



Spatio-temporal pattern formation in a nonlocal reaction-diffusion equation

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Abstract. We study a scalar reaction-diffusion equation which contains a nonlocal term in the form of an integral convolution in the spatial variable and demonstrate, using asymptotic, analytical and numerical techniques, that this scalar equation is capable of producing spatio-temporal patterns. Fisher's equation is a particular case of this equation. An asymptotic expansion is obtained for a travelling wavefront connecting the two uniform steady states and qualitative differences to the corresponding solution of Fisher's equation are noted. A stability analysis combined with numerical integration of the equation show that under certain circumstances non-uniform solutions are formed in the wake of this front. Using global bifurcation theory, we prove the existence of such non-uniform steady state solutions for a wide range of parameter values. Numerical bifurcation studies of the behaviour of steady state solutions as a certain parameter is varied, are also presented.

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1. Introduction and preliminaries

There has been some interest recently in the study of reaction-diffusion equations and systems incorporating nonlocal terms. These often arise in situations in ecological modelling where competition between individuals 'within a single species' and also between individuals of 'different species' (i.e. intra- and inter-specific interactions) cannot realistically be treated as local. For example, individuals in a population may compete with each other for a resource which can redistribute itself, or they may communicate with each other by chemical means (Furter and Grinfeld 1989). Alternatively in the models considered by Britton (1989, 1990) and Gourley and Britton (1996), nonlocal spatial effects are present as a consequence of the incorporation of time delays (because of the movement of individuals to their present position from their possible positions at previous times).

There has also been some interest in the effects of nonlocalities in reaction-convection equations with applications to cell population dynamics by investigators

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with interests in similar phenomena to what we are reporting in the present paper. Mackey and Rudnicki (1994) studied global convergence and Rey and Mackey (1995) studied travelling wavefront and pulse solutions.

It has been found by these and other authors that nonlocal terms can greatly enhance the richness of solution behaviour that can be expected from even a scalar reaction-diffusion equation. However, many ideas and techniques used to study standard reaction-diffusion systems can be carried over with relative ease. For example existence and uniqueness of solutions, linearized stability of equilibrium states and local bifurcation behaviour can be studied.

In the present paper we study an equation first proposed by Britton (1989, 1990), namely

$$u_t = ru \left(1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|x-y|} u(y, t) dy \right) + Du_{xx}, \quad (1)$$

for $(x, t) \in (-\infty, \infty) \times (0, \infty)$. The parameters r , D , α , β and λ are all positive constants and we further assume throughout that $1 + \alpha - \beta > 0$. With these assumptions (1) can be regarded as a model for a single animal species which is diffusing, aggregating, reproducing and competing for space and resources.

The terms in (1) have the following interpretation: the term αu , $\alpha > 0$, is a measure of the advantage to individuals in aggregating or grouping. Aggregation in a community of animals is often interpreted as a defence against predators (Hamilton 1971). Alternatively, it may be used for social reasons (Oster and Wilson 1978), as a means of foraging efficiently, or, in the case of flocks of birds or schools of fish, as a means of travelling advantageously, e.g. travelling together in formation is known to reduce drag. Good general discussions on aggregation in ecology and how it can be modelled can be found in Okubo (1986), Grunbaum and Okubo (1994), and Flierl *et al.* (1999).

The term $-\beta u^2$ in (1) represents competition for space (rather than resources). The presence of this particular term impedes population growth and stops the population density from ever exceeding a certain value (namely, with appropriate initial conditions, the positive root of $1 + \alpha u - \beta u^2 = 0$, cf. Britton (1990)).

Finally the integral (nonlocal) term of the equation represents competition between the individuals for food resources. Since this term is multiplied by $u(x, t)$, each individual is in competition with all others in the infinite spatial domain, but is in stronger competition with those nearby than those further away. This effect is tunable: the smaller λ is, the greater the nonlocal effect and, conversely, if $\lambda \rightarrow \infty$ the nonlocal term becomes local since

$$\lim_{\lambda \rightarrow \infty} \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|x-y|} u(y, t) dy = u(x, t).$$

The quantity $1/\lambda$ can therefore be considered as a measure of the spatial scale over which the nonlocal term acts.

Because Britton was interested only in the linear stability of the uniform states and local bifurcation phenomena, he restricted attention to the case $\beta = 0$ (in linearized stability analysis taking $\beta > 0$ just changes the coefficients in the linearized equation). However, Britton's nonlocal term is more general than ours, namely

$$\int_{-\infty}^t \int_{-\infty}^{\infty} G(x-y, t-s) u(y, s) dy ds,$$

with the kernel $G(x, t)$ suitably normalized. Our nonlocal term is a special case of this, arising by taking $G(x, t) = \delta(t) \frac{1}{2} \lambda \exp(-\lambda|x|)$. However, in the present paper we shall keep $\beta > 0$ wherever possible since our interest is mainly in solutions of (1) far from the uniform equilibria. We shall consider non-negative, classical solutions of (1), in particular, travelling front solutions and the global behaviour of bifurcating branches of steady solutions.

We start, in section 2, by using asymptotic methods to construct expressions for travelling wavefront solutions which connect the steady states $u \equiv 0$ and $u \equiv 1$ of (1) and compare these with the corresponding, well-known travelling wavefront solutions of Fisher's equation ($\alpha = \beta = 0, \lambda = \infty$). Then, in section 3, we present a stability analysis and numerical simulations of our equation which confirm the existence of the previously mentioned travelling waves when $u \equiv 1$ is stable. When it is not, the use of a suitably localized initial condition results in an invading wavefront moving out into the domain and leaving behind it a stable non-uniform steady state. More generally our simulations suggest that solutions of the equation always approach a steady state as $t \rightarrow \infty$, though this steady state may or may not be uniform (linearized analysis about $u \equiv 1$ confirms that Hopf bifurcations are impossible but that steady-state bifurcations may occur). Motivated by these observations, in section 4 we use global bifurcation theory to establish the existence of non-uniform steady states for a wide range of parameter values. For a particular set of parameter values, we use the numerical package AUTO to produce bifurcation diagrams that complement these analytical results. Finally some concluding remarks are made in the discussion section.

2. Travelling wavefront solutions

Equation (1) has two non-negative uniform steady states $u \equiv 0$ and $u \equiv 1$ (there is also a third steady state $u = -1/\beta$ which is not of biological relevance or interest here). In this section we show that there is a (non-monotonic) travelling wavefront solution connecting these two non-negative uniform states and construct an asymptotic expression for it. In the analysis of this section r and D can, without loss of generality, be taken to be unity so the equation under consideration is

$$u_t = u \left(1 + \alpha u - \beta u^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|x-y|} u(y, t) dy \right) + u_{xx}. \quad (2)$$

We seek travelling wave solutions and hence look for solutions of the form

$$u(x, t) = U(z), \quad z = x - ct,$$

with $c > 0$ without loss of generality. On substitution, (2) becomes

$$U'' + cU' + U \left(1 + \alpha U - \beta U^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|z-w|} U(w) dw \right) = 0, \quad (3)$$

where the prime denotes differentiation with respect to z . We look for a solution of this satisfying $U(-\infty) = 1$ and $U(\infty) = 0$. Since the equation is invariant with respect to translations in z we are free to prescribe $U(0)$, and for convenience take $U(0) = 1/2$.

By linearizing far ahead of the front in the usual way, we find that in order to have a solution that is positive for all z , the wave speed c must satisfy $c \geq c_{\min} = 2$. Guided

by the approach of Canosa (1973) (summarized in Murray (1989)) for constructing an asymptotic solution to Fisher's equation, we introduce the small parameter

$$\varepsilon = \frac{1}{c^2},$$

and look for a solution in the form

$$U(z) = g(\zeta), \quad \zeta = \varepsilon^{1/2}z.$$

Thus equation (3) becomes

$$\varepsilon g'' + g' + g \left(1 + \alpha g - \beta g^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|\zeta/\sqrt{\varepsilon}-w|} g(\sqrt{\varepsilon}w) dw \right) = 0,$$

or, after making the substitution $\eta = \sqrt{\varepsilon}w$ in the integral

$$\varepsilon g'' + g' + g \left(1 + \alpha g - \beta g^2 - (1 + \alpha - \beta) \int_{-\infty}^{\infty} \frac{\lambda}{2\sqrt{\varepsilon}} e^{-\lambda|\zeta-\eta/\sqrt{\varepsilon}|} g(\eta) d\eta \right) = 0. \quad (4)$$

The parameter ε appears not only as a coefficient of the highest derivative but also inside the integral term. In order to make progress the latter term must be expanded as a series in ε . Repeated integration by parts shows that

$$\int_{-\infty}^{\infty} \frac{\lambda}{2\sqrt{\varepsilon}} e^{-\lambda|\zeta-\eta/\sqrt{\varepsilon}|} g(\eta) d\eta = g(\zeta) + \frac{\varepsilon}{\lambda^2} g''(\zeta) + \dots$$

so that (4) may be approximated by

$$\varepsilon \left(1 - \frac{(1 + \alpha - \beta)}{\lambda^2} g \right) g'' + g' + g(1 - g)(1 + \beta g) = 0 \quad (5)$$

which we supplement with the boundary conditions

$$g(-\infty) = 1, \quad g(\infty) = 0.$$

Although (5) looks like a singular perturbation problem, ε multiplying the highest derivative, in fact a regular perturbation expansion in ε gives a uniformly valid first-order approximation. This is often the case in singular perturbation analysis of wavefronts and is essentially due to the fact that the nonlinear term $g(1 - g)(1 + \beta g)$ is zero at both boundaries (see Murray (1989)).

We therefore seek a solution of (5) of the form

$$g(\zeta) = g_0(\zeta) + \varepsilon g_1(\zeta) + O(\varepsilon^2),$$

with, since $U(0) = 1/2$

$$g_0(0) = \frac{1}{2} \quad \text{and} \quad g_n(0) = 0, \quad \text{for } n \geq 1.$$

Equating coefficients of ε^0 gives the differential equation

$$g_0'(\zeta) + g_0(\zeta)(1 - g_0(\zeta))(1 + \beta g_0(\zeta)) = 0, \quad g_0(0) = \frac{1}{2}, \quad (6)$$

which determines $g_0(\zeta)$, and equating coefficients of ε gives the following equation for $g_1(\zeta)$:

$$g_1'(\zeta) + g_1(\zeta) \left[1 + 2(\beta - 1)g_0(\zeta) - 3\beta(g_0(\zeta))^2 \right] = g_0''(\zeta) \left[\frac{(1 + \alpha - \beta)}{\lambda^2} g_0(\zeta) - 1 \right],$$

$$g_1(0) = 0. \quad (7)$$

When $\beta = 0$, (6) can be solved explicitly (an implicit solution is available more generally). We therefore proceed under the assumption that $\beta = 0$ after which we shall discuss what happens to the travelling wave when $\beta > 0$.

When $\beta = 0$ the solution to (6) is

$$g_0(\zeta) = \frac{1}{e^\zeta + 1}. \tag{8}$$

Substituting this into (7) and solving then gives

$$g_1(\zeta) = \frac{(e^\zeta + 1)(2\lambda^2 - \alpha - 1)(\ln(2) - \ln(e^\zeta + 1)) + (e^\zeta + 1)(\lambda^2 - \alpha - 1)\zeta + (\alpha + 1)(e^\zeta - 1)}{\lambda^2(e^\zeta + 1)(e^\zeta + e^{-\zeta} + 2)}. \tag{9}$$

Thus the approximation we have found to the solution of (3) (with $\beta = 0$) is

$$U(z) = g_0(z/c) + \frac{1}{c^2}g_1(z/c) + \dots \tag{10}$$

with g_0 and g_1 given by (8) and (9), respectively. This solution is shown in figure 1. Its most noteworthy feature is the hump immediately behind the front providing a travelling wave which, unlike in solutions of Fisher’s equation, is not monotonic. This hump is present even if $\alpha = 0$ and so it is genuinely a consequence of the nonlocal term in the equation rather than the aggregation term or the competition for space term (the β term) which has, of course, already been switched off.

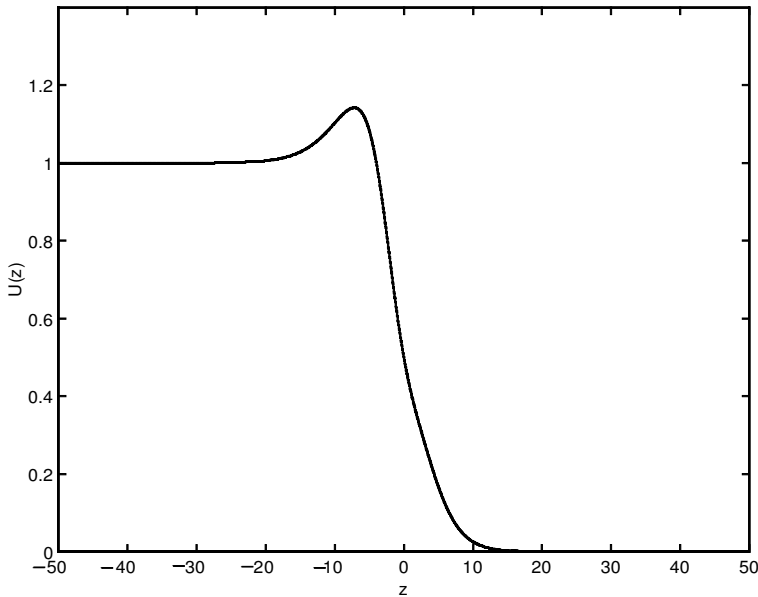


Figure 1. Plot of solution (10) to equation (3) (with $\beta = 0$). Other parameter values were: $\alpha = 0.2$, $\lambda = 0.25$, $c = 2.5$. The ‘hump’ immediately behind the front is the main difference between travelling wavefront solutions of our equation and those of Fisher’s equation.

The solution (10) is asymptotically accurate only in the limit $c \rightarrow \infty$ and therefore is expected to be least accurate when $c = 2$. However, Murray (1989) points out that when the method used here is applied to Fisher's equation, even when the least acceptable value of c is used the first term alone of the asymptotic solution is within a few per cent of the true solution. We can therefore view our solution with some confidence—it is also certainly very similar to the results of the numerical simulations of the full partial differential equation (1) presented in the next section (see figure 2 in particular).

It remains to discuss how the solution (10) will change when $\beta > 0$. Note that in the first two perturbation equations (6) and (7), the β terms do not arise in a way that would introduce major qualitative changes in the solutions. Indeed, an inspection of (6) shows that the effect of $\beta > 0$ is simply to make g_0' more negative. Thus the wavefront simply becomes steeper and so, with a given value for the wave speed c , the higher the value of β , the quicker is the transition from 0 to 1 as the front passes.

3. Linear stability analysis and numerical simulations

In this section we present the results of a linear stability analysis and some numerical simulations of (1). This serves to verify the analytical results of the previous section and is also a motivation for the global bifurcation analysis presented later. In order to carry out a linear stability analysis and to simulate (1), it is useful to recast the equation in a slightly different form. Let w denote the integral term, so that

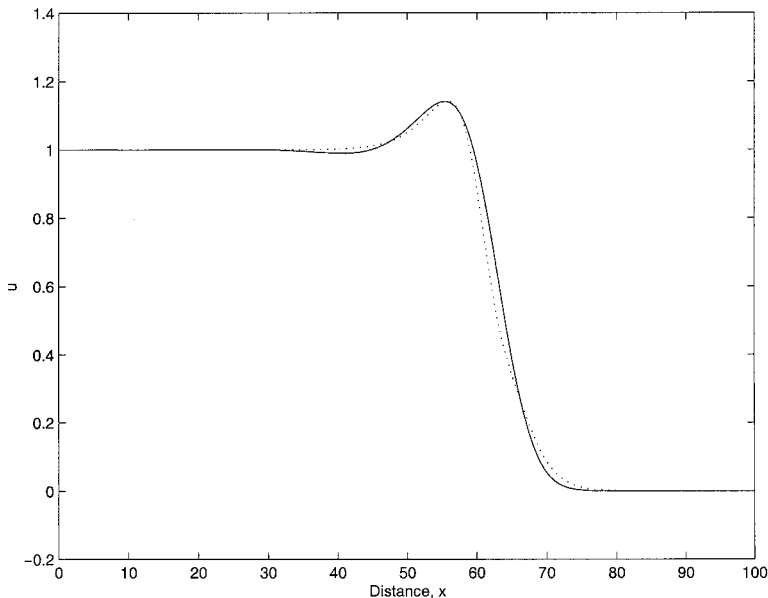


Figure 2. Typical solution profile (solid line) obtained by numerical simulation of (11). Parameter values were: $D = 1$, $r = 1$, $\alpha = 0.2$, $\lambda = 0.25$, $\beta = 0$. For comparison, a translate of the asymptotic solution (10), shown in figure 1, is also plotted (dotted line). The two solutions are in good agreement.

$$w(x, t) = \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|x-y|} u(y, t) dy.$$

Differentiating with respect to x twice shows that

$$w_{xx} = -\lambda^2(u - w).$$

Equation (1) may therefore be replaced by the coupled system

$$\begin{aligned} u_t &= ru(1 + \alpha u - \beta u^2 - (1 + \alpha - \beta)w) + Du_{xx}, \\ 0 &= \lambda^2(u - w) + w_{xx}, \end{aligned} \tag{11}$$

for $(x, t) \in (-\infty, \infty) \times (0, \infty)$. Equations (11) are now in a suitable form to carry out a standard linear stability analysis. Recasting the original equation in this coupled system form also has the advantage that, even though the second equation has no time derivative term, the system (11) may be solved by the method of lines and Gear’s method, as implemented in the NAG routine D03PCF. The absence of a time derivative term in one equation does have implications regarding what is required by way of initial conditions. We can prescribe $u(x, 0)$ at will but $w(x, 0)$ is then determined for us by the equation

$$w(x, 0) = \int_{-\infty}^{\infty} \frac{1}{2} \lambda e^{-\lambda|x-y|} u(y, 0) dy. \tag{12}$$

In simulations where travelling wavefront solutions are anticipated it is usual for $u(x, 0)$ to be taken in the form of a step function. Such initial data also reasonably represent the localized introduction of a species to the reaction domain. In this case, $w(x, 0)$ can easily be calculated explicitly and is simply a smoothed-out step function.

In the following, we focus our interest on the solution behaviour as the parameter α is varied, all other parameters are considered to be fixed. In particular, we consider values of α around the value for which the uniform steady state $(u, w) = (1, 1)$ changes stability; it is anticipated that changes to solution structure will occur at this point. The following formal calculations provide information concerning the (linear) stability of the uniform steady state.

Setting $u = 1 + \tilde{u}$ and $w = 1 + \tilde{w}$, substituting into (11) and linearizing gives

$$\begin{aligned} \tilde{u}_t &= r(\alpha - 2\beta)\tilde{u} - r(1 + \alpha - \beta)\tilde{w} + D\tilde{u}_{xx}, \\ 0 &= \lambda^2(\tilde{u} - \tilde{w}) + \tilde{w}_{xx}. \end{aligned} \tag{13}$$

Substituting a test function of the form

$$\begin{pmatrix} \tilde{u} \\ \tilde{w} \end{pmatrix} = \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} e^{\sigma t + ikx},$$

where k is real, provides the following dispersion relation:

$$(\sigma - r(\alpha - 2\beta) + Dk^2)(\lambda^2 + k^2) + r\lambda^2(1 + \alpha - \beta) = 0. \tag{14}$$

Note that this implies σ is real for all values of α and thus Hopf bifurcations from the uniform state $(u, w) = (1, 1)$ of (11) are impossible. Moreover, for α sufficiently small, σ as given by (14) is negative and hence $(u, w) = (1, 1)$ is stable. However, as α is increased it is possible for σ to pass through 0, indicating a loss of stability of the uniform steady state. For a fixed value of the wavenumber k this occurs when

$$\alpha = \frac{\lambda^2}{k^2}(1 - \beta) + \left(\frac{\lambda^2 + k^2}{rk^2} \right) (2r\beta + Dk^2). \quad (15)$$

This expression has a minimum (with respect to k) at the value $k = k_c$ given by

$$k_c^2 = \lambda \sqrt{\frac{r(1 + \beta)}{D}},$$

and the corresponding α value is α_c where

$$\alpha_c = 2\beta + \frac{\lambda^2 D}{r} + 2\lambda \sqrt{\frac{D(1 + \beta)}{r}}. \quad (16)$$

Thus as α is increased through α_c , the uniform steady state $(1, 1)$ loses stability and it is anticipated that a new, non-uniform steady state will appear having a spatial structure similar to $\exp(ik_c x)$. A full steady state bifurcation analysis is conducted in section 4.

It is possible to draw certain comparisons between the instability we are identifying here and the well known Turing, or diffusion-driven, instability which is described in detail in Murray (1989). We have noted that in our equation Hopf bifurcations are impossible; the only bifurcations that occur from the uniform steady state are steady-state bifurcations. But, note that the slightly different system

$$u_t = ru(1 + \alpha u - \beta u^2 - (1 + \alpha - \beta)w) + Du_{xx},$$

$$w_t = u - w + \lambda^{-2}w_{xx},$$

is equivalent to (11) as far as steady-state bifurcations are concerned, and the latter system is in the right form to draw comparisons with Turing bifurcations as described in Murray (1989). It is well known that Turing bifurcations can only occur when the ratio of the diffusivities of the two species or chemicals, which would be thought of as u and w here, is sufficiently large. For the above system, a necessary condition (see Murray (1989)) is that λ^{-2}/D has to be sufficiently large and one way to interpret this is that the nonlocality (measured by $1/\lambda$) has to be strong enough.

The link to Turing bifurcations is of mathematical, rather than ecological, interest. Ecologically speaking it is incorrect to think of w as a diffusing species with diffusivity λ^{-2} . In our model there is only one species, u , and w is just the spatio-temporal average thereof. The correct ecological interpretation of the quantity λ is that its reciprocal measures the strength of the nonlocality. For any value of the diffusivity D of our species, the steady-state bifurcation will occur for suitable values of the kinetic parameters r , α , β and λ though it can never occur if $\lambda = \infty$ (which, as we explained earlier, reduces the nonlocal term to a local one). Thus, we regard the bifurcation as having been induced by the nonlocality, not the diffusion as in Turing bifurcations.

Guided by the linear stability analysis we have carried out, we now present numerical simulations of (11) using the method of lines and Gear's method, as implemented in the NAG routine D03PCF. Our numerical simulations were all carried out on a finite spatial domain. The problem itself presumes the domain is infinite since it involves integration over all of \mathbf{R} . However, in view of the exponential decay of the integration kernel in (1) we can regard the integration variable y as effectively running over a finite interval centred on x and having width of order $1/\lambda$. We

therefore assume it is reasonable to use a finite domain which is large compared to $1/\lambda$. In our simulations we took the spatial domain to be either $0 \leq x \leq 100$ or $0 \leq x \leq 20$ (the latter being adequate for smaller diffusivities) and the values $\lambda = 0.25, 1$ and $\lambda = 6$ were used. Zero-flux boundary conditions were applied. The initial condition for u was taken to be

$$u(x, 0) = \begin{cases} 1, & 0 \leq x \leq 5, \\ 0, & 5 < x \leq 100, \end{cases}$$

for figure 2 and

$$u(x, 0) = \begin{cases} 1, & 0 \leq x \leq 10, \\ 0, & 10 < x \leq 20, \end{cases}$$

for figures 3–6. In both cases the initial condition for w was computed from this using (12), the limits of integration having been replaced by 0 and 100, or 0 and 20 as appropriate.

In figure 2 we show a snapshot of a numerical simulation of (11) using the same parameter values as those used for the plot of the asymptotic solution (10) in figure 1 (in particular, the diffusivity is 1 and because of this we needed to use a larger domain than in the subsequent simulations to allow the solution to evolve to a permanent profile before reaching the end of the domain). For comparison, in figure 2 we have also plotted a translate of the asymptotic solution (10). The two solutions are in remarkably good agreement. Figure 3, which uses a smaller diffusivity and different values for the other parameters, shows a snapshot of the solution of (11) at time $t = 2$. For $\alpha = 0.5$, the uniform state $u = 1$ is stable, and our numer-

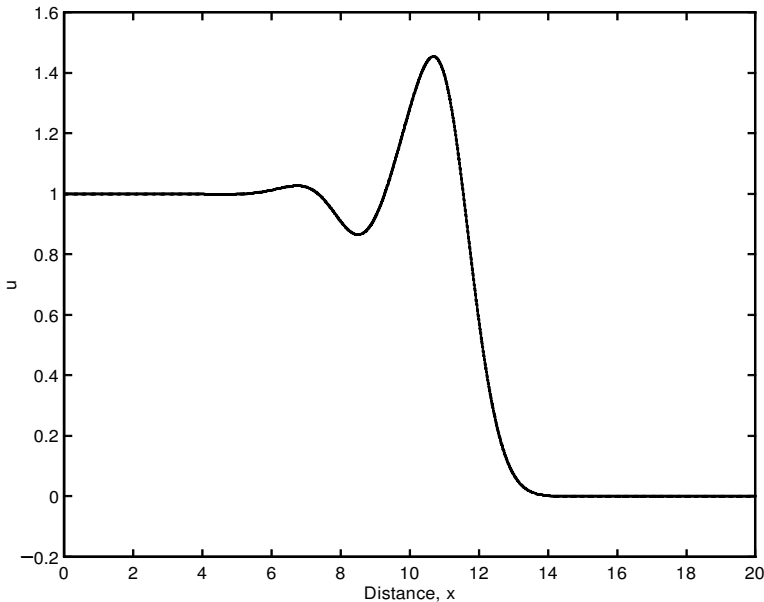


Figure 3. Solution of system (11) at time $t = 2$. Parameter values: $D = 0.1, r = 3, \alpha = 0.5, \lambda = 1, \beta = 0.1$. With these values the uniform steady state $u = 1$ is stable.

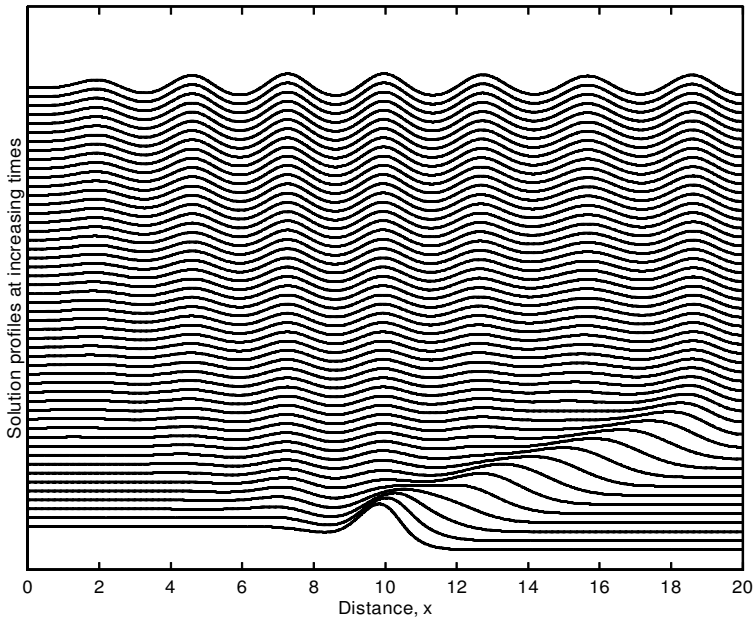


Figure 4. Profiles of the solution of system (11) at various equally spaced times in the range $1 \leq t \leq 40$. Parameter values: $D = 0.1$, $r = 3$, $\alpha = 0.65$, $\lambda = 1$, $\beta = 0.1$. With these values the uniform state $u = 1$ is just unstable.

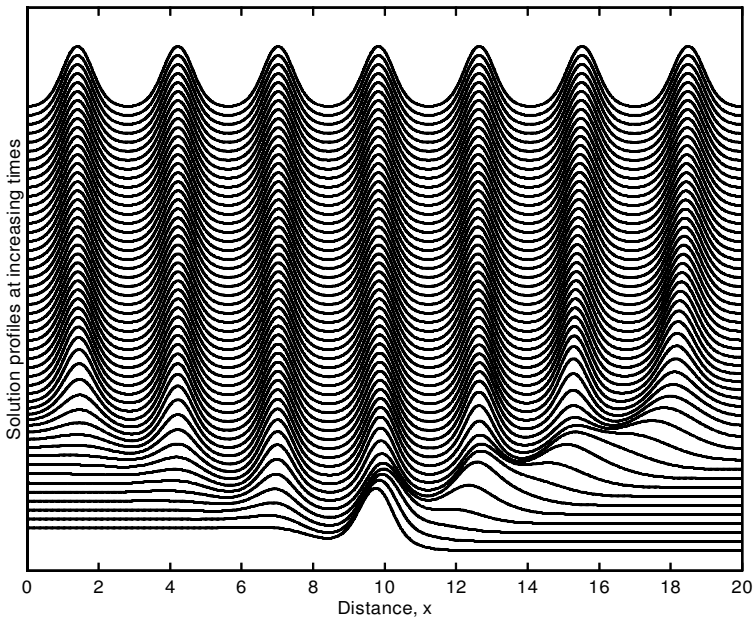


Figure 5. Profiles of the solution of system (11) at various equally spaced times in the range $1 \leq t \leq 40$. Parameter values: $D = 0.1$, $r = 3$, $\alpha = 0.8$, $\lambda = 1$, $\beta = 0.1$ (well beyond the bifurcation to instability of the uniform state $u = 1$).

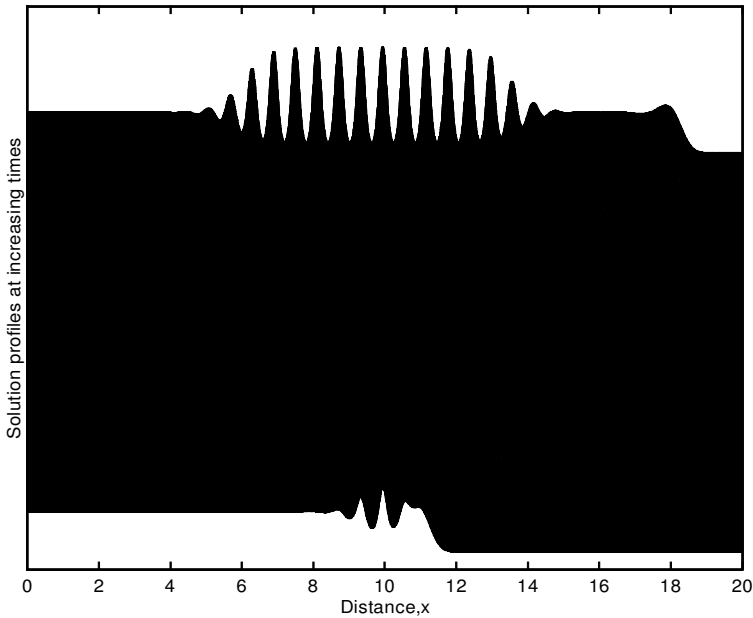


Figure 6. Profiles of the solution of system (11) at various equally spaced times in the range $1 \leq t \leq 25$. Parameter values: $D = 0.01$, $r = 3$, $\alpha = 1.2$, $\lambda = 6$, $\beta = 0.1$. These values indicate that when D is small, the final spatial pattern spreads through the domain more slowly than the advancing front.

ical simulation indicates that the solution evolves quickly to a permanent form travelling wave connecting the steady states $u = 0$ and $u = 1$, whose qualitative form is again consistent with the results of the asymptotic analysis of section 2. By increasing α to $\alpha = 0.65$, the uniform steady state $u = 1$ becomes unstable (the critical value for the parameter values used here is $\alpha_c = 0.616$) and as shown in figure 4, a non-uniform steady-state solution is left in the wake of the wavefront. The evolution to this steady state is slow. In figure 5, α is increased further still to $\alpha = 0.8$; the result is (a more rapid) evolution to a similar non-uniform steady state as that reached for values closer to the bifurcation value $\alpha = \alpha_c$. The resultant solution is qualitatively the same, comprising seven fixed peaks, differing only in amplitude from the solution shown in figure 4. In figure 6, a much lower value for the diffusivity D is used and the result is that the non-uniform steady state fills the domain more slowly than the speed of the advancing front. Thus at a given point x , immediately after the wavefront passes the solution will be very close to $u = 1$ and remains so for some time even though this uniform state is unstable.

A well-known result due to Casten and Holland (1978) states that a scalar reaction-diffusion equation comprising purely local terms and with homogeneous Neumann boundary conditions cannot have a stable non-uniform steady state solution. The above simulations clearly indicate that this situation no longer holds when nonlocal terms are included. The existence of non-uniform steady states is addressed in the following section.

All the numerical simulations carried out indicate that solutions always approach a steady state as $t \rightarrow \infty$, this steady state being either the uniform, $u = 1$, or some

non-uniform spatial pattern. Indeed, as we have already shown, Hopf bifurcations from this uniform state are impossible.

4. Bifurcation and global existence of non-uniform steady states

In this section we discuss the existence of steady state solutions to equation (1). The numerical simulations discussed above show that, depending on parameter values, either steady uniform or steady spatially periodic solutions are formed in the wake of a travelling front. Hence we will restrict our attention to the existence of such solutions. Using similar techniques to those used in Britton (1990), it is straightforward to show that in this case, seeking steady-state solutions of (1) is equivalent to finding solutions of the following system (cf. (11) above):

$$-Du_{xx} = ru(1 + \alpha u - \beta u^2 - (1 + \alpha - \beta)w), \quad \text{in } (0, \pi), \quad (17)$$

$$-w_{xx} = \lambda^2(u - w), \quad \text{in } (0, \pi), \quad (18)$$

$$u_x = w_x = 0, \quad \text{at } x = 0, \pi, \quad (19)$$

where $w(x)$ is defined in section 3 above. As u represents a population density, we are only interested in solutions for which u is non-negative and, by its definition, for which w is also non-negative. We also restrict our attention to classical solutions, i.e. solutions which are sufficiently differentiable to satisfy (17)–(19) in the standard sense. In particular, as in section 3, we are interested in how these steady-state solutions change as α is varied and so α will again be considered as the bifurcation parameter with all other parameters taken to be fixed and positive. We note that in order to obtain existence results, the technique of Defigueiredo and Mitidieri (1986) cannot be applied here as the nonlocal term in (1) is nonlinear. Also, our problem is not of a suitable form for application of the results of Cosner (1988) with regard to the existence and behaviour of global continua. Rather, we employ certain techniques similar to those used in Davidson and Rynne (2000).

First, it follows immediately that $(u, w) = (0, 0)$ and $(u, w) = (1, 1)$ are uniform solutions of (17)–(19). We will show that a branch of non-uniform solutions bifurcates from the solution $(1, 1)$ at a critical value of α and it is the solutions on this branch which are formed in the wake of the travelling front as depicted by the numerical solutions discussed above. (As will be discussed later, it can be shown that bifurcation from $(0, 0)$ happens only under non-generic conditions and will not be considered in this paper.)

Let $u = 1 + \hat{u}$ and $w = 1 + \hat{w}$. Then (17)–(19) are equivalent to

$$\begin{aligned} -D\hat{u}_{xx} &= r[(\alpha - 2\beta)\hat{u} - (1 + \alpha - \beta)\hat{w}] \\ &\quad + r\hat{u}[(\alpha - 3\beta)\hat{u} - \beta\hat{u}^2 - (1 + \alpha - \beta)\hat{w}], \quad \text{in } (0, \pi), \\ -\hat{w}_{xx} &= \lambda^2(\hat{u} - \hat{w}), \quad \text{in } (0, \pi), \\ \hat{u}_x &= \hat{w}_x = 0 \quad \text{at } x = 0, \pi. \end{aligned} \quad (20)$$

Thus $(\hat{u}, \hat{w}) = (0, 0)$ is a solution of (20) for all α and corresponds to the solution $(1, 1)$ of (17)–(19).

We now reformulate (20) in an appropriate function space setting in order to apply global bifurcation results. Let

$$X_k = \{\phi \in C^k[0, \pi] : \phi_x = 0 \text{ at } x = 0, \pi\}^2, \quad k = 1, 2, \quad Y = C[0, \pi]^2$$

(the superscript 2 denotes the Cartesian product of a pair of the corresponding spaces), and define the operators $\mathcal{L} : X_2 \rightarrow Y$, $\mathcal{M} : X_2 \rightarrow Y$, $\mathcal{F} : \mathbf{R} \times X_2 \rightarrow Y$, as follows:

$$v = \begin{pmatrix} \hat{u} \\ \hat{w} \end{pmatrix}, \quad \mathcal{L}v = \begin{pmatrix} D\Delta - 2\beta r & -r(1 - \beta) \\ \lambda^2 & \Delta - \lambda^2 \end{pmatrix}v, \quad \mathcal{M}v = \begin{pmatrix} r & -r \\ 0 & 0 \end{pmatrix}v \quad \text{and}$$

$$\mathcal{F}(\alpha, v) = \begin{pmatrix} r\hat{u}[(\alpha - 3\beta)\hat{u} - \beta\hat{u}^2 - (1 + \alpha - \beta)\hat{w}] \\ 0 \end{pmatrix}.$$

Clearly then, finding solutions of (20) is equivalent to finding an element in X_2 , which satisfies

$$(\mathcal{L} + \alpha\mathcal{M})v + \mathcal{F}(\alpha, v) = 0. \tag{21}$$

It is straightforward to show that the singular points of $\mathcal{L} + \alpha\mathcal{M}$ (the points at which 0 is an eigenvalue of $\mathcal{L} + \alpha\mathcal{M}$) are the numbers

$$\alpha = \frac{Dj^2}{r} + \frac{\lambda^2 D}{r} + 2\beta + \frac{\lambda^2(1 + \beta)}{j^2}, \tag{22}$$

for $j = 1, 2, \dots$ (Note that (22) is equivalent to (15) with j replacing k . Indeed, the eigenfunctions of $\mathcal{L} + \alpha\mathcal{M}$ with α given by (22) correspond to the unstable modes $\exp(ikx)$ discussed in section 3.) Hence, except for a countable set of values of the other parameters, no two singular points defined by (22) coincide. Thus, we will assume, without loss of generality, that parameters are chosen such that all the singular points of $\mathcal{L} + \alpha\mathcal{M}$ can be labelled by a strictly increasing sequence $0 < \alpha_1 < \alpha_2 < \dots$. Notice that, depending on the choice of parameter values, the i th element in this sequence, i.e. α_i , may not correspond to (22) with $j = i$; for the parameter values used in section 3, (22) has a minimum when $j = 2$.

It is now straightforward to show that standard local bifurcation results (see Crandall and Rabinowitz (1971)) apply to equation (21) and imply the existence of a local branch of non-uniform solutions bifurcating from each point $(\alpha, v) = (\alpha_i, 0)$ for $i \geq 1$.

It can be shown, using similar methods, that no such bifurcation occurs from $(\hat{u}, \hat{w}) = (-1, -1)$ (corresponding to the solution $(u, w) = (0, 0)$ of (17)–(19)) except for a particular choice of the other parameter values. As above, we ignore this non-generic case without loss of generality.

We now extend this local result to one concerning global existence in the following theorem.

Theorem 1. *A continuum of non-uniform solutions to the system (17)–(19) emanates from each bifurcation point $(u, w, \alpha) = (1, 1, \alpha_i)$, $i = 1, 2, \dots$. Moreover, each continuum either extends to unbounded α or intersects with at least one other bifurcation point.*

Proof. See Appendix for details.

For the parameter values used for figures 3–5 in section 3, the first bifurcation point on the line of uniform solutions $(1, 1)$ occurs at $\alpha \approx 0.642$ (from (22) with $j = 2$). Sufficiently close to this point, by the local results discussed above, it follows that solutions on the associated non-uniform branch have the form $(u, w) \approx (1 + c_1 \cos 2x, 1 + c_2 \cos 2x)$ where c_1 and c_2 are constants with $|c_1|, |c_2| \ll 1$. In section 3, it is shown that the uniform solution $(1, 1)$ is unstable for values of α above this first bifurcation point and numerical integration of the initial value problem suggests that a stable non-uniform solution does exist (see figure 4). Moreover, the underlying mode of this non-uniform solution is clearly $\cos 2x$ suggesting that it lies on the first branch of non-uniform solutions and that this branch bifurcates from the uniform branch in a supercritical manner. Theorem 1 ensures that this solution branch extends globally but cannot become unbounded for any finite value of α and cannot connect with the branch of trivial solutions. To gain further information regarding the global structure of this and other branches for the parameter values used for figures 3–5, we use the well known numerical continuation package AUTO.

Figure 7 is a bifurcation diagram for system (17)–(19) and shows how a measure of solution size, taken to be the value of the function $u(x)$ at the left-hand boundary $x = 0$, varies with the bifurcation parameter α . The diagram is somewhat complex with many secondary bifurcations but notice that the primary branches of non-uniform solutions bifurcate from the uniform branch $(1, 1)$ at the critical values of α given by (22). All primary branches above and below this line appear to remain distinct and are monotonically increasing (respectively decreasing) for a large range of values of α . This strongly suggests that the first alternative offered in Theorem 1 applies with these branches joining $\alpha = +\infty$. Notice that the branches are not symmetric about the line $u = 1$ reflecting the lack of symmetry in system (17)–(19). Bifurcation points are indicated by diamonds; all other crossings are not bifurcation

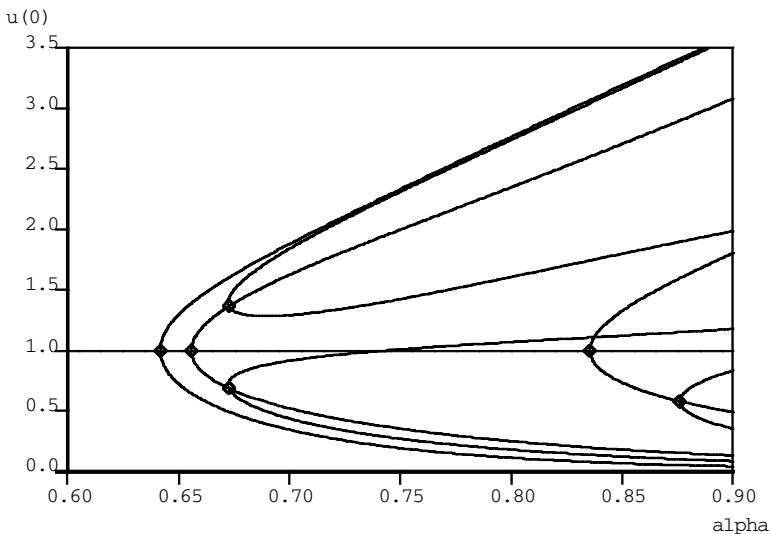


Figure 7. Bifurcation diagram for system (17)–(19). The value of $u(0)$ is shown as it varies with α indicating bifurcation of non-uniform branches of solutions from the uniform branch $(1, 1)$. Parameter values: $D = 0.1$, $r = 3$, $\lambda = 1$, $\beta = 0.1$.

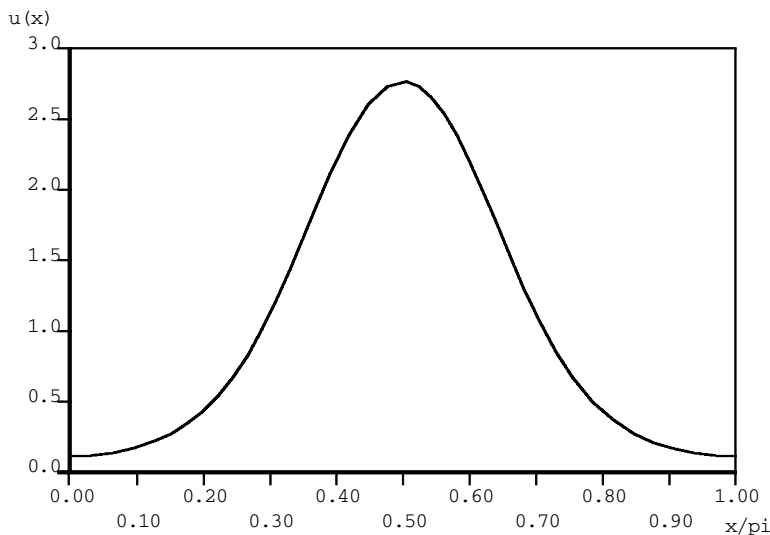


Figure 8. Steady state solution of system (17)–(19). The solution $u(x)$ is plotted against x/π (the scaling is a feature of AUTO) with $\alpha = 0.8$. Other parameter values are $D = 0.1$, $r = 3$, $\alpha = 0.8$, $\lambda = 1$, $\beta = 0.1$.

points, rather, they are a consequence of the projection of the solution–parameter space on to the plane. The formal calculations conducted in section 3 above, indicate that the uniform branch of solutions loses stability as α passes through the first critical value given by (22) (i.e. with $j = 2$). This, coupled with the supercritical nature of the bifurcation of the associated non-uniform branch, strongly suggests that the latter comprises stable solutions. Indeed, the solution on the lower component of this branch at the value $\alpha = 0.8$ as shown in figure 8, is very similar (modulo periodic extension) to the steady state solution reached in the wake of the travelling front shown in figure 5. (Solutions on the branch emanating from the second critical value have an underlying $\cos 3x$ mode at this value of α .)

5. Discussion

In this paper we have studied a reaction-diffusion equation derived to model the growth and dispersal of a single animal species. Of key interest is that this equation contains a nonlocal term which is necessary to accurately model intra-specific competition for resources. Standard techniques developed to study equations without nonlocal terms can be used to investigate certain properties of this more complex equation, such as linear stability of uniform states and local bifurcation phenomena, as other investigators have already noted. Our aim in this paper has therefore been to undertake a wider analysis of the structure of the solution set using asymptotic techniques, numerical simulations and ‘global’ bifurcation theory.

Specifically we first of all constructed an asymptotic expression for a travelling wave solution connecting the two uniform states, $u = 0, 1$, of equation (1), and noted that it differs qualitatively from the corresponding solution of Fisher’s equation. The main difference is the appearance of a hump immediately behind the wavefront. The

presence of this feature is entirely due to the nonlocal term in the equation, since it persists even when the α and β (local) terms are absent.

A biological interpretation of the hump is as follows. A travelling front solution connecting the zero (extinction) state with a positive uniform state can be interpreted as the species moving out (by diffusion) and colonizing a region of space that was previously uninhabited. Moreover, in our model it is assumed that each individual is competing for food with others at different points in space and, in this one-dimensional scenario, this means each individual is competing both with those in front and with those behind. In an invasion of a previously uninhabited region, those at the front of the invasion (mathematically, at the point where the travelling front is steepest) will find there are essentially no individuals ahead of them so that they are in competition only with those behind. This gives them an advantage and allows the population there to get above the carrying capacity level (the maximum the environment can sustain in the long term), but only in the vicinity of the front of the invading colony. As a result we see a hump in the front profile.

The asymptotic analysis does not address the stability of the travelling front, but numerical simulations confirm that the front exists and is stable. These simulations were conducted by first rewriting the single equation (1) as a coupled system containing only local terms (see section 3). The numerical simulations show that an invading wavefront moves out into the domain, leaving in its wake a steady state which is either uniform or non-uniform, depending on the chosen parameter values (it was shown that no temporally oscillatory behaviour was possible for the equation under consideration here; such behaviour is possible in certain scalar equations with delay). The existence of stable non-uniform steady state solutions is due entirely to the nonlocal term, since existing theory rules out such solutions for local scalar equations under the boundary conditions applied here. Motivated by these numerical simulations, a global analysis of a certain class of steady state solutions of (1) was conducted. *A priori* bounds were found and, using these in conjunction with global bifurcation theory, it was proved that non-uniform steady state solutions exist for a wide range of parameter values. Using the numerical package AUTO, we were able to demonstrate that stable non-uniform solutions are contained on a continuum emanating from the point at which the uniform solution $(u, w) = (1, 1)$ loses stability. Results suggest that this continuum joins $\alpha = +\infty$ and therefore there exists a non-uniform solution for all α greater than this critical value and all such solutions have the same underlying mode ($\cos 2x$ for the parameter values used in most of the simulations here). Our results suggest that it is always the first alternative of Theorem 1 that holds, i.e. that every continuum emanating from $(u, w) = (1, 1)$ extends to unbounded α and that no continuum enters another bifurcation point on the $(u, w) = (1, 1)$ branch (though secondary bifurcations may occur).

The fact that our original equation (1) is equivalent to the coupled system (11) enables us to draw certain links to the well-known Turing bifurcation, once the state variables and parameters have been suitably interpreted. The second equation in (11) does not have a time derivative term, but the stationary solutions of (11) are equivalent to those of a system where both variables have time derivative terms and it is this fact that enables us to draw comparisons to the Turing theory. When the parameters are interpreted with their correct ecological meaning, we see that it is the nonlocal term that causes the bifurcation in our model, and that the bifurcation can occur for any value of the diffusivity D of the species.

This paper has demonstrated the implications of nonlocal nonlinearities in ‘scalar’ reaction-diffusion equations and we have expanded on previous studies that have focused only on solutions near equilibrium. In ‘systems’ of local reaction-diffusion equations it has been shown (see, e.g. Sherratt *et al.* (1997)) that oscillatory spatial patterns and spatio-temporal chaos can form in the wake of an invading wavefront solution. It will be interesting to investigate the role of nonlocal terms in such systems, especially since it is known that in coupled systems (Gourley and Britton 1996) a nonlocal term of the type used in this paper can lead to a Hopf bifurcation (to a wave train solution or standing wave solution) in contrast to the case of a scalar equation when only a steady-state bifurcation is possible.

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Appendix

We present the full details of the proof of Theorem 1. First, we obtain a result concerning the boundedness of non-negative solutions to (17)–(19). In the following the notation $\| \cdot \|$ will denote the standard norm on the space $L^2(0, \pi)$ and the inner product referred to is the standard $L^2(0, \pi)$ inner product. Also $\| \cdot \|_{k,r}$ will denote the standard norm on the Sobolev space $W^{k,r}(0, \pi)$, for any integers $k, r \geq 1$. Furthermore, the notation $| \cdot |_k$ will denote the standard norm on the Banach space $C^k[0, \pi]$, for any $k \geq 0$ (see Adams (1975)).

Lemma A 1. *Let A be a positive number. Then there exists a constant K , which depends only on A, λ, r, D and β , such that if $0 < \alpha \leq A$, then every non-negative, classical solution (u, w) of the system (17)–(19) satisfies*

$$|u|_2 + |w|_2 \leq K.$$

Proof. Suppose that $(u, w) \in C^2[0, \pi] \times C^2[0, \pi]$ is a non-negative solution of the system (17)–(19). Integrating (17) over $(0, \pi)$, using the method of integration by parts and the boundary condition, yields

$$\int_0^\pi u(1 + \alpha u - \beta u^2) dx = (1 + \alpha - \beta) \int_0^\pi wu dx. \tag{A 1}$$

It follows from this and the modelling assumption $1 + \alpha - \beta > 0$, that

$$\beta \int_0^\pi u^3 dx \leq \int_0^\pi (u + \alpha u^2) dx$$

and hence, by Hölder’s inequality

$$\beta \int_0^\pi u^3 dx \leq \pi^{2/3} \left(\int_0^\pi u^3 dx \right)^{1/3} + \alpha \pi^{1/3} \left(\int_0^\pi u^3 dx \right)^{2/3}.$$

From this it is straightforward to show that

$$\begin{aligned} \int_0^\pi u^3 \, dx &\leq \max \left\{ 1, \frac{\pi}{\beta^3} (\pi^{1/3} + \alpha)^3 \right\} \\ &= \frac{\pi}{\beta^3} (\pi^{1/3} + \alpha)^3 \end{aligned} \tag{A 2}$$

by the assumption $1 + \alpha - \beta > 0$. It follows, again by Hölder’s inequality, that

$$\|u\| \leq K_1 \tag{A 3}$$

where $K_1 = (\pi^{1/2}/\beta)(\pi^{1/3} + \alpha)$. Taking the inner product of (18) with w gives

$$\|w_x\|^2 = \lambda^2 \int_0^\pi (uw - w^2) \, dx \tag{A 4}$$

and therefore

$$\int_0^\pi w^2 \, dx \leq \int_0^\pi wu \, dx \leq \left(\int_0^\pi w^2 \, dx \right)^{1/2} \left(\int_0^\pi u^2 \, dx \right)^{1/2}$$

by Schwarz’s inequality and so, by (A 3)

$$\|w\| \leq \|u\| \leq K_1. \tag{A 5}$$

Hence by (A 3)–(A 5), it follows after a little algebra that

$$\|w\|_{1,2} \leq K_1(\lambda^2 + 1)^{1/2}. \tag{A 6}$$

We now derive a similar bound for u . Taking the inner product of (17) with u gives

$$\begin{aligned} D\|u_x\|^2 &\leq r \int_0^\pi (u^2 + \alpha u^3 - \beta u^4 - (1 + \alpha - \beta)wu^2) \, dx \\ &\leq r \int_0^\pi (u^2 + \alpha u^3) \, dx \\ &\leq rK_1^2 + \frac{r\alpha}{\pi^{1/2}}K_1^3. \end{aligned}$$

Hence, from this, (A 3) and again after a little algebra, it follows that

$$\|u\|_{1,2} \leq K_2 \tag{A 7}$$

where

$$K_2 = K_1 \left(1 + \frac{r}{D} + \frac{r\alpha}{\pi^{1/2}D}K_1 \right)^{1/2}.$$

By the Sobolev embedding theorems (see Theorem 5.4 in Adams (1975)), the embedding $W^{1,2}(0, \pi) \hookrightarrow C^{0,\gamma}[0, \pi]$ is continuous for $0 < \gamma \leq 1/2$ (where $C^{k,\gamma}[0, \pi]$ represents the space of functions with k th derivative Hölder continuous as is standard). Hence the right-hand sides of (17) and (18) lie in $C^{0,1/2}[0, \pi]$ and the result follows standard regularity theory for elliptic operators (see, e.g. Theorem 6.31 in Gilbarg and Trudinger (1983)).

Using similar arguments, it is straightforward to show that Lemma A1 continues to hold when α has no designated sign, i.e. when the condition $0 < \alpha \leq A$ is replaced by $|\alpha| \leq A$ (although the constant K may be different). □

Proof of Theorem 1. For parameters chosen as above, the operator \mathcal{L} is non-singular and therefore (21) is equivalent to

$$v = \alpha \mathcal{K}v + \mathcal{H}(\alpha, v), \quad (\alpha, v) \in \mathbf{R} \times X_2 \quad (\text{A } 8)$$

where $\mathcal{K} = -\mathcal{L}^{-1}\mathcal{M}$ and $\mathcal{H}(\alpha, v) = -\mathcal{L}^{-1}\mathcal{F}(\alpha, v)$. It follows that (A 8) may be considered in the space $\mathbf{R} \times X_1$ (since $\mathcal{L}^{-1} : Y \rightarrow X_2$, any solution of (A 8) in $\mathbf{R} \times X_1$ automatically belongs to $\mathbf{R} \times X_2$). In this setting, equation (A 8) has the form considered in Rabinowitz (1971) and Dancer (1974) and also, since X_2 is compactly embedded in X_1 , the required compactness and other conditions in these papers hold. Hence the global existence results in Rabinowitz (1971) and Dancer (1974) apply to (A 8) as follows.

It is straightforward to show that each singular point α_i , $i = 1, 2, \dots$, of $\mathcal{L} + \alpha\mathcal{M}$ corresponds to a simple characteristic value of \mathcal{K} and hence for each $i = 1, 2, \dots$, there exists a global continuum $\hat{C}_i \subset \mathbf{R} \times X_1$ of solutions of (A 8) emanating from the point $(\alpha_i, 0)$. By the global theory, this continuum must either meet infinity or must meet an odd number of other such bifurcation points $(\alpha_j, 0)$, $\alpha_j \neq \alpha_i$. Except for such points, the solutions on \hat{C}_i are non-uniform. By the equivalence of (17)–(19) and (A 8), each continuum \hat{C}_i corresponds to a continuum C_i of solutions of (17)–(19). Now, the maximum principle implies that on each continuum, (u, w) must be positive and the values of the functions u and w are bounded away from 0 along C_i , at least on bounded α intervals. Therefore, if any continuum is unbounded, by Lemma A1, it must join ∞ in $\mathbf{R} \times X_1$ at $\alpha = \pm\infty$. If any continuum is bounded, then the second alternative given in the theorem follows by Theorem 1 in Dancer (1974). \square

References

- Adams, R. A., 1975, *Sobolev Spaces* (New York: Academic Press).
- Britton, N. F., 1989, Aggregation and the competitive exclusion principle. *Journal of Theoretical Biology*, **136**: 57–66.
- Britton, N. F., 1990, Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model. *SIAM Journal of Applied Mathematics*, **50**: 1663–1688.
- Canosa, J., 1973, On a nonlinear diffusion equation describing population growth. *IBM Journal of Research & Development*, **17**: 307–313.
- Casten, R. G., and Holland, C. J., 1978, Instability results for reaction-diffusion equations with Neumann boundary conditions. *Journal of Differential Equations*, **27**: 266–273.
- Cosner, C., 1988, Bifurcation from higher eigenvalues in nonlinear elliptic equations: continua that meet infinity. *Nonlinear Analysis, Theory, Methods & Applications*, **12**: 271–277.
- Crandall, M. G., and Rabinowitz, P. H., 1971, Bifurcation from simple eigenvalues. *Journal of Functional Analysis*, **8**: 321–340.
- Dancer, E. N., 1974, On the structure of solutions of non-linear eigenvalue problems. *Indiana University Mathematical Journal*, **23**: 1069–1076.
- Davidson, F. A., and Rynne, B. P., 2000, A priori bounds and global existence of solutions of the steady state Sel'kov model. *Proceedings of the Royal Society of Edinburgh*, **130**: 507–516.
- Defigueiredo, D. J., and Mitidieri, E., 1986, A maximum principle for an elliptic system and applications to semilinear problems. *SIAM Journal of Mathematical Analysis*, **17**: 836–846.
- Flierl, G., Grunbaum, D., Levin, S. A., and Olson, D., 1999, From individuals to aggregations: the interplay between behaviour and physics. *Journal of Theoretical Biology*, **196**: 397–454.
- Furter, J., and Grinfeld, M., 1989, Local vs. nonlocal interactions in population dynamics. *Journal of Mathematical Biology*, **27**: 65–80.
- Gilbarg, D., and Trudinger, N. S., 1983, *Elliptic Partial Differential Equations of Second Order* (Berlin: Springer).
- Gourley, S. A., and Britton, N. F., 1996, A predator prey reaction diffusion system with nonlocal effects. *Journal of Mathematical Biology*, **34**: 297–333.
- Grunbaum, D., and Okubo, A., 1994, Modeling social animal aggregations. *Frontiers of Theoretical Biology*, Lecture Notes in Biomathematics, Vol. 100, edited by S. A. Levin (Berlin: Springer).
- Hamilton, W. D., 1971, Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.

- Mackey, M. C., and Rudnicki, R., 1994, Global stability in a delayed partial differential equation describing cellular replication. *Journal of Mathematical Biology*, **33**: 89–109.
- Murray, J. D., 1989, *Mathematical Biology* (Berlin: Springer).
- Okubo, A., 1986, Dynamical aspects of animal grouping: swarms, schools, flocks and herds. *Advances in Biophysics*, **22**: 1–94.
- Oster, G. F., and Wilson, E. O., 1978, *Caste and Ecology in the Social Insects* (Princeton, NJ: Princeton University Press).
- Rabinowitz, P. H., 1971, Some global results for nonlinear eigenvalue problems. *Journal of Functional Analysis*, **7**: 487–513.
- Rey, A. D., and Mackey, M. C., 1995, Propagation of population pulses and fronts in a cell replication problem: non-locality and dependence on the initial function. *Physica D*, **86**: 373–395.
- Sherratt, J. A., Eagan, B. T., and Lewis, M. A., 1997, Oscillations and chaos behind predator-prey invasion: mathematical artifact or ecological reality? *Philosophical Transactions of the Royal Society of London Series B*, **352**: 21–38.