# Mathematical Biology A.A. 2009/10
# Exercises

## 1 Single population growth

1.1. Assume that growth of population $N$ depends on available resources $R$, according to a general law

$$\frac{dN}{dt} = NG(R). \tag{1}$$

Assume for the moment that the amount of resources is a fixed constant $C$, but they can be free (hence available) or used by the population. In other words

$$R = C - H(N). \tag{2}$$

The model will be specified when the functions $G$ and $H$ are given.

(a) Explain why reasonable assumptions are that both $G$ and $H$ are increasing functions with $G(0) < 0$, $H(0) = 0$.

(b) Choose a linear from for $G$ and $H$ and show that $N$ follows the logistic equation.

(c) In the previous case find the expressions for the intrinsic rate of growth $r$ and the carrying capacity $K$.

(d) Does equation (**??**) always have a positive equilibrium? If not, find the conditions under which it does.

(e) Using generic functions $G$ and $H$ satisfying the assumptions in a), under which conditions the equation (**??**) has a unique positive equilibrium. When is it asymptotically stable?

What could be other reasonable assumptions for $R$ instead of (**??**)?

1.2. A population $N$ is growing according to a logistic differential equation, and $N(t_1) = n_1$, $N(t_1 + \tau) = n_2$, $N(t_1 + 2\tau) = n_3$. Show that

$$K = \frac{1/n_1 + 1/n_3 - 2/n_2}{1/(n_1 n_3) - 1/n_2^2}.$$

1.3. It may be considered reasonable that, for a sexual species, growth is proportional to the number of encounters, hence, choosing appropriately the time unit:

$$\frac{dN}{dt} = N^2.$$

(a) Show that the solutions of this equation tend to infinity in a finite time.

(b) Let us correct the equation, by assuming that the term $N^2$ describes only the births, and that they are anyway limited by density dependence; deaths are proportional to $N$. Hence the resulting equation would be

$$\frac{dN}{dt} = N^2(1 - \frac{N}{K}) - \mu N.$$

Discuss whether it seems a reasonable equation. Find its positive equilibria and their stability properties. Does the equation still have the problem of solutions going to infinity in a finite time?

1.4. Harvesting problem.

Let us consider a population growing according to a logistic dynamics. Let assume that a constant effort $E$ of fishing[1] so that the yield per unit time is $qEx$, where $x$ is population size $q$ is a coefficient denoting the return to effort.

(a) Write down the differential equation for $x(t)$ which translate these assumptions; find its equilibria and the asymptotic behaviour of solutions, according to parameter values.

(b) Let assume that the unit price at which the fish is sold is $p$, and that the cost of fishing is proportional (through a coefficient $c$) to the effort $E$. Let assume that an enlightened dictator wants to set $E$ at the value that maximizes the gain (= revenue − cost) when the population is at its asymptotically stable equilibrium. Find the value of $E$ and the corresponding equilibrium value for $x$.

(c) Economic theory predicts that, for an open access fishery, the effort $E$ will in the long run reach the value at which the gain is equal to 0. Find the value of $E$ and the corresponding equilibrium value of $x$; compare them (i.e, find, if they are greater or smaller) than the previous case.

(d) Let assume that the government taxes at a percentage $\rho$ the gains obtained by fisheries. How does this affect the results obtained with open-access fishery?

[1] or hunting, or harvesting

(e) Let assume that the government taxes according to how much has been fished $Y$. Let us consisre two separate cases: a constant fraction $\rho Y$, or a progressive tax $\tau(Y)$ given by the formula

$$\tau(Y) = \begin{cases} 0 & \text{se } Y \leq Y_0 \\ \rho(Y - Y_0) & \text{se } Y > Y_0 \end{cases}$$

Which are the results of these regulations?

(f) Let us assume that the dynamics of $x$ be described, in absence of fishing, by the generalized logistic equation

$$x'(t) = rx(t)\left(1 - \left(\frac{x(t)}{K}\right)^{\alpha}\right). \qquad \alpha > 0$$

How do previous results change?

# 2 Analysis of planar systems

2.1. A theoretical model for mutual inhibition between two proteins is

$$\frac{dx}{dt} = \frac{\left(\frac{1}{2}\right)^n}{\left(\frac{1}{2}\right)^n + y^n} - x$$
$$\frac{dy}{dt} = \frac{\left(\frac{1}{2}\right)^n}{\left(\frac{1}{2}\right)^n + x^n} - y$$

where $x(t)$ and $y(t)$ represent the concentrations of the two proteins.

(a) Show that $\left(\frac{1}{2}, \frac{1}{2}\right)$ is an equilibrium for all $n > 0$.

(b) Study its stability in dependence of $n$.

(c) With the help of a computer, show that there exist other positive equilibria for $n > 2$.

2.2. The following system has been proposed to study a plant-herbivore system: $q$ represents plant quality (low $q$ means that the plant is toxic because of chemicals released, while high $q$ means that the plant is a good food for the herbivores). We assume that quality decreases (toxic compounds are synthetised) as a result of high herbivory). The density of herbivores is $H$ and their growth rate depends on the quality of food they consume. The model equations are

$$\frac{dq}{dt} = k_1 - k_2 qH(H - H_0)$$
$$\frac{dH}{dt} = k_3 H\left(1 - \frac{k_4 H}{q}\right).$$

(a) Explain why the equations correspond to the biological assumptions, and suggest possible meanings for its parameters.

(b) Show that the equations can be written in dimensionless form as

$$\frac{dx}{d\tau} = 1 - kxy(y-1)$$
$$\frac{dy}{d\tau} = \alpha y\left(1 - \frac{y}{x}\right).$$

Determine $k$ and $\alpha$ in terms of the original parameters.

(c) Show that there is only one positive equilibrium[2].

(d) Determine its stability[3]

# 3 Predator-prey

3.1. It is often observed that, in the pools where fish have been added, water has a greenish colour, indicating a high algal biomass. Try to explain this using a prey-predator system with functional and numerical response of Holling type, assuming that algae (the prey) follow the logistic equation (in absence of predators) and that zooplankton (predators) have mortality rate given by $d + bP$ where $P$ is fish density (assumed to be constant). Specifically, find how equilbrium algal biomass varies with fish density $P$, and comment the results.

3.2. In all Canada moose are preyed by packs of wolves that cause a relevant mortality. The ecologist Messier (1994) has collected data in different areas in the country and found that the following relation (approximately) holds between the density $L$ (# of wolves per km$^2$) of wolves and the density $A$ (# of moose per km$^2$) of moose:

$$L = \frac{0.0587(A - 0.03)}{0.76 + A}.$$

Let us interpret this relation as the isocline of predators, i.e. the equilibrium number of wolves for each constant density $A$ of moose. Is it possible to obtain such an isocline from a prey-predator system of Gause-Rosenzweig-McArthur type?

Messier has also obtained that, in absence of wolves, the growth of moose is logistic with intrinsic rate of growth equal to 0.51 years$^{-1}$ and carrying capacity equal to 1.96 moose per km$^2$ and that the rate of mortality bacause of predation (in years$^{-1}$) is proportional to wolf density and equal to $5.2L$.

[2]It is not possible computing it explicitly, but its uniqueness can easily be established graphically.

[3]It is not necessary to know explicitly the equilibrium; its sign is sufficient for the computations.

Draw the prey and predator isoclines and find the positive equilibrium of the system. Is such equilibrium stable[4]?

3.3. Consider a prey-predator system, in which prey dynamics, in absence of predators, is logistic, while predators interact among themselves. For instance, the number of preys captured per predator could increase with the number of predators (hunting in group could be more efficient) or decrease with the number of predators (predators could waste time fighting among them; or preys may be more careful when there are many predators around).

(a) Write a generic system according to these assumptions.

(b) Choose a specific model, corresponding to one of those cases.

(c) Analyse the equilibria and their stability (local) per the chosen model.

3.4. Leslie (1948) proposed the following system as a model for the prey-predator dynamics:

$$\frac{dH}{dt} = H(a - bH - cP), \qquad \frac{dP}{dt} = P(r - s\frac{P}{H}),$$

in other words, the predators ($P$) have a logistic type dynamics with carrying capacity proportional to the density of preys ($H$).

State clearly, and in case criticize, the assumptions of the model.

Draw the isoclines in the phase plane, and find the positive equilibrium.

Show that the function (where $(H^*, P^*)$ is the positive equilibrium)

$$V(H,P) = \log\left(\frac{H}{H^*}\right) + \frac{H^*}{H} + \frac{cH^*}{s}\left(\log\left(\frac{P}{P^*}\right) + \frac{P^*}{P}\right)$$

is a Liapunov function for the system[5]

3.5. Consider the following prey-predator system:

$$\begin{aligned}\frac{dH}{dt} &= H\left[r(1 - H/K) - \frac{\alpha HP}{(H^2 + \beta^2)}\right]\\ \frac{dP}{dt} &= P\left[-c + \frac{\gamma H^2}{(H^2 + \beta^2)}\right]\end{aligned}$$

where all parameters are positive.

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[4]think of the relation betwen isocline and the differential equation for predators

[5]The proof requires careful computations: 1. compute the derivative along the trajectories of $V$. 2. using the relations satisfied by $H^*$ and $P^*$, show that the terms including both $H$ and $P$ cancel, and the derivative is the sum of a term depending only on $H$ and one depending only on $P$. 3. using again the relations satisfied by $H^*$ and $P^*$, show that each term is a perfect square, so that the derivative has a definite sign.

(a) Give a biological interpretation to these equations.

(b) Find all equilibria (in the first quadrant) and study their stability for $\gamma < c$.

(c) Assume $\gamma > c$. Find the conditions on $K$ that make unstable the 'equilibrium without predators (but with a positive number of preys).

(d) Show that a positive equilibrium $(H^*, P^*)$, if it exists, is stable if $\frac{r}{K} + \alpha P^* \varphi'(H^*) > 0$ where $\varphi(H) = \frac{H}{H^2 + \beta^2}$.[6]

(e) Show that the condition of stability in (d) is equivalent[7] to

$$1 + \left(\frac{K - H^*}{H^*}\right)\left(\frac{\beta^2 - (H^*)^2}{\beta^2 + (H^*)^2}\right) > 0.$$

# 4 Two species competition

4.1. Show that in the Lotka-Volterra competition model, two species can coexist at a stable equilibrium only if the point representing the equilibrium densities of the two species $(N_1^*, N_2^*)$ lies above the line connecting the two equilibria with a single species $(K_1, 0)$ e $(0, K_2)$.

This represents a powerful test of the model: one can grow the two species in isolation, record their equilibrium densities; then grow the two species together and, if they reach a coexistence equilibrium, measure their densities and see whether the condition is satisfied.

Such an experiment was performed by Ayala (1969) with two species of fruit flies, *Drosophila pseudoobscura* and *D. serrata*, obtaining the following results:

| | Species grown in isolation | Species grown together |
|---|---|---|
| # D. pseudoobscura | 664 | 252 |
| # D. serrata | 1251 | 278 |

What can we conclude about the competition model? What may be reasons for the discrepancy from theoretical predictions?

4.2. For each of the following systems, determine the outcome of competition:

(a) $x' = x(60 - 3x - y)$, $y' = y(75 - 4x - y)$;

(b) $x' = x(80 - x - y)$, $y' = y(120 - x - 3y - 2y^2)$.

[6] To show this, it is convenient to rewrite the system using the function $\varphi$, and compute the positive equilibrium and the Jacobian through $\varphi(H^*)$ and $\varphi'(H^*)$, without explictly computing these.

[7] Use simple algebraic steps

4.3. Figure **??** shows some results of experiments by Tilman *et al.* (1981) with two species of algae (*Asterionella formosa* and *Cyclotella meneghiniana*) in two different circumstances: on the left when phosphates are limiting while silicates are abundant; on the right, when silicates are limiting while phosphates are abundant (see caption for details). Suppose that the two species are grown

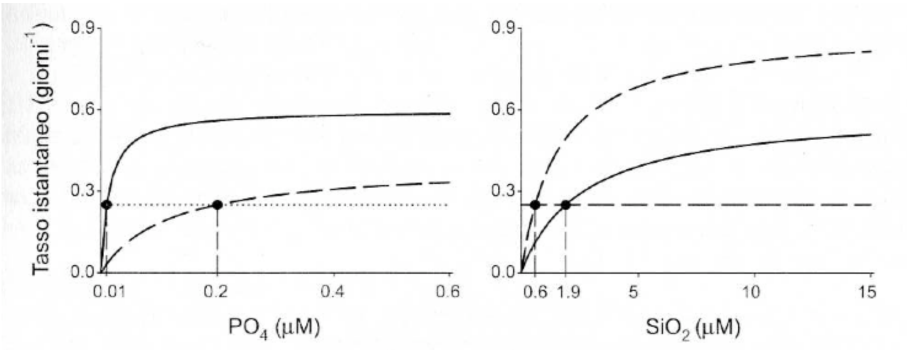



Figure 1: Rates of reproduction (in days$^{-1}$ of *Asterionella formosa* (continuous line) and *Cyclotella meneghiniana* (dashed line) as a function of $PO_4$ with abundant silicates (left panel), or of $SiO_2$ with abundant phosphates (right panel).

together in two different experimental set-ups: abundant silicates and limiting phosphates; or abundant phosphates and limiting silicates.

(a) Which of the two species will outcompete the other one in the two experiments?

(b) Assume that mortality is equal to 0.25 days$^{-1}$ for both species. Moreover, in the experiment with limiting phosphates the concentration of available phosphates $P$ is obtained from the total number $N$ of algae of the two species; similarly, in the experiment with limiting silicates the concentration of available silicates $S$ is obtained from the numbers (per $ml$) $N_1$ and $N_2$ of the two species, according to the following relations

$$P = \frac{2}{1 + 0.02N_1 + 0.01N_2} \qquad S = \frac{30}{1 + 0.04N_1 + 0.006N_2}.$$

Find the equilibrium concentrations towards which, in the two different experiments, the concentrations of the algae will converge.

(c) Assume that when a species is grown with limiting both phosphates and silicates, its rate of reproduction is given by the minimum of what shown in the two panels of Fig. **??** (Liebig's minimum law). Show that a coexistence equilibrium would then exist, and find its coordinates.

4.4. Assume that the dynamics of two competing species can be described by Lotka-Volterra system where the growth rates $r_1$ and $r_2$ are periodic functions of $t$ (positive at all times).

(a) Find the asymptotic behaviour of the system with only one species, say 1[8]

(b) Find the conditions under which species 2 would increase, if introduced in small numbers when species 1 has approached its asymptotic state. Is it possible to find parameter values such that species 2 would increase, if introduced in small numbers when species 1 is close to its asymptotic state[9], and vice versa?

(c) Repeat the scheme assuming that $r_1$ and $r_2$ are constant, but the carrying capacities $K_1$ and $K_2$ are periodic functions of $t$ (positive at all times). The computations are possible, but awful; it is enough describing the procedure conceptually, after having guessed correctly the asymptotic behaviour of the system with only species 1.

# 5 3 species ecological system

5.1. Consider the system con 2 prey species ($H_1$ and $H_2$) and 1 predator with Lotka-Volterra interactions:

$$H_1' = r_1 H_1 (1 - \frac{H_1}{K_1} - \alpha_{12}\frac{H_2}{K_1}) - c_1 H_1 P$$
$$H_2' = r_2 H_2 (1 - \alpha_{21}\frac{H_1}{K_2} - \frac{H_2}{K_2}) - c_2 H_2 P$$
$$P' = \gamma_1 c_1 H_1 P + \gamma_2 c_2 H_2 P - dP$$

(a) Make the equations non-dimensional, through suitable variable changes.

(b) List the possible equilibria with 1 or 2 species present, and examine the conditions for their existence and stability. As for positive equilibria, find the equations it must satisfy, without discussing its existence (in the positive quadrant) or its stability.

(c) Find parameter values[10] such that:

i. without predator the preys do not coexist, but will coexist together with the predator[11];

[8] the equation can be solved exactly using the transformation used for obtaining the exact solution of the logistic equation, or via separation of variables. This is actually not necessary, since the asymptotic behaviour of $N_1$ can be guessed intuitively, or obtained by plotting the vector field in the plane $(t, N_1)$.

[9] this verbal specification means that a linearization has to be performed

[10] a computer may help

[11] Note that I did not precise the meaning of 'coexistence'

ii. without predator the preys coexist, but the introduction of the predator causes extinction of one of them[12].

5.2. Consider the food-chain model with one prey species ($H$), a predator ($P$) and a predator of the predator ($Q$), using Holling-type laws:

$$\begin{aligned} H' &= rH(1 - \frac{H}{K}) - \frac{aHP}{1 + aTH} \\ P' &= \frac{\gamma aHP}{1 + aTH} - dP - \frac{bPQ}{1 + bSP} \\ Q' &= \frac{\rho bPQ}{1 + bSP} - eQ \end{aligned}$$

All parameters can be considered positive constants.

(a) Make the equations non-dimensional, through suitable variable changes.

(b) List the possible equilibria, and examine the conditions for their existence and stability.

(c) Does the enrichment paradox still hold?

# 6 Logistic equation with delay

6.1. Consider the equation

$$N'(t) = rN(t)\left(1 - \frac{N(t-\tau)}{K}\right).$$

(a) Find the linearized equation at the equilibrium $K$.

(b) Show that the corresponding characteristic equation is $\lambda = -re^{-\lambda\tau}$.

(c) Let $\lambda = x + iy$ and transform the characteristic equation into a couple of equations for $x$ and $y$.

(d) Show, using one of the previous equations, that, if $x \geq 0$, necessarily $|y| \leq r$.

(e) Using the previous relation in the other equation, show that, if $r\tau < \pi/2$, there are no solutions of the characteristic equation with $x \geq 0$.

6.2. Consider the equation

$$N'(t) = rN(t)\left(1 - \frac{\int_0^{+\infty} p(s)N(t-s)\,ds}{K}\right) \qquad \text{with } p(s) = \frac{1}{\tau}e^{-s/\tau}.$$

Let $P(t) = \int\limits_0^{+\infty} p(s)N(t-s)\,ds$.

[12] check the stability of the boundary equilibria

(a) Show[13] that $N(t)$ and $P(t)$ satisfy a two–dimensional system of ordinary differential equations.

(b) Show that the system has an equilibrium with the first component equal to $K$.

(c) Prove that that equilibrium is asymptotically stable.

# 7 Models in discrete time

7.1. Let $x_t$ the population of a species in year $t$. The dynamics is in discrete time; it is assumed that a fraction $p$ of the population survives to the following year. Moreover, each individual generates on average $2/(1+ax_t^2)$ children that survive to the following year: these are then identical to older individuals in terms of birth and death rates.

Write down $x_{t+1}$ in terms of $x_t$; make the equations non-dimensional in a way that reduces the number of parameters. Find the equilibria of the resulting discrete map. Study their stability according to the values of the (reduced) parameters.

7.2. According to Barrowclough and Rockwell (1993), the snow goose (*Anser caurulescens*) has the following demography:

| i | s | P |
|---|---|---|
| 0 | 0.46 | 0.00 |
| 1 | 0.76 | 0.00 |
| 2 | 0.76 | 0.50 |
| 3 | 0.76 | 0.86 |
| 4-7 | 0.81 | 1.00 |

| z | # number of chicks born alive | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| ⇓ | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 2 | 3 | 0 | 3 | 9 | 3 | 1 | 0 | 0 |
| 3 | 4 | 4 | 6 | 17 | 29 | 11 | 1 | 0 |
| 4 | 12 | 2 | 8 | 25 | 25 | 14 | 5 | 0 |
| 5 | 5 | 1 | 4 | 22 | 37 | 35 | 3 | 2 |
| 6 | 3 | 1 | 3 | 24 | 36 | 25 | 10 | 0 |
| 7 | 4 | 0 | 2 | 11 | 35 | 21 | 3 | 0 |

In the table to the left, $i$ denotes the age (in years), $s$ the probability of surviving to the following year, $P$ the probability of laying eggs. These probabilities refer to females only and, for simpliicity, let us assume that there is 0 probability of surviving to age 8 or beyond.

The table to the right shows, for each age of the mother ($z$), the number of observed nests with a certain number (between 0 and 7) of chicks born alive. Assume that on average 50% of them will be males, 50% females.

On the basis of these data prepare a Leslie matrix for female demography.

[13] a change of variable in the integral may be useful

Compute the expected life of a female at birth, and the expected number of female chicks produced over her life[14].

7.3. Consider an age-structured population growing according to a Leslie matrix. Suppose the population is in stable exponential growth (i.e. its age-structure is constant in time, while the total population is exponentially growing (or decreasing) with exponent $r$.

(a) Compute the two quantities:
   - $T_f$: the average age of the mothers of all children born at time $t$;
   - $T_m$: the average age at which the children born at time $t$ will give birth during their life.

(b) Show that $T_f < T_m$ if $r > 1$, and vice versa if $r < 1$.

(c) Show that, when $R \approx 1$, ($R$ the expected number of children born over a lifetime) the following relation holds in first approximation

$$(r-1)T_m \approx R - 1.$$

7.4. Consider an age-structured population growing according to a (2-dimensional) nonlinear Leslie model. Precisely, letting $u^t = \begin{pmatrix} u_1^t \\ u_2^t \end{pmatrix}$, the model is

$$u^{t+1} = \begin{pmatrix} m_1 & m_2 \\ \psi(N^t)s_1 & 0 \end{pmatrix} u^t$$

where $N^t = u_1^t + u_2^t$, $0 < m_1 < 1$, $0 < s_1 < 1$, $m_2 > 0$ and $\psi$ is a decreasing function such that $\psi(0) = 1$ and $\lim_{N\to\infty} \psi(N) = 0$.

(a) Find the conditions under which this system has a positive equilibrium.

(b) Study the conditions for its stability.

For answering this question, it is almost necessary to use the Jury conditions[15]: all the eigenvalues of a $2 \times 2$ matrix $A$ satisfy $|\lambda| < 1$ if and only if

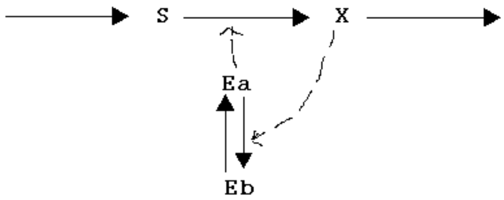
$$\det(A) < 1, \qquad -\det(A) - 1 < \mathrm{tr}(A) < \det(A) + 1.$$

[14] if such an exercise is given at the exam, the size of the matrices will be reduced, to decrease the number of computations

[15] one might wish to prove the Jury conditions, but this is not part of the exercise

# 8 Molecular and cellular biology

8.1. A molecule $X$ is synthetised from a substrate $S$ through an enzymatic reaction of Michaelis-Menten kinetics, proportionally to the concentration of the enzyme $E$ in active configuration. The enzyme $E$ moves from bound to active configuration at rate $k_1$, while the presence of $X$ helps the opposite transition that occurs at rate $k_{-1}X$, where $X$ is the concentration of $X$. These reactions can be summarised in the scheme to the right:




Finally the substrate is produced at constant rate, and $X$ dissociates proportionally to its concentrations.

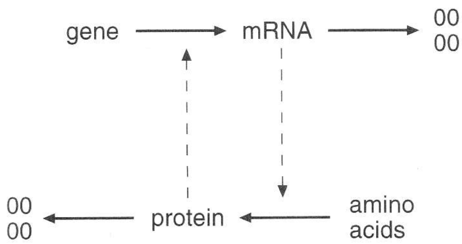
(a) Can we say that there is a positive or negative feedback of $X$ on its synthesis?

(b) Write down a system of differential equations corresponding to the assumptions.

(c) Compute the (unique) equilibrium of the system, finding conditions for its feasibility? *[Hint: consider the equation for the sum $S + X$]*

(d) Suggest what might be the behaviour of the system, when the conditions for the feasibility of the equilibrium are not satisfied.

8.2. *[Positive feedback on gene transcription (Griffith 1968).]* Consider the simple case of a protein that activates transcription of its own gene, as in the following figure:




This mechanism is described by a pair of ordinary differential equations:

$$\frac{d[M]}{dt} = \nu_1 \frac{\varepsilon^2 + ([P]/K_l)^2}{1 + ([P]/K_l)^2} - k_2[M], \qquad \frac{d[P]}{dt} = k_3[M] - k_4[P].$$

(a) How must the variables be scaled to write the ODEs in dimensionless form:

$$\frac{dx}{d\tau} = \frac{\varepsilon^2 + y^2}{1 + y^2} - x, \qquad \frac{dy}{d\tau} = \kappa(\sigma x - y) \; ?$$

(b) Assume $\varepsilon = 0.2$, $\kappa = 1$. Draw phase plane portraits for several values of $\sigma$.

(c) Show graphically how the number of equilibria of the system changes with $\sigma$.

(d) Plot the equilibrium value of $y$ as a function of $\sigma$. *[it is enough a picture showing the qualitative pattern.]*

8.3. In the derivation of Michaelis-Menten equation, it is assumed that the back-reaction $SE \overset{k_{-2}}{\longleftarrow} P + E$ is neglibly slow. Consider now the full system of reactions:

$$S + E \underset{k_{-1}}{\overset{k_1}{\rightleftarrows}} SE \underset{k_{-2}}{\overset{k_2}{\rightleftarrows}} P + E$$

(a) Write down the system of equations corresponding to this scheme. Assume that at the start, there is no complex $SE$ nor product $P$.

(b) Note that there are two quantities that are conserved: $[E] + [SE]$ and $[S] + [SE] + [P]$. Use this to decrease the number of equations.

(c) Make the equations non-dimensional, and in so doing introduce the paramete $\varepsilon = E_0/S_0$, ratio of initial values of enzyme and substrate.

(d) Go to the limit $\varepsilon \to 0^+$ which amounts to make the 'quasi-equilibrium' approximation.

(e) Consider the resulting differential equation for $S(t)$ and show that it will converge to an equilibrium $S^*$ where the concentrations of substrate and product will satisfy Haldane's relation

$$\frac{P^*}{S^*} = \frac{k_1 k_2}{k_{-1} k_{-2}}.$$

8.4. FitzHugh's original model for the action potential was

$$\frac{dx}{dt} = c\left(y + x - \frac{x^3}{3} - I\right), \qquad c\frac{dy}{dt} = a - x - by.$$

Here $x$ is an excitability variable such as membrane potential, $y$ is a recovery variable such as potassium permeability. $I$ is applied current (assumed to be constant), $a$, $b$ and $c$ are positive parameters such that $b < 1 < c$.

(a) Noting that equilibria are found through the intersections of a line and a cubic, show that, under the assumptions on parameters, there is always a unique equilibrium $(x^*, y^*)$. *[Hint: consider the slopes of the line and of the cubic.]*

(b) Computing the Jacobian at the equilibrium, show that it is asymptotically stable if

$$\frac{b}{c} - c(1 - (x^*)^2) > 0, \qquad 1 - b(1 - (x^*)^2) > 0.$$

(c) Show that the equilibrium is unstable if $x^*$ falls in the range $-r < x^* < r$ with $r = \sqrt{1 - b/c^2}$. Show that when this happens the equilibrium lies in the portion of the cubic between its local maximum and minimum.

(d) Show that at

$$I = I_c = \frac{a - r}{b} + r - \frac{r^3}{3}$$

the equilibrium is at $x^* = r$, and that the Jacobian has purely imaginary eigenvalues.

(e) Show, using the implicit function theorem, that the value of $x^*$ is a decreasing function of the applied current $I$.

(f) Deduce from this that the equilibrium will be unstable and that there will be a periodic solution of the system when $I$ belongs to the interval $(I_c, I_M)$ for an appropriate value of $I_M$.

(g) Assume that $c$ is very large. Changing the scale of time, rewrite the system as a pair of slow-fast equations. Show graphically what is the behaviour of the resulting system in the limit $c \to \infty$.

# 9 Travelling waves

9.1. Show that an exact travelling wave solution exists for the scalar reaction-diffusion equation

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

where $q > 0$ by looking for solutions in the form

$$u(x, t) = U(z) = \frac{1}{(1 + de^{bz})^s}, \ z = x - ct$$

where $c$ is the wave speed and $b$ and $s$ positive constants. Determine the values for $c$, $b$ and $s$ in terms of $q$ *[Hint: first choose $s$ such that $sq$ is simple, so that $u^{q+1}(1 - u^q)$ has a simple expression].*

Choose a value for $d$ such that the magnitude of the wave's gradient is maximal at $z = 0$.

# 10 Birth and death processes

10.1. The release of sterile males is a technique has sometimes been applied in the attempt to eradicate pests. The idea is that a certain proportion of females will mate with the released sterile males and will not produce offspring, leading to a reduction of the population. Clearly, this can be effective only if sterile males are quite abundant compared to normal males.

Repeating this process for a few generations (while normal males become less and less abundant) could lead to a strong reduction of the population, and possibly to extinction.

We make extreme assumptions, in order to be able to build a very simplified model of this mechanism in the form of a birth-and-death process.

First, assume that the number of females and 'normal' males is at all times equal: a male dies when and only when a female dies (at rate $\mu$, independently of population size); offspring are born in pairs (one male and one female).

Second, assume that the number of sterile males is kept constant at the value $S$ (as soon as one dies, it is replaced by a newly released one).

Finally, assume that each females mates at rate $\lambda$ (independently of population size) with a male chosen at random among the normal and sterile ones present in the population: if the male chosen is normal, it produces one female and one male; if it sterile, it does not produce offspring.

(a) Write the infinitesimal transition rates for this process (i.e., the rates at which the number of females changes from $j$ at a different value).

(b) Write down the corresponding Kolmogorov differential equations.

(c) Noting that 0 is an absorbing state for the process, write down a system for the probabilities of the population to become extinct sooner or later, conditional to the initial number of females (and males) being equal to $j$. Intuitively, will these probabilities be always equal to 1?

(d) Modify the model by assuming that there exists a level $K > 0$, such that when the number of females reaches the number $K$ the mating rate drops to 0, while being given by the model above for $j < K$. Write down a system of equation for the mean time to extinction, conditional on the number of females (and males) at time 0.

(e) Assume $K = 3$, $\lambda = 1.2$, $\mu = 1$. Find the value of $T_1$, the mean time to extinction, conditional on 1 being the number of females (and males) at time 0 *[I believe that a simple expression can be obtained using a generic value for $S$; if this seems too difficult, use $S = 2$]*

# 11 Models for infectious diseases

11.1. Considerate an infectious disease of $SIR$ type with an average period of infectivity of 7 days and a per-capita rate of being infected of 1/490.000 per day per infective individual [a mass-action law for infections is implicitly assumed]. Assume that the initial population is 1.4 millions of susceptibles, that the initial number of infectives be extremely low, and that births and deaths can be neglected.

(a) Determine the basic reproductive number $R_0$;

(b) Determine the number of infectives at the peak;

(c) Determine the fraction of the population that should be vaccinated at the start of the epidemic to prevent its spread.

(d) Approximate as well as you can the number of susceptibles at the end of the epidemic.

11.2. Let us assume that an infectious disease has a behviour of $S \to I \to R \to S$ type, i.e. infected individuals, once recovered, remain immune from the infection for some time (and can then be considered removed) but then become again susceptibles.

(a) Write a model for the spreas of an infectious disease of this type in a closed population, following the lines of the $SIR$ model analysed in class.

(b) Find the equilibria of such model and study their local stability, according to parameter values.

(c) Study the global behaviour of the system. *[Hint: it could be useful employing the function $(SI)^{-1}$ as a Bendixson-Dulac function.]*

11.3. Consider a Markov process modelling an $SIR$ epidemic (with closed population) in which 1 infected is introduced in a population with 3 susceptibles.

(a) Write down the infinitesimal transition rates

(b) Compute the probability that the epidemics ends after 0, 1, 2 or 3 new infections. *[Hint: sketch on a piece of paper all possible paths of infections and recoveries, and compute the probability of each path through the embedded jump Markov chain]*