1. An organism has a population density $U(X, T)$, which is assumed to obey the equation

$$U_T = rU(1 - \frac{U}{N}) + DU_{XX} \qquad \text{in} \quad 0 < T, \qquad 0 < X < L \; .$$

Explain the biological significance of the constants r, N and D. Rescale the variables to derive the non-dimensional equation for $u(x, t)$

$$u_t = u(1 - u) + u_{xx} \qquad \text{in} \quad 0 < t, \qquad 0 < x < l \; ,$$

where l is a constant to be determined.

At time $t = 0$, the population is at a very low level, $u \ll 1$. Discuss what will happen as $t \to \infty$ when the boundary conditions are

(a) $u_x = 0$ at $x = 0$ and $x = l$,

and

(b) $u = 0$ at $x = 0$ and $u_x = 0$ at $x = l$,

stating any critical relations between the parameters.

2. An enzyme E reacts with a substrate S to form an intermediate complex C, which then decomposes to form a product, P and the enzyme. At $t = 0$, the concentrations of E, S, C and P are, respectively, e_0, s_0, 0 and 0. The reactions are written

$$E + S \underset{k}{\overset{k}{\rightleftarrows}} C \qquad C \overset{k}{\longrightarrow} E + P \ .$$

where the reaction rates are all equal and scaled so that $k = 1$.

Obtain the equations for the concentrations of substrate, $s(t)$, and complex, $c(t) \equiv e_0 v(t)$ in the form

$$\frac{ds}{dt} = e_0[v - s(1 - v)] \qquad \text{and} \quad \frac{dv}{dt} = s(1 - v) - 2v \ .$$

Explain carefully the Michaelis-Menten steady state hypothesis, and show that it implies that $s(t)$ is given implicitly by

$$s + 2\ln s = s_0 + 2\ln s_0 - e_0 t \ .$$

Deduce that for large times $s \simeq s_0 \exp[\frac{1}{2}(s_0 - e_0 t)]$.

Describe what happens in the very early stages of the reaction.

3. The FitzHugh-Nagumo model of neurone behaviour can be written in the form

$$u' = \varepsilon(v - u) \qquad \text{and} \qquad v' = f(v) - u \ ,$$

where

$$f(v) = -v(v - v_1)(v - v_2) \qquad \text{with} \quad v_2 > v_1 > 0$$

and ε, v_1 and v_2 are positive constants.

Determine the condition for these equations to have a unique steady state and discuss its stability.

Assuming that there is only one steady state and that $\varepsilon \ll 1$, sketch in the $(v,\, u)$ plane the two trajectories starting at $u(0) = 0$ and $v(0) = v_1 \pm \delta$, for some small δ. You should include the curve $u = f(v)$ on your figure and give some indication of the time taken to traverse various portions of the trajectories.

Sketch also the potential $v(t)$ for each trajectory, and explain the biological significance of the difference in behaviour.

4. Cells in a tumour consume a nutrient of concentration u at a constant rate k. The cells die if the local concentration $u < u_0$ or $u > u_1$. If at the surface of the tumour $u < u_1$ then the cells divide and the tumour grows in size. The background concentration is $u = u_\infty$, where $u_\infty > u_1 > u_0 > 0$.

Assuming the tumour grows to an equilibrium size which is a sphere of radius a all parts of which are alive, the governing equations are

$$k = \nabla^2 u \equiv \frac{1}{r^2}\frac{d}{dr}\left(r^2 \frac{du}{dr}\right) \qquad \text{in} \quad 0 < r < a$$
$$0 = \nabla^2 u \qquad \text{in} \quad r > a\ .$$

Find $u(r)$ and deduce that the equilibrium radius is given by

$$a^2 = \frac{3}{k}(u_\infty - u_1)\ .$$

Show that the assumptions of the model require that

$$2u_0 + u_\infty \leqslant 3u_1\ .$$

5. The spread of rabies through the European fox population is modelled by the equations

$$S_t = -rSI$$

$$I_t = rSI - aI + dI_{xx} \ ,$$

where $S(x, t)$ and $I(x, t)$ are respectively the susceptible and infected populations, while r, a and d are given constants.

Discuss, briefly, the assumptions of the model.

Seek travelling wave solutions $S = S(z)$, $I = I(z)$, where $z = x - ct$ for some positive wave speed c. Show that

$$S' = \frac{r}{c} SI$$
$$I' = \frac{c}{d}\left[\tfrac{a}{r}\ln S - S - I + A\right] \ ,$$

where A is a constant. Show graphically or otherwise that this system can have two equilibrium points with $S = S_0$ or $S = S_1$, where $S_0 > S_1$.

Discuss the stability of these points, and explain why the speed of a travelling wave such that $S \to S_1$ as $x \to -\infty$ and $S \to S_0$ as $x \to \infty$ must satisfy

$$c \geqslant 2\left[d(rS_0 - a)\right]^{1/2} \ .$$

6. Explain qualitatively how a shear flow combined with weak cross-flow diffusion can lead effectively to strong downstream diffusion.

Flow of air or blood in a cleft $0 < y < 1$, can be modelled by a steady Poiseuille velocity in the x-direction,

$$V(y) = \beta y(1-y) \qquad \text{for some constant } \beta.$$

Defining y-averages over the cleft cross-section for some quantity w by

$$\overline{w}(x,\,t) = \int_0^1 w(x,\,y,\,t)\,dy\ ,$$

express β in terms of $\overline{V}$.

The concentration $u(x,y,t)$ of a chemical satisfies the equation

$$u_t + V(y)u_x = Du_{xx} + Du_{yy} \qquad \text{with} \quad u_y = 0 \qquad \text{on} \quad y = 0,1\ .$$

Writing $u = \overline{u}(x,\,t) + u'(x,\,y,\,t)$, and justifying carefully each stage of the argument, show that, approximately,

$$(V - \overline{V})\overline{u}_x = Du'_{yy}\ .$$

Deduce that

$$u' = \frac{\overline{V}\,\overline{u}_x}{D}\left(y^3 - \tfrac{1}{2}y^4 - \tfrac{1}{2}y^2 + \tfrac{1}{60}\right)$$

and hence that

$$\overline{u}_t + \overline{V}\,\overline{u}_x = D_{\text{eff}}\overline{u}_{xx} \qquad \text{where} \quad D_{\text{eff}} = D + \frac{\overline{V}^2}{210D}\ .$$

Interpret this equation and discuss its biological significance.