

PATTERN FORMATION OF THE ATTRACTION-REPULSION KELLER-SEGEL SYSTEM

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ABSTRACT. In this paper, the pattern formation of the attraction-repulsion Keller-Segel (ARKS) system is studied analytically and numerically. By the Hopf bifurcation theorem as well as the local and global bifurcation theorem, we rigorously establish the existence of time-periodic patterns and steady state patterns for the ARKS model in the full parameter regimes, which are identified by a linear stability analysis. We also show that when the chemotactic attraction is strong, a spiky steady state pattern can develop. Explicit time-periodic rippling wave patterns and spiky steady state patterns are obtained numerically by carefully selecting parameter values based on our theoretical results. The study in the paper asserts that chemotactic competitive interaction between attraction and repulsion can produce periodic patterns which are impossible for the chemotaxis model with a single chemical (either chemo-attractant or chemo-repellent).

1. Introduction. Chemotaxis is characterized by the sustained migration of cells in the direction of an increasing concentration of chemo-attractant or decreasing concentration of chemo-repellent, where the former is referred to as attractive chemotaxis and the latter to repulsive chemotaxis. Chemotactic pattern formation observed both experimentally and numerically exhibits rich interesting coherent structures such as aggregate, fruiting bodies, clusters, spirals, spots, rings, labyrinthine pattern, stripes and prorogating waves [1, 4, 11, 14, 16, 31, 55]. The patterns generated by chemotaxis models have been advocated to explain various biological processes/pattern formations, such as fish pigmentation patterning [36], angiogenesis in tumor progression [5], primitive streak formation [37], blood vessel formation [12], wound healing [40], and so on.

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The prototypical chemotaxis model was well-known as the Keller-Segel system [23] as follows

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\lambda u \nabla v), & x \in \Omega, t > 0, \\ v_t = \Delta v + \alpha u - \beta v, & x \in \Omega, t > 0, \end{cases} \quad (1.1)$$

where $u = u(x, t)$ denotes the cell density, $v = v(x, t)$ represents the chemical concentration, and Ω is a bounded domain in \mathbb{R}^n . Here the attractive (*resp.* repulsive) chemotaxis corresponds to $\lambda > 0$ (*resp.* $\lambda < 0$), and $|\lambda| \in \mathbb{R} \setminus \{0\}$ measures the strength of chemotactic response; parameters $\alpha, \beta > 0$ denote the production and degradation rates of the chemical. The Keller-Segel system (1.1) describes the chemotactic interaction between cells and one chemical signal (either attractive or repulsive), and it has triggered a tremendous amount of studies in the past four decades, *cf.* [16, 17, 38, 47] and references therein. However, in many biological processes, cells interact with combined attractive and repulsive chemical signals to achieve certain biological functions, for instance the leukocyte trafficking and neuronal pathfinding are governed by gradients of both chemical attractants and repellents [19]; see more examples in [6, 13, 28, 35].

In this paper, we shall consider the spatiotemporal pattern formation of the following dimensionless attraction-repulsion Keller-Segel (ARKS) system

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v) + \nabla \cdot (\xi u \nabla w), & x \in \Omega, t > 0 \\ v_t = \Delta v + \alpha u - \beta v, & x \in \Omega, t > 0, \\ w_t = \Delta w + \gamma u - \delta w, & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, & x \in \partial \Omega, t > 0, \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), w(x, 0) = w_0(x), & x \in \Omega, \end{cases} \quad (1.2)$$

where $u(x, t)$ denotes the cell density, $v(x, t)$ represents the concentration of an attractive signal (*i.e.* chemo-attractant), and $w(x, t)$ is the concentration of a repulsive signal (*i.e.* chemo-repellent); $\Omega \subset \mathbb{R}^n$ ($n \geq 1$) is a bounded connected domain with a smooth boundary $\partial \Omega$, and each of u , v and w satisfies a no-flux boundary condition; The parameters satisfy $\chi \geq 0, \xi \geq 0, \alpha, \beta, \gamma, \delta > 0$, where χ and ξ measure the strength of the attraction and repulsion, respectively, and $\alpha, \beta, \gamma, \delta$ represent the production and degradation rates of the two chemicals, respectively. The first cross-diffusive term in the first equation implies that the cell movement is directed up the chemo-attractant concentration, whereas the second cross-diffusive term indicates that cells move down the chemo-repellent concentration. The second and third equations in (1.2) state that chemo-attractant and chemo-repellent are released by cells and undergo natural decay.

The attraction-repulsion chemotaxis model (1.2) was proposed in [28] to describe the aggregation of microglia observed in Alzheimer's disease and in [35] to address the quorum effect in the chemotactic process. The system (1.2) can also be regarded as a particularized version of multi-species models proposed in a recent work [18], but the analysis there does not apply to (1.2) due to the lack of a Lyapunov functional. The global existence, asymptotic behavior and steady states of solutions to the model (1.2) were established in [25] for a one dimensional spatial domain and in [48] for the multi-dimensional case in some parameter regimes, where the existence of steady states was obtained only for the case $\beta = \delta$. It should be mentioned that when $\beta = \delta$, the system (1.2) can be reduced to the classical Keller-Segel model

(1.1) and hence conventional methods can be employed, see details in [48]. Traveling wave solutions of an attraction-repulsion chemotaxis model with volume-filling effect were recently studied in [39].

The purpose of this paper is to employ local and global bifurcation theory to study the time-periodic solutions and steady state solutions of (1.2) in the whole parameter regimes. We find that if $\beta \neq \delta$, the interaction between attraction and repulsion may lead to time-periodic rippling patterns which were not possible for the classical Keller-Segel model (1.1) due to the existence of a time-monotone Lyapunov functional. We note that the parameter regimes for the pattern formation of the ARKS model (1.2) was also identified in [28] by a linear stability analysis without rigorous proof, where time-periodic patterns were found under the argument of short ranged attraction and long ranged repulsion (*i.e.* the spatial range (length) of the attractant is longer than that of the repellent). In this paper, we study the pattern formation of the ARKS model (1.2) where the attractant and repellent have the same spatial range and identify the full parameter regimes in which the existence of time-periodic and steady state patterns are rigorously proved. Our results indicate that time-periodic patterns still can develop if the spatial range of attractant and repellent are the same. Moreover we explicitly find the numerical time-periodic rippling pattern which was not shown in [28]. To the best of our knowledge, this is the first time that the existence of time-periodic patterns is rigorously established for reaction-diffusion systems with chemotactic effect. For reaction-diffusion systems without chemotactic effect, time-periodic patterns have been found in many well-known systems via Hopf bifurcations [26, 56, 58]. In [30], Hopf bifurcation and time-periodic patterns were obtained for a three-dimensional diffusive competition system with cross-diffusion. Note that time-periodic pattern is one of the spatiotemporal patterns predicted by Turing in his seminal work [49] sixty years ago, and Turing also pointed out that such pattern can only occur with three or more morphogens, which resonates the fact that Hopf bifurcation cannot occur for the Keller-Segel system with only one chemical. In this paper, we assume that all three species u, v , and w have the same diffusion rate equal to one for simplicity and brevity; however our analysis and results directly extend to the case where the diffusion rates of u, v , and w are different. We shall discuss a general attraction-repulsion Keller-Segel model with different diffusion rates in a forthcoming paper.

In numerical simulation of (1.2) with parameters in the time-periodic pattern regime, propagating rippling waves which pass through one another without interference have been found. It is worth underlining that such patterns have been discovered experimentally in the early stage of starvation-induced fruiting body development of the starved myxobacteria ([20, 21, 57]) where the contact interaction between cells was postulated to be the underlying mechanism. However our results indicate that the chemotactic interaction of attraction and repulsion may offer an alternative mechanism, as indicated in [45].

For the steady state solutions, we recall that the existence of steady states to the Keller-Segel system was first analyzed in [42] by using local and global bifurcation techniques, and bifurcation of spatially heterogeneous steady state solutions were also obtained in [15, 29, 32]. Recently a global bifurcation analysis for steady states was carried out in [53] for a class of regularized models of the classical Keller-Segel models surveyed in [16], see also related work in [44, 51, 52]. On the other hand, the existence of spiky steady state solutions for chemotactic systems in the

small diffusion coefficient case has been shown in [22, 24] and many other work, see related surveys [33, 34]. The steady state solutions of the attraction-repulsion Keller-Segel model has not been considered in afore-mentioned works. Here we prove the existence of non-constant steady state solutions with bifurcation theory, and numerical simulation in the paper also shows spiky pattern although the diffusion coefficients are not small.

By integrating the first equation with the boundary conditions, one immediately observes that the cell mass is preserved for all $t > 0$. Hence the value of $\bar{u} = \frac{1}{|\Omega|} \int_{\Omega} u(x, t) dx$, will be prescribed in our study. Then the steady state solutions of (1.2) satisfy

$$\begin{cases} \Delta u - \nabla \cdot (\chi u \nabla v) + \nabla \cdot (\xi u \nabla w) = 0, & x \in \Omega, \\ \Delta v + \alpha u - \beta v = 0, & x \in \Omega \\ \Delta w + \gamma u - \delta w = 0, & x \in \Omega, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega, \\ \frac{1}{|\Omega|} \int_{\Omega} u(x) dx = \bar{u} > 0. \end{cases} \quad (1.3)$$

It is clear that $(\bar{u}, \bar{v}, \bar{w})$ is a constant steady state (i.e. equilibrium) solution of (1.3), where $\bar{v} = \alpha \bar{u} / \beta$, $\bar{w} = \gamma \bar{u} / \delta$. In the paper we shall show, given $\bar{u} > 0$, the system (1.3) has positive solutions for a suitable range of χ . The solutions will be the ones bifurcating from the constant steady states $(\bar{u}, \bar{v}, \bar{w})$. The chemotactic coefficient χ and ξ will be used as the bifurcation parameter, and the bifurcating solutions have arbitrarily fixed total cell mass.

The remaining part of the paper is organized as follows. In Section 2, we present the basic linear stability analysis for the constant steady state $(\bar{u}, \bar{v}, \bar{w})$; In Sections 3 and 4, we consider Hopf bifurcations and steady state bifurcations respectively; Discussion on pattern formation and numerical simulations are given in Section 5; and Section 6 is the appendix which collects the general Hopf bifurcation theorem, the local and global steady state bifurcation theorem, and the Routh-Hurwitz criterion for cubic equations, which are the analytic tools used in the paper.

2. Linearized stability analysis. Before proceeding, we introduce some important notations used in what follows. By \mathbb{N} , we denote the set of all the positive integers, and $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$. We use the Sobolev spaces $X = \{u \in W^{2,p}(\Omega) : \frac{\partial u}{\partial \nu} = 0\}$, $Y = L^p(\Omega)$, $Y_0 = \{u \in Y : \int_{\Omega} u(x) dx = 0\}$, and $X_0 = X \cap Y_0$. We always assume that $p > n$.

Linearizing the system (1.3) about the constant equilibrium solution $(\bar{u}, \bar{v}, \bar{w})$, we obtain an eigenvalue problem

$$\begin{cases} \Delta \phi - \chi \bar{u} \Delta \psi + \xi \bar{u} \Delta \varphi = \mu \phi, & x \in \Omega, \\ \Delta \psi + \alpha \phi - \beta \psi = \mu \psi, & x \in \Omega, \\ \Delta \varphi + \gamma \phi - \delta \varphi = \mu \varphi, & x \in \Omega, \\ \frac{\partial \phi}{\partial \nu} = \frac{\partial \psi}{\partial \nu} = \frac{\partial \varphi}{\partial \nu} = 0, & x \in \partial\Omega, \\ \int_{\Omega} \phi(x) dx = 0. \end{cases} \quad (2.1)$$

First we show that eigenvalue problem (2.1) can be reduced to a sequence of matrix eigenvalue problems.

Lemma 2.1. *Let $\{\lambda_n\}$ be the sequence of eigenvalues of $-\Delta$ with Neumann boundary condition, such that $0 = \lambda_0 < \lambda_1 \leq \lambda_2 \leq \dots$, and let $y_n(x)$ be its corresponding eigenfunction, $n \in \mathbb{N}$. Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium. Define*

$$A_n = \begin{pmatrix} -\lambda_n & \chi \bar{u} \lambda_n & -\xi \bar{u} \lambda_n \\ \alpha & -\lambda_n - \beta & 0 \\ \gamma & 0 & -\lambda_n - \delta \end{pmatrix}. \tag{2.2}$$

Then

1. *If μ is an eigenvalue of (2.1), then there exists $n \in \mathbb{N}$, such that μ is an eigenvalue of (2.2); if (a_n, b_n, c_n) is an eigenvector associated with μ for (2.2), then $(a_n, b_n, c_n)y_n$ is an eigenvector associated with μ for (2.1).*
2. *The constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2) if and only if for every $n \in \mathbb{N}$, all the eigenvalues of A_n have negative real part.*
3. *The constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$ is unstable with respect to (1.2) if and only if there exists an $n \in \mathbb{N}$, such that A_n has at least one eigenvalue with non-negative real part.*

Proof. Let μ be an eigenvalue of (2.1) with corresponding eigenfunction (ϕ, ψ, φ) . By using Fourier expansion, there exist $\{a_n\}$, $\{b_n\}$ and $\{c_n\}$ such that

$$\phi(x) = \sum_{n=0}^{\infty} a_n y_n(x), \quad \psi(x) = \sum_{n=0}^{\infty} b_n y_n(x), \quad \varphi(x) = \sum_{n=0}^{\infty} c_n y_n(x).$$

Since (ϕ, ψ, φ) is not identically zero, and due to the zero mass restriction, there exists $n \in \mathbb{N}$ such that $(a_n, b_n, c_n) \neq (0, 0, 0)$. Multiplying the first three equations in (2.1) by y_n and integrating over Ω , using the boundary conditions and assuming that $\|y_n\|_{L^2(\Omega)} = 1$, we obtain that

$$\begin{cases} -\lambda_n a_n + \chi \bar{u} \lambda_n b_n - \xi \bar{u} \lambda_n c_n = \mu a_n, \\ -\lambda_n b_n + \alpha a_n - \beta b_n = \mu b_n, \\ -\lambda_n c_n + \gamma a_n - \delta c_n = \mu c_n, \end{cases}$$

that is

$$A_n \begin{pmatrix} a_n \\ b_n \\ c_n \end{pmatrix} = \mu \begin{pmatrix} a_n \\ b_n \\ c_n \end{pmatrix},$$

where A_n is defined by (2.2). Hence the eigenvalues of (2.1) are determined by eigenvalues of A_n . By the principle of the linearized stability ([46, Thm. 8.6], [10, Thm. 5.2]), the constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2) if and only if the real part of the eigenvalues μ of the linearized elliptic problem (2.1) is negative. \square

With a direct calculation, one finds that the eigenvalues of A_n are determined by the characteristic polynomial

$$P(\mu) = \mu^3 + a_2(\chi, \lambda_n)\mu^2 + a_1(\chi, \lambda_n)\mu + a_0(\chi, \lambda_n), \tag{2.3}$$

where

$$a_2(\chi, \lambda_n) = 3\lambda_n + \beta + \delta, \tag{2.4}$$

$$a_1(\chi, \lambda_n) = 3\lambda_n^2 + [2(\beta + \delta) + (\xi\gamma - \alpha\chi)\bar{u}]\lambda_n + \delta\beta, \tag{2.5}$$

$$a_0(\chi, \lambda_n) = \lambda_n^3 + [\beta + \delta + (\xi\gamma - \alpha\chi)\bar{u}]\lambda_n^2 + [\beta\delta + (\beta\xi\gamma - \delta\alpha\chi)\bar{u}]\lambda_n. \tag{2.6}$$

It is clear that $a_2(\chi, \lambda_n) > 0$ for any $n \in \mathbb{N}$. Then the well-known Routh-Hurwitz criterion implies the following stability criterion:

Corollary 2.2. *Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium of (1.2). Then*

1. *The constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2) if and only if for every $n \in \mathbb{N}$, it holds that*
(S1) $a_0(\chi, \lambda_n) > 0$ and $a_2(\chi, \lambda_n)a_1(\chi, \lambda_n) - a_0(\chi, \lambda_n) > 0$.
2. *The constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$ is unstable with respect to (1.2) if and only if there exists an $n \in \mathbb{N}$ such that*
(S2) $a_0(\chi, \lambda_n) \leq 0$ or $a_2(\chi, \lambda_n)a_1(\chi, \lambda_n) \leq a_0(\chi, \lambda_n)$.

In view of Corollary 2.2, we define the quantity

$$\begin{aligned} T(\chi, \lambda_n) &:= a_2(\chi, \lambda_n)a_1(\chi, \lambda_n) - a_0(\chi, \lambda_n) \\ &= 8\lambda_n^3 + 2[4(\beta + \delta) + (\xi\gamma - \alpha\chi)\bar{u}]\lambda_n^2 \\ &\quad + [(\delta\xi\gamma - \beta\alpha\chi)\bar{u} + 2(\beta + \delta)^2 + 2\delta\beta]\lambda_n + (\beta + \delta)\beta\delta. \end{aligned} \quad (2.7)$$

Applying Corollary 2.2 and (2.4)-(2.7), we have the following rough results regarding the stability/instability of the constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$.

Proposition 2.3. *Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium of (1.2).*

1. *Assume that $\alpha, \beta, \gamma, \delta > 0$ are fixed. If $\chi \geq 0$, $\xi \geq 0$ satisfy*

$$\xi \geq \frac{\alpha}{\gamma} \max \left\{ \frac{\delta}{\beta}, \frac{\beta}{\delta} \right\} \chi, \quad (2.8)$$

then $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2).

2. *Assume that $\beta, \gamma, \delta, \bar{u} > 0$, $\xi \geq 0$ are fixed. If $\alpha\chi$ is large enough, then $(\bar{u}, \bar{v}, \bar{w})$ is unstable with respect to (1.2).*

Proof. If (χ, ξ) satisfies (2.8), then

$$\xi\gamma - \alpha\chi \geq 0, \quad \text{and} \quad \beta\xi\gamma - \delta\alpha\chi \geq 0. \quad (2.9)$$

From (2.4)-(2.7), the condition **(S1)** is satisfied for any $\lambda_n \geq 0$, hence $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable. On the other hand, we notice that a_0 can be written as

$$a_0(\chi, \lambda_n) = \lambda_n^3 + [\beta + \delta + \xi\gamma\bar{u}]\lambda_n^2 + \beta(\delta + \xi\gamma\bar{u})\lambda_n - \alpha\chi\bar{u}(\lambda_n^2 + \delta\lambda_n).$$

Thus for any fixed $\lambda_n > 0$, when $\alpha\chi$ is large enough, we have $a_0(\chi, \lambda_n) < 0$, and $(\bar{u}, \bar{v}, \bar{w})$ is unstable. \square

Remark 2.4. The stability condition (2.8) in Proposition 2.3 generalizes a result in [48], which asserts that in the absence of attraction ($\chi = 0$) or when the repulsion dominates over attraction (in the sense that $\xi\gamma \geq \alpha\chi$) under an additional assumption that $\delta = \beta$ (same death rate), the constant equilibrium is stable and hence there is no pattern formation. This is consistent with biological intuition since the repulsion acts as diffusion which helps to stabilize the system. However if the attraction dominates over the repulsion, spatiotemporal pattern formation may be expected.

To obtain more precise stability results, we look more carefully at the boundary between the stability and instability regimes

$$a_0(\chi, \lambda_n) = 0, \quad T(\chi, \lambda_n) = a_2(\chi, \lambda_n)a_1(\chi, \lambda_n) - a_0(\chi, \lambda_n) = 0.$$

For that purpose we define the set

$$S = \{(\chi, p) \in \mathbb{R}_+^2 : a_0(\chi, p) = 0\} \tag{2.10}$$

to be the steady state bifurcation curve, and

$$H = \{(\chi, p) \in \mathbb{R}_+^2 : T(\chi, p) = 0\} \tag{2.11}$$

to be the Hopf bifurcation curve (see [50]). The curves S and H are where the constant equilibrium is neutrally stable, *i.e.* the linearized equation has an eigenvalue with zero real part. Since the expression of $a_0(\chi, p)$ and $T(\chi, p)$ are linear in χ , then S and H are graphs of functions defined as follows:

$$\begin{aligned} \chi_S(p) &= \frac{1}{\alpha\bar{u}(p+\delta)} [p^2 + (\delta + \beta + \xi\gamma\bar{u})p + \beta\delta + \xi\gamma\beta\bar{u}] \\ &= \frac{1}{\alpha\bar{u}} \left[p + (\xi\gamma\bar{u} + \beta) + \frac{\xi\gamma\bar{u}(\beta - \delta)}{p + \delta} \right]; \end{aligned} \tag{2.12}$$

and

$$\begin{aligned} \chi_H(p) &= \frac{1}{\alpha\bar{u}p(2p + \beta)} \cdot \{8p^3 + 2[4(\delta + \beta) + \xi\gamma\bar{u}]p^2 \\ &\quad + [\delta\xi\gamma\bar{u} + 2(\delta + \beta)^2 + 2\beta\delta]p + (\delta + \beta)\delta\beta\} \\ &= \frac{1}{\alpha\bar{u}} \left[4p + (4\delta + 2\beta + \xi\gamma\bar{u}) + \frac{\delta(\delta + \beta)}{p} + \frac{\xi\gamma\bar{u}(\delta - \beta)}{2p + \beta} \right]. \end{aligned} \tag{2.13}$$

Then the functions $\chi_S(p)$ and $\chi_H(p)$ have the following properties.

Lemma 2.5. *Suppose that $\alpha, \beta, \gamma, \delta, \xi, \bar{u} > 0$ are fixed, and let $\chi_S(p)$ and $\chi_H(p)$ be defined as in (2.12) and (2.13).*

1. *If $\beta \leq \beta_* = \delta + \frac{\delta^2}{\xi\gamma\bar{u}}$, then $\chi_S(p)$ is strictly increasing for $p \in (0, \infty)$; and if $\beta > \beta_*$, then for $p_* = \sqrt{\xi\gamma\bar{u}(\beta - \delta)} - \delta$, $\chi_S(p)$ is strictly decreasing for $p \in (0, p_*)$, and $\chi_S(p)$ is strictly increasing for $p \in (p_*, \infty)$;*
2. *The function $\chi_H(p)$ satisfies $\lim_{p \rightarrow 0^+} \chi_H(p) = \infty$, $\lim_{p \rightarrow \infty} \chi_H(p) = \infty$, and there exists a unique critical point $p^* \in (0, \infty)$ of $\chi_H(p)$ which is the global minimum point.*

Proof. Differentiating (2.12), we get

$$\begin{aligned} \chi'_S(p) &= \frac{1}{\alpha\bar{u}} \left[1 + \frac{(\delta - \beta)\xi\gamma\bar{u}}{(p + \delta)^2} \right] \\ &= \frac{1}{\alpha\bar{u}} \frac{p^2 + 2\delta p + \delta^2 + (\delta - \beta)\xi\gamma\bar{u}}{(p + \delta)^2} \\ &> \frac{1}{\alpha\bar{u}} \frac{\delta^2 + \delta\xi\gamma\bar{u} - \beta\xi\gamma\bar{u}}{(p + \delta)^2}. \end{aligned}$$

If $\beta \leq \beta_*$, we have $\chi'_S(p) > 0$ for $p \in (0, \infty)$ and $\chi_S(p)$ is strictly increasing for $p \in (0, \infty)$; If $\beta > \beta_*$, we have

$$\chi'_S(p) = \frac{1}{\alpha\bar{u}} \frac{(p + \delta)^2 + \xi\gamma\bar{u}(\delta - \beta)}{(p + \delta)^2}.$$

Apparently $\chi'_S(p) < 0$ when $p \in (0, p_*)$ and $\chi'_S(p) > 0$ when $p \in (p_*, \infty)$. This proves the properties of $\chi_S(p)$.

Next we differentiate $\chi_H(p)$ and obtain

$$\chi'_H(p) = \frac{1}{\alpha\bar{u}} \left[4 - \frac{\delta(\delta + \beta)}{p^2} - \frac{2\xi\gamma\bar{u}(\delta - \beta)}{(2p + \beta)^2} \right].$$

If p^* is a critical point of $\chi_H(p)$, that is $\chi'_H(p^*) = 0$, then p^* satisfies

$$\frac{2\xi\gamma\bar{u}(\delta - \beta)}{(2p + \beta)^2} = 4 - \frac{\delta(\delta + \beta)}{p^2}. \quad (2.14)$$

Then

$$\begin{aligned} \chi''_H(p^*) &= \frac{1}{\alpha\bar{u}} \left[\frac{2\delta(\delta + \beta)}{(p^*)^3} + \frac{8\xi\gamma\bar{u}(\delta - \beta)}{(2p^* + \beta)^3} \right] \\ &= \frac{1}{\alpha\bar{u}} \left[\frac{2\delta(\delta + \beta)}{(p^*)^3} + \frac{4}{2p^* + \beta} \left(4 - \frac{\delta(\delta + \beta)}{(p^*)^2} \right) \right] \\ &= \frac{1}{\alpha\bar{u}(2p^* + \beta)} \left[\frac{2\delta\beta(\delta + \beta)}{(p^*)^3} + 16 \right] > 0. \end{aligned}$$

Hence any critical point of $\chi_H(p)$ must be a local minimum, and furthermore it must be unique since $\lim_{p \rightarrow 0^+} \chi_H(p) = \infty$ and $\lim_{p \rightarrow \infty} \chi_H(p) = \infty$. Therefore this critical point must be a global minimum point. \square

Now we can state a more precise stability result for the constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$.

Theorem 2.6. *Let $(\bar{u}, \bar{v}, \bar{w})$ be a constant equilibrium of (1.2). Assume that $\alpha, \beta, \gamma, \delta > 0$ and $\xi > 0$ are fixed. Let $\chi_S(p)$ and $\chi_H(p)$ be the functions defined in (2.12) and (2.13). If χ satisfies*

$$0 \leq \chi < \min_{n \in \mathbb{N}} \{ \chi_S(\lambda_n), \chi_H(\lambda_n) \}, \quad (2.15)$$

then $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2). In particular, $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2) if χ satisfies

$$0 < \chi < \min \{ \chi_S(p_*), \chi_H(p^*) \}, \quad (2.16)$$

where p_* and p^* are the global minimum points of $\chi_S(p)$ on $[0, \infty)$ and $\chi_H(p)$ on $(0, \infty)$ respectively.

The conclusions in Theorem 2.6 readily follow from Corollary 2.2 and Lemma 2.5. We notice that $\chi_S(p_*)$ can be explicitly calculated:

$$\chi_S(p_*) = \begin{cases} \frac{\beta}{\alpha\bar{u}} \left(1 + \frac{\xi\gamma\bar{u}}{\delta} \right), & \text{if } \beta \leq \beta_*; \\ \frac{1}{\alpha\bar{u}} (\sqrt{\xi\gamma\bar{u}} + \sqrt{\beta - \delta})^2, & \text{if } \beta > \beta_*, \end{cases} \quad (2.17)$$

where

$$\beta_* = \delta + \frac{\delta^2}{\xi\gamma\bar{u}}, \quad p_* = \begin{cases} 0, & \text{if } \beta \leq \beta_*; \\ \sqrt{\xi\gamma\bar{u}(\beta - \delta)} - \delta, & \text{if } \beta > \beta_*. \end{cases} \quad (2.18)$$

Both $\chi_S(p_*)$ and $\chi_H(p^*)$ can be computed if the parameter values are given. In Fig. 1, graphs of $\chi = \chi_S(p)$ and $\chi = \chi_H(p)$ for several different sets of parameters are illustrated.

If we increase the value of χ , then the positive constant equilibrium $(\bar{u}, \bar{v}, \bar{w})$ loses the stability at

$$\chi_* = \min_{n \in \mathbb{N}} \{ \chi_S(\lambda_n), \chi_H(\lambda_n) \}. \quad (2.19)$$

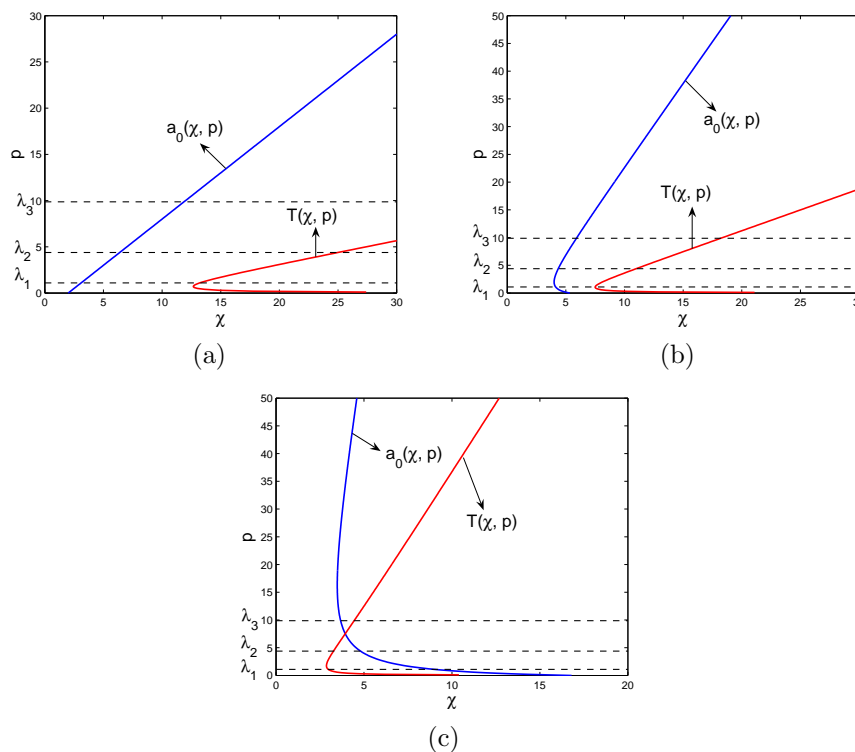


FIGURE 1. Graph of $a_0(\chi, p) = 0$ ($\chi = \chi_S(p)$) and $T(\chi, p) = 0$ ($\chi = \chi_H(p)$). Here the horizontal axis is χ and the vertical axis is p , and the dashed horizontal lines are $p = \lambda_n = (n\pi/3)^2$ for $n = 1, 2, 3$ (assuming that $\Omega = (0, 3)$ a one-dimensional spatial domain). Parameter values are: $\gamma = \alpha = \xi = \delta = 1$ for all three plots; (a) $\beta = 1, \bar{u} = 1$; (b) $\beta = 4, \bar{u} = 3$; (c) $\beta = 16, \bar{u} = 20$.

If $\chi_* = \min_{n \in \mathbb{N}} \chi_S(\lambda_n)$, then the linearized equation (2.1) has a zero eigenvalue at $\chi = \chi_*$, and a bifurcation of nontrivial steady state solutions of (1.2) occurs if some transversality conditions are met; similarly if $\chi_* = \min_{n \in \mathbb{N}} \chi_H(\lambda_n)$, then the linearized equation (2.1) has a pair of purely imaginary eigenvalues at $\chi = \chi_*$, and a Hopf bifurcation generating a family of periodic orbits of (1.2) occurs if some transversality conditions are met. We shall give more detailed analysis for both types of bifurcations in the next two sections. However one can see that whether the constant equilibrium loses stability to a spatial stationary pattern through a steady state bifurcation or to a spatial time-periodic pattern through a Hopf bifurcation is a delicate problem depending on the shape of the functions $\chi = \chi_S(p)$ and $\chi = \chi_H(p)$.

3. Hopf bifurcation. In this section we prove the existence of periodic orbits of (1.2) for a certain parameter range using the Hopf bifurcation theorem. For the reader’s convenience, a review of the Hopf bifurcation theorem for quasilinear parabolic systems is given in the appendix (subsection 6.2).

First we identify the parameter range of $\alpha, \beta, \delta, \gamma, \xi$ so that (2.1) could have purely imaginary eigenvalues. In the following lemma, we first show that if $\beta > \delta$ and $\xi\gamma\bar{u}$

is large, then $\chi_H(p) < \chi_S(p)$ for some p values, which indicates the possibility of a Hopf bifurcation.

Lemma 3.1. *Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium and define*

$$A^* =: A^*(\beta, \delta) = \frac{(\tilde{p} + \delta)^2(2\tilde{p} + \beta)}{(\beta - \delta)\tilde{p}}, \quad (3.1)$$

where \tilde{p} is the unique positive root of the equation

$$4\tilde{p}^3 + (4\delta + \beta)\tilde{p}^2 = \delta^2\beta. \quad (3.2)$$

1. If either

$$\delta \geq \beta \quad (3.3)$$

or

$$\beta > \delta \text{ and } \xi\gamma\bar{u} < A^*, \quad (3.4)$$

then $\chi_H(p) > \chi_S(p)$ for all $p > 0$.

2. If

$$\beta > \delta \text{ and } \xi\gamma\bar{u} > A^*, \quad (3.5)$$

then there exist $p_1, p_2 > 0$ such that $\chi_H(p) < \chi_S(p)$ for $p_1 < p < p_2$, and $\chi_H(p) > \chi_S(p)$ for $0 < p < p_1$ or $p > p_2$.

Proof. By (2.12) and (2.13), we have

$$\begin{aligned} & \chi_H(p) - \chi_S(p) \\ &= \frac{1}{\alpha\bar{u}} \left\{ 3p + 4\delta + \beta + \frac{\delta(\delta + \beta)}{p} + \xi\gamma\bar{u}(\delta - \beta) \left[\frac{1}{2p + \beta} + \frac{1}{p + \delta} \right] \right\}. \end{aligned}$$

Then it is apparent that when $\delta \geq \beta$, $\chi_H(p) > \chi_S(p)$ for all $p > 0$. For the case $\beta > \delta$, with $A = \xi\gamma\bar{u}$, $\chi_H - \chi_S$ can be expressed as

$$\chi_H(p) - \chi_S(p) = \frac{3p + \beta + \delta}{\alpha\bar{u}p(2p + \beta)(p + \delta)} \cdot Q_1(p),$$

where

$$Q_1(p) = (p + \delta)^2(2p + \beta) - A(\beta - \delta)p := Q_2(p) - Q_3(p).$$

Hence $\chi_H(p) - \chi_S(p) = (<)0$ for $p > 0$ if and only if $Q_1(p) = (<)0$. Since $Q_2(p)$ is a convex and increasing cubic function for $p > 0$, and $Q_3(p)$ is linear, then $Q_1(p) = 0$ has either 0, 1 or 2 roots when $A <, =$ or $> A^*$, for a critical value A^* . At the critical value $A = A^*$, we have a unique root \tilde{p} such that $Q_2(\tilde{p}) = Q_3(\tilde{p})$ and $Q_2'(\tilde{p}) = Q_3'(\tilde{p})$. Hence at $p = \tilde{p}$,

$$\begin{aligned} Q_2(\tilde{p}) &= (\tilde{p} + \delta)^2(2\tilde{p} + \beta) = A(\beta - \delta)\tilde{p} = Q_3(\tilde{p}), \\ Q_2'(\tilde{p}) &= 6\tilde{p}^2 + 2(4\delta + \beta)\tilde{p} + 2(\delta^2 + \beta\delta) = A(\beta - \delta) = Q_3'(\tilde{p}). \end{aligned} \quad (3.6)$$

Simplifying (3.6) we obtain

$$4\tilde{p}^3 + (4\delta + \beta)\tilde{p}^2 = \delta^2\beta. \quad (3.7)$$

Since (3.7) has a unique positive root \tilde{p} , then the critical value A^* is

$$A^* = \frac{Q_2(\tilde{p})}{(\beta - \delta)\tilde{p}} = \frac{(\tilde{p} + \delta)^2(2\tilde{p} + \beta)}{(\beta - \delta)\tilde{p}}.$$

Hence when $A > A^*$, $Q_1(p) = 0$ has two roots, denoted by p_1 and p_2 . Noticing that $Q_1(p)$ is convex, then the stated results follow. \square

Now we can determine the potential Hopf or steady state bifurcation points by using the Hopf bifurcation curve and steady state bifurcation curve.

Proposition 3.2. *Recall that $\{\lambda_n\}$ are the eigenvalues of $-\Delta$ with Neumann boundary condition, such that $0 = \lambda_0 < \lambda_1 \leq \lambda_2 \leq \dots$, and $y_n(x)$ is the corresponding eigenfunction for λ_n . Let $\chi_S(p)$ and $\chi_H(p)$ be defined as in (2.12) and (2.13), respectively. For $n \in \mathbb{N}$, define*

$$\chi_n^S = \chi_S(\lambda_n), \quad \chi_n^H = \chi_H(\lambda_n). \tag{3.8}$$

Then for fixed $\alpha, \beta, \delta, \gamma, \xi$,

1. the eigenvalue problem (2.1) has an eigenvalue $\mu = 0$ if and only if $\chi = \chi_n^S$ for some $n \in \mathbb{N}$, and the corresponding eigenfunction is $V_n y_n$, where V_n satisfies $A_n V_n = 0$ with A_n defined as in (2.2);
2. the eigenvalue problem (2.1) has a pair of purely imaginary eigenvalues $\mu = \pm i\nu$ if and only if (3.5) is satisfied, $\chi = \chi_n^H$ for some $n \in \mathbb{N}$ and $p_1 < \lambda_n < p_2$ where p_1 and p_2 are defined in Lemma 3.1, and the corresponding eigenfunction is $V_n^\pm y_n$, where V_n^\pm satisfies $A_n V_n^\pm = \pm i\nu V_n^\pm$.

Proof. The first part follows directly from part 1 of Lemma 2.1 and the fact that a zero eigenvalue of A_n is equivalent to $a_0(\chi, \lambda_n) = 0$. For the second part, (2.1) has a pair of purely imaginary eigenvalues if and only if for some $n \in \mathbb{N}$, A_n has a pair of purely imaginary conjugate eigenvalues. Suppose that A_n has eigenvalues $i\nu, -i\nu$ and θ where $\nu, \theta \in \mathbb{R}$ and $\nu \neq 0$. Then for a_0, a_1 and a_2 defined in (2.4)-(2.6), we have from the Routh-Hurwitz criterion (see Appendix 6.3)

$$a_2(\chi, \lambda_n) = -\theta, \quad a_1(\chi, \lambda_n) = \nu^2, \quad a_0(\chi, \lambda_n) = -\nu^2\theta. \tag{3.9}$$

Since from (2.4), $a_2(\chi, \lambda_n) = 3\lambda_n + \beta + \delta > 0$, hence $\theta < 0$ and $a_0(\chi, \lambda_n) > 0$. On the other hand, it is clear that $T(\chi, \lambda_n) = a_2(\chi, \lambda_n)a_1(\chi, \lambda_n) - a_0(\chi, \lambda_n) = 0$. Hence χ must satisfy $\chi_H(\lambda_n) = 0$ and $\chi_S(\lambda_n) > 0$. From Lemma 3.1, this can only occur when (3.4) is satisfied, $\chi = \chi_n^H$ for some $n \in \mathbb{N}$ and $p_1 < \lambda_n < p_2$. \square

Finally at a potential Hopf bifurcation point χ_n^H , we show that a nondegeneracy condition (see (H3) in Theorem 6.1) holds.

Lemma 3.3. *Suppose that (3.5) is satisfied and $p_1 < \lambda_n < p_2$ where p_1 and p_2 are defined as in Lemma 3.1, and χ_n^H is defined as in Proposition 3.2. Then for χ near χ_n^H , A_n has a unique eigenvalue $\sigma(\chi) + i\nu(\chi)$ such that $\sigma(\chi_n^H) = 0$ and $\nu(\chi_n^H) = \nu_0 > 0$, and $\sigma'(\chi_n^H) > 0$.*

Proof. The existence of a unique eigenvalue $\sigma(\chi) + i\nu(\chi)$ follows from the continuous dependence of eigenvalues on the parameter χ . For χ near χ_n^H , let the three roots of $A_n(\chi)$ be $\sigma(\chi) \pm i\nu(\chi)$ and $\theta(\chi)$ satisfying $\sigma(\chi_n^H) = 0, \nu(\chi_n^H) = \nu_0 > 0$. From (2.3), we have

$$\begin{aligned} -a_2(\chi, \lambda_n) &= 2\sigma(\chi) + \theta(\chi), \\ a_1(\chi, \lambda_n) &= \sigma^2(\chi) + \nu^2(\chi) + 2\sigma(\chi)\theta(\chi), \\ -a_0(\chi, \lambda_n) &= [\sigma^2(\chi) + \nu^2(\chi)]\theta(\chi). \end{aligned} \tag{3.10}$$

Differentiating (3.10) with respect to χ and using (2.4)-(2.6), we obtain

$$\begin{aligned} 2\sigma'(\chi) + \theta'(\chi) &= 0, \\ 2\sigma(\chi)\sigma'(\chi) + 2\nu(\chi)\nu'(\chi) + 2\sigma'(\chi)\theta(\chi) + 2\sigma(\chi)\theta'(\chi) &= -\alpha\bar{u}\lambda_n, \\ [2\sigma(\chi)\sigma'(\chi) + 2\nu(\chi)\nu'(\chi)]\theta(\chi) + [\sigma^2(\chi) + \nu^2(\chi)]\theta'(\chi) &= \alpha\bar{u}\lambda_n(\lambda_n + \delta). \end{aligned} \tag{3.11}$$

At $\chi = \chi_n^H$, since $\sigma(\chi_n^H) = 0$ and $\theta(\chi_n^H) := \theta_0 = -(3\lambda_n + \beta + \delta)$, we get

$$\begin{aligned} \theta'(\chi_n^H) &= -\frac{\alpha\bar{u}\lambda_n(2\lambda_n + \beta)}{\nu_0^2 + \theta_0^2} < 0, \\ \sigma'(\chi_n^H) &= -\frac{1}{2}\theta'(\chi_n^H) > 0. \end{aligned} \tag{3.12}$$

□

Now we state our main result in this section on the existence of nontrivial periodic orbits of (1.2).

Theorem 3.4. *Assume that the parameters $\alpha, \beta, \delta, \gamma, \xi, \bar{u}$ satisfy (3.4), and let χ_n^H and χ_n^S be defined as in (3.8). Suppose that*

- (A1) *for some $j \in \mathbb{N}$, λ_j is a simple eigenvalue of $-\Delta$ in Ω with Neumann boundary condition, and the corresponding eigenfunction is $y_j(x)$;*
- (A2) *The eigenvalue λ_j satisfies*

$$p_1(\beta, \delta) < \lambda_j < p_2(\beta, \delta), \tag{3.13}$$

where $p_1 = p_1(\beta, \delta)$ and $p_2 = p_2(\beta, \delta)$ are defined as in Lemma 3.1;

- (A3) *for any $n \in \mathbb{N}$, $\chi_j^H \neq \chi_n^S$, and for any $n \in \mathbb{N}$ and $n \neq j$, $\chi_j^H \neq \chi_n^H$.*

Then

1. (1.2) has a unique one-parameter family $\{\rho(s) : 0 < s < \varepsilon\}$ of nontrivial periodic orbits near $(\chi, u, v, w) = (\chi_j^H, \bar{u}, \bar{v}, \bar{w})$. More precisely, there exist $\varepsilon > 0$ and C^∞ function $s \mapsto (U_j(s), T_j(s), \chi_j(s))$ from $s \in (-\varepsilon, \varepsilon)$ to $C^1(\mathbb{R}, X^3) \times (0, \infty) \times \mathbb{R}$ satisfying

$$(U_j(0), T_j(0), \chi_j(0)) = ((\bar{u}, \bar{v}, \bar{w}), 2\pi/\nu_0, \chi_j^H), \tag{3.14}$$

and

$$U_j(s, x, t) = (\bar{u}, \bar{v}, \bar{w}) + sy_j(x) [V_j^+ \exp(i\nu_0 t) + V_j^- \exp(-i\nu_0 t)] + o(s), \tag{3.15}$$

where

$$\nu_0 = \sqrt{3\lambda_n^2 + [2(\beta + \delta) + (\xi\gamma - \alpha\chi_j^H)\bar{u}]\lambda_n + \delta\beta}, \tag{3.16}$$

and V_j^\pm is an eigenvector satisfying $A_j V_j^\pm = i\nu_0 V_j^\pm$;

2. for $0 < |s| < \varepsilon$, $\rho(s) = \rho(U_j(s)) = \{U_j(s, \cdot, t) : t \in \mathbb{R}\}$ is a nontrivial periodic orbit of (1.2) of period $T_j(s)$;
3. if $0 < s_1 < s_2 < \varepsilon$, then $\rho(s_1) \neq \rho(s_2)$;
4. there exists $\tau > 0$ such that if (1.2) has a nontrivial periodic solution $\tilde{U}(x, t)$ of period T for some $\chi \in \mathbb{R}$ with

$$|\chi - \chi_j^H| < \tau, \quad \left| T - \frac{2\pi}{\nu_0} \right| < \tau, \quad \max_{t \in \mathbb{R}, x \in \bar{\Omega}} |\tilde{U}(x, t) - (\bar{u}, \bar{v}, \bar{w})| < \tau,$$

then $\chi = \chi_j(s)$ and $\tilde{U}(x, t) = U_j(s, x, t + \theta)$ for some $s \in (0, \varepsilon)$ and some $\theta \in \mathbb{R}$.

Proof. We follow the general framework given in Section 6.1. Denote $U = (u, v, w)$. Define

$$a(U, \chi) = \begin{pmatrix} 1 & -\chi u & \xi u \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}, \quad a_0 = \begin{pmatrix} 0 & 0 & 0 \\ -\alpha & \beta & 0 \\ -\gamma & 0 & \delta \end{pmatrix}. \tag{3.17}$$

Then the chemotaxis system (1.2) is in a form of (6.6) with a and a_0 defined as in (3.17), $a_j \equiv 0$, $b \equiv 0$, $f \equiv 0$ and $g \equiv 0$. To apply Theorem 6.1, we make a change of

variables $(u, v, w) = (\bar{u} + \tilde{u}, \bar{v} + \tilde{v}, \bar{w} + \tilde{w})$. Denote $\tilde{U} = (\tilde{u}, \tilde{v}, \tilde{w})$ and $\bar{U} = (\bar{u}, \bar{v}, \bar{w})$. Then after the transformation, (1.2) becomes

$$\begin{cases} \partial_t \tilde{U} - \partial_j(a(\bar{U} + \tilde{U}, \chi)\partial_j \tilde{U}) + a_0 \tilde{U} = 0, & x \in \Omega, t > 0, \\ \partial_\nu \tilde{U} = 0, & x \in \partial\Omega, t > 0, \end{cases} \tag{3.18}$$

and for $\chi \geq 0$, $(\tilde{u}, \tilde{v}, \tilde{w}) = (0, 0, 0)$ is an equilibrium. The linearized equation (6.7) at \bar{U} is exactly (2.1). Hence to apply Theorem 6.1, we only need to verify conditions (H1)-(H3) are satisfied.

From Proposition 3.2, at $\chi = \chi_j^H$, the matrix A_j has a pair of purely imaginary eigenvalues $\pm i\nu_0$, with ν_0 given by (3.16) following (3.9) and (2.5). Since λ_n is a simple eigenvalue of $-\Delta$, and $\chi_j^H \neq \chi_n^H$ for $n \neq j$, then $\mu = \pm i\nu_0$ is a pair of simple eigenvalues of (2.1), and hence (H1) and (H2) (for $k \in \mathbb{Z} \setminus \{\pm 1, 0\}$) are satisfied. Since $\chi_j^H \neq \chi_n^S$ for any $n \in \mathbb{N}$, then 0 cannot be an eigenvalue for (2.1) when $\chi = \chi_j^H$, thus (H2) is also satisfied for $k = 0$. Finally Lemma 3.3 implies that (H3) is satisfied. Therefore we can apply Theorem 6.1 to obtain the results stated. The form (3.15) can be obtained by solving the linearized parabolic system. \square

Theorem 6.1 shows that the occurrence of a Hopf bifurcation in (1.2) depends on several factors: (i) parameters need to satisfy (3.4); (ii) the spatial domain Ω (or indeed the eigenvalue λ_j) need to satisfy conditions (A1)-(A3). The parameter choice (3.4) can be achieved when all parameters are properly chosen, and one example is shown in Fig. 1. The conditions (A1) and (A3) hold for generic spatial domains (*i.e.* all domains except a zero measure set), but (A2) means that the size and shape of the domain have to be chosen properly. For a parameter set satisfying (3.4), if the domain Ω is so small that $\lambda_1 > p_2$, then (A2) is not met.

When the Hopf bifurcations do occur in (1.2), results in this section give precise algorithm to determine the exact bifurcation points and the nature of the Hopf bifurcation. The parameter selection is achieved by using (3.4), and to satisfy (A2), one can use (3.1) and (3.2) and properly choose λ_j . The expression (3.15) gives the oscillation frequency, and the eigenfunction $y_j(x)$ gives the spatial profile of the oscillation. We also emphasize that Theorem 6.1 holds for domain Ω in any dimension $n \geq 1$. When $n = 1$ and $\Omega = (0, l)$, the eigenfunction is $y_j(x) = \cos(j\pi x/l)$ which shows the time-periodic orbit is also periodic in space.

4. Steady state bifurcation. In this section we prove the existence of nontrivial steady state solutions of (1.2), or equivalently solutions of (1.3). We use a bifurcation approach similar to the one in [53]. We first will consider the case of a general bounded domain $\Omega \subset \mathbb{R}^n$ ($n \geq 1$), and then we give some more specific results for the case $\Omega = (0, l)$ and $n = 1$. We first prove some nonexistence results of (1.3) for small $\chi \geq 0$.

Lemma 4.1. *Suppose that the parameters $\alpha, \beta, \delta, \gamma, \xi, \bar{u}$ are positive, then the only non-negative solution to (1.3) is $(\bar{u}, \bar{v}, \bar{w})$ if one of the following conditions is satisfied:*

1. $\xi\gamma \geq \chi\alpha$ and $\beta = \delta$; or
2. $\chi = 0$.

Proof. The first part is indeed proved in [48, Proposition 2.3], so we only prove the second part. When $\chi = 0$, the system (1.3) is reduced to

$$\begin{cases} \Delta u + \nabla \cdot (\xi u \nabla w) = 0, & x \in \Omega, \\ \Delta w + \gamma u - \delta w = 0, & x \in \Omega, \\ \frac{1}{|\Omega|} \int_{\Omega} u(x) dx = \bar{u} > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{4.1}$$

Note that the first equation of (4.1) can be written as $\nabla[u\nabla(\ln u + \xi w)] = 0$, then it follows that $\ln u(x) + \xi w(x) \equiv C_1$ or $u(x) \equiv C e^{-\xi w(x)}$ for a constant $C \in \mathbb{R}$. By using the mass conservation equality and the equation of w , we obtain that $w(x)$ satisfies

$$\Delta w + g(w) = 0, \quad x \in \Omega, \quad \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial\Omega, \tag{4.2}$$

where

$$g(w) = -\delta w + A e^{-\xi w}, \quad A = |\Omega| \bar{u} \gamma \left(\int_{\Omega} e^{-\xi w(x)} dx \right)^{-1}.$$

It is easy to verify that for a fixed $A > 0$, $g(w)(w - \bar{w}) < 0$ for any $w > 0$ and $w \neq \bar{w} = \gamma \bar{u} / \delta$. From the maximum principle, it follows that $0 \leq w(x) \leq \bar{w}$ for $x \in \bar{\Omega}$. Integrating the equation in (4.2) yields $\int_{\Omega} g(w(x)) dx = 0$. Hence $w(x) \equiv \bar{w}$ and consequently $(u, v, w) \equiv (\bar{u}, \bar{v}, \bar{w})$. \square

The main result for global bifurcation of steady state solutions in the attraction-repulsion chemotaxis system is as follows.

Theorem 4.2. *Assume that the parameters $\alpha, \beta, \delta, \gamma, \xi, \bar{u}$ are positive, and let χ_n^H and χ_n^S be defined as in (3.8). We assume that condition (A1) in Theorem 3.4 is satisfied, and also*

(A4) *for any $n \in \mathbb{N}$, $\chi_j^S \neq \chi_n^H$, and for any $n \in \mathbb{N}$ and $n \neq j$, $\chi_j^S \neq \chi_n^S$.*

Then

- (1.3) has a unique one-parameter family $\Gamma_j = \{(\hat{U}_j(s), \hat{\chi}_j(s)) : -\varepsilon < s < \varepsilon\}$ of nontrivial solutions near $(u, v, w, \chi) = (\bar{u}, \bar{v}, \bar{w}, \chi_j^S)$. More precisely, there exist $\varepsilon > 0$ and C^∞ function $s \mapsto (\hat{U}_j(s), \hat{\chi}_j(s))$ from $s \in (-\varepsilon, \varepsilon)$ to $X^3 \times \mathbb{R}$ satisfying

$$(\hat{U}_j(0), \hat{\chi}_j(0)) = ((\bar{u}, \bar{v}, \bar{w}), \chi_j^S), \tag{4.3}$$

and

$$\hat{U}_j(s, x) = (\bar{u}, \bar{v}, \bar{w}) + s y_j(x) \left(\lambda_j + \beta, \alpha, \frac{\gamma(\lambda_j + \beta)}{\lambda_j + \delta} \right) + s (h_{1,j}(s), h_{2,j}(s), h_{3,j}(s)), \tag{4.4}$$

such that $h_{1,j}(0) = h_{2,j}(0) = h_{3,j}(0) = 0$;

- The set Γ_j is a subset of a connected component \mathcal{C}_j of \bar{S} , where

$S = \{(u, v, w, \chi) \in X^3 \times \mathbb{R} : (u, v, w, \chi) \text{ is a nontrivial positive solution of (1.3)}\}$, and either \mathcal{C}_j contains another point $(\bar{u}, \bar{v}, \bar{w}, \chi_k^S)$ with $\chi_k^S \neq \chi_j^S$ or \mathcal{C}_j is unbounded.

- Let $\mathbf{proj}_\chi \mathcal{C}_j$ be the projection of \mathcal{C}_j onto the χ -axis. Then $\mathbf{proj}_\chi \mathcal{C}_j \subset (0, \infty)$, and if $\beta = \delta$, then $\mathbf{proj}_\chi \mathcal{C}_j \subset (\xi \gamma / \alpha, \infty)$.

Proof. Define a mapping $F : X^3 \times \mathbb{R} \rightarrow Y_0 \times Y^2 \times \mathbb{R}$ by

$$F(u, v, w, \chi) = \begin{pmatrix} \Delta u - \nabla \cdot (\chi u \nabla v) + \nabla \cdot (\xi u \nabla w) \\ \Delta v + \alpha u - \beta v \\ \Delta w + \gamma u - \delta w \\ \int_{\Omega} u(x) dx - |\Omega| \bar{u} \end{pmatrix}. \tag{4.5}$$

We apply Theorem 6.2 to the equation $F(u, v, w, \chi) = 0$ at $(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)$. Clearly, $F(\bar{u}, \bar{v}, \bar{w}, \chi_j^S) = 0$, and F is continuously differentiable. We verify the conditions in Theorem 6.2 in the following steps.

Step 1. $F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)$ is a Fredholm operator with index zero, and the kernel space $N(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S))$ is one-dimensional, where $U = (u, v, w)$.

By using the same argument as in Lemma 2.3 in [53], one can show that the linear operator $F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S) : X^3 \rightarrow Y_0 \times Y^2 \times \mathbb{R}$ is a Fredholm operator with index zero. To prove that $N(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)) \neq \{0\}$, we calculate that

$$F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)[\phi, \psi, \varphi] = \begin{pmatrix} \Delta \phi - \nabla \cdot (\chi_j^S \bar{u} \nabla \psi) + \nabla \cdot (\xi \bar{u} \nabla \varphi) \\ \Delta \psi + \alpha \phi - \beta \psi \\ \Delta \varphi + \gamma \phi - \delta \varphi \\ \int_{\Omega} \phi(x) dx \end{pmatrix}. \tag{4.6}$$

Let $(\phi, \psi, \varphi) (\neq 0) \in F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)$. Then from Lemma 2.1, there exists $j \in \mathbb{N}$ such that zero is an eigenvalue of A_j (defined in (2.2)), and the corresponding eigenvector is

$$(\bar{a}_j, \bar{b}_j, \bar{c}_j) y_j = \left(\lambda_j + \beta, \alpha, \frac{\gamma(\lambda_j + \beta)}{\lambda_j + \delta} \right) y_j. \tag{4.7}$$

From the condition (A1), the eigenvector is unique up to a constant multiple. Thus one has $N(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)) = \text{span}\{(\bar{a}_j, \bar{b}_j, \bar{c}_j) y_j\}$, which is one-dimensional.

Step 2. $F_{\chi_U}(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j) y_j] \notin R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S))$.

We claim that the range space $R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S))$ can be characterized as follows:

$$R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)) = \left\{ (h_1, h_2, h_3, r) \in Y_0 \times Y^2 \times \mathbb{R} : \int_{\Omega} (a_j^* h_1 + b_j^* h_2 + c_j^* h_3) y_j dx = 0 \right\}, \tag{4.8}$$

where (a_j^*, b_j^*, c_j^*) is a non-zero eigenvector for the eigenvalue $\mu = 0$ of A_n^T (the transpose of A_n defined in (2.2)):

$$(a_j^*, b_j^*, c_j^*) = \left(\lambda_j + \beta, \chi_j^S \bar{u} \lambda_j, -\frac{\chi_j^S \bar{u} \lambda_j}{\lambda_j + \delta} (\lambda_j + \beta) \right). \tag{4.9}$$

Indeed if $(h_1, h_2, h_3, r) \in R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S))$, then there exists $(\phi_1, \psi_1, \varphi_1) \in X^3$ such that

$$F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)[(\phi_1, \psi_1, \varphi_1)] = (h_1, h_2, h_3, r).$$

Define

$$L[\phi, \psi, \varphi] = \begin{pmatrix} \Delta \phi - \chi_j^S \bar{u} \Delta \psi + \xi \bar{u} \Delta \varphi \\ \Delta \psi + \alpha \phi - \beta \psi \\ \Delta \varphi + \gamma \phi - \delta \varphi \end{pmatrix}, \tag{4.10}$$

and its adjoint operator

$$L^*[\phi, \psi, \varphi] = \begin{pmatrix} \Delta\phi + \alpha\psi + \gamma\varphi \\ -\chi_j^S \bar{u} \Delta\phi + \Delta\psi - \beta\psi \\ \xi \bar{u} \Delta\phi + \Delta\varphi - \delta\varphi \end{pmatrix}. \tag{4.11}$$

Then we have

$$\begin{aligned} \langle (h_1, h_2, h_3), (a_j^*, b_j^*, c_j^*)y_j \rangle &= \langle L[(\phi_1, \psi_1, \varphi_1)], (a_j^*, b_j^*, c_j^*)y_j \rangle \\ &= \langle (\phi_1, \psi_1, \varphi_1), L^*[(a_j^*, b_j^*, c_j^*)y_j] \rangle = \langle (\phi_1, \psi_1, \varphi_1), A_n^*(a_j^*, b_j^*, c_j^*)y_j \rangle = 0, \end{aligned}$$

where $\langle \cdot, \cdot \rangle$ is the inner product in $[L^2(\Omega)]^3$. This proves that if

$$(h_1, h_2, h_3, r) \in R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)),$$

then

$$\int_{\Omega} (a_j^* h_1 + b_j^* h_2 + c_j^* h_3) y_j dx = 0. \tag{4.12}$$

Since (4.12) defines a codimension-1 set in $Y_0 \times Y^2 \times \mathbb{R}$, and we know that

$$\text{codim } R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)) = \dim N(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)) = 1,$$

then $R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S))$ must be in form of (4.8).

Now noting that

$$F_{\chi U}(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j] = (-\bar{u}\bar{b}_j \Delta y_j, 0, 0, 0) = (\bar{u}\alpha \lambda_j y_j, 0, 0, 0),$$

then from (4.8) we have

$$\int_{\Omega} (a_j^* h_1 + b_j^* h_2 + c_j^* h_3) y_j dx = \int_{\Omega} (\lambda_j + \beta) \bar{u} \alpha \lambda_j y_j^2 dx > 0.$$

Hence $F_{\chi U}(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)[(\bar{a}_j, \bar{b}_j, \bar{c}_j)y_j] \notin R(F_U(\bar{u}, \bar{v}, \bar{w}, \chi_j^S))$.

Finally we can use the arguments in Lemma 2.3 of [53] to show that for any $(u, v, w, \chi) \in X^3 \times \mathbb{R}$, the operator $F_U(u, v, w, \chi)$ is a Fredholm operator with index zero. Then all conditions in Theorem 6.2 are verified, and hence we obtain that solutions bifurcated from $(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)$ are on a connected component \mathcal{C}_j of the set of nontrivial solutions of (1.3). We shall show that all solutions on \mathcal{C}_j are positive. This is apparently true for solutions near the bifurcation point $(\bar{u}, \bar{v}, \bar{w}, \chi_j^S)$ since $\bar{u} > 0, \bar{v} > 0$ and $\bar{w} > 0$. From the equation of v and w in (1.3), one can see that if u is nonnegative, then v and w must be positive in $\bar{\Omega}$. Hence if not all solutions on \mathcal{C}_j are positive, then there exists $(u, v, w, \chi) \in \mathcal{C}_j$, such that $v(x) > 0, w(x) > 0$ in $\bar{\Omega}$, and $u(x) = 0$ for some $x \in \bar{\Omega}$. But from the equation of u in (1.3) (which is linear in u), and strong maximum principle, we have a contradiction. Hence all solutions on \mathcal{C}_j are positive.

For the last part, since the only nonnegative solution of (1.3) is $(\bar{u}, \bar{v}, \bar{w})$ when $\chi = 0$ from Lemma 4.1, and $\chi = 0$ cannot be a bifurcation point from Lemma 2.1, then the continuum \mathcal{C}_j cannot be extended to $\chi = 0$. Hence $\text{proj}_{\chi} \mathcal{C}_j \subset (0, \infty)$. The result for the case of $\beta = \delta$ is from the other result in Lemma 4.1. This completes the proof. \square

It is difficult to obtain more detailed information of the global branch \mathcal{C}_j in the general setting as in Theorem 4.2. When the spatial domain is one-dimensional,

a more precise description of \mathcal{C}_j can be obtained. In the remaining part of this section, we consider (1.3) in the case $n = 1$ and $\Omega = (0, l)$, that is

$$\begin{cases} (u' - \chi uv' + \xi uw')' = 0, & x \in (0, l), \\ v'' + \alpha u - \beta v = 0, & x \in (0, l), \\ w'' + \gamma u - \delta w = 0, & x \in (0, l), \\ u'(x) = v'(x) = w'(x) = 0, & x = 0, l, \\ \int_0^l u(x) dx = l\bar{u}. \end{cases} \tag{4.13}$$

To obtain a more precise global bifurcation diagram, we shall prove the following *a priori* estimates of positive solutions of (4.13) (the proof is similar to the one in [53]):

Lemma 4.3. *Suppose that $\alpha, \beta, \gamma, \delta > 0$ and $\chi, \xi \geq 0$, and $(u(x), v(x), w(x))$ is a non-negative solution of (4.13). Then either $(u(x), v(x), w(x))$ is the constant solution $(\bar{u}, \bar{v}, \bar{w})$ or for $x \in [0, l]$, $(u(x), v(x), w(x))$ satisfies*

$$\begin{aligned} 0 < u(x) &\leq \bar{u} \exp[2\bar{u}l^2(\chi\alpha + \xi\gamma)], \\ 0 < v(x) &\leq \alpha\bar{u} \left(\frac{1}{\beta} + 2l^2\right), \quad 0 < w(x) \leq \gamma\bar{u} \left(\frac{1}{\delta} + 2l^2\right). \end{aligned} \tag{4.14}$$

Proof. Clearly the constant $(\bar{u}, \bar{v}, \bar{w})$ is a solution to (4.13). Next we assume that $(u(x), v(x), w(x))$ is a non-constant nonnegative solution of (4.13). Assume that $v(x_0) = \min_{x \in [0, l]} v(x) = 0$. Then an application of Hopf’s lemma to the problem

$$\begin{cases} -v'' + \beta v = \alpha u \geq 0, & x \in (0, l), \\ v'(0) = v'(l) = 0, \end{cases}$$

tells us that $x_0 \neq 0, l$. Hence $x_0 \in (0, l)$ and applying the strong maximum principle to the problem above asserts that $v(x) = 0$ for all $x \in [0, l]$ and thus $u(x) = 0$ on $[0, l]$, which contradicts to the fact that $\int_0^l u(x) dx = l\bar{u} > 0$. Hence $v(x) > 0$ on $[0, l]$. Similar argument can be applied to

$$\begin{cases} -w'' + \delta w = \gamma u, & x \in (0, l), \\ w'(0) = w'(l) = 0, \end{cases}$$

to assert that $w(x) > 0$ on $[0, l]$. Next we show $u(x) > 0$ on $[0, l]$. Observe that $u(x)$ satisfies

$$\begin{cases} u'' - \chi u'v' - \chi uv'' + \xi u'w' + \xi uw'' = 0, & x \in (0, l), \\ u'(0) = u'(l) = 0, \end{cases}$$

and by the strong maximum principle, u cannot be zero in $(0, l)$. From Hopf boundary lemma and zero Neumann boundary condition, u cannot be zero at $0, l$ either. So $u(x) > 0$ on $[0, l]$.

Integrating the v -equation in (4.13) and using the boundary condition, we have

$$\begin{aligned} \int_0^l v(x) dx &= \frac{\alpha}{\beta} \int_0^l u(x) dx = \frac{\alpha}{\beta} \bar{u}l, \\ |v'(x)| &= \left| \int_0^x v''(\tau) d\tau \right| \leq \beta \int_0^x v(\tau) d\tau + \alpha \int_0^x u(\tau) d\tau \leq 2\alpha\bar{u}l. \end{aligned}$$

By the integral mean-value theorem, we may take $x_0 \in (0, l)$ such that $v(x_0) = \frac{1}{l} \int_0^l v(x) dx$. Then

$$v(x) = v(x_0) + \int_{x_0}^x v'(\tau) d\tau \leq \alpha \bar{u} \left(\frac{1}{\beta} + 2l^2 \right).$$

Similarly we obtain that $w(x) \leq \gamma \bar{u} \left(\frac{1}{\delta} + 2l^2 \right)$ and $|w'(x)| \leq 2\gamma \bar{u} l$ for $x \in (0, l)$.

On the other hand, since $u'(x) = \chi u(x)v'(x) - \xi u(x)w'(x)$, we have

$$\begin{aligned} |u'(x)| &\leq \chi u(x)|v'(x)| + \xi u(x)|w'(x)| \leq 2\bar{u}l(\chi\alpha + \xi\gamma)u(x), \\ |(\ln u(x))'| &\leq 2\bar{u}l(\chi\alpha + \xi\gamma). \end{aligned}$$

Taking $y_0 \in (0, l)$ such that $u(y_0) = \bar{u}$, we obtain $|\ln u(x) - \ln \bar{u}| \leq 2\bar{u}l^2(\chi\alpha + \xi\gamma)$. \square

Now we can prove the following result on the global bifurcation of monotone steady state solutions in one dimensional case under the assumption $\beta = \delta$ by using a earlier result by [53]:

Theorem 4.4. *Suppose that the constants $\xi, \alpha, \gamma, \beta, \delta, l > 0$, and $\beta = \delta$. Then for any $\chi > \chi_1^S$, there exists a positive solution (u, v, w) of (4.13) satisfying $u', v', w' < 0$ on $(0, l)$, where*

$$\chi_1^S = \frac{1}{\alpha \bar{u} (\frac{\pi^2}{l^2} + \delta)} \left[\frac{\pi^4}{l^4} + (\delta + \beta + \xi\gamma\bar{u}) \frac{\pi^2}{l^2} + \beta\delta + \xi\gamma\beta\bar{u} \right]. \quad (4.15)$$

Moreover when $\chi \rightarrow \infty$, we have

$$u(x) \rightarrow l\bar{u}\delta(x), \quad v(x) \rightarrow \frac{\sqrt{\beta}l\bar{v}}{e^{2\sqrt{\beta}l} - 1} (e^{\sqrt{\beta}x} + e^{\sqrt{\beta}(2l-x)}),$$

and $w(x) = (\gamma/\alpha)v(x)$, where $\bar{v} = \alpha\bar{u}/\beta$.

Proof. We can verify that all conditions in Theorem 6.3 are also satisfied, then Theorem 6.3 implies that \mathcal{C}_1 has a subset \mathcal{C}_1^+ , which contains the $s > 0$ part of the curve Γ_1 in Theorem 4.2 but excludes the $s < 0$ part. Note that it is easy to verify that χ_1^S can be calculated as in (4.15). From Lemma 4.1 and $\beta = \delta$, we know that $\mathbf{proj}_\chi \mathcal{C}_1^+ \subset (\xi\gamma/\alpha, \infty)$. On the other hand, from Lemma 4.3, all positive solutions (u, v, w) are bounded for χ in a compact subset of $(0, \infty)$. Hence when \mathcal{C}_1^+ is not compact, we must have $\mathbf{proj}_\chi \mathcal{C}_1^+ \supset (\chi_1^S, \infty)$. Furthermore when $\beta = \delta$, one has that $\chi_1^S > \xi\gamma/\alpha$ from Lemma 2.5 and (4.13) is then reduced to

$$\begin{cases} [u' - \chi uv' + (\xi\gamma/\alpha)uv']' = 0, & x \in (0, l), \\ v'' + \alpha u - \beta v = 0, & x \in (0, l), \\ u'(x) = v'(x) = 0, & x = 0, l, \\ \int_0^l u(x) dx = l\bar{u}, \end{cases} \quad (4.16)$$

with $w = (\gamma/\alpha)v$. Then we can apply Theorem 3.1 in [53] to obtain other assertions in the theorem. \square

We conjecture that the results in Theorem 4.4 hold at least for the case $\delta \geq \beta$, but a rigorous proof is difficult to obtain. Note that at the same bifurcation point $\chi = \chi_1^S$, another family of steady state solutions (u, v, w) satisfying $u', v', w' > 0$ also bifurcates from the line of trivial solutions $\{(\bar{u}, \bar{v}, \bar{w}, \chi)\}$ by taking the portion of Γ_1 with $s < 0$, hence a pitchfork bifurcation for (4.13) with $\beta = \delta$ occurs at

$\chi = \chi_1^S$. The stability of the bifurcating steady state solutions can be determined by calculation using formulas in [27, 43], but the calculation is lengthy hence not included here. From the numerical simulations in Section 5, the monotone steady state near $\chi = \chi_1^S$ appears to be locally asymptotically stable when $\delta \geq \beta$.

Finally we remark that in the results of Sections 2-4, we have used the attraction strength parameter χ as the bifurcation parameter. Indeed χ and ξ are both important parameters which measure the strength of the attraction and repulsion respectively. In this section we show that the bifurcation analysis in Sections 2-4 is still valid when we use ξ as the bifurcation parameter instead of χ . Since the proofs are all similar we only state the results for the stability analysis without proof. Similar to the functions $\chi_S(p)$ and $\chi_H(p)$ in Section 2, from (2.10) and (2.11) we can define

$$\xi_S(p) = \frac{p + \delta}{\gamma \bar{u}} \left(\frac{\alpha \chi \bar{u}}{p + \beta} - 1 \right), \tag{4.17}$$

and

$$\xi_H(p) = -\frac{1}{\gamma \bar{u}} \left[4p + 2(2\beta + \delta) + \frac{\beta(\delta + \beta)}{p} - \alpha \chi \bar{u} \cdot \frac{2p + \beta}{2p + \delta} \right]. \tag{4.18}$$

Then the properties of $\xi_S(p)$ and $\xi_H(p)$ are as follows:

Lemma 4.5. *Suppose that $\alpha, \beta, \gamma, \delta, \chi, \bar{u} > 0$ are fixed, and let $\xi_S(p)$ and $\xi_H(p)$ be defined as in (4.17) and (4.18).*

1. *If $\delta > \beta - \frac{\beta^2}{\alpha \chi \bar{u}}$, then $\xi_S(p)$ is strictly decreasing for $p \in (0, \infty)$; and if $\delta < \beta - \frac{\beta^2}{\alpha \chi \bar{u}}$, then for $p_* = \sqrt{\alpha \chi \bar{u}(\beta - \delta)} - \beta$, $\xi_S(p)$ is strictly increasing for $p \in (0, p_*)$, and $\xi_S(p)$ is strictly decreasing for $p \in (p_*, \infty)$;*
2. *The function $\xi_H(p)$ satisfies $\lim_{p \rightarrow 0^+} \xi_H(p) = -\infty$, $\lim_{p \rightarrow \infty} \xi_H(p) = -\infty$, and there exists a unique critical point $p^* \in (0, \infty)$ of $\xi_H(p)$ which is the global maximum point.*

The geometric properties of $\xi_S(p)$ and $\xi_H(p)$ clearly imply the following stability result for $(\bar{u}, \bar{v}, \bar{w})$.

Theorem 4.6. *Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium. Assume that $\alpha, \beta, \gamma, \delta > 0$ and $\chi > 0$ are fixed. Let $\xi_S(p)$ and $\xi_H(p)$ be the functions defined in (4.17) and (4.18). If ξ satisfies*

$$\xi > \max_{n \in \mathbb{N}} \{ \xi_S(\lambda_n), \xi_H(\lambda_n) \}, \tag{4.19}$$

then $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2). In particular, $(\bar{u}, \bar{v}, \bar{w})$ is locally asymptotically stable with respect to (1.2) if χ satisfies

$$\xi > \max \{ \chi_S(p_*), \chi_H(p^*) \}, \tag{4.20}$$

where p_ and p^* are the global maximum points of $\xi_S(p)$ on $[0, \infty)$ and $\xi_H(p)$ on $(0, \infty)$ respectively.*

We notice that $\xi_S(p_*)$ can be explicitly calculated:

$$\xi_S(p_*) = \begin{cases} \frac{\delta}{\gamma \bar{u}} \left(\frac{\alpha \chi \bar{u}}{\beta} - 1 \right), & \text{if } \delta \geq \delta_*; \\ \frac{1}{\gamma \bar{u}} \left(\sqrt{\alpha \chi \bar{u}} - \sqrt{\beta - \delta} \right)^2, & \text{if } \delta < \delta_*, \end{cases} \tag{4.21}$$

where

$$\delta_* = \beta - \frac{\beta^2}{\alpha\chi\bar{u}}, \quad p_* = \begin{cases} 0, & \text{if } \delta \geq \delta_*; \\ \sqrt{\alpha\chi\bar{u}(\beta - \delta)} - \beta & \text{if } \delta < \delta_*. \end{cases} \quad (4.22)$$

Both $\xi_S(p_*)$ and $\xi_H(p_*)$ can be computed if the parameter values are given. In Fig. 2, graphs of $\xi = \xi_S(p)$ and $\xi = \xi_H(p)$ for several different sets of parameters are shown.

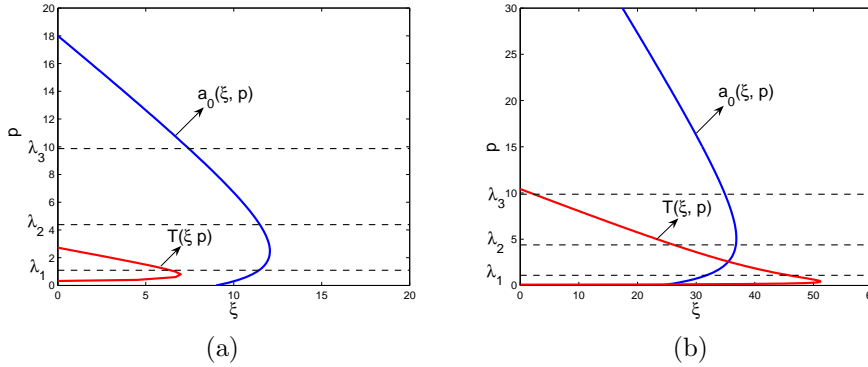


FIGURE 2. Graph of $a_0(\xi, p) = 0$ ($\xi = \xi_S(p)$) and $T(\xi, p) = 0$ ($\xi = \xi_H(p)$). Here the horizontal axis is ξ and the vertical axis is p , and the dashed horizontal lines are $p = \lambda_n = (n\pi/3)^2$ for $n = 1, 2, 3$, where we assume that $\Omega = (0, 3)$ a one-dimensional spatial domain). Parameters used: $\gamma = \alpha = \delta = \bar{u} = 1$, $\beta = 2$ for all three plots; (a) $\chi = 20$; (b) $\chi = 100$.

In particular if the graphic scenario in the right panel of Fig. 2 occurs, Hopf bifurcations are possible as we have shown in Section 3. Indeed similar to Lemma 3.1, we have the following result characterizing the parameter regimes for time-periodic patterns.

Lemma 4.7. *Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium and define*

$$A_* =: A_*(\beta, \delta) = \frac{(\hat{p} + \beta)^2(2\hat{p} + \delta)}{(\beta - \delta)\hat{p}},$$

where \hat{p} is the unique positive root of the equation

$$4p^3 + (\delta + 4\beta)p^2 = \beta^2\delta.$$

1. If either

$$\delta \geq \beta$$

or

$$\beta > \delta \text{ and } \chi\alpha\bar{u} < A_*,$$

then $\xi_S(p) > \xi_H(p)$ for all $p > 0$.

2. If

$$\beta > \delta \text{ and } \chi\alpha\bar{u} > A_*,$$

then there exist $p_1, p_2 > 0$ such that $\xi_S(p) < \xi_H(p)$ for $p_1 < p < p_2$, and $\xi_S(p) > \xi_H(p)$ for $0 < p < p_1$ or $p > p_2$.

5. Numerical simulations. The classical Keller-Segel model with one chemical does not admit time-periodic pattern solutions due to the existence of a time-monotone Lyapunov functional. In this paper, we prove that the attraction-repulsion Keller-Segel (ARKS) model (1.2), in which two competing chemicals (*i.e.* chemo-attractant and chemo-repellent) interact with one species, may produce time-periodic patterns. Our study shows that the death rates of two competing chemicals, denoted by β and δ , are critical in creating periodic patterns which arise only if the chemo-attractant has larger death rate than the chemo-repellent (*i.e.* $\delta < \beta$) and repulsion is large in the sense that $\xi\gamma\bar{u} > A^*$, where A^* is given in Lemma 3.1. The result was proved by the Hopf bifurcation theorems, see Lemma 3.1 and Theorem 3.4.

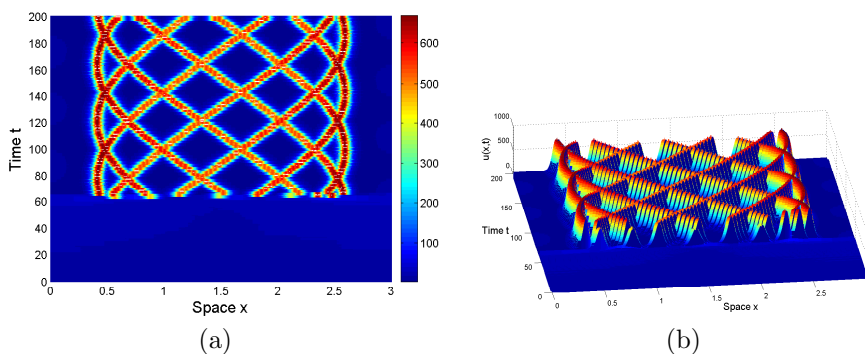


FIGURE 3. (a) Time-periodic rippling pattern formation of the solution component u to the ARKS system (1.2) in the interval $(0, 3)$; (b) A three dimensional view of spatiotemporal periodic rippling pattern of solution component u . The parameters values are: $\gamma = \alpha = \xi = \delta = 1, \beta = 16, \bar{u} = 20$, which are same as those in Fig. 1 (c). The initial conditions are set as a small random perturbation of the homogeneous steady state $(20, 5/4, 20)$.

In this section, we numerically explore the spatiotemporal patterns generated by the ARKS models (1.2) in different parameter regimes identified in the paper. The PDEPE computing package in `Matlab` is implemented to solve the system (1.2) in one dimension.

Lemma 3.1 presents complete parameter regimes in which various bifurcations occur, which are illustrated in Fig. 1. We first choose parameter values as in Fig. 1 (c) in an interval $\Omega = (0, l)$, then we obtain that

$$\chi_H(p) = \frac{1}{20} \left(4p + 56 - \frac{17}{p} - \frac{150}{p + 8} \right). \tag{5.1}$$

From Fig. 1 (c), we see that if we select χ slightly larger than the smallest Hopf bifurcation critical value χ_j^H given in (2.13) with $p = (j\pi/l)^2$, then only one Hopf bifurcation occurs and the constant steady state loses the stability through the Hopf bifurcation, and a time-periodic patterns is expected in this case (see Theorem 3.4). Indeed, in the simulation shown in Fig. 3, we choose $n = 1$ and $\Omega = (0, 3)$, and then it can be easily calculated that the smallest Hopf bifurcation value is $\chi_1^H = \chi_H(\pi^2/9) \approx 2.97$, while the next Hopf bifurcation value is $\chi_2^H = \chi_H(4\pi^2/9) \approx 3.27$.

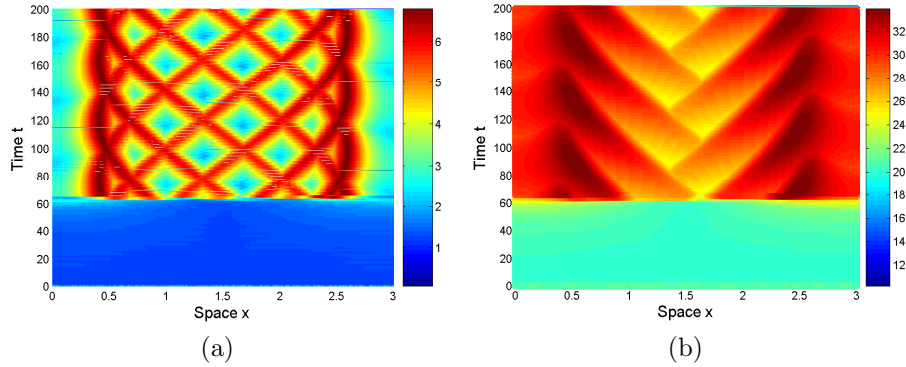


FIGURE 4. Time-periodic rippling pattern formation of the solution component v in (a) and w in (b) to the ARKS system (1.2) in the interval $(0, 3)$, where the parameter values and the initial data are the same as those in Fig. 3.

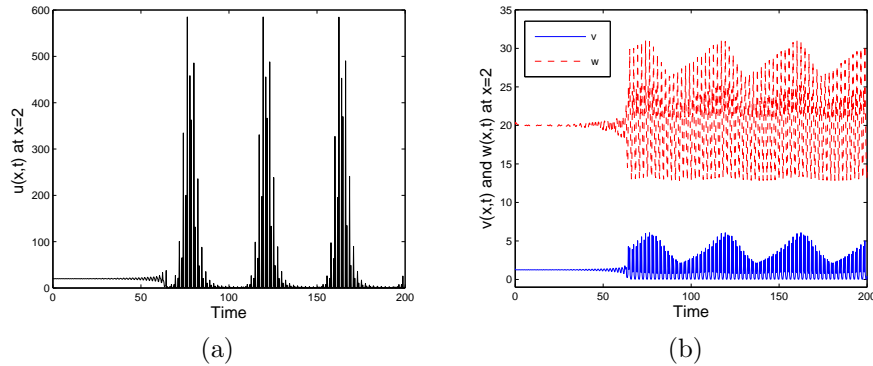


FIGURE 5. A visualization of the time-periodic solution (u, v, w) at a fixed spatial location $x = 2$. The parameter values and the initial conditions are the same as those in Fig. 3.

Here we choose $\chi = 3.07$ and set the initial condition as a small random perturbation of the homogeneous steady state $(u_s, v_s, w_s) = (20, 5/4, 20)$. Then the spatiotemporal pattern of the cell density u is plotted in Fig. 3 (a), in which we observe highly organized rippling periodic waves arise from an initially almost homogeneous colony and periodically reverse their directions. In a three dimensional visualization shown in Fig. 3 (b), we see that two wave crests pass through one another without interference when colliding, different from the typical chemotactic waves which coalesce upon collision (cf. [16, 54]). Fig. 4 plots the time-periodic patterns for the solution component (v, w) , and Fig. 5 plots a time-periodic evolution profile of the solution at a fixed location $x = 2$, where we see that the solution (u, v, w) of system (1.2) is periodic in time and the period can even be numerically counted. Hence we may conclude that the chemotactic interaction of attraction and repulsion can produce time-periodic patterns which cannot be generated in systems where each of them affects the cell by itself.

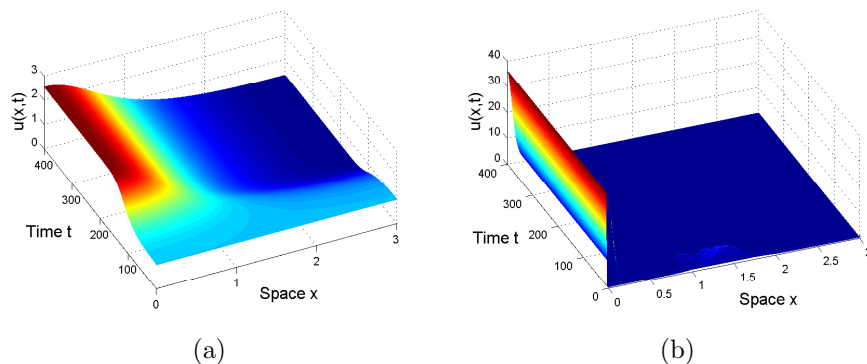


FIGURE 6. Numerical simulations of cell density u for different value of χ , where the steady state bifurcation occurs. (a) $\chi = 3.2$; (b) $\chi = 10$. Other parameter values are $\alpha = 1, \beta = 1, \gamma = 1, \delta = 1, \xi = 1, \bar{u} = 1$. The initial value is set as a small random perturbation of the homogeneous steady state $(1, 1, 1)$.

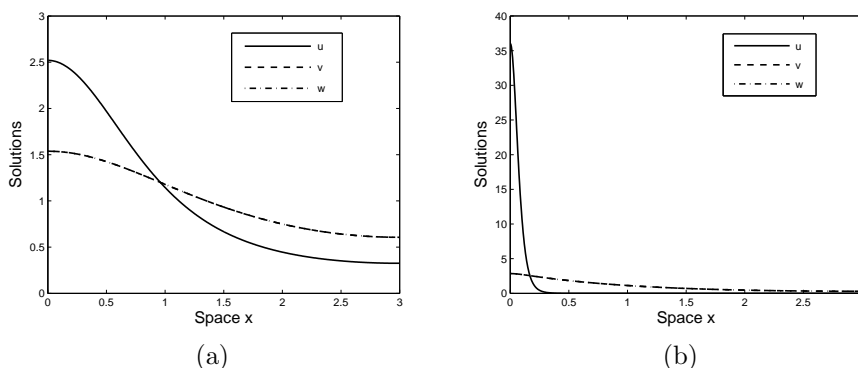


FIGURE 7. Plot of numerical profile of the monotone decreasing stationary solution (u, v, w) to the system (4.13) at time $t = 400$, where the parameter values in (a) and (b) are same as those in Fig. 6 (a) and Fig. 6 (b), respectively. Here the profile of v coincides with that of w due to $\alpha = \gamma$ as shown in the Theorem 4.4. The simulation shows that if the value of χ is increased, a spiky steady state pattern of cell density u will develop.

In the numerical simulation plotted in Fig. 3-5, time-periodic patterns are found by a careful selection of parameter values according to Fig. 1 (c) and Lemma 3.1 such that only Hopf bifurcations occur. It is also of interest to consider the pattern formation where only steady state bifurcations occur or both bifurcations occur. In the second simulation, we consider the parameter values given in Fig. 1 (a) so that

$$\chi_S(p) = p + 2, \quad \chi_H(p) = 4p + 7 + \frac{2}{p}. \tag{5.2}$$

In this case, no Hopf bifurcations can occur according to Lemma 3.1 and Theorem 3.4, but a steady state bifurcation occurs at every $\chi_j^S = \chi_S(\lambda_j)$. Again we choose

$\Omega = (0, 3)$. Then $\chi_1^S = \chi_S(\pi^2/9) = \pi^2/9 + 2 \approx 3.10$. In the numerical simulation shown in Fig. 6 (a), we choose $\chi = 3.20$ and set the initial condition as a small random perturbation of the homogeneous steady state $(1, 1, 1)$. We observe that a spatially monotone decreasing steady state pattern arises from the initial uniform colony. But the pattern solution u shown in Fig. 7 (a) is not spiky since the value of χ is not large (just slightly bigger than the bifurcation value). If we increase the value of χ , we find from the numerical simulation shown in Fig. 6 (b) that the spiky steady state pattern emerge, and the solution profile is monotone decreasing in space as shown Fig. 7 (b). These numerical simulations are entirely consistent with our theoretical results in Theorem 4.4.

6. Appendix: Bifurcation theorems.

6.1. Hopf bifurcation for quasilinear parabolic systems. We recall the Hopf bifurcation theorem for a quasilinear parabolic system from Amann [3] (see also Crandall and Rabinowitz [8], Da Prato and Lunardi [9]). For simplicity we only consider flux type boundary conditions not Dirichlet ones.

Let Ω be a bounded connected domain in \mathbb{R}^n ($n \geq 2$) with C^2 smooth boundary $\partial\Omega$, or an interval (a, b) in \mathbb{R} . Let $U(x) = (U_1(x), U_2(x), \dots, U_N(x))^T$ be a real N -dimensional column-vector-valued function, where $x \in \Omega$. Let the following be $N \times N$ real matrix-valued smooth functions:

$$\begin{aligned} & a(x, \eta, \lambda), \quad a_j(x, \eta, \lambda) \quad (j = 1, \dots, n), \quad a_0(x, \eta, \lambda), \quad \text{where } (x, \eta, \lambda) \in \bar{\Omega} \times G \times \mathbb{R}; \\ & b(x, \eta, \lambda) \quad \text{where } (x, \eta, \lambda) \in \partial\Omega \times G \times \mathbb{R}; \end{aligned} \quad (6.1)$$

and let the following be real N -dimensional column-vector-valued smooth functions:

$$f(x, \eta, \lambda), \quad \text{where } (x, \eta, \lambda) \in \bar{\Omega} \times G \times \mathbb{R}; \quad g(x, \eta, \lambda), \quad \text{where } (x, \eta, \lambda) \in \partial\Omega \times G \times \mathbb{R}. \quad (6.2)$$

Here G is an open subset of \mathbb{R}^N containing 0 and G is star-shaped with respect to 0. We assume that $a(x, \eta, \lambda)$ is elliptic in the sense that

$$\sigma(a(x, \eta, \lambda)) \subset \{z \in \mathbb{C} : \operatorname{Re}(z) > 0\}, \quad (x, \eta, \lambda) \in \bar{\Omega} \times G \times \mathbb{R}, \quad (6.3)$$

where $\sigma(\cdot)$ denotes the spectrum.

Fix $p > n + 1$ and let

$$\mathcal{V} = \{V \in H^{1,p}(\Omega, \mathbb{R}^N) : V(\Omega) \subset G\}, \quad (6.4)$$

which is an open subset of Banach space $H^{1,p}(\Omega, \mathbb{R}^N)$. Now given $(V, \lambda) \in \mathcal{V} \times \mathbb{R}$ and $U \in H^{2,p}(\Omega, \mathbb{R}^N)$, define

$$\begin{aligned} \mathcal{A}(V, \lambda)U &= -\partial_j(a(\cdot, V, \lambda)\partial_j U) + a_j(\cdot, V, \lambda)\partial_j U + a_0(\cdot, V, \lambda)U, \\ \mathcal{B}(V, \lambda)U &= a(\cdot, V, \lambda)\partial_\nu U + b(\cdot, V, \lambda)\gamma_\partial U, \end{aligned} \quad (6.5)$$

where matrix notation and summation convention are used with j running from 1 to n , ∂_ν is the outer normal derivative along $\partial\Omega$, and γ_∂ is the trace operator on $\partial\Omega$. Then a quasilinear parabolic system with nonlinear flux boundary condition can be written as

$$\begin{cases} \partial_t U + \mathcal{A}(U, \lambda)U = f(\cdot, U, \lambda), & x \in \Omega, t > 0, \\ \mathcal{B}(U, \lambda)U = g(\cdot, U, \lambda), & x \in \partial\Omega, t > 0, \\ U = U_0, & x \in \Omega, t = 0. \end{cases} \quad (6.6)$$

From the theory in [2], given $(V, \lambda) \in \mathcal{V} \times \mathbb{R}$, the pair $(\mathcal{A}(V, \lambda), \mathcal{B}(V, \lambda))$ is normally elliptic, and given an initial condition $U_0 \in \mathcal{V}$, there exists a unique maximal classical solution. To consider the related Hopf bifurcation, we further assume that

$$f(x, 0, \lambda) = g(x, 0, \lambda) = 0, \quad (x, \lambda) \in \bar{\Omega} \times \mathbb{R},$$

hence $U = 0$ is an equilibrium solution for (6.6) for any $\lambda \in \mathbb{R}$. By linearizing at $(U, \lambda) = (0, \lambda)$, we obtain a linear elliptic system:

$$\begin{cases} [-\mathcal{A}(0, \lambda) + \partial_U f(\cdot, 0, \lambda)]V = \mu(\lambda)V, & x \in \Omega, \\ [-\mathcal{B}(0, \lambda) + \partial_U g(\cdot, 0, \lambda)]V = 0, & x \in \partial\Omega. \end{cases} \tag{6.7}$$

Theorem 6.1. *Suppose that a, a_j, a_0, b, f, g are as defined above and are of class C^∞ , and the following conditions are satisfied:*

- (H1) *When $\lambda = \lambda_0$, $\mu = \pm\omega_0 i$ are simple eigenvalues of (6.7) for $\omega_0 > 0$;*
- (H2) *When $\lambda = \lambda_0$, (6.7) has no eigenvalues of the form $k\omega_0 i$ for $k \in \mathbb{Z} \setminus \{\pm 1\}$;*
- (H3) *Let $\mu(\lambda) = \alpha(\lambda) + i\beta(\lambda)$ be the unique eigenvalue of (6.7) for λ in a neighborhood of λ_0 satisfying $\mu(\lambda_0) = \omega_0 i$ and $\alpha'(\lambda_0) \neq 0$.*

Then (6.6) has a unique one-parameter family $\{\gamma(s) : 0 < s < \varepsilon\}$ of nontrivial periodic orbits near $(0, \lambda_0) \in \mathcal{V} \times \mathbb{R}$. More precisely, there exist $\varepsilon > 0$ and C^∞ function $s \mapsto (U(s), T(s), \lambda(s))$ from $s \in (-\varepsilon, \varepsilon)$ to $\mathcal{V} \times (0, \infty) \times \mathbb{R}$ satisfying

$$(U(0), T(0), \lambda(0)) = (0, 2\pi/\omega_0, \lambda_0),$$

and for $0 < |s| < \varepsilon$, $\gamma(s) = \gamma(U(s)) = \{U(s, \cdot, t) : t \in \mathbb{R}\}$ is a nontrivial periodic orbit of (6.6) of period $T(s)$; if $0 < s_1 < s_2 < \varepsilon$, then $\gamma(s_1) \neq \gamma(s_2)$; and there exists $\delta > 0$ such that if (6.6) has a nontrivial periodic solution $\tilde{U}(x, t)$ of period T for some $\lambda \in \mathbb{R}$ with

$$|\lambda - \lambda_0| < \delta, \quad \left| T - \frac{2\pi}{\omega_0} \right| < \delta, \quad \max_{t \in \mathbb{R}, x \in \bar{\Omega}} \left| \tilde{U}(x, t) \right| < \delta,$$

then $\lambda = \lambda(s)$ and $\tilde{U}(x, t) = U(s, x, t + \theta)$ for some $s \in (0, \varepsilon)$ and some $\theta \in \mathbb{R}$.

The theorem here is essentially the same as the theorem in [3] with some rephrasing. As mentioned in [3], the C^∞ smoothness assumption can be considerably weakened, which we do not need here as our system (1.2) does satisfy the C^∞ smoothness assumption.

6.2. Bifurcation of steady state solutions. We first 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, Y are Banach spaces. In the following $N(L)$ and $R(L)$ are the null space and the range of a linear operator L ; F_u is 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 arguments u and λ .

We recall the following global bifurcation theorem formulated in Shi and Wang [44, Theorem 4.3] which is based on almost the same conditions of the “bifurcation from a simple eigenvalue” theorem due to Crandall and Rabinowitz [7, Theorem 1.7], and it is also a generalization of the classical Rabinowitz global bifurcation theorem [41].

Theorem 6.2. *Let V be an open connected subset of $\mathbb{R} \times X$ and $(\lambda_0, u_0) \in V$, and let F be a continuously differentiable mapping from V into Y . Suppose that*

1. $F(\lambda, u_0) = 0$ for $(\lambda, u_0) \in V$,
2. The partial derivative $F_{\lambda u}(\lambda, u)$ exists and is continuous in (λ, u) near (λ_0, u_0) ,
3. $F_u(\lambda_0, u_0)$ is a Fredholm operator with index 0, and $\dim N(F_u(\lambda_0, u_0)) = 1$,
4. $F_{\lambda u}(\lambda_0, u_0)[w_0] \notin R(F_u(\lambda_0, u_0))$, where $w_0 \in X$ and $N(F_u(\lambda_0, u_0)) = \text{span}\{w_0\}$.

Let Z be any complement of $\text{span}\{w_0\}$ in X . Then there exist an open interval $I_1 = (-\epsilon, \epsilon)$ and continuous functions $\lambda : I_1 \rightarrow \mathbb{R}$, $\psi : I_1 \rightarrow Z$, such that $\lambda(0) = \lambda_0$, $\psi(0) = 0$, and, if $u(s) = u_0 + sw_0 + s\psi(s)$ for $s \in I_1$, then $F(\lambda(s), u(s)) = 0$. Moreover, $F^{-1}(\{0\})$ near (λ_0, u_0) consists precisely of the curves $u = u_0$ and $\Gamma = \{(\lambda(s), u(s)) : s \in I_1\}$. If in addition, $F_u(\lambda, u)$ is a Fredholm operator for all $(\lambda, u) \in V$, then the curve Γ is contained in \mathcal{C} , which is a connected component of \bar{S} where $S = \{(\lambda, u) \in V : F(\lambda, u) = 0, u \neq u_0\}$; and either \mathcal{C} is not compact in V , or \mathcal{C} contains a point (λ_*, u_0) with $\lambda_* \neq \lambda_0$.

The following unilateral global bifurcation theorem proved in [44, Theorem 4.4] is useful and the “positive part” of \mathcal{C} is of interest in the application.

Theorem 6.3. *Suppose that all conditions in Theorem 6.2 are satisfied. We define $\Gamma_+ = \{(u(s), \lambda(s)) : s \in (0, \delta)\}$ and $\Gamma_- = \{(u(s), \lambda(s)) : s \in (-\delta, 0)\}$. In addition we assume that*

1. $F_u(\lambda, u_0)$ is continuously differentiable in λ for $(\lambda, u_0) \in V$;
2. The norm function $u \mapsto \|u\|$ in X is continuously differentiable for any $u \neq 0$;
3. For $k \in (0, 1)$, if (λ, u_0) and (λ, u) are both in V , then $(1 - k)F_u(\lambda, u_0) + kF_u(\lambda, u)$ is a Fredholm operator.

Let \mathcal{C}^+ (resp. \mathcal{C}^-) be the component of $\mathcal{C}^+ \setminus \Gamma_-$ which contains Γ_+ (resp. the component of $\mathcal{C}^+ \setminus \Gamma_+$ which contains Γ_-). Then each of the sets \mathcal{C}^+ and \mathcal{C}^- satisfies one of the following: (i) it is not compact; (ii) it contains a point (λ_*, u_0) with $\lambda_0 \neq \lambda_*$; or (iii) it contains a point $(\lambda, u_0 + z)$, where $z \neq 0$ and $z \in Z$.

For the quasilinear parabolic system (6.6) defined in subsection 6.1, we define

$$F(\lambda, U) = \begin{pmatrix} -\mathcal{A}(U, \lambda)U + f(\cdot, U, \lambda) \\ -\mathcal{B}(U, \lambda)U + g(\cdot, U, \lambda) \end{pmatrix}, \tag{6.8}$$

where $\lambda \in \mathbb{R}$ and $U \in \mathcal{V}$. Then Theorem 3.3 in [44] can be reformulated in this simpler case as follows.

Lemma 6.4. *Suppose that $p > n$, $\partial\Omega \in C^3$, $a \in C^2$, $a_j, a_0, b, f, g \in C^1$, and the condition (6.3) is satisfied. Then $F : \mathbb{R} \times \mathcal{V} \rightarrow L^p(\Omega, \mathbb{R}^N) \times W^{1-1/p, p}(\partial\Omega, \mathbb{R}^N)$ is a Fredholm operator with index zero for every $(\lambda, U) \in \mathbb{R} \times \mathcal{V}$.*

This result follows directly from [44, Theorem 3.3], since the Augmon’s condition is satisfied from Case 1 of [44, Remark 2.5.5]. Hence the key condition on the Fredholm property of the linear operator in Theorems 6.2 and 6.3 is satisfied in this setting. We also remark that the differentiability of the norm function is also satisfied for L^p space (see the remark after [44, Theorem 4.4]).

6.3. Cubic roots. Next we consider the roots of the cubic equation with constants A, B and C

$$\lambda^3 + A\lambda^2 + B\lambda + C = 0, \quad A > 0.$$

Since the coefficients are real numbers, the equation has three roots, one of which must be real, two other can be either real or complex conjugate. The algebraic relation between the roots and the polynomial coefficients gives

$$A = -(\lambda_1 + \lambda_2 + \lambda_3), \quad B = \lambda_1\lambda_2 + \lambda_1\lambda_3 + \lambda_2\lambda_3, \quad C = -\lambda_1\lambda_2\lambda_3.$$

Then the Routh-Hurwitz criterion (e.g. see [31]) says that all the roots are negative or all the roots have negative real parts if and only if

$$A > 0, \quad C > 0, \quad AB - C^2 > 0.$$

Since $A > 0$, there is at least one root with negative real part. There are two cases to consider.

Case 1. $C = -\lambda_1\lambda_2\lambda_3 < 0$.

(1) If three roots are all real with $\lambda_1 < 0$, then $\lambda_2\lambda_3 < 0$. This indicates that either λ_2 or λ_3 is a positive number. Hence the equation has a positive root.

(2) If λ_1 is real and $\lambda_2 = a+bi$, $\lambda_3 = a-bi$, then $C = -\lambda_1\lambda_2\lambda_3 = -\lambda_1(a^2+b^2) < 0$ which implies that $\lambda_1 > 0$. Since at least one root has negative real part, we require $a < 0$.

Hence a necessary condition that the equation has complex roots with non-negative real part is $C = -\lambda_1\lambda_2\lambda_3 \geq 0$.

Case 2. $C = -\lambda_1\lambda_2\lambda_3 > 0$.

(1) If three roots are all real with $\lambda_1 < 0$, then $\lambda_2\lambda_3 > 0$ which indicates that λ_2 or λ_3 have the same sign. Since $A > 0, C > 0$, by the Routh-Hurwitz criterion, λ_2 and λ_3 are all negative iff $T = AB - C > 0$, and are all positive iff $T = AB - C < 0$. Hence only if $T = AB - C < 0$, there is positive root.

(2) If λ_1 is real and $\lambda_2 = a+bi$, $\lambda_3 = a-bi$, then $C = -\lambda_1\lambda_2\lambda_3 = -\lambda_1(a^2+b^2) > 0$ and hence $\lambda_1 < 0$. Since $A > 0, C > 0$, again by the Routh-Hurwitz criterion, $a > 0$ iff $T = AB - C < 0$.

Case 3. $C = -\lambda_1\lambda_2\lambda_3 = 0$. Then clearly there is a zero root.

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REFERENCES

- [1] J. Adler, Chemotaxis in bacteria, *Science*, **153** (1966), 708–716.
- [2] H. Amann, Dynamic theory of quasilinear parabolic equations. II. Reaction-diffusion systems, *Differential Integral Equations*, **3** (1990), 13–75.
- [3] H. Amann, Hopf bifurcation in quasilinear reaction-diffusion systems, in *Delay differential equations and dynamical systems (Claremont, CA, 1990)*, vol. 1475 of Lecture Notes in Math., Springer, Berlin, 1991, 53–63.
- [4] E. Budrene and H. Berg, Complex patterns formed by motile cells of *Escherichia coli*, *Nature*, **349** (1991), 630–633.
- [5] M. Chaplain and A. Stuart, A model mechanism for the chemotactic response of endothelial cells to tumor angiogenesis factor, *IMA J. Math. Appl. Med.*, **10** (1993), 149–168.
- [6] M. Chuai, W. Zeng, X. Yang, V. Boychenko, J. Glazier and C. Weijer, Cell movement during chick primitive streak formation, *Dev. Biol.*, **296** (2006), 137–149.
- [7] M. Crandall and P. Rabinowitz, Bifurcation from simple eigenvalues, *J. Functional Analysis*, **8** (1971), 321–340.

- [8] M. Crandall and P. Rabinowitz, [The Hopf bifurcation theorem in infinite dimensions](#), *Arch. Rational Mech. Anal.*, **67** (1977), 53–72.
- [9] G. Da Prato and A. Lunardi, Hopf bifurcation for fully nonlinear equations in Banach space, *Ann. Inst. H. Poincaré Anal. Non Linéaire*, **3** (1986), 315–329.
- [10] A.-K. Drangeid, [The principle of linearized stability for quasilinear parabolic evolution equations](#), *Nonlinear Anal.*, **13** (1989), 1091–1113.
- [11] R. Firtel, *Dictyostelium cinema*, <http://people.biology.ucsd.edu/firtel/video.htm>.
- [12] A. Gamba, D. Ambrosi, A. Coniglio, A. de Candia, S. Di Talia, E. Giraud, G. Serini, L. Preziosi and F. Bussolino, [Percolation, Morphogenesis, and Burgers dynamics in blood vessels Formation](#), *Phys. Rev. Lett.*, **90** (2003), 118101.
- [13] M. Gates, V. Coupe, E. Torres, R. Fricker-Gates and S. Dunnett, Spatially and temporally restricted chemoattractant and repulsive cues direct the formation of the nigro-striatal circuit, *Euro. J. Neuroscience*, **19** (2004), 831–844.
- [14] R. E. Goldstein, [Traveling-wave chemotaxis](#), *Phys. Rev. Lett.*, **77** (1996), 775–778.
- [15] P. Grindrod, J. D. Murray and S. Sinha, [Steady-state spatial patterns in a cell-chemotaxis model](#), *IMA J. Math. Appl. Med. Biol.*, **6** (1989), 69–79.
- [16] T. Hillen and K. J. Painter, [A user’s guide to PDE models for chemotaxis](#), *J. Math. Biol.*, **58** (2009), 183–217.
- [17] D. Horstmann, From 1970 until present: the Keller-Segel model in chemotaxis and its consequences. I, *Jahresber. Deutsch. Math.-Verein.*, **105** (2003), 103–165.
- [18] D. Horstmann, [Generalizing the Keller-Segel model: Lyapunov functionals, steady state analysis, and blow-up results for multi-species chemotaxis models in the presence of attraction and repulsion between competitive interacting species](#), *J. Nonlinear Sci.*, **21** (2011), 231–270.
- [19] A. Huttenlocher and M. Poznansky, [Reverse leukocyte migration can be attractive or repulsive](#), *Trends in Cell Biology*, **18** (2008), 298–306.
- [20] O. Igoshin and D. Kaiser, [Rippling of myxobacteria](#), Topics in biomathematics and related computational problems. *Math. Biosci.*, **188** (2004), 221–233.
- [21] O. Igoshin, R. Welch, D. Kaiser and G. Oster, [Waves and aggregation patterns in myxobacteria](#), *Proceedings of the National Academy of Sciences*, **101** (2004), 4256–4261.
- [22] Y. Kabeya and W.-M. Ni, Stationary Keller-Segel model with the linear sensitivity, Variational problems and related topics (Japanese) (Kyoto, 1997). *RIMS Kokyuroku*, **1025** (1998), 44–65.
- [23] E. Keller and L. Segel, [Initiation of slime mold aggregation viewed as an instability](#), *Journal of Theoretical Biology*, **26** (1970), 399–415.
- [24] C.-S. Lin, W.-M. Ni and I. Takagi, [Large amplitude stationary solutions to a chemotaxis system](#), *J. Differential Equations*, **72** (1988), 1–27.
- [25] J. Liu and Z.-A. Wang, [Classical solutions and steady states of an attraction-repulsion chemotaxis in one dimension](#), *J. Biol. Dyn.*, **6** (2012), 31–41.
- [26] J. Liu, F. Yi and J. Wei, [Multiple bifurcation analysis and spatiotemporal patterns in a 1-D Gierer-Meinhardt model of morphogenesis](#), *Internat. J. Bifur. Chaos Appl. Sci. Engrg.*, **20** (2010), 1007–1025.
- [27] P. Liu, J. Shi and Y. Wang, [Imperfect transcritical and pitchfork bifurcations](#), *J. Funct. Anal.*, **251** (2007), 573–600.
- [28] M. Luca, A. Chavez-Ross, L. Edelstein-Keshet and A. Mogilner, [Chemotactic signaling, microglia, and Alzheimer’s disease senile plaques: is there a connection?](#) *Bull. Math. Biol.*, **65** (2003), 693–730.
- [29] P. Maini, M. Myerscough, K. Winters and J. Murray, [Bifurcating spatially heterogeneous solutions in a chemotaxis model for biological pattern generation](#), *Bull. Math. Biol.*, **53** (1991), 701–719.
- [30] S. Martínez and W.-M. Ni, [Periodic solutions of a \$3 \times 3\$ competitive system with cross-diffusion](#), *Discrete Contin. Dyn. Syst.*, **15** (2006), 725–746.
- [31] J. Murray, *Mathematical Biology I: An Introduction*, 3rd edition, Springer, Berlin, 2002.
- [32] M. Myerscough, P. Maini and K. Painter, [Pattern formation in a generalized chemotactic model](#), *Bull. Math. Biol.*, **60** (1998), 1–26.
- [33] W.-M. Ni, Diffusion, cross-diffusion, and their spike-layer steady states, *Notices Amer. Math. Soc.*, **45** (1998), 9–18.
- [34] W.-M. Ni, [Qualitative properties of solutions to elliptic problems](#), in *Stationary partial differential equations. Vol. I*, Handb. Differ. Equ., North-Holland, Amsterdam, 2004, 157–233.

- [35] K. Painter and T. Hillen, Volume-filling and quorum-sensing in models for chemosensitive movement, *Can. Appl. Math. Q.*, **10** (2002), 501–543.
- [36] K. Painter, P. Maini and H. Othmer, Stripe formation in juvenile pomacanthus explained by a generalized turing mechanism with chemotaxis, *Proc. Natl. Acad. Sci.*, **96** (1999), 5549–5554.
- [37] K. Painter, P. Maini and H. Othmer, A chemotactic model for the advance and retreat of the primitive streak in avian development, *Bull. Math. Biol.*, **62** (2000), 501–525.
- [38] B. Perthame, *Transport Equations in Biology*, Birkhäuser Verlag, Basel, 2007.
- [39] B. Perthame, C. Schmeiser, M. Tang and N. Vauchelet, Traveling plateaus for a hyperbolic keller-segel system with attraction and repulsion-existence and branching instabilities, *Non-linearity*, **24** (2011), 1253–1270.
- [40] G. Petter, H. Byrne, D. Mcelwain and J. Norbury, A model of wound healing and angiogenesis in soft tissue, *Math. Biosci.*, **136** (2003), 35–63.
- [41] P. Rabinowitz, Some global results for nonlinear eigenvalue problems, *J. Functional Analysis*, **7** (1971), 487–513.
- [42] R. Schaaf, Stationary solutions of chemotaxis systems, *Trans. Amer. Math. Soc.*, **292** (1985), 531–556.
- [43] J. Shi, Persistence and bifurcation of degenerate solutions, *J. Funct. Anal.*, **169** (1999), 494–531.
- [44] J. Shi and X. Wang, On global bifurcation for quasilinear elliptic systems on bounded domains, *J. Differential Equations*, **246** (2009), 2788–2812.
- [45] W. Shi and D. Zusman, Sensory adaptation during negative chemotaxis in myxococcus xanthus, *J. Bacteriol.*, **176** (1994), 1517–1520.
- [46] G. Simonett, Center manifolds for quasilinear reaction-diffusion systems, *Differential Integral Equations*, **8** (1995), 753–796.
- [47] T. Suzuki, *Free energy and self-interaction particles*, Birkhäuser, Boston, 2005.
- [48] Y. Tao and Z.-A. Wang, Competing effects of attraction vs. repulsion in chemotaxis, *Math. Models Methods Appl. Sci.*, **23** (2013), 1–36.
- [49] A. Turing, The chemical basis of morphogenesis, *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **237** (1952), 37–72.
- [50] J. Wang, J. Shi and J. Wei, Dynamics and pattern formation in a diffusive predator-prey system with strong Allee effect in prey, *J. Differential Equations*, **251** (2011), 1276–1304.
- [51] X. Wang, Qualitative behavior of solutions of chemotactic diffusion systems: Effects of motility and chemotaxis and dynamics, *SIAM J. Math. Anal.*, **31** (2000), 535–560 (electronic).
- [52] X. Wang and Y. Wu, Qualitative analysis on a chemotactic diffusion model for two species competing for a limited resource, *Quart. Appl. Math.*, **60** (2002), 505–531.
- [53] X. Wang and Q. Xu, Spiky and transition layer steady states of chemotaxis systems via global bifurcation and Helly’s compactness theorem, *J. Mathematical Biology*, **66** (2013), 1241–1266.
- [54] Z.-A. Wang and T. Hillen, Classical solutions and pattern formation for a volume filling chemotaxis model, *Chaos*, **17** (2007), 037108, 13 pp.
- [55] Z.-A. Wang and T. Hillen, Shock formation in a chemotaxis model, *Math. Methods Appl. Sci.*, **31** (2008), 45–70.
- [56] M. J. Ward and J. Wei, Hopf bifurcations and oscillatory instabilities of spike solutions for the one-dimensional Gierer-Meinhardt model, *J. Nonlinear Sci.*, **13** (2003), 209–264.
- [57] R. Welch and D. Kaiser, Cell behavior in traveling wave patterns of myxobacteria, *Proceedings of the National Academy of Sciences*, **98** (2001), 14907–14912.
- [58] F. Yi, J. Wei and J. Shi, Bifurcation and spatiotemporal patterns in a homogeneous diffusive predator-prey system, *J. Differential Equations*, **246** (2009), 1944–1977.

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