Bifurcation Theory and its applications in PDEs and Mathematical Biology
Lecture 6: Delay Differential Equations

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First word

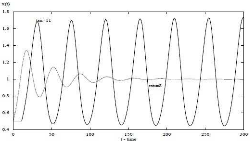
Michael Atiyah (1929-)

People think mathematics begins when you write down a theorem followed by a proof. That's not the beginning, that's the end. For me the creative place in mathematics comes before you start to put things down on paper, before you try to write a formula. You picture various things, you turn them over in your mind. You're trying to create, just as a musician is trying to create music, or a poet. There are no rules laid down. You have to do it your own way. But at the end, just as a composer has to put it down on paper, you have to write things down. But the most important stage is understanding. A proof by itself doesn't give you understanding. You can have a long proof and no idea at the end of why it works. But to understand why it works, you have to have a kind of gut reaction to the thing. You've got to feel it.

Hutchinson Equation

In the Logistic equation, the growth rate per capita is a decreasing function of the current population size. But in the reality, the female individual may need some maturing time to be able to reproduce. Hence in some cases, the growth rate per capita should instead depend on the population size of a past time. That is the delay effect in the density-dependent population growth. In 1948, British-American biologist George Evelyn Hutchinson (1903-1991) proposed the Logistic equation with delay (now called Hutchinson equation) (τ is the time delay).

$$\frac{dP(t)}{dt} = aP(t)\left(1 - \frac{P(t-\tau)}{K}\right)$$



Left: George Evelyn Hutchinson (1903-1991) Right: Simulation of Hutchinson equation

Mackey-Glass Equation and Nicholson's Blowfly equation

In 1977, Mackey and Glass constructed an equation of physiological control (for respiratory studies, or for white blood cells): $\dfrac{dx}{dt} = \lambda - \dfrac{\alpha V_m x(t-\tau)}{\theta^n + x^n(t-\tau)}$. It was shown that when λ increases, a sequence of period-doubling Hopf bifurcations occurs and chaotic behavior exists for some parameter values. A similar equation is Nicholson's equation for blowfly population $\dfrac{dx}{dt} = \beta x^n(t-\tau)\exp(-x(t-\tau)) - \alpha x(t)$

M.C. Mackey, L. Glass, Oscillation and chaos in physiological control systems. Science, 1977.
A. Nicholson, An outline of the dynamics of animal populations, Aust. J. Zool., 1954.
W. Gurney, S. Blythe, R. Nisbet, Nicholson's blowflies revisited, Nature, 1980.

Left: Michael Mackey; Right: Leon Glass

Delay-induced instability

$$\frac{dP(t)}{dt} = aP(t)\left(1 - P(t-\tau)\right)$$

Linearization at $P = 1$ without time delay:
$v'(t) = -av(t)$ (so $P = 1$ is stable when there is no time delay)

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So $\tau_0 = \dfrac{\pi}{2a}$ is the value where the stability is lost when $\tau > \tau_0$. And $\tau_n = \dfrac{(2n+1)\pi}{2a}$ is a Hopf bifurcation point.
(Thus $P = 1$ is stable when the time delay $\tau < \dfrac{\pi}{2a}$, but it is unstable if $\tau > \dfrac{\pi}{2a}$.)

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Basic lesson: a large delay destabilizes an equilibrium

Another example

$$\frac{du}{dt} = ru(t)[1 - au(t) - bu(t - \tau)].$$

Here a and b represent the portions of instantaneous and delayed dependence of the growth rate respectively, and we assume that $a, b \in (0, 1)$ and $a + b = 1$. Then $u_* = 1$ is an equilibrium.

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$\beta = r\sqrt{b^2 - a^2}$.

If $a \geq b$, then the neutral stability condition cannot be achieved. Indeed one can prove u_* is globally stable for any $\tau > 0$.
If $a < b$, then $\tau_0 = \frac{1}{r\sqrt{b^2 - a^2}} \arccos\left(-\frac{a}{b}\right)$ is the value where the stability is lost when $\tau > \tau_0$. And $\tau_n = \frac{1}{r\sqrt{b^2 - a^2}}\left(\arccos\left(-\frac{a}{b}\right) + 2n\pi\right)$ is a Hopf bifurcation point.

General case

$$\frac{du}{dt} = f(u(t), u(t-\tau)).$$

Here $f = f(u, w)$ is a smooth function, and we assume that $u = u_*$ is an equilibrium.

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If $|f_u| < |f_w|$, then $\tau_0 = \dfrac{1}{\sqrt{f_w^2 - f_u^2}} \arccos\left(-\dfrac{f_u}{f_w}\right)$ is the value where the stability is lost when $\tau > \tau_0$.

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Lesson: If the strength of instantaneous dependence is stronger than the delayed dependence, then the equilibrium is always stable; and if it is weaker, then the equilibrium loses the stability with a larger delay.

Stability

An equation with k different delays, and variable $x \in \mathbb{R}^n$:

$$\dot{x}(t) = f(x(t), x(t-\tau_1), \cdots, x(t-\tau_k)). \tag{1}$$

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The characteristic equation takes the form

$$det\left(\lambda I - A_0 - \sum_{j=1}^{m} A_j e^{-\lambda \eta_j}\right) = 0,$$

where A_j $(0 \leq j \leq m)$ is an $n \times n$ constant matrix, $\eta_j > 0$.

[Brauer, 1987, JDE], [Ruan, 2001, Quer.Appl.Math]
An steady state $x = x_*$ of system (27) is said to be absolutely stable (i.e., asymptotically stable independent of the delays) if it is asymptotically stable for all delays $\tau_j \geq 0$ $(1 \leq j \leq k)$; and $x = x_*$ is said to be conditionally stable (i.e., asymptotically stable depending on the delays) if it is asymptotically stable for τ_j $(1 \leq j \leq k)$ in some intervals, but not necessarily for all delays.

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$$P(\lambda) + e^{-\lambda\tau} Q(\lambda) = 0,$$

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1. scalar equations with a single delay or planar systems with only one delay term
2. planar system: $\dot{x}(t) = f(x(t), y(t-\tau_1))$, $\dot{y}(t) = g(x(t-\tau_2), y(t))$
3. planar system: $\dot{x}(t) = f(x(t), y(t)) \pm k_1 g(x(t-\tau), y(t-\tau))$,
$\dot{y}(t) = h(x(t), y(t)) \pm k_2 g(x(t-\tau), y(t-\tau))$.

General form

[Cooke-Grossman, 1982, JMAA], [Ruan, 2001, Quar.Appl.Math]
Characteristic equation

$$\lambda^2 + a\lambda + b + (c\lambda + d)e^{-\lambda\tau} = 0. \tag{2}$$

Neutral stability: $\pm i\omega$, $(\omega > 0)$, is a pair of roots.
$-\omega^2 + a\omega i + b + (c\omega i + d)e^{-i\omega\tau} = 0.$

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Let $T = c^2 - a^2 + 2b$, and $D = b^2 - d^2$. Then there is no positive root ω^2 if (i) $T < 0$ and $D > 0$; or (ii) $T^2 - 4D < 0$.

Theorem. If $a + c > 0$, $b + d > 0$, and either (i) $T < 0$ and $D > 0$; or (ii) $T^2 - 4D < 0$ is satisfied, then all roots of (2) have negative real part for any $\tau \geq 0$.

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On the other hand, if (i) $D < 0$ or (ii) $T > 0$, $D > 0$ and $T^2 - 4D \geq 0$, then $\omega^4 - (c^2 - a^2 + 2b)\omega^2 + (b^2 - d^2) = 0$ has one or two positive roots. And the critical delay value can be solved:

$$\tau_n = \frac{1}{\omega}\left(\arccos\left(\frac{(d - ac)\omega^2 - bd}{d^2 + c^2\omega^2}\right) + 2n\pi\right).$$

Example 1: Rosenzwing-MacArthur Model

[Chen-Shi-Wei, 2012, CPAA]

$$\begin{cases} \dfrac{\partial u}{\partial t} - d_1 u_{xx} = u\left(1 - \dfrac{u}{K}\right) - \dfrac{muv}{u+1}, & x \in (0, l\pi),\ t > 0, \\ \dfrac{\partial v}{\partial t} - d_2 v_{xx} = -dv + \dfrac{mu(t-\tau)v}{u(t-\tau)+1}, & x \in (0, l\pi),\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial x} = \dfrac{\partial v(x,t)}{\partial x} = 0, & x = 0, l\pi,\ t > 0, \\ u(x,t) = u_0(x,t) \geq 0, v(x,t) = v_0(x,t) \geq 0, & x \in (0, l\pi),\ t \in [-\tau, 0], \end{cases}$$

Constant steady state: (λ, v_λ) where $\lambda = \dfrac{d}{m-d}$ and $v_\lambda = \dfrac{(K-\lambda)(1+\lambda)}{Km}$.

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Constant steady state: (λ, v_λ) where $\lambda = \dfrac{d}{m-d}$ and $v_\lambda = \dfrac{(K-\lambda)(1+\lambda)}{Km}$.

Main result: For any $\lambda \in ((K-1)/2, K)$, there exists $\tau_0(\lambda) > 0$ such that (λ, v_λ) is stable when $\tau < \tau_0(\lambda)$, and (λ, v_λ) is unstable when $\tau > \tau_0(\lambda)$. Moreover $\lim_{\lambda\to(K-1)/2} \tau_0(\lambda) = 0$, and $\lim_{\lambda\to K} \tau_0(\lambda) = \infty$; At $\tau = \tau_0(\lambda)$, a branch of homogenous periodic orbits bifurcate from (λ, v_λ).

There is no parameter region in which the stability persists for all delay $\tau > 0$ (not absolutely stable).

Calculation

The characteristic equation

$$\Delta_n(\lambda,\tau)=\lambda^2+A_n\lambda+B_n+Ce^{-\lambda\tau}=0,\quad n=0,1,2,\cdots,$$

where

$$A_n=\frac{(d_1+d_2)n^2}{l^2}-\frac{\beta(k-1-2\beta)}{k(1+\beta)},$$

$$B_n=\frac{d_1d_2n^4}{l^4}-\frac{d_2n^2}{l^2}\frac{\beta(k-1-2\beta)}{k(1+\beta)},\quad C=\frac{r(k-\beta)}{k(\beta+1)}.$$

If $\pm i\sigma(\sigma>0)$ is a pair of roots of characteristic equation, then we have

$$\begin{cases}\sigma^2-B_n=C\cos\sigma\tau,\\ \sigma A_n=C\sin\sigma\tau,\end{cases}\quad n=0,1,2,\cdots,$$

which leads to

$$\sigma^4+(A_n^2-2B_n)\sigma^2+B_n^2-C^2=0,\quad n=0,1,2,\cdots,$$

where

$$A_n^2-2B_n=\frac{d_2^2n^4}{l^4}+\left(\frac{d_1n^2}{l^2}-\frac{\beta(k-1-2\beta)}{k(1+\beta)}\right)^2,$$

$$B_n^2-C^2=\frac{d_2^2n^4}{l^4}\left(\frac{d_1n^2}{l^2}-\frac{\beta(k-1-2\beta)}{k(1+\beta)}\right)^2-\frac{r^2(k-\beta)^2}{k^2(\beta+1)^2}.$$

Delayed Diffusive Leslie-Gower Predator-Prey Model

[Chen-Shi-Wei, 2012, IJBC]

$$
\begin{cases}
\dfrac{\partial u(t,x)}{\partial t} - d_1 \Delta u(t,x) = u(t,x)(p - \alpha u(t,x) - \beta v(t-\tau_1, x)), & x \in \Omega,\ t > 0, \\
\dfrac{\partial v(t,x)}{\partial t} - d_2 \Delta v(t,x) = \mu v(t,x) \left(1 - \dfrac{v(t,x)}{u(t-\tau_2, x)}\right), & x \in \Omega,\ t > 0, \\
\dfrac{\partial u(t,x)}{\partial \nu} = \dfrac{\partial v(t,x)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\
u(x,t) = u_0(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau_2, 0]. \\
v(x,t) = v_0(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau_1, 0].
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$$

Constant steady state: $(u_*, v_*) = \left(\dfrac{p}{\alpha+\beta}, \dfrac{p}{\alpha+\beta}\right)$.

Delayed Diffusive Leslie-Gower Predator-Prey Model

[Chen-Shi-Wei, 2012, IJBC]

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} - d_1 \Delta u(t,x) = u(t,x)(p - \alpha u(t,x) - \beta v(t-\tau_1, x)), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v(t,x)}{\partial t} - d_2 \Delta v(t,x) = \mu v(t,x) \left(1 - \dfrac{v(t,x)}{u(t-\tau_2, x)}\right), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(t,x)}{\partial \nu} = \dfrac{\partial v(t,x)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,t) = u_0(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau_2, 0]. \\ v(x,t) = v_0(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau_1, 0]. \end{cases}$$

Constant steady state: $(u_*, v_*) = \left(\dfrac{p}{\alpha+\beta}, \dfrac{p}{\alpha+\beta}\right)$.

Main result: (a) If $\alpha > \beta$, then (u_*, v_*) is globally asymptotically stable for any $\tau_1 \geq 0,\ \tau_2 \geq 0$. (proved with upper-lower solution method)
(b) If $\alpha < \beta$, then there exists $\tau_* > 0$ such that (u_*, v_*) is stable for $\tau_1 + \tau_2 < \tau_*$, and it is unstable for $\tau_1 + \tau_2 > \tau_*$.

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[Du-Hsu, 2004, JDE] When $\tau_1 = \tau_2 = 0$, if $\alpha > s_0 \beta$, for some $s_0 \in (1/5, 1/4)$, then (u_*, v_*) is globally asymptotically stable. (proved with Lyapunov function, and it is conjectured that the global stability holds for all $\alpha, \beta > 0$.)

Bifurcation diagram of Leslie-Gower system

There is a parameter region in which the global stability persists for all delay $\tau > 0$ (absolutely stable). The other region conditionally stability holds.

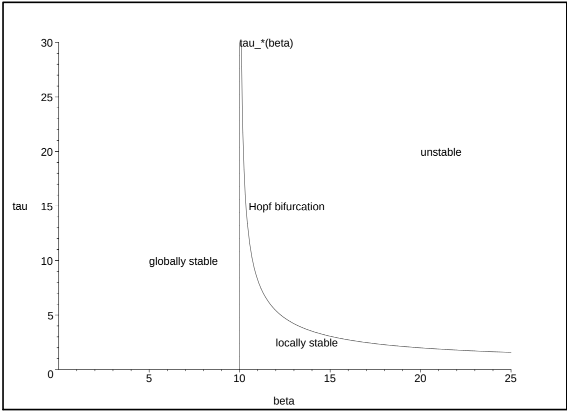

Figure: Bifurcation Diagram with parameters β and $\tau = \tau_1 + \tau_2$. Here $d_1 = 0.1,\ d_2 = 0.2,\ \alpha = 10,\ \mu = 1,\ p = 2.$

Calculation

The characteristic equation

$$\Delta_n(\lambda,\tau)=\lambda^2+A_n\lambda+B_n+Ce^{-\lambda\tau}=0,\quad n=0,1,2,\cdots,$$

where

$$A_n=\frac{\alpha}{\alpha+\beta}p+\mu+(d_1+d_2)\lambda_n,\quad B_n=\left(\lambda_n d_1+\frac{\alpha}{\alpha+\beta}p\right)(\lambda_n d_2+\mu),$$

$$C=\mu\frac{\beta}{\alpha+\beta}p,\quad \text{and}\quad \tau=\tau_1+\tau_2.$$

If $\pm i\sigma(\sigma>0)$ is a pair of roots of the characteristic equation, then we have

$$\begin{cases}\sigma^2-B_n=C\cos\sigma\tau,\\ \sigma A_n=C\sin\sigma\tau,\end{cases}\quad n=0,1,2,\cdots,$$

which lead to

$$\sigma^4+(A_n^2-2B_n)\sigma^2+B_n^2-C^2=0,\quad n=0,1,2,\cdots,$$

where

$$A_n^2-2B_n=\left(d_1\lambda_n+\frac{\alpha}{\alpha+\beta}p\right)^2+(d_2\lambda_n+\mu)^2,$$

$$B_n^2-C^2=\left(\lambda_n d_1+\frac{\alpha}{\alpha+\beta}p\right)^2(\lambda_n d_2+\mu)^2-\left(\mu\frac{\beta}{\alpha+\beta}p\right)^2.$$

Diffusive Hutchinson Model

no-flux boundary condition:

$$u_t = d\Delta u + ru(1 - u(t-\tau)), \quad x \in \Omega, \quad \frac{\partial u}{\partial n} = 0, \; x \in \partial\Omega.$$

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Same as non-spatial case: When $\tau < \dfrac{\pi}{2r}$, $u = K$ is locally stable;

When $\tau > \dfrac{\pi}{2r}$, $u = K$ is unstable, and $\tau = \pi/(2r)$ is a Hopf bifurcation point.

(Global stability of $u = K$ is only known when τ is sufficiently small)

[Yoshida, 1982, Hiroshima-MJ], [Memory, 1989, SIAM-JMA], [Friesecke, 1993, JDDE]

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[Green-Stech, 1981, book chap], [Busenberg-Huang, 1996, JDE],
[Su-Wei-Shi, 2009, JDE] more general case [Yan-Li, 2010, Nonlinearity]

Diffusive Hutchinson Model with Partial Delay

Assume that $a, b \geq 0$ and $a + b = 1$
no-flux boundary condition (and also non-spatial model):

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[Pao, 1996, JMAA], [Huang, 1998, JDE],

[Su-Wei-Shi, 2012, JDDE] global continuation of periodic orbits

Global Bifurcation

[Su-Wei-Shi, 2012, JDDE]

$u_t = du_{xx} + ru(1 - au - bu(t-\tau)), \quad x \in (0, \pi), \quad u(0) = u(\pi) = 0.$

assume $a < b$, $r > d$ but $r - d$ is small

There exists a unique positive steady state $u_r \approx (r - d) \sin x$.

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1. There exists infinitely many Hopf bifurcation points $\tau = \tau_n$ $(n = 0, 1, 2, \cdots)$ such that $\tau_{n+1} > \tau_n$ so that periodic orbits bifurcate from steady state u_r.
2. The connected component $\mathfrak{C}_n$ of the set of nontrivial periodic orbits bifurcating from $\tau = \tau_n$ is unbounded so that

$$\sup \left\{ \max_{t \in \mathbb{R}} |z(t)| + |\tau| + \omega + \omega^{-1} : (z, \tau, \omega) \in \mathfrak{C}_n \right\} = \infty,$$

   where $z(t)$ is the orbit and $2\pi/\omega$ is the period.
3. If $(z, \tau, \omega) \in \mathfrak{C}_n$, then $1/(n+1) < \omega < 1/n$ if $n \geq 1$, and $\omega > 1$ if $n = 0$.
4. For $n \neq m$, $\mathfrak{C}_n \bigcap \mathfrak{C}_m = \emptyset$; the projection of $\mathfrak{C}_n$ to τ component contains (τ_n, ∞).

[Wu, 1996, book], [Wu, 1998, Tran-AMS]

Diffusive Hutchinson Model with nonlocal effect

zero boundary condition:

$$u_t = d\Delta u + \lambda u \left(1 - \int_\Omega K(x,y)u(y,t-\tau)dy\right), \quad x \in \Omega, \quad u = 0, \quad x \in \partial\Omega.$$

assume $\lambda > d\lambda_1$ but $\lambda - d\lambda_1$ is small: there exists a $\tau_0(\lambda) > 0$ such that u_λ is locally asymptotically stable when $\tau \in [0, \tau_0(\lambda))$ and it is unstable when $\tau > \tau_0(\lambda)$. And $\tau = \tau_0(\lambda)$ is a Hopf bifurcation point.

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$$u_t = d\Delta u + \lambda u\left(1 - \int_0^\pi u(y,t-\tau)dy\right), \quad x \in (0,\pi), \quad u = 0, \quad x = 0, \pi.$$

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[Chen-Shi, 2012, JDE]

Simulation (1)

$$u_t = d\Delta u + \lambda u\left(1 - \int_0^\pi K(x,y)u(y,t-\tau)dy\right), \quad x \in (0,\pi), \quad u = 0, \quad x = 0, \pi.$$

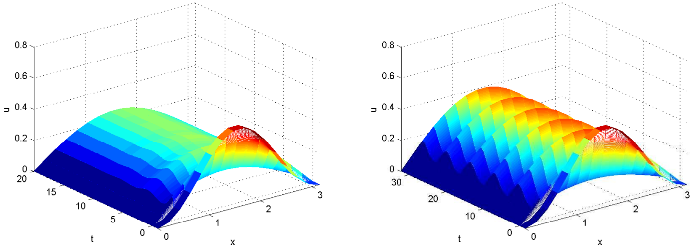


Figure: Spatially homogeneous kernel $K(x, y) = 1$. (Left): $\tau = 1$; (Right): $\tau = 1.6$.

Simulation (2)

$$u_t = d\Delta u + \lambda u\left(1 - \int_0^\pi K(x,y)u(y,t-\tau)dy\right), \quad x \in (0,\pi), \quad u = 0, \quad x = 0, \pi.$$

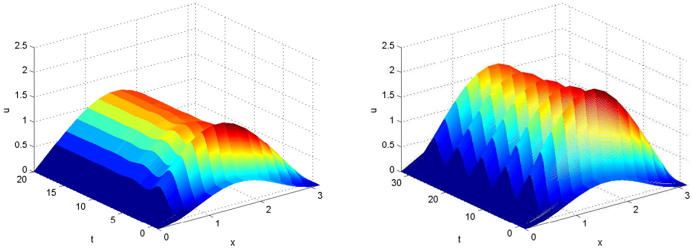


Figure: Spatially nonhomogeneous kernel $K(x,y) = \dfrac{|x-y|}{\pi}$. (Left): $\tau = 1$; (Right): $\tau = 1.6$.

Setting

[Su-Wei-Shi, 2009, JDE]

$$\begin{aligned} \frac{\partial u(x,t)}{\partial t} &= d\frac{\partial u^2(x,t)}{\partial x^2} + \lambda u(x,t)f(u(x,t-\tau)), \qquad x \in (0,l),\ t>0, \\ u(0,t) &= u(l,t) = 0, \qquad t \ge 0, \end{aligned} \tag{3}$$

where $d > 0$ is the diffusion coefficient, $\tau > 0$ is the time delay, and $\lambda > 0$ is a scaling constant; the spatial domain is the interval $(0, l)$, and Dirichlet boundary condition is imposed so the exterior environment is hostile. We consider Eq. (3) with the following initial value:

$$u(x,s) = \eta(x,s), \qquad x \in [0,l],\ s \in [-\tau, 0], \tag{4}$$

where $\eta \in \mathcal{C} \stackrel{def}{=} C([-\tau,0],Y)$ and $Y = L^2((0,l))$.

The following assumptions are always satisfied:

(A1) There exists $\delta > 0$ such that f is a C^4 function on $[0,\delta]$;

(A2) $f(0) = 1$, and $f'(u) < 0$ for $u \in [0,\delta]$.

Steady State

$$\frac{d^2u(x)}{dx^2} + \lambda u(x) f(u(x)) = 0, \quad x \in (0, l), \qquad (5)$$
$$u(0) = u(l) = 0.$$

It is well known that $Y = \mathscr{N}(dD^2 + \lambda_*) \oplus \mathscr{R}(dD^2 + \lambda_*)$, where

$$D^2 = \frac{\partial^2}{\partial x^2}, \qquad \mathscr{N}(dD^2 + \lambda_*) = \text{Span}\{\sin(\frac{\pi}{l}(\cdot))\}$$

and

$$\mathscr{R}(dD^2 + \lambda_*) = \left\{ y \in Y : \langle \sin(\frac{\pi}{l}(\cdot)), y \rangle = \int_0^l \sin(\frac{\pi}{l}x) y(x) dx = 0 \right\}.$$

Theorem 1 There exist $\lambda^* > \lambda_*$ and a continuously differentiable mapping $\lambda \mapsto (\xi_\lambda, \alpha_\lambda)$ from $[\lambda_*, \lambda^*]$ to $(X \cap \mathscr{R}(dD^2 + \lambda_*)) \times \mathbb{R}^+$ such that Eq.(3) has a positive steady state solution given by

$$u_\lambda = \alpha_\lambda(\lambda - \lambda_*)[\sin(\frac{\pi}{l}(\cdot)) + (\lambda - \lambda_*)\xi_\lambda], \qquad \lambda \in [\lambda_*, \lambda^*]. \qquad (6)$$

Moreover, $\alpha_{\lambda_*} = \dfrac{-\int_0^l \sin^2(\frac{\pi}{l}x)dx}{\lambda_* f'(0) \int_0^l \sin^3(\frac{\pi}{l}x)dx}$ and $\xi_{\lambda_*} \in X$ is the unique solution of the equation $(dD^2 + \lambda_*)\xi + [1 + \lambda_* \alpha_{\lambda_*} f'(0) \sin(\frac{\pi}{l}(\cdot))] \sin(\frac{\pi}{l}(\cdot)) = 0, \quad \langle \sin(\frac{\pi}{l}(\cdot)), \xi \rangle = 0.$

Linearization

$$\begin{aligned} \frac{\partial v(x,t)}{\partial t} &= d\frac{\partial^2 v(x,t)}{\partial x^2} + \lambda f(u_\lambda)v(x,t) + \lambda u_\lambda f'(u_\lambda)v(x,t-\tau), \quad t>0, \\ v(0,t) &= v(l,t) = 0, \quad t \geq 0, \\ v(x,t) &= \eta(x,t), \quad (x,t)\in[0,l]\times[-\tau,0], \end{aligned} \tag{7}$$

where $\eta \in \mathcal{C}$. We introduce the operator $A(\lambda) : \mathscr{D}(A(\lambda)) \to Y_{\mathbb{C}}$ defined by $A(\lambda) = dD^2 + \lambda f(u_\lambda)$, with domain

$$\mathscr{D}(A(\lambda)) = \{y \in Y_{\mathbb{C}} : \ \dot{y},\ \ddot{y} \in Y_{\mathbb{C}},\ y(0) = y(l) = 0\} = X_{\mathbb{C}},$$

and set $v(t) = v(\cdot,t)$, $\eta(t) = \eta(\cdot,t)$. Then Eq.(7) can be rewritten as

$$\begin{aligned} \frac{dv(t)}{dt} &= A(\lambda)v(t) + \lambda u_\lambda f'(u_\lambda)v(t-\tau), \quad t>0, \\ v(t) &= \eta(t), \quad t\in[-\tau,0], \quad \eta\in\mathcal{C}, \end{aligned} \tag{8}$$

with $A(\lambda)$ an infinitesimal generator of a compact C_0-semigroup. The semigroup induced by the solutions of Eq.(8) has the infinitesimal generator $A_\tau(\lambda)$ given by

$$\begin{aligned} A_\tau(\lambda)\phi &= \dot{\phi}, \\ \mathscr{D}(A_\tau(\lambda)) &= \{\phi \in \mathcal{C}_{\mathbb{C}} \cap \mathcal{C}^1_{\mathbb{C}} : \ \phi(0)\in X_{\mathbb{C}},\ \dot{\phi}(0) = A(\lambda)\phi(0) + \lambda u_\lambda f'(u_\lambda)\phi(-\tau)\}, \end{aligned}$$

where $\mathcal{C}^1_{\mathbb{C}} = C^1([-\tau,0], Y_{\mathbb{C}})$.

Spectral set

The spectral set $\sigma(A_\tau(\lambda)) = \{\mu \in \mathbb{C} : \ \Delta(\lambda, \mu, \tau) y = 0, \text{ for some } y \in X_{\mathbb{C}} \setminus \{0\}\}$, and

$$\Delta(\lambda, \mu, \tau) = A(\lambda) + \lambda u_\lambda f'(u_\lambda) e^{-\mu\tau} - \mu.$$

The eigenvalues of $A_\tau(\lambda)$ depend continuously on τ. It is clear that $A_\tau(\lambda)$ has an imaginary eigenvalue $\mu = i\nu$ $(\nu \neq 0)$ for some $\tau > 0$ if and only if

$$[A(\lambda) + \lambda u_\lambda f'(u_\lambda) e^{-i\theta} - i\nu] y = 0, \quad y(\neq 0) \in X_{\mathbb{C}} \tag{9}$$

is solvable for some value of $\nu > 0$, $\theta \in [0, 2\pi)$. One can see that if we find a pair of (ν, θ) such that Eq.(9) has a solution y, then

$$\Delta(\lambda, i\nu, \tau_n) y = 0, \qquad \tau_n = \frac{\theta + 2n\pi}{\nu}, \qquad n = 0, 1, 2, \cdots .$$

Decomposition

Suppose that (ν, θ, y) is a solution of Eq.(9) with $y(\neq 0) \in X_{\mathbb{C}}$. Then represented as

$$\begin{aligned} y = \beta \sin(\frac{\pi}{l}(\cdot)) + (\lambda - \lambda_*)z, \quad \langle \sin(\frac{\pi}{l}(\cdot)), z\rangle = 0, \quad \beta \geq 0, \\ \|y\|^2_{Y_{\mathbb{C}}} = \beta^2 \| \sin(\frac{\pi}{l}(\cdot))\|^2_{Y_{\mathbb{C}}} + (\lambda - \lambda_*)^2 \|z\|^2_{Y_{\mathbb{C}}} = \| \sin(\frac{\pi}{l}(\cdot))\|^2_{Y_{\mathbb{C}}}. \end{aligned} \tag{10}$$

Substituting these into Eq.(9), we obtain the equivalent system to Eq.(9):

$$\begin{aligned} g_1(z, \beta, h, \theta, \lambda) &\stackrel{def}{=} (dD^2 + \lambda_*)z + [\beta \sin(\frac{\pi}{l}(\cdot)) + (\lambda - \lambda_*)z] \\ &\cdot \left[1 + \lambda m_1(\xi_\lambda, \alpha_\lambda, \lambda) + \lambda \alpha_\lambda f'(u_\lambda) e^{-i\theta}[\sin(\frac{\pi}{l}(\cdot)) + (\lambda - \lambda_*)\xi_\lambda] - ih\right] = 0, \end{aligned}$$

$$g_2(z) \stackrel{def}{=} \mathrm{Re}\langle \sin(\frac{\pi}{l}(\cdot)), z\rangle = 0, \quad g_3(z) \stackrel{def}{=} \mathrm{Im}\langle \sin(\frac{\pi}{l}(\cdot)), z\rangle = 0,$$

$$g_4(z, \beta, \lambda) \stackrel{def}{=} (\beta^2 - 1)\| \sin(\frac{\pi}{l}(\cdot))\|^2_{Y_{\mathbb{C}}} + (\lambda - \lambda_*)^2 \|z\|^2_{Y_{\mathbb{C}}} = 0.$$

We define $G : X_{\mathbb{C}} \times \mathbb{R}^3 \times \mathbb{R} \mapsto Y_{\mathbb{C}} \times \mathbb{R}^3$ by $G = (g_1, g_2, g_3, g_4)$ and note

$$z_{\lambda_*} = (1 - i)\xi_{\lambda_*}, \quad \beta_{\lambda_*} = 1, \quad h_{\lambda_*} = 1, \quad \theta_{\lambda_*} = \frac{\pi}{2}, \tag{11}$$

with ξ_{λ_*} defined as in Theorem 1. An easy calculation shows that

$$G(z_{\lambda_*}, \beta_{\lambda_*}, h_{\lambda_*}, \theta_{\lambda_*}, \lambda_*) = 0.$$

Solving eigenvalue problem

Theorem 2. There exists a continuously differentiable mapping $\lambda \mapsto (z_\lambda, \beta_\lambda, h_\lambda, \theta_\lambda)$ from $[\lambda_*, \lambda^*]$ to $X_{\mathbb{C}} \times \mathbb{R}^3$ such that $G(z_\lambda, \beta_\lambda, h_\lambda, \theta_\lambda, \lambda) = 0$. Moreover, if $\lambda \in (\lambda_*, \lambda^*)$, and $(z^\lambda, \beta^\lambda, h^\lambda, \theta^\lambda, \lambda)$ solves the equation $G = 0$ with $h^\lambda > 0$, and $\theta^\lambda \in [0, 2\pi)$, then $(z^\lambda, \beta^\lambda, h^\lambda, \theta^\lambda) = (z_\lambda, \beta_\lambda, h_\lambda, \theta_\lambda)$.

Proof. Using Implicit function theorem.

Corollary. If $0 < \lambda^* - \lambda_* \ll 1$, then for each $\lambda \in (\lambda_*, \lambda^*)$, the eigenvalue problem

$$\Delta(\lambda, i\nu, \tau) y = 0, \quad \nu \geq 0, \quad \tau > 0, \quad y (\neq 0) \in X_{\mathbb{C}}$$

has a solution, or equivalently, $i\nu \in \sigma(A_\tau(\lambda))$ if and only if

$$\nu = \nu_\lambda = (\lambda - \lambda_*) h_\lambda, \quad \tau = \tau_n = \frac{\theta_\lambda + 2n\pi}{\nu_\lambda}, \quad n = 0, 1, 2, \cdots \tag{12}$$

and

$$y = r y_\lambda, \quad y_\lambda = \beta_\lambda \sin(\frac{\pi}{l}(\cdot)) + (\lambda - \lambda_*) z_\lambda,$$

where r is a nonzero constant, and $z_\lambda, \beta_\lambda, h_\lambda, \theta_\lambda$ are defined as in Theorem 2.

Stability of steady state solution

1. If $0 < \lambda^* - \lambda_* \ll 1$ and $\tau \geq 0$, then 0 is not an eigenvalue of $A_\tau(\lambda)$ for $\lambda \in (\lambda_*, \lambda^*]$.
2. If $0 < \lambda^* - \lambda_* \ll 1$ and $\tau = 0$, then all eigenvalues of $A_\tau(\lambda)$ have negative real parts for $\lambda \in (\lambda_*, \lambda^*]$.
3. If $0 < \lambda^* - \lambda_* \ll 1$, then for each fixed $\lambda \in (\lambda_*, \lambda^*]$, $\mu = i\nu_\lambda$ is a simple eigenvalue of A_{τ_n} for $n = 0, 1, 2, \cdots$.
4. Since $\mu = i\nu$ is a simple eigenvalue of A_{τ_n}, by using the implicit function theorem it is not difficult to show that there are a neighborhood $O_n \times D_n \times H_n \subset \mathbb{R} \times \mathbb{C} \times X_{\mathbb{C}}$ of $(\tau_n, i\nu_\lambda, y_\lambda)$ and a continuously differential function $(\mu, y) : O_n \to D_n \times H_n$ such that for each $\tau \in O_n$, the only eigenvalue of $A_\tau(\lambda)$ in D_n is $\mu(\tau)$, and

$$\mu(\tau_n) = i\nu_\lambda, \quad y(\tau_n) = y_\lambda,$$

$$\Delta(\lambda, \mu(\tau), \tau) = [A(\lambda) + \lambda u_\lambda f'(u_\lambda)e^{-\mu(\tau)\tau} - \mu(\tau)]y(\tau) = 0, \quad \tau \in O_n. \quad (13)$$

5. If $0 < \lambda^* - \lambda_* \ll 1$, then for each $\lambda \in (\lambda_*, \lambda^*]$,

$$\mathrm{Re}\frac{d\mu(\tau_n)}{d\tau} > 0, \quad n = 0, 1, 2, \cdots .$$

Hopf bifurcation

1. If $0 < \lambda^* - \lambda_* \ll 1$, then for each fixed $\lambda \in (\lambda_*, \lambda^*]$, the infinitesimal generator $A_\tau(\lambda)$ has exactly $2(n+1)$ eigenvalues with positive real part when $\tau \in (\tau_n, \tau_{\lambda_{n+1}}]$, $n = 0, 1, 2, \cdots$.
2. If $0 < \lambda^* - \lambda_* \ll 1$, then for each fixed $\lambda \in (\lambda_*, \lambda^*]$, the positive steady state solution u_λ of Eq.(3) is asymptotically stable when $\tau \in [0, \tau_0)$ and is unstable when $\tau \in (\tau_0, \infty)$.

Theorem 3. Suppose that $f(u)$ satisfies (A1) and (A2), and define $\lambda_* = d(\pi/l)^2$. Then there is a $\lambda^* > \lambda_*$ with $0 < \lambda^* - \lambda_* \ll 1$, and for each fixed $\lambda \in (\lambda_*, \lambda^*]$, there exist a sequence $\{\tau_n\}_{n=0}^{\infty}$ satisfying $0 < \tau_0 < \tau_1 < \cdots < \tau_n < \cdots$, such that Eq.(3) undergoes a Hopf bifurcation at $(\tau, u) = (\tau_n, u_\lambda)$ for $n = 0, 1, 2, \cdots$. More precisely, there is a family of periodic solutions in form of $(\tau_n(a), u_n(x, t; a))$ with period $T_n(a)$ for $a \in (0, a_1)$ with $a_1 > 0$, such that

$$\begin{aligned} &\tau_n(a) = \frac{\theta_\lambda + 2n\pi}{\nu_\lambda} + a^2 k_n^1(\lambda) + o(a^2), \quad T_n(a) = \frac{2\pi}{\nu_\lambda}\left(1 + a^2 k_n^2(\lambda) + o(a^2)\right), \\ &u_n(x, t; a) = u_\lambda(x) + \frac{a}{2}\left(y_\lambda(x)e^{i\nu_\lambda t} + \overline{y}_\lambda(x)e^{-i\nu_\lambda t}\right) + o(a), \end{aligned} \tag{14}$$

where

$$\begin{aligned} k_n^1(\lambda) &= \frac{d\gamma^*(0)}{da} := k_1(n,\lambda)(\lambda - \lambda_*)^{-3} + o((\lambda - \lambda_*)^{-3}), \\ k_n^2(\lambda) &= \frac{d\delta^*(0)}{da} := k_2(n,\lambda)(\lambda - \lambda_*)^{-2} + o((\lambda - \lambda_*)^{-2}), \end{aligned} \tag{15}$$

Hopf bifurcation (cont.)

$$
\begin{aligned}
k_1(n,\lambda) &= -\frac{\mathrm{Re}\int_0^l f'(u_\lambda)\bar{S}_n m_\lambda^1 \sin(\frac{\pi}{l}x) y_\lambda \bar{y}_\lambda (e^{i\theta_\lambda} + e^{-2i\theta_\lambda})dx}{h_\lambda \left| \int_0^l y_\lambda^2 dx \right| \mathrm{Re}\left\{ ie^{-i(\theta_\lambda+\rho_\lambda)} \int_0^l \frac{u_\lambda f'(u_\lambda) y_\lambda^2}{\lambda-\lambda_*} dx \right\}} \\
&= -\frac{\lambda_*^2 \left[f'(0)\right]^2 [1-3(\frac{\pi}{2}+2n\pi)](\int_0^l \sin^3(\frac{\pi}{l}x)dx)^2}{20(\int_0^l \sin^2(\frac{\pi}{l}x)dx)^2} + o(\lambda-\lambda_*),
\end{aligned}
$$

Hopf bifurcation (cont.)

$$
\begin{aligned}
k_2(n,\lambda) =& \frac{\mathrm{Re}\int_0^l f'(u_\lambda)\bar{S}_n m_\lambda^1 \sin(\frac{\pi}{l}x) y_\lambda \bar{y}_\lambda (e^{i\theta_\lambda} + e^{-2i\theta_\lambda})dx}{h_\lambda^2 |S_n|^2 \left|\int_0^l y_\lambda^2 dx\right| \mathrm{Re}\left\{ i e^{-i(\theta_\lambda+\rho_\lambda)} \int_0^l \frac{u_\lambda f'(u_\lambda) y_\lambda^2}{\lambda-\lambda_*} dx \right\}} \cdot \Bigg(\lambda h_\lambda \left|\int_0^l y_\lambda^2 dx\right| \\
& \cdot \mathrm{Im}\left\{ i e^{-i(\theta_\lambda+\rho_\lambda)} \int_0^l \frac{u_\lambda f'(u_\lambda) y_\lambda^2}{\lambda-\lambda_*} dx \right\} + \lambda^2(\theta_\lambda + 2n\pi) \left| \int_0^l \frac{u_\lambda f'(u_\lambda) y_\lambda^2}{\lambda-\lambda_*} dx \right|^2 \Bigg) \\
& + \frac{1}{h_\lambda |S_n|^2} \mathrm{Im} \int_0^l \lambda f'(u_\lambda) \bar{S}_n m_\lambda^1 y_\lambda \bar{y}_\lambda (e^{i\theta_\lambda} + e^{-2i\theta_\lambda}) dx \\
=& \frac{\lambda_*^2 [f'(0)]^2 [3(\frac{\pi}{2}+2n\pi)^2 - 2(\frac{\pi}{2}+2n\pi) - 3] (\int_0^l \sin^3(\frac{\pi}{l}x)dx)^2}{20[1+(\frac{\pi}{2}+2n\pi)]^2 (\int_0^l \sin^2(\frac{\pi}{l}x)dx)^2} + o(\lambda-\lambda_*),
\end{aligned}
$$

and $(\theta_\lambda, \nu_\lambda, y_\lambda)$ is the associated eigen-triple. In particular, $k_1(n,\lambda) > 0$ and $k_2(n,\lambda) > 0$ hence the Hopf bifurcation at (τ_n, u_λ) is forward with increasing period.

Nonlocal model

Delayed Fisher equation:

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d\Delta u(x,t) + \lambda u(x,t)\left(1 - u(x,t-\tau)\right), & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{16}$$

It has been pointed out by several authors that, in a reaction-diffusion model with time-delay effect, the effects of diffusion and time delays are not independent of each other, and the individuals which were at location x at previous times may not be at the same point in space presently. Hence the localized density-dependent growth rate per capita $1 - u(x, t-\tau)$ in (16) is not realistic. it is more reasonable to consider the diffusive logistic population model with nonlocal delay effect as follows:

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d\Delta u(x,t) + \lambda u(x,t)\left(1 - \displaystyle\int_\Omega K(x,y)u(y,t-\tau)dy\right), & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{17}$$

where $u(x,t)$ is the population density at time t and location x, $d > 0$ is the diffusion coefficient, $\tau > 0$ is the time delay representing the maturation time, and $\lambda > 0$ is a scaling constant; Ω is a connected bounded open domain in $\mathbb{R}^n$ $(n \geq 1)$, with a smooth boundary $\partial\Omega$, and Dirichlet boundary condition is imposed so the exterior environment is hostile; $K(x,y)$ is a kernel function which describes the dispersal behavior of the population. The nonlocal growth rate per capita in (17) incorporates the possible dispersal of the individuals during the maturation period, hence it is a more realistic model than (16).

Hopf bifurcation

Theorem 4. For $\lambda \in (\lambda_*, \lambda^*]$, the positive equilibrium solution u_λ of Eq.(17) is locally asymptotically stable when $\tau \in [0, \tau_0)$ and is unstable when $\tau \in (\tau_0, \infty)$. Moreover at $\tau = \tau_n$, $(n = 0, 1, 2, \cdots)$, a Hopf bifurcation occurs so that a branch of spatially nonhomogeneous periodic orbits of Eq. (17) emerges from (τ_n, u_λ).
More precisely, there exists $\varepsilon_0 > 0$ and continuously differentiable function $[-\varepsilon_0, \varepsilon_0] \mapsto (\tau_n(\varepsilon), T_n(\varepsilon), u_n(\varepsilon, x, t)) \in \mathbb{R} \times \mathbb{R} \times X$ satisfying $\tau_n(0) = \tau_n$, $T_n(0) = 2\pi/\nu_\lambda$, and $u_n(\varepsilon, x, t)$ is a $T_n(\varepsilon)$-periodic solution of Eq.(17) such that $u_n = u_\lambda + \varepsilon v_n(\varepsilon, x, t)$ where v_n satisfies $v_n(0, x, t)$ is a $2\pi/\nu_\lambda$-periodic solution of (7).
Moreover there exists $\delta > 0$ such that if Eq.(17) has a nonconstant periodic solution $u(x, t)$ of period T for some $\tau > 0$ with

$$|\tau - \tau_n| < \delta, \quad \left| T - \frac{2\pi}{\nu_\lambda} \right| < \delta, \quad \max_{t \in \mathbb{R}, x \in \overline{\Omega}} |u(x, t) - u_\lambda(x)| < \delta,$$

then $\tau = \tau_n(\varepsilon)$ and $u(x, t) = u_n(\varepsilon, x, t + \theta)$ for some $|\varepsilon| < \varepsilon_0$ and some $\theta \in \mathbb{R}$.

[Wu, 1995, book]

Homogenous kernel

When $K(x,y) \equiv 1$, $n = 1$ and $\Omega = (0, L)$ where $L > 0$, then the equation becomes

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = \dfrac{\partial^2 u(x,t)}{\partial x^2} + \lambda u(x,t)\left(1 - \displaystyle\int_0^\pi u(y, t-\tau)dy\right), & x \in (0,\pi),\ t > 0, \\ u(x,t) = 0, & x = 0,\ \pi,\ t > 0. \end{cases} \tag{18}$$

We can easily verify that Eq. (18) has a unique positive equilibrium solution $u_\lambda(x) = \dfrac{\lambda - 1}{2\lambda} \sin x$ for any $\lambda > 1$ (here $\lambda_* = 1$). Linearizing Eq. (18) at u_λ, we have that

$$\begin{cases} \dfrac{\partial v(x,t)}{\partial t} = \dfrac{\partial^2 v(x,t)}{\partial x^2} + v - \dfrac{\lambda - 1}{2} \sin x \displaystyle\int_0^\pi v(y, t-\tau)dy, & x \in (0,\pi),\ t > 0, \\ v(x,t) = 0, & x = 0,\ \pi,\ t > 0. \end{cases} \tag{19}$$

Note that μ is an eigenvalue of $A_\tau(\lambda)$ if and only if μ is an eigenvalue of the following nonlocal elliptic eigenvalue problem:

$$\begin{cases} \Delta(\lambda,\mu,\tau)\psi := \psi'' + \psi - \dfrac{\lambda - 1}{2} e^{-\mu\tau} \sin x \displaystyle\int_0^\pi \psi(y)dy - \mu\psi = 0, & x \in (0,\pi), \\ \psi(0) = \psi(\pi) = 0. \end{cases} \tag{20}$$

Eigenvalue probelm

Lemma. Suppose that $\lambda > 1$ and $\tau \geq 0$. Then $\mu \in \mathbb{C}$ is an eigenvalue of the problem (20) if and only if one of the following is satisfied:

1. $\mu = -n^2 + 1$ for $n = 2, 3, 4, \cdots$; or
2. μ satisfies

$$(\lambda - 1)e^{-\mu\tau} + \mu = 0. \tag{21}$$

Proof: Substituting the Fourier series $\psi = \sum_{n=1}^{\infty} c_n \sin nx$ into Eq. (20), we have:

$$\sum_{n=2}^{\infty} c_n \left(-n^2 + 1 - \mu\right) \sin nx - \left[(\lambda - 1) \sum_{n=0}^{\infty} \frac{c_{2n+1}}{2n+1} e^{-\mu\tau} + \mu c_1\right] \sin x = 0. \tag{22}$$

Case 1: Suppose that $\mu \in \mathbb{C}$ is an eigenvalue of (20), and $\mu \neq -n^2 + 1$ for each of $n = 2, 3, 4, \cdots$, then (22) implies each $c_n = 0$ for $n \geq 2$, and if $c_1 \neq 0$, then (21) is satisfied, and μ is an eigenvalue with an eigenfunction $\phi_1(x) = \sin x$.
Case 2: If (21) is not satisfied and for some $m = 2, 3, 4, \cdots$, $\mu = -m^2 + 1$, then $c_n = 0$ for $n \geq 2$ and $n \neq m$. If m is even, then $c_1 = 0$ as well, hence $\mu = -m^2 + 1$ is an eigenvalue with an eigenfunction $\phi_m(x) = \sin mx$; if m is odd, then $\mu = -m^2 + 1$ is an eigenvalue with an eigenfunction in form $\phi_m(x) = \sin x + c_m \sin mx$, where c_m satisfies

$$(\lambda - 1)\left(1 + \frac{c_m}{m}\right) e^{(-m^2+1)\tau} - m^2 + 1 = 0.$$

Distribution of eigenvalues

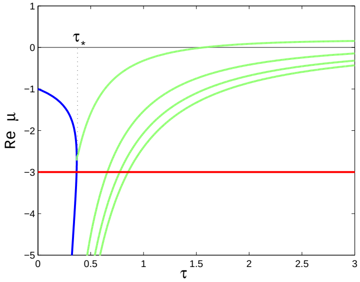


Figure: Relation between $\mathcal{R}e(\mu)$ and τ for Eq. (21). Here $\lambda = 2$. $\mu = -3$ is a fixed real-valued eigenvalue; on the left side of $\tau = \tau_*$ is the curve of real-valued eigenvalues μ satisfying $(\lambda - 1)e^{-\mu\tau} + \mu = 0$; and on the right side of $\tau = \tau_*$ are the curves of real part α_n of complex-valued eigenvalues $\alpha_n \pm i\beta_n$. The curve $\alpha_0(\tau)$ connects with the curve of real eigenvalues at $\tau = \tau_*$, and at $\tau = \pi/2$, $\alpha_0(\tau) = 0$ which gives rise of the first Hopf bifurcation point.

Hopf bifurcation

1. The eigenspace of (20) may not be one-dimensional. When $\mu = -n^2 + 1$ is also a root of (21), the eigenspace is two-dimensional. However as shown in [Davidson-Doods, 2006, AA], usually the eigenspace of such nonlocal problem is at most two-dimensional.
2. The eigenvalue problem (20) with $\tau = 0$ always has a principal eigenvalue μ_0 satisfying (21) with a positive eigenfunction $\sin x$. But μ_0 may not be the largest eigenvalue of (20). For example when $\tau = 0$ and $\lambda < 4$, the maximum eigenvalue of (20) is $1 - \lambda$ which is also the principal eigenvalue; but when $\tau = 0$ and $\lambda \geq 4$, then the maximum eigenvalue is -3 with the corresponding eigenfunction $\sin 2x$, and hence the maximum eigenvalue is not the principal eigenvalue.

Theorem 5. For each $\lambda > 1$, there exist

$$\tau_n(\lambda) = \frac{(4n+1)\pi}{2(\lambda - 1)}, \quad n = 0, 1, 2, \cdots, \tag{23}$$

such that when $\tau = \tau_n(\lambda)$, $n = 0, 1, 2 \cdots$, $A_\tau(\lambda)$ has a pair of simple purely imaginary roots $\pm i\nu_\lambda = \pm i(\lambda - 1)$. Consider the nonlocal problem (18). For each $\lambda > 1$ and $n \in \mathbb{N} \cup \{0\}$, there exists a $\tau_n(\lambda)$ defined as in (23) such that a Hopf bifurcation occurs for Eq. (18) at the unique positive equilibrium solution $u_\lambda = \dfrac{\lambda - 1}{2\lambda} \sin x$ when $\tau = \tau_n(\lambda)$. Moreover, u_λ is locally asymptotically stable when $0 \leq \tau < \tau_0(\lambda)$, and it is unstable when $\tau > \tau_0(\lambda)$.

An observation

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d\Delta u(x,t) + \lambda u(x,t)\left(1 - \displaystyle\int_\Omega K(x,y)u(y,t-\tau)dy\right), & x \in \Omega,\ t > 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{24}$$

suppose that a solution $u(x,t)$ of Eq. (24) is in a separable form

$$u(x,t) = \frac{\lambda - 1}{2\lambda} \sin x \cdot w(t). \tag{25}$$

Here we recall that $u_\lambda(x) = \dfrac{\lambda - 1}{2\lambda} \sin x$ is the unique positive equilibrium of Eq. (24) for $\lambda > 1$. Then it is easy to verify that $w(t)$ satisfies the well-known (non-spatial) Hutchinson equation

$$\frac{dw}{dt} = (\lambda - 1)w(t)(1 - w(t - \tau)). \tag{26}$$

It is also well-known that the Hopf bifurcation points of Eq. (26) are also given by (23), hence all the bifurcating periodic orbits obtained in Theorem 5 are indeed in separable form (25). This shows that the dynamics of Eq. (26) is embedded in the dynamics of Eq. (24) if the initial value is also in separable form (25). This is interesting for a Dirichlet boundary value problem, while it is common for Neumann (no-flux) boundary value problem. It would be interesting to know the stability of periodic solution with such separable form for all $\lambda > 1$, and whether a symmetry-breaking bifurcation can occur so that non-separable periodic orbits can arise.

Spatiotemporal Hutchinson model

[Zuo-Song, 2015, Non. Dyn.]

$$\begin{cases} u_t = d\Delta u + F(\lambda, u, g * u), & x \in (0,1),\ t \geq 0, \\ u_x = 0, & x = 0, 1,\ t \geq 0, \end{cases}$$

Here $(g * u)(x,t) = \int_{-\infty}^{t} g(t-s)u(x,s)ds$.

[Zuo-Song, 2015, JMAA]

$$\begin{cases} u_t = d\Delta u + F(\lambda, u, g * *u), & x \in (0,1),\ t \geq 0, \\ u_x = 0, & x = 0, 1,\ t \geq 0, \end{cases}$$

Here $(g * *u)(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y,t-s)g(t-s)u(y,s)dyds$.

[Guo, 2015, JDE] there is Hopf bifurcation for $u \approx \varepsilon\phi_1$

$$\begin{cases} u_t = d\Delta u + \lambda u F(g * *u), & x \in \Omega,\ t \geq 0, \\ u = 0, & x \in \partial\Omega,\ t \geq 0, \end{cases}$$

Here $(g * *u)(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y)g(t-s)u(y,s)dyds$.

Spatiotemporal Hutchinson model

[Chen-Yu, 2016] there is no Hopf bifurcation for $u \approx \varepsilon\phi_1$

$$\begin{cases} u_t = d\Delta u + \lambda u F(g**u), & x \in \Omega,\ t \geq 0, \\ u = 0, & x \in \partial\Omega,\ t \geq 0, \end{cases}$$

Here $(g**u)(x,t) = \int_{-\infty}^{t}\int_{\Omega} G(x,y,s)g(t-s)u(y,s)dyds$, and $g(t) = \dfrac{t^{m-1}e^{-t/\tau}}{\Gamma(m)\tau^m}$ or $g(t) = \delta(t-\tau)$ where $\tau, m > 0$, and $G(x,y,s)$ is the diffusion kernel.

Summary for spatiotemporal Hutchinson model:

$$\begin{cases} u_t = d\Delta u + \lambda u F(g**u), & x \in \Omega,\ t \geq 0, \\ u = 0, & x \in \partial\Omega,\ t \geq 0, \end{cases}$$

Here $(g**u)(x,t) = \int_{-\infty}^{t}\int_{\Omega} G(x,y,s)g(t-s)u(y,s)dyds.$

(i) $G(x,y,s) = \delta(x-y)$ and $g(t) = \delta(t-\tau)$: Hopf [Busenberg-Huang, 1996] [Su-Wei-Shi, 2009]
(ii) $G(x,y,s) = K(x,y)$ and $g(t) = \delta(t-\tau)$: Hopf [Chen-Shi, 2012]
(iii) $G(x,y,s) = K(x,y)$ and $g(t) = g(t)$: Hopf [Guo, 2015]
(iv) $G(x,y,s)$ is diffusion kernel and $g(t) = \delta(t-\tau)$: "no Hopf" [Chen-Yu, 2016]
(iv) $G(x,y,s)$ is diffusion kernel and $g(t)$ is Gamma: "no Hopf" [Chen-Yu, 2016]

Diffusive Nicholson's blowfly model

[So-Yang, 1998, JDE]

$$\begin{cases} u_t = d\Delta u - \tau u + \beta\tau u(t-1)e^{-u(t-1)}, & x \in \Omega,\ t \geq 0, \\ u = 0, & x \in \partial\Omega,\ t \geq 0. \end{cases}$$

1. When $(\beta - 1)\tau < d\lambda_1$, then $u = 0$ is globally asymptotically stable.
2. When $(\beta - 1)\tau > d\lambda_1$, there is a unique positive equilibrium solution.
3. When $1 < \beta < e^2$, the positive equilibrium solution is globally asymptotically stable.
4. When $\beta > e^2$, then the positive equilibrium solution is stable if $0 < \tau < \tau_0$, and it is unstable when $\tau > \tau_0$ (a Hopf bifurcation occurs at $\tau = \tau_0$).

[So-Wu-Yang, 2000, AMC], [Su-Wei-Shi, 2010, NARW], [Guo-Ma, JNS, 2016]

Neumann boundary condition:
[Yang-So, 1998, DCDS-Proc] [Yi-Zou, 2008, JDE]

Traveling wave:
[So-Zou, 2001, AMC]

Spatiotemporal Nicholson's blowfly model

[Gourley-Ruan, 2000, PRSE]

$$\begin{cases} u_t = d\Delta u - \tau u + \beta\tau F(g * u), & x \in \Omega,\ t \geq 0, \\ u = 0, & x \in \partial\Omega,\ t \geq 0. \end{cases}$$

Here $(g * u)(x, t) = \int_{-\infty}^{t} g(t - s)u(x, s)ds$, and $F(v) = ve^{-v}$.

[So-Wu-Zou, 2001, PRSL] traveling wave

$$u_t = d\Delta u - d_m u + \beta G * F(u), \quad x \in \mathbb{R},\ t \geq 0.$$

Here $G * v = \int_{\mathbb{R}} G(x - y)v(y)dy$, $G(y) = \frac{1}{\sqrt{4\pi\alpha}} e^{-y^2/(4\alpha)}$ and $F(v) = ve^{-v}$.

[Li-Ruan-Wang, 2007, JNS] traveling wave

$$u_t = d\Delta u - \tau u + \beta\tau F(g * *u), \quad x \in \mathbb{R}^N,\ t \geq 0.$$

Here $(g * *u)(x, t) = \int_{-\infty}^{t} \int_{\mathbb{R}^N} G(x, y, s)g(t - s)u(y, s)dyds$, and $F(v) = ve^{-v}$.

Spatiotemporal Nicholson's blowfly model

Bounded Domains:

[Zhao, 2009, CAMQ] [Su-Zou, 2014, Nonlinearity] (Neumann BC)
[Guo-Yang-Zou, 2012, CPAA] [Yi-Zou, 2013, JDDE] (Dirichlet BC)

$$\begin{cases} u_t = d\Delta u - d_m u + \beta G * F(u), & x \in \Omega, \ t \geq 0. \\ Bu = 0, & x \in \partial\Omega, \ t \geq 0. \end{cases}$$

Here $G * v = \int_\Omega G(x-y)v(y)dy$, and $F(v) = ve^{-v}$.
Global stability, Hopf bifurcation, Steady state solution.

[Hu-Yuan, 2012, EJAM]

$$u_t = d\Delta u - \tau u + \beta\tau F(g * *u), \quad x \in \Omega, \ t \geq 0.$$

Here $(g * *u)(x,t) = \int_{-\infty}^{t} \int_\Omega G(x,y,s)g(t-s)u(y,s)dyds$, and $F(v) = ve^{-v}$.
Global stability, Hopf bifurcation.

Surveys:
[Gourley-So-Wu, 2003, JMS] [Gourley-Wu, 2006, Book-chapter]

A Unified Model

[Zuo-Shi, 2016, preprint] We consider a general model in form:

$$\begin{cases} u_t(x,t) = d\Delta u(x,t) + F(\lambda, u(x,t), (g**H(u))(x,t)), & x \in \Omega,\ t \geq 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t \geq 0, \\ u(x,s) = \eta(x,s), & x \in \Omega,\ s \in (-\infty, 0], \end{cases}$$

Here

$$(g**u)(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y,t-s)g(t-s)u(y,s)dyds,$$

with G being
(i) the diffusion kernel $\Gamma(x,y,t)$, (ii) spatial kernel $K(x,y)$, (iii) delta kernel $\delta(x,y)$;

and the distribution function being
(i) Gamma distribution $g(t) = \dfrac{t^{m-1}e^{-t/\tau}}{\Gamma(m)\tau^m}$, (ii) discrete distribution $g(t) = \sum \delta(t - \tau_i)$.

Questions: Steady state, Stability, Hopf bifurcation, Traveling wave.

A Unified Model

[Zuo-Shi, 2016, preprint] We consider a general model in form:

$$\begin{cases} u_t(x,t) = d\Delta u(x,t) + F(\lambda, u(x,t), (g**H(u))(x,t)), & x \in \Omega,\ t \geq 0, \\ u(x,t) = 0, & x \in \partial\Omega,\ t \geq 0, \\ u(x,s) = \eta(x,s), & x \in \Omega,\ s \in (-\infty, 0], \end{cases} \tag{27}$$

Here

$$(g**u)(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y,t-s) g(t-s) u(y,s) dyds, \tag{28}$$

with G being the diffusion kernel

$$G(x,y,t) = \sum_{n=1}^{\infty} e^{-d\lambda_n t} \phi_n(x)\phi_n(y),$$

where (λ_n, ϕ_n) is the eigen-pair of the eigenvalue problem:

$$-\Delta\phi(x) = \lambda\phi(x), \quad x \in \Omega, \quad \phi(x) = 0, \quad x \in \partial\Omega,$$

and the distribution function being one of the following weak or strong kernel: $(\tau > 0)$

$$g_w(t) = \frac{1}{\tau} e^{-\frac{t}{\tau}}, \quad g_s(t) = \frac{t}{\tau^2} e^{-\frac{t}{\tau}}.$$

Conversion to a reaction-diffusion model

Proposition 1.

1. If $u(x,t)$ is a solution of (27) with the weak kernel function $g_w(t) = \frac{1}{\tau} e^{-\frac{t}{\tau}}$, then $(u(x,t), v(x,t))$ is the solution of

$$\begin{cases} u_t(x,t) = d\Delta u(x,t) + F(\lambda, u, v), & x \in \Omega,\ t > 0, \\ v_t(x,t) = d\Delta v(x,t) + \dfrac{1}{\tau}(H(u(x,t)) - v(x,t)), & x \in \Omega,\ t > 0, \\ u(x,t) = v(x,t) = 0, & x \in \partial\Omega,\ t \geq 0, \\ u(x,0) = \eta(x,0), & x \in \Omega, \\ v(x,0) = \dfrac{1}{\tau} \displaystyle\int_{-\infty}^{0} \int_{\Omega} G(x,y,-s) e^{-\frac{s}{\tau}} H(\eta(y,s)) dyds, & x \in \Omega. \end{cases} \tag{29}$$

2. If $(u(x,t), v(x,t))$ is a solution of

$$\begin{cases} u_t(x,t) = d\Delta u(x,t) + F(\lambda, u, v), & x \in \Omega,\ t \in \mathbb{R}, \\ v_t(x,t) = d\Delta v(x,t) + \dfrac{1}{\tau}(H(u(x,t)) - v(x,t)), & x \in \Omega,\ t \in \mathbb{R}, \\ u(x,t) = v(x,t) = 0, & x \in \partial\Omega,\ t \in \mathbb{R}, \end{cases} \tag{30}$$

Then $u(x,t)$ satisfies (27) such that $\eta(x,s) = u(x,s),\ -\infty < s < 0$.

Strong kernel and other cases

1. If $u(x,t)$ is a solution of (27) with the strong kernel function $g_s(t) = \frac{t}{\tau^2} e^{-\frac{t}{\tau}}$, then $(u(x,t), v(x,t), w(x,t))$ is the solution of

$$\begin{cases} u_t(x,t) = d\Delta u(x,t) + F(\lambda, u, v), & x \in \Omega, \ t > 0, \\ v_t(x,t) = d\Delta v(x,t) + \frac{1}{\tau}(w(x,t) - v(x,t)), & x \in \Omega, \ t > 0, \\ w_t(x,t) = d\Delta w(x,t) + \frac{1}{\tau}(H(u(x,t)) - w(x,t)), & x \in \Omega, \ t > 0, \\ u(x,t) = v(x,t) = w(x,t)0, & x \in \partial\Omega, \ t > 0, \\ u(x,0) = \eta(x,0), & x \in \Omega, \\ v(x,0) = \int_{-\infty}^{0} \int_\Omega G(x,y,-s) \frac{-s}{\tau^2} e^{\frac{s}{\tau}} H(\eta(y,s)) dyds, & x \in \Omega, \\ w(x,0) = \int_{-\infty}^{0} \int_\Omega G(x,y,-s) \frac{-1}{\tau} e^{\frac{s}{\tau}} H(\eta(y,s)) dyds, & x \in \Omega. \end{cases} \tag{31}$$

2. Similar conversion can be made if the bounded domain Ω is replaced by $\mathbb{R}^N$ (with G being the diffusion kernel in $\mathbb{R}^N$), or the Dirichlet boundary condition is replaced by Neumann or Robin boundary conditions.
3. There is a one-to-one correspondence between the steady state solutions and periodic orbits of the spatiotemporal distributed delayed system (27) and the reaction-diffusion system (with no delay and nonlocal effect) (29). And similar correspondence of traveling wave for the case of $\mathbb{R}^N$.

Local bifurcation of steady state solutions

$$\begin{cases} d\Delta u(x) + F(u(x), v(x)) = 0, & x \in \Omega, \\ d\Delta v(x) + \dfrac{1}{\tau}(H(u(x)) - v(x)) = 0, & x \in \Omega, \\ u(x) = v(x) = 0, & x \in \partial\Omega. \end{cases} \tag{32}$$

Define
$a = F_u(0,0)$, $b = F_v(0,0)$, $m = F_{uu}(0,0)$, $n = F_{uv}(0,0)$, $p = F_{vv}(0,0)$,
$d^* = \dfrac{1}{2\lambda_1\tau}(a\tau - 1 + \sqrt{(a\tau+1)^2 + 4bH'(0)})$, and $M = \dfrac{H'(0)}{d^*\lambda_1\tau + 1}$.

Theorem 2. Suppose that
(A1) F and H are C^2 near $(0,0)$ and 0 respectively, $F(0,0) = 0$, and $H(0) = 0$.
(A2) $a + H'(0)b > 0$ and $a + Mb \neq 0$.
Then $d = d^*$ is a unique bifurcation value of the system (32), where positive solutions bifurcate from the line of trivial solutions $\Gamma_0 = \{(d, 0, 0), d > 0\}$. Furthermore, if $(m + 2nM + pM^2)(a + bM) > 0$ (or < 0), then there exists $\delta > 0$ such that all positive solutions of (32) lie on a smooth curve
$\Gamma = \{(d, u_d(x), v_d(x)) : \ d \in (d^* - \delta, d^*) \text{ (or } (d^*, d^* - \delta))\}$, where

$$\begin{pmatrix} u_d(x) \\ v_d(x) \end{pmatrix} = k_d(d - d^*)\left(\begin{pmatrix} 1 \\ M \end{pmatrix}\phi_1(x) + o(d - d^*)\right), \tag{33}$$

where $k_{d^*} = \dfrac{2\lambda_1 \int_\Omega \phi_1^2(x)dx}{(m + 2nM + pM^2)\int_\Omega \phi_1^3(x)dx}$.

Stability

Theorem 3. Suppose that the conditions in Theorem 2 are satisfied, and $(m + 2nM + pM^2)(a + bM) > 0$. Then the positive solution $(u_d(x), v_d(x))$ obtained in Theorem 2 is locally asymptotically stable for $d \in (d^* - \delta, d^*)$.

Proof of Theorems 2 and 3: local bifurcation [Crandall-Rabinowitz, 1971, JFA], local stability [Crandall-Rabinowitz, 1973, ARMA]

Remark.

1. Theorems 2 and 3 are for a fixed $\tau > 0$, hence d_*, δ and (u_d, v_d) depend on τ.
2. When $b = F_v(0, 0) = 0$, then $d^* = a/\lambda_1$ which is independent of τ.
3. Theorem 3 implies that when $\tau > 0$ and $d \in (d^*(\tau) - \delta(\tau), d^*(\tau))$, there is no Hopf bifurcation occurring. Notice that (u_d, v_d) depends on τ as well.

Question. What happens outside of the narrow region $\tau > 0$ and $d \in (d^*(\tau) - \delta(\tau), d^*(\tau))$?

Global bifurcation and uniqueness (logistic type)

$$\begin{cases} d\Delta u(x) + F(u(x), v(x)) = 0, & x \in \Omega, \\ d\Delta v(x) + \dfrac{1}{\tau}(H(u(x)) - v(x)) = 0, & x \in \Omega, \\ u(x) = v(x) = 0, & x \in \partial\Omega. \end{cases}$$

Theorem 4. In additional to **(A1)**, **(A2)**, we assume that $a = F_u(0,0) > 0$, and

(B1) There exist a continuous function $F_1 : \overline{\mathbb{R}}_+ \to \mathbb{R}$ and a positive constant $K > 0$ such that $F(u,v) \le F_1(u)u$ for $(u,v) \in \overline{\mathbb{R}}_+ \times \overline{\mathbb{R}}_+$. And F_1 satisfies $F_1(u^*) = 0$ and $0 < F_1(u) < K$ for $u \in (0, u^*)$ and $F_1(u) < 0$ for $u > u^*$.

(B2) $H(u) \le H'(0)u$ for $u \in \overline{\mathbb{R}_+}$.

Then there exists a connected component Σ_1 of the set of positive solutions of (32) such that $\Gamma \subseteq \Sigma_1$, the projection $P_d\Sigma_1$ of Σ_1 into the d-component satisfies $P_d\Sigma_1 = (0, d_0)$ for some $d_0 \in [d^*, K/\lambda_1)$, and for every $(d,u,v) \in \Sigma_1$, $||u||_\infty + ||v||_\infty \le C$ for some $C > 0$ independent of d. Moreover if

(B3) $F_v(u,v) \le 0$ for $(u,v) \in \overline{\mathbb{R}}_+ \times \overline{\mathbb{R}}_+$,

and $N = 1$, then then for $\tau > 0$ and $0 < d < d^*$, (32) has a unique positive solution (u,v).

Example $F(u,v) = u(1 - au - bv)$, $H(u) = u$. [Su-Wei-Shi, 2012, JDDE]

Global bifurcation (Nicolson's blowfly type)

$$\begin{cases} d\Delta u(x) + F(u(x), v(x)) = 0, & x \in \Omega, \\ d\Delta v(x) + \dfrac{1}{\tau}(H(u(x)) - v(x)) = 0, & x \in \Omega, \\ u(x) = v(x) = 0, & x \in \partial\Omega. \end{cases}$$

Theorem 5. In additional to **(A1)**, **(A2)**, **(B2)**, we assume that $a = F_u(0,0) < 0$, and

(B4) There exist positive constants K_1, K_2, K_3 such that $F_u(0,0) \leq -K_1$, $F_v(0,0) \leq K_2$ and $F(u,v) \leq -K_1 u + K_3$.

Then there exists a connected component Σ_1 of the set of positive solutions of (32) such that $\Gamma \subseteq \Sigma_1$, the projection $P_d\Sigma_1$ of Σ_1 into the d-component satisfies $P_d\Sigma_1 = (0, d_0)$ for some $d_0 \geq d^*$, and for every $(d, u, v) \in \Sigma_1$, $||u||_\infty + ||v||_\infty \leq C$ for some $C > 0$ independent of d.

Example $F(u,v) = -au + bue^{-u}$, $H(u) = u$. [So-Yang, 1998, JDE]
$F(u,v) = -au + bv$, $H(u) = ue^{-u}$. [Li-Ruan-Wang, 2007, JNS] [Hu-Yuan, 2012, EJAM]

Logistic type equation

$$\begin{cases} u_t = d\Delta u + u(1 - Au - Bg * *u), & x \in \Omega, \ t \geq 0, \\ u = 0, & x \in \partial\Omega, \ t \geq 0. \end{cases} \tag{34}$$

Or equivalently

$$\begin{cases} u_t = d\Delta u + u(1 - Au - Bv), & x \in \Omega, \ t \in \mathbb{R}, \\ v_t = d\Delta v + \dfrac{1}{\tau}(u - v), & x \in \Omega, \ t \in \mathbb{R}, \\ u = v = 0, & x \in \partial\Omega, \ t \in \mathbb{R}. \end{cases}$$

Theorem 6. Suppose that $A > 0$ and $B > 0$. When $\tau > 0$ and $0 < d < \lambda_1^{-1}$, Equation (34) has a positive steady state solution $u_{\tau,d}$, and when $\tau > 0$ and $\lambda_1^{-1} - \delta(\tau) < d < \lambda_1^{-1}$, $u_{\tau,d}$ is locally asymptotically stable. Moreover if $N = 1$, then $u_{\tau,d}$ is the unique positive steady state solution, and its spectrum contains no nonnegative real eigenvalues.

Question. Can oscillations occur for some $(\tau, d) \in \{\tau > 0, 0 < d < \lambda_1^{-1}\}$?

Similar results hold for Nicholson's blowfly type models.

How do animals move over time?

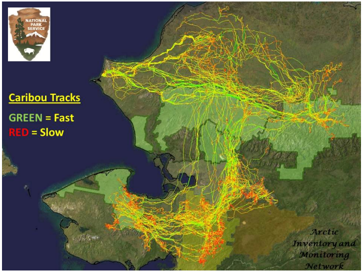
Left: Gazelles in Mongolia; Right: Sockeye salmon in Alaska

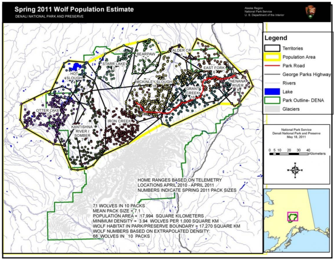
Above: North America sandhill cranes; Below: Wolf pack in Yellowstone National Park

news.bbc.co.uk/earth/hi/earth_news/newsid_8034000/8034392.stm, www.jasonsching.com/photography/
www.fws.gov/birds/surveys-and-data/webless-migratory-game-birds/sandhill-cranes.php
www.spokesman.com/stories/2012/jan/15/hungry-wolf-pack-rearranges-balance-in/

Animal movement data

GPS data received by collars on caribou, moose, muskox, and wolves is relayed via communication satellites to the desks of wildlife biologists. This technology allows biologists to track these animals in the remote areas of Alaska even during inclement weather and the dark.

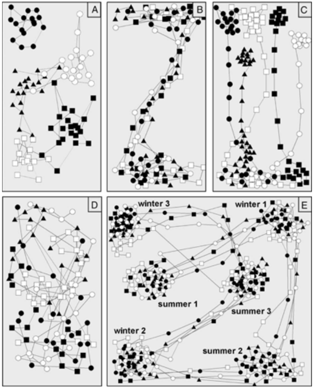




Left: migratory movements of female caribou of the Western Arctic Herd;
Right: wolf pack territories determined by GPS collar data and telemetry data.

`eros.usgs.gov/lir/wildlife-monitoring`

Animal Movement Patterns



Theoretical point patterns and trajectories of population distributions. (A) Sedentary ranges, (B) migration, (C) combination from (A) and (B), (D) nomadism type I, (E) nomadism type II. Boundary boxes indicate conceptual population ranges.

From: T. Muller and W. Fagan, Search and navigation in dynamic environments–from individual behaviors to population distributions. Oikos, 117, (2008), 654–664.

Memory-driven movements

[Fagan et.al., 2013, Ecol. Lett.] Spatial memory and animal movement

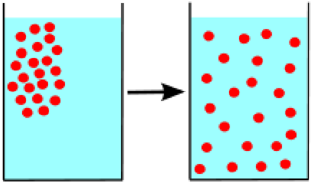
1. Central place foraging: regular return to central place (cognitive map of central place)
2. Migration: seasonal movement between two places (cognitive map, genetic memory, episodic-like memory)
3. Territoriality, home ranging: remaining and bounded in a bounded area (cognitive map, episodic-like memory) [Moorcroft-Lewis, 2006, book]
4. Predator avoidance: aversion from the area with high predator density (cognitive map, landscape of fear)
5. Memory-informed search: no typical pattern, in some rare cases systematic search patterns such as spirals possible (cognitive map, episodic-like memory)
6. and others

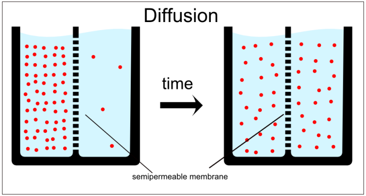
Diffusion

$u(x, y, t)$ is the population density at location (x, y) and time t:

$$\frac{\partial u}{\partial t}(x, y, t) = D\left(\frac{\partial^2 u}{\partial x^2}(x, y, t) + \frac{\partial^2}{\partial y^2}(x, y, t)\right).$$

1. Diffusion is the spontaneous spreading of matter (particles or molecules), heat, momentum, or light.
2. The rate of change w.r.t. time is caused by the the spatial movement, and it means the probability of moving to a neighboring location is the same for all directions.
3. Solved in a bounded region Ω with no-flux boundary condition:
   $$u(x, y, t) = \frac{\text{total population}}{\text{Area}(\Omega)} + Ce^{-kt}.$$
   (population tends to average, no spatial pattern)
4. Diffusion is passive and memoryless.



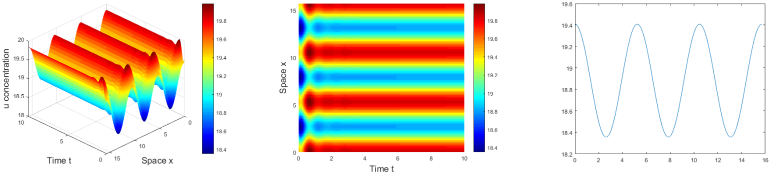


Turing diffusion-induced stability

Reaction-diffusion system of two chemicals

$$\begin{cases} u_t = d_1 u_{xx} + f(u,v), & x \in (0,L), \quad t > 0, \\ v_t = d_2 v_{xx} + g(u,v), & x \in (0,L), \quad t > 0, \\ u_x(0,t) = u_x(L,t) = v_x(0,t) = v_x(L,t) = 0, & t > 0. \end{cases}$$

Suppose that (x_*, y_*) is a stable equilibrium of the ODE model $\begin{cases} x_t = f(x,y), \\ y_t = g(x,y), \end{cases}$ but (x_*, y_*) is an unstable equilibrium for some choice of d_1, d_2, then it is likely the system can have a non-constant equilibrium which is a spatial pattern.



Turing pattern: (left) 3D view $(t, x, u(x,t))$; (middle) 2D view (t, x), and color is $u(x,t)$); (right) 2D view of equilibrium $(x, u(x))$.

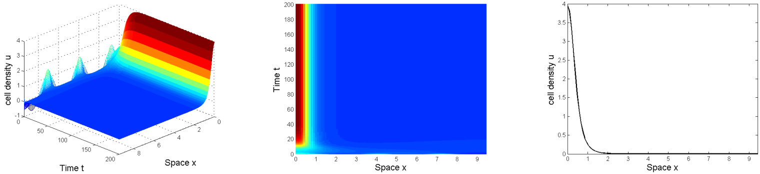
Keller-Segel Chemotaxis model

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

[Keller-Segel, 1970, JTB]: attractive chemotaxis for the aggregation of bacteria

$$\begin{cases} u_t = d_1 u_{xx} - \chi(uv_x)_x, & x \in (0, L), t > 0, \\ v_t = d_2 v_{xx} + \alpha u - \beta v, & x \in (0, L), t > 0, \\ u_x(0,t) = u_x(L,t) = v_x(0,t) = v_x(L,t) = 0, & t > 0. \end{cases}$$

- $u(x,t)$: concentration of cell, $v(x,t)$: concentration of chemical; $d_1, d_2 > 0$ (diffusion coefficients), $\chi \geq 0$ (strength of the attraction), $\alpha > 0$ (chemical generation rate), $\beta > 0$ (chemical decay rate).
- For large $\chi > 0$, the model produces non-constant equilibrium.

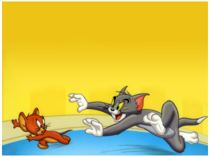


Aggregation of cell: (left) 3D view $(t, x, u(x,t))$; (middle) 2D view (t, x), and color is $u(x,t)$); (right) 2D view of equilibrium $(x, u(x))$. $d_1 = d_2 = \alpha = 1$, $\chi = 3$, $\beta = 0.2$.

Prey-taxis and predator-taxis

[Kareiva-Odell, 1987, Am.Nat.] [Wu-Shi-Wu, 2016, JDE]

For predator-prey models in ecology, in addition to random diffusion of predators, the spatial movement of predators and preys can be pursuit and evasion between them: predators pursuing preys and preys escaping from predators. Such movement is not random but directed: predators move toward the gradient direction of prey distribution (called "prey-taxis"), and/or preys move opposite to the gradient of predator distribution (called "predator-taxis").



$$\begin{cases} u_t = d_1 u_{xx} - \chi(p(u)v_x)_x + c\phi(u,v) - g(u), & x \in (0,L),\ t>0, \\ v_t = d_2 v_{xx} + \xi(q(v)u_x)_x + f(v) - \phi(u,v), & x \in (0,L),\ t>0. \end{cases}$$

$u(x,t)$, $v(x,t)$: densities of predator and prey at location x and time t;

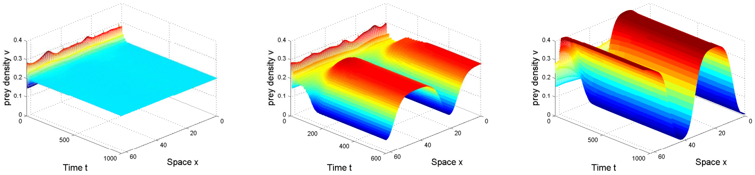
$-\chi(p(u)v_x)_x$: attractive prey-taxis (predator moves towards prey)

$+\xi(q(v)u_x)_x$: repulsive predator-taxis (prey moves away from predator)

Repulsive predator-taxis compressing spatial pattern

[Wu-Shi-Wang, 2018, M3AS to appear]

$$
\begin{cases}
u_t = d_1 u_{xx} + \dfrac{Buv}{h+v} - ku - lu^2, & x \in (0, L), t > 0, \\
v_t = d_2 v_{xx} + \xi(vu_x)_x + v(1-v) - \dfrac{uv}{h+v}, & x \in (0, L), t > 0, \\
u_x(0,t) = u_x(L,t) = v_x(0,t) = v_x(L,t) = 0, & t > 0.
\end{cases}
$$



Prey density: (left) $\xi = 330$; (middle) $\xi = 200$; (right) $\xi = 0$.
Here $d_1 = 400$, $d_2 = 1$, $h = 0.3$, $k = 0.2$, $l = 0.5$, $L = 30\pi$.

Turing patterns created by the different diffusion rates are compressed by the large repulsive predator-taxis.

Animal territory formation

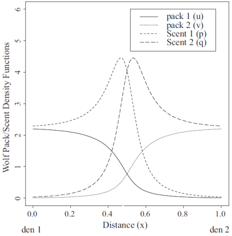
[Lewis-White-Murray, 1997, JMB] [Potts-Lewis, 2014, Amer. Math. Monthly]
Model of wolf pack formation

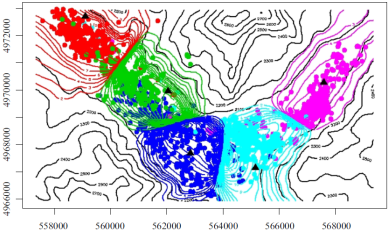
$$\begin{cases} u_t = du_{xx} + c(qu)_x, & x \in (0, L), t > 0, \\ v_t = dv_{xx} - c(pv)_x, & x \in (0, L), t > 0, \\ p_t = (l + \nu q)u - \mu p, & x \in (0, L), t > 0, \\ q_t = (l + \nu p)v - \mu q, & x \in (0, L), t > 0. \end{cases}$$

- $u(x, t), v(x, t)$: densities of two animal packs; $p(x, t), q(x, t)$: densities of scents of u, v respectively.
- $x = 0$: den site for u; $x = L$: den site for v.
- $+c(qu)_x$, $-c(pv)_x$: movement back towards the den.
- l: baseline scent deposition rate, ν: additional deposition in the presence of other pack's scent.

Animal territory formation

[Lewis-White-Murray, 1997, JMB] [Potts-Lewis, 2014, Amer. Math. Monthly]





(left): equilibrium solution of the 2-pack density-scent model;
(right): best fit of *n*-pack model to data on coyotes in Lamar Valley, Yellowstone National Park.

Predator-prey model with competition

[Berestycki-Zilio, 2017, preprint]

$$\begin{cases} w_{i,t} - d_i \Delta w_i = (-\omega_i + k_i u - \mu_i w_i - \beta \sum_{j \neq i} a_{ij} w_j) w_i, & x \in \Omega, t > 0, \\ u_t - D\Delta u = (\lambda - \mu u - \sum_{i=1}^{N} k_i w_i) u, & x \in \Omega, t > 0, \\ \partial_n w_i = \partial_n u = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

Here $w_i(x,t)$ is the population density of the i-th group of predators ($1 \leq i \leq N$), and $u(x,t)$ is the population of the prey.

Main results:

- For a given domain $\Omega \subset \mathbb{R}^n$, if β is sufficiently large, then for any steady state, there are only $\tilde{N}$ components of w_i are not zero, and $\tilde{N} \leq \dfrac{|\Omega|}{4\pi} \max_{1 \leq i \leq N} \dfrac{\lambda k_i - \mu \omega_i}{d_i \mu}$ if $n = 2$.
- For given Ω, there exists $\tilde{N}$ and a steady state solution (w_i, u) which maximizes $\displaystyle\int_\Omega \sum_{i=1}^{N} w_i$.
- As $\beta \to \infty$, the supports of w_i are separated.

Model of diffusion with spatial memory

[Shi-Wang Chuncheng-Wang Hao-Yan Xiangping, 2017, submitted]
Diffusion equation is based on the Fick's law: the movement flux is in the direction of negative gradient of the density distribution function. To include the episodic-like spatial memory of animals, we propose a modified Fick's law that in addition to the negative gradient of the density distribution function at the present time, there is a directed movement toward the negative gradient of the density distribution function at *past time*. Such movement is based on the memory (or history) of a particular past time density distribution:

$$u_t(x,t) = D_1 \Delta u(x,t) + D_2 div(u(x,t) \nabla u(x,t-\tau)) + g(x,t,u(x,t)),$$

where D_1 is the Fickian diffusion coefficient, D_2 is the memory-based diffusion coefficient, the time delay $\tau > 0$ represents the averaged memory period, and g describes the chemical reaction or biological birth/death.

- $D_2 < 0$: animals are attracted to their past track; $D_2 > 0$: animals avoid past track.
- This is similar to chemotaxis model before, but the chemical which attracts animals is the animals' past gradient.

Wellposedness

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \Delta u + D_2 div(u \nabla u_\tau) + g(u), & x \in \Omega, t > 0, \\ \dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,t) = \phi(x,t), & x \in \Omega, -\tau \le t \le 0. \end{cases}$$

Here $u = u(x,t)$, $u_\tau = u(x, t-\tau)$; Ω is a bounded domain in $\mathbb{R}^N$ $(N \ge 1)$ with a smooth boundary $\partial\Omega$; a homogeneous Neumann boundary condition is imposed so that there is no population movement across the boundary $\partial\Omega$. The initial condition $\phi(x,t)$ satisfies

$$\phi(x,t) \in C^{2,0}(\overline{\Omega} \times [-\tau, 0]), \quad \frac{\partial \phi}{\partial n}(x,t) = 0, \quad (x,t) \in \partial\Omega \times [-\tau, 0].$$

The growth rate $g(u)$ is always assumed to satisfy

$$g \in C^1([0,\infty), \mathbb{R}), \ g(0) = g(1) = 0, \ g(u) < 0, \quad \text{for } u > 1.$$

Theorem 1. Suppose that $D_1 > 0$ and $D_2 \in \mathbb{R}$. Then the above equation possesses a unique solution $u(x,t)$ for $(x,t) \in \overline{\Omega} \times [0,\infty)$. Moreover if $\phi(x,t) \ge 0$ for $(x,t) \in \partial\Omega \times [-\tau, 0]$, then $u(x,t) > 0$ for $(x,t) \in \overline{\Omega} \times (0,\infty)$.

Question: Are the solutions uniformly bounded for all $D_1 > 0$ and $D_2 \in \mathbb{R}$?

Stability

Linearizred equation around a constant equilibrium u^*:

$$\begin{cases} \dfrac{\partial \psi}{\partial t} = D_1 \Delta \psi + D_2 u^* \Delta \psi_\tau + g'(u^*)\psi, & x \in \Omega, t > 0, \\ \dfrac{\partial \psi}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0, \\ \psi(x,t) = \varphi_0(x,t), & x \in \Omega, -\tau \le t \le 0, \end{cases}$$

It can be solved by severation of variables $\psi(x,t) = \sum_{n=0}^{\infty} T_n(t)\phi_n(x)$, where ϕ_n are normalized eigenfunctions of $-\Delta \phi_n = \lambda_n \phi_n$ with Neumann boundary condition, and $T_n(t)$ satisfies the delay differential equation

$$\begin{cases} T_n'(t) = (-D_1 \lambda_n + g'(u^*))T_n(t) - D_2 u^* \lambda_n T_n(t-\tau), & t > 0, \\ T_n(t) = \tilde{\varphi}_n(t) := \displaystyle\int_\Omega \varphi_0(x,t)\phi_n(x)dx, & -\tau \le t \le 0. \end{cases}$$

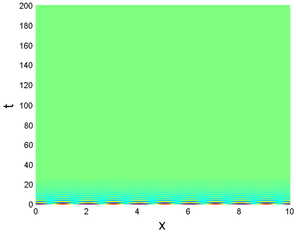
Theorem 2. Let u^* be a constant steady state. If $g'(u^*) > 0$, then u^* is unstable for any D_1, D_2 and $\tau \ge 0$; and if $g'(u^*) < 0$, then u^* is locally asymptotically stable when $D_1 \ge |D_2|u^*$ and $\tau \ge 0$, and it is unstable (with dim(unstable manifold)$=\infty$) when $D_1 < |D_2|u^*$ and $\tau > 0$.

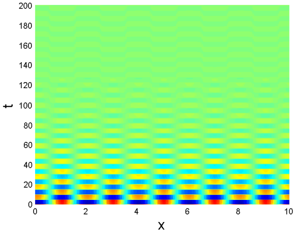
Example: Logistic Equation

$$\begin{cases} u_t = D_1 \Delta u + D_2 div(u(x,t) \nabla u(x, t-\tau)) + u(1-u), & x \in \Omega, t > 0, \\ \partial_n u(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,t) = \phi(x,t), & x \in \Omega, -\tau \le t \le 0. \end{cases}$$

Theorem 3. The equilibrium $u = 0$ is always unstable; the equilibrium $u = 1$ is locally asymptotically stable when $D_1 \ge |D_2|$ and $\tau \ge 0$, and it is unstable when $D_1 < |D_2|$ and $\tau > 0$. There are no other nonnegative equilibria.

Question: when $D_1 \ge |D_2|$ and $\tau > 0$, is $u = 1$ globally asymptotically stable?

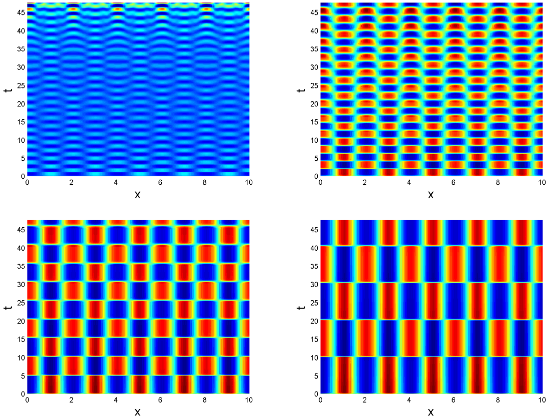




(left) $\tau = 1$; (right): $\tau = 5$. Here $D_1 = 1$ and $D_2 = 0.9$.

Checker board patterns

There are no spatially nonhomogeneous time-periodic patterns generated through Hopf bifurcations. But...



(top left) $\tau = 1$; (top right) $\tau = 2$; (bottom left) $\tau = 5$; (bottom right) $\tau = 10$. Here $D_1 = 1$, $D_2 = 1.1$.

Model with delays in both movement and growth

[Shi-Wang Chuncheng-Wang Hao, 2018, preprint]

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \Delta u + D_2 div(u \nabla u_\tau) + g(u, u_\sigma), & x \in \Omega, t > 0, \\ \dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0, \\ u(x,t) = \phi(x,t), & (x,t) \in \partial\Omega \times [-\max\{\tau,\sigma\}, 0]. \end{cases}$$

Here $u = u(x,t)$, $u_\tau = u(x, t-\tau)$ and $u_\sigma = u(x, t-\sigma)$.

- $\sigma = 0$ and $\tau > 0$: previous model with movement with delay: no bifurcation of stable periodic orbits;
- $\sigma > 0$ and $\tau = 0$: Diffusive Wright-Hutchinson equation: bifurcation of spatially homogeneous stable periodic orbits [Yoshida, 1982, Hiroshima-MJ], [Memory, 1989, SIAM-JMA], [Friesecke, 1993, JDDE];
- $\sigma > 0$ and $\tau = 0$ (Dirichlet boundary condition): bifurcation of spatially non-homogeneous stable periodic orbits from non-constant steady state [Green-Stech, 1981, book chap], [Busenberg-Huang, 1996, JDE] [Su-Wei-Shi, 2009, JDE] [Yan-Li, 2010, Nonlinearity] more general case

Stability

Characteristic equation: (μ is eigenvalue)

$$E(n,\tau,\sigma,\mu) := \mu + D_1\lambda_n - A + D_2 u^* \lambda_n e^{-\mu\tau} - Be^{-\mu\sigma} = 0, \;\; n = 0,1,2,3,\cdots .$$

Theorem 4.
1. When $D_1 < |D_2 u^*|$, for any $\tau > 0$ and $\sigma \geq 0$, there are infinitely many pairs of complex roots with positive real parts so u^* is linearly unstable.
2. When $D_1 > |D_2 u^*|$, for any $\tau > 0$ and $\sigma \geq 0$, there exists $N \in \mathbb{N}$ such that all the roots of have strictly negative real parts, for any $n > N$; and for $0 \leq n \leq N$, there is a spiral-like crossing curve in (τ,σ) plane which separates the parameter set which is stable or unstable in mode-n, and it defines a mode-n stable region Θ_n in (τ,σ) plane, and $\cap_{n=0}^{\infty}\Theta_n$ is the stable parameter region. (Note that only finitely many $\Theta_n \neq \emptyset$)

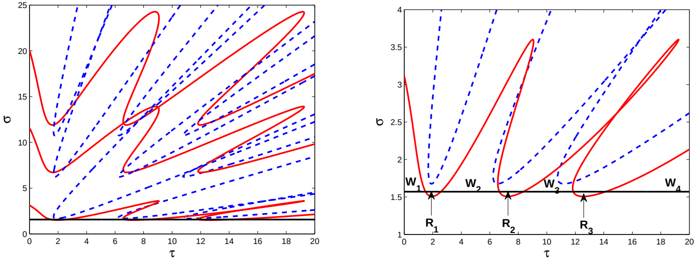
Eigenvalue problem with two delays:

[Hale-Huang, 1993, JMAA] [Ruan-Wei, 2003, DCDIS] [Gu et.al., 2005, JMAA]

Example: Wright-Hutchinson equation with memory

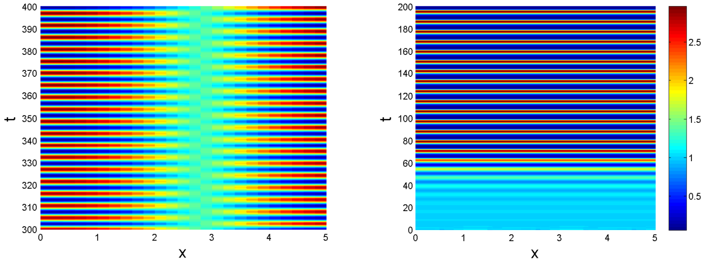
$$
\begin{cases}
\dfrac{\partial u}{\partial t} = \Delta u + D div(u\nabla u(x,t-\tau)) + u(1-u(x,t-\sigma)), & x \in \Omega, t > 0,\\
\dfrac{\partial u}{\partial n}(x,t) = 0, & x \in \partial\Omega, t > 0.
\end{cases}
$$

Stability change for $u = 1$: $(\mu + \lambda_n + D\lambda_n e^{-\mu\tau} + e^{-\mu\sigma} = 0)$



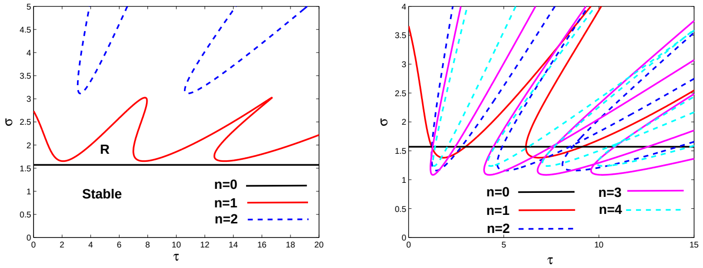
Left: crossing curves for $n = 0$ (black solid), $n = 1$ (red solid) and $n = 2$ (blue dotted); Right: zoom-in of the lower part. $\Omega = (0, 5)$ and $D = 0.7$.

Patterns



Periodic solutions with different delays. Left: a spatially nonhomogeneous periodic solution for $(\tau, \sigma) = (2, 1.52) \in R_1$; Right: a spatially homogeneous periodic solution for $(\tau, \sigma) = (1, 1.7) \in R_4$. Here, $\Omega = (0, 5)$, $D = 0.7$ and the initial function $u(\theta, x) = 1 + 0.1 \cos(\pi x/5)$ for $\theta \in [-\tau, 0]$.

Homogeneous or nonhomogeneous?

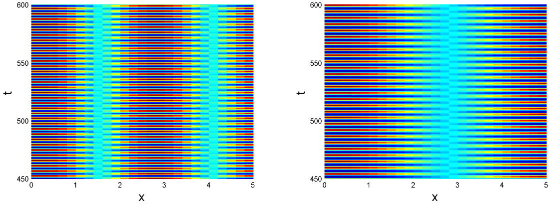


The crossing curves with different n, for $D = 0.5$ (left) and $D = 0.9$ (right). Here, $\Omega = (0, 5)$.

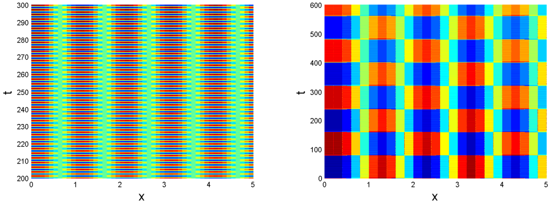
Proposition 5. There a threshold diffusion coefficient $D_0 \in (0, 1)$ such that nonhomogeneous periodic orbits emerge when $D \in (D_0, 1)$, and there are no nonhomogeneous periodic orbit Hopf bifurcations for $D \in (0, D_0)$.

More patterns

For $D = 0.9$ and $\tau = 2$, the spatially nonhomogeneous periodic solutions for $\sigma = 1.35$ (left) and $\sigma = 1.5$ (right).



(Left) For $D = 0.95$, $\tau = 1.18$ and $\sigma = 1.5$. Checker board again!
(Right) $g = ru\left(1 - \int_\Omega K(x,y)u(y,t-\sigma)dy\right)$ with triangular distribution function $K(x,y)$ such that $\int_\Omega K(x,y)dy = 1$ for any x. Here, $D = 0.95$, $\sigma = 1.5$ and $\tau = 80$.



Type of time delays

Discrete delay: past track at exactly time τ ago

$$u_t(x,t) = D_1 \Delta u(x,t) + D_2 div(u(x,t) \nabla u(x,t-\tau)) + g(u(x,t)).$$

Distributed delay: average of all past tracks for all past time:

$$u_t(x,t) = D_1 \Delta u(x,t) + D_2 div(u(x,t) \nabla v(x,t)) + g(u(x,t)), \quad x \in \Omega,$$

where

$$v(x,t) = g ** u(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y,t-s) g(t-s) u(y,s) dyds.$$

Here $G(x,y,t-s) = \sum_{n=1}^{\infty} e^{-D_1 n^2 (t-s)} \cos(nx) \cos(ny)$ (Green's function of diffusion equation) shows the movement under diffusion at the past time $t-s$, and the probability distribution functions

$$\text{(weak kernel)} \;\; g_w(t) = \frac{1}{\tau} e^{-\frac{t}{\tau}}, \quad \text{(strong kernel)} \;\; g_s(t) = \frac{t}{\tau^2} e^{-\frac{t}{\tau}},$$

show the decay of the memory.

Weak kernel system is equivalent to Keller-Segel model

[Shi Qingyan-Shi Junping-Wang Hao, 2018, in preparation]

$$u_t(x,t) = D_1 \Delta u(x,t) - D_2 div(u(x,t) \nabla v(x,t)) + g(u(x,t)), \quad x \in \Omega,$$

where

$$v(x,t) = g**u(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y,t-s) g(t-s) u(y,s) dyds.$$

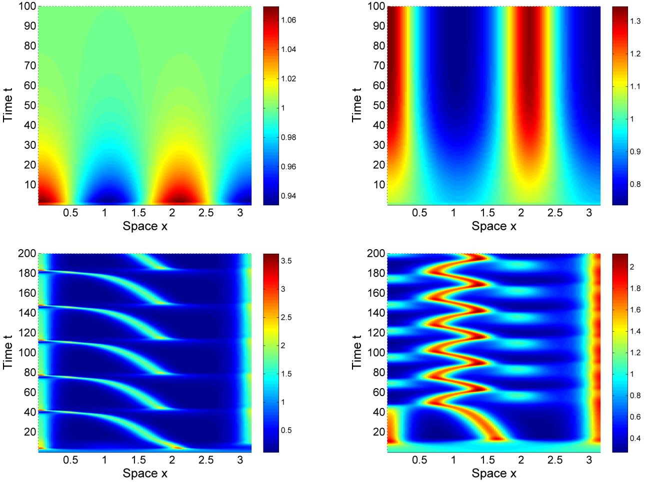
with weak kernel is equivalent to Keller-Segel chemotaxis model with logistic growth:

$$\begin{cases} u_t = D_1 \Delta u - D_2 div(u \nabla v) + g(u), & x \in \Omega, t > 0, \\ v_t = D_1 \Delta v + \tau^{-1} u - \tau^{-1} v, & x \in \Omega, t > 0. \end{cases}$$

- So that chemical attracting you is your decaying memory of all past movement!
- $v(x,t)$ is the memory (from $t = -\infty$ to now) at location x and time t, which decays at a rate $1/\tau$, and also increases at the same rate by the stimulate $u(x,t)$.

[Mimura-Tsujikawa, 1996, PhyA] [Hillen-Painter, 2011, PhyD]
[Kuto et.el., 2012, PhyD]

Weak kernel simulations



(upper left) no pattern; (upper right) non-constant equilibrium;
(lower left) drifting time-periodic solution; (lower right): wandering time-periodic solution.

Strong kernel system

$$u_t(x,t) = D_1\Delta u(x,t) - D_2 div(u(x,t)\nabla v(x,t)) + g(u(x,t)), \quad x \in \Omega,$$

where

$$v(x,t) = g**u(x,t) = \int_{-\infty}^{t}\int_{\Omega} G(x,y,t-s)g(t-s)u(y,s)dyds.$$

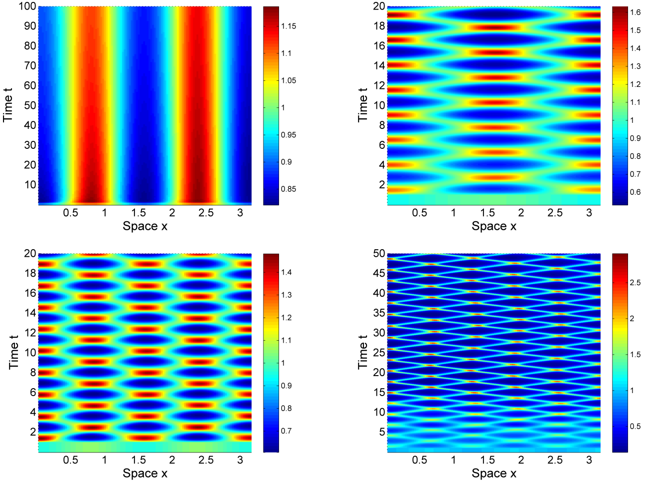
with weak kernel is equivalent to a Keller-Segel-like chemotaxis model with logistic growth:

$$\begin{cases} u_t = D_1\Delta u - D_2 div(u\nabla v) + g(u), & x \in \Omega, t > 0, \\ v_t = D_1\Delta v + \tau^{-1}w - \tau^{-1}v, & x \in \Omega, t > 0, \\ w_t = D_1\Delta w + \tau^{-1}u - \tau^{-1}w, & x \in \Omega, t > 0. \end{cases}$$

Here $v(x,t)$ is the past memory, $w(x,t)$ is another signal (secondary memory?) which stimulates the memory, and $u(x,t)$ stimulates $w(x,t)$.

- The memory may be a complicated cognitive process involving several levels of stimulations.
- More generally the degree-n Gamma distribution function $g_n(t) = \frac{t^n e^{-\frac{t}{\tau}}}{\tau^{n+1}\Gamma(n+1)}$ could induce an equivalent reaction-diffusion system with $n+1$ equations.

Strong kernel simulations



(upper left) non-constant equilibrium; (upper right) time-periodic solution; (lower left) time-periodic solution; (lower right): time-periodic solution.

Conclusions

- Partial differential equation with movement oriented by past gradient is one of ways of modeling memory-based animal movement.
- Similar to well-known Keller-Segel chemotaxis models, the memory-based PDE models can generate population aggregation in a stationary fashion. But they may also produce spatiotemporal time-periodic patterns, which may be more realistic for many repeatedly-occurring animal behavior.
- Future work:
  (i) numerically solving in two-dimensional region;
  (ii) fitting real ecological data;
  (iii) mathematical theory (non-standard PDE models: boundedness of solutions, asymptotic behavior, traveling waves).
  (iv) more general models:

$$u_t(x,t) = D_1 \Delta u(x,t) - D_2 div(f_1(u(x,t))\nabla f_2(v(x,t))) + g(u(x,t)), \quad x \in \Omega,$$

where

$$v(x,t) = g**u(x,t) = \int_{-\infty}^{t} \int_{\Omega} G(x,y,t-s)g(t-s)u(y,s)dyds,$$

and g and G are general kernel functions.
(v) multiple-species model: competition, predator-prey. (some work are underway)