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Oscillations and chaos behind predator-prey invasion: mathematical artifact or ecological reality?

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SUMMARY

A constant dilemma in theoretical ecology is knowing whether model predictions correspond to real phenomena or whether they are artifacts of the modelling framework. The frequent absence of detailed ecological data against which models can be tested gives this issue particular importance. We address this question in the specific case of invasion in a predator-prey system with oscillatory population kinetics, in which both species exhibit local random movement. Given only these two basic qualitative features, we consider whether we can deduce any properties of the behaviour following invasion. To do this we study four different types of mathematical model, which have no formal relationship, but which all reflect our two qualitative ingredients. The models are: reaction-diffusion equations, coupled map lattices, deterministic cellular automata, and integrodifference equations. We present results of numerical simulations of the invasion of prey by predators for each model, and show that although there are certain differences, the main qualitative features of the behaviour behind invasion are the same for all the models. Specifically, there are either irregular spatiotemporal oscillations behind the invasion, or regular spatiotemporal oscillations with the form of a periodic travelling 'wake', depending on parameter values. The observation of this behaviour in all types of model strongly suggests that it is a direct consequence of our basic qualitative assumptions, and as such is an ecologically reality which will always occur behind invasion in actual oscillatory predator-prey systems.

1. INTRODUCTION

Mathematical modelling plays a central role in studying ecological interactions. In many areas of biology, mathematical models, though important, play a subsidiary role to experimental research. Ecology, however, is different; experiments are often difficult to perform, and field data is often incomplete and hard to interpret. For this reason, the predictions of mathematical models in ecology have, in many cases, to be relied on without detailed experimental corroboration. There are of course many examples of models which build quantitatively on very detailed ecological data. However it is also common for models to be based on purely qualitative features of the ecological system. In such cases, a major difficulty is to determine which aspects of the model predictions are genuine consequences of the qualitative data used, and which are functions of the modelling framework.

In this paper we consider modelling a system of exactly this type, in which only basic qualitative features of the system are known, namely the invasion of a prey population by predators. The predator-prey systems we study are defined by two qualitative aspects of their behaviour. The first is that the local dynamics are oscillatory, so that in the absence of spatial variation, the stable coexistence state consists of periodic temporal oscillations in the predator and prey populations. The second qualitative feature we assume is that both predators and prey move randomly in

space. We ask the following question: are there properties of the invasion process that are common to all systems with these two simple ingredients?

To answer this, we will consider four quite different types of mathematical model: reaction-diffusion equations, coupled map lattice models, cellular automata, and integrodifference equations. These are the four types of spatiotemporal model most commonly used in ecology. We will use models of each type to study the invasion of prey by predators. We will show that although there are definite variations between the model types, there is a fundamental prediction that is common to all the models, namely that the behaviour behind the invasive front of predators consists of either irregular spatiotemporal oscillations, or periodic waves in population density. We have recently documented this behaviour in the context of reaction-diffusion models (Sherratt *et al.* 1995; see also Pascual 1993). In §§2–5 we describe our various models, and compare and contrast their solutions in one spatial dimension. Finally in §6 we discuss the new phenomena that enter the invasion process in a two-dimensional spatial domain.

2. REACTION-DIFFUSION MODEL

The first type of mathematical model we consider consists of reaction-diffusion equations, which were first applied to ecology in the pioneering work of Skellam (1951), and have subsequently been used by a

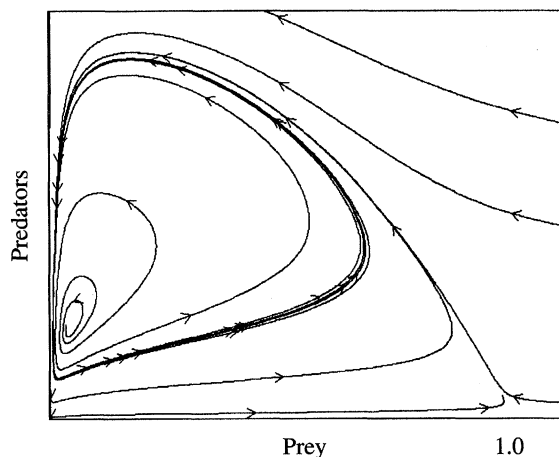


Figure 1. The qualitative form of a typical phase portrait of the population kinetics for an oscillatory predator-prey system. There is a prey-only steady state (1, 0) and also a coexistence steady state. Both of these are unstable, and the long-term behaviour is periodic oscillations in prey and predator densities, corresponding to a limit cycle in the phase plane. The actual phase plane shown is for kinetics (2) with parameter values $A = 3$, $B = 0.2$ and $C = 0.1$.

great many theoretical ecologists (see Holmes *et al.* (1994) for review). Our model equations express conservation of predator and prey population densities, and have the form

$$\partial p / \partial t = D_p \nabla^2 p + f_p(p, h), \quad (1a)$$

$$\partial h / \partial t = D_h \nabla^2 h + f_h(p, h). \quad (1b)$$

Here $p(x, t)$ and $h(x, t)$ are the population densities of predators and prey, with diffusion coefficients D_p and D_h , and x and t denote space and time. Models of the form (1) have been used by many authors to model both spatial patterns (Segel & Jackson 1972; Conway 1984) and wave phenomena (Murray 1975; Dunbar 1983) in predator-prey systems. Biologically realistic kinetic terms will have two non-trivial equilibria: a 'prey-only' state, $p = 0$, $h = h_0$, and a 'coexistence' state $p = p_s$, $h = h_s$. We are concerned with cyclical periodic populations, in which case the coexistence state will be unstable, and the kinetic ordinary differential equations governing local dynamics will have a stable limit cycle solution. A typical phase portrait of the kinetics is illustrated in figure 1. We consider specifically two sets of kinetics, both of which are well-known as predator-prey models:

$$\begin{aligned} f_p(p, h) &= A p h / (h + C) - B p \\ f_h(p, h) &= h(1 - h) - h p / (h + C) \end{aligned} \quad (2)$$

and

$$\begin{aligned} f_p(p, h) &= B p (A(1 - e^{-C h}) - 1) \\ f_h(p, h) &= h(1 - h) - p(1 - e^{-C h}). \end{aligned} \quad (3)$$

The historical origin and applicability of these models is discussed in detail elsewhere (Murray 1989; May 1981; Metz & Diekmann 1986; Freedman 1980). In both cases, A , B and C are positive parameters, and for appropriate parameter values (see May 1981; Murray 1989), the kinetics have the qualitative form illustrated in figure 1, including in particular a stable limit cycle.

For kinetics in which the coexistence steady state is stable, invasion of prey by predators in models of the form (1) has been studied by a number of authors. The invasive solution is a simple travelling wave, that is a transition front moving with constant shape and speed, with the prey-only steady state ahead of the front, and the coexistence state behind the front. This type of invasive front has been analysed mathematically in great detail (Chow & Tamm 1976; Dunbar 1983; Dunbar 1984; Dunbar 1986) and has been applied to a number of specific ecological situations, including plankton dynamics (Dubois 1975). Previous work on the corresponding behaviour in oscillatory systems has been applied to the geographical spread of epidemics (Murray 1989). In particular, mathematical models describing the spatial spread of rabies amongst foxes have been shown to demonstrate decaying oscillations in the wake of invasion (Anderson *et al.* 1981; Murray *et al.* 1986). However, to our surprise, we have been unable to find any previous work on the corresponding behaviour in predator-prey systems with cyclical behaviour. We consider the behaviour behind invasion in oscillatory predator-prey systems.

We have performed a large number of numerical simulations of invasion in the model (1) with kinetics (2) and (3). In this section we restrict attention to simulations in one spatial dimension; two-dimensional simulations are discussed in §6. We use a large spatial domain, with the system initially in the prey-only steady state, except for a small region in the centre of the domain, where a small density of predators is introduced. Here and in §§3–5, we stop our simulations before the invading wave reaches the end of the domain, so that the results are not sensitive to the boundary conditions, which can be either zero flux, periodic, or with population levels fixed at the prey-only steady state. In §6, we discuss the way in which the populations evolve after the invasion has reached the edge of the domain.

As expected, our initial condition results in a wave front of invading predators moving out from the initial perturbation. However, the behaviour behind the invasive front is quite different from the uniform population densities predicted by non-periodic kinetics. In all cases, we have found either regular spatio-temporal oscillations with the form of periodic travelling waves (figures 2a and 3a), or irregular spatio-temporal oscillations with no apparent order (figures 2b and 3b). We refer to this phenomenon as 'oscillatory wakes behind invasion'. The only exceptions are cases where travelling wakes degenerate into irregular fluctuations (figures 2c and 3c), which will be discussed below. In the case of regular oscillations, the periodic travelling waves move across the domain with a quite different speed from that of the invasive front; for the kinetics (2) and (3), we have found that their direction is always opposite to that of invasion, but for some other kinetic terms, the periodic waves move in same direction as the invasion, but with a faster speed (Sherratt *et al.* 1995).

The only previous work we are aware of on the behaviour behind invasion in oscillatory predator-prey systems is that of Dunbar (1986). In a piece of

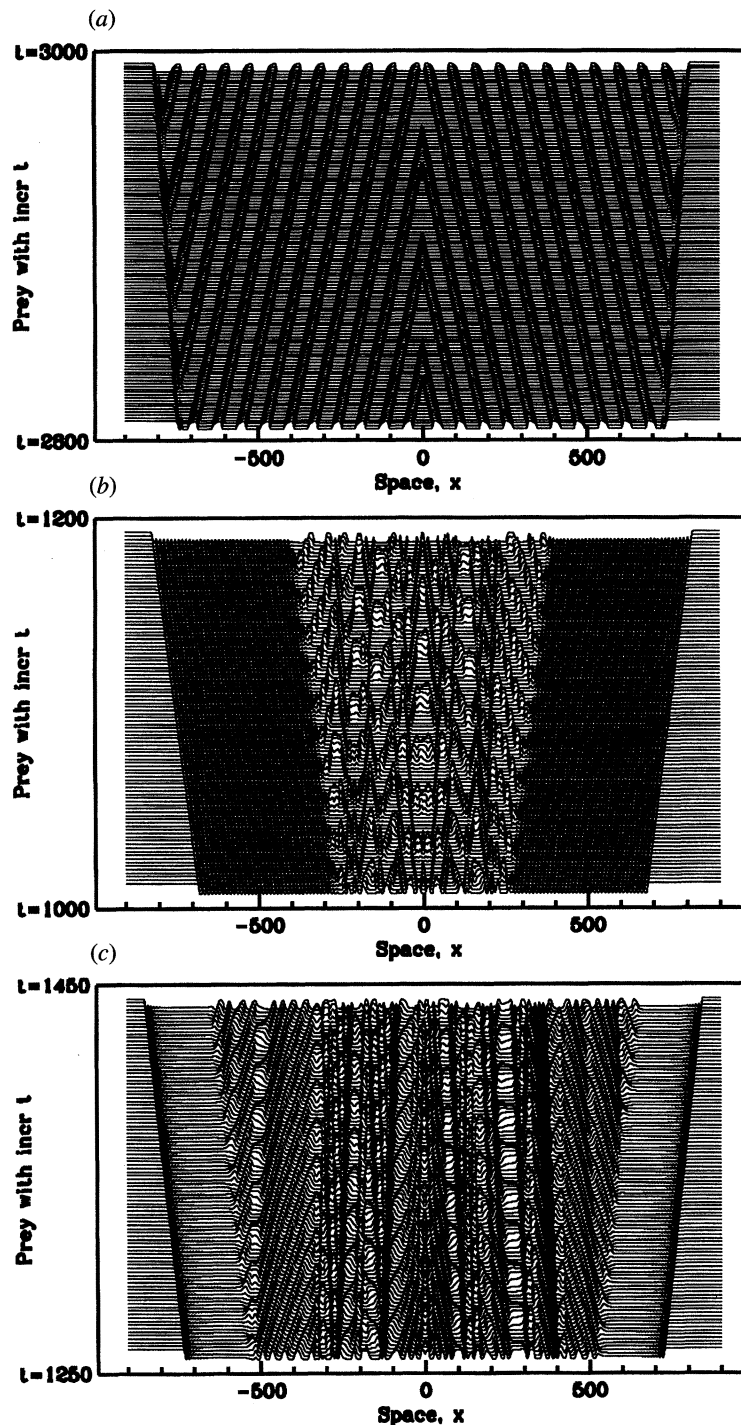


Figure 2. An illustration of the range of behaviours observed behind invasion in the reaction-diffusion model (1) with kinetics (2). We show space-time plots of the prey density; the predator density is qualitatively similar. In all cases, the initial condition at time $t = 0$ consists of the prey-only steady state everywhere, except for a small additional density of predators near $x = 0$. In all cases, this initial perturbation expands with time and gives rise to an invading wave of predators. However, the behaviour behind invasion depends crucially on the parameter values. In (a) there are regular periodic travelling waves behind the invasive, while in (b) there are irregular spatiotemporal oscillations. Work described elsewhere (Sherratt 1995; Sherratt *et al.* 1995) suggests that this behaviour is in fact spatiotemporal chaos. In (c) we illustrate a mixed case, in which there is a band of periodic waves immediately behind the invasive front, with irregular oscillations further back. In all cases, the initial perturbation is asymmetric about $x = 0$; in (a) this asymmetric rapidly disappears, while in (b) and (c) it is reflected in the long term solution. Note that in (b), there are low amplitude oscillatory waves parallel to invasion immediately behind the invasive front; this phenomenon is also exhibited in some simulations of the coupled map lattice model (see figure 5). The parameter values are (a) $A = 0.15$, $B = 0.05$, $C = 0.2$; (b) $A = 0.9$, $B = 0.3$, $C = 0.2$; (c) $A = 1.0$, $B = 0.5$, $C = 0.2$. The solution for $h(x, t)$ is plotted as a function of space x , with vertical separation proportional to the time interval between solutions. The equations were solved numerically using the method of lines and Gear's method.

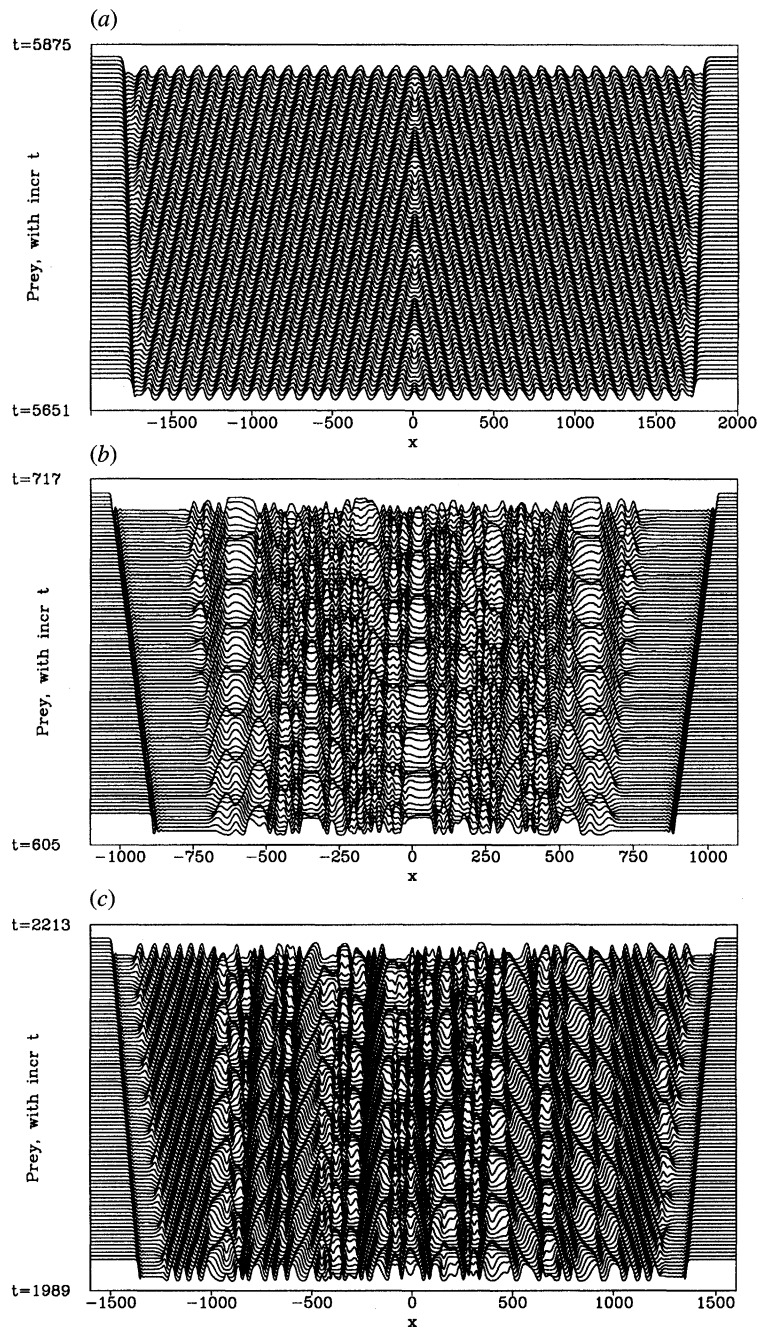


Figure 3. An illustration of the range of behaviours observed behind invasion in the reaction-diffusion model (1) with kinetics (3). We show space-time plots of the prey density; the predator density is qualitatively similar. In all cases, the initial condition at time $t = 0$ consists of the prey-only steady state everywhere, except for a small additional density of predators near $x = 0$. In all cases, this initial perturbation expands with time and gives rise to an invading wave of predators. However, the behaviour behind invasion depends crucially on the parameter values, and can be divided into one of three categories, as for kinetics (2) (see figure 2). In (a) there are regular periodic travelling waves behind the invasion, moving away from the invading front. In contrast to kinetics (2), we have never observed periodic waves moving in the same direction as invasion for kinetics (3). In (b) and (c) there are irregular spatiotemporal oscillations behind invasion; in (c), there is also a band of periodic waves immediately behind the invasive front. In all cases, the initial perturbation is asymmetric about $x = 0$; in (a) this asymmetric rapidly disappears, while in (b) and (c) it is reflected in the long term solution. The parameter values are (a) $A = 1.5$, $B = 0.05$, $C = 4$; (b) $A = 1.5$, $B = 1$, $C = 5$; (c) $A = 1.5$, $B = 0.22$, $C = 5$. The solution for $h(x, t)$ is plotted as a function of space x , with vertical separation proportional to the time interval between solutions. The equations were solved numerically using the method of lines and Gear's method.

extremely elegant mathematics, Dunbar proved the existence of an invasive wave solution for the kinetics (2), consisting of regular spatiotemporal oscillations behind and moving in parallel with the wave front. Our simulations show, however, that this solution is

not generated by the localized introduction of predators, at least for the parameter sets we have considered. In fact Dunbar's (1986) solution can be seen transiently in some of our simulations, but is ultimately unstable. Instead, when regular oscillations

do arise behind the invasive front, these have a considerably faster speed than the invasion itself, and sometimes travel in the opposite direction.

Of the four types of model we will consider, reaction-diffusion systems present the greatest opportunity for analytical study. The results of this study, which use a combination of numerical solution and mathematical analysis, and which rely heavily on caricature models, are published elsewhere (Sherratt 1993, 1994*a, b*), and we will give a brief summary here. In the model (1) with (2) or (3), there is a travelling transition wave solution, which is a wave front moving with constant shape and speed, connecting the prey-only steady state ahead of the wave and the coexistence steady state behind the wave. This solution is exactly the invasive wave observed in non-oscillatory predator-prey models of form (1) (Chow & Tamm 1976; Dunbar 1983, 1984, 1986). However, for oscillatory kinetics, the instability of the coexistence state causes new behaviour to develop behind the invasive front; the mathematical basis for this is well documented elsewhere (Sherratt 1994*b*; Sneyd & Sherratt 1996). Oscillatory reaction-diffusion equations have a family of periodic travelling wave solutions (Kopell & Howard 1973), and the particular wave selected behind invasion is determined by the exponential decay rate in the tail of the invasive front. For some parameters, the selected periodic wave is actually unstable as a reaction-diffusion solution, and in such cases the behaviour behind the front degenerates into irregular spatiotemporal oscillations. Numerical bifurcation studies of caricature models have provided strong evidence that these irregular oscillations are in fact spatiotemporal chaos (Sherratt 1995; Sherratt *et al.* 1995). Figures 2*c* and 3*c* illustrate cases in which periodic waves occur immediately behind the invasive front, with irregular oscillations further back; this occurs when the periodic waves are just unstable, so that they persist transiently before destabilizing into chaos.

In the solutions illustrated in figures 2 and 3, the dispersal rates D_h and D_p are taken to be equal, but essentially the same behaviour occurs for unequal dispersal rates. As D_h is increased for a fixed value of D_p (which fixes the invasion speed), the spatial period of the oscillations behind the invasive front increases, and there is a tendency for oscillations to become regular rather than irregular. This is very much as one would expect intuitively; increasing the prey dispersal rate has a homogenizing and stabilizing effect.

In some contexts, partial differential equation models for ecological interactions suffer from a dependence on very small population levels, at which a real population would be extinct (Mollinson 1993). A key issue to address is whether such ‘nano populations’ are playing a role in the model predictions we have discussed. We have been able to show that there is no such role, via a mathematical argument, the details of which will be presented elsewhere. Briefly, we have shown that in the case of equal dispersal rates for predators and prey, the region within the limit cycle solution of the kinetics is a confined set for the reaction-diffusion solution in the predator-prey plane. For unequal dispersal rates, we have constructed a confined

set which encloses the limit cycle. In either case, the key point is that the behaviour behind invasion is localized within this confined set, so that the predicted population levels do not drop below a finite minimum value. Thus infinitesimally small ‘nano populations’ do not arise in the wake of invasion.

3. COUPLED MAP LATTICE MODEL

In many ecological systems, populations are localized at discrete spatial sites; Taylor (1991) discusses predator-prey examples of this, and the detailed work of Kareiva (1987) on the ladybird-aphid system focuses specifically on the effects of spatial patchiness. A great many models of spatially discrete ecological systems have been proposed in recent years, with a very wide range of applications (Nee & May 1992; Bowers *et al.* 1994; Wiener & Tuljapurkar 1994; Harrison *et al.* 1995). Mathematically, such systems consist of discrete spatial sites, and can be modelled as either continuous in time, giving coupled ordinary differential equations (for a predator-prey example, see Sabelis *et al.* 1991), or discrete in time, giving a ‘coupled map lattice’. We consider a model of this latter type for an oscillatory predator-prey system. Thus, we take both space and time to be discrete, so that the model is formulated in terms of h_i^j and p_i^j , the prey and predator densities at spatial patch i and time j . Since we are restricting attention to one space dimension at this stage, we can represent the spatial patches by a single index i . Note that in contrast to the cellular automata discussed below in §4, the densities have a continuous range of possible values.

Our model is based closely on the Hassell–Comins–May model (Hassell *et al.* 1991; Comins *et al.* 1992), with each time step divided into two sub-steps, one representing local dynamics and one representing spatial dispersal. In the dispersal sub-step we use a standard discrete representation of local dispersal, which is taken directly from Hassell–Comins–May (Hassell *et al.* 1991; Comins *et al.* 1992):

$$h_i^{j+1/2} = (1 - \nu_h) h_i^j + \nu_h (h_{i+1}^j + h_{i-1}^j) / 2, \quad (4a)$$

$$h_i^{j+1/2} = (1 - \nu_p) p_i^j + \nu_p (p_{i+1}^j + p_{i-1}^j) / 2, \quad (4b)$$

where ν_h and ν_p are dispersal parameters for prey and predators, respectively. When ν_h and ν_p are small, this is a discrete analogue of spatial diffusion.

In the local dynamics sub-step of the time iteration, the densities at each spatial patch change independently. The kinetics rules thus have the form of coupled difference equations for predator and prey densities, which apply at each patch. There are many such models in the literature (see Murray (1989) or May (1981) for review), and we use the model initially proposed by Beddington *et al.* (1975)

$$h_i^{j+1} = h_i^{j+1/2} \exp [a(1 - h_i^{j+1/2}/b) - c p_i^{j+1/2}], \quad (5a)$$

$$p_i^{j+1} = h_i^{j+1/2} [1 - \exp(-c p_i^{j+1/2})], \quad (5b)$$

where a , b and c are positive parameters. This model has a prey-only steady state $h_i^j \equiv b$, $p_i^j \equiv 0$, and a unique coexistence steady state in which both prey and predator densities are non-zero, although this cannot be determined in a simple closed form. In the absence

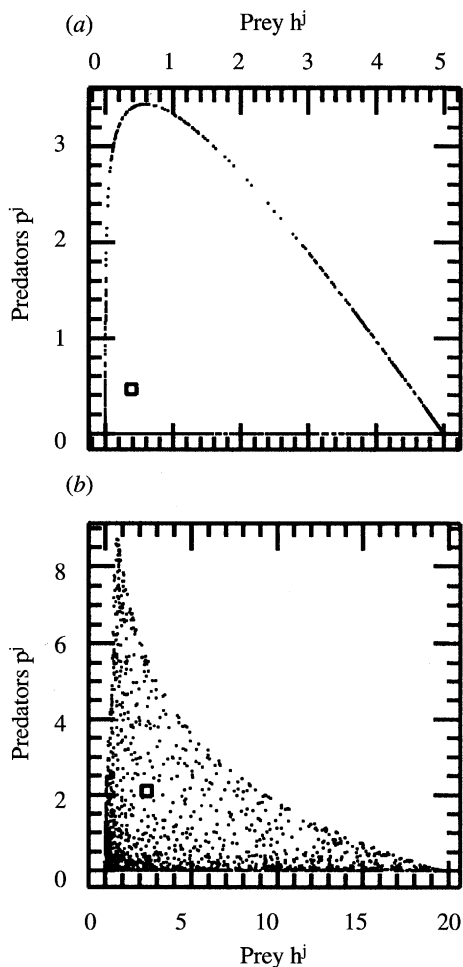


Figure 4. An illustration of the long-term behaviour of the kinetics (5) for the coupled map lattice model of predator-prey interaction. The kinetics have a prey-only and also a coexistence steady state; when the coexistence steady state is unstable, the long-term behaviour consists either of regular oscillations, as in (a), or chaos, as in (b). We plot the state at 2000 successive time step after allowing 5000 iterations for the dissipation of transients; the initial conditions at time step 0 is that the prey and predator densities are both 10% greater than their coexistence steady state values. The coexistence state is indicated in the figures by a small square. The parameter values are (a) $a = 1$, $b = 5$, $c = 2$, (b) $a = 3$, $b = 8$, $c = 1$. In studying invasion, we have only considered parameter sets for which the long-term behaviour consists of regular spatiotemporal oscillations as in (a). It is important to note that in such cases, although the densities trace out a limit cycle in the prey-predator plane, there is no periodicity in the actual population density values.

of spatial variations, this coexistence state is unstable for suitable parameter sets. Typical long-term behaviours in this case are illustrated in figure 4. For some parameters, the predator and prey densities trace out a limit cycle in the $h-p$ plane (figure 4a). The densities themselves are not periodic functions of time; rather the populations move in a non-periodic way around the limit cycle shown. This is the case of oscillatory local dynamics that is of interest to us. For other parameter sets for which the coexistence state is unstable, the long-term behaviour does not have such a simple form, and traces out a strange attractor in the $h-p$ plane (figure 4b). In such cases the local dynamics

are chaotic, a situation which cannot arise in two coupled ordinary differential equations such as the kinetics of the reaction-diffusion model (1), and we have not considered solutions of the spatiotemporal model for such parameter sets. We deliberately use (5) rather than the Nicholson-Bailey kinetics (Nicholson & Bailey 1935) used by Hassell, Comins and May (Hassell *et al.* 1991; Comins *et al.* 1992), which do not have a simple oscillatory solution; rather the coexistence steady state is unstable whenever it exists, giving rise to unbounded population growth (Murray 1989, §4.1).

To simulate invasion of prey by predators, we set up the system initially in the prey-only steady state everywhere except for a few patches in the centre of the domain, where a small predator density is also introduced. The predators then move outwards from this initial perturbation site, invading the domain at a rate of one patch per time iteration. The fact that the invasion occurs at this rate (except for very small ν_p and ν_h) shows that the spatial discretization is genuinely playing a key role. We have done a large number simulations of this invasive process for different parameter values, and typical results are illustrated in figure 5. In every case we have tried, there are periodic spatiotemporal oscillations immediately behind this invasive front, moving parallel to the front. The amplitude of these oscillations tends to decrease moving away from the front, and in some cases the solution becomes approximately uniform (figures 5a and 5c). Behind this band of periodic oscillations, there are either regular, periodic waves moving in the opposite direction to the invasion (figure 5a), irregular spatiotemporal oscillations (figure 5b), or a band of periodic waves with a region of irregularities further back (figure 5c). This behaviour is qualitatively identical to that in the reaction-diffusion models described in §2, with exactly the same three categories of behaviour, even though there is absolutely no formal relationship between the coupled map lattice model and either of the reaction-diffusion models. Note that there is a band of periodic waves moving with the invasion immediately behind the invasive front, which is also observed in some reaction-diffusion simulations (see figure 2b). For the coupled map lattice model, we do not have evidence from bifurcation studies to indicate the nature of the irregular behaviour, but for a wide range of parameters, we have found that localized perturbations applied in the irregular region both grow in time and expand spatially, suggesting that the irregularities are genuinely chaotic. In the case of regular oscillations behind invasion, such perturbations rapidly decay; these responses to perturbations are also observed in reaction-diffusion models.

In the reaction-diffusion model (1), the absolute values of the diffusion coefficients D_h and D_p are irrelevant, corresponding simply to a rescaling of the spatial coordinate: only the ratio D_h/D_p is significant. However, in (4), the actual values of ν_h and ν_p are important, and cannot be eliminated by scaling arguments; intuitively these values are a measure of dispersal potential relative to patch separation. In the solutions illustrated in figure 5, we have taken $\nu_h = \nu_p$, and as this common value is increased with fixed

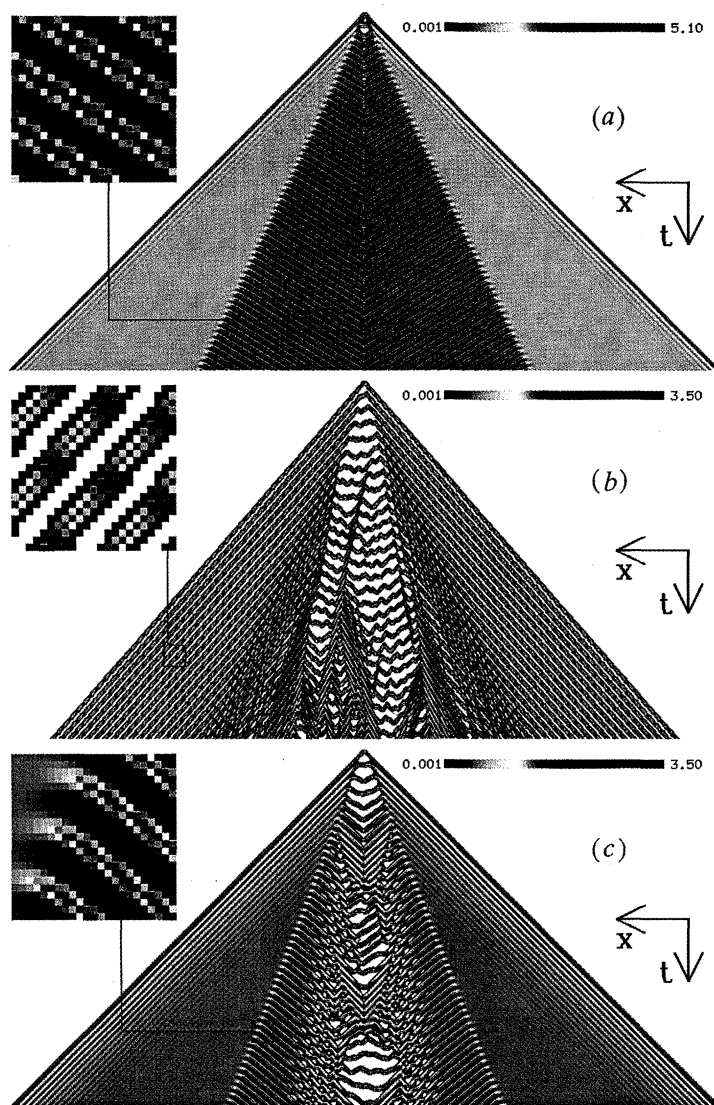


Figure 5. The behaviour behind invasion that is predicted by the coupled map lattice model (4, 5). We plot predator densities in the space-time plane; the behaviour of the prey population is qualitatively similar. The densities are represented by colours according to the scale bar shown, except that predator densities less than 0.001 are plotted in white, in order to better illustrate the progress of the invasion. We plot 398 successive time iterations on a spatial domain of 801 patches. At this scale the spatial discretization is not really visible, and therefore we have enlarged one region of the plane in each figure, in order to illustrate this discretization. Initially the system is in the prey-only steady state everywhere except in patches 400, 401 and 402, where small densities of predators are introduced. This initial perturbation rapidly grows, and invades the domain at a rate of one patch per time iteration, with periodic waves moving parallel to the front immediately behind. However, the behaviour in the wake of the invasion depends on parameters. In (a), there are regular spatiotemporal oscillations, with the form of periodic travelling waves, moving away from the invasive front, while in (b) there are irregular spatiotemporal oscillations in the wake region. In (c) we show a mixed case: there is a band of periodic waves, with irregular oscillations further back. The initial perturbation is asymmetric, and this asymmetry is reflected in the irregular oscillations in (b) and (c), but rapidly disappears in (a). The parameter values are (a) $a = 1.2$, $b = 8$, $c = 1$, $\nu_h = \nu_p = 0.7$; (b) $a = 1$, $b = 5$, $c = 2$, $\nu_h = \nu_p = 0.1$; (c) $a = 1$, $b = 5$, $c = 2$, $\nu_h = \nu_p = 0.5$.

kinetic parameters, there is a strong increase in the regularity of the behaviour behind invasion, as one would expect intuitively. If ν_h is increased with fixed ν_p , there is a tendency to regularity, as described in §2 for reaction-diffusion models. However, increasing ν_p with fixed ν_h shows a point of difference between the two types of model. In the reaction-diffusion case, increasing the predator dispersal rate with fixed prey dispersal reduces the regularity of the behaviour behind invasion, while in the coupled map lattice model there is a pronounced increase in regularity.

The reason for this difference is simply that in the latter case, there is an increase in the absolute value of dispersive potential, whereas in the former case only the ratio of prey to predator dispersal is affected.

4. CELLULAR AUTOMATA MODEL

Cellular automata are models in which, in addition to discrete space and time variables, the state space is also discretized. That is, the predator-prey system is assumed to be always in one of a finite number of states

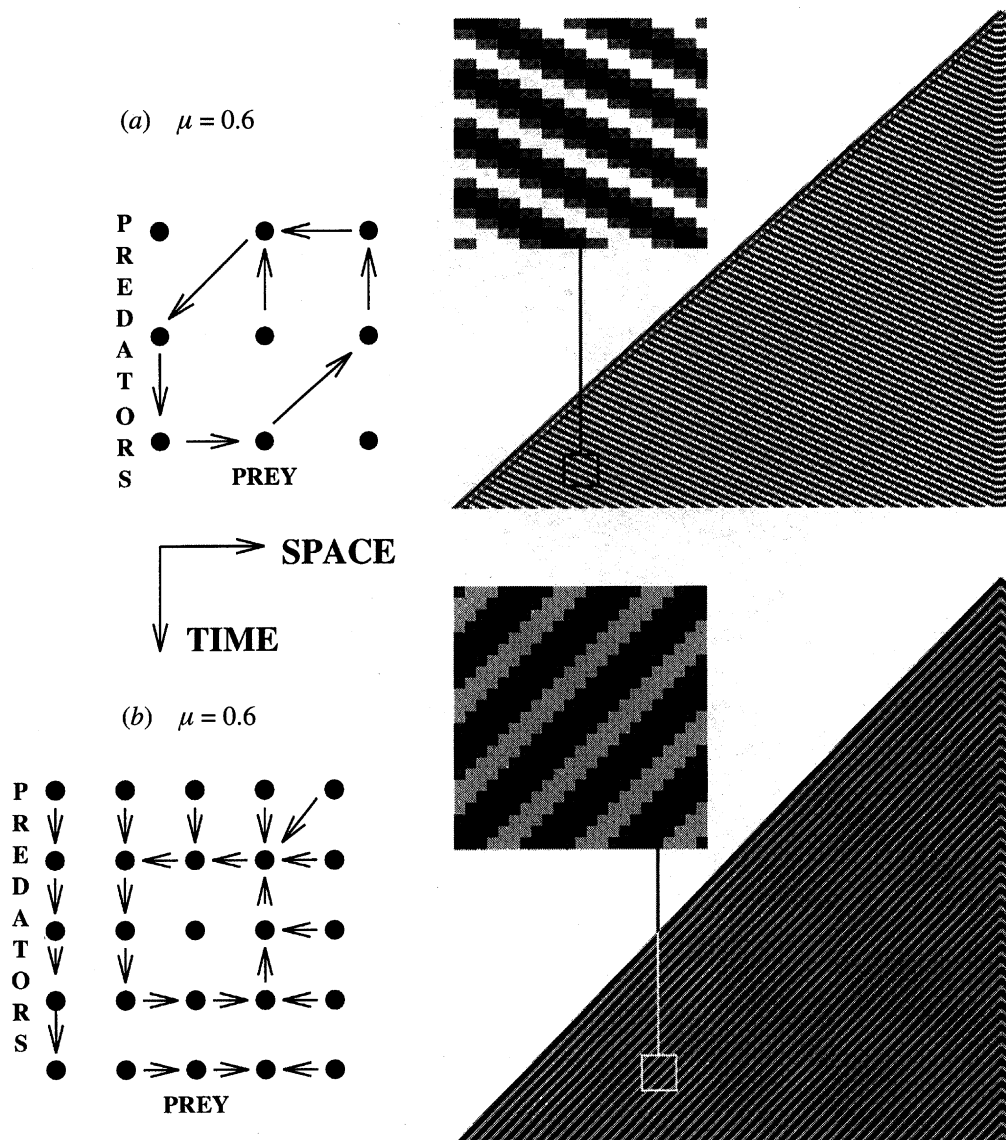


Figure 6. An illustration of the behaviour behind invasion in cellular automaton models. Parts (a), (c) and (d) show solutions of the 9-state automaton whose local dynamics are indicated schematically in the figure. Thus every time iteration is divided into two sub-steps; in the first of these, the state of the automaton changes at each spatial site according to the rule illustrated, while the second sub-step corresponds to unbiased local movement, using the rule (6). The common values of the dispersal parameters μ_p and μ_n are shown in each part of the figure. Part (b) illustrates a simulation of invasion in a 25-state automaton of the same basic form. The automata used in (a)–(d) are purely deterministic, but in (e), we show the solution for the same automaton as in (b), but with a probability $q = 0.2$ of extinction at the end of every iteration whenever the predator or prey populations are in their largest non-zero states; this is described in more detail in the main text. In each case, we use a spatial domain of 801 patches; 398 successive time iterations are plotted. At this scale the spatial discretization is not really visible, and therefore we have enlarged one region of the plane in each figure, in order to illustrate this discretization. Initially the system is in the prey-only steady state, everywhere except at patch numbers 400, 401 and 402, where an asymmetric perturbation to other states is applied. This asymmetry rapidly disappears in (a)–(d); it is just visible in the early part of the solution in (a). Therefore, in the interests of brevity, we only plot patches 1–409. Of course, the solution in (e) shows marked asymmetry because of the stochasticity. We plot predator density as a function of space and time on a grey scale, with white corresponding to the lowest-density state and black corresponding to the highest density state.

at each point in space and time. The majority of ecological cellular automata are stochastic, with transitions between states defined in terms of probabilities (Dytham & Shorrocks 1992; Hendry & McGlade 1995; Rand & Wilson 1995). However, we restrict attention to deterministic automata, since one of our aims is to demonstrate spatiotemporal irregularities arising from purely deterministic rules. Such deterministic automata are surprisingly rare in

ecology, although there are some important and influential exceptions (Crawley & May 1987; DeRoos *et al.* 1991; Hassell *et al.* 1991; Comins *et al.* 1992). Like most automata used in other applications, these models typically use rules in which each time iteration has only one stage, with the state at a patch changing according to the state both at that patch and at neighbouring patches. One effect of this is to combine the local dynamics and the dispersal process, so that we cannot

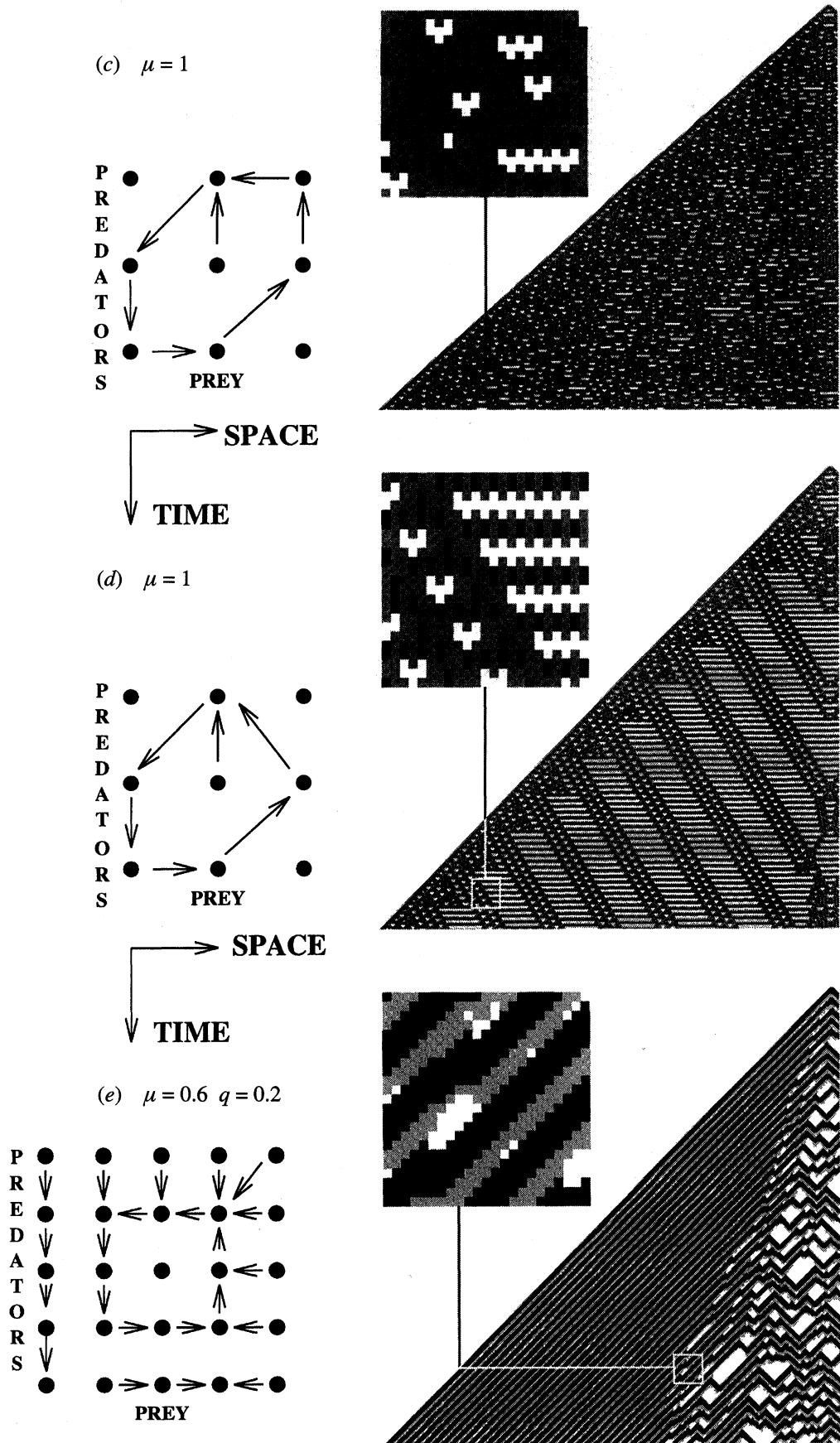


Figure 6(c-e). For legend see opposite.

be sure whether the automaton genuinely reflects our two key properties of local oscillations and unbiased local dispersal. Therefore we choose instead to develop a new automaton in which each time iteration is separated into two steps, corresponding to local kinetics and spatial dispersal.

We have considered automata with either 3 predator and 3 prey states (denoted by the integers 1, 2, 3), or 5 predator and 5 prey states (denotes by the integers 1–5); these systems therefore have a total of 9 and 25 possible states, respectively. The 25-state system enables a more accurate discrete representation of the continuum models we have been considering, and we interpret predator state 1 and prey state 1 as both being zero population levels. In the 9-state system, we take all the states as representing non-zero levels of both populations, except for the state (prey state 3, predator state 1), which we interpret as a prey-only equilibrium. The advantage of the 9-state system is that some mathematical analysis is possible, and this is described in detail elsewhere (Sherratt 1996).

In both systems, our model has the same basic framework. The first step of each time iteration corresponds to local dynamics, and the state at each spatial patch changes independently of the state at other patches. We have considered a wide range of different kinetic rules, all of the same basic form as the local dynamics for the reaction-diffusion and coupled map lattice models described above. In particular, all our kinetic rules have an oscillatory solution, and the ‘prey-only’ state is an equilibrium state.

The second part of each time step corresponds to unbiased spatial movement. To model this, we use a rule based on that described in Section 3 for the coupled map lattice model, in which the prey and predator states change independently. Again, we are considering solutions in one spatial dimension, and we denote by $H_i^{j+1/2}$ and $P_i^{j+1/2}$ the prey and predator states at patch i after the first half of the $(j+1)$ th iteration. Then our dispersal rule is

$$H_i^{j+1} = (1 - \mu_h) H_i^{j+1/2} + \mu_h (H_{i-1}^{j+1/2} + H_{i+1}^{j+1/2}) / 2, \quad (6a)$$

$$P_i^{j+1} = (1 - \mu_p) P_i^{j+1/2} + \mu_p (P_{i-1}^{j+1/2} + P_{i+1}^{j+1/2}) / 2, \quad (6b)$$

where μ_h and μ_p are motility parameters with values between 0 and 1; for simplicity we assume that $\mu_p = \mu_h = \mu$, say. In (6), the new states are initially calculated as real numbers, and then rounded to the nearest integer. This rounding means that our dispersal rule does not depend continuously on μ .

To study invasion, we consider a long, one-dimensional sequence of spatial patches, and assume that initially the system is in the prey-only steady state, except at a small number of patches in the centre of the domain. Examination of the dispersal rule (6) shows that this will result in invasion of the domain by predators provided the motility parameter μ is sufficiently large, and the invasion then moves outwards from the initial perturbation at a rate of one patch per time step. The behaviour behind invasion depends on both the form of the kinetics rule and the motility parameter μ , and some examples are illustrated in figure 6*a–d*. When $\mu < 1$, all our simulations

for both the 9 or 25 state automatas have shown periodic travelling waves behind the invasive front, in some cases moving parallel with the invasion (figure 6*b*), and in other cases moving in the opposite direction (figure 6*a*). This observation of periodic travelling waves in an oscillatory cellular automaton is to our knowledge quite novel, and in the case of the 9-state system, mathematical properties of these waves are discussed elsewhere (Sherratt 1996). For our purposes, the key fact is that these cellular automata solutions are remarkably similar to those of the reaction-diffusion and coupled map lattice models.

Notably, we have not observed spatiotemporal irregularities behind invasion in the cellular automaton model when $\mu < 1$. However, for $\mu = 1$ there is a wider range of behaviour behind invasion, including irregular wakes that are strongly reminiscent of the behaviour in reaction-diffusion and coupled map lattice models (compare figure 6*c* with figures 2*b*, 3*b*, and 5*b*). In one case, we have even observed the phenomenon of regular spatiotemporal oscillations immediately behind invasion, with irregular oscillations further back. This is illustrated in figure 6*d*, which should be compared with figures 2*c*, 3*c* and 5*c*. However, it is important to stress that the case $\mu = 1$ is of limited biological relevance.

One important issue which we have not considered thus far can easily be addressed using the 25-state cellular automaton framework, namely the possibility of extinction at small population levels. To model this we introduce a new ‘extinction sub step’ at the end of each iteration. In this new sub step, at each spatial site at which the predator or prey state is equal to 2, this state drops to 1 with a certain small probability q . We must stress that this is the only point in this paper in which we introduce an element of stochasticity into our modelling. In a large number of simulations, we have found that this extinction destabilizes the regular oscillations, resulting in an expanding region of irregular spatiotemporal oscillations, behind a transient band of regular oscillations (figure 6*e*). This solution is very reminiscent of the solutions illustrated previously in figures 2*c*, 3*c*, 5*c* and 6*d*, but it is important to stress that the origin of the irregularities is quite different in this present case. The width of this irregular region decreases with the extinction probability q , and in figure 5*e* we use a high probability ($q = 0.2$) for the purposes of illustration. The key implication of these results is that although local extinction does alter the behaviour behind invasion, the effects are only significant far behind the invasive wave front.

5. INTEGRODIFFERENCE EQUATION MODEL

The fourth and final category of model that we consider is an ‘integrodifference equation’ or ‘spatial contact’ model, in which population dispersal is represented by a probability distribution for the distance that an individual moves. Such models were first used for epidemics, with subpopulations represented as continuous functions of time (Kendall 1965;

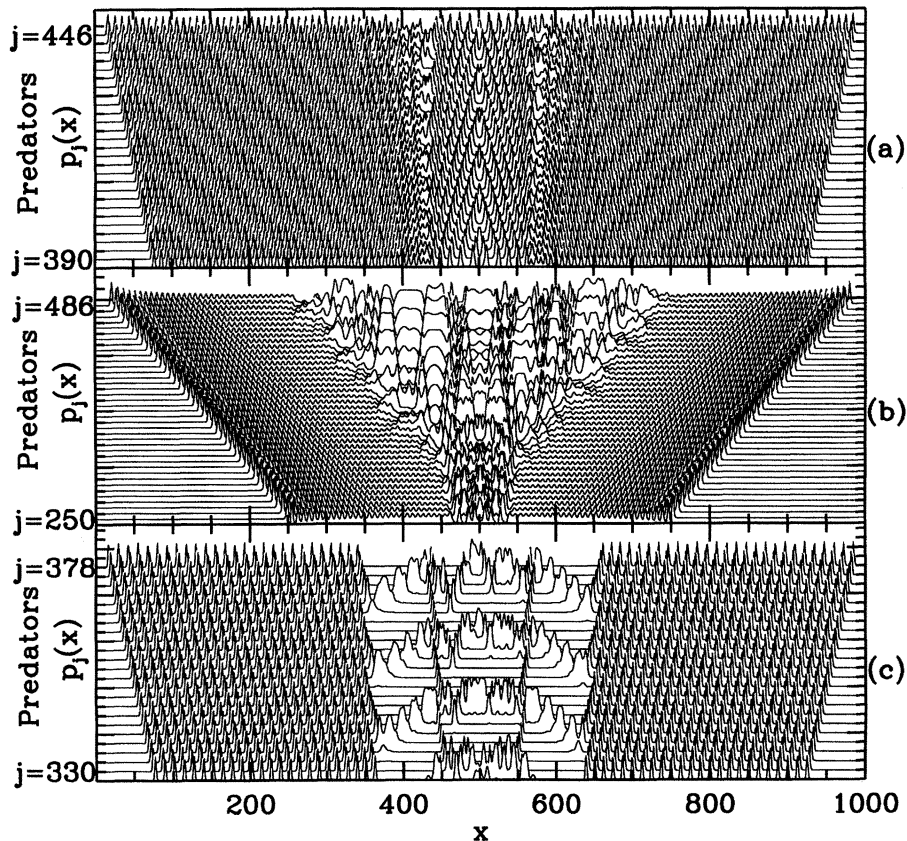


Figure 7. Oscillatory wakes behind invasion in the integrodifference equation model (7, 8, 9) for predator-prey interactions. We show space-time plots of the predator density; the solutions for the prey density are qualitatively similar. In all cases there are periodic travelling waves moving parallel to the invasion front immediately behind the front. The behaviour further back falls into one of the three categories familiar from the other types of model: periodic travelling waves moving away from the invasive front, as in (a); irregular spatiotemporal oscillations, as in (b); or mixed behaviour, as in (c). Initially the system is the prey only steady state everywhere except in a small region near $x = 500$, where a small distribution of predators is introduced; this perturbation rapidly expands, resulting in invasion. The parameter values are $\alpha_h = \alpha_p = 1$, with: (a) $a = 1$, $b = 5$, $c = 1$; (b) $a = 1$, $b = 2$, $c = 2$; (c) $a = 1.2$, $b = 8$, $c = 1$. The equation was solved numerically by calculating the integral using the extended trapezium rule with 6000 mesh points; our simple numerical tests suggest that this is more efficient than using more accurate integration schemes with fewer mesh points.

Mollison 1972). More recently, discrete-time contact models have been used in a number of models of population ecology (Kot 1989; Hardin *et al.* 1990; Andersen 1992; Kot 1992; Kot *et al.* 1995; Neubert *et al.* 1995), and it is this category of model that we use in our study. Our model is thus formulated in terms of $h^j(x)$ and $p^j(x)$, the prey and predator population densities at time step j , with x a coordinate for the infinite one-dimensional spatial domain.

The form of the model is taken from papers of Kot (1989, 1992):

$$h^{j+1}(x) = \int_{-\infty}^{+\infty} K_h(x-y) G_h[h^j(y), p^j(y)] dy, \quad (7a)$$

$$p^{j+1}(x) = \int_{-\infty}^{+\infty} K_p(x-y) G_p[h^j(y), p^j(y)] dy. \quad (7b)$$

Here $G_h(\cdot)$ and $G_p(\cdot)$ model the population kinetics, and the kernel functions K_h and K_p are distribution functions for spatial dispersal, and are subject to the constraint

$$\int_{-\infty}^{\infty} K_p(x) dx = \int_{-\infty}^{\infty} K_h(x) dx = 1.$$

The intuitive interpretation of (7) is that the birth-death processes represented in the kinetics cause the population densities to change from $h_j(y)$ and $p_j(y)$ to $G_h[h_j(y), p_j(y)]$ and $G_p[h_j(y), p_j(y)]$ between time steps j and $j+1$. Immediately afterwards, both populations undertake long-distance dispersal, and as a result become distributed around the point $x = y$ according to the distribution functions $K_p(\cdot)$ and $K_h(\cdot)$. Following Kot (1989, 1992), we use bilateral exponential distribution functions:

$$K_h(x-y) = \frac{1}{2}\alpha_h \exp(-\alpha_h|x-y|)$$

and

$$K_p(x-y) = \frac{1}{2}\alpha_p \exp(-\alpha_p|x-y|). \quad (8)$$

Such bilateral exponential kernels arise under assumptions of random movement and a constant probability per unit time of stopping during the dispersal period (Neubert *et al.* 1995). Here, α_h and α_p are motility parameters, which increase as motility decreases; as space is continuous in this model, their absolute values simply correspond to a rescaling of the spatial coordinate, and only the ratio α_h/α_p is significant.

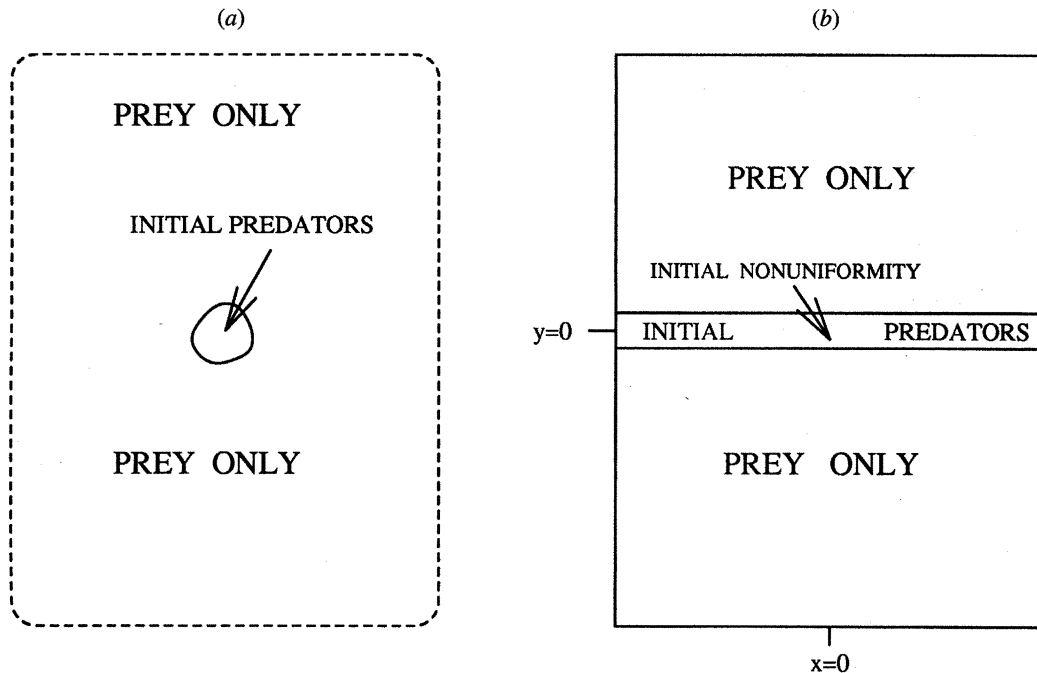


Figure 8. A schematic representation of the initial perturbations we use for our study of predator-prey invasions in two dimensions. In (a), we use initial conditions in which predators are introduced in a small, localized region of the domain, which is otherwise in the prey-only steady state. This is the natural two-dimensional analogue of the one-dimensional invasions we have discussed; the corresponding solutions are shown in figures 9 and 10. In (b), the initial conditions we use correspond to the introduction of predators along a line running parallel to one edge of the (rectangular) spatial domain. The perturbation has a small non-uniformity near the centre of the domain, and our main focus is to study the effects of this non-uniformity on what is otherwise a one-dimensional initial condition. In this case the boundary conditions are required at the ends of the domain perpendicular to the initial perturbation; we use either periodic or zero-flux boundary conditions, which give identical results for the time period we are considering. The corresponding solutions are illustrated in figures 11 and 12.

This model thus satisfies our requirement of random spatial movement, and will also exhibit oscillatory local dynamics provided suitable kinetic functions G_h and G_p are chosen. We use the same kinetics as in the coupled map lattice model described in §3, that is

$$G_h(h, p) = h \exp[a(1 - h/b) - cp] \quad (9a)$$

$$G_p(h, p) = h [1 - \exp(-cp)] \quad (9b)$$

where a , b and c are positive parameters. As discussed in §3, these kinetics are oscillatory for suitable parameter values.

Once again, we simulate invasion using initial conditions in which the system is in the prey-only steady state except in a small localized region, which we take as centred on $x = 0$. We have solved equations (7) with (9) numerically for a wide range of parameter values, and typical results are illustrated in figure 7. As in the coupled map lattice model, there is in every case an invasive wave front moving outwards from $x = 0$, with periodic travelling waves immediately behind it, moving parallel to the invasion. Periodic travelling waves have been observed previously in single species models of the form (7) (Kot 1992), although the particular kinetics (9) have not to our knowledge been used previously in the context of integrodifference equations. Behind this wavetrain moving parallel to invasion, there is one of the three familiar types of

behaviour, depending on parameter values: periodic travelling waves in the opposite direction to invasion (figure 7a), irregular spatiotemporal oscillations (figure 7b), and a mixture of the two (figure 7c). Again, localized perturbations applied to the irregular oscillations both grow in time and expand spatially, suggesting true spatiotemporal chaos. We must stress that although the kinetics (9) do exhibit temporally chaotic behaviour for some parameter sets (see figure 4), we have not used parameters in this region, and for all our simulations, the local behaviour is simple periodic oscillations.

6. INVASION IN TWO SPATIAL DIMENSIONS

In §§2–5, we have introduced four quite different types of model for predator-prey population dynamics. The models have no formal relationship, but all reflect the qualitative features of oscillatory local dynamics and random spatial movement. Using each of the models, we have simulated invasion of prey by predators. There are obviously differences in detail between the solution forms of the models, but much more striking is the strong qualitative similarity between the solutions, with the phenomena of periodic waves and irregular wakes behind invasion being ubiquitous features. This in turn provides very strong

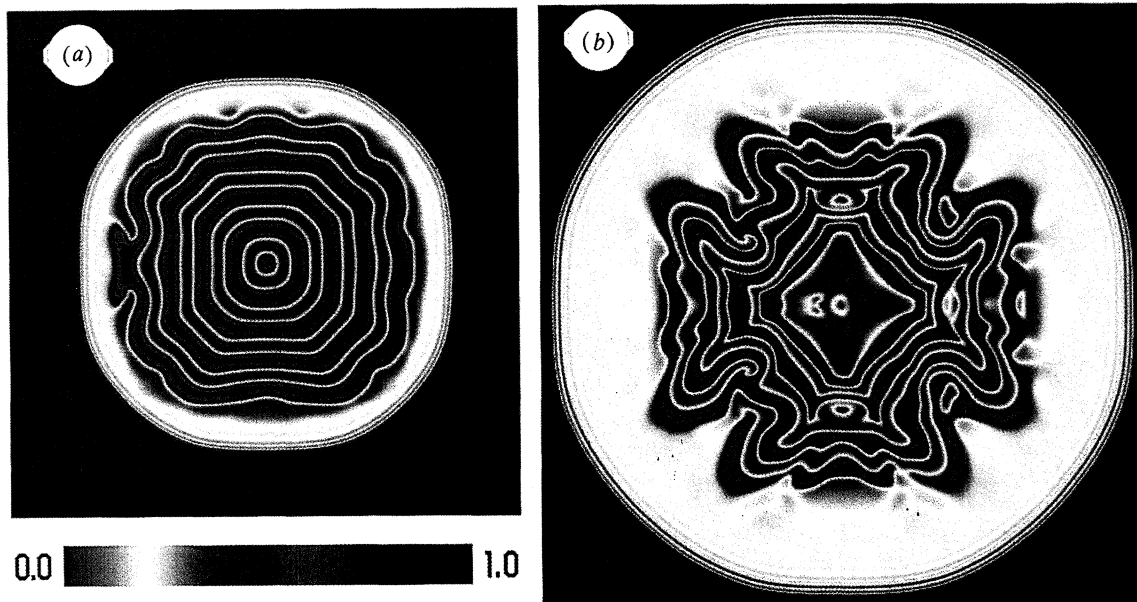


Figure 9. The behaviour in a two-dimensional predator-prey invasion following a localized introduction of predators, as predicted by the reaction-diffusion model (1) with kinetics (3). The initial conditions are as illustrated schematically in figure 8*a*; specifically, predators are introduced uniformly in a cylinder centered at the origin, and in addition a small perturbation is applied along the x axis. The solutions are shown as a function of space at one time point, with prey density indicated by the colour scheme shown in the bar chart; the predator density has a qualitatively similar form but is typically not in phase with the prey. In (a) there are regular periodic waves behind the invasive front, which are just unstable, causing a small asymmetry to develop near the x axis. In (b) there are highly irregular oscillations behind the invasive front. The parameter values are $A = 1.5$, $C = 5$ and (a) $B = 0.22$, (b) $B = 1$, and the time at which the solution is plotted is (a) 600; (b) 350. The equations were solved numerically using an alternating direction implicit method, with a block-centred Crank–Nicolson finite difference scheme. The spatial domain illustrated is $-500 < x, y < 500$ in both cases, and the spatial grid used was 1000×1000 .

evidence that these features are genuine consequences of the simple qualitative ingredients of oscillatory population kinetics and random spatial movement. Thus we can predict with some confidence that we do expect these features to appear in the wake of real predator-prey invasions.

We have thus far restricted attention to one-dimensional spatial domains, in order to simplify the model solutions and facilitate comparison. However, the vast majority of real ecological interactions occur in two-dimensional domains, and we now consider this more complex situation. Having used one-dimensional domains to establish the strong similarity between the different types of model, we now restrict attention to just two models: the reaction-diffusion model (1) with kinetics (3) and the coupled map lattice model (4, 5). The two-dimensional analogues of these models are very natural. In (1), the diffusion operator $\partial^2/\partial x^2$ is replaced by the two-dimensional Laplacian $\partial^2/\partial x^2 + \partial^2/\partial y^2$, where x and y are two-dimensional Cartesian coordinates, and the coupled map lattice dispersal rule (4) is replaced by

$$h_{(i_x, i_y)}^{j+1/2} = \nu_h h_{(i_x, i_y)}^j + (1 - \nu_h) \bar{h}_{(i_x, i_y)}^j, \quad (10a)$$

$$p_{(i_x, i_y)}^{j+1/2} = \nu_p p_{(i_x, i_y)}^j + (1 - \nu_p) \bar{p}_{(i_x, i_y)}^j. \quad (10b)$$

Here, (i_x, i_y) denotes the position in a two-dimensional rectangular array of patches, and $\bar{h}_{(i_x, i_y)}^j$, $\bar{p}_{(i_x, i_y)}^j$ denote the average of the prey and predator densities over the 8 neighbouring patches (this is the so-called Moore neighbourhood).

To study two-dimensional invasions, we consider two categories of initial perturbation (figure 8). In the first, predators are introduced in a small, localized region of the domain, which is otherwise in the prey-only steady state. This is the natural two-dimensional analogue of the one-dimensional invasions we have discussed, and the results are qualitatively similar; numerical simulations are shown in figure 9 for the reaction-diffusion model and figure 10 for the coupled map lattice model. These figures show the solutions at single instants in time; we have examined the temporal evolution by displaying successive time frames as a movie, but we are unable to represent this effectively on the printed page. The results have the same qualitative features as the one-dimensional solutions: periodic waves behind the invasive front, which may be unstable and thus degenerate into spatiotemporal irregularities. Again as in one dimension, the coupled map lattice model solutions also have a band of periodic waves immediately behind and moving parallel to the invasive front. An important new feature in the two-dimensional solutions is the way in which asymmetries in the initial introduction of predators are reflected in the long-time solutions. In both parts of figures 9 and 10, predators were initially introduced in a spatially asymmetric manner. However, in the cases in which only regular periodic waves are observed, this initial asymmetry rapidly disappears; by contrast, where there are irregular oscillations, the asymmetry persists. This provides additional evidence, on top of our previously presented

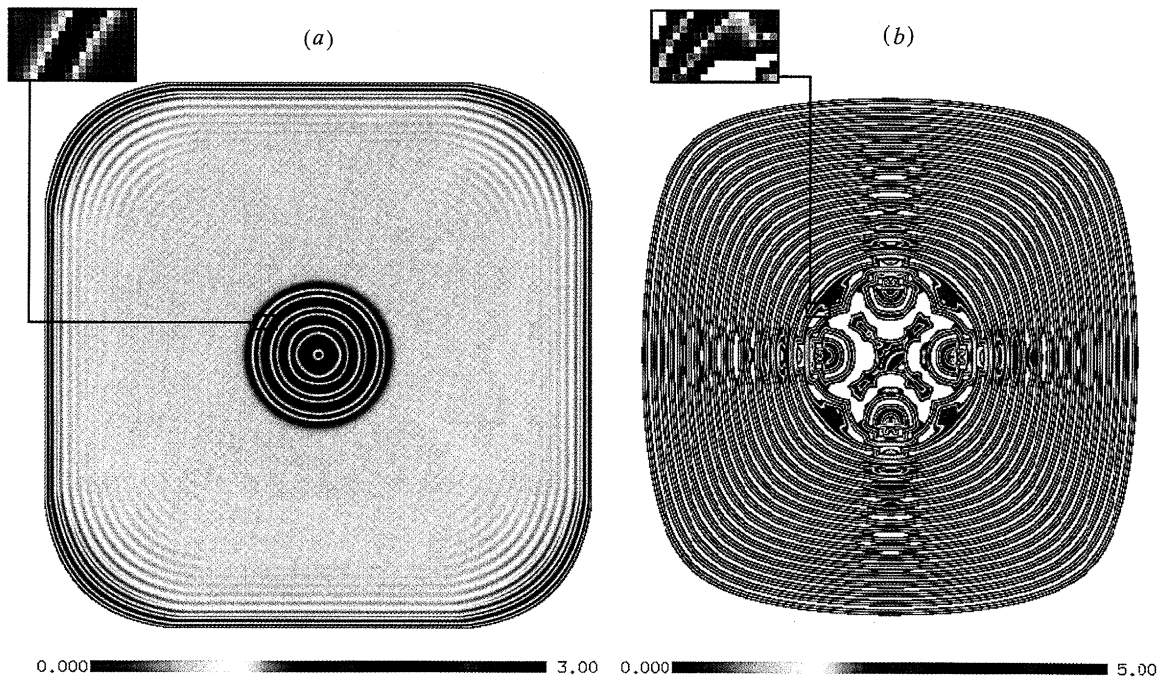


Figure 10. The behaviour in a two-dimensional predator-prey invasion following a localized introduction of predators, as predicted by the coupled map lattice model (10, 5). The solution is shown as a function of space at one instant of time, with predator density indicated by the colour scheme shown in the bar chart; predator densities less than 0.001 are shown in white. The prey distribution has a qualitatively similar form. In both (a) and (b) there is an expanding front of invading predators. In (a) this invasion leaves in its wake regular spatiotemporal oscillations with the form of a target pattern; these circular waves move away from the invasive front, towards the origin, although this cannot be seen in the single time frame illustrated. In (b), the behaviour behind invasion is irregular spatiotemporal oscillations, which retain the asymmetry of the initial conditions. The parameter values are: (a) $a = 1.2$, $b = 8$, $c = 1$, $\nu_h = \nu_p = 0.25$; (b) $a = 1$, $b = 5$, $c = 1$, $\nu_h = \nu_p = 0.7$. In both (a) and (b), the spatial domain is 512×512 patches, and the precise initial conditions are $h_{(i_x, i_y)} = b$ everywhere, and $p_{(i_x, i_y)} = 0.1$ for $225 \leq i_x, i_y \leq 257$, except that $p_{(255, 255)} = 0.2$ and $p_{(257, 257)} = 0.3$; otherwise $p_{(i_x, i_y)} = 0$. The solution is plotted after 263 time iterations in (a), and after 264 iterations in (b). In each part, one region of the domain is shown at an enlarged scale, in order to emphasize the spatial discretization of the domain.

bifurcation studies (Sherratt 1995; Sherratt *et al.* 1995), that these irregular oscillations are a genuine example of spatiotemporal chaos.

The second category of initial perturbation that we have used is the introduction of predators along a line running parallel to one edge of the (rectangular) spatial domain (figure 8b). We refer to the domain as $-L_x < x < L_x$, $-L_y < y < L_y$ in the reaction-diffusion model, and $-N_x < I_x < N_x$; $-N_y < i_y < N_y$ in the coupled map lattice model, where the initial perturbation line is $y = 0$ and $i_y = 0$, respectively; elsewhere in the domain, the system is initially in the prey-only steady state. If this perturbation were homogeneous in the x direction, the solution would of course remain independent of x , and have exactly the form of the one-dimensional solutions discussed above. However, the interest in this type of invasion is to consider the effect of a small non-uniformity in the initial perturbation, near $x = 0$ or $i_x = 0$. Figures 11 and 12 illustrate the behaviour behind invasion caused by such a non-uniform initial perturbation, in the reaction-diffusion and coupled map lattice models, respectively. When the corresponding one-dimensional solution consists of regular oscillations (periodic waves) behind invasion, the initial non-uniformity rapidly disappears, giving a purely one-dimensional solution (results not shown). However, when the corresponding

one-dimensional solution has irregular oscillations in the wake of invasion, as for the parameters used in figures 11 and 12, the initial nonuniformity spreads outwards through the domain from the centre. Again, this provides additional evidence for spatiotemporal chaos. Moreover, from an ecological viewpoint, it shows that the initial and relatively rapid invasion of prey by predators can be followed by two subsequent invasions. In the first of these, the regular behaviour behind the invasive front is replaced by irregular oscillations, which are nevertheless uniform parallel to the invasive front. Much later, these irregular oscillations are themselves invaded by very highly disordered oscillations that are irregular in both spatial directions as well as in time.

In the case of true spatiotemporal chaos, we are fully aware that, no matter how accurate our numerical methods, our numerical solutions are not exact solutions. The sensitivity to perturbations such as truncation error or roundoff error inherent in a chaotic system means that numerics simply amount to computational experiments where the true solution is subject to a minor perturbation at every time step. Nevertheless, the characteristic form of the numerical solution gives clear qualitative information about the underlying spatio-temporal dynamics. Also, any ecological system is likely to be subject to ongoing

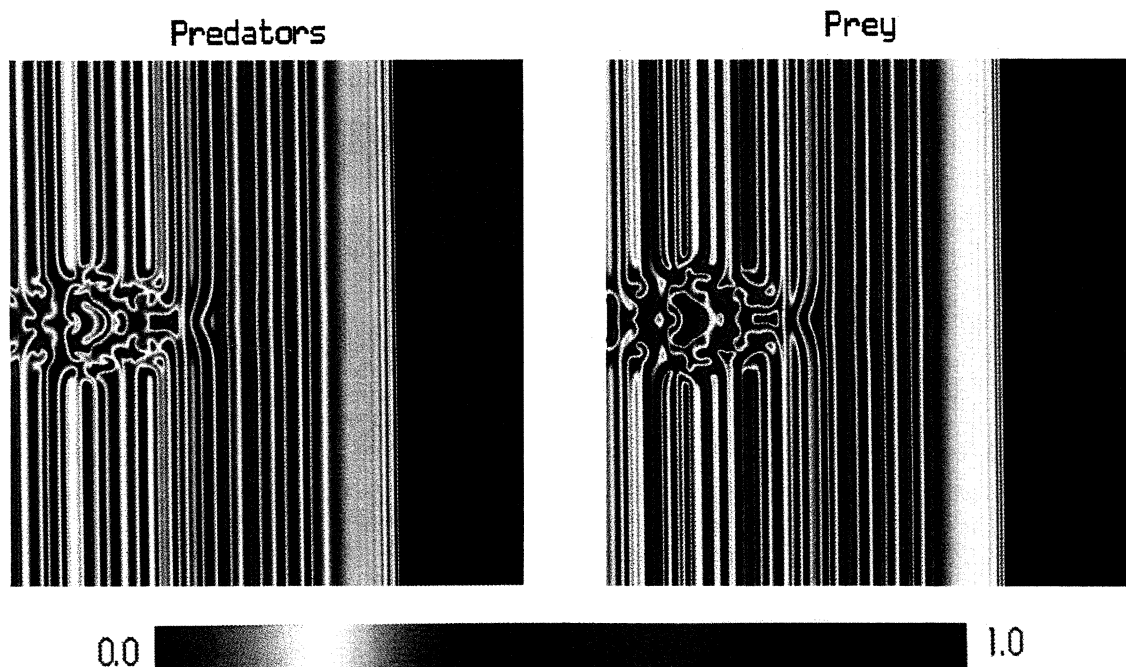


Figure 11. The behaviour in a two-dimensional predator-prey invasion following an introduction of predators along a line, as predicted by the reaction-diffusion model (1) with kinetics (3). The initial conditions are as illustrated schematically in figure 8*b*, except that to save computer time the equations are solved only in the region $x > 0$, with zero flux (Neumann) boundary conditions at $x = 0$. The solutions for both predators and prey are shown as a function of space at one time point, with population densities indicated by the colour scheme shown in the bar chart. The parameter values are $A = 1.5$, $B = 1$, $C = 5$ and the solution is plotted at time $t = 510$. The numerical method was as in figure 9. The spatial domain illustrated is $0 < x < 1000$, $-500 < y < 500$, and the spatial grid used is 1000×1000 . The precise initial conditions are as follows: $h = 0.8$, $p = 0$ everywhere except in the band $0 < x < 50$. In this band, $h = 0.6$, $p = 0.4$ (chosen arbitrarily), with the exception of the region $50 < x < 54$, $0 < y < 4$ in which an asymmetry was introduced, of the form $p = 0.4$.

perturbations, and in this sense the numerical solutions are more 'exact' than model itself.

7. DISCUSSION

Ecological invasions have become an important research topic in recent years. A number of different mathematical models have been proposed, although in almost all cases they focus entirely on the invading species without considering interactions with other species (see Williamson (1989) for a review). One reason for this is that experiments and field data on invasion are usually characterized in terms of the taxonomy of the invader, rather than functionality (Mooney *et al.* 1989). Nevertheless, there are a number of empirical and field studies of invasion in particular predator-prey systems (Robinson & Wellborn 1988; Fraser & Gilliam 1992; Nilssen *et al.* 1992; Greve 1994). These typically do not address the spatio-temporal structure behind invasion, which is the focus of our work; however, we are aware of one paper (Lehman & Caceres 1993) which describes the spatio-temporal pattern behind a specific invasion, namely the invasion of *Daphnia* by its crustacean predator *Bythotrephes* in Lake Michigan. This study does indeed find spatiotemporal oscillations consistent with the model predictions we have described. Very distinct oscillatory wakes were also found in data for the density of tephritid flies *Urophora carudi* L. (Diptera:

Tephritidae) as they invaded thistle populations (Jeltson *et al.* 1992). While the model used to explain this was a sum-difference equation, incorporating stages in the fly's development and vacancy/occupancy on the thistle sites, the basic ecological interaction is plant-herbivore, which can be considered a special form of prey-predator.

All of the simulations we have presented thus far have been stopped before the invasion reaches the edge of the domain. However, in applications a key issue is whether the behaviour observed behind invasion persists once the whole domain has been invaded. We have performed a preliminary investigation of this issue using the reaction-diffusion model, on one-dimensional domains with zero flux end conditions. This has revealed an interesting and important difference between regular and irregular wakes. When the behaviour behind invasion consists of regular spatio-temporal oscillations, these oscillations rapidly decay once the whole domain has been invaded, giving spatially homogeneous temporal oscillations within a fraction of the invasion time. These homogeneous oscillations are simply the limit cycle solution of the reaction kinetics. By contrast, when there is spatio-temporal chaos behind invasion, this persists for very long times. Indeed we have never observed significant changes in this behaviour, despite continuing solutions for 10 and sometimes 100 times longer than the time taken to initially invade the domain; for the domain sizes we are using, this is many tens of thousands of

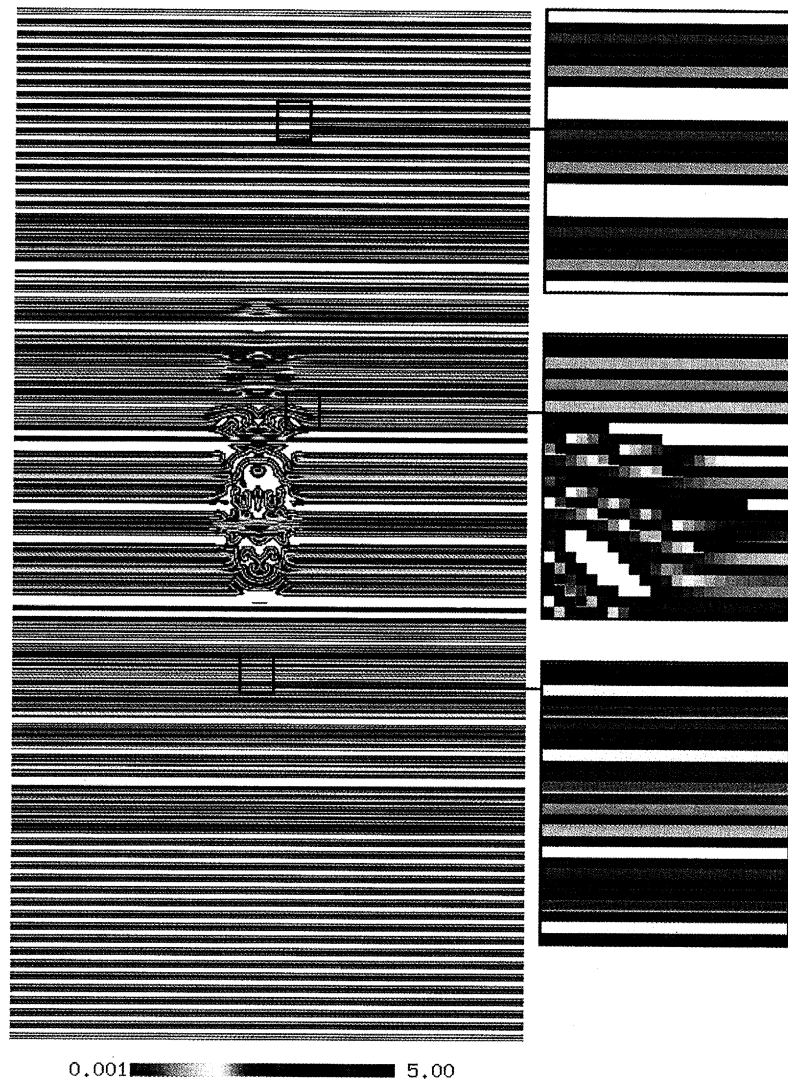


Figure 12. The behaviour in a two-dimensional predator-prey invasion from initial conditions in which predators are introduced along a line, as illustrated in figure 8*b*, as predicted by the coupled map lattice model (10, 5). The solution is shown as a function of space at one instant of time, with predator density indicated by the colour scheme shown in the bar chart; predator densities less than 0.001 are shown in white. The prey distribution has a qualitatively similar form. The solution divides naturally into three regions: periodic waves which move with the invasive front immediately behind the front, one-dimensional irregular oscillations further back, and two-dimensional irregularities near the centre of the domain. The spatial domain is 401 patches \times 801 patches; the precise initial conditions are $h_{(i_x, i_y)} = b$ everywhere, and $p_{(i_x, i_y)} = 0.1$ for $i_y = 399, 400, 401$ and all i_x , except that $p_{(399, 199)} = 0.2$ and $p_{(400, 201)} = 0.3$; otherwise $p_{(i_x, i_y)} = 0$. The solution is plotted after 392 time iterations. The parameter values are $a = 1.2$, $b = 8$, $c = 1$, $\nu_h = \nu_p = 0.22$. Three regions of the domain are shown at an enlarged scale, in order to emphasize the spatial discretization of the domain.

generations. This marked difference in persistence is a major difference between regular and irregular waves, and highlights the crucial importance of determining the anticipated behaviour for particular predator-prey systems.

Ecological data on spatiotemporal population interactions is rare (see Kareiva (1990) for a review), but perhaps the most unifying feature of this data is that it contains spatiotemporal irregularities. These irregularities may have a number of causes. Observational noise and environmental irregularities will have an effect in all studies. Therefore it is very difficult to say with confidence whether or not observed irregularities reflect chaos in the underlying population dynamics. However, the work in this paper goes some way to addressing this issue. We have shown that both regular

and irregular spatiotemporal oscillations arise very naturally behind invasion of prey by predators, as a direct consequence of two simple qualitative properties of the predator-prey system: oscillatory local dynamics and random movement. A single model alone would not allow this conclusion to be drawn, but we have demonstrated it in four quite different types of model, whose only common feature is these simple qualitative properties. We argue that from this we can conclude with confidence that spatiotemporal oscillations, either regular or irregular, will always occur behind invasion in real predator-prey systems of this type. Thus whatever noise is added by the environment and the observation method, these oscillations will be present as an underlying feature, and as a direct consequence of the population dynamics

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