

## Examples Sheet 2

1. Consider an infectious disease in some population where immunity wanes with time (and ignore births and deaths). This can be captured SIRS model of an infectious disease: start with the SIR model from lectures, but recovered individuals ( $R$ ) can lose their immunity and become susceptible again at a rate  $\gamma R$ . Using that the total population size remains constant ( $N$ ), reduce the system of equations to two, for  $S$  and  $I$  (the populations of susceptibles and infecteds respectively).

Give an expression for the basic reproduction ratio  $R_0$  and show that when  $R_0 > 1$  the system has a stable fixed point where both  $S > 0$  and  $I > 0$ .

Find the nullclines and sketch trajectories in the  $S - I$  plane. What happens in the long term?

2. A fungal disease is introduced into an isolated population of frogs. Without disease, the population size  $x$  would obey the (normalised) logistic equation  $\dot{x} = x(1 - x)$ , where the dot denotes differentiation with respect to time. The disease causes death at rate  $d$  and there is no recovery. The disease transmission rate is  $\beta$  and in addition, offspring of infected frogs are also infected from birth.

(a) Briefly explain why the population sizes of the uninfected  $x$  and infected  $y$  frogs now satisfy

$$\begin{aligned}\dot{x} &= x [1 - x - (1 + \beta)y] \\ \dot{y} &= y [(1 - d) - (1 - \beta)x - y] .\end{aligned}$$

(b) The population starts at the disease-free population size ( $x = 1$ ) and a small number of infected frogs are introduced. Show that the disease will successfully invade iff  $\beta > d$ .

(c) By finding all the equilibria in  $x, y \geq 0$  and considering their stability, find the long term outcome for the frog population. Specify  $d$  as a function of  $\beta$  at any boundaries.

(d) Plot the long-term steady *total* population size as a function of  $d$  for fixed  $\beta$ , and note that an intermediate mortality rate is actually the most harmful for overall population numbers. Explain why this is the case.

3. Let  $x, y$  be the normalised populations of phytoplankton and zooplankton respectively. The system is modelled by the following differential equations, where the constants  $\epsilon, b$  and  $c$  are positive:

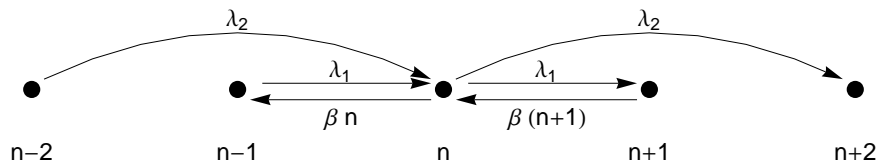
$$\begin{aligned} \frac{dx}{dt} &= bx(1-x) - y \frac{x^2}{\epsilon^2 + x^2} \\ \frac{dy}{dt} &= cy \frac{x^2}{\epsilon^2 + x^2} - y. \end{aligned}$$

Briefly explain the meaning of each term in these equations.

Assume that  $c > 2$  and  $\epsilon \ll 1$ . By finding the nullclines and carefully considering how they intersect show that there is one fixed point where both  $x > 0$  and  $y > 0$  and that it is stable.

The system is perturbed by the intrinsic growth rate  $b$  increasing as a result of a rise in the temperature of the sea. Consider how this changes the nullclines. If the system was at the stable fixed point before, what happens after the temperature rise? Deduce the possibility of excitable behaviour in which there can be a spike in the plankton population sizes.

4. Consider a birth and death process in which births can give rise to either one or two offspring, with probability  $\lambda_1$  and  $\lambda_2$  respectively, while the probability of death per individual is  $\beta$ ; i.e.



Write down the master equation ( $\dot{p}_n = \dots$ ) for this system, and show that the generating function  $\phi(s, t) = \sum_{n=0}^{\infty} s^n p_n$  satisfies the equation:

$$\frac{\partial \phi}{\partial t} = (s-1) \left[ (\lambda_1 + \lambda_2(s+1)) \phi - \beta \frac{\partial \phi}{\partial s} \right]$$

Use this equation in the steady state to show that

$$\langle n \rangle = \frac{1}{\beta}(\lambda_1 + 2\lambda_2), \quad \sigma^2 = \frac{1}{\beta}(\lambda_1 + 3\lambda_2).$$

5. Consider an experiment where two or three individuals are added to a population with probability  $\lambda_2$  and  $\lambda_3$  respectively per unit time. The death rate in the population is a constant  $\beta$  per individual per unit time. Write down the master equation and derive an equation for  $\frac{\partial \phi}{\partial t}$ , where  $\phi$  is the generating function (as above). Find the solution for  $\phi$  in steady state.

Show that for given target mean but otherwise a free choice of  $\lambda_2$  and  $\lambda_3$ , the experimenter can minimise the variance by only adding two individuals at a time. Find this minimum variance in terms of the mean.

6. Consider a birth-death process described by the following master equation:

$$\dot{p}_n = \lambda(p_{n-1} - p_n) + \beta[f(n+1)p_{n+1} - f(n)p_n], \quad f(n) = n(n-1).$$

- (i) Give an explanation of the terms on the right hand side.  
 (ii) Show that the equation satisfied by the generating function  $\phi(s, t)$  is

$$\frac{\partial \phi}{\partial t} = \lambda(s-1)\phi + \beta \left( (s-s^2) \frac{\partial^2 \phi}{\partial s^2} \right).$$

- (iii) Use the equation for  $\phi$  in the steady state, or the master equation directly, to obtain equations for  $\langle n^2 \rangle$  and  $\langle n^3 \rangle$ , in terms of  $\mu = \langle n \rangle$  and  $r = \lambda/\beta$  (do not try to evaluate  $\mu$  itself).  
 (iv) With the mean  $\mu$  unknown this system of equations is not closed. Nonetheless show that the variance  $\sigma^2 = \langle n^2 \rangle - \langle n \rangle^2 \leq r + \frac{1}{4}$ . Show also, using the inequality  $\langle n^2 \rangle \geq \langle n \rangle^2$ , that  $\langle n \rangle \leq (1 + \sqrt{1 + 4r})/2$ .

*In addition to the examples sheets, students are encouraged to do the exercises given in lectures (solutions available on Moodle).*