Instability in Diffusive Ecological Models with Nonlocal Delay Effects

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We propose a reaction−diffusion system with nonlocal delays to model the growth of plankton communities feeding on a limiting nutrient supplied at a constant rate. Two delays are incorporated into the model: one describes the delayed nutrient recycling process and the other models the delayed growth response of the plankton. It is assumed that both delays are nonlocal in the sense that there are delayed not only in time but also in space. Local and bifurcation analyses are carried out. It has been shown that Turing-type spatial patterns occur when the diffusion coefficients vary and temporal or spatial-temporal patterns occur when the delay involved in the growth response changes. © 2001 Academic Press

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1. INTRODUCTION

The effect of nutrient recycling on ecosystem stability has been previously studied for closed systems (see Nisbet and Gurney [15]) and usually nutrient recycling is regarded as an instantaneous term, thus neglecting the time required to regenerate nutrient from dead biomass by bacterial decomposition. However, a delay in nutrient recycling is always present in a natural system and it increases when temperature decreases (see Whittaker [25]). In order to simulate the growth of planktonic communities of unicellular algea in the lakes, Beretta *et al*. [1] constructed a chemostat-type model in which the plankton feeds on a limiting nutrient supplied at a constant rate. They assumed that the limiting nutrient is partially recycled after the death of the organisms and used a distributed delay to model nutrient recycling. It has been observed that plankton models with delayed nutrient recycling exhibit very interesting and rich dynamics (see Beretta and Takeuchi [2], He and Ruan [10], He, Ruan, and Xia [11], Ruan [21, 22], etc.).

In the lakes/oceans, plankton population movements are subject to many factors, such as currents and turbulent lateral diffusion (cf. Levin and Segel [12], Mimura [14], Okubo [16], Freedman and Ruan [4]). Ruan [22] proposed a diffusive plankton-nutrient interaction model with delayed nutrient recycling and delayed growth response and studied Turing instability and the existence of travelling wave solutions. However, the delay kernels used in [22] are spatial homogeneous.

In more realistic ecological models, the delays should be spatial inhomogeneous; that is, there are not only delays in the time variable but also delays in the space variable since the species were not necessarily at the same point in space at previous times. Such delays are called *nonlocal*. Recently, a great attention has been paid to the research on ecological models with nonlocal delays; see Gopalsamy [5], Gourley [6], Gourley and Bartuccelli [7], Gourley and Britton [8, 9], Levin and Segel [13], Pozio [19, 20], Yamada [27], etc. If delays appear in the time variable only, they are called *local* or time delays. Reaction−diffusion models with (local) time delays have been studied by many researchers; we refer to Feng and Lu [3], Pao [17, 18], Ruan and Wu [23] and a monograph by Wu [26].

In this paper, following the spirit of [22], we consider a reaction−diffusion plankton model with nonlocal delayed growth response and nonlocal delayed nutrient recycling. We are concerned with the effects of the nonlocal delays as well as the diffusions on the dynamics of the system.

The paper is organized as follows. Section 2 is devoted to the presentation of the model. In Section 3, we will study local stability of positive steady state of the model with delayed nutrient recycling. In Section 4 we discuss diffusion-driven instability of the model with both delayed nutrient

recycling and delayed growth response. In Section 5, we are concerned about the stability and bifurcation of the model with delayed growth response only and find that the delay in the growth response term induces oscillations via Hopf bifurcations. A brief discussion is given in Section 6.

2. THE MODEL

Let Ω be an open bounded set in R^3 with boundary $\partial\Omega$. $\partial/\partial n$ represents the outward normal derivative on $\partial\Omega$, Δ is the Laplace operator, and $d_i > 0 (i = 1, 2)$ are diffusion coefficients. Let $N(t, x)$ and $P(t, x)$ denote the biomass of nutrient and plankton, respectively, per unit of volume evaluated at the point x at time t. Consider the following reaction–diffusion plankton model with delayed nutrient recycling and delayed growth response

$$\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t, x)f(N(t, x))$$
$$+ \gamma_1 \int_{-\infty}^{t} \int_{\Omega} F(x, y, t - s) P(s, y) \, dy \, ds \tag{1}$$
$$\frac{\partial P}{\partial t} = d_2 \Delta P + P\left[-(\gamma + D) + a_1 \int_{-\infty}^{t} \int_{\Omega} G(x, y, t - s) f(N(t, x)) \right]$$

under the initial value conditions

$$N(\theta, x) = \phi(\theta, x), P(\theta, x) = \psi(\theta, x), \theta \in (-\infty, 0], x \in \Omega,$$

where ϕ and ψ are positive continuous functions, and the boundary value conditions

$$\frac{\partial N}{\partial n} = \frac{\partial P}{\partial n} = 0 \text{ on } \partial\Omega.$$

We suppose that all parameters are positive. They are interpreted as follows:

a, maximal nutrient uptake rate for plankton

N^0, input concentration of nutrient

D, washout rate of nutrient

γ, plankton mortality rate

γ_1, nutrient recycle rate after the death of plankton, $\gamma_1 \leq \gamma$

a_1, maximal conversion rate of the nutrient into planktonic biomass.

The function $f(N)$ describes the nutrient uptake rate of plankton. We assume the following general hypotheses on $f(N)$:

(1) $f(N)$ is nonnegative, increasing and vanishing where there is no nutrient;

(2) There is a saturation effect when the nutrient is very abundant.

That is, $f(N)$ is a continuously differentiable function defined on $[0, \infty)$ and

$$f(0) = 0, \ \frac{df}{dN} > 0, \ \lim_{N \to \infty} f(N) = 1.$$

These hypotheses are satisfied by the Michaelis−Menten function

$$f(N) = \frac{N}{K + N},$$

where $K > 0$ is the half-saturation constant or Michaelis−Menten constant.

The delay kernels F and G are nonnegative bounded functions defined on $\Omega \times [0, \infty)$. F describes the contribution of the average of the plankton population dead in the past in the domain Ω to the nutrient recycled at time t, and G describes the delayed growth response of the plankton. The double convolution kernels in both the time and space arise because of the fact that the species are moving (by diffusion), and therefore are not at the same point in space at previous times. Thus, the predation does not depend simply on population density at one point in space and time, but also on weighed average involving values at all previous times and all points in space. Typical kernels include (see Gourley [6], Gourley and Britton [9], etc.)

(i) $F(x, y, t) = \delta(x - y)\beta e^{-\beta t}(\beta > 0),$

(ii) $F(x, y, t) = \frac{\alpha}{2} e^{-\alpha |x - y|}\beta e^{-\beta t}(\alpha > 0, \beta > 0),$

(iii) $F(x, y, t) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(-\frac{|x - y|^2}{4Dt}\right)$

$$\times \beta e^{-\beta t}(D > 0, \beta > 0),$$

(iv) $F(x, y, t) = \delta(x - y)\delta(t - \tau)(\tau > 0).$

In kernel (i) the delta function suppresses the space integral

$$\int_{-\infty}^{t} \int_{\Omega} F(x, y, t - s)u(y, s) \, dy \, ds$$

and gives a term which is time delayed but local in space. When $1/\beta$ is small, kernels (i)−(iii) are weak delay kernels in the sense that, although all values of u in the past are taken into account, only recent values have a strong effect on the system. As $1/\beta$ increases, values of u further into the past become more important. Kernel (iv) gives a system of equations with a fixed discrete time delay τ (the double integral becomes $u(x, t − \tau)$).

Remark 2.1. We should mention that if the kernel (iii) is used, then the quantity D must be chosen to be d_2 so that it matches the diffusivity of the relevant species, which is the plankton P in Eq. (1). Also, if the kernel depends on $|x − y|$, then the domain must be large enough compared to the spatial extent of the kernel (in the case of kernel (ii), it is of order $1/\alpha$). In this paper, kernel (ii) will be used and the domain Ω is finite, therefore, α must be sufficiently large. This fact will be used repeatedly in studying the linearized systems.

When both N and P are space-independent and the two kernels are local, we have a special case of (1) which is the following delay system:

$$
\frac{dN}{dt} = D(N^0 − N) − aP(t, x)f(N(t)) + \gamma_1 \int_{-\infty}^{t} F(t − s)P(s)\,ds,
$$
$$
\frac{dP}{dt} = P\left[−(\gamma + D) + a_1 \int_{-\infty}^{t} G(t − s)f(N(s))\,ds \right]. \tag{2}
$$

System (2) was studied in He, Ruan, and Xia [11] and Ruan [22]. Note that a positive equilibrium of the delay system (2) is a spatial homogeneous steady state of the reaction−diffusion system (1). Thus, if

$$
\gamma + D < a_1 \text{ and } f^{-1}\left(\frac{\gamma + D}{a_1} \right) < N^0, \tag{3}
$$

then system (1) has a uniform steady state $E^* = (N^*, P^*)$ with

$$
N^* = f^{-1}\left(\frac{\gamma + D}{a_1} \right), \quad P^* = \frac{D(N^0 − N^*)}{af(N^*) − \gamma_1}. \tag{4}
$$

3. LOCAL STABILITY

In this section, we consider a special case of (1) with

$$
F(x, y, t) = \frac{\alpha}{2}e^{-\alpha|x−y|}\beta e^{-\beta t}, \ G(x, y, t) = \delta(x − y)\delta(t);
$$

that is, we consider the system

$$\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t, x) f(N(t, x))$$

$$+ \gamma_1 \int_{-\infty}^{t} \int_{\Omega} \frac{e^{-\alpha|x-y|} \beta e^{-\beta(t-s)} P(s, y)}{\int_{\Omega} e^{-\alpha|x-z|} dz} \, dy ds, \tag{5}$$

$$\frac{\partial P}{\partial t} = d_2 \Delta P + P\left[-(\gamma + D) + a_1 f(N(t, x))\right].$$

Notice that the steady state $E^* = (N^*, P^*)$ given by (4) is also a steady state of system (5). We shall use the linear-chain trick to study the stability of $E^* = (N^*, P^*)$. Define

$$R(t, x) = \int_{-\infty}^{t} \beta e^{-\beta(t-s)} P(s, x) \, ds.$$

Then system (5) is equivalent to the following system

$$\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t, x) f(N(t, x))$$

$$+ \gamma_1 \int_{\Omega} \frac{\exp(-\alpha|x-y|) R(t, y)}{\int_{\Omega} \exp(-\alpha|x-z|) \, dz} \, dy,$$

$$\frac{\partial P}{\partial t} = d_2 \Delta P + P\left[-(\gamma + D) + a_1 f(N(t, x))\right], \tag{6}$$

$$\frac{\partial R}{\partial t} = \beta\left[P(t, x) - R(t, x)\right].$$

The positive equilibrium of system (6) is $E^* = (N^*, P^*, R^*)$ with $P^* = R^*$; N^* and P^* are given by (4). Let

$$u_1 = N - N^*, \quad u_2 = P - P^*, \quad u_3 = R - R^*.$$

The linearized system of (6) takes the form

$$\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 - \left[D + aP^* f'(N^*)\right] u_1 - af'(N^*) u_2$$

$$+ \gamma_1 \int_{\Omega} \frac{\exp(-\alpha|x-y|) u_3(t, y)}{\int_{\Omega} \exp(-\alpha|x-z|) \, dz} \, dy,$$

$$\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + a_1 P^* f'(N^*) u_1, \tag{7}$$

$$\frac{\partial u_3}{\partial t} = \beta u_2 - \beta u_3.$$

Let

$$\begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \end{pmatrix} \cos(k_1 x_1)\cos(k_2 x_2)\cos(k_3 x_3)e^{\lambda t},$$

where $k_i(i = 1, 2, 3)$ is the wavenumber in the x_i direction and λ is the frequency. Suppose the domain has the form

$$\Omega = (0, l_1) \times (0, l_2) \times (0, l_3).$$

By Remark 2.1, α must be sufficiently large since Ω is finite. This ensures that the above vector $(u_1, u_2, u_3)^T$ is a solution of the linearized system (7). The boundary conditions on $\partial\Omega$ imply that

$$k_1 = \frac{n_1 \pi}{l_1}, \; k_2 = \frac{n_2 \pi}{l_2}, \; k_3 = \frac{n_3 \pi}{l_3},$$

where $n_i(i = 1, 2, 3)$ is the half-wavelength in the x_i direction. Denote

$$k^2 = k_1^2 + k_2^2 + k_3^2$$

and

$$\delta = \frac{1}{\int_\Omega \Psi^2(x)\, dx} \int_\Omega \left[\int_\Omega \frac{\exp(-\alpha|x-y|)\Psi(y)}{\int_\Omega \exp(-\alpha|x-z|)\, dz}\, dy \right] \Psi(x)\, dx \qquad (8)$$

with

$$\Psi(x) = \cos(k_1 x_1)\cos(k_2 x_2)\cos(k_3 x_3).$$

Then we have the characteristic equation

$$\lambda^3 + b_1 \lambda^2 + b_2 \lambda + b_3 = 0,$$

where

$$b_1 = \beta + (d_1 + d_2)k^2 + D + aP^* f'(N^*),$$

$$b_2 = \beta\big[(d_1 + d_2)k^2 + D + aP^* f'(N^*)\big] + d_1 d_2 k^4$$
$$+ d_2 k^2(D + aP^* f'(N^*)) + aa_1 P^* f'(N^*)f(N^*),$$

$$b_3 = \beta d_1 d_2 k^4 + \beta a_1 P^* f'(N^*)\big[af(N^*) - \gamma_1 \delta\big]$$
$$+ \beta d_2 k^2 \big[D + ap^* f'(N^*)\big].$$

By the Routh–Hurwitz criterion, the necessary and sufficient conditions for the characteristic roots λ_i $(i = 1, 2, 3, 4)$ to have negative real part are

$$\text{(i) } b_1 > 0, \text{ (ii) } b_3 > 0, \text{ (iii) } b_1 b_2 - b_3 > 0.$$

Obviously, (i) is satisfied. By (3) we have $af(N^*) - \gamma_1 > 0$ and from expression (8) we have $\delta \leq |1|$; thus (ii) holds. Since

$$
\begin{aligned}
\beta d_1 d_2 k^4 &+ \beta a a_1 P^* f'(N^*) f(N^*) \\
&+ \beta d_2 k^2 \big[D + ap^* f'(N^*) \big] + \text{positive terms} \\
> \beta d_1 d_2 k^4 &+ \beta a a_1 P^* f'(N^*) f(N^*) \\
&+ \beta d_2 k^2 \big[D + ap^* f'(N^*) \big] - \gamma_1 \beta a_1 P^* f'(N^*) \\
\geq \beta d_1 d_2 k^4 &+ \beta a a_1 P^* f'(N^*) f(N^*) \\
&+ \beta d_2 k^2 \big[D + ap^* f'(N^*) \big] - \delta \gamma_1 \beta a_1 P^* f'(N^*),
\end{aligned}
$$

it follows that (iii) is also satisfied. Hence, we have the following result about the linear stability of the uniform steady state.

THEOREM 3.1.   *If the inequalities in* (3) *hold, then the positive state E^* of system* (5) *exists and is locally stable.*

Remark 3.2.   The above result indicates that for system (5) with delayed nutrient recycling only, there is no spatial, temporal, or spatial-temporal structure and the effect of diffusion is to make the species distribution uniform over the region Ω as $t \to +\infty$.

4. DIFFUSION-DRIVEN INSTABILITY

We consider the delay model (1). Suppose

$$
F(x, y, t) = \frac{\alpha_1}{2} e^{-\alpha_1 |x-y|} \beta_1 e^{-\beta_1 t} (\alpha_1 > 0, \beta_1 > 0),
$$

$$
G(x, y, t) = \frac{\alpha_2}{2} e^{-\alpha_2 |x-y|} \beta_2 e^{-\beta_2 t} (\alpha_2 > 0, \beta_2 > 0).
$$

We have the following delay system

$$
\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t,x)f(N(t,x))
$$

$$
+ \gamma_1 \int_{-\infty}^{t} \int_{\Omega} \frac{e^{-\alpha_1|x-y|}\beta_1 e^{-\beta_1(t-s)}P(s,y)}{\int_{\Omega} e^{-\alpha_1|x-z|}\,dz}\,dy\,ds,
$$

$$
\frac{\partial P}{\partial t} = d_2 \Delta P + P\Bigg[-(\gamma + D)
$$

$$
+ a_1 \int_{-\infty}^{t} \int_{\Omega} \frac{e^{-\alpha_2|x-y|}\beta_2 e^{-\beta_2(t-s)}f(N(s,y))}{\int_{\Omega} e^{-\alpha_2|x-z|}\,dz}\,dy\,ds\Bigg].
$$

(9)

Define

$$
R(t,x) = \int_{-\infty}^{t} \beta_1 e^{-\beta_1(t-s)}P(s,x)\,ds,
$$

$$
Q(t,x) = \int_{-\infty}^{t} \beta_2 e^{-\beta_2(t-s)}f(N(s,y))\,ds.
$$

Then system (9) is equivalent to the following system

$$
\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t,x)f(N(t,x))
$$

$$
+ \gamma_1 \int_{\Omega} \frac{\exp(-\alpha_1|x-y|)R(t,y)}{\int_{\Omega} \exp(-\alpha_1|x-y|)\,dy}\,dy,
$$

$$
\frac{\partial P}{\partial t} = d_2 \Delta P + P\Bigg[-(\gamma+D) + a_1 \int_{\Omega} \frac{\exp(-\alpha_2|x-y|)Q(t,y)}{\int_{\Omega} \exp(-\alpha_2|x-z|)\,dz}\,dy\Bigg], \quad (10)
$$

$$
\frac{\partial R}{\partial t} = \beta_1[P(t,x) - R(t,x)],
$$

$$
\frac{\partial Q}{\partial t} = \beta_2[f(N(t,x)) - Q(t,x)].
$$

The positive equilibrium of system (10) is $E^* = (N^*, P^*, R^*, Q^*)$ with $R^* = P^*$, $Q^* = f(N^*)$; N^* and P^* are given by (4). Let

$$
u_1 = N - N^*,\ u_2 = P - P^*,\ u_3 = R - R^*,\ u_4 = Q - Q^*.
$$

The linearized system of (10) at E^* has the form

$$\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 - [D + aP^* f'(N^*)] u_1 - af(N^*) u_2$$

$$+ \gamma_1 \int_\Omega \frac{\exp(-\alpha_1|x-y|) u_3(t,y)}{\int_\Omega \exp(-\alpha_1|x-z|)\, dz}\, dy,$$

$$\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + a_1 P^* \int_\Omega \frac{\exp(-\alpha_1|x-y|) u_4(t,y)}{\int_\Omega \exp(-\alpha_1|x-z|)\, dz}\, dy, \qquad (11)$$

$$\frac{\partial u_3}{\partial t} = \beta_1 u_2 - \beta_1 u_3,$$

$$\frac{\partial u_4}{\partial t} = \beta_2 f(N^*) u_1 - \beta_2 u_4.$$

Thus, we have the characteristic equation

$$v^4 + b(k^2)v^3 + b_2(k^2)v^2 + b_3(k^2)v + b_4(k^2) = 0,$$

where

$$b_1(k^2) = (d_1 + d_2)k^2 + \beta_1 + \beta_2 + D + aP^* f'(N^*),$$

$$b_2(k^2) = d_1 d_2 k^4 + [(\beta_1 + \beta_2)(d_1 + d_2) - d_2(D + aP^* f'(N^*))]k^2$$
$$+ \beta_1 \beta_2 + (\beta_1 + \beta_2)(D + aP^* f'(N^*)),$$

$$b_3(k^2) = d_1 d_2(\beta_1 + \beta_2)k^4$$
$$+ [\beta_1 \beta_2(d_1 + d_2) + d_2(\beta_1 + \beta_2)(D + aP^* f'(N^*))]k^2$$
$$+ \beta_1 \beta_2(D + aP^* f'(N^*)) + a\beta_2(\gamma + D)P^* f'(N^*),$$

$$b_4(k^2) = \beta_1 \beta_2 d_1 d_2 k^4 + \beta_1 \beta_2 d_2(D + aP^* f'(N^*))k^2$$
$$+ \beta_1 \beta_2 a_1 \delta_2 P^* f'(N^*)[af(N^*) - \gamma_1 \delta_1],$$

where

$$\delta_1 = \frac{1}{\int_\Omega \Psi^2(x)\, dx} \int_\Omega \left[\int_\Omega \frac{\exp(-\alpha_1|x-y|)\Psi(y)}{\int_\Omega \exp(-\alpha_1|x-z|)\, dz}\, dy \right] \Psi(x)\, dx,$$

$$\delta_2 = \frac{1}{\int_\Omega \Psi^2(x)\, dx} \int_\Omega \left[\int_\Omega \frac{\exp(-\alpha_2|x-y|)\Psi(y)}{\int_\Omega \exp(-\alpha_2|x-z|)\, dz}\, dy \right] \Psi(x)\, dx$$

with

$$\Psi(x) = \cos(k_1 x_1)\cos(k_2 x_2)\cos(k_3 x_3).$$

Notice that $\delta_1 \le |1|$ and $\delta_2 \le |1|$. By the Routh–Hurwitz criterion, diffusion-driven instability or Turing instability occurs only if one of the following conditions is violated:

(i) $b_1(k^2) > 0,$

(ii) $b_4(k^2) > 0,$

(iii) $b_1(k^2)b_2(k^2) - b_3(k^2) > 0,$

(iv) $b_1(k^2)[b_2(k^2)b_3(k^2) - b_1(k^2)b_4(k^2)] - b_3(k^2) > 0.$

Clearly, (i) and (ii) cannot be violated. (iii) also cannot be violated if $b_1(0)b_2(0) - b_3(0) > 0$. To check (iv), denote

$$U(k^2) = b_1(k^2)\big[b_2(k^2)b_3(k^2) - b_1(k^2)b_4(k^2)\big] - b_3(k^2),$$

which is a fifth-order polynomial in k^2 and can be written as

$$U(k^2) = h_1(k^2)^5 + h_2(k^2)^4 + h_3(k^2)^3 + h_4(k^2)^2 + h_5(k^2) + h_6,$$

where $(A = D + aP^*f'(N^*))$, $B = a\beta_2(\gamma_1\delta_1 + D)P^*f'(N^*)$, $C = \beta_1\beta_2 a_1\delta_2 P^*f'(N^*)[af(N^*) - \gamma_1\delta_1])$, and

$$h_1 = (\beta_1 + \beta_2)(d_1 + d_2)d_1 d_2^3,$$

$$\begin{aligned}
h_2 = {}& (\beta_1 + \beta_2)^2 d_1 d_2^3 + (\beta_1 + \beta_2)^2(d_1 + d_2)^2 d_2^2 \\
& + A(\beta_1 + \beta_2)(d_1 + d_2)d_2^3 + A(\beta_1 + \beta_2)(d_1 + d_2)d_1 d_2^2 \\
& + A(\beta_1 + \beta_2)d_1 d_2^3 - (\beta_1 + \beta_2)^2 d_2^4,
\end{aligned}$$

$$\begin{aligned}
h_3 = {}& A^2(\beta_1 + \beta_2)d_2^3 + A^2(\beta_1 + \beta_2)d_1 d_2^2 \\
& + (\beta_1 + \beta_2)^3(d_1 + d_2)d_2^2 + A(\beta_1 + \beta_2)d_1 d_2^2 \\
& + \beta_1\beta_2(\beta_1 + \beta_2)(d_1 + d_2)d_2^2 \\
& + \beta_1\beta_2(\beta_1 + \beta_2)(d_1 + d_2)^3 + A(\beta_1 + \beta_2)^2(d_1 + d_2)^2 d_2 \\
& + A^2(\beta_1 + \beta_2)(d_1 + d_2)d_2^2 + B(d_1 + d_2)d_1 d_2 \\
& + 2A(\beta_1 + \beta_2)^2(d_1 + d_2)d_2^2 - A(\beta_1 + \beta_2)^2 d_2^3 \\
& - \beta_1\beta_2(\beta_1 + \beta_2)(d_1 + d_2)d_1 d_2,
\end{aligned}$$

$$h_4 = A^2(\beta_1 + \beta_2)d_2^2 + A^3(\beta_1 + \beta_2)d_2^2 + A^3(d_1 + d_2)d_2^3$$
$$+ \beta_1\beta_2(\beta_1 + \beta_2)^2 d_2^2 + A(\beta_1 + \beta_2)^2 d_2^2$$
$$+ \beta_1\beta_2(\beta_1 + \beta_2)^2 (d_1 + d_2)^2 + A(\beta_1 + \beta_2)^3 (d_1 + d_2)d_2$$
$$+ C(\beta_1 + \beta_2)(d_1 + d_2)^2 + ABd_2(d_1 + d_2)$$
$$+ 3A\beta_1\beta_2(\beta_1 + \beta_2)(d_1 + d_2)^2 + 2A^2(\beta_1 + \beta_2)^2 (d_1 + d_2)$$
$$+ ABd_1d_2 - \beta_1\beta_2(\beta_1 + \beta_2)^2 (d_1 + d_2) - C(d_1 + d_2)^2$$
$$- A\beta_1\beta_2(\beta_1 + \beta_2)d_2^2 - A\beta_1\beta_2 d_1 d_2,$$

$$h_5 = 3A^2\beta_1\beta_2(\beta_1 + \beta_2)(d_1 + d_2) + A^3(\beta_1 + \beta_2)d_2 + A^2 Bd_2$$
$$+ 2A\beta_1\beta_2(\beta_1 + \beta_2)^2 (d_1 + d_2) + A(\beta_1 + \beta_2)^3 d_2$$
$$+ C(\beta_1 + \beta_2)^2 (d_1 + d_2) + 2AB(\beta_1 + \beta_2)(d_1 + d_2)$$
$$+ B\beta_1\beta_2(d_1 + d_2) - 2A(\beta_1 + \beta_2)(d_1 + d_2) - AB(\beta_1 + \beta_2)d_2$$
$$- 2C(\beta_1 + \beta_2)(d_1 + d_2) - 2A^2\beta_1\beta_2(\beta_1 + \beta_2),$$

$$h_6 = A^2 B(\beta_1 + \beta_2) + AB(\beta_1 + \beta_2)^2 + A^3\beta_1\beta_2(\beta_1 + \beta_2)$$
$$+ A^2\beta_1\beta_2(\beta_1 + \beta_2)^2 + A\beta_1^2\beta_2^2(\beta_1 + \beta_2) + B\beta_1\beta_2(\beta_1 + \beta_2)$$
$$- A^2 C - B^2 - C(\beta_1 + \beta_2)^2 - 2AC(\beta_1 + \beta_2) - AB\beta_1\beta_2.$$

We have that $h_1 > 0$, so $U(k^2) \to \infty$ as $k^2 \to \infty$. Looking for extrema of $U(k^2)$, we need to find the roots of the equation

$$\frac{dU}{dk^2} = 5h_1(k^2)^4 + 4h_2(k^2)^3 + 3h_3(k^2)^2 + 2h_4(k^2) + h_5 = 0,$$

which can be written as

$$(k^2)^4 + p(k^2)^3 + q(k^2)^2 + r(k^2) + s = 0, \tag{12}$$

where

$$p = \frac{4h_2}{5h_1}, \quad q = \frac{3h_3}{5h_1}, \quad r = \frac{2h_4}{5h_1}, \quad s = \frac{h_5}{5h_1}.$$

Choose x, y and add $(xk^2 + y)$ to both sides of Eq. (12), such that

$$\left[(k^2)^2 + \frac{p}{2}(k^2) + \theta \right]^2 = (xk^2 + y)^2,$$

where θ is a real root of the cubic equation

$$8\theta^3 - 4q\theta^2 + 2(pr - 4s)\theta - p^2s + 4qs - r^2 = 0.$$

Thus, Eq. (12) is equivalent to a system of two quadratic equations:

$$(k^2)^2 + \left(\frac{p}{2} + x\right)k^2 + (\theta + y) = 0,$$

$$(k^2)^2 + \left(\frac{p}{2} - x\right)k^2 + (\theta - y) = 0,$$

from which we can find the possible local extrema:

$$k_{1,2}^2 = -\frac{1}{2}\left(\frac{p}{2} + x\right) \pm \frac{1}{2}\sqrt{\left(\frac{p}{2} + x\right)^2 - 4(\theta + y)},$$

$$k_{3,4}^2 = -\frac{1}{2}\left(\frac{p}{2} - x\right) \pm \frac{1}{2}\sqrt{\left(\frac{p}{2} - x\right)^2 - 4(\theta - y)}.$$

In order to determine the concavity of $U(k^2)$, we calculate the second derivative

$$\frac{d^2U}{d^2(k^2)} = 20h_1(k^2)^3 + 12h_2(k^2)^2 + 6h_3(k^2) + 2h_4.$$

Denote the local minimum by $k_{\min}^2$ (one of k_i^2, $i = 1, 2, 3, 4$). For diffusion-driven instability, we require that

$$k_{\min}^2 > 0$$

and

$$U(k_{\min}^2) < 0.$$

Notice that $U(0) > 0$, which is the stability condition of E^* (see Ruan [22]). We can state the following result.

THEOREM 4.1. *Turing instability occurs in system* (1) *if* $U(0) > 0$ *and there exists* $k_{min}^2 > 0$ *such that* $U(k_{min}^2) < 0$.

Remark 4.2. Theorem 4.1 shows that for the system (1) with both delayed nutrient recycling and delayed growth response, the diffusion could drive the homogeneous steady state into instability; thus certain Turing-type spatial patterns exist.

5. DELAY-INDUCED OSCILLATIONS

In this section, we determine the effect of the delay on the dynamics of the system; in particular we check if the delay in system (1) will induce oscillations in the N and P components. It is known that (see Beretta *et al*. [1] and Ruan [21]) the delay in the nutrient recycling term does not have a destabilizing effect. Thus, for the sake of convenience in discussion, we assume that the delay kernel in the nutrient recycling term in system (1) is a delta function and the delay kernel in the second equation is an exponential function:

$$F(x, y, t) = \delta(x - y)\delta(t), \; G(x, y, t) = \frac{\alpha}{2}e^{-\alpha|x-y|}\beta e^{-\beta t};$$

that is, we consider the system

$$\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t, x)f(N(t, x)) + \gamma_1 P(t, x),$$

$$\frac{\partial P}{\partial t} = d_2 \Delta P$$

$$+ P\left[-(\gamma + D) + a_1 \int_{-\infty}^{t} \int_{\Omega} \frac{e^{-\alpha|x-y|}\beta e^{-\beta(t-s)}f(N(s, y))}{\int_{\Omega} e^{-\alpha|x-z|} dz} \, dyds \right].$$

(13)

Define

$$Q(t, x) = \int_{-\infty}^{t} \beta e^{-\beta(t-s)}f(N(s, y)) \, ds.$$

Then system (13) is equivalent to the following system

$$\frac{\partial N}{\partial t} = d_1 \Delta N + D(N^0 - N) - aP(t, x)f(N(t, x)) + \gamma_1(P)(t, x),$$

$$\frac{\partial P}{\partial t} = d_2 \Delta P + P\left[-(\gamma + D) + a_1 \int_{\Omega} \frac{\exp(-\alpha|x - y|)Q(t, y)}{\int_{\Omega} \exp(-\alpha|x - z|) \, dz} \, dy \right], \quad (14)$$

$$\frac{\partial Q}{\partial t} = \beta[f(N(t, x)) - Q(t, x)].$$

The positive equilibrium of system (14) is $E^* = (N^*, P^*, Q^*)$, where N^* and P^* are the same as in section 2 and $Q^* = F(N^*)$. The characteristic equation of the linearized system (14) at E^* is given by

$$\lambda^3 + c_1(\beta)\lambda^2 + c_2(\beta)\lambda + c_3(\beta) = 0, \tag{15}$$

where

$$c_1(\beta) = \beta + (d_1 + d_2)k^2 + D + aP^*f'(N^*),$$

$$c_2(\beta) = \beta\left[(d_1 + d_2)k^2 + D + aP^*f'(N^*)\right]$$
$$+ k^4d_1d_2 + k^2d_2(D + aP^*f'(N^*)),$$

$$c_3(\beta) = \beta\left[k^4d_1d_2 + k^2d_2(D + aP^*f'(N^*))\right]$$
$$+ \beta f'(N^*)a_1P^*\delta_2\left[af(N^*) - \gamma_1\right].$$

By the Routh–Hurwitz criterion, the equilibrium E^* is locally stable if and only if

$$c_1(\beta) > 0,$$
$$c_3(\beta) > 0,$$
$$c_1(\beta)c_2(\beta) - c_3(\beta) > 0.$$

Clearly, the first two are always satisfied. Thus, the equilibrium E^* is locally stable if the third inequality holds. If for some value of β, say β_0, we have

$$c_1(\beta_0)c_2(\beta_0) = c_3(\beta_0),$$

then the characteristic Eq. (15) becomes

$$\left(\lambda + c_1(\beta_0)\right)\left(\lambda^2 + c_2(\beta_0)\right) = 0,$$

which has a negative real root $\lambda_1 = -c_1(\beta_0)$ and a pair of purely imaginary roots

$$\lambda_{2,3} = \pm i\sqrt{c_2(\beta_0)}.$$

By continuity, for $\beta \in (\beta_0 - \varepsilon, \beta_0 + \varepsilon)$, where $\varepsilon > 0$ is sufficiently small, the eigenvalues are of the form

$$\lambda_1 = -c_1(\beta); \ \lambda_{2,3} = \mu(\beta) \pm i\nu(\beta).$$

To determine if the Hopf bifurcation occurs when $\beta = \beta_0$, we need to verify the transversality condition. Substituting λ_2 into the characteristic Eq. (15), calculating the derivative with respect to β, and separating the real and imaginary parts, we obtain

$$A(\beta)\frac{d\mu(\beta)}{d\beta} - B(\beta)\frac{d\nu(\beta)}{d\beta} + C(\beta) = 0,$$

$$B(\beta)\frac{d\mu(\beta)}{d\beta} + A(\beta)\frac{d\nu(\beta)}{d\beta} + D(\beta) = 0,$$

where

$$A(\beta) = 3(\mu^2(\beta) - \nu^2(\beta)) + 2c_1(\beta)\mu(\beta) + c_2(\beta),$$
$$B(\beta) = 6\mu(\beta)\nu(\beta) + 2c_1(\beta)\nu(\beta),$$
$$C(\beta) = c_1'(\beta)(\mu^2(\beta) - \nu^2(\beta)) + c_2^2(\beta)\mu(\beta) + c_3'(\beta),$$
$$D(\beta) = 2c_1'(\beta)\mu(\beta)\nu(\beta) + c_2'(\beta)\nu(\beta).$$

Solving for $\frac{d\mu}{d\beta}$ and setting $\beta = \beta_0$, we have

$$\left.\frac{d\mu(\beta)}{d\beta}\right|_{\beta=\beta_0} = -\left.\frac{\dfrac{d}{d\beta}\left[c_1(\beta)c_2(\beta) - c_3(\beta)\right]}{4\left[c_1^2(\beta) + c_2(\beta)\right]}\right|_{\beta=\beta_0} \neq 0$$

if

$$\frac{d}{d\beta}\left[c_1(\beta)c_2(\beta) - c_3(\beta)\right]\big|_{\beta=\beta_0} \neq 0. \tag{16}$$

The transversality condition thus implies that a Hopf bifurcation occurs as β passes through the critical value β_0. We have the following result.

THEOREM 5.1.   *The positive equilibrium $E^* = (N^*, P^*)$ of system* (13) *is asymptotically stable if*

$$c_1(\beta)c_2(\beta) - c_3(\beta) > 0.$$

If there exists a $\beta_0 > 0$ such that

$$c_1(\beta_0)c_2(\beta_0) = c_3(\beta_0)$$

and condition (16) *holds, then there is a Hopf bifurcation at $E^* = (N^*, P^*)$ as β passes through β_0.*

Remark 5.2.   First, we would like to mention that the above bifurcation analysis is carried out for a fixed value of the wavenumber k. The above theorem indicates that the positive steady state of system (13) with delayed growth response is stable when the delay is less than a critical value and becomes unstable when it passes through the critical value. The oscillations of the components induced by a Hopf bifurcation demonstrate that the system exhibits certain temporal or spatial-temporal structures. On a finite domain, the oscillatory solutions are standing waves.

Remark 5.3.   There might be another $\beta_0' > 0$ such that $c_1(\beta_0')c_2(\beta_0') = c_3(\beta_0')$ and $\frac{d}{d\beta}\mu(\beta)|_{\beta=\beta_0'} \neq 0$. In this case, there are two Hopf bifurcations.

6. DISCUSSION

In this paper, we have considered a reaction−diffusion plankton model with nonlocal delayed growth response and nonlocal delayed nutrient recycling. The first inequality in (3) indicates that a_1, the maximum specific growth rate of plankton must be greater than $\gamma + D$, the total loss of plankton and the second inequality in (3) means that there must be enough nutrient input concentration. Notice that the inequalities in (3) are required throughout the paper to guarantee the existence of the positive uniform steady state and when the nonlocal delayed growth response is absent, they are exactly the local stability condition.

We first considered the model with nonlocal delayed nutrient recycling but without delay in the growth response and obtained local stability conditions. Our analysis once again shows that the delay in the nutrient recycling process does not have a destabilizing effect on the system (Beretta *et al*. [1] and Ruan [21]). Then we studied the general model with both nonlocal delayed nutrient recycling and nonlocal delayed growth response. We found that the system becomes unstable if the diffusion coefficients satisfy certain conditions; that is, Turing instability occurs. We thus generalized some of the results in Ruan [22] to the model with nonlocal delay. Finally, we analyzed the model with only nonlocal delayed growth response. It has shown that the delay does cause instability and thus oscillations in the components via a Hopf bifurcation.

ACKNOWLEDGMENTS

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