SPATIOTEMPORAL DYNAMICS IN ECOLOGY: INSIGHTS FROM PHYSICS

J. A. Sherratt

Department of Mathematics and Maxwell Institute for Mathematical Sciences,
Heriot-Watt University, Edinburgh EH14 4AS, UK
E-mail: jas@ma.hw.ac.uk

M. J. Smith

Microsoft Research,
7 J.J. Thompson Avenue, Cambridge, CB3 0FB, UK
E-mail: Matthew.Smith@microsoft.com

J. D. M. Rademacher

National Research Institute for Mathematics and Computer Science (CWI),
Science Park 123, 1098 XG Amsterdam, The Netherlands
E-mail: Jens.Rademacher@cwi.nl

Simulations of invasion in cyclic predator-prey systems show plane waves behind the invasion front. When the selected plane wave is unstable, there is a band of plane waves of constant width, followed by spatiotemporal chaos. We describe a new method for calculating the width of this band, based on the absolute stability of plane waves in moving frames of reference. This calculation shows that the band width can be very sensitive to changes in parameters, and we discuss the ecological implications of this result.

Keywords: Plane wave; Absolute Stability; complex Ginzburg-Landau equation

1. Invasions in Cyclic Predator-Prey Systems

Many natural populations exhibit multi-year cycles in abundance. These cycles arise from a variety of different mechanisms, but in some cases there is strong evidence that the underlying cause is the interaction between a predator population and its prey. For example, vole populations in Fennoscandia cycle with a period of 4 or 5 years [1]. The main terrestrial predator of voles is weasels, and when these are removed from a region of habitat via live trapping, the multi-year cycles in vole density disappear [2]. Predator-prey cycles have been studied mathematically for nearly 100 years, and a wide variety of different models have been proposed, including a large number consisting of two coupled ODEs (see the books [3, 4] for review). A typical example is the Rosenzweig-MacArthur model [5], which has the

2

dimensionless form

$$\boxed{\text{predators}} \quad dp/dt = \overbrace{ACph/B(1+Ch)}^{\substack{\text{benefit from}\\ \text{predation}}} - \overbrace{p/AB}^{\text{death}} \tag{1}$$

$$\boxed{\text{prey}} \quad dh/dt = \underbrace{h(1-h)}_{\substack{\text{intrinsic}\\ \text{birth \& death}}} - \underbrace{Cph/(1+Ch)}_{\text{predation}}. \tag{2}$$

Here p and h are the densities of predators and prey at time t, and A, B and C are positive parameters. Eqs. (1,2) have a unique "coexistence" steady state in which h and p are both non-zero, and as C increases through $(A+1)/(A-1)$, this steady state becomes unstable via undergo a standard supercritical Hopf bifurcation, leading to a stable limit cycle.

It is increasingly common for field studies of cyclic populations to record abundances at a number of different locations. In many cases this data reveals that the population is not spatially homogeneous; rather, there is a one-dimensional gradient in the phase of the cycles, so that the overall dynamics have the form of a plane wave [6]. By this, we mean that the population density is a periodic function of $x-at$, where x is a one-dimensional spatial coordinate, t is time, and a is the (phase) velocity. Note that the terms "plane wave", "wavetrain", and "periodic travelling wave" are synonymous. The model (1,2) can easily be adapted to study spatiotemporal behaviour, by adding diffusion terms to both equations, representing unbiased local dispersal. For simplicity, we assume that the populations have the same diffusion coefficient (which we arbitrarily set to 1); however, the phenomena that we will report also occur when the two coefficients are different [7] or even density-dependent [8]. Standard theory shows that oscillatory reaction-diffusion equations have a one-parameter family of plane wave solutions; some waves in the family are stable as solutions of the PDEs, but others are unstable [9].

For predator-prey systems, a particularly important spatiotemporal scenario is the invasion of prey by predators. We simulate this by solving our PDE model on a large spatial domain with zero Neumann boundary conditions, and with initial conditions consisting of a uniform prey density, with predators zero except near to one boundary. The PDE solutions exhibit an advancing wave of predators and a corresponding receding wave of prey. For C above the threshold for population cycles, the behaviour behind the invasion front consists of spatiotemporal oscillations [10–12]. In some cases, these are stable plane waves. However when the appropriate plane wave is unstable, more complicated dynamics occur. Immediately behind the invasion front, the population densities are almost constant, at their (unstable) coexistence steady state. Behind this, there is a plane wave band whose width remains constant as the invasion progresses, and which is followed by spatiotemporal chaos [11, 12, Fig. 1]. The width of the plane wave band is the key determinant of the behaviour observed in practice behind the invasion. We have recently developed a method that enables direct calculation of this width, for the first time [13].
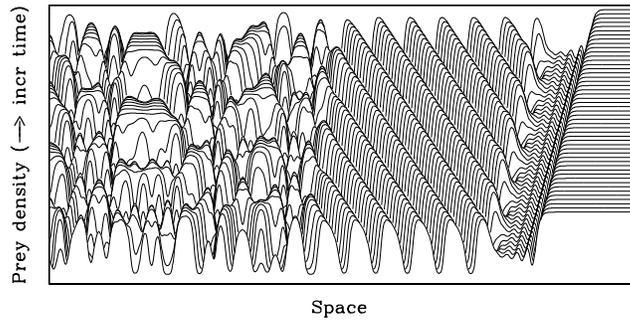
Fig. 1.   Plane wave generation in a simulated invasion of a prey population by predators, using
Eqs. (1,2) augmented by diffusion terms for p and h, with both diffusion coefficients set to 1. We
plot prey density h as a function of space and time. There is a receding invasive wave front, behind
which the solution settles at the (unstable) coexistence steady state. A plane wave band then
develops; the plane wave is unstable, and destabilises to give irregular spatiotemporal oscillations.
The predator dynamics are directly analogous, with the oscillations of the two populations being
out of phase. The initial conditions correspond to a prey-only state everywhere, except for a small
non-zero predator density at the left hand boundary. The parameters are $A = 1.3$, $B = 1.2$,
$C = 11.0$. The domain length is 1000, and the solution is plotted for $1155 \leq t \leq 1284$. The
equations were solved using a semi-implicit finite difference method, with a grid spacing of 0.5 and
a time step of 3×10^{-5}.

2. Amplitude Equation and Band Width Calculation

Detailed calculations show that the plane waves behind the invasion arise via the
invasion front leaving the system at the coexistence steady state and also initiating
an invasion of that state, in the opposite direction [14]. This means that close to Hopf
bifurcation in the kinetics, the plane wave band can be studied using an amplitude
equation. Since the Hopf bifurcation is supercritical and the diffusion coefficients
of predators and prey are equal, the appropriate amplitude equation is the cubic
complex Ginzburg-Landau equation with zero linear dispersion:

$$A_t = A_{xx} + A - (1 + \mathrm{i}c)|A|^2 A.$$

The relevant solution of this equation is a propagating front, with $A = 0$ ahead
of the front and a plane wave behind it [15, 16]. When the selected plane wave is
unstable, the plane waves occur in a band that is followed by spatiotemporal chaos.
The width of the band increases (from zero) in the early stages of the invasion, but
at large times it is constant.

   The key to understanding the width of the plane wave band is to consider
absolute stability [17, 18] when viewed in a frame of reference moving with a fixed,
arbitrary velocity V. That is, we consider whether perturbations to the plane wave
grow or decay over time when viewed at a fixed point travelling with velocity V. We
denote by $\lambda_{max}(V)$ the growth rate of the most unstable linear mode, with $\nu_{max}(V)$
being the corresponding spatial eigenvalue. Using general theory of absolute stability
[17, 18], we reduce the calculation of these quantities to the numerical tracking of

4

solutions of a quartic polynomial as parameters in the coefficients vary; details are given in [13]. There is a range of velocities (V_L, V_R) for which $\lambda_{max} > 0$; all perturbations decay in frames of reference moving with velocities outside this range.

Having calculated $\lambda_{max}(V)$, we can address the width of the plane wave band. For this, we require a precise definition of its left-hand edge, which we take as the first point at which the perturbations to the plane wave that are present immediately behind the invasion front become amplified by an arbitrary factor $\mathcal{F}$. We show in [13] that the dependence of the plane wave band width on $\mathcal{F}$ and c decouples, having the form $\log(\mathcal{F})\mathcal{W}(c)$. We refer to $\mathcal{W}(c)$ as the "band width coefficient"; it contains all of the dependence of the band width on ecological parameters. Let (x^*, t^*) be a point on the invasion front. We make the generic assumption that the most unstable linear modes are present in the perturbation given to the plane wave at such a point. As t increases above t^*, these perturbations will spread out in space and time, growing along all rays $x = x^* + (t - t^*)V$ with $V \in (V_L, V_R)$. On any such ray, the initial perturbation becomes amplified by the factor $\mathcal{F}$ at time $t_{crit}(V) = t^* + \log(\mathcal{F})/\text{Re}[\lambda_{max}(V)]$, at location $x_{crit}(V) = x^* + V\log(\mathcal{F})/\text{Re}[\lambda_{max}(V)]$. The left-hand edge of the plane wave band occurs at the point on the locus (as V varies) of $(x_{crit}(V), t_{crit}(V))$ that is closest to the invasion front. We show in [13] that this implies $\mathcal{W} = 1/\text{Re}[\nu_{max}(V_{band})]$, where

$$(V_{band} - c_{\text{inv}})\text{Re}[\nu_{max}(V_{band})] = \text{Re}[\lambda_{max}(V_{band})]. \tag{3}$$

It is of course entirely expected that $\mathcal{W}$ is the reciprocal of the real part of the spatial eigenvalue; our key result is Eq. (3) for the frame velocity V_{band} at which this eigenvalue should be calculated. Note that in general V_{band} is different from the velocity that maximises $\lambda_{max}(V)$.

3. Band Width Sensitivity and Ecological Implications

The parameter c in the complex Ginzburg-Landau equation can be related to ecological parameters via the standard process of reduction to normal form [19, 20]. Therefore our formula for the band width coefficient enables precise predictions of the variation in the width of the plane wave band as ecological parameters are altered. In [13] we show a contour plot of the width in a key ecological parameter plane. An important conclusion from such plots is that the width of the plane wave band can be very sensitive to parameters. For example, in the case of parameter estimates for the interaction between field voles and weasels [20], a 5% increase in vole birth rate increases the band width by 22%. An even more striking example of this sensitivity is provided by the interaction between the zooplankton *Daphnia pulex* and the phytoplankton *Chlamydomonas reinhardii*. Using estimates of the relevant parameters [21], we predict that the width of a plane wave band behind invasion would be extremely sensitive to the estimate of zooplankton birth rate, with a reduction of only 5.2% sufficient to double the band width. Such sensitivity is particularly important in the context of a changing climate, which is both increasing the frequency of ecological invasions [22] and also changing the parameters

of many oscillatory ecological systems [23, 24]. The sensitivity of the band width to such parameter changes suggests a very profound effect of climate change on the spatiotemporal dynamics of cyclic populations.

Acknowledgments

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