Introduction to Mathematical Biology
Exercises 6.1-6.5

6.1. *Undercompensation.* A discrete-time population model $N_{t+1} = F(N_t)$ is said to be undercompensating if F is a monotonically increasing function. The opposite case is overcompensation, when F is decreasing in some interval(s); in the latter case, starting from a larger population can result in a smaller population a year later.

(a) Show that an undercompensating model may not have a period-doubling bifurcation.
(b) Which of the three discrete-time population models discussed in the lecture (Beverton-Holt, Ricker, Skellam) is undercompensating?
(c) For the undercompensating models in (b), show that the nontrivial equilibrium is unique, and when positive, it is stable. Does this property hold for every undercompensating model? Or can you give an example with multiple equilibria (e.g. with an Allee effect)?

6.2. *The Ricker model.* Find the biologically relevant equilibria of the Ricker model

$$N_{t+1} = bN_t \exp(-aN_t)$$

Find the conditions under which these equilibria are asymptotically stable, and determine which type of bifurcation happens when the equilibrium loses its stability.

Optional: Obtain the bifurcation diagram of the Ricker model numerically, by iterating the dynamics and plotting the points of the attractor (the values that the iteration visits for high t, when the transient is over). To reduce the number of parameters to one, write $x_t = aN_t$, $x_{t+1} = bx_t \exp(-x_t)$ and investigate the attractor of x_t for different values of b (from x_t the dynamics of N_t follows trivially).

6.3 *The Ricker model as a model of cannibalistic fish.* Fish species are often cannibalistic, i.e., the adults feed on the juveniles (whereas the juveniles feed on plankton). Suppose that the juveniles are vulnerable to cannibalism for one year, after which they mature and are added to the adult population. Let N_t denote the number of adults at the beginning of year t, and let $x(\tau)$ and $n(\tau)$ denote respectively the number of juveniles and adults at time τ within the year, $0 \le \tau \le 1$. Reproduction occurs only at the beginning of each year in a discrete pulse, when each adult produces B juveniles, and hence the year starts with $x(0) = BN_t$ juveniles and $n(0) = N_t$ adults. The adults die at a time-variable rate $\delta(\tau)$. The juveniles die a natural death at a rate $\mu(\tau)$ and also die due to cannibalism at a rate $cn(\tau)$ (cannibalism follows mass action). This results in the within-year dynamics

$$\begin{aligned}\frac{dn(\tau)}{d\tau} &= -\delta(\tau)n(\tau) \\ \frac{dx(\tau)}{d\tau} &= -[\mu(\tau) + cn(\tau)]x(\tau)\end{aligned}$$

for $0 \leq \tau \leq 1$. At the beginning of the next year, the number of adults is the number of adults surviving from the previous year plus the number of surviving juveniles who now mature, i.e., $N_{t+1} = x(1) + n(1)$.

(a) Derive F that maps N_t into N_{t+1}.
(b) Investigate under which conditions we recover the Ricker map, $F(N) = bNe^{-aN}$.
(c) Assume that δ and μ are constants, and determine the conditions under which the model has a stable positive equilibrium. Suppose the adult mortality rate δ increases; will this stabilize or destabilize the nontrivial equilibrium, or have no effect?

6.4 *Optimization with cyclic dynamics.* Consider the discrete-time population model with k strains

$$N_{t+1}^{(i)} = \lambda_i(N_t)N_t^{(i)}$$

where $N_t^{(i)}$ is the population size of strain i, $\lambda_i(N_t)$ is its density-dependent annual growth rate, and $N_t = \sum_{j=1}^{k} N_t^{(j)}$ is total population size in year t. Suppose that $\lambda_i(N_t)$ can be factored into $\lambda_i(N_t) = \tilde{\lambda}_i \cdot f(N_t)$, i.e., it is the product of a strain-dependent factor $\tilde{\lambda}_i$ and a density-dependent factor $f(N_t)$. Show that generically only one strain can remain in this system, even if it exhibits cycles of arbitrary (finite) length.

6.5. *Iteroparity vs semelparity.* Some organisms reproduce repeatedly over their life (these are called iteroparous) whereas others reproduce only once (these are semelparous, like many insects and the annual plants). Consider a population with the annual growth rate

$$\lambda(n, N) = [ns + p(n)]f(N)$$

where n is fecundity, the number of offspring produced in one breeding season; $sf(N)$ is the probability of survival of each offspring; and $p(n)f(N)$ is the probability of survival of the parent till the next year. Both probabilities decrease with increasing population size (through the function f), and this regulates the size of the population (prevents exponential growth). If we assume that the offspring are mature adults when they are one year old, then we obtain the discrete-time model $N_{t+1} = \lambda(n, N_t)N_t$.

Different variants of this organism have different fecundity n and therefore also different probability of parental survival. p is assumed to decrease with increasing n because producing more offspring is only possible if the parent invests more of her resources into reproduction, whereby her own survival probability decreases (this trade-off is also called the "cost of reproduction"). It is reasonable to assume that there exists a positive value n_m at which all resources are used for the offspring such that $p(n_m) = 0$, and this marks the maximum number of offspring possible. Find the conditions under which this model (i) predicts an optimal fecundity n^* at which $p(n^*) > 0$ (iteroparity) and (ii) predicts that the parent should invest all her resources into the offspring, i.e., the optimal number of offspring is n_m and the parent does not survive (semelparity).