BIOL 410 Population and Community Ecology

Density-dependent growth 2
Objectives

- Time lags
- Amplitude, period
- Equilibrium
- Damped oscillations
- Stable limit cycles
- Discrete logistic growth model
- Chaos vs. stochasticity
Logistic population growth

\[ N < \text{seq}(0, 100, 1) \]
\[ t < \text{seq}(1, 20, 0.1) \]
\[ N_0 < 1 \]
\[ K < 60 \]
\[ r < 0.6 \]
\[ N_t < \frac{K}{1 + \left(\frac{K - N_0}{N_0}\right) \exp(-r \cdot t)} \]
Time Lags

• In a continuously growing population, adding new individuals into the population causes a continuous decrease in the per capita rate of population growth \[
\left(\frac{1}{N}\right)\left(\frac{dN}{dt}\right)
\]

• However, in many populations there are time lags \(\tau\) in response to changes in population size

What could cause these time lags?
What could produce time lags in density dependence?
\[
\frac{dN}{dt} = rN \left(1 - \frac{N_{t-\tau}}{K}\right) \quad \tau = \text{time lag}
\]
Time Lags

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

- Two things will affect this equation.
  1. The length of the time lag (\(\tau\))
  2. The response time of the population – this is inversely related to the intrinsic rate of increase (i.e. \(1/r\)).
Time Lags

• The ratio of the time lag to the response time $\frac{\tau}{1/r}$, (which is simply $r\tau$) controls population growth.

• If $r\tau$ is small (between 0 to 0.368)
  • the population increases smoothly to a carrying capacity

• If $r\tau$ is moderate (0.368 to 1.570)
  • the population first overshoots then undershoots carrying capacity, followed by dampening oscillation to reach carrying capacity over time.

• If $r\tau$ is large (>1.570)
  • the population goes into a stable limit cycle of oscillations above and below carrying capacity that go on indefinitely.
Cyclic Populations

- Population Size ($N$)
- Time ($t$)
- Amplitude
- Period
- $K$
Logistic population growth

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Time Lags

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

\[
\frac{\tau}{1/r'} = r\tau
\]
Time lags (continuous population)

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

\[
r \leftarrow 0.4 \\
K \leftarrow 1000 \\
\tau \leftarrow 0
\]

\[
t \leftarrow \text{seq}(1,100,1) \\
N0 \leftarrow 100 \\
r \leftarrow 0.4 \\
K \leftarrow 1000 \\
\tau \leftarrow 0 \\
r*tau \leftarrow r*tau \\
N \leftarrow \text{seq}(0,\text{length}(t),1) \\
N[1] \leftarrow N0 \\
lambda \leftarrow \exp(r) \\
\text{for}(ts \ in \ t)\{ \\
\text{etau} \leftarrow \tau \\
\text{if}(ts <= \tau) \ \text{etau} \leftarrow 0 \\
N[ts+1] \leftarrow \lambda*N[ts]/(1+((N[ts-\text{etau}]*\lambda-1))/K)) \\
\}
\]
Time lags (continuous population)

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

\[ \frac{\tau}{1/r'} = r\tau \]

\[ 0 < r\tau < 0.368 < r\tau < 1.57 \]

\[ r \leftarrow 0.4 \]
\[ K \leftarrow 1000 \]

\[ \tau \leftarrow 0, \quad r\tau = 0 \]
\[ \tau \leftarrow 2, \quad r\tau = 0.8 \]
Time lags (continuous population)

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

\[
\frac{\tau}{1/r'} = r\tau
\]

\[
0 < r\tau < 0.368 < r\tau < 1.57
\]

\[
r \leftarrow 0.4
\]

\[
K \leftarrow 1000
\]

\[
\tau \leftarrow 0, \quad r\tau = 0
\]

\[
\tau \leftarrow 2, \quad r\tau = 0.8
\]

\[
\tau \leftarrow 3, \quad r\tau = 1.2
\]
Time lags (continuous population)

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

\[
\frac{\tau}{1/r'} = r\tau
\]

\[
0 < r\tau < 0.368 < r\tau < 1.57
\]

\[
r < 0.4
\]
\[
K < 1000
\]
\[
\tau < 0, \quad r\tau = 0
\]
\[
\tau < 2, \quad r\tau = 0.8
\]
\[
\tau < 3, \quad r\tau = 1.2
\]
\[
\tau < 4, \quad r\tau = 1.6
\]
Time lags (continuous population)

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

\[
\frac{\tau}{1/r'} = r\tau
\]

\[
0 < r\tau < 0.368 < r\tau < 1.57
\]

\[
r < 0.4
\]

\[
K < 1000
\]

\[
\tau < 0, \ r\tau = 0
\]

\[
\tau < 4, \ r\tau = 1.6
\]

\[
\tau < 5, \ r\tau = 2.0
\]
Time lags (continuous population)

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

\[
\frac{\tau}{1/r'} = r\tau
\]

\[
0.368 < r\tau < 1.57 < r\tau
\]

\[
r \leftarrow 0.4
\]
\[
K \leftarrow 1000
\]

\[
\tau \leftarrow 0, \ r\tau = 0
\]
\[
\tau \leftarrow 5, \ r\tau = 2.0
\]
\[
\tau \leftarrow 6, \ r\tau = 2.4
\]
\[
\tau \leftarrow 7, \ r\tau = 2.8
\]
Time lags (continuous population)

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

- What will happen if these populations exhibiting limit cycles are disturbed?
- Land slip, fire?
Time lags (continuous population)

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

\[
r \leftarrow 0.4 \\
K \leftarrow 1000
\]

\[
\tau \leftarrow 0, \quad r\tau = 0
\]
Time lags (continuous population)

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

\[ \frac{\tau}{1/r} = r\tau \]

\[ 0.368 < r\tau < 1.57 < r\tau \]

\[ K \leq 1000 \]

\[ \tau \leq 0, \ r \leq 0.4, \ r\tau = 0 \]

\[ \tau \leq 3, \ r \leq 0.4, \ r\tau = 1.2 \]

\[ \tau \leq 3, \ r \leq 0.5, \ r\tau = 1.5 \]
Cycles in ecological populations

Canadian lynx data — the number of lynx trapped each year in the McKenzie river district of northwest Canada (1821–1934).
Daphnia pulex

Egg density dynamics during cycles.

St Kilda, Scotland
Soay Sheep

http://soaysheep.biology.ed.ac.uk/
• Approximately 3 years between population crashes
• What drives this cycle?

- Grenfell et al. 1992
  - Competition for food, highly overcompensating density-dependent mortality
- Grenfell et al. 1998
  - Weather and density dependence
- Coulson et al. 2001
  - Population age-structure, sex-structure, weather, density-dependence
- Ozgul et al. 2009
  - Size of sheep (as well as other factors)

http://soaysheep.biology.ed.ac.uk/
Discrete logistic models

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

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

- The discrete population growth model has a built in time lag of 1.0 (i.e. intergeneration time)
  - In continuous growing population, lag effects are influenced by the product of rate of increase and time lag \((r\tau)\).
  - In discrete population, time lag is 1, so dynamics of pop growth are essentially a function of discrete growth factor \((r_d)\).
Discrete Population Growth – Logistic Models

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

\[ r_d = 0.4 \]

```r

t <- seq(1,50,1)
N0 <- 100
rd <- 0.4
K <- 500

N <- seq(0,length(t),1)
N[1] <- N0

for(ts in t){
}
```
Discrete Population Growth – Logistic Models

- Dynamics of Discrete Population

1. If the Discrete Growth Factor is small ($r_d<2.0$), then you get dampened oscillations to a stable population at $K$.

\[ r_d = 1.5 \]
Discrete Population Growth – Logistic Models

• Dynamics of Discrete Population

2. If the Discrete Growth Factor is a bit larger ($r_d > 2.0$ but less than 2.449), then you get stable two-point limit cycles.

$r_d = 2.2$
Discrete Population Growth – Logistic Models

• Dynamics of Discrete Population

3. When the Discreet Growth Factor is between 2.449 to 2.570 (2.449 < \( r_d \) < 2.57), you get growth with complex limit cycles, with varying number of “points”.

\[ r_d = 2.56 \]
Discrete Population Growth – Logistic Models

• Dynamics of Discrete Population

4. When the Discreet Growth Factor is above 2.570, the limit cycles break down and the population grows in a non-repeating pattern (chaos)

\[ r_d = 2.7 \]
Discrete Population Growth – Logistic Models

- Chaos vs Stochasticity

\[ r_d = 2.7 \]

\[ N_0 = 100 \]

\[ N_0 = 101 \]
Variation in Carrying Capacity

• Environmental Variation may cause carrying capacity to change over time

• Variation could be:
  1. Random
  2. Cyclic
Variation in Carrying Capacity

- Random Variation in Carrying Capacity (K)
  - If \( r \) is not variable, but carrying capacity changes over time, result is complex growth patterns
  - When a population is above the carrying capacity, it declines at a faster rate than it will increase if it is at a corresponding similar point below the carrying capacity.
  - If the carrying capacity is described by a mean (\( \bar{K} \)) with an associated variance (\( \sigma_{K}^2 \)), a rough approximation of the mean population size will be:
    \[
    \bar{N} = \bar{K} - \frac{\sigma_{K}^2}{2}
    \]
Variation in Carrying Capacity

- **Random Variation in Carrying Capacity (K)**
  - The more variable the environment, the smaller the average population size.
  - If the intrinsic rate of increase \( r \) is large, the population closely tracks changes in carrying capacity.
  - If the small intrinsic rate of increase \( r \) is small, the population do not fluctuate much in size as carrying capacity varies, but the population size \( N \) will tend to be overall somewhat smaller than a population that has a rapid intrinsic growth rate.
Variation in Carrying Capacity

- Periodic (cyclic) variation in Carrying Capacity
  - e.g. seasonal variation in resources

\[ K_t = k_0 + k_1 \cos \left( \frac{2\pi t}{c} \right) \]

- \( K_t \) = carrying capacity at time \( t \)
- \( k_0 \) = is mean carrying capacity
- \( k_1 \) = the amplitude of the cycle
- \( c \) = the length of the cycle
Variation in Carrying Capacity

• Periodic (cyclic) variation in Carrying Capacity
  • length of the cycle acts as a time lag, so the behavior of the model depends on the factor $rc$ (as it did previously with $r\tau$)
Variation in Carrying Capacity

- If $rc$ is large (>>1.0), then the population tends to track the fluctuations in the environment:
  \[ N_t \approx k_0 + k_1 \cos\left(\frac{2\pi t}{c}\right) \]

- If $rc$ is very small (<<1.0), then the population tends to average out the fluctuations and persist at a level slightly below carrying capacity
  \[ \bar{N} \approx \sqrt{k_0^2 - k_t^2} \]