Homework 3

Due Friday, July 14 2017

Problem 1 (10 points)

The Beverton-Holt difference equation is given by

$$N_{t+1} = \frac{rKN_t}{K + (r-1)N_t}, \tag{1}$$

is widely used in the model of fisheries. Here, N_t is the population density of fish at time t and $r > 1$ is the "inherent growth rate" of the population and $K > 0$ is the carrying capacity.

(a) Find all the equilibria of this model and determine their stability. (You may want to use graphical approaches to check your results, but you should determine stability analytically.)

(b) Make the substitution $x_t = 1/N_t$ and show that this is a linear, inhomogeneous difference equation. Use this to find an explicit formula for N_t in terms of only r, K and N_0. Compare this solution to that of the logistic equation from homework 2.

(c) Now let $\mu = (r-1)/r$ and show that equation (1) can be rewritten as

$$N_{t+1} - N_t = \mu N_{t+1}\left(1 - \frac{N_t}{K}\right). \tag{2}$$

Use this to explain why the Beverton-Holt model is an approximation of the logistic equation.

Problem 2 (5 points)

The Ricker model is another difference equation used widely in fisheries biology. It is given by

$$N_{t+1} = N_t e^{r[1-N_t/K]}, \tag{3}$$

where N_t is the population density of fish at time t and r is the per capita growth rate and K is the carrying capacity. Find the fixed points of this map and determine their stability analytically. Draw a cobweb diagram for this map with a reasonable choice of r and N_0.

Problem 3 (15 points)

We proposed using the logistic map

$$x_{t+1} = \mu x_t(1 - x_t) \tag{4}$$

as a model of eel population growth. We argued that the growth rate should depend on how crowded the population was at an earlier time, not just on how crowded it is now. By this argument, it would probably be more accurate to use the following model (known as the *lagged logistic map* or *delayed logistic map*):

$$x_{t+1} = \mu x_t(1 - x_{t-\tau}), \tag{5}$$

where τ is a positive integer. We can think of this model as saying that the population depends on both how large the population is now (x_t) and how large the population was τ years ago ($x_{t-\tau}$). This seems somewhat reasonable – the population right now tells us how many breeding adults there are, which we certainly need to take into account, and the population τ years ago influences how much competition there was when the current adults were growing. This model is reasonable if, for instance, juvenile nutrition has a substantial effect on breeding success later in life.

(a) Show that equation (5) has two equilibria at $x^* = 0$ and $x^* = 1 - 1/\mu$. Note that x^* is an equilibrium if $x_{t+1} = x_t = x_{t-\tau} = x^*$.

(b) To determine the stability of equilibria for a delay difference equation $x_{t+1} = f(x_t, x_{t-\tau})$, we first need to find the linearization of our map. For delay equations, this linearization is given by

$$x_{t+1} \approx \left.\frac{\partial f(x,y)}{\partial x}\right|_{x=y=x^*} x_t + \left.\frac{\partial f(x,y)}{\partial y}\right|_{x=y=x^*} x_{t-\tau}. \tag{6}$$

Show that the linearization about $x^* = 0$ is given by

$$x_{t+1} \approx \mu x_t, \tag{7}$$

and that the linearization about $x^* = 1 - 1/\mu$ is given by

$$x_{t+1} \approx x_t + (1-\mu)x_{t-\tau}. \tag{8}$$

(c) In order to solve the linearized equations you found in part (b), we will try solutions of the form $x_t = \lambda^t$. Show that there is only one such solution to (7) and find the value of λ. Show that there are $\tau + 1$ possible solutions (i.e., $\tau + 1$ values of λ) to (8) and that these solutions satisfy

$$\mu = \lambda^\tau (1 - \lambda) + 1. \tag{9}$$

(d) Show that if $\mu < 1$, there is only one positive real solution λ of equation (9), and that this λ is larger than 1. In addition, show that there are two positive real solutions to (9) if μ is slightly larger than 1, and that both solutions are smaller than 1. Finally, show that if μ is too large, then there are no positive real solutions to (9). You may use graphical arguments for this part – you do not need to calculate the values of λ analytically.

(e) We are interested in the onset of oscillatory behavior. The equilibrium $x^* = 1 - 1/\mu$ will become a spiral instead of a node when the positive, real solutions of (9) disappear. The critical value μ_o where this occurs is the maximum value of (8). Calculate μ_o by setting $\mathrm{d}\mu/\mathrm{d}\lambda = 0$. Show that μ_o is a decreasing function of τ and that

$$\lim_{\tau \to \infty} \mu_o(\tau) = 1. \tag{10}$$

This means that larger delays make it easier to produce oscillations.

Problem 4 (10 points)

Another way to introduce a delay to the logistic equation is to assume that the density at all times in the past influences the per capita growth rate, and to assign a weight κ to each past density. For instance, we can write

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx(t) \int_0^\infty \kappa(\tau)\,(1 - x(t-\tau))\,\mathrm{d}\tau, \tag{11}$$

with

$$\kappa(\tau) = \alpha e^{-\alpha\tau}, \tag{12}$$

for some constant $\alpha > 0$. To solve this equation, we need to give an initial condition x for all past times. That is, we need to specify some function $x_0(t)$ such that

$$x(t) = x_0(t) \text{ for all } t \leq 0. \tag{13}$$

Equation (11) is called a Volterra integrodefferential equation.

(a) Show that $x(t) = 0$ for all $-\infty < t < \infty$ is a solution to (11). Show that $x(t) = 1$ for all $-\infty < t < \infty$ is a solution to (11). This means that 0 and 1 are equilibria of this equation.

(b) The linearization of (11) about $x^* = 1$ is

$$\frac{\mathrm{d}x}{\mathrm{d}t} \approx -r \int_0^\infty \kappa(\tau) x(t - \tau)\, \mathrm{d}\tau. \tag{14}$$

Solve equation (14) by trying a solution of the form $x(t) = e^{\lambda t}$. (You do not need to worry about initial conditions.)

(c) The equilibrium $x^* = 1$ is called stable if every λ you found in part (b) has negative real part. Find conditions on α and r such that $x^* = 1$ is stable.