Math332 January 2005 exam: solutions

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.

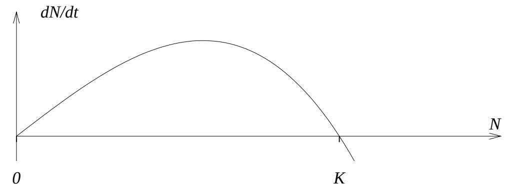
(a) **Question** *Explain the biological meaning of the function in the right hand side of equation (1) and of the parameters r and K.*

Answer This is a quasi-Malthusian form, where the reproduction coefficient decreases with the growth of the population, because of the intraspecific competition. r: the maximal, low-density, reproduction rate of the population . K: carrying capacity of the system .

4 marks for this part

(b) **Question** *Sketch the graph of the function in the right hand side of equation (1) for $N \geq 0$.*

Answer



Question *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.*

Answer Besides $N = 0$, the graph crosses the horizontal axis at only one point $N = K$, which is thus the requested nonzero equilibrium. The function is positive for $N < K$ and negative for $N > K$ therefore $N = K$ is stable with basin of attraction $(0, +\infty)$.

5 marks for this part

(c) **Question** *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*

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

Answer If $u = N^{-2}$, then $\mathrm{d}u/\mathrm{d}t = -2N^{-3}\mathrm{d}N/\mathrm{d}t$, then according to (1), we have

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -2N^{-3}rN(1 - N^2/K^2) = -2r(N^{-2} - K^{-2}) = 2r(K^{-2} - u).$$

This is a linear equation, its general solution is $u = K^{-2} + Ce^{-2rt}$. From initial conditions we determine $C = N_0^{-2} - K^{-2}$, so ultimately

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

as requested.

Question *Determine the behaviour of a typical solution in the limit $t \to +\infty$.*

Answer $N(t) \to K$ for any $N_0 > 0$.

Question *Compare this with your previous conclusion about the stability of the single nonzero equilibrium.*

Answer Both predict that K is stable with the basin of attraction $(0, +\infty)$

7 marks for this part

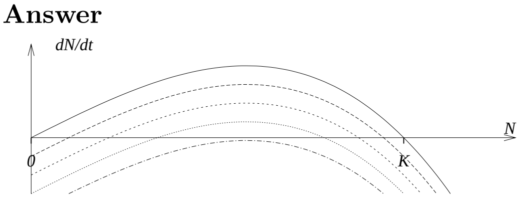
(d)

Question *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 $Y \geq 0$.

Answer



Question *Use it to explain how the population will respond to harvesting.*

Answer The stable population size will decrease as long as the graph of the right hand side intersects with the N axis; if Y is increased beyond that, the population will collaps.

Question *What is the maximal sustainable yield of the population?*

Answer As seen from the graph, intersection exists as long as Y does not exceed the maximum of $rN(1-(N/K)^2)$. This maximum is attained at $N = K/\sqrt{3}$ and is $Y_{\max} = 2rK/(3\sqrt{3})$.

4 marks for this part

Total for this question: 20 marks

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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) **Question** *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.*

Answer N_1 will be nonnegative iff $N_0 \in [0, 1]$. Maximum of function $F(x)$ is $R/4$ achieved at $x = 1/2 \in [0, 1]$, thus function $F(x)$ maps interval $[0, 1]$ onto the interval $[0, R/4]$. Thus $f : [0, 1] \to [0, 1]$ iff $R \in (0, 4]$

4 marks for this part

(b) **Question** *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.*

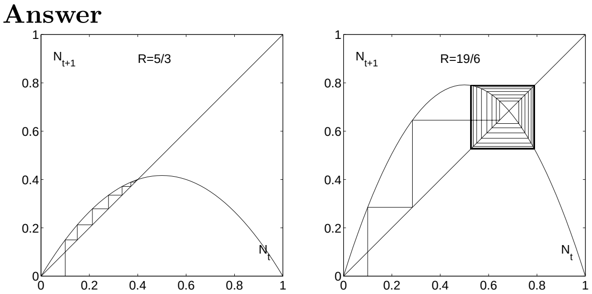
Answer Equilibrium N_* is a solution of equation $N_* = F(N_*)$ which for positive N_* requires $1 = R(1-N_*)$, or $N_* = 1 - 1/R$. It is positive if $R > 1$. Stability requires $|F'(N_*)| < 1$, which gives $|R(1 - 2N_*)| < 1$, $|R(1 - 2 + 2/R| < 1$, $-1 < -R + 2 < 1$, and finally $R \in (1, 3)$. We have $5/3 \in (1, 3)$ so equilibrium of *C. chinensis* is stable, and $19/6 \notin (1, 3)$ so equilibrium of *C. maculatus* is unstable.

5 marks for this part

(c)

Question *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 $N_0 = 0.1$.*

Answer



5 marks for this part

(d) **Question** *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).*

Answer $F(F(x)) = RF(x)(1 - F(x)) = R^2x(1-x)(1 - Rx(1-x))$.

Question *Express this second iteration function as a polynomial and determine its coefficients.*

Answer $F(F(x)) = R^2x(1-x)(Rx^2 - Rx + 1) = R^2x(-Rx^3 + Rx^2 + Rx^2 - Rx - x + 1 = -R^3x^4 - 2R^3x^3 - (R^3 + R^2)x^2 + R^2x$.

Question *Write down two point equilibria of this particular recurrence relation.*

Answer We already know two equilibria, i.e. two solutions to the equation $N = F(F(N))$. These are: $N_1 = 0$ and $N_2 = (R-1)/R$, which are equilibria of the original mapping, i.e. satisfy $N = F(N)$.

Question *Hence show that the the remaining point equilibiria are roots of the quadratic*

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

Answer Equation for the equlibria is $x - F(F(x)) = 0$, or $R^3x^4 + 2R^3x^3 + (R^3 + R^2)x^2 + (1 - R^2)x = 0$. To show the required, it is enough to obtain the same by multiplying out $x(Rx - R + 1)(R^2x^2 - R(R + 1)x + R + 1)$.

Question *Find these two solutions for C. maculatus and verify that these solutions are transformed one into the other by $F(x)$.*

Answer For $R = 19/6$, solutions of the quadratic $R^2x^2 - R(R+1)x + R + 1 = 0$ are $N_3 = 10/19$ and $N_4 = 15/19$. Direct calculation gives $F(10/19) = 15/19$ and $F(15/19) = 10/19$.

Question *Explain what this means for the evolution of the population.*

Answer This means that population of *C. maculatus* in the long run will oscillate with period 2 between these two values.

6 marks for this part

Total for this question: 20 marks

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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) **Question** *Suggest a biological interpretation of the terms in this model.*

Answer First term: egg hatching rate , Second term: decrease in the hatching rate due to density-depending decrease in laying . Third term: density-dependent mortality .

Question *Explain how one can see that, according to this model, the natural life expectancy of the birds in favourable conditions was very long.*

Answer The per capita death rate is mN, i.e. negligible at small N.

4 marks for this part

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

Answer (1) $N = 0$ (2) $N = b/(c+m)$ both exist for all positive parameters values .

3 marks for this part

(c) **Question** *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.*

Answer $\frac{\mathrm{d}h}{\mathrm{d}t}(t) = (b - 2cN_*)h(t-T) - 2mN_*h(t)$

Question *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*

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

Answer The suggested substitution, together with $N_* = b/(c+m)$, gives

$$\mu h_0 e^{\mu t} = \left(b - 2c\frac{b}{c+m}\right) h_0 e^{\mu(t-T)} - \frac{2mb}{c+m} h_0 e^{\mu(t)}$$

which, after cancelling $h_0 e^{\mu t}$ and simplifications becomes $\mu = \frac{b}{c+m}\left((m-c)e^{-\mu T} - 2m\right)$ from where the required equation (3a) follows

Question *Show that for $T = 0$ the equilibrium is stable,*

Answer If $T = 0$, (3a) becomes $m - c = 2m + (c+m)\mu/b$ from where $\mu = -b < 0$ i.e. asymptotic stability as required

Question *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:*

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

Answer When parameter T is continuously increased, any solution μ of (3a) changes continuously, as does its real part. When $\mathrm{Re}\,(\mu)$ changes sign from negative to positive, it goes through zero; at this moment $\mathrm{Re}\,(\mu) = 0$, and $\mu = i\omega$ for some ω. Substituting $\mu = i\omega$ into (3a) and separating real and imaginary parts, leads immediately to the system (3b).

7 marks for this part

(d) **Question** *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.*

Answer We need to satisfy equtions (3b), given that period of oscillations $2\pi/\omega = 3T$, i.e. $\omega T = 2\pi/3$. Thus $\cos(\omega T) = -1/2$, and the first of equations (3b) gives $c - m = 4m$, i.e. $c/m = 5$. Also, $\sin(\omega T) = \sqrt{3}/2$, and this together with the information on c/m transforms the second of equations (3b) into

$$4m \times \frac{\sqrt{3}}{2} = 6m\omega/b$$

from where

$$b = \omega\sqrt{3} = \sqrt{3}\frac{2\pi}{3T} = \frac{2\pi}{T\sqrt{3}}.$$

6 marks for this part

Total for this question: 20 marks

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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:*

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

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) **Question** *Explain briefly why this model simulates both intraspecific an interspecific competition,*

Answer Intraspecific competition: the denominator increases with increase of the same species. Interspecific competition: the denominator increases with increase of the competing species.

Question *and what is the biological significance of parameters β, R_1 and R_2.*

Answer β: the intensity of the interspecific competition. $R_{1,2}$: the low-density reproduction coefficients of the species 1 and 2 respectively.

4 marks for this part

(b) **Question** *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.*

Answer Equilibrium state satisfies $N_1^* = R_1 N_1^*/(1 + N_1^* + \beta N_2^*)$, $N_2^* = R_2 N_2^*/(1 + N_2^* + \beta N_1^*)$. As $N_{1,2}^* \neq 0$, this leads to system

$$N_1^* + \beta N_2^* = R_1^* - 1, \qquad N_2^* + \beta N_1^* = R_2^* - 1,$$

which has solution $N_1^* = \frac{\beta(R_2-1)-(R_1-1)}{\beta^2 2-1}$ and $N_2^* = \frac{\beta(R_1-1)-(R_2-1)}{\beta^2 2-1}$.

Question *Explain why $\beta > (R_2 - 1)/(R_1 - 1)$.*

Answer Since $\beta > 1$, positivity of $N_{1,2}^*$ requires positivity of both numerators. Thus β should exceed the larger of $(R_2 - 1)/(R_1 - 1)$ and $(R_1 - 1)/(R_2 - 1)$, and since $R_2 > R_1$, the required follows.

5 marks for this part

(c) **Question** *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 $p_j = N_j/R_j$, $j = 1,2$.

Answer Denoting the right-hand sides of the model equations as $F_1(x,y) = R_1x/(1+x+\beta y)$ and $F_2(x,y) = R_2y/(1+\beta x+y)$ for $x = N_1(t)$, $y = N_2(t)$, we have $\partial F_1/\partial x = R_1\frac{1+\beta y}{(1+x+\beta y)^2}$, which for $(x,y) = (N_1^*, N_2^*)$ as calculated above, becomes $1 - N_1^*/R_1 = 1 - p_1$ as requested. Also, $\partial F_1/\partial y = -\frac{\beta R_1 x}{(1+x+\beta y)^2} = -\beta N_1^*/R_1 = -\beta p_1$ as requested. Derivatives of F_2 are calculated similarly.

5 marks for this part

(d) **Question** *Show that the eigenvalues of* $\mathbf{A}$ *are always real and hence the equilibrium is always monotonic.*

Answer The characteristic equation is $\det(\mathbf{A} - \mu\mathbf{I}) = \mu^2 - \mathrm{Tr}\,\mathbf{A}\,\mu + \det\mathbf{A}$ and its discriminant is $\mathrm{Tr}\mathbf{A}^2 - 4\det\mathbf{A} = (p_1 - p_2)^2 + 4\beta^2 2p_1p_2 > 0$ thus there are always two real roots.

Question *Show that if Q is an asymptotically stable state,*

$$\beta < 1.$$

Answer One of conditions of stability is $\det\mathbf{A}+1 > \mathrm{Tr}\mathbf{A}$. This gives $(1-p_1)(1-p_2) - \beta^2 p_1p_2 + 1 > 2 - p_1 - p_2$, and the required follows.

6 marks for this part

Total for this question: 20 marks

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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) **Question** *Find all the equilibria in this model.*

Answer

- Q_0: $N_1 = N_2 = 0$ — extinction of both species.
- Q_1: $N_2 = 0, N_1 = 1/2$ — extinction of the second species.
- Q_2: $N_1 = 0, N_2 = 1$ — extinction of the first species.
- Q_{12}: Coexistence — both species survive. Then $\mathrm{d}N_1/\mathrm{d}t = \mathrm{d}N_2/\mathrm{d}t = 0$ leads to the system

$$2N_1 + 2N_2 = 1 \qquad 4N_1 + N_2 = 1$$

the unique solution of which is $N_1 = 1/6, N_2 = 1/3$.

4 marks for this part

(b) **Question** *For each of the equilibria, find the community matrix and its eigenvalues. Classify the equilibria.*

Answer The the Jacobian of the right-hand sides for arbitrary N_1, N_2 is

$$\mathbf{A} = \begin{bmatrix} 1 - 4N_1 - 2N_2 & -2N_1 \\ -4N_2 & 1 - 3N_1 - 2N_2 \end{bmatrix}.$$

For the four equilibria this gives the following community matrices $\mathbf{A}$ and eigenvalues λ_{12}.

- $Q_0(0,0)$: $\mathbf{A} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$, $\lambda_1 = \lambda_2 = 1$, unstable node..
- $Q_1(1/2,0)$: $\mathbf{A} = \begin{bmatrix} -1 & -1 \\ 0 & -1/2 \end{bmatrix}$, $\lambda_1 = -1$, $\lambda_2 = -1/2$, stable node.
- $Q_2(0,1)$: $\mathbf{A} = \begin{bmatrix} -1 & 0 \\ -4 & -1 \end{bmatrix}$, $\lambda_1 = \lambda_2 = -1$, stable node.

- $Q_{12}(1/6, 1/3)$: $\mathbf{A} = \begin{bmatrix} -1/3 & -1/3 \\ -4/3 & 1/3 \end{bmatrix}$, $\lambda_{1,2} = \pm\sqrt{5}/3$, saddle point

Question *Find also eigenvectors for the equilibrium in which both species survive.*

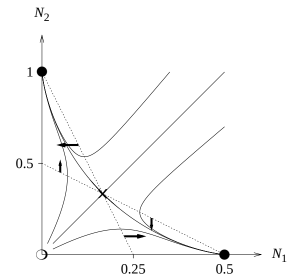
Answer For $\lambda_1 = \sqrt{5}/3$, $\mathbf{v}_1 = \begin{bmatrix} -1 \\ \sqrt{5}+1 \end{bmatrix}$; for $\lambda_2 = -\sqrt{5}/3$, $\mathbf{v}_1 = \begin{bmatrix} 1 \\ \sqrt{5}-1 \end{bmatrix}$.

6 marks for this part

(c) **Question** *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.*

Answer

The picture on the right shows the following features: (a) Null-clines (thin dashed lines), with direction of crossing of the nullclines shown by arrows; (b) Equilibria: the open circle=the unstable node; the filled circles=the stable nodes, the cross=the saddle point; (c) The four eparatrices of the saddle point (bold dashed lines). (d) Four typical trajectories, one from each class (thin solid lines).



Question *Are there any chances for the red squirrels to survive and what does that mean for the grey squirrels?*

Answer There are two stable equilibria in this system; for either of them, survival of one species corresponds to extinction of the other. Thus, red squirrels may survive if initial conditions are in the corresponding basin of attraction; in that case the grey squirrels will be extinct.

5 marks for this part

(d) **Question** *Determine the orbit derivative of the function $V = 2N_1 - N_2$.*

Answer $\mathrm{d}V/\mathrm{d}t = 2\frac{\mathrm{d}N_1}{\mathrm{d}t} - \frac{\mathrm{d}N_2}{\mathrm{d}t} = 2N_1(1 - 2N_1 - 2N_2) - N_2(1 - N_2 - 4N_1)$.

Question *Use it to prove that the line $N_2 = 2N_1$ is an invariant set.*

Answer Another definition for this line would be $V = 0$. Substitution of $N_2 = 2N_1$ gives $\mathrm{d}V/\mathrm{d}t = 2N_1(1 - 6N_1) - 2N_1(1 - 6N_1) = 0$. Thus, $V = 0 \Rightarrow \mathrm{d}V/\mathrm{d}t = 0$ and $\{V = 0\}$ is an invariant set q.e.d.

Question *Deduce from there, what would be the ultimate state of the system as $t \to +\infty$, if $N_1(0) = N_2(0) = 1$.*

Answer The invariant set $N_2 = 2N_1$ separates the phase plane onto two parts, either of which contains its own stable equilibrium, thus it is the separatrix. Therefore, the system will approach as $t \to +\infty$ that equilibrium which is on the same side of the line $N_2 = 2N_1$ that the initial condition $(N_1(0), N_2(0)) = (1, 1)$. This is $Q_1 = (1/2, 0)$, i.e. survival of grey squirrels and extintion of red squirrels.

5 marks for this part

Total for this question: 20 marks

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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) **Question** *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?*

Answer The right hand side of equation for $\mathrm{d}N_1/\mathrm{d}t$ decreases with N_2; the right hand side of equation for $\mathrm{d}N_2/\mathrm{d}t$ increases with N_1. So the first species suffers from the second, while the second benefits from the first. Therefore, the first species are the prey and the second species are the predators. In the first equation, the first term: Verhulst dynamics describing intraspecific competition of the prey. Second term in the first equation: mortality of prey due to predation, this is Holling type 2 functional response of predators. The second equation describes Verhulst intraspecific competition of predators, where the carrying capacity is determined by the density of the prey population.

6 marks for this part

(b) **Question** *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 $s = 1$.*

Answer Due to N_1 in the denominator, there are no equilibria with $N_1 = 0$. Thus we have only monopolistic survival of prey $(N_1, N_2) = (1, 0)$, or the coexistence, which is a solution of system

$$1 - N_1 - \frac{6N_2}{4N_1 + 1} = 0, \qquad 1 - N_2/N_1 = 0,$$

the only positive solution of which is $(N_1, N_2) = (1/4, 1/4)$. The Jacobian of the right-hand sides is $\mathbf{J} = \begin{bmatrix} 1 - 2N_1 - \frac{6N_2}{(4N_1+1)^2} & -\frac{6}{4N_1+1} \\ sN_2^2/N_1^2 & s(1 - 2N_2/N_1) \end{bmatrix}$. For $(N_1, N_2) = (1/4, 1/4)$ this gives community matrix $\mathbf{A} = \begin{bmatrix} 1/8 & -3 \\ s & -s \end{bmatrix}$ For $s = 1$, we have $\mathrm{Tr}\mathbf{A} = -7/8$, $\det \mathbf{A} = 23/8$, $\lambda^2 + \frac{7}{8}\lambda + \frac{23}{8} = 0$, $\lambda_{1,2} = -\frac{7}{16} \pm i\frac{\sqrt{687}}{16}$ so it is a stable focus.

6 marks for this part

(c) **Question** *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.*

Answer

4 marks for this part

(d) **Question** *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.*

Answer Hopf bifurcation corresponds to $\mathrm{Re}\,(\lambda) = 0$ and $\mathrm{Im}\,(\lambda) \neq 0$. The first of conditions is satisfied when $\mathrm{Tr}\mathbf{A} = \frac{1}{8} - s = 0$ so the critical value of the parameter is $s_{crit} = 1/8$. At that value of the parameter, $\omega = \mathrm{Im}\,(\lambda) = \sqrt{\begin{bmatrix} 1/8 & -3 \\ 1/8 & -1/8 \end{bmatrix}} = \sqrt{23}/8$, so the period of oscillations is $P = 2\pi/\omega = 16\pi/\sqrt{23} \approx 10.48$.

4 marks for this part

Total for this question: 20 marks

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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) **Question** *State, giving reasons, which of the two variables describes the hosts and which describes the parasitoids.*

Answer Population X will multiply exponentially in absence of Y, thus it is the population of hosts. Population Y will disappear in one generation in absence of X, thus it is the population of parasitoids.

Question *Explain the biological significance of the coefficients k and m and the factor e^{-aY_t} in these equations.*

Answer k, host reproduction coefficient without parasitoids; m, number of parasitoids progeny per parasitized host; e^{-aW_t}, probability of for a host to escape parasitism;

5 marks for this part

(b) **Question** *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.*

Answer For equilibrium we have

$$X_* = kX_* e^{-aY_*}, \qquad Y_* = kX_* \left(1 - e^{-aY_*}\right)$$

Since $X_* \neq 0$, cancelling it in the first equation, we find $Y_* = \ln(k)/a$. Then substituting this into the second equation, find $X_* = \dfrac{\ln(k)}{a(k-1)}$. This equilibrium is feasible for all $k > 1$ with no further restrictions on a.

4 marks for this part

(c) **Question** *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*

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

Answer The linearisation gives

$$x_{t+1} = kx_t e^{-aY_*} - kaX_* e^{-aY*} y_t, \qquad y_{t+1} = kx_t(1 - e^{-aY_*}) + kaB_* e^{-aY*} y_t.$$

or, after substituting the values of X_* and Y_*,

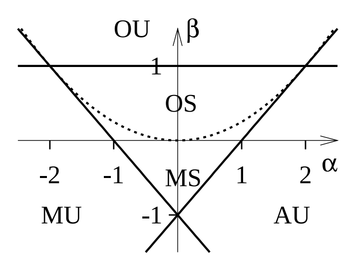
$$x_{t+1} = x_t - \frac{\ln(k)}{k-1} y_t \qquad y_{t+1} = (k-1)x_t + \frac{\ln(k)}{k-1} y_t.$$

The associated community matrix is therefore $\mathbf{L} = \begin{bmatrix} 1 & -\frac{\ln k}{k-1} \\ k-1 & \frac{\ln k}{k-1} \end{bmatrix}$ and its characteristic equation is $\det(\mathbf{L} - \mu\mathbf{I}) = \mu^2 - (1 + \frac{\ln k}{k-1})\mu + \frac{k \ln k}{k-1} = 0$ as requested

Question *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 $k > 1$.*

Answer

Let us consider functions $f_1(k) = k\ln(k)$ and $f_2(k) = k - 1$. As $f_1(1) = f_2(1) = 0$, and $\mathrm{d}f_1/\mathrm{d}k = 1 + \ln(k) > \mathrm{d}f_2/\mathrm{d}k = 1$ for all $k > 1$, thus $f_1(k) > f_2(k)$ for all $k > 1$, which is equivalent to $f_1(k)/f_2(k) > 1$ as requested. Stability triangle for equation $\mu^2 + \alpha\mu + \beta = 0$ is shown on the right. In our case $\beta = \frac{k\ln k}{k-1} > 1$, and the system is above the oscillatory instability line $\beta = 1$, — as requested.



7 marks for this part

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

Answer For $k = 1.01$, the characteristic equation has roots $\mu_{1,2} \approx 0.9975 \pm 0.09972i$. We see that $|\mu_{1,2}|$ is very close to 1 thus oscillations are diverging slowly. The period is $T = 2\pi/|\arg(\mu_{1,2})|$ which gives $T \approx 63$.

4 marks for this part

Total for this question: 20 marks