



Quantification of the Spatial Aspect of Chaotic Dynamics in Biological and Chemical Systems

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The need to study spatio-temporal chaos in a spatially extended dynamical system which exhibits not only irregular, initial-value sensitive temporal behavior but also the formation of irregular spatial patterns, has increasingly been recognized in biological science. While the temporal aspect of chaotic dynamics is usually characterized by the dominant Lyapunov exponent, the spatial aspect can be quantified by the correlation length. In this paper, using the diffusion-reaction model of population dynamics and considering the conditions of the system stability with respect to small heterogeneous perturbations, we derive an analytical formula for an ‘intrinsic length’ which appears to be in a very good agreement with the value of the correlation length of the system. Using this formula

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and numerical simulations, we analyze the dependence of the correlation length on the system parameters. We show that our findings may lead to a new understanding of some well-known experimental and field data as well as affect the choice of an adequate model of chaotic dynamics in biological and chemical systems.

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1. INTRODUCTION

Chaos in physical, chemical, biological and ecological systems has been a focus of attention of the scientific community for more than three decades (Lorenz, 1964; May, 1976; Kuramoto, 1984; Epstein and Showalter, 1996; Rai and Schaffer, 2001). While early studies were more concerned with the temporal aspects of the dynamics of spatially homogeneous ‘well-mixed’ systems, recent results have clearly shown that the impact of space is often crucial and can hardly be neglected (de Roos *et al.*, 1991; Bascompte and Solé, 1994; Rand and Wilson, 1995; Durrett and Levin, 2000). For nonlinear dynamical systems, the interplay between space and time is far from trivial and the existence of spatial dimension(s) can change the properties of the system essentially. Particularly, in the case of spatial uniformity and continuous time, deterministic chaos is only possible if the system consists of not less than three nonlinearly interacting species. For a spatially extended system, however, the existence of chaos was reported for a two-species chemical autocatalytic system (Merkin *et al.*, 1996; Rasmussen *et al.*, 1996; Davidson, 1998) and for a two-species predator–prey system (Pascual, 1993; Sherratt *et al.*, 1995, 1997; Petrovskii and Malchow, 1999, 2001a). In both cases, chaos is obviously impossible under the condition of spatial homogeneity. The dynamics of the system becomes chaotic as a result of spontaneous homogeneity breaking and formation of distinct spatial patterns. These and other results led to the contemporary concept of spatio-temporal chaos (Kuramoto, 1984; Kaneko, 1989; Hassell *et al.*, 1991; Bascompte and Solé, 1994; Solé and Bascompte, 1995; Petrovskii and Malchow, 1999, 2001a,b; Petrovskii *et al.*, 2001; Sherratt, 2001).

In the case of spatio-temporal chaos, the population densities fluctuate or oscillate with time in an irregular, stochastic manner. Furthermore, these irregular population oscillations in different sites, i.e., positions in space appear to be uncorrelated or only slightly correlated in the case that the distance between the sites is large enough [cf. de Roos *et al.* (1991)]; as a result, the spatial distribution of the species also exhibit a distinct irregularity. The spatial aspect of the community dynamics is usually described in terms of the correlation length L_{corr} (de Roos *et al.*, 1991; Pascual and Levin, 1999; Durrett and Levin, 2000): population fluctuations in points \mathbf{r}_1 and \mathbf{r}_2 are considered as independent (uncorrelated) in the case $|\mathbf{r}_1 - \mathbf{r}_2| > L_{\text{corr}}$. Within the distance L_{corr} , the population

oscillations are correlated due to the coupling between neighboring sites (e.g., due to migration of individuals). As a result, for a 1D system with a typical size L , the whole domain appears to be ‘split’ to $N \simeq L/L_{\text{corr}}$ sub-domains so that the dynamics of each sub-domain is only slightly affected by the dynamics of the others (de Roos *et al.*, 1991; Petrovskii and Malchow, 2001a). An important consequence of this type of population dynamics is that the danger of population extinction increases when the number N of sub-domains decreases, i.e., either with an increase in L_{corr} or with a decrease in the length L of the domain (Hassell *et al.*, 1991; Allen *et al.*, 1993; Bascompte and Solé, 1994; Jansen, 1995; Petrovskii and Malchow, 2001b).

In the light of the above description, it is clear that the correlation length is a quantity of significant ecological meaning. In order to calculate L_{corr} , a variety of approaches can be used (Pascual and Levin, 1999; Durrett and Levin, 2000), for a discussion of related issues also see Rand and Wilson (1995). Perhaps the most common way is to derive the value of L_{corr} from the properties of the spatial correlation function of the population fluctuations. Under this approach, L_{corr} is defined as the distance where the promptly (exponentially) decaying correlation function either reaches its first local minimum or has its first zero (Nayfeh and Balachandran, 1995; Abarbanel, 1996). In turn, the spatial correlation function can be calculated either based on spatio-temporal data of field observations [e.g., Ranta *et al.* (1997)] or from a corresponding model of the population dynamics. However, sufficiently detailed data are rarely available and obtaining L_{corr} from a model usually takes a lot of computer simulations for each parameter set. Moreover, numerical data alone usually provide only rather limited information about the dependence of L_{corr} on the parameters.

In this paper, we consider an alternative way to estimate the value of the correlation length. Using a rather general model of population dynamics and considering the conditions of stability of the population functioning at equilibrium, we obtain a simple analytical formula for an ‘intrinsic length’ which yields a very good estimate for L_{corr} . This formula is then used along with numerical simulations to quantify the spatial aspect of the system dynamics.

The paper is organized as follows. In Section 2, we consider conditions of stability of a homogeneous equilibrium state of a diffusion-reaction system of rather general type with respect to inhomogeneous perturbations and derive the formula for the ‘intrinsic length’. In Sections 3 and 4, we consider a few particular cases of spatio-temporal chaos in biological and chemical systems and show that, in a wide parameter range, the value of the intrinsic length coincides within the order of unity with the correlation length of a given system. In the last section, we discuss the ecological relevance of our results. We also show that our results may cast certain doubts upon the capability of some widely used models (e.g., λ - ω systems) to provide an appropriate description of spatio-temporal chaos in chemical and biological systems.

2. MAIN EQUATIONS

According to a widely accepted approach, the spatio-temporal dynamics of a system of n interacting biological (Hofbauer and Sigmund, 1988; Murray, 1989) or chemical (Kuramoto, 1984; Gray and Scott, 1990) species can be described by the following equations:

$$\frac{\partial u_i(\mathbf{r}, t)}{\partial t} = D_i \nabla^2 u_i(\mathbf{r}, t) + f_i(u_1, u_2, \dots, u_n), \quad i = 1, \dots, n, \quad (1)$$

where u_i is the density of the i th species, $\mathbf{r} = (X, Y, Z)$ is the position in space, t is the time and the nonlinear functions f_i describe the local kinetics of the system. Evidently, each function f_i depends on a number of parameters (e.g., the growth rates and the mortality rates in the case of biological species), so that all possible values of the parameters form the parameter space Γ . In case equation (1) is applied to a biological or ecological system, the ‘diffusion’ coefficients D_i describe the intensity of spatial mixing of the species either as a result of the motion of the individuals (Skellam, 1951; Okubo, 1986) or due to the properties of the environment, e.g., turbulence for plankton communities (Okubo, 1980).

We assume that the form of the functions f_i provides the existence of at least one nontrivial ‘coexistence’ steady state $(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n)$ inside a certain parameter range, so that

$$f_1(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n) = f_2(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n) = \dots = f_n(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n) = 0, \quad (2)$$

where $\bar{u}_i > 0, i = 1, \dots, n$. In order to induce a nontrivial local dynamics of the system, we assume below that $n \geq 2$. It is evident that each steady state defined by equation (2) corresponds to the homogeneous stationary state of system (1).

A coexistence state can be of different types, either stable or unstable. We begin with the purely temporal stability of the spatially homogeneous system, i.e., the stability of the kinetic system. Let us consider the case when a given steady state can change its stability depending on the value of parameters. Applying the standard linear stability analysis to system (1) without diffusion term, i.e., to

$$\frac{du_i(t)}{dt} = f_i(u_1, u_2, \dots, u_n), \quad i = 1, \dots, n, \quad (3)$$

the stability of the given steady state means that all the eigenvalues of system (3) linearized in the vicinity of $(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n)$ have negative real parts. Literally, denoting $u_i(t) - \bar{u}_i = \epsilon_i(t)$, we obtain from system (3):

$$\frac{d\epsilon_i(t)}{dt} = a_{i1}\epsilon_1 + a_{i2}\epsilon_2 + \dots + a_{in}\epsilon_n, \quad i = 1, \dots, n, \quad (4)$$

where $a_{ij} = \partial f_i(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n) / \partial u_j$ are the elements of the Jacobian of the kinetic system at the steady state. Then, the eigenvalues $\lambda_i (i = 1, \dots, n)$ are given by the following equation:

$$\det(A - \lambda E) = 0, \quad (5)$$

where $A = (a_{ij})$ and E is the identity matrix. Since the coefficients a_{ij} evidently depend on a number of parameters, cf. the comments after system (1), the eigenvalues also depend on the parameter values. Loss of stability means that the real parts of some eigenvalues become positive when a point in parameter space Γ crosses a certain critical hypersurface. A particular important example of such a situation is given by the Hopf bifurcation. Thus, if we denote the maximum real part of the eigenvalues as $\bar{\lambda}$, the system becomes (linearly) unstable when $\bar{\lambda}$ becomes positive. Note that, in terms of system (1), stability of system (3) means that we consider small spatially homogeneous perturbations of the stationary homogeneous state $u_i(x, t) = \bar{u}_i, i = 1, \dots, n$.

However, the situation becomes somewhat more complicated when we consider spatially inhomogeneous perturbations. Now, $u_i(x, t) = \bar{u}_i + \epsilon_i(x, t)$ and, substituting it into (1), we obtain:

$$\frac{\partial \epsilon_i(\mathbf{r}, t)}{\partial t} = D_i \nabla^2 \epsilon_i(\mathbf{r}, t) + a_{i1} \epsilon_1 + a_{i2} \epsilon_2 + \dots + a_{in} \epsilon_n, \quad i = 1, \dots, n. \quad (6)$$

Considering a perturbation with a certain wavenumber $|\mathbf{q}|$, i.e., $\epsilon_i = C_i e^{\nu t} \cos \mathbf{q}\mathbf{r}$, $i = 1, \dots, n$, from (6) we arrive at the following system:

$$\begin{aligned} (a_{11} - \nu - D_1 \mathbf{q}^2) C_1 + a_{12} C_2 + \dots + a_{1n} C_n &= 0, \\ a_{21} C_1 + (a_{22} - \nu - D_2 \mathbf{q}^2) C_2 + \dots + a_{2n} C_n &= 0, \\ &\vdots \\ a_{n1} C_1 + a_{n2} C_2 + \dots + (a_{nn} - \nu - D_n \mathbf{q}^2) C_n &= 0. \end{aligned}$$

A nontrivial solution exists if and only if

$$\det[A - (\nu E + \mathbf{q}^2 B)] = 0 \quad (7)$$

where $B = (b_{ij}), b_{ij} = D_i \delta_{ij}$ and δ_{ij} is the Kronecker symbol. If we assume that $D_1 = \dots = D_n = D$ (the case of unequal diffusivities will be treated in Section 4), it is readily seen that equation (7) coincides with (5) provided that $\lambda = \nu + D \mathbf{q}^2$. This means that the maximum real parts of the eigenvalues of the homogeneous and inhomogeneous problems are coupled by the following equation:

$$\bar{\nu} = \bar{\lambda} - D \mathbf{q}^2 \quad (8)$$

where $\bar{\nu} = \max_{(i)} \text{Re } \nu_i$ and ν_i ($i = 1, \dots, n$) are the solutions of (7). Apparently, a stationary homogeneous distribution is linearly stable with respect to the inhomogeneous perturbation with given wavelength $l = 2\pi/|\mathbf{q}|$ if the corresponding value of ν is less than or equal to zero and unstable otherwise.

Relation (8) has a clear meaning. When the steady state $(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_n)$ becomes locally unstable due to changing parameter values, i.e., $\bar{\lambda}$ becomes positive, it still remains stable in the distributed system with respect to inhomogeneous short-wave perturbations, i.e., for

$$|\mathbf{q}| > q_0 = (\bar{\lambda}/D)^{1/2}. \quad (9)$$

From equation (9) we arrive at the following formula for the critical wavelength:

$$l_0 = 2\pi(D/\bar{\lambda})^{1/2}. \quad (10)$$

The value of l_0 may be regarded as an ‘intrinsic length’ of system (1). Note that, in order to obtain equation (10), we did not make any specific assumptions about the local kinetics of the system, e.g., about the type of the inter-specific interactions. It should also be noted that, although we referred to a specific perturbation of the homogeneous steady state to arrive at equation (10), cf. the lines above equation (6), the meaning of the ‘intrinsic length’ is not limited to that case. The ‘intrinsic length’ l_0 gives the upper limit of the system stability with respect to small spatially inhomogeneous perturbations, i.e., the perturbations with a wavelength less than l_0 are damped by diffusion. In a more general case of a perturbation containing partial waves with length less as well as greater than l_0 , one can expect as an immediate consequence of relations (9) and (10) that the homogeneous steady state will be less stable against smooth ‘small-gradient’ than against sharp ‘large-gradient’ perturbations. This prediction is in very good agreement with other recent findings (Petrovskii and Malchow, 2001a).

If the perturbation exceeds the stability limits, the system can generate chaotic spatio-temporal patterns. Although the general dynamics of system (1) remains to be investigated, the existence of such patterns was reported for a few particular biological and chemical systems (Pascual, 1993; Sherratt *et al.*, 1995; Davidson, 1998; Petrovskii and Malchow, 1999, 2001a,b; Medvinsky *et al.*, 2001; Petrovskii *et al.*, 2001; Sherratt, 2001). In this case, the temporal variation of both the local and spatially averaged values of the species densities become remarkably irregular.

In the chaotic regime, the spatial properties of system (1) can be characterized by the correlation length L_{corr} (de Roos *et al.*, 1991; Durrett and Levin, 2000; Medvinsky *et al.*, 2001; Petrovskii and Malchow, 2001a,b) which has qualitatively the same origin as the ‘intrinsic length’ l_0 : it gives the maximum distance between two positions where the diffusive coupling is still essential. Thus, the effect of diffusion is quantified by l_0 at the early stage of system dynamics and by L_{corr} at its later stage after the transients have disappeared. The assumption we are going to make now is that the information about the short-time dynamics of the system is still important in the large-time limit. [Note that, although at first sight this assumption may seem exotic, recent findings by Neubert *et al.* (2002) give another example of a link between the early and the large-time dynamics of a diffusion-reaction system.] If this is the case, one can expect that the value of l_0 is to be seen also at the chaotic regime of the system dynamics. Since both l_0 and L_{corr} are related to the same process, i.e., diffusive coupling, we make a somewhat stronger conjecture about the existence of a scaling law:

$$\frac{L_{\text{corr}}}{l_0} = c^* \quad (11)$$

where c^* is a ‘structural’ coefficient of the order of unity, its numerical value

depending on the type of the interspecific interactions but not on particular parameter values once the model is fixed.

In order to test this hypothesis, we consider below a few particular cases of system (1) where the dependence of the maximum real part of the eigenvalues $\bar{\lambda}$ on the values of system parameters can be followed explicitly and the value of L_{corr} can be obtained from the results of numerical simulations.

3. NUMERICAL RESULTS

In this section, we present the results of numerical simulations for a predator–prey system, for a system of three competitive species and for a two-species chemical system. The equations were solved numerically by finite-differences using the semi-explicit scheme when, for each time-step, the diffusion terms are approximated on the upper layer of the numerical grid and the values of reaction terms are taken from the lower layer. The values of the grid steps Δx and Δt were chosen sufficiently small in order to avoid any essential numerical artifact. Furthermore, we tested the capability of the method by comparing numerical results with some known analytical predictions (Murray, 1989).

Before proceeding to the numerical simulations, the equations must be supplemented with boundary and initial conditions. At the boundaries of the numerical domain, we used the zero-flux conditions. For the initial values, we used the ‘constant-gradient’ species distribution when the density of one of the species is given by a linear function of X and the density of other species does not depend on space. It should be mentioned here that, actually, chaotic spatio-temporal dynamics appear for a wide class of initial conditions (Sherratt *et al.*, 1995; Petrovskii and Malchow, 1999, 2001a,b) and the properties of the corresponding spatial patterns do not show any dependence on the particulars of the initial species distribution.

3.1. Predator–prey system. The dynamics of a predator–prey system can be described, after choosing an appropriate parameterization for multiplication, predation and mortality (Murray, 1989; Pascual, 1993; Holmes *et al.*, 1994; Sherratt, 2001), by the following equations:

$$\frac{\partial U}{\partial T} = D \frac{\partial^2 U}{\partial X^2} + \alpha U \left(1 - \frac{U}{b} \right) - \gamma \frac{U}{U+h} V, \quad (12)$$

$$\frac{\partial V}{\partial T} = \epsilon D \frac{\partial^2 V}{\partial X^2} + \left(\kappa \gamma \frac{U}{U+h} - \mu \right) V, \quad (13)$$

where U and V are the densities of prey and predator, respectively, at position X and time T , α stands for the maximum *per capita* growth rate of the prey, b is its carrying capacity, h is the half-saturation prey density, coefficient γ describes the

intensity of predation, κ is the coefficient of food utilization, μ is the mortality rate of the predator, and ϵ is the ratio of the diffusion coefficients of predator and prey.

By re-scaling of the variables, $u = U/b$, $v = V\gamma/(\alpha b)$, $t = \alpha T$, $x = X(\alpha/D)^{1/2}$, we arrive at the system which contains only dimensionless variables and parameters:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u) - \frac{u}{u+H}v, \quad (14)$$

$$\frac{\partial v}{\partial t} = \epsilon \frac{\partial^2 v}{\partial x^2} + k \left(\frac{u}{u+H}v - rv \right), \quad (15)$$

where $H = h/b$, $k = \kappa\gamma/\alpha$ and $r = \mu/(\kappa\gamma)$. In this section, we assume $\epsilon = 1$.

It is readily seen [cf. Petrovskii and Malchow (1999, 2001a)] that the system (14) and (15) has only one homogeneous steady coexistence state (\bar{u}, \bar{v}) where

$$\bar{u} = \frac{rH}{1-r} \quad \text{and} \quad \bar{v} = (1-\bar{u})(H+\bar{u}) \quad (16)$$

which is located in the biologically meaningful domain $u, v \geq 0$ under the restraints $r < 1$ and $H \leq (1-r)/r$. For $H < H_c(r) = (1-r)/(1+r)$, the steady state (\bar{u}, \bar{v}) becomes unstable; in this case, the only attractor in the phase plane of the corresponding homogeneous system is the stable limit cycle which appears via the Hopf bifurcation. The real part of the eigenvalues of the system linearized in the vicinity of (\bar{u}, \bar{v}) is given by the following equation:

$$\bar{\lambda} = \frac{\text{tr } A}{2} \quad \text{where } \text{tr } A = \frac{r}{1-r}[(1-r) - H(1+r)], \quad (17)$$

where A is the matrix of the linearized system. Note that, although the parameter space Γ of the system (14) and (15) is 3-dimensional, the value of $\bar{\lambda}$ [and thus the stability of the system, see equation (9)] depends only on H and r . In a sufficiently small vicinity of the Hopf bifurcation curve, $\bar{\lambda}$ increases when the point in the parameter plane (r, H) of system (14) and (15) moves further away from the Hopf bifurcation curve $H_c(r)$; what follows from rigorous mathematical considerations (Marsden and McCracken, 1976).

Figure 1 gives a summary of the spatio-temporal dynamics of the system (14) and (15) in the chaotic regime which becomes possible when the coexistence state is unstable (Pascual, 1993; Sherratt *et al.*, 1995; Petrovskii and Malchow, 1999, 2001a,b; Sherratt, 2001). While Fig. 1(a) shows a snapshot of the spatial distribution of the populations, Fig. 1(b) and 1(c) give an account of the temporal dynamics of the system in terms of local and spatially averaged values of the population densities. Figure 1(d) shows the spatial correlation function of the prey (the spatial correlation function of the predator exhibits a qualitatively similar behavior), for more details see Petrovskii and Malchow (2001a).

Once the spatial correlation function is known, the correlation length can be derived out of its properties. Here and below, we define L_{corr} as the position of its

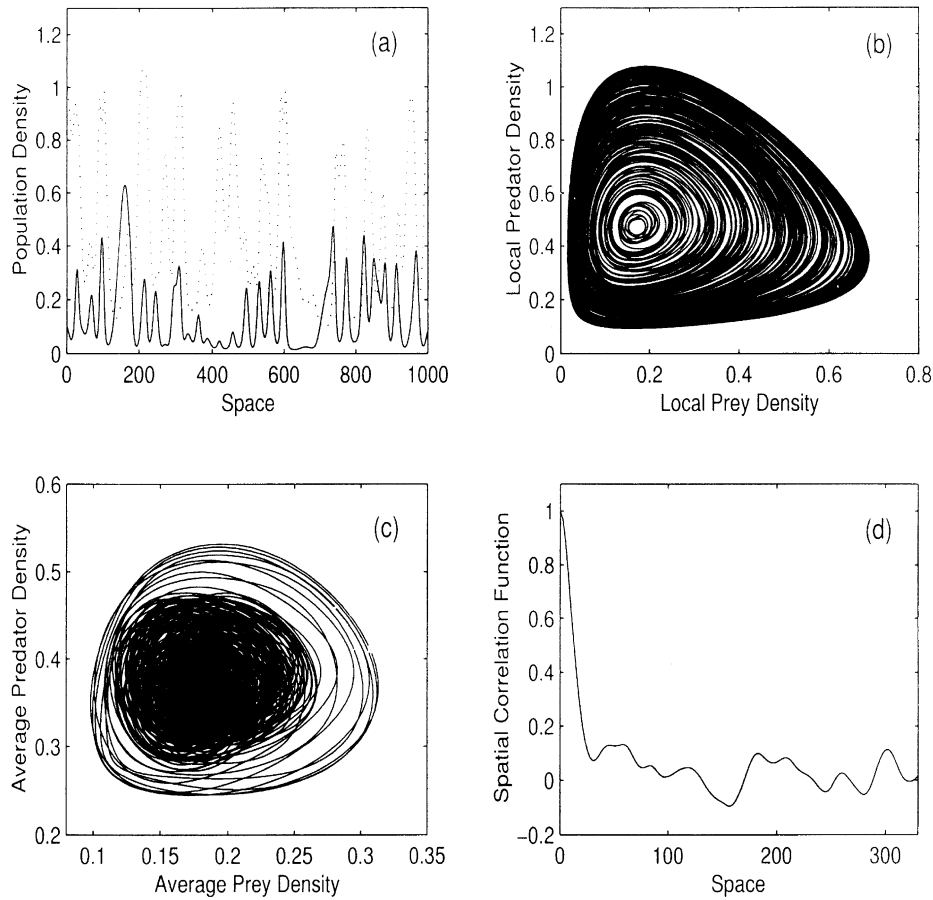


Figure 1. (a) A snapshot of the spatial distribution of the populations (solid curve for prey, dotted curve for predator) after onset of chaotic spatio-temporal oscillations in the predator-prey system (14) and (15) for parameters $k = 1.5$, $r = 0.3$, $h = 0.4$; (b) the 'local' phase plane of prey and predator densities calculated in a fixed point; (c) the phase plane of spatially averaged prey and predator densities; (d) the spatial correlation function of prey density.

first minimum (Nayfeh and Balachandran, 1995; Abarbanel, 1996). Table 1 shows the value of L_{corr} calculated for different sets of parameters as well as the value of l_0 obtained analytically from equations (10) and (17). One can see that the values of L_{corr} and l_0 are in a very good agreement in the case $\bar{\lambda}$ is sufficiently small, i.e., $\bar{\lambda} \sim 0.1$ or less, and there is a certain discrepancy for larger $\bar{\lambda}$, cf. the two lines at the bottom of Table 1.

3.2. A three-species system. Another example of a biological system showing the formation of chaotic spatio-temporal patterns is given by a community of three competitive species. For the sake of analytical simplicity, we restrict our analysis to the special case of 'cyclic competition' (May and Leonard, 1975) here.

Table 1. The (dimensionless) values of correlation and intrinsic lengths in the predator–prey system.

Parameters			$\bar{\lambda}$	l_0 (analytical)	L_{corr} (numerical)	L_{corr}/l_0
k	r	H				
2.0	0.40	0.40	0.013	54	60 ± 6	1.11
2.0	0.35	0.35	0.048	29	30 ± 3	1.03
1.5	0.30	0.40	0.039	32	33 ± 3	1.03
3.0	0.40	0.30	0.060	26	24 ± 3	0.92
2.0	0.25	0.25	0.073	23	21 ± 3	0.91
2.0	0.15	0.15	0.060	26	24 ± 3	0.92
2.0	0.05	0.05	0.024	41	39 ± 3	0.95
2.0	0.70	0.10	0.152	16	19 ± 3	1.19
2.0	0.80	0.05	0.220	13	18 ± 3	1.38

After a suitable re-scaling of the variables (Petrovskii *et al.*, 2001), the community dynamics is described by the following equations:

$$\frac{\partial u_1}{\partial t} = \frac{\partial^2 u_1}{\partial x^2} + (1 - u_1 - \alpha u_2 - \beta u_3)u_1, \quad (18)$$

$$\frac{\partial u_2}{\partial t} = \frac{\partial^2 u_2}{\partial x^2} + (1 - \beta u_1 - u_2 - \alpha u_3)u_2, \quad (19)$$

$$\frac{\partial u_3}{\partial t} = \frac{\partial^2 u_3}{\partial x^2} + (1 - \alpha u_1 - \beta u_2 - u_3)u_3. \quad (20)$$

System (18)–(20) without diffusion terms possesses a single coexistence steady state $(\bar{u}_1, \bar{u}_2, \bar{u}_3)$ where

$$\bar{u}_1 = \bar{u}_2 = \bar{u}_3 = \frac{1}{1 + \alpha + \beta}. \quad (21)$$

The maximum real part of the eigenvalues of the linearized system is given by the following formula (May and Leonard, 1975; Hofbauer and Sigmund, 1988):

$$\bar{\lambda} = \frac{1}{1 + \alpha + \beta} \left(-1 + \frac{\alpha + \beta}{2} \right). \quad (22)$$

When $\alpha + \beta > 2$, the steady state becomes locally unstable and perturbations of the homogeneous initial state can drive the system into spatio-temporal chaos (Petrovskii *et al.*, 2001). Figure 2 gives a brief account of the properties of the system dynamics in this case. Note that the structure of the phase space of system (18)–(20) is different, compared to the predator–prey system: in the case of cyclic competition, no stable limit cycle exists and the attractor is given by a heteroclinic trajectory connecting three unstable ‘one-species-only’ states $(1, 0, 0)$, $(0, 1, 0)$ and $(0, 0, 1)$, see May and Leonard (1975) and Hofbauer and Sigmund (1988) for details.

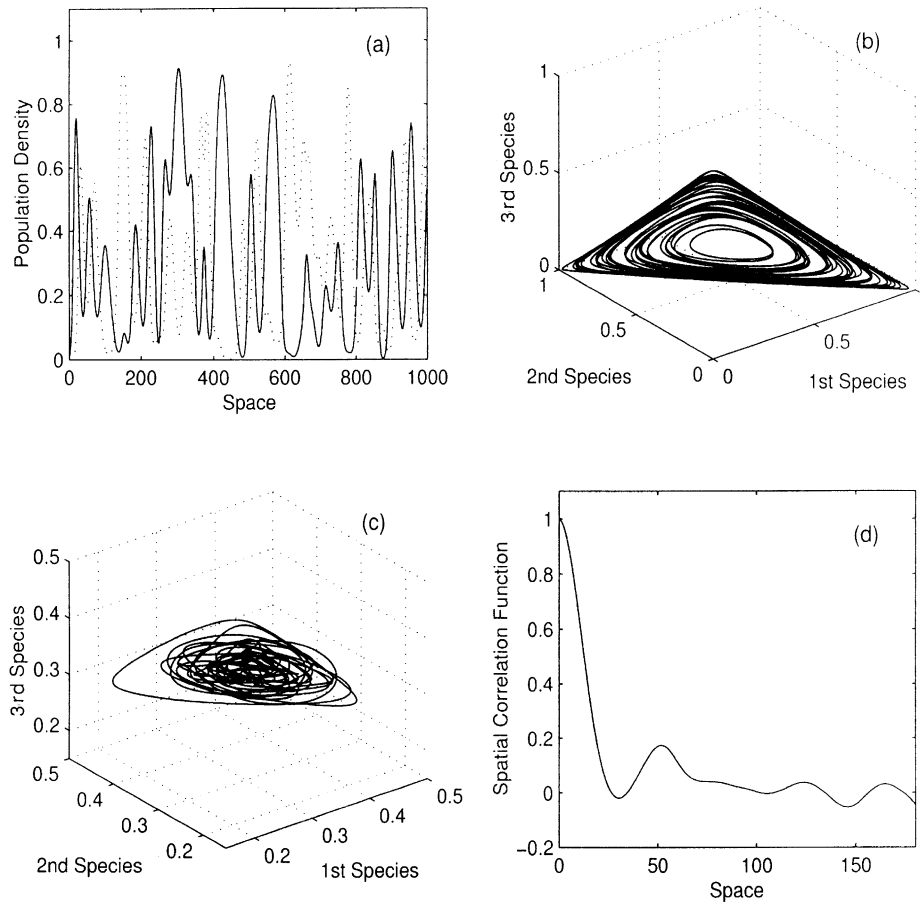


Figure 2. (a) A snapshot of the spatial distribution of the populations after onset of chaotic spatio-temporal oscillations in the system of three competitive species (18)–(20) for parameters $\alpha = 1.3$, $\beta = 0.8$ (solid curve for the first species, dotted curve for second species, the third species is not shown because it exhibits qualitatively similar behavior); (b) the trajectory of the system dynamics in the ‘local’ phase space of the system; (c) the trajectory of the system dynamics in the phase space of average densities; (d) the spatial correlation function of the first species density.

Table 2 shows the value of the correlation length L_{corr} calculated for different parameters α and β as well as the corresponding value of l_0 given by equations (10) and (22). It is readily seen that, although in this case numerical values of l_0 and L_{corr} are different, both quantities exhibit essentially the same type of dependence on the parameters because their ratio stays approximately constant (with small fluctuations within the computational error) for all checked parameter sets, cf. the right-hand column in Table 1. In particular, equation (10) apparently succeeds in predicting that the correlation length depends on the sum $\alpha + \beta$ rather than on α and β separately and that the value of L_{corr} increases when $\alpha + \beta$ tends to 2.

Table 2. Relation between the (dimensionless) values of correlation and intrinsic lengths in the three competitive species community.

Parameters		$\bar{\lambda}$	l_0 (analytical)	L_{corr} (numerical)	L_{corr}/l_0
α	β				
1.20	0.90	0.0161	49	30 ± 2	0.61
1.30	0.80	0.0161	49	30 ± 2	0.61
1.15	0.90	0.0082	69	41 ± 2	0.59
1.22	0.80	0.0033	109	65 ± 2	0.60
1.07	0.95	0.0033	109	67 ± 2	0.61
1.21	0.80	0.0017	154	93 ± 5	0.60

Due to specific properties of the system (18)–(20), it appears practically impossible to check hypothesis (11) for larger values of $\bar{\lambda}$. For parameter sets corresponding to a larger $\bar{\lambda}$, the rate of convergence of the trajectory to the heteroclinic attractor in phase space becomes very high. As a result, the time that the system spends in the vicinity of the ‘one-species-states’ increases dramatically and numerical simulations for those parameter values would demand incredibly large computer resources. Still, since even relatively small changes in the parameter values lead to a significant change of L_{corr} , the results given in Table 2 seem to provide a valuable portion of information to verify the scaling relation (11).

3.3. A two-species chemical system. The two cases considered above, although essentially different in the type of interspecific interactions, still exhibit a certain mathematical similarity; e.g., there is only one stationary coexistence state (either stable or unstable) in both cases. Meanwhile, it is well known that the existence of another steady state, particularly the existence of a saddle-point, can change the dynamics significantly (Rai and Schaffer, 2001). The interesting point is whether the applicability of equation (11) is restricted to a specific structure of the phase space of the system.

To address this issue, we consider another example now: the Gray–Scott model (Gray and Scott, 1990) of an autocatalytic reaction in an open 1D flow reactor:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + F(1 - u) - uv^2, \quad (23)$$

$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + uv^2 - (F + k)v, \quad (24)$$

with properly chosen dimensionless variables (Pearson, 1993). Now u and v are the concentrations of the substrate and the autocatalyst respectively, F is the flow rate and k is the effective rate constant of the decay of the autocatalyst.

One can readily see that, in the system (23) and (24), there are three spatially homogeneous steady states under condition $d = 1 - 4(F + k)^2/F > 0$: ‘substrate

Table 3. Relation between the dimensionless values of intrinsic and correlation lengths in the chemical autocatalytic system, cf. equation (10).

Parameters		$\bar{\lambda}$	l_0 (analytical)	L_{corr} (numerical)	L_{corr}/l_0
F	k				
0.015	0.04	0.0007	233	112 ± 4	0.48
0.024	0.05	0.0029	116	53 ± 2	0.46
0.019	0.045	0.0018	148	70 ± 2	0.47
0.0145	0.04	0.0020	139	67 ± 2	0.48
0.0083	0.03	0.0011	194	91 ± 3	0.47

only' $(1, 0)$, 'substrate dominated' (u_s, v_s) , and 'autocatalyst dominated' (u_a, v_a) where

$$u_s = \frac{1 + \sqrt{d}}{2}, \quad v_s = \left(\frac{F}{F+k} \right) \frac{1 - \sqrt{d}}{2}, \quad (25)$$

$$u_a = \frac{1 - \sqrt{d}}{2}, \quad v_a = \left(\frac{F}{F+k} \right) \frac{1 + \sqrt{d}}{2}. \quad (26)$$

When crossing the critical curve $d = 0$ in the (k, F) -plane towards smaller values of k , the two nontrivial states appear through a saddle-node bifurcation, the 'autocatalyst dominated' state being an unstable node.

The 'substrate only' state is always a stable node and the 'substrate dominated' state is always a saddle-point. A change in the local dynamics can be associated with the change of the type of the 'autocatalyst dominated' state, first of all, with the change of its stability. It is straightforward to see that the maximum real part of the eigenvalues of the Jacobian evaluated at the 'autocatalyst dominated' state is given by the following equation:

$$\bar{\lambda} = \frac{1}{2}(k - v_a^2). \quad (27)$$

The change of stability takes place when $\bar{\lambda} = 0$ which, after a little algebra, takes the following form:

$$\frac{k - F}{k + F} = \sqrt{d}. \quad (28)$$

The Hopf bifurcation that takes place when crossing the curve (28) is predicted to be supercritical for $k < k_{cr}$ (where k_{cr} is estimated as about 0.035), and only in this case a stable limit cycle appears (Rasmussen *et al.*, 1996). Otherwise, no limit cycle arises and any trajectory starting in the vicinity of the 'autocatalyst dominated' state after a number of expanding convolutions is finally attracted to the 'substrate only' state. Thus, the structure of the local phase plane of the Gray–Scott model is essentially different from the predator–prey system (14) and (15).

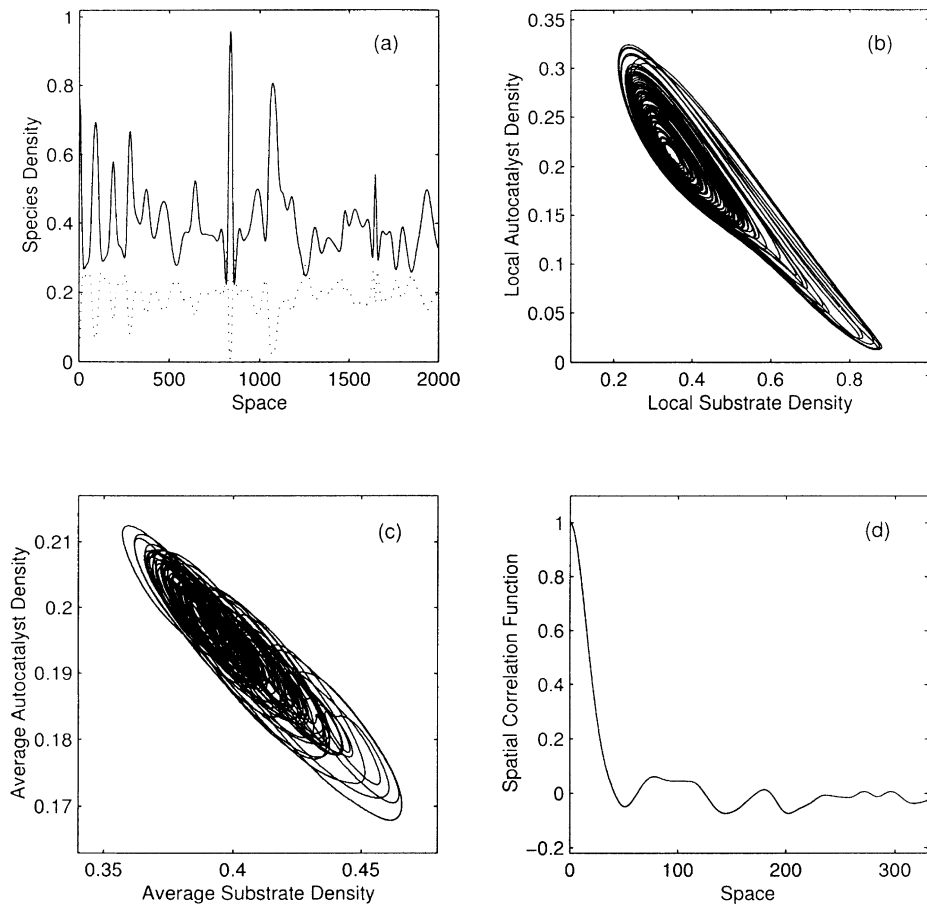


Figure 3. (a) A snapshot of the spatial distribution of the chemical species (solid curve for substrate, dotted curve for autocatalyst) after onset of chaotic spatio-temporal oscillations in the Gray–Scott model of an autocatalytic reaction, cf. equations (23) and (24), for parameters $F = 0.024$, $k = 0.05$; (b) the ‘local’ phase plane of the substrate–autocatalyst system; (c) the phase plane of spatially averaged species densities; (d) the spatial correlation function of the substrate density.

It was shown by Merkin *et al.* (1996) and Davidson (1998) that, for those parameter values when the ‘autocatalyst dominated’ state is unstable, the system (23) and (24) can exhibit spatio-temporal chaos. Figure 3 gives a brief account of the properties of the system dynamics in this case. Apparently, in the chaotic regime the spatial and temporal behavior of the reacting species is qualitatively similar to the behavior of the biological species, cf. Figs 1 and 3. Thus, although our main interest is focused on the dynamics of biological communities, the model (23) and (24) can be used for testing the hypothesis (11). Table 3 shows the value of L_{corr} obtained in our numerical simulations as well as the intrinsic length l_0 . Again, one can see the very good agreement between these two quantities up to an approximately constant factor on the order of unity.

As in the previous case, the properties of the system do not allow us to check hypothesis (11) for a wider parameter range. One can expect the formation of chaotic spatio-temporal patterns for such parameter values where the ‘autocatalyst dominated’ state exists and is unstable; the results of numerical simulations show that the actual parameter range is somewhat more narrow. However, the whole domain in the parameter (k, F) -plane where the structure of the phase plane is as described consists of a narrow strip located between $k = 0$ and $k \approx 0.06$ (Malchow and Petrovskii, 2002). Correspondingly, taking into account equation (10), $\bar{\lambda}$ is bounded in that domain so that the least upper bound appears to be on the order of 0.01.

4. A TWO-SPECIES SYSTEM WITH UNEQUAL DIFFUSIVITIES

Another interesting point is whether the above analysis can be extended to the case of unequal diffusivities. Since in this case an analytical treatment of the general n -species system appears to be very difficult, we restrict our consideration to a particular case of a two-species system.

Equation (7) now takes the following form:

$$\begin{vmatrix} a_{11} - v - D_1 \mathbf{q}^2 & a_{12} \\ a_{21} & a_{22} - v - D_2 \mathbf{q}^2 \end{vmatrix} = 0 \quad (29)$$

which is equivalent to

$$v^2 - \gamma v + \phi = 0 \quad (30)$$

where

$$\gamma = \text{tr } A - (D_1 + D_2) \mathbf{q}^2, \quad \phi = D_1 D_2 \mathbf{q}^4 - (a_{22} D_1 + a_{11} D_2) \mathbf{q}^2 + \det A. \quad (31)$$

Thus, since

$$v = \frac{1}{2} \left(\gamma \pm \sqrt{\gamma^2 - 4\phi} \right), \quad (32)$$

the homogeneous state of the system is linearly stable with respect to an inhomogeneous perturbation with wavelength $|\mathbf{q}|$ when $\gamma < 0$ and $\phi > 0$.

The results of further analysis depend on the sign of the following value:

$$\Delta = (a_{22} D_1 + a_{11} D_2)^2 - 4 D_1 D_2 \det A. \quad (33)$$

It is readily seen that the inequality $\phi > 0$ holds identically when $\Delta < 0$. In this case, the critical value q_{01} is given by the following equation:

$$\gamma = \text{tr } A - (D_1 + D_2) q_{01}^2 = 0, \quad (34)$$

Table 4. The dimensionless values of correlation and intrinsic lengths in the predator–prey system with unequal diffusivities for parameters $k = 2.0$, $r = H = 0.30$.

$\epsilon = D_2/D_1$	l_0 (analytical)	L_{corr} (numerical)	L_{corr}/l_0
0.1	18	17 ± 5	0.94
0.5	21	19 ± 5	0.90
1.0	24	24 ± 3	1.00
2.0	30	30 ± 3	1.00
5.0	42	42 ± 3	1.00
10.0	57	55 ± 5	0.96

so that $q_{01} = (\text{tr } A / (D_1 + D_2))^{1/2}$. Note that, in the case $D_1 = D_2$, Δ would be negative if and only if the steady state is a focus. In the case $D_1 \neq D_2$, however, the sign of Δ is not strictly related to the type of the steady state.

Since the steady state is assumed to be locally unstable, it holds $\text{tr } A > 0$. Taking into account that in a two-species system $\text{tr } A = 2\bar{\lambda}$, we arrive at the following equation for the critical wavenumber:

$$q_{01} = \left(\frac{\bar{\lambda}}{\langle D \rangle} \right)^{1/2} \quad \text{where } \langle D \rangle = \frac{D_1 + D_2}{2}. \quad (35)$$

Now let us consider the case $\Delta \geq 0$. In the case $\gamma > 0$ (which is equivalent to $|\mathbf{q}| < q_{01}$), $\max \text{Re } \nu_{1,2}$ is apparently positive. In the case $\gamma \leq 0$, the critical wavenumber is given by the equation $\phi = 0$ from which we obtain:

$$q_{02} = \left[\frac{(a_{22}D_1 + a_{11}D_2) + \sqrt{\Delta}}{2D_1D_2} \right]^{1/2}, \quad (36)$$

assuming that the numerator in square brackets is not negative. Thus, the homogeneous steady state appears to be stable with respect to small inhomogeneous perturbations with wavenumbers $|\mathbf{q}| > q_0$ where

$$q_0 = \max\{q_{01}, q_{02}\}. \quad (37)$$

In case parameter values are such that q_{02} does not exist [e.g., the numerator in (36) is negative], equation (37) is reduced to $q_0 = q_{01}$. It is readily seen that equation (37) coincides with (9) for $D_1 = D_2$.

Equations (10) and (37) give the value of the ‘intrinsic length’ l_0 for a two-species system with unequal diffusivities. However, whether hypothesis (11) about the relation between L_{corr} and l_0 remains true in this case is yet to be checked. To run computer experiments, we choose the predator–prey system (14) and (15) where ϵ can now be an arbitrary positive number. The results are shown in Table 4. As well as in the previous cases, one can see that hypothesis (11) is in very good agreement with numerical results.

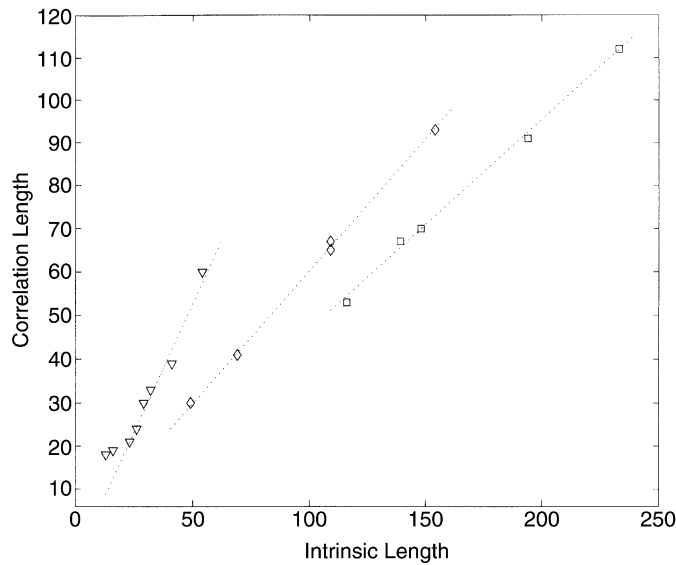


Figure 4. Numerically calculated correlation length L_{corr} plotted vs. intrinsic length l_0 for different systems: triangles for the predator–prey system, diamonds for the three competitive species system, squares for the substrate–autocatalyst system.

5. DISCUSSION AND CONCLUSIONS

The results of our numerical simulations of chaotic spatio-temporal dynamics in different systems show that hypothesis (11) about the relation between the intrinsic length l_0 and the correlation length L_{corr} of the system is valid in a wide parameter range, see Fig. 4. An immediate consequence of this conclusion is that the following equation can be used in order to estimate the value of L_{corr} :

$$L_{\text{corr}} = c^* l_0 \quad (38)$$

where l_0 is given by equation (10) and c^* is approximately constant, $c^* \approx 1$ for the predator–prey system, $c^* \approx 0.6$ for the system of three competitive species and $c^* \approx 0.47$ for the autocatalytic chemical system. In particular, we want to mention that equation (38) predicts an infinite growth of L_{corr} for parameters approaching their critical value when the coexistence state becomes stable. This is in good agreement with our numerical results, cf. Tables 1–3 and Fig. 4. However, there is a certain discrepancy between L_{corr} and l_0 that is not described by the linear relation (11) in the parameter range where $\bar{\lambda}$ becomes sufficiently large (correspondingly, L_{corr} sufficiently small). It may indicate that, in reality, c^* is a function of the system parameters with scaling properties so that $c^* \approx \text{const} \neq 0$ for $\bar{\lambda} \ll 1$.

It should be noted that the existence of a correlation length in a community of interacting species has important implications. In the diffusion-reaction system (1), spatio-temporal chaos, with its endogenous property of forming irregular uncorrelated spatial patterns, cannot be observed if the length of the

system is less than L_{corr} because in this case the species oscillations at all different sites are correlated due to diffusive coupling. (Note that this remark does not exclude a possibility of purely temporal chaos which can take place in a spatially homogeneous time-continuous system with three or more interacting species.) This prediction is in full coincidence with the results of our computer simulations. Since spatio-temporal chaos is shown to decrease the risk of population extinction (de Roos *et al.*, 1991; Hassell *et al.*, 1991; Allen *et al.*, 1993; Bascompte and Solé, 1994; Jansen, 1995; Petrovskii and Malchow, 2001b), the above conclusion may provide a new explanation of well-known experimental results [e.g., Luckinbill (1974)] when a predator–prey system goes extinct in a small domain but appears to be persistent in a larger domain.

In our study, we have used only purely deterministic models of population dynamics. That may raise certain doubts concerning the ecological relevance of our results since the actual dynamics of any community of interacting biological species arises from the interplay between various deterministic and stochastic factors. However, the relative importance of these factors remains obscure. Moreover, as has been shown recently by Malchow *et al.* (2002), there may exist a critical level of environmental noise so that the functioning of the systems with subcritical stochasticity is mainly controlled by deterministic processes.

Our results may also cast a new light on the long-standing enigma such as the ‘biological scale’ in the plankton dynamics. It is well known that while on a small scale (less than one hundred meters) and a large scale (more than a few dozens of kilometers) the spatial horizontal distribution of plankton in marine ecosystems is mainly controlled by the properties of the environment (Platt, 1972; Denman, 1976), on an intermediate scale the properties of the plankton spatial distribution are significantly modified by the biological interactions in the plankton community (Powell *et al.*, 1975; Weber *et al.*, 1986; Levin, 1990). The lower bound of this scale is called the KISS length, its origin is well understood and its value has been calculated consistently from a few different approaches. However, the origin of the upper bound remains a mystery.

In order to address this issue, we can apply the results obtained above for the predator–prey system. Such an approach is justified by the following two reasons. Firstly, it is widely accepted that the main biological phenomena affecting plankton dynamics are population growth and zooplankton grazing on phytoplankton. Secondly, although conclusive evidence is still lacking, there is a growing number of indications of chaos in the dynamics of ecological communities, see Medvinsky *et al.* (2001) for a review and an extended list of references. Thus, assuming that plankton dynamics is actually chaotic, the spatio-temporal patterns obtained in the predator–prey system (14) and (15) can be associated with the plankton patterns on the biological scale, its upper bound then being given by the correlation length.

In order to calculate L_{corr} , we use equations (10), (17) and (38). Referring to the parameter estimates provided by different authors (Nisbet *et al.*, 1991;

Truscott and Brindley, 1994; Sherratt, 2001), we choose the typical values $\alpha = 1.0 \text{ day}^{-1}$, $\gamma = 0.7 \text{ day}^{-1}$, $\mu = 0.05 \text{ day}^{-1}$, $\kappa = 0.15$, $h/b = 0.3$ [see the comments below equations (12) and (13)]. The turbulent diffusivity is roughly estimated as $D = 10^5 \text{ cm}^2 \text{ s}^{-1}$ (Nihoul, 1980). Using these values, we arrive at $L_{\text{corr}} \approx 30 \text{ km}$ which is in a very good agreement with the results of field observations (Weber *et al.*, 1986; Levin, 1990). Note that, since the value (dimensionless) of l_0 remains of the same order within a certain parameter range, see Table 1, this agreement is not violated by a reasonably small variation of parameter values.

A more general implication of our results concerns the choice of an adequate model to describe deterministic chaos. Namely, by now many theoretical results concerning spatio-temporal chaos in a system of interacting chemical and/or biological species have been obtained in terms of so-called λ - ω systems (the complex-variable analogue of the λ - ω systems is also known as the Ginzburg–Landau equation), cf. Kopell and Howard (1973), Kuramoto (1984), Bohr *et al.* (1998), Sherratt (2001) and the references therein. Briefly, a λ - ω system appears as the first-order approximation of a general diffusion-reaction system considering the size of the limit cycle as a small parameter. An advantage of this approach is that λ - ω systems often appear to be mathematically much simpler than the original diffusion-reaction systems, especially in the case when the original system consists of many species. The λ - ω systems are valid for parameter values near the Hopf bifurcation but there is also a strong opinion that they provide an adequate description of the dynamics of the corresponding diffusion-reaction systems in a much wider parameter range. Our results, however, seem to indicate that spatio-temporal chaos in the λ - ω systems is just a mathematical artifact without any clear relation to reality. It clearly follows from equations (10) and (38) as well as from the numerical simulations, see Tables 1 to 3, that the value of L_{corr} grows to infinity in the vicinity of the Hopf bifurcation. It means that, for corresponding parameter values, in any spatially bounded system (which is always the case for real biological or chemical systems) its size L appears to be less than the value of the correlation length in the system. That makes the existence of chaos impossible exactly in that parameter region where the λ - ω system is formally valid. This intrinsic contradiction might explain why the approach based on the λ - ω systems fails to describe the type of population dynamics correctly [cf. Sherratt (2001)], predicting spatio-temporal chaos for those cases where field observations report regular patterns.

In conclusion, we want to mention that our study leaves a few questions open. Firstly, it remains unclear how to calculate analytically the value of the structural coefficient c^* . Secondly, it will be interesting to see whether our analysis can be applied to the case when the diffusion coefficients are not constant, e.g., vary in space or are density dependent. Finally, an important question is how our results can be modified when stochastic factors are taken into account. These issues outline the direction of future research.

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