Introduction to Mathematical Biology
Exercises 2.1-2.5

2.1 *Logistic population growth.* (a) Solve the ODE of logistic population growth,

$$\frac{dN}{dt} = r_0\left(1 - \frac{N(t)}{K}\right)N(t) \tag{1}$$

given the initial condition $N(0) = N_0 > 0$.
(b) Assume $r_0 > 0$. Verify that $\lim_{t->\infty} N(t) = K$, i.e., that all orbits starting from a positive initial population size converge to the carrying capacity (K is globally stable).
(c) Suppose that we measure population size at discrete time steps, $T = 0, 1, 2, ...$, with τ time elapsed between each step (e.g. yearly census, τ =1 year) and let $N_T = N(T\tau)$. Show that if the population grows according to the logistic equation in (1), then the map $N_T \mapsto N_{T+1}$ is given by

$$N_{T+1} = \frac{\lambda N_T}{1 + \alpha N_T} \tag{2}$$

and express the new parameters λ, α with r_0, K, and τ. The discrete-time model in (2) is known as the *Beverton-Holt-model*.

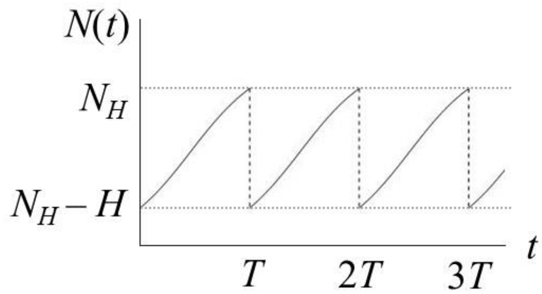
2.2 *Aggressive interactions.* Suppose that an animal has a constant *per capita* birth rate b and a constant natural death rate $\mu < b$. The individuals encounter each other at rate β according to mass action, and upon encounter, the two animals engage in a fight. When fighting, an individual gets killed with probability p. Construct a model for the dynamics of this population. Show that the model can be rewritten in the standard form of the logistic equation, and give the parameters of the logistic equation, r_0 and K, in terms of the original parameters b, μ, β, and p.

2.3 *Harvested logistic.* Find the optimal harvesting effort in the harvested logistic model,

$$\frac{dN}{dt} = r_0 N(t)\left(1 - \frac{N(t)}{K}\right) - \beta E N(t) \tag{3}$$

i.e., find the value of E such that the harvest per unit of time, βEN, is maximal at equilibrium. Show that with this optimal harvesting strategy, the equilibrium population density is $\hat{N} = K/2$. Explain verbally why one should keep the population at half the carrying capacity in order to achieve the maximal harvest.

2.4 *Optimizing fisheries with periodical removal.* Suppose a population of fish follows the logistic equation of population growth, except that after every time period T, we instantaneously remove H individuals (see figure below). For the management to be sustainable, we require the number of fish to be the same after each removal. This requirement determines H given the population size N_H where we harvest (see figure).



(a) For a given value of T, determine at which population size N_H we should harvest in order to maximize the number of harvested fish, H.
(b) Show that given the optimal harvesting strategy found in (a), the harvest obtained per unit of time, H/T, is a decreasing function of T (i.e., the more frequently we harvest, the better). Explain verbally why this is so (exercise 2.3 may give a hint).

2.5 *Fisheries with fixed quota.* A fishery might follow the simple rule "harvest H fish every day", with H an arbitrary constant. It is tempting to model this situation with the equation

$$\frac{dN}{dt} = r_0\left(1 - \frac{N(t)}{K}\right)N(t) - H$$

where the last term is the constant removal of H fish/day. (The difference from exercise 2.4 is that here we model removal as a process continuous in time, so that H is not a number but a rate; and H is an arbitrary constant, not determined by sustainability as in exercise 2.4.)
(a) $N = 0$ is not an equilibrium of this model; why? Does the model correctly describe any biological situation? Amend the model if necessary, while keeping it as close to the above as possible.
(b) Find the equilibria of the (amended) model and establish their stability. Does this model exhibit an Allee effect?
(c) Find the critical value of H above which the population cannot be maintained. Compare with exercise 2.3 (where the removal is $H = \beta EN$, E taking its optimal value and N the corresponding equilibrium value). In exercise 2.3, the harvested population is logistic, and therefore its nontrivial equilibrium, when positive, is stable. Explain the difference from the present model of a fixed quota.