2 Waves

2.11 Fisher's Equation for Population Dispersal Problems (9 units)

This project is essentially self-contained, and does not directly rely on any Part II lecture course. However, attendance at a Part II Numerical Analysis course may be of some help, as may attendance at the Part II course, Mathematical Biology.

Problem Formulation

An equation commonly encountered in population genetics is the one-dimensional diffusion equation

$$\frac{\partial \hat{\rho}}{\partial \hat{t}} = -\frac{\partial j}{\partial \hat{x}} + F(\hat{\rho}). \tag{1}$$

Here, $\hat{x}$ denotes the spatial position, $\hat{t}$ the time, $\hat{\rho}(\hat{x}, \hat{t})$ the population density, j the population flux, and $F(\hat{\rho})$ is a local source term that describes the net rate of growth in the population density.

A typical model for local population growth is given by the Pearl-Verhulst law

$$F(\hat{\rho}) = \begin{cases} \gamma\hat{\rho}(1 - \hat{\rho}/\hat{\rho}_s) & 0 < \hat{\rho} < \hat{\rho}_s; \\ 0 & \hat{\rho} \leqslant 0 \quad \hat{\rho} \geqslant \hat{\rho}_s. \end{cases} \tag{2}$$

This describes how a homogeneous population would grow, initially in an exponential manner, until the population saturated at some density $\hat{\rho}_s$.

The flux j is the source of the diffusive behaviour and is given by,

$$j = -D\frac{\partial \hat{\rho}}{\partial \hat{x}}. \tag{3}$$

If it is assumed that dispersal is due to random motion of individuals, then the diffusion coefficient D is constant and Fisher's equation is obtained. However, as a remedy to overcrowding, dispersal would be much more effective if the diffusion coefficient were population density-dependent. In fact this has been observed in populations of small animals. Here we consider the case $D = D_0\hat{\rho}$. With suitable non-dimensionalisation, we obtain the modified Fisher equation,

$$\frac{\partial \rho}{\partial t} = \frac{\partial}{\partial x}\left(\rho\frac{\partial \rho}{\partial x}\right) + \rho(1 - \rho). \tag{4}$$

A similar equation also arises in combustion dynamics.

Travelling wave solutions to this equation are the subject of project 2.11(a). A situation of more practical interest is when the population density is known at some initial time, and the subsequent evolution of the population is required. In projects 2.11(b) and 2.11(c) the expansion of a population which is initially limited to a finite spatial range is considered. Thus solutions to (4) are required subject to the following boundary conditions:

$$\begin{aligned} \rho(x, 0) &= \begin{cases} \rho_0(x), & 0 \leqslant x \leqslant 1, \\ 0, & x > 1, \end{cases} \qquad (5) \\ \frac{\partial \rho}{\partial x}(0, t) &= 0, \qquad t > 0, \\ \rho(x, t) &\to 0 \quad \text{as} \quad x \to \infty. \end{aligned}$$

The form of the initial data leads us to consider a solution which is piecewise continuous with a single jump across $x = s(t)$, where conditions given by conservation laws must be satisfied. The initial boundary-value problem can now be reformulated as follows:

$$
\begin{aligned}
&0 \leqslant x \leqslant s(t): \\
&\qquad \rho_t = (\rho\rho_x)_x + \rho(1-\rho), \\
&\qquad \rho(x,0) = \rho_0(x), \\
&\qquad \rho_x(0,t) = 0, \\
&\qquad \rho(s(t),t) = 0, \quad \rho_x(s(t),t) = -\dot{s}(t). \\
&s(t) < x: \\
&\qquad \rho(x,t) \equiv 0
\end{aligned}
\tag{6}
$$

We refer to $x = s(t)$ as the population front. From the initial population distribution (5) we see that $s(0) = 1$.

In project 2.11(b), solutions of (4) are obtained for a particular initial distribution, and the behaviour as $t \to \infty$ is examined. In project 2.11(c), the code developed in project 2.11(b) is used to examine the propagation of the population front.

Project 2.11(a): Travelling Wave Solutions

Here we consider solutions of (4) corresponding to steady expansion of a saturated population. By writing $\rho(x,t) = \phi(\xi)$, where $\xi = x - ct - x_0$, show that ϕ is governed by the nonlinear ODE,

$$\phi\phi'' + (\phi')^2 + c\phi' + \phi(1-\phi) = 0 \tag{7}$$

This is to be solved subject to the boundary conditions $\phi \to 1$ as $\xi \to -\infty$, $\phi \to 0$ as $\xi \to \infty$. General analytic solutions to (7) are not available and hence numerical solutions are required. Such solutions could be obtained by shooting, but here it is preferable to consider the asymptotic form of ϕ as $\xi \to -\infty$.

By linearising (7) about $\phi = 1$, show that as $\xi \to -\infty$,

$$\phi \sim 1 - Ae^{\lambda\xi} \tag{8}$$

where A is an arbitrary constant, due to the translational invariance of (7), and λ is to be determined as a function of c. This then provides suitable initial conditions for a forward integration in ξ, *ie.*,

$$\phi(\xi_0) = 1 - \delta, \qquad \phi'(\xi_0) = -\lambda\delta, \qquad \delta \ll 1, \tag{9}$$

for arbitrary ξ_0.

Obtain solutions for $c = 2.5, 1.75, 1$ and 0.75 using a suitable integration method. These travelling wave solutions should be plotted on axes with the origin chosen such that $\phi(\xi = 0) = \frac{1}{2}$ (to within graphical accuracy). Investigate the change in the wave profile as the wave speed c is decreased still further.

Show that

$$\phi(\xi) = \begin{cases} 1 - e^{(\xi-\xi_1)/\sqrt{2}}, & -\infty < \xi < \xi_1; \\ 0 & \xi_1 \leqslant \xi. \end{cases} \tag{10}$$

is an exact solution for a particular value of c to be determined. Comment on this solution, and plot the waveform, with ξ_1 chosen so that $\phi(\xi = 0) = \frac{1}{2}$, as before.

Project 2.11(b): Large-Time Limit for the Initial Value Problem

Travelling wave solutions often give clues to the general behaviour of solutions of a nonlinear wave equation. However, a more commonly encountered problem is when the population density is known at some initial time, and the subsequent evolution of the population is required. In this exercise we obtain solutions to (6). For numerical efficiency, renormalise the domain $[0, s(t)]$, to $[0, 1]$, by introducing a new spatial coordinate $y = x/s(t)$. Show that the evolution of $\rho(y, t)$ is given by

$$\frac{\partial \rho}{\partial t} = \frac{1}{2s^2}\frac{\partial^2(\rho^2)}{\partial y^2} + \frac{\dot{s}y}{s}\frac{\partial \rho}{\partial y} + \rho(1-\rho) \tag{11}$$

$$\rho_y(0,t) = 0, \qquad \rho(1,t) = 0, \qquad \rho_y(1,t) = -s\dot{s}. \tag{12}$$

The equation (11) is to be solved subject to the boundary conditions (12), and initial conditions

$$\rho(y, 0) = \rho_0(y). \tag{13}$$

The final condition in (12) then determines the motion of the population front, with $s(0) = 1$.

Many methods exist for the numerical solution of parabolic equations. Here we consider a very simple finite-difference method, where spatial derivatives are expressed using centred differences and the solution is advanced in time using forward Euler. Writing $t_j = j(\Delta t)$, $y_n = n/N$, $(n = 0, 1, \ldots, N)$, and using the notation $\rho_{j,n} \equiv \rho(t_j, y_n)$, $s_j \equiv s(t_j)$ we discretise (11) in the form,

$$\begin{aligned}
\frac{\rho_{j+1,n} - \rho_{j,n}}{\Delta t} &= \frac{1}{2s_j^2}\frac{\rho_{j,n+1}^2 - 2\rho_{j,n}^2 + \rho_{j,n-1}^2}{(\Delta y)^2} + \frac{\dot{s}_j y_n}{s_j}\frac{\rho_{j,n+1} - \rho_{j,n-1}}{2(\Delta y)} + \rho_{j,n}(1-\rho_{j,n}), \\
&\qquad\qquad n = 1, 2, \ldots, N-1 \\
\rho_{j,0} &= \rho_{j,1}, \\
\rho_{j,N} &= 0, \\
\frac{s_{j+1} - s_j}{\Delta t} &= \dot{s}_j = -s_j^{-1}\,\frac{\rho_{j,N-2} - 4\rho_{j,N-1}}{2\Delta y},
\end{aligned}$$

where $\Delta y = 1/N$. The expression for $\dot{s}_j$ is obtained by using the final condition in (12) with a three-point backward difference expression for $\rho_y(y = 1)$.

There are several more sophisticated numerical methods of solving this system of equations, but the method described is very simple to implement and proves sufficient for the current purposes. The main drawback is that Δt must be chosen very small to ensure numerical stability.

Write your own program to solve (11) using the discretisation given above. Obtain solutions for initial distribution $\rho_0(x) = 0.3e^x(1-x)$. Start with $N = 100$ and $\Delta t = 0.0001$, but confirm that your code produces solutions that are independent of mesh-size. Plot the solution as a function of the original spatial variable x at $t = 0.0$, 2.5, 5.0, 7.5, 10.0 and 12.5. Also plot the velocity of the wave front, $\dot{s}(t)$, as a function of time. Compare the large-time wave profile with the travelling wave solutions obtained in project 2.11(a).

Project 2.11(c): Motion of the Wave Front

Using the same program written for project 2.11(b), we now investigate the early evolution of the wave front for different classes of initial population distribution.

Consider three different initial profiles:

(i) $\rho_0(x) = A_1 e^x (1-x)$;

(ii) $\rho_0(x) = A_2 e^{2x} (1-x)^2$;

(iii) $\rho_0(x) = A_3 e^{3x} (1-x)^3$;

where A_i are numerical constants characterising the total initial population.

Using the same mesh-size as above, obtain solutions for $0 < t \leqslant 0.75$, for initial distribution (i). Consider various values of the coefficient A_1, in the range $0.1 \leqslant A_1 \leqslant 0.9$. For the larger values of A_1 it may be necessary to reduce the time step-size. Do not include plots of $\rho(x,t)$ in your report, but concentrate on the motion of the wave front. Write down a relationship between the initial velocity of the wave front and the initial profile and show that this is in agreement with your numerical results.

Calculate solutions for initial distribution (ii) with $A_2 = 0.25$ for $0 < t \leqslant 1$. As before plot $\dot{s}(t)$ as a function of time. Repeat these calculations with the spatial mesh-size reduced to $\Delta y = 0.002$ and then $\Delta y = 0.001$, adjusting Δt as necessary. Describe the movement of the wave front. Repeat these calculations with $A_2 = 0.05$, for $0 < t \leqslant 1$.

Analysis suggests that for some classes of initial distributions, the population front is fixed until a certain waiting time t_w has elapsed, after which the population expands. For initial distributions which are locally quadratic in the vicinity of the wavefront, it can be shown that the waiting time is given by

$$t_w = \log(1 + 16 g_2) \tag{14}$$

where $\rho_0(x) \sim g_2\,(1-x)^2$, as $x \to 1$. Are the numerical results you have obtained in broad agreement with this result? Discuss why such a phenomenon may occur in the evolution of a population.

Finally, calculate the motion of the population front for initial distribution (iii) with $A_3 = 0.2$. As with case (ii), reduce the mesh-size. Compare your results with the results of (ii).

References

A background to the biological models underlying these equations can be found in *Some exact solutions to a nonlinear diffusion problem in population genetics and combustion* by Newman (*J. Theoretical Biology* (1980) **85**, 325–334).

An in-depth analysis of equations of this form is presented in *The effects of variable diffusivity on the development of travelling waves in a class of reaction-diffusion equations* by King & Needham (*Phil. Trans. Roy. Soc. Lond.* A (1994) **348**, 229–260). This contains derivation of the results for waiting times, but reference to this paper is not necessary for the purposes of this project.

