

Turing bifurcations with a temporally varying diffusion coefficient

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Abstract. This paper is concerned with the possibility of Turing bifurcations in a reaction-diffusion system in which the diffusion coefficient of one species varies periodically in time. This problem was introduced and investigated numerically by Timm and Okubo (*J. Math. Biol.* **30**, 307, 1992) in the context of predator-prey interactions in plankton populations. Here, I consider the simple case in which the temporal variation in diffusivity has a square-tooth form, alternating between two constant values, with a period that is long compared with the time scale of the kinetics. The analysis is valid for any set of reaction kinetics. I derive explicit expressions for the Floquet multipliers that determine the stability of the steady state, and thereby obtain the conditions for diffusion driven instability to occur. These conditions imply that, depending on the kinetics, the homogeneous equilibrium may be either more or less stable than when the diffusion coefficient is a constant equal to the mean of the variable diffusivity. I go on to consider the form of the solution when diffusion driven instability does occur, and I use perturbation theory to determine the effect of a small temporal variation in the diffusion coefficient on the spatial wavelength of the pattern that results from diffusion driven instability.

Key words: Diffusion driven instability – Reaction diffusion equations – Pattern formation

Introduction

The evolution of spatial structure from an initially homogeneous state is one of the most widely studied problems in mathematical biology. Many of the proposed models consist of systems of reaction-diffusion equations, in which spatial pattern arises via a Turing bifurcation (Turing 1952). In this

mechanism, a homogeneous steady state that is stable to spatially uniform perturbations becomes unstable, in the presence of diffusion, to perturbations with appropriate spatial frequencies. This mechanism has been applied to spatial pattern formation in both embryology (Murray 1981; Meinhardt and Gierer 1974) and ecology (Segel and Jackson 1972; Levin and Segel 1976), and a detailed review is given in the book by Murray (1989). The Turing bifurcation was initially studied for reaction-diffusion systems in which the kinetic terms are functions of only the dependent variables, that is morphogen concentration or population density. Auchmuty and Nicolis (1975) extended the analysis by allowing the kinetic parameters to vary in space, and this has been developed by a number of subsequent authors (Pacala and Roughgarden 1982; Shigesada 1984; Cantrell and Cosner 1991). In particular, when the kinetic parameters are piecewise constant, the stability of the homogeneous state depends not only on the value and width of the regions of constant parameters, but also on their spatial arrangement. More recently it has been shown that spatially varying diffusion coefficients can produce patterns that vary in either amplitude or wavelength across the domain (Maini et al. 1992; Benson et al. 1993a,b).

In the context of developmental biology, such spatial variations in parameter values probably represent one of the main points of difference between the original theory of Turing (1952) and those actual biological systems in which chemical prepatterns regulate morphogenesis. However, in ecological contexts there is another point of difference, namely the temporal oscillations in parameter values due to seasonal variations. The effects of such oscillations were first considered by Timm and Okubo (1992). They studied the model of Levin and Segel (1976) for the predator-prey interaction between different species of plankton, with a sinusoidal temporal variation in the dispersal rate of the zooplankton (predators). In this case, such a variation arises from the combination of vertical migration and vertical current shear. Timm and Okubo (1992) presented numerical evidence that, for one particular set of kinetic parameters, the homogeneous steady state becomes more stable as the amplitude of the temporal variation in dispersal rate increases, with constant mean. They also used perturbation theory to prove this stabilising effect analytically when the temporal variation in dispersal rate is very small.

In this paper I present more general analytical results for the case of oscillations in predator dispersal rate. In order to facilitate analysis, I suppose that these oscillations take the form of the dispersal rate alternating between two constant values; moreover I consider only the case of very long period oscillations, such as seasonal variations. Within this context, I derive exact analytical conditions for diffusion driven patterns to form. In particular, my results show two separate regions of instability, only one of which was picked up in the numerical study of Timm and Okubo (1992). Moreover, I disprove their conjecture that diffusion driven instability always becomes less likely when temporal oscillations in dispersal rates are introduced.

The problem I consider concerns a system of two reaction-diffusion equations of the form

$$\partial u / \partial t = D_u \nabla^2 u + f(u, v) \quad (1a)$$

$$\partial v / \partial t = D_v(t) \nabla^2 v + g(u, v) \quad (1b)$$

where (u_s, v_s) is a homogeneous steady state of the system, and $D_v(t)$ is periodic with minimum period T . Specifically, I assume that $D_v(t)$ alternates between two constant values, that is $D_v(t) = D^+$ on $nT < t < (n + 1/2)T$ and $D_v(t) = D^-$ on $(n + 1/2)T < t < (n + 1)T$ ($n \in \mathbb{Z}$); the values of $D_v(nT)$ and $D_v(nT + T/2)$ are irrelevant. Henceforth, I will describe this functional form as a "square-tooth" form. The motivation for choosing this particular form of $D_v(t)$ is simply that it enables the conditions for diffusion driven instability to be determined explicitly, which is not possible more generally. This case therefore provides a method of gaining insight into the way in which the formation of spatial patterns can be altered by a temporal oscillation in dispersal rates. Note that in this case the existence of a solution to (1) and its continuous dependence on initial data follow immediately from the corresponding result for constant diffusion, since one is in effect solving a sequence of initial value problems, with constant diffusivity for each problem.

Linearising (1) about (u_s, v_s) gives, to leading order,

$$\partial \tilde{u} / \partial t = D_u \nabla^2 \tilde{u} + a \tilde{u} + b \tilde{v} \quad (2a)$$

$$\partial \tilde{v} / \partial t = D_v(t) \nabla^2 \tilde{v} + c \tilde{u} + d \tilde{v} \quad (2b)$$

where $\tilde{u} = u - u_s$ and $\tilde{v} = v - v_s$, with $|\tilde{u}|, |\tilde{v}| \ll 1$, and

$$a = \left. \frac{\partial f}{\partial u} \right|_{(u_s, v_s)} \quad b = \left. \frac{\partial f}{\partial v} \right|_{(u_s, v_s)} \quad c = \left. \frac{\partial g}{\partial u} \right|_{(u_s, v_s)} \quad d = \left. \frac{\partial g}{\partial v} \right|_{(u_s, v_s)}$$

Stability to homogeneous perturbations requires that $a + d < 0$ and $ad > bc$. In particular one of a and d must be negative, and throughout the paper I assume $d < 0$. I will show that diffusion driven instability then requires $a > 0$. Therefore, since only D_v varies in time, the assumption $d < 0$ is restrictive. It would be relatively straightforward to consider the case $a < 0$ and $d > 0$ (or equivalently, D_u varying in time) in the same way, but to be specific I consider only the one case, which is the one of interest in the application studied by Timm and Okubo (1992). In summary, I make the following assumptions throughout the paper:

$$a + d < 0 \quad (3a)$$

$$ad - bc > 0 \quad (3b)$$

$$d < 0 \quad (3c)$$

Fourier theory implies that at each point in time, the solution of (2) can be written as a sum of a suitable set of spatial modes $\exp(i\mathbf{k} \cdot \mathbf{x})$. I assume that this

Fourier series can be differentiated termwise with respect to both space and time, giving a series that is also convergent. To investigate the stability of (u_s, v_s) , one looks for solutions of (2) with the form $\tilde{u}(\underline{x}, t) = U(t)\exp(i\mathbf{k} \cdot \underline{x})$, $\tilde{v}(\underline{x}, t) = V(t)\exp(i\mathbf{k} \cdot \underline{x})$. This results in a system of linear ordinary differential equations in which one of the coefficients varies periodically in time:

$$dU/dt = [a - KD_u]U + bV \quad (4a)$$

$$dV/dt = cU + [d - KD_v(t)]V \quad (4b)$$

where $K = |\mathbf{k}|^2$. A general theory of equations such as this, that are linear with periodically varying coefficients, was developed by Floquet, and I will now briefly summarise this theory. A fuller account is given, for example, in the book by Iooss and Joseph (1980).

It is straightforward to show that any n th order homogeneous system of nonautonomous linear ordinary differential equations has n linearly independent solutions. An $n \times n$ matrix, $\underline{\Phi}(t)$ say, whose columns consist of such solutions is known as a "fundamental matrix" of the equations. When the coefficients of the equations are periodic in t , with minimum period T , say, the eigenvalues of $\underline{E} = \underline{\Phi}(t_0)^{-1}\underline{\Phi}(t_0 + T)$ are known as the "Floquet multipliers" of the system. It can be shown that the Floquet multipliers are independent of the choice of fundamental matrix, and thus of t_0 . Moreover, corresponding to the n multipliers μ_i ($i = 1, \dots, n$), there are n linearly independent solutions of the ordinary differential equations of the form $\sigma_i(t)\exp[(t/T)\log \mu_i]$, where each $\sigma_i(t)$ is periodic with period T . Therefore the homogeneous steady state is stable if and only if $|\mu_i| < 1$ for each i .

The difficulty with implementing this theory for a particular set of equations is in finding a linearly independent set of solutions. However for the simple form of $D_v(t)$ I am considering, (4) can be solved explicitly, enabling the Floquet multipliers to be determined.

The linear stability problem

In the original system of partial differential equations, one can rescale \underline{x} and D_v so that $D_u = 1$. Then, for the particular $D_v(t)$ we are considering, (4) has the following form:

$$d\underline{\omega}/dt = \underline{A}^+ \underline{\omega} \quad \text{on } nT < t < (n + 1/2)T \quad (5a)$$

$$d\underline{\omega}/dt = \underline{A}^- \underline{\omega} \quad \text{on } (n + 1/2)T < t < (n + 1)T \quad (5b)$$

($n \in \mathbb{Z}$). Here

$$\underline{\omega}(t) = \begin{bmatrix} U(t) \\ V(t) \end{bmatrix} \quad \text{and} \quad \underline{A}^\pm = \begin{bmatrix} a - K & b \\ c & d - KD^\pm \end{bmatrix}.$$

I denote the eigenvalues and corresponding eigenvectors of \underline{A}^\pm by λ_i^\pm and z_i^\pm , with $i = 1, 2$. I also write $\underline{A}^\pm(t) = \text{diag}[\exp(\lambda_1^\pm t), \exp(\lambda_2^\pm t)]$, and denote by \underline{Z}^\pm the matrix whose first and second columns are z_1^\pm and z_2^\pm . Then any fundamental matrices of (5a) and (5b) have the form $\underline{Z}^+ \underline{A}^+(t) \underline{C}^+$ and $\underline{Z}^- \underline{A}^-(t) \underline{C}^-$ respectively. Here \underline{C}^\pm are matrices whose entries are constants of integration; without loss of generality, I take $\underline{C}^+ = (\underline{A}^+(T/2))^{-1}$. Continuity at $t = T/2$ then requires that

$$\underline{C}^- = (\underline{A}^-(T/2))^{-1} (\underline{Z}^-)^{-1} \underline{Z}^+.$$

Therefore

$$\underline{E} \equiv (\underline{\Phi}(0))^{-1} \underline{\Phi}(T) = (\underline{Z}^+)^{-1} \underline{Z}^- \underline{A}^-(T/2) (\underline{Z}^-)^{-1} \underline{Z}^+ \underline{A}^+(T/2).$$

The homogeneous steady state (u_s, v_s) is stable if and only if both eigenvalues of \underline{E} have modulus less than 1.

The matrices \underline{Z}^\pm and \underline{A}^\pm can clearly be determined analytically, enabling calculation of \underline{E} . This shows that the eigenvalues μ of \underline{E} are given by $\mu = \hat{\mu} \cdot \exp(-\Gamma T/4)$, where $\hat{\mu}^2 - B\hat{\mu} + 1 = 0$. Here

$$\Gamma = (2 + D^+ + D^-)K - 2(a + d)$$

and

$$B = \frac{1}{2} e^{(P^+ + P^-)T/4} \left[(1 + e^{-P^+ T/2})(1 + e^{-P^- T/2}) + \frac{4bc + Q^+ Q^-}{P + P^-} (1 - e^{-P^+ T/2})(1 - e^{-P^- T/2}) \right]$$

with

$$Q^\pm = KD^\pm - K + a - d$$

$$P^\pm = \sqrt{4bc + Q^{\pm 2}}.$$

As expected, these expressions are all symmetric in D^+ and D^- , and thus without loss of generality I can assume that $|Q^+| > |Q^-|$. Note that (3a) implies that $\Gamma > 0$.

In applications, one is interested in the case in which the period T of $D_v(t)$ is much longer than the characteristic time scale of the reaction kinetics. This implies that $|P^\pm T| \gg 1$. Now P^\pm may be either real or pure imaginary, according to whether $Q^{\pm 2} + 4bc$ is positive or negative, respectively; however, $|Q^+| > |Q^-|$, and thus P^- can be real only if P^+ is also real. Therefore, if P^+ is pure imaginary, then both roots for $\hat{\mu}$ are $O(1)$ as $T \rightarrow \infty$, giving roots of μ that are $\ll 1$ in absolute value. The steady state (u_s, v_s) is then stable to a perturbation with wave number k . However, if P^+ is real, then $|B| \gg 1$ for large T , so that to leading order the roots for $\hat{\mu}$ are $1/B$ and B . Since $\Gamma > 0$, the first of these gives a root for μ that is $\ll 1$ in absolute value, whereas the second gives a root that is greater than one in absolute value if and only if $B > \exp(\Gamma T/4)$. Now $B = \beta \exp\{[P^+ + \text{Re}(P^-)]T/4\}$, where β is $O(1)$ as $T \rightarrow \infty$. Thus for sufficiently large T , the steady state is unstable to a perturbation of wave

number k if and only if

$$\begin{aligned}
 P^+ + \text{Re}(P^-) > \Gamma &\Leftrightarrow (P^- \notin \mathbb{R} \text{ and } P^+ > \Gamma) \quad \text{or} \quad (P^- \in \mathbb{R} \text{ and } P^- > \Gamma - P^+) \\
 &\Leftrightarrow (P^+ > \Gamma) \quad \text{or} \quad (P^- \in \mathbb{R} \text{ and } P^{-2} > (\Gamma - P^+)^2) \\
 &\Leftrightarrow P^+ > \Gamma \quad \text{or} \quad P^{-2} > (\Gamma - P^+)^2 \\
 &\Leftrightarrow P^+ > \Gamma \quad \text{or} \quad (\Gamma + P^{+2} - P^{-2})^2 < 4\Gamma^2 P^{+2},
 \end{aligned}$$

since P^- is either real and positive or pure imaginary, and $Q^{+2} > Q^{-2}$. I will now consider these two cases in turn.

Case (i): $P^+ > \Gamma$

I begin by considering the case $P^+ > \Gamma$. Both sides of this inequality are strictly positive, and squaring gives the condition for instability as $q_1(K) < 0$, where

$$\begin{aligned}
 q_1(K) \equiv (2D^+ + D^- + 1)(D^- + 3)K^2 - 2[(3a + d)D^+ \\
 + 2(a + d)D^- + (3a + 5d)]K + [3(a + d)^2 + 4(ad - bc)].
 \end{aligned}$$

Recall that stability to homogeneous perturbations requires that $ad > bc$, so that both the constant term and the coefficient of K^2 are positive. Therefore $q_1(K)$ will be negative for some positive values of $K \equiv |k|^2$ provided that it has real roots and that the coefficient of K is strictly negative. The quadratic will then have two real positive roots, and will be negative for values of K between these roots.

The analysis is simplified by writing $\delta = (D^+ - 1)/(D^- + 3)$. In terms of this quantity, the roots of $q_1(K)$ are real if and only if

$$q_2(\delta) \equiv (3a + d)^2 \delta^2 + 2(3a^2 - 2ad - d^2 + 4bc)\delta + (a^2 - 2ad + 4bc + d^2) > 0, \quad (6)$$

while the coefficient of K in $q_1(K)$ is negative provided that $3a + d > 0$ and $\delta > -2(a + d)/(3a + d) \equiv \delta_0$. If $3a + d < 0$, the coefficient is negative for all positive values of δ , and otherwise $\delta_0 > 0$, using (3a). Now

$$q_2(\delta_0) = [3(a + d)^2 + 4(ad - bc)](a + 3d)/(3a + d) < 0 \quad (7)$$

when $3a + d > 0$, using (3a). Therefore $q_1(K)$ will have real positive roots if and only if $3a + d > 0$ and $\delta > \delta_c$, where δ_c is the larger root of (6), and is greater than δ_0 . It is clear from (6) that δ_c depends only on the ratios $a/\sqrt{-bc}$ and $d/\sqrt{-bc}$, and this dependence is illustrated in Fig. 1. Note that since $d < 0$, $3a + d > 0 \Rightarrow a > 0 \Rightarrow ad < 0 \Rightarrow bc < 0$ using (3). Now when $a > 0$, straightforward substitution shows that $q_1(a)$ and $q'_1(a)$ are both strictly positive, so that $q_1(K)$ is only ever negative when $K < a$. Thus $Q^\pm > 0$, so that my assumption that $|Q^+| > |Q^-|$ implies that $D^+ > D^-$.

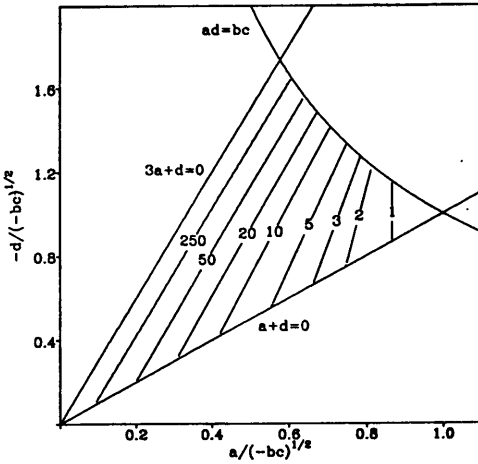


Fig. 1. A contour map of the variation of δ_c with the kinetics ratios $a/\sqrt{-bc}$ and $d/\sqrt{-bc}$. As discussed in the text, δ_c is defined only when $3a + d > 0$, $a + d < 0$ and $ad > bc$. In this case, the homogeneous steady state is driven unstable by diffusion when $(D^+ - 1)/(D^- + 3) > \delta_c$

Case (ii): $(\Gamma^2 + P^{+2} - P^{-2})^2 < 4\Gamma^2 P^{+2}$

This second condition for diffusion driven instability simplifies to

$$0 > \{ \bar{D}K^2 - (a\bar{D} + d)K + (ad - bc) \} + \Delta^2 \left\{ \frac{K^2(a - K)(\bar{D}K - d)}{[(1 + \bar{D})K - (a + d)]^2} \right\} \\ \equiv f(K) + \Delta^2 g(K), \tag{8}$$

say, where $\bar{D} = (D^+ - D^-)/2$ and $\Delta = |D^+ - D^-|/2$. When $D^+ = D^-$, (8) reduces to the quadratic dispersion relation for diffusion driven instability when the diffusion coefficients are constant (see, for example, Murray 1989, Chap. 14). More generally, this quadratic is altered by a positive multiple of the function $g(K)$. I begin by considering the case $a < 0$. Then $g(K) < 0$ for all $K > 0$. Moreover, I am only concerned with strictly positive D^\pm , so that $\Delta < \bar{D}$. Therefore

$$f(K) + \Delta^2 g(K) \\ > f(K) + \bar{D}^2 g(K) \\ > -ad + \frac{(K - a)(\bar{D}K - d)\{ (2\bar{D} + 1)K^2 - 2(a + d)(1 + \bar{D})K + (a + d)^2 \}}{[(1 + \bar{D})K - (a + d)]^2} \\ > 0 \quad \forall K > 0 \quad \text{when } a < 0. \tag{9}$$

Therefore, (8) never holds when $a < 0$.

Turning attention to the case $a > 0$, $g(K)$ then has the qualitative form illustrated in Fig. 2. In particular, $g(K) > 0$ on $0 < K < a$. Now when $a > 0$, (3b) implies that $bc < 0$, so that $f(a) = -bc$ and $f'(a) = a\bar{D} - d$ are both strictly positive. Therefore $f(K) > 0$ and $g(K) < 0$ for all $K > a$, implying that

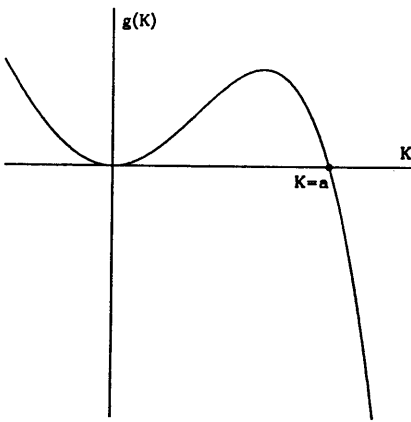


Fig. 2. The qualitative form of $g(K)$, defined in (8), when $a > 0$

$f(K) + \Delta^2 g(K) > f(K) + \bar{D}^2 g(K) > 0$, using (9). Therefore, (8) never holds when $K > a$. As above in case (i), this implies that $Q^\pm > 0$, so that $D^+ > D^-$.

When $K \in (0, a)$, $g(K) > 0$, so that $f(K) + \Delta^2 g(K)$ increases with Δ . Therefore, the range of unstable wave numbers decreases as the difference between D^+ and D^- increases, with constant mean, and the constant diffusivity case is the most unstable. The condition for (8) to hold for some K therefore falls naturally into two parts. Firstly, the system must be driven unstable by diffusion when the diffusion coefficient is constant with value \bar{D} , which requires that $a\bar{D} + d > 0$ and $(a\bar{D} + d)^2 > 4\bar{D}(ad - bc)$ (Murray 1989, Chap. 14). Secondly, it is necessary that $\Delta < \Delta_c$, where Δ_c is a critical value that depends on \bar{D} and the ratios $a/\sqrt{-bc}$ and $d/\sqrt{-bc}$. Straightforward differentiation shows that $\partial f/\partial \bar{D}$ and $\partial g/\partial \bar{D}$ are both strictly negative on $0 < K < a$, so that for given kinetics, Δ_c increases monotonically with \bar{D} . In some cases (e.g. $a/\sqrt{-bc} = 0.4$, $d/\sqrt{-bc} = -2$, $\bar{D} = 100$), $\Delta_c > \bar{D}$, so that the steady state can be driven unstable by diffusion even when $D^- = 0$.

The implications of linear theory

To summarise, the steady state (u_s, v_s) is stable to homogeneous perturbations if and only if $a + d < 0$ and $ad > bc$. This implies that one of a and d must be negative and I consider here only the case $d < 0$. Without loss of generality, I also take $D^+ > D^-$; physical realism further requires $D^- > 0$, that is $\Delta < \bar{D}$, where $\Delta = (D^+ - D^-)/2$ and $\bar{D} = (D^+ + D^-)/2$. Then, to leading order for large T , the steady state will be driven unstable by diffusion if and only if either

- (i) (a) $3a + d > 0$
- (b) $(D^+ - 1)/(D^- + 3) > \delta_c \Leftrightarrow (\delta_c + 1)\Delta + (\delta_c - 1)\bar{D} + (3\delta_c + 1)$

or

- (ii) (a) $a\bar{D} + d > 0$
- (b) $[a\bar{D} + d]^2 > 4\bar{D}(ad - bc)$
- (c) $\Delta < \Delta_c$

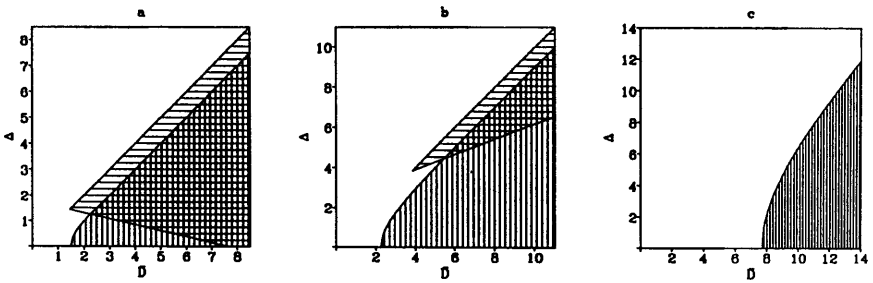


Fig. 3. Examples of the regions of $\bar{D} - \Delta$ parameter space in which diffusion driven instability occurs. The kinetics ratios are: **a** $a/\sqrt{-bc} = 0.9, d/\sqrt{-bc} = -1.1$; **b** $a/\sqrt{-bc} = 0.8, d/\sqrt{-bc} = -1.2$; **c** $a/\sqrt{-bc} = 0.5, d/\sqrt{-bc} = -1.7$. Shading by horizontal lines denotes that condition (i) is satisfied, and shading by vertical lines denotes that condition (ii) is satisfied. In c, $3a + d < 0$, so that condition (i) is not satisfied for any values of \bar{D} and Δ

Here $\delta_c > 0$ is the larger root of (6), and Δ_c is the unique value of Δ for which $f(K) + \Delta^2 g(K)$ touches the K axis on $(0, a)$; f and g are defined in (8). All of these inequalities depend only on the kinetics ratios $a/\sqrt{-bc}$ and $d/\sqrt{-bc}$, and on the two diffusion coefficients D^\pm . For given values of the kinetics ratios, conditions (i) and (ii) define different regions of the $\bar{D} - \Delta$ parameter space in which diffusion driven instability occurs. Some examples of these regions are illustrated in Fig. 3. Of particular interest is the fact that condition (ii) is an extension of the conditions for diffusion driven instability when $D^+ = D^-$, and that in this case the system is always made more stable by the temporal variation of the diffusion coefficients, in the sense that a necessary condition for instability is that the system is unstable in the case $D_v(t) \equiv (D^+ + D^-)/2$.

When $D^+ = D^-$, condition (i) holds if and only if $\delta_c < 1$ and $\bar{D} > (3\delta_c + 1)/(1 - \delta_c) \equiv \xi_c$, say, while condition (ii) holds if and only if $\bar{D} > D_c$. Here D_c is the critical diffusion coefficient for diffusion driven instability in the homogeneous case, and is the larger root of $(aD_c + d)^2 = 4(ad - bc)D_c$. I will now show that whenever $\delta_c < 1, D_c < \xi_c$, so that when $D^+ = D^-$, condition (i) implies condition (ii). Recall that δ_c is the larger root for δ of $q_2(\delta) = 0$ (defined in (6)). Now a necessary condition for $\delta_c < 1$ is

$$0 < q_2(1) = 4(4a^2 + 3bc) \Leftrightarrow a/\sqrt{-bc} > \sqrt{3}/2.$$

If this holds,

$$q'_2(1) = 8(3a^2 + ad + bc) > 8(3a^2 + 2bc) > 0$$

and thus $a/\sqrt{-bc} > \sqrt{3}/2$ is also sufficient for $\delta_c < 1$. Straightforward substitution shows that when this is satisfied, ξ_c is the larger root for ξ of

$$h_1(\xi) \equiv (a^2 + 3bc/4)\xi^2 - 2(ad - 5bc/4)\xi + (d^2 + 3bc/4),$$

while D_c is the larger root of

$$h_2(\xi) \equiv a^2\xi^2 - 2(ad - 2bc)\xi + d^2.$$

Now $h_2(\xi) - h_1(\xi) = 3(-bc)(\xi - 1)^2/4 \geq 0$, and thus $D_c < \xi_c$.

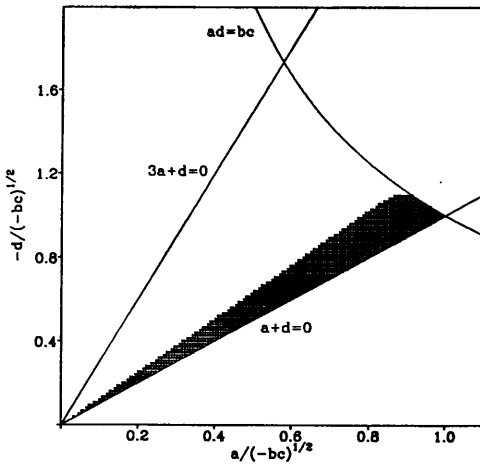


Fig. 4. An illustration of the parameter domain in which (10) is satisfied (denoted by dark shading). In this region of parameter space, the homogeneous steady state is driven unstable by diffusion for some values of $\bar{D} < D_c$ and $\Delta < \bar{D}$. The steady state will then be more unstable as a result of the temporal variation in D_v , in the sense that the steady state is stable when $D_v(t) \equiv \bar{D}$, with the same kinetics

This result implies that condition (i) defines an unstable region of the $D^+ - D^-$ parameter space that is not given by condition (ii) only when D^+ and D^- are sufficiently different. Of particular interest is whether condition (i) can imply diffusion driven instability in a case in which the steady state is stable when $D_v(t) \equiv (D^+ + D^-)/2$. Since $D^- > 0$, and $(D^+ - 1)/(D^- + 3)$ increases with Δ when \bar{D} is fixed, this occurs if and only if $(D^+ - 1)/(D^- + 3) > \delta_c$ when $\bar{D} \equiv \Delta = D_c$, that is, if and only if

$$2D_c - 1 > 3\delta_c. \quad (10)$$

The inequalities (10) and (3) and condition (ia) that $3a + d > 0$ together define the region of $(a/\sqrt{-bc}) - (d/\sqrt{-bc})$ parameter space in which (u_s, v_s) can be driven unstable by a sufficiently large temporal variation in D_v , even though (u_s, v_s) is stable when D_v is constant, with the same mean. This parameter domain is illustrated in Fig. 4. For the model and parameter values considered by Timm and Okubo (1992), the kinetic ratios lie outside this domain, and thus their conclusion, from numerical experiments, that a temporal variation in diffusivity stabilises the steady state is exactly right, at least for the square-tooth form of $D_v(t)$ I am considering. (It must be remembered that Timm and Okubo (1992) used a sinusoidal variation in D_v .) However, my analysis shows that this result is not general, and that for other sets of kinetics, a temporal variation in D_v can destabilise the steady state.

Behaviour when $D^+ \approx D^-$

When $D^+ = D^-$, with given values of the kinetic parameters, diffusion driven instability occurs if and only if the common value of D^+ and D^- is greater than D_c . If D^+ and D^- are different but sufficiently close, diffusion driven instability will occur only if both $(D^+ + D^-)/2 \equiv \bar{D} > D_c$ and $(D^+ - D^-)/2 \equiv$

$\Delta < \Delta_c(\bar{D})$. I now use perturbation theory to derive the asymptotic form of Δ_c when $\bar{D} = D_c + \varepsilon$, with $0 < \varepsilon \ll 1$.

When $\Delta = \Delta_c$, $f(K) + \Delta^2 g(K)$ has a double root at some value of K , say $K = \bar{K}$. The defining conditions for Δ_c and \bar{K} are therefore

$$f(\bar{K}; \bar{D}) + \Delta_c^2 g(\bar{K}; \bar{D}) = 0 \tag{11a}$$

$$\partial f / \partial K(\bar{K}; \bar{D}) + \Delta_c^2 \partial g / \partial K(\bar{K}; \bar{D}) = 0. \tag{11b}$$

For $\bar{D} = D_c + \varepsilon$, I look for solutions of these algebraic equations of the form $\bar{K} = \bar{K}_0 + \varepsilon \bar{K}_1 + \varepsilon^2 \bar{K}_2 + \dots$ and $\Delta_c = \varepsilon^{1/2} \Delta_{c,1} + \varepsilon^{3/2} \Delta_{c,2} + \varepsilon^{5/2} \Delta_{c,3} + \dots$. This expansion of Δ_c gives an expansion for Δ_c^2 in integer powers of ε .

Substituting these expansions into (11) and equating powers of ε gives, to order 1,

$$f(\bar{K}_0; D_c) = 0$$

$$\partial f / \partial K(\bar{K}_0; D_c) = 0.$$

These are the equations for the critical diffusion coefficient and wave number for diffusion driven instability with constant diffusivity, and give $\bar{K}_0 = (aD_c + d)/(2D_c)$, with D_c the larger root of $(aD_c + d)^2 = 4D_c(ad - bc)$. To order ε , (11) gives

$$\delta f / \partial \bar{D}(\bar{K}_0; D_c) + \Delta_{c,1}^2 g(\bar{K}_0; D_c) = 0$$

$$K_1 \partial^2 f / \partial K^2(\bar{K}_0; D_c) + \partial^2 f / \partial K \partial \bar{D}(\bar{K}_0; D_c) + \Delta_{c,1}^2 \partial g / \partial K(\bar{K}_0; D_c) = 0.$$

Solving these equations for $\Delta_{c,1}$ and \bar{K}_1 and simplifying gives

$$\Delta_{c,1} = \left[\frac{(aD_c - d)(D_c - 1)^2}{D_c(aD_c + d)} \right]^{1/2}$$

$$\bar{K}_1 = \frac{(2a + d)D_c + d}{2D_c^2(D_c - 1)}.$$

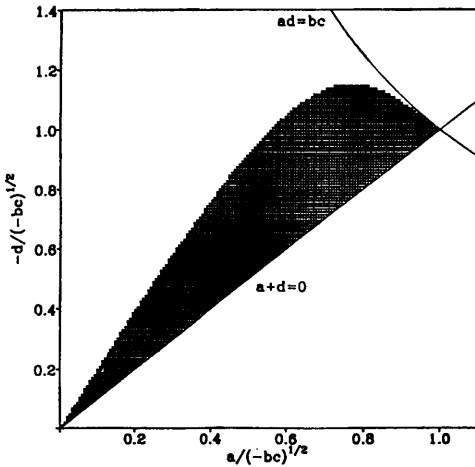


Fig. 5. An illustration of the parameter domain in which $(2a + d)D_c + d > 0$ (denoted by dark shading). In this region, a small temporal variation in D_c decreases the spatial wavelength of the pattern resulting from diffusion driven instability; elsewhere, the wavelength increases

Expressions can be derived for higher order terms in the same way. In particular, this analysis shows that the introduction of a small temporal variation in D_c tends to increase or decrease the wavelength of the resulting pattern according to whether $(2a + d)D_c + d$ is negative or positive respectively. This is a condition on the kinetic ratios $a/\sqrt{-bc}$ and $d/\sqrt{-bc}$, and divides the parameter space into two, as illustrated in Fig. 5.

Discussion

There are many points of difference between real ecological systems and corresponding reaction-diffusion models. Here I have focussed on just one of these differences, namely the seasonal variation of ecological parameters. My purpose is to understand the way in which such variations modify the pattern-forming ability predicted by reaction-diffusion models. As a mathematical problem, the investigation of pattern formation is considerably more complex for oscillating dispersal rates than for constant rates, requiring the solution of a Floquet problem rather than a simple eigenvalue problem.

I was motivated to study this topic in large part by the previous work of Timm and Okubo (1992). They investigated numerically the effects of periodically varying dispersal rates on pattern formation in a particular predator-prey reaction-diffusion model. It is notoriously dangerous to interpret such numerical studies, because one is inevitably restricted to a very small number of parameter sets. Therefore I have adopted an opposite approach to the problem – I consider a simple and admittedly less realistic form of temporal variation (namely piecewise linear rather than continuously varying), for which I can determine analytically the conditions for dispersal driven patterns. This analysis shows that several of the conclusions drawn by Timm and Okubo (1992) are not valid in more general contexts; in particular, oscillations in the predator dispersal rate can promote pattern formation in some cases. This is not to say that any of Timm and Okubo's results are wrong – rather that the conclusions they drew from numerical simulations cannot be generalised to all sets of parameter values.

An issue that I have not yet discussed is the form of the solution when diffusion driven instability does occur. The linear theory predicts a solution of constant shape, whose amplitude undergoes growing oscillations in time. However, we expect that nonlinearities in the system will limit the amplitude of the solution. I have investigated this numerically by focussing on the particular reaction-diffusion system proposed by Segel and Jackson (1972) as a model for predator-prey interactions; the kinetics are

$$f(u, v) = u + \kappa u^2 - \mu uv \quad (12a)$$

$$g(u, v) = uv - v^2, \quad (12b)$$

where $\kappa (< 1)$ and $\mu (> \kappa)$ are positive parameters. For this model, with a square-tooth form for $D_v(t)$, numerical solutions suggest that for parameter

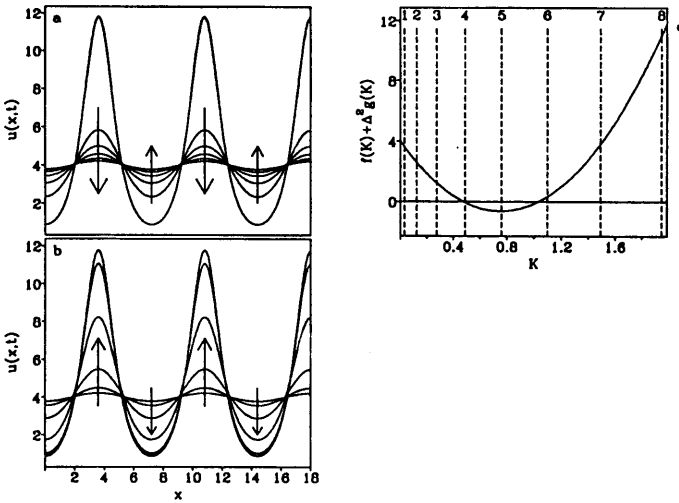


Fig. 6a–c. The numerical solution of (12) with $\kappa = 0.5$, $\mu = 0.75$, $D^+ = 10.5$, $D^- = 6.5$ and $T = 20$. The initial conditions consisted of small random perturbations about the homogeneous steady state $u = v = 4$, and I applied zero flux boundary conditions at the ends $x = 0$ and $x = 18$ of the spatial domain. The results are not at all sensitive to the details of the initial conditions, except that a mirror image solution (reflected about $x = 9$) is sometimes obtained. I plot u as a function of x at equally space times (time interval = 4) on a $30.5T \leq t \leq 31T$, b $31T \leq t \leq 31.5T$. By this time, transients have largely decayed, and the solution is approximately periodic with period T . The arrows indicate the way in which the solution evolves with time. As expected intuitively, the solution approaches the homogeneous steady state on the half of the period on which $D_v = D^-$ (a), and moves away again on the half of the period on which $D_v = D^+$ (b). For the parameter values used in this figure, condition (i) for diffusion driven instability is not satisfied, but condition (ii) holds. In c, I plot the corresponding dispersion relation, $f(K) + \Delta^2 g(K)$ (defined in (8)). The steady state is unstable to perturbations with all wave numbers for which $f(K) + \Delta^2 g(K) < 0$. I denote by dashed vertical lines the values of K for which a solution proportional to $\exp(ikx)$ can satisfy flux boundary conditions at $x = 0$ and $x = 18$ (recall that $K = k^2$). These values are given by $K = (n\pi/18)^2$ ($n \in \mathbf{Z}^+$), and the mode number n is indicated above each dashed vertical line. This shows that only mode 5 is unstable, and correspondingly the solutions illustrated in a and b have the same qualitative form as $\cos(5\pi x/18)$

values fairly close to a Turing bifurcation point, the solution evolves rapidly to a solution of approximately constant shape, whose amplitude varies periodically with period T ; an example is illustrated in Fig. 6. The spatial period of the solution is exactly that predicted by the linear theory (see Fig. 6).

To conclude, I will briefly discuss an obvious extension of the work presented here, namely the case of $D_v(t) = D^-$ on $(nT, nT + \xi T)$ and $D_v(t) = D^+$ on $(nT + \xi T, nT + T)$, where $n \in \mathbf{Z}$ and $0 < \xi < 1$. The extension to the case $\xi \neq 1/2$ is conceptually very simple, and can be analysed in exactly the same way as $\xi = 1/2$; however, it is algebraically much more complicated, and I have been unable to obtain simple expressions for the conditions for diffusion driven instability. One particularly striking feature is that the analogue of (8) is a cubic in Δ , with all coefficients non-zero in general, rather than

being linear in Δ^2 . In terms of the perturbation theory analysis discussed above, this means that when $\xi \neq 1/2$ and $\bar{D} = D_c + \varepsilon$, $\Delta_c = O(\varepsilon)$, in contrast to the case $\xi = 1/2$, when $\Delta_c = O(\varepsilon^{1/2})$. Put simply, this implies that the sensitivity of the stability of the steady state to a square-tooth temporal variation in diffusivity is greater when there is unequal weighting of the two diffusivities than in the case of equal weighting. However this does not mean that my results are particularly sensitive to the assumption $\xi = 1/2$, since the coefficient of $\varepsilon^{1/2}$ in the expansion of Δ_c is very small when ξ is close to $1/2$.

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References

- Auchmuty, J. F. G., Nicolis, G.: Bifurcation analysis of nonlinear reaction-diffusion equation – I. Evolution equations and the steady state solutions. *Bull. Math. Biol.* **37**, 323–365 (1975)
- Benson, D. L., Sherratt, J. A., Maini, P. K.: Diffusion driven instability in an inhomogeneous domain. *Bull. Math. Biol.* **55**, 365–384 (1993a)
- Benson, D. L., Maini, P. K., Sherratt, J. A.: Pattern formation in reaction-diffusion models with spatially inhomogeneous diffusion coefficients. *Math. Comp. Modelling* **17**, 29–34 (1993b)
- Cantrell, R. S., Cosner, C.: The effects of spatial heterogeneity in population dynamics. *J. Math. Biol.* **29**, 315–338 (1991)
- Iooss, G., Joseph, D. D.: *Elementary stability and bifurcation theory*. Berlin Heidelberg New York: Springer 1980
- Levin, G., Segel, L. A.: Hypothesis for origin of planktonic patchiness. *Nature* **259**, 259 (1976)
- Maini, P. K., Benson, D. L., Sherratt, J. A.: Pattern formation in reaction-diffusion models with spatially inhomogeneous diffusion coefficients. *IMA J. Math. Appl. Med. Biol.* **9**, 197–213 (1992)
- Menhardt, H., Gierer, A.: Applications of a theory of biological pattern formation based on lateral inhibition. *J. Cell Sci.* **15**, 321–346 (1974)
- Murray, J. D.: A pre-pattern formation mechanism for animal coat markings. *J. theor. Biol.* **88**, 161–199 (1981)
- Murray, J. D.: *Mathematical Biology*. Berlin Heidelberg New York: Springer 1989
- Pacala, S. W., Roughgarden, J.: Spatial heterogeneity and interspecific competition. *Theor. Pop. Biol.* **21**, 92–113 (1982)
- Segel, L. A., Jackson, J. L.: Dissipative structure: an explanation and an ecological example. *J. theor. Biol.* **37**, 545–559 (1972)
- Shigesada, N.: Spatial distribution of rapidly dispersing animals in heterogeneous environments. In: S. A. Levin, Hallan, T. G. (eds), *Lecture Notes in Biomathematics* **54**, pp. 478–491. Berlin Heidelberg New York: Springer
- Timm, U., Okubo, A.: Diffusion-driven instability in a predator-prey system with time-varying diffusivities. *J. Math. Biol.* **31**, 307–320 (1992)
- Turing, A. M.: The chemical basis of morphogenesis. *Phil. Trans. R. Soc. Lond.* **B237**, 37–72 (1952)