CHALMERS, GÖTEBORGS UNIVERSITET

EXAM for
COMPUTATIONAL BIOLOGY A

COURSE CODES: **FFR 110, FIM740GU, PhD**

Time:	June 9, 2017, at $08^{30} - 12^{30}$
Place:	Johanneberg
Teachers:	Kristian Gustafsson, 070-050 2211 (mobile), visits once at 10^{00}
Allowed material:	Mathematics Handbook for Science and Engineering
Not allowed:	any other written material, calculator

Maximum score on this exam: 12 points (need 5 points to pass).
Maximum score for homework problems: 18 points (need 7 points to pass).
CTH ≥17 grade 3; ≥22 grade 4; ≥26 grade 5,
GU ≥17 grade G; ≥ 24 grade VG.

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1. Effect of fishing on a predator-prey model [2 points] Consider a simple predator-prey model (Lotka-Volterra)

$$\begin{aligned}\dot{N} &= N(a - bP)\\ \dot{P} &= P(cN - d)\,.\end{aligned} \tag{1}$$

Assume N denotes the size of a prey population of fish that is eaten by predator fish of population size P. Assume a, b, c, d are positive constants.

a) Explain the forms of the terms on the right-hand side of Eq. (1).

Solution
See lecture notes, Section 3.1.1

b) Modify the model in Eq. (1) to include the effect of fishing by humans. Assume that the fishing tools do not distinguish between predator and prey fish, and assume that the total number of fish caught is proportional to the total fish population with proportionality coefficient f.

Solution
To include fishing as described above in the model in Eq. (1), we remove both predators and prey with the same rate coefficient. The modified model is therefore

$$\begin{aligned}\dot{N} &= N(a - bP) - fN\\ \dot{P} &= P(cN - d) - fP\,.\end{aligned}$$

c) Find all the steady states of the resulting model. How does the number of biologically relevant steady states depend on f?

Solution
The resulting model has two fixed points:
$(N^*, P^*) = (0, 0)$ and $(N^*, P^*) = ((d + f)/c, (a - f)/b)$. if $f < a$ there exists a non-trivial steady state, otherwise not.

d) Most solutions of Eq. (1) show oscillations with some period T. It is possible to show that the averages of the populations over one period (denoted $\overline{N}$ and $\overline{P}$) are equal to the values of the non-trivial steady state (denoted N^* and P^*), i.e.

$$\overline{N} \equiv \frac{1}{T}\int_0^T \mathrm{d}t' N(t') = N^* = \frac{d}{c}\,, \qquad \overline{P} \equiv \frac{1}{T}\int_0^T \mathrm{d}t' P(t') = P^* = \frac{a}{b}\,.$$

By using this result, explain what effect fishing has on the average populations of prey and predators.

Solution
When $f < a$, using that the model in subtask b) is on the form (1) with modified parameters, the average N and P are equal to the non-trivial fixed point found in subtask c:

$$\overline{N} = \frac{d+f}{c}$$
$$\overline{P} = \frac{a-f}{b}\,.$$

Comparing to the case without fishing

$$\overline{N}_0 = \frac{d}{c}$$
$$\overline{P}_0 = \frac{a}{b}\,,$$

we see that the prey population increases with increasing fishing, and the predator population decreases with increasing fishing. However, there is a limit, as f becomes larger than a, the non-trivial fixed point ceases to exist and the effect of fishing is to drive both populations extinct in the model.

2. Discrete growth models [2.5 points] Consider the following discrete growth model for a population of size N:

$$N_{t+1} = N_t \exp\left[r\left(1 - \frac{N_t}{K}\right)\right]\,, \tag{2}$$

where r and K are positive parameters.

a) Determine the non-negative steady states of the model (2) and give an interpretation of the parameter K.

Solution
Writing Eq. (2) as $N_{t+1} = F(N_t)$, the steady states are obtained by solving $F(N_t) = N_t$. We get $N_1^* = 0$ and $N_2^* = K$. We interpret K as the carrying capacity for the population.

b) Find a limit where the model (2) shows discrete Malthus growth:

$$N_{t+1} = N_t(1 + r)\,.$$

Give an interpretation of r in this limit (note that r must be dimensionless in Eq. (2)).

Solution
For small values of r and N/K the right-hand side of Eq. (2) simplifies to $N_t(1 + r)$, which is on the form of discrete Malthus growth.

The solution to this equation is $N_t = N_0(1+r)^t = N_0 e^{t\log(1+r)} \sim N_0 e^{rt}$, where we used that r is small. Since t takes discrete values at regular time intervals (for example at each generation of the population) we interpret r as the average growth rate during each time interval times the length of the time interval.

c) Determine the stability of the fixed points found in subtask a).

Solution
The stability can be read off from

$$\begin{aligned}
F'(N_t) &= \left(1 - \frac{r}{K}N_t\right)\exp\left[r\left(1 - \frac{N_t}{K}\right)\right]\\
F'(N_1^*) &= e^r > 1\\
F'(N_2^*) &= 1 - r
\end{aligned}$$

Thus N_1^* is always unstable and N_2^* is stable if $r < 2$ and unstable otherwise.

d) Show that Eq. (2) has a period-doubling bifurcation at $r = 2$.

Solution
One way to solve this problem is to solve it graphically, by sketching $F(N_t)$ and $F(F(N_t))$ when $\Lambda = F'(N_2^*)$ becomes smaller than -1.

Another way is to observe that close to the fixed point $N_2^* = K$ the exponent in the map (2) can be approximated by $1 + r\left(1 - \frac{N_t}{K}\right)$, i.e. the map locally behaves as the logistic map and one can proceed the analysis similar to that of the logistic map considered in the lectures.

As a third alternative we note that we have a period-doubling bifurcation if the map $F(N_t) \equiv N_{t+1}$ has a bifurcation such that $F'(N^*)$ passes -1 (such that no stable fixed points exists after the bifurcation) and the second-order iterate $F(F(N_t))$ has a supercritical pitchfork bifurcation (such that the second-order iterate has two stable fixed points, in addition to the unstable fixed points of $F(N_t)$). Showing these properties for the map (2) shows the period-doubling bifurcation.

3. Reaction-diffusion and travelling waves [2.5 points] Consider a reaction-diffusion equation in one spatial dimension

$$\frac{\partial n}{\partial t}(x,t) = rn(x,t)\left(1-\frac{n(x,t)}{K}\right)\left(\frac{n(x,t)}{A}-1\right) + D\frac{\partial^2 n}{\partial x^2}(x,t)\,. \qquad (3)$$

Here $n(x,t)$ denotes a population density of some species at position x at time t. Moreover r, K, A and D are non-negative parameters. Assume that $A < K$.

a) First consider the case where $D = 0$ in Eq. (3) and consider a homogeneous initial condition (i.e. you can neglect the spatial coordinate). By for example sketching the resulting flow, explain and give possible interpretations of the remaining parameters r, K, and A.

Solution
The resulting flow

$$\frac{dn}{\mathrm{d}t}(t) = rn(t)\left(1-\frac{n(t)}{K}\right)\left(\frac{n(t)}{A}-1\right)$$

has three fixed points located at $n^* = 0$, $n^* = A$ and $n^* = K$.

The parameters r and K are the (in this case negative) growth rate for small populations and the carrying capacity for the population. The additional parameter A introduces a threshold below which the growth rate is negative (Allee effect), and above which the growth rate is positive. This could model a population that suffers if the number of individuals are too few (some examples could be weaker group defence against predators or inbreeding when the population density is low).

b) To simplify the analysis, let $r = 1$, $A = 1/2$, $K = 1$ and $D = 1$. Assume that $n(x,t) = u(z)$ only depends on the combination $z = x - ct$. Starting from Eq. (3) derive an ordinary differential equation for $u(z)$.

Solution
For this coordinate change partial derivatives transform as

$$\frac{\partial n}{\partial t} = -c\frac{\mathrm{d}u}{\mathrm{d}z}$$
$$\frac{\partial n}{\partial x} = \frac{\mathrm{d}u}{\mathrm{d}z}$$

and Eq. (3) gives the ordinary differential equation

$$-c\frac{\mathrm{d}}{\mathrm{d}z}u(z) = u(z)\left(1-u(z)\right)\left(2u(z)-1\right) + \frac{\mathrm{d}^2}{\mathrm{d}z^2}u(z)\,.$$

c) Does the resulting equation in subtask b) allow travelling wave solutions? If so, for which values of c?

Solution

Introduce $v = \mathrm{d}u/\mathrm{d}z$ to write the equation for z as a first-order system

$$\frac{\mathrm{d}u}{\mathrm{d}z} = v$$
$$\frac{\mathrm{d}v}{\mathrm{d}z} = -u(1-u)(2u-1) - cv\,.$$

Travelling-wave solutions are orbits connecting fixed points in the u-v plane. The fixed points are given by $v^* = 0$ and $u_1^* = 0$, $u_2^* = 1/2$ and $u_3^* = 1$. The Jacobian evaluated at these fixed points is

$$\mathbb{J}(u) = \begin{pmatrix} 0 & 1 \\ 1-6u+6u^2 & -c \end{pmatrix}$$
$$\mathbb{J}(u_1^*) = \begin{pmatrix} 0 & 1 \\ 1 & -c \end{pmatrix}$$
$$\mathbb{J}(u_2^*) = \begin{pmatrix} 0 & 1 \\ -1/2 & -c \end{pmatrix}$$
$$\mathbb{J}(u_3^*) = \begin{pmatrix} 0 & 1 \\ 1 & -c \end{pmatrix}.$$

The corresponding eigenvalues are

$$\lambda_{1,\pm} = \frac{1}{2}(-c \pm \sqrt{c^2+4})$$
$$\lambda_{2,\pm} = \frac{1}{2}(-c \pm \sqrt{c^2-2})$$
$$\lambda_{3,\pm} = \frac{1}{2}(-c \pm \sqrt{c^2+4})\,.$$

Thus both $u_1^* = 0$ and $u_3^* = 1$ are saddle points no matter what c is. $u_2^* = 1/2$ is either a stable spiral if $|c| < \sqrt{2}$ or a stable node if $|c| > \sqrt{2}$. Sketching the phase-diagram it is possible to argue that the saddle points must be connected to the stable fixed point for any value of c. This implies that the system permits travelling-wave solutions for all values of c.

4. Diffusion-driven instability and pattern formation [2 points]
Turing showed that a two-dimensional reaction-diffusion system

$$\begin{aligned}\frac{\partial u}{\partial t} &= \gamma f(u,v) + \nabla^2 u \\ \frac{\partial v}{\partial t} &= \gamma g(u,v) + d\nabla^2 v\end{aligned}$$

is unstable to spatial wave-like perturbations in a range of wave numbers if the following conditions hold

$$\begin{aligned}\mathrm{tr}\mathbb{J} &< 0 \\ \det J &> 0 \\ dJ_{11} + J_{22} &> 0 \\ \frac{(dJ_{11}+J_{22})^2}{4d} &> \det \mathbb{J}\,.\end{aligned}$$

Here J_{ij} are elements of the Jacobian matrix of the homogeneous steady state

$$\mathbb{J} = \gamma \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}\,.$$

a) Consider the following reaction-diffusion system in one spatial dimension written in dimensionless units:

$$\begin{aligned}\frac{\partial u}{\partial t} &= \frac{u^2}{v} - bu + \frac{\partial^2 u}{\partial x^2} \\ \frac{\partial v}{\partial t} &= u^2 - v + d\frac{\partial^2 v}{\partial x^2}\,.\end{aligned} \tag{4}$$

Here b and d are positive constants.

Determine the positive spatially homogeneous steady states of the system (4). Is this state stable?

Solution
The positive steady state is $(u^*, v^*) = (1/b, 1/b^2)$. The Jacobian evaluated at the fixed point is

$$\begin{aligned}\mathbb{J}(u^*, v^*) &= \begin{pmatrix} b & -b^2 \\ 2/b & -1 \end{pmatrix} \\ \mathrm{tr}\mathbb{J} &= b - 1 \\ \det\mathbb{J} &= b\,.\end{aligned}$$

When $b < 1$ the fixed point is stable (spiral), otherwise it is unstable (spiral or node depending on b).

b) Determine the conditions for the steady state in subtask a) to be driven unstable by diffusion. Sketch the b-d parameter space in which diffusion-driven instability occurs.

Solution
Using Turing's conditions for the Jacobian gives $b < 1$ (homogeneous state should be stable) and

$$dJ_{11} + J_{22} = db - 1 > 0$$
$$\frac{(dJ_{11} + J_{22})^2}{4d} = \frac{(bd-1)^2}{4d} > \det \mathbb{J} = b\,.$$

giving an additional constraint on the parameters: $bd > 3 + 2\sqrt{2}$ (the condition $bd < 3 - 2\sqrt{2}$ is neglected because the additional condition $bd > 1$).

[Sketch]

c) Explain without calculations what it means that a system has a diffusion-driven instability, for example by sketching the response of the system to a small, suitable perturbation.

Solution
Lecture notes 8

d) An observation in nature is that there is (almost) no animal with striped body and spotted tail, but there is animal with spotted body and striped tail. Give one possible explanation (without calculations) for this observation.

Solution
Lecture notes 8

5. Disease spreading in large but finite populations [2 points] Assume that a population consists of N (constant in time) individuals. Each individual is either infected by, or susceptible to a disease. Assume that recovered individuals once again become susceptible (SIS model).

a) Denote the number of susceptible and infected individuals by S and I respectively. Assume that the rate at which susceptibles S turn into infectives I is $\beta SI/N$ and that the rate at which infectives turn into susceptibles is γI, where β and γ are positive constants.

Explain why the forms of these rates are reasonable. In particular, give an interpretation of β considering that the first rate is divided by the total population size N.

Solution
The rate at which susceptibles turn into infectives is proportional to the rate at which infected individuals encounter and infect susceptible individuals. β denotes the number of disease-spreading contacts per unit time for an infected individual. However, only contacts with susceptibles generate new infectives, hence each infected individual generates $\beta S/N$ new infectives per unit time. Finally, the rate at which susceptibles turn into infectives is proportional to the number of infectives, $\beta SI/N$.

The rate at which infectives turn into susceptibles is proportional to the number of infectives, i.e. infectives automatically recovers from the disease at some rate γ.

b) Assume that in a short time interval the number of infected individuals changes by $+1$ or -1 because of infections or due to recovery.

Using the rates introduced in subtask a), write down a Master equation for the probability $\rho_n(t)$ to observe n infected individuals at time t in a finite population consisting of N individuals.

Solution
Problem set 3.1b)

c) Contrast stochastic to deterministic models of disease spreading. Discuss under what conditions one should use either and discuss typical differences between the dynamics of the models.

6. Phase resetting of oscillators [1 point] Note: The theory for this problem is not covered in the course this year

a) Explain what is meant by phase resetting of an oscillating system.

Solution
Lecture notes 13.3

b) Give two examples of applications of phase resetting.

Solution
Lecture notes 13.3