Durham University

EXAMINATION PAPER

Examination Session:	Year:	Exam Code:
May	2018	MATH3171-WE01

Title:
Mathematical Biology III

Time Allowed:	3 hours	
Additional Material provided:	None	
Materials Permitted:	None	
Calculators Permitted:	No	Models Permitted: Use of electronic calculators is forbidden.
Visiting Students may use dictionaries: No		

Instructions to Candidates:	Credit will be given for: the best **FOUR** answers from Section A and the best **THREE** answers from Section B. Questions in Section B carry **TWICE** as many marks as those in Section A.

Revision:	

ED01/2018

SECTION A

1. **Similarity Solution** Consider the following non-autonomous partial differential equation for a function $c(x,t)$,

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} - \frac{1}{t^{1/2}}\frac{\partial c}{\partial x}, \tag{1}$$

where D is a positive constant, $x \in \mathbb{R}$ and $t > 0$.

(a) Assume a similarity solution v which relates to c as

$$c(x,t) = \frac{1}{t^{\alpha}}v(y), \quad y = x/t^{\beta}.$$

Show that, for a suitable choice of β, (1) reduces to the following O.D.E in y,

$$D\frac{\mathrm{d}^2 v}{\mathrm{d}y^2} - \frac{\mathrm{d}v}{\mathrm{d}y} + \alpha v + y\beta\frac{\mathrm{d}v}{\mathrm{d}y} = 0.$$

(b) Show by integration, that, for a suitable choice of α, this equation can be written as

$$D\frac{\mathrm{d}v}{\mathrm{d}y} + v\left(\frac{1}{2}y - 1\right) = C,$$

where C is a constant of integration.

(c) There is a turning point $\frac{\partial c}{\partial x} = 0$ whose position is $x = 2t^{1/2}$. Assuming α and β take the values found in (a) and (b), show that the solution to (1) takes the form

$$c(x,t) = t^{-1/2}A\exp\left(\frac{x(1-\frac{1}{4t^{1/2}}x)}{Dt^{1/2}}\right),$$

where A is a constant of integration.

2. **P.D.E. stability** Consider the following P.D.E. for a function $u(x, t)$,

$$\frac{\partial^2 u}{\partial t^2} = D\frac{\partial^2 u}{\partial x^2} - au\frac{\partial u}{\partial x} + \cos(u),$$

subject to no-flux boundary conditions on a domain $x \in [0, L]$, and where D and a are positive constants.

   (a) Find the homogeneous equilibrium for u on the domain $u \in [0, \pi]$.

   (b) Find a condition on the ratio a^2/D (if any) for which this equilibrium is asymptotically stable.

   (c) Consider a second homogeneous equilibrium on the domain $u \in [\pi, 2\pi]$. Find a condition on the ratio a^2/D (if any) for which this equilibrium is asymptotically stable.

3. **Spatial Lotka-Volterra** Consider the following spatial variant of the Lotka-Volterra system,

$$\frac{\partial u}{\partial t} = \nabla^2 u + u - uv,$$
$$\frac{\partial v}{\partial t} = D\nabla^2 v - \gamma(v - uv),$$

where γ and D are positive constants. The system is considered on a Cartesian domain $[0, L_1] \times [0, L_2]$ with a coordinate system (x_1, x_2). Both u and v take on (homogeneous) fixed values u_0 and v_0 on the boundaries at all times.

   (a) Find the system's homogeneous equilibria.

   (b) Determine any conditions on the domain lengths L_1 and L_2 for which the equilibria are asymptotically stable (if at all).

4. **Turing analysis** Consider the following **non-dimensionalised** reaction-diffusion system for scalar densities u and v

$$\frac{\partial u}{\partial t} = \nabla^2 u + \gamma F(u, v), \qquad (2)$$
$$\frac{\partial v}{\partial t} = D\nabla^2 v + \gamma G(u, v),$$

where D and γ are positive constants. We assume **no-flux** boundary conditions on a Cartesian domain $[0, L_1] \times [0, L_2]$ with coordinates (x_1, x_2). The Turing conditions for pattern formation are

$$F_u + G_v < 0, \quad F_u G_v - G_u F_v > 0, \qquad (3)$$
$$G_v + DF_u > 0, \quad (G_v + DF_u)^2 - 4D(F_u G_v - G_u F_v) > 0,$$

where we have used the notation

$$F_u = \left.\frac{\partial F}{\partial u}\right|_{u=u_0, v=v_0}, \quad F_v = \left.\frac{\partial F}{\partial v}\right|_{u=u_0, v=v_0},$$
$$G_u = \left.\frac{\partial G}{\partial u}\right|_{u=u_0, v=v_0}, \quad G_v = \left.\frac{\partial G}{\partial v}\right|_{u=u_0, v=v_0},$$

and (u_0, v_0) represent a homogeneous equilibrium of the system.

(a) Define what is meant by a pattern in this context, give the explicit mathematical form for the pattern and describe what the conditions (3) enforce.

(b) Assume $L_1 = 1$. Further assume there is a single permissible pattern number k_s which will grow in time (all others decaying). This mode leads to the formation of two possible patterns, one with five vertical stripes which run parallel to the x_2 axis, and one with 4 spots, each located at one of the domain's corners. Find the value of L_2.

5. **Population modelling** Consider the following model for the interaction of two populations $u(t)$ and $v(t)$,

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -au^2 + bu + cu^3 v, \qquad (4)$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = -duv + ev^2,$$

where a, b, c, d and e are positive constants.

(a) Show that (4) can be non-dimensionalised to take the form

$$\frac{\mathrm{d}\hat{u}}{\mathrm{d}\hat{t}} = -\hat{u}^2 + \hat{u} + \hat{u}^3\hat{v},$$
$$\frac{\mathrm{d}\hat{v}}{\mathrm{d}\hat{t}} = -\gamma_1\hat{u}\hat{v} + \gamma_2^2\hat{v}^2,$$

where $\gamma_1 = da^{-1}$ and $\gamma_2 = e^{1/2}ab^{-1}c^{-1/2}$ and $\hat{u}, \hat{v}$ and $\hat{t}$ are the non-dimensionalised variables.

(b) What do the constants γ_1 and γ_2 represent? In your answer you should consider if they represent self-interaction or mutual-interaction of the species.

(c) State all the physically permissible equilibria of the system for which one population is extinct.

6. **Chemotaxis and Slime mould** Consider the following generic model for bacterial growth in a semi-solid medium,

$$\frac{\partial n}{\partial t} = D_n\nabla^2 n - \alpha\nabla\cdot[nc\nabla c] + \rho n^2(\delta s - n),$$
$$\frac{\partial c}{\partial t} = D_c\nabla^2 c + \beta s(\mu n - s) - n^2 c,$$
$$\frac{\partial s}{\partial t} = D_s\nabla^2 s,$$

where $D_n, D_c, D_s, \alpha, \rho, \delta, \beta$ and μ are positive constants, n is the bacteria concentration, c is the chemotaxant concentration, and s is the nutrient concentration.

(a) Describe all the terms in this model. Describe their behaviour if we assume the populations are homogeneous.

(b) In an experiment a bacterial population is initially homogenously spread in its petri dish with a homogeneous distribution of nutrition s_0. A chemical is present whose only effect is to inhibit chemotaxant production. The chemical is then removed (almost instantaneously) and the chemotaxant population begins to grow. Assuming homogenous distributions for s, c and n, explain why the proposed model could be appropriate and state any requirements on the parameters for this to be the case. Hint: how can the parameter β be used to represent the presence/absence of the chemotaxant inhibitor?

SECTION B

7. **Turing Analysis** Consider the following hyperdiffusive reaction diffusion system,

$$\frac{\partial u}{\partial t} = \nabla^2 u - a\nabla^4 u + \gamma F(u, v),$$
$$\frac{\partial v}{\partial t} = D\left(\nabla^2 v - a\nabla^4 v\right) + \gamma G(u, v),$$

where D is the ratio of diffusion constants of v and u, and γ and a are positive constants. We assume the domain V is Cartesian, m-dimensional, and that all density fluxes vanish on its boundary. This model better captures the random motion of cells than the standard reaction-diffusion system for which $a = 0$ (with the other parameters identical and the same boundary conditions).

(a) State explicitly the boundary conditions of this system.

(b) State the equations which would determine the homogeneous equilibria (u_0, v_0) of this system.

(c) Carry out a Turing analysis for this system to show there will be a growing inhomogeneous pattern when

$$\begin{aligned} &F_u + G_v < 0, \quad F_u G_v - F_v G_u > 0, \\ &G_v + DF_u > 0, \quad [G_v + DF_u]^2 - 4D(F_u G_v - F_v G_u) \geq 0. \end{aligned} \tag{5}$$

Here we have used the notation

$$F_u = \left.\frac{\partial F}{\partial u}\right|_{u=u_0, v=v_0}, \quad F_v = \left.\frac{\partial F}{\partial v}\right|_{u=u_0, v=v_0},$$
$$G_u = \left.\frac{\partial G}{\partial u}\right|_{u=u_0, v=v_0}, \quad G_v = \left.\frac{\partial G}{\partial v}\right|_{u=u_0, v=v_0}.$$

(d) We set

$$F = \mathrm{e}^{-(u^2-1)} - 1, \quad G = u^2 - v^2.$$

Find the single permissible homogeneous equilibrium of the system, given we require $u_0, v_0 > 0$. Demonstrate that it cannot satisfy the Turing conditions for inhomogenous pattern formation derived in part (c).

(e) Observe that the Turing conditions for our hyperdiffusive system are the same as those for the standard reaction diffusion system $a = 0$. How do the pattern modes $(n_1, \ldots n_m)$ differ in the cases $a = 0$ and $a > 0$, leaving all other parameters unchanged?

8. **Species interaction** Consider the following system for modelling competitive species $u(t)$ and $v(t)$,

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -u^2 v + r_1 u, \qquad (6)$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = -uv^2 + r_2 v,$$

where $r_1, r_2 > 0$ are constants.

(a) Describe the effect of each term on the right hand side of the system and state which terms represent inter-species interactions. Is there any intra-species competition?

(b) Find the permissible equilibria when $r_1 \neq r_2$ and evaluate their stability.

(c) Now consider the case $r_1 = r_2$ and find the family of equilibria. Is this family asymptotically stable?

(d) The two populations have gestation periods of respectively 1 day (u) and 1 year (v), but produce the same number of offspring per individual per gestation period. The combined population system can approach an equilibrium state in which both species are non-zero. Can the system (6) represent these populations?

(e) It is suggested that the following might be a suitable model for the population interaction in which the population v can enter or leave the domain,

$$\frac{\mathrm{d}u}{\mathrm{d}t} = -u^2 v + r_1 u, \qquad (7)$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = -uv^2 + r_2 v + a.$$

As before r_1 and r_2 are positive constants and a is a real constant. There should be an equilibrium for which **both** populations are non-zero. The gestation periods given in (d) are assumed to apply. State whether a should be positive or negative.

(f) A hormone can be used to control the gestation period of u. On varying this hormone it is found the populations u and v can sustain oscillations about equilibrium with a very small fixed amplitude. Perform a linear stability analysis of (7) to establish if it is an appropriate model given this information.

9. **Spiral waves** Consider a reaction-diffusion system which is the asymptotic limit of a FitzHugh-Nagumo model for neuron firing. Here densities u and v represent respectively the neuronal firing activity and recovery response of this signal. These densities can be written as

$$u(r,\theta,t) = A(r,\theta,t)\cos(\phi(r,\theta,t)), \quad v(r,\theta,t) = A(r,\theta,t)\sin(\phi(r,\theta,t)),$$

where (r,θ) are polar coordinates for the plane $\mathbb{R}^2$. The functions A and ϕ satisfy the following system of P.D.E's

$$\begin{aligned} \frac{\partial A}{\partial t} &= D\nabla^2 A + Af(A) - D(A\nabla\phi)^2, \\ \frac{\partial \phi}{\partial t} &= D\nabla^2\phi + g(A) + 2\frac{D}{A}\nabla A\cdot\nabla\phi, \end{aligned} \tag{8}$$

with D a positive diffusion constant and f, g functions of A which represent the non linear rection part of the original FitzHugh-Nagumo system. A spiral wave limit-cycle occurs when A and ϕ take the following form

$$A = A(r), \quad \phi(r,\theta,t) = \Omega t + m\theta + \psi(r), \tag{9}$$

where m is a constant integer, Ω a real constant and $\psi(r)$ is a real function.

(a) Describe the effect of the of the parameters m and Ω and the functions A, ψ on the spiral limit cycle shape (9).

(b) For a limit cycle spiral wave (8) takes the following form,

$$\begin{aligned} D\left(\frac{\mathrm{d}^2 A}{\mathrm{d}r^2} + \frac{1}{r}\frac{\mathrm{d}A}{\mathrm{d}r}\right) + A\left[f - D\left(\frac{\mathrm{d}\psi}{\mathrm{d}r}\right)^2 - \frac{Dm^2}{r^2}\right] &= 0, \\ D\frac{\mathrm{d}^2\psi}{\mathrm{d}r^2} + D\left[\frac{1}{r} + \frac{2}{A}\frac{\mathrm{d}A}{\mathrm{d}r}\right]\frac{\mathrm{d}\psi}{\mathrm{d}r} &= \Omega - g. \end{aligned} \tag{10}$$

Show that the second equation of (10) can be rewritten as the following

$$\frac{\mathrm{d}\psi}{\mathrm{d}r} = \frac{1}{DrA^2}\int_0^r sA^2(\Omega - g)\mathrm{d}s.$$

(c) State and explain the boundary conditions on A and $\frac{\mathrm{d}\psi}{\mathrm{d}r}$ at $r = 0$, assuming $m \neq 0$.

(d) State a required condition on $\frac{\mathrm{d}\psi}{\mathrm{d}r}$ as $r \to \infty$ for reasonable physical behaviour.

(e) Use the condition of part (d) to place a specific constraint on the value of Ω in terms of the function g and hence obtain a limit for $\frac{\mathrm{d}\psi}{\mathrm{d}r}$ as $r \to \infty$.

(f) Consider the shape of a limit cycle spiral wave taking the form (10) on an annular domain with $r \in [1, \infty]$. Assume there are $m > 0$ spiral arms and that, for a fixed t, the peak of each spiral arm is along a line of fixed θ. The function f is,

$$f(A) = \frac{D + Dm^2}{r^2}. \tag{11}$$

State the form of the function g and solve for ψ and A assuming $A(1) = 1$ and $\frac{\mathrm{d}A}{\mathrm{d}r}(1) = 0$. Hint: seek a solution for A in the form $A = Cr^{\lambda}$, where C is a constant and use the identity

$$r^{\lambda} = \mathrm{e}^{\lambda \ln r},$$

at some point during the solution method.

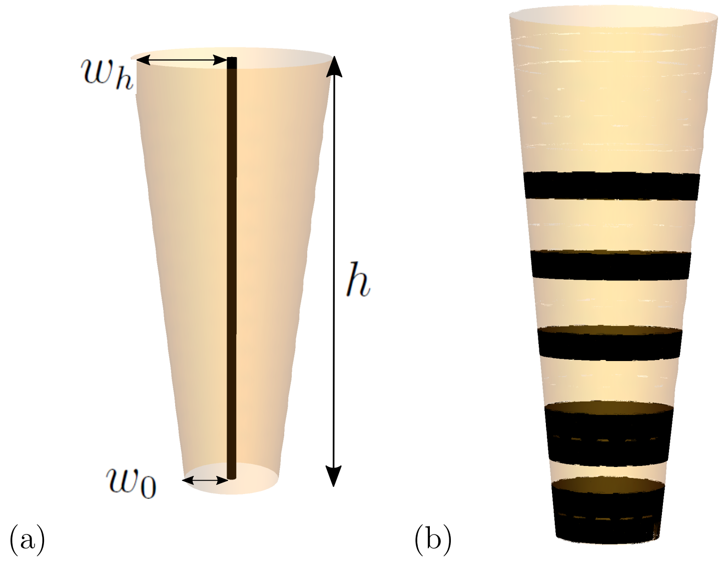

Figure 1: The tapered cylindrical surface used in question 10, the height h and boundary widths w_0 and w_h are shown.

10. **Pattern formation in a non-Cartesian domain** Consider the tapered cylindrical surface described by a vector $\mathbf{c}(\theta, z)$, shown in Figure 1(a), given by

$$\mathbf{c}(\theta, z) = bz\cos(\theta)\hat{\mathbf{x}} + bz\sin(\theta)\hat{\mathbf{y}} + z\hat{\mathbf{z}}.$$

for $z \in [w_0/b, h + w_0/b]$ and $\theta \in [0, 2\pi)$, where $(\hat{\mathbf{x}}, \hat{\mathbf{y}}, \hat{\mathbf{z}})$ are Cartesian basis vectors, w_0 is the minimum width of the surface, h the vertical length of the cylinder, $b = (w_h - w_0)/h$ and tapering gradient. This kind of surface has been used to model pattern formation on animal tails. In this domain the Laplacian of a function ψ takes the following form

$$\nabla^2\psi = \frac{\partial^2\psi}{\partial z^2} + \frac{1}{z}\frac{\partial\psi}{\partial z} + \frac{\gamma}{z^2}\frac{\partial^2\psi}{\partial\theta^2},$$

where $\gamma = (b^2+1)/b^2$. Consider the following reaction diffusion type system

$$\frac{\partial u}{\partial t} = \nabla^2 u + au\left(\frac{v}{1+v} - u\right),$$
$$\frac{\partial v}{\partial t} = D\nabla^2 v + b - uv,$$

on this tapered domain. There are no-flux boundary conditions at either end of the domain. The parameters D, a and b are positive constants.

(a) State explicitly the boundary conditions for this problem.

(b) Consider solutions $u(z,\theta,t) = u_0 + \epsilon u_1(z,\theta,t)$ and $v(z,\theta,t) = v_0 + \epsilon v_1(z,\theta,t)$, where u_0, v_0 are homogeneous equilibria of the system. Find the $\mathcal{O}(\epsilon)$ equations and assume their solutions take the form $u_1 = \psi_u(z,\theta)\mathrm{e}^{\lambda t}$ and $v_1 = \psi_v(z,\theta)\mathrm{e}^{\lambda t}$, where ψ_u and ψ_v satisfy

$$\nabla^2\psi_u + k^2\psi_u = 0, \text{ and } \nabla^2\psi_v + k^2\psi_v = 0.$$

Show that solutions to these eigen-equations take the form

$$\psi_{u/v}(z,\theta) = \sum_{n=0}^{\infty} \left[f_{n1}(z)\cos(n\theta) + f_{n2}(z)\sin(n\theta) \right],$$

where $f_{n\alpha}, \alpha = 1, 2$ solve the equation

$$\frac{\mathrm{d}^2 f_{n\alpha}}{\mathrm{d}z^2} + \frac{1}{z}\frac{\mathrm{d}f_{n\alpha}}{\mathrm{d}z} + \left(k^2 - \frac{\gamma n^2}{z^2}\right) f_{n\alpha} = 0. \tag{12}$$

(c) You are told that the observed pattern is a series of stripes, starting at $z = w_0/b$, as shown in Figure 1(b). State the form of the permissible spatial patterns ψ_u, given that the solution to (12) takes the form

$$f_{n\alpha}(z) = A_\alpha J_{\sqrt{\gamma}n}(kz) + B_\alpha Y_{\sqrt{\gamma}n}(kz),$$

with $J_{\sqrt{\gamma}n}(x)$ and $Y_{\sqrt{\gamma}n}(x)$ the (fractional) Bessel functions of the first and second kind.

(d) Find an algebraic equation for the permissible pattern numbers k.

(e) We note that the tapering parameter b takes the form

$$b = \frac{w_h - w_0}{h}.$$

Assume $w_h = 2$, $w_0 = 1$. You are told that the parameters of the model for two particular species of mammal are such that only modes for which $k \in [1, 2]$ will have positive temporal growth parameters λ. What is the expected effect of increasing the parameter h on the set of permissible stripe patterns of this system (Hint: think about the behaviour of the Bessel functions)?

(f) Assume the two populations have tails of significant difference in length but the same widths w_0 and w_h. How might we expect to see this tail length difference manifest itself between the two populations?