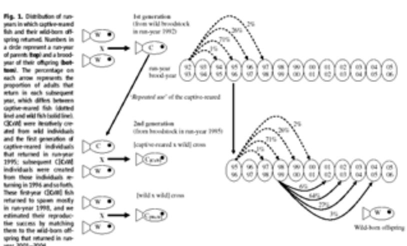
Population Models

- Introduction to population growth models
  - Unlimited resources, density independent growth
    - Deterministic models, simple exponential growth
    - Stochastic unlimited growth
  - Limited resources, density dependent growth

Araki et al. (2007): Genetic effects of captive breeding

- Hood River winter steelhead (Oregon)
- Estimated relative fitness for hatchery-reared adults reproducing in wild over several generations using microsatellite pedigree analyses.

Araki et al. (2007): Genetic effects of captive breeding



Effect of domestication on reproductive success? How does hatchery rearing alter adult life history traits and behavior affecting fitness?

Araki et al. (2007)5 OCTOBER 2007 VOL 318 SCIENCE www.sciencemag.org

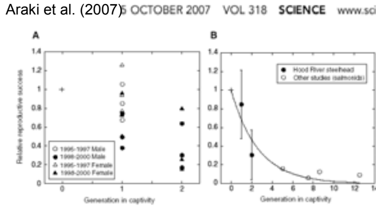


Fig. 2. (**A**) Estimated RRS of captive-reared fish relative to wild fish, plotted against generation time in captivity. Each point represents an estimate from a run-year and sex. The point at generation 0 represents wild fish as a control (marked as a cross). Estimates of the RRS of C[WxW] are plotted at generation 1 and C[CxW] at generation 2. Three years of data at generation 1 (open plots) are from (17). (**B**) Meta-analysis of the RRS of captive-reared versus wild fish plotted against generation time in captivity of other salmonid species. Solid circles are the estimates from our data (weighted geometric means from Fig. 2A). The bar represents 1 SD. The other four points are from two studies on steelhead, one on brown trout, and one on Atlantic salmon (table S4) from (25). The exponential regressions were obtained as $y = e^{-0.375x}$ (correlation coefficient = 0.962), which suggest that fitness in the wild is reduced 37.5% per generation of captive breeding.

~40% in relative fitness / generation in captivity when returned to the wild!

-Will this result be general for all animals?

Limited growth

- Last time we talked about unlimited growth where b and d did not vary or varied randomly around a constant value.
- Populations don't grow indefinitely

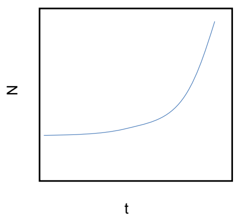
Growth rates

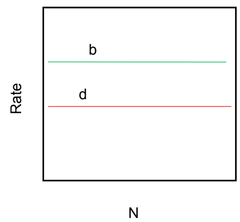
- In unlimited environments, birth rate is constant
- death rate is constant
- r = b - d

- dN / dt = f(N) N
- Exponential growth f(N) = r
- dN / dt = rN

Rates: unlimited growth

$N_t = N_o e^{rt} = N_o e^{(b-d)t}$





Limited growth

- Hastings (1997) Figure 4.1, Dynamics of sheep numbers in Tasmania after introduction (1820-1940).
- Hastings (1997) Figure 4.5 *E. coli* from experiment of McKendrick (1911).

Limited growth

- First, growth is exponential
- Then growth rate slows down as population increases (grow rate deccelarates)
- and then the population size fluctuates around a an apparent equilibrium population size
  - Why?

Growth rates

- birth rate declines
- and/or death rate increases

- One or more limiting resources at higher population size

Limited growth

- Rev. Thomas Malthus (1798), *An Essay on the Principles of Population*
- Human population grows expoentially, doubling ~30 years
- Food supply increases arthimetically

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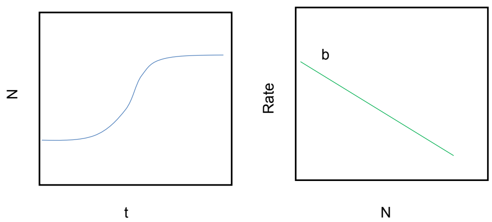
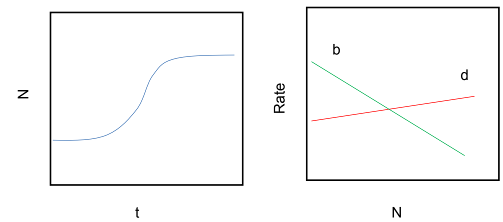
- Human population grows expoentially, doubling ~30 years
- Food supply increases arthimetically
- Verhulst (1800): environment is limited so there is some maximum number of organisms that can be supported in a area
- = K (the carrying capacity)

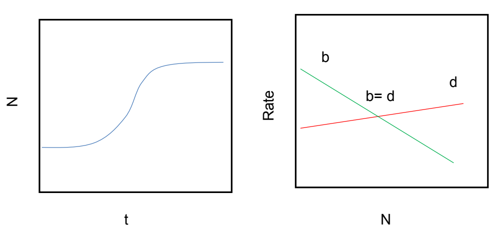
Rates: unlimited growth



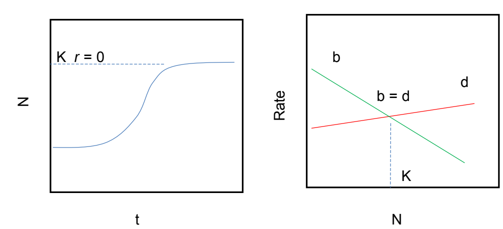
Rates: unlimited growth



Rates: unlimited growth



Rates: unlimited growth



Limited growth

- Population size N where b = d
  and r = b – d = 0
  is defined as K, the carrying capacity

Density dependent growth rates

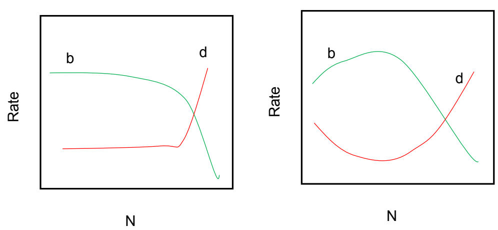
- dN / dt = *f*(N) N
  where *f*(N) describes how rate changes with increasing populations size

What if *f*(N) is non-linear?

Rates: unlimited growth

r = *f*(N) can take many non-linear forms to accommodate many underlying density dependent processes

Competition for nest holes | Finding mates
Disease dynamics | Predator swamping



Logistic growth: simplest assumptions

- Imagine an island with no predators or competitors where vegetation can support 500 deer
- How will rate of increase change as herd increases?

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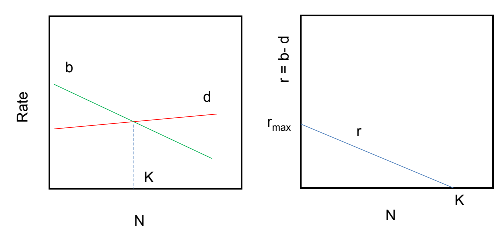
- Imagine an island with no predators or competitors where vegetation can support 500 deer
- How will rate of increase change as herd increases?
- Simplest case–each deer added to popupulation additively decreases population growth from some maximum rate (r_{max})
  - decrease in b with each deer added and
  - increase in d until b = d

Rates: unlimited growth



A simple model: Logistic growth

r = b - d

$r = r_{max}$ (K-N)/K

$r = r_{max}$ (1-N/K)

Therefore:

dN / dt = r N becomes

dN / dt = r_{max} (1 – N/K) N

usually written dN / dt = r N(1 – N/K)

Logistic growth

- The factor r_{max} (1-N/K) expresses the density dependence of population growth

dN / dt = r_{max} (1 – N/K) N

Integral form:

$N_t = K / (1 + e^{a-rt})$ where $a = \ln((K-N_0)/N_0)$

Caughley and Sinclair 1994

- What biological mechanisms explain logistic growth?
- Suggest logistic growth results from animals consuming a renewable resource where:
  - animals have no influence on rate of renewal
  - animals consume the “interest” (excess production)
  - don’t consume the “capital” (basis for production)

Caughley and Sinclair 1994

- i = satiating intake day^{-1}
- g = production of resource ha^{-1} day^{-1}
- b = maintenance intake individual-1 day-1
- N = no. individuals / ha
- proportion of resource channeled into maintenance and replacement = bN/g
- leaving rest, 1-(bN/g), for population growth

Caughley and Sinclair 1994

- when production is in excess, g/N > i, then
- $dN / dt = r_m N$
- when g/N < i, that is production is less than intake, then

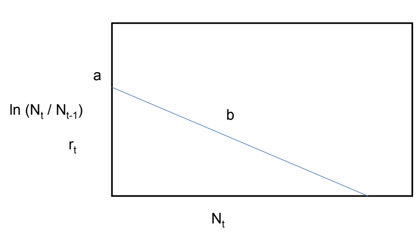
  $dN / dt = r_m N (1-bN/g)$
- If we set g/b (production/per captia maintenance)= K then we get :

  $dN / dt = r_m N (1-N/K)$

Estimating Parameters

- Dennis and Taper (1994) suggested a better way to estimate:
- $r_t = \ln (\lambda_t) = \ln (N_t / N_{t-1}) = a + bN_t$
- Do a regression of $\ln \lambda_t$ on N_t to statistically test for evidence of density dependence

Estimating Parameters



Logistic Growth Assumptions

- 1) The population starts with a stable age distribution
- 2) Density is measured in appropriate units
- 3) There is a real attribute of the population corresponding to r (or r_{max})

Assumptions: Age distribution

$N_t=$

N_0
N_1
N_2
N_3
N_4
N_5

A =

F_0	F_1	F_2	F_3	F_4	F_5
P_0	0	0	0	0	0
0	P_1	0	0	0	0
0	0	P_2	0	0	0
0	0	0	P_3	0	0
0	0	0	0	P_4	0

Where $F_x = f\,(N)$
and / or $P_x = f\,(N)$

Assumptions

- 4) Relationship between density and rate of increase per individual is linear
  - Fowler's work suggested that a non-linear relationship is more appropriate for large mammals
  - Non-linear models are commonly used:
    - The Beverton-Holt and Ricker spawner-recruit models used in fisheries assume two different non-linear relationships between *r* and N

Theta logistic model

- A more general form of the logistic model is the Theta logistic model (Ayalla 1973)
- Logistic model is a special case assuming a linear relationship between r and N
- Non-linear relationships modeled by adding a parameter (theta) that describes the shape of the relationship.

Assumptions

- 5) No time lags
- 6) K does not change through time
- 7) Population is large and the environment is constant so that there are no stochastic or random effects (i.e., no demographic or environmental stochasticity)
- 8) Population grows continuously with overlapping generations

Time lags?

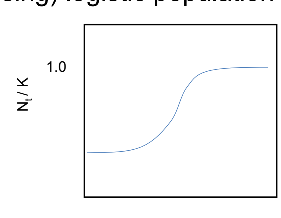
- Robert May (1974), in a famous paper in *Science* (186:645-647) explored implications of a discrete time version:

  $N_{t+1} = N_t\, e^{[r(1-N_t/K)]}$

  New individuals don't appear until next time step (i.e., annual breeding cycle)
- Simply adding a time lag produced some very surprising results

May (1974)

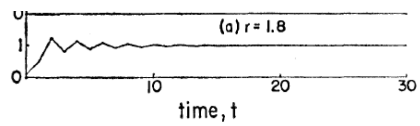
- when r < 1.0, smooth monotonic (only increasing) logistic population growth



May (1974)

- when 1.0 < r < 2.0, logistic growth with **damped oscillations** settling to K

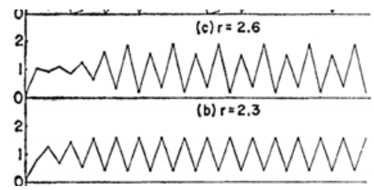
N$_t$ / K



May (1974)

- when 2.0 < r < 2.69, population shows **stable limit cycles**

N$_t$ / K



4 point cycle

2 point cycle

May (1974)

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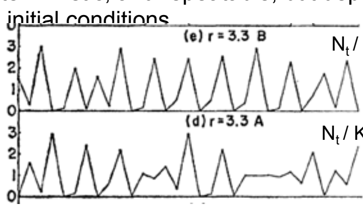

N$_t$ / K = 1.5

N$_t$ / K = 0.075

May (1974)

- Deterministic processes producing patterns of population dynamics that look like random processes
- While r > 2.69 (λ > 14.9) unlikely, chaos can occur at lower values of *r* when models assume time lags, non-linear dynamics etc.,
- May be very difficult to distinguish stable limit cycles, chaos, and stochastic processes in populations, but some evidence for all three.

Logistic Model Summary

- No population grows in an unlimited environment for long
- Simple model expressing an important biological attribute—that growth rate changes with population size
- Logistic model is most simple model that incorporates $r = f(N)$
- Important implications for population stability and harvest