



"Populační ekologie živočichů"

Stano Pekár

#### **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

 λ 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 constant

#### **Discrete (difference) model**

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

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



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

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

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



#### **Continuous (differential) model**

- logistic 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**

a) yeast (logistic curve)
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

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

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</li>
weak DD, population will return to K



### Models with time-lags

▶ species response to resource change is not immediate but delayed due to maternal effect, seasonal effect, predator pressure

• appropriate for species with long generation time where reproductive rate is dependent on density of a previous generation

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

discrete model

continuous model

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

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

- 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 ( $V_{max}$ ): - replace  $N^*$  by K/2

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

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

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

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

- Surplus production (catch-effort) models
- 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

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

