



Global bifurcation analysis and pattern formation in homogeneous diffusive predator–prey systems [☆]

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Received 5 February 2015; revised 2 September 2015

Available online 10 November 2015

Abstract

The dynamics of a general diffusive predator–prey system is considered. Existence and nonexistence of non-constant positive steady state solutions are shown to identify the ranges of parameters of spatial pattern formation. Bifurcations of spatially homogeneous and nonhomogeneous periodic solutions as well as non-constant steady state solutions are studied.

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MSC: 35K57; 37L10

Keywords: Reaction diffusion; Pattern formation; Global bifurcation; Predator prey

1. Introduction

In recent decades the role of spatial effects in maintaining biodiversity has received a great deal of attention in the literature on conservation, see for example [20,40]. One way of trying to understand how spatial effects such as habitat fragmentation influence populations and commu-

[☆] Partially supported by Natural Science Foundation of China (Nos. 11201101, 11371111), Natural Science Foundation of Heilongjiang Province (QC2015002).

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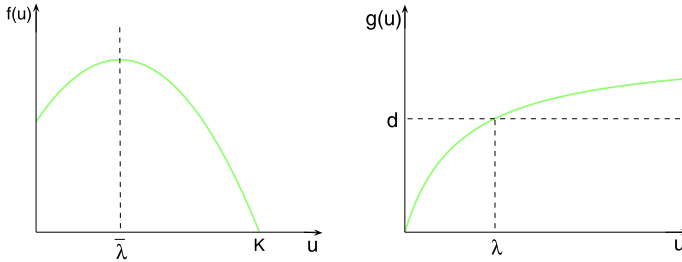


Fig. 1. Graph of $f(u)$ and $g(u)$.

nities is by using mathematical models [3]. Reaction–diffusion systems typically arise as models for interactions between different species (either chemical or biological) where the species can vary in density in space and move according to some processes such as physical diffusion or dispersal by random walks. Typical reaction–diffusion models are of form:

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + f_i(u), \quad x \in \Omega, \quad t > 0, \tag{1.1}$$

where $u = (u_1, u_2, \dots, u_n)$, with initial and boundary conditions.

The dynamical relationship between predators and their preys has been investigated widely in recent years due to its universal existence and importance in mathematical biology and ecology. A typical interaction of predator and prey is well known as the Rosenzweig–MacArthur model, which is widely used in real life ecological applications [26,36,37], and it has also been used to describe the spatiotemporal dynamics of an aquatic community of phytoplankton and zooplankton system [28]. The general model of interaction of predator and prey takes the form

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + g(u)(f(u) - v), & x \in \Omega, \quad t > 0, \\ \frac{\partial v}{\partial t} = d_2 \Delta v + v(g(u) - d), & x \in \Omega, \quad t > 0, \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega, \end{cases} \tag{1.2}$$

where f, g satisfy the following conditions:

- (a1) $f \in C^1(\overline{\mathbb{R}^+})$, $f(0) > 0$, there exists $K > 0$, such that for any $u > 0$, $u \neq K$, $f(u)(u - K) < 0$ and $f(K) = 0$; there exists $\bar{\lambda} \in (0, K)$ such that $f'(u) > 0$ on $[0, \bar{\lambda})$, $f'(u) < 0$ on $(\bar{\lambda}, K]$;
- (a2) $g \in C^1(\overline{\mathbb{R}^+})$, $g(0) = 0$; $g(u) > 0$ for $u > 0$ and $g'(u) > 0$ for $u \geq 0$; there exists a unique $\lambda > 0$ such that $g(\lambda) = d$.

The function $g(u)f(u)$ is the net growth rate of the prey in the absence of predators, $g(u)$ is the predator functional response, and d is the mortality rate of the predator which depends on the prey density. (See Fig. 1.) Similar formulation for predator–prey systems has been given in [43]. We consider the initial–boundary value problem over a bounded smooth domain $\Omega \subseteq \mathbb{R}^n$ for $n \geq 1$, and we impose a no-flux boundary condition so it is a closed ecosystem.

Some examples of $f(u)$ and $g(u)$ satisfying (a1) and (a2) are

$$\begin{aligned}
 \text{(logistic)} \quad f(u) &= \frac{(K - u)(u + a)}{mK}, \\
 \text{(weak Allee effect)} \quad f(u) &= \frac{(K - u)(u + a)(u + b)}{mK},
 \end{aligned} \tag{1.3}$$

where $m, K > 0$ and $0 < a < K$ (for logistic), or $m, K, a, b > 0$ and $K > (ab)/(a + b) > 0$ (for weak Allee effect), and

$$\begin{aligned}
 \text{(type I)} \quad g(u) &= mu, & \text{(type II)} \quad g(u) &= \frac{mu}{u + a}, \\
 \text{(Ivlev type)} \quad g(u) &= m(1 - e^{-au}),
 \end{aligned} \tag{1.4}$$

where $m, a > 0$.

The corresponding ODE system of (1.2) has been extensively studied in the existing literature, see for example [7,16,17]. The highlight of the study of the ODE system is the existence and uniqueness of a limit cycle (see also [42]). In [37], Rosenzweig et al. argued that enrichment of the environment (large carrying capacity) leads to destabilizing of the coexistence equilibrium, which is the so-called paradox of enrichment.

A complete and rigorous analysis of the global dynamics of the diffusive predator–prey system (1.2) has not been achieved. Ko and Ryu [21] obtained some results on the global stability of the equilibrium solution for certain parameter ranges. Du and Shi [9] considered a slightly different system in spatially heterogeneous environment. For a special nonlinearity, Yi, Wei and Shi [52] obtained a detailed bifurcation analysis from the constant coexistence equilibrium solution when the spatial domain Ω is one-dimensional. Recently Wang, Wang and Zhang [47] studied the pattern formation for (1.2) with prey-taxis.

In the early 1950s, the British mathematician Alan M. Turing [41] proposed a model that accounts for pattern formation in morphogenesis. Turing showed mathematically that a system of coupled reaction–diffusion equations could give rise to spatial concentration patterns of a fixed characteristic length from an arbitrary initial congratulation due to so called diffusion-driven instability, that is, diffusion could destabilize an otherwise stable equilibrium of the reaction–diffusion system and lead to nonuniform spatial patterns. Turing’s analysis stimulated considerable theoretical research on mathematical models of pattern formation, and a great deal of research have been devoted to the study of Turing instability in chemical and biology contexts, see for example, [2,5,10,22] for Brusselator model; [27,35] for Gray–Scott model; [19,30,51] for Lengyel–Epstein model, and [11,23,49] for Schnakenberg model.

Methods of analysis of reaction–diffusion systems have been developed since late 1970s (see for example, [1,3,8,32,39]). In this paper we apply some classical techniques like comparison methods, *a priori* estimates to prove the global existence of the solutions to (1.2), and in various situations, global asymptotical behavior of the solutions can be determined. We also use energy estimates to obtain the *a priori* bounds of the dynamic and steady state solutions, which also identifies the regions of parameters of nonexistence of nonconstant spatial patterns. We use the powerful Leray–Schauder degree theory to prove the existence of nonconstant steady states as in [24,25,33,34,45]. As a precise description of the global dynamics cannot be obtained as the case of ODE model, the PDE system possesses more spatiotemporal patterns: nonconstant spatial patterns and time-periodic orbits, at least. We use stability analysis and bifurcation theory to show

the existence of such nonconstant steady states and time-periodic orbits, which partially verifies the richness of the dynamics.

2. Basic dynamics and a priori bound

The system (1.2) has three non-negative constant equilibrium solutions $(0, 0)$, $(K, 0)$, (λ, v_λ) , where λ is the unique one satisfied $g(\lambda) = d$ and $v_\lambda = f(\lambda)$. In the following, we take λ as the main bifurcation parameter. The coexistence equilibrium (λ, v_λ) is in the first quadrant if and only if $0 < \lambda < K$. First we recall some well known results on the ODE dynamics of (1.2), see for example [7,16,17,37,42]:

$$\begin{cases} u' = g(u)(f(u) - v), \\ v' = v(g(u) - d). \end{cases} \tag{2.1}$$

1. when $\lambda \geq K$, $(K, 0)$ is globally asymptotically stable, see [16];
2. when $\lambda^0 < \lambda < K$, (λ, v_λ) is globally asymptotically stable, where $\lambda^0 \in (\bar{\lambda}, K)$ is the unique value satisfying $f(0) = f(\lambda^0)$, see [16];
3. $\bar{\lambda}$ is the unique bifurcation point where a Hopf bifurcation occurs, and the Hopf bifurcation is supercritical and backward;
4. when $0 < \lambda < \bar{\lambda}$, there is a globally asymptotically stable periodic orbit if $h_1(u) = f'(u)g(u)/[g(u) - g(\lambda)]$ is non-increasing in $(0, \lambda) \cup (\lambda, K)$, see [42];
5. when $\bar{\lambda} < \lambda < K$, if one of the following holds:
 (P1) $(uf'(u))'' \leq 0$, $(u/g(u))'' \geq 0$ for all $u \in [0, K]$, and $(uf'(u))' \leq 0$ for $u \in (\bar{\lambda}, K)$; or
 (P2) $f'''(u) \leq 0$ and $(1/g(u))'' \geq 0$ for all $u \in [0, K]$, and $f''(u) \leq 0$ for $u \in (\bar{\lambda}, K)$,
 then (2.1) has no closed orbits in the first quadrant and the positive equilibrium $(\lambda, v_\lambda) = (\lambda, f(\lambda))$ is globally asymptotically stable in the first quadrant, see [42].

In the following, the existence of solution to the dynamical equation (1.2) is proved, and a priori bound of the solution is also established.

2.1. Existence and a priori bound of solution to (1.2)

Theorem 2.1. *Suppose that f, g satisfy (a1)–(a2), $d, d_1, d_2 > 0$ and $\Omega \subset \mathbb{R}^n$ is a bounded domain with smooth boundary.*

- (a) *If $u_0(x) \geq 0$ ($\neq 0$), $v_0(x) \geq 0$ ($\neq 0$), then (1.2) has a unique solution $(u(x, t), v(x, t))$ such that $u(x, t) > 0, v(x, t) > 0$ for $t \in (0, \infty)$ and $x \in \bar{\Omega}$.*
- (b) *If $d > g(K)$ (equivalently $\lambda > K$), then $(u(x, t), v(x, t))$ converges to $(K, 0)$ uniformly as $t \rightarrow \infty$.*
- (c) *For any solution $(u(x, t), v(x, t))$ of (1.2),*

$$\limsup_{t \rightarrow \infty} u(x, t) \leq K, \quad \int_{\Omega} v(x, t) dx \leq \left(K + \frac{g(K)f(\bar{\lambda})}{d} \right) |\Omega|.$$

Moreover, there exists $d_{2*} > 0$ such that

$$\limsup_{t \rightarrow +\infty} v(x, t) \leq C$$

for all $d_2 \geq d_{2*}$, where the positive constant $C > 0$ is independent of u_0, v_0, d_1 but depends on d_{2*} only; if $d_1 = d_2$, then $v(x, t) \leq K + \frac{g(K)f(\bar{\lambda})}{d}$ for all $t > 0, x \in \bar{\Omega}$.

Proof. 1. Define

$$M(u, v) = g(u)f(u) - g(u)v, \quad N(u, v) = -dv + g(u)v,$$

then $M_v = -g(u) \leq 0$ and $N_u = g'(u)v \geq 0$ in $\mathbb{R}_+^2 = \{u \geq 0, v \geq 0\}$ and (1.2) is a mixed quasi-monotone system (see [32,50]). Let $(\underline{u}(x, t), \underline{v}(x, t)) = (0, 0)$ and $(\bar{u}(x, t), \bar{v}(x, t)) = (u^*(t), v^*(t))$, where $(u^*(t), v^*(t))$ is the unique solution to

$$\begin{cases} \frac{du}{dt} = g(u)f(u), \\ \frac{dv}{dt} = -dv + g(u)v, \\ u(0) = u^*, \quad v(0) = v^*, \end{cases} \tag{2.2}$$

where $u^* = \sup_{\bar{\Omega}} u_0(x)$ and $v^* = \sup_{\bar{\Omega}} v_0(x)$. Since $f(u)g(u) < 0$ for $u > K$, then for the first equation of (2.2), $u(t)$ exists globally and $u(t) < K + \varepsilon$ for $t > T$. Hence $(\underline{u}(x, t), \underline{v}(x, t)) = (0, 0)$ and $(\bar{u}(x, t), \bar{v}(x, t)) = (u^*(t), v^*(t))$ are a pair of lower-solution and upper-solution to (1.2), respectively, since

$$\begin{aligned} & \frac{\partial \bar{u}(x, t)}{\partial t} - d_1 \Delta \bar{u}(x, t) - M(\bar{u}(x, t), \underline{v}(x, t)) = 0 \\ & \geq 0 = \frac{\partial \underline{u}(x, t)}{\partial t} - d_1 \Delta \underline{u}(x, t) - M(\underline{u}(x, t), \bar{v}(x, t)), \end{aligned}$$

and

$$\begin{aligned} & \frac{\partial \bar{v}(x, t)}{\partial t} - d_2 \Delta \bar{v}(x, t) - N(\bar{u}(x, t), \bar{v}(x, t)) = -d\bar{v} + g(\bar{u})\bar{v} = 0 \\ & \geq 0 = \frac{\partial \underline{v}(x, t)}{\partial t} - d_2 \Delta \underline{v}(x, t) - N(\underline{u}(x, t), \underline{v}(x, t)), \end{aligned}$$

the boundary conditions are satisfied, and $0 \leq u_0(x) \leq u^*$ and $0 \leq v_0(x) \leq v^*$. Here we use the definition of lower/upper-solution in Definition 8.1.2 in [32] or Definition 5.3.1 in [50]. Therefore Theorem 8.3.3 in [32] or Theorem 5.3.3 in [50] shows that (2.2) has a unique globally defined solution $(u(x, t), v(x, t))$ which satisfies

$$0 \leq u(x, t) \leq u^*(t), \quad 0 \leq v(x, t) \leq v^*(t), \quad t \geq 0.$$

The strong maximum principle implies that $u(x, t), v(x, t) > 0$ when $t > 0$ for all $x \in \bar{\Omega}$. This proves part (a).

2. From proof above, we obtain that $u(x, t) \leq u^*(t)$ for all $t > 0$. From the ODE satisfied by $u^*(t)$ and f, g satisfying (a1), (a2), one can see that $u^*(t) \rightarrow K$ as $t \rightarrow \infty$. Thus for any $\varepsilon > 0$, there exists $T > 0$ such that $u(x, t) \leq K + \varepsilon$ in $\bar{\Omega} \times [T, +\infty)$.

If $d > g(K)$, then we can choose $\varepsilon > 0$ small enough so that $d > g(K + \varepsilon)$. Consequently the equation of $v^*(t)$ implies that $0 \leq v(x, t) \leq v^*(t) \rightarrow 0$ as $t \rightarrow \infty$ uniformly for $x \in \bar{\Omega}$. The equation of $u(x, t)$ is now asymptotically autonomous (see [6,18,29]), and its limit behavior is determined by the semiflow generated by the scalar parabolic equation:

$$\begin{cases} u_t = d_1 \Delta u + g(u)f(u), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{2.3}$$

It is well-known that (2.3) is a gradient system, and every orbit of (2.3) converges to the unique positive steady state $u = K$ (see [8,12]). Then from the theory of asymptotically autonomous dynamical systems, the solution $(u(x, t), v(x, t))$ of (1.2) converges to $(K, 0)$ as $t \rightarrow \infty$. This proves part (b).

3. For the estimate of $v(x, t)$, let $\int_{\Omega} u(x, t)dx = U(t)$, $\int_{\Omega} v(x, t)dx = V(t)$, then

$$\frac{dU}{dt} = \int_{\Omega} u_t dx = \int_{\Omega} d_1 \Delta u dx + \int_{\Omega} [g(u)(f(u) - v)] dx = \int_{\Omega} [g(u)(f(u) - v)] dx, \tag{2.4}$$

$$\frac{dV}{dt} = \int_{\Omega} v_t dx = \int_{\Omega} d_2 \Delta v dx - d \int_{\Omega} v dx + \int_{\Omega} g(u)v dx = -dV + \int_{\Omega} g(u)v dx. \tag{2.5}$$

Adding (2.4) and (2.5) and by virtue of the Neumann boundary condition, we obtain

$$\begin{aligned} (U + V)_t &= -dV + \int_{\Omega} g(u)f(u)dx = -d(U + V) + dU + \int_{\Omega} g(u)f(u)dx \\ &\leq -d(U + V) + (d(K + \varepsilon) + g(K + \varepsilon)f(\bar{\lambda}))|\Omega|. \end{aligned}$$

Integration of the inequality leads to

$$\int_{\Omega} v(x, t)dx = V(t) < U(t) + V(t) \leq \frac{1}{d} (d(K + \varepsilon) + g(K + \varepsilon)f(\bar{\lambda}))|\Omega|. \tag{2.6}$$

From (2.6), we know that any solution $v(x, t)$ satisfies an L^1 a priori estimate $K_1 = \frac{1}{d} (d(K + \varepsilon) + g(K + \varepsilon)f(\bar{\lambda}))|\Omega|$, which only depends on d, b and Ω . Furthermore we can use the L^1 bound to obtain an L^∞ bound K_2 from Theorem 3.1 in [1] (see also [4]), where K_2 depends on K_1 and v_0 .

Recall the proof of Lemma 4.7 in [4] (and also use the notation in that proof), when $d_2 > d_{2*}$, we can choose $2d_{2*}/(2 - d + g(K + \varepsilon)) < \varepsilon_0 < 2d_2/(2 - d + g(K + \varepsilon))$, then C_1 depends on a, m, d, Ω and d_{2*} . Therefore the L^∞ bound B^* only depends on C_1 and K_1 . Therefore, there exists $C > 0$ such that $\limsup_{t \rightarrow +\infty} v(x, t) \leq C$ with C independent of u_0, v_0, d_1, d_2 but only on a lower bound of d_2 .

4. If $d_1 = d_2$, we can add the two equations in (1.2) and obtain

$$\begin{cases} w_t - d_1 \Delta w = g(u) f(u) - dv, & \text{in } [T, +\infty) \times \Omega, \\ \frac{\partial w}{\partial n} = 0, & \text{on } [T, +\infty) \times \partial\Omega, \\ w(x, T) = u(x, T) + v(x, T), & \text{in } \Omega, \end{cases}$$

where $w(x, t) = u(x, t) + v(x, t)$. Since when $t > T$, we have

$$g(u) f(u) - dv = g(u) f(u) + du - dw \leq g(K + \varepsilon) f(\bar{\lambda}) + d(K + \varepsilon) - dw,$$

and for the equation

$$\begin{cases} \frac{\partial \phi}{\partial t} = d_1 \Delta \phi + g(K + \varepsilon) f(\bar{\lambda}) + d(K + \varepsilon) - d\phi, & x \in \Omega, t > T, \\ \frac{\partial \phi}{\partial n} = 0, & x \in \partial\Omega, t > T, \end{cases} \tag{2.7}$$

it is well known that the solution $\phi(x, t) \rightarrow d^{-1}[g(K + \varepsilon) f(\bar{\lambda}) + d(K + \varepsilon)]$, then the comparison argument shows that

$$\limsup_{t \rightarrow +\infty} v(x, t) \leq \limsup_{t \rightarrow +\infty} w(x, t) \leq d^{-1}[g(K + \varepsilon) f(\bar{\lambda}) + d(K + \varepsilon)],$$

which implies the last part of (c). \square

Remark 2.2. The global existence and boundedness of the positive solution to (1.2) can also be obtained from a general result of Hollis, Martin and Pierre [15] (see Theorems 1 and 2). Here we show the detailed construction to obtain specific bounds for this particular model.

The results on the dynamical behavior of (1.2) in Theorem 2.1 part (b) and (c) also imply the following results on the steady state solutions of (1.2), which satisfy:

$$\begin{cases} -d_1 \Delta u = g(u) (f(u) - v), & x \in \Omega, \\ -d_2 \Delta v = -dv + g(u)v, & x \in \Omega, \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{2.8}$$

Corollary 2.3. *Suppose that $d, d_1, d_2 > 0$ and Ω is a bounded domain with smooth boundary. Let $(u(x), v(x))$ be a non-negative solution of (2.8). If $d > g(K)$, then $(u(x), v(x))$ must be in form of $(0, 0)$ or $(K, 0)$.*

Proof. From Theorem 2.1 part (c), we have $u(x) \leq K$ and $-d + g(K) \leq 0$. By integrating the second equation of (2.8), we obtain

$$0 \leq d_2 \int_{\Omega} |\nabla v|^2 dx = \int_{\Omega} v^2 (-d + g(u)) dx \leq 0.$$

Hence $v \equiv 0$ on $\bar{\Omega}$. \square

2.2. Permanence

A system is said to be permanent if any state with all component positive initially must ultimately enter and remain within a fixed set of positive states that are strictly bounded away from zero in each component. An autonomous reaction–diffusion systems on a bounded domain which is permanent always exhibits a componentwise positive equilibrium [3]. Recall the definition of permanence of a reaction–diffusion system ([3, page 215]):

Definition 2.4. We shall say that (1.1) is ecologically permanent if there are positive numbers m and M with $m < M$ such that if $(u_1(x, t), \dots, u_n(x, t))$ denotes the solution trajectory to (1.1) with initial condition (u_1^0, \dots, u_n^0) and $u_i^0 > 0$ appropriately for $i = 1, \dots, n$, then there is a $t_0 > 0$ depending only on (u_1^0, \dots, u_n^0) such that

$$m \leq u_i(x, t) \leq M$$

for all $i \in \{1, \dots, n\}$, all $x \in \Omega$ and all $t \geq t_0$.

The criterion for permanence in [4] was expressed in terms of the signs of eigenvalues to linear elliptic differential equations whose coefficients are closely related to the coefficients in (1.1). For the system (1.2), the permanence can be obtained as follows.

Theorem 2.5. Suppose that the hypotheses in Theorem 2.1 are satisfied, and in addition g satisfies

$$(G) \quad g(u) = u\bar{g}(u) \text{ and } \bar{g}(0) \neq 0.$$

If $0 < \lambda < K$ (or equivalently $0 < d < g(K)$), then the system (1.2) is permanent with $u_0(x) \not\equiv 0$, $v_0(x) \not\equiv 0$.

Proof. According to Theorem 2.1, the solutions for the system (1.2) are bounded from above uniformly. Moreover, let σ_1 , σ_2 and ψ_1 , ψ_2 be the largest eigenvalue and the corresponding eigenfunctions of

$$\begin{cases} d_1 \Delta \psi + (\bar{g}(0)f(0)) \psi = \sigma \psi, & x \in \Omega, \\ \frac{\partial \psi}{\partial n} = 0, & x \in \partial \Omega, \end{cases} \quad \begin{cases} d_2 \Delta \psi + (-d + g(K)) \psi = \sigma \psi, & x \in \Omega, \\ \frac{\partial \psi}{\partial n} = 0, & x \in \partial \Omega, \end{cases}$$

respectively. If $g(K) > g(\lambda) = d$ (or equivalently $0 < \lambda < K$), then $\sigma_2 = g(K) - d > 0$. And we also know that $\sigma_1 = \bar{g}(0)f(0) > 0$. Therefore Theorem 5.7 and Theorem 5.8 in [4] show that the system (1.2) generates a semiflow on $C(\bar{\Omega}) \times C(\bar{\Omega})$ which is permanent. \square

The permanence implies the existence of a componentwise positive equilibrium for the reaction–diffusion system (see Theorem 4.6 in [3]), then Theorem 2.5 implies that (2.8) has a

positive solution when $0 < \lambda < K$. Indeed in this case (λ, v_λ) is a positive constant solution of (2.8).

2.3. Stability of nonnegative equilibria

In this subsection, we consider the local stability of nonnegative equilibria, and also obtain the global stability in some cases.

2.3.1. Local stability

From Theorem 2.1 part (c), the solutions of (1.2) tend to a constant equilibrium when $d > g(K)$. Therefore in the remaining part of the paper, we always assume that $d \leq g(K)$ (or equivalent to $0 < \lambda \leq K$). Recall that $-\Delta$ in $H^1(\Omega)$ under Neumann boundary condition has eigenvalues $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \dots$ and $\lim_{i \rightarrow \infty} \mu_i = \infty$. Let $S(\mu_i)$ be eigenspace corresponding to μ_i with multiplicity $m_i \geq 1$. Let ϕ_{ij} , $1 \leq j \leq m_i$, be the normalized eigenfunctions corresponding to μ_i . Then the set $\{\phi_{ij} : i \geq 0, 1 \leq j \leq m_i\}$ forms a complete orthonormal basis in $L^2(\Omega)$.

The local stability of steady state solutions can be analyzed as follows:

Theorem 2.6. *Suppose that $d, d_1, d_2 > 0$ and Ω is a bounded domain with smooth boundary. Then*

- (a) $(0, 0)$ is unstable for all $\lambda > 0$;
- (b) $(K, 0)$ is locally asymptotically stable for $\lambda > K$ and is unstable for $0 < \lambda < K$;
- (c) If $0 < \lambda < K$, then (λ, v_λ) is locally asymptotically stable for $\bar{\lambda} < \lambda < K$ and is unstable $0 < \lambda < \bar{\lambda}$.

Proof. The linearization of (1.2) at a constant solution $e^* = (u, v)$ can be expressed by

$$\begin{pmatrix} \phi_t \\ \psi_t \end{pmatrix} = L \begin{pmatrix} \phi \\ \psi \end{pmatrix} := D \begin{pmatrix} \Delta \phi \\ \Delta \psi \end{pmatrix} + J_{(u,v)} \begin{pmatrix} \phi \\ \psi \end{pmatrix} \tag{2.9}$$

with domain $X = \left\{ (\phi, \psi) \in H^2(\Omega) \times H^2(\Omega) : \frac{\partial \phi}{\partial n} = \frac{\partial \psi}{\partial n} = 0 \right\}$, where

$$D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}, \quad J_{(u,v)} = \begin{pmatrix} A(u, v) & B(u, v) \\ C(u, v) & D(u, v) \end{pmatrix},$$

and

$$\begin{aligned} A(u, v) &= g'(u)(f(u) - v) + g(u)f'(u), & B(u, v) &= -g(u), \\ C(u, v) &= g'(u)v, & D(u, v) &= g(u) - d. \end{aligned}$$

From Theorem 5.1.1 of [14], it is known that if all the eigenvalues of the operator L have negative real parts, then $e^* = (u, v)$ is asymptotically stable, otherwise, $e^* = (u, v)$ is unstable.

Let $X_{ij} = \{c \cdot \phi_{ij} : c \in \mathbb{R}^2\}$, where $\{\phi_{ij} : 1 \leq j \leq \dim[S(\mu_i)]\}$ is an orthonormal basis of $S(\mu_i)$. For $i \geq 0$, it can be observed that $X = \bigoplus_{i=1}^\infty X_i$ and $X_i = \bigoplus_{j=1}^{\dim[S(\mu_i)]} X_{ij}$ is invariant

under the operator L and σ is an eigenvalue of L if and only if σ is an eigenvalue of the matrix $J_i = -\mu_i D + J_{(u,v)}$ for some $i \geq 0$. So the stability is reduced to consider the characteristic equation

$$\det(\sigma I - J_i) = \sigma^2 - \text{trace } J_i \sigma + \det J_i, \tag{2.10}$$

with

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) + A(u, v) + D(u, v), \\ \det(J_i) &= d_1 d_2 \mu_i^2 - (A(u, v)d_2 + D(u, v)d_1) \mu_i + \det J_{(u,v)}. \end{aligned}$$

1. If $e^* = (0, 0)$, then $J_{(0,0)} = \begin{pmatrix} f(0)g'(0) & 0 \\ 0 & -d \end{pmatrix}$. For $i = 0$, one of the eigenvalues is $f(0)g'(0) > 0$, so $(0, 0)$ is unstable.
2. If $e^* = (K, 0)$, then $J_{(K,0)} = \begin{pmatrix} g(K)f'(K) & -g(K) \\ 0 & -d + g(K) \end{pmatrix}$.
 - (a) When $\lambda > K$, then $-d + g(K) < 0$, so for $i \geq 0$,

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) + g(K)f'(K) - d + g(K) < 0, \\ \det(J_i) &= d_1 d_2 \mu_i^2 + (-g(K)f'(K)d_2 + (d - g(K))d_1) \mu_i + g(K)f'(K)(-d + g(K)) > 0. \end{aligned}$$

Hence $(K, 0)$ is locally asymptotically stable.

- (b) When $\lambda < K$, then $-d + g(K) > 0$. For $i = 0$, $\det(J_i) = g(K)f'(K)(-d + g(K)) < 0$, which implies that (2.10) has at least one root with positive real part. Hence $(K, 0)$ is an unstable steady state solution of (1.2).

3. If $e^* = (\lambda, v_\lambda)$, then $J_{(\lambda,v_\lambda)} = \begin{pmatrix} A(\lambda) & B(\lambda) \\ C(\lambda) & 0 \end{pmatrix}$, where

$$A(\lambda) = g(\lambda)f'(\lambda), \quad B(\lambda) = -g(\lambda), \quad C(\lambda) = g'(\lambda)f(\lambda), \tag{2.11}$$

and we notice that $\bar{\lambda} \in (0, K)$ is the unique root of $f'(\lambda) = 0$.

- (a) When $\bar{\lambda} < \lambda < K$, then $A(\lambda) < 0$, so for $i \geq 0$,

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) + A(\lambda) < 0, \\ \det(J_i) &= d_1 d_2 \mu_i^2 - A(\lambda)d_2 \mu_i + g(\lambda)g'(\lambda)f(\lambda) > 0. \end{aligned} \tag{2.12}$$

Hence (λ, v_λ) is a locally asymptotically stable steady state solution of (1.2).

- (b) When $0 < \lambda < \bar{\lambda}$, then $A(\lambda) > 0$. For $i = 0$,

$$\text{trace}(J_i) = A(\lambda) > 0,$$

which implies that (2.10) has at least one root with positive real part. Hence (λ, v_λ) is an unstable steady state solution of (1.2). \square

2.3.2. Global stability

Now we consider the global stability of the semi-trivial solution $(K, 0)$ and the positive constant solution (λ, v_λ) , respectively.

Theorem 2.7.

- (a) If $\lambda^0 < \lambda \leq K$, where $\lambda^0 \in (\bar{\lambda}, K)$ is the unique λ satisfied $f(\lambda) = f(0)$, then (λ, v_λ) is globally asymptotically stable, that is to say, (λ, v_λ) attracts every positive solution of (1.2);
- (b) If $\lambda > K$ (equivalently $d > g(K)$), then $(K, 0)$ is globally asymptotically stable to the system (1.2).

Proof. We adopt the method of constructing Lyapunov functionals to derive the desired results.

1. When $\lambda^0 < \lambda \leq K$, (λ, v_λ) is the unique positive constant steady state solution to (1.2). We construct a well known Lyapunov functional as follows:

$$V(u(x, t), v(x, t)) = \int_{\Omega} \int_{\lambda}^u \frac{g(\xi) - d}{g(\xi)} d\xi dx + \int_{\Omega} \int_{v_\lambda}^v \frac{\eta - v_\lambda}{\eta} d\eta dx.$$

Then

$$\begin{aligned} V_t(u, v) &= \int_{\Omega} \frac{g(u) - d}{g(u)} u_t dx + \int_{\Omega} \frac{v - v_\lambda}{v} v_t dx \\ &= \int_{\Omega} (g(u) - g(\lambda))(f(u) - f(\lambda)) dx \\ &\quad - d_1 d \int_{\Omega} \frac{g'(u)}{g^2(u)} |\nabla u|^2 dx - d_2 v_\lambda \int_{\Omega} \frac{1}{v^2} |\nabla v|^2 dx. \end{aligned}$$

Therefore, the definition of λ^0 and (a2) imply that $V_t \leq 0$ along an orbit $(u(x, t), v(x, t))$ of system (1.2) with any non-negative initial value $(u_0, v_0) \neq (0, 0)$ or $(K, 0)$. And $V_t = 0$ if and only if $(u(x, t), v(x, t)) = (\lambda, v_\lambda)$, which proves the part (a).

2. When $\lambda > K$, we construct a similar Lyapunov functional as follows:

$$V(u(x, t), v(x, t)) = \int_{\Omega} \int_K^u \frac{g(\xi) - g(K)}{g(\xi)} d\xi dx + \int_{\Omega} v dx.$$

Then

$$\begin{aligned} V_t(u, v) &= \int_{\Omega} \frac{g(u) - g(K)}{g(u)} u_t dx + \int_{\Omega} v_t dx \\ &= \int_{\Omega} (g(u) - g(K)) f(u) dx + \int_{\Omega} (g(K) - d) v dx - d_1 g(K) \int_{\Omega} \frac{g'(u)}{g^2(u)} |\nabla u|^2 dx. \end{aligned}$$

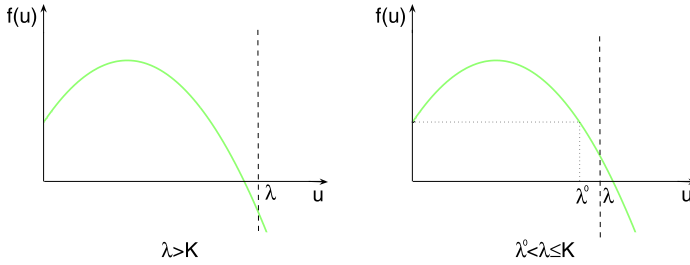


Fig. 2. The schematic diagram of equilibria as global stability.

Therefore, $g(K) < d$ and (a1), (a2) imply that $V_t \leq 0$ along an orbit $(u(x, t), v(x, t))$ of system (1.2) with any non-negative initial value $(u_0, v_0) \neq (0, 0)$ or $(K, 0)$. And $V_t = 0$ if and only if $(u(x, t), v(x, t)) = (K, 0)$, which completes the proof of (b). See Fig. 2. \square

3. Existence and nonexistence of nonconstant positive steady states

In this section we discuss the existence and nonexistence of nonconstant positive solutions of (2.8). Throughout the remaining part of this paper, the solutions refer to the classical solutions, by which we mean solutions in $C^2(\Omega) \cap C^1(\bar{\Omega})$. We will give *a priori* upper and lower bounds for the positive solutions of (2.8).

3.1. A priori estimates and nonexistence of solutions

In this section we discuss the nonexistence of nonconstant positive solutions of (2.8) for certain parameter ranges. To derive some *a priori* estimates for nonnegative solutions of (2.8), we recall the following maximum principle [34]:

Lemma 3.1. *Let Ω be a bounded Lipschitz domain in \mathbb{R}^n , and let $g \in C(\bar{\Omega} \times \mathbb{R})$. If $z \in H^1(\Omega)$ is a weak solution of the inequalities*

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

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

First we have the following *a priori* estimate for any nonnegative solutions for (2.8), using similar argument as the proof of Theorem 2.1 part (c) with $d_1 = d_2$.

Lemma 3.2. *Suppose that $(u(x), v(x))$ is a nonnegative solution of (2.8). Then either (u, v) is one of constant solutions: $(0, 0)$, $(K, 0)$, or for $x \in \bar{\Omega}$, $(u(x), v(x))$ satisfies*

$$0 < u(x) < K, \quad \text{and} \quad 0 < v(x) < C^* = \frac{1}{d}g(K)f(\bar{\lambda}) + \frac{d_1}{d_2}K, \tag{3.1}$$

where $d, d_1, d_2 > 0$.

Proof. Let $(u(x), v(x))$ be a nonnegative solution of (2.8). If there exists $x_0 \in \bar{\Omega}$ such that $v(x_0) = 0$, then $v(x) \equiv 0$ from the strong maximum principle and $u(x)$ satisfies

$$\begin{cases} -d_1 \Delta u = g(u) f(u), & x \in \Omega, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{3.2}$$

From Theorem 10.1.6 of [14], $u \equiv 0$ or $u \equiv K$. Hence if (u, v) is not $(0, 0)$ or $(K, 0)$, then $u(x) > 0$ and $v(x) > 0$ for $x \in \bar{\Omega}$.

From Lemma 3.1, $u(x) \leq K$ and from the strong maximum principle, $u(x) < K$ for all $x \in \bar{\Omega}$. By adding the two equations in (2.8), we have

$$\begin{aligned} -(d_1 \Delta u + d_2 \Delta v) &= g(u) f(u) - dv = \left(g(u) f(u) + \frac{dd_1 u}{d_2} \right) - \frac{d}{d_2} (d_1 u + d_2 v) \\ &\leq \left(g(K) f(\bar{\lambda}) + \frac{dd_1 K}{d_2} \right) - \frac{d}{d_2} (d_1 u + d_2 v). \end{aligned}$$

Then the maximum principle implies that

$$d_1 u + d_2 v < \frac{1}{d} (d_2 g(K) f(\bar{\lambda}) + dd_1 K),$$

which implies the desired estimate. \square

Now we can show the nonexistence of positive steady state solutions when the diffusion coefficients d_1 and d_2 are large.

Theorem 3.3. For any fixed $K, d > 0$, there exists $d^* = d^*(d, \Omega)$ such that if $\min\{d_1, d_2\} > d^*$, then the only nonnegative solutions to (2.8) are $(0, 0)$, $(K, 0)$ and (λ, v_λ) .

Proof. Let (u, v) be a nonnegative solution of (2.8), and denote $\bar{u} = |\Omega|^{-1} \int_{\Omega} u dx$, $\bar{v} = |\Omega|^{-1} \int_{\Omega} v dx$. Then

$$\int_{\Omega} (u - \bar{u}) dx = \int_{\Omega} (v - \bar{v}) dx = 0. \tag{3.3}$$

From (a2), we define $G_k = \max_{0 \leq u \leq K} g'(u)$. Multiplying the first equation in (2.8) by $u - \bar{u}$ and applying Lemma 3.2, we get

$$\begin{aligned} d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx &= \int_{\Omega} (u - \bar{u}) g(u) f(u) dx - \int_{\Omega} (u - \bar{u}) g(u) v dx \\ &= \int_{\Omega} (u - \bar{u}) [g(u) f(u) - g(\bar{u}) f(\bar{u})] dx - \int_{\Omega} (u - \bar{u}) [g(u) v - g(\bar{u}) \bar{v}] dx \end{aligned}$$

$$\begin{aligned}
 &= \int_{\Omega} (u - \bar{u})^2 [g'(\xi)f(\xi) + g(\xi)f'(\xi)] dx \\
 &\quad + \int_{\Omega} (u - \bar{u}) [-g(u)v + g(u)\bar{v} - g(u)\bar{v} + g(\bar{u})\bar{v}] dx \\
 &\leq [G_k f(\bar{\lambda}) + g(K)f'(0)] \int_{\Omega} (u - \bar{u})^2 dx + \int_{\Omega} (u - \bar{u})g(u)[\bar{v} - v] dx \\
 &\quad + \int_{\Omega} (u - \bar{u})\bar{v}[g(\bar{u}) - g(u)] dx \\
 &\leq [G_k f(\bar{\lambda}) + g(K)f'(0)] \int_{\Omega} (u - \bar{u})^2 dx \\
 &\quad + \frac{g^2(K)}{2} \int_{\Omega} (u - \bar{u})^2 dx + \frac{1}{2} \int_{\Omega} (\bar{v} - v)^2 dx. \tag{3.4}
 \end{aligned}$$

Furthermore, adding the two equations in (2.8) and integrating over Ω , we get

$$\int_{\Omega} (-d_1 \Delta u - d_2 \Delta v) dx = \int_{\Omega} [g(u)f(u) - dv] dx, \tag{3.5}$$

then the Neumann boundary conditions lead to

$$d \int_{\Omega} v dx = \int_{\Omega} g(u)f(u) dx \leq g(K)f(\bar{\lambda})|\Omega|. \tag{3.6}$$

Thus

$$\bar{v} = \frac{1}{|\Omega|} \int_{\Omega} v dx \leq \frac{g(K)f(\bar{\lambda})}{d} := V_k. \tag{3.7}$$

In a similar manner, we multiply the second equation in (2.8) by $v - \bar{v}$ to have

$$\begin{aligned}
 d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx &= \int_{\Omega} (v - \bar{v}) (-dv + g(u)v) dx \\
 &= \int_{\Omega} (v - \bar{v}) [(-dv + g(u)v) - (-d\bar{v} + g(\bar{u})\bar{v})] dx \\
 &= -d \int_{\Omega} (v - \bar{v})^2 dx + \int_{\Omega} (v - \bar{v}) [g(u)v - g(\bar{u})\bar{v}] dx
 \end{aligned}$$

$$\begin{aligned}
 &\leq \int_{\Omega} (v - \bar{v})[g(u)v - g(u)\bar{v} + g(u)\bar{v} - g(\bar{u})\bar{v}]dx \\
 &= \int_{\Omega} (v - \bar{v})^2 g(u)dx + \int_{\Omega} (v - \bar{v})\bar{v}[g(u) - g(\bar{u})]dx \\
 &\leq g(K) \int_{\Omega} (v - \bar{v})^2 dx + \int_{\Omega} (v - \bar{v})\bar{v}(u - \bar{u})g'(\xi)dx \\
 &\leq g(K) \int_{\Omega} (v - \bar{v})^2 dx + \frac{V_k^2}{2} \int_{\Omega} (v - \bar{v})^2 dx + \frac{G_k^2}{2} \int_{\Omega} (u - \bar{u})^2 dx. \tag{3.8}
 \end{aligned}$$

From (3.4), (3.8) and the Poincaré inequality, we obtain that

$$\begin{aligned}
 &d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx + d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx \\
 &\leq \frac{1}{\mu_1} \left(A \int_{\Omega} |\nabla(v - \bar{v})|^2 dx + B \int_{\Omega} |\nabla(u - \bar{u})|^2 dx \right),
 \end{aligned}$$

where

$$A = \frac{1}{2} + g(K) + \frac{V_k^2}{2}, \quad B = G_k f(\bar{\lambda}) + g(K)f'(0) + \frac{g^2(K)}{2} + \frac{G_k^2}{2}.$$

This shows that if

$$\min\{d_1, d_2\} > \frac{1}{\mu_1} \max\{A, B\},$$

then

$$\nabla(u - \bar{u}) = \nabla(v - \bar{v}) = 0,$$

and (u, v) must be a constant solution. \square

3.2. Existence of nonconstant positive steady states

From Theorem 2.7, we know that there is no non-constant nonnegative steady states when $\lambda^0 < \lambda \leq K$. In this section we consider the existence of non-constant positive steady states when $\lambda \leq \lambda^0$.

First we cite a Harnack inequality for weak solutions [34].

Lemma 3.4. *Let Ω be a bounded Lipschitz domain in \mathbb{R}^n , and let $c(x) \in L^q(\Omega)$ for some $q > n/2$. If $z \in H^1(\Omega)$ is a nonnegative weak solution of the boundary value problem*

$$\Delta z + c(x)z = 0 \quad \text{in } \Omega, \quad \frac{\partial z(x)}{\partial n} \leq 0 \quad \text{on } \partial\Omega,$$

then there is a constant C_1 , determined only by $\|c\|_q$, q and Ω such that

$$\sup_{\Omega} z \leq C_1 \inf_{\Omega} z.$$

Based on the above preparation, we are ready to derive *a priori* upper and lower bounds for all positive solutions to (2.8). More precisely, we have

Theorem 3.5. *Let Ω be a bounded smooth domain in \mathbb{R}^n . Then, for $\sigma \leq \lambda \leq K$ with some $\sigma > 0$ small enough, there exist two positive constants \underline{C} and \bar{C} with $\underline{C} < \bar{C}$ depending possibly on $d_1, d_2, d, K, \bar{\lambda}, \sigma$ and Ω , such that any positive solution $(u(x), v(x))$ of (2.8) satisfies*

$$\underline{C} \leq u(x), \quad v(x) \leq \bar{C} \quad \text{for any } x \in \bar{\Omega}. \tag{3.9}$$

Proof. From Lemma 3.2, we obtain that for any $x \in \bar{\Omega}$,

$$u(x), v(x) \leq \bar{C} := \max \left\{ K, \frac{1}{d}g(K)f(\bar{\lambda}) + \frac{d_1}{d_2}K \right\},$$

where \bar{C} depends on $d_1, d_2, d, \bar{\lambda}, K$. For the lower bound, let

$$L_1(x) := \frac{1}{d_1} \frac{g(u(x))}{u(x)} [f(u(x)) - v(x)], \quad L_2(x) := \frac{1}{d_2} [-d + g(u(x))],$$

then the mean value theorem implies that $g(u) = g(u) - g(0) = g'(\xi)u$, $\xi \in (0, u)$. Recall G_k defined in Theorem 3.3, we have

$$|L_1(x)| \leq \frac{1}{d_1} G_k (f(\bar{\lambda}) + \bar{C}), \quad |L_2(x)| \leq \frac{1}{d_2} (d + g(K)).$$

Thus Lemma 3.4 implies that there exists a positive constant C_2 depending on $d_1, d_2, d, \bar{\lambda}, K$, and Ω such that

$$\sup_{\Omega} u(x) \leq C_2 \inf_{\Omega} u(x), \quad \sup_{\Omega} v(x) \leq C_2 \inf_{\Omega} v(x).$$

It remains to prove that there exists $C_3 > 0$,

$$\sup_{\Omega} u(x) \geq C_3 \quad \text{and} \quad \sup_{\Omega} v(x) \geq C_3. \tag{3.10}$$

Suppose this is not true, then there exists a sequence of positive solutions $(u_n(x), v_n(x))$ such that

$$\sup_{\Omega} u_n(x) \rightarrow 0 \quad \text{or} \quad \sup_{\Omega} v_n(x) \rightarrow 0 \quad \text{as } n \rightarrow +\infty. \tag{3.11}$$

From the Sobolev embedding theorem and elliptic estimates, there exists a subsequence of (u_n, v_n) , which we still denote by (u_n, v_n) , such that $u_n \rightarrow u_0$ and $v_n \rightarrow v_0$ in $C^2(\bar{\Omega})$ as $n \rightarrow +\infty$. Observe that $u_0 \leq K$ and from (3.11), either $u_0 \equiv 0$ or $v_0 \equiv 0$, and (u_0, v_0) satisfies (2.8). Therefore, we have the following two cases:

- (i) $u_0 \equiv 0, v_0 \not\equiv 0$; or $u_0 \equiv 0, v_0 \equiv 0$.
- (ii) $u_0 \not\equiv 0, v_0 \equiv 0$.

Since (u_n, v_n) is a positive solution of (2.8), then by integrating the second equation in (2.8) for v_n over Ω , we obtain that

$$\int_{\Omega} v_n [-d + g(u_n)] dx = 0.$$

- (i) If $u_0 \equiv 0$, then we have

$$-d + g(u_n) \rightarrow -d + g(u_0) = -g(\lambda) + g(0) \leq -g(\sigma) < 0$$

for any $x \in \bar{\Omega}$ as $n \rightarrow \infty$. Since $v_n > 0$, then for sufficient large n , we obtain

$$\int_{\Omega} v_n (-d + g(u_n)) dx < 0, \tag{3.12}$$

which is a contradiction.

- (ii) If $u_0 \not\equiv 0$ and $v_0 \equiv 0$, then this implies that u_0 satisfies (3.2). So $u_0 \equiv K$ for large n . Thus, we have

$$-d + g(u_n) \rightarrow -d + g(K) \geq 0$$

for large n since $d = g(\lambda) \leq g(K)$.

Then a contradiction with (3.12) is reached. Therefore (3.10) holds and we complete the proof. We remark that the lower bound \underline{C} depends only on $d_1, d_2, d, K, \bar{\lambda}$. \square

When $\sigma \leq \lambda < K$ (where σ is defined in Theorem 3.5), (2.8) has a unique constant positive solution (λ, v_λ) . In this subsection we consider the existence of non-constant positive solutions of (2.8). To show the existence of non-constant positive solutions, we use Leray–Schauder degree theory (see [24,31,34,45,46]). Recall the definition of \underline{C} and \bar{C} from Theorem 3.5, we set

$$\mathbf{X} = \left\{ (u, v) \in [C^1(\bar{\Omega})]^2 : \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \text{ on } \partial\Omega \right\}, \quad \mathbf{X}^+ = \{(u, v) : u, v \geq 0, (u, v) \in \mathbf{X}\},$$

$$\Lambda = \{(u, v) \in \mathbf{X} : \underline{C}/2 \leq u(x), v(x) \leq 2\bar{C} \text{ for } x \in \bar{\Omega}\}.$$

Denote $\mathbf{u} = (u, v)$ and $e^* = (\lambda, v_\lambda)$, and

$$G(\mathbf{u}) = \begin{pmatrix} g(u)(f(u) - v) \\ v(-d + g(u)) \end{pmatrix}, \quad G_{\mathbf{u}}(e^*) = \begin{pmatrix} A(\lambda) & B(\lambda) \\ C(\lambda) & 0 \end{pmatrix},$$

where $A(\lambda), B(\lambda), C(\lambda)$ are defined as in subsection 2.2. Thus, (2.8) can be written as

$$-\Delta\Phi(\mathbf{u}) = G(\mathbf{u}) \quad \text{in } \Omega, \quad \frac{\partial \mathbf{u}}{\partial n} = 0 \quad \text{on } \partial\Omega, \tag{3.13}$$

with $\Phi(\mathbf{u}) = (d_1u, d_2v)^T$. Since the determinant $\det \Phi(\mathbf{u})$ is positive for all non-negative \mathbf{u} , $\Phi_{\mathbf{u}}^{-1}$ exists and for $\sigma \leq \lambda < K$, \mathbf{u} is a positive solution of (3.13) if and only if

$$\mathcal{F}(d_1, d_2, \lambda; \mathbf{u}) \equiv \mathbf{u} - (\mathbf{I} - \Delta)^{-1}[\Phi_{\mathbf{u}}^{-1}G(\mathbf{u}) + \mathbf{u}] = 0, \quad \mathbf{u} \text{ in } \mathbf{X}^+,$$

where $(\mathbf{I} - \Delta)^{-1}$ is the inverse of $\mathbf{I} - \Delta$ in \mathbf{X} with the Neumann boundary condition. As $\mathcal{F}(d_1, d_2, \lambda; \cdot)$ is a compact perturbation of the identity operator, the Leray–Schauder degree $\text{deg}(\mathcal{F}(d_1, d_2, \lambda; \cdot), \Lambda, 0)$ is well defined from Theorem 3.5, and by the homotopy invariance, it is constant for all $\lambda \geq \sigma$. Direct computation gives

$$\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*) = \mathbf{I} - (\mathbf{I} - \Delta)^{-1}[\Phi_{\mathbf{u}}^{-1}(e^*)G_{\mathbf{u}}(e^*) + \mathbf{I}].$$

If $\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*)$ is invertible, i.e. 0 is not an eigenvalue $\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*)$, then the Leray–Schauder Theorem (Theorem 2.8.1 in [31]) implies that

$$\text{index}(\mathcal{F}(d_1, d_2, \lambda; e^*)) = (-1)^\gamma,$$

where $\gamma = \sum \beta < 0 M_\beta$ and M_β is the multiplicity of any negative eigenvalue β of $\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*)$. Then $\text{deg}(\mathcal{F}(d_1, d_2, \lambda; \cdot), \Lambda, 0)$ is equal to the summation of the indices over all solutions to $\mathcal{F} = 0$ in Λ .

To calculate γ , we first define

$$\tilde{H}(d_1, d_2, \lambda; \mu) = \det[\mu\mathbf{I} - \Phi_{\mathbf{u}}^{-1}(e^*)G_{\mathbf{u}}(e^*)] = \frac{1}{d_1d_2}[d_1d_2\mu_i^2 - A(\lambda)d_2\mu_i - B(\lambda)C(\lambda)]. \tag{3.14}$$

By the same arguments as in [33,34,46], β is an eigenvalue of $\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*)$ on X_j if and only if $\beta(1 + \mu_j)$ is an eigenvalue of the matrix

$$M(\mu_j) := \mu_j\mathbf{I} - \Phi_{\mathbf{u}}^{-1}(e^*)G_{\mathbf{u}}(e^*) = \begin{pmatrix} \mu_j - \frac{A(\lambda)}{d_1} & -\frac{B(\lambda)}{d_1} \\ -\frac{C(\lambda)}{d_2} & \mu_j \end{pmatrix}.$$

Thus $\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*)$ is invertible if and only if the matrix $M(\mu_j)$ is non-singular for all $j \geq 0$. We also have that if $\tilde{H}(d_1, d_2, \lambda; \mu_j) \neq 0$, then $\tilde{H}(d_1, d_2, \lambda; \mu_j) < 0$ if and only if the number of negative eigenvalues of $\mathcal{F}_{\mathbf{u}}(d_1, d_2, \lambda; e^*)$ in X_j is odd. Then the following lemma (Theorem 6.1.1 in [46]) gives the explicit formula of calculating the index:

Lemma 3.6. *If $\tilde{H}(d_1, d_2, \lambda; \mu_i) \neq 0$ for all $i \geq 0$, then*

$$\text{index}(\mathcal{F}(d_1, d_2, \lambda; e^*)) = (-1)^\gamma, \quad \gamma = \sum_{i \geq 0, \tilde{H}(d_1, d_2, \lambda; \mu_i) < 0} m(\mu_i),$$

where $m(\mu_i)$ is the algebraic multiplicity of μ_i .

From Lemma 3.6 we see that to calculate the index of $\mathcal{F}(d_1, d_2, \lambda; e^*)$, the key step is to determine the range of μ for which $\tilde{H}(d_1, d_2, \lambda; \mu) < 0$. If $i = 0$, then $\tilde{H}(d_1, d_2, \lambda; 0) = \frac{-B(\lambda)C(\lambda)}{d_1 d_2} = \frac{g(\lambda)g'(\lambda)f(\lambda)}{d_1 d_2} > 0$ for all $\sigma \leq \lambda < K$, which has no contribution to the sum γ in Lemma 3.6. So we assume that $i \geq 1$ in the following.

Indeed non-negative roots of (3.14) exist if and only if $-4d_1 B(\lambda)C(\lambda) - d_2 A^2(\lambda) < 0$. Define $\mu^+(\lambda, d_1, d_2)$ and $\mu^-(\lambda, d_1, d_2)$ to be the two roots of

$$\tilde{H}(d_1, d_2, \lambda; \mu) = 0.$$

Now by using the same method as in [33,34,46], we have the following existence result for the non-constant steady state solutions:

Theorem 3.7. *Let $S = \{\mu_i : i \geq 0\}$ be the set of all eigenvalues of $-\Delta$ in $H^1(\Omega)$ under Neumann boundary condition, and let $A(\lambda)$, $B(\lambda)$ and $C(\lambda)$ be defined as in (2.11). Assume that $\sigma \leq \lambda < K$,*

$$\frac{d_2}{d_1} > \frac{-4B(\lambda)C(\lambda)}{A^2(\lambda)} = \frac{4g'(\lambda)f(\lambda)}{g(\lambda)[f'(\lambda)]^2}, \tag{3.15}$$

and there exist $i, j \in \mathbb{N}_0 = \mathbb{N} \cup \{0\}$, such that

- (a) $0 \leq \mu_j < \mu^-(\lambda, d_1, d_2) < \mu_{j+1} \leq \mu_i < \mu^+(\lambda, d_1, d_2) < \mu_{i+1}$ and
- (b) $\sum_{k=j+1}^i m(\mu_k)$ is odd.

Then (2.8) has at least one non-constant positive solution.

Proof. Consider a mapping $\hat{H} : \Lambda \times [0, 1] \rightarrow \mathbf{X}^+$ by

$$\hat{H}(\mathbf{u}, t) = (-\Delta + I)^{-1} \begin{pmatrix} u + \left(\frac{1-t}{d^*} + \frac{t}{d_1} \right) g(u)(f(u) - v) \\ v + \left(\frac{1-t}{d^*} + \frac{t}{d_2} \right) v(-d + g(u)) \end{pmatrix},$$

where d^* is defined as in Theorem 3.3. It is easy to see that solving (2.8) is equivalent to finding a fixed point of $\hat{H}(\cdot, 1)$ in Λ . According to the choice of d^* in Theorem 3.3, we have that $e^* = (\lambda, v_\lambda)$ is the only fixed point of $\hat{H}(\cdot, 0)$.

Furthermore, we have

$$\text{deg}(I - \hat{H}(\cdot, 0), \Lambda, e^*) = \text{index}(I - \hat{H}(\cdot, 0), e^*) = 1.$$

Since $I - \hat{H}(\cdot, 1) = \mathcal{F}$, and if (2.8) has no other solutions except the constant one e^* , then we have

$$\text{deg}(I - \hat{H}(\cdot, 1), \Lambda, (0, 0)) = \text{index}(\mathcal{F}, e^*) = (-1)^{\sum_{k=j+1}^i m(\mu_k)} = -1.$$

On the other hand, from the homotopy invariance of the Leray–Schauder degree, we have

$$1 = \text{deg}(I - \hat{H}(\cdot, 0), \Lambda, (0, 0)) = \text{deg}(I - \hat{H}(\cdot, 1), \Lambda, (0, 0)) = -1,$$

which is a contradiction. Therefore, there exists at least one non-constant solution of (2.8). \square

The conditions (a) and (b) in Theorem 3.7 define a region in the parameter space $\{(\lambda, d_1, d_2)\}$ for which a non-constant solution of (2.8) exists. This parameter region is usually a union of smaller connected components. When fixing all other parameters but freeing one, the parameter set is usually a union of non-overlapping intervals. This can be seen in the following corollary.

Corollary 3.8. *Let d (or λ) and d_1 be fixed so that (3.15) holds. Define*

$$d_2^j = \frac{B(\lambda)C(\lambda)}{d_1\mu_j^2 - A(\lambda)\mu_j}$$

for $j \in M := \{i \in \mathbb{N} : d_1\mu_i - A(\lambda) < 0\} = \{1, 2, \dots, |M|\}$. Assume that each of μ_j has odd multiplicity for $j \in M$, and the set $\{d_2^i : i \in M\}$ can be relabeled to $\{\widehat{d}_2^i : 1 \leq i \leq |M|\}$ so that

$$\widehat{d}_2^1 > \widehat{d}_2^2 > \dots > \widehat{d}_2^{|M|-1} > \widehat{d}_2^{|M|} > 0.$$

Then (2.8) has at least one non-constant solution for $d_2 \in \bigcup_{1 \leq i \leq \lfloor |M|/2 \rfloor} (\widehat{d}_2^{2i}, \widehat{d}_2^{2i-1})$.

Proof. It is easy to see that γ is odd when $d_2 \in \bigcup_{1 \leq i \leq \lfloor |M|/2 \rfloor} (\widehat{d}_2^{2i}, \widehat{d}_2^{2i-1})$. \square

4. Bifurcation analysis and existence of steady states

In this section we analyze patterned solutions of (1.2) bifurcating from the positive constant equilibrium, which include spatially homogeneous and nonhomogeneous periodic orbits as well as non-constant steady state solutions.

4.1. Determination of bifurcation points

To prove the existence of nonconstant steady state solutions and periodic solutions of (1.2), we further analyze the stability/instability of the constant coexistence steady state (λ, v_λ) . Recall from subsection 3.1, the positive constant coexistence steady state (λ, v_λ) exists if and only if $0 < \lambda < K$ and the precise stability information of (λ, v_λ) is determined by the trace and determinant of J_i ($i \geq 0$), which are defined in (2.12) with $A(\lambda)$, $B(\lambda)$ and $C(\lambda)$ defined in (2.11).

We define

$$\begin{aligned} T(\lambda, p) &= -p(d_1 + d_2) + A(\lambda), \\ D(\lambda, p) &= d_1 d_2 p^2 - d_2 A(\lambda)p - B(\lambda)C(\lambda). \end{aligned} \tag{4.1}$$

We call the set $\{(\lambda, p) \in \mathbb{R}_+^2 : T(\lambda, p) = 0\}$ to be the Hopf bifurcation curve, and the set $\{(\lambda, p) \in \mathbb{R}_+^2 : D(\lambda, p) = 0\}$ to be the steady state bifurcation curve. The studies in [19,42,52] show that the geometric properties of the Hopf and steady state bifurcation curves play an important role in the bifurcation analysis of (1.2).

First for the Hopf bifurcation curve, we notice that $T(\lambda, p) = 0$ is equivalent to $p = A(\lambda)/(d_1 + d_2) = g(\lambda)f'(\lambda)/(d_1 + d_2)$. Recall from subsection 2.2, the following lemma characterizes the profile of the function $A(\lambda)$, and its proof is straightforward calculation thus omitted:

Lemma 4.1. *Assume that (a1) and (a2) hold. Then there exist $0 < \lambda^* < \bar{\lambda} < K$ such that*

- (a) $A(0) = A(\bar{\lambda}) = 0$;
- (b) $A(\lambda) > 0$ in $(0, \bar{\lambda})$; $A(\lambda) < 0$ in $(\bar{\lambda}, \infty)$; $A(\lambda^*) = \max_{0 \leq \lambda \leq \bar{\lambda}} A(\lambda) := M^*$.
- (c) $A'(0) = g'(0)f'(0) + g(0)f''(0) = g'(0)f'(0) > 0$; $A'(\bar{\lambda}) = g'(\bar{\lambda})f'(\bar{\lambda}) + g(\bar{\lambda})f''(\bar{\lambda}) = g(\bar{\lambda})f''(\bar{\lambda}) < 0$. And $A'(\lambda^*) = 0$.

Secondly for the steady state bifurcation curve $D(\lambda, p) = 0$, we notice that for fixed λ , it is a quadratic in p . Indeed we can solve p from $D(p, \lambda) = 0$,

$$p = p_\pm(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{d_2^2 A^2(\lambda) + 4d_1 d_2 B(\lambda)C(\lambda)}}{2d_1 d_2}. \tag{4.2}$$

One can also see that the function $D(p, \lambda)$ has no critical points in the first quadrant, hence the set $\{(\lambda, p) \in \mathbb{R}_+^2 : D(\lambda, p) = 0\}$ must be a bounded connected smooth curve.

In order to analyze the property of p_\pm , (4.2) can be rewritten equivalently as,

$$p = p_\pm(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{C(\lambda) (d_2^2 h(\lambda) + 4d_1 d_2 B(\lambda))}}{2d_1 d_2}, \tag{4.3}$$

where $h(\lambda) = \frac{A(\lambda)^2}{C(\lambda)} = \frac{g(\lambda)^2 f'(\lambda)^2}{g'(\lambda) f(\lambda)}$. We have the following basic property of the function $h(\lambda)$.

Lemma 4.2. *For all $\lambda \in (0, \bar{\lambda})$, $h(\lambda) > 0$; $h(0) = h(\bar{\lambda}) = 0$. $h'(0) > 0$, $h'(\bar{\lambda}) < 0$ and there exists a unique $\lambda^\dagger \in (0, \bar{\lambda})$ such that $h'(\lambda^\dagger) = 0$ and $h(\lambda^\dagger) = \max_{0 \leq \lambda \leq \bar{\lambda}} h(\lambda)$.*

Proof. From the expression of $h(\lambda)$ and $g(0) = 0, f'(\bar{\lambda}) = 0$, it is clearly that $h(0) = h(\bar{\lambda}) = 0$. By direct calculation, it follows that

$$h'(\lambda) = \frac{A(\lambda)[2A'(\lambda)C(\lambda) - A(\lambda)C'(\lambda)]}{C(\lambda)^2}.$$

Denote $\tilde{h}(\lambda) = 2A'(\lambda)C(\lambda) - A(\lambda)C'(\lambda)$. Since $\tilde{h}(0) = 2A'(0)C(0) = 2f(0)f'(0)g'(0)^2 > 0$ and $\tilde{h}(\bar{\lambda}) = 2A'(\bar{\lambda})C(\bar{\lambda}) = 2g(\bar{\lambda})f''(\bar{\lambda})g'(\bar{\lambda})f(\bar{\lambda}) < 0$, then there exists at least one root of $\tilde{h}(\lambda) = 0$ in $(0, \bar{\lambda})$. Moreover, by the continuity of f' and g , $h(\lambda)$ attains its global maximum in $[0, \bar{\lambda}]$ at some $\lambda^\dagger \in (0, \bar{\lambda})$ such that $h(\lambda^\dagger) = \max_{0 \leq \lambda \leq \bar{\lambda}} h(\lambda)$, and apparently $h'(\lambda^\dagger) = 0$. \square

Let $S(\lambda) = d_2^2 A^2(\lambda) + 4d_1 d_2 B(\lambda)C(\lambda)$. From Lemma 4.2, there exist at least two roots of $S(\lambda) = 0$ in $(0, \bar{\lambda})$. We denote the minimal and maximal roots of $S(\lambda) = 0$ in $(0, \bar{\lambda})$ by $0 < \lambda_- < \lambda_+ < \bar{\lambda}$, thus $p_\pm(\lambda)$ exists only for $\lambda \in \Lambda_S := \{\lambda : \lambda_- \leq \lambda \leq \lambda_+ \text{ and } h(\lambda) > 4d_1 d / d_2\}$. We summarize the properties of $p_\pm(\lambda)$ as follows:

Lemma 4.3. *Let $p_\pm(\lambda)$ be the functions defined in (4.2). Then there exist $0 < \lambda_- < \lambda_+ < \bar{\lambda}$ such that $p_\pm(\lambda)$ exists for $\lambda \in \Lambda_S$. Moreover $p_+(\lambda) \geq p_-(\lambda)$ and*

$$\lim_{\lambda \rightarrow \lambda_+} p_\pm(\lambda) = \frac{A(\lambda_+)}{2d_1}, \quad \lim_{\lambda \rightarrow \lambda_-} p_\pm(\lambda) = \frac{A(\lambda_-)}{2d_1}.$$

Hence the steady state bifurcation curve $\{D(\lambda, p) = 0 : p \geq 0, \lambda \geq 0\}$ is a smooth curve connecting $(\lambda, p) = (\lambda_-, \frac{A(\lambda_-)}{2d_1})$ and $(\lambda, p) = (\lambda_+, \frac{A(\lambda_+)}{2d_1})$. Moreover, $p_+(\lambda)$ attains its maximum value M^{**} at $\lambda^{**} \in [\lambda_-, \lambda_+]$ and $p_-(\lambda)$ attains its minimal value M_{**} at $\lambda_{**} \in [\lambda_-, \lambda_+]$, thus the steady state bifurcation curve exists only for $p \in [M_{**}, M^{**}]$.

4.2. Steady state bifurcations

In this subsection we identify bifurcation points λ^S along the branch of the constant steady states $\{(\lambda, \lambda, v_\lambda) : 0 < \lambda < \bar{\lambda}\}$ where non-constant steady state solutions bifurcate from.

In this subsection and also in subsection 4.3, we assume that all eigenvalues μ_i of $-\Delta$ in $H^1(\Omega)$ with Neumann boundary condition are all simple, and denote corresponding eigenfunction by $\phi_i(x)$. Note that this assumption always holds when $n = 1$ for domain $\Omega = (0, \ell\pi)$ that for $i \in \mathbb{N}_0$,

$$\mu_i = \frac{i^2}{\ell^2}, \quad \text{and} \quad \phi_i(x) = \cos(ix/\ell);$$

and it also holds for a generic class of domains in higher dimensions.

Recall from Theorem 2.6, the linearization operator at (λ, v_λ) for (1.2) is

$$L(\lambda) \equiv \begin{pmatrix} d_1 \Delta + A(\lambda) & B(\lambda) \\ C(\lambda) & d_2 \Delta \end{pmatrix}. \tag{4.4}$$

Let

$$\begin{pmatrix} \psi \\ \varphi \end{pmatrix} = \sum_{i=0}^{\infty} \begin{pmatrix} a_i \\ b_i \end{pmatrix} \phi_i(x)$$

be an eigenfunction for $L(\lambda)$ with eigenvalue $\eta(\lambda)$ such that $L(\lambda)(\psi, \varphi)^T = \eta(\lambda)(\psi, \varphi)^T$. Then it is easy to show that for any $i \in \mathbb{N}_0$, $L_i(\lambda)(a_i, b_i)^T = \eta(\lambda)(a_i, b_i)^T$, where

$$L_i(\lambda) := \begin{pmatrix} A(\lambda) - d_1\mu_i & B(\lambda) \\ C(\lambda) & -d_2\mu_i \end{pmatrix}. \tag{4.5}$$

The characteristic equation of $L_i(\lambda)$ is given by

$$\xi^2 - T_i\xi + D_i = 0, \quad i = 0, 1, 2, \dots, \tag{4.6}$$

where

$$\begin{cases} T_i(\lambda) = A(\lambda) - (d_1 + d_2)\mu_i, \\ D_i(\lambda) = -B(\lambda)C(\lambda) - d_2A(\lambda)\mu_i + d_1d_2\mu_i^2. \end{cases} \tag{4.7}$$

From [52], we know that a bifurcation point λ^S satisfies the condition:

(H2): there exists $i \in \mathbb{N}_0$ such that

$$D_i(\lambda^S) = 0, \quad T_i(\lambda^S) \neq 0, \quad \text{and} \quad D_j(\lambda^S) \neq 0, \quad T_j(\lambda^S) \neq 0 \text{ for } j \neq i;$$

and

$$\frac{d}{d\lambda} D_i(\lambda^S) \neq 0.$$

It is well known that the principal eigenvalue of $-\Delta$ in $H^1(\Omega)$ under the Neumann boundary is $\mu_0 = 0$. Then $D_0(\lambda) = g(\lambda)g'(\lambda)f(\lambda) \neq 0$ for any $0 < \lambda < K$, hence we only consider $n \in \mathbb{N}$ and determine the set

$$\Omega_2 := \{\lambda \in (\lambda_-, \lambda_+) : \text{for some } n \in \mathbb{N}, \text{ (H}_2\text{) is satisfied}\}, \tag{4.8}$$

when a set of parameters (d_1, d_2) is given.

From Lemma 4.3, if $M_{**} > \mu_i = p$ or $\mu_i = p > M^{**}$, then there is no $\lambda \in (\lambda_-, \lambda_+]$ such that $D_i(\lambda) = 0$. But for any μ_i satisfying $M_{**} \leq \mu_i \leq M^{**}$, there exists λ_i^S such that $D(\lambda_i^S, \mu_i) = D_i(\lambda_i^S) = 0$ and these λ_i^S are potential steady state bifurcation points. Note that from Lemma 4.3 in subsection 4.1, for each given $i \in \mathbb{N}$, there are at least two λ such that $D(\lambda, \mu_i) = 0$ if $M_{**} \leq \mu_i \leq M^{**}$.

On the other hand, it is possible that for some $\lambda \in (\lambda_-, \lambda_+)$ and some $i \neq j$, we have

$$\mu_j = p_-(\lambda), \quad \text{and} \quad \mu_i = p_+(\lambda). \tag{4.9}$$

Then for this λ , 0 is not a simple eigenvalue of $L(\lambda)$ and we shall not consider bifurcations at such points. However from an argument in [52], for $n = 1$ and $\Omega = (0, \ell\pi)$, there are only

countably many ℓ , such that (4.9) occurs for some $i \neq j$. For general bounded domains in \mathbb{R}^n , one can also show that (4.9) does not occur for generic domains.

Next we verify $\frac{dD_i}{d\lambda}(\lambda_i^S) \neq 0$ if $\lambda_i^S \in \Lambda_S$ and $S(\lambda_i^S) \neq 0$. Indeed one has $D'_i(\lambda) = -B(\lambda)C'(\lambda) - d_2\mu_i A'(\lambda)$, and from the expression of p_{\pm} ,

$$p'_{\pm}(\lambda) = \frac{B(\lambda)C'(\lambda) + d_2A'(\lambda)p_{\pm}(\lambda)}{d_2(2d_1p_{\pm}(\lambda) - A(\lambda))}.$$

Therefore from Lemma 4.3, if $p'_{\pm}(\lambda_i^S) \neq 0$, then $\frac{dD_i}{d\lambda}(\lambda_i^S) \neq 0$ for $\lambda_i^S \in \Lambda_S$ and $S(\lambda_i^S) \neq 0$.

Summarizing the above discussions and using a general bifurcation theorem in [38], we obtain the main result of this section on the global bifurcation of steady state solutions:

Theorem 4.4. *Suppose that $d_1, d_2 > 0$ are fixed. Let Ω be a bounded smooth domain so that its spectral set $S = \{\mu_i : i \geq 0\}$ satisfies*

[S1] *All eigenvalues μ_i are simple for $i \geq 0$;*

[S2] *There exist $l, k \in \mathbb{N}$ such that $0 = \mu_0 < \dots < \mu_{l-1} < M_{**} < \mu_l < \dots < \mu_k < M^{**} < \mu_{k+1}$, where M_{**}, M^{**} are constants depending on d_1, d_2 defined in Lemma 4.3.*

Define $\Sigma_S = \{\lambda_i^S : 1 \leq i \leq 2(k - l + 1)\}$ to be the set of λ satisfying $D(\lambda, \mu_j) = 0$ for $l \leq j \leq k$, and with proper labeling,

$$\lambda_- \leq \lambda_{2(k-l+1)}^S \leq \dots \leq \lambda_2^S \leq \lambda_1^S < \lambda_+.$$

In addition, we assume that

$$\lambda_i^S \neq \lambda_j^S, \quad S(\lambda_i^S) \neq 0, \quad p'_{\pm}(\lambda_i^S) \neq 0 \quad \text{for any } 1 \leq i, j \leq 2(k - l + 1), \quad (4.10)$$

then for $1 \leq i \leq 2(k - l + 1)$:

1. *There is a smooth curve Γ_i of positive solutions of (2.8) bifurcating from $(\lambda, u, v) = (\lambda_i^S, \lambda_i^S, v_{\lambda_i^S})$, with Γ_i contained in a global branch \mathcal{C}_i of positive solutions of (2.8).*
2. *Near $(\lambda, u, v) = (\lambda_i^S, \lambda_i^S, v_{\lambda_i^S})$, $\Gamma_i = \{(\lambda_i(s), u_i(s), v_i(s)) : s \in (-\epsilon, \epsilon)\}$, where $u_i(s) = \lambda_i^S + sa_i\phi_i(x) + s\psi_{1,i}(s)$, $v_i(s) = \lambda_i^S + sb_i\phi_i(x) + s\psi_{2,i}(s)$ for some smooth functions $\lambda_i, \psi_{1,i}, \psi_{2,i}$ such that $\lambda_i(0) = \lambda_i^S$ and $\psi_{1,i}(0) = \psi_{2,i}(0) = 0$. Here (a_i, b_i) satisfies*

$$L(\lambda_i^S)[(a_i, b_i)^T \phi_i(x)] = (0, 0)^T.$$

3. *Either $\overline{\mathcal{C}_i}$ contains another $(\lambda_j^S, \lambda_j^S, v_{\lambda_j^S})$ for $j \neq i$ and $1 \leq j \leq 2(k - l + 1)$, or the projection of $\overline{\mathcal{C}_i}$ onto λ -axis contains the interval $(0, \lambda_i^S)$.*

Proof. The existence and uniqueness of λ_i^S follows from discussions above. Then the local bifurcation result follows from Theorem 3.2 in [52], and it is an application of a more general result Theorem 4.3 in [38].

For the global bifurcation, we apply Theorem 4.3 in [38]. After the change of variables:

$$w_1 = u - \lambda, \quad w_2 = v - v_\lambda,$$

we define a nonlinear equation:

$$F \left(\lambda, \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} \right) = \begin{pmatrix} d_1 \Delta w_1 + g(\lambda + w_1) [f(\lambda + w_1) - (v_\lambda + w_2)] \\ d_2 \Delta w_2 + (v_\lambda + w_2) [-d + g(\lambda + w_1)] \end{pmatrix},$$

with domain

$$V = \left\{ \left(\lambda, \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} \right) : 0 < \lambda < K, (w_1, w_2) \in X \text{ and } w_1 + \lambda \geq 0, w_2 + v_\lambda \geq 0 \right\}.$$

Then $\{(\lambda, 0, 0) : 0 < \lambda < K\}$ is a line of trivial solutions for $F = 0$ and Theorem 4.3 in [38] can be applied to each continuum \mathcal{C}_i bifurcated from $(\lambda_i^S, 0, 0)$. For each continuum \mathcal{C}_i , either $\overline{\mathcal{C}}_i$ contains another $(\lambda_j^S, 0, 0)$ or \mathcal{C}_i is not compact. (Here we do not make an extinction between the solutions of (2.8) and $F = 0$ as they are essentially same, hence we use \mathcal{C}_i for solution continuum for both equations.)

From Lemma 3.2, every solution (u, v) of (2.8) is bounded in L^∞ , then it is also bounded in X from L^p estimates and Schauder estimates. Therefore, if \mathcal{C}_i is not compact, then $\overline{\mathcal{C}}_i$ contains a boundary point $(\tilde{\lambda}, \tilde{w}_1, \tilde{w}_2)$. There are several cases for $\tilde{\lambda}$.

- (a) If $\tilde{\lambda} = 0$, then the projection of $\overline{\mathcal{C}}_i$ onto λ -axis contains $(0, \lambda_i^S)$;
- (b) If $\tilde{\lambda} = K$, then Corollary 2.3 implies that $(\tilde{\lambda} + \tilde{w}_1, v_\lambda + \tilde{w}_2) = (0, 0)$ or $(K, 0)$. But $(u, v) = (0, 0)$ is not a bifurcation point from Theorem 2.6, hence $(\tilde{w}_1 + \tilde{\lambda}, \tilde{w}_2 + v_\lambda)$ must be in a form of $(K, 0)$;
- (c) If $0 < \tilde{\lambda} < K$, then there exists $x_0 \in \bar{\Omega}$ such that $(\tilde{w}_1 + \tilde{\lambda})(x_0) = 0$ or $(\tilde{w}_2 + v_\lambda)(x_0) = 0$ since \tilde{w}_1 and \tilde{w}_2 are bounded from Lemma 3.2. The strong maximum principle implies that $(\tilde{w}_1 + \tilde{\lambda})(x) \equiv 0$ or $(\tilde{w}_2 + v_\lambda)(x) \equiv 0$ for all $x \in \Omega$. If $v \equiv 0$, then $(\tilde{\lambda}, u, v)$ is a solution in form $(\tilde{\lambda}, 0, 0)$ or $(\tilde{\lambda}, K, 0)$. If $u \equiv 0$, then $v \equiv 0$ from maximum principle. Same as in (b), $(\tilde{w}_1 + \tilde{\lambda}, \tilde{w}_2 + v_\lambda)$ also must be in a form of $(K, 0)$. \square

Remark 4.5. We remark that if one uses d_2 as bifurcation parameter, then $d_2 = d_2^j$ defined in Corollary 3.8 are indeed bifurcation points where non-constant solutions stem out from the branch of constant solutions, similar to Theorem 4.4. The result in Theorem 3.7 and Corollary 3.8 shows the existence of non-constant solutions in some more specific parameter regions, which cannot be achieved in bifurcation results since they are essentially local near bifurcation points.

4.3. Hopf bifurcations

In this subsection, we analyze the properties of Hopf bifurcations for (1.2), and we will show the existence of spatial-dependent and independent periodic solutions of system (1.2).

To identify Hopf bifurcation values λ^H , we recall the following sufficient condition from [13, 52]: ($T_i(\lambda)$ and $D_i(\lambda)$ are defined in (4.7))

(H1): There exists $i \in \mathbb{N}_0$ such that

$$T_i(\lambda_0) = 0, \quad D_i(\lambda_0) > 0 \quad \text{and} \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0 \quad \text{for } j \neq i; \quad (4.11)$$

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

$$\alpha'(\lambda_0) \neq 0, \quad \text{and} \quad \omega(\lambda_0) > 0. \quad (4.12)$$

From (4.7), $T_i(\lambda) < 0$ and $D_i(\lambda) > 0$ for all $i \in \mathbb{N}_0$ and $\lambda \in (\bar{\lambda}, 1)$, which implies that the trivial steady state (λ, v_λ) is locally asymptotically stable. Hence any potential Hopf bifurcation point λ^H must be in the interval $(0, \bar{\lambda}]$. In the following we assume that $d_1, d_2 > 0$ are fixed.

First $\lambda_0^H = \bar{\lambda}$ is always a Hopf bifurcation point since $T_0(\lambda_0^H) = A(\lambda_0^H) = 0$ and $T_j(\lambda_0^H) = -(d_1 + d_2)\mu_j^2 < 0$ for any $j \geq 1$; and

$$D_j(\lambda_0^H) = -B(\lambda_0^H)C(\lambda_0^H) + d_1d_2\mu_j^2 > 0$$

for any $j \in \mathbb{N}_0$. This corresponds to the Hopf bifurcation of spatially homogeneous periodic orbits which have been known from the studies in [16]. Apparently λ_0^H is also the unique value λ for the Hopf bifurcation of spatially homogeneous periodic orbits from the uniqueness result of limit cycle in [7,42].

Hence in the following we search for spatially non-homogeneous Hopf bifurcation for $i \geq 1$ in **(H1)**. Again we assume that **[S1]** holds, *i.e.* all eigenvalues μ_i are simple.

Lemma 4.1 implies that $A(0) = A(\bar{\lambda}) = 0$. Therefore we define λ_i^H to be the points λ in $0 < \lambda < \bar{\lambda}$ satisfying $A(\lambda) = (d_1 + d_2)\mu_i$, and such points always exist in pairs. Denote these points by $\lambda_{i,\pm}^H$ ($1 \leq i \leq m$), which satisfy

$$0 < \lambda_{1,-}^H < \dots < \lambda_{m,-}^H < \lambda^* < \lambda_{m,+}^H < \dots < \lambda_{1,+}^H < \lambda_0^H, \quad (4.13)$$

where $A(\lambda^*) = M^*$ is defined in **Lemma 4.1**. Clearly $T_i(\lambda_{i,\pm}^H) = 0$ and $T_j(\lambda_{i,\pm}^H) \neq 0$ for any $j \neq i$. Next we verify that $D_i(\lambda_{i,\pm}^H) > 0$. Indeed (a1) and (a2) imply that $f(\lambda) \geq f(0)$ and $g'(\lambda)$ has a minimum value G_* for $\lambda \in [0, \bar{\lambda}]$. Therefore, for any $\lambda \in [0, \bar{\lambda}]$,

$$\begin{aligned} D_i(\lambda_{i,\pm}^H) &= -B(\lambda_{i,\pm}^H)C(\lambda_{i,\pm}^H) - d_2A(\lambda_{i,\pm}^H)\mu_i + d_1d_2\mu_i^2 \\ &= g(\lambda_{i,\pm}^H)g'(\lambda_{i,\pm}^H)f(\lambda_{i,\pm}^H) - d_2(d_1 + d_2)\mu_i^2 + d_1d_2\mu_i^2 \\ &= g(\lambda_{i,\pm}^H)g'(\lambda_{i,\pm}^H)f(\lambda_{i,\pm}^H) - d_2^2\mu_i^2 \\ &= [g(\lambda_{i,\pm}^H)f'(\lambda_{i,\pm}^H)]^2 \left[\frac{g'(\lambda_{i,\pm}^H)f(\lambda_{i,\pm}^H)}{g(\lambda_{i,\pm}^H)[f'(\lambda_{i,\pm}^H)]^2} - \frac{d_2^2}{(d_1 + d_2)^2} \right] > 0, \end{aligned}$$

if d_1, d_2 satisfy

$$\frac{d_2}{d_1 + d_2} < \min_{\lambda \in [0, \bar{\lambda}]} \sqrt{\frac{g'(\lambda)f(\lambda)}{g(\lambda)[f'(\lambda)]^2}}. \quad (4.14)$$

Finally $D_j(\lambda_i^H) \neq 0$ if $\lambda_i^H \neq \lambda_j^S$ for $1 \leq j \leq k$, which also implies that a Hopf bifurcation point and a steady state bifurcation point do not overlap.

Summarizing our analysis above and applying Theorem 2.1 in [52], we obtain the following results on the Hopf bifurcations:

Theorem 4.6. Recall M^* defined in Lemma 4.1 and suppose that d_1, d_2 satisfy (4.14). Let Ω be a bounded smooth domain so that its spectral set $S = \{\mu_i\}$ satisfies [S1] and

[S3] There exists $m \in \mathbb{N}$ such that $\mu_m < \frac{M^*}{d_1 + d_2} < \mu_{m+1}$.

Define $\Sigma_H = \{\lambda_i^H : 0 \leq i \leq 2m\}$ to be the set of λ satisfying $T(\lambda, \mu_j) = 0$ for $0 \leq j \leq m$, and with proper labeling,

$$0 < \lambda_{2m}^H \leq \dots \leq \lambda_1^H = \lambda_0^H = \bar{\lambda}.$$

In addition, we assume for $0 \leq i \leq 2m$,

$$\lambda_i^H \neq \lambda_j^S, \quad \text{for any } 1 \leq j \leq 2(k - l + 1), \tag{4.15}$$

where λ_j^S are defined in Theorem 4.4. Then for each $0 \leq i \leq 2m$,

1. (1.2) undergoes a Hopf bifurcation at $\lambda = \lambda_i^H$; there is a smooth curve Λ_i of positive periodic orbits of (1.2) bifurcating from $(\lambda, u, v) = (\lambda_i^H, \lambda_i^H, v_{\lambda_i^H})$, with Λ_i contained in a global branch \mathcal{P}_i of positive periodic orbits of (1.2).
2. The bifurcating periodic orbits from $\lambda = \lambda_0^H$ are spatially homogeneous, which coincides with the periodic orbits of the corresponding ODE system (see [42]); the Hopf bifurcation at $\lambda = \lambda_0^H$ is supercritical and backward; the bifurcating spatially homogeneous periodic orbits are locally asymptotically stable near $\lambda = \lambda_0^H$.
3. The bifurcating periodic orbits from $\lambda = \lambda_i^H$ with $1 \leq i \leq 2m$ are spatially nonhomogeneous; near bifurcation point, they are in a form of

$$\begin{aligned} &(\lambda, u, v) \\ &= (\lambda_i^H + o(s), \lambda_i^H + se_i \cos(\omega(\lambda_i^H)t)\phi_i(x) + o(s), v_{\lambda_i^H} + sf_i \cos(\omega(\lambda_i^H)t)\phi_i(x) + o(s)), \end{aligned}$$

for $s \in (0, \delta)$, where $\omega(\lambda_i^H) = \sqrt{D_i(\lambda_i^H)}$ is the corresponding time frequency, $\phi_i(x)$ is the corresponding spatial eigenfunction, and (e_i, f_i) is a corresponding eigenvector.

4. For $1 \leq i \leq 2m$, the global branch of spatially nonhomogeneous periodic orbits \mathcal{P}_i satisfies either $\overline{\mathcal{P}_i}$ contains another bifurcation point $(\lambda, u, v) = (\lambda_j^H, \lambda_j^H, v_{\lambda_j^H})$ for $1 \leq j \leq 2m - 1$ and $j \neq i$, or $\overline{\mathcal{P}_i}$ contains a spatially homogeneous periodic orbit on \mathcal{P}_0 , or the projection of $\overline{\mathcal{P}_i}$ onto λ -axis contains the interval $(0, \lambda_i^H)$ or (λ_i^H, K) , or there exists $\hat{\lambda} \in (0, K)$ such that there exists a sequence of spatially nonhomogeneous periodic orbits $(\lambda_s, u_s, v_s) \in \mathcal{P}_i$ such that $\lambda_s \rightarrow \hat{\lambda}$ and the time period of (λ_s, u_s, v_s) tends to ∞ as $s \rightarrow \infty$.

Proof. The local bifurcation results in part 1 and 3 follow from discussions in this section and Theorem 2.1 in [52], and part 2 follows from [16,44] as any solutions of the ODE model are spatially homogeneous solutions of (1.2). The stability assertion in part 2 can be obtained in a similar way as [52] and the calculation in [16]. For the global bifurcation results, we use Theorem 3.3 in [48] for the abstract setting. Indeed to obtain the four alternatives stated here, we have to use a more general version of global bifurcation theorem restricted to the positive cone in the function space, which is similar to the corresponding result in [38] for steady state solutions. Note that from Theorem 2.1, we know that all periodic orbits are uniformly bounded for $\lambda \in [0, K]$. \square

Acknowledgments

We sincerely thank the very detailed and helpful referee reports by the anonymous reviewers and helpful suggestions by the editors.

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