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Turing instability and travelling waves in diffusive plankton models with delayed nutrient recycling

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In this paper we propose a reaction–diffusion system with two distributed delays to stimulate the growth of plankton communities in the lakes/oceans in which the plankton feeds on a limiting nutrient supplied at a constant rate. The limiting nutrient is partially recycled after the death of the organisms and a distributed delay is used to model nutrient recycling. The second delay is involved in the growth response of the plankton to nutrient uptake. We first show that there are oscillations (Hopf bifurcations) in the delay model induced by the second delay. Then we study Turing (diffusion-driven) instability of the reaction–diffusion system with delay. Finally, it is shown that if the delay model has a stable periodic solution, then the corresponding reaction–diffusion model with delay has a family of travelling waves.

1. Introduction

The effect of nutrient recycling on stability of ecosystems has been extensively studied (see Beretta *et al.*, 1990; Nisbet & Gurney, 1976). Nisbet & Gurney (1976) regarded nutrient recycling 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, 1975)). In order to simulate the growth of planktonic communities of unicellular algae in the lakes, Beretta *et al.* (1990) 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 in chemostat experiments that there is a delay in growth response even when the limiting nutrient is at undetectable small concentration (see (Caperon, 1969)). In a previous paper (Ruan, 1995a), we incorporated a discrete delay in the growth response of the species to nutrient uptake in the model of Beretta *et al.* (1990) and studied the effect of delays on the stability and persistence of the delay model. Further study of this model is carried out in (He & Ruan, 1998). Beretta & Takeuchi (1994) used another distributed delay to describe the delayed growth response, namely, they considered a system of two retarded functional differential equations with two distributed delays. They investigated the global stability of the positive equilibrium by using the Liapunov functionals method. See He, Ruan & Xia (1998) for related work.

In the lakes/oceans, plankton population movement is subject to many factors, such as currents and turbulent lateral diffusion, to name a few. Thus, it is more realistic to use reaction–diffusion equations to model the dynamics of plankton–nutrient interaction, cf. (Levin & Segel, 1976; Mimura, 1979; Okubo, 1980; Ruan, 1995b), etc. The object of the present paper is to propose a reaction–diffusion plankton model with delayed growth response and delayed nutrient recycling, that is, a reaction–diffusion system with two distributed (infinite) delays. This kind of system has been studied by many authors; we refer to (Kuang & Smith, 1993; Pao, 1996; Ruan & Wu, 1994) and references cited therein.

In studying morphogenesis, Turing (1952) considered reaction–diffusion equations of two chemicals and found that diffusion could destabilize an otherwise stable equilibrium. This leads to non-uniform spatial patterns which could then generate biological patterns by gene activation. This kind of instability is usually called *Turing instability* (Murray, 1989) or *diffusion-driven instability* (Okubo, 1980). For reviews and related work on Turing instability and spatial pattern formation, we refer to (Levin & Segel, 1985; Murray, 1989). Turing instability in reaction–diffusion systems with delay was first considered by Levin & Segel (1985). Recently, Choudhury & Fosser (1996) studied Turing instability in reaction–diffusion predator–prey models with distributed delay in the interspecies interaction terms. They derived necessary and sufficient conditions for Turing instability and found that these conditions are different from the classical conditions without delay. Gourley (1996) also studied instability of a predator–prey model with delay and spatial averaging.

Systems of reaction–diffusion equations from applied sciences such as chemistry, epidemiology and neurophysiology possess travelling wave solutions; for a survey see (Volpert *et al.*, 1994). More recently, travelling wave solutions have been established for reaction–diffusion equations with delay; we refer to (Bonilla & Liñán, 1984; Britton, 1990; Cavani, 1988; Gopalsamy, 1986; Gourley & Britton, 1996; de Oliveira, 1994; Rey & Mackey, 1992; Schaaf, 1987; Zou & Wu, 1997), etc.

Let $N(t,x)$ and $P(t,x)$ denote the densities of nutrient and plankton at time t and location x, where $0 \leqslant t < \infty$, $-\infty < x < \infty$. Let $d_i > 0$ denote the diffusion coefficients $(i = 1, 2)$. Consider the following reaction–diffusion plankton model with delayed nutrient recycling:

$$
\begin{aligned}
\frac{\partial N}{\partial t} &= d_1 \frac{\partial^2 N}{\partial x^2} + D(N^0 - N(t,x)) - aP(t,x) f(N(t,x)) + \gamma_1 \int_{-\infty}^{t} F(t-\tau) P(\tau,x)\,\mathrm{d}\tau, \\
\frac{\partial P}{\partial t} &= d_2 \frac{\partial^2 P}{\partial x^2} + P(t,x)\left[-(\gamma + D) + a_1 \int_{-\infty}^{t} G(t-\tau) f(N(\tau,x))\,\mathrm{d}\tau\right]
\end{aligned} \tag{1.1}
$$

under the initial value conditions

$$
N(\theta,x) = \phi(\theta,x), \quad P(\theta,x) = \psi(\theta,x), \quad \theta \in (-\infty, 0], \tag{1.2}
$$

where ϕ and ψ are positive continuous functions.

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

a	–	maximal nutrient uptake rate for the plankton
N^0	–	input concentration of the nutrient
D	–	washout rate of the nutrient
γ	–	plankton mortality rate
γ_1	–	nutrient recycle rate after the death of the plankton, $\gamma_1 \leqslant \gamma$
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 non-negative, increasing, and vanishes when 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

$$f(0) = 0, \quad \frac{\mathrm{d}f}{\mathrm{d}N} > 0, \quad \lim_{N\to\infty} f(N) = 1. \tag{1.3}$$

These hypotheses are satisfied by the Michaelis–Menton 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 non-negative bounded functions defined on $[0, \infty)$. Let F describe the contribution of the plankton population dead in the past to the nutrient recycled at time t and G describe the delayed growth response of the plankton. The presence of the distributed time delays must not affect the equilibrium values, so we normalize the kernels such that

$$\int_0^\infty F(s)\,\mathrm{d}s = \int_0^\infty G(s)\,\mathrm{d}s = 1. \tag{1.4}$$

In particular, the so-called *weak kernel* $\alpha \mathrm{e}^{-\alpha s}$ and *strong kernel* $\alpha^2 s\mathrm{e}^{-\alpha s}$, $\alpha > 0$ are frequently used in biological modelling; see (Cushing, 1977; MacDonald, 1978).

A special case of system (1.1) is the following delay system:

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= D(N^0 - N) - aPf(N) + \gamma_1 \int_{-\infty}^t F(t-\tau)P(\tau)\,\mathrm{d}\tau, \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= P\left[-(\gamma + D) + a_1 \int_{-\infty}^t G(t-\tau) f(N(\tau))\,\mathrm{d}\tau\right]. \end{aligned} \tag{1.5}$$

Note that a positive equilibrium of the delay system (1.5) is a spatial homogeneous steady state of the reaction–diffusion system (1.1). Thus, if

$$\gamma + D < a_1 \quad \text{and} \quad f^{-1}\left(\frac{\gamma + D}{a_1}\right) < N^0, \tag{1.6}$$

then system (1.1) has a uniform steady state $E^* = (N^*, P^*)$ with

$$N^* = f^{-1}\left(\frac{\gamma + D}{a_1}\right), \quad P^* = \frac{D(N^0 - N^*)}{af(N^*) - \gamma_1}. \tag{1.7}$$

In this paper, we first consider a special case, namely the delay model (1.5). By using the (average) delay involved in the growth response term as a bifurcation parameter, it is shown that when the delay is changed by a critical value, the positive equilibrium loses its stability and a Hopf bifurcation occurs, that is, a family of periodic solutions exists. Then we consider the delayed reaction–diffusion system (1.1). It is found that the diffusion can drive the spatial homogeneous steady state to unstable, that is, Turing instability occurs.

Finally, suppose that the set of bifurcating periodic solutions of the delay system (1.5) is orbitally asymptotically stable, then the corresponding delayed reaction–diffusion system (1.1) has a family of travelling waves. This is a generalization of the results of Koppel & Howard (1973) on classical reaction–diffusion systems and of de Oliveira (1994) on reaction–diffusion systems with finite delay.

2. Delay Induced Oscillations

First we consider the delay model (1.5), a special case of system (1.1). Suppose that $F(s) = \alpha e^{-\alpha s}$, $\alpha > 0$, $G(s) = \beta e^{-\beta s}$, $\beta > 0$. We have the following delay system:

$$\begin{aligned} \frac{dN}{dt} &= D(N^0 - N) - aPf(N) + \gamma_1 \int_{-\infty}^{t} \alpha e^{-\alpha(t-\tau)} P(\tau)\, d\tau, \\ \frac{dP}{dt} &= P\left[-(\gamma + D) + a_1 \int_{-\infty}^{t} \beta e^{-\beta(t-\tau)} f(N(\tau))\, d\tau\right]. \end{aligned} \tag{2.1}$$

The characteristic equation of the linearized system of (2.1) at the positive equilibrium $E^* = (N^*, P^*)$ is

$$\lambda^4 + c_1(\beta)\lambda^3 + c_2(\beta)\lambda^2 + c_3(\beta)\lambda + c_4(\beta) = 0, \tag{2.2}$$

where

$$\begin{aligned} c_1(\beta) &= \alpha + \beta + D + aP^* f'(N^*), \\ c_2(\beta) &= \alpha\beta + (\alpha + \beta)(D + aP^* f'(N^*)), \\ c_3(\beta) &= \alpha\beta(D + aP^* f'(N^*)) + a\beta(\gamma + D)P^* f'(N^*), \\ c_4(\beta) &= \alpha\beta a_1 P^* f'(N^*)[af(N^*) - \gamma_1]. \end{aligned}$$

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

$$\begin{aligned} c_1(\beta) &> 0, \\ c_4(\beta) &> 0, \\ c_1(\beta)c_2(\beta) - c_3(\beta) &> 0, \\ c_1(\beta)[c_2(\beta)c_3(\beta) - c_1(\beta)c_4(\beta)] - c_3^2(\beta) &> 0. \end{aligned}$$

Clearly, the first two hold. The third inequality holds if γ is not sufficiently large. Thus, the equilibrium is locally stable if the last inequality also holds. We want to know if there is a Hopf bifurcation at E^* when the delays are changed. It is known that (Beretta *et al.*, 1990; Ruan, 1995a) the delay in the nutrient recycling term does not have a destabilizing effect. So we choose β, the delay in the growth term, as a bifurcation parameter. Define

$$\phi(\beta) = c_1(\beta)[c_2(\beta)c_3(\beta) - c_1(\beta)c_4(\beta)] - c_3^2(\beta). \tag{2.3}$$

Then the local stability condition of E^* is $\phi(\beta) > 0$.

Let λ_i $(i = 1, 2, 3, 4)$ be the roots of the characteristic equation (2.2). Then we have

$$\begin{aligned} \lambda_1 + \lambda_2 + \lambda_3 + \lambda_4 &= -c_1(\beta), \\ \lambda_1\lambda_2 + \lambda_1\lambda_3 + \lambda_1\lambda_4 + \lambda_2\lambda_3 + \lambda_2\lambda_4 + \lambda_3\lambda_4 &= c_2(\beta), \\ \lambda_1\lambda_2\lambda_3 + \lambda_1\lambda_3\lambda_4 + \lambda_2\lambda_3\lambda_4 + \lambda_1\lambda_2\lambda_4 &= -c_3(\beta), \\ \lambda_1\lambda_2\lambda_3\lambda_4 &= c_4(\beta). \end{aligned} \tag{2.4}$$

If there exists $\beta_0 \in \mathbb{R} = (-\infty, \infty)$ such that $\phi(\beta_0) = 0$, then by the Routh–Hurwitz criterion there is at least one root, say λ_1, such that $\mathrm{Re}\lambda_1 = 0$. From the fourth equation of (2.4) it follows that $\mathrm{Im}\lambda_1 = \omega_0 \neq 0$, and hence there is another root, say λ_2, such that $\lambda_2 = \overline{\lambda}_1$. Since $\phi(\beta)$ is a polynomial, it is a continuous function of its roots, λ_1 and λ_2 are complex conjugate for $\beta \in (\beta_1, \beta_2)$ which includes β_0. Therefore, at β_0, equations (2.4) become

$$\begin{aligned} &\lambda_3 + \lambda_4 = -c_1(\beta), &\quad &\omega_0^2 + \lambda_3\lambda_4 = c_2(\beta), \\ &\omega_0^2(\lambda_3 + \lambda_4) = -c_3(\beta), &\quad &\omega_0^2\lambda_3\lambda_4 = c_4(\beta). \end{aligned} \tag{2.5}$$

If λ_3 and λ_4 are complex conjugate, from $(2.5)_1$ it follows that $2\mathrm{Re}\lambda_3 = -c_1(\beta)$. If λ_3 and λ_4 are real, from $(2.5)_{1,4}$ it follows that $\lambda_3 < 0$ and $\lambda_4 < 0$. Thus, when $\beta = \beta_0$, the characteristic equation (2.2) has a pair of purely imaginary roots λ_1 and λ_2, and a pair of other roots λ_3 and λ_4 with negative real part. To check if a Hopf bifurcation occurs, we need to verify the transversality condition. After some calculations it follows that

$$\frac{\mathrm{d}}{\mathrm{d}\beta}[\mathrm{Re}\lambda_{1,2}]_{\beta_0} = -\frac{c_1}{2[c_1^2 c_4 + (c_1 c_2 - 2c_3)^2]} \frac{\mathrm{d}\phi}{\mathrm{d}\beta}\bigg|_{\beta_0}. \tag{2.6}$$

The above analysis can be summarized as follows.

THEOREM 2.1 Suppose that the inequalities in (1.6) hold. If $\phi(\beta) > 0$, then the equilibrium E^* of system (1.1) is locally asymptotically stable. If there exists $\beta_0 \in R$ such that $\phi(\beta_0) = 0$ and $\mathrm{d}\phi/\mathrm{d}\beta$ is non-zero at β_0, then as β passes through the critical value β_0, a Hopf bifurcation occurs at E^*.

Notice that the average time delay is defined as $T = 1/\beta$; see (MacDonald, 1978). By the Hopf bifurcation theorem (Marsden & McCracken, 1976), a family of periodic solutions exists for values of $T = 1/\beta$ near $T_0 = 1/\beta_0$. By using the algorithm in (Hassard *et al.*, 1981), we can determine the stability of the bifurcating periodic solutions; see (Ruan & Wolkowicz, 1996).

Choose $f(N) = mN/(K + N)$ and parameter values $m = 1$, $K = 5{\cdot}85$, $D = 0{\cdot}08$, $N^0 = 3{\cdot}66$, $a = 4{\cdot}25$, $\gamma = 0{\cdot}58$, $\gamma_1 = 0{\cdot}12$, $a_1 = 3{\cdot}45$, $\alpha = 0{\cdot}45$. By Theorem 2.1, there is a critical value $\beta_0 = 0{\cdot}17$, the equilibrium $E^* = (1{\cdot}38, 0{\cdot}26)$ is locally stable when $T = 1/\beta < T_0 = 1/\beta_0 = 1/0{\cdot}17$, that is, when $\beta > 0{\cdot}17$; when β passes through the critical value $\beta_0 = 0{\cdot}17$, a Hopf bifurcation occurs at the equilibrium E^*; when $T > T_0$, that is when $\beta < \beta_0$, there is a periodic solution. Our numerical simulation indicates that an orbitally stable limit cycle exists for β slight less than $\beta_0 = 0{\cdot}17$ (see Fig. 1). In the following, we make an assumption:

(H) The bifurcating periodic solutions are orbitally asymptotically stable.

3. Diffusion-driven instability

Recall that if $\phi(\beta) > 0$, then the equilibrium E^* of the delay system (2.1) is stable. Now we shall determine the stability of E^* as a homogeneous solution of the reaction–diffusion system (1.1). We want to see if the diffusion coefficients induce instability; that is, if Turing instability occurs to model (1.1).

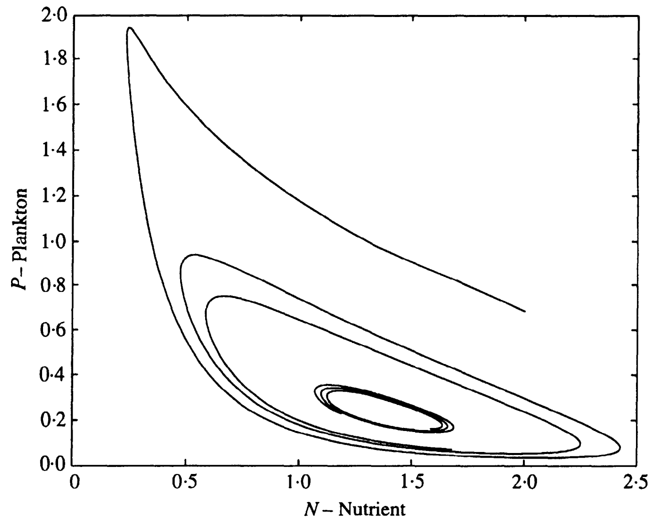

FIG. 1. With $\beta = 0{\cdot}1425$, there is an orbitally stable limit cycle attracting two trajectories. One trajectory has initial values outside the limit cycle, another has initial values inside the limit cycle near the equilibrium.

Suppose that $F(s)$ and $G(s)$ are weak kernels as given in Section 2. Define

$$R(t,x) = \int_{-\infty}^{t} \alpha e^{-\alpha(t-\tau)} P(\tau, x)\,d\tau, \qquad Q(t,x) = \int_{-\infty}^{t} \beta e^{-\beta(t-\tau)} f(N(\tau, x))\,d\tau.$$

Then system (1.1) is equivalent to the following system:

$$\begin{aligned}
\frac{\partial N}{\partial t} &= d_1 \frac{\partial^2 N}{\partial x^2} + D(N^0 - N(t,x)) - aP(t,x) f(N(t,x)) + \gamma_1 R(t,x),\\
\frac{\partial P}{\partial t} &= d_2 \frac{\partial^2 P}{\partial x^2} + P(t,x)[-(\gamma + D) + a_1 Q(t,x)],\\
\frac{\partial R}{\partial t} &= \alpha[P(t,x) - R(t,x)],\\
\frac{\partial Q}{\partial t} &= \beta[f(N(t,x)) - Q(t,x)].
\end{aligned} \tag{3.1}$$

The positive equilibrium of the system (3.1) is $E^* = (N^*, P^*, R^*, Q^*)$ with $R^* = P^*$, $Q^* = f(N^*)$; N^* and P^* are given by (1.7). Let

$$u_1 = N - N^*, \quad u_2 = P - P^*, \quad u_3 = R - R^*, \quad u_4 = Q - Q^*. \tag{3.2}$$

The linearized system of (3.1) at E^* has the form

$$\begin{aligned}
\frac{\partial u_1}{\partial t} &= d_1\frac{\partial^2 u_1}{\partial x^2} - [D + aP^* f'(N^*)]u_1 - af(N^*)u_2 + \gamma_1 u_3,\\
\frac{\partial u_2}{\partial t} &= d_2\frac{\partial^2 u_2}{\partial x^2} + a_1 P^* u_4,\\
\frac{\partial u_3}{\partial t} &= \alpha u_2 - \alpha u_3,\\
\frac{\partial u_4}{\partial t} &= \beta f'(N^*)u_1 - \beta u_4.
\end{aligned} \tag{3.3}$$

Let

$$\begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{pmatrix} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \alpha_4 \end{pmatrix} \cos(kx)\, \mathrm{e}^{\nu t},$$

where k is the wavenumber in the x-direction and ν is the frequency. Thus, we have the characteristic equation

$$\nu^4 + b_1(k^2)\nu^3 + b_2(k^2)\nu^2 + b_3(k^2)\nu + b_4(k^2) = 0, \tag{3.4}$$

where

$$\begin{aligned}
b_1(k^2) &= (d_1 + d_2)k^2 + \alpha + \beta + D + aP^* f'(N^*),\\
b_2(k^2) &= d_1 d_2 (k^2)^2 + [(\alpha + \beta)(d_1 + d_2) - d_2(D + aP^* f'(N^*))]k^2\\
&\quad + \alpha\beta + (\alpha + \beta)(D + aP^* f'(N^*)),\\
b_3(k^2) &= d_1 d_2(\alpha + \beta)(k^2)^2 + [\alpha\beta(d_1 + d_2) + d_2(\alpha + \beta)(D + aP^* f'(N^*))]k^2\\
&\quad + \alpha\beta(D + aP^* f'(N^*)) + a\beta(\gamma + D)P^* f'(N^*),\\
b_4(k^2) &= \alpha\beta d_1 d_2 (k^2)^2 + \alpha\beta d_2(D + aP^* f'(N^*))k^2\\
&\quad + \alpha\beta a_1 P^* f'(N^*)[af(N^*) - \gamma_1].
\end{aligned}$$

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

Notice that $b_i(0) = c_i(\beta)$ $(i = 1, 2, 3, 4)$. Clearly, (i) and (ii) cannot be violated; (iii) also cannot be violated if $c_1(\beta)c_2(\beta) - c_3(\beta) > 0$. To check (iv), denote

$$H(k^2) = b_1(k^2)[b_2(k^2)b_3(k^2) - b_1(k^2)b_4(k^2)] - b_3^2(k^2),$$

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

$$H(k^2) = a_1(k^2)^5 + a_2(k^2)^4 + a_3(k^2)^3 + a_4(k^2)^2 + a_5(k^2) + a_6, \tag{3.5}$$

where ($A = D+aP^* f'(N^*)$, $B = a\beta(\gamma+D)P^* f'(N^*)$, $C = \alpha\beta a_1 P^* f'(N^*)[af(N^*)-\gamma_1]$)

$$\begin{aligned}
a_1 &= (\alpha+\beta)(d_1+d_2)d_1 d_2^3,\\
a_2 &= (\alpha+\beta)^2 d_1 d_2^3 + (\alpha+\beta)^2 d_2^2(d_1+d_2)^2 + A(\alpha+\beta)(d_1+d_2)d_2^3\\
&\quad + A(\alpha+\beta)(d_1+d_2)d_1 d_2^2 + A(\alpha+\beta)d_1 d_2^3 - (\alpha+\beta)^2 d_2^4,\\
a_3 &= A^2(\alpha+\beta)d_2^3 + A^2(\alpha+\beta)d_1 d_2^2 + (\alpha+\beta)^3(d_1+d_2)d_2^2\\
&\quad + A(\alpha+\beta)d_1 d_2^2 + \alpha\beta(\alpha+\beta)(d_1+d_2)d_2^2 + \alpha\beta(\alpha+\beta)(d_1+d_2)^3\\
&\quad + A(\alpha+\beta)^2(d_1+d_2)^2 d_2 + A^2(\alpha+\beta)(d_1+d_2)d_2^2 + B(d_1+d_2)d_1 d_2\\
&\quad + 2A(\alpha+\beta)^2(d_1+d_2)d_2^2 - A(\alpha+\beta)^2 d_2^3 - \alpha\beta(\alpha+\beta)(d_1+d_2)d_1 d_2,\\
a_4 &= A^2(\alpha+\beta)^2 d_2^2 + A^3(\alpha+\beta)d_2^2 + A^3(d_1+d_2)d_2^3 + \alpha\beta(\alpha+\beta)^2 d_2^2\\
&\quad + A(\alpha+\beta)^2 d_2^2 + \alpha\beta(\alpha+\beta)^2(d_1+d_2)^2 + A(\alpha+\beta)^3(d_1+d_2)d_2\\
&\quad + C(\alpha+\beta)(d_1+d_2)^2 + ABd_2(d_1+d_2) + 3A\alpha\beta(\alpha+\beta)(d_1+d_2)^2\\
&\quad + 2A^2(\alpha+\beta)^2(d_1+d_2) + ABd_1 d_2 + C(\alpha+\beta)d_1 d_2\\
&\quad - \alpha\beta(\alpha+\beta)^2 d_1 d_2 - C(d_1+d_2)^2 - A\alpha\beta(\alpha+\beta)d_2^2 - A\alpha\beta(\alpha+\beta)d_1 d_2,\\
a_5 &= 3A^2\alpha\beta(\alpha+\beta)(d_1+d_2) + A^3(\alpha+\beta)d_2 + A^2 Bd_2 + 2A\alpha\beta(\alpha+\beta)^2(d_1+d_2)\\
&\quad + A^2(\alpha+\beta)^3 d_2 + C(\alpha+\beta)^2(d_1+d_2) + 2AB(\alpha+\beta)(d_1+d_2)\\
&\quad + B\alpha\beta(d_1+d_2) - 2A(\alpha+\beta)(d_1+d_2) - ABd_2(\alpha+\beta)\\
&\quad - 2C(\alpha+\beta)(d_1+d_2) - 2A^2\alpha\beta d_2(\alpha+\beta),\\
a_6 &= A^2 B(\alpha+\beta) + AB(\alpha+\beta)^2 + A^3\alpha\beta(\alpha+\beta) + A^2\alpha\beta(\alpha+\beta)^2 + A\alpha^2\beta^2(\alpha+\beta)\\
&\quad + B\alpha\beta(\alpha+\beta) - A^2 C - B^2 - C(\alpha+\beta)^2 - 2AC(\alpha+\beta) - AB\alpha\beta.
\end{aligned}$$

Notice that $a_1 > 0$, so $H(k^2) \to \infty$ as $k^2 \to \infty$. The first derivative of H with respect to k^2 is

$$\frac{\mathrm{d}H}{\mathrm{d}k^2} = 5a_1(k^2)^4 + 4a_2(k^2)^3 + 3a_3(k^2)^2 + 2a_4(k^2) + a_5. \tag{3.6}$$

To find the local extrema of $H(k^2)$, we need to find the roots of the equation $\mathrm{d}H/\mathrm{d}k^2 = 0$, which can be written as

$$(k^2)^4 + p(k^2)^3 + q(k^2)^2 + r(k^2) + s = 0, \tag{3.7}$$

where

$$p = \frac{4a_2}{5a_1}, \quad q = \frac{3a_3}{5a_1}, \quad r = \frac{2a_4}{5a_1}, \quad s = \frac{a_5}{5a_1}.$$

Choose a, b and add $(ak^2+b)^2$ to both sides of (3.7), such that

$$[(k^2)^2 + \tfrac{1}{2}p(k^2) + \theta]^2 = (ak^2+b)^2, \tag{3.8}$$

where θ is a real root of the cubic equation

$$8\theta^3 - 4q\theta^2 + 2(pr-4s)\theta - p^2 s + 4qs - r^2 = 0. \tag{3.9}$$

Thus, equation (3.7) is equivalent to a system of two quadratic equations:

$$(k^2)^2 + (\tfrac{1}{2}p + a)k^2 + (\theta + b) = 0, \quad (k^2)^2 + (\tfrac{1}{2}p - a)k^2 + (\theta - b) = 0, \tag{3.10}$$

from which we can find the possible local extrema:

$$\begin{aligned} k_{1,2}^2 &= -\tfrac{1}{2}(\tfrac{1}{2}p + a) \pm \tfrac{1}{2}\left((\tfrac{1}{2}p + a)^2 - 4(\theta + b)\right)^{\frac{1}{2}}, \\ k_{3,4}^2 &= -\tfrac{1}{2}(\tfrac{1}{2}p - a) \pm \tfrac{1}{2}\left((\tfrac{1}{2}p - a)^2 - 4(\theta - b)\right)^{\frac{1}{2}}. \end{aligned} \tag{3.11}$$

By using the second derivative

$$\frac{\mathrm{d}^2 H}{\mathrm{d}(k^2)^2} = 20a_1(k^2)^3 + 12a_2(k^2)^2 + 6a_3k^2 + 2a_4,$$

we can determine the concavity of $H(k^2)$. Denote the local minimum by $k^2_{\min}$ (one of k_i^2). For diffusive instability, we require that

$$k^2_{\min} > 0 \tag{3.12}$$

and

$$H(k^2_{\min}) < 0. \tag{3.13}$$

Notice that $H(0) = \phi(\beta)$. One can see that $\phi(\beta) > 0$, the stability criterion of E^*, is exactly $H(0) > 0$. Now we can state the following result.

THEOREM 3.1 Turing (diffusion-driven) instability occurs if $H(0) = \phi(\beta) > 0$, $k^2_{\min} > 0$ and $H(k^2_{\min}) < 0$.

Choose $f(N) = mN/(K + N)$ and parameter values $m = 1, K = 5{\cdot}85, D = 35{\cdot}77, N^0 = 3{\cdot}66, a = 1620, \gamma = 0{\cdot}58, \gamma_1 = 0{\cdot}12, a_1 = 190, \alpha = 0{\cdot}45, \beta = 8$. We can verify that $H(0) = \phi(\beta) > 0$, which implies that the equilibrium of the delay model (2.1) is stable. With the choice of $d_1 = 1, d_2 = 5$, the numerical computation indicates that the conditions in Theorem 3.1 are satisfied (see Fig. 2).

4. Travelling wave solutions

In this section, we suppose that there exists $\beta_0 \in \mathbb{R}$ such that $\phi(\beta_0) = 0$ and $\mathrm{d}\phi/\mathrm{d}\beta$ is non-zero at β_0. Then by Theorem 2.1 there is a periodic solution, say $(p_1(t), p_2(t))$, to the delay equations (2.1) bifurcating from E^* as β passes through the critical value β_0. We also assume that the assumption (H) holds, that is, $(p_1(t), p_2(t))$ is orbitally asymptotically stable. Furthermore, assume that the period of $(p_1(t), p_2(t))$ is $\omega := \omega(\beta)$.

To search travelling wave solutions of the equivalent system (3.1), let

$$N(t,x) = N(z), \quad P(t,x) = P(z), \quad R(t,x) = R(z), \quad Q(t,x) = Q(z), \tag{4.1}$$

where $z = kx + ct$, c is the velocity of the wave and k is the wavenumber. The equations

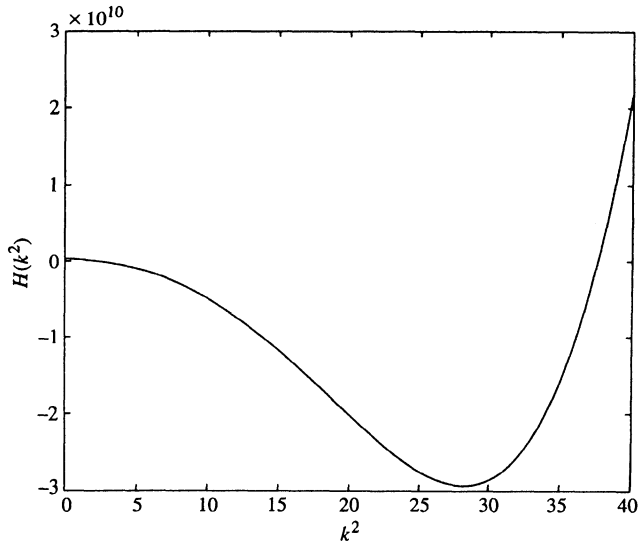

FIG. 2. With $d_1 = 1,\ d_2 = 5,\ H(k^2)$ becomes negative for a finite range of $k^2 > 0$.

in travelling wave form are

$$
\begin{aligned}
c\frac{\mathrm{d}N}{\mathrm{d}z} &= k^2 d_1 \frac{\mathrm{d}^2 N}{\mathrm{d}z^2} + D(N^0 - N(z)) - aP(z)f(N(z)) + \gamma_1 R(z),\\
c\frac{\mathrm{d}P}{\mathrm{d}z} &= k^2 d_2 \frac{\mathrm{d}^2 P}{\mathrm{d}z^2} + P(z)[-(\gamma + D) + a_1 Q(z)],\\
c\frac{\mathrm{d}R}{\mathrm{d}z} &= \alpha[P(z) - R(z)],\\
c\frac{\mathrm{d}Q}{\mathrm{d}z} &= \beta[f(N(z)) - Q(z)].
\end{aligned}
$$

Use the translation (3.2) once more, we have

$$
\begin{aligned}
c\frac{\mathrm{d}u_1}{\mathrm{d}z} &= k^2 d_1 \frac{\mathrm{d}^2 u_1}{\mathrm{d}z^2} - [D + P^* f'(N^*)]u_1 - af(N^*)u_2 + \gamma_1 u_3 - af'(N^*)u_1 u_2,\\
c\frac{\mathrm{d}u_2}{\mathrm{d}z} &= k^2 d_2 \frac{\mathrm{d}^2 u_2}{\mathrm{d}z^2} + a_1 P^* u_4 + a_1 u_2 u_4,\\
c\frac{\mathrm{d}u_3}{\mathrm{d}z} &= \alpha u_2 - \alpha u_3,\\
c\frac{\mathrm{d}u_4}{\mathrm{d}z} &= \beta f'(N^*)u_1 - \beta u_4.
\end{aligned} \tag{4.2}
$$

Introducing two new variables

$$
u_5 = c\frac{\mathrm{d}u_1}{\mathrm{d}z}, \quad u_6 = c\frac{\mathrm{d}u_2}{\mathrm{d}z},
$$

we have

$$
\begin{aligned}
c\frac{\mathrm{d}u_1}{\mathrm{d}z} &= u_5,\\
c\frac{\mathrm{d}u_2}{\mathrm{d}z} &= u_6,\\
c\frac{\mathrm{d}u_3}{\mathrm{d}z} &= \alpha u_2 - \alpha u_3,\\
c\frac{\mathrm{d}u_4}{\mathrm{d}z} &= \beta f'(N^*)u_1 - \beta u_4,\\
k^2\frac{\mathrm{d}u_5}{\mathrm{d}z} &= (c/d_1)\{[D + P^* f'(N^*)]u_1 + af(N^*)u_2 - \gamma_1 u_3 + u_5 + af'(N^*)u_1u_2\},\\
k^2\frac{\mathrm{d}u_6}{\mathrm{d}z} &= (c/d_2)[-a_1P^*u_4 + u_6 - a_1u_2u_4].
\end{aligned}
\tag{4.3}
$$

Denote $v = \mathrm{col}(u_1, u_2, u_3, u_4)$, $w = \mathrm{col}(u_5, u_6)$. Then the above system can be writen in the following abstract form:

$$
c\frac{\mathrm{d}v}{\mathrm{d}z} = Av + Bw, \qquad k^2\frac{\mathrm{d}w}{\mathrm{d}z} = tCw + G(v),
\tag{4.4}
$$

where

$$
A = \begin{pmatrix} 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & \alpha & -\alpha & 0\\ \beta f'(N^*) & 0 & 0 & -\beta \end{pmatrix}, \quad B = \begin{pmatrix} 1 & 0\\ 0 & 1\\ 0 & 0\\ 0 & 0 \end{pmatrix}, \quad C = \begin{pmatrix} c/d_1 & 0\\ 0 & c/d_2 \end{pmatrix}
$$

and

$$
G(v) = \begin{pmatrix} (c/d_1)[D + P^* f'(N^*)]v_1 + (c/d_1)af(N^*)v_2 - (c/d_1)\gamma_1 v_3 + (c/d_1)af'(N^*)v_1v_2\\ -(c/d_2)a_1P^*v_4 - (c/d_2)a_1v_2v_4 \end{pmatrix}.
$$

If $k^2 = 0$ in (4.4), then $w = -C^{-1}G(v)$ and $c\mathrm{d}v/\mathrm{d}z = Av - BC^{-1}G(v)$, that is,

$$
\begin{aligned}
c\frac{\mathrm{d}v_1}{\mathrm{d}z} &= -[D + P^* f'(N^*)]v_1 - af(N^*)v_2 + \gamma_1 v_3 - af'(N^*)v_1v_2,\\
c\frac{\mathrm{d}v_2}{\mathrm{d}z} &= a_1P^*v_4 + a_1v_2v_4,\\
c\frac{\mathrm{d}v_3}{\mathrm{d}z} &= \alpha v_2 - \alpha v_3,\\
c\frac{\mathrm{d}v_4}{\mathrm{d}z} &= \beta f'(N^*)v_1 - \beta v_4,
\end{aligned}
\tag{4.5}
$$

or

$$
c\frac{\mathrm{d}v}{\mathrm{d}z} = F(v).
\tag{4.6}
$$

This is the same system as in (4.2) with $k^2 = 0$. By assumption, for $c = 1$, system (4.4) has a periodic solution with period $\omega = \omega(\beta)$, then with $\overline{z} = z/c,\ c \neq 1$, system (4.6) takes the form

$$\mathrm{d}v/\mathrm{d}z = F(v), \tag{4.7}$$

which has a periodic solution of period ω. Thus, for $c \neq 1$, system (4.6) has a periodic solution of period $c\omega$.

Fix $c = c_0$ and denote the $c_0\omega$-periodic solution of (4.4) by $v^0 = \mathrm{col}(v_1^0, v_2^0, v_3^0, v_4^0)$. Hence, the degenerate case of (4.4) with $k^2 = 0$ has a $c_0\omega$-periodic solution $v = v^0,\ w = w^0$, where $w^0 = \mathrm{col}(c_0\mathrm{d}v_1^0/\mathrm{d}z, c_0\mathrm{d}v_2^0/\mathrm{d}z)$. Let $\xi = w - w^0$. Then $(4.4)_2$ becomes

$$k^2\frac{\mathrm{d}\xi}{\mathrm{d}z} = C\xi + G(v) + Cw^0 - k^2\frac{\mathrm{d}w^0}{\mathrm{d}z}. \tag{4.8}$$

Denote

$$\begin{aligned} C_\omega(\mathbb{R}, \mathbb{R}^3) &= \{f \mid f \in C(\mathbb{R}, \mathbb{R}^3), \quad f(t+\omega) = f(t)\}, \\ N[v^0, \rho] &= \{v \mid v \in C_{c_0\omega}(\mathbb{R}, \mathbb{R}^3), \quad \|v - v^0\| \leqslant \rho\}, \end{aligned}$$

where $\|v\| = \max_{0 \leqslant t \leqslant c_0\omega} \|v(t)\|_{\mathbb{R}^3}$. The following lemma is useful in estimating the solutions.

LEMMA 4.1 (Rozhkov, 1975) If C has no eigenvalue with zero real part, then the equation

$$k^2\frac{\mathrm{d}\xi}{\mathrm{d}z} = C\xi + f(t)$$

has a unique $c_0\omega$-periodic solution for each $f \in C_{c_0\omega}(\mathbb{R}, \mathbb{R}^2)$ and $0 < k^2 < k_0^2$, for some $k_0^2 \in (0, \infty)$. If this solution is denoted by $\xi = H_k(f)$, then the linear operator H_k is uniformly bounded:

$$\|H_k(f)\| \leqslant K\|f\|,$$

where the constant $K > 0$ is independent of k^2 and f.

If we fix $v \in N[v^0, \rho]$, then by Lemma 4.1, there exists $k_0^2 \in (0, \infty)$ such that (4.8) has a unique $c_0\omega$-periodic solution

$$\xi = H_k\left(G(v) + Cw^0 - k^2\frac{\mathrm{d}w^0}{\mathrm{d}z}\right)$$

for $0 < k^2 < k_0^2$ and

$$\begin{aligned} \|\xi\| &\leqslant K\left\|G(v) + Cw^0 - k^2\frac{\mathrm{d}w^0}{\mathrm{d}z}\right\| \leqslant K\left\|G(v) - G(v^0) - k^2\frac{\mathrm{d}w^0}{\mathrm{d}z}\right\| \\ &\leqslant K\left\|\frac{\partial G}{\partial v}(v^0)\right\| \|v^0\| + Kk^2\left\|\frac{\mathrm{d}w^0}{\mathrm{d}z}\right\| \leqslant K_1\rho + K_2k^2. \end{aligned}$$

Thus, if ρ and k^2 are small enough, $\|\xi\|$ is small too; if v is close to v^0, then the unique

$c_0\omega$-periodic solution w of (4.8) close to w^0 corresponds to v, represented by the operator π_k defined by

$$w = \pi_k(v).$$

Following Rozhkov (1975), we know that the system (4.4) is equivalent to the operator equations

$$c\frac{\mathrm{d}v}{\mathrm{d}z} = Av + Bw, \qquad w = w^0 + \pi_k(v) \tag{4.9}$$

and the following holds:

$$\left\| \pi_k(\eta + v^0) + C^{-1}\frac{\partial G}{\partial v}(v^0)\eta \right\| = o(k^2), \tag{4.10}$$

where $o(k^2) \to 0$ as $k^2 \to 0$.

Now we can state and prove the main result on the existence of travelling wave solutions.

THEOREM 4.2 Suppose that the delay system (2.1) has a bifurcating periodic solution $(p_1(t), p_2(t))$ for β close to the critical value β_0 which is orbitally asymptotically stable. Then there exists $k_0 > 0$ such that the delayed reaction–diffusion system (1.1) has a unique travelling wave solution

$$(N(t,x,k), P(t,x,k)) = (v_1(z) + N^*, v_2(z) + P^*),$$

which is $c_0\omega$-periodic in the variable $z = kx + c_0 t,\ 0 < k < k_0$. Moreover,

$$\lim_{k\to 0}(v_1(z), v_2(z)) = (p_1(t), p_2(t))$$

uniformly in t and x.

To prove the theorem, we need the following lemma.

LEMMA 4.3 (Howard & Koppel, 1973) Let $\Phi(t)$ be the fundamental matrix solution of the ω-periodic system $\mathrm{d}v/\mathrm{d}t = P(t),\ \Phi(0) = I$. Suppose the Floquet multiplier matrix $\Phi(\omega)$ has 1 as a simple eigenvalue, with corresponding right eigenvector r and left eigenvector l. (Thus, $p(t) = \Phi(t)r$ is a ω-periodic solution of the system, and any other ω-periodic solution is a multiple of $p(t)$. Also, the equation $(\Phi(t) - I)\xi = \eta$ has a solution if and only if $l \cdot \eta = 0$ and $r \cdot l \neq 0$ since the eigenvalue 1 is simple. We may assume r and l to be normalized so that $||r|| = 1$ and $r \cdot l = 1$). Let $b(t)$ be a ω-periodic vector. Then

(1) There is a unique value of m such that the system

$$\frac{\mathrm{d}v}{\mathrm{d}t} = P(t)v + mp(t) + b(t)$$

has a ω-periodic solution. If $q(t)$ is the solution to $\mathrm{d}v/\mathrm{d}t = P(t)v + b(t)$ with $q(0) = 0$, this value of m is $-l \cdot q(\omega)/\omega$.

(2) For this value of m there is a unique ω-periodic solution $p_1(t)$ which satisfies $l \cdot p_1(0) = 0$.

(3) There are constants k_1 and k_2, independent of $b(t)$, such that $m \leqslant k_1||b||$ and $||p_1|| \leqslant k_2||b||$.

Proof of Theorem 4.2. We shall prove that the equivalent reaction–diffusion system (3.1) has a unique travelling wave solution

$$(v_1(z) + N^*, v_2(z) + P^*, v_3(z) + R^*, v_4(z) + Q^*)$$

and

$$\lim_{k\to\infty} v_i(kx + c_0 t) = v_i^0(c_0 t), \qquad i = 1, 2, 3, 4$$

uniformly in t and x. Rewrite (4.9) as follows:

$$c\frac{\mathrm{d}v}{\mathrm{d}z} = Av + B(w^0 + \pi_k(v)) \tag{4.11}$$

and set $\eta = v - v^0$, $c = c_0 + m$, $|m| < c_0/2$. We have

$$\begin{aligned}\frac{\mathrm{d}\eta}{\mathrm{d}z} &= \frac{\mathrm{d}v}{\mathrm{d}z} - \frac{\mathrm{d}v^0}{\mathrm{d}z}\\ &= \frac{1}{c_0 + m}[A\eta + Av^0 + B(w^0 + \pi_k(v))] - \frac{\mathrm{d}v^0}{\mathrm{d}z}\\ &= \left(\frac{1}{c_0} - \frac{m}{c_0^2}\right)[A\eta + Av^0 + Bw^0] + \frac{1}{c_0 + m}B\pi_k(v) - \frac{\mathrm{d}v^0}{\mathrm{d}z} + o(c_0^2).\end{aligned}$$

Notice that $\mathrm{d}v^0/\mathrm{d}z = [Av^0 + Bw^0]/c_0 = F(v^0)$ and $P(z) = A - BC^{-1}D = (\partial F/\partial v)(v^0)$, where $D = (\partial G/\partial v)(v^0)$. It follows that

$$\begin{aligned}\frac{\mathrm{d}\eta}{\mathrm{d}z} &= \frac{1}{c_0}P(z)\eta - \frac{m}{c_0^2}F(v^0) + \frac{1}{c_0}B[\pi_k(\eta + v^0) + C^{-1}D\eta] - \frac{m}{c_0^2}[B\pi_k(\eta + v^0) + A\eta]\\ &\quad + o(c_0^2)\\ &= \frac{1}{c_0}P(z)\eta - \frac{m}{c_0^2}F(v^0) + J(z, \eta, m, k),\end{aligned}$$

where

$$J(z, \eta, m, k) = \frac{1}{c_0}B[\pi_k(\eta + v^0) + C^{-1}D\eta] - \frac{m}{c_0^2}[B\pi_k(\eta + v^0) + A\eta] + o(c_0^2).$$

Notice that $P(z)$ is the Jacobi matrix with respect to the $c_0\omega$-periodic solution v^0 to equation (4.6), thus $F(v^0)$ (and any of its multiples) is a $c_0\omega$-periodic solution of the linear equation

$$\frac{\mathrm{d}\eta}{\mathrm{d}z} = \frac{1}{c_0}P(z)\eta. \tag{4.12}$$

To apply Lemma 4.3, define

$$N[\rho] = \{\eta \in C_{c_0\omega}(\mathbb{R}, \mathbb{R}^3) : ||\eta|| \leqslant \eta,\ l \cdot \eta(0) = 0\}$$

and let $\overline{\eta} \in N[\rho]$. Since the unique $c_0\omega$-periodic solution of equation (4.6) is orbitally asymptotically stable, $\lambda = 1$ is a simple multiplier. Since $(m/c_0^2)F(v^0)$ is a $c_0\omega$-periodic solution of equation (4.12) and $J(z, \eta, m, k)$ is $c_0\omega$-periodic in z, Lemma 4.3 implies that the equation

$$\frac{d\overline{\eta}}{dz} = \frac{1}{c_0}P(z)\overline{\eta} - \frac{m}{c_0^2}F(v^0) + J(z, \overline{\eta}, m, k) \tag{4.13}$$

has a unique $c_0\omega$-periodic solution, say $\hat{\eta}$, satisfying $l \cdot \hat{\eta}(0) = 0$ for a unique value of m, say $\hat{m}$. Choose k_0^2 and ρ sufficiently small and c_0 sufficiently large such that

$$\max\{||\pi_k(\overline{\eta} + v^0) + C^{-1}D\overline{\eta}||,\ ||\overline{\eta}||,\ |o(c_0^2)|\} \leqslant \tfrac{1}{4}\hat{K}k^2 \tag{4.14}$$

and

$$\hat{K}k^2 \leqslant \tfrac{1}{4}, \tag{4.15}$$

for $0 < k^2 < k_0^2$, where $\hat{K} = \max_{i=1,2}\{k_i|1/c_0|\ ||B||, k_i/c_0^2\ ||A||\}$, k_1 and k_2 are given in Lemma 4.3. Thus, by Lemma 4.3 and (4.10), if $|m| \leqslant \hat{K}k^2$, $||\overline{\eta}|| \leqslant \hat{K}k^2$, we have

$$\begin{aligned} ||\hat{\eta}|| &\leqslant k_2||J(z, \overline{\eta}, m, k)|| \leqslant k_2\left|\frac{1}{c_0}\right|\ ||B||\ ||\pi_k(\overline{\eta} + v^0) + C^{-1}D\overline{\eta}|| \\ &+k_2|m|\frac{1}{c_0^2}\ ||B||\ ||\pi_k(\overline{\eta} + v^0)|| + k_2|m|\frac{1}{c_0^2}\ ||A||\ ||\overline{\eta}|| + |o(c_0^2)| \\ &\leqslant \frac{\hat{K}k^2}{4} + \frac{\hat{K}k^2}{4}\hat{K}k^2 + \frac{\hat{K}k^2}{4}\hat{K}k^2 + \frac{\hat{K}k^2}{4} \leqslant Kk^2. \end{aligned} \tag{4.16}$$

Similarly, we have

$$|\hat{m}| \leqslant Kk^2. \tag{4.17}$$

Define the set

$$S_k = \{(m, \overline{\eta}) : |m| \leqslant \hat{K}k^2,\ ||\overline{\eta}|| \leqslant \hat{K}k^2\}, \qquad 0 < k^2 < k_0^2$$

and a mapping $\mathcal{A} : S_k \to S_k$ by

$$\mathcal{A}(m, \overline{\eta}) = (\hat{m}, \hat{\eta}).$$

Then $\mathcal{A}(S_k) \subseteq S_k$. To show that the system (4.13) has a unique $c_0\omega$-periodic solution, we need to show that $\mathcal{A}$ is a contractive mapping. Let $(m_i, \overline{\eta}_i) \in S_k$, $i = 1, 2$ and write $\Delta\overline{\eta} = \overline{\eta}_1 - \overline{\eta}_2$, $\Delta m = m_1 - m_2$. Then

$$\frac{d\Delta\overline{\eta}}{dz} = \frac{1}{c_0}P(z)\Delta\overline{\eta} - \frac{\Delta m}{c_0^2}F(v^0) + \Delta J(z, \eta, m, k), \tag{4.18}$$

where $\Delta J = J(z, \eta_1, m_1, k) - J(z, \eta_2, m_2, k)$. Since $|\Delta m| \leqslant O(k^2)$, $|\Delta J| \leqslant O(k^2)$, once again by Lemma 4.3, there exist $\Delta\hat{m}$ and $\Delta\hat{\eta}$ satisfying (4.18) and

$$|\Delta\hat{m}| \leqslant O(k^2(|\Delta m| + ||\Delta\overline{\eta}||)), \quad ||\Delta\hat{\eta}|| \leqslant O(k^2(|\Delta m| + ||\Delta\overline{\eta}||)).$$

Therefore,

$$\begin{aligned} ||\mathcal{A}(m_1, \eta_1) - \mathcal{A}(m_2, \eta_2)|| &= ||(\hat{m}_1, \hat{\eta}_1) - (\hat{m}_2, \hat{\eta}_2)|| = ||(\hat{m}_1 - \hat{m}_2, \hat{\eta}_1 - \hat{\eta}_2)|| \\ &\leqslant \tilde{K}k^2(|\hat{m}_1 - \hat{m}_2| + ||\hat{\eta}_1 - \hat{\eta}_2||), \end{aligned}$$

where $\tilde{K} > 0$ is a constant. Choose k^2 sufficiently small such that $\tilde{K}k^2 \leqslant \frac{1}{4}$. Thus, we have

$$||\mathcal{A}(m_1, \eta_1) - \mathcal{A}(m_2, \eta_2)|| \leqslant \tfrac{1}{4}(|\hat{m}_1 - \hat{m}_2| + ||\hat{\eta}_1 - \hat{\eta}_2||),$$

which implies that $\mathcal{A}$ is a contractive mapping; this completes the proof. □

5. Discussion

In this paper we have proposed a plankton model with delayed nutrient recycling in the form of a coupled system of reaction–diffusion equations. Two distributed delays are incorporated in the model; one models the nutrient recycling and another describes the delayed growth response of the plankton to nutrient uptake. Our model is an extension of the delay models studied by Beretta *et al.* (1990), Beretta & Takeuchi (1994), He & Ruan (1998), He, Ruan and Xia (1998), Ruan (1995a) and of the reaction–diffusion model considered by Ruan (1995b).

We firstly studied the delay model without diffusion and obtained stability criteria for the positive equilibrium. The stability conditions depend on the (average) delay involved in the growth response of plankton. By using this delay as a bifurcation parameter, it was shown that when the delay passes through a critical value, the positive equilibrium loses its stability and a Hopf bifurcation occurs, that is, a family of periodic solutions bifurcates from the positive equilibrium. Though the stability conditions of the bifurcating periodic solutions were not analytically given, numerical simulation was carried out to show that with a chosen response function and suitable parameters, a stable limit cycle exists when the bifurcation parameter is near its critical value.

We then considered the reaction–diffusion equations with delays. It has been shown that the diffusion could drive the homogeneous steady state to unstable, thus certain Turing-type spatial patterns (non-constant stationary solutions) exist. Notice that if the delays are neglected, the reaction–diffusion system is globally stable; see (Ruan, 1995b). Therefore, we can see that the delays play a very important role in pattern formation. Numerical simulation confirmed our observation.

Finally, corresponding to the orbitally asymptotically stable periodic solutions of the delay model, we showed that there is a family of travelling wave solutions to the reaction–diffusion system with delay. However, we are unable to determine the stability of the travelling wave solutions. We conjecture that they are unstable, as observed by Cohen, Hagan & Simpson (1979) and with Gourley & Britton (1993) that, for certain classes of models with continuous time delay, the low-amplitude periodic steady and travelling wave solutions which arise via bifurcation from a uniform steady state are unstable.

We only considered spatial kernels in this paper. As argued by Britton (1990), since individuals in the populations are moving, they may not have been at the same point in space as at previous times, and hence the nutrient uptake and recycling are not measured pointwise in space. This leads to a second convolution (in space) in the integral terms in the equations, that is, the kernels are now spatio-temporal kernels. It would be very interesting to study the plankton models with non-local effects and we leave this for future consideration.

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