MORTALITY: a mathematical model for the death (survival) process

Let $N(t)$ denote the number of animals in some closed population. In this population there is no immigration, no emigration, and no reproduction. The only thing that can happen to change the number of animals is death.

Suppose some fraction $\mu$ die during one time interval; the fraction surviving is

$$S = 1 - \mu$$

$$N(t + 1) = S \cdot N(t) = (1 - \mu) \cdot N(t)$$

Let $\mu = 0.3$ (i.e. $S = 0.7$) and $N(0) = 1000$.

<table>
<thead>
<tr>
<th>$t$</th>
<th>$N(t)$</th>
<th>$N(t + 1)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1000.0</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>700.0</td>
<td>0.7</td>
</tr>
<tr>
<td>2</td>
<td>490.0</td>
<td>0.7</td>
</tr>
<tr>
<td>3</td>
<td>343.0</td>
<td>0.7</td>
</tr>
<tr>
<td>4</td>
<td>240.1</td>
<td>0.7</td>
</tr>
<tr>
<td>5</td>
<td>168.1</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Note that in reality there cannot be fractions of animals. This model is a continuous approximation to a process that is fundamentally discrete.

Algebraically, we have the following:

$$N(1) = S \cdot N(0) \quad N(2) = S \cdot N(1) = S \cdot (S \cdot N(0))$$

$$N(3) = S \cdot N(2) = S \cdot (S \cdot S \cdot N(0))$$

and in general

$$N(t) = S^t \cdot N(0)$$  \hspace{1cm} Here $t$ can be any positive number, not just an integer.

In fisheries we usually write the equation for $N(t)$ in an equivalent exponential form:

$$N(t) = N(0) \cdot \exp(-\lambda \cdot t)$$

$$\exp(X) = e^X$$

$$e = 2.71828...$$

To see the equivalence, let's convert $S^t$ to exponential form. Observe that

$$\ln(S^t) = t \cdot \ln(S)$$

$$\ln(X) = \log(X)$$
This means that \( S^t = \exp(t \cdot \ln(S)) \)

The exponentiation function is the inverse of the logarithm function, and vice versa. Exponentiation undoes the logarithm; the logarithm undoes the exponentiation.

Now substitute the right hand side into the equation \( N(t) = S^t \cdot N(0) \)

\[
\Rightarrow S^t \cdot N(0) = N(t) = \exp(t \cdot \ln(S)) \cdot N(0)
\]

\[
N(t) = N(0) \cdot \exp\left(-\ln\left(\frac{1}{S}\right) \cdot t\right)
\]

\[\ln(1/X) = -\ln(X)\]

Let \( M = \ln(1/S) \)

\[
\Rightarrow N(t) = N(0) \cdot \exp(-M \cdot t)
\]

We're done!

This coefficient \( M \) is usually described as the \textit{instantaneous rate of mortality.}

We have the following relationships: \( M = \ln\left(\frac{1}{S}\right) = -\ln(S) = -\ln(1 - \mu) \)

In the numerical example \( \mu = 0.3 \) and \( M = 0.3567... \)

In general, if \( \mu \) is small (say, less than 0.2), then \( M \equiv \mu \). Here are some examples:

\[-\ln(1 - 0.20) = 0.2231 \quad -\ln(1 - 0.10) = 0.1054 \quad -\ln(1 - 0.05) = 0.0513\]

One reason for working with instantaneous rates is that it is easy to change the time-step, by simple scaling. Implicit in the examples above is that each value of \( \mu, M, \) and \( S \) has an associated time-step, such as "per year" or "per month". To convert from an annual instantaneous rate to a monthly instantaneous rate, we just divide by 12. So, for example, an annual instantaneous mortality rate of 1.2 per year is equivalent to a monthly instantaneous rate of 0.1 per month. Note that we cannot convert between the annual \( M \) and an approximate value for the annual \( \mu \), using the rule \( M \equiv \mu \), but we can convert the monthly \( M \) to the approximate monthly \( \mu \), which is about 10% mortality per month.

\textbf{Review of Some Mathematics}

The course web-site includes a handout entitled "Review of Some Mathematics", which provides basic definitions and fundamental properties of some mathematical concepts. Most of the mathematics in this course involves basic algebra. However, I expect that your skills are a bit rusty. I will try to make it very clear how the models are set up and how to solve them. I will use exponents, logarithms, derivatives, limits, series, simple differential equations, and a few simple integrals. If you don't understand the terminology, my notation, or how I did some manipulation, please consult the "Review of Some Mathematics" and/or ask me.

In this course I will show you some applications of mathematics in population dynamics. This is a course in population dynamics not mathematics. What I want you to understand are how the models can be used and how they should not be used. I need to provide you some details regarding how the models are constructed so that you will understand the simplifying assumptions, which necessarily limit the applicability of the models. However, the risk is that you will get lost in the details of the mathematics.
Dimensional Methods

In mathematics we deal with numbers and abstractions, but in science we often measure physical quantities that have **dimensions**, such as length, mass, and time. We must specify magnitudes (unit scales) for these physical dimensions and we must be careful not to do nonsensical operations with the dimensions.

One common use of dimensions is to convert between different measurement units. To do these conversions we can manipulate the dimensions as if they were normal algebraic variables.

$$1\cdot \text{inch} = 2.54\cdot \text{cm} \quad \Rightarrow \quad 10\cdot \text{cm} \cdot \frac{1}{2.54} \left( \frac{\text{inch}}{\text{cm}} \right) = 3.937\cdot \text{inches}$$

$$16\cdot \text{oz} = 1\cdot \text{lb} \quad \Rightarrow \quad 2.5\cdot \text{lb} \cdot \frac{16\cdot \text{oz}}{1\cdot \text{lb}} = 40\cdot \text{oz}$$

We cannot do mathematical operations on physical quantities unless they have the same dimensions and scales. Here are some examples.

- $6\cdot \text{inches} + 12\cdot \text{cm}$
- $5\cdot \text{days} + 6\cdot \text{hours}$
- $3\cdot \text{lbs} + 9\cdot \text{inches}$

We can combine units with the same dimensions but different scales, but not units with different dimensions.

Equations must be **dimensionally homogeneous**. All terms in an equation must have the same fundamental dimensions. Also, it makes no sense to apply functions such as exp() or ln() to physical quantities. The terms within these functions must be **dimensionless**. Similarly, we cannot raise physical quantities to noninteger powers.

**Back to our equation for N(t).**

$$N(t) = N(0) \cdot \exp(-M \cdot t) \quad M \text{ has the dimension } [\text{Time}^{-1}].$$

It turns out that there is a very simple relationship between the function $N(t)$ and the derivative of this function, which I will denote as $N'(t)$. The variable $t$ in the parentheses in $N'(t)$ is the differentiation variable, what we are differentiating with respect to. The second term in the following equation is another way of representing the derivative of $N$ with respect to $t$.

$$N'(t) = \frac{dN}{dt} = N(0) \cdot \exp(-M \cdot t) \cdot (-M) \quad \text{Some authors use } N \text{ with a dot over it (dot notation) to signify } N'.$$

To derive this formula for $N'(t)$ I used the following basic rules of differentiation:

$$d(c \cdot X) = c \cdot d(X) \quad \text{and} \quad d(\exp(X)) = \exp(X) \cdot d(X)$$

where $c$ denotes a constant and $X$ denotes a variable.

Here are word translations of the differentiation rules:

- *The derivative of a constant times a function is the constant times the derivative of the function.*
- *The derivative of an exponential of a function is the exponential times the derivative of the function.*
To make this less abstract, below are some values for \( N(t) \) and \( N'(t) \); to the right are the graphs.

<table>
<thead>
<tr>
<th>( t )</th>
<th>( N(t) )</th>
<th>( N'(t) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1000.0</td>
<td>-356.7</td>
</tr>
<tr>
<td>1</td>
<td>700.0</td>
<td>-249.7</td>
</tr>
<tr>
<td>2</td>
<td>490.0</td>
<td>-174.8</td>
</tr>
<tr>
<td>3</td>
<td>343.0</td>
<td>-122.3</td>
</tr>
<tr>
<td>4</td>
<td>240.1</td>
<td>-85.6</td>
</tr>
<tr>
<td>5</td>
<td>168.1</td>
<td>-59.9</td>
</tr>
</tbody>
</table>

You should recall from calculus that the derivative of a function at a given point is the slope of the function at that point.

Notice in the graphs that there seems to be a simple linear relationship between \( N'(t) \) and \( N(t) \).

We can derive the relationship between \( N(t) \) and \( N'(t) \) using simple algebra.

\[
N(t) = N(0) \cdot \exp(-M \cdot t)
\]

and

\[
N'(t) = N(0) \cdot \exp(-M \cdot t) \cdot (-M)
\]

\[
\Rightarrow \quad N'(t) = -M \cdot N(t)
\]

This is an example of a first-order, ordinary differential equation (ODE). It is an equation that relates the function \( N \) with its first derivative \( N' \). It is described as ordinary because it has no partial derivatives. There is only one independent variable, \( t \). It is first-order because it involves only first derivatives.

Here is a second-order ODE.

\[
\frac{d^2}{dt^2}N + 2 \frac{d}{dt}N = -N + 3
\]
Analytical Solution to $N'(t) = -M \cdot N(t)$

For certain kinds of differential equations it is possible to derive a solution function using simple algebraic manipulations and then applying integration to undo the differentiation that produced the derivative. This is illustrated below.

\[
\frac{dN}{dt} = -M \cdot N
\]

\[
\frac{dN}{N} = -M \cdot dt
\]

\[
\int \frac{1}{N} \, dN = \int -M \, dt
\]

$N$ is the **dependent variable**; $t$ is the **independent variable**.

**Step 1:** separate the variables.

**Step 2:** integrate both sides to "undo" the differentiation.

We use the integration operation to undo the differentiation. This follows from the so-called Fundamental Rule of Calculus, which relates differentiation and integration as follows.

If $f(x)$ is continuous for $a \leq x \leq b$, and $F(x) = \int_a^x f(u) \, du$, then $F'(x) = f(x)$.

$F(x)$ is the area under the curve $f(u)$ over the interval $(a,x)$. The slope of $F(x)$ is $f(x)$.

When we differentiate the integral $F(x)$ we recover the function that was under the integral sign, which is called the integrand.

Returning to the equation, ...

... the left hand side is

\[
\int \frac{1}{N} \, dN = \ln(N) + C
\]

... and the right hand side is

\[
\int -M \, dt = -M \cdot t + C'
\]

Each process of integration produces a so-called arbitrary constant ($C$ and $C'$). They must be included to reflect the fact that differentiation of any constant is zero. Any solution curve to a differential equation has a family of parallel curves all having the same slope. They are also solutions to the differential equation.

Now we put the two pieces back together to get

\[
\ln(N) = -M \cdot t + C''
\]

The new arbitrary constant $C''$ is $C' - C$.

Exponentiate both sides.

\[
N(t) = \exp(-M \cdot t) \cdot \exp(C'')
\]

This is the so-called **general solution** to the differential equation. There is a family of solutions for the infinity of values that are possible for the arbitrary constant $C''$.

\[
N(t) = C'' \cdot \exp(-M \cdot t)
\]

Specify the **initial conditions**, to eliminate all but one member of the family of solutions.

\[
N = N(0) \quad \text{at} \quad t = 0
\]
\[ N(0) = C'''' \cdot \exp(-M \cdot 0) \]

\[ C'''' = N(0) \]

\[ N(t) = N(0) \cdot \exp(-M \cdot t) \]

\[ \text{Exp}(0) = 1. \]

\[ \text{Solve for } C''''. \]

\[ \text{This is the so-called specific solution to the differential equation.} \]

**Graphical Solution to \( N'(t) = -M \cdot N(t) \)**

With this simple differential equation we can also find a solution using a graphical technique.

Note that I rotated the axes 90°counterclockwise in the graph on the left so that in both graphs the N-axis is oriented vertically upwards.

The solution's slope at a particular value for \( t \) is just a constant \((-M)\) times the value of the solution.

The arbitrary constant in the general solution corresponds to the starting value in the time trajectory. The initial conditions fix the horizontal position of the vertical axis.

There will be an asymptote for \( N(t) \) at any value of \( N \) for which \( N'(t) = 0 \). In this example there is a horizontal asymptote at \( N = 0 \), and the graph of \( N(t) \) never crosses the horizontal line \( N = 0 \).

**Numerical Solution to \( N'(t) = -M \cdot N(t) \)**

We can develop a simple numerical method, akin to the graphical technique we just examined, to generate computer or spreadsheet solutions to a differential equation. The equation for \( N'(t) \) is used to generate the slope of \( N(t) \). We use the definition of the slope to derive an approximation for the value of \( N \) at a nearby value of \( t \).

The slope of \( N \) at point \( t \) is approximately equal to

\[ \frac{N(t + \Delta t) - N(t)}{(t + \Delta t) - t} = \frac{\Delta N}{\Delta t}. \]
By the way, the derivative of $N(t)$ is usually defined as the limiting value of the left hand expression as $\Delta t$ approaches zero. We can rearrange this approximation to get

$$\Rightarrow \quad \Delta N \equiv \Delta t \cdot \text{Slope}$$

If we increase $t$ by a small amount $\Delta t$ and calculate a new approximate value for $N$ at this new value of $t + \Delta t$, we get the following.

$$N(t + \Delta t) \equiv N(t) + \Delta N = N(t) + \Delta t \cdot (-M \cdot N(t))$$

To solve approximately for $N$ at a later point in time we can use the following algorithm:

1. take the current value for $N$;
2. calculate the value of the slope at that point;
3. multiply the slope times the time step;
4. add the product to the current value for $N$.

This general numerical method of solving a differential equation is known as Euler’s Method. If the function $N(t)$ is changing very rapidly the error of the approximation can be severe unless the $\Delta t$ value is very small. Other more sophisticated numerical methods are available. The advantage of Euler’s method is its simplicity.

*Explore the effects of $\Delta t$ using the Excel demonstration.*