Traveling wave solutions for a bacteria system with density-suppressed motility

R. Lui* and H. Ninomiya†

Abstract

In 2011, Liu et. al. proposed a three-component reaction-diffusion system to model the spread of bacteria and its signaling molecules (AHL) in an expanding cell population. At high AHL levels the bacteria are immotile, but diffuse with a positive diffusion constant at low distributions of AHL. In 2012, Fu et. al. studied a reduced system without considering nutrition and made heuristic arguments about the existence of traveling wave solutions. In this paper we provide rigorous proofs of the existence of traveling wave solutions for the reduced system under some simple conditions of the model parameters.

1 Introduction

It is well known that spatial patterns are ubiquitous in living organisms. For many years, scientists are intrigued by these patterns and have developed many mathematical models trying to explain them [5]. In the paper [4], the authors described a genetic circuit to suppress the motility of *Escherichia coli* cells at high cell level. They were able to observe periodic stripe patterns in their experiments. In the same paper, the authors also developed a three-component reaction-diffusion system involving the cell density and densities of the signaling molecules AHL and the nutrients to explain the observed phenomena. In the paper [3], the authors studied a reduced two-component system and gave heuristic arguments that traveling wave solutions exist. It is the purpose of this paper to give a rigorous proof of the existence of traveling wave solutions. The plots of the cell and AHL densities in [3] look remarkably similar to our traveling wave solutions.

The reduced-system studied in [3] is the following,

$$\left\{\begin{array}{rcl} \dfrac{\partial h}{\partial t} &=& D_h\dfrac{\partial^2 h}{\partial x^2} + \alpha\rho - \beta h, , \\ \dfrac{\partial \rho}{\partial t} &=& \dfrac{\partial^2}{\partial x^2}[\mu(h)\rho] + \gamma\rho\left(1 - \dfrac{\rho}{\rho_s}\right), \qquad \text{for } t > 0,\ x \in \mathbb{R}, \end{array}\right.$$

*Department of Mathematical Sciences, WPI, 100 Institute Road, Worcester, MA 01609, U.S.A.

†School of Interdisciplinary Mathematical Sciences, Meiji University 4-21-1 Nakano, Nakano-ku, Tokyo 164-8525, Japan

where $\mu(h)$ is the bacteria diffusion which decreases from D_ρ to a smaller value $D_{\rho,0}$ as h increases pass the threshold value h_0. In the above model, ρ is the density of the bacteria *Escherichia Coli*, which follow logistic growth. The bacteria excrete a small and rapidly degraded signaling molecules acyl-homoserine lactone (AHL) represented by h in the above model. At AHL level below h_0, the bacteria perform random walk via their run-and-tumble motion and are motile. At AHL level above h_0, the bacteria tumble incessantly and may be considered as immotile [1, 2]. In this paper, we assume that $D_{\rho,0} = 0$ and let $\mu(h) = D_\rho$ for $h < h_0$ and $\mu(h) = 0$ for $h > h_0$.

We first scale the system by dividing the first equation by h_0, the second equation by ρ_s. Then we scale time and space by letting $x = \sqrt{D_h/\beta}\, x'$, $t = t'/\beta$ to obtain the system

$$
\left\{
\begin{array}{rcl}
\dfrac{\partial h}{\partial t} & = & \dfrac{\partial^2 h}{\partial x^2} + \tilde{\alpha}\rho - h, \\
\dfrac{\partial \rho}{\partial t} & = & \dfrac{\partial^2}{\partial x^2}[\mu(h)\rho] + \tilde{\gamma}\rho(1-\rho),
\end{array}
\right.
\tag{1.1}
$$

where $\tilde{\alpha} = \alpha\rho_s/(h_0\beta)$, $\tilde{\gamma} = \gamma/\beta$ and

$$
\mu(h) = \begin{cases} D := \dfrac{D_\rho}{D_h} & \text{if } h < 1, \\ 0 & \text{if } h > 1. \end{cases}
$$

Suppose the location where $h = 1$ moves at a constant speed $c > 0$. We look for traveling wave solutions of the form $\hat{h}(z) = \hat{h}(x - ct)$, $\hat{\rho}(z) = \hat{\rho}(x - ct)$ that are non-constant on the intervals $(-\infty, 0)$ and $(0, \infty)$, and have constant limits as $z \to \pm\infty$. The constant c is called the wave speed and has to be determined together with $\hat{h}(z)$ and $\hat{\rho}(z)$. Substituting into (1.1), we have

$$
\hat{h}'' + c\hat{h}' - \hat{h} = -\hat{\alpha}\hat{\rho}, \tag{1.2}
$$

$$
(\mu(\hat{h})\hat{\rho})'' + c\hat{\rho}' + \gamma\hat{\rho}(1-\hat{\rho}) = 0. \tag{1.3}
$$

In what follows, we drop the 'hat' sign in equations (1.2) and (1.3). Let

$$
\begin{array}{rcl}
h(z) & = & \begin{cases} h_+(z) & (z \geq 0), \\ h_-(z) & (z < 0), \end{cases} \\
\rho(z) & = & \begin{cases} \rho_+(z) & (z \geq 0), \\ \rho_-(z) & (z < 0). \end{cases}
\end{array}
$$

We assume that h is a continuous function and ρ is discontinuous only at $z = 0$. We let

$$
\rho_{-0} := \lim_{z \uparrow 0} \rho(z) \tag{1.4}
$$

and assume that

$$h_-(z) > 1 \quad (z < 0), \quad h_+(z) \le 1 \quad (z > 0). \tag{1.5}$$

Note that from (1.5), $h(0) = 1$. The positive constants $\rho_{-0}, \alpha, \gamma$ and D are considered as model parameters in this paper.

The paper is organized as follows: In Section 2, we consider solutions of equations (1.2) and (1.3). In Section 3, we derive an equation the wave speed must satisfy and also give sufficient conditions that this equation has a root. The main results are given in Section 4. In Theorem 4.2, we give a sufficient condition for $h(z) \le 1$ when $z \ge 0$, which together with the existence of wave speed imply the existence of traveling waves. In Theorem 4.3, we give sufficient condition that given c greater than the minimum wave speed, there exists a unique ρ_{-0} (see (1.4)) such that traveling wave solutions exist with wave speed c. Section 5 is discussion.

2 Mathematical Preliminaries

2.1 The function ρ

When $z < 0$, $h > 1$, so that $\mu(h) = 0$. Solving (1.3) by separation of variables and using (1.4), we have

$$\rho_-(z) = \frac{\rho_{-0}}{\rho_{-0} + (1 - \rho_{-0})e^{\gamma z/c}}. \tag{2.1}$$

Note that

$$\lim_{z \to -\infty} \rho_-(z) = 1\,.$$

From the weak sense of (1.3), it follows that

$$\int_{-\infty}^{\infty} \mu(h(z))\rho(z)\,\psi''(z)\,dz - c\int_{-\infty}^{\infty} \rho(z)\psi'(z)\,dz + \int_{-\infty}^{\infty} \gamma\rho(z)(1-\rho(z))\psi(z)\,dz = 0$$

for any $\psi \in C^\infty(\mathbb{R})$. For any $\varepsilon > 0$, let $\psi \in C^\infty(\mathbb{R})$ vanish outside of $(-\varepsilon, \varepsilon)$ and satisfy $0 \le \psi \le 1$ and $\psi(0) = 1$. Assume that $\rho_+, \rho'_+, \rho''_+$ are bounded in $[0, \infty)$ and ρ_-, ρ'_- are bounded in $(-\infty, 0]$. The integration by parts yields

$$\int_{0+}^{\varepsilon} D\rho_+\psi''\,dz - c\,[\rho_+\psi]_{0+}^{\varepsilon} - c\,[\rho_-\psi]_{-\varepsilon}^{0-} + c\int_{0+}^{\varepsilon} \rho'_+\psi\,dz + c\int_{-\varepsilon}^{0-} \rho'_-\psi\,dz \;=\; o(1).$$

as $\varepsilon \downarrow 0$. Using the integration by parts twice, we get

$$-D\rho_+(0)\psi'(0) - \left[D\rho'_+\psi\right]_{0+}^{\varepsilon} + \int_{0+}^{\varepsilon} D\rho''_+\psi\,dz + c\rho_+(0)\psi(0) - c\rho_-(0)\psi(0) \;=\; o(1).$$

Here we used the notation as follows: $\rho_+(0) = \lim_{z\downarrow 0} \rho_+(z)$ and $\rho_-(0) = \lim_{z\uparrow 0} \rho_-(z)$ etc. By the assumption of $\rho_\pm$, we have

$$-D\rho_+(0)\psi'(0) + D\rho_+'(0)\psi(0) + c\rho_+(0)\psi(0) - c\rho_-(0)\psi(0) \quad = \quad o(1).$$

Letting $\varepsilon \downarrow 0$, we obtain that

$$\rho_+(0) = 0, \qquad \rho_+'(0) = \frac{c}{D}\,\rho_{-0}. \tag{2.2}$$

When $z > 0$, $\mu(h) = D$ and (1.3) becomes

$$D\rho_+'' + c\rho_+' + \gamma\rho_+(1-\rho_+) = 0\,, \quad \rho_+(0) = 0,\ \rho_+'(0) = \frac{c}{D}\,\rho_{-0}. \tag{2.3}$$

Writing this as a system, we have

$$\begin{aligned} \rho_+' &= q, \\ q' &= -\frac{c}{D}\,q - \frac{\gamma}{D}\rho_+(1-\rho_+). \end{aligned}$$

It is well known that $c \geq c_1^* := 2\sqrt{\gamma D}$ if $\rho_+(z)$ is to remain positive. The Jacobian matrix at the equilibrium point $(1,0)$ is

$$J = \begin{bmatrix} 0 & 1 \\ \dfrac{\gamma}{D} & -\dfrac{c}{D} \end{bmatrix}.$$

We see that $(1,0)$ is a saddle. Consider the line segment

$$q = -\frac{c}{D}(\rho_+ - 1)$$

for $\rho_+ \in [0,1]$ in the phase plane. Since $dq/d\rho_+ < -c/D$ for $\rho_+ \in (0,1]$ on this line segment, the orbit starting from the point $(0, c\rho_{-0}/D)$ for any $\rho_{-0} \in (0,1]$ cannot cross the line segment and has to cross the ρ_+-axis where $\rho_+(z)$ makes a maximum and then approaches the origin. We assume that $\rho_{-0} < 1$ for if $\rho_{-0} = 1$, then $\rho_-(z) = 1$. Hence, $0 < \rho_+(z) < 1$ for $z > 0$. Note that $\rho_-(z)$ is a decreasing function for $z < 0$.

Lemma 2.1. *Let $\rho(z;\rho_{-0})$ be the solution of* (1.3) *with $\lim\limits_{z\uparrow 0} \rho(z) = \rho_{-0} \in (0,1)$. If $0 < \rho_{-0} < \tilde{\rho}_{-0} < 1$, then $0 \leq \rho(z;\rho_{-0}) \leq \rho(z;\tilde{\rho}_{-0})$ for $z \in \mathbb{R}$.*

Proof. For $z < 0$, it is easily seen from (2.1) that $\rho_-(z,\rho_{-0})$ is increasing in ρ_{-0}. We only need to show $\rho(z;\tilde{\rho}_{-0}) \geq \rho(z;\rho_{-0})$ in $z > 0$. Denote $\rho(z;\tilde{\rho}_{-0})$ and $\rho(z;\rho_{-0})$ by $\tilde{\rho}(z)$ and $\rho(z)$, respectively. We prove by contradiction. By the third condition of (2.3), $0 < \rho(z) < \tilde{\rho}(z)$ for small positive z. Assume that there is a $z^* > 0$ such that $\tilde{\rho}(z^*) = \rho(z^*)$ and $0 < \rho(z) < \tilde{\rho}(z)$ for $0 < z < z^*$. Then

$$\begin{aligned} D(\tilde{\rho}'\rho - \tilde{\rho}\rho')' + c(\tilde{\rho}'\rho - \tilde{\rho}\rho') &= D(\tilde{\rho}''\rho - \tilde{\rho}\rho'') + c(\tilde{\rho}'\rho - \tilde{\rho}\rho') \\ &= -\gamma\tilde{\rho}(1-\tilde{\rho})\rho + \gamma\rho(1-\rho)\tilde{\rho} \\ &= \gamma\tilde{\rho}\rho(\tilde{\rho} - \rho) > 0 \end{aligned}$$

for $0 < z < z^*$. Multiplying the above by $e^{cz/D}$ and integrating both sides over $(0, z)$ yield

$$\tilde{\rho}'\rho - \tilde{\rho}\rho' > 0$$

for $0 < z \le z^*$. This implies that $\tilde{\rho}(z^*) > \rho(z^*)$, which contradicts the choice of z^*. The proof of the lemma is complete. $\square$

2.2 The function h

Consider the equation

$$h'' + ch' - h = -\alpha\rho(z). \tag{2.4}$$

Since $h(z)$ is continuous, integrating (2.4) from $-\varepsilon$ to ε and letting $\varepsilon \downarrow 0$, we have $h'(0-) = h'(0+)$ so that h is differentiable. Clearly, h is not C^2.

Consider the homogeneous differential equation

$$h'' + ch' - h = 0.$$

We denote the characteristic roots by

$$\lambda_\pm := \frac{-c \pm \sqrt{c^2+4}}{2}.$$

Applying the variation of constant formula to (2.4), we have

$$h(z) = (C_1 + A(z))\, e^{\lambda_+ z} + (C_2 + B(z))\, e^{\lambda_- z}, \tag{2.5}$$

where

$$\begin{aligned} A(z) &= -\frac{\alpha}{\sqrt{c^2+4}} \int_0^z \rho(\xi) e^{-\lambda_+ \xi} d\xi, \\ B(z) &= \frac{\alpha}{\sqrt{c^2+4}} \int_0^z \rho(\xi) e^{-\lambda_- \xi} d\xi. \end{aligned}$$

Here we have used the facts that

$$\lambda_+ - \lambda_- = \sqrt{c^2+4}, \quad \lambda_+\lambda_- = -1. \tag{2.6}$$

Since $A(0) = 0, B(0) = 0$, the condition $h(0) = 1$ implies that $C_1 + C_2 = 1$ so that $C_2 = 1 - C_1$.

In order for h to be bounded for $z > 0$, since $\lambda_+ > 0$, we need $C_1 = -A(\infty)$. Next we confirm that $(C_1 + A(z))e^{\lambda_+ z}$ in (2.5) converges as $z \to \infty$. Since $\lambda_+ > 0$,

$$(C_1 + A(z))e^{\lambda_+ z} = \frac{\alpha}{\sqrt{c^2+4}} \int_z^\infty \rho(\xi) e^{-\lambda_+(\xi - z)}\, d\xi$$

converges to zero if $\rho(z)$ is integrable near infinity. Now since $\lambda_- < 0$, $C_2\, e^{\lambda_- z}$ goes to zero as $z \to \infty$. Also

$$|B(z)|e^{\lambda_- z} = \frac{\alpha}{\sqrt{c^2+4}} \int_0^z \rho(\xi) e^{\lambda_-(z-\xi)}\, d\xi = \frac{\alpha}{\sqrt{c^2+4}} \int_0^z \rho(z-\tau)\, e^{\lambda_- \tau}\, d\tau\,.$$

Since $\rho(\infty) = 0$, the dominated convergence theorem implies that the above term goes to zero as $z \to \infty$. Hence we obtain

$$\lim_{z\to\infty} h(z) = 0.$$

From the above, we see that $h(z)$ can also be written as

$$h(z) = \frac{\alpha}{\sqrt{c^2+4}} \int_z^\infty \rho(\xi) e^{-\lambda_+(\xi - z)} d\xi + \frac{\alpha}{\sqrt{c^2+4}} \int_0^z \rho(\xi) e^{\lambda_-(z-\xi)} d\xi + K e^{\lambda_- z}, \tag{2.7}$$

where

$$K := 1 - \frac{\alpha}{\sqrt{c^2+4}} \int_0^\infty \rho(\xi) e^{-\lambda_+ \xi} d\xi.$$

3 The wave speed c

In this section, we first derive an equation for the wave speed, which is the equation (3.1) below. We then give sufficient conditions for the equation (3.1) to have a root.

Proposition 3.1. *If $c > 0$ is such that $h(z)$ is differentiable at the origin, then c satisfies the equation*

$$1 - \frac{\alpha}{\sqrt{c^2+4}} \int_{-\infty}^0 \rho(z;\rho_{-0}) e^{-\lambda_- z}\, dz - \frac{\alpha}{\sqrt{c^2+4}} \int_0^\infty \rho(z;\rho_{-0}) e^{-\lambda_+ z}\, dz = 0. \tag{3.1}$$

Proof. Multiplying equation (2.4) by $e^{-\lambda_+ z}$ and integrating the result from 0 to ∞, we have,

$$h'(0+) = \lambda_- + \alpha \int_0^\infty \rho(\xi) e^{-\lambda_+ \xi}\, d\xi.$$

Similarly, multiplying equation (2.4) by $e^{-\lambda_- z}$ and integrating the result from $-\infty$ to 0, we have

$$h'(0-) = \lambda_+ - \alpha \int_{-\infty}^0 \rho(\xi) e^{-\lambda_- \xi}\, d\xi.$$

Setting the two derivatives of h at the origin equal and using the fact $\lambda_+ - \lambda_- = \sqrt{c^2+1}$, we obtain equation (3.1). The proof of the proposition is complete. $\square$

Next, we want to give a sufficient condition that equation (3.1) has a root. From the paragraph above Lemma 2.1 the root lies in the interval (c_1^*, ∞) since we have assumed that $\rho_{-0} < 1$. Let

$$N(c, \rho_{-0}) := \frac{1}{\sqrt{c^2+4}} \left(\int_{-\infty}^{0} \rho(z; \rho_{-0}) e^{-\lambda_- z}\, dz + \int_0^\infty \rho(z; \rho_{-0}) e^{-\lambda_+ z}\, dz \right). \tag{3.2}$$

Then equation (3.1) is $1 - \alpha N(c, \rho_{-0}) = 0$.

Lemma 3.2. *If $\alpha\rho_{-0} > \gamma + 1$, then $\liminf_{c\to\infty} N(c, \rho_{-0}) > 1/\alpha$. Thus, if $N(c_1^*, \rho_{-0}) < 1/\alpha$, then equation (3.1) has a root.*

Proof. Define

$$I := \int_0^\infty \rho(s) e^{-\lambda_+ s} ds.$$

Multiplying (2.3) by $e^{-\lambda_+ z}$ and integrating the result over $(0, \infty)$ yield

$$D \int_0^\infty \rho''(z) e^{-\lambda_+ z} dz + c \int_0^\infty \rho'(z) e^{-\lambda_+ z} dz + \gamma \int_0^\infty \rho(z)(1 - \rho(z)) e^{-\lambda_+ z} dz = 0.$$

Since

$$\int_0^\infty \rho'(z) e^{-\lambda_+ z} dz = \lambda_+ I, \qquad \int_0^\infty \rho''(z) e^{-\lambda_+ z} dz = -\rho'_+(0) + \lambda_+^2 I,$$

we obtain

$$D(-\rho'_+(0) + \lambda_+^2 I) + c\lambda_+ I + \gamma I > 0.$$

From $\lambda_+^2 + c\lambda_+ - 1 = 0$,

$$I > \frac{D\rho'_+(0)}{c(1-D)\lambda_+ + \gamma + D} = \frac{c\rho_{-0}}{c(1-D)\lambda_+ + \gamma + D}.$$

Therefore,

$$N(c, \rho_{-0}) \geq \frac{1}{\sqrt{c^2+4}} I > \frac{c\rho_{-0}}{\{c(1-D)\lambda_+ + \gamma + D\}\sqrt{c^2+4}} = \frac{\eta(1+\eta)\rho_{-0}}{2(1-D)\eta + (\gamma+D)(1+\eta)},$$

where

$$\eta := \frac{c}{\sqrt{c^2+4}}.$$

Since $c \geq c_1^* = 2\sqrt{\gamma D}$,

$$\eta_1^* := \sqrt{\frac{\gamma D}{\gamma D + 1}} \leq \eta < 1. \tag{3.3}$$

The assumption of the theorem implies that

$$\liminf_{c\to\infty} N(c, \rho_{-0}) \geq \frac{\rho_{-0}}{1+\gamma} > \frac{1}{\alpha}.$$

Since equation (3.1) is $1 - \alpha N(c, \rho_{-0}) = 0$, the proof of the lemma is complete. $\square$

By Lemma 2.1, $N(c, \rho_{-0})$ is increasing in $\rho_{-0} \in (0,1)$. We also note that if (3.1) is satisfied, then

$$h(z) = \frac{\alpha}{\sqrt{c^2+4}} \int_z^\infty \rho(\xi) e^{-\lambda_+(\xi - z)} d\xi + \frac{\alpha}{\sqrt{c^2+4}} \int_{-\infty}^z \rho(\xi) e^{\lambda_-(z-\xi)} d\xi. \tag{3.4}$$

Proposition 3.3. *If $\alpha \leq 1$, then there are no bounded traveling wave solutions to* (1.1).

Proof. Note that $\lambda_- < 0 < \lambda_+$, $\lambda_+ + \lambda_- = -c$ and $\lambda_+ - \lambda_- = \sqrt{c^2+4}$. By (3.1) and $0 \leq \rho(z) < 1$, we have

$$\begin{aligned} N(c, \rho_{-0}) &< \frac{1}{\sqrt{c^2+4}} \left(\int_{-\infty}^0 e^{-\lambda_- z}\, dz + \int_0^\infty e^{-\lambda_+ z}\, dz \right) \\ &= \frac{1}{\sqrt{c^2+4}} \left(\frac{1}{\lambda_+} - \frac{1}{\lambda_-} \right) = 1. \end{aligned}$$

If $\alpha \leq 1$, then equation (3.1) is never satisfied. The proof of the proposition is complete. $\square$

4 Existence of traveling wave solutions

To show the existence of bounded traveling wave solutions, we must check that the solution h we constructed satisfies

$$h(z) > 1 \quad (z < 0), \qquad h(z) < 1 \quad (z > 0). \tag{4.1}$$

In the proof of Proposition 3.1, we have demonstrated that

$$h'(0) = \lambda_- + \alpha \int_0^\infty \rho(z) e^{-\lambda_+ z}\, dz = \lambda_+ - \alpha \int_{-\infty}^0 \rho(z) e^{-\lambda_- z}\, dz.$$

Now $\rho_-(z)$ decreases from 1 to ρ_{-0} as z increases from $-\infty$ to 0. Therefore,

$$h'(0) < \frac{-c + \sqrt{c^2+4}}{2} - \alpha \rho_{-0} \int_{-\infty}^0 e^{-\lambda_- z}\, dz = \frac{2(1 - \alpha \rho_{-0})}{c + \sqrt{c^2+4}}.$$

A sufficient condition for $h'(0) < 0$ is

$$\rho_{-0} > \frac{1}{\alpha} \tag{4.2}$$

The condition $h'(0) \leq 0$ is necessary since $h(0) = 1$.

Let us consider the first case of (4.1).

Lemma 4.1. *Let $\alpha > 1$ and let $1/\alpha < \rho_{-0} < 1$. Then $h(z)$ decreases from α to 1 as z increases from $-\infty$ to 0.*

Proof. Let $u(z) = h'(z)$. Then u satisfies $u'' + cu' - u > 0$ for $z < 0$. Thus u cannot have a positive local maximum. Every horizontal line above the z-axis can only intersect the graph of u once. Since $u(0) < 0$ by our assumption (4.2) and $h(z)$ is bounded, $u(z) < 0$ on $(-\infty, 0)$.

Now we show that $h(-\infty) = \alpha$. The first term of the right hand side of (3.4) can be rewritten as

$$\frac{\alpha}{\sqrt{c^2+4}} \int_z^\infty \rho(\xi) e^{-\lambda_+(\xi - z)} d\xi \;=\; \frac{\alpha}{\sqrt{c^2+4}} \int_0^\infty \rho(s+z) e^{-\lambda_+ s} ds \to \frac{\alpha}{\sqrt{c^2+4}} \frac{1}{\lambda_+}$$

because $\rho_-(z) \to 1$ as $z \to -\infty$. For the second term, we have

$$\frac{\alpha}{\sqrt{c^2+4}} \int_{-\infty}^z \rho(\xi) e^{\lambda_-(z-\xi)} d\xi \;=\; \frac{\alpha}{\sqrt{c^2+4}} \int_0^\infty \rho(z-s) e^{\lambda_- s} ds \to -\frac{\alpha}{\sqrt{c^2+4}} \frac{1}{\lambda_-}$$

as $z \to -\infty$. Therefore,

$$h(-\infty) = \frac{\alpha}{\sqrt{c^2+4}} \frac{1}{\lambda_+} - \frac{\alpha}{\sqrt{c^2+4}} \frac{1}{\lambda_-} = \alpha.$$

The proof of the lemma is complete. □

Theorem 4.2. *Let* (c, ρ_{-0}) *satisfy* (3.1) *and let* z_1, z_2 $(0 < z_1 < z_2)$ *be the two roots of* $\rho(z) = 1/\alpha$. *Suppose*

$$\int_{z_1}^\infty \rho(\xi) e^{-\lambda_+ \xi} d\xi \le \frac{|\lambda_-|}{\alpha} e^{-\lambda_+ z_1}. \tag{4.3}$$

Then there exists a traveling wave solution with speed c which satisfies $h(z) \le 1$ for any $z \ge 0$.

Proof. Set

$$\phi_1(z) := \frac{1}{\lambda_+ - \lambda_-} \int_z^\infty (\alpha\rho(\xi) - 1) e^{-\lambda_+(\xi - z)} d\xi, \quad \phi_2(z) := \frac{1}{\lambda_+ - \lambda_-} \int_{-\infty}^z (\alpha\rho(\xi) - 1) e^{\lambda_-(z-\xi)} d\xi.$$

From (2.6) and (3.4),

$$\begin{aligned} h(z) &= \phi_1(z) + \phi_2(z) + 1, \\ h'(z) &= \lambda_+ \phi_1(z) + \lambda_- \phi_2(z) = (\lambda_+ - \lambda_-)\phi_1(z) + \lambda_-(h(z) - 1). \end{aligned}$$

At a critical point of h, i.e., $h'(z) = 0$, the condition

$$h(z) - 1 = \frac{\lambda_+ - \lambda_-}{-\lambda_-} \phi_1(z) \le 0$$

is equivalent to

$$\phi_1(z) \le 0. \tag{4.4}$$

When $z \geq z_2$, $\alpha\rho(z) \leq 1$ and the definition of $\phi_1(z)$ implies (4.4). Thus, $h(z) \leq 1$ holds for $z \geq z_2$. It follows from (4.3) that

$$\int_{z_1}^{\infty} (\alpha\rho(\xi) - 1)e^{-\lambda_+\xi} d\xi \leq 0.$$

From the definitions of z_1, z_2, $\rho(z) \geq 1/\alpha$ in $[\alpha_1, \alpha_2]$ so that

$$\int_{z}^{\infty} (\alpha\rho(\xi) - 1)e^{-\lambda_+\xi} d\xi \leq 0$$

for any $z \in [z_1, z_2]$. Since $\alpha\rho(z) - 1 \leq 0$ for $z \in [0, z_1]$, $\phi_1(z) \leq 0$ for any $z \geq 0$ under (4.3). Therefore, we have $h(z) \leq 1$ for all $z > 0$. Note that if $\rho(z) \leq 1/\alpha$ for $z \geq 0$, then one can set $\alpha_1 = \alpha_2 = 0$. The proof of the theorem is complete. $\square$

Recall that $c_1^* = 2\sqrt{\gamma D}$. The following theorem gives a sufficient condition to the result that by changing ρ_{-0}, every $c\,(> c_1^*)$ can be a root of equation (3.1).

Theorem 4.3. *Assume that*

$$\frac{((4+\gamma-D)\sqrt{\gamma D} + (\gamma+D)\sqrt{\gamma D+1})(\sqrt{\gamma D+1} + \sqrt{\gamma D})}{\{4(1-D)\sqrt{\gamma D} + 2(\gamma+D)(\sqrt{\gamma D+1} + \sqrt{\gamma D})\}\sqrt{\gamma D+1}} \geq \frac{1}{\alpha}. \tag{4.5}$$

Then for any $c\,(> c_1^*)$, there exists a $\rho_{-0} \in (0, 1)$ such that c satisfies (3.1). Thus, there exists a traveling wave solution with speed c if $h(z) \leq 1$ for $z \geq 0$.

Proof. As $\rho_{-0} \to 0$, (ρ, h) converges to $(0, 0)$ locally uniformly as $z \to \infty$ and

$$\lim_{\rho_{-0}\to+0} N(c, \rho_{-0}) = 0\,.$$

If we take $\rho_{-0} = 1$, then $\rho_-(z) \equiv 1$. Therefore, from (3.2) and the proof of Lemma 3.2, we can replace η by η^* defined in (3.3) to obtain

$$\begin{aligned} N(c, 1) &\geq \frac{\eta+1}{2} + \frac{\eta(1+\eta)}{2(1-D)\eta + (\gamma+D)(1+\eta)} \\ &= \frac{((4+\gamma-D)\eta + \gamma + D)(1+\eta)}{4(1-D)\eta + 2(\gamma+D)(1+\eta)}. \end{aligned}$$

Because

$$\frac{\partial}{\partial\eta}\frac{\eta(1+\eta)}{2(1-D)\eta + (\gamma+D)(1+\eta)} = \frac{\eta^2(2+\gamma) + D\eta(1-\eta) + \gamma\eta + (\gamma+D)(1+\eta)}{\{2(1-D)\eta + (\gamma+D)(1+\eta)\}^2} > 0,$$

we can replace η by η^* defined in (3.3) to obtain

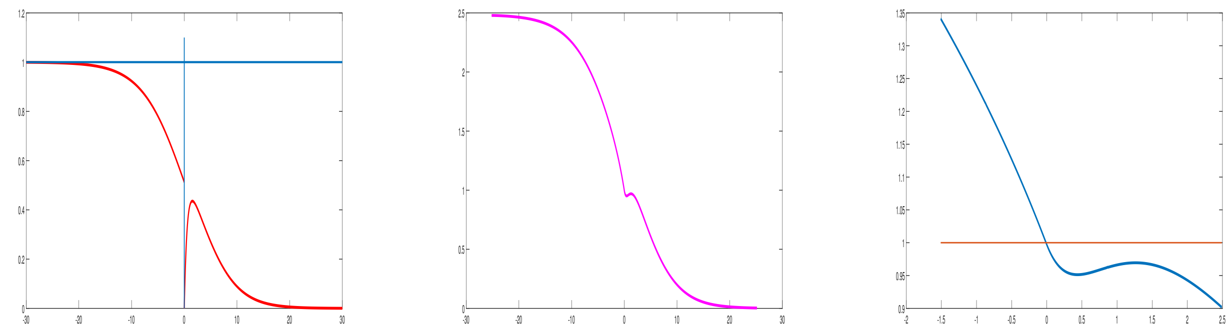
$$\begin{aligned} N(c, 1) &> \frac{((4+\gamma-D)\eta^* + \gamma + D)(1+\eta^*)}{4(1-D)\eta^* + 2(\gamma+D)(1+\eta^*)} \\ &= \frac{((4+\gamma-D)\sqrt{\gamma D} + (\gamma+D)\sqrt{\gamma D+1})(\sqrt{\gamma D+1} + \sqrt{\gamma D})}{\{4(1-D)\sqrt{\gamma D} + 2(\gamma+D)(\sqrt{\gamma D+1} + \sqrt{\gamma D})\}\sqrt{\gamma D+1}}. \end{aligned}$$

It follows from (4.5) and the monotonicity of $N(c, \rho_{-0})$ in ρ_{-0} that there is a unique $\rho_{-0} \in (0, 1)$ such that

$$N(c, \rho_{-0}) = \frac{1}{\alpha}.$$

The proof of the theorem is complete. $\square$

Figure 1 shows the profile of a traveling wave solution with parameter values and wave speed that satisfy equation (3.1) and ineuality (4.3). The parameter values and wave speed are given in the caption of Figure 1.



$\rho(z)$ $h(z)$ $h(z)$ near the origin

Figure 1: Traveling wave solutions with parameter values up to four places after decimal: $\alpha = 2.4862$, $\rho_{-0} = 0.5130$, $\gamma = 0.1565$, $D = 0.3439$. Wave speed is approximately $c = 0.6430$. Note that $h(z)$ lies below 1 and is not monotone for $z > 0$.

5 Discussion

The three-component model in [4] was constructed to explain the periodic stripes patterns the authors observed in their experiments. They simulated the system and the results are presented in the Movie S4 in the paper's Supporting Online Material. In [3], the authors mentioned that their reduced system is able to initiate stripe patterns and maintain them for a while, but the stripes are eventually lost when the cell density reaches ρ_s throughout the system. Such kind of transient patterns will be difficult to prove mathematically.

Acknowledgements

The last author was partially supported by JSPS KAKENHI Grant Numbers 26287024, 15K04963, 16K13778, 16KT0022.

References

[1] E. Ben-Jacob, I. Cohen, and H. Levine, Cooperative self-organization of microorganisms, Adv. Phys. 49, 395 (2000).

[2] E. O. Budrene and H. C. Berg, Complex patterns formed by motile cells of *Escherichia coli*, Nature (London) 349, 630 (1991).

[3] X. Fu, L.H. Tang, C. Liu, J.D. Huang, T. Hwa, and P. Lenz, Stripe formation in bacterial systems with density-suppressed motility, Physical Review Letters, **108(19)**, (2012), 198102. DOI: 10.1103/PhysRevLett.108.198102. Supplementary Material, http://link.aps.org/supplemental/10.1103/PhysRevLett.108.198102.

[4] C. Liu et al., Sequential establishment of stripe patterns in an expanding cell population, Science **334.6053**, (2011), 238–241. DOI: 10.1126/science.1209042. Supporting Online Material at www.sciencemag.org/cgi/content/full/334/6053/238/DC1.

[5] J.D. Murray, Mathematical Biology I. An Introduction, Springer, NY ed. 3, 2001.