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Wave train selection behind invasion fronts in reaction–diffusion predator–prey models

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ABSTRACT

Wave trains, or periodic travelling waves, can evolve behind invasion fronts in oscillatory reaction–diffusion models for predator–prey systems. Although there is a one-parameter family of possible wave train solutions, in a particular predator invasion a single member of this family is selected. Sherratt (1998) [13] has predicted this wave train selection, using a λ–ω system that is a valid approximation near a supercritical Hopf bifurcation in the corresponding kinetics and when the predator and prey diffusion coefficients are nearly equal. Away from a Hopf bifurcation, or if the diffusion coefficients differ somewhat, these predictions lose accuracy. We develop a more general wave train selection prediction for a two-component reaction–diffusion predator–prey system that depends on linearizations at the unstable homogeneous steady states involved in the invasion front. This prediction retains accuracy farther away from a Hopf bifurcation, and can also be applied when the predator and prey diffusion coefficients are unequal. We illustrate the selection prediction with its application to three models of predator invasions.

1. Introduction

The cause of temporal cycles in natural populations has been a focus of study by ecologists for many decades. A classical hypothesis is that this oscillatory behaviour arises from the interaction between a predator population and its prey, and many models have been constructed and studied to support this hypothesis (see, for example [1]). Such models have often taken the form of kinetics systems: ordinary differential equation models that describe the time evolution of predator and prey densities that are assumed to be spatially constant. More recently, however, field studies have shown that in some natural populations oscillations are not synchronized in space, and when viewed in one spatial dimension take the form of a wave train [2–7]. Wave trains, or periodic travelling waves, are spatio-temporal patterns that are periodic in both time and space and have the appearance of a spatially periodic solution that maintains its shape and moves at a constant speed. Consequently, there has been a great deal of study recently on oscillatory reaction–diffusion systems because these partial differential equation models possess wave train solutions (see [8] and references therein).

One way that wave trains can arise in oscillatory reaction–diffusion systems is following a predator invasion [9–11]. The initial condition for such a scenario consists of the prey at carrying capacity everywhere in the spatial domain, except in a localized region in which a predator is introduced. Typically, a travelling front evolves that maintains its shape and moves at a constant speed. In some cases, behind this primary invasion front a secondary transition occurs, and the solution takes the form of a wave train. Two numerical simulations where wave trains evolve following a predator invasion are illustrated in Fig. 1. We can see from these examples that the wave train behind the front does not necessarily move at the same speed, or even in the same direction, as the invasion front itself.

For oscillatory reaction–diffusion systems near a Hopf bifurcation in the corresponding kinetics, there exists a one-parameter family of wave train solutions and a range of corresponding speeds [12]. In a particular numerical simulation of an invasion, we typically observe only a single member of this family, and this seems robust to changes in initial or boundary conditions. Therefore, it appears that a particular wave train is somehow selected out of the family. We would like to find some means of predicting the selected wave train.

Sherratt has in fact already produced an explanation of the selection mechanism and a prediction for the wave train selected behind invasion fronts in reaction–diffusion systems with oscillatory kinetics [13]. The basis of his prediction is an approximating lambda–omega (λ–ω) system. The behaviour of

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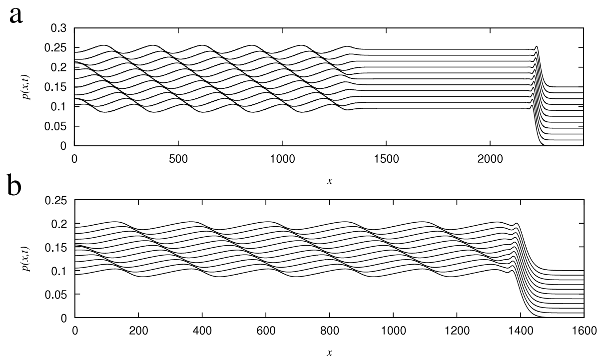

Fig. 1. Wave trains behind invasion fronts. The horizontal axis is the spatial coordinate x. Shown are equally spaced plots of the density of the predator $p(x, t)$ at ten equal time intervals with increasing time from bottom to top.

an oscillatory reaction–diffusion system near a nondegenerate supercritical Hopf bifurcation can be described by the simpler λ–ω system whose coefficients are obtained from the normal form of the Hopf bifurcation in the kinetics system. Predictions derived in this way are applicable near the Hopf bifurcation and when the predator and prey have nearly equal diffusion coefficients. For more widely applicable predictions, such as in cases where there are larger amplitude oscillations or unequal diffusion coefficients, it would be beneficial to develop a criterion to predict the selected wave train that does not directly depend on the λ–ω system.

In the remainder of this paper, we derive and test such a criterion. We first introduce in Section 2 the class of two-component reaction–diffusion systems we consider. These systems describe the evolution of population density distributions of two species, one a prey and the other a predator, in one space dimension. Two spatially homogeneous steady states are relevant: an unstable prey-only state that is invaded by a travelling front, and a coexistence state unstable to oscillatory modes that interacts with the invasion. In some cases, such as illustrated in Fig. 1(a), there is a secondary front that invades the coexistence state. The speed of a front invading an unstable steady state can be predicted by the linear spreading speed (see the review [14] and references therein) which depends only on linearization about the unstable state. In Section 3, we consider coherent structures in the complex Ginzburg–Landau (CGL) equation [14–18], of which the λ–ω system is a special case. The unstable state in this case is the origin, which corresponds to the coexistence state in predator–prey systems, and coherent structures represent travelling fronts that connect the steady state to wave trains. The linear spreading speed selects a particular coherent structure and wave train, and this retrieves the prediction developed in [13]. Coherent structures have been generalized as defects in general reaction–diffusion systems by Sandstede and Scheel in [19]. In Section 4, we extend the prediction for the λ–ω system to a new "pacemaker" criterion for defects in predator–prey reaction–diffusion systems that connect the unstable prey-only state with wave trains associated with oscillatory instabilities of the coexistence state. For the speed of the selected defect we take the minimum of the linear spreading speeds for the prey-only and coexistence states, and for the frequency of the selected wave train measured in the frame comoving with the defect we take the frequency of the linear Hopf instability of the coexistence state. The performance of the pacemaker criterion is then numerically tested in Section 5 on sample oscillatory reaction–diffusion systems. We find that the pacemaker criterion gives accurate predictions for a wider range of parameter values than the λ–ω criterion does, but still falls off in accuracy farther away from the Hopf bifurcation. Finally, Section 6 discusses and summarizes the key results.

2. Mathematical background

We consider predator–prey reaction–diffusion systems in one space dimension, of the form

$$\begin{aligned} \frac{\partial h}{\partial t} &= D_h \frac{\partial^2 h}{\partial x^2} + f(h,p) \\ \frac{\partial p}{\partial t} &= D_p \frac{\partial^2 p}{\partial x^2} + g(h,p), \end{aligned} \tag{1}$$

where $h(x, t)$ is the density of prey at position x and time t and $p(x, t)$ is the density of predator at (x, t). Both h and p are real-valued functions. The positive parameters D_h and D_p are the diffusion coefficients of the prey and predator, respectively, while the functions $f(h, p)$ and $g(h, p)$ depend on parameters not explicitly shown here, and describe the local population dynamics. For the invasion scenario of interest, we require (1) to have two spatially homogeneous steady states: a prey-only steady state $h(x, t) \equiv 1, p(x, t) \equiv 0$ and a coexistence steady state $h(x, t) \equiv h^*$, $p(x, t) \equiv p^*$ where both species persist at some non-zero levels.

We assume that both the prey-only state $(1, 0)$ and the coexistence state (h^*, p^*) are unstable as fixed points for the corresponding kinetics system

$$\begin{aligned} \frac{\mathrm{d}h}{\mathrm{d}t} &= f(h,p), \\ \frac{\mathrm{d}p}{\mathrm{d}t} &= g(h,p). \end{aligned} \tag{2}$$

In particular, we assume that the linearization of (2) about the prey-only state has real eigenvalues of opposite sign, while the linearization about the coexistence state has complex conjugate eigenvalues with positive real part and non-zero imaginary parts, and for some nearby parameter values the coexistence state (h^*, p^*) undergoes a supercritical Hopf bifurcation for (2).

Fig. 1(a) illustrates an invasion that appears to involve two travelling fronts, a primary front invading the unstable prey-only state, and a secondary front invading the unstable coexistence state. The two fronts do not necessarily travel at the same speed. Fig. 1(b) shows there may be a single front invading the prey-only state, but we consider only cases where the dynamics are still influenced by the coexistence state. The speed at which fronts invade an unstable steady state has been the subject of much study. A comprehensive review of this topic is provided by [14]. In this, van Saarloos defines a linear spreading speed ν^* given by solving the saddle point equations

$$\begin{cases} 0 = S(k^*, \omega^*) \\ 0 = (\partial_k + \nu^* \partial_\omega) S|_{(k^*,\omega^*)} \\ 0 = \Im(\omega^* - \nu^* k^*) \end{cases} \tag{3}$$

for (k^*, ω^*, ν^*), where $S(k, \omega) = 0$ is the characteristic equation for the linearization about the unstable steady state ahead of the front. While there may be multiple solutions to (3), only those for which

$$\Re(D) > 0, \quad \text{where } D = \left. \frac{-i(\partial_k + \nu^* \partial_\omega)^2 S}{2\partial_\omega S} \right|_{(k^*,\omega^*)}$$

are relevant. The equivalence of this approach with the historical pinch point analysis is discussed in [20]. When there are several dynamically relevant saddle points, we take the one with the largest corresponding ν^* to give the linear spreading speed. Details of how to compute linear spreading speeds using (3) for the system (1) are given in the Appendix. Fronts propagating into unstable states are grouped into two classes: pulled fronts that travel at speed ν^* and are in some sense generic, and pushed fronts that travel at a speed $\nu > \nu^*$. If the initial conditions decay sufficiently rapidly in space, faster than $e^{\lambda^* x}$ as $x \to \infty$, where $\lambda^* := \Im(k^*)$,