Simple Food Chain in a Chemostat with Distinct Removal Rates

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In this paper, we consider a model describing predator–prey interactions in a chemostat that incorporates both general response functions and distinct removal rates. In this case, the conservation law fails. To overcome this difficulty, we make use of a novel way of constructing a Lyapunov function in the study of the global stability of a predator-free steady state. Local and global stability of other steady states, persistence analysis, as well as numerical simulations are also presented. Our findings are largely in line with those of an identical removal rate case.

Key Words: chemostat; predator; prey; food chain; persistence.

1. INTRODUCTION

The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. It can be used to study competition between different populations of microorganisms, and has the advantage that the parameters are readily measurable. See the monograph of Smith and Waltman [10] for a detailed description of a chemostat and for various mathematical methods for analyzing chemostat models.

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Consider a food chain in a chemostat with one predator and one prey. We assume that the predator feeds exclusively on the prey, and the prey consumes the nutrient in the chemostat. This is an interesting practical problem both mathematically and biologically. In a waste treatment process, the bacteria live on the waste (or nutrient) while other organisms such as ciliates feed on the bacteria.

The equations of interest are

\[
S'(t) = (S^0 - S(t))D - \frac{1}{\gamma_1}F_1(S(t))x(t),
\]

\[
x'(t) = x(t)(F_1(S(t)) - \bar{D}_1) - \frac{1}{\gamma_2}F_2(x(t))y(t), \tag{1.1}
\]

\[
y'(t) = y(t)(F_2(x(t)) - \bar{D}_2),
\]

\[
S(0) > 0, \quad x(0) > 0, \quad y(0) > 0,
\]

where \(S(t)\) denotes the concentration of nutrient at time \(t\); \(x(t)\) denotes the concentration of prey at time \(t\); \(y(t)\) denotes the concentration of predator at time \(t\); \(S^0\) denotes the input concentration of the nutrient; \(\gamma_1\) and \(\gamma_2\) denote the yield constants; \(F_1\) and \(F_2\) denote the specific per-capita growth rates of prey and predator organisms, respectively; \(\bar{D}\) is the washout rate of the chemostat; each \(\bar{D}_i = D + \varepsilon_i, i = 1, 2\), where \(\varepsilon_1\) and \(\varepsilon_2\) denote the specific death rates of organisms \(x\) and \(y\), respectively. The values \(\bar{D}_1 = D\) and \(\bar{D}_2 = D\) result from assuming that the death rates of \(x\) and \(y\) are negligible so that the only loss of organisms is due to “washout” at the same rate that the nutrient is lost. If an organism’s death rate is significant, the removal rate of this organism should be the sum of \(D\) and the death rate.

We make the following assumptions on the response functions \(f_i\)

\[F_i: R_+ \rightarrow R_+,\]

\(F_i\) is continuously differentiable, \(F_i(0) = 0\), \(F_i'(S) > 0\) for all \(S \geq 0\) and \(F_2'(x) > 0\) for \(x \geq 0\). \(\tag{1.5}\)

By measuring concentrations of nutrient in units of \(S^0\), time in units of \(1/D\), \(x\) is units of \(\gamma_1 S^0\), and \(y\) in units of \(\gamma_1 \gamma_2 S^0\), one reduces the number
of parameters and obtains the following differential equations

$$S'(t) = 1 - S(t) - f_1(S(t)) x(t),$$
$$x'(t) = x(t) \left( f_1(S(t)) - D_1 \right) - f_2(x(t)) y(t),$$
$$y'(t) = y(t) \left( f_2(x(t)) - D_2 \right),$$

$$(1.6)$$

where $D_i = \bar{D}_i/D$, $i = 1, 2$; $f_1(S) = D^{-1}F_1(S^0S)$; and $f_2(x) = D^{-1}F_2(\gamma_1\gamma_2S^0x)$. Clearly, $f_i$ satisfy (1.2)–(1.5).

If the functional response functions are of the Michaelis–Menten form and $D_1 = D_2 = 1$, then system (1.6) becomes

$$S' = 1 - S - \frac{m_1S}{a_1 + S} x,$$

$$x' = x \left( \frac{m_1S}{a_1 + S} - 1 \right) - \frac{m_2x}{a_2 + x} y,$$

$$y' = y \left( \frac{m_2x}{a_2 + x} - 1 \right),$$

$$(1.7)$$

$S(0) > 0, \quad x(0) > 0, \quad y(0) > 0.$

System (1.7) has been studied in [1, 4, 9, and 12] and related experiments are described in [2, 4]. In [1], Butler et al. took advantage of the conservation principle and gave a global analysis of this model. The authors showed that the interior critical point is globally asymptotically stable if it is locally asymptotically stable, and if it is unstable then there exists a periodic orbit for (1.7).

The analysis in [1] critically depends on the assumption that removal rates for the prey and predator organisms are both equal to the washout rate of the chemostat. Consider the quantity

$$T = S + x + y,$$

where $S$, $x$, and $y$ are solutions of (1.7). Then $T$ satisfies the differential equality

$$T' = 1 - T.$$  

In this special case, the differential equality implies that all solutions approach the plane $S + x + y = 1$ at an exponential rate. This in turn implies that system (1.7) can be reduced to a planar system by dropping the $S$ equation and making the substitution $S = 1 - x - y$ in the remain-
ing two equations. This is often referred to as the conservation principle. However, a slight change in the removal rate of $x$ or $y$ destroys the form of the conservation principle and the reduction to a planar system is no longer possible.

This paper is organized as follows: In the next section, we present results on the positivity and boundedness of solutions. Section 3 deals with the existence and local stability of steady states. In Section 4, we shall provide global analysis, including global stability of the boundary steady states and persistence analysis. This paper ends with a discussion section which consists of comments and numerical simulations.

2. PRELIMINARIES

In this section, we shall present some preliminary results, including the positivity and boundedness of solutions. We consider first the positivity.

**Lemma 2.1.** The solutions $S(t), x(t), y(t)$ of (1.6) are positive, and for large $t$, $S(t) < 1$.

**Proof.** It is easy to see that $S(t)$ stays positive. Assume the lemma is false. Let $t_1 = \min \{ t: t > 0, x(t)y(t) = 0 \}$. Assume first that $x(t_1) = 0$. Then $y(t) \geq 0$ for $t \in [0, t_1]$. Let $A = \min_{0 \leq t \leq t_1} \{ f_1(S(t)) - D_1 - (f_2(x(t))/x(t))y(t) \}$. Then, for $t \in [0, t_1]$, $x'(t) \geq Ax(t)$, which implies that $x(t_1) \geq x(0)e^{At_1} > 0$, a contradiction. A similar argument shows that $y(t_1) = 0$ is absurd. Finally, $S' < 0$ for all $S \geq 1$. This proves the lemma.

Define

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

Adding the three equations in (1.6) yields

$$(S + x + y)' = 1 - (S + D_1x + D_2y).$$

This leads to

$$1 - D_{\text{max}}(S + x + y) \leq (S + x + y)' \leq 1 - D_{\text{min}}(S + x + y).$$

Solving this inequality yields the following lemma.

**Lemma 2.2.** For $\varepsilon > 0$, the solutions $S(t), x(t), y(t)$ of (1.6) satisfy

$$\frac{1}{D_{\text{max}}} - \varepsilon \leq S(t) + x(t) + y(t) \leq \frac{1}{D_{\text{min}}} + \varepsilon \quad (2.1)$$

for large $t$. 
3. STEADY STATES AND THEIR STABILITY

The washout steady state for system (1.6) is denoted by \( E_1 = (1, 0, 0). \) There is only one possible steady state involving prey organisms but not predator organisms, denoted by \( E_2 = (\lambda_s, (1 - \lambda_s)/D_1, 0) \) where \( \lambda_s \) is defined as the unique solution of

\[
f_1(S) - D_1 = 0
\]

(if it exists). The interior steady state is denoted by \( E_c = (S^*, \lambda_x, \lambda_x(f_1(S^*) - D_1)/D_2) \) where \( \lambda_x \) is defined as the unique solution of

\[
f_2(x) - D_2 = 0
\]

(if it exists), and \( S^* \) is defined as the unique solution of

\[
1 - S - f_1(S)\lambda_x = 0
\]

(3.1)

with \( S^* \in (0, 1) \). One can see that no steady state can exist where there is a predator species but no prey species. We say that \( E_2 \) or \( E_c \) does not exist if any one of its components is negative.

We now discuss the existence of steady states. The washout steady state \( E_1 = (1, 0, 0) \) always exists. Since \( f_1 \) is increasing with \( f_1(0) = 0 \),

\[
\lambda_s \text{ exists, satisfying } 0 < \lambda_s < 1 \text{ and } f_1(\lambda_s) = D_1 \iff f_1(1) > D_1.
\]

(3.2)

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 \( \lambda_s = +\infty \).

Next consider the mixed-culture (interior) steady state \( E_c \). Since \( f_2 \) is increasing with \( f_2(0) = 0 \),

\[
\lambda_x \text{ exists, satisfying } f_2(\lambda_x) = D_2 \iff \lim_{x \to \infty} f_2(x) > D_2.
\]

(3.3)

For \( E_c \) to exist, \( f_1(S^*) - D_1 \) must be positive or \( S^* > \lambda_s \). Note that

\[
F(S) = 1 - S - f_1(S)\lambda_x \text{ is decreasing in } S \text{ with } F(0) = 1 > 0, F(S^*) = 0, \text{ and } F(\lambda_s) = 1 - \lambda_s - D_1\lambda_x. \text{ So, } S^* > \lambda_s \text{ if and only if } (1 - \lambda_s)/D_1 > \lambda_x.
\]

In the case where \( f_2(S) < D_2 \) for all \( S > 0 \), 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 \( (1 - \lambda_s)/D_1 > \lambda_x \).

Next we investigate the local stability of these steady states by finding the eigenvalues of the associated Jacobian matrices.
The Jacobian matrix of (1.6) takes the form

\[ J = \begin{bmatrix}
-1 - xf_1'(S) & -f_1(S) & 0 \\
xf_1'(S) & f_1(S) - D_1 - yf_2'(x) & -f_2(x) \\
0 & yf_2'(x) & f_2(x) - D_2
\end{bmatrix}. \quad (3.4) \]

At \( E_1 \),

\[ J(E_1) = \begin{bmatrix}
-1 & -f_1(1) & 0 \\
0 & f_1(1) - D_1 & 0 \\
0 & 0 & -D_2
\end{bmatrix}. \quad (3.5) \]

The eigenvalues lie on the diagonal. They are all negative if and only if \( f_1(1) - D_1 < 0 \) or, equivalently, \( \lambda_x > 1 \).

When \( E_2 \) exists, the Jacobian matrix at \( E_2 \) is

\[ J(E_2) = \begin{bmatrix}
-1 - \frac{1 - \lambda_x}{D_1} f_1'(\lambda_x) & -f_1(\lambda_x) & 0 \\
\frac{1 - \lambda_x}{D_1} f_1'(\lambda_x) & 0 & -f_2 \left( \frac{1 - \lambda_x}{D_1} \right) \\
0 & 0 & f_2 \left( \frac{1 - \lambda_x}{D_1} \right) - D_2
\end{bmatrix}. \quad (3.6) \]

The determinant of the upper left-hand \( 2 \times 2 \) matrix is positive and its trace is negative, so its eigenvalues have negative real parts. The third eigenvalue of \( J(E_2) \) is \( f_2((1 - \lambda_x)/D_1) - D_2 \), the entry in the lower right-hand corner. Therefore \( E_2 \) is asymptotically stable if and only if \( f_2((1 - \lambda_x)/D_1) - D_2 < 0 \) or \( (1 - \lambda_x)/D_1 < \lambda_x \).

When \( E_c \) exists, the Jacobian matrix at \( E_c \) takes the form

\[ J(E_c) = \begin{bmatrix}
-1 - f_1'(S^*) \lambda_x & -f_1(S^*) & 0 \\
f_1'(S^*) \lambda_x & \left( 1 - \frac{\lambda_x}{D_2} f_2'(\lambda_x) \right) (f_1(S^*) - D_1) & -D_2 \\
0 & \frac{\lambda_x (f_1(S^*) - D_1)}{D_2} f_2'(\lambda_x) & 0
\end{bmatrix}. \quad (3.7) \]
The eigenvalues of $E(E_c)$ satisfy

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

where

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

$$a_2 = (1 + f_1'(S^*) \lambda_x) \left( \frac{\lambda_x}{D_x} f_2' (\lambda_x) - 1 \right) (f_1(S^*) - D_1) + \lambda_x (f_1(S^*) - D_1) f_2' (\lambda_x) + \lambda_x f_1(S^*) f_1'(S^*),$$

and

$$a_3 = \lambda_x f_2' (\lambda_x) (1 + f_1'(S^*) \lambda_x) (f_1(S^*) - D_1).$$

Note that the constant term $a_3$ is positive, so the Routh–Hurwitz criterion says that $E_c$ will be asymptotically stable if and only if $a_1 > 0$ and $a_1 a_2 > a_3$.

We summarize the above results in the following theorem.

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

If $D_1 = D_2 = 1$, then the limit plane of (1.6) is $\Sigma: S + x + y = 1$. If we drop the $S$ equation, then the limit system of (1.6) takes the form

$$x' = x(f_1(1-x-y) - 1) - f_2(x)y,$$

$$y' = y(f_2(x) - 1),$$

$$x(0) > 0, \quad y(0) > 0.$$

For this reduced system, if $E_c$ exists then the Jacobian matrix at $E_c$ is

$$J(E_c) = \begin{bmatrix}
-\lambda_x f_1'(S^*) - (\lambda_x f_2'(\lambda_x) - 1)(f_1(S^*) - 1) & -\lambda_x f_1'(S^*) - f_2(\lambda_x) \\
\lambda_x (f_1(S^*) - 1) f_2'(\lambda_x) & 0
\end{bmatrix}.$$

(3.10)
The determinant of this matrix is \([\lambda_x f'_1(S^*) + f_2(\lambda_x)][\lambda_x(f_1(S^* - 1) f'_2(\lambda_x)), which is positive, and the trace is \(-\lambda_x f'_1(S^*) - (\lambda_x f'_2(\lambda_x) - 1)(f_1(S^*) - 1). Therefore if \(-\lambda_x f'_1(S^*) - (\lambda_x f'_2(\lambda_x) - 1)(f_1(S^*) - 1) < 0\) then \(E_c\) is locally asymptotically stable; if \(-\lambda_x f'_1(S^*) - (\lambda_x f'_2(\lambda_x) - 1)(f_1(S^*) - 1) > 0\) then \(E_c\) is a repellor in \(\Sigma\), and in this case there is a periodic solution in \(\Sigma\) (by an application of the Poincaré–Bendixson theorem). We summarize these in the following theorem.

**Theorem 3.2.** Assume \(D_1 = D_2 = 1\) and \(E_c\) exists (i.e., \(\lambda_x + \lambda_x < 1\)). If \(-\lambda_x f'_1(S^*) - (\lambda_x f'_2(\lambda_x) - 1)(f_1(S^*) - 1) < 0\) then \(E_c\) is locally asymptotically stable. If \(-\lambda_x f'_1(S^*) - (\lambda_x f'_2(\lambda_x) - 1)(f_1(S^*) - 1) > 0\) then \(E_c\) is unstable, and there is a periodic solution in the plane \(\Sigma : S + x + y = 1\).

### 4. GLOBAL ANALYSIS

In the previous section, we showed that if only \(E_1\) exists then \(E_1\) is asymptotically stable, if \(E_1\) and \(E_2\) exist then \(E_1\) is unstable and \(E_2\) is (locally) asymptotically stable, if \(E_1\), \(E_2\), and \(E_c\) exist then \(E_1\) and \(E_2\) are unstable, and in this case \(E_c\) may or may not be stable. 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, under a reasonable additional assumption \(E_2\) 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 2.1 in Wolkowicz and Lu [13], which is a slightly modified version of the statements given in LaSalle [6] and Hale [3].) We shall also show that system (1.6) is uniformly persistent if \(E_c\) exists.

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

**Theorem 4.1.** If \(\lambda_x > 1\), then all solutions of (1.6) satisfy

\[
\lim_{t \to \infty} (S(t), x(t), y(t)) = (1, 0, 0).
\]

**Proof.** Since \(S(t) < 1\) for large \(t\) and \(f_1(1) - D_2 < 0\) (i.e., \(\lambda_x > 1\)), there is \(\alpha > 0\) such that \(x'(t) < -\alpha x(t)\) for \(t\) sufficiently large. This shows \(\lim_{t \to \infty} x(t) = 0\). It follows from the third equation of (1.6) that \(\lim_{t \to \infty} y(t) = 0\). Then the first equation of (1.6) yields \(\lim_{t \to \infty} S(t) = 1\). The proof is complete.

Note that if \((\lambda_x + \lambda_x)D_{\min} > 1\) then \(\lambda_x + D_1\lambda_x > 1\). That is, \(1/D_{\min} < \lambda_x + \lambda_x\) implies \((1 - \lambda_x)/D_1 < \lambda_x\).
THEOREM 4.2. If \( \lambda_s < 1 \) and

\[
\frac{1}{D_{\text{min}}} < \lambda_s + \lambda_x,
\]  
(4.1)

then all solutions of (1.6) satisfy

\[
\lim_{t \to \infty} (S(t), x(t), y(t)) = \left(\lambda_s, \frac{1 - \lambda_s}{D_1}, 0\right).
\]

Proof. We choose \( d_1 > D_{\text{max}} \) and \( d_2 < D_{\text{min}} \) such that

\[
\frac{1}{d_2} < \lambda_s + \lambda_x
\]  
(4.2)

and that, for large \( t \),

\[
\frac{1}{d_1} < S(t) + x(t) + y(t) < \frac{1}{d_2}.
\]  
(4.3)

Let

\[
\alpha = 1 + \max_{0 \leq x \leq (1 - \lambda_s)/D_1} \left\{ \frac{f_2(x)((1 - \lambda_s)/D_1 - x)}{x(D_2 - f_2(x))} \right\}
\]

and

\[
\beta = 1 + \max_{\lambda_x \leq x \leq 1/D_{\text{min}} + 1} \left\{ \frac{\alpha(f_2(x) - D_2)}{D_2} \right\}.
\]

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

\[
C'(u) = \begin{cases} 
0, & \text{if } u \leq \frac{1}{d_2} - \lambda_s, \\
\frac{\beta}{\lambda_x + \lambda_s - 1/d_2} \left( u + \lambda_x - \frac{1}{d_2} \right), & \text{if } \frac{1}{d_2} - \lambda_s < u < \lambda_x, \\
\beta, & u \geq \lambda_x.
\end{cases}
\]

\( C'(u) \) is simply linear on \([1/d_2 - \lambda_s, \lambda_x]\). In view of (4.3),

\[
x + y \leq \frac{1}{d_2} - \lambda_s \quad \text{if } S \geq \lambda_s.
\]
Therefore, if \( S \geq \lambda_s \), then \( C'(x + y) = 0 \). The graph of \( C'(x + y) \) is shown in Fig. 1.

Define the Lyapunov function \( V(S, x, y) \) as follows

\[
V = \int_{\lambda_s}^{S} \frac{(f_1(\xi) - D_1)(1 - \lambda_s)}{D_1(1 - \xi)} d\xi + \left(x - x^* - x^* \ln \frac{x}{x^*}\right) + \alpha y + C(x + y) \tag{4.4}
\]

on the set \( \Psi = \{(S, x, y) : S \in (0, 1), \; x, y \in (0, +\infty), \; S + x + y \in (1/d_1, 1/d_2)\} \), where \( x^* = (1 - \lambda_s)/D_1 \). Then the time derivative of \( V \) along solutions of the differential equation is

\[
\dot{V} = \left[C'(x + y) + 1 - \frac{(1 - \lambda_s)f_1(S)}{D_1(1 - S)}\right](f_1(S) - D_1)x
\]

\[
+ \left[\frac{f_2(x)}{x} \left(\frac{1 - \lambda_s}{D_1} - x\right) + \alpha (f_2(x) - D_2) - D_2 C'(x + y)\right]y.
\]

First, note that \( [1 - (1 - \lambda_s)f_1(S)/D_1(1 - S)](f_1(S) - D_1)x \) is nonpositive for \( 0 < S < 1 \) and equals 0 for \( S \in [0, 1) \) if and only if \( S = \lambda_s \) or \( x = 0 \). Since \( C'(x + y) = 0 \) for \( S \geq \lambda_s \) and \( C'(u) \geq 0 \) for \( u \geq 0 \), \( C'(x + y) \) \((f_1(S) - D_1)x \) is nonpositive for \( S \in [0, 1) \). Therefore the first term in \( \dot{V} \) is always nonpositive and equals 0 for \( S \in [0, 1) \) if and only if \( S = \lambda_s \) or \( x = 0 \).

\[\text{FIG. 1. A graphical depiction of} \; C'(x + y) \; \text{for} \; S \in [0, 1).}\]
Define

\[ h(S, x, y) = \frac{f_2(x)}{x} \left( \frac{1 - \lambda_s}{D_1} - x \right) + \alpha (f_2(x) - D_2) - D_2 C'(x + y). \]

If \( 0 < x \leq 1 - \lambda_s/D_1 \), then

\[ \frac{f_2(x)}{x} \left( \frac{1 - \lambda_s}{D_1} - x \right) \geq 0 \quad \text{and} \quad f_2(x) - D_2 \leq 0 \]

and they are equal to 0 if and only if \( x = (1 - \lambda_s)/D_1 \). Note that \( C'(x + y) \) is always nonnegative. By the definition of \( \alpha \), \( h(S, x, y) < 0 \) for \( 0 \leq x < (1 - \lambda_s)/D_1 \) and possibly \( h(S, x, y) = 0 \) if \( x = (1 - \lambda_s)/D_1 \). If \( (1 - \lambda_s)/D_1 < x \leq \lambda_s \), all three terms in \( h(S, x, y) \) are nonpositive and one can easily see \( h(S, x, y) < 0 \).

If \( x > \lambda_s \), then \( x + y > \lambda_s \) and therefore \( C'(x + y) = \beta \). Note that, if \( x > \lambda_s \), only the second term in \( h(S, x, y) \) is nonnegative. According to the definition of \( \beta \), \( h(S, x, y) < 0 \) if \( x > \lambda_s \). Therefore \( h(S, x, y) < 0 \) for \( x \geq 0 \) and \( x \neq (1 - \lambda_s)/D_1 \), and it is possibly 0 if \( x = (1 - \lambda_s)/D_1 \).

By Lemma 2.1 every bounded solution of (1.6) is contained in \( \Psi \), and hence by Theorem 2.1 in [13] every solution of (1.6) approaches the set \( \Lambda \), the largest invariant subset \( M \) of \( \Phi = \{(S, x, y) \in \Psi : \dot{V} = 0 \} \). \( \Phi \) is made up of points of the following forms

\[
\begin{align*}
(S, 0, 0), & \quad \text{where } S \in [0, 1], \\
\left( \lambda_s, \frac{1 - \lambda_s}{D_1}, y \right), & \quad \text{where } y \in [0, \infty), \\
(\lambda_s, x, 0), & \quad \text{where } x \in [0, \infty).
\end{align*}
\]

Since \( V \) is bounded above, any point of the form \((S, 0, 0)\) cannot be in the \( \omega \)-limit set \( \Omega \) of any solution initiating in the interior of \( R_+^3 \). \((\lambda_s, x, 0) \in M\) implies that \( S(t) = \lambda_s \) which in turn leads to \( 0 = S'(t) = 1 - \lambda_s - f_2(\lambda_s)x \) and hence \( x = (1 - \lambda_s)/D_1 \). \((\lambda_s, (1 - \lambda_s)/D_1, y) \in M\) implies that \( S(t) = \lambda_s \) and \( x(t) = (1 - \lambda_s)/D_1 \). The second equation of (1.6) implies that \( x' = 0 \), which yields \( y = 0 \). Therefore \( M = \{E_2\} \). This completes the proof.

**Theorem 4.3.** If \( \lambda_s < 1 \) and \( (1 - \lambda_s)/D_1 > \lambda_s \), then system (1.6) is uniformly persistent; i.e., there exists a constant \( \varepsilon > 0 \), independent of initial conditions, such that

\[
\liminf_{t \to \infty} S(t) \geq \varepsilon, \quad \liminf_{t \to \infty} x(t) \geq \varepsilon, \quad \liminf_{t \to \infty} y(t) \geq \varepsilon.
\]
Proof. Choose
\[ X_1 = \left\{ (S, x, y); 0 \leq S \leq 1, 0 < x \leq \frac{1}{D_{\text{min}}} + 1, 0 < y \leq \frac{1}{D_{\text{min}}} + 1 \right\}, \]
\[ Y_1 = \left\{ (S, x, 0); 0 \leq S \leq 1, 0 \leq x \leq \frac{1}{D_{\text{min}}} + 1 \right\}, \]
\[ Y_2 = \left\{ (S, 0, y); 0 \leq S \leq \frac{1}{D_{\text{min}}} + 1, 0 \leq y \leq \frac{1}{D_{\text{min}}} + 1 \right\}, \]

and
\[ X_2 = Y_1 \cup Y_2. \]

FIG. 2. \( m_1 = 3.6, \ a_1 = 0.8, \ D_1 = 1.4, \ m_2 = 3, \ a_2 = 0.6, \ D_2 = 1.2. \) \( (S(0), x(0), y(0)) = (0.6, 0.2, 0.7). \) The top curve depicts \( S(t), \) the middle one depicts \( x(t), \) and the bottom one depicts \( y(t). \) In this case, \( \lambda_y + \lambda_x < 1. \) Clearly, the solution approaches the predator-free steady state.
Then $X_1$ and $X_2$ are two disjoint subsets of $\mathbb{R}^3$, $X_2$ is compact, $\mathcal{X} = X_1 \cup X_2$ is also compact, and $X_1$ and $X_2$ are positively invariant for (1.6). By Lemma 2.2, $X_2$ and $\mathcal{X}$ are global attractors in the union of the $S-x$ plane and $S-y$ plane and in $\mathbb{R}^3_+$, 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 [11]).

$E_1$ and $E_2$ are the only steady states in $X_2$. $E_1$ is a saddle in $\mathbb{R}^3$ and its stable manifold is $\{(S,0,y); y \geq 0\}$. $E_2$ is also a saddle in $\mathbb{R}^3$ 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 [11], $X_2$ is a uniform strong repeller for $X_1$; that is, there are $\delta_1 > 0$ and $\delta_2 > 0$ such that $\liminf_{t \to \infty} x(t) > \delta_1$ and $\liminf_{t \to \infty} y(t) > \delta_2$ with $\delta_1$ and $\delta_2$ not depend-

![Graph showing $S(x,y)$ over time](image)

**FIG. 3.** $m_1 = 3.6, a_1 = 0.8, D_1 = 1.4, m_2 = 3, a_2 = 0.6, D_2 = 1$. $(S(0), x(0), y(0)) = (0.6, 0.2, 0.7)$. The top curve depicts $S(t)$, the middle one depicts $x(t)$, and the bottom one depicts $y(t)$. Clearly, the solution approaches a positive steady state.
ing on the initial values in $X_1$. Applying Proposition 2.2 of Thieme [11] to the first equation of (1.6) yields that there is $\delta_3 > 0$ such that $\liminf_{t \to \infty} S(t) > \delta_3$ with $\delta_3$ not depending 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 but the predator does not consume the nutrient. We assumed that the functional response functions are general monotone response functions and the removal rates are different. The model we considered is more general and realistic than the models in [1, 4, 9, 12].

FIG. 4. $m_1 = 8.5$, $a_1 = 0.6$, $D_1 = D_2 = 1$, $m_2 = 6$, $a_2 = 0.6$. $(S(0), x(0), y(0)) = (0.1, 0.7, 0.8)$. The top curve depicts $S(t)$, the middle one depicts $y(t)$, and the bottom one depicts $x(t)$. The solution appears to approach a periodic solution.
The main difficulty we faced was the lack of a conservation principle which 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 attractor if it is the only steady state (this happens when $\lambda_s > 1$). This confirms the intuition that both prey and predator cannot persist if the removal rate of the prey is relatively large. When $E_1$ and the predator-free steady state $E_2$ 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, under an additional assumption (see (4.1)), $E_2$ is a global attractor. The construction of the Lyapunov function is rather novel and nontrivial. This novel idea has been used in [7, 8]. This condition does not depend on the specific properties of the functional response functions, and it becomes necessary if $D_{\text{min}}$ is close to both $D_1$ and 1. The

\begin{figure}[h]
  \centering
  \includegraphics[width=\textwidth]{figure5.png}
  \caption{\textit{m}_1 = 8.5, \textit{a}_1 = 0.6, \textit{D}_1 = 1.1, \textit{m}_2 = 6, \textit{a}_2 = 0.6, \textit{D}_2 = 1. (S(0), x(0), y(0)) = (0.1, 0.7, 0.8). The top curve depicts \textit{S}(t), the middle one depicts \textit{y}(t), and the bottom one depicts \textit{x}(t). The solution oscillates but eventually approaches a positive steady state.}
\end{figure}
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.

$E_2$ is a global attractor if it is locally asymptotically stable and (4.1) holds. Based on our extensive simulation work where the functional response functions take the Michaelis–Menten form

$$f_1(S) = \frac{m_1S}{a_1 + S} \quad \text{and} \quad f_2(x) = \frac{m_2x}{a_2 + x},$$

we conjecture that this steady state remains globally asymptotically stable as long as it is locally stable (see Fig. 2). As $E_2$ becomes unstable, a locally asymptotically stable interior steady state $E_c$ bifurcates from it. Our simulation work (Fig. 3) suggests that $E_c$ is a global attractor if it is locally asymptotically stable. As certain parameters increase or decrease further away, $E_c$ loses its stability and oscillatory solutions appear. These oscillatory solutions (see Figs. 4 and 6) appear to be the results of Hopf bifurcations. Figure 4 shows a case in which $D_1 = D_2 = 1$ and system (1.6) possesses periodic solutions. Figure 5 indicates that perturbing $D_1$ (while keeping other parameters in Fig. 4 fixed) leads to a bifurcation. For example, changing $D_1 = 1$ in Fig. 4 to $D_1 = 1.1$ in Fig. 5 seems to destroy the periodic solutions and possibly leads to the global stability of $E_c$. Therefore varying the values of $D_1$ and $D_2$ may affect the dynamics of (1.6) in a very surprising and significant way.

Next, we see how the parameters $D_1$ and $D_2$ affect the dynamics of (1.6) if $S^0$ is fixed. $D_1 = 1 + \varepsilon_1$ and $D_2 = 1 + \varepsilon_2$, where $\varepsilon_1$ and $\varepsilon_2$ denote the scaled specific death rates of the prey and predator, respectively. (Note that the analysis of the model requires no assumptions on the sign of $\varepsilon_i$'s, as long as the $D_i$'s all remain positive. This leaves the ID_i's open to other interpretations.) Assume that $D_1$ and $D_2$ are large enough so that $\lambda_x > 1$, then both prey and predator populations will be washed out ($E_1$ is stable) in the chemostat. As $D_1$ is gradually decreased, eventually there is a bifurcation when $\lambda_x < 1$ and $(1 - \lambda_x)/D_1 < \lambda_x$. In this case, $E_1$ loses its stability and the new bifurcated steady state $E_2$ is asymptotically stable. As $D_2$ is gradually decreased, the next bifurcation occurs when $\lambda_x < 1$ and $(1 - \lambda_x)/D_1 > \lambda_x$ hold. In this case $E_2$ loses its stability, and a new interior steady state $E_c$ appears.

If $D_1 = D_2 = 1$, the conservation principle holds; that is, the $\omega$-limit sets of solutions of (1.6) 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 $f_1(S^*)(\lambda_x + (\lambda_x f^*_2(\lambda_x) - 1)(f_1(S^*) - 1) > 0$. When this in-
FIG. 6. \( m_1 = 4, \ a_1 = 0.6, \ D_1 = 1.1, \ m_2 = 5, \ a_2 = 0.5, \ D_2 = 1.2. \ (S(0), x(0), y(0)) = (0.1, 0.7, 0.8). \) In this case, it can be shown that \( E_c \) exists and is unstable. The top curve depicts \( S(t) \), the middle one depicts \( x(t) \), and the bottom one depicts \( y(t) \). The solution oscillates and seems to approach a periodic solution.

equality is reversed, \( E_c \) will be a repeller in \( \Sigma \), 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. Kuang [5] has shown in the case of Michaelis–Menten-type response functions, if \( -f_1'(S^*)\lambda_x - (\lambda_x f_2'(\lambda_x) - 1)(f_1(S^*) - 1) \) is small and positive, then the limit cycle is unique and asymptotically stable. We guess this is true for general response functions. 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. It remains open if this is true in the case of general response functions and different removal rates.
REFERENCES