INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

November 28, 2016

Exercise 9.1

(a) To compute the second iterated map for a generic vector $(N_1(t), N_2(t))^T$, we compute

$$\begin{aligned}
\mathbf{N}(t+1) &= \begin{pmatrix} 0 & F(N_1(t)+N_2(t)) \\ P & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix} = \begin{pmatrix} F(N_1(t)+N_2(t))N_2(t) \\ PN_1(t) \end{pmatrix} \\
\mathbf{N}(t+2) &= \begin{pmatrix} 0 & F(PN_1(t)+N_2(t)F(N_1(t)+N_2(t))) \\ P & 0 \end{pmatrix} \begin{pmatrix} F(N_1(t)+N_2(t))N_2(t) \\ PN_1(t) \end{pmatrix} \\
&= \begin{pmatrix} PF(PN_1(t)+N_2(t)F(N_1(t)+N_2(t)))N_1(t) \\ PF(N_1(t)+N_2(t))N_2(t) \end{pmatrix}
\end{aligned}$$

Hence, we can represent the second iterated map with the matrix

$$\mathbf{A}^{(2)}(N_1, N_2) = \begin{pmatrix} PF(PN_1+N_2F(N_1+N_2)) & 0 \\ 0 & PF(N_1+N_2) \end{pmatrix}$$

For an initial vector $\mathbf{N}(0) = (N_1(0), 0)^T$, the matrix reduces to

$$\mathbf{A}^{(2)}(N_1, 0) = \begin{pmatrix} PF(PN_1) & 0 \\ 0 & PF(N_1) \end{pmatrix} \tag{1}$$

Hence, every class evolves independently of the other and the second iterated map can be interpreted as a map for an unstructured population: defining $n(t) = N_1(t)$, we have

$$n(t+2) = F(Pn(t))Pn(t) = \frac{aPn(t)}{1+bPn(t)} =: f(n(t))$$

Let $\hat{n}$ such that $f(\hat{n}) = \hat{n}$, i.e.,

$$\hat{n} = \frac{aP-1}{bP}.$$

Notice that the equilibrium exists positive if and only if $aP > 1$. $\hat{n}$ is an equilibrium of the second iterated map, so it corresponds to a 2-year cycle of the population. We can prove that the 2-cycle is stable by considering the jacobian at $\hat{n}$:

$$f'(\hat{n}) = \frac{aP(1+bP\hat{n}) - abP^2\hat{n}}{(1+bP\hat{n})^2} = \frac{1}{aP}$$

Observe that $f'(\hat{n}) < 1$ whenever the equilibrium exists positive ($aP > 1$), hence we conclude its stability.

(b) In a stable population with density $(\hat{n}, 0)^T$ in even years, described by the second iterated map (1), we introduce some individuals with density ϵ in the empty year class. Notice that, since the original population is at equilibrium, its 2-years growth rate is equal to one: $PF(P\hat{n}) = 1$. The 2-years growth rate of the year class with density ϵ (obtained from (1)) is $PF(\hat{n} + \epsilon)$. Since $F(N)$ is a decreasing function of N we have

$$PF(\hat{n} + \epsilon) < PF(P\hat{n}) = 1,$$

hence the population with low density dies out. This happens because the alternative year class tries to reproduce in high-density years. So in the end there are two attractors, each year class alone is an attractor, and each makes high density in years it does not reproduce.

Exercise 9.2

(a) The second iterated map for a generic vector $(N_1(t), N_2(t))^T$ is now

$$\mathbf{A}^{(2)}(N_1, N_2) = \begin{pmatrix} PF(PN_1) & 0 \\ 0 & PF(N_2) \end{pmatrix}$$

For a stable population $(\hat{n}, 0)^T$, the 2-years growth rate is $PF(P\hat{n}) = 1$. The 2-years growth rate of the alternative year class introduced at low density $\epsilon \ll 1$ is

$$PF(\epsilon) > PF(P\hat{n}) = 1,$$

hence the new year class population invades (in this case, the low-density year class does not experience the competition from the stable population in its reproductive years).
(b) Consider the model

$$\begin{cases} N_1(t+1) = F(N_2(t))N_2(t) = \frac{aN_2(t)}{1+bN_2(t)} \\ N_2(t+1) = PN_1(t). \end{cases}$$

We calculate the equilibrium $(\hat{N}_1, \hat{N}_2)$:

$$\begin{cases} \hat{N}_1 = F(\hat{N}_2)\hat{N}_2 \\ \hat{N}_2 = P\hat{N}_1 \end{cases} \Leftrightarrow F(P\hat{N}_1) = 1 \Leftrightarrow \hat{N}_1 = \frac{a-1}{bP}, \quad \hat{N}_2 = \frac{a-1}{b}$$

which exists positive if and only if $a > 1$. The jacobian at equilibrium is

$$\mathbf{J} = \begin{pmatrix} 0 & \frac{a}{(1+b\hat{N}_2)^2} \\ P & 0 \end{pmatrix} = \begin{pmatrix} 0 & \frac{1}{a} \\ P & 0 \end{pmatrix}$$

The trace and determinant are

$$\text{tr}(\mathbf{J}) = 0, \qquad \det(\mathbf{J}) = -\frac{P}{a} > -P \geq -1,$$

and from the triangle of stability for discrete-time models we conclude that the equilibrium is always asymptotically stable when it is positive ($a > 1$).

Exercise 9.3

(a) We write the ODE for $x(a)$ from the ODE for $M(a) = \gamma x(a)^3$,

$$3\gamma x(a)^2 \frac{dx}{da} = \alpha c x(a)^2 - \nu\gamma x(a)^3$$
$$\Leftrightarrow \frac{dx}{da} = \frac{\alpha c}{3\gamma} - \frac{\nu}{3}x(a)$$

and we use the integrating factor $e^{\frac{\nu a}{3}}$ to solve the linear inhomogeneous ODE:

$$e^{\frac{\nu a}{3}}(\frac{dx}{da}(a) + \frac{\nu}{3}x(a)) = e^{\frac{\nu a}{3}}\frac{\alpha c}{3\gamma}$$
$$\frac{d}{da}\left(e^{\frac{\nu a}{3}}x(a)\right) = e^{\frac{\nu a}{3}}\frac{\alpha c}{3\gamma}$$
$$e^{\frac{\nu a}{3}}x(a) - x(0) = \frac{\alpha c}{\nu\gamma}(e^{\frac{\nu a}{3}} - 1)$$
$$x(a) = \frac{\alpha c}{\nu\gamma}(1 - e^{-\frac{\nu a}{3}}) + e^{-\frac{\nu a}{3}}x(0)$$

Finally, the thesis follows from the fact that

$$x_\infty := \lim_{a\to\infty} x(a) = \frac{\alpha c}{\nu\gamma}.$$

(b) The survival probability up to age a of an individual with constant death rate μ and having size y at age a is $\mathcal{F}(y,a) = \ell(a)\delta(y - x(a)) = e^{-\mu a}\delta(y - x(a))$. Hence, the expected number of offspring in a lifetime of an individual with birth rate $b(x) = \beta x$ is

$$\begin{aligned} R_0 &= \int_0^\infty b(x(a))\ell(a)da \\ &= \int_0^\infty \beta x(a)e^{-\mu a}da \\ &= \int_0^\infty \beta[x_\infty - e^{-\frac{\nu a}{3}}(x_\infty - x_0)]e^{-\mu a}da \\ &= \frac{\beta x_\infty}{\mu} - \frac{\beta(x_\infty - x_0)}{\mu + \nu/3} \end{aligned}$$

Exercise 9.4

(a) With stochasticity, the size of an individual depends on the environment:

$$x(a;\xi) = x_\infty(\xi) - e^{-\frac{\nu a}{3}}(x_\infty(\xi) - x_0) \tag{2}$$

where $x_\infty(\xi) = c\alpha(\xi)/\nu\gamma$. Since the environment is fixed for life, we can compute R_0 for an individual born in environment ξ as done in Exercise 9.3:

$$R_0(\xi) = \frac{\beta x_\infty(\xi)}{\mu} - \frac{\beta(x_\infty(\xi) - x_0)}{\mu + \nu/3}.$$

Then, R_0 is the average value

$$\overline{R}_0 = \int_\Xi f(\xi)R_0(\xi)d\xi.$$

(b) $\mathcal{F}(x,a)dx$ is given by the survival probability $e^{-\mu a}$ up to age a times the probability of having size in $(x, x+dx)$ at age a. We should now translate the condition of the size being in $(x, x+dx)$ with the condition of the environment being in $(\xi, \xi+d\xi)$.

The size at age a is in equal to x if and only if

$$
\begin{aligned}
x &= x_\infty(\xi) - e^{-\frac{\nu a}{3}}(x_\infty(\xi) - x_0) \\
\Leftrightarrow \quad x_\infty(\xi) &= \frac{x - e^{-\frac{\nu a}{3}} x_0}{1 - e^{-\frac{\nu a}{3}}} \\
\Leftrightarrow \quad \alpha(\xi) &= \frac{\nu\gamma}{c} \frac{x - e^{-\frac{\nu a}{3}} x_0}{1 - e^{-\frac{\nu a}{3}}} \\
\Leftrightarrow \quad \xi &= \alpha^{-1}\left(\frac{\nu\gamma}{c} \frac{x - e^{-\frac{\nu a}{3}} x_0}{1 - e^{-\frac{\nu a}{3}}}\right) =: \xi(x) \qquad (3)
\end{aligned}
$$

Moreover, the following relation holds between the differential elements dx and $d\xi$:

$$
\begin{aligned}
dx &= x'(\xi)d\xi = \frac{c\alpha'(\xi)}{\nu\gamma}(1 - e^{-\frac{\nu a}{3}})d\xi \\
\Leftrightarrow \quad d\xi &= \frac{\nu\gamma}{c\alpha'(\xi(x))} \frac{1}{(1 - e^{-\frac{\nu a}{3}})} dx
\end{aligned}
$$

Hence, we can write

$$
\begin{aligned}
\mathcal{F}(x,a)dx &= e^{-\mu a} f(\xi) d\xi \\
&= e^{-\mu a} f(\xi(x)) \frac{\nu\gamma}{c\alpha'(\xi(x))} \frac{1}{(1 - e^{-\frac{\nu a}{3}})} dx
\end{aligned}
$$

where $\xi(x)$ is defined in (3).

Exercise 9.5

(a) The individuals at time $t+1$ at location x are given by the adult individuals of the previous year, plus the offspring coming from the other points in space:

$$
N_{t+1}(x) = P(x)N_t(x) + \int_{-\infty}^{+\infty} N_t(\xi)F(\xi)\phi(x-\xi)d\xi.
$$

(b) We include age structure: $N_t(x,k)$ is the density of individuals of age k at location x in year t. Hence

$$
\begin{aligned}
N_{t+1}(x,1) &= \sum_{j=1}^{\infty} \int_{-\infty}^{+\infty} N_t(\xi, j)F_j(\xi)\phi(x-\xi)d\xi, \\
N_{t+1}(x,k+1) &= P_k(x)N_t(x,k), \qquad k \geq 1
\end{aligned}
$$