

Delay Models

A normal population model takes the form

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N(t)).$$

This is not necessarily, even in the most complex form that f can take, a realistic representation. Often, we need to know not just how many agents there are in the population, but how many have been alive long enough to know be able to reproduce. Therefore, we consider a delay:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N(t), N(t - T)).$$

Note here that we require in the initial conditions now not just $N(0)$, but $N(\tau)$ for $-T \leq \tau \leq 0$.

The delayed logistic model takes the form:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN(t) \left(1 - \frac{N(t - T)}{K} \right)$$

with $N(\tau)$ for $-T \leq \tau \leq 0$.

Now assume that at some point t_1 , $N(t_1) = K$, and that N has been increasing up to t_1 . Then we have that $f(N(t_1), N(t_1 - T)) > 0$, $f(N(t_1 + T), N(t_1)) = 0$, and that $f(N(t + T), N(t)) < 0$ for $t > t_1$. Thus we see that with these assumptions, we should get an oscillating system. We note that provided we get a symmetry, we can expect a period of roughly $4T$.

We non-dimensionalise to get the following:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(t)(1 - N(t - T)),$$

which has steady states $N^* \in \{0, 1\}$, as if the state is steady then $N^*(t - T) = N^*(t)$ (**investigate a bit further**).

Considering $N^* = 1$, write $N(t) = 1 + n(t)$ for $n(t) = o(1)$, and we have that (approximately) $\frac{\mathrm{d}n}{\mathrm{d}t} = -n(t - T)$, which with $n(t) = n(0)e^{\lambda t}$ gives $\lambda = -e^{-\lambda T}$. We then analyse λ , noting that for $\operatorname{Re} \lambda < 0$, we get that the steady state is stable.

Age-structured Models

A delay model may not capture the behaviour of the population properly, because while we can delay processes such as birth and death, we have difficulty capturing the population with a great deal of structure. In an age-structured model, we write the population as $n(t, a)$, the population density at time t of those with age a . Using the principle of mass conservation (**check**), we get von Foerster’s equation:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n$$

where $\mu(a)$ is the death rate of individuals of age a . We additionally have the initial and boundary conditions:

$$\begin{aligned} n(0, a) &= f(a) && \text{initial age-distribution} \\ n(t, 0) &= \int_0^\infty b(a)n(t, a) \, \mathrm{d}t && \text{birth rate of population} \end{aligned}$$

This requires that we use the method of characteristics, noting that we will have to split the problem into the regions $t > a$ and $t < a$, as the characteristic projections are the lines $t = a + t_0$, $t = a - a_0$. We then have $n(t, a) = n(t_0, 0)e^{-\int_0^a \mu(s) \, \mathrm{d}s}$, $n(t, a) = n(0, a_0)e^{-\int_0^a \mu(s) \, \mathrm{d}s}$.

In models for populations of proliferating cells, we wish to consider structuring the population as two types of cells: cycling cells, and quiescent (non-cycling) cells. This is considered according to models where a cell goes through a cycle of length T in which they have a choice once each cycle to become quiescent and duplicate themselves. We write $p(t, s)$, $q(t, s)$ for $t \in [0, \infty)$, $s \in [0, T)$, as the number of cells respectively cycling and quiescent at time t globally, time s in their own cell cycle.

Spatial Variation

Previously, models have tended to assume a ‘well-mixed’ assumption, that rate of change is constant across the space. This is clearly often not the case however, and therefore it is useful to consider spatial models.

Reaction-Diffusion

Suppose the chemical species C_i of concentration c_i undergoes a reaction with production levels according to

$$\frac{\mathrm{d}c_i}{\mathrm{d}t} = R_i(c_1, \dots, c_m).$$

Then we can write $c_i(\mathbf{x}, t)$ as the concentration at time t . We also write

$$\mathbf{q}(\mathbf{x}, t) = -D\nabla c$$

as the flux for some constant D .

Using the principle of mass balance, we have that for any closed volume V , $i \in \{1, \dots, m\}$,

$$\frac{\mathrm{d}}{\mathrm{d}t} \int_V c_i \, \mathrm{d}V = - \int_{\partial V} \mathbf{q} \cdot \mathrm{d}\mathbf{S} + \int_V R_i(c_1, \dots, c_m) \, \mathrm{d}V.$$

Consequently by the divergence theorem,

$$\frac{\mathrm{d}}{\mathrm{d}t} \int_V c_i \, \mathrm{d}V = \int_V \nabla \cdot (D_i \nabla c_i) + R_i(c_1, \dots, c_m) \, \mathrm{d}V$$

and as this volume V is arbitrary,

$$\frac{\partial c_i}{\partial t} = \nabla \cdot (D_i \nabla c_i) + R_i(c_1, \dots, c_m).$$

Positional information

One key consideration aided by spatial modelling is how domain size affects the growth of a population. Considering the budworm population on a one-dimensional domain, undergoing logistic growth and predation by birds, we have:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \left[ru \left(1 - \frac{u}{q} \right) - \frac{u^2}{1 + u^2} \right].$$

Note however that for $u(x, 0) = o(1)$, we can approximate the second term by ru . As we have x bounded (say in $[0, L]$), we can write $u(x, t)$ as a fourier series for each t ,

$$u(x, t) = \sum_{n=1}^{\infty} a_n(t) \sin \left(\frac{n\pi x}{L} \right)$$

and so

$$\frac{\mathrm{d}a_n}{\mathrm{d}t} = \left(-D \left(\frac{n\pi}{L} \right)^2 + r \right) a_n$$

which, by writing the coefficient of a_n as σ_n , gives us that

$$u(x, t) = \sum_{n=1}^{\infty} a_n(0) e^{\sigma_n t} \sin \left(\frac{n\pi x}{L} \right)$$

Travelling waves

We consider waves that travel with constant speed and shape, on the basis that there are many phenomena within biology which reflect wave-like behaviour.

Much of the study of this is based on the Fisher-KPP equation, also considered when investigating spatial variation:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + ru \left(1 - \frac{u}{K} \right)$$

for $x \in \mathbb{R}$, $t > 0$.

For analysis, we non-dimensionalise to get the slightly nicer form:

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1 - u)$$