BIOL 410 Population and Community Ecology

Mortality

Maximum sustainable yield

Methods for estimating survival rates Survival analysis

- Examines and models the time it take for events to occur
  - The event can be death, therefor “Survival analysis”

- Other names
  - “event-history analysis” : sociology
  - “failure-time analysis” : engineering

- Advantages:
  - Marked individuals checked on non-regular schedules
  - New left-censored individuals added to samples so that large n retained: “staggered entry design”
  - Accounts for right censored data – individuals lost to monitoring, but not assumed to have died
  - Right censored: unknown fate, radio failure or loss, emigration from study area.

Survival analysis

- Classically, the analysis focuses on time to death
  - But can be used anywhere you want to know what factors affect the time **for** an event to occur:
    - Germination timing
    - Arrival of a migrant or parasite
    - Dispersal of seeds or offspring
    - Failure time in mechanical systems
    - Response to stimulus

Censoring: dealing with uncertain data

- Censored survival times:
  - problem when event has not occurred (within the observation time) or the exact time of event is not known.

- Right censoring:
  - Where the date of death is unknown but is after some known date
  - true survival time > observed survival time

  e.g.
    - Organism alive at end of the observation period (study)
    - Subject is removed from the study
      - animal escapes, animal gets lost, plant gets eaten, etc.

Censoring

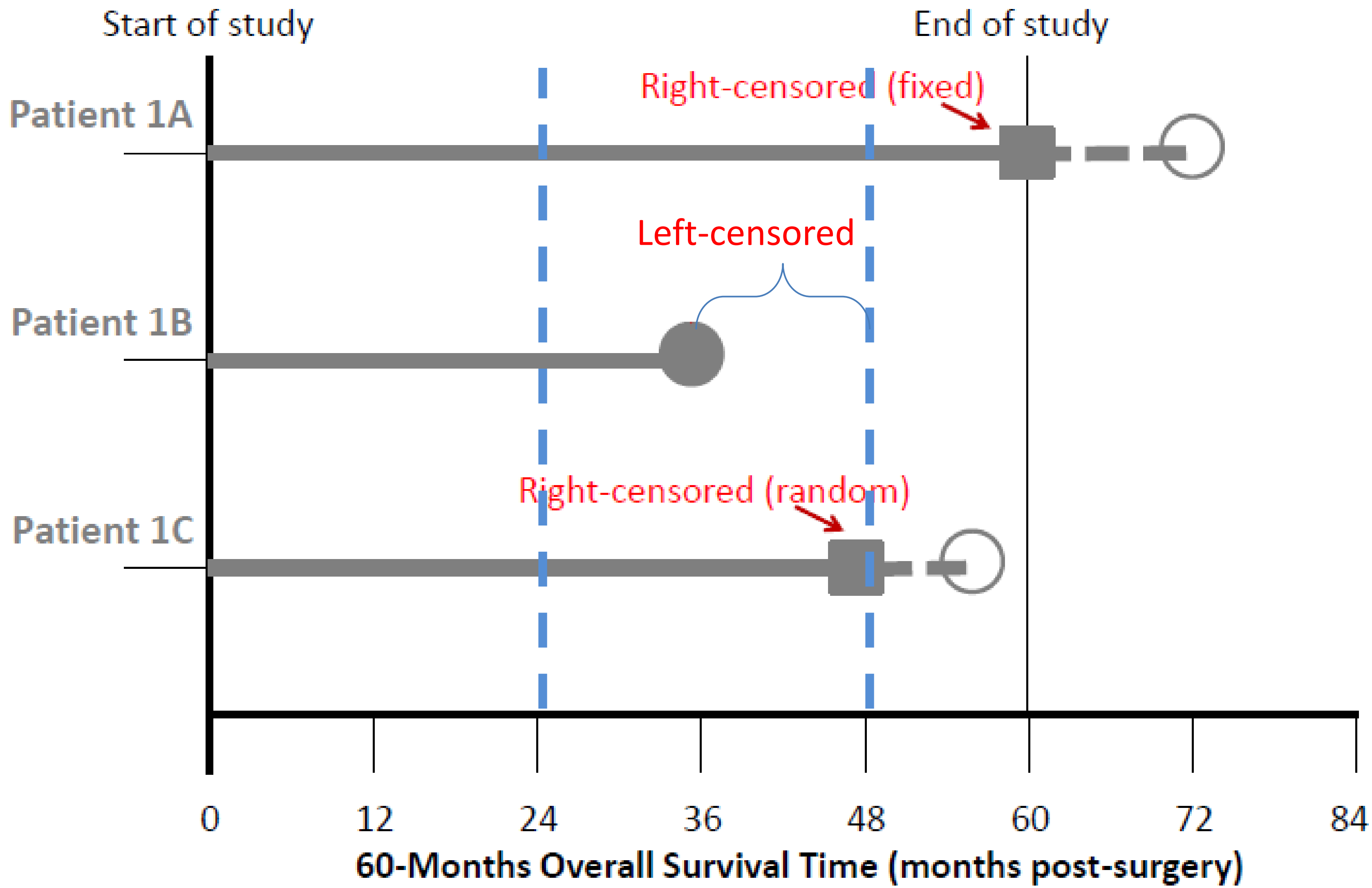
- Left censoring:
  - Occurs when a subject’s survival time is incomplete on the left side of the follow-up period.
  - True survival time < Observed survival time
  - Exact timing of event is uncertain: e.g..

e.g.

- We want to know time to death, but only assess survival when sampling

Censoring must be independent of the event being looked at

Censoring



Start of study
End of study
Right-censored (fixed)
Patient 1A
Left-censored
Patient 1B
Right-censored (random)
Patient 1C
0
12
24
36
48
60
72
84
60-Months Overall Survival Time (months post-surgery)

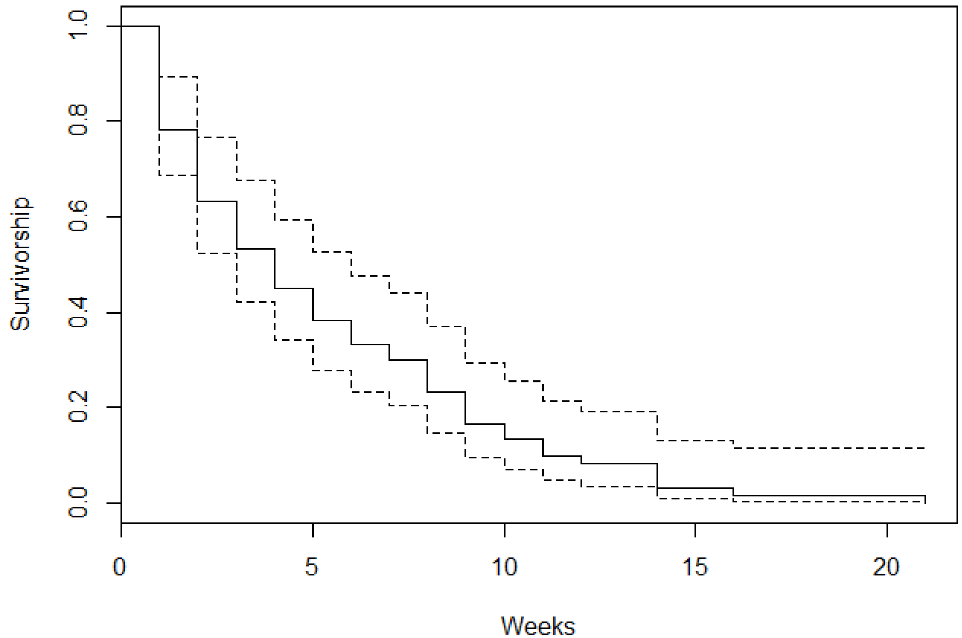
Estimated/Empirical survival curves

- Survival curve is estimated by Kaplan-Meier (KM) estimator, also know as “product estimator”

- The Kaplan-Meier estimate is a nonparametric maximum likelihood estimate of the survival function, S(t)

- The estimate is a step function with jumps at observe event times

Kaplan-Meier estimate



events (deaths)

$$\hat{S}_{KM} = \prod_{t_i < t} \frac{r(t_i) - d(t_i)}{r(t_i)}$$

at risk

$$\hat{S}_{KM} = \prod_{t_i < t} \left[1 - \left(\frac{d(t_i)}{r(t_i)} \right) \right]$$

Kaplan-Meier estimate

$$\hat{S}_{KM} = \prod_{t_i<t}\left[1 - \left(\frac{d(t_i)}{r(t_i)}\right)\right]$$

Sample period	# birds with radios	# found dead	# censored	# added	Survival estimate
1	20	0	0	1	1
2	21	0	0	1	1
3	22	2	1	0	0.909
4	19	5	0	0	0.670

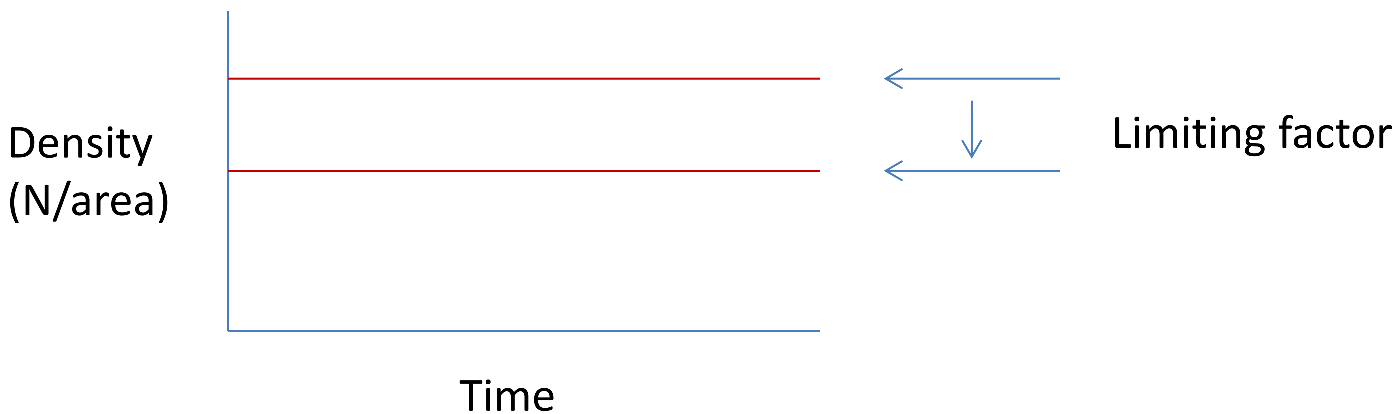
$$0.67 = \prod_{t_i<t}\left[\left(1 - \left(\frac{0}{20}\right)\right)\left(1 - \left(\frac{0}{21}\right)\right)\left(1 - \left(\frac{2}{22}\right)\right)\left(1 - \left(\frac{5}{19}\right)\right)\right]$$

What is mortality

Density dependent?
Density independent?

Population limitation and regulation

- Limitation:
  - A factor is defined to be a limiting factor if a change in the factor produces a change in average or equilibrium density



Population limitation

Journal of Animal Ecology 2006
75, 1269–1284

Population limitation of the northern red-backed vole in the boreal forests of northern Canada

RUDY BOONSTRA* and CHARLES J. KREBS†

Population limitation

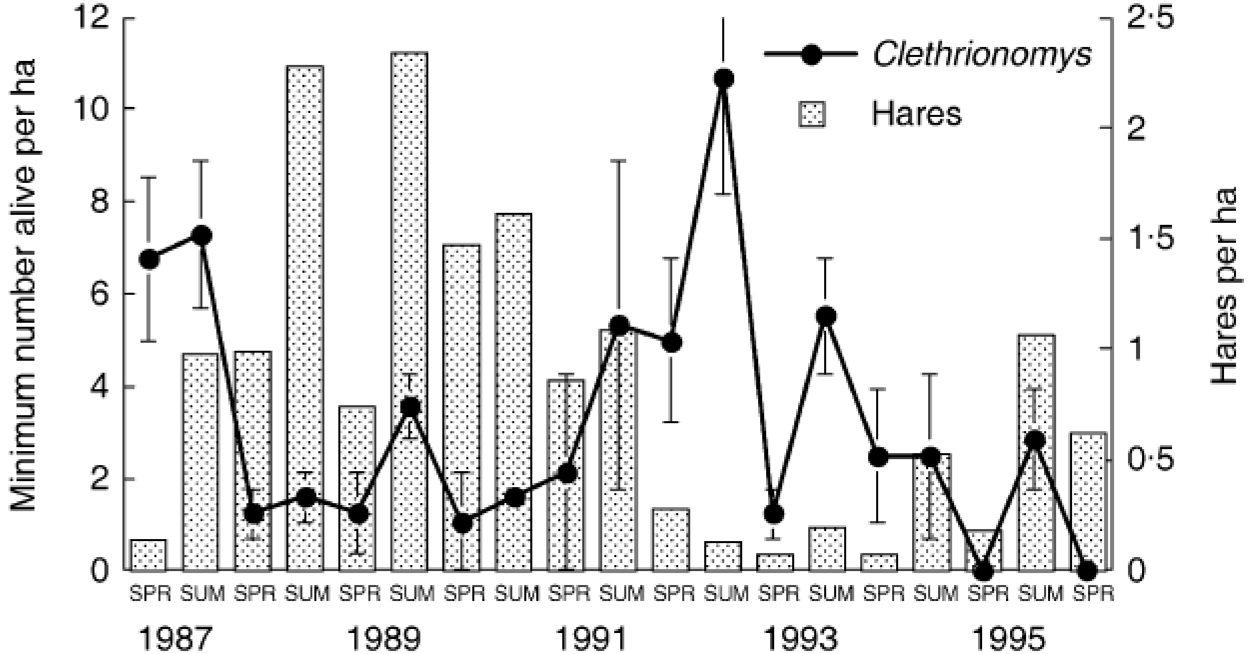


Fig. 1. Population changes of northern red-back voles on two control grids (means ± SE) from 1986 to 96 in south-western Yukon near Kluane Lake. Population changes of snowshoe hares (histograms) on control grids are presented for comparison.

Population limitation

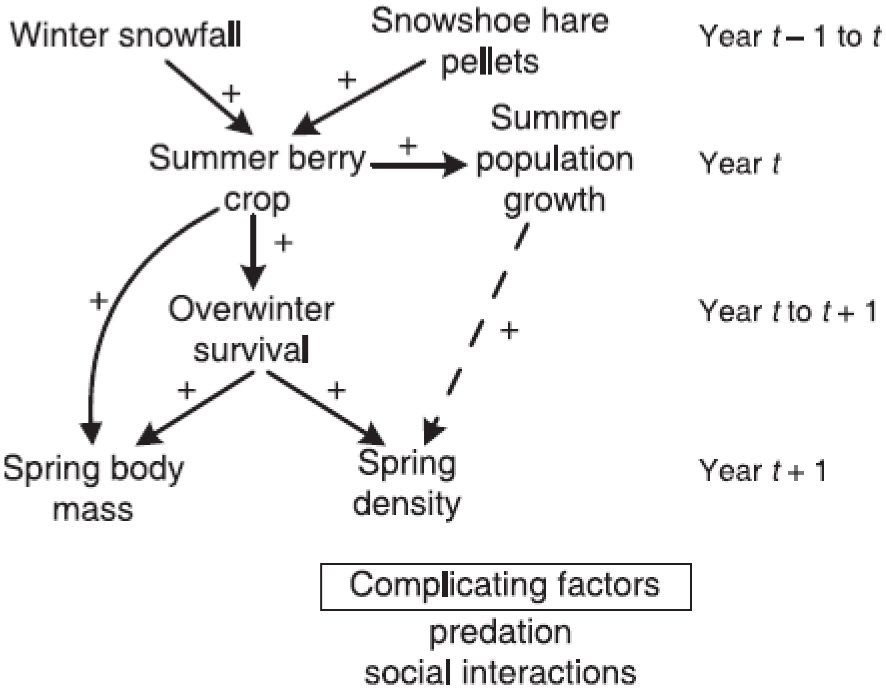


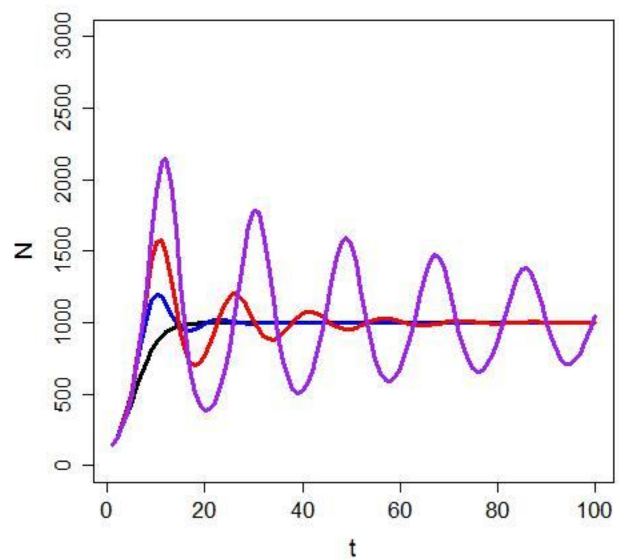
Fig. 6. Proposed model for population fluctuations in *Clethrionomys rutilus* from the boreal forest region of Canada and Alaska.

Population limitation

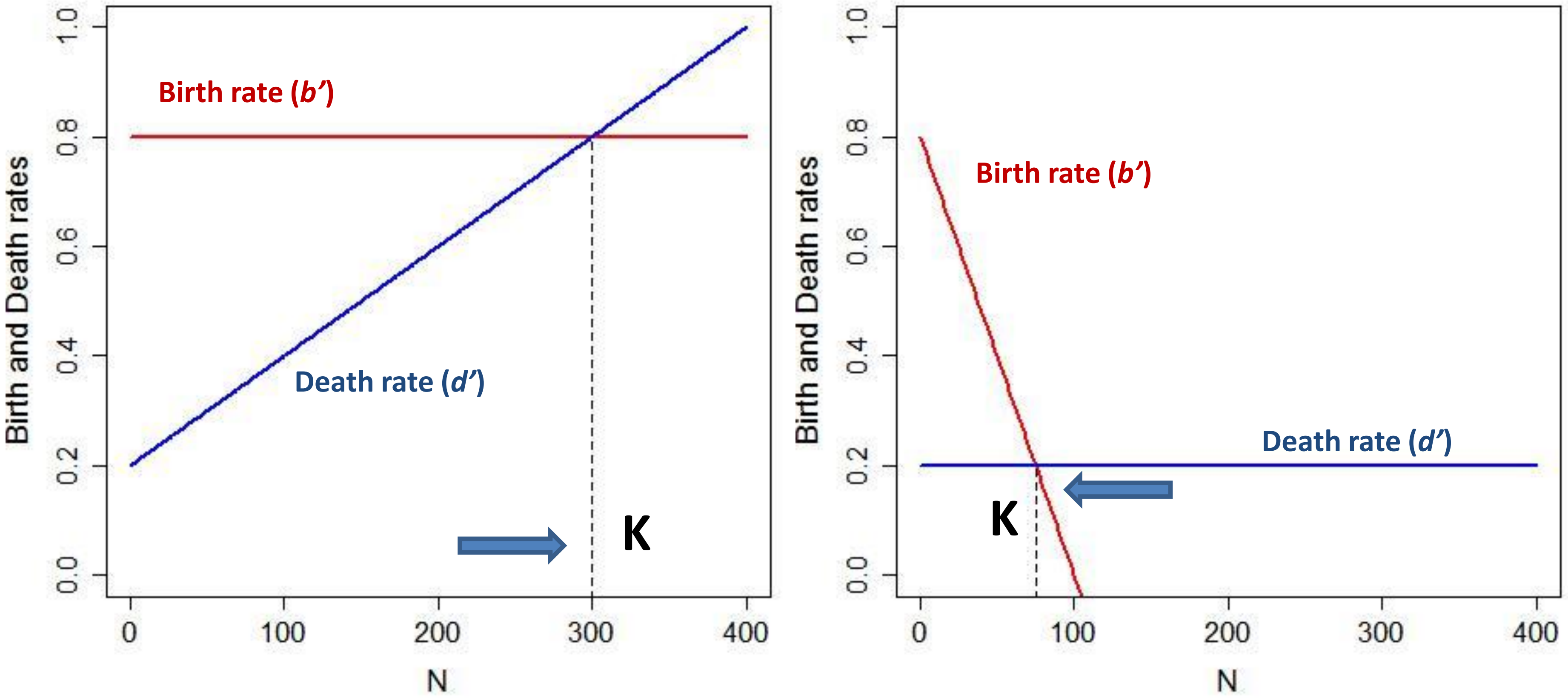
What other factors or processes would limit populations?

Population limitation and regulation

- Regulation:
  - A factor is defined to be a regulating factor if the percentage mortality caused by the factor increases with population density

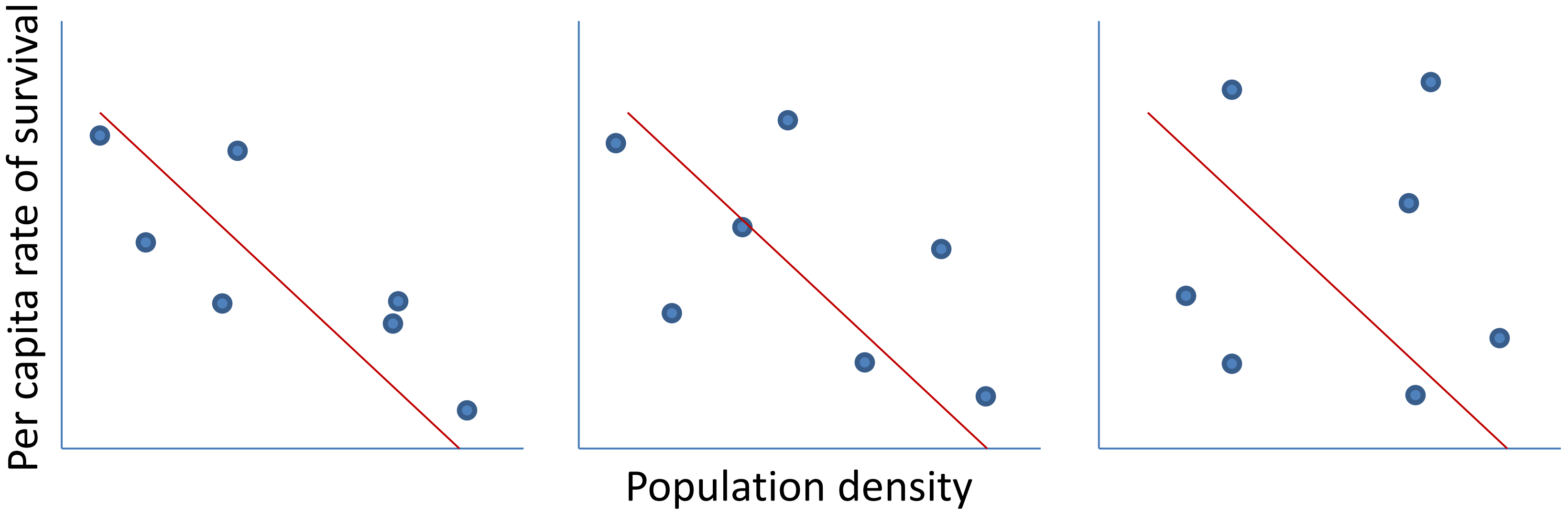


Regulation



Birth rate (b′)
Death rate (d′)
K
Birth and Death rates
N
0.0
0.2
0.4
0.6
0.8
1.0
0
100
200
300
400
Birth rate (b′)
Death rate (d′)
K
Birth and Death rates
N

Detecting population regulation



Detecting population regulation

1. Perturbation experiments
   - Manipulate population to decrease N (regulating factors are constant over time)
2. Relate variation in density of multiple populations to population growth rates
   - Regulated populations show decrease in growth rate with N (assume resources are constant across populations)
3. Relate individual populations to index of resource availability
   - Population growth is a function of resource/habitat.

Limitation vs. Regulation

- Food
- Weather
- Disease
- Cover
- Predation

Additive vs. compensatory mortality

How does natural mortality respond to exploitation?

Additive vs. compensatory mortality

- Compensatory mortality
  - Hunting reduces the number of individuals, reduces competition, and thus compensates for density-dependent mortality
  - Predation that does not affect the overall survival in a prey population
    - Merely replaces, or "compensates" for, existing sources of mortality.

Additive vs. compensatory mortality

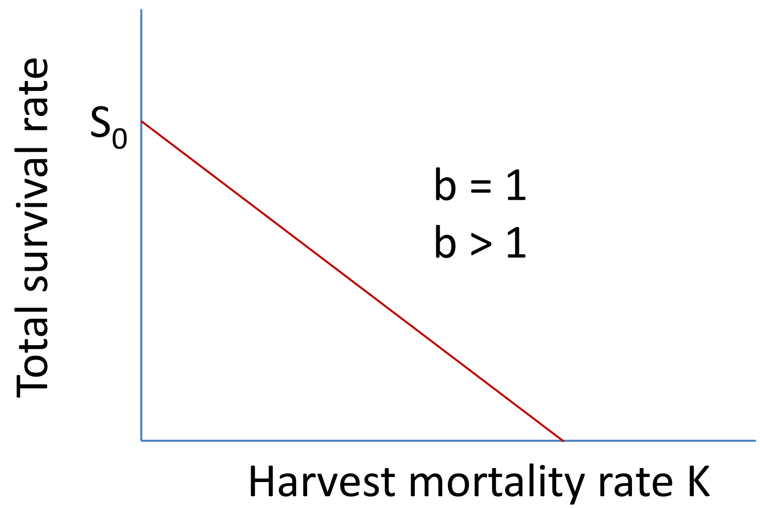
$$S_a = S_0(1 - bK)$$

- S_a = annual survival
- S_0 = baseline survival
- K = harvest mortality
- b = slope coefficient linking harvest mortality to annual survival

Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory Mortality in waterfowl populations: a review of the evidence and implications for research and management. Transactions of North American Wildlife and Natural Resources Conference 49:535-554.

Additive mortality

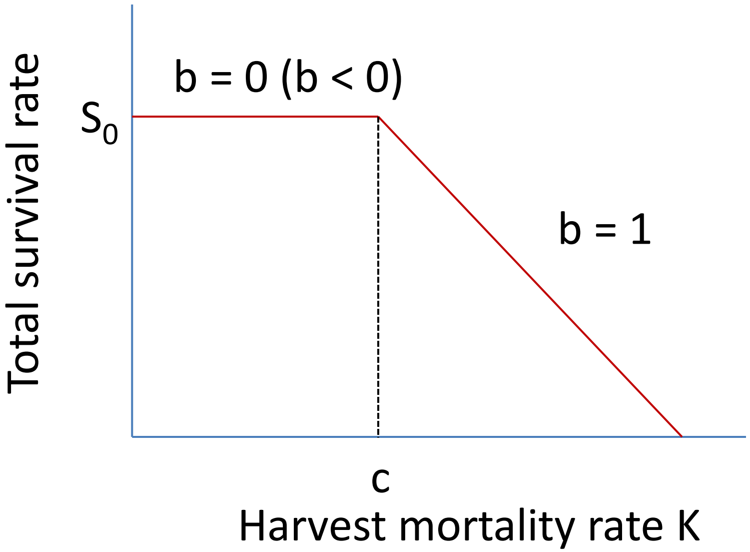
$$S_a = S_0(1 - bK)$$

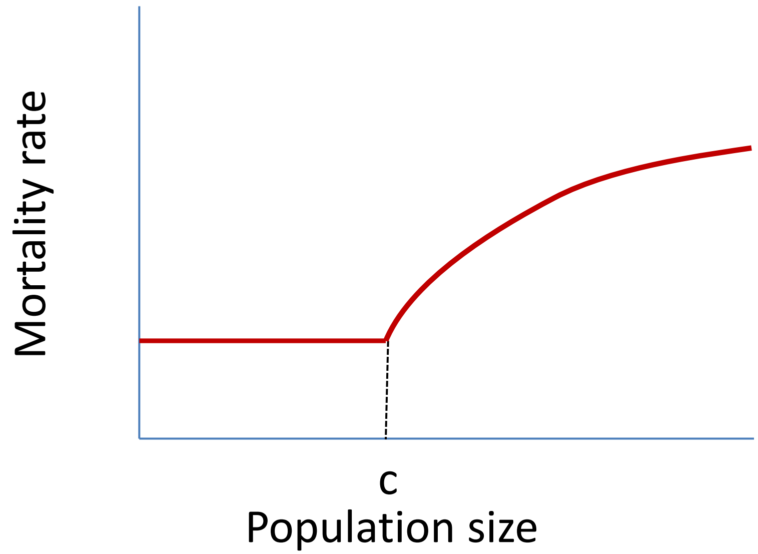


- One death from harvest is added to one natural death

Compensatory mortality

$$S_a = S_0(1 - bK)$$





- c = threshold below which compensatory mortality occurs
- $c = 1 - S_0$

Additive vs. compensatory mortality

Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 244–258 doi: 10.1111/j.1365-2656.2010.01769.x

Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan

Brett K. Sandercock[1,2]*, Erlend B. Nilsen[2], Henrik Brøseth[2] and Hans C. Pedersen[2]

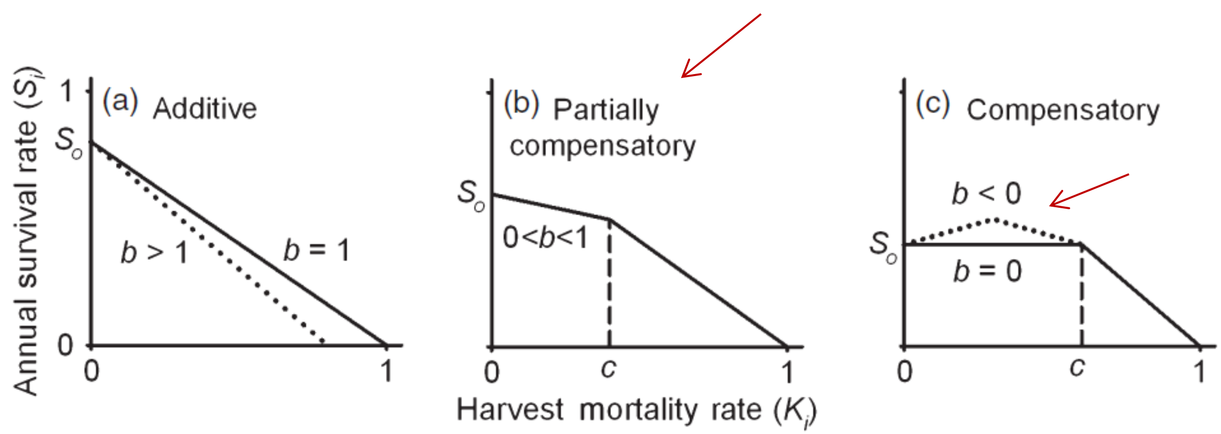
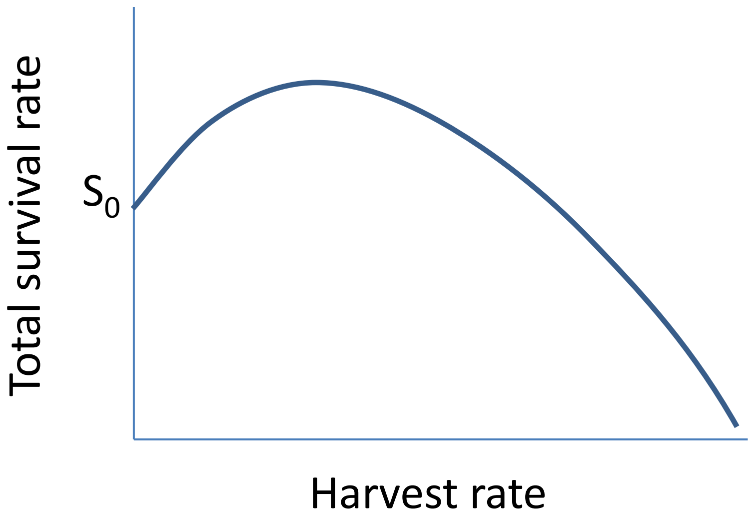


Fig. 1. Hypotheses for the effects of harvest mortality (K_i) on the annual survival (S_i) of exploited populations of animals. The (a) additive mortality hypothesis predicts that annual survival should decline with harvest ($b = 1$), the (b) partially compensatory mortality hypothesis predicts an intermediate response ($0 < b < 1$) and the (c) compensatory mortality hypothesis predicts that annual survival should be unaffected by harvest ($b = 0$), up to a threshold (c), determined by the complement of the baseline survival of an unharvested population ($c = 1 - S_o$). Models with sequential density dependence predict that the effects of harvest can be superadditive ($b > 1$) or lead to overcompensation ($b < 0$).

Overcompensation?



- Nicholson 1957
- Blowflies
  - Increase in adult mortality increased adult density if blowfly populations regulated by larval competition
- Agrawal 2000
- Plants
  - Overcompensation in seed production after herbivory

Additive vs. compensatory mortality

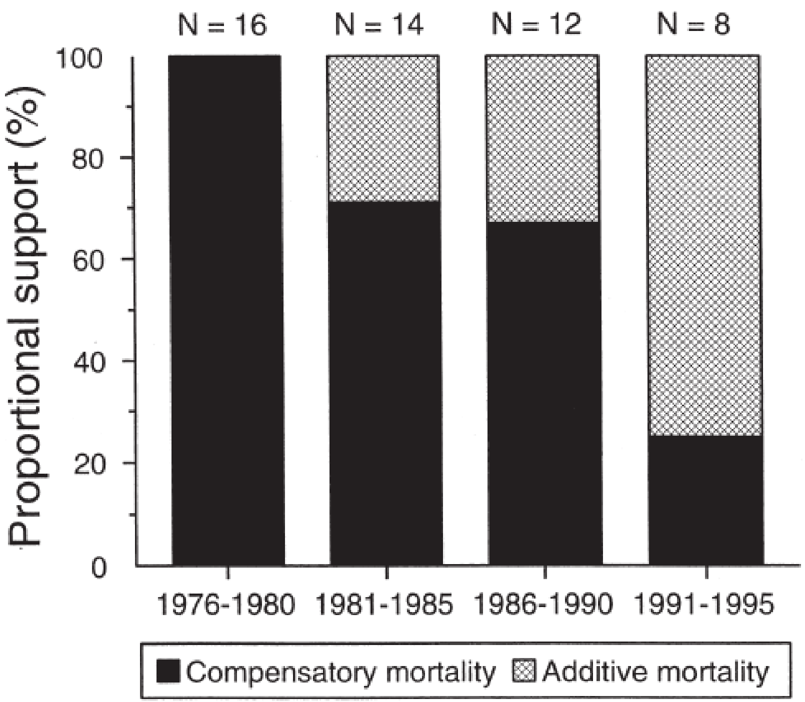


Fig. 1. Proportional support for the compensatory and the additive hunting mortality hypotheses in North American mallards from studies grouped into four time periods according to publication year. Total number of tests performed during each period is given above each column. See Table 1 for the original studies and the number of tests in each study.

Additive vs. compensatory mortality

Ecology, 90(10), 2009, pp. 2913–2921

Does hunting regulate cougar populations?
A test of the compensatory mortality hypothesis

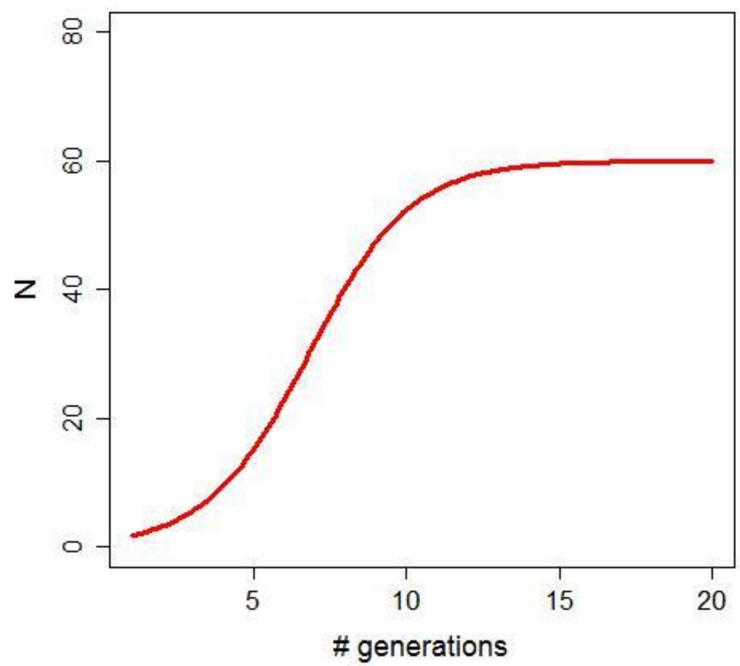
Hilary S. Cooley,[1,3] Robert B. Wielgus,[1] Gary M. Koehler,[2] Hugh S. Robinson,[1,4] and Benjamin T. Maletzke[1]

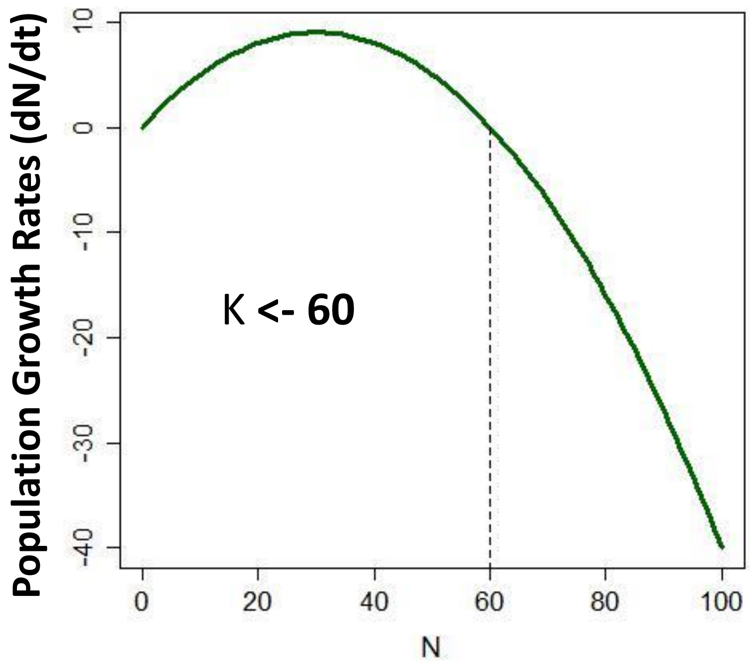
- Harvest mortality, particularly of adult males, triggers density-dependent responses in reproduction, offspring survival, and female population growth

- Vital rates did not compensate for hunting mortality

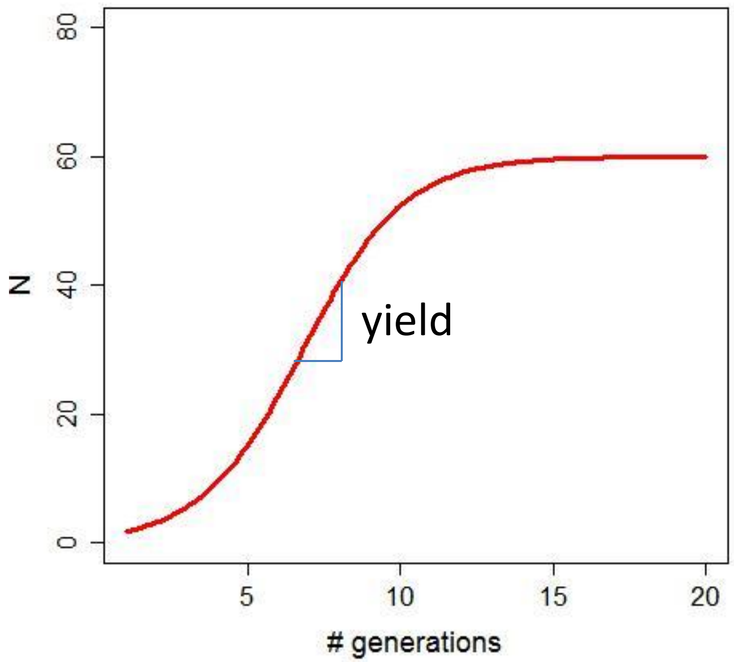
Density dependent mortality and sustainable yield

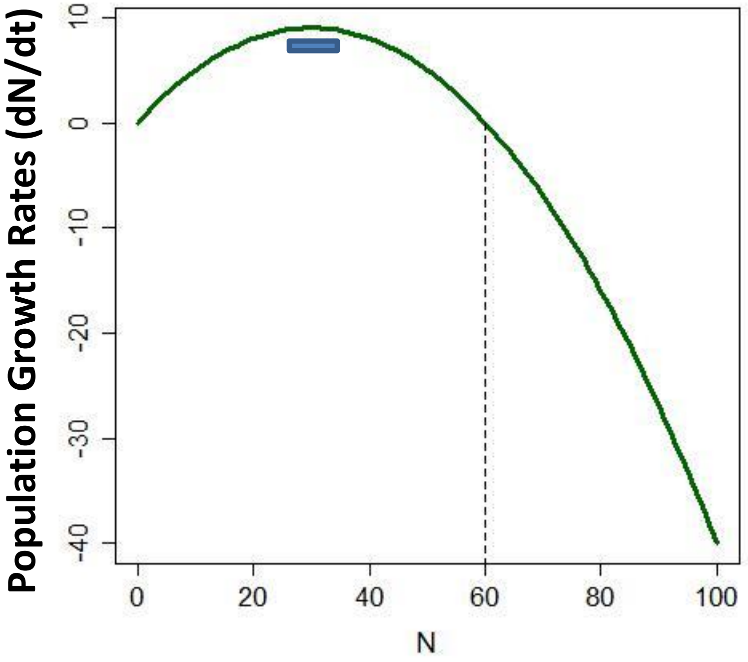
- Population growth under logistic population model





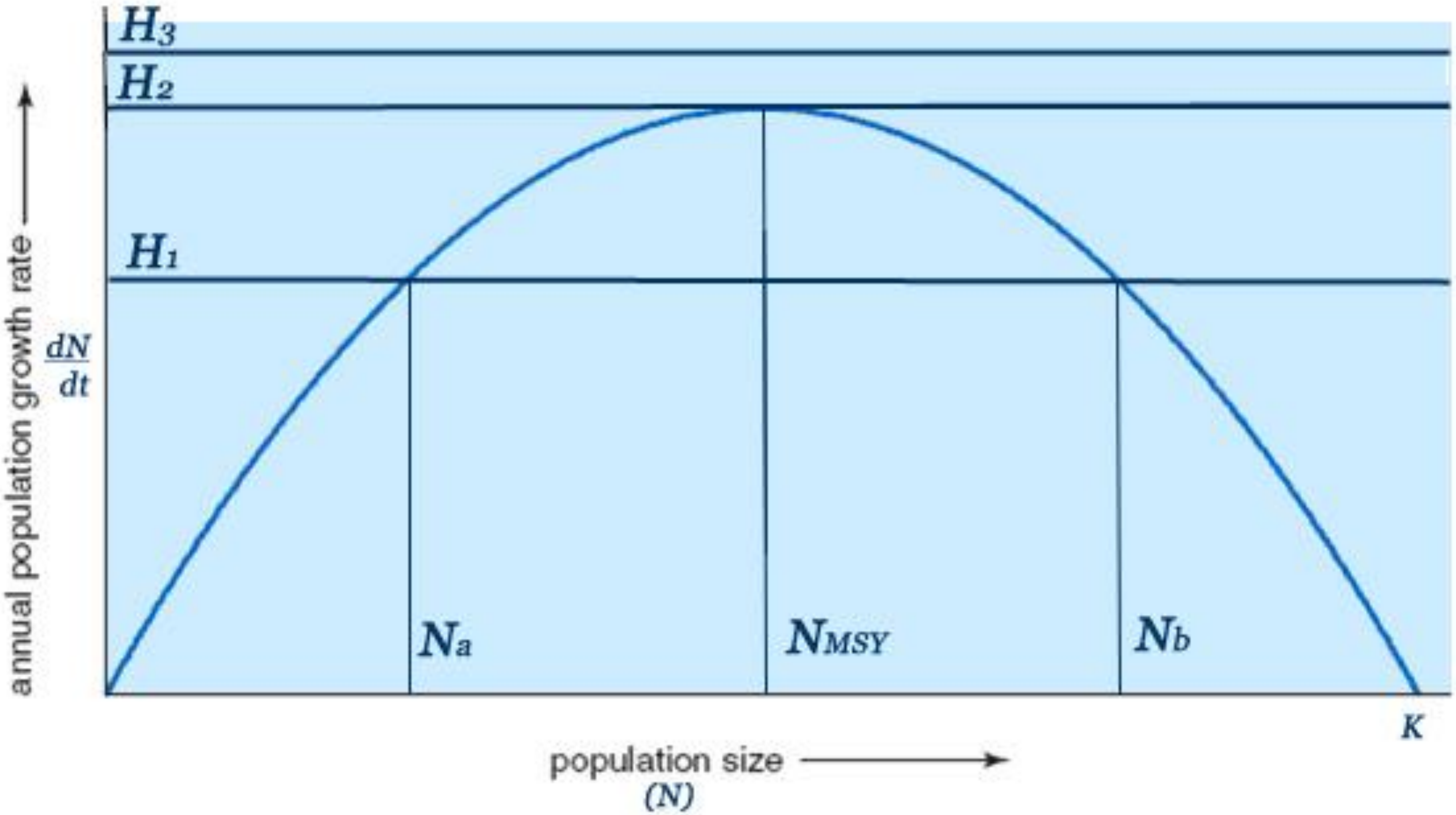
Optimal yield





- **Estimate Carrying Capacity**
- **Calculate Growth rate at point ½ Carrying Capacity.**
- **Maintain at population at N=K/2**
- **Set allowable harvest at dN/dt at this population size**
- ***Avoid overharvesting to drop population below N=K/2***

Optimal yield



- H = harvest rate
  - Estimated optimal sustainable yield
  - H_2 theoretical optimal harvest rate

$$H = \frac{Kr}{4}$$