1. A model for harvesting a population takes the form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(1 - \frac{N}{K}) - Y_0$$

where N(t) is the population density at time t, and r, K and  $Y_0$  are positive constants.

- (a) Explain why this is called a constant yield model.
- (b) Show that for  $Y_0 < \frac{rK}{4}$ , this equation has two steady states, and explain graphically why one of these steady states is linearly stable while the other is linearly unstable.
- (c) Show that the recovery time for harvesting at a yield  $Y_0$ ,  $T_R(Y_0)$ , satisfies

$$\frac{T_R(Y_0)}{T_R(0)} = \frac{1}{(1 - \frac{Y_0}{Y_M})^{\frac{1}{2}}}$$

for  $Y_0 < Y_M$  and  $Y_M = \frac{rK}{4}$ .

- (d) Why is this harvesting approach worse than the constant effort approach if we aim for maximum yield  $(Y_M)$ .
- (e) Explain why this model is unrealistic for  $Y_0 > Y_M$ .
- (f) Why might you have anticipated right from the outset that this model could be unrealistic in certain circumstances?
- 2. A continuous-time model for the evolution of a prey species (density N(t), where t is time), takes the form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = RN\left(1 - \frac{N}{K}\right) - P\left(1 - \exp\left[-\frac{N^2}{\epsilon A^2}\right]\right)$$

where  $0 < \epsilon \ll 1$  and R, K, P and A are positive constants.

- (a) Explain the biological interpretation of the different terms in the model.
- (b) If the units of N are density and those of t are time, what are the dimensions of R, K, P, A and ε? Hence show that

$$u = \frac{N}{A}, \qquad \tau = \frac{P}{A}t, \qquad r = \frac{AR}{P}, \qquad q = \frac{K}{A},$$

are non-dimensional.

(c) Show that the model can be non-dimensionalised to give

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} = ru\left(1 - \frac{u}{q}\right) - \left(1 - \exp\left[-\frac{u^2}{\epsilon}\right]\right),\,$$

where r and q are positive parameters.

- (d) Demonstrate that a necessary condition for there to be three non-zero steady states is that r and q must satisfy rq > 4.
- (e) Could this model exhibit hysteresis? Justify your answer.
- 3. Suppose that the evolution of a population can be described by a discrete-time Ricker model of the form

$$N_{t+1} = N_t \exp\left[r\left(1 - \frac{N_t}{K}\right)\right],$$

where 0 < r < 2.

- (a) Describe the biological interpretation of the model.
- (b) Determine any non-negative steady states and their linear stability.
- (c) Construct a cobweb map the model and discuss the global qualitative behaviour of the solutions.
- 4. Consider the effect of regularly harvesting the population of a species for which the model equation is

$$N_{t+1} = \frac{bN_t^2}{1 + N_t^2} - EN_t := f(N_t; E),$$

where E is a measure of the effort expended in obtaining the harvest,  $EN_t$ , and the parameters are such that b > 2 and E > 0.

- (a) Determine the steady states and hence show that if the effort  $E > E_M = (b-2)/2$ , then no harvest is obtained.
- (b) If  $E < E_M$  show by cob-webbing  $N_{t+1} = f(N_t; E)$ , or otherwise, that the model is realistic only if the population,  $N_t$ , always lies between two positive values for which you should find analytic expressions (but do not solve explicitly).
- (c) Demonstrate the existence of a tangent bifurcation as  $E \to E_M$ .
- 5. The interaction between two populations with densities  $N_1$  and  $N_2$  is modelled by

$$\frac{dN_1}{dt} = rN_1 \left( 1 - \frac{N_1}{K} \right) - aN_1N_2 \left( 1 - \exp[-bN_1] \right) 
\frac{dN_2}{dt} = -dN_2 + eN_2 \left( 1 - \exp[-bN_1] \right),$$

where a, b, d, e, r and K are positive constants.

- (a) What type of interaction exists between  $N_1$  and  $N_2$ ? What do the various terms imply ecologically?
- (b) Non-dimensionalise the system by writing

$$u = \frac{N_1}{K}, \qquad v = \frac{aN_2}{r}, \qquad \tau = rt, \qquad \alpha = \frac{e}{r}, \qquad \delta = \frac{d}{r}, \qquad \beta = bK.$$

- (c) Determine the non-negative equilibria and note any parameter restrictions.
- (d) Discuss the linear stability of the equilibria.
- (e) Show that a non-zero  $N_2$  population can exist if  $\beta > \beta_c = -\ln(1 \delta/\alpha)$ .
- (f) Briefly describe the bifurcation behaviour as  $\beta$  increases with  $0 < \delta/\alpha < 1$ .

## Optional

Consider a lake with some fish attractive to people who like to fish (from here on denoted "fishers"). We wish to model the fish-fishers interactions under the following assumptions:

6. • the fish population grows logistically in the absence of fishing;

- the presence of fishers depresses the fish growth rate at a rate jointly proportional to the size of the fish and fishers populations;
- fishing crew are attracted to the lake at a rate directly proportional to the number of fish in the lake;
- fishers are discouraged from the lake at a rate directly proportional to the number of fishers already there.
- (a) Write down a mathematical model for this situation, clearly defining your terms.
- (b) Show that a non-dimensionalised version of the model is

$$\frac{\mathrm{d}u}{\mathrm{d}\tau} = ru(1-u) - uv$$
$$\frac{\mathrm{d}v}{\mathrm{d}\tau} = \beta u - v,$$

where u and v represent the non-dimensionalised fish and fishers populations, respectively.

- (c) Calculate the steady states of the system and determine their stability.
- (d) Draw the phase plane, including the nullclines and phase trajectories.
- (e) What would be the effect of adding fish to the lake at a constant rate?
- 7. (a) What kind of interactive behaviour between two populations,  $N_1$  and  $N_2$ , is suggested by the model

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left( 1 - \frac{N_1}{K_1 + b_{12}N_2} \right), \frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left( 1 - \frac{N_2}{K_2 + b_{21}N_1} \right),$$

where  $r_1$ ,  $r_2$ ,  $K_1$ ,  $K_2$ ,  $b_{12}$  and  $b_{21}$  are positive constants?

(b) Show that, with appropriate non-dimensionalisation, this model takes the form

$$\begin{aligned} \frac{\mathrm{d}u_1}{\mathrm{d}\tau} &= u_1 \left( 1 - \frac{u_1}{1 + \alpha_{12} u_2} \right), \\ \frac{\mathrm{d}u_2}{\mathrm{d}\tau} &= \rho u_2 \left( 1 - \frac{u_2}{1 + \alpha_{21} u_1} \right), \end{aligned}$$

where

$$u_1 = \frac{N_1}{K_1}, \qquad u_2 = \frac{N_2}{K_2},$$

 $\tau$  is non-dimensionalised time and  $\alpha_{12}$ ,  $\alpha_{21}$  and  $\rho$  are positive parameters.

- (c) Determine the steady states and their linear stability, taking care to list any restrictions on parameters.
- (d) By drawing the nullclines and sketching phase trajectories, briefly discuss the behaviour of the model for the cases  $\alpha_{12}\alpha_{21} < 1$  and  $\alpha_{12}\alpha_{21} > 1$ .