

Three Species Food Web in a Chemostat

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Abstract: In this paper, we consider a model describing predator prey interaction in a chemostat that incorporates general response functions and identical removal rates. The existence of steady states, their local stability and persistence of the model are presented. We construct a Lyapunov function in the study of the global stability of a predator free steady state. We show that a slight fluctuation in the maximal growth rates of prey and/or predator devastate the form of conservation principle. Numerical simulations are also presented to analyze the model equations and determine the effect of the operating parameters of the chemostat on its dynamics.

Keywords: Chemostat; food web; predator; prey; stability.

1. Introduction

A standard example of an open system with purely exploitative competition in a laboratory device is called a chemostat. This device is important in studying the competition between different populations of microorganisms and has the advantage that the mathematics is tractable and the parameters are readily measurable. In a more hypothetical way it is also useful as a guide for isolation and identification of metabolic mutant strains. Its place in theoretical ecology is well documented in the surveys of [22, 23, 24]. Moreover, the chemostat model is the threshold for many variations (food chain, food web etc.) that yield more realistic biological and mathematical problems [5, 7, 12, 14, 17].

The dynamics of predator, prey and substrate interaction has become a ubiquitous tool for studying a number of industrial fields such as waste treatment bioreactors [2]. Over the years, researchers have come to appreciate that the study of predation could apply to studies of many natural ecosystems [10, 15,

19]. In the microbial ecology field, the dynamics of predator-prey interaction have also received a great deal of attention since they are the building elements of food chains and food webs. Early formulation of many simple two species models had been thoroughly explored [18]. After that, the discoveries expanded to include higher trophic levels [20, 16]. Zhu et al. [25] have extended the analysis of such models to the case where the growth rate has a restraint form. Li and Kuang [14] considered a simple food chain in a chemostat with one predator and one prey, where predator feeds exclusively on the prey and the prey consumes the nutrient. El-Owaidy and Moniem [5] also discussed a simple food chain with the extension that the predator feeds exclusively on the prey and the nutrient, and the prey consumes the nutrient in the chemostat. These two studies [5, 14] had limited to the case of single predator-prey-substrate in a chemostat with distinct removal rates for the competing species. More

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recently Alhumazi and Ajbar [1] examine the dynamics of predator-prey interaction for a general class of unstructured models where the growth rates are assumed to be general and without any restriction on their forms.

Before the works [1, 5, 14], the stability of simple food web model consisting of one predator and two preys with a growth limiting substrate had been theoretically investigated by Butler and Wolkowicz [4]. However they also had limited their investigation to the case where the predator consumes only one of the preys. Taking the above ideas into account, in this paper we are interested to examine the dynamics of a food web where the predator consumes both of the preys only and the preys consume the nutrient in the chemostat. It can be considered as resulting from the predator-prey system [5, 14] by adding a second prey population or from the competition system [12, 13] by adding a population preying upon both competing populations. Jost et al. [10] had been studied such a system experimentally in their lab by considering *Escherichia coli* and *Azotobacter vinelandii* (two bacteria) as preys, *Tetrahymena pyriformis* (a protozoan) as predator and glucose as the limiting substrate in the chemostat. Vayenas and Pavlou [21] had also been studied this model but they use numerical bifurcation techniques

to determine the effect of the operating conditions of the chemostat. In this work we derive the analytical results for which the model can predict the existence of populations in the chemostat at steady state level. For numerical techniques we use Michaelis-Menten/Monod's model for the dependence of the specific growth rates of the two prey populations on the concentration of the rate-limiting substrate and for the dependence of the specific growth rate of the predator on the concentrations of the prey populations to determine the effect of the operating parameters of the chemostat on the dynamics of the system.

2. The Model

We consider a chemostat in which all three microbial populations grow together and which is fed with medium containing the limiting nutrient for growth of the two competing bacterial populations. Let $s(t)$ denotes the nutrient concentration, $x_1(t)$ and $x_2(t)$ the concentrations of the competing prey populations and $y(t)$ the concentration of the predator population at time t . Then the food web can be represented as follows:

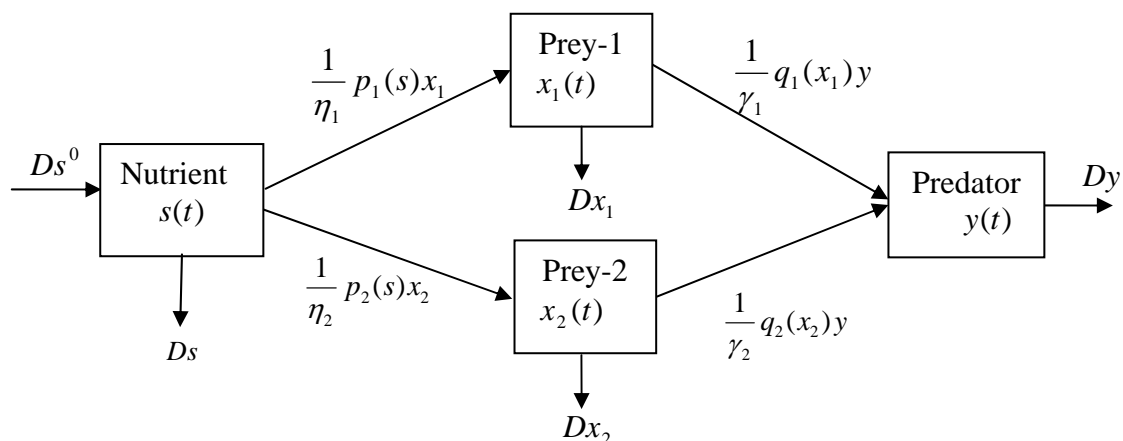


Figure 1. Flowchart diagram

The equations of the model take the form (see Figure 1 for a flowchart diagram):

$$\begin{aligned}
 s'(t) &= (s^0 - s(t))D - \sum_{i=1}^2 \frac{x_i(t)p_i(s(t))}{\eta_i} \\
 x_1'(t) &= x_1(t)(-D + p_1(s(t))) - \frac{1}{\gamma_1} y(t)q_1(x_1(t)) \quad (1) \\
 x_2'(t) &= x_2(t)(-D + p_2(s(t))) - \frac{1}{\gamma_2} y(t)q_2(x_2(t)) \\
 y'(t) &= y(t)(-D + q_1(x_1(t)) + q_2(x_2(t)))
 \end{aligned}$$

with

$$s(0) = s^0 \geq 0, x_i(0) = x_{i0} \geq 0, i=1,2, y(0) = y_0 \geq 0.$$

In the system (1), s^0 denotes the input concentration of the nutrient, η_i are the growth yield constants of the i th competitor and γ_i are the growth yield factors for the predator population feeding on the i th prey. $p_i(s)$ represent the specific per capita growth rate of the i th competitor, $q_i(x_i)$ the per capita growth rate of the predator population as a function of the respective prey population and D the input rate from the feed pump and the washout rate of the chemostat chamber.

We make the following assumptions considering the functions p_i and q_i of the model equation (1): $p_i, q_i : \mathbb{R}_+ \rightarrow \mathbb{R}_+$,

p_i, q_i are continuously differentiable,

$p_i'(s) \geq 0$ for all $s \in \mathbb{R}_+, q_i'(x_i) \geq 0$ for all

$x_i \in \mathbb{R}_+, p_i(0) = 0$ and $q_i(0) = 0$.

The system (1) describes a chemostat with a single, essential, growth limiting nutrient that is supplied at a constant rate from feed bottle, perfect mixing in the growth chamber, negligible death rates compared to the dilution rate and instantaneous balance of growth rates to the changes in the concentration of nutrient. Furthermore, we assume that the nutrient uptake rate is proportional to the rate of conversion of the prey biomass and similarly the prey uptake rate is proportional to the rate of conversion of the predator biomass. In this model, the two populations x_i compete solely for the nonreproducing substrate and they served individually and collectively as

prey for the predator population. When all three microorganisms are present, the system is a simple food web. In our model, when one or other of the prey is omitted, the system reduces to a simple food chain [14]. When the predator is omitted a simple competition symbiosis is obtained [24].

3. The Nondimensional Version of the Model

It will be more convenient to analyze the model after following substitutions are performed:

$$\bar{t} = tD, \bar{s} = \frac{s}{s^0}, \bar{x}_i = \frac{x_i}{\eta_i s^0}, \bar{y} = \frac{y}{\gamma_i \eta_i s^0}, i=1,2, \gamma_2 = \frac{\gamma_1 \eta_1}{\eta_2} \quad (2)$$

$$\bar{p}_i(\bar{s}) = \frac{p_i(s)}{D}, \bar{q}_i(\bar{x}_i) = \frac{q_i(x_i)}{D}, i=1,2 \quad (3)$$

We obtain the nondimensional version of the model (1) by omitting the bars for the simplification of the notation

$$\begin{aligned}
 s'(t) &= 1 - s(t) - \sum_{i=1}^2 x_i(t)p_i(s(t)) \\
 x_1'(t) &= x_1(t)(-1 + p_1(s(t))) - y(t)q_1(x_1(t)) \quad (4) \\
 x_2'(t) &= x_2(t)(-1 + p_2(s(t))) - y(t)q_2(x_2(t)) \\
 y'(t) &= y(t)(-1 + q_1(x_1(t)) + q_2(x_2(t)))
 \end{aligned}$$

with $s^0 \geq 0, x_{i0} \geq 0, i=1,2, y_0 \geq 0$.

All the above assumptions justified for this nondimensional version (4) of the system (1). Therefore, without loss of generality, we can consider the system (4) instead of (1) and we can always reinterpret our findings in terms of unscaled variables by the appropriate application of (2)-(3).

4. Preliminary Results

The following lemmas are straightforward and similar to the results given in [3] and [9].

Lemma 4.1. All solutions $s(t), x_1(t), x_2(t), y(t)$ of (4) for which $x_{i0} \geq 0, i=1,2$ and $y_0 > 0$ are positive and bounded for $t > 0$.

Lemma 4.2. The simplex

$L = \left\{ (s, x_1, x_2, y) : s, x_1, x_2, y \geq 0; s + \sum_{i=1}^2 x_i + y = 1 \right\}$
 is a global attractor for (4).

5. Steady States and Their Stability

The seven possible steady states (in the form $E \equiv (s, x_1, x_2, y)$) of the system (4) will be denoted $E_1 = (1,0,0,0)$, $E_{\lambda_1} = (\lambda_1, 1 - \lambda_1, 0, 0)$, $E_{\lambda_2} = (\lambda_2, 0, 1 - \lambda_2, 0)$, where λ_i is defined as the unique solution of $p_i(s) - 1 = 0$ (if it exists). $E^* = \left(s^*, x_1^*, x_2^*, 0 \right)$, where s^* is defined by the equations, $p_1(s) = p_2(s) = 1$ with $s^* \in (0,1)$ and x_1^*, x_2^* are the solutions of $1 - s^* = x_1^* + x_2^*$. $\tilde{E} = (\tilde{s}, \delta_1, 0, \tilde{y})$, where, $\tilde{y} = \delta_1(-1 + p_1(\tilde{s}))$ and \tilde{s} satisfies $1 - \tilde{s} = \delta_1 p_1(\tilde{s})$. $\hat{E} = (\hat{s}, 0, \delta_2, \hat{y})$, where, $\hat{y} = \delta_2(-1 + p_2(\hat{s}))$ and \hat{s} satisfies $1 - \hat{s} = \delta_2 p_2(\hat{s})$.

Also δ_i is defined as the unique solution of $q_i(x_i) - 1 = 0$ (if it exists). The values λ_i and δ_i represent the break-even concentration of nutrient and prey respectively. Note that, prey free with predator steady state does not exist.

$E_C = (\bar{s}, \bar{x}_1, \bar{x}_2, \bar{y})$ denotes the interior steady state where $\bar{s}, \bar{x}_1, \bar{x}_2$ are defined as the unique solution of the equation $1 - s - x_1 p_1(s) - x_2 p_2(s) = 0$ and $-1 + q_1(x_1) + q_2(x_2) = 0$ with $s \in (0,1)$ and they satisfy the equation $\frac{x_1(-1 + p_1(s))}{q_1(x_1)} = \frac{x_2(-1 + p_2(s))}{q_2(x_2)}$ and $y = \frac{x_1}{q_1(x_1)}(-1 + p_1(s)) = \frac{x_2}{q_2(x_2)}(-1 + p_2(s))$

To discuss the existence of steady states, their components must be non-negative. The

washout steady state $E_1 = (1,0,0,0)$ always exists. Since $p_i(s)$ is increasing with $p_i(0) = 0, \lambda_i$ exist, satisfying $0 < \lambda_i < 1$ and $p_i(\lambda_i) = 1 \Leftrightarrow p_i(1) > 1$

In this case, there is a predator-free steady state E_{λ_1} (resp. E_{λ_2}), otherwise, no such steady state exists. Now \tilde{E} is a steady state provided $\tilde{s} \geq 0$ is well defined and $\tilde{y} \geq 0$. \tilde{s} is defined by the equation $1 - \tilde{s} = \delta_1 p_1(\tilde{s})$. If we plot the functions $1 - s$ and $\delta_1 p_1(s)$ on the same graph, since $p_1(0) = 0$ and $p_1(s)$ strictly increasing function, it follows that there is a unique point \tilde{s} that satisfies the equation $1 - s = \delta_1 p_1(s)$ and $\tilde{s} \in (0,1)$. In order for $\tilde{y} \geq 0$, we require $\tilde{s} \geq \lambda_1$. But $\tilde{s} < \lambda_1$ if and only if $1 - \lambda_1 < 1 - \tilde{s} = \delta_1 p_1(\tilde{s}) < \delta_1 p_1(\lambda_1) \Rightarrow 1 - \lambda_1 < \delta_1$.

Thus, \tilde{E} is a steady state provided $\lambda_1 + \delta_1 \leq 1$. Actually, since in this case $\tilde{s} \geq \lambda_1$, it follows that $1 - \tilde{s} = \delta_1 p_1(\tilde{s}) \geq \delta_1$ and so \tilde{E} exists if $\lambda_1 \leq \tilde{s} \leq 1 - \delta_1$. Similar assumptions hold for the steady state \hat{E} also. In particular, the steady state \hat{E} exists if $\lambda_2 \leq \hat{s} \leq 1 - \delta_2$. Finally for the existence of E_C , we obtain the condition $p_1(s) = p_2(s) > 1$.

In the next step, we will investigate the local stability of these steady states by finding the eigenvalues of the associated Jacobian matrices. The Jacobian matrix of (4) takes the form

$$J = \begin{bmatrix} J_{11} & J_{12} & J_{13} & J_{14} \\ J_{21} & J_{22} & J_{23} & J_{24} \\ J_{31} & J_{32} & J_{33} & J_{34} \\ J_{41} & J_{42} & J_{43} & J_{44} \end{bmatrix} \tag{5}$$

where, $J_{11} = -1 - x_1 p_1'(s) - x_2 p_2'(s)$, $J_{12} = -p_1(s)$, $J_{13} = -p_2(s)$, $J_{14} = 0$, $J_{21} = x_1 p_1'(s)$, $J_{22} = -1 + p_1(s) - y q_1'(x_1)$, $J_{23} = 0$, $J_{24} = -q_1(x_1)$, $J_{31} = x_2 p_2'(s)$, $J_{32} = 0$, $J_{33} = -1 + p_2(s) - y q_2'(x_2)$, $J_{34} = -q_2(x_2)$, $J_{41} = 0$, $J_{42} = y q_1'(x_1)$, $J_{43} = y q_2'(x_2)$, $J_{44} = -1 + q_1(x_1) + q_2(x_2)$.

At E_1 ,

$$J(E_1) = \begin{bmatrix} -1 & -p_1(1) & -p_2(1) & 0 \\ 0 & -1 + p_1(1) & 0 & 0 \\ 0 & 0 & -1 + p_2(1) & 0 \\ 0 & 0 & 0 & -1 \end{bmatrix} \tag{6}$$

The eigenvalues lie on the diagonal. They are all negative if $-1 + p_i(1) < 0$ or, equivalently, $\lambda_i > 1$.

When E_{λ_1} exists, the Jacobian matrix at E_{λ_1} is given by

$$J(E_{\lambda_1}) = \begin{bmatrix} -1 - (1 - \lambda_1) p_1'(\lambda_1) & -p_1(\lambda_1) & -p_2(\lambda_1) & 0 \\ (1 - \lambda_1) p_1'(\lambda_1) & -1 + p_1(\lambda_1) & 0 & -q_1(1 - \lambda_1) \\ 0 & 0 & -1 + p_2(\lambda_1) & 0 \\ 0 & 0 & 0 & -1 + q_1(1 - \lambda_1) \end{bmatrix} \tag{7}$$

The determinant of the upper left hand 2×2 matrix is positive and its trace is negative, so its eigenvalues have negative real parts. The third and the fourth eigenvalues are $-1 + p_2(\lambda_1)$ and $-1 + q_1(1 - \lambda_1)$ respectively. Therefore, E_{λ_1} is asymptotically stable if and only if $-1 + p_2(\lambda_1) < 0$ and $-1 + q_1(1 - \lambda_1) < 0$ or, equivalently, $\lambda_1 < \lambda_2$ and $1 - \delta_1 < \lambda_1$. Similar calculation shows that E_{λ_2} is asymptotically stable if and only if $\lambda_2 < \lambda_1$ and $1 - \delta_2 < \lambda_2$.

When E^* , the steady state of the survival of two prey populations, exists, the Jacobian matrix $J(E^*)$ is given by,

$$J(E^*) = \begin{bmatrix} -1 - x_1 p_1' \left(s^* \right) - x_2 p_2' \left(s^* \right) & -p_1 \left(s^* \right) & -p_2 \left(s^* \right) & 0 \\ x_1 p_1' \left(s^* \right) & -1 + p_1 \left(s^* \right) & 0 & -q_1 \left(x_1^* \right) \\ x_2 p_2' \left(s^* \right) & 0 & -1 + p_2 \left(s^* \right) & -q_2 \left(x_2^* \right) \\ 0 & 0 & 0 & -1 + q_1 \left(x_1^* \right) + q_2 \left(x_2^* \right) \end{bmatrix} \tag{8}$$

The eigenvalues of $J(E^*)$ satisfy,

$$\left[\lambda - \left(-1 + q_1 \left(x_1^* \right) + q_2 \left(x_2^* \right) \right) \right] \left[\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 \right] = 0$$

where $a_1 = 1 + x_1 p_1'(s) + x_2 p_2'(s)$; $a_2 = x_1 p_1'(s) + x_2 p_2'(s)$; $a_3 = 0$.

Therefore, $a_1 > 0, a_2 > 0, a_1 a_2 > a_3$ and by Routh-Hurwitz criterion, the roots have negative real parts and so E is asymptotically stable if the fourth eigenvalue $\lambda = -1 + q_1(x_1) + q_2(x_2) < 0$.

When \tilde{E} exists, the Jacobian matrix $J(\tilde{E})$ at \tilde{E} is given by

$$J(\tilde{E}) = \begin{bmatrix} 1 - \delta_1 p_1'(\tilde{s}) & -p_1(\tilde{s}) & -p_2(\tilde{s}) & 0 \\ \delta_1 p_1'(\tilde{s}) & \frac{\tilde{y}}{\delta_1}(\delta_1 q_1'(\delta_1) - 1) & 0 & -1 \\ 0 & 0 & -1 + p_2(\tilde{s}) - \tilde{y} q_2'(0) & 0 \\ 0 & \tilde{y} q_1'(\delta_1) & \tilde{y} q_2'(0) & 0 \end{bmatrix} \tag{9}$$

The eigenvalues of $J(\tilde{E})$ satisfy $[\lambda - (-1 + p_2(\tilde{s}) - \tilde{y} q_2'(0))][\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3] = 0$

where $a_1 = 1 + \delta_1 p_1'(\tilde{s}) + \frac{\tilde{y}}{\delta_1}(\delta_1 q_1'(\delta_1) - 1)$,

$a_2 = (1 + \delta_1 p_1'(\tilde{s})) \frac{\tilde{y}}{\delta_1}(\delta_1 q_1'(\delta_1) - 1) + \tilde{y} q_1'(\delta_1) + p_1(\tilde{s}) \delta_1 p_1'(\tilde{s})$

$a_3 = (1 + \delta_1 p_1'(\tilde{s})) \tilde{y} q_1'(\delta_1)$.

Note that the constant term a_3 is positive. Therefore, if $\delta_1 q_1'(\delta_1) > 1$, then $a_1 > 0, a_2 > 0, a_1 a_2 > a_3$ and by Routh-Hurwitz criterion, the eigenvalues have negative real parts and so \tilde{E} is asymptotically stable if only the fourth eigenvalue $\lambda = -1 + p_2(\tilde{s}) - \tilde{y} q_2'(0) < 0$ or, equivalently, $p_2(\tilde{s}) < 1 + \tilde{y} q_2'(0)$.

Now if \hat{E} exists, then the Jacobian matrix $J(\hat{E})$ and the eigenvalues of $J(\hat{E})$ are quiet similar to $J(\tilde{E})$. It can be easily shown that the eigenvalues of $J(\hat{E})$ have negative real parts if and only if $\delta_2 q_2'(\delta_2) > 1$ and $p_1(\hat{s}) < 1 + \tilde{y} q_1'(0)$.

Finally, when the interior steady state, $E_C = (\bar{s}, \bar{x}_1, \bar{x}_2, \bar{y})$ exists, the Jacobian matrix $J(E_C)$ is

$$\text{given by } J(E_C) = \begin{bmatrix} J_{11} & J_{12} & J_{13} & J_{14} \\ J_{21} & J_{22} & J_{23} & J_{24} \\ J_{31} & J_{32} & J_{33} & J_{34} \\ J_{41} & J_{42} & J_{43} & J_{44} \end{bmatrix} \tag{10}$$

where, $J_{11} = -1 - \bar{x}_1 p_1'(\bar{s}) - \bar{x}_2 p_2'(\bar{s})$, $J_{12} = -p_1(\bar{s})$, $J_{13} = -p_2(\bar{s})$, $J_{14} = 0$, $J_{21} = \bar{x}_1 p_1'(\bar{s})$,

$J_{22} = -1 + p_1(\bar{s}) - \bar{y} q_1'(\bar{x}_1)$, $J_{23} = 0$, $J_{24} = -q_1(\bar{x}_1)$, $J_{31} = \bar{x}_2 p_2'(\bar{s})$, $J_{32} = 0$,

$J_{33} = -1 + p_2(\bar{s}) - \bar{y} q_2'(\bar{x}_2)$, $J_{34} = -q_2(\bar{x}_2)$, $J_{41} = 0$, $J_{42} = \bar{y} q_1'(\bar{x}_1)$, $J_{43} = \bar{y} q_2'(\bar{x}_2)$, $J_{44} = 0$

The eigenvalues of $J(E_C)$ satisfy $\lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0$

where, $a_1 = 3 + \bar{x}_1 p_1'(\bar{s}) + \bar{x}_2 p_2'(\bar{s}) + \bar{y} q_1'(\bar{x}_1) + \bar{y} q_2'(\bar{x}_2) - (p_1(\bar{s}) + p_2(\bar{s}))$,

$a_2 = \bar{y} q_1(\bar{x}_1) q_1'(\bar{x}_1) + \bar{y} q_2(\bar{x}_2) q_2'(\bar{x}_2) + \bar{y}^2 q_1'(\bar{x}_1) q_2'(\bar{x}_2) + 2\bar{y}(q_1(\bar{x}_1) + q_2(\bar{x}_2))$

$$\begin{aligned}
 & + 3 - \bar{y}(p_1(\bar{s})q_2'(\bar{x}_2) + p_2(\bar{s})q_1'(\bar{x}_1)) - 2(p_1(\bar{s}) + p_2(\bar{s})) + p_1(\bar{s})p_2(\bar{s}) + \\
 & (2 + \bar{y}q_1'(\bar{x}_1) + \bar{y}q_2'(\bar{x}_2))(\bar{x}_1p_1'(\bar{s}) + \bar{x}_2p_2'(\bar{s})) - (\bar{x}_1 + \bar{x}_2)p_1'(\bar{s})p_2(\bar{s}), \\
 a_3 = & (1 + \bar{x}_1p_1'(\bar{s}) + \bar{x}_2p_2'(\bar{s}))(\bar{y}q_1(\bar{x}_1)q_1'(\bar{x}_1) + \bar{y}q_2(\bar{x}_2)q_2'(\bar{x}_2) + \bar{y}q_1'(\bar{x}_1) + \bar{y}q_2'(\bar{x}_2) \\
 & - \bar{y}p_1(\bar{s})q_2'(\bar{x}_2) - \bar{y}p_2(\bar{s})q_1'(\bar{x}_1) + p_1(\bar{s})p_2(\bar{s}) + 1) + \bar{y}^2q_1'(\bar{x}_1)q_2'(\bar{x}_2)(q_1(\bar{x}_1) + \\
 & q_2(\bar{x}_2) + \bar{x}_1p_1'(\bar{s}) + \bar{x}_2p_2'(\bar{s})) - \bar{y}p_1(\bar{s})q_2(\bar{x}_2)q_2'(\bar{x}_2) - \bar{y}p_2(\bar{s})q_1(\bar{x}_1)q_1'(\bar{x}_1) \\
 & \bar{x}_2\bar{y}p_2(\bar{s})p_2'(\bar{s})q_1'(\bar{x}_1) - (p_1(\bar{s}) + p_2(\bar{s})) - \bar{x}_1p_1'(\bar{s})p_2(\bar{s}) - \bar{x}_2p_2'(\bar{s})p_1(\bar{s}). \\
 \text{and } a_4 = & (1 + \bar{x}_1p_1'(\bar{s}) + \bar{x}_2p_2'(\bar{s}))[\bar{y}q_1(\bar{x}_1)q_1'(\bar{x}_1)(1 - p_1(\bar{s}) + \bar{y}q_1'(\bar{x}_1)) + \bar{y}q_2(\bar{x}_2)q_2'(\bar{x}_2) \\
 & (1 - p_2(\bar{s}) + \bar{y}q_2'(\bar{x}_2))] + \bar{x}_1\bar{y}p_1(\bar{s})p_1'(\bar{s})q_2(\bar{x}_2)q_2'(\bar{x}_2) + \bar{x}_2\bar{y}p_2(\bar{s})p_2'(\bar{s})q_1(\bar{x}_1)q_1'(\bar{x}_1) \\
 & - \bar{x}_2\bar{y}p_1(\bar{s})p_2'(\bar{s})q_1(\bar{x}_1)q_2'(\bar{x}_2) - \bar{x}_1\bar{y}p_2(\bar{s})p_1'(\bar{s})q_2(\bar{x}_2)q_1'(\bar{x}_1).
 \end{aligned}$$

The Routh-Hurwitz criterion says that E_C will be locally asymptotically stable if and only if $a_1 > 0, a_2 > 0, a_3 > 0, a_4 > 0, a_1a_2 > a_3$ and $a_1a_2a_3 > a_3^2 + a_4a_1^2$.

We can summarize the above results in the following theorems.

Theorem 5.1. If $\lambda_i > 1, i = 1, 2$ then only E_1 exists and E_1 is locally asymptotically stable. If $\lambda_1 < 1$ and $1 - \delta_1 < \lambda_1 < \lambda_2$, then E_1 and E_{λ_1} exist, E_1 is unstable and E_{λ_1} is locally asymptotically stable. If $\lambda_2 < 1$ and $1 - \delta_2 < \lambda_2 < \lambda_1$, then E_1 and E_{λ_2} exist, E_1 is unstable and E_{λ_2} is locally asymptotically stable. If E^* exists and $q_1\left(x_1^*\right) + q_2\left(x_2^*\right) < 1$, then it is asymptotically stable. In these cases, the system is not uniformly persistent.

Theorem 5.2. If $\lambda_1 \leq \tilde{s} \leq 1 - \delta_1$, then \tilde{E} exists and \tilde{E} is locally asymptotically stable if $\delta_1q_1'(\delta_1) > 1$ and $p_2(\tilde{s}) < 1 + \tilde{y}q_2'(0)$. If $\lambda_2 \leq \hat{s} \leq 1 - \delta_2$, then \hat{E} exists and \hat{E} is locally asymptotically stable if $\delta_2q_2'(\delta_2) > 1$ and $p_1(\hat{s}) < 1 + \tilde{y}q_1'(0)$. In both cases, the system is not uniformly persistent. Finally, if $p_1(s) = p_2(s) > 1$, then E_C exists and E_C is locally asymptotically stable if $a_1 > 0, a_2 > 0, a_3 > 0, a_4 > 0, a_1a_2 > a_3, a_1a_2a_3 > a_3^2 + a_4a_1^2$ and therefore, the system will be uniformly persistent.

6. Global Analysis

In the previous section, we showed that if only E_1 exists, then E_1 is asymptotically stable, if E_1 and E_{λ_1} exist, then E_1 is unstable and E_{λ_1} is locally asymptotically stable. In this section, we will show that E_1 is globally asymptotically stable if E_1 exists. The proof is very straightforward. Most importantly we shall show that if only E_1 and E_{λ_1} exist,

under a reasonable assumption E_{λ_1} is globally asymptotically stable. 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 [24], which is a slightly modified version of the statements given in LaSalle [11] and Hale [8].)

The following theorem shows that E_1 is a global attractor if it is the only steady state (i.e., $\lambda_i > 1$).

Theorem 6.1. If $\lambda_i > 1$, then all solutions of (4) satisfy $\lim_{t \rightarrow +\infty} (s(t), x_1(t), x_2(t), y(t)) = (1, 0, 0, 0)$.

Proof. Since $s(t) < 1$ for large t and $p_i(1) - 1 < 0$ or $\lambda_i > 1$, there is a $v > 0$ such that $x_i'(t) < -vx_i(t)$ for t sufficiently large and $v = \min_{0 \leq t} \left\{ 1 - p_i(s) + \frac{q_i(x_i)}{x_i} y \right\}$. This shows that $\lim_{t \rightarrow \infty} x_i(t) = 0$. It follows from the forth equation of (4) that $y'(t) < -\mathcal{G}y(t)$ where $\mathcal{G} = \min_{0 \leq t} \{1 - q_1(x_1) - q_2(x_2)\}$ which implies that $\lim_{t \rightarrow \infty} y(t) = 0$. Then the first equation of (4) gives that $\lim_{t \rightarrow \infty} s(t) = 1$. This completes the proof.

Theorem 6.2. If $\lambda_i < 1$ and $1 - \delta_1 < \lambda_1 < \lambda_2$, then all solutions of (4) satisfy $\lim_{t \rightarrow +\infty} (s(t), x_1(t), x_2(t), y(t)) = (\lambda_1, 1 - \lambda_1, 0, 0)$.

Proof. From Lemma 4.2, we have $s(t) + x_1(t) + x_2(t) + y(t) = 1$ for large t . Let

$$\alpha = 1 + \max_{0 \leq x_i \leq 1 - \lambda_i} \left\{ \frac{q_1(x_1)(1 - \lambda_1 - x_1)}{x_1(1 - q_1(x_1) - q_2(x_2))} \right\} \text{ and } \beta = 1 + \max_{\bar{x}_i \leq x_i \leq 1} \left\{ \frac{(q_1(x_1) + q_2(x_2) - 1)}{q_2(x_2)} \right\}.$$

Let $C(u)$ be a continuously differentiable function and $C'(u)$ is given by

$$C'(u) = \begin{cases} 0 & , 0 \leq u \leq 1 - \lambda_1 \\ \frac{\beta}{\lambda_1 + \bar{x}_1 - 1} (u - (1 - \lambda_1)) & , 1 - \lambda_1 \leq u \leq \bar{x}_1 \\ \beta & , u \geq \bar{x}_1 \end{cases} \tag{11}$$

$C'(u)$ is linear on $[1 - \lambda_1, \bar{x}_1]$. In the view of Lemma 4.2, $u \leq 1 - \lambda_1$ if $s \geq \lambda_1$. Therefore, if $s \geq \lambda_1$, then $C'(x_1 + x_2 + y) = 0$.

Define a Lyapunov function as follows

$$V = \int_{\lambda_1}^s \frac{(p_1(\xi) - 1)(1 - \lambda_1)}{1 - \xi} d\xi + \int_{\bar{x}_1}^{x_1} \frac{\xi - \bar{x}_1}{\xi} d\xi + \alpha y + \beta x_2 + C(x_1 + x_2 + y)$$

on the set $\varphi = \{(s, x_1, x_2, y) : s \in (0, \lambda_2), x_1, x_2, y \in (0, \infty), s + x_1 + x_2 + y = 1\}$

where $\bar{x}_1 = 1 - \lambda_1$. Then the time derivative of V along the solution of the differential equation is

$$\begin{aligned} \dot{V} &= \left[C'(x_1 + x_2 + y) + 1 - \frac{(1 - \lambda_1)p_1(s) + \frac{x_2}{x_1}(1 - \lambda_1)p_2(s)}{1 - s} \right] (p_1(s) - 1)x_1 + \\ &\quad \left[\frac{(1 - \lambda_1 - x_1)q_1(x_1)}{x_1} + \alpha(q_1(x_1) + q_2(x_2) - 1) - \beta q_2(x_2) - C'(x_1 + x_2 + y) \right] y + \\ &\quad [\beta + C'(x_1 + x_2 + y)](p_2(s) - 1)x_2 \\ &= V_1 + V_2 + V_3. \end{aligned} \tag{12}$$

To discuss the sign of \dot{V} , we will investigate each term of \dot{V} . For V_1 , the term

$$\left[1 - \frac{(1 - \lambda_1)p_1(s) + \frac{x_2}{x_1}(1 - \lambda_1)p_2(s)}{1 - s} \right] (p_1(s) - 1)x_1 \text{ is nonpositive for } 0 < s < 1 \text{ and equals to}$$

zero for $s \in [0,1)$ if and only if $s = \lambda_1$. The term $C'(x_1 + x_2 + y)(p_1(s) - 1)x_1$ is nonpositive for $s \in [0,1)$, since $C'(x_1 + x_2 + y) = 0$ for $s \geq \lambda_1$ and $C'(u) \geq 0$ for $u \geq 0$ and $(p_1(s) - 1) < 0$ for $s < \lambda_1$. Therefore, V_1 is always nonpositive and equals to zero for $s \in [0,1)$ if and only if $s = \lambda_1$.

For V_2 , we will define

$$G(s, x_1, x_2, y) = \frac{(1 - \lambda_1 - x_1)q_1(x_1)}{x_1} + \alpha(q_1(x_1) + q_2(x_2) - 1) - \beta q_2(x_2) - C'(x_1 + x_2 + y) \tag{13}$$

If $0 \leq x_i \leq 1 - \lambda_i$, then by the definition of α and any choice of $\beta > 0$, we get

$$G(s, x_1, x_2, y) = (q_1(x_1) + q_2(x_2) - 1) - \beta q_2(x_2) - C'(x_1 + x_2 + y) < 0$$

If $1 - \lambda_i \leq x_i \leq \delta_i$, then all the terms of $G(s, x_1, x_2, y)$ are nonpositive and it can be easily shown that $G(s, x_1, x_2, y) < 0$. Also for $\delta_i \leq x_i \leq \bar{x}_i$, all the terms of $G(s, x_1, x_2, y)$ are nonpositive. If $x_i \geq \bar{x}_i$, and therefore $C'(x_1 + x_2 + y) = \beta$ then by definition of β , we have

$$G(s, x_1, x_2, y) = -q_2(x_2) - 1 - \frac{q_1(x_1) + q_2(x_2) - 1}{q_2(x_2)} < 0.$$

It follows that V_2 is always nonpositive. Finally, for V_3 , we will define

$$H(s, x_1, x_2, y) = [\beta + C'(x_1 + x_2 + y)](p_2(s) - 1)$$

The term $H(s, x_1, x_2, y)$ is nonpositive for $s \leq \lambda_2$ and equals to zero if and only if $s = \lambda_2$. It follows that each term of \dot{V} is nonpositive.

By lemma 4.2, every bounded solution of (4) is contained in φ and hence by theorem 1.2 in [24] every solution of (4) approaches the set ψ , the largest invariant subset M of $\eta = \{(s, x_1, x_2, y) \in \varphi : \dot{V} = 0\}$. η is made up of only one point of the form $(\lambda_1, x_1, 0, 0)$ where $x_1 \in [0, \infty)$. Since V is bounded above, the unique point of the form $(\lambda_1, x_1, 0, 0) \in M$ implies that $s(t) = \lambda_1$ and $x_2(t) = 0, y(t) = 0$ which in turn leads to $0 = s'(t) = 1 - \lambda_1 - p_1(\lambda_1)x_1$ and hence $x_1 = 1 - \lambda_1$. Therefore $M = \{E_{\lambda_1}\}$. This completes the proof.

7. Numerical Simulation

Based on our simulation work, we assume the functional response function takes the Michaelis-Menten/ Holling type II form:

$$p_i(s) = \frac{m_{1i}s}{a_{1i} + s} \text{ and } q_i(x_i) = \frac{m_{2i}x_i}{a_{2i} + x_i}, i = 1, 2.$$

where, m_{ij} are the maximal growth rates and a_{ij} are the half saturation constants. The nu-

merical experiments performed on the system (4) using experimental data confirm our theoretical findings. The model we considered exhibits a sequence of different stages of global behavior as various parameters change. The figures were constructed by proper choice of the kinetic parameters so that all the interesting behaviors of the system are observed.

At each stage, conditions have become sufficiently favorable for a new population to survive. Now we see how the parameters af-

fect the dynamics of (4) if s^0 is fixed. Assume that m_i ($i=1,2$) are small enough so that $\lambda_i > 1$, then all populations will be washed out (E_1 is stable) in the chemostat (Figure 2). As m_{11} is gradually increased, eventually there is a bifurcation when $\lambda_1 < 1$, and $1 - \delta_1 < \lambda_1 < \lambda_2$.

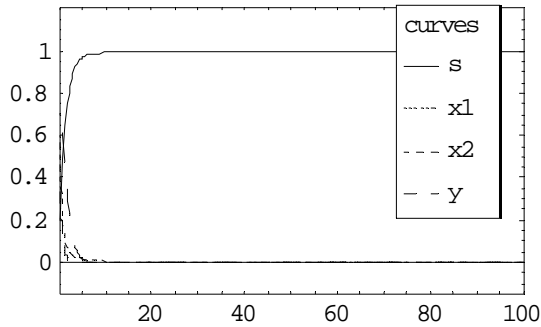


Figure 2. $m_{11} = 1.02, m_{12} = 1.01, m_{21} = 1.15, m_{22} = 1.1, a_{11} = 0.3, a_{12} = 0.5, a_{21} = 0.6, a_{22} = 0.3, (s_0, x_{10}, x_{20}, y_0) = (.2, .6, .4, .7)$. The solution curves tend to E_1 .

In this case, E_1 loses its stability and the new bifurcated steady state E_{λ_1} is asymptotically stable (Figure 3). This interprets that only the first.

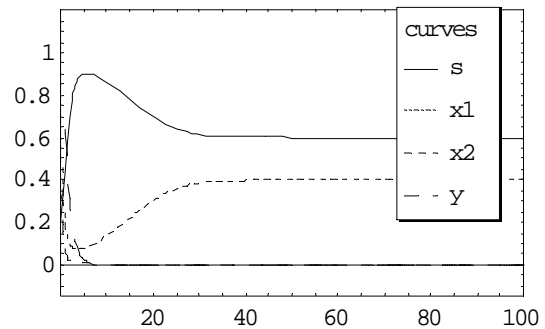


Figure 3. $m_{11} = 1.5$ and other parameter values are as given in Figure 2. The solution curves tend to E_{λ_1} .

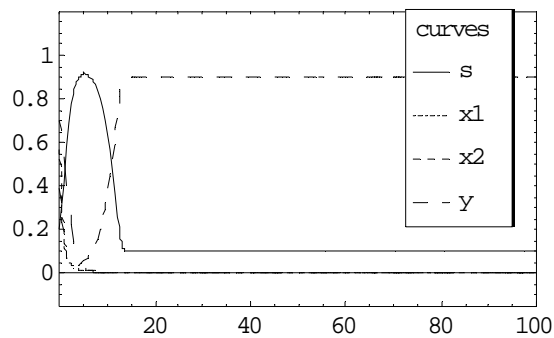


Figure 4. $m_{12} = 1.5$ and the other parameter values are as given in Figure 2. The solution curves tend to E_{λ_2} .

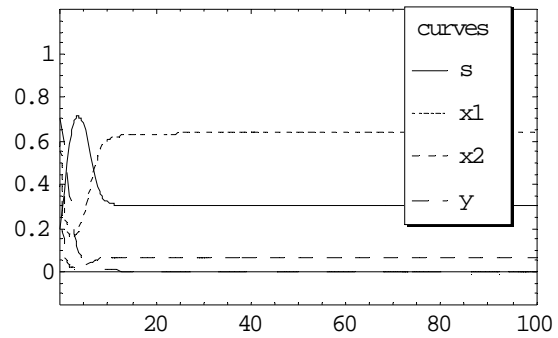


Figure 5. $m_{11} = 2.0, m_{12} = 2.67$ and the other parameter values are as given in Figure 2. The solution curves tend to E^* .

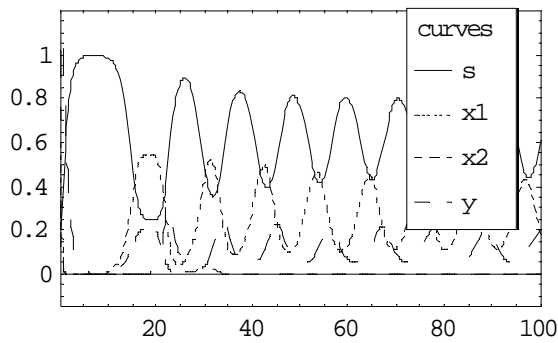


Figure 6. $m_{11} = 2.25, m_{12} = 2.25, m_{21} = 2.5, m_{22} = 2.5, a_{11} = 0.3, a_{12} = 0.3, a_{21} = 0.35, a_{22} = 0.35$. In this case \tilde{E} exists and is unstable. The solution oscillates and seems to approach a periodic solution.

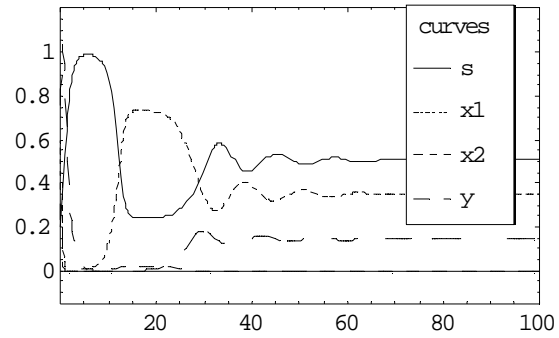


Figure 7. $m_{21} = 2.0$ and the other parameter values are as given in Figure 6. The solution oscillates but eventually approaches \tilde{E} .

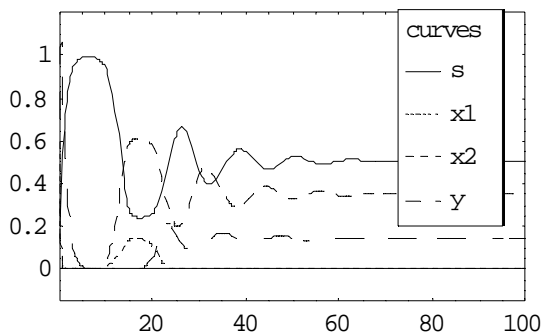


Figure 8. $m_{22} = 2.0$ and the other parameter values are as given in Figure 6. The solution oscillates but eventually approaches \hat{E} .

Furthermore, Figure 6 shows a case in which $m_{11} = m_{12} = 2.25, m_{21} = m_{22} = 2.5$ and the system possesses a periodic solutions of \tilde{E} . Figure 7 indicates that perturbing m_{21} (while keeping other parameters in Figure 6 fixed) in such a way that the conditions $\lambda_1 \leq \tilde{s} \leq 1 - \delta_1$, $\delta_1 q_1'(\delta_1) > 1$ and $p_2(\tilde{s}) < 1 + \tilde{y} q_2'(0)$ hold leads to a global stability of \tilde{E} whereas Figure 8 indicates that perturbing m_{22} (while keeping other parameters in Figure 6 fixed) so that the conditions of the local stability of \hat{E} hold leads to

a global stability of \hat{E} . Therefore, varying the values of maximal growth rates may affect the dynamics of (4) in a very significant way.

8. Discussion

Modeling microbial growth is a problem of special interest in mathematical biology and theoretical ecology. In this paper, we have been concerned with the qualitative behavior that can result when a predator invades a chemostat in which two prey populations are competing for a single, essential, growth limiting nutrient. In this model, the preys consume the nutrient and the predator consumes the preys only. We assume that the functional response functions are the general monotone response functions and the removal rates are identical. For this response function, we studied the local stability by using Routh-Hurwitz criterion and the global stability by using the methods of Lyapunov functions. In the case of identical removal rate the system can be reduced to a three dimensional system which is a slightly modified version given in [4]. We found that the washout steady state E_1 is a global attractor if it is the only steady state (this happens when $\lambda_i > 1$,). This confirms

the intuition that all the populations cannot persist if the growth rates of the preys are relatively small and close to one. When E_1 and E_{λ_1} are the only steady states, we found that E_1 is unstable and E_{λ_1} is locally asymptotically stable. By constructing a Lyapunov function, we were able to show that if E_1 and E_{λ_1} are the only steady states, E_{λ_1} is a global attractor. The construction of the Lyapunov function is rather novel and trivial. This novel idea has been used in [5, 12, 13, 14]. This condition does not depend on the specific properties of the functional response functions. The global stability of E_{λ_1} implies that the washout of the prey-2 and predator in the chemostat does not depend on the initial density levels of preys and predator. The global stability of E_{λ_2} implies that the predator and prey-1 will be washed out in the chemostat regardless of the initial density levels of preys and predator. Therefore, the principle of competitive exclusion of Gause [6] has been well established and confirmed. When two, and only two, species compete for a limiting substrate, one must be eliminated, as seen in Figure 3 and Figure 4. We showed that the steady states of coexisting of both preys as well as one of the preys with predator if exist are locally asymptotically stable. We also showed that when the interior steady state E_C exists and is locally asymptotically stable, then the preys and predator coexist in the sense that the system is uniformly persistent and the conservation principle is circumvented. In this case, a switch of the stability of the interior steady state E_C may occur.

Acknowledgements

The authors are thankful to the referees for their scrutiny.

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