Introduction to Mathematical Biology
Exercises 9.1-9.5

9.1. *Coexistence of year classes in semelparous populations with density-dependent fecundity.* Consider a population of a biennial organism, i.e., one that lives for at most two years and reproduces only when 2 years old. Population density affects only the effective fecundity; hence we shall assume that survival from age 1 to age 2 is constant and the number of offspring produced per reproducing individual is a decreasing function of total population size, $N_1 + N_2$. The population therefore grows according to

$$\mathbf{N}(t+1) = \begin{pmatrix} 0 & F(N_1(t) + N_2(t)) \\ P & 0 \end{pmatrix} \mathbf{N}(t) \tag{1}$$

Let the density-dependent fecundity be given by $F(N) = \frac{a}{1+bN}$. We have seen in the lecture that whenever this population has a positive equilibrium vector $\hat{\mathbf{N}}$, this equilibrium is unstable.

A population of biennial organisms consists of two sub-populations or "year classes": one year class reproduces in odd years, the other reproduces in even years. If F were constant, the population growth of the two year classes would be independent of one another; but here the two year-classes interact via density-dependence ($F(N)$).

(a) Assume that the initial population consists of only one year class, i.e., the initial population vector is of the form $\mathbf{N}(0) = (N_1(0), 0)^T$. Show that this population converges to a 2-cycle such that in every odd year the population vector is $(0, \hat{N})^T$, whereas in every even year it is $(\hat{N}/P, 0)^T$. (*Hint:* use the second iterated map to show convergence.)

(b) Show that this population is stable against introducing the missing year class at a low density: An initial population $\mathbf{N}(0) = (\hat{N}/P, \epsilon)^T$ with sufficiently small ϵ will converge to the 2-cycle described above, so that it will lose the year class introduced at density ϵ. Explain verbally why the initially rare year class is excluded.

9.2. *An alternative model for the coexistence of year classes.* As an alternative to the model in equation (1) above, assume that fecundity at age 2 depends on the population density of the 2-year old individuals only. This is the case, for example, when biennial plants are limited by their pollinator insects: the 1-year old plants do not flower and hence do not compete for pollinators. The model then becomes

$$\mathbf{N}(t+1) = \begin{pmatrix} 0 & F(N_2(t)) \\ P & 0 \end{pmatrix} \mathbf{N}(t) \tag{2}$$

Assume $F(N) = \frac{a}{1+bN}$ as above.

(a) Carry out the invasion analysis as in part (b) of the previous exercise. Explain verbally why the result is different.

(b) Show that the nontrivial equilibrium of (2) is asymptotically stable whenever it is positive, so that in the present model, the two year classes coexist at a stable equilibrium.

9.3. *R_0 in a size-structured population.*
(a) To derive R_0 in a population structured by body size, we first build a simple model for how the body size of an individual grows during its lifetime. Let $x(a)$ denote the length of the body at age a, with length at birth $x(0) = x_0$ given. We assume that the shape of the body remains the same, so that the organism's surface is given by $S(a) = c[x(a)]^2$ and its mass (proportional to volume) is $M(a) = \gamma[x(a)]^3$ at all ages. Suppose the food an individual obtains is proportional to its surface, whereas the amount of resources used for self-maintenance and reproduction is proportional to its mass. This yields a differential equation for mass,

$$\frac{dM}{da} = \alpha S(a) - \nu M(a)$$

Show that the length at age a is given by the *Von Bertalanffy equation* for body size,

$$x(a) = x_\infty - e^{-(\nu/3)a}(x_\infty - x_0)$$

where $x_\infty = \lim_{a\to\infty} x(a)$ is the asymptotic size to be determined from the parameters above.

(b) Assume that the birth rate is proportional to body size ($b(x) = \beta x$) and the death rate is constant (μ). Calculate R_0. (It would be more realistic to assume that the birth rate is proportional to body mass, not length; this results in a lengthier integral.)

9.4. *R_0 with stochastic growth of body size.* Extend the previous exercise assuming that at birth, each individual gets a random environment ξ (e.g. a territory of variable quality). The distribution of ξ is given by the probability density function f such that ξ takes a value between $\bar{\xi}$ and $\bar{\xi} + d\xi$ with probability $f(\bar{\xi})d\xi$. An individual's environment remains fixed for life and determines the food intake per unit surface, i.e., α in the above model becomes a function of ξ.

(a) Calculate R_0. (*Important hint:* Because the environment is fixed for life, there is a shortcut to spare the calculation of $\mathcal{F}(x, a)$.)

(b) Optional: Express $\mathcal{F}(x,a)$ (see lecture).

9.5. *A model with discrete time and continuous structure.* Consider a population where spatial location x determines the effective fecundity $F(x)$ and the probability that an adult survives till the next year, $P(x)$. For simplicity, we take a 1-dimensional physical space so that $x \in \mathbb{R}$. The offspring are dispersed around the location of their parent, so that an offspring of a parent at x lands at a location between ξ and $\xi + d\xi$ with probability $\phi(\xi - x)d\xi$. The adults are sessile (do not move). Let $N_t(x)$ be the population's density function in year t just before reproduction.

(a) Express $N_{t+1}(x)$.
(b) Extend this model to a population which has also age structure, such that a k-year old individual at location x has fecundity $F_k(x)$ and survival probability $P_k(x)$.

+1. *Stability conditions for* 2×2 *Jacobians.* For a 2×2 Jacobian, the characteristic equation is $\lambda^2 - \mathrm{tr}\,\lambda + \det = 0$ (where tr and det are respectively the trace and the determinant of the Jacobian). Find the pairs $(\mathrm{tr}, \det)$ for which the Jacobian has a complex conjugate pair of eigenvalues with absolute value 1 ($\lambda_{1,2} = e^{\pm i\phi}$). This completes the derivation of the "triangle of stability" we discussed in the lecture.