Noise-induced suppression of periodic travelling waves in oscillatory reaction–diffusion systems

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Ecological field data suggest that some species show periodic changes in abundance over time and in a specific spatial direction. Periodic travelling waves as solutions to reaction–diffusion equations have helped to identify possible scenarios, by which such spatio-temporal patterns may arise. In this paper, such solutions are tested for their robustness against an irregular temporal forcing, since most natural populations can be expected to be subject to erratic fluctuations imposed by the environment. It is found that small environmental noise is able to suppress periodic travelling waves in stochastic variants of oscillatory reaction–diffusion systems. Irregular spatio-temporal oscillations, however, appear to be more robust and persist under the same stochastic forcing.

Keywords: reaction–diffusion; travelling waves; spatio-temporal chaos; noise

1. Introduction

There is growing evidence that population densities of some species vary not only periodically over time (Turchin 2003), but also in a specific spatial direction. In this case, the temporal and spatial oscillations may resemble a periodic travelling wave in population density (Ranta & Kaitala 1997; Lambin *et al.* 1998; Bjørnstad *et al.* 2002; Tenow *et al.* 2007). Although such empirical evidence for periodic travelling waves in population dynamics was lacking at that time, this form of pattern formation had already been theoretically established for oscillatory reaction–diffusion equations by Kopell & Howard (1973). Since then, mathematical models have been used to understand the mechanisms behind the generation of periodic travelling waves, at first with applications to chemical reactions (Auchmuty & Nicolis 1976; Kuramoto 1984; Scott 1994). Subsequently, periodic travelling waves gained considerable attention in theoretical population dynamics and have been shown to exist in a variety of models. Examples are given by Shigesada *et al.* (1986) for a reaction–diffusion model with spatially varying diffusivity and population growth rate, Britton (1990) for an integro-differential reaction–diffusion model, Hassell *et al.* (1991) for a coupled map lattice and Sherratt (1996) for cellular automata.

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For the case of oscillatory reaction–diffusion systems, at least two realistic ecological scenarios have been identified, which may lead to periodic travelling waves. The first one is the formation of periodic travelling waves in the wake of a predator population invading a homogeneously distributed prey species (Petrovskii *et al.* 1998; Petrovskii & Malchow 2000; Sherratt 2001). The second one is associated with suitable boundary conditions applied to the edges of the habitat, reflecting some degree of hostility of the adjacent space (Sherratt *et al.* 2002; Sherratt 2003).

A key feature of periodic travelling waves in oscillatory reaction–diffusion systems is that there is always a whole family of feasible solutions. Depending on system parameters and boundary conditions, a particular member of this solution family is selected, which can be either stable or unstable as a solution to the reaction–diffusion equations. The question of stability of periodic travelling waves has been solved only for a few special cases (Kopell & Howard 1973; Maginu 1981), but extensive numerical studies indicate that whenever the selected solution is unstable, the long-term behaviour of the system dynamics consists of irregular spatio-temporal oscillations (Sherratt 1995; Petrovskii & Malchow 1999, 2001). For a comprehensive review of periodic travelling waves in field studies and reaction–diffusion systems, see Sherratt & Smith (2008).

To be applicable to real-world ecosystems, however, the results obtained from reaction–diffusion systems must be robust with respect to noisy perturbations induced by the environment. In the context of ecological modelling, this environmental stochasticity subsumes all processes that are not represented in the model, but for which an impact on the system dynamics cannot be ruled out. This could be the case for processes that are too poorly understood to allow for explicit description and/or for processes that are overly complex. Examples of such processes are rapidly changing atmospheric conditions, such as temperature, humidity, precipitation or wind stress; other species that interact with the modelled species; the availability of basic resources; the movement and salinity of the surrounding water column for aquatic species; intensity of light irradation for photosynthetic species and features of the habitat landscape.

Roughly speaking, there a three pathways over which such perturbations may influence a reaction–diffusion system. Firstly, there is purely spatial noise, reflecting a heterogeneous but fixed impact of landscape features on system dynamics. Secondly, there are purely temporal fluctuations. The most prominent of this type clearly is the periodic forcing imposed by the annual succession of the seasons. There are numerous models incorporating a periodic forcing of some kind to account for this type of large-scale fluctuation; a specific example for oscillatory reaction–diffusion equations is the work by Webb & Sherratt (2003). However, especially on smaller scales there are many processes that cannot be represented by a periodic forcing and when many of such processes come together, one can truly speak of erratic fluctuations or noise forcing the system. The combination of the two mentioned pathways leads to spatio-temporal noise, that is, fluctuations in both time and space. It depends on the scale of the problem at hand to decide which pathway may play a crucial role in the dynamics of the underlying system and which fluctuations may be neglected.

Now, there are several examples where the introduction of noise into an ecological model via one of the above-mentioned pathways may lead to a considerable shift in system dynamics, rather than just blurring the underlying

deterministic dynamics. Examples of such shifts include noise-triggered and noise-influenced transitions between alternative stable states (Scheffer & Carpenter 2003; D'Odorico *et al.* 2005; van Nes & Scheffer 2005; Guttal & Jayaprakashh 2007; Serizawa *et al.* 2009), sustained oscillations in an otherwise stationary system, which may give rise to regular spatio-temporal patterns (Aparicio & Solari 2001; Kuske *et al.* 2007; Sieber *et al.* 2007), the survival of species that would go extinct in a deterministic environment (Malchow *et al.* 2005), and the persistence of periodic travelling waves in situations where they would otherwise die out to spatially homogeneous oscillations (Kay & Sherratt 2000).

In this paper, we will investigate the impact of purely temporal noise on the propagation of travelling waves and irregular oscillations in reaction–diffusion models. It will be demonstrated that periodic travelling waves are very susceptible to small erratic fluctuations and that they are replaced by spatially homogeneous oscillations in the presence of noise. Irregular spatio-temporal oscillations, on the other hand, prove to be more robust against the noise. We begin by introducing a general stochastic reaction–diffusion model in §2 and define some basic notation. In §3, we present numerical simulations for a particular predator–prey model, indicating that a significant shift in spatiotemporal dynamics occurs under stochastic forcing. This example is used to motivate the use of a more generic oscillatory reaction–diffusion system in §4. Here, the effects are reproduced and investigated in more detail. The last section discusses the ecological and theoretical implications of the results.

2. Noise in reaction–diffusion systems

A general model for the interaction and dispersal of two species subject to noise is given by the two coupled stochastic reaction–diffusion equations

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + f_u(u,v) + g_u(u,v)\,\xi_t \tag{2.1}$$

and
$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + f_v(u,v) + g_v(u,v)\,\xi_t. \tag{2.2}$$

Here, $u = u(t,x)$ and $v = v(t,x)$ denote the densities of the species at time t and spatial location $x \in [0, L]$ on a spatially one-dimensional domain of length L. The spatially homogeneous diffusion coefficient D is assumed to be the same for both species. The two-dimensional vectorfield $F(u,v) = (f_u(u,v), f_v(u,v))$, which is assumed not to depend on time or space, forms the deterministic skeleton of the model. For our purpose, the skeleton will be required to contain a unique stable limit cycle, giving rise to oscillatory reaction kinetics. In the following, we will restrict our attention to Dirichlet boundary conditions $u = v = 0$ at $x = 0$ and $x = L$. In an ecological context, these boundary conditions reflect the assumption that the regions $x < 0$ and $x > L$ are hostile. As has been pointed out in §1, this scenario is known to give rise to periodic travelling waves.

Noise is introduced into the model via the real-valued stochastic process ξ_t and the coupling functions $g_u(u,v)$ and $g_v(u,v)$. The stochastic process ξ_t is essentially a family of real-valued random variables and for any fixed point in time, ξ_t

is a usual random variable mapping elements of some sample space Ω to real numbers. The sample space Ω can be viewed as the product of state spaces of any intrinsic or environmental process, which is not explicitly modelled by the reaction kinetics. Examples of such processes have been given in §1. These processes can be assumed to possess long-term mean values, and the parameters in the deterministic skeleton will usually reflect this assumed mean value. However, to account for the inevitable fluctuations around this mean, we will assume that the noise process ξ_t has a joint normal distribution with zero mean and unit variance, which does not change with time. Further, we require that the elements of this stationary noise process ξ_t at different times are uncorrelated. This gives rise to the autocorrelation function

$$C(h) = \mathrm{Cov}(\xi_t, \xi_{t+h}) = \begin{cases} 0 & \text{if } h \neq 0 \\ \infty & \text{if } h = 0 \end{cases}$$

or alternatively $C(h) = \delta(h)$, where δ is the Dirac delta function. A stochastic process fulfilling these requirements is commonly known as Gaussian white noise. By introducing the white noise process ξ_t into the reaction–diffusion model (2.1) and (2.2), the solution to this model will also be a stochastic process. Owing to the nature of the white noise ξ_t, equations (2.1) and (2.2) should merely be viewed as a more familiar abbrevation for the integral form of the underlying stochastic model (Walsh 1986).

There are three assumptions underlying the specific form of the noise process, which may need some clarification. Firstly, most of the mentioned environmental processes subsumed in the noise process are continuous functions of time and thus, in fact, autocorrelated at least on very small time scales. However, white noise has been widely used as an approximation to such processes, if they can be assumed to fluctuate rapidly on time scales that are small compared with the time scales of interaction and dispersal of the modelled species (Horsthemke & Lefever 1984). The analysis of datasets of environmental variables indicates that this assumption is acceptable for many terrestrial ecosystems (Steele 1985; Vasseur & Yodzis 2004). Secondly, an implicit assumption reflected by the model is that both species occupy the same habitat and thus experience the same noisy fluctuations. Consequently, the noise process ξ_t is the same for both species. Thirdly, we assume that the habitat is small enough so that spatial variations of the fluctuations can be neglected. Thus, ξ_t does not depend on space, but rather is a purely temporal stochastic process. However, the length of the habitat will be chosen well above the intrinsic length of the particular system (Petrovskii *et al.* 2003). This ensures that there is enough space for the spatial patterns to emerge, e.g. the length of the habitat will be larger than several times the spatial wave length of the observed periodic travelling waves.

Before proceeding, the forms of the coupling functions $g_u(u, v)$ and $g_v(u, v)$ need to be specified. Since ultimately, equations (2.1) and (2.2) are to describe the growth of populations, the coupling functions have to obey any conditions imposed by this modelling goal. For an isolated population surrounded by a hostile environment, which prevents immigration from outside into the habitat, a very general constraint is to require that population growth inside the habitat is zero if there is no population at all. For the deterministic reaction kinetics, this corresponds to $f_u(0, v) = f_v(u, 0) = 0$, and there is no reason to assume that

the introduction of noise renders void this postulate of parenthood (Hutchinson 1978). Since ξ_t is almost surely non-zero for all t, this leads us to also require $g_u(0, v) = g_v(u, 0) = 0$. This rules out the use of purely additive noise, where the coupling functions are essentially constants. However, the simplest coupling functions that fulfil the postulate of parenthood are homogeneous linear functions of the population densities, e.g. $g_u(u, v) = \eta u$ and $g_v(u, v) = \eta v$ with common noise strength η. This choice for the coupling functions leads to

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + f_u(u, v) + \eta u \xi_t \tag{2.3}$$

and
$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + f_v(u, v) + \eta v \xi_t. \tag{2.4}$$

This corresponds to multiplicative noise forcing the deterministic growth kinetics. In the next section, this general model will be used with specific oscillatory predator–prey growth kinetics.

3. Noise in a predator–prey system

Predator–prey models in the form of ordinary differential equations have been studied extensively over a period of almost a century in order to explain cyclic population dynamics. A vast number of models possessing a stable limit cycle have been proposed and as a consequence, there are numerous choices for the reaction kinetics. In order to motivate the use of more general cyclic kinetics, in this section, we will restrict our attention to the classic Rosenzweig–MacArthur model (Rosenzweig & MacArthur 1963). Under very general conditions, this model possesses a unique stable limit cycle and has been shown to generate travelling waves and spatio-temporal chaos when extended to a reaction–diffusion system (Petrovskii & Malchow 2001; Sherratt & Smith 2008). Using it as the deterministic skeleton in equations (2.3) and (2.4) yields the full stochastic reaction-diffusion model

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \left(r(1 - u) - \frac{av}{1 + h\,u} + \eta\xi_t\right)u \tag{3.1}$$

and
$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + \left(\epsilon\frac{au}{1 + hu} - m + \eta\xi_t\right)v. \tag{3.2}$$

Here, the prey population u grows logistically with intrinsic rate of growth r and a carrying capacity, which is scaled to unity in the above formulation. Predation follows a monod-type functional response (Holling 1959) with predation rate a and handling time h, which is characteristic for specialist predators preying on a single prey species. The numerical response of the predator v is scaled by the efficiency parameter ϵ and predators die with mortality rate m. The domain length will be fixed to $L = 20$ together with a diffusion coefficient of $D = 10^{-3}$. A typical parameter set yielding oscillatory behaviour of the reaction kinetics, which will
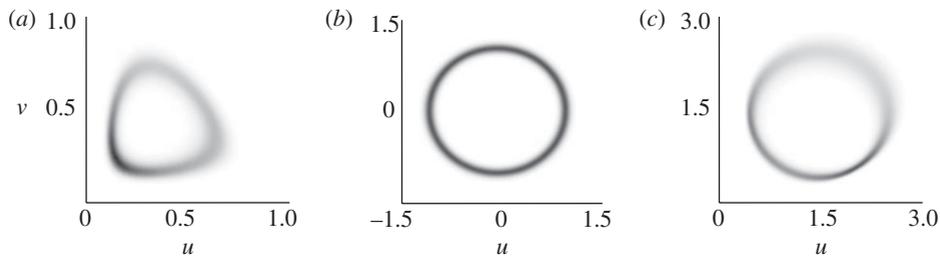
Figure 1. (*a*) Stationary probability distribution for the predator–prey system (3.1) and (3.2) with $\eta = 0.025$. Darker shade indicates higher probability. Stationary probability distribution for the λ–ω system (4.3) and (4.4) centred on the origin (*b*) and centred on (1.5, 1.5) (*c*). Noise strength is $\eta = 0.1$ in both cases.

be used from now on, is

$$r = 1, \quad a = \frac{10}{3}, \quad h = \frac{10}{3}, \quad \epsilon = 2 \quad \text{and} \quad m = 1. \tag{3.3}$$

Note that for this set of parameters and the chosen diffusion coefficient, the intrinsic length of the system is about $\pi/2$ and the habitat length is chosen well above this value.

As has been mentioned in the previous section, the solution to the stochastic system (3.1) and (3.2) is a stochastic process. Starting from a given initial condition, a particular stochastic trajectory through phase space is realized and these sample paths or realizations of the solution process are amenable to numerical approximation. The numerical data presented below is obtained by calculating particular realizations using the Euler–Maruyama method (Kloeden & Platen 1999) for the stochastic reaction kinetics and a Crank–Nicolson scheme for diffusion. The temporal step size is $\Delta t = 10^{-3}$ and spatial step size is $\Delta x = 2 \times 10^{-2}$.

Before proceeding to the spatial dynamics, figure 1*a* shows the stationary probability distribution for the reaction kinetics of equations (3.1) and (3.2) with parameters equation (3.3) and noise strength $\eta = 0.025$, obtained by averaging over many sample paths. The stable limit cycle appears smeared out in phase space, as would be expected for a system subject to stochastic forcing. However, the overall shape clearly resembles the deterministic orbit and in the following, care has been taken to ensure that the noise strength η is low enough so that the oscillatory behaviour of the local kinetics is qualitatively unaffected.

Turning to the full reaction–diffusion model, we start with a homogeneous distribution of the predator and prey populations and without stochastic forcing, that is $\eta = 0$. Without any perturbation, this homogeneous distribution would persist indefinitely. However, the fixed boundary conditions at both ends of the domain provide the necessary perturbations, from both of which a periodic travelling wave spreads across the entire domain. In figure 2*a*, a snapshot of the population densities is shown, after the periodic travelling wave occupies the whole domain. After this solution has settled, noisy perturbations are applied to the system by setting the noise strength η to some positive non-zero value. For very small values of η, the system dynamics does not change qualitatively.
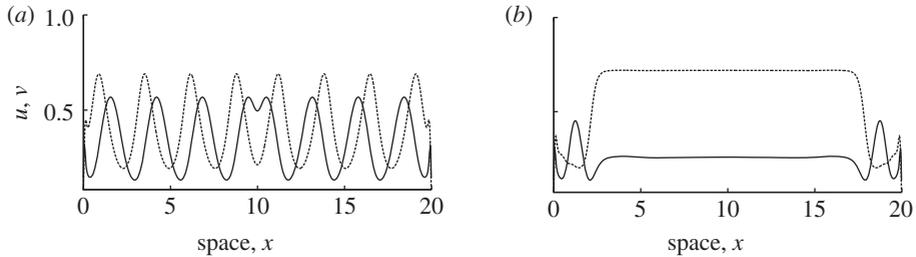
Figure 2. Snapshots of realizations of model (3.1) and (3.2), showing the spatial profile of prey u (solid) and predator v (dashed) densities. Periodic travelling waves for $\eta = 0$ at $t = 24\,500$ (a), which are suppressed to spatially homogeneous oscillations at $t = 28\,500$ (b), after noise intensity has been set to $\eta = 0.025$ at $t = 25\,000$. Note the disturbances at the boundaries, which are due to the Dirichlet boundary conditions.

If the noise strength exceeds some critical value, however, a significant shift in the system dynamics can be observed. Over the course of several time steps, the periodic travelling wave is gradually suppressed and replaced by spatially homogeneous oscillations. A snapshot of the spatial profile after noise has been set to $\eta = 0.025$ is shown in figure 2b. Disturbances of the otherwise spatially homogeneous profile are visible at the edges of the domain, which are due to the Dirichlet boundary conditions. For this noise strength, the local dynamics is clearly still oscillatory as shown in figure 1a and far away from the boundary, the homogeneous oscillations correspond to the local limit cycle oscillations.

An example of the entire process of noise-induced suppression of the periodic travelling wave is shown in figure 3a for the same noise strength $\eta = 0.025$. When the noise is switched off again, the periodic travelling wave again starts to spread from the boundaries to eventually reoccupy the whole domain. In fact, even for non-zero noise intensities, the local disturbances at the boundaries from time to time tend to spread from the edges before eventually being suppressed again by the noise. These intermittent break-ups of the spatially homogeneous oscillations are more frequent for lower noise intensities and their impact on regions far away from the boundaries is limited. This nevertheless shows that the noise-induced suppression of the periodic travelling wave is an unstable system state, which crucially depends on the presence and the strength of the stochastic forcing.

The next section investigates this suppression of travelling waves in more detail and it will be shown that it does not depend on the particular form of the oscillatory reaction kinetics, but rather may also be observed in a very generic setting.

4. Noise in a λ–ω system

Even the simplest reaction–diffusion systems of predator–prey interactions usually prove to be analytically intractable. Fortunately, in some cases, one can revert to much simpler models that under certain conditions mimic the dynamical behaviour of the more complicated one. In particular, there is a simpler
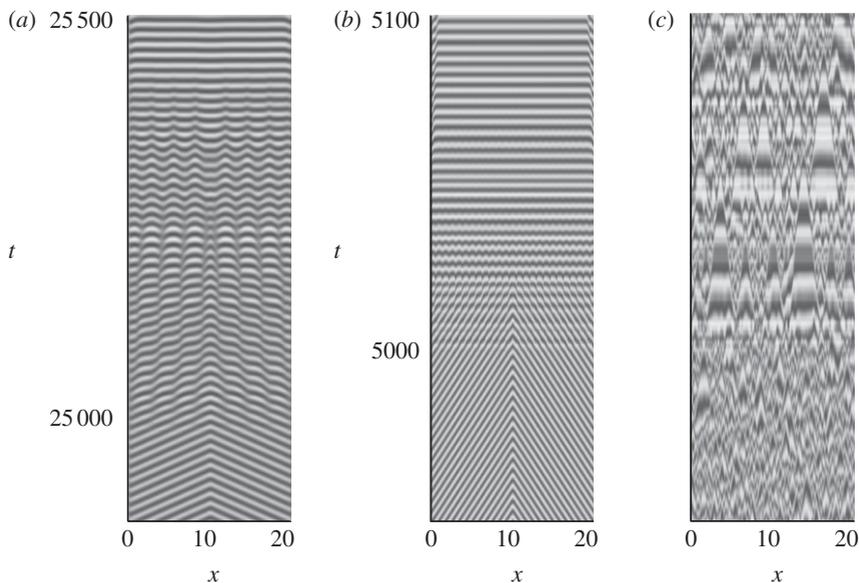
Figure 3. Suppression of travelling waves (*a*) in the predator–prey system (3.1) and (3.2). Noise strength is set to $\eta = 0.025$ at $t = 25\,000$. Suppression of travelling waves (*b*) and persistence of spatio-temporal chaos (*c*) in the λ–ω system (4.3) and (4.4). Here, in both cases, noise strength is set to $\eta = 0.1$ at $t = 5000$. Darker/lighter shades of grey indicate lower/higher population densities.

counterpart to predator–prey models whose reaction kinetics generate population cycles via a super-critical Hopf bifurcation of an equilibrium. These are the so-called λ–ω systems and reaction–diffusion equations based on these kinetics have the general form

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \lambda(r)u - \omega(r)v \tag{4.1}$$

and
$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + \omega(r)u + \lambda(r)v, \tag{4.2}$$

with $r = \sqrt{u^2 + v^2}$. In fact, systems of λ–ω type arise as the normal form of any system whose reaction kinetics possess an equilibrium close to a Hopf bifurcation. Therefore, these highly symmetric systems can be viewed as prototypical for more general oscillatory dynamics. Owing to this fact and because they are amenable to analytical investigation, periodic travelling waves as solutions to equations of the form (4.1) and (4.2) have been studied intensively. One of the most interesting results is that these periodic travelling waves can be stable or unstable as solutions to the reaction–diffusion equations and an analytical stability condition for the case of an infinite spatial domain have been derived by Kopell & Howard (1973). For a finite spatial domain subject to suitable boundary conditions, an equivalent stability condition is given by Sherratt (1995). In the same paper, it is shown by numerical analysis that when the periodic travelling wave is unstable, perturbations of the solution may lead to spatio-temporal chaos.

In the following, the effect of multiplicative noise on periodic travelling wave and chaotic solutions to a λ–ω system is investigated. We restrict our attention to a particular representative of the λ–ω class of reaction–diffusion systems whose stochastic equations on the one-dimensional spatial domain $[0, L]$ read

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + (1 - r^2)u - (3 - br^2)v + \eta u\xi_t \qquad (4.3)$$

and
$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + (3 - br^2)u + (1 - r^2)v + \eta v\xi_t. \qquad (4.4)$$

The local kinetics of equations (4.3) and (4.4) possess a circular limit cycle with unit radius, centred at the unstable equilibrium located at the origin. This periodic solution of the reaction kinetics reads

$$u_p(t) = \cos((3 - b)t)$$

and
$$v_p(t) = \sin((3 - b)t).$$

The form of these local solutions indicates that the parameter b determines the frequency of the local oscillation. In the deterministic reaction–diffusion system (4.3) and (4.4) on infinite and semi-infinite domains with $\eta = 0$, it depends on the parameter b whether the corresponding travelling wave solution is stable or unstable (Sherratt 1994). As will be shown below, also in the case of a finite domain subject to Dirichlet boundary conditions, b controls the observed spatio-temporal dynamics, e.g. whether the approached long-term behaviour will be periodic travelling waves or spatio-temporal chaos.

Note that we require $b \neq 3$, since otherwise the local kinetics reduce to

$$f_u(u, v) = (1 - r^2)(u - 3v)$$

and
$$f_v(u, v) = (1 - r^2)(3u + v).$$

It is readily seen that the unit circle is a continuum of non-hyperbolic equilibria, since, in addition to the origin, the reaction functions then vanish at all points $r^2 = u^2 + v^2 = 1$. While spatio-temporally irregular solutions may still be observed in the reaction–diffusion system with $b = 3$ (Sherratt 1995), the reaction kinetics in this case are clearly not oscillatory, e.g. they do not possess a limit cycle and thus they do not mimic the oscillatory predator–prey system.

Proceeding to the stochastic dynamics, firstly we again have a look at the stationary probability distribution of the stochastic λ–ω kinetics. This is shown in figure 1b for $b = 1$ and noise strength $\eta = 0.1$, where the distribution resembles the highly symmetric shape of the deterministic limit cycle.

For the oscillatory predator–prey system (3.1) and (3.2), a simple visual examination of the solution plot has shown that for a certain noise strength a fully developed periodic travelling wave is suppressed to spatially synchronized oscillations, except for small regions directly adjacent to the domain boundaries. To be able to quantify this effect of spatial synchronization at a fixed time t more exactly, in the following the current spatial mean value of a solution and the variation $\sigma(t)^2$ around this mean value with respect to the spatial position

will be calculated. For periodic travelling waves with fixed amplitude, the spatial variance is non-zero but constant over time, whereas $\sigma(t)^2 = 0$ corresponds to a perfectly homogeneous spatial distribution. Using a numerical realization, we calculate the empirical variation $\sigma(t)^2$ of all numerical mesh points on the subset $[x_0, L - x_0]$ of the domain. We will fix $x_0 = 1$ from now on, to avoid any influence of the fixed boundary conditions on the calculated spatial variance. Since there are $N = (L - 2x_0)/\Delta x$ mesh points in the interval, the spatial variation of $u(t, x)$ at time t is given by

$$\sigma(t)^2 = \frac{\Delta x}{L - 2x_0 - \Delta x} \sum_{i=0}^{N-1} \left(u(t, x_0 + i\Delta x) - \overline{u(t)} \right)^2, \tag{4.5}$$

with $\overline{u(t)}$ being the current spatial mean value of u on that interval.

Now, to investigate the effect of noise on periodic travelling wave solutions, we start with a small perturbation of the homogeneous distribution $u(0) = v(0) = 0$, and then numerically solve equations (4.3) and (4.4). As in the case of the predator–prey system, noise strength is kept at zero until the deterministic long-term behaviour has fully developed. In the case of $b = 1$, travelling waves spread from the local perturbation until they cover the whole domain. Setting the noise strength to $\eta > 0$ at some time t shows that this has no effect on the periodic travelling wave shape of the solution to the λ–ω system (4.3) and (4.4). Although the noisy perturbations lead to irregular temporal fluctuations of the amplitude of the waves, the qualitative form of the solution is not affected. This observation does not depend on the noise strength, as long as η is not too high and the limit cycle of the noisy local kinetics can still be clearly identified.

Apparently, the stochastic shift in system dynamics observed in the predator–prey system cannot be reproduced in the simpler λ–ω system (4.3) and (4.4). However, clearly there is a profound difference between the stochastic limit cycle of the λ–ω system and its predator–prey counterpart. The λ–ω system is radially symmetric around the origin and so are the multiplicative coupling functions. As a consequence, the effective noise strength of the stochastic forcing does not change along the limit cycle. Since the predator–prey system is neither radially symmetric around the non-trivial equilibrium nor centred at the origin, the situation is obviously not so simple in this system. Here the effective noise strength depends on the current position on the limit cycle, in general being higher further away from the origin and smaller when population densities are small.

Luckily, a similar situation can easily be mimicked in the λ–ω system by applying a simple coordinate transformation to the deterministic reaction kinetics. The linear transformation

$$u \mapsto u - u_s = u'$$

and

$$v \mapsto v - v_s = v'$$

moves the equilibrium away from the origin to (u_s, v_s). The surrounding limit cycle is then centred on this point rather than the origin. Note that the deterministic local dynamics remains qualitatively unchanged by this coordinate transformation. However, the symmetry between the vectorfield (f_u, f_v) and the coupling functions (g_u, g_v) is broken for $(u_s, v_s) \neq (0, 0)$. The effect of
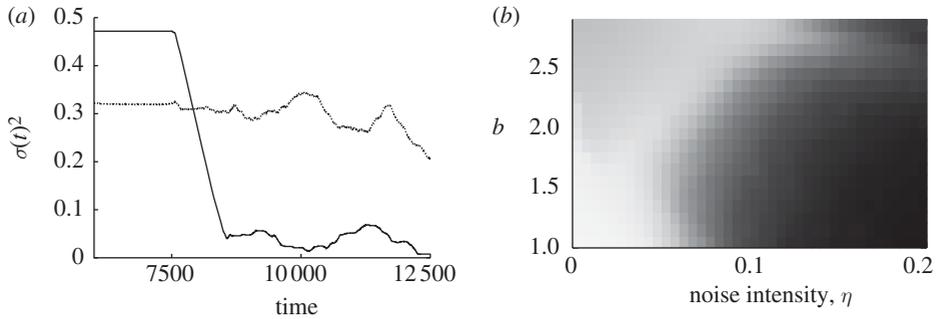
Figure 4. (*a*) Temporal evolution of the spatial variance shown for periodic travelling waves ($b = 1$, solid) and spatio-temporal chaos ($b = 2.5$, dashed), averaged over the preceding 1000 time steps. In both cases, noise is set from zero to $\eta = 0.1$ at $t = 7500$. The sharp decline in the spatial variance in the case of travelling waves is clearly visible. In contrast, spatial variance of the chaotic solution varies around its deterministic value and does not decrease significantly. (*b*) Mean spatial variance of solutions for different noise strengths and different values of the parameter b averaged over 50 000 time steps. Darker means lower spatial variance, e.g. spatially more homogeneous oscillations. Note, that solutions for $b \geq 2.5$ are chaotic rather than periodic travelling waves.

this broken symmetry is visible in the phase space diagram of the noisy system as shown in figure 1*c* for $(u_s, v_s) = (1.5, 1.5)$. Clearly, the effective noise strength is now different at different locations of the limit cycle. As in the predator–prey system, the limit cycle is more distorted now at high values of u and v, where the linear coupling functions attain higher values.

Fixing $(u_s, v_s) = (1.5, 1.5)$ and repeating the simulations as described above, the effect of noise that has been observed in the predator–prey system can then indeed be reproduced in the simpler λ–ω system. If the effective noise strength is high enough, the travelling waves observed for $b = 1$ are suppressed after a while and replaced by spatially homogeneous oscillations, as shown in figure 3*b*. These synchronized oscillations persist as long as the noise is present in the system.

Figure 4*a* shows a time lapse of the spatial variance $\sigma(t)^2$ for this case, with $\sigma(t)^2$ being averaged over the previous 1000 time steps. Prior to noise being set to $\eta = 0.1$ at $t = 7500$, the periodic travelling wave yields a constant spatial variance as expected and the immediate decline in spatial variance thereafter is clearly visible.

In contrast to periodic travelling waves for $b = 1$, for $b = 2.5$ irregular oscillations can be observed in the deterministic system. As has been shown, noise may suppress the periodic travelling waves to spatially homogeneous oscillations when the limit cycle is centred at $(1.5, 1.5)$. A natural question to ask now is what happens to spatio-temporally irregular solutions, if noise is applied to them in the same fashion as to the periodic travelling waves.

Interestingly, the chaotic dynamics observed for $b = 2.5$ proves to be more robust to noisy perturbations with noise strength $\eta = 0.1$ as shown in figure 3*c*. While the spatial variance decreases slightly in response to the stochastic forcing, the overall chaotic pattern remains. The temporal evolution of the spatial variance as shown in figure 4*a* reflects this observation. Note that if the limit cycle is centred at the origin, the qualitative behaviour of the chaotic solution is also not affected by the noise.

5. Discussion

Any model inherently is an idealization of the described natural processes. A plausible approach to account for processes that have been blinded out by this idealization is to treat them as some sort of noise. This point of view has been adopted in this paper and implies that the stochastic reaction–diffusion models presented in the previous sections provide a more complete description of the problem at hand. In many cases, a stochastic forcing may simply blur the known deterministic dynamics, giving it a more realistic appearance without actually leading to qualitatively different behaviour. However, of particular interest are results obtained from stochastic models, that indicate a significant noise-induced shift in system dynamics, that could not be anticipated from the deterministic skeleton.

This is the case for the results described above for a predator–prey model and a generic oscillatory reaction–diffusion system of λ–ω type. For the λ–ω system with the local limit cycle centred on (1.5, 1.5), an overview of the growing spatial synchronization in response to increasing noise strength is shown in figure 4*b*, displaying the mean spatial variance σ^2 for different values of the parameter b, averaged over a long time period after the noise has been switched on. Small noise below some critical noise strength has no significant effect, while suppression of travelling waves can be observed, if noise is above some critical value. With increasing b, higher noise levels are needed to suppress the travelling waves, which corresponds to the appearance of spatio-temporally irregular dynamics for these parameter values. For certain values of b, a small spatial variance is always present, even for high noise intensities. Heuristically, this robustness of the irregular oscillations seems plausbile, since they exhibit a higher spatio-temporal complexity than travelling waves and as such are not so easily suppressed to spatially homogeneous oscillations. In the light of these results, it is tempting to suggest that in natural populations spatio-temporal irregular oscillations should be observed more frequently than periodic travelling waves.

In conclusion, this indicates that periodic travelling waves as solutions to oscillatory reaction–diffusion systems are very sensitive to stochastic forcing. In particular, it has been shown that a rapidly fluctuating, highly non-periodic forcing of low intensity is able to suppress such travelling waves. The resulting spatially homogeneous oscillations resemble the limit cycle dynamics of the local reaction kinetics. This corresponds to a significant noise-induced shift in system dynamics, which is insofar a rather surprising result, as there is no corresponding shift in the stochastic local dynamics. Sample paths of the stochastic reaction kinetics still closely follow the deterministic limit cycle, as reflected by the stationary probability distributions shown in figure 1.

The apparent discrepancy between these results and the alleged travelling wave patterns in natural populations suggests at least two questions that are worth addressing in future research. The first question deals with the assumed properties of the noise process itself and the coupling functions used in the models above. This question is actually twofold, since the noise process may have a temporal as well as a spatial structure. Concerning the temporal properties, it has already been noted that despite its useful mathematical properties, temporal white noise does not correspond to any real-world process. This raises the question whether periodic travelling waves persist under the forcing of temporally autocorrelated or

coloured noise. The second part of the question concerns the spatial properties of the environmental fluctuations. The assumption of spatially invariant fluctuations certainly becomes invalid when considering large distribution areas. Even for a habitat covering a mostly homogeneous landscape, weather conditions can be expected to be significantly different at different spatial locations, if the habitat is larger than a few dozen kilometres. This leads one to impose some spatial structure on the noise process via the use of spatially non-uniform perturbations. Similar to temporal white noise, one could use noise that is white in space, which is somewhat at the other extreme compared with spatially constant noise. Not surprisingly, this does not lead to spatially homogeneous oscillations, but the travelling wave pattern is nevertheless destroyed already for small noise intensities.

The second major question concerns the fact that as indicated in the introduction, periodic travelling waves have been observed in model types other than reaction–diffusion systems. It is now natural to ask whether the travelling waves can be reproduced in appropriate stochastic variants of these models. If this is the case, this would give a hint towards which types of models may be more suitable than others to describe the travelling wave phenomenon observed in some natural populations.

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