GLOBAL DYNAMICS OF A CHEMOSTAT COMPETITION MODEL WITH DISTRIBUTED DELAY

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ABSTRACT

We study the global dynamics of n-species competition in a chemostat with distributed delay describing the time-lag involved in the conversion of nutrient to viable biomass. The delay phenomenon is modelled by the gamma distribution. The *linear chain trick* and a *fluctuation lemma* are applied to obtain the global limiting behavior of the model. When each population can survive if it is cultured alone, we prove that at most one competitor survives. The winner is the population that has the smallest *delayed break-even concentration*, provided that the orders of the delay kernels are large and the mean delays modified to include the washout rate (which we call the *virtual mean delays*) are bounded and close to each other, or the delay kernels modified to include the washout factor (which we call the *virtual delay kernels*) are close in L^1-norm. Also, when the virtual mean delays are relatively small, it is shown that the predictions of the distributed delay model are identical with the predictions of the corresponding ODEs model without delay. However, since the delayed break-even concentrations are functions of the parameters appearing in the delay kernels, if the delays are sufficiently large, the prediction of which competitor survives, given by the ODEs model, can differ from that given by the delay model.

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1. Introduction

In this paper, we study the global dynamics of the following model of n-species of microorganisms competing exploitatively for a single growth limiting nutrient in a well-stirred chemostat:

$$
\begin{aligned}
&S'(t) = \big(S^0 - S(t)\big)D - \sum_{i=1}^{n} x_i(t)p_i\big(S(t)\big),\\
&x_i'(t) = -Dx_i(t) + \int_{-\infty}^{t} x_i(\theta)p_i\big(S(\theta)\big)e^{-D(t-\theta)}K_i(t-\theta)\,d\theta, \quad i \in I(n),
\end{aligned}
\tag{1.1}
$$

where for any integer $m \geq 1$, $I(m) = \{1, 2, \ldots, m\}$, $\mathbb{R}_+ := [0, \infty)$ and the delay kernels $K_i : \mathbb{R}_+ \to \mathbb{R}_+$ take the form

$$
K_i(s) = \frac{\alpha_i^{r_i+1} s^{r_i}}{r_i!} e^{-\alpha_i s}, \quad s \in \mathbb{R}_+, \quad i \in I(n),
\tag{1.2}
$$

for constants $\alpha_i > 0$ and integers $r_i \geq 0$. Here $S(t)$ denotes the concentration of nutrient and $x_i(t)$ denotes the density of the i-th population of microorganisms in the culture vessel at time t. The parameter $D > 0$ is the dilution (or washout) rate. The concentration of the input nutrient in the feed vessel is denoted by a postive constant S^0. Species specific death rates are assumed to be insignificant compared to the dilution rate and are ignored. Each kernel K_i in (1.2) represents the distribution of the time delay involved in the conversion of nutrient to viable cells. Due to the outflow in the chemostat, only $x_i(\theta)e^{-D(t-\theta)}K_i(t-\theta)$, not $x_i(t)$, of the $x_i(\theta)$ microorganisms that consumed nutrient $t-\theta$ units previously, survive in the chemostat the $t-\theta$ units of time necessary to complete the process of converting the nutrient to new cells.

We are interested in the global asymptotic behavior of model (1.1). Throughout, we assume that each nutrient uptake function p_i, $i \in I(n)$, satisfies the following assumptions:

(1.3) $p_i : \mathbb{R}_+ \to \mathbb{R}_+$ is monotone increasing and locally Lipschitz with $p_i(0) = 0$;

(1.4) there exists a positive (possibly extended) real number λ_i such that

$$
\begin{aligned}
p_i(S) &< D\left(\frac{D+\alpha_i}{\alpha_i}\right)^{r_i+1} \quad \text{if } S < \lambda_i,\\
p_i(S) &> D\left(\frac{D+\alpha_i}{\alpha_i}\right)^{r_i+1} \quad \text{if } S > \lambda_i.
\end{aligned}
$$

Motivated by [4, 15], we call λ_i the *delayed break-even concentration* of population x_i. Under assumptions (1.3) and (1.4), system (1.1) always has the washout equilibrium $E_0 = (S^0, 0, 0)$. Moreover, for each $i \in I(n)$ such that $\lambda_i < S^0$, there is a nonnegative equilibrium of the form $E_i = (\lambda_i, x_1^*, x_2^*, \ldots, x_n^*)$, where $x_k^* = 0$ for all $k \neq i$ and

$$x_i^* = \left(\frac{\alpha_i}{D + \alpha_i}\right)^{r_i+1} (S^0 - \lambda_i). \tag{1.5}$$

Note that the presence of the washout (memory) factor $e^{-D(t-\theta)}$ in model (1.1) changes the equilibrium values for the corresponding ODEs model without delay. Therefore, the equilibria E_i, $i \in I(n)$, differ quantitatively from those when delays and washout effects are ignored.

A model similar to (1.1) but where all delays are discrete (i.e. the delay kernels are all degenerate Dirac Delta distributions), was recently studied in [27] where it was shown that under certain sufficient conditions, the discrete delay model exhibits competitive exclusion and the population that wins the competition is the one with the smallest break-even concentration. The time delay effect on the qualitative outcome of competition was explored and it was demonstrated that when the delays are relatively small, the predictions of the discrete delay model are identical with the predictions given by corresponding models without time delays, and that introducing large delays in the model may alter the predicted outcome of competition. More recently, in [28] model (1.1) was considered in the case where there are only two ($n = 2$) species engaged in competition. There the global limiting behavior of the model was completely determined under assumptions (1.3) and (1.4) and the generic condition $\lambda_1 \neq \lambda_2$.

The main purpose of this paper is to investigate the question as to whether and to what extent the global results of [28] can be extended to the general n -species model (1.1). By using the *linear chain trick technique* and a *fluctuation lemma*, we obtain sufficient conditions under which at most one population survives in the chemostat. We not only explore results that are analogues of those for the corresponding discrete delay model studied in [27], but also obtain new results that apply only to the distributed delay model (1.1). In the case where each population can survive in the chemostat when it is cultured alone, it is shown that the model exhibits competitive exclusion. The population that wins the competition is the one that has the smallest λ_i value, provided that either the *virtual* *delay kernels* are close in L^1-norm, or the orders of the delay kernels are large and the *virtual mean delays* are close to each other. Here the virtual delay kernel is a modification of the delay kernel K_i in (1.2) to include the washout factor e^{-Ds} and the virtual mean delay is a modification of the mean delay to include the washout rate D. These results are not restricted to the case where the K_i's are weak ($r_i = 0$) or strong ($r_i = 1$) kernels. In fact, they can be applied as well to kernels that have arbitrary orders.

We remark that chemostat models incorporating time delay have been studied by many authors. Models involving distributed delays are considered to be more realistic than discrete delay models (see [5, 6, 9, 12, 19-23]). We refer the reader to [27, 28] for an extensive literature review on chemostat modeling using time delays. In particular, we mention the papers [10, 11, 16], that are closely related to model (1.1). For the importance of including the washout factor over the time delay in chemostat models, we refer the reader to [18] and the survey paper [20]. It should be noted that the distributed delay model (1.1) may have more potential to mimic reality, compared to the corresponding ODEs model without delay, as computer simulations in [28] indicate.

This paper is organized as follows. In Section 2, we give two preliminary results on positivity and boundedness of solutions of (1.1). In Section 3, we state the main results. Some technical lemmas are proved in Section 4. Section 5 contains the proofs of the main results. Finally, we give some concluding remarks in Section 6.

2. Positivity and Boundedness

Throughout, we denote by BC^{n+1} the Banach space of bounded continuous functions mapping from $(-\infty, 0]$ to $\mathbb{R}^{n+1}$. From the general theory of integrodifferential equations (see [2, 24]), we know that for any initial data $\phi = (\phi_0, \phi_1, \ldots, \phi_n) \in BC_+^{n+1} := \{\phi \in BC^{n+1};\ \phi_i(\theta) \geq 0,\ 0 \leq i \leq n,\ \theta \leq 0\}$, there exists a unique solution $\pi(\phi; t) := \big(S(\phi; t), x_1(\phi; t), \ldots, x_n(\phi; t)\big)$ of (1.1) for all $t \geq 0$ such that $\pi(\phi; \cdot)\ |_{(-\infty,0]} = \phi$. For convenience, we will also use $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ to denote the solution $\pi(\phi; t)$ with $\phi \in BC_+^{n+1}$, if there is no confusion. When we say a solution $\pi(\phi; t)$ or $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ of (1.1) is positive, we mean that the solution has initial data $\phi \in BC_+^{n+1}$ and each component of the solution vector is positive for all $t > 0$.

In this section, we give two preliminary results on positivity and boundedness of solutions of (1.1). The proof of the following lemma is similar to the proof of Lemma 2.1 in [28].

Lemma 2.1. *For any* $\phi \in BC_+^{n+1}$ *with* $\phi_0(0) \geq 0$ *and* $\phi_i(0) > 0,\ i \in I(n)$, *the solution* $\pi(\phi; t)$ *is positive.*

In what follows, we derive a *conservation principle* for model (1.1). To see this, let $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ be an arbitrarily fixed positive solution. Using the linear chain trick technique as in [19], we define

$$y_{i,j}(t) = \int_{-\infty}^{t} x_i(\theta) p_i\big(S(\theta)\big) G^j_{D,\alpha_i}(t-\theta)\, d\theta, \tag{2.2}$$

$$G^j_{D,\alpha_i}(s) = \frac{{\alpha_i}^{j+1} s^j}{j!} e^{-(D+\alpha_i)s}, \quad s \in \mathbb{R}_+, \tag{2.3}$$

for $i \in I(n)$ and $j = 0, 1, 2, \ldots, r_i$. A direct verification using (1.2) implies that $S(t)$, $x_i(t)$ and $y_{i,j}(t)$, $i \in I(n)$, $j \in I(r_i)$ satisfy

$$\begin{aligned}
S'(t) &= \big(S^0 - S(t)\big)D - \sum_{i=1}^{n} x_i(t) p_i\big(S(t)\big),\\
x_i'(t) &= -D x_i(t) + y_{i,r_i}(t),\\
y_{i,0}'(t) &= -(D+\alpha_i)\, y_{i,0}(t) + \alpha_i\, x_i(t) p_i\big(S(t)\big),\\
y_{i,j}'(t) &= -(D+\alpha_i)\, y_{i,j}(t) + \alpha_i\, y_{i,j-1}(t).
\end{aligned} \tag{2.4}$$

Let

$$W(t) = S^0 - S(t) - \sum_{i=1}^{n} \Big(\sum_{j=0}^{r_i} \frac{y_{i,j}(t)}{\alpha_i} + x_i(t) \Big), \quad t \geq 0.$$

It follows from (2.4) that $W'(t) = -DW(t)$. Therefore

$$S(t) + \sum_{i=1}^{n} \Big(\sum_{j=0}^{r_i} \frac{y_{i,j}(t)}{\alpha_i} + x_i(t) \Big) = S^0 + \rho(t), \quad t \geq 0, \tag{2.5}$$

where the continuous function $\rho(t)$ depends on the initial data of the solution $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ and satisfies $\rho(t) \to 0$ exponentially as $t \to \infty$. Formula (2.5) therefore may be viewed as a conservation principle for the distributed delay model (1.1). We note that similar conservation principles for chemostat models with or without (discrete) delays can be found in [4, 10, 15, 26-28]. For more details on the role of conservation principles in analyzing chemostat models, we refer the reader to the recent monograph [26].

As a direct consequence of the above conservation principle (2.5), we obtain the following boundedness result.

Lemma 2.2. *All positive solutions of (1.1) are bounded for* $t > 0$.

Proof. If $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ is a positive solution of (1.1), then all $y_{i,j}(t)$ defined in (2.2) and (2.3) are positive for $t > 0$. The conclusion now follows from (2.5).

Remark 2.3. From formula (2.5), it can be seen that every positive solution $\big(S(t), x_1(t), \ldots, x_n(t)\big)$ satisfies

$$\limsup_{t\to\infty} S(t) \le S^0, \qquad \limsup_{t\to\infty} \sum_{i=1}^{n} x_i(t) \le S^0. \tag{2.6}$$

In later sections, we will obtain better upper limiting bounds for any positive solution of model (1.1). But (2.6) will be used in some preliminary estimates.

3. Main Results

By rearranging the equations in (1.1) if necessary, we may assume, without loss of generality, that $\lambda_1 \le \lambda_2 \le \cdots \le \lambda_n$. Our results on the global dynamics of (1.1) are proved under the following generic condition

$$\lambda_1 < \lambda_2 \le \cdots \le \lambda_n. \tag{3.1}$$

In all of the theorems stated below, except Theorems 3.1 and 3.2, we always assume that condition (3.1) is satisfied.

Theorem 3.1. *Let* $\pi(\phi; t)$ *be any given positive solution of (1.1). If* $\lambda_i \ge S^0$ *for some* $i \in I(n)$, *then* $x_i(\phi; t) \to 0$ *as* $t \to \infty$.

Theorem 3.1 states that if the delayed break-even concentration λ_i is larger than the input nutrient concentration, then population x_i dies out whether or not there is a competitor. This result immediately implies the following global result that describes outcomes in which all populations are eliminated from the chemostat. Note that this elimination is not a result of competition, but is due to the fact that the chemostat is an inadequate environment for any of the populations to survive.

Theorem 3.2. *If* $\lambda_1 \geq S^0$, *then* $\lim_{t\to\infty} \pi(\phi;t) = E_0$ *for every positive solution* $\pi(\phi;t)$ *of model (1.1).*

The case where some of the λ_i's are smaller than S^0 appears to be much more complicated. In [28], it was shown that any population x_i with $\lambda_i < S^0$ can survive in the chemostat when it is cultured alone. It is thus of interest to know whether such populations can coexist in the chemostat when they are cultured together. The following theorem provides a simple criterion to predict the outcome of such competition. It gives conditions under which model (1.1) exhibits *competitive exclusion.* The population that wins the competition is the one with the smallest λ_i value, that is, population x_1 survives in the chemostat, while all other populations die out.

For convenience, we define the index set

$$J = \{\, j \in I(n);\ \ j \geq 2 \text{ and } \lambda_j < S^0 \,\}. \tag{3.2}$$

Theorem 3.3. *Assume that* $\lambda_1 < S^0$ *and*

$$\sum_{j\in J} (S^0 - \lambda_j) < S^0 - \lambda_1. \tag{3.3}$$

Then $\lim_{t\to\infty} \pi(\phi;t) = E_1$ *for every positive solution* $\pi(\phi;t)$ *of model (1.1).*

Condition (3.3) in the above theorem requires that the λ_j value for population x_j, $j \in J$, should not be too "far away" from the input nutrient concentration S^0. If we regard $S^0 - \lambda_j$, $j \in J$, as an index measuring the ability of survival of the population x_j when it is cultured alone, condition (3.3) can be thought of as requiring the joint index of survival of all populations x_j, $j \in J$, to be less than the index of survival of population x_1. It is interesting to note that this condition is the same as condition (3.2) of [27] in the discrete delay case, except that the λ_i values are defined differently. Thus Theorem 3.3 provides an analogue of Theorem 3.1 in [27] for the corresponding discrete delay model. On the other hand, we should also note that condition (3.2) is equivalent to the generic condition

(3.1) when only two populations are involved in competition. Thus Theorem 3.3 includes the main results of Theorems 3.3 and 3.4 in [28].

The next result shows that even when condition (3.3) fails, the conclusion of Theorem 3.3 still holds if the delay kernels K_j, $j \in J$, modified to include the washout factor (a term that we will make clear now) are close to each other in $L^1[0,\infty)$-norm. To be more precise, let us define, for any real number $\gamma \geq 0$ and for any $j \in J$, the following quantity

$$\ell_j(\gamma) = S^0 - z_j^*, \tag{3.4}$$

where $z_j^* \in (0, S^0)$ is the unique solution of

$$\frac{D\,x}{\gamma + x} = \left(\frac{\alpha_j}{D + \alpha_j}\right)^{r_j+1} p_j(S^0 - x), \quad 0 < x < S^0. \tag{3.5}$$

Also, for a continuous function $K : \mathbb{R}_+ \to \mathbb{R}_+$ with $\int_0^\infty K(s)\,ds = 1$, we set

$$\gamma_1 = \frac{1}{D} \sum_{j \in J} x_j^*\, p_j(S^0) \int_0^\infty \left|Q_j^D(s) - K(s)\right| ds, \tag{3.6}$$

where J is the index set defined in (3.2), x_j^* is the number given by (1.5) and the function $Q_j^D : \mathbb{R}_+ \to \mathbb{R}_+$ is defined by

$$Q_j^D(s) = \left(\frac{D + \alpha_j}{\alpha_j}\right)^{r_j+1} G_{D,\alpha_j}^{r_j}(s), \quad s \in \mathbb{R}_+, \quad j \in J. \tag{3.7}$$

We note that the function Q_j^D as defined in (3.7) has the property that $\int_0^\infty Q_j^D(s)\,ds = 1$. Thus it can be viewed as a kernel that *modifies* the kernel K_j to include the washout factor e^{-Ds}. We call $Q_j^D(s)$ the *virtual delay kernel* corresponding to the (physical) delay kernel $K_j(s)$.

We can now state the following result.

Theorem 3.4. *Assume that* $\lambda_1 < S^0$. *Then every positive solution* $\pi(\phi;t)$ *of (1.1) satisfies* $\lim_{t\to\infty} \pi(\phi;t) = E_1$, *provided that there exists a continuous function* $K : \mathbb{R}_+ \to \mathbb{R}_+$ *with* $\lim_{t\to\infty} K(t) = 0$ *and* $\int_0^\infty K(s)\,ds = 1$ *such that* $\lambda_1 < \ell_j(\gamma_1)$ *for all* $j \in J$.

Remark 3.6. It can be seen from (3.4) and (3.5) that $\ell_j(\gamma)$ depends continuously on $\gamma \geq 0$. Moreover, it is decreasing with γ and satisfies $\ell_j(0) = \lambda_j$ and $\ell_j(\infty) = 0$ for each $j \in J$. Therefore, if γ is small, then condition $\lambda_1 < \ell_j(\gamma)$ for all $j \in J$ will follow from the generic assumption (3.1). In particular, if the *virtual delay kernels* Q_j^D, $j \in J$, are close to each other in $L^1[0,\infty)$ -norm, by choosing $K(u)$ to be any one of the $Q_j^D(u)$, it follows from (3.6) that γ_1 will be small and the hypotheses of Theorem 3.4 will be satisfied.

Our final result can be applied when the numbers $(r_j+1)/(D+\alpha_j)$, $j \in J$, are bounded and close to each other for large r_j 's. To state the result, we define, for any integer $r \geq 0$ and any real number $\alpha > 0$,

$$\gamma_2 = \frac{1}{D}\sum_{j\in J}\left(\frac{A_j}{\sqrt{r_j+1}} + \frac{B_j}{\sqrt{r+1}} + C_j|\tau_D - \tau_{D,j}|\right), \tag{3.8}$$

where the index set J is as before, and for each $j \in J$,

$$\begin{aligned}
&\tau_{D,j} = \frac{r_j+1}{D+\alpha_j}, \qquad \tau_D = \frac{r+1}{D+\alpha},\\
&A_j = \frac{2\,\tau_{D,j}\,C_j}{\sqrt{2\pi}}, \qquad B_j = \frac{2\,\tau_D\,C_j}{\sqrt{2\pi}},\\
&C_j = x_j^*\,p_j(S^0)\Big(p_j(S^0) + \mu_j\,S^0 p_j^{-1}(S^0)\big[D + \max_{j\in J} p_j(S^0)\big]\Big),
\end{aligned} \tag{3.9}$$

x_j^* is given by (1.5) and μ_j denotes the (global) Lipschitz constant of $p_j(S)$ on the interval $[0, S^0]$. Note that the number $\tau_{D,j}$ is the mean of the virtual delay kernel $Q_j^D(s)$, and it modifies the (physical) mean delay τ_j of $K_j(s)$ to include the washout rate D. In the sequel, we call $\tau_{D,j}$ the *virtual mean delay* of $Q_j^D(s)$.

Theorem 3.5. *Assume that* $\lambda_1 < S^0$. *Then every positive solution* $\pi(\phi;t)$ *of (1.1) satisfies* $\lim_{t\to\infty}\pi(\phi;t) = E_1$, *provided that there exist an* $\alpha > 0$ *and an integer* $r \geq 0$ *such that* $\lambda_1 < \ell_j(\gamma_2)$ *for all* $j \in J$.

Remark 3.7. Again, due to the continuity of $\ell_j(\gamma)$ in $\gamma \geq 0$ and due to the fact that $\ell_j(0) = \lambda_j \geq \lambda_1$ for $j \geq 2$, if either the orders r_j of the kernels K_j, $j \in J$, are large and the *virtual mean delays* $\tau_{D,j}$ are bounded and close to each other, or if the virtual mean delays $\tau_{D,j}$ are small for fixed orders r_j (not necessarily large), by choosing the pair (r,α) to be any one of (r_j,α_j), $j \in J$, it can be seen from (3.8) that γ_2 will be small and so the hypotheses of Theorem 3.5 will be satisfied.

Remark 3.8. In the statement of Theorem 3.3, it should be noted that if the index set J is empty, i.e. $\lambda_j \geq S^0$ for all $j \geq 2$, then condition (3.2) is not needed in Theorem 3.3. Similarly, if $J = \emptyset$, condition $\lambda_1 < \ell_j(\gamma_1)$ or $\lambda_1 < \ell_j(\gamma_2)$ is not needed in Theorems 3.4 and 3.5. For convenience, throughout, we adopt the convention that $\sum_{i=j}^{k} a_j \equiv 0$ if $k < j$, and $\sum_{i \in I} a_j \equiv 0$ if the index set I is empty. Also, a condition will be thought of as always being satisfied if it involves an index $i \in I$ where I is the empty set.

We conclude this section by noting that Theorems 3.4 and 3.5 are new and particular for the distributed delay model (1.1), iand no similar results seem to be available for the discrete delay models.

4. Some Technical Lemmas

In this section, we study a related system of ordinary differential equations and prove several technical lemmas describing some qualitative properties of positive solutions of the ODEs system. These lemmas will be useful in the proofs of the main theorems stated in the previous section.

Let $N \geq 1$ be a positive integer, $\omega : \mathbb{R}_+ \to \mathbb{R}$ be a continuous function with $\omega(t) \to 0$ as $t \to \infty$, and D, S^0, α_i, r_i, λ_i, p_i, $i \in I(N)$, be the same as in previous sections. We consider the following $\sum_{i=1}^{N}(r_i+2)$-dimensional system of ordinary differential equations for $u_{i,k}$, $i \in I(N)$, $k \in I(r_i+1)$:

$$
\begin{aligned}
&u'_{i,0}(t) = -D\, u_{i,0}(t) + u_{i,r_i+1}(t) p_i\big(S^0 - \sum_{j=1}^{N} u_{j,0}(t) + \omega(t)\big), \\
&u'_{i,k}(t) = -(D+\alpha_i)\, u_{i,k}(t) + \alpha_i\, u_{i,k-1}(t), \\
&S^0 - \sum_{j=1}^{N} u_{j,0}(0) + \omega(0) \geq 0.
\end{aligned}
\tag{4.1}
$$

We will only be interested in solutions of (4.1) for $t \geq 0$ that satisfy $S^0 - \sum_{j=1}^{N} u_{j,0}(t) + \omega(t) \geq 0$. Such solutions will be denoted by $u(t) = \big(u_{i,k}(t)\big)$ for $i \in I(N)$ and $k = 0, 1, 2, \ldots, r_i{+}1$, $t \geq 0$. We call such a solution of (4.1) a positive solution if each component $u_{i,k}(t)$ of $u(t)$ is positive for $t > 0$. By an argument similar to that for Lemma 2.1 in [28], we can show that every such solution of (4.1) with positive initial data is a positive solution. It follows easily that every positive solution $u(t)$ of (4.1) is bounded for $t > 0$.

Throughout this section, we always assume that the following condition is satisfied:

$$\lambda_1 < \lambda_2 \le \lambda_3 \le \cdots \le \lambda_N < S^0. \tag{4.2}$$

In the case that $N = 1$, condition (4.2) is simply $\lambda_1 < S^0$.

We begin with the following elementary but useful result.

Lemma 4.1. *Let $f : \mathbb{R}_+ \to \mathbb{R}$ be a bounded differentiable function.*

(i) If $\lim_{t\to\infty} f(t)$ exists (finite) and the derivative function $f'(t)$ is uniformly continuous on $\mathbb{R}_+$, then $\lim_{t\to\infty} f'(t) = 0$.

(ii) If $\lim_{t\to\infty} f(t)$ does not exist, then there exist sequences $\{t_m\} \uparrow \infty$ and $\{s_m\} \uparrow \infty$ such that

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

We remark that the first part of the lemma is due to Barbălat [1] and it is sometimes referred to as the *Barbălat lemma* in the literature. See [12] for a proof. The second part is proved in [14] and has been called the *fluctuation lemma.* This lemma will be useful, since if $u(t)$ is a positive solution of (4.1), then each component of this solution vector and its derivative function is a uniformly continuous function on $\mathbb{R}_+$ and Lemma 4.1 can be applied. To see this, note that all of the components of this solution vector are bounded functions on $\mathbb{R}_+$. Therefore, all of their derivatives are continuous and bounded functions on $\mathbb{R}_+$, as they are defined by (4.1). By the Mean Value Theorem, all the component functions are thus Lipschitz continuous and hence uniformly continuous. Note that each function p_i, $i \in I(N)$, is uniformly continuous on $[0, S^0]$. It follows from (4.1) that the derivative of each component of the solution vector is defined as the sum, difference, product and composition of uniformly continuous functions and hence, is also uniformly continuous. This lemma has played an important role in the analysis of chemostat models (see [10, 27, 28]).

We now study the asymptotic behavior of the positive solutions of (4.1). Let $u(t) = \big(u_{i,k}(t)\big)$ be such an arbitrarily fixed solution. We define

$$a_{i,k} = \liminf_{t\to\infty} u_{i,k}(t), \qquad b_{i,k} = \limsup_{t\to\infty} u_{i,k}(t),$$

for $i \in I(N)$ and $k = 0, 1, 2, \ldots, r_i + 1$. As we argued before, $a_{i,k}$ and $b_{i,k}$ are all finite nonnegative numbers. In the following two lemmas, we give some estimates for $a_{i,k}$ and $b_{i,k}$.

Lemma 4.2. *For every $i \in I(N)$ and $k \in I(r_i + 1)$,*

$$\left(\frac{\alpha_i}{D+\alpha_i}\right)^k a_{i,0} \le a_{i,k} \le b_{i,k} \le \left(\frac{\alpha_i}{D+\alpha_i}\right)^k b_{i,0}.$$

Proof. For any fixed $i \in I(N)$ and $k \in I(r_i+1)$, we apply Lemma 4.1 to find a sequence $\{s_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} u_{i,k}(s_m) = a_{i,k}, \quad \lim_{m\to\infty} u'_{i,k}(s_m) = 0.$$

By (4.1), this implies that

$$\lim_{m\to\infty} \left[-(D+\alpha_i)\, u_{i,k}(s_m) + \alpha_i\, u_{i,k-1}(s_m)\right] = 0.$$

Hence,

$$(D+\alpha_i)\, a_{i,k} = \alpha_i \lim_{m\to\infty} u_{i,k-1}(s_m) \ge \alpha_i\, a_{i,k-1},$$

which leads to

$$a_{i,k} \ge \left(\frac{\alpha_i}{D+\alpha_i}\right) a_{i,k-1} \ge \left(\frac{\alpha_i}{D+\alpha_i}\right)^k a_{i,0}.$$

Similarly, we can show that

$$b_{i,k} \le \left(\frac{\alpha_i}{D+\alpha_i}\right) b_{i,k-1} \le \left(\frac{\alpha_i}{D+\alpha_i}\right)^k b_{i,0}.$$

This establishes the lemma.

Lemma 4.3. *For each $i \in I(N)$, we have $b_{i,0} \le S^0 - \lambda_i$.*

Proof. By Lemma 4.1, there exists a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} u_{i,0}(t_m) = b_{i,0}, \quad \lim_{m\to\infty} u'_{i,0}(t_m) = 0.$$

Using (4.1), we obtain

$$
\begin{aligned}
D\, b_{i,0} &= \lim_{m\to\infty} \big[D\, u_{i,0}(t_m) + u'_{i,0}(t_m)\big] \\
&= \lim_{m\to\infty} u_{i,r_i+1}(t_m)\, p_i\big(S^0 - \sum_{j=1}^{N} u_{j,0}(t_m) + \omega(t_m)\big) \\
&\le b_{i,r_i+1}\, p_i\big(S^0 - \lim_{m\to\infty} u_{i,0}(t_m)\big) \\
&= b_{i,r_i+1}\, p_i\big(S^0 - b_{i,0}\big).
\end{aligned} \tag{4.3}
$$

Note that from Lemma 4.2,

$$
b_{i,r_i+1} \le \left(\frac{\alpha_i}{D+\alpha_i}\right)^{r_i+1} b_{i,0}.
$$

We substitute this into (4.3) to obtain

$$
D\, b_{i,0} \le b_{i,0} \left(\frac{\alpha_i}{D+\alpha_i}\right)^{r_i+1} p_i\big(S^0 - b_{i,0}\big). \tag{4.4}
$$

If $b_{i,0} = 0$, there is nothing to prove. If $b_{i,0} \neq 0$, then (4.4) implies that

$$
D \le \left(\frac{\alpha_i}{D+\alpha_i}\right)^{r_i+1} p_i\big(S^0 - b_{i,0}\big).
$$

By assumption (1.4), we have $S^0 - b_{i,0} \ge \lambda_i$.

This completes the proof.

We now introduce the following new variables

$$
\begin{aligned}
v_0(t) &= \sum_{i=2}^{N} u_{i,0}(t), \quad t \ge 0, \\
\beta &= \limsup_{t\to\infty} v_0(t).
\end{aligned} \tag{4.5}
$$

It is obvious that $0 \le \beta < \infty$. In the sequel, we call a positive solution $u(t)$ of (4.1) a *stack solution* if for all $k \in I(r_1+1)$, $u_{1,k}(t) \le u_{1,0}(t)$ for every $t > 0$. We study certain properties of the stack solutions of (4.1) in the next two lemmas.

Lemma 4.4. *Let $u(t)$ be a positive stack solution of (4.1). If $\beta < S^0 - \lambda_1$, then* $a_{1,0} > 0$.

Proof. In order to obtain a contradiction, assume that $a_{1,0} = 0$, i.e. $\liminf_{t\to\infty} u_{1,0}(t) = 0$. Define

$$
z(t) = \alpha_1\, u_{1,0}(t) + \sum_{k=1}^{r_1+1} D \left(\frac{D+\alpha_1}{\alpha_1}\right)^{k-1} u_{1,k}(t), \quad t > 0.
$$

It follows from (4.1) that

$$z'(t) = -\alpha_1\, u_{1,r_1+1}(t)\big[M - p_1\big(S^0 - u_{1,0}(t) - v_0(t) + \omega(t)\big)\big], \tag{4.6}$$

where

$$M = D\left(\frac{D+\alpha_1}{\alpha_1}\right)^{r_1+1}.$$

Note that $z(t) > 0$ for all $t > 0$. Since $a_{1,0} = 0$, and since $u(t)$ is a positive stack solution, i.e., for $k \in I(r_1+1)$, $0 < u_{1,k}(t) \le u_{1,0}(t)$ for all $t > 0$, it follows that $\liminf_{t\to\infty} z(t) = 0$. We can therefore find a sequence $\{\xi_m\} \uparrow \infty$ such that for all m, $z'(\xi_m) \le 0$, and as $m \to \infty$, $z(\xi_m) \to 0$ and so $u_{1,0}(\xi_m) \to 0$ since $0 < u_{1,0}(\xi_m) < \frac{z(\xi_m)}{\alpha_1}$.

Therefore, from (4.6) it follows that

$$-\alpha_1\, u_{1,r_1+1}(\xi_m)\big[M - p_1\big(S^0 - u_{1,0}(\xi_m) - v_0(\xi_m) + \omega(\xi_m)\big)\big] \le 0,$$

which implies that

$$p_1\big(S^0 - u_{1,0}(\xi_m) - v_0(\xi_m) + \omega(\xi_m)\big) \le D\left(\frac{D+\alpha_1}{\alpha_1}\right)^{r_1+1}.$$

By assumption (1.4), we obtain

$$S^0 - u_{1,0}(\xi_m) - v_0(\xi_m) + \omega(\xi_m) \le \lambda_1.$$

Consequently, for all m,

$$v_0(\xi_m) \ge S^0 - \lambda_1 - u_{1,0}(\xi_m) + \omega(\xi_m).$$

But then,

$$\beta \ge \limsup_{m\to\infty} v_0(\xi_m) \ge \lim_{m\to\infty} \big(S^0 - \lambda_1 - u_{1,0}(\xi_m) + \omega(\xi_m)\big) = S^0 - \lambda_1,$$

contradicting $\beta < S^0 - \lambda_1$. Therefore, $a_{1,0} > 0$ and the proof is complete.

Lemma 4.5. *Let $u(t)$ be a stack solution of (4.1). If*

$$\sum_{i=2}^{N} (S^0 - \lambda_i) < S^0 - \lambda_1, \tag{4.7}$$

then $a_{1,0} > 0$ *and* $a_{i,k} = b_{i,k} = 0$ *for all* $i \geq 2$ *and* $k = 0, 1, 2, \ldots, r_i + 1$.

Proof. First, we note that Lemma 4.3 and assumption (4.7) imply that

$$\beta \leq \sum_{i=2}^{N} b_{i,0} \leq \sum_{i=2}^{N} (S^0 - \lambda_i) < S^0 - \lambda_1.$$

Therefore, by Lemma 4.4, $a_{1,0} > 0$. To show that $a_{i,k} = b_{i,k} = 0$ for all $i \geq 2$ and $k \in I(r_i + 1)$, we need only to prove that $a_{i,0} = b_{i,0} = 0$ for all $i \geq 2$, since the conclusion will then follow from Lemma 4.2.

Suppose that $b_{i,0} \neq 0$ for some $i \geq 2$. By Lemma 4.1, there is a sequence $\{t_m\} \uparrow \infty$ such that

$$\lim_{m \to \infty} u_{i,0}(t_m) = b_{i,0}, \quad \lim_{m \to \infty} u'_{i,0}(t_m) = 0.$$

It then follows from (4.1) and Lemma 4.2 that

$$\begin{aligned} D\, b_{i,0} &= \lim_{m \to \infty} \left[D\, u_{i,0}(t_m) + u'_{i,0}(t_m) \right] \\ &= \lim_{m \to \infty} u_{i,r_i+1}(t_m)\, p_i\big(S^0 - \sum_{j=1}^{N} u_{j,0}(t_m) + \omega(t_m)\big) \\ &\leq b_{i,r_i+1}\, p_i\big(S^0 - a_{1,0} - b_{i,0}\big) \\ &\leq b_{i,0} \left(\frac{\alpha_i}{D + \alpha_i} \right)^{r_i+1} p_i\big(S^0 - a_{1,0} - b_{i,0}\big). \end{aligned}$$

This gives

$$p_i\big(S^0 - a_{1,0} - b_{i,0}\big) \geq D \left(\frac{\alpha_i}{D + \alpha_i} \right)^{r_i+1},$$

Consequently, by assumption (1.4),

$$S^0 - a_{1,0} - b_{i,0} \geq \lambda_i. \tag{4.8}$$

On the other hand, we can apply Lemma 4.1 again to obtain a sequence $\{s_m\} \uparrow \infty$ such that

$$\lim_{m \to \infty} u_{1,0}(s_m) = a_{1,0}, \quad \lim_{m \to \infty} u'_{1,0}(s_m) = 0.$$

From (4.1) and Lemma 4.2, we have

$$\begin{aligned} D\,a_{1,0} &= \lim_{m\to\infty}\big[D\,u_{1,0}(s_m) + u'_{1,0}(s_m)\big] \\ &= \lim_{m\to\infty} u_{1,r_1+1}(s_m)\,p_1\big(S^0 - u_{1,0}(s_m) - \sum_{j=2}^{N} u_{j,0}(s_m) + \omega(s_m)\big) \\ &\geq a_{1,r_1+1}\,p_1\big(S^0 - a_{1,0} - \sum_{j=2}^{N} b_{j,0}\big) \\ &\geq a_{1,0}\left(\frac{\alpha_1}{D+\alpha_1}\right)^{r_1+1} p_1\big(S^0 - a_{1,0} - \sum_{j=2}^{N} b_{j,0}\big). \end{aligned}$$

Since $a_{1,0} \neq 0$, it follows that

$$p_1\big(S^0 - a_{1,0} - \sum_{j=2}^{N} b_{j,0}\big) \leq D\left(\frac{D+\alpha_1}{\alpha_1}\right)^{r_1+1}.$$

Consequently, by assumption (1.4),

$$S^0 - a_{1,0} - \sum_{j=2}^{N} b_{j,0} \leq \lambda_1. \tag{4.9}$$

Combining (4.8) and (4.9), and applying Lemma 4.3, we obtain

$$\lambda_i - \lambda_1 \leq \sum_{j\neq 1,i} b_{j,0} \leq \sum_{j\neq 1,i} (S^0 - \lambda_j),$$

which contradicts assumption (4.7). Therefore, $b_{i,0} = 0$ for all $i \geq 2$. Since $0 \leq a_{i,0} \leq b_{i,0}$, $i \in I(N)$, we have $a_{i,0} = b_{i,0} = 0$ for all $i \geq 2$.

This completes the proof.

Lemma 4.6. *Let $\gamma \geq 0$ be a constant satisfying*

$$\limsup_{t\to\infty} \sum_{i=2}^{N} \left(\frac{D+\alpha_i}{\alpha_i}\right)^{r_i+1} u_{i,r_i+1}(t) \leq \gamma + \beta, \tag{4.10}$$

where β is the number defined by (4.5). If $\beta > 0$, then there exists $k \in \{2, 3, \ldots, N\}$ such that $\beta \leq S^0 - a_{1,0} - \ell_k(\gamma)$, where $\ell_k(\gamma)$ is defined in (3.4) and (3.5).

Proof. Recall that $v_0(t)$ is a differentiable function as defined in (4.5). It follows from (4.1) that $v_0(t)$ satisfies the system of differential equations:

$$
\begin{aligned}
&u'_{1,0}(t) = -D\,u_{1,0}(t) + u_{1,r_1+1}(t)p_1\big(S^0 - u_{1,0}(t) - v_0(t) + \omega(t)\big),\\
&u'_{1,k}(t) = -(D+\alpha_1)\,u_{1,k}(t) + \alpha_1\,u_{1,k-1}(t), \quad k \in I(r_1+1),\\
&v'_0(t) = -D\,v_0(t) + \sum_{i=2}^{N} u_{i,r_i+1}(t)p_i\big(S^0 - u_{1,0}(t) - v_0(t) + \omega(t)\big),\\
&u'_{i,k}(t) = -(D+\alpha_i)\,u_{i,k}(t) + \alpha_i\,u_{i,k-1}(t), \quad i \geq 2,\ \ k \in I(r_i+1).
\end{aligned} \tag{4.11}
$$

Let $\{\varepsilon_q\} \downarrow 0$ be a given positive sequence. Fix any $q > 0$. By Lemma 4.1 and assumption (4.10), we have a sequence $\{t_m\} \uparrow \infty$ such that for all m,

$$
\begin{aligned}
&\lim_{m\to\infty} v_0(t_m) = \beta, \quad \lim_{m\to\infty} v'_0(t_m) = 0,\\
&\beta - \frac{\varepsilon_q}{2} \leq v_0(t_m) \leq \beta + \frac{\varepsilon_q}{2},\\
&\sum_{i=2}^{N} U_{i,m} \leq \gamma + \beta + \varepsilon_q, \quad \omega(t_m) < \frac{\varepsilon_q}{2},
\end{aligned}
$$

where

$$
U_{i,m} = \left(\frac{D+\alpha_i}{\alpha_i}\right)^{r_i+1} u_{i,r_i+1}(t_m).
$$

Then it follows from (4.11) that

$$
\begin{aligned}
D\,\beta &= \lim_{m\to\infty}\big[D\,v_0(t_m) + v'_0(t_m)\big]\\
&= \lim_{m\to\infty} \sum_{i=2}^{N} u_{i,r_i+1}(t_m)p_i\big(S^0 - u_{1,0}(t_m) - v_0(t_m) + \omega(t_m)\big)\\
&\leq \limsup_{m\to\infty} \sum_{i=2}^{N} u_{i,r_i+1}(t_m)p_i\big(S^0 - a_{1,0} - \beta + \varepsilon_q\big)\\
&= \limsup_{m\to\infty} \sum_{i=2}^{N} \left(\frac{\alpha_i}{D+\alpha_i}\right)^{r_i+1} p_i\big(S^0 - a_{1,0} - \beta + \varepsilon_q\big)U_{i,m}\\
&\leq \left(\frac{\alpha_{k_q}}{D+\alpha_{k_q}}\right)^{r_{k_q}+1} p_{k_q}\big(S^0 - a_{1,0} - \beta + \varepsilon_q\big) \limsup_{m\to\infty} \sum_{i=2}^{N} U_{i,m}\\
&\leq \left(\frac{\alpha_{k_q}}{D+\alpha_{k_q}}\right)^{r_{k_q}+1} p_{k_q}\big(S^0 - a_{1,0} - \beta + \varepsilon_q\big)\big(\gamma + \beta + \varepsilon_q\big),
\end{aligned} \tag{4.12}
$$

where $k_q \in \{2, 3, \ldots, N\}$ is chosen so that for all $i \in \{2, 3, \ldots, N\}$,

$$
\begin{aligned}
&\left(\frac{\alpha_{k_q}}{D+\alpha_{k_q}}\right)^{r_{k_q}+1} p_{k_q}\big(S^0 - a_{1,0} - \beta + \varepsilon_q\big)\\
&\geq \left(\frac{\alpha_i}{D+\alpha_i}\right)^{r_i+1} p_i\big(S^0 - a_{1,0} - \beta + \varepsilon_q\big).
\end{aligned}
$$

By choosing a subsequence if necessary, we may assume that $\lim_{q\to\infty} k_q = k$ for some $k \in \{2, 3, \ldots, N\}$. Therefore, letting $q \to \infty$ in (4.12), we obtain

$$D\,\beta \le \left(\frac{\alpha_k}{D+\alpha_k}\right)^{r_k+1} p_k\big(S^0 - a_{1,0} - \beta\big)\big(\gamma + \beta\big).$$

Since $\beta > 0$, by (3.4) and (3.5), the above inequality yields $S^0 - a_{1,0} - \beta \ge \ell_k(\gamma)$, i.e. $\beta \le S^0 - a_{1,0} - \ell_k(\gamma)$, as desired.

This completes the proof.

Lemma 4.7. *Suppose that $u(t)$ is a stack solution of (4.1) and (4.10) holds for some constant $\gamma \ge 0$. If $\lambda_1 < \ell_j(\gamma) < S^0$ for all $2 \le j \le N$, then $a_{1,0} > 0$ and $a_{i,k} = b_{i,k} = 0$ for all $i \ge 2$ and $k = 0, 1, 2, \ldots, r_i + 1$.*

Proof. We first show that $a_{1,0} > 0$. By Lemma 4.4, this is clearly true if $\beta = 0$. In the case where $\beta > 0$, we apply Lemma 4.6 to obtain $\beta \le S^0 - \ell_k(\gamma)$ for some $k \ge 2$. But $\lambda_1 < \ell_k(\gamma) < S^0$, so Lemma 4.4 again implies that $a_{1,0} > 0$.

In view of Lemma 4.2, in order to show that $a_{i,k} = b_{i,k} = 0$ for all $i \ge 2$ and $k = 0, 1, 2, \ldots, r_i + 1$, we need only prove that $\beta = 0$. Suppose, to the contrary, that $\beta > 0$. Then by Lemma 4.6, there exists $k \ge 2$ such that

$$S^0 - a_{1,0} - \beta \ge \ell_k(\gamma). \tag{4.13}$$

On the other hand, applying Lemma 4.1, we can find a sequence $\{s_m\} \uparrow \infty$ such that

$$\lim_{m\to\infty} u_{1,0}(s_m) = a_{1,0}, \quad \lim_{m\to\infty} u'_{1,0}(s_m) = 0.$$

By the first equation of (4.11) and Lemma 4.2, we have

$$\begin{aligned} D\,a_{1,0} &= \lim_{m\to\infty}\big[D\,u_{1,0}(s_m) + u'_{1,0}(s_m)\big] \\ &= \lim_{m\to\infty} u_{1,r_1+1}(s_m)\,p_1\big(S^0 - u_{1,0}(s_m) - v_0(s_m) + \omega(s_m)\big) \\ &\ge a_{1,r_1+1}\,p_1\big(S^0 - a_{1,0} - \beta\big) \\ &\ge a_{1,0}\left(\frac{\alpha_1}{D+\alpha_1}\right)^{r_1+1} p_1\big(S^0 - a_{1,0} - \beta\big). \end{aligned}$$

Since $a_{1,0} > 0$, the above inequalities imply

$$D \ge \left(\frac{\alpha_1}{D+\alpha_1}\right)^{r_1+1} p_1\big(S^0 - a_{1,0} - \beta\big).$$

Consequently, by assumption (1.4),

$$S^0 - a_{1,0} - \beta \le \lambda_1. \tag{4.14}$$

By hypothesis, $\lambda_1 < \ell_j(\gamma)$ for all $j \ge 2$, and so $S^0 - a_{1,0} - \beta < \ell_k(\gamma)$, contradicting (4.13). Hence $\beta = 0$ and the proof is complete.

Lemma 4.8. *If* $a_{1,0} > 0$ *and* $a_{i,k} = b_{i,k} = 0$ *for all* $i \ge 2$, $k \in I(r_i + 1)$, *then*

$$a_{1,k} = b_{1,k} = \left(S^0 - \lambda_1\right)\left(\frac{\alpha_1}{D + \alpha_1}\right)^k, \quad k = 0, 1, 2, \ldots, r_1 + 1. \tag{4.15}$$

Proof. We first note that from the proof of Lemma 4.7, the inequality (4.14) holds if $a_{1,0} > 0$. Since $a_{i,k} = b_{i,k} = 0$ for every $i \ge 2$ and $k \in I(r_i + 1)$, it follows directly from definition (4.5) that $\beta = 0$. Hence (4.14) yields $S^0 - a_{1,0} \le \lambda_1$, i.e. $a_{1,0} \ge S^0 - \lambda_1$. On the other hand, applying Lemma 4.3, we obtain $b_{1,0} \le S^0 - \lambda_1$. This implies that $a_{1,0} = b_{1,0} = S^0 - \lambda_1$. Formula (4.15) now follows immediately from Lemma 4.2.

This completes the proof.

5. Proof of Main Results

This section is devoted to the proof of the main results stated in Section 3. The proofs of Theorems 3.1 and 3.2 are similar to the analogous theorems in [28] and hence are omitted. Before we prove Theorems 3.3-3.5, we make some observations. If $\lambda_1 < S^0$, then either the set $J := \{j \in I(n);\ j \ge 2 \text{ and } \lambda_j < S^0\} = \emptyset$, or there exists $N \ge 2$, such that $J = \{2, 3, \ldots, N\}$. In what follows, we write $N = 1$ if $J = \emptyset$. Let $\pi(\phi; t) = \left(S(t), x_1(t), \ldots, x_n(t)\right)$ be an arbitrarily fixed positive solution and $y_{i,j}(t)$ be defined as in (2.2) and (2.3). It follows from (2.5) that

$$S(t) = S^0 - \sum_{i=1}^{n}\Big(\sum_{j=0}^{r_i}\frac{y_{i,j}(t)}{\alpha_i} + x_i(t)\Big) + \rho(t), \quad t \ge 0, \tag{5.1}$$

for some continuous function $\rho(t)$ satisfying $\rho(t) \to 0$ as $t \to \infty$. Let

$$\omega(t) = -\sum_{i=N+1}^{n}\Big(\sum_{j=0}^{r_i}\frac{y_{i,j}(t)}{\alpha_i} + x_i(t)\Big) + \rho(t), \quad t \ge 0. \tag{5.2}$$

Since $\lambda_i \geq S^0$ for all $i \geq N+1$, by Theorem 3.1 and an argument similar to that in the proof of Theorem 3.1, $\lim_{t\to\infty} x_i(t) = \lim_{t\to\infty} y_{i,j}(t) = 0$ for all $i \geq N+1$ and $j = 0,1,2,\ldots,r_i$. Therefore, $\lim_{t\to\infty} \omega(t) = 0$. Substituting (5.1) and (5.2) into (2.4) and eliminating the first equation, we obtain

$$
\begin{aligned}
&x_i'(t) = -D\,x_i(t) + y_{i,r_i}(t),\\
(5.3)\quad &y_{i,0}'(t) = -(D+\alpha_i)\,y_{i,0}(t) + \alpha_i\,x_i(t)\,p_i\Big(S^0 - \textstyle\sum_{i=1}^N \Big(\sum_{j=0}^{r_i} \frac{y_{i,j}(t)}{\alpha_i} + x_i(t)\Big) + \omega(t)\Big),\\
&y_{i,j}'(t) = -(D+\alpha_i)\,y_{i,j}(t) + \alpha_i\,y_{i,j-1}(t), \quad i \in I(N),\ \ j \in I(r_i+1).
\end{aligned}
$$

Define

$$
(5.4)\qquad
\begin{aligned}
&u_{i,r_i+1}(t) = x_i(t), \quad i \in I(N),\\
&u_{i,k}(t) = x_i(t) + \sum_{j=k}^{r_i} \frac{y_{i,j}(t)}{\alpha_i}, \quad k = 0,1,2,\ldots,r_i+1.
\end{aligned}
$$

By using (5.3), it can be shown that $u(t) = \big(u_{i,k}(t)\big)$ defined by (5.4) is a positive solution of the ODEs system (4.1) with $\omega(t)$ given by (5.2). Moreover, since $\pi(\phi;t)$ is positive, $y_{i,j}(t)$ are all positive for $t > 0$, $i \in I(N)$ and $j = 0,1,2,\ldots,r_i$. So it follows from (5.4) that $u_{1,k}(t) \leq u_{1,0}(t)$ for all $k \in I(r_1+1)$ and $t > 0$. Therefore, according to Section 4, $u(t)$ as defined by (5.4) is a *stack solution* of (4.1). Clearly, assumption (4.2) is also satisfied.

We are now in a position to prove Theorem 3.3.

Proof of Theorem 3.3. We first note that the condition (3.2) implies that

$$
\sum_{i=2}^{N} (S^0 - \lambda_i) = \sum_{j\in J} (S^0 - \lambda_j) < S^0 - \lambda_1.
$$

Applying Lemma 4.5, we obtain $a_{1,0} > 0$ and $a_{i,k} = b_{i,k} = 0$ for all $2 \leq i \leq N$ and $k \in I(r_i+1)$. Furthermore, by Lemma 4.8, we have

$$
a_{1,k} = b_{1,k} = \big(S^0 - \lambda_1\big)\left(\frac{\alpha_1}{D+\alpha_1}\right)^k,
$$

for all $k = 0,1,2,\ldots,r_1+1$. Recall that $x_i(t) = u_{i,r_i+1}(t)$. Therefore,

$$
\begin{aligned}
&\lim_{t\to\infty} x_1(t) = a_{1,r_1+1} = \big(S^0 - \lambda_1\big)\left(\frac{\alpha_1}{D+\alpha_1}\right)^{r_1+1},\\
&\lim_{t\to\infty} x_i(t) = a_{i,r_i+1} = 0, \quad 2 \leq i \leq N.
\end{aligned}
$$

On the other hand, since $\lambda_i \geq S^0$ for $i \geq N$, we can apply Theorem 3.1 to obtain $\lim_{t\to\infty} x_i(t) = 0$ for all $N+1 \leq i \leq n$. Moreover, as in the proof of Theorem 3.2, we have $\lim_{t\to\infty} y_{i,j}(t) = 0$ for all $i \geq 2$, $j = 0, 1, 2, \dots, r_i$. Therefore, it follows from (5.1) that

$$\begin{aligned}\lim_{t\to\infty} S(t) =& S^0 - \lim_{t\to\infty} \Big(\sum_{j=0}^{r_1} \frac{y_{1,j}(t)}{\alpha_1} + x_1(t) \Big) \\ &- \lim_{t\to\infty} \sum_{i=2}^{n} \Big(\sum_{j=0}^{r_i} \frac{y_{i,j}(t)}{\alpha_i} + x_i(t) \Big) \\ =& S^0 - \lim_{t\to\infty} u_{1,0}(t) \\ =& S^0 - a_{1,0} \\ =& S^0 - (S^0 - \lambda_1) = \lambda_1 .\end{aligned}$$

Consequently,

$$\lim_{t\to\infty} \pi(\phi; t) = \Big(\lambda_1, (S^0 - \lambda_1) \left(\frac{\alpha_1}{D + \alpha_1} \right)^{r_1 + 1}, 0, \dots, 0 \Big) = E_1,$$

and the proof is complete.

To prove Theorems 3.4 and 3.5, we will need the following two lemmas.

Lemma 5.1. *Let $Q : \mathbb{R}_+ \to \mathbb{R}_+$ and $g : \mathbb{R} \to \mathbb{R}_+$ be continuous functions. If g is bounded and $\int_0^\infty Q(s)\, ds < \infty$, then*

$$\limsup_{t\to\infty} \int_{-\infty}^{t} g(\theta) Q(t - \theta)\, d\theta \leq \limsup_{t\to\infty} g(t) \int_0^\infty Q(s)\, ds. \tag{5.5}$$

Proof. Let $A = \sup_{t\in\mathbb{R}} g(t)$. If $A = 0$, then (5.1) holds trivially. So in what follows, we assume $A > 0$. Let $\varepsilon > 0$ be given. We choose $M = M(\varepsilon) > 0$ such that

$$\int_M^\infty Q(s)\, ds < \frac{\varepsilon}{2A} \int_0^\infty Q(s)\, ds.$$

Then we have

$$\begin{aligned}\int_{-\infty}^{t} g(\theta) Q(t - \theta)\, d\theta &= \int_0^\infty g(t - s) Q(s)\, ds \\ &= \int_0^M g(t - s) Q(s)\, ds + \int_M^\infty g(t - s) Q(s)\, ds \\ &\leq \int_0^M g(t - s) Q(s)\, ds + A \int_M^\infty Q(s)\, ds \\ &< \int_0^M g(t - s) Q(s)\, ds + \frac{\varepsilon}{2} \int_0^\infty Q(s)\, ds.\end{aligned} \tag{5.6}$$

Let $T = T(\varepsilon) > 0$ be such that for all $t \geq T$, $g(t-s) < \limsup_{t\to\infty} g(t) + \varepsilon/2$ for every $s \in [0, M]$. It then follows from (5.6) that for all $t \geq T$,

$$\begin{aligned}
&\int_{-\infty}^{t} g(\theta) Q(t-\theta)\, d\theta \\
&\quad < \int_0^M \left(\limsup_{t\to\infty} g(t) + \frac{\varepsilon}{2} \right) Q(s)\, ds + \frac{\varepsilon}{2} \int_0^\infty Q(s)\, ds \\
&\quad < \left(\limsup_{t\to\infty} g(t) + \varepsilon \right) \int_0^\infty Q(s)\, ds
\end{aligned}$$

from which (5.5) follows and the proof is complete.

Lemma 5.2. *Let* $h : \mathbb{R} \to \mathbb{R}_+$ *be a bounded continuous function. Suppose that for every* $\varepsilon > 0$, *there exist positive numbers* $M(\varepsilon)$, $L(\varepsilon)$, *and* L *such that* $\lim_{\varepsilon\to 0^+} L(\varepsilon) = L$ *and* $|h(t_2) - h(t_1)| \leq L(\varepsilon)\, |t_2 - t_1|$ *for all* $t_1, t_2 \geq M(\varepsilon)$. *Then for any* $\tau > 0$ *and any integer* $r \geq 0$,

$$\limsup_{t\to\infty} \left| \int_0^\infty h(t-s) G_r(s)\, ds - h(t-\tau) \right| \leq \frac{C}{\sqrt{r+1}}, \tag{5.7}$$

where

$$C = \frac{2\tau L}{\sqrt{2\pi}}, \qquad G_r(s) = \frac{\alpha^{r+1} s^r}{r!} e^{-\alpha s}, \qquad \alpha = \frac{r+1}{\tau}. \tag{5.8}$$

Proof. Let $\varepsilon > 0$ be given. Find $T = T(r, \varepsilon, \tau) > \max(M(\varepsilon), \tau)$ such that for $t \geq T$,

$$\int_t^\infty G_r(s)\, ds < \frac{\varepsilon}{2H},$$

where $H = \sup_{t\in\mathbb{R}} h(t)$. Note that for $t \geq 2T$ and $s \in [0, T]$, we have $|h(t-s) - h(t-\tau)| \leq L(\varepsilon)|s-\tau|$. Note that $\int_0^\infty G_r(s)\, ds = 1$. This implies that for all $t \geq 2T$,

$$\begin{aligned}
&\left| \int_0^\infty h(t-s) G_r(s)\, ds - h(t-\tau) \right| \\
&\leq \int_0^\infty |h(t-s) - h(t-\tau)| G_r(s)\, ds \\
&\leq \int_0^T |h(t-s) - h(t-\tau)| G_r(s)\, ds + 2H \int_T^\infty G_r(s)\, ds \\
&< L(\varepsilon) \int_0^\infty |s-\tau| G_r(s)\, ds + \varepsilon.
\end{aligned}$$

Let $I = \int_0^\infty |s-\tau| G_r(s)\, ds$. We rewrite this as

$$
\begin{aligned}
I =& \int_0^\tau (\tau - s) G_r(s)\, ds + \int_\tau^\infty (s-\tau) G_r(s)\, ds \\
=& \tau \left(\int_0^\tau - \int_\tau^\infty \right) G_r(s)\, ds - \left(\int_0^\tau - \int_\tau^\infty \right) s G_r(s)\, ds.
\end{aligned}
$$

Applying integration by parts repeatedly, we have

$$
\int_0^\tau G_r(s)\, ds - \int_\tau^\infty G_r(s)\, ds = 1 - 2e^{-\alpha\tau} \sum_{k=0}^{r} \frac{(\alpha\tau)^k}{k!},
$$

$$
\int_0^\tau s G_r(s)\, ds - \int_\tau^\infty s G_r(s)\, ds = \tau - 2\tau e^{-\alpha\tau} \sum_{k=0}^{r+1} \frac{(\alpha\tau)^k}{k!}.
$$

Hence,

$$
I = \frac{2\tau(\alpha\tau)^{r+1}}{(r+1)!} e^{-\alpha\tau} = \frac{2\tau(r+1)^{r+1}}{(r+1)!} e^{-(r+1)}.
$$

By Stirling's formula (see [17], Theorem 2, pp. 220), there exists $0 < \xi_r < 1$ such that

$$
(r+1)! = \sqrt{2\pi(r+1)} \left(\frac{r+1}{e} \right)^{r+1} e^{\frac{\xi_r}{12(r+1)}},
$$

and so it follows that

$$
\begin{aligned}
I =& \frac{2\tau}{\sqrt{2\pi(r+1)}} e^{-\frac{\xi_r}{12(r+1)}} \\
<& \frac{2\tau}{\sqrt{2\pi(r+1)}} = \frac{C}{L\sqrt{r+1}},
\end{aligned}
$$

where $C > 0$ is the constant given by (5.8). Consequently, for all $t \geq 2T$,

$$
\left| \int_0^\infty h(t-s) G_r(s)\, ds - h(t-\tau) \right| < \frac{L(\varepsilon)\, C}{L\sqrt{r+1}} + \varepsilon.
$$

This immediately leads to (5.7) and completes the proof.

Remark 5.3. The condition on h in the above lemma is satisfied if h is continuously differentiable and $\limsup_{t\to\infty} |h'(t)| \leq L$. In fact, for every $\varepsilon > 0$, we may choose $L(\varepsilon) = L + \varepsilon$, and appeal to the Mean Value Theorem.

We now give the proofs of Theorems 3.4 and 3.5.

Proof of Theorem 3.4. As in the proof of Theorem 3.3, it suffices to show that $a_{1,0} > 0$ and $a_{i,k} = b_{i,k} = 0$ for all $2 \leq i \leq N$ and $k = 0, 1, 2, \ldots, r_i + 1$. Recall that $u(t)$ is a stack solution of (4.1). By Lemma 4.7, it is sufficient to show that (4.10) holds for $\gamma = \gamma_1$, where $\gamma_1 \ge 0$ is the constant defined in (3.5). To this end, we first note that

$$
\begin{aligned}
\sum_{i=2}^{N}\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} u_{i,r_i+1}(t) &= \sum_{i=2}^{N}\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} x_i(t) \\
&= \sum_{i=2}^{N}\Big[\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} x_i(t) - \int_0^t u_{i,0}(t-s)K(s)\,ds\Big] \\
&\quad + \sum_{i=2}^{N}\int_0^t u_{i,0}(t-s)K(s)\,ds \\
&= \sum_{i=2}^{N} W_i(t) + \int_0^t v_0(t-s)K(s)\,ds,
\end{aligned}
\tag{5.9}
$$

where $v_0(t)$ is defined as in (4.5) and

$$
W_i(t) = \Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} x_i(t) - \int_0^t u_{i,0}(t-s)K(s)\,ds,
$$

for $i = 2, 3, \dots, N$. In what follows, we show that for each $2 \le i \le N$,

$$
\limsup_{t\to\infty} W_i(t) \le \frac{1}{D}\, x_i^*\, p_i(S^0)\int_0^\infty |Q_i^D(s) - K(s)|\,ds, \tag{5.10}
$$

where x_i^* is given by (1.5) and Q_i^D is the *virtual delay kernel* defined as in (3.8). Indeed, by using the equations in (5.3) and (5.4), we obtain

$$
\begin{aligned}
W_i'(t) =&\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1}\big(-Dx_i(t) + y_{i,r_i}(t)\big) \\
&- \int_0^t \Big(x_i'(t-s) + \textstyle\sum_{j=0}^{r_i} \frac{y_{i,j}'(t-s)}{\alpha_i}\Big)K(s)\,ds - u_{i,0}(0)K(t) \\
=& - D\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} x_i(t) + \Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} y_{i,r_i}(t) \\
&- \int_0^t \big[-Dx_i(t-s) + y_{i,r_i}(t-s)\big]K(s)\,ds \\
&- \int_0^t \Big[-\textstyle\sum_{j=0}^{r_i}\Big(\frac{D+\alpha_i}{\alpha_i}\Big)y_{i,j}(t-s) + \sum_{j=1}^{r_i} y_{i,j-1}(t-s)\Big]K(s)\,ds \\
&- \int_0^t x_i(t-s)p_i\big(S(t-s)\big)K(s)\,ds - u_{i,0}(0)K(t) \\
=& - D\Big[\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} x_i(t) - \int_0^t \Big(x_i(t-s) + \textstyle\sum_{j=0}^{r_i} \frac{y_{i,j}(t-s)}{\alpha_i}\Big)K(s)\,ds\Big]
\end{aligned}
\tag{5.11}
$$

$$
\begin{aligned}
&+\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} y_{i,r_i}(t) - \int_0^t x_i(t-s)p_i\big(S(t-s)\big)K(s)\,ds \\
=&-D\,W_i(t) + \int_0^\infty x_i(t-s)p_i\big(S(t-s)\big)\Big[\Big(\frac{D+\alpha_i}{\alpha_i}\Big)^{r_i+1} G^{r_i}_{D,\alpha_i}(s) - K(s)\Big]ds \\
&-u_{i,0}(0)K(t) - \int_t^\infty x_i(t-s)p_i\big(S(t-s)\big)K(s)\,ds \\
=&-D\,W_i(t) + \int_0^\infty x_i(t-s)p_i\big(S(t-s)\big)\big[Q_i^D(s) - K(s)\big]\,ds \\
&-u_{i,0}(0)K(t) - \int_t^\infty x_i(t-s)p_i\big(S(t-s)\big)K(s)\,ds,
\end{aligned}
$$

where we have used (2.2) and (2.3) for $y_{i,r_i}(t)$. Notice that $W_i(t)$ is bounded. It follows from (5.11) that $W_i'(t)$ is also bounded. This implies that $W_i(t)$ is uniformly continuous. By using (5.11) again, we see that $W_i'(t)$ is uniformly continuous as well. This allows us to apply Lemma 4.1. So we have a sequence $\{t_m\} \uparrow \infty$ such that

$$
\lim_{m\to\infty} W_i(t_m) = \limsup_{t\to\infty} W_i(t), \qquad \lim_{m\to\infty} W_i'(t_m) = 0.
$$

On the other hand, by assumption we have $\lim_{t\to\infty} K(t) = 0$ and

$$
\begin{aligned}
\lim_{t\to\infty} &\int_t^\infty x_i(t-s)p_i\big(S(t-s)\big)K(s)\,ds \\
&\le M_i \int_t^\infty K(s)\,ds = 0,
\end{aligned}
$$

where $M_i = \sup_{-\infty<\theta\le 0} |\phi_i(\theta)p_i\big(\phi_0(\theta)\big)|$ and $(\phi_0, \phi_1, \dots, \phi_N) \in BC_+^{N+1}$ is the initial data of $\big(S(t), x_1(t), \dots, x_N(t)\big)$. Therefore, it follows from (5.11) that

$$
\begin{aligned}
\limsup_{t\to\infty} W_i(t) =& \lim_{m\to\infty} W_i(t_m) \\
=&\frac{1}{D}\lim_{m\to\infty}\int_0^\infty x_i(t_m-s)p_i\big(S(t_m-s)\big)\big[Q_i^D(s)-K(s)\big]\,ds \\
&-\lim_{m\to\infty} u_{i,0}(0)K(t_m) - \lim_{m\to\infty}\int_{t_m}^\infty x_i(t-s)p_i\big(S(t-s)\big)K(s)\,ds \\
\le&\frac{1}{D}\limsup_{t\to\infty}\int_0^\infty x_i(t-s)p_i\big(S(t-s)\big)|Q_i^D(s)-K(s)|\,ds.
\end{aligned} \tag{5.12}
$$

Recall that $x_i(t) = u_{i,r_i+1}(t)$. By (2.6), Lemmas 4.2 and 4.3, we have

$$
\begin{aligned}
&\limsup_{t\to\infty} x_i(t) \le \left(\frac{\alpha_i}{D+\alpha_i}\right)^{r_i+1}\big(S^0-\lambda_i\big) = x_i^*, \\
&\limsup_{t\to\infty} p_i\big(S(t)\big) \le p_i\big(S^0\big).
\end{aligned} \tag{5.13}
$$

Applying Lemma 5.1 to (5.12) then gives (5.10).

Therefore, upon using Lemma 5.1 again, we obtain from (5.9) that

$$\begin{aligned}
&\limsup_{t\to\infty} \sum_{i=2}^{N} \left(\frac{D+\alpha_i}{\alpha_i}\right)^{r_i+1} u_{i,r_i+1}(t) \\
&\le \sum_{i=2}^{N} \limsup_{t\to\infty} W_i(t) + \limsup_{t\to\infty} \int_0^\infty v_0(t-s)K(s)\,ds \\
&\le \frac{1}{D}\sum_{i=2}^{N} x_i^*\, p_i(S^0) \int_0^\infty |Q_i^D(s) - K(s)|\,ds + \beta \int_0^\infty K(s)\,ds \\
&= \gamma_1 + \beta,
\end{aligned}$$

where $\beta = \limsup_{t\to\infty} v_0(t)$ is defined in (4.5). This proves (4.10) for $\gamma = \gamma_1$ and the conclusion follows.

Finally, we prove Theorem 3.5.

Proof of Theorem 3.5. As before, it suffices to show that (4.10) holds for $\gamma = \gamma_2$, where $\gamma_2 \ge 0$ is the constant defined by (3.7). We proceed as in the proof of Theorem 3.4 and arrive at (5.11) with $K(s)$ replaced by $Q(s)$, where

$$Q(s) = \left(\frac{D+\alpha}{\alpha}\right)^{r+1} G_{D,\alpha}^{r}(s)$$

and $G_{D,\alpha}^{r}(s)$ is defined as in (2.3). Let

$$\begin{aligned}
h_i(t) &= x_i(t) p_i\big(S(t)\big), \\
V_i(t) &= \int_0^\infty h_i(t-s)\big(Q_i^D(s) - Q(s)\big)\,ds,
\end{aligned}$$

for $i = 2, 3, \dots, N$. We rewrite each $V_i(t)$ as follows

$$\begin{aligned}
V_i(t) &= \int_0^\infty h_i(t-s) Q_i^D(s)\,ds - \int_0^\infty h_i(t-s) Q(s)\,ds \\
&= \int_0^\infty h_i(t-s) Q_i^D(s)\,ds - h_i(t-\tau_{D,i}) \\
&\quad - \Big(\int_0^\infty h_i(t-s) Q(s)\,ds - h_i(t-\tau_D)\Big) \\
&\quad + h_i(t-\tau_{D,i}) - h_i(t-\tau_D),
\end{aligned} \tag{5.14}$$

where $\tau_{D,i} = (r_i + 1)/(D + \alpha_i)$ and $\tau_D = (r + 1)/(D + \alpha)$ are the corresponding *virtual mean delays* of Q_i^D and Q. Note that by the first equation of (1.1), we have

$$\begin{aligned} |S'(t)| &= \big|S^0 D - DS(t) - \sum_{i=1}^{n} x_i(t) p_i\big(S(t)\big)\big| \\ &\le \max\{S^0 D, DS(t) + \sum_{i=1}^{n} x_i(t) p_i\big(S(t)\big)\}, \end{aligned}$$

where we have used the inequality $|a - b| \le \max\{a, b\}$ for all positive real numbers a and b. Thus by using (2.6), (5.13) and recalling that $\lim_{t\to\infty} x_i(t) = 0$ for all $i \ge N + 1$, we obtain

$$\begin{aligned} \limsup_{t\to\infty} |S'(t)| &\le \max\{\, S^0 D, S^0 D + P \limsup_{t\to\infty} \sum_{i=1}^{N} x_i(t)\,\} \\ &\le S^0 D + P S^0 = S^0 (D + P), \end{aligned} \tag{5.15}$$

where $P = \max_{1\le i\le N} p_i(S^0)$. Similarly, we can use (1.1), (5.13) and Lemma 5.1 to obtain

$$\begin{aligned} \limsup_{t\to\infty} |x_i'(t)| &\le \limsup_{t\to\infty} \max\big\{\, Dx_i(t), \textstyle\int_{-\infty}^{t} h_i(\theta) G_{D,\alpha_i}^{r_i}(t-\theta)\, d\theta\big\} \\ &\le \limsup_{t\to\infty} \max\big\{\, Dx_i(t), \textstyle\int_{-\infty}^{t} h_i(\theta) Q_i^D(t-\theta)\, d\theta\big\} \\ &\le \max\big\{\, Dx_i^*, \limsup_{t\to\infty} h_i(t)\big\} \\ &\le \max\big\{\, Dx_i^*, x_i^*\, p_i(S^0)\,\big\} \\ &= x_i^*\, p_i(S^0), \quad 2 \le i \le N. \end{aligned} \tag{5.16}$$

Hence, it follows from (5.15) and (5.16) that for any $\varepsilon > 0$, there exists $M_i = M_i(\varepsilon)$ such that for all t_1, $t_2 \ge M_i$,

$$\begin{aligned} |h_i(t_2) - h_i(t_1)| &= |x_i(t_2)\, p_i\big(S(t_2)\big) - x_i(t_1)\, p_i\big(S(t_1)\big)| \\ &\le p_i\big(S(t_2)\big)|x_i(t_2) - x_i(t_1)| + \mu_i\, x_i(t_1)|S(t_2) - S(t_1)| \\ &\le L_i(\varepsilon)|t_2 - t_1|, \end{aligned}$$

where μ_i is the global Lipschitz constant of p_i on the interval $[0, S^0]$, and

$$L_i(\varepsilon) = x_i^*\, p_i(S^0)\Big(p_i(S^0) + \mu_i\, S^0 p_i^{-1}(S^0)(D + P) + \varepsilon\Big).$$

This implies that for all $t \ge M_i + \max(\tau_{D,i}, \tau_D)$,

$$|h_i(t - \tau_{D,i}) - h_i(t - \tau_D)| \le L_i(\varepsilon)|\tau_D - \tau_{D,i}|.$$

Recall that A_i, B_i and C_i are the constants defined by (3.8). Since $\lim_{\varepsilon\to 0^+} L_i(\varepsilon) = C_i$, applying Lemma 5.2 to (5.14) gives

$$\begin{aligned}
\limsup_{t\to\infty} V_i(t) \le & \limsup_{t\to\infty} \left| \int_0^\infty h_i(t-\theta) Q_i^D(s)\, ds - h_i(t-\tau_{D,i}) \right| \\
& + \limsup_{t\to\infty} \left| \int_0^\infty h_i(t-\theta) Q(s)\, ds - h_i(t-\tau_D) \right| \\
& + \limsup_{t\to\infty} |h_i(t-\tau_{D,i}) - h_i(t-\tau_D)| \\
\le & \frac{2\tau_{D,i} C_i}{\sqrt{2\pi(r_i+1)}} + \frac{2\tau_D C_i}{\sqrt{2\pi(r+1)}} + C_i|\tau_D - \tau_{D,i}| \\
= & \frac{A_i}{\sqrt{r_i+1}} + \frac{B_i}{\sqrt{r+1}} + C_i|\tau_D - \tau_{D,i}|.
\end{aligned}$$

Therefore, as in (5.12), we obtain

$$\limsup_{t\to\infty} W_i(t) \le \frac{1}{D}\left(\frac{A_i}{\sqrt{r_i+1}} + \frac{B_i}{\sqrt{r+1}} + C_i|\tau_D - \tau_{D,i}| \right),$$

and consequently, by (5.9),

$$\begin{aligned}
& \limsup_{t\to\infty} \sum_{i=2}^{N} \left(\frac{D+\alpha_i}{\alpha_i} \right)^{r_i+1} u_{i,r_i+1}(t) \\
& \le \sum_{i=2}^{N} \limsup_{t\to\infty} W_i(t) + \beta \int_0^\infty Q(s)\, ds \\
& \le \frac{1}{D} \sum_{i=2}^{N} \left(\frac{A_i}{\sqrt{r_i+1}} + \frac{B_i}{\sqrt{r+1}} + C_i|\tau_D - \tau_{D,i}| \right) + \beta \\
& = \gamma_2 + \beta.
\end{aligned}$$

That is, (4.10) holds for $\gamma = \gamma_2$. This completes the proof of Theorem 3.5.

6. Concluding Remarks

In this paper, we considered the global dynamics of an exploitative competition model of n-species in the chemostat. We used distributed delays to model the time lag in the process of conversion of nutrient to new cells. Analogues of the results given in [27] for the corresponding discrete delay model are obtained and new results for the distributed delay model are proved. As well, the results extend the recent work [28] for the two species competition model to the general n-species case.

By selecting delay kernels of exponential type (see (1.2)), we obtained sufficient conditions under which the model exhibits competitive exclusion. In particular, we proved that the population that has the smallest delayed break-even concentration wins the competition, provided that either the *virtual delay kernels* are close to each other in L^1-norm, or the orders of the delay kernels are large and the *virtual mean delays* are close to each other. As noted before, different virtual delay kernels represent the distributions of the delay involved in the conversion of nutrient by the different species to new cells modified to include the washout factor. Also, as will be explained in the last paragraph of this concluding section, we know that the case where the order of the virtual delay kernel is large corresponds to a small stochastic perturbation of the discrete delay case (where the discrete delay is the virtual mean delay). Our results therefore indicate that the competitive exclusion principle remains true if the distributed delays for the different species (whether they are large or small) are close to each other in the L^1-sense or if the distributed delays are small perturbations of discrete delays, provided that the size of the discrete delays are similar for all of the species. Hence, if the delay kernels of the different species are similar (as might be expected for similar species), then our theorems are likely to apply.

The theorems we proved also imply that when the virtual mean delays are small, the predictions of the distributed delay model are identical to the predictions of the corresponding ODEs model without delay. To see this, let us assume, for simplicity, that the growth response functions p_i are strictly increasing. Then it follows from (1.4) that

$$\begin{aligned} \lambda_i &= p_i^{-1}\left(D\left(\tfrac{D+\alpha_i}{\alpha_i}\right)^{r_i+1}\right) \\ &= p_i^{-1}\left(D\left(1+\tfrac{D}{\alpha_i}\right)^{\alpha_i \tau_{D,i} \frac{D+\alpha_i}{\alpha_i}}\right). \end{aligned} \tag{6.1}$$

If the virtual mean delays $\tau_{D,i}$ are small, then the α_i's are large and so (6.1) implies that

$$\lambda_i \approx p_i^{-1}\left(De^{\tau_{D,i}}\right) \approx p_i^{-1}(D). \tag{6.2}$$

Since $p_i^{-1}(D)$ are the break-even concentrations for the corresponding ODEs model, it follows from (6.2) that if $\tau_{D,i}$ are small, then $\lambda_1 < \lambda_j$, $j \geq 2$, implies that $p_1^{-1}(D) < p_j^{-1}(D)$, $j \geq 2$. By Theorem 4.6 in [4], the ODEs model predicts that population x_1 is the sole survivor. This prediction is identical with the prediction given by the distributed delay model (1.1), as indicated by Theorem 3.5 and Remark 3.7. However, we should note that when the virtual mean delays are relatively large, from (6.1), it is possible that $\lambda_1 < \lambda_j$ and $p_1^{-1}(D) > p_j^{-1}(D)$ hold simultaneously. By Theorem 3.3, it follows that the distributed delay model may give predictions on the outcome of competition that are different from those given by the ODEs model. We refer to [27,28] for more details and a similar discussion of the effects of time delay on the outcome of competition in the chemostat.

One of the main findings in this paper is the role played by the so-called virtual delay kernels and the corresponding virtual mean delays (see Theorems 3.4 and 3.5) for predicting the global dynamics of model (1.1). To the best of our knowledge, this finding has not been reported in the literature. Although in [20] MacDonald seemed to have noticed this, he only gave a very brief discussion on a similar but different observation. We reiterate that the virtual delay kernels combine two modes of loss of memory of previous events, one occuring on a time scale $(r_i + 1)/\alpha_i$ appropriate to the particular mechanism conceived, and the other occuring on the time scale $1/D$ due to the outflow in the chemostat. Consequently, the virtual mean delay simulates the mean delay of this two-mode interaction of loss of memory. Observe that for any fixed $D > 0$, the virtual mean delay $\tau_{D,j}$ is always smaller than the (physical) mean delay $(r_i + 1)/\alpha_i$, and that they are close if α_i is large. This allows us to conclude that the results in Theorem 3.9 of [27] may be viewed as the limiting case of Theorem 3.5 of this paper, since the distributed delay model (1.1) approaches the corresponding discrete delay model when the α_i's go to infinity while the mean delays $\tau = (r_i + 1)/\alpha_i$ are kept fixed (see the Appendix of [28] for a proof). However, when the α_i's are relatively small, the results given in Theorems 3.4 and 3.5 appear to be new.

Finally, we remark that as in [28], we selected a particular class of delay kernels of the form (1.2) to analyze the global asymptotic behavior of model (1.1), and this selection allowed us to apply the *linear chain trick technique*. As discussed in [28], this class of delay kernels are of unimodal type and are generic in the sense that the linear span of the functions $\{e^{-s}, se^{-s}, s^2e^{-s}, \dots\}$ is dense in $L^1[0, \infty)$. Recently, in [13] the dependence of the global asymptotic dynamics on the delay kernels was studied and these results seem to provide some theoretical evidence for selecting delay kernels of unimodal type in some integral infinite delay differential equation models (see also [3, 7]). As well, it has been well-known that integral delay may take into account some stochastic behavior of species, and very long linear chains of differential equations provide multi-stages of biological processes with random passage through each and the overall distribution of the total passage time leads to a gamma distribution (see [21, 25]). This type of gamma distribution is known as the special Erlangian from renewal theory (see [8]), and the weak kernel and the Dirac distribution kernel corresponding to the discrete delay case represent the Erlangian distributions with the order $r = 0$ and $r = \infty$, respectively. Note that by the Central Limit Theorem, as r increases, the Erlangian distribution tends to become more normal around the mean. So, as indicated in [25], it is only necessary to choose a suitable value for r to obtain a good approximation to many unimodal distributions for t. From this point of view, in [21], MacDonald also comments that it is important to look for an overall picture of the dynamics for *general order* of the delay kernels. We have done so by committing ourselves to looking for global dynamics as well as allowing an arbitrary order in the delay kernels. For slightly more general delay kernels, i.e. gamma distribution kernels with non-integral orders (i.e. r_i 's are not integers in $K_i(s)$), our results may also be sufficient, as far as (local) *numerical solutions* are concerned, since as suggested by [8], solutions for non-integral orders may preferably be obtained by interpolating numerically between solutions for integral orders, rather than proceeding directly with the theory for the value of non-integral order r_i concerned. However, from the global dynamics point of view, it is important that we investigate the question as to whether or not the *global results* we proved in this paper hold for more general delay kernels. We leave this for future investigation.

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