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Research article

Diffusion-driven instability of both the equilibrium solution and the periodic solutions for the diffusive Sporns-Seelig model

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Abstract: In this paper, a reaction-diffusion Sporn-Seelig model subject to homogeneous Neumann boundary condition in the one dimensional spatial open bounded domain is considered. Of our particular interests, we are concerned with diffusion-driven instability of both the positive constant equilibrium solution and the Hopf bifurcating spatially homogeneous periodic solutions. To strengthen our analytical results, we also include some numerical simulations. These results allow for the clearer understanding the mechanisms of the spatiotemporal pattern formations of this chemical reaction model.

Keywords: the diffusive Sporns-Seelig model; Hopf bifurcations; spatially homogeneous periodic solutions; diffusion-driven instability; spatiotemporal patterns

1. Introduction

In 1952, A. Turing proposed a striking idea in his pioneering paper [1] that diffusion can destabilize an otherwise stable homogeneous equilibrium solution of the reaction-diffusion equations and trigger the emergence of new stable non-constant steady state solutions, which have non-uniform spatial patterns, now usually called Turing patterns. Since then, Turing's idea has been extensively used to model the spatial patterns in a variety of areas, including biology, physics and chemistry. In chemistry, the research of the spaito-temporal pattern formations has been a crucial issue. However, earlier results on this aspect in this area mainly concentrated on the temporal oscillations of the chemical models. For example, the well-known Belousov-Zhabontinskii chemical reaction was one of the earlier chemical reactions to report the temporal oscillatory patterns. Since then, more and more chemical reaction models have been proposed to exhibit temporal oscillatory patterns. In the course of the study of the oscillatory pattern in chemistry, Turing's 1952 paper was noticed by chemists who found with surprising that the system of the reaction-diffusion equations can be used to model the oscillatory patterns which can be observed by the solutions of the reaction diffusion equations; However, the Turing patterns (argued in Turing's 1952 paper) for the chemical reaction models have never been observed. Until 1990, D. Kepper and her collaborators [2] conducted a well-known CIMA chemical reaction observing the Turing patterns. This is the first experimental evidence of Turing pattern formation in chemistry. Since then, the spatiotemporal pattern formation (especially Turing pattern formation) in chemistry has sprung up.

On the other hand, the diffusion could also destabilize an otherwise stable spatially homogeneous periodic solution of the reaction-diffusion equations and then trigger the emergence of new irregular spatiotemporal patterns. This is known as diffusion-driven instability of the periodic solutions. Numerical simulations for the well-known Belousov-Zhabontinskii chemical reaction have shown that under suitable conditions on the diffusion rates, the spatially homogeneous periodic solutions of the reaction-diffusion equations do have the possibility to undergo diffusion-driven instability; In the past 40 years, diffusion-driven instability of the periodic solutions has been extensively studied. For example, in [3], K. Maginu used the regular perturbation methods to study the diffusion-driven instability of the spatially homogeneous periodic solution for the general reaction-diffusion equation on the entire space; After that, in [4], S. Ruan used Maginu's methods to study the diffusion-driven instability of the periodic solutions of the diffusive Gierer-Meinhardt system; In [5], M. Kuwamura, H. Izuhara considered diffusion-driven instability of the periodic solutions for the system with particular Hamiltonian structure; In [6], Y. Morita considered diffusion-driven instability of the periodic solutions for the partial functional differential equations with time delay; Recently, by using Maginu's idea, Yi [7] derived a general formula in terms of the diffusion rates (as well as the cross-diffusion rates) to determine the Hopf bifurcating spatially homogeneous periodic solutions for the general reaction-diffusion equations with 2-components. The abstract results obtained in [7] can be used to study the diffusion-driven instability of the Hopf bifurcating periodic solutions for all kinds of reaction-diffusion equations with 2-components.

In this paper, we are mainly concerned with the diffusive Sporns-Seelig model in the area of the chemical reactions. The original Sporns-Seelig model (indeed the ODE version) was first proposed in 1986 to characterize the influences of both negative (repression) and positive (inductive) feedbacks on the genetic regulatory mechanism of induction in the enzymatic chemical reaction [8]. The reaction involves a substrate S reacting with an enzyme E to form a complex ES which in turned is converted into an end-product P and the enzyme. Substrate S is supplied by a transport mechanism with autocatalysis characteristics obeying the logistic term. S and E react according to the following irreversible mechanism:

$$\mathrm{S} + \mathrm{E} \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \mathrm{ES} \xrightarrow{k_2} \mathrm{E} + \mathrm{P},$$

where S is depleted by reaction with the enzyme E, whose synthesis (forming ES with rate constant k_1) is induced by the action of S. Once ES is formed, it can not only produce E and S with reaction rate constant k_{-1}, but also can form E and P, with reaction rate k_2, which is usually called the enzymes catalytic constant. The end-product P is not interacting with enzymes (E and ES) or substrate S and is therefore eliminated in the analytical treatment. The enzyme E is then degraded or deactivated by first-order kinetics with rate constant k_0.

By the law of mass action, the scheme of the aforementioned enzymatic reaction can be characterized by the following ordinary differential equations:

$$\begin{cases} \frac{d[S]}{d\tau} = j_3 + j_2[S] - k_1[E][S] + k_{-1}[ES], \\ \frac{d[E]}{d\tau} = j_1[S] - k_0[E] - k_1[E][S] + k_{-1}[ES] + k_2[ES], \\ \frac{d[ES]}{d\tau} = k_1[E][S] - k_{-1}[ES] - k_2[ES], \end{cases} \tag{1.1}$$

where $[S] = [S](\tau)$, $[E] = [E](\tau)$ and $[ES] = [ES](\tau)$ stand for the concentrations of the substrate S, the enzyme E and the complex ES at time τ, respectively.

Let $[E]_{\text{total}} := [E] + [ES]$ be the total enzyme concentrations. Then, by (1.1), we have,

$$\frac{d[E]_{\text{total}}}{d\tau} = \frac{d[E]}{d\tau} + \frac{d[ES]}{d\tau} = j_1[S] - k_0[E]. \tag{1.2}$$

According to the Bodenstein hypothesis on the quasi-steady state for the complex $[ES]$, we can assume that $d[ES]/d\tau = 0$. Thus, from (1.1), we have $k_1[E][S] - k_{-1}[ES] - k_2[ES] = 0$. This together with $[E]_{\text{total}} := [E] + [ES]$ indicates that

$$[ES] = \frac{k_1[S][E]_{\text{total}}}{k_1[S] + k_{-1} + k_2}, [E] = \frac{(k_{-1} + k_2)[E]_{\text{total}}}{k_1[S] + k_{-1} + k_2}. \tag{1.3}$$

Substituting (1.3) into (1.1) and (1.2) , we have

$$\begin{aligned} \frac{d[S]}{d\tau} &= j_3 + j_2[S] - \frac{k_1 k_2}{k_{-1} + k_2}[E]_{\text{total}}[S]\frac{1}{\frac{k_1[S]}{k_{-1} + k_2} + 1}, \\ \frac{d[E]_{\text{total}}}{d\tau} &= j_1[S] - k_0[E]_{\text{total}}\frac{1}{\frac{k_1[S]}{k_{-1} + k_2} + 1}. \end{aligned}$$

Introducing new variables

$$u = \frac{k_1[S]}{k_{-1} + k_2}, \ v = \frac{k_1[E]_{\text{total}}}{k_{-1} + k_2}, \ t = k_0\tau, \ k = \frac{j_3 k_1}{k_0(k_{-1} + k_2)}, \ \xi = \frac{j_2}{k_0}, \ m = \frac{k_2}{k_0}, \ \theta = \frac{j_1}{k_0},$$

we obtain

$$\frac{du}{dt} = k + \xi u - \frac{muv}{1 + u}, \qquad \frac{dv}{dt} = \theta u - \frac{v}{1 + u}. \tag{1.4}$$

Adding the effect of spatial dispersal, we can obtain the following homogeneous diffusive reaction-diffusion Sporns-Seelig model for the generic regulatory mechanism of induction

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 u_{xx} + k + \xi u - \frac{muv}{1 + u}, & (x, t) \in (0, \ell\pi) \times (0, \infty), \\ \frac{\partial v}{\partial t} = d_2 v_{xx} + \theta u - \frac{v}{1 + u}, & (x, t) \in (0, \ell\pi) \times (0, \infty), \\ \partial_\nu u = \partial_\nu v = 0, x = 0, \ell\pi, & t > 0, \\ u(x, 0) = u_0(x) \geq 0, & v(x, 0) = v_0(x) \geq 0, x \in (0, \ell\pi), \end{cases} \tag{1.5}$$

where u and v stand for the re-scaled concentration of substrate and the enzyme at time t and position x. $d_1 > 0$ and $d_2 > 0$ are the diffusion rates of u and v respectively; For the convenience of our discussions (without loss of generality), we may assume that the spatial domain is $(0, \ell\pi)$, where $\ell > 0$.

Although system (1.5) has been proposed, our knowledge on the dynamics of the system still remains limited except that in [8] the authors showed the existence of the limit cycle for the kinetic ODE system from the numerical point of view. In this paper, of our particular interests, we focus on the diffusion-driven instability of two kinds of the solutions: one is the unique positive equilibrium solution and the other is the Hopf bifurcating periodic solutions. For the diffusion-driven instability analysis of the unique positive equilibrium solution, we use the linearized principle to deduce such instability; while for diffusion-driven instability of the bifurcating periodic solutions, we use the abstract results obtained in [7]. We choose the first component of the positive equilibrium solution, denoted by λ, as the bifurcation parameter, and show that the corresponding ODE system will undergo a Hopf bifurcation when the parameter λ crosses some critical value, denoted by λ_0. In particular, by computing the first Lyapunov coefficient, we find that the corresponding Hopf bifurcating periodic solution is always orbitally stable and the Hopf bifurcation is forward in the sense that the bifurcation occurs when the parameter λ is slightly larger than λ_0; Then, by using the abstract results in [7], we derive the relationship between the diffusion rates d_1 and d_2, such that under this relationship, the stable periodic solution (with respect to the ODEs) will become unstable with respect to the reaction-diffusion system (1.5).

We also include some numerical simulations to support our theoretical analysis. Our numerical simulations show that for fixed set of the system parameters, if the Hopf bifurcating spatially homogeneous periodic solutions of the reaction-diffusion system undergo diffusion-driven instability, then the new spatial patterns occur. In [1], A. Turing suggested that if the diffusion-driven instability of the constant positive equilibrium solution occurs, then around this equilibrium solution, new non-constant positive equilibrium solution will be generated; That is, diffusion-driven instability of the constant equilibrium solution will be one of the main mechanism for the emergence of spatial patterns; Our results shows that under certain conditions, diffusion-driven instability of the periodic solution can also generate new non-constant positive equilibrium solution.

The remaining part of the paper is organized as follows. In section 2, we perform detailed stability analysis and Hopf bifurcation analysis to the ODE system; In section 3, we consider diffusion-driven instability of the positive constant equilibrium solution; In section 4, we study diffusion-driven instability of the Hopf bifurcating periodic solutions; In section 5, we include some numerical simulations to support our theoretical analysis; In section 6, we end up our discussions by drawing some conclusions.

2. Stability and Hopf bifurcation analysis of the kinetic ODEs

In this section, we consider the dynamics of the ODE system (1.4). For convenience, we copy (1.4) here:

$$\frac{du}{dt} = k + \xi u - \frac{muv}{1+u}, \frac{dv}{dt} = \theta u - \frac{v}{1+u}. \tag{2.1}$$

Clearly, system (2.1) has a unique positive steady state solution (λ, v_λ), where λ is the unique positive root of $m\theta u^2 - \xi u - k = 0$ and $v_\lambda := \theta\lambda(\lambda + 1)$. We shall use λ as the bifurcation parameter (or equivalently m) by fixing ξ, θ and k.

The linearized operator of system (2.1) evaluated at (λ, v_λ) is given by:

$$J(\lambda) := \begin{pmatrix} a(\lambda) & b(\lambda) \\ c(\lambda) & d(\lambda) \end{pmatrix}, \tag{2.2}$$

where

$$a(\lambda) : = \frac{\xi\lambda^2 - k}{\lambda(1+\lambda)}, b(\lambda) := -\frac{\xi\lambda + k}{\theta\lambda(1+\lambda)}, c(\lambda) := \theta + \frac{\theta\lambda}{1+\lambda}, d(\lambda) := -\frac{1}{1+\lambda}. \tag{2.3}$$

The characteristic equation of $J(\lambda)$ is $\mu^2 - \mu T(\lambda) + D(\lambda) = 0$, where

$$T(\lambda) = \frac{\xi\lambda^2 - \lambda - k}{\lambda(\lambda+1)}, D(\lambda) = \frac{\xi\lambda + 2k}{\lambda(\lambda+1)}. \tag{2.4}$$

Clearly, the quadratic equation $\xi\lambda^2 - \lambda - k = 0$ will always have a unique positive root, denoted by λ_0. Then, we have the following results:

Theorem 2.1. *1. Let λ_0 be the unique positive root of $\xi\lambda^2 - \lambda - k = 0$. Then, (λ, v_λ) is locally asymptotically stable with respect to the ODE system* (2.1) *if $\lambda \in (0, \lambda_0)$, while unstable if $\lambda \in (\lambda_0, \infty)$.*

2. System (2.1) *undergoes a Hopf bifurcation around (λ, v_λ) at $\lambda = \lambda_0$. That is., there exists a $s^* > 0$, such that for $s \in (0, s^*)$, there exists $(\lambda(s), Z(s), u(\cdot, s), v(\cdot, s))$ so that $(u(\cdot, s), v(\cdot, s))$ is a periodic solution of* (2.1) *with minimum period $Z(s) \to 2\pi/\sqrt{D(\overline{\lambda})}$ and $(\lambda(s), u(\cdot, s), v(\cdot, s)) \to (\overline{\lambda}, 0, 0)$ as $s \to 0$. Moreover, the bifurcating periodic solution is always locally asymptotically stable. In particular, the Hopf bifurcation is forward in the sense that the bifurcating periodic solution occurs when λ is slightly larger than λ_0.*

Proof. 1. For $\lambda \in (0, \lambda_0)$, we have $T(\lambda) < 0$, and for $\lambda \in (\lambda_0, \infty)$, we have $T(\lambda) > 0$. On the other hand, for all $\lambda > 0$, $D(\lambda) > 0$. This induces the local stability and instability of (λ, v_λ). 2. At $\lambda = \lambda_0$, $L(\lambda)$ has a pair of imaginary eigenvalues $\mu = \pm i\sqrt{D(\lambda_0)}$. Let $\mu(\lambda) := \alpha(\lambda) \pm i\omega(\lambda)$ be the eigenvalue of $\mu^2 - \mu T(\lambda) + D(\lambda) = 0$ for λ close to λ_0. Then, we have

$$\alpha(\lambda) = \frac{1}{2}T(\lambda), \omega(\lambda) = \frac{1}{2}\sqrt{4D(\lambda) - T^2(\lambda)}. \tag{2.5}$$

In particular, a direct calculation shows that

$$\alpha'(\lambda_0) = \frac{(\xi+1)\lambda_0^2 + 2k\lambda_0 + k}{2\lambda_0^2(\lambda_0+1)^2} > 0. \tag{2.6}$$

Then, from the Poincaré-Andronov-Hopf Bifurcation Theorem [9], system (2.1) has a Hopf bifurcation at $(\lambda_0, v_{\lambda_0})$.

Next, we consider the direction of the Hopf bifurcation and the stability of bifurcating periodic solutions, denoted by $(u_p(t), v_p(t))$. To this end, we need to calculate the first Lyapunov coefficient. We translate (λ, v_λ) to $(0, 0)$ by the translation $\hat{u} = u - \lambda$ and $\hat{v} = v - v_\lambda$. If we still denote $\hat{u}$ and $\hat{v}$ by u and v, we can reduce system (2.1) to

$$u' = k + \xi\lambda + \xi u - \frac{m(u+\lambda)(v+v_\lambda)}{1+u+\lambda}, v' = \theta u + \theta\lambda - \frac{v+v_\lambda}{1+u+\lambda}. \tag{2.7}$$

Rewrite (2.7) in the following form:

$$\begin{pmatrix} u' \\ v' \end{pmatrix} = J(\lambda) \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} F_1(u, v, \lambda) \\ G_1(u, v, \lambda) \end{pmatrix}, \tag{2.8}$$

where $J(\lambda)$ is defined in (2.2) and

$$\begin{aligned} F_1(u, v, \lambda) :=& \frac{\xi\lambda + k}{\lambda(1+\lambda)^2} u^2 - \frac{\xi\lambda + k}{\theta\lambda^2(1+\lambda)^2} uv - \frac{\xi\lambda + k}{\lambda(1+\lambda)^3} u^3 + \frac{\xi\lambda + k}{\theta\lambda^2(1+\lambda)^3} u^2 v + O(|u|^4, |u|^3|v|), \\ G_1(u, v, \lambda) :=& -\frac{\theta\lambda}{(1+\lambda)^2} u^2 + \frac{1}{(1+\lambda)^2} uv + \frac{\theta\lambda}{(1+\lambda)^3} u^3 - \frac{1}{(1+\lambda)^3} u^2 v + O(|u|^4, |u|^3|v|). \end{aligned}$$

Define a real 2-by-2 matrix

$$P(\lambda) := \begin{pmatrix} 1 & 0 \\ N(\lambda) & M(\lambda) \end{pmatrix},$$

where

$$N(\lambda) := \frac{\theta(\xi\lambda^2 + \lambda - k)}{2(\xi\lambda + k)}, M(\lambda) := \frac{\theta\lambda(1+\lambda)\sqrt{4D(\lambda) - T^2(\lambda)}}{2(\xi\lambda + k)}.$$

By using the linear transformation $(u, v)^T = P(\lambda)(x, y)^T$, we can reduce (2.8) into the following equations

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} \alpha(\lambda) & -\omega(\lambda) \\ \omega(\lambda) & \alpha(\lambda) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} F(x, y, \lambda) \\ G(x, y, \lambda) \end{pmatrix}, \tag{2.9}$$

where $\alpha(\lambda)$ and $\omega(\lambda)$ are defined in (2.5), and

$$\begin{aligned} F(x, y, \lambda) :=& F_1\Big(x, N(\lambda)x + M(\lambda)y, \lambda\Big), \\ G(x, y, \lambda) :=& -\frac{N(\lambda)}{M(\lambda)} F_1\Big(x, N(\lambda)x + M(\lambda)y, \lambda\Big) + \frac{1}{M(\lambda)} G_1(x, N(\lambda)x + M(\lambda)y, \lambda). \end{aligned}$$

Taylor expanding $F(x, y, \lambda)$ at $(x, y) = (0, 0)$, we have

$$F(x, y, \lambda) = c_{20}x^2 + c_{11}xy + c_{21}x^2y + c_{30}x^3 + O(|x|^4, |x|^3|y|), \tag{2.10}$$

where

$$c_{20} := \frac{k}{\lambda^2(1+\lambda)}, c_{11} := \frac{-\sqrt{D(\lambda)}}{\lambda(1+\lambda)}, c_{21} := \frac{\sqrt{D(\lambda)}}{\lambda(1+\lambda)^2}, c_{30} := \frac{-k}{\lambda^2(1+\lambda)^2}.$$

Similarly, Taylor expanding $G(x, y, \lambda)$ at $(x, y) = (0, 0)$, we have

$$G(x, y, \lambda) = d_{20}x^2 + d_{11}xy + d_{30}x^3 + d_{21}x^2y + O(|x|^4, |x|^3|y|), \tag{2.11}$$

where

$$d_{20} := \frac{-k}{\lambda^2(1+\lambda)\sqrt{D(\lambda)}}, d_{11} := \frac{1}{\lambda(1+\lambda)}, d_{21} := \frac{-1}{\lambda(1+\lambda)^2}, d_{30} := \frac{k}{\lambda^2(1+\lambda)^2\sqrt{D(\lambda)}}.$$

Following [9] (see, for example, page 90), we define

$$c_1(\lambda_0) := \frac{i}{2\omega(\lambda_0)}\left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2\right) + \frac{g_{21}}{2}, \tag{2.12}$$

where

$$\begin{aligned}
g_{11} &:= \frac{1}{4}\big(F_{xx} + F_{yy} + i\big(G_{xx} + G_{yy}\big)\big),\\
g_{02} &:= \frac{1}{4}\big(F_{xx} - F_{yy} - 2G_{xy} + i\big(G_{xx} - G_{yy} + 2F_{xy}\big)\big),\\
g_{20} &:= \frac{1}{4}\big(F_{xx} - F_{yy} + 2G_{xy} + i\big(G_{xx} - G_{yy} - 2F_{xy}\big)\big),\\
g_{21} &:= \frac{1}{8}\big(F_{xxx} + F_{xyy} + G_{xxy} + G_{yyy} + i\big(G_{xxx} + G_{xyy} - F_{xxy} - F_{yyy}\big)\big),
\end{aligned} \tag{2.13}$$

where all the quantities are to be evaluated at $(0, 0, \lambda_0)$. Then, from (2.10) and (2.11), we have

$$\mathrm{Re}(\mathrm{c}_1(\lambda_0)) = -\frac{(1+k)\lambda_0^3 + (4k^2+3k)\lambda_0^2 + (3k^2+k)\lambda_0 + k^2}{8\lambda_0^4(1+\lambda_0)^2(\xi\lambda_0 + 2k)} < 0. \tag{2.14}$$

Then, by [7, 9], the bifurcating periodic solutions are orbitally asymptotically stable. On the other hand, by (2.6), we have $\alpha'(\lambda_0) > 0$. Thus, the Hopf bifurcation is forward in the sense that the bifurcating periodic solution occurs when λ is slightly larger than λ_0. We thus complete the proof. □

Remark 2.2. For convenience, we denote $(u(\cdot, s), v(\cdot, s))$ and $Z(s)$ by $(u_p(t), v_p(t))$ and P respectively.

3. Diffusion-driven instability of the constant equilibrium solution in the spatial system

In this section, we shall concentrate on the diffusion-driven instability of the the constant equilibrium solution (λ, v_λ) with respect to the spatial system (1.5).

To begin with, we assume that $\xi\lambda^2 - k > 0$ (or equivalently $\lambda > \sqrt{k/\xi}$), so that the diffusive system (1.5) is an activator-inhibitor system in the sense that the signs of the elements of the Jacobian matrix $J(\lambda)$, defined in (2.2), take in the following form:

$$J(\lambda) = \begin{pmatrix} + & - \\ + & - \end{pmatrix}. \tag{3.1}$$

By Theorem 2.1, (λ, v_λ) is locally asymptotically stable with respect to the ODE system (2.1) if $\lambda \in (0, \lambda_0)$, while unstable if $\lambda \in (\lambda_0, \infty)$. In the following, we shall assume that $\sqrt{k/\xi} < \lambda < \lambda_0$ so that (λ, v_λ) is stable in the diffusion-free activator-inhibitor system (2.1). Let $0 = \mu_0 < \mu_1 \le \mu_2 \le \cdots$ be the sequence of eigenvalues for the elliptic operator $-\Delta$ subject to the Neumann boundary condition on $(0, \ell\pi)$, where each μ_i has multiplicity one. Let ϕ_i be the normalized eigenfunctions corresponding to μ_i. Then, the set ϕ_i, $i \ge 0$, forms a complete orthonormal basis in $L^2(0, \ell\pi)$. Suppose that $d_1\mu_1 < \dfrac{\xi\lambda^2 - k}{\lambda(1+\lambda)}$ holds. Then, we define $i_\lambda = i_\lambda(\lambda, d_1, (0, \ell\pi))$ to be the largest positive integer such that for $i \le i_\lambda$, we have $d_1\mu_i < \dfrac{\xi\lambda^2 - k}{\lambda(1+\lambda)}$. Clearly, we have $1 \le i_\lambda < +\infty$. In this case, we define

$$\overline{d_2} = \overline{d_2}(\lambda, (0, \ell\pi)) = \min_{1 \le i \le i_\lambda}\left\{d_2^{(i)}\right\}, \text{ where, } d_2^{(i)} := \frac{d_1\lambda\mu_i + \xi\lambda + 2k}{\mu_i\left(\xi\lambda^2 - k - d_1\lambda(1+\lambda)\mu_i\right)}. \tag{3.2}$$

Theorem 3.1. *Let* $\sqrt{k/\xi} < \lambda < \lambda_0$ *and* $\overline{d_2}$ *be defined in* (3.2). *Then, the following conclusions hold true:*

1. *Suppose that* $d_1\mu_1 \geq \dfrac{\xi\lambda^2 - k}{\lambda(1+\lambda)}$ *holds. Then,* (λ, v_λ) *is locally asymptotically stable with respect to the reaction-diffusion system* (1.5).
2. *Suppose that* $d_1\mu_1 < \dfrac{\xi\lambda^2 - k}{\lambda(1+\lambda)}$ *holds. Then,* (λ, v_λ) *is locally asymptotically stable with respect to the reaction-diffusion system* (1.5) *if* $0 < d_2 < \overline{d_2}$, *while becomes Turing unstable if* $d_2 > \overline{d_2}$.

Proof. The linearized operator evaluated at (λ, v_λ) for system (1.5) is given by

$$L_{d_2}(\lambda) = \begin{pmatrix} d_1\Delta + a(\lambda) & b(\lambda) \\ c(\lambda) & d_2\Delta + d(\lambda) \end{pmatrix}, \tag{3.3}$$

where $a(\lambda)$, $b(\lambda)$, $c(\lambda)$ and $d(\lambda)$ are defined in (2.2). It follows from [11–13] that the eigenvalues of $L_{d_2}(\lambda)$ are determined by the eigenvalues of the operator $L_{d_2,i}(\lambda)$ which is given by

$$L_{d_2,i}(\lambda) = \begin{pmatrix} -d_1\mu_i + a(\lambda) & b(\lambda) \\ c(\lambda) & -d_2\mu_i + d(\lambda) \end{pmatrix}, \tag{3.4}$$

where $i = 0, 1, 2, \cdots$. The characteristic equation of $L_{d_2,i}(\lambda)$ is given by

$$\rho^2 + T_i(\lambda)\rho + D_i(\lambda) = 0,$$

where

$$\begin{aligned} T_i(\lambda) =& -(d_1 + d_2)\mu_i + \frac{\xi\lambda^2 - \lambda - k}{\lambda(\lambda+1)}, \\ D_i(\lambda) =& d_1 d_2 \mu_i^2 - (d_1 d(\lambda) + d_2 a(\lambda))\mu_i + D(\lambda) \\ =& d_1 d_2 \mu_i^2 - \left(\frac{d_2(\xi\lambda^2 - k)}{\lambda(1+\lambda)} - \frac{d_1}{1+\lambda}\right)\mu_i + \frac{\xi\lambda + 2k}{\lambda(\lambda+1)}. \end{aligned}$$

Since we assume that $\sqrt{k/\xi} < \lambda < \lambda_0$, we have $\dfrac{\xi\lambda^2 - \lambda - k}{\lambda(\lambda+1)} < 0$. Thus, for any $i \geq 0$, we have $T_i(\lambda) < 0$. Rewrite $D_i(\lambda)$ as

$$\begin{aligned} D_i(\lambda) =& d_1 d_2 \mu_i^2 - \left(\frac{d_2(\xi\lambda^2 - k)}{\lambda(1+\lambda)} - \frac{d_1}{1+\lambda}\right)\mu_i + \frac{\xi\lambda + 2k}{\lambda(\lambda+1)} \\ =& d_2\mu_i\left(d_1\mu_i - \frac{\xi\lambda^2 - k}{\lambda(1+\lambda)}\right) + \frac{d_1\mu_i}{1+\lambda} + \frac{\xi\lambda + 2k}{\lambda(\lambda+1)}. \end{aligned}$$

Suppose that $d_1\mu_1 \geq \dfrac{\xi\lambda^2 - k}{\lambda(1+\lambda)}$ holds. Then, for any $i \geq 1$, we have $D_i(\lambda) > 0$. Thus, all the eigenvalues of the linearized operator have negative real parts. This implies that in this case, (λ, v_λ) is locally asymptotically stable with respect to the reaction-diffusion system (1.5).

Suppose that $d_1\mu_1 < \dfrac{\xi\lambda^2 - k}{\lambda(1+\lambda)}$ holds. Then, for $0 < d_2 < \overline{d_2}$, we have for any $i \geq 1$, we have $D_i(\lambda) > 0$. Again, all the eigenvalues of the linearized operator have negative real parts. This implies that in this case, (λ, v_λ) is locally asymptotically stable with respect to the reaction-diffusion system (1.5). On the other hand, if $d_2 > \overline{d_2}$, then we may assume that the minimum in (3.2) is attained by some $j \in [1, i_\lambda]$. Thus, for $d_2 > d_2^{(j)}$, we have $D_j(\lambda) < 0$. Thus, there exists at least an eigenvalue having positive real parts. Hence, in this case, (λ, v_λ) is unstable with respect to the reaction-diffusion system (1.5); Moreover, by $\sqrt{k/\xi} < \lambda < \lambda_0$, (λ, v_λ) is locally asymptotically stable with respect to the ODE system; Therefore, in this case, (λ, v_λ) is Turing unstable. We complete the proof. □

Remark 3.2. In Theorem 3.1, we fix $d_1 > 0$, and choose d_2 as the bifurcation parameter and then define the "critical"value $\overline{d_2}$, such that if $0 < d_2 < \overline{d_2}$, then (λ, v_λ) is locally asymptotically stable with respect to the reaction-diffusion system (1.5); while if $d_2 > \overline{d_2}$, then (λ, v_λ) is Turing unstable with respect to the reaction-diffusion system (1.5). In fact, by rescaling the system parameters, we can also choose the ratio d_1/d_2 or d_2/d_1 as the bifurcation parameter. We would like to mention that in a recent paper by Jiang, Cao and Wang [10], the authors obtained sufficient and necessary conditions on diffusion-driven instability of the positive constant equilibrium solution by choosing the diffusion ratio as the bifurcation parameter. We refer interested readers to [10] for great details.

4. Diffusion-driven instability of periodic solutions in the spatial systems

To begin with, we shall first recall some preliminaries obtained by Yi in [7] on diffusion-driven instability of the periodic solutions for general reaction-diffusion system on bounded spatial domain subject to homogeneous Neumann boundary conditions.

Consider the following general reaction-diffusion equations with cross-diffusions and no-flux boundary conditions

$$\begin{aligned} \frac{\partial U}{\partial t} &= E\Delta U + F(U), t > 0, x \in \Omega_1, \\ \partial_\nu U &= 0, \qquad t > 0, x \in \partial\Omega_1. \end{aligned} \tag{4.1}$$

Here $x = (x_1, \cdots, x_n) \in \Omega_1 := \{\ell y : y \in \Omega_0\}$ which is star-shaped with respect to the origin, where $0 < \ell < \infty$ and Ω_0 is a fixed open bounded domain in $\mathbf{R}^n$ ($n \geq 1$) with sufficiently smooth boundary $\partial\Omega_0$, and

$$U(x,t) = \begin{pmatrix} u_1(x,t) \\ u_2(x,t) \\ \vdots \\ u_m(x,t) \end{pmatrix}, F(U) = \begin{pmatrix} f_1(u_1, \cdots, u_m) \\ f_2(u_1, \cdots, u_m) \\ \vdots \\ f_m(u_1, \cdots, u_m) \end{pmatrix}, E := \begin{pmatrix} d_{11} & d_{12} & \cdots & d_{1m} \\ d_{21} & d_{22} & \cdots & d_{2m} \\ \vdots & \vdots & \cdots & \vdots \\ d_{m1} & d_{m2} & \cdots & d_{mm} \end{pmatrix}, \tag{4.2}$$

where $d_{ii} > 0$ are the passive diffusion rates of the u_i for $i = 1, 2, \cdots, m$ with $m \geq 2$; $d_{ij} \in \mathbf{R}$, with $i \neq j$, are the cross-diffusion rates between u_i and u_j; f_i is assumed to be sufficiently smooth for $i = 1, \cdots, m$. In particular, all the eigenvalues of E have positive real parts (to guarantee the so-called "normally elliptic"condition).

Suppose that the corresponding ODE system of system (4.1)

$$\frac{dU}{dt} = F(U) \tag{4.3}$$

has a stable periodic solution $U = U_p(t)$ with the minimum period P, i.e.,

$$\frac{dU_p(t)}{dt} = F(U_p(t)), U_p(t+P) = U_p(t). \tag{4.4}$$

Let I_m be the $m \times m$ identity matrix. Then, the following perturbed ODEs

$$(I_m + \epsilon E)\frac{dU}{dt} = F(U), \tag{4.5}$$

has also a stable periodic solution, denoted by $U_p(\epsilon, t)$ with minimum period $P(\epsilon)$, which is continuously differentiable in ϵ for sufficiently small $|\epsilon|$. We state the following results:

Lemma 4.1. *([3, 7]) Suppose that the ODE system* (4.3) *has a stable periodic solution, denoted by $U_p(t)$ with the minimum period P. Then, for sufficiently small $|\epsilon|$, the perturbed system* (4.6) *will also have a stable periodic solution, denoted by $U_p(t, \epsilon)$ with the minimum period $P(\epsilon)$, a C^1 function of the perturbation parameter ϵ, such that as $\epsilon \to 0$, $U_p(t, \epsilon) \to U_p(t)$ and $P(\epsilon) \to P$.*

In [7], Yi obtained the following results:

Theorem 4.2. *Assume that $\Omega_1 = \ell\Omega_0$ is star-shaped with respect to the origin. Let $U_p(t)$ be a stable periodic solution of* (4.3)*, and let $P(\epsilon)$ be the period of periodic solution $U_p(t, \epsilon)$ of* (4.5)*. Then $U_p(t)$ is unstable with respect to* (4.1) *if $P'(0) < 0$ and ℓ is sufficiently large.*

Now, we are going to use Theorem 4.2 to consider diffusion-driven instability of the Hopf bifurcating spatially homogeneous periodic solution $(u_p(t), v_p(t))^T$ of system (1.5). Remember in the context of Theorem 4.2, our problem is the special case when $m = 2$, $\Omega_1 = (0, \ell\pi)$, and there is no cross-diffusion.

According to Theorem 4.2, we need to consider the following perturbed planar system

$$\left(I_2 + \epsilon\begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}\right)\begin{pmatrix} u' \\ v' \end{pmatrix} = \begin{pmatrix} k + \xi u - \dfrac{muv}{1+u} \\ \theta u - \dfrac{v}{1+u} \end{pmatrix}, \tag{4.6}$$

where $|\epsilon|$ is sufficiently small. By Theorem 3.3 of [7], if the aforementioned stable periodic solution of the ODE system (2.1) is the Hopf bifurcating periodic solution, then $P'(0) < 0$ can be clearly expressed in the language of the diffusion rates d_1 and d_2:

Lemma 4.3. *([7]) Suppose that λ is fixed to be sufficiently close to λ_0 so that $(u_p(t), v_p(t))$ is a stable periodic solution of system* (2.1) *bifurcating from $(\lambda, v_\lambda)^T$ at $\lambda = \lambda_0$, where λ_0 is the Hopf bifurcation value stated in Theorem 2.1. Then, we have*

$$\begin{aligned} P'(0) = &\sqrt{a(\lambda_0)d(\lambda_0) - b(\lambda_0)c(\lambda_0)}(d_1 + d_2) \\ &+ \frac{\mathrm{Im}(c_1(\lambda_0))}{\mathrm{Re}(c_1(\lambda_0))}\Big(d_1 d(\lambda_0) + d_2 a(\lambda_0)\Big) + o(|\lambda - \lambda_0|), \end{aligned} \tag{4.7}$$

where $a(\lambda)$, $b(\lambda)$, $c(\lambda)$ and $d(\lambda)$ are defined in (2.2)*,* $\mathrm{Re}(c_1(\lambda_0))$ *and* $\mathrm{Im}(c_1(\lambda_0))$ *are defined in* (2.14) *and* (4.13) *respectively.*

Then, we have the following results on diffusion-driven instability of the periodic solution $(u_p(t), v_p(t))$ with respect to the reaction-diffusion system (1.5):

Theorem 4.4. *Suppose that* $(u_p(t), v_p(t))$ *is the stable periodic solution of system* (2.1) *bifurcating from* $(\lambda_0, v_{\lambda_0})$ *as stated in Theorem 2.1. Then,* $(u_p(t), v_p(t))$ *undergoes diffusion-driven instability in system* (1.5) *if* ℓ *is sufficiently large and* $d_1\zeta + d_2\delta < 0$*, where*

$$\begin{aligned}\zeta :=&(2 + 16k + 14k^2)\lambda_0^5 + (-1 + 21k + 46k^2 + 24k^3)\lambda_0^4 + (-1 + 10k + 54k^2 + 46k^3)\lambda_0^3\\&+ (k + 25k^2 + 33k^3)\lambda_0^2 + (5k^2 + 14k^3)\lambda_0 + 3k^3,\\ \delta :=&(4 + 2k - 2k^2)\lambda_0^5 + (7 + 21k + 32k^2 + 24k^3)\lambda_0^4 + (1 + 20k + 60k^2 + 62k^3)\lambda_0^3\\&+ (5k + 35k^2 + 57k^3)\lambda_0^2 + (7k^2 + 22k^3)\lambda_0 + 3k^3.\end{aligned} \tag{4.8}$$

Proof. By (4.7), for λ sufficiently close to λ_0, it follows that the sign of $P'(0)$ is mainly determined by the first two terms of (4.7). We now calculate these first two terms of (4.7). Firstly, we have

$$\sqrt{a(\lambda_0)d(\lambda_0) - b(\lambda_0)c(\lambda_0)} = \sqrt{\frac{\xi\lambda_0 + 2k}{\lambda_0^2 + \lambda_0}}. \tag{4.9}$$

Define

$$\begin{aligned}\mathcal{M}_1(\lambda_0) :=&\eta_0\lambda_0^4 + \eta_1\lambda_0^3 + \eta_2\lambda_0^2 + \eta_3\lambda_0 + \eta_4,\\ \mathcal{N}_1(\lambda_0) :=&3(1 + \lambda_0)\Big((1 + k)\lambda_0^3 + (4k^2 + 3k)\lambda_0^2 + (3k^2 + k)\lambda_0 + k^2\Big),\end{aligned} \tag{4.10}$$

where

$$\begin{aligned}&\eta_0 :=8k^2 + 7k - 1, \eta_1 = 7k^2 - 4, \eta_2 = -8k^3 - 3k^2 - 5k - 1,\\ &\eta_3 := - 12k^3 - 5k^2 - 2k, \eta_4 = -4k^3 - k^2.\end{aligned} \tag{4.11}$$

By (2.14), we have

$$\mathrm{Re}(\mathrm{c}_1(\lambda_0)) = -\frac{(1 + k)\lambda_0^3 + (4k^2 + 3k)\lambda_0^2 + (3k^2 + k)\lambda_0 + k^2}{8\lambda_0^4(1 + \lambda_0)^2(\xi\lambda_0 + 2k)}. \tag{4.12}$$

On the other hand, from (2.10) and (2.11), we have

$$\begin{aligned}\mathrm{Im}(\mathrm{c}_1(\lambda_0)) =&\frac{1}{16}\big(G_{xxx} + G_{xyy} - F_{xxy} - F_{yyy}\big) - \frac{1}{16\omega(\lambda_0)}\big((F_{xx} + F_{yy})^2 + (G_{xx} + G_{yy})^2\big)\\&+ \frac{1}{32\omega(\lambda_0))}(F_{xx} + F_{yy})(F_{xx} - F_{yy} + 2G_{xy})\\&+ \frac{1}{32\omega(\lambda_0))}(G_{xx} + G_{yy})(G_{xx} - G_{yy} - 2F_{xy})\\&- \frac{1}{96\omega(\lambda_0)}\big((F_{xx} - F_{yy} - 2G_{xy})^2 + (G_{xx} - G_{yy} + 2F_{xy})^2\big)\\=&\frac{\eta_0\lambda_0^4 + \eta_1\lambda_0^3 + \eta_2\lambda_0^2 + \eta_3\lambda_0 + \eta_4}{24\lambda_0^5(1 + \lambda_0)^3(2k + \xi\lambda_0)\sqrt{\dfrac{\xi\lambda_0 + 2k}{\lambda_0(1 + \lambda_0)}}},\end{aligned} \tag{4.13}$$

where η_0, η_1, η_2, η_3 and η_4 are defined in (4.11) respectively.

Then, we have

$$\frac{\mathrm{Im}(c_1(\lambda_0))}{\mathrm{Re}(c_1(\lambda_0))} = -\sqrt{\frac{\lambda_0(1+\lambda_0)}{\xi\lambda_0 + 2k}} \cdot \frac{\mathcal{M}_1(\lambda_0)}{\lambda_0\mathcal{N}_1(\lambda_0)}, \tag{4.14}$$

where $\mathcal{M}_1(\lambda_0)$ and $\mathcal{N}_1(\lambda_0)$ are defined in (4.10) respectively.

After substituting (4.9), (4.12), (4.13) and (4.14) into (4.7), we find that, for λ sufficiently close to λ_0, $P'(0) < 0$ is equivalent to

$$\frac{d_1\zeta + d_2\delta}{2\xi\lambda_0 - 1} < 0, \tag{4.15}$$

where ζ and δ are defined by (4.8). Now, we argue that $2\xi\lambda_0 - 1 > 0$. In fact, we note that λ_0 satisfies $\xi\lambda_0^2 - \lambda_0 - k = 0$. By $\xi\left(\frac{1}{2\xi}\right)^2 - \left(\frac{1}{2\xi}\right) - k < 0$, we have $\frac{1}{2\xi} < \lambda_0$. Thus, we have $2\xi\lambda_0 - 1 > 0$. So far, we have proved that $p'(0) < 0$ is equivalent to $d_1\zeta + d_2\delta < 0$. Then, by Theorem 4.2 and Lemma 4.3, we complete the proof. □

5. Numerical simulations

In this section, we shall include some numerical simulations to strengthen our analytical analysis.

5.1. Diffusion-driven instability for the positive constant equilibrium solution

We simulate existence/nonexistence of diffusion-driven instability for the positive constant equilibrium solution. We choose the system parameters in the following way:

$$k = 5,\ \theta = 1,\ \xi = \frac{3795}{538756},\ m = \frac{40627825}{145129013768},\ \Omega = (0, 500). \tag{5.1}$$

Under (5.1), we have $\lambda_0 = 147$. Then, by Theorem 2.1, the unique positive constant equilibrium solution (λ, v_λ) is locally asymptotically stable with respect to the ODEs system (1.4) for any $\lambda \in (0, \lambda_0)$, while unstable for $\lambda \in (\lambda_0, +\infty)$. We now choose have $\lambda = \dfrac{734}{5}$. Then, (λ, v_λ) is locally asymptotically stable with respect to the ODEs system (1.4).

Case 1 (Diffusion-driven instability of the positive equilibrium solution fails): We choose $d_1 = d_2 = 1$, the initial values are chosen by: $u_0(x) = \lambda_0 + 0.01\sin(0.02x)$, $v_0(x) = v_{\lambda_0} + 0.01\cos(0.02x)$. In this case, no diffusion-driven instability of (λ, v_λ) could be found. That is, the equilbrium solution (λ, v_λ) is still stable with respect to the reaction-diffusion system (1.5). (See Figure 1)

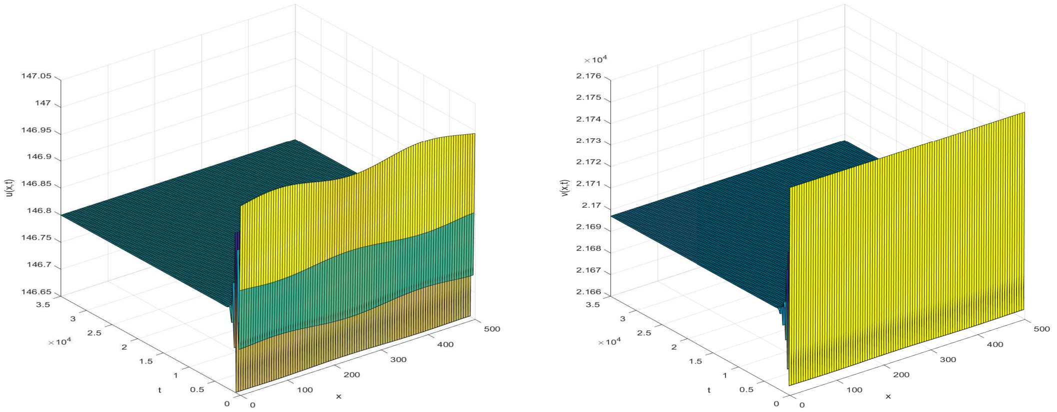

Figure 1. The case when $d_1 = d_2 = 1$, $x \in \ell(0, 1)$, where $\ell = 500$, and $t \in (0, 35000)$. Left: u-component; Right: v-component. The equilibrium solution (λ, v_λ) is still stable with respect the reaction-diffusion equations. In this case, diffusion-driven instability of the positive equilibrium solution does not occur.

Case 2 (Diffusion-driven instability of the positive equilibrium solution occurs): We choose $d_1 = 1, d_2 = 54$, the initial values are chosen by: $u_0(x) = \lambda_0 + 0.01\sin(0.02x)$, $v_0(x) = v_{\lambda_0} + 0.01\cos(0.02x)$. Clearly, d_1 and d_2 are satisfy conditions in Theorem 3.1. In this case, diffusion-driven instability of (λ, v_λ) occurs and new irregular spatiotemporal patterns are observed found. (See Figure 2)

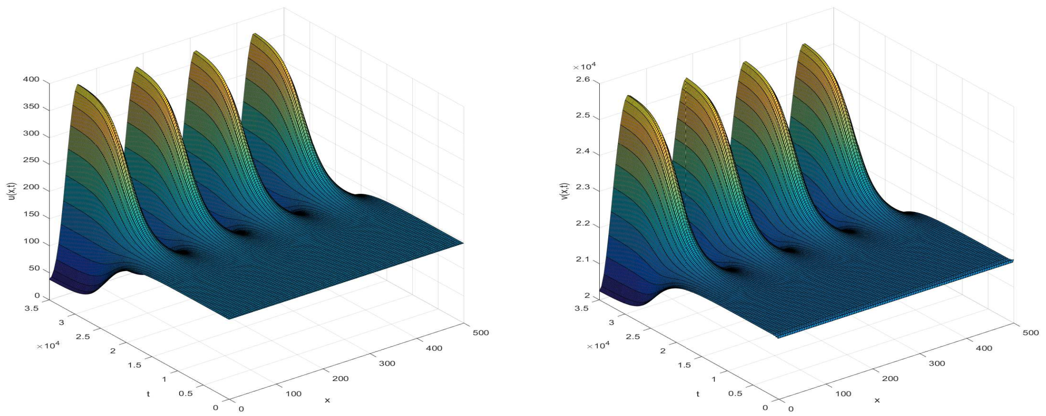

Figure 2. The case when $d_1 = 1, d_2 = 54$, $x \in \ell(0, 1)$, where $\ell = 500$, and $t \in (0, 35000)$. Left: u-component; Right: v-component. In this case, diffusion-driven instability of the positive equilibrium solution occurs.

5.2. *Diffusion-driven instability of the Hopf bifurcating periodic solution*

We simulate existence/nonexistence of diffusion-driven instability for the Hopf bifurcating periodic solution. We choose the system parameters in the following way:

$$k = \frac{22}{5}, \theta = 1, \xi = \frac{12132}{1734605}, m = \frac{150699184}{601770901205}, \Omega = (0, 500). \tag{5.2}$$

Under (5.2), we have $\lambda_0 = 147$. Choose $\lambda = 147.25$. Then, by Theorem 2.1, the ODEs system (1.4) has a stable periodic solution (denoted by $(u_p(t), v_p(t))$).

Case 1 (Diffusion-driven instability of the periodic solutions fails): We choose $d_1 = d_2 = 1$, the initial values are chosen by: $u_0(x) = \lambda_0 + 0.01\sin(0.02x)$, $v_0(x) = v_{\lambda_0} + 0.01\cos(0.02x)$. In this case, no diffusion-driven instability of $(u_p(t), v_p(t))$ could be found. That is, the periodic solution $(u_p(t), v_p(t))$ is still stable with respect to the reaction-diffusion system (1.5). (See Figure 3)

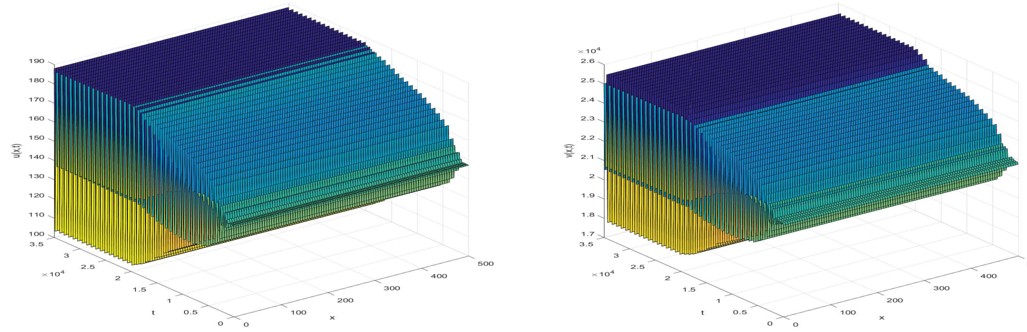

Figure 3. The case when $d_1 = d_2 = 1$, $x \in \ell(0, 1)$, where $\ell = 500$, and $t \in (0, 35000)$. Left: u-component; Right: v-component. The periodic solution $(u_p(t), v_p(t))^T$ is still stable with respect the reaction-diffusion equations. In this case, diffusion-driven instability of the periodic solutions does not occur.

Case 2 (Diffusion-driven instability of the periodic solution occurs): We choose $d_1 = 1, d_2 = 55$, the initial values are chosen by: $u_0(x) = \lambda_0 + 0.01\sin(0.02x)$, $v_0(x) = v_{\lambda_0} + 0.01\cos(0.02x)$. Clearly, d_1 and d_2 are satisfy (3.12). In this case, diffusion-driven instability of $(u_p(t), v_p(t))$ could be observed and new irregular spatiotemporal patterns are found. (See Figure 4)

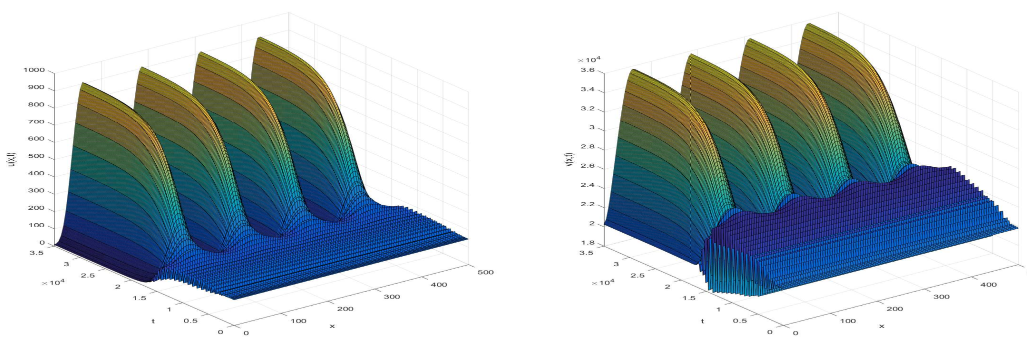

Figure 4. The case when $d_1 = 1, d_2 = 55$, $x \in \ell(0, 1)$, where $\ell = 500$, and $t \in (0, 35000)$. Left: u-component; Right: v-component. In this case, diffusion-driven instability of the periodic solutions occurs.

6. Conclusions

In this paper, we consider a homogeneous diffusive Sporns-Seelig model for the generic regulatory mechanism of induction subject to homogeneous Neumann boundary conditions. Of our particular interests, we are concerned with the diffusion-driven instability of both the positive constant equilibrium solution and the Hopf bifurcating spatially homogeneous periodic solutions. By using the linearized principle and the abstract results obtained in [7], we are able to derive precise conditions on the diffusion rates d_1 and d_2, such that under these conditions, both the stable positive constant equilibrium solution and the stable periodic solution (with respect to the kinetic ODE system) can undergo diffusion-driven instability in the reaction-diffusion system. Our numerical simulation shows that once the solutions undergo diffusion-driven instability, then new irregular spatial patterns occur. This kind of spatial patterns correspond to the existence of positive non-constant steady state solutions for the reaction-diffusion system. This suggests that, for this particular kind of diffusive Sporns-Seelig model, diffusion-driven instability of the two kinds of the solutions can be one of the mechanisms to generate new stable non-constant steady state solutions. To the best of our knowledge, our results on the aforementioned aspects are new for this particular homogeneous diffusive Sporns-Seelig model.

As the chemical reaction might have time delays in the process of reaction, one might think to include time delay into the diffusive Sporns-Seelig model. This reduce the original system to the partial functional differential equations. It is well-known that varying time delay can induce temporal oscillations. Now, a question arises naturally: if the kinetic Sporns-Seelig model with delay (functional differential equations) has a stable periodic solution, then in what relationship between d_1 and d_2, the stable periodic solution could become Turing unstable in the diffusive Sporns-Seelig model with delay (partial functional differential equations)? This is our future attempt for this particular model.

Finally, we would like to mention that there are several related works in this field to our present work, and we refer to interested readers to references [14–18].

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Conflict of interest

The authors declare there is no conflict of interest.

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