

### Examples Sheet 1

1. The population of a certain insect,  $N(t)$ , is modelled by the ODE

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) - p(N)$$

where  $p(N)$  is the sigmoidal function  $p(N) = BN/(A + N)$ .

- Give suggestions as to the meaning of the terms in this equation.
  - Show by rescaling that the dynamics depends only on the two parameters  $\alpha = A/K, \beta = B/rK$  [Hint: focus on simplifying the logistic terms first].
  - Investigate how many *positive* steady states there are, i.e. fixed points with  $N > 0$ . Sketch the  $(\alpha, \beta)$  plane, dividing it into regions where there are zero, one and two positive steady states.
  - What is the number of *stable* solutions, including the fixed point at  $N = 0$ , in each region? [Hint: investigating  $N = 0$  stability will be enough to deduce the rest]
2. A variant of the Hutchinson-Wright equation given by this equation:

$$\frac{dx(t)}{dt} = \alpha [x(t - T) - x(t)^2],$$

where  $\alpha, T > 0$ . Give a brief interpretation of what this might represent in terms of population dynamics. Show that the constant solution with  $x(t) = 1$  is stable for all  $\alpha, T > 0$ . [Hint: show that any 's' must have negative real part (as in lectures, the growth exponent of a small perturbation).]

3. Circulating red blood cells (RBCs) are destroyed in the spleen and created in the bone marrow in proportion to the number destroyed on the previous day.
- Treat days as discrete time units, and let  $R_n$  be the number of RBCs in circulation on day  $n$ , let  $M_n$  be the number produced by marrow on day  $n$ , let  $f$  be the fraction of RBCs removed by the spleen every day, and let  $\gamma$  be the number produced on day  $n$  for each cell lost on day  $n - 1$ .

Write down equations for  $R_{n+1}$  and  $M_{n+1}$  in terms of  $R_n$  and  $M_n$ , and show that

$$R_n = A\lambda_1^n + \beta\lambda_2^n,$$

where

$$\lambda_{1,2} = \frac{1 - f \pm \sqrt{(1 - f)^2 + 4\gamma f}}{2}.$$

Deduce that the RBC count may fluctuate, but that it will remain constant at large times if and only if  $\gamma = 1$ .

- (b) Start again, but this time formulate the model for RBC count as a delay differential equation for  $R(t)$ , where the production of new cells is proportional to  $R(t - T)$ . Now  $f$  should be a rate and  $\gamma$  is still the ratio of cells made for each one lost. Show that there exists a solution of the form  $R(t) = Ce^{\lambda t}$  if

$$\frac{1}{\gamma}(\lambda + 1) = e^{-\lambda f T}.$$

Show graphically that this equation has a positive real root if and only if  $\gamma > 1$ , and interpret this result.

4. The population density  $n(a, t)$  of individuals of age  $a$  at time  $t$  satisfies

$$\frac{\partial n(a, t)}{\partial t} + \frac{\partial n(a, t)}{\partial a} = -\mu(a)n(a, t), \quad \text{with} \quad n(0, t) = \int_0^\infty b(a)n(a, t)da,$$

where  $\mu(a)$  is the age-dependent death rate and  $b(a)$  is the birth rate per individual of age  $a$ .

Using the standard similarity solution  $n(a, t) = e^{\gamma t} r(a)$  for each of the examples below, give (i) the mean number of offspring, (ii) the population growth rate  $\gamma$  (solve where possible otherwise give an implicit expression) (iii) the value of the birth rate parameter  $B$  for which there is neither growth nor decay and sketch the age-profile of the population in this case.

- (a) The birth rate  $b(a)$  is a constant  $B$  for  $a_1 < a < a_2$  and zero otherwise. The death rate  $\mu(a)$  is a constant  $d$  for  $a > a_2$  and zero otherwise.
- (b) Individuals give birth only at age  $a^*$ :  $b(a) = B \delta(a - a^*)$ . The death rate  $\mu(a)$  is a constant  $d$  for all ages.
- (c) The birth rate  $b(a)$  is a constant  $B$  for all ages. All individuals die at age  $A$ . [Hint: in this extreme case, rather than using  $\mu(a)$ , just reformulate the standard approach slightly.]

5. Consider the difference equation with delay (note the  $n - 1$ ):

$$x_{n+1} = rx_n(1 - x_{n-1}).$$

This is the discrete equivalent of the delay differential equation for population discussed in lectures. Show that the fixed point  $x^* = 1 - r^{-1}$  is unstable if  $r$  is sufficiently large. [Hint: cannot use standard results for stability of 1D maps as this is NOT a 1D map!] Show that when  $r$  takes its marginal value for instability, the linearised stability problem has a periodic solution (to be determined).

6. A discrete-time model for breathing is given by

$$\begin{aligned} V_{n+1} &= \alpha C_{n-k} \\ C_{n+1} - C_n &= \gamma - \beta V_{n+1} \end{aligned}$$

where  $V_n$  is the volume of each breath at time step  $n$  and  $C_n$  is the concentration of carbon dioxide in the blood at the end of time step  $n$ . (This model was presented in lectures and we found and analysed the stability of the steady state when  $k = 0$  and  $k = 1$ .)

For general (integer)  $k > 1$ , by seeking parameter values when the modulus of a perturbation to the steady state is constant, show that the range of parameters where the solution is stable is

$$0 < \alpha\beta < 2 \sin\left(\frac{\pi}{4k + 2}\right).$$

Notice how this range shrinks as the time lag  $k$  increases. What is the periodicity of the constant-modulus solution at the upper end of this range?

7. A simple model of two competing populations eating the same food takes the form

$$\begin{aligned}\dot{N}_1 &= r_1 N_1 \left( 1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_2} \right), \\ \dot{N}_2 &= r_2 N_2 \left( 1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_1} \right).\end{aligned}$$

Rescale the equations to simplify them, and show that the solutions depend only on  $\rho = r_2/r_1$ ,  $b_{12}$  and  $b_{21}$ .

Now assume that  $\rho, b_{12}, b_{21} > 0$ . Find all the physically relevant fixed points and determine their stability. Give conditions on the coefficients such that there is a stable state of *coexistence*, with  $N_1, N_2 > 0$ .

8. Consider this ‘harvesting’ model:

$$\begin{aligned}\dot{u} &= u(1 - v) - \epsilon u^2 - f \\ \dot{v} &= -\alpha v(1 - u),\end{aligned}$$

with constants  $\alpha > 0$ ,  $f > 0$  and  $0 < \epsilon < 1/2$ .

Find all the biologically relevant fixed points of this system, and investigate their stability, distinguishing between different ranges of  $f$ :

- (a)  $0 < f < \epsilon$ ,
- (b)  $\epsilon < f < 1 - \epsilon$
- (c)  $1 - \epsilon < f < 1/(4\epsilon)$
- (d)  $1/(4\epsilon) < f$ .

In each case, sketch trajectories in the  $u-v$  phase-plane, and discuss what would happen to the predator and prey populations in practice.

Note that for this model something odd happens at  $u = 0$ . Comment on this, and discuss how the model might be improved in this respect.

*In addition to the examples sheets, students are encouraged to do the exercises given in lectures.*