Content: Single species models in continuous time

5.1.4.1-4.6

General considerations

Single species models in continuous time are based on differential equations of the form

\[ u'(t) = f(u(t)) \]

for some differentiable function \( f \). The solutions to such functions can be qualitatively analysed using only elementary knowledge of calculus. First we note that there is a unique solution to the equation with an auxiliary (initial) condition \( u(t_0) = u_0 \). In particular this means that the graphs of two solutions cannot intersect.

Next we note that any solution \( u^* \) to the equation \( f(u^*) = 0 \) will define a constant solution \( u(t) = u^* \) to the differential equation, which is an equilibrium. Since this is a solution, and since the graphs of two solutions cannot intersect, other solutions are confined to the bands defined by the equilibria. In each band the derivative has only one sign, and from this it is often simple to deduce the graphs of the solutions. This includes noting that as \( t \to \infty \) the solution must approach either \( \pm \infty \) or one of the steady states.

Example A simple but ecologically important case is the (normalized) logistic equation

\[ u'(t) = u(t)(1 - u(t)), \]

which has \( u^* = 0 \) and \( u^* = 1 \) as equilibria. The expression \( u(1 - u) \) is positive precisely when \( 0 < u < 1 \), from which we can deduce that the solutions look as in the graph below.

Clearly \( u^* = 1 \) is a stable equilibrium, whereas \( u^* = 0 \) is unstable. We can note that if we run time backwards, the opposite becomes true.

There is of course no problem in this case to find the actual solution.

Harvesting fish population

In the ecology of a single species we model by specifying an expression for the relative growth rate \( N'(t)/N(t) \). For a single species model this typically means an expression of the form \( f(N(t)) \), so that \( N'(t) = f(N(t))N(t) \). Simplest examples are (1) a constant, \( f(N(t)) = r \), giving exponential growth, and (2) \( f(N) = r(1 - N/K) \), defining the logistic equation

\[ N'(t) = rN(t)(1 - N(t)/K). \]

When analysing this equation we first non-dimensionalize by introducing \( u = N/K \) and the new time \( t' = rt \). That gives the equation

\[ u'(t) = u(t)(1 - u(t)), \]

which we analysed above. We see that \( N(t) \to K \) as \( t \to \infty \) and the time scale involved is \( 1/r \).

An important real-life problem is to develop ecologically acceptable strategies for harvesting a renewable resource, be it animals, fish, plants or whatever. The model usually asks for the maximum sustainable yield with minimum effort. We will consider the simplest such model, and look into some of its worrying conclusions.

We first assume that our technology allows us to harvest a fixed percentage of the resource, so that the model equation becomes

\[ N' = rN(1 - N/K) - EN = (r - E)(1 - N/K), \quad K(E) = K(1 - E/r). \]

This again is a logistic equation with a new carrying capacity \( K(E) \). It requires that \( E < r \); if \( E > r \), harvesting will drive the population to extinction.

The yield in turn is \( Y(E) = EK(E) \) and we see that we get the maximum sustainable yield \( Y_M = rK/4 \) if we take \( E = r/2 \). \( K(E) \) is stable and the recovery time is of the order \( T_K(E) = 1/(r - E) \). All this from our previous discussion.

A short calculation shows that

\[ \frac{Y}{Y_M} = \frac{4}{r^2} E(r - E) = \frac{4}{r^2} (r(r - E) - (r - E)^2) = 4\left(\frac{T_K(0)}{T_R(E)} - \frac{T_K(0)^2}{T_R(E)^2}\right), \]

and if we consider that our data is in the yield, we see that for each yield \( Y \) there are actually two possible values for \( T_R(Y) \):

\[ \frac{T_R(Y)}{T_R(0)} = \frac{2}{1 \pm \sqrt{1 - Y/Y_M}}. \]

A plot of this gives a curve with a lower segment \( L_- \) and an upper segment \( L_+ \).

If we start with a small \( E \), the equilibrium point is close to \( K \) and moves downwards with increasing \( E \) as long as we have \( K(E) > K/2 \). At the same time we move along the \( L_- \) branch and reach the point \( A \) in the graph. Further increase in \( E \) diminishes the yield, but also increase the recovery time since we now move on to the \( L_- \) branch. If we identify the maximum yield by increasing \( E \) until the yield diminishes, we will have moved on to the \( L_- \) branch and there will be a long recovery period needed!
An alternative model is to assume that a fixed amount $Y_0$ is harvested per time unit, so that the equation becomes

$$N' = rN(1 - N/K) - Y_0.$$ 

For relevant $Y_0$ there will be two positive equilibriums, with the lower unstable and the upper stable (move the first graph $Y_0$ up). The recovery time for the stable one can be computed to

$$\frac{T_R(Y_0)}{T_R(0)} = \frac{1}{\sqrt{1 - Y_0/Y_M}},$$

which shows that the recovery time goes to infinity as $Y_0 \to Y_M$. So reaching for maximum yield will deplete the resource!

Logistic law in discrete time

What happens with a logistic growth if we do not follow it continuously, but collect the information into bins covering time intervals of length $h$? This would give us a discrete dynamical system as an approximation of the original. The solution of $N' = rN(1 - N/K)$ is easily found to be

$$N(t) = \frac{K}{1 + a e^{-rt}}, \quad a = \frac{K - N(0)}{N(0)}.$$ 

Here we solve for $e^{-rt} = (K - N(t))/aN(t)$ from which we deduce that

$$N(t + h) = \frac{K}{1 + a e^{-hN(t)} e^{-rh}} = \frac{KN(t)}{N(t) + e^{-rh}(K - N(t))} = \frac{e^{rh}KN(t)}{(e^{rh}-1)N(t) + K}.$$ 

With $N_a = hN(nh)$ we get

$$N_{a+1} = \frac{N_a - hN_a}{1 + N_a/K_a}, \quad r_a = e^{rh}, \quad K_a = \frac{Kh}{e^{rh} - 1} \approx \frac{K}{r}.$$ 

Conversely, assume that

$$N_{a+1} = \frac{rN_a}{1 + N_a/K},$$

for which we have $N_a \to (r-1)K = K'$ as $n \to \infty$. Now write $N_a = hN(nh)$ with $r = r(h), K = K'/r(h) - 1$. We then have (with $t = nh$)

$$N(t + h) - N(t) = \frac{(r(h)-1)(1 - N(t)/K')N(t)}{1 + (r(h)-1)N(t)/K'},$$

from which we deduce that when $h \to 0$

$$N'(t) = \rho N(t)(1 - N(t)/K'), \quad \rho = r'(0).$$

Introducing predators

The logistic equation is usually not sufficient: most species are threatened also by some predator. Its interest in the prey in turn depends on the density of the latter. The interest is described by a function $g(N)$ called the functional response for the predator on the prey. If the number of predators is $P$, mass balance considerations suggests a model

$$N' = rN(1 - N/K) - Pg(N).$$ 

The two key functional responses are

$$g(N) = \frac{aN}{b + N}$$

which has the property of being proportional to $N$ for small prey population and approaching a limit for large. The latter is supposed to reflect that there is an upper limit for how much a single predator can eat. This response is considered to describe most invertebrates.

For vertebrate predators we also want to take into account that if prey is scares, the predator might not find it worth while to hunt it and choose something else to eat. We therefore want a more S-shaped functional response, for which we can use

$$g(N) = \frac{aN^2}{b^2 + N^2}.$$ 

The picture below is an experimental illustration of this behaviour. It illustrates the situation with the deer mouse (vertabrate predator) feeding on sawfly pupae in the laboratory. In the experiment the deer mouse could also eat dog biscuits (the horizontal line illustrates that the total intake was constant all the time).

If we can consider the population of predators constant (or at least independent of prey numbers), this gives us qualitative models to use in order to describe the dynamics of single prey species. If there is a dependence of predator numbers on prey numbers we need an equation for predator as well, giving us a system of nonlinear equations to solve. We will return to this situation soon.

Spruce budworm example - a project

In the north woods of Canada the balsam trees have a competitive advantage over the birches, in competing for sun light and nutrition. With time the balsam trees would outcompete the birch tree if there was no spruce budworm. The budworm harm the balsam trees but not the birch: when there is an outbreak of budworms the balsam trees gets defoliated, which with time leads to the death of the larvae. A cycle takes around 4 years. During that time the birch take advantage of the situation and increase their numbers. After some time, however, the balsam trees come back, which leads to an increase in budworm numbers and the cycle restarts. A total cycle takes between 40 and 100 years. There is a huge economic interest in the balsam trees, so understanding this ecological interest is of great importance.

There are different time scales in this problem:

1. the budworm density can increase hundredfold and more in months
2. the larvae are eaten by birds, which can change their diet on the same time scale
3. a defoliated tree can replace its foliation in 7–10 years
4. the life span of the trees involved is of size 100-150 yeras, but generation time are a few years.

We can describe the budworm density $B(t)$ by the following equation

$$B' = rB(1 - B/K) - \frac{aB^2}{b^2 + B^2},$$

where both $b$ and $K$ are assumed proportion to the total surface area of the trees.
Logistic growth as a consequence of limited resources

Let \( N(t) \) be the number of a species that feed on a resource with concentration \( S(t) \). The growth rate of the species depends on nutrient concentration:

\[
N'(t) = Y b(S(t)) N(t), \quad b(0) = 0.
\]

Here \( b(s) \) is the amount of nutrient taken up by each animal and \( Y \) is the yield per unit nutrient. Mass balance tells us that

\[
S'(t) = -b(S(t)) N(t)
\]

This is a system of differential equations, but such that \( N(t) + S(t) \) is constant, so that \( N(t) - N(0) = -Y(S(t) - S(0)) \). This means that we can solve for \( S(t) \) and insert in the first equation to get a single equation for the species population.

**Example** If we take \( b(r) = kr \), we get

\[
N'(t) = \kappa (S(0) + N(0) - N(t)) N(t) = r N(t)(1 - N(t)/K),
\]

where \( K = S(0) + N(0) \), \( r = \kappa K \), which is the logistic law.

The chemostat

A chemostat is a continuous culture device used for growing and studying bacteria.

Nutrient is added at a constant rate, say \( S_0 \lambda \) (mass/volume times volume/time), to the growth chamber where living cells are stirred in the enriched media. The growth chamber is continually adjusted to keep a constant volume by removing fluid at the flow rate \( \lambda \). Let \( S(t) \) be the concentration of nutrient in the growth chamber at time \( t \) and let \( B(t) \) denote the concentration of bacteria. The mathematical model that describes the chemostat is

\[
\begin{align*}
S'(t) &= \lambda(S_0 - S) - b(S) B/Y, \\
B'(t) &= b(S) B - \lambda B.
\end{align*}
\]

Note that change in notation from last paragraph: the yield is now part of the substrate equation (as in the book). For our analysis we choose

\[ b(S) = \frac{v m S}{K + S}. \]

We now want to make this system dimensionless in order to study it. Since \( b(S) = \frac{v m S(K)}{(K + S)} \), we try to replace \( S \) with \( s = S/K \) so that \( b(S) = \frac{v m s}{1 + s} \). At the same time we replace time with \( \lambda t \). With this substitution the system becomes

\[
\begin{align*}
s'(t) &= (s_0 - s) - \frac{v m S}{\lambda Y (1 + s)}, \\
b'(t) &= \frac{v m S}{\lambda(1 + s)} - B - B.
\end{align*}
\]

Finally we write \( b = \frac{v m B}{\lambda Y} \), and arrive at

\[
\begin{align*}
s'(t) &= (s_0 - s) - \frac{s b}{1 + s}, \\
b'(t) &= \frac{a s b}{1 + s} - b, \quad a = \frac{v m}{\lambda}.
\end{align*}
\]

This system of equations will be discussed and analysed next lecture.

Epilogue: On variolation of smallpox

An important reason for mathematical modelling is to get an understanding of what effect possible actions may have, in order to facilitate decision making. When calculus was still in its infancy it was used by one of the Bernouilli brothers to do just that. This was done in 1760 and discussed variolation (not vaccination) against smallpox (Edward Jenner’s work on inoculation with cowpox was still 30 years in the future). In variolation infectious material is inoculated into the skin of the susceptible in order to induce a mild infection. This was not an altogether harmless process; children could die from it, and it could trigger small epidemics. At the time physicians argued about whether the benefits of inoculation outweighed the risks, and the objective of Bernouillius paper was to provide some numbers to facilitate decision making.

Bernouilli introduced two unknowns \( x(a) \), the number of susceptibles at age \( a \), and \( n(a) \), the total number surviving to age \( a \) and wrote down the two differential equations

\[
x'(a) = -\lambda(x(a))x(a), \quad n'(a) = -p x(a) - \mu(a)n(a)
\]

subject to the initial conditions \( x(0) = n(0) = n \). Here \( \lambda \) is the force of infection, \( \mu(a) \) the age-dependent death rate, and \( p \) is the probability of dying from smallpox. He then derived the following differential equation for the prevalence \( f(a) = x(a)/n(a) \) of susceptibles:

\[
f'(a) = \lambda f(a)(p f(a) - 1), \quad f(0) = 1,
\]

(essentially the logistic equation) which he solved to get

\[
f(a) = \frac{1}{p + (1 - p) e^{\lambda a}}.
\]

He then could estimate the number of deaths due to smallpox, and deduce that in an environment free of smallpox the fraction surviving to age \( a \) should be given by \( e^{\lambda a}/(p + (1 - p) e^{\lambda a}) \). For number crunching he assumed that during one year smallpox attacks one in eight, so that \( \lambda = 1/8 \) and that it causes death also in one in eight, giving the same estimate for \( p \).

Using this model, and comparing it with actual life table data, Bernouilli was able to demonstrate that by eradicating smallpox the median age at death would increase by 12.4 years, from about 11.4 to 23.9 years.

Exercises

**Exercise 1** An alternative growth model to the logistic, much used in oncolgoy, is the Gompertz law:

\[
N'(t) = r(t) N(t), \quad r'(t) = -a r(t).
\]

1. Express this as a differential equation in \( N \) only and obtain the general solution. Sketch the solutions. This model agrees remarkably well with tumour growth data.

2. In a solid tumour the cells in the center do not get access to nutrients and oxygen and stop reproducing and die, leaving a necrotic center. Discuss why this might be modelled by Gompertz law.

**Exercise 2** Derive the general solution to the logistic equation.

**Exercise 3** Analyse the differential equation model for fixed amount harvesting

\[
N'(t) = r N (1 - \frac{N}{K}) - Y_0.
\]

**Exercise 4** Discuss how we can obtain estimates for the parameters \( r \) and \( K \) in a logistic model, and use this to find the parameters for the following data concerning the growth in volume of each of the two yeasts (growing separately):
Exercise 5  In cultures of the unicellular alga Daphnia magna it was observed that $f(N)$ decreased in a nonlinear fashion and not in the linear fashion of the logistic law. To account for this it was suggested that the growth rate depends on the rate at which food is utilized:

$$f(N) = \frac{rF_m - F}{F_m},$$

where $F$ is the rate of utilization when the population size is $N$ and $F_m$ is the maximal rate, when the population has reached a saturated level. Assume that

$$F = c_1N + c_2N',$$

(constant positive and $N' > 0$).

1. Derive the following equation

$$N' = r\frac{K - N}{K + \gamma N}.$$  

What are $K, \gamma$ in the original parameters?

2. Describe the qualitative behaviour of the solutions.

Exercise 6 Consider the discrete-time genetic model

$$p_{n+1} = \frac{\tau p_n^2 + p_n q_n}{\tau p_n^2 + 2p_n q_n + \sigma q_n}, \quad q_n = 1 - p_n$$

assume that the time step $i = h$, and that $\tau, \sigma$ are differentiable functions of $h$ which are one when $h = 0$. Show that the continuous time analogue is the differential equation

$$p'(t) = rp(t)(1 - p(t))(a - p(t)), \quad r = \tau'(0) + \sigma'(0), \quad a = \frac{\sigma'(0)}{\tau'(0) + \sigma'(0)}.$$