CANADIAN APPLIED
MATHEMATICS QUARTERLY
Volume 3, Number 2, Spring 1995

PERSISTENCE IN PLANKTON MODELS WITH DELAYED NUTRIENT RECYCLING

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ABSTRACT. A plankton-nutrient interaction model with delayed nutrient recycling is considered. The system consists of three components, autotrophic phytoplankton, herbivorous zooplankton and dissolved limiting nutrient. Distributed delays are used to describe the contribution of phytoplankton and zooplankton that died in the past to the nutrient recycled at the present time. Persistence criteria are derived for the model by using Liapunov-like functionals.

1. Introduction. The effect of nutrient recycling on ecosystem stability has been extensively studied for closed systems. Usually, nutrient recycling is considered as an instantaneous term, thus the time required to regenerate nutrient from dead biomass by bacterial decomposition is neglected. In a natural system, such a delay always presents and increases as temperature decreases (Whittaker [**28**]).

Beretta, Bischi and Solimano [**1**] considered an open system with a single species feeding on a limiting nutrient which is partially recycled after the death of the organisms. They inserted a distributed delay in the recycling term in order to study its effect on the stability of the positive equilibrium. In [**2**], Bischi studied the effects of the time delay involved in nutrient recycling on resilience, that is, the rate at which a system returns to a stable steady state following a perturbation. Bischi showed that when a system is characterized by oscillatory behavior, an increase in the distributed time delay can have a stabilizing effect. This is a counterintuitive result, because in general it has been found that the introduction of time delays is a destabilizing process, in the sense that increasing the time delay could cause a stable equilibrium to become unstable and/or cause the populations to fluctuate (see Cushing [**8**], Gopalsamy [**12**], Kuang [**21**], and MacDonald [**23**]). Freedman and Xu [**11**] extended the single species model in [**1**] to a competition model of chemostat-type with delayed nutrient recycling. They developed persistence and extinction criteria for the competing populations.

Received by the editor in February, 1994, and in revised form in October, 1994.
Research supported by the NSERC of Canada.

Persistence was studied for general dynamical systems by Butler, Freedman and Waltman [**5**], Butler and Waltman [**6**], and was developed to infinite dimensional systems by Hale and Waltman [**17**]. The concept of persistence has played an important role in mathematical ecology. Biologically, when a system of interacting species is persistent in a suitable sense, it means that all the species survive in the long term. Mathematically, persistence of a system means that strictly positive solutions do not have any ω limit points on the boundary of the nonnegative one. For more details and references on persistence and its applications in ecology, we refer to a survey paper by Hutson and Schmitt [**19**].

Recently, persistence in delayed ecological systems has been investigated by many authors. Freedman and Wu [**10**] discussed persistence of single species dispersal models with stage structure. By constructing suitable persistence functionals, Wang and Ma [**27**] obtained uniform persistence conditions for Lotka-Volterra predator-prey systems with a finite number of discrete delays. Their results suggested that delays are "harmless" for uniform persistence. By utilizing Liapunov-like functions, Freedman and Ruan [**9**] established some persistence criteria for functional differential equations with finite delay. See also Cao and Gard [**7**], Kuang and Tang [**22**], Ruan [**26**] and references cited therein.

In this paper, we consider a plankton-nutrient interaction model with delayed nutrient recycling. The system consists of autotrophic phytoplankton, herbivorous zooplankton and dissolved limiting nutrient. Distributed delays are used to describe the contribution of phytoplankton and zooplankton that died in the past to the nutrient recycled at the present time. The model is a system of functional differential equations with infinite delay. By using Liapunov-like functionals, we derive persistence criteria for the model.

This paper is organized as follows. The model is described in Section 2. In Section 3, we state some preliminary results about persistence and functional differential equations with infinite delay. The mathematical analysis of the model is carried out in Section 4. A discussion is given in Section 5.

2. The model. The plankton model with delayed nutrient recycling consists of three interacting components, herbivorous zooplankton (Z), autotrophic phytoplankton (P) and dissolved limiting nutrient (N), and is given by the following equations:

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) + (1-\delta)cZw(P) \\ &\qquad + \gamma_1 \int_{-\infty}^{t} F(t-s)P(s)\,ds + \varepsilon_1 \int_{-\infty}^{t} G(t-s)Z(s)\,ds \\ \frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P \\ \frac{dZ}{dt} &= Z[\delta cw(P) - (\varepsilon + D_2)], \end{aligned} \tag{2.1}$$

where all parameters are positive and are interpreted as follows:

a – maximal nutrient uptake rate for the phytoplankton
c – maximal zooplankton ingestion rate
N^0 – input concentration of the nutrient
D – washout rate of the nutrient
D_1 – washout rate of the phytoplankton
D_2 – washout rate of the zooplankton
γ – phytoplankton mortality rate
ε – zooplankton death rate
γ_1 – nutrient recycle rate after the death of the phytoplankton, $\gamma_1 \le \gamma$
ε_1 – nutrient recycle rate after the death of the zooplankton, $\varepsilon_1 \le \varepsilon$
δ – fraction of zooplankton nutrient conversion, $0 < \delta \le 1$

The function $u(N)$ describes the nutrient uptake rate of phytoplankton and satisfies the following general hypotheses (Hale and Somolinos [**16**]):

(i) the function is nonnegative, increasing and vanishes when there is no nutrient;

(ii) there is a saturation effect when the nutrient is very abundant.

That is, we assume that $u(N)$ is a continuous function defined on $[0, \infty)$, and satisfies

$$u(0) = 0, \qquad \frac{du}{dN} > 0 \quad \text{and} \quad \lim_{N \to \infty} u(N) = 1. \tag{2.2}$$

In particular, this kind of function includes the Michaelis-Menten function (Wroblewski and Richman [**30**])

$$u(N) = N/(k+N), \tag{2.3}$$

where k is the half-saturation constant or Michaelis-Menten constant.

The function $w(P)$ represents the response function describing herbivore grazing. It is also assumed that $w(P)$ is continuous on $[0,\infty)$ and satisfies

$$w(0) = 0, \qquad \frac{dw}{dP} > 0. \tag{2.4}$$

Usually, Ivlev's functional response formulation (Ivlev [**20**])

$$w(P) = 1 - e^{-\lambda P} \tag{2.5}$$

is used to describe the zooplankton grazing, where λ is the rate at which saturation is achieved with increasing phytoplankton levels (per unit concentration). Alternatively, Mayzaud and Poulet formulation [**24**]

$$w(P) = \lambda P(1 - e^{-\lambda P}) \tag{2.6}$$

is also used to describe the food-acclimatized herbivore grazing (Wroblewski and Richman [**30**]).

The delay-kernels $F(s)$ and $G(s)$ are nonnegative bounded functions defined on $[0,\infty)$ and describe the contribution of phytoplankton and zooplankton that died in the past to the nutrient recycled at time t. We assume that only fractions of the dead phytoplankton (γ_1) and the dead zooplankton (ε_1) are recycled into dissolved nutrient. The presence of the distributed time delay must not affect the equilibrium values, so we normalize the kernels such that

$$\int_0^\infty F(s)\,ds = 1, \qquad \int_0^\infty G(s)\,ds = 1. \tag{2.7}$$

According to MacDonald [**23**], we define the average time lag as

$$T = \int_0^\infty sF(s)\,ds. \tag{2.8}$$

In particular, the exponential kernel

$$\frac{\alpha^{n+1}}{n!}s^n e^{-\alpha s}, \qquad \alpha > 0 \tag{2.9}$$

is usually used (see Cushing [8]), where n is a nonnegative integer and α is linked to the mean time delay by

$$T = \frac{n+1}{\alpha}. \tag{2.10}$$

During consumption, only a fraction of the biomass removed from the resources compartment, δ, $\delta \leq 1$, is assumed to be assimilated by the consumer. The remainder goes directly to the dissolved nutrient. Besides the loss related to consumption, a second phytoplankton loss term, $-\gamma P$, represents loss due to extracellular release and senescent cell autolysis and sinking. The zooplankton dynamics includes growth as assimilated ingested ration and a loss rate (ε) due to high level predation, physiological death, etc. The parameters D, D_1 and D_2 are washout rates (or removal rates, diffusive rates) of biotic components from the system resulting from washout, diffusion, harvesting, burial in deep sediments, soluble metabolic loss or cell sinking, for example. Those processes in general do not take place in the same amount of time, so we suppose that D, D_1 and D_2 are different.

System (2.1) with initial conditions

$$N(0) = N_0 \geq 0, \qquad P(s) = \phi(s), \qquad Z(s) = \psi(x), \qquad -\infty < s \leq 0,$$

where $\phi, \psi : (-\infty, 0] \to [0, \infty)$ are bounded and continuous functions, possesses unique nonnegative solutions continuously dependent on parameters and initial data (see Cushing [8] and Gopalsamy [12]).

3. Preliminaries. Let X be a metric space with metric d. Consider a continuous flow $\mathcal{F} = (X, R^+, \pi)$ defined on X, where $\pi : X \times R^+ \to X$ is a continuous map such that $\pi(x, 0) = x$ for all $x \in X$ and $\pi(\pi(x,t), s) = \pi(x, t+s)$ for all $x \in X$, $t, s \in R^+ = [0, \infty)$. The boundary and interior of a set $M \subset X$ are denoted by ∂M and $\overset{\circ}{M}$, respectively. The ω limit set of $x \in X$ is defined to be $\omega(x) = \{y \in X :$ there is a sequence $\{t_n\} \subset R^+$ with $t_n \to \infty$ such that $\pi(x, t_n) \to y$ as $t \to \infty\}$.

Let E be a compact subset of X with ∂E and $\overset{\circ}{E}$ nonempty. Suppose that $\mathcal{F}$ is positively invariant over E. Then $\overset{\circ}{E}$ is also positively invariant, but the boundary ∂E may not be positively invariant.

Definition 3.1. The flow $\mathcal{F}$ is called *persistent* if, for all $x \in \overset{\circ}{E}$, we have

$$\liminf_{t\to\infty} d(\pi(x,t), \partial E) > 0$$

and *uniformly persistent* if there exists $\varepsilon_0 > 0$ such that for all $x \in \overset{\circ}{E}$ we have

$$\liminf_{t\to\infty} d(\pi(x,t), \partial E) > \varepsilon_0.$$

Let $|\cdot|$ denote a norm in R^n. Let C_g be the space of continuous functions mapping $(-\infty, 0]$ into R^n such that

$$\sup_{s\le 0} \frac{|\phi(s)|}{g(s)} < \infty,$$

where $g : (-\infty, 0] \to [1, \infty)$ is a continuous nonincreasing function such that

(g1) $g(0) = 1$;

(g2) $g(s+u)/g(s) \to 1$ uniformly on $(-\infty, 0]$ as $u \to 0^-$;

(g3) $g(s) \to \infty$ as $s \to -\infty$.

Define

$$|\phi|_g = \sup_{s\le 0} \frac{|\phi(s)|}{g(s)}.$$

Then $(C_g, |\cdot|_g)$ is a Banach space (see Haddock and Terjéki [**13**]).

If $x : (-\infty, A) \to R^n$, $0 < A \le \infty$, then for any $t \in [0, A)$, define $x_t : (-\infty, 0] \to R^n$ by $x_t(s) = x(t+s)$, $s \le 0$. For a given $t \ge 0$, x_t is the translation of x on $(-\infty, t]$ back to $(-\infty, 0]$, and x_0 is merely the restriction of x to $(-\infty, 0]$.

Let D be an open subset of C_g. Assume that $f : D \to R^n$ is continuous and maps bounded subsets of D into bounded sets in R^n (i.e., f is completely continuous on D). Consider the following functional differential equation with infinite delay:

$$\frac{dx}{dt} = f(x_t), \qquad t \geq 0 \tag{3.1}$$

with the initial value condition

$$x_0 = \phi \in D. \tag{3.2}$$

For the standard existence, uniqueness, continuous dependence and continuation theory for equation (3.1), we refer to Hale and Kato [**15**].

Suppose that equation (3.1) can be rewritten as follows:

$$\frac{dx_i}{dt} = f_i(x) + g_i(x) \int_{-\infty}^{0} q_i(-s, x_t(s))\, ds \tag{3.3}$$

for $t \geq 0$, $i = 1, 2, \dots, n$, where f_i and g_i are locally Lipschitzian and $q = (q_1, q_2, \dots, q_n)$ satisfies the following condition

$$\int_{-\infty}^{0} |q(-\theta, \phi(\theta))| g(\theta)\, d\theta < \infty. \tag{3.4}$$

The solution of (3.3) with $x_0 = \phi$ is denoted by $x(t, \phi)$. In terms of dynamical systems, we have

$$\pi(t, \phi) = \phi \cdot t = x_t(\phi) = x(t + s, \phi) \quad \text{for } -\infty < s \leq 0.$$

Let C_g^+ be the metric space with $\phi \in C_g$, each component $\phi_i(s) \geq 0$ for $-\infty < s \leq 0$. Then C_g^+ is contained in the nonnegative cone of C_g and contains the only biologically meaningful elements of C_g.

Definition 3.2. Solutions of (3.3) are said to be *point dissipative* if there is a constant B_1 such that, for any $\phi \in C_g^+$, there is a constant $T(\phi) > 0$ such that $|x(t, \phi)| < B_1$ for $t \geq T(\phi)$. Solutions of (3.3) are said to be *bounded dissipative* if there is a constant $B_1 > 0$ such that, for any $B_2 > 0$, there is a constant $T > 0$ such that $|x(t, \phi)| < B_1$ for $t \geq T$ and all $\phi \in C_g^+$ with $|\phi|_g \leq B_2$.

According to Hale [**14**], the above definitions of point dissipativity and bounded dissipativity coincide with the concepts of ultimate boundedness and uniformly ultimate boundedness, respectively. Clearly, if system (3.3) is bounded dissipative, it is point dissipative.

Let $E = C_g^+$, $d(\cdot,\cdot) = |\cdot|_g$, and denote

$$\partial C_g^+ = \{\phi \in C_g^+ : \phi_i(0) = 0 \text{ for at least one } i, i = 1, 2, \dots, n\}.$$

By following the procedure employed in Burton and Hutson [**4**] or in Freedman and Ruan [**9**], we can prove the following uniform persistence theorem for functional differential equations with infinite delay.

Theorem 3.3. *Suppose that*

(i) *System* (3.3) *is point dissipative*;

(ii) *Condition* (3.4) *holds*;

(iii) C_g^+ *is positively invariant*;

(iv) *for each* $\phi \in C_g^+$ *the solution* $x(t,\phi)$ *of* (3.3) *exists on* $[0,\infty)$ *and is continuous in* $|\cdot|_g$;

(v) *there exists a continuous functional* $\rho : C_g^+ \to R^+$ *satisfying*

  (a) $\rho(u) = 0$ *if and only if* $u \in \partial C_g^+$;

  (b) $\psi(u) = \dot{\rho}(u)/\rho(u) > 0$ *for* $u \in \omega(\partial C_g^+)$.

Then system (3.3) *is uniformly persistent.*

4. Mathematical analysis.

By (2.7) it is possible to find a function g satisfying the conditions (g1)–(g3) in Section 3 such that

$$\int_{-\infty}^{0} g(s)F(s)\,ds < \infty, \qquad \int_{-\infty}^{0} g(s)G(s)\,ds < \infty. \tag{4.1}$$

Let C_g be the Banach space of functions in $C((-\infty,0], R^3)$ with finite norm

$$|\phi|_g = \sup_{s\in(-\infty,0]} \frac{|\phi(s)|}{g(s)}, \tag{4.2}$$

and let $(C_g^+, |\cdot|_g)$ denote those $\phi \in C_g$ with $|\phi|_g < \infty$ and $\phi_i(s) \geq 0$ for $s \leq 0$, $i = 1, 2, 3$.

Given $\phi \in C_g^+$, we denote the solution of system (2.1) through ϕ by

$$U(t,\phi) = (N(t,\phi), P(t,\phi)Z(t,\phi)). \tag{4.3}$$

Theorem 4.1. *Suppose that*

$$\int_{-\infty}^{0}\int_{-\infty}^{s} F(u)\,du\,ds < \infty, \qquad \int_{-\infty}^{0}\int_{-\infty}^{s} G(u)\,du\,ds < \infty. \tag{4.4}$$

Then solutions of (2.1) *are point dissipative.*

Proof. Define

$$\begin{aligned} V(t,U_t) &= N(t) + P(t) + Z(t) \\ &\qquad + \gamma_1 \int_{-\infty}^{t}\int_{t-s}^{\infty} F(-u)P(s)\,du\,ds \\ &\qquad + \varepsilon_1 \int_{-\infty}^{t}\int_{t-s}^{\infty} G(-u)Z(s)\,du\,ds. \end{aligned} \tag{4.5}$$

We can see that $V \geq 0$ and $V \to \infty$ when $|(N,P,Z)|_g \to \infty$. The derivative of V along the trajectories of system (2.1) is

$$\begin{aligned} \frac{dV}{dt} &= \frac{dN}{dt} + \frac{dP}{dt} + \frac{dZ}{dt} \\ &\qquad + \gamma_1 \int_0^\infty F(s)[P(t) - P(t-s)]\,ds \\ &\qquad + \varepsilon_1 \int_0^\infty G(s)[Z(t) - Z(t-s)]\,ds \\ &= D(N^0 - N) - (\gamma + D_1)P - (\varepsilon + D_2)Z \\ &\qquad + \gamma_1 \int_0^\infty F(s)P(t)\,ds + \varepsilon_1 \int_0^\infty G(s)Z(t)\,ds \\ &= D(N^0 - N) - (\gamma + D_1 - \gamma_1)P - (\varepsilon + D_2 - \varepsilon_1)Z \\ &\leq -D_0(N + P + Z - N^0), \end{aligned} \tag{4.6}$$

where $D_0 = \min\{D, \gamma + D_1 - \gamma_1, \varepsilon + D_2 - \varepsilon_1\}$. If there is a constant $C > 0$ such that $|(N, P, Z)|_g \geq N_0 + C$, then (4.6) implies that

$$\frac{dV}{dt} \leq -CD_0.$$

Thus, all solutions of (2.1) are bounded dissipative (see Yoshizawa [**31**] or Burton [**3**]), and thus are point dissipative. □

Notice that a boundary equilibrium $E_0 = (N^0, 0, 0)$ always exists.

Theorem 4.2. *If $a \leq \gamma + D_1$, then E_0 is asymptotically stable.*

Proof. We have that

$$\begin{aligned}\frac{dP}{dt} &\leq P[au(N) - (\gamma + D_1)] \\ &\leq [a - (\gamma + D_1)]P \leq 0.\end{aligned}$$

Since there is no invariant set such that $P > 0$ is constant, we have $\lim_{t\to\infty} P(t) = 0$ and hence $\lim_{t\to\infty} Z(t) = 0$. From the first equation in system (2.1), it follows that $\lim_{t\to\infty} N(t) = N^0$. □

Consider the subsystem

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - aPu(N) + \gamma_1 \int_{-\infty}^{t} F(t-s)P(s)\,ds \\ \frac{dP}{dt} &= aPu(N) - (\gamma + D_1)P.\end{aligned} \tag{4.7}$$

If the following inequalities

$$a > \gamma + D_1 \tag{4.8}$$

and

$$N^0 > u^{-1}\left(\frac{\gamma + D_1}{a}\right) \tag{4.9}$$

hold, then system (4.7) has a positive steady state, say (N_1, P_1), where

$$N_1 = u^{-1}\left(\frac{\gamma + D_1}{a}\right), \qquad P_1 = \frac{D(N^0 - N^1)}{\gamma + D_1 - \gamma_1}. \tag{4.10}$$

By Theorem 4.1 of Beretta, Bischi and Solimano [**1**], if

$$(D + aP_1u'(N_1))^2 \geq 2aP_1u'(N_1)(\gamma + D_1), \tag{4.11}$$

then (N_1, P_1) is locally asymptotically stable. Thus, we have the following

Theorem 4.3. *If* (4.8), (4.9) *and* (4.11) *are satisfied, then the boundary equilibrium* $E_1 = (N_1, P_1, 0)$ *is asymptotically stable with respect to* $H_{12} = \{(N, P, Z) \in C_g^+ | Z = 0\}$.

Now we are in a position to state and prove our main theorem.

Theorem 4.4. *Suppose that F and G satisfy conditions* (4.4). *If the inequalities* (4.8), (4.9), (4.11),

$$\delta c > \varepsilon + D_2 \tag{4.12}$$

and

$$w(P_1) > \frac{\varepsilon + D_2}{\delta c} \tag{4.13}$$

hold, where N_1 *and* P_1 *are given by* (4.10), *then system* (2.1) *is uniformly persistent.*

Proof. In order to apply Theorem 3.2, we only need to verify condition (v). For any $(N, P, Z) \in \omega(\partial C_g^+)$, the ω limit set of the boundary of C_g^+, if $P = 0$, then $Z = 0$. From the first equation of (2.1), it follows that $\pi(N, t) = N \cdot t \to N^0$ as $t \to \infty$. If $Z = 0$, then Theorem 4.3 implies that $(\pi(N, t), \pi(P, t)) \to (N_1, P_1)$ as $t \to \infty$. Thus, $\omega(\partial C_g^+)$ is the union of $E_0 = (N^0, 0, 0)$ and $E_1 = (N_1, P_1, 0)$.

Now choose $\rho(U) = U_1^{\alpha_1} U_2^{\alpha_2} U_3^{\alpha_3}$, where $U = (U_1, U_2, U_3) = (N, P, Z)$ and α_1, α_2 and α_3 are positive, undetermined constants. We have

$$\begin{aligned}\psi(U) &= \frac{\dot{\rho}(U)}{\rho(U)} \\ &= \alpha_1 \left[D\left(\frac{N^0}{U_1(0)} - 1\right) - aU_2(0)\frac{u(U_1(0))}{U_1(0)} + (1-\delta)cU_3(0)\frac{w(U_2(0))}{U_1(0)} \right. \\ &\quad \left. + \frac{\gamma_1}{U_1(0)} \int_{-\infty}^{0} F(s)U_2(s)\, ds + \frac{\varepsilon_1}{U_1(0)} \int_{-\infty}^{0} G(s)U_3(s)\, ds \right] \\ &\quad + \alpha_2 \left[au(U_1(0)) - cU_3(0)\frac{w(U_2(0))}{U_2(0)} - (\gamma + D_1) \right] \\ &\quad + \alpha_3[\delta cw(U_2(0)) - (\varepsilon + D_2)].\end{aligned}$$

By (4.9) and (4.12), $\psi > 0$ at E_0. By (4.13), $\psi > 0$ at E_1 So there are always choices of α_1, α_2 and α_3 to ensure that $\psi > 0$. By Theorem 3.2, system (2.1) is uniformly persistent. □

As an example, we suppose that $u(N)$ is the Michaelis-Menten function, $w(P)$ is the Ivlev function, and $F(s)$ and $G(s)$ are strong kernels, i.e., we consider the following model

$$\begin{aligned}\frac{dN}{dt} &= D(N^0 - N) - aP\frac{N}{k+N} + (1-\delta)cZ(1 - e^{-\lambda P}) \\ &\quad + \gamma_1 \int_{-\infty}^{t} \frac{\alpha^{n+1}}{n!}(t-s)^n e^{-\alpha(t-s)} P(s)\, ds \\ &\quad + \varepsilon_1 \int_{-\infty}^{t} \frac{\beta^{m+1}}{m!}(t-s)^m e^{-\beta(t-s)} Z(s)\, ds \\ \frac{dP}{dt} &= aP\frac{N}{k+N} - cZ(1 - e^{-\lambda P}) - (\gamma + D_1)P \\ \frac{dZ}{dt} &= Z[\delta c(1 - e^{-\lambda P}) - (\varepsilon + D_2)],\end{aligned} \tag{4.14}$$

where m and n are positive integers, and all other parameters are positive numbers. Now inequality (4.9) becomes

$$N^0 > \frac{(\gamma + D_1)k}{a - (\gamma + D_1)}, \tag{4.15}$$

and the boundary equilibrium E_1 becomes

$$E_1 = \left(\frac{(\gamma + D_1)k}{a - (\gamma + D_1)}, \frac{D(N^0 - (\gamma + D_1)k/(a - (\gamma + D_1)))}{\gamma + D_1 - \gamma_1}, 0\right)$$

provided (4.8) and (4.9) hold. By Theorem 4.2 of Beretta, Bischi and Solimano [**1**] we know that E_1 is asymptotically stable with respect to H_{12}. By Theorem 4.4, we have

Theorem 4.5. *Suppose* (4.8), (4.13) *and* (4.15) *hold. System* (4.14) *is uniformly persistent if*

$$\exp\left[-\frac{\lambda D(N^0 - (\gamma + D_1)k/(a - (\gamma + D_1)))}{\gamma + D_1 - \gamma_1}\right] < \frac{\delta c - (\varepsilon + D_2)}{\delta c}.$$

5. Discussion. We have considered a model consisting of nutrient, phytoplankton and zooplankton with delayed nutrient recycling. Condition have been derived such that the system is uniformly persistent. For the case that the nutrient uptake function $u(N)$ is the Michaelis-Menten function, the herbivorous grazing function $w(P)$ is the Ivlev's functional response formulation, and the delayed kernels describing nutrient recycling are exponential kernels, the uniform persistence conditions can e summarized as follows:

$$a > \gamma + D_1, \tag{5.1}$$

$$\delta c > \varepsilon + D_2, \tag{5.2}$$

$$N^0 > \frac{(\gamma + D_1)k}{a - (\gamma + D_1)}, \tag{5.3}$$

and

$$\exp\left[-\frac{\lambda D(N^0 - (\gamma + D_1)k/(a - (\gamma + D_1)))}{\gamma + D_1 - \gamma_1}\right] < \frac{\delta c - (\varepsilon + D_2)}{\delta c}. \tag{5.4}$$

Conditions (5.1) and (5.2) indicate that the growth rates of phytoplankton and zooplankton must be greater than their loss rates, respectively. Condition (5.4) can be rewritten as follows:

$$N^0 > \frac{(\gamma + D_1)k}{a - (\gamma + D_1)} + \frac{\gamma + D_1 - \gamma_1}{\lambda D} \ln \frac{\delta c}{\delta c - (\varepsilon + D_2)}. \tag{5.5}$$

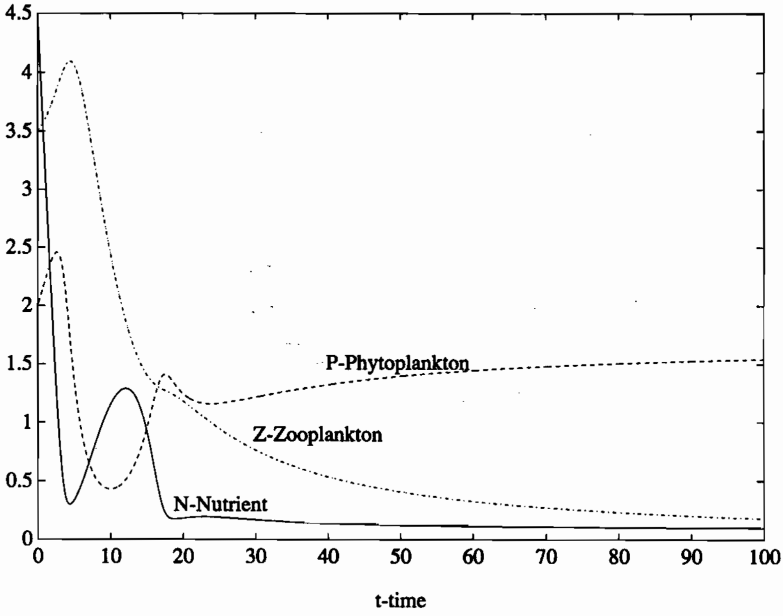

FIGURE 1. The model with instantaneous nutrient recycling. $u(N) = N/(k+N)$, $w(P) = 1 - e^{-\lambda P}$, $a = 1.0$, $k = 0.2$, $\gamma = 0.1$, $\varepsilon = 0.1$, $\lambda = 0.5$, $D = 0.1$, $c = 0.5$, $\delta = 0.7$, $D_1 = 0.2$, $D_2 = 0.1$, $N^0 = 5.75$, $\gamma_1 = 0.08$, $\varepsilon_1 = 0.05$.

Condition (5.1) guarantees that the first term on the righthand side of (5.5) is positive, and condition (5.2) guarantees that the second term on the righthand side of (5.5) is positive. Clearly, (5.5) implies (5.3).

The inequality (5.5) demonstrates that the model is nutrient controlled (Hallam [**18**]). Therefore, if nutrient concentration input is sufficient, then the system is uniformly persistent, that is, all components can survive in the long term.

If the distributed time delays in the nutrient recycling are neglected, that is, if we suppose that the nutrient recycling process is instantaneous, then system (2.1) reduces to the following ordinary differential equation model:

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPu(N) \\ &\quad + (1-\delta)cZw(P) + \gamma_1 P(t) + \varepsilon_1 Z(t) \end{aligned} \tag{5.6}$$

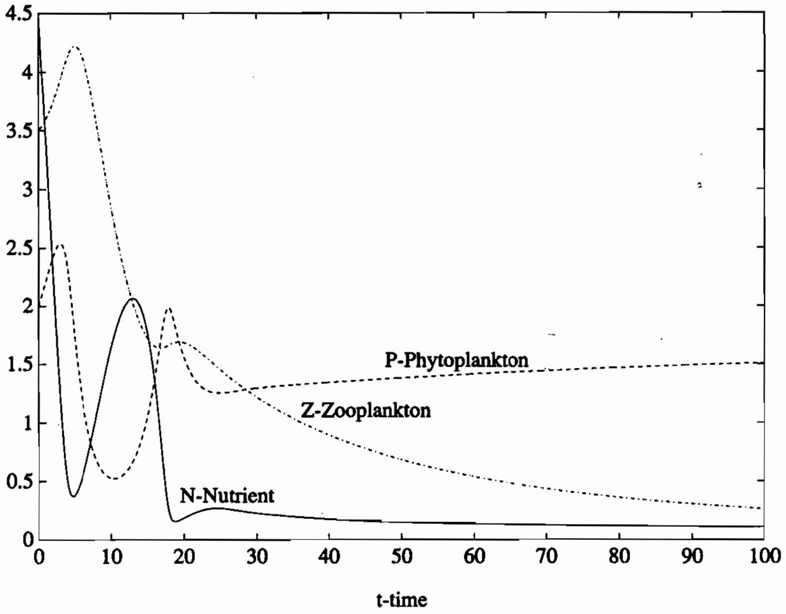

FIGURE 2. The model with delayed nutrient recycling. $u(N)=N/(k+N)$, $w(P)=1-e^{-\lambda P}$, $F(s)=\alpha^2 s e^{-\alpha s}(n=1)$, $G(s)=\beta^3 s^2 e^{-\beta s}/2(m=2)$, $a=1.0$, $k=0.2$, $\gamma=0.1$, $\varepsilon=0.1$, $\lambda=0.5$, $D=0.1$, $c=0.5$, $\delta=0.7$, $D_1=0.2$, $D_2=0.1$, $N^0=5.75$, $\gamma_1=0.08$, $\varepsilon_1=0.05$, $\alpha=0.2$, $\beta=0.15$.

$$\begin{aligned}\frac{dP}{dt} &= aPu(N) - cZw(P) - (\gamma + D_1)P\\ \frac{dZ}{dt} &= Z[\delta c w(P) - (\varepsilon + D_2)],\end{aligned}$$

which was studied by Ruan [**25**]. The uniform persistence conditions obtained in this article coincide with those derived in Ruan [**25**] for the ODE model (5.6). This means that the delays in model (2.1) do not affect the property of persistence. Similar phenomena has been observed by Burton and Hutson [**4**], Wang and Ma [**27**], Freedman and Ruan [**9**] and Ruang [**26**].

Finally, for the functional responses, parameters and initial values selected, solutions seem to be converging to the asymptotically stable equilibrium in the interior. Delays seem to slow down the convergence slightly and transients oscillate slightly more.

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