Further Mathematical Biology: Problem Sheet 2

Michaelmas Term 2020

Question 1.

The evolution of an age-structured population $N(t,a)$ satisfies

$$\frac{\partial N}{\partial t} + \frac{\partial N}{\partial a} = -\mu(a)N, \tag{1}$$

with $N(0,a) = F(a)$ and

$$N(t,0) = B(t) = \int_0^\infty \beta(a)N(t,a)\mathrm{d}a, \tag{2}$$

for some positive functions $\mu(a)$, $F(a)$ and $\beta(a)$.

(a) Use the method of characteristics to show that

$$N(t,a) = \begin{cases} F(a-t)\exp\left(-\int_{a-t}^{a}\mu(\tau)\mathrm{d}\tau\right) & \text{for } 0 < t < a, \\ \\ B(t-a)\exp\left(-\int_0^a \mu(\tau)\mathrm{d}\tau\right) & \text{for } a < t, \end{cases} \tag{3}$$

where

$$B(t) = \int_0^t \beta(\tau)B(t-\tau)\exp\left(-\int_0^\tau \mu(\theta)\mathrm{d}\theta\right)\mathrm{d}\tau + \int_t^\infty \beta(\tau)F(\tau-t)\exp\left(-\int_{\tau-t}^{\tau}\mu(\theta)\mathrm{d}\theta\right)\mathrm{d}\tau. \tag{4}$$

(b) Suppose that $\beta(a) = \beta > 0$, $\mu(a) = \mu > 0$ and that $N(t,a) \sim e^{\gamma t}S(a)$ as $t \to \infty$. Show that the growth rate γ is given by $\gamma = \beta - \mu$.

(c) Sketch the corresponding profiles $S(a)$ for the cases $\gamma > 0$, $\gamma = 0$ and $\gamma < 0$. Comment briefly on your results.

Question 2.

Consider a population of cells that are executing the cell cycle. We denote by $n(\phi,t)$ the number of cells at position $0 \le \phi \le 1$ in their cycle at time t. We introduce the following partial differential equation to model the evolution of the cell population:

$$\frac{\partial n}{\partial t} + (1+\beta\phi)\frac{\partial n}{\partial \phi} = -\mu n, \tag{5}$$

with $n(\phi,0) = f(\phi)$ and $n(0,t) = 2n(1,t)$ for some positive function $f(\phi)$ and positive constants β and μ.

By seeking a separable solution of the form $n(\phi,t) = e^{\gamma t}N(\phi)$, derive an expression for the unique value of $\mu = \mu^*(\beta)$ for which the population evolves, at long times, to a non-trivial, time-independent solution.

Question 3.

The distribution of a morphogen M is described by the following equations:

$$\frac{\partial M}{\partial t} = D\frac{\partial^2 M}{\partial x^2} - \lambda M, \qquad 0 < x < L, \tag{6}$$

with

$$\frac{\partial M}{\partial x}(0,t) = 0, \qquad M(L,t) = M_L, \qquad M(x,0) = 0, \tag{7}$$

where D, λ, M_L and L are positive constants.

(a) Determine the steady state distribution of $M(x,t)$, denoted $M_s(x)$.

(b) Cells contained in the domain mature into cells of type I where $M_s \geq \theta$ and into cells of type II otherwise. Given that $0 < \theta < M_L$, determine the position $x_\theta \in [0, L)$ at which cells switch from type I to type II.

(c) Explain how x_θ changes as the domain size $L \to \infty$.

Question 4.

A population of stem cells occupies the tissue region $0 \leq x \leq L$. Their fate is determined by the steady state distributions of two morphogens, M and A. The concentrations of M and A are described by the following (steady-state) ordinary differential equations

$$0 = \frac{\mathrm{d}^2 M}{\mathrm{d}x^2}, \qquad 0 = \frac{\mathrm{d}^2 A}{\mathrm{d}x^2} + \lambda M, \qquad \text{for } 0 < x < L, \tag{8}$$

with

$$M(0) = M_0, \qquad M(L) = 0 = A(0) = A(L). \tag{9}$$

(a) Determine the steady state concentration distributions of M and A.

(b) The stem cells differentiate (*i.e.* mature) where $A > A^* > 0$. Show that a necessary condition for generating differentiated cells is that $L^2 > (9\sqrt{3}A^*)/\lambda M_0$.

(c) Explain why stems cells will always persist in the tissue.

Question 5.

Suppose fishing is regulated in a zone H km from a country's shore (taken to be a straight line), but outside this zone over-fishing is so excessive that the population is effectively zero. Assume that the fish reproduce logistically, disperse by diffusion and within the zone are harvested with an effort E.

(a) Justify the following model of the fish population, $U(x,t)$,

$$\frac{\partial U}{\partial t} = D\frac{\partial^2 U}{\partial x^2} + rU\left(1 - \frac{U}{K}\right) - EU, \tag{10}$$

with boundary conditions

$$U = 0 \text{ on } x = H, \qquad \frac{\partial U}{\partial x} = 0 \text{ on } x = 0, \tag{11}$$

where r, K, $E(< r)$ and D are positive constants.

(b) Write down the spatially-uniform steady states of this system.

(c) Investigate the linear stability of the trivial steady state by writing

$$U(x,t) = \epsilon U_1(x)e^{\lambda t} + O(\epsilon^2), \tag{12}$$

and determining the equation and boundary conditions satisfied by U_1.

(d) Assuming *real* growth-rates λ, determine a condition on parameters r, E and λ for a solution U_1 to exist and, assuming that this is satisfied, give the general solution for U_1. [Note that we can *show* λ must be real, but this is a tedious exercise!]

(e) If the fish stock is not to collapse (*i.e.* the trivial solution is unstable), show that the fishing zone H must satisfy

$$H > \frac{\pi}{2}\left(\frac{r-E}{D}\right)^{-\frac{1}{2}}. \tag{13}$$

[Hint: you need to determine conditions for which the trivial solution $U = 0$ is *unstable*.]

(f) Discuss briefly the ecological implications of this result.