

FURTHER MATHEMATICAL BIOLOGY: PROBLEM SHEET 2
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MORPHOGEN GRADIENTS AND POSITIONAL INFORMATION.

Question 1.

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

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

with $\frac{\partial M}{\partial x}(0, t) = 0, \quad M(L, t) = M_L, \quad M(x, 0) = 0,$

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

- (a) Determine the steady state distribution of $M(x, t) \equiv M_s(x)$.
- (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 $L \rightarrow \infty$.

Question 2.

A population of stem cells occupy 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 equations

$$0 = \frac{d^2 M}{dx^2}, \quad 0 = \frac{d^2 A}{dx^2} + \lambda M, \quad \text{for } 0 < x < L,$$

with $M(0) = M_0, \quad M(L) = 0 = A(0) = A(L)$.

- (a) Determine the steady state 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 1.

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 $U(x, t)$:

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

with boundary conditions

$$U = 0 \text{ on } x = H, \quad \frac{\partial U}{\partial x} = 0 \text{ on } x = 0,$$

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

- (b) What are the spatially-uniform steady states of this system?
 (c) Investigate the linear stability of the trivial steady state by writing

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

and determining the equation and boundary conditions satisfied by U_1 .

- (d) Assuming *real* growth-rates λ , determine a condition on parameters r, E, λ for a solution U_1 to exist, and assuming that this is satisfied, give the general solution for U_1 . [Can *show* λ must be real, but tedious!]
 (e) If the fish stock is not to collapse (*i.e.* the trivial solution is unstable), show that the fishing zone H must satisfy

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

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

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

Question 2.

Consider a population of cells $u = u(x, t)$ that undergoes logistic growth but whose diffusion depends linearly on their their density so that

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \left(u \frac{\partial u}{\partial x} \right) + u(1 - u).$$

Seek travelling wave solutions of the form $u(x, t) = U(z)$ where $z = x - ct$ and $c > 0$. Determine the equations satisfied by $U(z)$ and $V(z) = U'(z)$. By looking for a solution of the form $V = c(U - 1)$, show that there is an exact solution for one value of the wave speed, c . You should state this value of c .

Question 3.

A non-dimensionalised version of the red squirrel-grey squirrel competition model takes the form

$$\begin{aligned}\frac{\partial G}{\partial t} &= \frac{\partial^2 G}{\partial x^2} + G(1 - G - \gamma_1 R), \\ \frac{\partial R}{\partial t} &= K \frac{\partial^2 R}{\partial x^2} + \alpha R(1 - R - \gamma_2 G),\end{aligned}$$

where $G(x, t)$ and $R(x, t)$ are the densities of grey and red squirrels, respectively, at time t and position x and K , α , γ_1 and γ_2 are positive constants with $\gamma_1 < 1$ and $\gamma_2 > 1$.

We seek travelling wave solutions of the form $G = G(z)$, $R = R(z)$ where $z = x - Vt$ and V is a positive constant, with $G(-\infty) = 1$, $R(-\infty) = 0$, $G(\infty) = 0$ and $R(\infty) = 1$.

- (a) Write down the system in travelling wave coordinates.
 (b) In the special case where $K = 1$, $\alpha = 1$, $\gamma_1 + \gamma_2 = 2$, show that $S = G + R$ satisfies the equation

$$\frac{d^2 S}{dz^2} + V \frac{dS}{dz} + S(1 - S) = 0,$$

and hence, by considering boundary conditions, that $S \equiv 1$ for all z is a solution.

- (c) Deduce that, for this special case,

$$\frac{d^2 G}{dz^2} + V \frac{dG}{dz} + (1 - \gamma_1)G(1 - G) = 0.$$

- (d) Show that, for this equation, travelling waves are possible if $V \geq 2(1 - \gamma_1)^{1/2}$ and sketch the wave.

Question 4.

A rabies model which includes logistic growth for the susceptibles, S , and diffusive dispersal for the infectives, I , is

$$\begin{aligned}\frac{\partial I}{\partial t} &= D \frac{\partial^2 I}{\partial x^2} + rIS - aI, \\ \frac{\partial S}{\partial t} &= -rIS + BS \left(1 - \frac{S}{S_0}\right),\end{aligned}$$

where r , a , B , D and s_0 are positive parameters.

- (a) Non-dimensionalise the system to give

$$\begin{aligned}\frac{\partial u}{\partial \tau} &= \frac{\partial^2 u}{\partial y^2} + uv - \lambda u, \\ \frac{\partial v}{\partial \tau} &= -uv + bv(1 - v),\end{aligned}$$

where u relates to I and v to S .

- (b) Look for travelling wave solutions with $u > 0$ and $v > 0$ and hence show, by linearising far ahead of a wavefront, where $v \rightarrow 1$ and $u \rightarrow 0$, *i.e.* far ahead where the population is still fully susceptible and the infection has not yet arrived, that a wave may exist if $\lambda < 1$ and, if so, the wave speed is $c \geq 2\sqrt{(1 - \lambda)}$.