

Hopf Bifurcations in Models with Chemotaxis or Advection

Junping Shi

Department of Mathematics,
College of William and Mary,
Williamsburg, Virginia 23187

Everything Disperses to Miami

The University of Miami

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Collaborators/Support



Zhian Wang (Hong Kong Polytechnic University, China)

Ping Liu (Harbin Normal University, China; visit College of William and Mary 2011-12)

Jun Zhou (Southwest University, Chongqing, China; visit College of William and Mary 2012-13)

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Stability of a Steady State Solution

For a continuous-time evolution equation $\frac{du}{dt} = F(\lambda, u)$, where $u \in X$ (state space), $\lambda \in \mathbb{R}$, a steady state solution u_* is **locally asymptotically stable** (or just stable) if for any $\epsilon > 0$, then there exists $\delta > 0$ such that when $\|u(0) - u_*\|_X < \delta$, then $\|u(t) - u_*\|_X < \epsilon$ for all $t > 0$ and $\lim_{t \rightarrow \infty} \|u(t) - u_*\|_X = 0$. Otherwise u_* is **unstable**.

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Bifurcation (change of stability): if when the parameter λ changes from $\lambda_* - \epsilon$ to $\lambda_* + \epsilon$, the steady state $u_*(\lambda)$ changes from stable to unstable; and other special solutions (steady states, periodic orbits) may emerge from the known solution $(\lambda, u_*(\lambda))$.

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Steady State Bifurcation (transcritical/pitchfork): if 0 is an eigenvalue of $D_u F(\lambda_*, u_*)$.

Hopf Bifurcation: if $\pm ki$ is a pair of eigenvalues of $D_u F(\lambda_*, u_*)$.

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ODE model: $\frac{dy}{dt} = f(\lambda, y), \quad y \in \mathbb{R}^n, f : \mathbb{R} \times \mathbb{R}^n \rightarrow \mathbb{R}^n$

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$$P(\lambda) = \text{Det}(\lambda I - J) = \lambda^n + a_1 \lambda^{n-1} + a_2 \lambda^{n-2} + \dots + a_{n-1} \lambda + a_n$$

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$n \geq 5$: check books

Alan Turing (1912-1954)



THE CHEMICAL BASIS OF MORPHOGENESIS

By A. M. TURING, F.R.S. *University of Manchester*

(Received 9 November 1951—Revised 13 March 1952)

It is suggested that a system of chemical substances, called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis. Such a system, although it may originally be quite homogeneous, may later develop a pattern or structure due to an instability of the homogeneous equilibrium, which is triggered off by random disturbances. Such reaction-diffusion systems are considered in some detail in the case of an isolated ring of cells, a mathematically convenient, though biologically unusual system. The investigation is chiefly concerned with the onset of instability. It is found that there are six essentially different forms which this may take. In the most interesting form stationary waves appear on the ring. It is suggested that this might account, for instance, for the transverse pattern on *Hydra* and for whorled leaves. A system of reactions and diffusion on a sphere is also considered. Such a system appears to account for gastrulation. Another reaction system in two dimensions gives rise to patterns reminiscent of dappling. It is also suggested that stationary waves in two dimensions could account for the phenomena of phyllotaxis.

The purpose of this paper is to discuss a possible mechanism by which the genes of a zygote may determine the anatomical structure of the resulting organism. The theory does not make any new hypotheses; it merely suggests that certain well-known physical laws are sufficient to account for many of the facts. The full understanding of the paper requires a good knowledge of mathematics, some biology, and some elementary chemistry. Since readers cannot be expected to be experts in all of these subjects, a number of elementary facts are explained, which can be found in text-books, but whose omission would make the paper difficult reading.

1. A MODEL OF THE EMBRYO. MORPHOGENS

In this section a mathematical model of the growing embryo will be described. This model will be a simplification and an idealization, and consequently a fabrication. It is to be hoped that the features retained for discussion are those of greatest importance in the present state of knowledge.

The model takes two slightly different forms. In one of them the cell theory is recognized but the cells are idealized into geometrical points. In the other the matter of the organism is imagined as continuously distributed. The cells are not, however, completely ignored, for various physical and physico-chemical characteristics of the matter as a whole are assumed to have values appropriate to the cellular matter.

With either of the models one proceeds as with a physical theory and defines an entity called 'the state of the system'. One then describes how that state is to be determined from the state at a moment very shortly before. With either model the description of the state consists of two parts, the mechanical and the chemical. The mechanical part of the state describes the positions, masses, velocities and elastic properties of the cells, and the forces between them. In the continuous form of the model essentially the same information is given in the form of the stress, velocity, density and elasticity of the matter. The chemical

[Turing, 1952] The Chemical Basis of Morphogenesis.
Phil. Trans. Royal Society London B

Turing's idea

Kinetic (K): $\frac{du}{dt} = f(u, v), \frac{dv}{dt} = g(u, v)$

Reaction-diffusion system (R-D): $u_t = d_1 \Delta u + f(u, v), v_t = d_2 \Delta v + g(u, v)$

Here $u(x, t)$ and $v(x, t)$ are the density functions of two chemicals (morphogen) or species which interact or react

- A constant solution $u(t, x) = u_0, v(t, x) = v_0$ can be a stable solution of **(K)**, but an unstable solution of **(R-D)**. Thus the instability is induced by diffusion. (Diffusion is generally a stabilizing force.)
- On the other hand, there must be stable non-constant equilibrium solutions, or stable non-equilibrium behavior, which have more complicated spatial-temporal structure.

Turing bifurcation in 1-D problem

For simplicity, we assume that $n = 1$ and $\Omega = (0, \ell\pi)$.

$$\begin{cases} u_t = du_{xx} + f(u, v), & x \in (0, \ell\pi), t > 0, \\ v_t = v_{xx} + g(u, v), & x \in (0, \ell\pi), t > 0, \\ u_x(t, 0) = u_x(t, \ell\pi) = v_x(t, 0) = v_x(t, \ell\pi) = 0, & t > 0, \\ u(0, x) = u_0(x), v(0, x) = v_0(x), & x \in (0, \ell\pi). \end{cases}$$

Equilibrium point: $f(u_0, v_0) = g(u_0, v_0) = 0$

Linearized equation:

$$L \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} d\phi_{xx} \\ \psi_{xx} \end{pmatrix} + \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}$$

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$$\begin{pmatrix} \phi \\ \psi \end{pmatrix} = \sum_{j=0}^{\infty} \begin{pmatrix} a_j \\ b_j \end{pmatrix} \cos\left(\frac{j\pi x}{\ell}\right).$$

Fourier theory: for an eigenfunction (ϕ, ψ) for eigenvalue μ , only one $(a_j, b_j) \neq 0$ and all other $(a_k, b_k) = 0$ for $k \neq j$, and (a_j, b_j) satisfies (where $\mu_j = j^2/\ell^2$, the eigenvalues of $-\phi'' = \mu\phi$ with no-flux boundary condition)

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Condition for Turing instability: $f_u > 0$, $g_v < 0$, $0 < d < 1$,

$$0 < d < \frac{\mu_j f_u - (f_u g_v - f_v g_u)}{\mu_j(\mu_j - g_v)} \equiv d_j \text{ (bifurcation point)}$$

Bifurcation of Nontrivial Steady State

Theorem: Suppose that $f(u_0, v_0) = g(u_0, v_0) = 0$, and at (u_0, v_0) ,

(A) $f_u > 0$ (activator), $g_v < 0$ (inhibitor);

(B) $D_1 = f_u g_v - f_v g_u > 0$ and $f_u + g_v < 0$.

If $d_k \equiv \frac{\mu_k f_u - (f_u g_v - f_v g_u)}{\mu_k (\mu_k - g_v)} \neq d_j$ for any $k \neq j$,

(i) $d = d_j$ is a bifurcation point where a continuum Σ of non-trivial solutions of

$$\begin{cases} du_{xx} + f(u, v) = 0, & v_{xx} + g(u, v) = 0, & x \in (0, \ell\pi), \\ u_x(0) = u_x(\ell\pi) = v_x(0) = v_x(\ell\pi) = 0, \end{cases}$$

bifurcates from the line of trivial solutions (d, u_0, v_0) ;

(ii) The continuum Σ is either unbounded in the space of (d, u, v) , or it connects to another (d_k, u_0, v_0) ;

(iii) Σ is locally a curve near (d_j, u_0, v_0) in form of

$(d, u, v) = (d(s), u_0 + sA \cos(jx) + o(s), v_0 + sB \cos(jx) + o(s))$, $|s| < \delta$, and $d'(0) = 0$ thus the bifurcation is of pitchfork type ($d''(0)$ can be computed in term of $D^3(f, g)$).

[Rabinowitz, 1971, JFA],

[Shi-Wang, 2009, JDE] [Shi, 2009, Frontier Math. China]

Example: Brusselator

[Prigogine-Lefever, 1968]

$$\begin{cases} u_t = du_{xx} + a - (b+1)u + u^2v, & x \in (0, \ell\pi), t > 0, \\ v_t = v_{xx} + bu - u^2v, & x \in (0, \ell\pi), t > 0, \\ u_x(t, 0) = u_x(t, \ell\pi) = v_x(t, 0) = v_x(t, \ell\pi) = 0, & t > 0, \\ u(0, x) = u_0(x), v(0, x) = v_0(x), & x \in (0, \ell\pi). \end{cases}$$

Unique constant steady state: $(a, b/a)$, Jacobian $J = \begin{pmatrix} b-1 & a^2 \\ -b & -a^2 \end{pmatrix}$.

Assume $1 < b < a^2 + 1$. $f_u > 0$, $g_v < 0$, $D_1 = f_u g_v - f_v g_u > 0$ and $f_u + g_v < 0$.

Bifurcation points: $d_j = \frac{(b-1)\mu_j - a^2}{(\mu_j + a^2)\mu_j}$ where $\mu_j = j^2/\ell^2$.

Choose $a = 1$ and $b = 1.5$. Then $d_j = \frac{\mu_j - 1}{2(\mu_j + 1)\mu_j}$ is the bifurcation point.

Result: if d is large, then no pattern; if d is small, then a nonconstant steady state emerges.

Simulation of non-constant steady state (Turing pattern)

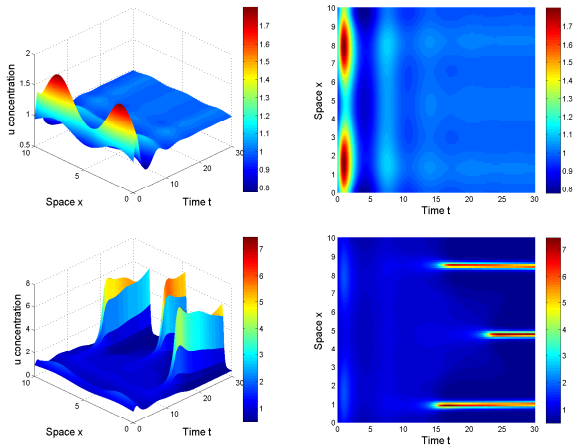


Figure : Numerical simulation for Brusselator model. Here $a = 1$, $b = 1.5$, $\Omega = (0, 10)$. Upper: $d = 0.05$; Lower: $d = 0.01$.

Time-periodic patterns

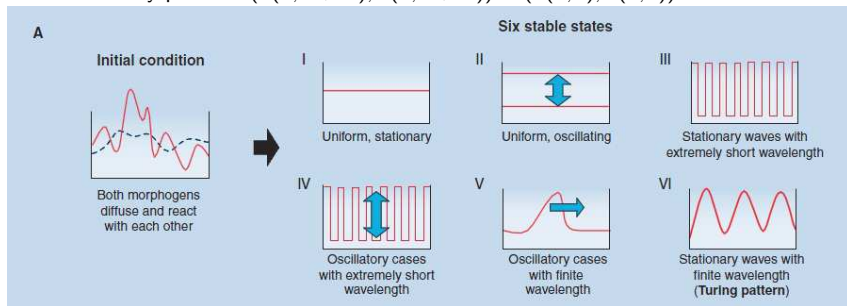
Steady state pattern: $(u(x, t), v(x, t)) = (u(x), v(x))$.

Time-oscillatory pattern: $(u(x, t + T), v(x, t + T)) = (u(x, t), v(x, t))$

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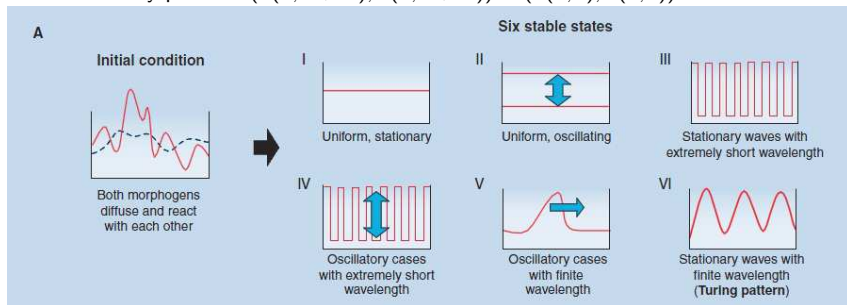


(Figure from: [\[Kondo-Miura, 2010, Science\]](#))

Time-periodic patterns

Steady state pattern: $(u(x, t), v(x, t)) = (u(x), v(x))$.

Time-oscillatory pattern: $(u(x, t + T), v(x, t + T)) = (u(x, t), v(x, t))$



(Figure from: [\[Kondo-Miura, 2010, Science\]](#))

[\[Turing, 1952\]](#): “The two remaining possibilities (oscillatory cases) can only occur with three or more morphogens.”

Conjecture?: If (u_0, v_0) is a constant steady state for a 2-D RD system which is stable for ODE dynamics, then the diffusive system cannot have (stable) periodic orbits.

Known: If (u_0, v_0) is a constant steady state for a 2-D RD system which is unstable for ODE dynamics, then the diffusive system can have (a lot of) periodic orbits.

[\[Yi-Wei-Shi, 2009, JDE\]](#)

Chemotaxis model

Diffusion: random movement of cells

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Chemotaxis: directional movement of cells due to attraction/repulsion to chemicals

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Chemotaxis: directional movement of cells due to attraction/repulsion to chemicals

[Keller-Segel, 1970, JTB]

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v), & x \in \Omega, t > 0, \\ v_t = \Delta v + \alpha u - \beta v, & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

- $u(x, t)$: cell density, $v(x, t)$: concentration of chemical; $\chi \geq 0$, $\alpha > 0$, $\beta > 0$,
- $\Omega \subset \mathbf{R}^n$ ($n \geq 1$) is a bounded connected domain with a smooth boundary $\partial\Omega$

Chemotaxis model

Diffusion: random movement of cells

Chemotaxis: directional movement of cells due to attraction/repulsion to chemicals

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[Wang-Xu, 2012, JMB] For $\chi > \chi_*$, the system has a non-constant steady state solution. For $\Omega = (0, L)$, it is shown that the steady state solutions bifurcated from the first bifurcation point are monotone ones, and they display spike patterns.

Earlier work: [Schaff, 1985, TAMS], [Lin-Ni-Takagi, 1988, JDE] and many others

There is no periodic-pattern: Lyapunov functional:

$$L(u, v) = \alpha \int_{\Omega} (u \log u - u - \chi uv) + \frac{\chi}{2} \int_{\Omega} (|\nabla v|^2 + \beta v^2)$$

Attractive and Repulsive Chemotaxis

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Repulsive Chemotaxis: move in the direction of decreasing concentration of chemo-repellent

[Painter-Hillen, 2002] [Wolansky, 2002] [Horstmann, 2011]
 [Liu-Wang, 2012] [Tao-Wang, 2013] [Liu-Shi-Wang, preprint]

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v) + \nabla \cdot (\xi u \nabla w), & x \in \Omega, t > 0 \\ v_t = \Delta v + \alpha u - \beta v, & x \in \Omega, t > 0, \\ w_t = \Delta w + \gamma u - \delta w, & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega, t > 0. \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), w(x, 0) = w_0(x), & x \in \Omega, \end{cases}$$

- $u(x, t)$: cell density, $v(x, t)$: concentration of chemo-attractant, $w(x, t)$: concentration of chemo-repellent
- $\chi \geq 0, \xi \geq 0, \alpha > 0, \beta > 0, \gamma > 0, \delta > 0$
- $\Omega \subset \mathbf{R}^n$ ($n \geq 1$) is a bounded connected domain with a smooth boundary $\partial\Omega$

Equilibrium and linearization

$$\begin{cases} u_t = \Delta u - \nabla \cdot (\chi u \nabla v) + \nabla \cdot (\xi u \nabla w), & x \in \Omega, t > 0, \\ v_t = \Delta v + \alpha u - \beta v, & x \in \Omega, t > 0, \\ w_t = \Delta w + \gamma u - \delta w, & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

$\int_{\Omega} u(x, t) dx = \int_{\Omega} u_0(x) dx$. Let $\bar{u} = \frac{1}{|\Omega|} \int_{\Omega} u(x, t) dx$ be fixed. Define $\bar{v} = \alpha \bar{u} / \beta$, $\bar{w} = \gamma \bar{u} / \delta$, then $(\bar{u}, \bar{v}, \bar{w})$ is a constant equilibrium.

Linearized equation

$$\begin{cases} \Delta \phi - \chi \bar{u} \Delta \psi + \xi \bar{u} \Delta \varphi = \mu \phi, & x \in \Omega, \\ \Delta \psi + \alpha \phi - \beta \psi = \mu \psi, & x \in \Omega, \\ \Delta \varphi + \gamma \phi - \delta \varphi = \mu \varphi, & x \in \Omega, \\ \int_{\Omega} \phi(x) dx = 0, & x \in \Omega, \\ \frac{\partial \phi}{\partial \nu} = \frac{\partial \psi}{\partial \nu} = \frac{\partial \varphi}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases}$$

Eigenvalue Problem

Fourier theory yields a matrix (here λ_n is eigenvalue of $-\Delta$)

$$A_n = \begin{pmatrix} -\lambda_n & \chi \bar{u} \lambda_n & -\xi \bar{u} \lambda_n \\ \alpha & -\lambda_n - \beta & 0 \\ \gamma & 0 & -\lambda_n - \delta \end{pmatrix}.$$

Characteristic polynomial

$$P(\mu) = \mu^3 + a_2(\chi, \lambda_n)\mu^2 + a_1(\chi, \lambda_n)\mu + a_0(\chi, \lambda_n),$$

where

$$a_2(\chi, \lambda_n) = 3\lambda_n + \beta + \delta,$$

$$a_1(\chi, \lambda_n) = 3\lambda_n^2 + [2(\beta + \delta) + (\xi\gamma - \alpha\chi)\bar{u}]\lambda_n + \delta\beta,$$

$$a_0(\chi, \lambda_n) = \lambda_n^3 + [\beta + \delta + (\xi\gamma - \alpha\chi)\bar{u}]\lambda_n^2 + [\beta\delta + (\beta\xi\gamma - \delta\alpha\chi)\bar{u}]\lambda_n.$$

Routh-Hurwitz: boundary of instability

$$a_0(\chi, \lambda_n) = 0, \quad T(\chi, \lambda_n) = a_2(\chi, \lambda_n)a_1(\chi, \lambda_n) - a_0(\chi, \lambda_n) = 0.$$

steady state bifurcation curve: $S = \{(\chi, p) \in \mathbf{R}_+^2 : a_0(\chi, p) = 0\}$

Hopf bifurcation curve: $H = \{(\chi, p) \in \mathbf{R}_+^2 : T(\chi, p) = 0\}$.

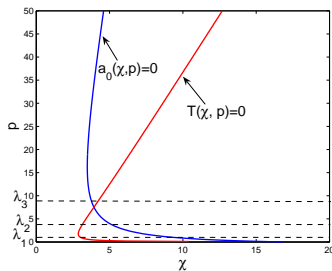
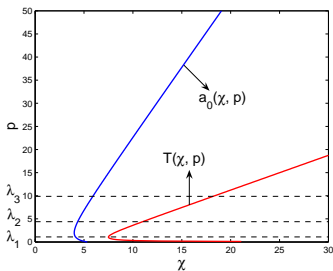


Figure : Graph of $a_0(\chi, p) = 0$ ($\chi = \chi_S(p)$) and $T(\chi, p) = 0$ ($\chi = \chi_H(p)$). Here the horizontal axis is χ and the vertical axis is p , and the dashed horizontal lines are $p = \lambda_n = n^2$ for $n = 1, 2, 3$ (assuming that $\Omega = (0, \pi)$ a one-dimensional spatial domain). Parameters used: $\gamma = \alpha = \xi = \delta = 1$ for both plots; (left) $\beta = 4$, $\bar{u} = 3$; (right) $\beta = 16$, $\bar{u} = 20$.

Hopf Bifurcation

[Liu-Shi-Wang, 2013, preprint]

Theorem. Let $(\bar{u}, \bar{v}, \bar{w})$ be a positive constant equilibrium point and define

$A^* =: A^*(\beta, \delta) = \frac{(p^* + \delta)^2(2p^* + \beta)}{(\beta - \delta)p^*}$, where p^* is the unique positive root of the equation $4p^3 + (4\delta + \beta)p^2 = \delta^2\beta$. If parameters satisfy

$$\beta > \delta \text{ and } \xi\gamma\bar{u} < A^*,$$

then for some appropriately chosen domain Ω , there exists a Hopf bifurcation point $\chi = \chi_j^H > 0$ for the system. More precisely,

- The system has a unique one-parameter family $\{\rho(s) : 0 < s < \varepsilon\}$ of nontrivial periodic orbits near $(\chi, u, v, w) = (\chi_j^H, \bar{u}, \bar{v}, \bar{w})$. More precisely, there exists $\varepsilon > 0$ and C^∞ function $s \mapsto (U_j(s), T_j(s), \chi_j(s))$ from $s \in (-\varepsilon, \varepsilon)$ to $W^{2,p}(\Omega, \mathbf{R}^3) \times (0, \infty) \times \mathbf{R}$ satisfying

$$(U_j(0), T_j(0), \chi_j(0)) = ((\bar{u}, \bar{v}, \bar{w}), 2\pi/\nu_0, \chi_j^H),$$

and

$$U_j(s, x, t) = (\bar{u}, \bar{v}, \bar{w}) + sy_j(x) [V_j \exp(i\nu_0 t) + \bar{V}_j \exp(-i\nu_0 t)] + o(s),$$

where

$$\nu_0 = \sqrt{3\lambda_n^2 + [2(\beta + \delta) + (\xi\gamma - \alpha\chi_j^H)\bar{u}]\lambda_n + \delta\beta},$$

and V_j is an eigenvector satisfying $A_j V_j = i\nu_0 V_j$;

Hopf Bifurcation

- for $0 < |s| < \varepsilon$, $\rho(s) = \rho(U_j(s)) = \{U_j(s, \cdot, t) : t \in \mathbf{R}\}$ is a nontrivial periodic orbit of the system with period $T_j(s)$;
- if $0 < s_1 < s_2 < \varepsilon$, then $\rho(s_1) \neq \rho(s_2)$;
- there exists $\tau > 0$ such that if the system has a nontrivial periodic solution $\tilde{U}(x, t)$ of period T for some $\chi \in \mathbf{R}$ with

$$|\chi - \chi_j^H| < \tau, \quad \left| T - \frac{2\pi}{\nu_0} \right| < \tau, \quad \max_{t \in \mathbf{R}, x \in \bar{\Omega}} \left| \tilde{U}(x, t) - (\bar{u}, \bar{v}, \bar{w}) \right| < \tau,$$

then $\chi = \chi_j(s)$ and $\tilde{U}(x, t) = U_j(s, x, t + \theta)$ for some $s \in (0, \varepsilon)$ and some $\theta \in \mathbf{R}$.

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Lesson: when the attractive chemotaxis is strong enough (χ large), a time-periodic pattern can emerge if all other parameters and domain are carefully chosen. In this case, Lyapunov functional is not possible.

For 2-D reaction-diffusion system (without chemotaxis), Hopf bifurcation cannot occur. Indeed [Turing, 1952] had already pointed out that time-periodic patterns can only occur if there are three or more chemicals involved in the reaction. Periodic patterns here are caused by chemotaxis.

Hopf bifurcation for quasilinear parabolic systems:

[Amann, 1991, book chapter] [Da Prado-Lunardi, 1985, AIHP] [Simonett, 1995, DIE]

Simulation of periodic patterns

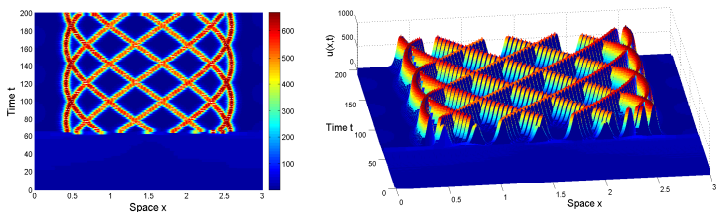


Figure : (a) A spatio-temporal periodic ripping pattern formation of solution component u of the system in an interval $(0, 3)$; (b) A three dimensional view of spatio-temporal periodic ripping pattern of solution component u . The parameters values are: $\gamma = \alpha = \xi = \delta = 1, \beta = 16, \bar{u} = 20$. The initial conditions are set as a small random perturbation of the homogeneous steady state $(20, 20/16, 20)$.

Simulation of periodic patterns

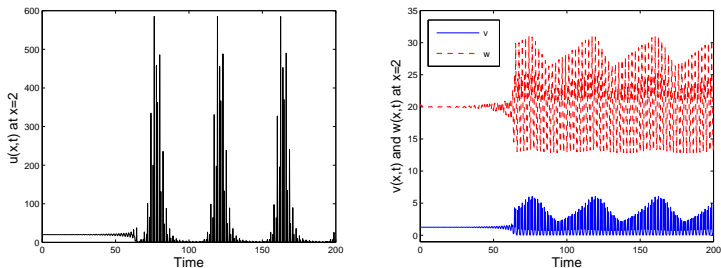


Figure : A visualization of the time-periodic solution (u, v, w) at fixed spatial location $x = 2$. The parameters values and the initial conditions are the same as before.

Simulation of steady state patterns

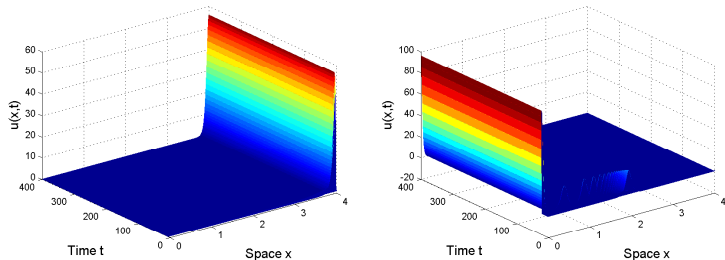


Figure : Numerical simulations of cell density u for different value of χ , where the steady state bifurcation occurs. (a) $\chi = 8.71$; (b) $\chi = 14.71$. Other parameter values are $\alpha = 1, \beta = 1, \gamma = 1, \delta = 1, \xi = 1, \bar{u} = 1$. The initial conditions are set as a small random perturbation of the homogeneous steady state $(1, 1, 1)$.

Ripple pattern in myxobacteria

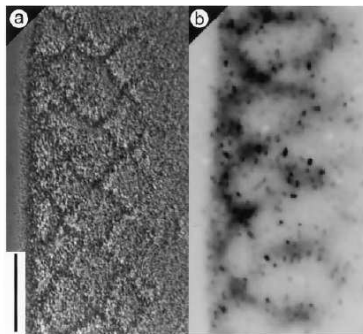
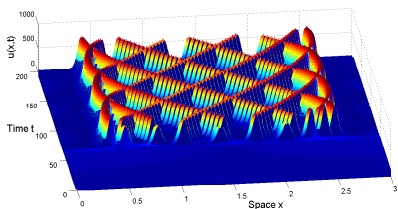


Figure : (left) Numerical simulation of attraction-repulsion Keller-Segel system; (right): ripple pattern in experiment [[Welch-Kaiser, 2001, PNAS](#)]

Question: existence of traveling wave or traveling pulse of attraction-repulsion Keller-Segel system.

Bifurcation from Grassland to Desert



$$\frac{\partial w}{\partial t} = a - w - wn^2 + \gamma \frac{\partial w}{\partial x}, \quad \frac{\partial n}{\partial t} = wn^2 - mn + \Delta n, \quad x \in \Omega.$$

$w(x, y, t)$: concentration of water; $n(x, y, t)$: concentration of plant,

Ω : a two-dimensional domain.

$a > 0$: rainfall; $-w$: evaporation; $-wn^2$: water uptake by plants; water flows downhill at speed γ ; wn^2 : plant growth; $-mn$: plant loss

[Klausmeier, 1999, [Science](#)]

PDE Model

[Zhou-Shi, 2012] preprint

We simplify it to 1-D domain $(0, L)$

$$\begin{cases} u_t - au_x = f(u) - u\phi(v), & 0 < x < L, \quad t > 0, \\ v_t - dv_{xx} = u\phi(v) - h(v), & 0 < x < L, \quad t > 0, \\ u(0, t) = u(L, t), & t > 0, \\ v(0, t) = v(L, t), \quad v_x(0, t) = v_x(L, t), & t > 0, \\ v(x, 0) = v_0(x), \quad u(x, 0) = u_0(x), & 0 \leq x \leq L, \end{cases}$$

We seek for solution which also satisfies $u_x(0, t) = u_x(L, t)$.

Local existence: can be proved through standard way using semigroup theory

Stability and bifurcation: suppose there is a unique constant steady state solution. Then what is the stability?

Eigenvalue problem

$$\begin{cases} A\phi' + a\phi + b\psi = \lambda\phi, & 0 < x < \pi, \\ D\psi'' + c\phi + d\psi = \lambda\psi, & 0 < x < \pi, \\ \phi(0) = \phi(\pi), \phi'(0) = \phi'(\pi), \\ \psi(0) = \psi(\pi), \psi'(0) = \psi'(\pi). \end{cases}$$

Let an eigenfunction be

$$\begin{aligned} \phi &= \sum_{n=0}^{\infty} (f_n^1 \sin(2nx) + f_n^2 \cos(2nx)), \\ \psi &= \sum_{n=0}^{\infty} (g_n^1 \sin(2nx) + g_n^2 \cos(2nx)). \end{aligned}$$

Then $(f_n^1, g_n^1, f_n^2, g_n^2)^T$ satisfies $\mathbb{A}_n (f_n^1, g_n^1, f_n^2, g_n^2)^T = \lambda (f_n^1, g_n^1, f_n^2, g_n^2)^T$, where

$$\mathbb{A}_n = \begin{pmatrix} a & b & -2nA & 0 \\ c & d - 4n^2D & 0 & 0 \\ 2nA & 0 & a & b \\ 0 & 0 & c & d - 4n^2D \end{pmatrix}.$$

Eigenvalue problem

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Characteristic equation:

$$\lambda^4 - 2B_n\lambda^3 + (B_n^2 + 2C_n + 4n^2\Lambda)\lambda^2 + (-2B_nC_n - 8k_n n^2\Lambda)\lambda + C_n^2 + 4k_n^2 n^2\Lambda = 0.$$

where $k_n = d - 4Dn^2$, $B_n = a + k_n$, $C_n = bc - ak_n$ and $\Lambda = A^2$.

Lemma.

- (i) If $B_n < 0$ and $C_n > 0$ for all $n \in \mathbb{N} \cup \{0\}$, then for $A = 0$, all eigenvalues have negative real parts.
- (ii) Assuming that $B_n < 0$ and $C_n > 0$ for all $n \in \mathbb{N} \cup \{0\}$ (which can be achieved if $a < 0$, $a + d < 0$, and $ad - bc > 0$). Then for $n \in \mathbb{N}$ such that $1 \leq n \leq \sqrt{d/(4D)}$ (so $d > 4D$), there exists

$$\Lambda_n^* = -\frac{B_n^2 C_n}{4ak_n n^2},$$

such that all eigenvalues of \mathbb{A} have negative real parts if $\Lambda < \Lambda_n^*$, and \mathbb{A} has exactly one pair of eigenvalues with positive real part when $\Lambda \in (\Lambda_n^*, \Lambda_n^* + \varepsilon)$.

Question: Hopf bifurcation theorem

Another approach

[Sherratt, 2005, JMB]

$$\begin{cases} A\phi' + a\phi + b\psi = \lambda\phi, \\ D\psi'' + c\phi + d\psi = \lambda\psi, \end{cases}$$

Solution form: $(\phi, \psi) = (f, g)\exp(-i2nx)$, $\begin{pmatrix} a + i2nA & b \\ c & d \end{pmatrix} \begin{pmatrix} f \\ g \end{pmatrix} = \lambda \begin{pmatrix} f \\ g \end{pmatrix}$

characteristic equation:

$$\lambda^2 + (4n^2D - a - d - i2nA) + (d - 4n^2D)(i2nA + a) - bc = 0, \text{ or}$$

$$\lambda^2 - (B_n - i2nAi)\lambda + k_n(a + i2nA) - bc = 0, \text{ where } k_n = d - 4Dn^2, B_n = a + k_n.$$

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Indeed, this is equivalent to our approach:

$$\begin{aligned} & \lambda^4 - 2B_n\lambda^3 + (B_n^2 + 2C_n + 4n^2\Lambda)\lambda^2 + (-2B_nC_n - 8k_nn^2\Lambda)\lambda + C_n^2 + 4k_n^2n^2\Lambda \\ & = (\lambda^2 - (B_n - i2nAi)\lambda + k_n(a + i2nA) - bc)(\lambda^2 - (B_n + i2nAi)\lambda + k_n(a - i2nA) - bc \end{aligned}$$

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Advantages and differences of our approach:

1. Our polynomial has real-value coefficients, so we have 2 pairs of conjugate complex root, not 2 non-conjugate complex roots;
2. We can use Routh-Hurwitz criterion for Hopf bifurcation analysis;
3. [Sherratt-Lord, 2007], [Sherratt, 2010] considered the traveling wave train solutions, and solutions are obtained from Hopf bifurcation of ODE system with wave speed c .

Simulation of Klausmeier model

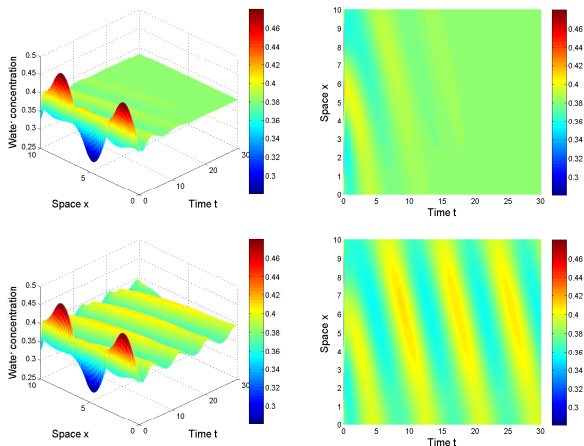


Figure : Numerical simulation for $u_t = \gamma u_x + a - u - uv^2$,
 $v_t = v_{xx} + uv^2 - mv$ with periodic boundary condition. Here $a = 3$,
 $m = 1$, $\Omega = (0, 10)$. Upper: $\gamma = -15$; Lower: $\gamma = -20$.

Conclusions

- Different diffusion rates produce nontrivial steady state patterns. [\[Turing, 1952\]](#)

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- Different diffusion rates produce nontrivial steady state patterns. [Turing, 1952]
- For diffusive systems (may with chemotaxis), usually 3 chemical species are needed for time-periodic patterns. In the minimal chemotactic system, a large attractive chemotactic force generates time-periodic patterns. Steady state patterns are still possible.
- For advective-diffusive systems in form

$$\begin{cases} u_t = Au_x + f(u) - \phi(u)v^p, & 0 < x < L, t > 0, \\ v_t = Dv_{xx} + \phi(u)v^p - h(v), & 0 < x < L, t > 0, \\ u(0, t) = u(L, t), u_x(0, t) = u_x(L, t), & t > 0, \\ v(0, t) = v(L, t), v_x(0, t) = v_x(L, t), & t > 0, \end{cases}$$

a large advection can generate time-periodic patterns. Nontrivial steady state patterns are not known yet (all washed away?)

Conclusions

- Different diffusion rates produce nontrivial steady state patterns. [Turing, 1952]
- For diffusive systems (may with chemotaxis), usually 3 chemical species are needed for time-periodic patterns. In the minimal chemotactic system, a large attractive chemotactic force generates time-periodic patterns. Steady state patterns are still possible.
- For advective-diffusive systems in form

$$\begin{cases} u_t = Au_x + f(u) - \phi(u)v^p, & 0 < x < L, t > 0, \\ v_t = Dv_{xx} + \phi(u)v^p - h(v), & 0 < x < L, t > 0, \\ u(0, t) = u(L, t), u_x(0, t) = u_x(L, t), & t > 0, \\ v(0, t) = v(L, t), v_x(0, t) = v_x(L, t), & t > 0, \end{cases}$$

a large advection can generate time-periodic patterns. Nontrivial steady state patterns are not known yet (all washed away?)

- [Kim-Shi-Zhou, preprint] For a system in form

$$\begin{cases} u_t = D_1u_{xx} + A_1u_x + f(u) - \phi(u)v^p, & 0 < x < L, t > 0, \\ v_t = D_2v_{xx} + A_2v_x + \phi(u)v^p - h(v), & 0 < x < L, t > 0, \\ u(0, t) = u(L, t), u_x(0, t) = u_x(L, t), & t > 0, \\ v(0, t) = v(L, t), v_x(0, t) = v_x(L, t), & t > 0, \end{cases}$$

time-periodic patterns can arise via a Hopf bifurcation if $|A_1|$ is large enough.

