SPIRAL WAVE GENERATION IN A DIFFUSIVE PREDATOR-PREY MODEL WITH TWO TIME DELAYS

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ABSTRACT. This paper is concerned with the pattern formation of a diffusive predator-prey model with two time delays. Based upon an analysis of Hopf bifurcation, we demonstrate that time delays can induce spatial patterns under some conditions. Moreover, by use of a series of numerical simulations, we show that the type of spatial patterns is the spiral wave. Finally, we demonstrate that the spiral wave is asymptotically stable.

1. Introduction

Pattern formation in reaction-diffusion systems is one of the most fascinating phenomena in nonlinear physics and has been observed in various mechanisms including chemical and biological systems. The most widely studied model for spatial pattern formation is the reaction-diffusion model proposed by Turing in 1952 [19]. He showed that a system of reacting and diffusing chemicals could evolve from the initial near-homogeneity into the inhomogeneous pattern of concentration.

There are two directions on current studies of spatial patterns. One is to study biological science by use of the theory of spatial patterns [1, 10, 11, 22], the other is to explore conditions enabling spatial patterns from mathematical aspect [2–9, 12–18, 20, 21, 23]. Kishimoto and Weinberger [6] proved the non-existence of stable positive stationary solution in the Lotka-Volterra competition-diffusion system without the cross-diffusion. However, when the cross-diffusion is present, Pang et al. [12] studied the existence of spatial patterns for the reaction-diffusion model with different kinds of diffusion terms and reaction terms. Shi et al. [14] proposed that the cross-diffusion can also destabilize a uniform equilibrium which is stable for the kinetic system and the self-diffusion reaction system. They gave an application to the predator-prey system with preytaxis and vegetation pattern formation in a water-limited

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ecosystem. Tian et al. [18] developed a theoretical framework for investigating spatial patterns on a plankton allelopathy with the cross-diffusion.

Recently, Sen et al. [13] showed that the time delay may induce spatial patterns in the reaction-diffusion system. Tian [15] discussed the formation of delay-induced Turing patterns in a model of allelopathic competition interactions and showed that the time delay plays an important role on pattern formation by use of a series of numerical simulations performed with a finite difference scheme. Lian et al. [7] investigated the pattern formation in a reaction-diffusion predator-prey model incorporating a prey refuge and illustrated the spatial patterns via numerical simulations. They found that the model dynamics exhibits a delay and diffusion controlled formation growth not only of spots, stripes and holes, but also of self-replicating spiral patterns.

In this paper, we will study spatial patterns of a reaction-diffusion predatorprey system with two delays which is written in the form:

$$\begin{cases}
\frac{\partial u_{1}}{\partial t} - d_{1}\Delta u_{1} = u_{1}(a_{1} - a_{11}u_{1} - \frac{a_{12}u_{2}(x, t - \tau_{2})}{\gamma + u_{2}(x, t - \tau_{2})}), & (x, t) \in \Omega \times (0, T), \\
\frac{\partial u_{2}}{\partial t} - d_{2}\Delta u_{2} = u_{2}(-a_{2} + a_{21}u_{1}(x, t - \tau_{1}) - a_{22}u_{2}), & (x, t) \in \Omega \times (0, T), \\
\frac{\partial u_{1}}{\partial \eta} = \frac{\partial u_{2}}{\partial \eta} = 0, & (x, t) \in \partial \Omega \times (0, T), \\
u_{i}(x, t) = \varphi_{i}(x, t), & i = 1, 2, & (x, t) \in \Omega \times [-\tau, 0],
\end{cases}$$

where $u_1(x,t)$ and $u_2(x,t)$ represent species densities of the prey and predator, respectively. Δ is the Laplacian operator and η is outward unit normal vector on $\partial\Omega$. d_1 and d_2 are diffusion coefficients. a_1 denotes intrinsic growth rate of prey species and a_2 denotes the death rate of predator species. a_{11} and a_{22} are rates of intra-specific competitions of prey species and predator species, respectively. $\frac{u_2(x,t-\tau_2)}{u_2(x,t-\tau_2)+\gamma}$ represents the Holling II type functional response. γ is the half-saturation abundance of prey species. a_{12} is the capture rate of predator species. a_{21} is the conversion rate of predator species. τ_1 is called hunting delay and τ_2 is the maturation time of the prey species. The parameters a_i , a_{ij} , d_i (i,j=1,2) and γ are positive constants. Initial value $\varphi_i(x,t)$ (i=1,2) is positive, Hölder continuous and satisfies $\partial\varphi_i/\partial\eta=0$ on the boundary. The homogeneous Neumann boundary condition biologically indicates that there is no population flux across the boundary.

The goal of this paper is to explore whether two time delays can drive the emergence of spatial patterns and how different time delays affect the stability of spatial patterns by numerical simulations. The structure of this paper is organized as follows: In Section 2, we analyze the role of time delays in the generation of spatial patterns from the mathematical point of view and derive conditions for these patterns to generate. In Section 3, we illustrate spatial

patterns via numerical simulations. Some discussions are presented in the last section.

2. Delay driven spatial patterns

In this section, we derive conditions for the generation of spatial patterns. In particular, we show that when the time delay is absent, the system (1.1) does not generate the spatial pattern. While, in the presence of time delays, the formation of spatial patterns is induced.

It is easy to see that the positive uniform equilibrium of the system (1.1) satisfies:

(2.1)
$$\begin{cases} a_1 - a_{11}u_1 - \frac{a_{12}u_2}{\gamma + u_2} = 0, \\ -a_2 + a_{21}u_1 - a_{22}u_2 = 0. \end{cases}$$

By a routine algebraic computation, sufficient condition can be obtained for the existence of the positive uniform equilibrium of the system (1.1).

Lemma 2.1. Assume that

$$(H_1): a_1a_{21} > a_{11}a_2.$$

Then the system (2.1) admits a unique positive uniform equilibrium $\mathbf{u}^* = (u_1^*, u_2^*)$.

Now we carry out the linear stability analysis of the system (1.1). Let $v_1 = u_1 - u_1^*$, $v_2 = u_2 - u_2^*$ and substitute them in the system (1.1). Retaining the linear terms in v_1 and v_2 gives rise to

$$(2.2) \qquad \begin{cases} \frac{\partial v_1}{\partial t} - \Delta v_1 = Av_1 + Bv_2(x, t - \tau_2), & (x, t) \in \Omega \times (0, T), \\ \frac{\partial v_2}{\partial t} - \Delta v_2 = Cv_2 + Dv_1(x, t - \tau_1), & (x, t) \in \Omega \times (0, T), \\ \frac{\partial v_1}{\partial \eta} = \frac{\partial v_2}{\partial \eta} = 0, & (x, t) \in \partial \Omega \times (0, T), \\ v_i(x, t) = \varphi_i(x, t) - u_i^*, & i = 1, 2, & (x, t) \in \Omega \times [-\tau, 0], \end{cases}$$

where

(2.3)
$$A = -a_{11}u_1^*, \quad B = \frac{-a_{12}\gamma u_1^*}{(\gamma + u_2^*)^2}, \quad C = -a_{22}u_2^*, \quad D = a_{21}u_2^*.$$

Since the boundary condition is homogeneous Neumann on the domain Ω , the appropriate eigenfunction of the system (2.2) is

$$(2.4) (v_1, v_2) = (c_1, c_2)e^{\lambda t} \cos kx,$$

where λ is the eigenvalue, k is the wavenumber and $0 \le k \in \mathbf{R}$. Substituting (2.4) in the system (2.2) yields

$$(2.5) \quad \left\{ \begin{array}{l} (\lambda c_1 + d_1 k^2 c_1) e^{\lambda t} \cos kx = (Ac_1 + Be^{-\lambda \tau_2} c_2) e^{\lambda t} \cos kx, \\ (\lambda c_2 + d_2 k^2 c_2) e^{\lambda t} \cos kx = (Cc_2 + De^{-\lambda \tau_1} c_1) e^{\lambda t} \cos kx. \end{array} \right.$$

Since $e^{\lambda t} \cos kx \neq 0$, equations (2.5) is equivalent to the following set of linear algebraic equations:

(2.6)
$$\begin{pmatrix} \lambda - A + d_1 k^2 & -Be^{-\lambda \tau_2} \\ -De^{-\lambda \tau_1} & \lambda - C + d_2 k^2 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}.$$

Nontrivial solutions of equations (2.6) exist if and only if

(2.7)
$$\det \begin{pmatrix} \lambda - A + d_1 k^2 & -Be^{-\lambda \tau_2} \\ -De^{-\lambda \tau_1} & \lambda - C + d_2 k^2 \end{pmatrix} = 0.$$

Let $\tau = \tau_1 + \tau_2$. Then the characteristic equation of the system (1.1) at the positive equilibrium \mathbf{u}^* is of the form

(2.8)
$$\Delta(\lambda, \tau) = \lambda^2 + \overline{A}_k \lambda + \overline{B}_k + \overline{C}_k e^{-\lambda \tau} = 0,$$

where

$$\overline{A}_k = -(A+C) + (d_1+d_2)k^2$$
, $\overline{B}_k = (-A+d_1k^2)(-C+d_2k^2)$, $\overline{C}_k = -BD$.

It is well known that \mathbf{u}^* is unstable if there is at least one root with $\mathrm{Re}\lambda>0$ and is stable if $\mathrm{Re}\lambda<0$ for all λ . That is to say, the stability of \mathbf{u}^* depends on the location of zeros of the associated characteristic equation. Thus, spatial patterns generate if $\mathrm{Re}\lambda=0$ with $\tau=\tau^*$, which is called delay driven spatial patterns. Moreover, τ^* is called the Hopf bifurcation threshold.

When the delay is absent (i.e., $\tau = 0$), the equation (2.8) becomes

(2.9)
$$\Delta(\lambda, 0) = \lambda^2 + \overline{A}_k \lambda + \overline{B}_k + \overline{C}_k = 0.$$

If

$$(H_2): a_{11}a_{22}(\gamma + u_2^*)^2 < a_{12}a_{21}$$

is satisfied, then it is easy to verify that $\overline{A}_k > 0$ and $\overline{B}_k + \overline{C}_k > 0$. These imply that the real parts of the roots of the equation (2.9) are negative. Firstly, we obtain the following stability result for the characteristic the equation (2.9).

Lemma 2.2. Roots of the equation (2.9) with $\tau = 0$ have always negative real parts, that is, the positive equilibrium \mathbf{u}^* for the system (1.1) with $\tau = \tau_1 = \tau_2 = 0$ is asymptotically stable.

When the time delay is present (i.e., $\tau \neq 0$) and if $\lambda = iw_0$ is a root of the equation (2.8), then we have

(2.10)
$$\begin{cases} w_0^2 - \overline{B}_k = \overline{C}_k \cos w_0 \tau, \\ w_0 \overline{A}_k = \overline{C}_k \sin w_0 \tau. \end{cases}$$

This leads to

(2.11)
$$w_0^4 + (\overline{A}_k^2 - 2\overline{B}_k)w_0^2 + \overline{B}_k^2 - \overline{C}_k^2 = 0,$$

where

(2.12)
$$\overline{A}_k^2 - 2\overline{B}_k = (-A + d_1 k^2)^2 + (-C + d_2 k^2)^2,$$

and

(2.13)
$$\overline{B}_k^2 - \overline{C}_k^2 = [AC - (Cd_1 + Ad_2)k^2 + d_1d_2k^4]^2 - (-BD)^2.$$

In view of the hypothesis (H_2) , it is easy to verify that $\overline{B}_k^2 - \overline{C}_k^2 < 0$ for some fixed k. Therefore, (2.11) has a unique positive real root:

$$w_0 = \sqrt{\frac{-\overline{A}_k^2 + 2\overline{B}_k + [(\overline{A}_k^2 - 2\overline{B}_k)^2 - 4(\overline{B}_k^2 - \overline{C}_k^2)]^{1/2}}{2}}.$$

Thus, the equation (2.8) has pure imaginary root iw_0 when

(2.14)
$$\tau = \tau^* + \frac{2j\pi}{w}, \ j = 1, 2, \dots, \ \tau^* = \frac{\arccos\frac{w_0^2 - \overline{B}(k)}{\overline{C}(k)}}{w_0}.$$

Next, applying the method developed by [10], we calculate the wavenumber k. From (2.12) and (2.13), we get

(2.15)
$$d_1 d_2 k^4 - (C d_1 + A d_2) k^2 + A C + B D = 0.$$

Clearly, (2.15) has a unique positive root

$$k^* = \sqrt{\frac{Cd_1 + Ad_2 + \sqrt{(Cd_1 + Ad_2)^2 - 4d_1d_2(AC + BD)}}{2d_1d_2}}.$$

Thus, $\overline{B}_k^2 - \overline{C}_k^2 < 0$ is satisfied if $k < k^*$. Moreover, the Hopf bifurcation threshold is given by τ^* from (2.14). In summary, we have the following result:

Theorem 2.1. Suppose that the system (1.1) satisfies hypothesis (H_1) and (H_2) , then time delays can induce spatial patterns. Moreover,

- (i) If $\tau_1 = \tau_2 = 0$, then the positive equilibrium \mathbf{u}^* of the system (1.1) is local asymptotically stable.
- (ii) If $\tau = \tau_1 + \tau_2 > \tau^*$, then the positive equilibrium \mathbf{u}^* of the system (1.1) is unstable.

Remark 2.1. If the sum of two time delays is large enough, then \mathbf{u}^* of the system (1.1) is unstable and the system (1.1) has spatial patterns.

3. Numerical results

In view of Theorem 2.1, fulfilments of hypothesis (H_1) and (H_2) are sufficient for the positive uniform equilibrium (u_1^*, u_2^*) being linearly unstable with respect to the particular case of the system (1.1). We take the following values:

$$(3.1) \quad a_1 = 1, a_{11} = 1, a_{12} = 1, \gamma = 1, a_2 = 1, a_{21} = 2, a_{22} = 1, \tau_1 = 2, \tau_2 = 2.$$

For this special choice, the positive uniform equilibrium is given by

$$(u_1^*, u_2^*) = (1.2858, 0.5616).$$

In this section, using the Euler difference method, we give some numerical results based on the formulae in Section 2. The domain of the system (1.1) is confined to a square domain $\Omega = [0, L_x] \times [0, L_y] \subset \mathbf{R}^2$. The wavenumber for the domain is thereby

$$\mathbf{k} = \pi(m/L_x, n/L_y), \text{ and } |\mathbf{k}| = \pi \sqrt{(m/L_x)^2 + (n/L_y)^2}, m, n = 0, 1, \dots$$

We consider the system (1.1) in a fixed domain $L_x = 900$ and $L_y = 300$ and solve it on a grid with 900×300 sites by a simple Euler method with a time step of $\Delta t = 0.1$ and a space step of $\Delta x = \Delta y = 1$. By discretizing the Laplacian in the grid with lattice sites denoted by (i, j), the numerical form is

$$\Delta u|_{(i,j)} = \frac{1}{\Delta x \Delta y} [a_l(i,j)u(i-1,j) + a_r(i,j)u(i+1,j) + a_d(i,j)u(i,j-1) + a_u(i,j)u(i,j+1) - 4u(i,j)],$$

where the matrix elements of a_l, a_r, a_d and a_u are unity except at the boundary. When (i,j) is at the left boundary (that is, i=0), we define $a_l(i,j)u(i-1,j) \equiv u(i+1,j)$, which guarantees zero-flux of reactants in the left boundary. Similarly we define $a_r(i,j), a_d(i,j)$ and $a_u(i,j)$ such that the boundary is no-flux.

It is well-known that for a purely spatial homogeneous initial distribution, the system always sustains homogeneous and the spatial pattern does not generate. So we take initial conditions with an inhomogeneous spatial perturbation. Our simulations indicate that the spiral wave emerges. Moreover, the number of spiral waves depends on the number of the critical point of the initial data. We recall that the critical point (x_c, y_c) of the initial data means that (x_c, y_c) satisfied that $u_1(x_c, y_c)|_{t=0} = u_1^*$ and $u_2(x_c, y_c)|_{t=0} = u_2^*$.

Here, we present the results of two computer experiments differing in the form of initial conditions. In the first case, the initial distribution of species is given in the following form:

$$u_1(x, y, t) = u_1^* - \epsilon_1(x - 40)(x - 160) - \epsilon_2(y - 60)(y - 140),$$

$$u_2(x, y, t) = u_2^* - \epsilon_3(x - 90) - \epsilon_4(y - 100),$$

where $\epsilon_1 = 2 \cdot 10^{-7}$, $\epsilon_2 = 3 \cdot 10^{-5}$, $\epsilon_3 = 1.2 \cdot 10^{-4}$ and $\epsilon_4 = 6 \cdot 10^{-4}$. In this case the initial data contains only one critical point $(x_c, y_c) = (277.9433, 62.4113)$. Snapshots of the spatial distribution are shown in Fig. 1 for t = 0, 1000, 2000, 3000, 4000, 12000. We find that distributions of prey and predator species are always of the same type, except in the early stages of the process when the influence of the initial condition is dominant. Hence, spatial patterns of predator species are shown. A spiral wave emerges in Fig. 1(c). After the formation of the spiral wave, it grows slightly for a certain time, with their spatial structure becoming more distinct (Fig. 1(d) and Fig. 1(e)). Moreover, the scale of spiral wave increases with the time and it eventually prevails to the whole domain. As the time goes on, the structure of the spatial pattern will sustain the spiral wave and the width of the spiral wave will be thin.

In the second case, the initial distribution of species is given in the following form:

$$u_1(x, y, t) = u_1^* - \epsilon_1(x - 0.1y - 225)(x - 0.1y - 675),$$

$$u_2(x, y, t) = u_2^* - \epsilon_2(x - 450) - \epsilon_3(y - 150),$$

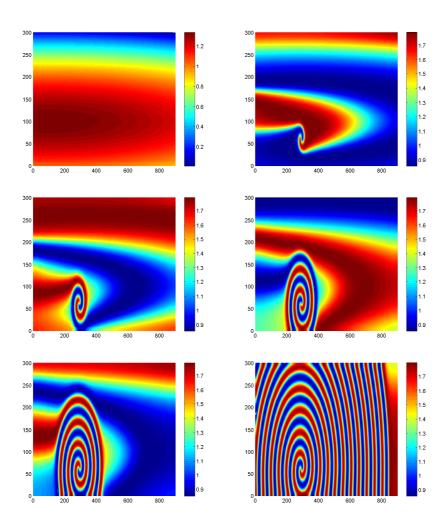


FIGURE 1. Spatial distribution of predator for (a) t=0, up and left location, (b) t=1000, up and right location, (c) t=2000, middle and left location, (d) t=3000, middle and right location, (e) t=4000, below and left location, (f) t=12000, below and right location. Parameters are given in (3.1). From (a)-(f), a spiral generates and prevails to the whole domain.

where $\epsilon_1=2\cdot 10^{-7}$, $\epsilon_2=3\cdot 10^{-5}$, and $\epsilon_3=1.2\cdot 10^{-4}$. In this case, the initial data contains only one critical points $(x_c,y_c)=(684.1463,245.1219)$ and (91.4634,201.2195). Snapshots of the spatial distribution are shown in Fig. 2 for t=0,1000,2000,3000,4000,36000. Two spiral waves simultaneously

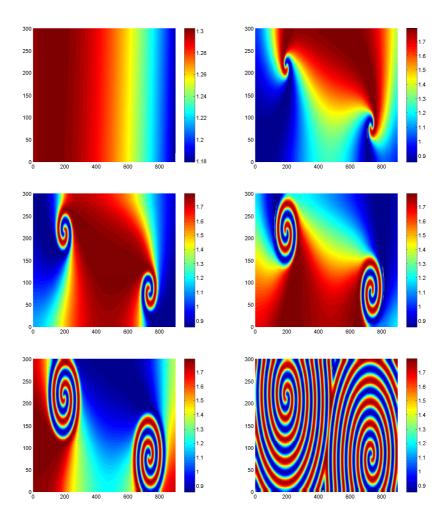


FIGURE 2. Spatial distribution of predator for (a) t=0, up and left location, (b) t=1000, up and right location, (c) t=2000, middle and left location, (d) t=3000, middle and right location, (e) t=4000, below and left location, (f) t=36000, below and right location. Parameters are given in (3.1). From (a)-(f), two spirals generate and prevail to the whole domain.

emerge in Fig. 2(c). After the formation of spiral waves, they grow slightly for a certain time, and get closer (Fig. 2(d) and Fig. 2(e)). Moreover, the scales of two spiral waves also increase with the time and they eventually prevail to the

whole domain. As the time goes on, the structure of spatial patterns will also sustain the spiral wave and the width of spiral waves will be thin.

4. Discussion

In this paper, we have developed a theoretical framework for studying the phenomenon of pattern formation in a 2D reaction-diffusion system with two time delays. Applying a stability analysis and suitable numerical simulations, we investigate the Hopf bifurcation, the pattern parameter space and the spiral wave pattern. We have shown that time delays can induce the existence of the Hopf bifurcation at the positive equilibrium and the system (1.1) can generate the spiral wave pattern under some special initial conditions. The stability of the positive uniform equilibrium is determined in parameter spaces (H_1) and (H_2) . In a biological sense, the existence of stability switch induced by the time delay is found in the region of the spatial pattern space of the large conversion rate of predator species.

Numerical studies have been employed to support and extend the obtained theoretical results. When interaction coefficients of two species are fixed and the conversation rate of predator species is large, the numerical simulations illustrate the existence of both stable and unstable equilibrium near the critical point of the time delay which is in good agreement with our theoretical analysis results. Our numerical results also show that spiral wave patterns are asymptotically stable, whereas in a plankton system spiral wave patterns are not stable [16]. Our study of PDE model simplifies the real ecological processes, which may not always be satisfactory. However, the mathematical model can help to clarify patterns of species interactions and guide further experiments. The proposed approach has applicability to other reaction-diffusion systems including time delays, such as competitive models and mutualistic models.

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