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A predator-prey reaction-diffusion system with nonlocal effects

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Abstract. We consider a predator-prey system in the form of a coupled system of reaction-diffusion equations with an integral term representing a weighted average of the values of the prey density function, both in past time and space. In a limiting case the system reduces to the Lotka Volterra diffusion system with logistic growth of the prey. We investigate the linear stability of the coexistence steady state and bifurcations occurring from it, and expressions for some of the bifurcating solutions are constructed. None of these bifurcations can occur in the degenerate case when the nonlocal term is in fact local.

Key words: Predator-prey – Reaction-diffusion – Time delay – Bifurcation – Pattern formation

1 Introduction

This paper is devoted to a study of the predator prey system

$$\begin{aligned} u_t &= u[1 + \alpha u - (1 + \alpha) G ** u] - uv + D\Delta u \\ v_t &= av(u - b) + \Delta v, \end{aligned} \tag{1.1}$$

for $(x, t) \in R^n \times (0, \infty)$, with $G ** u$ defined by

$$(G ** u)(x, t) = \int_{R^n} \int_{-\infty}^{t} G(x - y, t - s) u(y, s) \, ds \, dy \, . \tag{1.2}$$

In this system u and v are, respectively, prey and predator population densities and the quantities a, b and D are positive constants. We give a description of the various terms in this model below, but note that a special case of our model (with $v \equiv 0$) is the scalar equation

$$u_t = u[1 + \alpha u - (1 + \alpha) G ** u] + D\Delta u \tag{1.3}$$

introduced and studied by Britton (1990) as a model for a single diffusing animal species. Under certain assumptions on $G(x, t)$ (stated below), equation (1.3) has a uniform steady state solution $u = 1$, and Britton (1990) studied the linear stability of this solution and bifurcations occurring from it. It was found that the presence of the nonlocal term $G ** u$ brings about a variety of solution behaviour which it is impossible to obtain from a scalar *local* reaction diffusion equation, at least via bifurcation from a uniform state. Generally both the terms αu and $-(1 + \alpha) G ** u$ are required to destabilise the uniform state, but by suitable choice of G instability is possible with $\alpha = 0$ and the bifurcations are brought about by the nonlocal term $G ** u$ alone.

It is the object of the present paper to extend Britton's equation (1.3) to a predator prey system of two equations. We propose system (1.1) as the simplest reasonable such extension in the sense that all terms involving the predator density v are of classical Lotka Volterra type. The other terms in the model are also present in the single species case (1.3). The term $-(1 + \alpha) G ** u$, with $\alpha > -1$, represents intraspecific competition for resources. This term involves a temporal convolution and therefore introduces delay effects into the system, because of the need to consider the regeneration time of resources. The convolution in space then arises because of the fact that the animals are moving (by diffusion), and have therefore not been at the same point in space at previous times. Thus intraspecific competition for resources depends not simply on population density at one point in space and time, but on a weighted average involving values at all previous times and at all points in space.

Population models with delay have been considered before, e.g., by Cushing (1977), MacDonald (1978) and Gopalsamy (1992). Delays can arise for many reasons. For example, changes in a prey population will only result in a change in the predator population some time later, due to the predator's gestation time. Similarly, whilst the availability of food for a population of insects may immediately result in the laying of eggs, a larval stage will also result in a delay. But whatever the reason for introducing a delay into any population model in which the individuals are moving, the corresponding term in the model must be nonlocal in *space* as well as time. It would be realistic to incorporate delay effects in the interaction terms avu and possibly $-uv$ as well, but we will for the present paper restrict attention to (1.1), owing to the complexity of the analysis. In his study of the corresponding spatially uniform system, May (1973) gives examples of predator prey interactions in which the predator does have a fast response to numerical changes in the prey.

There has now been a great deal of research on purely time dependent systems with delay, and on reaction-diffusion systems containing terms which involve time delays. Some authors have proved results on global convergence in some rather general settings (e.g. Pozio 1983; Yamada 1984). There are comparison theorems for systems with delays which are often applicable (Ding 1989; Gourley and Britton 1993) and there has also been some work on permanence in systems with delay (Lu and Takeuchi 1994). Two recent papers by Choudhury (1994a, b) have considered competition and predator-prey reaction-diffusion systems with temporal convolution terms, and obtained results on the size of the Turing-unstable parameter spaces for the systems. However, even in this work the terms involving delay remain local in space. The emphasis of the present paper is that whenever delay is present in a model with diffusion, the term or terms involving delay must be *nonlocal* in space. There may be situations where on biological grounds it is reasonable to neglect spatial averaging, but this will be the exception rather than the rule.

The term αu in (1.1), when $\alpha > 0$, represents an advantage to the prey species in local aggregation. In a long paper, Okubo (1986) has described in detail some of the reasons for animal aggregation in nature, and the behaviour of the animals within the groups they have formed. Examples of aggregation fall into many categories, including the swarming of insects such as midges and locusts, the swarming of marine life forms such as zooplankton, the schooling of fish, the flocking of birds and the herding of mammals. A common interpretation of aggregation is as a defence against predators, especially in grassland herds and flocks of birds. Aggregations reduce the per-capita amount of time that has to be spent on predator detection, thereby increasing time available for other activities such as foraging. When threatened by predators, an individual prey will try to position itself as near to the centre of an aggregation as possible, so the aggregation can become very tight. Another reason for aggregation can be to optimise feeding efficiency, either by reducing per-capita foraging time, or it may be that large numbers can together kill a larger prey than a single individual could kill by itself, so in this sense a greater variety of food resources are being made available.

On biological grounds the quantity α clearly should be positive. However the mathematical analysis does not require such an assumption so we will in fact make no constraint on the sign of α at this stage.

Our assumptions on $G(\boldsymbol{x}, t)$ are as follows:

(H1) $G \in L^1(\boldsymbol{R}^n \times (0, \infty))$ and $tG \in L^1(\boldsymbol{R}^n \times (0, \infty))$. The former implies that the convolution $G ** u$ is spatio-temporal, but we also consider (in self contained sections) situations where (1.2) degenerates to a purely spatial or a purely temporal convolution. The integrability assumption on $tG(\boldsymbol{x}, t)$ is needed for technical reasons.

(H2) G satisfies the normalisation condition $G ** 1 = 1$, i.e.,

$$\int_{\boldsymbol{R}^n} \int_0^\infty G(\boldsymbol{x}, t)\, dt\, d\boldsymbol{x} = 1 .$$

This implies that the uniform steady state solutions of the model are the same as those of the corresponding purely local system, which is system (1.5) below.

(H3) $G = G(r, t)$ where $r = |\boldsymbol{x}|$. The kernel G quantifies the effect that $u(\boldsymbol{y}, s)$ has on $u(\boldsymbol{x}, t)$ $(s \leq t)$ and the form here assumes that the nonlocal effect depends only on the distance, and not the direction, of $\boldsymbol{y}$ from $\boldsymbol{x}$. Strictly speaking, we should use a different notation for $G(x, t)$ and $G(r, t)$, but no confusion should arise.

(H4) $G \geqq 0$, since G is a weighting function.

To make further progress it is sometimes appropriate to assume that $G(r, t)$ is differentiable as a function of r, with $\partial G/\partial r < 0$ for $r \geqq 0$, but the mathematical conclusions of the paper do not require this.

On the basis of a random walk argument, Britton (1990) derived the kernel

$$G(x, t) = \frac{1}{(4\pi Dt)^{n/2}} \exp\left(-\frac{|x|^2}{4Dt} \right) w(t), \quad \text{where} \int_0^\infty w(s)\, ds = 1 \ . \tag{1.4}$$

Here $w(s)$ represents the weight given at time t to time $t - s$. In this paper we allow other forms for G, and some of the results are for general G satisfying only hypotheses (H1)–(H4). Note that the double convolution $G ** u$ can be reduced to a purely temporal or to a purely spatial convolution, i.e.:

$$\int_{-\infty}^{t} \tilde{G}(t-s) u(x, s)\, ds \quad \text{or} \quad \int_{R^n} \tilde{G}(x-y) u(y, t)\, dy$$

by taking $G(x, t) = \delta(x)\tilde{G}(t)$ or $\delta(t)\tilde{G}(x)$ respectively. The most degenerate case, discussed below, is to take $G(x, t) = \delta(x)\delta(t)$ when $G ** u = u$. Kernels giving rise to purely temporal or purely spatial convolutions are referred to as *purely temporal* and *purely spatial* kernels. These degenerate cases do not satisfy (H1) and are considered in separate, self contained sections. When $G(x, t) = \delta(x)\delta(t)$ we recover the classical Lotka Volterra diffusion system with logistic growth of the prey

$$\begin{aligned} u_t &= u(1 - u - v) + D\Delta u \ , \\ v_t &= av(u - b) + \Delta v \ . \end{aligned} \tag{1.5}$$

In this system, and hence in (1.1), there are three spatially uniform steady state solutions $(u, v) = (0, 0)$, $(1, 0)$ and $(b, 1 - b)$. The latter is biologically relevant only if $0 < b < 1$ and in that case it represents coexistence of both species. The coexistence steady state is the one with which we shall be principally concerned, and it is important to point out at this stage that (when $0 < b < 1$) this steady state is linearly stable as a solution of (1.5); in other words it does not exhibit the phenomenon of diffusion-driven instability (Turing 1952). Thus if it becomes unstable as a solution of (1.1) for some kernel G, then the instability is not caused by diffusion alone.

Returning to (1.1), the plan of the paper is as follows. We carry out a linear stability analysis for each of the three steady states of (1.1), with particular attention on the coexistence steady state. We construct a stability diagram for this steady state and consider some of the bifurcations that occur from it, with α as bifurcation parameter. Specifically, we consider (i) bifurcation to steady spatially periodic and symmetric solutions, (ii) Hopf bifurcation to spatially and temporally periodic standing wave solutions and (iii) bifurcation to periodic travelling wave solutions. Our problem is of course on an infinite domain, but by restricting attention to plane periodic solutions we are able to effectively reduce the problem to a finite one dimensional domain with appropriate boundary conditions, extending the solution to the full domain only to ensure $G ** u$ is well defined, since this term involves integration over all of $\boldsymbol{R}^n$. The actual construction of the bifurcating solutions for the general case is deferred to §4. We also consider certain special cases, including a purely temporal convolution and a purely spatial convolution. For our purely temporal convolution bifurcations (ii) and (iii) occur and for our purely spatial convolution all three bifurcations occur (in contrast to the situation for equation (1.3)).

2 Linear stability of the uniform steady states

We present the linear stability analysis of our system (1.1) for its uniform steady state solutions, which are $(0,0)$, $(1,0)$ and $(b, 1-b)$ (if $0 < b < 1$). We are mainly interested in the coexistence steady state but first we consider the linear stability of $(0,0)$ and $(1,0)$.

Linear stability of $(0,0)$ is determined by the (uncoupled) system

$$\tilde{u}_t = \tilde{u} + D\Delta\tilde{u}$$
$$\tilde{v}_t = -ab\tilde{v} + \Delta\tilde{v}\,.$$

It follows that this steady state is linearly unstable to general perturbations, although perturbations involving no prey die out as expected.

To investigate the linear stability of $(1,0)$ we set $u = 1 + \tilde{u}, v = \tilde{v}$, substitute into (1.1) and retain only linear terms to obtain

$$\tilde{u}_t = \alpha\tilde{u} - (1+\alpha)\int_{\boldsymbol{R}^n}\int_{-\infty}^{t} G(\boldsymbol{x}-\boldsymbol{y}, t-s)\,\tilde{u}(\boldsymbol{y}, s)\,ds\,d\boldsymbol{y} - \tilde{v} + D\Delta\tilde{u}\,,$$
$$\tilde{v}_t = a(1-b)\tilde{v} + \Delta\tilde{v}\,.$$

The convolution term in (1.1) involves values of u at all times previous to t and so for a properly posed problem in $\boldsymbol{R}^n \times (0,\infty)$ we need to provide initial data for all $t \leqq 0$. We impose the conditions $u \equiv 1$ for $t < 0$ (so that $\tilde{u} \equiv 0$ for $t < 0$) and $u(\boldsymbol{x}, 0) = u_0(\boldsymbol{x})$, $v(\boldsymbol{x}, 0) = v_0(\boldsymbol{x})$. The time integral is then effectively from 0 to t only and so the Laplace convolution theorem applies. Taking Laplace transforms,

$$s\bar{\tilde{u}}(\boldsymbol{x}, s) - \tilde{u}_0(\boldsymbol{x}) = \alpha\bar{\tilde{u}} - (1+\alpha)\int_{\boldsymbol{R}^n}\bar{G}(\boldsymbol{x}-\boldsymbol{y}, s)\,\bar{\tilde{u}}(\boldsymbol{y}, s)\,d\boldsymbol{y} - \bar{\tilde{v}} + D\Delta\bar{\tilde{u}}\,,$$
$$s\bar{\tilde{v}}(\boldsymbol{x}, s) - \tilde{v}_0(\boldsymbol{x}) = a(1-b)\bar{\tilde{v}} + \Delta\bar{\tilde{v}}\,,$$

where bar denotes Laplace transform and s the transform variable. To test linear stability to plane perturbations of wave vector $\boldsymbol{k}$, we take as initial conditions

$$u_0(\boldsymbol{x}) = 1 + \varepsilon u' e^{i\boldsymbol{k}\cdot\boldsymbol{x}}, \qquad v_0(\boldsymbol{x}) = \varepsilon v' e^{i\boldsymbol{k}\cdot\boldsymbol{x}}$$

so that $\tilde{u}_0(\boldsymbol{x}) = \varepsilon u' e^{i\boldsymbol{k}\cdot\boldsymbol{x}}$ and $\tilde{v}_0(\boldsymbol{x}) = \varepsilon v' e^{i\boldsymbol{k}\cdot\boldsymbol{x}}$. Seeking solutions of the transformed system of the form

$$\begin{pmatrix} \bar{\tilde{u}}(\boldsymbol{x}, s) \\ \bar{\tilde{v}}(\boldsymbol{x}, s) \end{pmatrix} = \begin{pmatrix} A(s) \\ B(s) \end{pmatrix} e^{i\boldsymbol{k}\cdot\boldsymbol{x}}$$

we obtain

$$\begin{pmatrix} s - \alpha + (1 + \alpha)\bar{H}(s, k^2) + Dk^2 & 1 \\ 0 & s - a(1 - b) + k^2 \end{pmatrix} \begin{pmatrix} A(s) \\ B(s) \end{pmatrix} = \varepsilon \begin{pmatrix} u' \\ v' \end{pmatrix}$$

where $k^2 = \boldsymbol{k}.\boldsymbol{k}$ and

$$\bar{H}(s, k^2) = \int_{R^n} \int_0^\infty G(\boldsymbol{x}, t) e^{-st} e^{-i\boldsymbol{k}\cdot\boldsymbol{x}} \, dt \, d\boldsymbol{x} \, . \tag{2.1}$$

The singularities of $(\bar{\tilde{u}}, \bar{\tilde{v}})$ are therefore the roots of

$$(s - \alpha + (1 + \alpha)\bar{H}(s, k^2) + Dk^2)(s - a(1 - b) + k^2) = 0 \tag{2.2}$$

and if all these roots are in the left half complex plane then $(\tilde{u}, \tilde{v}) \to (0, 0)$ and the steady state is linearly stable. Before proceeding further we list certain properties of $\bar{H}(s, k^2)$.

(i) When s is real, $\bar{H}(s, k^2)$ is a real valued function of s and k^2.
(ii) $\bar{H}(0, 0) = 1$.
(iii) If $\operatorname{Re} s \geqq 0$ then $|\bar{H}(s, k^2)| \leqq 1$.
(iv) If s is real and non-negative then $\bar{H}(s, k^2) \leqq 1$.
(v) If s is real and non-negative and $(s, k^2) \neq (0, 0)$ then $\bar{H}(s, k^2) < 1$.
(vi) If $(\omega, k^2) \neq (0, 0)$ then $\bar{H}(i\omega, k^2) \neq 1$.

The proofs of these properties are all straightforward and with the exception of (vi) may be found in Britton (1990). Property (i), for example, is a consequence of hypothesis (H3) of G. Property (vi) is proved in Gourley (1993).

Returning to (2.2), we first consider the case $b > 1$ (i.e. there is no coexistence steady state). Then one root of (2.2) is $s = a(1 - b) - k^2 < 0$ and its other roots are the zero's of the first factor. However the first factor of (2.2) is the eigenvalue function studied by Britton (1990) and from the results proved in that paper it follows that if $\alpha < -\frac{1}{2}$ then for every $k^2 \geqq 0$ the roots of (2.2) all lie in the left half complex plane and the steady state $(1, 0)$ is linearly stable. If, however, $0 < b < 1$ (the criterion for the coexistence steady state $(b, 1 - b)$ to be biologically relevant), then the root $s = a(1 - b) - k^2$ is positive for sufficiently small k^2 and it follows that the steady state $(1, 0)$ is unstable to perturbations including such wave numbers.

We now investigate the linear stability of the steady state $(u, v) = (b, 1 - b)$, and we will assume that $0 < b < 1$ throughout the remainder of this paper. Setting $u = b + \tilde{u}$, $v = 1 - b + \tilde{v}$ in (1.1), neglecting higher order terms in

$\tilde{u}$ and $\tilde{v}$ and following the Laplace transform method just described, the eigenvalue equation this time turns out to be

$$f(s;\alpha,k^2) \equiv (s - \alpha b + (1+\alpha)b\bar{H}(s,k^2) + Dk^2)(s+k^2) + ab(1-b) = 0\,. \tag{2.3}$$

The roots of this equation occur in complex conjugate pairs. This fact is easily proved, in view of hypothesis (H3) of G. We present two theorems concerning the linear stability of $(b, 1-b)$ for general kernels $G(x,t)$. It is convenient to introduce the quantity

$$T = \int_{R^n}\int_0^\infty tG(x,t)\,dt\,dx \tag{2.4}$$

which measures the strength of the response delay described by the kernel G. The proof of the following theorem uses a method which is a modified version of one used by Cushing (1977) to investigate the eigenvalue equations arising from the linearisation of spatially uniform systems.

Theorem 2.1. *For any given k^2 the steady state $(b, 1-b)$ of* (1.1) *is linearly stable when*

$$\alpha < -\frac{1}{2} + \frac{Dk^2}{2b}\,.$$

In particular it is linearly stable to perturbations of arbitrary wave number if $\alpha < -1/2$.

Proof. Let $k^2 \geqq 0$ be fixed. We wish to show that the eigenvalue equation (2.3) has no roots with $\operatorname{Re} s \geqq 0$. First note that $\bar{H}(s,k^2)$ is analytic for $\operatorname{Re} s \geqq 0$. We denote by $\partial(R)$ the boundary of the semicircle $\operatorname{Re} z \geqq 0$, $|z| = R$ and let $\partial^1(R)$ be the circular part $\operatorname{Re} z > 0$ and $\partial^2(R) = \{z = iy,\ -R \leqq y \leqq R\}$ so that $\partial(R) = \partial^1(R) \cup \partial^2(R)$. The Argument Principle implies, provided

$$f(z;\alpha,k^2) \neq 0 \quad \text{when } \operatorname{Re} z = 0 \tag{2.5}$$

that the number of roots of $f(z;\alpha,k^2)$ inside $\partial(R)$ is

$$\nu(R) = \frac{1}{2\pi i}\int_{\partial(R)} \frac{f'(z;\alpha,k^2)}{f(z;\alpha,k^2)}\,dz = I_1(R) + I_2(R)$$

where prime denotes differentiation with respect to z and

$$I_j(R) = \frac{1}{2\pi i}\int_{\partial^j(R)} \frac{f'(z;\alpha,k^2)}{f(z;\alpha,k^2)}\,dz, \quad j = 1,2\,.$$

The number of roots with $\operatorname{Re} z \geqq 0$ is $\nu(\infty) = \lim_{R\to\infty}\nu(R)$ and we wish of course to show that this is zero. The fact that (2.5) is satisfied will become clear later in the proof. We first prove that $\lim_{R\to\infty} I_1(R) = 1$ and to do this we need some estimates. We introduce the function

$$h(z) = \frac{2 + (1+\alpha)b\bar{H}'(z,k^2)}{z}\,.$$

If we write $\phi(z) = -\alpha b + (1+\alpha)b\bar{H}(z,k^2) + Dk^2$, a calculation yields that

$$\frac{f'(z;\alpha,k^2)}{f(z;\alpha,k^2)} - h(z) =$$

$$\frac{z[-\phi(z) - k^2 - \phi(z)(1+\alpha)b\bar{H}'(z,k^2)] - [(2+(1+\alpha)b\bar{H}'(z,k^2))(\phi(z)k^2 + ab(1-b))]}{z(z^2 + [\phi(z)+k^2]z + [\phi(z)k^2 + ab(1-b)])}. \tag{2.6}$$

Next note that

$$\bar{H}'(z,k^2) = -\int_{R^n}\int_0^\infty t\,G(x,t)\ e^{-zt}e^{-ik.x}\,dt\,dx$$

so it follows that $|\bar{H}'(z,k^2)| \leqq T$ when $\operatorname{Re} z \geqq 0$. This and property (iii) of $\bar{H}$ imply that the square bracketed quantities in expression (2.6) are all bounded for $\operatorname{Re} z \geqq 0$; let $M > 0$ be sufficiently large as to serve as an upper bound for the absolute values of all these quantities. Then for $z \in \partial^1(R)$,

$$\left|\frac{f'(z;\alpha,k^2)}{f(z;\alpha,k^2)} - h(z)\right| \leqq \frac{(R+1)M}{R(R^2 - RM - M)}.$$

Next we need another estimate. Note that

$$|\bar{H}'(Re^{i\theta},k^2)| \leqq \int_{R^n}\int_0^\infty tG(x,t)\,e^{-(R\cos\theta)t}\,dt\,dx$$

and therefore

$$\begin{aligned}\int_{-\pi/2}^{\pi/2}|\bar{H}'(Re^{i\theta},k^2)|\,d\theta &\leqq 2\int_{R^n}\int_0^\infty t\,G(x,t)\int_{-\pi/2}^{0} e^{-(R\cos\theta)t}\,d\theta\,dt\,dx\\ &= 2\int_{R^n}\int_0^\infty tG(x,t)\int_0^{\pi/2} e^{-(R\sin\theta)t}\,d\theta\,dt\,dx\\ &\leqq 2\int_{R^n}\int_0^\infty tG(x,t)\int_0^{\pi/2} e^{-2Rt\theta/\pi}\,d\theta\,dt\,dx\\ &= \frac{\pi}{R}\int_{R^n}\int_0^\infty G(x,t)(1-e^{-Rt})\,dt\,dx \leqq \frac{\pi}{R}.\end{aligned}$$

Here we have used Jordans inequality $\sin\theta \geqq 2\theta/\pi$, valid for $\theta \in [0, \frac{1}{2}\pi]$. Having obtained these estimates we now have

$$\begin{aligned}|I_1(R) - 1| &= \left|\frac{1}{2\pi i}\int_{\partial^1(R)}\frac{f'(z;\alpha,k^2)}{f(z;\alpha,k^2)}\,dz - \frac{1}{2\pi i}\int_{\partial^1(R)}\frac{2}{z}\,dz\right|\\ &= \frac{1}{2\pi}\left|\int_{\partial^1(R)}\left(\frac{f'(z;\alpha,k^2)}{f(z;\alpha,k^2)} - h(z)\right)dz + (1+\alpha)b\int_{\partial^1(R)}\frac{\bar{H}'(z,k^2)}{z}\,dz\right|\end{aligned}$$

$$\leqq \frac{1}{2\pi}\left(\frac{\pi(R+1)M}{R^2-RM-M}+|1+\alpha|b\int_{-\pi/2}^{\pi/2}|\bar{H}'(Re^{i\theta},k^2)|\,d\theta\right)$$

$$\leqq \frac{1}{2\pi}\left(\frac{\pi(R+1)M}{R^2-RM-M}+\frac{|1+\alpha|b\pi}{R}\right)\to 0 \quad \text{as } R\to\infty \ .$$

This shows that $I_1(\infty)=1$.

Next we look at $I_2(R)$ for large R. We have

$$I_2(R)=\frac{1}{2\pi i}\int_R^{-R}\frac{f'(iy;\alpha,k^2)}{f(iy;\alpha,k^2)}i\,dy=\frac{1}{2\pi i}\Big(\log f(-iR;\alpha,k^2)-\log f(iR;\alpha,k^2)\Big)\,.$$

But $\overline{f(iR;\alpha,k^2)}=f(-iR;\alpha,k^2)$ so, using the principal branch $|\arg z|<\pi$ of the logarithm,

$$I_2(R)=\frac{1}{2\pi}(\arg f(-iR;\,\alpha,k^2)-\arg f(iR;\,\alpha,k^2))$$

$$=-1/\pi\arg f(iR;\,\alpha,k^2)$$

so we need to know what $\arg f(iR;\alpha,k^2)$ tends to as $R\to\infty$. Note that $\bar{H}(iR,k^2)=C(R)-iS(R)$ where

$$C(R)=\int_{R^n}\int_0^\infty G(\boldsymbol{x},t)\cos Rt\cos \boldsymbol{k}.\boldsymbol{x}\,dt\,d\boldsymbol{x}\ ,$$

$$S(R)=\int_{R^n}\int_0^\infty G(\boldsymbol{x},t)\sin Rt\cos \boldsymbol{k}.\boldsymbol{x}\,dt\,d\boldsymbol{x}\ .$$

Clearly $|C(R)|\leqq 1$ and $|S(R)|\leqq 1$ for all $R\geqq 0$. Now

$$\operatorname{Re} f(iR;\alpha,k^2)=-R^2+(1+\alpha)bRS(R)$$
$$+k^2(-\alpha b+(1+\alpha)\,bC(R)+Dk^2)+ab(1\text{-}b)$$

$$\operatorname{Im} f(iR;\alpha,k^2)=Rb(-\alpha+(1+\alpha)C(R))+k^2((D+1)R-(1+\alpha)bS(R))$$

so it is clear that when R is large,

$$\begin{aligned}&\operatorname{Re} f(iR;\alpha,k^2)\sim -R^2\ ,\\ &|\operatorname{Im} f(iR;\alpha,k^2)|\leqq \text{const.}R\ .\end{aligned}\tag{2.7}$$

The second of (2.7) in fact holds for all R because, using the inequality $|\sin x|\leqq|x|$, it is easily seen that $|S(R)|\leqq RT$ for all R. Now, the assumption $\alpha<-\frac{1}{2}+Dk^2/2b$ may be written

$$|1+\alpha|<-\alpha+\frac{Dk^2}{b}$$

and consequently $f(0;\alpha,k^2)>0$ since

$$f(0;\,\alpha,k^2)=k^2(-\alpha b+(1+\alpha)bC(0)+Dk^2)+ab(1-b)$$

$$\geqq k^2b\left(-\alpha-|1+\alpha|+\frac{Dk^2}{b}\right)+ab(1-b)>0\ .$$

This fact, together with the asymptotic behaviour of $f(iR;\alpha,k^2)$ given by (2.7), imply that as $R\to\infty$, $\arg f(iR;\alpha,k^2)$ tends to an odd multiple of π, say $\arg f(i\infty;\alpha,k^2)=(1-2m)\pi$ for some $m\in\boldsymbol{Z}$. Then $I_2(\infty)=2m-1$ and the number of roots in the right half complex plane is $\nu(\infty)=I_1(\infty)+I_2(\infty)=2m$ so $m\geqq 0$ and we must show that in fact $m=0$, i.e., that $\arg f(i\infty;\alpha,k^2)=\pi$. Geometrically, $m\geqq 2$ would correspond to a situation where as R ranges from 0 to ∞ the graph of $f(iR;\alpha,k^2)$ "winds around" the origin (in the clockwise sense) before permanently entering the left half of the complex plane, and $m=1$ simply means that the graph passes underneath the origin rather than over it. Therefore a sufficient condition to ensure that $\arg f(i\infty;\alpha,k^2)=\pi$ is that $\operatorname{Im} f(iR;\alpha,k^2)>0$ when $\operatorname{Re} f(iR;\alpha,k^2)=0$ (or, geometrically, that the graph of $f(iR;\alpha,k^2)$ does not cross over the negative imaginary axis). Now when $\operatorname{Re} f(iR;\alpha,k^2)=0$,

$$R(R-(1+\alpha)bS(R))=k^2(-\alpha b+(1+\alpha)bC(R)+Dk^2)+ab(1-b)\,.$$

Also $R>0$ at such points, since $f(0;\alpha,k^2)>0$. Hence when $\operatorname{Re} f(iR;\alpha,k^2)=0$ we have

$$\begin{aligned}\operatorname{Im} f(iR;\alpha,k^2)&=Rb(-\alpha+(1+\alpha)C(R))+k^2DR\\&\quad+\frac{k^2}{R}(k^2(-\alpha b+(1+\alpha)bC(R)+Dk^2)+ab(1-b))\\&\geqq\left(Rb+\frac{k^4b}{R}\right)\left(-\alpha+(1+\alpha)C(R)+\frac{Dk^2}{b}\right)\\&\geqq\left(Rb+\frac{k^4b}{R}\right)\left(-\alpha-|1+\alpha|+\frac{Dk^2}{b}\right)\\&>0\quad\text{since}\quad-\alpha-|1+\alpha|+Dk^2/b>0\end{aligned}$$

as desired. It is also clear now that (2.5) is verified. The proof of the theorem is complete. Next, we have the following instability result:

Theorem 2.2 *The steady state* $(b,1-b)$ *of* (1.1) *is linearly unstable for* α *sufficiently large and positive.*

The proof of this result is given in Gourley (1993) and will not be reproduced in detail here, except to note certain points. The cases $k^2\neq 0$ and $k^2=0$ are actually considered separately. When $k^2\neq 0$ we have that for α sufficiently large there are an odd number of real positive roots (counting multiplicity) of $f=0$. Since the roots are either real or in complex conjugate pairs it follows that there are an odd number of roots of positive real part, and therefore that as α is increased at least one of these roots must have crossed the imaginary axis through the origin. When $k^2=0$, $s=0$ cannot be a root of the eigenvalue equation, but when α is increased to a value sufficiently large there are at least two roots of positive real part. These must have crossed the imaginary axis as a pair of complex conjugates.

From Theorems 2.1 and 2.2 we know that as α increases from any value less than $-\frac{1}{2}$ to a value sufficiently large, certain roots of the eigenvalue equation $f=0$ cross the imaginary axis. Crossings may occur either through the origin or as pairs of complex conjugate roots, and we indicate how to sketch a stability diagram in the (α, k^2) plane for the steady state $(b, 1-b)$. We can explicitly calculate the locus of points in this plane such that $f=0$ has a root $s=0$. From (2.3), this locus is given by

$$\alpha = \frac{ab(1-b) + bk^2 \bar{H}(0,k^2) + Dk^4}{bk^2(1-\bar{H}(0,k^2))}\,.$$

This expression tends to infinity as $k^2 \to 0$ and asymptotes to Dk^2/b as $k^2 \to \infty$. It is not in general possible to find an explicit expression for the locus $\operatorname{Re} s = 0$, that is, the set of points in the (α, k^2) plane such that $f=0$ has purely imaginary roots. Explicit expressions for this locus are obtainable in certain special cases, but for the general case all we can do is attempt a rough sketch of the locus by considering limiting cases. We know that when $k^2=0$, $s=0$ is never a root of $f=0$ and so as α increases roots cross the imaginary axis as pairs of complex conjugates. Hence the locus $\operatorname{Re} s = 0$ meets the α-axis (at a value α^*, say). As $k^2 \to \infty$ some information can be gained by carrying out a rather heavy piece of asymptotic analysis, the full details of which are given in Gourley (1993). From Britton (1990) we have that as $k^2 \to \infty$, in n dimensions,

$$\bar{H}(s,k^2) \sim -\frac{2\pi^{n/2}}{\Gamma(n/2)k^2} G_n(s) + o\left(\frac{1}{k^2}\right) \tag{2.8}$$

where

$$G_n(s) = \lim_{r\to 0+} \bar{G}_r(r,s)\, r^{n-1} \tag{2.9}$$

and the bar denotes Laplace transform. Note that $G_n(0) < 0$ and $G_n'(0) > 0$. We may approximate the eigenvalue equation (2.3) by an equation of polynomial type if we approximate $G_n(s)$ using a Padé approximant. If the simplest approximation of this type:

$$G_n(s) \approx \frac{G_n(0)}{1-(G_n'(0)/G_n(0))s} \tag{2.10}$$

is used, then with (2.8) and (2.10) the eigenvalue equation (2.3) may be approximated by the cubic equation

$$\begin{aligned} &-\frac{G_n'(0)}{G_n(0)}s^3 + \left[1 + \frac{G_n'(0)}{G_n(0)}(\alpha b - (D+1)k^2)\right]s^2 + \left[k^2\left(1 + \frac{G_n'(0)}{G_n(0)}(\alpha b - Dk^2)\right)\right. \\ &\left. -\alpha b + Dk^2 - \frac{2(1+\alpha)b\pi^{n/2}}{\Gamma(n/2)k^2} G_n(0) - ab(1-b)\frac{G_n'(0)}{G_n(0)}\right]s \\ &+ ab(1-b) + k^2\left(-\alpha b + Dk^2 - \frac{2(1+\alpha)b\pi^{n/2}}{\Gamma(n/2)k^2}G_n(0)\right) = 0\,. \end{aligned} \tag{2.11}$$

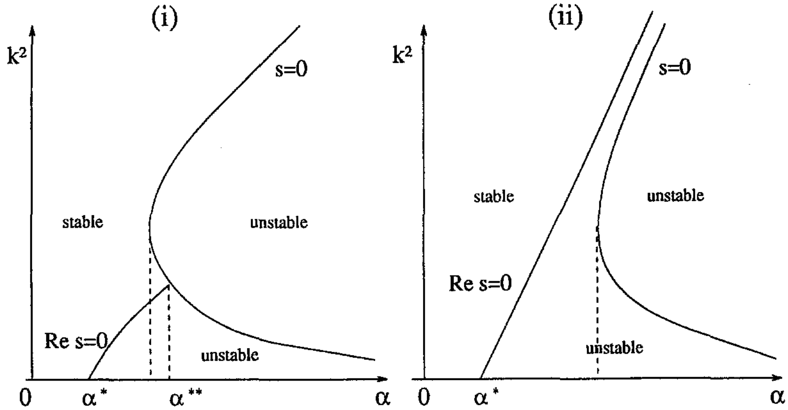

Fig. 1. Stability diagrams for the steady state solution $(u, v) = (b, 1 - b)$. Diagram (i) occurs when $2D\pi^{n/2}G_n'(0)/\Gamma(n/2) < 1$ and diagram (ii) occurs otherwise

We can then apply the standard conditions for a cubic equation to have purely imaginary roots. The analysis is particularly awkward, but the conclusion is that if $2D\pi^{n/2}G_n'(0)/\Gamma(n/2) > 1$ then for k^2 sufficiently large the root locus $\operatorname{Re} s = 0$ exists and is to the left of the locus $s = 0$ (in the (α, k^2) plane). If $2D\pi^{n/2}G_n'(0)/\Gamma(n/2) < 1$ then the root locus $\operatorname{Re} s = 0$ does not exist when k^2 is large. However, we know it exists for k^2 sufficiently small, so we can only conclude that it must meet the locus $s = 0$ and then cease to exist. Let α^{**} be the value of α at which the locus $\operatorname{Re} s = 0$ ceases to exist. The stability diagrams for the two cases are shown in Fig. 1 and are qualitatively similar to those in Britton (1990).

Our analysis suggests that if we focus attention on a certain particular wave number k (i.e. if we fix a wave vector $\boldsymbol{k}$ and only consider stability to perturbations of that particular wave vector) then, regarding α as bifurcation parameter, we should get a bifurcation at a simple eigenvalue to steady spatially periodic solutions, and a Hopf bifurcation to solutions which are spatially and temporally periodic. We will return to the general case in § 4 to confirm that these bifurcations occur and construct the bifurcating solutions using perturbation methods.

3 Some special kernels

We consider the system (1.1) with certain particular kernel functions G. In each case we examine in detail the linear stability of $(b, 1 - b)$ and some of the bifurcations that occur from this steady state, with α as bifurcation parameter. Some of the kernels are such that the integro-differential system (1.1) can be re-written as a system which is purely differential but of higher order. In these cases the eigenvalue equations may be re-written as polynomial equations, which may then be analysed using the Routh-Hurwitz criterion, yielding both necessary and sufficient conditions for stability.

Some of the kernels do not satisfy hypothesis (H1), but the analysis of this section is self contained. In § 4, when we consider bifurcations for general kernels G, we will always assume that the kernels are genuinely *spatio-temporal*, i.e., that they satisfy (H1).

3.1 A limiting case

By taking $G(x,t) = \delta(x)\delta(t)$ we eliminate nonlocal effects from (1.1) and the system reduces to (1.5). In this case $\bar{H}(s,k^2) \equiv 1$ and the eigenvalue equation (2.3) becomes

$$f(s;\alpha,k^2) \equiv (s + b + Dk^2)(s + k^2) + ab(1 - b) = 0\ .$$

For every $k^2 \geqq 0$ the roots of this equation both have negative real part so the steady state $(u,v) = (b, 1 - b)$ is stable. That is, in the purely local case our model does not exhibit diffusion-driven (Turing) instability. Hence the spatially structured solutions which exist in other cases are brought about by the nonlocal term $G ** u$ or by the interaction of this term with the aggregation term αu, but certainly not by diffusion alone.

3.2 A purely temporal kernel

A purely temporal kernel is one of the form $G(x,t) = \delta(x) g(t)$ where $g \in L^1(0,\infty)$ and $\int_0^\infty g(s)\,ds = 1$. For such a kernel $G ** u$ degenerates to the purely temporal convolution $\int_{-\infty}^t g(t-s)u(x,s)\,ds$. We consider the case which is simplest to deal with mathematically:

$$G(x,t) = \delta(x)\,\theta e^{-\theta t} \tag{3.1}$$

where $\theta > 0$. Then $\bar{H}(s,k^2) = \theta/(\theta + s)$ and the eigenvalue equation $f(s;\alpha,k^2) = 0$ determining stability of $(b, 1 - b)$ can be rewritten as a cubic equation

$$\begin{aligned} f^*(s;\alpha,k^2) = s^3 &+ [\theta - \alpha b + (D+1)k^2]s^2 \\ &+ [\theta b + ab(1-b) + k^2((D+1)\theta - \alpha b + Dk^2)]s \\ &+ [\theta ab(1-b) + \theta k^2(b + Dk^2)] = 0\ . \end{aligned} \tag{3.2}$$

Using the Routh Hurwitz criterion, we can show (Gourley 1993) that if

$$\alpha < \frac{\theta^2}{b(\theta + a(1-b))} \tag{3.3}$$

then for every $k^2 \geqq 0$ the roots of (3.2) all lie in the left half complex plane. Thus if (3.3) holds the steady state $(b, 1 - b)$ is linearly stable.

An obvious interpretation of condition (3.3) is that if the tendency of the prey species to aggregate is insufficiently great then aggregation cannot occur.

However an alternative way to view this condition would be to note that for any fixed α it holds when θ is sufficiently large. Now as θ increases, values of u in the past become progressively less important in their contribution to the average $G ** u$ at time t (see the expression (3.4) below) so that large θ implies a "weak" delay. Thus for the kernel of the present section if the delay effect is weak the steady state $(b, 1-b)$ remains stable. This is consistent with the usual observation, in spatially uniform systems, that delays are not destabilising unless they are in some sense significant (Cushing 1977). Note also that if $\alpha = 0$ then the steady state is stable for all $\theta > 0$.

We investigate two bifurcations which can occur from $(b, 1-b)$ as α is increased beyond the value in (3.3). Note that $s = 0$ is never a root of (3.2) (it cannot be a root of the eigenvalue equation corresponding to *any* purely temporal kernel), so we do not have bifurcation to periodic *steady* solutions. With the kernel (3.1) we let w denote the term $G ** u$ in (1.1) so that

$$w(x, t) = \int_{-\infty}^{t} \theta \mathrm{e}^{-\theta(t-s)} u(x, s)\, ds. \tag{3.4}$$

Differentiating (3.4) shows that $w_t = \theta(u - w)$. The integro-differential system may therefore be replaced by the system

$$\begin{aligned} u_t &= u(1 + \alpha u - (1+\alpha) w) - uv + D\Delta u \\ v_t &= av(u - b) + \Delta v \\ w_t &= \theta(u - w). \end{aligned} \tag{3.5}$$

It is not clear at this stage that the two systems are entirely equivalent since, in general, the third equation of (3.5) will, for a given u, have other solutions besides (3.4). However, in the classes of functions within which we work there is no such difficulty and the only solution of the third equation of (3.5) is given by the expression (3.4), as will be explained later.

We start by seeking periodic standing wave solutions of (3.5), by fixing $\boldsymbol{k}$ and looking for solutions which are 2π-periodic in $\xi = \boldsymbol{k} . \boldsymbol{x}$ and periodic in t. We write

$$u(x, t) = \hat{u}(\boldsymbol{k}\boldsymbol{x}, t) = \hat{u}(\xi, t)$$

and similarly for v and w. After dropping the hats the system becomes

$$\begin{aligned} u_t &= u(1 + \alpha u - (1+\alpha) w) - uv + Dk^2 u_{\xi\xi} \\ v_t &= av(u - b) + k^2 v_{\xi\xi} \\ w_t &= \theta(u - w) \end{aligned} \tag{3.6}$$

for $\xi \in (0, 2\pi)$ with periodic boundary conditions at $\xi = 0$ and $\xi = 2\pi$. Note that this problem is invariant under the transformation $\xi \to -\xi$; this means the eigenvalue of the linearised problem has multiplicity two (c.f. Britton (1990)). However we may overcome this problem as Britton did by restricting attention to solutions which are 2π-periodic and *symmetric* in ξ; this is equivalent to looking for solutions on $(0, \pi)$ which satisfy the homogeneous Neumann boundary conditions

$$\begin{aligned} u_\xi(0,t) &= v_\xi(0,t) = w_\xi(0,t) = 0 \\ u_\xi(\pi,t) &= v_\xi(\pi,t) = w_\xi(\pi,t) = 0 \; . \end{aligned} \tag{3.7}$$

Solutions satisfying (3.7) may be extended to an even function on $(-\pi, \pi)$ and then periodically over all of $\boldsymbol{R}$ (although for purely temporal kernels $G ** u$ involves values of u only at the point ξ itself so here we can actually consider the system for $\xi \in (0, \pi)$ only).

The boundary conditions (3.7) ensure periodicity in space, and we anticipate time periodicity arising via a Hopf bifurcation in an appropriate space of functions satisfying (3.7). Linearising the system about $(u, v, w) = (b, 1-b, b)$ by setting $u = b + \tilde{u}, v = 1 - b + \tilde{v}$ and $w = b + \tilde{w}$, the linearised system has solutions of the form $(\tilde{u}, \tilde{v}, \tilde{w}) = e^{st}\boldsymbol{X}(\xi)$ when

$$L\boldsymbol{X} = \begin{pmatrix} \alpha b + Dk^2 \dfrac{d^2}{d\xi^2} & -b & -(1+\alpha)b \\ a(1-b) & k^2 \dfrac{d^2}{d\xi^2} & 0 \\ \theta & 0 & -\theta \end{pmatrix} \boldsymbol{X} = s\boldsymbol{X} \tag{3.8}$$

with boundary conditions $\boldsymbol{X}_\xi(0) = \boldsymbol{X}_\xi(\pi) = 0$. Setting $\boldsymbol{X}(\xi) = \boldsymbol{c}\cos\xi$, with $\boldsymbol{c}$ a constant vector, we find that the eigenvalues s of the linear operator L satisfy $f^*(s; \alpha, k^2) = 0$ where f^* is the eigenvalue function (3.2). Purely imaginary roots of this equation occur only when

$$\begin{aligned} \alpha &= \alpha_0(k^2) \\ &= \frac{1}{2bk^2}\left[2k^2(\theta + Dk^2) + k^4 + \theta(b + Dk^2) + ab(1-b) - \sqrt{\Lambda(k^2)}\right] \end{aligned} \tag{3.9}$$

where

$$\begin{aligned} \Lambda(k^2) = \theta^2(b + Dk^2)^2 + (k^4 - ab(1-b))^2 + 2\theta(b + Dk^2)(ab(1-b) \\ + k^4) + 4k^2\theta ab(1-b) \, . \end{aligned} \tag{3.10}$$

Expression (3.9) therefore gives the locus $\operatorname{Re} s = 0$ in the (α, k^2) plane. The corresponding stability diagram for the steady state $(b, 1-b)$ is shown in Fig. 2.

It is shown in Gourley (1993) that the value $\alpha = \alpha_0(k^2)$ given by (3.9) is indeed a Hopf bifurcation point. The calculations are of a fairly standard nature but involve a great deal of algebra. We conclude that the system (3.6) admits solutions periodic in space and time (i.e. standing waves) and we now confirm that, as far as these solutions are concerned, the systems (3.6) and (1.1) (with this G) are equivalent. In other words, we show that if (u^*, v^*, w^*) is a periodic (in time) solution of (3.6) then w^* is necessarily equal to $\int_{-\infty}^{t} \theta e^{-\theta(t-s)} u^*(\xi, s)\, ds$. Now the third equation of (3.6) is linear, and this means

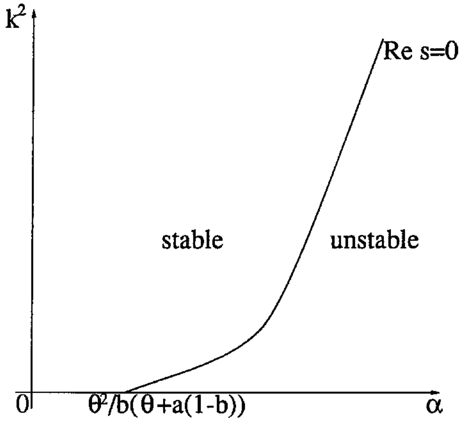

Fig. 2. Stability diagram for the steady state solution $(b, 1-b)$ for the system of § 3.2

we may write down its general solution as the sum of the particular integral (3.4) and a complementary function:

$$w^*(\xi, t) = \int_{-\infty}^{t} \theta e^{-\theta(t-s)} u^*(\xi, s)\, ds + A(\xi) e^{-\theta t} . \tag{3.11}$$

However if u^* and w^* are periodic in time, with period T, say, then it is straightforward to see that the first term in the RHS of (3.11) is also periodic in time with period T. The last term, however, will be non-periodic unless $A(\xi) = 0$. Thus the systems (3.6) and (1.1) are indeed equivalent.

In § 4 we show how to construct asymptotic expressions for standing wave solutions of (1.1) with general G.

Another bifurcation that occurs in system (3.5) is a Hopf bifurcation to periodic travelling wave solutions. Letting $z = \hat{\boldsymbol{k}}.\boldsymbol{x} + ct$ where $\hat{\boldsymbol{k}}$ is a unit vector the equations in travelling wave form are

$$\begin{aligned} cu' &= u(1 + \alpha u - (1 + \alpha)w) - uv + Du'' \\ cv' &= av(u - b) + v'' \\ cw' &= \theta(u - w) \end{aligned} \tag{3.12}$$

where prime denotes differentiation with respect to z. This is a system of ordinary differential equations of order five. It is again easy to show that if (u, v, w) is a *periodic* solution of (3.12) then it follows that

$$w(z) = \int_0^{\infty} \theta e^{-\theta s} u(z - cs)\, ds ,$$

the desired solution (expressed as a function of z) of the third equation of (3.12). So, as far as periodic travelling waves are concerned, the

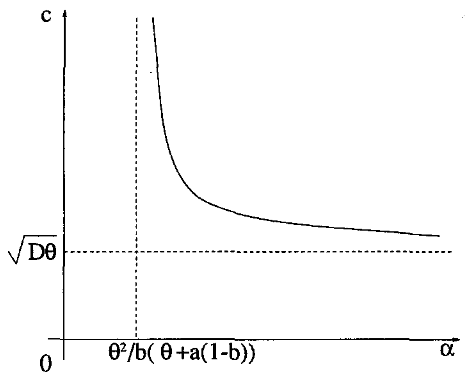

Fig. 3. Bifurcation curve in (α, c) parameter space for periodic travelling wave solutions for the system of § 3.2

integro-differential system and (3.12) are equivalent. If the system (3.12) is linearised about $(u, v, w) = (b, 1 - b, b)$, the linearised system has non-trivial solutions proportional to e^{sz} if and only if

$$Dcs^5 + (D\theta - (D+1)c^2)s^4 + (c^3 - (D+1)\theta c + \alpha bc)s^3$$
$$+ (c^2(\theta - \alpha b) - b\theta)s^2 + (cb\theta + cab(1-b))s + \theta ab(1-b) = 0\,. \quad (3.13)$$

Purely imaginary roots $s = i\omega$ of (3.13) cannot occur if $c = 0$ (as expected, since otherwise this would suggest bifurcation to a spatially periodic *steady* solution, and we know this cannot happen for a purely temporal kernel), but for $c \neq 0$ they occur for values of α and c on the curve given parametrically by

$$\alpha(\omega^2) = \frac{1}{2b\omega^2}[2\omega^2(\theta + D\omega^2) + \omega^4 + \theta(b + D\omega^2)$$
$$+ ab(1-b) - \sqrt{A(\omega^2)}]\,, \quad (3.14)$$

$$c(\omega^2) = \sqrt{\frac{1}{2\omega^2}\left[\theta(b + D\omega^2) - \omega^4 + ab(1-b) + \sqrt{A(\omega^2)}\right]} \quad (3.15)$$

for $\omega^2 > 0$, where A is the function defined by (3.10). This curve is shown in Fig. 3.

A Hopf bifurcation to periodic solutions occurs as this curve is crossed in the (α, c) plane. This is a Hopf bifurcation in $\boldsymbol{R}^5$, but the conditions can all be checked analytically and they hold everywhere on the curve. It follows that there are periodic travelling wave solutions of the system (3.12), and hence of the original integro-differential system.

3.3 A purely spatial kernel

A purely spatial kernel is one of the form $G(x, t) = g(x)\delta(t)$ where $g \in L^1(\boldsymbol{R}^n)$ and $\int_{\boldsymbol{R}^n} g(x)\,dx = 1$. For such a kernel $G ** u$ degenerates to $\int_{\boldsymbol{R}^n} g(x - y)u(y, t)\,dy$. We will work in one space dimension and consider the particular case

$$G(x,t) = \frac{1}{2}\lambda e^{-\lambda|x|}\delta(t) \tag{3.16}$$

where $\lambda > 0$. For this kernel $\bar{H}(s, k^2) = \lambda^2/(\lambda^2 + k^2)$ and the eigenvalue equation determining stability of $(b, 1 - b)$ can be put in the form

$$s^2 + \left((D+1)k^2 + \frac{b\lambda^2 - \alpha bk^2}{\lambda^2 + k^2}\right)s + k^2\left(\frac{b\lambda^2 - \alpha bk^2}{\lambda^2 + k^2} + Dk^2\right)$$
$$+ ab(1 - b) = 0\,. \tag{3.17}$$

This has a root $s = 0$ when

$$\alpha = \frac{Dk^2}{b} + \frac{D\lambda^2}{b} + \frac{\lambda^2 + a(1-b)}{k^2} + \frac{\lambda^2 a(1-b)}{k^4} \tag{3.18}$$

and purely imaginary roots when

$$\alpha = \frac{(D+1)k^2}{b} + \frac{(D+1)\lambda^2}{b} + \frac{\lambda^2}{k^2} \tag{3.19}$$

provided that

$$k^2\left(\frac{b\lambda^2 - \alpha bk^2}{\lambda^2 + k^2} + Dk^2\right) + ab(1-b) > 0$$

i.e., provided that

$$k^2 < \sqrt{ab(1-b)}\,. \tag{3.20}$$

Hence *non-stationary* solutions can only bifurcate from $(b, 1 - b)$ for sufficiently small wave numbers satisfying (3.20). The stability diagram is shown in Fig. 4. We have illustrated the situation when $\lambda^2 < (D + 1)a(1 - b)$; if this is not the case it simply means that the locus $\operatorname{Re} s = 0$ is everywhere to the right of the line $\alpha = \alpha^{**}$.

Note that purely imaginary eigenvalues cannot occur when $k^2 = 0$. Indeed, for a purely spatial kernel, spatially uniform oscillations would have to be governed by the nondelay system of § 3.1, which does not exhibit bifurcations from the steady state $(b, 1 - b)$. There is thus a significant qualitative difference between this particular case and the general spatio-temporal case of Fig. 1. Clearly there is a number $\alpha_c > 0$ such that when $\alpha < \alpha_c$ the steady state is linearly stable. It is easy to see that the number

$$\alpha_c = 2\lambda\sqrt{\frac{D}{b}} + \frac{D\lambda^2}{b} \tag{3.21}$$

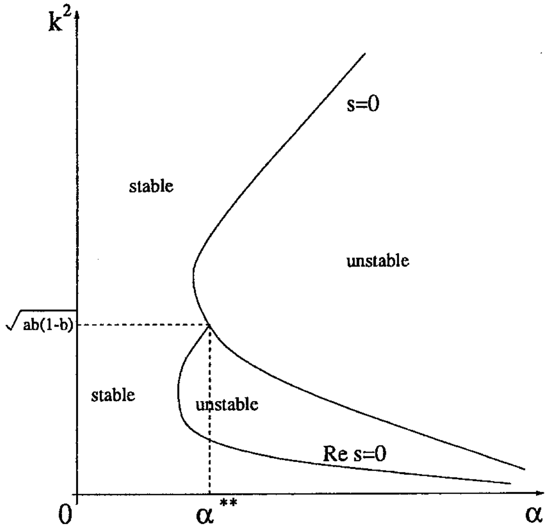

Fig. 4. Stability diagram for the steady state solution $(b, 1 - b)$ for the system of § 3.3 when $\lambda^2 < (D + 1)a(1 - b)$

will do, and although it is not the best possible such number it is adequate to illustrate certain points. For example, aggregation is not possible if the tendency to aggregate is too insignificant. But note also that for any fixed value of α we can have $\alpha < \alpha_c$ by taking λ sufficiently large. For the kernel of this section the parameter λ is a measure of how *localised* the average $G ** u$ of u is, and for large λ this average (at a point (x, t)) is strongly weighted towards values of u near to the point x itself. In fact as $\lambda \to \infty, G$ tends to a product of delta functions and the system reduces to that of § 3.1. Thus aggregation will not occur if the average is too localised; that is if the inhibitive effect of crowding of the prey species is sufficiently short-range (cf. Britton (1989)). The integro-differential equation (1.1) with this G can be analysed by defining

$$w(x, t) = \int_{-\infty}^{\infty} \tfrac{1}{2} \lambda e^{-\lambda|x-y|} u(y, t)\, dy \,. \tag{3.22}$$

Then, differentiating twice, $w_{xx} = -\lambda^2(u - w)$ and the equation may be replaced by the system

$$\begin{aligned} u_t &= u(1 + \alpha u - (1 + \alpha)w) - uv + Du_{xx} \\ v_t &= av(u - b) + v_{xx} \\ 0 &= \lambda^2(u - w) + w_{xx} \,. \end{aligned} \tag{3.23}$$

For solutions periodic in x this system is equivalent to the original integro-differential system since the general solution of the third equation of (3.23) is

$$w(x,t) = \int_{-\infty}^{\infty} \tfrac{1}{2}\lambda e^{-\lambda|x-y|} u(y,t)\,dy + A(t)\cosh\lambda x + B(t)\sinh\lambda x$$

so if u and w are periodic in x with the same period then the first term in the above is also periodic in x with this period and it follows that $A(t) = B(t) = 0$.

We analyse (3.23) using similar ideas to those of the previous section. We fix k and seek solutions of the form $u(x,t) = \hat{u}(kx,t) = \hat{u}(\xi,t)$ (similarly for v and w) which are 2π-periodic and symmetric in ξ, i.e., which satisfy homogeneous Neumann boundary conditions at $\xi = 0$ and $\xi = \pi$. In this set-up, bifurcation at a zero eigenvalue (i.e. $s = 0$) occurs at the value $\alpha = \alpha_0(k^2)$ given by (3.18), and a Hopf bifurcation occurs at (3.19). The detailed calculations are all given in Gourley (1993). Thus, with this kernel, the integro-differential equation admits stationary spatially periodic solutions and periodic standing wave solutions.

It also admits periodic travelling wave solutions, arising via Hopf bifurcation. In travelling wave form, with $z = x + ct$, the system reads

$$\begin{aligned} cu' &= u(1 + \alpha u - (1+\alpha)w) - uv + Du'' \\ cv' &= av(u - b) + v'' \\ 0 &= \lambda^2(u - w) + w'', \end{aligned} \tag{3.24}$$

a system of order six. The Hopf bifurcation occurs as we cross the curve

$$\left.\begin{aligned} \alpha(\omega^2) &= \frac{(D+1)\omega^2}{b} + \frac{(D+1)\lambda^2}{b} + \frac{\lambda^2}{\omega^2} \\ c(\omega^2) &= \sqrt{\frac{ab(1-b) - \omega^4}{\omega^2}} \end{aligned}\right\} \quad \text{for } \omega^2 \in [0, (ab(1-b))^{1/2}] \tag{3.25}$$

which is sketched in Fig. 5.

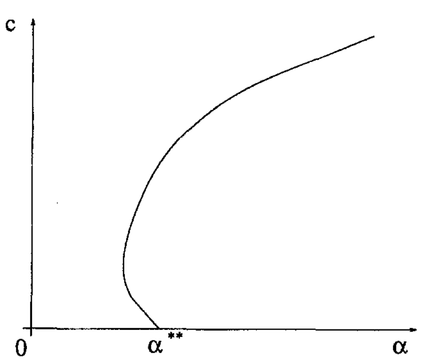

Fig. 5. Bifurcation curve in (α, c) parameter space for periodic travelling wave solutions for the system of § 3.3

It is worth noting that when Britton used a purely spatial kernel in his single species model, bifurcations to standing wave and travelling wave solutions did not occur. The eigenvalue equation there was linear so could not have purely imaginary roots, whereas here the equation is quadratic.

3.4 *The general exponential case*

Again we work in one spatial dimension and take

$$G(x, t) = \tfrac{1}{2}\lambda e^{-\lambda|x|}\theta e^{-\theta t} . \tag{3.26}$$

This kernel tends to the purely temporal kernel of § 3.2 when $\lambda \to \infty$, and to the purely spatial kernel of § 3.3 when $\theta \to \infty$. For finite (positive) λ and θ this kernel satisfies all the hypotheses on G of § 1.

The $s = 0$ root locus in the (α, k^2) plane for this kernel is given by

$$\alpha = \frac{Dk^2}{b} + \frac{D\lambda^2}{b} + \frac{\lambda^2 + a(1-b)}{k^2} + \frac{\lambda^2 a(1-b)}{k^4} \tag{3.27}$$

as in the case of the purely spatial kernel of § 3.3. Regarding the locus $\mathrm{Re}\, s = 0$, we can show (Gourley 1993) that if $\theta \leqq D\lambda^2$ then this locus exists for all $k^2 \geqq 0$, whereas if $\theta > D\lambda^2$ then the locus exists only as long as $k^2 < k_1^2$ where k_1^2 is the positive root of the quadratic equation

$$Q(x) \equiv (\theta - D\lambda^2)x^2 - b\lambda^2 x - (\lambda^2 + \theta)ab(1-b) = 0 .$$

It may be shown analytically that although the $\mathrm{Re}\, s = 0$ root locus meets the α-axis at the same value as for the purely temporal kernel of § 3.2, when λ is very small its qualitative behaviour is different (see Fig. 6), showing that instability sets in earlier when there is a significant (i.e. λ small) amount of spatial averaging. On the other hand as $\lambda \to \infty$, so the spatial averaging becomes more and more localised, the locus $s = 0$ goes to $+\infty$ and the locus $\mathrm{Re}\, s = 0$ tends to the corresponding one for the purely temporal case (Fig. 2) so that for all λ sufficiently large the condition $\alpha < \theta^2/b(\theta + a(1-b))$ is once again a necessary and sufficient condition for stability of $(b, 1-b)$.

For the kernel of this section the rough diagrams in Fig. 1 will apply (diagram (i) when $\theta > D\lambda^2$ and diagram (ii) when $\theta \leqq D\lambda^2$), but when λ is very small the situation is more accurately described by Fig. 6.

Since the kernel of the present section satisfies all the hypotheses of § 1, the bifurcation analysis for general kernels presented in § 4 applies. The system (1.1) will have steady spatially periodic solutions, standing waves and periodic travelling wave solutions.

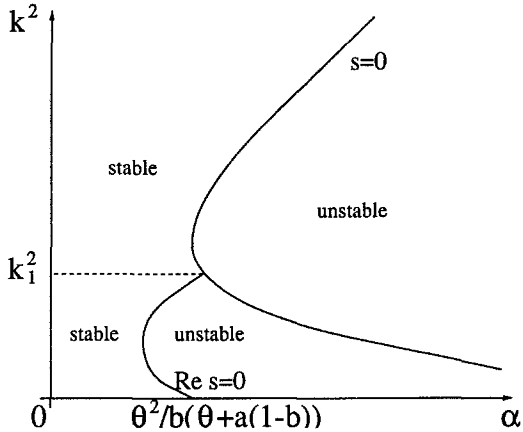

Fig. 6. Stability diagram for the steady state solution $(b, 1-b)$ for the system of § 3.4 when λ is sufficiently small

3.5 The simplest kernel based on a random walk

The kernel given by (1.4), with w a simple exponential, reads

$$G(\boldsymbol{x}, t) = \frac{1}{(4\pi D t)^{n/2}} \exp\left(-\frac{|\boldsymbol{x}|^2}{4Dt} \right) \theta e^{-\theta t} .$$

For this kernel the eigenvalue equation $f(s; \alpha, k^2) = 0$ can again be put into the form of a cubic equation in s. In the (α, k^2) plane the locus $\operatorname{Re} s = 0$ exists when, and only when, k^2 is less than the (unique) positive root of the cubic equation

$$C(x) = \frac{D^2}{D+1} x^3 - \frac{1}{D+1}(b\theta + D^2 ab(1-b))x - \theta ab(1-b) = 0 .$$

Thus for this kernel the stability diagram for the steady state $(b, 1-b)$ is as in Fig. 1, diagram (i). Again the hypotheses on G of § 1 are all satisfied so the bifurcation analysis for general kernels in § 4 applies. There are steady spatially periodic solutions and, for k^2 sufficiently small, standing waves and periodic travelling waves.

3.6 Delay induced instability

In all of the particular kernels considered so far, instability of the steady state $(b, 1-b)$ has set in for strictly *positive* values of α, the steady state being linearly stable when $\alpha = 0$. In this section we show that, by choosing the kernel G suitably, it is possible for instability to occur even when $\alpha = 0$. We consider the case

$$G(x, t) = \frac{1}{(4\pi Dt)^{n/2}} \exp\left(-\frac{|x|^2}{4Dt}\right) \delta(t - T) \tag{3.28}$$

where $T > 0$. With this kernel the nonlocal term in (1.1) becomes

$$(G** u)(x, t) = \int_{R^n} \frac{1}{(4\pi DT)^{n/2}} \exp\left(-\frac{|x-y|^2}{4DT}\right) u(y, t - T)\, dy$$

so the system (1.1) becomes one with a *fixed* time delay T. For this kernel, $\bar{H}(s, k^2) = e^{-sT} e^{-Dk^2T}$ and the eigenvalue equation determining stability of $(b, 1 - b)$ is

$$f(s; \alpha, k^2, T) = (s - \alpha b + (1 + \alpha) b e^{-sT} e^{-Dk^2T} + Dk^2)(s + k^2) + ab(1 - b) = 0 .$$

As we are interested in instability with $\alpha = 0$ we shall take $\alpha = 0$ in the remainder of this section and think of the delay T as bifurcation parameter. Note that in this case $s = 0$ cannot be a root of the eigenvalue equation, so instability can only set in (as T is varied) by two complex conjugate eigenvalues crossing the imaginary axis.

Let μ be the positive root of the quadratic equation

$$Q_1(x) = x^2 - bx - ab(1 - b) = 0 .$$

Then a direct calculation shows that

$$f\left(\mu i; 0, 0, \frac{\pi}{2\mu}\right) = 0 \tag{3.29}$$

so we expect that a bifurcation to spatially uniform temporally periodic solutions should occur at $T = \pi/2\mu$. If a stability diagram were plotted in the (T, k^2) plane the point $(\pi/2\mu, 0)$ would be on the locus $\operatorname{Re} s = 0$. It is in fact very easy to show that the *spatially uniform* mode is linearly stable for all $T < \pi/2\mu$, but rather less easy to analyse the eigenvalue equation when $k^2 \neq 0$. However, we have the following theorem which in particular concerns the $k^2 \neq 0$ case.

Theorem 3.1 *Let*

$$T < \frac{\pi}{2\mu} .$$

Then the steady state $(b, 1 - b)$ is linearly stable to perturbations of arbitrary wave number.

Proof. The method of proof we employ is similar to the method used in the proof of Theorem 2.1 (though the present theorem is not a special case of that theorem). We should point out that the kernel G of this section is, strictly speaking, not in $L^1(\boldsymbol{R}^n \times (0, \infty))$ owing to the presence of a delta function. However $\bar{H}(s, k^2)$ still satisfies properties (i)–(v) listed in § 2 and property (vi) of that section is not used in the proof of Theorem 2.1. Referring back to the proof of that theorem we have, for any fixed k^2, that the number of roots of $f(s; 0, k^2, T) = 0$ with $\operatorname{Re} s \geqq 0$ is

$$\lim_{R \to \infty} \left(1 - \frac{1}{\pi} \arg f(iR; 0, k^2, T)\right).$$

(The condition on α stated in the hypotheses of Theorem 2.1 is not used in this part of the proof). For stability we want to prove that $\arg f(i\infty; 0, k^2, T) = \pi$. Now

$$\begin{aligned} \operatorname{Re} f(iR; 0, k^2, T) = & -R^2 + bRe^{-Dk^2T} \sin RT \\ & + k^2(be^{-Dk^2T} \cos RT + Dk^2) + ab(1 - b) \end{aligned}$$

$$\operatorname{Im} f(iR; 0, k^2, T) = Rbe^{-Dk^2T} \cos RT + k^2((D + 1)R - be^{-Dk^2T} \sin RT)$$

so that $\operatorname{Re} f(iR; 0, k^2, T) \sim -R^2$ as $R \to \infty$ and $|\operatorname{Im} f(iR; 0, k^2, T)| \leqq$ const. R for all R.

Moreover $f(0; 0, k^2, T) \geqq ab(1 - b) > 0$ for any k^2. Hence, by considering the graph of $f(iR; 0, k^2, T)$ in the complex plane as R ranges from 0 to infinity it is clear that if we can show $\operatorname{Im} f(iR; 0, k^2, T) > 0$ when $\operatorname{Re} f(iR; 0, k^2, T) = 0$ then it will follow that $\arg f(iR; 0, k^2, T) \to \pi$ as $R \to \infty$.

When $\operatorname{Re} f(iR; 0, k^2, T) = 0$ we have

$$\operatorname{Im} f(iR; 0, k^2, T) = \left(R + \frac{k^4}{R}\right)(be^{-Dk^2T} \cos RT + Dk^2) + \frac{k^2}{R} ab(1 - b) \quad (3.30)$$

(note that R cannot be zero when $\operatorname{Re} f(iR; 0, k^2, T) = 0$, since $f(0; 0, k^2, T) > 0$). To show that expression (3.30) is positive it suffices to show that $be^{-Dk^2T} \cos RT + Dk^2 > 0$ when $\operatorname{Re} f(iR; 0, k^2, T) = 0$. Now when $\operatorname{Re} f(iR; 0, k^2, T) = 0$,

$$k^2(be^{-Dk^2T} \cos RT + Dk^2) = R^2 - bRe^{-Dk^2T} \sin RT - ab(1 - b) \qquad (3.31)$$

so suppose for contradiction that $be^{-Dk^2T} \cos RT + Dk^2 \leqq 0$. Then the right hand side of (3.31) is $\leqq 0$ and so it follows that

$$R^2 - bR - ab(1 - b) \leqq 0 .$$

It follows (by considering the quadratic equation that defines μ) that $R \leqq \mu$. However we also have $T < \pi/2\mu$ so, multiplying these inequalities we obtain $RT < \frac{1}{2}\pi$. But in that case $\cos RT > 0$ which contradicts our assumption that $be^{-Dk^2T} \cos RT + Dk^2 \leqq 0$. This completes the proof of the theorem.

There are certain points worth mentioning that come to light in proving this theorem. Note that, whether T satisfies $T < \pi/2\mu$ or not, expression (3.30) is positive when $Dk^2 > be^{-Dk^2T}$. The latter is true for all k^2 sufficiently large, and for any *fixed* k^2 it is true when T is sufficiently large. Thus large values of the delay are seen to have a stabilising effect, and bifurcations can only occur for k^2 sufficiently small.

4 Construction of the bifurcating solutions

In this section we construct, using perturbation methods, some of the solutions which bifurcate from the coexistence steady state $(b, 1-b)$ of the system (1.1). We are now studying this system for general $G(x, t)$ satisfying only hypotheses (H1)–(H4). Recall that the stability equation for perturbations of wave vector $\boldsymbol{k}$ is given by (2.3) and the stability boundaries in the (α, k^2) plane are as in Fig. 1.

We consider here two of the bifurcations, namely bifurcation to steady spatially periodic solutions, and Hopf bifurcation to periodic standing waves. There is also a Hopf bifurcation to periodic travelling wave solutions. The latter is described in Gourley (1993).

4.1 Bifurcation at a zero eigenvalue

We consider the bifurcation that occurs in (1.1) when as α is increased a root of the eigenvalue equation (2.3) crosses the imaginary axis through the origin. Such a crossing always occurs if $k^2 \neq 0$. When $s = 0$ is a root of (2.3) the linearised equations have solutions proportional to $e^{i\boldsymbol{k}.\boldsymbol{x}}$, so this suggests that we should consider the possibility of a bifurcation of steady spatially periodic plane wave solutions from the steady state solution $(b, 1-b)$. Let $\boldsymbol{k}$ be any non-zero vector (which we consider fixed), then we define $\xi = \boldsymbol{k}.\boldsymbol{x}$ and look for a solution which is 2π-periodic of the form $u(\boldsymbol{x}, t) = \hat{u}(\boldsymbol{k}.\boldsymbol{x}) = \hat{u}(\xi)$, $v(\boldsymbol{x}, t) = \hat{v}(\boldsymbol{k}.\boldsymbol{x}) = \hat{v}(\xi)$. Dropping the hats, the system (1.1) becomes (prime denoting differentiation with respect to ξ)

$$
\begin{aligned}
0 &= u\left(1 + \alpha u - (1+\alpha)\int_{\boldsymbol{R}^n}\int_0^\infty G(\boldsymbol{x}-\boldsymbol{y}, s)\,u(\boldsymbol{k}.\boldsymbol{y})\,ds\,dy\right) - uv + Dk^2u'' \\
0 &= av(u-b) + k^2v''
\end{aligned}
\tag{4.1}
$$

with periodic boundary conditions at $\xi = 0$ and $\xi = 2\pi$. Again the system is invariant under the transformation $\xi \to -\xi$ but we may ensure that the eigenvalue of the linearised system is simple if we look for solutions symmetric in ξ. Thus we look for solutions on $(0, \pi)$ which satisfy the conditions

$$
u'(0) = u'(\pi) = v'(0) = v'(\pi) = 0\,. \tag{4.2}
$$

For general kernels the term $G{**}u$ requires u to be defined on the whole real line; a solution on $(0, \pi)$ satisfying (4.2) is therefore understood to be extended to an even function on $(-\pi, \pi)$ and then periodically over all of $\boldsymbol{R}$.

We can check that an appropriate transversality condition holds as s passes through 0. Differentiating (2.3) with respect to α and setting $s = 0$ yields

$$
\frac{\partial s}{\partial \alpha} = \frac{bk^2(1-\bar{H}(0,k^2))}{-\alpha b + (1+\alpha)b\bar{H}(0,k^2) + k^2(D + 1 + (1+\alpha)b\bar{H}_s(0,k^2))}
$$

and since $k^2 \neq 0$, property (v) of $H(s, k^2)$ implies that the above quantity is nonzero and therefore that the transversality condition does indeed hold. We now construct the first few terms in the bifurcating solution using a standard perturbation procedure, regarding k^2 as fixed and working in a suitable space of functions satisfying (4.2) with the inner product

$$[(u_1, u_2), (v_1, v_2)] = \int_0^\pi (u_1(\xi)\bar{v}_1(\xi) + u_2(\xi)\bar{v}_2(\xi))\, d\xi .$$

We seek a solution of (4.1) with (4.2) of the form

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} b \\ 1-b \end{pmatrix} + \varepsilon \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + \varepsilon^2 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + \cdots , \tag{4.3}$$

$$\alpha = \alpha_0 + \varepsilon\alpha_1 + \varepsilon^2\alpha_2 + \cdots , \tag{4.4}$$

where

$$u_n'(0) = u_n'(\pi) = v_n'(0) = v_n'(\pi) = 0, \quad n = 1, 2, \ldots . \tag{4.5}$$

We substitute (4.3) into (4.1) and equate powers of ε up to the third power. If we define the linear operator L by

$$L = \begin{pmatrix} \alpha_0 b - (1+\alpha_0) b G{**} + Dk^2 \dfrac{d^2}{d\xi^2} & -b \\ a(1-b) & k^2 \dfrac{d^2}{d\xi^2} \end{pmatrix}$$

where the operator $G{**}$ is defined by (1.2), then the first three perturbation equations are

$$L\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \mathbf{0} \tag{4.6}$$

$$L\begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} -\alpha_1 b u_1 + \alpha_1 b\, G{**}u_1 - \alpha_0 u_1^2 + u_1 v_1 + (1+\alpha_0) u_1\, G{**}u_1 \\ -a u_1 v_1 \end{pmatrix} \tag{4.7}$$

$$L\begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} -\alpha_1 b u_2 - \alpha_2 b u_1 + \alpha_1 b\, G{**}u_2 + \alpha_2 b\, G{**}u_1 - 2\alpha_0 u_1 u_2 - \alpha_1 u_1^2 \\ + (1+\alpha_0) u_1\, G{**}u_2 + \alpha_1 u_1\, G{**}u_1 + (1+\alpha_0) u_2\, G{**}u_1 \\ + u_1 v_2 + u_2 v_1 \\ -a(v_1 u_2 + v_2 u_1) \end{pmatrix} \tag{4.8}$$

Next, a simple computation yields the useful formula

$$G{**}\cos n\xi = \bar{H}(0, n^2k^2)\cos n\xi, \quad n = 0, 1, 2, \ldots \tag{4.9}$$

which we will use in subsequent calculations. The non-trivial solution of (4.6) with (4.5) is of the form

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} \cos\xi \tag{4.10}$$

as long as

$$f(0;\alpha_0,k^2)=(-\alpha_0 b+(1+\alpha_0)b\bar{H}(0,k^2)+Dk^2)k^2+ab(1-b)=0 \quad (4.11)$$

and in this case either component of (4.6) gives the ratio of a_1 to a_2;

$$\frac{a_1}{a_2}=\frac{k^2}{a(1-b)}\,. \quad (4.12)$$

This is the only solution (up to scalar multiples) of (4.6) provided that

$$f(0;\alpha_0,n^2k^2)\neq 0 \quad \text{for all integers} \quad n\geqq 2 \quad (4.13)$$

which we assume to be the case. Then (4.11) defines α_0 as a function of k^2,

$$\alpha_0=\alpha_0(k^2)=\frac{ab(1-b)+bk^2\bar{H}(0,k^2)+Dk^4}{bk^2(1-\bar{H}(0,k^2))}\,. \quad (4.14)$$

We claim that the adjoint L^* of the linear operator L is given by

$$L^*=\begin{pmatrix}\alpha_0 b-(1+\alpha_0)b\,G{**}+Dk^2\dfrac{d^2}{d\xi^2} & a(1-b)\\ -b & k^2\dfrac{d^2}{d\xi^2}\end{pmatrix}.$$

The proof that L^* satisfies the defining property $[L\boldsymbol{u},\boldsymbol{v}]=[\boldsymbol{u},L^*\boldsymbol{v}]$ of adjoints is fairly routine but involves showing that

$$\int_0^\pi v\,G{**}u\,d\xi=\int_0^\pi u\,G{**}v\,d\xi$$

for all functions u, v such that $u'(0)=u'(\pi)=v'(0)=v'(\pi)=0$. This may easily be seen by expanding u and v in their Fourier cosine series, evaluating each integrand using formula (4.9) and then using the orthogonality of the functions $\cos n\xi$ over the interval $(0,\pi)$. Now in subsequent calculations we shall need to use the Fredholm Alternative so we need to know the solution $(u_1^*,v_1^*)^{\mathrm{T}}$ of the adjoint equation

$$L^*\begin{pmatrix}u_1^*\\ v_1^*\end{pmatrix}=\mathbf{0}\,. \quad (4.15)$$

Since (4.11) holds, the solution is $(u_1^*,v_1^*)^{\mathrm{T}}=(d_1,d_2)^{\mathrm{T}}\cos\xi$ where

$$\frac{d_1}{d_2}=-\frac{k^2}{b} \quad (4.16)$$

and this solution is again unique up to normalisation. With $u_1=a_1\cos\xi$ and $v_1=a_2\cos\xi$, it follows from the Fredholm Alternative that (4.7) has a solution if and only if the inner product of its right hand side with $(u_1^*,v_1^*)^{\mathrm{T}}$ is zero. Since the quadratic terms u_1^2, u_1v_1 and $u_1G{**}u_1$ do not involve first harmonics we are left with

$$\int_0^\pi(-\alpha_1 b+\alpha_1 b\bar{H}(0,k^2))a_1d_1\cos^2\xi\,d\xi=0$$

or $a_1 d_1 \alpha_1(1 - \bar{H}(0, k^2)) = 0$. From property (v) of $\bar{H}(s, k^2)$ and the fact that a_1 and d_1 cannot be zero it follows that $\alpha_1 = 0$. Then (4.7) becomes

$$L\begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} -\alpha_0 a_1^2 + a_1 a_2 + (1+\alpha_0) a_1^2 \bar{H}(0, k^2) \\ -a a_1 a_2 \end{pmatrix} \cos^2 \xi$$

$$= \begin{pmatrix} a_1 a_2 - a_1^2 (ab(1-b) + Dk^4)/bk^2 \\ -a a_1 a_2 \end{pmatrix} \cos^2 \xi \quad \text{using (4.11)}$$

$$= \frac{1}{2}\begin{pmatrix} -a_1 a_2 Dk^4/ab(1-b) \\ -a a_1 a_2 \end{pmatrix} (1 + \cos 2\xi) \quad \text{using (4.12)}\,.$$

This has solution

$$\begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} A_1 \\ A_2 \end{pmatrix} + \begin{pmatrix} B_1 \\ B_2 \end{pmatrix} \cos 2\xi$$

where, after some algebra,

$$A_1 = -\frac{a_1 a_2}{2(1-b)}, \qquad A_2 = \frac{a_1 a_2 (ab^2 + Dk^4)}{2ab^2(1-b)},$$

$$B_1 = \frac{a_1 a_2}{f(0; \alpha_0, 4k^2)} \left(\frac{2Dk^6}{ab(1-b)} - \frac{1}{2} ab \right),$$

$$B_2 = \frac{a_1 a_2}{f(0; \alpha_0, 4k^2)} \left(\frac{Dk^4}{2b} + \frac{a}{8k^2} (f(0; \alpha_0, 4k^2) - ab(1-b)) \right).$$

Note that assumption (4.13) guarantees that B_1 and B_2 are well defined. Then (4.8) becomes, after a lengthy calculation,

$$L\begin{pmatrix} u_3 \\ v_3 \end{pmatrix}$$

$$= \begin{pmatrix} \Big[-\alpha_2 b + \alpha_2 b \bar{H}(0, k^2) + A_1 + \frac{1}{2} B_1 \Big(\frac{1}{4k^2 b} (f(0; \alpha_0, 4k^2) - ab(1-b)) \\ \quad - \frac{4Dk^2}{b} \Big) + A_2 + \frac{1}{2} B_2 - \frac{Dk^2}{b} (A_1 + \frac{1}{2} B_1) \Big] a_1 \\ -a \Big[\frac{a(1-b)}{k^2} (A_1 + \frac{1}{2} B_1) + A_2 + \frac{1}{2} B_2 \Big] a_1 \end{pmatrix} \cos \xi$$

$$+ \begin{pmatrix} -\alpha_0 a_1 B_1 + \frac{1}{2} B_1 (1 + \alpha_0) a_1 (\bar{H}(0, 4k^2) + \bar{H}(0, k^2)) + \frac{1}{2}(a_2 B_1 + a_1 B_2) \\ -\frac{1}{2} a (a_2 B_1 + a_1 B_2) \end{pmatrix}$$

$$\times \cos 3\xi\,. \tag{4.17}$$

By the Fredholm Alternative, this has a solution if and only if

$$\left[-\alpha_2 b + \alpha_2 b\bar{H}(0,k^2) + A_1 + \frac{1}{2}B_1\left(\frac{1}{4k^2 b}(f(0;\alpha_0,4k^2) - ab(1-b)) - \frac{4Dk^2}{b}\right)\right.$$

$$\left. + A_2 + \frac{1}{2}B_2 - \frac{Dk^2}{b}(A_1 + \tfrac{1}{2}B_1)\right] d_1$$

$$- ad_2\left[\frac{a(1-b)}{k^2}(A_1 + \tfrac{1}{2}B_1) + A_2 + \tfrac{1}{2}B_2\right] = 0$$

Hence, using (4.16),

$$\alpha_2 b(1 - \bar{H}(0,k^2)) = A_1 + \frac{1}{2}B_1\left(\frac{1}{4k^2 b}(f(0;\alpha_0,4k^2) - ab(1-b)) - \frac{4Dk^2}{b}\right)$$

$$+ \left(\frac{a^2 b(1-b)}{k^4} - \frac{Dk^2}{b}\right)\left(A_1 + \frac{1}{2}B_1\right) + \left(1 + \frac{ab}{k^2}\right)\left(A_2 + \frac{1}{2}B_2\right)$$

so that after some algebra,

$$\alpha_2 = \frac{a_1 a_2}{b(1 - \bar{H}(0,k^2))}\left[\left(\frac{3Dk^4}{2ab^2} + \frac{2Dk^2}{b} + \frac{ab}{k^2} - \frac{7a^2 b(1-b)}{8k^4}\right)\Big/ 2(1-b)\right.$$

$$\left. - \left(\frac{5D^2k^8}{ab^2(1-b)} - \frac{5}{2}Dk^2 a + \frac{5a^3b^2(1-b)}{16k^4}\right)\Big/ f(0;\alpha_0,4k^2)\right].$$

Now $a_1 = k^2 a_2/a(1-b)$ so in the bifurcating solution a_2 only arises as a factor of ε, as expected. Hence we may take $a_2 = 1$ and $a_1 = k^2/a(1-b)$ and our construction of the first few terms in the bifurcating solution is complete.

The sign of α_2 determines whether the bifurcation is sub- or supercritical. It is straightforward to see that as $k^2 \to \infty$ (with $\alpha_0 = \alpha_0(k^2)$) we have $f(0;\alpha_0,4k^2) \to 12Dk^4$ and as $k^2 \to 0, f(0;\alpha_0,4k^2) \to -15ab(1-b)$. Hence

$$\alpha_2 \sim \frac{Dk^4 a_1 a_2}{3ab^3(1-b)} \quad \text{for } k^2 \text{ large},$$

$$\alpha_2 \sim -\frac{5a^2 a_1 a_2}{12k^4(1 - \bar{H}(0,k^2))} \quad \text{for } k^2 \text{ small},$$

so that this bifurcation is supercritical for k^2 sufficiently large and subcritical for k^2 sufficiently small.

4.2 *Hopf bifurcation to periodic standing waves*

We consider the bifurcation that occurs in (1.1) when as α is increased, two roots of the eigenvalue equation (2.3) cross the imaginary axis as a pair of complex conjugates. In this case the linearised equations have solutions proportional to $e^{ik\cdot x}e^{i\omega t}$ so this suggests that we should consider the possibility that from the uniform steady state solution $(u, v) = (b, 1-b)$ there bifurcates a family of plane wave solutions which are periodic in both space and time. To be specific, we look for a solution of (1.1) of the form $u(\boldsymbol{x}, t) = \hat{u}(\xi, \tau)$, $v(\boldsymbol{x}, t) = \hat{v}(\xi, \tau)$ where $\xi = \boldsymbol{k} . \boldsymbol{x}$ and $\tau = \omega t$ ($\boldsymbol{k}$ being any fixed non-zero vector) such that $\hat{u}$ and $\hat{v}$ are 2π-periodic in both arguments. After dropping the hats, the system (1.1) becomes

$$\begin{aligned} \omega u_\tau &= u[1 + \alpha u - (1+\alpha) G{**}u] - uv + Dk^2 u_{\xi\xi} \\ \omega v_\tau &= av(u-b) + k^2 v_{\xi\xi} \end{aligned} \tag{4.18}$$

for $(\xi, \tau) \in (0, 2\pi) \times (0, 2\pi)$ with periodic boundary conditions. We will again look for solutions which are symmetric in ξ by seeking solutions which satisfy the boundary conditions

$$u_\xi(0, \tau) = u_\xi(\pi, \tau) = v_\xi(0, \tau) = v_\xi(\pi, \tau) = 0 \tag{4.19}$$

and the conditions

$$\begin{aligned} u(\xi, 0) &= u(\xi, 2\pi), \qquad u_\tau(\xi, 0) = u_\tau(\xi, 2\pi)\,, \\ v(\xi, 0) &= v(\xi, 2\pi), \qquad v_\tau(\xi, 0) = v_\tau(\xi, 2\pi)\,. \end{aligned} \tag{4.20}$$

Thus the system is considered for $(\xi, \tau) \in (0, \pi) \times (0, 2\pi)$ only; it is clear how to define u outside this set so that $G{**}u$ is well defined. In this section we shall work in a suitable space of functions satisfying (4.19), (4.20) with the inner product

$$[(u_1, u_2), (v_1, v_2)] = \int_0^{2\pi} \int_0^{\pi} (u_1(\xi, \tau)\bar{v}_1(\xi, \tau) + u_2(\xi, \tau)\bar{v}_2(\xi, \tau))\, d\xi\, d\tau\,.$$

We shall construct the first few terms in the bifurcating solution using a Poincaré-Lindstedt procedure, that is, we seek a solution of (4.18) with (4.19) and (4.20) of the form

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} b \\ 1-b \end{pmatrix} + \varepsilon \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + \varepsilon^2 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + \cdots, \tag{4.21}$$

$$\alpha = \alpha_0 + \varepsilon\alpha_1 + \varepsilon^2\alpha_2 + \cdots, \tag{4.22}$$

$$\omega = \omega_0 + \varepsilon\omega_1 + \varepsilon^2\omega_2 + \cdots. \tag{4.23}$$

We substitute this into (4.18) and equate powers of ε up to the third power. Note however that since $G{**}u$ involves ω it is necessary to expand each $G{**}u_n$ in powers of ε,

$$\begin{aligned} G{**}u_n &= (G{**}u_n)|_{\varepsilon=0} + \varepsilon(G{**}u_n)_\varepsilon|_{\varepsilon=0} + \tfrac{1}{2}\varepsilon^2(G{**}u_n)_{\varepsilon\varepsilon}|_{\varepsilon=0} + \cdots \\ &= (G{**}u_n)^0 + \varepsilon(G{**}u_n)^0_\varepsilon + \tfrac{1}{2}\varepsilon^2(G{**}u_n)^0_{\varepsilon\varepsilon} + \cdots \end{aligned}$$

where the superscript zero denotes evaluation at $\varepsilon = 0$. If we define the linear operator M by

$$M = \omega_0 \frac{d}{d\tau} - \begin{pmatrix} \alpha_0 b - (1+\alpha_0) b (G{**}\cdot)^0 + Dk^2 \dfrac{d^2}{d\xi^2} & -b \\ a(1-b) & k^2 \dfrac{d^2}{d\xi^2} \end{pmatrix} \tag{4.24}$$

then the first three perturbation equations are

$$M\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \mathbf{0} \tag{4.25}$$

$$M\begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} -\omega_1 u_{1\tau} + \alpha_1 b u_1 - (1+\alpha_0) b (G{**}u_1)^0_\varepsilon - \alpha_1 b (G{**}u_1)^0 \\ +\alpha_0 u_1^2 - (1+\alpha_0) u_1 (G{**}u_1)^0 - u_1 v_1 \\ -\omega_1 v_{1\tau} + a u_1 v_1 \end{pmatrix} \tag{4.26}$$

$$M\begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} -\omega_1 u_{2\tau} - \omega_2 u_{1\tau} + \alpha_1 b u_2 + \alpha_2 b u_1 - (1+\alpha_0) b (G{**}u_2)^0_\varepsilon \\ -\frac{1}{2}(1+\alpha_0) b (G{**}u_1)^0_{\varepsilon\varepsilon} - \alpha_1 b (G{**}u_2)^0 - \alpha_1 b (G{**}u_1)^0_\varepsilon \\ -\alpha_2 b (G{**}u_1)^0 + 2\alpha_0 u_1 u_2 + \alpha_1 u_1^2 - (1+\alpha_0) u_1 (G{**}u_2)^0 \\ -(1+\alpha_0) u_1 (G{**}u_1)^0_\varepsilon - \alpha_1 u_1 (G{**}u_1)^0 - (1+\alpha_0) u_2 (G{**}u_1)^0 \\ -u_1 v_2 - u_2 v_1 \\ -\omega_1 v_{2\tau} - \omega_2 v_{1\tau} + a(v_1 u_2 + v_2 u_1) \end{pmatrix}$$

for $(\xi, \tau) \in (0, \pi) \times (0, 2\pi)$ with conditions of the form (4.19), (4.20) for each (u_n, v_n). A simple computation yields the formula

$$G{**}\,\mathrm{e}^{mi\tau} \cos n\xi = \bar{H}(mi\omega, n^2k^2)\,\mathrm{e}^{mi\tau} \cos n\xi, \quad m, n = 0, 1, 2, \ldots. \tag{4.28}$$

It is important to note the effect of the superscript zero in the term $(G{**}\cdot)^0$ of the operator M. For functions u of the form $u_{m,n}(\xi, \tau) = \mathrm{e}^{mi\tau} \cos n\xi$ we have, from (4.28), $(G{**}u_{m,n})^0 = \bar{H}(mi\omega_0, n^2k^2)u_{m,n}$. For other functions u, $(G{**}u)^0$ would be calculated by first writing u as a Fourier series in terms of the functions $u_{m,n}$.

The non-trivial solution of (4.25) is of the form

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \begin{pmatrix} a_1 \\ 1 \end{pmatrix} \mathrm{e}^{i\tau} \cos \xi + \text{c.c.} \tag{4.29}$$

where c.c. stands for complex conjugate, which satisfies (4.25) as long as

$$f(i\omega_0; \alpha_0, k^2) = (i\omega_0 - \alpha_0 b + (1+\alpha_0) b \bar{H}(i\omega_0, k^2) + Dk^2)(i\omega_0 + k^2) + ab(1-b) = 0 \tag{4.30}$$

and in this case either component of (4.25) implies that

$$a_1 = \frac{i\omega_0 + k^2}{a(1-b)}. \tag{4.31}$$

This is the only solution (up to scalar multiples) of (4.25) provided that

$$f(mi\omega_0; \alpha_0, n^2k^2) \neq 0 \quad \text{for any pair of non-negative integers } (m, n) \neq (1, 1) \tag{4.32}$$

which we assume to be the case. The real and imaginary parts of (4.30) give α_0 and ω_0 implicitly in terms of k^2, $\alpha_0 = \alpha_0(k^2)$, $\omega_0 = \omega_0(k^2)$.

It is fairly easy to see that the adjoint M^* of the linear operator M is given by

$$M^* = -\omega_0 \frac{d}{d\tau} - \begin{pmatrix} \alpha_0 b + Dk^2 \dfrac{d^2}{d\xi^2} & a(1-b) \\ -b & k^2 \dfrac{d^2}{d\xi^2} \end{pmatrix} + (1+\alpha_0) b M_1^* \tag{4.33}$$

where the linear operator M_1^* acts on Fourier components as follows:

$$M_1^* \left(\begin{pmatrix} a_1 \\ a_2 \end{pmatrix} e^{mi\tau} \cos n\xi \right) = \begin{pmatrix} a_1 \overline{\bar{H}(mi\omega_0, n^2k^2)}\, e^{mi\tau} \cos n\xi \\ 0 \end{pmatrix} \tag{4.34}$$

and on any other function (satisfying (4.19), (4.20)) by expressing it as a Fourier series and using linearity. The term M_1^* is in fact the contribution to the adjoint from the nonlocal term in the operator M.

The solution $(u_1^*, v_1^*)^{\mathrm{T}}$ of the adjoint equation

$$M^* \begin{pmatrix} u_1^* \\ v_1^* \end{pmatrix} = \mathbf{0}$$

is of the form

$$\begin{pmatrix} u_1^* \\ v_1^* \end{pmatrix} = \begin{pmatrix} d_1 \\ 1 \end{pmatrix} e^{i\tau} \cos \xi + \text{c.c.}$$

with

$$d_1 = \frac{i\omega_0 - k^2}{b}. \tag{4.35}$$

Let us now consider the transversality condition required for this bifurcation. For general kernels G the condition is, unfortunately, not easy to check. What we can do, however, is derive a certain formula which will be needed in later calculations, and we will demonstrate that the transversality condition does indeed hold at least for large k^2. For values of α near α_0, let $\mu(\alpha)$ be the root of the eigenvalue equation (2.3) such that $\mu(\alpha_0) = i\omega_0$. Then

$$(\mu(\alpha) - \alpha b + (1+\alpha) b \bar{H}(\mu(\alpha), k^2) + Dk^2)(\mu(\alpha) + k^2) + ab(1-b) = 0\ .$$

Differentiating with respect to α and evaluating at $\alpha = \alpha_0$, we can show that

$$\mu'(\alpha_0)[1 + a_1 \bar{d}_1 (1 + (1+\alpha_0) b \bar{H}_s(i\omega_0, k^2))] = a_1 \bar{d}_1 b (1 - \bar{H}(i\omega_0, k^2)). \tag{4.36}$$

We shall use this formula later. Referring back to the asymptotic analysis described in § 2, we can show that when $k^2 \to \infty$,

$$\mu'(\alpha_0) \sim \frac{b}{2} + i \frac{b G_n(0)}{2\omega_0^* G_n'(0)} \tag{4.37}$$

where

$$\omega_0^* = \sqrt{\frac{G_n(0)^2}{G_n'(0)} \left[\frac{2D\pi^{n/2}}{\Gamma(n/2)} - \frac{1}{G_n'(0)} \right]}\ . \tag{4.38}$$

This will be used later when we calculate the sub/supercriticality of this bifurcation as $k^2 \to \infty$. We return to our construction of the bifurcating solution, assuming that $\operatorname{Re}\mu'(\alpha_0) \neq 0$. Now

$$(G ** u_1)^0_\varepsilon = a_1 i\omega_1 \bar{H}_s(i\omega_0, k^2) e^{i\tau} \cos\xi + \text{c.c.}$$

and, taking the inner product of the right hand side of (4.26) with $(u_1^*, v_1^*)^{\mathrm{T}}$, we obtain after some algebra the solvability condition for (4.26):

$$i\omega_1[1 + a_1\bar{a}_1(1 + (1+\alpha_0)b\bar{H}_s(i\omega_0, k^2))] = \alpha_1 a_1 \bar{a}_1 b(1 - \bar{H}(i\omega_0, k^2)) .$$

Combining this with (4.36) yields

$$(i\omega_1 - \mu'(\alpha_0)\alpha_1)(1 - \bar{H}(i\omega_0, k^2)) = 0 .$$

From property (vi) of $\bar{H}$ it follows that $\mu'(\alpha_0)\alpha_1 = i\omega_1$. Hence $\alpha_1 \operatorname{Re}\mu'(\alpha_0) = 0$ and $\omega_1 = \alpha_1 \operatorname{Im}\mu'(\alpha_0)$. By the transversality assumption it follows that $\alpha_1 = 0$ and $\omega_1 = 0$. Consequently we also have $(G ** u_1)^0_\varepsilon = 0$ and (4.26) becomes

$$M\begin{pmatrix} u_2 \\ v_2 \end{pmatrix} =$$

$$\cos^2\xi \begin{pmatrix} \alpha_0(a_1^2 e^{2i\tau} + |a_1|^2) - (1+\alpha_0)a_1\bar{H}(i\omega_0, k^2)(a_1 e^{2i\tau} + \bar{a}_1) - a_1(e^{2i\tau} + 1) \\ a a_1(e^{2i\tau} + 1) \end{pmatrix}$$

$$+ \text{complex conjugate}$$

$$= \frac{1}{2}(1 + \cos 2\xi)\left\{\begin{pmatrix} \frac{a_1^2}{b}(i\omega_0 + Dk^2) \\ a a_1 \end{pmatrix} e^{2i\tau} + \begin{pmatrix} |a_1|^2 Dk^2/b \\ a a_1 \end{pmatrix}\right\} + \text{c.c.}$$

This has solution

$$\begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \left[\begin{pmatrix} A_1 \\ A_2 \end{pmatrix} + \begin{pmatrix} B_1 \\ B_2 \end{pmatrix}\cos 2\xi\right] e^{2i\tau} + \begin{pmatrix} C_1 \\ C_2 \end{pmatrix} + \begin{pmatrix} D_1 \\ D_2 \end{pmatrix}\cos 2\xi + \text{c.c.}$$

where, after some algebra and using (4.31),

$$A_1 = \frac{a_1}{2f(2i\omega_0; \alpha_0, 0)}\left(\frac{2i\omega_0(i\omega_0 + k^2)(i\omega_0 + Dk^2)}{ab(1-b)} - ab\right),$$

$$A_2 = \frac{a_1}{2f(2i\omega_0; \alpha_0, 0)}\left(\frac{(i\omega_0 + k^2)(i\omega_0 + Dk^2)}{b} + \frac{a}{2i\omega_0}(f(2i\omega_0; \alpha_0, 0) - ab(1-b))\right),$$

$$B_1 = \frac{a_1}{2f(2i\omega_0; \alpha_0, 4k^2)}\left(\frac{(i\omega_0 + k^2)(2i\omega_0 + 4k^2)(i\omega_0 + Dk^2)}{ab(1-b)} - ab\right),$$

$$B_2 = \frac{a_1}{2f(2i\omega_0; \alpha_0, 4k^2)}\left(\frac{(i\omega_0 + k^2)(i\omega_0 + Dk^2)}{b}\right.$$

$$\left. + a\frac{(f(2i\omega_0; \alpha_0, 4k^2) - ab(1-b))}{2i\omega_0 + 4k^2}\right),$$

$$C_1 = -\frac{a_1}{2(1-b)}, \qquad C_2 = \frac{a_1}{2ab^2(1-b)}(Dk^2(-i\omega_0 + k^2) + ab^2),$$

$$D_1 = \frac{a_1}{2f(0;\alpha_0, 4k^2)}\left(\frac{4Dk^4(-i\omega_0 + k^2)}{ab(1-b)} - ab\right),$$

$$D_2 = \frac{a_1}{2f(0;\alpha_0, 4k^2)}\left(\frac{Dk^2(-i\omega_0 + k^2)}{b} + \frac{a}{4k^2}(f(0;\alpha_0, 4k^2) - ab(1-b))\right).$$

Note that by assumption (4.32), all these coefficients are well defined. Now with $\alpha_1 = \omega_1 = 0$ we have $(G{**}u_2)^0_\varepsilon = 0$ and $(G{**}u_1)^0_{\varepsilon\varepsilon} = 2ia_1\omega_2\bar{H}_s(i\omega_0, k^2) \times e^{i\tau}\cos\xi$ + c.c.. The system (4.27) becomes

$$M\begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} -\omega_2 u_{1\tau} + \alpha_2 b u_1 - \frac{1}{2}(1+\alpha_0)b(G{**}u_1)^0_{\varepsilon\varepsilon} - \alpha_2 b(G{**}u_1)^0 \\ + 2\alpha_0 u_1 u_2 - (1+\alpha_0)u_1(G{**}u_2)^0 - (1+\alpha_0)u_2(G{**}u_1)^0 \\ - u_1 v_2 - u_2 v_1 \\ -\omega_2 v_{1\tau} + a(v_1 u_2 + v_2 u_1) \end{pmatrix} \tag{4.39}$$

After substitution of the expressions for u_1, v_1, u_2, v_2 and a rather lengthy calculation the system (4.39) yields a differential equation of the form

$$M\begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} \Phi_{11} \\ \Phi_{12} \end{pmatrix} e^{i\tau}\cos\xi + \begin{pmatrix} \Phi_{21} \\ \Phi_{22} \end{pmatrix} e^{i\tau}\cos 3\xi$$
$$+ \begin{pmatrix} \Phi_{31} \\ \Phi_{32} \end{pmatrix} e^{3i\tau}\cos\xi + \begin{pmatrix} \Phi_{41} \\ \Phi_{42} \end{pmatrix} e^{3i\tau}\cos 3\xi + \text{complex conjugate} \tag{4.40}$$

where

$$\begin{aligned} \Phi_{11} = & -ia_1\omega_2(1 + (1+\alpha_0)b\bar{H}_s(i\omega_0, k^2)) + \alpha_2 b a_1(1 - \bar{H}(i\omega_0, k^2)) \\ & + A_1(2\alpha_0\bar{a}_1 - (1+\alpha_0)\bar{a}_1\bar{H}(2i\omega_0, 0) - (1+\alpha_0)\bar{a}_1\overline{\bar{H}(i\omega_0, k^2)} - 1) - \bar{a}_1 A_2 \\ & + \tfrac{1}{2}B_1(2\alpha_0\bar{a}_1 - (1+\alpha_0)\bar{a}_1\bar{H}(2i\omega_0, 4k^2) - (1+\alpha_0)\bar{a}_1\overline{\bar{H}(i\omega_0, k^2)} - 1) - \tfrac{1}{2}\bar{a}_1 B_2 \\ & + 2\mathrm{Re}C_1(2\alpha_0 a_1 - (1+\alpha_0)a_1 - (1+\alpha_0)a_1\bar{H}(i\omega_0, k^2) - 1) - 2a_1\mathrm{Re}C_2 \\ & + \mathrm{Re}D_1(2\alpha_0 a_1 - (1+\alpha_0)a_1\bar{H}(0, 4k^2) - (1+\alpha_0)a_1\bar{H}(i\omega_0, k^2) - 1) - a_1\mathrm{Re}D_2, \end{aligned}$$

$$\begin{aligned} \Phi_{12} = & -i\omega_2 + a(A_1 + \bar{a}_1 A_2 + \tfrac{1}{2}B_1 + \tfrac{1}{2}\bar{a}_1 B_2 + 2\mathrm{Re}\,C_1 \\ & + 2a_1\mathrm{Re}\,C_2 + \mathrm{Re}\,D_1 + a_1\mathrm{Re}\,D_2) \end{aligned}$$

$$\begin{aligned} \Phi_{21} = & \tfrac{1}{2}B_1(2\alpha_0\bar{a}_1 - (1+\alpha_0)\bar{a}_1\bar{H}(2i\omega_0, 4k^2) - (1+\alpha_0)\bar{a}_1\overline{\bar{H}(i\omega_0, k^2)} - 1) - \tfrac{1}{2}\bar{a}_1 B_2 \\ & + \mathrm{Re}\,D_1(2\alpha_0 a_1 - (1+\alpha_0)a_1\bar{H}(0, 4k^2) - (1+\alpha_0)a_1\bar{H}(i\omega_0, k^2) - 1) - a_1\mathrm{Re}\,D_2, \end{aligned}$$

$$\Phi_{22} = a(\tfrac{1}{2}B_1 + \tfrac{1}{2}\bar{a}_1 B_2 + \mathrm{Re}\,D_1 + a_1\mathrm{Re}\,D_2),$$

$$\begin{aligned} \Phi_{31} = & A_1(2\alpha_0 a_1 - (1+\alpha_0)a_1\bar{H}(2i\omega_0, 0) - (1+\alpha_0)a_1\bar{H}(i\omega_0, k^2) - 1) - a_1 A_2 \\ & + \tfrac{1}{2}B_1(2\alpha_0 a_1 - (1+\alpha_0)a_1\bar{H}(2i\omega_0, 4k^2) - (1+\alpha_0)a_1\bar{H}(i\omega_0, k^2) - 1) - \tfrac{1}{2}a_1 B_2, \end{aligned}$$

$\Phi_{32} = a(A_1 + a_1 A_2 + \frac{1}{2}B_1 + \frac{1}{2}a_1 B_2)$,

$\Phi_{41} = \frac{1}{2}B_1(2\alpha_0 a_1 - (1+\alpha_0)a_1 \bar{H}(2i\omega_0, 4k^2) - (1+\alpha_0)a_1 \bar{H}(i\omega_0, k^2) - 1) - \frac{1}{2}a_1 B_2$,

$\Phi_{42} = a(\frac{1}{2}B_1 + \frac{1}{2}a_1 B_2)$.

The solvability condition for (4.40) is

$$\Phi_{11}\bar{d}_1 + \Phi_{12} = 0 . \tag{4.41}$$

Let us define $\tilde{\Phi}_{11}$ and $\tilde{\Phi}_{12}$ by writing

$$\Phi_{11} = -ia_1\omega_2(1 + (1+\alpha_0)b\bar{H}_s(i\omega_0, k^2)) + \alpha_2 b a_1(1 - \bar{H}(i\omega_0, k^2)) + \tilde{\Phi}_{11} ,$$

$$\Phi_{12} = -i\omega_2 + \tilde{\Phi}_{12} .$$

Then we have explicit expressions for $\tilde{\Phi}_{11}$ and $\tilde{\Phi}_{12}$, these expressions being independent of α_2 and ω_2. The solvability condition (4.41) reads, after some algebra,

$$i\omega_2[1 + a_1\bar{d}_1(1 + (1+\alpha_0)b\bar{H}_s(i\omega_0, k^2))] - \alpha_2 b a_1 \bar{d}_1(1 - \bar{H}(i\omega_0, k^2)) = \bar{d}_1\tilde{\Phi}_{11} + \tilde{\Phi}_{12}.$$

From (4.36) it follows that

$$i\omega_2 - \alpha_2\mu'(\alpha_0) = \frac{\mu'(\alpha_0)}{a_1\bar{d}_1 b(1 - \bar{H}(i\omega_0, k^2))}(\bar{d}_1\tilde{\Phi}_{11} + \tilde{\Phi}_{12})$$

so that

$$\alpha_2 = -\frac{1}{\operatorname{Re}\mu'(\alpha_0)}\operatorname{Re}\left[\frac{\mu'(\alpha_0)}{a_1\bar{d}_1 b(1 - \bar{H}(i\omega_0, k^2))}(\bar{d}_1\tilde{\Phi}_{11} + \tilde{\Phi}_{12})\right].$$

This quantity is well defined, and determines whether the bifurcation is sub- or supercritical. For k^2 large, with $\alpha_0 = \alpha_0(k^2)$ and $\omega_0 = \omega_0(k^2)$, we can use the expression for $\mu'(\alpha_0)$ given by (4.37) and a heavy piece of asymptotic analysis (Gourley 1993) to get

$$\alpha_2 \sim \frac{Dk^6}{b^4 a^2(1-b)^2}\operatorname{Re}\left[\left(\frac{b}{2} + i\frac{bG_n(0)}{2\omega_0^* G_n'(0)}\right)\left(\frac{2\bar{H}(2i\omega_0^*, 0) - 3}{\bar{H}(2i\omega_0^*, 0) - 1}\right)\right]$$

with ω_0^* given by (4.38). This is as far as we can go for general kernels G, so we shall consider in the remainder of this section what happens in the particular case of the kernel $G(x,t) = 1/2\lambda e^{-\lambda|x|}\theta e^{-\theta t}$ studied in § 3.4. Recall that for this kernel the locus $\operatorname{Re} s = 0$ only exists as $k^2 \to \infty$ if $\theta \leqq D\lambda^2$ so we assume this to be the case. For this kernel $\omega_0^* = \sqrt{\theta(D\lambda^2 - \theta)}$, $\mu'(\alpha_0) \sim b/2(1 - i\theta/\omega_0^*)$ and $\bar{H}(2i\omega_0^*, 0) = \theta/(\theta + 2i\omega_0^*)$. We find that α_2 has the same sign as $\operatorname{Re}(\omega_0^* - i\theta)(6\omega_0^* - i\theta)$, i.e., as $6D\lambda^2 - 7\theta$. Thus in the limit as $k^2 \to \infty$ the bifurcation is supercritical if $6D\lambda^2 > 7\theta$ and subcritical if $6/7 D\lambda^2 < \theta \leqq D\lambda^2$.

5 Conclusions

In this paper we have considered a predator prey system in the form of a coupled system of reaction diffusion equations containing a term which is nonlocal in both the spatial and the temporal variables. Our model is an extension, to a two-species predator prey system, of a single species model which had been studied previously. The system has the property that in the purely local case, when $G**u = u$, the coexistence steady state is not driven unstable by diffusion. However for spatio temporal convolutions, possible bifurcations from this steady state are (i) to steady spatially periodic solutions, (ii) to periodic standing wave solutions and (iii) to periodic travelling wave solutions. These bifurcations occur under only very minimal assumptions on G and the behaviour is evidently not brought about by diffusion alone, but rather by the nonlocal term in the system or by its interaction with the aggregation term αu. In the purely local case the system is very simple, being a Lotka Volterra diffusion system with logistic growth of the prey. Whilst integrodifferential systems tend to be rather complicated in appearance, all we have done essentially is to recognise that time delays should be included in the term representing intraspecific competition for resources for the prey species, and that the assumption of motion (through diffusion) means that any time delayed term should be nonlocal in space as well as in time. As a consequence, we have obtained a variety of solution behaviour which reflect phenomenon such as animal aggregation, population cycles and the motion of aggregations as observed in nature. We therefore claim that nonlocal effects play a very important role in pattern formation, and that our model is more realistic than the usual type of reaction diffusion system used to model predator prey interactions in which the species can diffuse.

We have noted that bifurcations (ii) and (iii) above can occur for purely temporal convolutions and that for purely spatial convolutions all three bifurcations can occur. The introduction of some spatial averaging (however little) has a significant effect by introducing a third bifurcation. The analysis in the purely temporal case of § 3.2 shows that for instability of the uniform steady state the parameter θ has to be sufficiently small, which means the delay has to be sufficiently large. This property of delays has been frequently observed in studies of spatially uniform systems, but little research has previously been done in establishing the property for reaction diffusion systems. In the purely spatial case of § 3.3 we observed that for instability to occur the spatial parameter λ has to be sufficiently small, meaning the average must not be too localised. With a suitable parameter to measure spatial averaging for more general kernels, this property could be established for whole classes of systems.

Many more questions are raised by this research. It would be interesting to investigate the stability of the bifurcating solutions we have obtained, and to investigate the possible existence of large amplitude waves. More work needs to be done on the global behaviour of solutions, and methods similar to those used by Ding (1989) may be useful in establishing global stability of steady states. It would also be interesting to consider nonlocal effects in other types of species interaction, such as competition models. Moreover, in (local) reaction diffusion systems where a steady state is diffusionally unstable, the regions of parameter space in which diffusive instability occurs are often very small

(Murray 1982). The incorporation of delay effects and the analogous mechanisms in space may considerably increase the size of these regions of parameter space.

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