# The Paradox of Enrichment:

## A fortifying concept or just well-fed theory?

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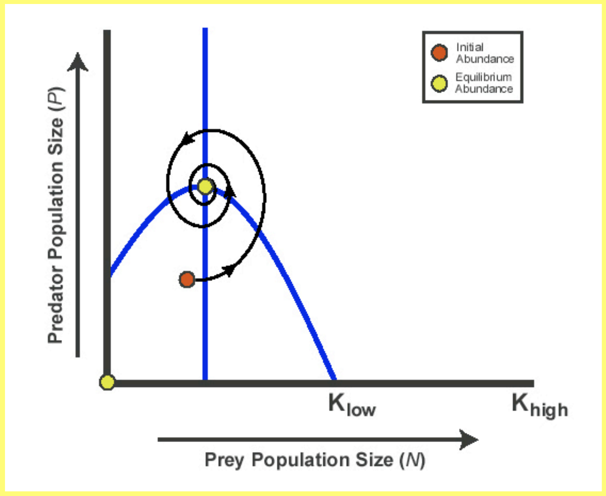
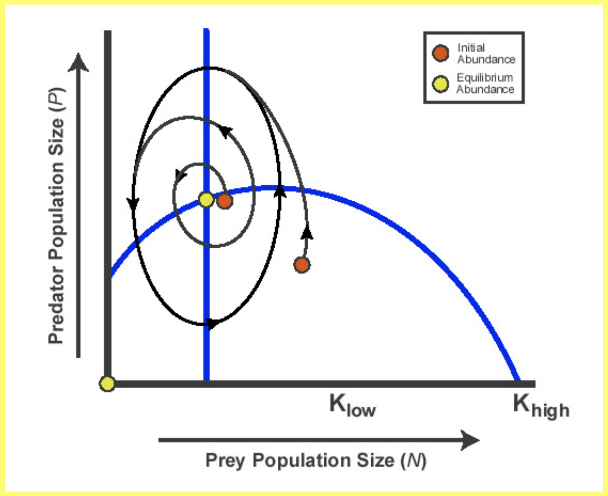
# The Paradox of Enrichment:




*"increasing the supply of limiting nutrients or energy tends to destroy the steady state"*

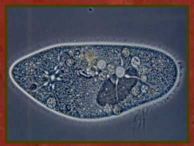
**(Rosenzweig 1971)**

# Evidence for the Paradox of Enrichment?

- Aquatic eutrophication
- Enrichment experiments
- *Paramecium-Didinium* experiments

# Why don't we see the Paradox of Enrichment?

1. Natural systems (and many laboratory systems) are too complex to show this simple phenomenon.
2. The underlying theory that produces the PoE is wrong.



Experiments needed!

# The *Paramecium-Didinium* system:

*Paramecium caudatum*

*Didinium nausatum*

- Meets major assumptions of simple predator-prey models:
  - Closed system
  - Can be maintained without heterogeneities/refugia
  - Single prey/single obligate predator
  - Prey food can be delivered as semi-continuous constant input

# Problems with *Paramecium-Didinium* data as evidence for the Paradox of Enrichment:

1. Does not conform to simple PoE explanation
2. Changes in prey nutrient input have been shown to change other parameters ($e$, $h$, $a$)

(Luckinbill 1973, Veilleux 1979)

# Alternative Models of Predation:

*Functional Responses:*

$$f\,(\mathrm{N}) \longleftrightarrow f\,(\mathrm{N/P})$$

*"Prey Dependent"*

*"Ratio Dependent"*

# Comparison of prey- vs. ratio dependent outcomes:

| Change in Parameter | Prey-Dependent Outcome | Ratio-Dependent Outcome |
|---|---|---|
| ***a*** ↓ (encounter rate) | DE → CoEx → PE | DE → PE; or DE → CoEx |
| ***K*** ↓ (carrying capacity) | DE → CoEx → PE | ***no change*** |
| ***r*** ↓ (prey growth rate) | ***no change*** | CoEx → DE |
| ***d*** ↓ (pred. death rate) | PE → CoEx → DE | PE → CoEx → DE |
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**Proportional removal of prey will decrease $r$ & $K$ without changing other parameters:**

$$dN/dt = r_0N\,(1 - N/K) - pN$$

$$r_p = (r_0 - p)$$

$$K_p = K(1 - p/r_0)$$

# Comparison of prey- vs. ratio dependent outcomes:

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|---|---|---|
| ***a*** ↓ (encounter rate) | DE → CoEx → PE | DE → PE; or DE → CoEx |
| Increasing levels of enforced proportional mortality (*p*) | DE → CoEx → PE | CoEx → DE |
| ***d*** ↓ (pred. death rate) | PE → CoEx → DE | PE → CoEx → DE |
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# Experiment: ***PoE in reverse***

$H_P$ = increasing ***p*** (*i.e.* reducing ***K***) in a stable system should **maintain stability**.

[prey-dependent prediction]

$H_R$ = increasing ***p*** (*i.e.* reducing ***r***) in a stable system should **destabilize the system**.

[ratio-dependent prediction]

# Experiment: ***PoE in reverse***

1. Using manipulations of methyl cellulose and prey nutrient input, find conditions under which long-term coexistence occurs
2. Impose proportional mortality of prey in as continuous a manner as possible
3. Continue to increase proportional mortality until *dual extinction* can be achieved
4. If dual extinction occurs, use a prey-only system with the same conditions to determine if the proportional mortality level at which *dual extinction* occurs corresponds to $r < 0$ or $r > 0$

# Experiment: ***PoE forward***

$H_R$ = decreasing ***p*** (*i.e.* increasing ***r***) in a stable system should **maintain stability**.

[ratio-dependent prediction]

$H_P$ = decreasing ***p*** (*i.e.* increasing ***K***) in a stable system should **destabilize the system**.

[prey-dependent prediction]

# Experiment: ***PoE forward***

1. Begin with a system where high proportional mortality is being enforced
2. Using manipulations of methyl cellulose and prey nutrient input, find conditions under which long-term coexistence occurs
3. Increase *r* by incrementally releasing the system from enforced proportional mortality
4. Continue to decrease proportional mortality until *dual extinction* can be achieved
5. Note the problem here with having to prove

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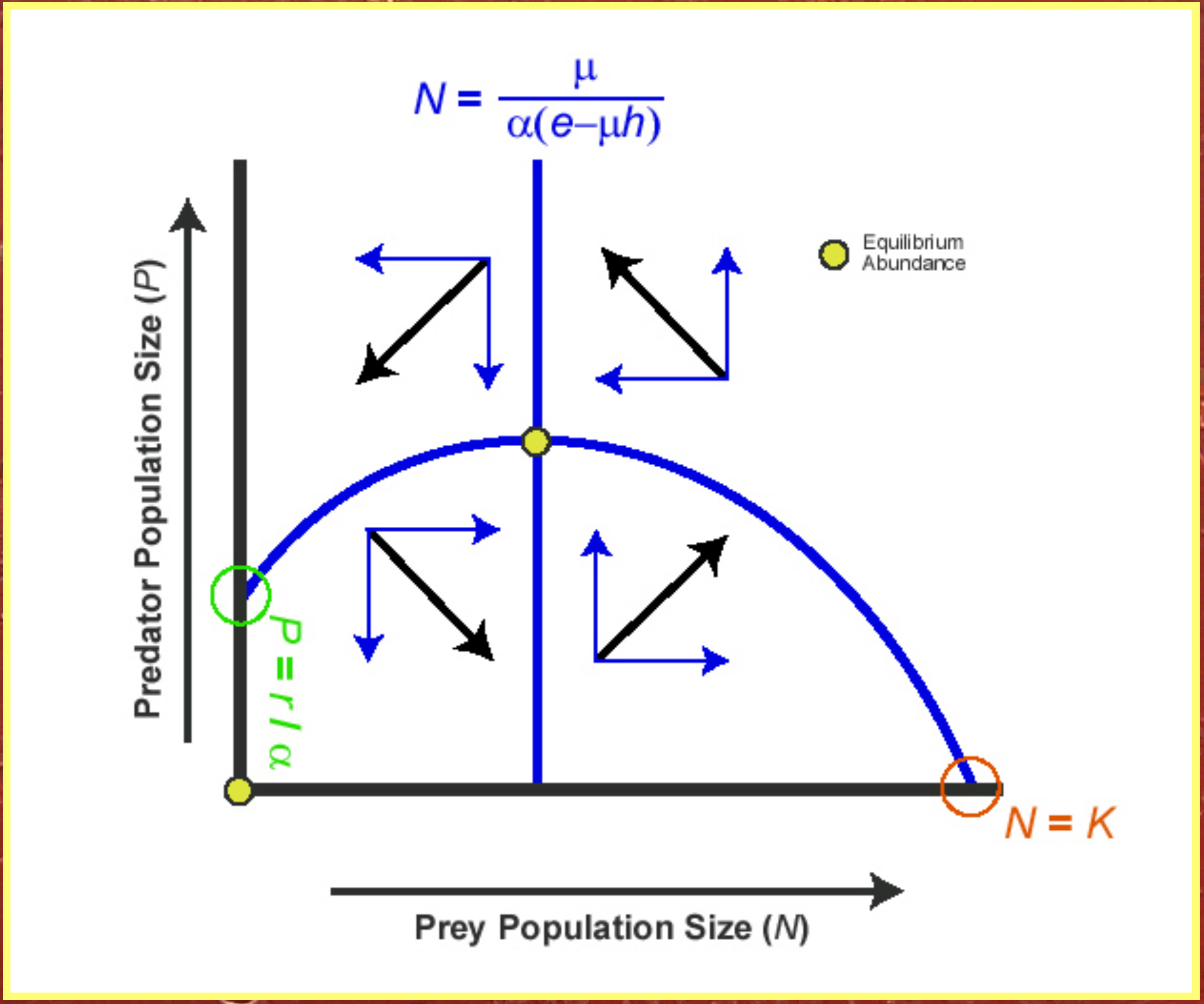
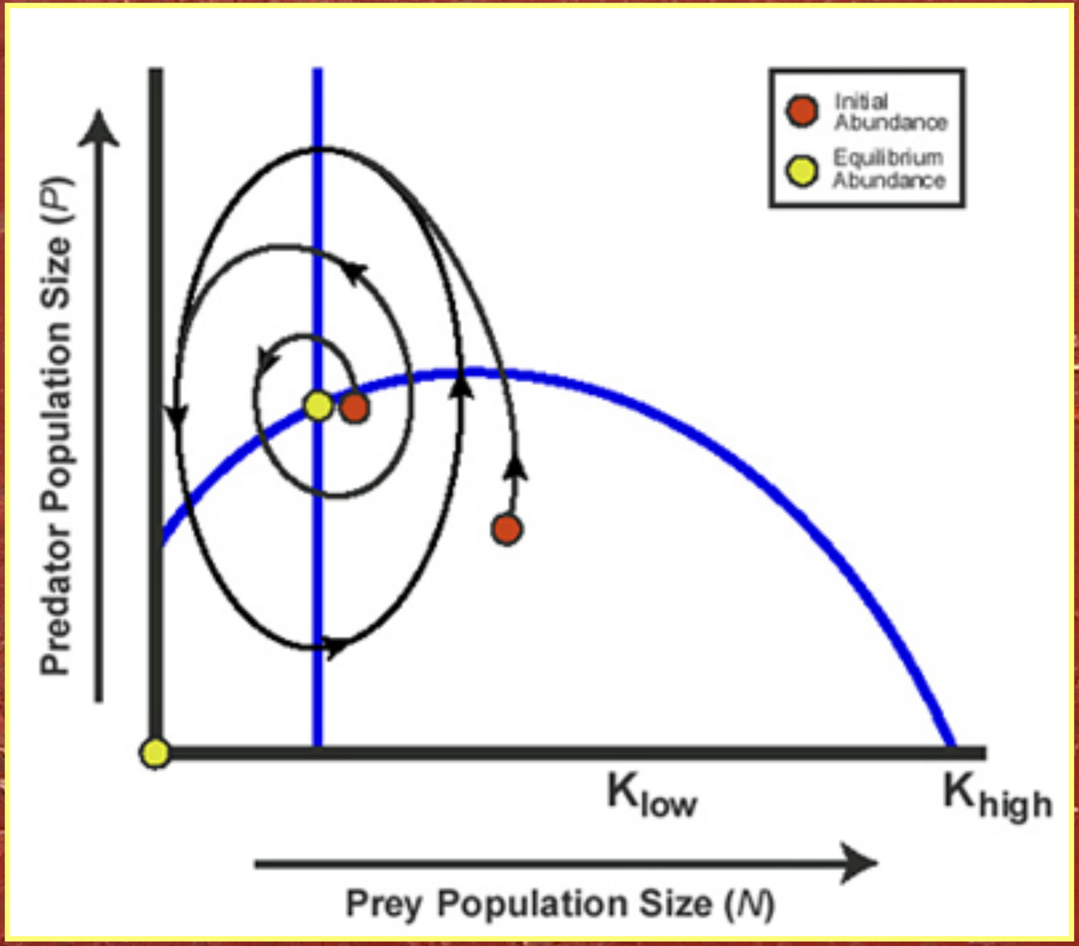
# Rosenzweig-MacArthur model:



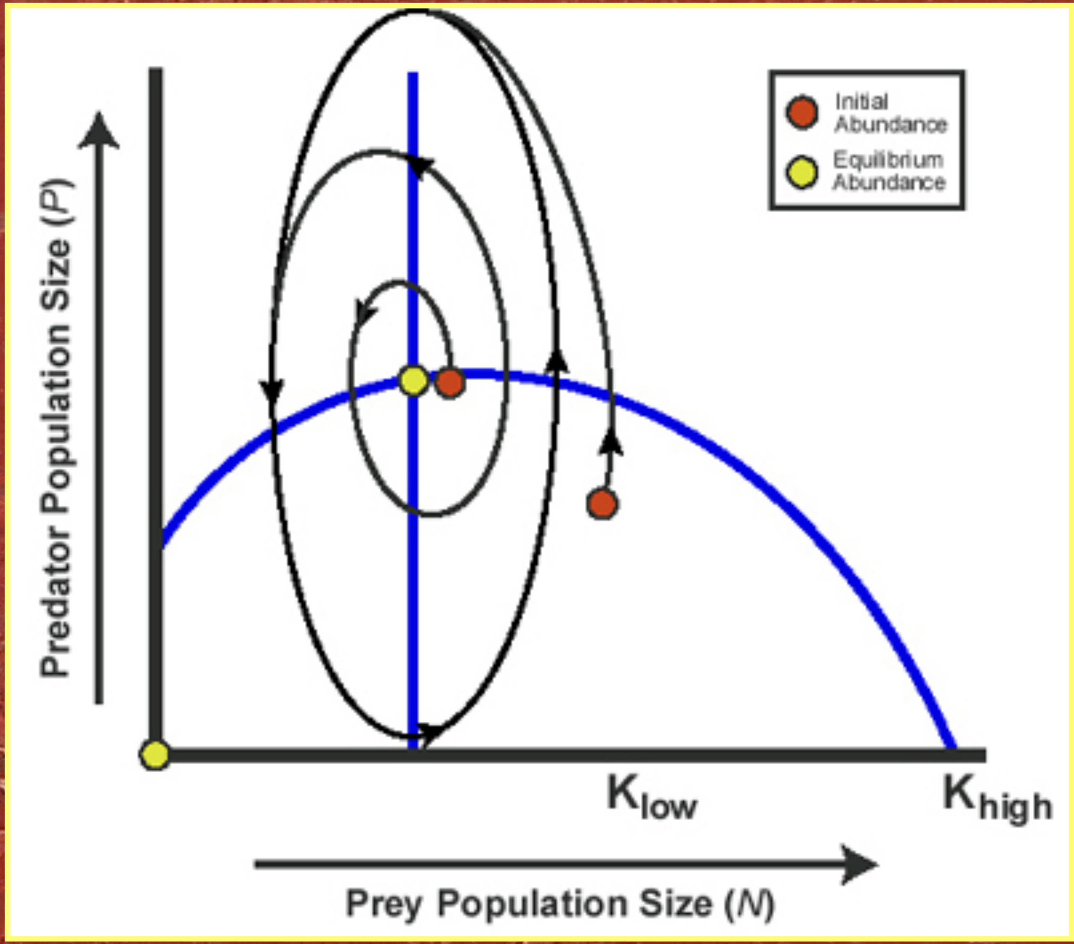

(*updated* Rosenzweig and MacArthur 1963)

# Luckinbill 1973:



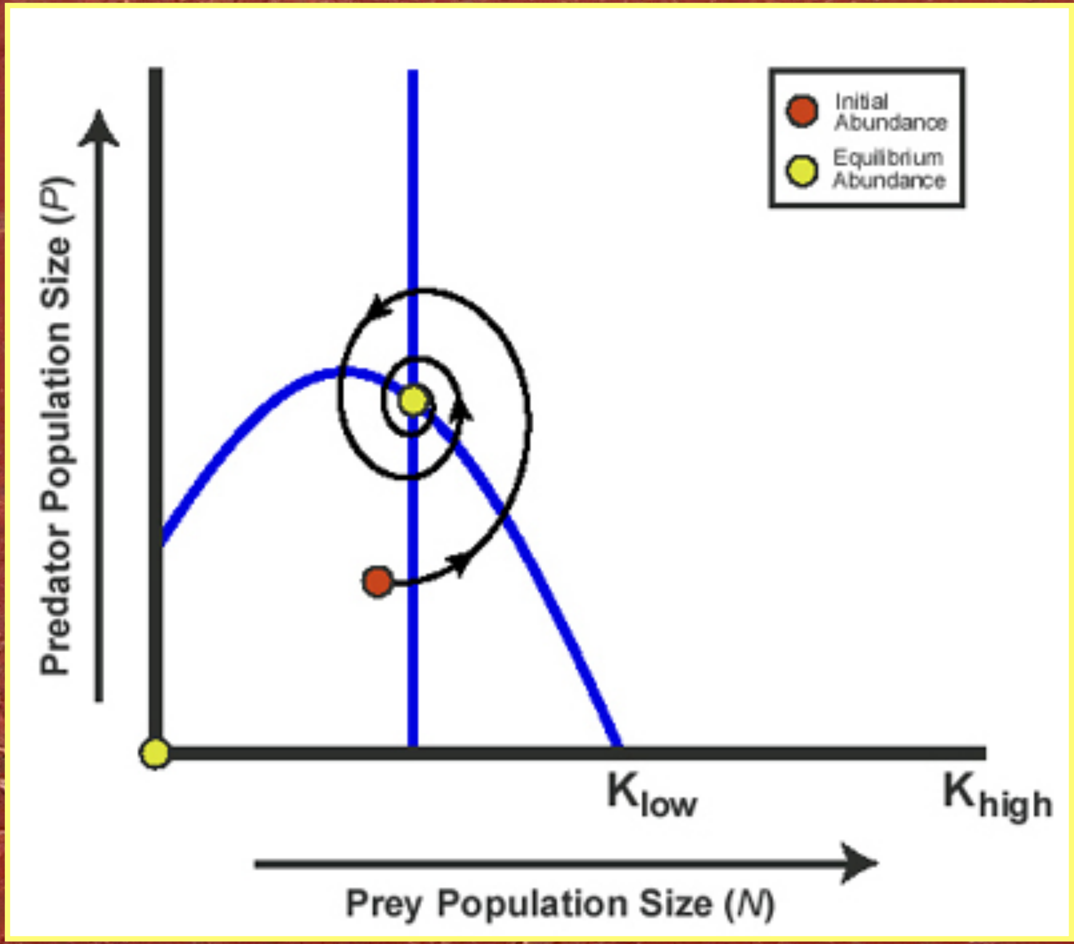

## *Dual Extinction*

# Luckinbill 1973:




## *Predator Extinction*

# Luckinbill 1973:




***Coexistence***