

On Food Chain In A Chemostat With Distinct Removal Rates *

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Abstract

A mathematical model of predator-prey interactions in a chemostat is considered. It incorporates both general response functions and distinct removal rates. A slight change in the removal rate of prey or predator destroys the form of the conservation principle. So, we construct a Lyapunov function in the study of the global stability of a predator-free and interior steady states. Local stability of steady states is studied by using the Routh-Hurwitz criterion.

1 Introduction

A simple example of exploitative competition occurs in a laboratory device, called a chemostat, that models competition in a very simple lake. This device is important in ecological studies because the mathematics is tractable and the relevant experiments are possible. Its place in theoretical ecology is well documented in the surveys of [11, 12, 13]. Moreover, the chemostat model is the starting point for many variations (food chain, etc.) that yield more realistic biological models and interesting mathematical problems [2, 8, 9].

A food chain in a chemostat with one predator and one prey is considered. In this case, the predator feeds exclusively on the prey and on the nutrient, and the prey consumes the nutrient in the chemostat.

A system of equations is considered in this paper:

$$\begin{aligned} s' &= (s^o - s(t))D - \frac{1}{\gamma_1}F_1(s(t))x(t) - \frac{1}{\gamma_2}F_2(s(t))y(t), \\ x'(t) &= x(t)(F_1(s(t)) - D - \epsilon_1) - \frac{1}{\gamma_3}F_3(x(t))y(t), \\ y'(t) &= y(t)(F_2(s(t)) + F_3(x(t)) - D - \epsilon_2), \end{aligned} \quad (1)$$

with $s(0) > 0$, $x(0) > 0$ and $y(0) > 0$.

The functions $s(t)$, $x(t)$ and $y(t)$ represent the concentration of nutrient, prey and predator at time t , respectively. s^o represents the input concentration of the nutrient. F_1 , F_2 and F_3 denote the specific growth rate of prey, predator on nutrient and on

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prey, respectively. D denotes the washout rate of the chemostat. ϵ_i denote the specific death rates of prey when $i = 1$ and of predator when $i = 2$, respectively.

If the death rates of prey and predator are insignificant (i.e. $\epsilon_i = 0$, $i = 1, 2$), then the only loss of organisms is due to “washout” at the same rate that the nutrient is lost. In this case, an organism’s death rate is not negligible, thus the removal rates of this organism should be the sum of washout rate of the chemostat and the death rate.

Assume that the functions F_i satisfy the following:

$$F_i : R_+ \rightarrow R_+, \quad (2)$$

$$F_i(0) = 0, \quad (3)$$

$$F_i \text{ is continuously differentiable,} \quad (4)$$

$$F_1'(s) > 0, F_2'(s) > 0 \text{ for all } s \geq 0 \text{ and } F_3'(x) > 0 \text{ for } x \geq 0. \quad (5)$$

We begin by scaling the equation (1) by $s(t) \rightarrow s^o s(t)$, $t \rightarrow t/D$, $x(t) \rightarrow s^o \gamma_1 x(t)$ and $y(t) \rightarrow s^o \gamma_2 y(t)$. Moreover, letting $\gamma_2 = \gamma_1 \gamma_3$, then we obtain the following differential equations:

$$\begin{aligned} s'(t) &= 1 - s(t) - f_1(s(t))x(t) - f_2(s(t))y(t), \\ x'(t) &= x(t)(f_1(s(t)) - D_1) - f_3(x(t))y(t), \\ y'(t) &= y(t)(f_2(s(t)) + f_3(x(t)) - D_2), \end{aligned} \quad (6)$$

with $s(0) > 0$, $x(0) > 0$ and $y(0) > 0$, where,

$$D_i = 1 - \frac{\epsilon_i}{D}, \quad f_i(s) = \frac{F_i(s^o s)}{D}, \quad i = 1, 2,$$

and

$$f_3(x) = \frac{F_3(\gamma_1 s^o x)}{D}.$$

It is easy to check that f_i satisfy (2)-(5).

The organization of this paper is as follows. In Section 2, the results on the positivity and boundedness of solutions are presented. An existence and local stability of steady states are studied in Section 3. Global stability of steady states and persistence analysis are provided in Section 4. Discussion is carried out in the last section.

2 Preliminaries

The positivity and boundedness are considered in the following two lemmas the proofs of which are similar to those in [8].

LEMMA 2.1 [8]. The solutions $(s(t), x(t), y(t))$ of (6) are positive, and for large t , $s(t) < 1$.

LEMMA 2.2 [8]. For $\epsilon > 0$, the solutions $(s(t), x(t), y(t))$ of (6) satisfy

$$\frac{1}{D_{\max}} - \epsilon \leq s(t) + x(t) + y(t) \leq \frac{1}{D_{\min}} + \epsilon, \quad (7)$$

for large t , where

$$D_{\max} = \max\{1, D_1, D_2\} \text{ and } D_{\min} = \min\{1, D_1, D_2\}. \quad (8)$$

3 Steady States and Their Stability

$E_1(1, 0, 0)$ denotes the washout steady state. $E_2 = (\lambda_s, (1 - \lambda_s)/D_1, 0)$ denotes the predator-free steady state, where λ_s is defined as the unique solution of $f_1(s) = D_1$ (if it exists). $E_c = (s^*, \lambda_x, \lambda_x(f_1(s^*) - D_1)/(D_2 - f_2(s^*)))$ denotes the interior steady state, where λ_x and s^* are defined as the unique solutions of $f_2(s) + f_3(x) = D_2$ and they satisfy the equation

$$s^* + f_1(s^*)\lambda_x + \frac{f_2(s^*)}{f_3(\lambda_x)}(f_1(s^*) - D_1)\lambda_x = 1 \tag{9}$$

with $s^* \in (0, 1)$. Prey-free with predator steady state does not exist. To discuss the existence of steady states, their components must be non-negative. Since all components of the washout rate is non-negative, E_1 always exists. Since f_1 is increasing with $f_1(0) = 0$, λ_s exists, satisfies $0 < \lambda_s < 1$ and

$$f_1(\lambda_s) = D_1 \iff D_1 < f_1(1). \tag{10}$$

In this case, there is a predator-free steady state $E_2 = (\lambda_s, (1 - \lambda_s)/D_1, 0)$, otherwise, no such steady state exists. In the case where $f_1(s) < D_1$ for all $s > 0$, we regard $\lambda_s = +\infty$. In case of the mixed-culture steady state E_c , since f_2 and f_3 are increasing with $f_2(0) = f_3(0) = 0$, s^* and λ_x exist and satisfy

$$f_2(s^*) + f_3(\lambda_x) = D_2 \iff f_2(1) + \lim_{x \rightarrow +\infty} f_3(x) > D_2. \tag{11}$$

For the existence of E_c , we have two cases:

CASE 1. $D_2 - f_2(s^*) = f_3(\lambda_x) > 0$, then no condition is necessary.

CASE 2. $f_1(s^*) - D_1 > 0$ or $s^* > \lambda_s$.

Note that

$$F(s) = 1 - s - f_1(s)\lambda_x - f_2(s)\lambda_x \frac{f_1(s) - D_1}{D_2 - f_2(s)} \tag{12}$$

is decreasing in S with $F(0) = 1 > 0$, $F(s^*) = 0$ and $F(\lambda_s) = 1 - \lambda_s - D\lambda_x$. So, $s^* > \lambda_s$ if, and only if, $\lambda_x < (1 - \lambda_s)/D_1$. In the case where $f_2(s) + f_3(x) < D_2$ for all $s, x > 0$, we regard $\lambda_x = +\infty$. Therefore, E_2 exists if, and only if, $\lambda_s < 1$, and E_c exists if, and only if, $\lambda_s < 1$ and $\lambda_x < (1 - \lambda_s)/D_1$.

Now, the local stability of these steady states will be investigated by studding the eigenvalues of the associated Jacobian matrices. The Jacobian matrix of (6) has the form

$$J = \begin{bmatrix} -1 - xf'_1(s) - yf'_2(s) & -f_1(s) & -f_2(s) \\ xf'_1(s) & f_1(s) - D_1 - yf'_3(x) & -f_3(x) \\ yf'_2(s) & yf'_3(x) & f_2(s) + f_3(x) - D_2 \end{bmatrix}. \tag{13}$$

At E_1 ,

$$J(E_1) = \begin{bmatrix} -1 & -f_1(1) & -f_2(1) \\ 0 & f_1(1) - D_1 & 0 \\ 0 & 0 & f_2(1) - D_2 \end{bmatrix}.$$

The eigenvalues lie on the diagonal. They are all negative if, and only if, $f_1(1) - D_1 < 0$ and $f_2(1) - D_2 < 0$ or, equivalently, $\lambda_s > 1$ and $\lambda_x > 0$, $s^* > 1$, respectively.

When E_2 exists, the Jacobian matrix at E_2 is

$$J(E_2) = \begin{bmatrix} -1 - \frac{(1-\lambda_s)f_1'(\lambda_s)}{D_1} & -f_1(\lambda_s) & -f_2(\lambda_s) \\ \frac{(1-\lambda_s)f_1'(\lambda_s)}{D_1} & 0 & -f_3\left(\frac{1-\lambda_s}{D_1}\right) \\ 0 & 0 & f_2(\lambda_s) + f_3\left(\frac{1-\lambda_s}{D_1}\right) - D_2 \end{bmatrix}.$$

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 eigenvalue of $J(E_2)$ is $f_2(\lambda_s) + f_3((1-\lambda_s)/D_1) - D_2$, the entry in the lower right-hand corner. Therefore E_2 is asymptotically stable if, and only if, $f_2(\lambda_s) + f_3((1-\lambda_s)/D_1) < D_2$ or $(1-\lambda_s)/D_1 < \lambda_x$ and $\lambda_s < s^*$.

When E_c exists, the Jacobian matrix $J(E_c)$ at E_c is given by

$$\begin{bmatrix} -1 - \lambda_x f_1'(s^*) - \frac{(f_1(s^*) - D_1)\lambda_x f_2'(s^*)}{(D_2 - f_2(s^*))} & -f_1(s^*) & -f_2(s^*) \\ \lambda_x f_1'(s^*) & f_1(s^*) - D_1 - \frac{(f_1(s^*) - D_1)\lambda_x f_3'(\lambda_x)}{(D_2 - f_2(s^*))} & -f_3(\lambda_x) \\ \frac{(f_1(s^*) - D_1)\lambda_x f_2'(s^*)}{(D_2 - f_2(s^*))} & \frac{(f_1(s^*) - D_1)\lambda_x f_3'(\lambda_x)}{(D_2 - f_2(s^*))} & 0 \end{bmatrix}.$$

The eigenvalues of $J(E_c)$ satisfy

$$\mu^3 + a_1\mu^2 + a_2\mu + a_3 = 0,$$

where

$$a_1 = 1 + \lambda_x f_1'(s^*) + \left(\frac{\lambda_x f_3'(\lambda_x)}{f_3(\lambda_x)} - 1 \right) (f_1(s^*) - D_1) + \lambda_x f_2'(s^*) \left(\frac{f_1(s^*) - D_1}{D_2 - f_2(s^*)} \right),$$

$$\begin{aligned} a_2 &= \left\{ 1 + \lambda_x f_1'(s^*) + \lambda_x f_2'(s^*) \left(\frac{f_1(s^*) - D_1}{D_2 - f_2(s^*)} \right) \right\} \left(\frac{\lambda_x f_3'(\lambda_x)}{f_3(\lambda_x)} - 1 \right) (f_1(s^*) - D_1) \\ &\quad + \lambda_x f_2(s^*) f_2'(s^*) \left(\frac{f_1(s^*) - D_1}{D_2 - f_2(s^*)} \right) + \lambda_x f_1(s^*) f_1'(s^*) + \lambda_x f_3'(\lambda_x) (f_1(s^*) - D_1) \end{aligned}$$

and

$$\begin{aligned} a_3 &= \lambda_x f_2(s^*) \left(\frac{f_1(s^*) - D_1}{D_2 - f_2(s^*)} \right) \\ &\quad \times \left\{ \lambda_x f_1'(s^*) f_3'(\lambda_x) + f_2'(s^*) \left(\frac{\lambda_x f_3'(\lambda_x)}{f_3(\lambda_x)} - 1 \right) (f_1(s^*) - D_1) \right\} \\ &\quad + \lambda_x f_2'(s^*) \left(\frac{f_1(s^*) - D_1}{D_2 - f_2(s^*)} \right) \{ \lambda_x f_3'(\lambda_x) (f_1(s^*) - D_1) + f_1(s^*) (f_2(s^*) - D_2) \} \\ &\quad + \lambda_x f_3'(\lambda_x) (f_1(s^*) - D_1) (1 + \lambda_x f_1'(s^*)). \end{aligned}$$

The Routh-Hurwitz criterion says that E_c will be asymptotically stable if, and only if, $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 > a_3$.

We can summarize the above results in the following theorem.

THEOREM 3.1. If $\lambda_s > 1$, then only E_1 exists and E_1 is locally asymptotically stable. If $\lambda_s < 1$ and $(1 - \lambda_s)/D_1 < \lambda_x$, then only E_1 and E_2 exist, E_1 is unstable and E_2 is locally asymptotically stable. If $\lambda_s < 1$ and $(1 - \lambda_s)/D_1 > \lambda_x$, then E_1 , E_2 and E_c exist, and E_1 and E_2 are unstable. E_c is locally asymptotically stable if $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 > a_3$.

4 Global Analysis

In the last section, we shall show that E_1 is globally asymptotically stable if only E_1 exists. The proof is very straightforward. Most importantly, we shall show that if only E_1 and E_2 exist then E_2 is globally asymptotically stable. The proofs involve the construction of a Lyapunov function and the application of the Lyapunov-LaSalle theorem. (We shall use Theorem 2.1 in Wolkowicz and Lu [13], which is a slightly modified version of the statements given in LaSalle [5] and Hale [3]). Also, if E_1 , E_2 and E_c exist, then E_c may be globally asymptotically stable by showing that system (6) is uniformly persistent.

The following theorem states that E_1 is a global attractor if it is the only steady state (i.e. $1 < \lambda_s$).

THEOREM 4.1. If $\lambda_s > 1$, then all solutions of (6) satisfy $\lim_{t \rightarrow +\infty} (s(t), x(t), y(t)) = (1, 0, 0)$.

PROOF. Since $s(t) < 1$ for large t and $f_1(1) - D_1 < 0$ or $1 < \lambda_s$, there is $\alpha > 0$ such that $x'(t) < -\alpha x(t)$ for t sufficiently large, and $\alpha = \min_{0 \leq t} \{D_1 - f_1(s) + (y/x)f_3(x)\}$. This shows that $\lim_{t \rightarrow +\infty} x(t) = 0$. It follows from the third equation of (6) that $y' < -\beta y(t)$ where $\beta = \min_{0 \leq t} \{D_2 - f_2(s)\}$ which implies that $\lim_{t \rightarrow +\infty} y(t) = 0$. Then the first equation of (6) yields $\lim_{t \rightarrow +\infty} s(t) = 1$. The proof is complete.

THEOREM 4.2. If $\lambda_s < 1$ and $D_{\min}^{-1} < \lambda_s + \lambda_x$, then all solutions of (6) satisfy $\lim_{t \rightarrow +\infty} (s(t), x(t), y(t)) = (\lambda_s, (1 - \lambda_s)/D_1, 0)$.

PROOF. If we have $(\lambda_s + \lambda_x)D_{\min} > 1$, then $\lambda_s + D_1 \lambda_x > 1$. That is, $D_{\min}^{-1} < \lambda_s + \lambda_x$ implies $(1 - \lambda_s)/D_1 < \lambda_x$. We choose $D_{\max} < d_1$ and $D_{\min} > d_2$ such that $d_2^{-1} < \lambda_s + \lambda_x$ and that (7) gives $d_1^{-1} < s(t) + x(t) + y(t) < d_2^{-1}$ for large t . Let

$$\alpha = 1 + \max_{\substack{0 \leq x \leq \frac{1-\lambda_s}{D_1} \\ 0 \leq s \leq \lambda_s}} \left\{ \frac{f_3(x)(\frac{1-\lambda_s}{D_1} - x)}{x(D_2 - f_2(s) - f_3(x))} \right\} \tag{14}$$

and

$$\beta = 1 + \max_{\substack{\lambda_x \leq x \leq \frac{1}{D_{\min}} + 1 \\ s^* \leq s \leq 1}} \left\{ \frac{\alpha(f_2(s) + f_3(x) - D_2)}{(D_2 - f_2(s))} \right\} \tag{15}$$

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

$$C'(u) = \begin{cases} 0 & u \leq \frac{1}{d_2} - \lambda_s, \\ \frac{\beta}{\lambda_x + \lambda_s - \frac{1}{d_2}} (u - (\frac{1}{d_2} - \lambda_s)) & \frac{1}{d_2} - \lambda_s \leq u < \lambda_x \\ \beta & u \geq \lambda_x \end{cases} . \quad (16)$$

$C'(u)$ is linear on $[\frac{1}{d_2} - \lambda_s, \lambda_x]$. Since, $x + y \leq \frac{1}{d_2} - \lambda_s$ if $s \geq \lambda_s$, therefore, if $s \geq \lambda_s$, then $C'(x + y) = 0$.

Define a Lyapunov function $V(s, x, y)$ as follows

$$V = \int_{\lambda_s}^s \frac{(f_1(\xi) - D_1)(1 - \lambda_s)}{D_1(1 - \xi)} d\xi + x - x^* \ln x + \alpha y + C(x + y), \quad (17)$$

on the set

$$\phi = \left\{ (s, x, y) : s \in (0, 1), x, y \in (0, +\infty), s + x + y \in \left(\frac{1}{d_1}, \frac{1}{d_2} \right) \right\},$$

where

$$x^* = \frac{1 - \lambda_s}{D_1}.$$

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

$$\begin{aligned} \dot{V} &= \left\{ C'(x + y) + 1 - \frac{(1 - \lambda_s)(f_1(s) + \frac{y}{x}f_2(s))}{D_1(1 - s)} \right\} (f_1(s) - D_1)x \\ &\quad + \left\{ \frac{f_3(x)}{x} \left(\frac{1 - \lambda_s}{D_1} - x \right) + \alpha(f_2(s) + f_3(x) - D_2) \right\} y \\ &\quad + (f_3(s) - D_2)C'(x + y)y. \end{aligned} \quad (18)$$

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

$$\left(1 - \frac{(1 - \lambda_s)(f_1(s) + \frac{y}{x}f_2(s))}{D_1(1 - s)} \right) (f_1(s) - D_1)x$$

is non-positive for $0 < s < 1$ and equals zero for $s \in [0, 1]$ if, and only if, $s = \lambda_s$. The term $C'(x + y)(f_1(s) - D_1)x$ is non-positive for $s \in [0, 1]$, since $C'(x + y) = 0$ for $s \geq \lambda_s$ and $C'(u) \geq 0$ for $u \geq 0$, and $f_1(s) - D_1 < 0$ for $s < \lambda_s$. Therefore, the first term in \dot{V} is always non-positive and equals zero for $s \in [0, 1]$ if and only if $s = \lambda_s$. Define

$$G(s, x, y) = \frac{f_3(x)}{x} \left(\frac{1 - \lambda_s}{D_1} - x \right) + \alpha(f_2(s) + f_3(x) - D_2) - (D_2 - f_2(s))C'(x + y). \quad (19)$$

Note that $(D_2 - f_2(s))C'(x + y)$ is always nonnegative. If $0 < x \leq (1 - \lambda_s)/D_1$ and $0 < s \leq \lambda_s$, then by the definition of α , we get

$$G(s, x, y) = (f_2(s) + f_3(x) - D_2) - (D_2 - f_2(s))C'(x + y) < 0.$$

If $(1 - \lambda_s)/D_1 < x \leq \lambda_x$ and $\lambda_s < s \leq s^*$, then all three terms in $G(s, x, y)$ are non-positive and one can easily see that $G(s, x, y) < 0$. If $x \geq \lambda_x$ and $s \geq s^*$, and therefore $C'(x + y) = \beta$, then by the definition of β , we have

$$G(s, x, y) = \frac{f_3(x)}{x} \left(\frac{1 - \lambda_s}{D_1} - x \right) - (D_2 - f_2(s)) < 0.$$

Therefore $G(s, x, y) < 0$ for $x \geq 0$ and $s \geq 0$.

By Lemma 2.1, every bounded solution of (6) is contained in ϕ , and hence by Theorem 2.1 in [13] every solution of (6) approaches the set ψ , the largest invariant subset M of $\eta = \{(s, x, y) \in \phi : \dot{V} = 0\}$. η is made up of only one point of the following form $(\lambda_s, x, 0)$, where $x \in [0, \infty)$. Since V is bounded above, the unique point of the form $(\lambda_s, x, 0) \in M$ implies that $s(t) = \lambda_s$ and $y(t) = 0$, which in turn leads to $0 = s'(t) = 1 - \lambda_s - f_1(\lambda_s)x(t)$ and hence $x = (1 - \lambda_s)/D_1$. Therefore $M = \{E_2\}$. This completes the proof.

THEOREM 4.3. If $\lambda_s < 1$ and $(1 - \lambda_s)/D_1 > \lambda_x$, then system (6) is uniformly persistent, i.e., there exists a constant $\epsilon > 0$, independent of initial conditions, such that

$$\liminf_{t \rightarrow +\infty} s(t) \geq \epsilon, \quad \liminf_{t \rightarrow +\infty} x(t) \geq \epsilon, \quad \text{and} \quad \liminf_{t \rightarrow +\infty} y(t) \geq \epsilon. \tag{20}$$

PROOF. Choose

$$X_1 = \{(s, x, y); 0 \leq s \leq 1, 0 < x \leq \frac{1}{D_{\min}} + 1, 0 < y \leq \frac{1}{D_{\min}} + 1\},$$

$$Y_1 = \{(s, x, 0); 0 \leq s \leq 1, 0 \leq x \leq \frac{1}{D_{\min}} + 1\},$$

$$Y_2 = \{(s, 0, y); 0 \leq s \leq 1, 0 \leq y \leq \frac{1}{D_{\min}} + 1\}$$

and

$$X_2 = Y_1 \cup Y_2.$$

Then X_1 and X_2 are two disjoint subsets of R^3 , X_2 is compact, $X = X_1 \cup X_2$ is also compact, and X_1 and X_2 are positively invariant for (6). By lemma 2.2, Y_1, Y_2 and X_1 are global attractors in the union of the $s - x$ plane and $s - y$ plane and in R^3 , respectively. We prove that X_2 is a uniformly strong repeller for X_1 (for the definitions of a uniformly strong repeller as well as a weak repeller, see Thieme [10]). E_1 and E_2 are the only steady states in X_2 . E_1 is a saddle in R^3 and its stable manifold is $\{(s, 0, y); y \geq 0\}$. E_2 is also a saddle in R^3 and its stable manifold is $\{(s, x, 0); x > 0\}$. Therefore E_1 and E_2 are weak repellers for X_1 .

The stable manifold structures of E_1 and E_2 (E_2 is a global attractor in the $s - x$ plane) imply that they are not cyclically chained to each other on the boundary X_2 . By Proposition 1.2 of Thieme [10], X_2 is a uniform strong repeller for X_1 ; that is, there are $\delta_1 > 0$ and $\delta_2 > 0$ such that $\liminf_{t \rightarrow +\infty} x(t) > \delta_1$ and $\liminf_{t \rightarrow +\infty} y(t) > \delta_2$ where δ_1 and δ_2 do not depend on the initial values in X_1 . Applying Proposition 2.2 of Thieme [10] to the first equation of (6) yields that there is $\delta_3 > 0$ such that $\liminf_{t \rightarrow +\infty} s(t) > \delta_3$ where δ_3 does not depend on the initial values of X_1 . This completes the proof.

5 Discussion

In this paper, we considered a food chain with one prey and one predator in the chemostat. In this model, the prey consumes the nutrient and the predator consumes the prey and the nutrient. We assumed that the functional response functions are general monotone response functions and the removal rates are different.

A conservation principle was lost due to the different removal rates. In the case of different removal rates, the system cannot be reduced to a two-dimensional system and we therefore must look at the full system. We found that the washout steady state E_1 is the global attractors if it is the only steady state (this happens when $\lambda_s > 1$). This confirms the intuition that both prey and predator can not persist if the removal rate of the prey is relatively large. When E_1 and E_2 are the only steady states, we found that E_1 is unstable and E_2 is locally asymptotically stable. By constructing a Lyapunov function, we were able to show that if E_1 and E_2 are the only steady states, E_2 is a global attractor. The construction of the Lyapunov function is rather novel and nontrivial. This novel idea has been used in [6, 7, 8]. This condition does not depend on the specific properties of the functional response functions, and it becomes necessary if D_{\min} is close to both D_1 and 1. The global stability of E_2 implies that the predator will be washed out in the chemostat regardless of the initial density levels of prey and predator. We also showed that, when E_c exists, the prey and predator coexist in the sense that the system is uniformly persistent. In this case, a switch of the stability of the interior steady state E_c may occur.

If $D_1 = D_2 = 1$, the conservation principle holds; that is, the w -limit sets of solutions of (6) lie in the plane $\Sigma : s + x + y = 1$. In this case, one can easily show that E_c (if it exists) is locally asymptotically stable if, and only if,

$$\frac{f_3'(\lambda_x)}{f_2'(s^*)}(f_3(\lambda_x) + \lambda_x f_1'(s^*)) > f_3(\lambda_x) + \left(1 - \frac{\lambda_x f_3'(\lambda_x)}{f_3(\lambda_x)}\right)(f_1(s^*) - 1), \quad (21)$$

and

$$\lambda_x f_1'(s^*) + \frac{\lambda_x f_2'(s^*)}{f_3(\lambda_x)}(f_1(s^*) - 1) > \left(1 - \frac{\lambda_x f_3'(\lambda_x)}{f_3(\lambda_x)}\right)(f_1(s^*) - 1). \quad (22)$$

When one of these inequality is reversed, E_c will be a repeller in Σ , and there will be at least one periodic orbit (by an application of the Poincaré-Bendixson theorem). Determining the number of periodic solutions is a deep mathematical problem. In case of $f_2(s) = 0$; $s \in [0, 1)$, and Michaelis-Menten-type response function, Kuang [4] has shown that if

$$f_1'(s^*)\lambda_x + (\lambda_x f_3'(\lambda_x) - 1)(f_1(s^*) - 1), \quad (23)$$

is small and negative, then the limit cycle is unique and asymptotically stable. Also, in [1] it was shown that in the case of Michaelis-Menten-type response functions and $D_1 = D_2 = 1$, E_c is globally asymptotically stable if it is locally asymptotically stable. In [8] it is asserted that this may be true for general response functions.

It remains open if this is true in the case of general response functions and different removal rates in [8] and in the current paper.

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