Dynamics of a strongly nonlocal reaction-diffusion population model

John Billingham
School of Mathematical Sciences, The University of Nottingham, University Park, Nottingham NG7 2RD, U.K.

Abstract. We study the development of travelling waves in a population that competes with itself for resources in a spatially nonlocal manner. We model this situation as an initial value problem for the integro-differential reaction-diffusion equation

\[ \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \left( 1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \lambda g(\lambda (x-y)) u(y,t) \, dy \right), \]

with \( g \) an even function that satisfies \( g(y) \to 0 \) as \( y \to \pm\infty \), \( \int_{-\infty}^{\infty} g(y) \, dy = 1 \), \( \alpha > 0 \), \( 0 < \beta < 1 + \alpha \) and \( \lambda > 0 \). We concentrate on the limit of highly nonlocal interactions, \( \lambda \ll 1 \), focussing on the particular case \( g(y) = \frac{1}{\sqrt{2\pi}} e^{-\frac{|y|^2}{2}} \), which is equivalent to the reaction-diffusion system

\[ \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \left( 1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) w \right), \]

\[ 0 = \frac{\partial^2 w}{\partial x^2} + \lambda^2 (u - w). \]

Using numerical and asymptotic methods, we show that in different, well-defined regions of parameter space, steady travelling waves, unsteady travelling waves and periodic travelling waves develop from localized initial conditions. A key feature of the system for \( \lambda \ll 1 \) is the local existence of travelling wave solutions that propagate with speed \( c < 2 \), and which, although they cannot exist globally, attract the solution of the initial value problem for an asymptotically long time. By using a Cole-Hopf transformation, we derive a first order hyperbolic equation for the gradient of log \( u \) ahead of the wavefront, where \( u \) is exponentially small. An analysis of this equation in terms of its characteristics, allowing for the formation of shocks where necessary, explains the dynamics of each of the different types of travelling wave. Moreover, we are able to show that the techniques which we develop for this particular case can be used for more general kernels \( g(y) \), and that we expect the same range of different types of travelling wave to be solutions of the initial value problem for appropriate parameter values. As another example, we briefly consider the case \( g(y) = e^{-y^2/\sqrt{\pi}} \), for which the system cannot be simplified to a pair of partial differential equations.

PACS numbers: 02.30.Jr, 02.30.Mv, 87.23Cc
AMS classification scheme numbers: 35K57, 41A60, 92D40

Submitted to: *Nonlinearity*
E-mail: J.Billingham@bham.ac.uk
1. Introduction

Over the past 15 years there has been much interest in reaction-diffusion equations that incorporate spatially and temporally nonlocal terms in the form of the convolution of a kernel function with the dependent variable (see, for example, Gourley and Britton (1993, 1996), Rey and Mackey (1995), Ashwin et al (2002), Zou (2002) and references therein). In this paper, we study the spatially nonlocal reaction-diffusion equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \left\{ 1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \lambda g(\lambda (x - y)) u(y,t) \, dy \right\}.$$  \hspace{1cm} (1)

for $-\infty < x < \infty$ and $t > 0$, with $g$ an even function that satisfies

$$\int_{-\infty}^{\infty} g(y) \, dy = 1.$$  \hspace{1cm} (2)

$\alpha > 0$, $0 < \beta < 1 + \alpha$ and $\lambda > 0$, subject to the localized initial condition

$$u(x,0) = \begin{cases} 1 & \text{for } |x| \leq L_0, \\ 0 & \text{for } |x| > L_0. \end{cases}$$  \hspace{1cm} (3)

Since this initial condition is symmetric about the origin, so is the solution, and we will consider the problem for $x > 0$, with boundary conditions

$$\frac{\partial u}{\partial x} (0, t) = 0, \quad u \to 0 \text{ as } x \to \infty.$$  \hspace{1cm} (4)

This type of equation was introduced by Britton (1989) to model the behaviour of a single species that derives some competitive advantage from local aggregation (modelled by the term $\alpha u$ in (1)) within the capacity of the local environment (modelled by the term $-\beta u^2$ in (1)), but also competes with itself through the depletion of resources in a neighbourhood of its original position (modelled by the convolution integral in (1)). For the biological background to the model, see Britton (1989, 1990). Note that (1) has been made dimensionless using the diffusion coefficient, the equilibrium population and the growth rate for small populations, so that $u = 1$ is an equilibrium state and $u_t \sim u_{xx} + u$ when $u \ll 1$.

In this paper, we begin by focussing on the simple kernel $g(y) = \frac{1}{2} e^{-|y|}$. Since this particular choice of $g(y)$ is the Green’s function for an ordinary differential equation, (1) is equivalent to the coupled equations

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u \left\{ 1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) w \right\},$$  \hspace{1cm} (5)

$$0 = \frac{\partial^2 w}{\partial x^2} + \lambda^2 (u - w),$$  \hspace{1cm} (6)

for $x > 0$, subject to (3) and (4) along with

$$\frac{\partial w}{\partial x} (0, t) = 0 \quad \text{and} \quad w \to 0 \text{ as } x \to \infty.$$  \hspace{1cm} (7)

The initial state of $w$ is

$$w(x,0) = \begin{cases} 1 - e^{-\lambda L_0} \cosh \lambda x & \text{for } x \leq L_0, \\ e^{-\lambda x} \sinh \lambda L_0 & \text{for } x > L_0. \end{cases}$$  \hspace{1cm} (8)

We will work with (5) and (6) since this system is easier to handle than (1), both numerically and analytically. Note that, in this paper, we will not be concerned with the details of the initiation of travelling waves, and have chosen the simple initial
condition (3) so that a travelling wave forms rapidly in our numerical simulations. This system was studied by Gourley, Chaplain and Davidson (2001), who examined the form of the travelling wave solutions and looked at the linear stability of the uniform steady state. They were particularly concerned with the development of travelling waves with oscillatory tails and the formation of standing waves behind the developing wavefront.

In this paper, we will consider solutions of the initial value problem when $\lambda \ll 1$. As discussed by Gourley (2000), we can think of this as the limit of a highly mobile resource on which the population represented by $u$ feeds. The population and the resource then vary over a long lengthscale of $O(\lambda^{-1})$. Indeed, Gourley (2000) shows how the kernel $g(y) = \frac{1}{2}e^{-|y|}$ arises as the solution of an equation for the resource very similar to (6), but with left hand side given by $\epsilon \partial w/\partial t$ with $\epsilon \ll 1$.

We begin in section 2 by explaining how we obtain numerical solutions of the initial value problem (3) to (7). These solutions will be used throughout the paper to illustrate our results. Section 3 is a short description of the various types of behaviour that solutions of the initial value problem can exhibit. In section 4 we construct the asymptotic, steady, travelling wave solutions of (5) and (6) when $\lambda \ll 1$. We then consider the initial value problem in the same limit in section 5. We show how the methods we have used can be generalized to other choices of $g(y)$ in section 6, and briefly consider the initial value problem with $g(y) = e^{-y^2}/\sqrt{\pi}$.

2. Numerical solution method

In order to capture the travelling waves that develop in the initial value problem, for our numerical solutions we work in a moving frame of reference by using the coordinate $Y = x - X(t)$, with $X(0) = 0$. We will describe below how we choose $X(t)$. We define $u = u(Y, t)$, $w = w(Y, t)$, so that (5) and (6) become

$$
u_t = \nu_{YY} + \dot{X} \nu_Y + u \left( 1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) w \right), \quad w_{YY} + \lambda^2 (u - w) = 0. \tag{9}$$

We truncate the domain of solution to $0 < Y < l$, and apply no flux boundary conditions,

$$\nu_Y = w_Y = 0 \text{ at } Y = 0 \text{ and } Y = l. \tag{10}$$

We calculate $u$ and $w$ at the equally-spaced set of $N$ discrete points, $Y = Y_i = (i - 1) \Delta Y$, $i = 1, 2, \ldots, N$, $\Delta Y = l/(N - 1)$. We evaluate the spatial derivatives in (9) using central differences and use a three point formula to discretize the no flux boundary conditions (10), so that we maintain second order spatial accuracy.

In order to advance the solution from $t$ to $t + \Delta t$, we calculate $u(Y_i, t + \Delta t)$ using explicit timestepping of (9a). We can then solve the linear equation (9b) to obtain $w(Y_i, t + \Delta t)$, which can be done efficiently in MATLAB using sparse LU decomposition. We choose our timestep to satisfy the stability criterion, $\Delta t < \frac{1}{2} (\Delta x)^2$, and also by imposing an upper bound on the maximum amount by which $u$ is allowed to change over a single timestep. This allows us to capture the rapidly-growing spike in $u$ that can occur in certain cases. We also calculate $x_{\text{max}}(t)$, the position of $u_{\text{max}}$, the maximum value of $u$. From this, we can estimate $c$, the speed of the wave that forms. After using $\dot{X}(t) = 0$ initially, at regular intervals we set $\dot{X} = c$. In this way, the frame of reference moves with the wave. This allows us to use a smaller value of $l$, the length of the domain of solution, than would be possible using a fixed frame of reference.
When $\lambda \ll 1$ there is a separation of lengthscales between the wavefront region, where $u$ varies on an $O(1)$ lengthscale, and the rest of the domain, where $u$ varies on an $O(\lambda^{-1})$ lengthscale (see figure 1). Although we could have tried to develop an adaptive gridding routine to cope with this, we decided to take the simpler option of a uniform grid and long computation times. We typically take $\Delta Y = 0.1$ and, for example, with $\lambda = 0.03$, use a domain of length $l = 400$, and hence 4000 grid points.

3. The solution of the initial value problem when $\lambda \ll 1$

Figure 1 shows the travelling wave that develops when $\alpha = 0.5$, $\beta = 1$ and $\lambda = 0.03$. Both $u$ and $w$ vary over the long lengthscale, $\lambda^{-1}$, away from the wavefront, where $u$ varies on an $O(1)$ lengthscale. There is also a local maximum in $u$ just behind the wavefront. In terms of the ecological model, the population at the wavefront suffers less competition than the population behind the wavefront, and is therefore able to grow larger. All of the travelling waves that we compute for $g(y) = \frac{1}{2}e^{-|y|}$ are qualitatively similar to that shown in figure 1. Figure 2 shows the seven regions in parameter space where travelling waves exist for $\lambda \ll 1$, in which the solution of the initial value problem behaves qualitatively differently. These behaviours are:

(i) Steady travelling waves (S). A travelling wave is formed, and propagates at constant speed, $c \geq 2$.

(ii) Periodic travelling waves (P1). A travelling wave is formed, and propagates at constant speed, but, with period of $O(\lambda^{-1})$, a spike in $u$ forms ahead of the wavefront and drags it forward by an $O(\lambda^{-1})$ distance over an $O(\lambda^{-1})$ timescale.

(iii) Periodic travelling waves (P2). As described above for P1 waves, but with stationary gaps in $u$ left behind the wavefront, formed when the gap between
spike and wavefront fails to close completely.

(iv) Spike decelerating travelling waves (SpD). A travelling wave is formed, and propagates at constant speed, but, after a delay of \( O(\lambda^{-1}) \), a spike in \( u \) forms ahead of the wavefront and drags it forward by an \( O(\lambda^{-1}) \) distance over an \( O(\lambda^{-1}) \) timescale. The resulting wave then decelerates smoothly, with \( c \to 2 \) as \( t \to \infty \) over an \( O(\lambda^{-1}) \) timescale.

(v) Discontinuously decelerating travelling waves (DD). A travelling wave is formed, and moves at constant speed. At some time later, of \( O(\lambda^{-1}) \), the wave accelerates rapidly over an \( O(1) \) timescale to a speed \( c > 2 \), then decelerates smoothly, with \( c \to 2 \) as \( t \to \infty \) over an \( O(\lambda^{-1}) \) timescale.

(vi) Discontinuously accelerating travelling waves (DA). A travelling wave is formed, and moves at constant speed. At some time later, of \( O(\lambda^{-1}) \), the wave accelerates rapidly over an \( O(1) \) timescale to a speed \( c < 2 \), then accelerates smoothly, with \( c \to 2 \) as \( t \to \infty \) over an \( O(\lambda^{-1}) \) timescale.

(vii) Smoothly accelerating travelling waves (SA). A travelling wave is formed and accelerates smoothly, with speed \( c \to 2 \) as \( t \to \infty \), over an \( O(\lambda^{-1}) \) timescale.

We will see how these regions can be determined when \( \lambda \ll 1 \), and meet examples of each type of wave in section 5.
4. Asymptotic solution of the travelling wave equations for $\lambda \ll 1$

We define a travelling wave coordinate $z = x - ct$, where $c$ is a constant wavespeed that is to be determined, and seek a steady, permanent form travelling wave solution $u = \hat{u}(z)$, $w = \hat{w}(z)$ with $\hat{u}$ and $\hat{w}$ positive. In terms of these new variables, (5) and (6) become

$$\hat{u}_{zz} + c\hat{u}_z + \hat{u} \left\{ 1 + \alpha \hat{u} - \beta \hat{u}^2 - (1 + \alpha - \beta) \hat{w} \right\} = 0,$$

$$\hat{w}_{zz} + \lambda^2 (\hat{u} - \hat{w}) = 0.$$  

Spatially uniform solutions of these equations have $\hat{u} = \hat{w}$, and hence $\hat{u} = 0$, 1 or $-1/\beta < 0$. From the initial conditions (3), we therefore expect the right-travelling wave that develops in the initial value problem to satisfy

$$\hat{u} \to 1, \quad \hat{w} \to 1 \quad \text{as } z \to -\infty,$$

$$\hat{u} \to 0, \quad \hat{w} \to 0 \quad \text{as } z \to \infty.$$  

We shall see below that this scaling of the problem is appropriate for an inner, or wavefront, region when $\lambda \ll 1$. At leading order, (12) shows that $\hat{w}$ varies linearly with $z$ and, as we shall see, matching with an outer region determines that $\hat{w}$ is constant at leading order. In order to fix this constant, we must consider the outer solution. Since the travelling wave solution is translationally invariant, we can, without loss of generality, let the wavefront lie at $z = 0$.

Before we continue, note that as $z \to \infty$, the leading order behaviour of $\hat{u} \ll 1$ is controlled by the linear equation

$$\hat{u}_{zz} + c\hat{u}_z + \hat{u} = 0.$$  

For $c < 2$ this equation has oscillatory solutions, so that $\hat{u}$ becomes negative and cannot therefore be the far field of a travelling wave solution. We conclude that travelling wave solutions of (11) and (12) can only exist for $c \geq 2$.

4.1. Outer solution

Let $Z = \lambda z$, $\hat{u} = U(Z)$, $\hat{w} = W(Z)$ with $U$, $W$, $Z = O(1)$ as $\lambda \to 0$. In terms of these scaled variables, (11), (12) and (13) become

$$\lambda^2 U_{ZZ} + \lambda c U_Z + U \left\{ 1 + \alpha U - \beta U^2 - (1 + \alpha - \beta) W \right\} = 0,$$

$$W_{ZZ} - W + U = 0,$$

subject to

$$U \to 1, \quad W \to 1 \quad \text{as } Z \to -\infty,$$

$$U \to 0, \quad W \to 0 \quad \text{as } Z \to \infty.$$  

At leading order, (15) becomes $U \left\{ 1 + \alpha U - \beta U^2 - (1 + \alpha - \beta) W \right\} = 0$. Physically, this means that the reaction terms in (1) dominate over the transport terms. One solution is

$$U = 0, \quad W = W_0 e^{-Z},$$  

which satisfies (17) as $Z \to \infty$. This is the outer solution ahead of the inner, or wavefront, region, so that (18) holds for $Z > 0$. As we shall see, $U$ is actually exponentially small ahead of the wavefront. The other solution is

$$W = \frac{1 + \alpha U - \beta U^2}{1 + \alpha - \beta}.$$  

On substituting this into (16), we can write the resulting system in phase plane form as

\[ U_Z = V, \quad (20) \]
\[ V_Z = \frac{2\beta V^2 + (1 - U)(1 + \beta U)}{\alpha - 2\beta U}. \quad (21) \]

If we can solve this system subject to the boundary condition (17a), which is equivalent to

\[ U \to 1, \quad V \to 0 \quad \text{as} \quad Z \to -\infty, \quad (22) \]

we will have found the solution in the outer region for \( Z < 0 \).

When \( \alpha > 2\beta \), a local analysis at the equilibrium point \((U, V) = (1, 0)\) shows that it is a linear centre, whilst the symmetry of the system under the transformation \( V \mapsto -V, \ Z \mapsto -Z \) reveals that \((1, 0)\) is also a nonlinear centre. We cannot, therefore, satisfy (22), and no travelling wave solution exists. Equation (16) of Gourley et al (2001) shows that, for \( \lambda \ll 1 \), the uniform steady state \( u = 1 \) of (1) is unstable when \( \alpha > 2\beta \), consistent with this observation. It is not difficult to show that this remains the stability boundary when \( \lambda \ll 1 \) for the more general equation (1). In this case, the travelling waves that develop in the initial value problem leave a stationary standing wave in their wake. We will not consider this type of behaviour here (see Gourley et al., 2001).

When \( \alpha < 2\beta \), \((1, 0)\) is a saddle point, and hence the only integral paths that satisfy (22) are its unstable separatrices. The separatrices of this saddle are shown in figure 3 for the typical case \( \alpha = 2, \ \beta = 1.25 \). In order to determine which of the unstable separatrices, and which part of that separatrix, forms the outer solution for

![Figure 3. The separatrices of the saddle point \( U = 1, V = 0 \) of the system (20), (21) when \( \alpha = 2 \) and \( \beta = 1.25 \). The broken line is the curve defined by (24), and \( S \) its intersection with the unstable separatrix of \((1, 0)\).](image-url)
Z < 0, we can use (16). If we integrate this equation over the real line, and note that, in a travelling wave solution, \( W_Z \to 0 \) as \( Z \to \pm \infty \), we find that
\[
\int_{-\infty}^{\infty} (U - W) \, dZ = 0. \tag{23}
\]
This can be seen to hold for the steady travelling wave shown in figure 1. Since we know that the solution is given, at leading order, by (18) for \( Z > 0 \) and that (19) holds for \( Z < 0 \), we can substitute into (23) and find, after some manipulation, making use of the fact that \( W \) is continuous at \( Z = 0 \), that
\[
U_Z = V = \frac{1 + \alpha U - \beta U^2}{2\beta U - \alpha} \quad \text{at} \quad Z = 0. \tag{24}
\]
This curve is shown as a broken line in figure 3. Equation (24) can also be obtained by noting that both \( W \) and \( W_Z \) are continuous at \( Z = 0 \).

Simple algebraic arguments, along with the monotonicity of \( U \), show that the unstable separatrix of \((1, 0)\) with \( V > 0 \) intersects the curve (24) at a unique point, \( S \). The stable separatrix between the saddle point and \( S \) therefore gives us the outer solution for \( Z < 0 \). It is straightforward to compute the position of \( S \) for given values of \( \alpha \) and \( \beta \) using the MATLAB routine ode45 to integrate (20) and (21). In particular, we can calculate the maximum value of \( U = U_{\text{max}} \), which occurs at \( S \), and deduce \( W_0 \), the value of \( W \) at \( Z = 0 \). These are connected by the relation
\[
U_{\text{max}} = \frac{\alpha + \sqrt{\alpha^2 + 4\beta L}}{2\beta} > 1, \tag{25}
\]
where
\[
L = 1 - (1 + \alpha - \beta) W_0 < 1. \tag{26}
\]
The parameter \( L \) plays an important role in what follows. The behaviour of \( U_{\text{max}} \) is plotted in figure 4. We can see that \( U_{\text{max}} = O(\beta^{-1}) \) when \( \beta \ll 1 \). The structure of the equations leads us to expect this, since the term \( -\beta u^2 \) in (1) acts to prevent \( u \) becoming unbounded. We will not consider this asymptotic limit here. Note that the wavespeed, \( c \), has yet to be determined. The range of possible wavespeeds will be fixed in the inner region, which we consider next.

### 4.2. Inner solution

In the inner region, where \( z = O(1) \), (12) shows that we need \( \tilde{w} = W_0 = (1 - L) / (1 + \alpha - \beta) \), in order to match with the outer solution. This means that (11) becomes
\[
\tilde{u}_{zz} + c\tilde{u}_z + \tilde{u} \left( L + \alpha \tilde{u} - \beta \tilde{u}^2 \right) = 0, \tag{27}
\]
to be solved subject to the matching conditions
\[
\tilde{u} \to 0 \quad \text{as} \quad z \to \infty, \quad \tilde{u} \to U_{\text{max}} \quad \text{as} \quad z \to -\infty. \tag{28}
\]
Fortunately for us, this system has been studied by Hadeler and Rothe (1975), and we need only rescale our equation in order to use their results. After making the definition,
\[
c_m(L) = \begin{cases} 
2\sqrt{L} & \text{for } 2\alpha^2 / \beta \leq L < 1, \\
\frac{3\sqrt{\alpha^2 + 4\beta L} - \alpha}{\sqrt{8\beta}} & \text{for } L \leq 2\alpha^2 / \beta,
\end{cases}
\tag{29}
\]
we find that:
Figure 4. The maximum value of $U, U_{\text{max}} > 1$, determined by the leading order, outer asymptotic solution for $\lambda \ll 1$.

(i) When $2\alpha^2/\beta \leq L < 1$, there is a unique solution for each $c \geq c_m(L)$. This restriction on $c$ arises from the fact that the equilibrium point at $(0, 0)$ in the $(\hat{u}, \hat{u}_z)$-phase plane changes from a stable node to a stable focus as $c$ decreases past $c_m$, so that $\hat{u}$ becomes negative for sufficiently large $z$ when $c < c_m(L)$. We also note that, for $z \gg 1$,

$$
\hat{u} = \begin{cases} 
O \left( z e^{-\frac{1}{2}c_m z} \right) & \text{when } c = c_m(L), \\
O \left( e^{\mu_+(L) z} \right) & \text{when } c > c_m(L),
\end{cases}
$$

(30)

where

$$
\mu_\pm = \frac{1}{2} \left( -c \pm \sqrt{c^2 - 4L} \right).
$$

(31)

(ii) When $0 \leq L < 2\alpha^2/\beta$, there is a unique solution for each $c \geq c_m(L)$. In this case, the restriction on $c$ arises from global, instead of local, considerations, with the solution of (27) becoming negative before approaching zero monotonically as $z \to \infty$ when $2\sqrt{L} \leq c < c_m$. For $z \gg 1$,

$$
\hat{u} = \begin{cases} 
O \left( e^{\mu_-(L) z} \right) & \text{when } c = c_m(L), \\
O \left( e^{\mu_+(L) z} \right) & \text{when } c > c_m(L),
\end{cases}
$$

(32)

(iii) When $L \leq 0$, there is a single solution, which exists only when $c = c_m(L)$. In this case, the solution is a saddle-saddle connection in the $(\hat{u}, \hat{u}_z)$-phase plane. For $z \gg 1$, $\hat{u} = O \left( e^{\mu_-(L) z} \right)$.

The regions in the $(\alpha, \beta)$-parameter space where these cases lie are shown in figure 5. Also shown, as a broken line, is the curve $c_m(L) = 2$. In the region below this curve,
As we have seen, it is straightforward to show that, for the full problem, no travelling waves exist for $c < 2$. Although these travelling waves cannot exist globally, they can exist within this inner region because, locally, $\dot{w} = W_0 > 0$ and the linearized form of the travelling wave equation, which governs the behaviour of $\tilde{u}$ ahead of the wavefront, is

$$\tilde{u}_{zz} + c\tilde{u}_z + L\tilde{u} = 0.$$ \[
\]

Local travelling wave solutions can therefore exist only for $c \geq 2\sqrt{L}$, consistent with the three cases that we described above. However, in the outer region, $W$ decays slowly, with $W = W_0 e^{-\lambda z} = W_0 e^{-\lambda z}$. We could now consider the leading order behaviour of $U$ in the outer region, where it is exponentially small. As we shall see in the next section, we would find that none of the travelling waves with $c < 2$ can match with a steady, exponentially small solution for $U$ ahead of the wavefront. However, when we consider the behaviour of the solution of the initial value problem, we will find that these nonexistent, slow waves have a crucial role to play. In fact, the solution can asymptote to a slow wave and travel with $c < 2$ for a time of $O(\lambda^{-1})$ before a different type of behaviour occurs.

**Figure 5.** The three regions in $(\alpha, \beta)$-parameter space, with $\beta < 1 + \alpha$ and $\alpha < 2\beta$, in which three different types of qualitative behaviour of solutions of (27) occur. The broken line is $c_m(L) = 2$, with $c_m(L) < 2$ below this line.

Figures 6 and 7 show a comparison between the asymptotic and numerical solutions when $\beta = 4 + 0.45\alpha$ with $5.5 < \alpha < 10$, a line that lies within the region of parameter space where $c_m > 2$. We can see that the solution of the initial value problem asymptotes to the minimum speed travelling wave, for reasons that we will explain in the next section. The agreement between numerical and asymptotic solutions is excellent for the maximum value of $u$, but slightly less good for the wave speed. As we explained in section 2, our resolution of the inner region is fairly low, with a grid spacing of 0.1. Since our analysis shows that the wave speed is fixed in the
inner region, whilst the maximum value of \( u \) is fixed in the outer region, where \( u \) and \( w \) vary slowly, on an \( O(\lambda^{-1}) \) lengthscale, it is not surprising that we can determine \( u_{\text{max}} \) more accurately than \( c \).

5. Asymptotic solution of the initial value problem for \( \lambda \ll 1 \)

5.1. Solution when \( t = O(1) \)

The leading order solution of the initial value problem when \( t = O(1) \) and \( \lambda \ll 1 \) cannot be found analytically. However, our numerical solutions of the full initial value problem suggest that a steady travelling wave emerges as \( t \to \infty \). Changes to this solution occur over a much longer timescale, of \( O(\lambda^{-1}) \). We will therefore assume that the solution of the initial value problem with \( t = O(1) \) for \( \lambda \ll 1 \) satisfies

\[
\begin{align*}
\begin{array}{ll}
\text{as } t \to \infty & \text{for } O(1) < x < L_0 + ct - O(1), \text{ where } Z = \lambda(x - L_0 - ct) \text{ and } U, W \text{ is the solution of the outer travelling wave problem, which we studied in the previous section, and} \\
\text{as } t \to \infty & \text{for } x - L_0 - ct = O(1), \text{ where } z = x - L_0 - ct \text{ and } \hat{u}, \hat{w} \text{ is a solution of the inner travelling wave problem. The value of the wave speed, } c, \text{ remains to be determined. When } x = O(1) \text{ there is a passive adjustment of the solution to accommodate the boundary condition at } x = 0, \text{ which we will not consider here. We will consider the form of the solution for } x > L_0 + ct + O(1) \text{ in the next section.}
\end{array}
\end{align*}
\]
5.2. Solution when \( t = O(\lambda^{-1}) \)

In order to determine the initial conditions ahead of the wavefront for the leading order problem when \( t = O(\lambda^{-1}) \), we can consider the asymptotic solution for \( \lambda = O(1) \) and \( t \ll 1 \), then the asymptotic solution for \( \lambda = O(1) \) and \( x \gg 1 \) consistent with the solution for \( t \ll 1 \). This idea originates with the work of Needham (see, for example, Needham and Leach, 2001).

It is straightforward to show that the asymptotic solution for \( t \ll 1 \) is

\[
\begin{align*}
    u &\sim 1 + (1 + \alpha - \beta) t \cosh \lambda x, \\
    w &\sim 1 - e^{-\lambda L_0} \cosh \lambda x + t \left\{ -\frac{1}{2} (1 + \alpha - \beta) \lambda x \sinh \lambda x + k_1 \cosh \lambda x \right\},
\end{align*}
\]

for \( 0 \leq x \leq L_0 - O(t^{1/2}) \),

\[
\begin{align*}
    u &\sim \frac{1}{2} \text{erfc} \left( \frac{x - L_0}{2 t^{1/2}} \right), \quad w \sim 1 - e^{-L_0} \cosh \lambda L_0,
\end{align*}
\]

for \( |x - L_0| = O(t^{1/2}) \), and

\[
\begin{align*}
    u &\sim \frac{1}{\pi^{1/2}} \frac{t^{1/2}}{x - L_0} \exp \left\{ -\frac{(x - L_0)^2}{4t} + o(1) \right\}, \\
    w &\sim e^{-\lambda(x-L_0)} \times \left[ e^{-\lambda L_0} \sinh \lambda L_0 + t \left\{ -\frac{1}{2} (1 + \alpha - \beta) \lambda L_0 \sinh \lambda L_0 + k_1 \cosh \lambda L_0 \right\} \right],
\end{align*}
\]

Figure 7. The leading order asymptotic value of \( c_m \) for \( \lambda \ll 1 \), and the speed of the travelling wave determined from numerical solutions of the initial value problem for various values of \( \lambda \) and \( \beta = 4 + 0.45\alpha \), so that \( c_m > 2 \).
for \(x > L_0 + O(t^{1/2})\), where \(k_1\) is a constant that can be determined by invoking the continuity of \(w_x\) at \(x = L_0\). The thin region around \(x = L_0\) is needed because the initial distribution of \(u\) is discontinuous there, and is immediately smoothed out by diffusion.

The asymptotic solution for \(x \gg 1\) and \(t = O(1)\) that is consistent with the solution for \(t \ll 1\) is

\[
  u \sim \frac{t^{1/2}}{\pi^{1/2} (x - L_0)} \exp \left\{ -\frac{(x - L_0)^2}{4t} + t + o(1) \right\}, \quad w \sim W_0(t) e^{-\lambda x},
\]

for some function \(W_0(t)\). In particular, we conclude that the solution for \(x - ct - L_0 > O(1)\) when \(t = O(1)\) and \(\lambda \ll 1\) satisfies

\[
  u \sim \frac{\lambda^{1/2}}{\pi^{1/2} (Z + \lambda ct)} \exp \left\{ -\frac{(Z + \lambda ct)^2}{4\lambda t} + t + o(1) \right\}, \quad w \sim W_0(t) e^{-Z} \quad \text{as} \quad t \to \infty.
\]

We can now define scaled variables \(T = \lambda t, u = \bar{U}(Z, T), w = \bar{W}(Z, T)\), with \(\bar{U}, \bar{W}, T = O(1)\) as \(\lambda \to 0\), in terms of which (5) and (6) become

\[
  \lambda \bar{U}_T = \bar{U} \left\{ 1 + \alpha \bar{U} - \beta \bar{U}^2 - (1 + \alpha - \beta) \bar{W} \right\} + \lambda c \bar{U}_Z + \lambda^2 \bar{U}_{ZZ},
\]

\[
  0 = \bar{W}_{ZZ} - \bar{W} + \bar{U},
\]

to be solved subject to matching with the solution for \(t = O(1)\), which gives

\[
  \bar{U}(Z, T) \sim U(Z), \quad \bar{W}(Z, T) \sim W(Z) \quad \text{as} \quad T \to 0 \quad \text{for} \quad Z < O(\lambda),
\]

where \(U(Z), W(Z)\) is the outer travelling wave solution, and

\[
  \bar{U}(Z, T) \sim \frac{\lambda^{1/2} T^{1/2}}{\pi^{1/2} (Z + cT)} \exp \left\{ -\frac{(Z + cT)^2}{4\lambda T} + \frac{T}{\lambda} + o(1) \right\},
\]

\[
  \bar{W}(Z, T) \sim W_0 e^{-Z},
\]

as \(T \to 0\) for \(Z > O(\lambda)\), where \(W_0 = (1 - L) / (1 + \alpha - \beta)\) is the value of \(W\) at the wavefront, which lies at \(Z = 0\). We can see from these initial conditions that the travelling wave solution emerges for \(T > 0\) and \(Z < O(\lambda)\), but should bear in mind that this is an assumption rather than a deduction, as discussed above. The asymptotic region that controls the dynamics of the solution for \(T = O(1)\) lies ahead of the wavefront, with \(Z > O(\lambda)\) and \(\bar{U}\) exponentially small. We consider this region in the next section.

5.3. Exponentially small solution ahead of the wavefront

We define the scaled variable \(\chi\) using \(\bar{U} = \exp(-\chi(Z, T)/\lambda)\), with \(\chi = O(1)\) and \(\chi > 0\) for \(T = O(1)\) and \(Z > O(\lambda)\). At leading order, \(\bar{W}\) satisfies

\[
  \bar{W}_{ZZ} - \bar{W} = 0,
\]

subject to \(\bar{W} \to 0\) as \(Z \to \infty\) and \(\bar{W} \to W_0\) as \(Z \to 0\). We conclude that \(\bar{W} = W_0 e^{-Z}\). If we now consider (40) and neglect exponentially small terms, we find that

\[
  \chi_T = (1 - L) e^{-Z} - 1 + cZ - \frac{\chi_Z^2}{2} + \lambda \chi_{ZZ}.
\]

This is to be solved subject to matching with the solution for \(t = O(1)\), which gives

\[
  \chi \sim \frac{(Z + cT)^2 - 4T^2}{4T} \quad \text{as} \quad T \to 0 \quad \text{for} \quad Z > 0,
\]
and matching with the wavefront solution, using (30) and (32), which gives
\[ \chi \sim kZ \text{ as } Z \to 0, \] (47)
where
\[ k = \begin{cases} \frac{1}{2} \left( c + \sqrt{c^2 - 4L} \right) & \text{for } c = c_m(L), \\ \frac{1}{2} \left( c - \sqrt{c^2 - 4L} \right) & \text{for } c > c_m(L). \end{cases} \] (48)
In order to solve this initial-boundary value problem, we differentiate and define \( y = \chi Z \), which leads to
\[ y_T + (2y - c) y_Z = -(1 - L) e^{-Z} + \lambda y ZZ, \] (49)
to be solved subject to
\[ y \sim \frac{Z + cT}{2T} \text{ as } T \to 0 \text{ for } Z > 0, \] (50)
\[ y = k \text{ at } Z = 0. \] (51)
At leading order for \( \lambda \ll 1 \), this is a hyperbolic problem, which we can solve using the method of characteristics. The diffusive term, \( \lambda y ZZ \), is negligible for \( \lambda \ll 1 \), unless a shock forms in the leading order problem, when it acts to smooth the shock over a lengthscale of \( O(\lambda) \).

We can understand how this hyperbolic problem arises by noting that ahead of the wavefront \( u \) is small, so that we have, at leading order,
\[ \lambda u_T = \lambda^2 u ZZ + \lambda cu_Z + u \{ 1 - (1 - L) e^{-Z} \}. \] (52)
The change of variable
\[ y = -\lambda u_Z / u, \] (53)
which gives us (49), is the Cole-Hopf transformation. Just as solving Burgers’ equation with small diffusivity using the method of characteristics is easier than solving the equivalent diffusion equation using a Laplace transform (see, for example, Billingham and King, 2001), it is easier to solve (49) than to solve (52) when \( \lambda \ll 1 \).

In order to proceed, it is convenient to make one further simple transformation,
\[ y = \frac{Z}{2T} + \frac{1}{2} c + \bar{y}, \] (54)
so that (49) to (51) become, neglecting the regularizing term, \( \lambda y ZZ \),
\[ \bar{y}_T + \left( 2\bar{y} + \frac{Z}{T} \right) \bar{y}_Z = -(1 - L) e^{-Z} - \frac{\bar{y}}{T}, \] (55)
to be solved subject to
\[ \bar{y} = 0 \text{ when } T = 0 \text{ for } Z > 0, \] (56)
\[ \bar{y} = k \text{ at } Z = 0 \text{ for } T > 0, \] (57)
where
\[ k = \begin{cases} \frac{1}{2} \sqrt{c^2 - 4L} & \text{for } c = c_m(L), \\ -\frac{1}{2} \sqrt{c^2 - 4L} & \text{for } c > c_m(L). \end{cases} \] (58)
The characteristics of (55) satisfy
\[ \frac{dT}{d\bar{y}} = 2\bar{y} + \frac{Z}{T}, \] (59)
on which
\[ \frac{d\bar{y}}{dT} = \frac{\bar{y}}{T} - (1 - L) e^{-Z}. \]  
(60)

If we now use (59) to eliminate \( \bar{y} \) from (60), we obtain the equation for the characteristics as
\[ \frac{d^2Z}{dT^2} = -2(1 - L) e^{-Z}. \]  
(61)

This can be integrated once to give
\[ \frac{dZ}{dT} = \pm \sqrt{A^2 + 4(1 - L) (e^{-Z} - 1)}, \]  
(62)

where \( A \) is the slope at \( Z = 0 \). If \( A^2 > 4(1 - L) \), \( Z_T \to \sqrt{A^2 - 4(1 - L)} \) as \( Z \to \infty \), whilst if \( A^2 < 4(1 - L) \), the characteristic has a turning point, with \( Z_T = 0 \) at \( Z = -\log \{1 - A^2/4(1 - L)\} \), and meets the \( T \)-axis at \( Z = -2\log \{1 - A^2/4(1 - L)\} \) with slope \( Z_T = -A \). The dividing characteristic, with \( A^2 = 4(1 - L) \), is \( T = (e^{Z/2} - 1) (1 - L)^{-1/2} \). We can deduce from this that the quarter plane \( Z > 0, T > 0 \) is completely filled by characteristics that originate at \( Z = T = 0 \), as shown in figure 8. We can see this algebraically by noting that (62) can be solved explicitly to give the equation of the characteristics through \( Z = T = 0 \). Parameterizing the characteristics using \( \gamma \), we find that
\[ Z = 2 \log \left[ \frac{1}{\gamma} \sin \left\{ (1 - L)^{1/2} \gamma T + \sin^{-1} \gamma \right\} \right], \]  
(63)
\[ \bar{y} = (1 - L)^{1/2} \gamma \cot \left\{ (1 - L)^{1/2} \gamma T + \sin^{-1} \gamma \right\} - \frac{Z}{2T}, \]  
(64)

with \( 0 < \gamma < 1 \), for \( T > (e^{Z/2} - 1) (1 - L)^{-1/2} \),
\[ Z = 2 \log \left[ \frac{1}{\gamma} \sinh \left\{ (1 - L)^{1/2} \gamma T + \log \left( \gamma + \sqrt{1 + \gamma^2} \right) \right\} \right], \]  
(65)
\[ \bar{y} = (1 - L)^{1/2} \gamma \coth \left\{ (1 - L)^{1/2} \gamma T + \log \left( \gamma + \sqrt{1 + \gamma^2} \right) \right\} - \frac{Z}{2T}, \]  
(66)

with \( \gamma > 0 \), for \( 0 < T < (e^{Z/2} - 1) (1 - L)^{-1/2} \). In order to determine the solution generated by these characteristics for any given \( Z \) and \( T \), we simply solve the nonlinear algebraic equation (63) or (65), as appropriate, to find \( \gamma \), and then \( \bar{y} \) is given by (64) or (66).

The characteristics that begin at \( Z = T = 0 \) do not, however, give us the whole picture, since we must also satisfy the boundary condition (57) at \( Z = 0 \) for \( T > 0 \), and hence need to consider the characteristics that start on the \( T \)-axis. Equation (59) shows that these have slope \( Z_T = 2\bar{k} \) at \( Z = 0 \). If \( c > c_m(L), \bar{k} < 0 \), and these characteristics point out of the domain of solution. It is not possible to construct a consistent solution in this case, and we have a simple criterion that shows why the wave with minimum speed, \( c = c_m(L) \), develops when \( t = O(1) \) instead of one of the faster waves. When \( c = c_m(L), \bar{k} = 0 \) for \( 2\alpha^2/\beta \leq L < 1 \), and we will defer discussion of this case until section 5.8. When \( L < 2\alpha^2/\beta, \bar{k} > 0 \), and the characteristics point into the domain \( Z > 0, T > 0 \). The solution is then determined by the characteristics that start on the \( T \)-axis and those that start at the origin with \( Z_T \geq 2\bar{k} \). We will consider this case first.
Dynamics of a strongly nonlocal reaction-diffusion population model

5. Steady travelling waves: \( c_m(L) \geq 2 \)

If the slope of the characteristics that start at the \( T \)-axis is less than that of the dividing characteristic, the solution is well-defined everywhere. For this to be the case, we need \( 2k = \sqrt{c^2_m - 4L} \geq 2\sqrt{1 - L} \) and hence \( c_m(L) \geq 2 \). The characteristics that start at the origin are then given by (65) and \( \bar{y} \) by (66) with \( \gamma \geq \gamma_0 = \sqrt{(c^2_m - 4)/(1 - L)} \).

The characteristics that start on the \( T \)-axis at \( T = T_0 \) have

\[
Z = 2\log\left[\frac{1}{\gamma_0} \sinh\left((1 - L)^{1/2} \gamma_0 (T - T_0) + \log\left(\gamma_0 + \sqrt{1 + \gamma_0^2}\right)\right)\right],
\]

with solution

\[
\bar{y} = \frac{1}{2} \sqrt{c^2_m - 4 + 4(1 - L)e^{-Z}} - \frac{Z}{2T}.
\]

This corresponds to the steady state solution

\[
y = \chi Z = \frac{1}{2} \left\{ c_m + \sqrt{c^2_m - 4 + 4(1 - L)e^{-Z}} \right\},
\]

which exists for all \( Z \geq 0 \) only when \( c_m \geq 2 \). Note that this steady state is the solution for \( Z \leq Z_0 \), where \( Z_0 \) is given by (67) with \( T_0 = 0 \). For \( T \gg 1 \), \( Z_0 \sim (c^2_m - 4)^{1/2} T \) when \( c_m > 2 \). This point is effectively a second wavefront moving, in terms of the fixed coordinate system, with speed \( c_m + \sqrt{c^2_m - 4} \), behind which the solution is a steady, permanent form travelling wave, and ahead of which the solution is developing with time under the action of reaction and diffusion. The characteristics are shown in figure 9, and the solution in figure 10 for a typical case. We can also compare this solution with the numerical solution of the full initial value problem. The development of \( y = \chi Z \) is shown in figure 11 for the same parameter values as for figure 10,
Figure 9. The characteristics with $\alpha = \beta = 8$, for which $c_m = 2.344$, $L = 0.486$ and $\gamma_0 = 0.853$.

Figure 10. The solution, $y(Z, T)$, with $\alpha = \beta = 8$ when $T = 0.1, 1, 3$ and $5$. The broken line is the steady solution, which holds for $Z \leq Z_0(T)$.

and $\lambda = 0.03$. The agreement is not perfect, but, since we obtain $y$ by taking the logarithm of $u$ where it is exponentially small and then use central differences to find the derivative, surprisingly good.
Dynamics of a strongly nonlocal reaction-diffusion population model

Figure 11. The development of $y = \chi_Z$ with $\alpha = \beta = 8$ and $\lambda = 0.03$, calculated from the numerical solution of the initial value problem when $T = 0.1, 1, 3$ and $5$. The broken line is the steady solution.

5.5. Periodic travelling waves: $L < 0$, $c_m(L) < 2$

We can now see that if $c_m < 2$, the steady solution (69) is only available for $Z \leq Z_{s0} = -\log \left\{ \left( 4 - c_m^2 \right) / 4 (1 - L) \right\}$. How does the solution develop for $Z \geq Z_{s0}$? We can find this out by looking at the characteristics. A typical example is shown in figure 12. Since $Z_T = 2k = \sqrt{c_m^2 - 4L} < 2\sqrt{1 - L}$ at $Z = 0$, the characteristics that start on the $T$-axis at $T = T_0$ are given by

$$ Z = 2 \log \left[ \frac{1}{\gamma_{s0}} \sin \left\{ (1 - L)^{1/2} \gamma_{s0} (T - T_0) + \sin^{-1} \gamma_{s0} \right\} \right], \quad (70) $$

with $\gamma_{s0} = \sqrt{(4 - c_m^2) / 4 (1 - L)}$. These turn back on themselves, and intersect both each other and the characteristics that start at the origin. The first intersection occurs when $T = T_{s0}$, where

$$ T_{s0} = \frac{1}{(1 - L)^{1/2} \gamma_{s0}} \left( \frac{\pi}{2} - \sin^{-1} \gamma_{s0} \right). \quad (71) $$

After this time, there is a range of values of $Z$ for which the solution carried by the characteristics is triple-valued. This indicates that a shock forms when $T = T_{s0}$ at $Z = Z_{s0}$, and propagates towards $Z = 0$. Figure 13 shows the triple-valued solution at various times, whilst figure 14 shows the solution computed from the full initial value problem with $\lambda = 0.01$ at the same times. Again, the agreement is good, and the shock can clearly be seen forming and starting to propagate. Since we have neglected the term $\lambda y ZZ$, the shock has thickness of $O(\lambda)$, consistent with figure 14.
Dynamics of a strongly nonlocal reaction-diffusion population model

Figure 12. The characteristics with $\alpha = 2$, $\beta = 1.2$, for which $c_m = 1.123$, $L = -0.139$ and $\gamma_0 = 0.776$.

Figure 13. The solution, $y(Z,T)$, with $\alpha = 2$, $\beta = 1.2$ when $T = 0.1, 0.5, 1, 1.5, 2, 2.5$ and $3$. The broken line is the steady solution.

In order to determine the dynamics of the shock, we write (55) in conservative form as

$$\bar{\dot{y}} T + \left\{ \dot{y}^2 + \frac{Z}{T} \dot{y} - (1 - L) e^{-Z} \right\} \frac{\partial}{\partial Z} = 0.$$  \hspace{1cm} (72)
Dynamics of a strongly nonlocal reaction-diffusion population model

Figure 14. The development of $y = \chi Z$ with $\alpha = 2$, $\beta = 1.2$ and $\lambda = 0.01$, calculated from the numerical solution of the initial value problem when $T = 0.1$, $0.5$, $1$, $1.5$, $2$, $2.5$ and $3$. The vertical dotted lines show the position of the shock when $T = 1$, $1.5$, $2$, $2.5$ and $3$, predicted by the asymptotic analysis. The broken line is the steady solution.

From this equation, it is straightforward to consider a small region around the shock, and thereby determine its velocity to be

$$\frac{dZ_s}{dT} = \frac{1}{2} \left( \frac{dZ}{dT} \bigg|_L + \frac{dZ}{dT} \bigg|_R \right),$$

(73)

where the subscripts $L$ and $R$ indicate values calculated to the left and the right of the shock. Since we know which characteristics enter the shock, we can determine the right hand side of (73), and find that

$$\frac{dZ_s}{dT} = (1 - L)^{1/2} \left\{ (e^{-Z_s} - \gamma_s^2)^{1/2} - (e^{-Z_s} - \gamma_s^2)^{1/2} \right\},$$

(74)

where $\gamma_s$ satisfies the algebraic equation

$$\gamma_s e^{Z_s/2} = \sin \left\{ \gamma_s (1 - L)^{1/2} T + \sin^{-1} \gamma_s \right\},$$

(75)

and $Z = Z_{s0}$ when $T = T_{s0}$. It is straightforward to integrate this system numerically for $T > T_{s0}$. The shock path that corresponds to the solution illustrated in figure 14 is shown in figure 15, along with the characteristics that carry the solution to the shock. The shock reaches the $T$-axis when $T = T_{s1} \approx 3.64$. The predicted positions of the shock at various times are also shown in figure 14, and are in reasonable agreement with the numerical solution of the full initial value problem.

At this point, we need to recall, firstly that $y = \chi Z$, and secondly that $u = \exp (-\chi / \lambda)$. For our assumption that $u$ is exponentially small when $\lambda \ll 1$ to remain valid, we need $\chi > 0$. This means that, if

$$\chi(Z, T) = \int_0^Z y(Z, T) \, dZ$$
Figure 15. The characteristics that carry the single-valued solution with $\alpha = 2$, $\beta = 1.2$. The broken line is the path of the shock.

first becomes zero when $T = T_{nu}$ for some positive $Z = Z_{nu}$, our approximation becomes nonuniform, and does so in the neighbourhood of $Z = Z_{nu}$. In other words, if the area under the curve $y = y(Z,T)$ between zero and $Z$ vanishes, our assumed solution structure breaks down. This must occur at some time $T_{nu}$ with $T_{s0} < T_{nu} < T_{s1}$ if $y_{s1}$, the value of $y$ to the right of the shock when it reaches $Z = 0$, is negative. This is clearly the case for the example illustrated in figure 14. It is straightforward to calculate the area under the curve numerically from the asymptotic solution for given values of $\alpha$ and $\beta$. For the particular case, $\alpha = 2$, $\beta = 1.2$, this nonuniformity occurs when $T = T_{nu} \approx 3.33$ at $Z = Z_{nu} \approx 0.55$, and manifests itself as the initiation at $Z = Z_{nu}$ of a region where $u$ grows, as shown in figure 16. The travelling wave then reforms itself, as shown in figure 17, and, numerical solutions suggest, relaxes onto a periodic solution in which a shock in $y$ repeatedly forms ahead of the wavefront, propagates back, and then initiates a growing region of $u$ ahead of the wavefront, as shown in figure 18. In this manner, the solution for $T \gg 1$ takes the form of a periodic travelling wave. Note that we chose to illustrate this behaviour with $\lambda = 0.01$ because the spike is not well separated from the wavefront when $\lambda = 0.03$, so that a simulation with $\lambda = 0.01$ gives a better indication of the nature of the solution. Although it is possible, in principle, to analyse the details of the subsequent periods of this cycle asymptotically, we have not attempted this here. The difficulty is that, ahead of the wavefront, $\bar{W}$ is no longer simply $W_0 e^{-Z}$, but depends upon the dynamics of the original wavefront and the pair of diverging wavefronts initiated at $Z = Z_{nu}$.

The position of the maximum value of $u$ as a function of time is shown in figure 19 for $\alpha = 2$, $\beta = 1.2$ and $\lambda = 0.01$. We can see that, although the minimum speed travelling wave solution, determined in the inner, wavefront region, has $c < 2$ for this range of parameter values, the solution actually lies close to this solution for much of
the time, punctuated by excursions when the wave jumps forwards by an amount of $O(1)$ ($O(\lambda^{-1})$ in terms of the original variables) by initiating a spike in $u$ ahead of the wavefront. It is crucial that $L < 0$ for this behaviour to occur, since there is then only one travelling wave solution for $\lambda \ll 1$, and hence no possibility of the wave reforming with a different wavespeed after the initiation of the spike in $u$. Note that, since the lower branch of the steady state solution has $y < 0$ at $Z = 0$, $y_{s1} < 0$ for all $L < 0$.

![Graph of $u$ and $w$](image.png)

**Figure 16.** The behaviour of $u$ and $w$ just after the spike in $u$ forms ahead of the wavefront, when $\alpha = 2$, $\beta = 1.2$ and $\lambda = 0.01$.

The periodic process that we have describe is not the only possibility. For some parameter values, the travelling wave does not reform itself after the initiation of
The behaviour of $u$ and $w$ as the travelling wave reforms, when $\alpha = 2$, $\beta = 1.2$ and $\lambda = 0.01$. Instead, the gap between spike and wavefront asymptotes to a steady state solution that remains fixed behind the wave. This steady state solution takes the form of a gap in $u$. As further spikes form ahead of the wave, more gaps form, so that the tail of the travelling wave is punctuated by a regular sequence of gaps, as shown in figure 20 for a typical case. We analyse the steady state gap solutions in the appendix, where we find that such solutions exist, and appear to be stable for $2\alpha > 3\beta$. In addition, we show how to calculate the width of the
gap, $2\lambda^{-1}H$ in terms of the original variables. The asymptotic solution for the case corresponding to figure 20 is shown in figure A1.

Numerical solutions show that the separation between spike and wavefront must exceed $2\lambda^{-1}H$ for the stationary gap solution to form. In other words, the gap between spike and wavefront can shrink onto a gap, but not grow into a gap. We refer to these solutions as P2 waves, whilst the periodic waves without gaps in their tails are P1 waves, as discussed in section 3. The regions of parameter space where P1 and P2
Figure 19. The position of the maximum value of $u$ when $\alpha = 2$, $\beta = 1.2$ and $\lambda = 0.01$. This is a periodic wave (P1).

waves occur are shown in figure 2.

Figure 20. The solution of the initial value problem when $\lambda = 0.03$, $\alpha = 5$ and $\beta = 2.8$ when $t = 375$. The gaps in the tail of the wave are the most obvious feature of this periodic wave (P2).
5.6. Spike decelerating travelling waves: \( L > 0, y_{s1} < 0, c_m < 2 \)

Figure 21 shows the region where \( y = y_{s1} \) is negative when the shock reaches \( Z = 0 \). We can see that this can occur for \( L > 0 \), when there is a range of possible wavespeeds with \( c \geq c_m(L) \). Numerical solutions show that after the spike in \( u \) forms ahead of the wavefront, the travelling wave reforms itself, as was the case for P1 waves, but now with wavespeed \( c > 2 > c_m(L) \). Subsequently, this wave decelerates, with \( c \to 2 \) as \( T \to \infty \). Note that a stationary gap solution does not form in the wake of these waves.

As we shall see below, unsteadiness is a typical feature of the solution when \( L > 0 \) and \( c_m(L) < 2 \), which we will analyse below. However, in this case, since we cannot describe the reformation of the wave analytically, we cannot make further progress. Figure 22 shows the dynamics of a typical spike decelerating wave.

5.7. Discontinuously accelerating and decelerating travelling waves: \( 0 < L < 2\alpha^2/\beta, y_{s1} > 0, c_m < 2 \)

When the shock reaches \( Z = 0 \) with \( y = y_{s1} \geq 0 \), the only possibility is that \( y(0, T) \) adjusts to to make \( y \), and hence \( \bar{y} \), continuous there. It is not possible to sustain a stationary shock at \( Z = 0 \). However, we know that \( \bar{y}(0, T) \) is given by (57). The only possibility is therefore that the wavespeed \( c \) adjusts (rapidly, on a \( T = O(\lambda) \) timescale) so that \( y_{s1} = \frac{1}{2} c + k \), and hence

\[
    c = c_{\text{new}} = y_{s1} + \frac{L}{y_{s1}}. \tag{76}
\]
Note that $L$ remains the same whatever the wavespeed, since it is determined in the outer region, away from the wavefront. After this rapid adjustment, the wavespeed cannot remain constant, since the solution must continue to satisfy the boundary condition at $Z = 0$. Figure 23 shows the position of the maximum value of $u$ as a function of time for a solution of the full initial value problem. It should be clear that the velocity does indeed remain constant, and then accelerate rapidly (on a $t = O(1)$, $T = O(\lambda)$ timescale), before accelerating on the $T = O(1)$ timescale to $c = 2$ as $T \to \infty$. This is the discontinuously accelerating wave shown as DA in figure 2. If $c_{\text{new}} > 2$, the wave must decelerate to $c = 2$, as in the example shown in figure 24. This is the discontinuously decelerating wave shown as DD in figure 2. The boundary between the regions DA and DD in figure 2 is given by the curve $c_{\text{new}} = 2$.

In order to analyse the acceleration of the travelling wave, we need to redefine our travelling wave variable as $Z = \lambda(x - L_0) - X(T)$, with $X(0) = 0$ and $X$ to be determined. If $X = c_m T$, we recover our original variable. Proceeding as before, we arrive at a problem for $\bar{y}$ that is only slightly different from (55) to (58), with

$$\chi_Z = y = \frac{Z + X}{2T} + \bar{y},$$

(77)

and

$$\bar{y}_T + \left(2\bar{y} + \frac{Z}{T} + \frac{X}{T} - \dot{X}\right)\bar{y}_Z = -(1 - L) e^{-Z} - \frac{\bar{y}}{T},$$

(78)

to be solved subject to

$$\bar{y} = 0 \text{ when } T = 0 \text{ for } Z > 0,$$

(79)
\[ \bar{y} = \bar{k}(T) \text{ at } Z = 0 \text{ for } T > 0, \]  
(80)

where

\[ \bar{k}(T) = \frac{1}{2} \left\{ \hat{X} - \frac{X}{T} + \sqrt{\hat{X}^2 - 4L} \right\}. \]  
(81)

The characteristics of (78) satisfy

\[ \frac{dZ}{dT} = 2\bar{y} + \frac{Z}{T} + \frac{X}{T} - \hat{X}, \]  
(82)

on which

\[ \frac{d\bar{y}}{dT} = -\frac{\bar{y}}{T} - (1 - L)e^{-Z}. \]  
(83)

If we now use (82) to eliminate \( \bar{y} \) from (83), we obtain the equation for the characteristics as

\[ \frac{d^2Z}{dT^2} = -2(1 - L)e^{-Z} - \hat{X}. \]  
(84)

This differs from (61) in the appearance of the acceleration of the wave in (84). Although we cannot now integrate this equation analytically, it is straightforward to solve numerically.

For \( 0 < T < T_{s1} \), \( V = \hat{X} = c_m(L) \), and the solution develops as described in the previous section. When the characteristics reach \( T = T_{s1} \), (84) shows that their slope changes discontinuously, with

\[ \left[ \frac{dZ}{dT} \right]_{x_{s1}^-}^{x_{s1}^+} = -[V]_{T_{s1}}, \]  
(85)
Dynamics of a strongly nonlocal reaction-diffusion population model

Figure 24. The position of the maximum value of $u$ when $\alpha = 3$ and $\beta = 3$ for $\lambda = 0.03$. The asymptotic solution has $c = c_m(L) \approx 1.60$ for $0 \leq T \leq T_{s1} \approx 6.2$, $t_{s1} \approx 206.7$. The broken lines have slopes $c_m(L)$ and 2. This is a discontinuously decelerating wave (DD).

From which we can deduce the new slope. To avoid confusion, we now parameterize the characteristics with $s$, so that $Z = Z(s)$, and solve the boundary value problem

$$\frac{d^2 Z}{ds^2} + 2 (1 - L) e^{-Z} = -\dot{V}(s) \text{ for } T_{s1} < s < T,$$

subject to

$$Z = 0 \text{ at } s = T, \quad (87)$$

$$\frac{dZ}{ds} = c_m - c_{\text{new}} + 2 (1 - L)^{1/2} \gamma \cot \left\{ (1 - L)^{1/2} \gamma T_{s1} + \sin^{-1} \gamma \right\} \text{ at } s = T_{s1}, \quad (88)$$

where $\gamma$ satisfies

$$\gamma e^{Z/2} = \sin \left\{ (1 - L)^{1/2} \gamma T_{s1} + \sin^{-1} \gamma \right\}, \quad (89)$$

and $V$ is determined by the boundary condition at $Z = 0$, which is

$$V(T) = \sqrt{4L + \left( \frac{dZ}{ds} \bigg|_{s=T} \right)^2}. \quad (90)$$

For a given value of $T$, if we know $V(s)$ for $0 \leq s < T$, we can solve this boundary value problem using finite differences, which then determines $V(T)$. We also use the asymptotic solution for $T - T_{s1} \ll 1$ to provide an appropriate initial condition. Figure 25 shows the behaviour of $V$ in two typical cases, whilst figures 23 and 24 show comparisons between numerical and asymptotic solutions, which are in good agreement.
5.8. Smoothly accelerating travelling waves: $c_m = 2\sqrt{L}$

When $c_m = 2\sqrt{L}$, we know that $\bar{g}(0,0) = \bar{k} = 0$. The wavespeed must therefore accelerate immediately, adjusting to satisfy the boundary condition at $Z = 0$. Figure 26 shows a solution of the full initial value problem, in which the wavespeed accelerates smoothly from $2\sqrt{L}$ to 2 as $T \to \infty$. This is the smoothly accelerating wave (SA), shown in figure 2. In order to determine the behaviour of the wavespeed asymptotically, we simply need to replace the boundary condition (88) with

$$Z = 0 \text{ at } s = 0,$$

and solve the initial-boundary value problem given by (86) to (90) as before, but now for $0 < s < T$. Figure 27 shows the behaviour of $V$ for various values of $L$. Note that the initially rather rapid variation in $V$ is followed by a slower approach to equilibrium. It is straightforward to show that $2 - V = O(T^{-2})$ for $T \gg 1$.

Figure 26 shows that the position of a smoothly accelerating wave calculated from the full initial value problem is in good agreement with that determined by solving (86) to (90) in a typical case.

6. Generalization to Other Kernels

Having worked through the details of the asymptotic analysis for $\lambda \ll 1$ with $g(y) = \frac{1}{2} e^{-|y|}$, can we generalize our results to other kernels? Let’s retain equation (5), and write

$$w = \lambda \int_{-\infty}^{\infty} g(\lambda(x-y)) u(y,t) \, dy.$$  

(92)
Using the travelling wave variables defined in section 4, we again find that ahead of the wavefront $U = 0$, whilst behind the wavefront (19) holds. Substituting this into
Dynamics of a strongly nonlocal reaction-diffusion population model

the scaled version of (92) leads to the nonlinear integral equation

\[ \frac{1 + \alpha U - \beta U^2}{1 + \alpha - \beta} = \int_{-\infty}^{0} g(Z - Y)U(Y) \, dY, \]  

which is to be solved subject to \( U \to 1 \) as \( Z \to -\infty \). Once \( U \) is known, \( W(Z) \) is given by

\[ W(Z) = \int_{-\infty}^{0} g(Z - Y)U(Y) \, dY \quad \text{for} \quad -\infty < Z < \infty. \]  

The phase plane problem that we considered in section 4 is therefore, in general, replaced by the solution of a nonlinear integral equation, (93), when the kernel, \( g \), is not the Green’s function of an ordinary differential equation. The inner problem at the wavefront then remains the same, (27) and (28), with \( L \) given by (26), and

\[ W_0 = W(0) = \int_{-\infty}^{0} g(-Y)U(Y) \, dY. \]

In particular, the wavespeed, \( c \), is determined by the value of \( L \) in the manner described in section 4.2. Note that if \( g(y) \) is monotonically increasing for \( y < 0 \), \( W(Z) \) is monotonically decreasing for \( Z > 0 \), since \( U > 0 \). We will assume that this is the case.

Ahead of the wavefront, the exponentially small part of the solution of the initial value problem now satisfies, using the same notation as section 5.3,

\[ \bar{y}_T + \left( 2\bar{y} + \frac{Z}{T} \right) \bar{y}_Z = (1 + \alpha - \beta) W_Z - \frac{\bar{y}}{T}, \]  

which means that the characteristics are given by

\[ \frac{dZ}{dT} = \pm \sqrt{A^2 + 4 (1 - L) \left( \frac{W(Z)}{W_0} - 1 \right)}. \]

Of course, in general, we cannot integrate this equation analytically as we could for the special case \( g = \frac{1}{2} e^{-|y|} \), but we can see that, since \( W \) is monotonically decreasing, the structure of the characteristics, and therefore the behaviour of the solution of the initial value problem, is qualitatively the same as it was for \( g(y) = \frac{1}{2} e^{-|y|} \). Without going into the details of the solution of (95), we can conclude that in the initial value problem, if \( L < 0 \) a periodic wave forms, driven by the formation of a spike ahead of the wavefront, if \( 0 < L < 2\alpha^2/\beta \) an unsteady wave forms with a discontinuous change in velocity at some well-defined time, and if \( 2\alpha^2/\beta < L < 1 \) a travelling wave forms that accelerates continuously for \( t > 0 \). In each of the final two cases, we expect \( c \to 2 \) as \( t \to \infty \).

We can illustrate this using the kernel \( g(y) = e^{-y^2/\sqrt{\pi}} \), which cannot be the Green’s function for an ordinary differential equation since it is continuous and twice-differentiable. We solve (93) numerically using the trapezium rule to evaluate the integral on a truncated domain \(-l < Z < 0\), assuming that \( U = 1 \) for \( Z < -l \), and solving the resulting set of nonlinear algebraic equations using Newton’s method. The regions of parameter space where we expect to find qualitatively different travelling wave solutions are illustrated in figure 28, which is very similar to the equivalent diagram for \( g(y) = \frac{1}{2} e^{-|y|} \), shown in figure 2. As we discussed earlier, the lower boundary of the region where travelling waves exist is given by \( \alpha = 2/\beta \). We found, as we should, that our numerical method failed to converge when \( \alpha > 2/\beta \).

In order to confirm these asymptotic predictions, we also solved the initial value problem numerically, evaluating \( w \) from (92) at each timestep using the trapezium rule.
Dynamics of a strongly nonlocal reaction-diffusion population model

rule. Figure 29 shows a comparison between the travelling wave that forms in the initial value problem and the asymptotic solution in two typical cases. Note that for $\beta$ sufficiently small, in contrast to the solutions when $g(y) = \frac{1}{2} e^{-|y|}$, the wave has a decaying oscillatory tail. In each of the cases for which we solved the initial value problem, the solution behaved as predicted by our asymptotic analysis, including the existence of stationary gap solutions and P2 waves.

Figure 28. The regions in parameter space where we predict different types of behaviour when $g(y) = e^{-y^2/\sqrt{\pi}}$. The broken line is $c_m = 2$.

7. Discussion

In this paper, we have considered a model for the behaviour of a species that derives an advantage from local cooperation, subject to both local environmental constraints and nonlocal intra-species competition. We concentrated on the case of highly nonlocal competition, and demonstrated that the species spreads by the propagation of travelling waves. These waves can be steady, unsteady or periodic, depending upon the dimensionless parameters. The key idea is the analysis of the hyperbolic initial value problem that determines the behaviour of the species ahead of the wavefront, where the population is exponentially small. This behaviour controls the dynamics of the wavefront, although we have seen that the dynamics behind the wavefront can vary (P1 and P2 waves).

The ideas that we have developed here could also be used for reaction-diffusion equations, or systems of such equations, whose behaviour ahead of the wavefront is governed by a linear equation of the form

$$\lambda u_t = u_{xx} + f(\lambda(x - ct)) u,$$
The asymptotic travelling wave solution for $\lambda \ll 1$ and the solution of the initial value problem when $\lambda = 0.03$, $\alpha = 5$ and $\beta = 2.8$.

which becomes

$$y_T + (2y - c)y_Z = f(Z) + \lambda y_{ZZ}$$

after the Cole-Hopf transformation, $y = -\lambda u_{Z}/u$, with $z = x - ct$, $Z = \lambda z$ and $T = \lambda t$. One such example is given by Billingham and Needham (1990), equation (106b), although the function $f(Z)$ is not available in closed form in this case.

Finally, three open questions.

- We have not investigated what happens for $\alpha > 2\beta$, when no travelling wave solutions exist for $\lambda \ll 1$. We know from Gourley et al (2001) that for $\lambda = O(1)$, stationary standing wave solutions form behind an advancing wavefront. What happens when $\lambda \ll 1$, and is it possible to solve the problem asymptotically?
- Does the range of behaviour that we have described for $\lambda \ll 1$ persist when $\lambda = O(1)$?
- Is a similar analysis possible when the nonlocal competition term in (1) also involves temporal nonlocality, as is the case in the original papers by Britton (1989, 1990)?

These questions are currently being investigated.

Acknowledgments

I would like to thank Fordyce Davidson for initial discussions about this problem, the organizers of the meeting ‘Dynamics of Reactive Fronts’ and the staff of the Institut Henri Poincaré in Paris for their hospitality whilst most of this work was carried out, and the other participants at the meeting for some helpful discussions.
Appendix. Stationary gap solutions

As we saw in section 5.5, stationary gap solutions form in the wake of P2 periodic waves, as shown in figure 20. In this appendix, we briefly show how these can be analysed for $\lambda \ll 1$ in the same way as we analysed the steady travelling waves in section 4. We begin by seeking a stationary solution on the infinite domain $-\infty < x < \infty$, symmetric about $x = 0$ with inner layers at $x = \pm \lambda^{-1} H$, within which $w = W_0$, a constant to be determined. Focussing on the layer at $x = -\lambda^{-1} H$, we define $x = -\lambda^{-1} H + \hat{x}$, in terms of which the steady version of (5) is, at leading order

$$u_{\hat{x}\hat{x}} + u \left( L + \alpha u - \beta u^2 \right) = 0,$$

where $L = 1 - (1 + \alpha - \beta) W_0$, and the matching conditions are

$$u \to U_{\text{max}} \text{ as } \hat{x} \to -\infty, \quad u \to 0 \text{ as } \hat{x} \to \infty,$$

with $U_{\text{max}}$ to be determined. Since $u_{\hat{x}}$ does not appear, we can integrate (A.1) once to obtain the equation of the integral paths. The condition for there to exist an integral path connecting the two steady states given by (A.2) as $\hat{x} \to \pm \infty$ is then easy to determine algebraically. We find that we need $L = -2\alpha^2 / 9\beta$, and hence

$$W_0 = \frac{1}{1 + \alpha - \beta} \left( 1 + \frac{2\alpha^2}{9\beta} \right), \quad U_{\text{max}} = \frac{2\alpha}{3\beta}.$$

We now define $X = \lambda x$ as the outer variable, in terms of which the steady versions of (5) and (6) are

$$\lambda^2 U_{XX} + U \left\{ 1 + \alpha U - \beta U^2 - (1 + \alpha - \beta) W \right\} = 0,$$

$$W_{XX} - W + U = 0.$$  

(A.4)

At leading order, as for the outer travelling wave solutions, we have $U = 0$ for $-H < X < H$, and hence

$$W = W_0 \frac{\cosh X}{\cosh H} \text{ for } -H < X < H.$$

(A.5)

For $|X| > H$, $W = (1 + \alpha U - \beta U^2) / (1 + \alpha - \beta)$, and hence we must solve the system (20) and (21) with $Z = X$, subject to

$$U \to 1 \text{ as } X \to -\infty, \quad U = \frac{2\alpha}{3\beta} \text{ at } X = -H.$$  

(A.6)

In addition, the continuity of $W_X$ at $X = -H$ leads to the condition

$$\tanh H = \frac{3\alpha\beta}{9\beta + 2\alpha^2} U_X(-H).$$

(A.7)

By solving (20) and (21) numerically, we are able to determine $H$ for given $\alpha$ and $\beta$. The outer solution for $\alpha = 5$ and $\beta = 2.8$ is shown in figure A1, and should be compared to figure 20.

We should also consider the exponentially small solution for $U$ in the gap, $-H < X < H$. If we write $U = \exp(-\chi(X)/\lambda)$ and neglect exponentially small terms, we find that

$$\chi_X^2 = \left( 1 + \frac{2\alpha^2}{9\beta} \right) \frac{\cosh X}{\cosh H} - 1.$$  

(A.8)
A steady solution therefore exists provided that

$$\cosh H < 1 + \frac{2\alpha^2}{9\beta}. \quad (A.9)$$

Numerically, we find that this condition is satisfied for all of the gap solutions.

Although solutions exist with $W_0 > 1$ and $U_{\text{max}} < 1$, these do not form in the solution of the initial value problem, and we speculate that they are either unstable, or simply cannot be accommodated in the tail of a travelling wave, where $u > 1$. The condition $U_{\text{max}} > 1$ is equivalent to $2\alpha > 3\beta$. In addition, it is not hard to see from the geometry of the phase plane solution of (20) and (21) that we can also construct a solution consisting of a sequence of gaps, such as is formed in the wake of a P2 wave, each of which can be closely approximated by the single gap solution, provided that the gap spacing is not too small.

References


Britton N F 1989 Aggregation and the competitive exclusion principle *J. Theoret. Biol.* **136** 57–66


