Trait-based models in plankton succession

Jorn Bruggeman
Department of Earth Sciences
University of Oxford

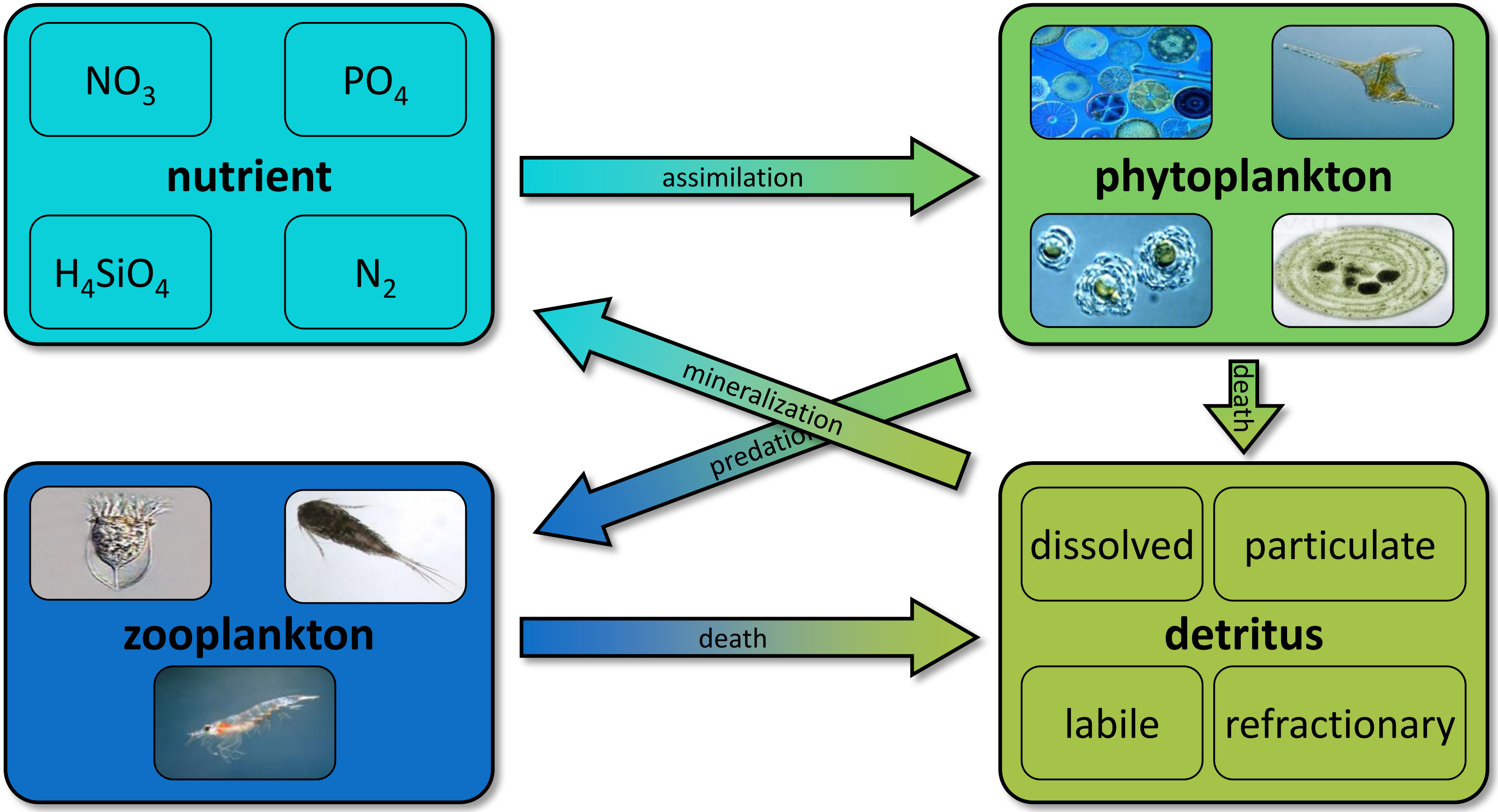
What is it all about?

- Small (0.5 - 200 µm) but important
  - up to 50 % of global photosynthesis
- High diversity
  - shape, form and function
- Studied in detail
  - laboratory
  - field
  - remote sensing

Toolbox

- Modularity
  1. Model individual organism
  2. Extrapolate to population
  3. Combine populations to build ecosystem
- Formulations
  - chemical kinetics [law of mass action, Michaelis-Menten]
  - co-limitation [multiplicative, law of the minimum]
  - temperature sensitivity [Q_{10}, Arrhenius]
  - storage [Droop]

Confronting complexity



NO_3

PO_4

nutrient

H_4SiO_4

N_2

assimilation

phytoplankton

death

mineralization

predation

zooplankton

death

dissolved

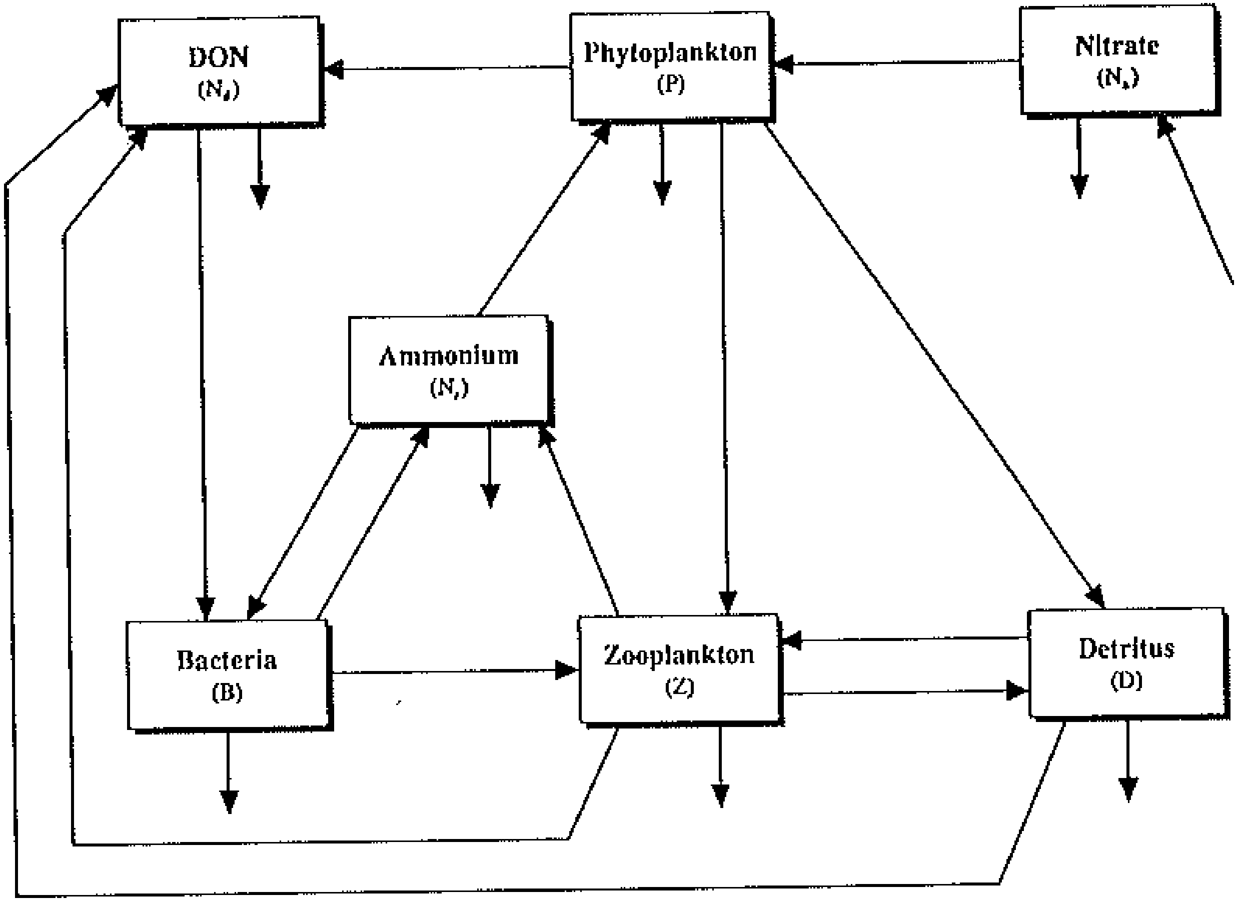
particulate

detritus

labile

refractionary

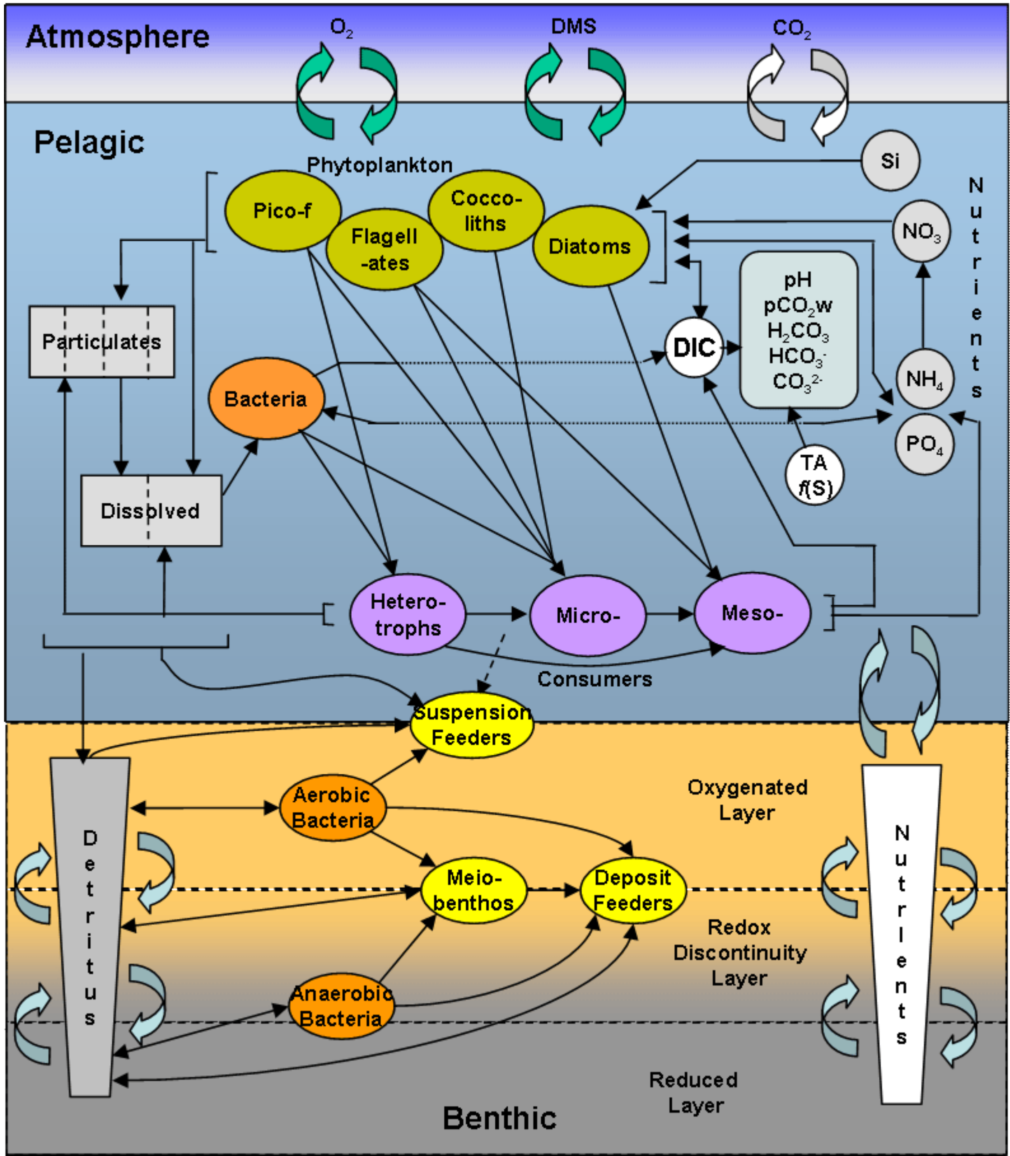
Classic NPZD



- Evans & Parslow (1985), Fasham et al. (1990)

“State of the art”

- <u>ERSEM</u>
- Green Ocean Model



But…

- Uncertainty
  - 100s of parameters: insufficient observations to constrain model behavior
  - 10s of state variables: insufficient observations to constrain initial state
- Complex behavior
  - limit cycles
  - chaos
  - qualitative and quantitative behavior depend strongly on parameter values and initial state

… and yet large-scale processes can seem so simple!

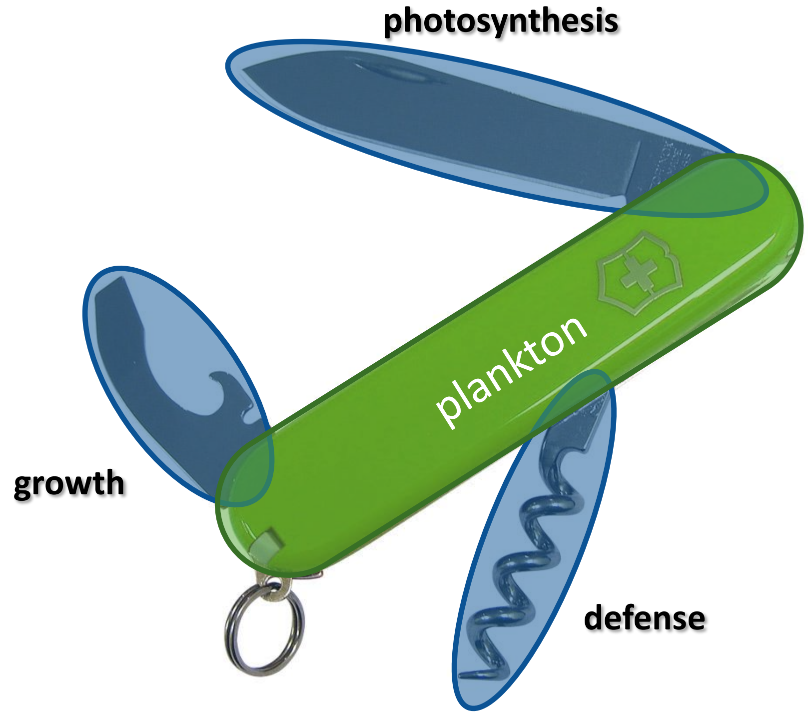
Alternatives
“Darwinian” approaches

- Replace modeller’s choices by random processes, and let competition do the rest

- Follows et al., Science, 2007
- Bruggeman & Kooijman, L&O, 2007

Principles

1. **Standardize** species: one model, different trait values

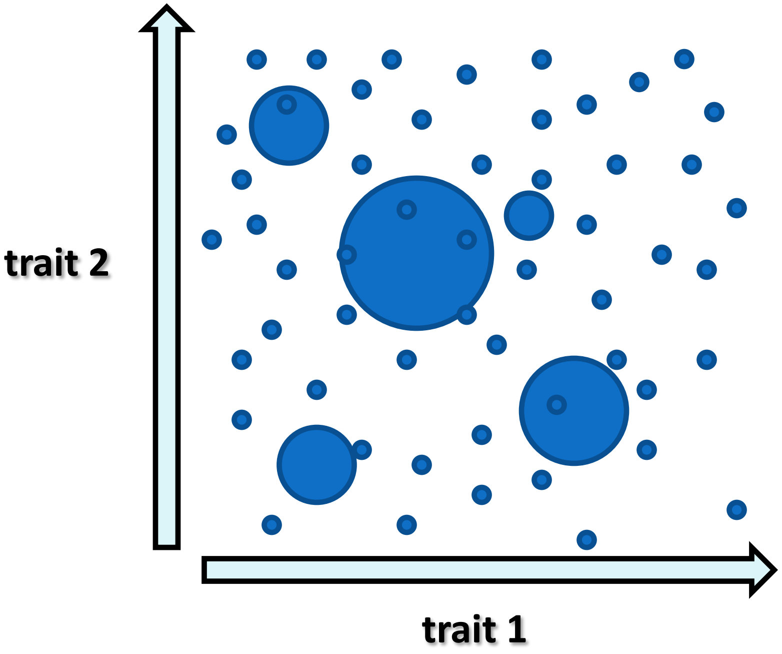


Bruggeman & Kooijman, Limnol. Oceanogr., 2007

Principles

1. **Standardize** species: one model, different trait values

2. **Add diversity**: introduce all possible species



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

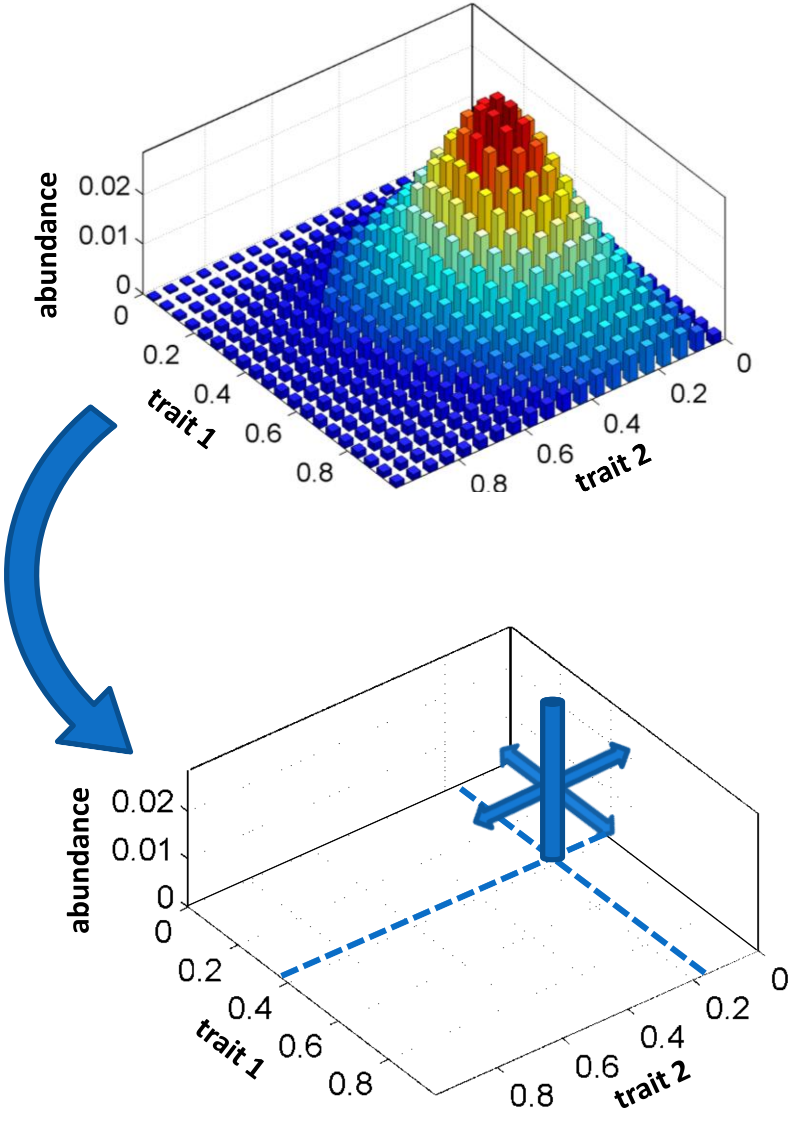
Bruggeman & Kooijman, Limnol. Oceanogr., 2007

Principles

1. **Standardize** species: one model, different trait values

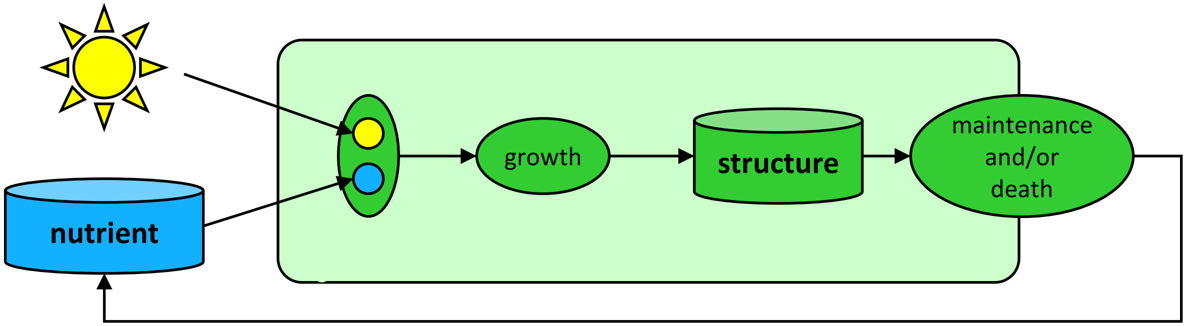
2. **Add diversity**: introduce all possible species

3. **Approximate**: characterize the community by key statistics



Bruggeman & Kooijman, Limnol. Oceanogr., 2007

Example: phytoplankton



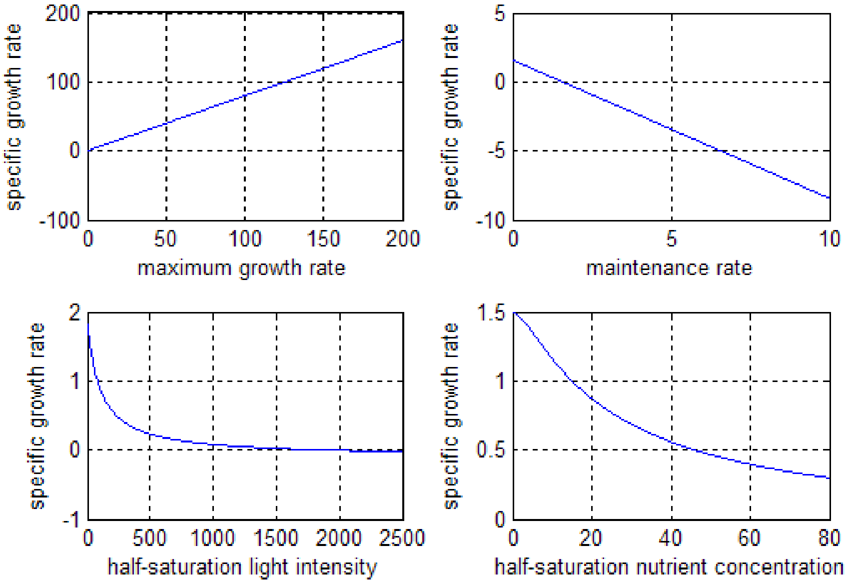
$$\frac{dX_V}{dt} = X_V \left(j_{V,Am} \frac{1}{1+\left(\frac{X_L}{K_L}\right)^{-1}+\left(\frac{X_N}{K_N}\right)^{-1}-\left(\frac{X_L}{K_L}+\frac{X_N}{K_N}\right)^{-1}} - j_{V,M} \right)$$

$j_{V,Am}$	maximum growth rate	d^{-1}
K_L	half-saturation light intensity	$\mathrm{W\ m}^{-2}$
K_N	half-saturation nutrient concentration	$\mu\mathrm{M}$
$j_{V,M}$	maintenance rate	d^{-1}

A thought-experiment

- What happens if we release all possible phytoplankton species in one environment?
- And the winner is…
  - highest maximum growth rate
  - lowest maintenance/death rate
  - lowest saturation coefficients

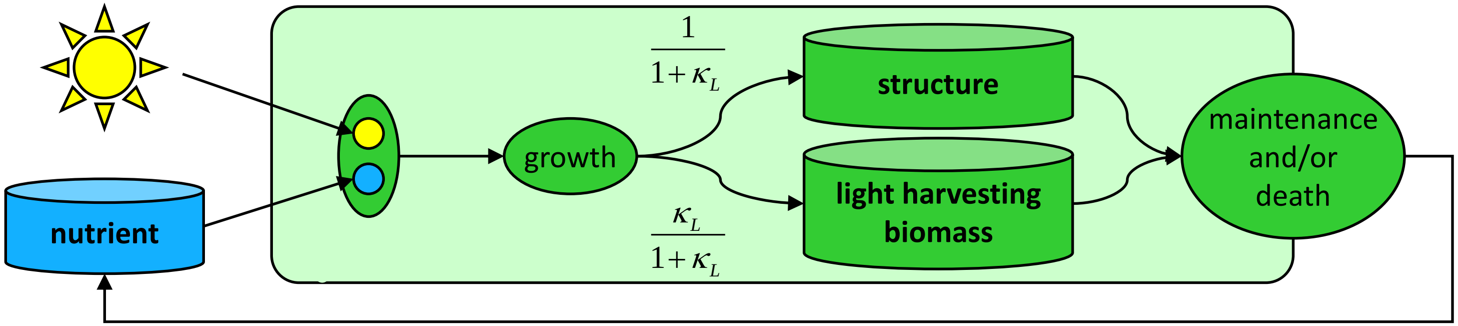
Unrealistic!



Trade-offs

- In reality, differences between species are supported by **trade-offs**
  - improvement of one feature comes at the expense of another
- For instance: *r*-*K* strategies
  - *r*-species: colonizers, high growth rate, low nutrient affinity
  - *K*-species: final stage of succession, low growth rate, high nutrient affinity
- Fitness and dominance of any species is time- and space-dependent, because the environment changes in time- and space

Phytoplankton with trade-off



$\frac{1}{1+\kappa_L}$

structure

growth

light harvesting biomass

$\frac{\kappa_L}{1+\kappa_L}$

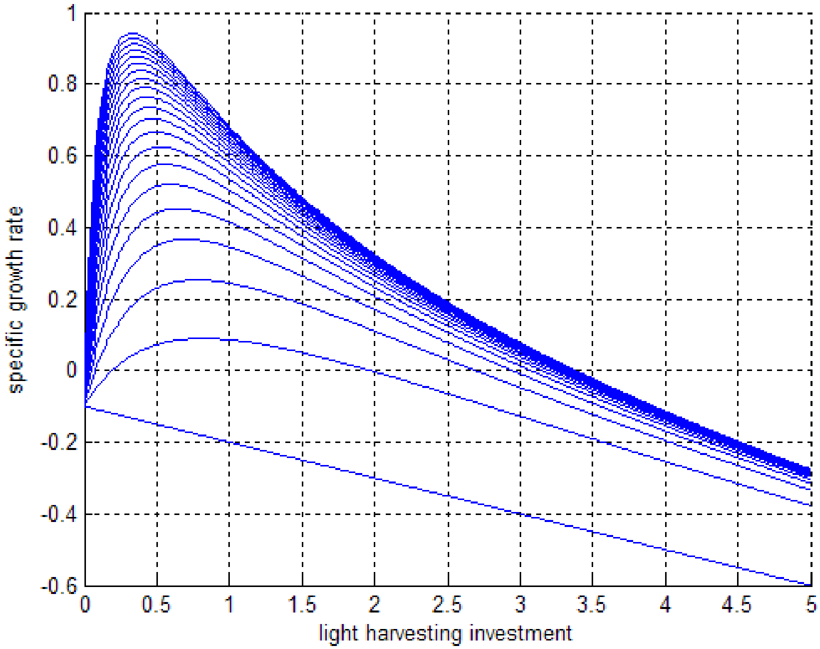
maintenance and/or death

nutrient

$$\frac{dX_V}{dt} = \frac{1}{1+\kappa_L} X_V \left(j_{V,Am} \frac{1}{1+\left(\kappa_L \frac{X_L}{K_L}\right)^{-1} + \left(\frac{X_N}{K_N}\right)^{-1} - \left(\kappa_L \frac{X_L}{K_L} + \frac{X_N}{K_N}\right)^{-1}} - (1+\kappa_L)\, j_{V,M} \right)$$

$j_{V,Am}$	maximum growth rate	d^{-1}
K_L	half-saturation light intensity	$W\ m^{-2}$
K_N	half-saturation nutrient concentration	μM
$j_{V,M}$	maintenance rate	d^{-1}
κ_L	investment in light harvesting	-

Phytoplankton trade-off curves

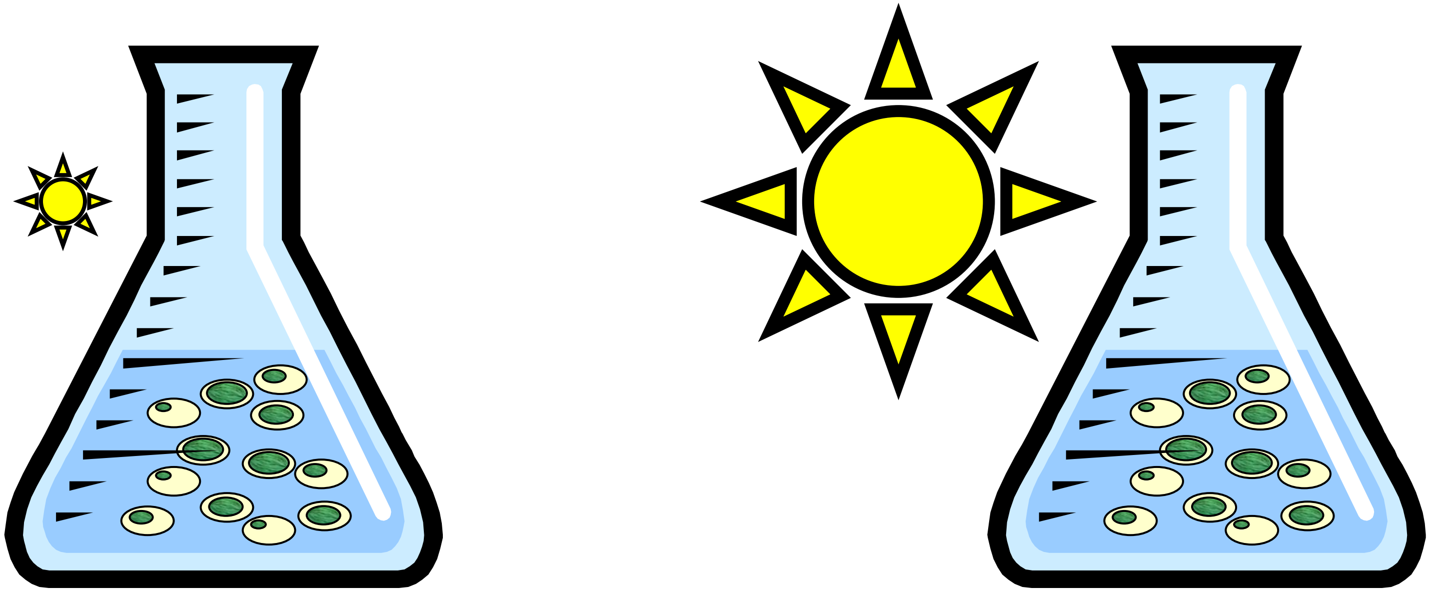


growth as function of light harvesting investment, for different light intensities

1. trade-off curve has optimum, prevents unrealistic drift to extremes
2. position of optimum depends on environment (here: light intensity)

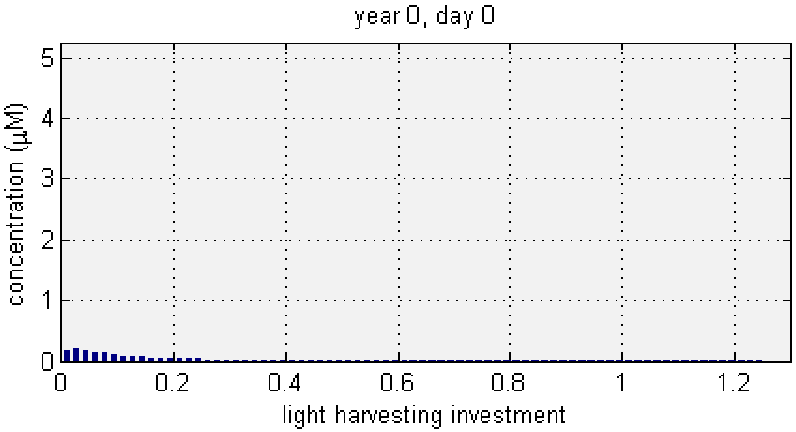
Setup 1: constant environment

- Closed bottles with all possible species
  - low initial biomasses
  - high initial nutrient
  - constant light intensity (bottle 1: low, bottle 2: high)

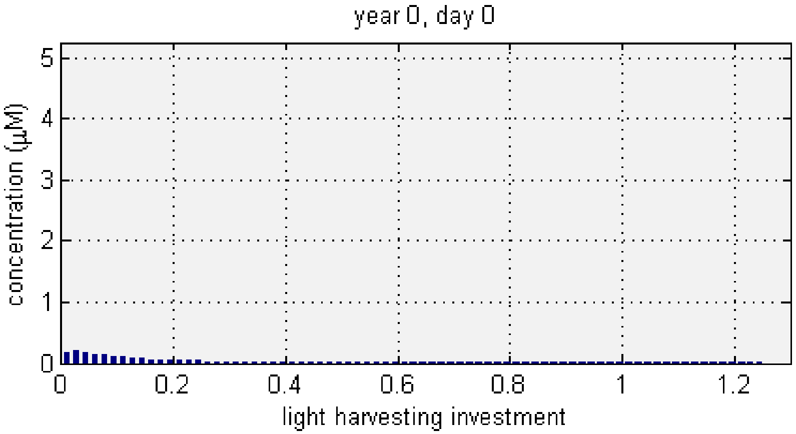


Effect: “survival of the fittest”

Low light

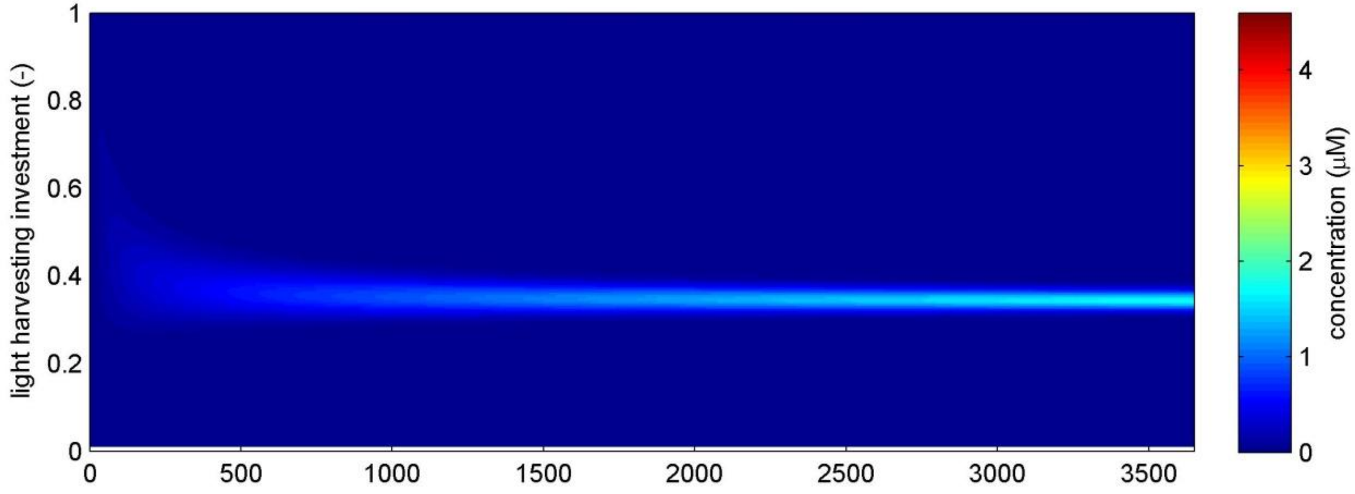


High light

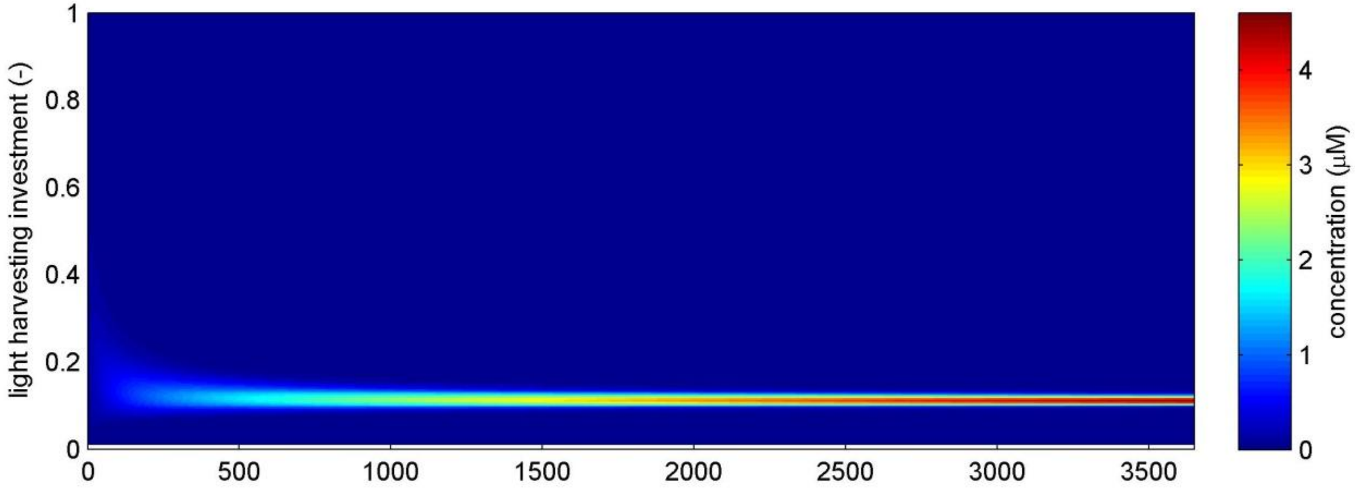


Trait distributions in time

Low light

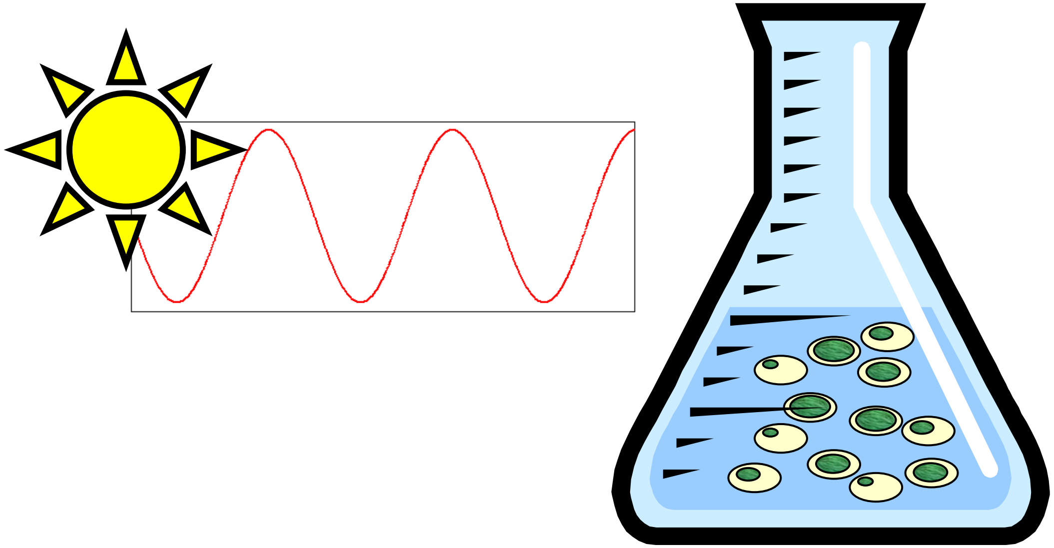


High light

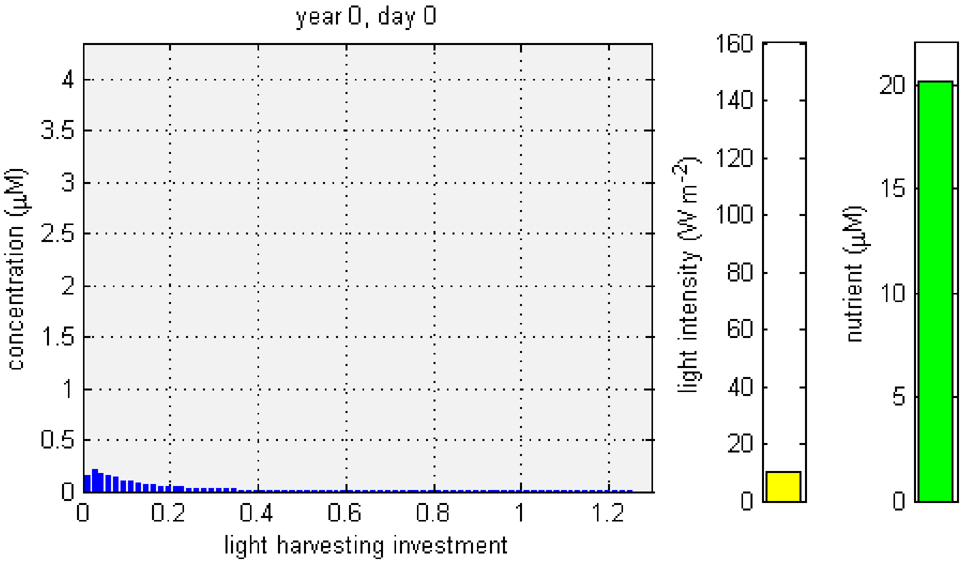


Setup 2: fluctuating environment

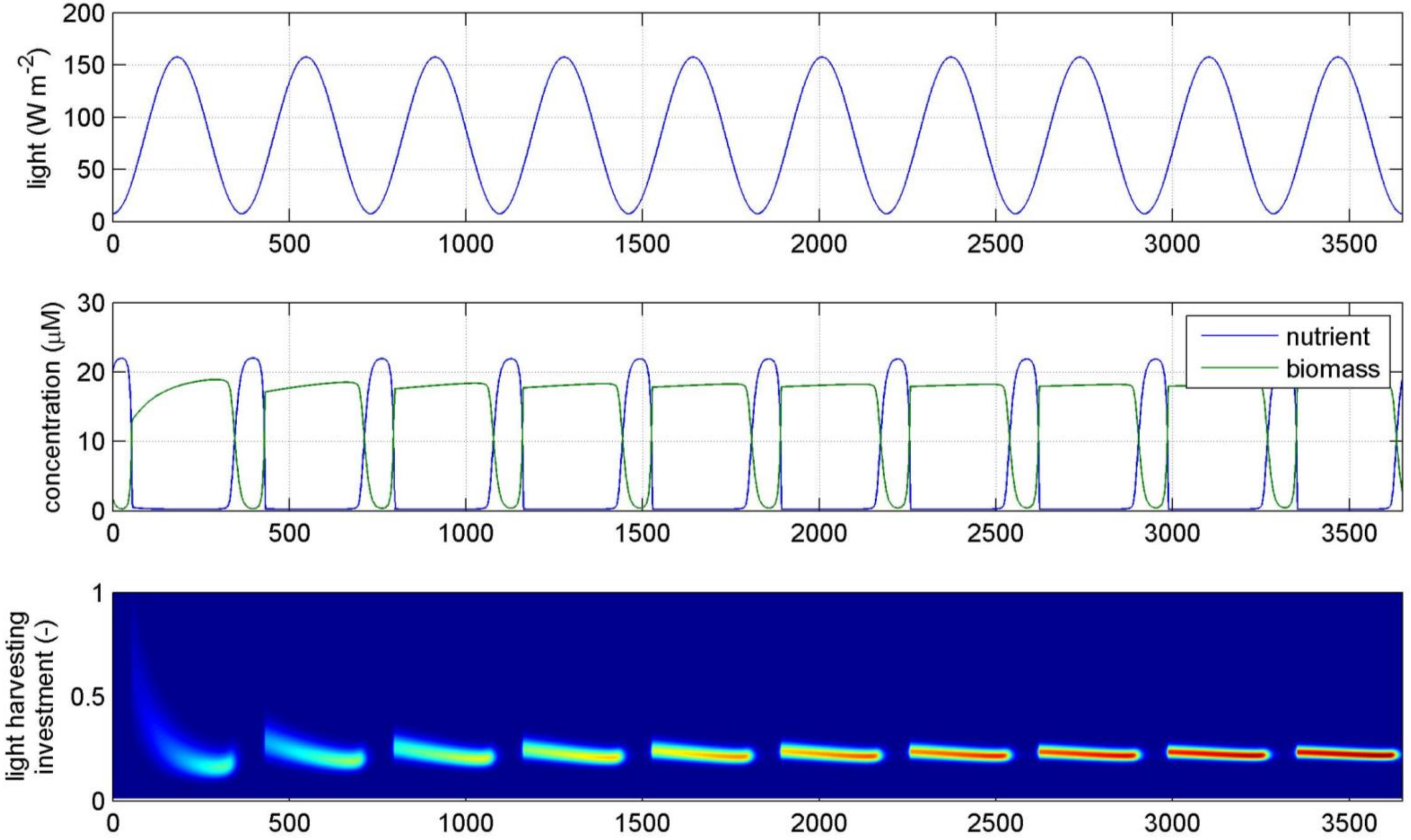
- Closed bottle with all possible species
  - low initial biomasses
  - high initial nutrient
  - **sinusoidal light intensity (‘seasonal cycle’)**



Effect: moderate seasonal succession



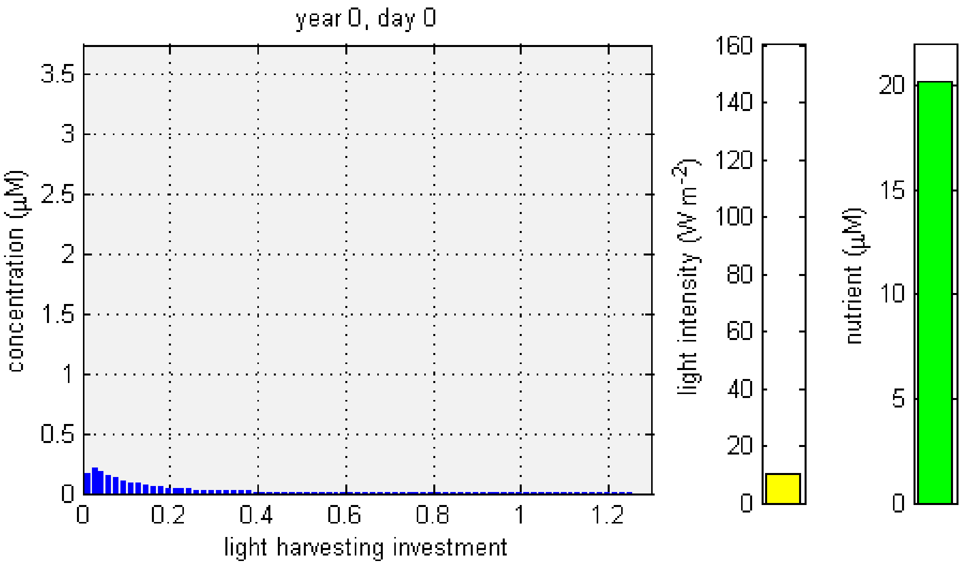
System dynamics in time



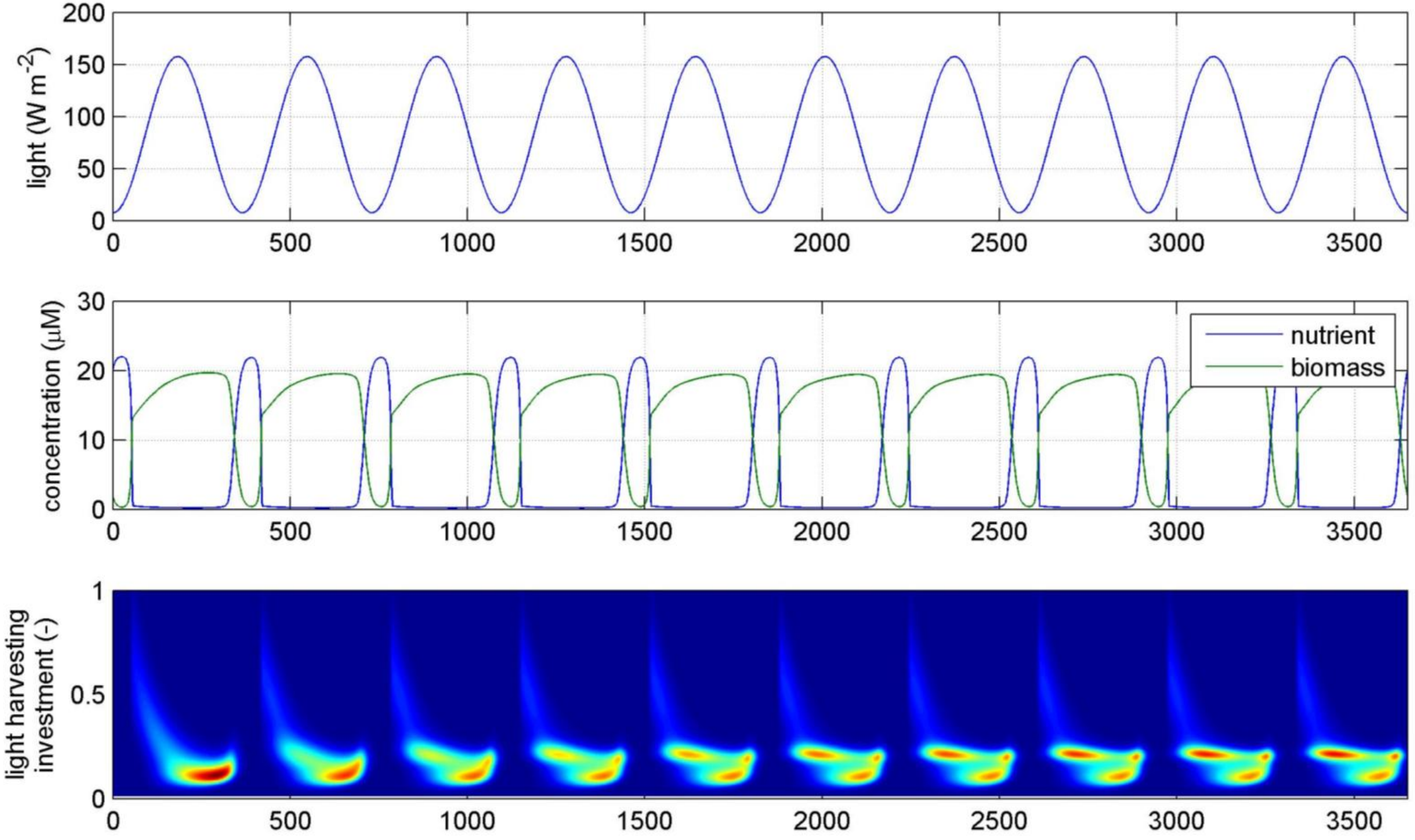
Competitive exclusion

- In changing environments, species can go extinct because:
  - they **always** perform worse than other species
  - they cannot survive long periods of (relatively) unfavorable conditions, **even if these are preceded/followed by good times**
- How to sustain a realistic level of diversity?
- Remedy:
  - Persistence of trace amounts of all species
  - Implementation: continuous mixing with reference state of infinite diversity (≈ 1‰ per day)

Effect: sustained diversity



System dynamics in time



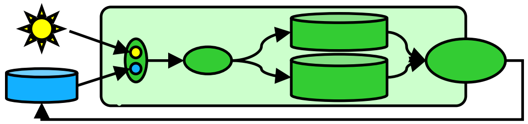
Where does this leave us?

- Less constant [arbitrary] parameters
  - All original parameters are now generic, not species-specific
  - Trait is species-specific, but does not require arbitrary values through assumption of “infinite diversity”
- Many state variables to simulate
  - Previous figures: 75-300 species to capture biodiversity
  - Computationally expensive, difficult to model more than 1 trait

But we are interested in large-scale processes (e.g. biomass), not those many species…

Less variables through approximation

$$f\left(\kappa_L\right)$$



$$\frac{dX_V}{dt}\left(\kappa_L\right)$$

1. **Taylor series approximation of growth rate**
2. **Neglect higher order terms (> 2nd order)**
3. **Approximate higher moments of distribution (skewness, kurtosis) by assuming distribution shape (e.g. normal, lognormal)**

(4. Multi-trait models: neglect correlation between traits)

$$\frac{d}{dt}X_{V,\mathrm{tot}}\left(X_{V,\mathrm{tot}},\kappa_{L,\mathrm{mean}},\kappa_{L,\mathrm{var}}\right)$$

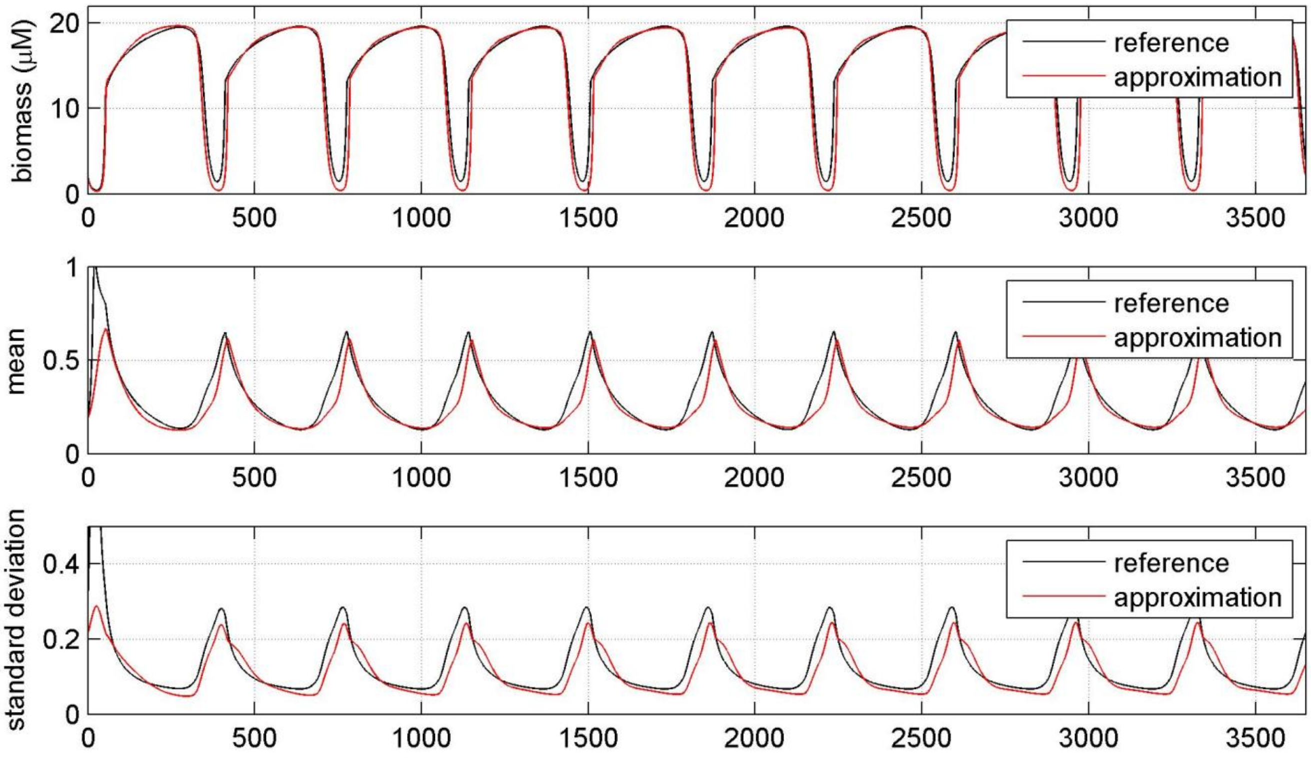
$$\frac{d}{dt}\kappa_{L,\mathrm{mean}}\left(X_{V,\mathrm{tot}},\kappa_{L,\mathrm{mean}},\kappa_{L,\mathrm{var}}\right)$$

$$\frac{d}{dt}\kappa_{L,\mathrm{var}}\left(X_{V,\mathrm{tot}},\kappa_{L,\mathrm{mean}},\kappa_{L,\mathrm{var}}\right)$$

Wirtz & Eckhardt (1996)
Norberg et al. (2001)
Savage et al. (2007)

Lande (1976)

Accuracy of approximation



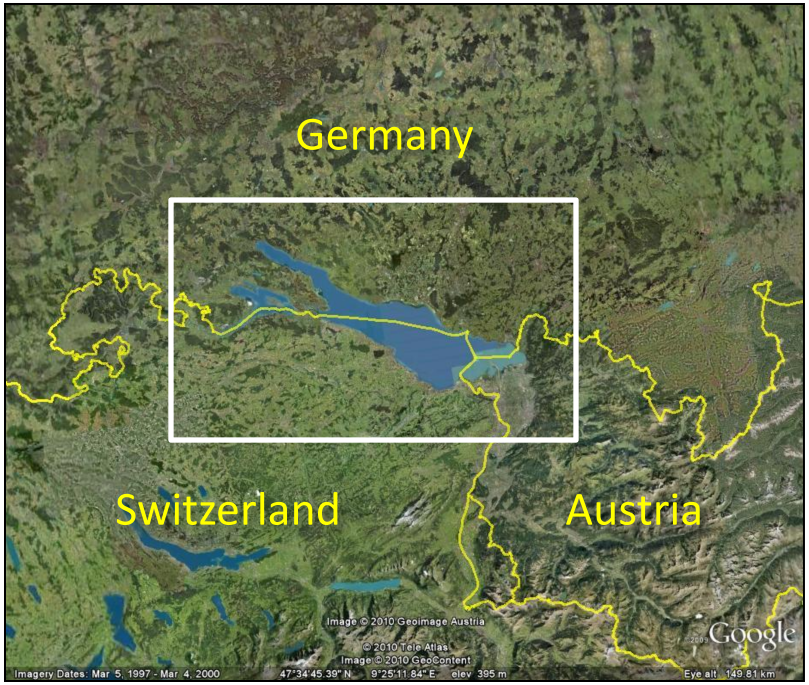
But 1: What traits matter, and how are they constrained by trade-offs?

- Impossible to tell without data
  - Databases with species vs. trait value (Litchman, Klausmeier, Bruggeman)
- Which traits matter?
  - component analysis to identify dominant traits
- What trade-offs?
  - regression to reconstruct linear and power law (allometric) relationships between traits

But 2: diversity

- Initial distribution
  - Follows et al. (2007): random, ensembles
  - Bruggeman & Kooijman (2007): continuous reference distributions
- Competitive exclusion
  - Hardin et al.
  - counteracted by spatiotemporal heterogeneity, self-repression (cannibalism, specific self-shading), interspecific dependencies
- Immigration and/or evolution

Test case 1: Lake Constance



Surface area	536 km^2
Average depth	90 m

Data sources

meteo

1979 – present
hourly values for surface irradiance, temperature, wind, ...

vertical profiles

1979 – present
monthly profiles of temperature

laboratory

database: > 1200 observed trait values for > 200 species

biomass

1979 – present
weekly biomass of 12 classes of plankton

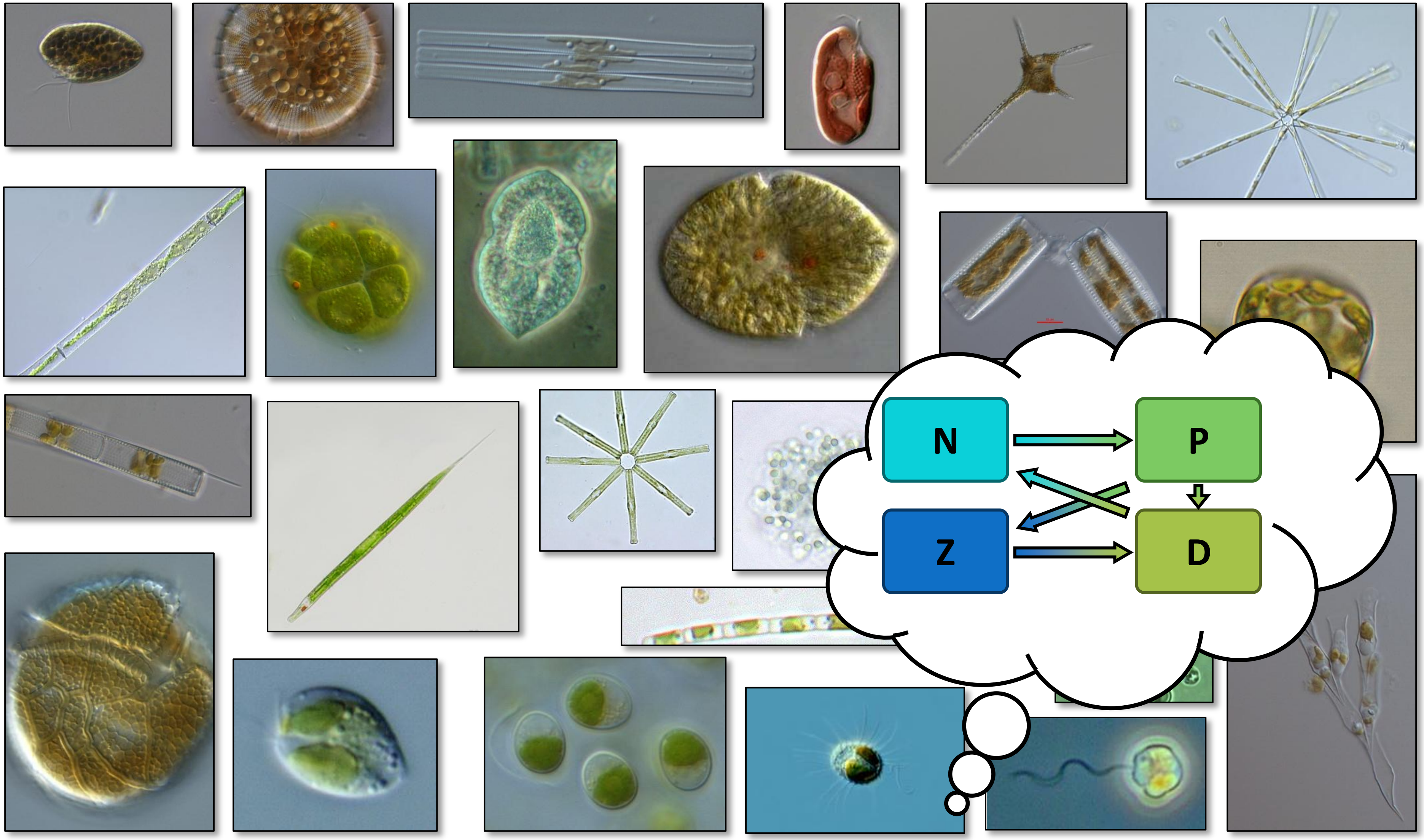
species

1979 – present
weekly counts of >200 phytoplankton species

evolution

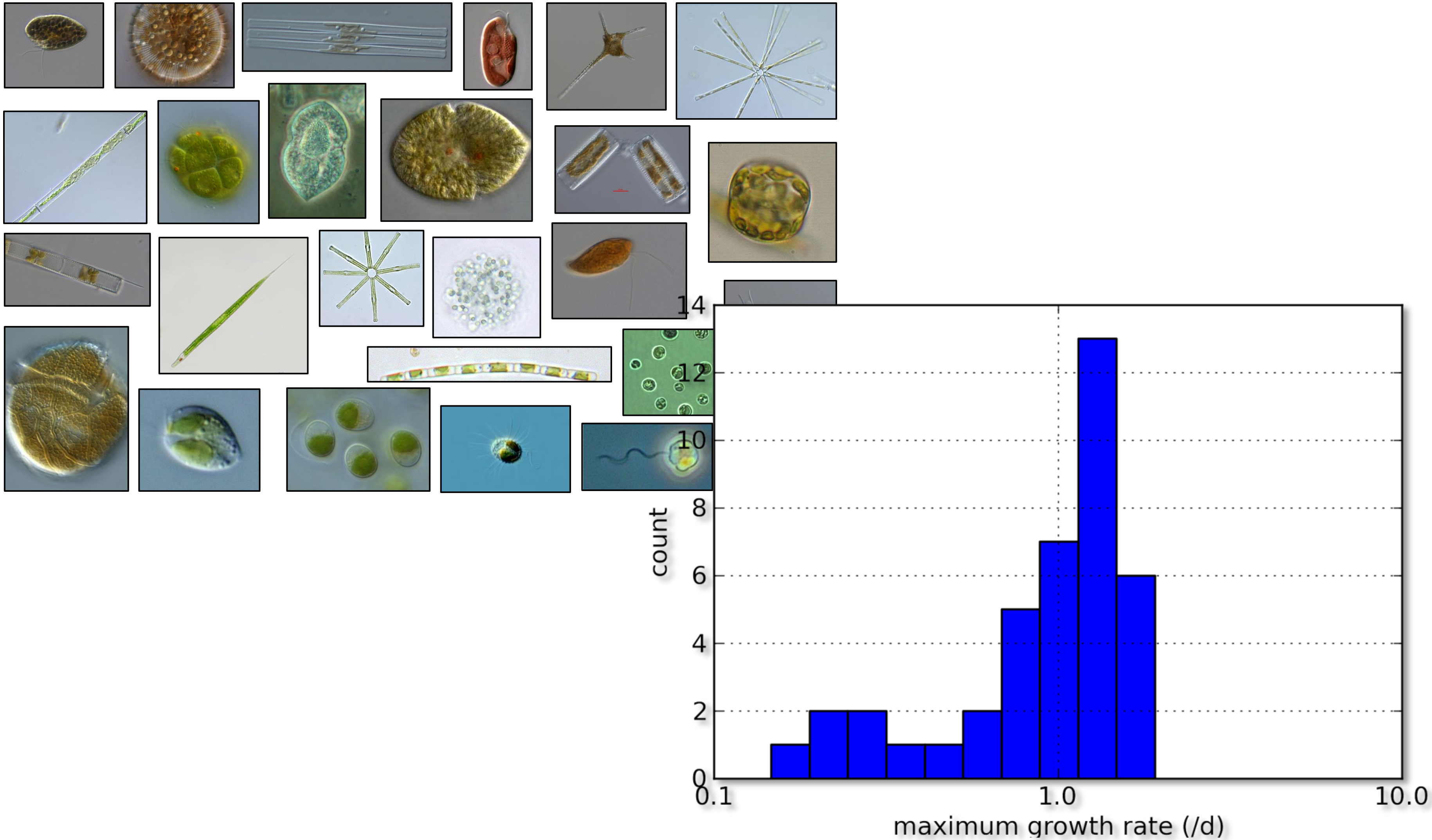
phylogenetic tree connecting all observed LC species

Observed phytoplankton species



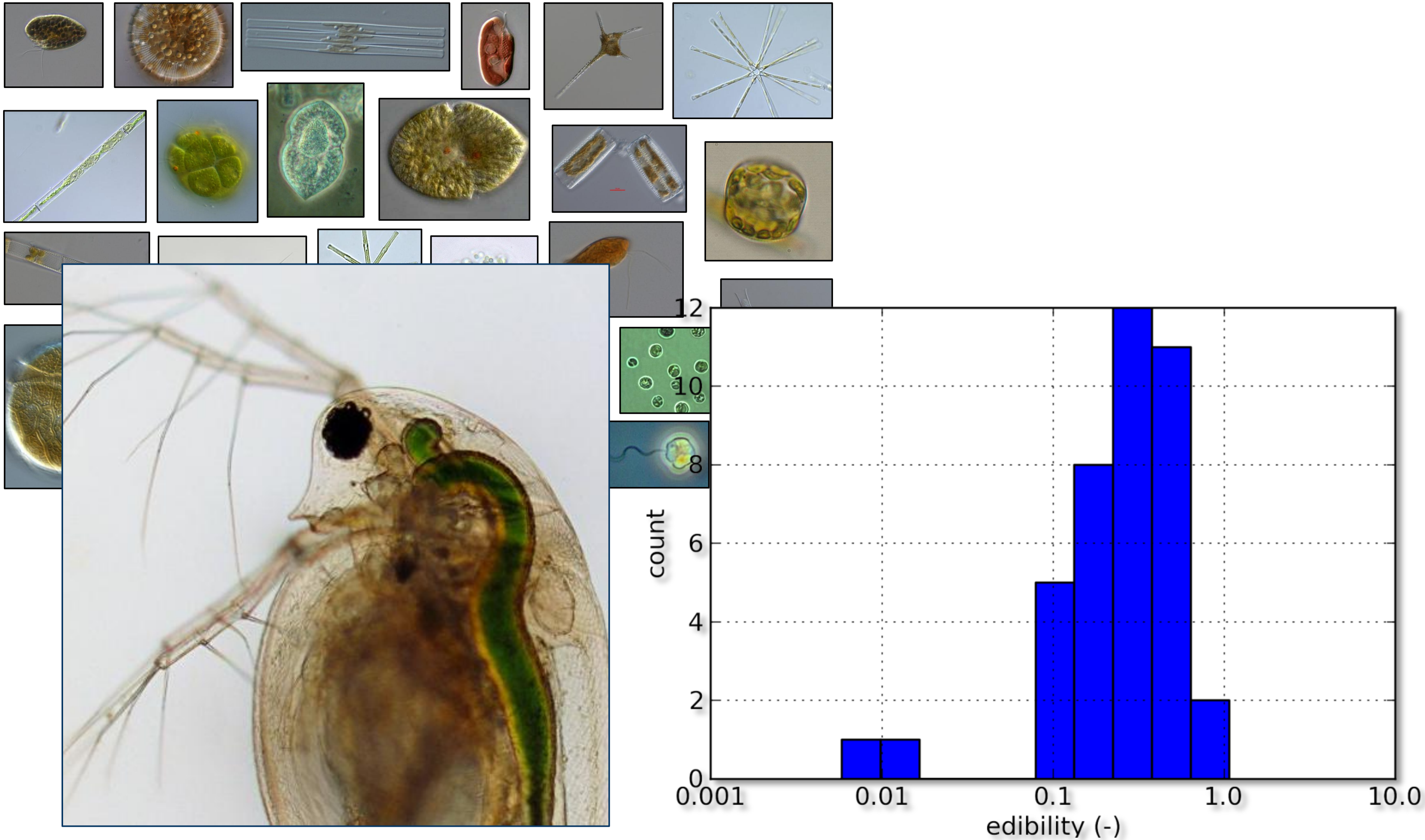
Variability

maximum growth rate



Variability

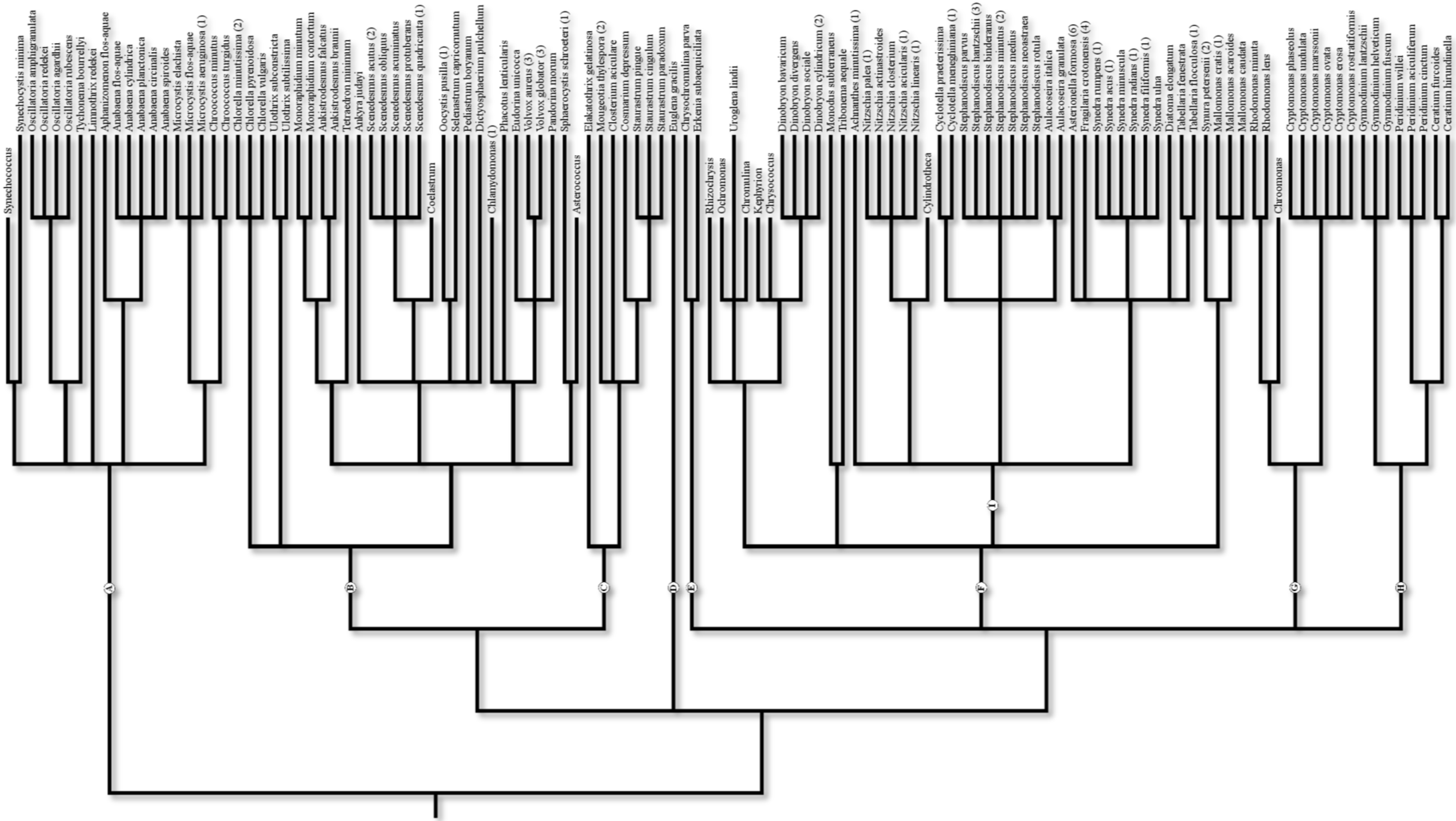
susceptibility to predation



Questions

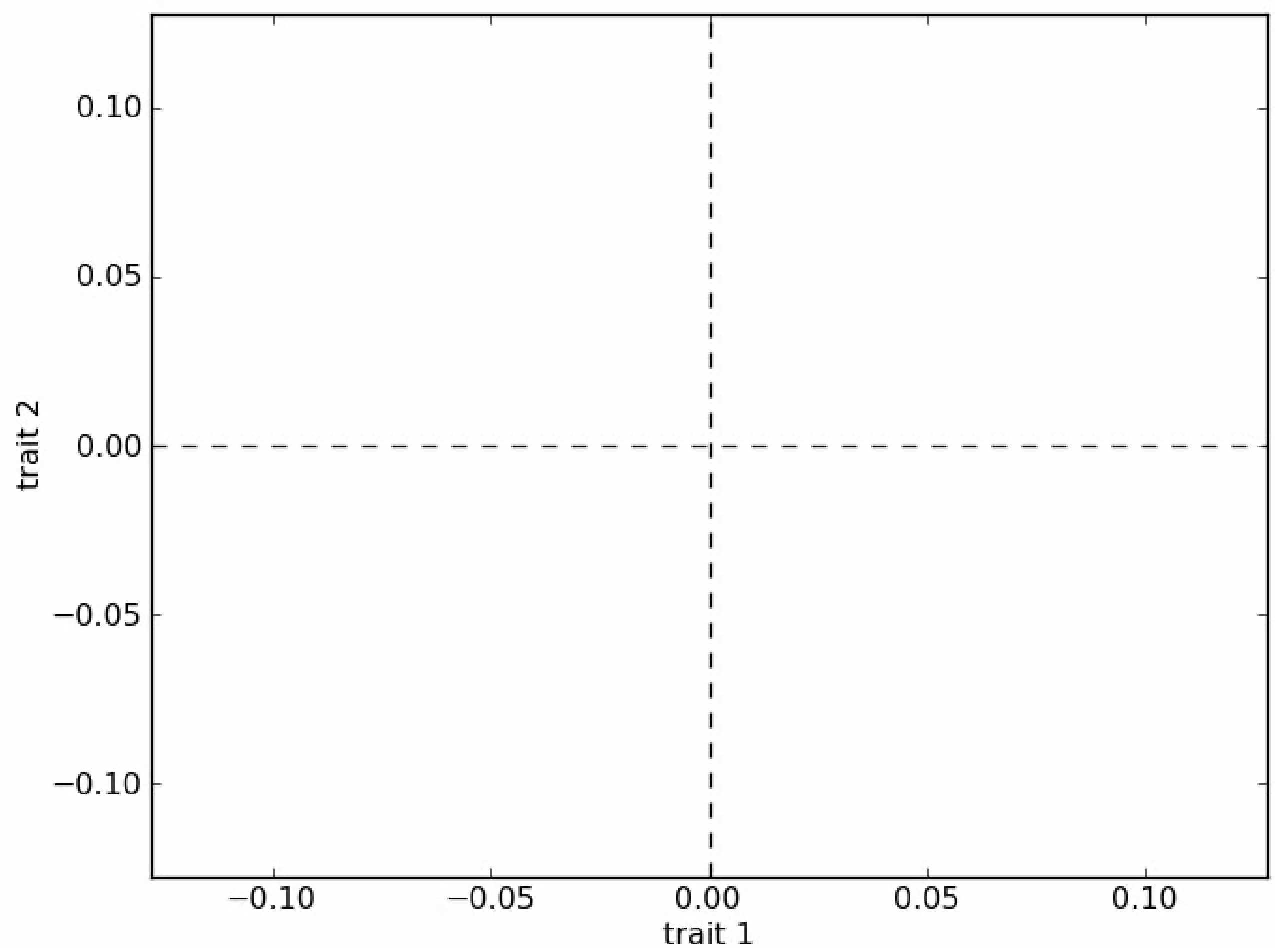
- Do we need to know all species?
  - Samples of present-day species are incomplete
  - Past and future species cannot be observed
- Do we need to know the value of every trait?
  - Measuring all traits of all known species is not feasible

Supplementary information: evolution



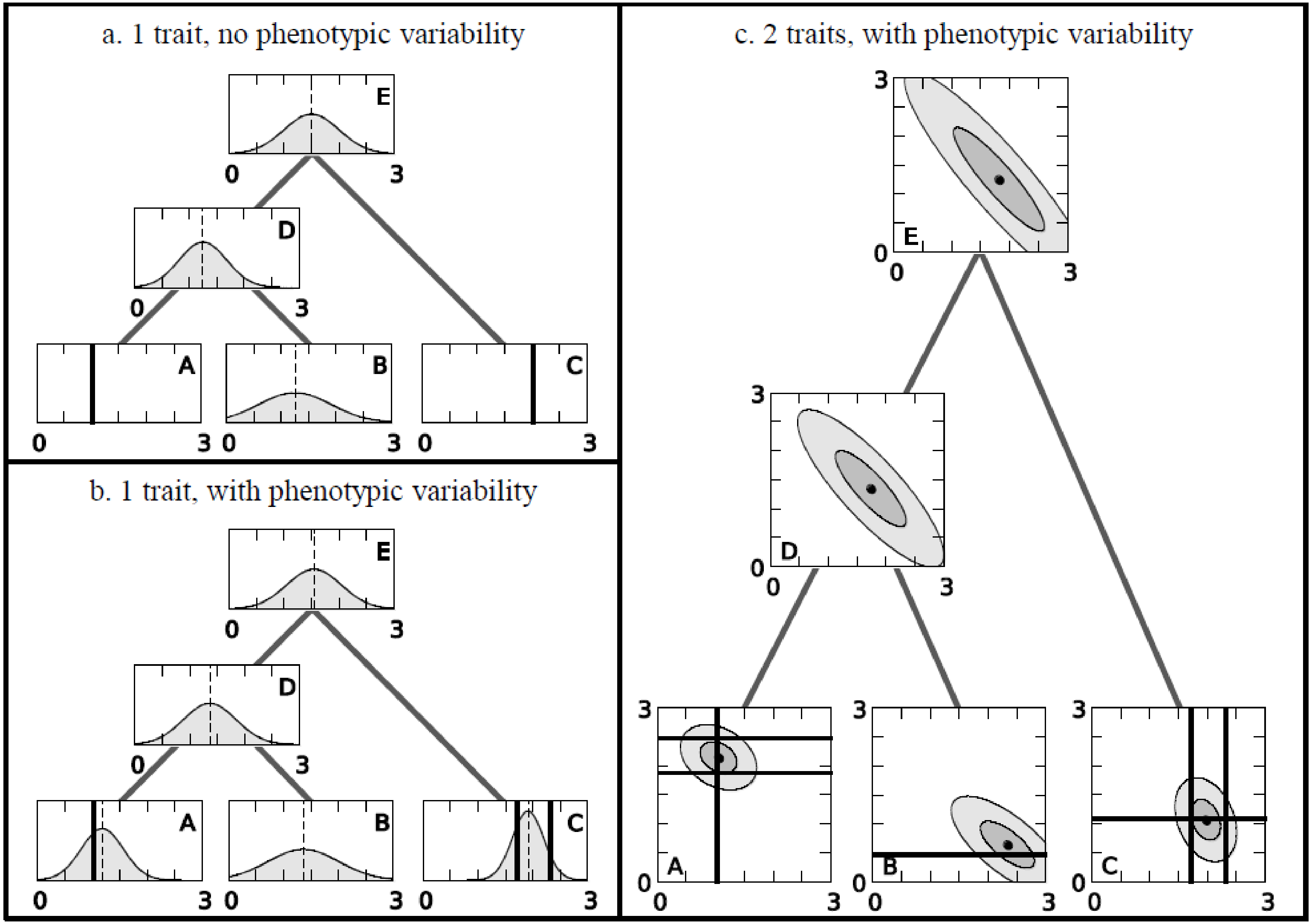
Bruggeman et al., Nucleic Acids Res., 2009
Bruggeman, J. Phycol., accepted

Getting grip on variability
Evolution as a random walk



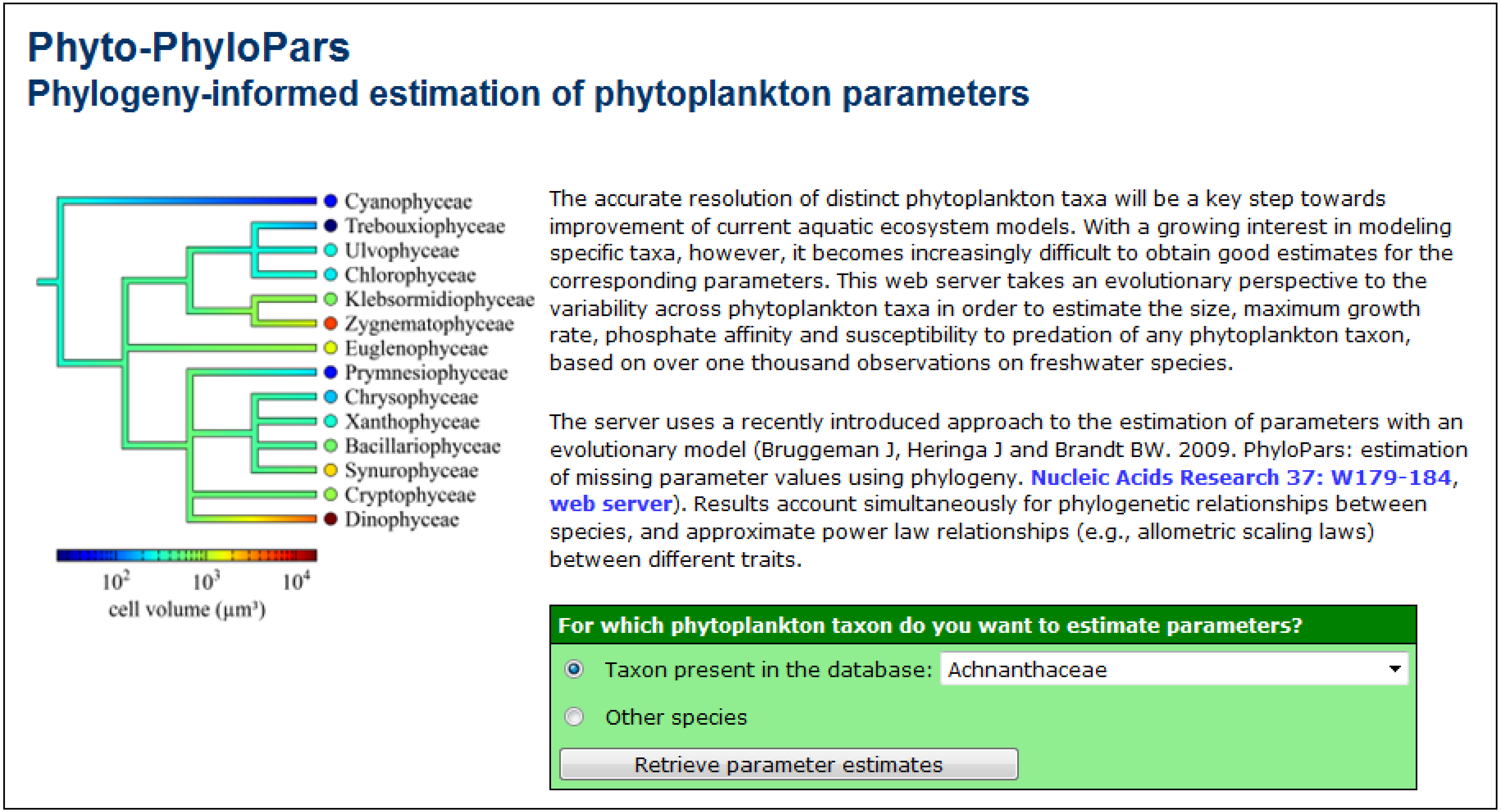
Bruggeman et al., Nucleic Acids Res., 2009
Bruggeman, J. Phycol., accepted

Reconstructing trait value variability



Demo

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



Phyto-PhyloPars

Phylogeny-informed estimation of phytoplankton parameters

The accurate resolution of distinct phytoplankton taxa will be a key step towards improvement of current aquatic ecosystem models. With a growing interest in modeling specific taxa, however, it becomes increasingly difficult to obtain good estimates for the corresponding parameters. This web server takes an evolutionary perspective to the variability across phytoplankton taxa in order to estimate the size, maximum growth rate, phosphate affinity and susceptibility to predation of any phytoplankton taxon, based on over one thousand observations on freshwater species.

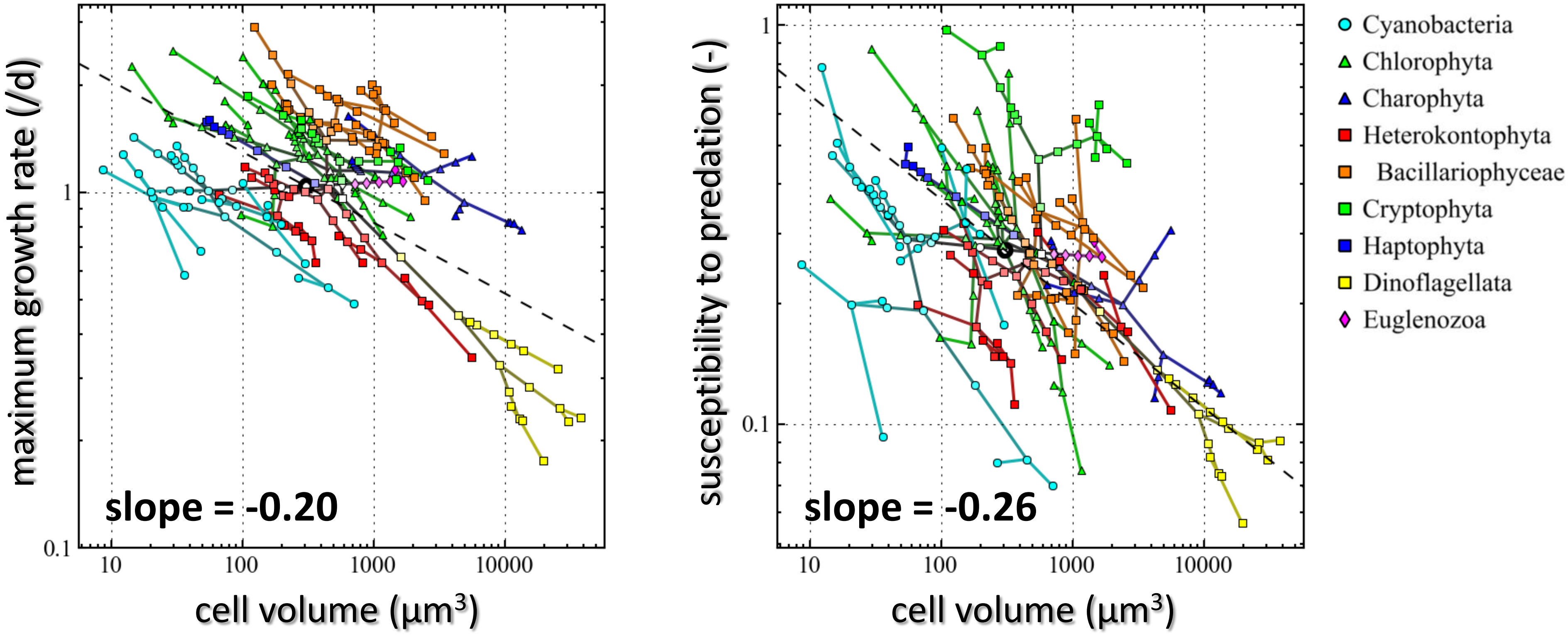
The server uses a recently introduced approach to the estimation of parameters with an evolutionary model (Bruggeman J, Heringa J and Brandt BW. 2009. PhyloPars: estimation of missing parameter values using phylogeny. **Nucleic Acids Research 37: W179-184**, **web server**). Results account simultaneously for phylogenetic relationships between species, and approximate power law relationships (e.g., allometric scaling laws) between different traits.

For which phytoplankton taxon do you want to estimate parameters?

● Taxon present in the database: Achnanthaceae

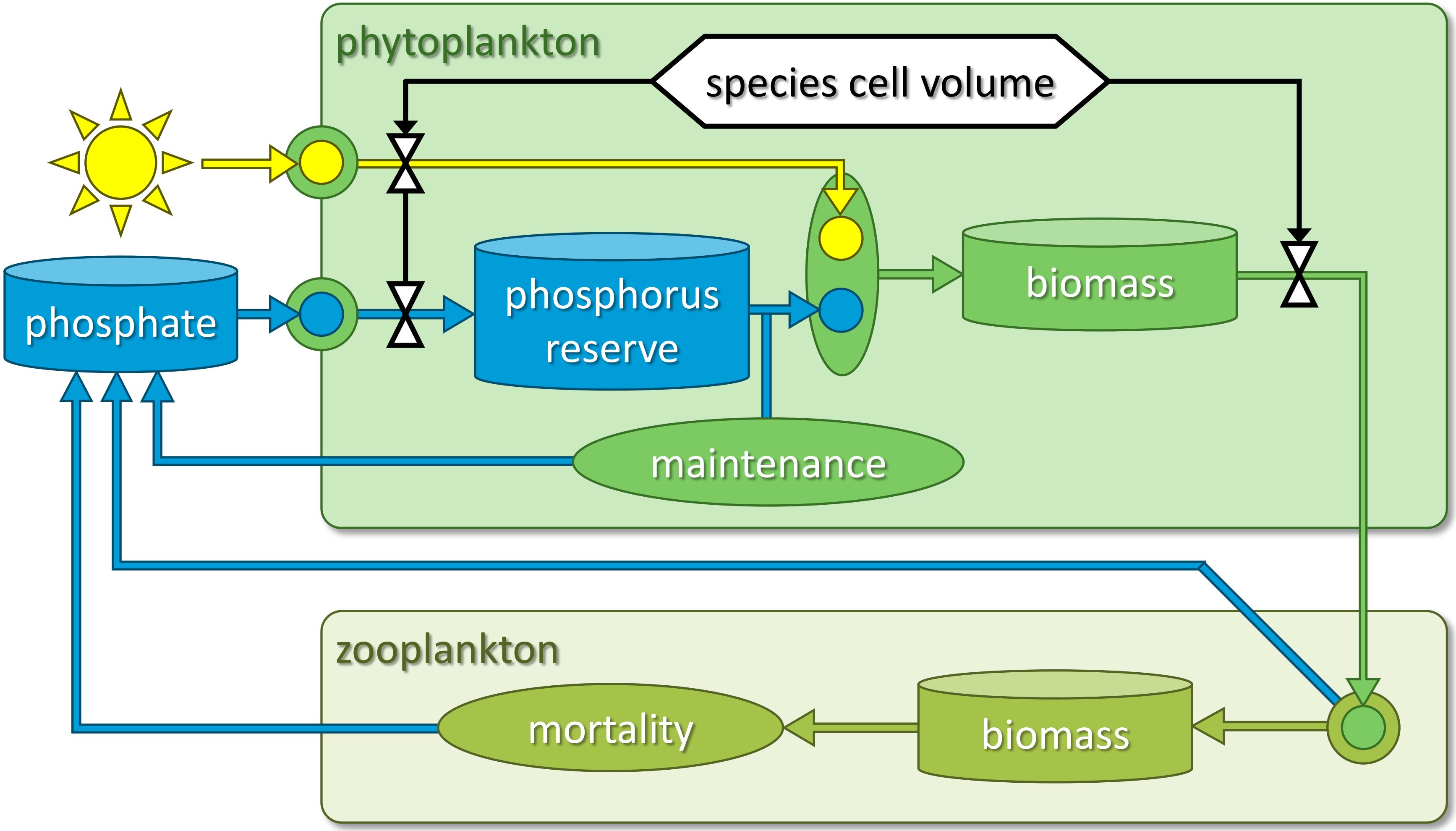
○ Other species

Reconstructing trait value variability



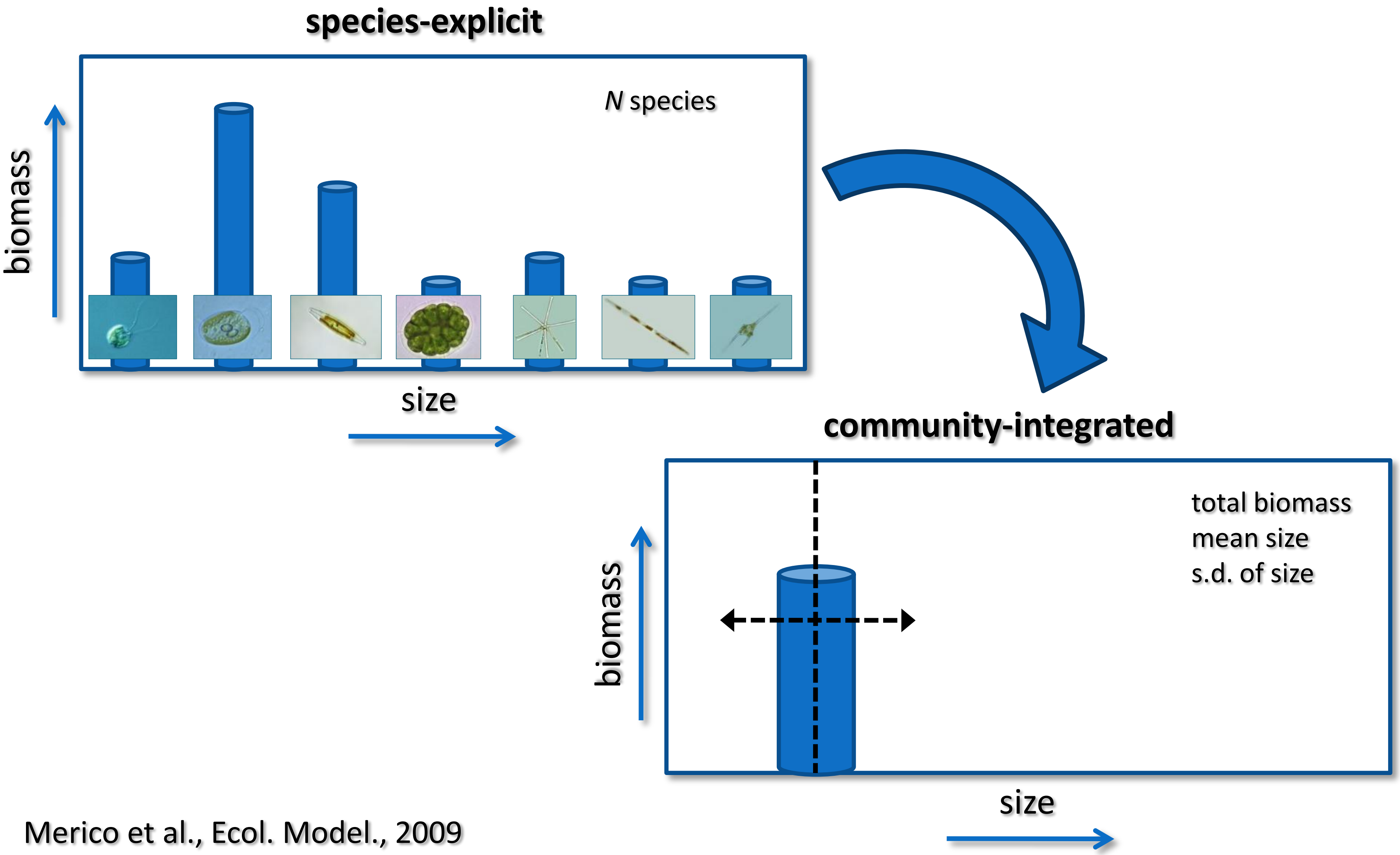
Bruggeman et al., Nucleic Acids Res., 2009
Bruggeman, J. Phycol., accepted

Describing the population
“size is everything”



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

Constructing a community



species-explicit

N species

biomass

size

community-integrated

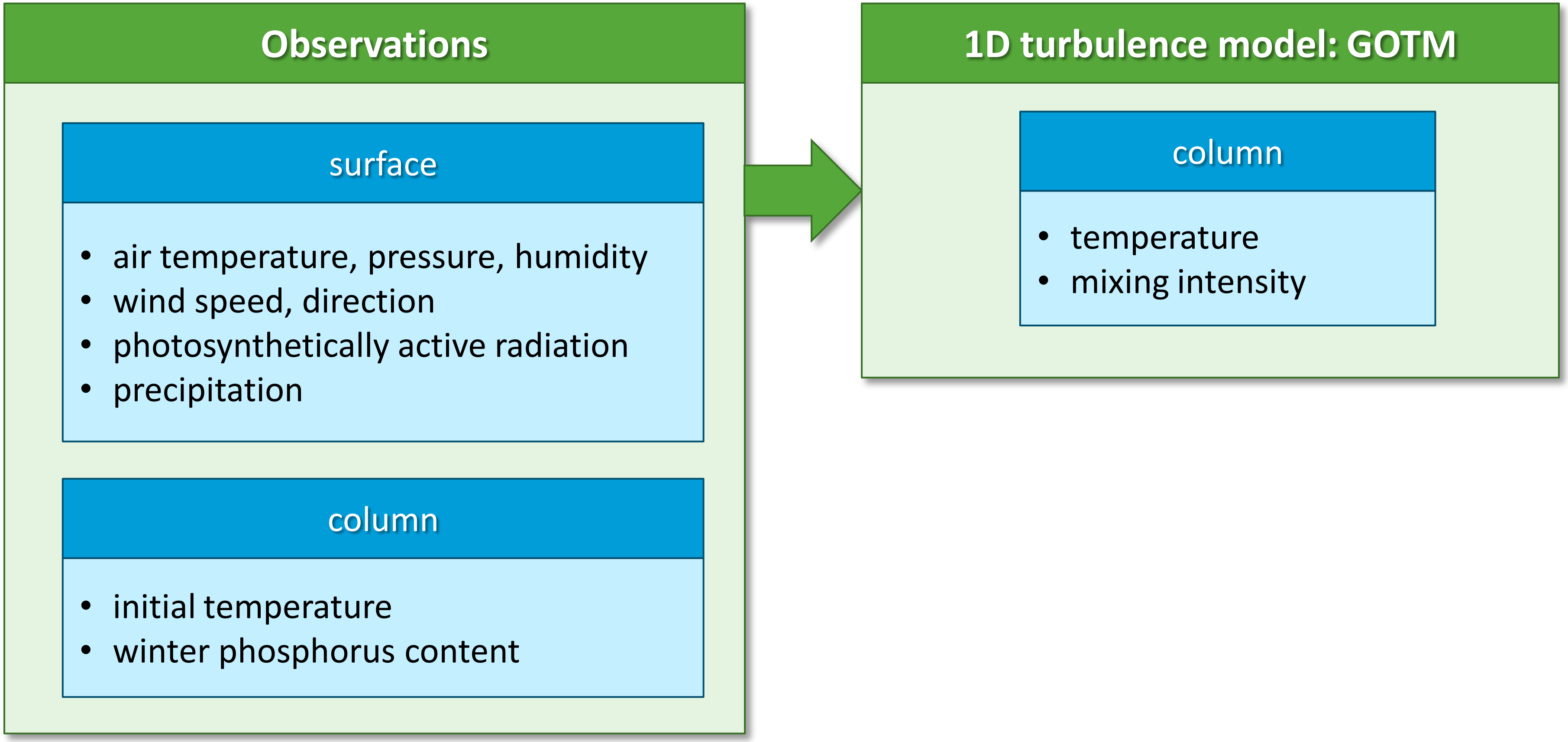
total biomass
mean size
s.d. of size

biomass

size

Merico et al., Ecol. Model., 2009

Modelling the environment



Observations

surface

- air temperature, pressure, humidity
- wind speed, direction
- photosynthetically active radiation
- precipitation

column

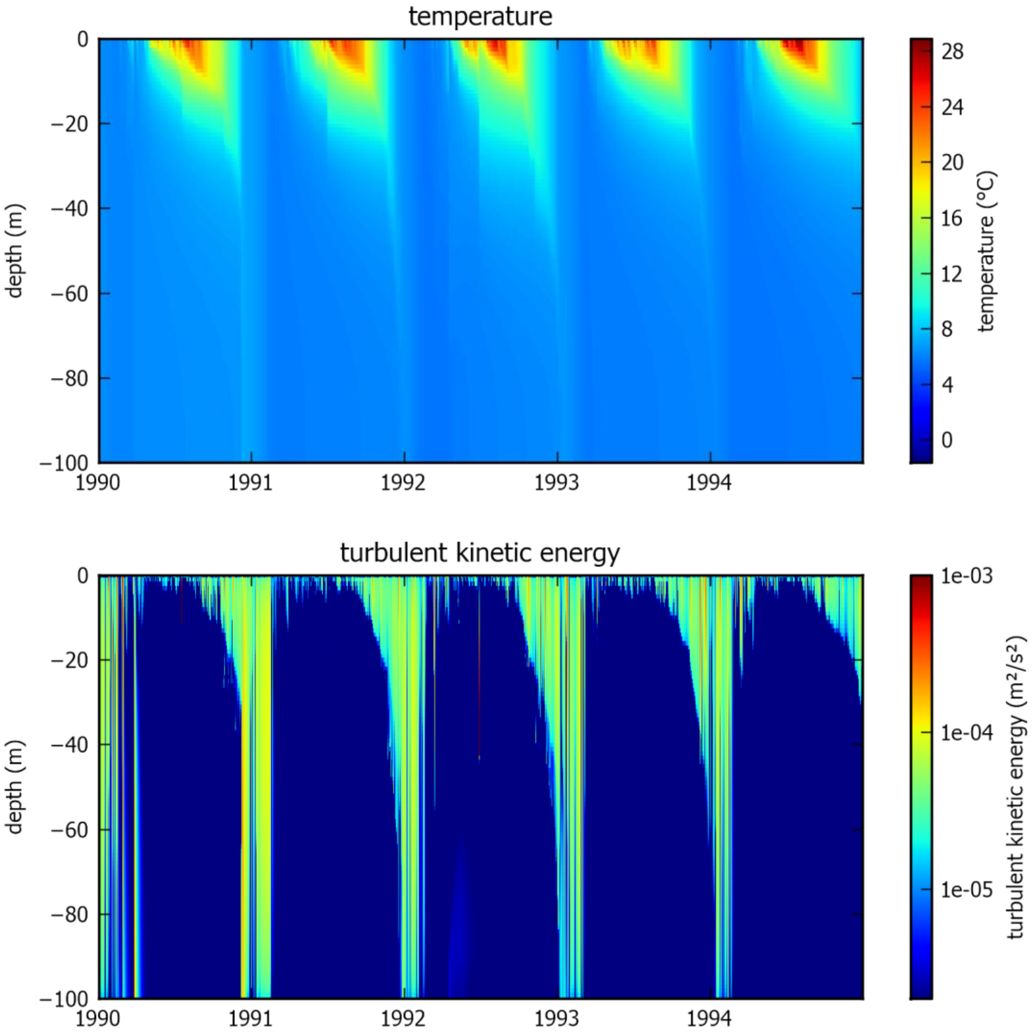
- initial temperature
- winter phosphorus content

1D turbulence model: GOTM

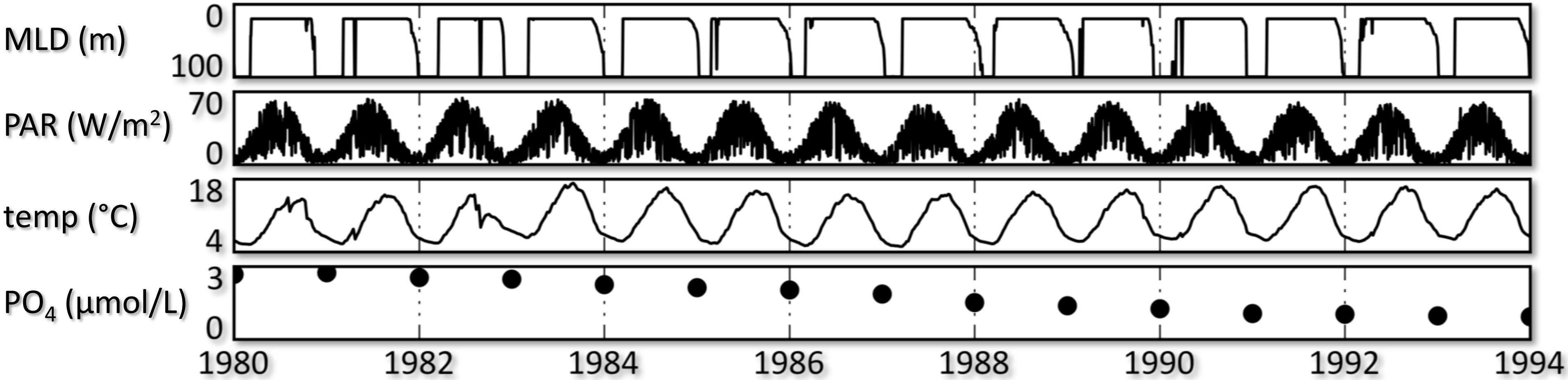
column

- temperature
- mixing intensity

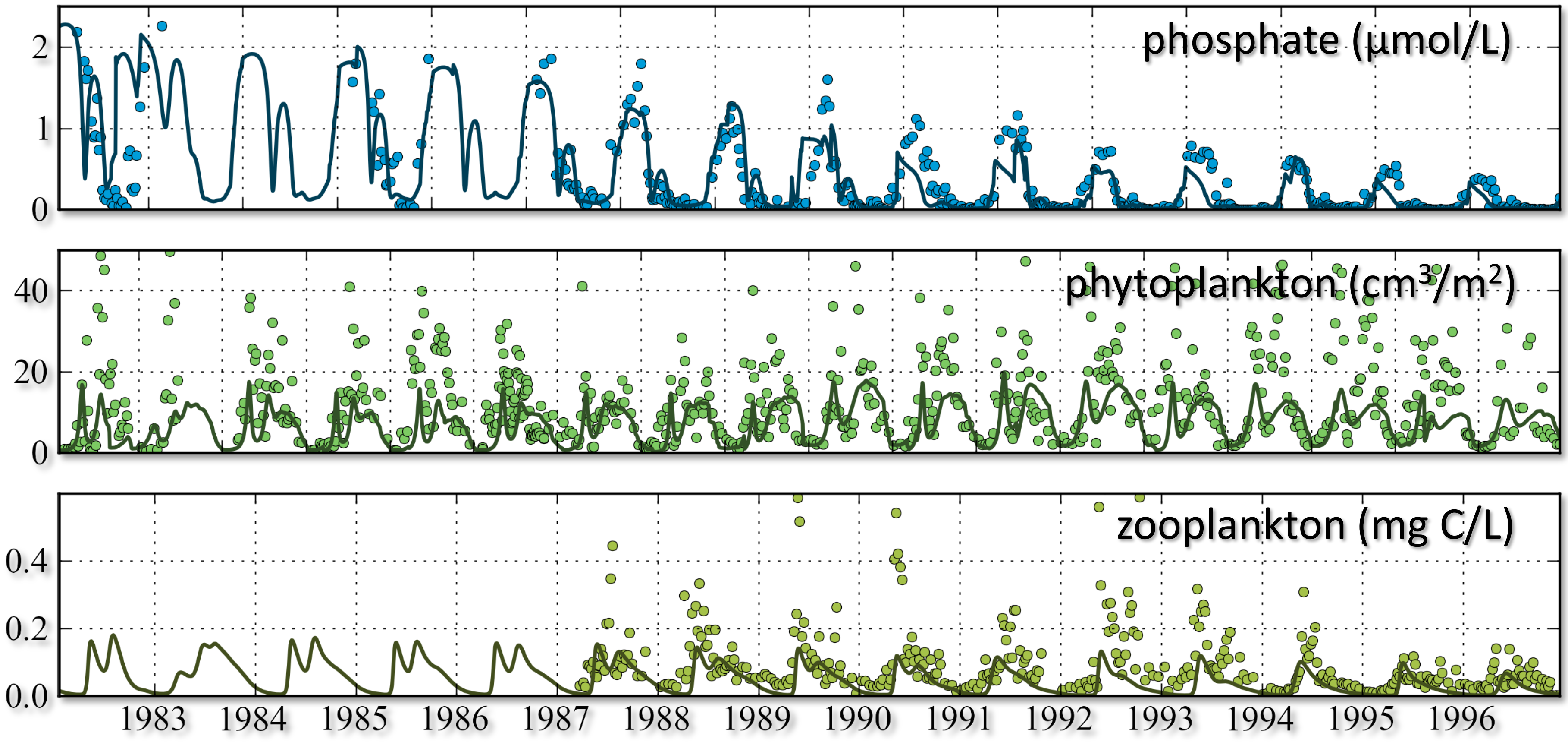
1D physics


temperature
0
−20
−40
−60
−80
−100
depth (m)
1990
1991
1992
1993
1994
28
24
20
16
12
8
4
0
temperature (°C)
turbulent kinetic energy
0
−20
−40
−60
−80
−100
depth (m)
1990
1991
1992
1993
1994
1e-03
1e-04
1e-05
turbulent kinetic energy (m²/s²)

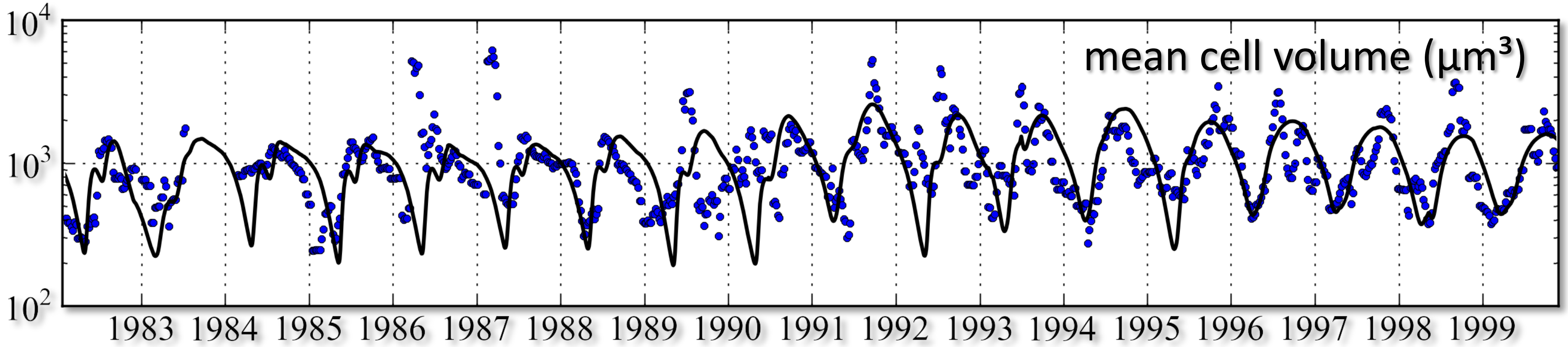
A mixed layer model



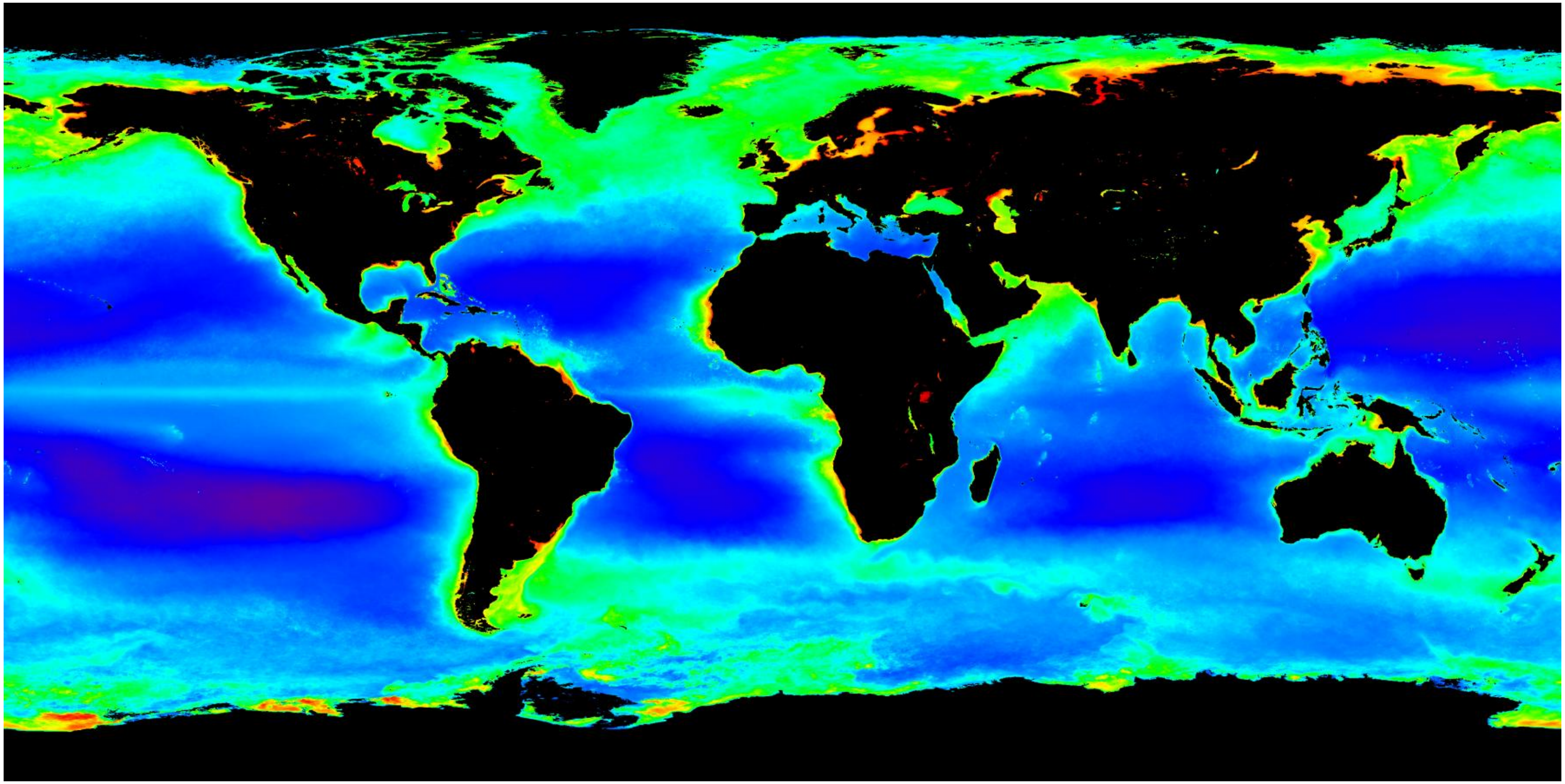
Calibration



Predictions
mean of cell size

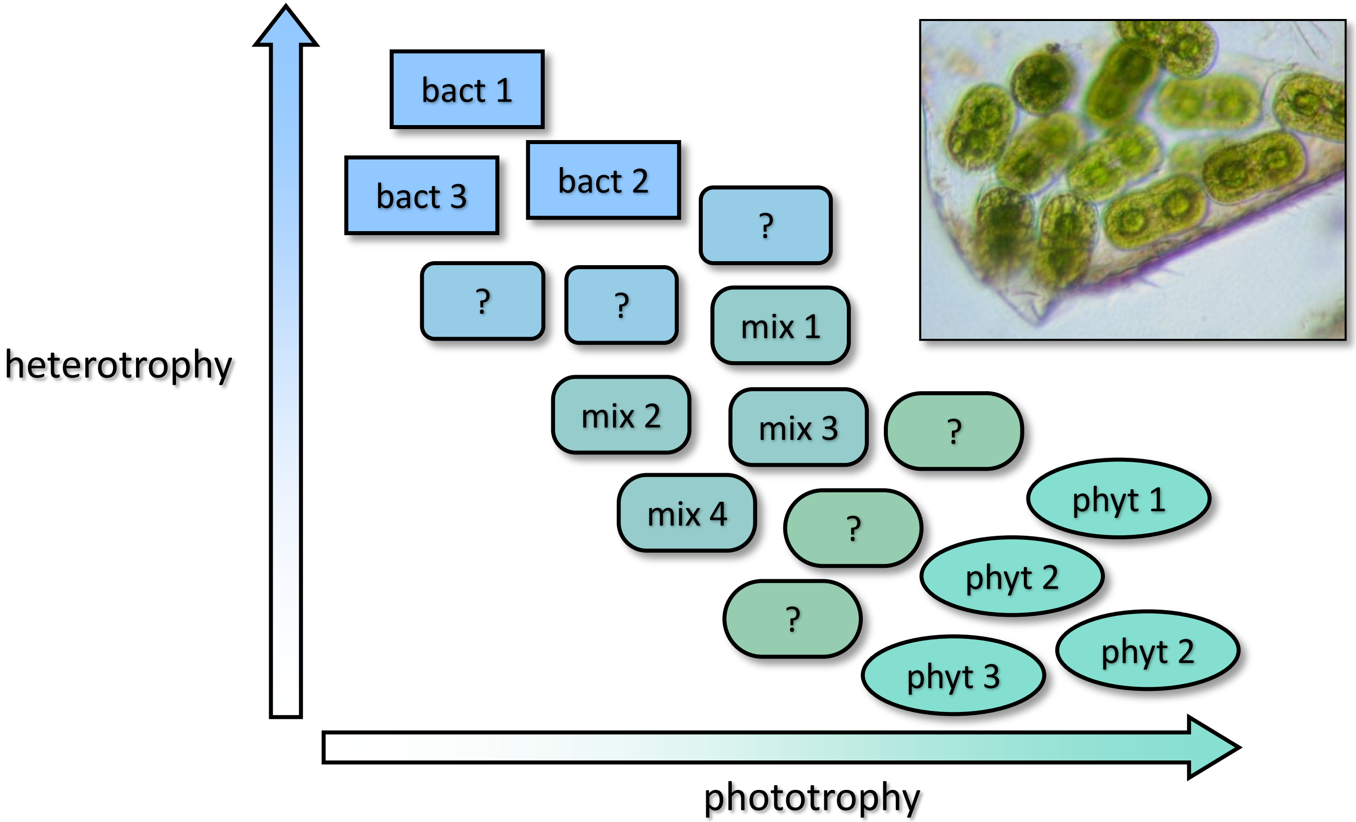


Test case 2: the world ocean



Looking at plankton: mixotrophy

Phototrophs and heterotrophs: a section through diversity


bact 1

bact 3

bact 2

?

?

?

mix 1

heterotrophy

mix 2

mix 3

?

phyt 1

mix 4

?

phyt 2

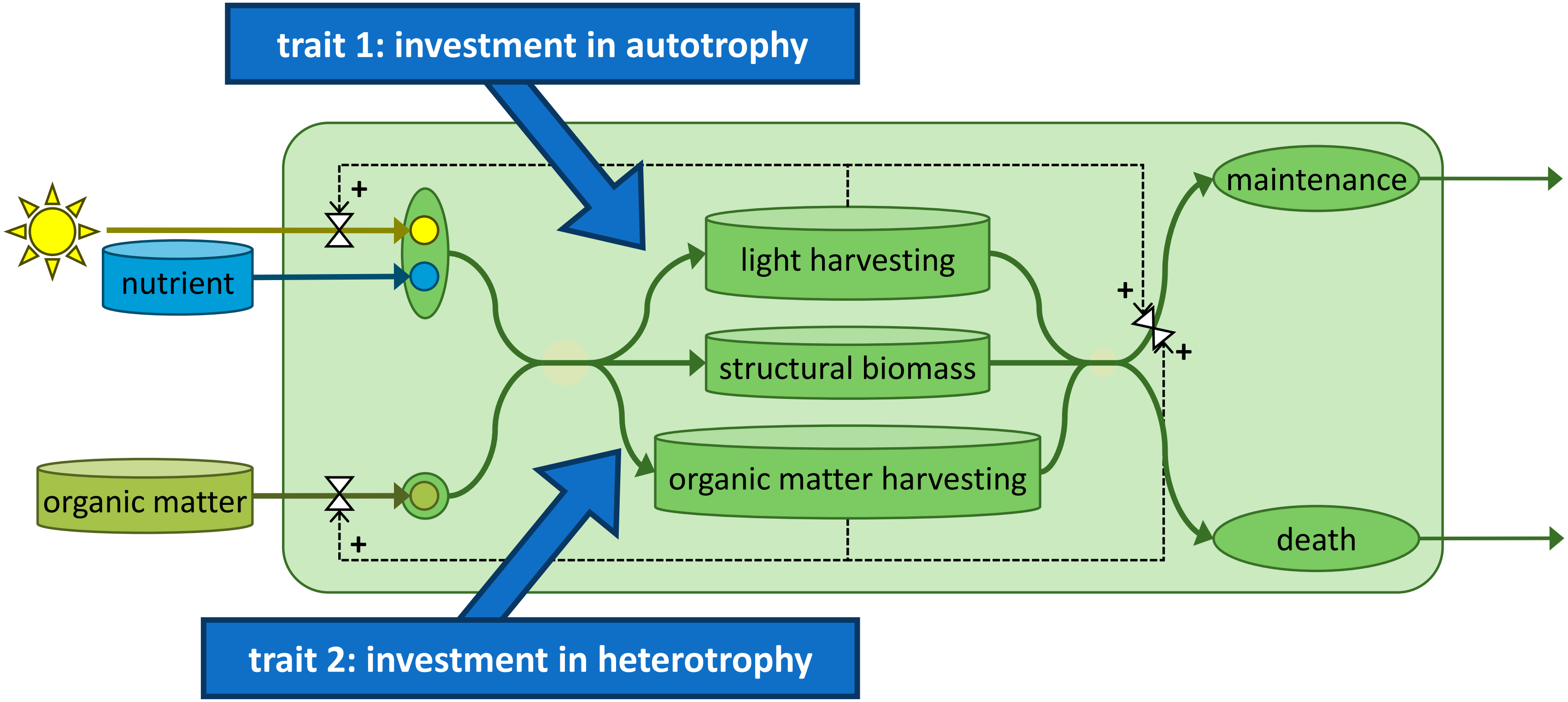
?

phyt 3

phyt 2

phototrophy

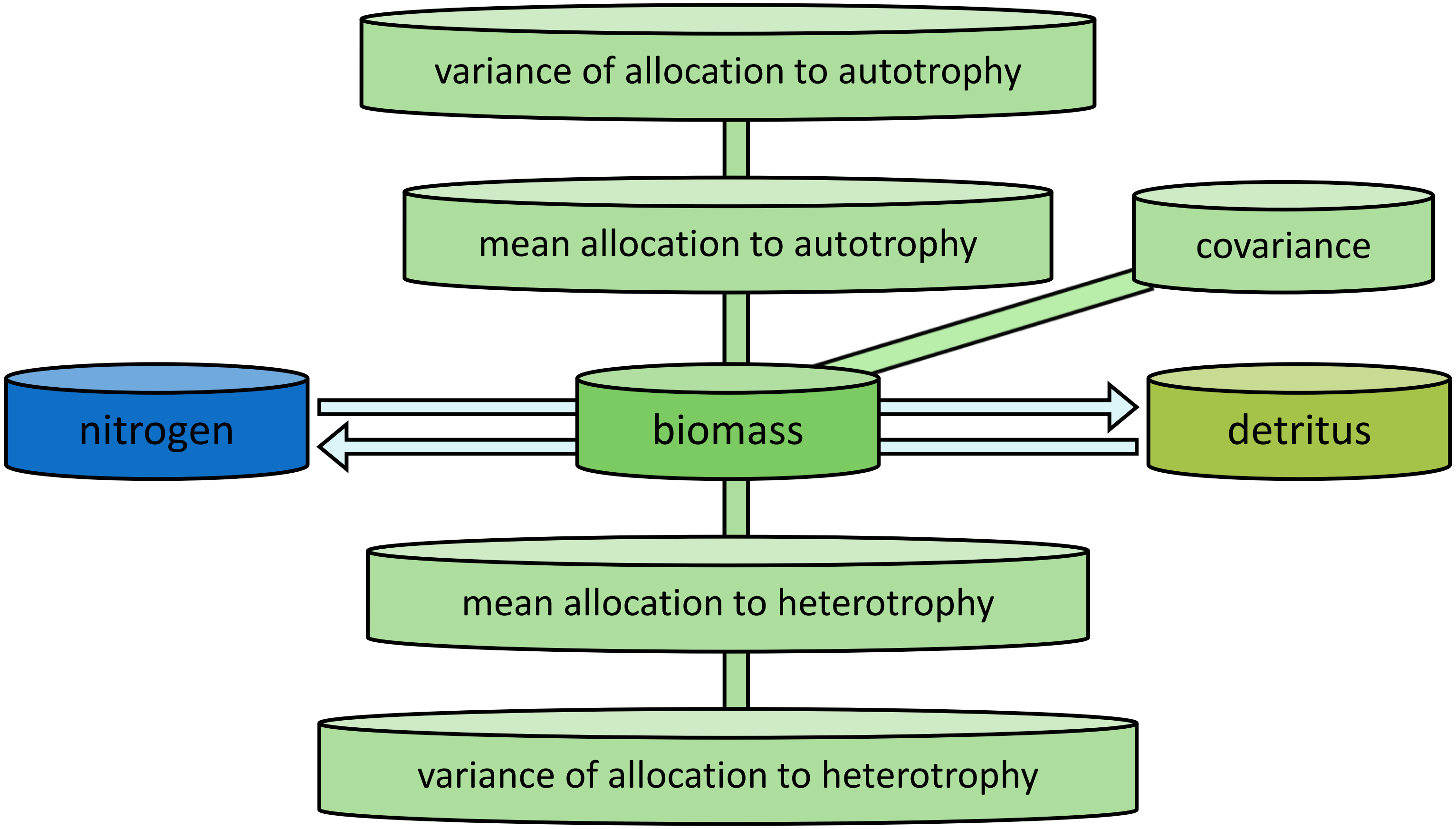
Generalizing the ecosystem: mixotrophy



trait 1: investment in autotrophy

trait 2: investment in heterotrophy

Model characteristics



7 physiological parameters

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

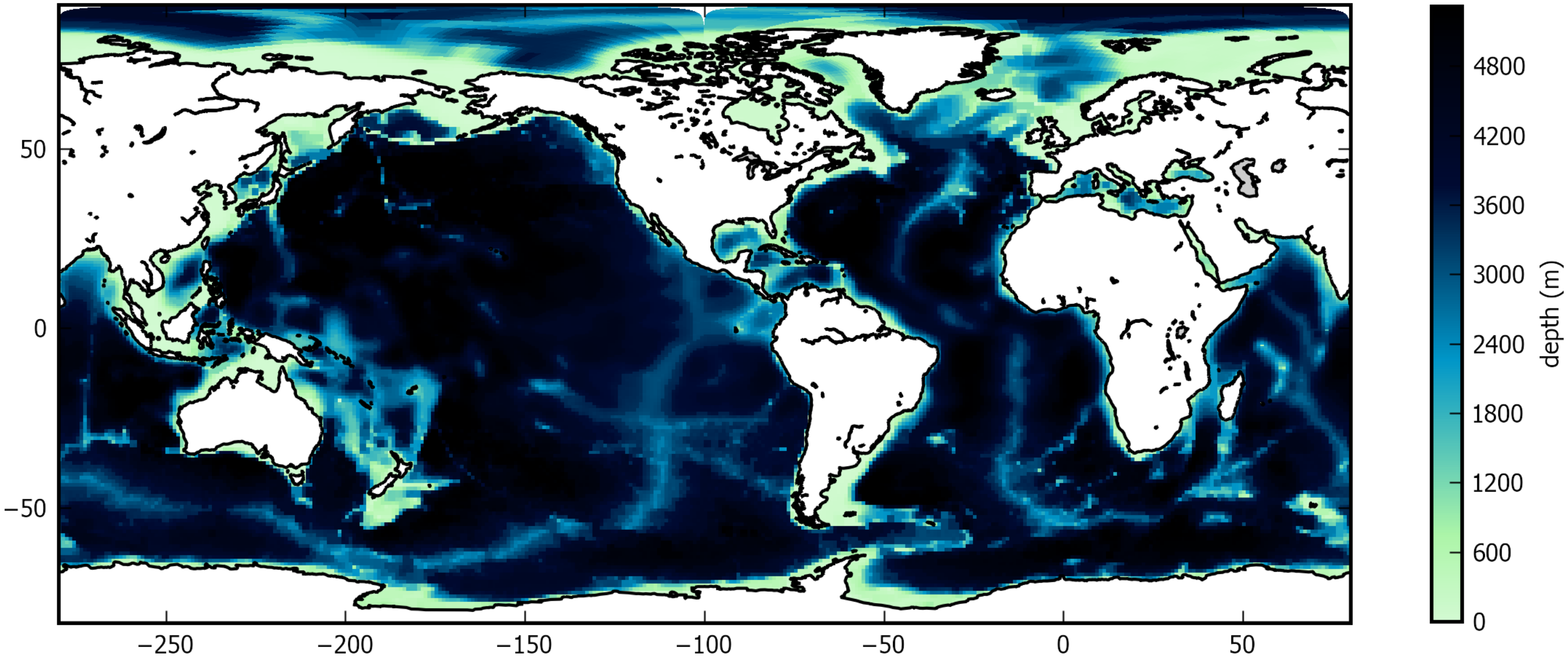
Bruggeman, Kooi & Kooijman (under rev.)

Calibration: 1D Bermuda profiles

- Bermuda Atlantic Time-series Study
- Column model
  - General Ocean Turbulence Model
  - ERA-40 meteorological forcing
  - Observed initial temperature, salinity, Dissolved Inorganic Nitrogen
  - 5 year period: 1989 – 1993
- Observed variables
  - Dissolved Inorganic Nitrogen
  - Chlorophyll
  - Export of Particulate Organic Nitrogen
  - Primary Production
- Parameter estimation
  - algorithm: Differential Evolution
  - all parameters free
  - 4 replica's (combined 300,000 runs)

Bruggeman, Kooi & Kooijman (under rev.)

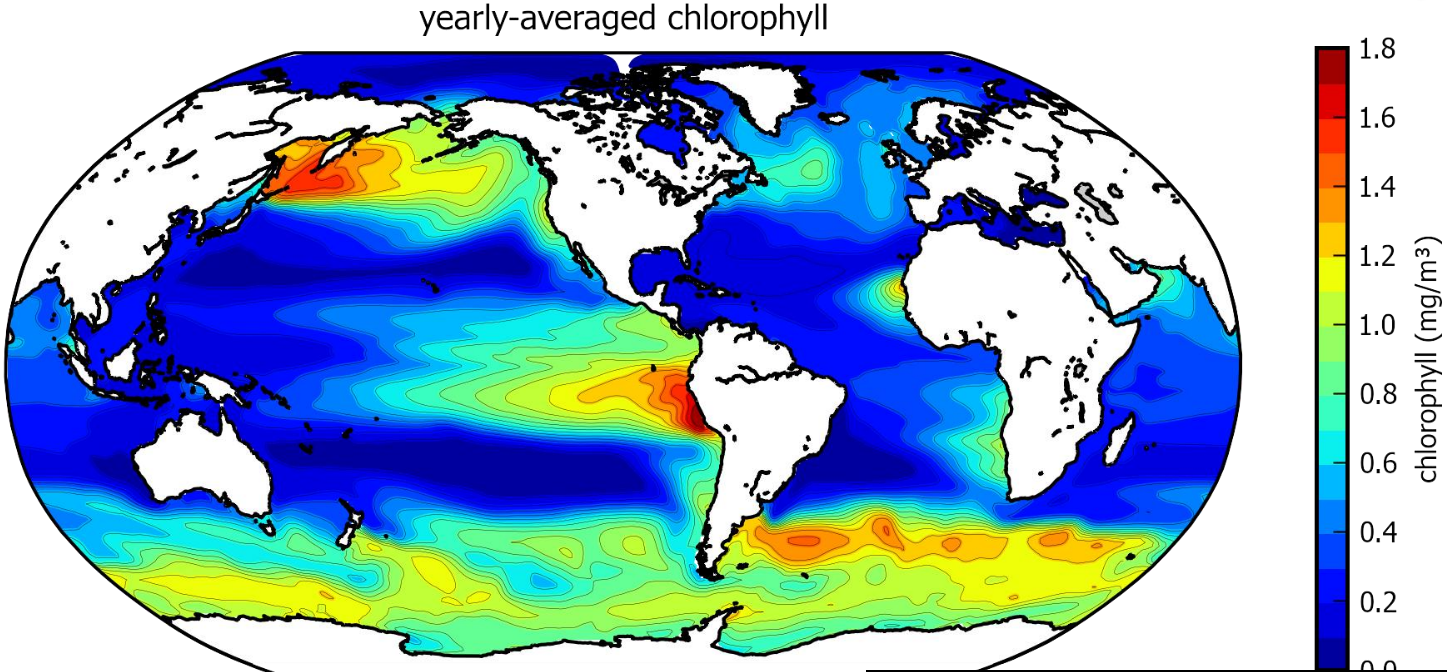
Simulation of the 3D world ocean

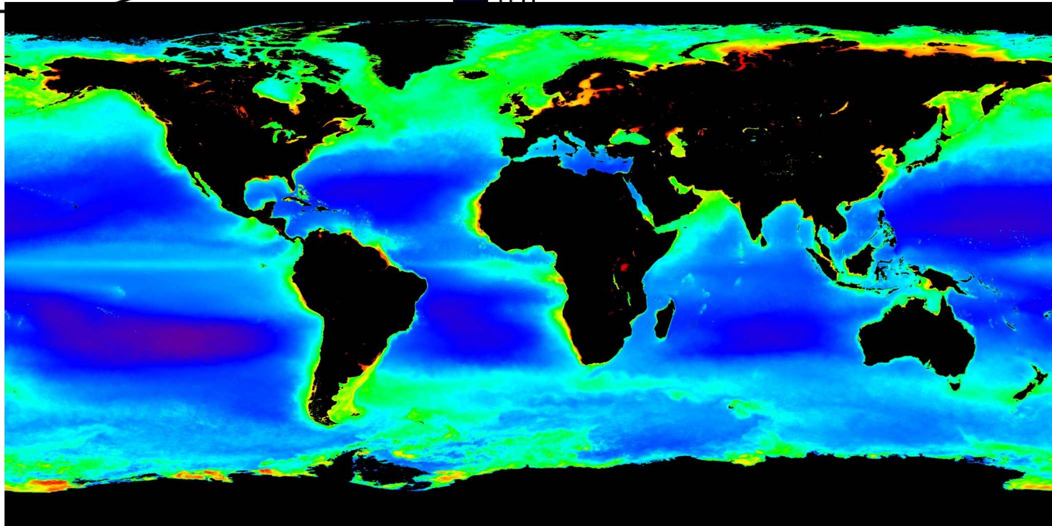


MOM 4, Griffies et al. (2005) setup

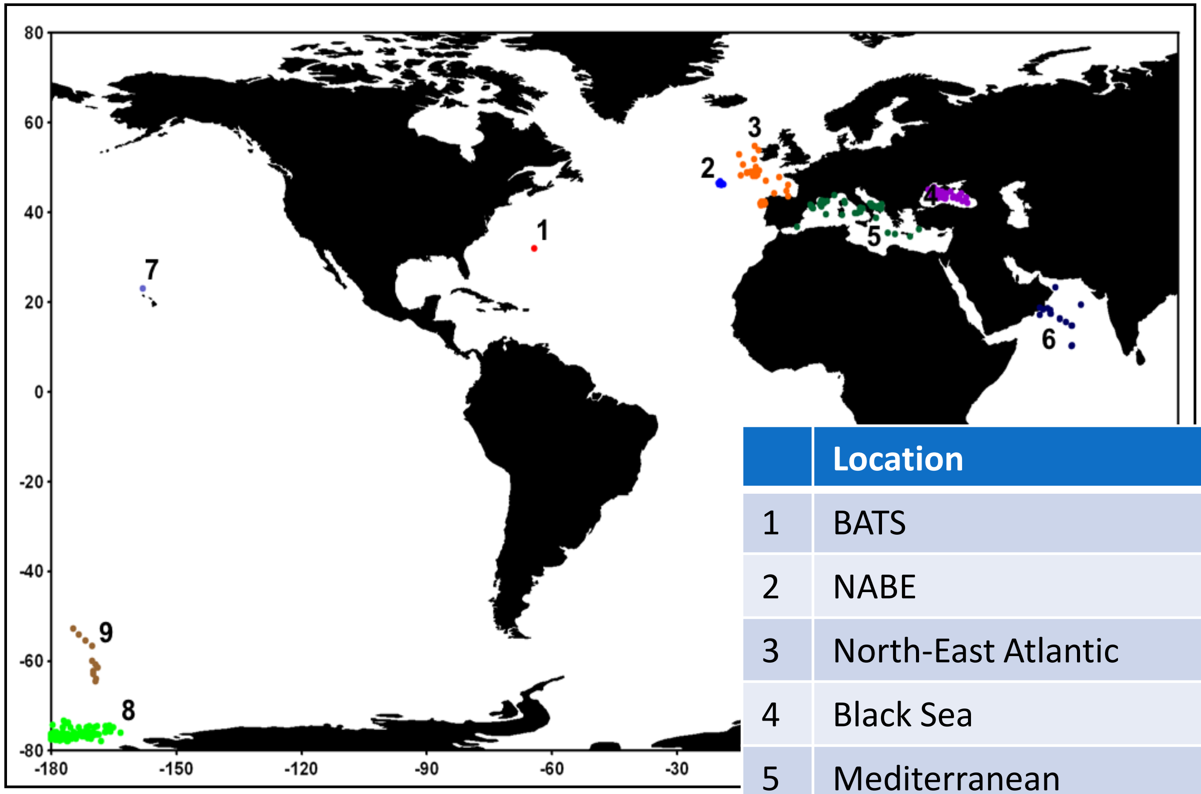
- 1° nominal horizontal resolution
- 50 depth levels, variable thickness (10 - 370 m)
- climatological forcing

Patterns: surface chlorophyll





Patterns: productivity



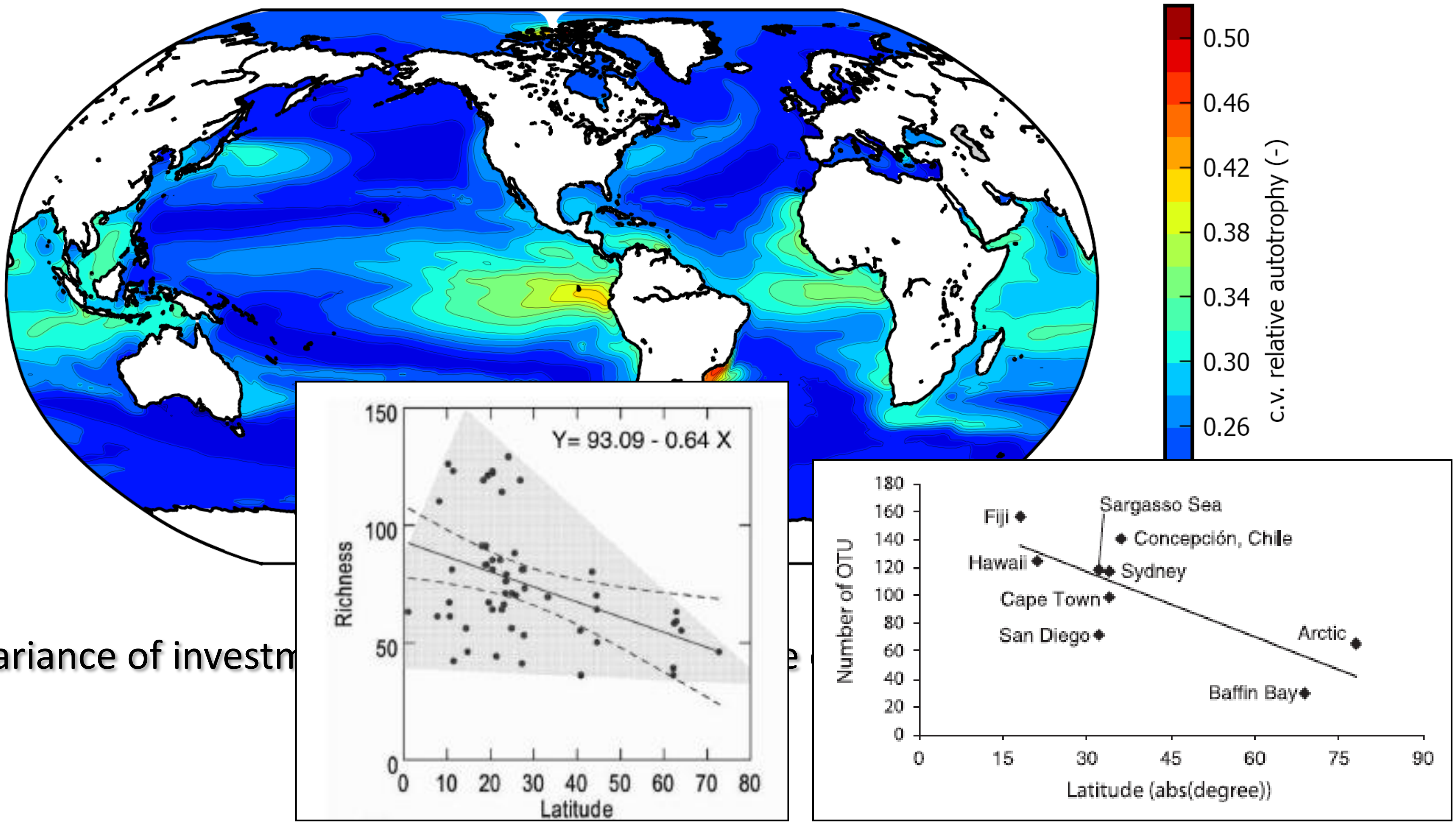
Mean rank: 4/10

	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

yearly-averaged coefficient of variation for autotrophy



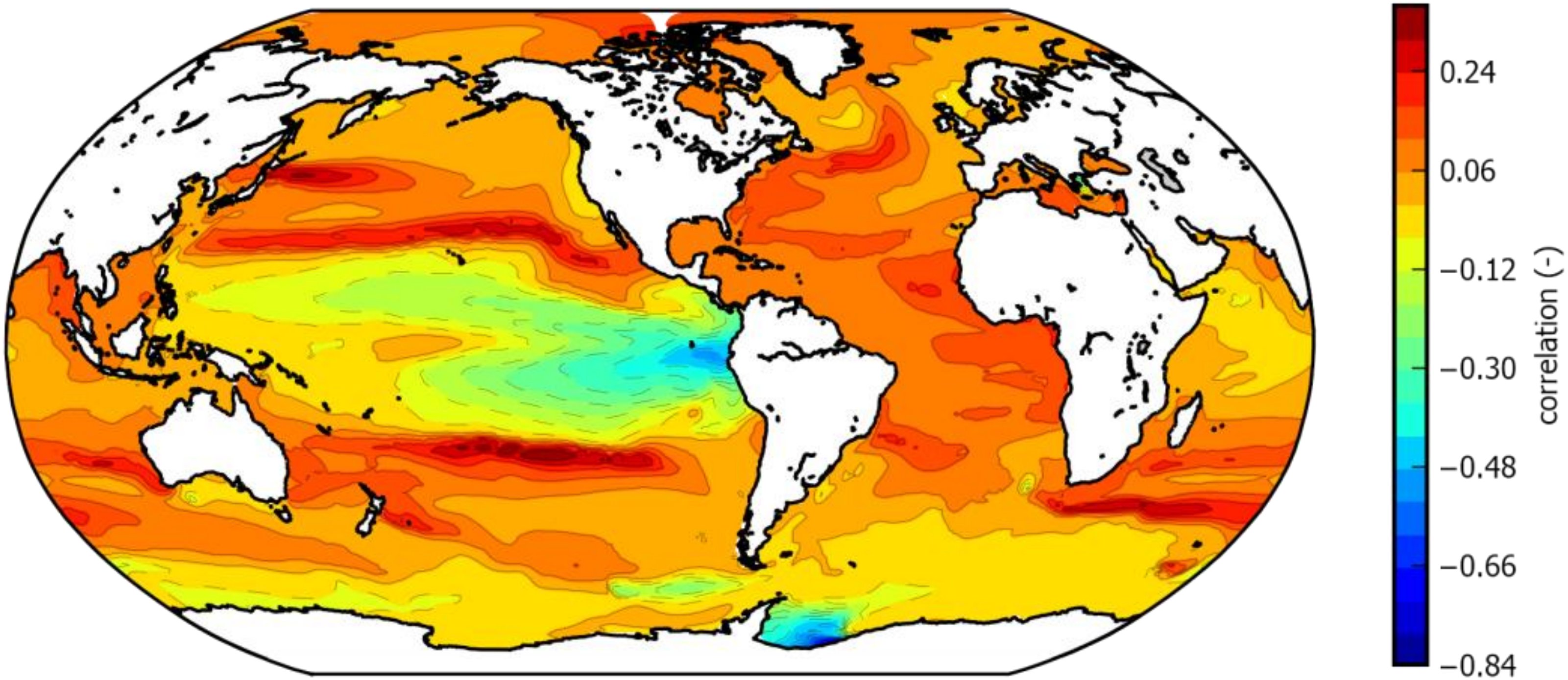
Variance of investm e

Fuhrman et al. (PNAS, 2008)

Pommier et al. (Molecular Ecology 2007)

Patterns: mixotrophy

Correlation between autotrophic and heterotrophic investment



Evaluation: 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

Wrapping up

- Darwinian approaches provide no magic solution...
  - They do not replace solid empirical knowledge – if anything, they require more!
- But they do change the way we look at systems
  - Traits, trade-offs and biodiversity instead of distinct, constant functional groups

Acknowledgements

Ursula Gaedke[1], Heiner Dietze[2], Andreas Oschlies[2], Elena Litchman[3], Heather Bouman[4], Kai Wirtz[5], Agostino Merico[6], Bas Kooijman[7], Bob Kooi[7], Mick Follows[8], Marjorie Friedrichs[9], Vincent Saba[10]

[1] University of Potsdam, Germany
[2] IFM-GEOMAR, Kiel, Germany
[3] Michigan State University, USA
[4] University of Oxford, UK
[5] GKSS Research Centre, Geesthacht, Germany
[6] ZMT Bremen, Germany
[7] Vrije Universteit Amsterdam, The Netherlands
[8] Massachusetts Institute of Technology, USA
[9] Virginia Institute of Marine Science, USA
[10] Princeton University, USA

NWO
Netherlands Organisation for Scientific Research

St John's College
Oxford