SUMMER 2003 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 endangered species of Cuban crocodiles *Crocodylus rhombifer* have a very long natural life expectancy and practically all their mortality is due to intraspecific competition. Dynamics of their population during a typical year is described by the following model:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \begin{cases} rN - mN^2, & \text{if } 0 < t < s, \\ -mN^2, & \text{if } s < t < 1. \end{cases} \tag{1}$$

Here N is the density of the population and time t is measured from the beginning of summer. The time unit is 1 year, and $0 < s < 1$.

(a) Explain the biological significance of the parameters s, r and m. What is the carrying capacity of the system for $t \in (0, s)$? There is no linear term in the right-hand side of (1) for $t \in (s, 1)$. Suggest what biological reality is reflected by this mathematical fact.

(5 marks)

(b) Integrate the differential equation (1) for $t \in (0, s)$ by separation of variables or otherwise, and show that

$$N(s) = \frac{e^{rs} N(0)}{1 + mN(0)\left(e^{rs} - 1\right)/r}.$$

(5 marks)

(c) By considering the limit $r \to 0$ in the previous result, or by integrating the differential equation (1) for $t \in (s, 1)$ by separation of variables, or otherwise, show that

$$N(1) = \frac{N(s)}{1 + m(1 - s)N(s)}.$$

(5 marks)

(d) By combining results of parts 1b and 1c, show that the long-term dynamics of the crocodile population can be described by the following discrete-time model:

$$N_{n+1} = \frac{RN_n}{1 + aN_n}$$

where N_n is the population size in the beginning of year n. Find coefficients R, a of this discrete-time model in terms of coefficients r, m, s of the original continuous-time model (1).

(5 marks)

2. Truscott and Brindley (1994) have suggested a model describing dynamics of plankton in the North Sea. In that model, the equation for the biomass of phytoplankton (microscopic algae), in suitably chosen units, is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx(1 - x/K) - \frac{x^2}{x^2 + 1}z \tag{2}$$

where x is phytoplankton biomass concentration and z is the biomass concentration of the zooplankton (microscopic crustaceans) grazing on the phytoplankton. For the purposes of the present problem, z can be considered constant, r and K are constant parameters.

(a) Explain biological significance of the two terms in the right-hand side of this equation, and of the parameters r and K. What is the Holling type of the predatory response of zooplankton to phytoplankton?

(5 marks)

(b) Assume from now on that $z = 1$. Draw carefully the graph of the function $y = f(x) = x/(x^2 + 1)$ in the range $x \in [0, 15]$. Explain how it can be used to find graphically the equilibrium values of x in this model. Use this method to demonstrate that at $K = 15$ and $r = 0.4$, there are three positive equilibrium states, and roughly estimate their values.

(7 marks)

(c) Based on the graphical method discussed in part 2b, or otherwise, derive conditions on parameters r, K and x for the bifurcation of double equilibria in this model. Solve these conditions for r and K as explicit functions of the double equilibrium position x.

(4 marks)

(d) In the end of winter, the parameters of the North Sea were $r \approx 0.4$ and $K \approx 15$, and the phytoplanton density was $x \approx 0.5$. During the spring, r and K slowly increased, and phytoplankton density x slowly increased too, until the "spring bloom", i.e. a sudden increase of the phytoplankton density to a very high value ($x > 20$), occurred. Use the result of part 2c to find, to 2 significant figures, what were the values of the parameters r and K at that moment, if the phytoplankton density immediately before the bloom was $x = 1.05$.

(4 marks)

3. The behaviour of a community of cowpea weevil *Callosobruchus maculatus* can be described by the discrete-time Hassell model:

$$N_{t+1} = \frac{RN_t}{(1 + aN_{t-T})^b} \tag{3}$$

(a) Explain the biological significance of the parameters R, a, b and T in this model. *(4 marks)*

(b) Find the equilibria in this model and the ranges of parameter values at which they exist and are biologically feasible. In particular, specify the equilibria possible for parameter values $a = 1$, $b = 2$ and $R = 9$.

(5 marks)

(c) Consider the case of $T = 0$, $a = 1$, $b = 2$ and $R = 9$. Sketch a cobweb or ladder diagram for this model, with the initial condition $x_0 = 0.1$. Deduce from it whether or not the nontrivial equilibrium in this model is stable. Is this equilibrium monotonic or oscillatory?

(5 marks)

(d) Consider the case of $T = 1$, $a = 1$, $b = 2$ and $R = 9$. Using the substitution $N_t = N^* + h_t$, where N^* is the nontrivial equilibrium, and $|h_t|$ is small, verify that the behaviour of the system close to this equilibrium is described by

$$h_{t+1} - h_t + \frac{4}{3}h_{t-1} = 0.$$

Hence show that this equilibrium is oscillatory unstable.

(6 marks)

4. The population of Kokanee salmon *Oncorhynchus nerka kennerlyi* living around lake Okanagan in British Columbia consists of five age groups: age 0 (eggs, larvae and fries) and 1 year old through to 4 years old fish. The fraction of the age 0 group surviving to age 1 is p_0; the fraction of the age 1 group surviving to age 2 is p_1 and the fraction of age 2 group surviving to age 3 is p_2. Half of the age 3 fish spawn at that age, producing Q eggs each in average and die after that; a fraction $p_3 < 1/2$ of age 3 fish (i.e. some of those who did not spawn) live on to age 4; the rest die without spawning. Of the age 4 fish, half spawn $2Q$ eggs each in average and die, and the other half dies without spawning, so none survive to age 5. This dynamics can be described by Leslie model

$$\mathbf{N}_{t+1} = \mathbf{L}\mathbf{N}_t \tag{4}$$

where $\mathbf{N}_t = (N_t^0, \dots N_t^4)^T$ is the column-vector describing the population in year t, and N_t^j is the size of the j-th age group at that year.

(a) Write down the system of discrete time evolution equations for the fish age groups. Thus construct the Leslie transition matrix $\mathbf{L}$.

(4 marks)

(b) Find the characteristic polynomial $P(\lambda)$ for $\mathbf{L}$. By considering the function $P(\lambda)/\lambda^5$ for positive λ, show that for all $p_0, \dots, p_3$ and Q positive, this polynomial always has exactly one positive root.

(9 marks)

(c) Recent years' observations have shown that $Q \approx 1000$ and that the population of fish each year is approximately $1/\sqrt{2}$ times the population the previous year. Assuming that $p_3 = 2^{-3/2}$, estimate the probability of a fish egg to survive to the mature stage (year 3). Find the stationary age distribution in terms of parameters p_0 and p_1. In particular, determine the established ratio of numbers of 3-year-old and 4-year-old fish.

(7 marks)

5. About 40 thousand years ago, the well established existence of the European population of *Homo neanderthalensis* has been challenged by a new aggressive species *Homo sapiens* which invaded from Africa. The two species competed for mammoths and caves, and their interaction could be described by a Lotka-Volterra-Gause model

$$\begin{aligned} \mathrm{d}N_1/\mathrm{d}t &= N_1\,(r_1 - a_1N_1 - b_{12}N_2) \\ \mathrm{d}N_2/\mathrm{d}t &= N_2\,(r_2 - a_2N_2 - b_{21}N_1) \end{aligned} \tag{5}$$

where N_1 and N_2 are densities of *H. sapiens* and *H. neanderthalensis* respectively, and the numerical values of the coefficients, in appropriate units, are $r_1 = 5$, $r_2 = 4$, $a_1 = a_2 = 2$, $b_{12} = b_{21} = 1$.

(a) Describe the biological significance of the parameters r_j, a_j and b_{jk}.

(3 marks)

(b) Assuming that the two species actually coexisted for some time, find their equilibrium densities. By how much did this unfortunate invasion decrease the population of the Neanderthals?

(6 marks)

(c) Rewrite the model (5) for new dynamic variables x, y defined by

$$N_1 = 2 + x, \qquad N_2 = 1 + y.$$

Find the orbit derivative of function V defined as

$$V(x, y) = x^2 + xy + y^2$$

and show that it is negatively definite in the region $\{N_1 > 0, N_2 > 0\} = \{x > -2, y > -1\}$. What does this result mean for (i) stability of the coexistence equilibrium, (ii) possibility of periodic solution in this model?

(7 marks)

(d) Only a few thousand years after the invasion, *H. sapiens* outperformed their competitors by inventing bone needles, which allowed them to make clothes out of mammoth wool and thus significantly decreased mortality due to harsh weather conditions. Specify which parameter in the model (5) would describe that change. Assuming that that was the only factor, find out the minimal change in that parameter necessary for complete extinction of the Neanderthals.

(4 marks)

6. The tachinid fly *Myiopharus doryphorae* parasitises on the beetle *Leptinotarsa decemlineata*, which is also known as the Colorado beetle and is a ferocious pest of potato plantations. An ecologically aware potato farmer decided, rather than using insecticides, to combat the beetles by keeping a population of these useful flies. Based on his own observation of the insects, the farmer developed a variant of the Lotka-Volterra predator-prey model to describe the interaction of the two species:

$$\begin{aligned} \frac{\mathrm{d}B}{\mathrm{d}t} &= B - B^2 - BF, \\ \frac{\mathrm{d}F}{\mathrm{d}t} &= BF - F^2. \end{aligned} \tag{6}$$

where B stands for the population of the beetles and F for the population of the flies.

(a) Describe the biological meaning of each of the five terms in the right-hand sides of equations (6).

(5 marks)

(b) Find the equilibria in this model and classify their stability. Thus explain why the farmer's first attempt to exterminate the beetles has failed.

(10 marks)

(c) Inspired by this mathematical model, the farmer has decided that he may be more successful if he supports his useful flies with some additional food source, which would allow them to survive even in the complete absence of beetles. To reflect this change, he modified his model in the following way:

$$\begin{aligned} \frac{\mathrm{d}B}{\mathrm{d}t} &= B - B^2 - BF, \\ \frac{\mathrm{d}F}{\mathrm{d}t} &= sF + BF - F^2, \end{aligned}$$

where parameter s represents the additional reproduction rate of the flies due to the supplement. Find what values of s would be sufficient to get rid of the beetles by making their coexistence with the flies impossible. Verify that the beetle-free existence of the flies in that case will be stable.

(5 marks)

7. To describe Bombay plague epidemic of 1905-6, Kermack and McKendrick (1927) have suggested the following model

$$\begin{aligned} \mathrm{d}S/\mathrm{d}t &= -\beta S I \\ \mathrm{d}I/\mathrm{d}t &= \beta S I - \nu I \end{aligned} \qquad (7)$$

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

(a) Explain the biological meaning of the terms in these equations, and what biological assumptions have been used in this model.

(6 marks)

(b) Perform the phase-plane analysis of the model (7): 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) The Bombay epidemic involved only a small fraction of the city population. Substitute $S = \nu/\beta + \sigma$ into (7) and assume that $|\sigma|$ and I are small. Simplify the first equation by keeping the main term and neglecting the smaller term. Verify by substitution that the following functions are a solution to the resulting system, for arbitrary p:

$$\sigma = -\frac{2}{\beta} p \tanh(pt); \qquad I = \frac{2}{\nu\beta} p^2 \operatorname{sech}^2(pt)$$

(remember that $(\tanh x)' = \operatorname{sech}^2 x = 1 - \tanh^2 x$).

(4 marks)

(d) The number of deaths per week in the Bombay epidemic can be approximately described by the following dependence:

$$800 \ \operatorname{sech}^2(0.2t),$$

where time is measured from the middle of the epidemic. Using the analytical solution discussed in part 7c, what information about the parameters of the model can be deduced from these statistical data?

(4 marks)