



A delayed chemostat model with general nonmonotone response functions and differential removal rates [☆]

Lin Wang, Gail S.K. Wolkowicz *

Department of Mathematics and Statistics, McMaster University, Hamilton, Ontario, L8S 4K1 Canada

Received 27 June 2005

Available online 15 September 2005

Submitted by William F. Ames

Abstract

A chemostat model with general nonmonotone response functions is considered. The nutrient conversion process involves time delay. We show that under certain conditions, when n species compete in the chemostat for a single resource that is allowed to be inhibitory at high concentrations, the competitive exclusion principle holds. In the case of insignificant death rates, the result concerning the attractivity of the single species survival equilibrium already appears in the literature several times (see [H.M. El-Owaidy, M. Ismail, Asymptotic behavior of the chemostat model with delayed response in growth, *Chaos Solitons Fractals* 13 (2002) 787–795; H.M. El-Owaidy, A.A. Moniem, Asymptotic behavior of a chemostat model with delayed response growth, *Appl. Math. Comput.* 147 (2004) 147–161; S. Yuan, M. Han, Z. Ma, Competition in the chemostat: convergence of a model with delayed response in growth, *Chaos Solitons Fractals* 17 (2003) 659–667]). However, the proofs are all incorrect. In this paper, we provide a correct proof that also applies in the case of differential death rates. In addition, we provide a local stability analysis that includes sufficient conditions for the bistability of the single species survival equilibrium and the washout equilibrium, thus showing the outcome can be initial condition dependent. Moreover, we show that when the species specific death rates are included, damped oscillations may occur even when there is no delay. Thus, the species specific death rates might also account for the damped oscillations in transient behavior observed in experiments.

© 2005 Elsevier Inc. All rights reserved.

Keywords: Global asymptotic stability; Nonmonotone response functions; Delay differential equations; Chemostat; Bistability; Competition; Transient dynamics; Species specific death rates

[☆] Research was partially supported by NSERC of Canada.

* Corresponding author.

E-mail address: wolkowicz@mcmaster.ca (G.S.K. Wolkowicz).

1. Introduction

In this paper, we consider the following chemostat model:

$$\begin{cases} \dot{S}(t) = (S^0 - S)D - \sum_{j=1}^n x_j(t)f_j(S(t)), \\ \dot{x}_j(t) = -D_jx_j(t) + \alpha_jx_j(t - \tau_j)f_j(S(t - \tau_j)), \quad j = 1, 2, \dots, n, \end{cases} \tag{1.1}$$

where $S(t)$ denotes the concentration of the nutrient at time t ; S^0 denotes the input nutrient concentration; D represents the washout rate of the nutrient; $x_j(t)$ represents the biomass of the j th population of microorganisms at time t ; $D_j, j \in N(1, n) := \{1, 2, \dots, n\}$ represents the specific removal rate of species x_j ($D_j = D + \epsilon_j$, where ϵ_j is the species specific death rate of species x_j); $f_j(S(t))$ indicates the consumption rate of nutrient by the j th species; the constant $\tau_j \geq 0$ stands for the time delay in conversion of nutrient to biomass for the j th species. Usually, as discussed in [6,15], the constant $\alpha_j = e^{-D_j\tau_j}$, and so $\alpha_jx_j(t - \tau_j)$ represents the biomass of those microorganisms in species x_j that consume nutrient τ_j units of time prior to time t and that survive in the chemostat the τ_j units of time necessary to complete the nutrient conversion process. However, in the proofs of this paper, we need only require that the constant α_j be positive. For example, $\alpha_j = Y_j e^{-D_j\tau_j}$, where Y_j is a yield constant, or even α_j independent of τ_j are permitted.

We assume that the growth response functions $f_j(S)$ in (1.1) satisfy:

- (i) $f_j : \mathbf{R}^+ \rightarrow \mathbf{R}^+$ is continuously differentiable and $f_j(0) = 0$ for each $j \in N(1, n)$;
- (ii) there exist uniquely defined positive (possibly extended) real numbers $\lambda_j \leq \mu_j \leq \infty$ such that

$$\begin{cases} \alpha_j f_j(S) < D_j, & \text{if } S \notin [\lambda_j, \mu_j]; \\ \alpha_j f_j(S) > D_j, & \text{if } S \in (\lambda_j, \mu_j). \end{cases}$$

Note that if $D_j = D$ for $j \in N(1, n)$, then (1.1) reduces to

$$\begin{cases} \dot{S}(t) = (S^0 - S)D - \sum_{j=1}^n x_j(t)f_j(S(t)), \\ \dot{x}_j(t) = -Dx_j(t) + \alpha_jx_j(t - \tau_j)f_j(S(t - \tau_j)), \quad j = 1, 2, \dots, n, \end{cases} \tag{1.2}$$

which was studied in [6,15] in the case of monotone response functions. Model (1.1) is a generalization of the model studied in [2,11,14], where the authors considered nonmonotone response functions but did not consider delays. An analogous model with monotone response functions involving distributed delays was investigated in [16,17]. For general theory on chemostat models, we refer to [12].

Model (1.2) under both assumptions (i) and (ii) when $n = 1$ was recently analyzed in [18], where the transient behavior is studied via local and global Hopf bifurcation analysis. In [13], Wang and Ma considered model (1.2) with $n = 2$ and they proved that if $\lambda_1 < \lambda_2 < S^0 < \mu_1$, then the equilibrium $E_{\lambda_1} = (\lambda_1, \alpha_1(S^0 - \lambda_1), 0)$ of (1.2) is globally attractive in the sense that all positive solutions converge to E_{λ_1} . The case with $n = 3$ was investigated in [4], where the authors attempted to establish convergence results similar to results in [13]. As well, in [5,19], the authors tried to obtain global convergence results for an arbitrary number of competitors. As we will explain in Section 3, the proofs in [4,5,19] are all incorrect.

In this paper, we consider model (1.1). We first establish some preliminary results in Section 2. Then in Section 3, we provide a correct proof for the attractivity of the single species survival equilibrium in the case of an arbitrary number of species. In a remark in this section, we point

out the specific errors in the literature. Global asymptotic stability results are given in Section 4, where it is also shown that bistability and damped oscillations are possible even in the case of no delay (i.e., $\tau_j = 0$). Some numerical simulations are given in Section 5. We conclude this paper in Section 6 with a discussion.

2. Preliminary results

We denote by C_{n+1}^+ the nonnegative cone of the Banach space of continuous functions $C_{n+1}^+ = \{\phi = (\phi_0, \phi_1, \phi_2, \dots, \phi_n) : [-r, 0] \rightarrow \mathbf{R}^{n+1} \text{ continuous}\}$, where $r = \max\{\tau_1, \tau_2, \dots, \tau_n\}$. By the method of steps [1], it can be shown that for each $\phi \in C_{n+1}^+$, there is a unique solution of (1.1) through ϕ , that we denote by $\pi(\phi; t) := (S(\phi; t), x_1(\phi, t), \dots, x_n(\phi, t)) \in \mathbf{R}_{n+1}^+$, which is well defined for all $t \geq 0$ and satisfies $\pi(\phi; \cdot)|_{[-r, 0]} = \phi$ and is positive provided $\phi_i(0) > 0, i \in N(1, n)$. Throughout this paper, when we say a solution $\pi(\phi; t)$ or $(S(t), x_1(t), \dots, x_n(t))$ of (1.1) is positive we mean that each component of the solution is positive for all $t \geq 0$.

We denote the washout equilibrium $E_{S^0} = (S^0, 0, \dots, 0)$ and the single species survival equilibrium

$$E_{\lambda_1} = \left(\lambda_1, \frac{\alpha_1(S^0 - \lambda_1)D}{D_1}, 0, \dots, 0 \right).$$

Let $(S(t), x_1(t), \dots, x_n(t)), t \geq 0$ be an arbitrary positive solution of (1.1). As in [15], we define

$$V(t) = S(t) + \sum_{i=1}^n \frac{1}{\alpha_i} x_i(t + \tau_i), \quad t \geq 0, \tag{2.1}$$

and $D_{\max} = \max(D, D_1, \dots, D_n), D_{\min} = \min(D, D_1, \dots, D_n)$. Then we have (see [15])

$$\frac{DS^0}{D_{\max}} + \epsilon_1(t) \leq V(t) \leq \frac{DS^0}{D_{\min}} + \epsilon_2(t), \quad t \geq 0, \tag{2.2}$$

where $\epsilon_i(t) \rightarrow 0$ exponentially for $i = 1, 2$ as $t \rightarrow \infty$. This leads to

$$\frac{DS^0}{D_{\max}} \leq \alpha = \liminf_{t \rightarrow \infty} V(t) \leq \limsup_{t \rightarrow \infty} V(t) = \beta \leq \frac{DS^0}{D_{\min}}. \tag{2.3}$$

This implies that $V(t)$ is bounded and all positive solutions of (1.1) are also bounded.

In what follows, we introduce some useful lemmas. Lemma 2.1 is due to Barbălat, which can be found in [7], and Lemma 2.2 is the so called fluctuation lemma [9].

Lemma 2.1. *Let $a \in (-\infty, \infty)$ and $f : [a, \infty) \rightarrow \mathbf{R}$ be a differentiable function. If $\lim_{t \rightarrow \infty} f(t)$ exists (finite) and $f'(t)$ is uniformly continuous on (a, ∞) , then $\lim_{t \rightarrow \infty} f'(t) = 0$.*

Lemma 2.2. *Let $f : \mathbf{R}^+ \rightarrow \mathbf{R}$ be a differentiable function. If $\liminf_{t \rightarrow \infty} f(t) < \limsup_{t \rightarrow \infty} f(t)$, then there are sequences $\{t_m\}$ and $\{s_m\}$ with $t_m \rightarrow \infty, s_m \rightarrow \infty$ as $m \rightarrow \infty$ such that for all m*

$$\lim_{m \rightarrow \infty} f(t_m) = \limsup_{t \rightarrow \infty} f(t), \quad f'(t_m) = 0$$

and

$$\lim_{m \rightarrow \infty} f(s_m) = \liminf_{t \rightarrow \infty} f(t), \quad f'(s_m) = 0.$$

Next we state a result concerning competitor-independent extinction.

Theorem 2.1. *If $\lambda_i \geq S^0$, then $\lim_{t \rightarrow \infty} x_i(t) = 0$. Moreover, if $\lambda_i \geq S^0$ for all $i \in N(1, n)$, then every solution $\pi(\phi; t)$ of system (1.1) satisfies*

$$\lim_{t \rightarrow \infty} \pi(\phi; t) = (S^0, 0, \dots, 0).$$

Proof. The proof is similar to that of Theorem 4.1 of [15]. \square

3. Global attractivity of the single species survival equilibrium

With Theorem 2.1 in mind, we next assume that

$$\lambda_1 < \lambda_j < S^0, \quad \text{for all } j \in N(2, n). \tag{3.1}$$

For each $i \in N(1, n)$, we define

$$b_i := \alpha_i \left(\frac{DS^0}{D_{\min}} - \lambda_i \right), \quad \delta_i := \liminf_{t \rightarrow \infty} x_i(t), \quad \gamma_i := \limsup_{t \rightarrow \infty} x_i(t).$$

Lemma 3.1. *If (3.1) holds, then*

$$\gamma_j := \limsup_{t \rightarrow \infty} x_j(t) \leq b_j, \quad \text{for all } j \in N(1, n).$$

Proof. Since $\gamma_j = \limsup_{t \rightarrow \infty} x_j(t)$, by Lemma 2.2, there exists a sequence $\{t_m\}$ with $t_m \rightarrow \infty$ as $m \rightarrow \infty$ and

$$x'_j(t_m) = 0, \quad \lim_{m \rightarrow \infty} x_j(t_m) = \limsup_{t \rightarrow \infty} x_j(t) = \gamma_j.$$

Notice that by (1.1) and (2.1), we have

$$\dot{x}_j(t) = -D_j x_j(t) + \alpha_j x_j(t - \tau_j) f_j \left(V(t - \tau_j) - \sum_{i=1}^n \frac{1}{\alpha_i} x_i(t + \tau_i - \tau_j) \right). \tag{3.2}$$

Therefore,

$$0 = x'_j(t_m) = -D_j x_j(t_m) + \alpha_j x_j(t_m - \tau_j) f_j \left(V(t_m - \tau_j) - \sum_{i=1}^n \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right),$$

that is,

$$f_j \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) = \frac{D_j x_j(t_m)}{\alpha_j x_j(t_m - \tau_j)}.$$

Note that $\gamma_j = \limsup_{t \rightarrow \infty} x_j(t)$. Then for any $\eta > 0$, there exists an $N > 0$ such that when $m > N$,

$$x_j(t_m - \tau_j) < \gamma_j + \eta.$$

This implies that

$$f_j \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) \geq \frac{D_j x_j(t_m)}{\alpha_j (\gamma_j + \eta)}, \quad m > N.$$

Consequently,

$$\liminf_{m \rightarrow \infty} f_j \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) \geq \frac{D_j \gamma_j}{\alpha_j (\gamma_j + \eta)}.$$

Letting $\eta \rightarrow 0$, we obtain

$$\liminf_{m \rightarrow \infty} f_j \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) \geq \frac{D_j}{\alpha_j},$$

which implies that

$$\liminf_{m \rightarrow \infty} \left[V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right] \geq \lambda_j.$$

By virtue of $\limsup_{t \rightarrow \infty} V(t) \leq \frac{DS^0}{D_{\min}}$ and $x_j(t) \geq 0$, we have

$$\frac{DS^0}{D_{\min}} - \frac{1}{\alpha_j} \gamma_j \geq \lambda_j,$$

which gives the desired

$$\gamma_j = \limsup_{t \rightarrow \infty} x_j(t) \leq \alpha_j \left(\frac{DS^0}{D_{\min}} - \lambda_j \right) = b_j, \quad j \in N(1, n). \quad \square$$

Lemma 3.2. *If*

$$\lambda_1 < \lambda_j < S^0 \leq \frac{DS^0}{D_{\min}} \leq \mu_1, \quad \text{for all } j \in N(2, n) \tag{3.3}$$

and

$$\frac{S^0 D}{D_{\max}} - \lambda_1 > \sum_{j=2}^n \left(\frac{S^0 D}{D_{\min}} - \lambda_j \right) \tag{3.4}$$

hold, then $\delta_1 > 0$.

Proof. The proof is similar to that of Lemma 5 in [13] and is omitted here (see also the proof of Lemma 3.5 in [15]). \square

Remark 3.1. The following lemma plays a crucial role in the proof of our convergence result, Theorem 3.1. It cannot be accomplished by the technique employed in the corresponding lemma in [15] where only the case of monotone response functions is considered. It is the proof of this result that is incorrect in [4,5,19] as will be explained in Remark 3.2.

Lemma 3.3. *If (3.3) and (3.4) hold, then $\delta_j = \gamma_j = 0$ for all $j \in N(2, n)$.*

Proof. The proof is divided into several steps.

Step 1. Since (3.3) implies (3.1) holds, by Lemma 3.1, it follows that $\gamma_j \leq b_j$. We show this implies

$$\delta_1 \geq e_1 := \alpha_1 \left[\left(\frac{DS^0}{D_{\max}} - \lambda_1 \right) - \sum_{j=2}^n \left(\frac{DS^0}{D_{\min}} - \lambda_j \right) \right].$$

This can be accomplished by considering two cases: $\delta_1 = \gamma_1$ and $\delta_1 < \gamma_1$.

Case 1.1. $\delta_1 = \gamma_1$, i.e., $\lim_{t \rightarrow \infty} x_1(t)$ exists. Then by Lemma 2.1, we know that $\lim_{t \rightarrow \infty} x'_1(t) = 0$. By Lemma 3.2, $\delta_1 > 0$ and so it follows from (3.2) that

$$f_1 \left(V(t - \tau_j) - \frac{1}{\alpha_1} x_1(t) - \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t + \tau_j - \tau_1) \right) = \frac{D_1 x_1(t) + x'_1(t)}{\alpha_1 x_1(t - \tau_1)}.$$

Hence,

$$\lim_{t \rightarrow \infty} f_1 \left(V(t - \tau_j) - \frac{1}{\alpha_1} x_1(t) - \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t + \tau_j - \tau_1) \right) = \frac{D_1}{\alpha_1},$$

which implies that either

$$\lim_{t \rightarrow \infty} \left[V(t - \tau_j) - \frac{1}{\alpha_1} x_1(t) - \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t + \tau_j - \tau_1) \right] = \lambda_1, \tag{3.5}$$

or

$$\lim_{t \rightarrow \infty} \left[V(t - \tau_j) - \frac{1}{\alpha_1} x_1(t) - \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t + \tau_j - \tau_1) \right] = \mu_1. \tag{3.6}$$

Note that (3.6) can be excluded due to (2.3) and $\delta_1 > 0$, therefore,

$$\frac{DS^0}{D_{\max}} - \frac{1}{\alpha_1} \delta_1 - \sum_{j=2}^n \frac{1}{\alpha_j} b_j \leq \lambda_1.$$

Consequently, we have

$$\delta_1 \geq \alpha_1 \left(\frac{DS^0}{D_{\max}} - \lambda_1 - \sum_{j=2}^n \left(\frac{DS^0}{D_{\min}} - \lambda_j \right) \right) = e_1$$

as desired.

Case 1.2. $\delta_1 < \gamma_1$. By Lemma 2.2, for $0 < \epsilon < \delta_1$, there exists a sequence $\{t_m\}$, with $t_m \rightarrow \infty$ as $m \rightarrow \infty$ such that

$$x'_1(t_m) = 0, \quad \lim_{m \rightarrow \infty} x_1(t_m) = \delta_1 \quad \text{and} \quad x_1(t_m - \tau_1) > \delta_1 - \epsilon > 0.$$

Then

$$\begin{aligned} & f_1 \left(V(t_m - \tau_1) - \frac{1}{\alpha_1} x_1(t_m) - \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t_m + \tau_j - \tau_1) \right) \\ &= \frac{D_1 x_1(t_m)}{\alpha_1 x_1(t_m - \tau_1)} \leq \frac{D_1 x_1(t_m)}{\alpha_1 (\delta_1 - \epsilon)}. \end{aligned}$$

This implies

$$\limsup_{m \rightarrow \infty} f_1 \left(V(t_m - \tau_1) - \frac{1}{\alpha_1} x_1(t_m) - \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t_m + \tau_j - \tau_1) \right) \leq \frac{D_1 \delta_1}{\alpha_1 (\delta_1 - \epsilon)}.$$

Thus, by continuity of the function f_1 , for $\epsilon > 0$ sufficiently small, there exists an $N > 0$ such that for $m > N$, $V(t_m - \tau_1) \geq \frac{DS^0}{D_{\max}} - \frac{\epsilon}{3}$,

$$V(t_m - \tau_1) - \frac{1}{\alpha_1}x_1(t_m) - \sum_{j=2}^n \frac{1}{\alpha_j}x_j(t_m + \tau_j - \tau_1) \leq \lambda_1 + \epsilon$$

and

$$x_1(t_m) \leq \delta_1 + \frac{\alpha_1 \epsilon}{3}, \quad x_j(t_m + \tau_j - \tau_1) \leq b_j + \frac{\alpha_j \epsilon}{3(n-1)}.$$

This shows that

$$\frac{DS^0}{D_{\max}} - \frac{1}{\alpha_1}\delta_1 - \sum_{j=2}^n \frac{1}{\alpha_j}b_j \leq \lambda_1 + 2\epsilon.$$

Letting $\epsilon \rightarrow 0$, we have

$$\frac{DS^0}{D_{\max}} - \frac{1}{\alpha_1}\delta_1 - \sum_{j=2}^n \frac{1}{\alpha_j}b_j \leq \lambda_1,$$

and thus

$$\delta_1 \geq \alpha_1 \left(\frac{DS^0}{D_{\max}} - \lambda_1 - \sum_{j=2}^n \left(\frac{DS^0}{D_{\min}} - \lambda_j \right) \right) = e_1.$$

Step 2. Using $\delta_1 \geq e_1$ established in Step 1, we next show that

$$\gamma_j \leq \max(0, e_2^j), \quad \text{where } e_2^j := \alpha_j \left(\frac{DS^0}{D_{\min}} - \lambda_j - \frac{e_1}{\alpha_1} \right).$$

We consider two cases: $\delta_j = \gamma_j$ and $\delta_j < \gamma_j$.

Case 2.1. First we assume that $\delta_j = \gamma_j$. Then we have $x_j'(t) \rightarrow 0$ as $t \rightarrow \infty$ and it follows from (3.2) that

$$f_j \left(V(t - \tau_j) - \frac{1}{\alpha_j}x_j(t) - \sum_{i \neq j}^n \frac{1}{\alpha_i}x_i(t + \tau_i - \tau_j) \right) = \frac{D_j x_j(t) + x_j'(t)}{\alpha_j x_j(t - \tau_j)}.$$

Since the limit on the right-hand side of the above equation exists, it follows from $\delta_1 > 0$ that

$$\lim_{t \rightarrow \infty} \left(V(t - \tau_j) - \frac{1}{\alpha_j}x_j(t) - \sum_{i \neq j}^n \frac{1}{\alpha_i}x_i(t + \tau_i - \tau_j) \right) = \lambda_j, \text{ or } \mu_j.$$

Note that $\mu_j > \lambda_j$. By (2.3), we have

$$\frac{DS^0}{D_{\min}} - \frac{1}{\alpha_j}\gamma_j - \frac{1}{\alpha_1}\delta_1 \geq \lambda_j.$$

This, combined with $\delta_1 \geq e_1$, yields

$$\frac{DS^0}{D_{\min}} - \frac{1}{\alpha_j}\gamma_j - \frac{1}{\alpha_1}e_1 \geq \lambda_j.$$

Consequently, we have

$$\gamma_j \leq \alpha_j \left(\frac{DS^0}{D_{\min}} - \lambda_j - \frac{1}{\alpha_1} e_1 \right) = e_2^j.$$

Hence, we have $\gamma_j \leq \max(0, e_2^j)$ as desired.

Case 2.2. Assume $\delta_j < \gamma_j$. By Lemma 2.2, given any $\eta > 0$, there exists a sequence $\{t_m\}$, with $t_m \rightarrow \infty$ as $m \rightarrow \infty$ such that

$$x_j'(t_m) = 0, \quad \lim_{m \rightarrow \infty} x_j(t_m) = \gamma_j, \quad \text{and} \quad x_j(t_m - \tau_j) < \gamma_j + \eta.$$

Then it follows from (3.2) that

$$\begin{aligned} & f_j \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) \\ &= \frac{D_j x_j(t_m)}{\alpha_j x_j(t_m - \tau_j)} \geq \frac{D_j x_j(t_m)}{\alpha_j (\gamma_j + \eta)}. \end{aligned}$$

This implies that

$$\liminf_{m \rightarrow \infty} f_j \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) \geq \frac{D_j \gamma_j}{\alpha_j (\gamma_j + \eta)}.$$

Therefore, letting $\eta \rightarrow 0$, we have

$$\liminf_{m \rightarrow \infty} \left(V(t_m - \tau_j) - \frac{1}{\alpha_j} x_j(t_m) - \sum_{i \neq j} \frac{1}{\alpha_i} x_i(t_m + \tau_i - \tau_j) \right) \geq \lambda_j.$$

It follows that

$$\frac{DS^0}{D_{\min}} - \frac{1}{\alpha_j} \gamma_j - \frac{1}{\alpha_1} \delta_1 \geq \lambda_j,$$

and hence

$$\frac{DS^0}{D_{\min}} - \frac{1}{\alpha_j} \gamma_j - \frac{1}{\alpha_1} e_1 \geq \lambda_j.$$

Then, as in Case 2.1, we have $\gamma_j \leq \max(0, e_2^j)$.

Step 3. If $e_2^j \leq 0$ for all $j \in N(2, n)$, then we are done. Without loss of generality, we assume that $e_2^j > 0$, $j = 2, 3, \dots, n_1$ and $e_2^j \leq 0$, $j = n_1 + 1, \dots, n$, where $2 < n_1 \leq n$. Then we have $\gamma_j \leq e_2^j$ for $j \in N(2, n_1)$ and $\gamma_j = 0$ for $j \in N(n_1 + 1, n)$. As in the proof of Step 1, with e_2^j playing the role of b_j , it follows that

$$\frac{DS^0}{D_{\max}} - \frac{1}{\alpha_1} \delta_1 - \sum_{j=2}^n \frac{1}{\alpha_j} e_2^j \leq \lambda_1.$$

Therefore, we have

$$\begin{aligned}
 \delta_1 &\geq \alpha_1 \left(\frac{DS^0}{D_{\max}} - \lambda_1 - \sum_{j=2}^{n_1} \frac{1}{\alpha_j} e_2^j \right) \\
 &= \alpha_1 \left(\frac{DS^0}{D_{\max}} - \lambda_1 - \sum_{j=2}^{n_1} \left(\frac{DS^0}{D_{\min}} - \lambda_j - \frac{e_1}{\alpha_1} \right) \right) \\
 &= \alpha_1 \left(\frac{DS^0}{D_{\max}} - \lambda_1 - \sum_{j=2}^{n_1} \left(\frac{DS^0}{D_{\min}} - \lambda_j \right) \right) + (n_1 - 1)e_1 \\
 &\geq \alpha_1 \left(\frac{DS^0}{D_{\max}} - \lambda_1 - \sum_{j=2}^n \left(\frac{DS^0}{D_{\min}} - \lambda_j \right) \right) + (n_1 - 1)e_1 \\
 &= e_1 + (n_1 - 1)e_1 =: e_3 > 2e_1.
 \end{aligned}$$

Using the same argument as in Step 2, we can show that if

$$\delta_1 \geq e_0 := \max \left\{ \alpha_1 \left(\frac{DS^0}{D_{\min}} - \lambda_j \right), j = 2, 3, \dots, n \right\},$$

then $\gamma_j = 0$ for all $j \in N(2, n)$. So if $e_3 \geq e_0$, then there is nothing to do. We next assume that $e_3 < e_0$. Then, as for Step 2, we can show that

$$\gamma_j \leq \max(0, e_4^j) \quad \text{with } e_4^j := \alpha_j \left(\frac{DS^0}{D_{\min}} - \lambda_j - \frac{1}{\alpha_1} e_3 \right).$$

Notice that $e_3 = n_1 e_1$, and so $e_4^j < e_2^j$. If for some $j \in N(2, n_1)$, $e_4^j \leq 0$, then for such j , $\gamma_j = 0$. Repeating the above procedure, we can obtain a sequence

$$e_1, e_2^j (j = 2, 3, \dots, n_1), e_3, e_4^j (j = 2, 3, \dots, n_2), \dots$$

with

$$n_1 \geq n_2 \geq \dots, \quad e_2^j > e_4^j > \dots,$$

and

$$e_{2k}^j = \alpha_j \left(\frac{DS^0}{D_{\min}} - \lambda_j - \frac{e_{2k-1}}{\alpha_1} \right), \quad e_{2k+1} = e_1 + (n_k - 1)e_{2k-1}, \quad k = 1, 2, \dots$$

Since $\frac{DS^0}{D_{\min}} - \lambda_j$ and e_0 are finite, then after a finite number of steps, say, after obtaining e_{2k+1} for some $k \in N$, we either have all $e_{2(k+1)}^j \leq 0$ or $e_{2k+3} \geq e_0$. This implies that $\gamma_j = 0$ for all $j \in N(2, n)$ and the proof is complete. \square

We are now in the position to state our result concerning the attractivity of E_{λ_1} .

Theorem 3.1. Assume that (3.3) and (3.4) hold. If $0 < D_1 < 2D$, then every solution $\pi(\phi; t)$ of (1.1) satisfies

$$\lim_{t \rightarrow \infty} \pi(\phi; t) = E_{\lambda_1}. \tag{3.7}$$

Proof. As in [15], it suffices to show that

$$\lim_{t \rightarrow \infty} (V(t), x_1(t)) = \left(S^0 + \frac{(D - D_1)(S^0 - \lambda_1)}{D_1}, \frac{\alpha_1(S^0 - \lambda_1)D}{D_1} \right). \tag{3.8}$$

Note that $(V(t), x_1(t))$ satisfies the following differential equations:

$$\begin{aligned} \dot{V}(t) &= -DV(t) + \frac{D - D_1}{\alpha_1} x_1(t) + DS^0 - \epsilon_1(t), \\ \dot{x}_1(t) &= -D_1 x_1(t) + \alpha_1 x_1(t - \tau_1) f_1 \left(V(t - \tau_1) - \frac{1}{\alpha_1} x_1(t) - \epsilon_2(t) \right), \end{aligned} \tag{3.9}$$

where

$$\epsilon_1(t) = \sum_{j=2}^n \frac{D_j - D}{\alpha_j} x_j(t + \tau_j) \quad \text{and} \quad \epsilon_2(t) = \sum_{j=2}^n \frac{1}{\alpha_j} x_j(t + \tau_j - \tau_1).$$

By Lemma 3.2, we know $\epsilon_i(t) \rightarrow 0, i = 1, 2$ as $t \rightarrow \infty$. We next show that

$$\beta - \alpha \geq \frac{\gamma_1 - \delta_1}{\alpha_1}, \tag{3.10}$$

where α and β are defined in (2.3). For any $\epsilon > 0$, we can find a sequence $\{t_m\}$ with $t_m \rightarrow \infty$ as $m \rightarrow \infty$ such that

$$\lim_{m \rightarrow \infty} x_1(t_m) = \gamma_1, \quad x'_1(t_m) = 0, \quad x_1(t_m - \tau_1) \leq \gamma_1 + \epsilon.$$

Then it follows from the second equation of (3.9) that

$$f_1 \left(V(t_m - \tau_1) - \frac{1}{\alpha_1} x_1(t_m) - \epsilon_2(t_m) \right) = \frac{D_1 x_1(t_m)}{\alpha_1 x_1(t_m - \tau_1)} \geq \frac{D_1 x_1(t_m)}{\alpha_1 (\gamma_1 + \epsilon)},$$

which implies

$$\liminf_{m \rightarrow \infty} f_1 \left(V(t_m - \tau_1) - \frac{1}{\alpha_1} x_1(t_m) - \epsilon_2(t_m) \right) \geq \frac{D_1 \gamma_1}{\alpha_1 (\gamma_1 + \epsilon)}.$$

Letting $\epsilon \rightarrow 0$, we have

$$\liminf_{m \rightarrow \infty} f_1 \left(V(t_m - \tau_1) - \frac{1}{\alpha_1} x_1(t_m) - \epsilon_2(t_m) \right) \geq \frac{D_1}{\alpha_1}.$$

This implies there is a subsequence $\{t_{m_k}\}$ of $\{t_m\}$ such that

$$t_{m_k} \rightarrow \infty, \quad \text{as } k \rightarrow \infty,$$

and

$$\begin{aligned} &\liminf_{m \rightarrow \infty} f_1 \left(V(t_m - \tau_1) - \frac{1}{\alpha_1} x_1(t_m) - \epsilon_2(t_m) \right) \\ &= \lim_{k \rightarrow \infty} f_1 \left(V(t_{m_k} - \tau_1) - \frac{1}{\alpha_1} x_1(t_{m_k}) - \epsilon(t_{m_k}) \right) \\ &\geq \frac{D_1}{\alpha_1}. \end{aligned}$$

Therefore, we have

$$\lim_{k \rightarrow \infty} \left(V(t_{m_k} - \tau_1) - \frac{1}{\alpha_1} x_1(t_{m_k}) - \epsilon(t_{m_k}) \right) \in [\lambda_1, \mu_1],$$

i.e.,

$$\lim_{k \rightarrow \infty} \left(V(t_{m_k} - \tau_1) - \frac{1}{\alpha_1} \gamma_1 \right) \geq \lambda_1.$$

This shows

$$\limsup_{t \rightarrow \infty} V(t) = \beta \geq \lim_{k \rightarrow \infty} V(t_{m_k} - \tau_1) \geq \lambda_1 + \frac{\gamma_1}{\alpha_1}. \tag{3.11}$$

Similarly, we can show that

$$\alpha \leq \frac{\delta_1}{\alpha_1} + \lambda_1. \tag{3.12}$$

Then (3.10) follows from (3.11) and (3.12). The rest of the proof is similar to the last part of the proof of Lemma 4.3 in [15] and we omit the details here. \square

Applying the above theorem to model (1.2), we immediately have the following result.

Corollary 3.1. *If*

$$\lambda_1 < \lambda_j < S^0 < \mu_1 \quad \text{for all } j \in N(2, n), \tag{3.13}$$

and

$$S^0 - \lambda_1 > \sum_{j=2}^n (S^0 - \lambda_j), \tag{3.14}$$

hold, then every positive solution $\pi(\phi; t)$ of (1.2) satisfies

$$\lim_{t \rightarrow \infty} \pi(\phi; t) = (\lambda_1, \alpha_1(S^0 - \lambda_1), 0, \dots, 0). \tag{3.15}$$

Proof. In model (1.2), $D_{\min} = D_{\max} = D_j = D$, $j \in N(1, n)$. Then (3.3) and (3.4) reduce to conditions (3.13) and (3.14), respectively, and $0 < D_1 = D < 2D$ holds automatically. Therefore the conclusion follows. \square

Remark 3.2. Here we discuss some errors in [4,5,19]. In these papers, the authors attempted to generalize the results given in [15] to the case with nonmonotone response functions, as in Corollary 3.1. Essentially, the same type of mistakes occurred in [4,5]. More specifically, the assertions (4) of [4] and (3.1) of [5] were incorrect. We also noticed that there was a mistake in [19]. Throughout, it was stated that the response functions were not necessarily monotone, but in the 6th line of the proof of [19, Lemma 3.3, p. 664], the monotonicity of f_j was used to derive an inequality which was crucial for the proof of their main result. In fact, the proof in [19] was very much the same as that of [15], where the monotonicity played an important role. Here in this paper, we establish Lemma 3.3 using a new approach that enables us to finally provide a correct proof.

4. Global stability, bistability and damped oscillations

4.1. Global stability

Note that in Theorem 3.1, we obtain the attractivity of the single species survival equilibrium E_{λ_1} . To show that E_{λ_1} is globally asymptotically stable, it only remains to prove E_{λ_1} is locally asymptotically stable.

Lemma 4.1. E_{λ_1} is locally asymptotically stable provided that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_j$ for all $j \in N(2, n)$.

Proof. The characteristic equation of the linearization of (1.1) at E_{λ_1} is $\Delta(\lambda) = 0$, with

$$\Delta(\lambda) = \Delta_1(\lambda) \prod_{j=2}^n (\lambda + D_j - \alpha_j f_j(\lambda_1) e^{-\lambda \tau_j}),$$

where

$$\Delta_1(\lambda) := \lambda^2 + [(1 + k)D_1 + kb]\lambda - (kD_1^2 + D_1\lambda)e^{-\lambda \tau_1} + kD_1(D_1 + b)$$

with $k := \frac{D}{D_1}$, $b := \alpha_1(S^0 - \lambda_1)f'(\lambda_1) > 0$. Note that $\lambda_1 < \lambda_j$, $j \in N(2, n)$, i.e., $\lambda_1 \notin [\lambda_j, \mu_j]$, $j \in N(2, n)$. This implies $\alpha_j f_j(\lambda_1) < \alpha_j f_j(\lambda_j) = D_j$ for all $j \in N(2, n)$. Then by Haye’s theorem [1], all roots of

$$\lambda + D_j - \alpha_j f_j(\lambda_1) e^{-\lambda \tau_j}, \quad j \in N(2, n),$$

have only negative real parts. It is only left to show that all roots of $\Delta_1(\lambda) = 0$ have negative real parts. It is easy to show this is true when $k = 1$, i.e., $D = D_1$. It is also clear that $\lambda = 0$ is not a root of $\Delta_1(\lambda) = 0$. Thus by Theorem 2.1 of [3], it suffices to show that $\Delta_1(\lambda) = 0$ does not admit a purely imaginary root. In fact, if $i\omega$ ($\omega > 0$) is a root of $\Delta_1(\lambda) = 0$, then we have, by separating the real and imaginary parts,

$$-\omega^2 + kD_1^2 + kbD_1 - \omega D_1 \sin(\omega \tau_1) - kD_1^2 \cos(\omega \tau_1) = 0 \tag{4.1}$$

and

$$(1 + k)D_1\omega + kb\omega - \omega D_1 \cos(\omega \tau_1) + kD_1^2 \sin(\omega \tau_1) = 0. \tag{4.2}$$

From (4.1) and (4.2), we obtain

$$-\omega^2 + kD_1^2 + kbD_1 = \omega D_1 \sin(\omega \tau_1) + kD_1^2 \cos(\omega \tau_1) \tag{4.3}$$

and

$$(1 + k)D_1\omega + kb\omega = \omega D_1 \cos(\omega \tau_1) - kD_1^2 \sin(\omega \tau_1). \tag{4.4}$$

Squaring both sides of (4.3) and (4.4) and adding, we have

$$\omega^2 [kb + (1 + k)D_1]^2 + (kD_1^2 + kbD_1 - \omega^2)^2 = \omega^2 D_1^2 + k^2 D_1^4,$$

which leads to

$$\omega^4 + B\omega^2 + C = 0, \tag{4.5}$$

with

$$B = [kb + (1 + k)D_1]^2 - D_1^2 - 2(kD_1^2 + kbD_1) \quad \text{and} \quad C = (kD_1^2 + kbD_1)^2 - k^2 D_1^4.$$

Letting $y = \omega^2 > 0$, we can write (4.5) as

$$F(y) = y^2 + By + C = 0. \tag{4.6}$$

Noting that $b = \alpha_1(S^0 - \lambda_1)f'(\lambda_1) > 0$, we have $F(0) = C > 0$. Also noting that

$$B = [kb + (1 + k)D_1]^2 - D_1^2 - 2(kD_1^2 + kbD_1) = (kb + kD_1)^2 > 0,$$

we conclude that $F(y) = 0$ for $y = \omega^2$ is impossible. Therefore $\Delta_1(\lambda) = 0$ has no purely imaginary roots and thus all roots of $\Delta(\lambda) = 0$ have negative real parts. The proof is complete. \square

Theorem 3.1 and Lemma 4.1 immediately give the following global stability result.

Theorem 4.1. *Consider model (1.1). The equilibrium E_{λ_1} is globally asymptotically stable with respect to C_{n+1}^+ provided that $0 < D_1 < 2D$, (3.3) and (3.4).*

Corollary 4.1. *Consider model (1.2). If (3.13) and (3.14) hold, then $E_{\lambda_1} = (\lambda_1, \alpha_1(S^0 - \lambda_1), 0, \dots, 0)$ is globally asymptotically stable with respect to C_{n+1}^+ .*

4.2. Bistability

Note that in Theorem 4.1 and Corollary 4.1, S^0 is assumed to be less than μ_1 . In fact, as can be seen from the following lemma, it is possible for system (1.1) to have two asymptotically stable equilibria when $S^0 > \mu_1$, and hence the single species survival equilibrium E_{λ_1} is not globally asymptotically stable. Suppose that $S^0 > \mu_1$. Then system (1.1) admits at least three nonnegative equilibrium points, namely, $E_{\lambda_1}, E_{S^0}, E_{\mu_1}$, where $E_{\mu_1} = (\mu_1, \frac{\alpha_1(S^0 - \mu_1)D}{D_1}, 0, \dots, 0)$.

Lemma 4.2. *Assume that $\lambda_1 < \mu_1 < S^0$ and $\lambda_1 < \lambda_j < \mu_j < S^0$ for all $j \in N(2, n)$. Then E_{λ_1} and E_{S^0} are both locally asymptotically stable.*

Proof. It is shown in Lemma 4.1 that E_{λ_1} is locally asymptotically stable. We only need show that E_{S^0} is also locally asymptotically stable. Linearizing (1.1) about E_{S^0} , we obtain the characteristic equation

$$\Delta(\lambda) = (\lambda + D) \prod_{j=1}^n (\lambda + D_j - \alpha_j f_j(S^0) e^{-\lambda \tau_j}) = 0. \tag{4.7}$$

Note that $\lambda_j < \mu_j < S^0$ for all $j \in N(1, n)$. This yields $\alpha_j f_j(S^0) < D_j, j \in N(1, n)$. By Hayes’s theorem, we know that for each $j \in N(1, n)$, equation $\lambda + D_j - \alpha_j f_j(S^0) e^{-\lambda \tau_j} = 0$ allows roots with negative real parts only. This shows that all roots of Eq. (4.7) have negative real parts. Thus the equilibrium E_{S^0} of model (1.1) is locally asymptotically stable. \square

Remark 4.1. The bistability result stated in Lemma 4.2 implies that initial condition dependent outcome in the chemostat is possible. This phenomenon never happens in the case when the response functions are monotone.

4.3. Damped oscillations

It is well known that if all removal rates are equal and the response functions are monotone, in the ODE system corresponding to (1.2), i.e., $\tau_j = 0, j \in N(1, n)$, if $\lambda_1 < S^0$, then every positive solution ultimately converges to the single species survival equilibrium monotonically. It is interesting to note that when there are differential removal rates, even in the no delay case with monotone response functions, it is possible for $\Delta_1(\lambda)$ to have complex roots resulting in damped oscillations. In fact, when $\tau_1 = 0$, $\Delta_1(\lambda)$ reduces to

$$\begin{aligned} \Delta_1(\lambda) &= \lambda^2 + [(1+k)D_1 + kb]\lambda - (D_1\lambda + kD_1^2) + kD_1(D_1 + b) \\ &= \lambda^2 + k(b + D_1)\lambda + kbD_1, \end{aligned}$$

with discriminant given by

$$\Delta_2 = k^2(D_1 + b)^2 - 4kbD_1 = k[(b + D_1)^2k - 4bD_1].$$

Clearly, Δ_2 is negative when $k \in (0, \frac{4bD_1}{(b+D_1)^2}) \subset (0, 1)$. This implies that whenever $D_1 > D$ and $\frac{D}{D_1} \in (0, \frac{4bD_1}{(b+D_1)^2}) \subset (0, 1)$, the characteristic equation of (1.1) always has complex roots with negative real parts, which results in damped oscillations near the stable equilibrium E_{λ_1} . This fact may partially explain why the transient behavior in some chemostat experiments involves damped oscillations, as some biological data seems to indicate (see [8]).

5. Numerical simulations

In this section, we present some numerical simulations. Throughout this section, the response functions $f_i(S) = \frac{m_i D_i S}{(a_i + S)(b_i + S)}$, $i = 1, 2, 3$, are used. The three response functions are all non-monotone and Theorem 3.9 of [15] does not apply.

Example 1. Letting $D = 1.0$, $D_1 = 1.5$, $D_2 = 1.2$, $D_3 = 0.9$, $S^0 = 6.0$, $\tau_1 = 0.2$, $\tau_2 = 0.05$, $\tau_3 = 0.04$, $a_1 = b_1 = 2$, $a_2 = b_2 = 7.2$, $a_3 = b_3 = 7.5$, $m_1 = 20$, $m_2 = 32$, $m_3 = 32$, we obtain $\lambda_1 = 0.3834$, $\mu_1 = 10.4330$, $\lambda_2 = 4.6951$, $\lambda_3 = 5.3454$ and $\frac{DS^0}{D_{\max}} - \lambda_1 = 3.6166 > \frac{DS^0}{D_{\min}} - \lambda_2 + \frac{DS^0}{D_{\min}} - \lambda_3 = 3.2930$. Theorem 4.1 applies. Hence, the equilibrium point $E_{\lambda_1} = (0.3834, 2.7739, 0, 0)$ is globally asymptotically stable and all positive solutions of (1.1) with the above choice of parameters converge to E_{λ_1} (see Fig. 1).

Example 2. We use the same parameters as in Example 1 except we choose $S^0 = 16$, which is now bigger than μ_1 . As can be seen from Fig. 2, the asymptotic behavior of (1.1) is initial condition dependent. For some initial conditions, x_1 is still the final survivor (see Fig. 2(a)) and for some initial conditions, all species will be washed out and no species can survive (see Fig. 2(b)).

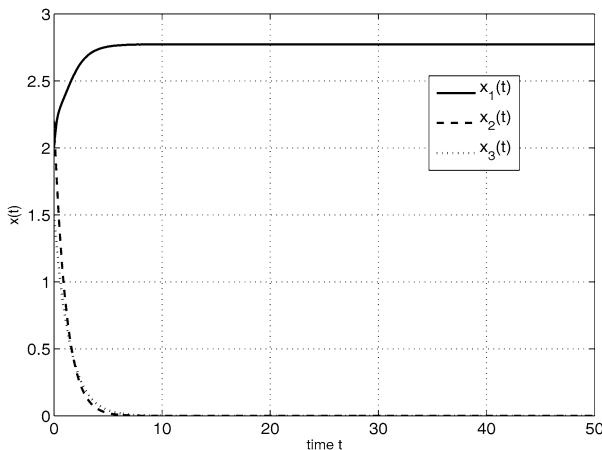


Fig. 1. Numerical simulations of Example 1. Initial data: $S(\theta) = 0.6$, $x_1(\theta) = 2.0$, $x_2(\theta) = 2.2$, $x_3(\theta) = 1.5$ for $\theta \in [-0.2, 0]$.

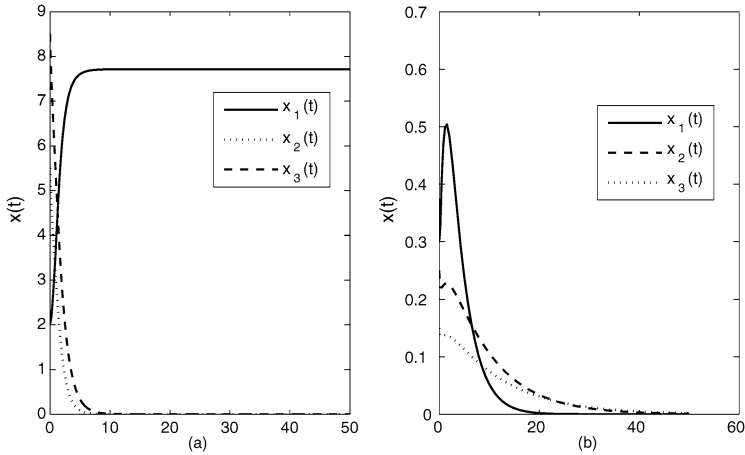


Fig. 2. Numerical simulations of Example 2. Initial data: (a) $S(\theta) = 0.6$, $x_1(\theta) = 2.0$, $x_2(\theta) = 5.5$, $x_3(\theta) = 8.5$ for $\theta \in [-0.2, 0]$; (b) $S(\theta) = 0.6$, $x_1(\theta) = 0.3$, $x_2(\theta) = 0.25$, $x_3(\theta) = 0.15$ for $\theta \in [-0.2, 0]$.

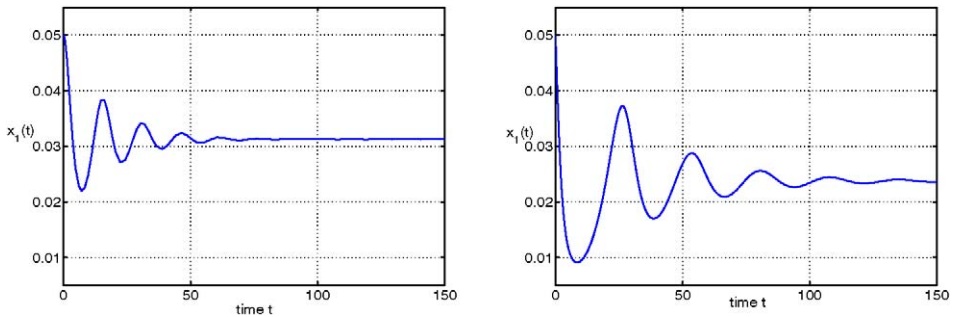


Fig. 3. (Left): Damped oscillations in the ODE system (5.1) given in Example 3. Initial data: $S(0) = 1.0002$, $x(0) = 0.05$; (right): Damped oscillations in the DDE system (5.2) given in Example 4 with $\tau = 0.02$. Initial data: $S(\theta) = 1.0002$, $x(\theta) = 0.05$ for $\theta \in [-0.02, 0]$.

Example 3. Here we provide an example illustrating damped oscillations in the associated ODE (no delay). Let $n = 1$, $\tau_1 = 0$, and $\alpha_1 = 1$ in (1.1). This results in a two-dimensional system

$$\begin{aligned} S'(t) &= (S^0 - S)D - x_1(t)f_1(S(t)), \\ x_1'(t) &= -D_1x_1(t) + x_1(t)f_1(S(t)). \end{aligned} \tag{5.1}$$

Let $S^0 = 3$, $D_1 = 4$, $f_1(s) = \frac{36s}{(2+s)^2}$. Then, we obtain $\lambda_1 = 1$ and $b := (S^0 - \lambda_1)f_1'(\lambda_1) = \frac{8}{3}$. The characteristic equation of the linearization of (5.1) about E_{λ_1} is $\Delta_1(\lambda) = \lambda^2 + \frac{20}{3}k\lambda + \frac{32}{3}k = 0$, which has two complex roots with negative real parts provided $k \in (0, 0.96)$. That is, whenever $D \in (0, 3.84)$, damped oscillations near E_{λ_1} appear due to the existence of two complex roots. This is shown in Fig. 3 (left), where $D = \frac{1}{16}$, $k = \frac{1}{64} \in (0, 0.96)$, and $\Delta_1(\lambda) = 0$ has the two complex roots: $-0.05208 \pm 0.4049i$.

Example 4. Next we illustrate how introduction of a small delay affects the damped oscillations in the previous example. We keep all parameters the same as in Example 3 except we let $\tau_1 = 0.02$, and $\alpha_1 = e^{-D_1\tau_1}$. Then we have

$$\begin{aligned} S'(t) &= (S^0 - S)D - x_1(t)f_1(S(t)), \\ x_1'(t) &= -D_1x_1(t) + \alpha_1x_1(t - \tau_1)f_1(S(t - \tau_1)). \end{aligned} \quad (5.2)$$

Again, we expect there are damped oscillations as confirmed in Fig. 3 (right). It is interesting to note that the introduction of a small delay increased both the period and the amplitude of the oscillations, and decreased the limiting biomass of the species.

6. Discussion

In this paper, we considered a delayed chemostat model (i.e., model (1.1)) with differential removal rates and with nonmonotone response functions. We showed that under certain conditions the single species survival equilibrium E_{λ_1} is globally asymptotically stable and hence the competitive exclusion principle holds.

The statement of one of our results, Corollary 3.1 has appeared in [19] and in special cases in [4,5]. The proof in each case required Lemma 3.3, but this was proved incorrectly as explained in Remark 3.2. We provided a correct proof of Lemma 3.3 in this paper.

We also analyzed local stability for the single species survival equilibrium E_{λ_1} and the washout equilibrium E_{S^0} . Bistability is possible when $S^0 > \mu_1$, which leads to initial condition dependent outcome of the competition. This is confirmed by our numerical simulations given in Example 2. This initial condition dependent outcome does not occur in analogous models with monotone response functions. This shows in the case of nonmonotone response functions, when $S^0 > \mu_1$, richer dynamics are possible. Indeed, when $n = 1$ in (1.2) with $\alpha_1 = e^{-D\tau_1}$, it is recently showed in [18] that Hopf bifurcations occur at critical values of the delay and the bifurcating periodic solutions persist when $S^0 > \mu_1$.

One of the reasons for including delay in the basic chemostat model (see [2,10] when the death rates are assumed to be insignificant compared to the dilution rate) was to try to account for differences between the model's predictions and the actual behavior seen in experiments. In particular, in experiments reported in [8], damped oscillatory convergence to the survival equilibrium was observed, whereas the basic model predicted monotone convergence. As well in experiments the species that died out, did so much faster than predicted by the basic model. Surprisingly, it is enough to allow differential removal rates to obtain damped oscillatory convergence to the survival equilibrium. Numerical simulations also showed that the more significant the death rates are, the faster the losing species died out. If in addition, a small delay is introduced, we observed, in our numerical simulations, an increase in the amplitude and period of the damped oscillations and it took longer for the oscillations to become difficult to observe. More experimental work is necessary to determine which it is, the delay or the species specific death rates or some combination of both that can help to account for the damped oscillations in experiments.

Note that our results allow the constants α_j 's to be quite general. Mathematically, model (1.1) is a generalization of the model considered in [5,15,19]. Our results predicted that at most one competitor survives, the competitor with the lowest break-even value. If the constants α_j , $j \in N(1, n)$ are independent of the delays τ_j , $j \in N(1, n)$, then the break-even values λ_j , $j \in N(1, n)$ do not depend on the corresponding delays τ_j , $j \in N(1, n)$ and hence the global convergence results established in Theorem 3.1 and Corollary 3.1 are also independent of delays τ_j , $j \in N(1, n)$. This implies that the delays do not affect the outcome in this case. On the other hand, if the constants α_j , $j \in N(1, n)$ depend on the delays, for instance, as in [15], in (1.1) $\alpha_j = e^{-D_j\tau_j}$,

then the break-even values do depend on τ_j 's and hence omitting appropriate delays in the model could lead to an incorrect prediction of the ultimate survival.

References

- [1] R. Bellman, K.L. Cooke, *Differential-Difference Equations*, Academic Press, New York, 1963.
- [2] G.J. Butler, G.S.K. Wolkowicz, A mathematical model of the chemostat with a general class of functions describing nutrient uptake, *SIAM J. Appl. Math.* 45 (1985) 138–151.
- [3] S.A. Campbell, S. Ruan, J. Wei, Qualitative analysis of a neural network model with multiple time delays, *Internat. J. Bifur. Chaos Appl. Sci. Engrg.* 9 (1999) 1585–1595.
- [4] H.M. El-Owaidy, M. Ismail, Asymptotic behavior of the chemostat model with delayed response in growth, *Chaos Solitons Fractals* 13 (2002) 787–795.
- [5] H.M. El-Owaidy, A.A. Moniem, Asymptotic behavior of a chemostat model with delayed response growth, *Appl. Math. Comput.* 147 (2004) 147–161.
- [6] S.F. Ellermeyer, Competition in the chemostat: global asymptotic behavior of a model with delayed response in growth, *SIAM J. Appl. Math.* 54 (1994) 456–465.
- [7] K. Gopalsamy, *Stability and Oscillations in Delay Differential Equations of Population Dynamics*, Math. Appl., vol. 74, Kluwer Academic, Dordrecht, 1992.
- [8] S.R. Hansen, S.P. Hubbell, Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes, *Science* 207 (1980) 1491–1493.
- [9] W.M. Hirsch, H. Hanisch, J.-P. Gabriel, Differential equation models of some parasitic infections: methods for the study of asymptotic behavior, *Comm. Pure Appl. Math.* 38 (1985) 733–753.
- [10] S.B. Hsu, S. Hubbell, P. Waltman, A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms, *SIAM J. Appl. Math.* 32 (1977) 366–383.
- [11] B. Li, Global asymptotic behavior of the chemostat: general response functions and different removal rates, *SIAM J. Appl. Math.* 59 (1999) 411–422 (electronic).
- [12] H.L. Smith, P. Waltman, *The Theory of the Chemostat. Dynamics of Microbial Competition*, Cambridge Stud. Math. Biology, vol. 13, Cambridge Univ. Press, Cambridge, 1995.
- [13] W. Wang, Z. Ma, Convergence in the chemostat model with delayed response in growth, *Systems Sci. Math. Sci.* 12 (1999) 23–32.
- [14] G.S.K. Wolkowicz, Z.Q. Lu, Global dynamics of a mathematical model of competition in the chemostat: general response functions and differential death rates, *SIAM J. Appl. Math.* 52 (1992) 222–233.
- [15] G.S.K. Wolkowicz, H. Xia, Global asymptotic behavior of a chemostat model with discrete delays, *SIAM J. Appl. Math.* 57 (1997) 1019–1043.
- [16] G.S.K. Wolkowicz, H. Xia, S. Ruan, Competition in the chemostat: a distributed delay model and its global asymptotic behavior, *SIAM J. Appl. Math.* 57 (1997) 1281–1310.
- [17] G.S.K. Wolkowicz, H. Xia, J. Wu, Global dynamics of a chemostat competition model with distributed delay, *J. Math. Biol.* 38 (1999) 285–316.
- [18] H. Xia, G.S.K. Wolkowicz, L. Wang, Transient oscillation induced by delayed growth response in the chemostat, *J. Math. Biol.* 50 (2005) 489–530.
- [19] S. Yuan, M. Han, Z. Ma, Competition in the chemostat: convergence of a model with delayed response in growth, *Chaos Solitons Fractals* 17 (2003) 659–667.