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Spatially Heterogeneous Discrete Waves in Predator–Prey Communities over a Patchy Environment

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ABSTRACT

A model motivated by the earlier work of J. D. Murray and D. Stirzaker is proposed to describe the dynamics of predator–prey communities over a patchy environment. The model is a system of delay differential equations. It is shown that if only one time lag is incorporated into the model, then a branch of spatially homogeneous periodic solutions occur as a primary Hopf bifurcation. However, if two time lags are used to measure different delayed factors in the process of growth, decay, and predator consumption of the prey population, then stable spatially heterogeneous periodic solutions (discrete waves or phase-locked oscillations) may exist. The utilized method is based on center manifold, normal form, and equivariant Hopf bifurcation theory.

1. INTRODUCTION

In [1] Murray showed that the coupling of continuous diffusion in space with time delay interacting population models can give rise to stable spatial and temporal fluctuations. In particular, for the proposed nonlinear scalar diffusion time delay equation, a spatial and temporal oscillatory traveling wave solution was obtained in which the amplitude depends only on the parameters of the equations.

The purpose of this paper is to demonstrate that the coupling of discrete diffusion in a patchy environment with a time delay interacting population model can also exhibit stable discrete waves, a special type of temporal periodic solutions representing oscillations in which the population in each patch oscillates like the others but in a different phase. We will show that in order to obtain stable spatially heterogeneous discrete waves, two time lags have to be incorporated into the model describing the dynamics of the population.

Time lags have been employed to model biological features such as

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regeneration time and reproductive lags. It is often biologically unrealistic to assume that the growth rate of the population depends on just one point in past time. For example, in the growth of an herbivore population grazing on vegetation, which was one of the motivations for [1], the time lag required for the reaction of the predator population to changes in the available amount of vegetation on which it depends is usually different from the time taken for the vegetation to recover.

On the other hand, much research has been devoted to the mathematical analysis of model equations for the growth of populations dispersing among patches in a heterogeneous environment in order to understand the effect of environmental changes on the growth of populations. We refer to [1–24] and references therein.

Delay differential equations with two time lags have been the subject of much literature. We refer to [24–30] and references therein. However, except for [24], where two lags come, respectively, from the self-regulating mechanism and the dispersion process, little has been done regarding stable spatially heterogeneous discrete waves for a predator–prey community. It should also be mentioned that the existence of stable spatially heterogeneous Hopf bifurcations has been obtained for a scalar reaction–diffusion equation with two delays in [30].

In this paper, we propose a system of delay differential equations with two time lags to model the growth of a predator–prey community over a ring of patches. We assume that the dynamics of the prey population in each patch is essentially governed by Murray's equation [1] and that the dispersion of the prey population occurs between nearest neighborhoods and is proportional to the difference between the densities of the populations. Our investigation indicates that introducing two time lags in the proposed model is not only biologically realistic but also mathematically necessary to observe stable spatially heterogeneous periodic solutions. In fact, we will show that if two delays are identical, then we will always obtain spatially homogeneous oscillations as the primary Hopf bifurcation. However, if two delays are different, then we can apply the center manifold, normal form, and equivariant Hopf bifurcation theory to show that stable spatially heterogeneous discrete waves may exist in some situations.

The rest of this paper is organized as follows. The model is described in Section 2 and is analyzed in Sections 3 (a single delay) and 4 (two time lags). Some remarks and discussions are provided in Section 5.

2. DISCRETE DIFFUSIONAL TIME DELAY MODEL

Consider a system consisting of a predator–prey interacting community distributed over a ring of n patches connected by dispersion between adjacent patches. In what follows, we will always, as an illustrative example of the considered predator–prey interaction, keep in mind herbivore vegetation and, in particular, planktonic populations in the sea in which herbivorous copepods live off phytoplankton. We refer to [1, 21] for more details about experimental observations and biological motivations of such a predator–prey interaction.

Following Murray [1] and Stirzaker [21], we assume that in each patch the population $u_i(t)$ of the prey at a time t satisfies, in the absence of predators,

$$\dot{u}_i(t) = h(u_i(t-\tau)),$$

where $\tau > 0$ is a constant. With herbivore vegetation in mind, $h(u_i(t-\tau))$ represents the growth and decay process of the population; τ is the time taken for the vegetation to regenerate.

We also assume that predator consumption depends only on their capacity $b > 0$ for the prey. Therefore, without dispersion from other patches, the equation for $u_i(t)$ in the predator–prey situation takes the form

$$\dot{u}_i(t) = h(u_i(t-\tau)) - bK_i(t),$$

where K_i is the number of predators in the patch at time t. The number of predators depends on the amount of food available to their offspring, so the total predator population also depends on the prey population at an earlier time. $K_i(t)$ is usually a rather complicated function of the prey population at a previous time. We assume, for simplicity, that

$$bK_i(t) = m(u_i(t-\tau^*)),$$

where τ^* is of the order of the regeneration time of the vegetation.

Finally, we assume that the dispersion occurs between adjacent patches and is proportional to the difference of the populations in these patches with a proportionality constant $p > 0$ measuring the strength of the dispersion. Therefore, the equation for $u(t) = (u_1(t), \ldots, u_n(t))^T$ in the situation of dispersion and predator–prey interaction becomes

$$\dot{u}_i(t) = h(u_i(t-\tau)) - m(u_i(t-\tau^*)) + p\left[u_{i+1}(t) - 2u_i(t) + u_{i-1}(t)\right], \tag{2.1}$$

where $i = 1, 2, \ldots, n \pmod{n}$, $\quad t \geqslant 0$.

As $h(u_i)$ must take into account crowding effects, for large u_i it must be a decreasing function. So, we expect that the isolated subsystem

$$\dot{u}_i(t) = h(u_i(t-\tau)) - m(u_i(t-\tau^*))$$

for the prey population without dispersion has a positive equilibrium K given by

$$h(K) - m(K) = 0$$

and

$$h'(K) < 0, \qquad m'(K) > 0. \tag{2.2}$$

This gives a spatially homogeneous equilibrium $K^* = (K, \dots, K)^T$ for system (2.1). Our primary goal is to look for Hopf bifurcation from this equilibrium. In what follows, we will also follow [1, 21] and assume that h and m are antisymmetric about the equilibrium K, resulting in

$$h''(K) = m''(K) = 0. \tag{2.3}$$

3. SPATIALLY HOMOGENEOUS HOPF BIFURCATIONS: SINGLE DELAY

In this section we consider (2.1) with a single delay τ. That is, we assume that $\tau = \tau^*$. Regarding τ as the parameter, we will show that the primary Hopf bifurcation consists of spatially homogeneous periodic solutions whose stability is determined by the sign of $h'''(K) - m'''(K)$.

The linearization of (2.1) about the spatially homogeneous equilibrium $K^* = (K, \dots, K)^T$ is

$$\dot{z}_i(t) = -rz_i(t - \tau) + p[z_{i+1}(t) + z_{i-1}(t) - 2z_i(t)],$$

where

$$r = -h'(K) + m'(K) > 0. \tag{3.1}$$

Normalizing the delay by $y_i(t) = z_i(\tau t)$, $t \in \mathbb{R}$, we get

$$\dot{y}_i(t) = -r\tau y_i(t-1) + p\tau[y_{i+1}(t) + y_{i-1}(t) - 2y_i(t)].$$

It is well known (see [31]) that the discrete Laplacian $\Delta: R^n \to R^n$ defined by

$$(\Delta y)_j = y_{j+1} + y_{j-1} - 2y_j, \qquad y \in R^n;\ j \ (\text{mod } n),$$

has eigenvalues $-4\sin^2(\pi j/n)$ with associated eigenvectors

$$v_j=\left(1,\exp\left[i\frac{2\pi}{n}j\right],\dots,\exp\left[i\frac{2\pi}{n}(n-1)j\right]\right)^T,\qquad 0\leqslant j\leqslant n-1.$$

Moreover,

$$\left[(\lambda+r\tau e^{-\lambda})Id-p\tau\Delta\right]v_j=\left[\lambda+r\tau e^{-\lambda}+4p\tau\sin^2\frac{\pi j}{n}\right]v_j.$$

Therefore, the corresponding characteristic equation takes the form

$$\prod_{j=0}^{n-1}\left[\lambda+r\tau e^{-\lambda}+4p\tau\sin^2\frac{\pi j}{n}\right]=0. \tag{3.2}$$

To analyze the distribution of characteristic values, we need the following result regarding equation

$$(z+a)e^z+b=0, \tag{3.3}$$

where $a\geqslant 0$, $b>0$ are given constants.

LEMMA 3.1

(i) *All roots of* (3.3) *have negative real parts if and only if* $b<\xi\sin\xi-\alpha\cos\xi$, *where* ξ *is the root of* $\xi=-\alpha\tan\xi$ *in* $(0,\pi)$ *if* $a\neq 0$, *or* $\xi=\pi/2$ *if* $a=0$.

(ii) *If* $a=0$ *and* $0<b<\pi/2$, *then every solution of Equation* (3.3) *has a negative real part.*

(iii) *If* $a=0$ *and* $b>e^{-1}$, *then* (3.3) *has a root* $u(b)+iv(b)$ *that is continuous together with its first derivative in b and satisfies* $0<v(b)<\pi$, $v(\pi/2)=\pi/2$, $u(\pi/2)=0$, $u'(\pi/2)>0$, *and* $u(b)>0$ *for* $b>\pi/2$.

We refer to [32] for a detailed proof of the above result.

Applying Lemma 3.1 to (3.2), we get

THEOREM 3.2

(i) *If* $\tau<\tau_0=\tau/2r$, *then all characteristic values of* (3.2) *have negative real parts.*

(ii) *If* $\tau=\tau_0$, *then* (3.2) *has a pair of purely imaginary characteristic values* $\pm i\pi/2$, *and all other characteristic values have negative real parts.*

(iii) *There exists* $\varepsilon>0$ *such that there is a characteristic value* $\lambda(\tau)=u(\tau)+iv(\tau)$ *of* (3.2) *that is continuous together with its first derivative in* $\tau\in(\tau_0-\varepsilon,\ \tau_0+\varepsilon)$ *and satisfies* $0<v(\tau)<\pi$, $v(\tau_0)=\pi/2$, $u(\tau_0)=0$, $u'(\tau_0)>0$, *and* $u(\tau)>0$ *for* $\tau\in(\tau_0,\ \tau_0+\varepsilon)$. *Moreover, for* $\tau\in(\tau_0-\varepsilon,\ \tau_0+\varepsilon)$, *all other characteristic values have negative real parts.*

Proof. Applying Lemma 3.1 to (3.2) with

$$a = 4p\tau \sin^2 \frac{\pi j}{n}, \qquad b = r\tau,$$

we can easily obtain the above results provided we can show that

$$r\tau < \xi \sin \xi - 4p\tau \left(\sin^2 \frac{\pi j}{n} \right) \cos \xi \tag{3.4}$$

if $\tau < \tau_0$, $1 \leqslant \mathrm{j} \leqslant \mathrm{n} - 1$, and $\xi \in (0, \pi)$ is the only solution of $\xi = -4p\tau \sin^2 \pi \mathrm{j}/n \tan \xi$. Note that (3.4) is equivalent to

$$r\tau < \frac{-4p\tau \sin^2 \pi j/n}{\cos \xi} = \frac{\xi}{\sin \xi}.$$

Consequently, (3.4) is true as the solution of $\xi = -4p\tau \sin^2(\pi j/n\tau) \tan \xi$ belongs to $(\pi/2, \pi)$, where $\xi/(\sin \xi) > \pi/2 = \tau_0 r$. ■

By using the standard Hopf bifurcation theorem for functional differential equations (see [32]), we can claim that near $\tau_0 = \pi/2r$ there is a Hopf bifurcation of periodic solutions. As the purely imaginary characteristic value corresponds to the zero of the first factor of (3.2), each periodic solution obtained from the above Hopf bifurcation theorem is spatially homogeneous (or synchronous), that is, $u_{i-1}(t) = u_i(t)$ for all $i(\mathrm{mod}\ n)$ and for all $t \in \mathbb{R}$, according to the general Hopf symmetric bifurcation theorem in [33, 34], which represents an analog for functional differential equations of the well-known Golubitsky–Stewart Hopf bifurcation theorem for ordinary differential equations in the presence of symmetry (see [31]). For the model equation (2.1), the spatial homogeneity of the periodic solution in the primary Hopf bifurcation is obvious. In fact, τ_0 is a Hopf bifurcation value of the scalar functional differential equation

$$\dot{w}(t) = h(w(t-\tau)) - m(w(t-\tau)),$$

and hence a Hopf bifurcation of periodic solution $w(t)$ occurs near $\tau = \tau_0$. This periodic solution then gives rise to a spatially homogeneous periodic solution $(w(t), \ldots, w(t))^T$ of (2.1) due to the internal D_n symmetry.

We now investigate the stability, direction of bifurcation, periods, and asymptotic forms of the small-amplitude periodic solutions bifurcating from the equilibrium $(K, \ldots, K)^T$. We will use the algorithm in the monograph of Hassard et al. [35] and assume $n = 3$ for the sake of simplicity.

THEOREM 3.3

Near $\tau = \tau_0 = \pi/2r$, system (2.1) *has a Hopf bifurcation of spatially homogeneous (or synchronous) periodic solutions bifurcating from the equilibrium $(K,\dots,K)^T$. If $m'''(K) < h'''(K)$, then the bifurcation takes place for $\tau < \tau_0$ and the bifurcating periodic solutions are unstable. If $m'''(K) > h'''(K)$, then the bifurcation takes place for $\tau > \tau_0$ and the bifurcating periodic solutions are orbitally asymptotically stable. Moreover, we have the following representation for the periodic solution u and the periods T*:

$$u(t, \tau(\varepsilon)) = K^* + 2\varepsilon(1,1,1)^T \cos\frac{\pi}{2\tau(\varepsilon)}t + O(\varepsilon^3),$$

$$T(\varepsilon) = 4\tau(\varepsilon)\left[1 - \frac{3b(\pi - 1)}{r\pi(1 + \pi^2/4)}\varepsilon^2 + O(\varepsilon^3)\right],$$

$$\tau(\varepsilon) = \tau_0 - \frac{3b\pi^2}{2r^2}\varepsilon^2 + O(\varepsilon^3),$$

$$r = -h'(K) + m'(K) > 0,$$

$$b = -h'''(K) + m'''(K).$$

Proof. We consider (2.1) when h and m are replaced by their Taylor expansions up to the third order. Making a change of variables $x_i(t) = u_i(\tau t) - K$, we get

$$\begin{aligned}\dot{x}_i(t) &= -r\tau x_i(t-1) - b\tau x^3(t-1) \\ &\quad + p\tau\left[x_{i+1}(t) + x_{i-1}(t) - 2x_i(t)\right], \qquad i(\operatorname{mod} n). \qquad (3.5)\end{aligned}$$

Let $\tau = \tau_0 + \mu$. We then have

$$\begin{aligned}\dot{x}_i(t) &= -r\left(\frac{\pi}{2r} + \mu\right)x_i(t-1) - b\left(\frac{\pi}{2r} + \mu\right)x_i^3(t-1) \\ &\quad + p\left(\frac{\pi}{2r} + \mu\right)\left[x_{i+1}(t) + x_{i-1}(t) - 2x_i(t)\right].\end{aligned}$$

The linearization of (3.5) is

$$\dot{x}(t) = \int_{-1}^{0} d\eta(\theta, \mu)x(t+\theta) \qquad (3.6)$$

with

$$d\eta(\theta,\mu) = p\left(\frac{\pi}{2r}+\mu\right)\begin{pmatrix} -2 & 1 & 1 \\ 1 & -2 & 1 \\ 1 & 1 & -2 \end{pmatrix}\delta(\theta)\,d\theta - \left(\frac{\pi}{2}+r\mu\right) I d\delta(\theta+1)\,d\theta,$$

where δ is the Dirac δ function. The generator of the semigroup defined by (3.6) is, see [32, 35],

$$A(\mu)\varphi = \begin{cases} \dot{\varphi}(\theta), & -1 \leqslant \theta < 0, \\ \int_{-1}^{0} d\eta(\theta,\mu)\varphi(\theta), & \theta = 0; \end{cases}$$

its adjoint operator is defined by

$$A^*(\mu)\alpha(s) = \begin{cases} -\dot{\alpha}(s), & 0 < s \leqslant 1, \\ \int_{-1}^{0} d\eta^T(\theta,\mu)\alpha(-\theta), & s = 0; \end{cases}$$

and the associated bilinear form is

$$\langle \alpha, \varphi \rangle = \bar{\alpha}(0)\varphi(0) - \int_{-1}^{0}\int_{0}^{\theta} \bar{\alpha}(\xi-\theta)\,d\eta(\theta,\mu)\varphi(\xi)\,d\xi.$$

Also note that $\lambda(0) = \pm i\pi/2$ is an eigenvalue of $A(0)$ with the eigenvector $q(\theta) = (1, 1, 1)^T e^{i(\pi/2)\theta}$, $-1 \leqslant \theta \leqslant 0$, and $\bar{\lambda}(0)$ is an eigenvalue of $A^*(0)$ with the eigenvector $q_1^*(s) = (1, 1, 1)e^{i(\pi/2)s}$, $0 \leqslant s \leqslant 1$. We can easily verify that

$$\langle q_1^*, q \rangle = \frac{3(1+\pi^2/4)}{1-i\pi/2}.$$

Hence, if we let

$$q^*(s) = \frac{1-(\pi/2)i}{3(1+\pi^2/4)}(1,1,1)e^{i(\pi/2)s}, \qquad 0 \leqslant s \leqslant 1,$$

then

$$\langle q^*, q \rangle = 1.$$

We now formally rewrite (3.5) as

$$\dot{x}_t = A(\mu)x_t + R(\mu)x_t$$

with

$$R(\mu)\varphi = \begin{cases} 0 & -1 \leqslant \theta < 0, \\ -b(\pi/2r + \mu)\left(\varphi_1^3(-1),\ \varphi_2^3(-1),\ \varphi_3^3(-1)\right)^T, & \theta = 0. \end{cases}$$

Carrying out the algorithm in [35, pp. 183–190] with $\omega_0 = \pi/2$, we get the bifurcating periodic solutions

$$\begin{aligned} x(t, \mu(\varepsilon)) &= 2\varepsilon \operatorname{Re}\left[q(0)e^{i\omega_0 t}\right] + 2\varepsilon^2 \operatorname{Re} q(0) \\ &\quad \times \left[\frac{g_{20}}{2i\omega_0}e^{2i\omega_0 t} - \frac{g_{11}}{i\omega_0} - \frac{g_{02}}{6i\omega_0}e^{-2i\omega_0 t}\right] \\ &\quad + \varepsilon^2 \operatorname{Re}\left[W_{20}(0)e^{2i\omega_0 t} + W_{11}(0)\right] + O(\varepsilon^3), \end{aligned}$$

whose periods are given by

$$T(\varepsilon) = \frac{2\pi}{\omega_0}\left[1 + \tau_2\varepsilon^2 + O(\varepsilon^3)\right],$$

where

$$\begin{aligned} \mu(\varepsilon) &= \mu_2\varepsilon^2 + O(\varepsilon^3), \\ \tau_2 &= -\frac{1}{\omega_0}\left[\operatorname{Im} c_1(0) + \mu_2\omega'(0)\right], \\ c_1(0) &= \frac{i}{2\omega_0}\left[g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}\right] + \frac{g_{21}}{2}, \\ g_{20} &= g_{11} = g_{02} = 0, \qquad W_{20} = W_{11} = 0, \\ g_{21} &= \frac{3b\pi}{r(1+\pi^2/4)}\left(\frac{\pi}{2} + i\right), \\ \omega'(0) &= \frac{r}{1+\pi^2/4}, \qquad \mu_2 = -\frac{\operatorname{Re} c_1(0)}{\alpha'(0)}, \\ \alpha'(0) &= \frac{d}{d\mu}\operatorname{Re}\lambda(\mu)|_{\mu=0} = \frac{r\pi}{2(1+\pi^2/4)}. \end{aligned}$$

The calculation is straightforward but tedious and thus is omitted. It is known that the direction of bifurcation is determined by μ_2 and the stability of bifurcating periodic solutions is determined by $\beta_2 = 2\operatorname{Re} c_1(0)$. Therefore, the conclusion follows. ■

It is natural to see that the parameter p, measuring the strength of dispersion between patches, does not appear in the representations of bifurcating periodic solutions and their periods, because each spatially homogeneous periodic solution of (2.1) corresponds to a periodic solution of the scalar equation $\dot{\omega}(t) = h(\omega(t-\tau)) - m(\omega(t-\tau))$. Theorem 3.3 also indicates that if $m'''(k) > h'''(k)$ and p is given, then there exists $\varepsilon_0 = \varepsilon_0(p) > 0$ such that for all $\tau = \tau(\varepsilon)$ with $\varepsilon \in (0, \varepsilon_0(p))$ the bifurcating periodic solution of (2.1) is asymptotically stable. The dependence of ε_0 on p, however, suggests that for a fixed small $\varepsilon > 0$ it is possible to destabilize this periodic solution by varying p. We will address this problem in a future paper.

4. SPATIALLY HETEROGENEOUS HOPF BIFURCATIONS: TWO DELAYS

The purpose of this section is to show that system (2.1) with two delays may exhibit primary Hopf bifurcation of stable spatially heterogeneous periodic solutions. Again, for simplicity, we assume $n = 3$, though our method can be applied to general situations.

Employing the same notations as those of Section 3, we can verify that the linearization of (2.1) about the equilibrium $K^* = (K, \ldots, K)^T$ is

$$\begin{aligned} \dot{z}_i(t) = &-r\alpha z_i(t-\tau) - r\beta z_i(t-\tau^*) \\ &+ p[z_{i+1}(t) + z_{i-1}(t) - 2z_i(t)], \qquad i(\text{mod } n), t \geqslant 0, \quad (4.1) \end{aligned}$$

where $r = -h'(k) + m'(k)$, $\alpha = -h'(k)/r$, and $\beta = m'(k)/r$. Normalizing one of the delays (τ) and renaming τ^*, we can assume that $\tau = 1$ and $\tau^* \geqslant 1$.

Let A denote the generator of the semigroup generated by (4.1). Then λ is an eigenvalue of A if and only if

$$\prod_{j=0}^{2} \left[\lambda + \alpha r e^{-\lambda} + \beta r e^{-\lambda \tau^*} + 4p \sin^2 \frac{\pi j}{3} \right] = 0.$$

We make the following assumption.

ASSUMPTION 1

All roots of $\lambda + \alpha r e^{-\lambda} + \beta r e^{-\lambda\tau^*} = 0$ *have negative real parts, and there exists* $p_0 > 0$ *so that* $\lambda + \alpha r e^{-\lambda} + \beta r e^{-\lambda\tau^*} + 3p_0 = 0$ *has a pair of purely imaginary solutions* $\pm i v_1$ *and all other solutions have negative real parts.*

General sufficient conditions to guarantee Assumption 1 seem difficult to obtain. However, we will provide some numerical results to support this assumption.

Note that the multiplicity of each of the eigenvalues $\pm iv_1$ is 2. Under Assumption 1, a theorem in [33, 34] guarantees that near $p = p_0$, system (2.1) has a Hopf bifurcation of periodic solutions satisfying $u_i(t) = u_{i-1}(t - T/n)$, $i(\text{mod } n)$, where $t \in R$ and T is the period of $u(t) = (u_1(t), \ldots, u_n(t))^T$. These periodic solutions are clearly spatially heterogeneous: the oscillations of prey populations in different patches are in different phases. In what follows, we call such periodic solutions discrete waves or phase-locked oscillations, following the work of Alexander and Auchmuty [36] and the monograph [31].

Our next goal is to develop an algorithm for determining the stability of discrete waves. Our approach is to reduce the semiflow of solutions of (2.1) to its center manifold (four-dimensional) and then appeal to the equivariant normal form of [31] for four-dimensional ordinary differential equations equivariant under the D_n action.

Note that the eigenvector of A corresponding to iv_1 is $(1, \xi, \xi^2)^T e^{iv_1\theta}$, $-\tau^* \leqslant \theta \leqslant 0$, where $\xi = e^{i\,2\pi/3}$. It can be easily verified that $\Phi = (\varphi_1, \varphi_2, \varphi_3, \varphi_4)$ is a basis for the generalized eigenspace $\mu_{iv_1}(A)$ of A associated with the eigenvalue iv_1 (of multiplicity 2), where

$$\varphi_1 = \left(1, -\frac{1}{2}, -\frac{1}{2}\right)^T \cos v_1\theta + \left(0, \frac{\sqrt{3}}{2}, -\frac{\sqrt{3}}{2}\right)^T \sin v_1\theta,$$

$$\varphi_2 = \left(1, -\frac{1}{2}, -\frac{1}{2}\right)^T \sin v_1\theta + \left(0, -\frac{\sqrt{3}}{2}, \frac{\sqrt{3}}{2}\right)^T \cos v_1\theta,$$

$$\varphi_3 = \left(1, -\frac{1}{2}, -\frac{1}{2}\right)^T \cos v_1\theta + \left(0, -\frac{\sqrt{3}}{2}, \frac{\sqrt{3}}{2}\right)^T \sin v_1\theta,$$

$$\varphi_1 = \left(1, -\frac{1}{2}, -\frac{1}{2}\right)^T \sin v_1\theta + \left(0, \frac{\sqrt{3}}{2}, -\frac{\sqrt{3}}{2}\right)^T \cos v_1\theta.$$

Similarly, $\Psi^* = (\psi_1^*, \psi_2^*, \psi_3^*, \psi_4^*)^T$ is a basis for the formal adjoint of A relative to the bilinear form

$$(\psi, \varphi) = \psi(0)\varphi(0) - \int_{-\tau^*}^{0}\int_{0}^{\theta}\psi(\xi - \theta)[d\eta(\theta)]\varphi(\xi)d\xi,$$

where

$$\psi_1^* = \left(1, -\frac{1}{2}, -\frac{1}{2}\right)\cos v_1 s - \left(0, \frac{\sqrt{3}}{2}, -\frac{\sqrt{3}}{2}\right)\sin v_1 s,$$

$$\psi_2^* = -\left(1, -\frac{1}{2}, -\frac{1}{2}\right)\sin v_1 s + \left(0, -\frac{\sqrt{3}}{2}, \frac{\sqrt{3}}{2}\right)\cos v_1 s,$$

$$\psi_3^* = \left(1, -\frac{1}{2}, -\frac{1}{2}\right)\cos v_1 s - \left(0, -\frac{\sqrt{3}}{2}, \frac{\sqrt{3}}{2}\right)\sin v_1 s,$$

$$\psi_4^* = -\left(1, -\frac{1}{2}, -\frac{1}{2}\right)\sin v_1 s + \left(0, \frac{\sqrt{3}}{2}, -\frac{\sqrt{3}}{2}\right)\cos v_1 s,$$

and

$$d\eta = p_0 \begin{bmatrix} -2 & 1 & 1 \\ 1 & -2 & 1 \\ 1 & 1 & -2 \end{bmatrix} \times \delta(\theta)d\theta - \alpha r I \delta(\theta+1)d\theta - r\beta I\delta(\theta+\tau^*)d\theta, \qquad \theta \in [-\tau^*, 0].$$

By direct calculations, we have

$$(\Psi^*, \Phi) = \begin{bmatrix} 0 & \Delta \\ \Delta & 0 \end{bmatrix}$$

where

$$\Delta = \begin{bmatrix} \frac{3}{2} - \frac{3}{2}r(\alpha\cos v_1 + \beta\tau^*\cos v_1\tau^*) & \frac{3}{2}r(\alpha\sin v_1 + \beta\tau^*\sin v_1\tau^*) \\ \frac{3}{2}r(\alpha\sin v_1 + \beta\tau^*\sin v_1\tau^*) & -\frac{3}{2} + \frac{3}{2}r(\alpha\cos v_1 + \beta\tau^*\cos v_1\tau^*) \end{bmatrix}$$

Hence

$$\Psi = (\Psi^*, \Phi)^{-1}(\psi_1^*, \psi_2^*, \psi_3^*, \psi_4^*)$$

is a basis of $\mu_{iv_1}(A^*)$ and $(\Psi, \Phi) = Id$. Let

$$M = \left[-\tfrac{3}{2} + \tfrac{3}{2}r(\alpha\cos v_1 + \beta\tau^*\cos v_1\tau^*)\right](\det\Delta)^{-1},$$

$$N = \left[-\tfrac{3}{2}r(\alpha\sin v_1 + \beta\tau^*\sin v_1\tau^*)\right](\det\Delta)^{-1}.$$

Then we have

$$\psi_1 = \Bigg(M\cos v_1 s - N\sin v_1 s, \left(-\frac{M}{2} + \frac{\sqrt{3}}{2}N\right)\cos v_1$$

$$+\left(\frac{\sqrt{3}}{2}M + \frac{N}{2}\right)\sin v_1 s,\ \left(-\frac{M}{2} - \frac{\sqrt{3}}{2}N\right)\cos v_1 s$$

$$+\left(-\frac{\sqrt{3}}{2}M + \frac{N}{2}\right)\sin v_1 s\Bigg),$$

$$\psi_2 = \Bigg(N\cos v_1 s + M\sin v_1 s, \left(-\frac{\sqrt{3}}{2}M - \frac{N}{2}\right)\cos v_1 s$$

$$+\left(-\frac{M}{2} + \frac{\sqrt{3}}{2}N\right)\sin v_1 s,\ \left(\frac{\sqrt{3}}{2}M - \frac{N}{2}\right)\cos v_1 s$$

$$+\left(-\frac{M}{2} - \frac{\sqrt{3}}{2}N\right)\sin v_1 s\Bigg),$$

$$\psi_3 = \Bigg(M\cos v_1 s - N\sin v_1 s, \left(-\frac{M}{2} - \frac{\sqrt{3}}{2}N\right)\cos v_1 s$$

$$+\left(-\frac{\sqrt{3}}{2}M + \frac{N}{2}\right)\sin v_1 s,\ \left(\frac{M}{2} + \frac{\sqrt{3}}{2}N\right)\cos v_1$$

$$+\left(\frac{\sqrt{3}}{2}M + \frac{N}{2}\right)\sin v_1 s\Bigg),$$

$$\psi_4 = \Bigg(N\cos v_1 s + M\sin v_1 s, \left(\frac{\sqrt{3}}{2}M - \frac{N}{2}\right)\cos v_1 s$$

$$+\left(-\frac{M}{2} - \frac{\sqrt{3}}{2}N\right)\sin v_1 s,\ \left(-\frac{\sqrt{3}}{2}M - \frac{N}{2}\right)\cos v_1 s$$

$$+\left(-\frac{M}{2} + \frac{\sqrt{3}}{2}N\right)\sin v_1 s\Bigg).$$

The center manifold theory ensures that there exists a smooth functional $g:\mu_{iv_1}(A) \to C([-\tau^*, 0]; \mathbb{R}^n)$ with $g(0)=0$, $Dg(0)=0$ and such that if $u(t)$ is a solution on the center manifold then

$$u_t - K^* = \Phi(\Psi, u_t - K^*) + g(\Phi(\Psi, u_t - K^*)).$$

Moreover, if we let

$$y(t) = (\Psi, u_t - K^*) \in \mathbb{R}^4,$$

then $y(t)$ satisfies the following system of ordinary differential equations:

$$\dot{y}(t) = By(t) + \Psi(0)\left[(p - p_0)\begin{pmatrix} -2 & 1 & 1 \\ 1 & -2 & 1 \\ 1 & 1 & -2 \end{pmatrix} u(t) \right.$$
$$\left. + \begin{pmatrix} h(u_1(t-1)) - m(u_1(t-\tau^*)) + \alpha r[u_1(t-1) - K] + \beta r[u_1(t-\tau^*) - K] \\ h(u_2(t-1)) - m(u_2(t-\tau^*)) + \alpha r[u_2(t-1) - K] + \beta r[u_2(t-\tau^*) - K] \\ h(u_3(t-1)) - m(u_3(t-\tau^*)) + \alpha r[u_3(t-1) - K] + \beta r[u_3(t-\tau^*) - K] \end{pmatrix}\right],$$

where

$$B = \begin{bmatrix} 0 & -v_1 & 0 & 0 \\ v_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -v_1 \\ 0 & 0 & v_1 & 0 \end{bmatrix}.$$

After some manipulations, we get

$$\dot{y}(t) = A_1 y(t) + \Psi(0)\begin{pmatrix} -\alpha^* b u_1^{*3}(t-1) - \beta^* b u_1^{*3}(t-\tau^*) \\ -\alpha^* b u_2^{*3}(t-1) - \beta^* b u_2^{*3}(t-\tau^*) \\ -\alpha^* b u_3^{*3}(t-1) - \beta^* b u_3^{*3}(t-\tau^*) \end{pmatrix}$$
$$+ O\left(|p - p_0||y|^2\right) + O\left(|y|^4\right),$$

where

$$A_1 = \begin{bmatrix} -\frac{9}{2}M(p-p_0) & -v_1 + \frac{9}{2}N(p-p_0) & -\frac{9}{2}M(p-p_0) & -\frac{9}{2}N(p-p_0) \\ v_1 - \frac{9}{2}N(p-p_0) & -\frac{9}{2}M(p-p_0) & -\frac{9}{2}N(p-p_0) & \frac{9}{2}M(p-p_0) \\ -\frac{9}{2}M(p-p_0) & -\frac{9}{2}N(p-p_0) & -\frac{9}{2}M(p-p_0) & -v_1 + \frac{9}{2}N(p-p_0) \\ -\frac{9}{2}N(p-p_0) & \frac{9}{2}M(p-p_0) & v_1 - \frac{9}{2}N(p-p_0) & -\frac{9}{2}M(p-p_0) \end{bmatrix},$$

$$b = m'''(K) - h'''(k), \qquad \alpha^* = -\frac{h'''(k)}{b}, \qquad \beta^* = \frac{m'''(k)}{b},$$

and

$$(u_1^*(t-j), u_2^*(t-j), u_3^*(t-j))^T = \Phi(-j)y(t), \qquad j = 1, \tau^*.$$

It can be easily shown that A_1 has two double eigenvalues given by

$$\lambda_{1,2} = -\tfrac{9}{2}M(p-p_0) \pm \tfrac{1}{2}\left\{81(p-p_0)^2M^2 - 4v_1[v_1 - 9M(p-p_0)]\right\}^{1/2}.$$

Let

$$PQ = \begin{bmatrix} 0 & 0 & 0 & 2 \\ M_1 & M_2 & M_3 & M_4 \\ -M_3 & -M_4 & -M_1 & -M_2 \\ 0 & 2 & 0 & 0 \end{bmatrix},$$

where

$$M_1 = \frac{18(p-p_0)MC}{81(p-p_0)^2(M^2-N^2) - 4v_1[v_1 - 9N(p-p_0)]},$$

$$M_2 = \frac{18(p-p_0)N[2v_1 - 9(p-p_0)N]}{81(p-p_0)^2(M^2-N^2) - 4v_1[v_1 - 9N(p-p_0)]},$$

$$M_3 = \frac{2[2v_1 - 9N(p-p_0)]C}{81(p-p_0)^2(M^2-N^2) - 4v_1[v_1 - 9N(p-p_0)]},$$

$$M_4 = \frac{162(p-p_0)^2MN}{81(p-p_0)^2(M^2-N^2) - 4v_1[v_1 - 9N(p-p_0)]},$$

$$C = \frac{\left\{4v_1[v_1 - 9(p-p_0)N] - 81(p-p_0)^2M^2\right\}^{1/2}}{2}.$$

Then

$$(PQ)^{-1}A_1PQ = A :=$$

$$\begin{bmatrix} -\tfrac{9}{2}(p-p_0)M & C & 0 & 0 \\ -C & -\tfrac{9}{2}(p-p_0)M & 0 & 0 \\ 0 & 0 & -\tfrac{9}{2}(p-p_0)M & C \\ 0 & 0 & -C & -\tfrac{9}{2}(p-p_0)M \end{bmatrix}.$$

Making a change of variable,

$$y = PQz, \tag{4.2}$$

we get

$$\dot{z}(t) = Az(t) + (PQ)^{-1}\Psi(0)\begin{bmatrix} -\alpha^* b u_1^{*3}(t-1) - \beta^* b u_1^{*3}(t-\tau^*) \\ -\alpha^* b u_2^{*3}(t-1) - \beta^* b u_2^{*3}(t-\tau^*) \\ -\alpha^* b u_3^{*3}(t-1) - \beta^* b u_3^{*3}(t-\tau^*) \end{bmatrix}$$

$$+ O\left(|p-p_0||z|^2\right) + O\left(|z|^3\right). \tag{4.3}$$

A straightforward but tedious calculation leads to

$$(PQ)^{-1}\Psi(0)\left(M_1^2 - M_3^2\right)$$

$$= \begin{bmatrix} \frac{-MM^* + N}{2} & \frac{\left(M - \sqrt{3}N\right)M^* + \sqrt{3}M - N}{4} & \frac{\left(M + \sqrt{3}N\right)M^* - \sqrt{3}M - N}{4} \\ MM_1 - MM_3 & -M_1\left(\frac{M}{2} - \frac{\sqrt{3}}{2}N\right) + M_3\left(\frac{M}{2} + \frac{\sqrt{3}}{2}N\right) & -M_1\left(\frac{M}{2} + \frac{\sqrt{3}}{2}N\right) + M_3\left(\frac{M}{2} - \frac{\sqrt{3}}{2}N\right) \\ MM_3 - MM_1 & -M_3\left(\frac{M}{2} - \frac{\sqrt{3}}{2}N\right) + M_1\left(\frac{M}{2} + \frac{\sqrt{3}}{2}N\right) & -M_3\left(\frac{M}{2} + \frac{\sqrt{3}}{2}N\right) + M_1\left(\frac{M}{2} - \frac{\sqrt{3}}{2}N\right) \\ \frac{-MM^* + N}{2} & \frac{-\sqrt{3}M - N + \left(M + \sqrt{3}N\right)M^*}{4} & \frac{\sqrt{3}M - N + \left(M - \sqrt{3}N\right)M^*}{4} \end{bmatrix},$$

and $M^* = M_1 M_4 - M_2 M_3$.

According to [31], the equivariant norm form of (4.3) to third order is

$$\dot{z}(t) = Az(t) + a_1\left(z_1^2 + z_2^2 + z_3^2 + z_4^2\right)z(t)$$

$$+ b_0 \begin{pmatrix} z_1^2 + z_2^2 & 0 & 0 & 0 \\ 0 & z_1^2 + z_2^2 & 0 & 0 \\ 0 & 0 & z_3^2 + z_4^2 & 0 \\ 0 & 0 & 0 & z_3^2 + z_4^2 \end{pmatrix} z(t), \tag{4.4}$$

which can be expressed in its polar form

$$\begin{aligned} \dot{r}_1 &= -\tfrac{9}{2}M(p-p_0)r_1 + \left[a_1\left(r_1^2 + r_2^2\right) + b_0 r_2^2\right]r_1, \\ \dot{r}_2 &= -\tfrac{9}{2}M(p-p_0)r_2 + \left[a_1\left(r_1^2 + r_2^2\right) + b_0 r_2^2\right]r_2, \\ \dot{p}_1 &= C, \qquad p_2 = C. \end{aligned} \tag{4.5}$$

Comparing the coefficients of $z_1^2 z_2$ and $z_3^2 z_1$ between the first equation of (4.3) and (4.4), we get

$$a_1 + b_0 = \frac{-b(\alpha^* a_1 + \beta^* a_{\tau^*})}{M_1^2 - M_3^2},$$
$$a_1 = \frac{-b(\alpha^* c_1 + \beta^* c_{\tau^*})}{M_1^2 - M_3^2}, \tag{4.6}$$

where

$$\begin{aligned} a_j = {} & \tfrac{1}{2}[M^* - N][M_3 \cos jv_1 + M_1 \sin jv_1]^3 \\ & + \tfrac{1}{4}\left[MM^* - \sqrt{3}NM^* + \sqrt{3}M - N\right] \\ & \times\left[\left(-\frac{\sqrt{3}}{2}M_1 + \frac{1}{2}M_3\right)\cos jv_1 + \left(\frac{1}{2}M_1 - \frac{\sqrt{3}}{2}M_3\right)\sin jv_1\right]^3 \\ & + \tfrac{1}{4}\left[MM^* + \sqrt{3}NM^* - \sqrt{3}M - N\right] \\ & \times\left[\left(\frac{\sqrt{3}}{2}M_1 + \frac{1}{2}M_3\right)\cos jv_1 + \left(\frac{1}{2}M_1 + \frac{\sqrt{3}}{2}M_3\right)\sin jv_1\right]^3, \end{aligned}$$

$$\begin{aligned} c_j = {} & -\tfrac{3}{2}[-MM^* + N][M_1 \cos jv_1 + M_3 \sin jv_1]^2[M_3 \cos jv_1 + M_1 \sin jv_1] \\ & + \tfrac{3}{8}\left[(M - \sqrt{3}N)M^* + \sqrt{3}M - N\right] \\ & \times\left[(M_1 - \sqrt{3}M_3)\cos jv_1 - (\sqrt{3}M_1 - M_3)\sin jv_1\right]^2 \\ & \times\left[-(\sqrt{3}M_1 - M_3)\cos jv_1 + (M_1 - \sqrt{3}M_3)\sin jv_1\right] \\ & + \tfrac{3}{8}\left[(M + \sqrt{3}N)M^* - \sqrt{3}M - N\right] \\ & \times\left[(M_1 + \sqrt{3}M_3)\cos jv_1 + (\sqrt{3}M_1 + M_3)\sin jv_1\right]^2 \\ & \times\left[(\sqrt{3}M_1 + M_3)\cos jv_1 + (M_1 + \sqrt{3}M_3)\sin jv_1\right], \end{aligned}$$

with $j = 1$ or τ^*.

It can be easily verified that the amplitude equation in system (4.5) has a nontrivial equilibrium (r^*, r^*) with

$$r^{*2} = 9M(p - p_0)/2(2a_1 + b_0)$$

or

$$r^{*2} = \frac{-9M(M_1^2 - M_3^2)}{2b[\alpha(a_1 + c_1) + \beta(a_{\tau^*} + c_{\tau^*})]}(p - p_0). \tag{4.7}$$

The eigenvalues of the linearization of (4.5) at (r^*, r^*) are given by

$$\lambda_1 = 2r^{*2}(2a_1 + b_0), \qquad \lambda_2 = 2r^{*2}b_0.$$

Consequently, we have the following conclusion:

THEOREM 4.1

Assume that Assumption 1 *is satisfied. Then system* (2.1) *has a Hopf bifurcation of discrete waves. For the equivariant normal form* (4.4) *of* (2.1) *up to third order, the bifurcation takes place for* $p > p_0$ *if*

$$\Delta_1 := \frac{M(M_1^2 - M_3^2)}{b[\alpha(a_1 + c_1) + \beta(a_{\tau^*} + c_{\tau^*})]} < 0,$$

or for $p < p_0$ *if* $\Delta_1 > 0$. *Moreover, the discrete waves are asymptotically stable if*

$$\Delta_2 := \frac{b[\alpha(a_1 + c_1) + \beta(a_{\tau^*} + c_{\tau^*})]}{M_1^2 - M_3^2} > 0,$$

$$\Delta_3 := \frac{b[\alpha(a_1 + c_1) + \beta(a_{\tau^*} - c_{\tau^*})]}{M_1^2 - M_3^2} > 0$$

and unstable if at least one of Δ_2 *and* Δ_3 *is negative.*

The conclusion about the normal form (4.4) gives us some insight into the dynamics of the full system (2.1), which can be verified with numerical simulations at appropriate parameter values. But it remains an interesting open problem to determine if the normal form (4.4) captures all of the essential dynamics of the full system.

The analysis of the characteristic equation of (4.1) is very complicated, and the complete description of the distribution of characteristic values is still remote. However, we are able to use the Maple program to carry out some numerical simulations. In particular, for $\alpha = 0.7333333333$, $\beta = 0.2666666666$, $\tau = 1$, $\tau^* = 3.05$, $p_0 = 0.1068436529$, $r = 3.1591596998$, $m'''(k) = -0.2666666666$, $h'''(k) = 0.7333333333$, we can also verify that Assumption 1 is satisfied and

$$\alpha^*(a_1 + c_1) + \beta^*(a_{\tau*} + c_{\tau*}) = 0.0519500609,$$

$$\alpha^*(a_1 - c_1) + \beta^*(a_{\tau*} - c_{\tau*}) = 0.07341308855,$$

$$M = -0.04963129536, \qquad M_1 = 0.05506232503, \qquad M_3 = -0.9438832338.$$

Therefore, the bifurcation of discrete waves takes place for $p > p_0$, and the discrete waves are asymptotically stable.

5. DISCUSSION

Multiple time lags and dispersion occur in many biological processes, and the mathematical analysis of the model equations is usually very complicated. Our focus in this paper is on a model motivated by the earlier work of Murray [1] and describing the dynamics of predator–prey communities over a ring of patches. In the case of a single delay, we have shown that the primary Hopf bifurcation consists of spatially homogeneous periodic solutions that represent synchronous oscillations in the patchy environment. The bifurcation direction and stability have also been studied, but the global existence of synchronous oscillations and their stability analysis remain an open problem. In the case of two time lags, we have developed an algorithm to determine the existence of discrete waves and their stability. Computer simulations show that stable discrete waves representing spatially heterogeneous oscillations or phase-locked oscillations may occur, and consequently the presence of multiple time lags may give rise to spatial heterogeneity in a system of functional differential equations. Some results about characteristic values of a system of delay differential equations with two delays can be found in the literature, but a complete description still remains a challenging problem.

The ring structure of the patchy environment greatly simplifies our mathematical analysis and enables us to apply some recent results in [33, 34] for symmetric Hopf bifurcation theory of functional differential equations and the equivariant normal form in [31] for ordinary differential equations. This is clearly a simplification of the real situation, and the more general structure of the patchy environment should be addressed in the future.

Finally, we emphasize that a more realistic model should include distributed delays and take the form

$$\dot{u}_i(t) = \int_{-\infty}^{t} K_1^i(t-s)h(u_i(s))ds - \int_{-\infty}^{t} K_2^i(t-s)m(u_i(s))ds + \sum_{j\neq i} D_{ji}\left[u_j(t) - u_i(t)\right].$$

Though our method can, in principle, be applied to the above system, the corresponding analysis can be quite difficult but should be pursued in the future.

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