

Capturing Evolution and Ecology in a Global Ocean Model

Tim Lenton,

Stuart Daines, James Clark, Hywel Williams



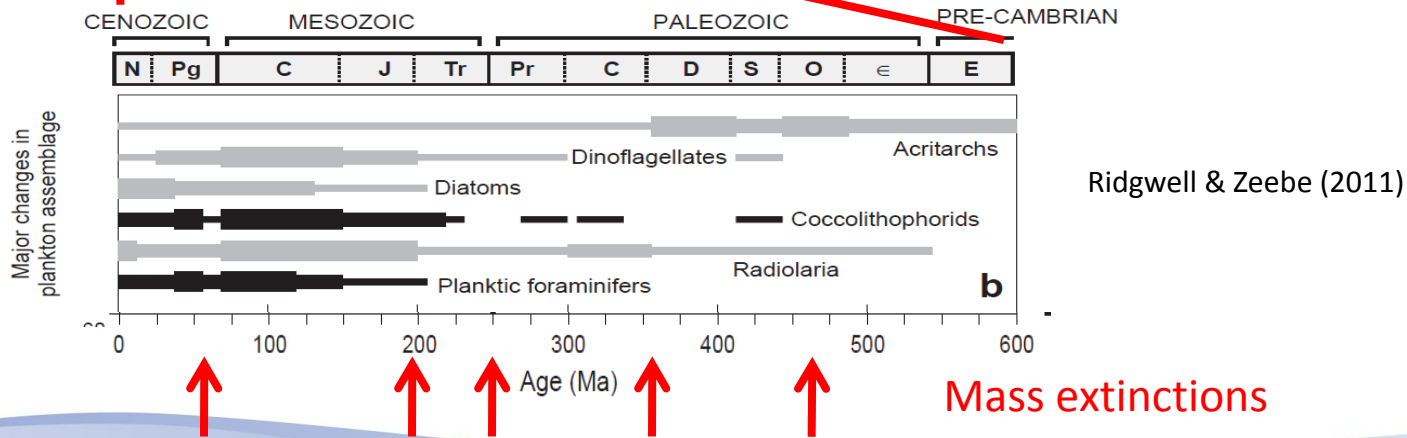
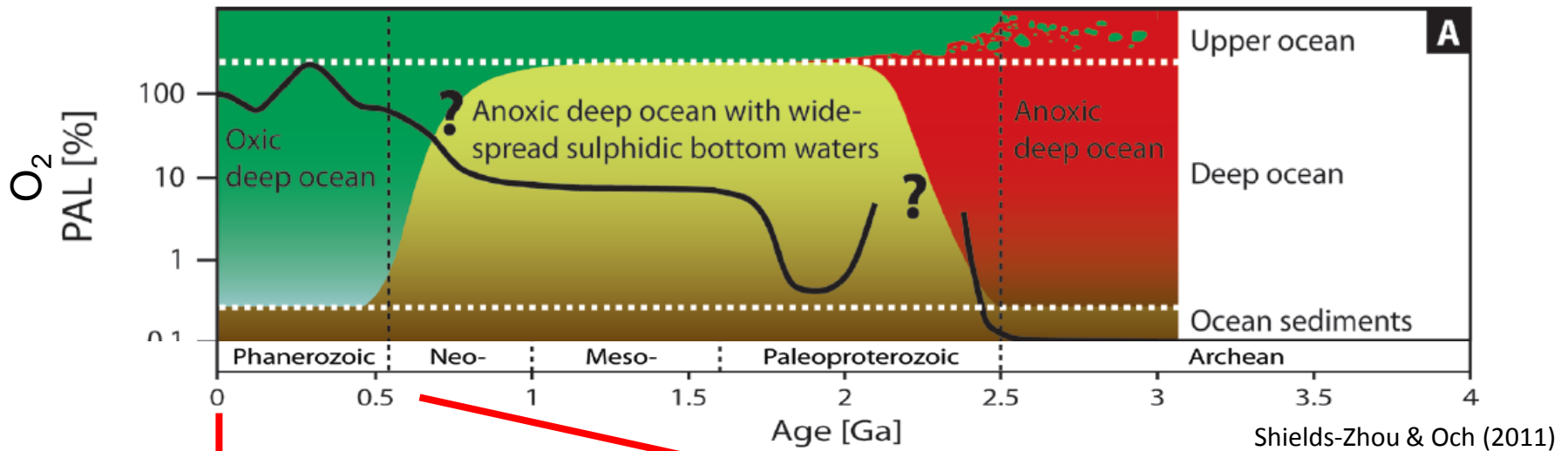
College of Life and Environmental Sciences, University of Exeter, UK

t.m.lenton@exeter.ac.uk

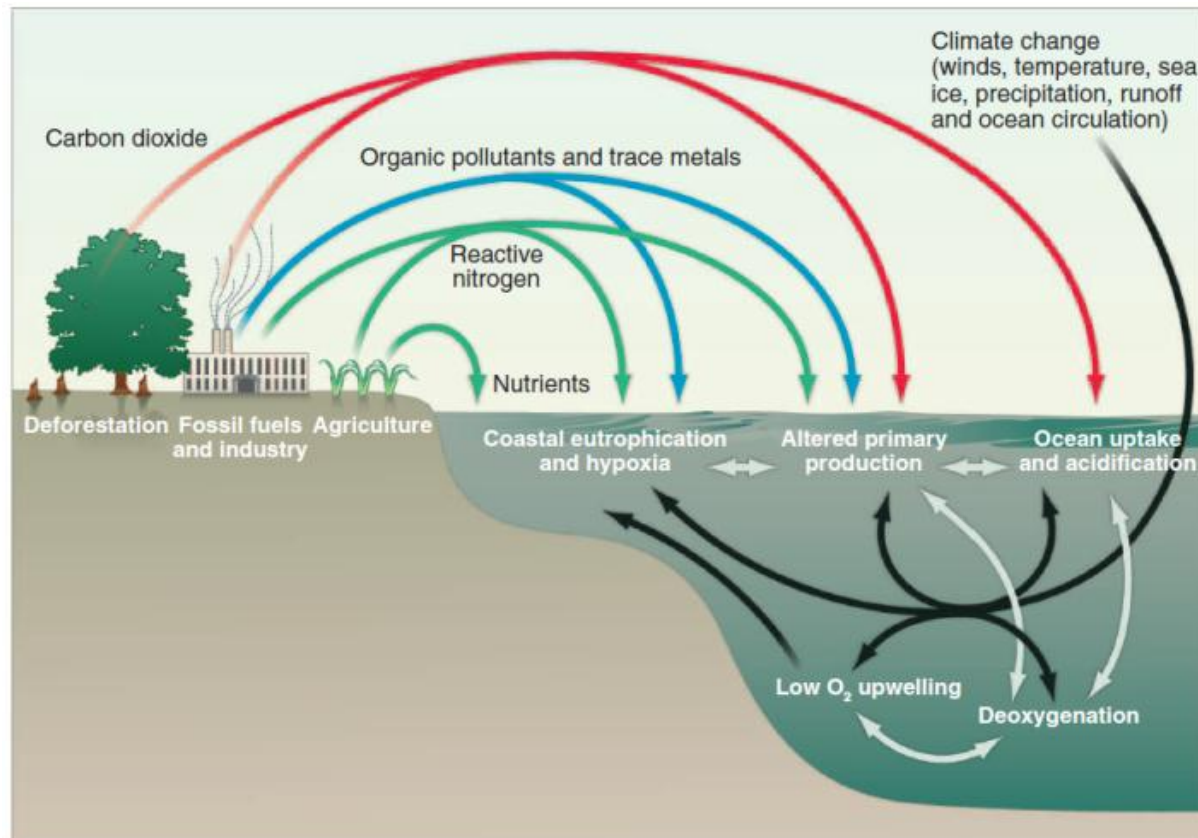
Outline

- Challenges
 - Motivating scientific questions
- Approach
 - Existing models and their limitations
 - Evolutionary Ecosystem (EVE) model
- Results
 - Emergent phytoplankton growth strategies
 - Cell size, N:P composition, dynamic storage

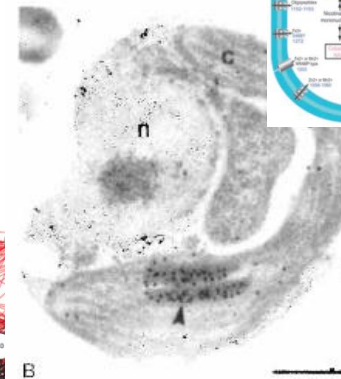
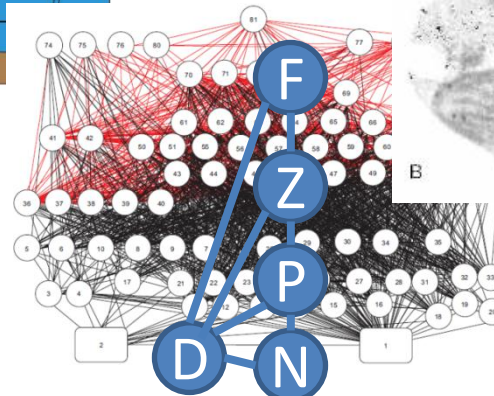
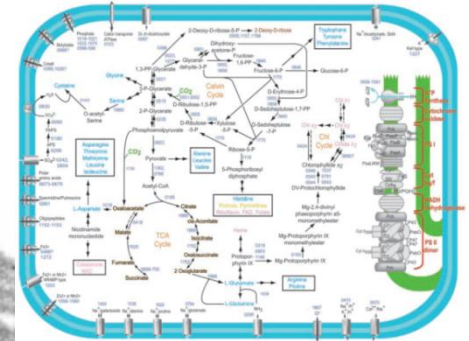
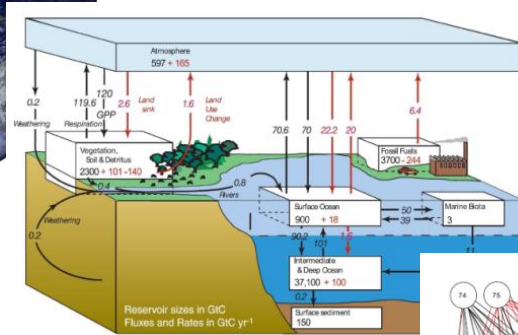
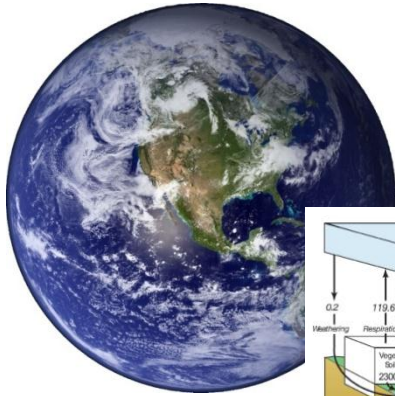
How have Earth and life co-evolved in the past?



How will the (rest of the) biosphere respond to anthropogenic global change?



How can we use (molecular) biological data to produce better predictive biosphere models?



Overarching challenges

- Life is (very) diverse
- Life adapts
 - Organisms acclimate
 - Populations evolve by natural selection
- Organisms have life histories
- Evolution is contingent

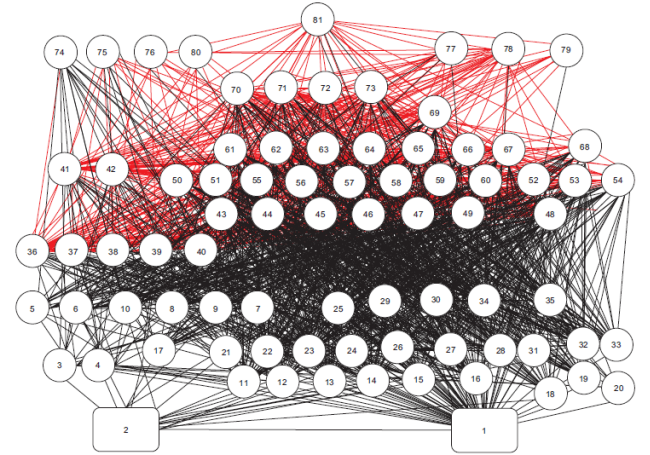
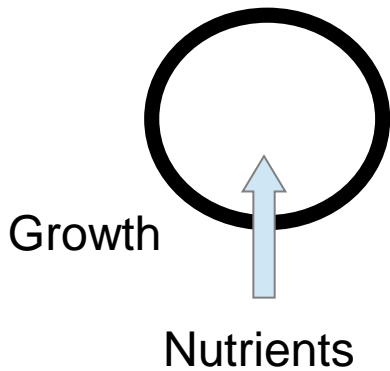
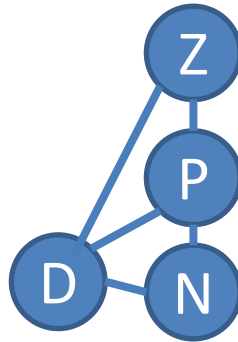


figure Mike St John, Link (2002)

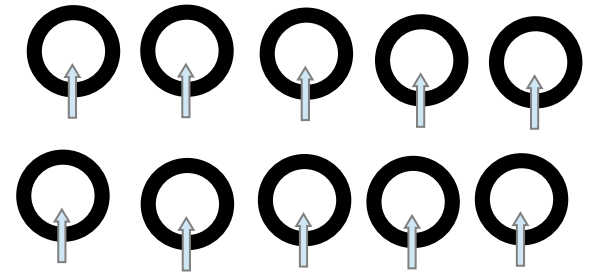
Traditional approaches to modelling the marine ecosystem



Monod (1942)



Riley (1946)

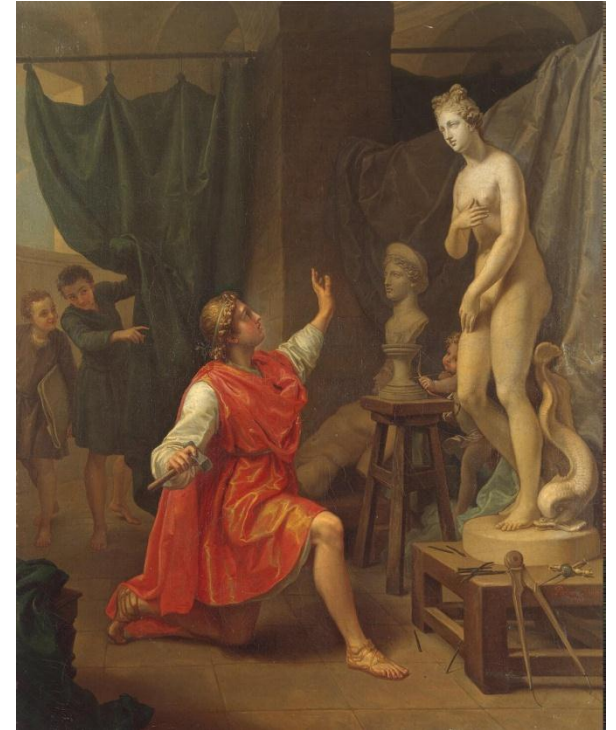


LeQuere et al (2000s)

Aggregated models - effective locally when tuned to observations in a region of space and time ...but not portable

Limitations of traditional models

- Lack of diversity
- Fixed responses
 - No acclimation or adaptation
- Lack of life histories
 - Important for storage and acclimation strategies in dynamic environments, seasonality, dispersal
- Lack of evolutionary contingency
 - Can access anywhere in trait space

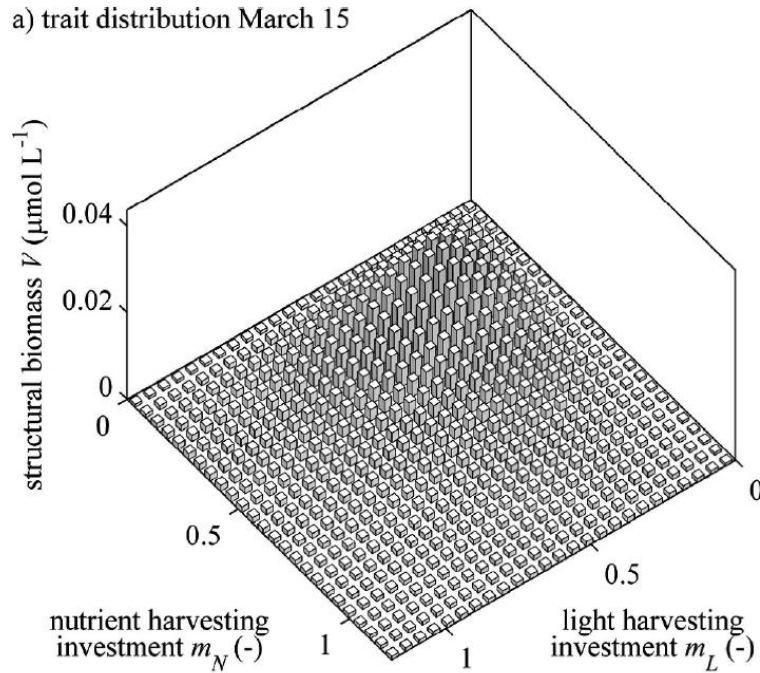


Pygmalion and Galatea
by Pecheux (1784)

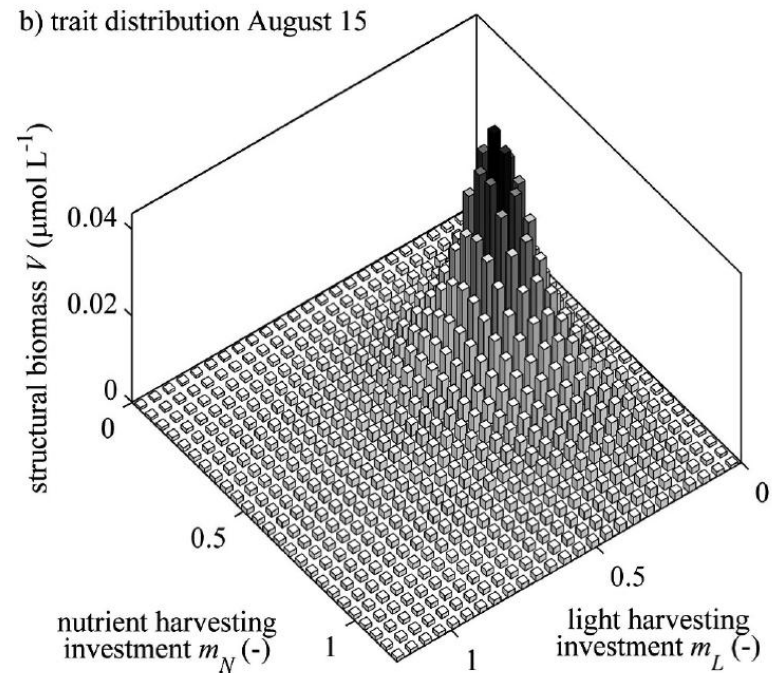
“A biodiversity-inspired approach to aquatic ecosystem modelling”



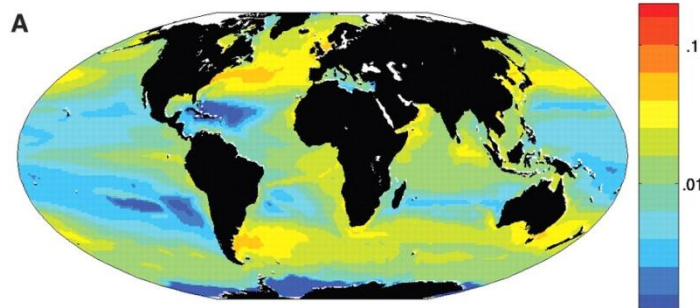
a) trait distribution March 15



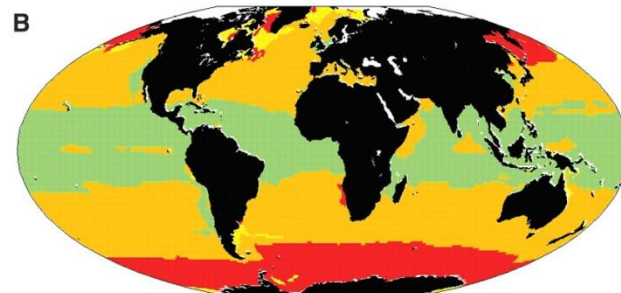
b) trait distribution August 15



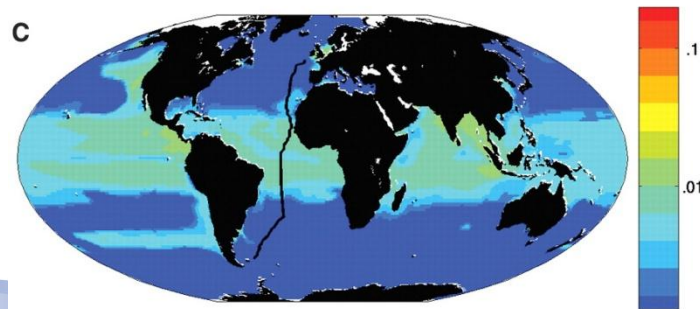
“Emergent biogeography of microbial communities in a model ocean”



Total phytoplankton biomass
($\mu\text{M P}$, 0 to 50 m average)



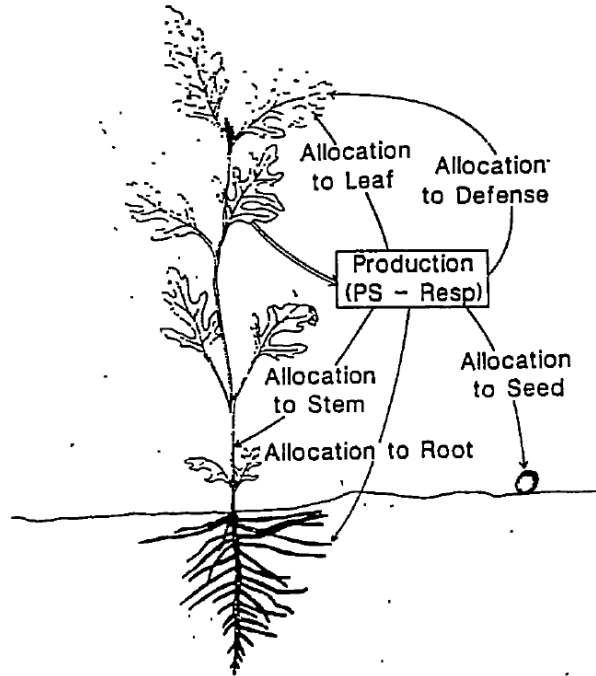
Group locally dominating annual mean biomass:
analogs of *Prochlorococcus*
other small photo-autotrophs
Diatoms
other large phytoplankton



Total biomass of
Prochlorococcus analogs
($\mu\text{M P}$, 0 to 50 m average)

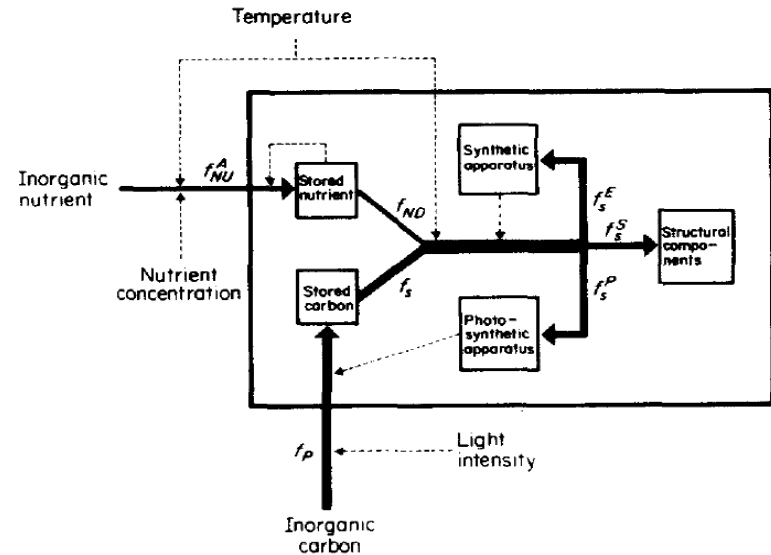
Evolutionary ecology: Traits, trade-offs, emergent strategies

Terrestrial plants



Bloom (1985), Tilman (1990)

Phytoplankton



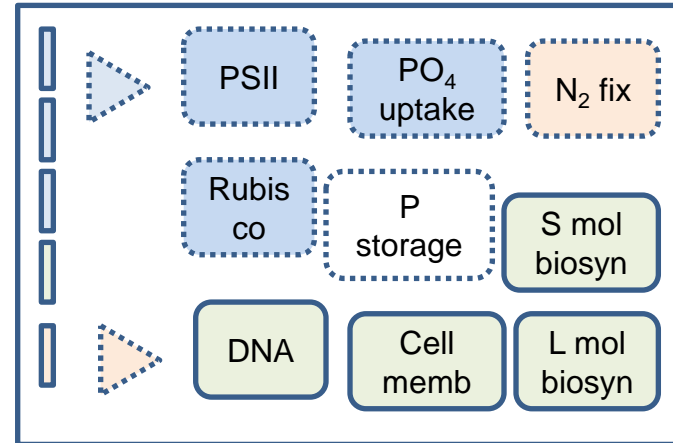
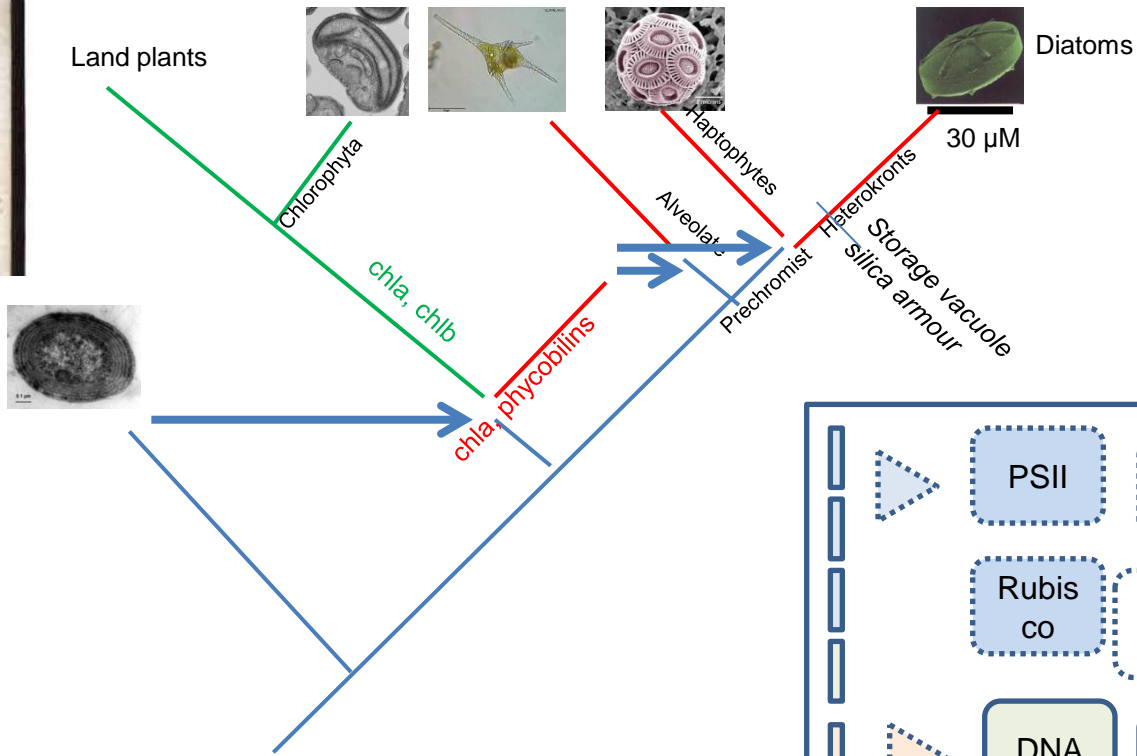
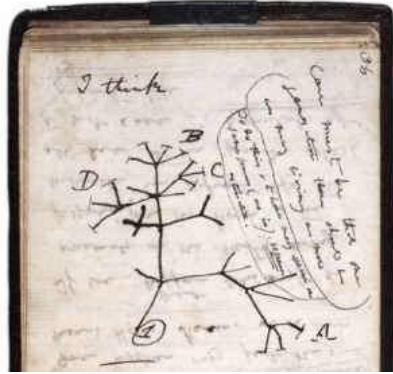
Shuter (1979), Raven (1984), Vallino *et al.* (1996)

EVolutionary Ecosystem (EVE) Model Approach

- **Individuals:**
 - Functional traits
 - Physiologically constrained model organisms
 - Trade-offs and resource allocation
- **Community and ecosystem:**
 - Selection in model environment
 - Interactions and trophic structure
 - Community assembly (dispersal...)
 - Biogeochemical cycles



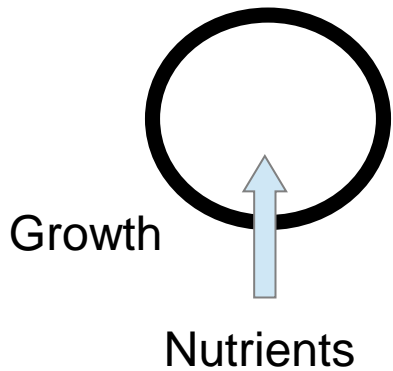
Conserved, phylogenetically-related building blocks



Physiology, 'cellular economics'

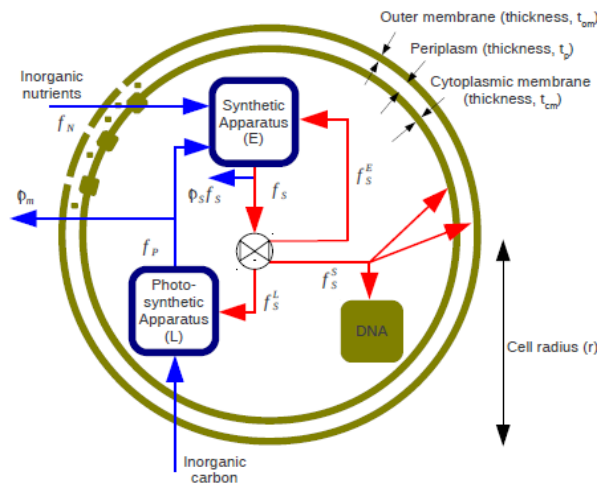
COMPLEXITY

Monod-type models



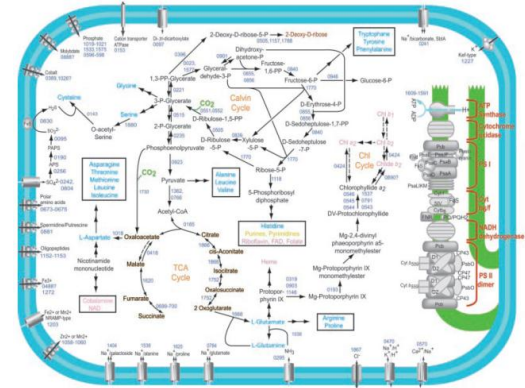
Monod (1942)

EVE model



Inspired by Shuter (1979)

Metabolic networks (systems biology)

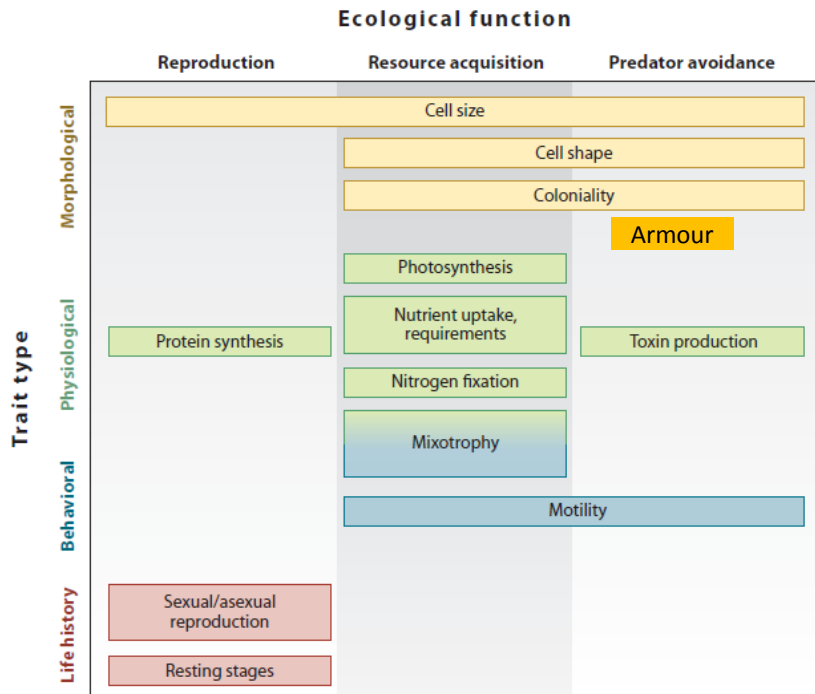


Dufresne (2003)

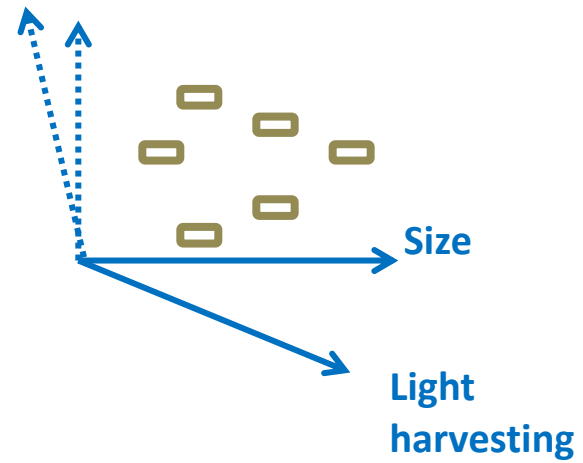
⇒ Parameter-sparse representation of diversity and adaptation based on common physiology

Functional traits and trade-offs

Phytoplankton traits



Trait space

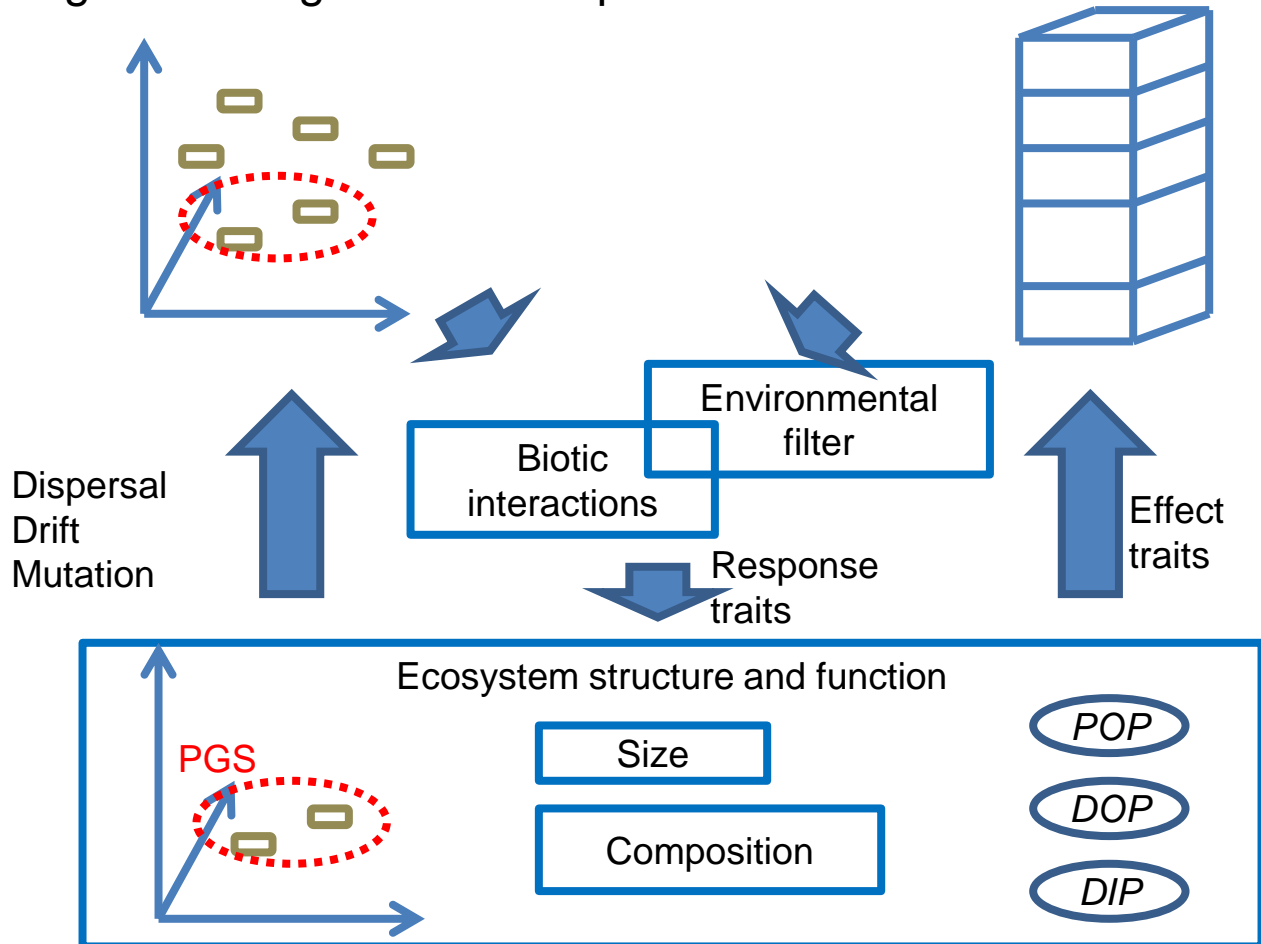


Trade-offs emerge from physiological constraints and cost-benefit

Environmental selection

Organisms: Agents in trait space

Environment: MIT gcm

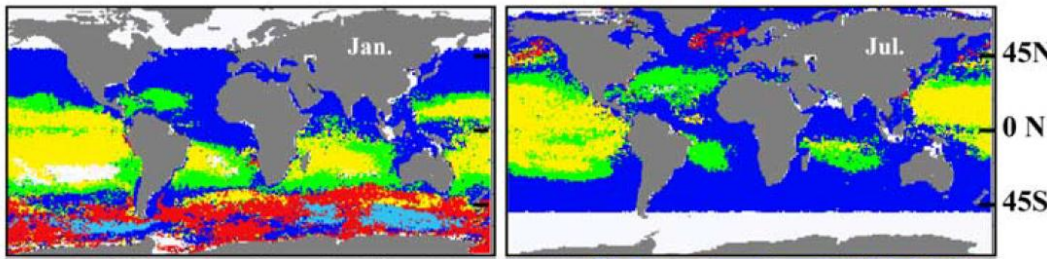


Applications

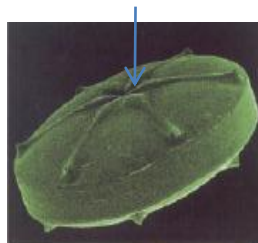
- Emergent phytoplankton growth strategies and biogeography
 1. Cell (minimum) size
 2. Composition and N:P stoichiometry
 3. Dynamic strategies

1. Patterns in phytoplankton size

Biogeography (Alvain 2008)



Nano. Prochl. SLC Diatoms Phaeo.



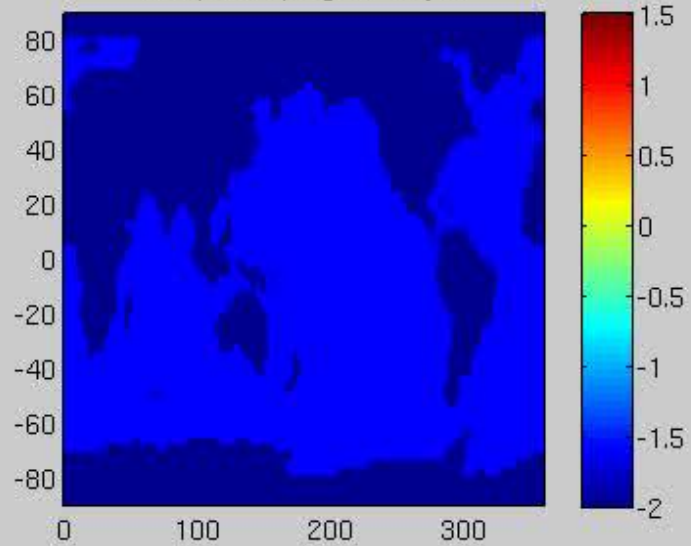
Pico < 2 μm
 Nano 2 - 20 μm
 Micro 20 - 200 μm



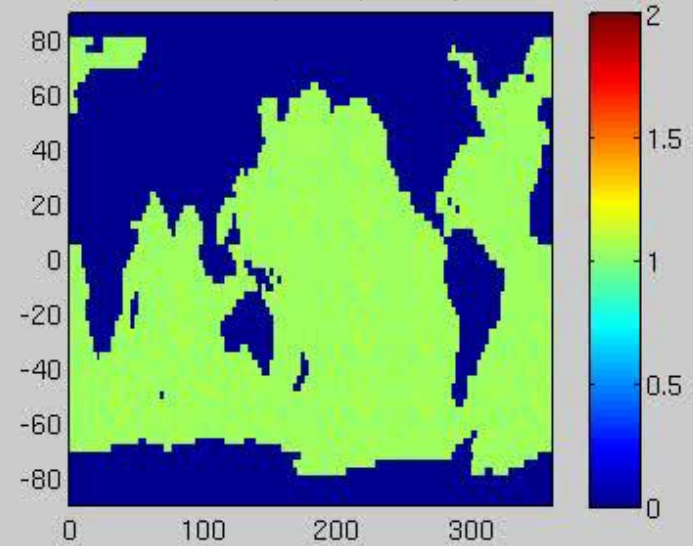
Oligotrophs / gleaners
 'K strategists'
 Nutrient limited
 < 1 μm prokaryotes
 95% efficient microbial loop
R*, small size

Copiotrophs / opportunists
 'r strategists'
 Light-limited
 >10 μm eukaryotes
Growth rate
Storage strategies

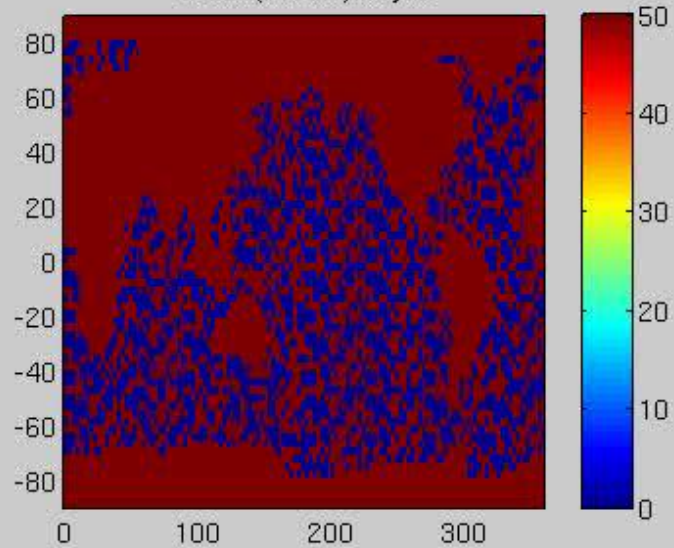
chl (0-50m) mg m^{-3} day 0



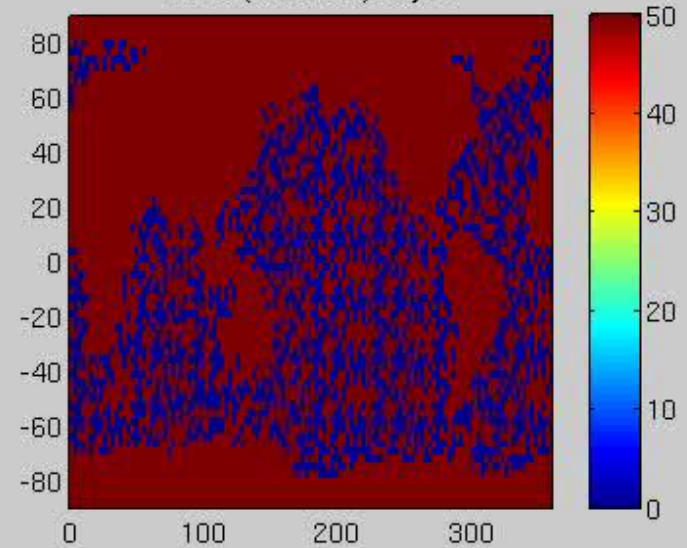
CellRadius (0-50m) μm day 0

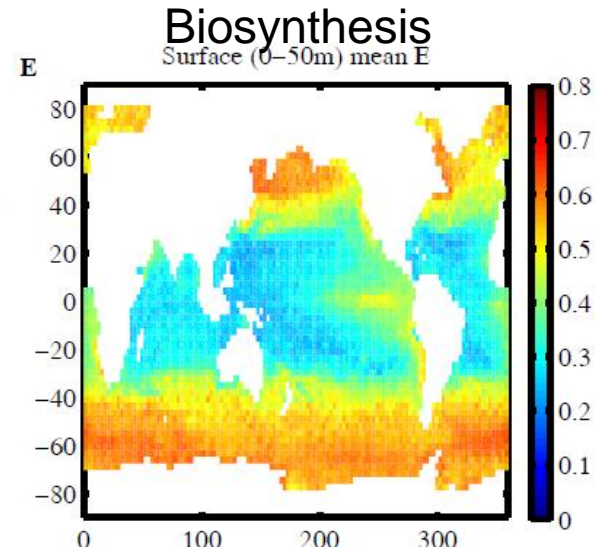
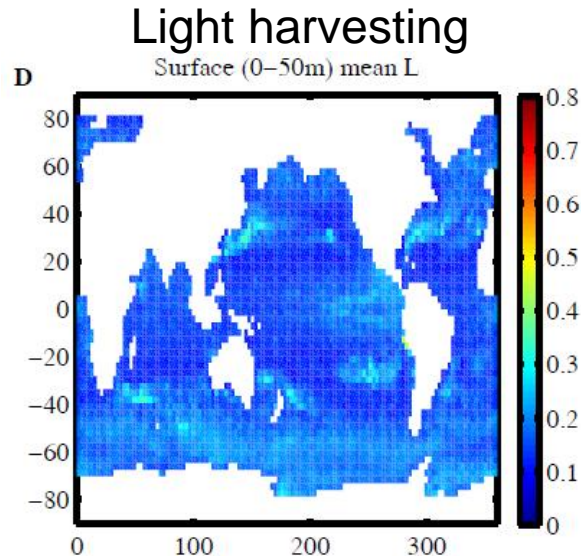
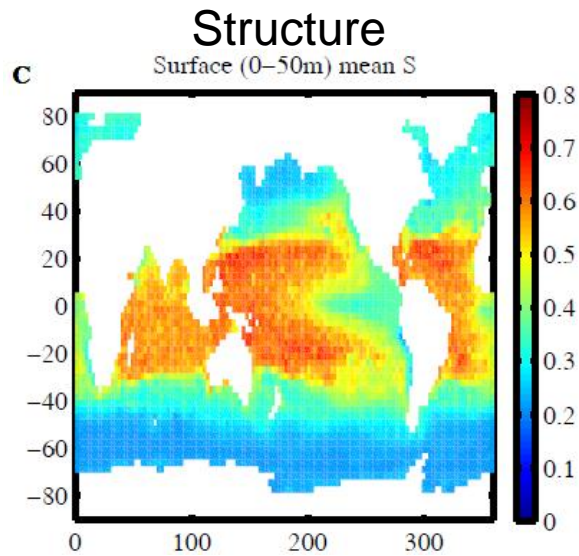
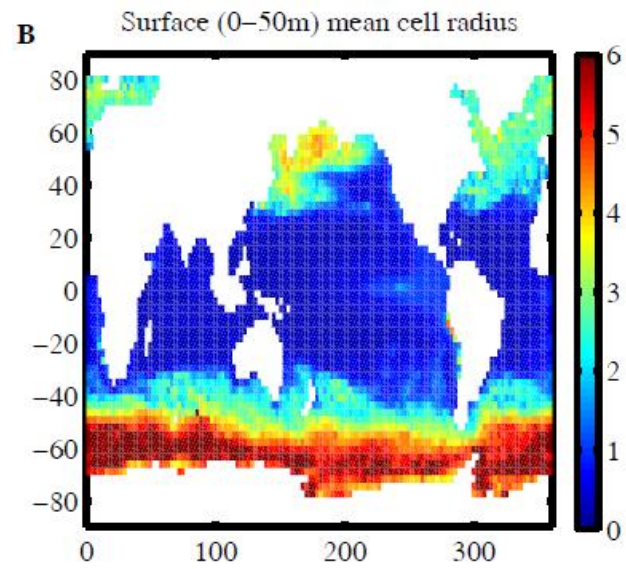
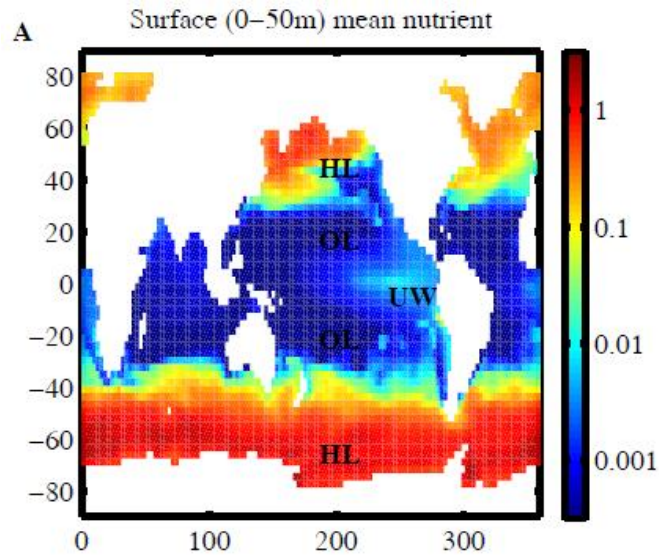


C/chl (0-50m) day 0

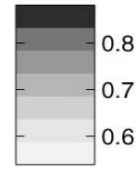
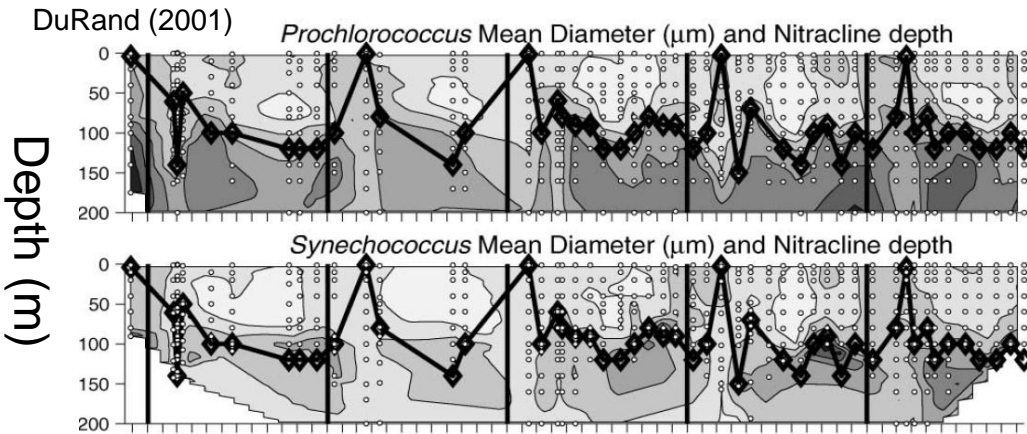


C/chl (50-120m) day 0

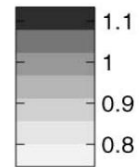




Cell size and adaptation to low light (BATS)

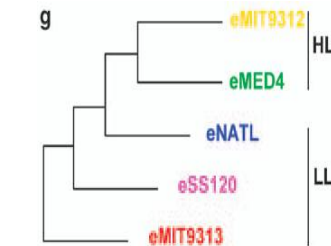


- Shift to larger cell sizes ($\sim 0.7\mu\text{m}$) in *Prochlorococcus* during the spring bloom.

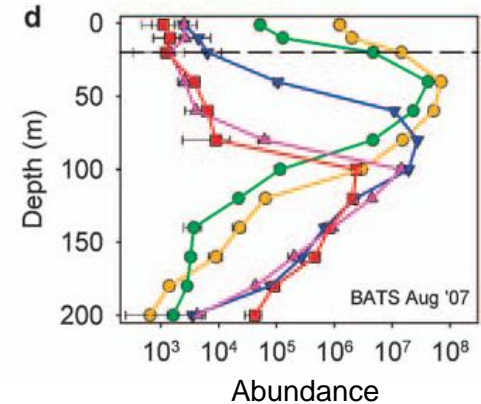
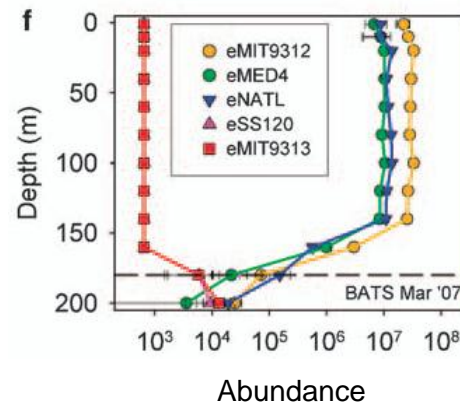


- Larger cell sizes generally observed at depth, around the deep chlorophyll maximum.

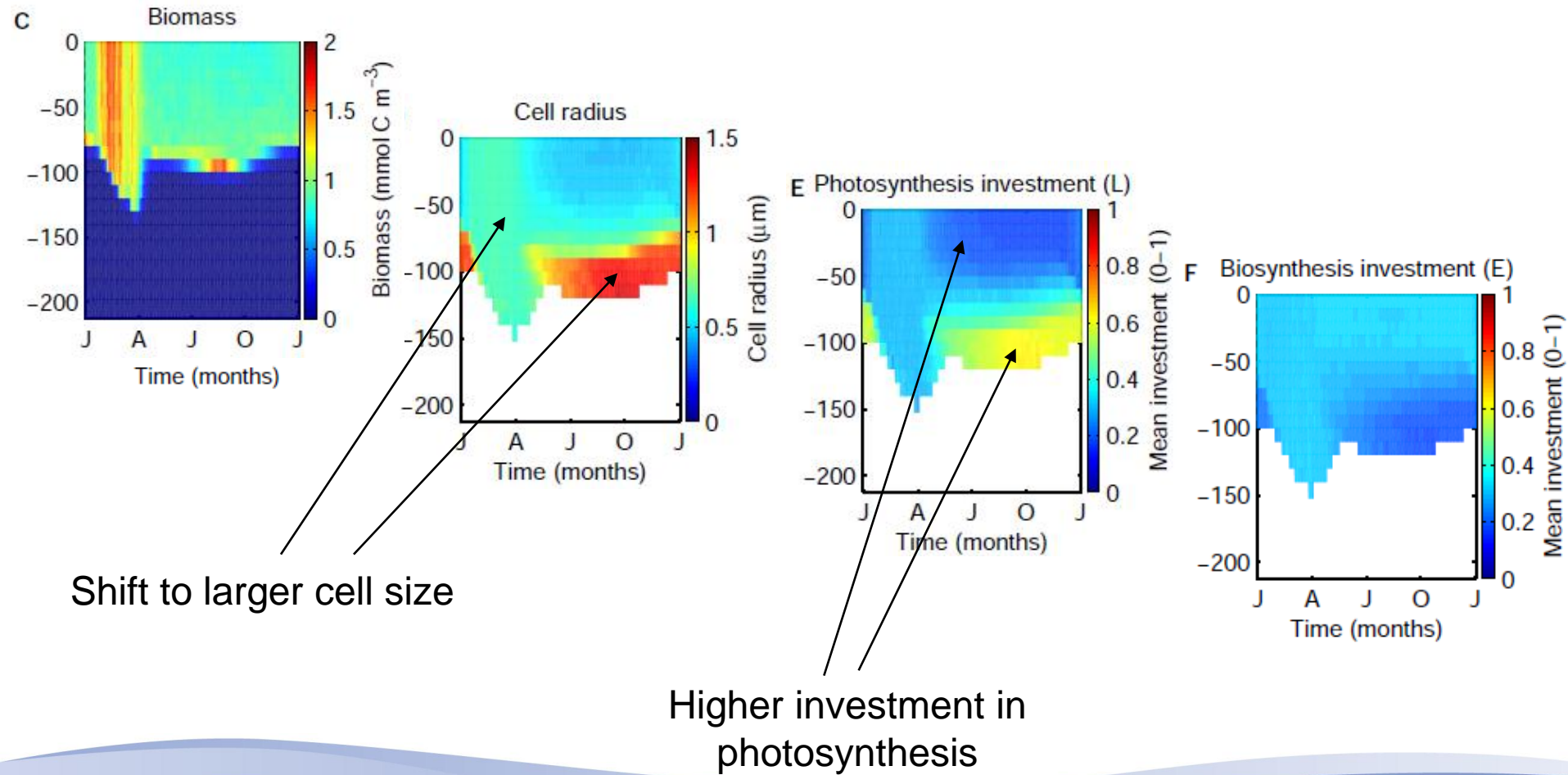
- High light adapted species dominate in well mixed surface waters.
- In stratified conditions, shift to low light adapted species at depth.



Malmstrom (2010)

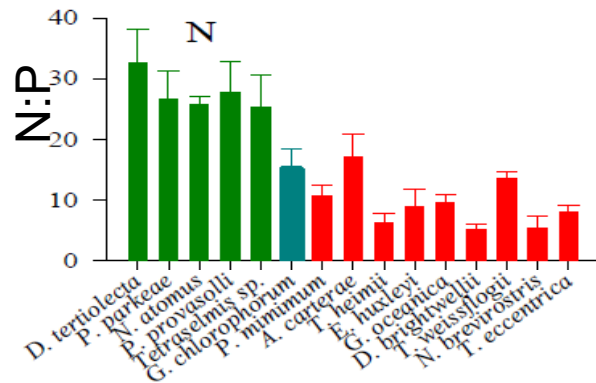


Phytoplankton population dynamics at BATS



2. Patterns in phytoplankton N:P stoichiometry

Phytoplankton stoichiometry in laboratory culture
 Quigg et al (2003) Nature



'Greens'

Ostreococcus

Prokaryotes:

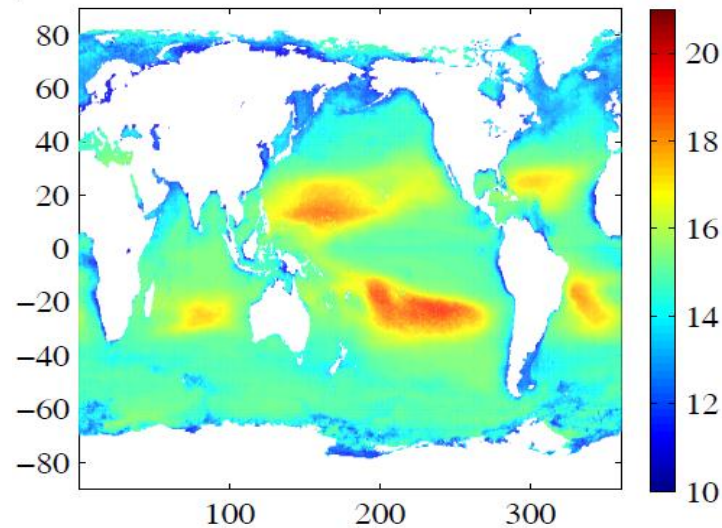
Prochl.

Synechococcus

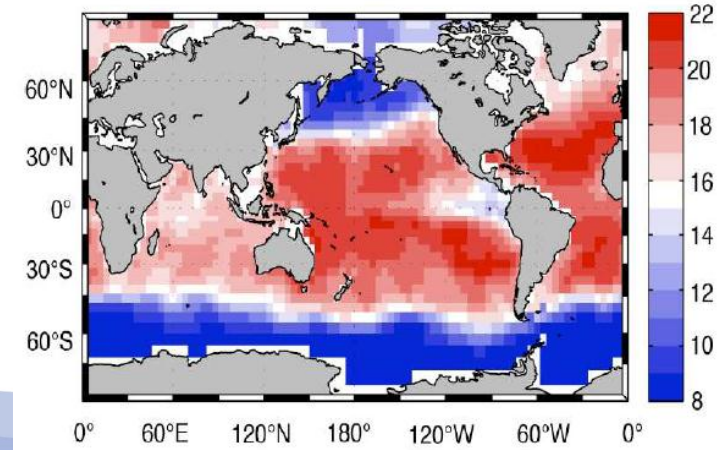
'Reds'

Diatoms

Coccolithophores



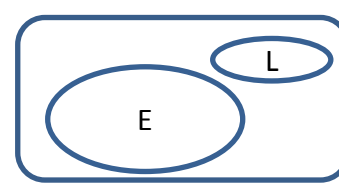
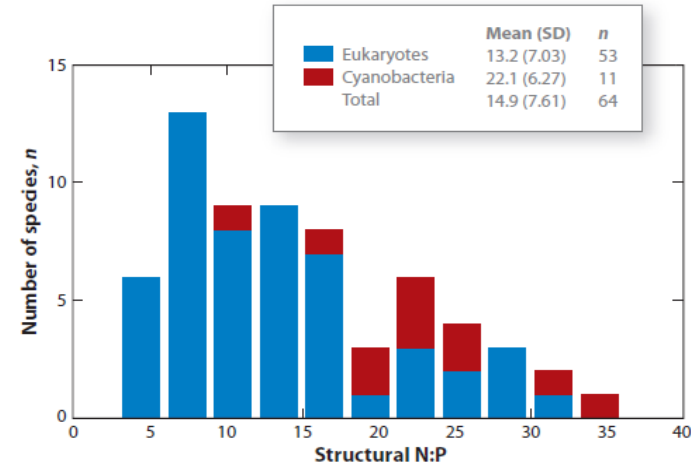
N:P from chl and size-class weighting (Daines et al. 2013)



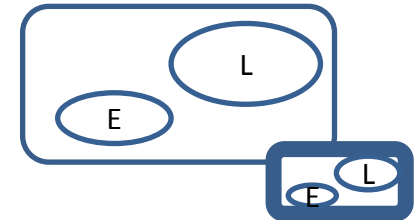
N:P from diatom (Si export) weighting (Weber & Deutsch 2012)

The growth rate hypothesis, rRNA and N:P

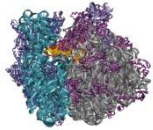
- Maintaining high growth rates requires high concentrations of P-rich ribosomes (rRNA)
- Predict that faster growth rate produces lower N:P organisms
- Crucial to determining how low N:P can go is the rRNA 'rate constant' for protein synthesis ($\text{aa rib}^{-1} \text{s}^{-1}$)



Fast growth
P rich ribosomes
Low N:P



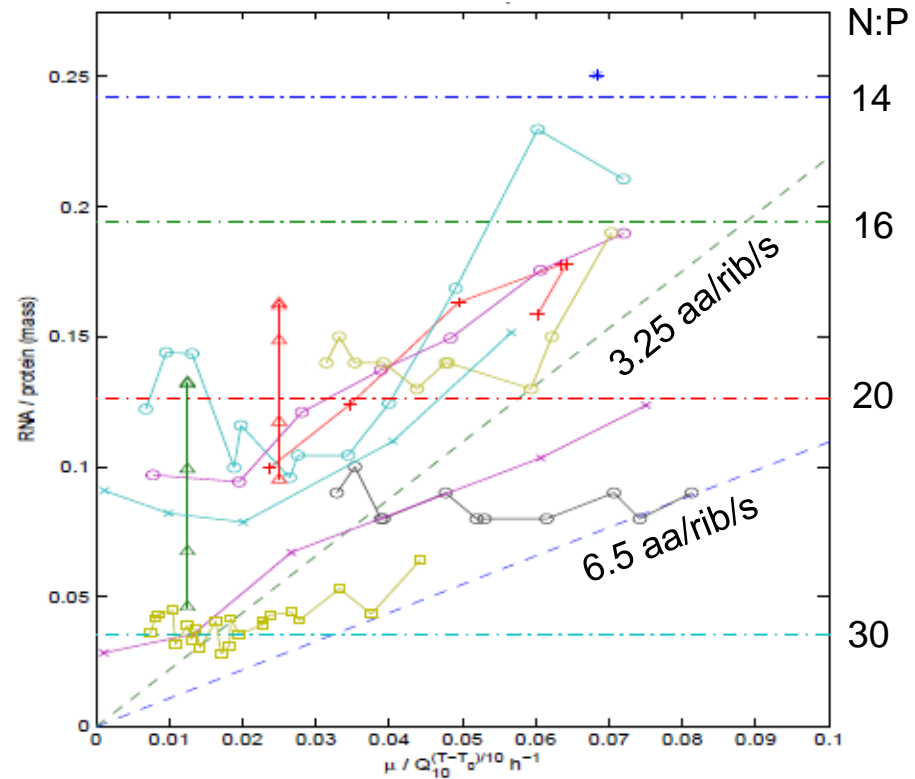
Resource limited
Slow growth
High N:P



rRNA required for protein synthesis

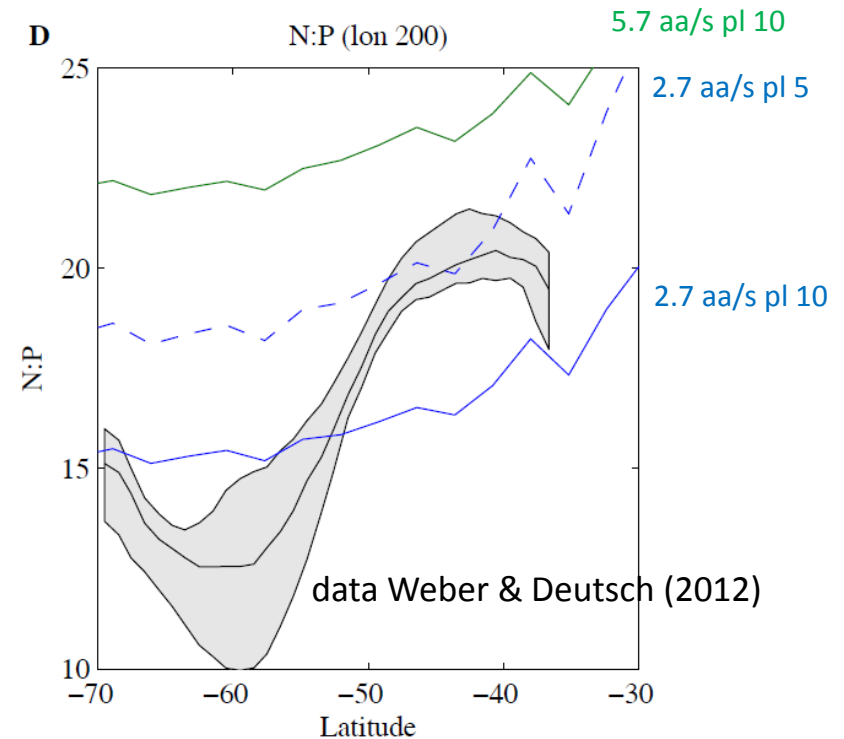
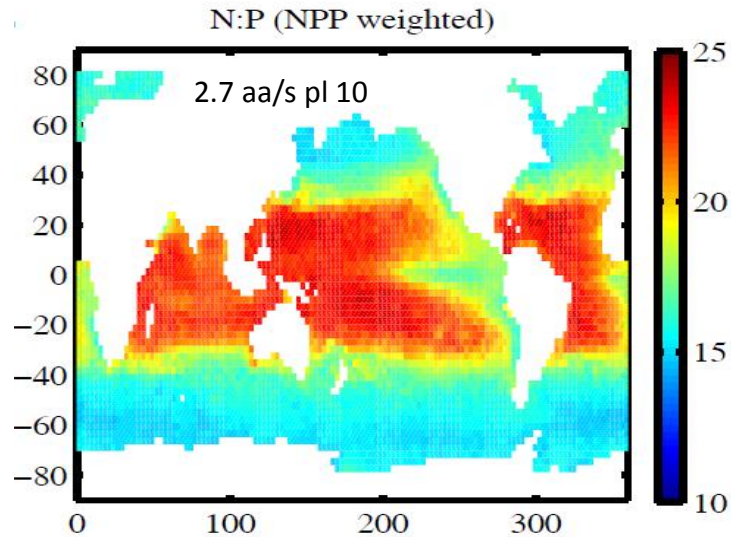
- Existing models span a range 2.7–5.7 aa rib⁻¹ s⁻¹
- High value is from yeast (heterotrophic fungus!)
- New compilation of data for photoautotrophs

RNA/protein



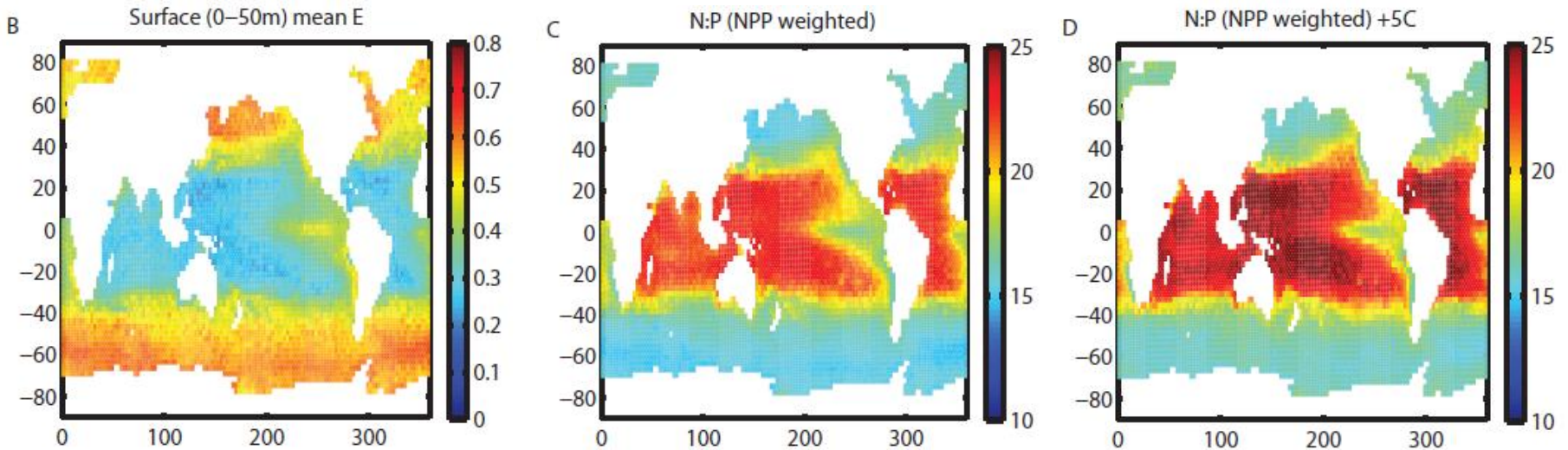
Growth rate (T normalised)

Predictions from the growth rate hypothesis



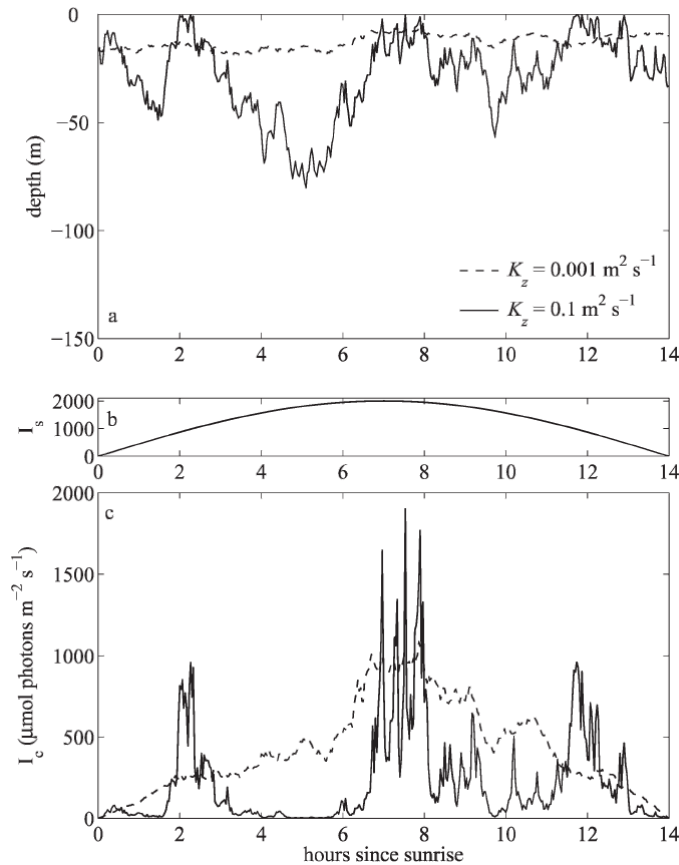
- Explains overall patterns in N:P
- But not lowest observed N:P
- Additional contribution from P storage?

Physiological effect of warming



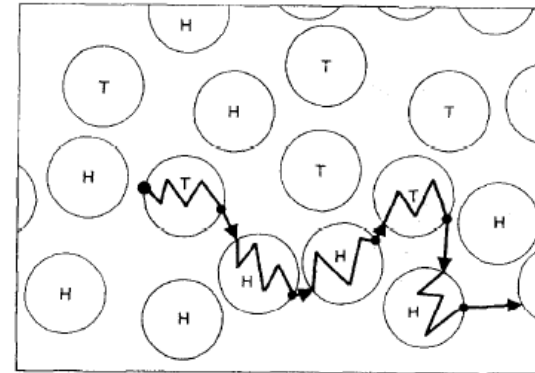
- Rate of protein synthesis increases strongly with temperature
- Less P-rich ribosomes required to produce required N-rich protein at higher T
- Therefore physiological effect of warming is to increase organism N:P
- But must also consider effects of increased stratification reducing nutrient supply...

3. Strategies for dynamic environments



e.g. Fluctuating light environment in mixed layer (Ross *et al.* 2008)

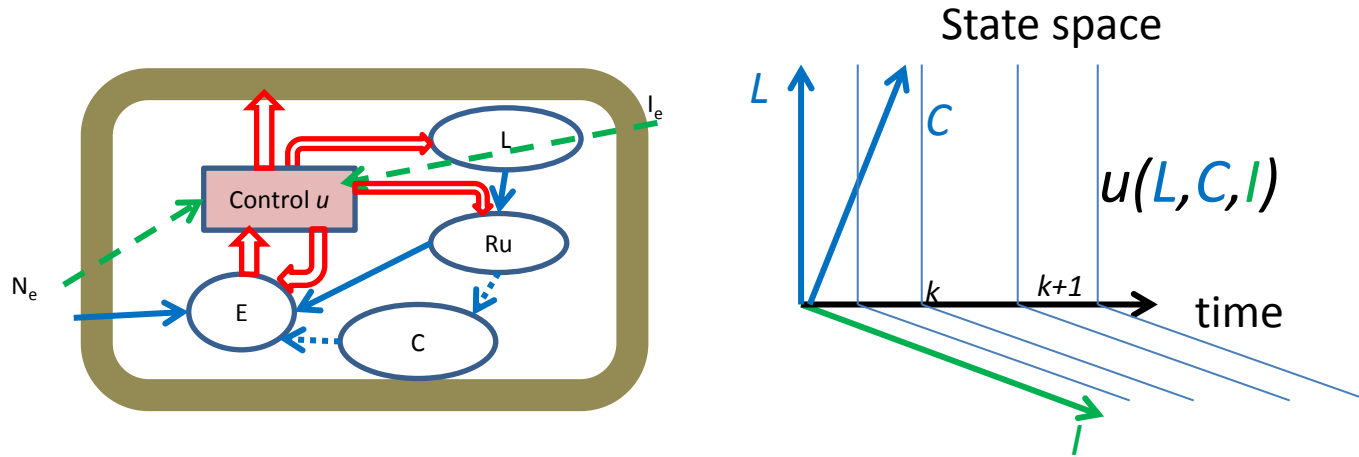
- Autotroph storage pools even out stochastic supply of light, N, P
- But how to model this?...



Optimal foraging – MacArthur & Pianka (1966), Emlen (1966), Charnov (1976)...

Storage and acclimation as optimal control

- Fitness benefit of dynamic allocation (acclimation, storage)



Expectation over stochastic environment

control

state evolution (growth!)

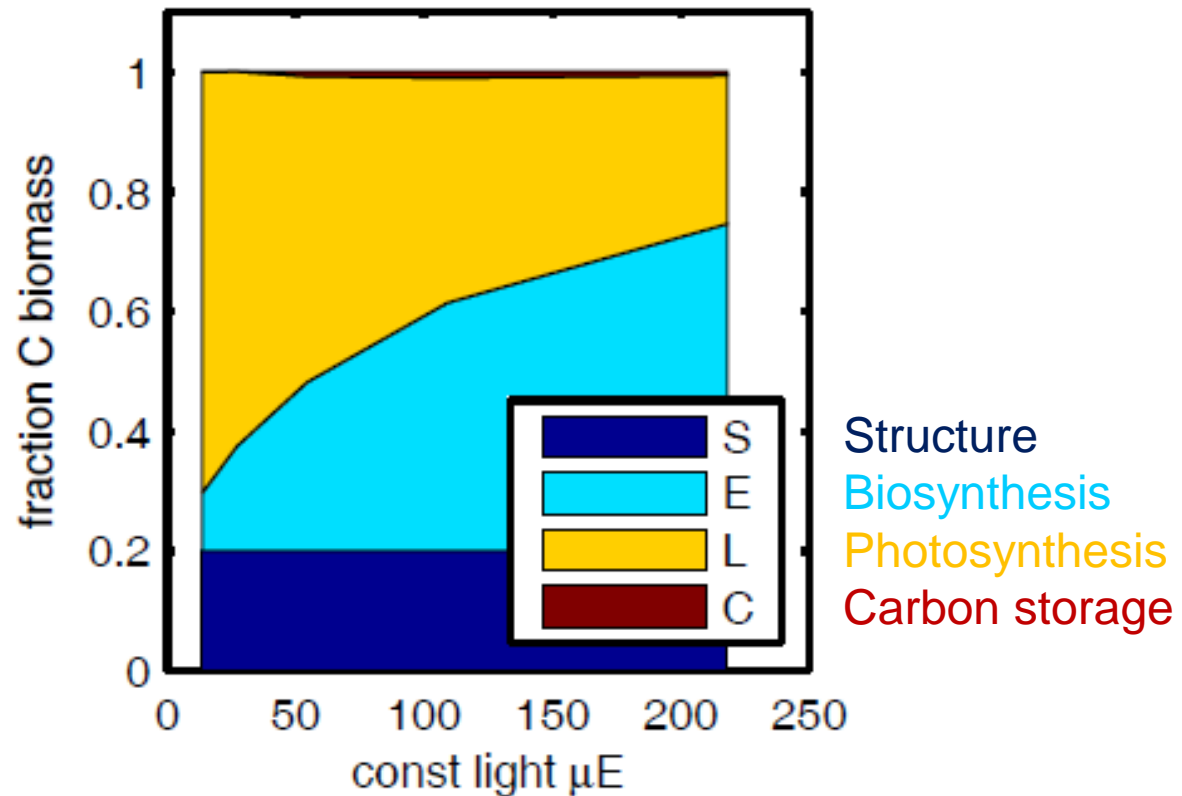
$$J_k^*(x_k, e_k) = \max_{u_k} \mathbb{E}_{w_k} \left\{ g_k(x_k, e_k, u_k(x_k, e_k), w_k) + J_{k+1}^*(F_k(x_k, e_k, u_k, w_k)) \right\}$$

Fitness (eg biomass)

Instantaneous benefit

Future benefit

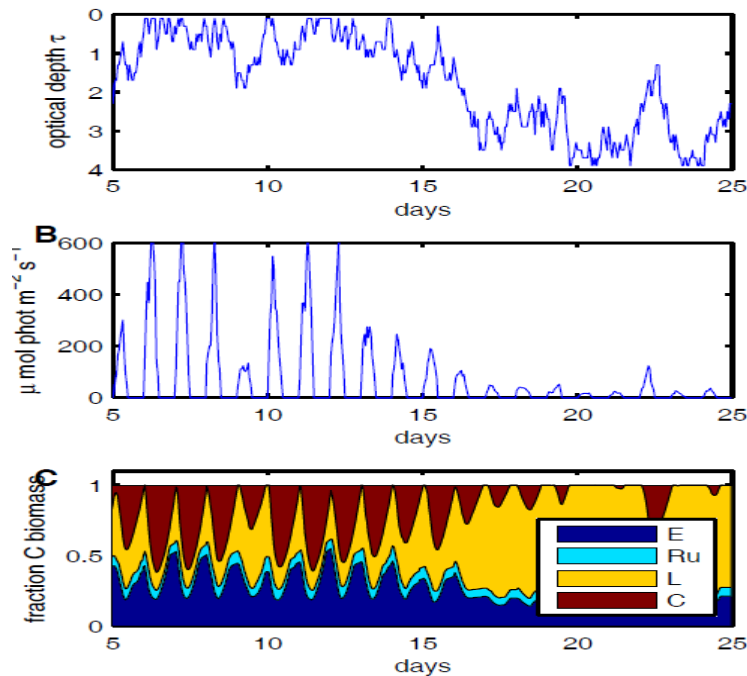
One optimal strategy in constant environment – no C storage



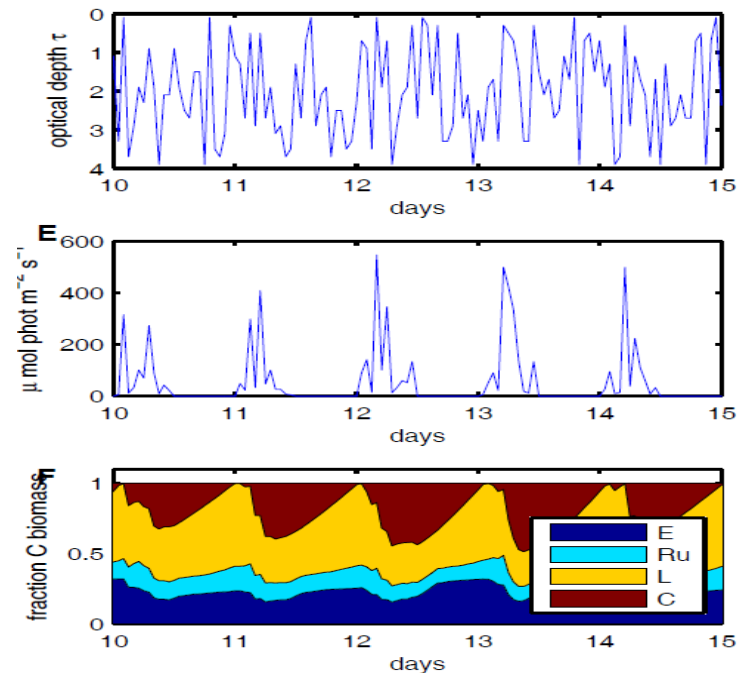
Emergent strategies in fluctuating environments

Slow variability – C storage over diel cycle, acclimation

cf Ross & Geider (2009)



Fast variability – fitness maximisation
⇒ increased allocation to Rubisco, C storage buffering of short light pulses



Summary

- Approach of physiology + resource allocation + optimality gives a parameter-sparse representation of diversity:
 - Environmental selection on *traits (population adaptation)*
 - Dynamic environments: fitness maximising behaviour as *optimal control (acclimation, storage strategies)*
- Environmental selection for phytoplankton growth strategies
 - Size: Nutrients \Rightarrow (minimum) size
 - Composition: overall patterns in N:P
 - ... but growth rate requirements for rRNA can only explain part of N:P
 - Dynamic strategies as fitness maximisation
- Functional trait and physiological approach is *unreasonably* effective ...as an approach to evolutionary ecology

Implications for the carbon cycle

- C:N is relatively conserved therefore predicted increase in N:P under warming implies increased C:P and potentially greater export
 - But need to consider changes in multiple environmental controls
- Increase in phytoplankton N:P will tend to produce more N limitation, but may also select more strongly for diazotrophs
- Need dynamic strategies to capture storage of C, P and N in phytoplankton properly

Integrative Terrestrial-Marine Lessons

- Traits and physiologically-grounded trade-offs is the way forward for process-based prediction (cf Tilman 1990, JeDi terrestrial model)
- Marine: Primary production by microbes in fluid
 - Relatively direct link from cellular economics and ecophysiology to biogeochemical cycles (but recycling still ‘complicated’ and higher organisms and trophic structure important for biological pump)
 - High diversity and rapid adaptation of microbial ecosystem
 - Fluid physical environment ‘easy’ to model
- Terrestrial: Primary production by higher plants in soil
 - Multi-cellular complexity and soil formation means indirect link from ecophysiology and cellular economics to biogeochemical cycles
 - Long lifetimes, slow dispersal, slower adaptation timescales
 - Solid phase of physical environment ‘hard’ to model