GLOBAL STABILITY IN CHEMOSTAT-TYPE COMPETITION MODELS WITH NUTRIENT RECYCLING

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Abstract. Freedman and Xu (*J. Math. Biol.* 31(1993), 513-527) proposed two chemostat-type competition models with nutrient recycling. In the first model the recycling is instantaneous, whereas in the second, the recycling is delayed. They carried out the equilibrium analysis and obtained persistence criteria for the models. In this paper, by applying the method of Liapunov functionals we study the global asymptotic stability of the positive equilibria of the models. We also generalize the results to the multi-species competition models with instantaneous and delayed nutrient recycling, respectively. Differing from the dynamics of the usual chemostat models, we find that the competing populations could coexist if there is nutrient recycling and they compete directly.

Key words. competition model, nutrient recycling, time delay, Liapunov functional, global stability.

AMS subject classifications. 34K15, 34K20, 92A15

Short title. Competition Models with Nutrient Recycling

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1. Introduction

An important factor among the many processes which influence ecosystem dynamics is nutrient (material) recycling. The effect of nutrient recycling on ecosystem stability and persistence has been studied by Antonios and Hallam [1], DeAngelis, Bartell and Brenker [10], Nisbet and Gurney [18], Nisbet, McKinstry and Gurney [19], Powell and Richerson [20], Ruan [21, 22], and Ulanowicz [26], etc. Usually, nutrient recycling is regarded as an instantaneous term, thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition. However, in natural systems such as a lake, generally there is a residence time of nutrient and sediments measured in years (Powell and Richerson [20]). Thus a time delay is always present in a natural system and it increases when temperature decreases (Whittaker [27]).

In order to model the growth of planktonic communities in lakes, where the plankton feeds on a limiting nutrient supplied as a constant rate, such as unicellular algae feeds on phosphorus, Beretta, Bischi and Solomano [3] proposed a chemostat-type model with delayed nutrient recycling. They supposed that the limiting nutrient is partially recycled due to bacterial decomposition of dead planktonic biomass and used a distributed delay to model the nutrient recycling in order to study its effect on the stability of the positive equilibrium. In a consecutive paper, Bischi [7] studied the effect of the time delay on resilience, the rate at which a system returns to a stable steady state following a perturbation. Bischi showed that if the system is characterized by oscillating behavior, an increase of the time delay involved in nutrient recycling can have a stabilizing effect. This is counter-intuitive to the usual observation the time delay has a destabilizing effect in the sense that increasing the time delay could cause a stable steady state to become unstable and/or cause the population to fluctuate (Cushing [9], Gopalsamy [12], Kuang [16], and MacDonald [17]). Recently, Beretta and Takeuchi [4-6] and He and Ruan [13] studied the global asymptotic stability of the positive equilibrium by applying Liapunov functional method. For other related work, we refer to Beretta and Takeuchi [4-6] and Ruan [23].

Freedman and Xu [11] extended the single species model proposed by Beretta, Bischi and Solomano [3] to two-species competition models with instantaneous and delayed nutrient recycling. Their models differ from the usual chemostat models (see Butler and Wolkowicz [8], Hsu [14], Hsu, Hubbell and Waltman [15], Smith and Waltman [24], etc.). Firstly, A chemostat model is thought of as referring to a stirred tank with a substantial washout rate. Hence all "death" in chemostat models are due to washout. Secondly, there is no direct competition between the two microorganisms. Thirdly, there is no nutrient recycling. Freedman and Xu developed persistence and extinction criteria for the competing populations. But they did not study the global stability of the positive equilibrium.

Our goal in this paper is to discuss the global asymptotic stability of the models proposed by Freedman and Xu [11] and of the n -species competition models with instantaneous and delayed nutrient recycling. Namely, we consider the following competition model with delayed nutrient recycling

$$\begin{aligned}\dot{S} &= D(S^0 - S) - \sum_{i=1}^{n} \mu_i N_i p(S) + \int_0^{\infty} F(u)\Big(\sum_{i=1}^{n} b_i D_i N_i(t-u)\Big)du \\ \dot{N}_i &= N_i\Big[-(D+D_i) + m_i p(S) - \sum_{j=1}^{n} \delta_{ij} N_j\Big], \quad i = 1,2,\dots,n\end{aligned} \tag{1.1}$$

and its special cases, where $S(t)$ denotes the nutrient concentration and $N_i(t)\,(i = 1,2,\dots,n)$ is the competitor concentration at time t.

In system (1.1), S^0 is the input concentration of the limiting nutrient; D is the washout rate; $\mu_i\,(i = 1,2,\dots,n)$ is the maximal nutrient uptake rate of the i th competitor; $D_i\,(i = 1,2,\dots,n)$ is the linear component of the i th competitor's death rate, whereas $\delta_{ii}\,(i = 1,2,\dots,n)$ is its quadratic component; δ_{ij} are the competition coefficients; $m_i\,(i = 1,2,\dots,n)$ is the maximal conversion rate of the nutrient into planktonic biomass; $b_i\,(i = 1,2,\dots,n)$ is the recycling rate of the i th competitor. Notice that system (1.1) can be thought to represent a real lake system, so the washout rate D is small and other plankton death rates $D_i(i = 1,2,\dots,n)$ are significant.

We assume that the competing microorganisms are sufficiently similar such that their nutrient uptake functions have similar properties, that is, have similar geometrical shapes with different maximal values. These maximal values represent a saturation effect in the nutrient uptake. In system (1.1), $p(S)$ is the nutrient uptake function and satisfies the following properties:

$$p(0) = 0, \quad p'(S) > 0, \quad \lim_{S\to\infty} p(S) = 1. \tag{1.2}$$

In particular, the Michaelis-Menten function $p(S) = S/(k+S)$ satisfies the assumptions, where $k > 0$ is the half-saturation constant.

We also assume that the competing populations are sufficiently similar in their uptake of nutrient so that the resultant delays are the same. The kernel $F : R \to R^+$ is continuous and satisfies

$$\int_0^\infty F(u)\,du = 1, \quad T_f = \int_0^\infty uF(u)\,du < \infty. \tag{1.3}$$

The solutions of system (1.1) exist for all $t \geq 0$ under the initial conditions

$$S(0) = S_0 > 0, \quad N_i(u) = \phi_i(u), \;\; i = 1, 2, \dots, n, \quad u \in (-\infty, 0], \tag{1.4}$$

where $\phi_i \; (i = 1, 2, \dots, n)$ are positive linear continuous functions on $(-\infty, 0]$.

The paper is organized as follows. In Section 2, we first consider the two-species competition model with instantaneous nutrient recycling. The two-species competition model with delayed nutrient recycling is discussed in Section 3. In Section 4, we generalize the results in Sections 2 and 3 to the n -species competition models with instantaneous and delayed nutrient recycling, respectively. Finally, a discussion and numerical simulations are presented in Section 5.

2. Competition Models with Instantaneous Nutrient Recycling

Let $S(t)$ denote the nutrient concentration and $N_i(t)\,(i = 1, 2)$ be the competitor concentration at time t. To model a real lake system, it is reasonable to expect that direct competition occurs between two microorganisms. We consider the following two-species competition model with instantaneous nutrient recycling

$$\begin{aligned}
\dot{S} &= D(S^o - S) - (\mu_1 N_1 + \mu_2 N_2)p(S) + b_1 D_1 N_1 + b_2 D_2 N_2 \\
\dot{N}_1 &= N_1[-(D + D_1) + m_1 p(S) - (\delta_{11} N_1 + \delta_{12} N_2)] \\
\dot{N}_2 &= N_2[-(D + D_2) + m_2 p(S) - (\delta_{21} N_1 + \delta_{22} N_2)]
\end{aligned} \tag{2.1}$$

under nonnegative initial values

$$S(0) = S_0 \geq 0, \quad N_i(0) = N_{i0} \geq 0, \quad i = 1, 2.$$

Theorem 2.1. *All the solutions of (2.1) are bounded.*

Proof. As in the proof of Theorem 2.5 in [11], let

$$V(S, N_1, N_2) = S(t) + \frac{\mu_1}{m_1} N_1(t) + \frac{\mu_2}{m_2} N_2(t). \tag{2.2}$$

Then, along the solutions of (2.1),

$$\dot{V} = D(S^0 - S) - \mu_1\left(\frac{D+D_1}{m_1} - \frac{b_1 D_1}{\mu_1}\right)N_1 - \mu_2\left(\frac{D+D_2}{m_2} - \frac{b_2 D_2}{\mu_2}\right)N_2$$
$$- \frac{\mu_1}{m_1}\delta_{11}N_1^2 - \left(\frac{\mu_1}{m_1}\delta_{12} + \frac{\mu_2}{m_2}\delta_{21}\right)N_1 N_2 - \frac{\mu_2}{m_2}\delta_{22}N_2^2. \tag{2.3}$$

Let $\gamma_i = (D+D_i)/m_i - b_i D_i/\mu_i \, (i = 1,2)$. If $\gamma_i > 0$ for $i = 1,2$, then the conclusion follows from Theorem 2.5 in [11]. Now let us first suppose that $\gamma_i \leq 0$ for $i = 1,2$. We rewrite (2.3) in the following form

$$\begin{aligned}\dot{V} &= D(S^0 - S) - \mu_1\gamma_1 N_1 - \mu_2\gamma_2 N_2 \\ &\quad - \frac{\mu_1}{m_1}\delta_{11}N_1^2 - \left(\frac{\mu_1}{m_1}\delta_{12} + \frac{\mu_2}{m_2}\delta_{21}\right)N_1 N_2 - \frac{\mu_2}{m_2}\delta_{22}N_2^2 \\ &= D(S^o - S) - \frac{\mu_1}{m_1}\delta_{11}\left(N_1 - \frac{\gamma_1 m_1}{2\delta_{11}}\right)^2 - \frac{\mu_2}{m_1}\delta_{22}\left(N_2 - \frac{\gamma_2 m_2}{2\delta_{22}}\right)^2 \\ &\quad - \left(\frac{\mu_1}{m_1}\delta_{12} + \frac{\mu_2}{m_2}\delta_{21}\right)N_1 N_2 + \frac{\mu_1\gamma_1^2 m_1}{4\delta_{11}} + \frac{\mu_2\gamma_2^2 m_2}{4\delta_{22}}.\end{aligned} \tag{2.4}$$

Thus, outside the region of the positive cone bounded by the three positive coordinate planes and by the surface

$$\begin{aligned}DS &+ \frac{\mu_1}{m_1}\delta_{11}\left(N_1 - \frac{\gamma_1 m_1}{2\delta_{11}}\right)^2 + \frac{\mu_2}{m_1}\delta_{22}\left(N_2 - \frac{\gamma_2 m_2}{2\delta_{22}}\right)^2 \\ &+ \left(\frac{\mu_1}{m_1}\delta_{12} + \frac{\mu_2}{m_2}\delta_{21}\right)N_1 N_2 = DS^0 + \frac{\mu_1\gamma_1^2 m_1}{4\delta_{11}} + \frac{\mu_2\gamma_2^2 m_2}{4\delta_{22}},\end{aligned}$$

$\dot{V}$ is negative and hence the boundedness follows. For the rest cases $\gamma_1\gamma_2 \leq 0$, similar argument can be used. This completes the proof. □

Remark 2.2. In Theorem 2.5 in [11], the boundedness of the solutions is guaranteed under the condition $(D + D_i)/m_i > b_i D_i/\mu_i$ for $i = 1,2$. Obviously, Theorem 2.1 improves Theorem 2.5 in [11].

We note that $E_0 = (S^0, 0, 0)$ is always an equilibrium for the system (2.1). The following result about the stability of E_0 was proved in [11].

Theorem 2.3. (Theorem 2.3 in [11]) *Suppose that*

$$m_i p(S^o) < D + D_i, \quad i = 1,2 \tag{2.4}$$

and

$$m_i b_i < \mu_i, \quad i = 1, 2. \tag{2.5}$$

Then $\lim_{t\to\infty}(S(t), N_1(t), N_2(t)) = E_0$.

In fact, the condition (2.4) in Theorem 2.3 is also necessary.

Theorem 2.4. E_0 *is local asymptotical stable if and only if (2.4) holds.*

Proof. The linearized system of (2.1) at E_0 is given by

$$\begin{aligned} \dot{x}(t) &= -Dx + [-\mu p(S^0) + b_1 D_1]y_1 + [-\mu p(S^0) + b_2 D_2]y_2 \\ \dot{y}_1(t) &= [-(D + D_1) + m_1 p(S^0)]y_1 \\ \dot{y}_2(t) &= [-(D + D_2) + m_2 p(S^0)]y_2. \end{aligned} \tag{2.6}$$

From (2.6), one can easily obtain the conclusion. □

Notice that inequalities (2.4) and (2.5) can be rewritten as

$$S_0 < \min\{p^{-1}\left(\frac{D + D_1}{m_1}\right),\ p^{-1}\left(\frac{D + D_2}{m_2}\right)\} \tag{2.4a}$$

and

$$b_i < \frac{\mu_i}{m_i}, \quad i = 1, 2. \tag{2.5a}$$

Inequaliy (2.4a) means that the nutrient input concentration S^0 is very small, inequality (2.5a) means that the nutrient recycling rate b_i of the i th-competitor is less than the ratio of its maximal uptake rate and maximal conversion rate. Thus, the above results indicate that if there is no enough nutrient input and the nutrient recycling rates are relatively low, then no population can survive indefinitely.

Giving more detailed analysis on the proof of Theorem 2.4 in [11], we can obtain the following necessary and sufficient condition on the existence of a unique non-negative equilibrium $\hat{E}_i$ in the $S - N_i$ plane, $i = 1$ or 2, which is an improvement of Theorem 2.4 in [11].

Theorem 2.5. *System (2.1) has a unique non-negative equilibrium* $\hat{E}_i$ *with* $\hat{S}_i < S^0$ *in the* $S - N_i$ *plane if and only if*

$$p(S^0) > \frac{D + D_i}{m_i} \qquad \text{for} \quad i = 1 \quad \text{or} \quad 2. \tag{2.7}$$

Proof. As in the proof of Theorem 2.4 in [11], let $\hat{S}_i$ and $\hat{N}_i$ be the coordinate components of $\hat{E}_i$ in the $S-N_i$ plane and denote $\alpha_i = D + D_i$ and $\beta_i = b_i D_i$. Then $\hat{S}_i$ and $\hat{N}_i$ must be the roots of the following equations:

$$\hat{N}_i = \frac{m_i}{\delta_{ii}}[p(\hat{S}_i) - \frac{\alpha_i}{m_i}], \tag{2.8}$$

$$\hat{S}_i = S^0 - \frac{m_i\mu_i}{D\delta_{ii}}[p(\hat{S}_i) - \frac{\alpha_i}{m_i}][p(\hat{S}_i) - \frac{\beta_i}{\mu_i}]. \tag{2.9}$$

Define two functions ϕ and ψ on $[0, S^0 + T]$ by

$$\phi(S) := \frac{1}{2}\left[\frac{\alpha_i}{m_i} + \frac{\beta_i}{\mu_i} + \left(\left(\frac{\alpha_i}{m_i} - \frac{\beta_i}{\mu_i}\right)^2 + \frac{4D\delta_{ii}(S^0 - S)}{m_i\mu_i}\right)^{1/2}\right],$$

$$\psi(S) := \frac{1}{2}\left[\frac{\alpha_i}{m_i} + \frac{\beta_i}{\mu_i} - \left(\left(\frac{\alpha_i}{m_i} - \frac{\beta_i}{\mu_i}\right)^2 + \frac{4D\delta_{ii}(S^0 - S)}{m_i\mu_i}\right)^{1/2}\right],$$

where $T = m_i\mu_i(\alpha_i/m_i - \beta_i/\mu_i)^2/4D\delta_{ii}$. Then $\hat{S}_i$ is a root of (2.9) if and only if

$$p(\hat{S}_i) = \phi(\hat{S}_i) \qquad \text{or} \qquad p(\hat{S}_i) = \psi(\hat{S}_i). \tag{2.10}$$

Sufficiency: We first prove that, under the condition (2.7), system (2.1) has a unique nonnegative equilibrium $\hat{E}_i$ with $\hat{S}_i < S^0$. Indeed, $\psi(S)$ is increasing on $[0, S^0 + T]$ and

$$\psi(S^0 + T) = \frac{1}{2}[\frac{\alpha_i}{m_i} + \frac{\beta_i}{\mu_i}].$$

We consider the following two cases.

Case 1: $\alpha_i/m_i > \beta_i/\mu_i$. Following the argument of proof of Theorem 2.4 in [11], one can derive $\hat{N}_i < 0$, which is impossible.

Case 2: $\alpha_i/m_i \leq \beta_i/\mu_i$. Suppose $\hat{N}_i > 0$ and there exists $\hat{S}_i < S^0$ such that $p(\hat{S}_i) = \psi(\hat{S}_i)$. Then it follows from (2.8) that $p(\hat{S}_i) > \alpha_i/m_i$, which implies

$$\frac{\beta_i}{\mu_i} - \frac{\alpha_i}{\mu_i} > \left[\left(\frac{\beta_i}{\mu_i} - \frac{\alpha_i}{\mu_i}\right)^2 + \frac{4D\delta_{ii}(S^o - \hat{S}_i)}{m_i\mu_i}\right]^{1/2}.$$

Squaring both sides in the above inequality, one can see that $\hat{S}_i > S^0$, which contradicts $\hat{S}_i < S^0$. Hence $\hat{S}_i$ must satisfy $p(\hat{S}_i) = \phi(\hat{S}_i)$.

Since $\phi(S)$ is decreasing and $\phi(0) > 0 = p(0)$ and $\phi(S^0) = \alpha_i/m_i < p(S^0)$ by (2.7), there must be a unique $\hat{S}_i \in (0, S^0)$ such that $p(\hat{S}_i) = \phi(\hat{S}_i)$ and consequently, $\hat{N}_i > 0$. Therefore the sufficiency is proved.

Necessary: We now prove that, if (2.7) does not hold, then (2.1) does not have nonnegative equilibrium $\hat{E}_i$ with $\hat{S}_i < S^0$ in the $S - N_i$ plane. In fact, if $p(S^0) \le \alpha_i/m_i$, then $p(\hat{S}_i) < p(S^0) \le \alpha_i/m_i$ and hence, from (2.8) $\hat{N}_i < 0$. This leads to a contradiction. The proof is completed. □

Remark 2.6. Theorem 2.4 in [11] gives sufficient conditions for the existence of $\hat{E}_i$ under an addition condition

$$\frac{D + D_i}{m_i} > \frac{b_i D_i}{\mu_i} \qquad (i = 1.2).$$

Obviously Theorem 2.5 improves Theorem 2.4 in [11].

The stability of $\hat{E}_i$ was studied in [11]. The following theorem improves the conditions in [11] and can be proved by using the similar argument in proving Theorem 2.8.

Theorem 2.7. *Assume that system (2.1) has a positive equilibrium* $\hat{E}_i$ *on* $S - N_i$ *plane. If* $\mu_i p(\hat{S}_i) > b_i D_i$ *, then the positive equilibrium* $\hat{E}_i$ *of (2.1) is globally asymptotically stable in the* $S - N_i$ *plane.*

Notice that condition (2.7) can be rewritten as $S^0 > p^{-1}((D + D_i)/m_i)$ for $i = 1, 2$ and $\mu_i p(\hat{S}_i)$ represents the nutrient uptake rate of the i th-competitor. Thus, Theorems 2.6 and 2.7 demonstrate that if there is enough nutrient input, then either population can live on the nutrient in the absence of the other, provided it uptakes nutrient sufficiently.

In [11], Freedman and Xu also studied the persistence of system (2.1). Then, under persistence and boundedness, the ω limit set of (2.1) may contain positive equilibria or possibly, periodic solutions. In the following, we intend to study the global stability of the positive equilibrium of (2.1) if it exists.

Let $E^* = (S^*, N_1^*, N_2^*)$ be a positive equilibrium of (2.1). Define

$$x = S - S^*, \qquad y_i = \ln(N_i/N_i^*) \qquad (i = 1, 2), \tag{2.10}$$

that is

$$S = x + S^*, \qquad N_i = N_i^* e^{y_i} \qquad (i = 1, 2).$$

Also, denote

$$\xi(x(t)) = p(x(t) + S^*) - p(S^*). \tag{2.11}$$

Then

$$-S^* < x < +\infty, \quad -\infty < y_i < +\infty, \quad i = 1, 2, \quad -p(S^*) \le \xi(x(t)) < 1 - p(S^*)$$

and $x\xi(x) > 0$ for $x \neq 0$, $x\xi(x) = 0$ if and only if $x = 0$. It follows from (2.10) and (2.1) that

$$\begin{aligned}
\dot{x} &= D[S^0 - x - S^*] - (\mu_1 N_1^* e^{y_1} + \mu_2 N_2^* e^{y_2}) p(x + S^*) \\
&\quad + b_1 D_1 N_1^* e^{y_1} + b_2 D_2 N_2^* e^{y_2} \\
&= -Dx - \mu_1 N_1^* [e^{y_1} p(x + S^*) - p(S^*)] - \mu_2 N_2^* [e^{y_2} p(x + S^*) - p(S^*)] \\
&\quad + b_1 D_1 N_1^* [e^{y_1} - 1] + b_2 D_2 N_2^* [e^{y_2} - 1] \\
&= -Dx - \mu_1 N_1^* \Big(e^{y_1} [p(x + S^*) - p(S^*)] + p(S^*)[e^{y_1} - 1] \Big) \\
&\quad - \mu_2 N_2^* \Big(e^{y_2} [p(x + S^*) - p(S^*)] + p(S^*)[e^{y_2} - 1] \Big) \\
&\quad + b_1 D_1 N_1^* [e^{y_1} - 1] + b_2 D_2 N_2^* [e^{y_2} - 1], \\
\dot{y}_1 &= -(D + D_1) + m_1 p(x + S^*) - [\delta_{11} N_1^* e^{y_1} + \delta_{12} N_2^* e^{y_2}] \\
&= m_1 [p(x + S^*) - p(S^*)] - (\delta_{11} N_1^* [e^{y_1} - 1] + \delta_{12} N_2^* [e^{y_2} - 1]), \\
\dot{y}_2 &= -(D + D_2) + m_2 p(x + S^*) - [\delta_{21} N_1^* e^{y_1} + \delta_{22} N_2^* e^{y_2}] \\
&= m_2 [p(x + S^*) - p(S^*)] - (\delta_{21} N_1^* [e^{y_1} - 1] + \delta_{22} N_2^* [e^{y_2} - 1]).
\end{aligned}$$

By using the function $\xi(x(t))$, we can rewrite the above equations as follows:

$$\begin{aligned}
\dot{x}(t) &= -Dx(t) - \mu_1 N_1^* e^{y_1(t)} \xi(x(t)) - \mu_2 N_2^* e^{y_2} \xi(x(t)) \\
&\quad - N_1^* [\mu_1 p(S^*) - b_1 D_1][e^{y_1(t)} - 1] - N_2^* [\mu_2 p(S^*) - b_2 D_2][e^{y_2(t)} - 1] \\
\dot{y}_1(t) &= m_1 \xi(x(t)) - (\delta_{11} N_1^* [e^{y_1(t)} - 1] + \delta_{12} N_2^* [e^{y_2(t)} - 1]) \\
\dot{y}_2(t) &= m_2 \xi(x(t)) - (\delta_{21} N_1^* [e^{y_1(t)} - 1] + \delta_{22} N_2^* [e^{y_2(t)} - 1]).
\end{aligned} \tag{2.12}$$

Let $z(t) = (x(t), y_1(t), y_2(t))$ be the solutions of (2.12) with initial values $x(0) > -S^*$, $y_i(0) \in R$, $i = 1, 2$. Define

$$V_i(z(t)) = N_i^* \int_0^{y_i} [e^u - 1]\, du \quad (i = 1, 2), \qquad V_3(z(t)) = \int_0^x \xi(u)\, du. \tag{2.13}$$

Then $V_i > 0$ $(i = 1, 2)$. Along the solutions of (2.12), we have

$$\dot{V}_1(z(t)) = N_1^* [e^{y_1(t)} - 1] \dot{y}_1(t)$$

$$
\begin{aligned}
&= m_1 N_1^* \xi(x(t))[e^{y_1(t)} - 1] - (\delta_{11}(N_1^*)^2[e^{y_1(t)} - 1]^2 \\
&\quad + \delta_{12} N_1^* N_2^* [e^{y_1(t)} - 1][e^{y_2(t)} - 1]), \qquad (2.14) \\
\dot{V}_2(z(t)) &= N_2^*[e^{y_2(t)} - 1]\dot{y}_2(t) \\
&= m_2 N_2^* \xi(x(t))[e^{y_2(t)} - 1] - (\delta_{21} N_1^* N_2^* [e^{y_1(t)} - 1][e^{y_2(t)} - 1] \\
&\quad + \delta_{22}(N_2^*)^2[e^{y_2(t)} - 1]^2), \qquad (2.15) \\
\dot{V}_3(z(t)) &= \xi(x(t))\dot{x}(t) \\
&= -Dx(t)\xi(x(t)) - \mu_1 N_1^* e^{y_1(t)} \xi^2(x(t)) - \mu_2 N_2^* e^{y_2(t)} \xi^2(x(t)) \\
&\quad - N_1^*[\mu_1 p(S^*) - b_1 D_1]\xi(x(t))[e^{y_1(t)} - 1] \\
&\quad - N_2^*[\mu_2 p(S^*) - b_2 D_2]\xi(x(t))[e^{y_2(t)} - 1]. \qquad (2.16)
\end{aligned}
$$

Assume

$$\mu_i p(S^*) > b_i D_i \qquad (i = 1, 2). \qquad (2.17)$$

One can select $\alpha_i > 0\,(i = 1, 2)$ such that

$$\alpha_i = \frac{1}{m_i}[\mu_i p(S^*) - b_i D_i] \qquad (i = 1, 2).$$

Now define a Liapunov function as follows:

$$V(z(t)) = \alpha_1 V_1(z(t)) + \alpha_2 V_2(z(t)) + V_3(z(t)). \qquad (2.18)$$

Thus,

$$
\begin{aligned}
\dot{V}(z(t)) &= -Dx(t)\xi(x(t)) - \mu_1 N_1(t)\xi^2(x(t)) - \mu_2 N_2(t)\xi^2(x(t)) \\
&\quad - \alpha_1(\delta_{11}(N_1^*)^2[e^{y_1(t)} - 1]^2 + \delta_{12} N_1^* N_2^*[e^{y_1(t)} - 1][e^{y_2(t)} - 1]) \\
&\quad - \alpha_2(\delta_{21} N_1^* N_2^*[e^{y_1(t)} - 1][e^{y_2(t)} - 1] + \delta_{22}(N_2^*)^2[e^{y_2(t)} - 1]^2) \\
&= -Dx(t)\xi(x(t)) - \mu_1 N_1(t)\xi^2(x(t)) - \mu_2 N_2(t)\xi^2(x(t)) \\
&\quad - \alpha_1(\delta_{11}[N_1(t) - N_1^*]^2 + \delta_{12}[N_1(t) - N_1^*][N_2(t) - N_2^*]) \\
&\quad - \alpha_2(\delta_{21}[N_1(t) - N_1^*][N_2(t) - N_2^*] + \delta_{22}[N_2(t) - N_2^*]^2) \\
&= -Dx(t)\xi(x(t)) - \mu_1 N_1(t)\xi^2(x(t)) - \mu_2 N_2(t)\xi^2(x(t)) - N(t)ABN^T(t), \qquad (2.19)
\end{aligned}
$$

in which

$$N(t) = (N_1(t) - N_1^*, N_2(t) - N_2^*), \qquad A = diag(\alpha_1, \alpha_2) \qquad B = (\delta_{ij})_{2\times 2}.$$

Based on the above analysis, we conclude the following result on the global stability of the positive equilibrium of (2.1).

Theorem 2.8. *Assume that*

(i) *system (2.1) has a positive equilibrium* $E^* = (S^*, N_1^*, N_2^*)$;

(ii) $\mu_i p(S^*) > b_i D_i$ *for* $i = 1, 2$;

(iii) *the matrix* $B = (\delta_{ij})_{2\times 2}$ *is semi-positive definite.*

Then E^* *of (2.1) is globally asymptotically stable.*

3. Competition Models with Delayed Nutrient Recycling

In this section, we assume that there is a distributed delay in the nutrient recycling process. We also assume that the competing populations are sufficiently similar in their uptake of nutrient so that the resultant delays are the same. Consider following delay equations

$$\begin{aligned} \dot{S} &= D(S^0 - S) - (\mu_1 N_1 + \mu_2 N_2)p(S) \\ &\quad + \int_0^\infty F(u)[b_1 D_1 N_1(t-u) + b_2 D_2 N_2(t-u)]\,du \\ \dot{N}_1 &= N_1[-(D + D_1) + m_1 p(S) - (\delta_{11} N_1 + \delta_{12} N_2)] \\ \dot{N}_2 &= N_2[-(D + D_2) + m_2 p(S) - (\delta_{21} N_1 + \delta_{22} N_2)], \end{aligned} \tag{3.1}$$

in which the kernal function $F : R \to R^+$ is continuous and satisfies (1.3). Solutions of system (3.1) exist for all $t \geq 0$ under the initial conditions

$$S(0) = S_0 > 0, \quad N_i(u) = \phi_i(u), \;\; i = 1, 2, \quad u \in (-\infty, 0],$$

where $\phi_i \; (i = 1, 2)$ are positive linear continuous functions on $(-\infty, 0]$.

Following the argument in the proof of Theorem 2.1 in this paper and Theorem 4.1 in [11], one can derive the boundedness of the solutions of (3.1).

Theorem 3.1. *All solutions of system (3.1) are bounded.*

Note that system (3.1) always has an equilibrium of the form $E_0 = (S^0, 0, 0)$. Following the arguments in Theorem 2.1 and Corollary 2.2 in [11], we can prove the following convergence result on the equilibrium E_0.

Theorem 3.2. *(a) Let the ineqality*

$$m_i < D + D_i \tag{3.2}$$

hold, where $i = 1$ *or* 2. *Then* $\lim_{t\to\infty} N_i(t) = 0$.

(b) If (3.2) holds for $i = 1$ *and* 2, *then* $\lim_{t\to\infty}(S(t), N_1(t), N_2(t)) = E_0$.

In the following, we generalize Theorem 2.3 in [11] to the delay model (3.1).

Theorem 3.3. *Assume* $\hat{D}T_f < 1$ *and*

$$m_i b_i < \mu_i, \qquad m_i p(\tilde{S}) < D + D_i \qquad (i = 1, 2), \tag{3.3}$$

where $\hat{D} = \max\{b_1 m_1 D_1/\mu_1, b_2 m_2 D_2/\mu_2\}$ *and* $\tilde{S} = S^0/(1 - \hat{D}T_f)$. *Then*

$$\lim_{t\to\infty}(S(t), N_1(t), N_2(t)) = E_0.$$

Proof. Let

$$Z_1(t) = m_1 m_2 S(t) + m_2 \mu_1 N_1(t) + m_1 \mu_2 N_2(t). \tag{3.4}$$

Then, along the solutions of (3.1), we have

$$\begin{aligned}
\dot{Z}_1(t) &= m_1 m_2 \dot{S}(t) + m_2 \mu_1 \dot{N}_1(t) + m_1 \mu_2 \dot{N}_2(t) \\
&= m_1 m_2 \Big[D(S^0 - S(t)) - (\mu_1 N_1 + \mu_2 N_2) p(S(t)) \\
&\quad + \int_0^\infty F(u)[b_1 D_1 N_1(t-u) + b_2 D_2 N_2(t-u)]\, ds \Big] \\
&\quad + m_2 \mu_1 N_1(t)[-(D + D_1) + m_1 p(S(t)) - (\delta_{11} N_1(t) + \delta_{12} N_2(t))] \\
&\quad + m_1 \mu_2 N_2(t)[-(D + D_2) + m_2 p(S(t)) - (\delta_{21} N_1(t) + \delta_{22} N_2(t))] \\
&= m_1 m_2 D S^0 - D Z_1(t) \\
&\quad + m_1 m_2 \int_0^\infty F(u)[b_1 D_1 N_1(t-u) + b_2 D_2 N_2(t-u)]\, du \\
&\quad - m_2 \mu_1 D_1 N_1(t) - m_2 \mu_1 [\delta_{11} N_1(t) + \delta_{12} N_2(t)] N_1(t) \\
&\quad - m_1 \mu_2 D_2 N_2(t) - m_1 \mu_2 [\delta_{21} N_1(t) + \delta_{22} N_2(t)] N_2(t).
\end{aligned} \tag{3.5}$$

Define

$$Z_2(t) = m_1 m_2 \int_0^\infty F(u) \int_{t-u}^u [b_1 D_1 N_1(v) + b_2 D_2 N_2(v)] dv du \tag{3.6}$$

and

$$Z(t) = Z_1(t) + Z_2(t). \tag{3.7}$$

The, from (3.5)-(3.7) and by the nonnegativity of Z_2, we have

$$\begin{aligned}\dot{Z}(t) &\leq -DZ_1(t) + m_1m_2DS^0 + m_2D_1(m_1b_1-\mu_1)N_1(t) + m_1D_2(m_2b_2-\mu_2)N_2(t)\\ &\leq -DZ(t) + m_1m_2DS^0 + m_2D_1(m_1b_1-\mu_1)N_1(t) + m_1D_2(m_2b_2-\mu_2)N_2(t)\\ &\quad + m_1m_2D\int_0^\infty F(u)\int_{t-u}^u [b_1D_1N_1(v)+b_2D_2N_2(v)]\,dv\,du\\ &\leq -DZ(t) + m_1m_2DS^0 + m_2D_1(m_1b_1-\mu_1)N_1(t) + m_1D_2(m_2b_2-\mu_2)N_2(t)\\ &\quad + D\hat{D}\int_0^\infty F(u)\int_{t-u}^u Z(v)\,dv\,du, \qquad (3.8)\end{aligned}$$

where $\hat{D} = \max\{b_1m_1D_1/\mu_1, b_2m_2D_2/\mu_2\}$. By assumption (3.3), it then follows from (3.8) that

$$\dot{Z}(t) \leq -DZ(t) + m_1m_2DS^0 + D\hat{D}\int_0^\infty F(u)\int_{t-u}^u Z(v)\,dv\,du. \qquad (3.9)$$

Multiplying e^{Dt} on both sides of (3.9) and then integrating over $[0,t]\,(t\geq 0)$, we have

$$Z(t)e^{Dt} \leq Z(0) + m_1m_2S^o[e^{Dt}-1] + D\hat{D}\int_0^t e^{Dr}\int_0^\infty F(u)\int_{r-u}^r Z(v)\,dv\,du\,dr. \qquad (3.10)$$

Define

$$\|Z(t)\| = \sup_{-\infty<u\leq t} Z(u). \qquad (3.11)$$

Then (3.10) leads to

$$\begin{aligned}Z(t)e^{Dt} &\leq Z(0) + m_1m_2S^0[e^{Dt}-1] + D\hat{D}\|Z(t)\|\int_0^t e^{Dr}\int_0^\infty F(u)\int_{r-u}^r dv\,du\,dr\\ &= Z(0) + m_1m_2S^0[e^{Dt}-1] + D\hat{D}\left(\int_0^t e^{Dr}\,dr\right)\|Z(t)\|\int_0^\infty uF(u)\,du\\ &= Z(0) + m_1m_2S^0[e^{Dt}-1] + \hat{D}T_f[e^{Dt}-1]\|Z(t)\|\end{aligned}$$

and hence

$$\begin{aligned}\|Z(t)\|e^{Dt} &= \sup_{-\infty<u\leq t} Z(u)e^{Du}\\ &\leq Z(0) + m_1m_2S^0[e^{Dt}-1] + \hat{D}T_f[e^{Dt}-1]\|Z(t)\|.\end{aligned}$$

That is,

$$\|Z(t)\| \leq Z(0)e^{-Dt} + m_1m_2S^0[1-e^{-Dt}] + \hat{D}T_f[1-e^{-Dt}]\|Z(t)\|. \qquad (3.12)$$

Since $\hat{D}T_f < 1$, there exists a T_1 such that

$$L(t) \equiv \hat{D}T_f[1 - e^{-Dt}] < 1 \qquad \text{for} \qquad t \geq T_1. \tag{3.13}$$

By (3.12) and (3.13), we obtain

$$\begin{aligned} \|Z(t)\| &\leq \frac{1}{1 - L(t)}\left[Z(0)e^{-Dt} + m_1 m_2 S^0[1 - e^{-Dt}]\right] \\ &\to \frac{m_1 m_2 S^0}{1 - \hat{D}T_f} = m_1 m_2 \tilde{S} \qquad \text{as} \qquad t \to \infty, \end{aligned} \tag{3.14}$$

which, together with (3.4) and (3.7), implies that

$$\lim_{t\to\infty} S(t) \leq \tilde{S} = \frac{S^0}{1 - \hat{D}T_f}.$$

By assumption (3.3), there exits $T_2 > 0$ such that

$$m_i p(S(t)) < D + D_i \qquad (i = 1, 2), \quad t \geq T_2.$$

Then $\dot{N}_i(t) \leq 0 (i = 1, 2)$ for $t \geq T = \max\{T_1, T_2\}$, which implies that $\lim_{t\to\infty} N_i(t) = 0 (i = 1, 2)$ and in turn implies that $\lim_{t\to\infty} S(t) = S^0$. □

Remark 3.4. When the kernel $F(u)$ is a delta function, system (3.1) becomes to the ODE model (2.1) and Theorem 3.3 reduces to Theorem 2.3 in [11].

From the Remark in Section 4 in [11], we can see the following estimates for the upper bound of $N_i(t)(i = 1, 2)$.

Lemma 3.5. *If* $D + D_i < m_i (i = 1, 2)$, *then*

$$\limsup_{t\to\infty} N_i(t) \leq M_i = \frac{m_i - (D + D_i)}{\delta_{ii}}, \quad i = 1, 2. \tag{3.15}$$

Similar to the analysis in Section 2, we know that the system (3.1) has a unique non-negative equilibrium $\hat{E}_i$ with $\hat{S}_i < S^0$ in the $S - N_i$ plane $(i = 1$ or $2)$ if (2.7) holds true. In the following, we study the stability of $\hat{E}_i$.

Theorem 3.6. *Assume that*

(i) *(2.7) holds;*

(ii) $b_i D_i < \mu_i p(\hat{S}_i)$;

(iii) $T_f < \infty$ and $T_f^* \equiv (1/d_i)\int_0^\infty F(s)[e^{d_i s} - 1]\,ds < \infty$ *with* $d_i = (D + D_i) + \delta_{ii} M_i$;

(iv) $b_i D_i[(m_i + \delta_{ii}\hat{N}_i)T_f^* + m_i T_f]/2 < \mu_i$;

(v) *either* $\delta_{ii} = 0$ or $\hat{N}_i[\mu_i p(\hat{N}_i) - b_i D_i]/m_i > b_i D_i T_f M_i/2$.

Then $\hat{E}_i$ *is global asymptotically asymptotically stable in the* $S - N_i$ *plane.*

Proof. Consider the subsystem

$$\begin{aligned} \dot{S} &= D(S^0 - S) - \mu_i N_i + b_i D_i \int_0^\infty F(u) N_i(t-u)ds \\ \dot{N}_i &= N_i[-(D + D_i) + m_i p(S) - \delta_{ii} N_i]. \end{aligned} \tag{3.17}$$

Let

$$x = S - \hat{S}_i, \qquad y_i = \ell n \frac{N_i}{\hat{N}_i}.$$

Then system (3.17) can be written as

$$\begin{aligned} \dot{x}(t) &= -Dx(t) - \mu_i \hat{N}_i e^{y_i(t)}\xi(x) - \mu_i \hat{N}_i p(\hat{S}_i)[e^{y_i(t)} - 1] \\ &\quad + b_i D_i \hat{N}_i \int_0^\infty F(s)[e^{y_i(t-s)} - 1]\,ds \\ \dot{y}_i(t) &= m_i \xi(x(t)) - \delta_{ii}\hat{N}_i[e^{y_i(t)} - 1], \end{aligned} \tag{3.18}$$

where $\xi(x(t)) = p(x(t) + \hat{S}_i) - p(\hat{S}_i)$. Define

$$V_1(x(t)) = \int_0^x \xi(u)\,du, \qquad W_1(y_i(t)) = \int_0^{y_i} [e^u - 1]\,du. \tag{3.19}$$

Then

$$\begin{aligned} \dot{W}_1 &= [e^{y_i(t)} - 1]\dot{y}_i(t) \\ &= m_i \xi(x(t))[e^{y_i(t)} - 1] - \delta_{ii}\hat{N}_i[e^{y_i(t)} - 1]^2, \\ \dot{V}_1 &= -Dx(t)\xi(x(t)) - \mu_i \hat{N}_i e^{y_i(t)}\xi^2(x(t)) - \mu_i \hat{N}_i p(\hat{S}_i)\xi(x(t))[e^{y_i(t)} - 1] \\ &\quad + b_i D_i \hat{N}_i \xi(x(t)) \int_0^\infty F(s)[e^{y_i(t-s)} - 1]\,ds \\ &= -Dx(t)\xi(x(t)) - \mu_i \hat{N}_i e^{y_i(t)}\xi^2(x(t)) - \hat{N}_i[\mu_i p(\hat{S}_i) - b_i D_i]\xi(x(t))[e^{y_i(t)} - 1] \end{aligned}$$

$$
\begin{aligned}
&- b_iD_i\hat{N}_i\xi(x(t))\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}\dot{y}_i(u)\,du\,ds\\
&= -Dx(t)\xi(x(t)) - \mu_i\hat{N}_ie^{y_i(t)}\xi^2(x(t)) - \hat{N}_i[\mu_ip(\hat{S}_i) - b_iD_i]\xi(x(t))[e^{y_i(t)} - 1]\\
&\quad - b_iD_i\hat{N}_i\xi(x(t))\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}\Big(m_i\xi(x(u)) - \delta_{ii}\hat{N}_i[e^{y_i(u)} - 1]\Big)\,du\,ds\\
&\le -Dx(t)\xi(x(t)) - \mu_i\hat{N}_ie^{y_i(t)}\xi^2(x(t)) - \hat{N}_i[\mu_ip(\hat{S}_i) - b_iD_i]\xi(x(t))[e^{y_i(t)} - 1]\\
&\quad + \frac{b_iD_i\hat{N}_i}{2}\Bigg[m_i\Big(\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}\,du\,ds\Big)\xi^2(x(t))\\
&\quad + m_i\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}\xi^2(x(u))\,du\,ds\\
&\quad + \delta_{ii}\hat{N}_i\Big(\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}\,du\,ds\Big)\xi^2(x(t))\\
&\quad + \delta_{ii}\hat{N}_i\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}[e^{y_i(u)} - 1]^2\,du\,ds\Bigg].
\end{aligned}
$$

Next, we define

$$
\begin{aligned}
V_2(t) = \frac{b_iD_i\hat{N}_i}{2}\Bigg[&m_i\int_0^\infty F(s)\int_{t-s}^t\int_v^t e^{y_i(u)}\xi^2(x(u))\,du\,dv\,ds\\
&+ \delta_{ii}\hat{N}_i\int_0^\infty F(s)\int_{t-s}^t\int_v^t e^{y_i(u)}[e^{y_i(u)} - 1]^2\,du\,dv\,ds\Bigg]
\end{aligned}
\tag{3.20}
$$

and

$$
V_3(t) = V_1(t) + V_2(t). \tag{3.21}
$$

Thus,

$$
\begin{aligned}
\dot{V}_3 \le{}& -Dx(t)\xi(x(t)) - \mu_i\hat{N}_ie^{y_i(t)}\xi^2(x(t)) - \hat{N}_i[\mu_ip(\hat{S}_i) - b_iD_i]\xi(x(t))[e^{y_i(t)} - 1]\\
&+ \frac{b_iD_i\hat{N}_i}{2}\Bigg\{\Bigg[(m_i + \delta_{ii}\hat{N}_i)\Big(\int_0^\infty F(s)\int_{t-s}^t e^{y_i(u)}\,du\,ds\Big) + m_iT_fe^{y_i(t)}\Bigg]\xi^2(x(t))\\
&+ \delta_{ii}\hat{N}_iT_fe^{y_i(t)}[e^{y_i(t)} - 1]^2\Bigg\}.
\end{aligned}
\tag{3.22}
$$

Choose $\alpha > 0$ such that

$$
\alpha\hat{N}_i[\mu_ip(\hat{S}_i) - b_iD_i] = m_i
$$

and define

$$
V(t) = \alpha V_3(t) + W_1(t). \tag{3.23}
$$

We have

$$
\begin{aligned}
\dot V \le & -\delta_{ii}\hat N_i[e^{y_i}-1]^2 \\
& + \alpha\Big\{ - Dx\xi(x) - \mu_i N_i(t)\xi^2(x) \\
& + \frac{b_iD_i}{2}\Big[(m_i+\delta_{ii}\hat N_i)\Big(\int_0^\infty F(s)\int_{t-s}^t N_i(u)\,du\,ds\Big) + m_iT_fN_i(t)\Big]\xi^2(x(t)) \\
& + \delta_{ii}T_fN_i(t)[e^{y_i(t)}-1]^2\Big\}.
\end{aligned} \tag{3.24}
$$

On the other hand, Lemma 3.5 and (3.17) imply that

$$
\dot N_i(t) \ge N_i(t)[-(D+D_i)-\delta_{ii}M_i] = -d_iN_i(t) \quad \text{for all large} \quad t. \tag{3.25}
$$

Integrating (3.25) from s to $t (t > s)$ and using the fact that $N_i(s) \le e^{d_i(t-s)}N_i(t)$, one can obtain from assumption (iii) that

$$
\int_0^\infty F(s)\int_{t-s}^t N_i(u)\,du\,ds \le T_f^* N_i(t).
$$

Hence, by (3.24) and assumptions (iv) and (v), we have

$$
\begin{aligned}
\dot V \le & -\delta_{ii}\hat N_i[e^{y_i}-1]^2 \\
& + \alpha\Big\{ - Dx\xi(x) - \mu_i N_i(t)\xi^2(x) \\
& + \frac{b_iD_i}{2}\Big[(m_i+\delta_{ii}\hat N_i)T_f^* + m_iT_f\Big]N_i(t)\xi^2(x(t)) \\
& + \delta_{ii}T_fM_i[e^{y_i(t)}-1]^2\Big\} \\
< & \ 0.
\end{aligned}
$$

This completes the proof. □

Remark 3.7. The stability of $\hat E_i$ of the system (3.17) has been studied by Beretta and Takeuchi [6]. Our conditions in Theorem 2.5 are different from those in Theorems 4.1 and 4.3 in their paper, in which $\delta_{ii} > 0$ is required to be sufficiently large and is used to control other terms.

The persistence of system (3.1) has been studied by Freedman and Xu [11], which implies that there exists an interior equilibrium. Now we discuss the global stability of the positive equilibrium by applying Liapunov functional method.

Theorem 3.8. *Assume that*

(i) *system (3.1) has a positive equilibrium* $N^* = (S^*, N_1^*, N_2^*)$;

(ii) $D + D_i < m_i,\ b_i D_i < \mu_i p(S_i^*),\quad i = 1, 2;$

(iii) $T_f < \infty,\quad T_i^* = (1/d_i^*)\int_0^\infty F(s)[e^{d_i^* s} - 1]\,ds < \infty$ *with* $d_i^* := (D + D_i) + \sum_{j=1}^2 \delta_{ij} M_j,\ i = 1, 2;$

(iv) $b_i D_i[(m_i + \sum_{j=1}^2 \delta_{ij} N_j^*)T_i^* + m_i T_f]/2 < \mu_i,\ i = 1, 2;$

(v) $B = (b_{ij})_{2\times 2}$ *is semi-positive finite with* $b_{ij} \geq 0$ *defined by*

$$b_{ij} = \begin{cases} \delta_{ii} - \frac{T_f m_i}{2[\mu_i p(S^*) - b_i D_i] N_i^*} \sum_{j=1}^2 b_j D_j \delta_{ji} M_j & \text{if } i = j \\ \delta_{ij} & \text{if } i \neq j. \end{cases} \tag{3.26}$$

Then E_i^* *is global asymptotically stable.*

Proof. By using the same transform in Section 2, system (3.1) can be rewritten as

$$\begin{aligned} \dot{x}(t) &= -Dx(t) - \sum_{i=1}^2 \Big\{ \mu_i N_i^* e^{y_i(t)} \xi(x) \mu_i N_i^* p(S^*)[e^{y_i(t)} - 1] \\ &\quad - b_i D_i N_i^* \int_0^\infty F(s)[e^{y_i(t-s)} - 1]\,ds \Big\} \\ \dot{y}_i(t) &= m_i \xi(x(t)) - \sum_{j=1}^2 \delta_{ij} N_j^* [e^{y_j(t)} - 1] \quad (i = 1, 2). \end{aligned} \tag{3.27}$$

Define

$$V_1(x(t)) = \int_0^x \xi(u)\,du, \qquad W_i(y_i(t)) = N_i^* \int_0^{y_i} [e^u - 1]\,du \qquad (i = 1, 2). \tag{3.28}$$

Then, we have

$$\begin{aligned} \dot{W}_i &= N_i^*[e^{y_i(t)} - 1]\dot{y}_i(t) \\ &= m_i N_i^* \xi(x(t))[e^{y_i(t)} - 1] - \sum_{j=1}^2 \delta_{ij} N_i^* N_j^* [e^{y_i(t)} - 1][e^{y_j(t)} - 1] \end{aligned} \tag{3.29}$$

and

$$
\begin{aligned}
\dot V_1 &= -Dx(t)\xi(x(t)) - \sum_{i=1}^{2}\Big\{\mu_i N_i^* e^{y_i(t)}\xi^2(x(t)) + N_i^*[\mu_i p(\hat S_i) - b_i D_i]\xi(x(t))[e^{y_i(t)}-1] \\
&\quad + b_i D_i N_i^* \xi(x(t))\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}\dot y_i(u)\,du\,ds\Big\} \\
&= -Dx(t)\xi(x(t)) - \sum_{i=1}^{2}\Big\{\mu_i N_i^* e^{y_i(t)}\xi^2(x(t)) + N_i^*[\mu_i p(\hat S_i) - b_i D_i]\xi(x(t))[e^{y_i(t)}-1] \\
&\quad + b_i D_i N_i^* \xi(x(t))\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}\Big(m_i\xi(x(u)) - \sum_{j=1}^{2}\delta_{ij}N_j^*[e^{y_j(u)}-1]\Big)\,du\,ds\Big\} \\
&\le -Dx(t)\xi(x(t)) + \sum_{i=1}^{2}\Big\{-\mu_i N_i^* e^{y_i(t)}\xi^2(x(t)) - N_i^*[\mu_i p(\hat S_i) - b_i D_i]\xi(x(t))[e^{y_i(t)}-1] \\
&\quad + \frac{b_i D_i N_i^*}{2}\Big[m_i\Big(\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}\,du\,ds\Big)\xi^2(x(t)) \\
&\quad + m_i\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}\xi^2(x(u))\,du\,ds \\
&\quad + \sum_{j=1}^{2}\Big[\delta_{ij}N_j^*\Big(\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}\,du\,ds\Big)\xi^2(x(t)) \\
&\quad + \delta_{ij}N_j^*\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}[e^{y_j(u)}-1]^2\,du\,ds\Big]\Big]\Big\}. \qquad (3.30)
\end{aligned}
$$

Next, we define

$$
\begin{aligned}
V_2(t) = \sum_{i=1}^{2}\frac{b_i D_i N_i^*}{2}\Big[& m_i\int_0^\infty F(s)\int_{t-s}^{t}\int_v^t e^{y_i(u)}\xi^2(x(u))\,du\,dv\,ds \\
&+ \sum_{j=1}^{2}\delta_{ij}N_j^*\int_0^\infty F(s)\int_{t-s}^{t}\int_v^t e^{y_i(u)}[e^{y_j(u)}-1]^2\,du\,dv\,ds\Big] \qquad (3.31)
\end{aligned}
$$

and

$$
V_3(t) = V_1(t) + V_2(t). \qquad (3.32)
$$

Notice that $\dot{N}(t) \geq -d_i^* N_i(t)$. Then, by Lemma 3.5 we have from (3.30) - (3.32) that

$$\dot{V}_3 \leq -Dx(t)\xi(x(t)) + \sum_{i=1}^{2}\Bigg\{ -\mu_i N_i^* e^{y_i(t)}\xi^2(x(t)) - N_i^*[\mu_i p(S^*) - b_i D_i]\xi(x(t))[e^{y_i(t)} - 1]$$
$$+ \frac{b_i D_i N_i^*}{2}\Bigg\{\Bigg[(m_i + \sum_{j=1}^{2}\delta_{ij}N_j^*)\Bigg(\int_0^\infty F(s)\int_{t-s}^{t} e^{y_i(u)}\,du\,ds\Bigg) + m_i T_f e^{y_i(t)}\Bigg]\xi^2(x(t))$$
$$+ \sum_{j=1}^{2}\delta_{ij}N_j^* T_f e^{y_i(t)}[e^{y_j(t)} - 1]^2\Bigg\}\Bigg\}$$
$$\leq -Dx(t)\xi(x(t)) + \sum_{i=1}^{2}\Bigg\{ -\mu_i N_i(t)\xi^2(x(t)) - N_i^*[\mu_i p(S^*) - b_i D_i]\xi(x(t))[e^{y_i(t)} - 1]$$
$$+ \frac{b_i D_i}{2}\Bigg\{\Bigg[(m_i + \sum_{j=1}^{2}\delta_{ij}N_j^*)T_i^* + m_i T_f\Bigg]N_i(t)\xi^2(x(t))$$
$$+ \sum_{j=1}^{2}\delta_{ij}N_j^* T_f M_i[e^{y_j(t)} - 1]^2\Bigg\}\Bigg\}. \tag{3.33}$$

Choose $\alpha_i > 0$ such that

$$[\mu_i p(S_i^*) - b_i D_i] = \alpha_i m_i \qquad (i = 1, 2)$$

and define

$$V(t) = V_3(t) + \alpha_1 W_1(t) + \alpha_2 W_2(t). \tag{3.34}$$

It follows from (3.33) and (3.34) that

$$\dot{V} \leq -n(t)ABn^T(t) + \Bigg\{ -Dx\xi(x)$$
$$- \sum_{i=1}^{2}\Bigg[\mu_i - \frac{b_i D_i}{2}\Bigg([m_i + \sum_{j=1}^{2}\delta_{ij}N_j^*]T_i^* + m_i T_f\Bigg)\Bigg]\Bigg\}N_i(t)\xi^2(x(t)), \tag{3.35}$$

where

$$n(t) = (N_1(t) - N_1^*, N_2(t) - N_2^*), \quad A = diag(\alpha_1, \alpha_2), \quad B = (b_{ij})_{2\times 2}$$

with b_{ij} defined in assumption (vi). Thus, by the assumptions, (3.35) implies that $\dot{V} < 0$. Applying the standard theorem on the method of Liapunov functionals (cf, e.g. Theorem 2.5.1 in Kuang [16]), we obtain the global asymptotic stability of E^*. This completes the proof. □

4. n -Species Competition Models

In this section, we generalize the results in the previous sections on two-species competition models to multi-species competition models.

4.1. The Instantaneous Model. First we consider the following n -species competition model with instantaneous nutrient recycling:

$$\begin{aligned} \dot{S} &= D(S^0 - S) - \sum_{i=1}^{n} \mu_i N_i p(S) + \sum_{i=1}^{n} b_i D_i N_i \\ \dot{N}_i &= N_i \Big[-(D + D_i) + m_i p(S) - \sum_{i=1}^{n} \delta_{ij} N_j \Big], \quad i = 1, 2, \dots, n. \end{aligned} \tag{4.1}$$

First we have the following result about the boundedness of solutions to system (4.1).

Theorem 4.1. *If*

$$\frac{D + D_i}{m_i} > \frac{b_i D_i}{\mu_i}, \quad i = 1, 2, \dots, n, \tag{4.2}$$

then all the solutions of (4.1) are bounded.

Proof. Following the argument in [11], choose

$$V(t) = S(t) + \sum_{i=1}^{n} \frac{\mu_i}{m_i} N_i(t). \tag{4.3}$$

Then $V \geq 0$ and $V \to \infty$ when $\|(S(t), N_1(t), \dots, N_n(t))\| \to \infty$. Along solutions of (4.2), we have

$$\dot{V} = D(S^0 - S) - \sum_{i=1}^{n} \mu_i \left(\frac{D + D_i}{m_i} - \frac{b_i D_i}{\mu_i} \right) N_i - \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{\mu_i \delta_{ij}}{m_i} N_i N_j.$$

By the assumptions, the coeffifients of N_i are negative. Thus, $\dot{V} < 0$ outside the region of the positive cone bounded by the positive coordinate planes and by the hypersurface

$$DS + \sum_{i=1}^{n} \mu_i \left(\frac{D + D_i}{m_i} - \frac{b_i D_i}{\mu_i} \right) N_i + \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{\mu_i \delta_{ij}}{m_i} N_i N_j = DS^0.$$

Boundedness follows by Yoshizawa's Theorem (see Yoshizawa [30]). □

Note that $E_0 = (S^0, 0, \dots, 0)$ is always an equilibrium for system (4.1).

Theorem 4.2. *If*

$$m_i p(S^0) < D + D_i, \quad m_i b_i < \mu_i, \quad i = 1, 2, \ldots, n, \tag{4.4}$$

then E_0 *is asymptotically stable.*

Proof. Define a Liapunov function as follows:

$$V(t) = \Big(\prod_{j=1}^{n} m_j\Big) S(t) + \Big(\prod_{\substack{j=1\\ j\neq i}}^{n} m_j\Big)\Big(\sum_{i=1}^{n} \mu_i N_i\Big). \tag{4.5}$$

Then we have

$$\begin{aligned}
\dot V &= -DV(t) + \Big(\prod_{j=1}^{n} m_j\Big) DS^0 \\
&\quad - \Big(\prod_{\substack{j=1\\ j\neq i}}^{n} m_j\Big) \sum_{i=1}^{n} (\mu_i - m_i b_i) D_i N_i - \Big(\prod_{\substack{j=1\\ j\neq i}}^{n} m_j\Big) \sum_{i=1}^{n}\sum_{j=1}^{n} \mu_i \delta_{ij} N_i N_j \\
&\le -DV(t) + \Big(\prod_{j=1}^{n} m_j\Big) DS^0,
\end{aligned}$$

which implies that

$$V(t) \le V(0) e^{-Dt} + \Big(\prod_{j=1}^{n} m_j\Big) S^0.$$

Thus,

$$\lim_{t\to\infty} V(t) = \Big(\prod_{j=1}^{n} m_j\Big) S^0,$$

which in turn implies that

$$\lim_{t\to\infty} S(t) \le S^0. \tag{4.6}$$

Hence, by (4.4), there exists $T > 0$ such that for $t \ge T$, $m_i p(S(t)) \le D + D_i$. By the second equation in system (4.1), we have $\dot N_i(t) \le 0$ for $i = 1, 2, \ldots, n$. Since there are no invariant sets such that $N_i > 0$ is constant, it follows that $\lim_{t\to\infty} N_i(t) = 0$ for $i = 1, 2, \ldots, n$ and then (4.6) implies $\lim_{t\to\infty} S(t) = S^0$. □

Now suppose that there is a positive equilibrium $E^* = (S^*, N_1^*, \ldots, N_n^*)$ for system (4.1). Define

$$x = S - S^*, \quad y_i = \ln(N_i/N_i^*) \quad i = 1, 2, \ldots, n. \tag{4.7}$$

Thus, system (4.1) can be written as follows:

$$
\begin{aligned}
\dot{x}(t) &= -Dx(t) - \sum_{i=1}^{n} \mu_i N_i^* e^{y_i(t)} \xi(x(t)) - \sum_{i=1}^{n} N_i^* [\mu_i p(S^*) - b_i D_i][e^{y_i(t)} - 1] \\
\dot{y}_i(t) &= m_i \xi(x(t)) - \sum_{j=1}^{n} \delta_{ij} N_j^* [e^{y_j(t)} - 1], \quad i = 1, 2, \ldots, n,
\end{aligned}
\tag{4.8}
$$

where $\xi(x(t))$ is defined in (2.11).

Theorem 4.3. *Suppose that*

(i) *system (4.1) has a positive equilibrium* E^*;

(ii) $\mu_i p(S^*) > b_i D_i$ *for* $i = 1, 2, \ldots, n$;

(iii) *the matrix* $B = (\delta_{ij})_{n \times n}$ *is semi-positive definite.*

Then the positive equilibrium E^* *is globally asymptotically stable.*

Proof. Let $z(t) = (x(t), y_1(t), \ldots, y_n(t))$ be the solutions of (4.8) with positive initial values. Set

$$
V_0(z(t)) = \int_0^x \xi(u)\, du, \quad V_i(z(t)) = N_i^* \int_0^{y_i} [e^u - 1]\, du, \quad i = 1, 2, \ldots, n. \tag{4.9}
$$

By assumption (ii), we can choose $\alpha_i > 0\, (i = 1, 2, \ldots, n)$ such that

$$
\alpha_i = \frac{1}{m_i} [\mu_i p(S^*) - b_i D_i], \quad i = 1, 2, \ldots, n.
$$

Now define a Liapunov functional as follows:

$$
V(z(t)) = V_0(z(t)) + \sum_{i=1}^{n} \alpha_i V_i(z(t)). \tag{4.10}
$$

Denote

$$
N(t) = (N_1(t) - N_1^*, \ldots, N_n(t) - N_n^*), \quad A = diag(\alpha_1, \ldots, \alpha_n), \quad B = (\delta_{ij})_{n \times n}.
$$

Then, along the solutions of system (4.8), we obtain

$$
\dot{V}(z(t)) = -Dx(t)\xi(x(t)) - \sum_{i=1}^{n} \mu_i N_i(t) \xi^2(x(t))
$$

$$
\begin{aligned}
&-\sum_{i=1}^{n}\sum_{j=1}^{n}\alpha_i\delta_{ij}N_i^*N_j^*[e^{y_i}-1][e^{y_j}-1] \\
&= -Dx(t)\xi(x(t)) - \sum_{i=1}^{n}\mu_iN_i(t)\xi^2(x(t)) - N(t)ABN^T(t) \\
&< 0
\end{aligned}
$$

followed by assumption (iii). This completes the proof. □

4.2. Delayed Model. Suppose that there is a delay involved in nutrient recycling, that is, we consider the following n -species competition model with delayed nutrient recycling:

$$
\begin{aligned}
\dot{S} &= D(S^0 - S) - \sum_{i=1}^{n}\mu_iN_ip(S) + \int_0^\infty F(u)\Big(\sum_{i=1}^{n}b_iD_iN_i(t-u)\Big)du \\
\dot{N}_i &= N_i\Big[-(D+D_i) + m_ip(S) - \sum_{j=1}^{n}\delta_{ij}N_j\Big], \quad i = 1, 2, \dots, n,
\end{aligned}
\tag{4.11}
$$

in which the kernel F is continuous and satisfies (1.3).

Theorem 4.4. *If (4.2) in Theorem 4.1 is satisfied, then all the solutions of (4.11) are bounded.*

Proof. Choose

$$
V(t) = S(t) + \sum_{i=1}^{n}\frac{\mu_i}{m_i}N_i(t) + \int_0^\infty F(u)\Big[\int_{t-u}^{t}\sum_{i=1}^{n}b_iD_iN_i(v)dv\Big]\,du. \tag{4.12}
$$

Then, along solutions of (4.11), we have

$$
\begin{aligned}
\dot{V} &= D(S^0 - S(t)) - \sum_{i=1}^{n}\mu_iN_i(t)p(S(t)) + \int_0^\infty F(u)\Big(\sum_{i=1}^{n}b_iD_iN_i(t-u)\Big)du \\
&\quad + \sum_{i=1}^{n}\frac{\mu_i}{m_i}N_i(t)\Big[-(D+D_i) + m_ip(S) - \sum_{j=1}^{n}\delta_{ij}N_j\Big] \\
&\quad + \int_0^\infty F(u)\sum_{i=1}^{n}b_iD_i\big(N_i(t) - N_i(t-u)\big)du \\
&= D(S^0 - S(t)) - \sum_{i=1}^{n}\mu_i\Big(\frac{D+D_i}{m_i} - \frac{b_iD_i}{\mu_i}\Big)N_i(t) - \sum_{i=1}^{n}\sum_{j=1}^{n}\frac{\mu_i\delta_{ij}}{m_i}N_iN_j.
\end{aligned}
$$

The rest is same as in the proof of Theorem 4.1. □

Notice that $E_0 = (S^0, 0, \ldots, 0)$ is an equilibruium of system (4.11). Using the same function $V(t)$ defined in (4.5) and following the arguments in Section 3, we can prove the following theorem on the stability of E_0.

Theorem 4.5. *If* $\hat{D}T_f < 1$ *and*

$$m_i b_i < \mu_i, \qquad m_i p(\tilde{S}) < D + D_i, \quad i = 1, 2, \ldots, n,$$

where T_f *is defined in Section 3,* $\hat{D} = \max_{1 \le i \le 2}\{b_i m_i D_i/\mu_i\}$, *and* $\tilde{S} = S^0/(1 - \hat{D}T_f)$. *Then* E_0 *is asymptotically stable.*

If $D + D_i < m_i$, $i = 1, 2, \ldots, n$, following the arguments in Section 4 in Freedman and Xu [11], we can obtain the following upper bound for $N_i(t)$, that is,

$$\limsup_{t \to \infty} N_i(t) \le M_i := \frac{m_i - (D + D_i)}{\delta_{ii}}, \quad i = 1, 2, \ldots, n. \tag{4.13}$$

Finally, by using similar functionals constructed in the proof of Theorem 3.8, we can prove the following theorem.

Theorem 4.6. *Assume that*

(i) *system (4.11) has a positive equilibrium* $E^* = (S^*, N_1^*, \ldots, N_n^*)$;

(ii) $D + D_i < m_i$, $b_i D_i < \mu_i p(S_i^*)$, $i = 1, 2, \ldots, n$;

(iii) $T_f < \infty$, $T_i^* = (1/d_i^*) \int_0^\infty F(s)[e^{d_i^* s} - 1]\, ds < \infty$, $i = 1, 2, \ldots, n$, *where* $d_i^* = (D + D_i) + \sum_{j=1}^n \delta_{ij} M_j$;

(iv) $b_i D_i[(m_i + \sum_{j=1}^n \delta_{ij} N_j^*)T_i^* + m_i T_f]/2 < \mu_i$, $i = 1, 2, \ldots, n$;

(v) *the matrix* $B = (b_{ij})_{n \times n}$ *is semi-positive definite with* $b_{ij} \ge 0$ *defined as follows:*

$$b_{ij} = \begin{cases} \delta_{ii} - \frac{T_f m_i}{2[\mu_i p(S^*) - b_i D_i] N_i^*} \sum_{j=1}^n b_j D_j \delta_{ji} M_j & \text{if } i = j \\ \delta_{ij} & \text{if } i \ne j. \end{cases}$$

Then E^* *is globally asymptotically stable.*

Note that Theorem 4.6 can be regarded as a generalization of Theorem 3.8 on the two-species model (3.1) to the n -species competition model (4.11) as well as a generalization of Theorem 4.3 on the ODE model (4.1) to the delayed model (4.11).

5. Discussion

In this paper, we first considered the chemostat-type two-species competition models with instantaneous or delayed nutrient recycling proposed by Freedman and Xu [11]. Freedman and Xu carried out the equilibrium analysis and derived persistence and extinction crtiria for the competing populations. We studied the global asymptotic stability of the positive equilibrium by using the method of Liapunov functionals. We also generalized the obtained results to n -species competion models with instantaneous and delayed nutrient recycling, respectively.

The models we studied differ from the usual chemostat models in several aspects due to the fact that a chemostat model is refered as a stirred tank with a constant washout rate, where all death is due to washout, there is no direct competition between/among the competing microorganisms, and there is no nutrient recycling. The dynamics of our models is also different from that of the classic chemostat models. It is known (see Hsu, Hubbell and Waltman [15], Hsu [14], Butler and Wolkowicz [8] and Wolkowicz and Lu [28]) that in chemostat models all species concentration evetually approach equilibrium concentrations and at most one population avoids dying out, that is, the *competive exclusion principle* (Armstrong and McHehee [2]) occurs. By using the classical method of Liapunov function(al), we were able to show that under certain assumptions, the positive equilibrium is globally asymptotically stable. Thus, the competitors could coexist if they compete directly and there is nutrient recycling that provides extra foods for the populations. The same difference exists between the competiton models with delayed nutrient recycling and the chemostat models with delay (see Wolkowicz and Xia [29]).

Finally, for selected functional respose, kernel, initial values and parameters, numerical simulations show that solutions are converging to the positive equilibrium in the models with instantaneous and delayed nutrient recycling, respectively (Fig. I and II). However, if the two populations only compete indirectly for the nutrient and do not compete directly, then only one population can survive (Fig. III). This is similar to the phenomenon obeserved in chemostat models (see Hsu, Hubbell and Waltman [15]).

It would be interesting to study the global asymptotic stability of the diffusion-competion models or predator-prey models with nutrient recycling (instantaneous or delayed). We leave this for future consideration.

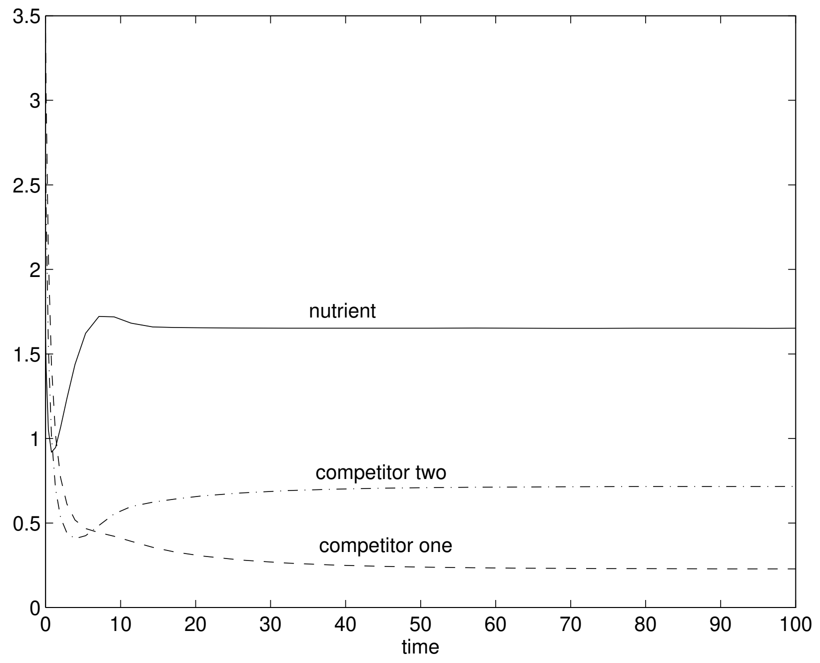

FIG. I. The model with instantaneous nutrient recycling. $p(S) = \frac{S}{k+S}$, $k = 4.0$, $D = 0.15$, $S^0 = 5.75$, $\mu_1 = 2.0$, $\mu_2 = 3.0$, $b_1 = 0.4$, $b_2 = 0.6$, $D_1 = 0.2$, $D_2 = 0.3$, $\delta_{11} = 0.4$, $\delta_{12} = 0.2$, $\delta_{21} = 0.3$, $\delta_{22} = 0.5$.

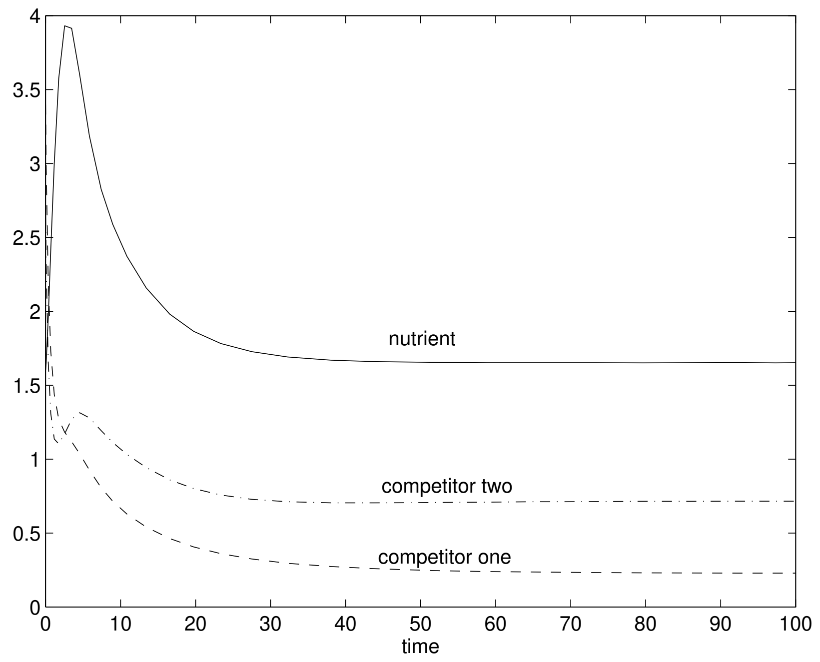

FIG. II. The model with delayed nutrient recycling. $F(u) = \alpha e^{-\alpha u}$, $\alpha = 0.15$, all other parameters are the same as in Fig. I.

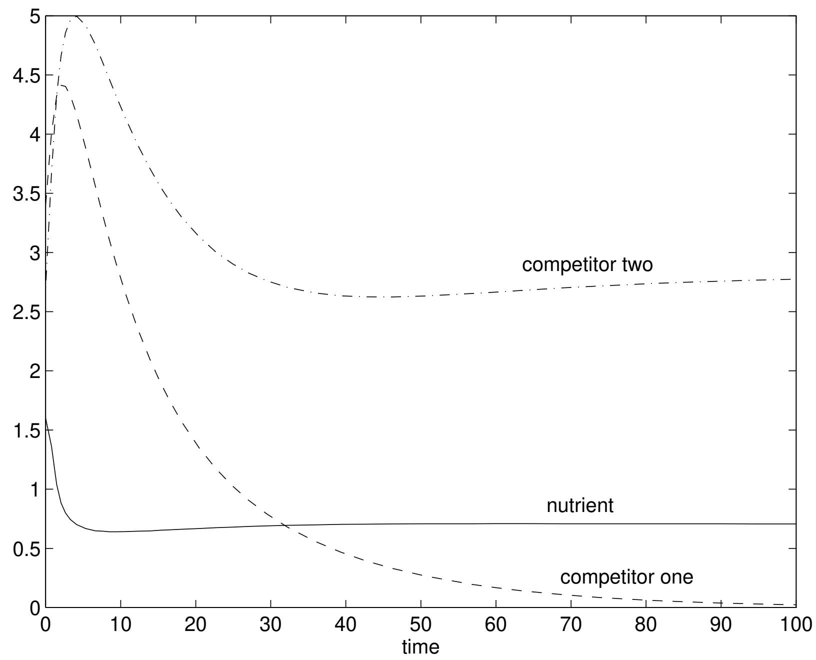

FIG. III. The model with delayed nutrient recycling but without direct competition. $\delta_{ij} = 0\,(i,j = 1,2)$.

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