SUMMER 2004 EXAMINATIONS

Degree of Bachelor of Arts : Year 3
Degree of Bachelor of Science : Year 3
Degree of Master of Mathematics : Year 3

NON-PHYSICAL APPLICATIONS II
(POPULATION DYNAMICS)

TIME ALLOWED : Two Hours and a Half

INSTRUCTIONS TO CANDIDATES

Full marks can be obtained for complete answers to FIVE questions.
Only the best FIVE answers will be counted.

1. The behaviour of a population is described by the Richards growth law

$$\mathrm{d}N/\mathrm{d}t = rN\left(1 - \sqrt{N/K}\right) \tag{1}$$

where N is the population size depending on the continuous time variable t and r and K are positive constants.

(a) Explain the biological meaning of the terms rN and $-rN\sqrt{N/K}$ in the right hand side of (1) and of the parameters r and K.

(4 marks)

(b) Sketch the graph of the function in the right hand side of the above equation for $N \geq 0$. Use your graph to show that the system possesses a single non-zero equilibrium, find the corresponding population size, and characterise its stability (including the basin of attraction if appropriate).

(5 marks)

(c) Use the substitution $u = N^{-1/2}$ to show that exact solution of equation (1) satisfying the initial condition $N(0) = N_0 > 0$ is given by

$$N(t) = \left(K^{-1/2} + (N_0^{-1/2} - K^{-1/2})e^{-rt/2}\right)^{-2}. \tag{1a}$$

Determine the behaviour of a typical solution in the limit $t \to +\infty$. Compare this with your previous conclusions about the stability and the basin of the single nonzero equilibrium.

(7 marks)

(d) Use equation (1a) in part 1(c) above to show that this population can be also described by a discrete time model (difference equation) with time step $T > 0$, equivalent to (1), of the following form

$$N(t+T) = \frac{RN(t)}{\left(1 + aN(t)^{1/2}\right)^2}$$

and determine the parameters R and a. Without further calculations, explain why this discrete-time model has at least one non-zero equilibrium and characterise its stability (including the basin of attraction if appropriate).

(4 marks)

2. The Hassell model for a single species with population N_t at discrete time t changing with step 1 is described by

$$N_{t+1} = \frac{RN_t}{(1+aN_t)^b} \qquad (2)$$

where $R > 1$, $a > 0$ and $b > 0$ are constants.

(a) Explain the biological meaning of the numerator (RN_t) and of the denominator $((1+aN_t)^b)$ in this formula. Give biological interpretations of the three parameters R, a and b.

(5 marks)

(b) Find the non-zero equilibrium value, N_*, in this model. Determine the local stability condition for this equilibrium in terms of R and b. In particular, find the nonzero equilibrium for $a = 1$, $b = 3$ and $R = 125$ and determine its stability.

(5 marks)

(c) Draw carefully the graph of the function $F(N) = 125N/(1+N)^3$ for $N \in [0, 20]$, and use it to sketch a stepladder/cobweb diagram for the solution of model (2) at $a = 1$, $b = 3$ and $R = 125$, and initial condition $N(0) = 3$.

(4 marks)

(d) For the same values of the parameters $a = 1$, $b = 3$ and $R = 125$, determine N_{t+2} in terms of N_t, i.e. the second iteration of the succession function. Find all solutions of the equation $N_{t+2}(N_t) = N_t$. How many cycles of period 2 are in this model at these parameter values? Identify all such cycles.

(6 marks)

3. The growth of an age-structured population of weed, consisting of three age groups (age 0, 1 and 2 years) is described by Leslie's linear matrix equation

$$\mathbf{N}_{t+1} = \mathbf{L}\mathbf{N}_t, \tag{3}$$

where

$$\mathbf{N}_t = \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \end{bmatrix},$$

$N_j(t)$ is the population density of the age group j at the time t and $\mathbf{L}$ is the Leslie transition matrix:

$$\mathbf{L} = \begin{bmatrix} F_0 & F_1 & F_2 \\ P_0 & 0 & 0 \\ 0 & P_1 & 0 \end{bmatrix}.$$

(a) Explain the biological meaning of the constants F_j and P_j, and point out what constraints on the possible values of these coefficients this meaning imposes.

(5 marks)

(b) Find the characteristic polynomial $P(\mu)$ for $\mathbf{L}$. By considering the function $P(\mu)/\mu^3$ for positive μ, show that this polynomial always has exactly one positive root.

(c) In the unchecked population of weed, parameter values are $F_0 = 0$, $F_1 = 10$, $F_2 = 600$, $P_0 = 0.1$, $P_1 = 0.1$. Determine whether the the population will grow or decay in the long run, and how fast.

(5 marks)

(d) A herbicide is suggested against this weed, which works by reducing the fertility of the two-year old plants. Find out, to what extent coefficient F_2 should be reduced to eradicate the weed.

(4 marks)

4. Interaction between two closely related species sharing common resources can be investigated using the discrete-time model of Law and Watkinson, with the growth equations

$$\begin{aligned} x_{t+1} &= \frac{Rx_t}{1+(ax_t+by_t)^n}, \\ y_{t+1} &= \frac{Ry_t}{1+(bx_t+ay_t)^n}. \end{aligned} \tag{4}$$

(a) Explain the biological significance of the constants R, a and b. Suppose the species are in a coexistence equilibrium. Based on the biological meaning of parameter b, predict whether the populations will increase or decrease if b increases?

(4 marks)

(b) Let $R = 2$, $n = 3$ and $a = 1$. Assuming $b \neq 1$, find the coexistence equilibrium population densities $x_t = x_*$ and $y_t = y_*$ in terms of b. Verify that the answer is consistent with the conclusion on the role of parameter b from part (a) above.

(5 marks)

(c) With the same assumptions, $R = 2$, $n = 3$, $a = 1$ and $b \neq 1$, find the community matrix $\mathbf{A}$ of the coexistence equilibrium, and determine at which values of b it will be stable in linear approximation.

(7 marks)

(d) Consider the case $b = 1$, with other parameters the same as before, $R = 2$, $n = 3$, $a = 1$. Find out the behaviour of the system in the long run, if the initial conditions are $x = 1$, $y = 2$.

(4 marks)

5. The behaviour of an ecosystem involving three species is modelled by the linearised growth equations:

$$\begin{aligned} \mathrm{d}N_1/\mathrm{d}t &= a_1 - b_{11}N_1 + b_{12}N_2 - b_{13}N_3 \\ \mathrm{d}N_2/\mathrm{d}t &= a_2 + b_{21}N_1 - b_{22}N_2 \\ \mathrm{d}N_3/\mathrm{d}t &= a_3 - b_{31}N_1 - b_{33}N_3. \end{aligned} \tag{5}$$

(a) Assuming that all parameters a_j, b_{jk} in this model are positive, briefly discuss the character of the interaction within and between the species.

(4 marks)

(b) State carefully a theorem involving Lyapunov function V which guarantees stability of an equilibrium in a system of autonomous differential equations.

(3 marks)

(c) Consider system (5) at the following values of the parameters: $a_1 = 4$, $a_2 = 3$, $a_3 = 5$, $b_{11} = b_{22} = b_{33} = 4$, $b_{12} = b_{21} = b_{31} = b_{13} = 1$. Show that this system has an equilibrium at $N_1 = N_2 = N_3 = 1$. Show that this equilibrium is isolated. Verify that the system (5) can be written in the matrix form.

$$\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = -\mathbf{M}\mathbf{x}, \qquad \text{where } \mathbf{x}(t) = \begin{bmatrix} N_1(t) - 1 \\ N_2(t) - 1 \\ N_3(t) - 1 \end{bmatrix} \tag{5a}$$

and $\mathbf{M}$ is a real symmetric matrix. Find the eigenvalues of $\mathbf{M}$, verifying that they are all positive, i.e. $\mathbf{M}$ is positive definite.

(6 marks)

(d) Consider the function $V = \mathbf{x}^T\mathbf{M}\mathbf{x}$, where $\mathbf{M}$ is the symmetric positive definite matrix introduced above. Show that the orbit derivative of V by the system (5a) is

$$\frac{\mathrm{d}V}{\mathrm{d}t} = -2\mathbf{x}^T\left(\mathbf{M}^2\right)\mathbf{x}.$$

Hence, by means of the Lyapunov theorem referred to above, show that the equilibrium state $N_1 = N_2 = N_3 = 1$ is asymptotically stable, and specify its basin of attraction. You may use without proof the following statements: (1) A quadratic form with a positive definite matrix is a positive definite function; (2) The square of a positive definite matrix is a positive definite matrix.

(7 marks)

6. A predator-prey system is described by the following system of differential equations:

$$\begin{aligned} \mathrm{d}N_1/\mathrm{d}t &= r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - p_1 \frac{N_1 N_2}{N_1 + A} \\ \mathrm{d}N_2/\mathrm{d}t &= -m_2 N_2 + p_2 \frac{N_1 N_2}{N_1 + A} \end{aligned} \tag{6}$$

where N_1 is the density of the population of prey and N_2 is density of the population of predators.

(a) Explain briefly the biological significance of the coefficients r_1, m_2, K_1, and A in equations (6), and state which of p_1, p_2 characterises the functional response and which characterises the numerical response of predators to prey

(5 marks)

(b) Consider the following values of parameters: $r_1 = 1$, $K_1 = 4$, $p_1 = 1$, $m_2 = 1$, $p_2 = 2$, $A = 1$. Find the values of N_1, N_2 for all equilibria predicted by the model. Show that the community matrix $\mathbf{A}$ associated with the equilibrium state with both species present is given by

$$\mathbf{A} = \begin{bmatrix} 1/8 & -1/2 \\ 3/4 & 0 \end{bmatrix}.$$

Thus show that the equilibrium is unstable.

(7 marks)

(c) State carefully theorems by Poincaré and Bendixson which guarantee the existence and stability of periodic solutions in a system of two autonomous differential equations with an absorbing region without stable equilibria.

(3 marks)

(d) Find the orbit derivative of function $V = 2N_1 + N_2$ due to system (6) and prove that if $V = 8$ then $\mathrm{d}V/\mathrm{d}t \leq 0$. Thus identify a triangle in the (N_1, N_2) plane which is an absorbing region. Specify what further conditions would need to be ascertained to apply the Poincaré-Bendixson theory mentioned in question 6c (you are not required to check these conditions).

(5 marks)

7. The classical model of an epidemic of an infectious disease due to Kermack and McKendrick (1927) has the form

$$dS/dt = -\beta SI, \qquad dI/dt = \beta SI - \nu I, \qquad dR/dt = \nu I, \tag{7}$$

where S is the number of susceptible, I the number of infected and R is the number of removed individuals of the population, and β and ν are non-negative parameters.

(a) Explain the biological meaning of the terms and biological assumptions used in this model.

(6 marks)

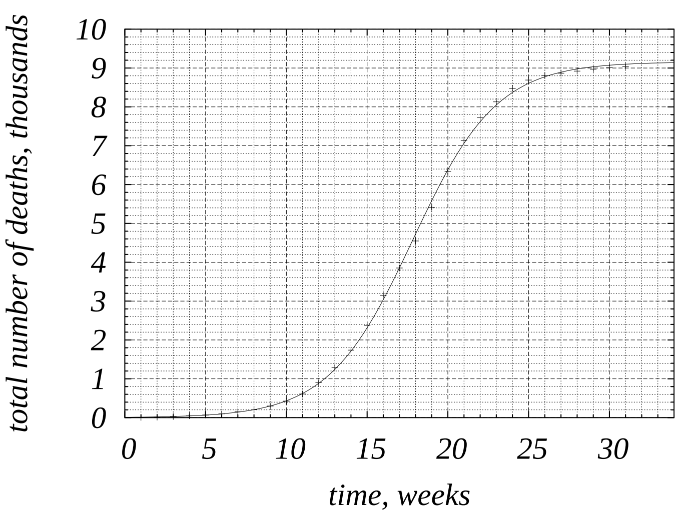
(b) Perform a phase-plane analysis of the model (7) in the plane (S, I): draw the null-clines, indicate equilibria, show the general direction of trajectories in different parts of the phase plane, and sketch a typical trajectory representing an epidemic.

(6 marks)

(c) This model was applied to the Bombay plague epidemic of 1905-6 in which only a small fraction of the city population were infected. Substitute $S = \nu/\beta + \sigma$ into (7) and assume that $|\sigma|$ and I are small. Simplify the first equation by neglecting the smaller term. Verify by substitution that $\sigma = -\frac{2p}{\beta}\tanh(p(t - t_*))$ and $I = \frac{2}{\nu\beta}p^2\,\mathrm{sech}^2(p(t - t_*))$ are a solution to the resulting system for arbitrary p and t_* (remember that $(\tanh x)' = \mathrm{sech}^2 x = 1 - \tanh^2 x$).

(4 marks)

(d)



This is the graph of mortality data of the Bombay epidemic of 1905-6. Estimate (to 1 significant figure) the values of the coefficients of the model (7). Assume that the part of city population potentially involved in the epidemics was 100 thousand.

(4 marks)