A phytoplankton cellular allocation model

David (Roo) Nicholson, Scott Doney, Rachel Stanley

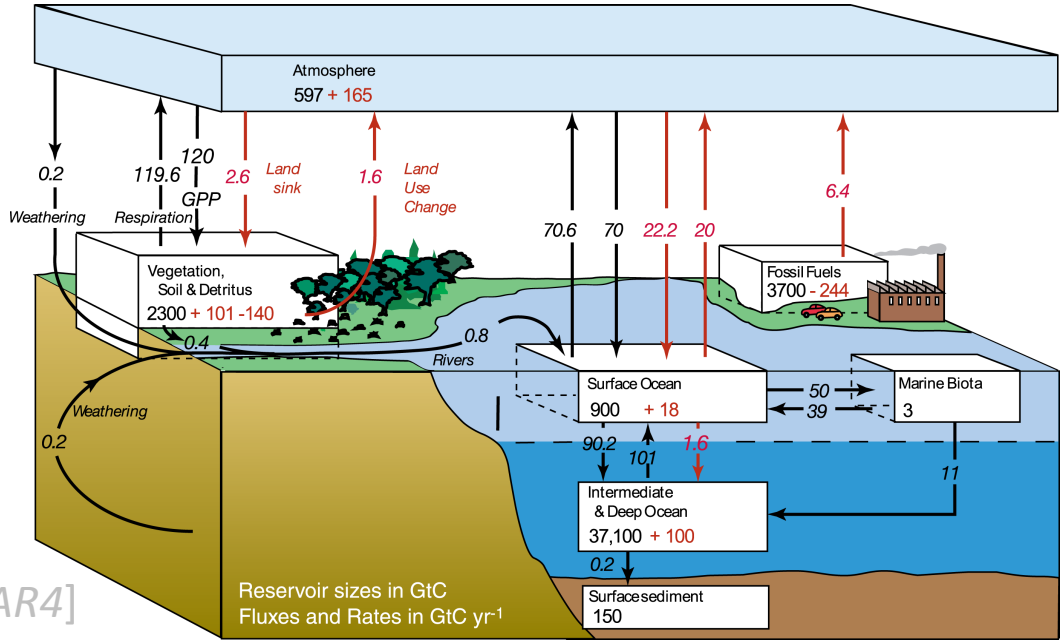
Woods Hole Oceanographic Institution

Overview

- Background information
  - Phytoplankton and the global carbon cycle
  - Relating biodiversity to biogeochemistry
  - Environmental controls on growth and composition
- Optimal cell allocation model (CAM) overview
  - Functional pools and physiological processes
  - Dynamic nutrient uptake
  - Photosynthesis, carbon fixation and ATP balance
  - Size and a ‘master’ variable
- CAM model results
  - Comparison to culture studies
  - Evaluation against primary production field observations
  - Future directions: nitrogen fixation as an example

The global carbon cycle

- Terrestrial C_{org} = 2300 Pg C (big number) // Gross Primary Prod. = 120 GtC yr^{-1}
- Marine Biota = 3 Pg C (small number) // Net Primary Prod. = 50 GtC yr^{-1}



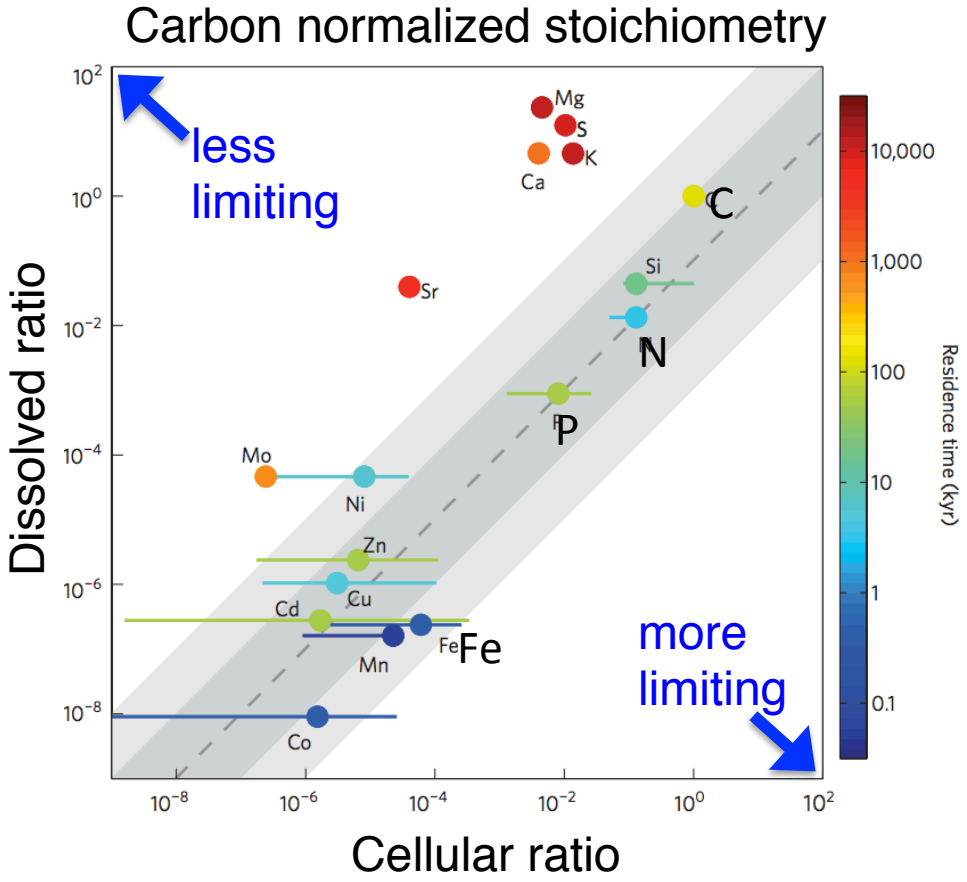
[IPCC AR4]

Unicellular phytoplankton mediate large carbon fluxes and have a short (~day) residence time in the upper ocean. Community composition responds to changes in the physical environment on these short time scales.

What limits phytoplankton growth?

Stoichiometry is critical. Variations from canonical Redfield Ratio (C:N:P = 106:16:1) are significant, especially for less abundant elements

- Light for photosynthesis
- Carbon
- Macronutrients (N and P)
  - P more variable than N
- Micronutrients (e.g. metals)
  - More flexible than macro
- Limitation is dictated by supply versus demand

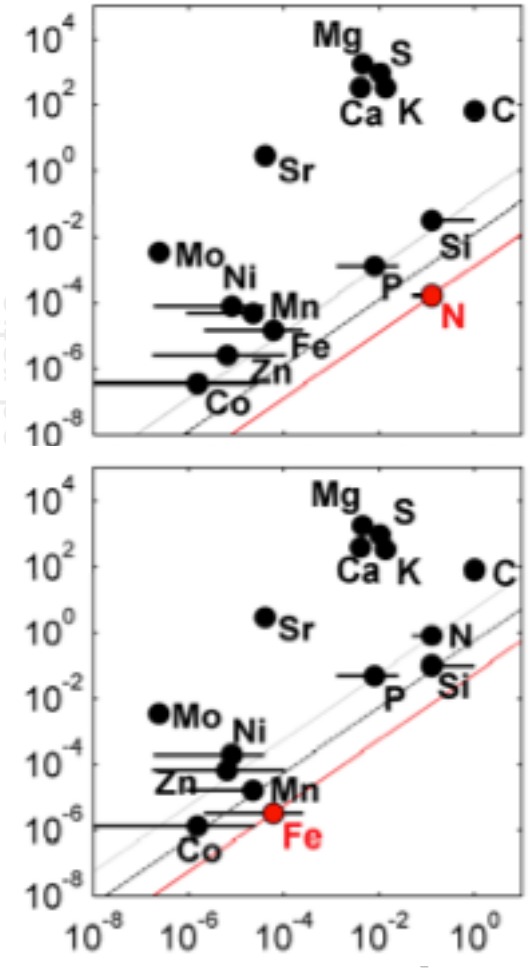


[*Moore et al.* 2013]

What limits phytoplankton growth?

Stoichiometry is critical. Variations from canonical Redfield Ratio (C:N:P = 106:16:1) are significant, especially for less abundant elements

- Light for photosynthesis
- Carbon
- Macronutrients (N and P)
  - P more variable than N
- Micronutrients (e.g. metals)
  - More flexible than macro
- Limitation is dictated by supply versus demand



N. Pac. Gyre (HOT)

N is proximal limiting

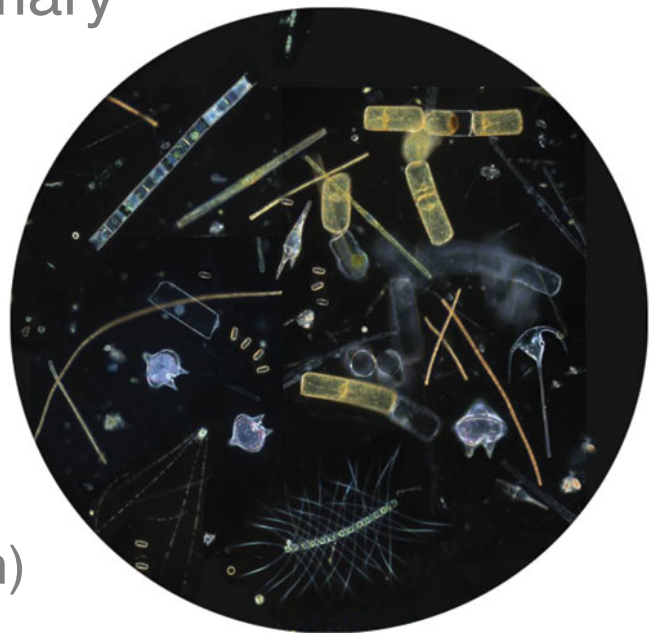
SAZ S. Ocean

Fe is proximal limiting nutrient

[*et al.* 2013]

Phytoplankton diversity

- A wide diversity of phytoplankton is responsible for the vast majority of primary productivity in the ocean
- Classified by cell size:
  - picoplankton (< 2 µm)
  - nanoplankton (2 – 20 µm)
  - Microplankton (20 – 200 µm)
- Classified by pathways:
  - Diazotrophs (N-fixing) (e.g. Trichodesmium)
  - Calcifiers (e.g. E. Huxlei)
  - Silicifiers (e.g. diatoms)
- Challenge: to model ocean diversity given observational and computational limits

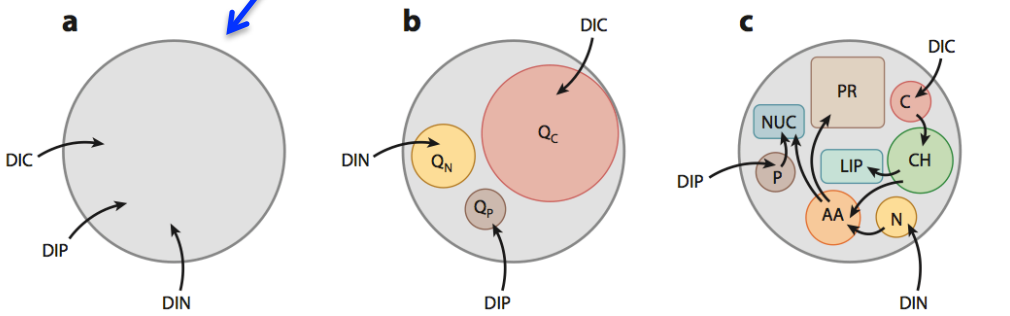


Modeling marine microbes

$$\mu = f(E, T, N, P, Fe, ...)$$

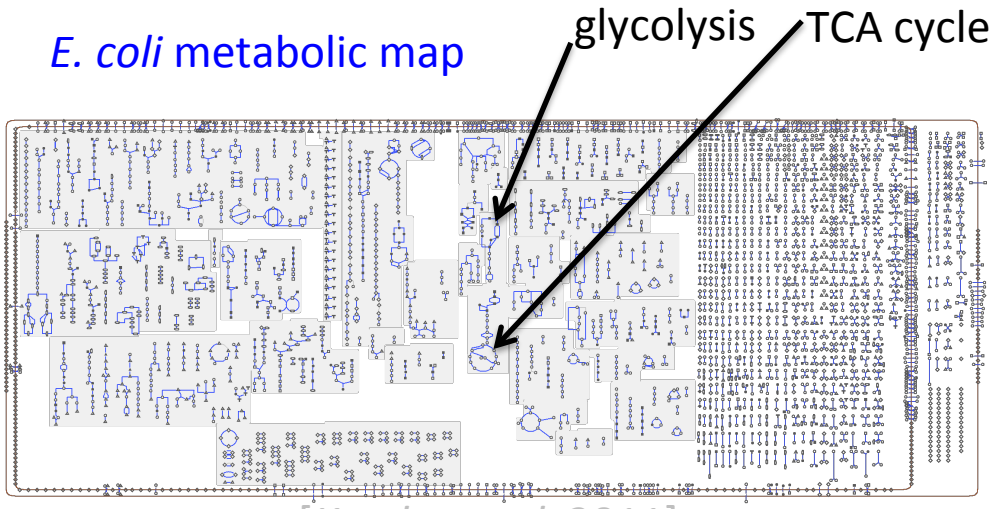
- What level of complexity is appropriate?
  - Computational limitations
  - Number of functional types, vs. cell complexity
  - How many unconstrained parameters?
- Optimal cellular allocation
  - Functional pools
  - Metabolic processes
  - Optimal resource allocation
  - Defining tradeoffs reduces free parameters

Most CMIP5 models



Monod Droop [*Follows et al.* 2011]

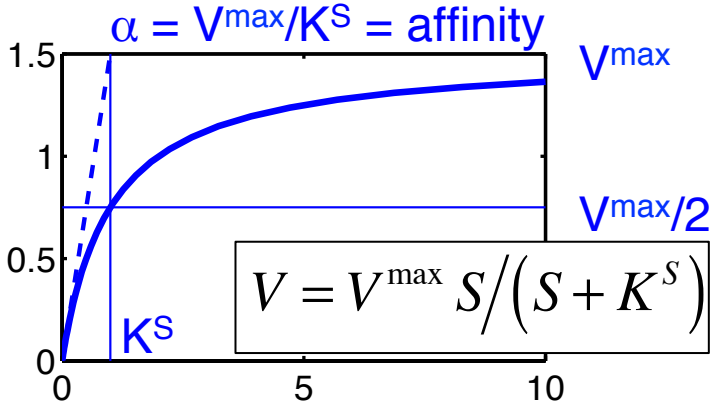
E. coli metabolic map

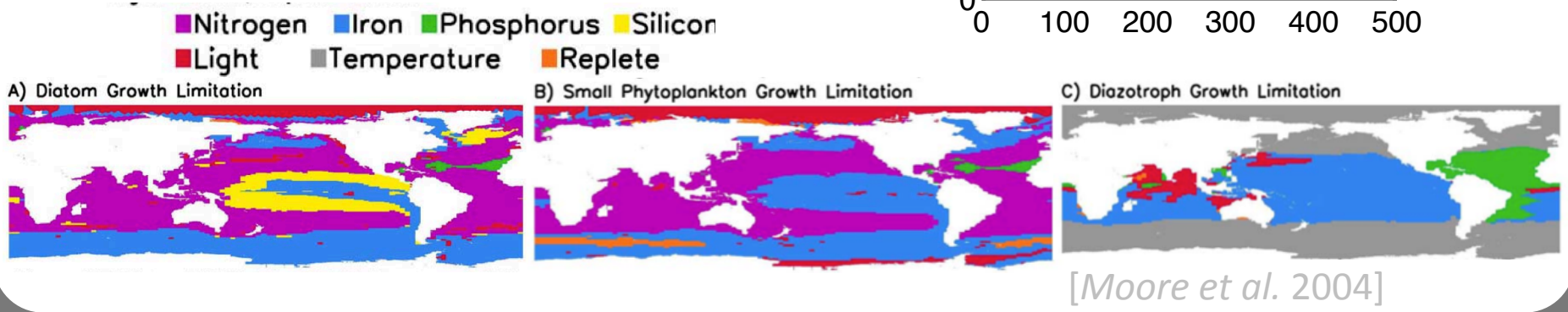


[*Kessler et al.* 2011]

CESM Ocean Ecosystem Model

- 3 phytoplankton functional types
  - Pico/nano, Diatom, Diazatroph
  - Calcifiers = fraction of Pico/nano
- Photoadaptation (Geider 98)
  - Variable chl:
  - Initial slope of P vs I: $\alpha = \alpha^{chl}(chl{:}C)$
- Modified Redfield Stoichiometry
  - Fixed C:N:P per functional type
  - Monod: uptake = growth
- Variable Fe and Si Quotas

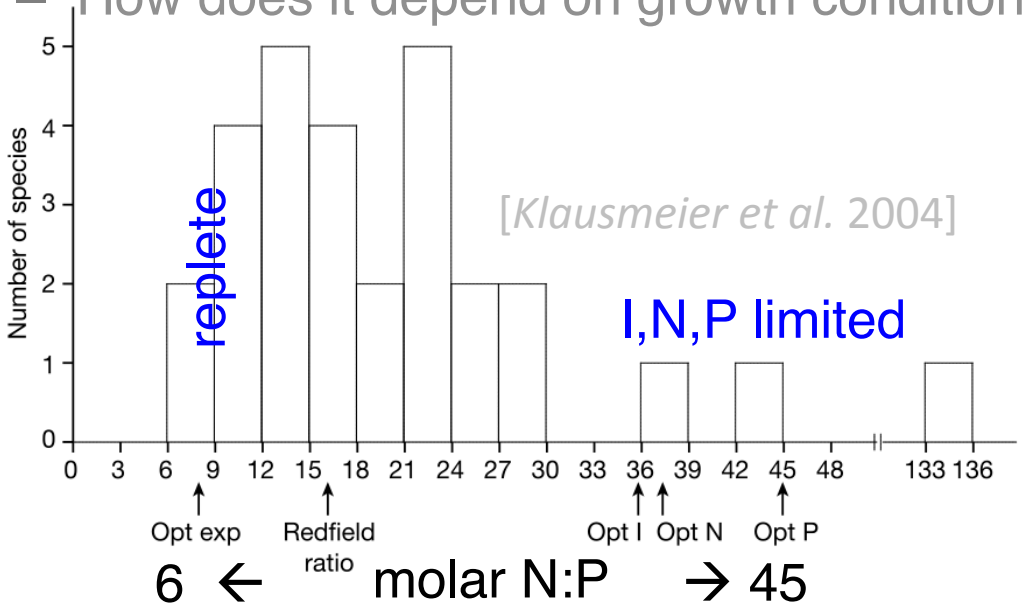




[Moore et al. 2004]

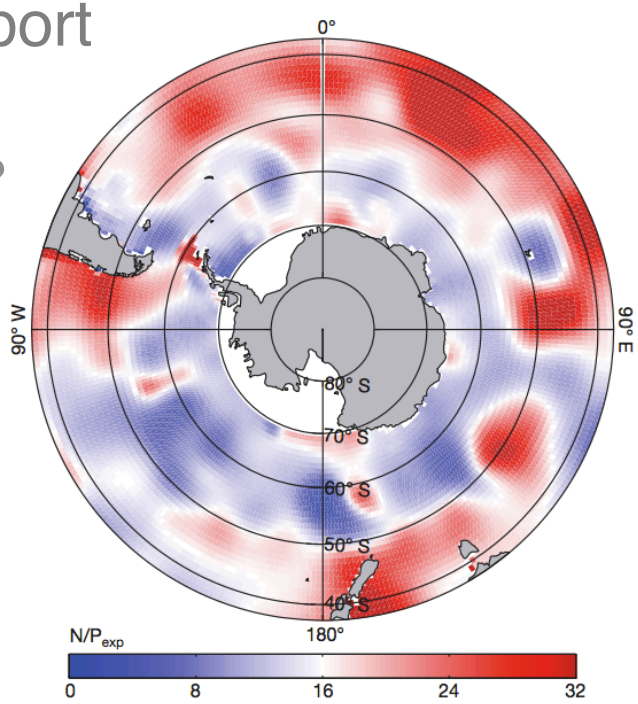
Implications for the carbon cycle

- What controls export and export efficiency (e-ratio)
  - Mineral ballast hypothesis: calcifiers and silicifiers more efficient?
  - Large cells more efficient than small cells?
  - Models need to predict the role of individuals
- Variability in C:N:P impacts carbon export
  - How does it depend on functional type?
  - How does it depend on growth conditions?



[*Klausmeier et al.* 2004]

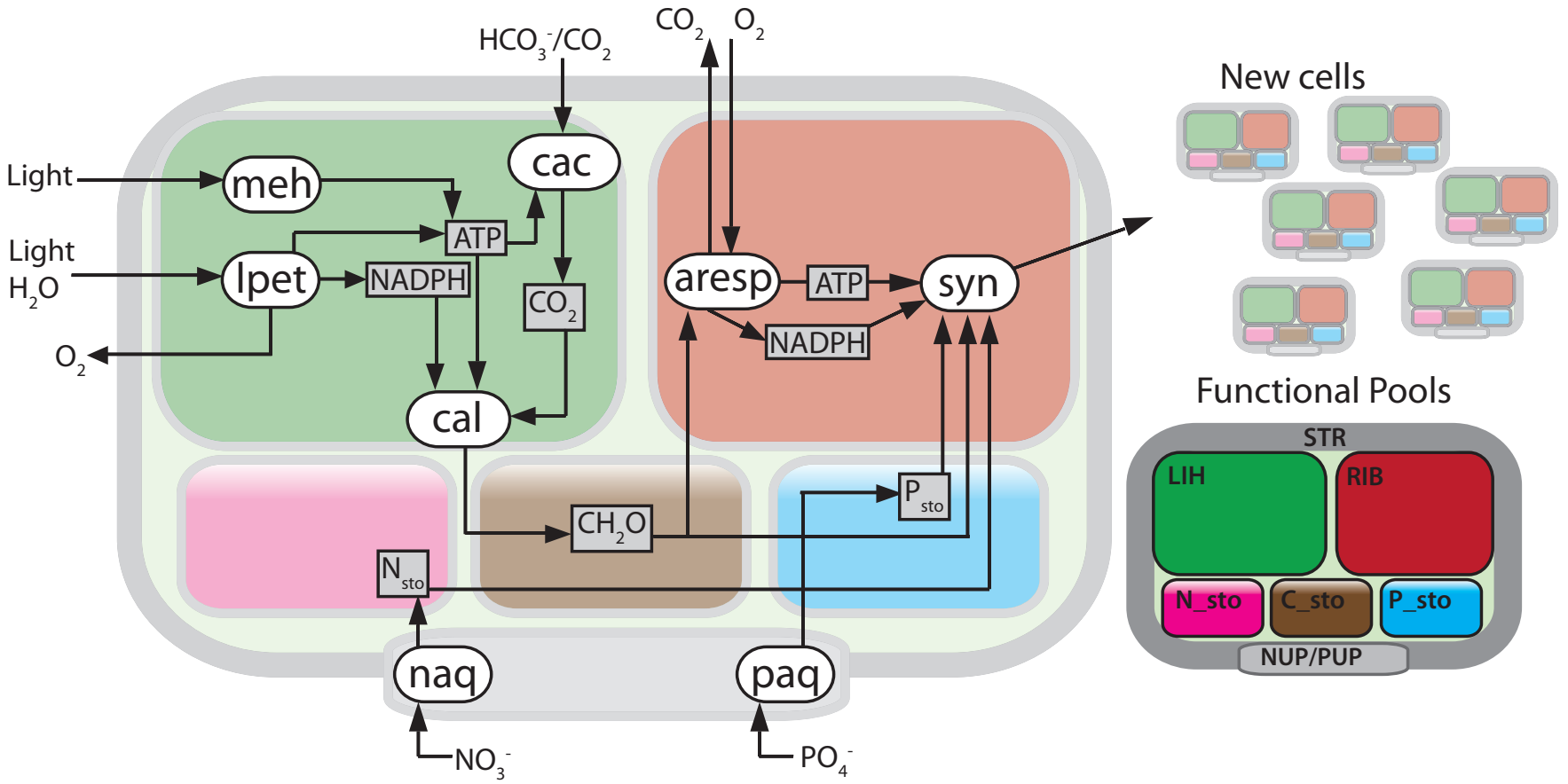
Export N:P



[*Weber and Deutsch* 2010]

CAM model principles

1. A cell as a number of functional pools interconnected by metabolic processes (e.g., Shuter, 1979)
2. Distinct C:N:P stoichiometry of functional pools (e.g., Klausmeier et al., 2004)
3. Dynamic nutrient uptake kinetics (e.g., Aksnes and Egge, 1991; Morel, 1987)
4. Allometric scaling of cell physiology/metabolism: cell radius as a master trait (e.g., Litchman et al., 2007)
5. Variable chl:C ratio (e.g., Geider et al. 1997,1998; Laws and Bannister 1980)
6. Quantifying both gross and net primary production (e.g., Halsey et al., 2010, 2013)

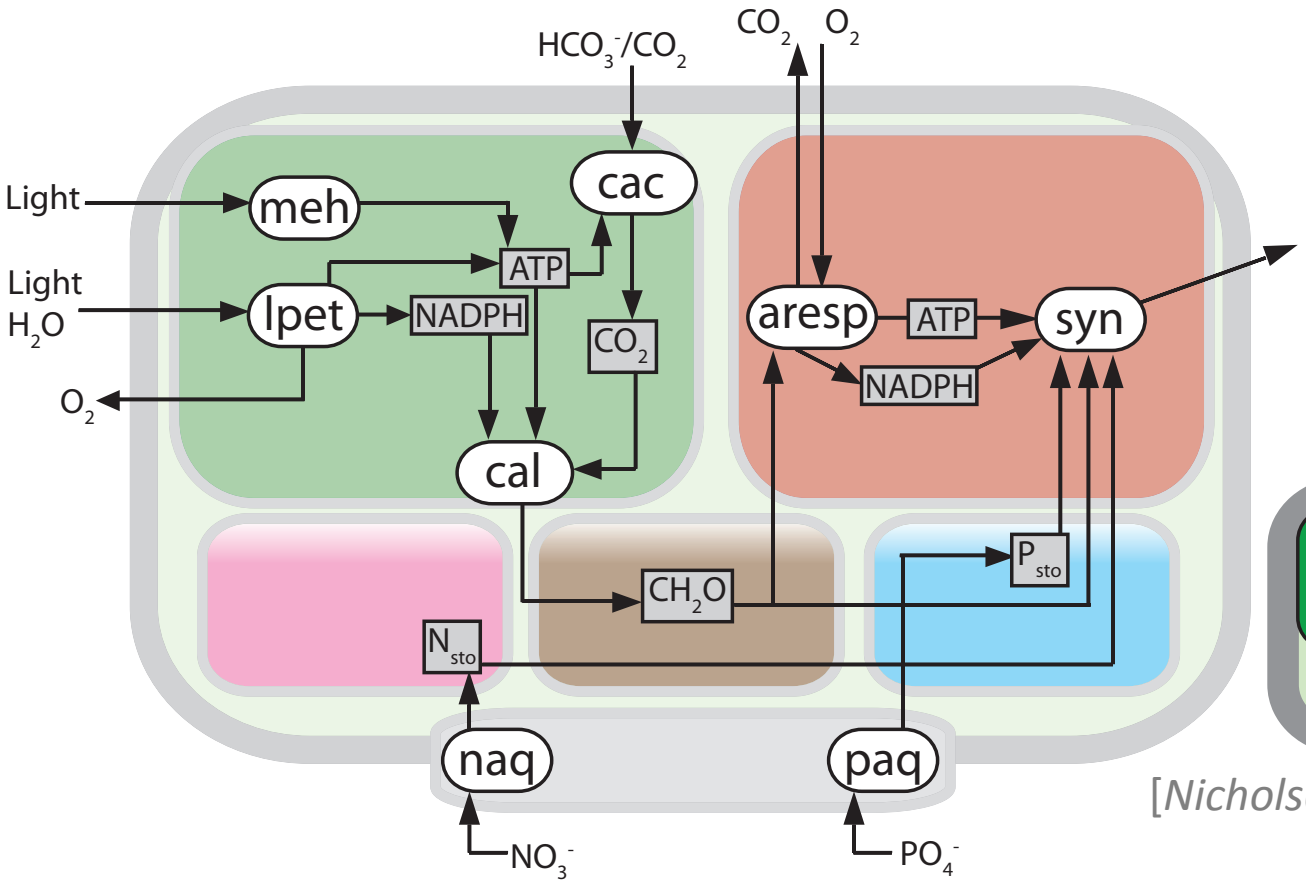


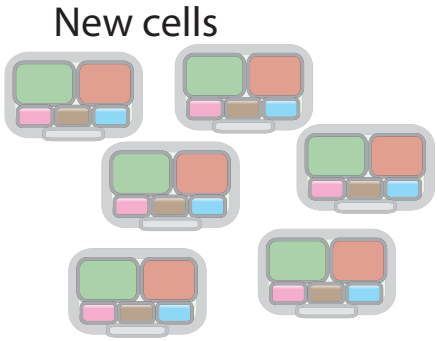
Functional Pools

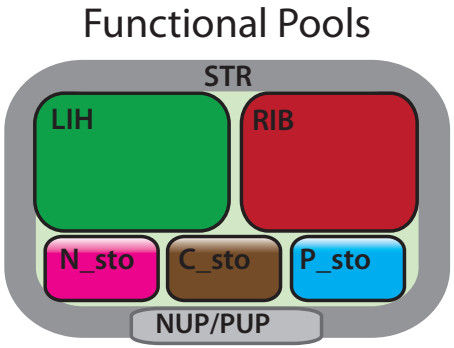
STR: Structural/cell wall
LIH: Light harvesting complex
RIB: Ribosomes and biosynthesis
STO: Storage of C, N and P
NUP/PUP: N and P transporter proteins

Metabolic processes

meh: Mehler/cyclic photosythetic pathways
lpet: Linear photosynthetic electron transfer
cac: Carbon acquisition and concentration
cal: Calvin cycle carbon fixation
aresp: Autotrophic respiration/catabolism
syn: Biosynthesis of new cells
naq:paq: Uptake/acquisition of inorganic N/P

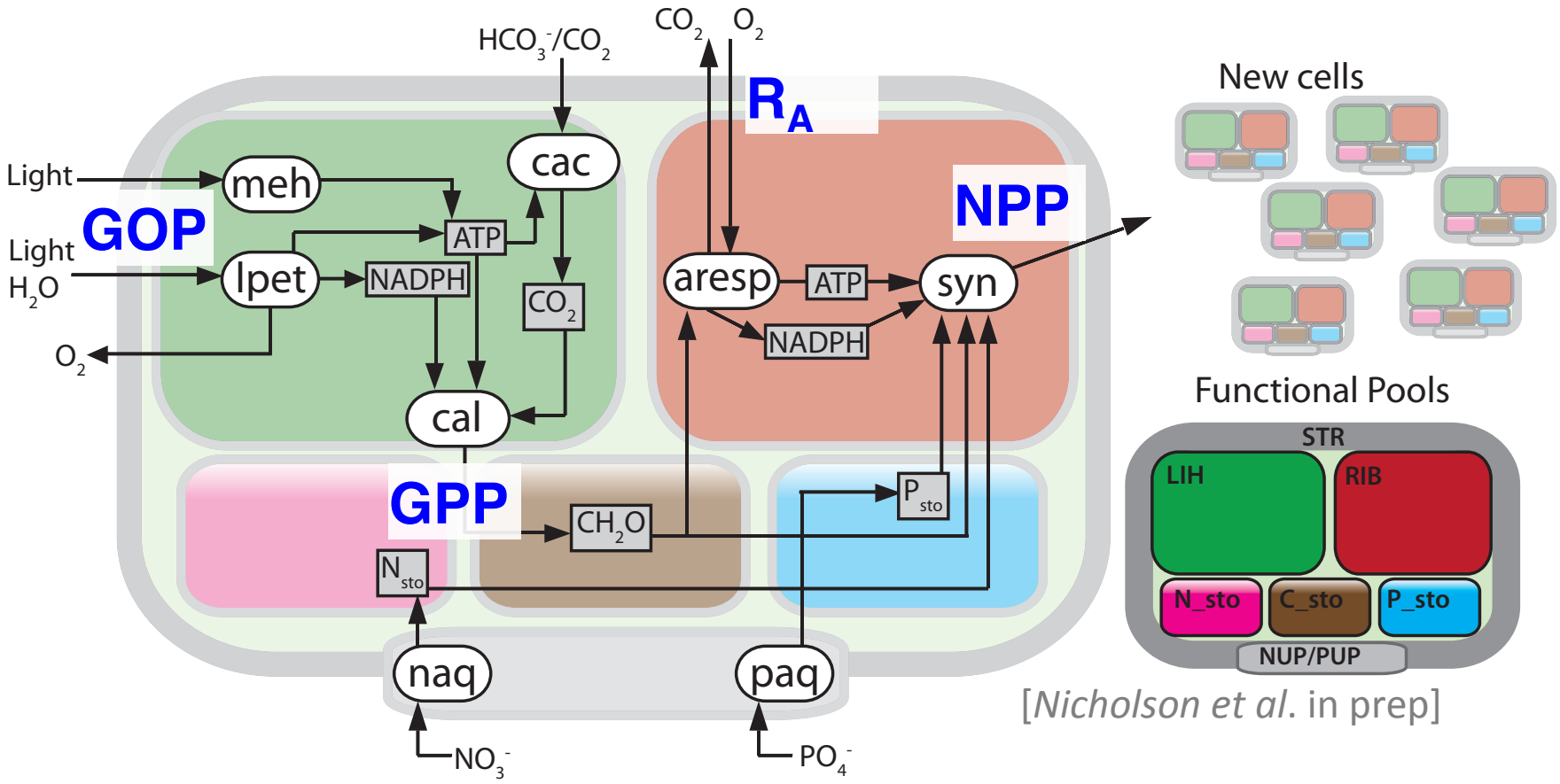






[*Nicholson et al.* in prep]

- Functional Pool Stoichiometry: **RIB** is P-rich. **LIH** is N-rich
  - P:C has more variability than N:C [e.g. *Klausmeier* 2004;*Sterner Elser* 2002]
- Photosynthetic pathways for ATP (**meh**) versus C-fixing (**lpet**)
  - ATP needed for carbon acquisition, nutrient uptake
- Autotrophic respiration (**aresp**) fuels biosynthesis

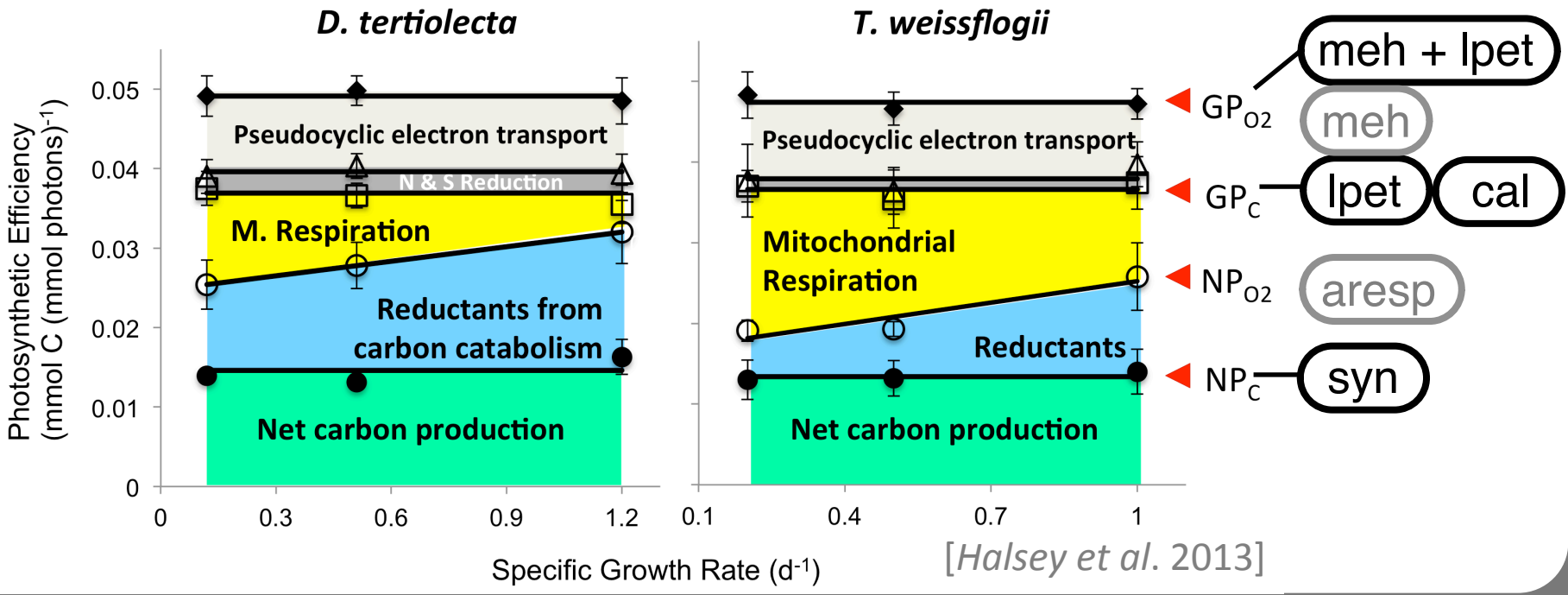


[*Nicholson et al.* in prep]

- Functional Pool Stoichiometry: **RIB** is P-rich. **LIH** is N-rich
  - P:C has more variability than N:C [e.g. *Klausmeier* 2004;*Sterner Elser* 2002]
- Photosynthetic pathways for ATP (**meh**) versus C-fixing (**lpet**)
  - ATP needed for carbon acquisition, nutrient uptake
- Autotrophic respiration (**aresp**) fuels biosynthesis

From photosynthesis to growth

- Allocation of photosynthate conserved across phytoplankton types
  - Chemostat cultures grown under nitrate limitation
  - Light limitation? Fe limitation? N-fixation?
- Only a fraction of GPP_{O2} ends up as net production (NPP_C)
  - GPP_C = 75% of GPP_{O2} and NPP_C = 40% of GPP_C
  - Ratios are constant under nitrate limited growth conditions



[*Halsey et al.* 2013]

CAM nutrient uptake

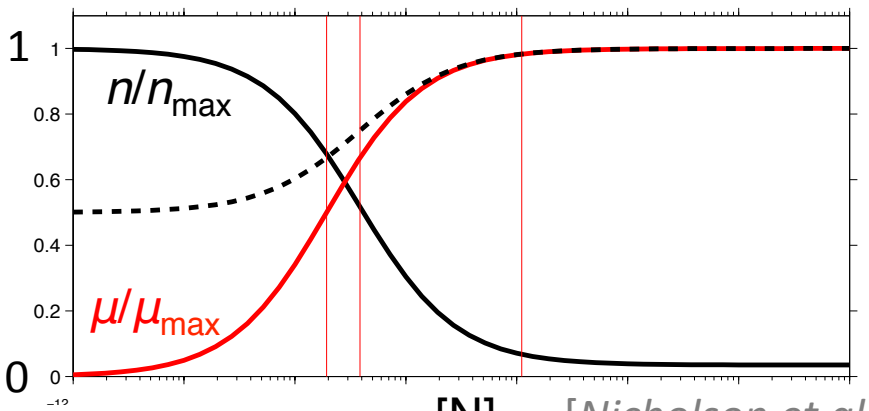
- Cells adjusts number of uptake sites on cell surface
  - Maximum density of nutrient transporters on cell surface
  - Fixed ion handling time, Diffusive supply inversely related to radius
  - Luxury uptake when acclimated to low nutrients
  - Small cells are more competitive for C-normalized uptake

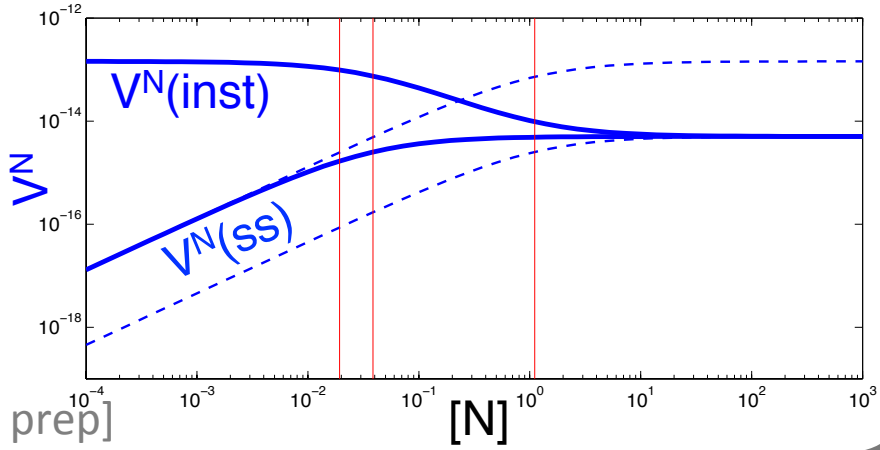
$$V^N = (n/h)\frac{N}{(Avh)^{-1} + N}$$

Affinity: $\alpha^N = nAD/r \propto r$

n = number of uptake sites
h = ion handling time (s^{-1})
A = ion catch area per site (m^2)
v = mass transfer coeff. (D/r) (m s^{-1})

Nutrient uptake kinetics

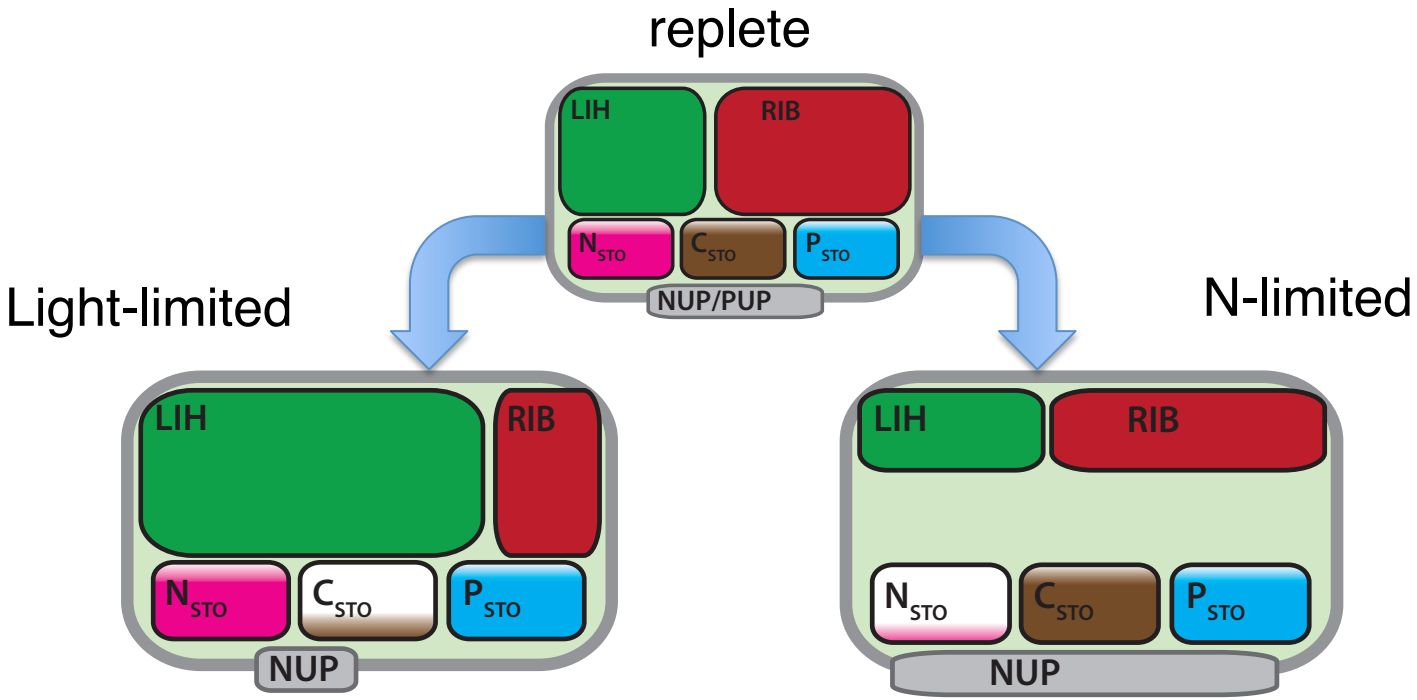




[*Nicholson et al.* in prep]

Acclimation to resource limitation

- Cells acclimate to maximize growth rate for given environment
  - Resources optimally allocated to functional pools



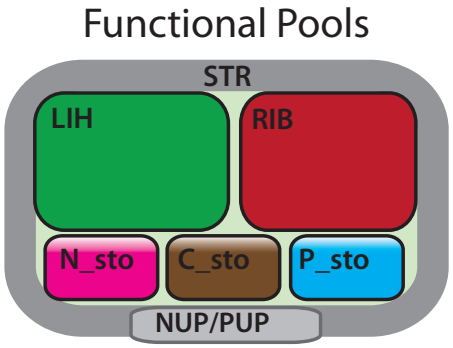
↑↓ in LIH to ↑ photosynthesis
↓ RIB as μ decreases
↓ In NUP

↓ in LIH and RIB as μ decreases
- lower N-Quota
- SA:C increases

↑ in NUP

Optimal allocation

- Solve for functional pool allocation that optimizes balanced growth (cell composition constant with time)
- System of equations



ATP production = ATP demand

$$A_{meh} + A_{lpet} = A_{cal} + A_{caq} + A_{nup/pup}$$

Growth rate * (N:C) = N uptake

$$V^N = \mu r_{tot}^N = \frac{a_{syn}\phi_{RIB}\left(1 - R_A\right)}{\phi_{TOT}} r_{tot}^N$$

Conservation of mass: ϕ_i = optimal allocation to pool *i*

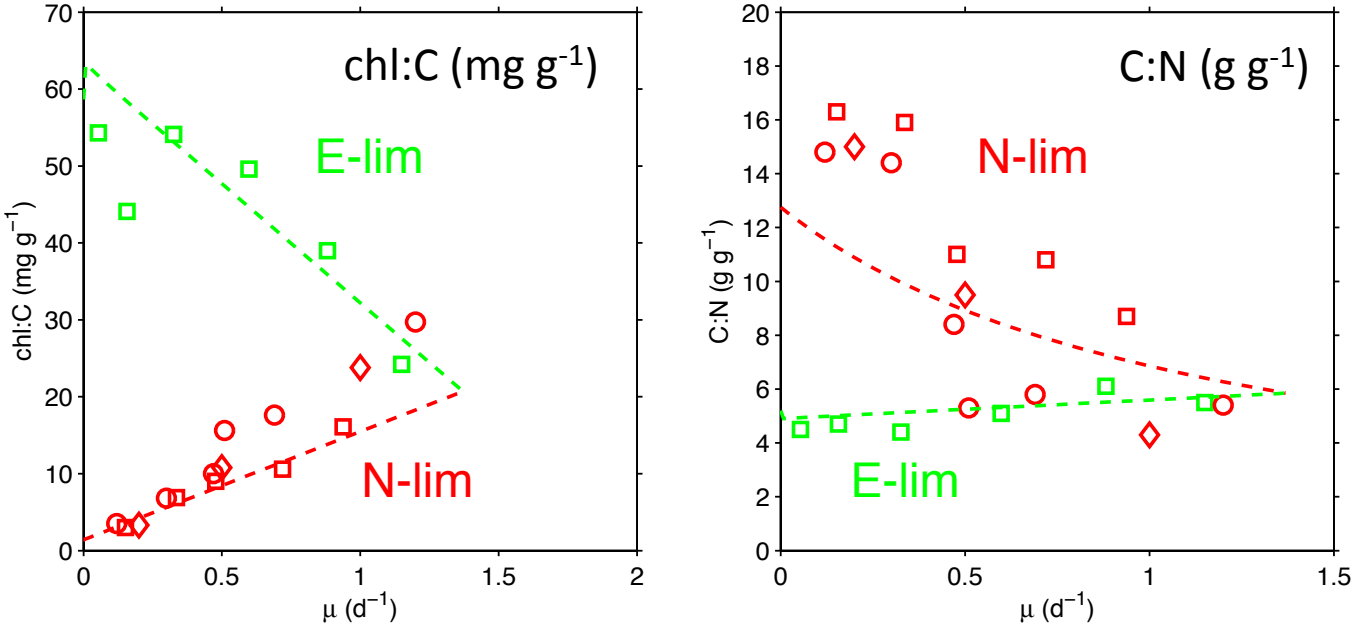
$$\phi_{tot} = \phi_{LIH} + \phi_{RIB} + \phi_{UP} + \phi_{STR} + \phi_{STO}$$

Solve for: ϕ_{LIH}, ϕ_{RIB}, ϕ_{STO}, n_{NUP}

- Cell shifts allocation towards optimal allocation at prescribed timescale (τ = 1 day)

Acclimation to light and nutrient limitation

- Continuous cultures grown under nutrient and light limited conditions [*Laws and Bannister* 1980; *Halsey et al.* 2010]
  - chl:C varies by factor of ~30, C:N by factor of 2
  - Chlorophyll is not a good direct proxy for phytoplankton biomass



[*Nicholson et al.* in prep]

Cell size and growth rate

- Growth rate decreases with increasing cell size
  - Predicted by metabolic theory of ecology (Brown et al. 2004)
  - Biomass normalized metabolism: $B/M = B_0 M^{-1/4} f(T)$
  - Trend does not hold for smallest cell sizes in observations

fixed fraction e.g. DNA scales with cell volume

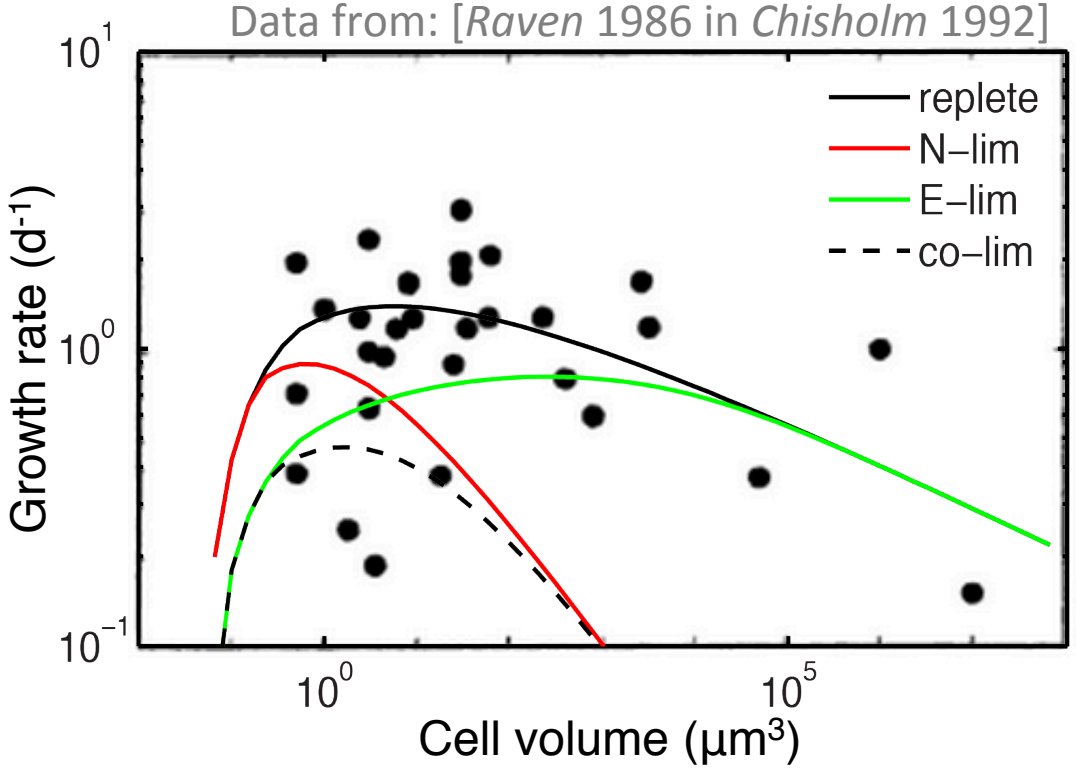
$$f_{STR} = f_{STR}^{0} + r^{-1} f_{STR}^{r}$$

Cell membrane scales with surface area (r^2/r^3)

Light limitation favors larger cell size

NO3 limitation favors smaller cells

Data from: [*Raven* 1986 in *Chisholm* 1992]



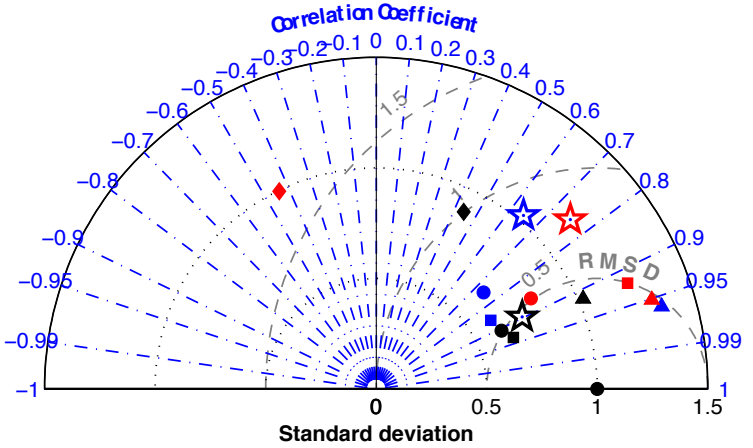
[*Nicholson et al.* in prep]

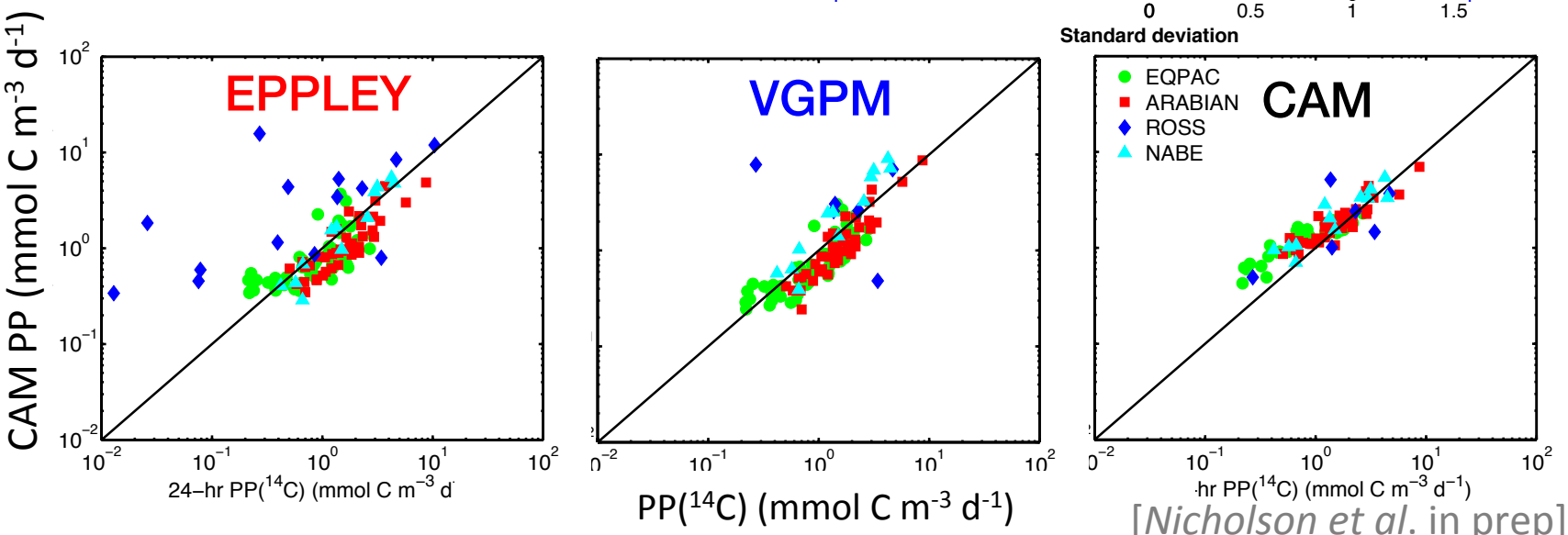
CAM applied to JGOFS data

- Process studies conducted in 1990's in the Equatorial Pacific, Arabian Sea, Ross Sea, North Atlantic

$PP_{CAM} = \mu_{CAM} \bullet chl_{OBS}/(chl:C)_{CAM}$

where, μ_{CAM} and $(chl:C)_{CAM}$ are $f(NO_3, PO_4, PAR, T)$

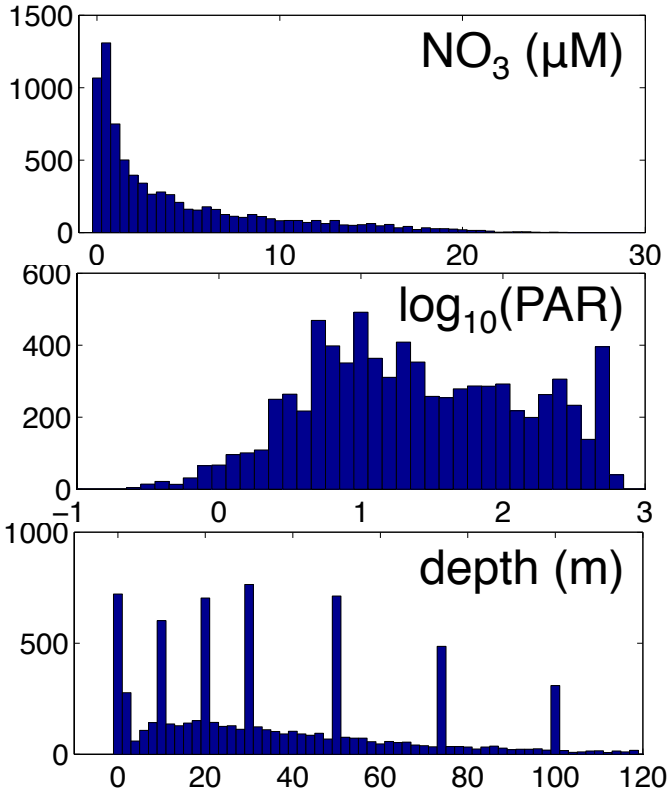


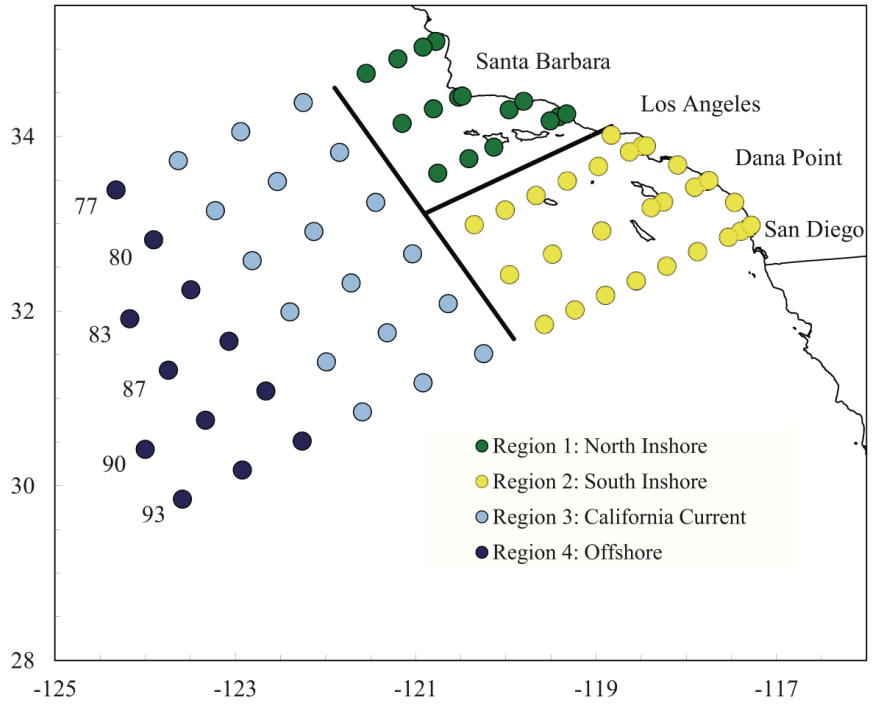


[*Nicholson et al.* in prep]

CAM applied to CalCOFI data

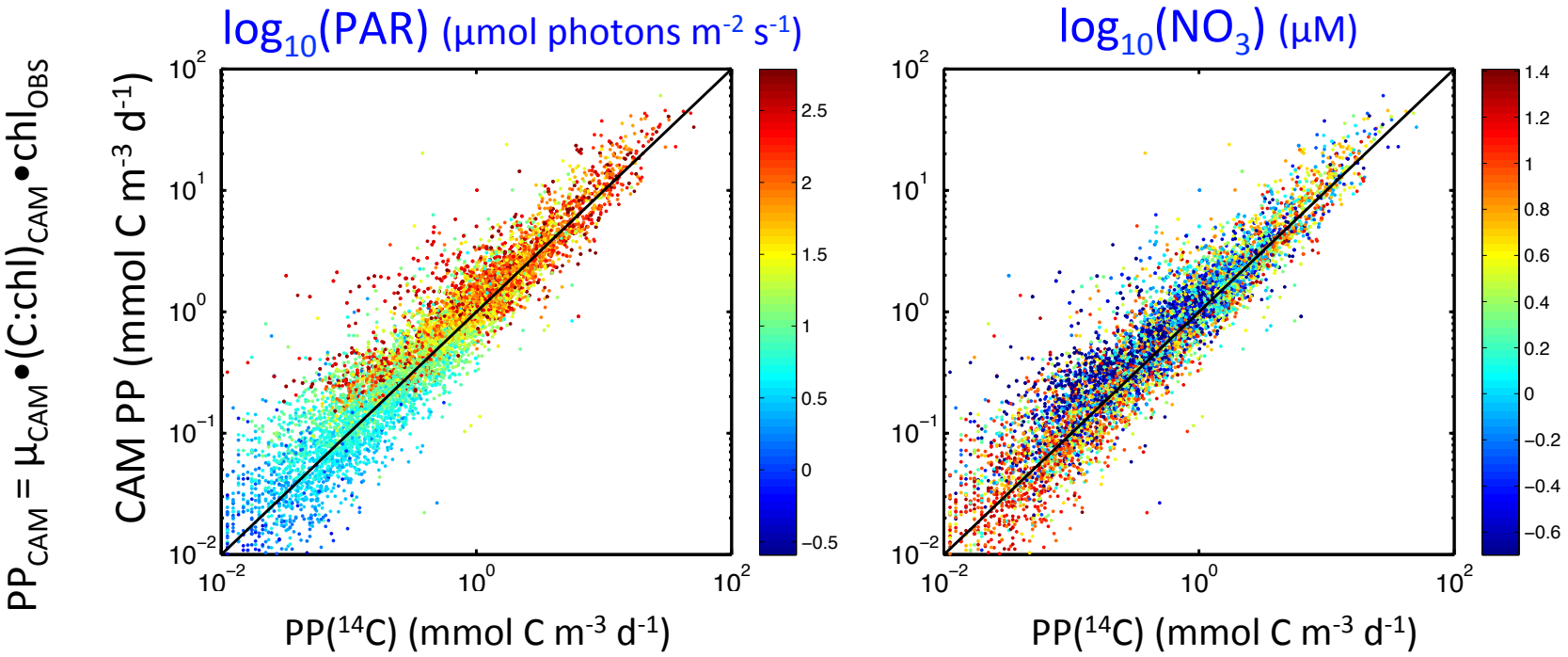
- Long term time-series program across California Margin
  - Biomes: nearshore upwelling to California Current to oligotrophic
  - Measurements include PP(^{14}C), PAR(z), Nutrients
  - Used data from 1985-2012, *n* = 7848





CAM applied to CalCOFI data

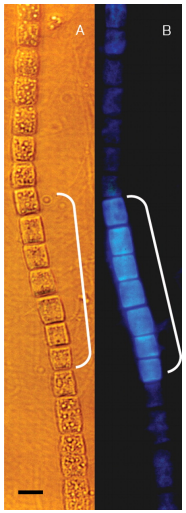
- Model parameters are same as used for JGOFS comparison and Laws and Bannister comparison
- Slight positive bias when high light/low nutrient
  - Is this a photoinhibition effect?



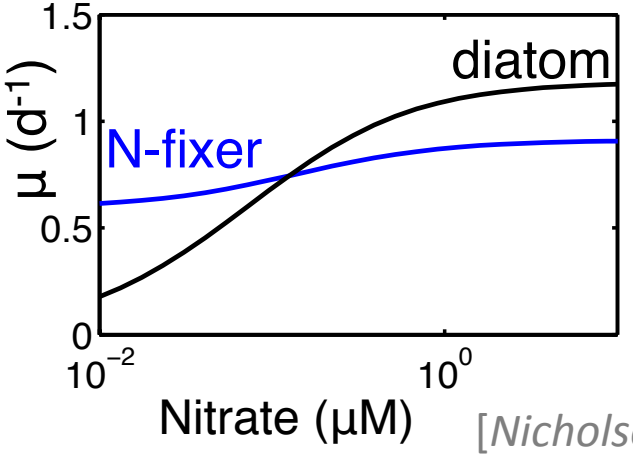
[*Nicholson et al.* in prep]

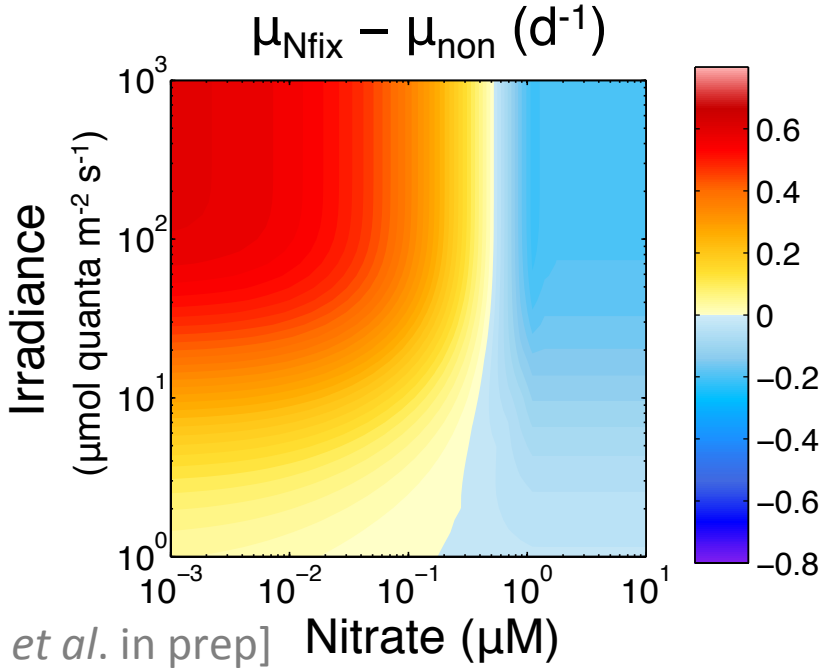
Future directions: nitrogen fixation

- Nitrogen fixation is energetically costly (16 ATP per N fixed)
  - Greater fraction of photosynthesis devoted to generating ATP
  - **meh** pathway must provide additional 16 ATP demand per N fixed
- Additional N-fixing 'functional pool' separated in space/time
  - Diazocytes in Trichodesmium make up ~20% of cells
  - 20% of cell carbon devoted to new Diazocyte pool



[El-Shehawy et al. 2003]



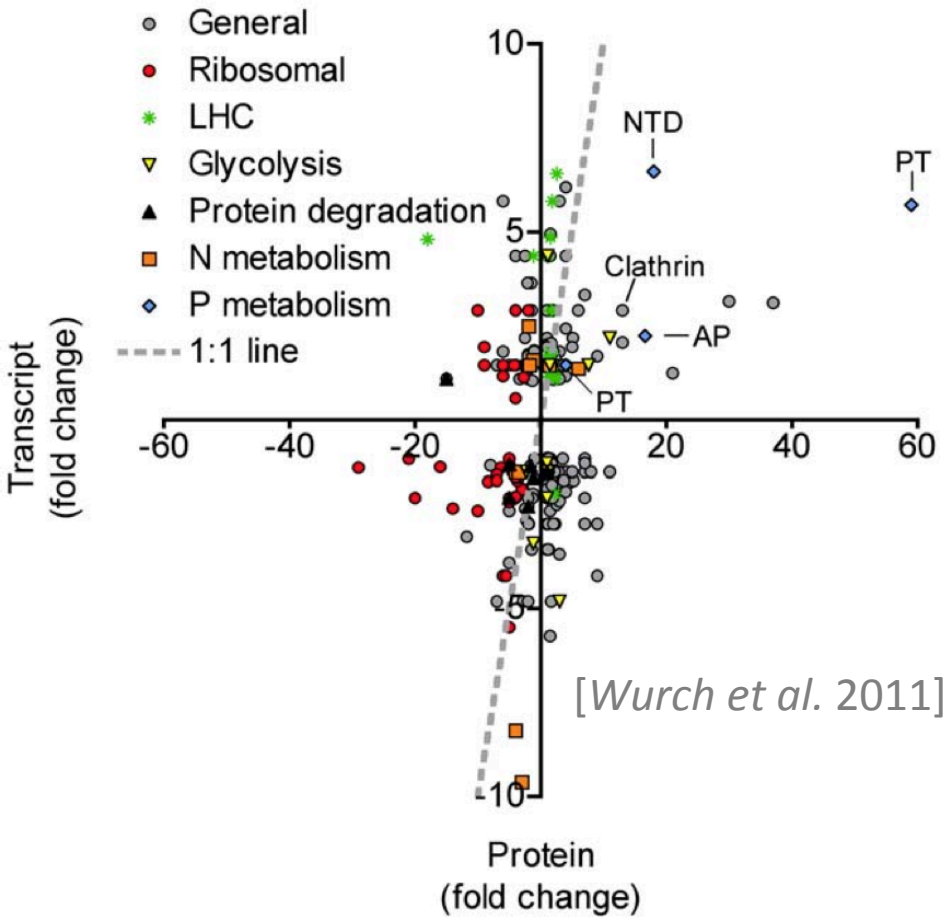


[Nicholson et al. in prep]

Future directions: 'omic' constraints

- 'Omic' approaches can inform model
  - P-uptake proteins/ transcriptome upregulated
  - Ribosomal protein abundance reduced under P-stress
- Transcriptome and proteome map to functional pools and physicological processes

Response of Aureococcus to P-limitation



[*Wurch et al.* 2011]

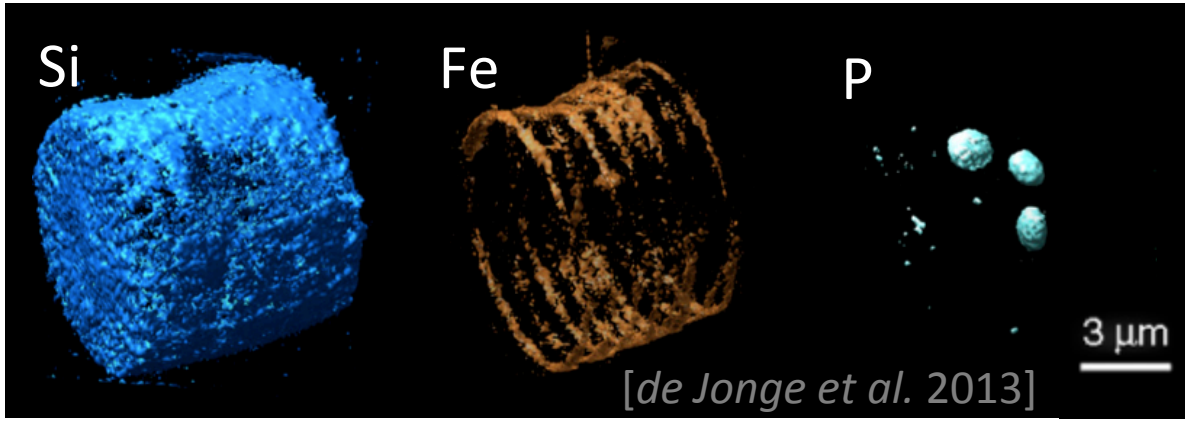
Future directions: trace metals

- Cell Fe quota primarily associated with light harvesting complex and nitrogen fixation

[*Twinning and Baines* 2013]

Protein(s)	Function(s)
Cytochromes	Electron transport in photosynthesis and respiration
Ferredoxin	Electron transport in photosynthesis and N fixation
Other Fe-S proteins	Electron transport in photosynthesis and respiration
Nitrate and nitrite reductase	Conversion of nitrate to ammonia
Chelatase	Porphyrin and phycobiliprotein synthesis
Nitrogenase	N fixation
Catalase	Conversion of hydrogen peroxide to water
Peroxidase	Reduction of reactive oxygen species
Superoxide dismutase	Disproportionation of superoxide to hydrogen peroxide and O_2

X-ray fluorescence tomography of a diatom (*Cyclotella meneghiniana*)



Conclusions

- Limitations of the current generation of IPCC models
  - Not mechanistic enough
  - Fixed C:N:P stoichiometry
  - Limited number of functional types
  - Parameters ‘tuned’ to current ocean conditions?
- An optimal allocation approach
  - More mechanistic basis
  - Modular structure: stoichiometry and function tied to
  - Cells acclimate – optimize growth under future conditions
  - Allometric scaling reduces number of independent parameters
- Future challenges:
  - Integrate into 1D and 3D models
  - Some trade-offs need to be better quantified
  - Timescales for acclimation are poorly constrained
  - Hierarchical complexity –flexibility to divide or merge cellular components

end

- Questions?

end

- Questions?