Lecture 5:
Modelling Population Dynamics – $N(t)$

Part I: Limited and unlimited growth

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Topics: Top down models (equation based) of population dynamics N(t)

<table>
<thead>
<tr>
<th>Time discrete</th>
<th>Time continuous</th>
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<td>Unlimited growth</td>
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<td>Limited growth</td>
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<td>Stochastic limited growth</td>
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Example: linkage of simulation and equation based models (Fahse et al. 1998)

Application/Model analysis: Protocol for a PVA from first principles (Grimm & Wissel 2004)

Nice Introductions:

Equation based Models

J Roughgarden - Primer of ecological theory – all examples in matlab

M Kot – Elements of Mathematical Ecology

WSC Gurney & RM Nisbet – Ecological Dynamics

But there are many more…

C. Wissel – Theoretische Ökologie – Eine Einführung
What are (non-spatial, unstructured) population dynamics?

*Paramecium aurelia* - based on G.F. Gause 1934 as presented in: Primer of Ecological Theory, Joan Roughgarden

![Graph showing population growth of Paramecium aurelia](Source: www.wikipedia.de)

Why modelling it?

*Paramecium aurelia* - based on G.F. Gause 1934 as presented in: Primer of Ecological Theory, Joan Roughgarden

- Process based understanding
- Predictions, long term dynamics
- (Computer) experiments
Lets get started – unlimited growth – time discrete $N_t$

$$N_{t+1} = BN_t - DN_t + N_t$$

B: birth rate  
D: death rate

Quite often B and D are merged to the per capita growth rate R

$$N_{t+1} = RN_t$$

Geometric growth - Recursion:

$$N_{t=1} = 1$$

$$N_{t=2} = RN_{t=1}$$

$$N_{t+1} = 2N_t = 2 \cdot 2 \cdot N_{t-1} = \ldots = 2^t N_0 = R^t N_0$$

Source: www.wikipedia.de
So what have we got? \[ N_{t+1} = R^t N_0 \]

Parameterizing the model using R-function nls: \( R \sim 1.4 \)
MLE of \( R \sim 1.44 \) and \( N_0 \sim 1.3 \), using optim() in R

Parameterizing the model using R-function nls using only the first seven data points: \( R \sim 2.3 \)

Early dynamics can be described by geometric growth!

We could quantify "growth rate" R.
Unlimited growth – time continuous $N(t)$

So far discrete, i.e. events happen in finite time steps

$$N_{t+1} = RN_t$$

Inconvenient for mathematical analysis and sometime biologically not plausible

Let's make time step, small, very small, and assume that birth and death processes can occur any time, than the change in population time is given by

$$\frac{dN(t)}{dt} = rN(t)$$

Is called an ordinary differential equation (ODE) and can be solved analytically, e.g. separation of variables.
Separation of variables:

\[
\frac{dN(t)}{dt} = rN(t)
\]

\[\iff \frac{dN}{N(t)} = rdt\]

\[\iff \int \frac{dN}{N(t)} = \int rdt\]

\[
\Rightarrow \ln(N(t)) = rt + C
\]

\[
\Rightarrow N(t) = \exp(C) \exp(rt)
\]
Separation of variables:

\[ N(t) = \exp(C) \exp(rt) \]

With \( N(0) = N_0 \)

\[ \Rightarrow C = \ln(N_0) \]

finally

\[ \Rightarrow N(t) = N_0 \exp(rt) \]

Unlimited growth

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<thead>
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<tr>
<td>( N_{t+1} = R'N_0 )</td>
<td>( N(t) = N(0) \exp(rt) )</td>
</tr>
<tr>
<td>( N_{t+1} = N_0 \exp(\ln(R')) )</td>
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</table>

\[ \ln(R) = r \]
Some remarks on models of (age) structured population dynamics \( N(t) \) – (Leslie) Matrix models

**Leslie Matrix**

\[
\begin{pmatrix}
F_1 & F_2 & F_3 \\
0 & 0 & 0
\end{pmatrix}
\begin{pmatrix}
n_{1,t} \\
n_{2,t} \\
n_{3,t}
\end{pmatrix}
= 
\begin{pmatrix}
n_{1,t+1} \\
n_{2,t+1} \\
n_{3,t+1}
\end{pmatrix}
\]

Matrix models frequently used in applied conservation studies of population viability analysis (PVA)

**Leslie Matrix**

\[
\begin{pmatrix}
F_1 & F_2 & F_3 \\
0 & 0 & 0
\end{pmatrix}
\begin{pmatrix}
n_{1,t} \\
n_{2,t} \\
n_{3,t}
\end{pmatrix}
= 
\begin{pmatrix}
F_1 \cdot n_{1,t} + F_2 \cdot n_{2,t} + F_3 \cdot n_{3,t} \\
P_1 \cdot n_{1,t} + 0 \cdot n_{2,t} + 0 \cdot n_{3,t} \\
0 \cdot n_{1,t} + P_2 \cdot n_{2,t} + 0 \cdot n_{3,t}
\end{pmatrix}
\]

Simple set of linear equations

\[
M \cdot \tilde{n}(t) = \tilde{n}(t + 1)
\]
If there is an equilibrium population structure (e.g., negative exponential age structure), then….

\[ M \cdot \vec{n}_i(t) = \lambda_i \cdot \vec{n}_i(t) \]

\( \vec{n}_i \) - i-th eigenvector – corresponding to the leading eigenvalue \( \lambda_i \)

\( \lambda_i \) - leading eigenvalue \( \lambda_i \)

\[ \vec{n}_i(t + t_0) = \lambda_i^t \cdot \vec{n}_i(t_0) \]

Calculating \( \lambda_i \) is difficult (characteristic polynomial of \( M \) has to be solved), but numerics will mostly do the job – (e.g., \texttt{eigen(M)} in R)

\[ N(t) = \lambda_i^t \cdot N(t_0) \]

for a reasonable large \( t_0 \)

\( \lambda_i > 1 \) – geometric growth

\( \lambda_i = 1 \) – constant population size

\( \lambda_i < 1 \) – exponential decline

But please remember
Back to unstructured population dynamics $N(t)$
– limited growth - continuous

Many possible models:

- Logistic
- Ricker model – fish cannibalism
- Gompertz
- Maynard-Smith and Slatkin

Logistic equation:

\[
\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t)}{K}\right)
\]

$K$: Capacity

$r = 0.81$

$K = 582.5$
Logistic equation – time continuous

\[
\frac{dN(t)}{dt} = r N(t) \left( 1 - \frac{N(t)}{K} \right)
\]

K: Capacity

Solving by separation of variables. Integration already needs some experience (partial fraction decomposition).

Analytical solution:

\[
N(t) = \frac{K}{\left( \frac{K}{N_0} - 1 \right) \exp(-rt) + 1}
\]

(Bronstein)

Analytical solutions are great for understanding!
Parameter estimation for K and r with R-function nls:
K = 582.5 and r = 0.83

So what's the problem with ODE models?

1. Technical problems – Integrating is a problem!
2. Overlapping generations
3. No variability
1. Technical problems

\[ \frac{dN(t)}{dt} = rN(t) \left( 1 - \frac{N(t)}{K} \right) \]

What to do if analytical solution cannot be found?

Numerical approximation of the problem

Principle idea – discretize the problem for small time steps and compute (iterate) the solution!

Many ways to do – one standard technique is called Runge Kutte, also implemented in R

An introduction to R for dynamic modeling, Stephen Ellner
Ecology and Evolutionary Biology, Cornell, March 19, 2003

But use lsoda() instead of rk4() – help for rk4

```r
#numerical solution
library(odesolve)
times <- c(1:20)
f <- function(t,x,parms){a=parms[1];b=parms[2];xdot=c(1);xdot=x*a*(1-x/b);return(list(xdot));}
out1<-lsoda(y=2,times,f,parms=c(a=0.81,b=582.5))
plot(out1,col=2)
```

```r
# numerical solution
library(odesolve)
times <- c(1:20)
f <- function(t,x,parms){a=parms[1];b=parms[2];xdot=c(1);xdot=x*a*(1-x/b);return(list(xdot));}
out1<-lsoda(y=2,times,f,parms=c(a=0.81,b=582.5))
plot(out1,col=2)
```
Numerical solution (red line, points belong to analytical solution)

Major disadvantage: numerical solution has to be determined for each set of parameterization independently. Does not always work!

Problem for parameter fitting! Computational demanding!

2. Non-overlapping generations

Time discrete Logistic equation

If individuals reproduce and die at a certain point in time rather than continuously

\[
\frac{\Delta N}{\Delta t} = RN_t \left(1 - \frac{N_t}{K}\right)
\]

with \(\Delta t = 1\) and \(\Delta N = N_{t+1} - N_t\)

\[
N_{t+1} = RN_t \left(1 - \frac{N_t}{K}\right) + N_t
\]
Is there a simple recursion?

Exponential growth

\[ N_{t=1} = N_1 \]

\[ N_{t=2} = R N_1 \]

\[ N_{t+1} = R^t N_0 \]

Logistic equation

\[ N_{t=1} = N_1 \]

\[ N_{t=2} = R N_1 \left(1 - \frac{N_1}{K}\right) + N_1 \]

\[ N_{t+1} = R N_1 \left(1 - \frac{N_t}{K}\right) + N_t \]

No

That means this time we will not find a solution \( N(t) = \ldots \)

Well, we can discuss attributes of the potential solution!

\[ N_{t=2} = R N_{t=1} \left(1 - \frac{N_{t=1}}{K}\right) + N_{t=1} \]

We are looking for \( N^* \) that

\[ N^* = R N^* \left(1 - \frac{N^*}{K}\right) + N^* \]
That’s true for $N^* = 0$ or $N^* = K$

Equilibrium solutions

Stability:

Continuous case: $N = K$ is always stable
And
$N = 0$ always unstable
Perturbation experiment:

Local stability analysis:

\[ N_{t+1} = RN_t \left(1 - \frac{N_t}{K}\right) + N_t = F(N_t) \]

Using:

\[ N^* = F(N^*) \]
\[ N_t = n_t + N^* \]

Thus we can write

\[ N_{t+1} = n_{t+1} + N^* = F(N_t) = F(n_t + N^*) \]
\[ n_{t+1} + N^* = F(n_t + N^*) \]
F is not specified, but non-linear problems are mostly not tractable, this is why scientists love to linearise…

Taylor expansion:

\[
F(N^* + n_i) = \sum_{i=0}^{\infty} \left( \frac{1}{i!} \frac{d^i F(N^*)}{dN^i} \right) (n_i)^i
\]

Which is for quadratic functions as the logistic functions:

\[
F_q(N^* + n_i) = F(N^*) + \frac{dF_q(N^*)}{dN} n_i + \frac{d^2 F_q(N^*)}{dN^2} \frac{n_i^2}{2}
\]

If \( F \) is the logistic equation:

\[
\frac{dF_q(N)}{dN} = R - \frac{2R}{K} N + 1
\]
\[
\frac{d^2 F_q(N)}{dN^2} = -\frac{2R}{K}
\]

For \( N^* = K \)

\[
F_{q,1}(N^* + n_i) \sim N^*
\]
\[
F_{q,2}(N^* + n_i) \sim N^* + (1 - R)n_i
\]
\[
F_{q,3}(N^* + n_i) \sim N^* + (1 - R)n_i - \frac{R}{K} n_i^2
\]
\[ F_{q,1} (N^* + n_t) - N^* \]

\[ F_{q,2} (N^* + n_t) \sim N^* + (1-R)n_t \]
\[ n_{t+1} + N^* = F(n_t + N^*) \]

Well, finally replacing \( F \) by its linear approximation (Taylor expansion)

\[ n_{t+1} + N^* \approx N^* + (1 - R)n_t \]

\( \Leftrightarrow n_{t+1} \approx (1 - R)n_t \)

Geometric growth again!

\[ n_t \to 0 \quad \text{if} \quad |1 - R| < 1 \]

The equilibrium at \( N = K \) is only stable for \( 0 < R < 2 \)

The equilibrium at \( N = 0 \) is never stable for \( 0 < R \) – not shown here

\[
\begin{align*}
\text{Cobweb – Analysis – } R &= 1.25 - \text{stable} \quad \text{(Graph)}
\end{align*}
\]
So, we have learned quite a bit, without knowing the solution!

\[ N_{t+1} = RN_t \left(1 - \frac{N_t}{K}\right) + N_t \]

Equilibrium at \( N=0 \) and \( N=K \)

The equilibrium at \( N = K \) is only stable for \( 0 < R < 2 \)

The equilibrium at \( N = 0 \) is never stable for \( 0 < R \) – not shown here

But we have computers, we can iterate the solution!
Iteration in R

```r
# function for time discrete population dynamics
logist <- function (r)
{
  N <- rep(1, times = 1000)
  K <- 582.5
  ti <- c(1:1000)
  for (i in 1:999)
  {
    N[i+1] <- N[i]+r*N[i]*(1-N[i]/K)
  }
  plot (N[1:100], type = "l")
  lines(ti,582.5/(1+(582.5-1)*exp(-log(r+1)*ti)), col = "green",type = "l")
}
```

Parameter estimation for K and R with R-function nls:
K = 582.5 and R = exp(0.83)-1=1.3

Analytical solution of the time continuous problem is not the same as the solution of the time discrete problem. Mathematicians tend to call this a numerical artefact, but there is a ecological meaning behind this difference – non-overlapping generations.
Equilibrium stable if $0 \leq R < 2$, but what happens for $R \geq 2$?

```r
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{
  N <- rep(1, times = 1000)
  K <- 582.5
  ti <- c(1:1000)

  for (i in 1:999)
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    N[i+1] <- N[i]+r*N[i]*(1-N[i]/K)
  }

  plot (N[1:100], type = "l")
  lines(ti,582.5/(1+(582.5-1)*exp(-log(r+1)*ti)), col = "green",type = "l")
}
```
Discrete population dynamics – non-overlapping generations, can show complex dynamics

Will never happen for the continuous description!

Often called deterministic chaos!

Very nice way to illustrate dependency of population dynamics on its parameterization R Bifurcation diagram

```r
bifurcation <- function (n)
{
  plot(0,0,ylim = c(0,800),xlim = c(1.8,3),xlab = "r",ylab="N")
  N <- rep(1, times = (100+n))
  K <- 582.5
  ti <- c(t(100+n))
  r <- c(1:400)
  r <- 1.8+1.2*(r-1)/399
  for(i in 1:399)
  {
    for (t in 1:(99+n))
    {
      N[t+1] <- N[t]+r[i]*N[t]*(1-N[t]/K)
      if (t > 99)
      {
        points(r[i],N[t+1],cex=0.75,pch=19)
      }
    }
  }
}
```

Jürgen Groeneveld – Lecture 5 „Equation based population models“ (Part I, Day 5)
Self similarity
Scientists fell in love with complex dynamics:

MAY RM
SIMPLE MATHEMATICAL-MODELS WITH VERY COMPLICATED DYNAMICS
NATURE 261 (5560): 459-467 1976
Times Cited: 1928

Solving our problem?
What is the role of „deterministic chaos“ in Ecology?

Hardly any application!

Too sensitive against noise!