IMA Journal of Applied Mathematics (1999) 63, 199–216

On the persistence of spatiotemporal oscillations generated by invasion

ALISON L. KAY[†] Mathematics Institute, University of Warwick, Coventry CV4 7AL, UK

AND

JONATHAN A. SHERRATT[‡] Department of Mathematics, Heriot-Watt University, Edinburgh EH14 4AS, UK [Received 13 March 1998]

Many systems in biology and chemistry are oscillatory, with a stable, spatially homogeneous steady state which consists of periodic temporal oscillations in the interacting species, and such systems have been extensively studied on infinite or semi-infinite spatial domains. We consider the effect of a finite domain, with zero-flux boundary conditions, on the behaviour of solutions to oscillatory reaction-diffusion equations after invasion. We begin by considering numerical simulations of various oscillatory predator-prey systems. We conclude that when regular spatiotemporal oscillations are left in the wake of invasion, these die out, beginning with a decrease in the spatial frequency of the oscillations at one boundary, which then propagates across the domain. The long-time solution in this case is purely temporal oscillations, corresponding to the limit cycle of the kinetics. Contrastingly, when irregular spatiotemporal oscillations are left in the wake of invasion, they persist, even in very long time simulations. To study this phenomenon in more detail, we consider the $\lambda - \omega$ class of reaction-diffusion systems. Numerical simulations show that these systems also exhibit die-out of regular spatiotemporal oscillations and persistence of irregular spatiotemporal oscillations. Exploiting the mathematical simplicity of the $\lambda - \omega$ form, we derive analytically an approximation to the transition fronts in r and θ_x which occur during the die-out of the regular oscillations. We then use this approximation to describe how the die-out occurs, and to derive a measure of its rate, as a function of parameter values. We discuss applications of our results to ecology, calcium signalling and chemistry.

1. Introduction

Many systems in biology and chemistry are intrinsically oscillatory, with a stable, spatially homogeneous steady state that is not stationary, but rather consists of periodic temporal oscillations in the interacting biological or chemical species. Classic examples include the Belousov–Zhabotinskii reaction (Leach *et al.* 1994), the intra-cellular calcium system (Sneyd *et al.* 1995), and a number of predator–prey interactions (May 1981; Hassell *et al.* 1991). Spatiotemporal behaviour in these systems is often modelled using oscillatory reaction–diffusion equations (Cross & Hohenberg 1993), although spatially or temporally

© Oxford University Press 1999

[†](akay@maths.warwick.ac.uk)

[‡](jas@ma.hw.ac.uk)

discrete models are a popular alternative in ecological applications (Hassell *et al.* 1991; Rohani *et al.* 1997); we use the word 'oscillatory' to indicate that the reaction–diffusion kinetics have a stable limit cycle.

In one space dimension, the majority of work on oscillatory reaction-diffusion equations has focused on two solution forms, namely periodic wave-trains and spatiotemporal chaos. Periodic wave-trains were first studied by Kopell & Howard (1973b), who showed that all oscillatory reaction-diffusion systems have a one-parameter family of periodic wave-train solutions, and subsequently a series of authors considered the form of such waves, and their stability as reaction-diffusion solutions (Othmer 1977; Ermentrout 1980; Maginu 1981; Koga 1993). Spatiotemporal chaos was originally studied in the 'Brussellator' chemical model, where it arises via differences in the diffusion rates of reactants (Kuramoto 1984; Rovinsky 1987); more recently, spatiotemporal chaos has been found in systems with equal diffusion rates (Pascual 1993; Sherratt et al. 1995). In the last few years, work on oscillatory reaction-diffusion equations has shifted from the study of these two solution forms, to the potential to generate them from simple initial conditions, of the type that would arise naturally in applications. The essential conclusion of this work is that invasion processes generate both periodic wave-trains (Sherratt 1994b; Koga 1995; Ermentrout et al. 1997) and spatiotemporal chaos (Sherratt 1994a; Rasmussen et al. 1996; Merkin & Sadiq 1997; Davidson 1998). A simple context for the discussion of such invasions is predator-prey systems, and we will focus on these for most of the paper, returning to other applications in the discussion.

Mathematical modelling of ecological invasions has a very long history, dating back to the pioneering work of Skellam (1951). However, the vast majority of models focus entirely on the invading species, without considering its interactions with existing species. The effects of this interaction are most pronounced in the case of cyclical predator–prey systems, in which the spatially homogeneous coexistence equilibrium consists of periodic oscillations in predator and prey densities; a detailed discussion of this homogeneous behaviour is given in the book of May (1981). Sherratt *et al.* have previously used oscillatory reaction–diffusion models to study the invasion of a prey population by predators in such a cyclical system (1997). This work shows that the invasion process leaves in its wake spatiotemporal oscillations that are either regular, with the form of a periodic wave-train, or irregular, with evolution towards at least temporal chaos; typical examples of the two behaviours are illustrated in Fig. 1. Detailed explanations of these solution forms is given elsewhere (Sherratt 1994a, 1999); briefly, a particular member of the periodic wave-train family is selected by the leading invasive front, and irregular oscillations result if this wave-train is unstable as a reaction–diffusion solution.

The studies of invasion in (Sherratt *et al.* 1997) apply only to an infinite or semi-infinite domain. In practice, ecological domains are finite, typically bounded by changes in terrain. A key issue thus concerns the long-term behaviour after a solution of the form illustrated in Fig. 1 has invaded the whole of a finite domain. The object of this paper is to address this issue. We begin (Section 2) by presenting numerical results, and then in Sections 3 and 4 we use a caricature model to study the behaviour analytically. Boundary conditions are clearly important factors, and we restrict attention throughout to the case of zero-flux conditions at both ends of the (one-dimensional) domain.



FIG. 1. Numerical simulations of invasion in cyclical predator-prey systems, showing the progress of invasion fronts with regular and irregular oscillatory wakes. The solutions have the form of an advancing wave front of predators and a receding wave front of prey; in (a) there is a periodic wave-train solution behind these fronts, while in (b) there are irregular spatiotemporal oscillations. We show solutions of (1) with $D_h = D_p = 1$ and with kinetics (2). Graph (a) illustrates a regular oscillatory wake, and is for parameter values a = 1.5, b = 0.05 and c = 4, while (b) illustrates an irregular oscillatory wake, and is for parameter values a = 1.5, b = 1 and c = 5. The numerical simulations were done using the method of lines and Gear's method, with initial conditions consisting of the prey-only steady state everywhere, except on the left-hand boundary, where the coexistence steady state is imposed initially

2. Simulations of invasion on finite domains

We begin by presenting the results of numerical simulations of invasion on finite spatial domains. We consider reaction-diffusion models for predator-prey interactions with the

form

$$\frac{\partial h}{\partial t} = D_h \frac{\partial^2 h}{\partial x^2} + f_h(h, p), \qquad (1a)$$

$$\frac{\partial p}{\partial t} = D_p \frac{\partial^2 p}{\partial x^2} + f_p(h, p).$$
(1b)

Here p(x, t) and h(x, t) denote predator and prey densities respectively, at time t and position x on a one-dimensional spatial domain. Biologically realistic kinetic terms f_p and f_h will have two non-trivial equilibria, a 'prey-only' steady state which we take to be p = 0, h = 1 by suitable rescaling, and a 'coexistence' state, $p = p_s, h = h_s$. For cyclical populations, this coexistence state will also be unstable, and will lie inside a stable limit cycle in the kinetic phase plane. We have considered three standard sets of predator–prey kinetics, all of which have such a stable limit cycle for appropriate parameter values:

$$f_h(h, p) = h(1-h) - p(1-e^{-ch}), \qquad f_p(h, p) = bp(a-1-ae^{-ch}),$$
 (2)

$$f_h(h, p) = h(1-h) - \frac{hp}{h+c}, \qquad f_p(h, p) = \frac{aph}{h+c} - bp,$$
 (3)

$$f_h(h, p) = h(1-h) - \frac{ahp}{h+c}, \qquad f_p(h, p) = bp\left(1 - \frac{p}{h}\right).$$
 (4)

Here *a*, *b* and *c* are positive parameters in all cases. The historical origin and applicability of these models is discussed in detail elsewhere (May 1981; Metz & Diekmann 1986; Dunbar 1986; Murray 1989). On an infinite or semi-infinite domain, numerical simulations of invasion with these kinetics, in the oscillatory regimes, give solutions of the form illustrated in either Fig. 1a or Fig. 1b, depending on parameter values. In these figures, the system is initially in the prey-only state h = 1, p = 0, except for a small perturbation close to the x = 0 boundary. A boundary condition is of course required at x = 0, but is not significant: for instance, imposing values of *h* and *p* on this boundary, rather than using zero-flux conditions as in the figures, does not significantly affect the solution. Note that in oscillatory reaction–diffusion equations with more complex kinetics, behaviours other than periodic wave-trains and spatiotemporal chaos can be generated, such as groups of propagating pulses and breather solutions (Rasmussen *et al.* 1996; Ermentrout *et al.* 1997; Merkin & Sadiq 1997; Davidson 1998). However, extensive numerical simulations of a range of different predator–prey models always gives behaviour of one of the forms illustrated in Fig. 1a,b.

To study the behaviour on a finite domain, we solved (1) with (2), (3) or (4) numerically on 0 < x < L, with zero-flux boundary conditions $h_x = p_x = 0$ at x = 0 and x = L, and initial conditions h = 1, p = 0 for $\epsilon < x < L$ for some $\epsilon \ll L$, with a non-zero initial value of p on $0 < x < \epsilon$. This corresponds to the introduction of predators at one edge of a domain that is otherwise occupied entirely by prey. Of course, numerical solutions inevitably involve a finite spatial domain: the key difference between the simulations we consider now and those presented above is the time period over which the equations are solved. In Fig. 1, the invading wave of predators is some distance from the right-hand boundary at the end of the simulation; in our 'finite domain' simulations, we continue the solution for a period many times that required for the whole domain to be invaded. Our numerical solutions have used both the method of lines with Gear's method, and a Crank–Nicolson scheme; these two methods have very different convergence properties for oscillatory reaction–diffusion equations (Sherratt 1997), making their comparison a good test for convergence.

Numerical simulations for a wide range of parameters show a very clear pattern of behaviour. Initially, the solution has the same qualitative form as shown in Fig. 1, namely an invading front of predators moving across the domain, with either a periodic wave-train or irregular spatiotemporal oscillations behind it. Once the whole domain has been invaded, the behaviour depends crucially on whether the oscillations behind invasion fall into the regular or irregular category (Figs 2 and 3). In the former case, the oscillations gradually die out, with the frequency of the spatial oscillations decreasing first at one boundary of the domain, followed by a progression of this change across the domain. The solution evolves in this manner towards a spatially homogeneous, temporal oscillation, corresponding to the limit-cycle solution of the kinetics. The die-out usually begins at the edge of the domain opposite to that at which the predators were initially introduced, although for some parameter sets it occurs in the opposite direction (for example, kinetics (4) with a = 3, b = c = 0.1). In sharp contrast, when irregular spatiotemporal oscillations are left in the wake of the invasion, these persist, even in very long-time numerical solutions. This is consistent with numerical results of Rasmussen et al. (1996) and Davidson (1998) for other oscillatory reaction-diffusion systems (with, respectively, periodic and zero-flux boundary conditions), although these studies do not specifically investigate long-time persistence. There are in fact 'intermediate cases' between regular and irregular wakes behind invasion, in which there is a band of periodic waves immediately behind the invasive front, which changes into irregular oscillations further back; this corresponds mathematically to the selection by the invasion process of a periodic wave that is only just unstable, so that the periodic waves appear as a transient (Sherratt 1994a). In such cases, our simulations of invasion on a finite domain suggest that again there are either long-term persistent spatiotemporal irregularities, or that the system evolves towards a homogeneous temporal oscillation; however, the division between these cases depends sensitively on parameter values near the division between regular and irregular oscillatory wakes.

Ecological implications of these results will be discussed in Section 5. Prior to this, we study in more detail the rather striking way in which the periodic wave-train evolves to spatial homogeneity in the regular case, using a caricature system of oscillatory reaction–diffusion equations.

3. Persistence of oscillations in $\lambda - \omega$ systems

Background

We have been unable to make any progress studying the predator-prey models (1) with (2), (3) or (4) analytically, for general parameter values. However, there is a special case in which the systems are much more amenable to analysis, namely for kinetic parameters close to the Hopf bifurcation, and for equal predator and prey diffusion coefficients. In this



FIG. 2. A numerical simulation of invasion in a cyclic predator–prey system, showing the behaviour after an invasive front with a regular oscillatory wake has reached the far side of a finite domain, with zero-flux boundary conditions. The figure clearly illustrates the dying out of the regular oscillations; beginning with a decrease in frequency at the right-hand side of the domain, which then progresses across the rest of the domain. The long-time behaviour consists of spatially homogeneous, temporal oscillations around the limit cycle of the kinetics. The solution shown is for (1) with kinetics (2) for parameter values $D_h = D_p = 1$, a = 1.5, b = 0.05 and c = 4. The solution is plotted in blocks, each of which is a space-time plot, so that the variation in the solution can be seen over long time, and at small intervals through that time; the time at the first line of each block corresponds to successive multiples of the time at which the plot begins

case the kinetics can be approximated by the Hopf normal form, giving

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \lambda(r)u - \omega(r)v, \qquad (5a)$$

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + \omega(r)u + \lambda(r)v, \tag{5b}$$

where *u* and *v* represent appropriate linear combinations of the predator and prey densities *p* and *h*. Here $r = (u^2 + v^2)^{\frac{1}{2}}$, with $\lambda(r) = \lambda_0 - \lambda_1 r^2$ and $\omega(r) = \omega_0 + \omega_1 r^2$, where $\lambda_0, \lambda_1 > 0$. Note that the system (5) is very general, being the normal form of any oscillatory reaction–diffusion system close to Hopf bifurcation, provided the variables have the same diffusion coefficient. Thus our calculations will apply to a range of applications in addition to ecology, and this is discussed further in Section 5.

Reaction–diffusion systems of the form (5) are known as ' $\lambda - \omega$ systems', and were first

204



FIG. 3. A numerical simulation of invasion in a cyclic predator-prey system, showing the behaviour after an invasion front with an irregular oscillatory wake has reached the far side of a finite domain, with zero-flux boundary conditions. The figure illustrates the long-time persistence of the irregular oscillations. The solution shown is for (1) with kinetics (2), for parameter values $D_h = D_p = 1$, a = 1.5, b = 1 and c = 5. The solution is again plotted in blocks, as described in the legend to Fig. 2

studied by Kopell & Howard (1973b). The key to the analytical study of such systems is to work in terms of polar coordinates in the (u, v)-plane, r and $\theta = \tan^{-1} v/u$, in terms of which (5) becomes

$$\frac{\partial r}{\partial t} = \frac{\partial^2 r}{\partial x^2} - r \left(\frac{\partial \theta}{\partial x}\right)^2 + r(\lambda_0 - \lambda_1 r^2),\tag{6a}$$

$$\frac{\partial\theta}{\partial t} = \frac{\partial^2\theta}{\partial x^2} + \frac{2}{r}\frac{\partial r}{\partial x}\frac{\partial\theta}{\partial x} + (\omega_0 + \omega_1 r^2).$$
(6b)

From this formulation, it is clear that there is a spatially homogeneous circular limit-cycle solution, with amplitude (radius) $r_c = (\lambda_0/\lambda_1)^{\frac{1}{2}}$. Also there is a family of periodic wave-train solutions, which are also circular in the (u, v)-plane, with amplitude \hat{r} for any $\hat{r} < r_c$. The form of these wave-train solutions is easily determined: substituting $r(x, t) = \hat{r}$, a constant, into (6) implies that $\theta(x, t) = \sqrt{(\lambda(\hat{r}))x + \omega(\hat{r})t + \theta_0}$, where θ_0 is an arbitrary constant, which may be set to zero without loss of generality. Thus the periodic waves have

the form

$$u(x, t) = \hat{r} \cos \theta(x, t) = \hat{r} \cos(\sqrt{\lambda(\hat{r})x} + \omega(\hat{r})t),$$

$$v(x, t) = \hat{r} \sin \theta(x, t) = \hat{r} \sin(\sqrt{\lambda(\hat{r})x} + \omega(\hat{r})t).$$

Thus we have a sinusoidal periodic plane wave moving with speed $\omega(\hat{r})/\sqrt{(\lambda(\hat{r}))}$ in the negative *x*-direction. There is also the mirror image wave, where $\theta(x, t) = -\sqrt{(\lambda(\hat{r}))x} + \omega(\hat{r})t$, which moves with the same speed in the positive *x*-direction.

Kopell & Howard (1973b) derived a stability condition for the periodic wave-train solutions of $\lambda - \omega$ systems, which in the case of (6) shows that the periodic plane waves are stable if and only if their amplitude \hat{r} is larger than \hat{r}_c , where

$$\hat{r}_c = \left[\frac{2\lambda_0}{\lambda 1} \left(\frac{\lambda_1^2 + \omega_1^2}{3\lambda_1^2 + 2\omega_1^2}\right)\right]^{1/2}.$$

The existence of this precise stability result is in sharp contrast to more general oscillatory reaction–diffusion systems, for which results on stability of periodic waves are quite limited (Othmer 1977; Maginu 1981).

Numerical simulations

The equilibrium point u = v = 0 in a $\lambda - \omega$ system corresponds to the coexistence steady state $h = h_s$, $p = p_s$ in the predator-prey systems. However, $\lambda - \omega$ systems have no equilibrium corresponding to the prey-only state of predator-prey models, and thus cannot be used to mimic the invasion process. Investigation of the persistence of spatiotemporal oscillations is possible, though, by using appropriate initial conditions.

To study the persistence of regular oscillations (periodic plane waves) in the $\lambda - \omega$ case, we solved the equations numerically with initial conditions consisting of a periodic planewave solution of stable amplitude $\hat{r} > \hat{r}_c$ on the whole of a finite domain, again using zero-flux boundary conditions ($u_x = v_x = 0$). We found that such regular spatiotemporal oscillations die out, starting from one side of the domain, in a manner very similar to that for predator-prey systems. An example of this is illustrated in Fig. 4a.

For the corresponding case of irregular oscillations in $\lambda - \omega$ systems, the natural initial condition to use is a periodic wave-train of unstable amplitude ($\hat{r} < \hat{r}_c$). However, perturbation of an unstable wave-train does not always generate spatiotemporal irregularities; the resultant behaviour in fact depends sensitively on the wave-train amplitude and domain length. This was studied in detail by Sherratt (1995) for periodically forced boundary conditions, demonstrating a range of possible long-term behaviours, including complex periodic oscillations and quasi-periodicity. We have not attempted a corresponding detailed numerical bifurcation study for zero-flux boundary conditions; however, our simulations indicate that once spatiotemporal irregularities have been formed somewhere on the domain, they spread throughout the domain and persist for long times. This is illustrated in Fig. 4b.

We also mention here that our numerical results indicate that the regular oscillations die out from the right-hand side of the domain if $w(\cdot)$ is a decreasing function (that is, if $\omega_1 < 0$), and from the left-hand side if $w(\cdot)$ is an increasing function ($\omega_1 > 0$). If $w(\cdot)$ is

206



FIG. 4. An illustration of the fact that persistence of spatiotemporal oscillations in $\lambda - \omega$ systems mimics that in oscillatory predator-prey systems after the invasion of an entire domain. Graph (a) is for $\lambda(r) = 1 - r^2$ and $\omega(r) = 1 + r^2$, with an initial periodic plane wave of stable amplitude $\hat{r} = 0.9$, and shows the regular oscillations dying out, from the left-hand side of the domain. Graph (b) is for $\lambda(r) = 1 - r^2$ and $\omega(r) = 1 + 3r^2$, with an initial periodic plane wave of stable amplitude $\hat{r} = 0.4$, and shows irregular oscillations developing from the unstable plane wave, and then persisting. The solutions are plotted in blocks, as explained in the legend to Fig. 2



FIG. 5. An illustration of the solution in Fig. 4a, replotted in terms of r and θ_x . This shows in more detail the way in which stable periodic waves die out across the domain. As in Fig. 4a, $\lambda(r) = 1 - r^2$, $\omega(r) = 1 + r^2$ and the initial periodic plane wave has amplitude $\hat{r} = 0.9$. The solutions are plotted as a function of space x at equally spaced times (time interval 10); the arrows indicate the way in which the solutions evolve as time increases

a constant ($\omega_1 = 0$) then the die-out occurs much more slowly, and symmetrically from each side of the domain. Henceforth we shall concentrate on the case of $w(\cdot)$ increasing; there is no loss of generality, since the equations (6) are invariant under the transformation $\omega_1 \mapsto -\omega_1, x \mapsto L - x$, where the domain is 0 < x < L.

4. Analytical study of the die-out of regular oscillations

Details of the way in which the regular oscillations die out are revealed by replotting solutions such as those in Fig. 4a in terms of r and θ_x rather than u and v, as illustrated in Fig. 5. This shows transition fronts in r and θ_x moving across the domain, starting from the left-hand side. The r transition front joins $r = r_c$ to $r = \hat{r}$, and has negative gradient, the size of which decreases with time, while the θ_x transition front joins $\theta_x = 0$ to $\theta_x = \sqrt{(\lambda(\hat{r}))}$, and has positive gradient which decreases with time.

An obvious possible explanation for the solutions in Fig. 5 is that they are transients in the evolution towards a travelling wave front in r and θ_x , and we begin by presenting results arguing against this explanation. If such a wave front were to be forming in Fig. 5, then the finite boundaries would be preventing the evolution of a constant shape profile. To study the possibility of such a wave, we neglect these boundary effects, and use the travelling wave variable z = x - ct, looking for solutions of the form $r(x, t) = \tilde{r}(z)$ and $\theta_x(x, t) = \psi(x, t) = \tilde{\psi}(z)$. We also write $\tilde{\phi}(z) = \tilde{r}'/\tilde{r}$, where the prime represents differentiation with respect to z. Substitution of these solution forms into (6) gives three coupled ordinary

differential equations, which have been studied previously by a number of authors working on amplitude transition fronts in λ - ω systems (Howard & Kopell 1977; Sherratt 1994b). Using the boundary conditions $\tilde{r} = r_c$, $\tilde{\phi} = 0$, $\tilde{\psi} = 0$ as $z \to -\infty$ and $\tilde{r} = \hat{r}$, $\tilde{\phi} = 0$, $\tilde{\psi} = \sqrt{(\lambda(\hat{r}))}$ as $z \to \infty$ these equations show that, if such a travelling wave were to exist, it would have a positive wave speed c, so that $r = r_c$, $\theta_x = 0$ behind the wave, with $r = \hat{r}, \theta_x = \sqrt{(\lambda(\hat{r}))}$ ahead, as would be required in our case. Straightforward calculation shows that the $\tilde{r} - \phi - \psi$ equations have exactly one unstable eigenvector at $(r_c, 0, 0)$ and at least one stable eigenvector at $(\hat{r}, 0, \sqrt{\lambda(\hat{r})})$, which is compatible with a travellingfront trajectory. However, when we attempted to construct this trajectory by numerical solution of the $\tilde{r} - \tilde{\phi} - \tilde{\psi}$ ordinary differential equations, we found that solutions starting on the unstable eigenvector at $(r_c, 0, 0)$ evolved to infinity, rather than towards $(\hat{r}, 0, \sqrt{\lambda(\hat{r})})$; it is not clear whether this is due to non-existence or structural instability of the trajectory. In fact, Howard & Kopell (1977) conjectured that for such a trajectory to exist and to be stable as a partial differential equation solution, the number of unstable eigenvectors at the initial steady state plus the number of stable eigenvectors at final point must be at least 4. Calculations show that this condition is not satisfied in our case; we omit the details for brevity. This combination of results suggests that a travelling front in r and θ_x of the required form does not exist, although we have been unable to formally eliminate the possibility. Moreover, when the domain length L is long, numerical simulations as in Fig. 5 do not show evolution towards a constant shape profile.

Having rejected the possibility of travelling wave fronts in r and θ_x , we now consider other possible forms for the observed transition fronts. In the solution illustrated in Fig. 5 it is very noticeable that the θ_x transition appears linear in space, with gradient decreasing in time, but independent of x (until θ_x gets close to its periodic plane-wave steady-state value, when it tails off). This same observation holds in numerical simulations for a wide range of parameters. Prompted by this, we look for solutions satisfying $\theta_{xx}(x, t) = f(t)$, where $f(\cdot)$ is an unknown function of time only, satisfying f(t), $f'(t) \to 0$ as $t \to \infty$. Then $\theta_x(x, t) = f(t)x + g(t)$ for an arbitrary function of time $g(\cdot)$, and the boundary condition $\theta_x(0, t) = 0$ gives $g(t) \equiv 0$. Thus

$$\theta(x,t) = \frac{1}{2}f(t)x^2 + h(t)$$
(7)

for a further arbitrary function of time h(t). Substituting (7) into (6b) and evaluating at x = 0 gives $h'(t) = f(t) + \omega(r_c)$, using the boundary conditions $r_x = \theta_x = 0$ at x = 0. Thus we have

$$\theta(x,t) = \frac{f(t)x^2}{2} + \int^t f + \omega(r_c)t.$$
 (8)

Substituting (8) into (6) gives

$$r_t = r_{xx} - rf^2(t)x^2 + r(\lambda_0 - \lambda_1 r^2),$$
(9a)

$$r_x = \frac{r}{2f(t)x} \left(\frac{x^2}{2} f'(t) + \omega_1 (r_c^2 - r^2) \right).$$
(9b)

Thus we have two equations which determine r(x, t); we will consider whether these equations together determine the unknown function f(t).

To make calculations algebraically simpler, we rescale the system using

$$l_0 = \omega_0 / \lambda_0,$$
 $x = X / \sqrt{\lambda_0},$ $\theta = \Theta,$

$$l_1 = \omega_1 / \lambda_1, \qquad t = T / \lambda_0, \qquad r = R \sqrt{\lambda_0 / \lambda_1}.$$
 (10)

In terms of these new variables, the equations (9) become

$$R_T = R_{XX} - RF^2(T)X^2 + R(1 - R^2),$$
(11)

$$R_X = \left(\frac{X^2}{2}F'(T) + l_1\right)\frac{R}{2F(T)X} - \frac{l_1}{2F(T)X}R^3,$$
(12)

where $\Theta_X(X, T) = F(T)X$, for $F(T) = f(T/\lambda_0)/\lambda_0$. These equations depend only on the single parameter l_1 .

In equation (12), time enters only as a parameter, so that it is an ordinary differential equation, which is in fact of a standard form known as a *Bernoulli equation*. The solution is available from standard textbooks (for example, Murphy 1960),

$$R = X^{k(T)} e^{-b(\bar{X},T)/2} \left(C(T) + 2k(T) \int_{0}^{X} \bar{X}^{2k(T)-1} e^{-b(\bar{X},T)} \,\mathrm{d}\bar{X} \right)^{-1/2},$$

where $b(X, T) = -X^2 F'(T)/4F(T)$, $k(T) = l_1/2F(T)$ and $C(\cdot)$ is an arbitrary function of time resulting from the integration. Figure 5 shows that R(0, T) goes from its initial value of \hat{r} to 1 very quickly, so at all but small times we can take R(0, T) = 1 to a very good approximation, which means that $C(T) \equiv 0$, using l'Hôpital's rule. Thus we have

$$R = \frac{X^{k(T)} e^{-b(X,T)/2}}{k(T)^{1/2}} \left(2 \int_{0}^{X} \bar{X}^{2(k(T)-1)} e^{-b(\bar{X},T)} \bar{X} \, \mathrm{d}\bar{X} \right)^{-1/2}$$
$$= \frac{b(X,T)^{k(T)/2} e^{-b(X,T)/2}}{k(T)^{1/2}} \left(\int_{0}^{b(X,T)} z^{k(T)-1} e^{-z} \, \mathrm{d}z \right)^{-1/2}$$
$$= \left(\frac{b(X,T)^{k(T)} e^{-b(X,T)}}{k(T) \gamma(k(T), b(X,T))} \right)^{1/2},$$
(13)

where we have used the change of variables $z = b(X, T)\bar{X}^2/X^2$. The integral $\gamma(k, b) = \int_0^b z^{k-1} e^{-z} dz$ is a special function known as the incomplete gamma function.

The solution (13) for R is implied by our assumed form for Θ and the boundary conditions. This is only an exact solution of the $\lambda-\omega$ system if (13) also satisfies (11). However, substitution of (13) into (11) gives an extremely complicated equation for F(T) which we were unable to solve exactly. In reality though, we are only interested in the solution at relatively large times (in the sense that the numerically estimated values of b and k are large), and thus we restrict our attention to approximating the form of F, as

210

 $T \to \infty$. To do this we need to have a limiting form for $\gamma(k(T), b(X, T))$ at large k and b. Standard books of tables typically contain asymptotic expansions for γ as one of k and b approach ∞ , with the other remaining fixed. However, we require an expansion valid as $T \to \infty$, which implies that $k \to \infty$, with b varying too (and possibly $b \to \infty$). Such an expansion has been found only relatively recently, by Temme (1975). The expansion given therein is for a non-normalized form of the incomplete gamma function; suitable manipulation, using the well-known asymptotic expansions of the gamma function, gives

$$\gamma(k,b) \sim \frac{k^{k-1}\mu^k e^{-b}}{1-\mu} = \frac{b^k e^{-b}}{k(1-b/k)}$$
(14)

to leading order as one (or both) of the parameters k and b tend to infinity. The result is uniformly valid in $\mu = b/k \ge 0$, provided $\mu \ne 1$; the case $\mu = 1$ can be considered separately, but in fact never gives a suitable form for r in our problem. This expansion has recently been extended to the complex plane by Dunster (1996), but (14) is sufficient for our purposes. Substituting (14) into (13) and simplifying implies that to leading order as $T \rightarrow \infty$,

$$R = \sqrt{1 - \frac{b}{k}} = \sqrt{1 + \frac{F'(T)X^2}{2l_1}}.$$
(15)

Our objective is to determine the form of the function F(T) as $T \to \infty$. From Fig. 5 and corresponding simulations for other parameter values, it appears that the transition fronts in θ_x and r move in parallel, even at quite large times. Since $\Theta_X = F(T)X$ and $R = \{1 + F'(T)X^2/2l_1\}^{1/2}$, this implies that if both X and $T \to \infty$ with F(T)X finite, then $F'(T)X^2$ must also be finite. Therefore $F'(T) \sim -AF(T)^2$ as $T \to \infty$, for some positive constant A; the minus sign enters because we know that F(.) is decreasing. Thus F(T) = 1/(AT). Hence (15) becomes

$$R = \sqrt{1 - \frac{X^2}{2l_1 A T^2}},$$

and for notational simplicity we write $\phi(X, T) = X^2/2l_1AT^2$. We can now substitute $R^2 = 1 - \phi(X, T)$ into equation (11), and using $X^2 = 2l_1AT^2\phi$ we obtain an equation completely in terms of ϕ and T;

$$\phi(1-\phi)(A-2l_1) - \frac{2\phi}{l_1T^2} - \frac{1}{2l_1T^2} + \frac{\phi}{T} = 0.$$
 (16)

We are concerned with the behaviour at large times for *R* lying between \hat{r} and 1; thus we require (16) to be satisfied to leading order as $T \to \infty$ with ϕ fixed, implying that $A = 2l_1$. Our approximation to the transition fronts is thus

$$R = \sqrt{1 - \frac{X^2}{4l_1^2 T^2}}, \qquad \Theta_X = F(T)X = \frac{X}{2l_1 T}.$$

Returning to the original, non-rescaled system using (10), we determine the leading-order form of the transition fronts at large t as

$$r = \sqrt{\frac{\lambda_0}{\lambda_1} - \frac{\lambda_1}{4\omega_1^2} \frac{x^2}{t^2}},$$
 (17a)

$$\theta_x = \frac{\lambda_1 x}{2\omega_1 t}.$$
(17b)

Figure 6 shows the *r*-transition fronts determined by numerical solution of (6) compared to our approximation (17a), for two different values of $l_1 = \omega_1/\lambda_1$. The comparison in each case is good, although there are clearly differences in quantitative detail. Numerical investigation shows that the main source of these errors in the calculations is higher-order terms in the expansion of the incomplete gamma function, rather than higher-order terms in (16). Crucially, our approximation deals well with the dependence of the solution on parameter values, and as an example of this we show in Fig. 6 that the approximation reflects the change in the speed of advance of the transition front when λ_1 is altered.

Equation (17a) shows that at fixed r, the speed of our calculated transition is constant in time, as the front progresses, but that the speed is larger at smaller values of r; that is, the higher parts of the front lag further and further behind the lower parts. The spatial frequency of the oscillations is $\theta_x = \lambda_1 x/2\omega_1 t$, and is thus directly related to the amplitude. As a measure of the rate at which the regular oscillations are dying out, we calculate the time, t^* , at which the area under the r transition front has reached half of its value as $t \to \infty$, $L(r_c - \hat{r})$. Thus a lower value of t^* means that the regular spatiotemporal oscillations die out more quickly. The value of t^* is thus given by the equation $L(r_c - \hat{r})/2 = \int_{\hat{r}}^{r_c} x(r; t^*) dr$, where x(r; t) is given by (17a), $r_c = \sqrt{(\lambda_0/\lambda_1)}$ and \hat{r} is the amplitude of the initial periodic plane wave. This gives

$$t^* = \frac{L\lambda_1}{\omega_1\sqrt{\lambda_0}} \left[\frac{(1-\hat{r}/r_c)}{\pi - 2\sin^{-1}(\hat{r}/r_c) - 2(\hat{r}/r_c)\sqrt{1 - (\hat{r}/r_c)^2}} \right]$$
(18)

and from this we can see how the speed of die-out depends upon the various parameters involved. In particular, the expression in square brackets is a strictly increasing function of \hat{r}/r_c for $0 < \hat{r}/r_c < 1$, tending to infinity as $\hat{r} \rightarrow r_c$. This is quite a counter-intuitive result, implying that the die-out actually occurs more slowly when the initial periodic plane-wave amplitude \hat{r} is closer to the limit cycle amplitude r_c . For the two transitions shown in Fig. 6, the corresponding values of t^* are about 85 and 140, where L = 100 is the domain size.

5. Discussion

In this paper we have considered the long-term behaviour after invasion of a finite region with zero-flux boundary conditions in oscillatory reaction–diffusion equations. In Section 2, we used numerical simulations of several different predator–prey systems. This showed that regular oscillatory wakes died out after the initial invasion, leaving purely temporal oscillations around the limit cycle of the kinetics. Contrastingly, irregular oscillatory wakes led to persistence of irregular oscillations across the whole domain after invasion. In Section 3, we introduced $\lambda - \omega$ systems, and verified that they mimic the die-out of regular



FIG. 6. Comparison of the numerically determined *r*-transition fronts, r_{pde} , with those of our analytic approximation (17a), r_{approx} , at times t = 10, 20, ..., 90. The left-hand graphs are for $l_1 = \omega_1/\lambda_1 = 1$, where we have taken $\lambda(r) = 1 - r^2$, $\omega(r) = 1 + r^2$ and $\hat{r} = 0.9$. The right-hand graphs are for $l_1 = \omega_1/\lambda_1 = 0.5$, where $\lambda(r) = 1 - 2r^2$, $\omega(r) = 1 + r^2$ and $\hat{r} = 0.6$. In both cases the comparison is good, and our approximation to the transition reflects the different speeds of advance of the front for different values of l_1

oscillations and persistence of irregular oscillations that was observed for predator-prey models. Plotting these solutions in terms of amplitude and phase gradient revealed details of the die-out in the regular case, and in Section 4 we used this to derive an approximation to the die-out, valid to leading order at large times. In particular, this yielded an estimate for the rate of die-out, as a function of parameters.

Any oscillatory reaction–diffusion system with equal diffusion coefficients has a form that is approximately of $\lambda - \omega$ type when the kinetic parameters are sufficiently close to Hopf bifurcation. Thus the calculation in Section 4 applies in these cases. In particular, λ_0 , λ_1 and ω_1 could be related to the parameters in any particular chemical or biological model by explicit calculation of the Hopf normal form, yielding an estimate of the rate of die-out in terms of model parameters. The numerical simulations illustrated in Fig. 2 are in fact for parameters quite far from Hopf bifurcation, and the compelling similarity between this simulation and the $\lambda - \omega$ case, which also holds for a wide range of other parameters, suggests that the analysis in Section 4 actually gives a good approximation to behaviour quite far from Hopf bifurcation.

In the context of ecology, the observation of long-term irregular spatiotemporal

oscillations is highly significant. The possibility that irregularities in ecological data might arise from population dynamics rather than environmental noise was first proposed by May more than 20 years ago (May & Oster 1976), but traditional explanations for such irregularities depend either on discretization of time and/or space, or on the interaction of more than two species. Our results show that a system of just one predator and one prey species can exhibit long-term spatiotemporal irregularities provided that the prey is present initially, and is subsequently invaded by the predator.

Our results also have implications for a number of applications quite different from ecology. The intra-cellular calcium system is either oscillatory or excitable, depending on certain conditions, and has been extensively modelled by systems of reaction–diffusion equations (Sneyd *et al.* 1993; Borghans *et al.* 1997). Numerical simulations of these models in the oscillatory regime also show oscillatory wakes generated by invasion, either regular or irregular (Sneyd & Sherratt 1997). The possibility of irregular oscillations that are persistent at large times in a finite domain is very significant in this case, because it provides a potential method for distinguishing experimentally between the oscillatory and excitable kinetics, which is an important controversy for calcium dynamics: in the excitable cases one does not expect the same type of persistence behaviour.

Experimentally, the most promising systems for quantitatively reproducing the behaviour we have predicted are oscillatory chemical reactions, such as the Belousov-Zhabotinskii reaction (Leach et al. 1994). Such systems have been extensively studied mathematically, so that detailed models are available (reviewed by Scott (1994)). In chemical systems, invasion is not a particularly natural way to generate periodic waves, but a number of other approaches have been used successfully, in particular for the Belousov-Zhabotinskii system (Kopell & Howard 1973a; Pagola et al. 1988; Stössel & Münster 1995). A procedure that is particularly relevant to our modelling is that of Stössel & Münster (1995), who imposed temporal oscillations at the ends of a one-dimensional reaction vessel, for a Belousov-Zhabotinskii system in an excitable regime. If this were repeated for the reaction in the oscillatory regime, mathematical simulations predict that, for suitable oscillation frequencies at the boundaries, both stable periodic waves and spatiotemporal irregularities could be generated. Our work predicts that if the boundaries were then altered to give zero flux conditions (quite straightforward experimentally), the irregular oscillations would persist while the periodic waves would die out, at a rate that we have predicted in our analysis.

References

- BORGHANS, J. A. M., DUPONT, G., & GOLDBETER, A. 1997 Complex intra-cellular calcium oscillations—a theoretical exploration of possible mechanisms. J. Biophys. Chem. 66, 25–41.
- CROSS, M. C. & HOHENBERG, P. C. 1993 Pattern formation outside of equilibrium. *Rev. Mod. Phys.* **65**, 851–1112.
- DAVIDSON, F. A. 1998 Chaotic wakes and other wave-induced behavior in a system of reaction– diffusion equations. Int. J. Bif. Chaos 8, 1303–1313.
- DUNBAR, S. R. 1986 Traveling waves in diffusive predator-prey equations: Periodic orbits and point-to-periodic heteroclinic orbits. *SIAM J. Appl. Math.* **46**, 1057–1077.
- DUNSTER, T. M. 1996 Asymptotic solutions of second order linear differential equations having almost coalescent turning points, with an application to the incomplete gamma function. *Proc.*

R. Soc. A **452**, 1331–1349.

- ERMENTROUT, G. B. 1980 Small amplitude stable wave-trains in reaction–diffusion systems. *Lect. Notes Pure Appl. Math.* **54**, 217–228.
- ERMENTROUT, G. B., CHEN, X., & CHEN, Z. 1997 Transition fronts and localised structures in bistable reaction-diffusion systems. *Physica* D **108**, 147–167.
- HASSELL. M. P. COMINS, H. N., & MAY, R. M. 1991 Spatial structure and chaos in insect population dynamics. *Nature* **353**, 255–258.
- HOWARD, L. N. & KOPELL, N. 1977 Slowly varying waves and shock structures in reaction– diffusion equations. *Stud. Appl. Math.* 56, 95–145.
- KOGA, S. 1993 Coexistence of stably propagating periodic wave trains in intrinsically bistable reaction–diffusion systems. *Phys. Lett.* **191**, 251–256.
- KOGA, S. 1995 A variety of stable persistent waves in intrinsically bistable reaction-diffusion systems—from one-dimensional periodic waves to one-armed and 2-armed rotating spiral waves. *Physica* D 84, 148–161.
- KOPELL, N. & HOWARD, L. N. 1973a Horizontal bands in the Belousov reaction. *Science* 180, 1171–1175.
- KOPELL, N. & HOWARD, L. N. 1973b Plane wave solutions to reaction-diffusion equations. *Stud. Appl. Math.* 52, 291–328.
- KURAMOTO, Y. 1984 Chemical Oscillations, Waves and Turbulence. Berlin: Springer.
- LEACH, J. A., MERKIN, T. H., & SCOTT, S. K. 1994 Oscillations and waves in the Belousov– Zhabotinskii reaction in a finite medium. J. Math. Chem. 16, 115–124.
- MAGINU, K. 1981 Stability of periodic travelling wave solutions with large spatial periods in reaction–diffusion equations. J. Diff. Eq. 39, 73–99.
- MAY, R. M. 1981 Stability and Complexity in Model Ecosystems. Princeton: University Press.
- MAY, R. M. & OSTER, G. F. 1976 Bifurcations and dynamics complexity in simple ecological models. *Amer. Nat.* **110**, 573–599.
- MERKIN, J. H. & SADIQ, M. A. 1997 The propagation of travelling waves in an open cubic autocatalytic chemical system. IMA J. Appl. Math. 57, 273–309.
- METZ, J. A. J. & DIEKMANN, O. 1986 A gentle introduction to structured population models: three worked examples. In: *The Dynamics of Physiologically Structured Populations*, Vol. 68. Berlin: Springer.
- MURPHY, G. M. 1960 Ordinary Differential Equations and their Solutions. New York: Van Nostrand.
- MURRAY, J. D. 1989 Mathematical Biology. Berlin: Springer.
- OTHMER, H. G. 1977 Current problems in pattern formation. Lect. Math. Life Sci. 9, 57-86.
- PAGOLA, A., ROSS, J., & VIDAL, C. 1988 Measurement of dispersion-relation of chemical waves in an oscillatory reacting medium. *J. Phys. Chem.* **92**, 163–166.
- PASCUAL, M. 1993 Diffusion induced chaos in a spatial predator-prey system. *Proc. R. Soc* B **251**, 1–7.
- RASMUSSEN, K. E., MAZIN, W. & MOSEKILDE, E. 1996 Wave-splitting in the bistable Gray–Scott model. *Int. J. Bif. Chaos* 6, 1077–1092.
- ROHANI, P., LEWIS, T. J., GRUNBAUM, D., & RUXTON, G. D. 1997 Spatial self-organization in ecology: Pretty patterns or robust reality? *TREE* 12, 70–74
- ROVINSKY, A. B. 1987 Twinkling patterns and diffusion-induced chaos in a model of the Belousov– Zhabotinsky chemical medium. *J. Phys. Chem.* **91**, 5113–5118

SCOTT, S. K. 1994 Oscillations, Waves and Chaos in Chemical Kinetics. Oxford: University Press.

SHERRATT, J. A. 1994a Irregular wakes in reaction-diffusion waves. Physica D 70, 370-382.

- SHERRATT, J. A. 1994b On the speed of amplitude transition waves in reaction–diffusion systems of $\lambda \omega$ type. *IMA J. Appl. Math.* **52**, 79–92.
- SHERRATT, J. A. 1995 Unstable wave-trains and chaotic wakes in reaction–diffusion systems of $\lambda \omega$ type. *Physica* D **82**, 165–179.
- SHERRATT, J. A. 1997 A comparison of two numerical methods for oscillatory reaction-diffusion equations. *Appl. Math. Lett.* **10**, 1–5.
- SHERRATT, J. A. 1999 Invading wave fronts and their oscilatory wakes are linked by a modulated travelling phase resetting wave. *Physica* D to appear.
- SHERRATT, J. A., EAGAN, B. T., & LEWIS, M. A. 1997 Oscillations and chaos behind predatorprey invasion: mathematical artifact or ecological reality. *Phil. Trans. R. Soc.* B 352, 21–38.
- SHERRATT, J. A., LEWIS, M. A., & FOWLER, A. C. 1995 Ecological chaos in the wake of invasion. Proc. Nat. Acad. Sci. USA 92, 2524–2528.
- SKELLAM, J. C. 1951 Random dispersal in theoretical populations. Biometrika 38, 196-218.
- SNEYD, J., GIRARD, S., & CLAPHAM, D. 1993 Calcium wave propagation by calcium-induced calcium release: an unusual excitable system. *Bull. Math. Biol.* 55, 315–344.
- SNEYD, J., KEIZER, J., & SANDERSON, M. J. 1995 Mechanisms of calcium oscillations and waves: a quantative analysis. *FASEB J.* 14, 1463–1472.
- SNEYD, J. & SHERRATT, J. A. 1997 On the propagation of calcium waves in an inhomogeneous medium. SIAM J. Appl. Math. 57, 73–94.
- STÖSSEL, R. & MÜNSTER, A. F. 1995 Periodic and irregular wave patterns in an open tubular gel reactor. *Chem. Phys. Lett.* 239, 354–360.
- TEMME, N. M. 1975 Uniform asymptotic expansions of the incomplete gamma functions and the incomplete beta function. *Math. Comp.* **29**, 1109–1114.