INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

September 26, 2016

Exercise 2.1

(a) We can solve the logistic equation by separation of variables:

$$\int_{N_0}^{N(t)} \frac{dN}{\left(1 - \frac{N}{K}\right) N} = \int_0^t r_0 ds \tag{1}$$

By solving the integral at the left-hand side, we obtain the explicit solution

$$N(t) = \frac{KN_0}{N_0(1 - e^{-r_0 t}) + Ke^{-r_0 t}}.$$

Remark: instead of using separation of variables, you can use the change of variable $x = K/N$ and solve the equivalent linear equation for x by using the variation of constants formula.

(b) Assume $r_0 > 0$. Then, by taking the limit $t \to \infty$, we easily obtain

$$\lim_{t \to \infty} N(t) = K$$

for any initial value N_0. Hence K is *globally* stable.

(c) Let $N_T = N(T\tau)$. Since the logistic equation is autonomous, the initial time does not matter, but only the initial value. Hence, to get the value N_{T+1} we can use the explicit solution (1) for $t = \tau$ and $N_0 = N_T$, and rearrange the terms:

$$\begin{aligned} N_{T+1} &= \frac{KN_T}{N_T(1 - e^{-r_0\tau}) + Ke^{-r_0\tau}} \\ &= \frac{e^{r_0\tau} N_T}{1 + \frac{1}{K}(e^{r_0\tau} - 1)N_T} \\ &= \frac{\lambda N_T}{1 + \alpha N_T} \end{aligned}$$

with

$$\lambda = e^{r_0\tau}, \qquad \alpha = \frac{e^{r_0\tau} - 1}{K}.$$

Exercise 2.2

Given the rates, we can write the following ODE model for the density N of individuals:

$$
\begin{aligned}
\frac{\mathrm{d}N}{\mathrm{d}t} &= bN - \mu N - p\beta N^2 \\
&= (b-\mu)\left(1 - \frac{N}{\frac{b-\mu}{p\beta}}\right) N
\end{aligned}
$$

hence it is in the standard form of the logistic equation, with

$$r_0 = b - \mu, \quad K = \frac{b-\mu}{p\beta}.$$

Exercise 2.3

The nontrivial equilibrium is

$$\hat{N} = K - \frac{K\beta}{r_0} E.$$

Denote

$$h(E) = \beta \hat{N} E = \beta K E - \frac{K\beta^2 E^2}{r_0}.$$

the harvest rate at equilibrium. We notice that $h(E)$ is a parabola which attains its maximum at $E^* = \frac{r_0}{2\beta}$. The equilibrium value corresponding to E^* is

$$\hat{N}^* = K - \frac{K\beta}{r_0}\frac{r_0}{2\beta} = \frac{K}{2}.$$

Intuitively, you should keep the population at the value $K/2$ because this is the value at which the growth rate of the population is maximal.

Finally, notice that

$$\hat{H}^* = \beta \hat{N}^* E^* = \frac{K r_0}{4}.$$

Exercise 2.4

We use the explicit solution (1) calculated in Exercise 2.1, with initial value $N_H - H$ up to time $t = T$

$$N(T) = \frac{K(N_H - H)}{(N_H - H)(1 - e^{-r_0 T}) + K e^{-r_0 T}}$$

Then, we impose that $N(T) = N_H$ and we solve for H as a function of T and N_H (you can also directly use the calculation for the Beverton-Holt model of Exercise 2.1(c)).

We obtain

$$
\begin{aligned}
H &= \frac{N_H(K - N_H)(1 - e^{-r_0 T})}{K - N_H(1 - e^{-r_0 T})} \\
&= N_H - \frac{N_H K e^{-r_0 T}}{K - N_H(1 - e^{-r_0 T})} =: h(N_H)
\end{aligned}
$$

and we need to maximize h with respect to N_H.

In particular,

$$h'(N_H) = 1 - \frac{Ke^{-r_0 T}(K - N_H(1 - e^{-r_0 T})) + N_H K e^{-r_0 T}(1 - e^{-r_0 T})}{(K - N_H(1 - e^{-r_0 T}))^2}$$
$$= 1 - \frac{K^2 e^{-r_0 T}}{(K - N_H(1 - e^{-r_0 T}))^2}$$

and

$$h'(N_H^*) = 0 \Leftrightarrow (K - N_H(1 - e^{-r_0 T}))^2 = K^2 e^{-r_0 T}$$
$$\Leftrightarrow N_H^* = \frac{1 - e^{\frac{-r_0 T}{2}}}{1 - e^{-r_0 T}} K$$

and this is actually a maximum (check second derivative or sign of h').

The maximal harvest is

$$H^* = h(N_H^*) = N_H^* - \frac{N_H^* K e^{-r_0 T}}{K - N_H^*(1 - e^{-r_0 T})}$$
$$= \frac{1 - e^{\frac{-r_0 T}{2}}}{1 + e^{\frac{-r_0 T}{2}}} K$$

(b) We have

$$\frac{H^*}{T} = \frac{K}{T} \frac{1 - e^{\frac{-r_0 T}{2}}}{1 + e^{\frac{-r_0 T}{2}}}$$

We can now compute the derivative with respect to T:

$$\frac{d}{dt}\frac{H^*}{T} = \frac{K}{T} \frac{\frac{r_0}{2} e^{\frac{-r_0 T}{2}}(1 + e^{\frac{-r_0 T}{2}}) + (1 - e^{\frac{-r_0 T}{2}})\frac{r_0}{2} e^{\frac{-r_0 T}{2}}}{(1 + e^{\frac{-r_0 T}{2}})^2} - \frac{K}{T^2} \frac{1 - e^{\frac{-r_0 T}{2}}}{1 + e^{\frac{-r_0 T}{2}}}$$
$$= \frac{K}{T^2 (1 + e^{\frac{-r_0 T}{2}})^2} \left[e^{-r_0 T} + T r_0 e^{\frac{-r_0 T}{2}} - 1 \right]$$

Consider the function $g(x) = e^{-2x} + xe^{-x} - 1$. Then $g(0) = 0$ and

$$g'(x) = e^{-x}\left(1 - x - 2e^{-x}\right) < 0 \quad \text{for all } x \neq 0$$

hence we conclude that $\frac{d}{dt}\frac{H^*}{T} < 0$ for all $T > 0$ (i.e., is better to harvest often when the population has the highest growth rate).

Exercise 2.5

(a) The problem here is that we are assuming to harvest fish at a constant rate, even in the situation when there is no fish left. This translates into the fact that the mathematical model is not positivity preserving: it may predict negative population densities, which is clearly not biologically meaningful.

We can consider a model where we harvest at a constant rate $H > 0$ as long as the population density is positive, i.e.,

$$\text{harvest rate } h(N) = \begin{cases} H & \text{if } N > 0 \\ 0 & \text{if } N = 0. \end{cases}$$

and the ODE model is

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

(b) The equilibria are $N = 0$ and $N^* > 0$ such that

$$r_0 \left(1 - \frac{N^*}{K}\right) N^* - H = 0$$

(notice that we may have 0, 1, or 2 equilibria depending on the values of the parameters $r_0, K, H \rightarrow$ *fold bifurcation*).

The model exhibit Allee effect because the growth rate is negative close to $N = 0$.

(c) There exists a stable positive equilibrium if and only if

$$0 \leq H < H_{\text{cr}},$$

where

$$H_{\text{crit}} = \max_{N \geq 0} \left[r_0 \left(1 - \frac{N}{K}\right) N \right] = \frac{r_0 K}{4}$$

For $H \geq H_{\text{crit}}$, there exists no positive stable equilibrium and the population goes extinct.

Notice that the critical harvest rate H_{crit} coincides with the maximal harvest rate H^* of exercise 2.3, but now the harvest is constant independently of the population density (which is the mechanism leading to the extinction of the population), while in the previous exercise the harvest rate was relative to population size, allowing a positive stable equilibrium to occur.