What is it?
- Individuals are seperated by their age
- Populations are not tracked in their totality

Why do you need it?
- For investigating future demograpfics
- Understanding specie's life-history

3 Questions to answer:
I. How many individuals of a given age class die during each time interval?

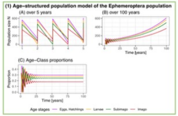
II. How many move into the next age class?

III. How many newborns are created by the member of each age class?

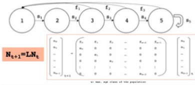
Good resources:
- Crouse et al. (1987)
- Crowder et al. (1994)
- tinyurl.com/2mvnp6j6

$$\begin{pmatrix} 140 \\ 0 \\ 90 \\ 75 \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0.8 & 0.6 \\ 0.95 & 0 & 0 & 0 \\ 0 & 0.95 & 0 & 0 \\ 0 & 0 & 0.75 & 0 \end{pmatrix} \begin{pmatrix} 0 \\ 100 \\ 100 \\ 100 \end{pmatrix}_{t}$$

„The population grows exponentially over 100 years, but the proportion in each class reaches an equilibrium."



AGE-STRUCTURED POPULATION MODEL



$N_{t+1}=LN_t$

N= Vector of abundances at time t
L= Population transition matrix (Leslie matrix)

s= Probability of transition
f= Fecundities

Equilibrium analysis:
- = Point when the dynamics of the system stop changing (see (C))
- Each population matrix L has a corresponding eigenvector v and eigenvalue λ
  - v: represents the stable stage distribution of the population
  - λ: gives the growth rate at the stable age distribution
  - $Lv = \lambda v$
- Eigenvalue λ is equal to e^r
  - r: intrinsic rate of increase of the population in the equation: $N_t=N_0e^{rt}$
- If $\lambda=e^r=1$, then $r=0$ → population size remains stable
- In a constant environment, the proportion of individuals in different age classes of a populations tends toward a stable age distribution
- Once the stable age distribution has been reached, a population undergoes exponential growth at rate λ (see (B))

What is the logistic growth model?
- The logistic growth model is a mathematical model to describe the change of a population size over time ($\frac{dn}{dt}$).
- **The intrinsic growth rate (*r*)** indicates whether a population is growing (*r* > 0), decreasing (*r* < 0) or sustaining itself (*r* = 0).
- The logistic growth model features the parameter ***K***, which represents the **carrying capacity.** An ecological system can only sustain a limited number of one species at the same time, e.g. due to competition for resources.
- In continuous time, the model assumes that the per capita growth rate decreases linearly with population size.

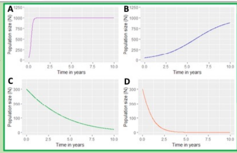


*Figure 1: Plotting the continuous time equation with different growth rate values (r). The carrying capacity K is constant for A-D (K = 1000); the starting population is N = 50 for A and B, N = 300 for C and D. **A**: r = 10.0, population size increases rapidly until it reaches the carrying capacity, from this time the system is at equilibrium (K = N). **B**: r = 0.5, population size increases in an almost S-shaped curve. Carrying capacity is not reached in the displayed time period; **C**: r = -0.3, population size decreases slowly; **D**: r = -1.2, the population size decreases more rapidly than C and reaches equilibrium, because N turns zero.*

Logistic growth model

Logistic growth model – Equation in continuous time

$$\frac{dn}{dt} = rn(t)\left(1-\frac{n(t)}{K}\right)$$

Parameter	Description	Range
r	Population growth rate per capita	[-∞,∞]
K	Carrying capacity	[0, ∞]
t	Time	[0, ∞]
State variable		
n(t)	Population size at time t	[0, ∞]

Equilibrium analysis

When is a system at equilibrium?

In population ecology, a system is at equilibrium when the population size doesn't change over time and becomes constant.

To analyze a system regarding its equilibrium, $\frac{dn}{dt}$ is replaced with the equilibrium value (0). The equation is then solved for each variable:

$$rn(t)\left(1-\frac{n(t)}{K}\right) = \frac{dn}{dt}$$

$rn(t) = 0$
$r^* = 0$
$n(t)^* = 0$

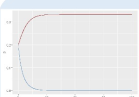
$\left(1-\frac{n(t)}{K}\right) = 0$
$-\frac{n(t)}{K} = -1$
$-K = -n(t)$
$K^* = n(t)$

For the logistic growth model, there are three cases in which the system reaches an equilibrium:

I. the intrinsic growth rate *r* equals zero.

II. The population size $n(t)$ equals zero.

III. The carrying capacity *K* equals the population size.



Parameter values

time	0-100 years
P	0.2
c	0.6
c	0.4
e	0.4
e	0.6

What is the difference between both plots?
- The parameters c and e differ between the red and the blue graph
- At the red line: c>e → the population can grow
- At the blue line: c<e → more patches, and with that more metapopulations/individuals in them, die, than there are new patches that get colonized →With that, the population shrinks and will go extinct within a few decades.

Useful additional information

Parameter	Description	Range
N	Total number of available patches	[0;∞], but constant
U	Number of unoccupied patches	N-O
O	Number of occupied patches	N-U

Parameter	Description	Range
c	Probability of occurance of a colonization	[0;1]
p	Probability, that a patch is initially occupied	[0;1]
e	Extinction rate per patch	[0;1]
t	time	[0;+∞]

What is a metapopulation?
- An ensemble of interacting populations connected by dispersal of individuals among them
- Many species exist as metapopulations
  - The amount is increasing due to habitat loss, degradation, fragmentation
  → landscapes become patchy

Levins metapopulation model

$$\frac{dp}{dt} = cp(1-p) - ep \qquad \frac{O}{N} = p \qquad \frac{U}{N} = 1-p$$

Interpreting model terms

1-p	Pobability of an empty patch
cp(1-p)	Colonization rate

What is the Levins metapopulation model?
- Was first introduced in 1969 → the pioneer of metapopulation models
- Assumptions:
  - There is a large number of patches which all have identical colonization(c) and extinction(e) rates
  - Across patches, c and e are uncorrelated and the population size can be ignored
  - There is only absence or presence of the species in a patch
- Appropiate for systems with intermediate levels of migration between patches
- If movement is extremely common: the system behaves as a single, larger population
- If migration is extremely rare: each patch can properly be considered in isolation

Equilibrium behaviour

1) Under what conditions does the system reach equilibrium?

The population reaches equilibrium, if $\frac{dp}{dt}=0$, then $cp(1-p)=ep$ and $(1-p)=\frac{e}{c}$, so the equilibrium is $P=1-\frac{e}{c}$.
At equilibrium, not all patches are occupied, unless $\frac{e}{c}=0$.
For persistence c>e is needed.

2) Under what parameter values is the system at 0 (for example, when is population size 0)?

The population will go extinct, if e≥c.

What is Lotka-Volterra Model?

The Lotka–Volterra model is frequently used to describe the dynamics of ecological systems in which two species, the predator (y) and the prey (x), interacting each other in limited space. The Lotka–Volterra model assumes that the prey consumption rate by a predator is directly proportional to the prey abundance. This means that predator feeding is limited only by the amount of prey in the environment.

In Figure 1, I designed a conceptual model with *Noctiluca sp.* as a predator and *Cymbella sp.* as a prey. *Noctiluca* is a marine dinoflagellate, which is large and has an increase population at night. *Noctiluca* feeds on various minute marine organisms, including also marine diatoms. *Cymbella sp.* on the other hand is a marine diatom, which has a high population growth rate, as a primary producents of photosynthesis.

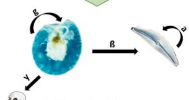


Fig. 1. Conceptual model

On this table are given the parameters, which we need to calculate the Lotka-Volterra Model, in this case the prey-predator behavior between *Noctiluca sp.* and *Cymbella sp.*

Parameter	
a	Prey population growth rate
β	Predation rate
δ	Predator population growth rate
γ	Predator mortality rate
x	Prey species
y	Predator species

The equations governing the dynamics of the prey and predator are: The prey grows at a linear rate (alpha) and gets eaten by the predator at the rate of (beta). The predator gains a certain amount vitality by eating the prey at a rate (delta), while dying off at another rate (gamma).

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y$$

In Figure 2 we see the behavior of a prey (a) and a predator (b) when they are not interacting with each other. They have both a high growth rate, when there are not other factors, which impact their growth rate.

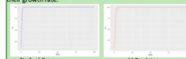


Fig 2. a) Prey b) Predator

When they are competing with each other, we have an other outcome.

Results

This choice of parameters leads to periodic dynamics in which the prey population initially increases, leading to an abundance of food for the predators. The predators increase in response (lagging the prey population), eventually overwhelming the prey population, which crashes. This in turn causes the predators to crash, and the cycle repeats. The period of these dynamics is about 15 seconds, with the predators lagging the prey by about a second.

Equilibrium

The system is at equilibrium if the variables don't change anymore and are static. In a continuous-time model, the derivatives over time are 0. In Fig 3 there is no equilibrium because the variables are not static. But here you can find stable cycles, because the height and the bottom part of the model-curve are repeating again and again in cycles.

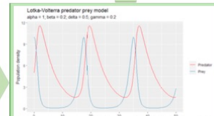
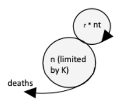


Fig 3. Lotka-Volterra Model

Logistic growth model: **cheat sheet**

Conceptual diagram



Definition

The logistic growth model in continuous time describes the change in population size ***n*** over time ***t***, with a per capita growth rate ***r*** that decreases as the population size increases towards the carrying capacity ***K***.

Equation

$$\frac{dn}{dt} = rn_t\left(1-\frac{n_t}{K}\right)$$

Equilibrium

The population is at equilibrium when *total* deaths equal *total* births.

$$0 = rn_t\left(1-\frac{n_t}{K}\right)$$
$$\rightarrow n_t = K$$

Parameter	Description	Range
n	population size	[0, K]
n_t	population size at time t	[in progress]
r	intrinsic rate of growth (per capita change in number of individuals in a population over time)	[- ∞, ∞]
K	carrying capacity: maximum population size at which the population can sustain itself	dependent on N

Example plot

The values of parameters used for this plot are n=42 and K=100. The range of r is shown in the right legend. When r is positive, n_t increases towards K, when r is negative n_t decreases. When r equals zero, n_t is equal to K.