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Persistence of travelling waves in a generalized Fisher equation

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ABSTRACT

Travelling waves of the Fisher equation with arbitrary power of nonlinearity are studied in the presence of long-range diffusion. Using analogy between travelling waves and heteroclinic solutions of corresponding ODEs, we employ the geometric singular perturbation theory to prove the persistence of these waves when the influence of long-range effects is small. When the long-range diffusion coefficient becomes larger, the behaviour of travelling waves can only be studied numerically. In this case we find that starting with some values, solutions of the model lose monotonicity and become oscillatory.

1. Introduction

One of the cornerstones of modern mathematical biology is the Fisher equation. Being originally derived as a model for the propagation of a favoured gene in a population [10,15], this equation has since served as a basic model for numerous physical and biological phenomena characterized by local interactions, linear growth and competition [18]. In its simplest form, the Fisher equation for a scalar function $u(x,t)$ is given by

$$u_t = u_{xx} + u(1-u). \tag{1}$$

In order to account for more involved competition, this equation can be generalized by allowing a higher degree of nonlinearity:

$$u_t = u_{xx} + pu\left(1-u^r\right)\left(q+u^r\right). \tag{2}$$

Using a combination of nonlinear transformations and symbolic computations, an analytic solution of the latter equation has been recently found [6]. This solution has the form

$$u(x,t) = \left\{\frac{1}{2} - \frac{1}{2}\tanh\left[\frac{r}{2}\sqrt{\frac{p}{r+1}}\left(x-(1+q+qr)\sqrt{\frac{p}{r+1}}t\right)\right]\right\}^{\frac{1}{r}}, \tag{3}$$

and represents a wave travelling with a speed

$$c = (1+q+qr)\sqrt{\frac{p}{r+1}}, \tag{4}$$

in the positive x direction. The solution (3) is shown in Fig. 1 for several values of the power of nonlinearity q. When $p=q=1$ and $r=1/2$, Eq. (2) reduces to the Fisher equation (1), and the solution (3) becomes the classical closed form solution of the Fisher equation with the wavespeed $c=5/\sqrt{6}$, found by Ablowitz and Zeppetella [1].

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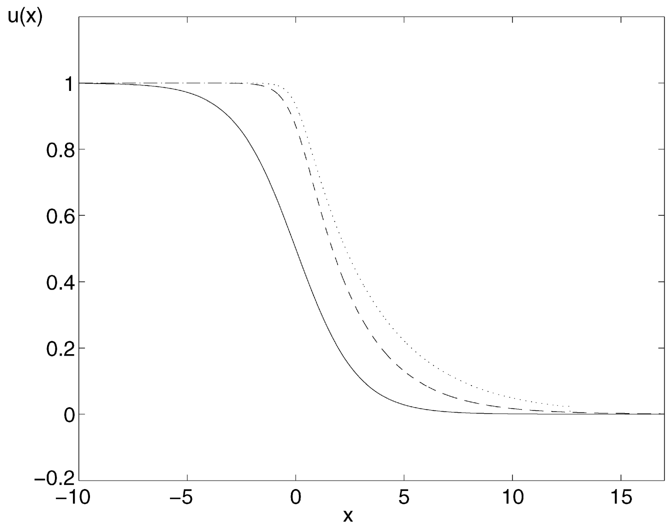

Fig. 1. Shape of solitary wave solution (3). Parameters are $p = q = 1$ and $r = 1$ (solid), $r = 5$ (dashed) and $r = 10$ (dotted).

In the context of population dynamics several other generalizations of the Fisher equation have been investigated. These include non-locality, spatial averaging of nonlinearity, temporal delays and a long-range diffusion [4,7,11,12]. Recently, effects of transport memory for Eq. (1) have been included to describe the coherent motion of individuals between collisions [2,17]. The influence of these effects leads to a marked difference in the dynamics from that of the original equation, such as the possibility of "inverse fronts", in which the state $u = 0$ invades the state $u = 1$.

In this Letter we are interested in the travelling wave solutions of the generalized Fisher equation with fourth-order derivative

$$u_t = -Du_{xxxx} + u_{xx} + pu\left(1 - u^r\right)\left(q + u^r\right), \tag{5}$$

for a scalar function $u = u(x,t)$, with $p, q > 0$ and $r \geqslant 1$. When $D = 0$, this equation describes the situation of a local diffusion and a generalized competition. At the same time, when $D > 0$, this equation includes the effects of a long-range diffusion as introduced by Cohen and Murray in their study of pattern formation in a single species population [7]. These authors demonstrated how fourth-order and higher derivatives can appear in approximations of equations including "non-local" terms.

Several particular cases of Eq. (5) have been studied for different values of parameters. When $p = q = r = 1$, Eq. (5) becomes an extended Fisher–Kolmogorov equation, which has been used to model phase transitions and other bistable phenomena [8]. It has been shown that this equation can exhibit a range of periodic and chaotic spatial patterns [19]. For a slightly different form of a cubic nonlinearity travelling wave solutions have also been studied by Akveld and Hulshof [3].

The aim of this Letter is to investigate, within the context of our model, what happens to travelling wave solutions (3) of Eq. (2) when the long-range effects are included. In order to address this problem we use dynamical systems methods. Namely, the equation for travelling wave solutions can be written as a dynamical system, and for D small it can be analysed with the help of a geometric singular perturbation theory [14]. Using this theory, we will show that the travelling waves (3) persist under small fourth-order perturbation in Eq. (5). Similar techniques have been used to show the persistence of travelling waves in a delayed Fisher equation [4], a fourth-order diffusion system with a slightly different nonlinearity [3], as well as an extended Burgers–Huxley model [16].

When the effects of a long-range diffusion become significant, analytical approach fails to provide the persistence of travelling waves. Therefore, we will resort to numerical solution of an appropriate boundary value problem to establish the existence of such solutions.

2. Dynamical systems reformulation

We begin our analysis by looking for the travelling wave solutions of Eq. (5) of the form

$$u(x,t) = U(z), \quad \text{where } z = x - ct.$$

Substituting this into Eq. (5) gives

$$-DU'''' + U'' + cU' + pU\left(1 - U^r\right)\left(q + U^r\right) = 0, \tag{6}$$

where prime denotes differentiation with respect to z. After introducing the quantities $U' = v$, $v' = y$, $y' = w$ one can recast (6) as

$$Y_z = F(Y), \quad F(Y) = \begin{pmatrix} v \\ y \\ w \\ \frac{1}{D}[y + cv + pU(1 - U^r)(q + U^r)] \end{pmatrix}, \quad Y = \begin{pmatrix} U \\ v \\ y \\ w \end{pmatrix}. \tag{7}$$

The steady states for this system are

$$Y^0 = (0,0,0,0)^T \quad \text{and} \quad Y^1 = (1,0,0,0)^T,$$

and we have discarded the steady states with negative values of the variables as biologically irrelevant. Linearization matrix near the steady state Y^0 has the form

$$A_0 = DF\big(Y^0\big) = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ pq/D & c/D & 1/D & 0 \end{pmatrix},$$

with the corresponding characteristic equation

$$D\lambda^4 - \lambda^2 - c\lambda - pq = 0. \tag{8}$$

Similarly, the linearization near Y^1 has the form

$$A_1 = DF\big(Y^1\big) = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ -pr(q+1)/D & c/D & 1/D & 0 \end{pmatrix},$$

with the characteristic equation

$$D\lambda^4 - \lambda^2 - c\lambda + pr(q+1) = 0. \tag{9}$$

We have the following result regarding the linearization of (7).

Proposition 1. *Let $c > 0$. Then the stable manifold of the steady state Y^0 in system (7) has dimension three, and the unstable manifold at Y^1 has dimension two.*

Proof. Spectrum of linearization near the steady state Y^0 is determined by the roots of the characteristic equation (8), which can be written as $\Delta(\lambda) = 0$ with

$$\Delta(\lambda) = D\lambda^4 - \lambda^2 - c\lambda - pq.$$

We need to show that $\Delta(\lambda)$ has three roots in the left half of the complex plane. Since Δ is analytic, the number of roots in the left half complex plane is

$$\frac{1}{2\pi i}\lim_{R\to\infty}\int_{\gamma_R}\frac{\Delta'(\lambda)}{\Delta(\lambda)}d\lambda, \tag{10}$$

where the contour γ_R is the boundary, traversed anticlockwise, of the semicircle of radius R, centred at the origin, contained in $\operatorname{Re}\lambda \leqslant 0$. This integral equals

$$2 + \frac{1}{\pi}\big[\arg\Delta(iR)\big]_{R=0}^{R=\infty}.$$

The quantity in brackets denotes the total change in the argument of $\Delta(iR)$ as R goes from zero to infinity, and hence we have to compute the number of times the image $\Delta(iR)$, $R > 0$, winds around the origin. Now, when $R = 0$, the image of $\Delta(iR)$ starts on the negative real axis, and for R sufficiently large it ends up in the fourth quadrant with asymptotic behaviour

$$\operatorname{Re}\Delta(iR) \sim DR^4, \quad \operatorname{Im}\Delta(iR) \sim -cR \quad \text{as } R \to \infty.$$

Therefore,

$$\big[\arg\Delta(iR)\big]_{R=0}^{R=\infty} = n\pi$$

for some odd integer n. However, since $\operatorname{Im}\Delta(iR) = -cR < 0$ for all $R > 0$, thus $n = 1$, and consequently, the number of the roots of characteristic roots in the left complex half plane is three.

Similarly, for Y^1 we have to find the winding number of the image of the function $\Delta(iR)$, $R > 0$ around the origin, where now

$$\Delta(\lambda) = D\lambda^4 - \lambda^2 - c\lambda + pr(q+1).$$

The same argument as before shows that this number is equal to

$$2 - \frac{1}{\pi}\big[\arg\Delta(iR)\big]_{R=0}^{R=\infty}.$$

It is easy to see that since the imaginary part $\operatorname{Im}\Delta(iR)$ never crosses zero, therefore $[\arg\Delta(iR)]_{R=0}^{R=\infty} = 0$, and this concludes the proof. □

Proposition 1 yields that the sum of the dimensions of the stable manifold $W^s(Y^0)$ and the unstable manifold $W^u(Y^1)$ is five, while the phase space has the dimension four. Hence, *generically* these two manifolds intersect in $\mathbb{R}^4$ along one-dimensional curve, which is our travelling wave solution. To prove rigourously the existence this intersection a further analysis is required.

3. Persistence of travelling waves for small long-range diffusion

In this section we consider the case of D small. Let $D=\varepsilon^2 \ll 1$. Introducing the coordinates $v=U'$, $y=v'$ and a stretched variable $w=\varepsilon y'$, the system (5) can be rewritten as

$$U_z=v, \qquad v_z=y, \qquad \varepsilon y_z=w, \qquad \varepsilon w_z=y+cv+pU\big(1-U^r\big)\big(q+U^r\big). \tag{11}$$

Now, with $\zeta=z/\varepsilon$, the dual "fast system" associated with (11) has the form

$$U_\zeta=\varepsilon v, \qquad v_\zeta=\varepsilon y, \qquad y_\zeta=w, \qquad w_\zeta=y+cv+pU\big(1-U^r\big)\big(q+U^r\big). \tag{12}$$

If in (11) ε is set to zero, then U and v are governed by

$$\frac{d^2U}{dz^2}+c\frac{dU}{dz}+pU\big(1-U^r\big)\big(q+U^r\big)=0, \qquad v=\frac{dU}{dz},$$

while y and w must lie on the set

$$M_0:=\big\{(U,v,y,w)\in\mathbb{R}^4\colon\ w=0 \text{ and } y+cv+pU\big(1-U^r\big)\big(q+U^r\big)=0\big\},$$

which is a two-dimensional submanifold of $\mathbb{R}^4$.

By definition [9], the manifold M_0 is said to be normally hyperbolic if the linearization of the *fast system*, restricted to M_0, has exactly $\dim M_0$ eigenvalues on the imaginary axis, with the remainder of the system hyperbolic. The linearization of the fast system (12), restricted to M_0 (i.e. $\varepsilon=0$), has the matrix

$$\mathcal{A}=\begin{pmatrix} 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 1\\ s & c & 1 & 0\end{pmatrix}, \tag{13}$$

with

$$s=pq+p(r+1)(1-q)U^r-p(2r+1)U^{2r}.$$

This matrix $\mathcal{A}$ has the eigenvalues $0,0,-1,1$, and thus we conclude that M_0 is normally hyperbolic. Therefore, by Fenichel's invariant manifold theory [9], for ε sufficiently small there exists a two-dimensional sub-manifold M_ε of $\mathbb{R}^4$ which is within the distance ε of M_0 and which is invariant for the flow (11).

Next, we shall determine the dynamics on M_ε. One can write

$$M_\varepsilon=\big\{(U,v,y,w)\in\mathbb{R}^4\colon\ w=g(U,v,\varepsilon),\ \ y=h(U,v,\varepsilon)-cv-pU\big(1-U^r\big)\big(q+U^r\big)\big\}, \tag{14}$$

where the functions g and h yet to be determined satisfy

$$g(U,v,0)=h(U,v,0)=0.$$

Substituting the representation of M_ε from (14) into (11), one obtains that $g(U,v,\varepsilon)$ and $h(U,v,\varepsilon)$ satisfy the coupled system of equations

$$g=\varepsilon\bigg[v\frac{\partial h}{\partial U}+\frac{\partial h}{\partial v}\big(h-cv-pU\big(1-U^r\big)\big(q+U^r\big)\big)-ch+c^2v+cpU\big(1-U^r\big)\big(q+U^r\big)-pqv-p(1-q)(r+1)U^rv+p(2r+1)U^{2r}v\bigg],$$

$$h=\varepsilon\bigg[v\frac{\partial g}{\partial U}+\frac{\partial g}{\partial v}\big(h-cv-pU\big(1-U^r\big)\big(q+U^r\big)\big)\bigg].$$

Now, we expand g and h in Taylor series in ε

$$g(U,v,\varepsilon)=g(U,v,0)+\varepsilon g_\varepsilon(U,v,0)+\frac{1}{2}\varepsilon^2 g_{\varepsilon\varepsilon}(U,v,0)+\cdots,$$

$$h(U,v,\varepsilon)=h(U,v,0)+\varepsilon h_\varepsilon(U,v,0)+\frac{1}{2}\varepsilon^2 h_{\varepsilon\varepsilon}(U,v,0)+\cdots$$

and equate same orders in ε. At zeroth order, we have

$$g(U,v,0)=h(U,v,0)=0,$$

as expected. Powers of ε give

$$g_\varepsilon(U,v,0)=c^2v+cpU\big(1-U^r\big)\big(q+U^r\big)-pv\big[q+(1-q)(r+1)U^r-(2r+1)U^{2r}\big],$$

$$h_\varepsilon(U,v,0)=0,$$

and at the second order in ε one has

$$\frac{1}{2}g_{\varepsilon\varepsilon}(U,v,0)=0,$$

$$\begin{aligned}\frac{1}{2}h_{\varepsilon\varepsilon}(U,v,0)={}&v\big\{c\big[pq+p(r+1)(1-q)U^r-p(2r+1)U^{2r}\big]-pv\big[r(1-q)(r+1)U^{r-1}-2r(2r+1)U^{2r-1}\big]\big\}\\ &+\big[h-cv-pU\big(1-U^r\big)\big(q+U^r\big)\big]\big[c^2-p\big(q+(1-q)(r+1)U^r-(2r+1)U^{2r}\big)\big].\end{aligned}$$

Thus,

$$h(U, v, \varepsilon) = \varepsilon^2 h_1(U, v, \varepsilon),$$

where

$$h_1(U, v, \varepsilon) = \frac{1}{2} h_{\varepsilon\varepsilon}(U, v, 0) + \mathcal{O}(\varepsilon).$$

This allows one to write the system (11) as a following system

$$U_z = v, \qquad v_z = -cv - pU\left(1 - U^r\right)\left(q + U^r\right) + \varepsilon^2 h_1(U, v, \varepsilon), \tag{15}$$

which determines the dynamics on the "slow" manifold M_ε.

4. The flow on the manifold M_ε

When $\varepsilon = 0$, system (15) reduces to a system of coupled first-order ODEs. Let (U_0, v_0) be the solution of (15) when $\varepsilon = 0$. This can be any travelling wave solution of the original system (2), including a particular closed form solution (3). In the (U, v) phase plane this solution is a connection between $(1, 0)$ and $(0, 0)$. We shall use Fredholm theory to show that for $\varepsilon > 0$ sufficiently small there exists a heteroclinic connection between the critical points $(1, 0)$ and $(0, 0)$ of (15). This connection corresponds to a travelling wave solution of (5).

When $\varepsilon \neq 0$, we set

$$U = U_0 + \varepsilon^2 \tilde{U}, \qquad v = v_0 + \varepsilon^2 \tilde{v},$$

and substitute this into (15). To the lowest order in ε the system governing $\tilde{U}, \tilde{v}$ is

$$\frac{d}{dz}\begin{pmatrix} \tilde{U} \\ \tilde{v} \end{pmatrix} - \begin{pmatrix} 0 & 1 \\ -pq - p(r+1)(1-q)U_0^r + p(2r+1)U_0^{2r} & -c \end{pmatrix}\begin{pmatrix} \tilde{U} \\ \tilde{v} \end{pmatrix} = \begin{pmatrix} 0 \\ h_1(U_0, v_0, 0) \end{pmatrix}, \tag{16}$$

which can be written as

$$\mathcal{L}\begin{pmatrix} \tilde{U} \\ \tilde{v} \end{pmatrix} = \begin{pmatrix} 0 \\ h_1(U_0, v_0, 0) \end{pmatrix}, \tag{17}$$

with $\mathcal{L}$ being a linear differential operator defined by the left-hand side of Eq. (16). We want to prove that this system has a solution satisfying

$$\tilde{U}, \tilde{v} \to 0 \quad \text{as } z \to \pm\infty.$$

Working in the space L^2 of square integrable functions, we introduce the inner product as $\int_{-\infty}^{\infty} \langle \mathbf{x}(z), \mathbf{y}(z) \rangle \, dz$, with $\langle \cdot, \cdot \rangle$ being the inner product on $\mathbb{R}^2$. Note that the operator $\mathcal{L}$ is not self-adjoint. Taking an inner product between a function $\mathbf{x}(z)$ in the kernel of the adjoint operator $\mathcal{L}^*$ and the right-hand side of (17) gives

$$\int_{-\infty}^{\infty} \left\langle \mathbf{x}(z), \begin{pmatrix} 0 \\ h_1(U_0(z), v_0(z), 0) \end{pmatrix} \right\rangle dz = \int_{-\infty}^{\infty} \left\langle \mathbf{x}(z), \mathcal{L}\begin{pmatrix} \tilde{U} \\ \tilde{v} \end{pmatrix} \right\rangle dz = \int_{-\infty}^{\infty} \left\langle \mathcal{L}^* \mathbf{x}(z), \begin{pmatrix} \tilde{U} \\ \tilde{v} \end{pmatrix} \right\rangle dz = 0.$$

This implies the Fredholm alternative, which states that the system (17) has a solution if and only if

$$\int_{-\infty}^{\infty} \left\langle \mathbf{x}(z), \begin{pmatrix} 0 \\ h_1(U_0(z), v_0(z), 0) \end{pmatrix} \right\rangle dz = 0, \tag{18}$$

for all functions $\mathbf{x}(z)$ in the kernel of the adjoint operator $\mathcal{L}^*$, see [20].

In order to find the kernel of the adjoint problem, we consider the adjoint equation which has the form

$$\frac{d\mathbf{x}}{dt} = \begin{pmatrix} 0 & pq + p(r+1)(1-q)U_0^r - p(2r+1)U_0^{2r} \\ -1 & c \end{pmatrix} \mathbf{x}. \tag{19}$$

Letting $z \to \infty$, one has $U_0 \to 0$ and the matrix in (19) is then a constant matrix with eigenvalues λ satisfying

$$\lambda^2 - c\lambda + pq = 0. \tag{20}$$

From (20) it follows that both eigenvalues are positive or have a positive real part (since $q > 0$, $p > 0$), and as $z \to \infty$ any solutions of (19), other then the zero solution, must grow exponentially. The only solution in L^2 is therefore a zero solution $\mathbf{x}(z) = \mathbf{0}$, and consequently the Fredholm orthogonality condition (18) trivially holds. Thus, we have proved the existence of the desired connection in manifold M_ε.

Theorem 2. *For every $c > 0$ defined in (4), there exists ε_0 such that, for every $\varepsilon \in (0, \varepsilon_0]$, Eq. (5) admits a monotone travelling front solution $u(x, t) = U(z)$ satisfying $U(-\infty) = 1$ and $U(\infty) = 0$, where $z = x - ct$.*

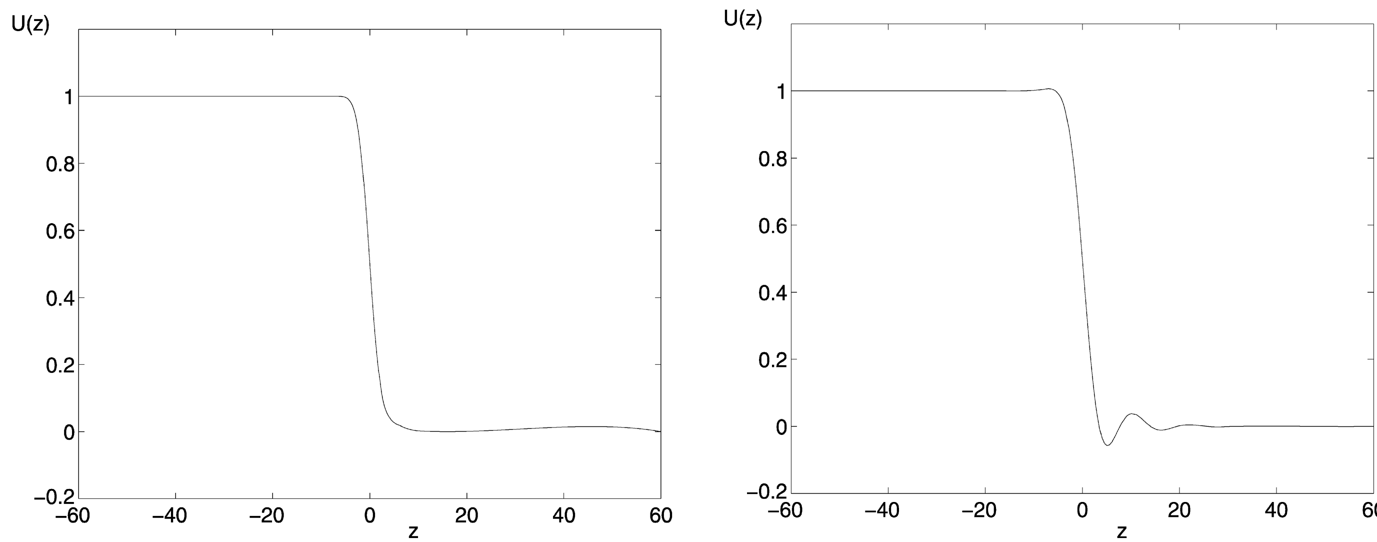

Fig. 2. Heteroclinic connections of (6) with $p = q = 1$, $r = 2$, and $D = 1$ (left) and $D = 10$ (right). The wavespeed c given by (4) is $c = 4/\sqrt{3}$.

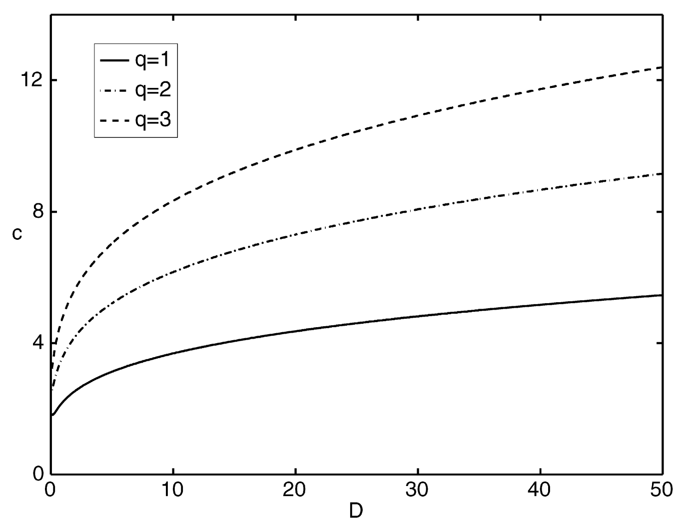

Fig. 3. Boundary of asymptotic behaviour of the leading edge of the travelling wave solution of Eq. (6) with $p = 1$ and different values of q. For any parameter values above each boundary, there is a monotone decay, while below each boundary the decay is oscillatory.

5. Persistence of travelling waves for large long-range diffusion

So far, we have established that the travelling waves of the generalized Fisher equation persist under the influence of a long-range diffusion, when it is small. For larger values of D, this problem does not lend itself to the analytical treatment, and therefore one has to use numerical methods. Our presentation here follows Ashwin et al. [4], where a similar problem was considered for the KPP–Fisher equation with a delay in the form of a convolution term.

We look for solutions $U(z)$ of Eq. (6) subject to boundary conditions

$$U(-\infty) = 1, \qquad U(+\infty) = 0. \tag{21}$$

To this end, we consider the system (6), (21) on a long finite interval $z = [-L, L]$ with the approximation converging to a correct solution in the limit $L \to \infty$ [5,13]. Using argument similar to the one in [4], we require the solution to have no projection on the stable manifold of Y^1 at $z = -L$ and no projection on the unstable manifold of Y^0 at $z = L$. Due to translational symmetry of Eq. (6), one can fix the value of $U(0)$ as a fourth boundary condition, and we take this to be $U(0) = 0.5$. Numerical solution of the above problem was performed using a finite difference method realized in a NAG boundary value solver *D02RAF*. This routine was run successively until the required absolute tolerance of 10^{-6} was achieved, with the collocation points being distributed unevenly along the interval $[-60, 60]$.

Results of numerical simulations are shown in Fig. 2 for some particular values of parameters. This figure suggests that as the long-range diffusion coefficient D increases from zero, perturbed heteroclinic orbits remain close in shape to the unperturbed solutions. However, starting with some critical D, two of the negative eigenvalues of matrix A_0 (linearization matrix near the steady state Y^0) form a leading complex conjugate pair, and this results in oscillations of the solution at $z \to \infty$. Biologically, this situation is not plausible since it allows population density to become negative for some values of z thus invalidating the model. Fig. 3 shows the boundaries in the parameter space of wavespeed c and long-range diffusion coefficient D, which separate the regions of monotone (above the boundary) and oscillatory (below the boundary) decay of the leading edge of the travelling wave for different values of q. One can observe that the higher q, the larger is the minimal wavespeed for which the travelling waves have a monotone decay as $z \to \infty$.

6. Conclusions

Travelling wave solutions of the generalized Fisher equation have been considered in the presence of the long-range diffusion. Using analytical and numerical tools we have shown that the travelling fronts (3) are robust and persist when the strength of long-range diffusion is sufficiently small. In this case, the geometric singular perturbation theory and invariant manifold theory have allowed us to prove rigourously the existence of perturbed heteroclinic connections in the system. This result is quite powerful since it is simultaneously valid for various types of competition modelled by Eq. (5) with different values of parameters.

For larger values of the long-range diffusion coefficient, heteroclinic fronts have been obtained numerically as a solution of a boundary-value problem for a reduced dynamical system. Numerical simulations suggest that starting with some value of D, solutions acquire oscillatory behaviour at the right end, where they approach zero. This implies that at this moment the model loses its validity in representing biological quantities (such as population dynamics), and consequently another description should be used to capture the dynamics of competition in the presence of long-range diffusion.

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