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Pattern formation in reaction diffusion systems: a Galerkin model

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Abstract. Reaction diffusion systems are extremely useful for studying pattern formation in biological systems. We carry out a Lorenz like few mode truncation of a reaction diffusion system and show that it not only gives the same qualitative behaviour as the more complicated systems but also indicates of the existence of a Hopf-bifurcation in the turing region.

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1 Introduction

It was first suggested by Turing that interaction of two substances A and B with differing diffusivities can cause pattern formation. The two important features in pattern formation are local self enhancement and long range inhibition. Self enhancement amplifies small local inhomogeneities. If a small increase of A beyond its homogeneous steady state value causes further increase of A then A is self enhancing. However self enhancement alone can not produce stable pattern. For a stable pattern an overall increase of A due to the positive feedback has to be checked. This is done by having a fast diffusing antagonist B which prevents the spread of the self enhancing reaction. A host of different kinds of reaction-diffusion pattern generation and transition between these patterned states are being given attention to these days [1,2]. The two species A and B constitute a reaction diffusion system. A much studied model [3] is

$$\frac{\partial A}{\partial t} = D\nabla^2 A + \frac{A^2}{B} - A + \sigma \tag{1}$$

$$\frac{\partial B}{\partial t} = \nabla^2 B + \mu (A^2 - B) \tag{2}$$

where σ is the rate of production of species A and μ is the rate of removal of B through interaction. The diffusivity D is much smaller than unity.

The general procedure for studying such systems has been a linear stability analysis on the basic homogeneous steady state followed by numerical integration. The phase diagram obtained in this fashion is shown in Figure 1. The boundary marked '1' separates a steady homogeneous state from a steady patterned state while the boundary marked '2' separates the homogeneous steady state from a homogeneous time periodic state. These boundaries come from a linear stability analysis. Numerical analysis gives

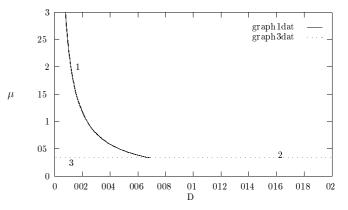


Fig. 1. Phase diagram that comes from the linear stability analysis of equations (1) and (2). The boundary marked '1' and that marked '3' encloses a steady patterned state, the boundary '1' separates the steady patterned state from steady homogeneous state and the boundary '2' separates the steady homogeneous state from an oscillatory homogeneous state.

the region marked '3' where one has a time dependent patterned state. Analytic treatment of the nonlinear states has not been done as yet. Our emphasis here has been on showing the very crucial Hopf bifurcation over a Turing region. This Hopf-Turing [4] mixed mode region is of much importance because of the phase instability that subsequently developed to render the system chaotic, characterised by a comparatively higher dimensional attractor [5,6]. In a different field, where pattern formation [7] is common - namely hydrodynamic instabilities - various theoretical techniques have been used to analyse the nonlinear state. These can be generally classified into two categories a) amplitude equation [8] and b) Galerkin models [9]. The latter involves replacing the partial differential equation by a few judiciously chosen ordinary differential equations and led to the study of Lorenz model [10]

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which had a strong impact on the field of nonlinear dynamics. In this paper our aim will be to write a Lorenz like model for the reaction diffusion system. Analysis of the model along the standard lines, then shows a phase diagram which is similar to the one shown in Figure 1. Consequently, we believe that low order Galerkin models can be a useful tool for discussing pattern formation in reaction diffusion systems. In Section 2, we discuss the simplest situation namely the pattern formation in onedimensional systems. The success in one dimension leads us to consider the two-dimensional situation in Section 3. In this case, on the basis of a truncation, we actually predict that by varying a parameter, a transition can occur between different patterns.

2 One-dimensional system

In setting up our Galerkin model, we would keep the number of modes at a minimum. For a dynamical system, interesting behaviour obtains for dimension greater than two [11]. Consequently, if a three mode truncation is done, then it will be capable of exhibiting nontrivial dynamics. This is precisely the lesson of Lorenz model. We expand

$$A(x,t) = A_0(t) + A_1(t)\cos(kx) B(x,t) = B_0(t) + B_1(t)\cos(kx).$$
(3)

The variable A is slowly diffusing which implies that $D \ll 1$. The modes A_0 and A_1 decay with approximately the same time constant if they were acting alone. For the modes B_0 and B_1 on the other hand, B_1 is a fast decaying mode compared to B_0 , for small values of μ and not so small value of k. In this situation, one can drop the mode B_1 and have a three mode truncation – the simplest situation which can lead to complicated behaviour. It should be noted that the wave number k is a constant parameter with above truncation. Matching Fourier coefficients on either side of equations (1) and (2) with the modes of equation (3) we have

$$\dot{A}_{0} = -A_{0} + \frac{A_{0}^{2}}{B_{0}} + \frac{A_{1}^{2}}{2B_{0}} + \sigma$$
$$\dot{A}_{1} = -(1 + Dk^{2})A_{1} + \frac{2A_{0}A_{1}}{B_{0}}$$
$$\dot{B}_{0} = -\mu B_{0} + \mu A_{0}^{2} + \mu \frac{A_{1}^{2}}{2} \cdot$$
(4)

We now need to look at the fixed points: 1) $A_1 = 0$, $A_0^2 = B_0$, $A_0 = 1 + \sigma$. This is the steady homogeneous phase, 2) $A_0 = 1 + \sigma$, $B_0 = 2\frac{1+\sigma}{1+Dk^2}$, $\frac{A_1^2}{2} = \left[\frac{2}{1+Dk^2} - (1+\sigma)\right](1+\sigma)$. This fixed point exists for $\frac{1-Dk^2}{1+Dk^2} > \sigma$ and corresponds to a steady patterned state. These are the two basic states in the system, captured correctly by the truncated system. We first look at the stability analysis of the steady

homogeneous state

$$\delta \dot{A}_{0} = -\delta A_{0} \left(1 - \frac{2A_{0}}{B_{0}} \right) - \frac{\delta B_{0}}{(1+\sigma)^{2}}$$

$$\delta \dot{B}_{0} = -\mu \delta B_{0} + 2\mu A_{0} \delta A_{0}$$

$$\delta \dot{A}_{1} = \left(-[1+Dk^{2}] + \frac{2}{1+\sigma} \right) \delta A_{1}.$$
 (5)

Instability in the independent subspace of A_1 corresponding to the zero relaxation rate sets in for $\frac{1-Dk^2}{1+Dk^2} > \sigma$, which is the same as for the existence of A_1^2 . Since the above condition for instability can be rewritten as $Dk^2 < \frac{1-\sigma}{1+\sigma}$, we will henceforth treat the wave number as one of the constant parameters along with the reaction rate μ . We now look for possible Hopf bifurcation of the basic steady state. For this we need to keep $Dk^2 > \frac{1-\sigma}{1+\sigma}$, so that the mode A_1 is a decaying mode and we look for the relaxation rate p of the fluctuations δA_0 and δB_0 . Clearly the growth rate p can be found from

$$p^{2} + p\left[1 + \mu - \frac{2}{1 + \sigma}\right] + \mu = 0.$$
 (6)

The roots are complex if $\frac{2}{1+\sigma} > (1-\sqrt{\mu})^2$, an inequality which is satisfied for $\sigma < 1$ and $\mu < 1$. The real part of p vanishes if

$$\mu = \mu_{\rm c} = \frac{1 - \sigma}{1 + \sigma} \tag{7}$$

and fluctuations grow if $\mu < \mu_c$. In the $\mu - Dk^2$ plane, the instability boundary has the structure shown in Figure 2a.

The phase boundaries shown in Figure 1 are qualitatively the same as that found. Having established the credibility of the truncated model, we now explore the stability of the patterned steady state against a Hopf bifurcation. This is what is achievable easily in the truncated model, but difficult to sort out in the full differential equation. To do this we write $A_0 = 1 + \sigma + \delta \tilde{A}_0$, $B_0 = \frac{2(1+\sigma)}{1+Dk^2} + \delta \tilde{B}_0$ and $A_1 = \tilde{A}_1 + \delta \tilde{A}_1$, where $\tilde{A}_1 = 2\sqrt{\left(\frac{1}{1+Dk^2} - \frac{1+\sigma}{2}\right)(1+\sigma)}$.

Linearising the equation of motions for $\delta \tilde{A}_0, \delta \tilde{A}_1$ and $\delta \tilde{B}_0$ in equation (4), we get

$$\delta \dot{\tilde{A}}_{0} = Dk^{2} \delta \tilde{A}_{0} - \delta \tilde{B}_{0} \frac{1 + Dk^{2}}{2(1 + \sigma)} + \frac{\tilde{A}_{1}(1 + Dk^{2})}{2(1 + \sigma)} \delta A_{1}$$

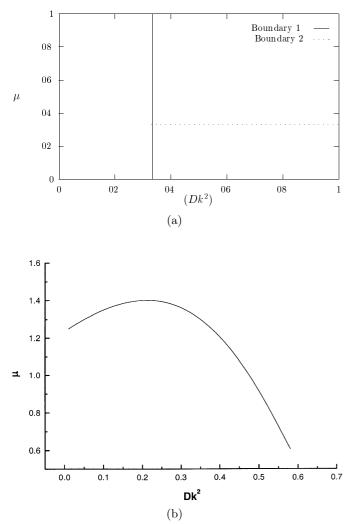
$$\delta \dot{\tilde{B}}_{0} = -\mu \delta \tilde{B}_{0} + 2\mu (1 + \sigma) \delta \tilde{A}_{0} + \mu \tilde{A}_{1} \delta \tilde{A}_{1}$$

$$\delta \dot{\tilde{A}}_{1} = \frac{\tilde{A}_{1}(1 + Dk^{2})}{1 + \sigma} \delta \tilde{A}_{0} - \frac{\tilde{A}_{1}(1 + Dk^{2})^{2}}{2(1 + \sigma)} \delta \tilde{B}_{0}.$$
(8)

The growth rate p now satisfies

$$p^{3} + p^{2}(\mu - Dk^{2}) + p\left(\mu + \frac{\mu \tilde{A}_{1}^{2}(1 + Dk^{2})^{2}}{2(1 + \sigma)} - \frac{\tilde{A}_{1}^{2}(1 + Dk^{2})^{2}}{2(1 + \sigma)^{2}}\right) + \frac{\mu \tilde{A}_{1}^{2}(1 + Dk^{2})^{2}}{2(1 + \sigma)} = 0.$$
(9)

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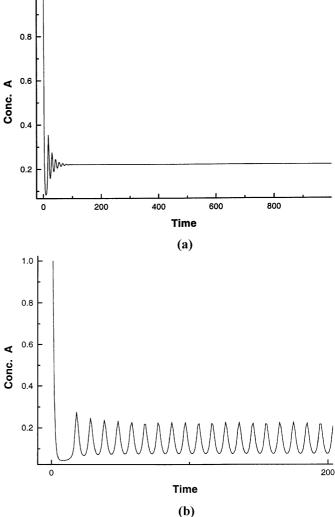


Fig. 2. (a) Phase diagram that comes from the stability analysis of equation (5). The boundary '1' is the zero instability boundary, on the right hand side of which A_1 exists. The boundary '2' is another instability boundary at $\mu = \mu_c$ below which the temporal instability grows. (b) The Hopf bifurcation boundary obtained from equation (10) for $\sigma = 0.5$. In the μ_0 - Dk^2 plane the region below the graph there is a steady patterned state and above it there is an oscillatory patterned state.

A Hopf bifurcation occurs for $\mu = \mu_0$ which for a particular σ is given by

$$\frac{\mu_0 \tilde{A_1}^2 (1+Dk^2)^2}{2(1+\sigma)} = (\mu_0 - Dk^2) \left(\mu_0 + \frac{\mu_0 \tilde{A_1}^2 (1+Dk^2)^2}{2(1+\sigma)} - \frac{\tilde{A_1}^2 (1+Dk^2)^2}{2(1+\sigma)^2} \right).$$
(10)

We show the boundary for $\sigma = 1/2$ in the $\mu - Dk^2$ plane in Figure 2b. A numerical integration of the actual model

Fig. 3. (a) Time series for the activator concentration A obtained by time integrating the actual model for $Dk^2 = 0.35$, $\mu = 0.5$ and $\sigma = 0.5$. (b) Time series for the activator concentration A obtained by time integrating the actual model for $Dk^2 = 0.35$, $\mu = 0.9$ and $\sigma = 0.5$. Here we see that the patterned state is oscillating.

(Eq. (1) and Eq. (2)) for a range of Dk^2 values and σ values shows a Hopf bifurcation to occur at a $\mu > \mu_0$. In Figure 3a the time series shows the existence of a fixed point at $Dk^2 = 0.35$, $\mu = 0.5$ (which is greater than μ_0) and $\sigma = 0.5$. Figure 3b shows the oscillating time series for $\mu = 0.9$ and Dk^2 , σ set at the same values as in Figure 3a. Therefore it is clear from Figure 3b that a Hopf bifurcation occurs at some μ value within 0.5 and 0.9.

For $\mu > \mu_0$, we should have a patterned oscillatory state, is also evident from the study of the nature of the roots of equation (9). Now, is this limit cycle stable? The truncated system allows us an analytic handling of this question as well. To see how this works we write equation (4) in terms of shifted variables X, Y, Z defined as

$$A_{0} = 1 + \sigma + X$$

$$B_{0} = \frac{2(1 + \sigma)}{1 + Dk^{2}} + Y$$

$$A_{1} = \tilde{A}_{1} + Z.$$
 (11)

In terms of X, Y, Z, we can write equation (4) as

$$L\begin{pmatrix} X\\ Y\\ Z \end{pmatrix} = \begin{pmatrix} \frac{\frac{2(1+\sigma)}{1+Dk^2} \left(X^2 + \frac{Z^2}{2}\right) - 2(1+\sigma)XY - \tilde{A}_1YZ + Y^2}{\frac{2(1+\sigma)}{1+Dk^2} \left[\frac{2(1+\sigma)}{1+Dk^2} + Y\right]} \\ \mu \left(X^2 + \frac{Z^2}{2}\right) \\ \frac{\frac{(1+\sigma)}{1+Dk^2}XZ - (1+\sigma)ZY - \tilde{A}_1YX + \frac{\tilde{A}_1}{2}(1+Dk^2)Y^2}{\frac{(1+\sigma)}{1+Dk^2} \left[\frac{2(1+\sigma)}{1+Dk^2} + Y\right]} \end{pmatrix}$$
(12)

where L is the linear operator

$$L = \begin{pmatrix} \frac{\partial}{\partial t} - Dk^2 & \frac{1+Dk^2}{2(1+\sigma)} & \frac{\tilde{A}_1(1+Dk^2)}{2(1+\sigma)} \\ -2\mu(1+\sigma) & \frac{\partial}{\partial t} + \mu & \mu\tilde{A}_1 \\ \frac{\tilde{A}_1(1+Dk^2)}{(1+\sigma)} & \frac{(1+Dk^2)^2}{2(1+\sigma)} & \frac{\partial}{\partial t} \end{pmatrix}.$$
 (13)

For $\mu = \mu_0$ (Eq. (10)), L has a eigenvector of the form

 $\begin{pmatrix} X_0 \\ Y_0 \\ Z_0 \end{pmatrix} \exp(\mathrm{i}\omega t).$ For $\mu \simeq \mu_0$, we ask the question whether

a limit cycle solution of the form

$$\begin{pmatrix} X \\ Y \\ Z \end{pmatrix} = A(T) \begin{pmatrix} X_0 \\ Y_0 \\ Z_0 \end{pmatrix} \exp(\mathrm{i}\omega t)$$
(14)

where A(T) is a slowly varying function, exists. With the dynamics governed by equations (12) and (13), standard techniques (multiple scale perturbation theory) leads to an amplitude equation

$$\frac{\mathrm{d}A}{\mathrm{d}t} = (\mu_0 - \mu)A - f(\mu_0, Dk^2, \sigma)A^3$$
(15)

where $f(\mu_0, Dk^2, \sigma)$ is a complicated function which one finds can be both of positive and negative values. For positive value of f, the limit cycle is stabilized, while for negative value of f, the state for $\mu < \mu_0$, shows complicated time dependence. This is entirely consistent with the findings reported by Koch and Meinhardt. In conclusions we have shown that the very complicated problem of pattern formation can be profitably studied via a Galerkin transformation and there is also a new result in the form of a Hopf bifurcation in a region where linear stability analysis predicts a steady patterned state. As in the field of hydrodynamic instabilities, this could be a very effective way of studying pattern forming instabilities.

3 Two-dimensional system

Having noted that the severe truncation of the partial differential equations governing the reaction diffusion system in one dimension gives results in qualitative agreement with the numerical integration, we carry this procedure one step further and investigate the two-dimensional system. This is far richer than the one-dimensional system because of the variety of patterns that can be generated. Can a truncated model capture all the patterns? The answer is clearly negative. The goal of the truncated model is certainly more restrictive. However if the class of patterns can be narrowed down, then the truncated model can come in very handy to capture the central features. We will illustrate the solution by studying the possible competition between a striped pattern and a rectangular pattern.

It should be fairly obvious that the modes we choose have two mirror subclass of patterns that we are interested in. For the specific class of patterns mentioned, the choice of modes would be

$$A(x,t) = A_0(t) + A_1(t)\cos(k_1x) + A_2\cos(k_2y) + A_{12}\cos(k_1x)\cos(k_2y) B(x,t) = B_0(t) + B_{12}\cos(k_1x)\cos(k_2y).$$
(16)

For $A_1 = A_2 = A_{12} = B_{12} = 0$, we would have the homogeneous state. For $A_2 = A_{12} = B_{12} = 0$, we would have stripes in the x-direction, while $A_1 = A_{12} = B_{12} = 0$, would give stripes in the y-direction. For $A_1 = A_2 = 0$, we would have a rectangular pattern. Thus for studying the possibility of competition between stripes and rectangles, we would need a 6-mode model. We insert the expansion for A and B given in equations (1) and (2) in the governing equations and equating the coefficients of the same Fourier terms on either side, obtain

$$\dot{A}_{0} = -A_{0} + \frac{A_{0}^{2}}{B_{0}} + \frac{A_{1}^{2}}{2B_{0}} + \frac{A_{2}^{2}}{2B_{0}} + \frac{A_{12}^{2}}{4B_{0}} - \frac{A_{0}A_{12}B_{12}}{2B_{0}^{2}}\sigma$$

$$\dot{A}_{1} = -(1+Dk^{2})A_{1} + \frac{2A_{0}A_{1}}{B_{0}}$$

$$\dot{A}_{2} = -(1+Dk^{2})A_{2} + \frac{2A_{0}A_{2}}{B_{0}} + \frac{A_{12}A_{1}}{B_{0}} - \frac{A_{0}A_{1}B_{12}}{B_{0}^{2}}$$

$$\dot{A}_{12} = -(1+2Dk^{2})A_{12} + \frac{2A_{0}A_{12}}{B_{0}} + \frac{2A_{1}A_{2}}{B_{0}} - \frac{A_{0}^{2}B_{12}}{B_{0}^{2}}$$

$$\dot{B}_{0} = -\mu B_{0} + \mu A_{0}^{2} + \mu \frac{A_{1}^{2}}{2}$$

$$\dot{B}_{12} = -(\mu + 2k^{2})B_{12} + 2\mu A_{1}A_{2} + 2\mu A_{0}A_{12}.$$
(17)

The stripe fixed point corresponds to either

$$A_0 = 1 + \sigma$$

$$B_0 = 2(1 + \sigma)/(1 + Dk^2)$$

$$A_1^2 = 2(B_0 - A_0^2)$$
(18)

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and others zero, or

$$A_0 = 1 + \sigma$$

$$B_0 = 2(1 + \sigma)/(1 + Dk^2)$$

$$A_2^2 = 2(B_0 - A_0^2)$$
(19)

with all other modes zero.

The square fixed point corresponds to $A_0 = A_0^*$, $A_1 = A_2 = A^*$, $A_{12} = A_{12}^*$, $B_0 = B_0^*$ and $B_{12} = B_{12}^*$, with the starred quantities satisfying

$$A_{0}^{*} = \frac{(A_{0}^{*})^{2}}{(B_{0}^{*})^{2}} + \frac{A^{*}}{B_{0}^{*}} + \frac{(A_{12}^{*})}{(B_{0}^{*})}(A_{12}^{*} - \frac{2A_{0}^{*}B_{12}^{*}}{B_{0}^{*}}) + \sigma$$

$$(1 + Dk^{2}) = \frac{2A_{0}^{*}}{B_{0}^{*}} + \frac{(A_{12}^{*})}{(B_{0}^{*})} - \frac{A_{0}^{*}B_{12}^{*}}{(B_{0}^{*})^{2}}$$

$$(1 + Dk^{2} - \frac{2A_{0}^{*}}{B_{0}^{*}})A_{12}^{*} = \frac{2B_{0}^{*}A^{*2} - A_{0}^{*2}B_{12}}{B_{0}^{*2}}$$

$$B_{0}^{*} = A_{0}^{*} + A_{1}^{*} + \frac{A_{12}^{*}}{4}$$

$$B_{12}^{*} = \frac{2\mu(A^{*2} + A_{0}^{*}A_{12}^{*})}{\mu + 2k^{2}}.$$
(20)

To answer the question whether the pattern is striped or square, one imagine that a striped pattern is formed (say along the *x*-direction) and ask if it is stable against a square like perturbation. Consequently, we consider the fixed point $A_0 = 1 + \sigma$, $B_0 = \frac{2(1+\sigma)}{1+Dk^2}$, and $A_1^2 = (B_0 - A_0^2)$ and examine its stability against perturbation by $\delta A_2, \delta A_{12}$ and δB_{12} . Doing a linear stability analysis, we obtain the system

$$\delta \dot{A}_{2} = \frac{A_{1}}{B_{0}} \delta A_{12} - \frac{A_{0}A_{1}}{B_{0}^{2}} \delta B_{12}$$

$$\delta \dot{A}_{12} = -Dk^{2} \delta A_{12} + \frac{2A_{1}}{B_{0}} \delta A_{2} - \frac{A_{0}^{2}}{B_{0}^{2}} \delta B_{12}$$

$$\delta \dot{B}_{12} = -(\mu + 2k^{2}) \delta B_{12} + 2\mu A_{1} \delta A_{2} + 2\mu A_{0} \delta A_{12}. \quad (21)$$

The growth rate 'p' satisfies the cubic

$$p^{3} + p^{2}(Dk^{2} + 2k^{2} + \mu) + p \left[Dk^{2}(\mu + 2k^{2}) + \frac{2\mu A_{0}^{3}}{B_{0}^{2}} + \frac{2\mu\sigma A_{1}^{2}}{B_{0}^{2}} \right] + \frac{6\mu A_{1}^{2}A_{0}^{2}}{B_{0}^{3}} + \frac{2\mu Dk^{2}A_{0}A_{1}^{2}}{B_{0}^{2}} - (\mu + 2k^{2})\frac{2A_{1}^{2}}{B_{0}^{2}} = 0.$$
(22)

The cubic for 'p' has a zero root at $k^2 = k_c^2$ with $(2 - \frac{5\mu(1+\sigma)D}{2})k_c^2 = \mu \frac{1+3\sigma}{2}$ for $k^2 > k_c^2$, the last term in equation (22) is negative and the cubic has a positive root. Thus for wave numbers greater than a critical value, the striped pattern is unstable against the square like perturbation, while for small wave numbers the striped pattern is stable. In this two-dimensional system we have also carried out a numerical integration of the whole 8-mode truncated system consisting of modes $A_0, A_1, A_2, A_{12}, B_0, B_1, B_2, B_{12}$, and the results as shown in Figure 4 are in good qualitative agreement with analytic study the wave no on the instability boundary [3] is

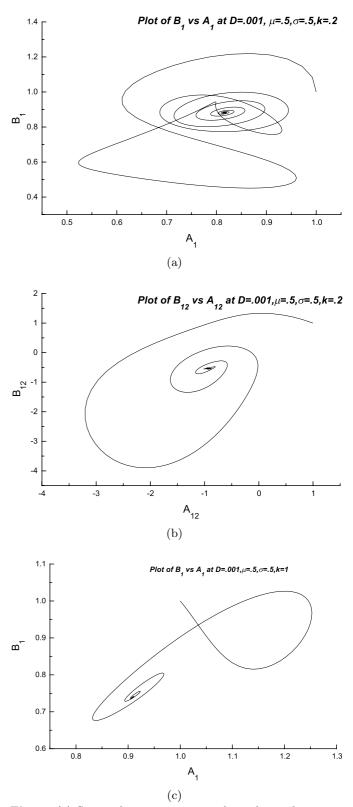


Fig. 4. (a) Stripped pattern state in the eight mode system at parameter values as depicted in the figure. (b) Unphysical square pattern fixed point in the eight mode system at parameter values as depicted in the figure. (c) Stripped pattern state in the eight mode system at parameter values as depicted in the figure. (d) Square pattern state in the eight mode system at parameter values as depicted in the figure.

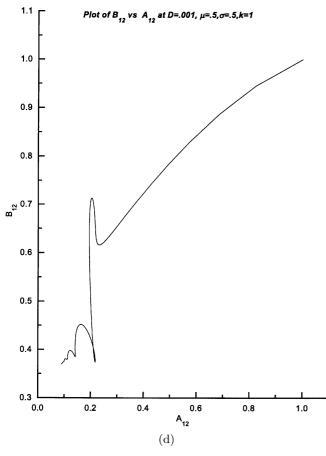


Fig. 4. Continued.

determined by D and σ and thus we finally arrive at the conclusion that parameter σ determines the pattern and by tuning σ , we can observe a cross over from a striped to a square pattern.

Conclusion

The Galerkin model, frequently used in handling with hydrodynamic instabilities, turns out to be a very useful and handy technique in reaction-diffusion systems too. The first part of our analysis using Galerkin model shows the existence of a temporal oscillation over the Turing region. Existence of such a Hopf-Turing mixed state, being a precondition for the development of chaos via phase instability, is worth studying. In the second part our analysis shows that a transition from stripe to square pattern. This result has been arrived at by the effective use of three modes only. Still the result is in good qualitative agreement with the numerics done on 8-mode truncated system. Here lies the advantage of using Galerkin model in the analysis of reaction-diffusion systems at least for the models having the nonlinear terms of the same symmetry as that in Gierer-Meinhardt model [12].

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