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Pattern formation in a general glycolysis reaction–diffusion system

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A general reaction–diffusion system modelling glycolysis is investigated. The parameter regions for the stability and instability of the unique constant steady-state solution is derived, and the existence of time-periodic orbits and non-constant steady-state solutions are proved by the bifurcation method and Leray–Schauder degree theory. The effect of various parameters on the existence and non-existence of spatiotemporal patterns is analysed.

Keywords: reaction–diffusion system; glycolysis model; stability, Hopf bifurcation; steady-state bifurcation; non-constant positive solutions.

1. Introduction

In the early 1950s, the British mathematician Turing (1952) 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 configuration due to so-called *diffusion-driven instability*, that is, diffusion could destabilize an otherwise stable equilibrium of the reaction–diffusion system and lead to non-uniform 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, Auchmuty & Nicolis (1975a,b), Brown & Davidson (1995), Catllá *et al.* (2012), Ghergu (2008), Ghergu & Rădulescu (2010), Kolokolnikov *et al.* (2006), Peng & Wang (2005), You (2007) and Zhou & Mu (2010) for Brusselator model; Doelman *et al.* (1997), Hale *et al.* (1999), Mazin *et al.* (1996), McGough & Riley (2004), Peng & Wang (2009), Wei (2001) and You (2011a,b, 2012b) for Gray–Scott model; Du & Wang (2010), Jang *et al.* (2004), Jin *et al.* (2013), Ni (2004), Ni & Tang (2005) and Yi *et al.* (2008, 2009b) for Lengyel–Epstein model; Peng & Sun (2010), You (2012a) for a Oregonator model and Ghergu & Radulescu (2011), Iron *et al.* (2004), Schnakenberg (1979), Ward & Wei (2002) and Wei & Winter (2008, 2012) for Schnakenberg model.

Glycolysis, which occurs in the cytosol, is thought to be the archetype of a universal metabolic pathway for cellular energy requirement. The wide occurrence of glycolysis indicates that it is one of the most ancient known metabolic pathways and a common way of providing limited energy for the organism in living nature. However, its significance lies in that it can supply the energy with a rapid speed, but more importantly under oxygen-free conditions such as strenuous exercise and high-altitude hypoxia. Glycolysis model turns out to be a classic and representative system in biochemical reaction. All glycolysis models are based on the same reaction scheme. The difference between the model stems from the difference in the mechanism for key enzyme reaction (see Bhargava, 1980; Guo *et al.*, 2012; Higgins, 1964; Peng *et al.*, 2008; Sel'Kov, 1968). In Segel (1980), Othmer & Aldridge (1977) and Tyson & Kauffman (1975), the following dimensionless glycolysis system was proposed:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \dfrac{\partial^2 u}{\partial x^2} + bv - u + u^2 v, & x \in (0, \ell),\ t > 0, \\ \dfrac{\partial v}{\partial t} = d_2 \dfrac{\partial^2 v}{\partial x^2} + a - bv - u^2 v, & x \in (0, \ell),\ t > 0. \end{cases} \tag{1.1}$$

Here, the reactions occur in an interval $(0, \ell)$, $u(x,t)$ and $v(x,t)$ represent chemical concentrations, d_1 and d_2 are the diffusion coefficients, a is the dimensionless input flux and b is the dimensionless constant rate for the low activity state. Concerning this model for a two-cell system, there are some stability results (see Ashkenazi & Othmer, 1977; Tyson & Kauffman, 1975). For $b = 0$, the model is called Sel'klov model, which was studied extensively in recent years (see Davidson & Rynne, 2000; Furter & Eilbeck, 1995; López-Gómez *et al.*, 1992; Peng, 2007; Peng *et al.*, 2006; Sel'Kov, 1968; Wang, 2003).

The goal of this paper is to give a comprehensive mathematical study of the general glycolysis model. In particular, we are interested in the spatiotemporal pattern formation and bifurcations in the glycolysis model, and the effect of system parameters and diffusion coefficients on the glycolysis model dynamics. For that purpose, we consider the following system defined in a general bounded domain:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + bv - u + f(u)v, & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + a - bv - f(u)v, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geqslant 0,\ v(x,0) = v_0(x) \geqslant 0, & x \in \Omega, \end{cases} \tag{1.2}$$

where $\Omega \subset \mathbb{R}^N$, $N \geqslant 1$, is a bounded domain with a smooth boundary $\partial\Omega$, Δ is the Laplace operator with respect to the spatial variable $x = (x_1, \ldots, x_N)$ and a no-flux boundary condition is assumed so that the chemical reactions occur in a closed reactor. The parameters a, b, d_1 and d_2 are the same as in (1.1), and a, b, d_1 and d_2 positive constants. The function f is always assumed to satisfy

(f_0) $f \in C^1(0,\infty) \cap C[0,\infty), f(0) = 0, f(u) > 0$ and $f'(u) > 0$ for $u \in (0,\infty)$.

A typical choice of $f(u)$ is $f(u) = u^m$ for $m \geqslant 1$ in the context of autocatalytic chemical reactions, and m is the order of chemical reaction. It is known that the exponent m may have an impact on the stability of non-constant steady-state solutions of (1.2) (Iron *et al.*, 2004; Wei & Winter, 2014). Here we use a rather general form of $f(u)$, so it can also be used for non-power function-type reaction rates. For example, the Hill function $f(u) = u^m/(h^m + u^m)$ is often used in chemical kinetics when (1.2) is derived from a larger system under a quasi-steady-state assumption (Higgins, 1964; Sel'Kov, 1968).

The existence and uniqueness of a solution $u(x,t), v(x,t)$ to the evolution system (1.2) for $t \in (0,\infty)$, $x \in \bar{\Omega}$ can be obtained by applying a result in Hollis & Pierre (1987) if (f_0) is strengthened to

(f_1) $f \in C^1[0,\infty)$ and there exist constants $C > 0$ and $\gamma > 1$ such that $|f(u)| \leqslant C(1+u)^{\gamma}$ for any $u \geqslant 0$.

If f only satisfies (f_0) and f is assumed to be sublinear, that is,

(f_2) for $u \in (0,\infty)$, the function $f(u)/u$ is non-increasing and $\lim_{u\to\infty}(f(u)/u) = 0$,

then the existence of a global solution to (1.2) follows from the proof of Theorem 2.1 in Ghergu & Rădulescu (2010). In this paper, we focus on the question of existence and stability of steady-state solutions and periodic orbits of (1.2). The steady-state equation associated with (1.2) is

$$\begin{cases} d_1 \Delta u + bv - u + f(u)v = 0, & x \in \Omega, \\ d_2 \Delta v + a - bv - f(u)v = 0, & x \in \Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{1.3}$$

It is easy to see that (1.3) possesses a unique positive constant steady-state solution

$$(u, v) = (a, a/\lambda), \tag{1.4}$$

where $\lambda := f(a) + b$. Since f is increasing, then λ is a more convenient parameter to use than b, and we will use λ as an equivalent parameter in many places of the paper.

Our main results for (1.2) and (1.3) can be summarized as follows:

(a) The constant steady-state solution $(a, a/\lambda)$ is locally asymptotically stable either when b is large or a is small (regardless of d_1 and d_2), or when d_1/d_2 is large (regardless of a and b); in a certain more special choice of parameters and function $f(u)$, it is shown that $(a, a/\lambda)$ is globally asymptotically stable (see Section 2.2).

(b) The constant steady-state solution $(a, a/\lambda)$ is the only steady-state solution of (1.2) either when a is small (regardless of b, d_1 and d_2), or when d_1 is large (regardless of a, b and d_2) (see Section 3.2).

(c) Fixing a, d_1 and d_2, and using b as the bifurcation parameter, there exist $n_0 + 1$ Hopf bifurcation points where periodic orbits of (1.2) bifurcating from the constant solution $(a, a/\lambda)$, and there exist n_1 steady-state bifurcation points where non-constant steady-state solutions of (1.2) bifurcating from the constant solution $(a, a/\lambda)$. Here n_0 and n_1 are non-negative integers which are determined by the domain Ω, and parameters a, d_1 and d_2 (see Sections 2.3 and 2.4).

(d) When the fixed-point index of the constant steady-state solution $(a, a/\lambda)$ is -1, then there exists at least a non-constant steady-state solution of (1.2). It is shown that the fixed-point index of $(a, a/\lambda)$ being -1 can be achieved for a non-empty region in the parameter space of (a, b, d_1, d_2). In particular, for fixed a, d_1 and d_2, such region for b is the union of finitely many non-overlapping intervals; and for fixed a, b, d_2 satisfying an additional condition, such region for d_1 is the union of infinitely many non-overlapping intervals which converge to $d_1 = 0$. All these intervals can be explicitly calculated (see Section 3.3).

The results in parts (a) and (b) indicate for what parameter ranges, non-constant patterns are not possible for (1.3); and the results in parts (c) and (d) show that, for other parameter ranges, time-periodic patterns and non-constant stationary patterns are possible. These patterns have been predicted by Turing (1952) for a wide class of reaction–diffusion models. The results in part (c) are proved using bifurcation theory, and the ones in part (d) are proved by using topological degree theory. These results complement each other nicely: the bifurcation results can show the rough spatial profile of the patterns, but patterns are only shown for parameters near bifurcation points; on the other hand, the degree theoretical results hold for a larger parameter region, but there is no information about the pattern profile. By using both techniques, a better picture of the non-constant patterns is obtained here.

The organization of the remaining part of the paper is as follows. In Section 2, we analyse the stability of the uniform steady state $(u, v) = (a, a/\lambda)$, and we use bifurcation theory to prove the existence of periodic orbits and non-constant steady-state solutions. Some numerical simulations of periodic orbits and non-constant steady-state solutions are also shown at the end of Section 2. In Section 3, we prove the existence and non-existence of positive steady-state solutions by using *a priori* estimates, energy estimates, asymptotic analysis and Leray–Schauder degree theory. Throughout this paper, $\mathbb{N}$ is the set of natural numbers and $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$. The eigenvalues of operator $-\Delta$ with homogeneous Neumann boundary condition in Ω are denoted by $0 = \mu_0 < \mu_1 \leqslant \mu_2 \leqslant \cdots \leqslant \mu_n \leqslant \cdots$, and the eigenfunction corresponding to μ_n is $\phi_n(x)$.

2. Stability and bifurcation

2.1 *Stability with respect to the ODE model*

We first consider the ODE model corresponding to (1.2) with f satisfying (f_0):

$$\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = bv - u + f(u)v, & t > 0, \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = a - bv - f(u)v, & t > 0. \end{cases} \tag{2.1}$$

By (1.4), $(a, a/\lambda)$ is the unique positive equilibrium of (2.1). In the following, we fix the parameter $a > 0$ and use λ as the main bifurcation parameter. Note that the parameter λ is equivalent to b with $b > 0$ corresponds to $\lambda > f(a)$. The Jacobian matrix of system (2.1) at $(a, a/\lambda)$ is

$$L_0(\lambda) = \begin{pmatrix} A(\lambda) & \lambda \\ B(\lambda) & -\lambda \end{pmatrix}, \tag{2.2}$$

where

$$A(\lambda) = \frac{af'(a)}{\lambda} - 1 \quad \text{and} \quad B(\lambda) = -\frac{af'(a)}{\lambda}. \tag{2.3}$$

The characteristic equation of $L_0(\lambda)$ is

$$\xi^2 - T(\lambda)\xi + D(\lambda) = 0, \tag{2.4}$$

where

$$\begin{cases} T(\lambda) = A(\lambda) - \lambda, \\ D(\lambda) = -\lambda(A(\lambda) + B(\lambda)) = \lambda. \end{cases}$$

The equilibrium $(a, a/\lambda)$ is locally asymptotically stable if $T(\lambda) < 0$ and $D(\lambda) > 0$. Apparently, $D(\lambda) > 0$ holds for any $\lambda > f(a)$, thus $(a, a/\lambda)$ is locally asymptotically stable if $A(\lambda) < \lambda$. Indeed, define

$$\bar{\lambda}_0 := \frac{-1 + \sqrt{1 + 4af'(a)}}{2}. \tag{2.5}$$

Then $\lambda = \bar{\lambda}_0$ is the only root of $T(\lambda) = 0$. The equilibrium $(a, a/\lambda)$ is locally asymptotically stable if $\lambda > \bar{\lambda}_0$, and it is unstable if $\lambda < \bar{\lambda}_0$. This bifurcation point $\lambda = \bar{\lambda}_0$ is only valid if $\bar{\lambda}_0 > f(a)$. Recall that a Hopf bifurcation value λ satisfies the following conditions:

$$T(\lambda) = 0, \quad D(\lambda) > 0 \quad \text{and} \quad T'(\lambda) \neq 0.$$

Since $T'(\lambda) = -af'(a)/\lambda^2 - 1 < -1 < 0$, then $\lambda = \bar{\lambda}_0$ is the unique Hopf bifurcation point for (2.2) if $f(a) < \bar{\lambda}_0$. From Poincaré–Bendixson theory, the system (2.1) possesses a periodic orbit when $\lambda < \bar{\lambda}_0$, but the uniqueness is not known.

2.2 *Stability with respect to the PDE model*

Next, we consider the stability of the constant equilibrium $(a, a/\lambda)$ with respect to the PDE model (1.2). Linearizing the system (1.2) about the constant equilibrium $(a, a/\lambda)$, we obtain an eigenvalue problem

$$\begin{cases} d_1 \Delta\phi + A(\lambda)\phi + \lambda\psi = \mu\phi, & x \in \Omega, \\ d_2 \Delta\psi + B(\lambda)\phi - \lambda\psi = \mu\psi, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial\nu} = \dfrac{\partial\psi}{\partial\nu} = 0, & x \in \partial\Omega, \end{cases} \tag{2.6}$$

where $A(\lambda)$ and $B(\lambda)$ are defined as in (2.3).

Denote

$$L(\lambda) := \begin{pmatrix} d_1\Delta + A(\lambda) & \lambda \\ B(\lambda) & d_2\Delta - \lambda \end{pmatrix}. \tag{2.7}$$

For each $n \in \mathbb{N}_0$, we define a 2×2 matrix

$$L_n(\lambda) := \begin{pmatrix} -d_1\mu_n + A(\lambda) & \lambda \\ B(\lambda) & -d_2\mu_n - \lambda \end{pmatrix}. \tag{2.8}$$

Then, the following statements hold true by using Fourier decomposition:

1. If μ is an eigenvalue of (2.6), then there exists $n \in \mathbb{N}_0$ such that μ is an eigenvalue of $L_n(\lambda)$.
2. The constant equilibrium $(a, a/\lambda)$ is locally asymptotically stable with respect to (1.2) if and only if, for every $n \in \mathbb{N}_0$, all eigenvalues of $L_n(\lambda)$ have negative real part.

3. The constant equilibrium $(a, a/\lambda)$ is unstable with respect to (1.2) if there exists an $n \in \mathbb{N}_0$ such that $L_n(\lambda)$ has at least one eigenvalue with non-negative real part.

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

$$\mu^2 - T_n(\lambda)\mu + D_n(\lambda) = 0, \tag{2.9}$$

where

$$T_n(\lambda) = A(\lambda) - \lambda - (d_1 + d_2)\mu_n, \tag{2.10}$$

$$D_n(\lambda) = d_1 d_2 \mu_n^2 + (d_1\lambda - d_2 A(\lambda))\mu_n - \lambda(A(\lambda) + B(\lambda)). \tag{2.11}$$

Then $(a, a/\lambda)$ is locally asymptotically stable if $T_n(\lambda) < 0$ and $D_n(\lambda) > 0$ for all $n \in \mathbb{N}_0$, and $(a, a/\lambda)$ is unstable if there exists $n \in \mathbb{N}_0$ such that $T_n(\lambda) \geqslant 0$ or $D_n(\lambda) \leqslant 0$.

To obtain more precise stability results, we define

$$\begin{aligned} T(\lambda, \mu) &:= A(\lambda) - \lambda - (d_1 + d_2)\mu = \frac{af'(a)}{\lambda} - 1 - \lambda - (d_1 + d_2)\mu \\ D(\lambda, \mu) &:= d_1 d_2 \mu^2 + (d_1\lambda - d_2 A(\lambda))\mu - \lambda(A(\lambda) + B(\lambda)) \\ &= (d_1\mu + 1)(d_2\mu + \lambda) - \frac{d_2 af'(a)\mu}{\lambda}, \end{aligned} \tag{2.12}$$

and

$$H := \{(\lambda, \mu) \in (0, \infty) \times [0, \infty) : T(\lambda, \mu) = 0\},$$
$$S := \{(\lambda, \mu) \in (0, \infty) \times [0, \infty) : D(\lambda, \mu) = 0\}.$$

Then H is the Hopf bifurcation curve and S is the steady-state bifurcation curve (see Wang *et al.*, 2011; Yi *et al.*, 2009a). Furthermore, the sets H and S are graphs of functions defined as follows:

$$\begin{aligned} \lambda_H(\mu) &= \frac{1}{2}[-((d_1 + d_2)\mu + 1) + \sqrt{((d_1 + d_2)\mu + 1)^2 + 4af'(a)}], \\ \lambda_S(\mu) &= \frac{1}{2}\left(-d_2\mu + \sqrt{d_2^2\mu^2 + \frac{4d_2 af'(a)\mu}{d_1\mu + 1}}\right). \end{aligned} \tag{2.13}$$

We also solve μ from $D(\lambda, \mu) = 0$:

$$\mu = \mu_\pm(\lambda) = \frac{d_2 A(\lambda) - d_1\lambda \pm \sqrt{(d_2 A(\lambda) - d_1\lambda)^2 - 4d_1 d_2 \lambda}}{2d_1 d_2}. \tag{2.14}$$

We have the following properties of the functions $\lambda_H(\mu)$ and $\lambda_S(\mu)$ (see Fig. 1).

LEMMA 2.1 Suppose that $a, d_1, d_2 > 0$ are fixed. Let $\bar{\lambda}_0$ be defined as in (2.5), and let $\lambda_H(\mu)$ and $\lambda_S(\mu)$ be the functions defined in (2.13). Then the following conditions are satisfied:

1. The function $\lambda_H(\mu)$ is strictly decreasing for $\mu \in [0, \infty)$ such that $\lambda_H(0) = \bar{\lambda}_0$ and $\lim_{\mu\to\infty} \lambda_H(\mu) = 0$.

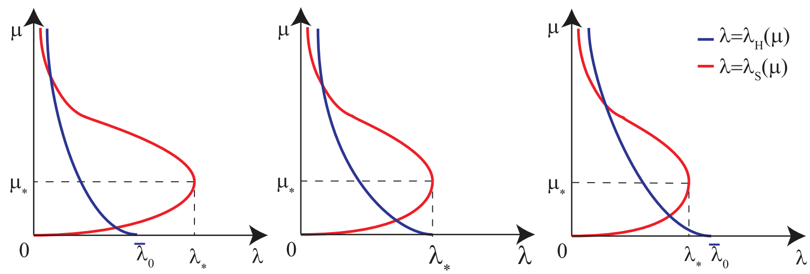

FIG. 1. The graphs of $\lambda_H(\mu)$ (decreasing curve) and $\lambda_S(\mu)$ (parabola-like curve). Left: $\bar{\lambda}_0 < \lambda_*$; middle: $\bar{\lambda}_0 = \lambda_*$ and right: $\lambda_* < \bar{\lambda}_0$.

2. Define

$$\mu_* := \frac{-\sqrt{d_1 d_2} + \sqrt{d_1 d_2 + 4d_1\sqrt{d_1 d_2 a f'(a)}}}{2d_1\sqrt{d_1 d_2}}. \tag{2.15}$$

Then $\mu = \mu_*$ is the unique critical point of $\lambda_S(\mu)$, the function $\lambda_S(\mu)$ is strictly increasing for $\mu \in (0, \mu_*)$ and $\lambda_S(\mu)$ is strictly decreasing for $\mu \in (\mu_*, \infty)$. Furthermore,

$$\lambda_S(0) = 0, \quad \lambda_S(\mu) \leqslant \lambda_S(\mu_*) = d_1 d_2 \mu_*^2 := \lambda_*, \quad \lim_{\mu\to\infty} \lambda_S(\mu) = 0.$$

Moreover, if $f(a) < \lambda_*$, then there exists exactly two positive constants $\mu^1 < \mu_* < \mu < \mu^2$ such that $\lambda_S(\mu^1) = \lambda_S(\mu^2) = f(a)$, $\lambda_S(\mu) \in (f(a), \lambda_*]$ if $\mu \in (\mu^1, \mu^2)$, and $0 < \lambda_S(\mu) < f(a)$ if $\mu \in (0, \mu^1) \cup (\mu^2, \infty)$. Consequently, for $f(a) \leqslant \lambda \leqslant \lambda_*$, $\mu_\pm(\lambda)$ are well defined as in (2.14); $\mu_+(\lambda)$ is strictly decreasing in $(f(a), \lambda_*)$, $\mu_-(\lambda)$ is strictly increasing in $(f(a), \lambda_*)$, $\mu_+(f(a)) = \mu^2$, $\mu_-(f(a)) = \mu^1$ and $\mu_+(\lambda_*) = \mu_-(\lambda_*) = \mu_*$.

3. $\{(\lambda, \mu) \in (0, \infty) \times [0, \infty) : T(\lambda, \mu) < 0\} = \{\lambda > \lambda_H(\mu),\ \mu \geqslant 0\}$ and $\{(\lambda, \mu) \in (0, \infty) \times [0, \infty) : D(\lambda, \mu) > 0\} = \{\lambda > \lambda_S(\mu),\ \mu \geqslant 0\}$.

Proof. We only prove the second conclusion since the first one is obvious by the fact that $\lambda_H(\mu)$ is the inverse function of $\mu_H(\lambda) := (1/(d_1 + d_2))(af'(a)/\lambda - 1 - \lambda)$, and the third one follows from the first one and the second one. Differentiating $\lambda_S(\mu)$, we get

$$\begin{aligned}
2\lambda_S'(\mu) &= \frac{d_2}{\sqrt{d_2^2\mu^2 + 4d_2 af'(a)\mu/(d_1\mu + 1)}}\left(-\sqrt{d_2^2\mu^2 + \frac{4d_2 af'(a)\mu}{d_1\mu + 1}} + d_2\mu + \frac{2af'(a)}{(d_1\mu + 1)^2}\right)\\
&= M(d_1, d_2, a, \mu)(af'(a) + d_2\mu(d_1\mu + 1)^2 - d_2\mu(d_1\mu + 1)^3)\\
&= M(d_1, d_2, a, \mu)(af'(a) - d_1 d_2\mu^2(d_1\mu + 1)^2)\\
&= M(d_1, d_2, a, \mu)(\sqrt{af'(a)} + \sqrt{d_1 d_2}\mu(d_1\mu + 1))(\sqrt{af'(a)} - \sqrt{d_1 d_2}\mu(d_1\mu + 1))\\
&= M'(d_1, d_2, a, \mu)(\mu_* - \mu),
\end{aligned}$$

where

$$M(d_1,d_2,a,\mu)=\frac{4d_2af'(a)}{\sqrt{d_2^2\mu^2+\frac{4d_2af'(a)\mu}{d_1\mu+1}}\left(\sqrt{d_2^2\mu^2+\frac{4d_2af'(a)\mu}{d_1\mu+1}}+d_2\mu+\frac{2af'(a)}{d_1\mu+1^2}\right)(d_1\mu+1)^4}>0,$$

$$M'(d_1,d_2,a,\mu)=M(d_1,d_2,a,\mu)(\sqrt{af'(a)}+\sqrt{d_1d_2}\mu(d_1\mu+1))\times\left(\mu+\frac{\sqrt{d_1d_2}+\sqrt{d_1d_2+4d_1\sqrt{d_1d_2af'(a)}}}{2d_1\sqrt{d_1d_2}}\right)>0.$$

Furthermore,

$$\lim_{\mu\to\infty}2\lambda_S(\mu)=\lim_{\mu\to\infty}\frac{4d_2af'(a)\mu/(d_1\mu+1)}{d_2\mu+\sqrt{d_2^2\mu^2+4d_2af'(a)\mu/(d_1\mu+1)}}=0.$$

So the second conclusion follows. □

REMARK 2.2 After some calculations, we obtain that

$$\lambda_*=\lambda_*(D)=\frac{1}{2D}\sqrt{1+4\sqrt{Daf'(a)}}\left(\sqrt{1+4\sqrt{Daf'(a)}}-1\right),$$

where $D=d_1/d_2$. Then it is obvious that $\lim_{D\to 0}\lambda_*=\infty$ and $\lim_{D\to\infty}\lambda_*=0$. Furthermore, by the fact of $\lambda_*(D)$ is a continuous function for $D\in(0,\infty)$, we can confirm that all cases listed in Fig. 1 are possible by choosing D properly.

Now, we can give a stability result regarding the constant equilibrium $(a,a/\lambda)$ by the analysis above and the restriction $\lambda>f(a)$. To this end, we define

$$\bar{\lambda}_1=\max_{n\in\mathbb{N}}\lambda_S(\mu_n)\leqslant\lambda_*. \tag{2.16}$$

THEOREM 2.3 Assume a,d_1,d_2 are fixed. Let $\bar{\lambda}_0$, λ_* and $\bar{\lambda}_1$ be the constants defined in (2.5), (2.15) and (2.16), respectively. Then the constant equilibrium $(a,a/\lambda)$ is locally asymptotically stable with respect to (1.2) if λ satisfies

$$\lambda>\max\{f(a),\bar{\lambda}_0,\bar{\lambda}_1\}. \tag{2.17}$$

In particular (2.17) holds if $\lambda>\max\{f(a),\bar{\lambda}_0,\lambda_*\}$.

The result in Theorem 2.3 implies that the constant equilibrium $(a,a/\lambda)$ is locally asymptotically stable when the parameter b satisfies $b>\max\{\bar{\lambda}_0-f(a),\lambda_*-f(a)\}$. Note that $\bar{\lambda}_0$ only depends on a while λ_* depends on $D=d_1/d_2$. Hence a diffusion-induced instability can be achieved if $D=d_1/d_2$ is small.

In general, it is hard to determine whether $(a, a/\lambda)$ is globally asymptotically stable with respect to all initial conditions. In the remaining part of this section, we prove the global stability of $(a, a/\lambda)$ with respect to (1.2) for the special case $f(s) = s^m$ with $m = 1$ or 2:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + bv - u + u^m v, & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + a - bv - u^m v, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geqslant 0,\ v(x,0) = v_0(x) \geqslant 0, & x \in \Omega. \end{cases} \tag{2.18}$$

For the special system (2.18), we have the following global convergence result.

THEOREM 2.4 Let $(u(x,t), v(x,t))$ be a solution of (2.18) with $(u_0(x), v_0(x)) \geqslant (\not\equiv)(0,0)$. Then $\lim_{t\to\infty}(u(x,t), v(x,t)) = (a, a/\lambda)$ if

(1) $m = 1$ and $b > a$; or

(2) $m = 2$, $b > 4a^2$ and $b \geqslant (\max_{x\in\bar{\Omega}} u_0(x))^2$.

The proof of Theorem 2.4 is given in Appendix. The convergence result in Theorem 2.4 for $m = 2$ also holds when

$$b > \frac{a^m}{m^{-1} - m^{-m}} \quad \text{and} \quad b > am\left(\max_{x\in\bar{\Omega}} u_0(x)\right)^{m-1}. \tag{2.19}$$

The convergence result for $m = 1$ is global for any initial conditions, and the one for $m \geqslant 2$ is not global as the initial value u_0 has to be small. If $d_1 = d_2 = d > 0$, we can remove the condition on initial data in (2.19) and get a global stability result as the $m = 1$ case. In fact, by letting $w(x,t) = u(x,t) + v(x,t)$, it follows from (2.18) that w satisfies $w_t = d\Delta w + a - u \leqslant d\Delta w + a + a/b + \varepsilon - w$ for $t \geqslant T_1^\varepsilon$ for some T_1^ε since $v(x,t) \leqslant a/b + \varepsilon$. Thus $\limsup_{t\to\infty} \max_{x\in\bar{\Omega}} w(x,t) \leqslant a + a/b + \varepsilon$. Then there exists $T_2^\varepsilon > T_1^\varepsilon$ such that $u(x,t) \leqslant w(x,t) \leqslant a + a/b + 2\varepsilon$ for $t \geqslant T_2^\varepsilon$. So, $\lim_{t\to\infty}(u(x,t), v(x,t)) = (a, a/\lambda)$ if b is large enough such that

$$b > \frac{a^m}{m^{-1} - m^{-m}} \quad \text{and} \quad b > am\left(a + \frac{a}{b}\right)^{m-1}.$$

2.3 *Hopf bifurcations*

In this subsection, we analyse the Hopf bifurcations from the constant equilibrium $(a, a/\lambda)$ for (1.2), and we will show the existence of spatially homogeneous and spatially inhomogeneous periodic orbits of system (1.2). In this subsection and also Section 2.4, we assume that all eigenvalues μ_i of $-\Delta$ in $H^1(\Omega)$ are simple, and denote the corresponding eigenfunction by $\phi_i(x)$ where $i \in \mathbb{N}_0$. Note that this assumption always holds when $N = 1$ for domain $\Omega = (0, \ell\pi)$, as for $i \in \mathbb{N}_0$, $\mu_i = i^2/\ell^2$ and $\phi_i(x) = \cos(ix/\ell)$, where ℓ is a positive constant; and it also holds for a generic class of domains in higher dimensions.

Recall that $b = \lambda - f(a)$; then (1.2) is equivalent to

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + (\lambda - f(a))v - u + f(u)v, & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + a - (\lambda - f(a))v - f(u)v, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x),\ v(x,0) = v_0(x), & x \in \Omega. \end{cases} \tag{2.20}$$

Again (2.20) has a unique positive constant equilibrium $(a, a/\lambda)$, and we use λ as the main bifurcation parameter. To identify possible Hopf bifurcation value λ^H, we recall the following necessary and sufficient condition from (Hassard *et al.*, 1981; Yi *et al.*, 2009a).

($\mathrm{A_H}$) There exists $i \in \mathbb{N}_0$ such that

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

where $T_i(\lambda)$ and $D_i(\lambda)$ are defined in (2.10) and (2.11), respectively; and for the unique pair of complex eigenvalues $\alpha(\lambda) \pm i\omega(\lambda)$ near the imaginary axis,

$$\alpha'(\lambda^H) \neq 0 \quad \text{and} \quad \omega(\lambda^H) > 0.$$

For $i \in \mathbb{N}_0$, we define

$$\lambda_i^H = \lambda_H(\mu_i), \tag{2.21}$$

where the function $\lambda_H(\mu)$ is defined in (2.13). Then $T_i(\lambda_i^H) = 0$ and $T_j(\lambda_i^H) \neq 0$ for $j \neq i$. By Lemma 2.1, it is easy to see that λ_i^H is strictly decreasing in i and

$$\max_{i \in \mathbb{N}_0} \lambda_i^H = \lambda_0^H = \bar{\lambda}_0 \quad \text{and} \quad \lim_{i \to \infty} \lambda_i^H = 0,$$

where $\bar{\lambda}_0$ is defined in (2.5). Since we require $f(a) < \bar{\lambda}_0$, then there exists an $n_0 \in \mathbb{N}_0$ such that $\lambda_{n_0+1}^H \leqslant f(a) < \lambda_{n_0}^H$. Then we have $n_0 + 1$ possible Hopf bifurcation points at $\lambda = \lambda_j^H$ $(0 \leqslant j \leqslant n_0)$ defined by (2.21), and these points satisfy

$$f(a) < \lambda_{n_0}^H < \lambda_{n_0-1}^H < \cdots < \lambda_1^H < \lambda_0^H.$$

Next, we show that under some additional conditions, $D_j(\lambda_i^H) > 0$ for $0 \leqslant i \leqslant n_0$ and $j \in \mathbb{N}_0$; then in this case we must have $D_i(\lambda_i^H) > 0$ and $D_j(\lambda_i^H) \neq 0$ for $0 \leqslant i \leqslant n_0$ and $j \in \mathbb{N}_0$, as required in the condition ($\mathrm{A_H}$).

If

$$d_1 f^2(a) + d_2 f(a) - d_2 a f'(a) \geqslant 0, \tag{2.22}$$

then

$$D_j(\lambda_i^H) = d_1 d_2 \mu_j^2 + \frac{1}{\lambda_i^H}(d_1(\lambda_i^H)^2 + d_2\lambda_i^H - d_2 a f'(a))\mu_j + \lambda > 0.$$

On the other hand, if (2.22) does not hold, then we still have

$$D_j(\lambda_i^H) \geqslant d_1 d_2 \mu_j^2 + \left(2\sqrt{d_1 d_2} - \frac{d_2 a f'(a)}{f(a)}\right)\mu_j + \lambda$$

$$\geqslant \frac{4d_1 d_2 \lambda - (2\sqrt{d_1 d_2} - d_2 a f'(a)/f(a))^2}{4d_1 d_2} \geqslant \frac{4d_1 d_2 f(a) - (2\sqrt{d_1 d_2} - d_2 a f'(a)/f(a))^2}{4d_1 d_2} > 0,$$

given that

$$4d_1 d_2 f(a) > \left(2\sqrt{d_1 d_2} - \frac{d_2 a f'(a)}{f(a)}\right)^2. \tag{2.23}$$

Finally, let the eigenvalues close to the pure imaginary one near $\lambda = \lambda_i^H$, $0 \leqslant i \leqslant n_0$ be $\alpha(\lambda) \pm i\omega(\lambda)$. Then

$$\alpha'(\lambda_i^H) = \frac{T_i'(\lambda_i^H)}{2} = \frac{1}{2}\left(-\frac{af'(a)}{\lambda_i^H} - 1\right) < -\frac{1}{2} < 0,$$

$$\omega(\lambda_i^H) = \sqrt{D_i(\lambda_i^H)} > 0.$$

Now, by using the Hopf bifurcation theorem in Yi *et al.* (2009a), we have the following theorem.

THEOREM 2.5 Suppose that $a, d_1, d_2 > 0$ are fixed such that $f(a) < \bar{\lambda}_0$ and either (2.22) or (2.23) holds, where $\bar{\lambda}_0$ is defined in (2.5). Let Ω be a bounded smooth domain so that the spectral set $S = \{\mu_i\}_{i\in\mathbb{N}_0}$ satisfies that:

(S_1) all eigenvalues μ_i are simple for $i \in \mathbb{N}_0$.

Then there exists an $n_0 \in \mathbb{N}_0$ such that $\lambda_{n_0+1}^H \leqslant f(a) < \lambda_{n_0}^H$ and for (2.20), there exist $n_0 + 1$ Hopf bifurcation points $\lambda_j^H, j = 0, 1, 2, \ldots, n_0$, defined by (2.21), satisfying

$$f(a) < \lambda_{n_0}^H < \lambda_{n_0-1}^H < \cdots < \lambda_1^H < \lambda_0^H = \bar{\lambda}_0.$$

At each $\lambda = \lambda_j^H$, the system (2.20) undergos a Hopf bifurcation, and the bifurcation periodic orbits near $(\lambda, u, v) = (\lambda_j^H, a, a/\lambda_j^H)$ can be parameterized as $(\lambda(s), u(s), v(s))$, so that $\lambda(s) \in C^\infty$ in the form of $\lambda(s) = \lambda_j^H + o(s)$ for $s \in (0, \delta)$ for some small $\delta > 0$, and

$$\begin{cases} u(s)(x,t) = a + s a_j \cos(\omega(\lambda_j^H)t)\phi_j(x) + o(s), \\ v(s)(x,t) = a/\lambda_j^H + s b_j \cos(\omega(\lambda_j^H)t)\phi_j(x) + o(s), \end{cases}$$

where $\omega(\lambda_j^H) = \sqrt{D_j(\lambda_j^H)}$ is the corresponding time frequency, $\phi_j(x)$ is the corresponding spatial eigenfunction and (a_j, b_j) is the corresponding eigenvector, i.e.

$$[L(\lambda_j^H) - i\omega(\lambda_j^H)I][(a_j, b_j)^\top \phi_j(x)] = (0,0)^\top,$$

where $L(\lambda)$ is defined in (2.7) and I is the identity map. Moreover, the following conditions are satisfied:

1. The bifurcating periodic orbits from $\lambda = \lambda_0^H = \bar{\lambda}_0$ are spatially homogeneous, which coincide with the periodic orbits of the corresponding ODE system.
2. The bifurcating periodic orbits from $\lambda = \lambda_j^H$, $1 \leqslant j \leqslant n_0$, are spatially non-homogeneous.

REMARK 2.6 (i) If $f(a) \geqslant \bar{\lambda}_0$ does not hold, then $(a, a/\lambda)$ is locally asymptotic stable for every $b > 0$ or $\lambda > f(a)$. This occurs for $f(u) = u$ for which $f(a) = a > (-1 + \sqrt{1+4a^2})/2 = \bar{\lambda}_0$ for any $a > 0$.

(ii) If $f(u) = u^m$ with $m > 1$, then the assumptions $f(a) < \bar{\lambda}_0$, and (2.22) or (2.23) are all satisfied if

$$d_2 < d_1, \quad \text{and} \quad \min\left\{\sqrt[m]{\frac{d_2(m-1)}{d_1}}, \sqrt[m]{\frac{(2\sqrt{d_1} - m\sqrt{d_2})^2}{4d_1}}\right\} \leqslant a < \sqrt[m]{m-1}. \tag{2.24}$$

When $m = 2$, then (2.24) becomes

$$d_2 < d_1, \quad \text{and} \quad \min\left\{\sqrt{\frac{d_2}{d_1}}, 1 - \sqrt{\frac{d_2}{d_1}}\right\} \leqslant a < 1. \tag{2.25}$$

(iii) The condition (2.22) or (2.23) is sufficient but not necessary, and Hopf bifurcations indeed occur for a much wider range of parameters (a, d_1, d_2) described by (2.22) or (2.23).

The spatially non-homogeneous periodic orbits bifurcating from $\lambda = \lambda_j^H$, $1 \leqslant j \leqslant n_0$, are all unstable as $L(\lambda_j^H)$ possesses at least one pair of eigenvalues with positive real part. The stability of the spatially homogeneous periodic orbits bifurcating from $\lambda = \lambda_j^0$ can be determined via calculation of normal form. In the next result, we consider the bifurcation direction and stability of the bifurcating periodic orbits bifurcating from $\lambda = \lambda_0^H$ for the case of $f(s) = s^2$ according to Yi *et al.* (2009a).

THEOREM 2.7 Let λ_0^H be defined as in Theorem 2.5. Then, for the system (2.20) with $f(u) = u^2$,

1. If $a > \sqrt{2}/4$ (or equivalently $\lambda_0^H > 1/2$), then the Hopf bifurcation at $\lambda = \lambda_0^H$ is supercritical. That is, for small $\epsilon > 0$ and $\lambda \in (\lambda_0^H, \lambda_0^H + \epsilon)$, there is a small amplitude spatially homogeneous periodic orbit, and this periodic orbit is locally asymptotically stable.
2. If $a < \sqrt{2}/4$ (or equivalently $\lambda_0^H < 1/2$), then the Hopf bifurcation at $\lambda = \lambda_0^H$ is subcritical. That is, for small $\varepsilon > 0$ and $\lambda \in (\lambda_0^H - \varepsilon, \lambda_0^H)$, there is a small amplitude spatially homogeneous periodic orbit, and this periodic orbit is unstable.

The proof of Theorem 2.7 is given in Appendix. Note that in the case of a subcritical Hopf bifurcation, there must be another large amplitude spatially homogeneous limit cycle for $\lambda \in (\lambda_0^H - \varepsilon, \lambda_0^H)$ from the Poincaré–Bendixson theory.

2.4 *Steady-state bifurcation*

In this part, we analyse the properties of steady-state solution bifurcations for (1.3). Similarly to (2.20), we make the transformation $\lambda = f(a) + b > f(a)$, then (1.3) becomes

$$\begin{cases} d_1 \Delta u + (\lambda - f(a))v - u + f(u)v = 0, & x \in \Omega, \\ d_2 \Delta v + a - (\lambda - f(a))v - f(u)v = 0, & x \in \Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{2.26}$$

We identify steady-state bifurcation value λ^S of (2.26), which satisfies the following steady-state bifurcation condition (Yi *et al.*, 2009a):

(A_S) there exists $n \in \mathbb{N}_0$ such that

$$D_n(\lambda^S) = 0, \quad T_n(\lambda^S) \neq 0, \quad D_j(\lambda^S) \neq 0v \quad \text{and} \quad T_j(\lambda^S) \neq 0 \text{ for any } j \in \mathbb{N}_0 \text{ and } j \neq n,$$

and

$$D_n'(\lambda^S) \neq 0,$$

where $T_n(\lambda)$ and $D_n(\lambda)$ are defined in (2.10) and (2.11), respectively.

Apparently, $D_0(\lambda) = \lambda > f(a)$, hence we only consider $n \in \mathbb{N}$. In the following, we fix an arbitrary $a > 0$, and determine λ-values satisfying condition (A_S). We note that $D_n(\lambda) = 0$ is equivalent to $\lambda = \lambda_S(\mu_n)$, where $\lambda_S(\mu)$ is defined in (2.13). Here, we make the following additional assumption on the spectral set $S = \{\mu_i\}_{i \in \mathbb{N}_0}$ according to Lemma 2.1:

(S_2) There exist $p, q \in \mathbb{N}$, $p \leqslant q$ such that $\mu_{p-1} \leqslant \mu^1 < \mu_p \leqslant \mu_q < \mu^2 \leqslant \mu_{q+1}$, where μ^1 and μ^2 are defined in Lemma 2.1.

In the following, for $p, q \in \mathbb{N}$, we denote

$$\langle p, q \rangle := \begin{cases} [p, q] \cap \mathbb{N}, & \text{if } p < q; \\ \{p\}, & \text{if } p = q, \end{cases} \qquad \lambda_n^S := \lambda_S(\mu_n) \quad \text{for } n \in \langle p, q \rangle. \tag{2.27}$$

The points λ_n^S defined above are potential steady-state bifurcation points. It follows from Lemma 2.1 that, for each $n \in \langle p, q \rangle$, there exists only one point $\lambda = \lambda_n^S$ such that $D_n(\lambda_n^S) = 0$. On the other hand, it is possible that, for some $\lambda \in (f(a), \lambda_*)$ and some $i, j \in \langle p, q \rangle$, $i < j$ such that

$$\mu_i = \mu_-(\lambda) \quad \text{and} \quad \mu_j = \mu_+(\lambda), \tag{2.28}$$

where $\mu_\pm(\lambda)$ is defined in (2.14). Then for this λ, 0 is not a simple eigenvalue of $L(\lambda)$, which is defined in (2.7), and we shall not consider bifurcations at such points. On the other hand, it is also possible that

$$\lambda_i^S = \lambda_j^H \text{ (a Hopf bifurcation point) for some } i, j \in \langle p, q \rangle. \tag{2.29}$$

However, from an argument in Yi *et al.* (2009a), for $N = 1$ and $\Omega = (0, \ell\pi)$, there are only countably many ℓ, such that (2.28) or (2.29) occurs for some $i \neq j$. For general bounded domains in $\mathbb{R}^N$, one can also show that (2.28) or (2.29) does not occur for generic domains (Wang *et al.*, 2011).

To satisfy the bifurcation condition (A_S), we only need to verify whether $D'_n(\lambda_n^S) \neq 0$, which is proved in the following lemma.

LEMMA 2.8 Let λ_n^S and λ_* be defined in (2.27) and Lemma 2.1, respectively. If $\lambda_n^S \neq \lambda_*$, then $D'_n(\lambda_n^S) \neq 0$.

Proof. By differentiating $D(\lambda_S(\mu), \mu) = 0$ with respect to μ, where $D(\lambda, \mu)$ is defined in (2.12), we have

$$\frac{\partial D}{\partial \lambda}\frac{d\lambda_S}{d\mu} + \frac{\partial D}{\partial \mu} = 0.$$

If, to the contrary, we assume that $D'_n(\lambda_n^S) = 0$, then

$$\frac{\partial D}{\partial \lambda}(\lambda_n^S, \mu_n) = 0.$$

From $\lambda_n^S \neq \lambda_*$, it follows from Lemma 2.1 that $(d\lambda_S/d\mu)(\mu_n) \neq 0$. Hence, we have

$$\frac{\partial D}{\partial \mu}(\lambda_n^S, \mu_n) = 0.$$

Then, we can deduce $\lambda_n^S = \lambda_*$ from above relation, which is a contradiction. □

Summarizing the above discussion and using a general bifurcation theorem (Shi & Wang, 2009; Wang *et al.*, 2011), we obtain the main result of this part on bifurcation of steady-state solutions.

THEOREM 2.9 Suppose that $a, d_1, d_2 > 0$ are fixed such that $f(a) < \lambda_*$, where λ_* is defined in Lemma 2.1. Let Ω be a bounded smooth domain so that the spectral set $S = \{\mu_i\}_{i=\in\mathbb{N}_0}$ satisfy that (S_1) and (S_2). Then for any $n \in \langle p, q\rangle$, which is defined in (2.27), there exists a unique $\lambda_n^S \in (f(a), \lambda_*]$ such that $D_n(\lambda_n^S) = 0$. If in addition, we assume $\lambda_n^S \neq \lambda_*$, and

$$\lambda_n^S \neq \lambda_j^S \text{ for any } j \in \langle p, q\rangle \text{ and } n \neq j, \text{ and } \lambda_n^S \neq \lambda_j^H \text{ for any } j \in \langle p, q\rangle, \tag{2.30}$$

where λ_j^H is defined in (2.21), then

1. there is a smooth curve Γ_n of positive solutions of (2.26) bifurcating from $(\lambda, u, v) = (\lambda_n^S, a, a/\lambda_n^S)$, with Γ_n contained in a global branch Σ_n of positive non-trivial solutions of (2.26);
2. near $(\lambda, u, v) = (\lambda_n^S, a, a/\lambda_n^S)$, $\Gamma_n = \{\lambda_n(s), u_n(s), v_n(s) : s \in (-\epsilon, \epsilon)\}$, where

$$\begin{cases} u_n(s) = a + s a_n \phi_n(x) + s\psi_{1,n}(s), \\ v_n(s) = a/\lambda_n^S + s b_n \phi_n(x) + s\psi_{2,n}(s), \end{cases}$$

for some C^∞ smooth functions $\lambda_n, \psi_{1,n}, \psi_{2,n}$ such that $\lambda_n(0) = \lambda_n^S$ and $\psi_{1,n}(0) = \psi_{2,n}(0) = 0$. Here (a_n, b_n) satisfies

$$L(\lambda_n^S)[(a_n, b_n)^\top \phi_n(x)] = (0, 0)^\top,$$

where $L(\lambda)$ is defined in (2.7).

Proof. Since $f(a) < \lambda_*$, then $f(a) < \lambda_n^S < \lambda_*$. Thus the condition ($A_S$) has been proved in the previous paragraphs, and the bifurcation of solutions to (2.26) occur at $\lambda = \lambda_n^S$. Note that we assume (2.30) holds, so $\lambda = \lambda_n^S$ is always a bifurcation from simple eigenvalue point. From the global bifurcation theorem in Shi & Wang (2009), Γ_n is contained in a global branch Σ_n of solutions. Hence the results stated here are all proved except proving that Σ_n only consists of positive solutions to (2.26). This is true for solutions on Γ_n as $a > 0$ and $a/\lambda_n^S > 0$. Suppose that there is a solution on Σ_n which is not positive. Then by the continuity of Σ_n, there exists a point $(\hat{\lambda}, \hat{u}, \hat{v}) \in \Sigma_n$ such that $\hat{\lambda} \in \mathbb{R}$, $\hat{u}(x) \geqslant 0$, $\hat{v}(x) \geqslant 0$ for all $x \in \bar{\Omega}$, and there exists $x_0 \in \bar{\Omega}$ such that $\hat{u}(x_0) = 0$ or $\hat{v}(x_0) = 0$. We discuss the following possible cases:

(a) $x_0 \in \Omega$ and $\hat{v}(x_0) = 0$. By the second equation of (2.26), we have $0 \geqslant -d_2 \Delta \hat{v}(x_0) = a > 0$, which is a contradiction to the fact that x_0 is the minimum of $\hat{v}$.

(b) $x_0 \in \Omega$, $\hat{u}(x_0) = 0$ and $\hat{v}(x_0) > 0$. By the first equation of (2.26), we have $0 \geqslant -d_1 \Delta \hat{u}(x_0) = (\hat{\lambda} - f(a))\hat{v}(x_0) > 0$, which is again a contradiction to the fact that x_0 is the minimum of $\hat{u}$.

(c) $x_0 \in \partial\Omega$, and $\hat{v}(x_0) = 0$. Since $d_2 \Delta \hat{v} - b\hat{v} - f(\hat{u})\hat{v} = -a \leqslant 0$ in Ω, and $\hat{v}$ reaches its minimum at $x_0 \in \partial\Omega$, it follows that by the Hopf boundary lemma, either $v \equiv 0$ or $\partial \hat{v}(x_0)/\partial \nu < 0$. However, $a > 0$; then $\hat{v} = 0$ is not possible for a solution $(\hat{u}, \hat{v})$ of (2.26), and the other alternative contradicts with the Neumann boundary condition in (2.26).

(d) $x_0 \in \partial\Omega$, and $\hat{u}(x_0) = 0$. Since $d_1 \Delta \hat{u} - \hat{u} = -b\hat{v} - f(\hat{u})\hat{v} \leqslant 0$ in Ω, it follows that we can get a similar contradiction as (c).

Therefore any solution of (2.26) on Σ_n is positive. This completes the proof. □

2.5 *Numerical simulations*

To visualize the cascade of Hopf bifurcations and steady-state bifurcations described in Theorems 2.5 and 2.9, we consider two numerical examples. In both examples, we assume the spatial dimension $N = 1$, $\Omega = (0, 3\pi)$ and $f(u) = u^2$. Then $\mu_i = i^2/9$, $i \in \mathbb{N}_0$.

EXAMPLE 2.10 We choose $a = 0.5$, $d_1 = 1$ and $d_2 = 0.8$. Then the conditions in Theorem 2.5 (especially (2.22)) are satisfied; then steady-state bifurcations cannot occur and Hopf bifurcation points are

$$\lambda_0^H \approx 0.366 > \lambda_1^H \approx 0.3274 > f(a) = 0.25 > \lambda_2^H \approx 0.2446.$$

The curves $\Gamma_H = \{(a,b) : \lambda = b + a^2 = \bar{\lambda}_0\}$ and several $\Gamma_i = \{(a,b) : \lambda = b + a^2 = \lambda_i^S\}$ $(i \in \mathbb{N})$ are shown in Fig. 2. The region below the curve Γ_H is the parameter set (a,b) so that the equilibrium $(a, a/\lambda)$ is unstable for the ODE dynamics and a spatially homogeneous periodic orbit exists for such (a,b). The parameter region below Γ_i is where $D_i(\lambda) < 0$, but these regions are all below Γ_H, hence non-homogeneous steady-state solutions may be unstable or do not exist (in case $a = 0.5$. Figure 3 shows a numerical simulation for $(a,b) = (0.5, 0.1)$ so that (a,b) in the region $\{b < \bar{\lambda}_0 - a^2\}$, and the solution converges to a spatially homogeneous periodic orbit.

EXAMPLE 2.11 We choose $a = 3.5$, $d_1 = 0.01$ and $d_2 = 1$. Then μ_*, μ^1, μ^2 in Lemma 2.1 can be calculated as

$$\mu_* \approx 36.312, \quad f(a) = 12.25 < 13.186 \approx d_1 d_2 \mu_*^2, \quad \mu^1 \approx 17.417, \quad \mu^2 \approx 70.333.$$

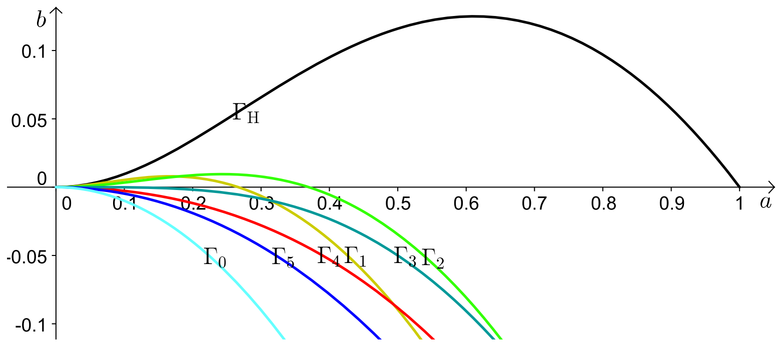

FIG. 2. Graph of $\Gamma_i : b = \lambda_i^S - a^2$, $0 \leqslant i \leqslant 5$ and $\Gamma_{\rm H} : b = \bar{\lambda}_0 - a^2$, where $d_1 = 1$ and $d_2 = 0.8$.

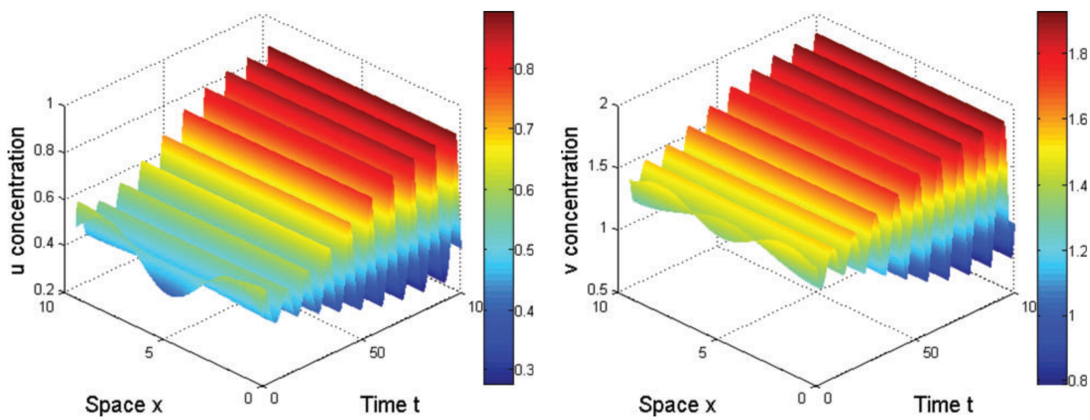

FIG. 3. Numerical simulation of the system (2.20) with $f(u) = u^2$, $d_1 = 1$, $d_2 = 0.8$, $a = 0.5$, $b = 0.1$ ($\lambda = 0.35$) and initial values $u_0(x) = 0.5 + 0.1\sin(x)$, $v_0(x) = 1.429 + 0.1\sin(x)$. The solution converges to a spatially homogeneous periodic orbit.

We can easily find that

$$\begin{aligned}\mu_{12} = 16 < \mu^1 < \mu_{13} \approx 18.778 < \mu_{14} < \cdots < \mu_{18}\\ = 36 < \mu_* < \mu_{19} \approx 40.111 < \mu_9 < \cdots < \mu_{25} \approx 69.444 < \mu^2 < \mu_{30} \approx 75.111,\end{aligned}$$

hence the interval (μ^1, μ^2) contains the eigenvalues μ_i $(13 \leqslant i \leqslant 25)$. This gives possible steady-state bifurcation points

$$\begin{aligned}\lambda_{18}^S \approx 13.185 > \lambda_{19}^S \approx 13.165 > \lambda_{17}^S \approx 13.155 > \lambda_{20}^S \approx 13.100 > \lambda_{16}^S \approx 13.069\\ > \lambda_{21}^S \approx 12.996 > \lambda_{15}^S \approx 12.921 > \lambda_{22}^S \approx 12.858 > \lambda_{14}^S \approx 12.706\\ > \lambda_{23}^S \approx 12.690 > \lambda_{24}^S \approx 12.498 > \lambda_{13}^S \approx 12.417 > \lambda_{25}^S \approx 12.286,\end{aligned}$$

while the largest Hopf bifurcation point $\lambda_0^H = \bar{\lambda}_0 \approx 4.4749$ which is much smaller. Hence, for this parameter set $(a, d_1, d_2) = (3.5, 0.01, 1)$, when b or λ decreases, the first bifurcation point encountered is $\lambda_{18}^S \approx 13.185$, and a steady-state bifurcation (Turing bifurcation) occurs there. Figure 4 shows the curves

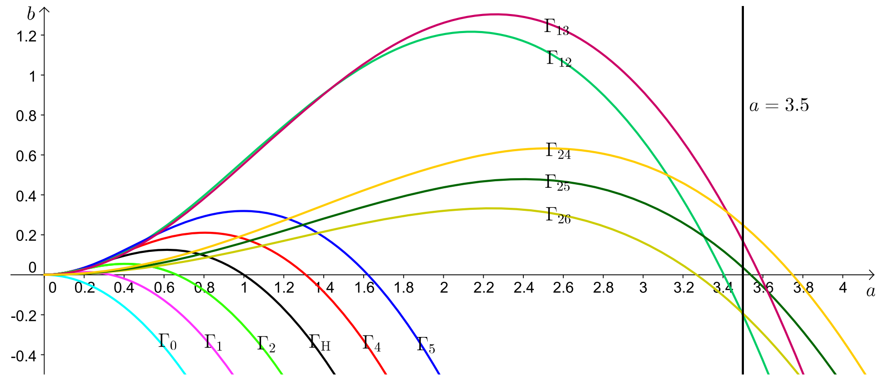

FIG. 4. Graph of $\Gamma_i : b = \lambda_i^S - a^2$, $i = 0, 1, 2, 4, 5, 12, 13, 24, 25, 26$ and $\Gamma_{\rm H} : b = \bar{\lambda}_0 - a^2$, where $d_1 = 0.01$ and $d_2 = 1$.

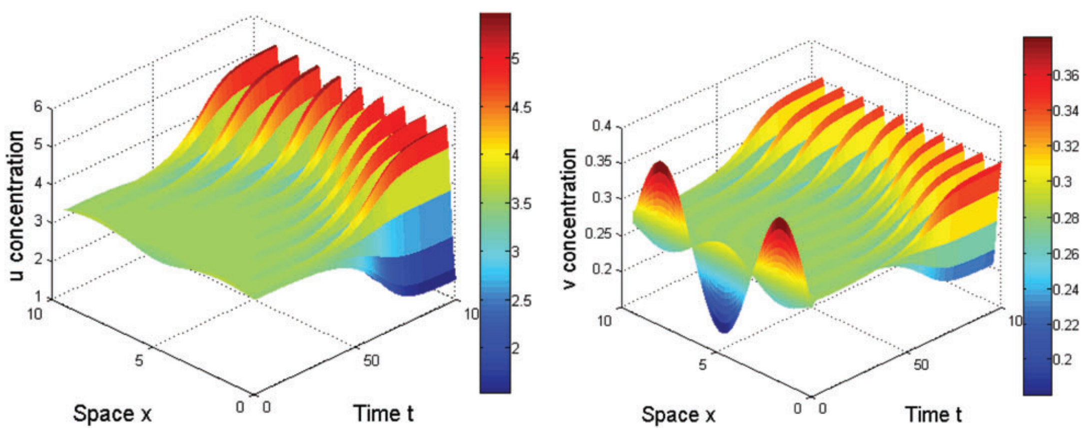

FIG. 5. Numerical simulation of the system (2.20) with $f(u) = u^2$, $d_1 = 0.01$ and $d_2 = 1$, $a = 3.5$, $b = 0.25$ ($\lambda = 12.5$) and initial values $u_0(x) = 3.5 + 0.1\sin(x)$, $v_0(x) = 0.28 + 0.1\sin(x)$. The solution converges to a spatially non-homogeneous steady-state solution.

Γ_i and Γ_H in the case. At any parameter value (a, b) satisfying $\bar{\lambda}_0 - a^2 < b < \lambda_i^S - a^2$ for some i, such Turing bifurcation can occur. In the (a, b)-plane shown in Fig. 4, this corresponds to the region above the curve Γ_H but below some Γ_i. A numerical simulation for $(a, b) = (3.5, 0.25)$ is shown in Fig. 5, where a non-homogeneous steady-state solution can be observed for large time t.

3. A further analysis of the steady-state solutions

In Section 2.4, we obtain the existence of non-constant solutions of (1.3) by using bifurcation methods. Since the global structure of the set of positive solutions to (1.3) is still not clear despite the results in Theorem 2.9, the bifurcation result is most useful near the bifurcation points. In this section, we obtain some further existence/non-existence results for the steady-state system (1.3) by using energy estimates and topological methods. The section is divided into three parts. In the first part, we give some *a priori* estimates of the solution of (1.3), which are useful in the later discussions. In Part 2, we study the non-existence of non-constant solutions of (1.3), while in Part 3 we study the existence of non-constant solutions via Leray–Schauder degree.

3.1 *A priori estimates*

First, we recall the following maximum principle (see Lou & Ni, 1996, Proposition 2.2 or Lou & Ni, 1999, Lemma 2.1).

LEMMA 3.1 Let $g \in C(\bar{\Omega} \times \mathbb{R})$ and $b_j(x) \in C(\bar{\Omega})$, $j = 1, 2, \ldots, N$. Then the following conditions are satisfied.

(i) If $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ satisfies

$$\begin{cases} \Delta w + \displaystyle\sum_{j=1}^{N} b_j(x) w_{x_j} + g(x, w(x)) \geqslant 0 & \text{in } \Omega, \\ \dfrac{\partial w}{\partial \nu} \leqslant 0 & \text{on } \partial\Omega, \end{cases}$$

and $w(x_0) = \max_{x \in \bar{\Omega}} w(x)$, then $g(x_0, w(x_0)) \geqslant 0$.

(ii) If $w \in C^2(\Omega) \cap C^1(\bar{\Omega})$ satisfies

$$\begin{cases} \Delta w + \displaystyle\sum_{j=1}^{N} b_j(x) w_{x_j} + g(x, w(x)) \leqslant 0 & \text{in } \Omega, \\ \dfrac{\partial w}{\partial \nu} \geqslant 0 & \text{on } \partial\Omega, \end{cases}$$

and $w(x_0) = \min_{x \in \bar{\Omega}} w(x)$, then $g(x_0, w(x_0)) \leqslant 0$.

A key result in our further analysis is the next lemma which establishes basic *a priori* estimates for the solutions of (1.3).

LEMMA 3.2 Any solution (u, v) of (1.3) satisfies

$$\frac{ab}{b + f(a + ad_2/(bd_1))} \leqslant u(x) \leqslant a + \frac{ad_2}{bd_1}, \quad x \in \bar{\Omega}, \tag{3.1}$$

$$\frac{a}{b + f(a + ad_2/(bd_1))} \leqslant v(x) \leqslant \frac{a}{b}, \quad x \in \bar{\Omega}. \tag{3.2}$$

Proof. Let $x_0 \in \bar{\Omega}$ be a maximum point of v. Then it follows from Lemma 3.1(i) that $a - bv(x_0) - f(u(x_0))v(x_0) \geqslant 0$, which implies $v(x) \leqslant v(x_0) \leqslant a/b$ for $x \in \bar{\Omega}$. Let $w = d_1 u + d_2 v$. Adding the first two equations in (1.3), we have

$$-\Delta w = a - u, \quad x \in \Omega, \quad \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega.$$

Let $x_1 \in \bar{\Omega}$ be a maximum point of w; then it follows from Lemma 3.1(i) that $u(x_1) \leqslant a$. Hence we have

$$d_1 u(x) \leqslant w(x) \leqslant w(x_1) = d_1 u(x_1) + d_2 v(x_1) \leqslant a d_1 + \frac{a d_2}{b}, \quad x \in \bar{\Omega}.$$

This yields the upper bound of u in (3.1).

Let $x_2 \in \bar{\Omega}$ be a minimum point of v; then it follows from Lemma 3.1(ii) that $a - bv(x_2) - f(u(x_2))v(x_2) \leqslant 0$, thus it follows from the upper bound of u in (3.1) that

$$a \leqslant (b + f(u(x_2)))v(x_2) \leqslant (b + f(a + ad_2/(bd_1)))v(x_2),$$

which provides the lower bound of v in (3.2). Finally, let $x_3 \in \bar{\Omega}$ be a minimum point of u, then it follows from Lemma 3.1(ii) that $0 \geqslant bv(x_3) - u(x_3) + f(u(x_3))v(x_3) \geqslant bv(x_3) - u(x_3)$. Then it follows from the lower bound of v in (3.2) that

$$u(x) \geqslant u(x_3) \geqslant bv(x_3) \geqslant \frac{ab}{b + f(a + ad_2/(bd_1))}, \quad x \in \bar{\Omega}.$$

□

Furthermore by standard elliptic regularity theory and Lemma 3.2, we obtain the following proposition.

PROPOSITION 3.3 Let $\varepsilon, A, b, D_1, D_2, \Theta > 0$ be fixed. Then we have the following conditions:

(i) there exist two positive constants C_1 and C_2 depending only on $\varepsilon, A, b, \Theta$ such that any solution (u, v) of (1.3) satisfies $C_1 < u(x), v(x) < C_2$ for $x \in \bar{\Omega}$ if $\varepsilon \leqslant a \leqslant A$ and $0 < d_2/d_1 < \Theta$;

(ii) for any $\alpha \in (0, 1)$, there exist a positive constant C depending on $A, b, D_1, D_2, \Theta, \alpha, N, \Omega$ such that, for all $0 < a \leqslant A$, $d_1 \geqslant D_1$, $d_2 \geqslant D_2$ and $0 < d_2/d_1 \leqslant \Theta$, any solution (u, v) of (1.3) satisfies $\|u\|_{C^{2+\alpha}(\bar{\Omega})} + \|v\|_{C^{2+\alpha}(\bar{\Omega})} \leqslant C$.

Proof. (i) It follows from Lemma 3.2 that, for all $\varepsilon \leqslant a \leqslant A$, $d_1 \geqslant D_1$ and $0 < d_2 \leqslant D_2$, any solution (u, v) of (1.3) satisfies

$$\begin{aligned} \frac{\varepsilon b}{b + f(A + A\Theta/b)} &\leqslant u(x) \leqslant A + \frac{A\Theta}{b}, \quad x \in \bar{\Omega}, \\ \frac{\varepsilon}{b + f(A + A\Theta/b)} &\leqslant v(x) \leqslant \frac{A}{b}, \quad x \in \bar{\Omega}. \end{aligned} \tag{3.3}$$

Then the conclusion of (i) follows. For (ii), we first rewrite (1.3) as follows:

$$\begin{cases} -\Delta u = \dfrac{1}{d_1}(bv - u + f(u)v), & x \in \Omega, \\ -\Delta v = \dfrac{1}{d_2}(a - bv - f(u)v), & x \in \Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases}$$

Define

$$\Lambda_1 := \frac{1}{D_1}\left(2A + A\Theta + \frac{A}{b}f(A\Theta)\right), \quad \Lambda_2 := \frac{1}{D_2}\left(2A + \frac{A}{b}f(A\Theta)\right);$$

by (3.3), it holds

$$\left\|\frac{1}{d_1}(bv - u + f(u)v)\right\|_{L^\infty(\Omega)} \leqslant \Lambda_1 \quad \text{and} \quad \left\|\frac{1}{d_2}(a - bv - f(u)v)\right\|_{L^\infty(\Omega)} \leqslant \Lambda_2.$$

Then, the conclusion can be obtained by a bootstrap argument. □

For any solution (u, v) of (1.3), we denote by $\bar{u}$ and $\bar{v}$ the average over Ω of u and v, respectively, i.e.

$$\bar{u} = \frac{1}{|\Omega|}\int_\Omega u\,dx, \quad \bar{v} = \frac{1}{|\Omega|}\int_\Omega v\,dx,$$

where $|\Omega|$ denotes the Lebesgue measure of Ω. Integrating (1.3) over Ω, we obtain that

$$\bar{u} = a \quad \text{and} \quad \int_\Omega (b + f(u))v\,dx = a|\Omega|. \tag{3.4}$$

Let $\phi = u - \bar{u}$ and $\psi = v - \bar{v}$. The next result provides *a priori* L^2-estimates for ϕ, ψ and their gradients.

PROPOSITION 3.4 Let (u, v) be a non-constant solution of (1.3). Then

(i)

$$\frac{d_2^2\mu_1^2}{2d_1^2\mu_1^2 + 2d_1\mu_1 + 1} \leqslant \frac{\|\nabla\phi\|^2_{L^2(\Omega)}}{\|\nabla\psi\|^2_{L^2(\Omega)}} \leqslant \left(\frac{d_2}{d_1}\right)^2;$$

(ii)

$$\frac{d_2^2\mu_1^3}{(\mu_1+1)(2d_1^2\mu_1^2 + 2d_1\mu_1 + 1)} \leqslant \frac{\|\nabla\phi\|^2_{L^2(\Omega)} + \|\phi\|^2_{L^2(\Omega)}}{\|\nabla\psi\|^2_{L^2(\Omega)} + \|\psi\|^2_{L^2(\Omega)}} \leqslant \left(1 + \frac{1}{\mu_1}\right)\left(\frac{d_2}{d_1}\right)^2.$$

Proof. Let $w = d_1\phi + d_2\psi$; then it follows from (1.3) and (3.4) that

$$\Delta w = \phi, \quad x \in \Omega, \quad \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega. \tag{3.5}$$

Multiplying the equation in (3.5) by ϕ and integrating over Ω, we have

$$\int_\Omega \nabla w \cdot \nabla\phi\,dx = -\int_\Omega \phi^2\,dx,$$

which yields

$$d_2\int_\Omega \nabla\phi\cdot\nabla\psi\,dx = -\int_\Omega \phi^2\,dx - d_1\int_\Omega |\nabla\phi|^2\,dx. \tag{3.6}$$

By using (3.6), we obtain that

$$
\begin{aligned}
0 &\leqslant \int_\Omega |\nabla w|^2\,\mathrm{d}x = d_1^2 \int_\Omega |\nabla \phi|^2\,\mathrm{d}x + 2d_1 d_2 \int_\Omega \nabla\phi\cdot\nabla\psi\,\mathrm{d}x + d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x \\
&= -d_1^2 \int_\Omega |\nabla\phi|^2\,\mathrm{d}x - 2d_1 \int_\Omega \phi^2\,\mathrm{d}x + d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x \\
&\leqslant d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x - d_1^2 \int_\Omega |\nabla\phi|^2\,\mathrm{d}x,
\end{aligned}
$$

which implies the upper bound in (i).

Next, by multiplying the equation in (3.5) by w and integrating over Ω, we obtain

$$
\int_\Omega |\nabla w|^2\,\mathrm{d}x = -\int_\Omega w\phi\,\mathrm{d}x,
$$

which can be expanded as

$$
d_1^2 \int_\Omega |\nabla\phi|^2\,\mathrm{d}x + 2d_1 d_2 \int_\Omega \nabla\phi\cdot\nabla\psi\,\mathrm{d}x + d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x = -d_1 \int_\Omega \phi^2\,\mathrm{d}x - d_2 \int_\Omega \phi\psi\,\mathrm{d}x.
$$

By using (3.6), it follows that

$$
d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x = d_1^2 \int_\Omega |\nabla\phi|^2\,\mathrm{d}x + d_1 \int_\Omega \phi^2\,\mathrm{d}x - d_2 \int_\Omega \phi\psi\,\mathrm{d}x.
$$

On the other hand, by using Young's inequality, we have

$$
-d_2 \int_\Omega \phi\psi\,\mathrm{d}x \leqslant \frac{1}{2\mu_1} \int_\Omega \phi^2\,\mathrm{d}x + \frac{d_2^2\mu_1}{2} \int_\Omega \psi^2\,\mathrm{d}x.
$$

Combining the last two relations, we obtain that

$$
d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x \leqslant d_1^2 \int_\Omega |\nabla\phi|^2\,\mathrm{d}x + \left(d_1 + \frac{1}{2\mu_1}\right) \int_\Omega \phi^2\,\mathrm{d}x + \frac{d_2^2\mu_1}{2} \int_\Omega \psi^2\,\mathrm{d}x. \tag{3.7}
$$

By Poincaré's inequality we have

$$
\int_\Omega \phi^2\,\mathrm{d}x \leqslant \frac{1}{\mu_1} \int_\Omega |\nabla\psi|^2\,\mathrm{d}x, \quad \int_\Omega \psi^2\,\mathrm{d}x \leqslant \frac{1}{\mu_1} \int_\Omega |\nabla\psi|^2\,\mathrm{d}x. \tag{3.8}
$$

Therefore, from (3.7) and (3.8) we obtain

$$
d_2^2 \int_\Omega |\nabla\psi|^2\,\mathrm{d}x \leqslant \frac{2d_1^2\mu_1^2 + 2d_1\mu_1 + 1}{\mu_1^2} \int_\Omega |\nabla\phi|^2\,\mathrm{d}x,
$$

which completes the proof of (i).

The proof of (ii) follows directly from (i) together with the following estimate, which is a direct consequence of Poincaré's inequality:

$$\frac{\mu_1\|\nabla\phi\|^2_{L^2(\Omega)}}{(\mu_1+1)\|\nabla\psi\|^2_{L^2(\Omega)}} \leqslant \frac{\|\nabla\phi\|^2_{L^2(\Omega)}+\|\phi\|^2_{L^2(\Omega)}}{\|\nabla\psi\|^2_{L^2(\Omega)}+\|\psi\|^2_{L^2(\Omega)}} \leqslant \frac{(\mu_1+1)\|\nabla\phi\|^2_{L^2(\Omega)}}{\mu_1\|\nabla\psi\|^2_{L^2(\Omega)}}.$$

□

3.2 *Non-existence of non-constant steady-state solutions*

Here, we first prove that (1.3) has no non-constant solutions if the first non-zero eigenvalue μ_1 is large.

THEOREM 3.5 Let $a, b, d_1, d_2 > 0$ be fixed. Then there exists a positive constant L depending only on a, b, d_1 and d_2 such that (1.3) has no non-constant solutions if $\mu_1 > L$.

Proof. Let $\phi = u - \bar{u}$ and $\psi = v - \bar{v}$, where (u, v) is any solution of (1.3). Multiplying the first equation of (1.3) with ϕ and integrating over Ω. By Lemma 3.2, Young's inequality and Poincaré's inequality, we obtain

$$\begin{aligned}
d_1\int_\Omega |\nabla\phi|^2\,\mathrm{d}x &= b\int_\Omega v\phi\,\mathrm{d}x - \int_\Omega \phi^2\,\mathrm{d}x + \int_\Omega f(u)v\phi\,\mathrm{d}x\\
&= b\int_\Omega \phi\psi\,\mathrm{d}x - \int_\Omega \phi^2\,\mathrm{d}x + \int_\Omega f(u)\phi\psi\,\mathrm{d}x + \int_\Omega \bar{v}(f(u)-f(\bar{u}))\phi\,\mathrm{d}x\\
&\leqslant C_3\int_\Omega |\phi\psi|\,\mathrm{d}x + \bar{v}\int_\Omega \left(\int_0^1 f'(\theta u+(1-\theta)\bar{u})\,\mathrm{d}\theta\right)\phi^2\,\mathrm{d}x\\
&\leqslant C_4\int_\Omega (|\phi\psi|+\phi^2)\,\mathrm{d}x \leqslant 2C_4\int_\Omega(\phi^2+\psi^2)\,\mathrm{d}x\\
&\leqslant \frac{2C_4}{\mu_1}\int_\Omega(|\nabla\phi|^2+|\nabla\psi|^2)\,\mathrm{d}x,
\end{aligned}$$

where C_3, C_4 depend only on a, b, d_1 and d_2. Similarly, we get

$$d_2\int_\Omega |\nabla\psi|^2\,\mathrm{d}x \leqslant \frac{2C_5}{\mu_1}\int_\Omega(|\nabla\phi|^2+|\nabla\psi|^2)\,\mathrm{d}x,$$

where C_5 depends only on a, b, d_1 and d_2. Adding the above two inequalities, we find

$$\min\{d_1,d_2\}(\|\nabla\phi\|^2_{L^2(\Omega)}+\|\nabla\psi\|^2_{L^2(\Omega)}) \leqslant \frac{C_6}{\mu_1}(\|\nabla\phi\|^2_{L^2(\Omega)}+\|\nabla\psi\|^2_{L^2(\Omega)}), \tag{3.9}$$

where C_6 depends only on a, b, d_1 and d_2. Then it follows from (3.9) that $\|\nabla\phi\|^2_{L^2(\Omega)} = \|\nabla\psi\|^2_{L^2(\Omega)} = 0$, that is, u and v are constant functions if $\mu_1 > C_6/\min\{d_1, d_2\}$. □

Next, we prove the non-existence of non-constant solutions of (1.3) when d_1 is large or a is small. To achieve that, we first prove the following lemma.

LEMMA 3.6 (i) Let $a, b, d_2 > 0$ be fixed and let $\{\sigma_n\} \subset (0, \infty)$ be such that $\sigma_n \to \infty$ as $n \to \infty$. If (u_n, v_n) is a solution of (1.3) with $d_1 = \sigma_n$, then

$$\lim_{n\to\infty}\left(\|u_n - a\|_{C^2(\bar{\Omega})} + \left\|v_n - \frac{a}{f(a)+b}\right\|_{C^2(\bar{\Omega})}\right) = 0.$$

(ii) Let $b, d_1, d_2 > 0$ be fixed and let $\{a_n\} \subset (0, \infty)$ be such that $a_n \to 0$ as $n \to \infty$. If (u_n, v_n) is a solution of (1.3) with $a = a_n$, then

$$\lim_{n\to\infty}(\|u_n\|_{C^2(\bar{\Omega})} +]\|v_n\|_{C^2(\bar{\Omega})}) = 0.$$

Proof. We only give the proof of (i) since the proof is similar for the second one. By Proposition 3.3, the sequence $\{(u_n, v_n)\}$ is bounded in $C^{2+\alpha}(\bar{\Omega}) \times C^{2+\alpha}(\bar{\Omega})$ for any $\alpha \in (0, 1)$. Hence, by passing to a subsequence if necessary, $\{(u_n, v_n)\}$ converges in $C^2(\bar{\Omega}) \times C^2(\bar{\Omega})$ to some $(u, v) \in C^2(\bar{\Omega}) \times C^2(\bar{\Omega})$. Dividing the first equation of (1.3) by d_1 and then passing to the limit with $n \to \infty$, we obtain that (u, v) satisfies the following relations in view of (3.4):

$$\begin{cases} -\Delta u = 0, & x \in \Omega, \\ -d_2\Delta v = a - bv - f(u)v, & x \in \Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \\ \displaystyle\int_\Omega u(x)\,\mathrm{d}x = a|\Omega| = \int_\Omega (b + f(u(x)))v(x)\,\mathrm{d}x. \end{cases} \tag{3.10}$$

From the first, third and fourth relations in (3.10), we know that $u \equiv a$. Thus v satisfies

$$\begin{cases} -d_2\Delta v = a - (b + f(a))v, & x \in \Omega, \\ \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{3.11}$$

which has the unique non-negative solution $v(x) \equiv a/(b + f(a))$. □

Now we can prove the non-existence of non-constant solutions of (1.3) when d_1 is large or a is small.

THEOREM 3.7 (i) Let $a, b, d_2 > 0$ be fixed. Then there exists a positive constant D depending only on a, b and d_2 such that (1.3) has no non-constant solutions if $d_1 > D$.

(ii) Let $b, d_1, d_2 > 0$ be fixed. Then there exists a positive constant A depending only on b, d_1 and d_2 such that (1.3) has no non-constant solutions if $0 < a < A$.

Proof. Denote

$$H_\nu(\Omega) = \left\{w \in W^{2,2}(\Omega) : \frac{\partial w}{\partial \nu} = 0 \text{ on } \partial\Omega\right\} \quad \text{and} \quad L_0^2(\Omega) = \left\{w \in L^2(\Omega) : \int_\Omega w\,\mathrm{d}x = 0\right\}.$$

Let $w = u - a$ and $\sigma = 1/d_1$; then by (3.4), the weak formulation of (1.3) is equivalent to

$$\begin{cases} -\Delta w = \sigma(bv - a - w + f(w+a)v), & x \in \Omega, \\ -d_2\Delta v = a - bv - f(w+a)v, & x \in \Omega, \\ w \in H_\nu(\Omega) \cap L_0^2(\Omega), & v \in H_\nu(\Omega). \end{cases} \tag{3.12}$$

Define $F : \mathbb{R} \times (H_\nu(\Omega) \cap L_0^2(\Omega)) \times H_\nu(\Omega) \to L_0^2(\Omega) \times L^2(\Omega)$ by

$$F(\sigma, w, v) := \begin{pmatrix} \Delta w + \sigma P(bv - w + f(w+a)v) \\ d_2\Delta v + a - bv - f(w+a)v \end{pmatrix},$$

where $P : L^2(\Omega) \to L_0^2(\Omega)$ is the projection operator form $L^2(\Omega)$ into $L_0^2(\Omega)$, i.e.

$$P\varphi = \varphi - \frac{1}{|\Omega|}\int_\Omega \varphi \, \mathrm{d}x \quad \text{for any } \varphi \in L^2(\Omega).$$

We claim that (3.12) is equivalent to $F(\sigma, w, v) = (0,0)^\top$. Indeed, if (σ, w, v) is a solution of (3.12), it is obvious that $F(\sigma, w, v) = (0,0)^\top$. On the other hand, if $F(\sigma, w, v) = (0,0)^\top$, then

$$d_2\Delta v + a - bv - f(w+a)v = 0 \text{ in } \Omega, \quad v \in H_\nu(\Omega).$$

By integration, it is easy to see that the above equation implies $bv - a + f(w+a)v \in L_0^2(\Omega)$. Since $w \in L_0^2(\Omega)$, this yields $bv - a - w + f(w+a)v \in L_0^2(\Omega)$, so we have

$$P(bv - w + f(w+a)v) = bv - a - w + f(w+a)v.$$

Therefore, (σ, w, v) satisfies (3.12).

The proof of Lemma 3.6 implies that the equation $F(0, w, v) = (0,0)^\top$ has a unique non-negative solution $(w, v) = (0, a/(f(a)+b))$. Furthermore, the Frechét derivative of F at $(\sigma, 0, a/(f(a)+b))$ is given by

$$D_{(w,v)}F(0,0,a/(f(a)+b)) := \begin{pmatrix} \Delta - \sigma & \sigma(b + f(a))P \\ 0 & d_2\Delta - b - f(a) \end{pmatrix}.$$

It is easy to see that $D_{(w,v)}F(0,0,a/(f(a)+b))$ is invertible, so it follows from the Implicit Function Theorem that there exist positive constants σ_0 and r such that $(0,0,a/(f(a)+b))$ is the unique solution of $F(\sigma, w, v) = (0,0)^\top$ if $(\sigma, w, v) \in [0, \sigma_0] \times B_r(0, a/(f(a)+b))$, where $B_r(0, a/(f(a)+b))$ denotes the open ball in $(H_\nu(\Omega) \cap L_0^2(\Omega)) \times H_\nu(\Omega)$ centred at $(0, a/(f(a)+b))$ with radius r.

Now, let $\{\sigma_n\}$ be a sequence of positive numbers such that $\sigma_n \to \infty$ as $n \to \infty$ and let (u_n, v_n) be a solution of (1.3) for a, b, d_2 fixed and $d_1 = \sigma_n$. Letting $w_n = u_n - a$, it follows that $F(1/\sigma_n, w_n, v_n) = (0,0)^\top$. According to Lemma 3.6(i), we have $(w_n, v_n) \to (0, a/(f(a)+b))$ in $C^2(\bar{\Omega})$ as $n \to \infty$. This means that, for $n \geqslant 1$ large enough, $(1/\sigma_n, w_n, v_n) \in [0, \sigma_0] \times B_r(0, a/(f(a)+b))$ which yields $(w_n, v_n) = (0, a/(f(a)+b))$. Hence, for $d_1 = \sigma_n$ large enough, the only non-negative solution of (1.3) is the constant solution $(a, a/(f(a)+b))$, which is part (i).

For part (ii), we consider a solution sequence $\{(u_n, v_n)\}_{n=1}^\infty$ of (1.3) with $a = a_n$ such that $a_n \to 0$ as $n \to \infty$. In view of Lemma 3.6(ii), we obtain $(u_n, v_n) \to (0,0)$ in $C^2(\bar{\Omega}) \times C^2(\bar{\Omega})$. Obviously, $(0,0)$

is the unique solution of (1.3) with $a = 0$. Furthermore, by Theorem 2.3, $(0,0)$ is locally asymptotically stable for (1.2) with $a = 0$. Since (1.3) is a regular perturbation problem for $a \to 0$, it follows from the regular perturbation theory of linear operators (Kato, 1976) that the solution (u_n, v_n) is also linearly stable if n is large enough. Consequently, the well-known implicit function theorem shows that $(a, a/(f(a)+b))$ is the unique positive solution to (1.3) if a is sufficiently small. □

3.3 *Existence of non-constant steady-state solutions*

In this section, we use degree theory to prove the existence of non-constant solutions of (1.3) for a certain parameter range. For that purpose, we define

$$\mathbf{X} := \left\{ \mathbf{w} = (u,v) \in [C^1(\bar{\Omega}) \cap C^2(\Omega)]^2 : \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0 \text{ on } \partial\Omega \right\}, \tag{3.13}$$

and let

$$\mathbf{X}^+ := \{(u,v) \in \mathbf{X} : u(x) > 0,\ v(x) > 0,\ x \in \bar{\Omega}\}.$$

We rewrite (2.26) (or equivalently (1.3)) in the following form:

$$-\mathcal{D}\Delta \mathbf{w} = G(\mathbf{w}), \quad \mathbf{w} \in \mathbf{X}^+, \tag{3.14}$$

where

$$\mathcal{D} = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}, \quad G(\mathbf{w}) = \begin{pmatrix} (\lambda - f(a))v - u + f(u)v \\ a - (\lambda - f(a))v - f(u)v \end{pmatrix}$$

For the calculation of degree, it is more convenient to write (3.14) as

$$H(\mathbf{w}) = 0, \quad \mathbf{w} \in \mathbf{X}^+,$$

where

$$H(\mathbf{w}) = \mathbf{w} - (-\Delta + I)^{-1}(\mathcal{D}^{-1}G(\mathbf{w}) + \mathbf{w}), \quad \mathbf{w} \in \mathbf{X}^+. \tag{3.15}$$

Let $\mathbf{w_0} = (a, a/\lambda)$ be the positive constant equilibrium of (1.2); then we have

$$D_{\mathbf{w}}H(\mathbf{w}_0) = I - (-\Delta + I)^{-1}(I + \mathcal{D}^{-1}L_0(\lambda)),$$

where $L_0(\lambda)$ is defined in (2.2). If $D_{\mathbf{w}}H(\mathbf{w}_0)$ is invertible, by Nirenberg (2001, Theorem 2.8.1), the index of H at $\mathbf{w}_0$ is given by

$$\text{index}(H, \mathbf{w}_0) = (-1)^{\gamma}, \tag{3.16}$$

where γ is the number of negative eigenvalues of $D_{\mathbf{w}}H(\mathbf{w}_0)$. On the other hand, using the decomposition

$$\mathbf{X} = \bigoplus_{k \geqslant 0} \mathbf{X}_k, \tag{3.17}$$

where $\mathbf{X}_k$ is the eigenspace corresponding to μ_k, $k \in \mathbb{N}_0$. Since $\mathbf{X}_k$ is an invariant subspace of the linear compact operator $D_{\mathbf{w}}H(\mathbf{w}_0)$, then $\xi \in \mathbb{R}$ is an eigenvalue of $D_{\mathbf{w}}H(\mathbf{w}_0)$ in $\mathbf{X}_k$ if and only if ξ is an eigenvalue of $(\mu_i+1)^{-1}(\mu_i I - \mathcal{D}^{-1}L_0(\lambda))$. Therefore, $D_{\mathbf{w}}H(\mathbf{w}_0)$ is invertible if, and only if for any $i \in \mathbb{N}_0$, the matrix $\mu_i I - \mathcal{D}^{-1}L_0(\lambda)$ is invertible. Define

$$Q(a,\lambda,d_1,d_2,\mu) := \det(\mu I - \mathcal{D}^{-1}L_0(\lambda)). \tag{3.18}$$

Hence, if $\mu_i I - D^{-1}L_0(\lambda)$ is invertible for any $i \in \mathbb{N}_0$, then it is well known (see, for example Peng *et al.*, 2008) that

$$\gamma = \sum_{i\in\mathbb{N}_0,\ Q(a,\lambda,d_1,d_2,\mu_i)<0} e(\mu_i), \tag{3.19}$$

where $e(\mu_i)$ is the algebraic multiplicity of μ_i. A straightforward computation yields that

$$Q(a,\lambda,d_1,d_2,\mu) = \frac{1}{d_1 d_2} D(\lambda,\mu), \tag{3.20}$$

where $D(\lambda,\mu)$ is defined in (2.12). Here, we emphasize the dependence of Q on a, d_1, d_2 as well. If $\lambda < \lambda_*$ (which is defined in Lemma 2.1), i.e.

$$af'(a) > \lambda(1+\sqrt{d_1\lambda/d_2})^2, \tag{3.21}$$

then, from Lemma 2.1, the equation $Q(a,\lambda,d_1,d_2,\cdot)=0$ has two positive roots $\mu^{\pm}(a,\lambda,d_1,d_2)$ which are defined as in (2.14). Now, by using the same method as in Peng *et al.* (2008) (see also Ghergu, 2008; Pang & Wang, 2004; Peng & Wang, 2005; Zhou & Mu, 2010), we have the following result.

THEOREM 3.8 Assume that a,λ,d_1,d_2 satisfy (3.21), and there exist $i,j \in \mathbb{N}_0$ such that

(i) $0 \leqslant \mu_j < \mu^-(a,\lambda,d_1,d_2) < \mu_{j+1} \leqslant \mu_i < \mu^+(a,\lambda,d_1,d_2) < \mu_{i+1}$ and

(ii) $\sum_{k=j+1}^{i} e(\mu_k)$ is odd.

Then (2.26) (or equivalently (1.3)) possesses at least one non-constant solution.

Proof. We prove the result by using a degree theory via a homotopy argument in the parameter d_1. Suppose that $(a,\lambda,d_1,d_2) = (\bar{a},\bar{\lambda},\bar{d}_1,\bar{d}_2)$ are given and satisfy (3.21). From Theorem 3.7, for the given $(a,\lambda,d_2) = (\bar{a},\bar{\lambda},\bar{d}_2)$, there exists $D_1 > 0$ such that when $d_1 > D_1$, system (2.26) has no non-constant solutions. From Lemma 2.1 and Remark 2.2, one can choose $D_2 > 0$ such that, for the given $(a,\lambda,d_2) = (\bar{a},\bar{\lambda},\bar{d}_2)$, when $d_1 > D_2$, then the corresponding $\lambda_*(\bar{a},\bar{\lambda},d_1,\bar{d}_2) < \lambda$ (where λ_* is defined in Lemma 2.1). Hence we have

$$Q(\bar{a},\bar{\lambda},d_1,\bar{d}_2,\mu) > 0, \quad \text{if } \mu \geqslant 0,\ d_1 > D_2. \tag{3.22}$$

Furthermore, by Proposition 3.3, for the given $(a,\lambda,d_2) = (\bar{a},\bar{\lambda},\bar{d}_2)$, there exist positive $D_3 > 0$ and two constants C_1 and C_2 depending only on D_3 such that any solution (u,v) of (2.26) with $(a,\lambda,d_2) = (\bar{a},\bar{\lambda},\bar{d}_2)$ and $d_1 \geqslant D_3$ satisfies $C_1 < u(x), v(x) < C_2$ for $x \in \bar{\Omega}$. We define $D = \max\{D_1, D_2, D_3\}$.

Consider a mapping $\hat{F} : \mathcal{M} \times [0,1] \to C(\bar{\Omega}) \times C(\bar{\Omega})$ by

$$\hat{F}(\mathbf{w},t) = (-\Delta + I)^{-1} \begin{pmatrix} u + \left(\frac{1-t}{D} + \frac{t}{d_1}\right)[(\bar{\lambda} - f(\bar{a}))v - u + f(u)v] \\ v + \frac{1}{d_2}[\bar{a} - (\bar{\lambda} - f(\bar{a}))v - f(u)v] \end{pmatrix},$$

where

$$\mathcal{M} = \{\mathbf{w} = (u,v) \in C(\bar{\Omega}) \times C(\bar{\Omega}) : C_1 < u, v < C_2 \text{ in } \bar{\Omega}\}.$$

It is easy to see that solving (2.26) is equivalent to finding a fixed point of $\hat{F}(\cdot,1)$ in $\mathcal{M}$. According to the choice of D, we have that $\mathbf{w}_0 = (a, a/\lambda)$ is the only fixed point of $\hat{F}(\cdot,0)$. Furthermore, by (3.22) we have

$$\deg(I - \hat{F}(\cdot,0), \mathcal{M}, (0,0)) = \text{index}(I - \hat{F}(\cdot,0), \mathbf{w}_0) = 1. \tag{3.23}$$

Since $I - \hat{F}(\cdot,1) = H$, and if (2.26) has no other solutions except the constant one $\mathbf{w}_0$, then, by (3.16) and (3.19), we have

$$\deg(I - \hat{F}(\cdot,1)) = \text{index}(H, \mathbf{w}_0) = (-1)^{\sum_{k=j+1}^{i} e(\mu_k)} = -1. \tag{3.24}$$

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

$$1 = \deg(I - \hat{F}(\cdot,0), \mathcal{M}, (0,0)) = \deg(I - \hat{F}(\cdot,1)) = -1,$$

which is a contradiction. Therefore, there exists a non-constant solution of (2.26). □

The conditions (i) and (ii) in Theorem 3.8 defines a region in the parameter space $\{(a, \lambda, d_1, d_2)\}$ for which a non-constant solution of (1.3) exists. Because of the binary nature of the index, 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 3.9 Suppose that all eigenvalues μ_i ($i \in \mathbb{N}_0$) have odd algebraic multiplicity.

(i) Let $a, d_1, d_2 > 0$ be fixed, and let μ^1, μ^2 be defined as in Lemma 2.1. Suppose that the condition (S_2) in Section 2.4 is satisfied, and λ_n^S are defined as in (2.27). Assume that the set $\{\lambda_n^S : n \in \langle p, q\rangle\}$ can be relabelled to $\{\widehat{\lambda_i^S} : 1 \leqslant i \leqslant q - p + 1\}$ such that

$$f(a) < \widehat{\lambda_{q-p+1}^S} < \cdots < \widehat{\lambda_{i+1}^S} < \widehat{\lambda_i^S} < \cdots \cdot \widehat{\lambda_2^S} < \widehat{\lambda_1^S} < \lambda_*.$$

Then (2.26) (or equivalently (1.3)) has at least one non-constant solution for

$$\lambda \in \bigcup_{1 \leqslant i \leqslant q-p+1,\, i \text{ is odd}} (\widehat{\lambda_{i+1}^S}, \widehat{\lambda_i^S}). \tag{3.25}$$

(ii) Let $a, \lambda, d_2 > 0$ be fixed so that a, λ satisfy

$$af'(a) > \lambda > f(a). \tag{3.26}$$

Define

$$d_1^n = \frac{d_2\mu_n(af'(a) - \lambda) - \lambda^2}{\mu_n\lambda(d_2\mu_n + \lambda)}, \tag{3.27}$$

for $n \in \{n \in \mathbb{N} : d_2\mu_n(af'(a) - \lambda) - \lambda^2 > 0\}$. Assume that the set $\{d_1^n : n \in \mathbb{N}, d_2\mu_n(af'(a) - \lambda) - \lambda^2 > 0\}$ can be relabelled to $\{\widehat{d_1^n} : n \in \mathbb{N}\}$ such that

$$\widehat{d_1^1} > \widehat{d_1^2} > \cdots > \widehat{d_1^i} > \widehat{d_1^{i+1}} > \cdots, \quad \lim_{i\to\infty} \widehat{d_1^i} = 0.$$

Then (2.26) (or equivalently (1.3)) has at least one non-constant solution for

$$d_1 \in \bigcup_{i\in\mathbb{N}} (\widehat{d_1^{2i}}, \widehat{d_1^{2i-1}}). \tag{3.28}$$

Proof. For (i), it is easy to see that γ defined in (3.19) is odd if λ satisfies (3.25); and for (ii), it is easy to see that γ is odd when d_1 satisfies (3.28). □

We remark that one can indeed show that $\lambda = \lambda_n^S$ and $d_1 = d_1^n$ defined in Corollary 3.9 are bifurcation points where non-constant solutions stem out from the branch of constant solution, by using the global bifurcation theorem in Rabinowitz (1971). This would partially generalize the result in Theorem 2.9 where the eigenvalues μ_i are assumed to be simple. However, the result in Corollary 3.9 shows the existence of non-constant solutions in some more specific parameter regions, which cannot be achieved in bifurcation results.

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Appendix

A.1 *Proof of Theorem* 2.4

We first consider the following scalar problem:

$$\begin{cases} \dfrac{\partial w}{\partial t} = d\Delta w + \zeta(w), & x \in \Omega,\ t > 0, \\ \dfrac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ w(x,0) = w_0(x) \geqslant 0, \not\equiv 0, & x \in \Omega, \end{cases} \tag{A.1}$$

where $d > 0$ is a constant. Then we have the following result for (A.1).

LEMMA A.1 Assume $\zeta \in C[0,\infty] \cap C^1(0,\infty)$ satisfies that there exists a constant $\varepsilon > 0$ such that ζ has only one root $C_w \in (0, \max_{x\in\bar\Omega} w_0(x) + \varepsilon]$ and $\zeta'(C_w) < 0$. Then $w(x,t)$ exists for all $t > 0$, and $\lim_{t\to\infty} w(x,t) = C_w$ uniformly in $\bar\Omega$.

Proof. Let $z(t,z_0)$ be the solution of the following equation:

$$\begin{cases} \dfrac{\mathrm{d}z}{\mathrm{d}t} = \zeta(z), & t > 0, \\ z(0) = z_0, \end{cases}$$

where $0 < z_0 \leqslant \max_{x\in\bar\Omega} w_0(x) + \varepsilon$. It follows from the assumption on ζ and theory of ODE that $\lim\limits_{t\to\infty} z(t,z_0) = C_w$. By the strong maximum of parabolic equation, we know that $w(x,t) > 0$ in $\bar\Omega$ for $t > 0$. Then we can take $\delta > 0$ small enough so that

$$\bar w_0 := \max_{x\in\bar\Omega} w(x,t+\delta) \in \left(0, \max_{x\in\bar\Omega} w_0(x) + \varepsilon\right],$$
$$\underline{w}_0 := \min_{x\in\bar\Omega} w(x,t+\delta) \in \left(0, \max_{x\in\bar\Omega} w_0(x) + \varepsilon\right].$$

Then $z(t,\underline{w}_0) \leqslant w(x,t+\delta) \leqslant z(t,\bar w_0)$ by the comparison principle. Then the conclusion follows by the fact that $\lim_{t\to\infty} z(t,\underline{w}_0) = C_w = \lim_{t\to\infty} z(t,\bar w_0)$. □

Proof of Theorem 2.4. We only give the proof of case $m = 2$ since the proof of $m = 1$ is easier by using similar methods. It follows from the second equation of (2.18) that $v_t - d_2\Delta v \leqslant a - bv$; then, by

Lemma A.1 and the comparison principle, we get

$$\limsup_{t\to\infty}\max_{x\in\bar{\Omega}} v(x,t) \leqslant \frac{a}{b} := \bar{v}_1.$$

Since $b > 4a^2$, we can choose $\epsilon > 0$ small enough so that $1 - 4b(\bar{v}_1+\epsilon)^2 > 0$. Then there exists a constant $T_1^\epsilon \gg 1$ such that $v(x,t) \leqslant \bar{v}_1 + \epsilon$ for $x \in \bar{\Omega}$ and $t \geqslant T_1^\epsilon$. By the first equation of (2.18) we have, for $x \in \bar{\Omega}$ and $t > t \geqslant T_1^\epsilon$,

$$u_t - d_1\Delta u \leqslant (\bar{v}_1+\epsilon)u^2 - u + b(\bar{v}_1+\epsilon) := \zeta_1(u).$$

It is easy to verify that $\zeta_1(u)$ has two roots u_ϵ^1, u_ϵ^2 and $\zeta_1'(u_\epsilon^1) < 0$, where

$$u_\epsilon^1 = \frac{1-\sqrt{1-4b(\bar{v}_1+\epsilon)^2}}{2(\bar{v}_1+\epsilon)}, \quad u_\epsilon^2 = \frac{1+\sqrt{1-4b(\bar{v}_1+\epsilon)^2}}{2(\bar{v}_1+\epsilon)} > \sqrt{b}.$$

Since $\max_{x\in\bar{\Omega}} u_0(x) \leqslant \sqrt{b}$, there exists a positive constant ε such that $\zeta_1(u)$ has only one root $u_\epsilon^1 \in (0, \max_{x\in\bar{\Omega}} u_0(x) + \varepsilon]$, by Lemma A.1, the comparison principle and letting $\epsilon \to 0$, we have

$$\limsup_{t\to\infty}\max_{x\in\bar{\Omega}} u(x,t) \leqslant \frac{1-\sqrt{1-4b\bar{v}_1^2}}{2\bar{v}_1} = \frac{b-\sqrt{b^2-4a^2b}}{2a} := \bar{u}_1. \tag{A.2}$$

Then, for $\epsilon > 0$ small enough, there exists a constant $T_2^\epsilon \gg 1$ such that $u(x,t) \leqslant \bar{u}_1 + \epsilon$ for $x \in \bar{\Omega}$ and $t \geqslant T_2^\epsilon$. Then, by the second equation of (2.18), Lemma A.1 and letting $\epsilon \to 0$, we get

$$\liminf_{t\to\infty}\min_{x\in\bar{\Omega}} v(x,t) \geqslant \frac{a}{b+\bar{u}_1^2} := \underline{v}_1 \leqslant \bar{v}_1. \tag{A.3}$$

Since $\underline{v}_1 \leqslant \bar{v}_1$, we can choose $0 < \epsilon < \underline{v}_1$ such that $1 - 4b(\underline{v}_1 - \epsilon)^2 > 0$. Then there exists a constant $T_3^\epsilon \gg 1$ such that $v(x,t) \geqslant \underline{v}_1 - \epsilon$ for $x \in \bar{\Omega}$ and $t \geqslant T_3^\epsilon$. By similar analysis as (A.2), we get

$$\liminf_{t\to\infty}\min_{x\in\bar{\Omega}} u(x,t) \geqslant \frac{1-\sqrt{1-4b\underline{v}_1^2}}{2\underline{v}_1} := \underline{u}_1 \leqslant \bar{u}_1.$$

Then, for any $0 < \epsilon < \underline{u}_1$, there exists a constant $T_4^\epsilon \gg 1$ such that $u(x,t) \geqslant \underline{u}_1 - \epsilon$ for $x \in \bar{\Omega}$ and $t \geqslant T_4^\epsilon$. By similar analysis as (A.3), we get

$$\limsup_{t\to\infty}\max_{x\in\bar{\Omega}} v(x,t) \leqslant \frac{a}{b+\underline{u}_1^2} := \bar{v}_2.$$

Furthermore, one can show $\underline{v}_1 \leqslant \bar{v}_2 \leqslant \bar{v}_1$ by direct calculation. Similarly, we have

$$\limsup_{t\to\infty}\max_{x\in\bar{\Omega}} u(x,t) \leqslant \frac{1-\sqrt{1-4b\bar{v}_2^2}}{2\bar{v}_2} := \bar{u}_2,$$

and $\underline{u}_1 \leqslant \bar{u}_2 \leqslant \bar{u}_1$.

Let

$$\varphi(s)=\frac{a}{b+s^2},\quad s>0,$$
$$\psi(s)=\frac{1-\sqrt{1-4bs^2}}{2s},\quad 0<s<\frac{1}{2\sqrt{b}}.$$

Then φ is decreasing and ψ is increasing. The constants $\bar{u}_i, \bar{v}_i, \underline{u}_i, \underline{v}_i$, $i=1,2$, constructed above satisfy

$$\begin{cases} \underline{v}_1=\varphi(\bar{u}_1)\leqslant\varphi(\underline{u}_1)=\bar{v}_2\leqslant\bar{v}_1=\dfrac{a}{b}, \\ \underline{u}_1=\psi(\underline{v}_1)\leqslant\psi(\bar{v}_2)=\bar{u}_2\leqslant\bar{u}_1=\psi(\bar{v}_1), \\ \underline{v}_1\leqslant\liminf\limits_{t\to\infty}\min\limits_{x\in\bar{\Omega}}v(x,t)\leqslant\limsup\limits_{t\to\infty}\max\limits_{x\in\bar{\Omega}}v(x,t)\leqslant\bar{v}_2, \\ \underline{u}_1\leqslant\liminf\limits_{t\to\infty}\min\limits_{x\in\bar{\Omega}}u(x,t)\leqslant\limsup\limits_{t\to\infty}\max\limits_{x\in\bar{\Omega}}u(x,t)\leqslant\bar{u}_2. \end{cases} \tag{A.4}$$

By induction, we can construct four sequences $\{\bar{v}_i\}_{i=1}^{\infty}$, $\{\bar{u}_i\}_{i=1}^{\infty}$, $\{\underline{v}_i\}_{i=1}^{\infty}$ and $\{\underline{u}_i\}_{i=1}^{\infty}$ by

$$\bar{v}_1=\frac{a}{b},\quad \bar{u}_i=\psi(\bar{v}_i),\quad \underline{v}_i=\varphi(\bar{u}_i),\quad \underline{u}_i=\psi(\underline{v}_i),\quad \bar{v}_{i+1}=\varphi(\underline{u}_i), \tag{A.5}$$

such that

$$\begin{cases} \underline{v}_i\leqslant\liminf\limits_{t\to\infty}\min\limits_{x\in\bar{\Omega}}v(x,t)\leqslant\limsup\limits_{t\to\infty}\max\limits_{x\in\bar{\Omega}}v(x,t)\leqslant\bar{v}_i, \\ \underline{u}_i\leqslant\liminf\limits_{t\to\infty}\min\limits_{x\in\bar{\Omega}}u(x,t)\leqslant\limsup\limits_{t\to\infty}\max\limits_{x\in\bar{\Omega}}u(x,t)\leqslant\bar{u}_i. \end{cases}$$

In view of (A.4), (A.5) and the monotonicity of ϕ and ψ, it follows

$$\begin{cases} \underline{v}_i\leqslant\underline{v}_{i+1}=\varphi(\bar{u}_{i+1})\leqslant\varphi(\underline{u}_i)=\bar{v}_{i+1}\leqslant\bar{v}_i, \\ \underline{u}_i\leqslant\underline{u}_{i+1}=\psi(\underline{v}_{i+1})\leqslant\psi(\bar{v}_{i+1})=\bar{u}_{i+1}\leqslant\bar{u}_i \end{cases}$$

by induction. From the monotonicity of the sequences, we may assume

$$\lim_{i\to\infty}\underline{u}_i=\underline{u},\quad \lim_{i\to\infty}\bar{u}_i=\bar{u},\quad \lim_{i\to\infty}\underline{v}_i=\underline{v},\quad \lim_{i\to\infty}\bar{v}_i=\bar{v}.$$

It is obvious that $0<\underline{u}\leqslant\bar{u}$, $0<\underline{v}\leqslant\bar{v}$ and $\underline{u},\bar{u},\underline{v},\bar{v}$ satisfy

$$\bar{u}=\psi(\bar{v}),\quad \bar{v}=\varphi(\underline{u}),\quad \underline{u}=\psi(\underline{v}),\quad \underline{v}=\varphi(\bar{u}). \tag{A.6}$$

With some elementary calculations, one can show that (A.6) is equivalent to

$$\begin{cases} \bar{u}^2\bar{v}-\bar{u}+b\bar{v}=0, \\ \underline{u}^2\underline{v}-\underline{u}+b\underline{v}=0, \\ \bar{u}^2\underline{v}+b\underline{v}-a=0, \\ \underline{u}^2\bar{v}+b\bar{v}-a=0. \end{cases} \tag{A.7}$$

It follows from the first and fourth equations of (A.7) that

$$\bar{v}(\bar{u}+\underline{u})(\bar{u}-\underline{u})+a-\bar{u}=0. \tag{A.8}$$

By the second and third equations of (A.7), we have

$$\underline{v}(\bar{u}+\underline{u})(\bar{u}-\underline{u})+\underline{u}-a=0. \tag{A.9}$$

Then it follows from (A.8) and (A.9) that

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

i.e. $\bar{u}=\underline{u}=a$. Then, by (A.7), we obtain $\bar{v}=\underline{v}=a/(a^2+b)$. □

A.2 *Proof of Theorem* 2.7

Proof of Theorem 2.7. Here we follow the notations and calculations in Yi *et al.* (2009a). When $\lambda=\lambda_0^H=\bar{\lambda}_0=(-1+\sqrt{1+8a^2})/2$, (2.9) has a pair of purely imaginary eigenvalues $\mu=\pm i\sqrt{\bar{\lambda}_0}$. Let $\beta=\sqrt{\bar{\lambda}_0}$; then for Jacobin matrix

$$L_0(\lambda)=\begin{pmatrix}A(\bar{\lambda}_0) & \bar{\lambda}_0\\ B(\bar{\lambda}_0) & -\bar{\lambda}_0\end{pmatrix}=\begin{pmatrix}\bar{\lambda}_0 & \bar{\lambda}_0\\ -1-\bar{\lambda}_0 & -\bar{\lambda}_0\end{pmatrix}=\begin{pmatrix}\beta^2 & \beta^2\\ -1-\beta^2 & -\beta^2\end{pmatrix}, \tag{A.10}$$

and eigenvector q of eigenvalue $i\beta$ satisfying

$$L_0q=i\beta q$$

can be chosen as $q:=(a_0,b_0)^\top=(-\beta,\beta-i)^\top$. Define the inner product in $X_{\mathbb{C}}:=X\bigoplus iX=\{x_1+ix_2: x_1,x_2\in X\}$ by

$$\langle \mathbf{w}_1,\mathbf{w}_2\rangle=\int_\Omega(\bar{u}_1u_2+\bar{v}_1v_2)\,\mathrm{d}x,$$

where $\mathbf{w}_i=(u_i,v_i)^\top\in X_{\mathbb{C}}$, $i=1,2$. We choose an associated eigenvector q^* for the eigenvalue $\mu=-i\beta$ satisfying

$$L_0^*q^*=-i\beta q^*,\quad \langle q^*,q\rangle=1,\quad \langle q^*,\bar{q}\rangle=0.$$

Then $q^*=(a_0^*,b_0^*)^\top=((-1-i\beta)/2\beta|\Omega|,-i/2|\Omega|)^\top$.

Let $h(u,v)=bv-u+u^2v$ and $g(u,v)=a-bv-u^2v$, by calculation, at

$$\left(a,\frac{a}{\bar{\lambda}_0}\right)=\left(\frac{\beta}{\sqrt{2}}\sqrt{1+\beta^2},\frac{1}{\sqrt{2}\beta}\sqrt{1+\beta^2}\right),$$

we have

$$\begin{cases} g_{uu}=-h_{uu},\ g_{uv}=-h_{uv},\ g_{uuv}=-h_{uuv},\\ h_{vv}=h_{vvv}=h_{uvv}=h_{uuu}=g_{uuu}=g_{vv}=g_{uvv}=g_{vvv}=0,\\ h_{uu}=\dfrac{\sqrt{2}}{\beta}\sqrt{1+\beta^2},\ h_{uv}=\sqrt{2}\beta\sqrt{1+\beta^2},\ h_{uuv}=2.\end{cases} \tag{A.11}$$

By direct calculation, it follows that

$$\begin{aligned}
c_0 &= h_{uu}a_0^2 + 2h_{uv}a_0b_0 + h_{vv}b_0^2 = (\sqrt{2} - 2\sqrt{2}\beta^2)\beta\sqrt{1+\beta^2} + 2\sqrt{2}\beta^2\sqrt{1+\beta^2}i,\\
d_0 &= g_{uu}a_0^2 + 2g_{uv}a_0b_0 + g_{vv}b_0^2 = -c_0,\\
e_0 &= h_{uu}|a_0|^2 + h_{uv}(a_0\bar{b}_0 + \bar{a}_0b_0) + h_{vv}|b_0|^2 = (\sqrt{2} - 2\sqrt{2}\beta^2)\beta\sqrt{1+\beta^2},\\
f_0 &= g_{uu}|a_0|^2 + g_{uv}(a_0\bar{b}_0 + \bar{a}_0b_0) + g_{vv}|b_0|^2 = -e_0,\\
g_0 &= h_{uuu}|a_0|^2a_0 + h_{uuv}(2|a_0|^2b_0 + a_0^2\bar{b}_0) + h_{uvv}(2|b_0|^2a_0 + b_0^2\bar{a}_0) + h_{vvv}|b_0|^2b_0\\
&= 2\beta^2(3\beta - i),\\
h_0 &= g_{uuu}|a_0|^2a_0 + g_{uuv}(2|a_0|^2b_0 + a_0^2\bar{b}_0) + g_{uvv}(2|b_0|^2a_0 + b_0^2\bar{a}_0) + g_{vvv}|b_0|^2b_0 = -g_0.
\end{aligned}$$

Denote

$$Q_{q,q} = \begin{pmatrix} c_0 \\ d_0 \end{pmatrix}, \quad Q_{q,\bar{q}} = \begin{pmatrix} e_0 \\ f_0 \end{pmatrix}, \quad C_{q,q,\bar{q}} = \begin{pmatrix} g_0 \\ h_0 \end{pmatrix}. \tag{A.12}$$

Then

$$\begin{aligned}
\langle q^*, Q_{q,q}\rangle &= \int_\Omega \left(\frac{-1+i\beta}{2\beta\ell\pi}c_0 + \frac{id_0}{2\ell\pi}\right)\mathrm{d}x = -\frac{c_0}{2\beta},\\
\langle q^*, Q_{q,\bar{q}}\rangle &= \int_\Omega \left(\frac{-1+i\beta}{2\beta\ell\pi}e_0 + \frac{if_0}{2\ell\pi}\right)\mathrm{d}x = -\frac{e_0}{2\beta},\\
\langle q^*, C_{q,q,\bar{q}}\rangle &= \int_\Omega \left(\frac{-1+i\beta}{2\beta\ell\pi}g_0 + \frac{ih_0}{2\ell\pi}\right)\mathrm{d}x = -\frac{g_0}{2\beta},\\
\langle \bar{q}^*, Q_{q,q}\rangle &= \int_\Omega (-\beta c_0 + (\beta+i)d_0)\,\mathrm{d}x = -\frac{c_0}{2\beta},\\
\langle \bar{q}^*, Q_{q,\bar{q}}\rangle &= \int_\Omega (-\beta e_0 + (\beta+i)f_0)\,\mathrm{d}x = -\frac{e_0}{2\beta},\\
\langle q^*, Q_{q,q}\rangle &= \langle \bar{q}^*, Q_{q,q}\rangle, \quad \langle q^*, C_{q,q,\bar{q}}\rangle = \langle \bar{q}^*, Q_{q,\bar{q}}\rangle.
\end{aligned}$$

Hence,

$$\begin{aligned}
H_{20} &= (c_0, d_0)^\top + \frac{c_0}{2\beta_0}(a_0, b_0)^\top + \frac{c_0}{2\beta_0}(\bar{a}_0, \bar{b}_0)^\top = c_0(1,-1)^\top + c_0(-1,1)^\top = 0,\\
H_{11} &= (e_0, f_0)^\top + \frac{e_0}{2\beta}(a_0, b_0)^\top + \frac{e_0}{2\beta}(\bar{a}_0, \bar{b}_0)^\top = e_0(1,-1)^\top + e_0(-1,1)^\top = 0,
\end{aligned}$$

which implies that $\omega_{20} = \omega_{11} = 0$, then

$$\langle q^*, Q_{\omega_{11},q}\rangle = \langle q^*, Q_{\omega_{20},\bar{q}}\rangle = 0. \tag{A.13}$$

Thus,

$$\begin{aligned}\mathrm{Re}(c_1(\lambda_0^H)) &= \mathrm{Re}\left\{\frac{i}{2\omega_0}\langle q^*, Q_{q,q}\rangle \cdot \langle q^*, Q_{q,\bar{q}}\rangle + \frac{1}{2}\langle q^*, C_{q,q,\bar{q}}\rangle\right\} \\ &= \left(\beta^2 - \frac{1}{2}\right)\left(1 + \beta^2 + \frac{\sqrt{2}}{2}\sqrt{1+\beta^2}\right),\end{aligned} \tag{A.14}$$

where $\omega_0 = \beta$. From (A.14), we know that if $0 < \beta < \sqrt{2}/2$, then $\mathrm{Re}(c_1(\lambda_0^H)) < 0$, and if $\beta > \sqrt{2}/2$, then $\mathrm{Re}(c_1(\lambda_0^H)) > 0$. From the proof of Theorem 2.5, we know that $\gamma'(\lambda_0^H) < 0$. Hence we obtain the direction of bifurcation according to Jin *et al.* (2013, Lemma 5.1). □