Problems

Problem 1. Solve the Gompertz equation

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

Problem 2. Check that if f is a differentiable and strictly decreasing function such that $f(K) = 0$, then the positive solutions of the equation

$$N'(t) = f(N(t))N(t) \tag{2}$$

have the property $\lim_{t\to\infty} N(t) = K$.

Problem 3. Check how the properties of the solutions of the equation

$$N'(t) = \lambda\left(1 - \frac{N(t)}{K} - \frac{A}{1 + BN(t)}\right)N(t) \tag{3}$$

depend on the coefficients A, B, K and λ.

Problem 4. Prove that if $\lambda(t)$ is a continuous and periodic function with the period T and with the mean value $\bar{\lambda} < 0$ and $c(t)$ is a continous bounded function then every solution of the equation $N'(t) = \lambda(t)N(t)+c(t)$ is bounded for $t \geq t_0$.

Problem 5. Prove that if $\lambda(t)$ is a continuous and periodic function with the period T and mean value $\bar{\lambda} = 0$, and $c(t)$ is a continuous periodic function with the period T, then each solution of the equation $N'(t) = \lambda(t)N(t)+c(t)$ satisfies

$$N(t+T) = N(t) + C\exp\Big(\int_0^t \lambda(s)\,ds\Big), \tag{4}$$

where C is the same constant for all solutions. Check that $N(mT) = N(0)+mC$ and find C.

Problem 6. Equation

$$V' = \alpha(t)V^{2/3} - \beta(t)V$$

describes the growth of the volume of a cell. In this case we assume that the amount of the food provided to the cell is proportional to the surface of a cell $S \sim V^{2/3}$, and the food is consuming with the rate proportional to the volume. Functions $\alpha(t)$ and $\beta(t)$ are respective coefficients. What can you say about the function $V(t)$ if $\alpha(t)$ and $\beta(t)$ are continuous and periodic functions with the same period.
Hint. Substitute $L = V^{1/3}$ and apply a theorem from the lectures.

Problem 7. We assume that a differentiable function $f : [0,\infty) \times [0,\infty) \to [0,\infty)$ has the following properties:
(a) $\frac{\partial f}{\partial N_1}(N_1,N_2) > 0$, $\frac{\partial f}{\partial N_2}(N_1,N_2) > 0$ for all N_1 and N_2,
(b) $f(0,0) = 0$,
(c) $\lim_{N_1\to\infty} f(N_1,0) > \varepsilon_1/\gamma_1$ and $\lim_{N_2\to\infty} f(0,N_2) > \varepsilon_2/\gamma_2$.

Check that the solutions of the system

$$
\begin{cases}
\dfrac{dN_1}{dt} = (\varepsilon_1 - \gamma_1 f(N_1, N_2))N_1, \\
\dfrac{dN_2}{dt} = (\varepsilon_2 - \gamma_2 f\big(N_1, N_2)\big)N_2
\end{cases}
\tag{5}
$$

have the same properties as the solution of the system

$$
\begin{cases}
\dfrac{dN_1}{dt} = \big(\varepsilon_1 - \gamma_1 (h_1 N_1 + h_2 N_2)\big)N_1 \\
\dfrac{dN_2}{dt} = \big(\varepsilon_2 - \gamma_2 \big(h_1 N_1 + h_2 N_2)\big)N_2
\end{cases}
\tag{6}
$$

Problem 8. Find stationary points of the system

$$
\begin{cases}
\dfrac{dN_1}{dt} = \big(\varepsilon_1 - \gamma_1 (N_1 + \beta N_2)\big)N_1, \\
\dfrac{dN_2}{dt} = \big(\varepsilon_2 - \gamma_2 (N_2 + \beta N_1)\big)N_2,
\end{cases}
,
\tag{7}
$$

where $\varepsilon_1, \varepsilon_2, \gamma_1, \gamma_2, \beta > 0$. Check how the properties of the stationary points depends on the parameters $\varepsilon_1, \varepsilon_2, \gamma_1, \gamma_2, \beta$.
Hint. Check that if $(\overline{N}_1, \overline{N}_2)$ is a stationary point with positive co-ordinates then the Frechét derivative $\dfrac{df}{dN}$ equals

$$
A = \begin{bmatrix} -\gamma_1 \overline{N}_1 & -\beta\gamma_1 \overline{N}_1 \\ -\beta\gamma_2 \overline{N}_2 & -\gamma_2 \overline{N}_2 \end{bmatrix}.
$$

Show that if $\beta < 1$, then the point $(\overline{N}_1, \overline{N}_2)$ is stable and if $\beta > 1$, then it is a saddle point.

Problem 9. Prove that all nonnegative solutions of the system (7) are bounded.

Problem 10. Check that each nonnegative solution of system (7) converges to a stationary point.
Hint. Consider a Lapunov function:

$$
Q(N_1, N_2) = \frac{1}{2}N_1^2 + \beta N_1 N_2 + \frac{1}{2}N_2^2 - \frac{\varepsilon_1}{\gamma_1}N_1 - \frac{\varepsilon_2}{\gamma_2}N_2.
$$

Check that

$$
\begin{aligned}
\frac{d}{dt}Q(N_1(t), N_2(t)) = &- \gamma_1 N_1(t)\left(N_1(t) + \beta N_2(t) - \frac{\varepsilon_1}{\gamma_1}\right)^2 \\
&- \gamma_2 N_2(t)\left(N_2(t) + \beta N_1(t) - \frac{\varepsilon_2}{\gamma_2}\right)^2
\end{aligned}
$$

and conclude from this inequality each nonnegative solution converges to a stationary point.

Problem 11. Consider a system of equations describing two species living in symbiosis:

$$\begin{cases} \dfrac{dN_1}{dt} = (\varepsilon_1 - \lambda_1 N_1 + \gamma_1 N_2)N_1, \\ \dfrac{dN_2}{dt} = (\varepsilon_2 + \gamma_2 N_1 - \lambda_2 N_2)N_2. \end{cases} \tag{8}$$

Give the interpretation of the coefficients appearing in this system. Check that if $\lambda_1\lambda_2 > \gamma_1\gamma_2$, then all positive solutions of this system converges to the stationary solution (K_1, K_2), where

$$K_1 = \frac{\varepsilon_1\lambda_2 + \varepsilon_2\gamma_1}{\lambda_1\lambda_2 - \gamma_1\gamma_2}, \quad K_2 = \frac{\varepsilon_2\lambda_1 + \varepsilon_1\gamma_2}{\lambda_1\lambda_2 - \gamma_1\gamma_2}.$$

Hint. Consider the Lapunov function:

$$V(N_1, N_2) = \gamma_2 K_1 F\left(\frac{N_1}{K_1}\right) + \gamma_1 K_2 F\left(\frac{N_2}{K_2}\right),$$

where $F(x) = x - \ln x - 1$.

Problem 12. Check that systems (7), (8) satisfy the Dulac-Bendixson criteria.

Problem 13. Consider the following system of equations

$$\begin{cases} x' = \alpha(r)x - \beta(r)y \\ y' = \beta(r)x + \alpha(r)y, \end{cases} \tag{9}$$

where $r = \sqrt{x^2 + y^2}$. Check if the periodic solutions of this system are stable if $\beta(r) = 1$ and

(a) $\alpha(r) = 1 - r$,
(b) $\alpha(r) = r - 1$,
(c) $\alpha(r) = (1 - r)^2$,
(d) $\alpha(r) = -(1 - r)^2$,
(e) $\alpha(r) = (r - 1)(r - 2)$,
(f) $\alpha(r) = (1 - r)(r - 2)^2$,
(g) $\alpha(r) = (1 - r)^2(r - 2)$,
(h) $\alpha(r) = (r - 1)^2(2 - r)$,

Hint. System (9) in the polar coordinates (r, φ) have the form

$$\begin{cases} r' = \alpha(r)r \\ \varphi' = \beta(r). \end{cases} \tag{10}$$

Problem 14. Check if the periodic solution $\bar{x}(t) = \cos t$, $\bar{y}(t) = \sin t$ of system (9) with $\beta(r) = r$ is stable in the Lapunov sense if

(a) $\alpha(r) = (1 - r)/r$,
(b) $\alpha(r) = (1 - r)^3/r$.

Problem 15. Let $\mathbf{f} : \mathbb{R}^2 \to \mathbb{R}^2$ be a C^1 -function such that $\mathbf{f}(\mathbf{0}) = \mathbf{0}$ and let $A = \mathbf{f}'(\mathbf{0})$. Assume that the matrix A has two real eigenvalues λ_1 and λ_2 corresponding to independent eigenvectors $\mathbf{v}_1$ and $\mathbf{v}_2$. Define the function $V : \mathbb{R}^2 \to [0, \infty)$ by $V(\mathbf{x}) = c_1^2 + c_2^2$, if $\mathbf{x} = c_1\mathbf{v}_1 + c_2\mathbf{v}_2$. Check that

$$V'(\mathbf{x}) \cdot \mathbf{f}(\mathbf{x}) = 2c_1^2\lambda_1 + 2c_2^2\lambda_2 + o(\|\mathbf{c}\|^2). \tag{11}$$

Hint. You can apply the formula:

$$\frac{dV}{d\mathbf{x}} = \frac{dV}{d\mathbf{c}} \cdot \left(\frac{d\mathbf{x}}{d\mathbf{c}}\right)^{-1}.$$

Problem 16. Check what kind of bifurcation we have at the point $(0, 0)$ for $\mu = 0$ for the system of equations

$$\begin{cases} x' = y + \varphi(\mu, x^2 + y^2)x \\ y' = -x + \varphi(\mu, x^2 + y^2)y. \end{cases} \tag{12}$$

if

(a) $\varphi(\mu, r^2) = \mu + r^2$,
(b) $\varphi(\mu, r^2) = (r^2 - 1)^2 - 1 + \mu$,
(c) $\varphi(\mu, r^2) = -(r^2 - \mu)^2(r^2 - 2\mu)$,
(d) $\varphi(\mu, r^2) = -(r^2 - \sqrt[3]{\mu})^2(r^2 - 2\sqrt[3]{\mu})$.

Problem 17. Consider the following system of equations

$$\begin{cases} x' = (\mu - x^2 - y^2)x - a(\mu)y \\ y' = (\mu - x^2 - y^2)y + a(\mu)x, \end{cases}$$

where $a(\mu)$ is an arbitrary C^3 function. Check that if $a(0) \neq 0$, then this system satisfies all assumption of the bifurcation theorem, thus for $\mu = 0$ we have the Hopf bifurcation. Describe the bifurcation if

(a) $a(\mu) = \mu$,
(b) $a \equiv 0$.

Problem 18. Consider a special case of the Kolmogorov model

$$\begin{cases} x' = (2 - x)x - xe^{(1-x)c}y \\ y' = (x - 1)y. \end{cases}$$

Check that in the point $(x, y) = (1, 1)$ and for $c = 1$ the Hopf bifurcation appears.
Hint. Substitute $x := x - 1$, $y := y - 1$ and $\mu := c - 1$ and apply formulae for the system in the normal form.

Problem 19. Consider an epidemic model in a population with a constant number N with two groups of individuals: susceptible and infected and S is the number of susceptible individuals and I is the number of infected individuals. We assume that in a unit of time μN new individuals enter the population and at the same time μS and μI of individual leave both groups. We assume that γI of infected individuals recover in a unit of time and $\beta(S,I)$ is the probability of being infected in a unit of time. Check S and I satisfies the following system of equations

$$\begin{cases} S' = \mu N - \beta(S,I)S - \mu S + \gamma I \\ I' = \beta(S,I)S - (\mu+\gamma)I. \end{cases} \tag{13}$$

Find an equation for infected group. Assume that

$$\beta(S,I) = \beta\frac{I}{N}. \tag{14}$$

Check that the function satisfies a logistic equation. Check how the epidemic courses depend on N, β, μ, γ.

Problem 20. Using equations $S' = -\alpha SI$ and $R' = \beta I$ check that

$$\ln S(t) + \tfrac{\alpha}{\beta}R(t) = \ln S_0 + \tfrac{\alpha}{\beta}R_0, \tag{15}$$

where $R_0 = R(0)$.

Problem 21. Let $R_\infty = \lim_{t\to\infty} R(t)$. Using (15) and the equation $S(t)+I(t)+R(t) = \text{const}$ show that

$$R_\infty = I_0 + R_0 + S_0\big(1 - e^{\frac{\alpha}{\beta}(R_0 - R_\infty)}\big). \tag{16}$$

Problem 22. Assume that $R_0 = 0$ and that the initial number of infected individuals is small. Let $S_{\infty,0}$ and $R_{\infty,0}$ be the limits S_∞ and R_∞, as $I_0 \to 0$. Find an equation for $S_{\infty,0}$ and $R_{\infty,0}$.

Problem 23. Assume that we know S_0 and S_∞. Find $\frac{\beta}{\alpha}$, $\frac{\alpha}{\beta}S_0$ and $I_{\max}$ – the maximal size the infected part of the population. We assume that the initial number of infected individuals is small and we can neglect it.

Problem 24. Let us assume that the initial number of infected indviduals is small and we can neglect it. Check that if $x_\infty = S_\infty/S_0$, then

$$x_\infty = e^{\mathcal{R}_0(x_\infty - 1)}. \tag{17}$$

Prove that

a) $x_\infty > e^{-\mathcal{R}_0}$,
b) $x_\infty \approx e^{-\mathcal{R}_0}$ for large $\mathcal{R}_0$,
c) $x_\infty < \frac{1}{\mathcal{R}_0}$,
d) if $\mathcal{R}_0 > 1$ and $\mathcal{R}_0 \approx 1$, then $x_\infty \approx 3 - 2\mathcal{R}_0$.

Let $\mathcal{R}_0 > 1$ and $f(x) = e^{\mathcal{R}_0(x-1)}$. Check the inequalities $x_\infty < f(x) < x$ for $x \in (x_\infty, 1)$. Using these inequalities and and the inequality $x_\infty < \frac{1}{\mathcal{R}_0}$ prove that x_∞ is a limit of a decreasing recurrent sequence $x_1 = \frac{1}{\mathcal{R}_0}$, $x_{n+1} = f(x_n)$ for $n \geq 1$. In particular $x_\infty < x_2 = e^{1-\mathcal{R}_0}$.

Problem 25. Propose a continuous time version of the model of telomere shortening.

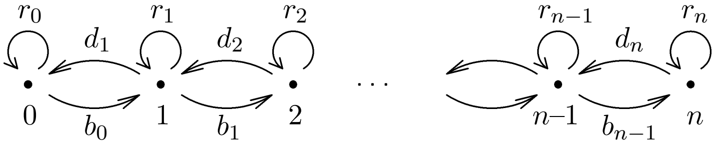

FIGURE 1. The graph of connections in the discrete generalized birth-death process (Problem 28). In this case $p_{i+1,i} = b_i$, $p_{i,i+1} = d_i$ and $p_{i,i} = r_i$.

Problem 26. Consider the model of telomere shortening with $d_i = d$ and $r_i = r$ for $i = 1, 2, \dots, n$. Find the formula for the matrix P^k and check the asymptotic behaviour of the sequence $(\mathbf{x}^k)$ as $k \to \infty$.

Problem 27. Consider the model of the age structure of a population. We assume that $b_{n-2} > 0$, $b_n > 0$ and $b_i = 0$ in other cases. Check that we have asynchronous exponential growth in this model.

Problem 28. Consider a discrete model of the generalized birth-death process (see Fig. 1) Check that
a) if $r_i = 0$ for $i = 0, 1, \dots, n$, then it has no the property of the asynchronous exponential growth.
b) if $b_i > 0$ and $d_j > 0$ for all possible i, j and $r_i > 0$ for some i, then we have asynchronous exponential growth in this model.

Problem 29. Consider the model from Problem 28 with $d_i = 0$, $r_i = \lambda > 0$ and $b_i > 0$ for all possible i. Find a formula for the matrix P^k and check the asymptotic behaviour of the sequence $(\mathbf{x}^k)$ as $k \to \infty$.
Hint. Write the matrix P in the form $P = \lambda I + B$ and check that $B^{n+1} = 0$.

Problem 30. Prove the continuous version of the Perron theorem.
Hint. Replace the matrix Q which appears in the equation $\mathbf{x}' = Q\mathbf{x}$ by $Q = -\lambda I + B$ where $\lambda = \max\{-a_{ii} : i = 1, \dots, n\}$. Check that $x(t) = e^{\lambda t} e^{Bt} x$. Then apply the discrete version of the Perron theorem. From the condition (**K**) it follows that the matrix $P = e^{Bt}$ has all entrances positive.

Problem 31. Consider the system

$$\begin{aligned} x_1' &= b_n x_n - a_1 x_1, \\ x_i' &= b_{i-1} x_{i-1} - a_i x_i, \quad \text{for } i = 2, \dots, n, \end{aligned} \tag{18}$$

where $b_i > 0$ for $1 \le i \le n$. Check that system (18) satisfies the law of asynchronous exponential growth.

Problem 32. Consider a model given by the system of equations

$$x_i'(t) = -a_i x_i(t) + b_{i-1} x_{i-1}(t) + d_{i+1} x_{i+1}(t), \tag{19}$$

for $i = 0, 1, \ldots,$. We assume that $b_{-1} = 0$, $d_0 = 0$. Check that the matrix A of this system is a Kolmogorov matrix if and only if $a_i = b_i + d_i$ for $i = 0, 1, 2, \ldots$. Check that the matrix A generates a Markov semigroup if and only if the sequence (x_n) defined by the recurent formulae $x_0 = 1$, $x_1 = 1 + \frac{\theta}{b_0}$ and

$$x_{n+1} = \left(1 + \frac{d_n + \theta}{b_n}\right)x_n - \frac{d_n}{b_n}x_{n-1}, \quad n \geq 1, \quad \theta > 0, \tag{20}$$

is unbounded. Check that the sequence x_n is unbounded if a) $\displaystyle\sum_{n=0}^{\infty} \frac{1}{b_n} = \infty$, b) $d_n \geq b_n$ for sufficiently large n.

Check that the sequence x_n is bounded if $d_n = 0$ for $n \in \mathbb{N}$ and $\displaystyle\sum_{n=0}^{\infty} \frac{1}{b_n} < \infty$.

Problem 33. Consider the following system of equations

$$\begin{aligned} y_1' &= -2ry_1 + (2m_2 + d)y_2 + \sum_{n=3}^{\infty} m_n y_n, \\ y_n' &= -(d + r + m_n + \tfrac{r-d}{n})ny_n + rny_{n-1} + (d + m_{n+1})ny_{n+1} \end{aligned} \tag{21}$$

for $n \geq 2$. We assume that $r > 0$, $d > 0$ and (m_n) is a sequence of positive numbers. Check that the system (21) generates a Markov semigroup on l^1. *Hint.* Apply Theorem 5 from the lectures. Check that $x \neq 0$ is a solution of the equation $Ax = \theta x$ if and only if

(22)
$$x_{n+1} = \left(1 + \frac{\theta}{(n+1)r}\right)x_n + \frac{(n-1)(d + m_n)}{(n+1)r}(x_n - x_{n-1}) + \frac{m_n}{(n+1)r}(x_n - x_1)$$

for $n \geq 1$. Let us assume that $x_1 > 0$. Then check that the sequence is increasing. Show that

$$x_n \geq x_1 \prod_{i=2}^{n} \left(1 + \frac{\theta}{ri}\right)$$

and prove that $\lim_{n\to\infty} x_n = \infty$.

Problem 34. Check when the solutions $N(t) \equiv 0$ and $N(t) \equiv K$ of the equation

$$N'(t) = \sigma\left(1 - \frac{1}{K}\int_0^{\infty} w(h)N(t-h)\,dh\right)N(t) \tag{23}$$

are asymptotically stable.

Problem 35. Check that if f and g are differentiable functions, $f(x)x > 0$ i $f^2(x) - g^2(x) > 0$ for $x \not\equiv 0$ and $\liminf_{|x|\to\infty} |f(x)| > 0$, then the zero solution of the equation

$$x'(t) = -f\big(x(t)\big) + g\big(x(t-h)\big)$$

is globally stable.

Hint. The Lapunov functional is given by the formula

$$V(\varphi) = F(\varphi(0)) + \frac{1}{2}\int_{-h}^{0} f^2\varphi(r))\,dr,$$

where $F(x) = \int_0^x f(r)\,dr$.

Problem 36. Solve the equation

$$\frac{\partial u}{\partial t} + \frac{\partial}{\partial x}(xu) = -\mu(x)u \tag{24}$$

with the initial condtion $u(0,x) = u_0(x)$ for $x \geq 0$.
Hint. For each $c \geq 0$ we define the function $\varphi_c(t) = u(t, ce^t)$. Check that

$$\varphi_c'(t) = -(1 + \mu(ce^t))\varphi_c(t)$$

and solve this equation. Check that $\varphi_c(0) = u_0(c)$. Observe that if $c = xe^{-t}$ then $u(t,x) = \varphi_c(t)$.

Problem 37. Solve the equation

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u \tag{25}$$

with the initial condtion $u(0,a) = u_0(a)$ for $a \geq 0$ and the boundary condition $u(t,0) = \psi(t)$ for $t \geq 0$.
Hint. For each $c \in \mathbb{R}$ we define the function $\varphi_c(t) = u(t, c+t)$. Check that

$$\varphi_c'(t) = -\varphi_c(t)$$

and solve this equation. Check that $\varphi_c(0) = u_0(c)$ if $c \geq 0$ and $\varphi_c(-c) = \psi(-c)$ for $c < 0$. Then give the formula for $u(t,x)$ using the function $\varphi_c(t)$.

Problem 38. Consider the McKendrick's model:

$$\begin{aligned}
&\frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu(a)u(t,a),\\
&u(t,0) = 2\int_0^\infty u(t,a)b(a),\, da\\
&u(0,a) = u_0(a).
\end{aligned}$$

Check that the function $u(t,0)$ satisfies the following integral equation

$$\begin{aligned}
u(t,0) = &\int_0^t b(a)u(t-a,0)\exp\Big\{-\int_0^a \mu(s)\,ds\Big\}\,da\\
&+\int_t^\infty b(a)u_0(a-t)\exp\Big\{-\int_{a-t}^a \mu(s)\,ds\Big\}\,da.
\end{aligned}$$

Hint. Apply the result from the problem 37.

Problem 39. Consider the McKendrick's model with coefficients independent of t. Give a biological interpretation of the constant

$$R = \int_0^{a_m} b(a)\exp\Big\{-\int_0^a \mu(s)\,ds\Big\}\,da. \tag{26}$$

What is the influence of the constant R on the relation between the stationary age profile $p_*(a)$ and the survival function $\Phi(a)$.

Problem 40. Consider the McKendrick's model with a constant death rate μ. Find the survival function $\Phi(a)$.

Problem 41. Consider the McKendrick's model with the death rate $\mu = \gamma$, where $\gamma > 0$ is a constant. Find the survival function $\Phi(a)$.

Problem 42. Consider the McKendrick's model with the death rate μ which satisfies the differential equation $\mu'(a) = \alpha\mu(a)$, where $\alpha > 0$ Find the survival function $\Phi(a)$.