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EXISTENCE OF TRAVELING WAVE SOLUTIONS FOR A ONE-DIMENSIONAL CELL MOTILITY MODEL

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Abstract. In this paper, we extend the existence of traveling wave result in [1] to the case where the rate of disassembly of free polymers is non-zero. Mathematical methods used include dynamical system techniques and global bifurcation theory.

1. Introduction

The movement of cells along surfaces is fundamental to many important biological processes such as metastatic cancer, wound healing and functioning of the cellular immune system. The process of cell movement has been a subject of investigation for more than a hundred years and today remains one of the outstanding questions in cell biology. It is generally agreed among the biologists [3] that cell movement is a three-step process that involves protrusion at the front end, graded adhesion to the substratum (stronger at the front and weaker at the rear) and contraction which pulls the cell body and rear end forward. Recently, many mathematical models have been developed to describe various aspects of cell movements. However, a two-dimensional model describing the movement of an entire cell has not yet been accomplished due to the difficulties involved in modeling protrusion and contraction together.

In 2003, Mogilner and Verzi [3] developed a one-dimensional model that describes the movement of a nematode sperm cell whose uniform crawling motion is observed experimentally. They document some numerical evidence that their model supports traveling wave solutions. Subsequently, Choi, Lee and Lui [1] proved rigorously that traveling wave solutions indeed exist assuming that there is no disassembly of the free filaments. The purpose of this paper is to remove this

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assumption and prove that traveling wave solutions also exist assuming constant rates of disassembly and unbundling.

The paper is organized as follows. In the next section, the model and the derivations leading to the traveling system and boundary conditions are described. The proof of the main theorem is given in section three.

2. Mathematical Model

In 2003, Mogilner and Verzi [3] proposed the following system of strongly-coupled parabolic system to model the movement of a nematode sperm cell

$$\left\{\begin{aligned} \frac{\partial b}{\partial t} &= -\frac{\partial}{\partial x}(bv) - \gamma_b(y)b\,, \\ \frac{\partial p}{\partial t} &= -\frac{\partial}{\partial x}(pv) + \gamma_b(y)b - \gamma_p(y)p\,, \\ \frac{\partial c}{\partial t} &= -\frac{\partial}{\partial x}(cv)\,. \end{aligned}\right. \tag{2.1}$$

In the above system, v is the cytoskeletal velocity which is assumed to be

$$v(x,t) = \frac{1}{\xi(y)}\frac{\partial \sigma}{\partial x}\,.$$

In the above equations, σ is the stress in the cell, $\xi = \xi(y)$ is the effective drag coefficient between the cell and the substratum and y is the distance from the rear end of the cell. Also, b and p denote the length densities of the bundled and free filaments, respectively and c denotes the length density of the cytoskeletal nodes. The function γ_b is the rate of unbundling of the bundled filament and γ_p is the rate of disassembly of the free filaments.

In [3], Mogilner and Verzi assumed that σ is of the form

$$\sigma = Kb\left(\frac{1}{c} - \rho\right) + \kappa\frac{p}{c} \tag{2.2}$$

where K and κ are the effective spring constants for the bundled and free filaments, respectively and ρ is the rest length of the bundled filament.

The boundary conditions for (2.1) are as follow. The front and back ends of the cell are located at $f(t)$ and $r(t)$, respectively so that $y = x - r(t)$. At the front we assume that $\sigma = 0$, there is no free filament and the amount of bundled filaments is known. These conditions and (2.2) imply that $c = 1/\rho$. Hence, the boundary conditions at the front are:

$$\sigma = 0\,, \quad b = b_0\,, \quad p = 0 \quad \text{and} \quad c = \frac{1}{\rho}\,. \tag{2.3}$$

The boundary condition at the back is simply $\sigma = 0$.

In [3], Mogilner and Verzi assumed that the front and back movements are governed by the equations

$$\left\{ \begin{array}{rcl} \frac{df}{dt} & = & V_p \mid_{f(t)} + v \mid_{f(t)}, \\ \frac{dr}{dt} & = & V_d + v \mid_{r(t)} \end{array} \right. \tag{2.4}$$

where

$$V_p = V_0 \left[0.5 + \frac{1}{\pi} \arctan(\eta(y-L)) \right] \frac{L}{f(t) - r(t)}$$

is the rate of MSP (major sperm protein) polymerization and V_d is a given positive constant.

In 2003, Choi, Lee and Lui [1] proved the existence of traveling wave solutions for the above model. Their analysis proceeds as follow. Suppose the cell is of length ℓ and travels with a velocity k so that the front is located at $f(t) = kt + \ell$ and the back is located at $r(t) = kt$. Then (2.4) reduces to

$$\left\{ \begin{array}{rcl} k & = & V_0 \left[0.5 + \frac{1}{\pi} \arctan(\eta(\ell - L)) \right] \frac{L}{\ell} + v \mid_{kt+\ell}, \\ k & = & V_d + v \mid_{kt} . \end{array} \right. \tag{2.5}$$

Traveling wave solutions to (2.1) are by definition special solutions of the form $b(x,t) = b(x-kt)$, $p(x,t) = p(x-kt)$ and $c(x,t) = c(x-kt)$. They maintain a constant shape and move with a constant speed k. Substituting these solutions into (2.1), one obtains the system

$$\left\{ \begin{array}{rcl} -kb' & = & -\left[\frac{b}{\xi(y)} \sigma' \right]' - \gamma_b(y) b, \\ -kp' & = & -\left[\frac{p}{\xi(y)} \sigma' \right]' + \gamma_b(y) b - \gamma_p(y) p, \\ -kc' & = & -\left[\frac{c}{\xi(y)} \sigma' \right]' \end{array} \right. \tag{2.6}$$

where $' = d/dy$. The last equation can be integrated to yield

$$-kc = -\frac{c}{\xi(y)} \sigma' - A = -cv - A. \tag{2.7}$$

Evaluating this expression at the front using (2.5a),

$$A(\ell) = \frac{V_0 L}{\rho \ell} \left[0.5 + \frac{1}{\pi} \arctan(\eta(\ell - L)) \right]. \tag{2.8}$$

From (2.5b),

$$k = V_d + \frac{kc - A(\ell)}{c} \,|_{kt}$$

which simplifies to

$$c \,|_{kt} = \frac{A(\ell)}{V_d}\,. \tag{2.9}$$

This condition holds at the back of the wave.

From equation (2.7)

$$\sigma' = \xi \left(k - \frac{A(\ell)}{c} \right)\,. \tag{2.10}$$

Substituting this into (2.6), the first two equations of (2.6) become

$$\begin{cases} \left(\dfrac{bA}{c}\right)' - \gamma_b(y)b &= 0\,, \\ \left(\dfrac{pA}{c}\right)' + \gamma_b(y)b - \gamma_p(y)p &= 0\,. \end{cases} \tag{2.11}$$

The traveling wave system therefore consists of equations (2.11), (2.10) and (2.2). The boundary conditions are (2.3) at the front ($y = \ell$) and $\sigma = 0$, $c = A(\ell)/V_d$ at the back ($y = 0$). To prove the existence of traveling wave solutions, one must demonstrate that there exist k and $\ell > 0$ such that the traveling wave system has a solution (b, p, σ, c) satisfying both the front and back conditions mentioned above. In [1], Choi, Lee and Lui proved, among other things, the existence of traveling wave solutions assuming that $\gamma_p = 0$. In this paper, we shall remove this assumption. For technical reason, we shall assume that γ_p and γ_b are positive constants which are not assumed in [1].

Let $u = b/c, v = p/c$, then the traveling wave system can be written as

$$\begin{pmatrix} u \\ v \\ \sigma \\ c \end{pmatrix}' = \begin{pmatrix} \gamma_b \dfrac{uc}{A} \\ \gamma_p \dfrac{vc}{A} - \gamma_b \dfrac{uc}{A} \\ \xi(y)(k - \dfrac{A}{c}) \\ -\dfrac{(\rho c - 1)\gamma_b c}{\rho A} + \dfrac{\kappa(\gamma_p vc - \gamma_b uc)}{KA\rho u} - \dfrac{\xi(y)(k - A/c)}{K\rho u} \end{pmatrix}. \tag{2.12}$$

For the rest of the paper we let $\gamma = \gamma_p/\gamma_b$. We shall make the following assumptions on A rather than assuming it to be of the form (2.8).

(HA) There exists $\ell^* > 0$ such that $A(\ell^*) = V_d/\rho$. Furthermore,

$A : (0, \ell^*] \to (0, \infty)$ is a C^1 function with

(a) $A(\ell) \to \infty$ as $\ell \to 0^+$,

(b) $A(\ell) > A(\ell^*)$ for all $\ell \in (0, \ell^*)$,

(c) $A'(\ell^*) < 0$,

(d) Let $\ell_1^* = 0$ if $\gamma \le 1$ and there exists a unique $0 < \ell_1^* < \ell^*$ such that

$$\left(\frac{\rho A(\ell_1^*)}{V_d} - 1\right)\frac{(1-\gamma)K}{\kappa} + 1 = 0 \qquad if \qquad \gamma > 1\,. \tag{2.13}$$

Remark If $A(\ell)$ is decreasing on $(0, \infty)$, then the existence of ℓ^* as well as conditions (b) to (d) above will all be satisfied.
The main result of this paper is

Theorem 2.1. *Let γ_p and γ_b be positive constants. Suppose $\xi \in C^1[0, \ell^*]$, there exist ξ_0 and ξ_1 such that $0 < \xi_0 \le \xi(y) \le \xi_1$ for all $y \in [0, \ell^*]$ and $A(\ell)$ satisfies hypotheses (HA), then there exist positive constants k and ℓ such that system (2.12) has a solution on the interval $[0, \ell]$ satisfying the condition (2.3) at $y = \ell$ and the conditions $\sigma = 0$ and (2.9) at $y = 0$.*

3. Proof of Theorem 2.1

Let $w = 1/(uA),\ \tilde{z} = vA$ and $\tilde{c} = c/A$. Then from (2.12),

$$\begin{pmatrix} w \\ \tilde{z} \\ \tilde{c} \end{pmatrix}' = \begin{pmatrix} -\gamma_b w\tilde{c} \\ \gamma_p \tilde{c}\tilde{z} - \gamma_b \dfrac{\tilde{c}}{w} \\ -(\tilde{c} - \dfrac{1}{\rho A})\gamma_b\tilde{c} + \dfrac{\kappa}{KA\rho}(\gamma_p w\tilde{z}\tilde{c} - \gamma_b\tilde{c}) - \dfrac{\xi(y)}{K\rho}(k - \dfrac{1}{\tilde{c}})w \end{pmatrix}. \tag{3.1}$$

From (2.3), the boundary conditions at $y = \ell$ are

$$w = 1/(b_0\rho A), \quad \tilde{z} = 0 \quad \text{and} \quad \tilde{c} = 1/(\rho A)\,. \tag{3.2}$$

From (2.9) and $\sigma = 0$, the boundary conditions at $y = 0$ are

$$(A\rho\tilde{c} - 1) = (\kappa/K)\tilde{z}w \quad \text{and} \quad \tilde{c} = 1/V_d\,. \tag{3.3}$$

From (3.1), we have

$$(3.4)\qquad \begin{cases} \dfrac{d\tilde{c}}{dw} = \dfrac{\tilde{c}}{w} - \dfrac{\kappa\gamma}{KA\rho}\tilde{z} - \dfrac{1}{\rho A w}\left(1-\dfrac{\kappa}{K}\right) + \dfrac{\xi(y)}{\gamma_b K\rho}\left(k - \dfrac{1}{\tilde{c}}\right)\dfrac{1}{\tilde{c}} \\ \dfrac{d\tilde{z}}{dw} = -\dfrac{\gamma\tilde{z}}{w} + \dfrac{1}{w^2} \end{cases}$$

where $\gamma = \gamma_p/\gamma_b$. The solution to (3.4b) satisfying the condition $\tilde{z}(1/b_0\rho A) = 0$ is given by

$$(3.5)\qquad \tilde{z} = \frac{1}{(\gamma-1)w} + \frac{C_1}{w^\gamma} \qquad if \quad \gamma \neq 1$$

where

$$C_1 = \frac{(b_0\rho A)^{-\gamma+1}}{(1-\gamma)}$$

and

$$\tilde{z} = \frac{\ln(wb_0A\rho)}{w} \qquad if \quad \gamma = 1\,.$$

Note that $\tilde{z}(w) > 0$ for $w > 1/b_0\rho A$. For the rest of the argument, we shall define $\tilde{w} = wb_0\rho A$.

Lemma 3.1. *The solution to equation* $(3.4a)$ *without the last term, with* $\tilde{z}$ *replaced by the formula above and satisfies the boundary condition* $\tilde{c}(1/b_{\,0}\rho A) = 1/\rho A$ *is given by*

$$(i)\ \ \bar{c}(\tilde{w}) = \frac{1}{\rho A}\left[1 - \frac{\kappa}{(1-\gamma)K}\right] + \frac{\kappa}{K(1-\gamma)\rho A}\tilde{w}^{1-\gamma} \qquad if \quad \gamma \neq 1,$$

$$(ii)\ \ \bar{c}(\tilde{w}) = \left(\frac{\kappa}{K}\ln\tilde{w} + 1\right)\frac{1}{\rho A} \qquad if \quad \gamma = 1\,.$$

Proof. We first assume that $\gamma \neq 1$. Dropping the last term of (3.4a) and letting

$$\mu_1 = \frac{\kappa\gamma}{KA\rho}\,, \qquad \mu_2 = \frac{1}{\rho A}\left(1 - \frac{\kappa}{K}\right)\,,$$

(3.4a) can be rewritten as

$$(3.6)\qquad \frac{d\bar{c}}{dw} - \frac{\bar{c}}{w} = -\mu_1\left(\frac{1}{(\gamma-1)w} + \frac{C_1}{w^\gamma}\right) - \mu_2\frac{1}{w}\,.$$

Integrating, we have

$$(3.7)\qquad \bar{c}(w) = C_2 + \frac{C_1\mu_1}{\gamma}\frac{1}{w^{\gamma-1}} + C_3 w$$

where

$$C_2 = \frac{\mu_1}{(\gamma-1)} + \mu_2 \,.$$

Using the boundary condition, we obtain

$$C_3 = b_0 - C_2 b_0 \rho A - \frac{C_1 \mu_1}{\gamma (b_0 \rho A)^{-\gamma}} \,.$$

Therefore, from (3.7), we have

$$\bar{c}(w) = b_0 w + C_2(1 - b_0 \rho A w) + \frac{C_1 \mu_1 w}{\gamma}\left[\frac{1}{w^\gamma} - (b_0 \rho A)^\gamma\right] \,.$$

Substituting in the definitions of C_1, C_2, μ_1 and μ_2, we have

$$\begin{aligned}
\bar{c}(w) &= b_0 w + \left[\frac{\kappa\gamma}{KA\rho(\gamma-1)} + \frac{1}{\rho A}(1 - \frac{\kappa}{K})\right](1 - b_0 \rho A w) \\
&\quad + \frac{\kappa C_1}{KA\rho}\left[\frac{1}{w^{\gamma-1}} - (b_0 \rho A)^\gamma w\right] \\
&= b_0 w + \left[\frac{\kappa}{KA\rho(\gamma-1)} + \frac{1}{\rho A}\right](1 - b_0 \rho A w) \\
&\quad + \frac{\kappa}{KA\rho(1-\gamma)}\left[\frac{(b_0 \rho A)^{1-\gamma}}{w^{\gamma-1}} - (b_0 \rho A) w\right] \\
&= b_0 w + \frac{1}{\rho A}(1 - b_0 \rho A w) + \frac{\kappa}{KA\rho(\gamma-1)} + \frac{\kappa \tilde{w}^{1-\gamma}}{KA\rho(1-\gamma)}
\end{aligned}$$

which is the same as (i) above.

If $\gamma = 1$, then from (3.4a) without the last term, we have

$$\frac{d\bar{c}}{dw} = \frac{\bar{c}}{w} - \frac{\kappa}{KA\rho}\left[\frac{\ln(w b_0 A\rho)}{w}\right] - \frac{1}{wA\rho}\left(1 - \frac{\kappa}{K}\right).$$

Integrating this equation, we have

$$\begin{aligned}
\frac{\bar{c}}{w} &= \frac{1}{wA\rho}\left(1 - \frac{\kappa}{K}\right) - \frac{\kappa}{KA\rho}\int \frac{\ln(w b_0 A\rho)}{w^2}\, dw + C \\
&= \frac{\kappa}{KA\rho}\frac{\ln(w b_0 A\rho)}{w} + \frac{\kappa}{wKA\rho} + \frac{1}{wA\rho}\left(1 - \frac{\kappa}{K}\right) + C \,.
\end{aligned}$$

Since $\bar{c} = 1/(A\rho)$ when $w = 1/(b_0 A\rho)$, we see that $C = 0$. Hence,

$$\bar{c} = \frac{1}{A\rho}\left[\frac{\kappa}{K}\ln\tilde{w} + 1\right]$$

which is the same as (ii) above. The proof of the lemma is complete. ∎

Lemma 3.2. *Recall the definition of ℓ_1^* in (HA)(d). For a given $\ell \in (\ell_1^*, \ell^*)$, define*

$$(i)\;\; \tilde{w}_0 = \left[\left(\frac{\rho A(\ell)}{V_d} - 1\right)\frac{(1-\gamma)K}{\kappa} + 1\right]^{1/(1-\gamma)} \qquad if \quad \gamma \neq 1$$

$$(ii)\;\; \tilde{w}_0 = exp\left(\frac{K}{\kappa}\left(\frac{\rho A(\ell)}{V_d} - 1\right)\right) \qquad if \quad \gamma = 1\,.$$

Then $\tilde{w}_0 > 1$ and the function $\bar{c}(\tilde{w})$ defined in Lemma 3.1 is increasing on the interval $(1, \tilde{w}_0)$.

Proof. Since $\rho A(\ell) > V_d$ if $\ell < \ell^*$, it is clear that $\tilde{w}_0 > 1$ for all $\gamma \geq 0$. The fact that $\bar{c}(\tilde{w})$ is increasing is obvious from its definition. The proof of the lemma is complete. ∎

For the rest of the proof, we shall define $\tilde{c}_0 = \bar{c}(\tilde{w}_0) = 1/V_d$, $\tilde{c}_1 = \bar{c}(1) = 1/\rho A(\ell)$ and S, Q to be the points $S = (1, \tilde{c}_1)$, $Q = (\tilde{w}_0, \tilde{c}_0)$ in the $\tilde{w} - \tilde{c}$ plane. From the above lemma, for $\ell \in (\ell_1^*, \ell^*)$, the point Q is to the right of and above S. The graph of the function $\bar{c}(\tilde{w})$ passes through S and Q. Furthermore, from (3.2) and (3.3), Q corresponds to the back of the wave and S corresponds to the front of the wave.

Lemma 3.3. *Let $\ell \in (\ell_1^*, \ell^*)$, then*

(i) *there exists a $k(\ell) \in (V_d, \rho A(\ell))$ such that the solution to (3.1) with initial condition Q passes through S in a finite amount of time denoted by $y^*(\ell)$.*

(ii) *any trajectory of (3.1) passing through Q and S must have $V_d < k < \rho A(\ell)$. Moreover such a trajectory lies strictly below $\bar{c}(\tilde{w})$ on the interval $(1, \tilde{w}_0)$.*

Proof. We first prove the first part of (ii). Observe from (3.1a) that $\tilde{w} = wb_0\rho A$ is decreasing in y if $\tilde{w}$ and $\tilde{c}$ are positive. We shall use $\bar{c}(\tilde{w})$ defined in Lemma 3.1 as a comparison function.

Suppose $k < V_d$, then at the point Q, the last term in (3.4a) equals $\xi(0)(k - V_d)V_d/(\gamma_b K\rho) < 0$ and hence $d\tilde{c}/dw < d\bar{c}/dw$ at Q. From Taylor series expansion, $\tilde{c}(\tilde{w}) > \bar{c}(\tilde{w})$ for $\tilde{w}$ sufficiently close and less than $\tilde{w}_0$. Suppose $\tilde{c}$ intersects $\bar{c}$ from above at some point $P = (w^*, \tilde{c}(w^*))$ where $w^* \in [1, \tilde{w}_0)$. Then since $\bar{c}(\tilde{w})$ is increasing on $[1, \tilde{w}_0]$, we have $1/\rho A(\ell) \leq \tilde{c}(w^*) < 1/V_d$ so that $(k - 1/\tilde{c}(w^*)) < k - V_d < 0$. Therefore, $d\tilde{c}/dw < d\bar{c}/dw$ at P which is a contradiction. Thus, $\tilde{c}$ must lie above $\bar{c}$ on the interval $[1, \tilde{w}_0]$ if $k < V_d$. Actually, since $\tilde{c} > 1/\rho A(\ell)$, $d\tilde{c}/dw$ is bounded so $\tilde{c}(\tilde{w})$ cannot blow up on the interval $[1, \tilde{w}_0]$. Therefore, the trajectory $\tilde{c}$ starting from Q must cross L, defined as the vertical line $\tilde{w} = 1$ passing through S, at a point above S in finite time y.

Now suppose $k > \rho A(\ell)$, then at Q, $k - 1/\tilde{c} = k - V_d > 0$ so that $\tilde{c}(\tilde{w})$ is below $\bar{c}(\tilde{w})$ for $\tilde{w}$ sufficiently close and less than $\tilde{w}_0$. If $\tilde{c}$ crosses $\bar{c}$ from below at some point $P = (w^*, \tilde{c}(w^*))$ where $w^* \in [1, \tilde{w}_0)$, then since $\tilde{c}(w^*) \geq 1/\rho A(\ell)$, we have $k - 1/\tilde{c}(w^*) \geq k - \rho A(\ell) > 0$ which means that $d\tilde{c}/dw > d\bar{c}/dw$ at P, a contradiction. Therefore, $\tilde{c}$ lies below $\bar{c}$ on the interval $[1, \tilde{w}_0]$. For the given ℓ, let $c_{min} > 0$ be chosen so small that

$$\frac{c_{min}}{1} + \frac{|1-\kappa/K|}{\rho A(\ell)} + \frac{\xi_0}{\gamma_b K \rho}\left(k - \frac{1}{c_{min}}\right)\frac{1}{c_{min}} < 0\,. \tag{3.8}$$

Then since $\tilde{z} \geq 0$ for $\tilde{w} > 1$, (3.4a) implies that $d\tilde{c}/dw < 0$ if $\tilde{c} = c_{min}$ and $\tilde{w} \geq 1$. Therefore, $\tilde{c}(\tilde{w})$ cannot be less than c_{min}. Thus if $k > \rho A(\ell)$, the trajectory $\tilde{c}(\tilde{w})$ must cross L below S and at a value above c_{min} in finite time y.

Next we consider the cases when $k = V_d$ and $k = \rho A(\ell)$. Suppose $k = V_d$, then the slope of the curves $\tilde{c}$ and $\bar{c}$ are the same at Q and we need to consider second derivatives. We have

$$\frac{d^2\tilde{c}}{dw^2}\,|_Q = \frac{d^2\bar{c}}{dw^2}\,|_Q + \frac{\xi(0)V_d^3}{\gamma_b K\rho}\frac{d\tilde{c}}{dw}\,|_Q\ .$$

Since the last term in the above expression is positive, $d^2\tilde{c}/dw^2\,|_Q > d^2\bar{c}/dw^2\,|_Q$ and hence $\tilde{c}(\tilde{w}) > \bar{c}(\tilde{w})$ for $\tilde{w}$ sufficiently close and less than $\tilde{w}_0$. The rest of the argument proceeds as before so that $\tilde{c} \geq \bar{c}$ on the interval $[1, \tilde{w}_0]$ if $k = V_d$.

Suppose $k = \rho A(\ell)$, then as before $\tilde{c}$ lies strictly below $\bar{c}$ on the interval $(1, \tilde{w}_0)$. Suppose $\tilde{c}(1) = \bar{c}(1)$, then since $k - 1/\tilde{c} = 0$ at S, we need to consider the second derivative. Since

$$\frac{d^2\tilde{c}}{dw^2}\,|_S = \frac{d^2\bar{c}}{dw^2}\,|_S + \frac{\xi(y)[\rho A(\ell)]^3}{\gamma_b K\rho}\frac{d\tilde{c}}{dw}\,|_S,$$

Taylor series expansion at $\tilde{w} = 1$ implies that $\tilde{c}(\tilde{w}) > \bar{c}(\tilde{w})$ to the right and near $\tilde{w} = 1$. This is a contradiction and hence $\tilde{c}(1) < 1/\rho A(\ell)$. This completes the proof of the first part of (ii).

Since the trajectory $\tilde{c}$ starting from Q crosses L above S in finite time y if $k \leq V_d$ and below S in finite time y if $k \geq \rho A(\ell)$ and since the point of crossing depends continuously on k, there exists a $k(\ell) \in (V_d, \rho A(\ell))$ where the trajectory passes through S. We denote the amount of time it takes for the trajectory to arrive at S by $y^*(\ell)$. This completes the proof of part (i) of the lemma.

We now turn to the proof of second half of (ii). Suppose we have a trajectory connecting Q and S for some value of $k(\ell) \in (V_d, \rho A(\ell))$. Then from the above argument, $\tilde{c}(\tilde{w})$ is below $\bar{c}(\tilde{w})$ near the endpoints on the interval $(1, \tilde{w}_0)$. Suppose the trajectory $\tilde{c}(\tilde{w})$ crosses $\bar{c}(\tilde{w})$ at two consecutive points $B_1 = (\tilde{w}_1, \tilde{c}_1)$ and $B_2 = (\tilde{w}_2, \tilde{c}_2)$ with the trajectory lying above $\bar{c}(\tilde{w})$ on the interval $(\tilde{w}_1, \tilde{w}_2)$. Then from the directions the trajectory crosses $\bar{c}(\tilde{w})$ at B_1 and B_2, we have $k - 1/\tilde{c}_1 \geq 0$ and $k - 1/\tilde{c}_2 \leq 0$ which contradicts the fact that $\tilde{c}_2 > \tilde{c}_1$. Thus $\tilde{c}$ lies below $\bar{c}$ on $[1, \tilde{w}_0]$.

The trajectory mentioned above actually stays strictly below $\bar{c}(\tilde{w})$. For if it touches $\bar{c}$ at the point $(\tilde{w}_1, \tilde{c}_1)$, we have $k = 1/\tilde{c}_1$. Since there can be at most one such point of tangency, the trajectory lies strictly below $\bar{c}(\tilde{w})$ on $(1, \tilde{w}_1)$ leading to $k < 1/\tilde{c}(\tilde{w})$ on this interval. Let the expression on the right of (3.4a) without the last term and with obvious modifications be denoted by $f(\tilde{w}, \tilde{c})$. Then $d\tilde{c}/d\tilde{w} < f(\tilde{w}, \tilde{c})$ and $d\bar{c}/d\tilde{w} = f(\tilde{w}, \bar{c})$ on the interval $(1, \tilde{w}_1)$. Comparison principle implies that the trajectory $\tilde{c}$ cannot reach S which is a contradiction. Thus the trajectory connecting Q and S must lie strictly below $\bar{c}$. The proof of the lemma is complete. ∎

Corollary 3.1. *$\sigma > 0$ along the trajectory connecting Q and S described in the above lemma.*

Proof. We prove the corollary for the case $\gamma \neq 1$ only. Since $\tilde{c} < \bar{c}$, we have

$$\frac{c}{A} < \frac{1}{\rho A}\left[1 - \frac{\kappa}{(1-\gamma)K}\right] + \frac{\kappa}{K(1-\gamma)A\rho}\tilde{w}^{1-\gamma}.$$

Rearranging and substituting in $wb_0\rho A$ for $\tilde{w}$, we have

$$\frac{\kappa b}{(1-\gamma)c}\left[1 - (wb_0\rho A)^{1-\gamma}\right] < Kb\left(\frac{1}{c} - \rho\right).$$

From (2.2) and the fact that $w = 1/uA = c/bA$, we have

$$\sigma > \frac{\kappa b}{(1-\gamma)c}\left[1 - \left(\frac{cb_0\rho}{b}\right)^{1-\gamma}\right] + \kappa\frac{p}{c}.$$

Since $\tilde{z} = pA/c$, from (3.5) the expression on the right equals to

$$\frac{\kappa b}{(1-\gamma)c}\left[1 - \left(\frac{cb_0\rho}{b}\right)^{1-\gamma}\right] + \frac{\kappa}{A}\left[\frac{1}{(\gamma-1)w} + \frac{(b_0\rho A)^{-\gamma+1}}{(1-\gamma)w^{\gamma}}\right].$$

Replacing $1/wA$ by $u = b/c$, the above expression equals zero. Thus $\sigma > 0$ and the proof of the corollary is complete. ∎

Lemma 3.4. *The arrival time function $y^*(\ell)$ satisfies: (i) $\ell \downarrow \ell_1^*$ if and only if $y^*(\ell) \to \infty$, (ii) $\ell \uparrow \ell^*$ if and only if $y^*(\ell) \to 0$.*

Proof. We prove the lemma for the case $\gamma \neq 1$ only. Multiplying equation (3.1a) by $b_0\rho A$, dividing by $\tilde{w}$, integrating from 0 to $y^*(\ell)$ and rearranging, we obtain

$$\frac{\tilde{w}(y^*(\ell))}{\tilde{w}(0)} = exp\,\{-\int_0^{y^*(\ell)} \gamma_b\,\tilde{c}(y;\ell)\,dy\}.$$

From the definition of $\tilde{w}_0$, we have

$$\frac{1}{\left[\left(\frac{\rho A(\ell)}{V_d}-1\right)\frac{(1-\gamma)K}{\kappa}+1\right]^{1/(1-\gamma)}} = exp\left\{-\int_0^{y^*(\ell)}\gamma_b\,\tilde{c}(y;\ell)\,dy\right\}. \tag{3.9}$$

We first examine statement (i). If $0 \le \gamma < 1$, then $\ell_1^* = 0$. From our hypotheses (HA), the left-side of (3.9) goes to zero as $\ell \downarrow 0$. If $\gamma > 1$, then ℓ_1^* is by definition the value where the term inside the square bracket equals zero so the left side also goes to zero as $\ell \downarrow \ell_1^*$. From Lemma 3.3, $\tilde{c}$ is bounded above and hence (3.9) implies that $y^*(\ell) \to \infty$ as $\ell \downarrow \ell_1^*$.

Conversely, let $\{\ell_n\}$ be a sequence in (ℓ_1^*, ℓ^*) with the corresponding arrival time $y_n^* \equiv y^*(\ell_n) \to \infty$ as $n \to \infty$. We claim that $\ell_n \to \ell_1^*$. For suppose not, then there exists a subsequence still labeled as $\{\ell_n\}$ such that $\ell_n \to \hat{\ell} > 0$ as $n \to \infty$. From hypotheses (HA), $\hat{c} = \liminf_{n\to\infty} c_{min}(\ell_n) > 0$ where c_{min} is defined in (3.8) with k replaced by $\rho A(\ell_n)$ there. From (3.9),

$$\frac{1}{\left[\left(\frac{\rho A(\ell_n)}{V_d}-1\right)\frac{(1-\gamma)K}{\kappa}+1\right]^{1/(1-\gamma)}} \le \exp(-\gamma_b\hat{c}y_n^*)\,.$$

Taking the limit as $n \to \infty$, we arrive at a contradiction. The proof of statement (i) is complete.

We now turn to statement (ii). From (HA), $\lim_{\ell\to\ell^*}\rho A(\ell) = V_d$. Since $\tilde{c} \ge \inf_{\{\ell^*/2<\ell<\ell^*\}} c_{min}(\ell) > 0$, (3.9) implies that $y^*(\ell) \to 0$ as $\ell \to \ell^*$.

Conversely, let $\{\ell_n\}$ be a sequence in (ℓ_1^*, ℓ^*) with the corresponding arrival time $y_n^* \equiv y^*(\ell_n) \to 0$ as $n \to \infty$. We claim that $\ell_n \to \ell^*$. For suppose not, then there exists a subsequence, still labeled as $\{\ell_n\}$, such that $\ell_n \to \hat{\ell} < \ell^*$ as $n \to \infty$. From (3.9),

$$\frac{1}{\left[\left(\frac{\rho A(\ell_n)}{V_d}-1\right)\frac{(1-\gamma)K}{\kappa}+1\right]^{1/(1-\gamma)}} \ge \exp(-My_n^*)\,.$$

Since $\rho A(\hat{\ell}) > V_d$, we arrive at a contradiction in the above inequality by letting $n \to \infty$. The proof of statement (ii) as well as the lemma is complete. ■

We now prove that the function $y^*(\ell)$ has a fixed-point on the interval $(0, \ell^*)$.

From (3.1) and (3.5), we have

$$\text{(3.10)}\quad \begin{cases} \tilde{w}' &= -\gamma_b \tilde{w}\tilde{c} \\ \tilde{c}' &= -\left(\tilde{c} - \dfrac{1}{\rho A}\right)\gamma_b \tilde{c} + \dfrac{\kappa \tilde{c}}{K\rho A}\left[\gamma_p\left(\dfrac{1}{\gamma - 1} + \dfrac{\tilde{w}^{1-\gamma}}{1-\gamma}\right) - \gamma_b\right] \\ & \quad -\dfrac{\xi(y)}{K\rho^2 b_0 A}\left(k - \dfrac{1}{\tilde{c}}\right)\tilde{w}\,. \end{cases}$$

Let

$$\text{(3.11)}\quad \begin{cases} F_1 &= \tilde{c}(y,k,\ell) - \dfrac{1}{\rho A(\ell)}\,, \\ F_2 &= \tilde{w}(y,k,\ell) - 1\,, \\ F_3 &= y - \ell\,. \end{cases}$$

where $\tilde{w}(y,k,\ell)$ and $\tilde{c}(y,k,\ell)$ are solutions of (3.10) satisfying the initial conditions $\tilde{w}(0,k,\ell) = \tilde{w}_0$, $\tilde{c}(0,k,\ell) = 1/V_d$.

Lemma 3.5. *The set* $\mathcal{S} = \{(y^*, k, \ell) \in \mathbf{R}^3 : \ell_1^* < \ell < \ell^*,\ k(\ell),\ y^*(\ell)$ *defined in Lemma 3.3* $\}$ *contains an unbounded continuum (closed connected set) which approaches the point* $(0, V_d, \ell^*)$.

Proof. We consider the case $\gamma \neq 1$ only. Let $\alpha \equiv A'(\ell^*)$ and let $\mathbf{F} = (F_1, F_2)^T$. We consider k as a bifurcation parameter. If $\ell = \ell^*$, then from Lemma 3.4, $y^* = 0$ and $\mathbf{F}(0,k,\ell^*) = 0$ for all k. From [2, p. 23],

$$\mathbf{F} = \mathcal{L}\begin{pmatrix} y \\ \ell - \ell^* \end{pmatrix} + (k - V_d)\mathcal{B}\begin{pmatrix} y \\ \ell - \ell^* \end{pmatrix} + \mathbf{p}$$

where

$$\text{(3.12)}\quad \mathcal{L} \equiv \begin{pmatrix} \partial F_1/\partial y & \partial F_1/\partial \ell \\ \partial F_2/\partial y & \partial F_2/\partial \ell \end{pmatrix}\Bigg|_{(0,V_d,\ell^*)} = \begin{pmatrix} -\kappa\gamma_b/KV_d^2 & \alpha\rho/V_d^2 \\ -\gamma_b/V_d & \alpha\rho K/\kappa V_d \end{pmatrix},$$

$$\text{(3.13)}\quad \mathcal{B} \equiv \begin{pmatrix} \partial^2 F_1/\partial k\partial y & \partial^2 F_1/\partial k\partial \ell \\ \partial^2 F_2/\partial k\partial y & \partial^2 F_2/\partial k\partial \ell \end{pmatrix}\Bigg|_{(0,V_d,\ell^*)} = \begin{pmatrix} -\xi(0)/K\rho b_0 V_d & 0 \\ 0 & 0 \end{pmatrix}$$

and $\mathbf{p}$ satisfies the properties listed in [2, (3.2)]. In the above calculations, we have used system (3.10), the facts that $\tilde{w}(0,k,\ell) = \tilde{w}_0$, $\tilde{w}_0 = 1$ if $\ell = \ell^*$ and $\rho A(\ell^*) = V_d$.

It can be readily checked that $\det(\mathcal{L}) = 0$. The null space of $\mathcal{L}$ is spanned by $\mathbf{n} \equiv (\alpha\rho, \kappa\gamma_b/K)^T$ and $\mathbf{z} \equiv (-\kappa\gamma_b/K, \alpha\rho)^T$ is perpendicular to $\mathbf{n}$. To employ the result in [2], we check that $\{\mathcal{L}\mathbf{z}, \mathcal{B}\mathbf{n}\}$ is a basis of $\mathbf{R}^2$. From [2, Theorem 1], a simple bifurcation occurs at $(0, V_d, \ell^*)$ with a trivial solution branch: $y = 0$, $\ell = \ell^*$ and k being arbitrary and another non-trivial C^1 solution curve Γ (see Figure 1). From Lemma 3.4, as $y \to 0$, we have $\ell \to \ell^*$ and $k \to V_d$. From Lemma 3.5, it is easy to see that for $0 < \ell < \ell^*$, points on Γ correspond to solutions of (3.1) connecting Q and S. Moreover, Γ cannot return to the trivial branch elsewhere, as there is no other bifurcation point there.

Fig. 1.

From the structure of $\mathbf{n}$, we have

$$\left\{ \begin{array}{rcl} y(s) & = & \alpha\rho s + o(s)\,, \\ \ell(s) & = & \ell^* + (\kappa\gamma_b/K)s + o(s)\,, \\ k(s) & = & V_d + o(1) \end{array} \right. \tag{3.14}$$

in a neighborhood of the bifurcation point where s parameterizes Γ. Since $dy/ds \neq 0$, locally near the bifurcation point, we can parameterize Γ by y.

Next, we need to compute

$$\begin{aligned} \mathcal{J} &= \begin{pmatrix} \partial F_1/\partial k & \partial F_1/\partial \ell \\ \partial F_2/\partial k & \partial F_2/\partial \ell \end{pmatrix} \\ &= \begin{pmatrix} \partial \tilde{c}/\partial k & \partial \tilde{c}/\partial \ell + A'(\ell)/\rho A^2(\ell) \\ \partial \tilde{w}/\partial k & \partial \tilde{w}/\partial \ell \end{pmatrix} \end{aligned} \tag{3.15}$$

and show that $det\mathcal{J} \neq 0$ on Γ near the bifurcation point $(0, V_d, \ell^*)$. From (3.10b), we have

$$
\begin{aligned}
(\tilde{c}_k)' &= -\gamma_b \tilde{c}\tilde{c}_k - \left(\tilde{c} - \frac{1}{\rho A(\ell)}\right)\gamma_b \tilde{c}_k + \frac{\kappa \tilde{c}_k}{K A(\ell)}[\cdots] + \frac{\kappa \tilde{c}}{K\rho A(\ell)}\left[\gamma_p \tilde{w}^{-\gamma}\tilde{w}_k\right] \\
&- \frac{\xi(y)}{K\rho^2 b_0 A(\ell)}\left(k - \frac{1}{\tilde{c}}\right)\tilde{w}_k - \frac{\xi(y)}{K\rho^2 b_0 A(\ell)}\left(1 + \frac{\tilde{c}_k}{\tilde{c}^2}\right)\tilde{w}
\end{aligned} \tag{3.16}
$$

where subscripts in k denote partial derivatives with respect to k. From this and (3.10a), we have

$$
\begin{pmatrix} \partial\tilde{w}/\partial k \\ \partial\tilde{c}/\partial k \end{pmatrix}' = \begin{pmatrix} -\gamma_b\tilde{c} & -\gamma_b\tilde{w} \\ \cdots & \cdots \end{pmatrix}\begin{pmatrix} \partial\tilde{w}/\partial k \\ \partial\tilde{c}/\partial k \end{pmatrix} + \begin{pmatrix} 0 \\ \dfrac{-\xi(y)\tilde{w}}{K\rho^2 b_0 A(\ell)} \end{pmatrix}. \tag{3.17}
$$

Since $\tilde{w}(0,k,\ell) = \tilde{w}_0$ and $\tilde{c}(0,k,\ell) = 1/V_d$ are both independent of k, we have from (3.17a),

$$
\frac{\partial\tilde{w}}{\partial k}(y,k,\ell) = o(y)
$$

and from (3.17b)

$$
\frac{\partial\tilde{c}}{\partial k}(y,k,\ell) = \frac{-\xi(0)}{K b_0 \rho V_d}\, y + o(y)
$$

near the bifurcation point $(0, V_d, \ell^*)$.

To continue, from (3.10b), we have

$$
\begin{aligned}
(\tilde{c}_\ell)' &= -\left(\tilde{c}_\ell + \frac{A'(\ell)}{\rho A^2(\ell)}\right)\gamma_b\tilde{c} - \left(\tilde{c} - \frac{1}{\rho A}\right)\gamma_b\tilde{c}_\ell + \frac{\kappa\tilde{c}_\ell}{K\rho A}[\cdots] - \frac{\kappa\tilde{c}A'(\ell)}{K\rho A^2(\ell)}[\cdots] \\
&+ \frac{\kappa\tilde{c}}{K\rho A(\ell)}\left[\gamma_p\tilde{w}^{-\gamma}\tilde{w}_\ell\right] + \frac{\xi(y)A'(\ell)}{K\rho^2 b_0 A^2(\ell)}\left(k - \frac{1}{\tilde{c}}\right)\tilde{w} \\
&- \frac{\xi(y)}{K\rho^2 b_0 A(\ell)}\left(\frac{\tilde{c}_\ell}{\tilde{c}^2}\right)\tilde{w} - \frac{\xi(y)}{K\rho^2 b_0 A(\ell)}\left(k - \frac{1}{\tilde{c}}\right)\tilde{w}_\ell\,.
\end{aligned} \tag{3.18}
$$

Therefore,

$$
\begin{aligned}
\begin{pmatrix} \partial\tilde{w}/\partial\ell \\ \partial\tilde{c}/\partial\ell \end{pmatrix}' &= \begin{pmatrix} -\gamma_b\tilde{c} & -\gamma_b\tilde{w} \\ \cdots & \cdots \end{pmatrix}\begin{pmatrix} \partial\tilde{w}/\partial\ell \\ \partial\tilde{c}/\partial\ell \end{pmatrix} \\
&+ \begin{pmatrix} 0 \\ -\dfrac{A'(\ell)}{\rho A^2(\ell)}\gamma_b\tilde{c} + \dfrac{\xi(y)A'(\ell)}{K\rho^2 b_0 A^2(\ell)}\left(k - \dfrac{1}{\tilde{c}}\right)\tilde{w} - \dfrac{\kappa\tilde{c}A'(\ell)}{K\rho A^2(\ell)}[\cdots] \end{pmatrix}.
\end{aligned}
$$

From the definition of $\tilde{w}_0$, we have

$$
\begin{aligned}
\frac{\partial\tilde{w}}{\partial\ell}(0,k,\ell) &= [\cdots]^{\gamma/(1-\gamma)}\,\frac{\rho A'(\ell)}{V_d}\,\frac{K}{\kappa} \\
&= \frac{\rho A'(\ell)K}{\kappa V_d}\tilde{w}_0^{\gamma}\,.
\end{aligned}
$$

Therefore,

$$\frac{\partial \tilde{w}}{\partial \ell}(y,k,\ell) = \frac{\rho\alpha K}{\kappa V_d} + o(1)$$

near $(0, V_d, \ell^*)$. Since $\tilde{c}(0,k,\ell) = 1/V_d$, we have

$$\frac{\partial \tilde{c}}{\partial \ell}(y,k,\ell) = o(1)$$

near $(0, V_d, \ell^*)$. Therefore,

$$\mathcal{J} = \begin{pmatrix} \dfrac{-\xi(0)}{Kb_0\rho V_d}\, y + o(y) & o(1) + \dfrac{\rho\alpha}{V_d^2} \\ o(y) & \dfrac{\rho\alpha K}{\kappa V_d} + o(1) \end{pmatrix}$$

and

$$det\,\mathcal{J} = -\frac{\xi(0)\alpha}{\kappa b_0 V_d^2}\, y + o(y)$$

near the bifurcation point $(0, V_d, \ell^*)$ and is non-zero for $y > 0$ since $\alpha < 0$.

Let $B_R(y) = \{(y,k,\ell) : |k - V_d|^2 + |\ell - \ell^*|^2 < R^2\}$ and let $B_R = B_R(0)$. Suppose $\mathcal{S}$ is bounded, then there exists $R > 0$ and $y_2 > 0$ such that the non-trivial solution is contained in the interior of the cylinder $\mathcal{C} = \{(y,k,\ell) : 0 \le y < y_2, (k,\ell) \in B_R\}$. Since $\mathbf{F}$ does not vanish on $[y_1, y_2] \times \partial B_R$ for a sufficiently small $y_1 > 0$, we have $deg(\mathbf{F}, B_R(y_1), 0) = deg(\mathbf{F}, B_R(y_2), 0)$. From the fact that there is no other solution for small $y_1 > 0$, the above calculation on the determinant of $\mathcal{J}$ implies that $deg(\mathbf{F}, B_R(y_1), 0) = 1$. This is a contradiction since $deg(\mathbf{F}, B_R(y_2), 0) = 0$. Hence $\mathcal{S}$ cannot be bounded.

To prove that the set $\mathcal{S}$ in Lemma 3.5 contains a connected continuum, we simply observe that the set $\mathcal{C}$ in the above argument can be replaced by a bounded neighborhood containing the maximal continuum approaching the point $(0, V_d, \ell^*)$ (see Lemma 1.2 in [4]). The rest of the proof is then identical to the above argument.

Proof of Theorem2.1 In the unbounded continuum of $\mathcal{S}$ in Lemma 3.5, y^* must be unbounded for if otherwise, ℓ is bounded away from ℓ_1^* and $A(\ell)$ is bounded away from infinity and hence $k \in (V_d, \rho A(\ell))$ is also bounded which is a contradiction. Because the unbounded continuum is connected and approaching the point $(0, V_d, \ell^*)$, there exists an ℓ such that $y^* = \ell$ which implies the existence of traveling wave. The proof of Theorem 2.1 is complete.

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