

LARGE LAKES OBSERVATORY

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UNIVERSITY OF MINNESOTA DULUTH

Driven to Discover™

# Stoichiometry of consumer-driven nutrient cycling: Background and theory

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**TRIGGER  
WARNING**

oCB

# Stoichiometry

Mass balance of multiple  
conserved substances in  
ecological interactions

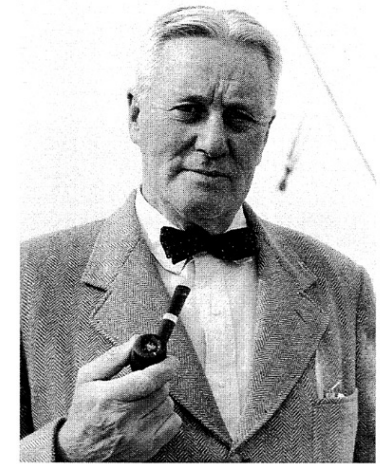
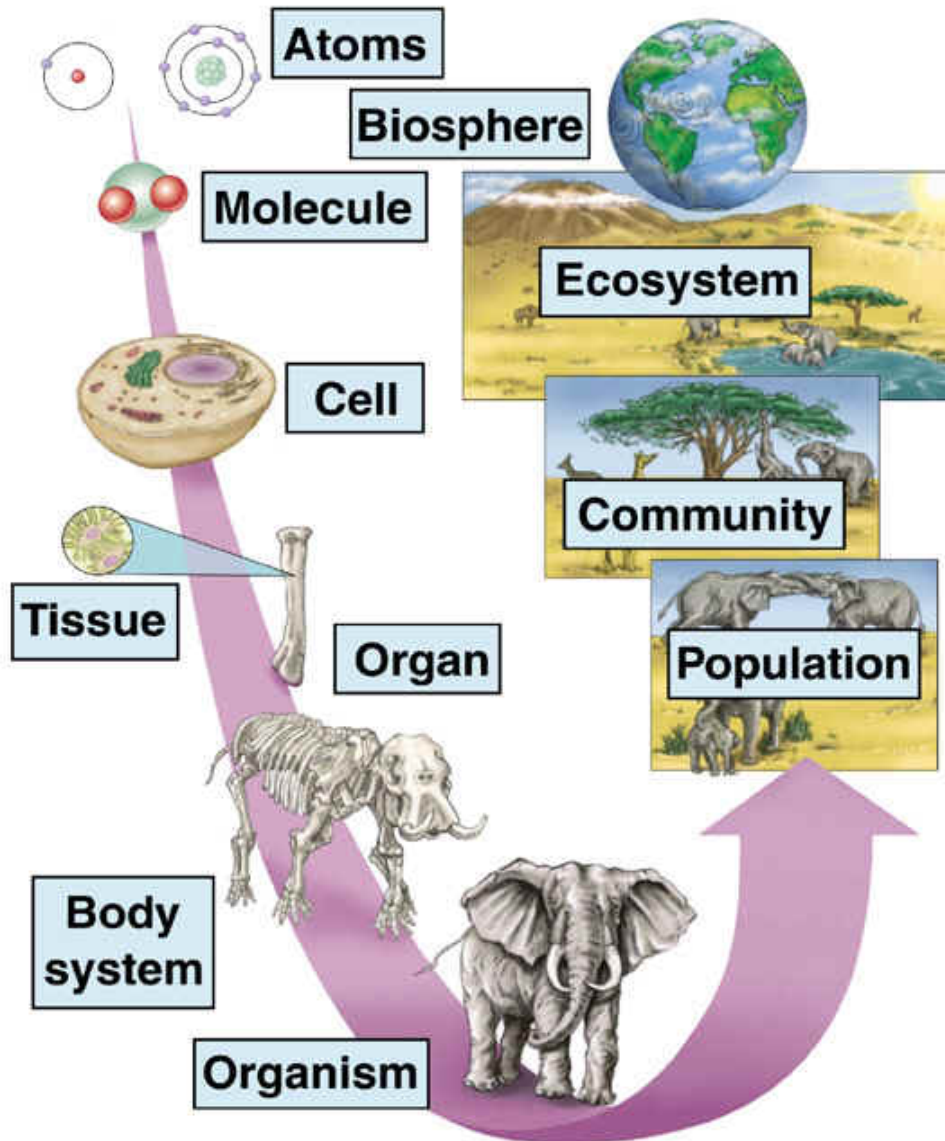
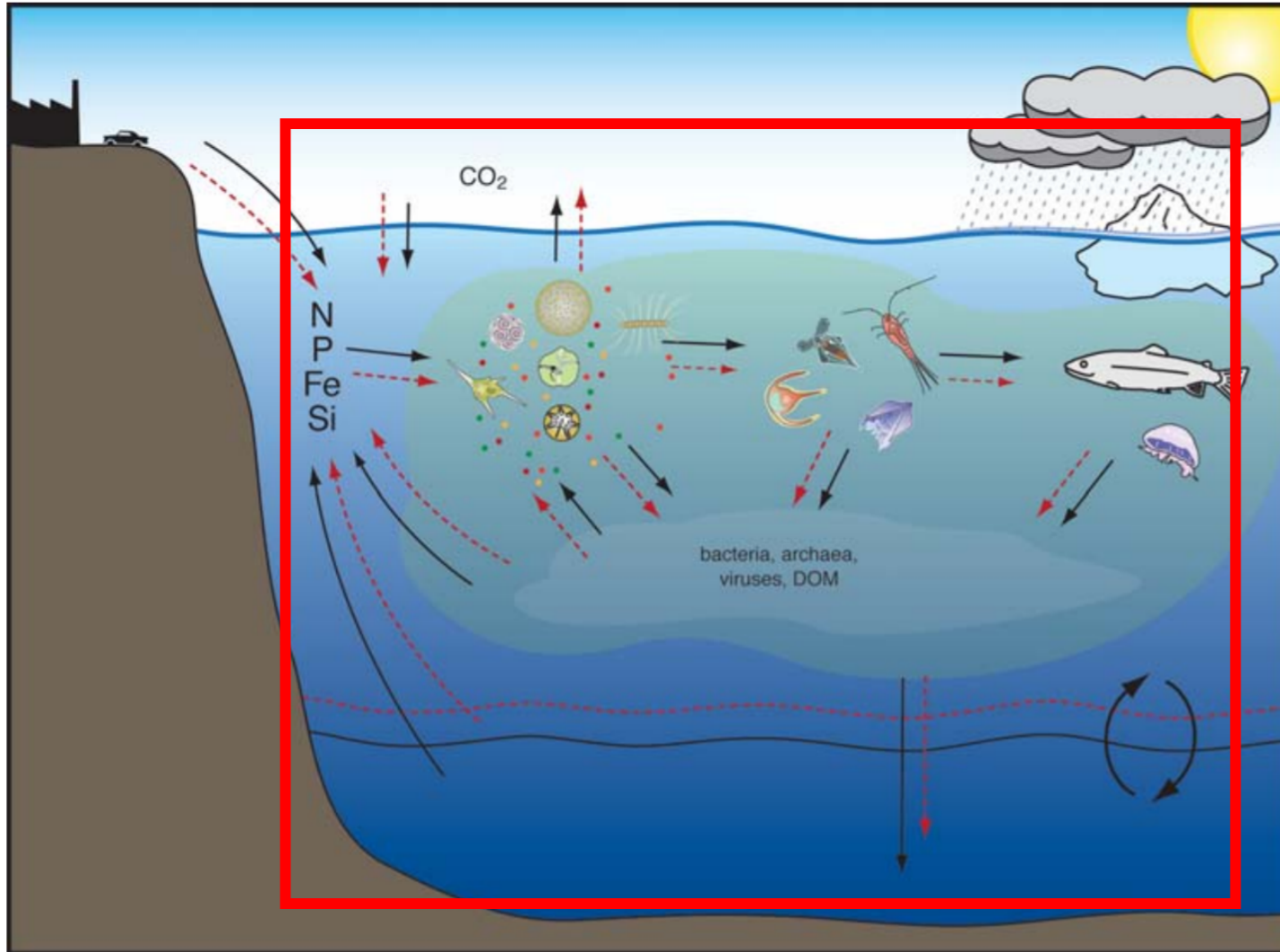


Photo by John Hahn, Woods Hole Oceanographic Institution

*Alfred Russel Wallace*

There are stoichiometric stories across all levels of organization – and they relate!

I'll be spending most of my time around the organism level.



A highly multidimensional problem!

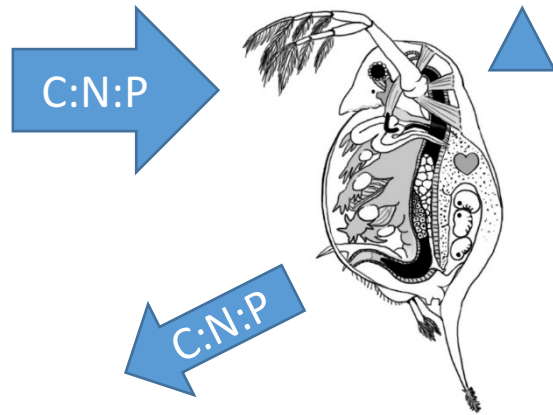
How do we unpack this box?

What are the functional couplings?

How do we overlay multiple cycles?

Consumers are important as nutrient recyclers (Ketchum 1962, Lehman 1980, Vanni, Atkinson and others).

Might we build up an understanding species by species, “wiring” in measured values.



The P released per biomass ingested varied with P:C of food, and became zero at low food P levels.

Animals were actively maintaining their P balance by adjusting C vs. P budgets.

Y. Olsen et al. L&O 1986

10x

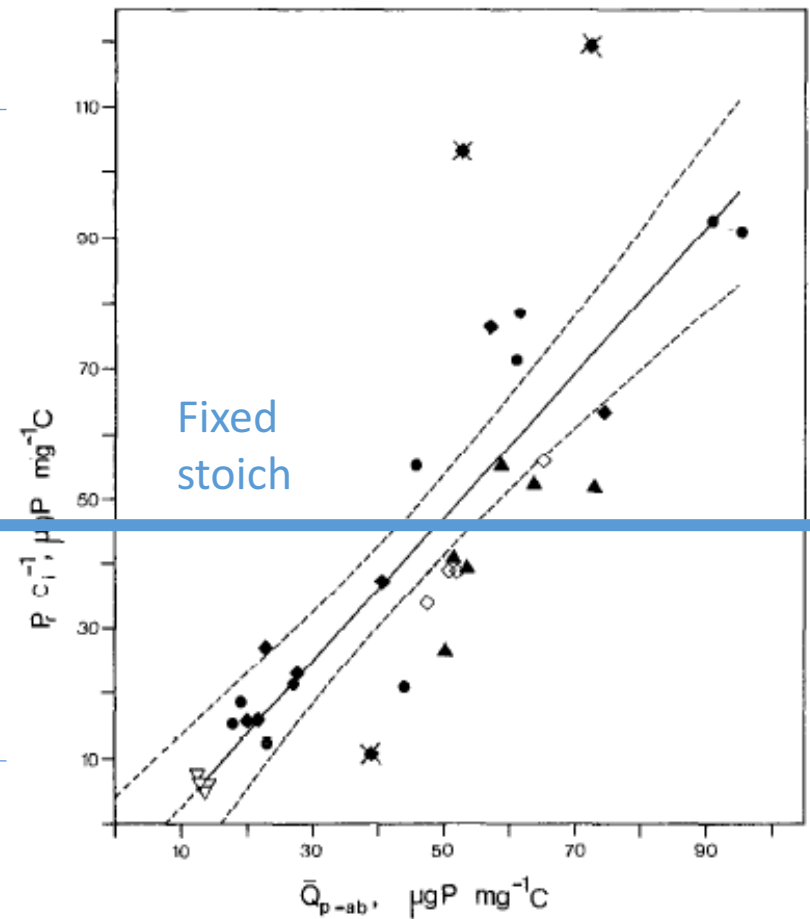


Fig. 6. The amount of phosphorus released by the animals ( $P_r$ ) per unit of algal and bacterial carbon which is ingested ( $c_i$ ) as a function of the mean phosphorus content of the respective food ( $\bar{Q}_{p-ab}$ ). Regression line and its 95% C.I. for all experimental values is drawn.  $\bar{Q}_{p-ab}$  is defined as the mean  $Q_{p-ab}$  of experimental and control bottles. Enclosure 1—●; enclosure 2—◆; preliminary experiment—▲; experiment 1 (Olsen and Østgaard 1985)—▽; experiment 2 (Olsen and Østgaard 1985)—◇; values omitted in regression (cf. Table 9)—✱.

C:N:P



Dominance by larger grazers was associated with P instead of N limitation.

Food web shifts result in biogeochemical adjustments.

Elser et al. L&O 1988

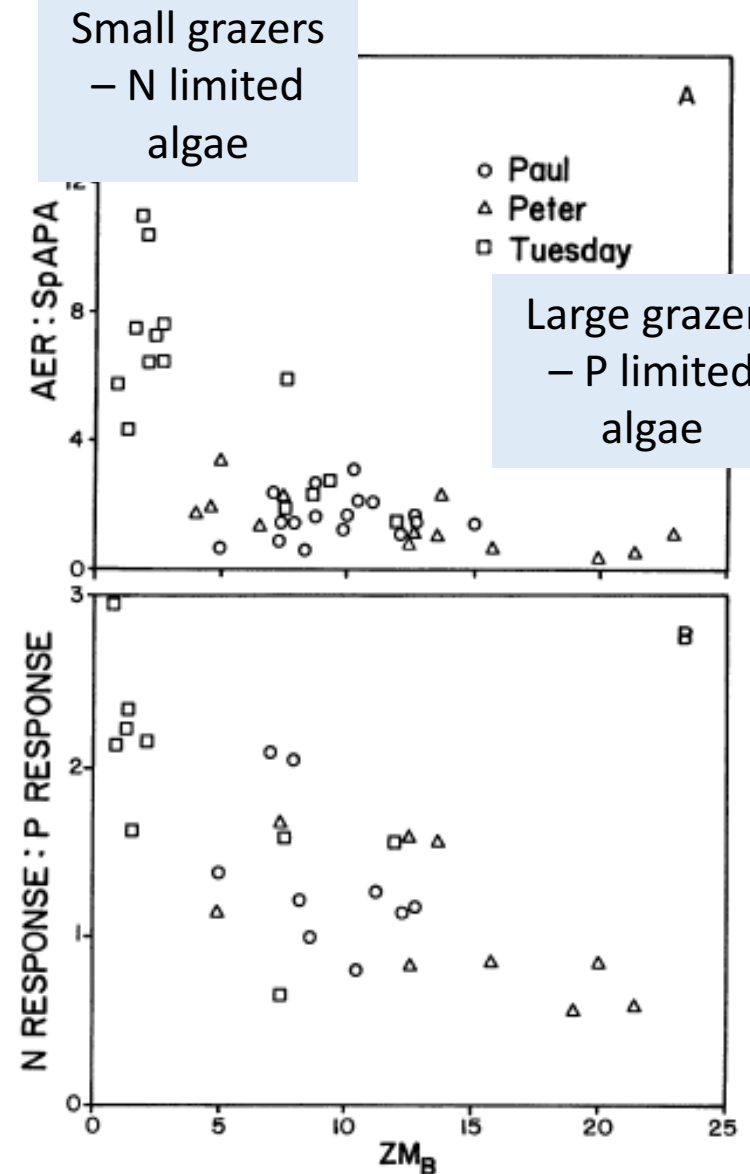


Fig. 5. AER:SpAPA (A) and N response:P response (B) vs.  $ZM_B$ .



Homeostasis “inflected” the relationships, depressing N:P released at low food N:P and increasing N:P released at high food N:P.

At the time of this paper, open Q was what was best value for zooplankton N:P. So calculated model with a range of values.

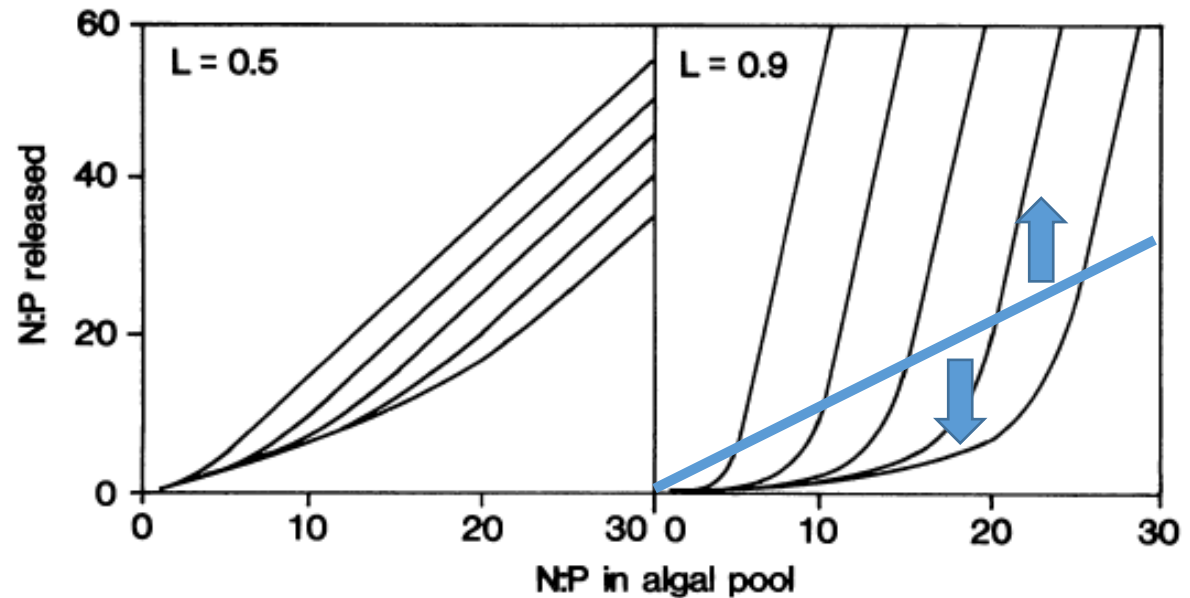


FIG. 3.—Under the model of strict homeostasis, the ratio of nitrogen to phosphorus (N:P) released and therefore resupplied to algae ( $s$ ) is predicted to vary with the N:P in the algal pool ( $f$ ) according to the curvilinear relationships pictured. Shown are solutions to equations (9) using  $L = 0.5$  (left) and  $L = 0.9$  (right) when  $b = 5$  (left curve), 10, 15, 20, and 25 (right curve).

Sterner AmNat 1990

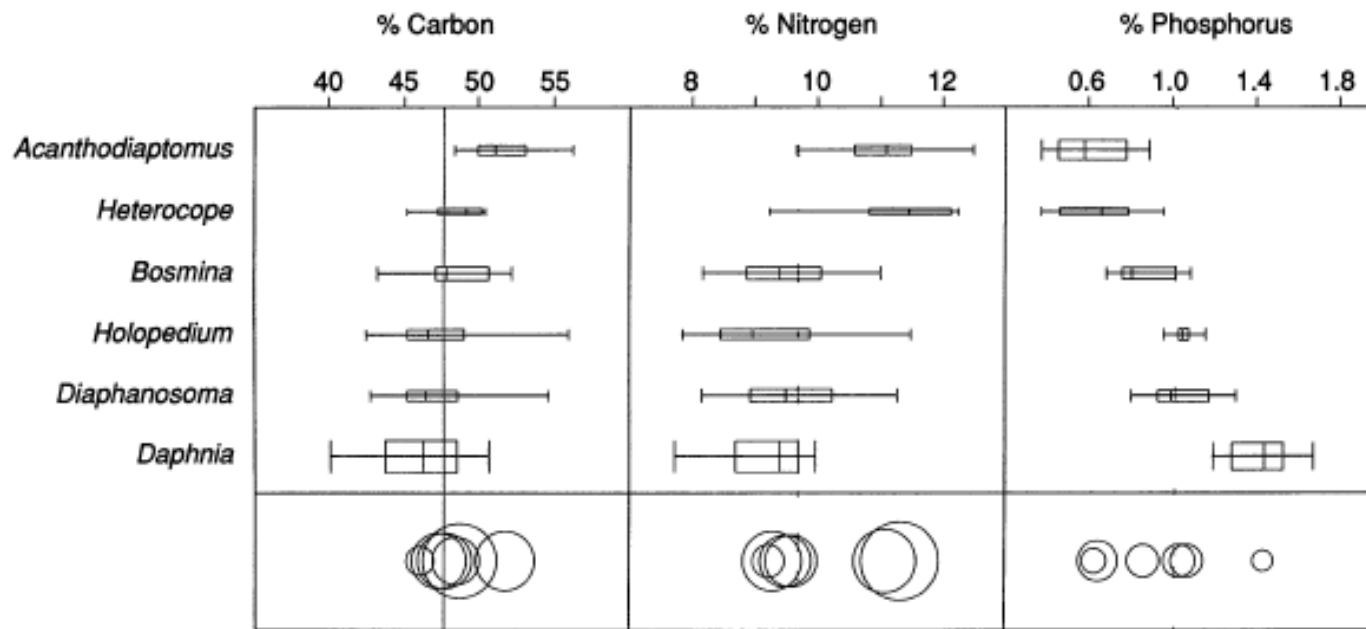
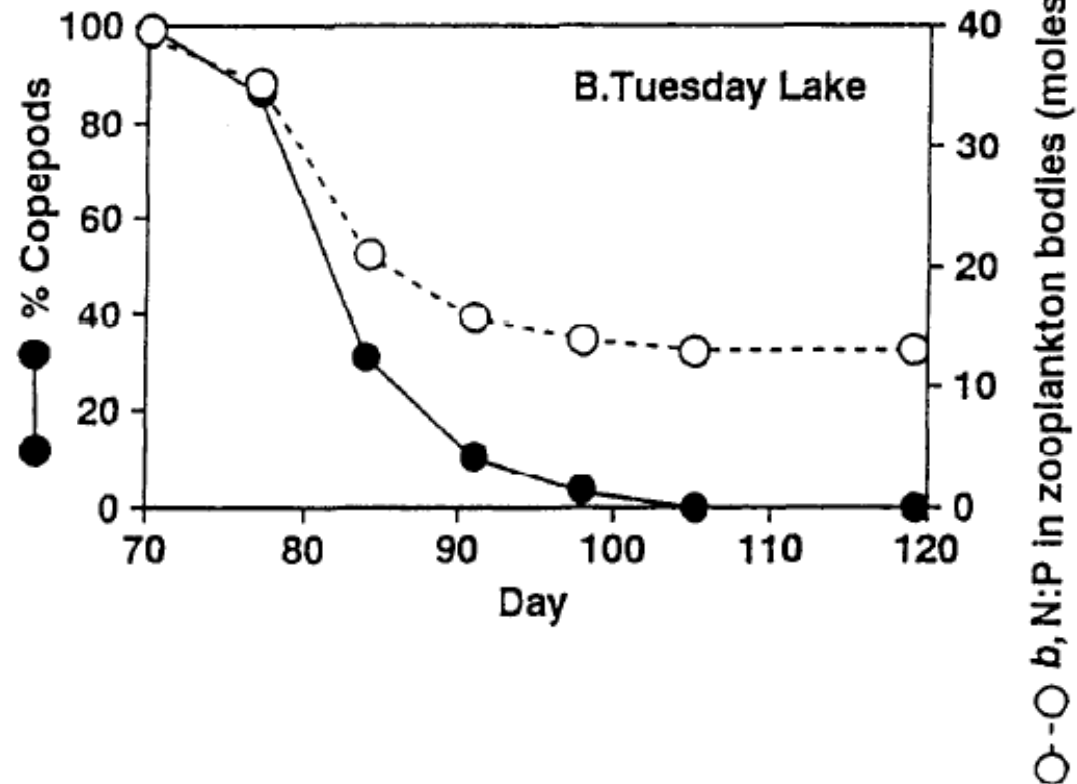
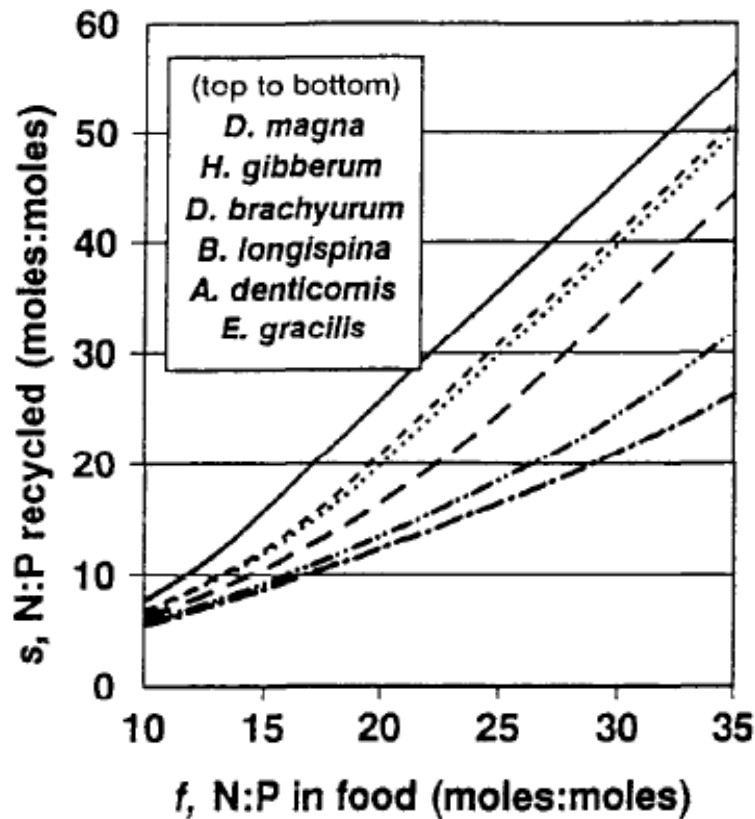


Fig. 2. Box-and-whisker displays of distributions of all field samples by zooplankton species and element (C, N, and P as percent of dry wt). Boxes indicate medians and the middle two quartiles; whiskers indicate the limits of the 10–90% percentiles. Box heights are proportional to sample sizes. Lower panels show comparison circles among species within an element; two distributions are considered different at a 95% C.L. if their circles are disjunct or have an outside angle of intersection  $< 90^\circ$ .

Not all crustacean zooplankton have same C, N, P.  
Daphnia high P, low N. Copepods high N, low P.

Andersen and Hessen L&O 1991



Used Sterner's recycling model and Andersen/Hessen measurements of zoop N:P to retroactively "predict" biogeochemical shifts observed by Elser et al. 1988.

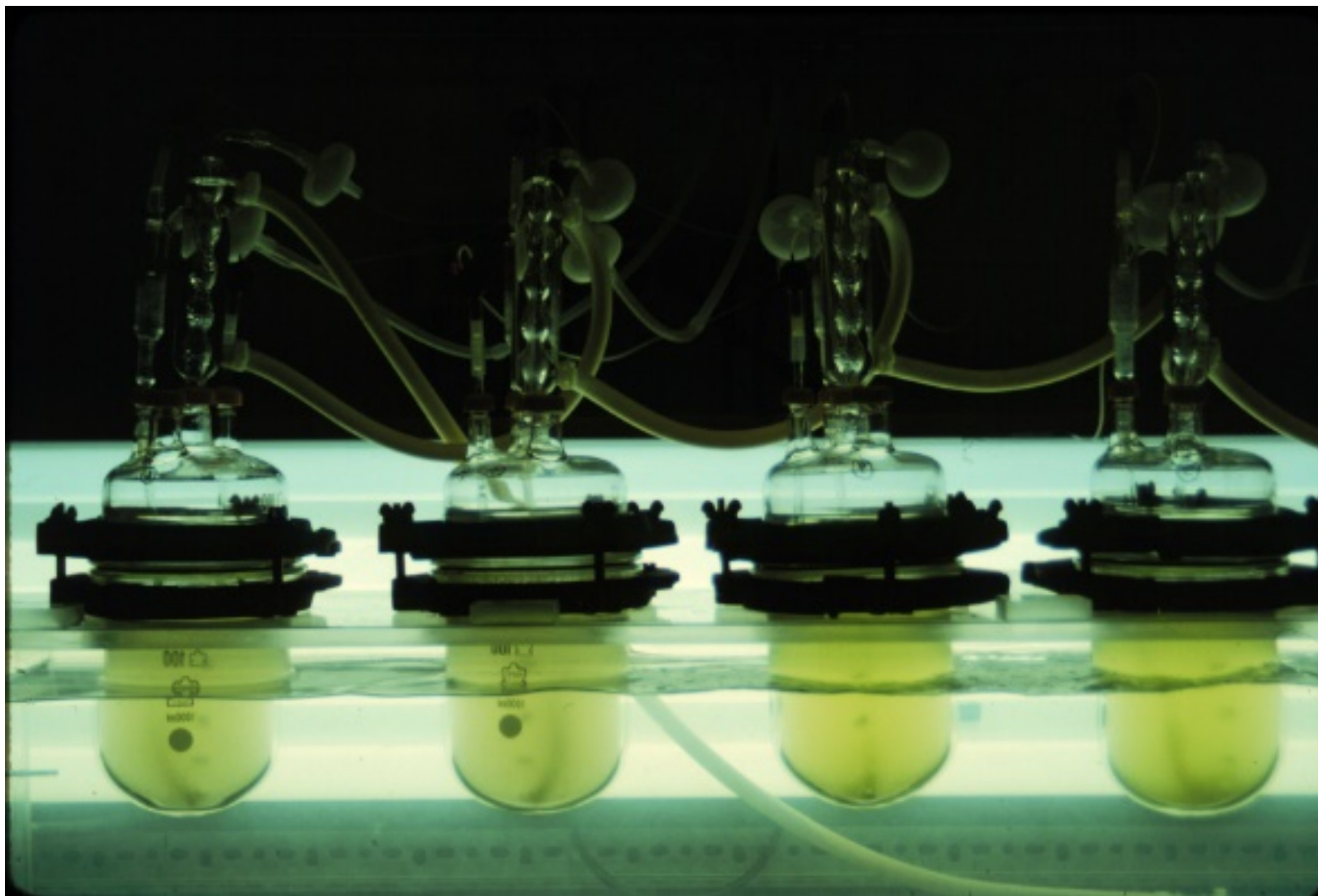
Linked food web shifts to biogeochemical cycling through stoichiometrically explicit modeling.

Sterner et al. Biogeochem 1992

# Stoichiometric building blocks

1. Species in ecosystems have multiple roles and affect biogeochemical cycling of multiple substances including the primary limiting nutrients.
2. We might predict some complex ecosystem dynamics with relatively simple mass-balance relationships.
3. Organisms are biodiverse and ALIVE!  
They don't fit into food webs/OCB like passive, linear transducers.

# Implications of stoichiometric mismatches



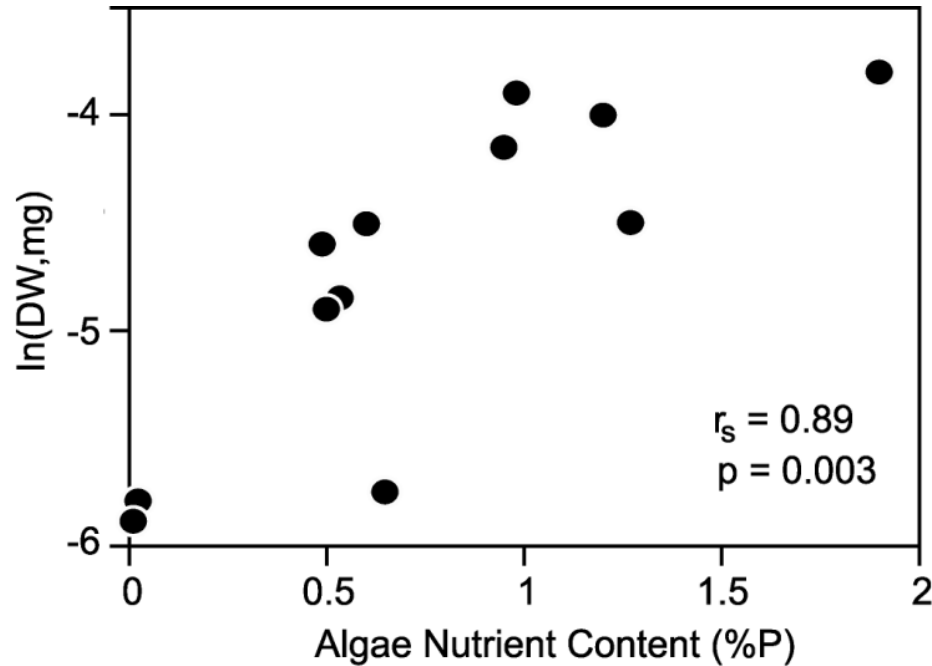
10-d old *Daphnia obtusa*.

One species of zooplankton herbivore, consuming one species of algae, had very different growth dynamics depending on how algae were grown.

Only years later did we learn that *D. obtusa* had very high body P and thus high P demands.

Photo: R. Sterner



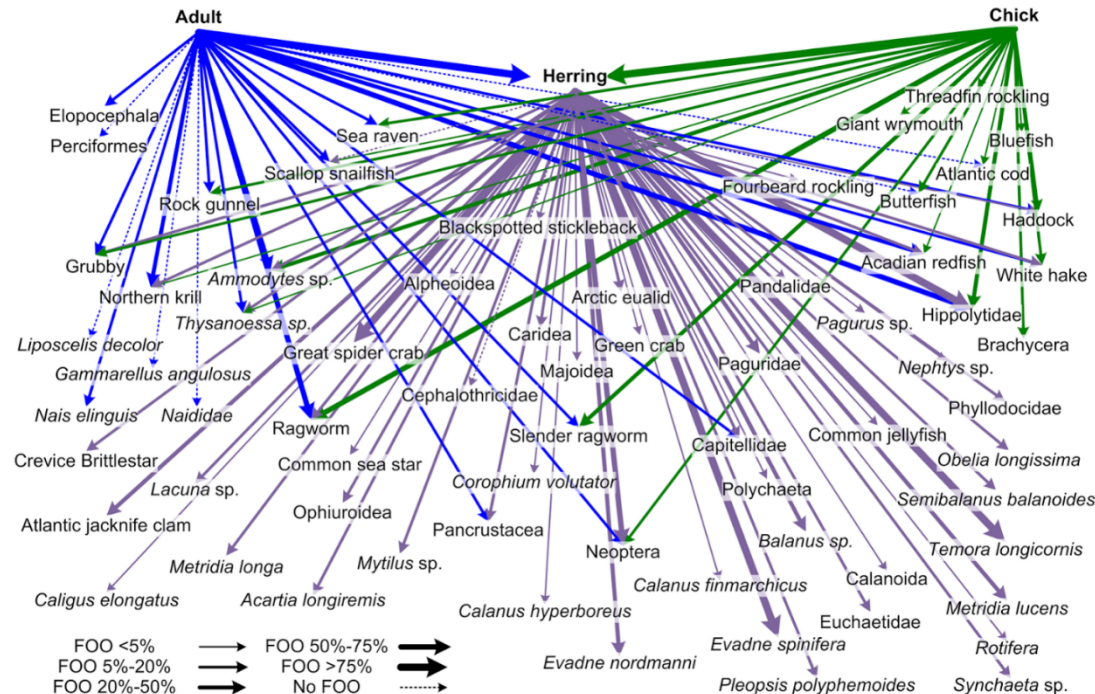


Variation in  
nutrient content of  
algae affects  
zooplankton  
growth.



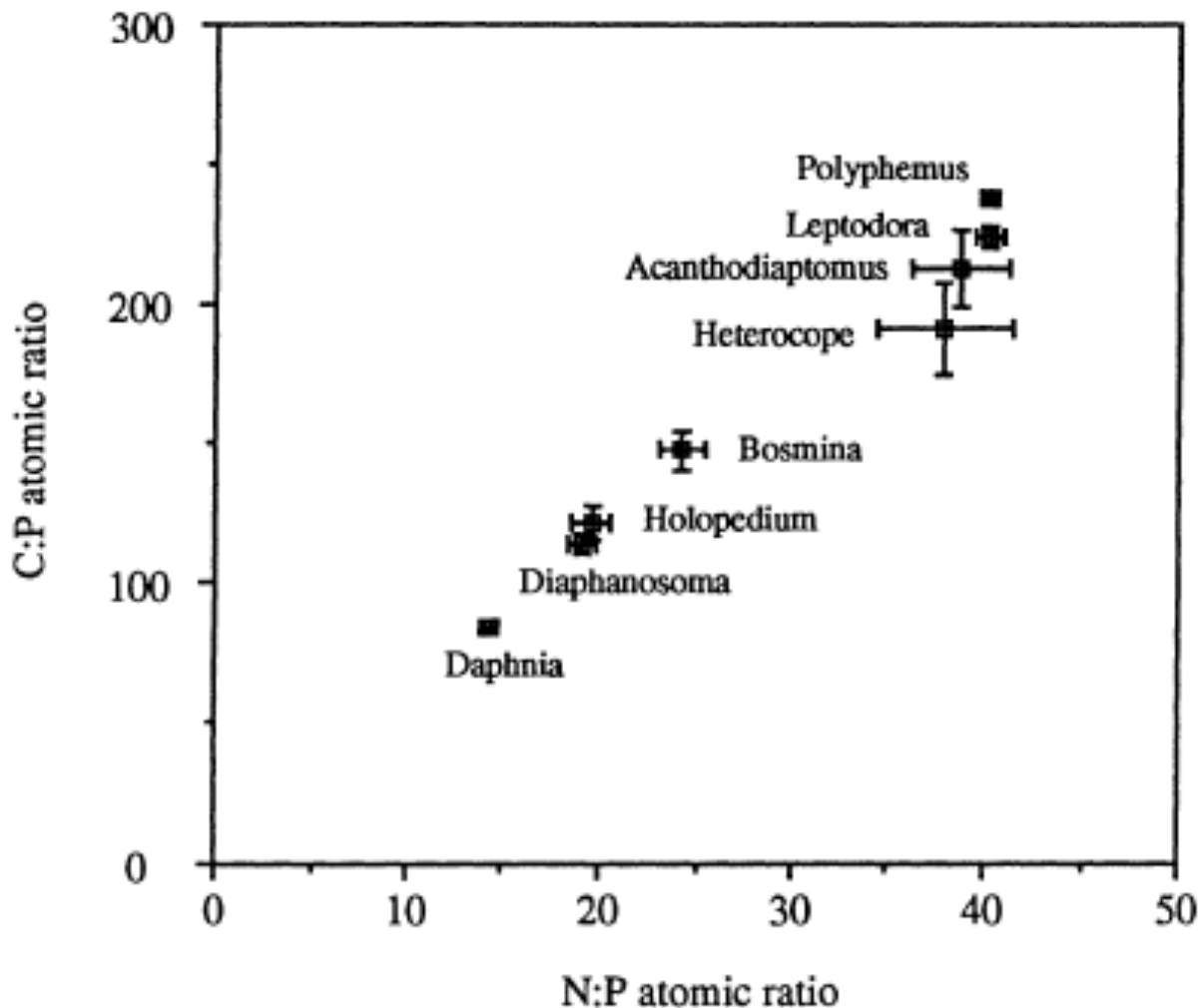
Biodiversity as a challenge, made more acute by advances in barcoding, etc.

Do we need a “new theory” for every subspecies of consumer?



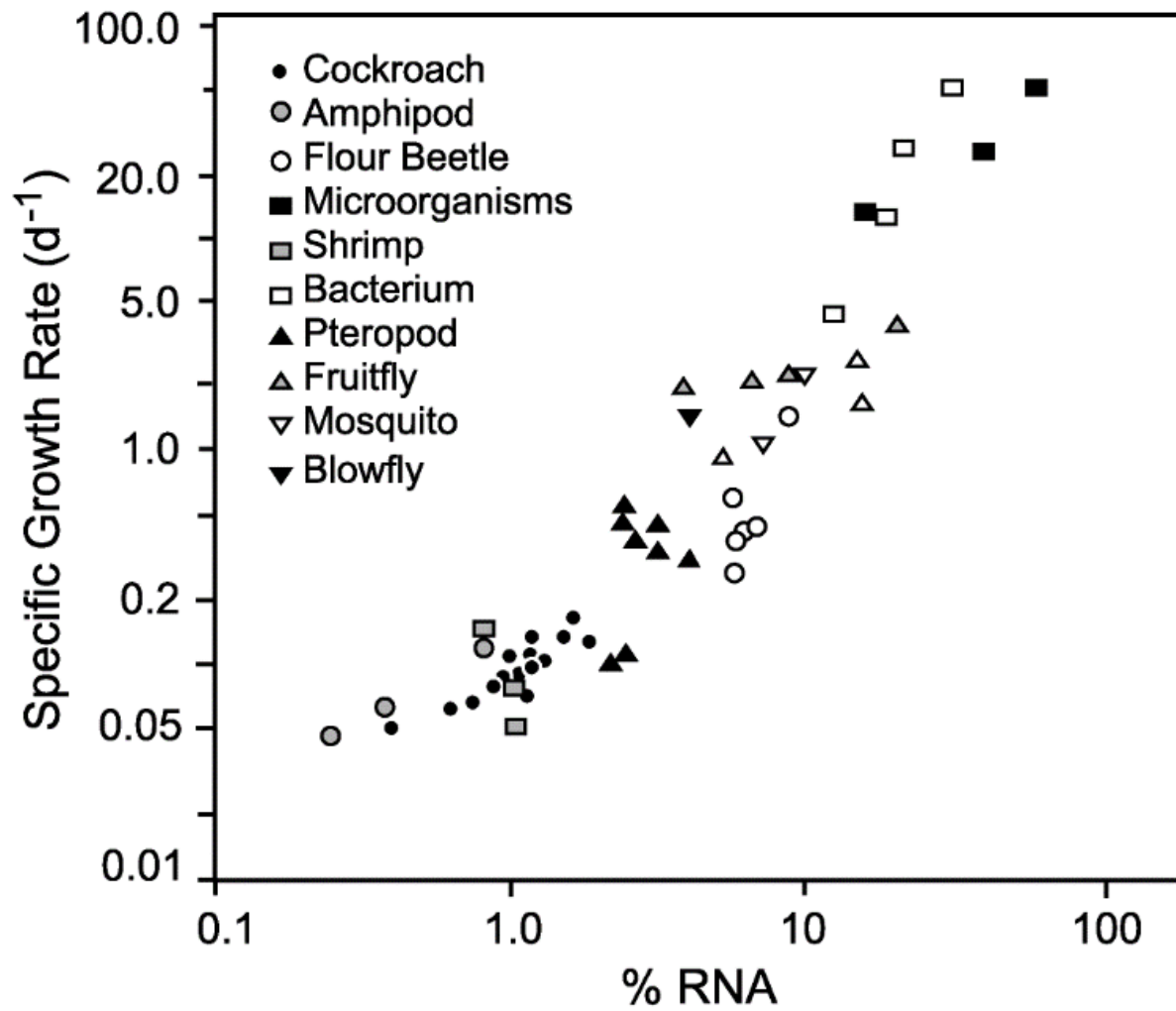
<http://dna-barcoding.blogspot.com/2014/03/from-puffins-to-plankton.html>

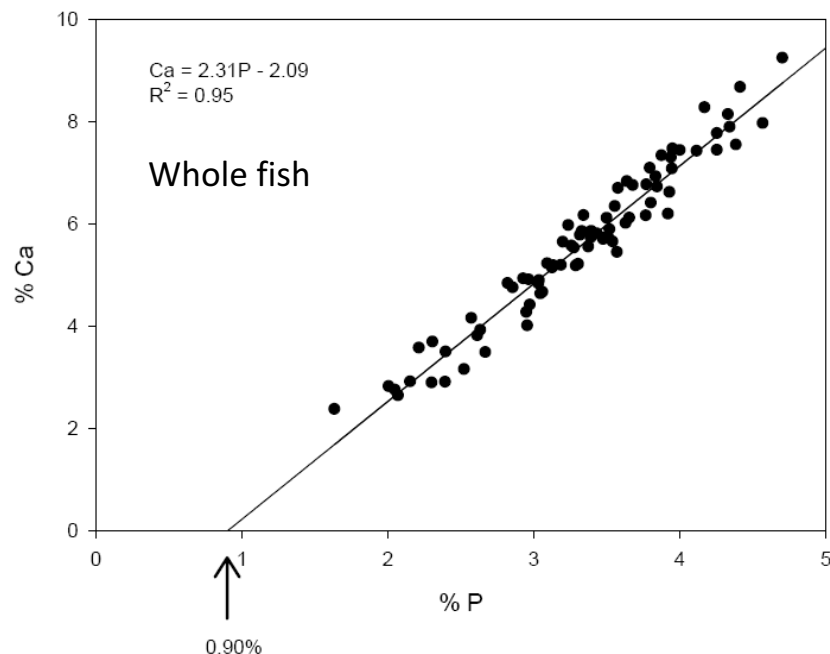
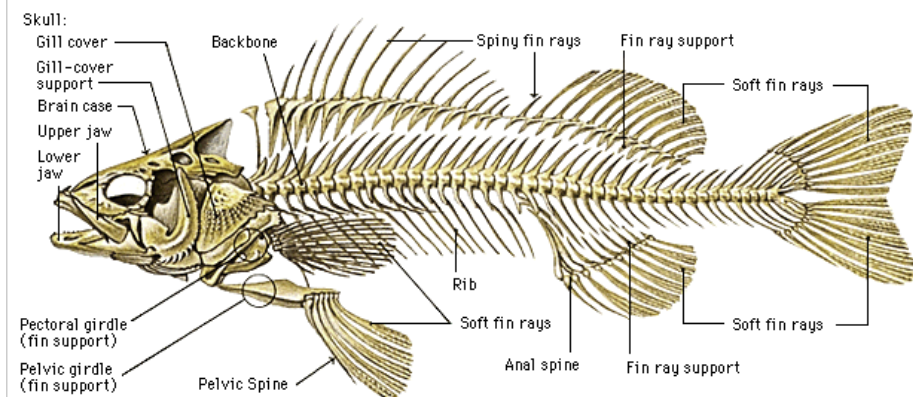
“Rules of Life”? (J. Olds, NSF-BIO)



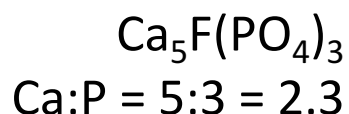
Unexpectedly high variation in elemental content of freshwater zooplankton while intraspecific variation was comparatively small.

Hypothesized that high P was related to high RNA and thus there was a tradeoff between high growth with good food and good growth on poor food.





Mineral form of P: Apatite



chlorine, hydroxyl, or carbonate  
often replacing the fluoride

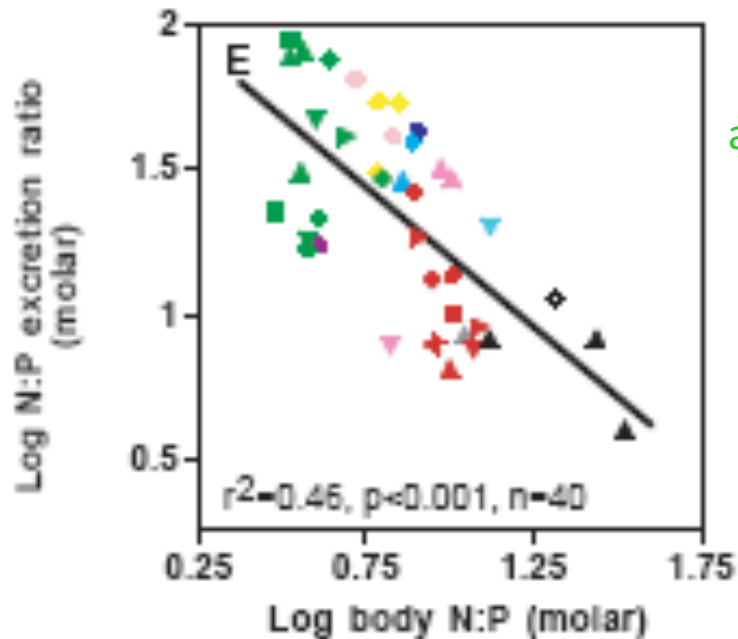


Hendrixson, H. A., R. W. Sterner, and A. D. Kay. 2007. Elemental stoichiometry of freshwater fish in relation to phylogeny, allometry and ecology. *Journal of Fish Biology* **70**: 121-140.

## REPORT

# Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes

Vanni, M. J., Flecker, A. S., Hood, J. M. & Headworth, J. L. (2002). *Ecology Letters* 5, 285–293.

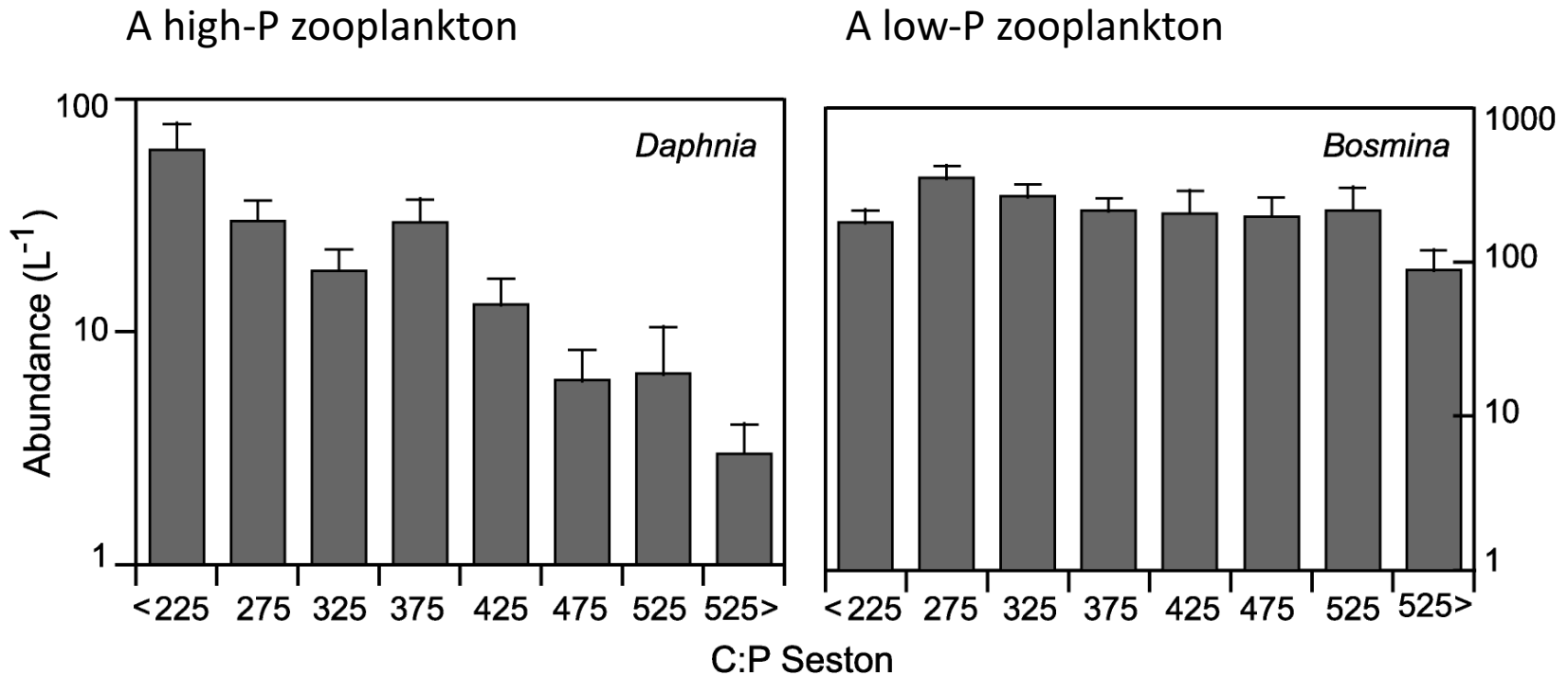


armored catfish

Characidae

tadpoles





Promising! A simple measure (P content of animal) was associated with something potentially very complicated – how fast that animal grows on different living foods.

There have been some great successes in applying stoichiometric relationships to organism growth and nutrient cycling.

But not all studies that attempt this find high predictive power with stoichiometry.

More on the importance of  
growth



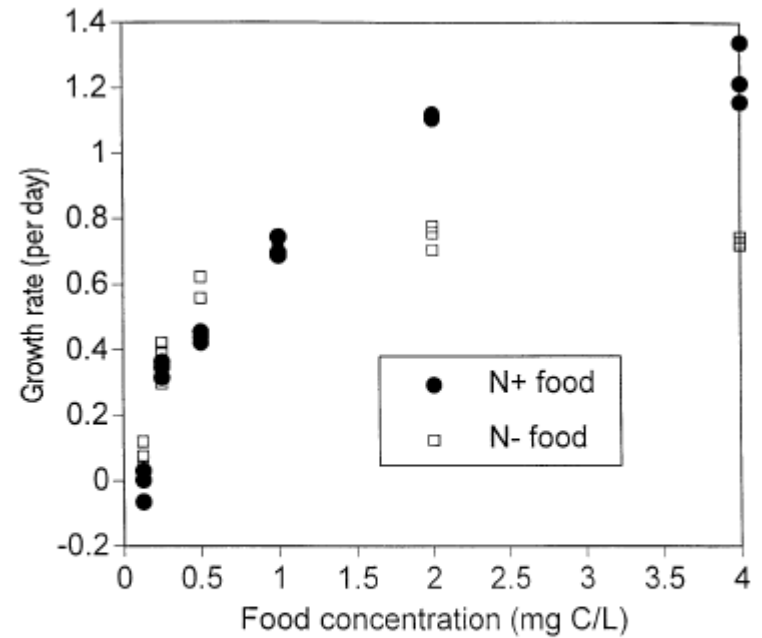
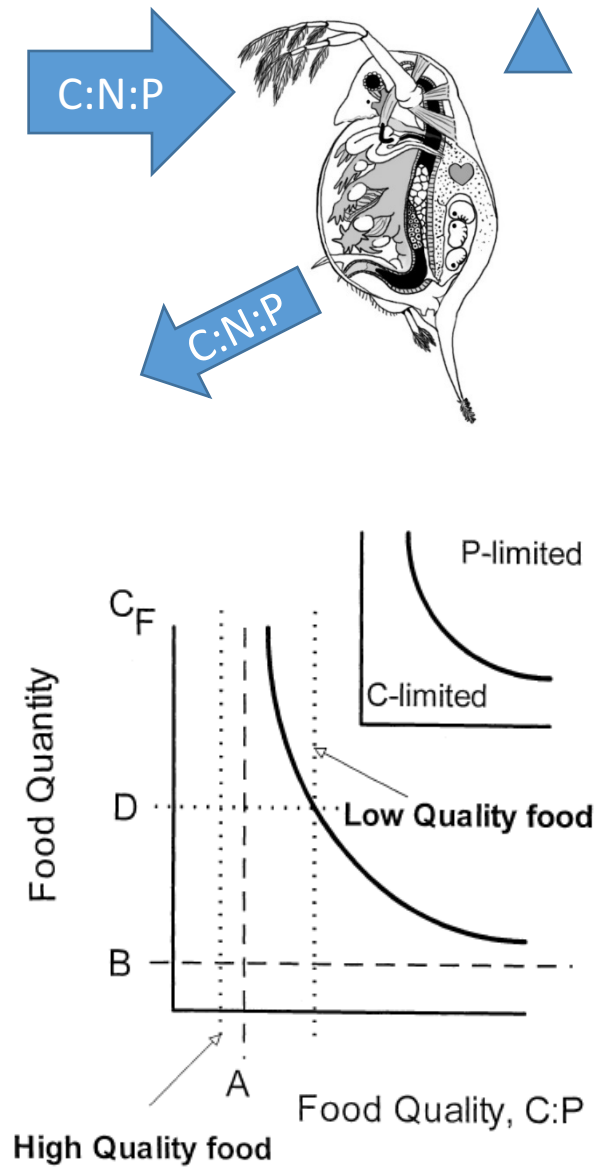


Fig. 3 Growth rates of the rotifer *Brachionus rubens* as a function of food quantity and quality (redrawn from original data provided by K.-O. Rothhaupt, published originally in Rothhaupt, 1995).

Sterner Freshwater Biology 1997

## Carbon and phosphorus linkages in *Daphnia* growth are determined by growth rate, not species or diet

James M. Hood<sup>†,\*</sup> and Robert W. Sterner

Department of Ecology, Evolution and Behavior, University of Minnesota–Twin Cities, St. Paul, Minnesota 55108, USA

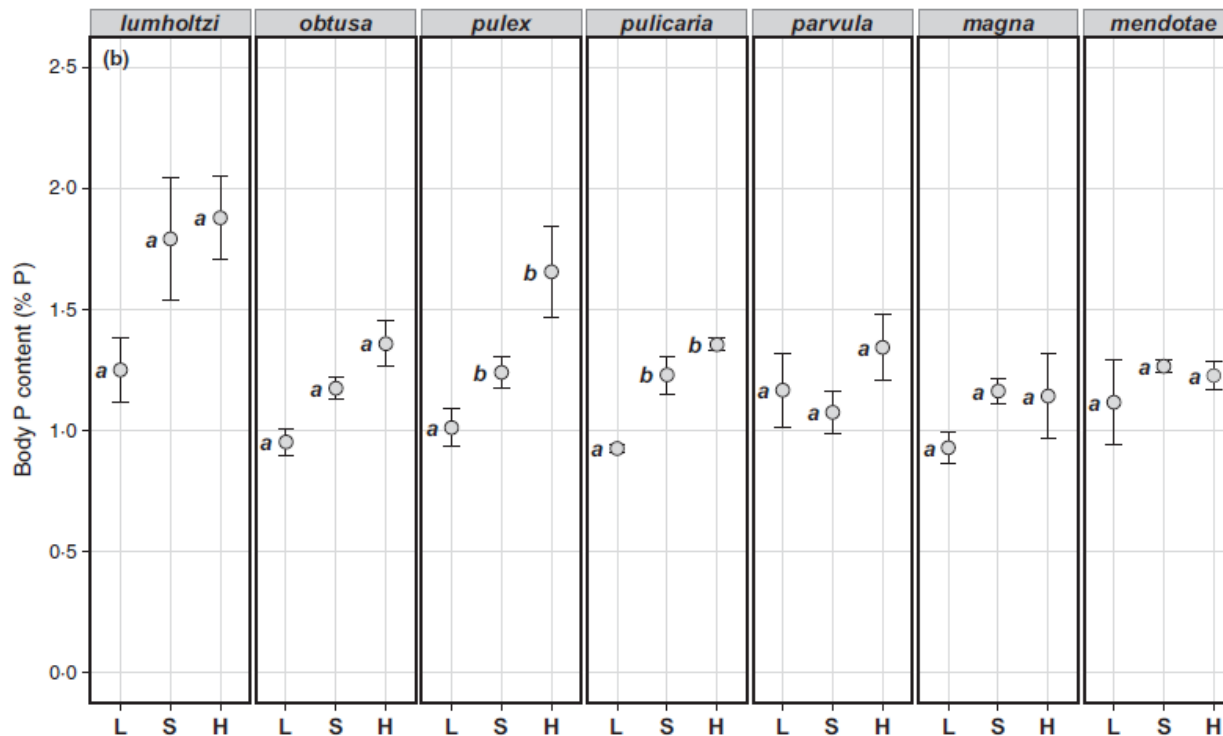


Fig. 2. Diet P strongly influences growth rates ( $F_{6,14} = 36.32$ ,  $P < 0.001$ ) and P contents ( $F_{6,14} = 5.45$ ,  $P < 0.001$ ). Mean dry mass growth ( $\text{day}^{-1}$ , a) and percent P (b) for all seven species grown on three diets (L = low P, S = switch treatment and H = high P). Error bars are 1 standard error. Letters represent significant differences within a species among diets (Tukey HSD,  $P < 0.05$ ). Species are sorted by  $\mu_{DM}$  in the HP treatment.

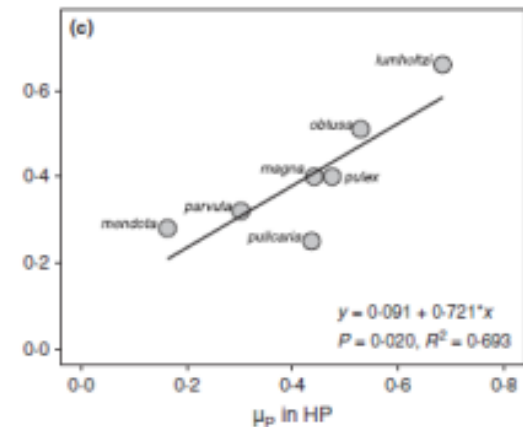
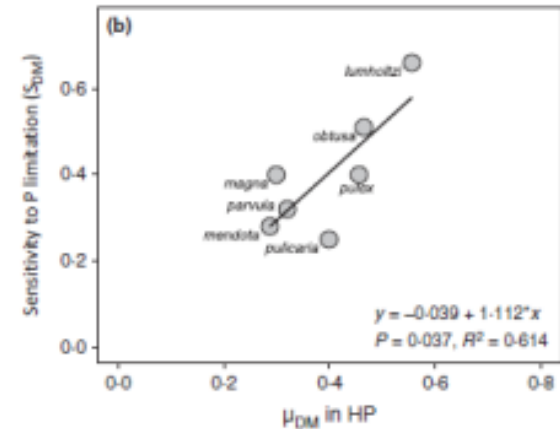
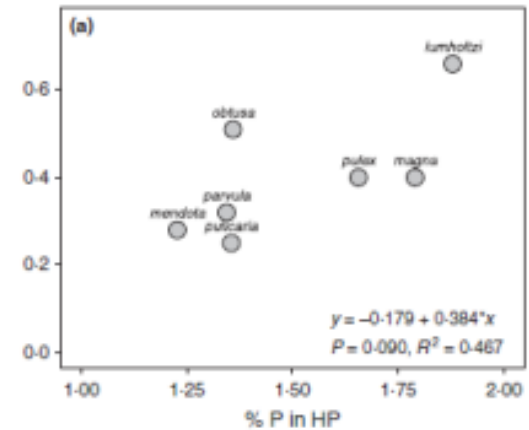
Q: What determines the sensitivity of growth to P limitation? Are “high P” species more sensitive?

Fast growing species more susceptible to P limitation.

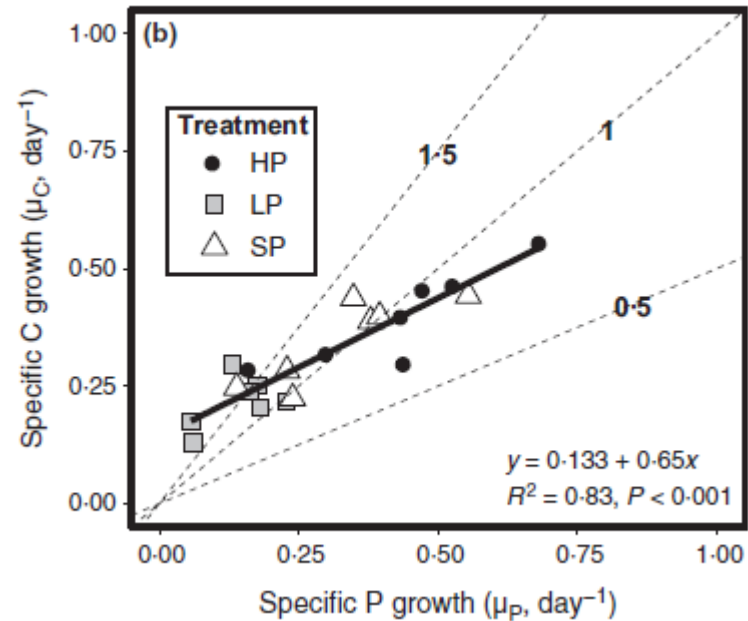
Growth:efficiency tradeoff.

“No” relation with P content at HP algae:

Plus relation with growth at HP algae:

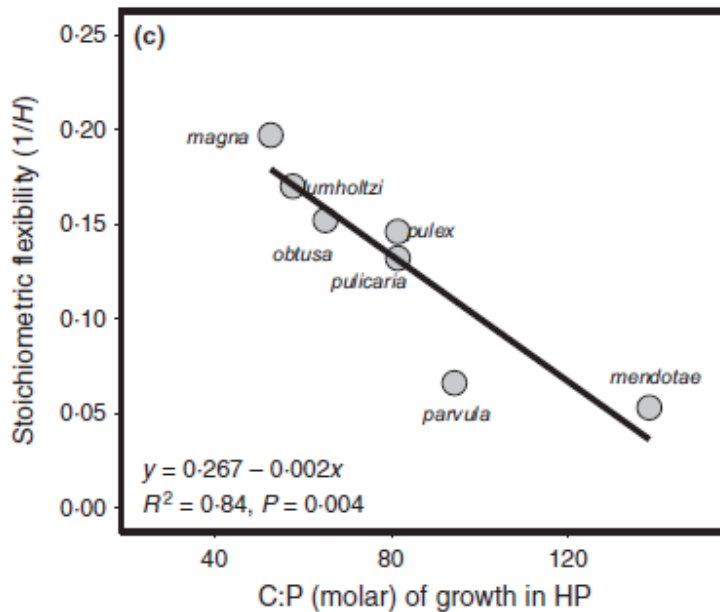


A perhaps universal relationship linking C and P additions associated with growth: As more P is added to body, relatively more C is added but not proportionately. Works across species and across treatment.



Species with low max growth, small scope for change in C:P.

Species with high max growth, large scope for change in C:P.



# Take Homes

Ecological stoichiometry is based on rules for linking elements during organism growth. These then feed back on production dynamics and ecosystem properties.

The art of making things just complicated enough to explain patterns but not more so remains a challenge.

# Thank you!



@bobsterner