

## Asymptotic Behavior of Single Species Chemostat Model

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### Abstract

In this paper, we consider a basic resource-based single species model in a well-stirred chemostat that incorporates general response function. Conditions for positivity, boundedness and persistence of solutions and the existence of nonnegative steady states are given. Local stability of steady states are studied by using the Routh-Hurwitz criterion. Global stability of the steady states are also presented. Computer algebra system MATHEMATICA is used extensively for symbolic and numerical simulations.

**Key words:** chemostat; local stability; global stability; persistence.

### I. Introduction

Modeling microbial growth is a problem of special interest in mathematical biology and theoretical ecology. The device ‘CHEMOSTAT’ is a laboratory apparatus used for the continuous culture of the microorganisms. It is important in ecological studies because the mathematics is tractable and the relevant experiments are possible. The purpose of this paper is to study the asymptotic behavior of single species model in a well-stirred chemostat. Our model consists of a system of two autonomous differential equations. This paper extends the work done by Kapur [2]. For a detailed description of a chemostat, the general formulation of our model and for various mathematical methods for analyzing chemostat models, we refer the reader to [2], [4], [5] and [6].

This paper is organized as follows. In section II, the model is described. In section III, the results on the positivity and boundedness of solutions are presented. An existence and the local stability of steady states are studied in section IV. Section V deals with global stability of steady states and persistence analysis. Numerical simulations and discussion are carried out in the last section.

### II. The Model

We assume that the population of microorganism consumes the nutrient in the chemostat. A system of equations is considered in this paper:

$$\begin{aligned} s'(t) &= D(s^0 - s(t)) - u(s(t))p(t) \\ p'(t) &= (F(s(t)) - D - \varepsilon)p(t) \\ s(0) &\geq 0, p(0) \geq 0. \end{aligned} \quad (1)$$

The functions  $s(t)$  and  $p(t)$  denote respectively the concentration (weight per unit volume) of the growth limiting nutrient and of the nutrient-sensitive microorganism in the chemostat at time  $t$ .  $s^0$  represents the input concentration of growth limiting nutrient;  $u(s)$  and  $F(s)$  represent the specific per capita nutrient uptake function and the specific per capita growth rate of microorganism on nutrient respectively;  $D$  is the dilution rate of the chemostat;  $\varepsilon$  denotes the specific death rate of

microorganism. If the death rate of microorganism is insignificant, then the only loss of microorganism is due to “washout” at the same rate that the nutrient is lost. In this case, we assume that the death rate is not negligible, thus the removal rate of microorganism will be the sum of  $D$  and the death rate. We specially assume that nutrient is nonreproducing, input concentration and dilution rate are constants and that the mixing in the vessel is perfect. In our model, we shall consider the following expression relating growth and uptake as [2]

$$\gamma u(s) = F(s) \quad (2)$$

where  $\gamma$  is yield constant, represents the conversion factor of nutrient to microorganism.

We assume that the function  $F$  satisfies the following:

$$F : R_+ \rightarrow R_+ \text{ is continuously differentiable,} \quad (3)$$

$$F(0) = 0, \quad (4)$$

$$F \text{ is monotonically increasing,} \quad (5)$$

$$\lim_{s \rightarrow \infty} F(s) < \infty \quad (6)$$

We begin by scaling the equation (1) by  $s(t) \rightarrow s^0 s(t)$ ,  $t \rightarrow t/D$  and  $p(t) \rightarrow \gamma s^0 p(t)$ .

Then we obtain the following differential equations:

$$\begin{aligned} s'(t) &= 1 - s(t) - f(s(t))p(t) \\ p'(t) &= f(s(t))p(t) - D_1 p(t) \\ s(0) &\geq 0, p(0) \geq 0 \end{aligned} \quad (7)$$

where,  $f(s) = \frac{F(s^0 s)}{D}$  and  $D_1 = 1 + \frac{\varepsilon}{D}$ .

It is observed that  $f$  satisfies (3)-(6).

### III. Preliminaries

The positivity and boundedness of solution are considered in the following two lemmas.

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**Lemma 3.1:** *The solutions  $s(t), p(t)$  of (7) are positive and for large  $t$ ,  $s(t) < 1$ .*

**Proof:** Suppose it is not true that  $s(t) > 0$  for all  $t > 0$ . Let  $t_1 = \min\{t : t > 0 \ \& \ s(t) = 0\}$ . Then  $s(t) > 0, \forall t \in [0, t_1)$ . But from the first equation of (7), we have  $s'(t_1) = 1 > 0$ . That is,  $s'(t) > 0$  on a neighborhood of  $t_1$ . This implies there exists  $\varepsilon > 0$  such that  $s(t)$  is increasing on  $(t_1 - \varepsilon, t_1 + \varepsilon)$ . Therefore we have  $0 < s(t_1 - \varepsilon/2) < s(t_1)$ , a contradiction. Thus  $s(t) > 0$  for all  $t > 0$ . Again, from the second equation of (7) we have  $p'(t) = (f(s) - D_1)p$ . This gives  $p(t) = p_0 \exp[\int_0^t (f(s(\theta)) - D_1)d\theta]$ , which shows that  $p(t) > 0$  for all  $t \geq 0$ . Therefore, the system (7) with positive initial conditions at  $t = 0$  produces positive solution for  $t > 0$ . Finally, from the first equation of (7), we have  $s'(t) = 1 - s(t) - D_1 p(t)$  for  $t > 0$ . This implies  $s(t) < 1 + (s(0) - 1)\exp[-t]$  and hence if  $t$  becomes large then  $s(t) < 1$ . This completes the proof.  $\square$

**Lemma 3.2:** *For  $\varepsilon > 0$ , the solutions  $s(t), p(t)$  of (7) satisfy*

$$\frac{1}{D_{\max}} - \varepsilon \leq s(t) + p(t) \leq \frac{1}{D_{\min}} + \varepsilon \tag{8}$$

for large  $t$ , where

$$D_{\max} = \max\{1, D_1\} \text{ and } D_{\min} = \min\{1, D_1\} \tag{9}$$

**Proof:** Let  $z(t) = s(t) + p(t)$ . From (7) we have

$$z'(t) = s'(t) + p'(t) = 1 - (s(t) + D_1 p(t)).$$

This leads to  $1 - D_{\max} z(t) \leq z'(t) \leq 1 - D_{\min} z(t)$ .

Solving the differential inequality, we obtain

$$\begin{aligned} \frac{1}{D_{\max}} + \left(z(0) - \frac{1}{D_{\max}}\right) \exp[-D_{\max} t] \leq \\ z(t) \leq \frac{1}{D_{\min}} + \left(z(0) - \frac{1}{D_{\min}}\right) \exp[-D_{\min} t]. \end{aligned}$$

Therefore, if  $t$  becomes large then for  $\varepsilon > 0$ ,

$$\frac{1}{D_{\max}} - \varepsilon \leq z(t) \leq \frac{1}{D_{\min}} + \varepsilon$$

Hence  $\frac{1}{D_{\max}} - \varepsilon \leq s(t) + p(t) \leq \frac{1}{D_{\min}} + \varepsilon$ , for large  $t$ . This completes the proof.  $\square$

**IV. Steady states and their local Stability**

The model (7) has two steady states. These are  $E_0 \equiv (1, 0)$  and  $E_c \equiv (\lambda_s, (1 - \lambda_s)/D_1)$ , denote the wash-out steady state and the interior steady states in the  $(s, p)$ -plane, where  $\lambda_s$  is defined as the unique solution of  $f(s) = D_1$ . To discuss the existence of steady states, their components must be nonnegative. Since all the components of the washout steady state are nonnegative,  $E_0$  always exists. Since  $f$  is increasing with  $f(0) = 0$ ,  $\lambda_s$  exists, satisfying  $0 < \lambda_s < 1$  and

$$f(s) = D_1 \Leftrightarrow D_1 < f(1).$$

In this case, there is an interior steady state  $E_c$ , otherwise no such steady state exists. The parameter  $\lambda_s$  represents the break-even concentration value of the nutrient where derivative of  $p$  is zero.

**Remark:** From (7), we get  $s'(t) + p'(t) = 1 - s(t) - D_1 p(t)$  so that if  $\bar{S}$  and  $\bar{P}$  are steady state values, then  $\bar{S} + D_1 \bar{P} = 1$  and hence all steady state values lie on the line  $s + D_1 p = 1$  in the nonnegative cone of the  $(s, p)$ -plane.

Now, the local stability of the steady states  $E_0$  and  $E_c$  will be investigated by studying the eigenvalues of the associated Jacobian matrices. The Jacobian matrix of (7) takes the form:

$$J(s, p) = \begin{pmatrix} -1 - f'(s)p & -f(s) \\ f'(s)p & f(s) - D_1 \end{pmatrix}.$$

**Theorem 4.1:** *If  $\lambda_s > 1$ , then only  $E_0$  exists and is locally asymptotically stable. If  $\lambda_s < 1$ , then both  $E_0$  and  $E_c$  exist,  $E_0$  is unstable and  $E_c$  is locally asymptotically stable.*

**Proof:** At  $E_0$ ,

$$J(E_0) = \begin{pmatrix} -1 & -f(1) \\ 0 & f(1) - D_1 \end{pmatrix}$$

and the eigenvalues of  $J(E_0)$  are  $\mu_1 = -1 < 0$

and  $\mu_2 = f(1) - D_1$ .

They are all negative if and only if  $\lambda_s > 1$  and therefore  $E_0$  is locally asymptotically stable. Otherwise,  $E_0$  is unstable.

At  $E_c$ , the Jacobian matrix takes the form

$$J(E_c) = \begin{pmatrix} -1 - ((1 - \lambda_s)/D_1)f'(\lambda_s) & -f(\lambda_s) \\ ((1 - \lambda_s)/D_1)f'(\lambda_s) & 0 \end{pmatrix}$$

The eigenvalues of  $J(E_c)$  satisfy the equation

$$\mu^2 + a_1\mu + a_2 = 0 \quad (10)$$

where

$$a_1 = -\text{Trace}(J(E_1)) = ((1 - \lambda_s)/D_1)f'(\lambda_s) + 1 > 0$$

and  $a_2 = \text{Det}(J(E_1)) = (1 - \lambda_s)f(\lambda_s)f'(\lambda_s) > 0$  if and only if  $\lambda_s < 1$ .

Hence, by Routh-Hurwitz criterion the roots of (10) have negative real parts and therefore,  $E_c$  is locally asymptotically stable.  $\square$

## V. Global analysis

In this section, we shall show that  $E_0$  is globally asymptotically stable if only  $E_0$  exists. If  $E_0$  and  $E_c$  exist, then  $E_c$  is globally asymptotically stable by showing that the system (7) is uniformly persistence. The proof involves the construction of a Lyapunov function and the application of the Lyapunov-LaSalle theorem. (We shall use Theorem 1.2 in Wolkowicz and Lu [7], which is slightly modified version of the statement given in LaSalle [3] and Hale [1].) The following theorem shows that  $E_0$  is a global attractor if it is the only steady state (i.e.,  $\lambda_s > 1$ ).

**Theorem 5.1:** *If  $\lambda_s > 1$ , then the solutions of (7) satisfy  $\lim_{t \rightarrow \infty} (s(t), p(t)) = (1, 0)$ .*

**Proof:** Since  $s(t) < 1$  for large  $t$  and  $\lambda_s > 1$  or  $D_1 = f(\lambda_s) > f(1)$ , we have  $D_1 - f(s) > D_1 - f(1) > 0$ . Thus there is  $0 < \alpha = \min_{t \geq 0} \{D_1 - f(s)\}$  such that  $p'(t) < -\alpha p(t)$  for sufficiently large  $t$  by the second equation of (7). This shows  $p(t) < p(0) \exp[-\alpha t]$  and since  $p(t) > 0$  for  $t > 0$ , so we have  $\lim_{t \rightarrow \infty} p(t) = 0$ . Then the first equation of (7) yields  $\lim_{t \rightarrow \infty} s(t) = 1$ . This completes the proof.  $\square$

**Theorem 5.2:** *If  $\lambda_s < 1$ , then the solutions of (7) satisfy*

$$\lim_{t \rightarrow \infty} (s(t), p(t)) = \left( \lambda_s, \frac{1 - \lambda_s}{D_1} \right).$$

**Proof:** We choose  $d_1 > D_{\max}$  and  $d_2 < D_{\min}$  such that for large  $t$ ,

$$\frac{1}{d_1} \leq s(t) + p(t) \leq \frac{1}{d_2}.$$

Define the Lyapunov function  $V(s, p)$  as follows

$$V = \int_{\lambda_s}^s \frac{(f(\xi) - D_1)(1 - \lambda_s)}{D_1(1 - \xi)} d\xi + \int_{p^*}^p \frac{\xi - p^*}{\xi} d\xi$$

on the set

$$\psi = \{(s, p) : s \in (0, 1), p > 0, s + p \in (1/d_1, 1/d_2)\},$$

where  $p^* = (1 - \lambda_s)/D_1$ .

Then the time derivative of  $V$  along solutions of the differential equation is

$$\dot{V} = \left( 1 - \frac{(1 - \lambda_s)f(s)}{D_1(1 - s)} \right) (f(s) - D_1)p.$$

Therefore,  $\dot{V}$  is nonpositive for  $0 < s < 1$  and equals 0 for  $s \in [0, 1)$  if and only if  $s = \lambda_s$  or  $p = 0$ .

By Lemma 3.1 every bounded solution of (7) is contained in  $\psi$  and hence by Theorem 1.2 in [7] every solution of (7) approaches the set  $\Lambda$ , the largest invariant subset  $M$  of  $\phi = \{(s, p) \in \psi : \dot{V} = 0\}$ .  $\phi$  is made up of points of the following forms

$$(s, 0), \text{ where } s \in [0, 1]$$

$$(\lambda_s, p), \text{ where } p \in [0, \infty).$$

Since  $V$  is bounded above, any solution of the form  $(s, 0)$  can not be in the omega limit set of any solution initiating in the interior of  $R_+^2$ .  $(\lambda_s, p) \in M$  implies that  $s(t) = \lambda_s$ , which in turn leads to  $0 = s'(t) = 1 - \lambda_s - f(\lambda_s)p$  and hence  $p = (1 - \lambda_s)/D_1$ . Therefore  $M = \{E_c\}$ . This completes the proof.  $\square$

## VI. Discussion

In this paper, we considered a basic resource-based single species chemostat model which is the modified form of the model given in Kapur [2]. In this model, the population of microorganism consumes the nutrient. Kapur carried out the equilibrium analysis and extinction criteria for monotone response function and presented graphical results for Monod type response function. We assumed that the functional response is general monotone function. For this response function we proved the positivity and boundedness of solutions of our model. We also studied the local stability of steady states by using the Routh-Hurwitz criterion and global stability of the steady states by using the method of Lyapunov functionals.

The model (7) has two steady states. One is associated with extinction, the other with survival. We found that the washout steady state  $E_0$  is the global attractor if it is the

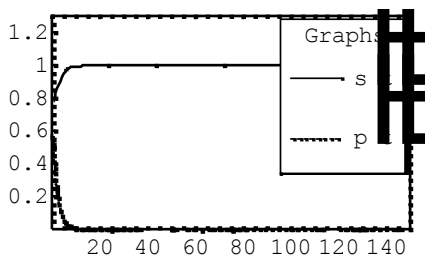
only steady state (this happens when  $\lambda_s > 1$ ). This confirms that the system is not persistent. When  $E_0$  and  $E_c$  both exist, we found that  $E_0$  is unstable and  $E_c$  is locally asymptotically stable. By constructing a Lyapunov function, we were able to show that  $E_c$  is a global attractor and that the system is uniformly persistent. Based on our simulation work we assume the functional response function takes the Moser form:

$$f(s) = \frac{ms^n}{a^n + s^n}$$

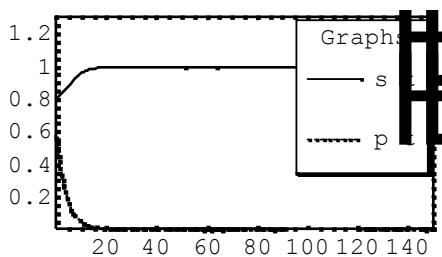
where  $m$  is the maximal growth rate and  $a$  is the half saturation constant and  $n \in N$ .

The numerical experiments performed on the system (7) using experimental data confirm our theoretical findings. Figures 1-2 show the solution trajectories as a function of time, where the parameters are set so that the steady states  $E_0$  and  $E_c$  are stable for all  $n \in N$ . Figure 3 deals with a different case. This Shows that the solution trajectories tend to  $E_0$  for  $n = 1$  and tend to  $E_c$  for  $n \geq 2$  respectively. The initial value  $(s(0), p(0)) = (0.8, 0.6)$  was taken for the graphs in figures 1-3.

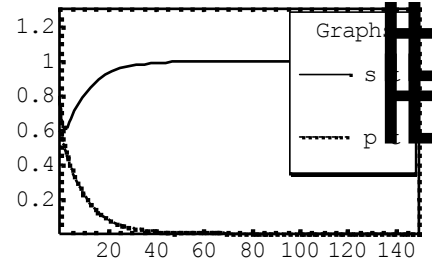
Figures 4-5 contain the trajectories of the system (7) initiating in the nonnegative cone of the  $(s, p)$ -plane. The two plots in figure-4 have  $\lambda_s > 1$  and the extinction steady state is stable. All plotted trajectories tend to  $E_0$ , extinction of the species. The two plots in figure-5 have  $\lambda_s < 1$  and all plotted trajectories tend to  $E_c$ , resulting in a stable survival steady state. Therefore, we now can conclude that the extinction and survival of population of microorganism depend on the break-even concentration,  $\lambda_s$ .



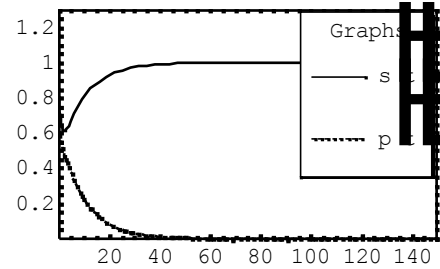
$m = .5, a = .2, D_1 = .9, n = 1$



$m = .8, a = .2, D_1 = .9, n = 1$

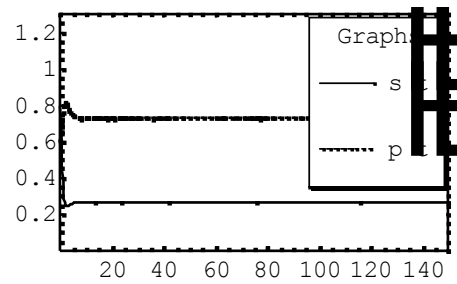


$m = .8, a = .2, D_1 = .9, n = 10$

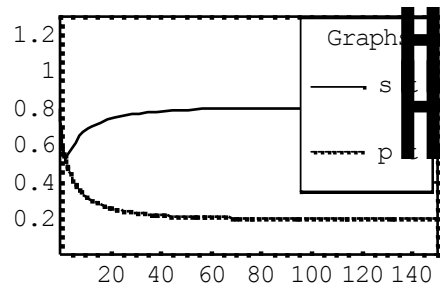


$m = .8, a = .2, D_1 = .9, n = 30$

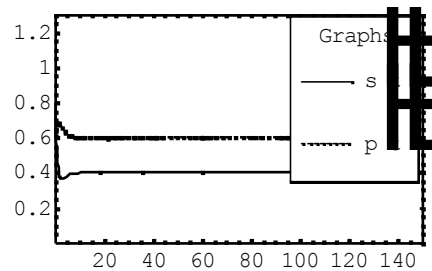
**Fig. 1.** Solution trajectories as function of time, tending to the stable steady state  $E_0$ .



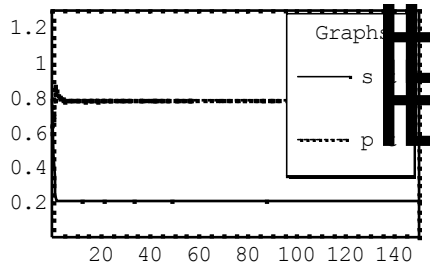
$m = 1.75, a = .2, D_1 = 1., n = 1$



$m = 1.25, a = .2, D_1 = 1., n = 1$

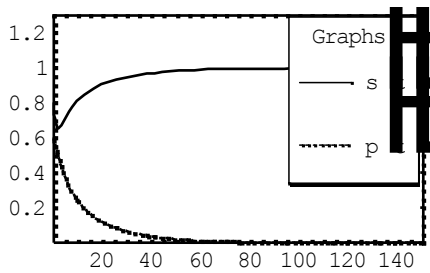


$m = 1.25, a = .2, D_1 = 1., n = 2$

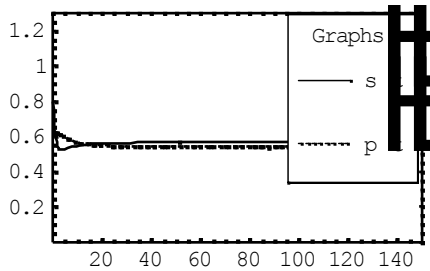


$$m = 1.25, a = .2, D_1 = 1., n = 25$$

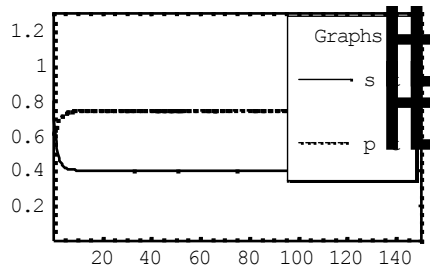
**Fig. 2.** Solution trajectories as function of time, tending to the stable steady state  $E_c$ .



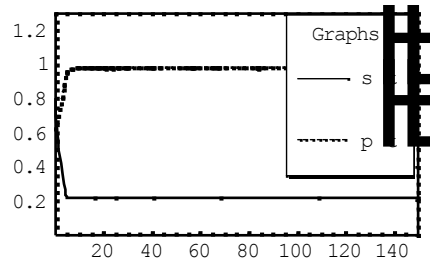
$$m = .9, a = .2, D_1 = .8, n = 1$$



$$m = .9, a = .2, D_1 = .8, n = 2$$

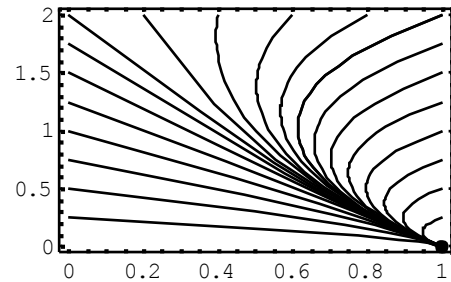


$$m = .9, a = .2, D_1 = .8, n = 3$$

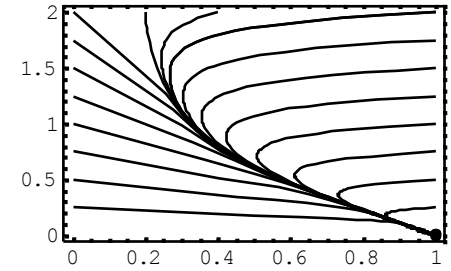


$$m = .9, a = .2, D_1 = .8, n = 25$$

**Fig. 3.** Solution trajectories as function of time, tend to  $E_0$  for  $n = 1$  and tend to  $E_c$  for  $n \geq 2$ .

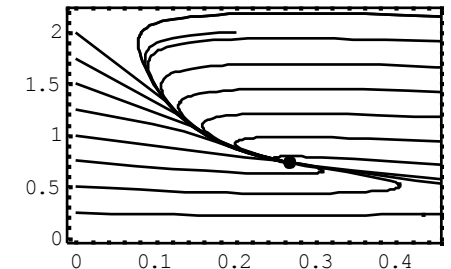


$$m = .5, a = .2, D_1 = .9, n = 1$$

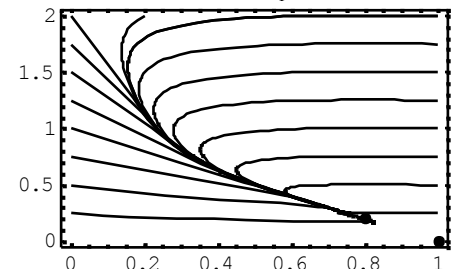


$$m = .8, a = .2, D_1 = .9, n = 2$$

**Fig. 4.** Trajectories for the system (7) tend to  $E_0$ .



$$m = 1.75, a = .2, D_1 = 1., n = 1$$



$$m = 1.25, a = .2, D_1 = 1., n = 1$$

**Fig. 5.** Trajectories for the system (7) tend to  $E_c$ .

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