

Steady states and pattern formation of the density-suppressed motility model

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This paper considers the stationary problem of density-suppressed motility models proposed in [Fu et al. \(2012\)](#) and [Liu et al. \(2011\)](#) in one dimension with Neumann boundary conditions. The models consist of parabolic equations with cross-diffusion and degeneracy. We employ the global bifurcation theory and Helly compactness theorem to explore the conditions under which non-constant stationary (pattern) solutions exist and asymptotic profiles of solutions as some parameter value is small. When the cell growth is not considered, we are able to show the monotonicity of solutions and hence achieve a global bifurcation diagram by treating the chemical diffusion rate as a bifurcation parameter. Furthermore, we show that the solutions have boundary spikes as the chemical diffusion rate tends to zero and identify the conditions for the non-existence of non-constant solutions. When transformed to specific motility functions, our results indeed give sharp conditions on the existence of non-constant stationary solutions. While with the cell growth, the structure of global bifurcation diagram is much more complicated and in particular the solution loses the monotonicity property. By treating the growth rate as a bifurcation parameter, we identify a minimum range of growth rate in which non-constant stationary solutions are warranted, while a global bifurcation diagram can still be attained in a special situation. We use numerical simulations to test our analytical results and illustrate that patterns can be very intricate and stable stationary solutions may not exist when the parameter value is outside the minimal range identified in our paper.

Keywords: density-suppressed motility; stationary solutions; global bifurcation theory; Helly compactness theorem; pattern formation.

1. Introduction

The reaction–diffusion models have played key roles in mathematical biology in reproducing a wide variety of exquisite spatio-temporal patterns arising in embryogenesis, development and population dynamics due to the diffusion-driven (Turing) instability ([Kondo & Miura, 2010](#); [Murray, 2001](#)). Many of them invoke nonlinear diffusion enhanced by the local environment condition to accounting for population pressure (cf. [Méndez et al., 2012](#)), volume exclusion (cf. [Dyson & Bakerm, 2015](#); [Painter & Hillen, 2002](#)) or avoidance of danger (cf. [Murray, 2001](#)), and so on. However, the opposite situation may occur where the species will slow down its random diffusion rate when encountering external signals such as the predator in pursuit of the prey ([Jin & Wang, 2021b](#); [Kareiva & Odell, 1987](#)) and

the bacterial in searching food (Keller & Segel, 1971, 1970). Recently, a so-called ‘self-trapping’ mechanism was introduced in Liu *et al.* (2011) by a synthetic biology approach onto programmed bacterial *Escherichia coli* cells, which excrete signalling molecules acyl-homoserine lactone (AHL) such that at low AHL level, the bacteria undergo run-and-tumble random motion and are motile, while at high AHL levels, the bacteria tumble incessantly and become immotile due to the vanishing macroscopic motility. Remarkably, *E. coli* cells formed the outward expanding stripe (wave) patterns in the petri dish. To understand the underlying patterning mechanism, the following three-component reaction–diffusion system has been proposed in Liu *et al.* (2011)

$$\begin{cases} u_t = \Delta(\gamma(v)u) + \frac{\alpha w^2 u}{w^2 + \mu}, & x \in \Omega, \quad t > 0, \\ v_t = d\Delta v + u - v, & x \in \Omega, \quad t > 0, \\ w_t = \Delta w - \frac{w^2 u}{w^2 + \mu}, & x \in \Omega, \quad t > 0, \end{cases} \quad (1.1)$$

where $u(x, t)$, $v(x, t)$ and $w(x, t)$ denote the bacterial cell density, concentration of AHL and nutrient density, respectively; $\alpha, \mu, d > 0$ are constants and Ω is bounded domain in $\mathbb{R}^N (N \geq 1)$. The first equation of (1.1) describes the random motion of bacterial cells with an AHL-dependent motility coefficient $\gamma(v)$, and a cell growth due to the nutrient intake. The second equation of (1.1) describes the diffusion, production and turnover of AHL, while the third equation describes the dynamics of diffusion and consumption on nutrient. The most of existing reaction–diffusion systems usually assume that the diffusion rate is constant or depend on the density of species itself, except the cross-diffusion systems (cf. Lou & Ni, 1996). The prominent feature of the system (1.1) is that the bacterial diffusion rate is a function $\gamma(v)$ depending on external signal density v , which satisfies $\gamma'(v) < 0$ by taking into account the repressive effect of AHL concentration on the bacterial motility (cf. Liu *et al.*, 2011). This monotone decreasing property of $\gamma(v)$ distinguishes the nonlinear diffusion in (1.1) from the cross-diffusion systems (cf. Lou & Ni, 1996).

Though the system (1.1) may numerically reproduce some key features of experimental observations as illustrated in Liu *et al.* (2011), its mathematical analysis seems not easy. Later, an alternative simplified two-component so-called ‘density-suppressed motility’ model was proposed in Fu *et al.* (2012):

$$\begin{cases} u_t = \Delta(\gamma(v)u) + \sigma u(1 - u), & x \in \Omega, \quad t > 0, \\ v_t = d\Delta v + u - v, & x \in \Omega, \quad t > 0, \end{cases} \quad (1.2)$$

where the reduced growth rate of cells at high density was used to approximate the nutrient depletion effect in the system (1.1). By expanding the Laplacian term in the first equation of (1.2), we shall find the motility function $\gamma(v)$ produces cross-diffusion effect, and more importantly the decay property $\gamma'(v) < 0$ may lead to degenerate diffusion. Therefore the mathematical analysis of the above systems is non-trivial and no mathematical result has been available for (1.1) as we know. There are only few results obtained recently for the simplified system (1.2) with Neumann boundary conditions as recalled below.

- (i) $\sigma = 0$. The existence of global classical solutions of (1.2) in any dimensions has been established in Yoon & Kim (2017) in the case of $\gamma(v) = c_0/v^k (k > 0)$ for small $c_0 > 0$. The smallness assumption on c_0 is removed lately for the parabolic-elliptic case with $0 < k < \frac{2}{n-2}$

in Ahn & Yoon (2019). When $\gamma(v) = \frac{1}{c+\gamma^k}$ ($k > 0, c \geq 0$), the existence of global weak solutions of (1.2) with large initial data in dimensions $n \in \{1, 2, 3\}$ was established in Desvillettes *et al.* (2019) under some constraints for k in different dimensions. However, the solution of (1.2) with $\sigma = 0$ may blow up if $\gamma(v)$ has a faster decay than algebraic decay. For example, if $\gamma(v) = e^{-\chi v}$, by constructing a Lyapunov functional, it is proved in Jin & Wang (2020) that there exists a critical mass $m_* = \frac{4\pi}{\chi}$ such that the solution of (1.2) with $\sigma = 0$ exists globally with uniform-in-time bound if $\int_{\Omega} u_0 dx < m_*$ while blows up if $\int_{\Omega} u_0 dx > m_*$ in two dimensions, where u_0 denotes the initial value of u . It was further shown in Fujie & Jiang (2020a) that the blow-up time is infinity.

- (ii) $\sigma > 0$. It appears that the cell growth (i.e. $\sigma > 0$) has a strong impact on the dynamics of (1.2) and bring many differences than the case $\sigma = 0$. The first result on the global existence and large time behavior of solutions was established in Jin *et al.* (2018). More precisely, it is shown in Jin *et al.* (2018) that the system (1.2) with $\sigma > 0$ has a unique global classical solution in two dimensions under the following assumptions on the motility function $\gamma(v)$:

$$(H0) \quad \gamma(v) \in C^3([0, \infty)), \gamma(v) > 0 \text{ and } \gamma'(v) < 0 \text{ on } [0, \infty), \lim_{v \rightarrow \infty} \gamma(v) = 0 \text{ and } \lim_{v \rightarrow \infty} \frac{\gamma'(v)}{\gamma(v)} \text{ exists.}$$

Moreover, the constant steady state (1, 1) of (1.2) is proved to be globally asymptotically stable if $\sigma > \frac{K_0}{16}$ where $K_0 = \max_{0 \leq v \leq \infty} \frac{|\gamma'(v)|^2}{\gamma(v)}$. The global existence result has been extended to higher dimensions ($n \geq 3$) for large $\sigma > 0$ in Wang & Wang (2019). Recently, the last condition ‘ $\lim_{v \rightarrow \infty} \frac{\gamma'(v)}{\gamma(v)}$ exists’ was improved in Jin & Wang (2021a) and removed in Fujie & Jiang (2020b) in the case of parabolic-elliptic case (i.e. the second equation of (1.2) is replaced by $d\Delta v + u - v = 0$). On the other hand, for small $\sigma > 0$, the existence/non-existence of non-constant steady states of (1.2) was rigorously established under some constraints on the parameters in Ma *et al.* (2020) and the periodic pulsating wave is analytically approximated by the multi-scale analysis. When $\gamma(v)$ is a piecewise constant function, the dynamics of discontinuity interface was studied in Smith-Roberge *et al.* (2019).

The above-mentioned are the results available to the system (1.2). It appears that the results for (1.1) are very limited and there is only one work (Jin *et al.*, 2020) addressing the global existence and asymptotic behavior of solutions under some stringent assumption on the motility function $\gamma(v)$. The purpose of this paper is to investigate the existence of non-constant stationary (classical) solutions to the density-suppressed motility models (1.1) and (1.2) with Neumann boundary conditions. First the stationary problem of (1.2) with Neumann boundary conditions reads as

$$\begin{cases} \Delta(\gamma(v)u) + \sigma u(1 - u) = 0, & x \in \Omega, \\ d\Delta v + u - v = 0, & x \in \Omega, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{1.3}$$

where ν denotes the unit outward normal vector of $\partial\Omega$. Next we claim that the non-constant stationary solutions of (1.1) are also determined by the above stationary problem (1.3) with $\sigma = 0$. Indeed the

stationary problem of (1.1) with Neumann boundary conditions is given by

$$\begin{cases} \Delta(\gamma(v)u) + \frac{\alpha w^2 u}{w^2 + \lambda} = 0, & x \in \Omega, \\ d\Delta v + u - v = 0, & x \in \Omega, \\ \Delta w - \frac{w^2 u}{w^2 + \lambda} = 0, & x \in \Omega, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \quad (1.4)$$

Multiplying the third equation of (1.4) by w and then integrating the result by part, we end up with

$$\int_{\Omega} |\nabla w|^2 + \int_{\Omega} \frac{uw^3}{w^2 + \lambda} = 0. \quad (1.5)$$

For biologically meaningful solution $u \geq 0, w \geq 0$, we have two conclusions from (1.5): (1) w is a non-zero constant and $u \equiv 0$; or (2) $w \equiv 0$ and $u \geq 0$ satisfies (1.3) with $\sigma = 0$. However, the case (1) gives only constant solutions, which is not our interest. In case (2), the non-constant solution of (1.4) will be $(u, v, 0)$ where (u, v) is determined by (1.3) with $\sigma = 0$. Therefore, in this paper, we shall focus on the stationary problem (1.3) with $\sigma \geq 0$ and explore the existence of non-constant solutions. Note that stationary problem (1.3) with $\sigma > 0$ has been studied recently in [Ma et al. \(2020\)](#) under the hypotheses (H0). This paper will complement the results by [Ma et al. \(2020\)](#) with the case $\sigma = 0$. For the case $\sigma > 0$, the system (1.3) was only partially understood and many interesting questions still open. This paper will fill some gaps left in [Ma et al. \(2020\)](#) for the case $\sigma > 0$.

Due to the appearance of cross-diffusion and possible degeneracy as mentioned above, the mathematical study of (1.3) is non-trivial. The paper ([Ma et al., 2020](#)) cleverly uses an idea by defining $\tilde{u} = \gamma(v)u$ to transform the system (1.3) into an elliptic system without cross-diffusion and degeneracy, but the reaction terms become very complicated. Hence, the non-existence of non-constant solutions is partially obtained under certain assumptions, and the existence results established by the method of topological degree are rather weak. In this paper, we shall explore the existence of non-constant classical solutions of (1.3) in one dimension with explicit conditions on parameters. For the case $\sigma = 0$, we treat the chemical diffusion rate $d > 0$ as a bifurcation parameter and find explicit sharp parameter regimes for the existence of monotone solutions of (1.3) by the global bifurcation theory. Moreover, we show that the solution (u, v) has a boundary spike as $d \rightarrow 0$ by using the Helly compactness theorem. For the case $\sigma > 0$, it is very hard to find monotone solutions and hence a complete global bifurcation diagram becomes elusive. Luckily we still can use the global bifurcation to find a specific (minimal) range of $\sigma > 0$ so that (1.3) admits non-constant solutions. This is an essential improvement of the results by [Ma et al. \(2020\)](#) where no any specific range of σ was found to warrant the existence of non-constant solutions to (1.3). We shall detail these in the upcoming sections. Throughout paper, whenever we say a solution of (1.3), it always means a positive classical solution without particular mention.

The rest of this paper is organized as follows. In section 2, we shall perform the global bifurcation analysis for system (1.3) with $\sigma = 0$ and identify the range of d for the existence of non-constant solutions. In section 3, the case $\sigma > 0$ will be explored and a minimal range of $\sigma > 0$ is explicitly found to warrant the existence of non-constant solutions. Numerical simulations are shown to verify our analytical results and predict the possible results for the situations not proved in the paper. Finally, in section 4, we summarize our results and discuss some open questions with some speculations based on numerical simulations.

2. Steady states without growth (i.e. $\sigma = 0$)

In this section, we shall consider the steady state problem (1.3) with $\sigma = 0$ with Neumann boundary condition in one dimension. Without loss of generality, we assume $\Omega = (0, l)$. Then the concerned problem is the following:

$$\begin{cases} (\gamma(v)u)_{xx} = 0, & x \in (0, l), \\ dv_{xx} - v + u = 0, & x \in (0, l), \\ v_x = u_x = 0, & x = 0, l, \end{cases} \tag{2.6}$$

where $d > 0$ is a constant and the motility function satisfies the following mild condition:

$$(H1) \quad \gamma(v) \in C^2(0, \infty), \gamma(v) > 0 \text{ and } \gamma'(v) < 0.$$

Note that the conditions (H1) are much weaker than (H0) imposed in Jin *et al.* (2018) for time-dependent problem (1.2).

2.1 Existence

The first equation of (2.6) with Neumann boundary conditions implies that total mass of u is conserved, and the second equation of (2.6) with the Neumann boundary condition entails that the cell and chemical have the same mass (i.e. $\int_0^l u dx = \int_0^l v dx$). Therefore, in the sequel, we suppose

$$\frac{1}{l} \int_0^l u(x) dx = \frac{1}{l} \int_0^l v(x) dx = \omega, \tag{2.7}$$

where $\omega > 0$ is a fixed number denoting the cell mass. Then the stationary problem with mass restriction becomes

$$\begin{cases} [\gamma(v)u]_{xx} = 0, & x \in (0, l), \\ dv_{xx} - v + u = 0, & x \in (0, l), \\ v_x = u_x = 0, & x = 0, l, \\ \frac{1}{l} \int_{\Omega} u(x) dx = \omega. \end{cases} \tag{2.8}$$

We give *a priori* estimates first.

LEMMA 2.1 Let (u, v) be a positive classical solution of (2.8) in $[0, l]$ with the hypothesis (H1). Then it holds that

$$\frac{\omega l}{\sqrt{d} \sinh \frac{l}{\sqrt{d}}} = \vartheta_1 \leq v(x) \leq \vartheta_2 = \omega + \frac{\omega l^2}{d} \tag{2.9}$$

and

$$\omega \exp\left(-\frac{\omega l^2}{d}\mathcal{K}\right) \leq u \leq \omega \exp\left(\frac{\omega l^2}{d}\mathcal{K}\right), \quad (2.10)$$

where $\mathcal{K} = \sup_{\vartheta_1 \leq v \leq \vartheta_2} \frac{|\gamma'(v)|}{\gamma(v)}$.

Proof. Denote $G(x; x_0)$ as the Green's function for any fixed $x_0 \in (0, l)$ and it satisfies

$$\begin{cases} -dG_{xx} + G = \delta(x - x_0), & x \in (0, l), \\ G_x(0; x_0) = G_x(l; x_0) = 0. \end{cases}$$

Then G can be explicitly given by

$$G(x; x_0) = \begin{cases} \frac{\cosh \frac{(l-x_0)}{\sqrt{d}}}{\sqrt{d} \sinh \frac{l}{\sqrt{d}}} \cosh \frac{1}{\sqrt{d}}x, & x \in (0, x_0), \\ \frac{\cosh \frac{1}{\sqrt{d}}x_0}{\sqrt{d} \sinh \frac{l}{\sqrt{d}}} \cosh \frac{(l-x)}{\sqrt{d}}, & x \in (x_0, l). \end{cases}$$

Obviously, $G(x; x_0) \geq \frac{1}{\sqrt{d} \sinh \frac{l}{\sqrt{d}}}$ for $x, x_0 \in (0, l)$. By the v -equation we have

$$v(x_0) = \int_0^l G(x; x_0)u(x)dx \geq \frac{1}{\sqrt{d} \sinh \frac{l}{\sqrt{d}}} \int_0^l u(x)dx = \frac{\omega l}{\sqrt{d} \sinh \frac{l}{\sqrt{d}}} = \vartheta_1, \quad \forall x_0 \in (0, l).$$

This prove the first inequality in (2.9).

Recall that

$$\int_0^l v(x)dx = \omega l.$$

With the fact that $v'(x) = \int_0^x v''(y)dy$ and $v'(0) = 0$, and we again use the v -equation to obtain

$$dv'(x) = \int_0^x (v - u)dy.$$

Note that $u, v \geq 0$. Then it follows from (2.7) that $|dv'(x)| \leq \omega l$. Take $x_0 \in [0, l]$ such that $v(x_0) = \frac{\int_0^l v(x)dx}{l} = \omega$ by the mean value theorem for integrals. Then we have the following estimate for $v(x)$:

$$v(x) = v(x_0) + \int_{x_0}^x v'(y)dy \leq \omega + \frac{\omega l^2}{d} = \vartheta_2.$$

By u -equation in (2.6) and Neumann boundary conditions, we have

$$\gamma(v)u' = -\gamma'(v)uv' \text{ or } \frac{u'}{u} = -\frac{\gamma'(v)v'}{\gamma(v)}. \tag{2.11}$$

So

$$|(\ln u)'| = \left| \frac{\gamma'(v)}{\gamma(v)} v' \right| \leq \frac{\omega l |\gamma'(v)|}{d \gamma(v)}.$$

Take $y_0 \in [0, l]$ such that $u(y_0) = \omega$. Then the integration from y_0 to x gives us (2.10). □

We shall use the diffusion rate d as the bifurcation value for the bifurcation theory. To this end, we introduce some notations. Let $X = H_N^2(0, l) = \{u \in H^2(0, l) | u'(0) = 0 = u'(l)\}$, $Y = L^2(0, l)$, $Y_0 = \{u \in L^2(0, l) | \int_0^l u(x)dx = 0\}$. Define $\mathcal{F} : \mathbb{R}^+ \times X \times X \rightarrow Y_0 \times Y \times \mathbb{R}$ such that

$$\mathcal{F}(d, u, v) = \begin{pmatrix} -[\gamma(v)u]_{xx} \\ -dv_{xx} + v - u \\ \int_0^l u(x)dx - \omega l \end{pmatrix}.$$

Observe that (u, v) is a solution of system $\mathcal{F}(d, u, v) = 0$ is equivalent to that (u, v) is a solution of (2.8). For any fixed point $(d, u_1, v_1) \in \mathbb{R}^+ \times X \times X$, we have the Fréchet derivative

$$D_{(u,v)}\mathcal{F}(d, u_1, v_1)(u, v) = \begin{pmatrix} -[\gamma'(v_1)u_1v + \gamma(v_1)u]_{xx} \\ -dv_{xx} + v - u \\ \int_0^l u(x)dx \end{pmatrix}. \tag{2.12}$$

Then the following results can be obtained.

LEMMA 2.2 For any fixed point $(u_1, v_1) \in X \times X$, the Fréchet derivative

$$D_{(u,v)}\mathcal{F}(d, u_1, v_1) : X \times X \rightarrow Y_0 \times Y \times \mathbb{R}$$

is a Fredholm operator with index 0.

Proof. Note that the second-order derivative terms of u and v in the first line of (2.12) are $-\gamma'(v_1)u_1v_{xx}$ and $-\gamma(v_1)u_{xx}$. Denote

$$D_{(u,v)}\mathcal{F}(d, u_1, v_1)(u, v) \triangleq \mathcal{F}_1(u, v) + \mathcal{F}_2(u, v),$$

where

$$\mathcal{F}_1(u, v) = \begin{pmatrix} -[\gamma'(v_1)u_1v + \gamma(v_1)u]_{xx} \\ -dv_{xx} + v - u \\ 0 \end{pmatrix}, \mathcal{F}_2(u, v) = \begin{pmatrix} 0 \\ 0 \\ \int_0^l u(x)dx \end{pmatrix}.$$

For \mathcal{F}_1 , the second-order derivatives of u and v in \mathcal{F}_1 can be written as

$$-\begin{pmatrix} \gamma(v_1) & \gamma'(v_1)u_1 \\ 0 & d \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}_{xx},$$

and then we have the conclusion that

$$D_{(u,v)}\mathcal{F}(\sigma, u_1, v_1)(u, v) : X \times X \rightarrow Y_0 \times Y \times \mathbb{R}$$

is a Fredholm operator with index zero by a similar argument as in the proof of Lemma 2.3 in Wang & Xu (2013). Clearly, \mathcal{F}_2 is linear and compact. So the compact perturbation, \mathcal{F}_2 , does not change the Fredholmness and the Fredholm index of \mathcal{F}_1 . This completes the proof. \square

We aim to find all possible bifurcation values of d . Recall for a positive constant steady state (d, ω, ω) ($\omega > 0$), the necessary condition for bifurcation to occur is that the null space of $D_{(u,v)}\mathcal{F}(d, \omega, \omega)$ is non-trivial, i.e. $N(D_{(u,v)}\mathcal{F}(d, \omega, \omega)) \neq \{0\}$. According to (2.12), we know the null space of $D_{(u,v)}\mathcal{F}(d, \omega, \omega)$ is the space of solution (u, v) satisfying

$$\begin{cases} -\gamma(\omega)u_{xx} - \gamma'(\omega)\omega v_{xx} = 0, & x \in (0, l), \\ -dv_{xx} + v - u = 0, & x \in (0, l), \\ u_x = v_x = 0, & x = 0, l, \\ \int_0^l u(x)dx = 0. \end{cases} \tag{2.13}$$

Since the system (2.13) is linear with Neumann boundary conditions, its solution is of the form

$$u = \sum_{m=0}^{\infty} t_m \cos \frac{m\pi x}{l} \text{ and } v = \sum_{m=0}^{\infty} s_m \cos \frac{m\pi x}{l}. \tag{2.14}$$

Substituting above expansions of u, v into (2.13), we arrive at

$$\begin{cases} \gamma(\omega)t_m + \gamma'(\omega)\omega s_m = 0, \\ \frac{dm^2\pi^2}{l^2}s_m + s_m - t_m = 0. \end{cases} \tag{2.15}$$

The condition $\int_0^l u(x)dx = 0$ applied to (2.14) immediately implies that $t_0 = s_0 = 0$. So the equation (2.15) have non-trivial solutions if and only if $d = \bar{d}_m$ such that

$$-\frac{\gamma'(\omega)\omega}{\gamma(\omega)} = 1 + \frac{\bar{d}_m m^2 \pi^2}{l^2}, \quad m = 1, 2, \dots \tag{2.16}$$

Clearly, the null space is one-dimensional and

$$N(D_{(u,v)}\mathcal{F}(\bar{d}_m, \omega, \omega)) = \text{span}\{(\bar{u}_m, \bar{v}_m)\},$$

where $(\bar{u}_m, \bar{v}_m) = (\frac{\bar{d}_m m^2 \pi^2}{\rho^2} + 1, 1) \cos \frac{m\pi x}{l}$, $m = 1, 2, \dots$. So if we can choose (ω, ω) such that $\bar{d}_m = (-\frac{\gamma'(\omega)\omega}{\gamma(\omega)} - 1) \frac{\rho^2}{m^2 \pi^2} > 0$ along with the condition $\frac{|\gamma'(\omega)\omega|}{\gamma(\omega)} - 1 > 0$, we can carry out the bifurcation analysis for the chemical diffusion rate $d > 0$.

To use the local bifurcation theorem (Theorem A.1), we need to check the transversality condition:

$$D_{(u,v)d} \mathcal{F}(\bar{d}_m, \omega, \omega)(\bar{u}_m, \bar{v}_m) \notin R(D_{(u,v)} \mathcal{F}(\bar{d}_m, \omega, \omega)). \tag{2.17}$$

Assuming, by contradiction, that (2.17) is false, then there exists $(\tilde{u}, \tilde{v}) \in X \times X$ such that

$$\begin{cases} -\gamma(\omega)\tilde{u}_{xx} - \gamma'(\omega)\omega\tilde{v}_{xx} = 0, & x \in (0, l), \\ -\bar{d}_m\tilde{v}_{xx} + \tilde{v} - \tilde{u} = \frac{m^2\pi^2}{\rho^2} \cos \frac{m\pi x}{l}, & x \in (0, l), \\ \tilde{u}_x = \tilde{v}_x = 0, & x = 0, l, \\ \int_0^l \tilde{u}(x)dx = 0. \end{cases}$$

Similarly, we substitute the expansions $\tilde{u} = \sum_{m=0}^\infty \tilde{t}_m \cos \frac{m\pi x}{l}$ and $\tilde{v} = \sum_{m=0}^\infty \tilde{s}_m \cos \frac{m\pi x}{l}$ into the above system and find that \tilde{t}_m and \tilde{s}_m satisfy

$$\begin{cases} \gamma(\omega)\tilde{t}_m + \gamma'(\omega)\omega\tilde{s}_m = 0, \\ \frac{\bar{d}_m m^2 \pi^2}{\rho^2} \tilde{s}_m + \tilde{s}_m - \tilde{t}_m = \frac{m^2 \pi^2}{\rho^2}. \end{cases} \tag{2.18}$$

With (2.16), the second equation of (2.18) can be written as $\gamma(\omega)\tilde{t}_m + \gamma'(\omega)\omega\tilde{s}_m = -\frac{m^2\pi^2\gamma(\omega)}{\rho^2}$. Inserting this into the first equation of (2.18), we have $-\frac{m^2\pi^2\gamma(\omega)}{\rho^2} = 0$, which is impossible since $m \geq 1$. This verifies the transversality condition.

Applying Theorem A.1, we obtain that $\forall m \geq 1$, \bar{d}_m is a bifurcation value and hence there exists a $\delta > 0$ and continuous functions: $s \in (-\delta, \delta) \mapsto d_m(s) \in \mathbb{R}$ and $s \in (-\delta, \delta) \mapsto (u_m(s), v_m(s)) \in X \times X$ such that $d_m(0) = \bar{d}_m$ and

$$(u_m(s, x), v_m(s, x)) = (\omega, \omega) + s(\bar{u}_m(x), \bar{v}_m(x)) + o(s) \tag{2.19}$$

is a solution of (2.8). Moreover, all non-constant solutions of (2.8) near the bifurcation point $(\bar{d}_m, \omega, \omega)$ lie on the curve

$$\mathcal{C}_m = (d_m(s), u_m(s, x), v_m(s, x)), s \in (-\delta, \delta).$$

Now we are ready to prove the following existence result on the non-constant solutions to (2.8).

THEOREM 2.1 For any fixed constant $\omega > 0$ such that $\frac{|\gamma'(\omega)\omega|}{\gamma(\omega)} - 1 > 0$, if

$$0 < d < \bar{d}_1,$$

where $\bar{d}_1 = (\frac{|\gamma'(\omega)\omega|}{\gamma(\omega)} - 1) \frac{\rho^2}{\pi^2}$, then there exists a positive solution (u, v) to (2.8) satisfying $u', v' < 0$ on $(0, l)$.

Proof. The proof consists of several steps.

Step 1. Denote by \mathcal{C} the component of non-trivial solutions that contains \mathcal{C}_1 . We show if $(d, u, v) \in \mathcal{C}$, then $u(x) > 0$ and $v(x) > 0$ for $x \in [0, l]$. Define

$$\mathcal{A} = \{(d, u, v) \in \mathcal{C} | u > 0, v > 0 \text{ in } [0, l]\}.$$

First \mathcal{A} is non-empty since $(\bar{d}_1, \omega, \omega) \in \mathcal{A}$. Clearly, \mathcal{A} is open in \mathcal{C} . Suppose that a sequence $(d_m, u_m, v_m) \in \mathcal{A}$ converges to $(d, u, v) \in \mathcal{C}$ as $m \rightarrow \infty$ in the norm of $\mathbb{R}^+ \times X \times X$ and also $\mathbb{R} \times C^2([0, l]) \times C^2([0, l])$ by elliptic regularity theorem. Obviously $u \geq 0, v \geq 0$ on $[0, l]$ because $u_m > 0, v_m > 0$ on $[0, l]$. We can show that $u \neq 0, v \neq 0$ on $[0, l]$. Consider the value of v first. Assume that there exists $x_0 \in [0, l]$ such that $v(x_0) = 0$. Recall v satisfies

$$\begin{cases} dv'' - v = -u, & \text{in } (0, l), \\ v'(0) = v'(l) = 0. \end{cases}$$

Applying strong maximum principle and Hopf boundary point lemma, we have $v \equiv 0$ on $[0, l]$, which implies $u \equiv 0$, contradicting $\int_0^l u(x)dx = \omega > 0$. Thus $v > 0$ on $[0, l]$. To show $u > 0$ on $[0, l]$, observe that u satisfies

$$\gamma(v)u_{xx} + 2\gamma'(v)v_x u_x + u(\gamma''(v)v_x^2 + \gamma'(v)v_{xx}) = 0, \tag{2.20}$$

where the coefficients $\gamma(v), \gamma'(v), \gamma''(v)$ are all bounded since v is bounded (see Lemma 2.1). Similarly, if $u(x_0) = 0$ for some $x_0 \in [0, l]$, then again we can apply strong maximum principle and Hopf boundary point lemma to obtain $u \equiv 0$, which is impossible. Then we have $u(x) > 0$ on $[0, l]$, which means $(d, u, v) \in \mathcal{A}$, i.e. \mathcal{A} is closed. Hence $\mathcal{A} = \mathcal{C}$.

Step 2. We now study \mathcal{C}^+ , the ‘upper’ branch of \mathcal{C} . The existence of \mathcal{C}^+ is guaranteed by the bifurcation Theorem A.1. So \mathcal{C}^+ contains the part of the curve \mathcal{C}_1 corresponding to $s > 0$. Next we show that $u', v' < 0$ on $(0, l), \forall (d, u, v) \in \mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\}$.

Define $\mathcal{B} = \{(d, u, v) \in \mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\} | u', v' < 0 \text{ on } (0, l)\}$. First, we prove that \mathcal{B} is non-empty. By (2.19), for $(d, u, v) \in \mathcal{C}^+$ near $(\bar{d}_1, \omega, \omega)$, we have

$$(u(s, x), v(s, x)) = (\omega, \omega) + s(\bar{u}_1(x), \bar{v}_1(x)) + o(s)$$

for some $s \in (0, \delta)$, where

$$(\bar{u}_1(x), \bar{v}_1(x)) = \left(\frac{\bar{d}_1 \pi^2}{l^2} + 1, 1 \right) \cos \frac{\pi x}{l}.$$

Obviously, $u' < 0$ and $v' < 0$ on $(0, l)$. So \mathcal{B} is non-empty.

Then we proceed to prove \mathcal{B} is open in $\mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\}$. Suppose $(d, u, v) \in \mathcal{B}$ and $(d_m, u_m, v_m) \in \mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\} \rightarrow (d, u, v)$ as $m \rightarrow \infty$. We want to show $(d_m, u_m, v_m) \in \mathcal{B}$ i.e. $u'_m, v'_m < 0$ in $(0, l)$ for large m . Since $u', v' < 0$ on $(0, l)$, then for large $m, u'_m, v'_m < 0$ on any fixed compact subinterval of $(0, l)$. We just need to consider the sign of u'_m, v'_m near the end points $x = 0, l$. It suffices to show the

‘non-degeneracy’ of u and v at $x = 0, l$, which is $u'', v'' \neq 0$ at $x = 0, l$. To show this, we differentiate the v -equation and get

$$\begin{cases} d(v')'' - v' = -u' > 0, & \text{in } (0, l), \\ v'(0) = 0 = v'(l), v' < 0, & \text{in } (0, l). \end{cases} \tag{2.21}$$

Applying Hopf boundary point lemma we have $v''(l) > 0 > v''(0)$. Using (2.20) for $x = 0$ and $x = l$, we have $u''(l) > 0 > u''(0)$. Now for large m , $u'_m, v'_m < 0$ on $(0, l)$ and then \mathcal{B} is open.

Finally we shall prove \mathcal{B} is closed in $\mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\}$. Suppose $(d_m, u_m, v_m) \in \mathcal{B} \rightarrow (d, u, v) \in \mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\}$ as $m \rightarrow \infty$. We want to show $u', v' < 0$ in $(0, l)$. We know $u', v' \leq 0$ on $[0, l]$ since $u'_m, v'_m < 0$. Applying strong maximum principal to (2.21), $v' \equiv 0$ or $v' < 0$ on $(0, l)$. If $v' \equiv 0$, by (2.11), we have $u' \equiv 0$. Recall $\int_0^l u(x)dx = \omega l = \int_0^l v(x)dx$, so $u \equiv v \equiv \omega$, which implies d is a bifurcation value and then $d = \bar{d}_n$ for some $n \geq 1$. $n = 1$ is impossible because $(d, u, v) \in \mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\}$. If $n \geq 2$, then (d_m, u_m, v_m) must be on the bifurcation curve $\mathcal{C}_n = \{(d_n(s), u_n(s, x), v_n(s, x)) | s \in (-\delta, \delta), s \neq 0\}$ for large m . Recall

$$(u_n(s, x), v_n(s, x)) = (\omega, \omega) + s(\bar{u}_n(x), \bar{v}_n(x)) + o(s)$$

and $(\bar{u}_n, \bar{v}_n) = (\frac{\bar{d}_n n^2 \pi^2}{l^2} + 1, 1) \cos \frac{n\pi x}{l}, n = 2, 3, \dots$. Obviously $u_n(s, x)$ and $v_n(s, x)$ are not decreasing on $(0, l)$ while $u_m(x)$ and $v_m(x)$ are decreasing, which is impossible. Thus $v' < 0$ on $(0, l)$. Using (2.11), we also have $u' < 0$ in $(0, l)$.

Step 3. Now by Theorem A.2, \mathcal{C}^+ satisfies at least one of the following alternatives:

- (a) it is not compact in $\mathbb{R}^+ \times X \times X$;
- (b) it contains a point (d^*, ω, ω) with $d^* \neq \bar{d}_1$;
- (c) it contains a point $(d, \omega + \hat{u}, \omega + \hat{v})$ where $0 \neq (\hat{u}, \hat{v}) \in Z$ and Z is a closed linear subspace of $X \times X$, complementing to $N(D_{(u,v)}\mathcal{F}(\bar{d}_1, \omega, \omega)) = \text{span}\{(\bar{u}_1, \bar{v}_1)\}$. We can take

$$Z = \left\{ (u, v) \in X \times X \mid \int_0^l (\bar{u}_1(x)u(x) + \bar{v}_1(x)v(x))dx = 0 \right\}.$$

Next we prove the alternatives (b) and (c) cannot happen to our problem.

If (b) occurs, then d^* shall be some bifurcation value \bar{d}_n and $n \geq 1$. This situation cannot happen according to the proof in Step 2.

If (c) occurs, $(d, \omega + \hat{u}, \omega + \hat{v}) \in \mathcal{C}^+ \setminus \{(\bar{d}_1, \omega, \omega)\}$ and by Step 2, we know $\hat{u}', \hat{v}' < 0$ on $(0, l)$. Since $(\hat{u}, \hat{v}) \in Z$, with the definition of Z , we have

$$\begin{aligned} 0 &= \int_0^l \left[\left(\frac{d\pi^2}{l^2} + 1 \right) \hat{u}(x) + \hat{v}(x) \right] \cos \frac{\pi x}{l} dx \\ &= -\frac{l}{\pi} \int_0^l \left[\left(\frac{d\pi^2}{l^2} + 1 \right) \hat{u}'(x) + \hat{v}'(x) \right] \sin \frac{\pi x}{l} dx > 0, \end{aligned}$$

which raises a contradiction. Hence (c) can not happen and the situation (a) will occur.

Step 4. We finally show that the ‘ d -coordinate’ on \mathcal{C}^+ is full of $(0, \bar{d}_1)$.

Recall (2.9) and (2.10), we know u and v are all bounded for any fixed $d > 0$. The function $\gamma(\cdot)$ is C^2 -smooth in $(0, \infty)$, so $-\frac{\gamma'(v)}{\gamma(v)}$ is bounded for bounded v . If d is strictly larger than a positive number, (u, v) is bounded in the norm of $C^3(0, l) \times C^3(0, l)$. So if d -coordinate on \mathcal{C}^+ is not full of $(0, \bar{d}_1)$, situation (a) implies that on the curve \mathcal{C}^+ , d shall go to infinity. By Lemma 2.1, we see that all positive solutions (u, v) of (2.8) tend to (ω, ω) as $d \rightarrow \infty$. Recall the null space of $N(D_{(u,v)}\mathcal{F}(\bar{d}_m, \omega, \omega))$ is $\{0\}$ for large d . Using implicit function theorem, we know for large d , (2.8) only has positive constant solution (ω, ω) . Since we have proved that on the curve \mathcal{C}^+ , $u', v' < 0$ by step 2, we have that d -coordinate on \mathcal{C}^+ is full of $(0, \bar{d}_1)$. This implies that for any d satisfying $0 < d < \bar{d}_1$, there exists a positive solution (u, v) to (2.8) satisfying $u', v' < 0$ on $(0, l)$, and the proof of Theorem 2.1 is complete. \square

2.2 Asymptotic profiles as $d \rightarrow 0$

In this section, we shall find the asymptotic profiles of positive monotone decreasing solutions (u, v) of (2.8) as $d \rightarrow 0$ by using the Helly compactness theorem. We remark that the idea of using Helly compactness theorem to explore the asymptotic dynamics of solutions to chemotaxis models first appeared in Wang (2000) and then in Wang & Xu (2013). Here we extend their ideas to density-suppressed motility models.

THEOREM 2.2 Let (u, v) be the positive monotone decreasing solutions of (2.8) obtained in Theorem 2.1. If $\sup_{v>0} \frac{\gamma(v)}{|\gamma'(v)|} < \omega$, then both u and v have spikes at $x = 0$ as $d \rightarrow 0$ (i.e. namely $u, v \rightarrow \infty$ in L^∞ -norm at $x = 0$ as $d \rightarrow 0$, and u, v are bounded in any $(\varepsilon, 1)$ for $0 < \varepsilon < 1$).

Proof. Since (u, v) is the solution of (2.8), we have $\frac{1}{l} \int_0^l u(x) = \omega$. By the monotonicity of u , \forall small $\varepsilon > 0$, u is uniformly bounded in $[\varepsilon, l]$ for any small d . Observe that the differentiation of $dv'' - v + u = 0$ yields

$$(dv')'' - v' + u' = 0.$$

Recall $u' = -\frac{\gamma'(v)uv'}{\gamma(v)}$, see (2.11). Inserting u' into the above differentiated v -equation, we have

$$(dv')'' + \left(-\frac{\gamma'(v)}{\gamma(v)}u - 1\right)v' = 0. \quad (2.22)$$

Consider the coefficient of v' of equation (2.22), if $-\frac{\gamma'(v(z))}{\gamma(v(z))}u(z) - 1 > \frac{d\pi^2}{z^2}$ for any $z \in (0, l)$, then by Sturm's oscillation theorem via a comparison between v' and $\sin(\frac{\pi x}{z})$, v' must change sign in $[0, z]$. So we have

$$-\frac{\gamma'(v(z))}{\gamma(v(z))}u(z) - 1 \leq \frac{d\pi^2}{z^2}.$$

Rearranging the equation and writing $u(z) = u(d; z)$, we have

$$u(d; z) \leq \left(\frac{d\pi^2}{z^2} + 1\right) \left(-\frac{\gamma(v)}{\gamma'(v)}\right) \leq \left(\frac{d\pi^2}{z^2} + 1\right) G_1, \quad \forall z \in (0, l), \quad (2.23)$$

where we have denoted $G_1 =: \sup_{v>0} \frac{\gamma(v)}{|\gamma'(v)|}$ for convenience. Then for any $\mu \in (0, \frac{l}{d}]$, we have the following estimate

$$\int_{d\mu}^l u(x)dx \leq \int_{d\mu}^l G_1 \left(\frac{d\pi^2}{x^2} + 1 \right) dx \leq G_1 \left(\frac{\pi^2}{\mu} + l \right).$$

From the assumption, we see that $\omega > G_1$. Then there exists a positive small constant c such that $\omega > G_1 + c$. Then for small d , we can take $\mu = \frac{G_1\pi^2}{cl}$, then

$$\omega l = \int_{\frac{dG_1\pi^2}{cl}}^l u(x)dx + \int_0^{\frac{dG_1\pi^2}{cl}} u(x)dx \leq (G_1 + c)l + u(0) \frac{dG_1\pi^2}{cl}.$$

Rearrangement of the above equation, we end up with

$$u(d; 0) \geq \frac{(\omega l - (G_1 + c)l)cl}{dG_1\pi^2}.$$

Since $\omega l - (G_1 + c)l > 0$, $u(d; 0)$ tends to infinity as $d \rightarrow 0$.

Now we consider the asymptotic behaviour of v as $d \rightarrow 0$. Recall that (u, v) is a pair of C^2 smooth bounded decreasing function in $(0, l)$ solving (2.6). Let us denote $v(x) = v(d; x)$. Since $v' < 0$ for $x \in (0, l)$ and $\int_0^l v(d; x) = \omega l$, it can be easily shown by a contradiction argument that $v(d; x) < \frac{\omega l}{x}$. For any fixed small $\epsilon > 0$ and for any interval W embedded in (ϵ, l) , one can check directly that

$$\sup_{n \in \mathbb{N}} \left(\left\| v \left(\frac{1}{n}; x \right) \right\|_{L^1(W)} + \left\| \frac{dv(\frac{1}{n}; x)}{dx} \right\|_{L^1(W)} \right) = \omega l + \frac{\omega l}{\epsilon} < \infty.$$

Moreover, $v(\frac{1}{n}; x)$ is uniformly bounded in n at a point in $(0, l)$, e.g. $v(\frac{1}{n}; \frac{l}{2}) < 2\omega$. So by Helly's compactness theorem, after passing to a subsequence of $n \rightarrow \infty$, which implies $d \rightarrow 0$, we have $v(x) \rightarrow$ some $v_0^k(x)$ pointwise in C^2 on $[\frac{1}{k}, l]$ for any fixed large integer k . Hence, $(v_0^k(x))_{xx}$ is bounded in $[\frac{1}{k}, l]$. In a same manner, we can find $u_0^k(x)$ such that passing the limit $d \rightarrow 0$ to the v -equation in (2.8), $u_0^k(x)$ and $v_0^k(x)$ satisfy

$$u_0^k(x) = v_0^k(x), \quad x \in \left[\frac{1}{k}, l \right].$$

By the standard diagonal argument of compactness (cf. Giga *et al.*, 2010), after passing to a subsequence of $d \rightarrow 0$, we have $v(x) \rightarrow$ some $v_0(x)$ pointwise in C^2 on $(0, l]$. The uniqueness of limit implies that $v_0(x) = v_0^k(x)$ in $[\frac{1}{k}, l]$. Similarly, we can find $u_0(x)$ such that the following holds thanks to the fact $\int_0^l u(x)dx = \int_0^l v(x)dx$:

$$\int_0^{\frac{1}{k}} u_0(x)dx + \int_{\frac{1}{k}}^l u_0^k(x)dx = \int_0^l u_0(x)dx = \int_0^l v_0(x)dx = \int_0^{\frac{1}{k}} v_0(x)dx + \int_{\frac{1}{k}}^l v_0^k(x)dx,$$

i.e. $\int_0^{\frac{1}{k}} u_0(x)dx = \int_0^{\frac{1}{k}} v_0(x)dx$. Then

$$\frac{1}{k}u_0\left(\frac{1}{k}\right) \leq \int_0^{\frac{1}{k}} u_0(x)dx = \int_0^{\frac{1}{k}} v_0(x)dx \leq \frac{1}{k}v_0(0),$$

which is $u_0\left(\frac{1}{k}\right) \leq v_0(0)$ for any large integer k . Since $u(d; 0) \rightarrow \infty$ as $d \rightarrow 0$, sending $k \rightarrow \infty$, we immediately have $v(d; 0) \rightarrow \infty$ as $d \rightarrow 0$ and conclude the proof. \square

LEMMA 2.3 Assume $\inf_{v>0} \frac{\gamma(v)}{|\gamma'(v)|} = G_2 > 0$. If $\omega \leq G_2$, (2.8) only has constant positive solution for any fixed $d > 0$.

Proof. We prove the results by contradiction. With Neumann boundary conditions, we assume, without loss of generality, that there exists a non-constant positive solution (u, v) to (2.8) with $v' < 0$ in $(0, l)$. Recall that

$$(dv')'' + \left(-\frac{\gamma'(v)}{\gamma(v)}u - 1\right)v' = 0.$$

Since $\omega l = \int_0^l u(x)dx \leq lG_2$ and u is decreasing, $u(x) < G_2$ for $x \in (0, l)$ or there exists an interval (a, l) with $a > 0$ such that $u(x) < G_2$ for $x \in (a, l)$ and $u(a) = G_2$. If $u(x) < G_2$ for $x \in (0, l)$, one has

$$(dv')'' = (-v')\left(-\frac{\gamma'(v)}{\gamma(v)}u - 1\right) \leq (-v')\left(\frac{u}{G_2} - 1\right) \leq 0, \text{ for } x \in (0, l). \tag{2.24}$$

Then applying strong maximum principle to the above equation with boundary condition $v'(0) = v'(l) = 0$, we have $v'(x) \equiv 0$ for $x \in (0, l)$, which is impossible because $v'(x) < 0$. So we alternatively have that $u(x) < G_2$ for $x \in (a, l)$ and $u(a) = G_2$. By (2.24), $(v')'' < 0$ in (a, l) . Since $v'(x) < 0$ in (a, l) and $v'(l) = 0$, it can be shown that $v''(a) > 0$. Recall u' has the same sign with v' . Then u is decreasing in $(0, l)$. Hence $u(x) \geq G_2$ in $[0, a]$. With similar arguments as above, we have $v''(a) < 0$. This raises a contradiction and completes the proof. \square

2.3 Transformation to explicit motility functions

The conditions in Theorem 2.1, Theorem 2.2 and Lemma 2.3 can be explicitly found as long as the motility function $\gamma(v)$ is known. Therefore, it would be of interest to transform these results to typical motility functions and make the results more transparent. Notice that $\gamma(v)$ is a smooth decreasing function, which typically may be of exponential or algebraic decay. Then we can present the following more specific results.

COROLLARY 2.1 For any fixed constant $\omega > 0$, the following results hold.

- (i) If $\gamma(v) = e^{-\chi v}$ with $\chi > 0$, then (2.8) has a positive non-constant solution satisfying $u', v' < 0$ on $(0, l)$ for any $d > 0$ if $\chi\omega > 1 + \frac{d\pi^2}{l^2}$, where u and v have boundary

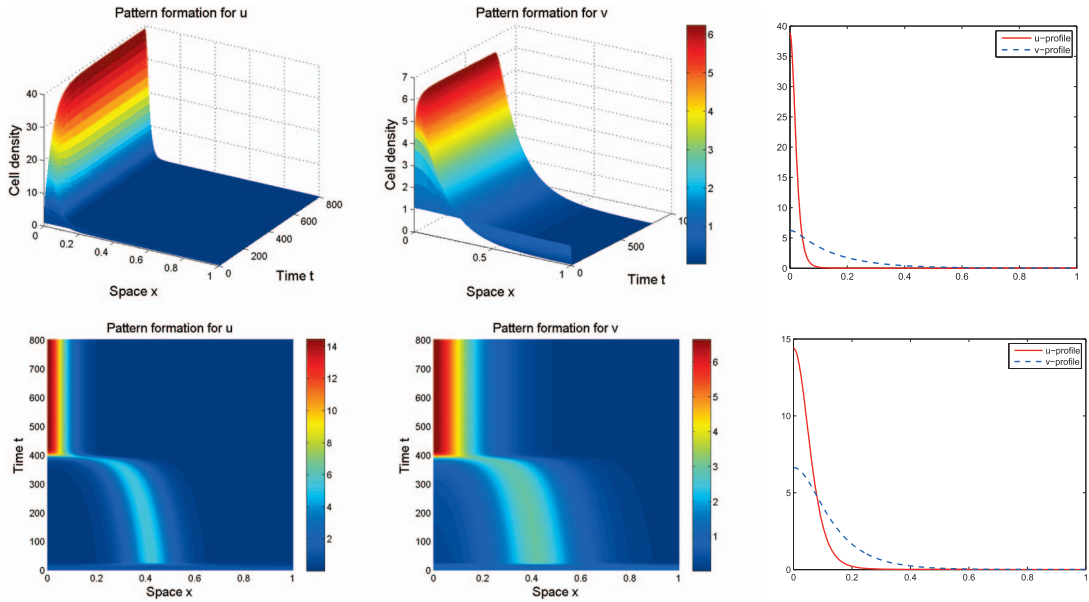


FIG. 1. Numerical simulations of monotone decreasing solutions of the system (1.2) with $\sigma = 0$ and $d = 0.02$ in $(0, \pi)$, where the initial value (u_0, v_0) is set as a small random perturbation of a constant steady state $(1, 1)$. In the first panel (row), we choose $\gamma(v) = e^{-2v}$, and in the second panel (row) we choose $\gamma(v) = \frac{1}{v^{12}}$.

spikes at $x = 0$ as $d \rightarrow 0$. Moreover, if $\chi\omega \leq 1$, then (2.8) has only constant solution $(u, v) = (\omega, \omega)$.

- (ii) If $\gamma(v) = \frac{1}{v^\lambda}$ with $\lambda > 0$, then (2.8) has a positive non-constant solution satisfying $u', v' < 0$ on $(0, l)$ for any $d > 0$ if $\lambda > 1 + \frac{d\pi^2}{\rho^2}$, where u and v have boundary spikes at $x = 0$ as $d \rightarrow 0$. In addition, if $\lambda \leq 1$, then (2.8) has only constant solution $(u, v) = (\omega, \omega)$.

Proof. When $\gamma(v) = e^{-\chi v}$ with $\chi > 0$, the conditions $\frac{|\gamma'(\omega)|\omega}{\gamma(\omega)} - 1 > 0$ and $0 < d < \bar{d}_1$ become $\chi\omega > 1 + \frac{d\pi^2}{\rho^2}$. Furthermore $\frac{\gamma(v)}{|\gamma'(v)|} = \frac{1}{\chi}$. Hence substituting these results to Theorem 2.1, Theorem 2.2 and Lemma 2.3, the results in (i) are directly obtained. Similarly, if $\gamma(v) = \frac{1}{v^\lambda}$ with $\lambda > 0$, then $\frac{\gamma(v)}{|\gamma'(v)|} = \frac{v}{\lambda}$. By simple calculations with results of Lemma 2.1, the first part result in (ii) with $\lambda > 1 + \frac{d\pi^2}{\rho^2}$ follows from Theorem 2.1 and Theorem 2.2. The second part result in (ii) with $\lambda \leq 1$ comes from Yoon & Kim (2017, Theorem 3.3) directly. \square

From the above results, we find that the existence of non-constant solutions may essentially depend on the decay rate of $\gamma(v)$ for given chemical diffusion rate $d > 0$. However, the results have a difference between exponential decay and algebraic decay motility function: the cell mass ω plays a role in the former one while does not in the latter one. We numerically test the results in Corollary 2.1 in Fig.1 where we do find the monotone decreasing solution by choosing parameters fulfilling the conditions in Corollary 2.1.

3. Steady states with growth (i.e. $\sigma > 0$)

Consider the steady-state problem (1.3) with $\sigma > 0$ and Neumann boundary condition in one dimension

$$\begin{cases} (\gamma(v)u)_{xx} + \sigma u(1 - u) = 0, & x \in (0, l), \\ dv_{xx} - v + u = 0, & x \in (0, l), \\ u_x = v_x = 0, & x = 0, l, \end{cases} \tag{3.25}$$

where $\sigma > 0, d > 0$ are constants. Observe that $(0, 0)$ and $(1, 1)$ are two only constant solutions of (3.25). We impose the following assumption on the motility function:

(H2) $\gamma(v)$ is C^2 -smooth in $(0, \infty)$ with $\gamma'(v) < 0$ and $-\frac{\gamma'(1)}{\gamma(1)} > \frac{d\pi^2}{l^2} + 1$.

We remark that the quantity $-\frac{\gamma'(1)}{\gamma(1)}$ characterizes the decay rate of motility function $\gamma(v)$. For example, if $\gamma(v) = e^{-kv}$ or $\gamma(v) = \frac{1}{v^k}$, then it can easily checked that $-\frac{\gamma'(1)}{\gamma(1)} = k$.

3.1 *Existence of non-constant solutions*

Define $\mathcal{F} : \mathcal{V} \rightarrow Y \times Y$ by

$$\mathcal{F}(\sigma, u, v) = \begin{pmatrix} -[(\gamma(v)u)_{xx} + \sigma u(1 - u)] \\ -dv_{xx} + v - u \end{pmatrix},$$

where $\mathcal{V} = (0, \infty) \times X \times X$ is an open set and X, Y have been defined before. Clearly, if (u, v) is the solution of system $\mathcal{F}(\sigma, u, v) = 0$, (u, v) is the solution of (3.25) and vice versa. For any fixed $(\sigma, u_1, v_1) \in \mathcal{V}$, consider the Fréchet derivative

$$D_{(u,v)}\mathcal{F}(\sigma, u_1, v_1) = \begin{pmatrix} -[(\gamma'(v_1)u_1v + \gamma(v_1)u)_{xx} + \sigma u(1 - u_1) - \sigma uu_1] \\ -dv_{xx} + v - u \end{pmatrix}. \tag{3.26}$$

LEMMA 3.1 For any fixed $(u_1, v_1) \in X \times X$, the Fréchet derivative

$$D_{(u,v)}\mathcal{F}(\sigma, u_1, v_1) : X \times X \rightarrow Y \times Y$$

is a Fredholm operator with index zero.

Proof. Consider the Fréchet derivative at a fixed point (σ, u_1, v_1) in \mathcal{V} , which is (3.26). The second-order derivatives of u and v in the first line of (3.26) are $-\gamma'(v_1)u_1v_{xx}$ and $-\gamma(v_1)u_{xx}$. So the second-order derivatives part of $D_{(u,v)}\mathcal{F}$ can be written as

$$-\begin{pmatrix} \gamma(v_1) & \gamma'(v_1)u_1 \\ 0 & d \end{pmatrix} \begin{pmatrix} u_{xx} \\ v_{xx} \end{pmatrix}$$

and hence we have the conclusion that

$$D_{(u,v)}\mathcal{F}(\sigma, u_1, v_1) : X \times X \rightarrow Y \times Y$$

is elliptic and satisfies Agmon’s condition by Remark 2.5 case 3 in Shi & Wang (2009). By Theorem 3.3 and Remark 3.4 in Shi & Wang (2009), $D_{(u,v)}\mathcal{F}(\sigma, u_1, v_1) : X \times X \rightarrow Y \times Y$ is a Fredholm operator with zero index. \square

Now we try to find all the possible bifurcation value of σ . Recall there are only two constant steady states of (3.25), $(0, 0)$ and $(1, 1)$. The necessary condition for bifurcation is that the null space of $D_{(u,v)}\mathcal{F}(\sigma, 0, 0)$ or $D_{(u,v)}\mathcal{F}(\sigma, 1, 1)$ is non-trivial, i.e.

$$N(D_{(u,v)}\mathcal{F}(\sigma, 0, 0)) \neq \{0\} \text{ or } N(D_{(u,v)}\mathcal{F}(\sigma, 1, 1)) \neq \{0\}.$$

According to (3.26), we know the null space of $D_{(u,v)}\mathcal{F}(\sigma, 0, 0)$ is the space of solution (u, v) of

$$\begin{cases} -\gamma(0)u_{xx} - \sigma u = 0, \\ -dv_{xx} + v - u = 0, \end{cases}$$

and the null space of $D_{(u,v)}\mathcal{F}(\sigma, 1, 1)$ is the space of solution (u, v) of

$$\begin{cases} -\gamma'(1)v_{xx} - \gamma(1)u_{xx} + \sigma u = 0, \\ -dv_{xx} + v - u = 0. \end{cases}$$

With a similar discussion in Section 2.1, we have the following results:

For any positive integer m such that $\sigma_m = (-\gamma(1) - \frac{\gamma'(1)}{\frac{dm^2\pi^2}{l^2} + 1})\frac{m^2\pi^2}{l^2} > 0$, σ_m is a positive bifurcation value and $(\sigma_m, 1, 1)$ is a bifurcation point in \mathcal{V} . By theorem A.1, there exists a $\delta > 0$ and continuous functions: $s \in (-\delta, \delta) \mapsto \sigma_m(s) \in (0, \infty)$, $s \in (-\delta, \delta) \mapsto (u_m(s, x), v_m(s, x)) \in X \times X$ such that $\sigma_m(0) = \sigma_m$ and

$$(u_m(s, x), v_m(s, x)) = (1, 1) + s(u_m(x), v_m(x)) + o(s)$$

is a solution of (3.25), where $(u_m(x), v_m(x)) = (a_m, b_m) \cos \frac{m\pi x}{l}$ for any constants a_m, b_m satisfying $\frac{a_m}{b_m} = \frac{dm^2\pi^2}{l^2} + 1$. Furthermore, all non-constant solutions of (3.25) near the bifurcation point $(\sigma_m, 1, 1)$ are on the curve

$$\bar{C}_m = (\sigma_m(s), u_m(s, x), v_m(s, x)), s \in (-\delta, \delta).$$

For any positive integer m , $\tilde{\sigma}_m = \gamma(0)\frac{m^2\pi^2}{l^2}$ is a bifurcation value and $(\tilde{\sigma}_m, 0, 0)$ is a bifurcation point in \mathcal{V} . Similarly, there exists $\tilde{\delta} > 0$ and continuous functions: $s \in (-\tilde{\delta}, \tilde{\delta}) \mapsto \tilde{\sigma}_m(s) \in (0, \infty)$, $s \in (-\tilde{\delta}, \tilde{\delta}) \mapsto (\tilde{u}_m(s, x), \tilde{v}_m(s, x)) \in X \times X$ such that $\tilde{\sigma}_m(0) = \tilde{\sigma}_m$ and

$$(\tilde{u}_m(s, x), \tilde{v}_m(s, x)) = (0, 0) + s(u_m(x), v_m(x)) + o(s)$$

is a solution of (3.25), where $(u_m(x), v_m(x))$ are defined above. Moreover, all non-constant solutions of (3.25) near the bifurcation point $(\tilde{\sigma}_m, 0, 0)$ are on the curve

$$\tilde{C}_m = (\tilde{\sigma}_m(s), \tilde{u}_m(s, x), \tilde{v}_m(s, x)), s \in (-\delta, \delta).$$

Observe that for any $s \in (-\delta, \delta), s \neq 0, \tilde{u}_m(s, x)$ and $\tilde{v}_m(s, x)$ must change signs for $x \in [0, l]$, which are not meaningful solutions in applications of biology. So we shall not perform the global bifurcation analysis for the trivial steady state $(0, 0)$. Below by \mathcal{C}_m we denote the component of non-trivial solutions that contains $\bar{\mathcal{C}}_m$. The existence of \mathcal{C}_1 is guaranteed by Theorem A.1 and assumption (H2). However, for $m > 1$, we do not know σ_m is non-negative or negative and cannot make sure \mathcal{C}_m is exist. By assumption (H2), we know there exists a positive integer M such that

$$\frac{dM^2\pi^2}{l^2} + 1 < -\frac{\gamma'(1)}{\gamma(1)} \leq \frac{d(M+1)^2\pi^2}{l^2} + 1 \tag{3.27}$$

with $\sigma_m > 0$ for $1 \leq m \leq M$ and $\sigma_m \leq 0$ for $m \geq M + 1$. Hence for $m = 1, 2, \dots, M$, the existence of \mathcal{C}_m is guaranteed. Then we have the following theorem.

THEOREM 3.1 Let the assumption (H2) hold and $\sigma_m = \left(-\gamma(1) - \frac{\gamma'(1)}{\frac{dm^2\pi^2}{l^2} + 1}\right) \frac{m^2\pi^2}{l^2}$ with m being a positive integer. Then there exists a positive integer M such that (3.27) and the following results hold.

- (i) If $M = 1$, then the problem (3.25) has a non-constant solution for $\sigma \in (0, \sigma_1)$.
- (ii) If $M \geq 2$, then the problem (3.25) has a non-constant solution for $\sigma \in (\sigma_*, \sigma^*)$, where $\sigma^* = \max_{1 \leq m \leq M} \{\sigma_m\}$ and $\sigma_* = \max_{1 \leq m \leq M} \{\sigma_m | \sigma_m < \sigma^*\}$ (namely σ^* and σ_* are the largest and second largest numbers of σ_m for $1 \leq m \leq M$, respectively).

Proof. We start the proof with a claim: if $(\sigma, u, v) \in \mathcal{C}_m (m = 1, 2, \dots, M)$, then $u(x) > 0$ and $v(x) > 0$ for all $x \in [0, l]$.

Define

$$\mathcal{A}_m = \{(\sigma, u, v) \in \mathcal{C}_m | u(x) > 0, v(x) > 0 \text{ in } [0, l]\} \text{ for } m = 1, 2, \dots, M.$$

For any fixed m, \mathcal{A}_m is non-empty since $(\sigma_m, 1, 1) \in \mathcal{A}_m$. We can easily see that \mathcal{A}_m is open in \mathcal{C}_m . So it suffices to show \mathcal{A}_m is closed in \mathcal{C}_m to prove the claim because the connectedness of \mathcal{C}_m will give us $\mathcal{C}_m = \mathcal{A}_m$. Suppose a sequence $(\sigma_k, u_k, v_k) \in \mathcal{A}_m$ converges to $(\sigma, u, v) \in \mathcal{C}_m$ as $k \rightarrow \infty$ in the norm of $\mathbb{R} \times X \times X$ and hence in the norm of $\mathbb{R} \times C^2([0, l]) \times C^2([0, l])$ by elliptic regularity theory. To show \mathcal{A}_m is closed, we just need to show $(\sigma, u, v) \in \mathcal{A}_m$. Since $u_k > 0, v_k > 0$ in $[0, l], u \geq 0, v \geq 0$ in $[0, l]$. We only need to show $u \neq 0, v \neq 0$ in $[0, l]$. First we consider the value of v and assume that there exists $x_0 \in [0, l]$ such that $v(x_0) = 0$. Recall v satisfies

$$\begin{cases} dv'' - v = -u \leq 0, & \text{in } (0, l), \\ v'(0) = v'(l) = 0. \end{cases}$$

Applying strong maximum principle and Hopf boundary point lemma, we have $v \equiv 0$ in $[0, l]$. Hence $u \equiv v \equiv 0$ in $[0, l]$, which implies $(\sigma, u, v) = (\sigma, 0, 0)$ is a bifurcation point on the curve \mathcal{C}_n for some $n \geq 1$. So when k is large, there exists $\delta > 0$, such that $(u_k, v_k) = (0, 0) + s(u_n(x), v_n(x)) + o(s)$ for $s \in (-\delta, \delta)$ for some n . Recall that $v_n(x) = b_n \cos \frac{n\pi x}{l}$, where b_n is a constant. So v_k must be negative or zero in $[0, l]$. This contradicts the fact $v_k > 0$ in $[0, l]$. So our assumption is false and $v > 0$ in $[0, l]$.

Now we show $u > 0$ in $[0, l]$. Observe that u satisfies

$$\gamma(v)u_{xx} + 2\gamma'(v)v_x u_x + [\sigma(1 - u) + \gamma''(v)(v_x)^2 + \gamma'(v)v_{xx}]u = 0.$$

The ‘coefficient’ of u is bounded by *a priori* estimate of u and v , which is given in Proposition 2.1 in [Ma et al. \(2020\)](#). Similarly, if $u(x_0) = 0$ for some $x_0 \in [0, l]$, again we can apply strong maximum principle and Hopf boundary point lemma to obtain $u \equiv v \equiv 0$, which is impossible. Now we have $(\sigma, u, v) \in \mathcal{A}_m$ and the claim is proved.

Since all the constant solutions can only be $(0, 0)$ or $(1, 1)$, and $(\sigma, 0, 0)$ is not on the curve \mathcal{C}_m by our former discussion, all points (σ, u, v) on the curve \mathcal{C}_m must be non-constant solutions of (3.25) except the points on the σ -coordinate, which are $(\sigma, 1, 1)$ for some $\sigma > 0$. From Theorem A.1, we know \mathcal{C}_m is either not compact in \mathcal{V} or contains a point $(\sigma_n, 1, 1)$ with $\sigma_n \neq \sigma_m$. First, we know (u, v) is bounded by Proposition 2.1 in [Ma et al. \(2020\)](#) with $\sigma > 0$ and when $\sigma = 0$, (u, v) is bounded by Lemma 2.1. By Theorem 3.1 (a) in [Ma et al. \(2020\)](#), we know (3.25) does not have non-constant solutions for large σ . We immediately have the conclusion that if \mathcal{C}_m is not compact, the σ -coordinate must cover $(0, \sigma_m)$. Clearly, if \mathcal{C}_m contains a point $(\sigma_n, 1, 1)$ with $\sigma_n \neq \sigma_m$, the σ -coordinate must cover the interval with endpoints σ_n and σ_m . Consider the curve bifurcating from the largest positive bifurcation value σ^* , the σ -coordinate must cover (σ_*, σ^*) for $M \geq 2$ and $(0, \sigma_1)$ for $M = 1$. This completes the proof. \square

REMARK 3.1 If we use d as the bifurcation parameter, then bifurcations may occur at

$$\hat{d}_m = \frac{l^2}{(\sigma l^2 + \gamma(1)\pi^2 m^2)} \left(-\gamma'(1) - \gamma(1) - \frac{\sigma l^2}{\pi^2 m^2} \right), m = 1, 2, \dots \tag{3.28}$$

and the counterpart of assumption (H2) is

$$(H3) \quad \gamma(v) \text{ is } C^2\text{-smooth in } (0, \infty) \text{ with } \gamma'(v) < 0 \text{ and } -\frac{\gamma'(1)}{\gamma(1)} > 1,$$

which ensures that there exists a positive integer M such that $\hat{d}_m > 0$ for $m \geq M + 1$ and $\hat{d}_m \leq 0$ for $m = 1, 2, \dots, M$, i.e.

$$1 + \frac{\sigma l^2}{\pi^2 (M + 1)^2} < \frac{|\gamma'(1)|}{\gamma(1)} \leq 1 + \frac{\sigma l^2}{\pi^2 M^2}. \tag{3.29}$$

Since there exist infinitely many positive bifurcation numbers and $\hat{d}_m \rightarrow 0$ as $m \rightarrow \infty$, we cannot assert the global bifurcation result as Theorem 3.1(i). However, the similar result to Theorem 3.1(ii) will hold for $d \in (d_*, d^*)$ where d^* and d_* are the largest and second largest numbers of \hat{d}_m for $m \geq M + 1$ respectively. That is, we have the following results.

COROLLARY 3.1 Let the assumption (H3) hold and \hat{d}_m defined in (3.28). Then there exists a positive integer M such that (3.29) holds and the problem (3.25) has a non-constant solution for $d \in (d_*, d^*)$, where $d^* = \max_{m \geq M+1} \{\hat{d}_m\}$ and $d_* = \max_{m \geq M+1} \{\hat{d}_m | \hat{d}_m < d^*\}$.

REMARK 3.2 The dynamics of (1.2) with $\sigma > 0$ is much more complicated than the case $\sigma = 0$ as numerically illustrated in [Jin et al. \(2018\)](#). Theorem 3.1 gives the minimum ranges of σ for the existence

of non-constant stationary solutions of (3.25). This is the first result that can assert the existence of non-constant stationary solutions for (3.25) in a specified range of σ . In this sense, our results improve the one-dimensional existence results by Ma *et al.* (2020, Theorem 4.1) in one dimension where the conditions can only be checked for a given value of σ . However, the results in Theorem 3.1 by no means rule out the possibility that (3.25) has non-constant solutions outside the range (σ_*, σ^*) . The existence of non-constant solutions of (3.25) is far from being completely understood.

REMARK 3.3 If M is not large, we can easily find all values of σ_m for $m = 1, 2, \dots, M$ and reorder the largest and second largest value of bifurcation values σ_m (i.e. σ^* and σ_* , respectively). However, if M is large, it is cumbersome to compute all positive bifurcation values to make comparison. Notice that the function $\sigma(x) = -\frac{\gamma(1)\pi^2}{l^2}x^2 - \frac{\gamma'(1)}{d+\frac{l^2}{\pi^2x^2}}$, where $\sigma(m) = \sigma_m$ if m is a positive integer, has a unique maximum at

$$x = \frac{l}{\sqrt{d\pi}} \sqrt{\sqrt{-\frac{\gamma'(1)}{\gamma(1)}} - 1} \triangleq \bar{x} \tag{3.30}$$

and $\sigma(x)$ is strictly increasing in $(0, \bar{x})$ while strictly decreasing in (\bar{x}, M) . Since we are mainly concerned with two numbers: the largest and second largest values of bifurcation values, we find a short algorithm to quickly find σ_* and σ^* for any $M \geq 2$ as given in the following lemma.

LEMMA 3.2 Let $M \geq 2$ in (3.27) and \bar{x} be defined in (3.30). Then the two numbers σ^* and σ_* can be explicitly found in the following ways.

- If \bar{x} is an integer, then

$$\sigma^* = \sigma_{\bar{x}} = \frac{1}{d}(\sqrt{-\gamma'(1)} - \sqrt{\gamma(1)})^2, \quad \sigma_* = \max\{\sigma_{\bar{x}-1}, \sigma_{\bar{x}+1}\}.$$

- If \bar{x} is not an integer, then

$$\sigma^* = \max\{\sigma_{[\bar{x}]}, \sigma_{\lceil\bar{x}\rceil}\}, \quad \sigma_* = \max\{\sigma_{\bar{x}-1}, \sigma_{\bar{x}+1}\}$$

where $[\bar{x}]$ denotes the largest integer less than \bar{x} while $\lceil\bar{x}\rceil$ denotes the smallest integer greater than \bar{x} , and \tilde{x} is the integer such that $\sigma^* = \sigma_{\tilde{x}}$ (i.e. \bar{x} is either $[\bar{x}]$ or $\lceil\bar{x}\rceil$).

Proof. We divide two cases to proceed.

Case 1: \bar{x} is an integer. It is obvious that $\sigma^* = \sigma_{\bar{x}}$ and $\sigma_* = \max\{\sigma_{\bar{x}-1}, \sigma_{\bar{x}+1}\}$.

Case 2: \bar{x} is not an integer. Consider $[\bar{x}]$ and $\lceil\bar{x}\rceil$. If $\sigma_{[\bar{x}]} > \sigma_{\lceil\bar{x}\rceil}$, then $\sigma^* = \sigma_{[\bar{x}]}$ and we need to compare the value of $\sigma_{[\bar{x}]}$ and $\sigma_{[\bar{x}]-1}$ to take $\sigma_* = \max\{\sigma_{[\bar{x}]}, \sigma_{[\bar{x}]-1}\}$. Similarly, if $\sigma_{\lceil\bar{x}\rceil} > \sigma_{[\bar{x}]}$, $\sigma^* = \sigma_{\lceil\bar{x}\rceil}$ and we need to compare the value of $\sigma_{\lceil\bar{x}\rceil}$ and $\sigma_{\lceil\bar{x}\rceil+1}$ to take $\sigma_* = \max\{\sigma_{\lceil\bar{x}\rceil}, \sigma_{\lceil\bar{x}\rceil+1}\}$. If $\sigma_{[\bar{x}]} = \sigma_{\lceil\bar{x}\rceil}$, $\sigma^* = \sigma_{[\bar{x}]} = \sigma_{\lceil\bar{x}\rceil}$, $\sigma_* = \max\{\sigma_{[\bar{x}]-1}, \sigma_{\lceil\bar{x}\rceil+1}\}$. Observe that $[\bar{x}] + 1 = \lceil\bar{x}\rceil$. So if we denote \tilde{x} as the integer such that $\sigma^* = \sigma_{\tilde{x}}$, then $\sigma_* = \max\{\sigma_{\tilde{x}+1}, \sigma_{\tilde{x}-1}\}$. \square

REMARK 3.4 If $M = 1$ and \bar{x} is an integer for given motility function $\gamma(v)$, then $\sigma^* = \sigma_{\bar{x}}$ and $\sigma_* = 0$. Note that $\sigma_{\bar{x}} = \sigma_1 = \frac{1}{d}(\sqrt{-\gamma'(1)} - \sqrt{\gamma(1)})^2$ is the maximal value of σ to allow the pattern formation (see Jin *et al.*, 2018). Hence in this case the global bifurcation diagram full of $(0, \sigma_1)$ is achieved on

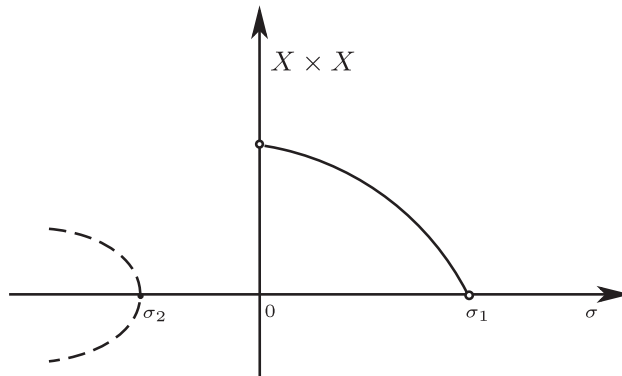


FIG. 2. Bifurcation diagram of the solution (u, v) in the space $X \times X$ vs. σ in the case that $M = 1$ and \bar{x} is an integer. When $\sigma > \sigma_1$, the constant steady state $(1, 1)$ is asymptotically stable and no non-constant solutions will bifurcate, while for each $\sigma \in (0, \sigma_1)$, there is at least one non-constant solution (indicated by solid curve). Here we only plot the half bifurcation curve above σ -axis, which can be connected to vertical axis. Other bifurcation points $\sigma_m (m \geq 2)$ are negative and hence are out of our interest although there are also non-constant solutions bifurcating from them (indicated by dashed curve).

the σ -axis and our result gives the largest parameter regime for the existence of pattern (i.e. stationary non-constant) solutions, see a plot of bifurcation diagram in Fig. 2. For example, if $l = \pi$, $d = 1$ and $\gamma(v) = 1/(1 + e^{8(v-1)})$. Then a simple calculation shows that (3.27) holds with $M = 1$ and $\bar{x} = \frac{l}{\sqrt{d\pi}} \sqrt{\sqrt{4} - 1} = 1$, where $\sigma^* = \sigma_1 = 0.5, \sigma_* = 0$ and $\sigma_2 = -0.4$.

3.2 Examples

We shall use some examples to numerically illustrate that stationary patterns will arise from the model (1.2) under the assumptions in Theorem 3.1. We also numerically demonstrate that the patterns may be intricate if the parameter value of σ is outside the range (σ_*, σ^*) . In particular, unstable or periodic patterns may arise. This indicates that the global bifurcation diagram in the full regime $(0, \sigma^*)$ cannot be expected for any motility function $\gamma(v)$ satisfying (3.27) except the case $M = 1$ as discussed in Remark 3.4. We also numerically show the possible differences in pattern formations between exponentially and algebraically decay motility functions, which have not been qualitatively characterized in any existing works.

Example 1: Theorem 3.1 provides a simple algorithm to identify the minimal range (σ_*, σ^*) in which the existence of non-constant steady states to density-suppressed motility models is ensured. We present an example for $M \geq 2$ to illustrate the patterns for σ inside and outside this range. Consider $\gamma(v) = 1/(1 + e^{9(v-1)})$, $l = 4\pi$ and $d = 1$. By a simple calculation, we know (3.27) holds for $M = 7$ and $\bar{x} = \frac{l}{\sqrt{d\pi}} \sqrt{\sqrt{4.5} - 1} = 4.2357$. Hence $[\bar{x}] = 4, \lceil \bar{x} \rceil = 5$. By the algorithm stated in Lemma 3.2, we find that $\sigma_* = \sigma_3 = 0.5287$ and $\sigma^* = \sigma_4 = 0.6250$. Therefore, we can confirm by Theorem 3.1 that the system (3.25) has a non-constant solution for any $\sigma \in (0.5287, 0.6250)$. This is numerically verified by the simulations shown in Fig. 3 for $\sigma = 0.6$ where we find the stable stationary patterns. However, an interesting question arises as whether the elliptic problem (3.25) has non-constant solutions outside this range $(\sigma_*, \sigma^*) = (0.5287, 0.6250)$, which remains an open question in this paper. Here we

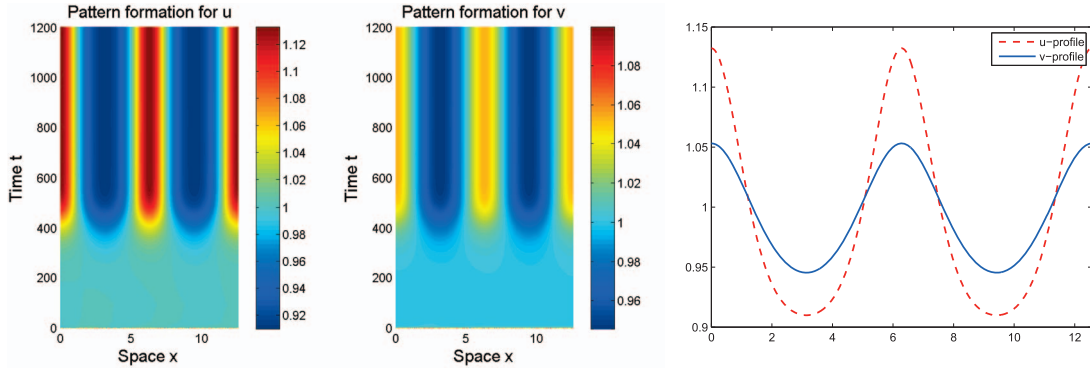


FIG. 3. Numerical stationary patterns generated by the system (1.2) with $\sigma = 0.6$ in $(0, 4\pi)$, where $\gamma(v) = 1/(1 + e^{9(v-1)})$, $d = 1$ and the initial value (u_0, v_0) is set as a small random perturbation of constant steady state $(1, 1)$.

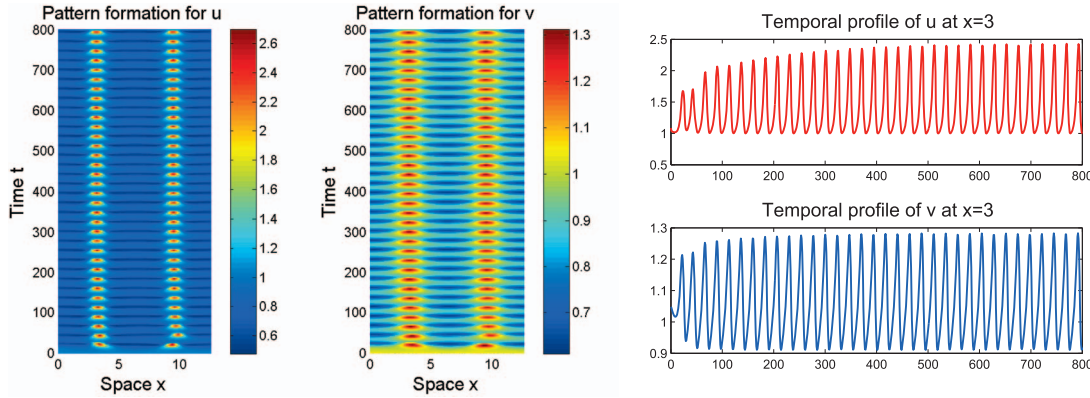


FIG. 4. Numerical periodic patterns generated by the system (1.2) with $\sigma = 0.2$ in $(0, 4\pi)$, where $\gamma(v) = 1/(1 + e^{9(v-1)})$, $d = 1$ and the initial value (u_0, v_0) is set as a small random perturbation of constant steady state $(1, 1)$.

numerically illustrate the possibilities. To this end, we first choose $\sigma = 0.2$, which is less than the value of σ_* , and numerical simulations shown in Fig. 4 show that time-periodic patterns will arise and hence the system (1.3) may not have stable steady states. This implies that it is perhaps impossible to get a global bifurcation diagram full of $(0, \sigma^*)$ to ensure the existence of stationary solutions.

Example 2: We consider two examples for $\gamma(v)$: $\gamma(v) = 1/(1 + e^{9(v-1)})$ and $\gamma(v) = \frac{1}{(1+v)^9}$, to look at the differences of patterning processes between exponential and algebraic decay motility functions. For this, we choose the parameter values of σ to be outside the identified range (σ_*, σ^*) where we do not know whether the system allows stationary patterns. The simulations in Fig. 5 illustrate that the exponentially decay motility function generates unstable (chaotic) temporal-spatio patterns while the algebraically decay one produces stationary patterns. This indicates that the patterning process may be very different for motility functions with different decay rates in some (narrow) parameter regimes.

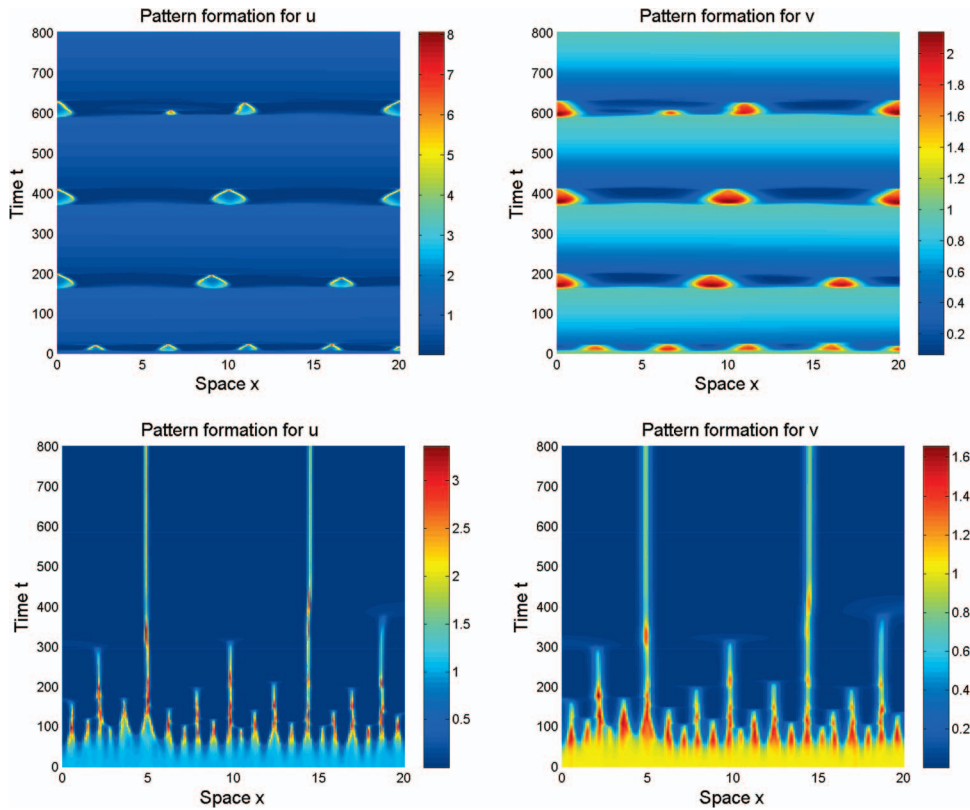


FIG. 5. Numerical patterns generated by the system (1.2) with $\sigma = 0.02$ in $(0, 20)$, where $\gamma(v) = 1/(1 + e^{9(v-1)})$ and $d = 0.3$ in the first panel (row) and $\gamma(v) = 1/(1 + v)^9$ and $d = 0.02$ in the second panel (row). The initial value (u_0, v_0) is set as a small random perturbation of constant steady state $(1, 1)$.

4. Summary and discussion

In this paper, we find the explicit parameter regimes for the existence of non-constant solutions to the one-dimensional stationary Neumann problem (1.3). When the cell growth rate $\sigma = 0$, (1.3) corresponds to the stationary problem of density-suppressed motility systems (1.1) with Neumann boundary conditions, while $\sigma > 0$, it corresponds to the stationary problem of (1.2) subject to Neumann boundary conditions. The one-dimensional problem (1.3) with $\sigma = 0$ and $\sigma > 0$ is formulated by (2.6) and (3.25), respectively. Using the global bifurcation theory by treating the chemical diffusion rate $d > 0$ as a bifurcation parameter, we show that the problem (2.6) admits monotone solutions as $0 < d < \bar{d}_1$ (see Theorem 2.1). Furthermore, we show that the monotone solutions have boundary spikes as $d \rightarrow 0$ in Theorem 2.2. With the help of maximum principle, we find conditions such that (2.6) admits only constant solutions (see Lemma 2.3). These results, if they are transformed to specific motility function $\gamma(v)$, lead to sharp (threshold) conditions on the existence of non-constant stationary solutions (see Corollary 2.1). Numerical simulations shown in Fig. 1 well agree with our analytical results. When $\sigma > 0$, the bifurcation analysis is more complicated and a global bifurcation diagram is elusive. By bifurcation theorems, we are able to identify a minimal range, denoted by (σ_*, σ^*) of σ , to

guarantee the existence of non-constant solutions of (3.25) (Theorem 3.1). But for a special case $M = 1$ and \bar{x} is an integer, the global bifurcation diagram is indeed achieved (see Remark 3.4 and Fig. 2). When $\sigma > 0$ is large, say $\sigma > \sigma^*$, the logistic damping will be strong enough to homogenize the dynamics and hence erase any patterns. This fact is rigorously shown in both papers (Jin *et al.*, 2018, and Ma *et al.*, 2020) that non-constant solutions of (1.3) will not exist if σ is larger than some number. Hence, the existence of upper bound σ^* for σ in Theorem 3.1 is necessary although our methods are different from Jin *et al.* (2018); Ma *et al.* (2020). The concerned issue is the existence of a lower bound σ_* since the global bifurcation diagram exists when $\sigma = 0$. However, this is indeed the case for the sublinear and linear algebraic decay motility function as shown in Ma *et al.* (2020, Theorem 3.1 and Remark 3.1). In other words, when the decay of motility function $\gamma(v)$ is linear or sub-linear, the bifurcation range for σ cannot be decreasingly extended from σ^* to zero but to some positive number. Nevertheless, the assumption in (H2) requires that the decay rate of motility function $\gamma(v)$ must be super-linear, and we are unable to prove that there is no non-constant solution if $\sigma < \sigma_*$. Hence an open question arises as

- If the decay rate of $\gamma(v)$ is superlinear like $\gamma(v) = \frac{1}{v^k}(k > 1)$ or $\gamma(v) = e^{-\chi v}$ with $\chi > 0$, whether the lower bound σ_* in Theorem 3.1 can be zero or arbitrarily close to zero?

The answer of the above question seems elusive from numerical simulations. In Fig. 4, we show that when σ is inside the range (σ_*, σ^*) , the stationary pattern exists. However, if the value of σ is decreased to be outside the range (σ_*, σ^*) , periodic patterns instead of stationary patterns will develop. If we further decrease the value of σ , then chaotic (unstable) temporal-spatio pattern will arise (see the first row of Fig. 5). This indicates that for exponentially decay motility function, stationary pattern may only exist for a medium range of σ , namely σ_* cannot be arbitrarily close to zero. However, for the algebraic decay motility function with superlinear decay rate, the situations seem different as shown in the second row of Fig. 5 where we observe the stationary patterns and no periodic or chaotic patterns can be found. This implies that to investigate the above question, we may need to differentiate fast (like exponential) and slow (like algebraic) decay motility function $\gamma(v)$. This makes the question even more delicate and exploration of this question will be rewarding.

In this paper, we consider the system (1.3) only in one dimension for $\sigma \geq 0$. The multi-dimensional problem of (1.3) with $\sigma > 0$ has been investigated in Ma *et al.* (2020). But the results are far from being complete and solution profiles/patterns have not been qualitatively characterized. Hence the multi-dimensional problem of (1.3) has a demand for further investigation. Lastly, we discuss the patterning processes caused by the logistic growth in the density-suppressed motility model (1.2). By expanding the diffusion term $\Delta(\gamma(v)u) = \nabla \cdot (\gamma(v)\nabla u + \gamma'(v)u\nabla v)$, we find that the system (1.2) is analogous to chemotaxis models with logistic growth. The difference is that in (1.2), both diffusion and chemotactic coefficient are not constant but chemical-density dependent functions that not only make the analysis different but also lead to different patterning processes. As shown in Kolokolnikov *et al.* (2014); Ma *et al.* (2012); Painter & Hillen (2011); Wang & Hillen (2007), pattern formation of chemotaxis models with logistic growth typically has the so-called merging and emerging dynamics. But no merging and emerging patterning process is identified for the system (1.2) as shown in our various numerical simulations in this paper and in Ma *et al.* (2020). This implies that the motility function $\gamma(v)$ plays an important role in determining the pattern profiles.

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REFERENCES

- AHN, J. & YOON, C. (2019) Global well-posedness and stability of constant equilibria in parabolic-elliptic chemotaxis systems without gradient sensing. *Nonlinearity*, **32**, 1327–1351.
- CRANDALL, M. G. & RABINOWITZ, P. H. (1971) Bifurcation from simple eigenvalues. *J. Funct. Anal.*, **8**, 321–340.
- DESUILLETES, L., KIM, Y. J., TRESCASES, A. & YOON, C. (2019) A logarithmic chemotaxis model featuring global existence and aggregation. *Nonlinear Anal. Real World Appl.*, **50**, 562–582.
- DYSON, L. & BAKERM, R. E. (2015) The importance of volume exclusion in modelling cellular migration. *J. Math. Biol.*, **71**, 691–711.
- FITZPATRICK, P. M. & PEJSACHOWICZ, J. (1991) Parity and generalized multiplicity. *Trans. Amer. Math. Soc.*, **326**, 281–305.
- FU, X., TANG, L. H., LIU, C., HUANG, J. D., HWA, T. & LENZ, P. (2012) Stripe formation in bacterial system with density-suppressed motility. *Phys. Rev. Lett.*, **108**, 198102.
- FUJIE, K. & JIANG J. (2020a) Comparison methods for a Keller–Segel-type model of pattern formations with density-suppressed motilities. arXiv:2001.01288.
- FUJIE, K. & JIANG, J. (2020b) Global existence for a kinetic model of pattern formation with density-suppressed motilities. *J. Differential Equations*, **269**, 5338–5378.
- GIGA, M. H., GIGA, Y. & SAAL, J. (2010) Compactness theorems. *Nonlinear Partial Differential Equations*. Progress in Nonlinear Differential Equations and Their Applications, vol **79**. Birkhäuser Boston.
- JIN, H. Y. & WANG, Z. A. (2021a) The Keller–Segel system with logistic growth and signal-dependent motility. *Disc. Cont. Dyn. Syst.-B*, **26**, 3023–3041. doi: [10.3934/dcdsb.2020218](https://doi.org/10.3934/dcdsb.2020218).
- JIN, H. Y., KIM, Y. J. & WANG, Z. A. (2018) Boundedness, stabilization, and pattern formation driven by density-suppressed motility. *SIAM J. Appl. Math.*, **78**, 1632–1657.
- JIN, H. Y., SHI, S. & WANG, Z. A. (2020) Boundedness and asymptotics of a reaction–diffusion system with density-dependent motility. *J. Differential Equations*, **269**, 6758–6793.
- JIN, H. Y. & WANG, Z. A. (2021b) Global dynamics and spatio-temporal patterns of predator–prey systems with density-dependent motion. *Eur. J. Appl. Math.* doi: [10.1017/S09567925200002482](https://doi.org/10.1017/S09567925200002482).
- JIN, H. Y. & WANG, Z. A. (2020) Critical mass on the Keller–Segel system with signal-dependent motility. *Proc. Amer. Math. Soc.*, **148**, 4855–4873.
- KAREIVA, P. & ODELL, G. (1987) Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *Amer. Nat.*, **130**, 233–270.
- KELLER, E. F. & SEGEL, L. A. (1971) Models for chemotaxis. *J. Theor. Biol.*, **30**, 225–234.
- KELLER, E. F. & SEGEL, L. A. (1970) Initiation of slime mold aggregation viewed as an instability. *J. Theor. Biol.*, **26**, 399–415.
- KOLOKOLNIKOV, T., WEI, J. & ALCOLADO, A. (2014) Basic mechanisms driving complex spike dynamics in a chemotaxis model with logistic growth. *SIAM J. Appl. Math.*, **74**, 1375–1396.
- KONDO, S. & MIURA, T. (2010) Reaction–diffusion model as a framework for understanding biological pattern formation. *Science*, **329**, 1616–1620.
- LIU, C., et al. (2011) Sequential establishment of stripe patterns in an expanding cell population. *Science*, **334**, 238–241.
- LOU, Y. & NI, W.-M. (1996) Diffusion, self-diffusion and cross-diffusion. *J. Differential Equations*, **131**, 79–131.
- MA, M., OU, C. H. & WANG, Z. A. (2012) Stationary solutions of a volume filling chemotaxis model with logistic growth and their stability. *SIAM J. Appl. Math.*, **72**, 740–766.
- MA, M., PENG, R. & WANG, Z. (2020) Stationary and non-stationary patterns of the density-suppressed motility model. *Phys. D*, **402**, 132259, 13pp.
- MURRAY, J. D. (2001) *Mathematical Biology*. New York: Springer.

- MÉNDEZ, V., CAMPOS, D., PAGONABARRAGA, I. & FEDOTOV, S. (2012) Density-dependent dispersal and population aggregation patterns. *J. Theor. Biol.*, **309**, 113–120.
- PEJSACHOWICZ, J. & RABIER, P. J. (1998) Degree theory for C^1 Fredholm mappings of index 0. *J. Anal. Math.*, **76**, 289–319.
- PAINTER, K. J. & HILLEN, T. (2002) Volume-filling and quorum-sensing in models for chemosensitive movement. *Can. Appl. Math. Q.*, **10**, 501–543.
- PAINTER, K. & HILLEN, T. (2011) Spatio-temporal chaos in a chemotaxis model. *Phys. D*, **240**, 363–375.
- SMITH-ROBERGE, J., IRON, D. & KOLOKOLNIKOV, T. (2019) Pattern formation in bacterial colonies with density-dependent diffusion. *Eur. J. Appl. Math.*, **30**, 196–218.
- SHI, J. & WANG, X. (2009) On global bifurcation for quasilinear elliptic systems on bounded domains. *J. Differential Equations*, **246**, 2788–2812.
- WANG, J. & WANG, M. (2019) Boundedness in the higher-dimensional Keller–Segel model with signal-dependent motility and logistic growth. *J. Math. Phys.*, **60**, 011507.
- WANG, X. (2000) Qualitative behavior of solutions of chemotactic diffusion systems: effects of motility and chemotaxis and dynamics. *SIAM J. Math. Anal.*, **31**, 535–560.
- WANG, X. & XU, Q. (2013) Spiky and transition layer steady state of chemotaxis systems via global bifurcation and Helly’s compactness theorem. *J. Math. Biol.*, **66**, 1241–1266.
- WANG, Z. A. & HILLEN, T. (2007) Classical solutions and pattern formation for a volume filling chemotaxis model. *Chaos*, **17**, 037108.
- YOON, C. & KIM, Y. J. (2017) Global existence and aggregation in a Keller–Segel model with Fokker–Planck diffusion. *Acta Appl. Math.*, **149**, 101–123.

Appendix A. Bifurcation theorem

For convenience, we hereby recall some bifurcation theorems for an abstract equation

$$F(\lambda, u) = 0,$$

where $F : \mathbb{R} \times X \rightarrow Y$ is a nonlinear differentiable mapping and X and Y are Banach spaces. In the following $N(L)$ and $R(L)$ are the null space and the range of a linear operator L , respectively; F_u denotes the Fréchet partial derivatives of F with respect to argument u , and $F_{\lambda u}$ is the mixed Fréchet partial derivatives of F with respect to u and λ .

We revisit the following global bifurcation theorem formulated in Shi & Wang (2009, Theorem 4.3), which was based on almost the same conditions of local bifurcation theorem by Crandall & Rabinowitz (1971) and the global bifurcation theorem for Fredholm operators developed by Fitzpatrick, Pejsachowicz and Rabier (Fitzpatrick & Pejsachowicz, 1991, and Pejsachowicz & Rabier, 1998).

THEOREM A.1 Let X, Y be Banach spaces and V be an open connected subset of $\mathbb{R} \times X$. Let $(\lambda_0, u_0) \in V$ and F be a continuously differentiable mapping from V to Y . Assume that

- $F(\lambda, u_0) = 0$ for $(\lambda, u_0) \in V$;
- $D_{\lambda u}F(\lambda, u)$ exists and is continuous for (λ, u) near (λ_0, u_0) ;
- $D_uF(\lambda_0, u_0)$ is a Fredholm operator with index zero;
- $D_{\lambda u}F(\lambda_0, u_0)w_0 \notin R(D_uF(\lambda_0, u_0))$ for $w_0 \in X$ and $\dim N(D_uF(\lambda, u_0)) = 1$ with $N(D_uF(\lambda_0, u_0)) = \text{span}\{w_0\}$ (transversality condition).

Let Z be a closed complement of $\text{span}\{w_0\}$ in X . Then there exists an open interval $(-\delta, \delta)$ and continuous functions $\lambda : (-\delta, \delta) \mapsto \mathbb{R}$, $\psi : (-\delta, \delta) \mapsto Z$ such that $\lambda(0) = \lambda_0$, $\psi(0) = 0$, and if $u(s) = u_0 + sw_0 + s\psi(s)$ for all $s \in (-\delta, \delta)$, then

$$F(\lambda(s), u(s)) = 0.$$

In addition, $F^{-1}(0)$ near (λ_0, u_0) consists precisely of the curves $u = u_0$ and $S = \{(\lambda(s), u(s)) | s \in (-\delta, \delta)\}$. Furthermore, if $D_u F(\lambda, u)$ is a Fredholm operator $\forall (\lambda, u) \in V$, then the curve S is contained in a connected component C of \bar{S} where $S = \{(\lambda, u) \in V | F(\lambda, u) = 0, u \neq u_0\}$, and C is either not compact in V or contains a point (λ^*, u_0) with $\lambda^* \neq \lambda_0$.

Consider the ‘positive part and negative part’ of C . Let $\Gamma_+ = \{(\lambda(s), u(s)) | s \in (0, \delta)\}$, and $\Gamma_- = \{(\lambda(s), u(s)) | s \in (-\delta, 0)\}$. Let C^+ be the component of $C \setminus \Gamma_-$ that contains Γ_+ and C^- be the component of $C \setminus \Gamma_+$ that contains Γ_- , we have the following convenient results from Shi & Wang (2009, Theorem 4.4).

THEOREM A.2 Suppose that all conditions in the Theorem A.1 are satisfied. Furthermore, we assume that

- $D_u F(\lambda, u_0)$ is continuously differentiable w.r.t. λ for $(\lambda, u_0) \in V$;
- The norm function: $u \in X \mapsto \|u\|$ is $C^1(X \setminus \{0\})$;
- For $k \in (0, 1)$, if (λ, u_0) and (λ, u) are both in V , then $(1 - kF_u(\lambda, u_0)) + kF_u(\lambda, u)$ is a Fredholm operator.

Then each of C^+ and C_- satisfies one of the following:

- (i) it is not compact in V ;
- (ii) it contains a point (λ^*, u_0) with $\lambda^* \neq \lambda_0$;
- (iii) it contains a point $(\lambda, u_0 + z)$ where $z \neq 0 \in Z$.

It is well known that if X is the usual Sobolev space $W^{m,p}(\Omega)$ with $1 < p < \infty$, the second condition in Theorem A.2 is always satisfied. The third condition is true for elliptic operator considered in Section 2 and 3 in Shi & Wang (2009).