Pergamon

Appl. Math. Lett. Vol. 10, No. 1, pp. 1–4, 1997

0893-9659/97 $17.00 + 0.00

PII: S0893-9659(96)00101-2

Boundary-Driven Instability

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(Received March 1996; accepted June 1996)

Abstract—We analyse a reaction-diffusion system and show that complex spatial patterns can be generated by imposing Dirichlet boundary conditions on one or more of the reactant concentrations. This pattern persists even when the homogeneous steady state with Neumann conditions is stable.

Keywords—Turing systems, Pattern formation, Environmental instability, Asymmetry.

1. STABILITY, INSTABILITY AND PATTERN

In 1952, Turing [1] considered a mathematical model for two interacting chemicals of the form:

$$\frac{\partial u}{\partial t} = \nabla \cdot (D_u \nabla u) + f(u,v), \tag{1}$$

$$\frac{\partial v}{\partial t} = \nabla \cdot (D_v \nabla v) + g(u,v), \tag{2}$$

where $u(\mathbf{r},t), v(\mathbf{r},t)$ are chemical concentrations at position $\mathbf{r}$ and time t, and D_u and D_v are diffusion coefficients which are usually assumed constant. The functions f and g model the chemical kinetics and are usually polynomials or rational functions (although Turing considered the simple case in which these functions were linear in the chemical concentrations). Using periodic boundary conditions, Turing showed that a steady state of the system, stable in the absence of diffusion, could be driven unstable by the presence of diffusion, resulting in the system evolving to a spatially-varying solution in u and v, that is, to a *spatial pattern*. This phenomenon is now known as *Turing-* or *diffusion-driven-instability* and, for the case where f and g are nonlinear, the growing spatial patterns predicted by linear stability analysis can evolve into bounded, spatially-varying, stable steady state solutions.

Subsequent to Turing, reaction-diffusion equations have been extensively studied for the case of Neumann, or zero flux, boundary conditions, and applied to many patterning phenomena in biology, where u and v are concentrations of chemicals or morphogens, and ecology, where u and v are species densities (see, for example, [2–5]). Most studies focus on how either the chemical kinetics/species interactions, or diffusion, can destabilize the uniform steady state. In such studies, the boundary behaves as a passive, impermeable membrane. Recently, it was

†P.K.M. would like to thank the School of Mathematics and Statistics, University of Sydney, for its hospitality and support.
‡This work was supported by an Australian Research Council small grant (to M.R.M.).

Typeset by $\mathcal{A}_{\mathcal{M}}\mathcal{S}$-TEX shown that using mixed boundary conditions, for example, zero flux for one chemical and fixed conditions for the other, results in significant changes in the pattern properties exhibited by a reaction-diffusion system [6]. For example, under certain mixed boundary conditions, a stable, spatially-nonuniform solution existed for arbitrarily small domain size, when, with zero flux boundary conditions, the uniform steady state was the only stable solution. In this note, we show how Dirichlet boundary conditions are able to destabilise the uniform steady state and generate complex patterns in a reaction-diffusion system when the uniform steady state is stable with Neumann boundary conditions.

2. BOUNDARY-DRIVEN INSTABILITY: AN EXAMPLE

In this section we consider, in one spatial dimension, the following equations, originally proposed in [7] as a predator-prey model:

$$\frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial x^2} + (\alpha + \beta u)u - \gamma uv, \tag{3}$$

$$\frac{\partial v}{\partial t} = D_v \frac{\partial^2 v}{\partial x^2} + \delta uv - \rho v^2, \tag{4}$$

where α, β, γ, δ, and ρ are positive parameters, and u and v depend on x and t. For Neumann boundary conditions, this system has the nontrivial uniform steady state

$$u_s = \frac{\rho\alpha}{\gamma\delta - \rho\beta}, \qquad v_s = \frac{\delta\alpha}{\gamma\delta - \rho\beta}. \tag{5}$$

For parameter values $\alpha = 1$, $\beta = 0.5$, $\gamma = 1$, $\delta = 1$, $\rho = 1$, the uniform steady state is $u = v = 2$. We set $D_u = 1$ and use D_v as the bifurcation parameter. With Neumann boundary conditions the uniform steady state becomes unstable at $D_v = D_v^c = 11.68$. For higher values of D_v the system evolves to give spatial pattern (Figure 1). For $D_v < D_v^c$ the uniform steady state is stable. Figure 2 shows the effect of imposing a Dirichlet boundary condition on u at $x = 0$. Figure 2a shows the steady state solution for $D_v = 12$. As expected, away from the left-hand boundary, it is similar to the pattern shown in Figure 1. The leftmost, highest peak in both u and v at small x is an effect of the boundary condition on u. When $D_v = 11.5$, that is, below the critical value 11.68, the Dirichlet boundary condition destabilises the uniform steady state and a pattern is generated. The amplitude of this pattern is increasingly damped as x becomes larger. As we continue to decrease D_v, the damping becomes stronger and the number of peaks becomes fewer (Figure 2c). Finally only the leftmost peak remains (Figure 2d). This disappears for $D_v < 1$.

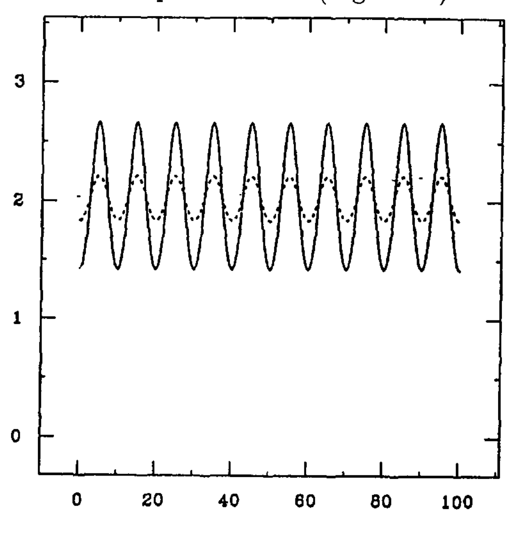
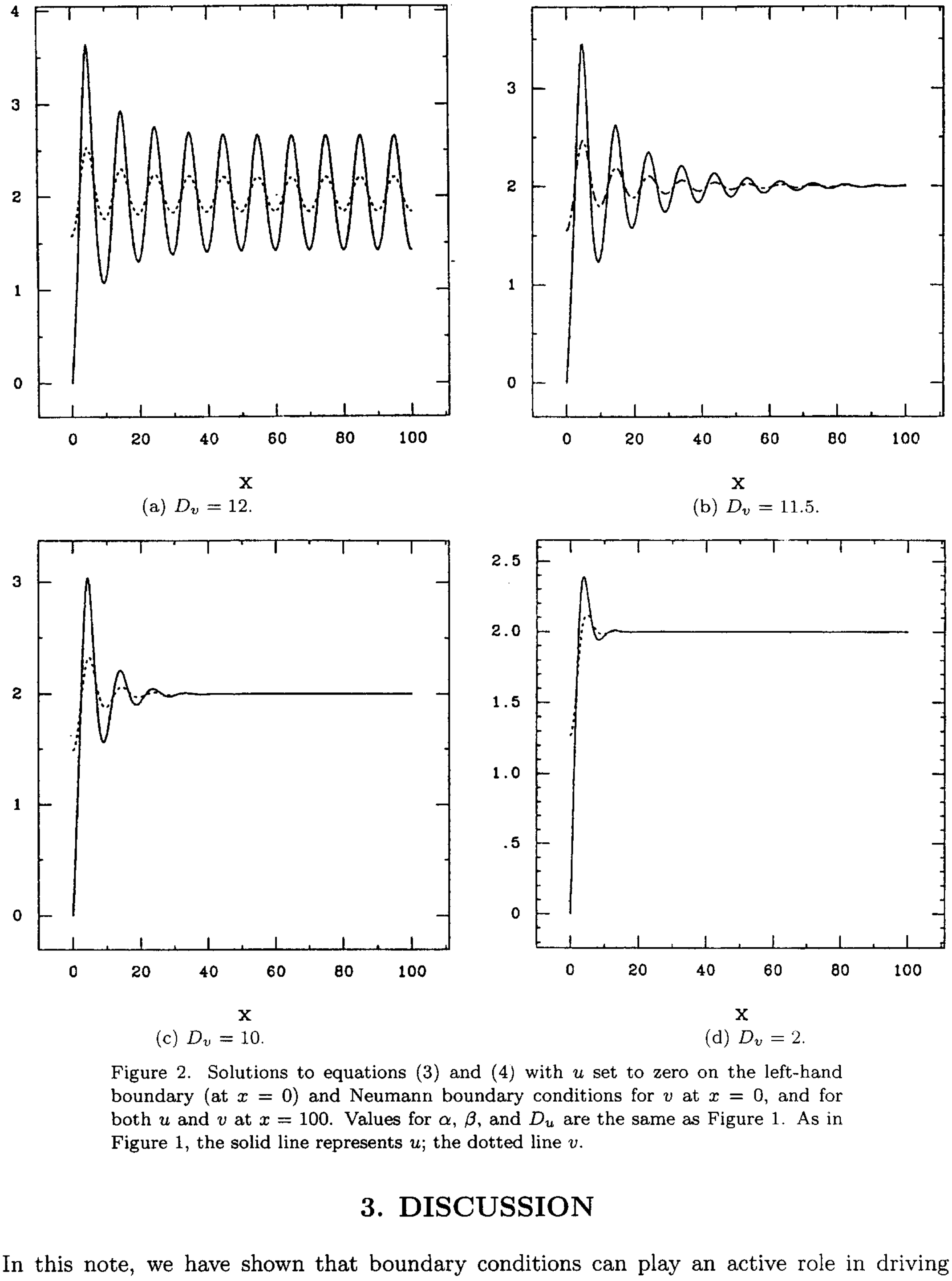


Figure 1. Pattern generated by equations (3) and (4) with Neumann boundary conditions. Parameter values: $\alpha = 1$, $\beta = 0.5$, and $D_u = 1$. Here $D_v = 12$; for these parameter values $D_v^c = 11.68$. The solid line represents u; the dotted line v.



(a) $D_v = 12$.

(b) $D_v = 11.5$.

(c) $D_v = 10$.

(d) $D_v = 2$.

Figure 2. Solutions to equations (3) and (4) with u set to zero on the left-hand boundary (at $x = 0$) and Neumann boundary conditions for v at $x = 0$, and for both u and v at $x = 100$. Values for α, β, and D_u are the same as Figure 1. As in Figure 1, the solid line represents u; the dotted line v.

3. DISCUSSION

In this note, we have shown that boundary conditions can play an active role in driving a uniform steady state of a reaction diffusion system unstable, leading to a stable, spatial pattern. We have observed similar effects in the modified glycolysis system analysed in [6] and also in the chemotaxis model studied in [8] (results not shown). A crucial difference between the patterns observed here, and those observed in [6], is their complexity. The patterns obtained in [6] with mixed boundary conditions, for the case where the uniform steady state was stable for Neumann boundary conditions, were simple in the sense that they had only one turning point. In our case, by extending the domain length, we have found solutions that have several turning points and the effect of the boundary condition is felt far into the domain. This is another example of *environmental instability* discussed in [9]. There, it was shown that a spatially-varying diffusion coefficient could induce the model (3),(4) to form a spatial pattern which encroached into the domain in which the uniform steady state was stable.

The patterns we observe here are spatially asymmetric. Maini *et al.* [10] considered a reaction diffusion model for skeletal patterning in the chick limb, and showed how a spatially-varying diffusion coefficient led to asymmetric patterns in a Turing model which were consistent with the results of biological experiments which contradicted the standard Turing model with constant diffusion coefficients. Here, we have presented an alternative way to produce spatially-asymmetric patterns. In this note, we have considered only the final, steady state to which solutions evolve. However, the patterns produced here exhibit an interesting spatio-temporal dynamics which will be examined in a subsequent publication [11].

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