

A Generalized Diffusion Model for Growth and Dispersal in a Population

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Abstract. A reaction-diffusion model is presented in which spatial structure is maintained by means of a diffusive mechanism more general than classical Fickian diffusion. This generalized diffusion takes into account the diffusive gradient (or gradient energy) necessary to maintain a pattern even in a single diffusing species. The approach is based on a Landau-Ginzburg free energy model. A problem involving simple logistic kinetics is fully analyzed, and a nonlinear stability analysis based on a multi-scale perturbation method shows bifurcation to non-uniform states.

Key words: Diffusion model – Populations – Ginzburg-Landau model

1. Introduction

Dispersal effects in deterministic models for interacting populations are usually taken to be diffusive in a Fickian sense with the resulting equations of reaction diffusion type: See Okubo [1] for an up to date review. Steady state heterogeneous structures and wave phenomena are a consequence of the interplay between the nonlinear interaction and diffusion. If $n(\mathbf{x}, t)$ denotes the population density vector, the equations are typically of the form

$$\frac{\partial n}{\partial t} = G(n) + \nabla \cdot D \nabla n, \quad (1.1)$$

where G is the nonlinear growth interaction (or in the chemical sense the kinetics), and D the diffusion matrix. If n is a scalar then (1.1) cannot sustain steady state spatial structures in a finite domain with Neumann boundary conditions.

With the complexity of ecological systems it seems restrictive to consider spatial effects (other than convection) to be simply Fickian diffusion. An approach based on a Landau-Ginzburg free energy model is more general and contains the Fickian model as a special case. We show in Section 2 below that in the scalar case

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$n(\mathbf{x}, t)$, satisfies an equation of the form

$$\frac{\partial n}{\partial t} = G(n) + DA \nabla^2 n + DB \nabla^2 n^3 - DK \nabla^4 n, \quad (1.2)$$

where D , B and k are positive constants and A may be a positive or negative constant. When $A < 0$ this is in essence equivalent to a negative diffusion coefficient in a Fickian sense. Taylor and Taylor [2] from their field work on insect migration have proposed a mechanism in which the diffusion coefficient exhibits population pressure which effectively gives a negative diffusion for small enough population densities. In more primitive organisms it is like an alternative to chemotaxis. Okubo [1] in an attempt to model schooling of fish and several other authors (see [1] for a discussion and references) in attempts to study aggregative behavior have proposed other generalizations of (1.1). These are all second order differential equations, however, and in the scalar case none of these models can exhibit bifurcation from a uniform state to a stable heterogeneous spatial structure. In (1.2) the last two terms have a spatially stabilizing effect while $DA \nabla^2 n$ with $A < 0$ is destabilizing. Such a model equation (1.2) can exhibit bifurcation to stable heterogeneous spatial structures, as we show below.

In Section 2 we discuss diffusion in the general non-Fickian sense and derive the governing equation. In Section 3 we consider the single scalar equation for a simple logistic kinetics and give the linear stability results. In Section 4 we discuss the nonlinear stability and show the bifurcation to nonuniform states. The form for the energy density which results in the model equation (1.2) is described in the appendix.

2. Generalized Diffusion

In various fields of physics, chemistry, and engineering in the last one hundred years Fick's law of diffusion has been inadequate to describe diffusive processes. In many cases generalizations and alternatives, based on fundamental physical processes, have been proposed which successfully describe and predict the experimental observations. Three main periods and problems have provided the major impetus for this development. (i) The work of Gibbs and van der Waals around the turn of the century on coexistence near the critical point led to the concepts of nucleation, metastability, and spinodal decomposition in an attempt to understand the simultaneous existence of two spatially distributed states of matter (i.e., pattern formation). The fundamental role of diffusion and its physical nature was carefully studied. (ii) The work of Cahn and his co-workers in the period 1950 – 1970 on the structure of metal alloys (again, pattern formation) led to a successful analytical formulation incorporating the concepts of a negative diffusion gradient which had been experimentally observed by x-ray techniques and which is necessary in the theory of metal alloys to account for molecular clumping (or aggregation). (iii) The recent work (1970 – 1980) on striations or patterns (in the phonon or quasi-particle density) on super-conducting thin films led to a re-examination and further development of the Gibbs-van der Waals theories this time based on the pioneering work of Landau. At about the same time as the work on metal alloys was going on, the Landau-Ginzburg theory of non-equilibrium thermodynamics was proposed to

account for the phase co-existence patterns. Inherent in this theory is a non-Fickian mechanism of diffusion. The recent work in super-conductivity has led to a satisfying theory based on the Landau-Ginzburg description. Excellent papers describing the work on metal alloys and the earlier phase co-existence problems are the major survey paper of Cahn [3] and his paper [4]. The more recent work in super-conductivity can be found in [5], [6].

In all theories the generalized diffusion reduces to simple Fickian diffusion when spatially homogeneous states are produced. The generalized diffusion takes into account the diffusive gradient (or gradient energy) necessary to maintain a pattern even in the experimentally observed situation of a single diffusing species.

Perhaps the best way to present the derivation is first to discuss the classical Fick's law in the relevant notation. Thus, suppose $n(\mathbf{x}, t)$ represents the concentration of some diffusing species. Let $f(n)$ represent the energy density (i.e., internal energy per unit volume) of some evolving pattern, so that the total energy $F[n]$ in a volume V is

$$F[n] = \int_V f(n) dx. \tag{2.1}$$

The variational derivative $\delta F/\delta n$ (that is, the change in energy or work done in changing states by an amount δn) defines a (chemical) potential $\mu(n)$; that is,

$$\mu(n) = \frac{\delta F}{\delta n} = f'(n). \tag{2.2}$$

Now, a gradient of the potential μ will drive a current \mathbf{J} , or equivalently, the flux \mathbf{J} is proportional to the gradient of μ . This is Fick's law. Thus,

$$\mathbf{J} = -D \text{grad } \mu(n), \tag{2.3}$$

where D is a proportionality constant. The basic equation of continuity (i.e., conservation of mass) then becomes

$$\frac{\partial n}{\partial t} = -\text{div } \mathbf{J} = \text{div}(D \text{grad } \mu(n)) = \text{div}(Df''(n) \text{grad } n). \tag{2.4}$$

Hence,

$$\frac{\partial n}{\partial t} = \text{div}(\tilde{D}(n) \text{grad } n), \tag{2.5}$$

where

$$\tilde{D}(n) = Df''(n). \tag{2.6}$$

In the case of the simple heat equation or a situation with constant diffusion, the internal energy density is the standard quadratic form $f(n) = \frac{1}{2}n^2$. Then, $\mu(n) = n$, and (2.5) becomes

$$\frac{\partial n}{\partial t} = D \nabla^2 n \tag{2.7}$$

with $\tilde{D}(n) \equiv D$ representing the constant diffusion coefficient. Classical Fickian nonlinear diffusion is represented by (2.5) with a nonlinear diffusivity $\tilde{D}(n)$. Clearly, the derivation remains the same if we allow D to have spatial and temporal

dependence, if we allow n to be a vector of concentrations, and if we add sources and sinks (i.e., dynamics or reaction terms) to the continuity equation to obtain the standard reaction-diffusion system

$$\frac{\partial \mathbf{n}}{\partial t} = \text{div}(\tilde{D}(\mathbf{n}, \mathbf{x}, t) \text{grad } \mathbf{n}) + G(\mathbf{n}) \quad (2.8)$$

in place of (2.5). Here $G(\mathbf{n})$ represents the dynamics (or reaction terms). This completes our derivation of Fickian diffusion.

Most derivations of (2.5) or (2.8) start at equation (2.3); that is, Fick's law as given in (2.3) is simply postulated. All we have done is to start with the internal energy (consistent with Fick's law) necessary to maintain states described by Fick's law. The pertinent feature of this energy functional (2.1) is that it depends only on the state n of the system through the density $f(n)$. However, stable inhomogeneous states (i.e., patterns) exist in many fields. These patterns often contain large changes in concentrations (i.e., concentration gradients), and thus, there must be a gradient energy necessary to maintain such a state. That is, phenomenologically instead of (2.1) a more realistic energy functional is

$$F[n] = \int_V [f(n) + \frac{1}{2}k(\nabla n)^2 + \dots] dx. \quad (2.9)$$

Here $f(n)$ represents the energy density which this volume would have in a homogeneous composition, and the other terms represent the energy density (a "gradient" energy) which is a function of local composition and which clearly will be significant in non-homogeneous states. The proof that (2.9) is the precise form of the integrand necessary to preserve various physical and geometrical quantities is given in Appendix A. In one form or another this is the crucial step in all the fields mentioned above. Our derivation most closely follows the work of Cahn and Landau-Ginzburg.

Now, we simply re-trace the steps in going from (2.1) to (2.8). The potential μ induced by our energy functional (2.9) is given by

$$\mu = \mu(n, \nabla n) = \frac{\delta F}{\delta n} = -k \nabla^2 n + f'(n), \quad (2.10)$$

so that the flux \mathbf{J} is given by

$$\mathbf{J} = -D \text{grad } \mu(n, \nabla n). \quad (2.11)$$

Incorporating first order spatial effects the equation of continuity then becomes

$$\begin{aligned} \frac{\partial n}{\partial t} &= -\text{div } \mathbf{J} = \text{div}(D \text{grad } \mu) \\ &= D \nabla^2 (-k \nabla^2 n + f'(n)) \\ &= -kD \nabla^4 n + \text{div}(Df''(n) \text{grad } n). \end{aligned} \quad (2.12)$$

We show in Appendix A that the appropriate form for $f(n)$ is

$$f(n) = \frac{1}{2}An^2 + \frac{1}{4}Bn^4. \quad (2.13)$$

Thus, (2.12) becomes

$$\frac{\partial n}{\partial t} = -Dk\nabla^4 n + DA\nabla^2 n + DB\nabla^2 n^3. \quad (2.14)$$

Finally, if we incorporate the dynamics (or reaction terms), we obtain

$$\frac{\partial n}{\partial t} = -Dk\nabla^4 n + DA\nabla^2 n + DB\nabla^2 n^3 + G(n). \quad (2.15)$$

The equations (2.14), (2.15) are the generalizations of equations (2.5), (2.8) respectively. In the one-dimensional case, which we study in detail in the next sections, equation (2.15) becomes

$$\frac{\partial n}{\partial t} = -Dk\frac{\partial^4 n}{\partial x^4} + D(A + 3Bn^2)\frac{\partial^2 n}{\partial x^2} + 6DBn\left(\frac{\partial n}{\partial x}\right)^2 + G(n). \quad (2.16)$$

3. Patterns for a Single Diffusion Species

We shall consider the interaction of our generalized diffusion with kinetics of logistic type by way of example. Thus, we analyze

$$\frac{\partial n}{\partial t} = -Dk\frac{\partial^4 n}{\partial x^4} + D(A + 3Bn^2)\frac{\partial^2 n}{\partial x^2} + 6DBn\left(\frac{\partial n}{\partial x}\right)^2 + k_1 n - k_2 n^2. \quad (3.1)$$

This model has been proposed by Huberman [5] to study strictions in chemical reactions. Huberman presented only a plausibility argument based on linear analysis. Coutsias [7], using more advanced perturbation methods, then derived the nonlinear exchange of stability mechanism. Our presentation follows the work of Coutsias who used the multi-scale methods suggested by Boa and Cohen [8]. Coutsias and Huberman [9] have examined the implications of this generalized diffusion in general Ginzburg-Landau systems.

Our major results are that while much of the structure contained in the standard second order reaction-diffusion equation (with the same non-linearity) is totally preserved, significant qualitative changes are produced especially near bifurcation points. We are able to assess clearly the role of the Fickian part of the diffusion in its attempt to produce homogeneous equilibrium states and the non-Fickian part in maintaining species aggregation.

Uniform (i.e., homogeneous) steady states are given by

$$n \equiv 0 \quad \text{and} \quad n \equiv \frac{k_1}{k_2}. \quad (3.2)$$

With k_1 as parameter the bifurcation theory for the standard second order reaction-diffusion equation is illustrated in Figure 1. As k_1 varies from negative to positive (for fixed $k_2 > 0$) the steady state $n \equiv 0$ loses its stability at $k_1 = 0$ and the system changes to the stable steady state $n \equiv k_1/k_2$. Both states are uniform, with no pattern formed.

We now present the linearized stability analysis of (3.1) for the basic steady states (3.2). Some of the algebraic manipulation, while straight-forward, is lengthy.

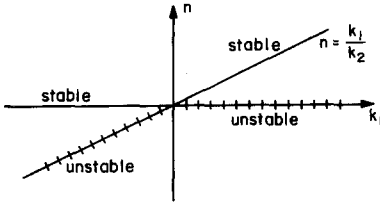


Fig. 1

We shall exhibit only the major steps referring the reader to [7] where the detailed algebraic manipulation is carried out.

To carry out the linearized stability analysis of the state $n \equiv k_1/k_2$, let $n(x, t) = (k_1/k_2) + n_1(x, t)$, substitute into (3.1), and retain only linear terms to obtain in the usual way

$$\frac{\partial n_1}{\partial t} = -k_1 n_1 + \left(DA + 3DB \frac{k_1^2}{k_2^2} \right) \frac{\partial^2 n_1}{\partial x^2} - Dk \frac{\partial^4 n_1}{\partial x^4}. \tag{3.3}$$

Solutions are

$$n_1(x, t) = e^{\sigma t} e^{iqx}, \tag{3.4}$$

where

$$\sigma = -k_1 - \left(DA + 3DB \frac{k_1^2}{k_2^2} \right) q^2 - Dkq^4. \tag{3.5}$$

Similarly, if we linearize about the state $n \equiv 0$, we find that the perturbation term $n_1(x, t)$ satisfies

$$\frac{\partial n_1}{\partial t} = k_1 n_1 + DA \frac{\partial^2 n_1}{\partial x^2} - Dk \frac{\partial^4 n_1}{\partial x^4}, \tag{3.6}$$

solutions of which are again of the form (3.4) where now

$$\sigma = k_1 - DAq^2 - Dkq^4. \tag{3.7}$$

These dispersion relations (3.5) and (3.7) are illustrated in Fig. 2.

The mechanism for pattern formation and the structure of the bifurcation diagram is now clearly revealed. Consider, for example, the stability of the state $n \equiv 0$. From Fig. 3 we see that as we vary k_1 , the state $n \equiv 0$, which is stable for $k_1 < k_{1c}^-$, loses its stability at $k_1 = k_{1c}^-$. As we pass through this critical value we expect a new state to evolve with the spatial structure $e^{\pm iq_c x}$. Here

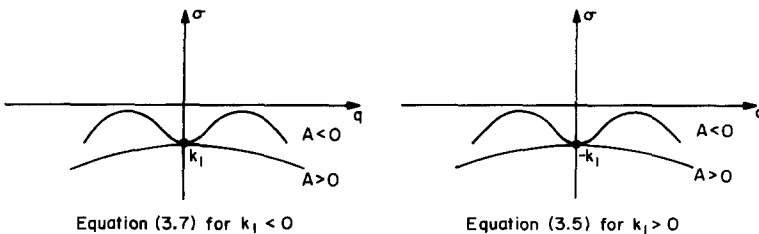


Fig. 2

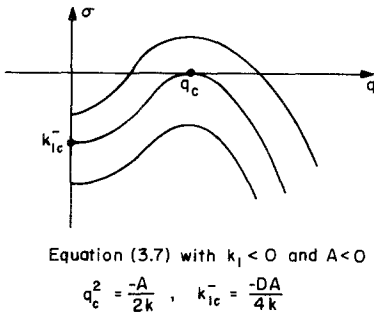


Fig. 3

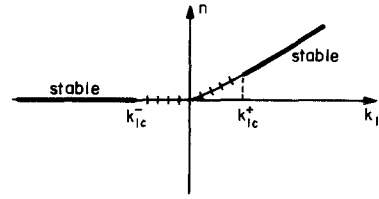


Fig. 4

$$q_c^2 = \frac{-A}{4k}, \quad k_{1c}^- = \frac{-DA^2}{4k}. \tag{3.8}$$

Similar considerations apply for the stability of the state $n \equiv k_1/k_2$, where k_{1c}^+ is the positive solution of

$$\frac{3B}{k_2^2} k_{1c}^{+2} + \left(\frac{2k}{D}\right)^{1/2} (k_{1c}^+)^{1/2} + A = 0, \quad q_c^2 = \left(\frac{k_{1c}^+}{2kD}\right)^{1/2}. \tag{3.9}$$

These results are best understood by a glance at the bifurcation diagram of Fig. 4. As k_1 varies from negative to positive, we clearly see the loss of stability of the state $n \equiv 0$ at $k_1 = k_{1c}^-$ and the onset of the stability of the state $n \equiv k_1/k_2$ at $k_1 = k_{1c}^+$. Our linearized theory clearly indicates (and we shall confirm it with our nonlinear analysis of Section 4) that stable patterns (with spatial structure of the form $\frac{\sin}{\cos} q_c x$) can develop at the bifurcation points $k = k_{1c}^-, k_{1c}^+$. In fact, branches connecting the stable state at $k_1 < k_{1c}^-$ with that at $k_1 > k_{1c}^+$ may take several different shapes depending on various relationships among the parameters of the problem; we now present this in Section 4.

4. Nonlinear Stability Analysis: Bifurcation of Nonuniform States

When the uniform state is unstable, solutions starting with initial conditions near the solutions can be calculated asymptotically when k_1 is near k_{1c}^- or k_{1c}^+ . We shall carry out such an analysis using a multi-scale perturbation method.

Let k_1 be close to the critical value k_1 , where k_1 represents either k_{1c}^- or k_{1c}^+ ; that is, we define a small parameter ε ($0 < \varepsilon \ll 1$) by

$$k_1 = \overline{k_1} + \varepsilon^2 \delta \quad (\varepsilon \ll q_c), \tag{4.1}$$

and assume a solution of (3.1) of the form

$$n = n_0 + \varepsilon n_1(x, t, \xi, \tau) + \varepsilon^2 n_2(x, t, \xi, \tau) + \dots, \tag{4.2}$$

where n_0 represents either 0 or k_1/k_2 , and where

$$\xi = \varepsilon x, \quad \tau = \varepsilon^2 t. \tag{4.3}$$

The critical part of our analysis is clearly the assumed structure (4.1)–(4.3). The justification for this form and the scaling used in x is suggested by the geometry of the problem and in t from the structure of the equations. With wave numbers in a neighborhood of q_c , say $q_1 = q_c - \varepsilon/2$, $q_2 = q_c + \varepsilon/2$, combining two cosines for example gives $\cos q_1 x \cos q_2 x = \frac{1}{2}(\cos 2q_c x + \cos \varepsilon x)$: this suggests εx as the x -scaling.

We now carry out the perturbation procedure. Upon inserting (4.1)–(4.3) into (3.1) and equating coefficients of like powers of ε , we obtain

$$Ln_1 = 0, \quad (4.4)$$

where the operator L is defined by

$$Ln \equiv \left[\partial_t + |k_1| \left(\frac{1}{q_c^4} \partial_{xxxx} + \frac{1}{q_c^2} \partial_{xx} + 1 \right) \right] n, \quad (4.5)$$

$$Ln_2 = -\frac{4|k_1|}{q_c^2} \partial_{x\xi} \left(\frac{1}{q_c^2} \partial_{xx} + 1 \right) n_1 + \delta n_0 + (3n_0 DB \partial_{xx} - k_2) n_1^2, \quad (4.6)$$

$$Ln_3 = -\partial_t n_1 + \delta n_1 + \frac{4|k_1|}{q_c^2} \partial_{\xi\xi} n_1 - 2(k_2 - 3DBn_0) \partial_{xx} n_1 n_2 + DB \partial_{xx} n_1^3 \\ + \left[6DBn_0 \partial_{x\xi} n_1^2 - \frac{4|k_1|}{q_c^2} \partial_{x\xi} \left(\frac{1}{q_c^2} \partial_{xx} + 1 \right) n_2 \right]. \quad (4.7)$$

The general solution of (4.4) is

$$n_1 = \int_{-\infty}^{\infty} (\tilde{A}(\xi, \tau, q) \cos qx + \tilde{B}(\xi, \tau, q) \sin qx) \exp[\sigma(q)t] dq, \quad (4.8)$$

where the unknown functions \tilde{A} and \tilde{B} will be determined at a later stage of the perturbation procedure. Equation (4.8) represents the full solution n_1 , valid for all time, but it leads to expressions of unmanageable complexity in the further analysis. Things can be simplified considerably and the equations for \tilde{A} and \tilde{B} can be determined if we perform an asymptotic analysis for large time at every step. Hence, since $\alpha(q)$ has a maximum at $q = q_c$, we can use the standard method of Laplace to get the asymptotic form of the integral in (4.8). We obtain

$$n_1 \sim \tilde{A}(\xi, \tau) \cos q_c x + \tilde{B}(\xi, \tau) \sin q_c x. \quad (4.9)$$

Assuming that such a calculation can be carried out at every step, we can in effect ignore t -dependence in our further analysis and carry out all calculations asymptotically for large time. Thus, we substitute (4.9) into the right-hand side of (4.6) to obtain

$$Ln_2 = \left[\delta n_0 - k_2 \left(\frac{\tilde{A}^2 + \tilde{B}^2}{2} \right) \right] \\ - (12DBn_0 q_c^2 + k_2) \left[\frac{1}{2}(\tilde{A}^2 - \tilde{B}^2) \cos 2q_c x + \tilde{A}\tilde{B} \sin 2q_c x \right], \quad (4.10)$$

the solution of which is

$$\begin{aligned}
 n_2 = & \frac{1}{|k_1|} \left[\delta n_0 - k_2 \left(\frac{\tilde{A}^2 + \tilde{B}^2}{2} \right) \right] \\
 & + \frac{1}{9|k_1|} (12DBn_0q_c^2 + k_2) \left[\frac{1}{2}(\tilde{A}^2 + \tilde{B}^2) \cos 2q_c x + \tilde{A}\tilde{B} \sin 2q_c x \right] \\
 & + \text{homogeneous solution.}
 \end{aligned} \tag{4.11}$$

At the next stage we have

$$\begin{aligned}
 Ln_3 = & \left[-\partial_\tau + \delta + \frac{4|k_1|}{q_c^2} \partial_{\xi\xi} - \frac{2}{|k_1|} \left\{ \delta n_0 - \frac{(19k_2 + 12DBn_0q_c^2)}{36} (\tilde{A}^2 + \tilde{B}^2) \right\} \right. \\
 & \left. \times (k_2 + 3BDn_0q_c^2) - \frac{3}{4} DBq_c^2 (\tilde{A}^2 + \tilde{B}^2) \right] n_1 + \text{higher harmonics.}
 \end{aligned} \tag{4.12}$$

The solution n_3 will become unbounded, due to the appearance of secular terms, unless we require the square bracket on the right of (4.12) to vanish [with n_1 from (4.9)] which gives the equations for A and B at $n_0 = 0$ and $n_0 = k_1/k_2$. At $n_0 = 0$ ($k_1 < 0$, $k_{1c}^- = -DA^2/8k$, $q_c^2 = |A|/4k$), suppression of secular terms gives

$$\begin{aligned}
 \frac{\partial \tilde{A}}{\partial \tau} &= [\delta - \lambda(\tilde{A}^2 + \tilde{B}^2)]\tilde{A} + 2D|A|\tilde{A}_{\xi\xi}, \\
 \frac{\partial \tilde{B}}{\partial \tau} &= [\delta - \lambda(\tilde{A}^2 + \tilde{B}^2)]\tilde{B} + 2D|A|\tilde{B}_{\xi\xi},
 \end{aligned} \tag{4.13}$$

where

$$\lambda = \frac{3DB|A|}{16k} - \frac{76kk_2^2}{9DA^2}. \tag{4.14}$$

The behavior of n_1 in (4.9) with \tilde{A} , \tilde{B} from (4.13) is summarized in Table 1: There is a threshold effect in the case $\lambda < 0$, $\delta < 0$.

At $n_0 = k_1/k_2$ suppression of secular terms gives equations similar to (4.13) from which an equivalent table to Table 1 can be obtained: the results are illustrated qualitatively in Figs. 5–7 with the parameter ranges given in the legends.

Table 1. Behavior near the bifurcation when $n_0 = 0$; λ as in (4.14)

	$\lambda < 0$	$\lambda > 0$
$\delta < 0$	n_1 blows up unless it is small enough initially ($\tilde{A}^2(\xi, 0) + \tilde{B}^2(\xi, 0) < \delta/\lambda$) in which case it decays to zero	$n_1 \rightarrow 0$
$\delta > 0$	n_1 blows up	n_1 evolves to some bounded steady state with $\tilde{A}^2 + \tilde{B}^2 \rightarrow \delta/\lambda > 0$

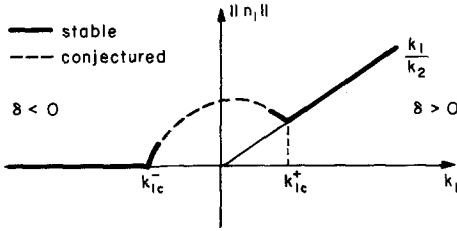


Fig. 5. Bifurcation diagram for

$$DBq_+^2 > \frac{38}{27} \frac{k_2^2}{k_+} \left(1 + 3BDq_+^2 \frac{k_+}{k_2^2}\right) \left(1 + 12BDq_+^2 \frac{k_+}{19k_2^2}\right), \quad DBq_-^2 > \frac{-38}{27} \frac{k_2^2}{k_-}.$$

Here q_+ , k_+ and q_- , k_- correspond to q_c and k_{1c} in (3.9) and (3.8) respectively

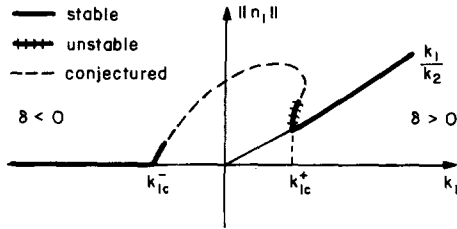


Fig. 6. Bifurcation diagram for

$$DBq_+^2 < \frac{38}{27} \frac{k_2^2}{k_+} \left(1 + 3BDq_+^2 \frac{k_+}{k_2^2}\right) \left(1 + 12BDq_+^2 \frac{k_2}{19k_2^2}\right), \quad DBq_-^2 > \frac{-38}{27} \frac{k_2^2}{k_-}$$

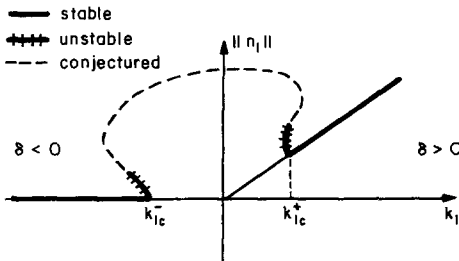


Fig. 7. Bifurcation diagram for

$$DBq_+^2 < \frac{38}{27} \frac{k_2^2}{k_+} \left(1 + 3BDq_+^2 \frac{k_+}{k_2^2}\right) \left(1 + 12BDq_+^2 \frac{k_+}{19k_2^2}\right), \quad DBq_-^2 < \frac{-38}{27} \frac{k_2^2}{k_-}$$

Therefore, to leading order in ϵ the solutions of (3.1) near the bifurcation points are given by (4.9), where the evolution equations for $\tilde{A}(\xi, \tau)$ and $\tilde{B}(\xi, \tau)$ are given by (4.13), near $n_0 = 0$ with similar equations near $n_0 = k_1/k_2$. These equations determine both the stability and the bifurcation structure both of which are illustrated in Figs. 5–7. The dashed continuation lines are conjectures.

5. Analysis of the Smooth Transition Case

Consider Fig. 5 near $k_1 = k_{1c}^-$ which we shall analyze by way of illustration. The evolution equations for \tilde{A} and \tilde{B} in the solution (4.9) for n_1 are given by (4.13). Evolution to a stable state requires $\lambda > 0$ and $\delta > 0$, where λ is given by (4.14). By appropriate scaling we need only consider

$$\tilde{A}_\tau = \tilde{A}[1 - (\tilde{A}^2 + \tilde{B}^2)] + \tilde{A}_{\xi\xi}, \quad \tilde{B}_\tau = \tilde{B}[1 - (\tilde{A}^2 + \tilde{B}^2)] + \tilde{B}_{\xi\xi}. \quad (5.1)$$

The form of (5.1) suggests transforming the system according to

$$\tilde{A} = R \cos \phi, \quad \tilde{B} = R \sin \phi,$$

where R, ϕ satisfy

$$R_\tau = R(1 - R^2) + R_{\xi\xi} - R\phi_\xi^2, \quad \phi_\tau = \frac{1}{R^2}(R^2\phi_\xi)_\xi. \quad (5.2)$$

A one-parameter family of solutions is

$$\begin{aligned} \phi &= c\xi + (\text{arbitrary constant}), \\ R &= R(\tau; c) \quad \text{where} \quad R_\tau = R(1 - R^2) - Rc^2, \end{aligned} \quad (5.3)$$

which, as $\tau \rightarrow \infty$, evolve to

$$\phi = c\xi, \quad R = (1 - c^2)^{1/2} \equiv R_0, \quad |c| < 1. \quad (5.4)$$

Such solutions are linearly stable if $|c| < 1/\sqrt{3}$. This gives

$$n_1(x, t \rightarrow \infty) = (1 - c^2)^{1/2} \text{Re}[\exp(ix(q_c + \varepsilon c))],$$

to within some scaling constants. A similar solution for n_1 obtains near $n = n_0 \neq 0$.

The $R - \phi$ equations (5.2) have another family of solutions given by

$$\phi = c, \quad R = R(\xi); \quad R_{\xi\xi} + R(1 - R^2) = 0,$$

and so $R(\xi)$ is a Jacobian elliptic function. If R is linearized about a periodic function a partial differential equation is obtained the spatial part of which is a Hill operator. This means that positive eigenvalues always exist [10] which lead to growing exponentials: this means that such periodic solutions for R are unstable.

6. Conclusions

By considering a more general non-Fickian approach we have obtained a model equation, namely (2.14), which we propose as a mechanism governing population growth and dispersal of a single species. It takes into account, in a fuller way, effects of population pressure which is now fairly widely accepted as an ecological factor. Population aggregation against a concentration gradient, as is observed in many insect populations, is possible with such a model. We have investigated the consequences of this by considering the solution behaviour near bifurcation points. In the case of a specific growth, namely logistic, we have found spatial structures which result from a nonlinear stability analysis near bifurcation. From Figs. 5–7 the solution behaviour near the bifurcation points is non-standard and exhibits a variety of possible behavior.

Appendix A. The Energy Density

The energy density must be invariant under reflections ($x_i \rightarrow -x_i$) and rotations ($x_i \rightarrow x_j$). Thus

$$F[n] = \int_N [f(n) + k_1 \nabla^2 n + k_2 (\nabla n)^2 + \dots] dx. \quad (\text{A.1})$$

Consider the term involving $k_1 \nabla^2 n$. Green's Theorem implies that we can write this term as

$$\int_V k_1 \nabla^2 n dx + \int_V \nabla k_1 \cdot \nabla n dx = \int_S k_1 \frac{\partial n}{\partial \mathbf{N}} d\sigma, \quad (\text{A.2})$$

where \mathbf{N} represents the outward pointing normal to the surface S bounding the volume V . We are allowing k_1 to depend on n so that $\nabla k_1 = k'_1(n) \nabla n$. Thus

$$\int_V k_1 \nabla^2 n dx = - \int_V k'_1(n) (\nabla n)^2 dx + \int_S k_1 \frac{\partial n}{\partial \mathbf{N}} d\sigma. \quad (\text{A.3})$$

Since we are not concerned with the effects at the external surface, we can choose the boundary S such that $\partial n / \partial \mathbf{N} = 0$ on S . Therefore, (A.1) becomes

$$F[n] = \int_V [f(n) + \frac{1}{2} k (\nabla n)^2 + \dots] dx \quad (\text{A.4})$$

where

$$\frac{1}{2} k = -k'_1(n) + k_2. \quad (\text{A.5})$$

The basic Landau-Ginzburg assumption for $f(n)$ is that

$$f(n) = \frac{1}{2} A n^2 + \frac{1}{4} B n^4. \quad (\text{A.6})$$

Only even powers of n appear because the energy density cannot depend on the sign of n . For example in the context of the thermodynamics of phase transition given by

$$A = A_0(T - T_c), \quad (\text{A.7})$$

where A_0 is some constant, T is the temperature, and T_c is the critical temperature. In our usage in this paper the parameter T (with a critical value $T = T_c$) is a parameter associated with the species' environment or the population's behavior when near an aggregative state. Just as in all previous physical contexts, the parameter A can assume positive or negative values. Note that if we designate the coefficient DA of the second derivative in (2.14) as the "diffusion coefficient," then negative diffusion is possible. However, the stabilizing mechanism then becomes the fourth order term in the production of a pattern. In the previous applications to metal alloys and super-conducting thin films, this theory has been successful both qualitatively and quantitatively.

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