


Next time...

LETTER

ECOLOGY LETTERS  WILEY

Interactions between temperature and nutrients determine the population dynamics of primary producers

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Funding information

Yale Center for Natural Carbon Capture; Natural Sciences and Engineering Research Council of Canada

Editor: Roberto Salguero-Gomez

Abstract

Global change is rapidly and fundamentally altering many of the processes regulating the flux of energy throughout ecosystems, and although researchers now understand the effect of temperature on key rates (such as aquatic primary productivity), the theoretical foundation needed to generate forecasts of biomass dynamics and extinction risk remains underdeveloped. We develop new theory that describes the interconnected effects of nutrients and temperature on phytoplankton populations and show that the thermal response of equilibrium biomass (i.e. carrying capacity) always peaks at a lower temperature than for productivity (i.e. growth rate). This mismatch is driven by differences in the thermal responses of growth, death, and per-capita impact on the nutrient pool, making our results highly general and applicable to widely used population models beyond phytoplankton. We further show that non-equilibrium dynamics depend on the pace of environmental change relative to underlying vital rates and that populations respond to variable environments differently at high versus low temperatures due to thermal asymmetries.

KEYWORDS

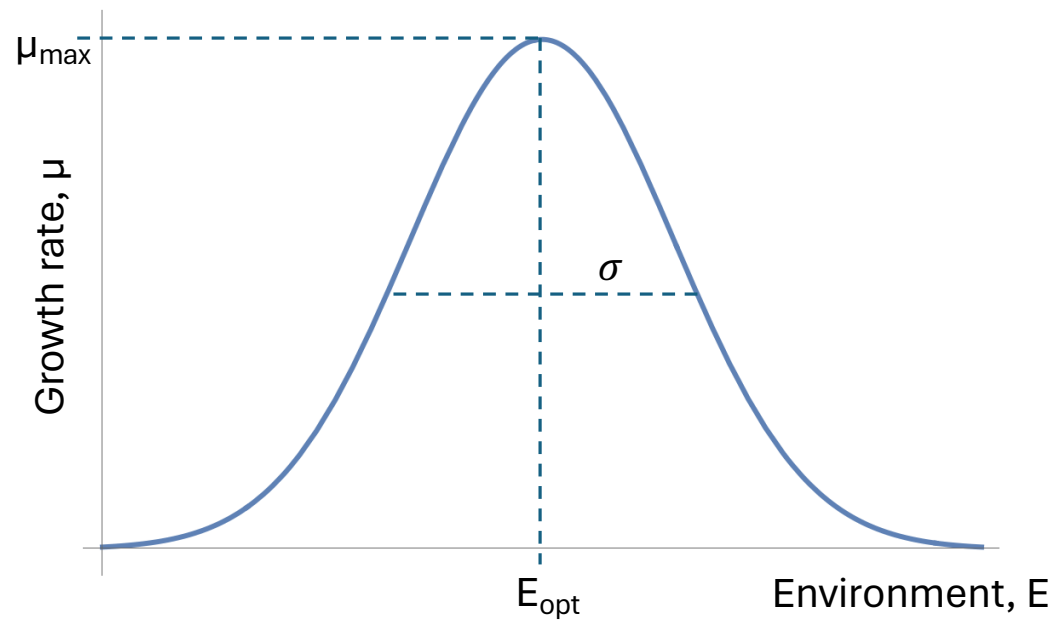
carrying capacity, Droop model, nutrient limitation, phytoplankton, population dynamics, theoretical ecology, thermal performance

More Environmental & Physiological Realism

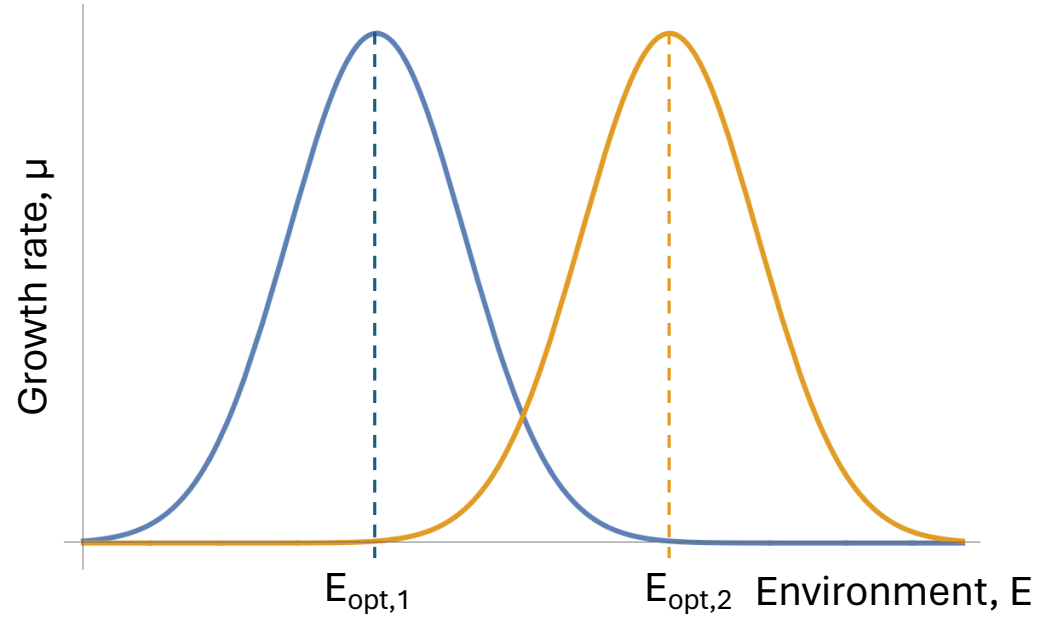
Environmental factors, temperature & variable nutrient quotas

Environmental factors

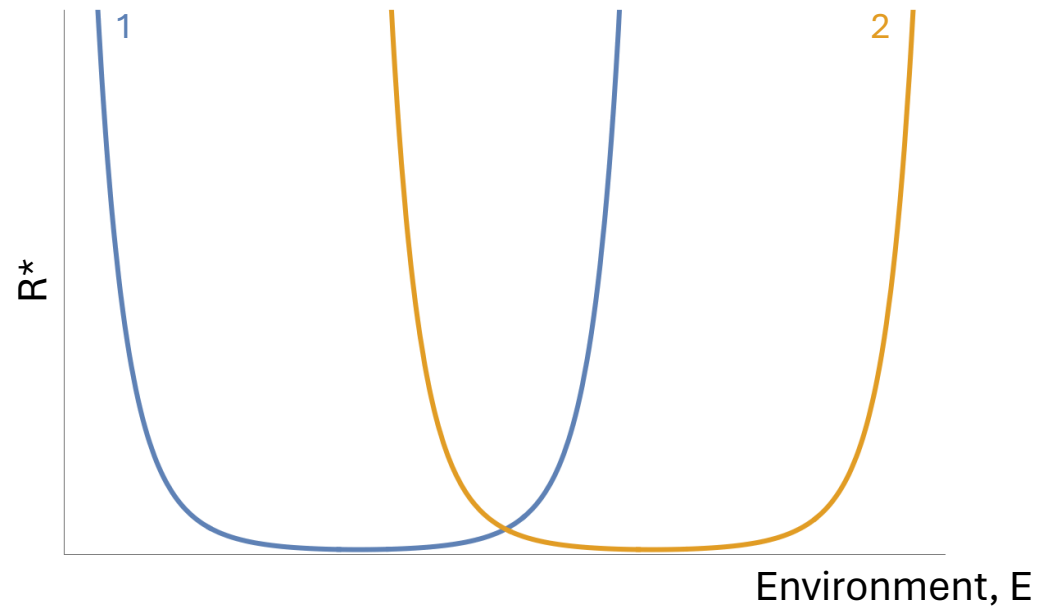
- Environmental factors affect growth but are not consumed / impacted
- Classic assumption: Gaussian (Gauch & Whittaker *Ecology* 1972)



Trade-off in optimum

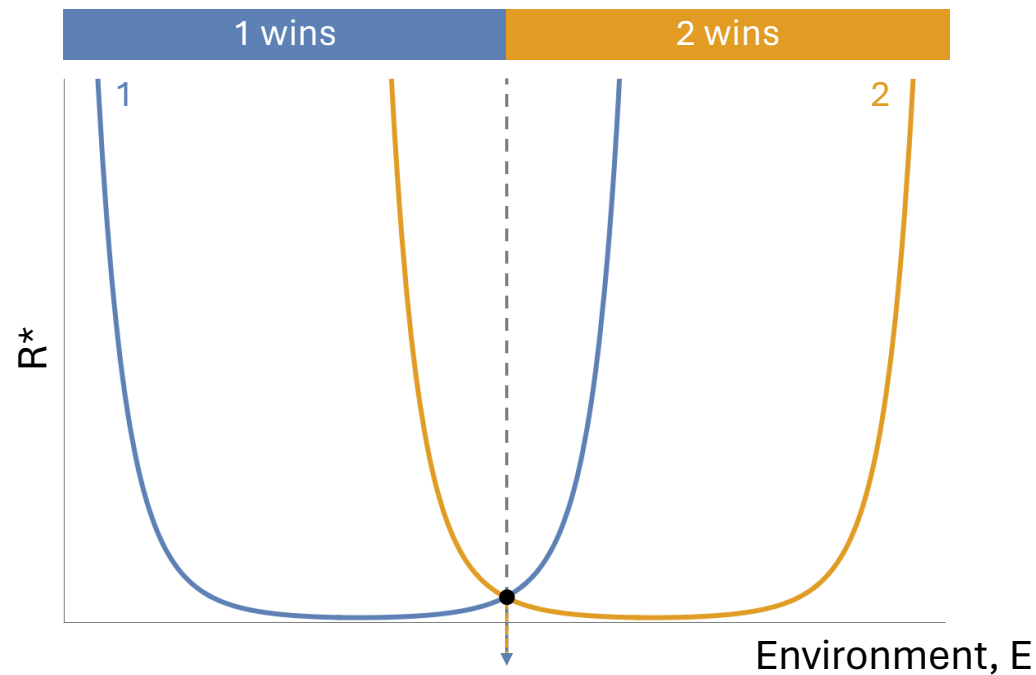


R^* vs Environment

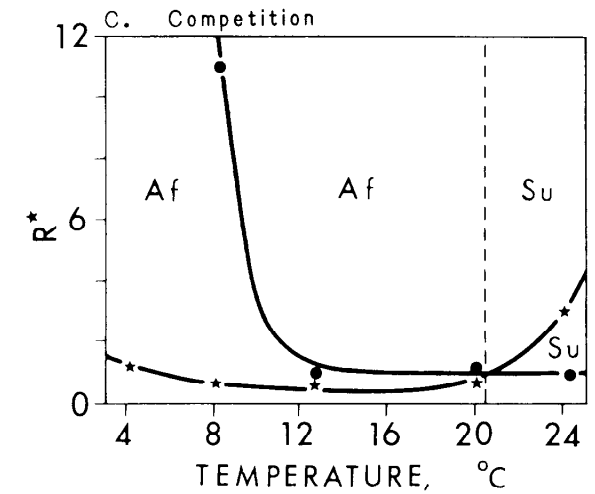
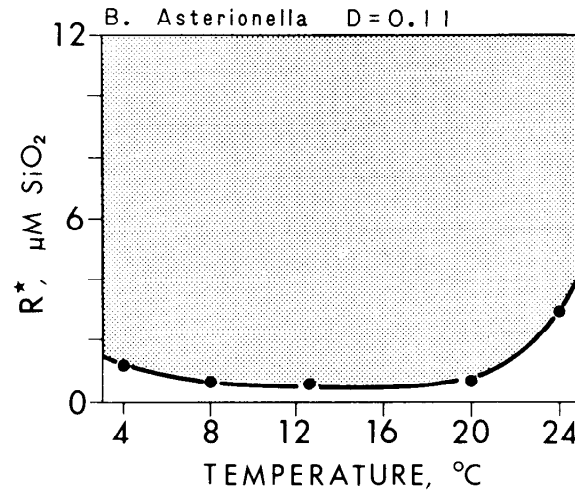
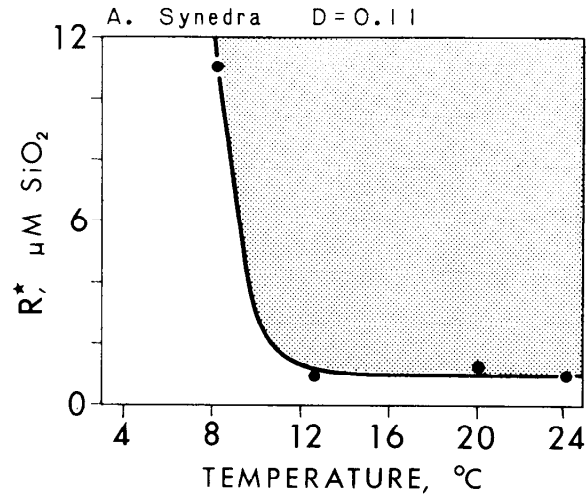


Trade-off in optimum

- Shift in superior competitor possible
- Equal impact (no impact) means no stable coexistence



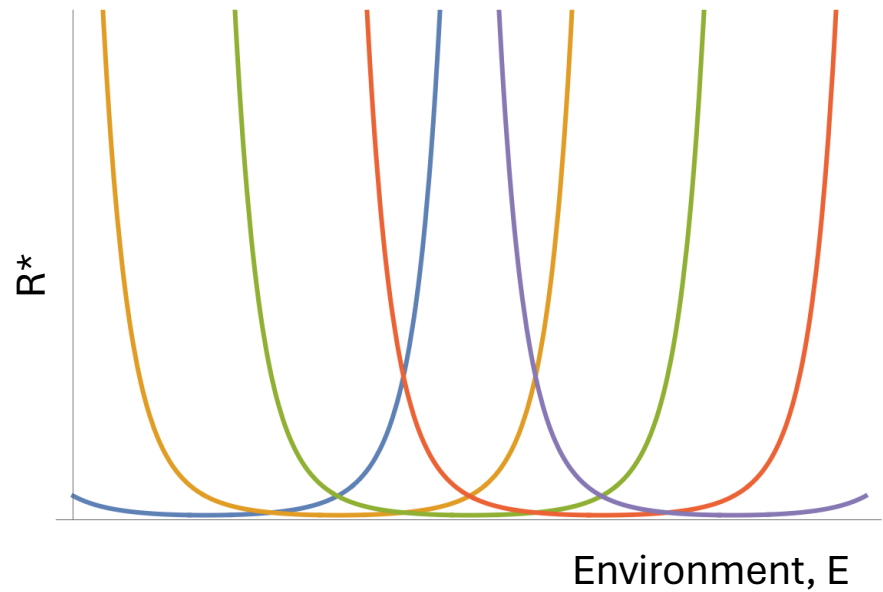
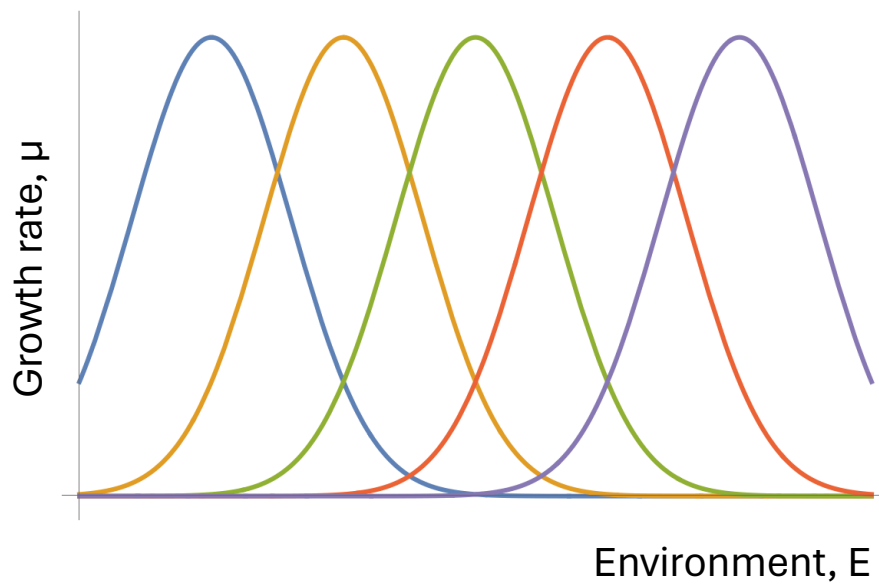
Experimental verification



(Tilman et al. *L&O* 1981)

Environmental gradients

- Predicts species replacements along environmental gradients



Temperature

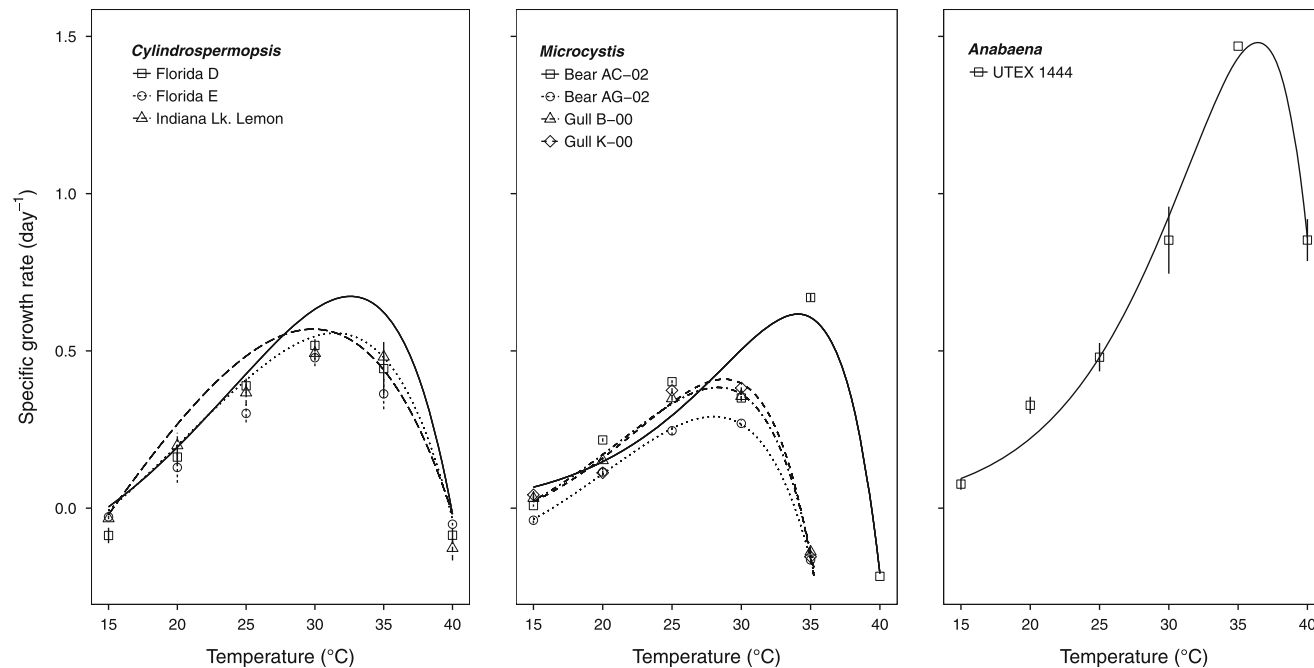
- Metabolic theory of ecology (Brown et al. *Ecology* 2004)
- Arrhenius function: rate $\propto e^{-E/(kT)}$ (E=activation energy, k=Boltzman constant, T=temperature)
- Hotter = faster



JAMES H. BROWN, MacArthur Award Recipient, 2002

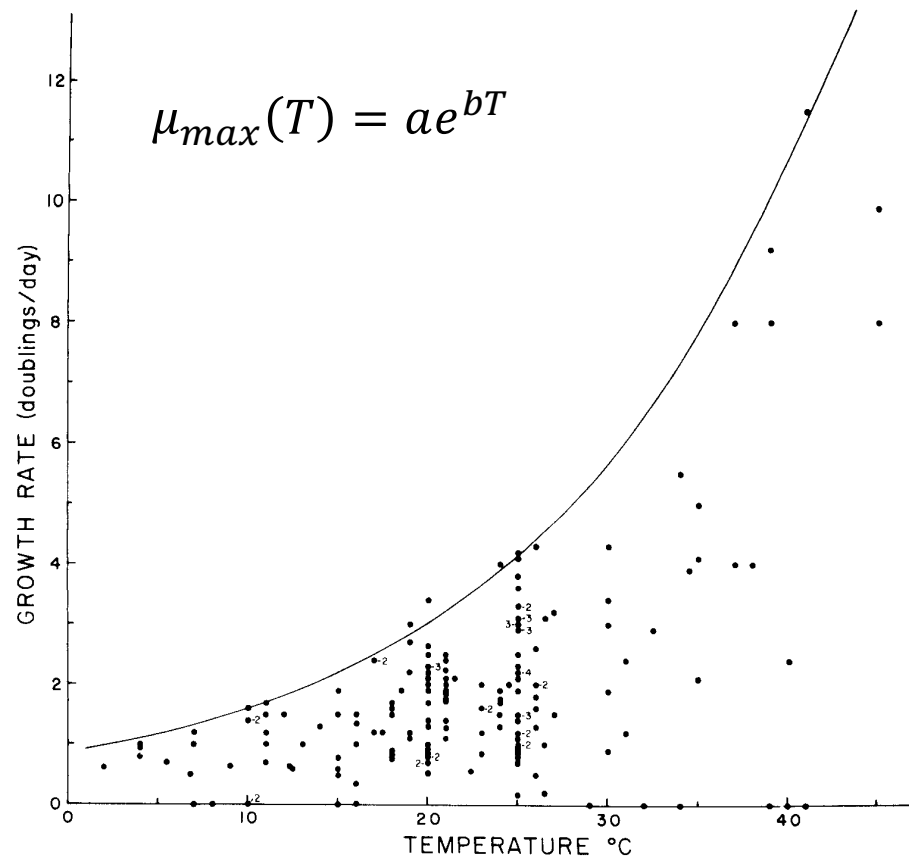
Real TPCs

- Real organisms have upper and lower bounds – response is unimodal (often skewed)



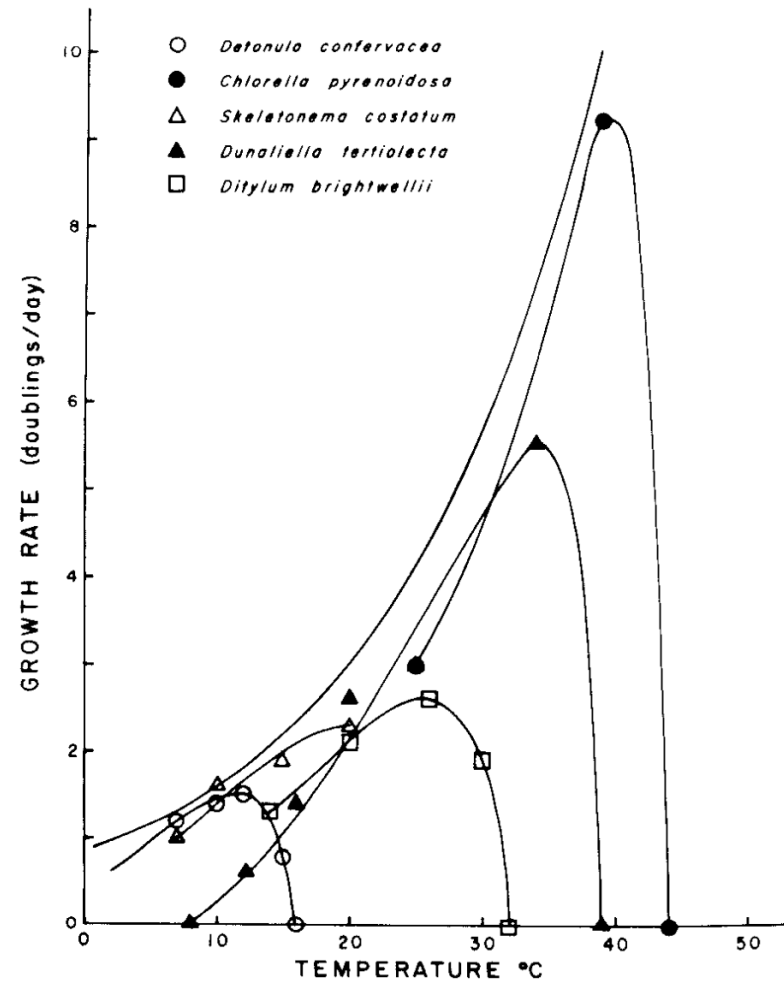
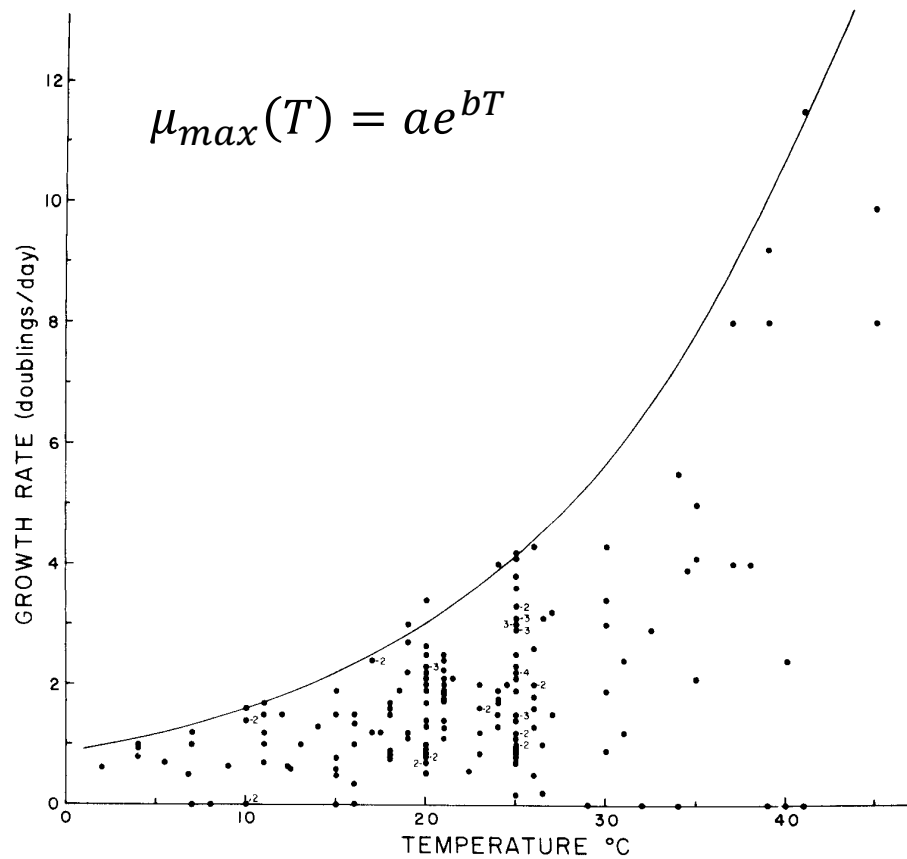
(Thomas & Litchman *Hydrobiologia* 2015)

Eppley curve



(Eppley 1972)

Eppley curve

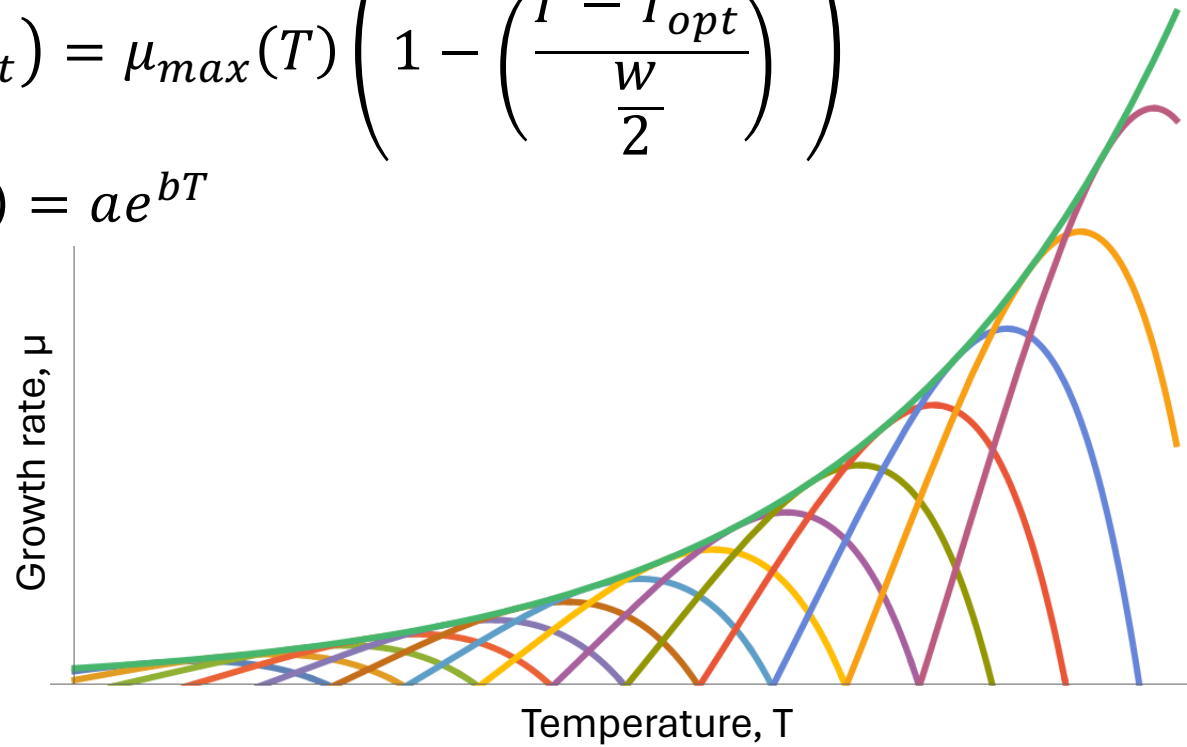


(Eppley 1972)

Norberg model

$$\mu(T, T_{opt}) = \mu_{max}(T) \left(1 - \left(\frac{T - T_{opt}}{\frac{w}{2}} \right)^2 \right)$$

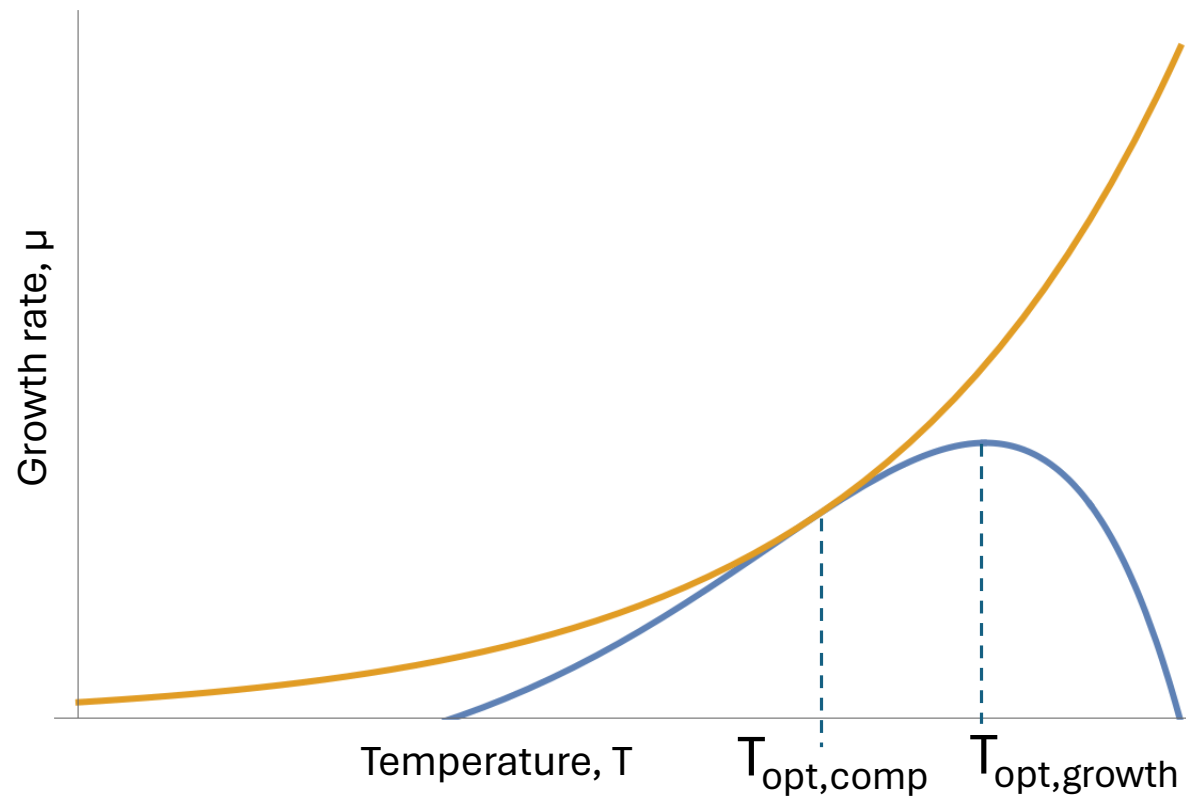
$$\mu_{max}(T) = ae^{bT}$$



(Norberg L&O 2004)

Norberg model

- Competitive $T_{opt} \neq$ growth T_{opt}



(Thomas et al. *Science* 2012)

Nutrient-temperature interactions

- Modeling nutrient-temperature interaction can be tricky!

$$\begin{aligned}\frac{dR}{dt} &= a(R_{in} - R) - Q\mu_T(T, T_{opt})\mu_R(R)N \\ \frac{dN}{dt} &= \mu_T(T, T_{opt})\mu_R(R)N - mN\end{aligned}$$

- What if you're outside your thermal niche ($\mu_T < 0$)?

Double-exponential model

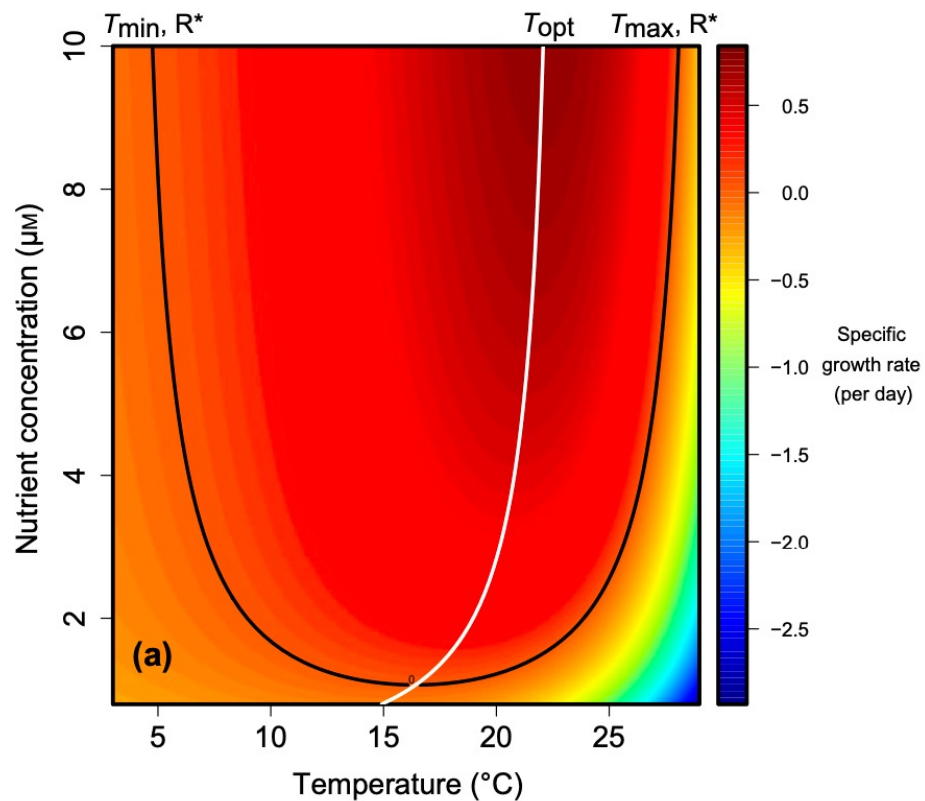
- Double-exponential model:

$$\begin{aligned}\frac{dR}{dt} &= a(R_{in} - R) - Q\mu_T(T)\mu_R(R)N \\ \frac{dN}{dt} &= \mu_T(T)\mu_R(R)N - m(T)N\end{aligned}$$

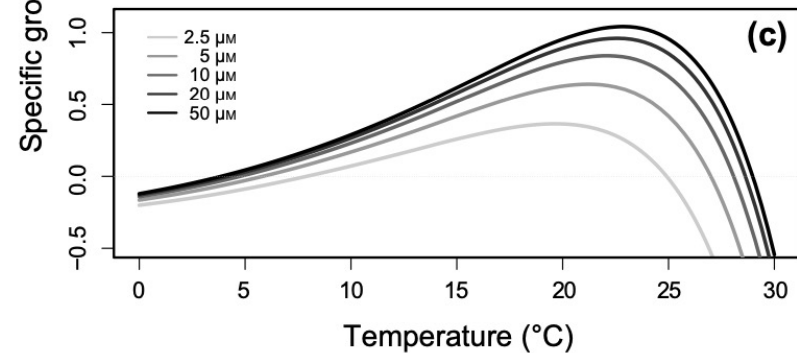
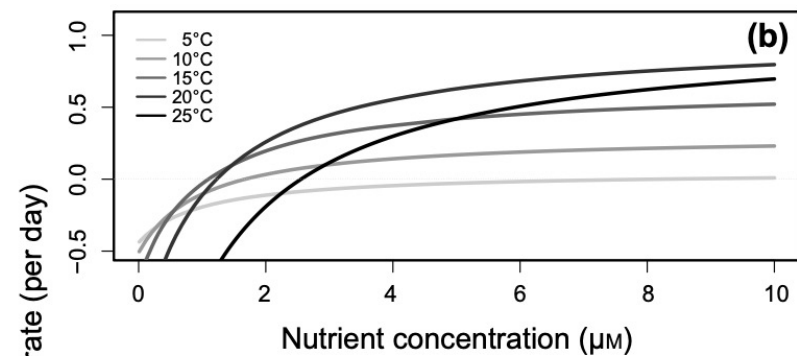
- Both births and deaths are exponential functions of T
 $\mu(T) = \mu_0 e^{\mu_1 T}, m(T) = m_0 e^{m_1 T}$

(Thomas et al. *Global Change Biology* 2017)

Double-exponential model



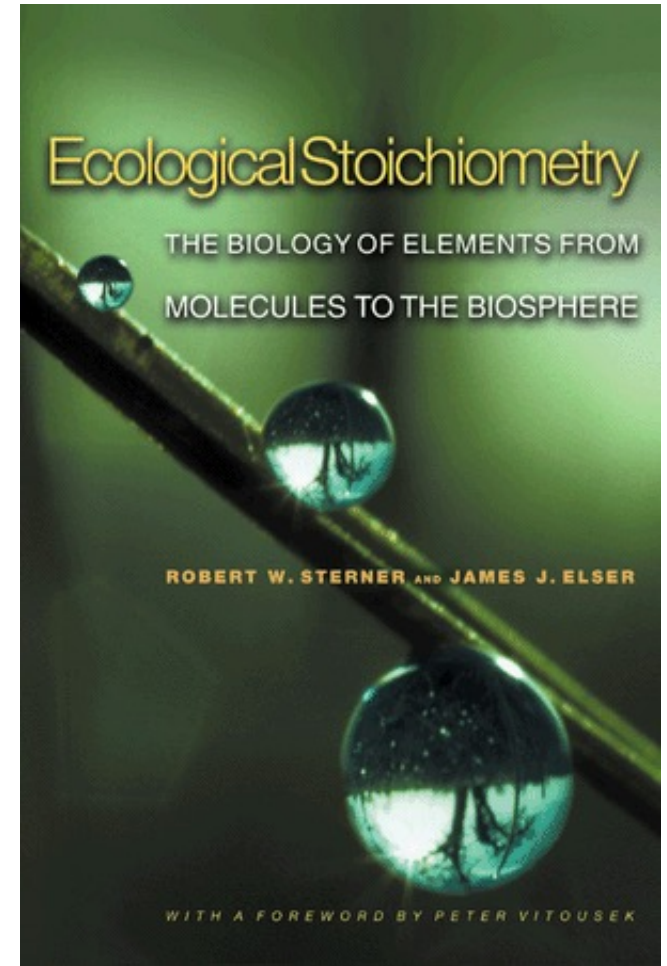
T_{opt} is a function of R !



(Thomas et al. *Global Change Biology* 2017)

Variable nutrient quota

- Resource-consumer models we've looked at so far assume fixed nutrient content (quotas / yields)
- Good approximation for some organisms/resources (animals) not so good for others (plants/nutrients)

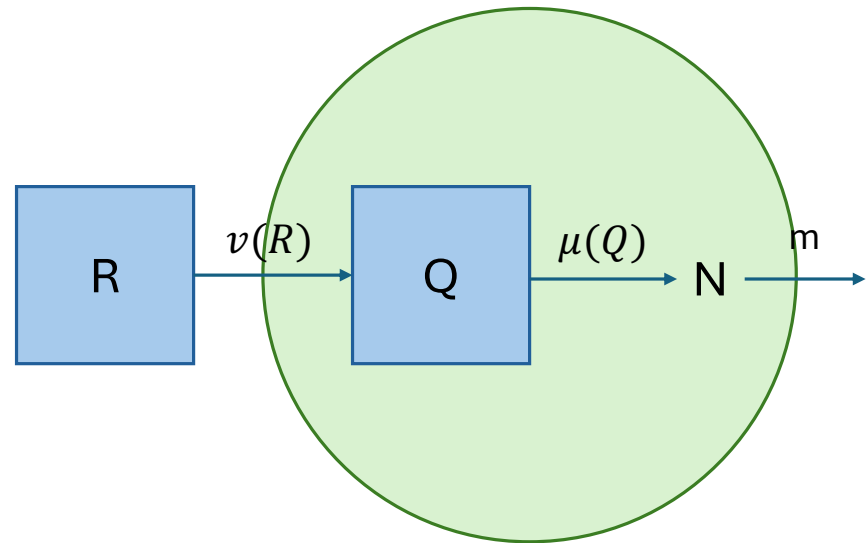


Variable internal stores model

$$\frac{dR}{dt} = a(R_{in} - R) - v(R)N$$

$$\frac{dQ}{dt} = v(R) - \mu(Q)Q$$

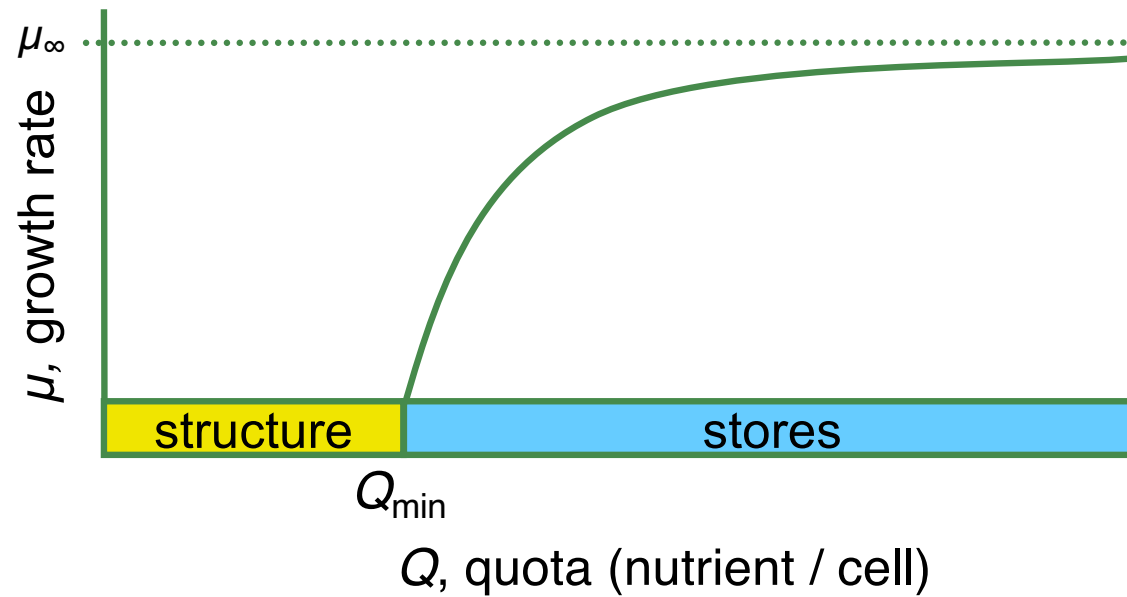
$$\frac{dN}{dt} = (\mu(Q) - m)N$$



a “structured” population model — population can’t be fully described by a single number

Droop function

$$\mu(Q) = \mu_{\infty} \left(1 - \frac{Q_{min}}{Q} \right)$$



(Droop 1968, Caperon 1968)

Variable internal stores model

Extensive variable S:

$$\frac{dS}{dt} = v(R)N - mS$$

$$\frac{dN}{dt} = (\mu(Q) - m)N$$

$$Q = S/N$$

Variable internal stores model

Extensive variable S:

$$\frac{dS}{dt} = v(R)N - mS$$

$$\frac{dN}{dt} = (\mu(Q) - m)N$$

$$Q = S/N$$

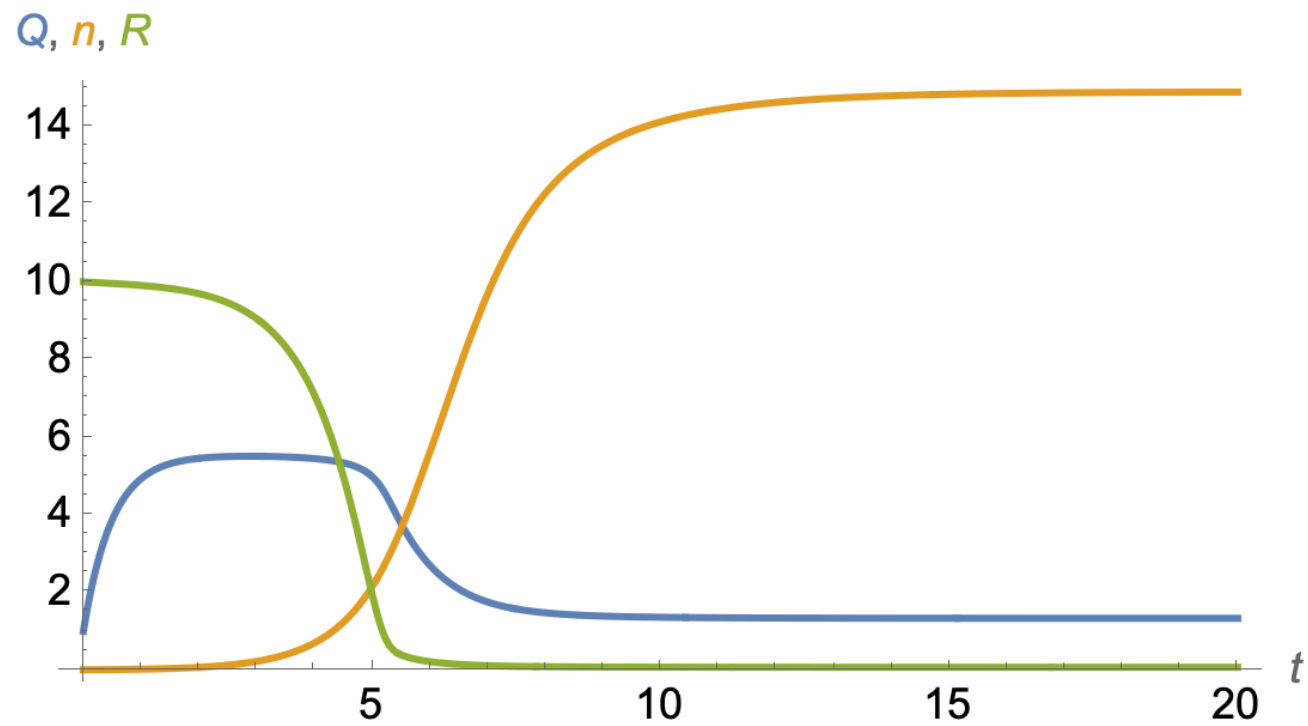
Intensive variable Q:

$$\frac{dQ}{dt} = \frac{N (dS/dt) - S (dN/dt)}{N^2}$$

$$\frac{dQ}{dt} = \frac{N(v(R)N - mS) - S(\mu(Q) - m)N}{N^2}$$

$$\frac{dQ}{dt} = v(R) - \mu(Q)Q$$

Simulate



Exponential phase

Quasi-steady state approximation

$$0 \approx \frac{dQ}{dt} = v(R_{in}) - \mu_{\infty}(\tilde{Q} - Q_{min})$$

$$\tilde{Q} \approx Q_{min} + \frac{v(R_{in})}{\mu_{\infty}}$$

$$\tilde{\mu} \approx \frac{\mu_{\infty} v(R_{in})}{\mu_{\infty} Q_{min} + v(R_{in})}$$

(Klausmeier et al. *L&O* 2004)

Equilibrium phase

$$\begin{aligned}\hat{R} = R^* &= \frac{Q_{min} m \mu_{\infty} H}{v_{max}(\mu_{\infty} - m) - Q_{min} m \mu_{\infty}} \\ \hat{Q} &= Q_{min} \frac{\mu_{\infty}}{\mu_{\infty} - m} \\ \hat{N} &= \frac{a(R_{in} - R^*)}{\hat{Q} m}\end{aligned}$$

(Burmester 1979, Klausmeier et al. *L&O* 2004)

Why bother?

- Important for non-equilibrium conditions
- Experimentally measured uptake rates, etc.
- Interested in questions of ecological stoichiometry (varying Q)

70s Chemostat Classics

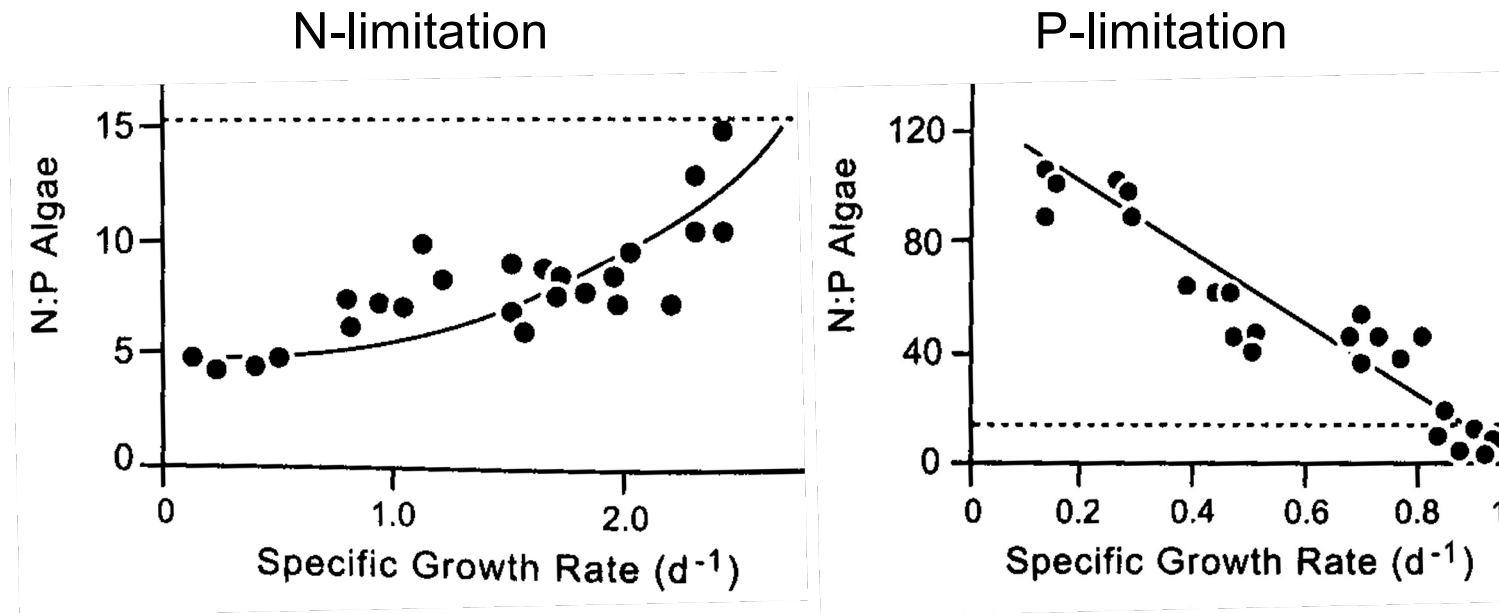
★ volume 1



Goldman experiments: vary growth

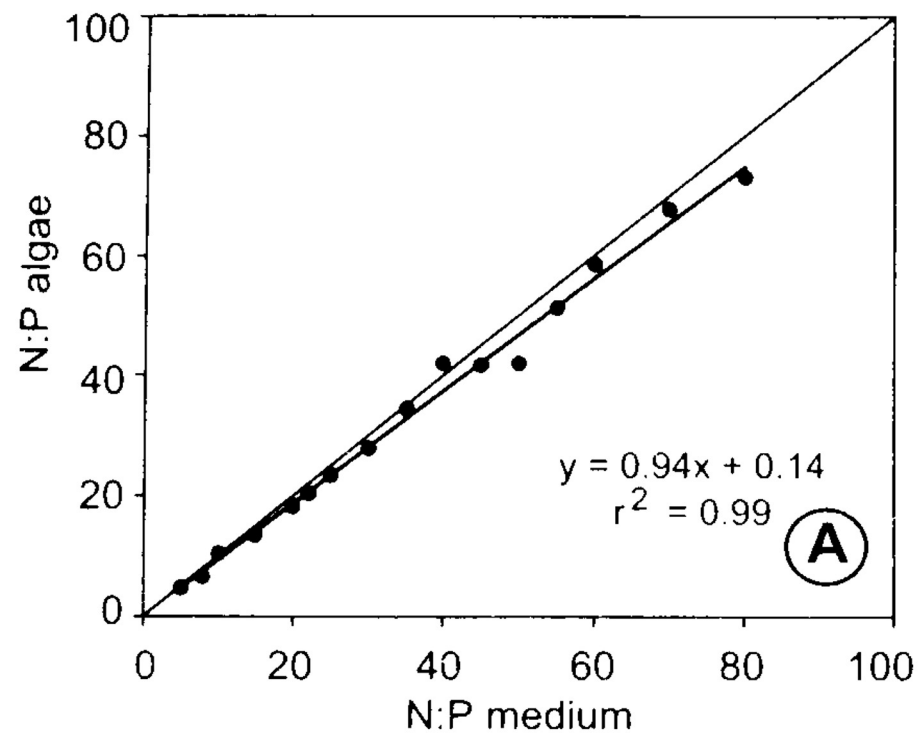
Rhee experiments: vary N:P

“Goldman” Experiments Vary Growth Rate



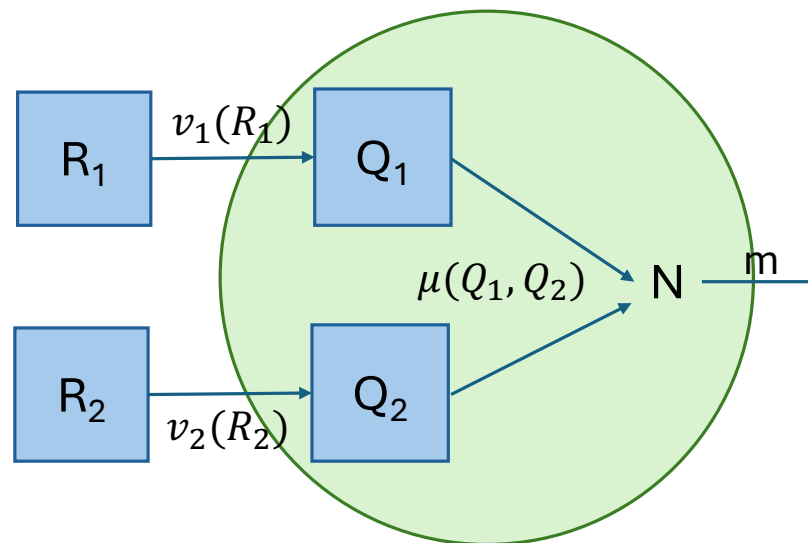
(Goldman et al. 1979, reprinted from Sterner & Elser 2002)

“Rhee” Experiments Vary N:P Supply



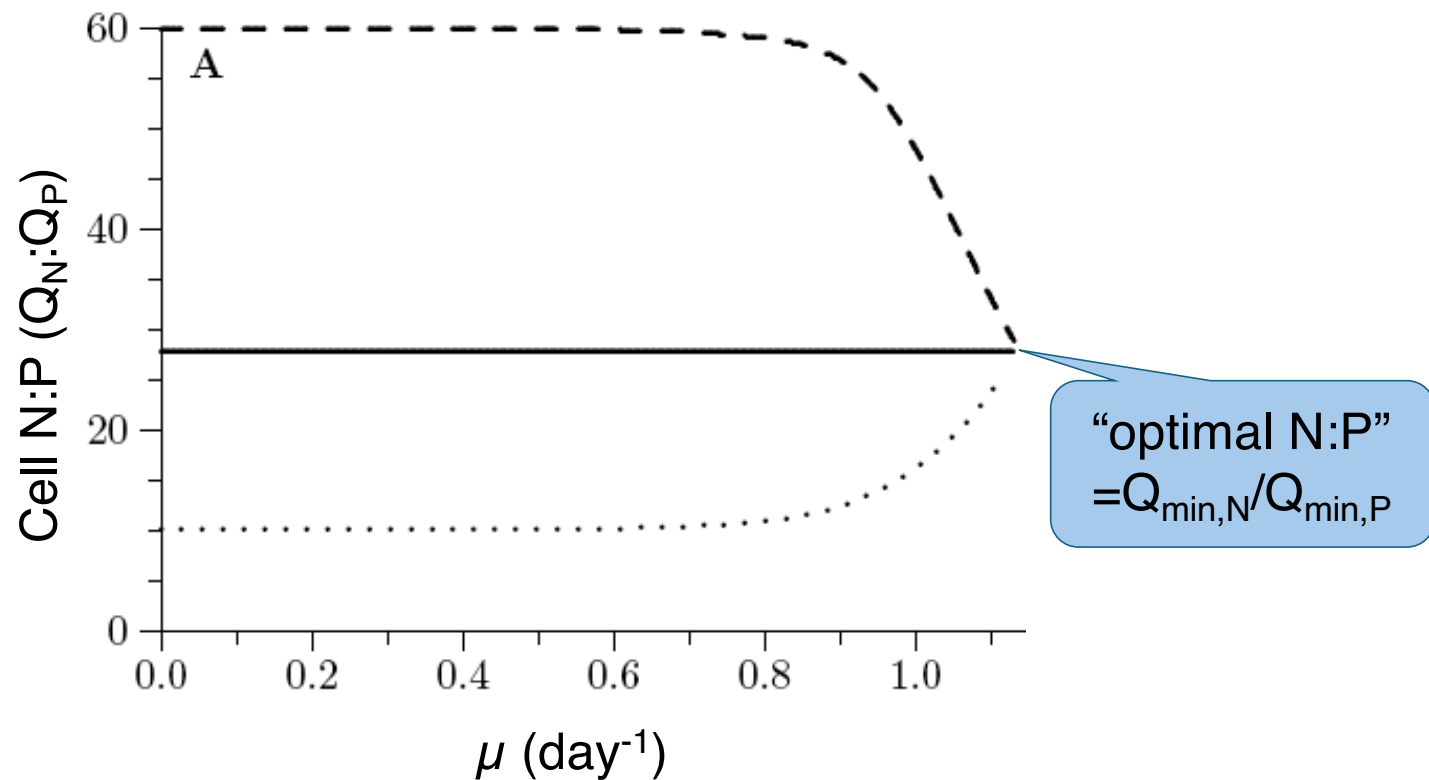
(Rhee 1974, reprinted from Sterner & Elser 2002)

Two essential resources



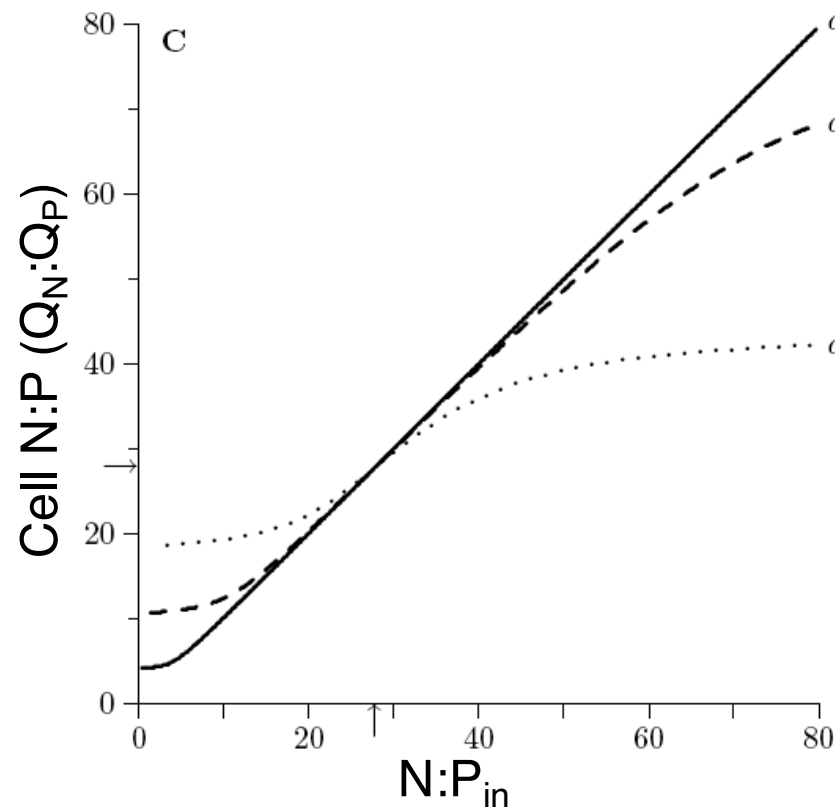
$$\mu(Q_1, Q_2) = \min(\mu_1(Q_1), \mu_2(Q_2))$$

“Goldman” Experiments Vary Growth Rate



(Klausmeier et al. *L&O* 2004)

“Rhee” Experiments Vary N:P Supply



(Klausmeier et al. *L&O* 2004)

A Critical Review of Twenty Years' Use of the Resource-Ratio Theory

Thomas E. Miller,^{1,*} Jean H. Burns,^{1,†} Pablo Munguia,^{1,‡} Eric L. Walters,^{1,§} Jamie M. Kneitel,^{1,||}
Paul M. Richards,^{1,#} Nicolas Mouquet,^{2,**} and Hannah L. Buckley^{1,††}

Table 1. Predictions

1. The species that can survive at the lowest levels of a limiting resource will be the best competitor for that resource
2. Species dominance varies with the ratio of the availabilities of two resources
3. The number of coexisting species is less than or equal to the number of limiting resources
4. The vector describing the resource supply rate to an environment will affect whether competing species coexist and, if not, which species will competitively exclude the other
5. The vectors describing the consumption rates of resources for two species will determine whether competing species coexist or, if not, which species will dominate competitively
6. Trade-offs in resource use must occur for species to co- exist along a gradient of ratios of the availabilities of two resources
7. The highest diversity of competing species will occur at an intermediate ratio of the availabilities of two resources

1333 articles cite Tilman 80, 82

85% cite in passing

7.2% extend theory

5% tested model predictions / assumptions

26/68 papers: acceptable experimental design

32/42 tests: microcosm experiments

6/42 tests: field observations

4/42 tests: field experiments

Table 2: Number of individual tests of the seven predictions of the resource-ratio theory listed in table 1

Prediction number	Test adequate?			Total
	Yes; prediction supported?		No	
	Yes	No		
1	8	5	9	22
2	13	3	31	47
3	1	1	1	3
4	5	1	5	11
5	2	0	1	3
6	2	1	2	5
7	0	0	10	10
Total	31	11	59	101

Table 3: The habitat type used for each of the 42 adequate tests shown in table 2

Prediction supported?	Freshwater	Marine	Terrestrial
Yes	23	5	3
No	8	1	2

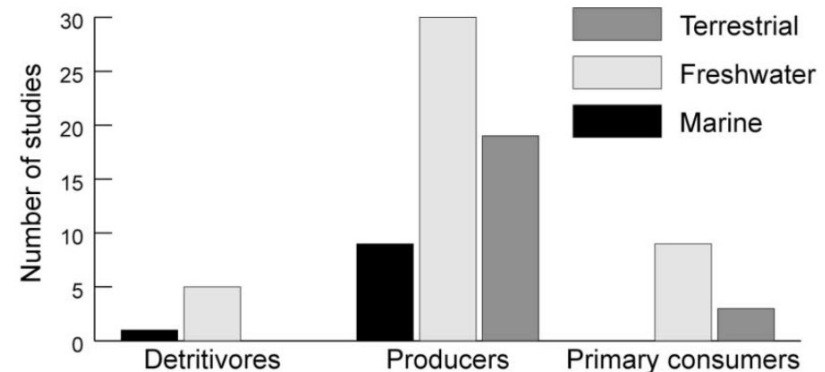


Table 4: Trophic groups used in each of the 42 adequate tests shown in table 2

Prediction supported?	Producer	Primary consumer	Detritivore
Yes	22.5	5.5	3
No	8.5	1.5	1

Some discussion questions

- Do you agree with the authors' conclusions that resource-ratio theory is inadequately tested?
- What are challenges of testing resource-ratio theory?
- Why is there bias in terms of systems used?
- In general, how should we test general theories?
- Do you think other theories are better / worse supported?