

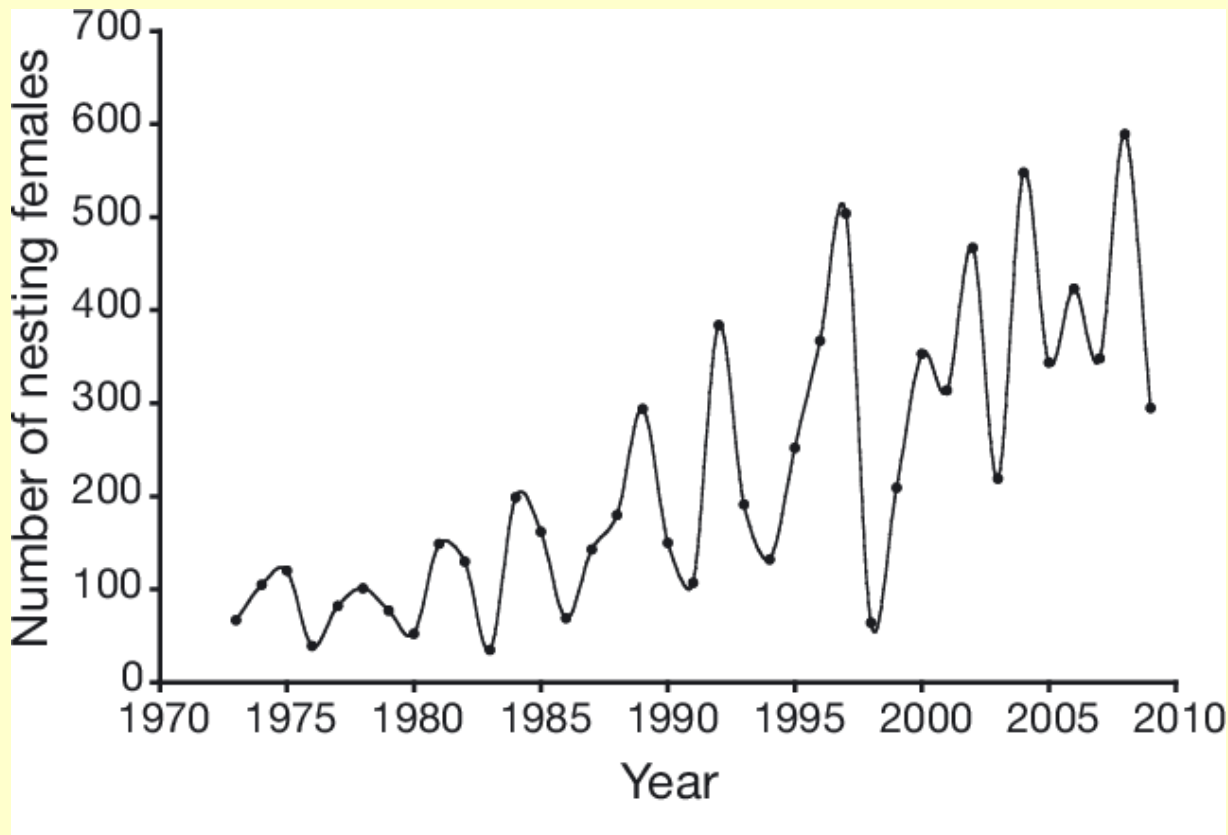
Theory and Math of Modelling Carrying Capacity



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Motivation

1. Review theory and math of carrying capacity.
2. Highlight two challenges to apply this concept.



Estimated number of green turtles nesting on East Island, French Frigate Shoals, 1973-2009

(Tiwari et al. 2010)

Carrying Capacity in Ecology

Definition 1: Basic Ecology

Maximum population size (number or organisms) that can be supported **indefinitely** by a given environment.

- Simple definition
- Complex application

Sliding Baselines and Anecdotes

Table 2. Historical accounts of the early great abundance of green turtles in the Caribbean

Reefs before Columbus **(Jackson 1997)**

Andres Bernaldez, writing about Columbus' 2nd voyage in 1494	Southeastern Cuba	But in those twenty leagues, they saw very many more, for the sea was thick with them, and they were of the very largest, so numerous that it seemed that the ships would run aground on them and were as if bathing in them.
Ferdinand Columbus, writing about the 4th voyage in 1503 ^a	Cayman Islands	... in sight of two very small and low islands, full of tortoises, as was all the sea about, insomuch that they looked like little rocks ...
Edward Long (1774), writing of the late 1600s	West of the Cayman Islands	... it is affirmed, that vessels, which have lost their latitude in hazy weather, have steered entirely by the noise which these creatures make in swimming, to attain the Cayman isles.

^anot seen, cited in Lewis 1940

How many sea turtles lived in the Caribbean in 1492?

Historical catches **(6.5 million)**

Carrying capacity models **(660 million)**

Implications: Management & Conservation

Conceptual Framework

- Relationship between population growth and resource availability (assume limiting resources).
- Limiting factors: food, space, water (predation and competition).

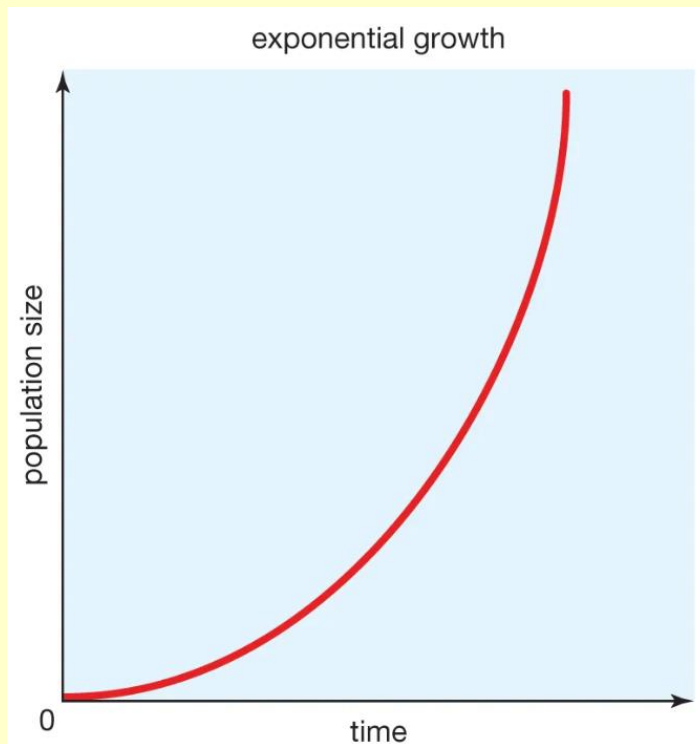
Application for Understanding Carrying Capacity

- Estimate resources necessary per individual.
- Calculate number of individuals supported.

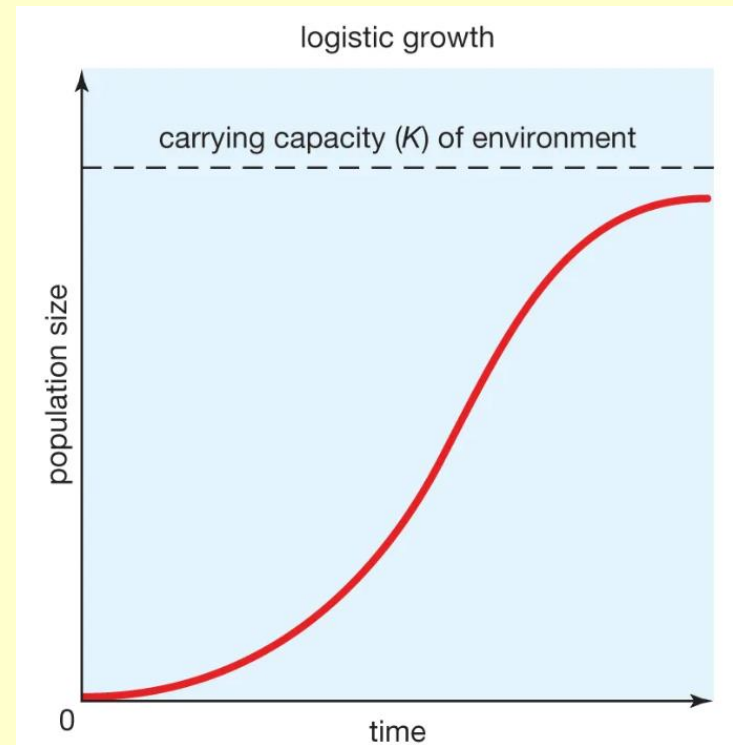
Carrying Capacity Definitions

Definition 2: Population Dynamics

Equilibrium population size where birth rate equals death rate due to density dependent processes.



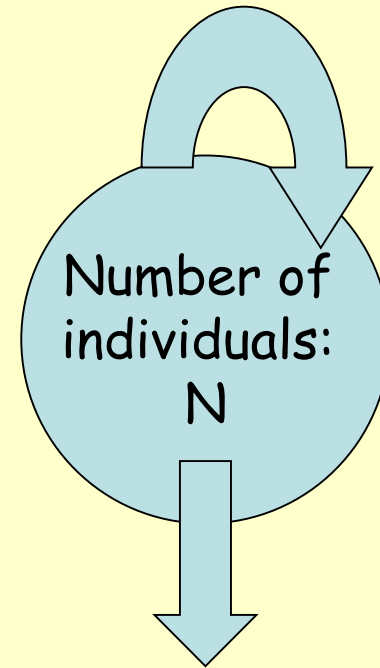
Exponential



Logistic

Modelling Population Growth

Change in population
(plus births, minus deaths)



**Birth
rate:
bN**

**Death
rate:
dN**

$$dN / dt = (bN) - (dN) = (b - d) * N$$

$$dN / dt = (bN) - (dN) = r * N$$

Carrying Capacity (K)

Logistic growth model
(Pearl & Reed, 1920):

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

N : population size or density

r : intrinsic rate of increase

(maximum per capita growth rate in absence of competition)

Expression in brackets: density-dependent growth potential:

~ 1 at low N (logistic growth \rightarrow exponential growth)

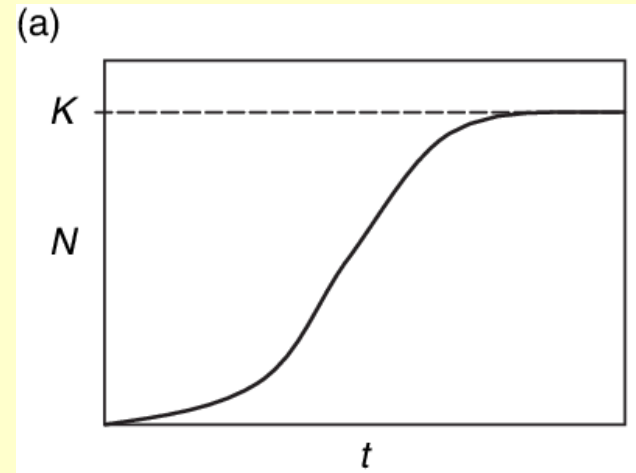
~ 0 when $N = K$, where population growth ceases.

Carrying Capacity (K)

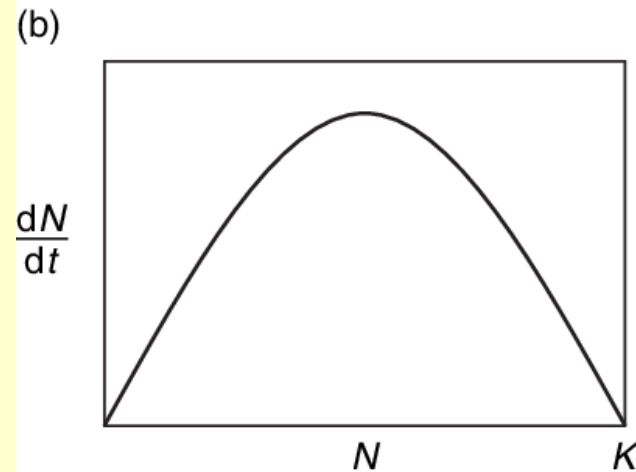
Logistic growth model
(Pearl & Reed, 1920):

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

(a) Logistic population growth model, shows population size (N) leveling off at a fixed carrying capacity (K) over time (t).



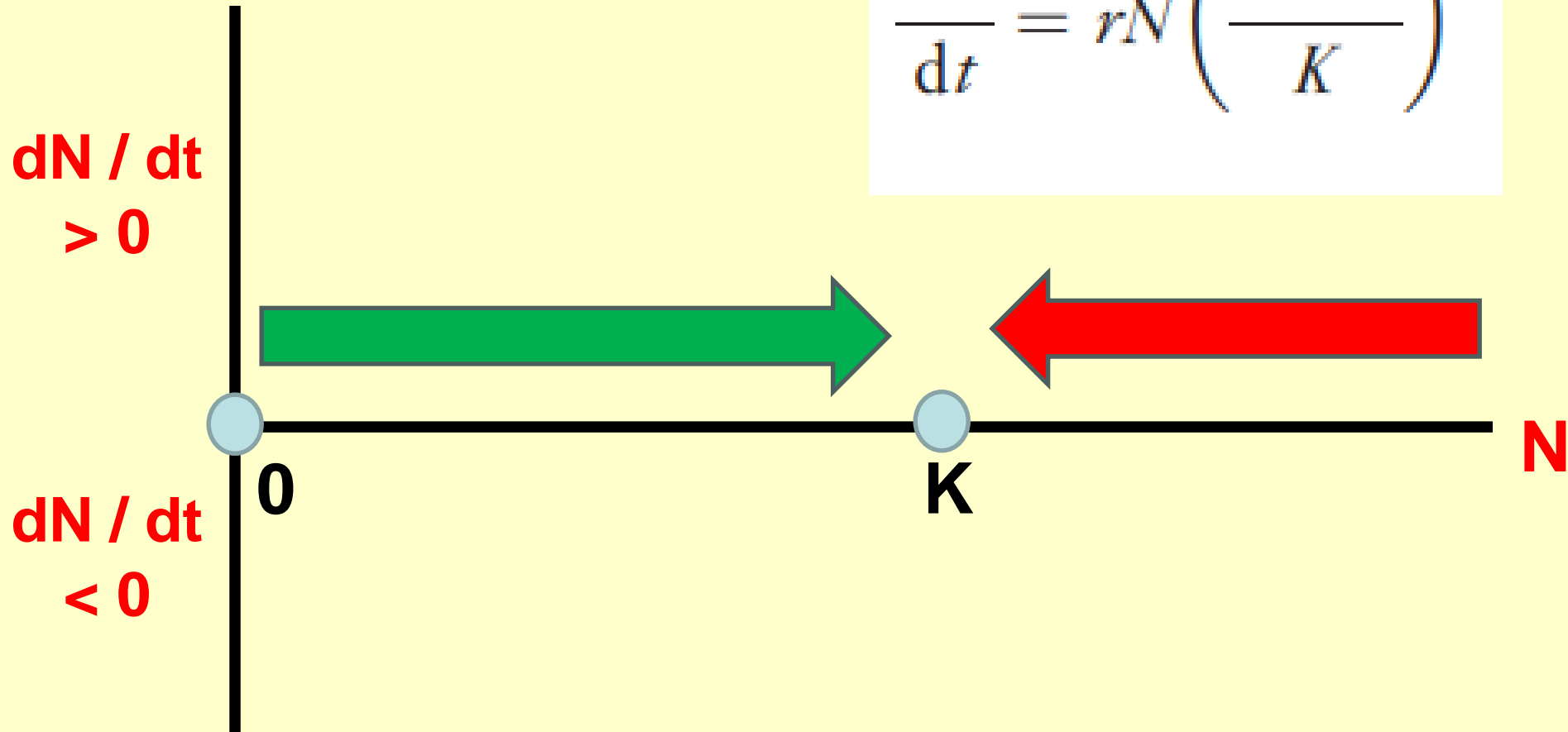
(b) Logistic population growth rate (dN/dt) as function of population size. The growth rate peaks at $N = 0.5 K$ and equals zero at $N = K$ and $N = 0$.



Carrying Capacity (K)

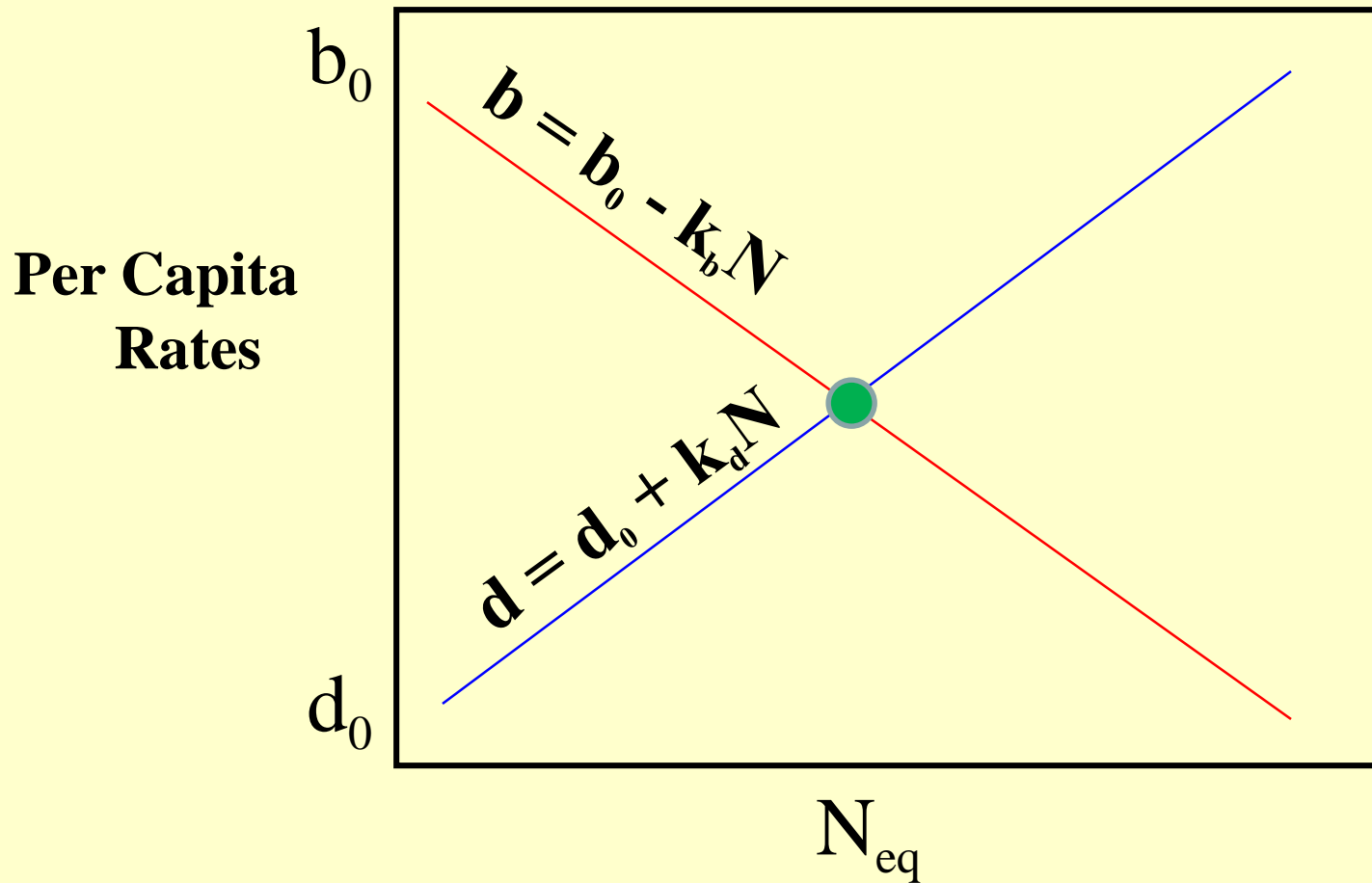
Logistic growth model (Pearl & Reed, 1920):

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

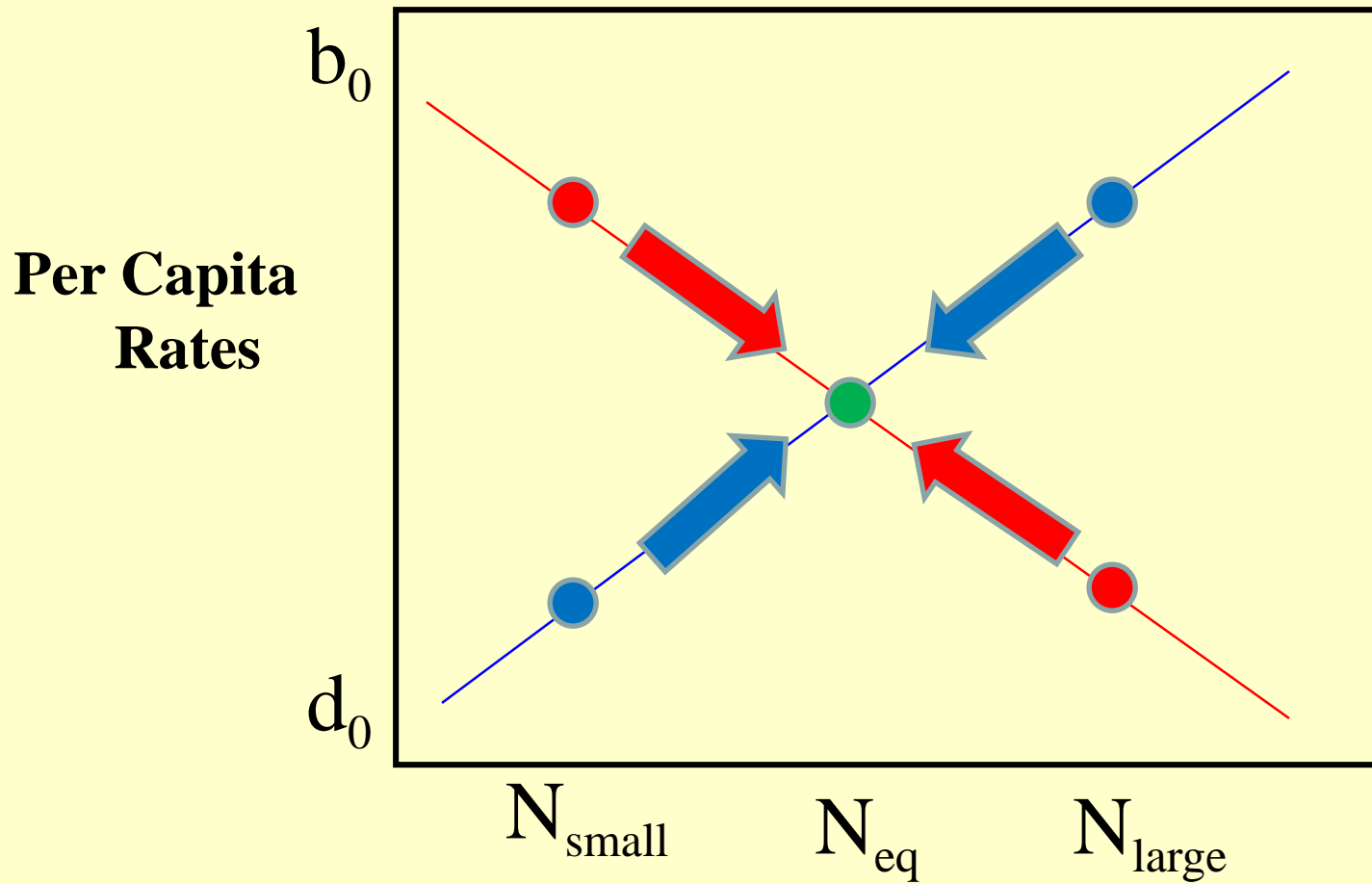


K affects birth / death rates

$N = K$ is a stable equilibrium



Stable Equilibrium Point



Implications: Management & Conservation

Conceptual Framework

- Focus on dynamics rather than static value.
- Equilibrium between death and birth rates.

Application for Understanding Carrying Capacity

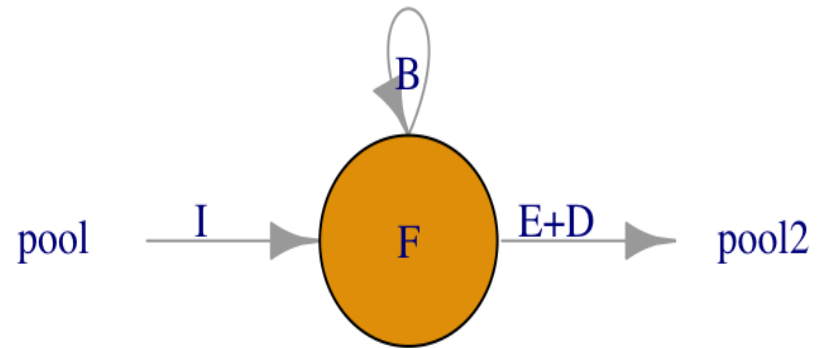
- Empirical evidence of density dependence.

Carrying Capacity Definitions

Definition 3: Average population size over time.

Birth and death rates need not be equal, if there is migration (unlike logistic model).

Despite population fluctuations, no change in "average" population abundance over time.



$$\frac{\Delta N}{\Delta t} = \frac{B + I - D - E}{\Delta t}$$

Implications: Management & Conservation

Conceptual Framework

- Focus on abundance.
- Equilibrium of death and birth and emigration.

Application for Understanding Carrying Capacity

- Empirical evidence of population stability.
- No abundance trend over time.



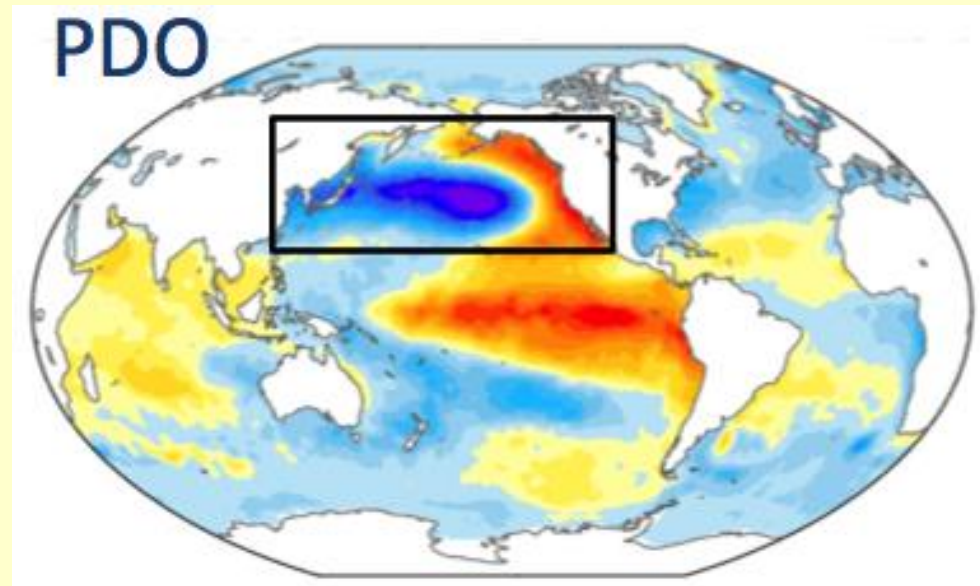
Mass-nesting by olive ridley sea turtles at Ostional, Costa Rica. Photograph by Vanessa Bézy.

Challenges - Equilibrium Points

Simple population models can produce complex (unpredictable) behavior.



Ocean's dominant physical forcing is "red" (long wavelength low frequency)



Logistic Growth Without K

Nature **261** 459–67 (1976)



Simple mathematical models with very complicated dynamics

Robert M. May*

First-order difference equations arise in many contexts in the biological, economic and social sciences. Such equations, even though simple and deterministic, can exhibit a surprising array of dynamical behaviour, from stable points, to a bifurcating hierarchy of stable cycles, to apparently random fluctuations. There are consequently many fascinating problems, some concerned with delicate mathematical aspects of the fine structure of the trajectories, and some concerned with the practical implications and applications. This is an interpretive review of them.

$$N_{t+1} = a * N_t * (1 - b * N_t)$$

Logistic Growth Without K

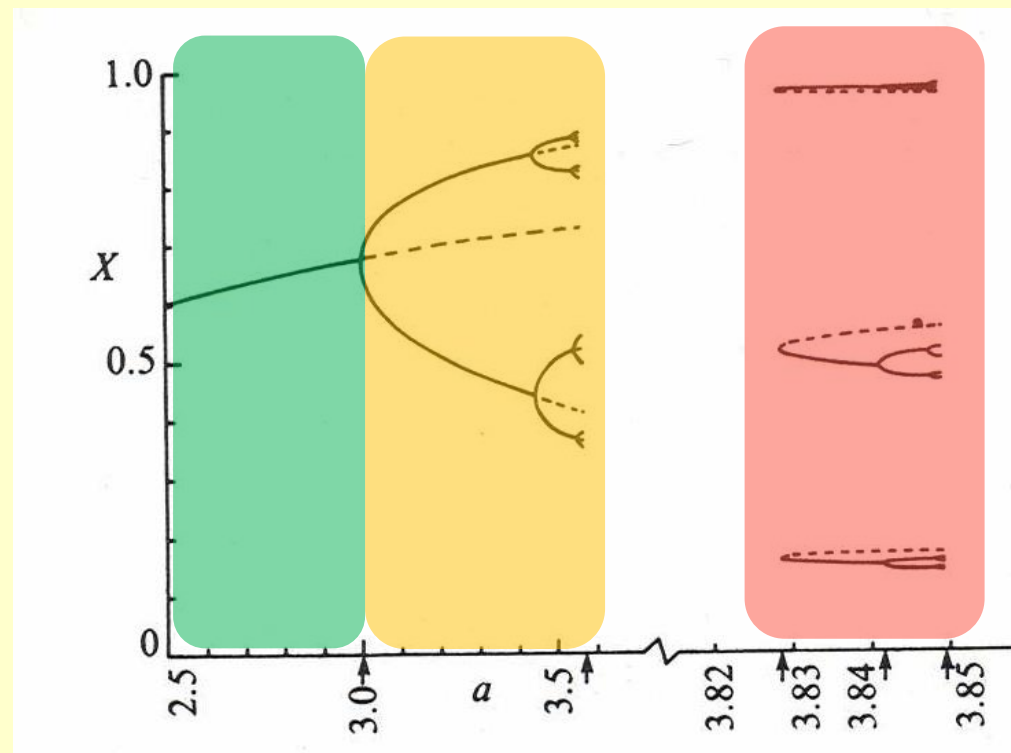
$$N_{t+1} = N_t * a * (1 - b * N_t)$$

$a = \text{Lambda}$

$b = \text{density dependence}$

As population growth rate (a) increases... something odd happens

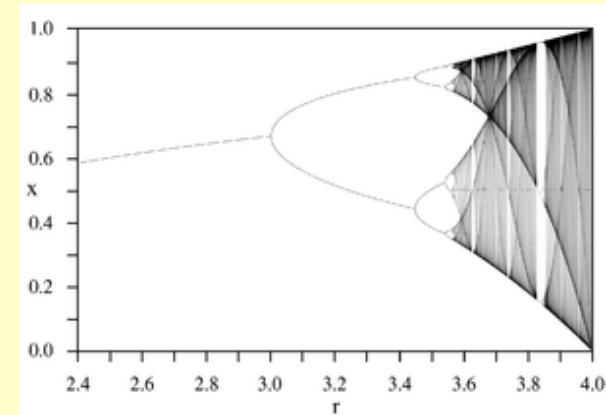
Deterministic model causes unpredictable chaotic behavior



Implications: Management & Conservation

- Single populations cycle (without predators / prey)
- Initial conditions influence predictive capability
- If natural processes (e.g., precipitation, storms) are chaotic... populations tracking these physical drivers may also follow chaotic patterns indirectly

Main Idea: Deterministic nature of many natural systems does not make them predictable.



Low Frequency Physical Forcing

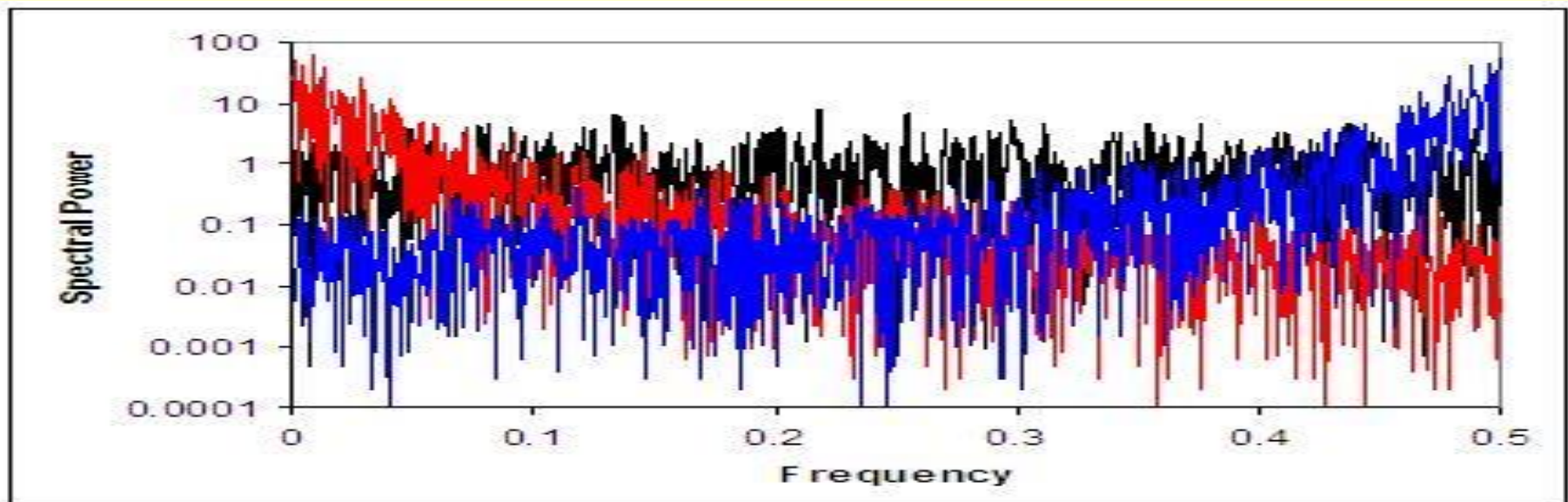
A comparison of terrestrial and marine ecological systems

John H. Steele

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

I review here the differences between temporal variability in terrestrial and marine environments and consider how this external forcing may affect population fluctuations in the two systems. The internal dynamics and community responses are expected to differ significantly with marine populations more likely to show longer term changes between alternative community structures.

(Steele 1985)



Implications of a "Red" Ocean

Many marine species undergo periodic (large wavelength) oscillations even without harvest.

Species dynamics recreated with simple models, when forcing frequency less than population response rate (r).

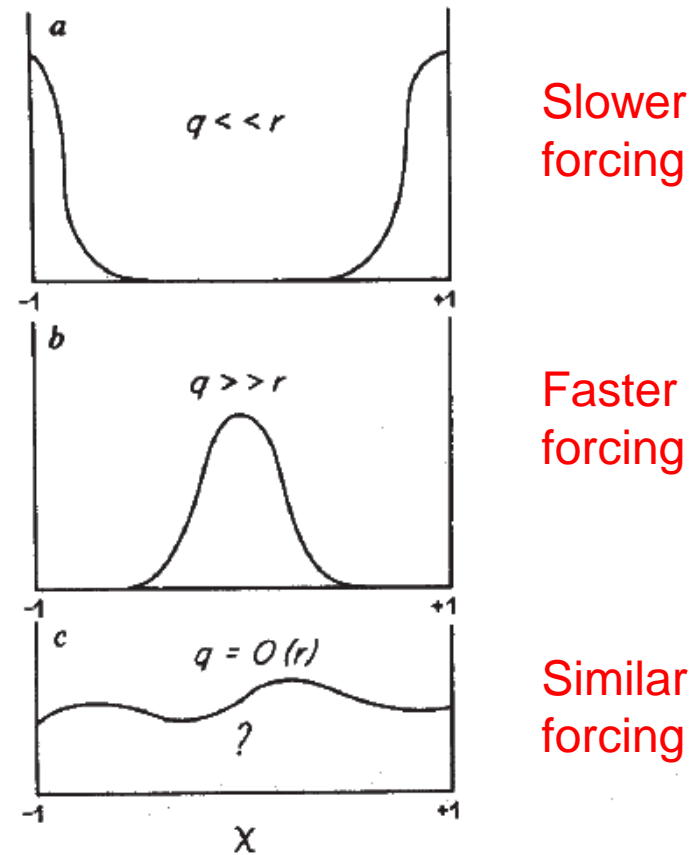


Fig. 4 Response of a two-equilibria system to stochastic forcing at frequencies: *a*, much less than and *b*, much greater than the intrinsic response rate of the system. *c*, Indeterminacy of the system when the rates are comparable.

(Steele 1985)

Decadal Oscillations

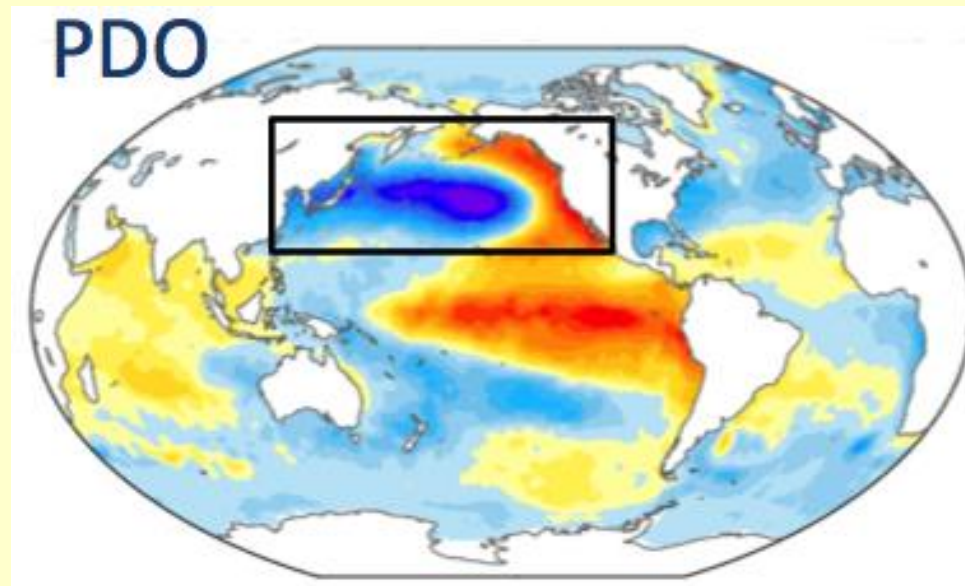
FISHERIES OCEANOGRAPHY

Fish. Oceanogr. 3:1, 15–21, 1994

Physical and biological consequences of a climate event in the central North Pacific (Polovina et al. 1994)

JEFFREY J. POLOVINA,^{1,2} GARY T. MITCHUM,² NICK E. GRAHAM,³ MITCHELL P. CRAIG,¹ EDWARD E. DEMARTINI¹ AND ELIZABETH N. FLINT⁴

important goal in marine science, and now, with concerns over climate change, is even more critical. However, given the lack of coherent climate and ecosystem data sets, most studies have relied only on fishery data



(Mantua et al. 1997)

Conclusions

Basic Definition:

Maximum population size (number that can be supported indefinitely by a given environment).

Updated Definition:

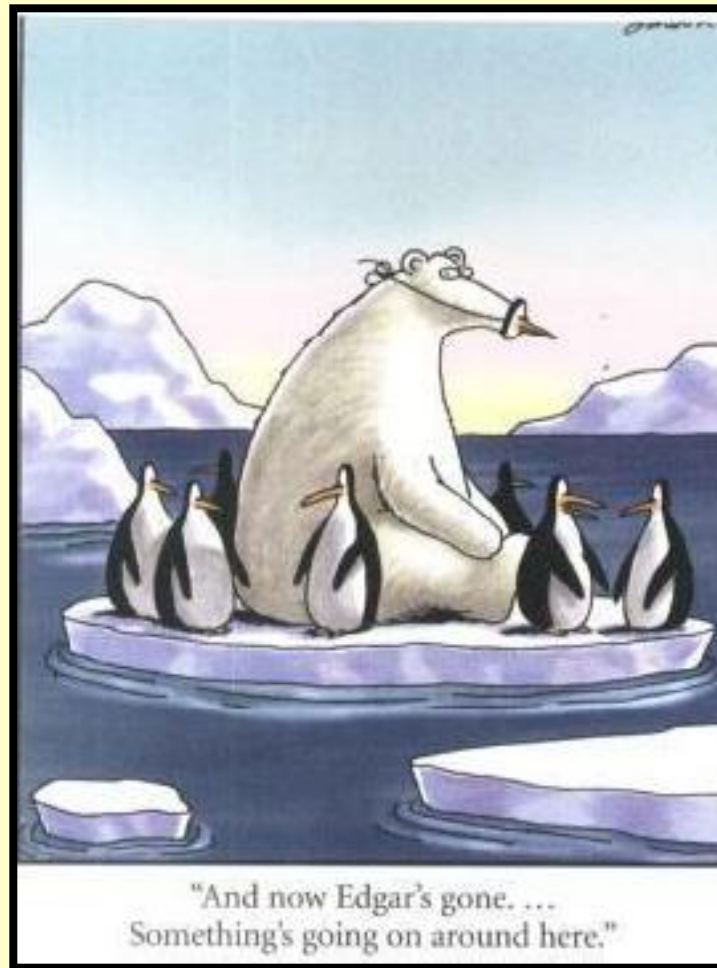
Average population size over time.

Birth and death rates.

Emigration, Range Expansion.

New Resources, New Behaviors.

Conclusions



Are vital rates (or behavior) influenced by number of individuals in population ?

Population Growth Model Assumptions

(Hastings et al. 2011)

1. **Closed Population:** migration in /out of population.
2. **Homogeneous Population:** All individuals identical.
(All we need to know is the number of individuals)

Thus, the number of offspring per individual
(or the per capita birth and death rates) are:

- (i) constant through time, and
- (ii) independent of population size.

Fishery Implications - MSY

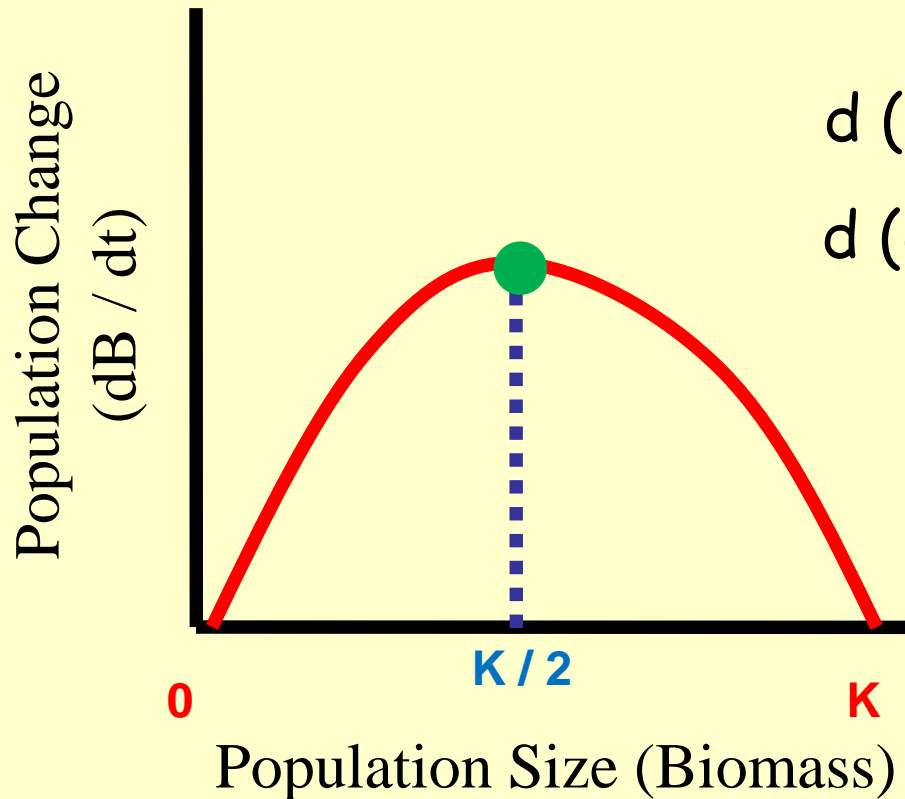
Assumptions: *Static Carrying Capacity, No Stochasticity*

Finding Maximum: **(slope = 0)**

Derivative of B with respect to B

$$dB / dt = r B (B - K)$$

$$dB / dt = rBB - rBK$$



$$d (dB / dt) / dB = 2rB - rK$$

$$d (dB / dt) / dB = r * (2B - K)$$

How do we make
 $d (dB / dt) / dB = 0$?

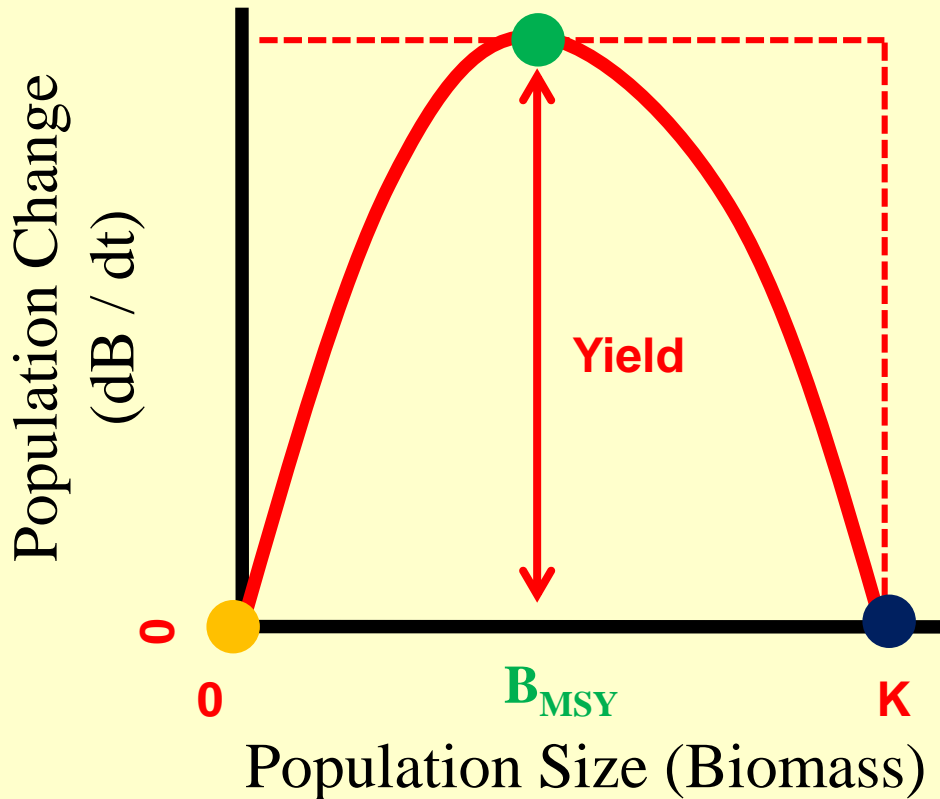
$$(2B - K) = 0$$

$$(B = K / 2)$$

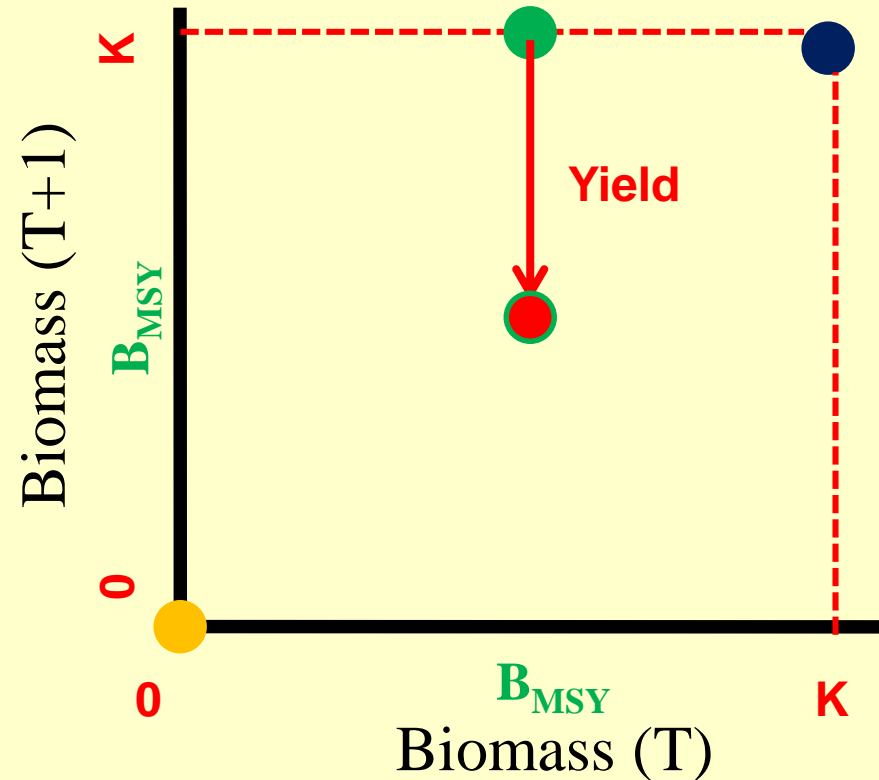
Fishery Implication - MSY

Relates current biomass and yield to the optimum yield that could be sustained indefinitely

Recruitment Curve



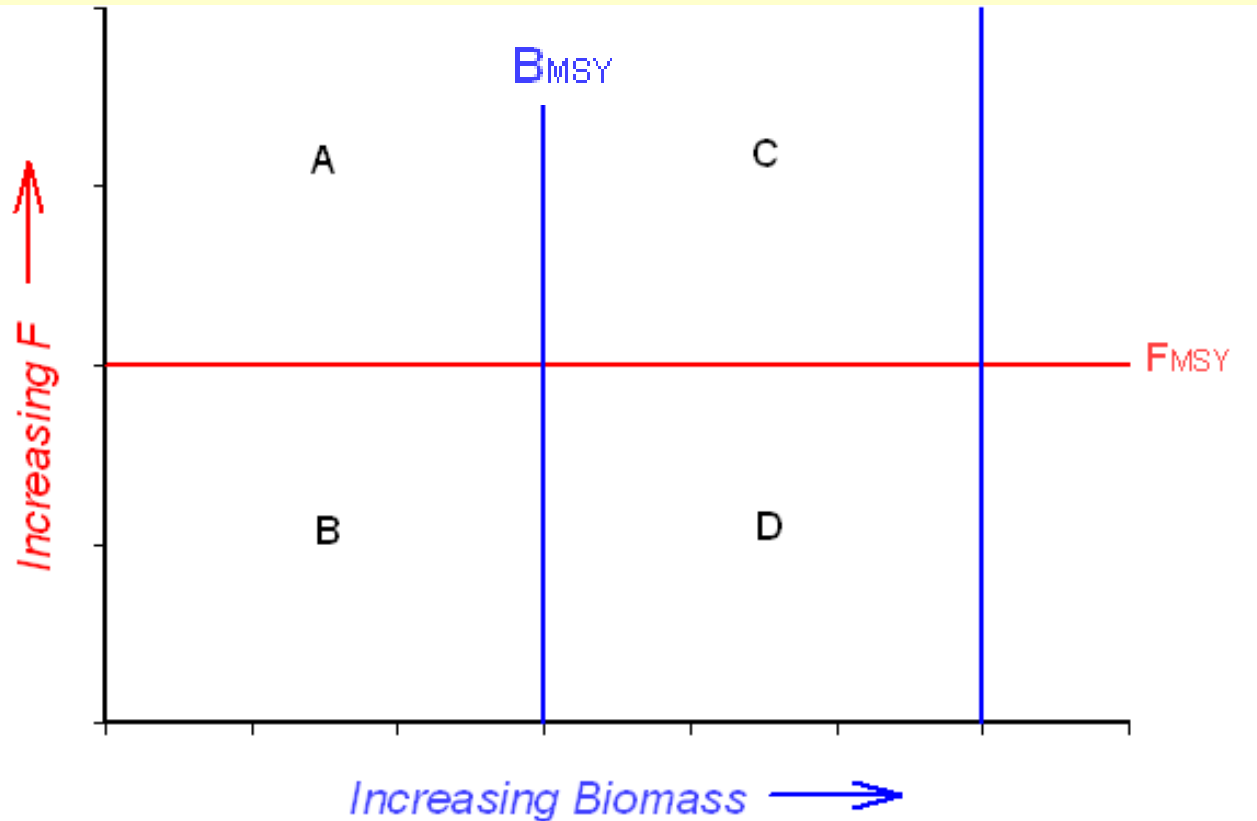
Phase Diagram



Fishery Implications: MSY

$K/2$

K



Overfishing:
Defined by
fishing
mortality (F)

**Overfished
Stock:**
Defined by
stock
biomass (B)

- A. Overfishing is occurring; stock is overfished
- B. Overfishing is not occurring; stock is overfished
- C. Overfishing is occurring; stock not overfished
- D. Overfishing is not occurring; stock is not overfished

(www.nefsc.noaa.gov)