SUMMER 2005 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. Rainbow trout *Oncorhynchus mykiss* is a highly commercial fish, found naturally all round the Pacific basin. A company wishes to exploit a river abundant with the fish. The company's ecologists have found that the behaviour of the trout population is well described by the Richards growth law

$$\mathrm{d}N/\mathrm{d}t = rN(1 - (N/K)^2), \tag{1}$$

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 function in the right hand side of equation (1) and of the parameters r and K.

(4 marks)

(b) Sketch the graph of the function in the right hand side of equation (1) for $N \geq 0$. Use your graph to show that the system possesses a single non-zero equilibrium, find the corresponding population size in terms of the parameters r and K, and characterise its stability.

(5 marks)

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

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

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

(7 marks)

(d) If the trout are harvested with a constant yield Y, the growth law is modified to

$$\mathrm{d}N/\mathrm{d}t = rN(1 - (N/K)^2) - Y.$$

Sketch graphs of the function in the right hand side of this equation for a selection of values of $Y \geq 0$. Use it to explain how the population will respond to harvesting. What is the maximal sustainable yield of the population?

(4 marks)

2. The dynamics populations of weavels of the genus *Callosobruchus* can be described by a simplified discrete-time model

$$N_{t+1} = F(N_t),$$
$$F(x) = Rx(1-x), \tag{2}$$

where N_t is population size in appropriate units, time is measured in generations and $R > 0$ is a constant. Species *C. chinensis* is best described by $R = 5/3$, and species *C. maculatus* is best described by $R = 19/6$.

(a) This model will only be biologically sensible if N_t remains non-negative for all t. Find out what limitations this requirement imposes on possible values of N_0 and R.

(4 marks)

(b) Find all values of parameter R at which this model has a positive equilibrium, and all values of R for which this equilibrium is stable. Show that the equilibrium is stable for *C. chinensis* but unstable for *C. maculatus*.

(5 marks)

(c) Draw carefully the graph of the succession functions $F(x)$ of (2) for $R = 5/3$ and $R = 19/6$. Use these graphs to draw stepladder/cobweb diagrams corresponding to each of these values of R, with the same initial condition $N_0 = 0.1$.

(5 marks)

(d) Find, for general R, the explicit form of the 2-step recurrence relation $N_{t+2} = F(F(N_t))$, where $F(x) = Rx(1-x)$ is the succession function of (2). Express this second iteration function as a polynomial and determine its coefficients. Write down two point equilibria of this particular recurrence relation. Hence show that the the remaining point equilibiria are roots of the quadratic

$$R^2x^2 - R(R+1)x + R + 1 = 0.$$

Find these two solutions for *C. maculatus* and verify that these solutions are transformed one into the other by $F(x)$. Explain what this means for the evolution of the population.

(6 marks)

3. On a small tropical island without any predators, there once lived a population of flightless birds *Raphus cucullatus*, also known as dodo. The weather stayed the same throughout the year, and so the birds could lay eggs at arbitrary times. The dynamics of that population could be described by the following delay-differential equation:

$$\frac{\mathrm{d}N}{\mathrm{d}t}(t) = bN(t-T) - c[N(t-T)]^2 - m[N(t)]^2, \tag{3}$$

where $T > 0$ is the time delay between laying the eggs and those eggs hatching, and b, c and m are some positive parameters.

(a) Suggest a biological interpretation of the terms in this model. Explain how one can see that, according to this model, the natural life expectancy of the birds in favourable conditions was very long.

(4 marks)

(b) Find the equilibria in this model and the ranges of parameter values at which they exist. *(3 marks)*

(c) By putting $N(t) = N_* + h(t)$ in (3), where N_* is an equilibrium in (3) and h is small, derive the linear delay-differential equation for h. Show that for the nonzero equilibrium, solutions of this linearised equation in the form $h(t) = \mathrm{Re}\left(h_0 e^{\mu t}\right)$ exist if μ satisfies the transcendental equation

$$(m-c)e^{-\mu T} = 2m + (c+m)\mu/b. \tag{3a}$$

Show that for $T = 0$ the equilibrium is stable, and that while T is increased from zero with other parameters fixed, the stability will first, if ever, be violated when the following system of equations has real solutions for T and ω:

$$(c-m)\cos(\omega T) = -2m, \qquad (c-m)\sin(\omega T) = (c+m)\omega/b. \tag{3b}$$

(7 marks)

(d) A study of historical records of sightings of dodo suggest that during a certain period, their population showed periodic oscillations with a period three times longer than the egg incubation time T. Assuming that these oscillations correspond to the instability described in part 3c, use these data to evaluate (a) the ratio c/m, (b) the value of coefficient b in terms of incubation time T.

(6 marks)

4. Interaction between two closely related species sharing common resources can be investigated using the following simple variant of the discrete-time model of Hassel and Comins:

$$\begin{aligned} N_1(t+1) &= \frac{R_1 N_1(t)}{1 + N_1(t) + \beta N_2(t)}, \\ N_2(t+1) &= \frac{R_2 N_2(t)}{1 + \beta N_1(t) + N_2(t)}, \end{aligned} \tag{4}$$

in which $N_1(t)$, $N_2(t)$ are the respective population densities at time t and β, R_1 and R_2 are constants with $\beta > 1$ and $R_2 > R_1 > 1$.

(a) Explain briefly why this model simulates both intraspecific an interspecific competition, and what is the biological significance of parameters β, R_1 and R_2.

(4 marks)

(b) The system possesses an equilibrium state Q with both species present at densities $(N_1, N_2) = (N_1^*, N_2^*)$. Find N_1^* and N_2^* in terms of β, R_1 and R_2. Explain why $\beta > (R_2 - 1)/(R_1 - 1)$.

(5 marks)

(c) Show that the community matrix $\mathbf{A}$ associated with Q is given by

$$\mathbf{A} = \begin{bmatrix} 1 - p_1 & -\beta p_1 \\ -\beta p_2 & 1 - p_2 \end{bmatrix}$$

where $p_j = N_j / R_j$, $j = 1, 2$.

(5 marks)

(d) Show that the eigenvalues of $\mathbf{A}$ are always real and hence the equilibrium is always monotonic. Show that if Q is an asymptotically stable state,

$$\beta < 1.$$

(6 marks)

5. Red squirrel *Sciurus vulgaris*, native inhabitant of Britain, since 1876 has been subjected to a fierce competition from its American cousin, grey squirrel *Scirus carolinensis*. A hopeful conservationist has suggested that, given appropriate protective measures, *S. vulgaris* can stand up to the competition. He believes that given their reproductive and foraging habits, interaction of the two species would be described by Lotka-Volterra-Gause equations with the following parameters

$$\begin{aligned} \frac{\mathrm{d}N_1}{\mathrm{d}t} &= N_1(1 - 2N_1 - 2N_2), \\ \frac{\mathrm{d}N_2}{\mathrm{d}t} &= N_2(1 - N_2 - 4N_1), \end{aligned}$$

where $N_1 = N_1(t)$ is the population density of *S. carolinensis* and and $N_2 = N_2(t)$ is the population density of *S. vulgaris*, measured in appropriately chosen units.

(a) Find all the equilibria in this model.

(4 marks)

(b) For each of the equilibria, find the community matrix and its eigenvalues. Classify the equilibria. Find also eigenvectors for the equilibrium in which both species survive.

(6 marks)

(c) Sketch the phase portrait of this system in the biologically sensible region: draw the null-clines of the system and determine the crude directions of the trajectories in parts of the phase plane cut by the null-clines, designate the equilibria in the phase plane, and sketch a few typical trajectories. Are there any chances for the red squirrels to survive and what does that mean for the grey squirrels?

(5 marks)

(d) Determine the orbit derivative of the function $V = 2N_1 - N_2$. Use it to prove that the line $N_2 = 2N_1$ is an invariant set. Deduce from there, what would be the ultimate state of the system as $t \to +\infty$, if $N_1(0) = N_2(0) = 1$.

(5 marks)

6. The favourite food of haddock *Melanogrammus aeglefinus* are microscopic crustaceans *Calanus finmarchicus.* A simplified model describing the interaction of the populations of the two species in the Irish Sea, in suitably chosen units, has the form

$$\begin{aligned} \mathrm{d}N_1/\mathrm{d}t &= N_1(1-N_1) - \frac{6N_1N_2}{4N_1+1}, \\ \mathrm{d}N_2/\mathrm{d}t &= sN_2(1-N_2/N_1), \end{aligned} \tag{5}$$

where $s > 0$ is a dimensionless parameter.

(a) Explain which of the variables N_1, N_2 describes predators (fish) and which describes prey (crustaceans)? Describe the biological significance of all the terms in this model. What is the Holling class of the functional response of the predators?

(6 marks)

(b) Find all biologically feasible equilbria possible in this model. Find the community matrix associated with the equilibrium (N_1^*, N_2^*), corresponding to survival of both species, as a function of the parameter s. Investigate the stability of that equilibrium for $s = 1$.

(6 marks)

(c) State the theorem by Hopf and others about the birth of a limit cycle in a system where an equilibrium changes its stability due to a change in the system parameters.

(4 marks)

(d) An expert analysis of possible consequences of environmental changes and fishing policy predicts a decrease of parameter s in the model. Find the value of parameter s which corresponds to the loss of stability of the equilibrium (N_1^*, N_2^*) via the Hopf bifurcation. Calculate the period of oscillations at the critical value of the parameter s.

(4 marks)

7. The interaction between a host and a parasitoid is described using the discrete-time model of Nicholson and Bailey,

$$\begin{aligned} X_{t+1} &= kX_t e^{-aY_t}, \\ Y_{t+1} &= mX_t\left(1 - e^{-aY_t}\right), \end{aligned} \tag{6}$$

with parameters $a > 0$ and $k > 0$.

(a) State, giving reasons, which of the two variables describes the hosts and which describes the parasitoids. Explain the biological significance of the coefficients k and m and the factor e^{-aY_t} in these equations.

(5 marks)

(b) From now on, assume that $m = k$. For system (6), determine the conditions on the parameters a and k at which a biologically feasible nonzero equilibrium (X^*, Y^*) exists, and find this equilibrium.

(4 marks)

(c) Given that x_t, y_t are the respective deviations of the densities X_t, Y_t from their equilibrium values X_*, Y_* at the time t, show that if both x_t and y_t are small, then in the linear approximation, their growth in one generation is described by the factor μ which is a root of

$$\mu^2 - \left(1 + \frac{\ln(k)}{k-1}\right)\mu + \frac{k\ln(k)}{k-1} = 0.$$

Show that $\frac{k\ln(k)}{k-1} > 1$ for all $k > 1$. Hence, by referring to a diagram involving a stability triangle, or otherwise, show that the equilibrium (X_*, Y_*) is unstable with divergent oscillations for all values $k > 1$.

(7 marks)

(d) Show that, in the case $k = 1.01$, the oscillations are diverging very slowly and find their period to 2 significant figures.

(4 marks)