DISCRETE AND CONTINUOUS
DYNAMICAL SYSTEMS–SERIES B
Volume **1**, Number **3**, August **2001**

Website: http://AIMsciences.org

pp. **339–362**

TRAVELLING WAVES IN A NONLINEAR DEGENERATE DIFFUSION MODEL FOR BACTERIAL PATTERN FORMATION

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Abstract. We study a reaction diffusion model recently proposed in [5] to describe the spatiotemporal evolution of the bacterium *Bacillus subtilis* on agar plates containing nutrient. An interesting mathematical feature of the model, which is a coupled pair of partial differential equations, is that the bacterial density satisfies a degenerate nonlinear diffusion equation. It was shown numerically that this model can exhibit quasi-one-dimensional constant speed travelling wave solutions. We present an analytic study of the existence and uniqueness problem for constant speed travelling wave solutions. We find that such solutions exist only for speeds greater than some threshold speed giving minimum speed waves which have a sharp profile. For speeds greater than this minimum speed the waves are smooth. We also characterise the dependence of the wave profile on the decay of the front of the initial perturbation in bacterial density. An investigation of the partial differential equation problem establishes, via a global existence and uniqueness argument, that these waves are the only long time solutions supported by the problem. Numerical solutions of the partial differential equation problem are presented and they confirm the results of the analysis.

1. **Introduction.** Many biological systems exhibit the phenomenon of self organisation, whereby complex spatiotemporal patterns emerge from the biochemical processes occurring within the system (for review see, for example, Murray [15]). One very widely studied system is the spatiotemporal patterning behaviour in bacterial colonies. Not only does this serve as a model paradigm for patterning in higher organisms, its study also has important implications in biotechnology and related areas.

1991 *Mathematics Subject Classification.* 37C45.
Key words and phrases. degenerate diffusion, travelling waves, bacterial chemotaxis, phase plane analysis, nonlinear coupled parabolic equations.

Bacterial colonies grown on the surface of thin agar plates can develop various types of spatial patterns including rings, spots, disks and patterns with a dense-branching morphology (DBM). The nature of the pattern exhibited depends on the particular bacterial species used and the environmental conditions imposed. The spatio-temporal patterns generated by the bacterium *Bacillus subtilis* were investigated in Kawasaki *et al.* [5] using a reaction diffusion type model, and the authors presented the first demonstration of branching pattern formation of bacterial colonies in the framework of a reaction diffusion system. Closer investigation of these patterns revealed that, although the colony grows on the two-dimensional surface of the agar plate, each tip elongates in one dimension apart from occasionally branching. The authors therefore considered a one-dimensional version of their model and showed, using numerical simulations, that the model exhibited travelling wave solutions with a constant speed that closely approximated the speed of the solution profile to the full two-dimensional problem.

This model has a very interesting mathematical structure, involving nonlinear degenerate diffusion in a coupled system of reaction diffusion equations. To our knowledge, there is little theory on travelling wave solutions in such coupled systems. The aim of this paper is to: address the existence and uniqueness problem for this type of solution, determine speed selection, investigate the role of initial conditions, and study robustness. These are key issues from the biological viewpoint. In fact, we consider a simplified version of the model in which one of the diffusion coefficients is set to zero, so that the system is now an ordinary differential equation coupled with a nonlinear degenerate diffusion reaction equation. Surprisingly, we find that this simplified version of the model captures much of the behaviour of the full system, in particular the wave speed predicted by our analytic study is in close agreement with that exhibited by travelling wave solutions to the full system.

We briefly describe the model proposed in Kawasaki *et al.* [5] (section 2) and in section 3 carry out a detailed analysis of the travelling wave solutions of the simplified version of the model. The partial differential equation problem is considered in section 4 and in section 5 we show how our analysis can be extended to other models of similar form. The results are then discussed in the context of the original paper (section 6).

2. The Model.

Kawasaki *et al.* [5] considered a model of the form

$$\frac{\partial n}{\partial t} = D_n \nabla^2 n - knb \tag{2.1}$$

$$\frac{\partial b}{\partial t} = \nabla \cdot D_b \nabla b + knb \tag{2.2}$$

to describe the spatiotemporal dynamics on a planar surface of bacterial cell density $b(x, y, t)$ and nutrient concentration $n(x, y, t)$ at spatial position (x, y) and time t. The model equations assume that the nutrient diffuses in a Fickian sense with constant diffusion coefficient D_n and is consumed by bacteria at a rate k. The bacteria are assumed to have diffusion coefficient $D_b = \sigma_0 nb$, where σ_0 is a positive constant and the nonlinearity accounts, in a phenomenological way, for experimental observations on bacterial motion.

They showed, via numerical simulation, that this model gave rise to a vast array of patterns in different parameter regimes. They focussed on the formation of dense branching patterns and investigated how the model parameters controlled the rate of branch tip elongation. Considering a branch as a one-dimensional structure, they argued that a simplied version of the model,

$$\frac{\partial b}{\partial t} = \sigma_0 \frac{\partial}{\partial x}[b\frac{\partial b}{\partial x}] + b(1 - b/K) \tag{2.3}$$

where K is a positive constant, could approximate the motion. They were then able to quote analytic results on the travelling wave speed of this type of equation and compare the results with those observed in the full two-dimensional simulations. We refer the reader to the original paper for full details.

Here we consider the one-dimensional version of the model and carry out a more detailed analysis. Specifically, denoting the nutrient concentration and bacterial density by $n(x,t)$ and $b(x,t)$, respectively, at position x and time t, we consider a nondimensionalised version of the model taking the form:

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - nb \tag{2.4}$$

$$\frac{\partial b}{\partial t} = D_b \frac{\partial}{\partial x}\left(nb\frac{\partial b}{\partial x}\right) + nb \tag{2.5}$$

where $\{(x,t) : x \in \mathbf{R}, \quad t \in \mathbf{R}^+\}$ and D_n and D_b are the non-dimensionalised diffusion coefficients of n and b, respectively. Here there is a slight abuse of notation as b, n, x and t now represent non-dimensional quantities.

This system has a continuum of spatially uniform steady states of the form $(n,b) = (n_s, 0), (0, b_s)$, where n_s and b_s are arbitrary constants. The laboratory set-up consists of a nutrient-enriched agar plate on which an initial innoculum of bacteria is placed. Therefore the appropriate steady state to consider initially is the one (which we denote by $\mathcal{S}$) given by

$$n = 1, \quad b = 0 \quad \text{for all} \quad -\infty < x < \infty. \tag{2.6}$$

The biological interpretation of this condition is that the nutrient is at a uniform concentration level of 1 (nondimensionalised) and there are no bacteria present. We then assume that at time $t = 0$ there is an initial innoculum of bacteria at $x = 0$, that is a (small) perturbation to the original state is made at $t = 0$ to the b values in a region localized around $x = 0$. We take conditions to be uniform at infinity so that

$$\frac{\partial n}{\partial x} \to 0, \ \frac{\partial b}{\partial x} \to 0 \text{ as } |x| \to \infty, \quad \text{for all} \quad t > 0. \tag{2.7}$$

In the following we shall assume that $D_n = 0$. This is in effect modelling the case of so called "hard agar". The implications of this assumption will be discussed in section 6. Without restriction we shall take $D_b = 1$. Our main aim is to explore what are the possible long time stationary states of this system. Specifically, given the experimental and numerical evidence for travelling wave solutions presented in [5] we start by considering the possible constant speed travelling wave solutions to the system described by equations (2.4)–(2.7).

3. **Permanent-form travelling waves.** To discuss the permanent-form travelling wave solutions (TWS) that can arise as large time structures within the system of equations (2.4)–(2.5) under the conditions (2.6)–(2.7) we introduce the travelling coordinate $y = x - vt$, where v is the (constant) wave velocity. Because this system is invariant for symmetric initial conditions to a change of coordinates $x \to -x$ we can choose to take $v > 0$ in the above coordinate transformation. Substituting $n(x,t) = (\tilde{n}(x-vt), \tilde{b}(x-vt))$ into (2.4)–(2.5) transforms the latter into travelling wave coordinates:

$$vn' = nb \tag{3.1}$$

$$(nbb')' + vb' + nb = 0 \tag{3.2}$$

where $'$ denotes derivative with respect to y and, for notational simplicity, we have dropped the tildes. Equations (3.1)–(3.2) are to be solved subject to the following boundary conditions ahead of the wave

$$n \to 1, \ b \to 0 \text{ as } y \to \infty \tag{3.3}$$

so that the wave is propagating into the fresh nutrient region of the plate while behind the wave

$$n \to n_s, \ b \to b_s \text{ as } y \to -\infty, \tag{3.4}$$

that is, the nutrient concentration and bacterial density have relaxed to spatially uniform values after the wave has passed. Here n_s and b_s are constant and, from equations (2.4)–(2.5), at least one of them is zero (steady state value). Also note that for physically realistic solutions we require that $n, b \geq 0$ (see Section 4.2 for a mathematical proof that this is indeed the case for the model). Simple integration of (3.1) with respect to y shows that, under these conditions, v is non-negative, consistent with our assumption on the wave speed. We note that our numerical solutions, presented later, confirm this result.

Here we have adopted the standard approach of establishing the existence of travelling wave solutions of the full partial differential equation system by looking for heteroclinic trajectories of the associated ordinary differential equation system with appropriate boundary conditions.

3.1. **Properties of the travelling wave solutions.** General properties of TWS for systems having kinetics of the form in (2.4)–(2.5), but with constant diffusion coefficients for both species, have been given in [2, 10, 13]. Some of these properties are preserved in the present case and we shall recall them without proof. However, the presence of the nonlinear diffusion term leads to some significant differences in general. We start with a list of all these properties.

P1 *There are no TWS with* $n \equiv 1$ *or* $b \equiv 0$.

Proof: This follows directly from [10].◇

P2 *There exists* $y_0 \in \mathbf{R}$ *such that* $nb(y_0) \neq 0$.

Proof: This follows from **P1**, equation (3.1) and boundary condition (3.3).◇

P3 *Of the continuum of spatially uniform steady states $(n_s, 0)$, $(0, b_s)$ for the initial value problem (2.4)–(2.5), we require that $n_s = 0$, $b_s = 1$ for travelling waves.*

Proof: If we integrate with respect to y both sides of equation (3.2) once and apply boundary conditions (3.3)–(3.4) we obtain

$$vb_s = \int_{-\infty}^{\infty} (nb)dy > 0 \tag{3.5}$$

and thus $b_s > 0$ via **P1** and the fact that v is non-negative. But $n_s b_s = 0$ so that $n_s = 0$. Now if we integrate equations (3.1)–(3.2) from $-\infty$ to y (some finite value) we have

$$nbb' + v(b - b_s) + vn = 0. \tag{3.6}$$

By taking $y \to \infty$ here and using boundary condition (3.3) we finally get $vb_s = v$ giving $b_s = 1$. Therefore equation (3.2) can be replaced by equation (3.6) with $b_s = 1$.$\diamondsuit$

P4 *n is monotone increasing and b is monotone decreasing.*

Proof: For the case of n this results directly from (3.1) and the definition of TWS. From the b equation we have

$$b' = \frac{-v}{n} - \frac{\int_{-\infty}^{y} (nb)ds}{nb} \leq 0 \tag{3.7}$$

for $nb \neq 0$. Suppose now that $nb(y_1) = 0$ for some $y_1 \in \mathbf{R}$. Two cases may arise from (3.6), namely either $n(y_1) = 0$, $b(y_1) = 1$ or $n(y_1) = 1$, $b(y_1) = 0$. The first situation is impossible. This is easily seen since from the monotonicity of n we have that $n(y) = 0$ and therefore from (3.6) $b(y) = 1$ for all y such that $-\infty < y \leq y_1$. We can take without restriction y_1 such that $n(y) > 0$ for all $y > y_1$. From equation (3.1) and the uniqueness theorem for initial value problems we have that $n(y) \equiv 0, \forall y \in \mathbf{R}$. Hence we have a contradiction with boundary condition (3.3). For the second possibility assume that there exists y_2 such that $n(y_2) = 1$ and $b(y_2) = 0$. The monotonicity property of n and the boundary condition (3.3) then means that $n(y) = 1$ for all $y > y_2$. From **P3** we can chose y_2 such that $n(y) < 1$ for all $y < y_2$. Then equation (3.6) implies that $b(y) > 0$ for all $y < y_2$. Hence we can apply the above monotonicity property since we have nb nonzero.$\diamondsuit$

From **P4** we deduce that $1 \geq n(y), b(y) \geq 0$, for all $y \in (-\infty, \infty)$.

By using the above properties we can re-write the system (3.1)–(3.2) as

$$n' = nb/v, \qquad nbb' = v(1 - n - b)$$

which is singular on the vertical and horizontal axes of the $n - b$ plane. The singularity can be removed by using a standard re-parametrization [17, 18]. Let z be such that $dz/dy = nb$ for $nb(y) > 0$ for all y. In terms of z and keeping the same $'$ sign notation for the derivative with respect to z (for notational simplicity) the above re-written form of (3.1)–(3.2) becomes:

$$n' = \frac{(nb)^2}{v} \tag{3.8}$$

$$b' = v(1 - n - b), \tag{3.9}$$

which is not singular. Moreover, given that $1/(nb) > 0$ for $n > 0$ and $b > 0$, the dynamics given by (3.1)–(3.2) and that associated with (3.8)–(3.9) are the same in the first quadrant. Thus, we are interested in analysing the dynamics given by (3.8)–(3.9) with the boundary conditions (3.3)–(3.4) together with those given by **P3**.

P5 *Let* $(n(z), b(z))$ *be a travelling wave solution to equations (3.8)–(3.9). Then* $n(z) + b(z) \geq 1$ *for all* $z \in \mathbf{R}$.

Proof: This follows easily from equation (3.9) and **P4** if we note that $1 - n - b = \frac{b'}{v} \leq 0$.♢

P6 The velocity, v, of the travelling wave solutions satisfies $v \geq v_0 = \frac{1}{\sqrt{6}}$.

Proof: This can be seen by first differentiating equation (3.9) once with respect to z to obtain

$$b'' = -v(n' + b') \tag{3.10}$$

From equations (3.8) and (3.9), the above can be rewritten as

$$b'' + vb' + b^2 \left(1 - b - \frac{b'}{v}\right)^2 = 0. \tag{3.11}$$

Integrating this equation with respect to z from $-\infty$ to ∞ and using the boundary conditions (3.3)–(3.4) with $b_s = 1$ we find that

$$v \geq \frac{1}{6v}, \tag{3.12}$$

that is, $v \geq \frac{1}{\sqrt{6}}$.♢

An important consequence of **P6** is that the waves can only exist for speeds greater than a minimum (strictly positive) speed. However, we shall see later that the bound given in **P6** is not the best one achievable.

We now discuss the correspondence between the solutions of the systems (3.1)–(3.2) and (3.8)–(3.9). Clearly if every solution pair $(n,\ b)$ to (3.1)–(3.2) is nonzero everywhere then (3.1)–(3.2) would be equivalent to (3.8)–(3.9). Let us analyse what happens if this is not the case. Then there would be a $y_* \in \mathbf{R}$ such that

$$nb(y_*) = 0. \tag{3.13}$$

In view of equation (3.6) it is clear that this implies that $(n + b)(y_*) = 1$. Two possibilities may arise from equations (3.6) and (3.13) which we analyse in turn.

Case 1: $n(y_*) = 0$ and $b(y_*) = 1$. This case is actually impossible (this was already established in the proof of **P4**).

Case 2: $n(y_*) = 1$ and $b(y_*) = 0$. Then **P3** and **P4** imply that $n(y) = 1$, $b(y) = 0$ for all $\infty > y \geq y_*$. Also from (3.2) we find that $b'(v + nb') = 0$ at y_* so that

$lim_{y \to y_*^-} b'(y) \equiv b'(y_*^-) = 0$ or $b'(y_*^-) = -v$ (we do not know if $b'(y_*)$ exists, that is, we are considering weak solutions (continuous and piecewise differentiable) rather than classical solutions). Now suppose that $b'(y_*^-) = 0$. With this hypothesis we note that neither n nor b can decay exponentially for y close to y_*. Otherwise we could arrive at a contradiction in the same way as we did in *Case 1* above. Next we see from equations (3.1) and (3.6) that $\frac{d^k}{dy^k}(n)(y_*) = 0$, $\frac{d^k}{dy^k}(b)(y_*^-) = 0$ for all $k \geq 1$, k integer (by induction on k from repeated differentiation of equations (3.1) and (3.6)). But we know from monotonicity that $b(y) \equiv 0 \ \forall y > y_*$. Thus $b'(y_*^+) = 0$. Therefore for the case $b'(y_*^-) = 0$, $b'(y_*)$ exists and by induction b is of class C^∞ around y_* so we can also rule out algebraic decay around y_*. This shows that the case $b'(y_*^-) = 0$ is impossible. We note in passing that this also implies that b is not an analytic function on $\mathbf{R}$.

The above argument shows that in *Case 2* the only possibility is $b(y_*) = 0, b'(y_*^-) = -v$. We investigate this possibility below.

3.2. **Phase plane analysis of equations (3.8)–(3.9).** We now consider the system of equations (3.8)–(3.9) with the boundary conditions (3.3)–(3.4). We shall see in due course that the behaviour of this simpler system is entirely equivalent to that of the full initial system (3.1)–(3.2) even if we remember that (3.8)–(3.9) was obtained from (3.1)–(3.2) only in the case $nb(y) \neq 0$. Also it is clear that in this case all the properties above for TWS to (3.1)–(3.2) remain valid for (3.8)–(3.9).

Our aim is to establish the existence of an integral connection between the two steady states $R = (0, 1)$ and $S = (1, 0)$ of system (3.8)–(3.9) which enters S along its stable manifold (whose existence is established). This will be shown to correspond to a sharp type solution for the original system (3.1)–(3.2). First we will analyse the local dynamical behaviour of system (3.8)–(3.9) around the two equilibrium points. We then go on to study the change in the phase plane as the parameter v is varied from $v > 0$ small (when no connection between R and S is possible) up to $v \to \infty$ (when all the connections from R enter S along a certain centre manifold, which is explicitly calculated). Finally, we show that the direction of any trajectory leaving R changes monotonically with increasing v. These properties will allow us to ascertain that there is only one positive speed $v_{min} > 0$ for which a connection from R to S is via the stable manifold.

Any TWS of (2.4)–(2.5) under the conditions (2.6)–(2.7) corresponds to an integral path of the system (3.8)–(3.9) connecting the two stationary states R =(0,1) to S=(1,0)[1]. By simple direct calculation one can see that R is a non-hyperbolic point and the eigenvalues of the Jacobian matrix associated with the system (3.8)–(3.9) at R are $\lambda_1 = 0, \lambda_2 = -v$. The corresponding eigenvectors are $\underline{e_1} = (1, -1)$ and $\underline{e_2} = (0, 1)$. Clearly $\underline{e_2}$ points towards R locally around R so that any TWS must originate from R along the $\underline{e_1}$ direction. Because of the nature of this point we need to use the Centre Manifold Theorem to obtain the equation of this path locally around R. We find that

$$n = 1 - b + \frac{1}{v^2}(1 - b)^2 + \dots . \tag{3.14}$$

Similarly, we find that S is a non-hyperbolic point. The eigenvalues of the Jacobian matrix associated with the system (3.8)–(3.9) at S are $\lambda_3 = 0, \lambda_4 = -v$, with

[1]Because of this equivalence we will use the term TWS to also denote the appropriate heteroclinic trajectory in the $n - b$ phase plane.

the corresponding eigenvectors $\underline{e_3} = (1, -1)$ and $\underline{e_4} = (0, 1)$. Any TWS must end at S = (1,0). Now both $\underline{e_3}$ and $\underline{e_4}$ point towards S around S so that we now have two possible ways to enter S. If the TWS enters along $\underline{e_3}$ then the decay is along the central manifold whose equation is given locally by

$$b = 1 - n + \frac{1}{v^2}(1-n)^2 + \dots \tag{3.15}$$

(we note that (3.14) and (3.15) are symmetric because the right-hand sides of equations (3.8) and (3.9) are symmetric in n and b respectively, that is $(n, b) \to (b, n)$).

If the decay to S is along $\underline{e_4}$ then it does so such that $\frac{db}{dn} \to -\infty$ for $z \to \infty$. A short calculation similar to the one in [13] shows that the local form of the trajectory is

$$b = v\sqrt{2(1-n)} + \dots. \tag{3.16}$$

On eliminating the variable z from (3.8)–(3.9) we obtain the following ordinary differential equation for the trajectories of this system:

$$\frac{db}{dn} = \frac{v^2(1-b-n)}{(nb)^2} \tag{3.17}$$

for $nb \neq 0$. However, from the preceding paragraph we know that $nb = 0$ for some finite z value would only be possible with $b'(y_*^-) = -v,\ n'(y_*) = 0$. This implies that $\frac{db}{dn} \to -\infty$ for $y \to y_*^-$ which is also a property of the dynamical system given by equation (3.17). This remark coupled with the analysis from the last paragraph in section 3.1 shows that the systems (3.1)–(3.2) (or (3.1) and (3.6)) and (3.8)–(3.9) in the form (3.17) have equivalent behaviour, i.e. both sustain sharp and smooth TWS and no other type of waves and there is a one-to-one correspondence between these two types of solution and the two systems.

For the analysis which follows we shall focus on the triangular region T given by (see figure 1):

$$T = \{(n, b) : 0 \leq n \leq 1 \,\text{and}\, (1-n) \leq b \leq 1\}. \tag{3.18}$$

We now examine the behaviour of the field associated with the system (3.8)–(3.9) along the boundary of T. Along the line $n = 1$ we have that $n' > 0, b' = -vb < 0$. On $b = 1$ we have $n' > 0, b' = -vn < 0$ whilst on $b = (1-n),\ n' > 0, b' = 0$. Furthermore, on the line $n = 0$ we have that $b' > 0$ for $b < 1$ and $b' < 0$ for $b > 1$. On $b = 0, n' = 0, b' = v(1-n)$ which is positive in $n < 1$ and negative in $n > 1$. Due to this local behaviour along the T boundary we note that any allowable solution must leave T only across the line $n = 1$.

We next look at the behaviour of the trajectory R_v originating from R=(0,1) for v positive but close to zero. In this case either from equation (3.14) or from equation (3.15) we would find that locally n (or b) becomes greater than 1 which is

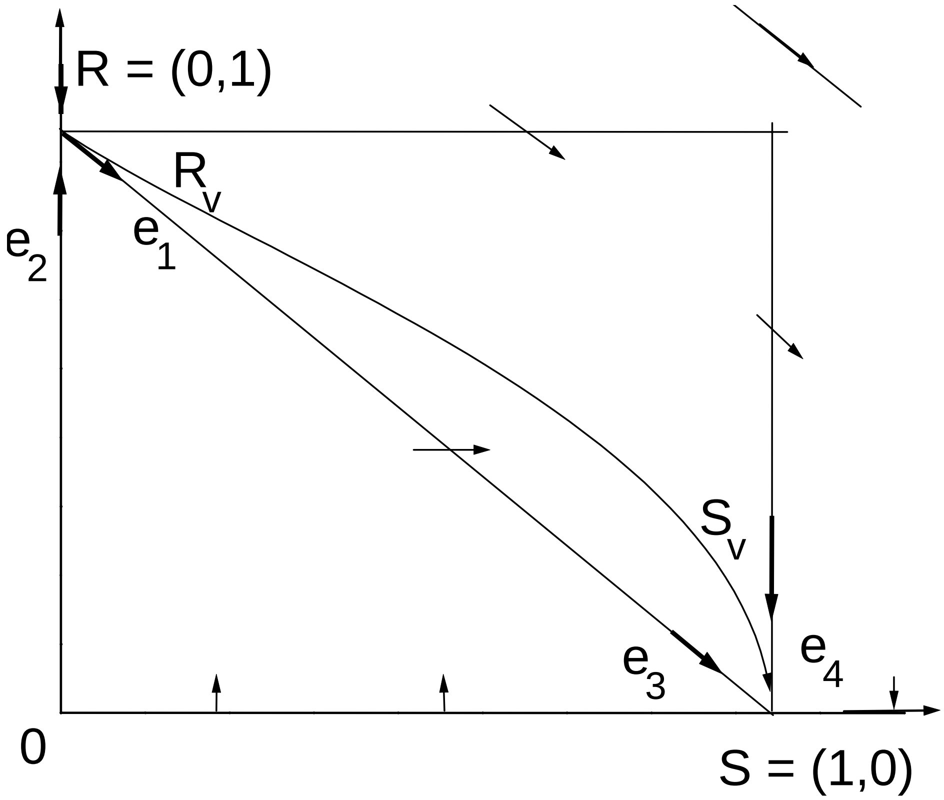


FIGURE 1. A sketch of the phase plane for system (3.8)–(3.9) showing the triangle T (vertices $(0,0), (1,0)$ and $(1,1)$) and illustrating the relevant trajectories and field directions (see text for full details).

in contradiction with the conclusion of **P4**. In fact from **P6** we already know that there are TWS only for $v \geq v_0 \geq \frac{1}{\sqrt{6}}$.

The next key step is to see from **P5** and equation (3.17) that

$$\frac{db}{dn} < 0 \tag{3.19}$$

so that $\frac{db}{dn}$ decreases as v increases for fixed (n,b) in T and away from R and S (where $n+b=1$). This then implies that any trajectory R_v originating from R must move down below its previous position in the (n,b) plane as v increases for fixed n and b. However, for the same reason the opposite is true for any trajectory S_v which enters S tangential to $\underline{e_4}$ (the same conclusion holds if S_v would have entered S along $\underline{e_3}$). For fixed values of n and b, R_v must move above its previous position so as to satisfy (3.19). This fact then establishes that if there is at least a trajectory connecting R to S then it is unique. In particular there is a unique connection from R to S entering S along $\underline{e_4}$.

An alternative way to see this is to note that the angle $\theta(v)$ formed for the vector field defined by (3.8)–(3.9) and the positive (in the clockwise direction) n axis is given by

$$\theta(v) = tan^{-1}\left(\frac{v^2(1-b-n)}{(nb)^2}\right).$$

This is a monotonic decreasing function of v for all interior points of T. The uniqueness result immediately follows.

We have already shown that for small values of v there are no TWS. In fact any such trajectory will leave T across the boundary $n = 1$ after which it terminates at infinity. However, because of the monotonicity properties of the trajectories described above we deduce that if there is a solution connecting R to S and entering S along $\underline{e_4}$ then this is the TWS with the minimum speed v_{min}. All the other solutions (if they exist) must therefore enter S along the central manifold (3.15). This last fact is easy to prove. To see this we need to show that any trajectory S_v terminating at S does so along the centre manifold (3.15) for $v > v_{min}$. This is readily established because S_v cannot escape along the boundary $b = 1 - n$ and if it would not terminate at S then it would intersect the boundary $n = 1$ at some interior point. This fact then would produce a contradiction by employing arguments similar to those used to establish the existence of the solution with minimum speed v_{min}.

All that remains now is to prove that a connection between R and S exists which gives the TWS with the minimum speed. We do this by studying the behaviour of the stable manifold S_v of S as b is increased away from 0. The method we employ is similar to the technique used in [2] (even though they dealt with a scalar equation). First we remark that for v close to 0, S_v must cross the line $b = 1 - n$. We next examine the behaviour of S_v for $v >> 1$ and show that, in this case, S_v intersects the line $b = 1$. Then from a continuity argument it is clear that there must be a finite value of v for which R_v and S_v coincide, thus concluding the proof. We put $N = 1 - n$ and work in the (b, N) phase-plane. Therefore we have

$$\frac{dN}{db} = \frac{(1-N)^2 b^2}{v^2(b-N)} \tag{3.20}$$

for which S_v is given, from equation (3.16), by

$$N = \frac{b^2}{2v^2} + O(v^{-2}). \tag{3.21}$$

This approximation suggests the change of variable

$$N = \frac{N_0}{v^2} \tag{3.22}$$

where N_0 is a function which will be determined below. Equation (3.20) now becomes

$$\frac{dN_0}{db} = \frac{b^2(1-\frac{N_0}{v^2})^2}{b-\frac{N_0}{v^2}} \quad \text{and} \quad N_0 \sim \frac{b^2}{2} \text{ as } b \to 0^+. \tag{3.23}$$

If $v >> 1$, then from equation (3.23) an asymptotic expansion is suggested for N_0 of the form

$$N_0 = N_1(b) + \frac{N_2(b)}{v^2} + ... \tag{3.24}$$

where the functions $N_1, N_2, ...,$ can be determined from substituting (3.24) into (3.23) and solving at each order in turn. We find

$$N_0(b) = \frac{b^2}{2} + \frac{1}{2}\left(\frac{b^3}{3} - \frac{b^4}{2}\right)\frac{1}{v^2} + ... \tag{3.25}$$

It is therefore clear from equation (3.25) that we have $N_0(1) < 1$ and thus N crosses the line $b = 1$ in $b > 0$ which is what we wanted to establish. This then ends the proof of the existence and uniqueness of the TWS to system (3.8)–(3.9).

We conclude this part by noting the following characterization of the minimum speed v_{min}: $v = v_{min}$ is the minimum value of $v > 0$ such that $R_v(S_v)$ remains in the triangle T.

Finally it is worth commenting on the behaviour of the n solution in the case of the minimum speed solution which results from the preceding analysis. The issue here is related to whether there is any sharp decay in the n profile. A quick calculation shows that this is not the case, however. Indeed suppose that y_* is such that $b(y_*^-) = 0,\ b'(y_*^-) = -v$. Then equation (3.1) implies that n is locally given by

$$n \sim e^{-(y-y_*)^2/2}, \quad \text{for} \quad y < y_*. \tag{3.26}$$

with $n = 1$ for $y \geq y_*$. Hence from (3.16) n is smooth at $y = y_*$ (i.e. $n = 1$, $\frac{dn}{dy} = 0$ for all $y \geq y_*$).

This minimum speed can be computed numerically on using the methods described in Merkin *et al.* [13]. We integrate equation (3.17) with the local form given by equations (3.14) and (3.16) by applying a shooting method as implemented by the NAG routine DO2AGF. Figure 2 shows a plot of the resulting numerical solution. The minimum speed was found to be $v_{min} = 0.700$. This value of the minimum speed is in very good agreement with the value of the speed for the wave solutions obtained by solving the full partial differential equation problem (2.4)–(2.7). Finally we conjecture that $v_{min} = \frac{1}{\sqrt{2}}$.

We now proceed to study the partial differential equation (PDE) problem posed by equations (2.4)–(2.7).

4. **The Partial Differential Equation Problem (2.4)–(2.7).** We now investigate the local and global existence of solutions to the partial differential equation problem (2.4)–(2.7) and then explore the numerical solutions obtained from various initial conditions. In particular we will see that all the TWS (i.e. the travelling waves with speeds $v \geq v_{min} = 0.7$) predicted by the theory from the previous section are realizable as long term solutions to (2.4)–(2.7) provided the appropriate initial condition is chosen.

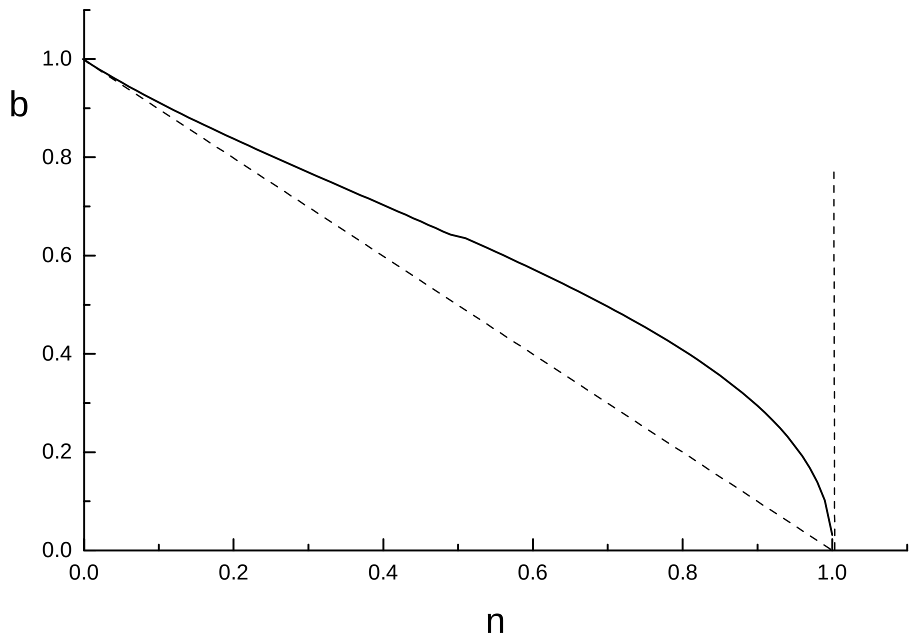


FIGURE 2. Plot of the numerical solution to equation (3.17) with minimum speed $v_{min} = 0.700$ in the (n, b) phase-plane, with local forms at $(0, 1)$ and $(1, 0)$ given by equations (3.14) and (3.16), respectively. The dashed lines represent $n + b = 1$ and the normal to the n-axis at $n = 1$.

4.1. **Local existence and uniqueness.** In general the initial value problem posed by the system (2.4)–(2.7) is well posed although the solutions are not necessarily classical because of the density dependent diffusion coefficient of the b species in equation (2.5). For initial data with compact and/or semi-infinite support it is possible to show that the solution exists and is piecewise classical in $(-\infty, \infty) \times [0, T)$. However, a proper analysis of this question is very technical and falls outside the primary scope of this work, namely the analysis of the travelling wave solutions. It will be presented elsewhere. For the remainder of this section we shall assume that if the initial data is smooth, with compact support, then the initial value problem (2.4)–(2.7) has a unique solution which is at least piecewise differentiable in $(-\infty, \infty) \times [0, T)$ for some $T > 0$.

4.2. **Global existence theory.** We now show that the solutions (n, b) whose existence was assumed above for all (x, t) with $-\infty < x < \infty$, $0 \leq t < T$ can be continued for any $0 \leq t < \infty$. There is however a difficulty with the PDE problem (2.4)–(2.7) in that the second equation has a density dependent diffusion equation and as such there is no immediately available comparison principle. Nevertheless this can be overcome in a simple way.

We first establish that any solution to system (2.4)–(2.5) with $D_n = 0$ and boundary conditions (2.6)–(2.7) which has positive initial data remains positive for any positive time. Moreover it is easy to establish an upper bound for n directly.

R1 *Let $n(x,t)$, $b(x,t)$ be a solution of our PDE problem for $(x,t) \in (-\infty,\infty) \times [0,T)$. Then*

$$0 \le n \le 1, \ 0 \le b \tag{4.1}$$

for all $(x,t) \in (-\infty,\infty) \times [0,T)$.

Proof: The proof is carried out in two steps:
A) The region $\Omega = \{(n,b) \mid n,b \ge 0\}$ is a positively invariant region for the PDE system with initial condition taken as a small perturbation to the uniform steady state (2.6) for all $(x,t) \in (-\infty,\infty) \times [0,T)$. By considering the kinetic term $g = (-nb, nb)$ and taking due regard of the behaviour as $|x| \to \infty$ along the lines described by Merkin *et al.* [12] we see that the system (2.4)–(2.5) is g-stable and the result follows by applying Theorem 14.11 from Smoller [20].

B) The upper bound for n in (4.1) is readily obtained by the same method as above (or by direct scalar comparison principle) and from the initial condition (2.6) the result follows easily.$\diamondsuit$

From **R1** it follows that in order to establish global existence we need to ascertain that b is *a priori* bounded as well. To do this we shall establish a maximum principle for the equation of the form satisfied by b.

R2 *Suppose that u satisfies the problem*

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(u\frac{\partial u}{\partial x}\right) \tag{4.2}$$

for $-\infty < x < \infty$ with $u(x,0) = u_0(x)$ being a positive, compact supported function on **R**. *Suppose also that*

$$\frac{\partial u}{\partial x} \to 0 \ \textit{as} \ |x| \to \infty, \quad t > 0. \tag{4.3}$$

Then the solution to the problem (4.2)–(4.3) is bounded.

Proof: The proof follows from King and Needham [7] (Prop. 3.1). $\diamondsuit$

From **R3** it is easy to obtain in a standard way a comparison principle for an equation having the spatial operator of the form as in (4.2). A particular form for which this theory is amenable is the form satisfied by the b species in (2.5) because we know that n is already positive and *a priori* bounded on the domain. Let us denote by $\overline{b}$ the solution to the problem

$$\frac{\partial \overline{b}}{\partial t} = \frac{\partial}{\partial x}\left(\overline{b}\frac{\partial \overline{b}}{\partial x}\right) + \overline{b} \tag{4.4}$$

with the same boundary and initial data as in (2.6)–(2.7) for the PDE system (2.4)–(2.5). Then by the above comparison principle we have the following bound for b:

R3 $b \leq \overline{b}$, *for all* $(x,t) \in (-\infty,\infty) \times [0,T)$.

Now it remains to show that the solution to equation (4.4) is *a priori* bounded on the domain. This follows easily by noting that we have

$$\overline{b} \leq ue^t \tag{4.5}$$

for all $(x,t) \in (-\infty,\infty) \times [0,T)$ and where u is the solution to the problem (4.2)–(4.3) which we know is *a priori* bounded.

Results **R1**–**R3** establish *a priori* bounds for n, b and the global existence of the solutions to our PDE problem follows by an application of Theorem 14.4 from Smoller [20].

We note that the above results essentially say that the PDE problem (2.4)–(2.7) has a unique pair of solutions (n, b) which exist for all positive times given suitable initial and boundary conditions. We then deduce, via the results established in section 3, that the travelling wave solutions are the only long time solutions supported by the PDE problem (2.4)–(2.7).

4.3. **Numerical solutions of the PDE problem.** In this section we solve numerically the system (2.4)–(2.7) and explore the possibility of travelling wave solutions for speeds greater than v_{min}=0.700.

A property of all the solutions to be presented here is that any spatially localised input of bacteria results in the formation of symmetrically propagating structures, of non-zero bacterial density, to the left and right directions simultaneously. This property is clear from the structure of the governing equations (2.4)–(2.5) and boundary conditions (2.6)–(2.7) which are all invariant to the change of coordinate $x \to -x$. This enables us to solve the problem on the semi-infinite spatial domain: $K = (x : 0 \leq x < \infty)$. Therefore we solve the PDE problem (2.4)–(2.7) on $K \times [0,T)$. The boundary condition at $x = 0$ is the symmetry boundary condition. The numerical solutions have been obtained in two different (independent) ways. The first method uses a standard fully implicit Crank-Nicolson finite-difference discretization algorithm with the resulting nonlinear algebraic equations being solved by employing a Newton-Raphson iteration with LU decomposition for the linear matrices. This algorithm has been used successfully before for a similar problem (but with constant diffusion for b, see Merkin and Needham [10], Merkin *et al.* [13]). The present situation of density-dependent, nonlinear diffusion poses no new difficulties except for the cases when $b = 0$. In such cases the resulting equations become only time-dependent and so the integration is quicker. Care has been taken that

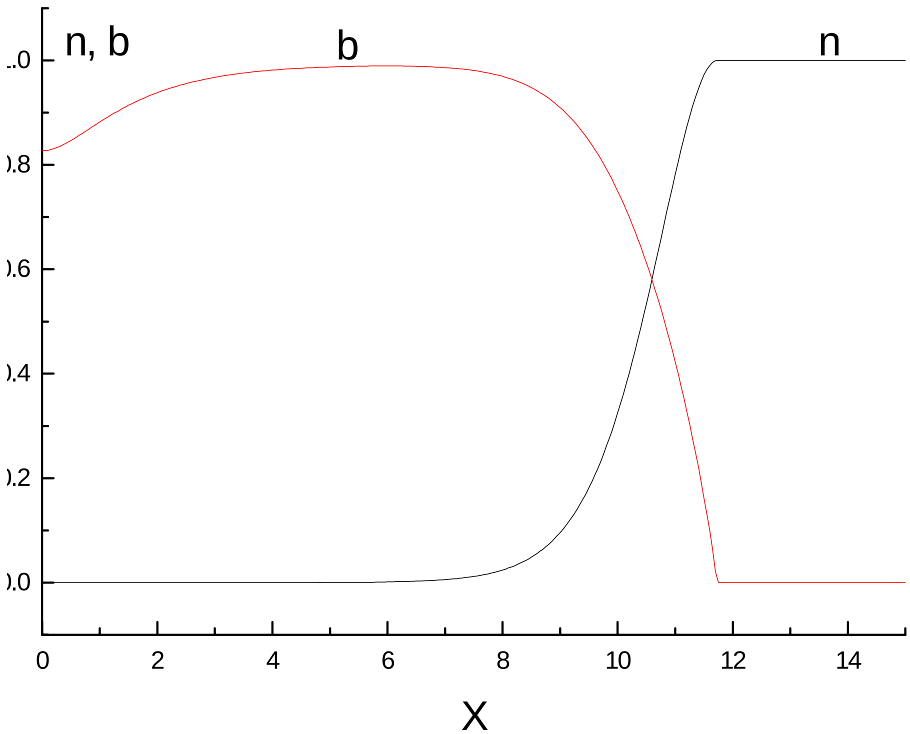


FIGURE 3. Plot of the numerical solution of the full PDE problem (2.4)–(2.7) for time = 20.0 obtained from the initial conditions $n(x,0) = 1, b(x,0) = 0$ for all x such that $0 \le x < \infty$ and $b(0,0) = 1.0, n(0,0) = 1.0$. For details of the other conditions see text. All the solutions in figures 3, 4a-b and 5 were first obtained on the spatial domain $0 \le x \le l$ and then repeated on the $0 \le x \le 2l$ where $l = 200h$, $h = 0.1$ to insure that they are independent of the length of the physical domain. We also checked that the choice $h = 0.1$ leads to sufficiently accurate simulations by obtaining solutions with $h = 0.05,\ h = 0.2$. In all these cases the solutions obtained are graphically indistinguishable.

at these points we do not introduce additional errors by the truncation which has been implemented such that the condition $b = 0 \Longleftrightarrow |b| \le 10.0^{-10}$ is satisfied. The second method uses the method of lines with the resulting time-dependent equations being solved by a Runge-Kutta routine. The solutions obtained by these two different methods have been checked against each other in all the cases analysed and the agreement was found to be very good (better than the graphical accuracy).

Our simulations show that a large set of initial conditions initiates a travelling wave propagating with the minimum speed (for example any compactly supported initial perturbation in b). This wave is of sharp type as expected from the theory in section 3. In figure 3 we show such a situation for the case when the initial condition is $b(x,0) = 0$ for all $0 < x < \infty$ with $b(0,0) = 1$. The numerical solution also confirms the speed of the wave to be $v_{numerical} = 0.693$ which is in good agreement with the minimum speed ($v_{min} = 0.700$) given by our theory in section 3. We have computed this speed by two independent methods so as to check the accuracy of the calculations against each other. The first method used simple linear interpolation to locate the position of the front after which the speed was computed by a simple difference formula. The second method is based on computing the front location by an integral method, thus being more accurate, which is similar to the one used in Merkin *et al.* [13]. The results are illustrated in figure 4a) where we plot the position of the travelling wave fronts evolving from the initial-value problem for the case $v = v_{min}$. This figure clearly shows that the front position describes a straight line in time with constant slope giving the minimum speed. Figure 4c) shows a plot of the speed of the wave with time showing the approach from below to the minimum speed value $v = v_{min} = 0.700$.

It is interesting to see whether the other TWS established by the theory in section 3 (i.e. the faster, smooth waves) are also realisable as solutions to the PDE problem. This is indeed the case and in figures 5 and 6 we show the transition from the sharp type wave to the smoother waves for three different initial conditions in b. The initial conditions have decay of the form $b = e^{-\gamma x}$. For this decay we have numerically obtained that the speed of the waves follows the "dispersion relation":

$$v = \begin{cases} \frac{1}{\gamma}, \ \gamma < \frac{1}{v_{min}} \\ v_{min}, \ \gamma > \frac{1}{v_{min}} \end{cases} \tag{4.6}$$

The above relation can be justified in a simple way. Note that the leading edge of the wave front has $n \sim 1, b \sim 0$. So that from equation (2.5) we have, by linearising at the leading edge of the TWS,

$$\frac{\partial b}{\partial t} = b, \tag{4.7}$$

because all the spatial terms contribute only to higher order terms. If initially $b = e^{-\gamma x}$ then a TWS evolves of the form $b(x,t) = e^{-\gamma(x-vt)}$. By substituting this in (4.7) we find that $v = \frac{1}{\gamma}$. However, it is clear that this relation can only subsist for $v \geq v_{min}$ leading to (4.6) above.

5. **Other similar models.** In this section we indicate briefly that the analysis presented above for the model system (2.4)-(2.7) is applicable to other problems. In fact in Kawasaki *et al.* [5], the authors mentioned a possible extension of (2.4)–(2.5) of the following form

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - nb \tag{5.1}$$

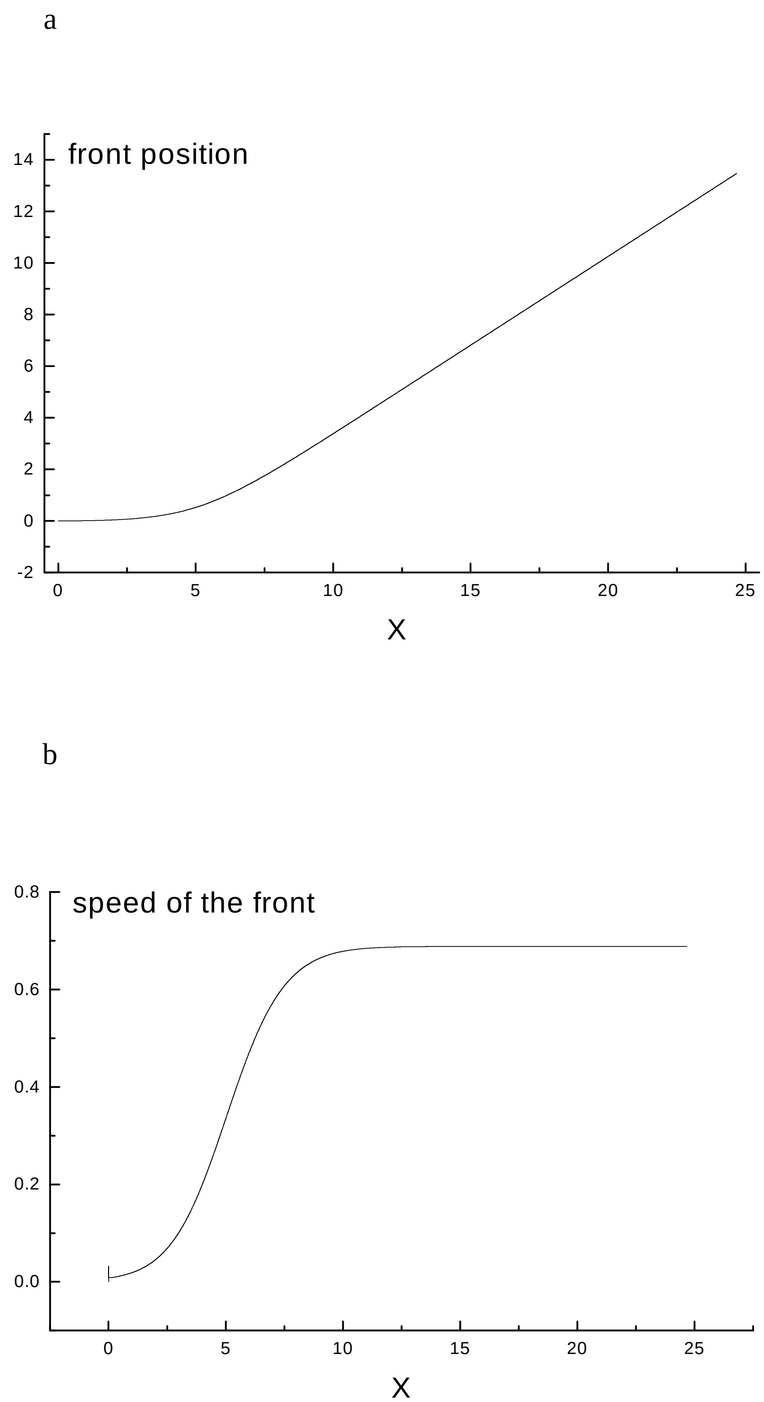
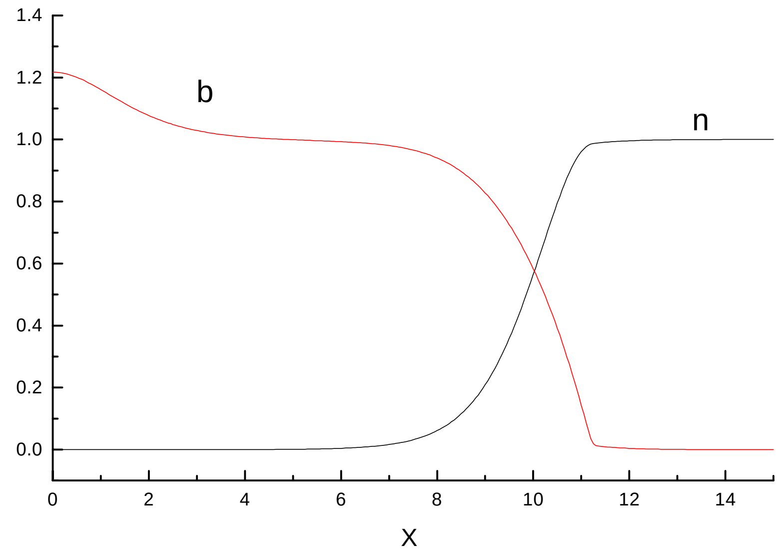


FIGURE 4. a) Successive positions of the TWS for the case $v = v_{min}$. b) Plot showing the approach to the constant minimum speed value $v = v_{min} = 0.700$ of the sharp front.



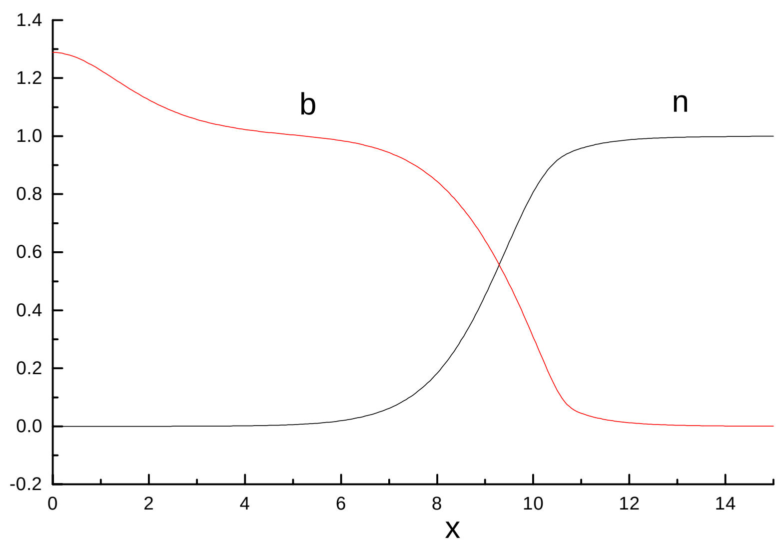


FIGURE 5. a) Plot of the numerical solution of the cell density profile from the full PDE problem (2.4)–(2.7) for time = 15.0 obtained from the initial conditions $n(x,0) = 1, b(x,0) = e^{-1.5x}$ for all x such that $0 \leq x < \infty$. b) Same as in a) but for the initial data: $n(x,0) = 1, b(x,0) = e^{-1.2x}$ for all $0 \leq x < \infty$.

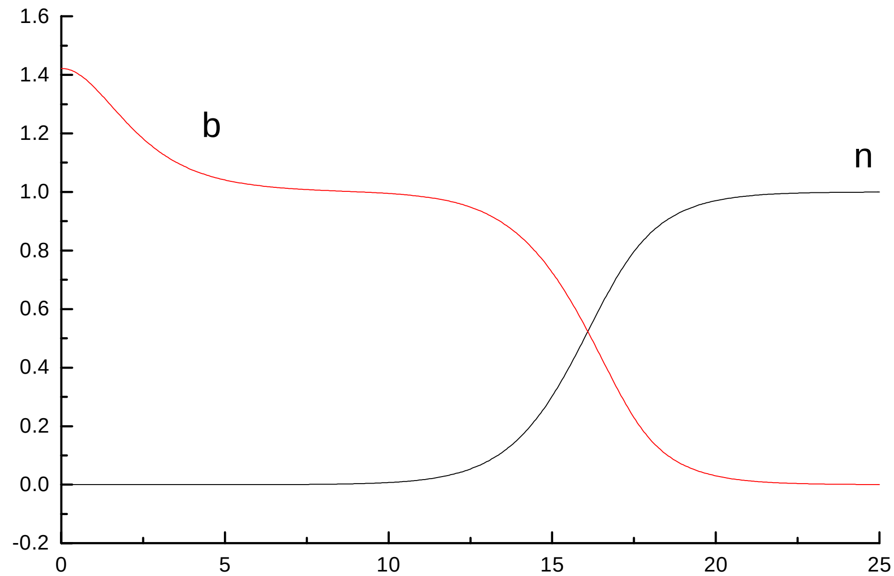


FIGURE 6. Same as figure 5a) but for the initial data: $n(x,0) = 1, b(x,0) = e^{-0.8x}$ for all x such that $0 \le x < \infty$.

$$\frac{\partial b}{\partial t} = D_b \frac{\partial}{\partial x}\left(nb^m \frac{\partial b}{\partial x}\right) + nb, \tag{5.2}$$

where $m > 1$.

Our theoretical treatment developed above is directly applicable to equations (5.1)–(5.2). Figure 7 shows a plot of the minimum speed of the TWS (still of sharp type) for the problem (5.1)–(5.2) as a function of m for a range of values of $m \ge 1$ obtained from the above travelling wave analysis using numerical integration with the NAG DO2AGF routine. These results are in very good agreement with numerical simulations of the full partial differential equation system (results not shown). Note that from this figure we see that the front speed converges to zero from above as $m \to \infty$. This is intuitively obvious because with $0 \le b \le 1$ we have that $b^m \to 0$ so the flux term for bacteria tends to zero. Similar calculations can be done for the model with bacterial diffusion taking the form $(b^m b_x)_x$ for $m \ge 1$.

6. **Conclusions.** One of the most intriguing problems in biology concerns spatio-temporal pattern formation. It is now well-known that a number of different types of bacterial colonies exhibit very rich patterning behaviour, for example, spreading disks, rings, spots, dense-branching morphologies with finger-like protrusions. Several models have been proposed to describe these behaviours see, for example, Woodward *et al.* [21], Mimura *et al.* [14], Ben-Jacob *et al.* [1], and references therein). Many of these models are very sophisticated, involving the interaction of a number of chemotactic agents, or the production of wetting agents. The simplest model proposed for this type of behaviour is that of Kawasaki *et al.* [5], in which it

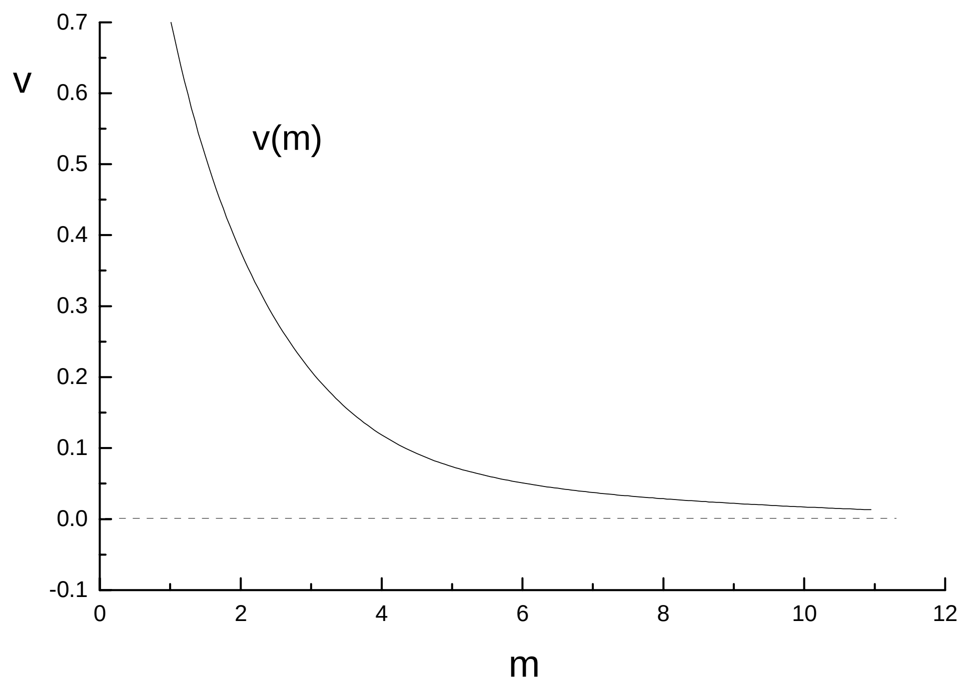


FIGURE 7. Plot of the minimum speed of the sharp type wave front as a function of m for a range of values of m with $m \geq 1$ obtained from numerical integration of the travelling wave equations corresponding to system (5.1)–(5.2). Note the asymptotic convergence of the speed to 0 as $m \to \infty$.

is shown that reaction diffusion models can produce the DBM type of behaviour, and this is the model on which we have chosen to focus, as it provides the challenge of developing travelling wave theory for coupled PDE systems with degenerate diffusion. We note that the behaviour observed by Kawasaki *et al.* is an extension of the branching patterns observed by Meinhardt [11] in a generic activator-inhibitor reaction diffusion model.

By simplifying one of the equations, we have been able to carry out a detailed analysis on the existence and uniqueness of travelling wave solutions showing, in particular, the existence of sharp type solutions. We have also derived a minimum wave speed. A problem that we have not addressed here is that of asymptotic stability of the travelling wave solution of sharp type. Our numerical simulations do suggest stability of this solution, but a mathematical analysis of stability remains to be done. Our analysis, which is on a coupled system of one ODE and one PDE gives results very similar to those obtained for the system of two coupled PDEs (and those obtained in Kawasaki *et al.* [5]). It would be of interest to determine under what general conditions this agreement holds.

We note that similar conclusions regarding sharp type travelling wave solutions have been previously reported for scalar nonlinear diffusion problems (Sherratt and Marchant [19]). To our knowledge there is no work on similar problems for a coupled system of equations (see also the equation (6.1) below). We note that the singular space operator in equation (2.5) fits into the more general class of cross-diffusion and chemotactic type models. The analysis of travelling waves in chemotactic systems began with the classical paper of Keller and Segel [6]. More recently Feltham and Chaplain [3] have determined analytically the properties of the associated travelling wave solutions in some special cases.

At this point it is worth commenting on a feature of equation (4.6). Clearly the dispersion relation (4.6) gives a continuous function (of γ) which is non-differentiable at $\gamma = v_{min}$. This is in contrast to the Fisher equation, for which the corresponding dispersion relation is differentiable everywhere. Indeed, for this latter case we know from Larson [8] that the behaviour of the solution to the system with linear diffusion in both n, b is dependent of the form of the initial data. If, say, initially we have $b(x,0) \sim e^{\sigma x}$, $0 < \sigma \leq 1$, then as $x \to \infty$ we have the selected speed as $v = \sigma + 1/\sigma \geq v_{min} = 2$.

As we mentioned already our treatment can be applied for more general degenerate diffusion equations of the form

$$\frac{\partial b}{\partial t} = \frac{\partial}{\partial x}\left(D(n,b)\frac{\partial b}{\partial x}\right) + nb \tag{6.1}$$

with $D(n,b)$ positive for the case when both n and b are positive, but zero when n and/or b are zero. It is clear that any such equation will give rise to a dispersion relation like (4.6), i.e. continuous but nondifferentiable at $v = v_{min}$. From the above we can state that the non-differentiable property of the dispersion relation is an indicator that the system supports sharp type solutions through degenerate diffusion terms of this type. In fact we conjecture that this is true whenever there is at least a parameterized set (depending on one parameter) of initial data for which the dependence of the speed on this parameter is a continuous but non-differentiable function. However, much more detailed work on this is required.

We have also considered equations (2.4)–(2.7) under different initial conditions for the nutrient level, i.e. we set

$$n(x,0) = \nu_0. \tag{6.2}$$

As expected the speed of the resulting sharp TWS has a monotonic dependence on this parameter with the wave speed vanishing for low nutrient levels and increasing exponential-like (unbounded) with increasing initial nutrient value, ν_0. The results (illustrated in Figure 8) agree with those in Kawasaki *et al.* [5], showing that our simple caricature system (2.4)–(2.7) can capture the key features of the more complicated system studied in the original paper, at least in one spatial dimension.

If we require the conservation of total mass in our system (i.e. $\frac{d}{dt}(n+b) = 0$) then a scalar equation in b can be obtained from (2.4)–(2.5) by replacing n in equation (2.5) with $1 - b$. This results in the equation:

$$\frac{\partial b}{\partial t} = \frac{\partial}{\partial x}\left((1-b)b\frac{\partial b}{\partial x}\right) + (1-b)b \tag{6.3}$$

with the same initial and boundary conditions (2.6)–(2.7) for b. We have solved equation (6.3) numerically and found that the behaviour is in good qualitative agreement with that given by our original, more complicated system (2.4)–(2.7).

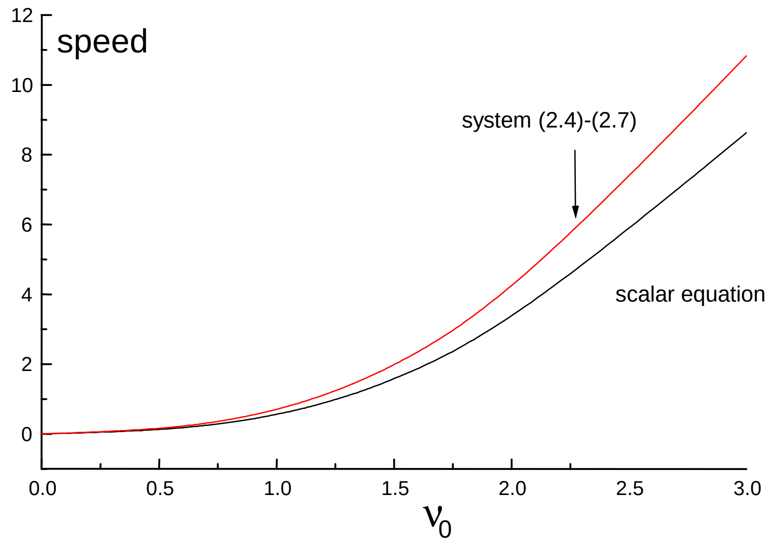


FIGURE 8. Plots of the speed of sharp TWS as a function of different nutrient levels ν_0. The top curve corresponds to the solutions of (2.4)–(2.7) modified with the initial condition (6.2) and the lower curve to the solutions of the scalar equation (6.3). Note that at high levels of nutrient concentration, experiments have shown that that cell response saturates. Therefore the model equations (2.4)–(2.5) are not valid in this regime.

The resulting speed of the sharp TWS obtained as solution to (6.3) corresponding to the same different nutrient levels ν_0 is also plotted in Figure 8. Note that although this procedure was applied in the original paper their scalar equation was further simplified (by assuming that $n = ct$). Nevertheless we show here that a more realistic form is still capable of capturing all the behaviour shown by the full system (2.4)–(2.7). Note that the travelling wave solution dynamics of doubly degenerate diffusion equations (of which (6.3) is a particular case) has been studied in detail by Sánchez-Garduño [16]. Here a possible generalisation of the problem posed by equation (6.3) would be the study of the existence of travelling waves for the problem

$$\frac{\partial b}{\partial t} = \frac{\partial}{\partial x}\left(g(b)\frac{\partial b}{\partial x}\right) + (1-b)b \tag{6.4}$$

where g satisfies $g(0) = g(1)$ and $g > 0$ in $(0,1)$ but not necessarily with $g'(0) >$ or $g'(1) < 0$. Recent techniques introduced by Malaguti and Marcelli [9] may offer possibilities for studying this type of equation.

As mentioned above, there are now a number of models, based on very different biological assumptions, which can exhibit patterns that are consistent qualitatively with those observed experimentally. This is the first step in the modelling process. It is now necessary to carry out a detailed quantitative study to determine if these models exhibit the appropriate patterns for realistic parameter values. This procedure may well distinguish between models, allowing us to have a fuller understanding of the underlying processes involved in bacterial motion, and is the subject of present experimental research.

Finally, we note that in this paper we have extended and generalised previous analyses for a scalar equation to the more general system

$$n_t = -f(n, b); \qquad b_t = [D(n, b)b_x]_x + f(n, b) \tag{6.5}$$

where $D(n, b)$ has more than one zero and may be degenerate, f is smooth, bounded, non-negative and has two zeroes. Thus, our analyses provides a basis on which to build a more thorough mathematical understanding of more biologically realistic models.

Acknowledgments. RAS is supported by the joint BBSRC/EPSRC Initiative in "Mathematical Modelling, Simulation and Prediction of Biological Systems", Grant No 43–MMI 09782. FSG thanks the hospitality of the Centre for Mathematical Biology, Oxford, where part of this research was carried out during his visit under the academic exchange scheme between the Royal Society of London and the Academia Mexicana de Ciencias. We thank Drs Robert Beadmore and Angela Stevens for reading the manuscript and making helpful comments.

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Received November 2000; revised April 2001.

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