

# **Masnedic** narations

"Populační ekologie živočichů"

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## **Density-dependent growth**

• includes all mechanisms of population growth that change with density

- population structure is ignored
- extrinsic effects are negligible
- response of  $\lambda$  and *r* to *N* is immediate

 $\lambda$  and *r* decrease with population density either because natality decreases or mortality increases or both

- negative feedback of the 1st order

*K*.. carrying capacity
upper limit of population growth where λ = 1 or r = 0

- is a constant

### Discrete (difference) model

- there is linear dependence of  $\lambda$  on N



$$N_{t+1} = \frac{N_t \lambda}{1 + \frac{(\lambda - 1)N_t}{K}}$$

f 
$$a = \frac{\lambda - 1}{K}$$
 then

$$N_{t+1} = \frac{N_t \lambda}{1 + aN_t}$$



## **Continuous (differential) model**

- Iogistic growth
- First used by Verhulst (1838) to describe growth of human population
- there is linear dependence of r on N



$$\frac{dN}{dt} = Nr \quad \rightarrow \quad \frac{dN}{dt} \frac{1}{N} = r$$

- when  $N \to K$  then  $r \to 0$ 

$$\frac{dN}{dt} = Nr\left(1 - \frac{N}{K}\right)$$

#### Solution of the differential equation

$$N_{t} = \frac{KN_{0}}{(K - N_{0})e^{-rt} + N_{0}}$$

# Examination of the logistic model



#### Model equilibria

1. N = 0 .. unstable equilibrium

2. N = K .. stable equilibrium .. if 0 < r < 2

 "Monotonous increase" and "Damping oscillations" has a stable equilibrium

"Limit cycle" and "Chaos"
 has no equilibrium

r < 2 .. stable equilibrium r = 2 .. 2-point limit cycle r = 2.5 .. 4-point limit cycle r = 2.692 .. chaos

 chaos can be produced by deterministic process

 density-dependence is stabilising only when
 r is rather low



## **Observed population dynamics**

b) sheep (logistic curve with oscillations)

c) Callosobruchus (damping oscillations)

d) Parus (chaos)

e) Daphnia

of 28 insect species in one species chaos was identified, one other showed limit cycles, all other were in stable equilibrium



# **Evidence of DD**

- in case of density-independence  $\lambda$  is constant independent of N
- in case of DD  $\lambda$  is changing with N:  $\ln(\lambda) = a bN_{t}$
- plot  $\ln(\lambda)$  against  $N_t$
- estimate  $\lambda$  and K



# General logistic model

Hassell (1975) proposed general model for DD *r* is not linearly dependent on N

$$N_{t+1} = \frac{N_t \lambda}{\left(1 + aN_t\right)^{\theta}} \qquad \qquad \frac{\mathrm{d}N}{\mathrm{d}t} = rN \left(1 - \left(1 - \frac{1}{2}\right)^{\theta}\right)$$

where  $\theta$ .. the strength of competition

•  $\theta < 1$  .. scramble competition (over-compensation), strong DD, leads to fluctuations around *K* 

•  $\theta = 1$  .. contest competition (exact compensation), stable density

θ >> 1 .. under-compensation
- weak DD, population will return to K



 $\frac{N}{K}$ 

## Models with time-lags

species response to resource change is not immediate (as in case of hunger) but delayed due to maternal effect, seasonal effect, predator pressure

• appropriate for species with long generation time where reproductive rate is dependent on the past (previous generations)

• time lag (d or  $\tau$ ) .. negative feedback of the 2nd order

discrete model

 $N_{t+1} = \frac{N_t \lambda}{1 + a N_{t-d}}$ 

continuous model

$$\frac{dN}{dt} = N_t r \left( 1 - \frac{N_{t-\tau}}{K} \right)$$

- many populations of mammals cycle with 3-4 year periods
- time-lag provokes fluctuations of certain amplitude at certain periods
- period of the cycle in continuous model is always  $4\tau$

#### Solution of the continuous model:

$$N_{t+1} = N_t e^{r\left(1 - \frac{N_{t-\tau}}{K}\right)}$$

 $r \tau < 1 \rightarrow$  monotonous increase  $r \tau < 3 \rightarrow$  damping fluctuations  $r \tau < 4 \rightarrow$  limit cycle fluctuations  $r \tau > 5 \rightarrow$  extinction



## Harvesting

- Maximum Sustainable Harvest (MSH)
- to harvest as much as possible with the least negative effect on N
- ignore population structure
- ignore stochasticity

$$\frac{\mathrm{d}N}{\mathrm{d}t} = Nr\left(1 - \frac{N}{K}\right) = 0$$



local maximum:  $N^* = \frac{K}{2}$ 

Amount of MSH ( $V_{max}$ ): at K/2:

$$MSH = \frac{rK}{4}$$

Robinson & Redford (1991)
Maximum Sustainable Yield (MSY)

$$MSY = a\left(\frac{\lambda K - K}{2}\right)$$

here 
$$a = 0.6$$
 for longevity < 5  
 $a = 0.4$  for longevity = (5,10)  
 $a = 0.2$  for longevity > 10

Surplus production (catch-effort) models

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- when r,  $\lambda$  and K are not known
- effort and catch over several years is known
- Schaefer quadratic model

$$catch = \alpha + \beta E + \gamma E^2$$

- local maximum of the function identifies optimal effort (*OE*)



# Alee effect

individuals in a population may cooperate in hunting, breeding – positive effect on population increase

- ► Allee (1931) discovered inverse DD
- genetic inbreeding decrease in fertility
- demographic stochasticity biased sex ratio
- small groups cooperation in foraging, defence, mating, thermoregulation
- K<sub>2</sub>.. extinction threshold,
  unstable equilibrium
  population increase is slow
  at low density but fast at higher density

$$\frac{dN}{dt} = Nr\left(1 - \frac{N}{K_1}\right)\left(\frac{N}{K_2} - 1\right)$$

