

Intraspetif Inchaet ons

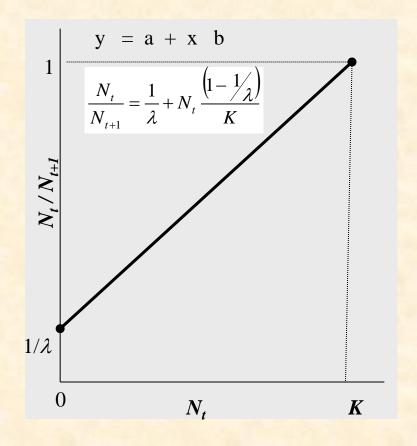
Density-dependent growth

- ▶ includes all mechanisms of population growth that change with density
- population structure is ignored
- extrinsic effects are negligible
- response of λ and r to N is immediate
- \blacktriangleright 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 $\lambda = 1$ or r = 0
- is a constant

Discrete (difference) model

- there is linear dependence of λ on N

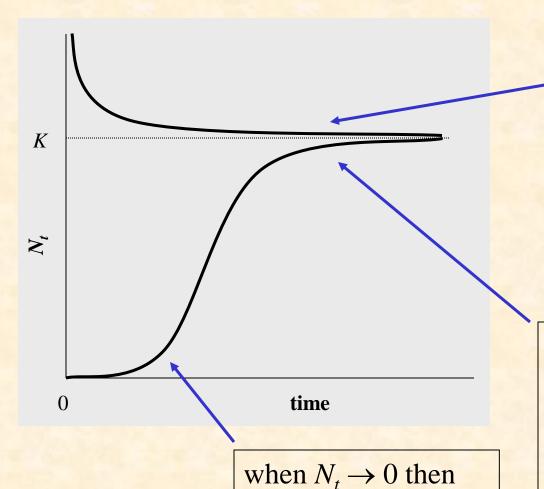
$$N_{t+1} = N_t \lambda \frac{N_t}{N_{t+1}} = \frac{1}{\lambda}$$



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

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

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



 $\frac{\lambda}{1 + aN_t} \approx \lambda$

no competition

exponential growth

when $N_t > K$ then

$$\frac{\lambda}{1 + aN_t} < 1$$

• population returns to K

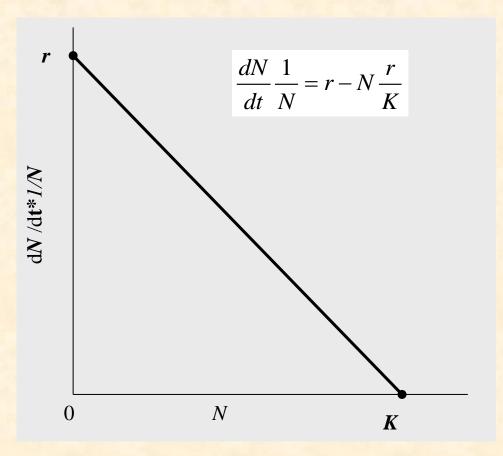
when $N_t \to K$ then

$$\frac{\lambda}{1 + aN_t} \approx 1$$

- density-dependent control
- S-shaped (sigmoid) growth

Continuous (differential) model

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



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

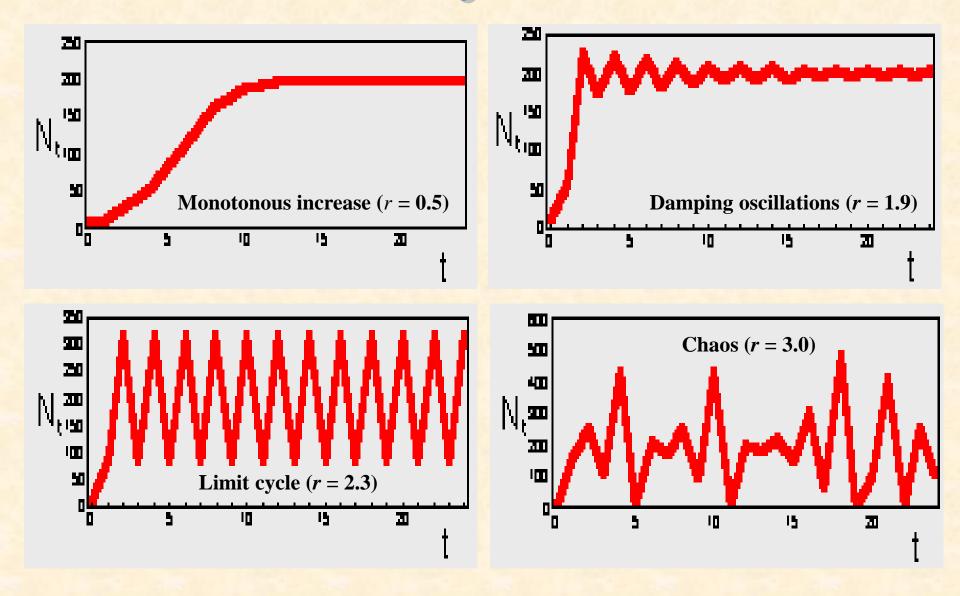
- when $N \to K$ then $r \to 0$

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

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

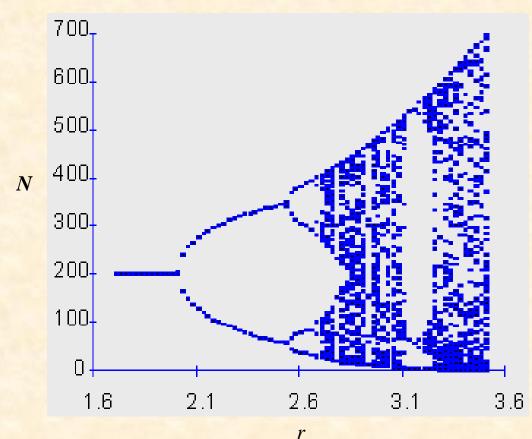
r < 2 .. stable equilibrium

r = 2 ... 2-point limit cycle

r = 2.5 ... 4-point limit cycle

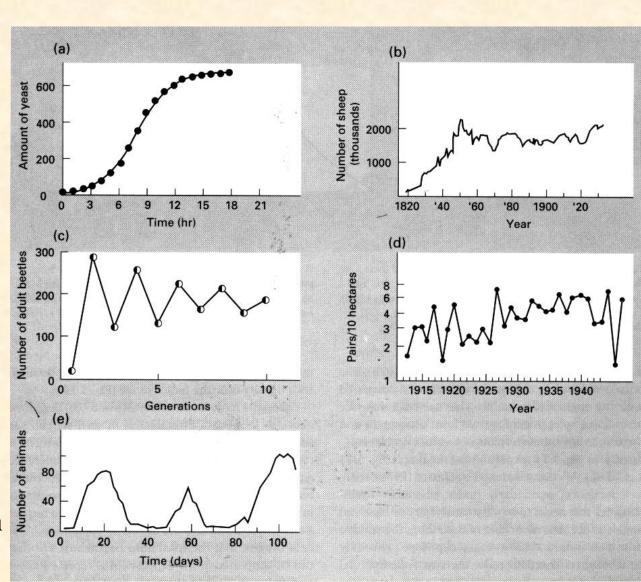
r = 2.692 ... chaos

- chaos can be produced by deterministic process
- ▶ density-dependence is stabilising only whenr is rather low



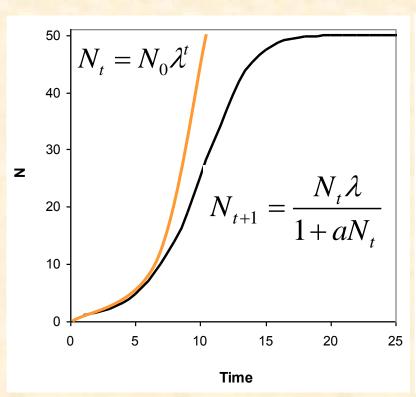
Observed population dynamics

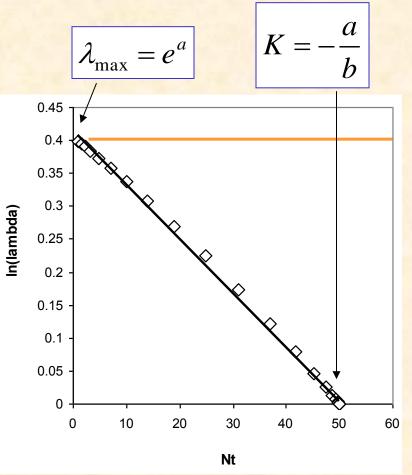
- a) yeast (logistic curve)
- b) sheep (logistic curve with oscillations)
- c) Callosobruchus (damping oscillations)
- d) Parus (chaos)
- e) Daphnia
- ▶ of 28 insect species in one species chaos was identified, one other showed limit cycles, all other were in stable equilibrium



Evidence of DD

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





General logistic model

- rate may not be linearly dependent on N_t
- ▶ Hassell (1975) proposed general model for DD
- r is not linearly dependent on N

$$N_{t+1} = \frac{N_t \lambda}{\left(1 + aN_t\right)^{\theta}}$$

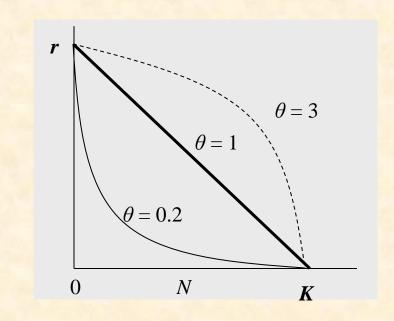
$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \left(\frac{N}{K}\right)^{\theta}\right)$$

where θ .. the strength of competition

 θ < 1 .. scramble competition, strong DD, leads to fluctuations around K

 $\theta = 1$.. contest competition, stable density

 $\theta >> 1$.. weak DD, strong competition near to K, population will return to 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)
 - \blacktriangleright time lag (d or τ) .. negative feedback of the 2nd order

discrete model

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

continuous model

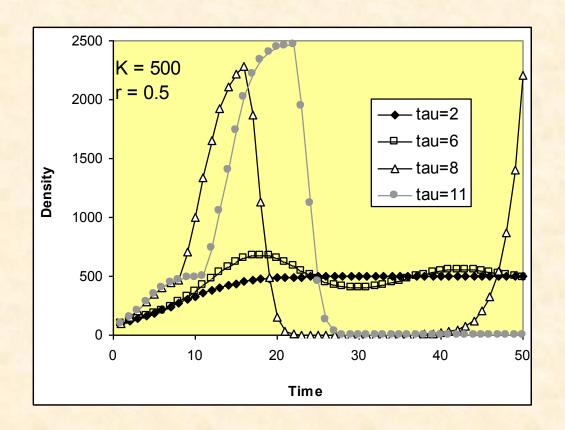
$$\left| \frac{dN}{dt} = N_t r \left(1 - \frac{N_{t-\tau}}{K} \right) \right|$$

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

Solution of the continuous model:

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

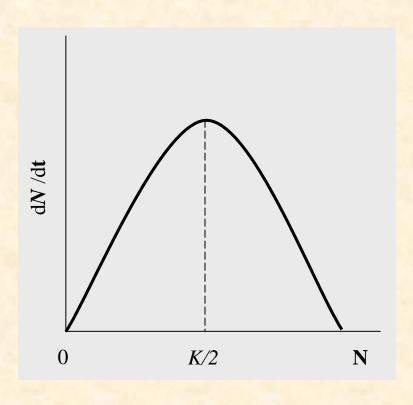
 $r \tau < 1 \rightarrow$ monotonous increase $r \tau < 3 \rightarrow$ damping fluctuations $r \tau < 4 \rightarrow$ limit cycle fluctuations $r \tau > 5 \rightarrow$ extinction



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:

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

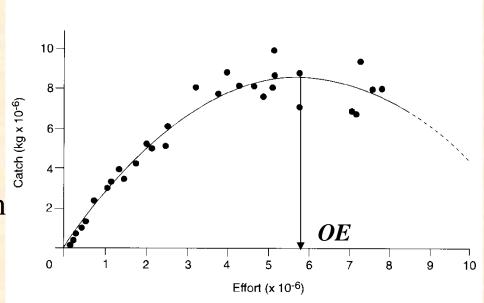
- ▶ Robinson & Redford (1991)
- Maximum Sustainable Yield (MSY)

MSY =
$$a \left(\frac{\lambda K - K}{2} \right)$$
 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, λ 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
- $\blacktriangleright K_2$.. extinction threshold,
- unstable equilibrium
- population increase is slow at low density but fast at higher density

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

