

**Problem set 1**  
for February 10, 23.59, 2023

**Problem 1, Time delayed model with Allee effect [6p]** It is well-known that individuals in many biological populations suffer from a reduced capacity to reproduce or survive when the population density (that is, size) is small. As a consequence, the population may experience extinction depending on its density. This effect is known as Allee effect [W. C. Allee et al. Principles of animal ecology (1949)]. The Allee effect can arise due to several different mechanisms, such as difficulty of finding a mate, inefficient antipredator strategies in small groups of prey (due to reduced cooperation) etc. Mechanisms that allow for the Allee effect to appear (for example reduced cooperation) are often time delayed. Denoting the population size by  $N$ , a time-delayed growth with Allee effect can be modelled as follows:

$$\dot{N}(t) = rN(t) \left( 1 - \frac{N(t-T)}{K} \right) \left( \frac{N(t)}{A} - 1 \right). \quad (1)$$

Here  $T$  is a time-delay parameter. Your task is to analyse how the dynamics in this model depends on the time-delay parameter  $T$ . Solve Eq. (1) numerically by either writing your own solver, or using a solver from scientific software such as Mathematica or Matlab. Integrate Eq. (1) for  $T = 0.1, 0.2, \dots$ , up to 5. Set the remaining parameters to:  $A = 20$ ,  $K = 100$ ,  $r = 0.1$ , and  $N_0 = 50$  (where  $N_0$  denotes the population size at time  $t = 0$ ). Assume further that during the time interval  $[-T, 0]$  the population size was constant and equal to  $N_0$ .

- a) Show examples of the different dynamics obtained in this model: no oscillations, damped oscillations, and stable oscillations (limit cycle).
- b) Estimate numerically the value of  $T$  at which the dynamics starts exhibiting damped oscillations.
- c) Estimate numerically the value of  $T$  (denoted by  $T_H$ ) at which a bifurcation (Hopf bifurcation) occurs.
- d) Use linear stability analysis to analytically compute the value of  $T_H$ . Do this by linearising Eq. (1) around the steady state  $N^* = K$  and use a perturbation that is proportional to  $\exp(\lambda t)$ . Compare  $T_H$  that you obtain analytically to the estimate found in subtask c). Discuss your results.

**Problem 2, Discrete growth models [5p]** Assume that the population size  $N_\tau$  depends on discrete time ( $\tau = 0, 1, 2, \dots$ ) as follows

$$N_{\tau+1} = \frac{(r+1)N_\tau}{1 + \left(\frac{N_\tau}{K}\right)^b}. \quad (2)$$

Here, the parameters satisfy:  $K > 0$ ,  $r > 0$ , and  $b \geq 1$ .

- a) Analytically determine the non-negative steady states of the model (2).
- b) Perform linear stability analysis and discuss how the linear stability of the non-negative steady states depends on the parameters.
- c) Analytically find all conditions on the parameters (within their ranges of validity) where a bifurcation from a stable steady state to an unstable steady state occurs.

In the following, use the parameter values:  $K = 10^3$ ,  $r = 0.1$  and  $b = 1$ .

- d) Investigate how the population size depends on time for the following values of the initial population size:  $N_0 = 1, 2, 3$  and  $10$ . For each case, use the linear stability analysis performed in task b) to approximate the population dynamics in the vicinity of the unstable steady state. [Hint: treat the initial condition as a small perturbation around the unstable steady state, and plot how this perturbation, and consequently the population size, is expected to change over time according to the linear stability analysis.] Plot this approximation together with the corresponding (exact) population dynamics obtained by iterating Eq. (2). Use log-log scale for plotting to distinguish well between the different curves.
- e) Discuss how well the stability analysis approximates the exact dynamics. How does the initial condition influence the approximation?
- f) Use linear stability analysis to approximate the dynamics in the vicinity of the stable steady state. Use initial population size  $N_0 = N^* + \delta N_0$ , where  $N^*$  is the value of the stable steady state and  $\delta N_0$  is an initial perturbation around  $N^*$ . Choose  $\delta N_0 = -10, -3, -2, -1, 1, 2, 3$  and  $10$ . Proceed as follows. Starting from an initial perturbation  $\delta N_0$ , approximate the dynamics until the system comes close to  $N^*$  using the linear stability analysis around the stable steady state. Plot this approximation together with the exact dynamics, starting at  $N_0$ . Perform the approximation for the different values of the initial perturbation  $\delta N_0$ . How does the initial perturbation influence the approximation?

**Problem 3, A route to chaos [5p]** The dynamics of a population with adults cannibalising on their offspring can be described by the Ricker map [W. E. Ricker, J. Fish. Res. Board. Can. **11**, 559-623 (1954)]:

$$\eta_{\tau+1} = R\eta_{\tau}e^{-\alpha\eta_{\tau}},$$

where  $\eta_{\tau}$  denotes the number of adults in generation  $\tau = 0, 1, 2, \dots$ ,  $R$  is related to the number of offspring produced by each adult and  $\alpha$  is the incidence rate of cannibalism. The factor  $e^{-\alpha\eta_{\tau}}$  describes the probability of offspring survival to maturity. In this task you will analyse the stability of the steady states of the Ricker map as a function of the parameter  $R$  for  $\alpha = 0.01$  and  $\eta_0 = 900$ .

- a) Assume that  $R$  takes the values from 1 to 30 in steps of 0.1 and plot the bifurcation diagram of  $\eta$  against  $R$  as follows. For each value of  $R$ , run the model for 300 generations and plot the last 100 values of  $\eta_{\tau}$  versus the value of  $R$ . The final plot should show the results for all values of  $R$  tested. Describe the result.
- b) Plot the population dynamics  $\eta_{\tau}$  versus  $\tau$  (where  $\tau = 0, \dots, 40$ ) for four values of  $R$ . Choose four representative values of  $R$  where  $\eta_{\tau}$  has a stable fixed point, a 2-point cycle, a 3-point cycle, and a 4-point cycle. Describe the dynamics observed for the four values of  $R$ .
- c) Numerically investigate at which value  $R_1$  of  $R$  does the population dynamics bifurcate from a stable equilibrium to a stable 2-point cycle? At which value  $R_2$  does the dynamics bifurcate to a stable 4-point cycle?
- d) By making zooms and refining the  $R$ -grid, make a rough estimate of  $R_{\infty}$ , the first parameter value where the period-doubling bifurcation has repeated an infinite number of times. Explain how you come to this estimate of  $R_{\infty}$ .