Bacterial chemotaxis without gradient-sensing

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Abstract. Chemotaxis models are based on spatial or temporal gradient measurements of by individual organisms. The key contribution of Keller and Segel [15,16] is showing that erratic measurements of individuals may result in an accurate chemotaxis phenomenon as a group. In this paper we provide another option to understand chemotactic behavior when individuals do not sense the gradient of chemical concentration by any means. We show that, if individuals increase their dispersal rate to find food when there is not enough food, an accurate chemotactic behavior may be obtained without sensing the gradient. Such a dispersal has been suggested by Cho and Kim [5] and was called starvation driven diffusion. This model is surprisingly similar to the original Keller-Segel model. A comprehensive picture of traveling bands and fronts is provided.

Key words. chemotaxis, phase plane analysis, starvation driven diffusion, Keller-Segel equation, pulse and front type traveling waves

1. Introduction

In chemotaxis a surprising and mysterious phenomenon is how microscopic scale organisms figure out the macroscopic scale concentration gradient and find the correct direction to resources such as food. One may say that the main contribution of the classical Keller-Segel model on this issue is to show that, even if the individuals sense the chemical gradient inaccurately, the chemotactic phenomenon can be accurate in an averaged sense. The purpose of this paper is to go one step further from Keller and Segel's idea and conclude that, if individual organisms increase the dispersal rate when starvation begins, accurate chemotactic behavior is obtained without sensing the gradient. We will achieve this goal by introducing a new chemotaxis model based on a starvation driven diffusion and showing the existence of traveling waves.

Chemotactic behaviors of single-celled organisms have been intensively studied for a long time. It is believed that the dynamics behind them will help us to understand other migration phenomenon such as the cell movements within a human body. Bonner's *Dictyostelium* [3] and Matsushita *et al.*'s *Bacillus subtilis* [24] show interesting chemotactic behavior and patterns. The chemotaxis model in this paper is closely related to the the pioneering works of Adler which made a significant turning point in the theory of intracellular signal transduction of bacteria. Adler showed in his paper [1,2] that motile *Escherichia coli* placed at one end of a capillary tube containing food and oxygen migrate through the tube in one or two traveling wave bands, which is clearly a chemotaxis phenomenon. This phenomenon has been mathematically modeled by Keller and Segel [15,16] and Adler's experiment data were successfully fit by the model.

Keller and Segel's equations are written as

$$\begin{cases} u_t = (\mu(m)u_x - \chi(m)u\,m_x)_x, \\ m_t = \epsilon\, m_{xx} - k(m)u, \end{cases} \tag{1}$$

where $u \geq 0$ is the population density, $m \geq 0$ is the nutrient concentration, $\epsilon > 0$ is the diffusivity of the nutrient, and $k(m) \geq 0$ is the consumption rate. The population reproduction term such as the logistic one is omitted since chemotaxis models are to understand the migration effect. The diffusivity $\mu(m) > 0$ and the chemosensitivity $\chi(m) > 0$ come from the bacteria's dispersal strategy and are related. In the derivation of the model bacteria are assumed to measure the nutrient concentration using receptors placed along the body and move toward higher concentration. Let $0 < a < 1$ be the ratio of effective body length, i.e., the largest distance between receptors over the body length of bacteria. In the derivation of the Keller-Segel model, μ and χ satisfy

$$\chi(m) = -(1-a)\mu'(m), \quad \mu'(m) \leq 0. \tag{2}$$

Notice that the ratio becomes $a = 0$ if there is only one receptor or if the concentration gradient is not actually measured. One may find a detailed mechanism of chemotactic systems and related mathematical approaches from Tindall *et al.* [31,32].

Traveling wave solutions of (1) have been intensively studied after various simplifications. In fact, Keller and Segel by themselves broke the link between μ and χ in (2) by assuming

$$\epsilon = \mu' = k' = 0 \quad \text{and} \quad \chi(m) = m^{-1}, \tag{3}$$

and then found explicit traveling wave solutions [16].

Nonconstant consumption rates such as

$$k(m) = m^p, \qquad p \geq 0 \tag{4}$$

have been considered by many authors. The consumption rate represents the feeding style of organisms and decides traveling wave types. Organisms may consume more if there is more food. However, it is more realistic to assume $0 \leq p < 1$ since, even if the amount of food is doubled, organisms do not consume two times more usually. For the case with $0 \leq p < 1$, we have traveling band solutions and the existence, stability and convergence as $\epsilon \to 0$ have been intensively studied (see [11,17,18,23,25,27–30,34]). The case with $p = 1$ gives traveling fronts instead of bands (see [14,21,33]). In fact, this case models vascular growth of angiogenesis and has been well-documented (see [4,8,9,20,22]). These traveling wave band and front solutions are obtained using a chemotaxis model introduced in the next section.

The rest of this paper is organized as follows. In Section 2, the chemotaxis model of this paper is introduced, which is based on starvation driven diffusion. Main theorems and results are in Section 3, which consists of two lemmas and three theorems. The proofs of the three theorems are in Section 4. A phase plane analysis for traveling wave solutions are done in Section 5. Examples of traveling wave solutions are given in Section 6 by computing ordinary differential equations and compared with the cases in Theorems. Conclusions and discussions on possible biological applications are given in Section 7.

2. The Model

The main feature of the chemotaxis model presented in this paper is that we do not assume that species sense the gradient of chemical concentration. The only hypothesis of the theory presented here is that organisms increase their motility to find food when there is not enough food. In other words, if nutrient is abundant, species decrease their motility and stay in place. Such behavior of bacterial species can be found from the literature and we took an example from Matsushita *et al.* [24]. A cartoon of a growing tip of *Bacillus subtilis* is given in Figure 1 (see [24, Figure 3] for the actual photo).

The fingernail structure consists of actively moving cells. The cells surrounding the nail are inactive in movement. The ones in the site without nutrient are inactive since they have no energy to move. However, the boundary ones in the site with nutrient, which take most of the resources, are inactive in movement and active in multiplying. The influx of the nutrient to the fingernail region is limited due to the consumption by the boundary cells and the cells in the region

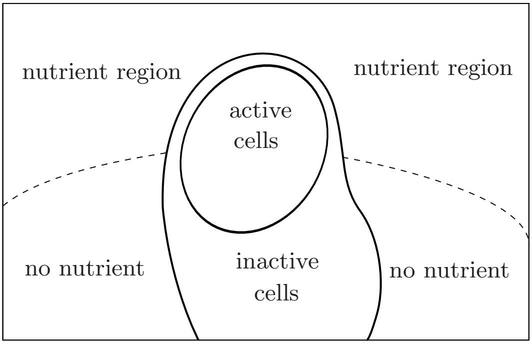


Fig. 1. A cartoon of the tip of a upward growing branch of *Bacillus subtilis*. The Fingernail structure consists of actively moving cells. Inactive cells surrounding the nail are of two types. The ones in the site with nutrient are inactive in movement and active in multiplying. However, the ones in the site without nutrient are inactive in both. The actual photo is from [24, Figure 3] and the width of the finger is 0.5 mm.

are actively moving to find food. This is a clear example that shows starvation increases dispersal as long as species has energy to move. *Dictyostelium* also provides an example of dispersal increase under starvation in a different level of ecological evolution. It is well known that, if starvation has started, *Dictyostelium* aggregates to form a stalk like structure. The single purpose of this process is to eventually increase their dispersal ability. Dispersal increase under starvation can be found in various sizes and levels of biological organisms and more discussions can be found from [5].

The chemotaxis model of this paper does not have the usual drift term and is written as

$$\begin{cases} u_t = \quad (\gamma\, u)_{xx}, \\ m_t = -k(m)u, \end{cases} \qquad x \in \boldsymbol{R},\ t > 0, \tag{5}$$

where the motility γ is understood as the *departing probability* (see Appendix A for a derivation of the first equation). Directional information is not included and the motility $\gamma = \gamma(m, u)$ is a function of concentrations u and m, but not their gradients. In other words, organisms decide their movement without any gradient information. The required hypotheses on the motility function γ are:

$$\gamma > 0, \quad \gamma_u \geq 0 \quad \text{and} \quad \gamma_m \leq 0. \tag{6}$$

If the population increases or the resource decreases, the starvation will increase. Therefore, these hypotheses imply that starvation increases the motility of species and hence we call the corresponding dispersal process a *starvation driven diffusion*. The first equation in (5) is written as

$$u_t = \big((\gamma + \gamma_u u)u_x + \gamma_m u\, m_x\big)_x. \tag{7}$$

The first two conditions in (6) make the model parabolic and the third one gives an advection toward the resource but not against it. Therefore, if one choose a motility function that starvation reduces motility, the problem will become invalid.

Remark 1. The Keller-Segel model in (1) is identical to (7) when the motility depends on the resource concentration only, i.e., $\gamma = \gamma(m)$, and the ratio of the effective body length is $a = 0$. Then, the corresponding chemosensitivity and the diffusivity in (7) satisfy the relation in (2). In fact, it is not surprising since $a = 0$ implies that bacteria do not sense the gradient, but sense the concentration only, which is exactly the assumption of our model.

Next, we will restrict our motility functions further as a function of a *satisfaction measure* only,

$$s = \frac{m}{u}, \tag{8}$$

which measures the average amount of resources available for each individual. Individuals does not know the total size of resource nor population. However, they know the amount of the resource they obtain and hence the use of the above measure is biologically reasonable. We will abuse notation by writing $\gamma(m,u) = \gamma(\frac{m}{u})$. The main hypothesis of the motility function $\gamma(s)$ is that it is a decreasing function of the satisfaction measure. The motility function is also assumed to be smooth and bounded below, i.e.,

$$\lim_{s\to\infty} \gamma(s) = \ell > 0, \quad \gamma'(s) \le 0 \ \text{ on } \ (0,\infty). \tag{9}$$

Then, the hypotheses in (6) are satisfied, i.e.,

$$\gamma_m = \gamma'(s)\frac{1}{u} \le 0 \quad \text{and} \quad \gamma_u = -\gamma'(s)\frac{m}{u^2} \ge 0, \tag{10}$$

and hence the diffusion in the model is still a starvation driven one.

The consumption rate $k(m)$ is assumed to satisfy two hypotheses:

$$k'(m) \ge 0, \quad \lim_{m\to 0} k(m) = 0. \tag{11}$$

The first one indicates that organisms consume more if there is more food. The second one says that the organisms do not consume food at all if there is nothing left. Two typical examples in the literature are $k(m) = m^p$ and $k(m) = \frac{m^p}{1+m^p}$ with $p > 0$. The second one has bounded consumption rate as $m \to \infty$, which is more realistic. However, since we will consider uniformly bounded nutrient concentration, there is no essential difference in our context. On the other hand, the choice of p makes a difference. The regime with $p \le 1$ is more realistic in the context of this paper since, even if the amount of resource is doubled, the consumption rate is not usually doubled. However, the case with $p > 1$ provides mathematically interesting phenomena and we consider both cases.

Remark 2 (Supersensitivity). The Weber-Fechner law, $\chi(m) = \frac{1}{m}$, blows up as $m \to 0$ and such a singularity is called a chemotactic supersensitivity. Notice that one needs both the chemotactic behavior and the population reproduction to get a traveling wave band phenomenon, where a persistent traveling wave does not exist in reality without reproduction. The contribution of chemotaxis theory is to show that the chemotactic behavior is so important in the phenomenon that this supersensitivity is enough to allow a traveling wave band even without any reproduction. However, if the relation (2) is taken instead of the simplification assumption $\mu'(m) = 0$ in (3), the diffusivity $\mu(m)$ also blows up as $m \to 0$ and it is unclear whether there exists a traveling wave band or not. We will obtain traveling waves under such a relation between the diffusivity and the chemosensitivity. To obtain a traveling wave band without such singularities, one should consider a problem with a population reproduction.

3. Main Theorems and Results

A traveling wave solution of speed $c \in \boldsymbol{R}$ is a solution in the form of

$$u(x,t) = u(x-ct), \quad m(x,t) = m(x-ct).$$

Introduce the variable for a traveling wave solution,

$$\xi = x - ct.$$

Then, from Equation (5), we obtain a system of ODEs

$$c\,u' = -(\gamma(s)u)'', \quad \xi \in \boldsymbol{R}, \tag{12}$$

$$c\,m' = k(m)u, \qquad \xi \in \boldsymbol{R}, \tag{13}$$

where the notation $'$ is to denote ordinary differentiation with respect to the single variable ξ. The boundary conditions are

$$u' \to 0,\ m' \to 0,\ u \to u_\pm \geq 0,\ m \to m_\pm \geq 0 \ \text{ as } \xi \to \pm\infty. \tag{14}$$

Lemma 1. *Let $(u(\xi), m(\xi))$ be a nonnegative traveling wave solution of (12)–(14). If u is not identically zero, then $m(\xi)$ is strictly monotone.*

Proof. Since the motility function satisfies (9), Equation (7) is uniformly parabolic. Hence, if a traveling wave solution u is not identically zero, it is strictly positive everywhere, i.e., $u(\xi) > 0$ for all $\xi \in \boldsymbol{R}$. Therefore, by (13), we have

$$m'(\xi) = \frac{k(m)u}{c} \neq 0.$$

Hence, m is strictly monotone. □

A traveling wave is called a *front type* if the boundary values at $\xi = \pm\infty$ are different. Lemma 1 implies that a nontrivial traveling wave of the resource distribution m is always a front type with a monotone profile. In the rest of this paper we consider the case when m is increasing under a boundary condition

$$0 \le m_- < m_+.$$

Then, the solution m is strictly increasing and we may consider $\xi = \xi(m)$ as the inverse function of $m = m(\xi)$. This choice of boundary data, $m_+ > 0$, forces us to choose $u_+ = 0$ since (11) and (13) imply that (m_+, u_+) is not a steady state for any $u_+ > 0$ if $m_+ > 0$. One can easily see that this steady state is unstable. In the rest of the paper the boundary values of the traveling wave at $\xi = \infty$ are fixed with

$$u_+ = 0, \quad m_+ > 0. \tag{15}$$

We will investigate the sufficient and necessary conditions of other boundary conditions u_-, m_- and the wave speed $c \in \boldsymbol{R}$ that give the existence of a traveling wave.

Lemma 2. *If $m_- > 0$ or $\int_0^{m_+} \frac{1}{k(\eta)} d\eta < \infty$, then the population size of the species is finite. Hence $u_- = 0$ is a necessary condition for the existence of a traveling wave solution.*

Proof. Equation (13) can be written as $u = c\frac{m'}{k(m)}$. Its integration over the whole real line gives the total population of the species, which is

$$\int_{-\infty}^{\infty} u(\xi) d\xi = c \int_{-\infty}^{\infty} \frac{m'}{k(m)} d\xi = c \int_{m_-}^{m_+} \frac{1}{k(m)} dm.$$

Under the hypotheses in (11) the right side is finite for all $m_- > 0$. Therefore, the population size is finite under the assumptions of the lemma. However, if $u_- > 0$, the total population size becomes infinite and hence $u_- = 0$ is a necessary condition. □

A traveling wave is called a *pulse type*, band, or localized if the boundary values at $\xi = \pm\infty$ are identical. Lemma 2 implies that there exists only a pulse type traveling wave if $\int_0^{m_+} \frac{1}{k(\eta)} d\eta < \infty$. We first consider necessary conditions to have a traveling wave solution and the possibility $m_- > 0$ is deleted.

Theorem 1. *Let $u_+ = 0$ and $0 \le m_- < m_+ < \infty$.*
(i) $m_- = 0$ and $c > 0$ are necessary conditions for the existence of a nontrivial traveling wave solution of (12)–(14).
(ii) If $\gamma(s)$ is bounded, there is no nontrivial traveling wave solution.

Proofs of this and subsequent theorems will be given in the next section. The types of traveling waves depends on the consumption rate $k = k(m)$ and the asymptotic behavior of the motility function $\gamma(s)$ as $s \to 0$. The following two theorems are for the two cases with $\int_0^{m_+} \frac{1}{k(\eta)} d\eta < \infty$ and $\int_0^{m_+} \frac{1}{k(\eta)} d\eta = \infty$.

Theorem 2. *Let* $u_+ = 0$, $0 \le m_- < m_+ < \infty$, *and* $\int_0^{m_+} \frac{1}{k(\eta)} d\eta < \infty$. *There exists a traveling wave solution of (12)–(14) if and only if* $u_- = m_- = 0$ *and* $\gamma(s) \to \infty$ *as* $s \to 0$. *The total population of the traveling species is*

$$N := c \int_0^{m_+} \frac{1}{k(\eta)} d\eta. \tag{16}$$

Theorem 2 gives the conditions of boundary values and the motility function for the existence of a traveling wave band solution. The condition $\int_0^{m_+} \frac{1}{k(\eta)} d\eta < \infty$ is the case with $0 < p < 1$ if the consumption rate is given by (4). The relation (16) shows that the wave speed c is related to the population size $N > 0$ and the consumption rate $k(m)$, but not to the motility function γ.

Remark 3. Keller and Odell [17, Theorem] found necessary and sufficient conditions for the existence of traveling wave band of finite size, which are

$$\lim_{m \to 0+} \frac{1}{k(m)\chi(m)} = 0, \tag{17}$$

$$\lim_{m \to 0+} \int_0^{m_+} \frac{\exp\left(- \int_m^{m_+} \frac{\chi(\eta)}{\mu(\eta)} d\eta \right)}{\mu(m) k(m)} dm = 0. \tag{18}$$

For the case with

$$\mu = m^r, \quad \chi = m^{-q} \quad \text{and} \quad k = m^p,$$

the corresponding conditions are

$$p < \min(1, q) \quad \text{and} \quad r + q \ge 1.$$

The two hypotheses of Keller and Odell are resolved in the unboundedness of the motility $\gamma(s)$ as $s \to 0$ in Theorem 2.

Next, we will go one step further for the case $\int_0^{m_+} \frac{1}{k(m)} dm = \infty$. The condition (17) appears in a slightly modified form in the following theorem. In this case we obtain front type traveling waves and pulse type ones of infinite mass. Non-existence of a traveling wave solution is also shown.

Theorem 3. *Let* $u_+ = 0$, $0 \le m_- < m_+ < \infty$, *and* $\int_0^{m_+} \frac{1}{k(\eta)} d\eta = \infty$.
(*i*) *Suppose that there exists* $0 < u_0 < \infty$ *such that*

$$-\lim_{m\to 0} \gamma'\Big(\frac{m}{u_0}\Big) k(m) = c^2. \tag{19}$$

Then, there exists a traveling wave solution of (12)–(14) if and only if $u_- = u_0$ *and* $m_- = 0$.
(*ii*) *Suppose that*

$$-\lim_{m\to 0} \gamma'\Big(\frac{m}{u_0}\Big) k(m) > c^2 \tag{20}$$

for any $u_0 > 0$. *Then, there exists a traveling wave solution of (12)–(14) if and only if* $u_- = m_- = 0$. *Furthermore, the traveling wave solution has infinite population mass.*
(*iii*) *Otherwise, there is no traveling wave solution for any boundary values* $u_-, m_- < \infty$.

The relation (19) shows that the speed of the traveling wave is independent of the amount of nutrient on the right side, $m_+ > 0$, for a case with $\int_0^{m_+} \frac{1}{k(\eta)} d\eta = \infty$. However, the amount of population density on the left side, $u_- = u_0$, and the asymptotic behavior of the motility function and the consumption rate at zero decide the traveling speed $c > 0$. If (20) is satisfied for all $u_0 > 0$ with a given $c = c_0 > 0$, then it is so for any given positive speed $c < c_0$. Hence there exists a traveling wave solution for any speed $c \ge c_0$. If the limit diverges to infinity, Theorem 3(*ii*) implies that there exists a localized traveling wave solution with any speed $c > 0$ with infinite population mass. To our knowledge this is the first proof of the existence of a localized traveling wave solution of a chemotaxis model with infinite population mass.

4. Proofs of Theorems

In this section we prove the three theorems stated in the previous section. We first clarify the exactness in the traveling wave system, which makes proofs a lot simpler than the original Keller-Segel cases. Let $0 \le m_- < m_+ < \infty$ and $u_+ = 0$. Then, the integration of (12) on (ξ, ∞) gives

$$-cu = (\gamma(s)u)' = \gamma_m m' u + \gamma_u u u' + \gamma(s) u',$$

where the boundary terms disappear by the boundary condition (14). Divide both sides by m' and substitute the relation $\frac{u}{m'} = \frac{c}{k(m)}$, which is from Equation (13), and obtain

$$\Big(\gamma_m u + \frac{c^2}{k(m)}\Big) + (\gamma_u u + \gamma)\frac{u'}{m'} = 0. \tag{21}$$

Therefore, the system (21) and (13) is equivalent to (12) and (13) under the boundary condition $m_+ > 0$ and $u_+ = 0$.

Next we consider a relation in the phase plane. (A detailed phase plane analysis is given in Section 5.) Since $m > 0$ and m is strictly increasing, one may consider u as a function of m by changing the variable. Hence the relation in (21) can be written as

$$M dm + U du = 0, \tag{22}$$

where $M := \gamma_m u + \frac{c^2}{k(m)}$ and $U := \gamma_u u + \gamma$. Then,

$$M_u = \gamma_{mu} u + \gamma_m = U_m,$$

which shows the equation for the traveling wave solution (22) is exact. This exactness is the key advantage of the chemotaxis model and gives a complete picture of traveling waves. Define

$$\psi(m,u) := \gamma u - c^2 H(m), \quad H'(m) = \frac{1}{k(m)}. \tag{23}$$

Then, the solution is implicitly given by

$$\psi(m,u) = \text{constant}.$$

Since $u \to u_+ = 0$, $s \to \lim_{m \to m_+} \frac{m}{u} = \infty$, and hence $\gamma \to \ell > 0$ as $m \to m_+$, we have the constant is $c^2 H(m_+)$. Hence, we have $H(m) = -\int_m^{m_+} \frac{1}{k(\eta)} d\eta$ and obtain

$$\psi(m,u) = \gamma u - c^2 \int_m^{m_+} \frac{1}{k(\eta)} d\eta = 0, \quad m_- < m < m_+. \tag{24}$$

Then, since

$$\psi_u = \gamma_u \, u + \gamma > 0, \quad m_- < m < m_+,$$

the implicit function theorem implies that there is a function $u = u(m)$ on (m_-, m_+).

Remark 4. It is clear that $u(m) \to 0\,(= u_+)$ as $m \to m_+$. Hence, for the existence of the traveling wave solution of (12)–(14), we only need to check if $u(m) \to u_-$ as $m \to m_-$. Therefore, showing a necessary condition for the boundary condition also gives a sufficient condition.

Remark 5. Consider the case when the motility is a function of m only, i.e., $\gamma = \gamma(m)$. In this case, the trajectory of a traveling wave is given explicitly by

$$u(m) = \frac{c^2}{\gamma(m)} \int_m^{m_+} \frac{1}{k(\eta)} d\eta.$$

Having the chemotaxis model in the form of (7) is highly advantageous since it gives an exact form for the traveling wave solution and makes a complete picture accessible.

Proof (of Theorem 1).

(i). From Equation (13) we obtain

$$u = c\frac{m'}{k(m)}.$$

Since $m > 0, u > 0$ and $m' > 0$ for all $\xi \in \boldsymbol{R}$, the wave speed is strictly positive by the relation, i.e., $c > 0$. Suppose that $m_- > 0$. Then, taking $m \to m_-$ limit for (24) gives

$$\lim_{m\to m_-} \gamma\Big(\frac{m}{u(m)}\Big)u(m) = c^2\int_{m_-}^{m_+}\frac{1}{k(\eta)}d\eta > 0.$$

If $u_- = 0$, then $\displaystyle\lim_{m\to m_-}\gamma(\frac{m}{u(m)})u(m) = \ell \times 0 = 0$ which contradicts the above relation. Hence $u_- > 0$, which also contradicts Lemma 2. Therefore $m_- = 0$ is a necessary condition.

(ii). Suppose that the motility function is bounded by $\gamma < A$ for some constant $A > 0$. Then, the relation (24) is written by

$$Au \geq c^2\int_m^{m_+}\frac{1}{k(\eta)}d\eta > 0.$$

If we let $m \to m_-(=0)$, we find $u_- \geq \frac{c^2}{A}\int_0^{m_+}\frac{1}{k(\eta)}d\eta > 0$. Hence, if $\int_0^{m_+}\frac{1}{k(\eta)}d\eta < \infty$, Lemma 2 is contradicted and there is no traveling wave solution. On the other hand, if $\int_0^{m_+}\frac{1}{k(\eta)}d\eta = \infty$, then $u(m) \to \infty$ as $m \to 0$ and hence there is again no traveling wave solution. Therefore, for any boundary condition $u_- \in \boldsymbol{R}$, we conclude that there is no traveling wave solution if γ is bounded. □

Proof (of Theorem 2).

($\Rightarrow$) We have $u_- = 0$ by Lemma 2 and $m_- = 0$ by Theorem 1(i). If γ is bounded, then $u_- > 0$ by the relation (24). Therefore, γ should be unbounded. Since γ is smooth on $(0,\infty)$ and $\gamma(s) \to \ell$ as $s \to \infty$, we have $\gamma(s) \to \infty$ as $s \to 0$.

($\Leftarrow$) It is enough to show that $u(m) \to u_-\,(=0)$ as $m \to m_-\,(=0)$, where $u = u(m)$ satisfies (24), i.e.,

$$\gamma\Big(\frac{m}{u(m)}\Big)u(m) = c^2\int_m^{m_+}\frac{1}{k(\eta)}d\eta, \quad m_- < m < m_+.$$

Suppose that $u(m) \to u_0 > 0$ as $m \to 0$. Then, for any c finite, as $m \to 0$,

$$\begin{aligned} &\gamma\Big(\frac{m}{u(m)}\Big)u(m) \to \infty, \\ &c^2 \int_m^{m_+} \frac{1}{k(\eta)} d\eta \to c^2 \int_0^{m_+} \frac{1}{k(\eta)} d\eta < \infty, \end{aligned}$$

which is a contradiction. Hence $u(m) \to 0$ as $m \to 0$.

The total population of the traveling wave band is computed by (13). Then,

$$\int_{-\infty}^{\infty} u(\xi) d\xi = \int_{-\infty}^{\infty} \frac{cm'}{k(m)} d\xi = \int_0^{m_+} \frac{c}{k(m)} dm,$$

which gives (16). □

Proof (of Theorem 3). We already have in Theorem 1(i) that $m_- = 0$ is a necessary condition. The other necessary condition for u_- comes from the relation (24) which can be written as

$$\gamma\Big(\frac{m}{u(m)}\Big)u(m) = c^2 \int_m^{m_+} \frac{1}{k(\eta)} d\eta. \tag{25}$$

Since the right side diverges to ∞ as $m \to 0$, the derivatives of both sides with respect to m should have the same asymptotics as $m \to 0$ if $u(m) \to u_- > 0$ as $m \to 0$. In other words, L'Hopital's rule is applicable and is the key of the following proof.

(i) Suppose that there exists a traveling wave solution and $u(m) \to u_- < u_0$ as $m \to 0$. Choose $u_1 > 0$ such that $u_- < u_1 < u_0$. From the relation (25) and the monotonicity of γ, we have

$$c^2 = \lim_{m\to 0} \frac{\gamma(\frac{m}{u})u}{\int_m^{m_+} \frac{1}{k(\eta)} d\eta} < \lim_{m\to 0} \frac{\gamma(\frac{m}{u_1})u_1}{\int_m^{m_+} \frac{1}{k(\eta)} d\eta}.$$

Since $\int_m^{m_+} \frac{1}{k(\eta)} d\eta \to \infty$ as $m \to 0$, we may apply L'Hopital's rule and obtain

$$-\lim_{m\to 0} \gamma'\Big(\frac{m}{u_1}\Big)k(m) > c^2.$$

However, this contradicts the assumption (19) since $\frac{m}{u_0} < \frac{m}{u_1}$ and no one diverges faster from the behind. One may similarly derive a contradiction if $u(m) \to u_- > u_0$ as $m \to 0$ and conclude that $u(m) \to u_0$ as $m \to 0$.

(ii) Suppose that there exists a traveling wave and $u(m) \to u_- > 0$ or $u(m) \to \infty$ as $m \to 0$. Take $u_1 > 0$ such that $u_1 < u_-$. Then, similarly,

$$c^2 = \lim_{m\to 0} \frac{\gamma(\frac{m}{u})u}{\int_m^{m_+} \frac{1}{k(\eta)} d\eta} > \lim_{m\to 0} \frac{\gamma(\frac{m}{u_1})u_1}{\int_m^{m_+} \frac{1}{k(\eta)} d\eta}.$$

Apply L'Hopital's rule and obtain

$$-\lim_{m\to 0}\gamma'\Big(\frac{m}{u_1}\Big)k(m) < c^2,$$

which contradicts the assumption (20). Hence $u(m)\to 0$ as $m\to 0$ if and only if there exists a traveling wave solution. The total population of the traveling wave band is computed by (13). Then, since $c\neq 0$,

$$\int_{-\infty}^{\infty} u(\xi)d\xi = \int_{-\infty}^{\infty}\frac{cm'}{k(m)}d\xi = \int_0^{m_+}\frac{c}{k(m)}dm = \infty.$$

(*iii*) Suppose that there exists a traveling wave such that $u(m)\to u_-$ as $m\to 0$. If $u_->0$, then (19) is satisfied with $u_0=u_-$. If $u_-=0$, then (20) is satisfied. Hence, if (19) and (20) fail, the only possibility is $u(m)\to\infty$ as $m\to 0$ and there is no traveling wave solution for any boundary condition $u_-\geq 0$. □

5. Phase Plane Analysis

contradicts to We study the structure of traveling wave solutions in this section using phase plane analysis. This study shows that the proofs in the previous section are closely related to this analysis. The basic relation satisfied by a traveling wave is (24). Note that Equation (22) gives a regularity to the solution, i.e.,

$$\frac{du}{dm} = \frac{-1}{\gamma_u u+\gamma}\Big(\gamma_m u + \frac{c^2}{k(m)}\Big), \quad m_- < m < m_+. \tag{26}$$

Hence, the derivative of $u=u(m)$ is continuous and bounded. This relation also implies that the monotonicity of the solution is divided along a curve

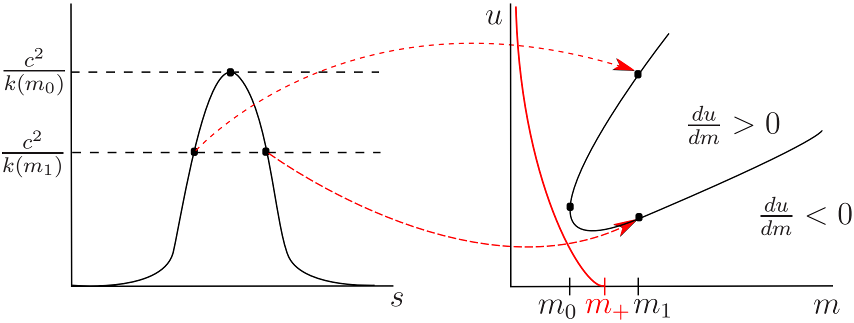
$$\gamma_m u + \frac{c^2}{k(m)} = 0.$$

We will call this curve a *separatrix* since the monotonicity of trajectories $u=u(m)$ are different in the two regions separated by this curve. Since $\gamma_m u = \gamma'(s)$, this separatrix satisfies

$$-\gamma'(s) = \frac{c^2}{k(m)}, \tag{27}$$

which is the relation used to characterize the traveling waves in Theorem 3 as in (19). In this section we analyze the trajectories of traveling waves in the phase plane using the separatrix.

First, consider a case when $-\gamma'(s)$ is bounded (see Figure 2(a)). Let $-\gamma'(s)\leq\kappa_0$ and $-\gamma'(s_0)=\kappa_0$ with $s_0\neq 0$. Then, since $k(m)\to 0$



(a) a graph of bounded $-\gamma'(s)$ (b) the separatrix and a trajectory

Fig. 2. The monotonicity of a traveling wave trajectory in the phase plane is divided by a curve called 'separatrix' in (b). This diagram shows its relation to the graph of γ' in (a) when γ' is bounded.

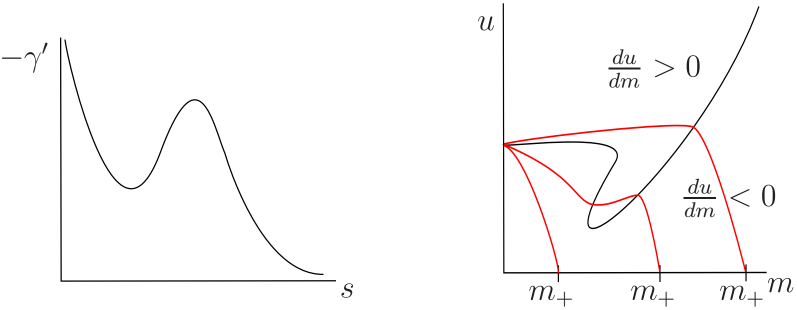
monotone as $m \to 0$, there exists a unique $m_0 > 0$ such that $\frac{c^2}{k(m_0)} = \kappa_0$. Therefore, a point (m_0, u_0) is on the curve if $s_0 = \frac{m_0}{u_0}$ or $u_0 = \frac{m_0}{s_0}$. Since $\frac{c^2}{k(m)} > \kappa_0$ for all $m < m_0$, the separatrix does not enter the region $m < m_0$ (see Figure 2(b)). Let $m_1 > m_0$. Then, there exists at least one $s > 0$ such that $\frac{c^2}{k(m_1)} = -\gamma'(s)$. For example, in Figure 2(a), there are two such points. Therefore, there should be two points in the separatrix corresponding the value $m = m_1$. Since $u = \frac{m}{s}$, the point with smaller satisfaction measure s corresponds to the upper point as in Figure 2. A rough sketch of the separatrix is given in Figure 2(b). If the maximum point is $s_0 = 0$, then the vertical line $m = m_0$ becomes an asymptote of the separatrix.

Next, consider the other limit of the trajectory $u = u(m)$ of a traveling wave which starts from an unstable steady state $(m_+, 0)$. Since $\frac{du}{dm} < 0$ for all $m < m_0$, there is no chance that the trajectory connects the origin as $m \to 0$. One might guess that $u(m) \to u_0 > 0$ as $m \to 0$. However, that is not possible by Theorem 3. Clearly,

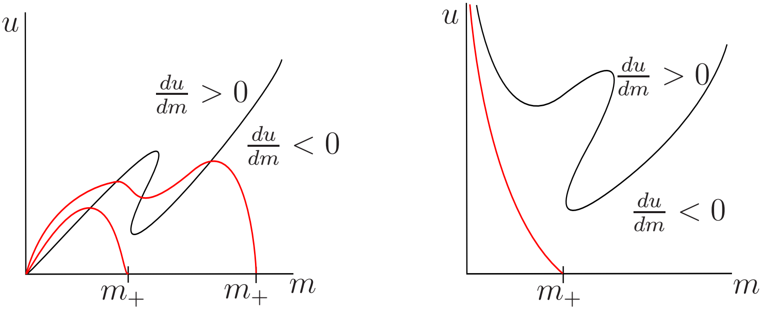
$$-\lim_{m\to 0} \gamma'\Big(\frac{m}{u_0}\Big)k(m) = 0$$

for any $u_0 > 0$ since γ' is bounded and $k(m) \to 0$ as $m \to 0$. Therefore, Theorem 3(*iii*) implies that $u(m) \to \infty$ as $m \to 0$. The only possibility is that the population u blows up as in Figure 2(b) as $m \to 0$.

The second case is when $\gamma'(s)$ is unbounded. Since $\gamma'(s) \to 0$ as $s \to \infty$ and γ is smooth on $(0, \infty)$, $-\gamma'(s) \to \infty$ as $s \to 0$ (see Figure 3(a)). Since γ' is unbounded, there exists at least one point in the separatrix for each $m > 0$. We assume that γ' is monotone for s small enough as in Theorem 3. Then, there are three possible cases for the limit of the separatrix as $m \to 0$ which are given in Figures 3(b), 3(c)



(a) a graph of unbounded $-\gamma'(s)$ (b) trajectories of case in Thm 3(i)



(c) trajectories related to Thm 2,3(ii) (d) trajectories related to Thm 3(iii)

Fig. 3. A graph of $-\gamma'$ is given in (a) when $-\gamma'(s) \to \infty$ as $s \to 0$. Three types trajectories of traveling waves are given with dashed lines in (b),(c) and (d). The monotonicity of a traveling wave trajectory is divided by a curve called 'separatrix' given in solid lines.

and 3(d). These three cases correspond to the three cases of Theorem 3 in that order. In fact the conditions of (19) and (20) are the ones of (27) for m small.

Similarly, consider the other limit of the trajectory $u = u(m)$ that starts from $(m_+, 0)$. Theorem 3 implies that the trajectory connects the same limit of the separatrix as $m \to 0$ (see Figures 3(b),3(c) and 3(d)). One can formally see the reason directly from (24). If $u(m) \to u_0 > 0$ as $m \to 0$, the relation gives

$$\gamma\Big(\frac{m}{u_0}\Big)u_0 - \int_m^{m_+} \frac{c^2}{k(\eta)}d\eta \to 0 \quad \text{as} \quad m \to 0.$$

Therefore, this convergence is possible only if two terms diverge with the same speed. If the integral term grows slow in comparison with a given motility function or vice-versa as $m \to 0$, then there is no such $u_0 > 0$. Hence, derivatives of both terms with respect to m decides the limit, which are

$$\frac{\partial}{\partial m}\Big(\gamma\Big(\frac{m}{u_0}\Big)u_0\Big) = \gamma'\Big(\frac{m}{u_0}\Big), \quad \frac{\partial}{\partial m}\int_m^{m_+} \frac{c^2}{k(\eta)}d\eta = -\frac{c^2}{k(m)}.$$

In other words, even if the separatrix and the traveling wave trajectories satisfy different relations, their behaviors near $m = 0$ are decided by the same dynamics and hence they have the same limit as $m \to 0$.

Remark 6 (Monotonicity of traveling waves). Lemma 1 implies that the resource distribution $m = m(\xi)$ of a traveling wave is always monotone and hence it is a front type. However, the profile of the population distribution $u = u(\xi)$ is not monotone in general. A pulse type traveling wave is not monotone of course. However, even if $u = u(\xi)$ is a front type, it is not necessarily monotone. If the trajectory of a traveling wave stays in one of the two regions divided by the separatrix, then u is monotone. However, if it crosses the boundary as in Figures 3(b) and 3(c), then $u = u(\xi)$ is not monotone.

6. Numerical Simulations

The purpose of this section is to provide specific examples of traveling wave solutions by numerically computing the differential equations and to compare them with the theorems. Hence we will choose specific γ and k for each of the three cases. We also simulate the appearance of a localized traveling wave and compare it to the theoretical traveling waves. Consider a Cauchy problem of our chemotaxis model

$$\begin{cases} u_t = (\gamma(s)u)_{xx}, & m_t = -k(m)u, \\ u(x,0) = 0.1\chi_{(-0.2,0.2)}, & m(x,0) = 0.1, \end{cases} \qquad x \in \boldsymbol{R},\ t > 0, \tag{28}$$

where

$$\gamma(s) = 0.005(s^{-4} + 1), \quad k(m) = 5\, m^{1/2}. \tag{29}$$

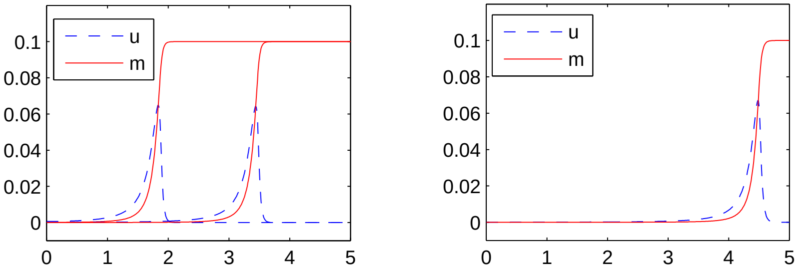
Since both the equation and the initial value are symmetric with respect to the origin, so is the solution. The initial population distribution splits in two pieces and then propagates into opposite directions symmetrically. The population size of each piece is $N = 0.02$. The consumption rate of this example gives

$$\int_0^{m_+} \frac{1}{k(m)} dm = \frac{1}{5} \int_0^{0.1} m^{-1/2} dm = \frac{2\sqrt{0.1}}{5} < \infty.$$

Therefore, we are in the case of Theorem 2 and the traveling wave speed is given by (16), which is

$$c = 0.02 \times \frac{5}{2\sqrt{0.1}} \cong 0.158.$$

A numerical simulation for the traveling wave moving to right is given in Figure 4(a). The profile of the wave has been displayed at two different incidents $t = 10$ and 20. The numerical wave speed is



(a) Traveling waves at two different moments $t = 10$ and 20

(b)Pulse type traveling wave for (29)–(31) with $c = 0.158$

Fig. 4. [A case with $\int_0^1 \frac{1}{k(m)} dm < \infty$] The numerical simulations for (28) is given in (a) at two different times $t = 10$ and 20. A pulse type traveling band of finite population is formed and moves with a constant speed. The ode system (30) for traveling wave solution gives the same traveling wave solution.

about $c = 0.160$. The shape and the speed of the traveling wave fits to the simulation of the model case (28).

Consider the solution of the ODE system (12)–(13). Since $m_- = u_+ = 0$ are necessary conditions and $m_+ = 0.1$ is given, we take them. Then, the second order equation in the first row is turned into a first order one after integration on (ξ, ∞). Then the equations are written as

$$\begin{cases} c(\gamma'(s)s - \gamma)u' = c^2 u + \gamma'(s)k(m)u, \\ c\,m' = k(m)u, \end{cases} \qquad \xi \in \boldsymbol{R}, \tag{30}$$

where the boundary values are

$$u_- = u_+ = m_- = 0, \qquad m_+ = 0.1.$$

A solution of this traveling wave equation is given in Figure 4(b). For the computation, boundary conditions and the wave speed are given as

$$m(5) = 0.1, \quad u(5) = 10^{-7}, \quad c = 0.158. \tag{31}$$

The solution is then computed for $x < 5$. For the comparison with the numerical simulation of (28) in Figure 4(a), we have used the same wave speed in this computation. One may observe the same structure of the solution.

Next we consider an example of a front type traveling wave corresponding to the case in Theorem 3(i). First, let

$$\gamma(s) = 0.005(s^{-2} + 1), \quad k(m) = 10\,m^3. \tag{32}$$

In this example we took a consumption rate k satisfying $\int_0^{m_+} \frac{1}{k(m)} dm = \infty$. We are looking for a front type traveling wave with $m_+ = u_- =$

0.1 and $u_+ = m_- = 0$. Then, the relation (19) is written as

$$-\lim_{m\to 0}\gamma'\Big(\frac{m}{0.1}\Big)k(m) = 0.01\Big(\frac{m}{0.1}\Big)^{-3}10m^3 = (0.1)^4 = c^2.$$

Hence the traveling wave speed should be $c = 0.01$. The traveling wave for this case can be numerically computed by solving the ordinary differential equation (30). In Figure 5(a), a traveling wave is given after solving it with boundary conditions,

$$m(100) = 0.1, \quad u(100) = 10^{-7}, \tag{33}$$

and a wave speed $c = 0.01$. One may observe that the population density u converges exactly to $u_- = 0.1$ as $\xi \to -\infty$. In Figure 5(b), the traveling wave with a wave speed $c = 0.005$ is given with the same boundary conditions. In this case the population density u converges approximately to $u_- = 0.061$ as $\xi \to -\infty$. One may check that this is the value that approximately satisfies the relation (19).

Next we consider an example of a localized traveling wave corresponding to the case of Theorem 3(*ii*). First, let

$$\gamma(s) = 0.005(s^{-3}+1), \quad k(m) = 10\,m^2. \tag{34}$$

Then, for any given $u_0 > 0$, one may easily see that

$$-\lim_{m\to 0}\gamma'\Big(\frac{m}{u_0}\Big)k(m) = \infty.$$

Therefore, Theorem 3(*ii*) implies that, for any given wave speed $c > 0$, there exists a pulse type traveling wave solution of infinite population mass having the speed. Therefore, the waves are not distinguishable in terms of the population size or the boundary condition u_-. The only measure to distinguish them is the wave speed. In Figures 5(c) and 5(d), two pulse type traveling waves are displayed with wave speeds $c = 0.0077$ and 0.0039, respectively. Roughly speaking, we may say from these examples that a faster traveling wave is bigger than a slower one.

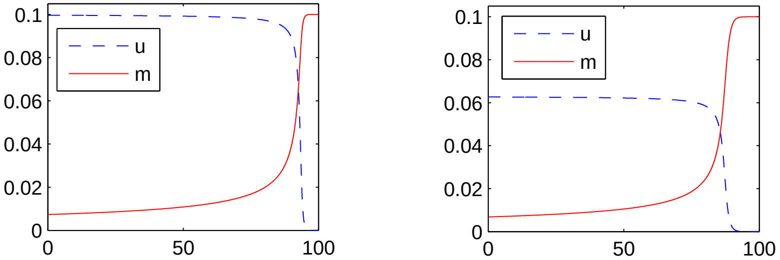
Finally we consider blowing up solutions in Theorem 3(*iii*). Let

$$\gamma(s) = 0.005(s^{-1}+1), \quad k(m) = 10\,m^4. \tag{35}$$

Then, for any $u_0 > 0$, we have

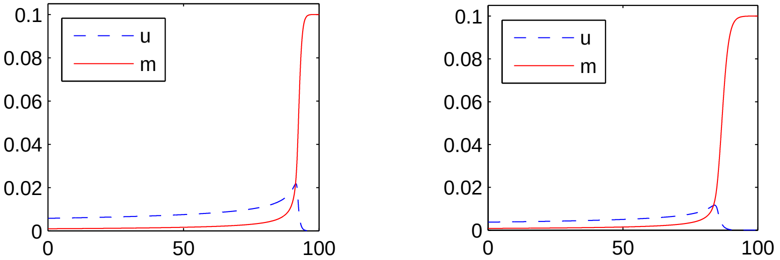
$$-\lim_{m\to 0}\gamma'\Big(\frac{m}{u_0}\Big)k(m) = 0,$$

and hence Theorem 3(*iii*) implies that there is no traveling wave solution for any given boundary data $0 \le u_- < \infty$. In Figures 5(e) and 5(f), two examples of blowing up solution of (30) with wave speeds $c = 0.0224$ and 0.0112, respectively. One may observe that the population $u(\xi)$ increases as $\xi \to -\infty$.



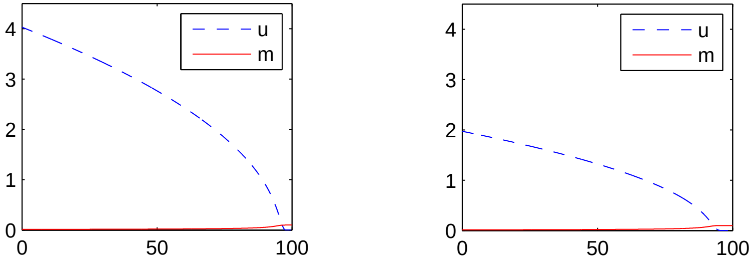
(a) Front type traveling wave with (32), (33) and $c = 0.01$

(b) Front type traveling wave with (32), (33) and $c = 0.005$



(c) Pulse type traveling wave with (34), (33) and $c = 0.0077$

(d) Pulse type traveling wave with (34), (33) and $c = 0.0039$



(e) Blowing up solution with (35), (33) and $c = 0.0224$

(f) Blowing up solution with (35), (33) and $c = 0.0112$

Fig. 5. [Three cases with $\int_0^1 \frac{1}{k(m)} dm = \infty$] Front type traveling waves are given in (a) and (b) with different wave speed. The pulse type traveling waves in (c) and (d) are of infinite population mass. Figures (e) and (f) are examples that traveling wave solutions blow up. One may observe a logarithmic growth of the population $u(\xi)$ as $\xi \to -\infty$. In these cases there is no traveling wave solution for any boundary value $u_- < \infty$.

7. Discussions

Chemotaxis is the phenomenon whereby biological organisms move toward or away from higher concentration of signaling chemicals such as pheromone or nutrients. Most of chemotaxis models are based on the assumption that organisms measure the concentration gradient. There are several models on sensing spatial or temporal gradients of chemical concentrations. However, it is still puzzling if micro-scale organisms such as bacteria really recognize the macro-scale concentration gradient of chemicals.

In this paper we propose a new theory for the chemotaxis phenomenon without the usual assumption of gradient-sensing. In the context of Adler's [1,2] traveling wave band phenomenon, the microscopic scale organism, or *Escherichia coli*, was assumed to disperse more actively to find food if there is not enough food, i.e., the dispersal is driven by starvation. In this case the individuals have the intention to move to other place without knowing the direction with more food and hence the movement is in a complete random manner. However, this conditional eagerness for migration produces advection and we have still observed chemotaxis phenomenon. In fact, we have easily obtained all previously obtained traveling waves using our model.

The chemotaxis phenomenon of single-celled organisms has attracted attention because of its role in various biological phenomena including multicellular organisms (see [13]). For example, the movement of sperm towards the egg during fertilization or the cell positioning during embryonic development is sometimes guided by chemical signals [10,12]. The invasion of tumor cells and their stimulation for new blood vessel growth are also guided by chemotactic phenomena [6,7,19]. The theory in this paper suggests that motility control is another possibility to guide cell migration. We have seen that, even if bacteria do not sense the concentration gradient, they may escape a place and move to a preferred place by simply increasing their motility. This behavior may give exactly the same chemotactic term of the Keller-Segel model. In other words, if cell motility is activated in one place and deactivated in another place, then cell migration to a specific place can be obtained.

Appendix A. Derivation of a starvation driven diffusion

In this section we introduce a short derivation of a starvation driven diffusion (see [5] for detailed discussions). Consider a random walk system with a constant walk length Δx and a constant jumping time interval Δt. Let $0 < \gamma(x_i) \leq 1$ be the probability for a particle to depart a grid point x_i at each jumping time. (For a usual random walk system every particle departs at each jumping time and hence $\gamma = 1$.) Each particle moves to one of two adjacent grid points, x_{i+1} or x_{i-1}, randomly. Let $U(x_i)$ be the number of particles placed at the grid point x_i. Then, the particle density is $u = U/\Delta x$. Hence the net flux that crosses a middle point $x_{i+1/2} := \frac{x_i+x_{i+1}}{2}$ is

$$\begin{aligned} J\Big|_{x_{i+1/2}} &= \frac{\gamma(x_i)|\Delta x|u(x_i)}{2|\Delta t|} - \frac{\gamma(x_{i+1})|\Delta x|u(x_{i+1})}{2|\Delta t|} \\ &\cong -\frac{|\Delta x|^2}{2\Delta t}(\gamma u)_x\Big|_{x_{i+1/2}}. \end{aligned}$$

The corresponding diffusion equation comes from the conservation law

$$u_t = -\nabla \cdot J = \frac{|\Delta x|^2}{2\Delta t}(\gamma u)_{xx}.$$

After a time rescaling we obtain the desired equation

$$u_t = (\gamma u)_{xx}.$$

Notice that the probability γ depends only on the departing point x_i, which indicates the concentration gradient is not measured. If the probability depends on nearby points, then it implies gradient information is used to decide the migration probability. For more discussion including other cases, see Okubo and Levin [26, §5.4].

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