Imperial College London

MATH97018 MATH97096

BSc, MSci and MSc EXAMINATIONS (MATHEMATICS)
May-June 2020

This paper is also taken for the relevant examination for the Associateship of the Royal College of Science

Mathematical Biology

Date: 21st May 2020

Time: 13.00pm - 15.30pm (BST)

Time Allowed: 2 Hours 30 Minutes

Upload Time Allowed: 30 Minutes

This paper has 5 Questions.

Candidates should start their solutions to each question on a new sheet of paper.

Each sheet of paper should have your CID, Question Number and Page Number on the top.

Only use 1 side of the paper.

Allow margins for marking.

Any required additional material(s) will be provided.

Credit will be given for all questions attempted.

Each question carries equal weight.

SUBMIT YOUR ANSWERS AS ONE PDF TO THE RELEVANT DROPBOX ON BLACKBOARD INCLUDING A COMPLETED COVERSHEET WITH YOUR CID NUMBER, QUESTION NUMBERS ANSWERED AND PAGE NUMBERS PER QUESTION.

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1. **(20 marks) Competition of rabbits vs sheep.** A farmer tries to prevent an invasion of rabbits by introducing sheep to his grassland. He seeks help from a pedantic mathematician who suggests the following ODE model based on the assumption that rabbits and sheep compete for a limited grass supply:

$$\frac{\partial x}{\partial t} = x(3 - x - 2y), \quad \frac{\partial y}{\partial t} = y(2 - x - y).$$

The variables x and y model the respective nondimensional population sizes of rabbits and sheep.

(a) (5 marks) Find the steady states of the model and give an interpretation for each of these possible outcomes to inform the farmer.

(b) (10 marks) Classify the phase portraits in the vicinity of the steady states using linear stability analysis.

(c) (5 marks) Draw the qualitative global phase portrait and use it to provide an answer to the farmer's question of how many sheep are needed to eradicate a rabbit population with $x < 1$.

2. **(20 marks) Hysteresis in gene expression.** A deterministic ODE model for the expression of a protein with positive feedback is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \alpha + g(x) - x,$$

where $g(x) = \beta \frac{x^n}{1+x^n}$ is a nonlinear activation function with Hill coefficient n and $\alpha, \beta > 0$ are non-dimensional rate constants.

(a) (i) (2 marks) Provide an argument why there is only one positive stable steady state for $n = 1$.

(ii) (3 marks) Sketch the graph of the function $g(x)$ for $n \gg 1$. What simple shape does it approach as $n \to \infty$?

(b) In the following assume $n \gg 1$.

(i) (5 marks) The right hand side of the equation for $\dot{x}$ can be rewritten as $g(x) - h(x)$, where $h(x) = x - \alpha$. Use this decomposition to draw the phase portrait for (1) $\alpha + \beta < 1$, (2) $\alpha + \beta > 1$ for $\alpha < 1$ and (3) $\alpha + \beta > 1$ for $\alpha > 1$ and indicate the stability of the possible steady states.

(ii) (3 marks) Draw the phase diagram in the α-β-plane showing the regions where the system has 1 or 2 stable steady states.

(iii) (4 marks) Draw the bifurcation diagram of the steady state x^* in the $(x^*$,$\alpha)$-plane.

(iv) (3 marks) Assume $\beta > 1$ and discuss how the protein level x behaves if α is slowly increased from 0 to a value $\alpha > 1$ and then slowly decreased back to $\alpha = 0$. [Hint: Your result should depend on the initial state!]

3. **(20 marks) Stochastic amplification in enzymatic reactions.** We will assume that production and consumption of a metabolite X inside a living cell follows a birth-death process

$$\varnothing \xrightarrow{w_+(x)} X, \quad X \xrightarrow{w_-(x)} \varnothing.$$

The production rate is constant while the consumption rate follows Michaelis-Menten kinetics:

$$w_+(x) = a, \quad w_-(x) = \frac{x}{x+K},$$

where $a > 0$ and K is the Michaelis-Menten constant. *Hint: A special case of the binomial series is*

$$\frac{1}{(1-z)^{\beta+1}} = \sum_{k=0}^{\infty} \binom{k+\beta}{k} z^k.$$

(a) (3 marks) Write down the ODE model and obtain the steady state solution. For which parameter ranges does the steady state solution exist?

(b) (8 marks) Give the master equation for the probability $p(x,t)$ that there are x proteins at time t and show that the stationary distribution $p(x)$ is the negative binomial distribution. Use the result to show that the probability generating function is

$$G(z) = \sum_{x=0}^{\infty} z^x p(x) = \left(\frac{a-1}{az-1}\right)^{K+1}.$$

For which parameter ranges does the stationary distribution exist?

(c) (4 marks) Use the probability generating function to obtain the mean number of molecules in steady state. Compare your result to the steady state solution of the deterministic ODEs and discuss the parameter regimes where you expect agreement or disagreement.

(d) (5 marks) Find an expression for the coefficient of variation (standard deviation/mean) as a function of the mean number of molecules. How does it scale for low mean numbers and large mean numbers? *Hint: Considering squared coefficient of variation eases the calculation.*

4. **(20 marks) Turing pattern formation.** The colour pattern on the tail of an animal is assumed to depend on the concentrations of two chemicals, $u(\vec{x}, t)$ and $v(\vec{x},\, t)$, which interact and diffuse according to the reaction-diffusion equations

$$\begin{aligned}\frac{\partial u}{\partial t} &= \nabla^2 u + u(1 + u - 2v) \\ \frac{\partial v}{\partial t} &= d\nabla^2 v + v(1 + 2u - 3v), \quad \forall \vec{x} \in \Omega\end{aligned}$$

subject to the no-flux boundary conditions

$$\hat{u} \cdot \nabla u = \hat{u} \cdot \nabla v = 0 \quad \forall \vec{x} \in \partial\Omega \ .$$

(a) (5 marks) Show that there is a spatially uniform steady state $u = u_0 > 0$, $v = v_0 > 0$ which is stable to spatially uniform perturbations.

(b) (4 marks) Consider a small non-uniform perturbation about the uniform steady state to be separable in the form $u \approx u_0 + A_1\phi(\vec{x})e^{\lambda t}$, $v \approx v_0 + A_2\phi(\vec{x})e^{\lambda t}$. Find the PDE satisfied by $\phi(\vec{x})$ and the equation for the growth rates λ of perturbations.

(c) (6 marks) Find the least value of $d > 0$ such that this state may be unstable to spatially dependent perturbations, i.e., the Turing bifurcation point, and calculate the range of unstable wave-numbers when $d = 10$.

(d) (5 marks) Describe the plausible patterns when the tail is approximately one-dimensional, $\Omega = (0, 5)$ and $d = 10$. What patterns do you expect if the animal's tail grows longer?

5. **(20 marks)** Describe the use of phase space analysis for the analysis of spatially-homogeneous deterministic, spatially-extended and stochastic models of population dynamics. Provide interpretations for the involved quantities determining the phase portraits and give qualitative examples of the population dynamics.

Module:	MATH96006/MATH97018/MATH97096
Setter:	Thomas
Checker:	Mestel
Editor:	Wu
External:	Alexander
Date:	March 18, 2020
Version:	Final version

BSc, MSci and MSc EXAMINATIONS (MATHEMATICS)

May – June 2020

MATH96006/MATH97018/MATH97096 Mathematical Biology

The following information must be completed:

Is the paper suitable for resitting students from previous years: No (detailed balance condition not studied in previous years)

Category A marks: available for basic, routine material (excluding any mastery question) (40 percent = 32/80 for 4 questions):
1(a) 5 marks; 1(b) 10 marks; 2(a) 5 marks; 3(a) 3 marks; 4(a), (b) 9 marks.

Category B marks: Further 25 percent of marks (20/ 80 for 4 questions) for demonstration of a sound knowledge of a good part of the material and the solution of straightforward problems and examples with reasonable accuracy (excluding mastery question):
1(c) 5 marks; 2(b) (i) 5 marks; 3(c) 4 marks; 4(c) 6 marks.

Category C marks: the next 15 percent of the marks (= 12/80 for 4 questions) for parts of questions at the high 2:1 or 1st class level (excluding mastery question):
2(b) (ii) 3 marks, 2(b)(iii) 4 marks; 3(d) 5 marks;

Category D marks: Most challenging 20 percent (16/80 marks for 4 questions) of the paper (excluding mastery question):
2(b) (iv) 3 marks; 3(b) 8 marks; 4(d) 5 marks.

Signatures are required for the final version:

Setter's signature	Checker's signature	Editor's signature
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BSc, MSc and MSci EXAMINATIONS (MATHEMATICS)

May – June 2020

This paper is also taken for the relevant examination for the Associateship of the Royal College of Science.

Mathematical Biology

Date: ??

Time: ??

Time Allowed: 2 Hours for MATH96 paper; 2.5 Hours for MATH97 papers

This paper has *4 Questions (MATH96 version); 5 Questions (MATH97 versions)*.

Candidates should start their solutions to each question in a new main answer book.

Supplementary books may only be used after the relevant main book(s) are full.

Statistical tables will not be provided.

- DO NOT OPEN THIS PAPER UNTIL THE INVIGILATOR TELLS YOU TO.
- Affix one of the labels provided to each answer book that you use, but DO NOT USE THE LABEL WITH YOUR NAME ON IT.
- Credit will be given for all questions attempted.
- Each question carries equal weight.
- Calculators may not be used.

1. **(20 marks) Competition of rabbits vs sheep.** A farmer tries to prevent an invasion of rabbits by introducing sheep to his grassland. He seeks help from a pedantic mathematician who suggests the following ODE model based on the assumption that rabbits and sheep compete for a limited grass supply:

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(b) (10 marks) Classify the phase portraits in the vicinity of the steady states using linear stability analysis.

(c) (5 marks) Draw the qualitative global phase portrait and use it to provide an answer to the farmer's question of how many sheep are needed to eradicate a rabbit population with $x < 1$.

Solution: Similar question has been SEEN by students in the context of competition models.

(a)
1. $(x^*, y^*) = (0, 0)$ sheep and rabbits go extinct
2. $(x^*, y^*) = (0, 2)$ rabbits go extinct
3. $(x^*, y^*) = (3, 0)$ sheep go extinct
4. $(x^*, y^*) = (1, 1)$ coexistence.

(b) The Jacobian matrix is

$$J = \begin{pmatrix} -2x^* - 2y^* + 3 & -2x^* \\ -y^* & -x^* - 2y^* + 2 \end{pmatrix}.$$

This yields the following classification of steady states:

1.
$$J = \begin{pmatrix} 3 & 0 \\ 0 & 2 \end{pmatrix}$$
$\implies$ unstable node.

2.
$$J = \begin{pmatrix} -1 & 0 \\ -2 & -2 \end{pmatrix}$$
Eigenvalues are $\{-2, -1\}$ $\implies$ stable node.

3.

$$J = \begin{pmatrix} -3 & -6 \\ 0 & -1 \end{pmatrix}$$

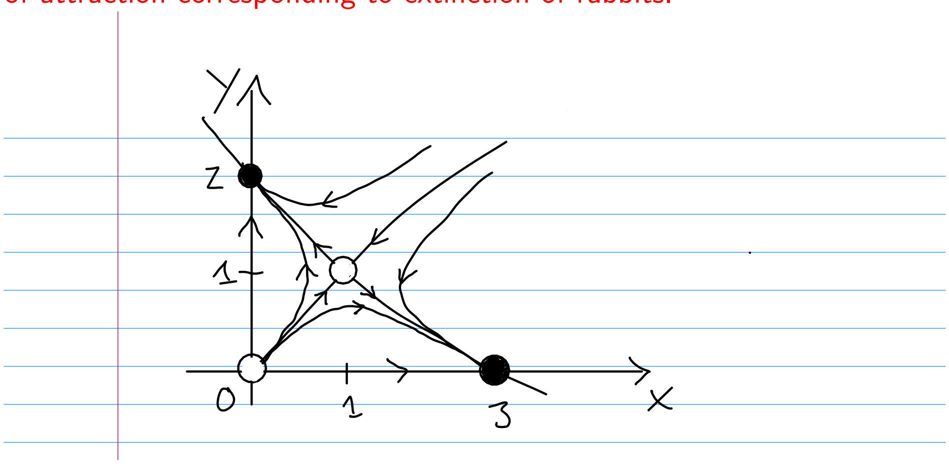
Eigenvalues are $\{-3, -1\} \implies$ stable node.

4.

$$J = \begin{pmatrix} -1 & -2 \\ -1 & -1 \end{pmatrix}$$

Eigenvalues are $\lambda = -1 \pm \sqrt{2} \implies$ saddle.

(c) Accept rough sketches of the phase portrait. A calculation of the eigenvectors is not explicitly required. From the phase portrait, we see that $y > 1$ sheep are sufficient to eradicate a rabbit population of $x < 1$. Accept also answers that identify the area above the separatrix as the basin of attraction corresponding to extinction of rabbits.



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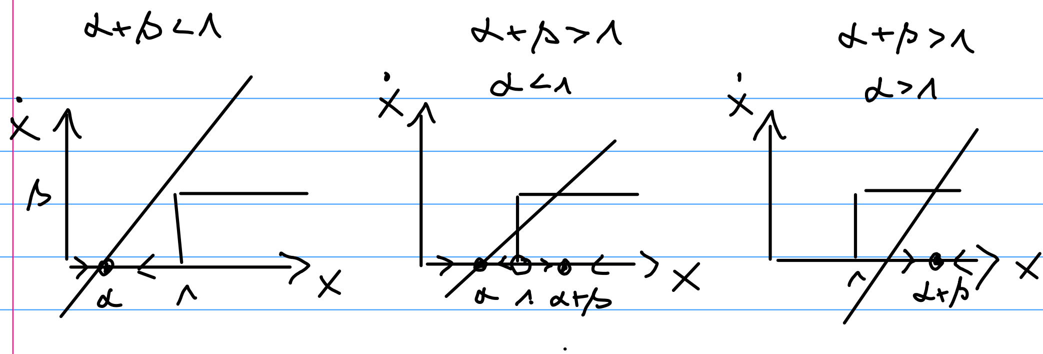
(iv) (3 marks) Assume $\beta > 1$ and discuss how the protein level x behaves if α is slowly increased from 0 to a value $\alpha > 1$ and then slowly decreased back to $\alpha = 0$. [Hint: Your result should depend on the initial state!]

Solution: The question is UNSEEN but students should be familiar with concepts as bistability, hysteresis, phase portraits and diagrams.

(a) (i) Setting $\dot{x} = 0$ and multiplying with $(1 + x)$ leads to a quadratic polynomial equation, which can have at most two positive roots. Since $\dot{x}$ is bounded from above and $\dot{x}(0) > 0$ there must be one stable solution. Accept answers that point to quadratic polynomials.

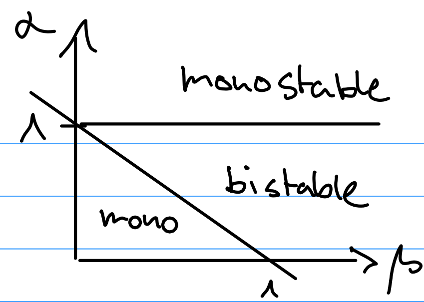
(ii) g approaches a Heaviside step function $\beta\theta(x - 1)$ and the graph should resemble this limiting function. The value at $x = 1$ is always $1/2$ but this is less important if n is large but finite.

(b) (i) The graphs should resemble:

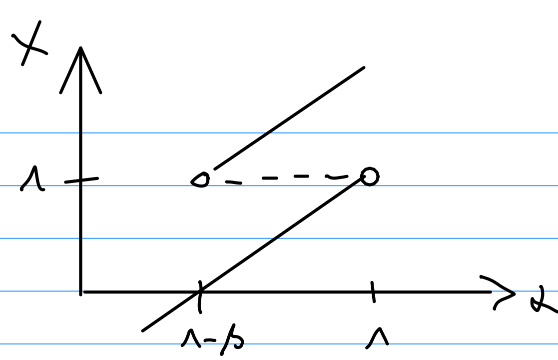


Marks are given for correctly drawing the two functions, indicating the possible steady states at $x = \alpha$, 1 and $\alpha + \beta$, their stability indicated by dots and the flow towards them by arrows.

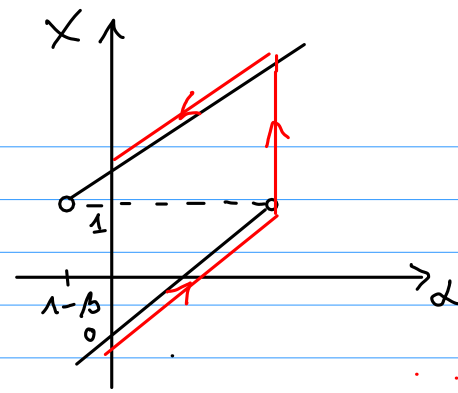
(ii) This follows directly from Part (i) by considering that for case (1) and (3) there is only one stable state but there are two stable states for case (2).



(iii) The stable states are α (case (1) and (2)) and $\alpha + \beta$ (case (2) and (3)). The unstable state is located at 1 if $1 - \beta < \alpha < 1$ as seen from (i). The phase diagram then follows as:



(iv) If initially there are $x > 1$ proteins, the system stays at the upper branch. If initially there are $x < 1$ proteins, the system stays at the lower branch until $\alpha = 1$, then jumps to the upper branch as α increases. When α is decreased again it always remains on the upper branch. The phenomenon is called hysteresis (SEEN), which is irreversible in this case.


x
1
1-β
0
α

3. **(20 marks) Stochastic amplification in enzymatic reactions.** We will assume that production and consumption of a metabolite X inside a living cell follows a birth-death process

$$\varnothing \xrightarrow{w_+(x)} X, \quad X \xrightarrow{w_-(x)} \varnothing.$$

The production rate is constant while the consumption rate follows Michaelis-Menten kinetics:

$$w_+(x) = a, \quad w_-(x) = \frac{x}{x+K},$$

where $a > 0$ and K is the Michaelis-Menten constant. *Hint: A special case of the binomial series is*

$$\frac{1}{(1-z)^{\beta+1}} = \sum_{k=0}^{\infty} \binom{k+\beta}{k} z^k.$$

(a) (3 marks) Write down the ODE model and obtain the steady state solution. For which parameter ranges does the steady state solution exist?

(b) (8 marks) Give the master equation for the probability $p(x,t)$ that there are x proteins at time t and show that the stationary distribution $p(x)$ is the negative binomial distribution. Use the result to show that the probability generating function is

$$G(z) = \sum_{x=0}^{\infty} z^x p(x) = \left(\frac{a-1}{az-1}\right)^{K+1}.$$

For which parameter ranges does the stationary distribution exist?

(c) (4 marks) Use the probability generating function to obtain the mean number of molecules in steady state. Compare your result to the steady state solution of the deterministic ODEs and discuss the parameter regimes where you expect agreement or disagreement.

(d) (5 marks) Find an expression for the coefficient of variation (standard deviation/mean) as a function of the mean number of molecules. How does it scale for low mean numbers and large mean numbers? *Hint: Considering squared coefficient of variation eases the calculation.*

Solution: The question is mostly UNSEEN but students should be familiar with the concepts of master equations, stationary distributions, detailed balance, negative binomial distribution and generating functions.

(a) (SEEN) The steady state follows from

$$w_+(x^*) = w_-(x^*) \implies x^* = K\frac{a}{1-a},$$

which exists for $a < 1$, i.e., the production rate needs to be less than the maximum consumption rate.

(b) This is a birth-death process and the master equation (SEEN) is

$$\frac{\mathrm{d}p(x,t)}{\mathrm{d}t} = w_+(x-1)p(x-1,t) - w_+(x)p(x,t) + w_-(x+1)p(x+1,t) - w_-(x)p(x,t).$$

The steady state distribution can be found by setting $\frac{\mathrm{d}p(x,t)}{\mathrm{d}t} = 0$ and using the detailed balance condition (SEEN)

$$w_+(x-1)p(x-1) = w_-(x)p(x), \quad \text{or} \quad w_+(x)p(x,t) = w_-(x+1)p(x+1),$$

which are equivalent. This gives the detailed balance solution:

$$\begin{aligned}
p(x) &= p(0)\prod_{i=1}^{x}\frac{w_+(i-1)}{w_-(x)} \quad \text{(SEEN)} \\
&= p(0)\prod_{i=1}^{x} a\,(i-1+K)\,\frac{1}{i-1} \\
&= p(0)a^x\frac{\Gamma(K+x+1)}{\Gamma(K+1)\Gamma(x+1)} = p(0)a^x\binom{K+x}{x} = p(0)a^x\binom{K+x}{K} \quad \text{(UNSEEN)},
\end{aligned}$$

which is the negative binomial distribution. $p(0)$ is a normalising factor found using the binomial series

$$\frac{1}{p(0)} = \sum_{x\geq 0} a^x\binom{K+x}{x} = (1-a)^{-K-1}.$$

Thus the stationary distribution exists if $a < 1$ and is given by

$$p(x) = (1-a)^{K+1}\,a^x\binom{K+x}{K}.$$

Finally, the probability generating function is found directly using the binomial series, which gives

$$G(z) = \sum_{x=0}^{\infty} z^x p(x) = (1-a)^{K+1}\sum_{x=0}^{\infty}(az)^x\binom{K+x}{K} = \left(\frac{az-1}{a-1}\right)^{-K-1}.$$

(c) (UNSEEN) Using the characteristic function, we find the mean

$$\mathrm{E}[x] = G'(1) = \frac{aK}{1-a}\left(1+\frac{1}{K}\right) = x^*\left(1+\frac{1}{K}\right) > x^*.$$

Thus the stochastic model always predicts higher protein levels than ODE model. However, this amplification may be small if $K \gg 1$.

(d) (UNSEEN) The derivatives of the generating function can be related to the factorial moments

$$G'(1) = \mathrm{E}[x] = \frac{a}{1-a}(K+1)\,, \quad G''(1) = \mathrm{E}[x(x-1)] = \frac{a^2}{(1-a)^2}(K+1)(K+2)$$

Thus

$$\mathrm{Var}(x) = G''(1) + G'(1) - [G'(1)]^2,$$

and

$$\mathrm{CV}^2(\mathrm{E}[x]) = \frac{1}{\mathrm{E}[x]} + \frac{G''(1)}{[G'(1)]^2} - 1 = \frac{1}{\mathrm{E}[x]} + \frac{K+2}{K+1} - 1 = \frac{1}{\mathrm{E}[x]} + \frac{1}{K+1}.$$

This relation is UNSEEN but the technique should be familiar from first year courses. For $\mathrm{E}[x] \ll K+1$, the CV scales with the inverse square root of the mean. For $\mathrm{E}[x] \gg K+1$, the CV is practically constant. The result is surprising as large numbers do not guarantee deterministic behaviour.

4. **(20 marks) Turing pattern formation.** The colour pattern on the tail of an animal is assumed to depend on the concentrations of two chemicals, $u(\vec{x},t)$ and $v(\vec{x},\,t)$, which interact and diffuse according to the reaction-diffusion equations

$$\frac{\partial u}{\partial t} = \nabla^2 u + u(1+u-2v)$$
$$\frac{\partial v}{\partial t} = d\nabla^2 v + v(1+2u-3v), \quad \forall \vec{x} \in \Omega$$

subject to the no-flux boundary conditions

$$\hat{u}\cdot\nabla u = \hat{u}\cdot\nabla v = 0 \;\; \forall \vec{x} \in \partial\Omega\ .$$

(a) (5 marks) Show that there is a spatially uniform steady state $u = u_0 > 0$, $v = v_0 > 0$ which is stable to spatially uniform perturbations.

(b) (4 marks) Consider a small non-uniform perturbation about the uniform steady state to be separable in the form $u \approx u_0 + A_1\phi(\vec{x})e^{\lambda t}$, $v \approx v_0 + A_2\phi(\vec{x})e^{\lambda t}$. Find the PDE satisfied by $\phi(\vec{x})$ and the equation for the growth rates λ of perturbations.

(c) (6 marks) Find the least value of $d > 0$ such that this state may be unstable to spatially dependent perturbations, i.e., the Turing bifurcation point, and calculate the range of unstable wave-numbers when $d = 10$.

(d) (5 marks) Describe the plausible patterns when the tail is approximately one-dimensional, $\Omega = (0,5)$ and $d = 10$. What patterns do you expect if the animal's tail grows longer?

Solution:

(a) (UNSEEN) The steady states are $(u^*,v^*) = (-1,0)$, $(0,1/3)$, $(1,1)$ and $(0,0)$. The only positive stable steady state is $(1,1)$ corresponds to a stable node with Jacobian

$$J = \begin{pmatrix} 1 & -2 \\ 2 & -3 \end{pmatrix}.$$

(b) (SEEN) Students should have seen this exercise a couple of times. It follows from direct substitution that

$$\lambda\vec{A} = \frac{1}{\phi(\vec{x})}\nabla^2\phi(\vec{x})D\vec{A} + J\vec{A},$$

where $D = \mathrm{diag}(1,d)$, and hence the second term must be constant, i.e., $\nabla^2\phi = -k^2\phi$ for a positive constant k^2 (Helmholtz equation). The above equation has non-trivial solutions if

$$\det(\lambda\underline{1} + Dk^2 - J) = 0,$$

which is called the characteristic equation.

(c) (UNSEEN) The range of unstable modes is determined by characteristic equation for $\lambda = 0$:

$$0 = \det(Dk^2 - J) = dk^4 + (3-d)k^2 + 1, \tag{1}$$

which has roots

$$k_\pm^2 = \frac{1}{2d}\left(d - 3 \pm \sqrt{d^2 - 10d + 9}\right).$$

There is only one root when

$$0 = d^2 - 10d + 9.$$

Hence, either $d = 1$ or $d = 9$. The case $d = 1$ leads to $k_\pm^2 < 0$ and thus no Turing bifurcation occurs. $d = 9$ leads to a solution $k_+^2 > 0$, which determines the Turing bifurcation point. For $d = 10$, the band of unstable modes is $k_-^2 = 1/5$ and $k_+^2 = 1/2$.

(d) The eigenfunctions of the Helmholtz equation satisfying the Neumann boundary conditions are $\cos(kx)$ with

$$k = \frac{n\pi}{L},$$

for $n = 0, 1, 2, ...$ We have $L = 5$ and hence $k^2 = \frac{n^2\pi^2}{L^2} = \frac{n^2\pi^2}{25} > \frac{n^2 3^2}{25} = n^2\frac{9}{5}\cdot\frac{1}{5} > \frac{1}{5}$ for $n \geq 1$. However, $k^2 = \frac{n^2\pi^2}{25} < \frac{1}{2}$ only for $n = 1$. Hence the plausible patterns are $\pm\cos(\pi x/5)$ depending on initial conditions (marks are given for both patterns). When the tail grows longer the spacing of wave-numbers k becomes closer and periodic patterns, i.e., stripes with $n \geq 2$, may develop. Students have SEEN the reasoning on more complex 2D domains in the lecture. The emphasis of the question is on checking the two conditions, identifying both patterns ($\pm$) and commenting on periodicity.

5. **(20 marks)** Describe the use of phase space analysis for the analysis of spatially-homogeneous deterministic, spatially-extended and stochastic models of population dynamics. Provide interpretations for the involved quantities determining the phase portraits and give qualitative examples of the population dynamics.

Solution: The mastery question can be answered qualitatively or using explicit examples. The phase space should be identified as the space in which all possible states of a system are uniquely represented, which often allows to analyse the dynamics graphically, i.e., in a plane. Accept answers that comment on the phase space variables in the three cases and provide qualitative examples of the dynamics, i.e., spatial/stochastic solutions propagating from deterministically stable into stable/unstable states that are impossible in deterministic ODE models (such as fronts and switching paths).

A particular example discussed extensively in the lectures could be Schloegl's 2nd model whose ODE model has two stable steady states separated by an unstable state. For small perturbations, transitions between stable states are impossible. In the stochastic model, however, stable and unstable states are saddle points and transitions between stable (and unstable) states become possible. The switching phenomenon leads to a bimodal probability distribution. Similarly, in the spatial model there are phase space trajectories propagating into unstable or stable states. These solutions correspond to fronts.

Alternatively, Schloegl's 1st model corresponds to a logistic growth model. Spatial versions of this model give rise to fronts (or stationary patterns depending on boundary conditions) propagating into the deterministically unstable extinct state. Similarly, in the stochastic model, population extinction is often inevitable.

A more general account would be:

- Deterministic models such as deterministic reaction networks
  Examples: ODE models describing continuous population size x, e.g., logistic growth model etc.
  Phase space variables: x and the associated vector field $\dot{x}$.

- Spatial models such as reaction-diffusion systems.
  Examples: PDE models describing continuous population size $\rho(x - vt)$ varying in space and time such as steady fronts/travelling waves/spatio-temporal patterns or even stationary pattern as a special case.
  Phase space variables: Examples of phase space variables are (ρ, ρ'), where ρ is the population size determining wave profile/pattern and ρ' its spatial gradient. The associated vector field is (ρ', ρ'').

- Stochastic models such as stochastic reaction networks
  Examples: Dynamics of discrete population size x. Can be approximated using the WKB approximation and quasi-potential.
  Phase space variables: (x, p), where $p = S'(x)$ is the derivative of the quasi-potential. The associated vector field is $(\dot{x}, \dot{p})$.

If your module is taught across multiple year levels, you might have received this form for each level of the module. You are only required to fill this out once for each question.

Please record below, some brief but non-trivial comments for students about how well (or otherwise) the questions were answered. For example, you may wish to comment on common errors and misconceptions, or areas where students have done well. These comments should note any errors in and corrections to the paper. These comments will be made available to students via the MathsCentral Blackboard site and should not contain any information which identifies individual candidates. Any comments which should be kept confidential should be included as confidential comments for the Exam Board and Externals. If you would like to add formulas, please include a sperate pdf file with your email.

ExamModuleCode	Question	Comments for Students	
MATH97018_MATH970	1	Many of you have excelled in this question. Well done.	
MATH97018_MATH970	2	Some students missed that the limit of the function depends on the value of x but still succeeded in identifying the stability of steady states. The tricky part of the last part was that for the parameter regime the hysteresis was irreversible.	
MATH97018_MATH970	3	Almost everyone succeeded in deriving the binomial distribution, well done. The more tricky part of this question was to notice that the coefficient of variation does not necessarily decay with the mean (as hinted to in the title of the question).	
MATH97018_MATH970	4	As you have realised most of this question was outlined in the lecture notes. Surprisingly, many of you missed to describe the corresponding pattern by solving for the eigenfunctions of the Helmholtz equation (also in the notes). The tricky part was that there are two possible pattern depending on sign of amplitudes.	
MATH97018_MATH970	5	Many of you have done well. While everyone has commented on applications in ODE systems, some missed to comment on spatial and stochastic systems discussed in the lecture and notes.	