Prof. Dr. Joachim Krug
Alexander Klug
Benjamin Schmiegelt
Suman G. Das

Summer term 2021

Biological Physics II

Problem Set 4

Please hand in your solutions before 12:00 noon on Wednesday, June 9, 2021.

1. The Ricker Model

4+6+3+6+6+5 = 30 pts

The Ricker Model can be used to model population dynamics with discrete generations[1]. It is defined as an iterated map:

$$N_{t+1} = N_t e^{r\left(1-\frac{N_t}{K}\right)}, \tag{1.1}$$

where $N_t \geq 0$ is the population at time (generation) t. The parameters r and K are positive.

a) Find a transformation that reduces the above equation to

$$x_{t+1} = x_t e^{r(1-x_t)}, \tag{1.2}$$

where $x_t \geq 0$. The equation has a trivial fixed point at $x = 0$. Show that it is unstable. Find the non-trivial fixed point x^* (there is only one). By linear stability analysis, find the thresholds r_l and r_u such that x^* is stable for $r_l < r < r_u$.

b) Consider the quantity $V_t = (x_t - x^*)^2$. Show that $V_{t+1} \leq V_t$ in the stability range of x^*. When is the equality achieved? Use these properties of the function to argue that the non-trivial fixed point is in fact the only attractor in the system in its stability range. For $r = 1$ and starting from $x_0 = 0.2$, numerically generate and plot V_t for long enough time to clearly see its asymptotic behavior. Also plot x_t over the same time range.

c) For $r = 1$ and starting at $x_0 \simeq 0.2$, sketch (by hand) the cobweb plot for the dynamics and compare it with your simulation results in the previous part.

d) Write down the expression for the twice iterated map, $g(x) = f(f(x))$, where $f(x) = xe^{r(1-x)}$ is the Ricker map in (1.2). Note that $x = 0$ and $x = x^*$ must always be fixed points of $g(x)$. Slightly above r_u, x^* is no longer a stable fixed point of the Ricker map and a stable 2-cycle emerges, i.e in steady state the system oscillates between two values x_1 and x_2. For $r = 2.4$, numerically plot the function $x - g(x)$ and from it determine x_1 and x_2 approximately. Now simulate (1.2) for $r = 2.4$ starting from a generic initial condition and plot x_t in the steady state. Check if your simulation result is consistent with the values of x_1 and x_2 you found.

[1] See (1) Ricker, William Edwin. "Stock and recruitment." Journal of the Fisheries Board of Canada 11.5 (1954): 559-623, and (2) May, Robert M. "Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos." Science 186.4164 (1974): 645-647.

e) The Ricker map shows a period doubling route to chaos, i.e as r is increased, a stable fixed point gives way to a stable 2-cycle, which is followed by a stable 4-cycle, followed by a stable 8-cycle and so on till the behavior becomes chaotic at some finite r. A good way to visualise this is through the *bifurcation diagram*[2], which plots the asymptotically visited values of x as a function of r. Numerically plot the bifurcation diagram for the Ricker map between $r = 1.8$ and $r = 3.0$. Based on the data generated for this plot, estimate the range of r over which the 2-cycle is stable, and the smallest value of r at which the system exhibits chaotic behavior.

f) Define the constants

$$\delta_n = \frac{r_{n+1} - r_n}{r_{n+2} - r_{n+1}},$$

where r_n is the value of r at which the n-th period doubling occurs. For example, r_1 is the lowest value of r at which the 2-cycle occurs. Further, define $\delta = \lim_{n\to\infty} \delta_n$. Plot δ_n for $n = 1, 2, 3, 4, 5$ using the data from the previous part. (Hint: If necessary, generate the bifurcation diagram with higher resolution on the r-axis.) It can be shown that δ is the so-called Feigenbaum constant, with the value $\delta \simeq 4.669$. Does your curve for δ_n approach this value?

[2] See Wikipedia for some examples: https://en.wikipedia.org/wiki/Bifurcation_diagram.