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Travelling fronts in a food-limited population model with time delay

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In this paper we study travelling front solutions of a certain food-limited population model incorporating time-delays and diffusion. Special attention is paid to the modelling of the time delays to incorporate associated non-local spatial terms which account for the drift of individuals to their present position from their possible positions at previous times. For a particular class of delay kernels, existence of travelling front solutions connecting the two spatially uniform steady states is established for sufficiently small delays. The approach is to reformulate the problem as an existence question for a heteroclinic connection in $\mathbb{R}^4$. The problem is then tackled using dynamical systems techniques, in particular, Fenichel's invariant manifold theory. For larger delays, numerical simulations reveal changes in the front's profile which develops a prominent hump.

1. Introduction

The differential equation

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\frac{K - N(t)}{K + \gamma N(t)}, \tag{1.1}$$

where r, K and γ are positive constants, was first proposed by Smith [12] as a mathematical model for populations of *Daphnia* (water flea) and a derivation of this equation is given in [10]. The equation has also been used in the study of the effects of environmental toxicants on populations [8]. The above type of equation is often referred to as a food-limited or resource-limited model.

The time-delay version of the model

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\frac{K - N(t-\tau)}{K + \gamma N(t-\tau)}, \quad \tau > 0, \tag{1.2}$$

has been studied by several investigators in recent years. Gopalsamy *et al.* [5] investigated the $N = K$ equilibrium, showing it to be globally stable if $r\tau e^{r\tau} < 1$, and they followed up their investigation in [6] by allowing the coefficients r and γ to become periodic functions of t (see also [9]). More recently, global stability in a slightly more general equation was studied by So and Yu [13].

There has been relatively little investigation of the consequences of allowing spatial dispersal in such food-limited models, but, in a recent paper, Feng and Lu [3] studied the following food-limited model without time delay,

$$\frac{\partial u(\boldsymbol{x},t)}{\partial t} - Au(\boldsymbol{x},t) = r(\boldsymbol{x})u(\boldsymbol{x},t)\frac{K(\boldsymbol{x}) - u(\boldsymbol{x},t)}{K(\boldsymbol{x}) + \gamma(\boldsymbol{x})u(\boldsymbol{x},t)} \tag{1.3}$$

and the time-delay model

$$\frac{\partial u(\boldsymbol{x},t)}{\partial t} - Au(\boldsymbol{x},t) = r(\boldsymbol{x})u(\boldsymbol{x},t)\frac{K(\boldsymbol{x}) - au(\boldsymbol{x},t) - bu(\boldsymbol{x},t-\tau)}{K(\boldsymbol{x}) + a\gamma(\boldsymbol{x})u(\boldsymbol{x},t) + b\gamma(\boldsymbol{x})u(\boldsymbol{x},t-\tau)}, \tag{1.4}$$

where $\boldsymbol{x} = (x_1, x_2, \ldots x_n) \in \Omega \subset \mathbb{R}^n$, with Ω bounded, and the operator A, given by

$$A = \sum_{i,j=1}^{n} \alpha_{ij}(\boldsymbol{x})\frac{\partial^2}{\partial x_i \partial x_j} + \sum_{j=1}^{n} \beta_j(\boldsymbol{x})\frac{\partial}{\partial x_j},$$

is uniformly strongly elliptic and has coefficient functions that are uniformly Hölder continuous in $\bar{\Omega}$. Of course, this includes the operator $A = \nabla^2$ (the Laplacian), usually seen in reaction-diffusion equations. Feng and Lu studied both of the above problems under a general boundary condition that includes both the zero-Dirichlet and zero-Neumann cases, establishing a global convergence result to a non-zero steady-state (which may be $\boldsymbol{x}$ dependent), under certain assumptions that, in the case of (1.4), included the condition that $a > b$. It would be interesting to investigate the global stability in the case $a = 0$.

Travelling front solutions have not yet been investigated in the literature for this particular type of population model, although there has recently been a great deal of interest in travelling front solutions of other scalar time-delay models. For example, travelling front solutions of the well-known Nicholson's blowflies equation were shown to exist by So and Zou [14] for discrete time delays and by Gourley [7] for a certain class of distributed delays. A general method for establishing existence of such solutions in reaction-diffusion equations (including coupled systems) with discrete delays was developed by Wu and Zou [15], although their approach does not apply to the particular type of delay (i.e. delays with associated spatial averaging) considered in the present paper. Furthermore, in this paper we also want to study distributed delays.

Since we wish to study wavefront solutions, we shall take the parameters r, K and γ to be constant. However, we wish the delay to be incorporated in a way that allows for associated spatial averaging due to the diffusion, and which also allows the discrete delay considered in other works to emerge as a particular case. Since the above-mentioned parameters will be constant in the present paper, and since we work on the infinite one-dimensional spatial domain $x \in (-\infty, \infty)$, certain non-dimensionalizations will be possible and we may study, without loss of generality, the equation

$$\frac{\partial u}{\partial t}(x,t) = u(x,t)\left(\frac{1 - (f * u)(x,t)}{1 + \gamma(f * u)(x,t)}\right) + \frac{\partial^2 u}{\partial x^2}(x,t), \tag{1.5}$$

where the parameter $\gamma > 0$ and the spatio-temporal convolution $f * u$ is defined by

$$(f * u)(x,t) = \int_{-\infty}^{t} \int_{-\infty}^{\infty} f(x-y, t-s)u(y,s)\,\mathrm{d}y\mathrm{d}s \tag{1.6}$$

and we make the usual normalization assumption on the kernel f, namely

$$\int_{0}^{\infty} \int_{-\infty}^{\infty} f(x,t)\,\mathrm{d}x\mathrm{d}t = 1,$$

so that the kernel does not affect the spatially uniform steady states, which in this model will be $u \equiv 0$ and $u \equiv 1$.

If the kernel f is taken to be

$$f(x,t) = \delta(x)\delta(t-\tau), \tag{1.7}$$

then (1.5) becomes

$$\frac{\partial u}{\partial t}(x,t) = u(x,t)\left(\frac{1-u(x,t-\tau)}{1+\gamma u(x,t-\tau)}\right) + \frac{\partial^2 u}{\partial x^2}(x,t), \tag{1.8}$$

which is the reaction-diffusion analogue of (1.2). However, it has become recognized in recent years that, in fact, one cannot simply incorporate diffusion into a delay equation (or, indeed, insert a delay of the kind in (1.8) into a reaction-diffusion equation) and still have a model that makes sense ecologically. It is an implicit assumption in any diffusion equation that individuals in the population are moving around randomly with no preferred direction. Simple linear diffusion implies that an individual occupying a particular point in space at a particular time could have been anywhere in the domain (even in an infinite domain) at a given time in the past, though with a higher probability of being somewhere nearby than somewhere further away. To allow for this, one can instead take f to be

$$f(x,t) = \frac{1}{\sqrt{4\pi t}}\mathrm{e}^{-x^2/(4t)}\delta(t-\tau), \tag{1.9}$$

which, when inserted into (1.5), gives

$$\frac{\partial u}{\partial t}(x,t) = u(x,t)\left(\frac{1-\int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-(x-y)^2/(4\tau)}u(y,t-\tau)\,\mathrm{d}y}{1+\gamma\int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-(x-y)^2/(4\tau)}u(y,t-\tau)\,\mathrm{d}y}\right) + \frac{\partial^2 u}{\partial x^2}(x,t). \tag{1.10}$$

One can now see that the movement of individuals to their present position from where they have been at previous times is accounted for by a spatial convolution with a kernel that spreads normally with a dependence on the delay. A derivation of this type of formulation, using probabilistic arguments, is given in [1].

The type of equation discussed in the previous paragraph, whether with spatial convolution or not, is called a *discrete-delay equation*. In the literature, one frequently also encounters *distributed-delay* equations. These are equations where the entire past history of the population density contributes to its current growth rate (but usually with a greater emphasis to recent densities), rather than just the density τ time units ago, as in (1.8) or (1.10). Of course, the formulation (1.5), (1.6) allows both discrete and distributed delays.

We are interested in travelling front solutions, both for distributed delays and for discrete delays. The study of travelling front solutions is a challenging problem in delay differential equations, since the ordinary differential equations (ODEs) that any travelling wave solutions must satisfy are usually posed in a high-dimensional (possibly infinite-dimensional) space and so one must find a way to attack this problem of the dimensionality of the phase space. In the present paper, we can make progress for the distributed-delay case by studying a particular class of kernels of the form,

$$f(x,t) = \frac{1}{\sqrt{4\pi t}} \mathrm{e}^{-x^2/(4t)} \frac{1}{\tau} \mathrm{e}^{-t/\tau}, \tag{1.11}$$

in which the parameter τ is representative of the delay, as can be seen by substituting the kernel into (1.5). For this class of kernels, the phase space of the system of travelling wave ODEs is four dimensional. A travelling wave front can be characterized as a heteroclinic connection in this phase space, and the existence of such a connection can then be established for sufficiently small τ (small delay) by using dynamical systems theory and, in particular, Fenichel's invariant manifold theory.

In this paper we shall also study the discrete-delay equation (1.10). In this case, the travelling wave equations are not posed in a finite-dimensional space and the aforementioned dynamical systems techniques are not applicable. Neither are any of the available methods for discrete-delay equations, such as those of [15], since they cannot handle the spatial convolution. In this case, we are not able to rigorously establish the existence of fronts, but can obtain some information via a formal asymptotic analysis for large values of the front's speed.

2. The distributed-delay case

In this section, equation (1.5) will be considered for the case when

$$f(x,t) = \frac{1}{\sqrt{4\pi t}} \mathrm{e}^{-x^2/(4t)} \frac{1}{\tau} \mathrm{e}^{-t/\tau}, \tag{2.1}$$

with τ, which measures the delay, being a positive parameter. This case is known in the literature as the weak generic delay case and is possibly the simplest case to which the methods of the present section will apply. For this kernel, if we define $v = f * u$, i.e.

$$v(x,t) = \int_{-\infty}^{t} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi(t-s)}} \mathrm{e}^{-(x-y)^2/(4(t-s))} \frac{1}{\tau} \mathrm{e}^{-(t-s)/\tau} u(y,s)\,\mathrm{d}y\mathrm{d}s, \tag{2.2}$$

it is straightforward to see that v satisfies

$$\frac{\partial v}{\partial t} = \frac{1}{\tau}(u-v) + \frac{\partial^2 v}{\partial x^2},$$

and thus it is possible to reformulate the integro-differential equation (1.5) as the system

$$u_t = u\left(\frac{1-v}{1+\gamma v}\right) + u_{xx}, \qquad v_t = \frac{1}{\tau}(u-v) + v_{xx}. \tag{2.3}$$

Of course, this is not a delay differential system. The delay in the original problem now plays its role through the parameter τ. This method of conversion of an integro-differential system into a coupled system of non-delay equations is called the linear chain technique and has been used by many investigators over the years, though only relatively recently for spatio-temporal delay kernels such as (2.1). It is impossible to carry out any such technique on an equation with discrete delay.

Our intention is to establish the existence of travelling wavefront solutions of (2.3) connecting the two uniform steady-states $(u, v) = (0, 0)$ and $(1, 1)$, for sufficiently small delay. We first need to establish the existence of such solutions when the delay is zero. Allowing τ to approach zero, it can be seen that $v \to u$ (this can be most easily seen by examining (2.2)). Thus, in this limit, we arrive at the non-delay version of the model,

$$u_t = u\left(\frac{1-u}{1+\gamma u}\right) + u_{xx}. \tag{2.4}$$

Converting to travelling wave form in the usual manner by setting $u(x, t) = U(z)$ with $z = x - ct$, $c > 0$, yields the following second-order ODE for $U(z)$,

$$U'' + cU' + U\left(\frac{1-U}{1+\gamma U}\right) = 0, \tag{2.5}$$

where primes denote differentiation with respect to z. We seek solutions such that $U(-\infty) = 1$ and $U(\infty) = 0$. Any such wavefront will move from left to right along the z-axis ($c > 0$). Since (2.5) is a second-order ODE, it is possible to establish existence of such fronts by using phase-plane techniques. The details are standard and will be omitted. We summarize the results as follows.

THEOREM 2.1. *For any $c \geqslant 2$, there exists a function $U(z)$ that satisfies (2.5), together with $U(-\infty) = 1$ and $U(\infty) = 0$, and which is strictly monotonically decreasing for all $z \in (-\infty, \infty)$.*

When the delay τ is non-zero, the governing equations are (2.3) and we now aim to show that travelling front solutions of these equations exist for small $\tau > 0$. Converting to travelling wave form, by setting

$$u(x, t) = U(z), \qquad v(x, t) = V(z), \qquad z = x - ct,$$

we have

$$\left.\begin{aligned} U'' + cU' + U\left(\frac{1-V}{1+\gamma V}\right) &= 0, \\ V'' + cV' + \frac{1}{\tau}(U - V) &= 0. \end{aligned}\right\} \tag{2.6}$$

This system is invariant under the transformation $(c, z) \to (-c, -z)$ and thus we may assume, without loss of generality, that $c > 0$. Solutions are sought satisfying $U(-\infty) = 1$, $U(\infty) = 0$, $V(-\infty) = 1$ and $V(\infty) = 0$. It is convenient to introduce the new variables

$$\tilde{U} = U' + \tfrac{1}{2}cU, \qquad \tilde{V} = V' + \tfrac{1}{2}cV,$$

in terms of which (2.6) can be reformulated as

$$\frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix} U \\ \tilde{U} \\ V \\ \tilde{V} \end{pmatrix} = \begin{pmatrix} \tilde{U} - \frac{1}{2}cU \\ \frac{1}{4}c^2U - \frac{1}{2}c\tilde{U} - U\left(\dfrac{1-V}{1+\gamma V}\right) \\ \tilde{V} - \frac{1}{2}cV \\ \frac{1}{4}c^2V - \frac{1}{2}c\tilde{V} + \dfrac{1}{\tau}(V-U) \end{pmatrix}. \tag{2.7}$$

This system has two equilibria, both of which are independent of τ, namely

$$(U, \tilde{U}, V, \tilde{V}) = (0,0,0,0) \quad \text{and} \quad (1, \tfrac{1}{2}c, 1, \tfrac{1}{2}c),$$

and we are seeking a heteroclinic connection between these. The plausibility of this can be seen by a simple dimension-counting argument. For system (2.7), the linearized or Jacobian matrix J is given by

$$J(U,\tilde{U},V,\tilde{V}) = \begin{pmatrix} -\frac{1}{2}c & 1 & 0 & 0 \\ \frac{1}{4}c^2 - \left(\dfrac{1-V}{1+\gamma V}\right) & -\frac{1}{2}c & \dfrac{(1+\gamma)U}{(1+\gamma V)^2} & 0 \\ 0 & 0 & -\frac{1}{2}c & 1 \\ -\dfrac{1}{\tau} & 0 & \frac{1}{4}c^2 + \dfrac{1}{\tau} & -\frac{1}{2}c \end{pmatrix}.$$

Thus

$$J(0,0,0,0) = \begin{pmatrix} -\frac{1}{2}c & 1 & 0 & 0 \\ \frac{1}{4}c^2 - 1 & -\frac{1}{2}c & 0 & 0 \\ 0 & 0 & -\frac{1}{2}c & 1 \\ -\dfrac{1}{\tau} & 0 & \frac{1}{4}c^2 + \dfrac{1}{\tau} & -\frac{1}{2}c \end{pmatrix},$$

whose eigenvalues λ satisfy

$$(\lambda^2 + c\lambda + 1)\left(\lambda^2 + c\lambda - \frac{1}{\tau}\right) = 0.$$

We are assuming here that $c \geqslant 2$, so that monotone travelling fronts exist for the unperturbed problem. Under this assumption, we therefore have three negative eigenvalues and one positive one and thus $\dim W^{\mathrm{s}}(0,0,0,0) = 3$, where W^{s} denotes the stable manifold.

We can also compute the eigenvalue equation for the other equilibrium state $(1, \frac{1}{2}c, 1, \frac{1}{2}c)$. Its eigenvalues λ satisfy

$$Q(\lambda;\tau) := \tau\lambda^4 + 2c\tau\lambda^3 + (\tau c^2 - 1)\lambda^2 - c\lambda + \frac{1}{1+\gamma} = 0$$

and we are interested in the situation when the delay τ is small. When it is zero, we are solving $Q(\lambda;0) = 0$, which has two real roots of opposite sign. When τ is positive but small, simple graphical arguments will show that the above two roots change little, but two new real roots appear, both large in magnitude but opposite in sign. Thus $\dim W^{\mathrm{u}}(1, \frac{1}{2}c, 1, \frac{1}{2}c) = 2$, where W^{u} denotes the unstable manifold.

The sum of the dimensions of the stable and unstable manifolds computed is five, while the phase space has dimension four. This lends plausibility to the idea that they might intersect along a one-dimensional curve in $\mathbb{R}^4$. Our aim now is to rigorously establish the existence of this curve, which is a heteroclinic connection between the two equilibrium points of (2.7) and corresponds to the travelling front we are seeking.

A further transformation of the variables is now necessary. With minimal risk of confusion of notation we shall switch to lowercase letters. We introduce the small parameter

$$\varepsilon = \sqrt{\tau}$$

and define

$$u = U, \qquad \tilde{u} = \tilde{U}, \qquad v = V, \qquad \tilde{v} = \varepsilon \tilde{V}.$$

We also move to subscript notation for the derivatives, since a new independent variable is going to be introduced shortly. With this notation, the system (2.7) becomes

$$\left.\begin{aligned} u_z &= \tilde{u} - \tfrac{1}{2}cu, \\ \tilde{u}_z &= \tfrac{1}{4}c^2 u - \tfrac{1}{2}c\tilde{u} - u\left(\frac{1-v}{1+\gamma v}\right), \\ \varepsilon v_z &= -\tfrac{1}{2}\varepsilon c v + \tilde{v}, \\ \varepsilon \tilde{v}_z &= v - u + \tfrac{1}{4}\varepsilon^2 c^2 v - \tfrac{1}{2}\varepsilon c \tilde{v}. \end{aligned}\right\} \tag{2.8}$$

It can easily be verified that when $\varepsilon = 0$, system (2.8) reduces to the second-order ODE for fronts in the non-delay case. System (2.8) is referred to as the slow system. Note that when $\varepsilon = 0$ it does not define a dynamical system in $\mathbb{R}^4$. This problem may be overcome by the transformation

$$z = \varepsilon \eta,$$

under which the system becomes

$$\left.\begin{aligned} u_\eta &= \varepsilon(\tilde{u} - \tfrac{1}{2}cu), \\ \tilde{u}_\eta &= \varepsilon\left(\tfrac{1}{4}c^2 u - \tfrac{1}{2}c\tilde{u} - u\left(\frac{1-v}{1+\gamma v}\right)\right), \\ v_\eta &= -\tfrac{1}{2}\varepsilon c v + \tilde{v}, \\ \tilde{v}_\eta &= v - u + \tfrac{1}{4}\varepsilon^2 c^2 v - \tfrac{1}{2}\varepsilon c \tilde{v}. \end{aligned}\right\} \tag{2.9}$$

This is called the fast system. The slow and fast systems are equivalent when $\varepsilon > 0$.

In the slow system (2.8), note that if ε is set to zero, then the flow of that system is confined to the set

$$M_0 := \{(u, \tilde{u}, v, \tilde{v}) \in \mathbb{R}^4 : \tilde{v} = 0 \text{ and } v = u\},$$

which is a two-dimensional invariant manifold for (2.8), with $\varepsilon = 0$. What we claim is that M_0 is a normally hyperbolic manifold in the sense of Fenichel [4] and that the hypotheses of Fenichel's invariant manifold theorem are satisfied. For $\varepsilon > 0$

sufficiently small, this theorem then furnishes us with a manifold M_ε, which is close to M_0 and which is invariant for the flow when $\varepsilon > 0$. The restriction of (2.8) to this manifold M_ε then yields a two-dimensional system of ODEs, which we shall then analyse using a perturbation argument, together with Fredholm orthogonality theory, to establish the existence of the heteroclinic connection we are seeking.

Verifying normal hyperbolicity of M_0 involves checking that the linearization of the fast system (2.9), restricted to M_0, has precisely $\dim M_0$ eigenvalues on the imaginary axis, with the remainder of the spectrum being hyperbolic. The linearization of (2.9) restricted to M_0 is given by the matrix

$$\begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ -1 & 0 & 1 & 0 \end{pmatrix},$$

the eigenvalues of which are 0, 0, 1, −1. Thus we have the correct number of eigenvalues on the imaginary axis and normal hyperbolicity of M_0 is verified.

By Fenichel's theory, we know that a two-dimensional invariant manifold M_ε exists with the properties described above. It can be written in the form

$$M_\varepsilon := \{(u, \tilde{u}, v, \tilde{v}) \in \mathbb{R}^4 : \tilde{v} = g(u, \tilde{u}; \varepsilon) \text{ and } v = u + h(u, \tilde{u}; \varepsilon)\},$$

where the functions g and h, which we must determine, satisfy

$$g(u, \tilde{u}; 0) = h(u, \tilde{u}; 0) = 0. \tag{2.10}$$

To determine these two functions we use the fact that M_ε is an invariant manifold for the flow of (2.8). Substitution yields that g and h satisfy

$$\varepsilon\left[\left(1 + \frac{\partial h}{\partial u}\right)(\tilde{u} - \tfrac{1}{2}cu) + \frac{\partial h}{\partial \tilde{u}}\left(\tfrac{1}{4}c^2 u - \tfrac{1}{2}c\tilde{u} - u\left(\frac{1 - u - h}{1 + \gamma u + \gamma h}\right)\right)\right] = -\tfrac{1}{2}\varepsilon c(u + h) + g$$

and

$$\varepsilon\left[\frac{\partial g}{\partial u}(\tilde{u} - \tfrac{1}{2}cu) + \frac{\partial g}{\partial \tilde{u}}\left(\tfrac{1}{4}c^2 u - \tfrac{1}{2}c\tilde{u} - u\left(\frac{1 - u - h}{1 + \gamma u + \gamma h}\right)\right)\right] = h + \tfrac{1}{4}\varepsilon^2 c^2(u + h) - \tfrac{1}{2}\varepsilon c g.$$

Exploiting the smallness of ε, we may attempt solutions of these in the form of regular perturbation series in ε. In view of (2.10), such series may be started at the ε term, so we try

$$g(u, \tilde{u}; \varepsilon) = \varepsilon g_1(u, \tilde{u}) + \varepsilon^2 g_2(u, \tilde{u}) + \cdots,$$
$$h(u, \tilde{u}; \varepsilon) = \varepsilon h_1(u, \tilde{u}) + \varepsilon^2 h_2(u, \tilde{u}) + \cdots.$$

Substituting and comparing coefficients of ε and ε^2 gives us

$$\left.\begin{aligned} g_1(u, \tilde{u}) &= \tilde{u}, & g_2(u, \tilde{u}) &= 0, \\ h_1(u, \tilde{u}) &= 0, & h_2(u, \tilde{u}) &= -u\left(\frac{1 - u}{1 + \gamma u}\right). \end{aligned}\right\} \tag{2.11}$$

Although g and h have both been calculated, it is really only h that we need and it is given by

$$h(u,\tilde{u};\varepsilon) = -\varepsilon^2 u\left(\frac{1-u}{1+\gamma u}\right) + O(\varepsilon^3) \tag{2.12}$$

$$=: -\varepsilon^2 H(u) + O(\varepsilon^3). \tag{2.13}$$

The slow system, restricted to M_ε, is then given by

$$\left.\begin{aligned} u_z &= \tilde{u} - \tfrac{1}{2}cu, \\ \tilde{u}_z &= \tfrac{1}{4}c^2 u - \tfrac{1}{2}c\tilde{u} - u\left(\frac{1-u-h(u,\tilde{u};\varepsilon)}{1+\gamma u+\gamma h(u,\tilde{u};\varepsilon)}\right), \end{aligned}\right\} \tag{2.14}$$

where h is given by (2.12).

It is easily verified that when $\varepsilon = 0$, system (2.14) reduces to the corresponding ODE for travelling fronts of the non-delay problem (equation (2.5)) and also that for any $\varepsilon > 0$, system (2.14) has equilibrium points $(u,\tilde{u}) = (0,0)$ and $(1,\tfrac{1}{2}c)$ and we wish now to establish the existence of a heteroclinic connection between these two critical points. We know that such a connection exists when $\varepsilon = 0$ (theorem 2.1) and we shall seek a solution of (2.14) that is a perturbation of this.

Let $(u_0,\tilde{u}_0)$ be the solution of (2.14) when $\varepsilon = 0$. To solve the system for $\varepsilon > 0$ small, we try

$$u = u_0 + \varepsilon^2\phi + \cdots, \qquad \tilde{u} = \tilde{u}_0 + \varepsilon^2\psi + \cdots.$$

Substituting, we find that, to lowest order, the differential equation system determining ϕ and ψ is

$$\frac{\mathrm{d}}{\mathrm{d}z}\begin{pmatrix}\phi\\ \psi\end{pmatrix} + \begin{pmatrix} \tfrac{1}{2}c & -1 \\ \dfrac{1-2u_0-\gamma u_0^2}{(1+\gamma u_0)^2} - \tfrac{1}{4}c^2 & \tfrac{1}{2}c \end{pmatrix}\begin{pmatrix}\phi\\ \psi\end{pmatrix} = \begin{pmatrix} 0 \\ -\dfrac{(1+\gamma)u_0 H(u_0)}{(1+\gamma u_0)^2}\end{pmatrix}, \tag{2.15}$$

and we seek to prove that this system has a solution satisfying $\phi(\pm\infty) = 0$ and $\psi(\pm\infty) = 0$.

Working in the space L^2 of square integrable functions, with inner product

$$\int_{-\infty}^{\infty} (\boldsymbol{x}(z), \boldsymbol{y}(z))\,\mathrm{d}z,$$

$(\cdot,\cdot)$ being the Euclidean inner product on $\mathbb{R}^2$, Fredholm theory states that (2.15) will have a solution if and only if

$$\int_{-\infty}^{\infty}\left(\boldsymbol{x}(z), \begin{pmatrix} 0 \\ -\dfrac{(1+\gamma)u_0(z)H(u_0(z))}{(1+\gamma u_0(z))^2}\end{pmatrix}\right)\mathrm{d}z = 0$$

for all functions $\boldsymbol{x}(z)$ in the kernel of the adjoint of the operator $\mathcal{L}$ defined by the left-hand side of (2.15). It is easy to verify that the adjoint operator $\mathcal{L}^*$ is given by

$$\mathcal{L}^* = -\frac{\mathrm{d}}{\mathrm{d}z} + \begin{pmatrix} \tfrac{1}{2}c & -\tfrac{1}{4}c^2 + \dfrac{1-2u_0-\gamma u_0^2}{(1+\gamma u_0)^2} \\ -1 & \tfrac{1}{2}c \end{pmatrix},$$

and thus to compute $\ker \mathcal{L}^*$ we have to find all $\boldsymbol{x}(z)$ satisfying

$$\frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}z} = \begin{pmatrix} \frac{1}{2}c & -\frac{1}{4}c^2 + \dfrac{1-2u_0(z)-\gamma u_0^2(z)}{(1+\gamma u_0(z))^2} \\ -1 & \frac{1}{2}c \end{pmatrix} \boldsymbol{x}, \tag{2.16}$$

the general solution of which will be difficult to find because the matrix is, of course, non-constant. However, we are only looking for solutions satisfying $\boldsymbol{x}(\pm\infty) = \mathbf{0}$ and, in fact, the only such solution is the zero solution. Recall that $u_0(z)$ is the solution of the unperturbed problem and although we have no explicit expression for it, we do know that it tends to zero as $z \to \infty$. Letting $z \to \infty$ in (2.16), the matrix becomes a constant matrix, with eigenvalues λ satisfying

$$\lambda^2 - c\lambda + 1 = 0$$

and, since $c \geqslant 2$, the eigenvalues are therefore both real and positive. So, as $z \to \infty$, any solution of (2.16) other than the zero solution must be growing exponentially for large z. So the only solution satisfying $\boldsymbol{x}(\pm\infty) = \mathbf{0}$ is the zero solution. This means, of course, that the Fredholm orthogonality condition trivially holds and so solutions of (2.15) exist. This completes the proof that a heteroclinic connection exists between the two equilibrium points $(0, 0, 0, 0)$ and $(1, \frac{1}{2}c, 1, \frac{1}{2}c)$ of (2.7) and we may summarize our findings in the following theorem.

THEOREM 2.2. *For any fixed $c \geqslant 2$, equation (1.5), for the case when the kernel f is given by (2.1), possesses a travelling front solution $u(x, t) = U(x - ct)$ satisfying $U(-\infty) = 1$ and $U(\infty) = 0$, provided the delay τ is sufficiently small.*

Finally, we remark that it is actually very unusual for a Fredholm orthogonality condition to hold trivially by virtue of the kernel of the adjoint operator consisting only of the zero vector, as is the case in this application. Indeed, $\ker \mathcal{L}$ can be shown to contain more than just the zero vector. The operator $\mathcal{L}$ is, in fact, an operator of non-zero index. Its index, given by

$$\dim \ker \mathcal{L} - \dim \ker \mathcal{L}^*$$

can be shown to be 1.

The question remains as to whether the fronts continue to persist when the delay is not so small, and what they look like in this case. We can gain some information by a numerical simulation of the system (2.3), with a diffusivity d scaled in to give greater control of the propagation speed and to improve numerical stability. Thus we simulate

$$u_t = u\left(\frac{1-v}{1+\gamma v}\right) + \mathrm{d}u_{xx}, \qquad v_t = \frac{1}{\tau}(u - v) + \mathrm{d}v_{xx} \tag{2.17}$$

on a large spatial domain $x \in [0, 2000]$, with homogeneous Neumann boundary conditions and initial conditions appropriate for the study of wavefront problems, which we take to be

$$u(x, 0) = v(x, 0) = 1 - H(x - 200),$$

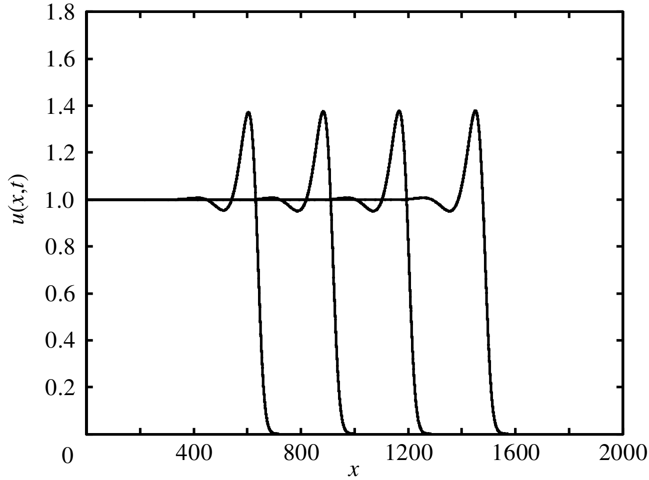

Figure 1. Numerical simulation of (2.17) on the domain $x \in [0, 2000]$ with homogeneous Neumann boundary conditions and initial data as described in the text. Parameter values were $d = 50$, $\gamma = 0.5$ and $\tau = 2$.

$H(x)$ being Heaviside's function. For small values of the delay τ, we observed rapid evolution to a monotone wavefront solution looking very similar to the corresponding solution to the non-delay problem. However, as the delay was increased, monotonicity was eventually lost and the front then developed quite a prominent hump, the height of which increased with the delay (see figure 1).

3. The discrete-delay case

In the discrete-delay case, i.e. the delayed term involves evaluation of the density u exactly τ time units ago, the original equation (1.5) becomes

$$\frac{\partial u}{\partial t}(x,t) = u(x,t)\left(\frac{1 - \int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-(x-y)^2/(4\tau)}u(y,t-\tau)\,\mathrm{d}y}{1 + \gamma\int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-(x-y)^2/(4\tau)}u(y,t-\tau)\,\mathrm{d}y}\right) + \frac{\partial^2 u}{\partial x^2}(x,t). \tag{3.1}$$

As in the distributed-delay case, this equation involves a convolution in space to allow for the movement of individuals to their present position from their possible positions at previous times.

Equation (3.1) is much more difficult to study than the distributed-delay equation with exponentially decaying kernel that was the focus of attention in the previous section. This is because there is no way to recast (3.1) as a non-delay equation. The travelling wave equations are infinite dimensional and thus the search for travelling front solutions is a much deeper and more difficult problem. There are, however, some results on existence of such solutions for discrete-delay equations without associated spatial non-localness (i.e. all terms in the equation are evaluated at the same point in space) (see, for example, [15]). The methods are based on upper and lower solutions, require a certain quasimonotonicity assumption and are very different from the methods described in the previous section.

We can, however, employ some simple asymptotics to try to resolve some questions on the monotonicity or otherwise of travelling front solutions to (3.1) and how this depends on the delay τ. Seeking travelling wave solutions for (3.1), by setting $u(x,t) = U(z) = U(x-ct)$, we find that the travelling wave equations can be cast into the form

$$U''(z) + cU'(z) + U(z)\left(\frac{1 - \int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-w^2/(4\tau)}U(z-w+c\tau)\,\mathrm{d}w}{1 + \gamma\int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-w^2/(4\tau)}U(z-w+c\tau)\,\mathrm{d}w}\right) = 0, \tag{3.2}$$

and we are interested in rightward moving waves ($c > 0$); thus the boundary conditions are $U(-\infty) = 1$ and $U(\infty) = 0$. A great deal of information on the monotonicity or otherwise of such fronts for large values of c can be gained by using the method developed by Canosa [2] for the Fisher equation. Although the method is an asymptotic analysis as the front speed approaches infinity, it is known that for Fisher's equation the method generates a solution that is accurate to within a few percent of the true solution, even at the minimum wave speed. The method has also been applied to other reaction-diffusion equations, including coupled systems, with very good results [11].

Linearizing (3.2) far ahead of the front, where $U \to 0$, gives

$$U''(z) + cU'(z) + U(z) = 0,$$

and thus we assume, as in Fisher's equation, that $c \geqslant 2$ to ensure we are studying ecologically realistic fronts that are positive for all values of z. Following Canosa's [2] approach, we introduce the small parameter

$$\varepsilon = 1/c^2$$

and seek a solution in the form

$$U(z) = g(\zeta), \qquad \zeta = \sqrt{\varepsilon}z.$$

Equation (3.2) then becomes

$$\varepsilon g''(\zeta)+g'(\zeta)+g(\zeta)\left(\frac{1 - \int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-w^2/(4\tau)}g(\zeta-\sqrt{\varepsilon}w+\tau)\,\mathrm{d}w}{1 + \gamma\int_{-\infty}^{\infty}(1/\sqrt{4\pi\tau})\mathrm{e}^{-w^2/(4\tau)}g(\zeta-\sqrt{\varepsilon}w+\tau)\,\mathrm{d}w}\right) = 0 \tag{3.3}$$

and the integral term in (3.3) can be expanded in a Taylor series to give

$$g(\zeta+\tau)\int_{-\infty}^{\infty}\frac{1}{\sqrt{4\pi\tau}}\mathrm{e}^{-w^2/(4\tau)}\,\mathrm{d}w + \tfrac{1}{2}\varepsilon g''(\zeta+\tau)\int_{-\infty}^{\infty}\frac{w^2}{\sqrt{4\pi\tau}}\mathrm{e}^{-w^2/(4\tau)}\,\mathrm{d}w + \cdots,$$

which equals

$$g(\zeta+\tau) + \varepsilon\tau g''(\zeta+\tau).$$

Thus equation (3.3) can be approximated by

$$\varepsilon g''(\zeta) + g'(\zeta) + g(\zeta)\left(\frac{1 - g(\zeta+\tau) - \varepsilon\tau g''(\zeta+\tau)}{1 + \gamma g(\zeta+\tau) + \gamma\varepsilon\tau g''(\zeta+\tau)}\right) = 0,$$

the boundary conditions for which are $g(-\infty) = 1$ and $g(\infty) = 0$. In order to fix the position of the front in the moving frame, we may also take $g(0) = \frac{1}{2}$ without loss of generality. Following the Canosa approach, we attempt a regular perturbation series solution in the form

$$g(\zeta) = g_0(\zeta) + \varepsilon g_1(\zeta) + \cdots$$

and assume that the leading-order term g_0 is sufficient to give a good qualitative description of the solution. The differential equation for g_0 is

$$g_0'(\zeta) + g_0(\zeta)\left(\frac{1 - g_0(\zeta + \tau)}{1 + \gamma g_0(\zeta + \tau)}\right) = 0, \qquad g_0(0) = \tfrac{1}{2}. \tag{3.4}$$

In delay equations, it is quite usual for the equation determining a wavefront to be an equation of advanced type, as in this case. With a view to examining the potential onset of a hump in the travelling front profile as τ is increased (as happened in the distributed-delay model of the previous section), we now ask the question of whether the solution of (3.4) is monotone or not. Of course, it is monotone when $\tau = 0$, since it is then a one-dimensional ODE. Monotonicity is not immediately lost for positive τ; the delay has to be above a certain critical value. On reversing the independent variable ζ, equation (3.4) becomes the non-dimensionalized version of the delay equation considered in [5], which is (1.2) of this paper. In [5], conditions are given that are both necessary and sufficient for monotonicity. Thus, drawing analogy with the approach of [5], we can state that the condition for the solution of (3.4) to be monotone is that the delay τ should satisfy

$$\tau \leqslant \tau_{\mathrm{c}} := \frac{1 + \gamma}{\mathrm{e}}. \tag{3.5}$$

In our model, this criterion would, of course, be an approximate one. Nonetheless, the indication is that a non-monotone travelling front with a hump, as in the distributed-delay case, is to be expected for values of τ very much bigger than τ_{c}. In fact, it can be shown that if τ is further increased, there is another critical value at which the $u = 1$ steady-state of (3.1) loses stability and thus stable permanent form travelling fronts are no longer to be expected. This does not happen in the distributed-delay case of the previous section.

4. Conclusion

In this paper we have studied travelling front solutions of Smith's well-known 'food-limited' population model with time delay. We considered both discrete and distributed delays and in both cases we have incorporated spatial averaging, which is necessary to properly account for the consequences of the motion of individuals in a delay model. In the distributed-delay case, for a particular class of kernels, we have proved existence of travelling front solutions for sufficiently small delays by using linear chain techniques to recast the travelling wave equations as a finite-dimensional system of ODEs to which geometric singular perturbation theory applies. The travelling fronts, which are modelled as heterclinic orbits, are shown to exist by employing Fenichel's invariant manifold theory, together with a perturbation method and the Fredholm alternative. The approach also shows that for small delays the fronts are qualitatively similar to those of the non-delay equation.

It is important to note that at no stage did we require an explicit expression for the travelling front solution of the unperturbed problem (i.e. the non-delay equation). We only needed to know that such a solution exists and its general qualitative properties. This is important because it indicates that our approach is probably quite widely applicable to studying travelling fronts in delay equations, and is almost certainly also applicable to the study of fronts in time-delayed predator–prey and competition equations.

Furthermore, although we have confined attention to a very specific nonlinear reaction term, our approach will generalize to the equation

$$\frac{\partial u}{\partial t}(x,t) = u(x,t)G((f*u)(x,t)) + \frac{\partial^2 u}{\partial x^2}(x,t), \tag{4.1}$$

with $f*u$ still given by (1.6) and f some kernel such that the linear chain techniques will be available. We have concentrated on the case when G in (4.1) is taken to be $G(v) = (1-v)/(1+\gamma v)$, but in fact all that is really required is that G have one positive zero. Our approach has also been applied to the Nicholson's blowflies equation [7], which has a very different nonlinearity (not even containing a factor of $u(x,t)$), although in that application a purely temporal delay kernel was used rather than the spatio-temporal delay considered here. In fact, the applicability or otherwise of our approach depends rather more on the delay kernel f than on the function G in (4.1). Thus it remains to consider whether the method can be extended to other kernels. Certainly if the kernel f is replaced by

$$f(x,t) = \frac{1}{\sqrt{4\pi t}} \mathrm{e}^{-x^2/(4t)} \frac{t}{\tau^2} \mathrm{e}^{-t/\tau},$$

known in the literature as the strong generic delay case, linear chain techniques are still applicable, but the system of travelling wave equations is six dimensional. Our methods can still be applied in principle, but it will be much more difficult in practice.

For larger delays, numerical study of the distributed-delay problem and some simple asymptotics in the discrete-delay case both indicated the formation of a prominent hump in the front profile the height of which grows with the delay.

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