EXAMINATION PAPER

Examination Session:	Year:	Exam Code:
May	2019	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:	

ED01/2019

SECTION A

1. **Travelling waves in predator-prey** Consider the spatial Lotka-Volterra system on a one dimensional domain, the whole real line, with coordinate $x \in \mathbb{R}$:

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} - \alpha u v, \qquad (1)$$
$$\frac{\partial v}{\partial t} = D_2 \frac{\partial^2 v}{\partial x^2} + \beta u v.$$

Here D_1, D_2 are constant positive diffusion coefficients and the interaction constants α and β are also positive.

(a) Consider travelling wave solutions to (1) in the form $u(z), v(z)$ where $z = x - ct$. Show that under this assumption the equations take the following form

$$D_1 \frac{\mathrm{d}^2 u}{\mathrm{d}z^2} + c\frac{\mathrm{d}u}{\mathrm{d}z} - \alpha u v = 0,$$
$$D_2 \frac{\mathrm{d}^2 v}{\mathrm{d}z^2} + c\frac{\mathrm{d}v}{\mathrm{d}z} + \beta u v = 0.$$

(b) The predator v invades the prey environment in which initially there is a homogeneous prey population u_0. We assume a small predator invasion in the form

$$u(z) = u_0 - \epsilon u_c \mathrm{e}^{\lambda z},$$
$$v(z) = \epsilon u_c \mathrm{e}^{\lambda z},$$

where λ is **real** for a valid travelling wave disturbance. Find the $\mathcal{O}(\epsilon)$ equations for λ under this assumption.

(c) Assume the interaction constants are identical and that both populations diffuse at the same rate. Show that the minimum velocity c for a valid travelling wave solution is

$$c_{min} = \sqrt{4D_1\alpha u_0}.$$

2. **Fourier transform solution of a P.D.E** Consider the following P.D.E. and its fundamental problem:

$$\frac{\partial c}{\partial t} = t^n D \frac{\partial^2 c}{\partial x^2}, \quad c(x,0) = \delta(x), \quad c(\pm\infty, t) = 0, \tag{2}$$

with $n > 0$. Here $\delta(x)$ is the Dirac delta distribution and $D > 0$. We define the Fourier Transform as

$$F[c](k) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \mathrm{e}^{-\mathrm{i}kx} c(x) \mathrm{d}x,$$

and its inverse as

$$F^{-1}[c](x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \mathrm{e}^{\mathrm{i}kx} c(k) \mathrm{d}k.$$

(a) Show that the solution to (2) in Fourier space is

$$F[c](k) = \frac{1}{\sqrt{2\pi}} \mathrm{e}^{-\frac{Dk^2 t^{n+1}}{n+1}}.$$

(b) Find the solution in real space $c(x,t)$. You may use the following identity

$$F[\mathrm{e}^{-ax^2}](k) = \frac{1}{\sqrt{2a}} \mathrm{e}^{-k^2/4a}.$$

(c) Compare this solution to the fundamental solution of the standard diffusion equation $n = 0$, focusing on the physical plausibility of the solution and the difference in the solution's expansion as a function of time.

3. **Population modelling** Consider the following model for the interaction of population densities $u(t), v(t)$,

$$\frac{\mathrm{d}u}{\mathrm{d}t} = u - \left[u^2 + v^2 - c/4\right], \tag{3}$$

$$\frac{\mathrm{d}v}{\mathrm{d}t} = v(1 - v), \tag{4}$$

where $c > 0$ is a positive constant.

(a) Describe the terms on the right hand side of the system. Pay attention to which terms are self interactions or mutual interactions. Treat the term in square brackets as one type of interaction.

(b) Find all **physically permissible** equilibria of the system.

(c) Argue why the equilibria for which $v = 0$ are unstable. You may freely state any facts from the course notes and need not perform a stability analysis.

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

$$\frac{\partial u}{\partial t} = \nabla^2 u + \gamma F(u,v), \tag{5}$$
$$\frac{\partial v}{\partial t} = D\nabla^2 v + \gamma G(u,v),$$

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

$$F_u + G_v < 0, \quad F_u G_v - G_u F_v > 0, \tag{6}$$
$$G_v + DF_u > 0, \quad (G_v + DF_u)^2 - 4D(F_u G_v - G_u F_v) > 0,$$

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 (6) enforce.

(b) A particular version of (5) can be used to model a growing animal epithelial layer. Assume the growth is modelled as uniform continuous (in time) increase of the domain lengths L_1 and L_2. Consider an equilibrium (u_0, v_0) of this system and assume it is **independent** of the value of the lengths L_1 and L_2. Assume the changing lengths do not change the constants D, γ or the functions F and G and finally that the growth is sufficiently slow that the system remains in equilibrium under this growth (if the equilibrium is stable).

For some initial lengths L_1 and L_2 the Turing conditions (6) are satisfied, however, no patterns are formed. Then, when the lengths increase to some value aL_1 and aL_2, $a > 1$, a pattern of spots forms. Explain why the pattern formation is delayed until the length has increased, despite always satisfying the Turing conditions. You should use your answer to part (a).

5. **Lotka-Volterra Periodicity** Consider the non-dimensionalised Lotka-Volterra equation for densities $u(t), v(t)$,

$$\frac{\mathrm{d}u}{\mathrm{d}t} = u - uv,$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = \gamma(-v + uv),$$

with $\gamma > 0$ a constant.

(a) Show that the system can be integrated to give

$$\log(v) - v = -\gamma(\log(u) - u) + C,$$

where C is a constant of integration.

(b) Use the result of (a) to demonstrate that the solutions to the Lotka Volterra system are periodic close to the equilibrium $(u, v) = (1, 1)$. To do so you may use the fact that for some two-dimensional surface $F(u, v)$ a local extremum is a local maximum if the function

$$D = \frac{\partial^2 F}{\partial v^2}\frac{\partial^2 F}{\partial u^2} - \left(\frac{\partial^2 F}{\partial u \partial v}\right)^2,$$

is positive and $\frac{\partial^2 F}{\partial u^2} < 0$.

6. **The Acetabularia model** Consider a model for hair tip growth from an Acetabularia cell stalk. We model the stalk in its cross-section as an annular domain with polar coordinates (r, θ). A morphogen represented by a chemical density $u(r, \theta, t)$ generates hair growth in a given region if $u > u_c$ for some critical value u_c. Its distribution is controlled by a source of calcium density $v(r, \theta, t)$ and their interaction is modelled by the following system.

$$\begin{aligned}\frac{\partial u}{\partial t} &= \nabla^2 u + R^2(a - u + u^2 v), \qquad (7)\\ \frac{\partial v}{\partial t} &= D\nabla^2 v + R^2(b - u^2 v),\end{aligned}$$

where $D > 0$ is the constant ratio of diffusion of u and v, R is a constant proportional to the mean radius of the stalk and $b \in \mathbb{R}^+, a \in \mathbb{R}$ are also constants. In particular b represents the calcium concentration of the surrounding solvent. It is believed the spontaneous hair formation can be modelled by a Turing instability of this system where both u and v have no flux boundary conditions.

(a) Find the homogeneous equilibrium (u_0, v_0) of (7).

(b) Solutions for u to the linearised system of (7) in the neighbourhood of this equilibrium take the form

$$AJ_n(k_n r)\cos(n\theta)\mathrm{e}^{\lambda(k_n)t},$$

for some constant $A > 0$, n an integer and $k_n \geq 0$ constant. Here J_n is the n^{th} Bessel function of the first kind. Assume the domain is thin *i.e.* $r \in [R - \epsilon, R + \epsilon]$, $\epsilon \ll R$. It can be shown under this assumption that $k_n = n$ to a good approximation. Assume further that $u_c > u_0$, that there is only one value of k_n for which $\lambda(k_n) > 0$ and that this $k_n \propto R$. What is the expected relationship between the stalk's radius and the pattern of hair growth?

(c) The Turing conditions of this system can be shown to be satisfied if the following two inequalities hold

$$a < \frac{u_0}{2}\left(1 - \frac{2u_0}{\sqrt{D}} - \frac{u_0^2}{D}\right), \quad a > \frac{u_0(1 - u_0^2)}{2}. \qquad (8)$$

Argue, based on these inequalities, that if $D > 1$ tip growth is promoted when the surrounding calcium concentration belongs to an interval $b \in [b_l, b_h]$ but is suppressed otherwise.

SECTION B

7. **Turing Analysis** Consider the following non-linear reaction diffusion system for the interaction of a bacterial species, via its population density u and its food source, represented by a population density v,

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

where the constant D is the ratio of diffusion constants of v and u, and γ is also a positive constant. We assume the domain V is Cartesian, m-dimensional, and that all density fluxes vanish on its boundary.

(a) Write equations expressing the boundary conditions.

(b) What are the conditions on u and v for the solutions to be physically valid?

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

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

$$F_u + G_v < 0, \quad F_uG_v - F_vG_u > 0,$$
$$G_vu_0v_0 + DF_u > 0, \quad (G_vu_0v_0 + DF_u)^2 - 4u_0v_0D(F_uG_v - F_vG_u) \geq 0. \qquad (9)$$

Here we have used the notation

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

(e) Consider the following reaction functions,

$$F(u,v) = u^2 - v^2/a^2, \quad G(u,v) = \sin(u)\sin(v), \qquad (10)$$

for $a > 0$ with a constant. Find all physically valid homogeneous equilibria and show that none of them can satisfy the Turing conditions.

(f) Give the physical interpretation of the specific reason the Turing conditions were not satisfied in part (e).

8. **Species interaction** Consider the following purely temporal model for the expansion of bacterial colony $u(t)$ into an environment filled with a food supply $v(t)$:

$$\frac{\mathrm{d}u}{\mathrm{d}t} = au - b\sin(u)\sin(v), \qquad (11)$$
$$\frac{\mathrm{d}v}{\mathrm{d}t} = cv\left(1 - \frac{uv}{d}\right),$$

where a, b, c, d are positive constants. The solutions $u(t), v(t)$ should be positive to be considered physically valid.

(a) Show that we can introduce scaled variables $\hat{u}, \hat{v}, \hat{t}$ such that the system (11) can be written as

$$\frac{\mathrm{d}\hat{u}}{\mathrm{d}\hat{t}} = \hat{u} - \beta\sin(d\hat{u})\sin(\hat{v}), \qquad (12)$$
$$\frac{\mathrm{d}\hat{v}}{\mathrm{d}\hat{t}} = \gamma\hat{v}\left(1 - \hat{u}\hat{v}\right),$$

where $\gamma = c/a$ and $\beta = b/ad$.

(b) Find all equilibria of the system (12) for which **at least** one of the bacteria/food supply is extinguished. Perform a linear stability analysis of these equilibria.

(c) Show that, in order for the bacteria to be in equilibrium with a non-zero food supply, its population must satisfy.

$$\hat{u} = \beta\sin(d\hat{u})\sin(1/\hat{u}), \qquad (13)$$

and argue that this implies we require $\beta d > 1$ for such equilibria to exist.

(d) Observations of an example bacterial colony for which this model is intended indicate that the variables u and v should exhibit limit cycle behaviour. Assume this can occur in the model when there is an equilibrium $du_0 = \pi/2$ satisfying (13). Show, using a linear stability analysis, that limit cycles close to this equilibrium must satisfy the following inequality

$$\frac{2}{n\pi} > \hat{u} > \frac{2}{(n+2)\pi},$$

where $n = 4k + 1\ldots$ for integer $k \geq 0$.

9. **Chemotaxis and pattern formation** Consider the following one-dimensional chemotactic slime mould model,

$$\frac{\partial n}{\partial t} = -\alpha \frac{\partial}{\partial x}\left[\chi(n,c)\frac{\partial c}{\partial x}\right],$$
$$\frac{\partial c}{\partial t} = \frac{\partial^2 c}{\partial x^2} + nc(1-\gamma n),$$

where α and γ are positive constants. Here $n(x,t)$ is the slime mould density and $c(x,t)$ the chemotaxant density and $\chi(n,c)$ is a smooth function which determines the chemotaxic behaviour. We consider the model on a Cartesian domain $x \in [0, L]$.

(a) If we assume that c has a spatially homogeneous profile, then show there exists a non-zero homogeneous equilibrium for n, which we label n_0. Then, assuming c initially takes a value $c(0) = 1$, show that

$$c(t) = \mathrm{e}^{n_0(1-\gamma n_0)t}.$$

(b) Now consider small spatial variations around this solution in the form

$$n(x,t) = n_0 + \epsilon \sum_{n=0}^{\infty} f_{k_n}(t)\mathrm{e}^{ik_n x}, \quad c(x,t) = c_0(t) + \epsilon \sum_{n=0}^{\infty} g_{k_n}(t)\mathrm{e}^{ik_n x},$$
$$c_0(t) = \mathrm{e}^{n_0(1-\gamma n_0)t},$$

where $\epsilon \ll 1$ and $k_n = n\pi/L$. Show that, for each k_n, the $\mathcal{O}(\epsilon)$ equations are

$$\frac{\mathrm{d}f_{k_n}}{\mathrm{d}t} = k_n^2 \alpha \chi_0(n_0, c_0) g_{k_n},$$
$$\frac{\mathrm{d}g_{k_n}}{\mathrm{d}t} = -k_n^2 g_{k_n} + (1-\gamma 2n_0)\mathrm{e}^{n_0(1-\gamma n_0)t} f_{k_n} + n_0(1-\gamma n_0) g_{k_n},$$

(c) Consider the case $n_0 = 1/(2\gamma)$. Solve to find $g(t)$ and give its interpretation in terms of mode growth.

(d) Now assume also $\chi(n,c) = nc$. Consider two sets of boundary conditions. First no-flux boundary conditions

$$\frac{\partial n}{\partial x}(0,t) = \frac{\partial n}{\partial x}(L,t) = \frac{\partial c}{\partial x}(0,t) = \frac{\partial c}{\partial x}(L,t) = 0,$$

and second, zero Dirichlet boundary conditions,

$$n(0,t) = n(L,t) = c(0,t) = c(L,t) = 0.$$

State in each case whether pattern formation can occur and if so, state the conditions on the domain length L for pattern formation to occur.

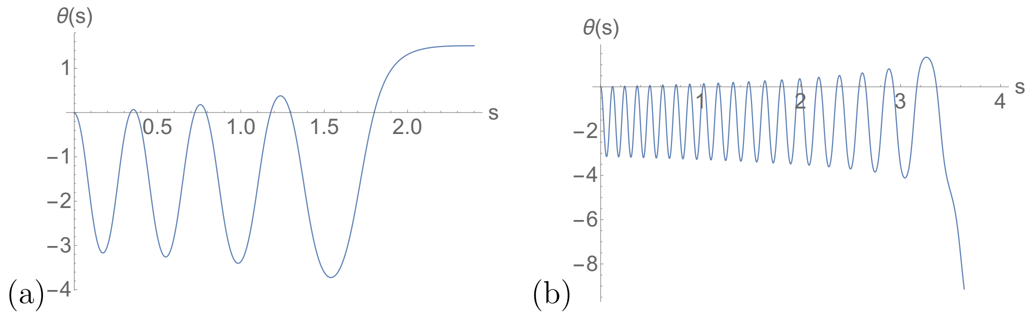

Figure 1: Solutions $\theta(s)$ to (15) used in question 10(f).

10. **Elastic rods** Consider a thin slender body whose central axis is represented by a curve $\mathbf{r}(s) : [0, L] \to \mathbb{R}^3$, where s is the body's arclength. The coordinates of $\mathbb{R}^3$ take the form (x, y, z) with unit vectors $\hat{x}, \hat{y}$ and $\hat{z}$ respectively. A force $\mathbf{n}(s)$ represents the internal force acting on each cross-section of the the body and $\mathbf{m}(s)$ represents the internal couple acting on each cross section. Net forces and couples can be applied at $s = 0$ and $s = L$.

(a) Demonstrate using force and moment balance that the equilibrium equations for this body are

$$\frac{\mathrm{d}\mathbf{n}}{\mathrm{d}s} + \mathbf{f} = \mathbf{0},$$
$$\frac{\mathrm{d}\mathbf{m}}{\mathrm{d}s} + \frac{\mathrm{d}\mathbf{r}}{\mathrm{d}s} \times \mathbf{n} + \mathbf{l} = \mathbf{0},$$

where $\mathbf{f}$ is an external force per unit length acting on the body and $\mathbf{l}$ an external couple per unit length acting on the body.

(b) For all permissible configurations the curve $\mathbf{r}(s)$ can, for some vector $\mathbf{u}(s)$, be determined by solving the following system of differential equations

$$\frac{\mathrm{d}\mathbf{r}}{\mathrm{d}s} = \mathbf{d}_3, \quad \frac{\mathrm{d}}{\mathrm{d}s}\mathbf{d}_j = \mathbf{u} \times \mathbf{d}_j, \quad \mathbf{u} = u_1\mathbf{d}_1 + u_2\mathbf{d}_2 + u_3\mathbf{d}_3,$$

(up to a choice of initial conditions). Here $\mathbf{d}_3$ is the unit tangent vector of $\mathbf{r}$ and $\mathbf{d}_1$ and $\mathbf{d}_2$ form an orthonormal frame with $\mathbf{d}_3$.

What does this imply about the slender rod with regards to its potential deformation?

(c) Assume the rod is in equilibrium and subjected to a gravitational body force $\mathbf{f} = -g\hat{z}$. Further assume there is no net force applied at $s = L$. Show that

$$\mathbf{n} = g(s - L)\hat{z}.$$

(d) We now consider the following further restriction on its potential deformation. The tangent vector is described by an angle function $\theta(s)$

$$\mathbf{d}_3 = (\cos\theta(s), 0, \sin\theta(s))\,.$$

Construct a right-handed orthonormal frame $(\mathbf{d}_3, \mathbf{d}_1, \mathbf{d}_2)$ for the curve $\mathbf{r}$ on the further assumption that it has no twist ($u_3 = 0$).

(e) Assume that there is no body moment $\mathbf{l}$ and the material couple $\mathbf{m}$ takes the form

$$\mathbf{m} = Bu_1\mathbf{d}_1 + Bu_2\mathbf{d}_2 + Cu_3\mathbf{d}_3, \tag{14}$$

where B and C are constants. Demonstrate that the moment equation reduces to the following non-linear O.D.E.

$$B\frac{\mathrm{d}^2\theta}{\mathrm{d}s^2} + g(s-L)\cos\theta = 0. \tag{15}$$

(f) Solutions to (15) are shown in Figure 1. These solutions are from a model for a human hair hanging under gravity. Describe briefly the shape of the rod $\mathbf{r}(s)$ for solution (a) and briefly comment on the difference one would expect to see for rod (b).