Math332 Summer 2004 exam: solutions

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.

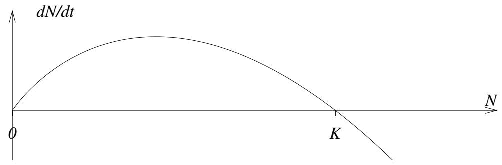
(a) **Question** *Explain the biological meaning of the terms rN and $-rN\sqrt{N/K}$ in the right hand side of (1) and of the parameters r and K.*

Answer First term: growth of the population without account of the intraspecific competition. Second term: decrease of the growth rate due to intraspecific competition. r: the maximal per capita reproduction rate 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 the above equation 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, and characterise its stability (including the basin of attraction if appropriate).*

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

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

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

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

This is a linear equation, its general solution is $u = K^{-1/2} + Ce^{-rt/2}$. From initial conditions we determine $C = N_0^{-1/2} - K^{-1/2}$, so ultimately

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

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 conclusions about the stability and the basin 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** *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.

Answer Replacing in (1a) $N(0) \to N(t)$, $N(t) \to N(t+T)$, $t \to T$, we get
$N(t+T) = \left(K^{-1/2}(1-e^{-rT/2}) + N(t)^{-1/2}e^{-rT/2}\right)^{-2} = \left(N(t)^{-1/2}e^{-rT/2}((e^{rT/2}-1)N(t)^{1/2}K^{-1/2}+1\right)^{-2} = \frac{e^{rT}N(t)}{\left(1+(e^{rT/2}-1)K^{-1/2}N(t)^{1/2}\right)^2}$ as requested, with $R = e^{rT}$ and $a = (e^{rT/2} - 1)K^{-1/2}$.

Question *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).*

Answer Since this model is in exact correspondence equivalent of (1), the stable equilibrium $N = K$ of (1) is also a stable equilibrium of this model, with the same basin of attraction $(0, +\infty)$.

4 marks for this part

Total for this question: 20 marks

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

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

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

(a) **Question** *Explain the biological meaning of the numerator (RN_t) and of the denominator ($(1+aN_t)^b$) in this formula.*

Answer Numerator: growth of the population without account of the intraspecific competition. Denominator: decrease of the growth rate due to intraspecific competition.

Question *Give biological interpretations of the three parameters R, a and b.*

Answer R: if N is so small the denominator can be replaced with 1, the dynamic equation becomes Malthusian with R as the reproduction coefficient. Thus R is the low-density reproduction coefficient, or r.c. in the absence of intraspecific competition. b: all other things being equal, the denominator increases with b increasing, so this parameter characterizes intensity of the i.s.c. a: at a fixed value of b, it is the combination aN_t that determines the i.s.c., so i.s.c. is negligible when $aN_1 \ll 1$ and becomes significant when $aN_t \sim 1$ or more. Thus a is the inverse of the typical population after which the i.s.c. is significant.

5 marks for this part

(b) **Question** *Find the non-zero equilibrium value, N_*, in this model.*

Answer

$$\frac{RN}{(1+aN)^b} = F(N) = N, \quad N \neq 0 \quad \Rightarrow N = \underline{N_* = \frac{R^{1/b} - 1}{a}}$$

Question *Determine the local stability condition for this equilibrium in terms of R and b.*

Answer Stability condition is $-1 < F'(N_*) < 1$. We have N_*, $F'(N) = R\frac{1+(1-b)aN}{(1+aN)^{b+1}}$, $F'(N_*) = 1 - b + bR^{-1/b}$, we get $-1 < F'(N_*) < 1 \quad \Leftrightarrow \quad 0 < b(1 - R^{-1/b}) < 2$ or, since $R > 1$,

$$\underline{\frac{2}{b} + R^{-1/b} > 1}$$

Question *In particular, find the nonzero equilibrium for $a = 1$, $b = 3$ and $R = 125$*

Answer

$$N_* = \frac{R^{1/b} - 1}{a} = \frac{125^{1/3} - 1}{1} = \underline{4}$$

Question *and determine its stability.*

Answer

$$\frac{2}{b} + R^{-1/b} = 13/15 \underline{< 1}$$

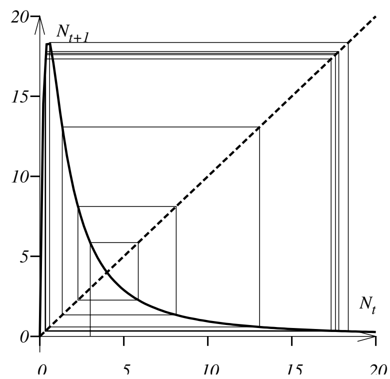
so the equilibrium is unstable.

5 marks for this part

(c)

Question *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 $N(0) = 3$.*

Answer



4 marks for this part

(d) **Question** *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.*

Answer

$$N_{t+1} = F(N_t) = \frac{125N}{(1+N)^3}, \quad N_{t+2} = F(F(N_t)) = \frac{125F(N)}{(1+F(N))^2} = \underline{\frac{125^2 N(1+N)^6}{(125N+(1+N)^3)^3}}$$

Question *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.*

Answer Equilibria of $F(F(N))$ are equilibria of $F(N)$ or 2-cycles of $F(N)$. Find them:

$$F(F(N)) = \frac{125^2 N(1+N)^6}{(125N+(1+N)^3)^3} = N; \frac{5^6(1+N)^6}{(125N+(1+N)^3)^3} = 1; \quad 5^2(1+N)^2 = 125N + (1+N)^3.$$

It is more convenient to write in terms of $x = N + 1$, which gives $x^3 - 25x^2 + 125x - 125 = 0$. The solution corresponding to equilibrium is $x = 5$ which is factored out to produce $(x^3 - 125) + 25x(5 - x) = 0$; $x^2 + 5x + 25 - 25x = 0$; and eventually $x^2 - 20x + 25 = 0$, $N_{1,2} = 9 \pm 5\sqrt{3}$ which is one 2-cycle.

6 marks for this part

Total for this question: 20 marks

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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) **Question** *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.*

Answer F_j: fertility of age group j. P_j: probability of age group j to survive to age $j+1$. $F_j \geq 0$, $0 < P_j \leq 1$.

5 marks for this part

(b) **Question** *Find the characteristic polynomial $P(\mu)$ for $\mathbf{L}$.*

Answer

$$P(\mu) = \mu^3 - F_0\mu^2 - P_0F_1\mu - P_0P_1F_2$$

Question *By considering the function $P(\mu)/\mu^3$ for positive μ, show that this polynomial always has exactly one positive root.*

Answer (bookwork) $P(\mu)/\mu^3 = 1 - F_0/\mu - P_0F_1/\mu^2 - P_0P_1F_2/\mu^3$. This function is negative for small positive μ, tends to 1 for large μ and thus must change the sign at some $\mu > 0$; as it is continuous, it must be zero at the point of change of the sign. Since it is monotone, it may only change the sign once, thus there is only one positive root.

6 marks for this part

(c) **Question** *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.*

Answer The characteristic equation is then $\mu^3 - \mu - 6 = 0$ which by inspection or otherwise, has solution $\mu = 2$. The other two roots are smaller by absolute value: this follows from the fact that the principal root must be positive, and results of the previous section, or can be established directly by finding the other two roots $\mu_{2,3} = -1 \pm i\sqrt{2}$. Thus, in the long run, population will double every year.

5 marks for this part

(d) **Question** *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.*

Answer At given parameter values, characteristic equation is

$$P(\mu) = \mu^3 - \mu - 0.01F_2 = 0$$

Population is marginally viable if $\mu = 1$; substituting this into the characteristic equation we find $F_2 = 0$. Any bigger fertility will only make the population more viable, thus eradication by reducing F_2 is not possible.

4 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 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) **Question** *Explain the biological significance of the constants R, a and b.*

Answer R: low-density reproduction coefficient of either species. a: determines intraspecific competition. b: determines interspecific competition.

Question *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?*

Answer They will decrease, since greater value of b means the species suppress stronger each other.

4 marks for this part

(b) **Question** *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.*

Answer Equilibrium corresponds to $x_{t+1} = x_t = x_*$, $y_{t+1} = y_t = y_*$, which for coexistence $x_* \neq 0$, $y_* \neq 0$ gives system of equations $1 = \frac{2}{1+(x_*+by_*)^3}$, $1 = \frac{2}{1+(y_*+bx_*)^3}$, or $x_* + by_* = 1$, $bx_* + y_* = 1$, wherefrom, if $b \neq 1$,

$$x_* = y_* = 1/(1+b).$$

Question *Verify that the answer is consistent with the conclusion on the role of parameter b from part (a) above.*

Answer Indeed, as b increases, x_* and y_* decrease.

5 marks for this part

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

Answer At given parameter values, model (4) becomes

$$x_{t+1} = \frac{2x_t}{1+(x_t+by_t)^3} = F(x_t, y_t), \qquad y_{t+1} = \frac{2y_t}{1+(bx_t+y_t)^3} = G(x_t, y_t)$$

Differentiation of the first right-hand side gives $\frac{\partial F}{\partial x} = 2\frac{1+(by-2x)(x+by)^2}{(1+(x+by)^3)^2}$, $\frac{\partial F}{\partial y} = -6\frac{bx(x+by)^2}{(1+(x+by)^3)^2}$ and similarly for the derivatives of G. Substituting $x = y = 1/(b+1)$ gives the community matrix in the form

$$\mathbf{A} = \begin{bmatrix} \frac{\partial F}{\partial x} & \frac{\partial F}{\partial y} \\ \frac{\partial G}{\partial x} & \frac{\partial G}{\partial y} \end{bmatrix} = \begin{bmatrix} p & -q \\ -q & p \end{bmatrix},$$

where $p = \frac{2b-1}{2b+2}$, $q = \frac{3b}{2b+2}$. The eigenvalues of **A** are $\mu_{1,2} = p \pm q = \left\{\frac{5b-1}{2b+b}, -\frac{1}{2}\right\}$. Stability requires that $|\mu_{1,2}| < 1$. The second root always satisfies . For the first root, we need $\lambda_1 > -1$, which requires $b > -1/7$, and $\lambda_1 < 1$, which requires $b < 1$.

7 marks for this part

(d) **Question** *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 $x = 1$, $y = 2$.*

Answer Since now we have $a = b$, dividing one equation by the other gives $\frac{y_{t+1}}{x_{t+1}} = \frac{y_t}{x_t}$, that is, the ratio of population sizes remains constant. With given initial conditions, we have $y_t = 2x_t$ for all t. Substituting this into the first equation, we have $x_{t+1} = \frac{2x_t}{1+(3x)^3}$ which has a unique positive equilibrium $x = 1/3$. The derivative of the R.H.S. at it is $-1/2$ so it is stable. Thus in the long run, the system will approach the state $x = 1/3$, $y = 2/3$.

4 marks for this part

Total for this question: 20 marks

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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) **Question** *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.*

Answer Parameters b_{11}, b_{22}, b_{33}: all three species demonstrate intraspecific competition. Parameters b_{12}, b_{21}: Species 1 and 2 benefit from each other, so they are in mutualist/symbiotic relationship. Parameters b_{13}, b_{31}: species 1 and 3 suffer from each other, so they are in inter-specific competition. Species 2 and 3 do not interact in this model.

4 marks for this part

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

Answer Let Q be an isolated equilibrium in a domain D; and V be a continuously differentiable function which is positive definite on D (i.e. zero at Q and positive elsewhere on D). If the orbit derivative of V is negatively definite on D, then Q is asymptotically stable.

3 marks for this part

(c) **Question** *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 $N_1 = N_2 = N_3 = 1$.*

Answer Direct substitution of these values into (5) renders all three right-hand sides zero .

Question *Show that this equilibrium is isolated.*

Answer The equilibrium is a solution of system of linear algebraic equations,

$$\mathbf{A}\mathbf{N}_* = \mathbf{a}$$

where

$$\mathbf{A} = \begin{bmatrix} 4 & -1 & 1 \\ -1 & 4 & 0 \\ 1 & 0 & 4 \end{bmatrix}, \quad \mathbf{N}_* = \begin{bmatrix} N_1^* \\ N_2^* \\ N_3^* \end{bmatrix}, \quad \mathbf{a} = \begin{bmatrix} 4 \\ 3 \\ 5 \end{bmatrix}.$$

Matrix $\mathbf{A}$ is non-singular $\det \mathbf{A} = 56 \neq 0$, thus the solution is unique and therefore isolated.

Question *Verify that the system (5) can be written in the matrix form.*

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

and $\mathbf{M}$ is a real symmetric matrix.

Answer Indeed, substitution of $\mathbf{x}$ as said produces this matrix form with $\mathbf{M}$ identical to matrix $\mathbf{A}$ introduced above,

$$\mathbf{M} = \begin{bmatrix} 4 & -1 & 1 \\ -1 & 4 & 0 \\ 1 & 0 & 4 \end{bmatrix}$$

Question *Find the eigenvalues of $\mathbf{M}$, verifying that they are all positive, i.e. $\mathbf{M}$ is positive definite.*

Answer

$$\det(\mathbf{M} - \lambda\mathbf{I}) = (4-\lambda)^3 - 2(4-\lambda) = (4-\lambda)(\lambda^2 - 8\lambda + 14)$$

thus the eigenvalues are

$$\lambda_1 = 4, \quad \lambda_{2,3} = 4 \pm \sqrt{2},$$

all positive .

6 marks for this part

(d) **Question** *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*

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

Answer By definition of the orbit derivative,

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

as requested

Question *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.*

Answer From the above results, we can now assert that:

— Function $V(\mathbf{x})$ is continuously differentiable and positive definite, as a quadratic form with positive definite matrix $\mathbf{M}$;

— Its orbit derivative $\mathrm{d}V/\mathrm{d}t(\mathbf{x})$ is negatively definite, as an opposite of a quadratic form with a positive definite matrix $\mathbf{M}^2$;

— Equilibrium $\mathbf{x} = \mathbf{0}$ is isolated. Thus all conditions of the Lyapunov theorem are satisfied, and the equilibrium is asymptotically stable. Region D to which the assumptions of the theorem apply, is the whole space, thus the equilibrium is globally attractive.

7 marks for this part

Total for this question: 20 marks

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

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

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

(a) **Question** *Explain briefly the biological significance of the coefficients r_1, m_2, K_1, and A in equations (6),*

Answer r_1: low-density reproduction rate of prey in absence of predators. K_1: carrying capacity of prey in absence of predators. m_2: mortality of predators in absence of prey. A: saturation constant for the predators functional and numerical response: prey population at which intensity of predation decreases two-fold.

Question *and state which of p_1, p_2 characterises the functional response and which characterises the numerical response of predators to prey*

Answer p_1: functional response; p_2: numerical response.

5 marks for this part

(b) **Question** *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.*

Answer

- $N_1 = N_2 = 0$ (extinction of both species) .
- $N_1 = 0,\ N_2 \neq 0$ (extinction of the prey only) — no such solutions.
- $N_1 = 0,\ N_2 \neq 0 \Rightarrow N_1 = 4$ (extinction of the predator only) .
- $N_1 \neq 0,\ N_2 \neq 0$ (coexistence) — this leads to the system

$$\begin{aligned} \left(1 - \frac{N_1}{4}\right) - \frac{N_2}{N_1 + 1} &= 0 \\ -1 + \frac{2N_1}{N_1 + 1} &= 0 \end{aligned}$$

From the second equation $\underline{N_1 = 1}$, substituting this into the first equation yields $\underline{N_2 = 3/2}$.

Question *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.

Answer To prove instability, it is sufficient to notice that $\mathrm{Tr}\mathbf{A} = 1/2 > 0$.

7 marks for this part

(c) **Question** *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.*

Answer A1 If D is an absorbing region and contains a single unstable equilibrium, **or**

A2 If D is an annulus-shape absorbing region and contains no equilibria, **then**
Th2 D contains at least one periodic orbit; **and, moreover,**
Th3 If D contains only one periodic orbit, it is a stable limit cycle.
.

3 marks for this part

(d) **Question** *Find the orbit derivative of function $V = 2N_1 + N_2$ due to system (6)*
Answer

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

Question *and prove that if $V = 8$ then $\mathrm{d}V/\mathrm{d}t \le 0$. Thus identify a triangle in the (N_1, N_2) plane which is an absorbing region.*
Answer If $V = 8$ then $N_2 = V - 2N_1 = 8 - 2N_1$ and

$$\mathrm{d}V/\mathrm{d}t = -N_1^2/2 + 4N_1 - 8 = -\frac{1}{2}(N_1 - 4)^2 \le 0$$

The absorbing region is the triangle bounded by the lines $N_1 = 0$, $N_2 = 0$ and $2N_1 + N_2 = 8$.
Question *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).*
Answer Further condition to satisfy: that the unstable coexistence equilibrium is inside this triangle, and that there are no other equilibria in this triangle

5 marks for this part

Total for this question: 20 marks

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

$$\mathrm{d}S/\mathrm{d}t = -\beta SI, \qquad \mathrm{d}I/\mathrm{d}t = \beta SI - \nu I, \qquad \mathrm{d}R/\mathrm{d}t = \nu I, \tag{7}$$

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.

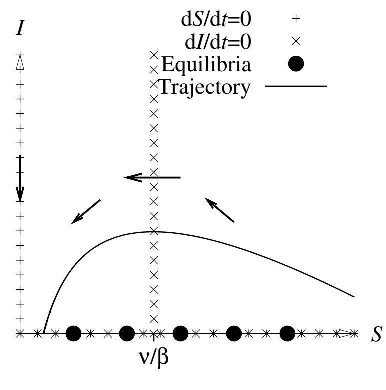
(a) **Question** *Explain the biological meaning of the terms and biological assumptions used in this model.*
Answer Terms: βSI — the rate of transmission of the disease νI — rate of removal . Assumptions:
— Rate of transmission is proportional to the rate of encounter of susceptibles and infectives, meeting at random.
— Removals of individuals are independent events with certain probabilities per capita per unit of time.
— The removed individuals never return to the epidemics, e.g. die or acquire permanent immunity. — All vital dymamics (number of births and disease-unrelated mortalities) neglected.

6 marks for this part

(b) **Question** *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.*
Answer

Null clines:
— $\dot{S} = 0$: two lines, $S = 0$ and $I = 0$
— $\dot{I} = 0$: two lines, $S = \nu/\beta$ and $I = 0$
Equilibria: the two sets of null-clines have the whole line $I = 0$, and only that line, as an intersection, thus this whole line consists of equilibria. General direction of trajectories: since $\dot{S} < 0$, all trajectories move leftwards, since $\dot{I} = \beta I(S - \frac{\nu}{\beta})$, trajectories go up where $S > \nu/\beta$ and down where $S < \nu/\beta$.

Phase portrait:



6 marks for this part

(c) **Question** *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* $I = \frac{2}{\nu\beta}p^2\operatorname{sech}^2(p(t-t_*))$ *are a solution to the resulting system for arbitrary* p *and* t_* *(remember that* $(\tanh x)' = \operatorname{sech}^2 x = 1 - \tanh^2 x$*).*

Answer The suggested substitution leads to the system

$$\begin{aligned} \mathrm{d}\sigma/\mathrm{d}t &= -\nu I - \beta\sigma I \\ \mathrm{d}I/\mathrm{d}t &= \beta\sigma I \end{aligned}$$

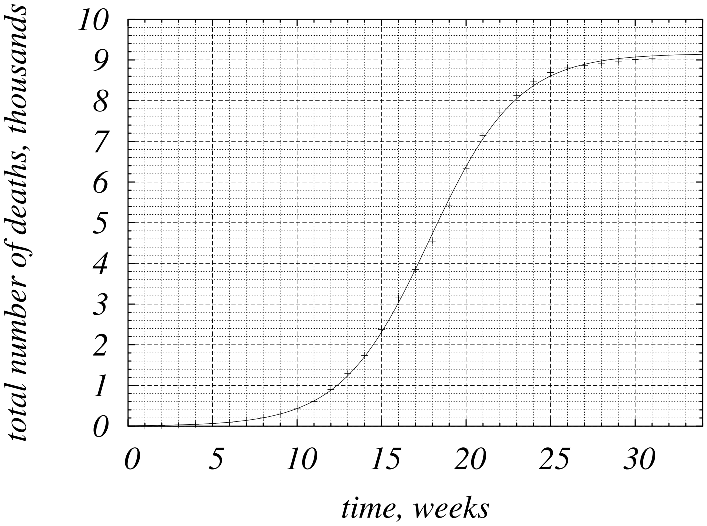
In the first equation, the second term is much smaller than the first term because σ is assumed small; discarding that term gives

$$\begin{aligned} \mathrm{d}\sigma/\mathrm{d}t &= -\nu I \\ \mathrm{d}I/\mathrm{d}t &= \beta\sigma I. \end{aligned}$$

Substitution of the given solution gives: $\dot\sigma = -\frac{2}{\beta}p^2\operatorname{sech}^2(p(t-t_*)) = -\nu I$, and $-\nu I = -\frac{2}{\beta}p^2\operatorname{sech}^2(p(t-t_*)) = \dot\sigma$, thus the first equation is satisfied. Similarly, $\dot I = \frac{2}{\nu\beta}p^2\left(1-\tanh^2(p(t-t_*))\right)' = -\frac{2}{\nu\beta}p^2(2\tanh pt)(p\operatorname{sech}^2 pt)$ $= -\frac{2}{\nu\beta}p^3\tanh pt\,\operatorname{sech}^2 pt$, and $\beta\sigma I = \beta\left(-\frac{2}{\beta}p\right)\left(\frac{2}{\nu\beta}p^2\right)\tanh p(t-t_*)\operatorname{sech}^2 p(t-t_*) = -\frac{4}{\nu\beta}p^3\tanh p(t-t_*)\operatorname{sech}^2 p(t-t_*) = \dot I$ and the second equation is satisfied.

4 marks for this part

(d) **Question**



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 for this part

Answer This is the graph of function $R(t)$ which for the analytical solution obtained above has the form

$$R(t) = R_{-\infty} + \Delta_R\left[1 + \tanh(p(t-t_*))\right]$$

where $\Delta_R = 2p/\beta$ and p, $R_{-\infty}$ and t_* are arbitrary constants. From the graph we estimate $R_{-\infty} = 0$, $t_* \approx 18$, and $\Delta_R \approx 4600$. The levels $R = \Delta_R(1 \pm \tanh(1)) = \{1100, 8100\}$ are achieved at $t \approx t_* \pm 5$, thus $p \approx 1/5 = 0.2$. Thus $\beta = 2p/\Delta_R \approx 10^{-4}$. Since the epidemic is weak, $S_* = \nu/\beta \approx S$, thus $\nu \approx S\beta \approx 10$.

Total for this question: 20 marks