

## REACTION, DIFFUSION AND CHEMOTAXIS IN WAVE PROPAGATION

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**ABSTRACT.** By constructing an invariant set in the three dimensional space, we establish the existence of traveling wave solutions to a reaction-diffusion-chemotaxis model describing biological processes such as the bacterial chemotactic movement in response to oxygen and the initiation of angiogenesis. The minimal wave speed is shown to exist and the role of each process of reaction, diffusion and chemotaxis in the wave propagation is investigated. Our results reveal three essential biological implications: (1) the cell growth increases the wave speed; (2) the chemotaxis must be strong enough to make a contribution to the increment of the wave speed; (3) the diffusion rate plays a role in increasing the wave speed only when the cell growth is present.

**1. Introduction.** In this paper, we study the traveling wave solutions to the following reaction-diffusion-chemotaxis model

$$\begin{cases} u_t = [du_x - \chi u(\log s)_x]_x + \mu u(1 - u), \\ s_t = \varepsilon s_{xx} - us \end{cases} \quad (1.1)$$

for  $(x, t) \in \mathbb{R} \times [0, \infty)$ , where  $u(x, t)$  and  $s(x, t)$  denote the cell density and chemical concentration, respectively. The parameter  $\chi > 0$  is called the chemotactic coefficient,  $\mu > 0$  denotes the cell growth rate,  $d$  and  $\varepsilon > 0$  are cell and the chemical diffusion coefficients respectively.

With the logistic cell growth term included, the model (1.1) is a generalization of the well studied Keller-Segel's chemotaxis model [10]

$$\begin{cases} u_t = [du_x - \chi u(\log s)_x]_x, \\ s_t = \varepsilon s_{xx} - us^m, \end{cases} \quad (1.2)$$

which was proposed to interpret the propagation of traveling bands of chemotactic bacteria with a constant speed observed in the celebrated experiment of Adler [1, 2], where  $u(x, t)$  denotes the bacterial density and  $s(x, t)$  the oxygen concentration. The term  $-us^m$  describes the consumption of oxygen (i.e. chemical) by the bacteria with

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a consumption rate parameter  $m \geq 0$ . When  $m < (=, \text{ or } >) 1$ , the consumption rate is called sub-linear (linear or super-linear).

The theoretical study of traveling wave solutions of chemotaxis model (1.2) was started with the Keller-Segel's work [10] where they showed that model (1.2) with  $0 \leq m < 1$  can reproduce the traveling bands (i.e. pulses) whose speeds were in satisfactory agreement with experimental observation of [1, 2]. Subsequently, a flurry of refined works on traveling wave solutions of (1.2) have been carried out, cf. [3, 17, 20, 25, 26, 28, 29, 35] and references therein. When  $m = 1$ , model (1.2) was used by Nossal [22] to describe the chemotactic boundary formation by bacterial population in response to the substrate consisting of nutrients if  $\varepsilon = 0$ , and by Rosen [26, 27] to show the phenomenological theory for the chemotaxis and consumption of oxygen by motile aerobic bacteria if  $\varepsilon > 0$ . Moreover model (1.2) with  $\varepsilon \geq 0$  may be used to describe the directed movement of endothelial cells toward the signaling molecule vascular endothelial growth factor (VEGF) during the initiation of angiogenesis [4, 5, 6, 11, 32], where  $u$  denotes the density of endothelial cells and  $s$  stands for the concentration of VEGF. The existence and stability of traveling wave solutions of the model (1.2) with  $m = 1$  were established in [15, 16, 18, 32, 34], while the initial-boundary value problem and Cauchy problem were studied in [14, 30]. For the study of traveling wave solutions to other chemotaxis models with logarithmic sensitivities, we refer to [3, 9] and references therein. Finally we mention that, when  $m \geq 1$ , the global solutions of (1.2) with other forms of chemotactic sensitivity function were studied in [5, 6, 7, 13, 31] for both bounded and unbounded domains.

The cell kinetics was not considered in all above mentioned studies. However both Keller-Segel [10, Introduction] and Nossal [22, Introduction] mentioned that the cell (i.e. bacterial) growth is a process possibly taking place in the experiment although they didn't consider explicitly this effect in their model analysis. If the model (1.2) were to describe the initiation of angiogenesis as in [6, 32], it is of importance to incorporate the cell growth, since angiogenesis activator promotes the growth of vascular endothelial cells to facilitate the formation of new blood vessels [21] during the initiation of angiogenesis. Hence it would be interesting to inspect the effect of cell growth using mathematical models. In this paper we consider logistic growth which is often used in the context of chemotaxis (e.g. see [19, 23, 24, 33]). Nevertheless other cell kinetic forms are possible in chemotaxis, such as bistable kinetics in [8]. The purpose of this paper is to investigate the existence of traveling wave solutions and the minimal wave speed to the model (1.1), namely the model (1.2) with  $m = 1$  and the addition of logistic cell growth.

The study of traveling wave solutions of (1.1) is generally formidable due to the logarithmic singularity, high dimensionality and failure of maximum principle. The idea in this paper is to employ the Hopf-Cole transformation

$$w = -(\log s)_x = -\frac{s_x}{s} \quad (1.3)$$

and transform the reaction-diffusion-chemotaxis system (1.1) into a new system without singularity

$$\begin{cases} u_t = (du_x + \chi uw)_x + \mu u(1 - u), \\ w_t = \varepsilon w_{xx} - (\varepsilon w^2 - u)_x. \end{cases} \quad (1.4)$$

The transformation (1.3) was first applied in [12] for system (1.2) with  $\varepsilon = 0$  and later was further applied to model (1.2) with  $\varepsilon > 0$  in [16] to study the existence and stability of traveling wave solutions. The transformation (1.3) is apparently

not helpful for the model (1.2) with  $m \neq 1$ . Our plan is to study the traveling wave solutions of transformed system (1.4) first and then transfer the results back to the original system (1.1). It is easily observed that the phase plane analysis can be applied to the traveling wave system of (1.4) without cell growth (i.e.  $\mu = 0$ ). However once the cell growth ( $\mu > 0$ ) is taken into account, the corresponding traveling wave system can only be reduced to three-dimensional and the difficulty of analysis is drastically increased. Luckily we can construct a positively invariant set in the three dimensional phase space to prove the existence of traveling wave solutions for the transformed system (1.4), and then use the comparison arguments to establish the existence of the minimal speed and derive both very good upper and lower bounds for the minimal speed. It is worth mentioning that our approach and arguments in obtaining the lower bound for the minimal speed are new and, we believe, may have broad applicability in a large class of reaction-diffusion systems. Moreover the presence of cell growth makes the dynamics of the model more complicated. There are three processes contained in the model (1.1): reaction, diffusion and chemotaxis. The most significant feature, which will be shown in the paper, is that traveling waves can arise from the interaction of any two of these processes. That is, any single process is not necessary for wave propagation. This is different from the Keller-Segel model (1.2) where both cell diffusion and chemotaxis are essential to support the wave propagation. Hence it is of interest and importance to examine the effect of each process and the integrated effect on the wave propagation. These important (biological) questions will be discussed in the last section of this paper and three essential implications of our results will be presented.

In this paper, we shall consider  $u(x, t) \geq 0, s(x, t) \geq 0$  only since they denote densities of biological species. Because the model (1.1) describes the directed movement of cells toward the chemical which is degraded by cells when they encounter, the wave propagation can be regarded as an “invasive” pattern. That is, the wave profile  $u$  decreases from its tail to front and  $s$  increases from its tail to the front, which means  $u_x < 0$  and  $s_x > 0$  if we suppose the traveling waves propagate from the left to the right. By transformation (1.3), we have  $w \leq 0$ . Hence, the biologically meaningful traveling wave solutions of (1.4) satisfy  $u \geq 0, u_x < 0, w \leq 0$ .

To state the results for the system (1.1), we first state the existence theorem of traveling wave solutions to the transformed system (1.4) as follows.

**Theorem 1.1.** *For any given  $d > 0, \chi > 0, \varepsilon > 0$  and  $\mu > 0$ , there exists the minimal speed  $c_* = c_*(d, \chi, \varepsilon, \mu) > 0$  such that*

- (i) *the system (1.4) has a traveling wave solution  $(u(x, t), w(x, t)) = (u_c(\xi), w_c(\xi))$ ,  $\xi := x - ct$ , that satisfies*

$$\begin{cases} 0 < u_c(\xi), & u'_c(\xi) < 0, & w_c(\xi) < 0, & \forall \xi \in (-\infty, \infty), \\ (u_c(-\infty), w_c(-\infty)) = \left(1, -\frac{2}{c + \sqrt{c^2 + 4\varepsilon}}\right), & (u_c(\infty), w_c(\infty)) = (0, 0) \end{cases} \quad (1.5)$$

*if and only if  $c \geq c_*$ . Moreover,  $w'_c(\xi) > 0$  for  $\xi \in (-\infty, \infty)$  and the traveling wave solution is unique (up to a translation in  $\xi$ );*

- (ii) *furthermore, the following estimates for  $c_*$  hold:*

$$\bar{c}_* \leq c_*(d, \chi, \varepsilon, \mu) \leq 2\sqrt{d\mu} + \frac{\chi}{\sqrt{d\mu} + \sqrt{d\mu} + \varepsilon + \chi}, \quad (1.6)$$

where

$$\bar{c}_* = 2\sqrt{d\mu} > \frac{\chi}{\sqrt{\chi + \varepsilon}} \quad \text{if } \chi \leq d\mu + \sqrt{d\mu(d\mu + \varepsilon)} \quad (1.7)$$

and

$$\bar{c}_* = \frac{\chi^2 + d\varepsilon\mu}{\sqrt{\chi(\chi + \varepsilon)(\chi - d\mu)}} > \max \left\{ 2\sqrt{d\mu}, \frac{\chi}{\sqrt{\chi + \varepsilon}} \right\} \quad \text{if } \chi > d\mu + \sqrt{d\mu(d\mu + \varepsilon)}. \quad (1.8)$$

Since the cell density  $u$  in the original model (1.1) remains the same as the one in the transformed model (1.4), we transform the results in Theorem 1.1 to  $s$  from  $w$  and obtain the following theorem for (1.1).

**Theorem 1.2.** *Let  $c_*$  be given in Theorem 1.1. For any given  $c \geq c_*$  and  $s^+ > 0$ , let  $(u_c, w_c)$  be the traveling wave solution given in Theorem 1.1 and let*

$$s_c(\xi) = s^+ \cdot \exp \left( \int_{\xi}^{\infty} w_c(u) du \right), \quad \xi = x - ct.$$

Then  $(u(x, t), s(x, t)) = (u_c(\xi), s_c(\xi))$  is the unique (up to a translation) traveling wave solution of the system (1.1) satisfying

$$\begin{cases} u'_c(\xi) < 0, & s'_c(\xi) > 0 & \forall \xi \in (-\infty, \infty), \\ (u_c(-\infty), s_c(-\infty)) = (1, 0), & (u_c(\infty), s_c(\infty)) = (0, s^+). \end{cases} \quad (1.9)$$

**Remark 1.** From (1.6) - (1.8) we see  $c_* \rightarrow 2\sqrt{d\mu}$  as  $\chi \rightarrow 0$  and  $c_* \rightarrow \chi/\sqrt{\chi + \varepsilon}$  as  $d \rightarrow 0$  or  $\mu \rightarrow 0$ . We shall give the corresponding results for these limiting cases in Section 6.

**Remark 2.** In a previous paper [32], the existence of traveling wave solutions to the chemotaxis model (1.1) without cell growth, namely  $\mu = 0$ , was established and the unique wave speed was found to be  $c = \chi/\sqrt{\chi + \varepsilon}$ . When the cell growth is incorporated into the model, Theorem 1.1 shows that the wave speed is no longer unique; instead, all the wave speeds form the interval  $[c_*, \infty)$ . The estimates in (1.6) and (1.8) imply that the cell growth in the model (1.1) increases the wave speed, with  $c_* \searrow \chi/\sqrt{\chi + \varepsilon}$  as  $\mu \searrow 0$ . This implies that, all traveling wave solutions, except the one with the minimum wave speed, disappear as  $\mu \searrow 0$ . In other words, there undergoes a bifurcation of infinitely many traveling waves when cell growth is present.

The outline of the paper is as follows. For simplicity, in the beginning of Section 2, we use suitable scalings to change the system (1.4) into the system (2.2) with the diffusion coefficient  $d = 1$ , and then prove the existence of traveling wave solutions of (2.2) for every  $c > 2\sqrt{\mu} + \frac{\chi}{\sqrt{\mu} + \sqrt{\mu + \varepsilon} + \chi}$  in the rest of Section 2. We prove the existence of the minimal speed  $c_0$  for the system (2.2) in Section 3. We then establish an estimate of the lower bound  $\bar{c}$  for  $c_0$  in Section 4. We finally complete the proofs of Theorems 1.1 and 1.2 in Section 5. In Section 6, we discuss the traveling waves for three limiting cases of (1.1), namely,  $d = 0$ ,  $\chi = 0$  and  $\mu = 0$ , respectively. In the last Section 7, we briefly summarize our main results and discuss the effect of reaction, diffusion and chemotaxis on the wave propagation and biological implications of our results. We remark that, with little difficulty, the results of the paper can be extended to the system (1.1) with a general mono-stable growth function for cells.

**2. Existence of traveling wave solutions.** To investigate the existence of traveling wave solutions of the transformed system (1.4), let us first reduce  $d = 1$  in (1.4) by the scalings

$$\tilde{\chi} = \chi/d, \quad \tilde{\varepsilon} = \varepsilon/d, \quad \tilde{u}(x, t) = u(\sqrt{d}x, t), \quad \tilde{w}(x, t) = \sqrt{d}w(\sqrt{d}x, t), \quad (2.1)$$

so that  $\tilde{u}_x(x, t) = \sqrt{d}u_x(\sqrt{d}x, t)$ ,  $\tilde{u}_{xx}(x, t) = du_{xx}(\sqrt{d}x, t)$ ,  $\tilde{w}_x(x, t) = dw_x(\sqrt{d}x, t)$ ,  $\tilde{w}_{xx}(x, t) = d\sqrt{d}w_{xx}(\sqrt{d}x, t)$ , and (1.4) is then transformed to

$$\begin{aligned} \tilde{u}_t &= (\tilde{u}_x + \tilde{\chi}\tilde{u}\tilde{w})_x + \mu\tilde{u}(1 - \tilde{u}), \\ \tilde{w}_t &= \tilde{\varepsilon}\tilde{w}_{xx} - (\tilde{\varepsilon}\tilde{w}^2 - \tilde{u})_x. \end{aligned} \quad (2.2)$$

For the transformed system (2.2), biologically interesting traveling wave solutions are of the form  $\tilde{u}(x, t) := \tilde{U}(\xi)$ ,  $\tilde{w}(x, t) := \tilde{W}(\xi)$ ,  $\xi = x - ct$ , with the properties  $0 < \tilde{U} < 1$ ,  $\tilde{U}(-\infty) = 1$ ,  $\tilde{U}(\infty) = 0$ ,  $\tilde{W} < 0$ ,  $\tilde{W}(\infty) = 0$ , where  $c > 0$  is the wave speed. For notational convenience, we denote  $\tilde{U}$  and  $\tilde{W}$  by the lower cases  $u$  and  $w$ , and still use  $\chi$  and  $\varepsilon$  for  $\tilde{\chi}$  and  $\tilde{\varepsilon}$  respectively. Then  $(u, w)$  satisfies the coupled ODEs

$$\begin{cases} -cu' = (u' + \chi uw)' + \mu u(1 - u), \\ -cw' = \varepsilon w'' - (\varepsilon w^2 - u)'. \end{cases}$$

Integrating the second equation and using  $u(\infty) = w(\infty) = 0$  yields  $-cw = \varepsilon w' - \varepsilon w^2 + u$ . By introducing a new variable  $v := u' + \chi uw + cu$ , the resulting variables  $(u, v, w)$  satisfy the first order system of ODEs

$$\begin{cases} u' = v - \chi uw - cu, \\ v' = -f(u) := -\mu u(1 - u), \\ w' = w^2 - \frac{c}{\varepsilon}w - \frac{1}{\varepsilon}u. \end{cases} \quad (2.3)$$

A simple algebra yields that (2.3) has two equilibria  $(0, 0, 0)$  and  $(1, v_c^*, w_c^*)$  in the half space  $w \leq 0$ , where

$$w_c^* = \frac{-2}{c + \sqrt{c^2 + 4\varepsilon}} < 0, \quad v_c^* = \chi w_c^* + c. \quad (2.4)$$

Since  $0 < u(\xi) < 1$  for the interested waves, the second equation of (2.3) implies that  $v'(\xi) < 0$  so that  $0 < v(\xi) < v_c^*$  for  $\xi \in (-\infty, \infty)$ . Using the formula for  $v_c^*$  in (2.4) we deduce that

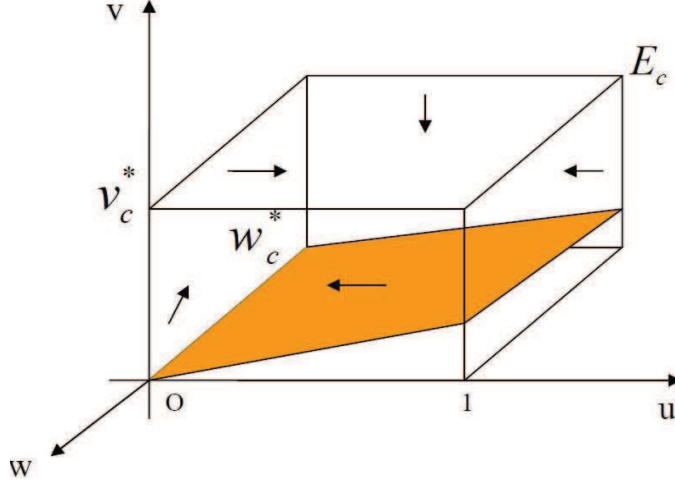
$$v_c^* > 0 \iff c > \frac{\chi}{\sqrt{\varepsilon + \chi}}. \quad (2.5)$$

Therefore, if  $(u, w)$  is a traveling wave solution of (2.2) with the speed  $c$ , then it is necessary that  $c > \chi/\sqrt{\varepsilon + \chi}$  and that  $(u, v, w)$  is a heteroclinic solution of (2.3) satisfying the conditions

$$\begin{cases} 0 < u(\xi) < 1, \quad 0 < v(\xi) < v_c^*, \quad w(\xi) < 0 \quad \forall \xi \in (-\infty, \infty), \\ (u, v, w)(-\infty) = E_c := (1, v_c^*, w_c^*), \quad (u, v, w)(\infty) = O := (0, 0, 0). \end{cases} \quad (2.6)$$

In this section we shall establish the following theorem which provides a sufficient condition on  $c$  for the existence of heteroclinic solutions of (2.3) satisfying the conditions (2.6).

**Theorem 2.1.** *Let  $c > 2\sqrt{\mu} + \frac{\chi}{\sqrt{\mu + \sqrt{\mu + \varepsilon + \chi}}}$ . Then there is a unique (up to a translation) heteroclinic solution  $(u_c, v_c, w_c)$  of (2.3) and (2.6). Furthermore,  $u'_c < 0$ ,  $v'_c < 0$  and  $w'_c > 0$  on  $(-\infty, \infty)$ .*

FIGURE 1. Sketch of the closed box  $\mathcal{B}_c$ .

The proof of Theorem 2.1 is based on the construction of a subset  $\mathcal{B}_1$  of  $\mathcal{B}_c$  (see Fig. 1) that is positively invariant to the flows of (2.3). The set  $\mathcal{B}_1$  has the properties: (i) the 1-dimensional unstable manifold  $W^u(E_c)$  of (2.3) at  $E_c$  is tangent to an eigenvector pointing to the interior of  $\mathcal{B}_1$ ; (ii) each component of the solutions  $(u, v, w)$  of (2.3) starting from  $W^u(E_c)$  lying in  $\mathcal{B}_1$  is monotone. We shall prove these facts and then Theorem 2.1 via the following three lemmas.

For a fixed  $c > \chi/\sqrt{\chi + \varepsilon}$ , let us begin by defining a closed box in the  $uvw$  phase space  $\mathbb{R}^3$  (see Fig. 1)

$$\mathcal{B}_c := \{(u, v, w) : 0 \leq u \leq 1, 0 \leq v \leq v_c^*, w_c^* \leq w \leq 0\}.$$

**Lemma 2.2.** *Let  $c > \chi/\sqrt{\chi + \varepsilon}$ . Then the following hold.*

- (i) *The locally unstable manifold  $W^u(E_c)$  of (2.3) is 1-dimensional and tangent to the eigenvector  $\mathcal{V}$  of the Jacobian matrix of (2.3) at  $E_c$  associated with its unique positive eigenvalue  $\lambda_+$ , where  $\mathcal{V}$  is given by*

$$\mathcal{V} := \left(-1, -\frac{\mu}{\lambda_+}, \frac{1}{\varepsilon(\lambda_+ + \varepsilon/c - 2w_c^*)}\right)^\top, \quad (2.7)$$

*which points to the interior of  $\mathcal{B}_c$ .*

- (ii) *The equilibrium  $O$  is a stable node (including the degenerated stable node) of (2.3) if  $c \geq 2\sqrt{\mu}$ , and stable focus if  $c < 2\sqrt{\mu}$ . In particular, (2.3) has not heteroclinic orbit satisfying the limit condition 2.6 if  $c < 2\sqrt{\mu}$ .*

*Proof.* The Jacobian matrices of (2.3) at  $O$  and  $E_c$  are, respectively,

$$J_0 = \begin{pmatrix} -c & 1 & 0 \\ -\mu & 0 & 0 \\ -\frac{1}{\varepsilon} & 0 & -\frac{c}{\varepsilon} \end{pmatrix}, \quad J_c = \begin{pmatrix} -v_c^* & 1 & -\chi \\ \mu & 0 & 0 \\ -\frac{1}{\varepsilon} & 0 & 2w_c^* - \frac{c}{\varepsilon} \end{pmatrix}.$$

The eigenvalues of  $J_0$  are

$$\lambda_1 = \frac{1}{2}(-c + \sqrt{c^2 - 4\mu}), \quad \lambda_2 = \frac{1}{2}(-c - \sqrt{c^2 - 4\mu}), \quad \lambda_0 = -\frac{c}{\varepsilon} \quad (2.8)$$

with associated eigenvectors (using  $\lambda_1\lambda_2 = \mu$ )

$$\begin{pmatrix} 1 \\ \mu/|\lambda_1| \\ -1/(\varepsilon\lambda_1 + c) \end{pmatrix}, \quad \begin{pmatrix} 1 \\ \mu/|\lambda_2| \\ -1/(\varepsilon\lambda_2 + c) \end{pmatrix}, \quad \begin{pmatrix} 0 \\ 0 \\ -1 \end{pmatrix}. \quad (2.9)$$

The characteristic equation of  $J_c$  is

$$\begin{aligned} P(\lambda) &:= \left(\lambda + \frac{c}{\varepsilon} - 2w_c^*\right)(\lambda^2 + v_c^*\lambda - \mu) - \frac{\chi}{\varepsilon}\lambda \\ &= \lambda^3 + \left(\frac{c}{\varepsilon} - 2w_c^* + v_c^*\right)\lambda^2 + \left[v_c^*\left(\frac{c}{\varepsilon} - 2w_c^*\right) - \mu - \frac{\chi}{\varepsilon}\right]\lambda + \mu\left(2w_c^* - \frac{c}{\varepsilon}\right) = 0. \end{aligned} \quad (2.10)$$

Since  $P(2w_c^* - c/\varepsilon) = \chi(c/\varepsilon - 2w_c^*)/\varepsilon > 0$  and  $P(0) = \mu(2w_c^* - c/\varepsilon) < 0$  by virtue of  $w_c^* < 0$ , and the coefficient of  $\lambda^3$  in  $P(\lambda)$  is positive, we conclude that  $P(\lambda) = 0$  has a unique positive root  $\lambda_+$  and two negative roots. A direct verification shows that  $\mathcal{V}$  defined in (2.7) is an eigenvector of  $J_c$  associated with  $\lambda_+$ . It follows from the signs of its components that  $\mathcal{V}$  points to the interior of  $\mathcal{B}_c$ . Applying the unstable manifold theorem yields the conclusions of Lemma 2.2 (i). Part (ii) of Lemma 2.2 follows easily from the expresses (2.8) and (2.9). In particular, if  $c < 2\sqrt{\mu}$ , then the eigenvalues  $\lambda_1$  and  $\lambda_2$  are complex while the eigenvalue  $\lambda_0$  corresponds to the invariant line  $\{u = v = 0\}$  of the system (2.3). This implies that any solution of (2.3) that converges to the origin  $O$  but does not stay in the line  $\{u = v = 0\}$  must be oscillatory around the origin  $O$ .  $\square$

**Lemma 2.3.** *Let  $c > \chi/\sqrt{\chi + \varepsilon}$ . Then the following hold.*

- (i) *Any solution of (2.3) starting at a point in  $\mathcal{B}_c$  can only exit  $\mathcal{B}_c$  from its bottom face  $v = 0$ .*
- (ii) *If  $c > 2\sqrt{\mu} + \frac{\chi}{\sqrt{\mu} + \sqrt{\mu + \varepsilon + \chi}}$ , then  $v_c^* > 2\sqrt{\mu}$  and the subset  $\mathcal{B}_1$  of  $\mathcal{B}_c$  defined by*

$$\mathcal{B}_1 := \{(u, v, w) \in \mathcal{B}_c : v \geq ku\}, \quad k := \frac{1}{2} \left( v_c^* + \sqrt{(v_c^*)^2 - 4\mu} \right),$$

*i.e., the subset of  $\mathcal{B}_c$  lying above the shaded region in Fig. 1, is a positively invariant set of (2.3).*

*Proof.* To show (i), it suffices to check the vector field of (2.3) on the surfaces of  $\mathcal{B}_c$ . Let  $(u, v, w) \in \partial\mathcal{B}_c$ .

On the face  $u = 0$ ,  $u' = v > 0$  if  $v > 0$ ; its edge  $v = 0$  lies on the  $w$ -axis which is an invariant set of (2.3) with  $w' = w^2 - \frac{c}{\varepsilon}w > 0$  for  $w < 0$ .

On the face  $u = 1$ ,  $u' = v - \chi w - c = v - \chi w - v_c^* + \chi w_c^* = (v - v_c^*) - \chi(w - w_c^*) < 0$  except at the equilibrium point  $E_c$ .

On the face  $v = v_c^*$ ,  $v' = -f(u) < 0$  if  $u \in (0, 1)$ ; on its edge  $u = 0$ ,  $v' = 0$  and  $v'' = -f'(0)u' = -f'(0) < 0$ ; on its edge  $u = 1$ ,  $v' = 0$  and  $v'' = f'(1)\chi(w - w_c^*) < 0$  except at  $E_c$ .

On the face  $v = 0$ ,  $v' = -f(u) < 0$  if  $u \in (0, 1)$ ; on its edge  $u = 1$ ,  $v' = 0$  and  $v'' = -f'(1)u' = -f'(1)[- \chi(w - w_c^*) + v - v_c^*] < 0$ .

On the face  $w = 0$ ,  $w' = -u/\varepsilon < 0$  if  $u \in (0, 1]$ ; on its edge  $u = 0$ ,  $w' = 0$  and  $w'' = -v/\varepsilon > 0$  except at  $O$ .

On the face  $w = w_c^*$ ,  $w' = (w_c^*)^2 - cw_c^*/\varepsilon - u/\varepsilon = (1 - u)/\varepsilon > 0$  if  $u \in [0, 1)$ ; on its edge  $u = 1$ ,  $w' = 0$  and  $w'' = -(v - v_c^*)/\varepsilon > 0$  except at  $E_c$ .

The above vector field analysis establishes (i).

To show (ii), first we have

$$\begin{aligned}
v_c^* = \chi w_c^* + c > 2\sqrt{\mu} &\iff \frac{-2\chi}{c + \sqrt{c^2 + 4\varepsilon}} + c > 2\sqrt{\mu} \\
&\iff (c - 2\sqrt{\mu})\sqrt{c^2 + 4\varepsilon} > 2\chi - c(c - 2\sqrt{\mu}) \\
&\iff \varepsilon(c - 2\sqrt{\mu})^2 > \chi^2 - \chi(c - 2\sqrt{\mu})^2 - 2\chi\sqrt{\mu}(c - 2\sqrt{\mu}) \\
&\iff (\varepsilon + \chi)(c - 2\sqrt{\mu})^2 + 2\chi\sqrt{\mu}(c - 2\sqrt{\mu}) - \chi^2 > 0 \\
&\iff c > 2\sqrt{\mu} + \frac{\chi}{\sqrt{\mu} + \sqrt{\mu + \varepsilon + \chi}}.
\end{aligned}$$

It remains to check the vector field of (2.3) at every point  $(u, v, w)$  on the bottom face  $v = ku$  of  $\mathcal{B}_1$ . At such a point, noting that the outer normal vector of the plane is  $n = (k, -1, 0)^\top$ , and  $u' \leq v - \chi w_c^* u - cu = [k - v_c^*]u$ , we have for  $u > 0$  (using  $k^2 - kv_c^* + \mu = 0$ )

$$n \cdot (u', v', w')^\top = ku' - v' \leq [k^2 - kv_c^* + \mu(1 - u)]u = -\mu u^2 < 0,$$

while its edge with  $u = 0$  lies on the invariant set of (2.3). This yields (ii).  $\square$

**Lemma 2.4.** *Let  $c > \chi/\sqrt{\chi + \varepsilon}$  and  $\varphi_c(\xi) := (u_c(\xi), v_c(\xi), w_c(\xi))$  be a solution of (2.3) lying in  $W^u(E_c) \cap \text{Int}(\mathcal{B}_c)$  for all sufficiently negative  $\xi$ . Let*

$$T := \sup\{\tilde{\xi} \in \mathbb{R} : \varphi_c(\xi) \in \mathcal{B}_c, \forall \xi \in (-\infty, \tilde{\xi}]\}.$$

Then the following hold.

- (i)  $u'_c(\xi) < 0$ ,  $v'_c(\xi) < 0$ ,  $w'_c(\xi) > 0$ , and  $\varphi_c(\xi) \in \text{Int}(\mathcal{B}_c)$  for all  $\xi \in (-\infty, T)$ .
- (ii) If  $T = \infty$ , then  $\varphi_c(\infty) = O$ . That is,  $\varphi_c$  is a heteroclinic solution of (2.3) and (2.6). If  $T < \infty$ , then  $u_c(T) > 0$ ,  $v_c(T) = 0$ , and  $w_c(T) < 0$ .

*Proof.* Since the eigenvector  $\mathcal{V}$  points into the interior of  $\mathcal{B}_c$  and  $\varphi_c(\xi)$  is tangent to  $\mathcal{V}$  as  $\xi \rightarrow -\infty$ , we deduce that for sufficiently negative  $\xi$ ,  $\varphi_c(\xi) \in \text{Int}(\mathcal{B}_c)$  and  $u'_c(\xi) < 0$ ,  $v'_c(\xi) < 0$ , and  $w'_c(\xi) > 0$ .

**Claim A.**  $u'_c(\xi) < 0$ ,  $v'_c(\xi) < 0$ , and  $w'_c(\xi) > 0$  for all  $\xi \in (-\infty, T)$  as well as for  $\xi = T$  if  $T < \infty$ .

From (2.3) we have  $u_c'' + cu_c' = -f(u_c) - \chi u_c' w_c - \chi u_c w_c'$ , and a differentiation of the third equation of (2.3) gives  $w_c'' - p(\xi)w_c' = -u_c'/\varepsilon$  where  $p(\xi) := 2w_c(\xi) - c/\varepsilon$ . Take  $\xi_0$  to be sufficiently negative such that  $u_c'(\xi) < 0$  and  $w_c'(\xi) > 0$  for  $\xi \in (-\infty, \xi_0]$ . Applying the variation of constants formula yields, for every  $\xi \in [\xi_0, T)$  or  $\xi = T$  if  $T < \infty$ ,

$$\begin{aligned}
u'_c(\xi) &= e^{-c(\xi - \xi_0)} u'_c(\xi_0) - \int_{\xi_0}^{\xi} e^{-c(\xi - s)} [f(u_c(s)) + \chi u'_c(s) w_c(s) + \chi u_c(s) w'_c(s)] ds, \\
w'_c(\xi) &= e^{\int_{\xi_0}^{\xi} p(s) ds} w'_c(\xi_0) - \frac{1}{\varepsilon} \int_{\xi_0}^{\xi} e^{\int_s^{\xi} p(\eta) d\eta} u'_c(s) ds.
\end{aligned} \tag{2.11}$$

Let  $T_1 = \{\tilde{\xi} \in [\xi_0, T) : u'_c(\xi) < 0, w'_c(\xi) > 0, \forall \xi \in (-\infty, \tilde{\xi}]\}$ . Then we have,  $f(u_c) + \chi u'_c w_c + \chi u_c w'_c \geq 0$  on  $[\xi_0, T_1)$  and  $f(u_c) + \chi u'_c w_c + \chi u_c w'_c > 0$  at  $\xi_0$ . It follows from (2.11) and the continuity of  $f(u_c) + \chi u'_c w_c + \chi u_c w'_c$  that if  $T_1 < T$ , then  $T_1 < \infty$ ,  $u'_c(T_1) < 0$  and  $w'_c(T_1) > 0$ , contradicting the definition of  $T_1$ . Thus,  $T_1 = T$  so that  $u'_c(\xi) < 0$ ,  $w'_c(\xi) > 0$  for  $\xi \in (-\infty, T)$  and for  $\xi = T$  if  $T < \infty$ .

Since  $0 \leq u_c(\xi) < 1$  and  $u'_c(\xi) < 0$  for  $\xi \in (-\infty, T)$  and for  $\xi = T$  if  $T < \infty$ , it follows that  $0 < u_c(\xi) < 1$  for  $\xi \in (-\infty, \infty)$  if  $T = \infty$ , or  $u_c(T) > 0$  if  $T < \infty$  (since



from Lemma 2.3 (i)  $\varphi_c$  cannot exit  $\mathcal{B}_c$  from the face  $u = 0$ ) so that  $0 < u_c(\xi) < 1$  for  $\xi \in (-\infty, T]$ . Thus, from the second equation in (2.3) we get  $v'_c = -f(u_c) < 0$  for all  $\xi \in (-\infty, T)$  and for  $\xi = T$  if  $T < \infty$ . This shows Claim A.

Since  $\varphi_c \in \mathcal{B}_c$  on  $(-\infty, T)$  and the strict monotonicity of the components of  $\varphi_c$  from Claim A, we conclude that  $\varphi_c(\xi) \in \text{Int}(\mathcal{B}_c)$  for all  $\xi \in (-\infty, T)$ . If  $T = \infty$ , then clearly  $\varphi_c(\infty)$  exists with  $\varphi_c(\infty) \in \mathcal{B}_c$ . Since  $\varphi_c(\infty)$  has to be an equilibrium point of (2.3) (from the theory of dynamical systems) lying in  $\mathcal{B}_c$ , it follows that  $\varphi_c(\infty) = O$ . If  $T < \infty$ , then Lemma 2.3 (i) and the signs of  $u'_c(T)$ ,  $v'_c(T)$ , and  $w'_c(T)$  give that  $u_c(T) > 0$ ,  $v_c(T) = O$ , and  $w_c(T) < 0$ . The lemma is thus proved.  $\square$

*Proof of Theorem 2.1.* It follows from Lemma 2.3 (ii) that  $\varphi_c(\xi) \in \mathcal{B}_1 \subset \mathcal{B}_c$  for all  $\xi \in (-\infty, \infty)$ . Then by applying Lemma 2.4 (ii) we conclude that  $\varphi_c$  is a heteroclinic solution of (2.3) and (2.6) with the claimed monotone property. Since  $W^u(E_c)$  is 1-dimensional, it follows that  $\varphi_c$  is unique (up to a translation). Theorem 2.1 is thus proved.  $\square$

**3. Minimal wave speed.** Wave speed is always important in applications, since it may describe, for example, how fast the disease is transmitted in epidemiology or cancer cells spread in tissue in cancer biology. Therefore determining the range of wave speeds (i.e, determining the minimum wave speed) is an essential ingredient in the study of traveling wave solutions for many biological and physical models. In this section, we establish the existence of minimal speed  $c_0 > 0$  and show that  $\varphi_c$  is a heteroclinic solution of (2.3) and (2.6) if and only if  $c \geq c_0$ .

**Lemma 3.1.** *Let  $c_0 \geq 2\sqrt{\mu}$  and  $c_0 > \chi/\sqrt{\chi + \varepsilon}$ . If  $\varphi_{c_0}$  is a heteroclinic solution of (2.3) and (2.6) with  $c = c_0$ , then for every  $c > c_0$ ,  $\varphi_c$  is a heteroclinic solution of (2.3) and (2.6), where  $\varphi_c$  is the solution defined in Lemma 2.4 for  $c > \chi/\sqrt{\chi + \varepsilon}$  and  $c \geq 2\sqrt{\mu}$ .*

*Proof.* Fix an arbitrary  $c > c_0$ . To prove that  $\varphi_c$  is a heteroclinic solution of (2.3) and (2.6), it suffices to show from Lemma 2.4 that  $T = \infty$ .

Assume on the contrary that  $T < \infty$ . Lemma 2.4 gives that  $u'_c < 0$ ,  $v'_c < 0$ ,  $w'_c > 0$ , and  $0 < u_c < 1$  on  $(-\infty, T]$ , and  $\varphi_c(\xi) \in \text{Int}(\mathcal{B}_c)$  for  $\xi \in (-\infty, T)$  and  $v_c(T) = 0$ . This implies that  $u = u_c(\xi)$  is strictly decreasing over  $(-\infty, T]$  with the range  $[\gamma, 1)$  where  $\gamma = u_c(T) > 0$ . We now use  $u$  as the independent variable and define  $V_c(u) := v_c(u_c^{-1}(u))$  and  $W_c(u) := w_c(u_c^{-1}(u))$  for  $u \in [\gamma, 1)$ , which satisfy, for  $u \in [\gamma, 1)$ ,

$$\begin{aligned} \frac{dV_c}{du} &= F_1(u, V_c, W_c, c) := -\frac{f(u)}{V_c - \chi u W_c - cu}, \\ \frac{dW_c}{du} &= F_2(u, V_c, W_c, c) := \frac{W_c^2 - \frac{c}{\varepsilon} W_c - \frac{1}{\varepsilon} u}{V_c - \chi u W_c - cu}, \\ V_c - \chi u W_c - cu &< 0, \quad W_c^2 - \frac{c}{\varepsilon} W_c - \frac{1}{\varepsilon} u > 0, \\ (V_c(1), W_c(1)) &:= \lim_{u \rightarrow 1^-} (V_c(u), W_c(u)) = (v_c^*, w_c^*). \end{aligned} \tag{3.1}$$

Similarly, we define  $V_0(u) := v_{c_0}(u_{c_0}^{-1}(u))$  and  $W_0(u) := w_{c_0}(u_{c_0}^{-1}(u))$  for  $u \in (0, 1)$ , which solve (3.1) for  $u \in (0, 1)$ , with  $V_c$ ,  $W_c$ ,  $c$ , and  $(v_c^*, w_c^*)$  being replaced by  $V_0$ ,  $W_0$ ,  $c_0$ , and  $(v_{c_0}^*, w_{c_0}^*)$ , respectively.

We claim that

$$V_0(u) < V_c(u), \quad W_0(u) < W_c(u) \quad \forall u \in [\gamma, 1]. \quad (3.2)$$

First, since  $v_c^*$  and  $w_c^*$  are increasing functions of  $c \in (\chi/\sqrt{\chi + \varepsilon}, \infty)$ , it follows that (3.2) holds for  $u$  sufficiently close to 1. Suppose by contradiction that the claim is false. Then there exists  $u_1 \in [\gamma, 1)$  such that either

$$W_0(u_1) = W_c(u_1), \quad W'_0(u_1) \leq W'_c(u_1), \quad (3.3)$$

or

$$V_0(u_1) = V_c(u_1), \quad V'_0(u_1) \leq V'_c(u_1). \quad (3.4)$$

**Case 1.** Assume that (3.3) holds and let  $W := W_0(u_1) = W_c(u_1)$ . Write  $\frac{A_c}{B_c} := F_2(u_1, V_c, W, c)$  and  $\frac{A_0}{B_0} := F_2(u_1, V_0, W, c_0)$ . We have

$$\begin{aligned} \frac{dW_c}{du}(u_1) - \frac{dW_0}{du}(u_1) &= \frac{A_c}{B_c} - \frac{A_0}{B_0} = \frac{A_c(B_0 - B_c)}{B_c B_0} + \frac{A_c - A_0}{B_0} \\ &= \frac{-A_c}{B_c B_0} [(V_c - V_0) - (c - c_0)u] - \frac{W}{\varepsilon B_0} (c - c_0). \end{aligned} \quad (3.5)$$

Since  $W < 0$ ,  $B_0 < 0$ , and  $c - c_0 > 0$ , the second term of (3.5) is less than zero. We want to show the first term is also negative. For this purpose we claim that

$$(V_c - V_0) - (c - c_0)u > 0 \text{ for all } u \in [u_1, 1]. \quad (3.6)$$

Note that  $V_c(1) - V_0(1) = v_c^* - v_{c_0}^* = c - c_0 + \chi(w_c^* - w_{c_0}^*) > c - c_0$ , it follows that (3.6) holds for all  $1 - u > 0$  sufficiently small. Assume by contradiction that  $u_0$  is the largest number in  $[u_1, 1)$  such that  $(V_c - V_0) - (c - c_0)u = 0$  at  $u = u_0$ . Since  $W_c(u_0) \geq W_0(u_0)$ , it follows that  $\chi u W_c - V_c + cu \geq \chi u W_{c_0} - V_{c_0} + c_0 u$  at  $u = u_0$ . Then using  $\chi u W_{c_0} - V_{c_0} + c_0 u > 0$  at  $u = u_0$  and the equations for  $V_c$  and  $V_0$  in (3.1), we derive  $\frac{dV_c}{du} \leq \frac{dV_0}{du}$  at  $u = u_0$ , and thus  $\frac{d}{du} [(V_c - V_0) - (c - c_0)u] \leq -(c - c_0) < 0$  at  $u = u_0$ , which contradicts the definition of  $u_0$ . Therefore, (3.6) holds.

Since  $A_c > 0$ ,  $B_c < 0$  and  $B_0 < 0$ , it follows from (3.6) that the first term of (3.5) is also less than zero. Therefore,  $\frac{dW_c}{du}(u_1) - \frac{dW_0}{du}(u_1) < 0$ . However, this contradicts the second inequality in (3.3). Whence we conclude that (3.3) cannot hold.

**Case 2.** Assume that (3.4) holds and let  $V := V_c(u_1) = V_0(u_1)$ . Write  $\tilde{B}_c := V - \chi u_1 W_c(u_1) - c u_1$  and  $\tilde{B}_0 := V - \chi u_1 W_0(u_1) - c_0 u_1$ . We have, at  $u = u_1$ ,

$$\frac{dV_c}{du} - \frac{dV_0}{du} = \frac{f(u_1)}{\tilde{B}_c \tilde{B}_0} (\tilde{B}_c - \tilde{B}_0) = -\frac{f(u_1)u_1}{\tilde{B}_c \tilde{B}_0} [\chi(W_c - W_0) + (c - c_0)].$$

Since  $\tilde{B}_c < 0$ ,  $\tilde{B}_0 < 0$ ,  $W_c(u_1) - W_0(u_1) > 0$  and  $(c - c_0) > 0$ , it follows that  $\frac{dV_c}{du}(u_1) - \frac{dV_0}{du}(u_1) < 0$ , which contradicts the second inequality in (3.4). This shows that (3.4) cannot hold.

Combining the above two cases we conclude that (3.2) holds for all  $u \in [\gamma, 1)$ . In particular, this implies that  $V_c(\gamma) > V_0(\gamma) > 0$  so that  $v_c(T) = V_c(\gamma) > 0$ . However, this contradicts the assertion that  $v_c(T) = 0$  stated at the beginning of the proof. This contradiction yields that  $T = \infty$ , and thus Lemma 3.1 is proved.  $\square$

**Lemma 3.2.** *Let  $\varphi_c$  be the solution defined in Lemma 2.4 for  $c > \chi/\sqrt{\chi + \varepsilon}$  and  $c \geq 2\sqrt{\mu}$ . Let*

$$c_0 = \inf \left\{ c > \max \left\{ \frac{\chi}{\sqrt{\chi + \varepsilon}}, 2\sqrt{\mu} \right\} : \varphi_c \text{ is a heteroclinic solution of (2.3) and (2.6) with } u_c(0) = 1/2 \right\}.$$

If  $c_0 > \chi/\sqrt{\chi + \varepsilon}$ , then  $\varphi_{c_0}$  is a heteroclinic solution of (2.3) and (2.6) with  $\varphi_{c_0}(\xi) \in \text{Int}(\mathcal{B}_c)$ ,  $u'_{c_0}(\xi) < 0$ ,  $v'_{c_0}(\xi) < 0$  and  $w'_{c_0}(\xi) > 0$  for  $\xi \in (-\infty, \infty)$ .

*Proof.* First, it follows from Theorem 2.1 that  $c_0$  is well defined and  $c_0 \geq \chi/\sqrt{\chi + \varepsilon}$ . Now assume that  $c_0 > \chi/\sqrt{\chi + \varepsilon}$ . We shall show that  $\varphi_{c_0}$  is a heteroclinic solution of (2.3) and (2.6) with

$$\varphi_{c_0}(\xi) \in \text{Int}(\mathcal{B}_{c_0}), \quad u'_{c_0}(\xi) < 0, \quad v'_{c_0}(\xi) < 0, \quad w'_{c_0}(\xi) > 0 \quad \forall \xi \in (-\infty, \infty).$$

First, the definition of  $c_0$  implies that there exists a sequence  $\{c_k\}_{k=1}^\infty$  with  $c_k > c_0$  and  $c_k \rightarrow c_0$  as  $k \rightarrow \infty$ . that every  $\varphi_{c_k}$  with  $u_{c_k}(0) = 1/2$  is a heteroclinic solution of (2.3) and (2.6); and moreover, from Lemma 2.4,  $\varphi_{c_k}(\xi) \in \text{Int}(\mathcal{B}_{c_k})$ ,  $u'_{c_k}(\xi) < 0$ ,  $v'_{c_k}(\xi) < 0$  and  $w'_{c_k}(\xi) > 0$  for all  $\xi \in (-\infty, \infty)$ . Clearly, (2.3) yields that  $\varphi'_{c_k}$  ( $k = 1, \dots$ ) are uniformly bounded over  $(-\infty, \infty)$ . Therefore applying Arzela-Ascoli theorem and diagonal selection process there exists a subsequence of  $\{c_k\}_{k=1}^\infty$ , which is still denoted by  $\{c_k\}_{k=1}^\infty$ , such that  $\{\varphi_{c_k}\}$  converges uniformly on every compact set of  $(-\infty, \infty)$ . Let  $\varphi_0$  be the limit function of  $\varphi_{c_k}$ . It follows that  $\varphi_0 := (u_0, v_0, w_0)$  is a solution of (2.3) on  $(-\infty, \infty)$ , whose components are monotone in  $(-\infty, \infty)$  with  $u_0(0) = 1/2$ . Consequently,  $\varphi_0(\pm\infty)$  exist with  $\varphi_0(-\infty) = E_{c_0}$  and  $\varphi_0(\infty) = O$ . Since  $W^u(E_{c_0})$  is 1-dimensional, it follows that  $\varphi_0(\xi)$  lies in  $W^u(E_{c_0}) \cap \text{Int}(\mathcal{B}_{c_0})$  for all sufficiently negative  $\xi$ , and is equal to  $\varphi_{c_0}$  or a translation of it. The remaining assertions of Lemma 3.2 follow from Lemma 2.4.  $\square$

**Theorem 3.3.**  $c_0$  defined in Lemma 3.2 is the minimum wave speed of the biologically relevant traveling waves of the system (2.2).

*Proof.* It will be shown in Lemma 4.1 and Theorem 4.2 in Section 4 that the assumption  $c_0 > \frac{\chi}{\sqrt{\chi + \varepsilon}}$  in Lemma 3.2 is always satisfied. Whence, the assertion of Theorem 3.3 follows from the definition of  $c_0$ , Lemma 2.2 (ii), and Lemmas 3.1 and 3.2.  $\square$

**4. A lower bound for  $c_0$ .** The aim of this section is to establish the estimates in (1.6). To this end we need the following lemma.

**Lemma 4.1.** For given positive numbers  $\chi$ ,  $\mu$  and  $\varepsilon$ , the following results hold.

- (i) If  $\chi \leq \mu + \sqrt{\mu(\mu + \varepsilon)}$ , then  $2\sqrt{\mu} > \frac{\chi}{\sqrt{\chi + \varepsilon}}$ ;
- (ii) If  $\chi > \mu + \sqrt{\mu(\mu + \varepsilon)}$ , then the equation

$$\bar{c} = \frac{2\mu}{\bar{c} + \sqrt{\bar{c}^2 - 4\mu}} + \frac{2\chi}{\bar{c} + \sqrt{\bar{c}^2 + 4\varepsilon}} \quad (4.1)$$

has a unique positive solution

$$\bar{c} = \frac{\chi^2 + \varepsilon\mu}{\sqrt{\chi(\chi + \varepsilon)(\chi - \mu)}}. \quad (4.2)$$

Moreover,  $\bar{c} > \max \left\{ 2\sqrt{\mu}, \frac{\chi}{\sqrt{\chi + \varepsilon}} \right\}$ .

*Proof.* First, a straightforward computation yields that  $2\sqrt{\mu} = \frac{\bar{\chi}}{\sqrt{\bar{\chi} + \varepsilon}}$  with

$$\bar{\chi} = 2[\mu + \sqrt{\mu(\mu + \varepsilon)}].$$

It is obvious that the function  $\frac{\chi}{\sqrt{\chi + \varepsilon}}$  is strictly monotone increasing on  $\chi$ . Hence  $\chi \leq \mu + \sqrt{\mu(\mu + \varepsilon)} < \bar{\chi}$  implies that

$$\frac{\chi}{\sqrt{\chi + \varepsilon}} < \frac{\bar{\chi}}{\sqrt{\bar{\chi} + \varepsilon}} = 2\sqrt{\mu}.$$

This confirms Part (i) of the lemma.

Next, note that the function

$$h(c) := \frac{2\mu}{c + \sqrt{c^2 - 4\mu}} + \frac{2\chi}{c + \sqrt{c^2 + 4\varepsilon}}.$$

is a strictly monotone decreasing function of  $c$  on  $[2\sqrt{\mu}, \infty)$ , with the maximum value  $h(2\sqrt{\mu}) = \sqrt{\mu} + \frac{\chi}{\sqrt{\mu} + \sqrt{\mu + \varepsilon}}$ . It follows that in order for  $\bar{c} \in (2\sqrt{\mu}, \infty)$  in (4.1) to be (uniquely) defined, it is necessary and sufficient to require  $\sqrt{\mu} + \frac{\chi}{\sqrt{\mu} + \sqrt{\mu + \varepsilon}} > 2\sqrt{\mu}$ , which is equivalent to the assumption made in Part (ii) of the lemma. Now one easily sees that the equation (4.1) is equivalent to (upon rationalizations)

$$(1 + \frac{\chi}{\varepsilon})\bar{c} = \frac{\chi}{\varepsilon}\sqrt{\bar{c}^2 + 4\varepsilon} - \sqrt{\bar{c}^2 - 4\mu},$$

which can be simplified to (upon squaring two times)

$$(\chi + \varepsilon)(1 - \frac{\mu}{\chi})\bar{c}^2 = (\chi + \frac{\varepsilon\mu}{\chi})^2,$$

from which we find  $\bar{c}$  as defined in (4.2). It is obvious that  $\bar{c} > 2\sqrt{\mu}$  since  $\bar{c} \in (2\sqrt{\mu}, \infty)$ . Finally, by the definition of  $v_{\bar{c}}^*$  and (4.1) we deduce that

$$v_{\bar{c}}^* = \bar{c} - \frac{2\chi}{\bar{c} + \sqrt{\bar{c}^2 + 4\varepsilon}} = \frac{2\mu}{\bar{c} + \sqrt{\bar{c}^2 - 4\mu}} > 0.$$

Thus from (2.5) it follows that  $\bar{c} > \frac{\chi}{\sqrt{\chi + \varepsilon}}$ . This shows Part (ii) of the lemma.  $\square$

**Theorem 4.2.** *Let  $c_0$  be defined in Lemma 3.2 and  $\bar{c}$  be given in (4.2). Then*

- (a)  $2\sqrt{\mu} \leq c_0$ , if  $\chi \leq \mu + \sqrt{\mu(\mu + \varepsilon)}$ ;
- (b)  $\bar{c} < c_0$ , if  $\chi > \mu + \sqrt{\mu(\mu + \varepsilon)}$ .

Before proving Theorem 4.2, let us first give an outline of our approach. Recall that the number  $\bar{c}$  defined in (4.2) satisfies

$$v_{\bar{c}}^* = \frac{\mu}{|\lambda_2|} = |\lambda_1|, \quad (4.3)$$

where  $\lambda_1$  and  $\lambda_2$  are defined in (2.8) in which  $c = \bar{c}$ .

Suppose  $\varphi_{\bar{c}} = (u_{\bar{c}}, v_{\bar{c}}, w_{\bar{c}})$  given in Lemma 2.4 is a heteroclinic orbit connecting  $E_{\bar{c}}$  and  $O$ . Then

$$(u_{\bar{c}}, v_{\bar{c}})(-\infty) = (1, v_{\bar{c}}^*), \quad (u_{\bar{c}}, v_{\bar{c}})(\infty) = (0, 0). \quad (4.4)$$

Since  $w'_{\bar{c}} = w_{\bar{c}}^2 - (\bar{c}w_{\bar{c}} + u_{\bar{c}})/\varepsilon > 0$  and  $w_{\bar{c}} < 0$  on  $(-\infty, \infty)$ , we have on  $(-\infty, \infty)$

$$w_{\bar{c}} < \frac{1}{2\varepsilon} \left[ \bar{c} - \sqrt{\bar{c}^2 + 4\varepsilon u_{\bar{c}}} \right] = -\frac{2u_{\bar{c}}}{\bar{c} + \sqrt{\bar{c}^2 + 4\varepsilon u_{\bar{c}}}}.$$

It follows from the first two equations of (2.3) that

$$u'_{\bar{c}} > v_{\bar{c}} - [\bar{c} - \chi g(u_{\bar{c}})]u_{\bar{c}}, \quad v'_{\bar{c}} = -f(u_{\bar{c}}), \quad (4.5)$$

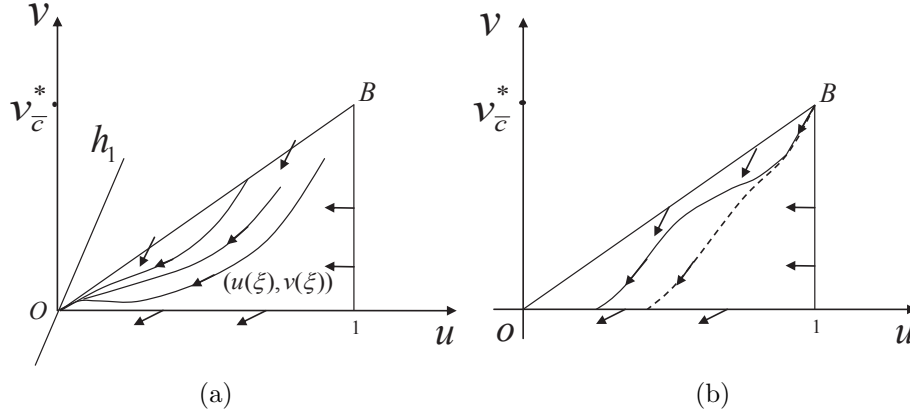


FIGURE 2. In Fig. (a): There are infinitely many solutions of (4.6) that converge to the equilibrium  $O$  but are not tangent to  $\mathbf{h}_1$  at  $O$ , a violation to the stable manifold theorem. In Fig. (b): The solid curve is the orbit of a solution of (4.6) and the dotted curve is the projection of the orbit of  $\varphi_{\bar{c}}(\xi)$  onto the  $uv$  plane.

where

$$g(u) = \frac{2u}{\bar{c} + \sqrt{\bar{c}^2 + 4\epsilon u}} = \frac{1}{2\epsilon}(\sqrt{\bar{c}^2 + 4\epsilon u} - \bar{c}).$$

Using (4.5) and the comparison argument we shall show that  $(u_{\bar{c}}(\xi), v_{\bar{c}}(\xi))$  will be bounded above, in the  $uv$  plane, by a solution of the associated planar system

$$u' = v - [\bar{c} - \chi g(u)]u, \quad v' = -f(u), \quad (4.6)$$

that will eventually push  $(u_{\bar{c}}(\xi), v_{\bar{c}}(\xi))$  out of the nonnegative region of the  $uv$  plane. Hence  $\varphi_{\bar{c}} = (u_{\bar{c}}, v_{\bar{c}}, w_{\bar{c}})$  can not be a biologically relevant heteroclinic orbit connecting  $E_{\bar{c}}$  and  $O$ . This gives that  $c_0 > \bar{c}$ , as claimed in Theorem 4.2 (b).

We first establish in the following lemma on the planar system (4.6).

**Lemma 4.3.** *Assume that  $\chi > \mu + \sqrt{\mu(\mu + \epsilon)}$  and let  $\bar{c} > 2\sqrt{\mu}$  be defined in (4.1). Let*

$$\Omega = \{(u, v) : 0 \leq u \leq 1, 0 \leq v \leq v_{\bar{c}}^* u\}$$

be the triangular region with the vertices  $O := (0, 0)$ ,  $B := (1, v_{\bar{c}}^*)$  and  $(1, 0)$  (see Fig. 2). Then for any point  $(u_0, v_0) \in \text{Int}(\Omega)$ , the solution  $(u(\xi), v(\xi))$  of (4.6) with  $(u(0), v(0)) = (u_0, v_0)$  will exit the region  $\Omega$  from its bottom at some positive time  $\xi_1$ . i.e.,  $v(\xi_1) = 0$  for some  $\xi_1 > 0$ .

*Proof. Step 1.* We first study the local dynamics of (4.6) at the equilibrium  $O$ . The Jacobian matrix of (4.6) at  $O$  is  $\begin{pmatrix} -\bar{c} & 1 \\ -\mu & 0 \end{pmatrix}$ , which has two negative eigenvalues  $\lambda_1$  and  $\lambda_2$  given in (2.8) with  $c := \bar{c}$  and their associated eigenvectors  $\mathbf{h}_1 = (1, \mu/|\lambda_1|)^\top$  and  $\mathbf{h}_2 = (1, \mu/|\lambda_2|)^\top$  respectively. Thus,  $O$  is a stable node of (4.6). Noticing  $\lambda_2 < \lambda_1$ , it follows from the stable manifold theorem that, in a neighborhood of the equilibrium  $O$ , all nontrivial orbits of (4.6), except two of them, approach  $O$  as  $\xi \rightarrow \infty$  in the direction tangent to the eigenvector  $\mathbf{h}_1$ .

*Step 2.* We study the vector field of (4.6) on the line segment  $OB$  given by  $v = v_{\bar{c}}^* u = \mu u/|\lambda_2|$  with  $u \in [0, 1]$  (see Fig. 2). Here we have used the equalities

$v_{\bar{c}}^* = \mu/|\lambda_2|$  from (4.1). We claim that the flows of (4.6) cross the segment  $OB$  downward, i.e.,

$$\frac{dv}{du} = \frac{-f(u)}{v - [\bar{c} - \chi g(u)]u} > \frac{\mu}{|\lambda_2|} \quad \forall (u, v) \in OB, \quad u \in (0, 1). \quad (4.7)$$

In fact, this follows from the equation  $|\lambda_2|^2 - \bar{c}|\lambda_2| + \mu = 0$ , the definition of  $\bar{c}$  in (4.1), the properties of  $g$ , and the following:

$$\begin{aligned} \frac{dv}{du} > \frac{\mu}{|\lambda_2|} &\iff \frac{1-u}{\bar{c} - \chi g(u) - \frac{\mu}{|\lambda_2|}} > \frac{1}{|\lambda_2|} \\ &\iff (1-u)|\lambda_2|^2 > \bar{c}|\lambda_2| - \chi g(u)|\lambda_2| - \mu \\ &\iff -|\lambda_2| + \chi \frac{g(u)}{u} > 0 \\ &\iff \frac{\mu}{|\lambda_2|} > \bar{c} - \chi \frac{g(u)}{u} \quad (\text{since } |\lambda_2| = \bar{c} - \frac{\mu}{|\lambda_2|}) \\ &\iff \frac{g(u)}{u} > g(1) \quad (\text{from (4.1)}) \\ &\iff \frac{2}{\bar{c} + \sqrt{\bar{c}^2 + 4\epsilon u}} > \frac{2}{\bar{c} + \sqrt{\bar{c}^2 + 4\epsilon}}. \end{aligned}$$

**Step 3.** Let us consider the vector field  $(u', v')$  of (4.6) at an arbitrary point  $(u, v) \in \text{Int}(\Omega)$ . It is obvious that  $v \leq v_{\bar{c}}^* u = \frac{\mu}{|\lambda_2|} u = |\lambda_1|u$  and

$$v' < 0. \quad (4.8)$$

Moreover by (4.1), one easily deduces that

$$|\lambda_2| = \bar{c} - |\lambda_1| = \frac{2\chi}{\bar{c} + \sqrt{\bar{c}^2 + 4\epsilon}} = \frac{\chi}{2\epsilon} (\sqrt{\bar{c}^2 + 4\epsilon} - \bar{c}). \quad (4.9)$$

From (4.9) and the definition of  $g(u)$  it therefore follows that

$$\begin{aligned} u' &= v - [\bar{c} - \chi g(u)]u \\ &\leq [|\lambda_1| - \bar{c} + \chi g(u)]u \\ &= - \left[ \frac{\chi}{2\epsilon} (\sqrt{\bar{c}^2 + 4\epsilon} - \bar{c}) - \frac{\chi}{2\epsilon} (\sqrt{\bar{c}^2 + 4\epsilon u} - \bar{c}) \right] u \\ &< 0. \end{aligned} \quad (4.10)$$

Now for any solution  $(u(\xi), v(\xi))$  of (4.6) with  $(u(0), v(0)) \in \text{Int}(\Omega)$ , we claim that  $(u(\xi), v(\xi))$  must exit  $\Omega$  from the bottom of  $\Omega$  at some positive time  $\xi_1$ . Suppose this is not the case, then  $(u(\xi), v(\xi)) \in \Omega$  for all  $\xi \geq 0$  since it can not leave  $\Omega$  from the line segment  $OB$ . Then both  $u(\xi)$  and  $v(\xi)$  are decreasing as  $\xi$  increases by (4.8) and (4.10). This yields that  $(u(\xi), v(\xi)) \rightarrow O$  as  $\xi \rightarrow \infty$ . By this fact and the result obtained in Step 2 we immediately conclude that any solution of (4.6) through a point in the region bounded above by the line segment  $OB$  and below by the orbit  $\{(u(\xi), v(\xi)) : \xi \geq 0\}$  will stay this region and converges to the equilibrium 0 as  $\xi \rightarrow \infty$ . That is, (4.6) would have infinitely many solutions that converge to  $O$  but not in the direction tangent to the eigenvector  $\mathbf{h}_1$  (see Fig. 2 (a)). This leads to a contradiction. Thus, Lemma 4.3 is proved.  $\square$

We need the following lemma before completing the Theorem 4.2.

**Lemma 4.4.** *Let  $\lambda_+$  be the unique positive root of the characteristic polynomial  $P(\lambda)$  given in (2.10) with  $c = \bar{c}$ . Then*

$$\lambda_+ < |\lambda_2|, \quad (4.11)$$

where  $\lambda_2$  is defined as in Step 1 of the proof of Lemma 4.3.

*Proof.* Since  $P(0) < 0$  and  $P(\lambda)$  has a unique positive root  $\lambda_+$ , it is sufficient to show that  $P(|\lambda_2|) > 0$ . By (2.10), (4.9) and the equalities

$$v_{\bar{c}}^* |\lambda_2| = |\lambda_1| |\lambda_2| = \mu, \quad -w_{\bar{c}}^* = \frac{\sqrt{\bar{c}^2 + 4\varepsilon} - \bar{c}}{2\varepsilon},$$

we have

$$\begin{aligned} P(|\lambda_2|) &= \left(|\lambda_2| + \frac{c}{\varepsilon} - 2w_{\bar{c}}^*\right) (|\lambda_2|^2 + v_{\bar{c}}^* |\lambda_2| - \mu) - \frac{\chi}{\varepsilon} |\lambda_2| \\ &= \left(|\lambda_2| + \frac{\sqrt{\bar{c}^2 + 4\varepsilon}}{\varepsilon}\right) |\lambda_2|^2 - \frac{\chi}{\varepsilon} |\lambda_2| \\ &> |\lambda_2| \left(|\lambda_2| \frac{\sqrt{\bar{c}^2 + 4\varepsilon}}{\varepsilon} - \frac{\chi}{\varepsilon}\right) \\ &= \frac{|\lambda_2| \chi}{\varepsilon} \left(\frac{2\sqrt{\bar{c}^2 + 4\varepsilon}}{\bar{c} + \sqrt{\bar{c}^2 + 4\varepsilon}} - 1\right) \\ &> 0. \end{aligned} \quad (4.12)$$

□

With Lemmas 4.3 and 4.4 in hand, we are ready to prove Theorem 4.2.

*Proof of Theorem 4.2.* Part (a) of Theorem 4.2 is a straightforward consequence of Lemma 2.2 (ii), Lemma 3.1, Lemma 3.2 and Lemma 4.1 (i). In order to show  $c_0 > \bar{c}$  when  $\chi > \mu + \sqrt{\mu(\mu + \varepsilon)}$ , it suffices to show by Lemma 3.1 and Lemma 4.1 (ii) that  $\varphi_{\bar{c}}$  is not a heteroclinic solution of (2.3) and (2.6). Assume on the contrary that  $\varphi_{\bar{c}}$  is a heteroclinic solution of (2.3) and (2.6). Then the unstable manifold theorem implies that the orbit of  $\varphi_{\bar{c}}(\xi)$  is tangent to the eigenvector  $\mathcal{V}$  defined in (2.7) at  $\xi = -\infty$ . Hence  $(u_{\bar{c}}(\xi), v_{\bar{c}}(\xi))$ , the projection of  $\varphi_{\bar{c}}(\xi)$  onto the  $uv$ -plane, is tangent to a line of slope  $\mu/\lambda_+$  at the point  $B$  for  $\xi = -\infty$ . Note that the line segment  $OB$  defined in Lemma 4.3 has the slope  $v_{\bar{c}}^* = \mu/|\lambda_2|$ . By Lemma 4.4 we have  $v_{\bar{c}}^* < \mu/\lambda_+$ . It follows that  $(u_{\bar{c}}(\xi), v_{\bar{c}}(\xi)) \in \text{Int}(\Omega)$  for all sufficiently negative  $\xi$  (see Fig.2 (b)). So we can pick a  $\xi_0$  such that  $(u_{\bar{c}}(\xi_0), v_{\bar{c}}(\xi_0)) \in \text{Int}(\Omega)$ . Let  $(u(\xi), v(\xi))$  be a solution of (4.6) with  $(u(0), v(0)) = (u_{\bar{c}}(\xi_0), v_{\bar{c}}(\xi_0))$ . Recall that  $(u_{\bar{c}}(\xi_0), v_{\bar{c}}(\xi_0))$  satisfies (4.5) for all  $\xi \in (-\infty, \infty)$ . Then a comparison argument shows that the orbit  $\{(u(\xi), v(\xi)) : \xi \geq 0\}$  lies above the projection  $\{(u_{\bar{c}}(\xi), v_{\bar{c}}(\xi)) : \xi \in (\xi_0, \infty)\}$  of the orbit of  $\varphi_{\bar{c}}$  in the  $uv$  plane. On the other hand,  $(u(\xi), v(\xi))$  must exit the triangular region  $\Omega$  from its bottom at some positive time  $\xi_1$  by Lemma 4.3. So that  $(u_{\bar{c}}(\xi), v_{\bar{c}}(\xi))$  must leave the region  $\Omega$  from its bottom too (see Fig. 2 (b)). This contradicts the fact that  $0 < v_{\bar{c}}(\xi) < v_{\bar{c}}^*$  for all  $\xi \in (-\infty, \infty)$ . Whence, Theorem 4.2 is proved. □

**5. Proofs of Theorems 1.1 and 1.2.** Let us first prove Theorem 1.1. Observe that, by the scalings in (2.1),  $(\tilde{u}(x, t), \tilde{w}(x, t)) = \left(\tilde{U}\left(x - \frac{c}{\sqrt{d}}t\right), \tilde{W}\left(x - \frac{c}{\sqrt{d}}t\right)\right)$  is a

traveling wave of (2.2) with the speed  $c/\sqrt{d}$  if and only if

$$(u(x, t), w(x, t)) = (U(x - ct), W(x - ct)) = \left( \tilde{U}\left(\frac{x - ct}{\sqrt{d}}\right), \frac{1}{\sqrt{d}}\tilde{W}\left(\frac{x - ct}{\sqrt{d}}\right) \right) \quad (5.1)$$

is a traveling wave of (1.4) with the speed  $c$ . Hence the system (1.4) has the minimum wave speed  $c_*(d, \chi, \varepsilon, \mu) = \sqrt{d}c_0$  with  $c_0$  defined in Lemma 3.2. Moreover, recalling that  $\chi$  and  $\varepsilon$  in the system (2.3) stand for  $\chi/d$  and  $\varepsilon/d$  respectively, one then easily deduces the estimate given in Part (ii) of Theorem 1.1 from Theorems 2.1, 4.2, and the equality  $c_* = c_*(d, \chi, \varepsilon, \mu) = \sqrt{d}c_0$ . This completes the proof of Theorem 1.1.

To show Theorem 1.2, we may assume that  $d = 1$ . Given  $c \geq c_0$  and  $s^+ > 0$ , let  $(u_c, s_c)$  be defined in Theorem 1.2. It follows from the properties of  $w_c$ , in particular,  $w_c(\xi) \rightarrow 0$  exponentially fast as  $\xi \rightarrow \infty$  (from the stable manifold theorem), that  $s_c$  is well-defined with  $s_c > 0$  and  $s'_c = -w_c s_c > 0$  on  $(-\infty, \infty)$ ,  $s_c(-\infty) = 0$  and  $s_c(\infty) = s^+$ . Furthermore, using  $(\ln s_c)' = -w_c$ ,  $s''_c = (-w'_c + w_c^2)s_c$ , and the equations in (2.3) we obtain that  $cu'_c + (u'_c - \chi(u_c(\ln s_c))')' + \mu u_c(1 - u_c) = 0$  and  $\varepsilon s''_c + cs'_c - u_c s_c = 0$ . This shows that  $(u_c, s_c)$  is a monotone traveling wave solution of (1.1) as described in Theorem 1.2. The uniqueness of such a solution follows from Lemma 2.2 (i). This completes the proof of Theorem 1.2.

**6. Traveling waves of limiting systems.** In order to discuss the effect of each process of reaction, diffusion and chemotaxis on the traveling waves as well as the biological implications of our results, in this section, we discuss the traveling waves for limiting cases of (1.1), namely,  $\chi = 0$ ,  $d = 0$  and  $\mu = 0$ , respectively.

**6.1. No chemotaxis:**  $\chi = 0$ . When  $\chi = 0$ , the original system (1.1) and the transformed (1.4) reduce to, respectively,

$$u_t = du_{xx} + \mu u(1 - u), \quad s_t = \varepsilon s_{xx} - us, \quad (6.1)$$

and

$$u_t = du_{xx} + \mu u(1 - u), \quad w_t = \varepsilon w_{xx} - (\varepsilon w^2 - u)_x. \quad (6.2)$$

We have:

**Theorem 6.1.** *For every  $c \geq 2\sqrt{d\mu}$ , there is a unique traveling wave  $(u_c, s_c)$  for (6.1) satisfying (1.9).*

*Proof.* From the analysis in preceding sections and proof in section 5, it suffices to prove the existence of traveling wave solution  $(u_c, w_c)$  of the transformed system (6.2).

For a given  $c \geq 2\sqrt{\mu}$ , we pick a sequence  $\chi_n > 0$  such that  $\chi_n \rightarrow 0$  as  $n \rightarrow \infty$  (e.g.  $\chi_n = 1/n$ ), and define  $c_n$  as

$$c_n = c + \frac{\chi_n}{\sqrt{d\mu} + \sqrt{d\mu + \varepsilon + \chi_n}}$$

for all  $n$ . Using the existence of  $(u_{c_n}, w_{c_n})$  for each  $n$  by virtue of Theorem 1.1 and a standard limiting procedure we derive the existence of  $(u_c, w_c)$  for (6.2).  $\square$



**6.2. No diffusion:**  $d = 0$ . When  $d = 0$ , the systems (1.1) reduces to

$$u_t = -[\chi u(\ln s)]_x + \mu u(1 - u), \quad s_t = \varepsilon s_{xx} - us, \quad (6.3)$$

and the transformed system (1.4) becomes

$$u_t = (\chi uw)_x + \mu u(1 - u), \quad w_t = \varepsilon w_{xx} - (\varepsilon w^2 - u)_x. \quad (6.4)$$

We have:

**Theorem 6.2.** *For every  $c > \chi/\sqrt{\chi + \varepsilon}$ , there is a unique traveling wave solution  $(u_c, s_c)$  of (6.3) satisfying (1.9).*

*Proof.* Again, we only need to prove the existence of traveling wave of the transformed system (6.4). If  $c > \chi/\sqrt{\chi + \varepsilon}$ , then we can pick a sequence  $d_n \searrow 0$  as  $n \rightarrow \infty$  such that for all  $n$ ,

$$c_* < 2\sqrt{d_n\mu} + \frac{\chi}{\sqrt{d_n\mu} + \sqrt{d_n\mu + \varepsilon + \chi}}.$$

It follows from Theorem 1.1 and the above inequality that there exists a sequence of traveling wave solutions  $(u_{c,n}(\xi), w_{c,n}(\xi))$  satisfying the condition (1.5) for all  $n$ . Then, by a limiting process we obtain a traveling wave solution of the system (1.4) with  $d = 0$ .  $\square$

**6.3. No cell growth:**  $\mu = 0$ . When  $\mu = 0$ , the model (1.1) reduces to

$$u_t = [du_x - \chi u(\ln s)]_x, \quad s_t = \varepsilon s_{xx} - us, \quad (6.5)$$

which is the model considered in [32]. Here we cite the following result for reference.

**Theorem 6.3** ([32]). *The system (6.5) admits a unique (up to a translation) traveling wave  $(u_c, s_c)$  satisfying (1.9), where the wave speed  $c = \chi/\sqrt{\chi + \varepsilon}$ .*

**7. Summary and discussion.** In this paper, we investigate the traveling waves of a biological system (1.1) which contains three processes: reaction, diffusion and chemotaxis. The main result of this paper is to prove that the interaction of these three processes can generate traveling waves with a minimal wave speed (see Theorem 1.1). We also show in section 6 that any single process is not necessary for the existence of traveling waves, namely the interaction of any two processes can give rise to traveling waves with a minimum (or unique) wave speed as summarized in Table 1. In each parameter regime  $R_i$  ( $i = 1, 2, 3, 4$ ), the corresponding system can produce the traveling waves with the same asymptotics and monotonicity in (1.9). Hence the role of each single process in the wave propagation is unclear. However the (minimal) wave speed, which was rigorously derived in this paper, can be used to examine the effect of each single process on the traveling waves. In the first three limiting parameter regimes  $R_i$  ( $i = 1, 2, 3$ ), the dependencies of the (minimal) wave speed on system parameters are explicit and hence the role of each process is quite clear. In the parameter regime  $R_4$ , the minimal wave speed requires further interpretations and effect of each process needs to be clarified with our results. There are three important biological implications of our results as to be explained below.

It can be found from Table 1 that without logistic reaction (growth) term (i.e.  $\mu = 0$ ), the wave propagation is driven by both diffusion and chemotaxis with a unique wave speed  $\frac{\chi}{\sqrt{\chi + \varepsilon}}$ . Once the cell growth is included, there exist infinitely many wave speeds with the minimal wave speed  $c_*$  greater than  $\frac{\chi}{\sqrt{\chi + \varepsilon}}$ , which indicates that the cell growth facilitates the wave propagation to regions of higher chemical concentration. This is the first biological implication of our results. We

TABLE 1. A comparison of the (minimal) wave speed of traveling waves of the model (1.1) in different parameter regimes, where the minimal wave speed  $c_*$  is given in (1.6).

Parameter regimes	Wave speed $c$
$R_1 : d = 0, \chi, \mu > 0$	$c > \frac{\chi}{\sqrt{\chi + \varepsilon}}$
$R_2 : \chi = 0, d, \mu > 0$	$c \geq 2\sqrt{d\mu}$
$R_3 : \mu = 0, d, \chi > 0$	$c = \frac{\chi}{\sqrt{\chi + \varepsilon}}$
$R_4 : d, \chi, \mu > 0$	$c \geq c_*$

show the numerical wave profile  $u(x, t)$  without and with cell growth at the same time  $t = 200$  numerically in Fig. 3 (a), where it is found that the wavefront with  $\mu > 0$  (dashed line) precedes the one with  $\mu = 0$  (solid line). This numerically verifies that cells with growth propagate faster than cells without growth. In the parameter regime  $R_4$  where all processes participate the wave propagation, we see that integrated interaction of reaction and diffusion competes with chemotaxis in the sense of selecting the minimal wave speed by noting (1.6). Furthermore (1.7) shows that if the chemotaxis is weak (i.e.  $\chi$  is small), the interaction of reaction and diffusion will play a dominant role and the minimal wave speed will be selected as the minimal wave speed of simple reaction-diffusion wave (i.e. Fisher wave). However if the chemotactic strength  $\chi$  is increased to exceed a threshold number  $\chi_* = d\mu + \sqrt{d\mu(d\mu + \varepsilon)}$ , then chemotaxis will come to play a role by increasing the wave speed but can not entirely suppress the interaction of reaction and diffusion, since from (1.8) we see that each parameter  $\chi, d, \mu$  makes a contribution to  $\bar{c}_*$ . Hence we can conclude that the chemotaxis must be strong enough ( $\chi > \chi_*$ ) in order to increase the wave speed. This is the second implication of our results. From regime  $R_3$ , we find that if there is no cell growth, the wave speed is independent of the cell diffusion (see Theorem 6.3). This indicates that cell diffusion does not contribute to wave speed if the cell growth is absent although it decreases the asymptotic decay rates of traveling waves at far field (see [32, Theorem 3.3]). However if the cell growth is present, the quantity  $\bar{c}_*$  (see (1.6)-(1.8)) will depend on the cell diffusion rate  $d$ . This entails that cell diffusion has to combine with cell growth to make a contribution to the increment of the minimal wave speed, which is the third implication of our results.

The stability of traveling waves of the model (1.1) without cell growth (i.e.  $\mu = 0$ ), for which the wave speed is unique and hence the asymptotic profile is apparently determined, has been established in [16]. However if the cell growth is present, the wave speed is no longer unique but has a minimal speed  $c_*$ . Hence the description of asymptotic stability of traveling wave solutions is more complicated due to the presence of logistic growth. We expect for a large class of initial distributions, the minimum wave speed will be the stable one. The critical factor in controlling this selection is the asymptotic behavior of the initial data as  $x \rightarrow +\infty$ . The preliminary numerical simulation in Fig. 3 (b) illustrates the (nonlinear) asymptotic stability of traveling waves of (1.1). However, the precise description and rigorous verification

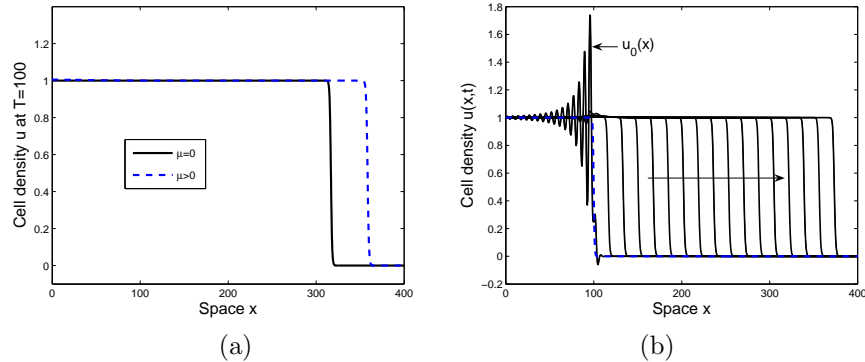


FIGURE 3. (a) Wave propagation profile of  $u$  for the model (1.4) with  $\mu = 0$  and  $\mu > 0$  at the time step  $T = 100$ , where the time step size  $\Delta t = 0.1$  and initial value  $u_0(x) = 1/(1 + \exp(2(x - 100)))$ ,  $w_0(x) = -0.33 + 0.33/(1 + \exp(-2(x - 100)))$  and parameter values are  $d = 2$ ,  $\chi = 9$ ,  $\varepsilon = 0.1$ , and  $\mu = 0.1$  (for dashed curve); (b) The numerical illustration of the evolution of stable traveling waves, where the initial value is given as a perturbation of the initial value given in (a); other parameters are same as those in (a) with  $\mu = 0.1$ . The arrow indicates the wave propagation direction.

of the stability of traveling waves for  $\mu > 0$  of (1.1) are non-trivial and we leave them for the future research.

Finally we remark that the logistic growth considered in this paper does not exclude other possible cell kinetics in general, for instance the bistable kinetics [8]. If the chemical is a nutrient source (like food or oxygen) for cells, then the cell growth may rely on the chemical concentration and can be of the form  $rus$  or  $rus(1 - u)$  ( $r > 0$ ). The traveling waves of the model with these kinetic forms are also of interest to investigate.

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