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# Spatial Structures in Nonlinear Interaction-Diffusion Systems

by

Masayasu Mimura

Dept. of Applied Mathematics, Konan University, Kobe, Japan

1. INTRODUCTION. Recently nonlinear "reaction-diffusion" or "interaction-diffusion" equations have been studied as models for problems in chemical reactor[1,2], in genetics[3,4], in morphogenesis[5,6], in ecology[7,8], in plasma physics[9] and other fields. As will be seen, the most interesting work is to analyze qualitative behaviors of solutions of the equations. Most of equations are described by

$$U_t = DU_{xx} + F(x,U).$$

Here the state variable $U$ denotes certain measures such as density, concentration, etc.. Restricting the boundary condition to no flux one, we may say that the environment govering the state is homogeneous if $F(x,U)$ is independent of $x$, on the other hand, if $F(x,U)$ depends on $x$, it is inhomogeneous. In this paper we are interested in the latter case when the heterogeneity is sufficiently small. This study is motivated by Gierer and Meinhardt[6]. They proposed some models to explain the mechanism of re-generation on hydra. The models are constructed such that Child's gradient theory[10] is combined with usual chemical reaction-diffusion

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A part of this note is a short version of Mimura and Murray.[21]

equations in Turing's sense[5]. This theory necessarily makes the environment inhomogeneous. The analyses of this model system were done theoretically as well as numerically[6,11]

In this paper we consider a particular system which is one of prey-predator interaction models with diffusion processes

$$u_t = d_1 u_{xx} + f(x,u)u - uv$$

$$v_t = d_2 v_{xx} - g(v)v + kuv.$$

Here u and v represent the population densities of a prey species and its predator, f(x,u) is the reproductive rate of u which depends on position x, g(v) is the death rate of u and k is the frequency of encounters. We intend to discuss spatial structures of solutions under no flux boundary conditions. The mathematical tool used here is a perturbed bifurcation theory. The rest of this paper is an application of a singular perturbation theory to the above system.

We show that there appears a striking spatial pattern although the environment is slightly homogeneous. This result seems to explain the bloom phenomenon of plankton in ecology.

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2. FORMULATION OF THE PROBLEM. From the discussion in Section 1, our study of prey-predator population interaction will be described by

$$(2\text{-}1)_1 \qquad U_t = DU_{xx} + F(x,U),$$

Here $U = {}^t(u,v)$, $D$ is a diagonal matrix whose elements are non-negative constants $d_1$ and $d_2$ and $F(x,U)$ is given by

$$F(x,U) = {}^t(\, e(x)f(u)u - uv,\ - g(v)v + uv\,),$$

where we put $k = 1$ for simplicity. We assume that $f$ and $g$ are both appropriately smooth in the quadrant $(u,v) \geqq 0$, and that they satisfy the following conditions:

(f-1) There is a constant $c_1 > 0$ s.t. $f(u) < 0$ for $u > c_1$.

(f-2) The $f(u)$ curve satisfies the Allee effect as shown in Fig.1.

(g-1) There is a constant $c_2 > 0$ s.t. $g(v) > c_2$ for $v \geqq 0$.

(g-2) $g(v)$ is strictly monotone increasing as shown in Fig.2.

We assume that $e(x) = e + \varepsilon\bar{e}(x)$ for some positive constant $e$ and a bounded function $\bar{e}(x)$. $\varepsilon$ is a constant which measures heterogeneity in environment. Moreover, we assume

(fg-1) There exists at least one positive constant solution $\bar{U} = {}^t(\bar{u},\bar{v})$ satisfying $ef(\bar{u}) = \bar{v}$ and $g(\bar{v}) = \bar{u}$.

We consider the initial-boundary value problem for $(2\text{-}1)_1$ in $(t,x) \in R^1_+ \times I = (0,\ell)$ subject to the boundary and initial conditions

$$(2\text{-}1)_2 \qquad U_x(t,0) = U_x(t,\ell) = 0, \quad t \in R^1_+$$

and

$$(2\text{-}1)_3 \qquad U(0,x) = U_0(x), \ x \in \bar{I}.$$

The global existence and uniqueness of smooth solutions to this problem have been proved fully in various function spaces, if $\varepsilon$ is sufficiently small.[12,13]

Remark 2-1. If $d_1$ and $d_2$ are both large enough, and $\varepsilon = 0$, the solution of (2-1) tends to be homogeneous asymptotically. That is, it tends to a solution of an associated system of ordinary differential equations.[14] Accordingly, our interest in (2-1) is that either $d_1$ or $d_2$ is not large. In ecology, we sometimes encounter such cases, for a special example, the reader may imagine "plant-herbivore systems".

3. BIFURCATION ANALYSIS. Employing the Lyapunov-Schmidt method,[15,16] one can demonstrate small amplitude heterogeneous steady state solutions of (2-1). It is convenient to introduce a vector $V = U - \bar{U}$. The resulting system for $V$ is

$(3\text{-}1)_1$ $$V_t = DV_{xx} + G(x,V), \quad (t,x) \in R^1_+ \times I,$$

$(3\text{-}1)_2$ $$V_x(t,0) = V_x(t,\ell) = 0, \quad t \in R^1_+$$

and

$(3\text{-}1)_3$ $$V(0,x) = V_0(x) = U_0(x) - \bar{U}, \quad x \in \bar{I}.$$

Here $G(x,V) = F(x,V + \bar{U})$. We may write $G$ as

$$G(x,V) = BV + H(V) + \varepsilon R(x,V),$$

where $B = \{b_{ij}\}$ is the Jacobi matrix of ${}^t(ef(u)u - uv, - g(v)v + uv)$ at $U = \bar{U}$, $H(V)$ is a smooth nonlinear term satisfying $H(0) = H_V(0) = 0$, and $G(x,V)$ is a function of $x$ and $U$ such that $G(x,0) \neq 0$.

Our discussion is restricted to the case when B satisfies

(B-1) $b_{11} > 0$,

(B-2) $\det B > 0$

and

(B-3) $\operatorname{tr} B < 0$.

Under the above conditions, we consider the bifurcation problem of the stationary problem for (3-1)

$$(3\text{-}2)_1 \qquad DV^s_{xx} + BV^s + H(V^s) + \varepsilon R(x,V^s) = 0, \quad x \in I,$$

$$(3\text{-}2)_2 \qquad V^s_x(0) = V^s_x(\ell) = 0.$$

Here $d = (d_1, d_2)$ is used as bifurcation parameters and it is assumed to vary along any fixed path $d = d(\sigma)$ with one parameter $\sigma$.

Lemma 3-1. Let the curves $C_n$ be

$$C_n: \ \{b_{11} - d_1(\frac{n\pi}{\ell})^2\}\{b_{22} - d_2(\frac{n\pi}{\ell})^2\} = b_{12}b_{21}$$

for $n \geqq 1$. Then the bifurcation curve $\Gamma$ is given by

$$\Gamma = \bigcup_{n=1}^{\infty} \{d \in C_n \,|\, P_n \leqq d_1 < P_{n-1}\},$$

where $P_0 = b_{11}(\frac{\ell}{\pi})^2$ and $P_n$ $(n \geqq 1)$ is an abscissa of the intersecting point of $C_n$ and $C_{n+1}$.

(proof) The details are given in Mimura-Nishiura-Yamaguti.[17]

Here $d = d(\sigma)$ is defined more explicitly as follows:

(d-1) $d: I_0 \to R^2_+$ is a smooth mapping, where $I_0$ is an open interval in $R^1$ which contains 0.

(d-2) $d(0)$ lies on $\Gamma$ and $d$ intersects transversally with $\Gamma$.

(d-3) $d(0)$ is not an intersecting point of two points of $\{C_n\}$.

Theorem 3-1. Let $\varepsilon$ be fixed sufficiently small. There exists some constant $\mu_0 > 0$ s.t. (3-2) has a unique one parameter family of solutions $(\sigma(\mu), v^s(\mu)) \in R^1 \times \{(H_N^2(I))^2 \cap \hat{O}\}$ for $|\mu| < \mu_0$, where $H_N^2(I)$ = closure of $\{\cos\frac{n\pi x}{\ell}\}_{n=0}^{\infty}$ in $H^2(I)$ and $\hat{O}$ is an open set in $(L^2(I))^2$ with $0 \in O$. Here $\sigma(0) = \hat{0}$ when $\varepsilon = 0$ and

$$v^s(\mu) = \mu\Phi_n + o(\mu),$$

where $\Phi_n$ is the normalized eigenvector corresponding to the zero eigenvalue of

(3-3)$_1$ $\qquad L(0)\Psi = \lambda\Psi, \quad x \in I,$

(3-3)$_2$ $\qquad \Psi_x(0) = \Psi_x(\ell) = 0$

for $L(0) = D(0)\dfrac{d^2}{dx^2} + B$.

Theorem 3-2. The relation between $\sigma$, $\varepsilon$ and $\mu$ is determined by the scalar equation

$$\alpha\mu\sigma + \beta\mu^3 + \gamma\varepsilon + \eta(\sigma,\varepsilon,\mu) = 0,$$

where $\eta$ is higher order terms compared with the first three terms. $\alpha$ and $\beta$ are both some constants and $\gamma$ is defined by

$$\gamma = (R(x,0), \Phi_n^*),$$

$\Phi_n^*$ is the normalized eigenvector corresponding to the zero eigenvalue of

(3-4)$_1$ $\qquad L^*(0)\Psi = \lambda\Psi, \quad x \in I,$

$$(3\text{-}4)_2 \qquad \Psi_x(0) = \Psi_x(\ell) = 0$$

The proofs can be obtained with the framework of "perturbed bifurcation theory at simple eigenvalues"[17,18]

4. APPLICATION. Using the result in Section 3, we try to explain the behavior of planktonic bloom. Assuming that the bifurcation path $d = d(\sigma)$ starts from the stable region and goes into the unstable region, that is,

$$d_1(\sigma) = d_1(0) + k_1\sigma + 0(\sigma) \ ,$$

$$d_2(\sigma) = d_2(0) + k_2\sigma + 0(\sigma)$$

for some konstants $k_1 < 0$ and $k_2 > 0$, then, after some calculation, we see $\alpha > 0$. Moreover we assume that $d = d(\sigma)$ intersects with $\Gamma \cap C_2$, and that $\bar{e}(x)$ is defined by

$$\bar{e}(x) = \begin{cases} 1, & x \in \left(\frac{\ell}{4}, \frac{3\ell}{4}\right) \\ 0, & \text{otherwise} \ , \end{cases}$$

for simplicity. Noting that

$$R(x,0) = {}^t(\ \bar{e}(x) f(\bar{u})\bar{u},\ 0\ ) \quad \text{and}$$

$$\Phi_2^* = \frac{2}{\ell} \frac{\cos \frac{2\pi x}{\ell}}{\sqrt{\{d_2(0)(\frac{2\pi}{\ell})^2 - m_{22}\}^2 + m_{12}^2}} \, {}^t(d_2(0)(\tfrac{2\pi}{\ell})^2 - m_{22}, m_{12}),$$

we find $\gamma < 0$. Finally from an actual point of view, restricting to stable solutions, $\beta < 0$ must be satisfied.[18] Thus, the bifurcation equation in Theorem 3-2 leads to the bifurcation diagram displayed in Fig. 3. This picture can be obtained by use of Thom's transversality.[19] Thus, in the neighborhood of $\sigma = 0$, there appears spatial pattern and both densities are higher on $(\frac{\ell}{4}, \frac{3\ell}{4})$ compared with other interval. Here we emphasize that the heterogeneity of both densities is striking compared with that of environment. The picture is drawn in Fig.4.

5. SINGULAR PERTURBATION ANALYSIS. We next construct large amplitude steady state solutions of (3-1) when $d_1$ is zero or sufficiently small. We assume in this section that $\bar{U}$ is unique, and that $\varepsilon = 0$. We consider (3-2) in the special case $d_1 = 0$. The resulting system has the form

$$(5\text{-}1)_{1a} \qquad ef(u)u - uv = 0, \quad x \in I,$$

$$(5\text{-}1)_{1b} \qquad d_2 v_{xx} - g(v)v + uv = 0, \quad x \in I.$$

The boundary conditions are

$$(5\text{-}1)_2 \qquad u_x(x) = v_x(x) = 0 \quad \text{at} \quad x = 0 \quad \text{and} \quad \ell.$$

It follows from $(5\text{-}1)_{1a}$ that

$$(5\text{-}2) \qquad u = 0 \quad \text{or} \quad ef(u) = v.$$

Since $f(u)$ has the nonlinearity called the Allee effect, (5-2) implies that $u$ generally takes three different values for $v$, say $h_1(v)\,(= 0)$, $h_2(v)$ or $h_3(v)$ $(h_2 < h_3)$. Thus three single equations are derived from $(5\text{-}1)_{1b}$:

$$(5\text{-}3)_i \qquad d_2 v^i_{xx} + G_i(v^i) = 0 \quad \text{for} \quad i = 1,2 \text{ and } 3,$$

where $G_i(v) = -g(v)v - h_i(v)v$. Now we can consider two different kind of boundary value problems. One is that $(5\text{-}3)_i$ is satisfied in the whole domain $I$, the other is that $I$ consists of at least two different parts of $I_i$ ( $i = 1,2$ and $3$ ) and that $(5\text{-}3)_i$ is satisfied on each domain $I_i$. It is easy to infer that the former case implies small amplitude waves, on the other hand, the latter produces large amplitude waves. The latter seems to be interesting, though the following problem happens: How $I_i$ can be determined in $I$ ? In order to study this problem, we use a singular perturbation technique.[20,21] We first consider the stationary problem (3-2) with non zero but sufficiently small $d_1$,

$$(5\text{-}4)_{1a} \qquad d_1 u^s_{xx} + ef(u^s)u^s - u^s v^s = 0, \quad x \in I$$

$$(5\text{-}4)_{1b} \qquad d_2 v^s_{xx} - g(v^s)v^s + u^s v^s = 0, \quad x \in I.$$

Suppose that there exists a solution $(u(x),v(x))$ of the problem (5-1) such that

$$\lim_{d_1 \to 0} u^s(x) = u(x) \quad \text{for almost all } x \in \bar{I}$$

and

$$\lim_{d_1 \to 0} v^s(x) = v(x) \quad \text{for all } x \in \bar{I} .$$

Numerical evidences confirm the validity of this assumption. By transforming from $x$ to $\frac{x - x^*}{\sqrt{d_1}} = y$ where $x^*$ is an arbitrary fixed seperating point between $I_i$ and $I_j$ $(i \neq j)$, $(5\text{-}4)_{1a}$ is reduced to

$$(5\text{-}5)_{1a} \qquad u^s_{yy} + ef(u^s)u^s - u^s v^s = 0.$$

With the aid of the continuity of $v^s(x)$ at the point $x^*$, it follows

(5-6)$_{1a}$ $$u^s_{yy} + ef(u^s)u^s - v(x^*)u^s = 0, \quad x \in R^1,$$

The reasonable boundary conditions for (5-6)$_{1a}$ is assumed to be

(5-6)$_2$ $$\lim_{y \to -\infty} u^s(y) = u^i(x^*) \quad \text{and}$$
$$\lim_{y \to +\infty} u^s(y) = u^j(x^*).$$

Here we must note that (5-6) is valid to O(1). Concerning the problem (5-6), it is known that ther exists a solution if and only if

(5-7) $$\int_{u_i(x^*)}^{u_j(x^*)} [\{ef(z) - v(x^*)\}z]dz = 0.^{22},$$

This relation leads to the following results:

(1) $I = I_1 \bigcup I_3$ and

(2) $v(x^*)$ is determined uniquely, say $v^*_x$, which is independent of seperating points $x^*$.

Thus we can formulate the well defined boundary value problem in the whole domain $I$, that is,

(5-8)$_{1b}$ $$d_2 v_{xx} + G(v) = 0, \quad x \in I,$$

(5-8)$_2$ $$v_x(0) = v_x(\ell) = 0,$$

where $G(v)$ is defined by

(5-9) $$G(v) = \begin{cases} G_1(v) & \text{for } 0 \leqq v < v^*_c \\ G_3(v) & \text{for } v^*_c < v \leqq ef(u_{max}). \end{cases}$$

For the problem (5-8), we can see that there exist heterogeneous solutions $v(x)$. Thus we find that there appear remarkable heterogeneity in the solution $u(x)$ which is determined by $ef(u) = v$.

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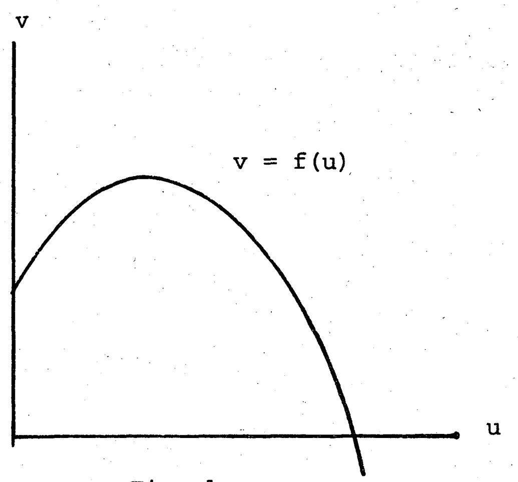


Fig. 1.

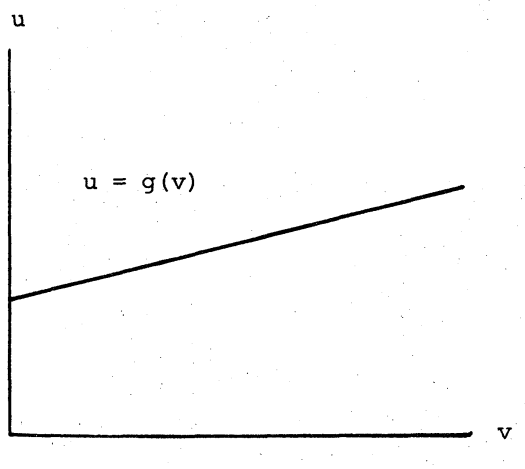


Fig. 2.

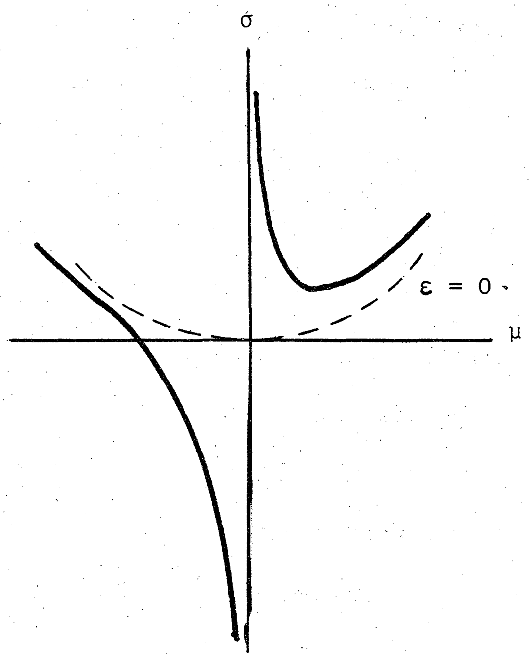


Fig. 3.