# 第 1 回「応用数学特論 III, IIIa」 2022 年 10 月 3 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Population dynamics

Let $N(t)$ be the **population** at time $t$. The simplest mathematical model of the population dynamics is given by

$$\frac{dN(t)}{dt} = bN(t) - dN(t), \quad N(0) = N_0,$$

where $b$ and $d$ denote the birth and death rates, respectively. The solution is given by

$$N(t) = N_0 e^{(b-d)t}.$$

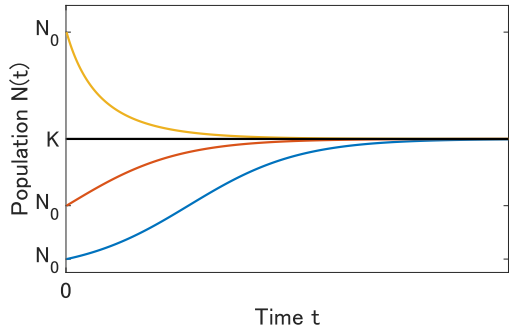
Here $r := b - d$ is called the **Malthusian parameter**, which determines whether the population increases or decreases:

- If $r > 0$, then the population $N(t)$ increases exponentially to $+\infty$ as $t \to +\infty$.
- If $r < 0$, then the population $N(t)$ decreases exponentially to 0 as $t \to +\infty$.

However, the infinitely increasing population seems unrealistic. The following modified model is called the **logistic equation**, developed by Verhulst:

$$\frac{dN(t)}{dt} = rN(t)\left[1 - \frac{N(t)}{K}\right],$$

where $K$ is called the **carrying capacity**. This equation has two steady states: $N = 0$ and $K$. We can check that 0 is unstable and $K$ is stable.




## 2 Insect outbreak

The model for budworm population dynamics, considered by Ludwig et al. (1978) is

$$\frac{dN(t)}{dt} = r_B N(t)\left[1 - \frac{N(t)}{K_B}\right] - \frac{BN^2}{A^2 + N^2}.$$

We perform nondimensionalization by introducing

$$u = \frac{N}{A}, \quad r = \frac{Ar_B}{B}, \quad q = \frac{K_B}{A}, \quad \tau = \frac{Bt}{A}.$$

We then have

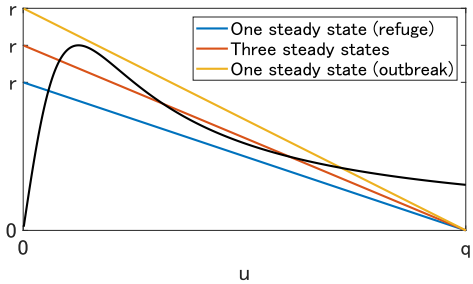
$$\frac{du}{d\tau} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2} =: f(u).$$

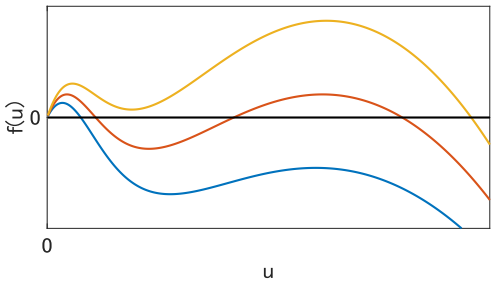
The steady states are the solutions of

$$ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2} = 0.$$

It is obvious that $u = 0$ is always one of the steady state, which is unstable. The existence and stability of other solutions can be studied by considering the following equation:

$$r\left(1 - \frac{u}{q}\right) = \frac{u}{1+u^2}.$$



# 第 2 回「応用数学特論 III, IIIa」 2022 年 10 月 17 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Difference equation

Let $f$ be a smooth function. The following recurrence relation is called a **difference equation**:

$$u_{t+1} = f(u_t), \quad t = 0, 1, 2, \ldots.$$

The equilibrium point $u^*$ is a solution of

$$u^* = f(u^*).$$

To investigate the **stability** of $u^*$, we write

$$u_t = u^* + v_t, \quad |v_t| \ll 1.$$

By the Taylor expansion, we obtain

$$v_{t+1} \approx \lambda v_t,$$

where $\lambda := f'(u^*)$. We then see that

- If $|\lambda| < 1$, then $u^*$ is stable.
- If $|\lambda| > 1$, then $u^*$ is unstable.

For example, $u_{t+1} = \cos u_t$ has only one stable equilibrium point $u^* \approx 0.739$. $u_{t+1} = \sin u_t$ has only one stable equilibrium point $u^* = 0$, which stablity can be checked by writing a cobweb plot.

**Exercise** Find all equilibrium points of $u_{t+1} = u_t e^{1-u_t}$ and investigate their stability.

## 2 Logistic map

The difference form of the logistic equation is

$$N(t+1) - N(t) = r_d N(t) \left[1 - \frac{N(t)}{K_d}\right].$$

By changing the variable as

$$N(t) = \frac{1 + r_d}{r_d} K_d u_t, \quad r = 1 + r_d,$$

we arrive at

$$u_{t+1} = r u_t (1 - u_t),$$

which is called a **logistic map**.

We assume that $0 < u_0 < 1$ and $r > 0$. If $r < 1$, then there exists only one stable equilibrium $u^* = 0$. If $r > 1$, then another equilibrium point $u^* = 1 - r^{-1}$ exists. It is stable for $1 < r < 3$, but unstable for $r > 3$.

For $r > 3$, we consider the following second iteration:

$$\begin{aligned} u_{t+2} =& f(f(u_t)) \\ =& r\left[r u_t (1 - u_t)\right]\left[1 - r u_t (1 - u_t)\right]. \end{aligned}$$

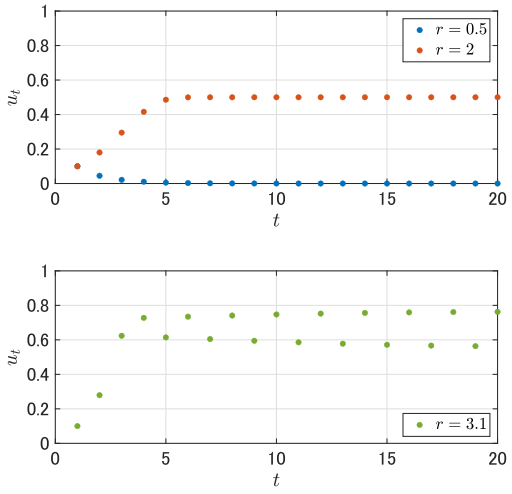
The equilibrium points $u_2^*$ of this equation can correspond to a 2-periodic solution. We write them by $p$ and $q$, that is, $f(p) = q$, $f(q) = p$ and $p \neq q$. By a calculation, we obtain

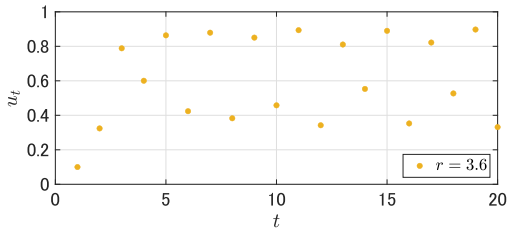
$$p, q = \frac{r + 1 \pm \sqrt{(r+1)(r-3)}}{2r}.$$

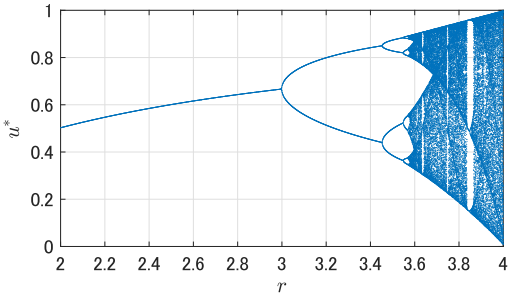
The stability of the 2-periodic solution can be checked by

$$\lambda_2 := \left.\frac{d}{du} f^2(u)\right|_{u=p,q} = f'(p) f'(q).$$

That is, if $|\lambda_2| < 1$, then it is stable, whereas if $|\lambda_2| > 1$, then it is unstable. We can check that if $3 < r < 1 + \sqrt{6}$, then the 2-periodic solution is stable. For $r > 1 + \sqrt{6}$, the period-doublings to 4, 8, 16,...-periodic solutions occur as $r$ increases. For $r > r_\infty \approx 3.57$, a **chaotic behavior** appears.




1
0.8
0.6
0.4
0.2
0
$u_t$
0
5
10
15
20
$t$
$r = 3.6$


1
0.8
0.6
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0
$u^*$
2
2.2
2.4
2.6
2.8
3
3.2
3.4
3.6
3.8
4
$r$

# 第 3 回「応用数学特論 III, IIIa」 2022 年 10 月 24 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Lotka-Volterra model

Let $N(t)$ and $P(t)$ be the populations of prey and predator at time $t$, respectively. The **Lotka-Volterra model** is given by

$$\frac{dN}{dt} = N(a - bP), \quad \frac{dP}{dt} = P(cN - d),$$

where $a, b, c$ and $d$ are positive parameters. More precisely, $aN$ denotes the growth term of prey; $-bNP$ and $cNP$ denote the effects of predation in decreasing the prey population and increasing the predator population, respectively; $-dP$ denotes the death rate of the predator population. Let

$$\tau = at, \ \ \alpha = \frac{d}{a}, \ \ u(\tau) = \frac{cN(\tau)}{d}, \ \ v(\tau) = \frac{bP(\tau)}{a}.$$

The Lotka-Volterra model can then be rewritten as

$$\frac{du}{d\tau} = u(1 - v), \quad \frac{dv}{d\tau} = \alpha v(u - 1).$$

The equilibrium points of this model are

$$(u^*, v^*) = (0, 0), \ (1, 1).$$

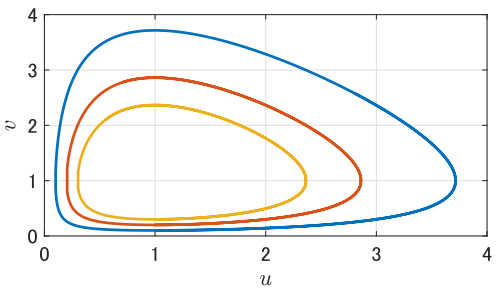
In the $u$-$v$ phase plane, we have

$$\frac{dv}{du} = \alpha \frac{v(u-1)}{u(1-v)}.$$

By solving this, we have

$$\alpha u + v - \ln u^\alpha v = H,$$

where $H > H_{min} = 1 + \alpha$. This forms a closed trajectory in the $u$-$v$ phase plane. The solution is the periodic solution moving on this trajectory.




## 2 Phase plane analysis

We consider the following general system of ordinary differential equations:

$$\frac{dx}{dt} = f(x, y), \quad \frac{dy}{dt} = g(x, y).$$

The equilibrium point $(x^*, y^*)$ satisfies

$$f(x^*, y^*) = g(x^*, y^*) = 0.$$

Let $A$ be the Jacobian matrix at $(x^*, y^*)$, that is,

$$A = \begin{bmatrix} \frac{\partial f(x^*,y^*)}{\partial x} & \frac{\partial f(x^*,y^*)}{\partial y} \\ \frac{\partial g(x^*,y^*)}{\partial x} & \frac{\partial g(x^*,y^*)}{\partial y} \end{bmatrix}.$$

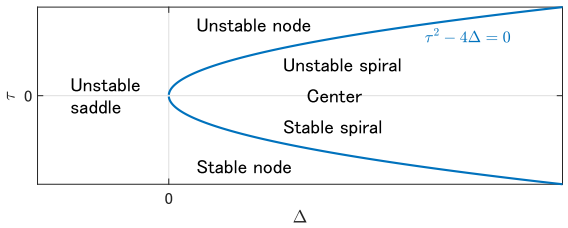
Let $\lambda_1, \lambda_2$ be the eigenvalues of $A$. The stability of equilibrium point $(x^*, y^*)$ can be investigated as follows:

- If both $\mathrm{Re}\,\lambda_1$ and $\mathrm{Re}\,\lambda_2$ are negative, then $(x^*, y^*)$ is **asymptotically stable**.
- If either or both $\mathrm{Re}\,\lambda_1$ and $\mathrm{Re}\,\lambda_2$ are positive, then $(x^*, y^*)$ is unstable.

Let $\tau$ and $\Delta$ be the trace and determinant of $A$. We then have

$$\lambda_1, \lambda_2 = \frac{\tau \pm \sqrt{\tau^2 - 4\Delta}}{2}.$$

That is, the stability is determined only by $\tau$ and $\Delta$.




**Exercise** Answer the stability of all equilibrium points of the following system:

$$\frac{dx}{dt} = x(3 - 2x - y), \quad \frac{dy}{dt} = y(2 - x - y).$$

# 第 4 回「応用数学特論 III, IIIa」 2022 年 10 月 31 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Competition

Let us consider the competition of two species whose populations are $N_1$ and $N_2$, respectively. The **Lotka-Volterra competition model** is given by

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right),$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_2}{K_2}\right),$$

where all parameters are positive. Let

$$u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1},$$
$$a_{12} = b_{12}\frac{K_2}{K_1}, \quad a_{21} = b_{21}\frac{K_1}{K_2}.$$

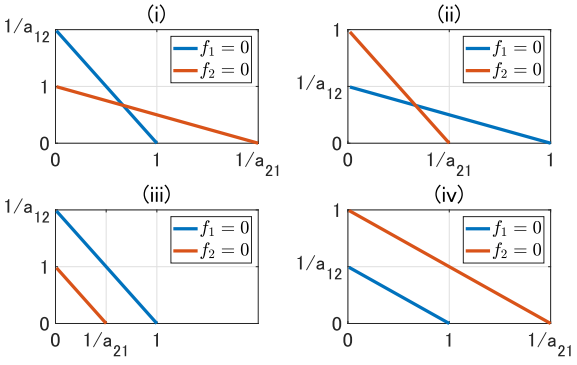
Then, the model can be rewritten as

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2) =: f_1(u_1, u_2),$$
$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1) =: f_2(u_1, u_2).$$

The equilibrium points $(u_1, u_2) = (u_1^*, u_2^*)$ are

$$(u_1^*, u_2^*) = (0,0),\ (1,0),\ (0,1),$$
$$\left(\frac{1-a_{12}}{\delta}, \frac{1-a_{21}}{\delta}\right),\ \delta = 1 - a_{12}a_{21}.$$

The stability of each equilibrium point can be investigated by using the Jacobian matrix. There are four cases: (i) $a_{12} < 1$ and $a_{21} < 1$. (ii) $a_{12} > 1$ and $a_{21} > 1$. (iii) $a_{12} < 1 < a_{21}$. (iv) $a_{21} < 1 < a_{12}$. The dynamics can also be investigated by drawing **nullclines** in the $u_1$-$u_2$ plane.




## 2 Mutualism

The **mutualism** can be modeled by the following system:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_1}\right),$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21}\frac{N_2}{K_2}\right).$$

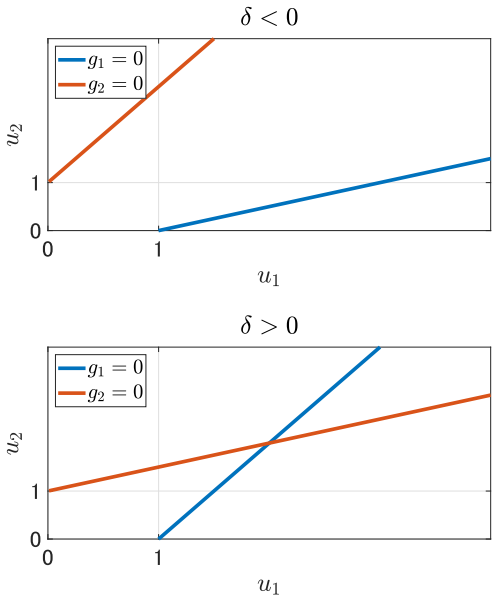
Similar to the competition model, this system can be rewritten as

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2) =: g_1(u_1, u_2),$$
$$\frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1) =: g_2(u_1, u_2).$$

The equilibrium points are

$$(u_1^*, u_2^*) = (0,0),\ (1,0),\ (0,1),$$
$$\left(\frac{1+a_{12}}{\delta}, \frac{1+a_{21}}{\delta}\right),\ \delta = 1 - a_{12}a_{21}.$$

We can easily check that $(0,0)$, $(1,0)$ and $(0,1)$ are always unstable. If $\delta < 0$, then the fourth equilibrium point does not exist, and hence, the solution goes to infinity as $t$ increases. If $\delta > 0$, then the fourth equilibrium point exists and it is a stable node.



# 第 5 回「応用数学特論 III, IIIa」 2022 年 11 月 7 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Basic enzyme reaction

Let $S$ be a substrate, $E$ be an enzyme, $SE$ be a complex and $P$ be a product. The basic **enzyme reaction** can be represented by

$$S + E \rightleftharpoons_{k_{-1}}^{k_1} SE \xrightarrow{k_2} P + E.$$

Let $[\cdot]$ denote concentration and let

$$s = [S], \quad e = [E], \quad c = [SE], \quad p = [P].$$

We then have the following system:

$$\frac{ds}{dt} = -k_1 es + k_{-1} c, \quad \frac{de}{dt} = -k_1 es + (k_{-1} + k_2)c,$$
$$\frac{dc}{dt} = k_1 es - (k_{-1} + k_2)c, \quad \frac{dp}{dt} = k_2 c$$

with initial condition

$$s(0) = s_0, \quad e(0) = e_0, \quad c(0) = p(0) = 0.$$

We easily see that the first three equations of the system are independent of $p$. Moreover,

$$\frac{de}{dt} + \frac{dc}{dt} = 0 \quad \Leftrightarrow \quad e + c = e_0.$$

Hence, the system can be reduced to

$$\frac{ds}{dt} = -k_1 e_0 s + (k_1 s + k_{-1})c,$$
$$\frac{dc}{dt} = k_1 e_0 s - (k_1 s + k_{-1} + k_2)c.$$

In the initial stage of the complex, $c$, we can assume that $dc/dt \approx 0$ (quasi-steady state approximation) and we get

$$c = \frac{e_0 s}{s + K_m}, \quad K_m = \frac{k_{-1} + k_2}{k_1},$$

where $K_m$ is called the **Michaelis constant**. The equation of $s$ can be rewritten as

$$\frac{ds}{dt} = -\frac{k_2 e_0 s}{s + K_m}.$$

## 2 Autocatalysis and inhibition

Autocatalysis is represented by

$$A + X \rightleftharpoons_{k_{-1}}^{k_1} 2X.$$

If the concentration of $A$ is constant $a$, then

$$\frac{dx}{dt} = k_1 ax - k_{-1} x^2,$$

which is no other than the logistic equation.

If the reaction system is

$$A + X \rightleftharpoons_{k_{-1}}^{k_1} 2X, \quad B + X \xrightarrow{k_2} C,$$

and the concentration of $B$ is constant $b$, then

$$\frac{dx}{dt} = (k_1 a - k_2 b)x - k_{-1} x^2.$$

In this case, a **transcritical bifurcation** occurs at $k_1 a - k_2 b = 0$.

If the reaction system is

$$A + X \xrightarrow{k_1} 2X, \quad X + Y \xrightarrow{k_2} 2Y, \quad Y \xrightarrow{k_3} B,$$

then

$$\frac{dx}{dt} = k_1 ax - k_2 xy, \quad \frac{dy}{dt} = k_2 xy - k_3 y,$$

which is equivalent to the Lotka-Volterra model.

Thomas (1975) formulated the following equations of the uric acid $u$ and the oxygen $v$:

$$\frac{du}{dt} = a - u - \rho R(u, v) = f(u, v),$$
$$\frac{dv}{dt} = \alpha(b - v) - \rho R(u, v) = g(u, v),$$
$$R(u, v) = \frac{uv}{1 + u + Ku^2}.$$

**Exercise** A gene product with autocatalysis can be represented by

$$\frac{dx}{dt} = s + k_1 \frac{x^2}{1 + x^2} - k_2 x.$$

Suppose that $s = 0$ and $k_1, k_2 > 0$. Show a condition for which the equation has two positive equilibrium points. Moreover, answer their stability.

# 第 6 回「応用数学特論 III, IIIa」 2022 年 11 月 14 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Limit cycle

We consider the following system in the polar coordinates:

$$\frac{dr}{dt} = r(1-r^2), \quad \frac{d\theta}{dt} = 1.$$

We can easily check that the equilibrium pont $r^* = 0$ is unstable and $r^* = 1$ is stable. Hence, $(x, y) = (r\cos\theta, r\sin\theta)$ converges to a closed orbit with radius 1. This is a **limit cycle**.

We consider the following general system:

$$\frac{dx}{dt} = f(x, y), \quad \frac{dy}{dt} = g(x, y).$$

The following theorem gives a sufficient condition for the existence of a limit cycle.

**Poincaré-Bendixson Theorem**

Suppose that

1) $R$ is a bounded closed set in the $x-y$ plane.
2) $f$ and $g$ are continuously differentiable in a domain that includes $R$.
3) $R$ does not include any equilibria.
4) There is an orbit $C$ that stays in $R$.

Then, $C$ is either a closed orbit or an orbit approaching to a limit cycle.

We now apply the Poincaré-Bendixson theorem to the following system:

$$\frac{dr}{dt} = r(1-r^2) + \mu r\cos\theta, \quad \frac{d\theta}{dt} = 1.$$

If we find $r_M > r_m > 0$ such that $r' > 0$ at $r = r_m$ and $r' < 0$ at $r = r_M$, then the following set $R$ (confined set) satisfies the condition of the Poincaré-Bendixson theorem:

$$R = \{(x, y) = (r\cos\theta, r\sin\theta) : r_m \le r \le r_M\}.$$

If $\mu < 1$, we can set

$$r_m = 0.999\sqrt{1-\mu}, \quad r_M = 1.001\sqrt{1+\mu}.$$

## 2 Simple two-species oscillators

Schnackenberg (1979) considered the following reaction mechanism which will admit periodic solutions:

$$X \rightleftharpoons_{k_{-1}}^{k_1} A, \quad B \xrightarrow{k_2} Y, \quad 2X + Y \xrightarrow{k_3} 3X.$$

The nondimensional form is

$$\frac{du}{dt} = a - u + u^2 v = f(u, v), \quad \frac{dv}{dt} = b - u^2 v = g(u, v),$$

where $a$ and $b$ are positive constants. The equilibrium point $(u^*, v^*)$ is

$$u^* = a + b, \quad v^* = \frac{b}{(a+b)^2}.$$

The trace $\tau$ and determinant $\Delta$ of the Jacobian matrix can be calculated as

$$\tau = \frac{b-a}{a+b} - (a+b)^2, \quad \Delta = (a+b)^2 > 0.$$

To apply the Poincaré-Bendixson theorem, $(u^*, v^*)$ should be unstable. This holds if

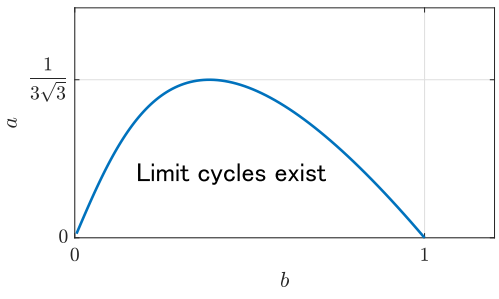
$$\tau > 0 \quad \Leftrightarrow \quad b - a > (a+b)^3.$$

To depict a parameter region where a limit cyle exists, we rewrite the condition $\tau > 0$ in terms of $u^*$, that is,

$$\tau > 0 \quad \Leftrightarrow \quad a < \frac{u^*[1-(u^*)^2]}{2}.$$

Since $b = u^* - a$, we obtain the following parameter boundary:

$$a = \frac{x(1-x^2)}{2}, \quad b = \frac{x(1+x^2)}{2}, \quad x > 0.$$



# 第 7 回「応用数学特論 III, IIIa」 2022 年 11 月 21 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Flows on the circle

Consider the following differential equation:

$$\theta' = f(\theta), \quad f(\theta) = f(\theta + 2\pi).$$

This equation corresponds to a **vector field on the circle**. Examples are as follows:

- $\theta' = \sin\theta$.
- $\theta' = \omega$ ($\omega$: constant).

Two people, A and B, are running around a circular track. To run once around the track, they take $T_1$ and $T_2$ seconds ($T_1 < T_2$), respectively. If they start together, how long does it take for A to lap B once? Let

$$\theta_1' = \omega_1, \quad \theta_2' = \omega_2.$$

We then have that $\omega_i = 2\pi/T_i$, $i = 1, 2$. By considering the phase difference $\phi = \theta_1 - \theta_2$, we obtain the answer to the above question as

$$\frac{2\pi}{\omega_1 - \omega_2} = \left(\frac{1}{T_1} - \frac{1}{T_2}\right)^{-1}.$$

The following equation corresponds to the nonuniform oscillator:

$$\theta' = \omega - a\sin\theta,$$

where $\omega$ and $a$ are positive constants. For $a < \omega$, there is no equilibrium. An equilibrium arises in a saddle-node bifurcation at $a = \omega$, and it splits into two equilibria for $a > \omega$. For $a < \omega$, the period of oscillation (from $\theta$ to $\theta + 2\pi$) is caluculated as

$$T = \int_0^{2\pi} \frac{1}{\omega - a\sin\theta} d\theta.$$

We can calculate it as

$$T = \frac{2\pi}{\sqrt{\omega^2 - a^2}}.$$

## 2 Firefly's flashing rhythm

Assume that $\theta$ is the phase of the firefly's flashing rhythm and $\theta = 0$ corresponds to the instant when a flash is emitted. The model is as follows:

$$\theta' = \omega + a\sin(\Theta - \theta),$$

where $\omega$ and $a$ are positive constants and $\Theta$ is the phase of the periodic stimulus satisfying

$$\Theta' = \Omega,$$

where $\Omega$ is a positive constant. Let $\phi = \Theta - \theta$ be the phase difference and

$$\tau = at, \quad \mu = \frac{\Omega - \omega}{a},$$

we obtain the following dimensionless equation:

$$\phi' = \mu - \sin\phi.$$

For $\mu \geq 0$, we see that

- If $\mu = 0$, then the firefly and the stimulus eventually keep flashing simultaneously.
- If $0 < \mu < 1$, then the firefly's rhythm is phase-locked to the stimulus.
- A saddle-node bifurcation occurs at $\mu = 1$.
- If $\mu > 1$, then the phase drift occurs. The period of phse drift (from $\phi$ to $\phi + 2\pi$) can be calculated as

$$T = \frac{2\pi}{\sqrt{(\Omega - \omega)^2 - a^2}}.$$

The situation for $\mu < 0$ is similar. The phase locking by the stimulus is possible if $|\mu| \leq 1$, that is, $\Omega$ satisfies

$$\omega - a \leq \Omega \leq \omega + a.$$

This range is called the range of entrainment.

# 第 8 回「応用数学特論 III, IIIb」 2022 年 11 月 28 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 The SIR epidemic model

In 1927, Kermack and McKendrick proposed a mathematical model for epidemics, which is called the **SIR epidemic model**. Here, $S(t)$, $I(t)$ and $R(t)$ denote the **susceptible**, **infective** and **removed** populations at time $t \geq 0$, respectively. The model in a simple form is given by the following system of ordinary differential equations:

$$\begin{cases} \dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = -\beta S(t)I(t), \\ \dfrac{\mathrm{d}I(t)}{\mathrm{d}t} = \beta S(t)I(t) - \gamma I(t), \\ \dfrac{\mathrm{d}R(t)}{\mathrm{d}t} = \gamma I(t), \quad t > 0. \end{cases}$$

where $\beta > 0$ is the infection rate and $\gamma > 0$ is the removal rate. The initial condition is

$$S(0) = S_0 > 0, \quad I(0) = I_0 > 0, \quad R(0) = 0.$$

We can easily confirm that the total population $N := S + I + R$ is constant. Since $N = S_0 + I_0 > 0$, $S'(t) < 0$ and $R'(t) > 0$,

$$0 < S(t) + I(t) < N \quad \text{for all } t > 0.$$

If $S(0) \approx N$, then the infective population in the initial invasion phase is governed by the following equation:

$$\frac{\mathrm{d}I(t)}{\mathrm{d}t} = \beta N I(t) - \gamma I(t), \quad t > 0.$$

Hence, the infective populatin increases as time evolves if $\beta N - \gamma > 0$. This condition can be rewritten as

$$\mathcal{R}_0 := \frac{\beta N}{\gamma} > 1.$$

$\mathcal{R}_0$ is called **the basic reproduction number**. We can obtain the following threshold statement.

$$\mathcal{R}_0 > 1 \Rightarrow \text{the outbreak occurs.}$$
$$\mathcal{R}_0 < 1 \Rightarrow \text{there is no outbreak.}$$

$\mathcal{R}_0$ means the average number of secondary cases produced by an infected individual during their entire infectious period in a completely susceptible population. Note that $\gamma \mathrm{e}^{-\gamma t}$ is the probability density function of recovery occurring, and hence,

$$\int_0^{+\infty} t\gamma \mathrm{e}^{-\gamma t} \mathrm{d}t = \frac{1}{\gamma}$$

is the average duration in the infectious state.

## 2 The final size equation

Let $N_{cr} := \gamma/\beta$. We then see that if $S(0) < N_{cr}$, then the infective population is monotone decreasing, whereas if $S(0) > N_{cr}$, then it is not monotne. We have

$$\frac{\mathrm{d}I}{\mathrm{d}S} = -1 + \frac{N_{cr}}{S}.$$

By integraion, we have, for $t > 0$,

$$I(t) = I(0) + S(0) - S(t) + N_{cr} \log \frac{S(t)}{S(0)}.$$

Since $S(t) \to S(\infty) > 0$ and $I(t) \to 0$ as $t \to +\infty$, we obtain

$$S(\infty) = S(0)\mathrm{e}^{-\frac{N - S(\infty)}{N_{cr}}}.$$

Let $p = (N - S(\infty))/N$ be **the final size of epidemic**. We then have

$$1 - p = \left(1 - \frac{I(0)}{N}\right) \mathrm{e}^{-\mathcal{R}_0 p}.$$

For $I(0) \approx 0$, we have

$$1 - p_\infty = \mathrm{e}^{-\mathcal{R}_0 p_\infty}.$$

This equation is called **the final size equation**.

**Exercise**

Show that $p_\infty > 0$ if and only if $\mathcal{R}_0 > 1$.

# 第 9 回「応用数学特論 III, IIIb」 2022 年 12 月 5 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 SIR model with demography

Let $b > 0$ be the birth rate and $\mu > 0$ be the mortality rate. The **SIR model with demography** is given by

$$\begin{cases} \dfrac{\mathrm{d}S}{\mathrm{d}t} = b - \beta SI - \mu S, \\ \dfrac{\mathrm{d}I}{\mathrm{d}t} = \beta SI - (\gamma + \mu)I, \\ \dfrac{\mathrm{d}R}{\mathrm{d}t} = \gamma I - \mu R. \end{cases}$$

This model has two equilibrium points. The first one is the **disease-free** equilibrium:

$$E^0 = (S^0, 0, 0) = \left(\frac{b}{\mu}, 0, 0\right).$$

The second one is the **endemic** equilibrium:

$$\begin{aligned} E^* &= (S^*, I^*, R^*) \\ &= \left(\frac{\gamma+\mu}{\beta}, \frac{\mu}{\beta}\left(\frac{b\beta}{\mu(\gamma+\mu)} - 1\right), \frac{\gamma I^*}{\mu}\right). \end{aligned}$$

The disease-free equilibrium $E^0$ always exists. The endemic equilibrium $E^*$ exists if and only if

$$\frac{b\beta}{\mu(\gamma+\mu)} > 1.$$

In fact, for this model, the basic reproduction number $\mathcal{R}_0$ is defined by

$$\mathcal{R}_0 = \frac{b\beta}{\mu(\gamma+\mu)},$$

and $\mathcal{R}_0 = 1$ is the threshold value for the existence of $E^*$. More precisely, by peforming stability analysis, one can see that

- If $\mathcal{R}_0 < 1$, then the disease-free equilibrium $E^0$ is asymptotically stable, and no endemic equilibrium $E^*$ exists.
- If $\mathcal{R}_0 > 1$, then the disease-free equilibrium $E^0$ is unstable, the endemic equlibrium $E^*$ exists, and it is stable.

That is, $\mathcal{R}_0$ determines whether the disease dies out or persists. In this case, a forward transcritical bifurcation occurs at $\mathcal{R}_0 = 1$.

## 2 Control of disease

If the infection rate $\beta$ is reduced to $(1-e)\beta$, $0 < e < 1$ by social distancing, then we obtain

$$\mathcal{R}_e = \frac{(1-e)b\beta}{\mu(\gamma+\mu)} = (1-e)\mathcal{R}_0,$$

and the threshold value is changed to $\mathcal{R}_e = 1$. This $\mathcal{R}_e$ is called the **effective** (or, control) reproduction number. The condition $\mathcal{R}_e < 1$ can be rewritten as

$$e > 1 - \frac{1}{\mathcal{R}_0} = e^*.$$

That is, to suppress the epidemic, the reduction rate $e$ of infection rate should be greater than the critical value $e^*$. A similar conclusion can be obtained if $b$ is reduced to $(1-e)b$ by vaccination.

The following model is called an asymptomatic transmission model:

$$\begin{cases} \dfrac{\mathrm{d}S}{\mathrm{d}t} = -(\beta_1 E + \beta_2 I)S, \\ \dfrac{\mathrm{d}E}{\mathrm{d}t} = (\beta_1 E + \beta_2 I)S - \varepsilon E, \\ \dfrac{\mathrm{d}I}{\mathrm{d}t} = \varepsilon E - \gamma I. \end{cases}$$

The basic reproduction number is $\mathcal{R}_0 = \mathcal{R}_1 + \mathcal{R}_2$, where

$$\mathcal{R}_1 = \frac{\beta_1 N}{\varepsilon}, \quad \mathcal{R}_2 = \frac{\beta_2 N}{\gamma}, \quad N : \text{total population}.$$

If $\mathcal{R}_1 < 1$, then $\mathcal{R}_0 < 1$ is equivalent to $T < 1$, where

$$T = \frac{\mathcal{R}_2}{1 - \mathcal{R}_1}.$$

This $T$ is called the **type reproduction number**. If we can reduce only the infection rate $\beta_2$ of symptomatic transmission to $(1-e)\beta_2$ by quarantine, then the condtion for disease suppression is

$$e > 1 - \frac{1}{T}.$$

# 第 10 回「応用数学特論 III, IIIb」 2022 年 12 月 12 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Diffusion and traveling wave

Let $\Delta x, \Delta t > 0$ and

$$x_i = i\Delta x, \quad i = 0, \pm 1, \pm 2, \dots,$$
$$t_n = n\Delta t, \quad n = 0, 1, 2, \dots.$$

Let $N(x,t)$ be number of individuals in position $x \in \mathbb{R}$ at time $t \geq 0$. The following model is obtained by assuming **random walk**.

$$N(x_i, t_{n+1}) = \frac{1}{2}N(x_{i-1}, t_n) + \frac{1}{2}N(x_{i+1}, t_n).$$

By Taylor expansion, we obtain

$$\frac{\partial N(x_i,t_n)}{\partial t}\Delta t = \frac{1}{2}\frac{\partial^2 N(x_i,t_n)}{\partial x^2}(\Delta x)^2 + O((\Delta t)^2 + (\Delta x)^4).$$

We then obtain by $\Delta t \to 0$

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2}, \quad D = \frac{1}{2}\lim_{\Delta t \to 0}\frac{(\Delta x)^2}{\Delta t}.$$

This equation is called a **diffusion equation**, and $D$ is called a **diffusion coefficient**.

If a logistic term $rN(1-N)$ is added, the following **Fisher-KPP equation** is obtained.

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN(1-N).$$

This equation belongs to the class of **reaction-diffusion equations**. Let $z = x - ct$ and substituting $N(x,t) = U(z)$, we obtain

$$DU''(z) + cU'(z) + rU(1-U) = 0.$$

This solution is called a **traveling wave**. We can easily check that

$$N(x,t) = N(x + cT, t + T),$$

which implies that a wave in position $x$ at time $t$ moves to position $x + cT$ at time $t + T$.

## 2 Geographical spread of disease

The SI(R) epidemic model can be extented to the following reaction-diffusion equations.

$$\begin{cases} \dfrac{\partial S}{\partial t} = D\dfrac{\partial^2 S}{\partial x^2} - \beta SI, \\ \dfrac{\partial I}{\partial t} = D\dfrac{\partial^2 I}{\partial x^2} + \beta SI - \gamma I, \end{cases}$$

where $S = S(x,t)$ and $I = I(x,t)$, $x \in \mathbb{R}$, $t \geq 0$. By changing the variables, we obtain

$$\begin{cases} \dfrac{\partial S}{\partial t} = \dfrac{\partial^2 S}{\partial x^2} - SI, \\ \dfrac{\partial I}{\partial t} = \dfrac{\partial^2 I}{\partial x^2} + SI - \lambda I, \end{cases}$$

where $\lambda = \gamma/(\beta S^0) = 1/\mathcal{R}_0$. Let $z = x - ct$, $U(z) = S(x,t)$ and $V(z) = I(x,t)$, we obtain

$$U'' + cU' - UV = 0,$$
$$V'' + cV' + V(U - \lambda) = 0.$$

We seek a traveing wave solution $(U, V)$ satisfying

$$0 \leq U(-\infty) < U(+\infty) = 1,$$
$$V(-\infty) = V(\infty) = 0.$$

Liniearizing near the leading edge of the wave (where $S \to 1$) gives

$$V'' + cV' + V(1 - \lambda) = 0,$$

which solution is

$$V(z) = C\exp^{\frac{-c \pm \sqrt{c^2 - 4(1-\lambda)}}{2}z}.$$

If a traveling wave solution exists, $c$ and $\lambda$ must satisfy

$$c \geq 2\sqrt{1-\lambda}, \quad \lambda < 1.$$

$\lambda < 1$ is equivalent to $\mathcal{R}_0 > 1$.

# 第 11 回「応用数学特論 III, IIIb」 2022 年 12 月 19 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Infection age

Let $\tau$ be the **infection age** that implies the time elapsed since the infection. Let $i(t,\tau)$ be the infective population at time $t$ with infection age $\tau$. Let $S(t)$ and $R(t)$ be the susceptible and recovered populations at time $t$. The **infection age-structured SIR epidemic model** is given by

$$\begin{cases} S'(t) = -\lambda(t)S(t), \\ i_t(t,\tau) + i_\tau(t,\tau) = -\gamma(\tau)i(t,\tau), \\ i(t,0) = \lambda(t)S(t), \\ R'(t) = \int_0^\infty \gamma(\tau)i(t,\tau)d\tau, \end{cases}$$

where $\lambda(t)$ denotes the **force of infection** given by

$$\lambda(t) = \int_0^\infty \beta(\tau)i(t,\tau)d\tau.$$

$\beta(\tau)$ and $\gamma(\tau)$ are age-dependent infection rate and recovery rate, respectively. Let

$$\Gamma(\tau) = e^{-\int_0^\tau \gamma(\sigma)d\sigma}$$

be the survival probability at the infective state. By integrating along the characteristic line, we obtain

$$i(t,\tau) = \begin{cases} i(t-\tau,0)\Gamma(\tau), & t-\tau > 0, \\ i(0,\tau-t)\dfrac{\Gamma(\tau)}{\Gamma(\tau-t)}, & \tau-t > 0. \end{cases}$$

We consider the initial invasion phase $(S,i,R) \approx (N,0,0)$. Let $v(t) = \lambda(t)N$ be the newly infected population. We then obtain the renewal equation

$$v(t) = g(t) + \int_0^t \Psi(\tau)v(t-\tau)d\tau,$$

where

$$g(t) = N\int_t^\infty \beta(\tau)i(0,\tau-t)\frac{\Gamma(\tau)}{\Gamma(\tau-t)}d\tau,$$
$$\Psi(\tau) = N\beta(\tau)\Gamma(\tau).$$

Hence, the basic reproduction number $\mathcal{R}_0$ is given by

$$\mathcal{R}_0 = \int_0^\infty \Psi(\tau)d\tau = N\int_0^\infty \beta(\tau)\Gamma(\tau)d\tau.$$

## 2 Equilibrium

The infection age-structured SIR epidemic model with demography is given by

$$\begin{cases} S'(t) = b - \lambda(t)S(t) - \mu S(t), \\ i_t(t,\tau) + i_\tau(t,\tau) = -\left[\mu + \gamma(\tau)\right] i(t,\tau), \\ i(t,0) = \lambda(t)S(t), \\ R'(t) = \int_0^\infty \gamma(\tau)i(t,\tau)d\tau - \mu R(t). \end{cases}$$

The disease-free equilibrium is given by $(S,i,R) = (b/\mu,0,0)$. By considering the initial invasion phase $(S,i,R) \approx (b/\mu,0,0)$ as in the previous model, we obtain

$$\mathcal{R}_0 = \frac{b}{\mu}\int_0^\infty \beta(\tau)e^{-\mu\tau}\Gamma(\tau)d\tau.$$

The endemic equilibrium is give by $(S,i,R) = (S^*,i^*,R^*)$, where

$$S^* = \frac{b}{\lambda^*+\mu}, \quad i^*(\tau) = \lambda^* S^* e^{-\mu\tau}\Gamma(\tau),$$
$$R^* = \frac{1}{\mu}\int_0^\infty \gamma(\tau)i^*(\tau)d\tau, \quad \lambda^* = \int_0^\infty \beta(\tau)i^*(\tau)d\tau.$$

We obtain the characteristic equation of $\lambda^*$ as

$$1 = \frac{b}{\lambda^*+\mu}\int_0^\infty \beta(\tau)e^{-\mu\tau}\Gamma(\tau)d\tau =: \Phi(\lambda^*).$$

Since $\Phi(\lambda^*)$ is monotone decreasing and converges to zero as $\lambda^* \to \infty$, we can see that if $\Phi(0) > 1$, then a positive $\lambda^*$ exists. Since $\mathcal{R}_0 = \Phi(0)$, we can conclude that the endemic equilibrium exists if $\mathcal{R}_0 > 1$.

**Exercise**

Find the basic reprodution number $\mathcal{R}_0$ of the following model.

$$\begin{cases} S'(t) = b - \lambda(t)S(t) - \mu S(t), \\ e_t(t,\tau) + e_\tau(t,\tau) = -\left[\mu + \varepsilon(\tau)\right] e(t,\tau), \\ i_t(t,\tau) + i_\tau(t,\tau) = -\left[\mu + \gamma(\tau)\right] i(t,\tau), \\ e(t,0) = \lambda(t)S(t), \\ i(t,0) = \int_0^\infty \varepsilon(\tau)e(t,\tau)d\tau, \\ \lambda(t) = \int_0^\infty \beta(\tau)i(t,\tau)d\tau. \end{cases}$$

# 第 12 回「応用数学特論 III, IIIb」 2022 年 12 月 26 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Steepness of wave front

Let $u = u(x,t)$ and consider the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u).$$

Let $z = x - ct$ and $U(z) = u(x,t)$. It then satisfies

$$U'' + cU' + U(1-U) = 0.$$

This equation has a motone nonincreasing solution with $U(-\infty) = 1$ and $U(\infty) = 0$ for all $c > 2$.

Since the wave solutions are invariant to any shift $z \to z +$ constant, we can assume that $U(0) = 1/2$. Let $\varepsilon = 1/c^2$ and consider the following transformation.

$$U(z) = g(\xi), \quad \xi = \frac{z}{c} = \sqrt{\varepsilon} z.$$

We then have

$$\begin{aligned} &\varepsilon g'' + g' + g(1-g) = 0, \\ &g(-\infty) = 1, \quad g(0) = \frac{1}{2}, \quad g(\infty) = 0. \end{aligned}$$

We look for solutions in the following form:

$$g(\xi) = g_0(\xi) + g_1(\xi)\varepsilon + O(\varepsilon^2)$$

for $0 < \varepsilon \ll 1$. The boundary condition becomes

$$\begin{aligned} &g_0(-\infty) = 1, \quad g_0(0) = \frac{1}{2}, \quad g_0(\infty) = 0, \\ &g_i(\pm\infty) = g_i(0) = 0, \quad i = 1, 2, \ldots. \end{aligned}$$

Equating powers of $\varepsilon$, we get

$$\begin{aligned} &O(1): \ g_0'(\xi) = -g_0(1-g_0), \\ &O(\varepsilon): \ g_1' + (1-2g_0)g_1 = -g_0''. \end{aligned}$$

Solving these equations, we have

$$\begin{aligned} g_0(\xi) &= \frac{1}{1+e^{\xi}}, \\ g_1(\xi) &= \frac{e^{\xi}}{(1+e^{\xi})^2} \ln \frac{4e^{\xi}}{(1+e^{\xi})^2}. \end{aligned}$$

The original function $U$ then becomes

$$U(z) = \frac{1}{1+e^{z/c}} + \frac{1}{c^2} \frac{e^{z/c}}{(1+e^{z/c})^2} \ln \frac{4e^{z/c}}{(1+e^{z/c})^2} + O\left(\frac{1}{c^4}\right).$$

We now investigate the steepness of the wave front in terms of the wave speed $c$. Let $s$ be a measure of the steepness, which is the magnitude of the maximum of $U'$. It attains as the point where $U'' = 0$, that is,

$$g_0'' + g_1''\varepsilon + O(\varepsilon^2) = 0.$$

We then see that $z = \xi = 0$ gives such a point, that is,

$$s = -U'(0) = \frac{1}{4c} + O\left(\frac{1}{c^5}\right).$$

This implies that the faster the wave moves, the less steep is the wavefront.

## 2 Stability of wave solutions

To consider the stability of the wave solution $u_c(z) = U(z)$, let

$$u(z,t) = u_c(z) + \omega v(z,t), \quad 0 < \omega \ll 1.$$

$v$ satisfies

$$v_t = [1 - 2u_c(z)]v + cv_z + v_{zz}.$$

The solution $u_c(z)$ is stable if $\lim_{t\to\infty} v(z,t) = 0$ or $\lim_{t\to\infty} v(z,t) = u_c'(z)$. Set $v(z,t) = g(z)e^{-\lambda t}$ with $g(\pm L) = 0$ for some $L$. We then have

$$g'' + cg' + [\lambda + 1 - 2u_c(z)]\, g = 0.$$

If $g(z) = h(z)e^{-cz/2}$, we have

$$h'' + \left[\lambda - \left\{2u_c(z) + \frac{c^2}{4} - 1\right\}\right] h = 0, \ \ h(\pm L) = 0.$$

As $2u_c(z) + c^2/4 - 1 > 0$, the standard theory gives that all eigenvalues $\lambda$ are real and positive. Hence, $v(z,t) = g(z)e^{-\lambda t}$ tends to zero as $t \to \infty$, which implies that the wave equation $u_c$ is stable.

# 第 13 回「応用数学特論 III, IIIb」 2023 年 1 月 16 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## 1 Density-dependent diffusion

Let $n = n(x,t)$ be the population density at location $x \in \mathbb{R}$ and time $t \geq 0$. Usually, the **flux** $J$ is supposed to be proportional to the gradient of $n$:

$$J = -D\frac{\partial n}{\partial x}, \quad D > 0.$$

If no newborn is crated, the rate of change of the population in a region $(x_0, x_1)$ is equal to the rate of flow across the boundary:

$$\frac{\partial}{\partial t}\int_{x_0}^{x_1} n(x,t)dx = J(x_0,t) - J(x_1,t).$$

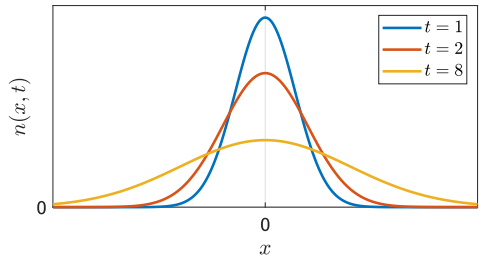
Let $x_1 = x_0 + \Delta x$ and $\Delta x \to 0$. We then have

$$\frac{\partial n}{\partial t} = -\frac{\partial J}{\partial x} = \frac{\partial}{\partial x}\left(D\frac{\partial n}{\partial x}\right).$$

If $D$ is a constant, we obtain the diffusion equation $\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2}$, which solution is

$$n(x,t) = \frac{N}{2\sqrt{\pi D t}} e^{-\frac{x^2}{4Dt}},$$

where $N > 0$ is the total population.




If $D$ depends on $n$, then it is called the density-dependent diffusion. The flux is changed to

$$J = -D(n)\frac{\partial n}{\partial x}, \quad \frac{dD}{dn} > 0.$$

A typical form for $D(n)$ is $D_0(n/n_0)^m$, where $D_0, n_0, m_0 > 0$ are positive constants. The equation is then given by

$$\frac{\partial n}{\partial t} = D_0\frac{\partial}{\partial x}\left[\left(\frac{n}{n_0}\right)^m \frac{\partial n}{\partial x}\right].$$

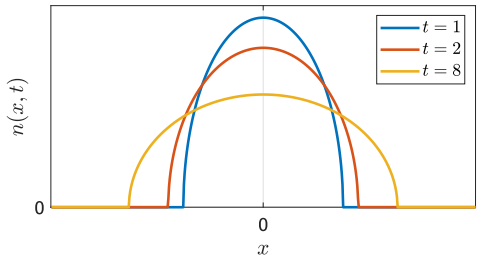
An analytical solution is

$$n(x,t) = \begin{cases} \dfrac{n_0}{\lambda(t)}\left[1 - \left\{\dfrac{x}{r_0\lambda(t)}\right\}^2\right]^{\frac{1}{m}}, & |x| \leq r_0\lambda(t), \\ 0, & |x| > r_0\lambda(t), \end{cases}$$

where

$$\lambda(t) = \left(\frac{t}{t_0}\right)^{\frac{1}{2+m}}, \quad r_0 = \frac{N\Gamma\left(\frac{1}{m}+\frac{3}{2}\right)}{\sqrt{\pi}n_0\Gamma\left(\frac{1}{m}+1\right)},$$
$$t_0 = \frac{r_0^2 m}{2D_0(m+2)},$$

where $\Gamma$ is the gamma function.




## 2 Chemotaxis

The chemically directed movement induced by pheromones is called the **chemotaxis**. The flux is $J = J_{\text{diffusion}} + J_{\text{chemotaxis}}$, where

$$J_{\text{diffusion}} = -D\frac{\partial n}{\partial x}, \quad J_{\text{chemotaxis}} = n\chi(a)\frac{\partial a}{\partial x},$$

and $a = a(x,t)$ is the concentration of an attractant. A simple example of the model is as follows:

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} - \chi_0\frac{\partial}{\partial x}\left(n\frac{\partial a}{\partial x}\right),$$
$$\frac{\partial a}{\partial t} = hn - ka + D_a\frac{\partial^2 a}{\partial x^2}.$$

Here, the attractant is assumed to be produced as $hn$, diffuse with diffusion coefficient $D_a$, and exponentially decay as $-ka$.

# 第 14 回「応用数学特論 III, IIIb」 2023 年 1 月 23 日

教科書：J.D. Murray, Mathematical Biology, Springer, 1993.

## Pattern formation

The modeling of **pattern formation** in biology is one of the important applications of the diffusion equation. Turing (1952) suggested that chemical concentration can produce spatially heterogeneous patterns. We first study the following basic system: for $t > 0$ and $0 < x < p$,

$$u_t = \gamma f(u,v) + u_{xx},$$
$$v_t = \gamma g(u,v) + dv_{xx},$$

with boundary condition, for $t > 0$,

$$u_x(t,0) = u_x(t,p) = v_x(t,0) = v_x(t,p) = 0.$$

Here $u = u(t,x)$ and $v = v(t,x)$ are two chemical species, $\gamma$ is a parameter and $d$ is the diffusion coefficient. $f$ and $g$ are nonlinear reaction terms such as

$$f(u,v) = a - u + u^2 v, \quad g(u,v) = b - u^2 v, \quad (1)$$

where $a$ and $b$ are parameters.

The spatially heterogeneous patterns can arise by **diffusion driven instability**, which means that an equilibrium solution, which is stable in the absence of diffusion, is destabilized by diffusion. The equilibrium solution $(u_0, v_0)$ in the absence of diffusion satisfies

$$f(u_0, v_0) = g(u_0, v_0) = 0.$$

The linearized system around $(u_0, v_0)$ is

$$w_t = \gamma A w,$$

where

$$A = \begin{bmatrix} f_u(u_0,v_0) & f_v(u_0,v_0) \\ g_u(u_0,v_0) & g_v(u_0,v_0) \end{bmatrix}.$$

The condition for $(u_0, v_0)$ to be stable is as follows:

$$\mathrm{tr}A = f_u + g_v < 0, \quad (2)$$
$$\det A = |A| = f_u g_v - f_v g_u > 0, \quad (3)$$

where $f_u = f_u(u_0, v_0)$, etc.

The linearized system with diffusion is

$$w_t = \gamma A w + D w_{xx},$$

where $D = \begin{bmatrix} 1 & 0 \\ 0 & d \end{bmatrix}$. We now consider the eigenvalue problem

$$\frac{\partial^2 W_k}{\partial x^2} + k^2 W_k = 0, \quad \frac{\partial W_k}{\partial x} = 0 \ \ (x = 0, p).$$

Substituting $w = \sum_k c_k e^{\lambda t} W_k$ into the lineaized system, we obtain the following characteristic equation:

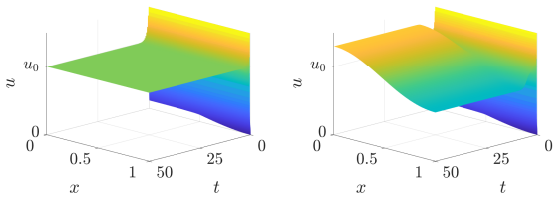
$$\lambda^2 + [k^2(1+d) - \gamma(f_u + g_v)]\lambda + h(k^2) = 0,$$
$$h(k^2) = dk^4 - \gamma(df_u + g_v)k^2 + \gamma^2 |A|.$$

If this equation has a root $\lambda$ with positive real part, then the equilibrium solution $(u_0, v_0)$ is destabilized. We can check that the condition for this to be satisfied is

$$df_u + g_v > 0, \quad (4)$$
$$(df_u + g_v)^2 - 4d|A| > 0. \quad (5)$$

For example, for reaction terms $f$ and $g$ given by (1), conditions (2)-(4) are respectively rewritten as follows.

$$0 < b - a < (a+b)^3.$$
$$(a+b)^2 > 0.$$
$$d(b-a) > (a+b)^3.$$




(a) Stable case (b) Unstable case

**Exercise**

Suppose that $f$ and $g$ are given by (1). Rewrite (5) by using $a, b$ and $d$.

# 第 15 回「応用数学特論 III, IIIb」 2023 年 1 月 30 日

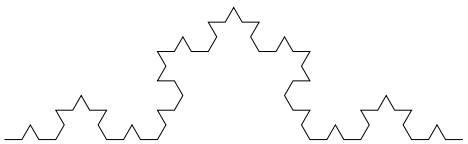
教科書 : J.D. Murray, Mathematical Biology, Springer, 1993.
参考書 : S.H. Strogatz, Nonlinear Dynamics and Chaos, 1994.

## 1 Fractals

**Fractals** are complex geometric shapes with fine structure at arbitrarily small scales. Usually, they have some degree of self-similarity. Fractal theory is related to the measurement of biological structures at different magnifications. Now we give two examples of fractals.

**Cantor set.** Let $S_0 = [0, 1]$. Removing its open middle third, we obtain $S_1 = [0, 1/3) \cup (2/3, 1]$. Removing the open middle thirds of two intervals in $S_1$, we obtain $S_2$. The limiting set $C = S_\infty$ is the **Cantor set**. The Cantor set has a total length of zero.

**The von Koch curve.** Let $S_0$ be a line segment. $S_n$ is obtained by replacing the middle third of each eadge in $S_{n-1}$ by the other two sides of an equilateral triangle. $K = S_\infty$ is the **von Koch curve**. The arc length between any two points on $K$ is infinite.



## 2 Similarity dimension

For a self-similar fractal, let $m$ be the number of copies and $r$ be the scale factor. Then, the **similarity dimension** $d$ of it is defined by

$$d = \frac{\ln m}{\ln r}.$$

For the Cantor set $C$, we have $m = 2$ and $r = 3$. We then have $d = \ln 2/\ln 3 \approx 0.63$.

For the von Koch curve, we have $m = 4$ and $r = 3$. We then have $d = \ln 4/\ln 3 \approx 1.26$.

## 3 Box dimension

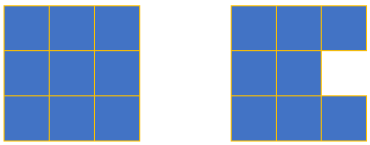
Let $S$ be a subset of $\mathbb{R}^D$, and $N(\varepsilon)$ be the minimun number of $D$-dimensional cubes of side $\varepsilon$ needed to cover $S$. The **box dimension** of $S$ is defined by

$$d = \lim_{\varepsilon \to 0} \frac{\ln N(\varepsilon)}{\ln(1/\varepsilon)}.$$

For the Cantor set, $d$ can be calculated as

$$d = \lim_{n \to \infty} \frac{\ln 2^n}{\ln 3^n} = \frac{\ln 2}{\ln 3}.$$

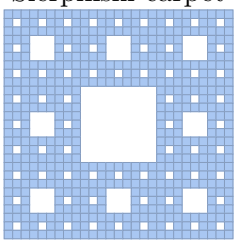
Let $S_0$ be a squre divided into nine equal squares, and then one of the squares is selected at rondam and discarded. Then, the process is repeated on each of the eight remaining small squares. The limit is a nonself-similar fractal. What is the box dimension of it?




$S_1$ is covered by $N = 8$ squares of side $\varepsilon = 1/3$. $S_2$ is covered by $n = 8^2$ squares of side $\varepsilon = 1/3^2$. In general, $N = 8^n$ and $\varepsilon = 1/3^n$, and hence,

$$d = \lim_{n \to \infty} \frac{\ln 8^n}{\ln 3^n} = \frac{\ln 8}{\ln 3} \approx 1.89.$$

Sierpinski carpet



**Exercise**

Consider a new kind of Cantor set by removing the middle half of each subinterval, rather than the middle third. Find the similarity dimension of the set.