J. Math. Biol. (1996) 34: 857–877

Journal of
Mathematical
Biology

Mechanisms for stabilisation and destabilisation of systems of reaction-diffusion equations

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Received 10 January 1995; received in revised form 5 June 1995

Abstract. Potential mechanisms for stabilising and destabilising the spatially uniform steady states of systems of reaction-diffusion equations are examined. In the first instance the effect of introducing small periodic perturbations of the diffusion coefficients in a general system of reaction-diffusion equations is studied. Analytical results are proved for the case where the uniform steady state is marginally stable and demonstrate that the effect on the original system of such perturbations is one of stabilisation. Numerical simulations carried out on an ecological model of Levin and Segel (1976) confirm the analysis as well as extending it to the case where the perturbations are no longer small. Spatio-temporal delay is then introduced into the model. Analytical and numerical results are presented which show that the effect of the delay is to destabilise the original system.

Key words: Reaction-diffusion equations – Time-periodic diffusion coefficients – Spatio-temporal delay

1 Introduction

The development of a heterogeneous spatial pattern from an underlying homogeneous steady-state via diffusion-driven instability is well known and so-called "Turing-systems" have been postulated to explain the occurrence of pattern formation arising in many biological situations (e.g. Turing, 1952; Gierer and Meinhardt, 1972). Indeed it has recently been realised that the question to be asked should not be "how does pattern arise?" but rather "how does pattern not arise?" (Dillon et al., 1994), since the crucial aspect of pattern formation is that it should occur in a robust way, time after time, generation after generation, largely unaffected by any noise in the system. It has been shown (Murray, 1982) that the difference between different reaction-diffusion systems is the size of the region of parameter space which gives rise to pattern.

Questions of stability are then crucial to the development of pattern and it is in this context that we examine two possible mechanisms and their potential to stabilise or destabilise a system of reaction-diffusion equations. These questions are investigated in the following sections by examining the effect of

(a) periodic diffusion coefficients and

(b) spatio-temporal delays

on the stability of the spatially uniform steady-state of a system of reaction-diffusion equations which is assumed initially to be marginally stable. Asymptotic methods are used to obtain results for the case of marginal stability of a general system and then illustrated numerically using the specific ecological model of Levin and Segel (1976). These results are then extended by considering numerical simulations in the case where the uniform steady state is not necessarily marginally stable and where the perturbations are not necessarily small.

2 Periodic perturbations of diffusion coefficients

In 1992 Timm and Okubo considered the effect of small periodic perturbations in one of the diffusion coefficients on the stability of a spatially uniform steady state solution of a particular reaction-diffusion system, and showed that the effect was always stabilising. In this section we use the two-timing method to generalise their work by considering more general reaction-diffusion systems and allowing small periodic perturbations in all the diffusion coefficients. We shall develop the argument in the context of the homogeneous Neumann problem, but other initial boundary value problems and the Cauchy problem may be analysed similarly. The problem $P(\varepsilon)$ is

$$\boldsymbol{S}_t = \boldsymbol{f}(\boldsymbol{S}) + D(t;\varepsilon)\Delta\boldsymbol{S} \quad \text{in } \Omega\times(0,\ \infty) \tag{2.1}$$

with homogeneous Neumann boundary conditions, and initial conditions to be specified later. For simplicity we shall take $\boldsymbol{S}$ to be two-dimensional, $\boldsymbol{S} = (S_1, S_2)^T$, and D to be a positive diagonal matrix. Let $D(t;\varepsilon)$ be periodic of period T, but let $D(t;0)$ be independent of t, so that the periodic perturbations are small. We write

$$D(t;\varepsilon) = D^0 + \varepsilon D^1(t)\ .$$

Let $\boldsymbol{S}^*$ be a steady spatially uniform marginally stable solution of the problem $P(\varepsilon)$, so that $\boldsymbol{f}(\boldsymbol{S}^*) = \boldsymbol{0}$. For any n let v_n and ψ_n be the n-th eigenvalue and eigenfunction of $-\Delta$ on Ω with homogeneous Neumann boundary conditions, so $v_0 = 0$, $v_n > 0$ for $n > 0$, and let the marginally stable mode be the m-th, for some $m \neq 0$. Let the initial conditions be given by

$$\boldsymbol{S}_0 = \sum_{n=0}^{\infty} (B_n^1 \boldsymbol{c}_n^1 + B_n^2 \boldsymbol{c}_n^2)\psi_n\ , \tag{2.2}$$

where c_n^1 and c_n^2 are the eigenvectors with eigenvalues σ_n^1 and σ_n^2 of the eigenvalue problem

$$\sigma_n c_n = df(S^*)c_n - \nu_n D^0 c_n =: Ac_n - \nu_n D^0 c_n \,. \tag{2.3}$$

We assume that such distinct eigenvectors exist for each n purely for simplicity in the exposition. Then the linearised unperturbed problem $Q(0)$ given by

$$\tilde{S}_t = df(S^*)\tilde{S} + D^0 \Delta \tilde{S} = A\tilde{S} + D^0 \Delta \tilde{S} \quad \text{in } \Omega \times (0, \infty)\,, \tag{2.4}$$

with boundary and initial conditions as for $P(\varepsilon)$, has solution

$$\tilde{S}(t) = \sum_{n=0}^{\infty} \{B_n^1 c_n^1 \exp(\sigma_n^1 t) + B_n^2 c_n^2 \exp(\sigma_n^2 t)\}\,\psi_n \,. \tag{2.5}$$

Let us investigate the consequences of the assumption of marginal stability. The eigenvalues σ_n^1 and σ_n^2 satisfy the quadratic

$$\begin{vmatrix} \sigma_n - a_{11} + \nu_n D_1^0 & -a_{12} \\ -a_{21} & \sigma_n - a_{22} + \nu_n D_2^0 \end{vmatrix} = 0$$

Thus

$$\sigma_n^2 - (a_{11} + a_{22} - \nu_n D_1^0 - \nu_n D_2^0)\sigma_n + H^0(\nu_n) = 0$$

where

$$H^0(\nu_n) = a_{11}a_{22} - a_{12}a_{21} - (a_{11}D_2^0 + a_{22}D_1^0)\nu_n + D_1^0 D_2^0 \nu_n^2 \,. \tag{2.6}$$

The condition of stability for $n = 0$ implies that

$$\left.\begin{aligned} tr(A) &= a_{11} + a_{22} < 0 \\ \det(A) &= a_{11}a_{22} - a_{12}a_{21} > 0 \end{aligned}\right\} . \tag{2.7}$$

That of marginal stability for $n = m$ therefore gives $H^0(\nu_m) = 0$, and hence that one and only one of a_{11} and a_{22} is positive; let us take

$$a_{11} > 0, \qquad a_{22} < 0 \tag{2.8}$$

without loss of generality. The marginal stability assumption and the restriction to two dimensions therefore implies that there is a single zero eigenvalue $\sigma_m^1 = 0$ of the problem at $\varepsilon = 0$; the analysis is easily extended to higher dimensions under this condition. Now (2.6) implies that

$$\tilde{S}(t) = B_m^1 c_m^1 \psi_m + \text{EST} =: B_0 c\psi + \text{EST}\,,$$

say, where EST stands for exponentially small terms.

Based on this analysis we shall construct a solution of the linearised problem $Q(\varepsilon)$, given by

$$\tilde{S}_t = df(S^*)\tilde{S} + D(t;\varepsilon)\Delta\tilde{S} = A\tilde{S} + D(t;\varepsilon)\Delta\tilde{S}$$

in $\Omega \times (0, \infty)$ with the usual boundary and initial conditions, by the two-timing method. This will determine the linearised stability, and hence (by standard results) the stability, of the solution $\boldsymbol{S}^*$ of the problem $P(\varepsilon)$. Since the problem is linear, and neglecting exponentially small terms, we may restrict attention to the m-th mode. Defining $\boldsymbol{w}$ by $\tilde{\boldsymbol{S}} = \boldsymbol{w}\psi + \mathrm{EST}$, the problem reduces to the ordinary differential equation in $\mathbb{R}^2$,

$$\frac{d\boldsymbol{w}}{dt} = A\boldsymbol{w} - vD(t;\varepsilon)\boldsymbol{w} =: M(t;\varepsilon)\boldsymbol{w}$$

with initial conditions $\boldsymbol{w}(0) = B_0\boldsymbol{c}$.

For small ε, we are close to the boundary between stable and unstable behaviour, so we expect growth or decay of solutions on a slow time scale. Let $T_0 = \omega t$, $T_1 = \Omega_1 t$, where $\omega = 1$, $\Omega_1 \approx \varepsilon + \varepsilon^2\Omega_1^2 + \cdots$. It is not necessary to expand ω as a power series in ε as the fast time scale is determined by the periodic forcing of the problem. Define $\boldsymbol{W}$ by $\boldsymbol{W}(T_0, T_1;\varepsilon) := \boldsymbol{w}(t;\varepsilon)$, and the problem becomes

$$\frac{\partial \boldsymbol{W}}{\partial T_0} + \Omega_1 \frac{\partial \boldsymbol{W}}{\partial T_1} = A\boldsymbol{W} - vD(T_0;\varepsilon)\boldsymbol{W} = M(T_0;\varepsilon)\boldsymbol{W},$$

say, with initial conditions

$$\boldsymbol{W}(0, T_1;\varepsilon) = B(T_1)\boldsymbol{c}, \qquad B(0) = B_0 .$$

The function B is determined by requiring that $\boldsymbol{W}$ be bounded in $T_0 \in \mathbb{R}$; its behaviour as a function of T_1 determines the stability of $\boldsymbol{S}^*$ as a solution of $P(\varepsilon)$.

We expand $\boldsymbol{W}$ in powers of ε, $\boldsymbol{W} \approx \boldsymbol{W}^0 + \varepsilon\boldsymbol{W}^1 + \cdots$, and equate coefficients of each power. We also write $M = M^0 + \varepsilon M^1$. The $O(1)$ terms give

$$\frac{\partial \boldsymbol{W}^0}{\partial T_0} = A\boldsymbol{W}^0 - vD^0\boldsymbol{W}^0 = M^0\boldsymbol{W}^0,\ \boldsymbol{W}^0(0, T_1) = B(T_1)\boldsymbol{c}$$

which, by the assumption of marginal stability and the fact that $\boldsymbol{c}$ is an eigenvector of M^0 with zero eigenvalue, has a solution bounded in $T_0 \in \mathbb{R}$ given by $\boldsymbol{W}^0(T_0, T_1) = B(T_1)\boldsymbol{c}$. The $O(\varepsilon)$ terms give

$$\frac{\partial \boldsymbol{W}^1}{\partial T_0} - A\boldsymbol{W}^1 + vD^0\boldsymbol{W}^1 = -\frac{\partial \boldsymbol{W}^0}{\partial T_1} - vD^1(T_0)\boldsymbol{W}^0$$

or

$$L\boldsymbol{W}^1 := \left(\frac{\partial}{\partial T_0} - M^0\right)\boldsymbol{W}^1 = \boldsymbol{h}^1(T_0) := \left(-\frac{\partial}{\partial T_1} + M^1(T_0)\right)\boldsymbol{W}^0$$

which by Fredholm theory has a solution bounded for $T_0 \in \mathbb{R}$ iff $[\boldsymbol{h}^1, \boldsymbol{c}^*] = 0$, where $[\cdot,\cdot]$ is the standard inner product for $\mathbb{R}^2$-valued functions periodic of period T, namely the average as a function of T_0 over a period of the Euclidean inner product $\langle\cdot,\cdot\rangle$, and $\boldsymbol{c}^*$ is the adjoint eigenvector to $\boldsymbol{c}$ in this set-up. Since $\boldsymbol{W}^0$ is constant as a function of T_0 the Fredholm orthogonality condition reduces to

$$\langle\boldsymbol{c}^*, \boldsymbol{c}\rangle B' = \langle\boldsymbol{c}^*, \bar{M}^1\boldsymbol{c}\rangle B$$

where $\bar{M}^1$ is the average value of M^1 over a period. Stability is determined by the sign of $\langle \boldsymbol{c}^*, \bar{M}^1 \boldsymbol{c} \rangle / \langle \boldsymbol{c}^*, \boldsymbol{c} \rangle$, stable if negative and unstable if positive.

The result above essentially says that the stability of the solution of the linearised problem (up to $O(\varepsilon)$), and hence the stability boundary for the nonlinear problem, depends on the *average* value of the coefficients in the problem over their period (up to $O(\varepsilon)$). There is to this order no effect due to their periodicity itself. To determine this effect we need to go to $O(\varepsilon^2)$, and to simplify the calculations we shall assume that the periodic perturbations to the coefficients have average value zero (if necessary by incorporating non-zero average values into the leading order term). Thus from now on we have $\bar{M}^1 = 0$. It is a consequence of the fact that this is an $O(\varepsilon^2)$ effect that the slow time scale must be changed, and we define $T_2 = \Omega_2 t$, $\Omega_2 \approx \varepsilon^2 + \varepsilon^3 \Omega_2^3 + \cdots$.

With obvious consequent changes, the problem becomes

$$\frac{\partial \boldsymbol{W}}{\partial T_0} + \Omega_2 \frac{\partial \boldsymbol{W}}{\partial T_2} = M \boldsymbol{W}$$

$$\boldsymbol{W}(0, T_2; \varepsilon) = B(T_2)\boldsymbol{c}, \qquad B(0) = B_0 .$$

Leading order terms give $\boldsymbol{W}^0(T_0, T_2) = B(T_2)\boldsymbol{c}$, and $O(\varepsilon)$ terms

$$L\boldsymbol{W}^1 = M^1(T_0)\boldsymbol{W}^0 \tag{2.9}$$

for which the Fredholm orthogonality condition is trivially satisfied since $\boldsymbol{W}^0$ is independent of T_0 and M^1 is a function T_0 with average value zero. The $O(\varepsilon^2)$ terms give

$$L\boldsymbol{W}^2 = -\frac{\partial \boldsymbol{W}^0}{\partial T_2} + M^1(T_0)\boldsymbol{W}^1 .$$

The Fredholm orthogonality condition gives

$$\langle \boldsymbol{c}^*, \boldsymbol{c} \rangle B' = [\boldsymbol{c}^*, M^1 \boldsymbol{W}^1] .$$

Stability is determined by the sign of α, defined by

$$\langle \boldsymbol{c}^*, \boldsymbol{c} \rangle \alpha B := [\boldsymbol{c}^*, M^1 \boldsymbol{W}^1] .$$

This is easily calculated in any given instance, using the explicit formula

$$\boldsymbol{W}^1(T_0) = \exp(M^0 T_0) \int_0^{T_0} \exp(-M^0 \tau_0) M^1(\tau_0) \boldsymbol{W}^0 \, d\tau_0 . \tag{2.10}$$

But M^1 is a diagonal matrix,

$$M^1 = \begin{pmatrix} m_{11}^1 & 0 \\ 0 & m_{22}^1 \end{pmatrix} .$$

Therefore (2.10) gives

$$m_{11}^1 Bc_1 = \frac{\partial W_1^1}{\partial T_0} - m_{11}^0 W_1^1 - m_{12}^0 W_2^1$$

$$m_{22}^1 Bc_2 = \frac{\partial W_2^1}{\partial T_0} - m_{21}^0 W_1^1 - m_{22}^0 W_2^1$$

and therefore

$$\begin{aligned}\langle \boldsymbol{c}^*, M^1 \boldsymbol{W}^1 \rangle &= c_1^* m_{11}^1 W_1^1 + c_2^* m_{22}^1 W_2^1 \\ &= \frac{c_1^*}{Bc_1} W_1^1 \left(\frac{\partial W_1^1}{\partial T_0} - m_{11}^0 W_1^1 - m_{12}^0 W_2^1 \right) \\ &+ \frac{c_2^*}{Bc_2} W_2^1 \left(\frac{\partial W_2^1}{\partial T_0} - m_{21}^0 W_1^1 - m_{22}^0 W_2^1 \right)\end{aligned}$$

Integrating over a period, recalling that $\boldsymbol{W}^1$ is periodic and $\boldsymbol{c}, \boldsymbol{c}^*$ and B are independent of T_0,

$$\begin{aligned}B[\boldsymbol{c}^*, M^1 \boldsymbol{W}^1] = \frac{1}{T} \int_0^T & \left\{ \frac{c_1^*}{c_1} W_1^1 (-m_{11}^0 W_1^1 - m_{12}^0 W_2^1) \right. \\ & \left. + \frac{c_2^*}{c_2} W_2^1 (-m_{21}^0 W_1^1 - m_{22}^0 W_2^1) \right\} .\end{aligned}$$

By a simple calculation we may take $c_1 = -m_{12}^0, c_2 = m_{11}^0$, $c_1^* = -m_{21}^0$, $c_2^* = m_{11}^0$. Note that $m_{11}^0 m_{22}^0 = m_{12}^0 m_{21}^0$; this follows from the marginal stability of the mth mode. Using this, we get $\langle \boldsymbol{c}^*, \boldsymbol{c} \rangle = m_{11}^0 (m_{11}^0 + m_{22}^0)$, and, after some algebra,

$$B[\boldsymbol{c}^*, M^1 \boldsymbol{W}^1] = -m_{11}^0 \frac{m_{21}^0}{m_{12}^0} \frac{1}{T} \int_0^T \left(W_1^1 + \frac{m_{12}^0}{m_{11}^0} W_2^1 \right)^2 .$$

It follows that

$$\begin{aligned}\operatorname{sgn} \alpha &= -\operatorname{sgn} m_{12}^0 m_{21}^0 (m_{11}^0 + m_{22}^0) \\ &= -\operatorname{sgn} a_{12} a_{21} (a_{11} + a_{22} - v(D_1^0 + D_2^0)) \\ &= -1\end{aligned}$$

and so the system is always stabilised by the perturbation.

The above results show that all *small amplitude* periodic perturbations with average zero in the diffusion coefficients are stabilising, but if the perturbations are $O(\varepsilon)$ then the stabilising effect is $O(\varepsilon^2)$. This generalises the results of Timm and Okubo (1992) to models other than that of Levin and Segel (1976), and to the case of perturbations in more than one diffusion coefficient. In the next section we conduct a numerical investigation of a particular case when the periodic perturbation is sinusoidal, but not necessarily of small amplitude. We find that when the amplitude is large, stabilisation still results. However, for large amplitude oscillations in diffusivity, the precise nature of the oscillations must be important because Sherratt (1995) has shown that when the diffusivity of one species alternates between two constant values (i.e. has a square tooth form), the uniform state can be driven unstable.

We have tried other perturbations, which have also resulted in stabilisation (cf. Appendix 1). However, a more general result than given here has yet to be proved.

3 Numerical simulations

In this section we examine the predator-prey (zooplankton-phytoplankton) model of Levin and Segel (1976) and carry out some numerical simulations in order to demonstrate the analytical results of the previous section. Thus we take

$$\begin{aligned} f_1(\boldsymbol{S}) &= a_1 S_1 + c_1 S_1^2 - b_1 S_1 S_2 \\ f_2(\boldsymbol{S}) &= -c_2 S_2^2 + b_2 S_1 S_2 \end{aligned} \tag{3.1}$$

The steady states $\boldsymbol{S}^*$ satisfy $f_1(\boldsymbol{S}^*) = f_2(\boldsymbol{S}^*) = 0$ and correspondingly the Jacobian evaluated at the steady states ($d\boldsymbol{f}^0(\boldsymbol{S}^*) = A^0$) is given by

$$A^0 = \begin{pmatrix} c_1^0 S_1^* & -b_1^0 S_1^* \\ b_1^0 S_2^* & -c_2^0 S_2^* \end{pmatrix}$$

Following Timm and Okubo (1992), we use the data of Wroblewski and O'Brien (1976) to estimate the parameters of the model as

$$a_1 = 0.2 \times 10^{-5} \text{s}^{-1}, \qquad b_1 = b_2 = 0.0383 \times 10^{-5} \text{s}^{-1} (\mu\text{g N l}^{-1})^{-1},$$

$$c_1 = 0.02 \times 10^{-5} \text{s}^{-1} (\mu\text{g N l}^{-1})^{-1}, \qquad c_2 = 0.0575 \times 10^{-5} \text{s}^{-1} (\mu\text{g N l}^{-1})^{-1}. \tag{3.2}$$

Again, following Timm and Okubo (1992) we investigate the effect on the stability of the system by introducing a time-varying diffusion coefficient D_2, where D_2 is of the particular form

$$D_2(\tau) = D_1(a + b \sin \tau) \quad a > 1, \quad a > |b|, \tag{3.3}$$

with τ a dimensionless time given by $\tau \equiv \omega t$, $\omega > 0$ being the frequency of variation in D_2 which we take as 2π (per day) $= 7.272 \times 10^{-5} \text{s}^{-1}$. Considering the case $b = 0$, it is straightforward to show that the linearised problem (with the above set of parameters and particular scaling in time) is marginally stable for some critical value of $a = a_{\text{cr}} = 5.24$ and it is a straightforward task to show

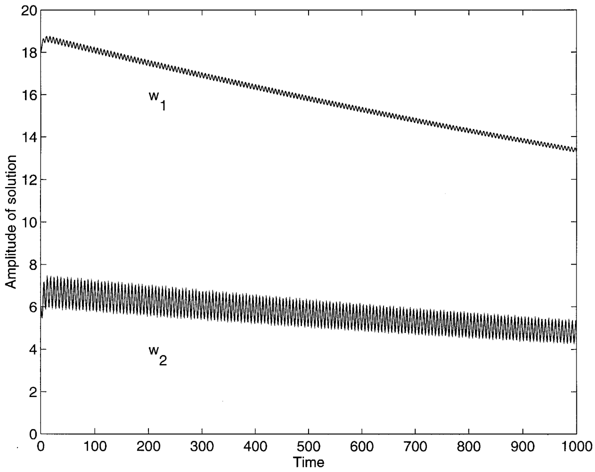

Fig. 1. Long time behaviour of w_1 and w_2 obtained by numerical integration of (3.4) showing the stabilising $O(\varepsilon^2)$ effect of the time-dependent diffusion coefficient $D_2 = D_1(a + b \sin \tau)$ i.e. the solutions of both w_1 and w_2 tend slowly to zero due to the time-varying diffusivity. The values of a and b used are $a = a_{cr} = 5.24$ and $b = 3.5$. w_1 denotes amplitude of prey, while w_2 denotes amplitude of predator

that the stability analysis with $b \neq 0$ reduces to solving the following pair of ordinary differential equations

$$\begin{aligned} \frac{dw_1}{d\tau} &= 0.0682 w_1 - 0.1911 w_2 \\ \frac{dw_2}{d\tau} &= 0.1273 w_1 - (0.3572 + 0.0317 b \sin \tau)\, w_2 \end{aligned} \tag{3.4}$$

where $b < a_{cr} = 5.24$. Figure 1 shows the results of solving the above system of equations using second and third order Runge–Kutta formulas with initial conditions $[w_1(0), w_2(0)]^T = [18, 6]^T$ and $b = 3.5$. The $O(\varepsilon^2)$ stabilising effect of the time-dependent diffusion coefficient D_2 is clearly seen with the solutions w_1, w_2 both slowly tending to zero (as is to be expected from the previous analytical results).

A more general study of the stability of the system when b is not necessarily small (but satisfies $a > b > 0$) and away from the critical point a_{cr}, where the uniform steady-state is not marginally stable, may be carried out numerically. This involves a similar system of ODEs as (3.4) with the only difference being in the value chosen for the wavenumber k. Figure 2 illustrates the domains of instability and stability in the ab-plane which are separated by the stability curve. This diagram was obtained using numerical continuation by integrating the system of ODEs numerically with a fixed initial value of $a = a^* > a_{cr}$ and an initial value of $b = b_1$ satisfying $a^* > b_1 > 0$. Solutions which diverged from the initial conditions were considered unstable, the point

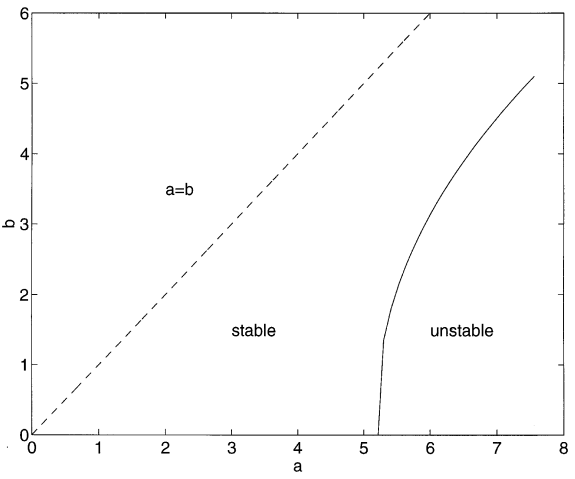

Fig. 2. Stability diagram showing regions of stability and instability in the (a, b) plane separated by the stability boundary

(a^*, b_1) lying in the unstable region. The process was then repeated a number of times with the same value of a^*, but with the value for b_1 increased by 0.05 each time, until the solutions converged to zero at some $b = b^*$ and were considered stable. The point (a^*, b^*) was then deemed to lie on the stability curve. The whole process was then repeated using a new initial point $(a^* + 0.05, b_1)$ until the stability curve shown in Fig. 2 was obtained. The results show that for a sufficiently large value of b the effect of the perturbation is one of stability.

4 Delay-induced instability

In the previous sections we considered how the stability of a uniform steady state solution of a system changes when small amplitude temporally periodic perturbations were added to the diffusion coefficients of the system. In the remainder of this paper we shall work with constant diffusivities once more (in the notation of Sect. 2, our problem $P(0)$ becomes problem P), and consider how the stability of the uniform steady state changes when a time delay is introduced into the predator equation to take account of the delayed predator growth rate response to a change in prey density, due to the predator's gestation period. In this section it is convenient to work on an infinite spatial domain $x \in (-\infty, \infty)$ because of the way we incorporate averaging in space that arises as a consequence of incorporating delay into a diffusion model. Throughout the remainder of the paper, and following on from the example at the end of the previous section, we concentrate on the model of Levin and Segel (1976) as a specific case-study to illustrate the effect of introducing a delay term into a system of reaction-diffusion equations. We shall then compare and contrast these effects with those of time-dependent periodic diffusion coefficients. Let us restate for convenience the system with constant diffusivities:

$$\begin{aligned} \partial S_1/\partial t &= D_1 \partial^2 S_1/\partial x^2 + S_1(a_1 + c_1 S_1 - b_1 S_2) , \\ \partial S_2/\partial t &= a D_1 \partial^2 S_2/\partial x^2 + S_2(b_2 S_1 - c_2 S_2) . \end{aligned} \tag{4.1}$$

In order to model the predator's gestation period, we will replace S_1, in the second equation only, by

$$S_3(x,t) := \int_{-\infty}^{t} \int_{-\infty}^{\infty} g(x-y, t-s) S_1(y,s)\, dy\, ds \tag{4.2}$$

so we shall be studying the system

$$\begin{aligned} \partial S_1/\partial t &= D_1 \partial^2 S_1/\partial x^2 + S_1(a_1 + c_1 S_1 - b_1 S_2) , \\ \partial S_2/\partial t &= a D_1 \partial^2 S_2/\partial x^2 + S_2\left(b_2 \int_{-\infty}^{t} \int_{-\infty}^{\infty} g(x-y,t-s) S_1(y,s)\, dy\, ds - c_2 S_2 \right) . \end{aligned} \tag{4.3}$$

The kernel $g(x,t)$ satisfies

$$\int_0^\infty \int_{-\infty}^{\infty} g(x,t)\, dx\, dt = 1$$

and so S_3 is a spatio-temporal average of S_1. It follows that the uniform steady states of the new model (4.3) will be the same as those of (4.1) and so we are particularly interested in the stability of the steady state (S_1^*, S_2^*) given by

$$S_1^* = \frac{a_1 c_2}{b_1 b_2 - c_1 c_2}, \qquad S_2^* = \frac{a_1 b_2}{b_1 b_2 - c_1 c_2}. \tag{4.4}$$

We will consider the two cases

$$g(x,t) = \frac{1}{\sqrt{4\pi D_1 t}}\, e^{-x^2/(4D_1 t)}\, \frac{1}{T}\, e^{-t/T} , \tag{4.5}$$

$$g(x,t) = \frac{1}{\sqrt{4\pi D_1 t}}\, e^{-x^2/(4D_1 t)}\, \delta(t - T) \tag{4.6}$$

where in each case T is a positive constant measuring the delay in the system (in a sense to be discussed shortly), and is quite unrelated to the T of Sect. 2.

The use of a spatio-temporal average of the form (4.2) to model delay effects follows the ideas of Britton (1990) and Gourley (1993). The kernel $g(x,t)$ specifies how important the prey population density is at each past time. The integral in space arises because at previous times individual animals will not have been at the same point in space. Thus spatial averaging arises because of our incorporation of delay into a model where there is motion of individuals in the population, and $g(x, t)$ will in fact act as a weighting function for both the spatial and the temporal averaging.

When kernel (4.5) is used, the entire past history of S_1 is taken into account in the temporal averaging and so the delay is of a "distributed" type. However, the importance of individual "events" depends on how long ago they happened, and this importance can be thought of as being measured by $\frac{1}{T}\exp(-(t-s)/T)$ where $s < t$ is some particular time in the past and t is current time. So this kernel implies exponentially decreasing importance of the past. However the rate at which the exponential decays can be reduced by increasing T, so T in this sense can be taken as a quantitative measure of the delay. The other part of the expression for this kernel accounts for the movement of animals by diffusion and was derived on the basis of a simple random walk argument by Britton (1990).

When kernel (4.6) is used the spatio-temporal average (4.2) becomes

$$S_3 = \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi D_1 T}} \mathrm{e}^{-(x-y)^2/(4D_1 T)} S_1(y, t-T)\, dy$$

so that only the density at time $t - T$ is taken into account in the temporal averaging, and not the entire past history. Here, T would be the predator's gestation period.

Now, we know (Timm and Okubo, 1992), that the system without delay, namely (4.1), may exhibit diffusion-driven instability whenever

$$a > a_{\mathrm{cr}} = a_{11}^{-2}[(a_{11}a_{22} - a_{12}a_{21})^{1/2} + |a_{12}a_{21}|^{1/2}]^2 \tag{4.7}$$

with the a_{ij} given by

$$\begin{aligned} a_{11} &= c_1 S_1^* > 0, \qquad a_{12} = -b_1 S_1^* < 0\,, \\ a_{21} &= b_2 S_2^* > 0, \qquad a_{22} = -c_2 S_2^* < 0\,. \end{aligned} \tag{4.8}$$

In this section we are interested in the possibility of destabilisation of the uniform steady state that is delay-induced rather than diffusion-induced. Consequently we shall assume henceforth that $a < a_{\mathrm{cr}}$. This is equivalent to assuming that

$$H(k^2) > 0 \quad \text{for all } k^2 \geqq 0 \tag{4.9}$$

where

$$H(k^2) \equiv D_1^2 a k^4 - D_1(a_{11}a + a_{22})k^2 + a_{11}a_{22} - a_{12}a_{21}\,, \tag{4.10}$$

where we note that we now have $D_2 = aD_1$, H is equivalent to H^0 and k^2 is equivalent to v in the notation of Sect. 2. Our intention is to compute, for each of kernels (4.5, 4.6), stability diagrams in the (T, a) plane for the uniform steady state solution (S_1^*, S_2^*). For both of these kernels we have been speaking of the quantity T as the delay, but it is important at this stage to assure ourselves that we are making a valid comparison. We need to work with a definition of delay that is independent of the specific functional form of the kernel. Following Gourley (1993), given any kernel $g(x,t)$ we define the delay associated with this kernel to be

$$\int_0^\infty \int_{-\infty}^\infty t g(x,t)\,dx\,dt\ . \tag{4.11}$$

This definition (without the space integral) has been commonly used in studying spatially uniform systems (e.g. Cushing (1977)). When applied to the kernels (4.5, 4.6), the integral (4.11) yields the value T in both cases.

We will now consider in detail each of the two kernels (4.5, 4.6).

4.1 The distributed delay case

When

$$g(x,t) = \frac{1}{\sqrt{4\pi D_1 t}}\,\mathrm{e}^{-x^2/(4D_1 t)}\,\frac{1}{T}\,\mathrm{e}^{-t/T}\ , \tag{4.12}$$

a calculation shows that $S_3(x,t)$, defined by (4.2), satisfies

$$\frac{\partial S_3}{\partial t} = D_1\frac{\partial^2 S_3}{\partial x^2} + \frac{1}{T}(S_1 - S_3)\ .$$

Consequently, the original system (4.1) may be replaced by the system

$$\begin{aligned} \partial S_1/\partial t &= D_1 \partial^2 S_1/\partial x^2 + S_1(a_1 + c_1 S_1 - b_1 S_2)\ ,\\ \partial S_2/\partial t &= a D_1 \partial^2 S_2/\partial x^2 + S_2(b_2 S_3 - c_2 S_2)\ ,\\ \partial S_3/\partial t &= D_1 \partial^2 S_3/\partial x^2 + \tfrac{1}{T}(S_1 - S_3)\ . \end{aligned} \tag{4.13}$$

Note that in this system the first and third equations have the same diffusion coefficient. This system has a spatially uniform steady state $S_1 = S_1^*$, $S_2 = S_2^*$ and $S_3 = S_3^*$. Here S_1^* and S_2^* are as for the non-delay case (see (4.4)), and $S_3^* = S_1^*$. We are interested in the linear stability of this steady state. Defining

$$S_i = S_i^* + \tilde{S}_i, \quad i = 1, 2, 3$$

where the $\tilde{S}_i$ are small, we obtain the linearised system

$$\tilde{\boldsymbol{S}}_t = A\tilde{\boldsymbol{S}} + D\Delta\tilde{\boldsymbol{S}}$$

where now $D = \mathrm{diag}(D_1, aD_1, D_1)$ (equivalent to D^0 of Sect. 2), $\tilde{\boldsymbol{S}} = (\tilde{S}_1, \tilde{S}_2, \tilde{S}_3)^{\mathrm{T}}$ and

$$A = \begin{pmatrix} a_{11} & a_{12} & 0 \\ 0 & a_{22} & a_{21} \\ \frac{1}{T} & 0 & -\frac{1}{T} \end{pmatrix}.$$

Here the a_{ij} are as per (4.8).

Solutions of the linearised system proportional to $\exp(\sigma t + ikx)$ exist whenever

$$(\sigma - a_{11} + D_1 k^2)(\sigma - a_{22} + aD_1 k^2)\left(\sigma + \frac{1}{T} + D_1 k^2\right) = \frac{1}{T} a_{12} a_{21} \tag{4.14}$$

and this can of course be rearranged to yield a cubic equation in σ.

For a system of two reaction-diffusion equations, the corresponding eigenvalue equation would be a quadratic in σ. It is a consequence of the assumption of stability in the absence of diffusion that this quadratic eigenvalue equation cannot have purely imaginary roots, so that when a diffusion driven instability occurs, it does so by a root of the eigenvalue equation passing through the origin in the complex plane, i.e., a bifurcation to a new (non-uniform) steady state. Our system, with the delay, is different because instability may also occur by a pair of complex conjugate roots crossing the imaginary axis, i.e., a Hopf bifurcation. We have to consider both possibilities.

The algebra is complicated in places, so we present only the overall conclusions, which were obtained with the aid of the symbolic manipulation package MAPLE. We use values for the parameters of the model as per (3.2) with a scaling of 10^5 for convenience. This scaling does not affect the steady state values S_i^* ($i = 1, 2$) for the non-delay model (4.1), nor the stability of this steady state, since we work on an infinite domain. The critical value a_{cr} is also unaffected by this scaling.

The (scaled) parameter values (3.2) lead to

$$\begin{aligned} S_1^* &= 36.29, & S_2^* &= 24.17\ , \\ a_{11} &= 0.7258, & a_{12} &= -1.39\ , \\ a_{21} &= 0.926, & a_{22} &= -1.39, \\ a_{cr} &= 5.24 \end{aligned} \tag{4.15}$$

and for numerical work we have taken $D_1 = 10^{-3}$.

The eigenvalue equation (4.14) will have a root $\sigma = 0$ whenever $T = T_0(k^2; a)$ where

$$T_0(k^2; a) = \frac{H(k^2)}{D_1 k^2 (a_{11} - D_1 k^2)(aD_1 k^2 - a_{22})}\,. \tag{4.16}$$

The subscript 0 refers to the fact that this expression gives the locus, in the (T, k^2) plane, of the root $\sigma = 0$. The function $H(k^2)$ is given by (4.10) and is a strictly positive function, since we are assuming $a \in (0, a_{cr})$ (i.e., that the system is stable in the absence of delay). Recalling that $a_{11} > 0$ and $a_{22} < 0$, the expression (4.16) is singular when $k^2 = 0$ and when $k^2 = a_{11}/D_1$. Its graph is shown in Fig. 3 for a typical $a \in (0, a_{cr})$. We have also shown the locus of Hopf bifurcations (Re $\sigma = 0$), denoted $T_H(k^2; a)$. This locus can be obtained by applying the standard conditions for a cubic equation to have purely imaginary roots, but closed form expressions for the locus are messy.

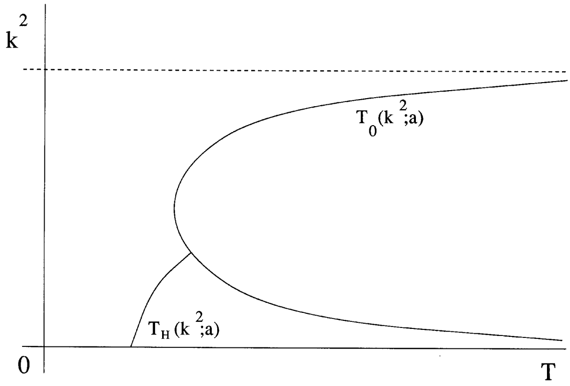

Fig. 3. Stability diagram for the steady state (S_1^*, S_2^*, S_3^*) of the system (4.13) for a typical $a \in (0, a_{cr})$, with parameter values given by (3.2), scaled by 10^5

With the (scaled) parameter values (3.2), a MAPLE plot of T_H (as a function of two variables) demonstrates that for any a in the range $(0, 5.24)$, $T_H(k^2; a)$ is a monotonically increasing function of k^2.

Now for any fixed $a \in (0, a_{cr})$ we wish to establish the critical T, which we call $T_{cr}(a)$, when instability first sets in. From Fig. 3 this critical T will be either the leftmost point on the $T_0(k^2; a)$ curve, or the leftmost point on the $T_H(k^2; a)$ curve, whichever value is least. The leftmost point on the latter curve is at $k^2 = 0$ because of the monotonicity of this curve. Thus the critical T when instability sets in is

$$T_{cr}(a) = \min\left(T_H(0; a), \min_{k^2 > 0} T_0(k^2; a) \right). \tag{4.17}$$

The above curve, plotted in the (T, a) parameter plane, is shown in Fig. 4. For a range of values of a the destabilising value for the delay T is $T_H(0; a)$ (which is actually independent of a). For higher a the destabilising value is the leftmost point on the $T_0(k^2; a)$ curve in Fig. 3.

Recall that for the non-delay system (4.1), diffusion-driven instability is possible if $a > a_{cr}$. Figure 4 shows that the introduction of delay has a very dramatic effect on the stability of the uniform steady state. For any $a < a_{cr}$, instability will set in if the delay is sufficiently large, and if T exceeds a finite value then the steady state is unstable for all a.

The system (4.13) may be solved numerically, using the Method of Lines and Gear's Method, as implemented by the NAG Fortran Library routine DO3PGF. This routine requires the problem to be posed on a finite spatial domain, whereas the definition of $S_3(x, t)$ (eqn. (4.2)) shows that, for the time-delayed version of our problem to make sense, $S_1(x, t)$ must be defined for all $x \in (-\infty, \infty)$. However, for any kernel $g(x, t)$ that is an even function of x (as both (4.5) and (4.6) are), it is not hard to see that, given a solution of (4.3), the transformation $x \to -x$ will yield another solution. Moreover if S_1 is

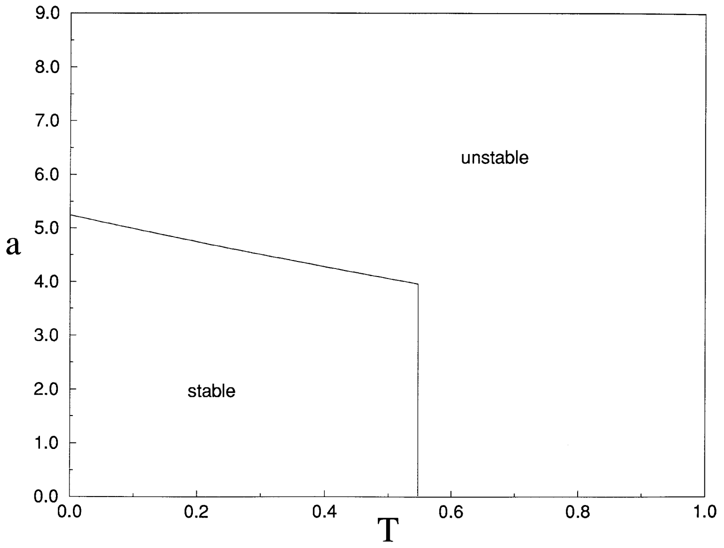

Fig. 4. Stability boundary in (T, a) plane for the system (4.13) with parameter values given by (3.2), scaled by 10^5

periodic in x then S_3 is periodic in x with the same period. In view of these considerations, we can seek solutions of (4.3) on $(-\infty, \infty)$ periodic in x by looking for solutions of (4.13) for $x \in (0, 1)$ satisfying the homogeneous Neumann boundary conditions

$$\frac{\partial S_i}{\partial x}(0, t) = \frac{\partial S_i}{\partial x}(1, t) = 0 \quad i = 1, 2, 3 \tag{4.18}$$

and by extending such a solution to an even function on $(-1, 1)$ and then periodically over all of $(-\infty, \infty)$ so that S_3 is well defined. With this understanding, our problem is henceforth one of considering the system (4.13) on the finite domain $x \in (0, 1)$. The domain $(0, 1)$ was of course chosen for convenience, and could be replaced by $(0, L)$ for any $L > 0$, although clearly once the domain is chosen, we are restricting attention to solutions of certain periods only. However for large domains we could, in view of the exponential decay of the kernel, simply interpret the problem as one on a finite spatial domain with homogeneous Neumann boundary conditions.

In Fig. 5 we have shown the evolution of a solution of (4.13) with boundary conditions (4.18) and with initial conditions taken as small random perturbations from the uniform state (S_1^*, S_2^*, S_3^*). For this numerical simulation the parameter values are again given by (3.2), scaled by 10^5, and $D_1 = 10^{-3}$. We have taken $a = 5.2$ (which is only just below the critical value of 5.24 for the non-delay case), and $T = \frac{2}{7}$. With $a = 5.2$ the critical delay obtained from (4.17) is 0.0169, although of course this is for an infinite spatial domain. We are now effectively working on a finite domain, so that in (4.17) the minimum will

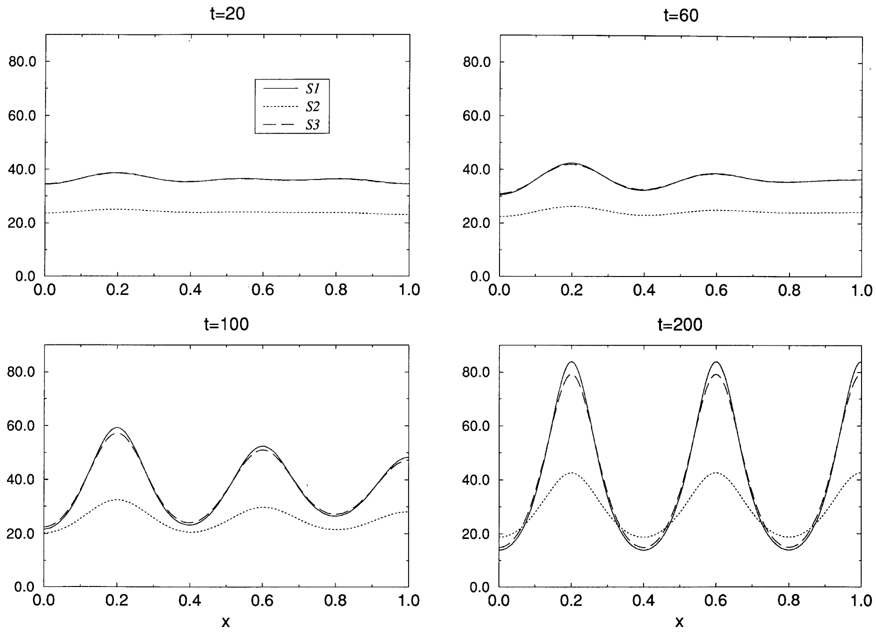

Fig. 5. Evolution of solution of (4.13) with boundary conditions (4.18). Initial conditions are small random perturbations from the uniform state (S_1^*, S_2^*, S_3^*)

be taken over a discrete set of values of the wavenumber k^2. This will have the effect of increasing the critical delay.

With the above parameter values, Fig. 5 shows convergence to a large amplitude steady state solution. The quantities of principal interest are the prey and predator densities S_1 and S_2, but we have also plotted S_3, the spatio-temporal average of S_1. In the earlier stages of the evolution the S_1 and S_3 curves are nearly coincident as we are using a small value of the delay (the use of a *zero* delay would, of course, result in convergence to the uniform state, since $a < a_{cr}$). Later in the evolution, when the steady state has been reached and there is more spatial variation, these two curves are more distinguishable since S_3 represents spatial, as well as temporal, averaging.

4.2 The fixed delay case

When

$$g(x,t) = \frac{1}{\sqrt{4\pi D_1 t}} \, e^{-x^2/(4D_1 t)} \, \delta(t - T)$$

the system (4.3) has to be linearised as an integro-differential system. It is not possible in this case to re-write the system as a system of reaction-diffusion equations without delay. However, the linearisation method for integro-differential systems in convolution form is well developed; the linearised equations are solved either by Laplace transforms or trial solutions. The associated calculations for the present model are comparable with those in the models studied by Gourley (1993). The eigenvalue equation corresponding to perturbations proportional to $\exp(\sigma t + ikx)$ turns out to be

$$(\sigma - a_{11} + D_1 k^2)(\sigma - a_{22} + aD_1 k^2) = a_{12}a_{21}e^{-\sigma T}e^{-D_1 T k^2}\,. \tag{4.19}$$

Adopting the same notation as for the previous kernel, the $\sigma = 0$ root locus for this case is given by

$$T_0(k^2; a) = \frac{1}{D_1 k^2}\log\frac{a_{12}a_{21}}{(D_1 k^2 - a_{11})(aD_1 k^2 - a_{22})}\,. \tag{4.20}$$

This locus is qualitatively similar to the corresponding one for the previous kernel (Fig. 3), and it is defined for the same range of values of k^2.

The locus $T_H(k^2; a)$ of Hopf bifurcation points for this kernel is much more difficult to detect. When $k^2 = 0$, equation (4.19) is in a standard, well studied, form (see, for example, Marshall et al (1992)), and in this case one can seek purely imaginary roots of the equation by setting $\sigma = i\omega$, and ω^2 will satisfy a certain polynomial equation that does not involve T. The value of T giving rise to these roots is then found from the original equation. The difficulty comes when $k^2 > 0$, because the equation determining ω^2 still involves T and it becomes difficult to proceed with the method.

We can obtain some information by using the Padé approximant

$$e^{-x} \sim \frac{1}{1 + x}$$

applied to both the terms $e^{-\sigma T}$ and $e^{-D_1 T k^2}$ in (4.19). The approximated equation can be rewritten as a cubic equation in σ and the conditions applied for the latter equation to have purely imaginary roots. This results in a polynomial in T of degree four, and numerically it may be demonstrated that for appropriate values of a this polynomial has only one positive root. Furthermore if we increase k^2 the root increases. Therefore on the basis of this analysis we conclude that $T_H(k^2; a)$ is a monotonically increasing function of k^2 and, as for the previous kernel, we should therefore like to know the value $T_H(0; a)$. But we can obtain this by studying the eigenvalue equation (4.19) without the Padé approximant. With $k^2 = 0$ the equation reads

$$(\sigma - a_{11})(\sigma - a_{22}) = a_{12}a_{21}e^{-\sigma T}$$

and, using the methods described in Marshall et al (1992) and the (scaled) parameter values (3.2), we obtain $T_H(0; a) = 0.5216$ (for all $a \in (0, a_{cr})$). Accordingly, the stability boundary in the (T, a) parameter plane is given by

$$T_{cr}(a) = \min\left(0.5216, \min_{k^2 > 0} T_0(k^2; a)\right). \tag{4.21}$$

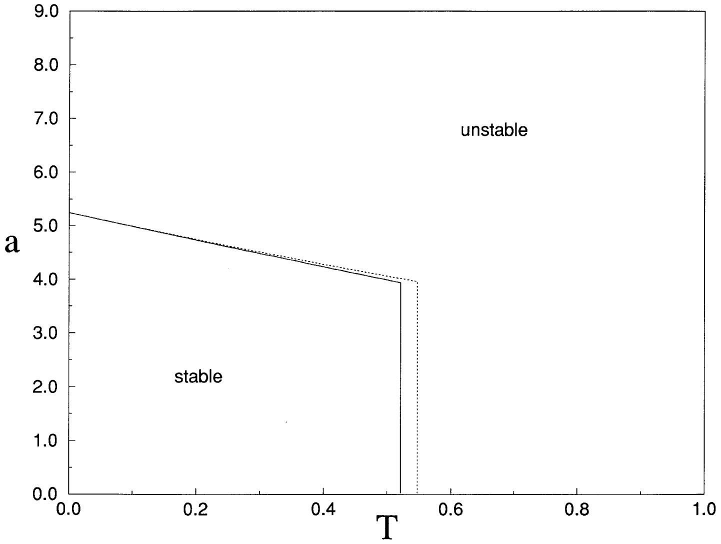

Fig. 6. Comparison of stability boundaries in (T, a) parameter plane for the kernels (4.5) and (4.6)

where $T_0(k^2; a)$ is now given by (4.20). This curve is plotted in Fig. 6, and the corresponding curve for the previous kernel is shown with a dotted line for comparison. Note that the two curves are very similar indeed, despite the distinct difference in the functional forms of the two kernels.

5 Conclusions

We have shown that the stability of the spatially uniform steady state of a system of reaction-diffusion equations may be altered by introducing time-dependent periodic diffusion coefficients into the original system or by introducing delays into the original system. Generalising the results of Timm and Okubo (1992), we have shown that small amplitude temporally periodic perturbations of the diffusion coefficients have a stabilising effect, but that it is a weak effect in the sense that convergence to the uniform steady state after a perturbation occurs on a very slow time scale. The incorporation of a single delay term, on the other hand, has a dramatic destabilising effect. Moreover, the instability domains in the (T, a) parameter plane for the two kernels we have considered illustrate not only this destabilising tendency but also suggest that the overall "amount of delay" in the system, measured by a quantity such as (4.11), is more important than the precise weighting given to individual times or periods in the past, i.e. the specific functional form of the delay kernel $g(x, t)$.

In systems without delay, regions of parameter space corresponding to instability of the uniform state of the system are commonly called the Turing space of the system. In an interesting paper, Murray (1982) considers various non-delay reaction-diffusion systems and compares their (two-parameter) Turing spaces, showing how these change in size when different values are taken for other parameters. The size of the Turing space of a system varies considerably from one system to another but it is often rather small, which could be interpreted as saying that instability is the exception rather than the rule.

In the present paper we have started with a known result concerning how, in the absence of delay, the stability or instability of the system depends on the value of a, which is the ratio of diffusivities. As usual, all other quantities being fixed, this ratio has to exceed a critical value for the system to initiate spatial patterns. We have now seen how this critical value drops when a delay is introduced into the system. We conjecture that the introduction of a delay into a system of reaction diffusion equations will have the effect of greatly increasing its corresponding Turing space for the other parameters, so that in fact it is *stability* that is the exception rather than the rule. Thus the emergence of spatial patterns is a typical phenomenon, holding in large regions of parameter space, and the question to be asked therefore becomes "how does pattern not arise". It is of course, very natural on biological grounds to incorporate delays into reaction-diffusion systems; in fact in virtually any biological system, responses to changes do occur with a delay and instantaneous responses are less common. Thus the use of models with delay terms (possibly several) should be quite natural.

Appendix

In this appendix we apply the method of multiple scales to the predator-prey model of Levin and Segel (1976) with diffusion included (Timm and Okubo, 1992). We show how the introduction of a small amplitude, temporally-periodic perturbation to one of the diffusion coefficients extends the domain of stability of the uniform steady state in a neighbourhood of the critical ratio of diffusion coefficients $a = D_2/D_1 = a_{cr}$. (When $a > a_{cr}$ diffusion-driven instability is realised (Turing, 1952).)

In the notation of Sect. 2, we once again study (2.1) with $\boldsymbol{f} = (f_1, f_2)^T$ defined by (3.1) and $D_2 = D_2(\tau)$ defined by (3.3). At the uniform steady-state we have $\boldsymbol{S} = \boldsymbol{S}^*$ with $f_1(\boldsymbol{S}^*) = 0 = f_2(\boldsymbol{S}^*)$. Following Timm and Okubo (1992), we consider small perturbations to $\boldsymbol{S}$ about the steady-state of the form:

$$\boldsymbol{S} = \boldsymbol{S}^* + \boldsymbol{s}(x, t) \,. \tag{5.1}$$

Linearization of (2.1) about $\boldsymbol{S}^*$ with the above $\mathbf{f}$ and D_2 leads to

$$\begin{aligned} \frac{\partial s_1}{\partial \tau} &= D_1 \frac{\partial^2 s_1}{\partial x^2} + a_{11} s_1 + a_{12} s_2 \,, \\ \frac{\partial s_2}{\partial \tau} &= D_1 (a + b \sin \tau) \frac{\partial^2 s_2}{\partial x^2} + a_{21} s_1 + a_{22} s_2 \,, \end{aligned} \tag{5.2}$$

where $[a_{ij}]$ are the elements of the Jacobian matrix of (3.1) evaluated at $\boldsymbol{S}^*$. Seeking solutions of (5.2) in the form

$$\boldsymbol{s} = \boldsymbol{\phi}(\tau)\mathrm{e}^{ikx} ,$$

we obtain the following system of equations for $\boldsymbol{\phi} = (\phi_1, \phi_2)$:

$$\begin{aligned} \frac{d\phi_1}{d\tau} &= (a_{11} - k^2 D_1)\phi_1 + a_{12}\phi_2 , \\ \frac{d\phi_2}{d\tau} &= a_{21}\phi_1 + [a_{22} - k^2 D_1(a + b\sin\tau)]\,\phi_1 . \end{aligned} \tag{5.3}$$

Differentiating (5.3) with respect to τ and eliminating ϕ_2 we obtain the following second-order differential equation for $\phi_1 = \varphi$:

$$\begin{aligned} 0 = {} & \frac{d^2\varphi}{d\tau^2} - \{Tr(A) - k^2 D_1(1 + a + b\sin\tau\}\,\frac{d\varphi}{d\tau} \\ & + \{det(A) - k^2 D_1(aa_{11} + a_{22}) + k^4 D_1^2 a - bk^2(a_{11} - k^2 D_1)\sin\tau\}\,\varphi . \end{aligned} \tag{5.4}$$

For small amplitude perturbations to D_2 we fix $0 < b = \varepsilon \ll 1$ and construct regular power series expansions for a and φ:

$$\begin{aligned} a &= a_0 + \varepsilon a_1 + \varepsilon^2 a_2 + \cdots \\ \varphi &= \varphi_0 + \varepsilon\varphi_1 + \varepsilon^2\varphi_2 + \cdots . \end{aligned} \tag{5.5}$$

Substituting with (5.5) in (5.4) and equating to zero coefficients of ε^n we obtain at leading order:

$$\begin{aligned} 0 &= \varphi_0'' - (Tr(A) - k^2 D_1(1 + a_0))\varphi_0' \\ &\Rightarrow \varphi_0 = 1 + \Delta\mathrm{e}^{-\mu\tau} , \end{aligned}$$

where primes denote differentiation with respect to τ and we have introduced

$$\mu = k^2 D_1(1 + a_0) - Tr(A) .$$

Thus, for $a_0 < a_{\mathrm{cr}}$ the perturbation is stable at leading order whereas for $a_0 > a_{\mathrm{cr}}$ the perturbation is unstable; $a_0 = a_{\mathrm{cr}}$ denotes the stability boundary in the case $b = \varepsilon = 0$. Fixing $a_0 = a_{\mathrm{cr}}$, and $\mu = 0$, we parameterize the stability boundary in a neighbourhood of a_{cr} in terms of the small parameter $b = \varepsilon$ by calculating corrections to a_0.

At $O(\varepsilon)$ we obtain:

$$\begin{aligned} 0 &= \varphi_1'' - k^2(a_{11} - k^2 D_1)\,(\sin\tau + D_a a_1)\varphi_0 , \\ &\Rightarrow \varphi_1 = \varphi_{10} + \alpha_1 \sin\tau , \end{aligned}$$

where $\alpha_1 = k^2(a_{11} - k^2 D_1)$, and we fix $a_1 = 0$ to eliminate secular terms along the stability boundary.

Continuing to $O(\varepsilon^2)$ we deduce further that:

$$0 = \varphi_2'' + k^2\varphi_1' \sin\tau - k^2(a_{11} - k^2 D_1)\,(\varphi_1 \sin\tau - D_1 a_2) . \tag{5.6}$$

Once again, to prevent secular terms appearing, we require that the coefficient of the constant forcing term vanish in (5.6). Substitution with φ_1 and noting that $2k^2\varphi_1' \sin\tau = \alpha_1(1 - \cos 2\tau)$, we obtain the following expression for the $O(\varepsilon^2)$ correction to a:

$$a_2 = -\frac{k^2(a_{11} - k^2 D_1)}{2D_1} > 0 ,$$

for k sufficiently large. Thus $a(\varepsilon) = a_{\text{cr}} + \varepsilon^2 a_2 > a_{\text{cr}} = a(\varepsilon = 0)$ so that the effect of introducing small amplitude, temporally periodic perturbations to the ratio of diffusion coefficients D_2/D_1 does indeed extend the domain of stability. However, once again we see that this effect is indeed a small one of $O(\varepsilon^2)$.

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