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Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator–prey system [☆]

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ABSTRACT

A diffusive predator–prey system with Holling type-II predator functional response subject to Neumann boundary conditions is considered. Hopf and steady state bifurcation analysis are carried out in details. In particular we show the existence of multiple spatially non-homogeneous periodic orbits while the system parameters are all spatially homogeneous. Our results and global bifurcation theory also suggest the existence of loops of spatially non-homogeneous periodic orbits and steady state solutions. These results provide theoretical evidences to the complex spatiotemporal dynamics found by numerical simulation.

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1. Introduction

Consumer–resource (predator–prey) type interactions can generate rich dynamics [34,40,41], and the spatial structure can further affect the population dynamics of both species [4,11,17,25,29,35,43]. In particular, it is known that spatial heterogeneity may induce complex spatiotemporal patterns [11–13]. On the other hand, for the spatially homogeneous reaction–diffusion predator–prey model with classical Lotka–Volterra interaction and no flux boundary conditions, it is known that the unique coexistence steady state solution is globally asymptotically stable, and thus no non-trivial spatial patterns are possible in that case [8,11]. In this article, we consider a homogeneous reaction–diffusion

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predator–prey model with no flux boundary conditions and Holling type-II functional response [19], and we will rigorously show that the system possesses rich spatiotemporal dynamical structure.

The reaction–diffusion system which we consider is

$$\begin{cases} U_t - d_1 \Delta U = AU \left(1 - \frac{U}{N} \right) - \frac{BUV}{C + U}, & x \in \Omega, t > 0, \\ V_t - d_2 \Delta V = -DV + \frac{EUV}{C + U}, & x \in \Omega, t > 0, \\ \partial_\nu U = \partial_\nu V = 0, & x \in \partial\Omega, t > 0, \\ U(x, 0) = U_0(x) \geq 0, \quad V(x, 0) = V_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{1.1}$$

Here Ω is a bounded domain in \mathbf{R}^N , $N \geq 1$, with a smooth boundary $\partial\Omega$; ∂_ν is the outer flux, and no flux boundary condition is imposed so the system is a closed one; $U = U(x, t)$ and $V = V(x, t)$ stand for the densities of the prey and predator at time $t > 0$ and a spatial position $x \in \Omega$ respectively; $d_1, d_2 > 0$ are the diffusion coefficients of the species; the parameters A, B, C, D, E, N are positive real numbers; the prey population follows a logistic growth, A is the intrinsic growth rate, and N is the carrying capacity; D is the death rate of the predator; B and E represent the strength of the relative effect of the interaction on the two species; the function $U/(C + U)$ denotes the functional response of the predator to the prey density, which refers to the change in the density of prey attached per unit time per predator as the prey density changes. The positive parameter C measures the “saturation” effect: the consumption of prey by a unit number of predators cannot continue to grow linearly with the number of prey available but must saturate at value $1/C$ (see [14,19] for more details).

The interaction of predator and prey in (1.1) is well known as the Rosenzweig–MacArthur model, which is widely used in real-life ecological applications [34,41]. The reaction–diffusion model (1.1) has also been used to describe the spatiotemporal dynamics of an aquatic community of phytoplankton and zooplankton system [35].

With a nondimensionalized change of variables:

$$s = At, \quad u = \frac{U}{C}, \quad v = \frac{B}{EC}V,$$

and let $d'_1 = A^{-1}d_1$ and $d'_2 = A^{-1}d_2$, we obtain

$$\begin{cases} u_s - d'_1 \Delta u = u \left(1 - \frac{u}{NC^{-1}} \right) - \frac{E}{A} \frac{uv}{u + 1}, & x \in \Omega, s > 0, \\ v_s - d'_2 \Delta v = -\frac{D}{A}v + \frac{E}{A} \frac{uv}{u + 1}, & x \in \Omega, s > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, s > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Let

$$k = \frac{N}{C}, \quad m = \frac{E}{A}, \quad \theta = \frac{D}{A},$$

and still denote s, d'_1, d'_2 by t, d_1, d_2 respectively. Then we obtain the simplified dimensionless system of equations:

$$\begin{cases} u_t - d_1 \Delta u = u \left(1 - \frac{u}{k} \right) - \frac{muv}{u + 1}, & x \in \Omega, t > 0, \\ v_t - d_2 \Delta v = -\theta v + \frac{muv}{u + 1}, & x \in \Omega, t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases} \tag{1.2}$$

In the remaining part of this article, we focus on the system (1.2). For the new parameters, k is a rescaled carrying capacity; θ is the death rate of the predator, and m is the strength of the interaction.

The ODE system of (1.2) has been extensively studied in the existing literature, see for example [3,20,21], and a summary of the ODE dynamics will be given in Section 2.2. The highlight of the study of the ODE model corresponding to (1.2)

$$\frac{du}{dt} = u \left(1 - \frac{u}{k} \right) - \frac{mu v}{u + 1}, \quad \frac{dv}{dt} = -\theta v + \frac{mu v}{u + 1} \quad (1.3)$$

is the existence and uniqueness of a limit cycle. In [40], Rosenzweig argued that enrichment of the environment (larger carrying capacity k in (1.3)) leads to destabilizing of the coexistence equilibrium, which is the so-called paradox of enrichment. May [34] pointed out the importance of the limit cycle in the population dynamics, but the uniqueness of the limit cycle turns out to be a difficult mathematical question (see Albrecht et al. [1]). Hsu, Hubbell and Waltman [20,23] considered the global stability of coexistence equilibrium and Cheng [3] first proved the uniqueness of limit cycle of (1.3) (see also [28,50]). More recently, Hsu and Shi [24] discussed the relaxation oscillator profile of the unique limit cycle of (1.3).

A complete and rigorous analysis of the global dynamics of the diffusive predator–prey system (1.2) has not been achieved. Ko and Ryu [27] obtained some results on the global stability of the constant steady state solutions and the existence of at least one non-constant equilibrium solution for certain parameter ranges. Du and Lou [10] studied a slightly different model and obtained various asymptotic behavior of the steady state solutions when some parameters are large or small. On the other hand, Medvinsky et al. [35] used (1.2) as a simplest possible mathematical model to investigate the pattern formation of a phytoplankton–zooplankton system, and their numerical studies show a rich spectrum of spatiotemporal patterns. We also mention that for the equations in (1.2) with Dirichlet boundary conditions, many mathematical results have been obtained in the last 30 years, and we refer to Du and Shi [11] for a comprehensive review on that issue.

We point out that most studies of diffusive predator–prey systems such as (1.2) and the like concentrate on the steady state solutions, while periodic solutions play an important role even in ODE dynamics of (1.3). Overall there are few results regarding the periodic solutions of spatially homogeneous reaction–diffusion systems. Notice that under Neumann boundary conditions, the periodic orbit of the ODE system (1.3) becomes a spatially homogeneous periodic orbit of the reaction–diffusion system (1.2). Hopf bifurcations of such spatially homogeneous periodic orbits in reaction–diffusion systems have been considered for Brusselator system (Hassard et al. [16]), Gierer–Meinhardt system (Ruan [42]) and CIMA reaction (Yi et al. [48,49]). But the bifurcating periodic orbits in these work are spatially homogeneous thus the same ones as in ODE systems. In Du and Lou [9], Hopf bifurcation points are obtained in a predator–prey system with Dirichlet boundary condition for some carefully chosen parameters.

Our main contribution in this article is a detailed bifurcation analysis from the constant coexistence equilibrium solution of (1.2) when the spatial domain Ω is one-dimensional. Following the geometric approach in [20,23,24], we use the coordinate λ of the vertical nullcline of (1.3) (i.e. λ solves u in $-\theta + mu/(1 + u) = 0$) as the main bifurcation parameter. Under certain conditions on other parameters, we show that there exist exactly $2n$ Hopf bifurcation points where *spatially non-homogeneous periodic orbits* bifurcate from the curve of the constant coexistence steady state solutions (see Theorems 2.4 and 3.8 for details). These periodic orbits correspond to the spatial eigen-mode $\cos(kx/\ell)$ ($1 \leq k \leq n$) where $\ell\pi$ is the length of the spatial domain. The integer n is determined by ℓ , and n is larger for larger ℓ . For those parameter values, there are no steady state bifurcations from the curve of the constant coexistence steady state solutions. Hence the complexity of the spatiotemporal dynamics here is indicated by these spatially non-homogeneous periodic orbits, and available methods cannot yield existence of non-constant steady state patterns in these parameter ranges. We also remark that such Hopf bifurcation points always exist in pairs, and for each fixed eigen-mode, there is exactly one pair of Hopf bifurcation points associated with it. This suggests possible loop branches of periodic orbits with a fixed spatial nodal pattern, but we do not have rigorous proof of that fact due to the difficulty of the analysis of global branches of periodic orbits.

In some different parameter ranges, both Hopf and steady state bifurcations occur along the curve of the constant coexistence steady state solutions, and the intertwining of the two type of bifurcations is delicate (see Theorem 3.10). Indeed either type of bifurcations occur for certain eigen-modes, and the complexity of the bifurcation diagrams implies the complexity of the real dynamics of (1.2). This provides some theoretical evidences for the complex dynamical behavior found through numerical simulation in [35].

The emergence of these complicated spatiotemporal patterns is clearly due to the effect of the diffusion. But we point out that the bifurcations in this article are not diffusion-induced Turing bifurcations [45] where the diffusion coefficients are used as bifurcation parameters and they are often large or small. Our bifurcation analysis is performed with fixed arbitrary diffusion coefficients d_1 and d_2 in (1.2), and for any diffusion coefficients, certain complicated spatiotemporal patterns exist. But the variety of the patterns does depend on the diffusion coefficients as shown in Theorems 2.4, 3.8 and 3.10. Also in (1.2), there are no Turing type bifurcations where stable non-constant steady state solutions bifurcate from the constant ones. In many pattern formation problems, certain parameters need to be small or large so that singular perturbation theory can be applied, and our results do not assume such properties of parameters.

The periodic patterns found here are “self-organized” in the sense that the system parameters in (1.2) are all spatially and temporally constant. Periodic orbits driven by periodic system parameters or delay mechanism have been extensively studied in recent years, but rigorous proof of existence of self-organized spatiotemporal patterns is rare in literature of nonlinear sciences.

The remaining parts of the paper are structured in the following way. In Section 2, stability and Hopf bifurcation analysis are considered for system (1.2). The Hopf bifurcation formulas for the general reaction–diffusion systems consisting of two equations are derived in Section 2.1 and the results obtained there are applied in Hopf bifurcation analysis of (1.2) in Section 2.2. In Section 3, steady state bifurcations and the interaction between Hopf and steady state bifurcations are studied. Again we recall some general steady state bifurcation results in Section 3.1, and applications to (1.2) are given in Section 3.2. The paper ends with some concluding remarks. Two longer proofs are given in Appendices A and B. Throughout the paper, we denote by \mathbb{N} the set of all the positive integers, and $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$.

2. Hopf bifurcations

In this section, we derive an explicit algorithm for determining the direction of Hopf bifurcation and stability of the bifurcating periodic solutions for a reaction–diffusion (R–D) system consisting of two equations with Neumann boundary condition, by using the center manifold theory and normal form method. While our calculations can be carried over to higher spatial domains, we restrict ourselves to the case of one-dimensional spatial domain $(0, \ell\pi)$, for which the structure of the eigenvalues is clear. Then we apply the theory to the predator–prey system (1.2).

2.1. Hopf bifurcation for general R–D systems

This subsection is devoted to deriving an explicit algorithm for determining the properties of Hopf bifurcation of a general R–D system on the spatial domain $\Omega = (0, \ell\pi)$, with $\ell \in \mathbb{R}^+$. Our results are mostly extracted from [16] but we summarize the necessary results specifically for the one-dimensional R–D system for the convenience of readers and future applications. A number of authors have established abstract Hopf bifurcation theorems for PDEs, see [7,18,26,33]. Our results here can be adapted to other boundary conditions and higher spatial domains.

We consider a general R–D system subject to Neumann boundary condition on spatial domain $\Omega = (0, \ell\pi)$, with $\ell \in \mathbb{R}^+$,

$$\begin{cases} u_t - d_1 u_{xx} = f(\lambda, u, v), & x \in (0, \ell\pi), t > 0, \\ v_t - d_2 v_{xx} = g(\lambda, u, v), & x \in (0, \ell\pi), t > 0, \\ u_x(0, t) = v_x(0, t) = 0, \quad u_x(\ell\pi, t) = v_x(\ell\pi, t) = 0, & t > 0, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x), & x \in (0, \ell\pi), \end{cases} \quad (2.1)$$

where $d_1, d_2, \lambda \in \mathbb{R}^+, f, g: \mathbb{R} \times \mathbb{R}^2 \rightarrow \mathbb{R}$ are C^k ($k \geq 5$) with $f(\lambda, 0, 0) = g(\lambda, 0, 0) = 0$. Define the real-valued Sobolev space

$$X := \{(u, v) \in H^2(0, \ell\pi) \times H^2(0, \ell\pi) \mid (u_x, v_x)|_{x=0, \ell\pi} = 0\}. \tag{2.2}$$

We also define the complexification of X to be $X_{\mathbb{C}} := X \oplus iX = \{x_1 + ix_2 \mid x_1, x_2 \in X\}$.

The linearized operator of the steady state system of (2.1) evaluated at $(\lambda, 0, 0)$ is

$$L(\lambda) := \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + A(\lambda) & B(\lambda) \\ C(\lambda) & d_2 \frac{\partial^2}{\partial x^2} + D(\lambda) \end{pmatrix}, \tag{2.3}$$

with the domain $D_{L(\lambda)} = X_{\mathbb{C}}$, where $A(\lambda) = f_u(\lambda, 0, 0)$, $B(\lambda) = f_v(\lambda, 0, 0)$, $C(\lambda) = g_u(\lambda, 0, 0)$, and $D(\lambda) = g_v(\lambda, 0, 0)$. To consider Hopf bifurcations, we assume that for some $\lambda_0 \in \mathbb{R}$, the following condition holds:

(H₁) There exists a neighborhood O of λ_0 such that for $\lambda \in O$, $L(\lambda)$ has a pair of complex, simple, conjugate eigenvalues $\alpha(\lambda) \pm i\omega(\lambda)$, continuously differentiable in λ , with $\alpha(\lambda_0) = 0$, $\omega(\lambda_0) = \omega_0 > 0$, and $\alpha'(\lambda_0) \neq 0$; all other eigenvalues of $L(\lambda)$ have non-zero real parts for $\lambda \in O$.

It is well known that the eigenvalue problem

$$-\varphi'' = \mu\varphi, \quad x \in (0, \ell\pi), \quad \varphi'(0) = \varphi'(\ell\pi) = 0$$

has eigenvalues $\mu_n = \frac{n^2}{\ell^2}$ ($n = 0, 1, 2, \dots$), with corresponding eigenfunctions $\varphi_n(x) = \cos \frac{n}{\ell}x$. Let

$$\begin{pmatrix} \phi \\ \psi \end{pmatrix} = \sum_{n=0}^{\infty} \cos \frac{n}{\ell}x \begin{pmatrix} a_n \\ b_n \end{pmatrix} \tag{2.4}$$

be an eigenfunction for $L(\lambda)$ with eigenvalue $\beta(\lambda)$, that is, $L(\lambda)(\phi, \psi)^T = \beta(\lambda)(\phi, \psi)^T$. Then from a straightforward analysis, we obtain

$$L_n(\lambda) \begin{pmatrix} a_n \\ b_n \end{pmatrix} = \beta(\lambda) \begin{pmatrix} a_n \\ b_n \end{pmatrix}, \quad n = 0, 1, 2, \dots, \tag{2.5}$$

where

$$L_n(\lambda) := \begin{pmatrix} A(\lambda) - \frac{d_1 n^2}{\ell^2} & B(\lambda) \\ C(\lambda) & D(\lambda) - \frac{d_2 n^2}{\ell^2} \end{pmatrix}. \tag{2.6}$$

It follows that the eigenvalues of $L(\lambda)$ are given by the eigenvalues of $L_n(\lambda)$ for $n = 0, 1, 2, \dots$. The characteristic equation of $L_n(\lambda)$ is

$$\beta^2 - \beta T_n(\lambda) + D_n(\lambda) = 0, \quad n = 0, 1, 2, \dots, \tag{2.7}$$

where

$$\begin{cases} T_n(\lambda) = A(\lambda) + D(\lambda) - \frac{(d_1 + d_2)n^2}{\ell^2}, \\ D_n(\lambda) = \frac{d_1 d_2 n^4}{\ell^4} - \frac{n^2}{\ell^2} (d_2 A(\lambda) + d_1 D(\lambda)) + A(\lambda)D(\lambda) - B(\lambda)C(\lambda), \end{cases}$$

and the eigenvalues $\beta(\lambda)$ are given by

$$\beta(\lambda) = \frac{T_n(\lambda) \pm \sqrt{T_n^2(\lambda) - 4D_n(\lambda)}}{2}, \quad n = 0, 1, 2, \dots \tag{2.8}$$

We assume that (H_1) holds at $\lambda = \lambda_0$. Then at $\lambda = \lambda_0$, $L(\lambda)$ has a pair of simple purely imaginary eigenvalues $\pm i\omega_0$ if and only if there exists a unique $n \in \mathbb{N}_0$ such that $\pm i\omega_0$ are the purely imaginary eigenvalues of $L_n(\lambda)$. We denote the associated eigenvector by $q = \cos \frac{n}{\ell} x (a_n, b_n)^T$, with $a_n, b_n \in \mathbb{C}$, such that $L(\lambda_0)q = i\omega_0 q$.

We adopt the framework of [16, Chapter 5]. We rewrite system (2.1) in the abstract form

$$\frac{dU}{dt} = L(\lambda)U + F(\lambda, U), \tag{2.9}$$

where

$$F(\lambda, U) := \begin{pmatrix} f(\lambda, u, v) - A(\lambda)u - B(\lambda)v \\ g(\lambda, u, v) - C(\lambda)u - D(\lambda)v \end{pmatrix}, \tag{2.10}$$

with $U = (u, v)^T \in X$. At $\lambda = \lambda_0$, the system (2.9) reduces to

$$\frac{dU}{dt} = L(\lambda_0)U + F_0(U), \tag{2.11}$$

where $F_0(U) := F(\lambda, U)|_{\lambda=\lambda_0}$.

Let $\langle \cdot, \cdot \rangle$ be the complex-valued L^2 inner product on Hilbert space $X_{\mathbb{C}}$, defined as

$$\langle U_1, U_2 \rangle = \int_0^{\ell\pi} (\bar{u}_1 u_2 + \bar{v}_1 v_2) dx, \tag{2.12}$$

with $U_i = (u_i, v_i)^T \in X_{\mathbb{C}}$ ($i = 1, 2$). Notice that $\langle \lambda U_1, U_2 \rangle = \bar{\lambda} \langle U_1, U_2 \rangle$. Denote by $L^*(\lambda_0)$ the adjoint operator of the operator $L(\lambda_0)$ such that $\langle u, L(\lambda_0)v \rangle = \langle L^*(\lambda_0)u, v \rangle$, also defined on $D_{L^*(\lambda_0)} = X_{\mathbb{C}}$,

$$L^*(\lambda_0) := \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + A(\lambda_0) & C(\lambda_0) \\ B(\lambda_0) & d_2 \frac{\partial^2}{\partial x^2} + D(\lambda_0) \end{pmatrix}. \tag{2.13}$$

From (H_1) , we can choose $q^* := \cos \frac{n}{\ell} x (a_n^*, b_n^*)^T \in X_{\mathbb{C}}$ so that

$$L^*(\lambda_0)q^* = -i\omega_0 q^*, \quad \langle q^*, q \rangle = 1, \quad \text{and} \quad \langle q^*, \bar{q} \rangle = 0.$$

We decompose $X = X^c \oplus X^s$, with $X^c := \{zq + \bar{z}\bar{q} \mid z \in \mathbb{C}\}$, $X^s := \{u \in X \mid \langle q^*, u \rangle = 0\}$. For any $(u, v) \in X$, there exists $z \in \mathbb{C}$ and $w = (w_1, w_2) \in X^s$ such that

$$\begin{pmatrix} u \\ v \end{pmatrix} = zq + \bar{z}\bar{q} + \begin{pmatrix} w_1 \\ w_2 \end{pmatrix}, \quad \text{or} \quad \begin{cases} u = za_n \cos \frac{n}{\ell} x + \bar{z}\bar{a}_n \cos \frac{n}{\ell} x + w_1, \\ v = zb_n \cos \frac{n}{\ell} x + \bar{z}\bar{b}_n \cos \frac{n}{\ell} x + w_2. \end{cases} \tag{2.14}$$

Thus the system (2.11) is reduced to the following system in (z, w) coordinates:

$$\begin{cases} \frac{dz}{dt} = i\omega_0 z + \langle q^*, F_0 \rangle, \\ \frac{dw}{dt} = L(\lambda_0)w + H(z, \bar{z}, w), \end{cases} \tag{2.15}$$

where

$$H(z, \bar{z}, w) := F_0 - \langle q^*, F_0 \rangle q - \langle \bar{q}^*, F_0 \rangle \bar{q}, \quad \text{and} \quad F_0 := F_0(zq + \bar{z}\bar{q} + w). \tag{2.16}$$

As in [16], we write F_0 in the form:

$$F_0(U) := \frac{1}{2}Q(U, U) + \frac{1}{6}C(U, U, U) + O(|U|^4), \quad \text{where } U = (u, v), \tag{2.17}$$

and Q, C are symmetric multilinear forms. For simplicity, we write $Q_{XY} = Q(X, Y)$, and $C_{XYZ} = C(X, Y, Z)$. For later uses, we calculate Q_{qq} , $Q_{q\bar{q}}$ and $C_{qq\bar{q}}$ as follows:

$$\begin{aligned} Q_{qq} &= \cos^2 \frac{n}{\ell} x \begin{pmatrix} c_n \\ d_n \end{pmatrix}, & Q_{q\bar{q}} &= \cos^2 \frac{n}{\ell} x \begin{pmatrix} e_n \\ f_n \end{pmatrix}, \\ C_{qq\bar{q}} &= \cos^3 \frac{n}{\ell} x \begin{pmatrix} g_n \\ h_n \end{pmatrix}, \end{aligned} \tag{2.18}$$

where (with all the partial derivatives evaluated at $(\lambda_0, 0, 0)$)

$$\begin{cases} c_n = f_{uu}a_n^2 + 2f_{uv}a_nb_n + f_{vv}b_n^2, \\ d_n = g_{uu}a_n^2 + 2g_{uv}a_nb_n + g_{vv}b_n^2, \\ e_n = f_{uu}|a_n|^2 + f_{uv}(a_n\bar{b}_n + \bar{a}_nb_n) + f_{vv}|b_n|^2, \\ f_n = g_{uu}|a_n|^2 + g_{uv}(a_n\bar{b}_n + \bar{a}_nb_n) + g_{vv}|b_n|^2, \\ g_n = f_{uuu}|a_n|^2a_n + f_{uuv}(2|a_n|^2b_n + a_n^2\bar{b}_n) + f_{uvv}(2|b_n|^2a_n + b_n^2\bar{a}_n) + f_{vvv}|b_n|^2b_n, \\ h_n = g_{uuu}|a_n|^2a_n + g_{uuv}(2|a_n|^2b_n + a_n^2\bar{b}_n) + g_{uvv}(2|b_n|^2a_n + b_n^2\bar{a}_n) + g_{vvv}|b_n|^2b_n. \end{cases} \tag{2.19}$$

Let

$$H(z, \bar{z}, w) = \frac{H_{20}}{2}z^2 + H_{11}z\bar{z} + \frac{H_{02}}{2}\bar{z}^2 + o(|z|^3) + o(|z| \cdot |w|), \tag{2.20}$$

then by (2.16) and (2.17), we have

$$\begin{cases} H_{20} = Q_{qq} - \langle q^*, Q_{qq} \rangle q - \langle \bar{q}^*, Q_{qq} \rangle \bar{q}, \\ H_{11} = Q_{q\bar{q}} - \langle q^*, Q_{q\bar{q}} \rangle q - \langle \bar{q}^*, Q_{q\bar{q}} \rangle \bar{q}. \end{cases} \tag{2.21}$$

It follows from Appendix A of [16] that the system (2.15) possesses a center manifold, and then we can write w in the form:

$$w = \frac{w_{20}}{2}z^2 + w_{11}z\bar{z} + \frac{w_{02}}{2}\bar{z}^2 + o(|z|^3). \tag{2.22}$$

By (2.20), (2.22), and together with

$$L(\lambda_0)w + H(z, \bar{z}, w) = \frac{dw}{dt} = \frac{\partial w}{\partial z} \frac{dz}{dt} + \frac{\partial w}{\partial \bar{z}} \frac{d\bar{z}}{dt}, \tag{2.23}$$

we have

$$w_{20} = [2i\omega_0 I - L(\lambda_0)]^{-1} H_{20} \quad \text{and} \quad w_{11} = -[L(\lambda_0)]^{-1} H_{11}.$$

We claim that

$$w_{20} = \begin{cases} \frac{1}{2}[2i\omega_0 I - L(\lambda_0)]^{-1}[(\cos \frac{2n}{\ell}x + 1)\binom{c_n}{d_n}], & \text{if } n \in \mathbb{N}, \\ [2i\omega_0 I - L(\lambda_0)]^{-1}[\binom{c_0}{d_0} - \langle q^*, Q_{qq} \rangle \binom{a_0}{b_0} - \langle \bar{q}^*, Q_{qq} \rangle \binom{\bar{a}_0}{\bar{b}_0}], & \text{if } n = 0. \end{cases} \tag{2.24}$$

In fact, if $n \in \mathbb{N}$, then noticing that

$$\int_0^{\ell\pi} \cos^3 \frac{n}{\ell}x \, dx = 0,$$

and by calculation, we have

$$\langle q^*, Q_{qq} \rangle = \langle q^*, Q_{q\bar{q}} \rangle = \langle \bar{q}^*, Q_{qq} \rangle = \langle \bar{q}^*, Q_{q\bar{q}} \rangle = 0. \tag{2.25}$$

Then, by (2.18) and (2.21), we have

$$H_{20} = \begin{cases} Q_{qq} = \cos^2 \frac{n}{\ell}x \binom{c_n}{d_n} = (\frac{1}{2} \cos \frac{2n}{\ell}x + \frac{1}{2}) \binom{c_n}{d_n}, & \text{if } n \in \mathbb{N}, \\ \binom{c_0}{d_0} - \langle q^*, Q_{qq} \rangle \binom{a_0}{b_0} - \langle \bar{q}^*, Q_{qq} \rangle \binom{\bar{a}_0}{\bar{b}_0}, & \text{if } n = 0, \end{cases} \tag{2.26}$$

which implies (2.24).

Likewise we have

$$w_{11} = \begin{cases} -\frac{1}{2}[L(\lambda_0)]^{-1}[(\cos \frac{2n}{\ell}x + 1)\binom{e_n}{f_n}], & \text{if } n \in \mathbb{N}, \\ -[L(\lambda_0)]^{-1}[\binom{e_0}{f_0} - \langle q^*, Q_{q\bar{q}} \rangle \binom{a_0}{b_0} - \langle \bar{q}^*, Q_{q\bar{q}} \rangle \binom{\bar{a}_0}{\bar{b}_0}], & \text{if } n = 0. \end{cases} \tag{2.27}$$

Notice that the calculation of $[2i\omega_0 I - L(\lambda_0)]^{-1}$ and $[L(\lambda_0)]^{-1}$ in (2.24) and (2.27) are restricted to the subspaces spanned by the eigen-modes 1 and $\cos(2nx/\ell)$.

Therefore the reaction–diffusion system restricted to the center manifold is given by

$$\frac{dz}{dt} = i\omega_0 z + \langle q^*, F_0 \rangle = i\omega_0 z + \sum_{2 \leq i+j \leq 3} \frac{g_{ij}}{i!j!} z^i \bar{z}^j + \mathcal{O}(|z|^4), \tag{2.28}$$

where $g_{20} = \langle q^*, Q_{qq} \rangle$, $g_{11} = \langle q^*, Q_{q\bar{q}} \rangle$, $g_{02} = \langle q^*, Q_{\bar{q}\bar{q}} \rangle$, and

$$g_{21} = 2\langle q^*, Q_{w_{11}q} \rangle + \langle q^*, Q_{w_{20}\bar{q}} \rangle + \langle q^*, C_{qq\bar{q}} \rangle.$$

The dynamics of (2.15) can be determined by the dynamics of (2.28).

As in page 28 of [16], we write the Poincaré normal form of (2.9) (for λ in a neighborhood of λ_0) in the form:

$$\dot{z} = (\alpha(\lambda) + i\omega(\lambda))z + z \sum_{j=1}^M c_j(\lambda)(z\bar{z})^j, \tag{2.29}$$

where z is a complex variable, $M \geq 1$ and $c_j(\lambda)$ are complex-valued coefficients. Then from page 47 of [16], we have

$$c_1(\lambda) = \frac{g_{20}g_{11}(3\alpha(\lambda) + i\omega(\lambda))}{2(\alpha^2(\lambda) + \omega^2(\lambda))} + \frac{|g_{11}|^2}{\alpha(\lambda) + i\omega(\lambda)} + \frac{|g_{02}|^2}{2(\alpha(\lambda) + 3i\omega(\lambda))} + \frac{g_{21}}{2}. \tag{2.30}$$

Thus

$$\begin{aligned} c_1(\lambda_0) &= \frac{i}{2\omega_0} \left(g_{20}g_{11} - 2|g_{11}|^2 - \frac{1}{3}|g_{02}|^2 \right) + \frac{g_{21}}{2} \\ &= \frac{i}{2\omega_0} \langle q^*, Q_{qq} \rangle \cdot \langle q^*, Q_{q\bar{q}} \rangle + \langle q^*, Q_{w_{11}q} \rangle + \frac{1}{2} \langle q^*, Q_{w_{20}\bar{q}} \rangle + \frac{1}{2} \langle q^*, C_{qq\bar{q}} \rangle, \end{aligned} \tag{2.31}$$

with w_{20} and w_{11} in the form of (2.24) and (2.27) respectively.

From Theorem II and Remark 3 in Chapter 1 of [16], under (H_1) , the system (2.28), or (2.15) or equivalently (2.1), undergoes a Hopf bifurcation at $\lambda = \lambda_0$. With s sufficiently small, for $\lambda = \lambda(s)$, there exists a family of $T(s)$ -periodic continuously differentiable solutions $(u(s)(x, t), v(s)(x, t))$ of system (2.1) such that $u(0) = v(0) = 0$. More precisely, from page 30 of [16], it follows that $z(t) = se^{2\pi it/T(s)}$, and substituting it into (2.14), we obtain

$$\begin{cases} u(s)(x, t) = s(a_n e^{2\pi it/T(s)} + \bar{a}_n e^{-2\pi it/T(s)}) \cos \frac{n}{\ell} x + o(s^2), \\ v(s)(x, t) = s(b_n e^{2\pi it/T(s)} + \bar{b}_n e^{-2\pi it/T(s)}) \cos \frac{n}{\ell} x + o(s^2), \end{cases} \tag{2.32}$$

where

$$T(s) = \frac{2\pi}{\omega_0} (1 + \tau_2 s^2) + o(s^4), \quad \tau_2 := -\frac{1}{\omega_0} \left[\text{Im}(c_1(\lambda_0)) - \frac{\text{Re}(c_1(\lambda_0))}{\alpha'(\lambda_0)} \omega'(\lambda_0) \right], \tag{2.33}$$

and

$$T''(0) = \frac{4\pi}{\omega_0} \tau_2 = -\frac{4\pi}{\omega_0^2} \left[\text{Im}(c_1(\lambda_0)) - \frac{\text{Re}(c_1(\lambda_0))}{\alpha'(\lambda_0)} \omega'(\lambda_0) \right]. \tag{2.34}$$

Also from the results in Section 1.3 of [16], $\lambda(0) = \lambda_0$ and $\lambda'(0) = 0$. Then the bifurcation direction and the stability of the bifurcating periodic solutions are determined by $\lambda''(0)$, which is given by

$$\lambda''(0) = -\frac{1}{\alpha'(\lambda_0)} \text{Re}(c_1(\lambda_0)).$$

To summarize we have the following Hopf bifurcation theorem for the general R–D equations (2.1).

Theorem 2.1. *Suppose (H_1) is satisfied. Then (2.1) possesses a family of real-valued $T(s)$ -periodic solutions $(\lambda(s), u(s)(x, t), v(s)(x, t))$, for s sufficiently small, bifurcating from $(\lambda_0, 0, 0)$ at $\lambda = \lambda_0$ in the space $\mathbb{R} \times X$, and there exists a unique $n \in \mathbb{N}_0$, such that $(u(s)(x, t), v(s)(x, t))$ can be parameterized in the form of (2.32). Furthermore:*

1. *The bifurcation is supercritical (resp. subcritical) if*

$$\frac{1}{\alpha'(\lambda_0)} \operatorname{Re}(c_1(\lambda_0)) < 0 \quad (\text{resp. } > 0). \tag{2.35}$$

2. *If in addition all other eigenvalues of $L(\lambda_0)$ have negative real parts, then the bifurcating periodic solutions are stable (resp. unstable) if $\operatorname{Re}(c_1(\lambda_0)) < 0$ (resp. > 0).*

Remark 2.2.

1. Under (H_1) , if additionally there exists at least one eigenvalue of $L(\lambda)$ having positive real part, then the bifurcating periodic solutions are always unstable because the eigenvalues with positive real parts give rise to characteristic (Floquet) exponents with positive real parts.
2. For ODEs, $\operatorname{Re} c_1(\lambda_0)$ can be formulated in an explicit form (see, for example, page 277 of [46]). In PDEs, however, in order to compute $\operatorname{Re} c_1(\lambda_0)$, we need first to calculate $\langle q^*, Q_{qq} \rangle$, $\langle q^*, Q_{q\bar{q}} \rangle$, $\langle q^*, Q_{w_{11}q} \rangle$, $\langle q^*, Q_{w_{20}\bar{q}} \rangle$, and $\langle q^*, C_{qq\bar{q}} \rangle$. Since they are defined in other formulas as mentioned above, and substituting these definitions into the formula (2.31) will be lengthy, we leave $\operatorname{Re}(c_1(\lambda_0))$ in the form of (2.31) instead of a lengthy two-page formula. For concrete PDE examples (like the one in next subsection), we use (2.31) and corresponding substitutions to calculate these related quantities.

2.2. Hopf bifurcation in diffusive predator–prey system

In this subsection, we analyze the stability of the constant coexistence steady state of (1.2), and consider the related Hopf bifurcation for (1.2) with the spatial domain $\Omega = (0, \ell\pi)$, $\ell \in \mathbb{R}^+$, which is

$$\begin{cases} u_t - d_1 u_{xx} = u \left(1 - \frac{u}{k} \right) - \frac{mu v}{u + 1}, & x \in (0, \ell\pi), \quad t > 0, \\ v_t - d_2 v_{xx} = -\theta v + \frac{mu v}{u + 1}, & x \in (0, \ell\pi), \quad t > 0, \\ u_x(0, t) = v_x(0, t) = 0, \quad u_x(\ell\pi, t) = v_x(\ell\pi, t) = 0, & t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in (0, \ell\pi). \end{cases} \tag{2.36}$$

First we recall some well-known results on the ODE dynamics of (2.36), see [20,22–24] for more details and related references. The system (2.36) has three non-negative constant equilibrium solutions: $(0, 0)$, $(k, 0)$, (λ, v_λ) , where

$$\lambda = \frac{\theta}{m - \theta}, \quad v_\lambda = \frac{(k - \lambda)(1 + \lambda)}{km}.$$

In the following, we shall fix θ and k and use λ as the main bifurcation parameter (or equivalently m as a parameter). The coexistence equilibrium (λ, v_λ) is in the first quadrant if and only if $m > \theta(1 + k)/k$ (or $0 < \lambda < k$). For the ODE system in (2.36) without the diffusion:

$$u' = u \left(1 - \frac{u}{k} \right) - \frac{mu v}{u + 1}, \quad v' = -\theta v + \frac{mu v}{u + 1},$$

we have the following stability information: when $\lambda \geq k$, $(k, 0)$ is globally asymptotically stable; when $(k - 1)/2 < \lambda < k$, the coexistence equilibrium (λ, v_λ) is globally asymptotically stable; and when

$0 < \lambda < (k - 1)/2$, there is a globally asymptotically stable periodic orbit [3]. $\lambda = (k - 1)/2$ is a bifurcation point where a subcritical Hopf bifurcation occurs.

Some of the global dynamics described above still hold for reaction–diffusion dynamics (2.36) (indeed even for arbitrary higher-dimensional spacial domains). When $\lambda \geq k$ (or $0 < m < \theta(1 + k)/k$), it is well known that $(k, 0)$ is globally asymptotically stable (see for example [13,27]). Hence we always assume that $0 < \lambda < k$ (or $m > \theta(1 + k)/k$) in the following. On the other hand, we have the following global stability theorem about (λ, v_λ) , which is essentially known [21] but we include here for the sake of completeness:

Theorem 2.3. *Suppose that $0 < k \leq 1$, or $k > 1$ but $k - 1 \leq \lambda < k$. Then (λ, v_λ) is globally asymptotically stable for the dynamics of (2.36).*

Proof. We define

$$E(u(x, t), v(x, t)) = \int_0^{\ell\pi} \int_\lambda^u \frac{mh(\xi) - \theta}{h(\xi)} d\xi dx + m \int_0^{\ell\pi} \int_{v_\lambda}^v \frac{\eta - v_\lambda}{\eta} d\eta dx.$$

Then

$$\begin{aligned} E_t(u, v) &= \int_0^{\ell\pi} \frac{mh(u) - \theta}{h(u)} u_t dx + m \int_0^{\ell\pi} \frac{v - v_\lambda}{v} v_t dx \\ &= m \int_0^{\ell\pi} (h(u) - h(\lambda))(g(u) - g(\lambda)) dx - I(t), \end{aligned}$$

where $h(u) := \frac{u}{u+1}$, $g(u) := (1 - \frac{u}{k})(u + 1)$ and

$$I(t) := d_1 \theta \int_0^{\ell\pi} \frac{h'(u)}{h^2(u)} u_x^2 dx + d_2 v_\lambda m \int_0^{\ell\pi} \frac{1}{v^2} v_x^2 dx.$$

Notice that, for any $u > 0$, $h'(u) > 0$, and when $0 < k \leq 1$, $g'(u) < 0$ for any $u > 0$. Thus, $[h(u) - h(\lambda)] \cdot [g(u) - g(\lambda)] \leq 0$ for any $u > 0$. When $k > 1$, but $v_\lambda \leq 1/m$ (which is equivalent to $g(\lambda) \leq g(0)$), then $[h(u) - h(\lambda)] \cdot [g(u) - g(\lambda)] \leq 0$ for any $u > 0$. Thus, in both cases, $E_t < 0$ along an orbit $(u(x, t), v(x, t))$ of system (2.36) with any non-negative initial value $(u_0, v_0) \neq (0, 0)$ or $(k, 0)$, and $E_t = 0$ only if $(u(x, t), v(x, t)) = (\lambda, v_\lambda)$. Notice that $v_\lambda \leq 1/m$ is equivalent to $\lambda \geq k - 1$, which completes the proof. \square

It is obvious that the proof above also works for the arbitrary higher spatial domain Ω . For $(k - 1)/2 < \lambda < k - 1$, a Lyapunov functional is known for ODE in (2.36) [2], but it cannot be generalized to the R–D system case [21].

Due to the global stability in Theorem 2.3, and in order to concentrate on the investigation of Hopf bifurcation, in the remaining part of this subsection, we always assume that $k > 1$, and we consider λ in the range of $0 < \lambda < k - 1$.

To cast our discussion into the framework of Section 2.1, we translate (2.36) into the following system by the translation $\hat{u} = u - \lambda$ and $\hat{v} = v - v_\lambda$, and still let u and v denote \hat{u} and \hat{v} respectively. We have

$$\begin{cases} u_t - d_1 u_{xx} = (u + \lambda) \left(1 - \frac{u + \lambda}{k} \right) - \frac{m(u + \lambda)(v + v_\lambda)}{1 + u + \lambda}, & x \in (0, \ell\pi), t > 0, \\ v_t - d_2 v_{xx} = -\theta(v + v_\lambda) + \frac{m(u + \lambda)(v + v_\lambda)}{1 + u + \lambda}, & x \in (0, \ell\pi), t > 0, \\ u_x(0, t) = v_x(0, t) = 0, \quad u_x(\ell\pi, t) = v_x(\ell\pi, t) = 0, & t > 0. \end{cases} \tag{2.37}$$

As in Section 2.1, we consider the linearization near $(0, 0)$ for (2.37):

$$L(\lambda) := \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + A(\lambda) & B(\lambda) \\ C(\lambda) & d_2 \frac{\partial^2}{\partial x^2} \end{pmatrix} \quad \text{and} \quad L_n(\lambda) := \begin{pmatrix} A(\lambda) - \frac{d_1 n^2}{\ell^2} & B(\lambda) \\ C(\lambda) & -\frac{d_2 n^2}{\ell^2} \end{pmatrix},$$

where

$$A(\lambda) := \frac{\lambda(k - 1 - 2\lambda)}{k(1 + \lambda)}, \quad B(\lambda) := -\theta, \quad \text{and} \quad C(\lambda) := \frac{k - \lambda}{k(1 + \lambda)}. \tag{2.38}$$

The characteristic equation of $L_n(\lambda)$ is

$$\beta^2 - \beta T_n(\lambda) + D_n(\lambda) = 0, \quad n = 0, 1, 2, \dots, \tag{2.39}$$

where

$$\begin{cases} T_n(\lambda) = \frac{\lambda(k - 1 - 2\lambda)}{k(1 + \lambda)} - \frac{(d_1 + d_2)n^2}{\ell^2}, \\ D_n(\lambda) = \frac{\theta(k - \lambda)}{k(1 + \lambda)} - \left[\frac{d_2 \lambda(k - 1 - 2\lambda)}{k(1 + \lambda)} \right] \frac{n^2}{\ell^2} + \frac{d_1 d_2 n^4}{\ell^4}. \end{cases} \tag{2.40}$$

We shall identify Hopf bifurcation values λ_0 which satisfy the condition (H_1) , which takes the following form now: there exists $n \in \mathbb{N}_0$ such that

$$T_n(\lambda_0) = 0, \quad D_n(\lambda_0) > 0, \quad \text{and} \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0 \quad \text{for } j \neq n; \tag{2.41}$$

and for the unique pair of complex eigenvalues near the imaginary axis $\alpha(\lambda) \pm i\omega(\lambda)$,

$$\alpha'(\lambda_0) \neq 0. \tag{2.42}$$

From (2.40), $T_n(\lambda) < 0$ and $D_n(\lambda) > 0$ for $\lambda \in ((k - 1)/2, k - 1)$, which implies that the trivial steady state (λ, v_λ) is locally asymptotically stable. Hence any potential bifurcation point λ_0 must be in the interval $(0, (k - 1)/2]$. For any Hopf bifurcation point λ_0 in $(0, (k - 1)/2]$, $\alpha(\lambda) \pm i\omega(\lambda)$ are the eigenvalues of $L_n(\lambda)$, so

$$\alpha(\lambda) = \frac{A(\lambda)}{2} - \frac{(d_1 + d_2)n^2}{2\ell^2}, \quad \omega(\lambda) = \sqrt{D_n(\lambda) - \alpha^2(\lambda)}, \tag{2.43}$$

and

$$\begin{aligned} \alpha'(\lambda_0) &= \frac{A'(\lambda)}{2} \Big|_{\lambda=\lambda_0} \\ &= \frac{k-1-4\lambda-2\lambda^2}{2k(1+\lambda)^2} \Big|_{\lambda=\lambda_0} \begin{cases} > 0, & \text{if } 0 < \lambda_0 < \lambda_*, \\ < 0, & \text{if } \lambda_* < \lambda_0 \leq (k-1)/2, \end{cases} \end{aligned} \tag{2.44}$$

where (recall that we assume $k > 1$)

$$\lambda_* := \sqrt{\frac{k+1}{2}} - 1 \in \left(0, \frac{k-1}{2}\right). \tag{2.45}$$

Hence the transversality condition (2.42) is always satisfied as long as $\lambda_0 \neq \lambda_*$. Moreover when $\lambda_* < \lambda_0 < (k-1)/2$, the real part of one pair of complex eigenvalues of $L(\lambda)$ becomes positive when λ decreases crossing λ_0 , and when $0 < \lambda_0 < \lambda_*$, the real part of one pair of complex eigenvalues of $L(\lambda)$ becomes negative when λ decreases crossing λ_0 . That is, in $(\lambda_*, (k-1)/2)$, the constant steady state loses stability when λ decreases across a bifurcation point, but in $(0, \lambda_*)$ it regains the stability when λ decreases across a bifurcation point.

From discussions above, the determination of Hopf bifurcation points reduces to describing the set

$$\Lambda_1 := \{ \lambda \in (0, (k-1)/2) \setminus \{ \lambda_* \} : \text{for some } n \in \mathbb{N}, (2.41) \text{ is satisfied} \}, \tag{2.46}$$

when a set of parameters $(\ell, d_1, d_2, \theta, k)$ is given. In the following we fix $d_1, d_2, \theta > 0$ and $k > 1$, but choose ℓ appropriately. First $\lambda_0^H := (k-1)/2$ is always an element of Λ_1 for any $\ell > 0$ since $T_0(\lambda_0^H) = 0$, $T_j(\lambda_0^H) < 0$ for any $j \geq 1$, and $D_m(\lambda_0^H) > 0$ for any $m \in \mathbb{N}_0$. This corresponds to the Hopf bifurcation of spatially homogeneous periodic solution which has been known from the studies of ODE model. Apparently λ_0^H is also the unique value λ for the Hopf bifurcation of spatially homogeneous periodic solution for any $\ell > 0$.

Hence in the following we look for spatially non-homogeneous Hopf bifurcation for $n \geq 1$. We notice that $A(0) = A(\lambda_0^H) = 0$, and $A(\lambda) > 0$ in $(0, \lambda_0^H)$, and $A(\lambda)$ has a unique critical point $\lambda = \lambda_*$ at which $A(\lambda)$ achieves a local maximum $A(\lambda_*) = 2\lambda_*^2/k := M_* > 0$. Define

$$\ell_n = n \sqrt{\frac{d_1 + d_2}{M_*}}, \quad n \in \mathbb{N}, \quad \text{where } M_* = \frac{(\sqrt{k+1} - \sqrt{2})^2}{k} > 0. \tag{2.47}$$

Then for $\ell_n < \ell \leq \ell_{n+1}$, and $1 \leq j \leq n$, we define $\lambda_{j,-}^H$ and $\lambda_{j,+}^H$ to be the roots of $A(\lambda) = \frac{(d_1+d_2)j^2}{\ell^2}$ satisfying $0 < \lambda_{j,-}^H < \lambda_* < \lambda_{j,+}^H < \lambda_0^H$. These points satisfy

$$0 < \lambda_{1,-}^H < \lambda_{2,-}^H < \dots < \lambda_{n,-}^H < \lambda_* < \lambda_{n,+}^H < \dots < \lambda_{2,+}^H < \lambda_{1,+}^H < \lambda_0^H.$$

Clearly $T_j(\lambda_{j,\pm}^H) = 0$ and $T_i(\lambda_{j,\pm}^H) \neq 0$ for $i \neq j$. Now we only need to verify whether $D_i(\lambda_{j,\pm}^H) \neq 0$ for all $i \in \mathbb{N}_0$, and in particular, $D_j(\lambda_{j,\pm}^H) > 0$.

Here we derive a condition on the parameters so that $D_i(\lambda) > 0$ for all $\lambda \in [0, \lambda_0^H]$ so that $D_i(\lambda_{j,\pm}^H) > 0$. Indeed if $\lambda \in [0, \lambda_0^H]$, then

$$D_i(\lambda) \geq \frac{\theta}{k} - d_2 M_* \frac{i^2}{\ell^2} + d_1 d_2 \frac{i^4}{\ell^4} := g\left(\frac{i^2}{\ell^2}\right). \tag{2.48}$$

The quadratic function $g(y) = \theta/k - d_2 M_* y + d_1 d_2 y^2$ is positive for all $y \in \mathbb{R}$ if

$$\frac{\theta}{k} > \frac{d_2 M_*^2}{4d_1}. \tag{2.49}$$

Summarizing our analysis above, and applying Theorem 2.1, we obtain our main result in this subsection:

Theorem 2.4. *Suppose that the constants $d_1, d_2, m, \theta > 0$ and $k > 1$ satisfy*

$$\frac{d_1}{d_2} > \frac{(\sqrt{k+1} - \sqrt{2})^4}{4\theta k}, \tag{2.50}$$

and ℓ_n are defined as in (2.47). Then for any ℓ in $(\ell_n, \ell_{n+1}]$, there exist $2n$ points $\lambda_{j,\pm}^H(\ell)$, $1 \leq j \leq n$, satisfying

$$0 < \lambda_{1,-}^H(\ell) < \lambda_{2,-}^H(\ell) < \dots < \lambda_{n,-}^H(\ell) < \lambda_* < \lambda_{n,+}^H(\ell) < \dots < \lambda_{2,+}^H(\ell) < \lambda_{1,+}^H(\ell) < \lambda_0^H,$$

such that the system (2.36) undergoes a Hopf bifurcation at $\lambda = \lambda_{j,\pm}^H$ or $\lambda = \lambda_0^H$, and the bifurcating periodic solutions can be parameterized in the form of (2.32). Moreover:

1. The bifurcating periodic solutions from $\lambda = \lambda_0^H$ are spatially homogeneous, which coincides with the periodic solution of the corresponding ODE system.
2. The bifurcating periodic solutions from $\lambda = \lambda_{j,\pm}^H$ are spatially non-homogeneous.

Remark 2.5.

1. We emphasize that we not only have shown the existence of Hopf bifurcation points $\lambda_{j,\pm}^H$, but all the points $\lambda_{j,\pm}^H$ can be explicitly calculated according to our discussion above. See the examples following the remarks.
2. If $0 < \ell \leq \ell_1$, then the only Hopf bifurcation point is λ_0^H . Hence

$$\ell_1 = \frac{\sqrt{(d_1 + d_2)k}}{\sqrt{k+1} - \sqrt{2}}$$

is a minimal spatial size for the system to have a time-periodic spatial pattern, and ℓ_1 can be viewed as a characteristic spatial scale of periodic pattern. On the other hand, more periodic patterns are possible as ℓ grows. This minimal patch size can be compared with the “minimal patch size” $\sqrt{d_1}$ for the existence of non-constant solutions of $-d_1 u'' = u(1 - u/k)$ with $u'(0) = u'(\ell\pi) = 0$. While the two minimal patch sizes are in the same order (square root of diffusion coefficients), the former also depends on the carrying capacity (which is in the nonlinear part of the equation). It is also interesting to note that if one increases the carrying capacity, this minimal patch size decreases so the threshold value for spatial periodic pattern formation is lowered. This is in the same spirit of Rosenzweig’s paradox of enrichment [40]—the increase of the carrying capacity induces oscillation of the populations.

3. The condition (2.50) is satisfied if (a) for any given $\theta > 0$ and $k > 1$, d_1/d_2 is large; or (b) for any given $d_1, d_2 > 0$, θ is large or $k - 1$ is small. We also remark that (2.50) is mainly a sufficient condition so that no steady state bifurcations will occur in $(0, \lambda_0^H)$ and only Hopf bifurcations can occur. Some Hopf bifurcations could still occur when (2.50) is not satisfied, see more discussions in Section 3.2.
4. The bifurcation at λ_0^H holds without any restriction on ℓ and (2.50).
5. The existence and uniqueness of the spatially homogeneous periodic solution for $\lambda \in (0, \lambda_0^H)$ follows from [3]. The spatially non-homogeneous periodic solutions near the bifurcation points are apparently positive. Indeed, from a global bifurcation theorem of Wu [47], these bifurcating solutions belong to some global branches (connected components) of periodic orbits. From the maximum principle of parabolic equations, every periodic orbit on these branches is positive. However it is not clear whether the branch of periodic orbits bifurcating from $\lambda_{j,-}^H$ connects to

the one from $\lambda_{j,+}^H$. From the result of [47], the global branch of periodic orbits can also be unbounded or be bounded but the periods are unbounded. It is known that (see [24]) the period of spatially homogeneous periodic orbit tends to ∞ as $\lambda \rightarrow 0^+$ while the orbit is bounded. The bound of periodic orbits can be obtained if *a priori* estimate of solutions to (2.36) is known. Such *a priori* estimate can be obtained when $d_1 = d_2$, see the remark after Lemma 3.5.

Example 2.6. Let $\Omega = (0, \ell\pi)$, $d_1 = 1$, $d_2 = 3$, $k = 17$, $\theta = 4$. From calculation, $\lambda_0^H = 8$, $\lambda_* = 2$, $M_* := 2\lambda_*^2/k = 8/17$, $\ell_n := n\sqrt{(d_1 + d_2)/M_*} = \sqrt{34}n/2 \approx 2.915n$ and (2.50) is satisfied so $D_i(\lambda_{j,\pm}^H) > 0$.

1. Let $\ell = 2\sqrt{119}/7 \approx 3.116$, then $\ell \in (\ell_1, \ell_2] \approx (2.915, 5.830]$. Solving $A(\lambda) = (d_1 + d_2)n^2/\ell^2$, or equivalently, $2\lambda^2 - 9\lambda + 7 = 0$, we have $\lambda_{1,-}^H = 1$ and $\lambda_{1,+}^H = 3.5$. Then the set of Hopf bifurcation points $\Lambda_1 = \{\lambda_{1,-}^H, \lambda_{1,+}^H, \lambda_0^H\} = \{1, 3.5, 8\}$.
2. Let $\ell = 4\sqrt{85}/5 \approx 7.375$, then $\ell \in (\ell_2, \ell_3] \approx (5.830, 8.745]$. Likewise, we can obtain $\lambda_{1,-}^H \approx 0.0862$, $\lambda_{2,-}^H = 0.5$, $\lambda_{2,+}^H = 5$, $\lambda_{1,+}^H \approx 7.288$. Then

$$\Lambda_1 = \{\lambda_{1,-}^H, \lambda_{2,-}^H, \lambda_{2,+}^H, \lambda_{1,+}^H, \lambda_0^H\} = \{0.0862, 0.5, 5, 7.288, 8\}. \tag{2.51}$$

Next we consider the bifurcation direction and stability of the bifurcating periodic solutions.

Theorem 2.7. For the system (2.36), the Hopf bifurcation at $\lambda = \lambda_0^H$ is subcritical, and the bifurcating (spatially homogeneous) periodic solutions are locally asymptotically stable.

Proof. By Theorem 2.1, in order to determine the stability and bifurcation direction of the bifurcating periodic solution, we need to calculate $\text{Re}(c_1(\lambda_0^H))$, with $c_1(\lambda_0^H)$ defined by (2.31). When $\lambda = \lambda_0^H$, we put

$$q := \begin{pmatrix} a_0 \\ b_0 \end{pmatrix} = \begin{pmatrix} 1 \\ -i\omega_0/\theta \end{pmatrix} \quad \text{and} \quad q^* := \begin{pmatrix} a_0^* \\ b_0^* \end{pmatrix} = \begin{pmatrix} 1/(2\ell\pi) \\ -\theta i/(2\omega_0\ell\pi) \end{pmatrix}, \tag{2.52}$$

where $\omega_0 = \sqrt{\theta/k}$.

Recall that in our context,

$$\begin{aligned} f(\lambda, u, v) &= (u + \lambda) \left(1 - \frac{u + \lambda}{k} \right) - \frac{m(u + \lambda)(v + v_\lambda)}{1 + u + \lambda}, \\ g(\lambda, u, v) &= -\theta(v + v_\lambda) + \frac{m(u + \lambda)(v + v_\lambda)}{1 + u + \lambda}, \end{aligned} \tag{2.53}$$

then we have, by (2.19),

$$\begin{aligned} c_0 &= \frac{-2(k-1)^2 + 8i\omega_0k}{k(k-1)(k+1)}, & d_0 &= -\frac{4(k-1) + 8i\omega_0k}{k(k-1)(k+1)}, \\ e_0 &= \frac{2(1-k)}{k(k+1)}, & f_0 &= -\frac{4}{k(k+1)}, & g_0 = -h_0 &= -\frac{24(k-1) + 16i\omega_0k}{k(k-1)(k+1)^2}, \end{aligned} \tag{2.54}$$

and

$$\begin{aligned} \langle q^*, Q_{qq} \rangle &= \frac{4\theta\omega_0k - (k-1)^2\omega_0 + 2\theta(3-k)i}{k(k-1)(k+1)\omega_0}, \\ \langle q^*, Q_{q\bar{q}} \rangle &= \frac{(1-k)\omega_0 - 2\theta i}{k(k+1)\omega_0}, \end{aligned}$$

$$\begin{aligned} \langle \bar{q}^*, Q_{qq} \rangle &= -\frac{(k-1)^2\omega_0 + 2\theta k\omega_0 - 4\theta ki}{k(k-1)(k+1)\omega_0}, \\ \langle \bar{q}^*, C_{qq\bar{q}} \rangle &= \frac{-12(k-1)\omega_0 - 8\theta k\omega_0 + 4\theta(3k-5)i}{k(k-1)(k+1)^2\omega_0}. \end{aligned} \tag{2.55}$$

Hence it is straightforward to calculate

$$\begin{aligned} H_{20} &= \begin{pmatrix} c_0 \\ d_0 \end{pmatrix} - \langle q^*, Q_{qq} \rangle \begin{pmatrix} a_0 \\ b_0 \end{pmatrix} - \langle \bar{q}^*, Q_{qq} \rangle \begin{pmatrix} \bar{a}_0 \\ \bar{b}_0 \end{pmatrix} = 0, \\ H_{11} &= \begin{pmatrix} e_0 \\ f_0 \end{pmatrix} - \langle q^*, Q_{q\bar{q}} \rangle \begin{pmatrix} a_0 \\ b_0 \end{pmatrix} - \langle \bar{q}^*, Q_{q\bar{q}} \rangle \begin{pmatrix} \bar{a}_0 \\ \bar{b}_0 \end{pmatrix} = 0, \end{aligned} \tag{2.56}$$

which implies that $w_{20} = w_{11} = 0$. So

$$\langle q^*, Q_{w_{11}q} \rangle = \langle q^*, Q_{w_{20}\bar{q}} \rangle = 0. \tag{2.57}$$

Therefore

$$\begin{aligned} \operatorname{Re}(c_1(\lambda_0^H)) &= \operatorname{Re} \left\{ \frac{i}{2\omega_0} \langle q^*, Q_{qq} \rangle \cdot \langle q^*, Q_{q\bar{q}} \rangle + \frac{1}{2} \langle q^*, C_{qq\bar{q}} \rangle \right\} \\ &= \frac{\theta(4\theta k - (k-1)^2 - (3-k)(1-k))}{k^2(k-1)(k+1)^2\omega_0^2} + \frac{6\omega_0(1-k) - 4\theta\omega_0 k}{k(k-1)(k+1)^2\omega_0} \\ &= \frac{\theta(4\theta k - (k-1)^2 - (3-k)(1-k))}{k^2(k-1)(k+1)^2\omega_0^2} - \frac{6(k-1) + 4\theta k}{k(k-1)(k+1)^2} \\ &= \frac{4\theta k - (k-1)^2 - (3-k)(1-k) - 6(k-1) - 4\theta k}{k(k-1)(k+1)^2} \\ &= -\frac{2(k-1)(k+1)}{k(k-1)(k+1)^2} = -\frac{2}{k(k+1)} < 0. \end{aligned} \tag{2.58}$$

From (2.44), it follows that $\alpha'(\lambda_0^H) < 0$, and then by Theorem 2.1, the bifurcation is subcritical. On the other hand, from (2.40), $T_n(\lambda_0^H) < 0$ and $D_n(\lambda_0^H) > 0$ for any $n \geq 1$, so the bifurcating periodic solutions are stable since $\operatorname{Re}(c_1(\lambda_0^H)) < 0$. \square

Remark 2.8. We point out that it was proved in [3] that the ODE system of (2.36) possesses a unique periodic orbit which is globally asymptotically stable. Our result here shows that near the Hopf bifurcation point, this spatially homogeneous periodic solution (the same one as in ODE) is locally asymptotically stable with respect to the R–D system. Its global stability with respect to the R–D system is not known.

For the spatially non-homogeneous periodic solutions in Theorem 2.4, we have

Theorem 2.9. For the system (2.36), the Hopf bifurcation at $\lambda = \lambda_{j,-}^H$ is subcritical (supercritical) if $\operatorname{Re}(c_1(\lambda_{j,-}^H)) > 0$ (< 0), while the one at $\lambda = \lambda_{j,+}^H$ is subcritical (supercritical) if $\operatorname{Re}(c_1(\lambda_{j,+}^H)) < 0$ (> 0), where $\operatorname{Re}(c_1(\lambda_{j,\pm}^H))$ is defined in (A.18); and the bifurcating (spatially non-homogeneous) periodic solutions are unstable.

Proof. The bifurcation direction is determined by Theorem 2.1 and (2.44). The calculation of $\text{Re}(c_1(\lambda_{j,+}^H)) < 0$ is lengthy, and we will give it in Appendix A. The bifurcating periodic solutions are clearly unstable since the steady state (λ, v_λ) is unstable. \square

We conclude the section with the following example illustrate Theorem 2.9, which also continues Example 2.6.

Example 2.10. Let $\Omega = (0, \frac{2\sqrt{119}}{7}\pi)$, $d_1 = 1$, $d_2 = 3$, $k = 17$, $\theta = 4$. Then by Example 2.6, $\Lambda_1 = \{\lambda_{1,-}^H, \lambda_{1,+}^H, \lambda_0^H\} = \{1, 3.5, 8\}$. From the computation by `Matlab` and by (A.18), it follows that $\text{Re}(c_1(\lambda_{1,-}^H)) \approx 0.59746 > 0$, $\text{Re}(c_1(\lambda_{1,+}^H)) \approx 0.23125 > 0$ and by (2.44), $\alpha'(\lambda_{1,-}^H) = A'(\lambda_{1,-}^H) > 0$ and $\alpha'(\lambda_{1,+}^H) = A'(\lambda_{1,+}^H) < 0$, thus the bifurcation direction is subcritical and supercritical at $\lambda = \lambda_{1,-}^H$ and $\lambda = \lambda_{1,+}^H$ respectively.

3. Steady state bifurcations

3.1. Steady state bifurcation for general R–D systems

Again we consider the general R–D system (2.1) with Neumann boundary condition on spatial domain $\Omega = (0, \ell\pi)$, where $d_1, d_2, \lambda \in \mathbb{R}^+$, $f, g: \mathbb{R} \times \mathbb{R}^2 \rightarrow \mathbb{R}$ are C^k ($k \geq 2$) with $f(\lambda, 0, 0) = g(\lambda, 0, 0) = 0$. We assume that $X, L(\lambda), L_n(\lambda)$ are as defined in Section 2.1, but now the domain of linear operators is X not X_C . Our main assumption is that, for some $\lambda_0 \in \mathbb{R}$, the following condition holds:

(H₂) There exists a neighborhood O of λ_0 such that for $\lambda \in O$, $L(\lambda)$ has a simple real eigenvalue $\gamma(\lambda)$, continuously differentiable in λ , with $\gamma(\lambda_0) = 0$, and $\gamma'(\lambda_0) \neq 0$; all other eigenvalues of $L(\lambda)$ have non-zero real parts for $\lambda \in O$.

To apply an abstract bifurcation theorem, we define

$$\mathbf{F}(\lambda, u, v) = \begin{pmatrix} d_1 u_{xx} + f(\lambda, u, v) \\ d_2 v_{xx} + g(\lambda, u, v) \end{pmatrix}, \tag{3.1}$$

where $\lambda \in \mathbb{R}^+$, and $(u, v) \in X$. Then $\mathbf{F}(\lambda, 0, 0) \equiv (0, 0)$, and from (H₂), the Fréchet derivative $D_{(u,v)}\mathbf{F}(\lambda_0, 0, 0) = L(\lambda_0)$ has a simple eigenvalue 0, with eigenvector $q = (a_n, b_n)^T \cos \frac{n}{\ell}x$ and $a_n, b_n \in \mathbb{R}$, such that $L(\lambda_0)q = 0$. The range \mathcal{R} of $L(\lambda_0)$ is given by $\{(u, v) \in Y: \langle q^*, (u, v) \rangle = 0\}$, where q^* is the eigenvector corresponding to eigenvalue 0 of $L^*(\lambda_0)$, the adjoint operator of $L(\lambda_0)$, $\langle q, q^* \rangle = 1$, and $Y = L^2(0, \ell\pi) \times L^2(0, \ell\pi)$. Hence \mathcal{R} is codimension-one in Y . Finally we claim that $D_{\lambda(u,v)}\mathbf{F}(\lambda_0, 0, 0)q \notin \mathcal{R}$ from (H₂). Indeed, let $q(\lambda)$ be a differentiable family of eigenvectors associated with $\gamma(\lambda)$ such that $q(\lambda_0) = q$, and differentiating $L(\lambda)q(\lambda) = \gamma(\lambda)q(\lambda)$ with respect to λ , we obtain $L'(\lambda_0)q + L(\lambda_0)q'(\lambda_0) = \gamma'(\lambda_0)q$, and $\langle L'(\lambda_0)q, q^* \rangle = \gamma'(\lambda_0)\langle q, q^* \rangle = \gamma'(\lambda_0) \neq 0$. Hence $D_{\lambda(u,v)}\mathbf{F}(\lambda_0, 0, 0)q = L'(\lambda_0)q \notin \mathcal{R}$.

Thus we are in the position to apply a well-known abstract bifurcation theorem of Crandall and Rabinowitz [6]. In fact, we will use a strengthened form of their classical theorem by Pejsachowicz and Rabier [36] which also generalizes the global bifurcation theorem of Rabinowitz [39]. The following result is from Shi and Wang [44] (here $\mathcal{N}(L)$ and $\mathcal{R}(L)$ are the null space and range space respectively):

Theorem 3.1. Let X, Y be Banach spaces, let V be an open connected subset of $\mathbb{R} \times X$ and $(\lambda_0, u_0) \in V$, and let \mathbf{F} be a continuously differentiable mapping from V into Y . Suppose that:

1. $\mathbf{F}(\lambda, u_0) = 0$ for $(\lambda, u_0) \in V$.
2. The partial derivative $D_{\lambda u}\mathbf{F}(\lambda, u_0)$ exists and is continuous in λ near λ_0 .

3. $D_u \mathbf{F}(\lambda_0, u_0)$ is a Fredholm operator with index 0, and $\dim \mathcal{N}(D_u \mathbf{F}(\lambda_0, u_0)) = 1$.
4. $D_{\lambda u} \mathbf{F}(\lambda_0, u_0)[w_0] \notin \mathcal{R}(D_u \mathbf{F}(\lambda_0, u_0))$, where $w_0 \in X$ spans $\mathcal{N}(D_u \mathbf{F}(\lambda_0, u_0))$.

Let Z be any complement of $\text{span}\{w_0\}$ in X . Then there exist an open interval $I_1 = (-\epsilon, \epsilon)$ and continuous functions $\lambda : I_1 \rightarrow \mathbf{R}, \psi : I_1 \rightarrow Z$, such that $\lambda(0) = \lambda_0, \psi(0) = 0$, and, if $u(s) = u_0 + s w_0 + s \psi(s)$ for $s \in I_1$, then $\mathbf{F}(\lambda(s), u(s)) = 0$. Moreover:

1. $\mathbf{F}^{-1}(\{0\})$ near (λ_0, u_0) consists precisely of the curves $u = u_0$ and $\Gamma = \{(\lambda(s), u(s)) : s \in I_1\}$.
2. If in addition, $D_u \mathbf{F}(\lambda, u)$ is a Fredholm operator for all $(\lambda, u) \in V$, then the curve Γ is contained in \mathcal{C} , which is a connected component of \bar{S} where $S = \{(\lambda, u) \in V : \mathbf{F}(\lambda, u) = 0, u \neq u_0\}$; and either \mathcal{C} is not compact in V , or \mathcal{C} contains a point (λ_*, u_0) with $\lambda_* \neq \lambda_0$.
3. If in addition \mathbf{F} is C^k with $k \geq 2$, then the curve Γ is C^{k-1} smooth near (λ_0, u_0) .

The smoothness of the curve of the non-trivial solutions is well known, and it follows from a more general bifurcation theorem of Liu, Shi and Wang [31]. From the results of [44], for \mathbf{F} defined here, $D_{(u,v)} \mathbf{F}(\lambda, u, v)$ is a Fredholm operator for all $(\lambda, u, v) \in \mathbf{R} \times X$. Thus we have the following global bifurcation theorem regarding the steady state bifurcation of (2.1):

Theorem 3.2. *Let I be a closed interval which contains $\lambda_0 \in \mathbf{R}$. Suppose that (H_2) is satisfied at $\lambda = \lambda_0$. Then there is a smooth curve Γ of the steady state solutions of (2.1) bifurcating from $(\lambda_0, 0, 0)$, and Γ is contained in a connected component \mathcal{C} of the set of non-zero steady state solutions of (2.1) in $I \times X$. Either \mathcal{C} is unbounded in $I \times X$, or $\mathcal{C} \cap (\partial I \times X) \neq \emptyset$, or \mathcal{C} contains a further bifurcation point $(\lambda_*, 0, 0)$ with $\lambda_* \neq \lambda_0$ such that 0 is an eigenvalue of $L(\lambda_*)$. More precisely, near $(\lambda_0, 0, 0)$, Γ can be expressed as $\Gamma = \{(\lambda(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$, where $u(s) = s \mathbf{a}_n \cos(nx/\ell) + s \psi_1(s), v(s) = s \mathbf{b}_n \cos(nx/\ell) + s \psi_2(s)$ for $s \in (-\epsilon, \epsilon)$, and $\lambda : (-\epsilon, \epsilon) \rightarrow \mathbf{R}, \psi_1, \psi_2 : (-\epsilon, \epsilon) \rightarrow Z$ are C^1 functions, such that $\lambda(0) = \lambda_0, \psi_1(0) = \psi_2(0) = 0$. Here $Z = Z_1 \times Z_1$, with $Z_1 = \{u \in Y : \int_0^{\ell\pi} u(x) \cos(nx/\ell) dx = 0\}$, and $\mathbf{a}_n, \mathbf{b}_n$ satisfy $L_n(\lambda_0)(\mathbf{a}_n, \mathbf{b}_n)^T = (0, 0)^T$.*

Remark 3.3.

1. The interval I in Theorem 3.2 can be the entire \mathbf{R} , and in that case, the alternative of \mathcal{C} intersects with the boundary is not needed.
2. The theory in [44] also holds for higher-dimensional domain Ω and $X = W^{2,p}(\Omega)$ where $p > 2$. Theorem 3.2 for $p > 2$ is useful when considering the classical solutions and positive solutions. One can choose p large so that $C^\alpha(\bar{\Omega})$ is embedded in $W^{2,p}(\Omega)$ and thus the positive cone X_1 in X has nonempty interior. Then one can apply the bifurcation theorem above in X_1 instead of X , but now another possible alternative is that $\mathcal{C} \cap (I \times \partial X_1) \neq \emptyset$. This fact will be useful in later discussions.

3.2. Steady state bifurcation in diffusive predator–prey system

In this subsection, we consider the steady state bifurcations for predator–prey system (2.36). The non-negative steady state solutions of (2.36) satisfy the semilinear elliptic system:

$$\begin{cases} -d_1 u_{xx} = u \left(1 - \frac{u}{k} \right) - \frac{muv}{1+u}, & x \in (0, \ell\pi), \\ -d_2 v_{xx} = -\theta v + \frac{muv}{1+u}, & x \in (0, \ell\pi), \\ (u_x(x), v_x(x)) = 0, & x = 0, \ell\pi. \end{cases} \tag{3.2}$$

Clearly (3.2) has spatially homogeneous solutions $(0, 0), (k, 0)$ and (λ, v_λ) (defined as in Section 2.2, and exists when $\lambda < k$). Moreover from the results in Section 2.2, $(k, 0)$ is globally asymptotically

stable when $\lambda \geq k$, and (λ, v_λ) is globally asymptotically stable when $\lambda \in [k - 1, k)$. Hence (3.2) has no spatially non-homogeneous steady state solutions when $\lambda \geq k - 1$. We always assume $0 < \lambda < k - 1$ (or equivalently $m > \theta k / (k - 1)$) in the following. To derive some *a priori* estimates for the non-negative solutions of (3.2), we recall the following maximum principle (see [32,38]):

Lemma 3.4. *Let Ω be a bounded Lipschitz domain in \mathbb{R}^n , and let $g \in C(\overline{\Omega} \times \mathbb{R})$. If $z \in W^{1,2}(\Omega)$ is a weak solution of the inequalities*

$$\Delta z + g(x, z) \geq 0 \quad \text{in } \Omega, \quad \partial_\nu z \leq 0 \quad \text{on } \partial\Omega,$$

and if there is a constant K such that $g(x, z) < 0$ for $z > K$, then $z \leq K$ a.e. in Ω .

We have the following *a priori* estimate for the non-negative solutions of (3.2) (similar to Theorem 3.3 in [27]):

Lemma 3.5. *Suppose that $d_1, d_2, m, \theta, \ell > 0, k > 1$, and $(u(x), v(x))$ is a non-negative solution of (3.2). Then either (u, v) is one of constant solutions: $(0, 0)$, $(k, 0)$, or for $x \in [0, \ell\pi]$, $(u(x), v(x))$ satisfies*

$$0 < u(x) < k \quad \text{and} \quad 0 < v(x) < \frac{k(d_2 + \theta d_1)}{\theta d_2}. \tag{3.3}$$

Proof. If there exists $x_0 \in [0, \ell\pi]$ such that $v(x_0) = 0$, then $v(x) \equiv 0$ from strong maximum principle (for example, Theorem 2.10 of [15]), and u satisfies $-d_1 u'' = u(1 - u/k)$, $u'(0) = u'(\ell\pi) = 0$. From the well-known result (for example, Theorem 10.1.6 of [18]), $u \equiv 0$ or $u \equiv k$. Hence if (u, v) is not $(0, 0)$ or $(k, 0)$, then $u(x) > 0$ and $v(x) > 0$ for $x \in [0, \ell\pi]$.

From Lemma 3.4, $u(x) \leq k$ and from the strong maximum principle, $u(x) < k$ for $x \in [0, \ell\pi]$. On the other hand, by adding the two equations in (3.2), we have

$$-(d_1 u + d_2 v)'' \leq \left(1 + \frac{d_1}{d_2} \theta\right) k - \frac{\theta}{d_2} (d_1 u + d_2 v), \tag{3.4}$$

then from Lemma 3.4 and the strong maximum principle,

$$d_1 u + d_2 v < \frac{(d_1 \theta + d_2) k}{\theta}, \tag{3.5}$$

which implies (3.3). \square

We remark that if $d_1 = d_2$, then by using arguments in the proof of Lemma 3.5 and the maximum principle of parabolic equations, one can also prove the solution $(u(x, t), v(x, t))$ of (2.36) satisfies the *a priori* bound:

$$\limsup_{t \rightarrow \infty} u(x, t) \leq k, \quad \limsup_{t \rightarrow \infty} v(x, t) \leq \frac{k(d_2 + \theta d_1)}{d_2 \theta}. \tag{3.6}$$

This implies in that case all the periodic orbits obtained in Theorem 2.4 satisfy the bound in (3.6).

A positive lower bound of steady states is also useful. But such bound cannot be uniform as $\lambda \rightarrow 0$ (or $m \rightarrow \infty$) since $(\lambda, v_\lambda) \rightarrow (0, 0)$ when $m \rightarrow \infty$. From Theorem 2.3, (3.2) has no non-constant solution when $\lambda > k - 1$ or equivalently $m < \theta k / (k - 1)$. Hence we only need to consider the case that $m \geq \theta k / (k - 1)$. For bounded m (or λ away from 0), we have the following result (similar to Theorem 3.4 in [27]):

Lemma 3.6. *Suppose that $d_1, d_2, \theta, \ell > 0$ and $k > 1$ are fixed, $\theta k / (k - 1) \leq m \leq M$ for some $M > 0$. Then there exists a positive constant $\underline{\mathcal{C}}$ depending possibly on $d_1, d_2, \theta, \ell, k$ and M , such that any positive solution $(u(x), v(x))$ of (3.2) satisfies*

$$u(x), v(x) \geq \underline{\mathcal{C}} \quad \text{for any } x \in \overline{\Omega}. \tag{3.7}$$

Proof. From Lemma 3.5, we obtain that for $x \in \overline{\Omega}$,

$$u(x), v(x) \leq \overline{\mathcal{C}} := \max \left\{ k, \frac{(d_1\theta + d_2)k}{\theta} \right\}, \tag{3.8}$$

where $\overline{\mathcal{C}}$ depends on d_1, d_2, k, θ . Let

$$c_1(x) := 1 - \frac{u(x)}{k} - \frac{mv(x)}{1 + u(x)} \quad \text{and} \quad c_2(x) := -\theta + \frac{mu(x)}{1 + u(x)}. \tag{3.9}$$

Then

$$|c_1(x)| \leq 2 + m\overline{\mathcal{C}} \leq 2 + M\overline{\mathcal{C}} \quad \text{and} \quad |c_2(x)| \leq \theta + M. \tag{3.10}$$

From Harnack inequality (see [30,38]), there exists a positive constant C , depending on $M, \theta, \overline{\mathcal{C}}$ and ℓ such that

$$\sup_{\overline{\Omega}} u(x) \leq C \inf_{\overline{\Omega}} u(x), \quad \sup_{\overline{\Omega}} v(x) \leq C \inf_{\overline{\Omega}} v(x). \tag{3.11}$$

Hence it remains to prove that $\sup_{\overline{\Omega}} u(x) > c$ and $\sup_{\overline{\Omega}} v(x) > c$ for some $c > 0$, which is independent of choice of solution. Suppose this is not true. Then there exists a sequence of positive solutions (u_n, v_n) (with $m = m_n \geq \theta k / (k - 1)$) such that $\sup_{\overline{\Omega}} u_n(x) \rightarrow 0$ or $\sup_{\overline{\Omega}} v_n(x) \rightarrow 0$ as $n \rightarrow \infty$. From elliptic regularity theory, there exists a subsequence of (m_n, u_n, v_n) , which we still denote by (m_n, u_n, v_n) , such that $m_n \rightarrow m_\infty, u_n \rightarrow u_\infty$ and $v_n \rightarrow v_\infty$ in $C^2(\overline{\Omega})$ as $n \rightarrow \infty$ for some (u_∞, v_∞) . From the assumption, either $u_\infty \equiv 0$ or $v_\infty \equiv 0$, and (u_∞, v_∞) satisfies (3.2) with some $m = m_\infty$ such that $\theta k / (k - 1) \leq m_\infty \leq M$. If $u_\infty \equiv 0$, then for large n , we have $-\theta + m_n u_n / (1 + u_n) < -\theta / 2 < 0$ for any $x \in \overline{\Omega}$. But integrating the equation of v_n , we obtain

$$\int_0^{\ell\pi} v_n \left(-\theta + \frac{m_n u_n}{1 + u_n} \right) dx = 0, \tag{3.12}$$

that is a contradiction. Hence $u_\infty \not\equiv 0$ and $v_\infty \equiv 0$, which implies that u_∞ satisfies $-d_1 u'' = u(1 - u/k), u'(0) = u'(\ell\pi) = 0$. So $u_\infty \equiv k$, and for large n , we have $-\theta + m_n u_n / (1 + u_n) > \varepsilon > 0$ since $\theta k / (k - 1) \leq m_\infty$. This again contradicts with (3.12). Therefore $\sup_{\overline{\Omega}} u(x) > 0$ and $\sup_{\overline{\Omega}} v(x) > 0$, and consequently (3.7) holds. \square

Now we start the bifurcation analysis. Consider the non-zero solutions of

$$\begin{cases} -d_1 u_{xx} = (u + \lambda) \left(1 - \frac{u + \lambda}{k} \right) - \frac{m(u + \lambda)(v + v_\lambda)}{1 + u + \lambda}, & x \in (0, \ell\pi), \\ -d_2 v_{xx} = -\theta(v + v_\lambda) + \frac{m(u + \lambda)(v + v_\lambda)}{1 + u + \lambda}, & x \in (0, \ell\pi), \\ u_x(0) = v_x(0) = u_x(\ell\pi) = v_x(\ell\pi) = 0. \end{cases} \tag{3.13}$$

Here again we use the translation $\hat{u} = u - \lambda$ and $\hat{v} = v - v_\lambda$, and with (3.13) we are in the setting of Section 3.1 with $f(\lambda, u, v)$ and $g(\lambda, u, v)$ the same as the ones in (2.53).

We identify steady state bifurcation values λ_0 which satisfy the steady state bifurcation condition (H_2) , which is: there exists $n \in \mathbb{N}_0$ such that

$$D_n(\lambda_0) = 0, \quad T_n(\lambda_0) \neq 0, \quad \text{and} \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0 \quad \text{for } j \neq n; \tag{3.14}$$

and

$$\frac{d}{d\lambda} D_n(\lambda_0) \neq 0. \tag{3.15}$$

Notice that (3.15) is equivalent to $\gamma'(\lambda_0) \neq 0$ in (H_2) . Again from (2.40), $T_n(\lambda) \leq 0$ and $D_n(\lambda) > 0$ for $\lambda \in [\lambda_0^H, k - 1)$. So any potential bifurcation point λ_0 must be in the interval $(0, \lambda_0^H)$. Then the determination of steady state bifurcation points reduces to describing the set

$$\Lambda_2 := \{ \lambda \in (0, \lambda_0^H) : \text{for some } n \in \mathbb{N}, (3.14) \text{ and } (3.15) \text{ are satisfied} \}, \tag{3.16}$$

when a set of parameters $(\ell, d_1, d_2, \theta, k)$ is given.

To determine Λ_2 , we rewrite $D_n(\lambda)$ as $D_n(\lambda) = \theta C(\lambda) - d_2 A(\lambda)p + d_1 d_2 p^2$, where $p = n^2/\ell^2$. Solving p from $D_n(\lambda) = 0$, we have

$$p = p_\pm(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{d_2^2 A(\lambda)^2 - 4d_1 d_2 \theta C(\lambda)}}{2d_1 d_2}, \tag{3.17}$$

or equivalently,

$$p = p_\pm(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{C(\lambda)(d_2^2 h(\lambda) - 4d_1 d_2 \theta)}}{2d_1 d_2},$$

where $h(\lambda) := \frac{A(\lambda)^2}{C(\lambda)} = \frac{\lambda^2(k-1-2\lambda)^2}{k(1+\lambda)(k-\lambda)}$. We have the following basic property of the function $h(\lambda)$.

Lemma 3.7. *For all $\lambda \in (0, \lambda_0^H)$, $h(\lambda) > 0$, $h(0) = h(\lambda_0^H) = 0$, and there exists a unique $\lambda^\# \in (0, \lambda_0^H)$, such that $h'(\lambda^\#) = 0$, $h'(\lambda) > 0$ in $(0, \lambda^\#)$ and $h'(\lambda) < 0$ in $(\lambda^\#, \lambda_0^H)$.*

Proof. Clearly, $h(0) = h(\lambda_0^H) = 0$, and $h(\lambda) > 0$ in $(0, \lambda_0^H)$. By direct calculation, it follows that

$$h'(\lambda) = \frac{\lambda(k-1-2\lambda)}{k(1+\lambda)^2(k-\lambda)^2} g(\lambda), \tag{3.18}$$

where $g(\lambda) = 4\lambda^3 - 6(k-1)\lambda^2 + (k^2 - 10k + 1)\lambda + 2k(k-1)$. Since $g(0) = 2k(k-1) > 0$ and $g(\lambda_0^H) = -\lambda_0^H(k+1)^2 < 0$, there exists at least one root of $g(\lambda) = 0$ in $(0, \lambda_0^H)$. If g has more than one root in $(0, \lambda_0^H)$, then g must have exactly three roots in $(0, \lambda_0^H)$ counting multiplicity. Denote these three roots by λ^1, λ^2 and λ^3 , then $\lambda^1 \lambda^2 \lambda^3 = -k(k-1)/2 < 0$ since $k > 1$, which is a contradiction. Hence in $(0, \lambda_0^H)$, $h(\lambda) = 0$ has a unique critical point $\lambda^\#$, where $h(\lambda)$ attains its maximal value. \square

Thus, if $d_1/d_2 > h(\lambda^\#)/(4\theta)$, $D_n(\lambda) > 0$ for all possible $n \in \mathbb{N}_0$, and no steady state bifurcation could occur. If $d_1/d_2 < h(\lambda^\#)/(4\theta)$, then from Lemma 3.7, there exist $\underline{\lambda} < \bar{\lambda} \in (0, \lambda_0^H)$, such that $h(\underline{\lambda})/(4\theta) = h(\bar{\lambda})/(4\theta) = d_1/d_2$. For all $\lambda \in [0, \underline{\lambda}) \cup (\bar{\lambda}, \lambda_0^H)$, $D_n(\lambda) > 0$, there is no steady state bifurcation occurring. Thus Λ_2 is empty if $d_1/d_2 > h(\lambda^\#)/(4\theta)$ holds; and in order for Λ_2 to be a nonempty subset of $[\underline{\lambda}, \bar{\lambda}]$

we need $d_1/d_2 < h(\lambda^\#)/(4\theta)$. On the other hand, $D_n(\lambda) > 0$ implies that Hopf bifurcation occurs at $\lambda_{j,\pm}^H$ defined in Section 2.2. We have the following strengthened version of Theorem 2.4:

Theorem 3.8. *Suppose that the constants $d_1, d_2, m, \theta > 0$ and $k > 1$, ℓ_n are defined as in (2.47), and $\lambda_{j,\pm}^H$ are defined as in Section 2.2. Define*

$$h(\lambda) := \frac{A(\lambda)^2}{C(\lambda)} = \frac{\lambda^2(k-1-2\lambda)^2}{k(1+\lambda)(k-\lambda)}. \tag{3.19}$$

1. If

$$\frac{d_1}{d_2} > \frac{h(\lambda^\#)}{4\theta}, \tag{3.20}$$

then the system (2.36) undergoes a Hopf bifurcation at $\lambda = \lambda_{j,\pm}^H$, and there is no steady state bifurcation along the curve $\{(\lambda, v_\lambda) : 0 < \lambda < \lambda_0^H\}$.

2. If

$$\frac{d_1}{d_2} < \frac{h(\lambda^\#)}{4\theta} \tag{3.21}$$

and $\lambda_{j,\pm}^H \notin [\underline{\lambda}, \bar{\lambda}]$, where $0 < \underline{\lambda} < \bar{\lambda}$ are the only two roots of $h(\lambda) = 4\theta d_1/d_2$ in $(0, \lambda_0^H)$, then the system (2.36) undergoes a Hopf bifurcation at $\lambda = \lambda_{j,\pm}^H \notin [\underline{\lambda}, \bar{\lambda}]$.

It is easy to verify that (2.50) implies (3.20), but the algebraic expression of $h(\lambda^\#)$ is cumbersome to be stated here while (2.50) is more explicit.

Next we assume that (3.21) holds and investigate the steady state bifurcations, and the interaction between the Hopf bifurcation and steady state bifurcation. The following lemma describes the basic properties of $p_\pm(\lambda)$, defined in $[\underline{\lambda}, \bar{\lambda}]$. The proof of the lemma is elementary but long, so we postpone it to Appendix B.

Lemma 3.9. *Suppose that the constants $d_1, d_2, \theta > 0$ and $k > 1$ satisfy (3.21), then there exists a $\lambda_c \in (\underline{\lambda}, \lambda^\#)$, such that $p_+(\lambda)$ is increasing in $(\underline{\lambda}, \lambda_c)$, and is decreasing in $(\lambda_c, \bar{\lambda})$; and there exists a further $\lambda'_c \in (\lambda_c, \bar{\lambda})$, such that $p_-(\lambda)$ is decreasing in $(\underline{\lambda}, \lambda'_c)$, and is increasing in $(\lambda'_c, \bar{\lambda})$; $0 < p_-(\lambda'_c) < p_+(\lambda_c) < \infty$; $p_+(\underline{\lambda}) = p_-(\underline{\lambda})$ and $p_+(\bar{\lambda}) = p_-(\bar{\lambda})$; moreover*

$$\lim_{\lambda \rightarrow \underline{\lambda}} p'_+(\lambda) = +\infty, \quad \lim_{\lambda \rightarrow \bar{\lambda}} p'_+(\lambda) = -\infty, \quad \lim_{\lambda \rightarrow \underline{\lambda}} p'_-(\lambda) = -\infty, \quad \lim_{\lambda \rightarrow \bar{\lambda}} p'_-(\lambda) = +\infty. \tag{3.22}$$

From Lemma 3.9, the graph $(\lambda, p_\pm(\lambda))$ forms a closed loop in \mathbb{R}^2 with only four critical points, see Figs. 1–3 for some examples. We define $p_+ := p_+(\lambda_c)$ and $p_- := p_-(\lambda'_c)$. From the properties of $p_\pm(\lambda)$ listed in Lemma 3.9, if $p_- < n^2/\ell^2 < p_+$, then there exist $\lambda_{n,\pm}^S \in [\underline{\lambda}, \bar{\lambda}]$, such that $\underline{\lambda} < \lambda_{n,-}^S < \lambda_{n,+}^S < \bar{\lambda}$, $p_\pm(\lambda_{n,\pm}^S) = n^2/\ell^2$ and thus $D_n(\lambda_{n,\pm}^S) = 0$. Define $\tilde{\ell}_{n,\pm} = n/\sqrt{p_\pm}$, then for any $\ell \in (\tilde{\ell}_{n,+}, \tilde{\ell}_{n,-})$, there exist $\lambda_{n,\pm}^S$ such that $D_n(\lambda_{n,\pm}^S) = 0$.

These points $\lambda_{n,\pm}^S$ are potential steady state bifurcation points. But it is possible that for some $i < j$, $p_-(\lambda_{i,-}^S) = p_+(\lambda_{j,-}^S)$ or $p_-(\lambda_{i,+}^S) = p_+(\lambda_{j,+}^S)$. In this case, for $\lambda = \lambda_{i,-}^S = \lambda_{j,-}^S$, 0 is not a simple eigenvalue of $L(\lambda)$, and we shall not consider bifurcations at such points. We notice that, from the properties of $p_\pm(\lambda)$ in Lemma 3.9, the multiplicity of 0 as eigenvalue of $L(\lambda)$ is at most 2. On the other hand, it is also possible that some $\lambda_{i,\pm}^S = \lambda_{j,\pm}^H$. So the dimension of center manifold of the equilibrium (λ, v_λ) can be as high as 4.

We claim that there are only countably many $\ell > 0$, in fact only finitely many $\ell \in (0, M)$ for any given $M > 0$, such that $\lambda = \lambda_{i,-}^S = \lambda_{j,-}^S$ or $\lambda_{i,\pm}^S = \lambda_{j,\pm}^H$ for these ℓ and some $i, j \in \mathbb{N}$. Let $E_n(\lambda, \ell) = k\ell^4(1 + \lambda)D_n(\lambda)$ and $F_n(\lambda, \ell) = k\ell^2(1 + \lambda)T_n(\lambda)$. Then for any $n \in \mathbb{N}$, $E_n(\lambda, \ell)$ and $F_n(\lambda, \ell)$ are polynomials of λ and ℓ with real coefficients. Hence on (λ, ℓ) -plane, the set $q_n = \{(\lambda, \ell): E_n(\lambda, \ell) = 0\}$ or $p_n = \{(\lambda, \ell): F_n(\lambda, \ell) = 0\}$ is the union of countably many analytic curves. Moreover, we require $\lambda \in [\underline{\lambda}, \bar{\lambda}]$, so for any $M > 0$, there are only finitely many $i, j \in \mathbb{N}$ such that $q_i \cap ([\underline{\lambda}, \bar{\lambda}] \times [0, M]) \neq \emptyset$ and $p_j \cap ([\underline{\lambda}, \bar{\lambda}] \times [0, M]) \neq \emptyset$, and these finitely many q_i, p_j only have finitely many intersection points in $[\underline{\lambda}, \bar{\lambda}] \times [0, M]$ due to the analyticity, and thus the intersection points of different q_i, p_j in $[\underline{\lambda}, \bar{\lambda}] \times [0, \infty)$ are countable. We define

$$L^E = \{\ell > 0: E_i(\lambda, \ell) = E_j(\lambda, \ell) \text{ or } E_i(\lambda, \ell) = F_j(\lambda, \ell) \text{ for some } \lambda \in [\underline{\lambda}, \bar{\lambda}], \text{ and } i, j \in \mathbb{N}\}.$$

Then the points in L^E can be arranged as a sequence whose only limit point is ∞ .

So for bifurcation from simple eigenvalue to occur, we assume that $\ell \in \mathbb{R} \setminus L^E$, and we consider the corresponding possible bifurcation points $\lambda_{n,\pm}^S$. Now we only need to verify whether $\frac{d}{d\lambda} D_n(\lambda_{n,\pm}^S) \neq 0$. We claim that whenever $\lambda_{n,-}^S \neq \underline{\lambda}$ and $\lambda_{n,+}^S \neq \bar{\lambda}$, then $\frac{d}{d\lambda} D_n(\lambda_{n,\pm}^S) \neq 0$ holds. Suppose that $\frac{d}{d\lambda} D_n(\lambda_{n,-}^S) = 0$. Since $D_n(\lambda_{n,-}^S) = 0$, we have $p_+(\lambda_{n,-}^S) = n^2/\ell^2$, or $p_-(\lambda_{n,-}^S) = n^2/\ell^2$. By (2.40), $\lambda_{n,-}^S$ satisfies

$$\frac{\theta C'(\lambda)}{d_2 A'(\lambda)} = \frac{\theta(k+1)}{d_2(2\lambda^2 + 4\lambda + 1 - k)} = \frac{n^2}{\ell^2} = p_+(\lambda) \quad (\text{or } p_-(\lambda)). \tag{3.23}$$

By differentiating $D_n(\lambda)|_{p=p_+(\lambda)} = 0$ with respect to λ , we obtain that

$$\theta C'(\lambda) - d_2 A'(\lambda)p_+(\lambda) - d_2 A(\lambda)p'_+(\lambda) + 2d_1 d_2 p_+(\lambda)p'_+(\lambda) = 0. \tag{3.24}$$

Substituting (3.23) into (3.24), we obtain that

$$(2d_1 d_2 p_+(\lambda_{n,-}^S) - d_2 A(\lambda_{n,-}^S))p'_+(\lambda_{n,-}^S) = 0,$$

or

$$(2d_1 d_2 p_-(\lambda_{n,-}^S) - d_2 A(\lambda_{n,-}^S))p'_-(\lambda_{n,-}^S) = 0.$$

Since $\ell \in (\tilde{\ell}_{n,+}, \tilde{\ell}_{n,-})$, we have $p'_\pm(\lambda_{n,-}^S) \neq 0$. Thus, $2d_1 d_2 p_-(\lambda_{n,-}^S) - d_2 A(\lambda_{n,-}^S) = 0$ or $2d_1 d_2 p_+(\lambda_{n,-}^S) - d_2 A(\lambda_{n,-}^S) = 0$. Then by the definition of $\lambda_{n,-}^S$ and (3.17), we have $\lambda_{n,-}^S = \underline{\lambda}$. Likewise, if $\frac{d}{d\lambda} D_n(\lambda_{n,+}^S) = 0$, we have $\lambda_{n,+}^S = \bar{\lambda}$. Thus the claim holds.

Summarizing the preparation above, we are now ready to state the main result of this subsection on the global bifurcation of steady state solutions:

Theorem 3.10. *Suppose that the constants $d_1, d_2, m, \theta > 0$ and $k > 1$ satisfy (3.21), $p_\pm(\lambda)$ are defined as in (3.17) and*

$$\tilde{\ell}_{n,+} := \frac{n}{\sqrt{\max p_+(\lambda)}}, \quad \tilde{\ell}_{n,-} := \frac{n}{\sqrt{\min p_-(\lambda)}}.$$

If for some $n \in \mathbb{N}$, $\ell \in (\tilde{\ell}_{n,+}, \tilde{\ell}_{n,-}) \setminus L^E$, there exist exactly two points $\lambda_{n,\pm}^S \in (\underline{\lambda}, \bar{\lambda})$, with $\lambda_{n,-}^S < \lambda_{n,+}^S$ such that $p_\pm(\lambda_{n,\pm}^S) = n^2/\ell^2$. Then there is a smooth curve $\Gamma_{n,\pm}$ of positive solutions of (3.2) bifurcating from $(\lambda, u, v) = (\lambda_{n,\pm}^S, \lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S})$, with $\Gamma_{n,\pm}$ contained in a global branch $C_{n,\pm}$ of the positive solutions of (3.2). Moreover:

1. Near $(\lambda, u, v) = (\lambda_{n,\pm}^S, \lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S})$, $\Gamma_{n,\pm} = \{(\lambda(s), u(s), v(s)): s \in (-\epsilon, \epsilon)\}$, where $u(s) = \lambda_{n,\pm}^S + \mathbf{a}_n \cos(nx/\ell) + s\psi_1(s)$, $v(s) = v_{\lambda_{n,\pm}^S} + s\mathbf{b}_n \cos(nx/\ell) + s\psi_2(s)$ for $s \in (-\epsilon, \epsilon)$ for some C^∞ smooth functions λ, ϕ_1, ψ_2 such that $\lambda(0) = \lambda_{n,\pm}^S$ and $\psi_1(0) = \psi_2(0) = 0$. Here \mathbf{a}_n and \mathbf{b}_n satisfy $L_n(\lambda_0)(\mathbf{a}_n, \mathbf{b}_n)^T = (0, 0)^T$, with $\lambda_0 = \lambda_{n,+}^S$ or $\lambda_0 = \lambda_{n,-}^S$.
2. Either $C_{n,\pm}$ contains another $(\lambda_{j,\pm}^S, \lambda_{j,\pm}^S, v_{\lambda_{j,\pm}^S})$, or the projection of $C_{n,\pm}$ onto λ -axis contains the interval $(0, \lambda_{j,\pm}^S)$.

Proof. From the discussion above, if at $\lambda = \lambda_{n,\pm}^S$ the conditions in the theorem are satisfied, then $\lambda_{n,\pm}^S \in \Lambda_2$, and one can apply Theorem 3.2. For the global bifurcation, we use the interval $\lambda \in (0, k - 1)$. Here we use parameter m instead of λ , then $m \in (\theta k / (k - 1), \infty)$. From Lemma 3.5, any positive solution of (3.2) is bounded in L^∞ with bound independent of m . From Lemma 3.6, if $m \leq M$, then all positive solutions of (3.2) are uniformly bounded in X . Hence the global branch $C_{n,\pm}$ is bounded in X if $m \leq M$. The solutions near bifurcation points are apparently positive. We also claim that any solution on $C_{n,\pm}$ is positive. In fact, if this is not true, then from Lemma 3.5, $C_{n,\pm}$ contains either $(0, 0)$ or $(k, 0)$. However from linearization around $(0, 0)$ or $(k, 0)$, any solutions bifurcating from $(u, v) = (0, 0)$ or $(k, 0)$ are not positive near bifurcation points, and hence the positive solution branches cannot be connected to $(0, 0)$ or $(k, 0)$. Finally from discussion earlier, there are no positive solutions of (3.2) when $\lambda \geq k - 1$ other than the constant ones. Hence $C_{n,\pm}$ cannot intersect the boundary $\{\lambda = k - 1\} \times X$. Therefore, either $C_{n,\pm}$ contains another $(\lambda_{j,\pm}^S, \lambda_{j,\pm}^S, v_{\lambda_{j,\pm}^S})$, or the projection of $C_{n,\pm}$ onto λ -axis contains the interval $(0, \lambda_{j,\pm}^S)$. \square

Remark 3.11.

1. $\tilde{\ell}_{1,+} = (1/p_+)^{1/2}$ is a minimal spatial size for the system (2.36) to have a steady state bifurcation.
2. Theorem 3.10 shows that each bifurcating branch is either a loop connecting two bifurcation points or a branch consisting solutions for all large m . Possibility of latter case will need a further understanding of solutions of (3.2) as $m \rightarrow \infty$.
3. The existence of multiple bifurcation points does not imply existence of non-homogeneous steady states for all $\lambda \in (\lambda_{j,-}^S, \lambda_{j,+}^S)$. However a degree theory argument similar to the ones in [27,37, 38] could be used to prove the existence of spatially non-homogeneous steady states for some values of λ based on our analysis. Here we only sketch the idea but omit the details: Suppose the conditions in Theorem 3.10 are satisfied. Then the steady state bifurcation points in $(\underline{\lambda}, \bar{\lambda})$ can be ordered and relabeled as $\underline{\lambda} < \tilde{\lambda}_1 < \tilde{\lambda}_2 < \dots < \tilde{\lambda}_{2k} < \bar{\lambda}$. At each bifurcation point, the index of (λ, v_λ) changes by 1 from our assumption. Then from degree counting and the *a priori* estimates in Lemma 3.6, there exists at least one non-homogeneous solution of (3.2) when $\lambda \in (\tilde{\lambda}_{2i-1}, \tilde{\lambda}_{2i})$ with $i = 1, 2, \dots, k$.

Finally we discuss the interaction between the Hopf and steady state bifurcations. A set of possible Hopf bifurcation points $\lambda_{j,\pm}^H$ is identified in Section 2.2, and similarly a set of possible steady state bifurcation points $\lambda_{j,\pm}^S$ is identified in this subsection. For a countable set of exceptional values $\ell \in L^E$, $\lambda_{j,\pm}^H$ and $\lambda_{j,\pm}^S$ can be identical for some i, j , so that (2.36) has a higher-dimensional center manifold near (λ, v_λ) at such λ . Bifurcations from these points with higher-dimensional degeneracy are still possible, but we do not consider them here. For other $\ell \notin L^E$ satisfying $\ell > \max\{\ell_1, \tilde{\ell}_{1,+}\}$, we have shown that with some necessary transversality conditions, Hopf bifurcations or steady state bifurcations could occur at these points (see Theorems 2.4, 3.8 and 3.10). In fact the occurrence of bifurcation depends only on the specific eigen-mode $\cos(nx/\ell)$, and the bifurcation related to this mode has the following possible scenarios (here we assume that $d_1, d_2, \theta > 0$ and $k > 1$ are given, $\ell \notin L^E$, $\ell > \max\{\ell_1, \tilde{\ell}_{1,+}\}$, and all transversality conditions are met):

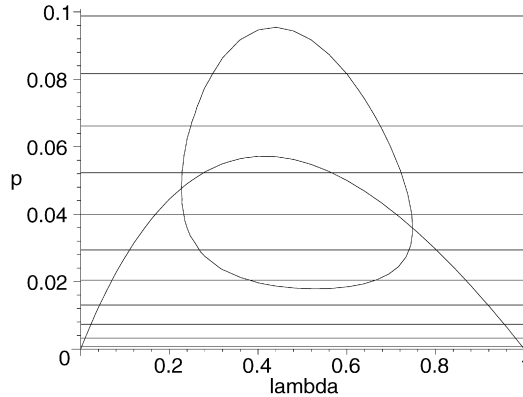


Fig. 1. Graph of $T(\lambda, p)$ and $D(\lambda, p)$. Here $d_1 = d_2 = 1, k = 3, \theta = 0.003$. The horizontal lines are $p = n^2/\ell^2$ where $1 \leq n \leq 11$ and $\ell = 35$.

- (Case 1) Neither of $\lambda_{n,\pm}^H$ and $\lambda_{n,\pm}^S$ exist, then there is no bifurcation for this mode.
- (Case 2) $\lambda_{n,\pm}^H$ exist but not $\lambda_{n,\pm}^S$, then there are two Hopf bifurcations and no steady state bifurcations for this eigen-mode.
- (Case 3) $\lambda_{n,\pm}^S$ exist but not $\lambda_{n,\pm}^H$, then there are two steady state bifurcations and no Hopf bifurcations for this eigen-mode.
- (Case 4) Both of $\lambda_{n,\pm}^H$ and $\lambda_{n,\pm}^S$ exist, then:
 - (a) if $\lambda_{n,-}^S < \lambda_{n,+}^S < \lambda_{n,-}^H < \lambda_{n,+}^H$ or $\lambda_{n,-}^H < \lambda_{n,+}^H < \lambda_{n,-}^S < \lambda_{n,+}^S$, then there are two steady state bifurcations and two Hopf bifurcations;
 - (b) if $\lambda_{n,-}^S < \lambda_{n,-}^H < \lambda_{n,+}^H < \lambda_{n,+}^S$, then there are two steady state bifurcations but no Hopf bifurcations as $D_n(\lambda) < 0$ at $\lambda = \lambda_{n,+}^H$;
 - (c) if $\lambda_{n,-}^H < \lambda_{n,-}^S < \lambda_{n,+}^S < \lambda_{n,+}^H$, then there are two steady state bifurcations and two Hopf bifurcations;
 - (d) if $\lambda_{n,-}^H < \lambda_{n,-}^S < \lambda_{n,+}^H < \lambda_{n,+}^S$, then there are two steady state bifurcations and one Hopf bifurcation (at $\lambda_{n,-}^H$), and there is no Hopf bifurcation at $\lambda = \lambda_{n,+}^H$ since $D_n(\lambda_{n,+}^H) < 0$;
 - (e) if $\lambda_{n,-}^S < \lambda_{n,-}^H < \lambda_{n,+}^S < \lambda_{n,+}^H$, then there are two steady state bifurcations and one Hopf bifurcation (at $\lambda_{n,+}^H$), and there is no Hopf bifurcation at $\lambda = \lambda_{n,-}^H$ since $D_n(\lambda_{n,-}^H) < 0$.

We remark that all these scenarios are possible by modifying parameters d_1, d_2, θ, k and ℓ . Given the parameters (d_1, d_2, θ, k) , the bifurcation points are essentially determined by the graphs of $p = A(\lambda)/(d_1 + d_2)$ and $p = p_{\pm}(\lambda)$, where $p = n^2/\ell^2$. We illustrate these different possibilities by some examples. In the following, we use $T(\lambda, p) := A(\lambda) - (d_1 + d_2)p = 0$ and $D(\lambda, p) := \theta C(\lambda) - d_2 A(\lambda)p + d_1 d_2 p^2 = 0$. We show the graph of $D = 0$ can be contained in that of $T = 0$, can intersect $T = 0$, and can be above $T = 0$.

Example 3.12. In Fig. 1, for $1 \leq n \leq 4$, Case 2 occurs, and there exist 8 Hopf bifurcation points but no steady state bifurcation points. More precisely, $\lambda_{1,-}^H \approx 0.0026 < \lambda_{2,-}^H \approx 0.0098 < \lambda_{3,-}^H \approx 0.0231 < \lambda_{4,-}^H \approx 0.0428 < 0.1$, and $0.9 < \lambda_{4,+}^H \approx 0.9180 < \lambda_{3,+}^H \approx 0.9549 < \lambda_{2,+}^H \approx 0.9804 < \lambda_{1,+}^H \approx 0.9950 < 1$. For $5 \leq n \leq 6$, Case 4(c) occurs, and there exist 4 Hopf bifurcation points and 4 steady state bifurcation points. More precisely, $\lambda_{5,-}^S \approx 0.0706 < \lambda_{5,-}^S \approx 0.3772 < \lambda_{5,+}^S \approx 0.6656 < \lambda_{5,+}^S \approx 0.8682 < 0.9$ and $\lambda_{6,-}^H \approx 0.1099 < \lambda_{6,-}^S \approx 0.2662 < \lambda_{6,+}^S \approx 0.7407 < \lambda_{6,+}^H \approx 0.8019 < 0.9$. For $n = 7$, Case 4(d) occurs, there exist 2 steady state bifurcation points $\lambda_{7,-}^S \approx 0.2311$ and $\lambda_{7,+}^S \approx 0.7463 < 0.9$ and only one Hopf bifurcation at $\lambda_{7,-}^H \approx 0.1867$, but not at $\lambda_{7,+}^H \approx 0.7113$, since $D_7(\lambda_{7,+}^H) < 0$. For $n = 8$, Case 4(b) occurs, and there are only 2 steady state bifurcation points $\lambda_{8,-}^S \approx 0.2276$ and $\lambda_{8,+}^S \approx 0.7227$ and no Hopf bifurcation points, since $D_8(\lambda_{8,\pm}^H) < 0$. For $9 \leq n \leq 10$, Case 3 occurs, and there exist 4 steady state

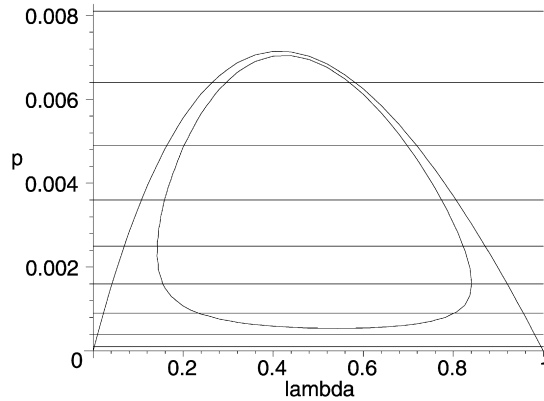


Fig. 2. Graph of $T(\lambda, p)$ and $D(\lambda, p)$. Here $d_1 = 15, d_2 = 1, k = 3, \theta = 0.0001$. The horizontal lines are $p = n^2/\ell^2$ where $1 \leq n \leq 9$ and $\ell = 100$.

bifurcation points $\lambda_{9,-}^S \approx 0.1629 < \lambda_{10,-}^S \approx 0.2959 < \lambda_{10,+}^S \approx 0.5999 < \lambda_{9,+}^S \approx 0.7978$, but no Hopf bifurcation points. For $n \geq 11$, Case 1 occurs, and there is no bifurcation points.

Example 3.13. In Fig. 2, for $n = 1, 2$, Case 2 occurs, and there exist 4 Hopf bifurcation points but no steady state bifurcations. More precisely, $0 < \lambda_{1,-}^H \approx 0.0024 < \lambda_{2,-}^H \approx 0.0098 < 0.1$, and $0.9 < \lambda_{2,+}^H \approx 0.9806 < \lambda_{1,+}^H \approx 0.9952 < 1$. For $3 \leq n \leq 8$, Case 4(c) occurs, and we have

$$\lambda_{3,-}^H < \lambda_{4,-}^H < \lambda_{5,-}^H < \lambda_{6,-}^H < \lambda_{5,-}^S < \lambda_{4,-}^S < \lambda_{6,-}^S < \lambda_{7,-}^H < \lambda_{7,-}^S < \lambda_{3,-}^S < \lambda_{8,-}^H < \lambda_{8,-}^S < \lambda_{8,+}^S < \lambda_{8,+}^H < \lambda_{7,+}^S < \lambda_{7,+}^H < \lambda_{6,+}^S < \lambda_{6,+}^H < \lambda_{5,+}^S < \lambda_{5,+}^H < \lambda_{4,+}^S < \lambda_{4,+}^H < \lambda_{3,+}^H < \lambda_{3,+}^S,$$

where

$$\begin{aligned} \lambda_{3,-}^H &\approx 0.0224, & \lambda_{3,+}^H &\approx 0.9560, & \lambda_{4,-}^H &\approx 0.0418, & \lambda_{4,+}^H &\approx 0.9198, \\ \lambda_{5,-}^H &\approx 0.0689, & \lambda_{5,+}^H &\approx 0.8711, & \lambda_{6,-}^H &\approx 0.1072, & \lambda_{6,+}^H &\approx 0.8064, \\ \lambda_{7,-}^H &\approx 0.1636, & \lambda_{7,+}^H &\approx 0.7188, & \lambda_{8,-}^H &\approx 0.2635, & \lambda_{8,+}^H &\approx 0.5829, \\ \lambda_{3,-}^S &\approx 0.2329, & \lambda_{3,+}^S &\approx 0.8023, & \lambda_{4,-}^S &\approx 0.1542, & \lambda_{4,+}^S &\approx 0.8409, \\ \lambda_{5,-}^S &\approx 0.1413, & \lambda_{5,+}^S &\approx 0.8223, & \lambda_{6,-}^S &\approx 0.1583, & \lambda_{6,+}^S &\approx 0.7745, \\ \lambda_{7,-}^S &\approx 0.2017, & \lambda_{7,+}^S &\approx 0.6982, & \lambda_{8,-}^S &\approx 0.2936, & \lambda_{8,+}^S &\approx 0.5701. \end{aligned}$$

Thus there exist 12 Hopf bifurcation points and 12 steady state bifurcation points for the modes $3 \leq n \leq 8$. There is no bifurcation for $n \geq 9$.

Example 3.14. In Fig. 3, for $1 \leq n \leq 5$, Case 2 occurs, there are 10 Hopf bifurcation points but no steady state bifurcation points. More precisely, $0 < \lambda_{1,-}^H \approx 0.0050 < \lambda_{2,-}^H \approx 0.0209 < \lambda_{3,-}^H \approx 0.0497 < \lambda_{4,-}^H \approx 0.0972 < \lambda_{5,-}^H \approx 0.1798 < 0.2$ and $0.6 < \lambda_{5,+}^H \approx 0.6952 < \lambda_{4,+}^H \approx 0.8228 < \lambda_{3,+}^H \approx 0.9053 < \lambda_{2,+}^H \approx 0.9591 < \lambda_{1,+}^H \approx 0.9900 < 1$. For $n = 6$, Case 1 occurs, and there exist no Hopf bifurcation and steady state bifurcation points. For $n = 7$, Case 3 occurs and there exist 2 steady state bifurcation points $\lambda_{7,-}^S \approx 0.2293$ and $\lambda_{7,+}^S \approx 0.7165$, but no Hopf bifurcation points. For $n \geq 8$, no bifurcation occurs. In this example the mode $n = 6$ is skipped in bifurcation sequence.

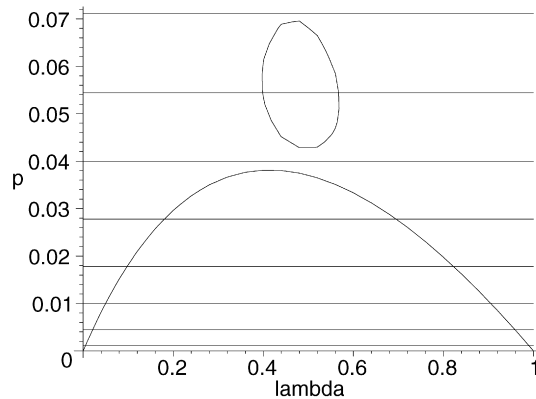


Fig. 3. Graph of $T(\lambda, p)$ and $D(\lambda, p)$. Here $d_1 = 1, d_2 = 2, k = 3, \theta = 0.0105$. The horizontal lines are $p = n^2/\ell^2$ where $1 \leq n \leq 8$ and $\ell = 30$.

4. Concluding remarks

A rigorous investigation of the global dynamics and bifurcation of patterned solutions of the diffusive predator–prey system with Holling type-II functional response is given, and the parameter ranges of existence of multiple bifurcations are identified.

Three parameter sets play essential roles in the pattern formation mechanism of (1.2): the kinetic dynamics parameters (m, k, θ) , the diffusion coefficients (d_1, d_2) (or essentially the ratio d_1/d_2), and the spatial scale ℓ . It is well known that pattern formation is not possible for small spatial domains [5], and we determine the minimum ℓ for the existence of spatially non-homogeneous oscillatory or steady states. Notice that these minimum domain sizes depend on both the kinetic dynamics parameters and the diffusion coefficients. For larger spatial domains, more patterns and more bifurcations are possible as shown by our results.

Diffusion coefficients are not the main driving force of the bifurcation and pattern formation discovered here. But Theorem 3.8 shows the subtle dependence of the spatiotemporal patterns on the ratio d_1/d_2 of the diffusion coefficients. Biologically this can be interpreted as: if the prey moves relatively faster compared to the predator, then oscillatory patterns are more likely (only Hopf bifurcations are possible); and if the dispersal of the prey is not as fast, both oscillatory and equilibrium patterns will appear.

The main bifurcation parameter in this work is from the kinetic dynamics parameters (m, k, θ) or $\lambda = \theta/(m - \theta)$. The cascade of Hopf and steady state bifurcations shown in this paper represents the rich self-organized spatiotemporal dynamics of the diffusive predator–prey system (1.2). As shown in previous work, the reaction–diffusion system (1.2) is one of prototypical pattern formation models with wide applications in population biology including phytoplankton and zooplankton interactions as well as more general consumer–resource interactions. The bifurcation approach given here provides another aspect of such pattern formation problem. We believe it can also be applied to other activator–inhibitor type systems.

Further analysis of the bifurcating solutions of (1.2) remains a challenging problem. Our results show that global branches of periodic orbits or steady state solutions exist, and they can be unbounded or form loops. We conjecture that all these branches are indeed loops in the space (λ, u, v) . The stability of these patterned solutions are also not known except near the bifurcation points.

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Appendix A. Bifurcation direction of the spatially non-homogeneous periodic solutions

In this appendix, we determine the bifurcation direction of the spatially non-homogeneous periodic solutions found in Theorem 2.4. Recall that the bifurcating periodic solution is supercritical (resp. subcritical) if $\frac{1}{\alpha'(\lambda_{j,\pm}^H)} \operatorname{Re}(c_1(\lambda_{j,\pm}^H)) < 0$ (resp. > 0). We calculate $\operatorname{Re}(c_1(\lambda_{j,\pm}^H))$, with $c_1(\lambda_{j,\pm}^H)$ defined in (2.31). When $\lambda = \lambda_{j,\pm}^H$ ($j \in \mathbb{N}$), then we set

$$\begin{aligned} q &:= \cos \frac{j}{\ell} x(a_j, b_j)^T = \cos \frac{j}{\ell} x \left(1, \frac{d_2 j^2}{\ell^2 \theta} - \frac{i \omega_0}{\theta} \right)^T, \\ q^* &:= \cos \frac{j}{\ell} x(a_j^*, b_j^*)^T = \cos \frac{j}{\ell} x \left(\frac{1}{\ell \pi} + \frac{d_2 j^2}{\omega_0 \ell^3 \pi} i, -\frac{\theta i}{\ell \pi \omega_0} \right)^T, \end{aligned} \tag{A.1}$$

where

$$\omega_0 = \left(\theta C(\lambda_{j,\pm}^H) - \frac{d_2^2 j^4}{\ell^4} \right)^{1/2}.$$

By (2.25), when $j \in \mathbb{N}$, it follows that $\langle q^*, Q_{qq} \rangle = \langle q^*, Q_{q\bar{q}} \rangle = 0$. Thus, in order to calculate $\operatorname{Re}(c_1(\lambda_{j,\pm}^H))$, it remains to calculate

$$\langle q^*, Q_{w_{11}q} \rangle, \quad \langle q^*, Q_{w_{20}\bar{q}} \rangle \quad \text{and} \quad \langle q^*, C_{qq\bar{q}} \rangle. \tag{A.2}$$

It is straightforward to compute that

$$[2i\omega_0 I - L_{2j}(\lambda_{j,\pm}^H)]^{-1} = (\alpha_1 + \alpha_2 i)^{-1} \begin{pmatrix} 2i\omega_0 + \frac{4d_2 j^2}{\ell^2} & -\theta \\ C(\lambda_{j,\pm}^H) & 2i\omega_0 - \frac{(d_2 - 3d_1)j^2}{\ell^2} \end{pmatrix}, \tag{A.3}$$

with

$$\alpha_1 := \frac{(12d_1 d_2 - 3d_2^2)j^4 - 3\omega_0^2 \ell^4}{\ell^4}, \quad \alpha_2 := \frac{6\omega_0(d_1 + d_2)j^2}{\ell^2}; \tag{A.4}$$

and

$$[2i\omega_0 I - L_0(\lambda_{j,\pm}^H)]^{-1} = (\alpha_3 + \alpha_4 i)^{-1} \begin{pmatrix} 2i\omega_0 & -\theta \\ C(\lambda_{j,\pm}^H) & 2i\omega_0 - \frac{(d_1 + d_2)j^2}{\ell^2} \end{pmatrix}, \tag{A.5}$$

with

$$\alpha_3 := \frac{d_2^2 j^4 - 3\omega_0^2 \ell^4}{\ell^4}, \quad \alpha_4 := -\frac{2\omega_0(d_1 + d_2)j^2}{\ell^2}. \tag{A.6}$$

Then we have by (2.24), when $j \in \mathbb{N}$,

$$\begin{aligned} w_{20} &= \left[\frac{[2i\omega_0 I - L_{2j}(\lambda_{j,\pm}^H)]^{-1}}{2} \cos \frac{2j}{\ell} x + \frac{[2i\omega_0 I - L_0(\lambda_{j,\pm}^H)]^{-1}}{2} \right] \cdot \begin{pmatrix} c_j \\ d_j \end{pmatrix} \\ &= \frac{[\alpha_1 + \alpha_2 i]^{-1}}{2} \begin{pmatrix} [2i\omega_0 + \frac{4d_2 j^2}{\ell^2}]c_j - \theta d_j \\ C(\lambda_{j,\pm}^H)c_j + [2i\omega_0 - \frac{(d_2 - 3d_1)j^2}{\ell^2}]d_j \end{pmatrix} \cos \frac{2jx}{\ell} \\ &\quad + \frac{[\alpha_3 + \alpha_4 i]^{-1}}{2} \begin{pmatrix} 2i\omega_0 c_j - \theta d_j \\ C(\lambda_{j,\pm}^H)c_j + [2i\omega_0 - \frac{(d_1 + d_2)j^2}{\ell^2}]d_j \end{pmatrix}. \end{aligned} \tag{A.7}$$

Likewise when $j \in \mathbb{N}$, we have

$$w_{11} = \frac{\alpha_5^{-1}}{2} \left(C(\lambda_{j,\pm}^H) e_j - \frac{(d_2 - 3d_1)j^2}{\ell^2} f_j \right) \cos \frac{2jx}{\ell} - \frac{1}{2C(\lambda_{j,\pm}^H)} \left(-C(\lambda_{j,\pm}^H) e_j + \frac{(d_1 + d_2)j^2}{\ell^2} f_j \right), \tag{A.8}$$

with $\alpha_5 := [(12d_1d_2 - 3d_2^2)j^4 + \omega_0^2\ell^4]/\ell^4$. From computation, it follows that

$$\begin{cases} f_{uu} = -\frac{2\lambda^2 + 6\lambda + 2 - 2k}{k(1 + \lambda)^2}, & f_{uv} = -\frac{\theta}{\lambda(\lambda + 1)}, & f_{vv} = f_{v\bar{v}\bar{v}} = f_{u\bar{v}\bar{v}} = 0, \\ f_{uuu} = -\frac{6(k - \lambda)}{k(1 + \lambda)^3}, & f_{uuv} = \frac{2\theta}{\lambda(\lambda + 1)^2}, & g_{uu} = -\frac{2(k - \lambda)}{k(\lambda + 1)^2}, & g_{vv} = g_{u\bar{v}\bar{v}} = 0, \\ g_{uv} = \frac{\theta}{\lambda(\lambda + 1)}, & g_{uuu} = \frac{6(k - \lambda)}{k(1 + \lambda)^3}, & g_{uuv} = -\frac{2\theta}{\lambda(\lambda + 1)^2}, & g_{v\bar{v}\bar{v}} = 0. \end{cases} \tag{A.9}$$

Here and in the following we always assume that all the partial derivatives of f and g are evaluated at $(\lambda_{j,\pm}^H, 0, 0)$. Then we have

$$Q_{w_{20},\bar{q}} = \begin{pmatrix} f_{uu}\xi + f_{uv}\eta + f_{uv}\bar{b}_j\bar{\xi} \\ g_{uu}\xi + g_{uv}\eta + g_{uv}\bar{b}_j\bar{\xi} \end{pmatrix} \cos \frac{jx}{\ell} \cos \frac{2jx}{\ell} + \begin{pmatrix} f_{uu}\tau + f_{uv}\chi + f_{uv}\bar{b}_j\tau \\ g_{uu}\tau + g_{uv}\chi + g_{uv}\bar{b}_j\tau \end{pmatrix} \cos \frac{jx}{\ell} \tag{A.10}$$

and

$$Q_{w_{11},q} = \begin{pmatrix} f_{uu}\tilde{\xi} + f_{uv}\tilde{\eta} + f_{uv}b_j\tilde{\xi} \\ g_{uu}\tilde{\xi} + g_{uv}\tilde{\eta} + g_{uv}b_j\tilde{\xi} \end{pmatrix} \cos \frac{2jx}{\ell} \cos \frac{jx}{\ell} + \begin{pmatrix} f_{uu}\tilde{\tau} + f_{uv}\tilde{\chi} + f_{uv}b_j\tilde{\tau} \\ g_{uu}\tilde{\tau} + g_{uv}\tilde{\chi} + f_{uv}b_j\tilde{\tau} \end{pmatrix} \cos \frac{jx}{\ell}, \tag{A.11}$$

with

$$\begin{aligned} \xi &= \frac{(\alpha_1 + \alpha_2 i)^{-1}}{2} \left[\left(2i\omega_0 + \frac{4d_2j^2}{\ell^2} \right) c_j - \theta d_j \right], \\ \eta &= \frac{(\alpha_1 + \alpha_2 i)^{-1}}{2} \left[C(\lambda_{j,\pm}^H) c_j + \left(2i\omega_0 - \frac{(d_2 - 3d_1)j^2}{\ell^2} \right) d_j \right], \\ \tau &= \frac{(\alpha_3 + \alpha_4 i)^{-1}}{2} (2i\omega_0 c_j - \theta d_j), \\ \chi &= \frac{(\alpha_3 + \alpha_4 i)^{-1}}{2} \left[C(\lambda_{j,\pm}^H) c_j + \left(2i\omega_0 - \frac{(d_1 + d_2)j^2}{\ell^2} \right) d_j \right], \\ \tilde{\xi} &= \frac{1}{2\alpha_5} \left(-\frac{4d_2j^2}{\ell^2} e_j + \theta f_j \right), \\ \tilde{\eta} &= \frac{1}{2\alpha_5} \left(-C(\lambda_{j,\pm}^H) e_j + \frac{(d_2 - 3d_1)j^2}{\ell^2} f_j \right), \\ \tilde{\tau} &= -\frac{1}{2C(\lambda_{j,\pm}^H)} f_j, \\ \tilde{\chi} &= \frac{1}{2C(\lambda_{j,\pm}^H)} \left(-C(\lambda_{j,\pm}^H) e_j + \frac{(d_1 + d_2)j^2}{\ell^2} f_j \right), \end{aligned} \tag{A.12}$$

where by (2.19),

$$\begin{cases} c_j = f_{uu} - \frac{2i\omega_0}{\theta} f_{uv}, & d_j = g_{uu} - \frac{2i\omega_0}{\theta} g_{uv}, & e_j = f_{uu}, \\ f_j = g_{uu}, & g_j = f_{uuu} - \frac{i\omega_0}{\theta} f_{uuv}, & h_j = g_{uuu} - \frac{i\omega_0}{\theta} g_{uuv}. \end{cases} \tag{A.13}$$

Notice that for any $j \in \mathbb{N}$,

$$\int_0^{\ell\pi} \cos^2 \frac{jx}{\ell} dx = \frac{1}{2} \ell\pi, \quad \int_0^{\ell\pi} \cos \frac{2jx}{\ell} \cos^2 \frac{jx}{\ell} dx = \frac{1}{4} \ell\pi, \quad \int_0^{\ell\pi} \cos^4 \frac{jx}{\ell} dx = \frac{3}{8} \ell\pi,$$

we have

$$\begin{aligned} \langle q^*, Q_{w_{20}\bar{q}} \rangle &= \frac{\ell\pi}{4} \{ \bar{a}_j^* (f_{uu}\xi + f_{uv}\eta + f_{uv}\xi\bar{b}_j) + \bar{b}_j^* (g_{uu}\xi + g_{uv}\eta + g_{uv}\xi\bar{b}_j) \} \\ &\quad + \frac{\ell\pi}{2} \{ \bar{a}_j^* (f_{uu}\tau + f_{uv}\chi + f_{uv}\tau\bar{b}_j) + \bar{b}_j^* (g_{uu}\tau + g_{uv}\chi + g_{uv}\tau\bar{b}_j) \}, \\ \langle q^*, Q_{w_{11}q} \rangle &= \frac{\ell\pi}{4} \{ \bar{a}_j^* (f_{uu}\tilde{\xi} + f_{uv}\tilde{\eta} + f_{uv}\tilde{\xi}b_j) + \bar{b}_j^* (g_{uu}\tilde{\xi} + g_{uv}\tilde{\eta} + g_{uv}\tilde{\xi}b_j) \} \\ &\quad + \frac{\ell\pi}{2} \{ \bar{a}_j^* (f_{uu}\tilde{\tau} + f_{uv}\tilde{\chi} + f_{uv}\tilde{\tau}b_j) + \bar{b}_j^* (g_{uu}\tilde{\tau} + g_{uv}\tilde{\chi} + g_{uv}\tilde{\tau}b_j) \}, \\ \langle q^*, C_{qq\bar{q}} \rangle &= \frac{3\ell\pi}{4} (\bar{a}_j^* g_j + \bar{b}_j^* h_j). \end{aligned} \tag{A.14}$$

Since $\ell\pi\bar{a}_j^* = 1 - \frac{d_2j^2}{\omega_0\ell^2}i$, and $\ell\pi\bar{b}_j^* = \frac{\theta}{\omega_j}i$, it follows that

$$\operatorname{Re}\langle q^*, C_{qq\bar{q}} \rangle = \frac{3}{8} \left(f_{uuu} + \frac{d_2j^2}{\ell^2\theta} f_{uuv} + g_{uuv} \right), \tag{A.15}$$

and

$$\begin{aligned} \operatorname{Re}\langle q^*, Q_{w_{20}q} \rangle &= \frac{1}{4} \left[f_{uu}(\xi_R + 2\tau_R) + f_{uv}(\eta_R + 2\chi_R) - g_{uv}(\xi_R + 2\tau_R) - \frac{\omega_0}{\theta} f_{uv}(\xi_R + 2\tau_R) \right] \\ &\quad + \frac{d_2j^2}{4\omega_0\ell^2} \left[f_{uu}(\xi_I + 2\tau_I) + f_{uv}(\eta_I + 2\chi_I) + \frac{\omega_0}{\theta} f_{uv}(\xi_R + 2\tau_R) \right] \\ &\quad - \frac{\theta}{4\omega_0} [g_{uu}(\xi_I + 2\tau_I) + g_{uv}(\eta_I + 2\chi_I)], \\ \operatorname{Re}\langle q^*, Q_{w_{11}q} \rangle &= \frac{1}{4} \left[f_{uu}(\tilde{\xi} + 2\tilde{\tau}) + f_{uv}(\tilde{\eta} + 2\tilde{\chi}) + \frac{d_2j^2}{\ell^2\theta} f_{uv}(\tilde{\xi} + 2\tilde{\tau}) - g_{uv}(\tilde{\xi} + 2\tilde{\tau}) \right], \end{aligned} \tag{A.16}$$

where we define $\Gamma_R := \operatorname{Re} \Gamma$ and $\Gamma_I := \operatorname{Im} \Gamma$ for $\Gamma = \xi, \eta, \tau, \chi$. More precisely,

$$\begin{aligned}
 \xi_R &= \frac{\alpha_1}{2(\alpha_1^2 + \alpha_2^2)} \left(\frac{4\omega_0^2}{\theta} f_{uv} + \frac{4d_2 j^2}{\ell^2} f_{uu} - \theta g_{uu} \right) \\
 &\quad + \frac{\alpha_2}{2(\alpha_1^2 + \alpha_2^2)} \left(2\omega_0 f_{uu} - \frac{8\omega_0 d_2 j^2}{\ell^2 \theta} f_{uv} + 2\omega_0 g_{uv} \right), \\
 \xi_I &= \frac{\alpha_1}{2(\alpha_1^2 + \alpha_2^2)} \left(2\omega_0 f_{uu} - \frac{8\omega_0 d_2 j^2}{\ell^2 \theta} f_{uv} + 2\omega_0 g_{uv} \right) \\
 &\quad - \frac{\alpha_2}{2(\alpha_1^2 + \alpha_2^2)} \left(\frac{4\omega_0^2}{\theta} f_{uv} + \frac{4d_2 j^2}{\ell^2} f_{uu} - \theta g_{uu} \right), \\
 \eta_R &= \frac{\alpha_1}{2(\alpha_1^2 + \alpha_2^2)} \left(C(\lambda_{j,\pm}^H) f_{uu} + \frac{4\omega_0^2}{\theta} g_{uv} - \frac{(d_2 - 3d_1)j^2}{\ell^2} g_{uu} \right) \\
 &\quad + \frac{\alpha_2}{2(\alpha_1^2 + \alpha_2^2)} \left(-\frac{2\omega_0}{\theta} C(\lambda_{j,\pm}^H) f_{uv} + \frac{2\omega_0(d_2 - 3d_1)j^2}{\ell^2 \theta} g_{uv} + 2\omega_0 g_{uu} \right), \\
 \eta_I &= \frac{\alpha_1}{2(\alpha_1^2 + \alpha_2^2)} \left(-\frac{2\omega_0}{\theta} C(\lambda_{j,\pm}^H) f_{uv} + \frac{2\omega_0(d_2 - 3d_1)j^2}{\ell^2 \theta} g_{uv} + 2\omega_0 g_{uu} \right) \\
 &\quad - \frac{\alpha_2}{2(\alpha_1^2 + \alpha_2^2)} \left(C(\lambda_{j,\pm}^H) f_{uu} + \frac{4\omega_0^2}{\theta} g_{uv} - \frac{(d_2 - 3d_1)j^2}{\ell^2} g_{uu} \right), \\
 \tau_R &= \frac{\alpha_3}{2(\alpha_3^2 + \alpha_4^2)} \left(\frac{4\omega_0^2}{\theta} f_{uv} - \theta g_{uu} \right) + \frac{\alpha_4}{2(\alpha_3^2 + \alpha_4^2)} (2\omega_0 f_{uu} + 2\omega_0 g_{uv}), \\
 \tau_I &= \frac{\alpha_3}{2(\alpha_3^2 + \alpha_4^2)} (2\omega_0 f_{uu} + 2\omega_0 g_{uv}) - \frac{\alpha_4}{2(\alpha_3^2 + \alpha_4^2)} \left(\frac{4\omega_0^2}{\theta} f_{uv} - \theta g_{uu} \right), \\
 \chi_R &= \frac{\alpha_3}{2(\alpha_3^2 + \alpha_4^2)} \left(C(\lambda_{j,\pm}^H) f_{uu} + \frac{4\omega_0^2}{\theta} g_{uv} - \frac{(d_1 + d_2)j^2}{\ell^2} g_{uu} \right) \\
 &\quad + \frac{\alpha_4}{2(\alpha_3^2 + \alpha_4^2)} \left(-\frac{2\omega_0}{\theta} C(\lambda_{j,\pm}^H) f_{uv} + \frac{2\omega_0(d_1 + d_2)j^2}{\ell^2 \theta} g_{uv} + 2\omega_0 g_{uu} \right), \\
 \chi_I &= \frac{\alpha_3}{2(\alpha_3^2 + \alpha_4^2)} \left(-\frac{2\omega_0}{\theta} C(\lambda_{j,\pm}^H) f_{uv} + \frac{2\omega_0(d_1 + d_2)j^2}{\ell^2 \theta} g_{uv} + 2\omega_0 g_{uu} \right) \\
 &\quad - \frac{\alpha_4}{2(\alpha_3^2 + \alpha_4^2)} \left(C(\lambda_{j,\pm}^H) f_{uu} + \frac{4\omega_0^2}{\theta} g_{uv} - \frac{(d_1 + d_2)j^2}{\ell^2} g_{uu} \right). \tag{A.17}
 \end{aligned}$$

So far, by (2.31), we have

$$\begin{aligned}
 \operatorname{Re}(c_1(\lambda_{j,\pm}^H)) &= \operatorname{Re}(q^*, Q_{w_{11}q}) + \frac{1}{2} \operatorname{Re}(q^*, Q_{w_{20}\bar{q}}) + \frac{1}{2} \operatorname{Re}(q^*, C_{qq\bar{q}}) \\
 &= \frac{1}{4} \left[f_{uu}(\tilde{\xi} + 2\tilde{\tau}) + f_{uv}(\tilde{\eta} + 2\tilde{\chi}) + \frac{d_2 j^2}{\ell^2 \theta} f_{uv}(\tilde{\xi} + 2\tilde{\tau}) - g_{uv}(\tilde{\xi} + 2\tilde{\tau}) \right] \\
 &\quad + \frac{1}{8} \left[f_{uu}(\xi_R + 2\tau_R) + f_{uv}(\eta_R + 2\chi_R) - g_{uv}(\xi_R + 2\tau_R) - \frac{\omega_0}{\theta} f_{uv}(\xi_R + 2\tau_R) \right]
 \end{aligned}$$

$$\begin{aligned}
 & + \frac{d_2 j^2}{8\omega_0 \ell^2} \left[f_{uu}(\xi_I + 2\tau_I) + f_{uv}(\eta_I + 2\chi_I) + \frac{\omega_0}{\theta} f_{uv}(\xi_R + 2\tau_R) \right] \\
 & - \frac{\theta}{8\omega_0} [g_{uu}(\xi_I + 2\tau_I) + g_{uv}(\eta_I + 2\chi_I)] + \frac{3}{32} \left(f_{uuu} + \frac{d_2 j^2}{\ell^2 \theta} f_{uuv} + g_{uuv} \right). \tag{A.18}
 \end{aligned}$$

Thus the bifurcating periodic solution is supercritical (resp. subcritical) if $\frac{1}{\alpha'(\lambda_{j,\pm}^H)} \operatorname{Re}(c_1(\lambda_{j,\pm}^H)) < 0$ (resp. > 0), which is given in (A.18).

Appendix B. Proof of Lemma 3.9

Proof. It is clear that $\lambda^\# \in (\underline{\lambda}, \bar{\lambda})$. Recall λ_* is defined in (2.45). We claim that $\lambda_* < \lambda^\#$. In fact, since $h'(\lambda_*) = -A^2(\lambda_*)C'(\lambda_*)/C^2(\lambda_*) > 0$, and $h'(\lambda^\#) = 0$, we have $\lambda_* < \lambda^\#$. There are two cases to consider: $\lambda_* \in (\underline{\lambda}, \bar{\lambda})$ and $\lambda_* \leq \underline{\lambda}$. We will only consider the former case, since the latter one is similar. Now we suppose that $\lambda_* \in (\underline{\lambda}, \bar{\lambda})$ holds. In $(\underline{\lambda}, \lambda_*)$, since $A(\lambda)$ is increasing, and $C(\lambda)$ is decreasing, then by

$$p_+(\lambda) = \frac{d_2 A(\lambda) + \sqrt{d_2^2 A(\lambda)^2 - 4d_1 d_2 \theta C(\lambda)}}{2d_1 d_2},$$

$p_+(\lambda)$ is increasing in $(\underline{\lambda}, \lambda_*)$. Then $p'_+(\lambda) > 0$ for $\lambda \in (\underline{\lambda}, \lambda_*)$. In $(\lambda^\#, \bar{\lambda})$, since $A(\lambda)$, $C(\lambda)$ and $h(\lambda)$ are all decreasing, then by

$$p_+(\lambda) = \frac{d_2 A(\lambda) + \sqrt{C(\lambda)(d_2^2 h(\lambda) - 4d_1 d_2 \theta)}}{2d_1 d_2},$$

$p_+(\lambda)$ is decreasing in $(\lambda^\#, \bar{\lambda})$. Then $p'_+(\lambda) < 0$ for $\lambda \in (\lambda^\#, \bar{\lambda})$. It remains to consider the case when $\lambda \in [\lambda_*, \lambda^\#]$. In fact, by calculating $p'_+(\lambda)$ in (3.17), we can obtain that $\lim_{\lambda \rightarrow \underline{\lambda}} p'_+(\lambda) = +\infty$, $\lim_{\lambda \rightarrow \bar{\lambda}} p'_+(\lambda) = -\infty$, and for small $\varepsilon_1, \varepsilon_2 > 0$, $p'_+(\underline{\lambda} + \varepsilon_1) > 0$, $p'_+(\bar{\lambda} - \varepsilon_2) < 0$. Then there exists at least one $\lambda_c \in (\underline{\lambda} + \varepsilon_1, \bar{\lambda} - \varepsilon_2)$, such that $p'_+(\lambda_c) = 0$. Since for $\lambda \in (\underline{\lambda}, \lambda_*) \cup (\lambda^\#, \bar{\lambda})$, $p'_+(\lambda) \neq 0$, we have $\lambda_c \in [\lambda_*, \lambda^\#]$. We claim that $\lambda_c \neq \lambda_*, \lambda^\#$. In fact, by differentiating $D_n(\lambda)|_{p=p_+(\lambda)} = 0$ with respect to λ at $\lambda = \lambda_*$, we obtain

$$\theta C'(\lambda_*) - d_2 A'(\lambda_*) p_+(\lambda_*) - d_2 A(\lambda_*) p'_+(\lambda_*) + 2d_1 d_2 p_+(\lambda_*) p'_+(\lambda_*) = 0,$$

and then (noticing that $A'(\lambda_*) = 0$)

$$p'_+(\lambda_*) = -\frac{\theta C'(\lambda_*)}{2d_1 d_2 p_+(\lambda_*) - d_2 A(\lambda_*)} = -\frac{\theta C'(\lambda_*)}{\sqrt{d_2^2 A^2(\lambda_*) - 4d_1 d_2 \theta C(\lambda_*)}} > 0,$$

then $\lambda_c \neq \lambda_*$. Similarly we have

$$p'_+(\lambda^\#) = \frac{d_2 A'(\lambda^\#) p_+(\lambda^\#) - \theta C'(\lambda^\#)}{\sqrt{d_2^2 A^2(\lambda^\#) - 4d_1 d_2 \theta C(\lambda^\#)}}.$$

Since $h'(\lambda^\#) = 0$, we have $2A'(\lambda^\#)C(\lambda^\#) = A(\lambda^\#)C'(\lambda^\#)$. Then it follows that

$$p'_+(\lambda^\#) = \frac{C'(\lambda^\#)[d_2 A(\lambda^\#) p_+(\lambda^\#) - 2\theta C(\lambda^\#)]}{2C(\lambda^\#) \sqrt{d_2^2 A^2(\lambda^\#) - 4d_1 d_2 \theta C(\lambda^\#)}}.$$

Suppose that $d_2A(\lambda^\#)p(\lambda^\#) - 2\theta C(\lambda^\#) = 0$, we have $p_+(\lambda^\#) = 2\theta C(\lambda^\#)/(d_2A(\lambda^\#))$, thus $p_+^2(\lambda^\#) = 4\theta^2C^2(\lambda^\#)/(d_2^2A^2(\lambda^\#))$. Together with $d_1d_2p^2(\lambda^\#) = d_2A(\lambda^\#)p(\lambda^\#) - \theta C(\lambda^\#)$, we have $d_1/d_2 = A^2(\lambda^\#)/(4\theta C(\lambda^\#)) = h(\lambda^\#)/(4\theta)$, which is impossible by our assumption. Thus $p'_+(\lambda^\#) \neq 0$ (actually < 0), then $\lambda_c \neq \lambda^\#$.

We claim that λ_c is unique in $(\lambda_*, \lambda^\#)$. Suppose not, let λ_c and λ_d , with $\lambda_* < \lambda_c < \lambda_d < \lambda^\#$, be the last two consecutive points, such that $p'_+(\lambda_c) = p'_+(\lambda_d) = 0$. Since $p_+(\lambda)$ is decreasing in $(\lambda^\#, \bar{\lambda})$, λ_d is the local maximal point of $p_+(\lambda)$. Also by the fact that λ_c and λ_d are consecutive and $\lambda_c < \lambda_d$, we obtain that λ_c is the local minimal point of $p_+(\lambda)$. Thus $p_+(\lambda_c) \leq p_+(\lambda_d)$. Substituting $p'_+(\lambda_c) = p'_+(\lambda_d) = 0$ into (3.24) respectively, we have

$$p_+(\lambda_c) = \frac{\theta(k+1)}{d_2(2\lambda_c^2 + 4\lambda_c + 1 - k)}, \quad p_+(\lambda_d) = \frac{\theta(k+1)}{d_2(2\lambda_d^2 + 4\lambda_d + 1 - k)}. \tag{B.1}$$

Since $\lambda_* < \lambda_c < \lambda_d$, we have $p_+(\lambda_c) > p_+(\lambda_d) > 0$, which is impossible since we have $p_+(\lambda_c) \leq p_+(\lambda_d)$. Thus the critical point λ_c is unique in $(\lambda_*, \lambda^\#)$. And by the continuity of $p_+(\lambda)$, it follows that $p_+(\lambda)$ is increasing in $(\underline{\lambda}, \lambda_c)$, is decreasing in $(\lambda_c, \bar{\lambda})$, and at λ_c , $p_+(\lambda)$ attains its maximal value $p_+(\lambda_c)$. In the case when $\lambda_* \leq \underline{\lambda}$, we can use the same methods to prove the results, which we omit here.

Now we consider the properties of $p_-(\lambda)$. Since $p_+(\lambda)p_-(\lambda) = \theta C(\lambda)/(d_1d_2)$, we write $p_-(\lambda) = \theta C(\lambda)/(d_1d_2p_+(\lambda))$. Since $p_+(\lambda)$ is increasing in $(\underline{\lambda}, \lambda_c)$, $p_-(\lambda)$ is decreasing in $(\underline{\lambda}, \lambda_c)$. Since $p'_+(\lambda_c) = 0$, by the same analysis as (3.24) and (B.1), it follows that $p'_-(\lambda_c) \neq 0$. Thus, repeating the analysis in the last paragraph, we can show that there exists a unique point $\lambda'_c \in (\lambda_c, \bar{\lambda})$, such that $p_-(\lambda)$ is decreasing in $(\underline{\lambda}, \lambda'_c)$, while it is increasing in $(\lambda'_c, \bar{\lambda})$, and at λ'_c , $p_-(\lambda)$ attains its minimal value.

Finally we calculate

$$p_+(\underline{\lambda}) = p_-(\underline{\lambda}) = A(\underline{\lambda})/(2d_1) = \sqrt{\theta C(\underline{\lambda})/(d_1d_2)},$$

$$p_+(\bar{\lambda}) = p_-(\bar{\lambda}) = A(\bar{\lambda})/(2d_1) = \sqrt{\theta C(\bar{\lambda})/(d_1d_2)},$$

since $d_2^2A^2(\underline{\lambda}) - 4\theta d_1d_2C(\underline{\lambda}) = 0$, and $d_2^2A^2(\bar{\lambda}) - 4\theta d_1d_2C(\bar{\lambda}) = 0$. Then, we can obtain $p_+(\underline{\lambda}) = p_-(\underline{\lambda}) > p_+(\bar{\lambda}) = p_-(\bar{\lambda})$, since $C(\lambda)$ is decreasing. In summary we have $0 < p_-(\lambda'_c) < p_+(\bar{\lambda}) = p_-(\bar{\lambda}) < p_+(\underline{\lambda}) = p_-(\underline{\lambda}) < p_+(\lambda_c) < \infty$, the last inequality of which holds by (B.1). \square

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