Modelling diverse communities

Trade-offs and species diversity pull the strings

Jorn Bruggeman

Department of Earth Sciences/St. John's College

University of Oxford

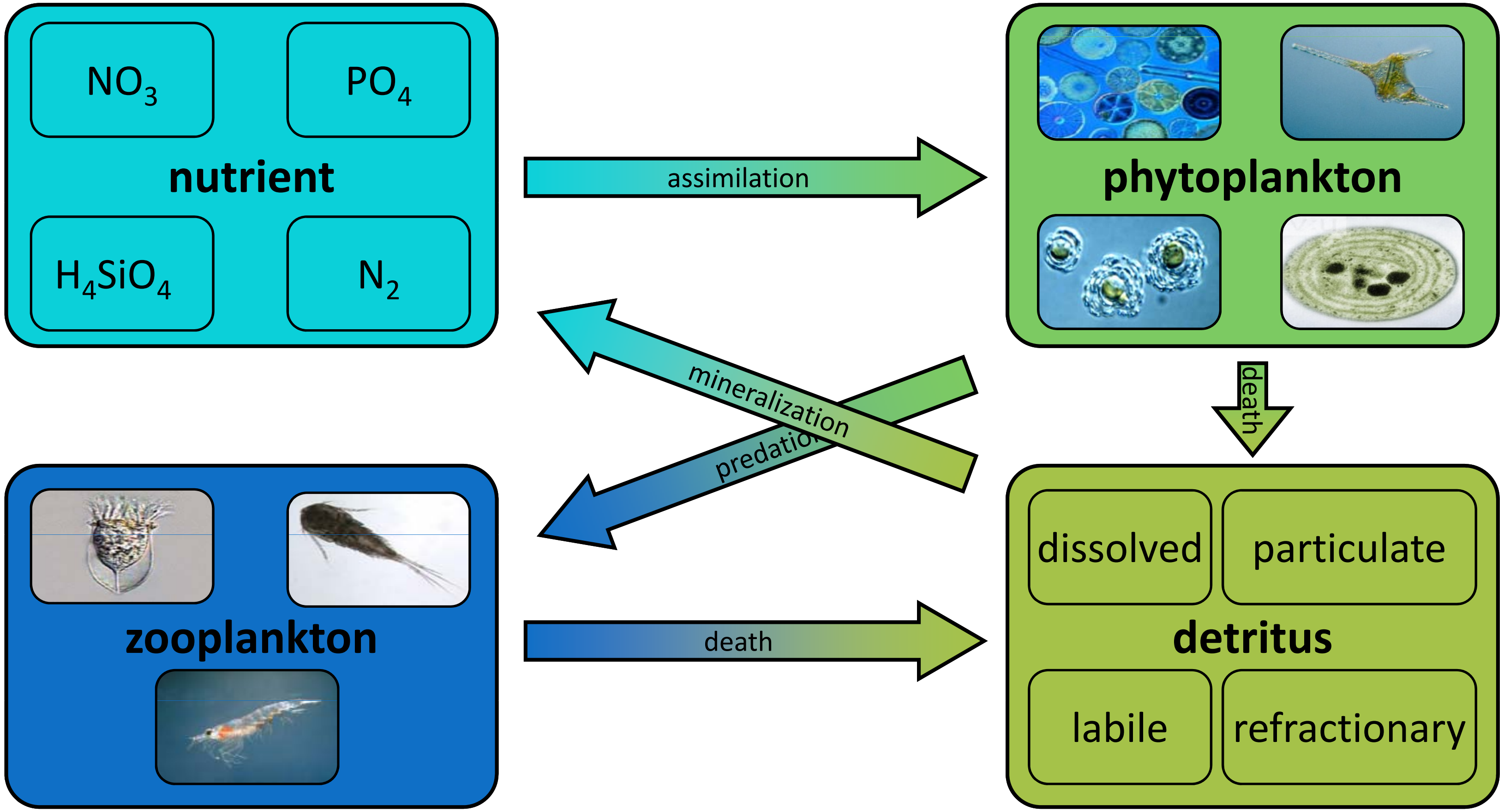
St John's College Oxford

UNIVERSITY OF OXFORD

Natural diversity

- Up to 50 % of global primary production
- Key role in biogeochemical cycles
- High diversity = adaptability

Confronting complexity in models



NPZD: Evans & Parslow (Biol Oceanog 1985), Franks et al., (Mar Biol 1986), Fasham et al. (J Mar Res 1990)

Plankton Functional Types: ERSEM/BFM, MEDUSA, Diat-HadOCC, PlankTOM, PISCES, TOPAZ

The desired outcome?

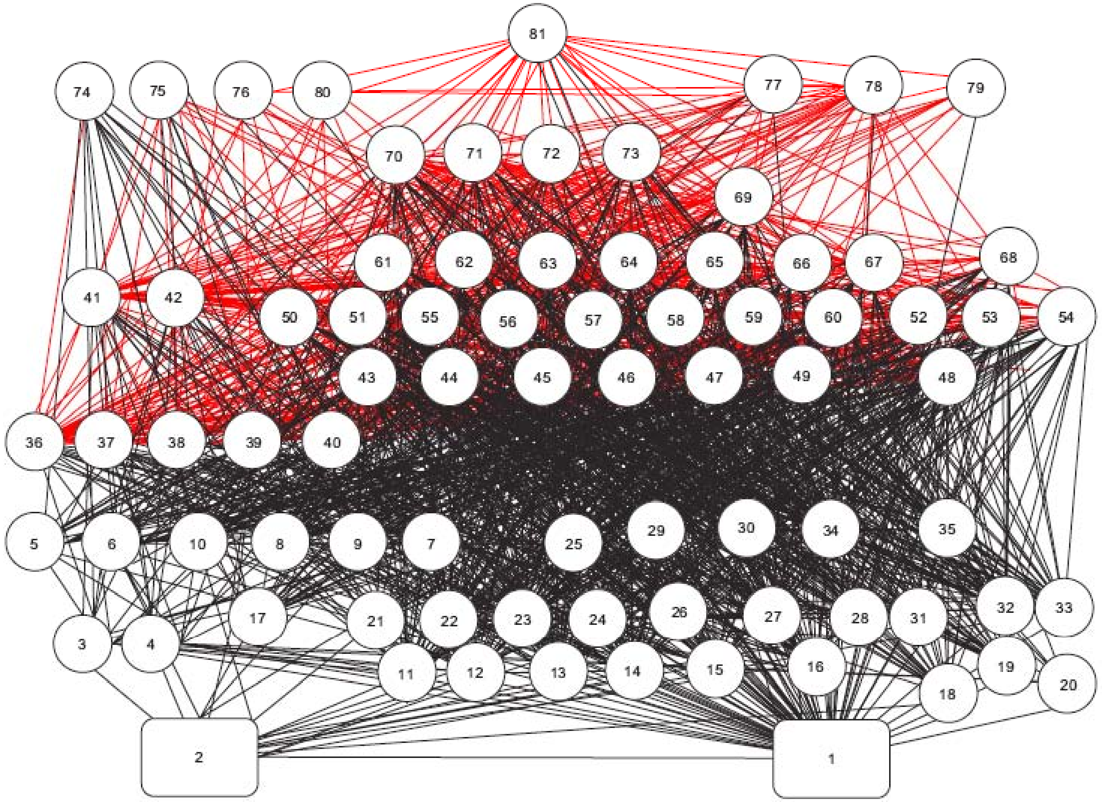
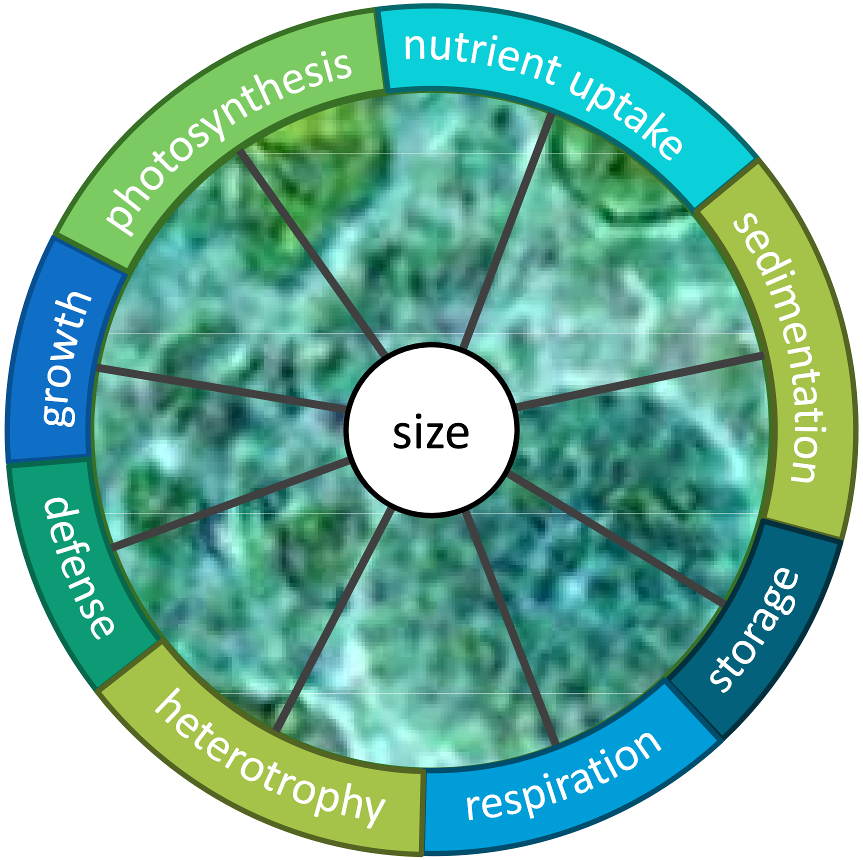


Fig. 1. Species and links of the northwest Atlantic food web. This tangled 'bird's nest' represents interactions at the approximate trophic level of each species, with increasing trophic level towards the top of the web. The left side of the web generally typifies pelagic organisms, and the right to middle represents more benthic/demersally oriented organisms. Red lines indicate predation on fish. 1 = detritus, 2 = phytoplankton, 3 = *Calanus* sp., 4 = other copepods, 5 = ctenophores, 6 = chaetognatha (i.e. arrow worms), 7 = jellyfish, 8 = euphasiids, 9 = *Crangon* sp., 10 = mysids, 11 = pandalids, 12 = other decapods, 13 = gammarids, 14 = hyperiids, 15 = caprellids, 16 = isopods, 17 = pteropods, 18 = cumaceans, 19 = mantis shrimps, 20 = tunicates, 21 = porifera, 22 = cancer crabs, 23 = other crabs, 24 = lobster, 25 = hydroids, 26 = corals and anemones, 27 = polychaetes, 28 = other worms, 29 = starfish, 30 = brittle stars, 31 = sea cucumbers, 32 = scallops, 33 = clams and mussels, 34 = snails, 35 = urchins, 36 = sand lance, 37 = Atlantic herring, 38 = alewife, 39 = Atlantic mackerel, 40 = butterfish, 41 = loligo, 42 = illex, 43 = pollock, 44 = silver hake, 45 = spotted hake, 46 = white hake, 47 = red hake, 48 = Atlantic cod, 49 = haddock, 50 = sea raven, 51 = longhorn sculpin, 52 = little skate, 53 = winter skate, 54 = thorny skate, 55 = ocean pout, 56 = cusk, 57 = wolfish, 58 = cunner, 59 = sea robins, 60 = redfish, 61 = yellowtail flounder, 62 = windowpane flounder, 63 = summer flounder, 64 = witch flounder, 65 = four-spot flounder, 66 = winter flounder, 67 = American plaice, 68 = American halibut, 69 = smooth dogfish, 70 = spiny dogfish, 71 = goosefish, 72 = weakfish, 73 = bluefish, 74 = baleen whales, 75 = toothed whales and porpoises, 76 = seals, 77 = migratory scombrids, 78 = migratory sharks, 79 = migratory billfish, 80 = birds, 81 = humans

Adaptive approaches

1. **Standardize** species
   - unified model
   - *traits* describe interspecific variability
   - *trade-offs* link costs and benefits

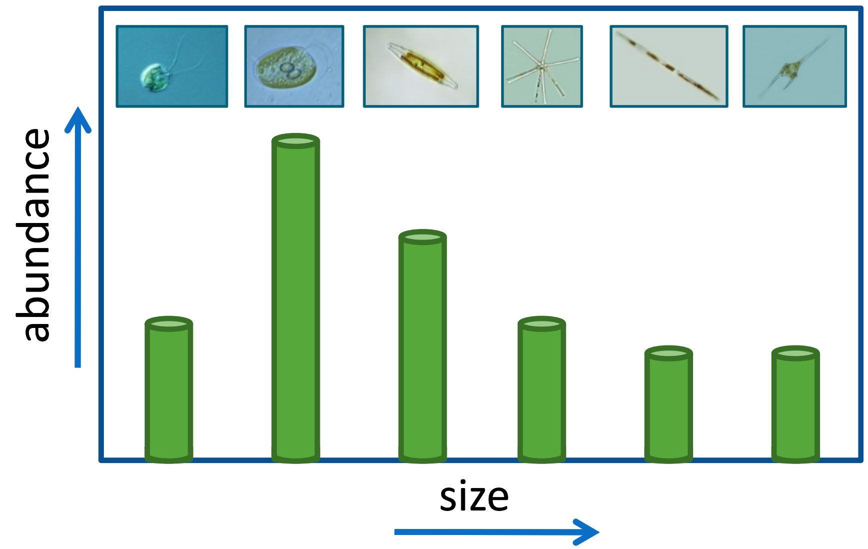


Adaptive approaches

1. **Standardize** species
   - unified model
   - *traits* describe interspecific variability
   - *trade-offs* link costs and benefits

2. **Generate** multi-species community
   - introduce "all possible" species or randomly draw trait values

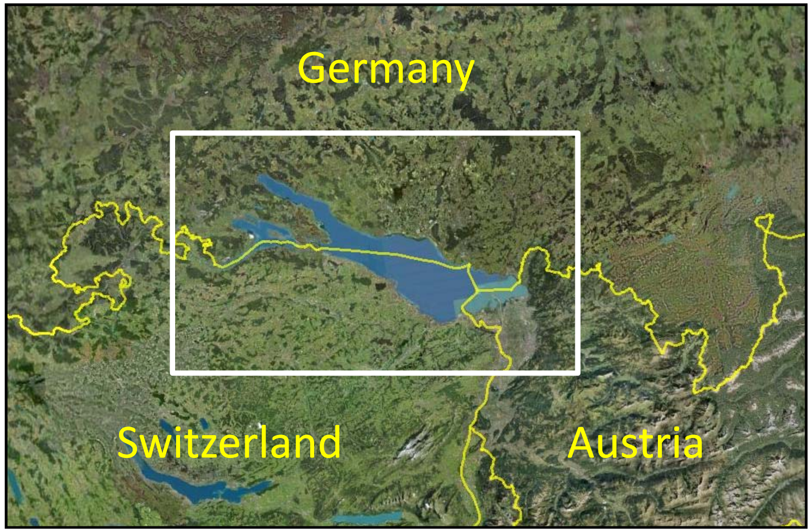
3. **Study** evolution in spatial and temporal varying environments
   - Community self-assembles through interspecific competition



"Everything is everywhere, the environment selects"
Beijerinck (1913) & Baas-Becking (1934)

Example

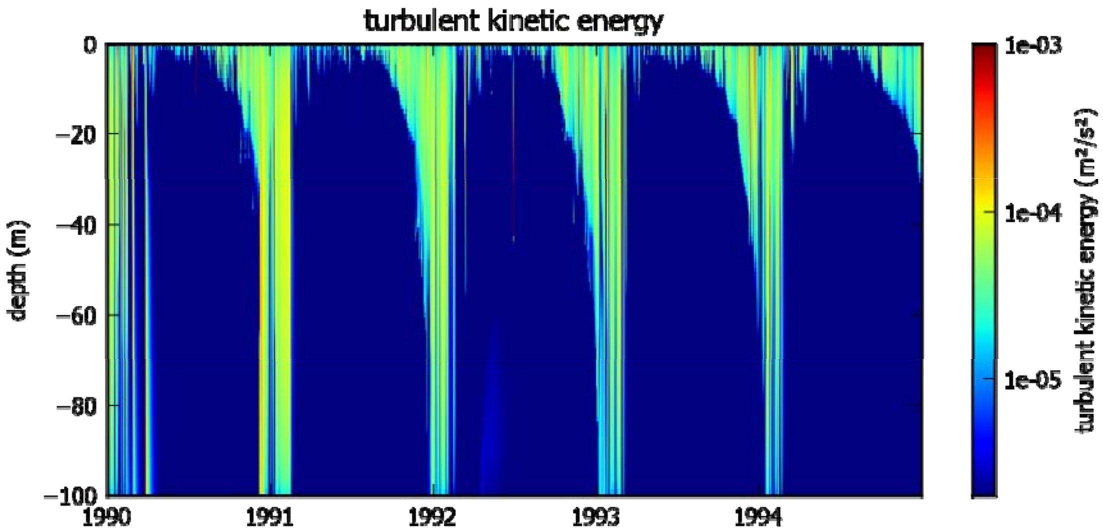
Phytoplankton succession in Lake Constance



Surface area	536 km²
Depth	101 m on average, 254 m maximum
Limiting nutrient	P
Dominant grazer	*Daphnia* sp.
Seasonality	physics-driven: summer stratification, winter deep mixing

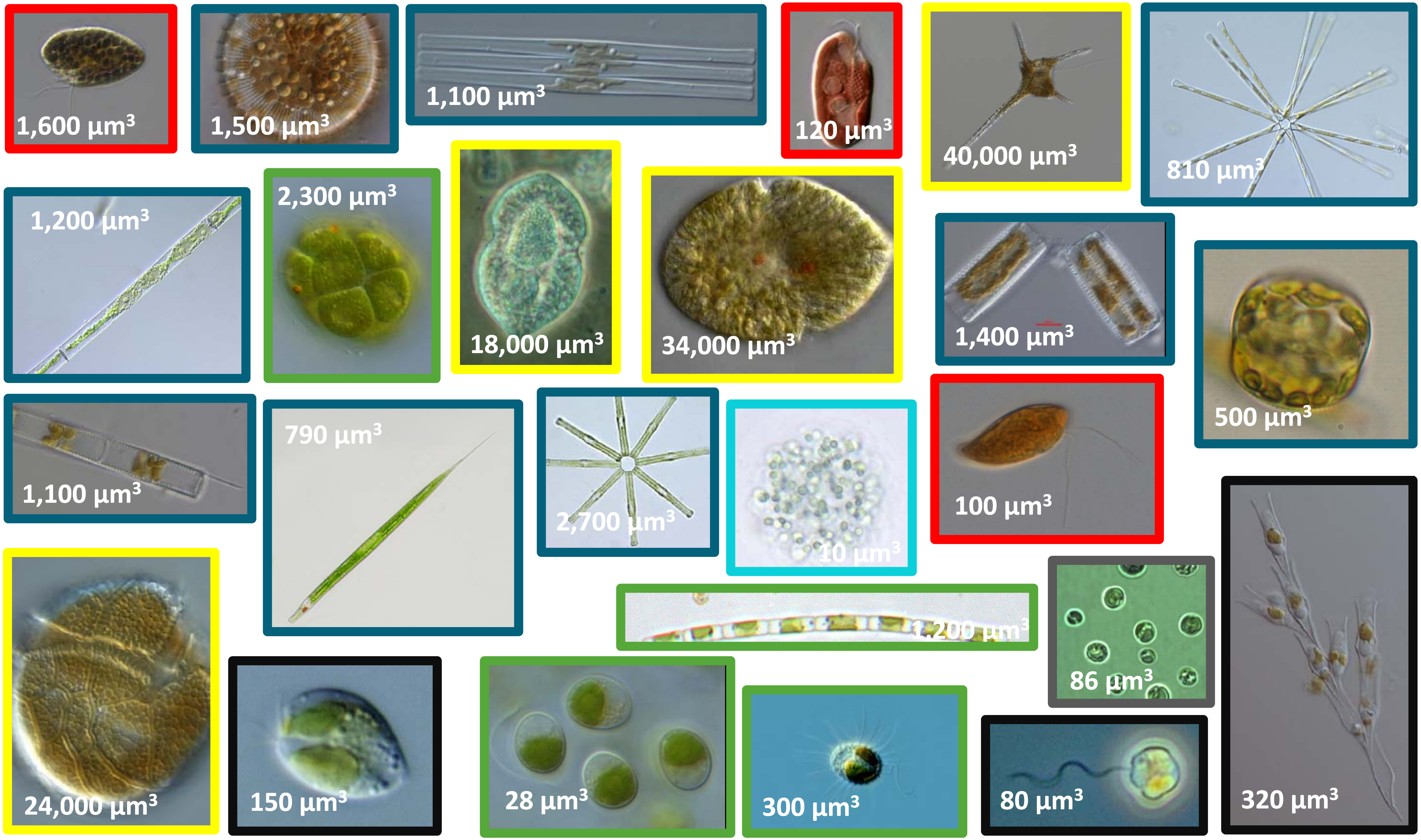
34 years of observations

- Physics
  - hourly meteo
  - monthly temperature profiles

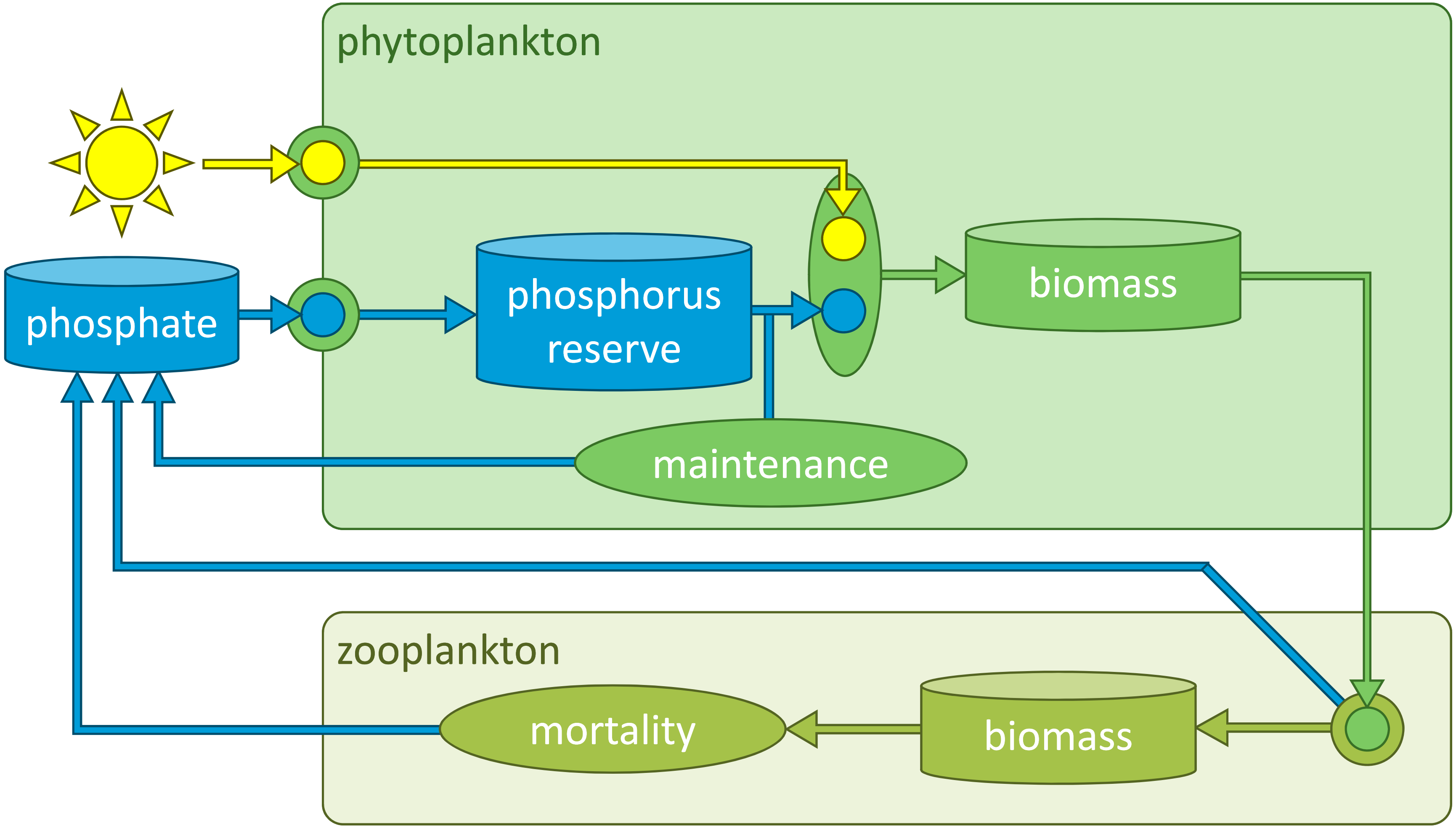


- Biochemistry
  - biweekly bulk nutrients & biomass
  - weekly counts of **200+** phytoplankton species

Observed phytoplankton species

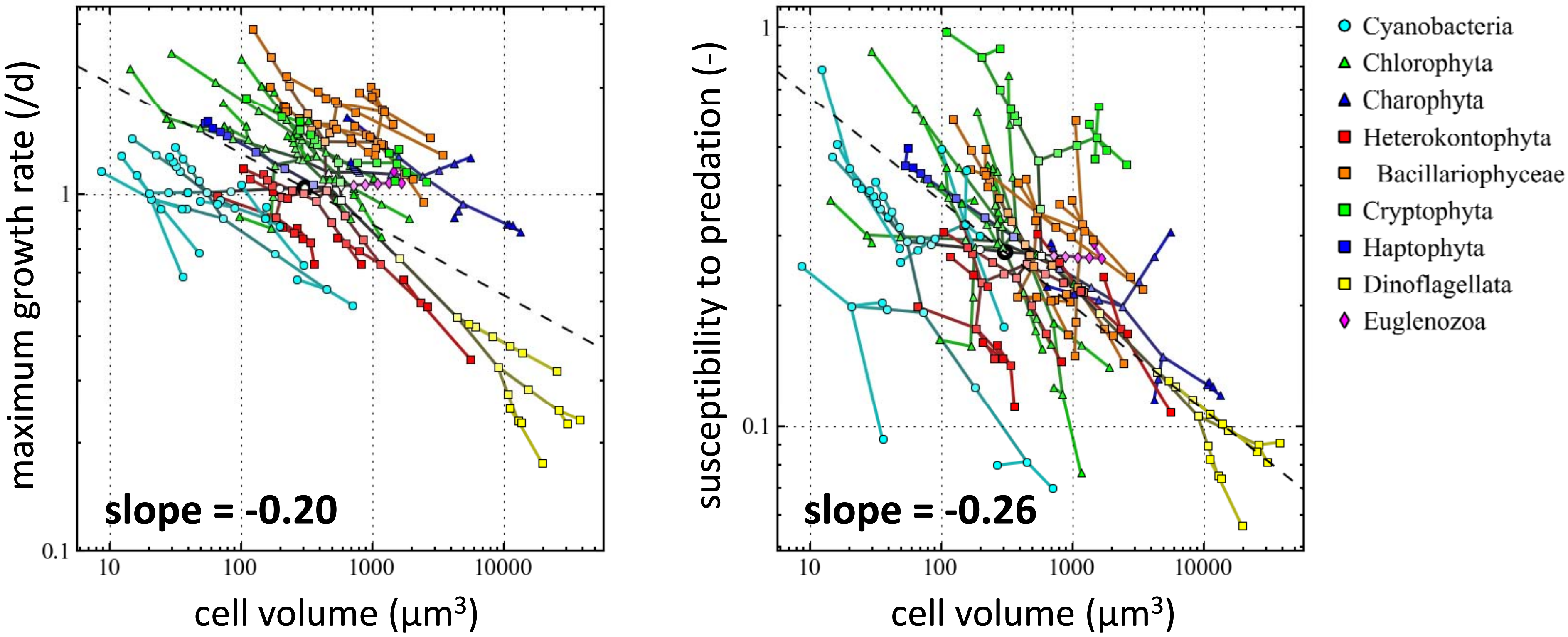


A generic phytoplankton model



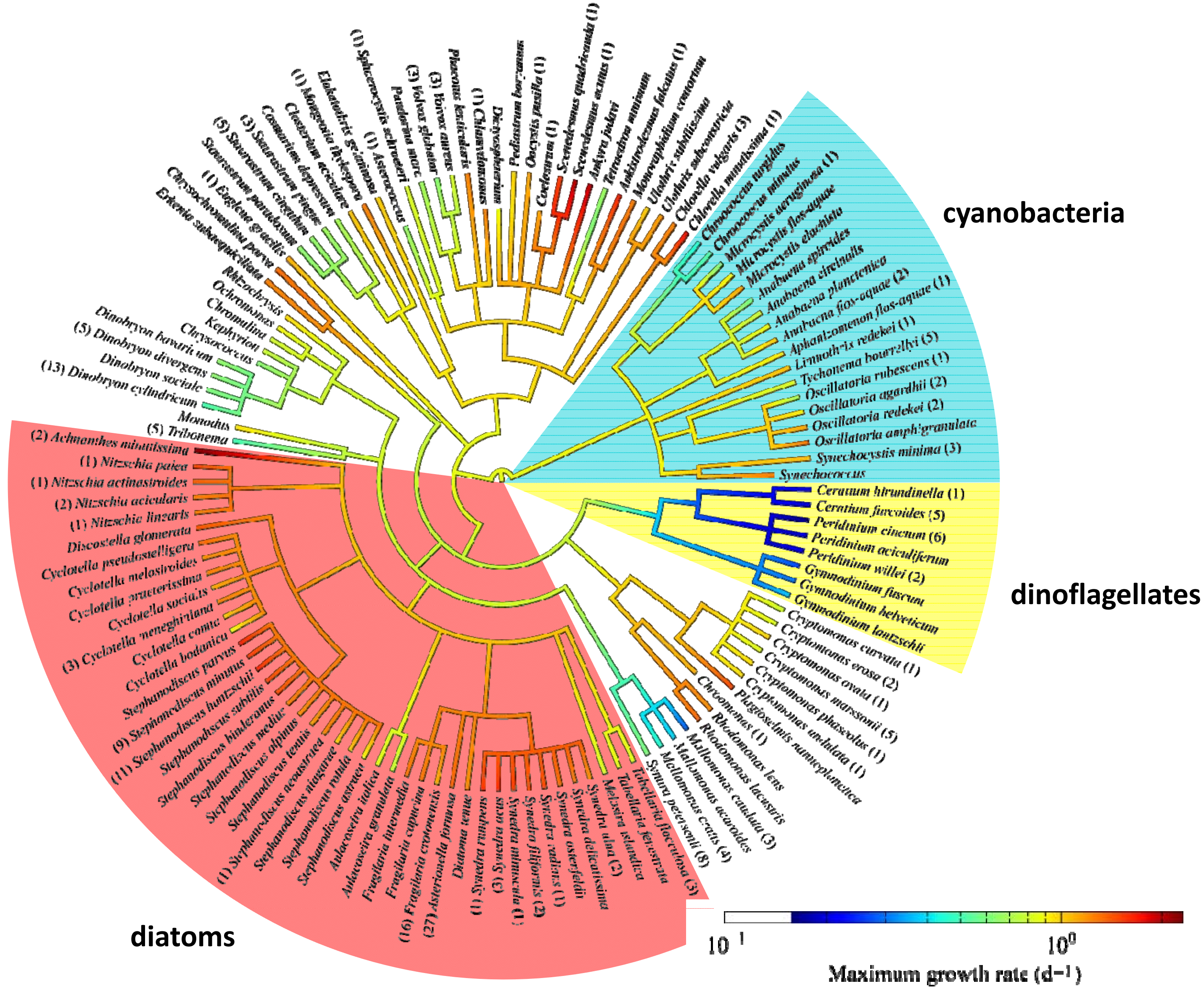
Dynamic Energy Budget (DEB) theory (Kooijman 2000;2010)

What traits govern interspecific variability?



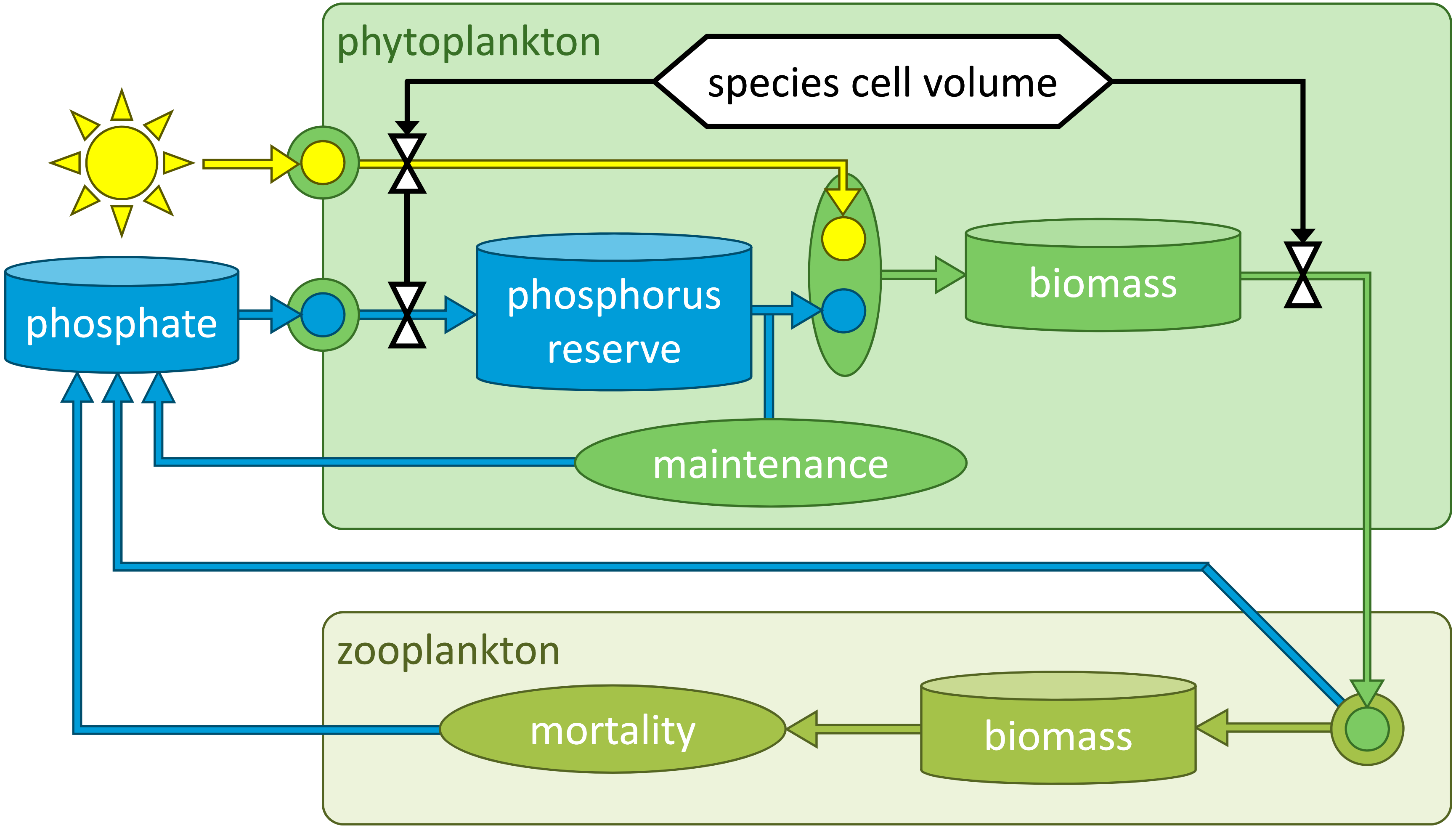
Bruggeman et al. (Nucleic Acids Res 2009), Bruggeman (J Phycol 2011)

By-product: trait values for all taxa



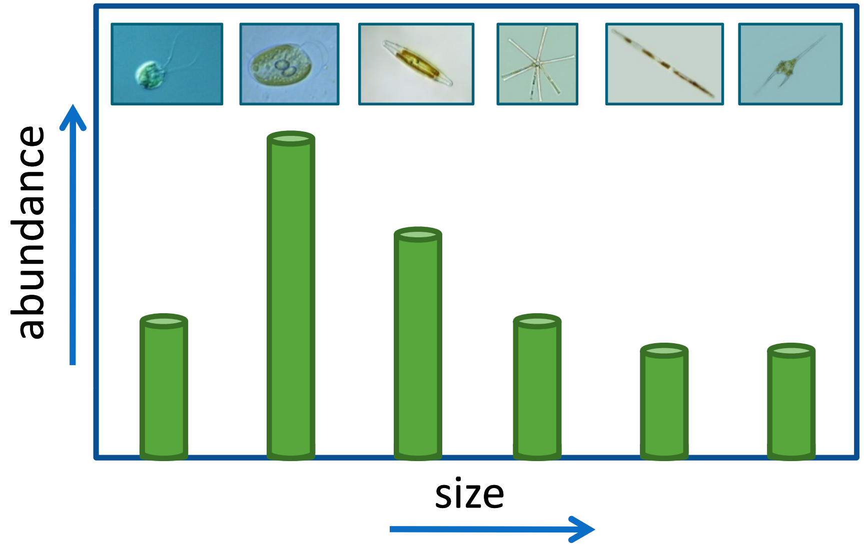
http://www.ibi.vu.nl/programs/phylopars/phytoplankton

Inserting size-dependencies



Dynamic Energy Budget (DEB) theory (Kooijman 2000;2010)

A size-structured community

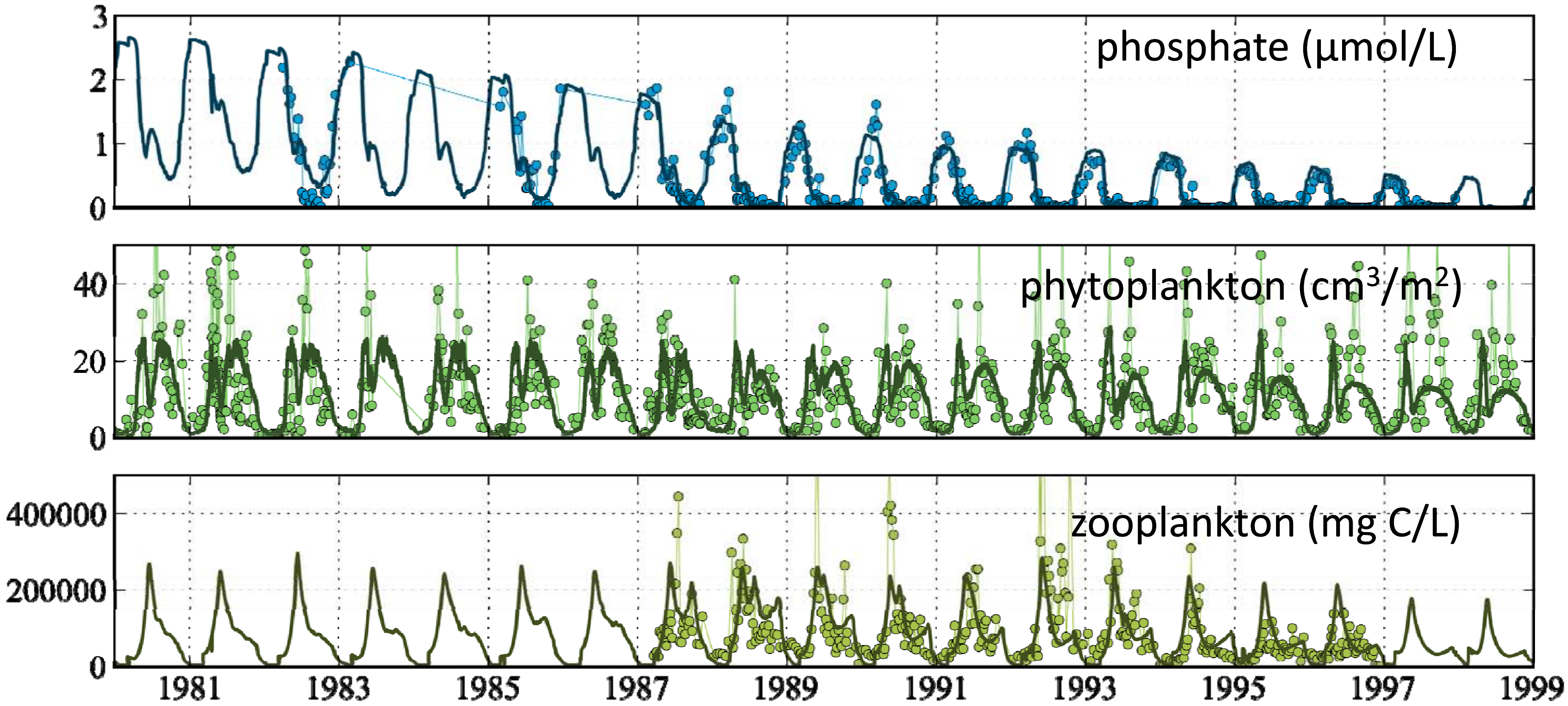


"Everything is everywhere, the environment selects"
Beijerinck (1913) & Baas-Becking (1934)

For instance:

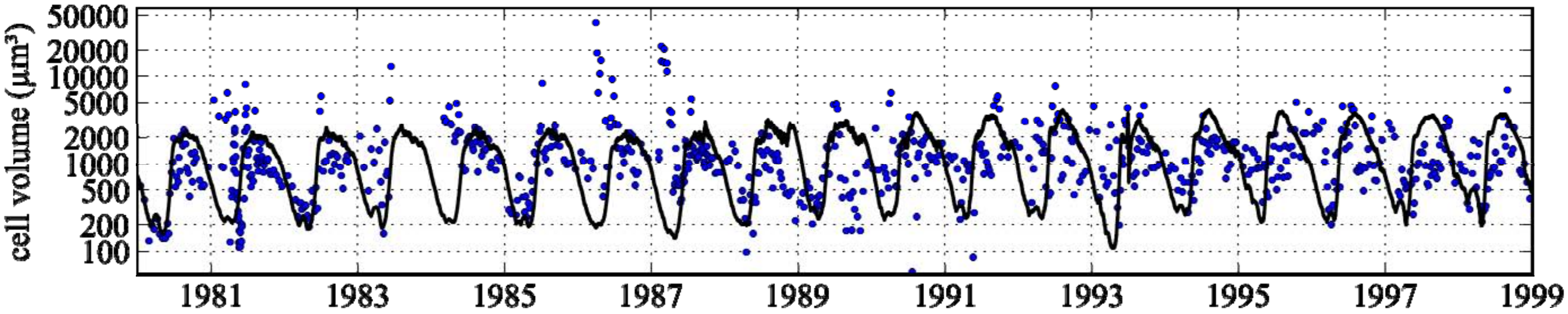
Moloney & Field (J Plankton Res 1991)
Gin et al. (Ecol Mod 1998)
Armstrong (J Plankton Res 1999)
Baird & Suthers (Ecol Mod 2007)
Banas (Ecol Mod 2011)
Ward et al. (Limnol Oceanog 2012)

Calibration: bulk nutrients and biomass

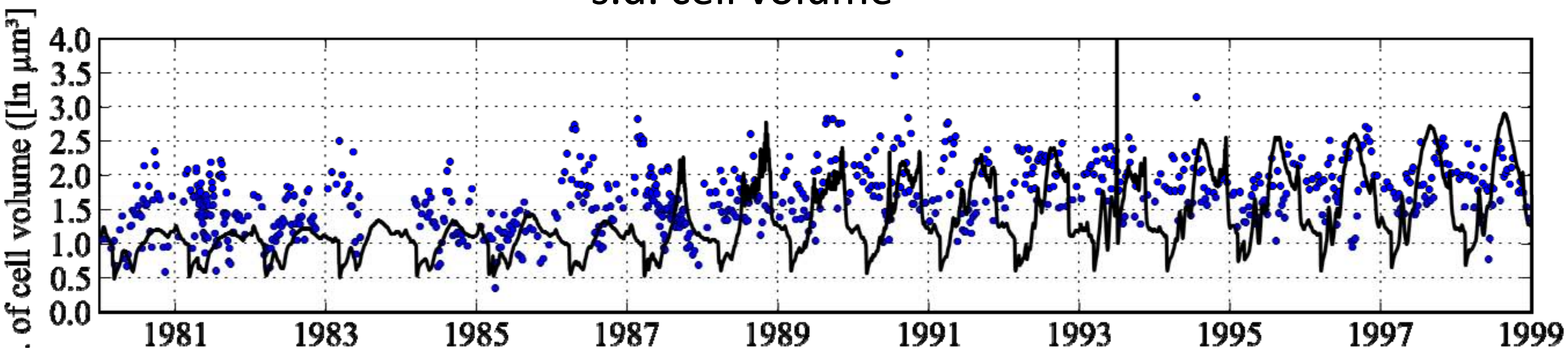


Validation: the size distribution

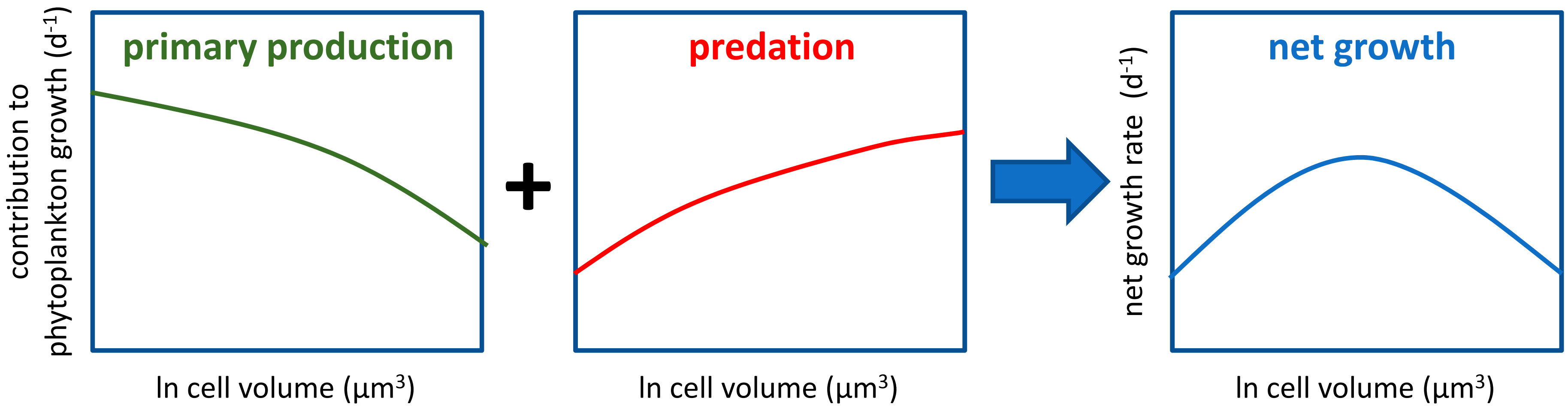
mean cell volume

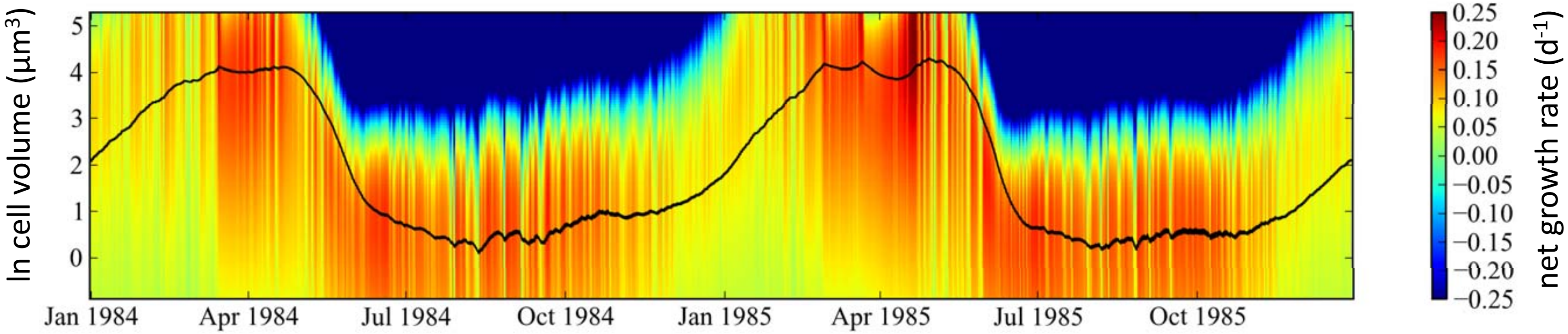


s.d. cell volume



Selection pressures





Interim conclusions

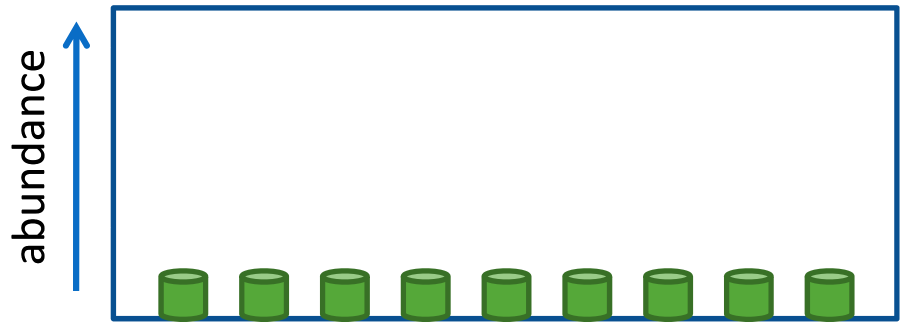
- A size-based approach captures *seasonal variation* in the *size structure* of the phytoplankton community
- Size structure is controlled by:
  - Bottom-up pressure (resource limitation favours small species)
  - Top-down pressure (grazers prefer small prey)

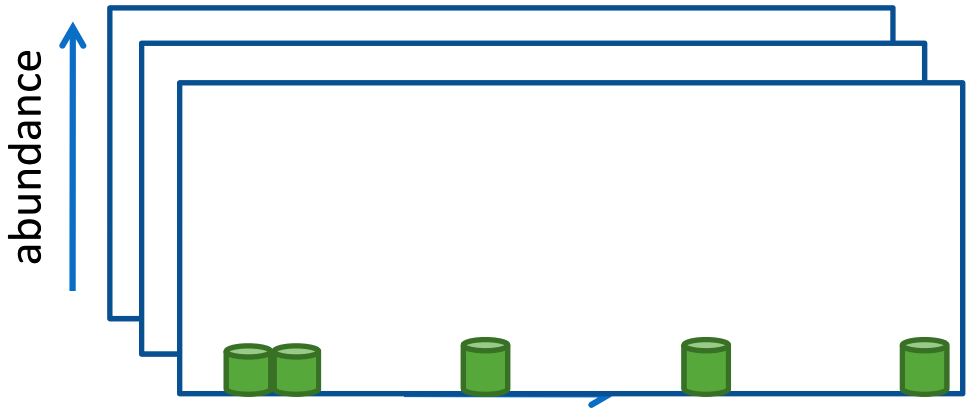
Revisiting adaptive approaches - differences

- How do you generate a multi-species community?
  - Sample trait space, repeat many times (ensemble simulation)
  - Grid all of trait space
- What processes control species diversity?
  - initial assemblage
  - immigration
  - background diversity/dormant communities
  - genetic mutation
- How do you represent a multi-species community?
  - Explicitly model many species
  - Implicitly represent community with aggregate statistics

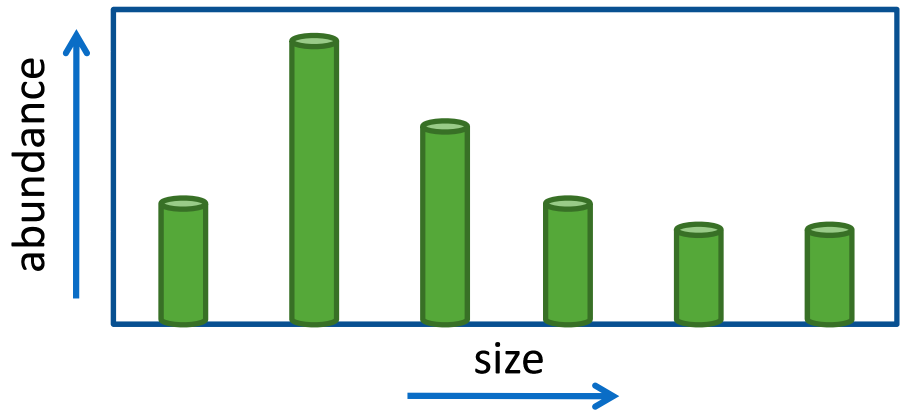
Generating a multi-species community

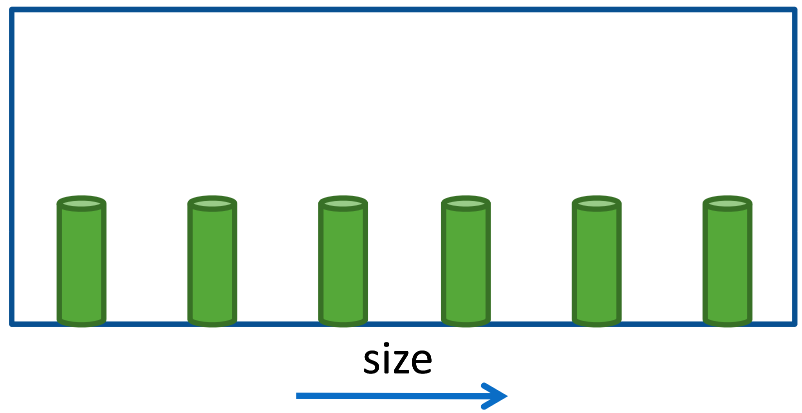
- Gridding vs. repeated sampling





- Distribution shape

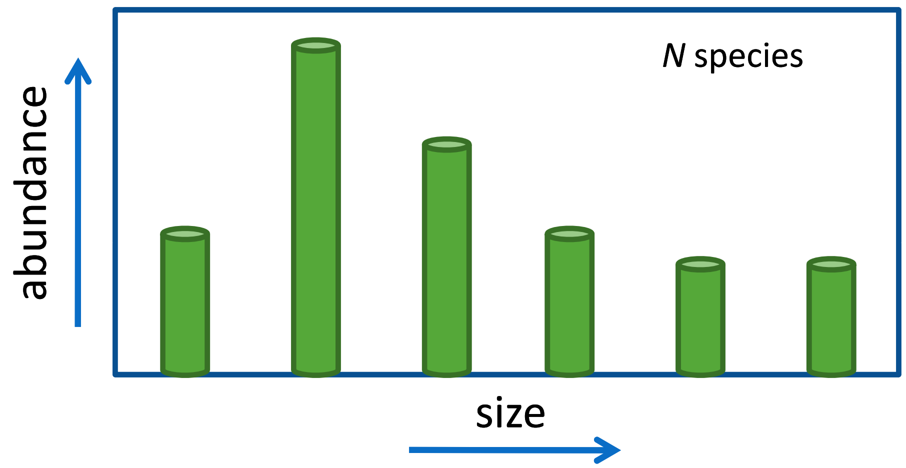




Sustaining diversity

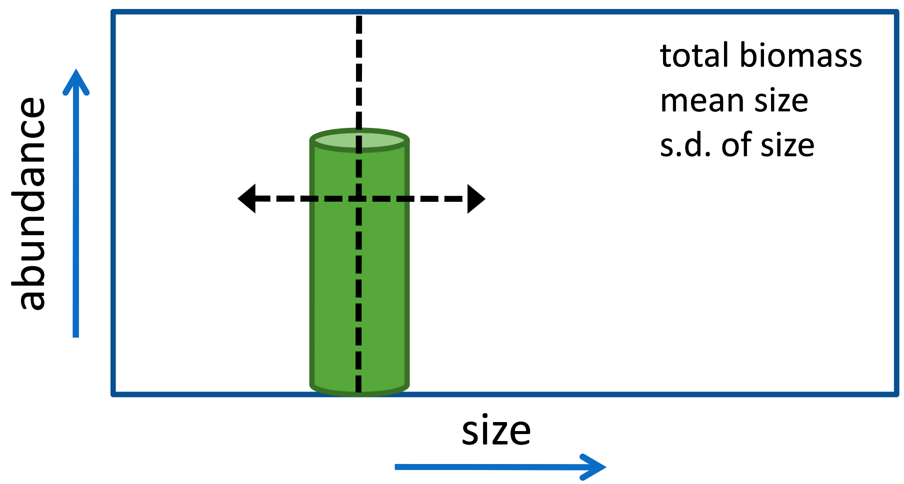
- Competitive exclusion is ubiquitous in models
- Why not in reality? Proposed reasons:
  - Spatial variability
  - Temporal variability
  - “Kill the winner”: frequency dependent specific growth. For instance: adaptive predator preferences (Fasham et al. 1990), viruses, interference feeding
- In models
  - Background species concentration
    - Source terms: $P+P_0$, sink terms: P
  - Mix in new species (laterally, vertically)
  - Mutate (Clark et al. Ecol Mod 2011)

From explicit species to aggregate statistics



Explicitly-modelled species

Follows et al. (Science 2007)
Bruggeman & Kooijman (Limnol Oceanog 2007)



Approximation in terms of "moments":
total biomass, trait mean and variance

Wirtz & Eckhardt (Ecol Mod 1996)
Norberg et al. (PNAS 2001)
Merico et al. (Ecol Mod 2009)

Close similarities with **A**daptive **D**ynamics and **a**daptive **d**ynamics

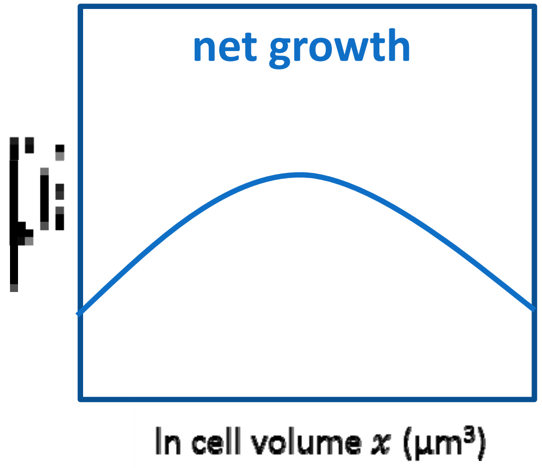
Dynamics of aggregate statistics

- Approximate equations

Total biomass $$\frac{d}{dt}C_T \approx C_T\left(r + \frac{1}{2}v\frac{\partial^2 r}{\partial x^2}\right)$$

Mean trait value $$\frac{d}{dt}\bar{x} \approx v\frac{\partial r}{\partial x}$$

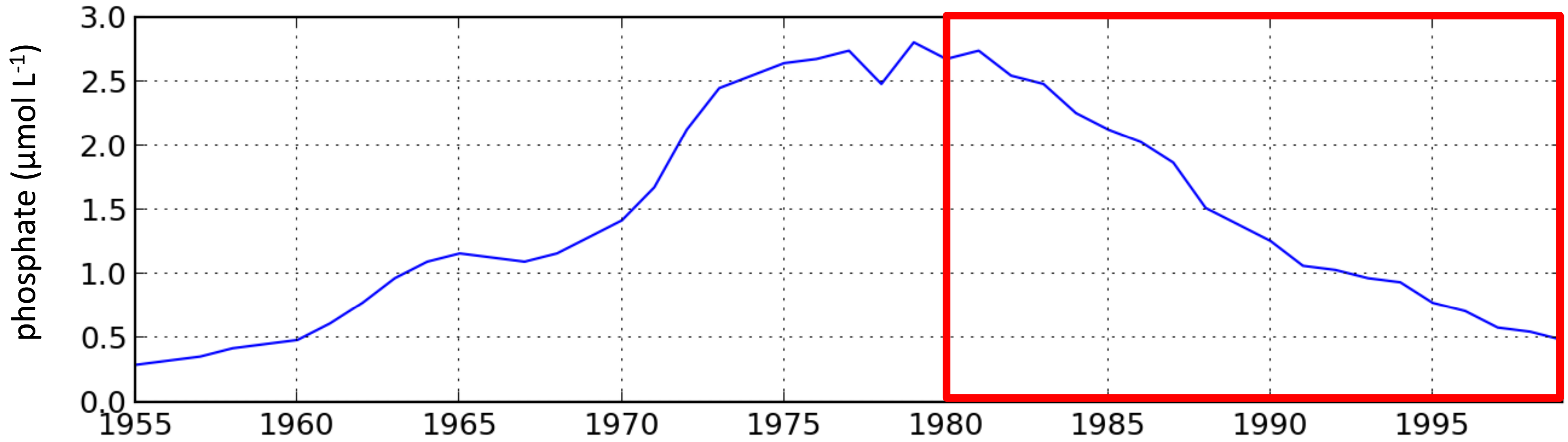
Variance $$\frac{d}{dt}v \approx v^2\frac{\partial^2 r}{\partial x^2}$$



Wirtz & Eckhardt (Ecol Mod 1996)
Norberg et al. (PNAS 2001)
Merico et al. (Ecol Mod 2009)

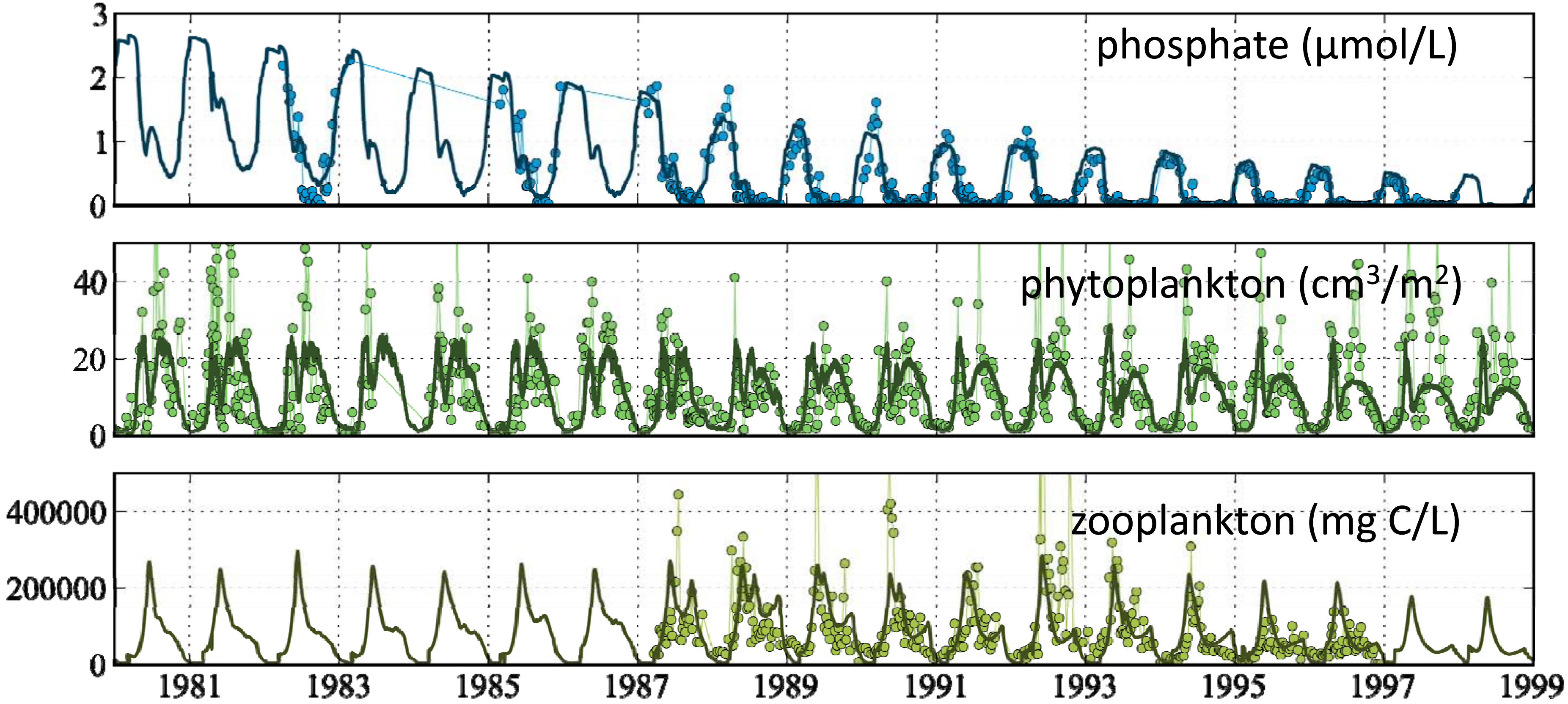
- The change in (mean) trait value is set by
  - fitness gradient $\frac{\partial r}{\partial x}$
  - diversity/trait variance v

Revisiting Lake Constance – long-term change

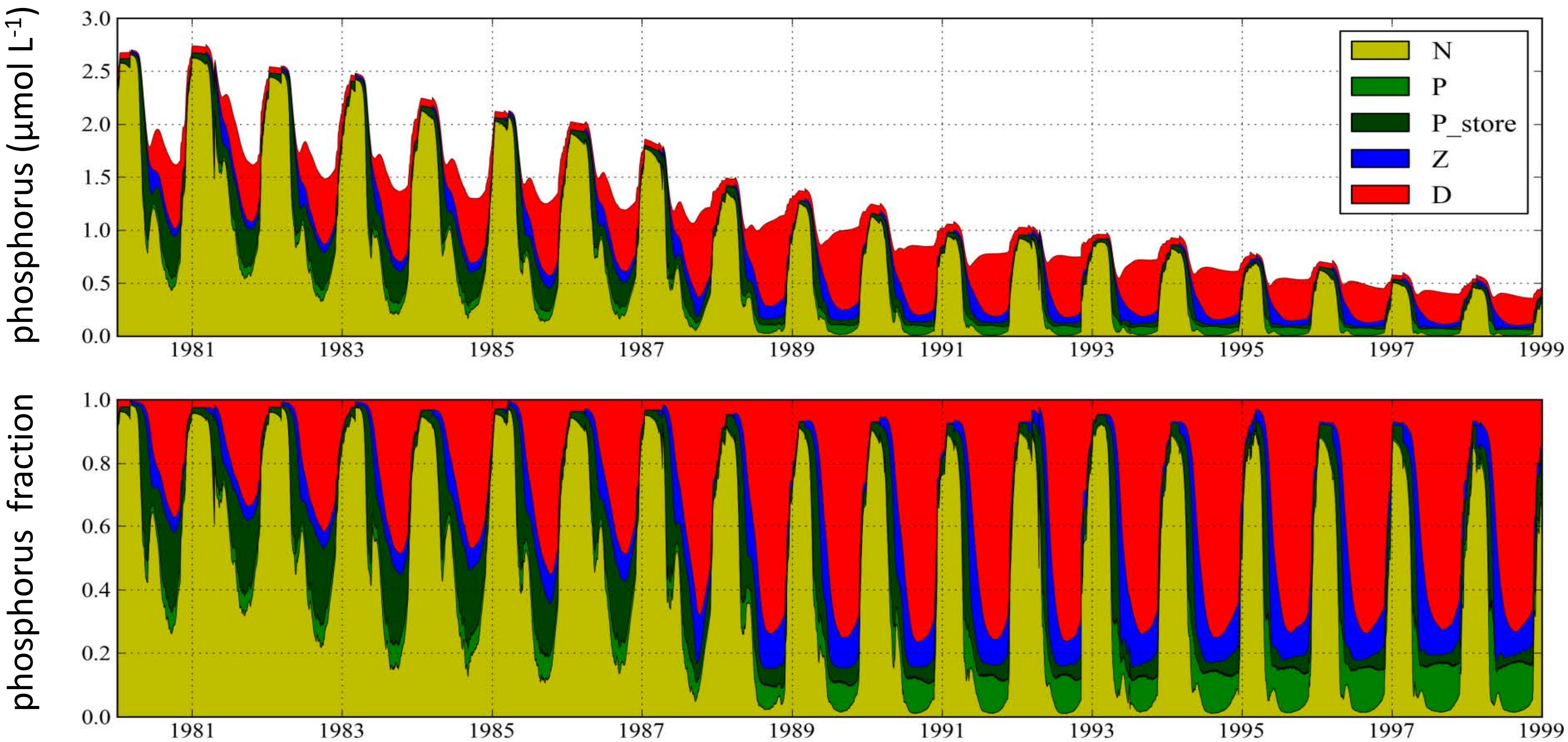


6-fold reduction in PO_4 between 1980 and 2000

Calibration: bulk nutrients and biomass

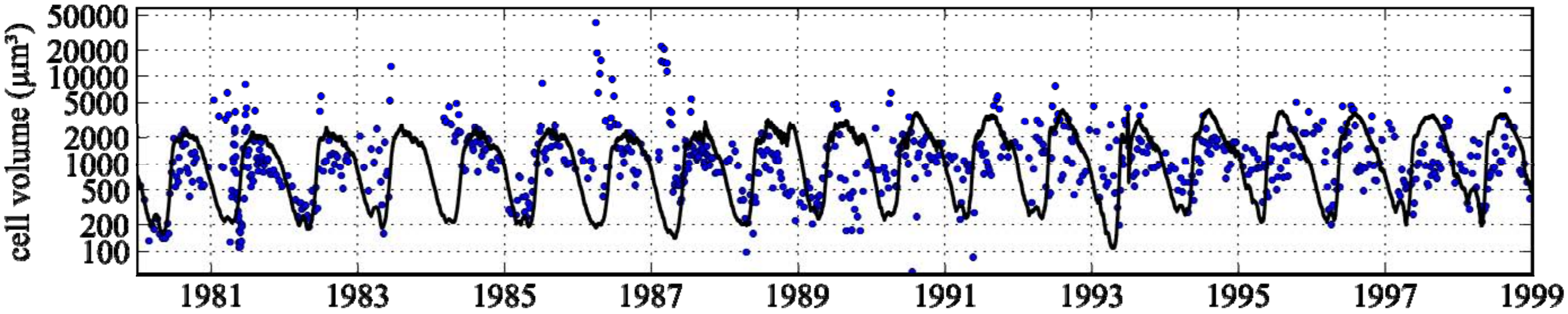


Where does the nutrient go?

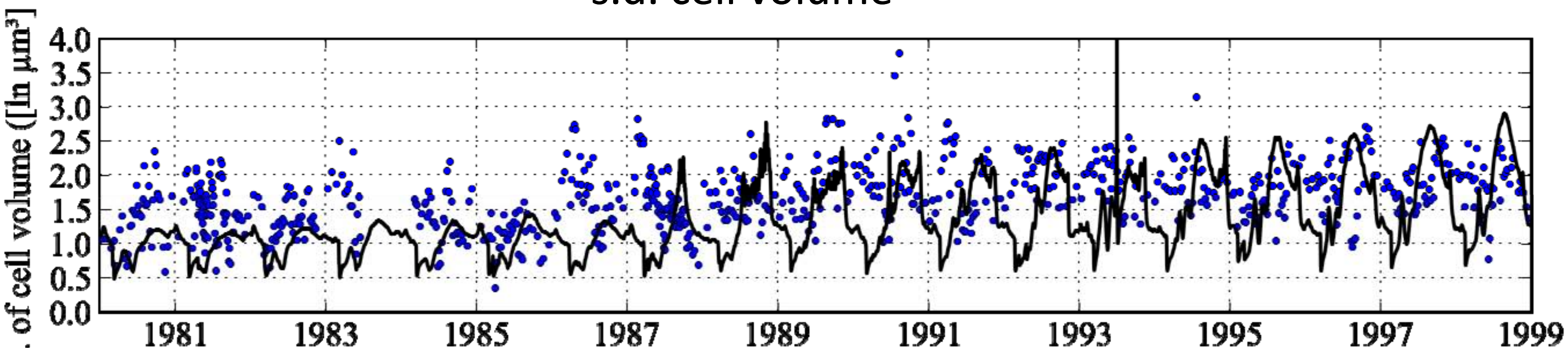


Another look at the size distribution

mean cell volume



s.d. cell volume



Proposed chain of events

1980 – 1988

[PO_4] reduction only affects internal P store

1988 – 1992

internal P store drops to critical level

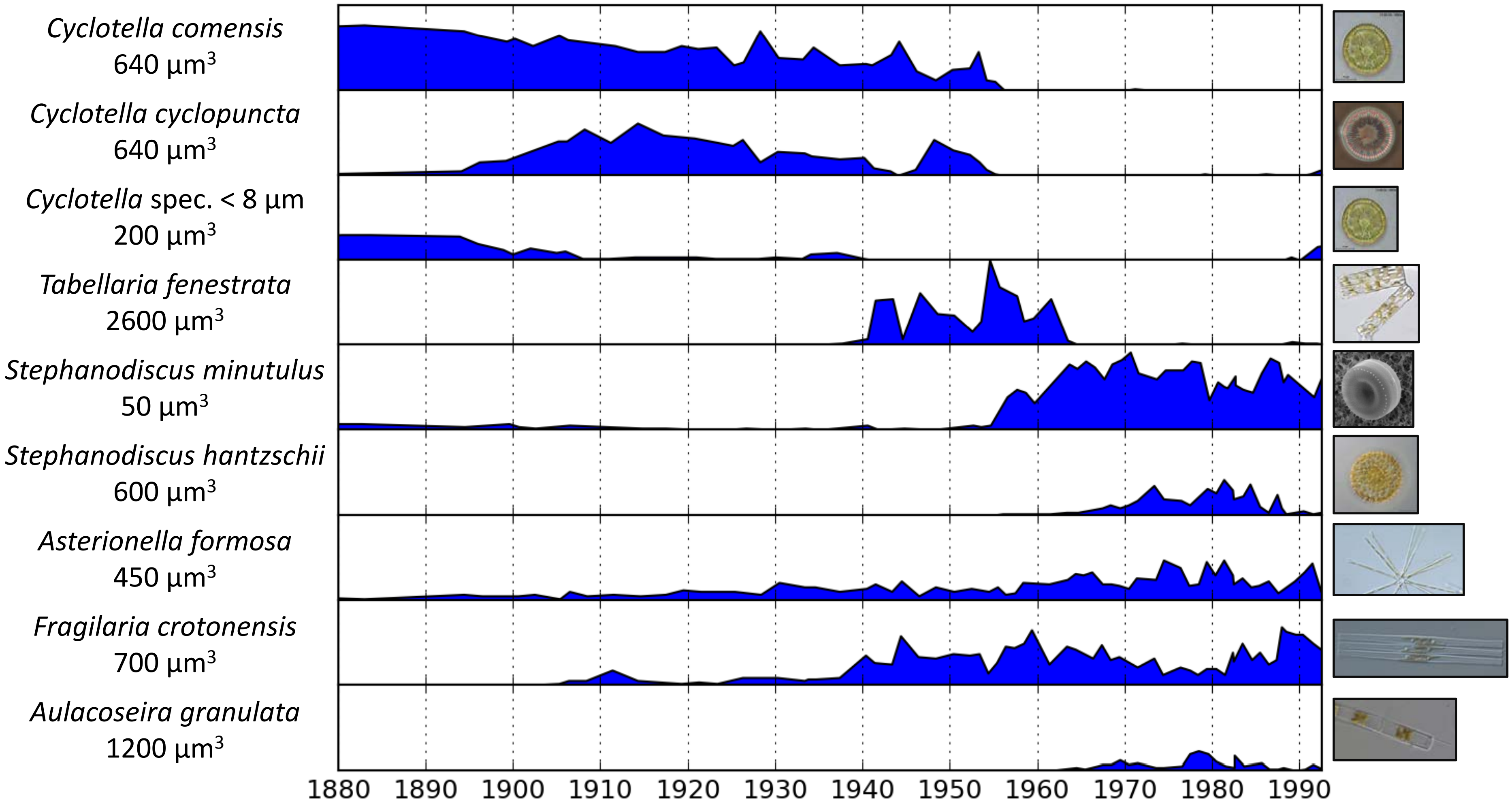
→ reduced dominance by fast growers
→ increased diversity
→ increased prey availability for grazer
→ increase in grazers
→ selection towards larger phytoplankton

1992 –

further nutrient reduction, increased bottom-up pressure

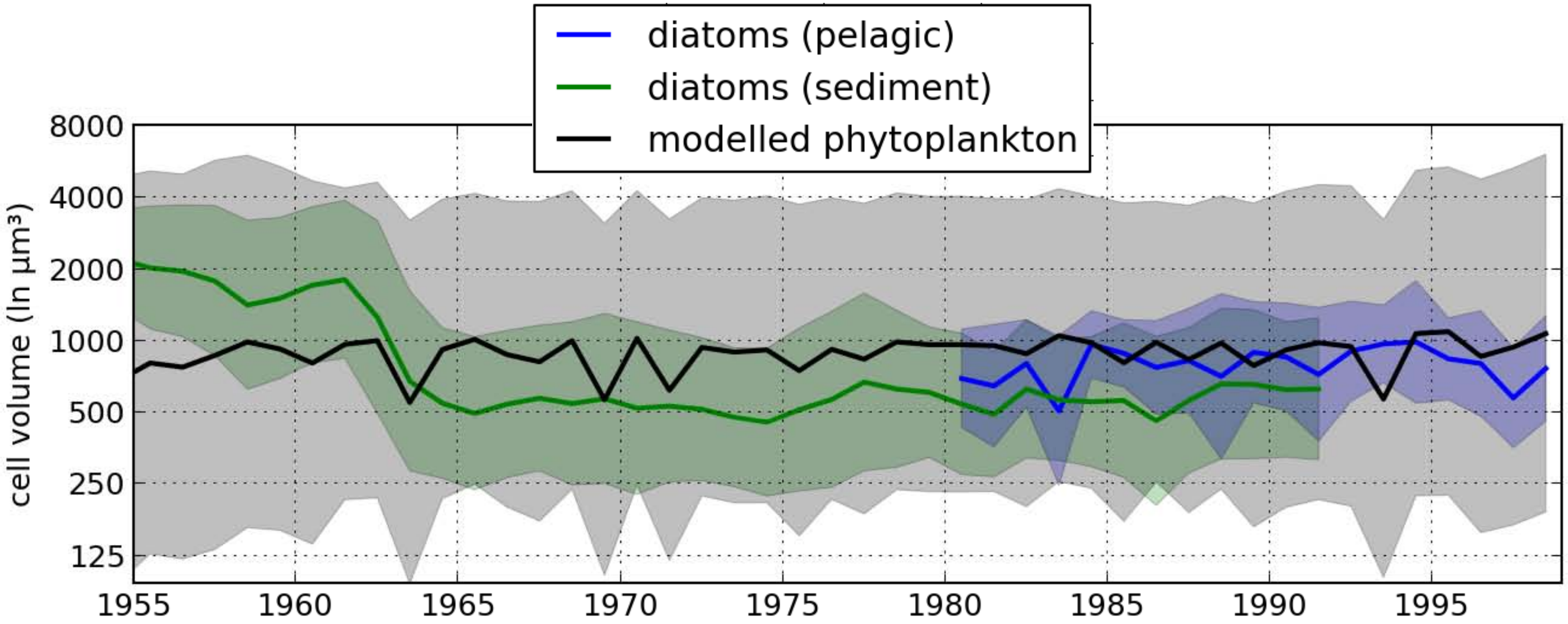
→ decreases in phytoplankton and grazer
→ selection towards smaller phytoplankton

Sedimentary record: diatom frustules



Wessels et al. (J Paleolimnol 1999)

Long-term diatom size



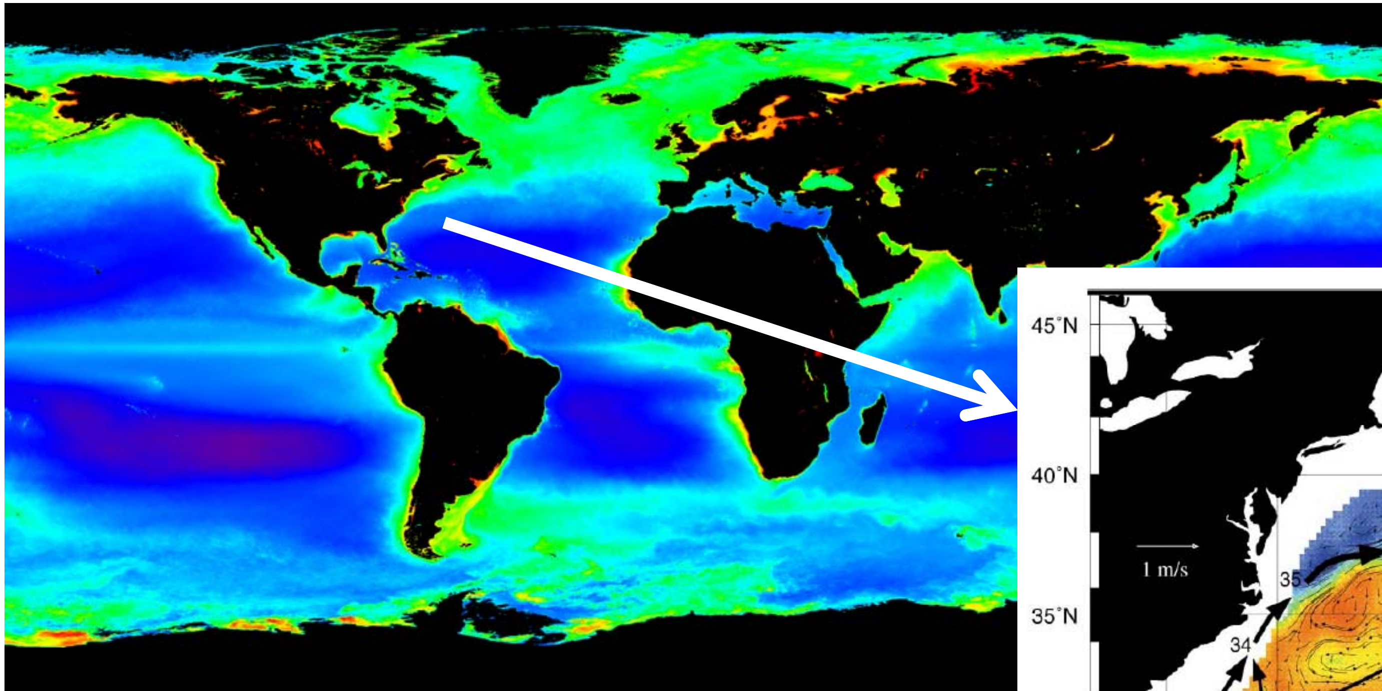
Tentative conclusions

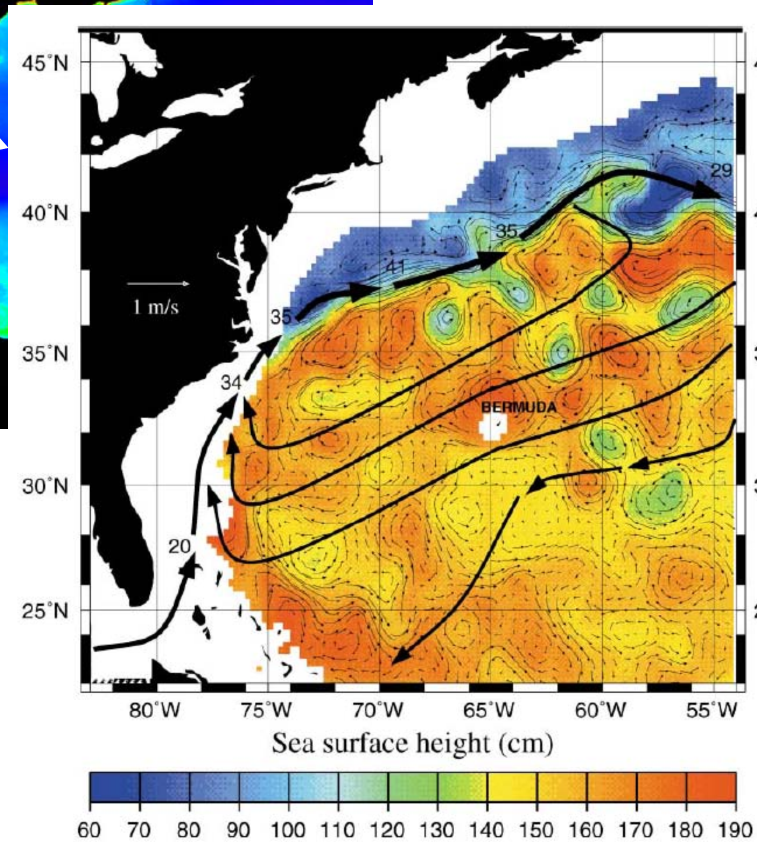
- Phytoplankton response to oligotrophication
  1. no response for 5-8 years
  2. increase in grazer concentration
  3. increase in phytoplankton size
- Causes
  - intracellular storage of nutrients delays response
  - interaction between resource limitation, *diversity*, and predation

Towards global, IPCC-class models

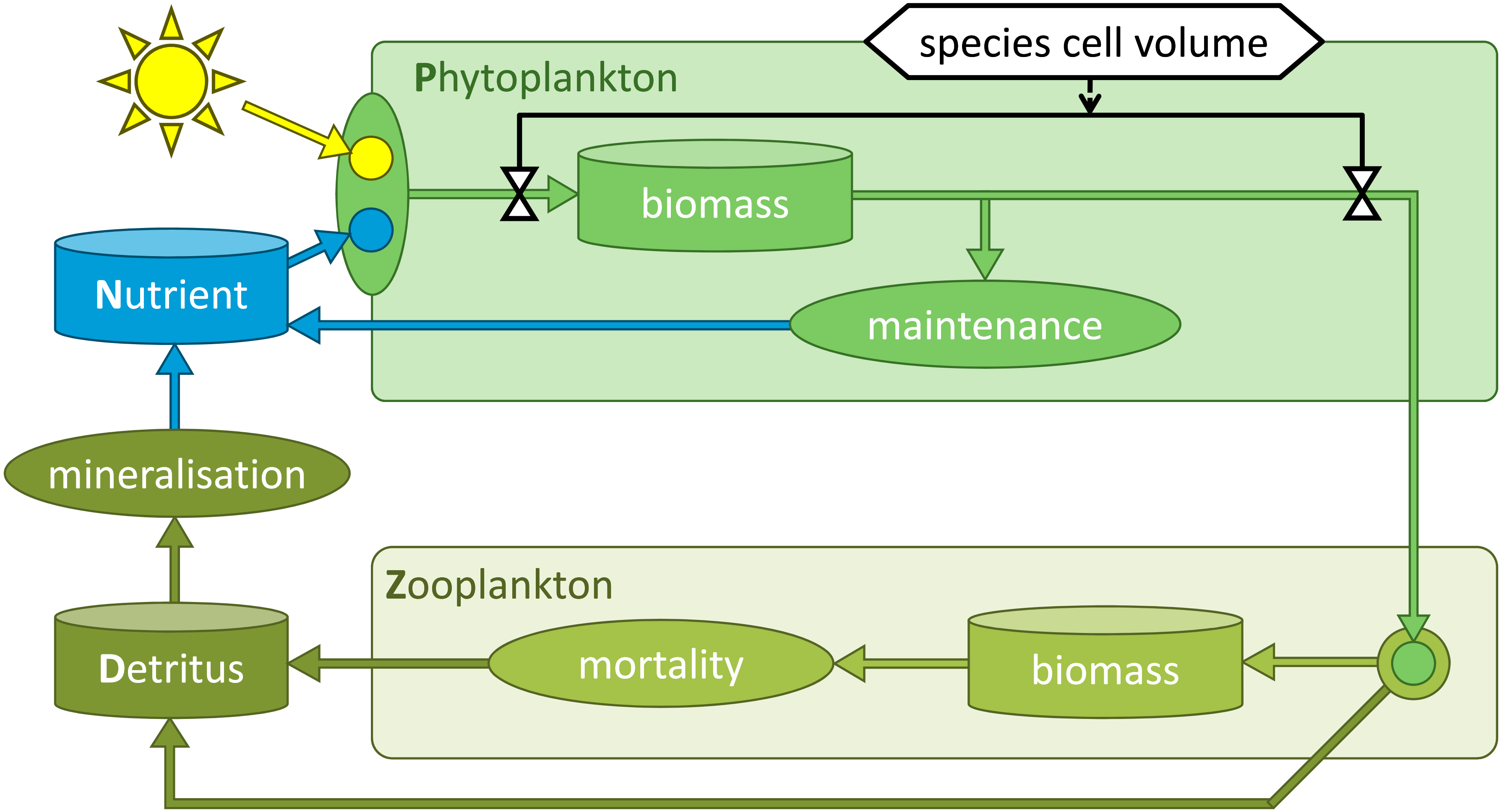
- 3D hydrodynamic models, >1.6 million grid points
- Explicit multi-species
  - Straightforward but expensive: many tracers, repeated runs
- Aggregate statistics
  - Fewer state variables, more complex local dynamics
  - But how do you transport mean and variance?
  - $\bar{x}C_T$ and $(v + \bar{x}^2)\ C_T$ behave as standard passive tracers (Bruggeman 2009)

Towards the world ocean

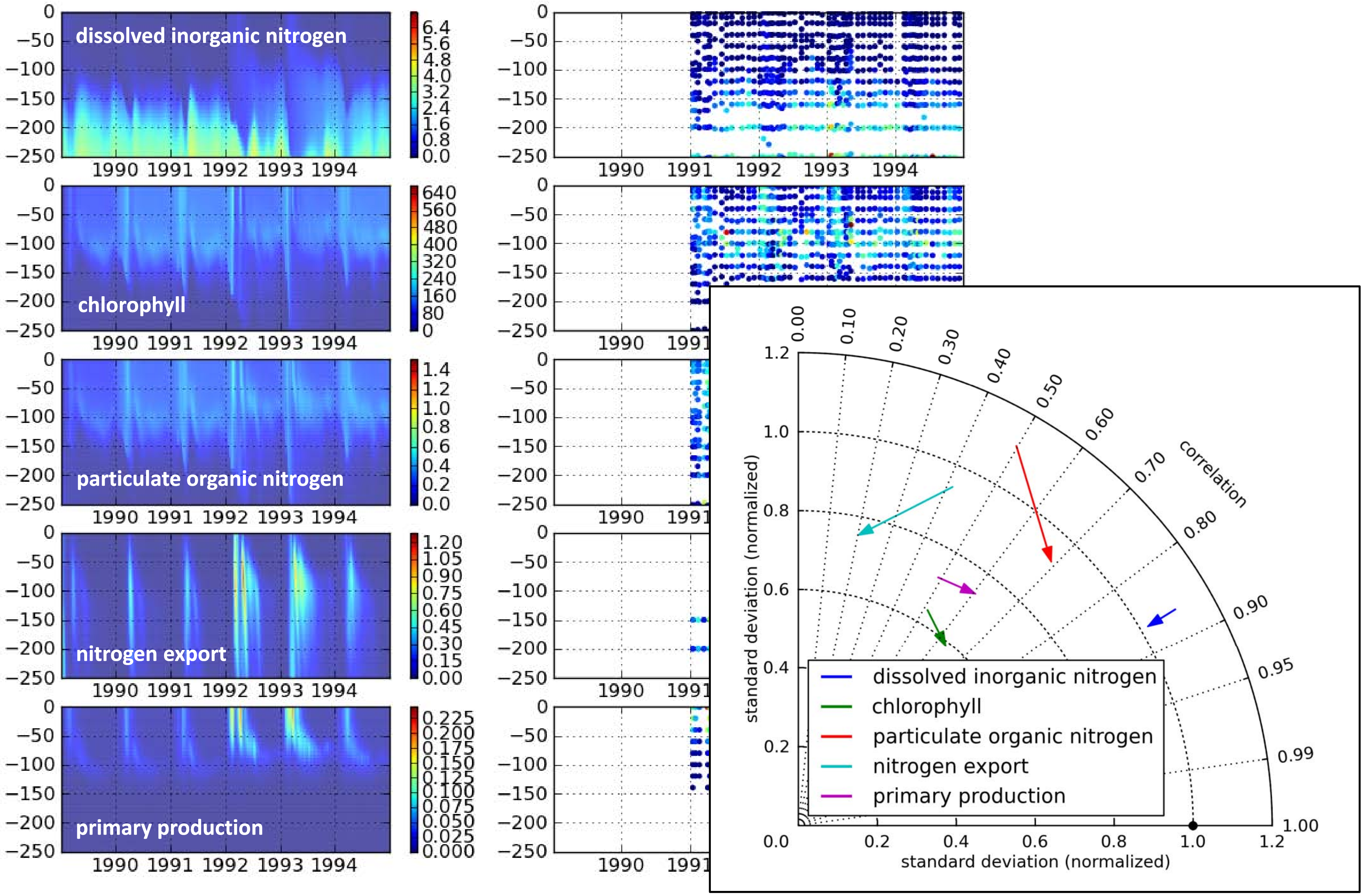




Stripped model

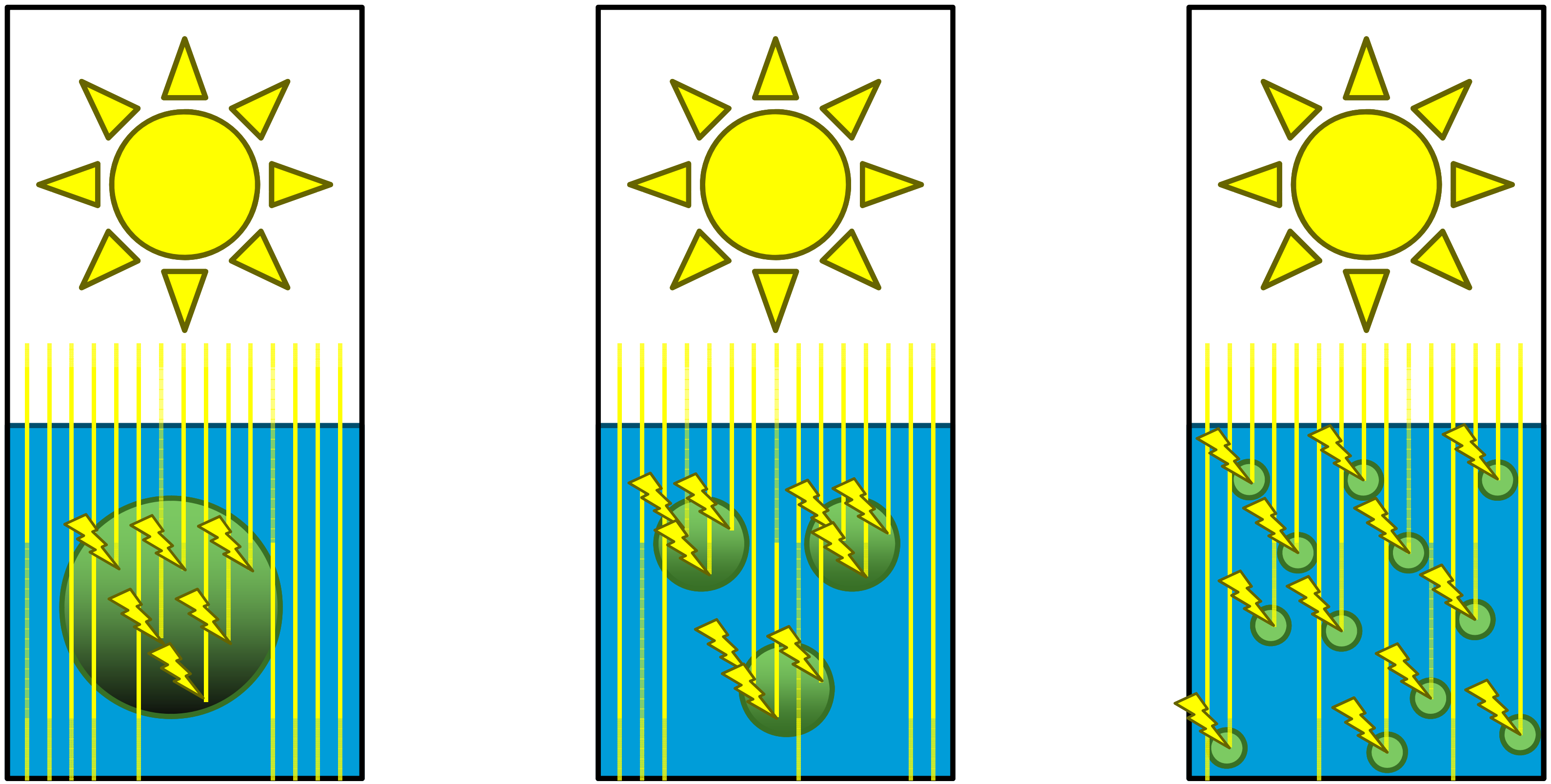


Bermuda – calibration



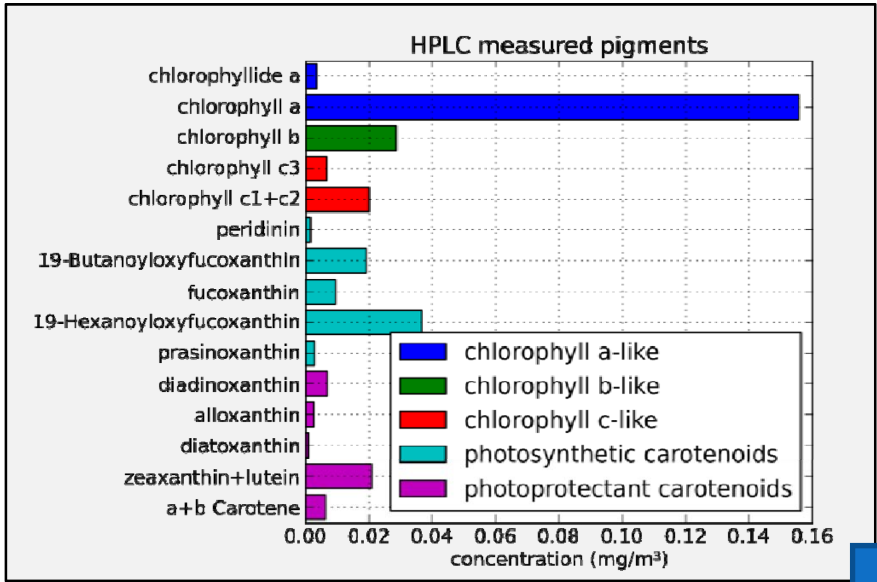
Size from optics: concepts

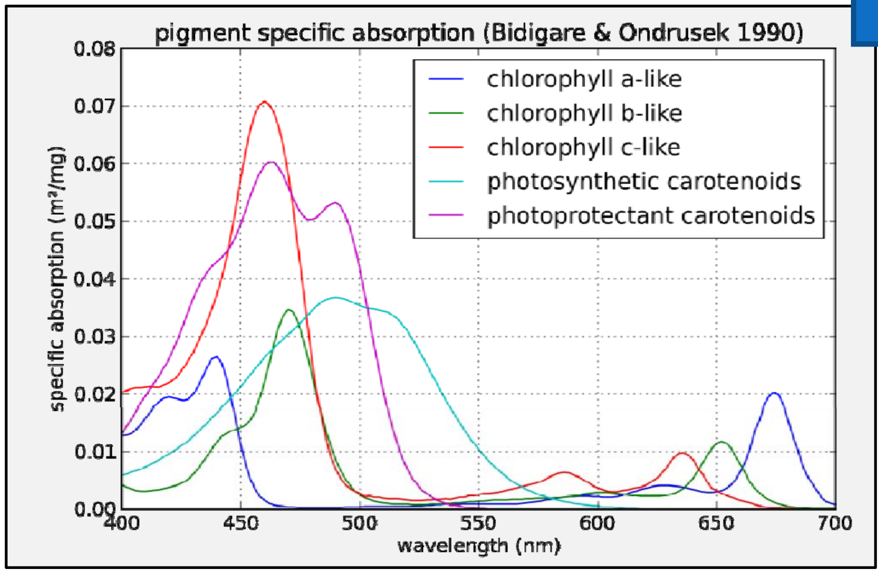
Take a fixed quantity of pigment, and distribute it over cells of different sizes.
What happens to light absorption?

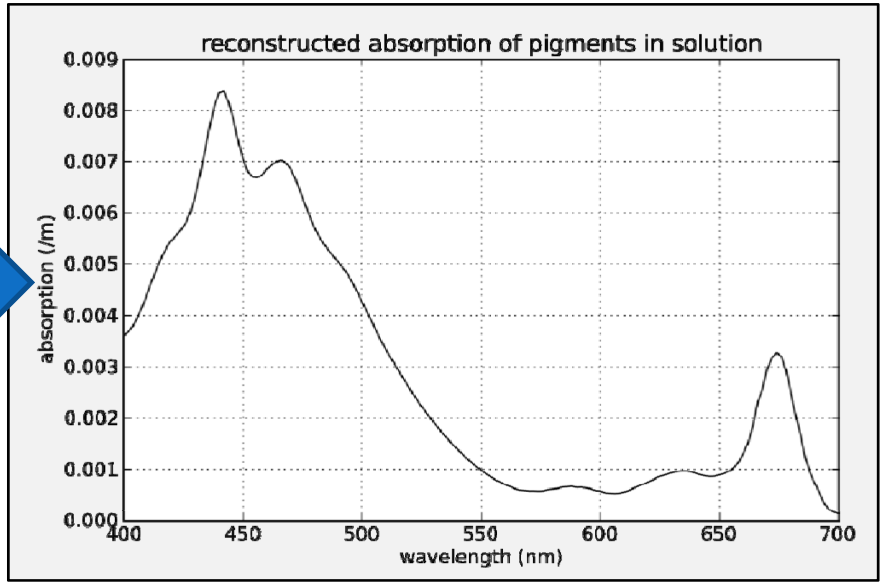


40 % absorption | 60 % absorption | 80 % absorption

Size from optics: pigments and absorption



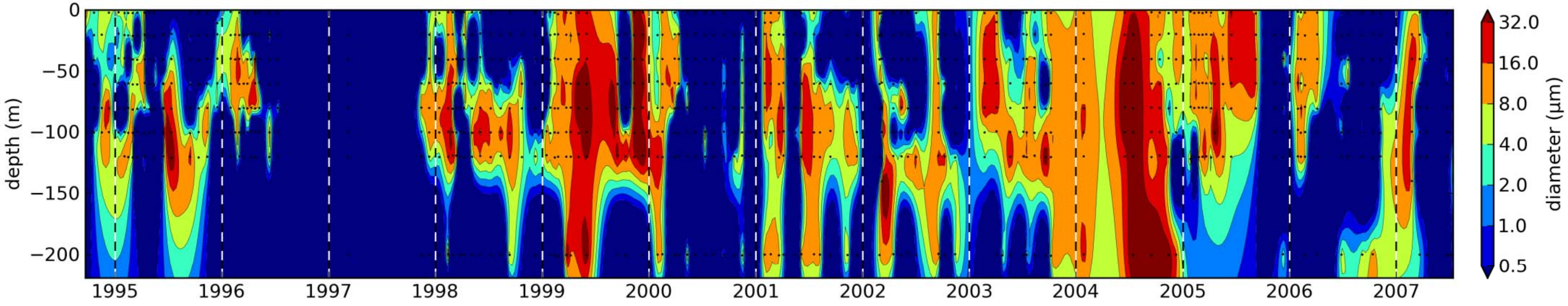




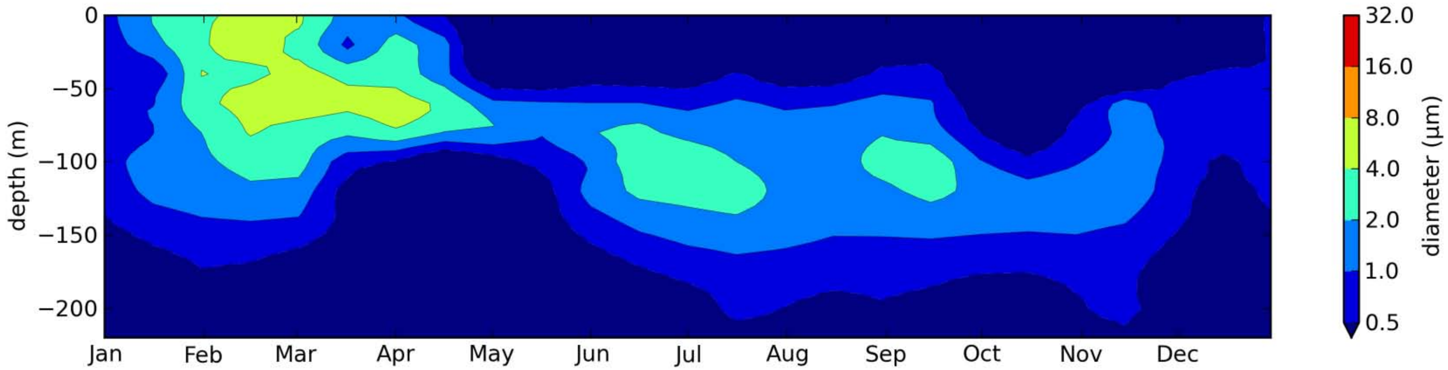
Morel & Bricaud (Deep-Sea Res A 1981)
Roy et al. (J R Soc Interface 2010)

Reconstructed Bermuda cell size

1994 – 2007

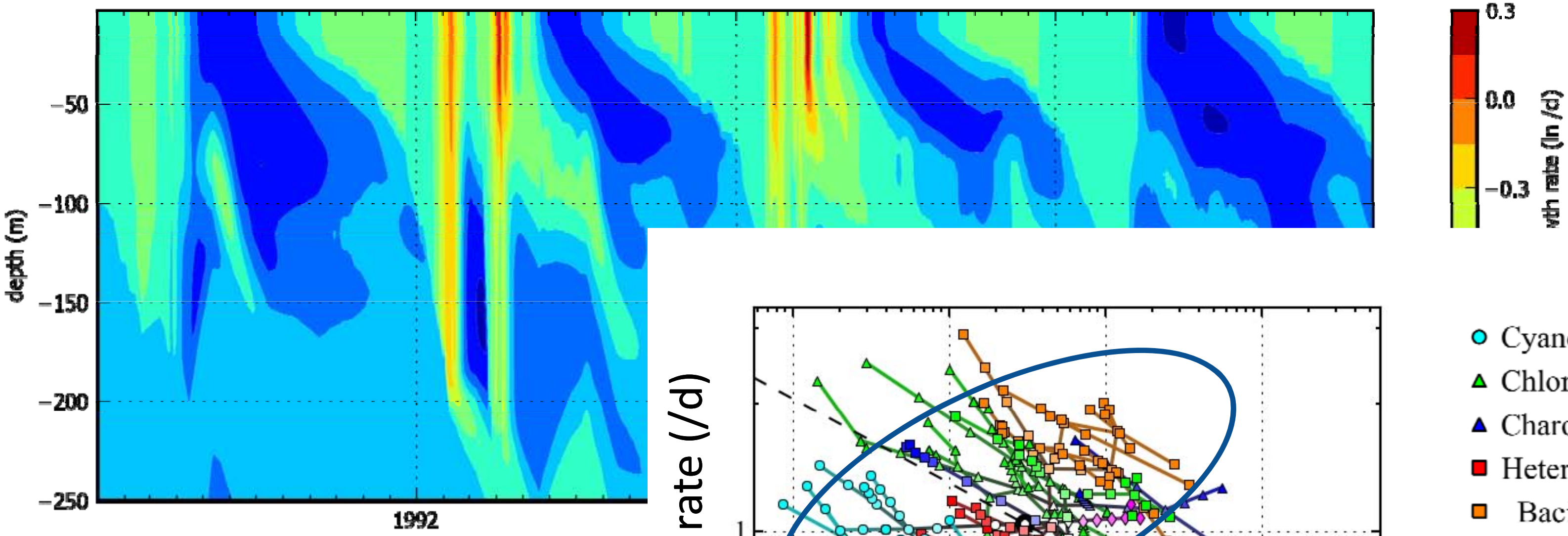


annual mean

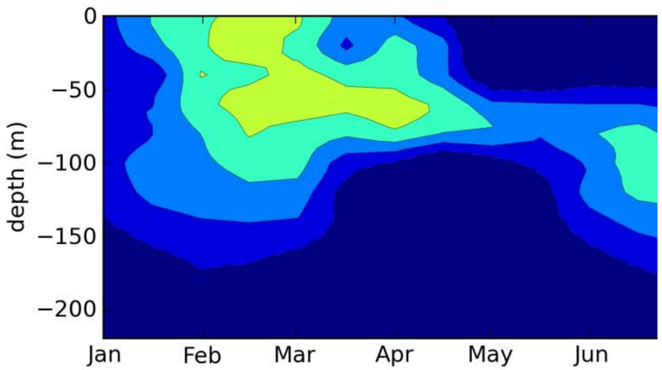


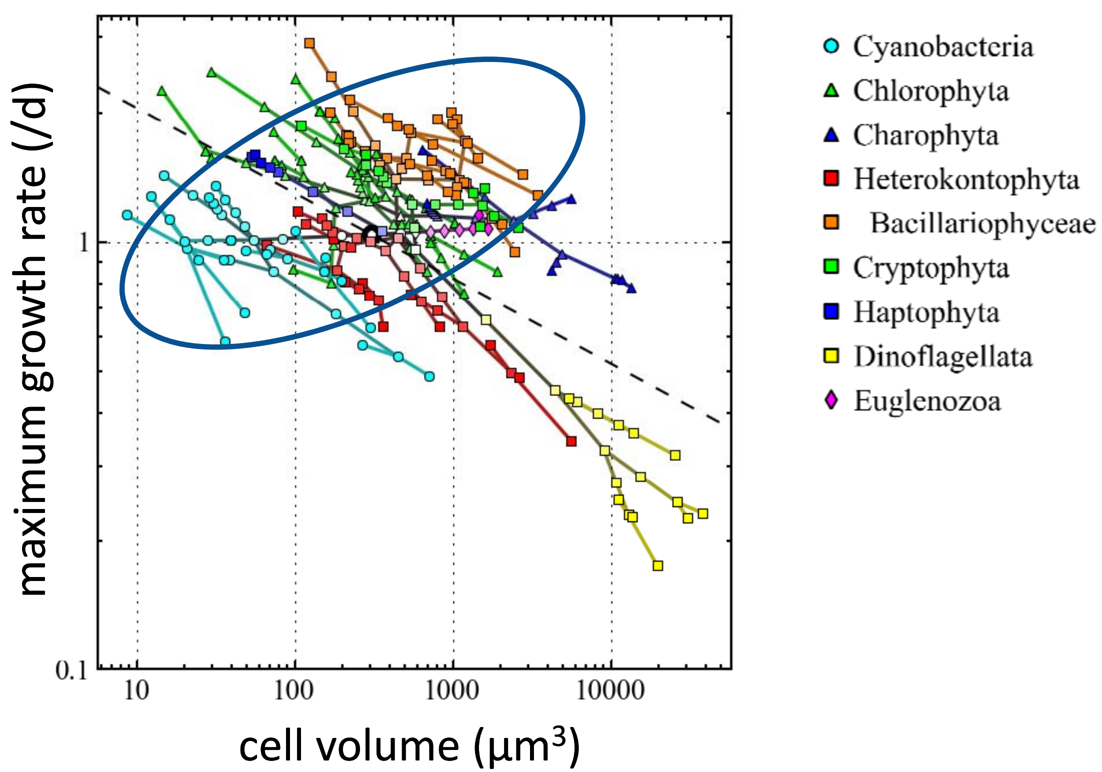
Bermuda: size vs. growth rate

modelled mean of maximum growth rate

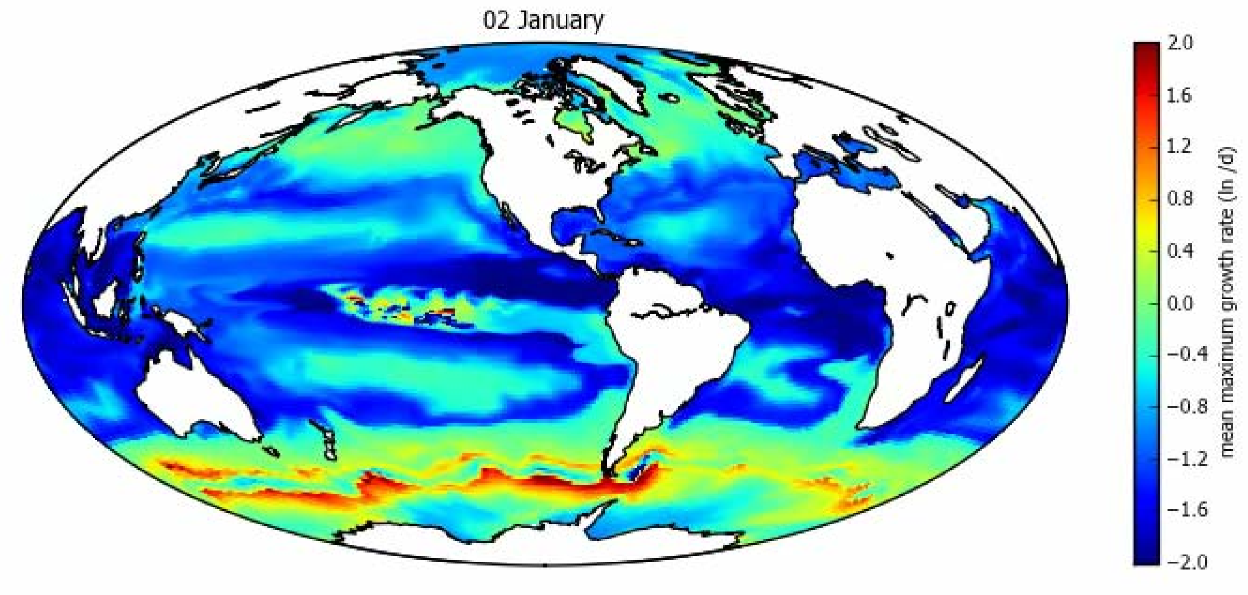


observed annual mean cell size –





In the global ocean



3D global simulation

- MOM4p1
- 1° resolution
- climatological forcing (CORE)

Multiple traits: mixotrophy

Biogeosciences Discuss., 10, 13535–13562, 2013
www.biogeosciences-discuss.net/10/13535/2013/
doi:10.5194/bgd-10-13535-2013

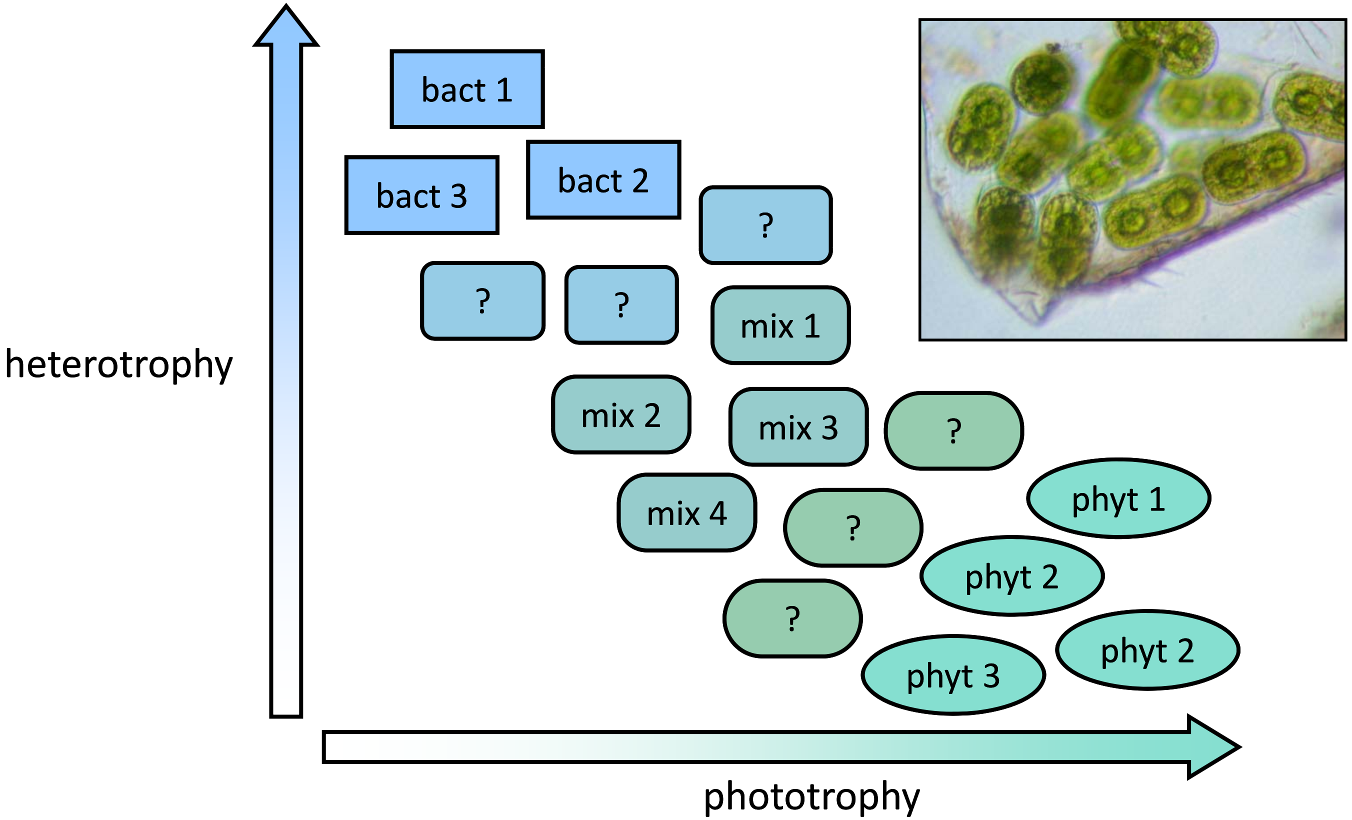
Biogeosciences
Discussions
Open Access

The role of mixotrophic protists in the biological carbon pump

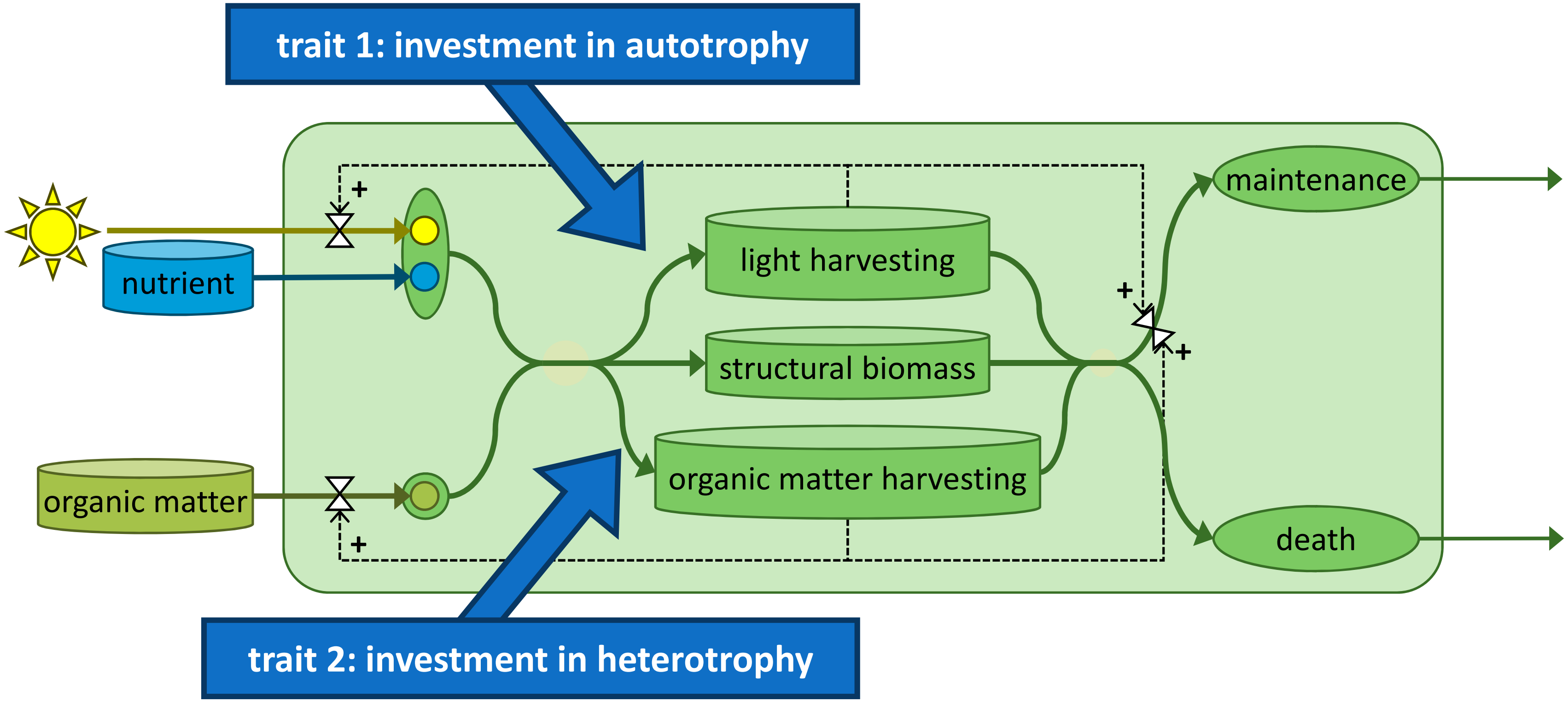
A. Mitra[1], K. J. Flynn[1], J. M. Burkholder[2], T. Berge[3], A. Calbet[4], J. A. Raven[5], E. Granéli[6], P. M. Glibert[7], P. J. Hansen[3], D. K. Stoecker[7], F. Thingstad[8], U. Tillmann[9], S. Våge[8], S. Wilken[10], and M. V. Zubkov[11]

Multiple traits: mixotrophy

Phototrophs and heterotrophs: a section through diversity

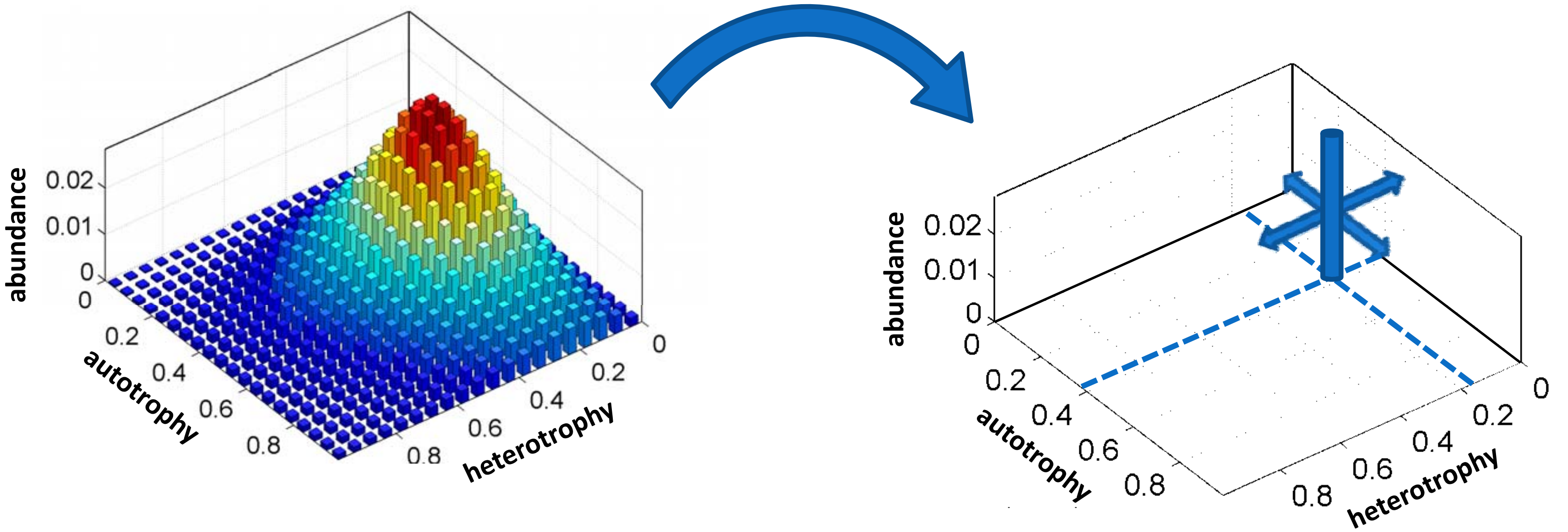


Generalizing the ecosystem: mixotrophy



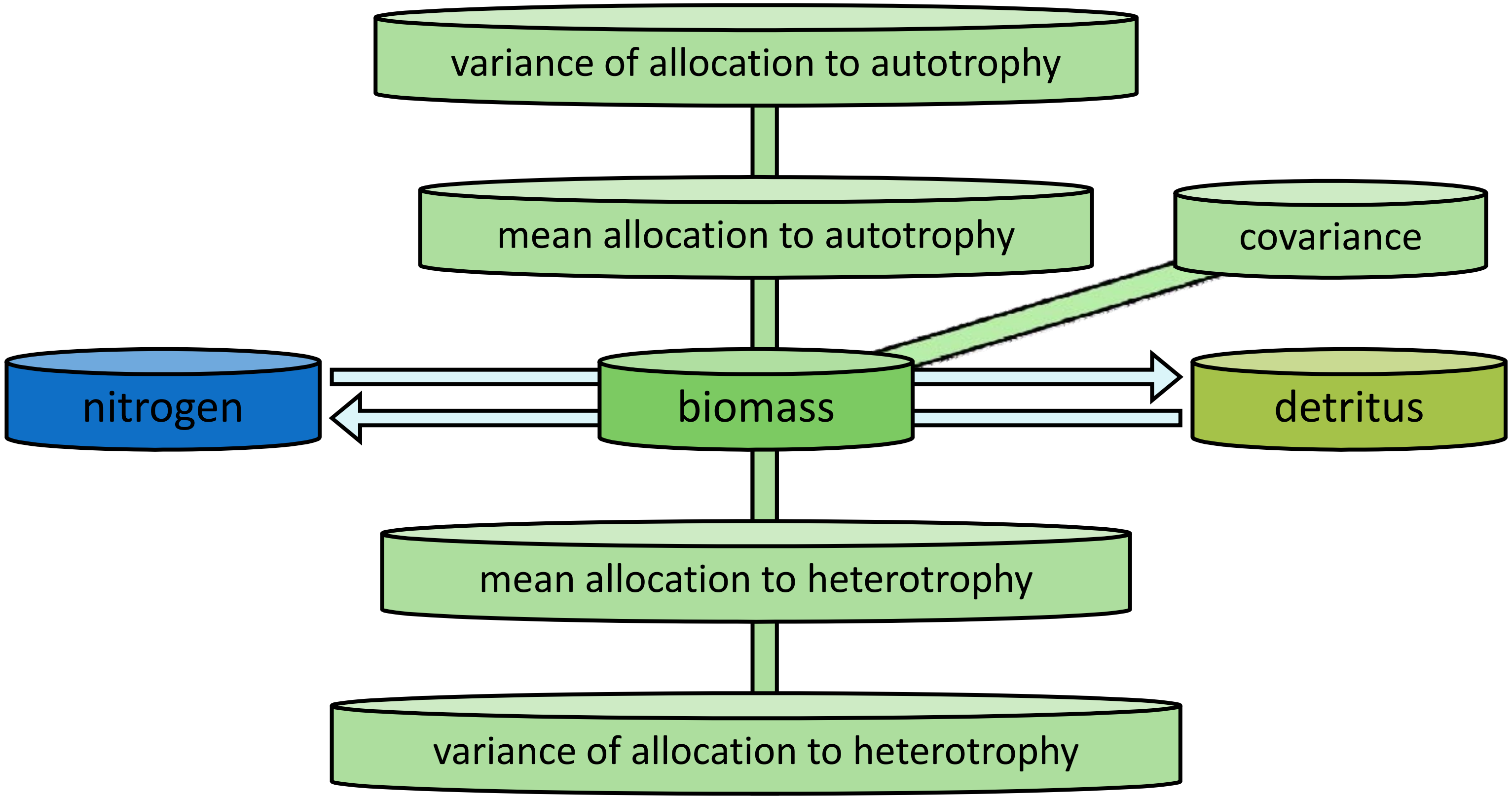
Bruggeman (2009)

Community representation



Bruggeman (2009)

Model characteristics

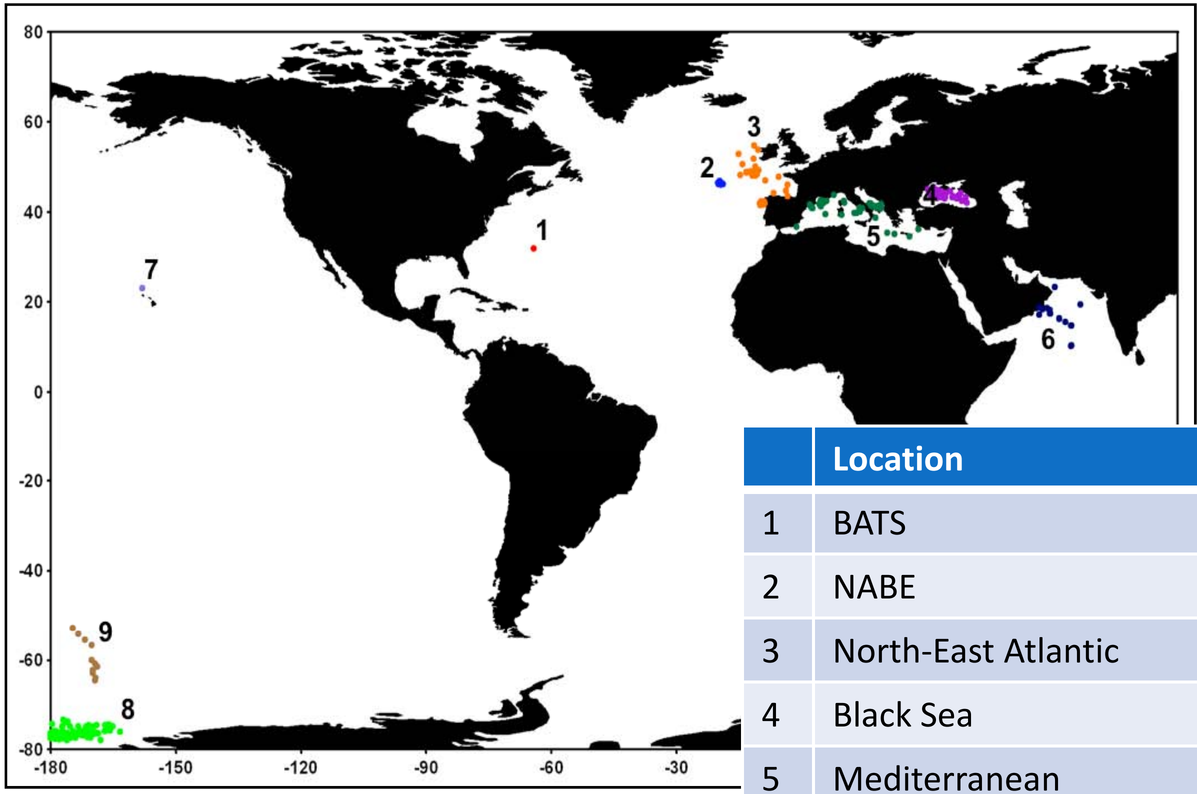


7 physiological parameters

- maximum autotrophic and heterotrophic production
- half-saturation constants for light, nutrient, organic matter
- maintenance rate, death rate

Bruggeman (2009)

Patterns: productivity

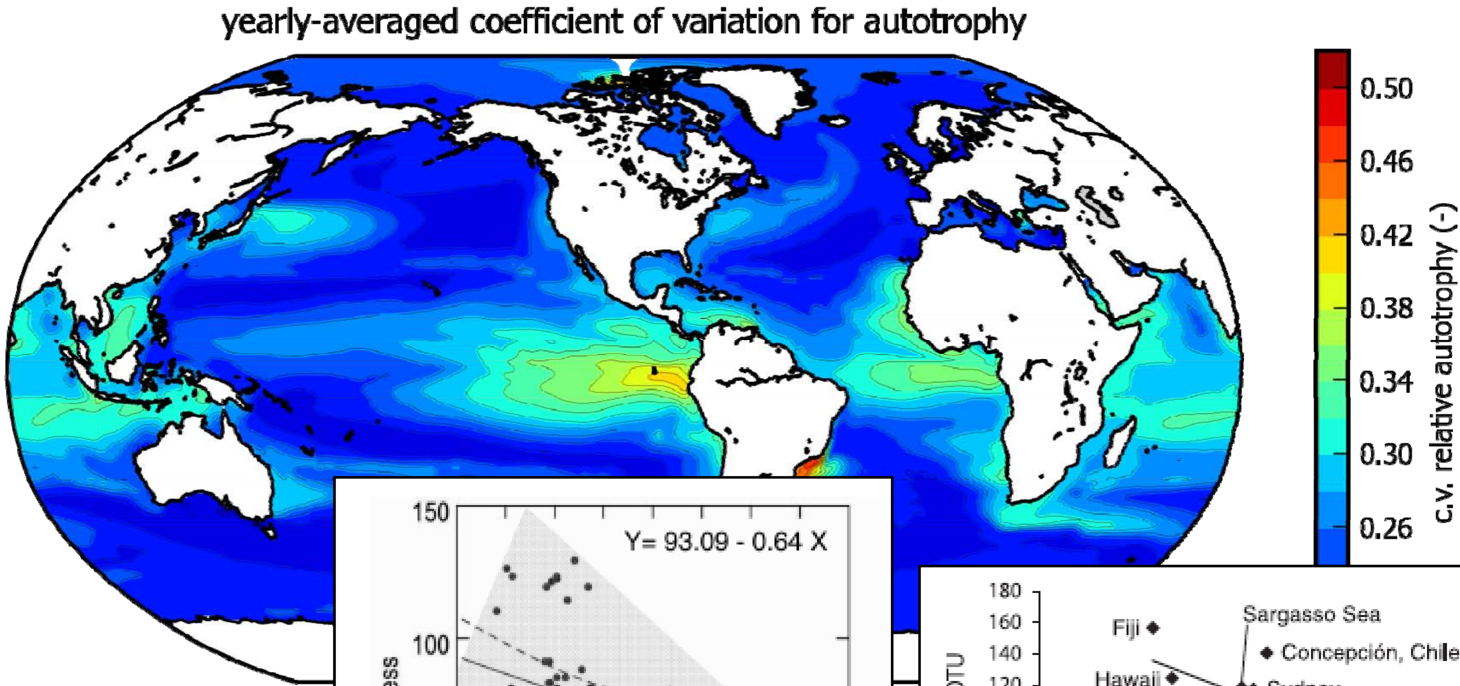


Mean rank: 4/10

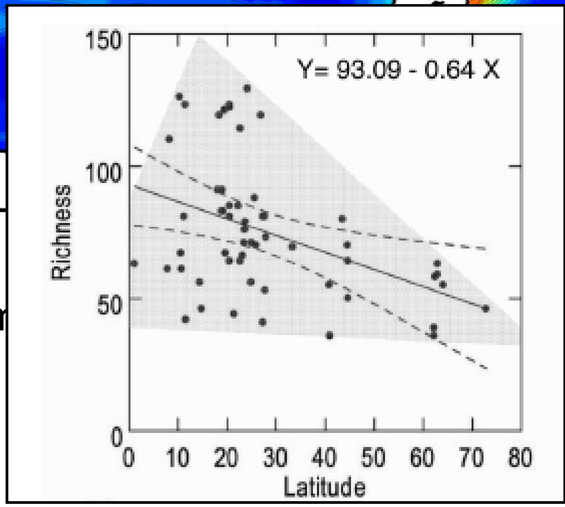
	Location	Rank	Percentile
1	BATS	6/13	42 %
2	NABE	7/13	50 %
3	North-East Atlantic	7/13	50 %
4	Black Sea	2/2	75 %
5	Mediterranean	1/5	10 %
6	Arabian Sea	2/12	13 %
7	HOT	5/12	38 %
8	Ross Sea	2/5	30 %
9	Antarctic Polar Frontal Zone	6/10	55 %

Saba et al. (Global Biogeochem. Cycles)
Saba et al. (in prep.)

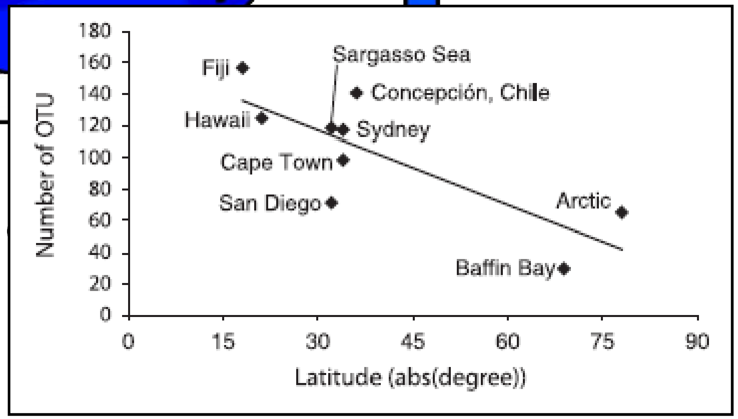
Patterns: biodiversity



Variance of investm



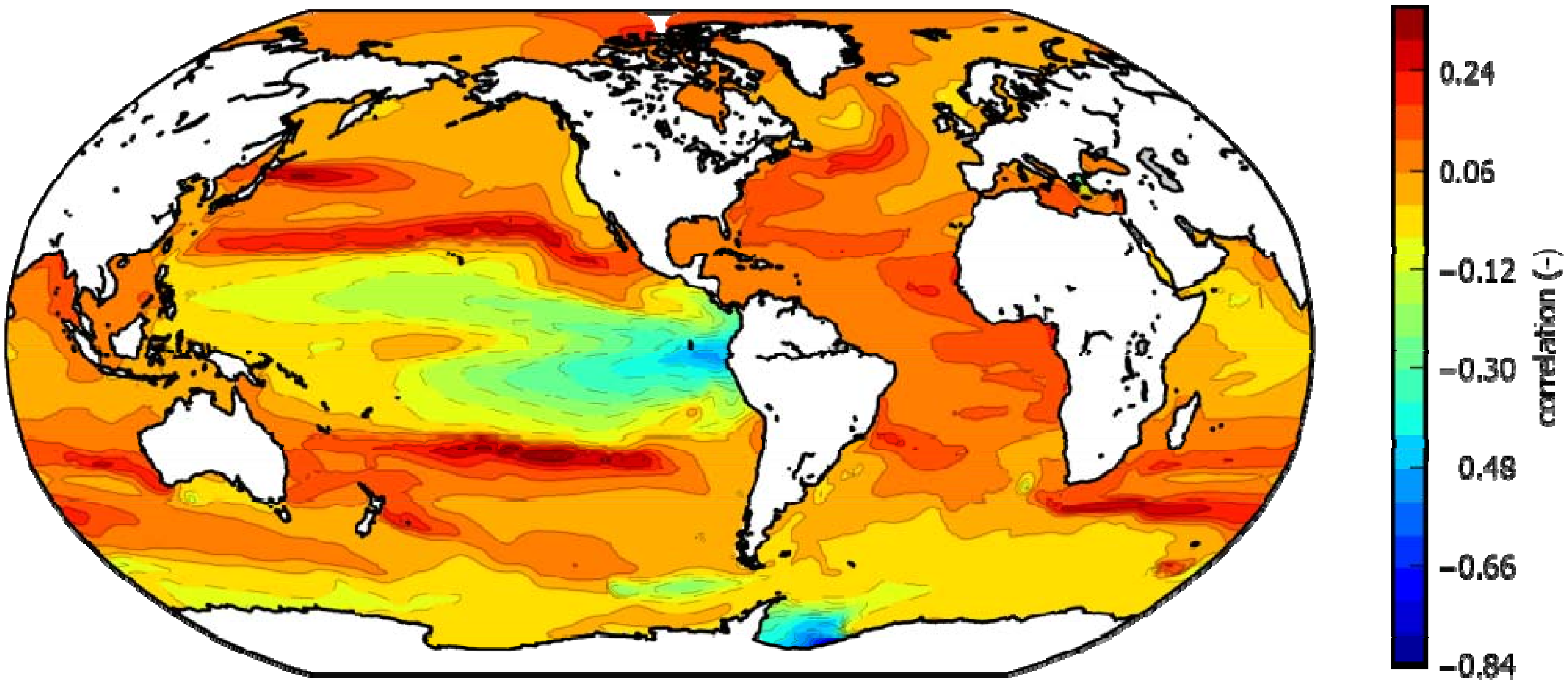
Fuhrman et al. (PNAS, 2008)



Pommier et al. (Molecular Ecology 2007)

Patterns: mixotrophy

Correlation between autotrophic and heterotrophic investment

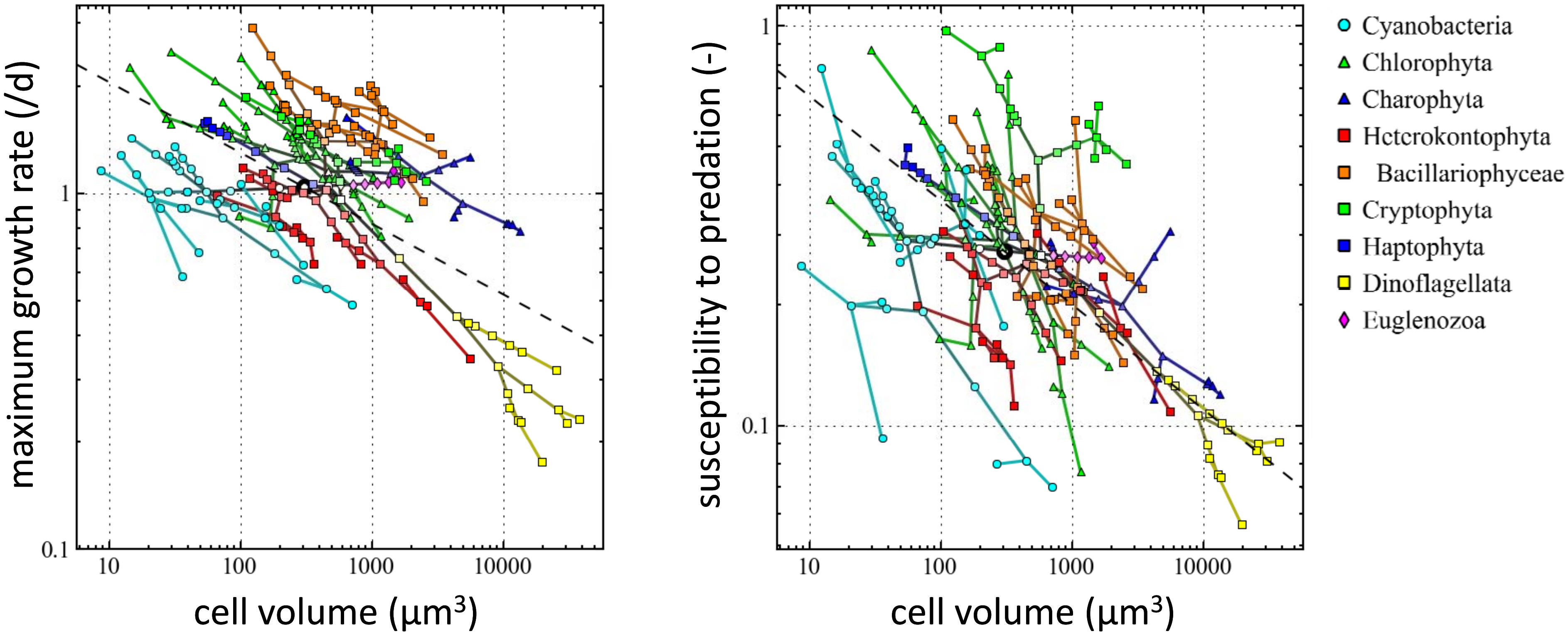


Extensions

- Discretely-valued traits
  - diatom vs. non-diatom, calcifyer vs. non-calcifyer
  - Wirtz & Eckhardt (Ecol Mod 1996)
- Biomass-dependent specific growth rates
  - Predation
  - Frequency dependent pop. growth (Savage et al. J Theor Biol 2007)
- Indirect dependencies between growth and traits
  - Trait controls nutrient uptake, nutrient store control growth

Note: Limitations of allometry

- Non-monotonic trade-offs



Wirtz (J Plankton Res 2011; Mar Ecol Prog Ser 2012)

Aggregate statistics: costs and benefits

- Approximation = reduced accuracy
  - Errors: 1 % biomass, 10 % mean, 25 % variance
- No more distinct species
  - No harmful algae, invasive species, commercial targets
- Non-standard tracers
  - Requires transformations and custom clipping logic in GCMs

- Insightful
  - Direct measures of community strategy & functional diversity
- Well-constrained and fast
  - Minimal number of parameters and state variables
- Flexible
  - Accommodates succession, genotypic evolution

Recipe

- A standard model for "all species"
- Knowledge about interspecific variability
  - Measured trait values
  - Principal traits
  - Trait covariance and trade-offs
- Assemble a community
  - Explicit species, optionally aggregate statistics
- Expose to environmental variability
  - Seasonality, interannual variability, spatial gradients