

Written examination, TATM38 Mathematical Models in Biology

2021-01-08, 8.00 - 13.00

Each problem is worth 4 points. To obtain a grade 3, 4 or 5, you need 10, 14 or 18 points, respectively. You must not use any aids (no textbooks, notes, calculators or other electronic tools).

1. A population  $N(t)$  is described by the modified logistic equation

$$\frac{dN}{dt} = r \left( 1 - \left( \frac{N}{B} \right)^\alpha \right) N$$

Here  $r > 0$ ,  $\alpha > 0$ , and  $B > 0$  are constants.

Find all steady states (= equilibrium points) and determine their stability. Sketch the phase line for  $N \geq 0$ . What happens to the population as  $t \rightarrow \infty$ ?

2. Let  $x_n$  and  $y_n$  be two populations of organisms at discrete time  $n = 0, 1, 2, \dots$ . From one time step to the next, the first population becomes twice the previous level of the second, and the second becomes the sum of the two previous populations. Therefore they satisfy the equations

$$\begin{cases} x_{n+1} = 2y_n \\ y_{n+1} = x_n + y_n \end{cases}$$

Find the general solution to this system.

It has been observed that at time  $n = 5$ , the populations are  $x_5 = 62$  and  $y_5 = 65$ . Find the solution that satisfies this condition. What were the initial values  $(x_0, y_0)$  for this solution? Also give  $(x_1, y_1)$ ,  $(x_2, y_2)$ ,  $(x_3, y_3)$ , and  $(x_4, y_4)$  for this solution.

3. Consider the chemostat equations

$$\begin{cases} \frac{dN}{dt} = \frac{2CN}{1+C} - N \\ \frac{dC}{dt} = -\frac{CN}{1+C} - C + \alpha \end{cases},$$

where  $\alpha > 0$  is a constant. Verify that  $(\bar{N}_1, \bar{C}_1) = (0, \alpha)$  and  $(\bar{N}_2, \bar{C}_2) = (2\alpha - 2, 1)$  are steady states. Show that  $(\bar{N}_2, \bar{C}_2)$  is stable whenever  $\bar{N}_2 > 0$ . Show that  $(\bar{N}_1, \bar{C}_1)$  is unstable when  $\bar{N}_2 > 0$  and stable when  $\bar{N}_2 < 0$ .

PLEASE TURN

4. Let  $x(t)$  and  $y(t)$  be prey and predator populations, respectively, described by a Lotka-Volterra predator-prey model with logistic prey growth:

$$\begin{cases} \frac{dx}{dt} = 2x\left(1 - \frac{x}{K}\right) - xy \\ \frac{dy}{dt} = -y + 2xy \end{cases},$$

where  $K > 0$  is a constant. Show that there is a steady state  $(\bar{x}, \bar{y})$  with  $\bar{x} > 0$  and  $\bar{y} > 0$  if  $K > \frac{1}{2}$ .

Let  $K = 1$ . Find all steady states (= equilibrium points) and determine their stability. Draw a phase plane picture (with nullclines and directions of the vector field). Do the solution solutions move in a spiral towards the stable steady state?

5. For  $0 < x < 2\pi$  and  $t > 0$ , solve the initial-boundary value problem (IBVP) for  $u(t, x)$

$$\begin{cases} 3u_t = u_{xx} - 2u \\ u_x(t, 0) = 0 \\ u_x(t, 2\pi) = 0 \\ u(0, x) = 3 + 4 \cos x \end{cases}$$

Hint: put  $u(t, x) = v(t, x)e^{\alpha t}$ .

6. A model with spatial diffusion of a phytoplankton-herbivore system in two space dimensions is given by

$$\begin{cases} u_t = u + u^2 - uv + D_1(u_{xx} + u_{yy}) \\ v_t = 2uv - v^2 + D_2(v_{xx} + v_{yy}) \end{cases}$$

Here  $u(t, x, y)$  and  $v(t, x, y)$  are the phytoplankton and herbivore concentrations.

Find the spatially uniform steady state  $(\bar{u}, \bar{v})$  which has  $\bar{u} > 0$  and  $\bar{v} > 0$ , and show that it is stable if there is no diffusion ( $D_1 = D_2 = 0$ ).

Show that the condition for Turing diffusive instability is  $D_2 - 2D_1 > 2\sqrt{2D_1D_2}$ .

If  $0 < x < L$  and  $0 < y < L/2$  with  $L = \sqrt{15}\pi$ ,  $D_1 = \frac{1}{2}$  and  $D_2 = 6$ , find the only value of  $(m, n)$  for which an unstable (pattern forming) mode  $e^{\sigma t} \cos \frac{m\pi x}{L} \cos \frac{n\pi y}{L/2}$  ( $\sigma > 0$ ) appears, and sketch the resulting pattern.

TATM38, Math. Bio 8/1 2021, solution sketches

① Steady states  $\frac{dN}{dt} = f(N) = r(1 - \frac{N}{B}^\alpha)N = 0 \Rightarrow \bar{N}_1 = 0, \bar{N}_2 = B$

$f(N) = r(N - \frac{N^{\alpha+1}}{B^\alpha}) \Rightarrow f'(N) = r(1 - (\alpha+1)\frac{N^\alpha}{B^\alpha}) \Rightarrow$

$f'(\bar{N}_1) = f'(0) = r > 0 \Rightarrow \bar{N}_1$  unstable

$f'(\bar{N}_2) = f'(B) = r(1 - (\alpha+1) \cdot 1) = -r\alpha < 0 \Rightarrow \bar{N}_2$  stable

Phase line



$N(t) \rightarrow \begin{cases} B & \text{if } N(0) > 0 \\ 0 & \text{if } N(0) = 0 \end{cases}$

②  $\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = A \begin{pmatrix} x_n \\ y_n \end{pmatrix}, A = \begin{pmatrix} 0 & 2 \\ 1 & 1 \end{pmatrix}$ . Eigenvalues  $|\begin{matrix} -\lambda & 2 \\ 1 & 1-\lambda \end{matrix}| = \lambda^2 - \lambda - 2 = 0$

$\Rightarrow \lambda_1 = 2, \lambda_2 = -1$ . Eigenvectors  $\lambda_1 = 2 \begin{pmatrix} -2 & 2 & | & 0 \\ -1 & 1 & | & 0 \end{pmatrix} \sim \begin{pmatrix} -1 & 1 & | & 0 \\ 0 & 0 & | & 0 \end{pmatrix} \bar{v}_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$

$\lambda_2 = -1 \begin{pmatrix} 1 & 2 & | & 0 \\ 1 & 2 & | & 0 \end{pmatrix} \sim \begin{pmatrix} 1 & 2 & | & 0 \\ 0 & 0 & | & 0 \end{pmatrix} \bar{v}_2 = \begin{pmatrix} 2 \\ -1 \end{pmatrix} \Rightarrow$  General solution is

$\begin{pmatrix} x_n \\ y_n \end{pmatrix} = c_1 \lambda_1^n \bar{v}_1 + c_2 \lambda_2^n \bar{v}_2 = c_1 2^n \begin{pmatrix} 1 \\ 1 \end{pmatrix} + c_2 (-1)^n \begin{pmatrix} 2 \\ -1 \end{pmatrix}$

Condition  $\begin{pmatrix} x_5 \\ y_5 \end{pmatrix} = 32c_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} - c_2 \begin{pmatrix} 2 \\ -1 \end{pmatrix} = \begin{pmatrix} 62 \\ 65 \end{pmatrix} \Rightarrow \begin{cases} 32c_1 - 2c_2 = 62 \\ 32c_1 + c_2 = 65 \end{cases} \Rightarrow \begin{cases} c_1 = 2 \\ c_2 = 1 \end{cases} \Rightarrow$

$\begin{pmatrix} x_n \\ y_n \end{pmatrix} = 2^{n+1} \begin{pmatrix} 1 \\ 1 \end{pmatrix} + (-1)^n \begin{pmatrix} 2 \\ -1 \end{pmatrix}$ . One finds  $\begin{pmatrix} x_0 \\ y_0 \end{pmatrix} = 2 \cdot \begin{pmatrix} 1 \\ 1 \end{pmatrix} + \begin{pmatrix} 2 \\ -1 \end{pmatrix} = \begin{pmatrix} 4 \\ 1 \end{pmatrix}$  and

$\begin{pmatrix} x_1 \\ y_1 \end{pmatrix} = \begin{pmatrix} 2 \\ 5 \end{pmatrix}, \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} = \begin{pmatrix} 10 \\ 7 \end{pmatrix}, \begin{pmatrix} x_3 \\ y_3 \end{pmatrix} = \begin{pmatrix} 14 \\ 17 \end{pmatrix}, \begin{pmatrix} x_4 \\ y_4 \end{pmatrix} = \begin{pmatrix} 34 \\ 31 \end{pmatrix}$

③  $\begin{cases} \frac{dN}{dt} = F(N, C) = \frac{2CN}{1+C} - N \\ \frac{dC}{dt} = G(N, C) = -\frac{CN}{1+C} - C + \alpha \end{cases}$   $\begin{cases} F(0, \alpha) = 0 - 0 = 0 \\ G(0, \alpha) = 0 - \alpha + \alpha = 0 \end{cases} \Rightarrow (0, \alpha)$  and  $(2\alpha - 2, 1)$  steady states

Jacobian  $J(N, C) = \begin{pmatrix} F'_N & F'_C \\ G'_N & G'_C \end{pmatrix} = \begin{pmatrix} \frac{2C}{1+C} - 1 & \frac{2N}{(1+C)^2} \\ -\frac{C}{1+C} & -\frac{N}{(1+C)^2} - 1 \end{pmatrix} \Rightarrow J_1 = J(0, \alpha) = \begin{pmatrix} \frac{2\alpha}{1+\alpha} - 1 & 0 \\ -\frac{\alpha}{1+\alpha} & -1 \end{pmatrix}$

$J_2 = J(2\alpha - 2, 1) = \begin{pmatrix} 0 & \alpha - 1 \\ -\frac{1}{2} & \frac{1-\alpha}{2} - 1 \end{pmatrix}$

Case 1:  $\bar{N}_2 = 2\alpha - 2 > 0 \Leftrightarrow \alpha > 1 \Rightarrow \begin{cases} \text{Tr } J_2 = -\frac{\alpha+1}{2} < 0 \\ \det J_2 = \frac{\alpha-1}{2} > 0 \end{cases} \Rightarrow (\bar{N}_2, \bar{C}_2) = (2\alpha - 2, 1)$  stable

$J_1$  has eigenvalues  $\lambda_1 = \frac{2\alpha - (1+\alpha)}{1+\alpha} = \frac{\alpha-1}{1+\alpha} > 0$  and  $\lambda_2 = -1 < 0 \Rightarrow$  saddle  $\Rightarrow (\bar{N}_1, \bar{C}_1) = (0, \alpha)$  unstable

Case 2  $\bar{N}_2 < 0 \Leftrightarrow \alpha < 1$ .  $J_1$  has  $\lambda_1 = \frac{\alpha-1}{1+\alpha} < 0$  and  $\lambda_2 = -1 < 0 \Rightarrow (\bar{N}_1, \bar{C}_1)$  stable

[for  $J_2$  the eigenvalues are  $\frac{1-\alpha}{2}$  and  $-1$ ]

$$\textcircled{4} \begin{cases} x' = 2x(1 - \frac{x}{k}) - xy = x(2 - \frac{2x}{k} - y) & \text{x-nullclines } x=0, \frac{2x}{k} + y = 2 \\ y' = -y + 2xy = y(-1 + 2x) & \text{y-nullclines } y=0, x = \frac{1}{2} \end{cases}$$

Steady states  $y=0$  in  $\textcircled{*} \Rightarrow x=0, x=k$  }  $\Rightarrow$  3 steady states  
 $x = \frac{1}{2}$  in  $\textcircled{*} \Rightarrow y = 2 - \frac{1}{k}$  }  $(\bar{x}_1, \bar{y}_1) = (0, 0), (\bar{x}_2, \bar{y}_2) = (k, 0)$   
 $(\bar{x}_3, \bar{y}_3) = (\frac{1}{2}, 2 - \frac{1}{k})$

$$\bar{y}_3 > 0 \text{ if } 2 - \frac{1}{k} > 0 \Rightarrow k > \frac{1}{2}$$

With  $k=1$ :  $(\bar{x}_1, \bar{y}_1) = (0, 0), (\bar{x}_2, \bar{y}_2) = (1, 0), (\bar{x}_3, \bar{y}_3) = (\frac{1}{2}, 1)$   
 x-nullclines  $x=0, 2x+y=2$ , y-nullclines  $y=0, x=\frac{1}{2}$

$$J(x, y) = \begin{pmatrix} 2-4x-y & -x \\ 2y & 2x-1 \end{pmatrix} \Rightarrow J(0, 0) = \begin{pmatrix} 2 & 0 \\ 0 & -1 \end{pmatrix} \lambda_1 = 2 > 0, \lambda_2 = -1 < 0 \text{ saddle, unstable}$$

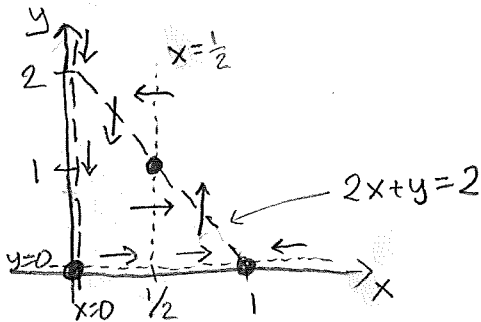
$$J(1, 0) = \begin{pmatrix} -2 & -1 \\ 0 & 1 \end{pmatrix}, \lambda_1 = -2 < 0, \lambda_2 = 1 > 0 \Rightarrow \text{saddle, unstable}$$

$$J(\frac{1}{2}, 1) = \begin{pmatrix} -1 & -\frac{1}{2} \\ 2 & 0 \end{pmatrix} = J \quad \left. \begin{array}{l} \text{Tr} J = -1 < 0 \\ \det J = 1 > 0 \end{array} \right\} \Rightarrow \text{stable. Or } \lambda^2 + \lambda + 1 = 0 \Rightarrow \lambda_{1,2} = \frac{-1 \pm i\sqrt{3}}{2}$$

$$\text{Re } \lambda_{1,2} = -\frac{1}{2} < 0 \Rightarrow \text{stable}$$

complex  
 $\downarrow$   
 spiral

$$(\text{or } (\text{Tr} J)^2 - 4 \det J = 1 - 4 < 0 \Rightarrow \text{spiral})$$



$$\textcircled{5} u(t, x) = v(t, x) e^{\alpha t} \Rightarrow u_x = v_x e^{\alpha t}, u_{xx} = v_{xx} e^{\alpha t}, u_t = (v_t + \alpha v) e^{\alpha t} \Rightarrow$$

$$3u_t = u_{xx} - 2u \Rightarrow 3(v_t + \alpha v) e^{\alpha t} = v_{xx} e^{\alpha t} - 2v e^{\alpha t} \text{ with } \alpha = -\frac{2}{3}$$

IBVP for  $v(t, x)$ :

$$\begin{cases} 3v_t = v_{xx} & 0 < x < 2\pi, t > 0 \\ v_x(t, 0) = u_x(t, 0) e^{-\alpha t} = 0 \\ v_x(t, 2\pi) = u_x(t, 2\pi) e^{-\alpha t} = 0 \\ v(0, x) = u(0, x) e^0 = 3 + 4 \cos x \end{cases}$$

$$v(t, x) = T(t) X(x) \Rightarrow \frac{3T'(t)}{T(t)} = \frac{X''(x)}{X(x)} = \lambda$$

$$X'(0) = X'(2\pi) \text{ from boundary conditions}$$

$$\text{Solutions to } X\text{-eq: } X_n(x) = \cos \frac{n x}{2}, n=0, 1, 2, \dots, \lambda = -\frac{n^2}{4} \Rightarrow$$

$$\text{--- II --- } T\text{-eq: } T_n(t) = e^{\lambda t/3} = e^{-n^2 t/12}$$

$$v(t, x) = \sum_{n=0}^{\infty} a_n e^{-n^2 t/12} \cos \frac{n x}{2}, \text{ initial condition } \Rightarrow$$

$$v(0, x) = \sum_{n=0}^{\infty} a_n \cos \frac{n x}{2} = 3 + 4 \cos x \Rightarrow a_0 = 3, a_2 = 4, a_n = 0, n \neq 0, 2 \Rightarrow$$

$$v(t, x) = 3e^{0t} \cos 0x + 4e^{-4t/12} \cos x = 3 + 4e^{-t/3} \cos x \Rightarrow$$

$$\underline{\underline{u(t, x) = v(t, x) e^{-2t/3} = 3e^{-2t/3} + 4e^{-t} \cos x}}$$

⑥ Spatially uniform steady state  $\bar{u}, \bar{v}$  satisfies

$$\begin{cases} \bar{u} + \bar{u}^2 - \bar{u}\bar{v} = 0 \\ 2\bar{u}\bar{v} - \bar{v}^2 = 0 \end{cases} \Leftrightarrow \begin{cases} \bar{u}(1 + \bar{u} - \bar{v}) = 0 \\ \bar{v}(2\bar{u} - \bar{v}) = 0 \end{cases} \xrightarrow{\substack{\text{if } \bar{u} > 0 \\ \bar{v} > 0}} \begin{cases} 1 + \bar{u} - \bar{v} = 0 \\ 2\bar{u} - \bar{v} = 0 \end{cases} \Rightarrow (\bar{u}, \bar{v}) = (1, 2)$$

$$J(u, v) = \begin{pmatrix} 1+2u-v & -u \\ 2v & 2u-2v \end{pmatrix} \Rightarrow J(1, 2) = \begin{pmatrix} 1 & -1 \\ 4 & -2 \end{pmatrix} = A$$

$$\left. \begin{array}{l} \text{Tr } A = -1 < 0 \\ \det A = 2 > 0 \end{array} \right\} \Rightarrow \text{stable if no diffusion}$$

Condition for Turing diffusive instability:  $a_{11}D_2 + a_{22}D_1 > 2\sqrt{D_1D_2\det A}$

$$\Rightarrow D_2 - 2D_1 > 2\sqrt{2D_1D_2}$$

$$D_1 = \frac{1}{2}, D_2 = 6 \text{ gives } D_2 - 2D_1 = 6 - 1 = 5 \text{ and } 2\sqrt{2D_1D_2} = 2\sqrt{6} < 5 \text{ OK.}$$

$$\text{With } P = \frac{a_{11}D_2 + a_{22}D_1}{D_1D_2} = \frac{5}{3}, W = \frac{\det A}{D_1D_2} = \frac{2}{3} \text{ and } \Delta = \sqrt{\frac{P^2}{4} - W} = \sqrt{\frac{25}{36} - \frac{2}{36}} = \frac{1}{6}$$

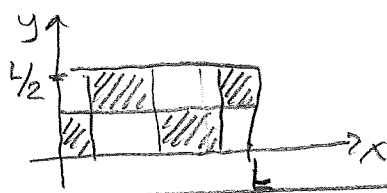
unstable perturbations appear for

$$-\Delta < Q^2 - \frac{P}{2} < \Delta \Leftrightarrow -\frac{1}{6} < Q^2 - \frac{5}{6} < \frac{1}{6} \Leftrightarrow \frac{2}{3} < Q^2 < 1$$

$$\text{where } Q^2 = \pi^2 \left( \frac{m^2}{L_x^2} + \frac{n^2}{L_y^2} \right) = \pi^2 \left( \frac{m^2}{L^2} + \frac{n^2}{L^2/4} \right) = \pi^2 \left( \frac{m^2}{15\pi^2} + \frac{4n^2}{15\pi^2} \right) = \frac{1}{15}(m^2 + 4n^2)$$

$$\Rightarrow \frac{2}{3} < \frac{m^2 + 4n^2}{15} < 1 \Rightarrow 10 < m^2 + 4n^2 < 15, \text{ only satisfied for } \underline{m=3, n=1}$$

$$\cos \frac{3\pi x}{L} \cdot \cos \frac{\pi y}{L/2}$$



$$\left[ \begin{array}{l} > 0 \text{ if } \boxed{\text{shaded}} \\ < 0 \text{ if } \boxed{\text{unshaded}} \end{array} \right]$$