Physiological diversity matters: a modelling perspective

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Acknowledgments:

Ben Ward

Chris Follett

Mick Follows

Oliver Jahn

Anna Hickman

NASA

NSF

SIMONS FOUNDATION

Gordon and Betty MOORE FOUNDATION

OUTLINE

Global 3-D biogeochemical, ecosystem models

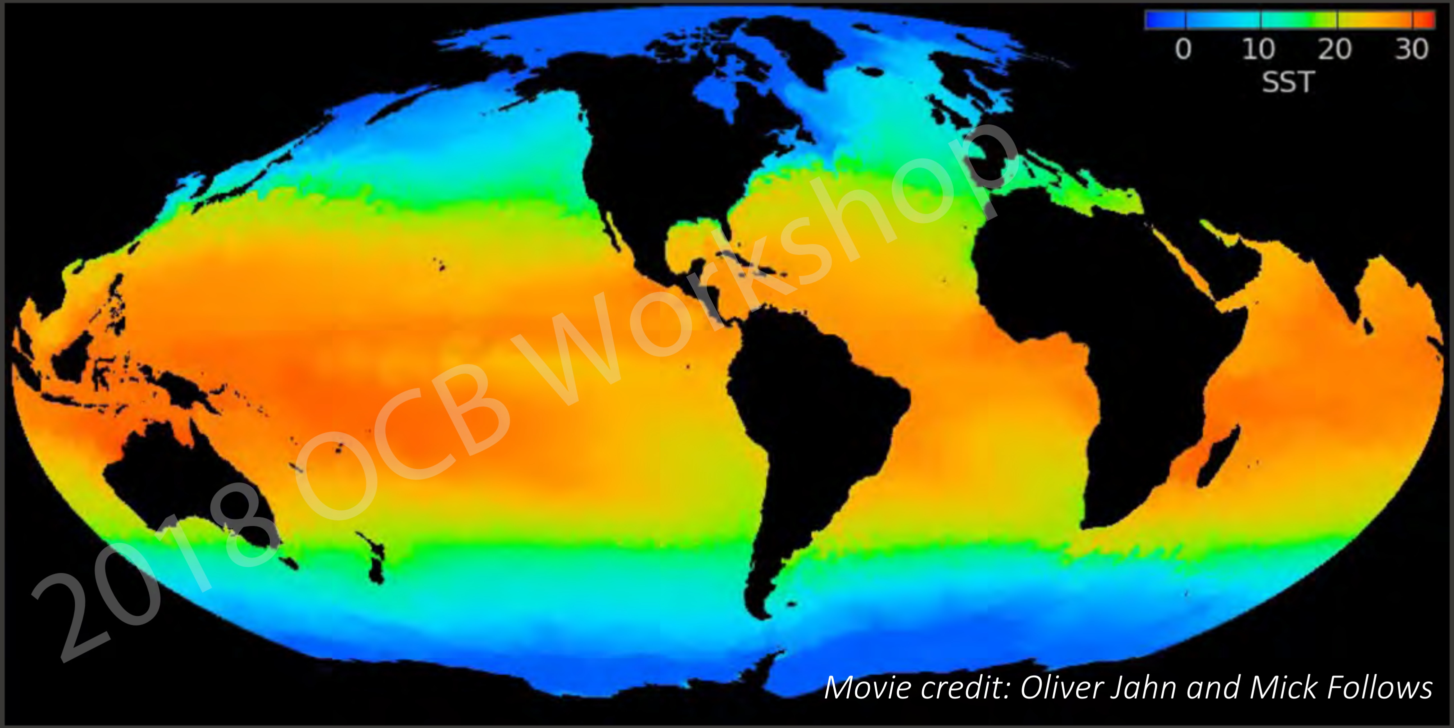
- What is state of the art in terms of diversity?
- Why including physiological diversity matters?
  - some examples
- Other aspects of physiological parameterization
  (hopefully to lead to discussion)

Global 3-D biogeochemical, ecosystem models

Physics:
velocity, mixing, temperature

Biogeochemistry:
nutrients, DOM, POM

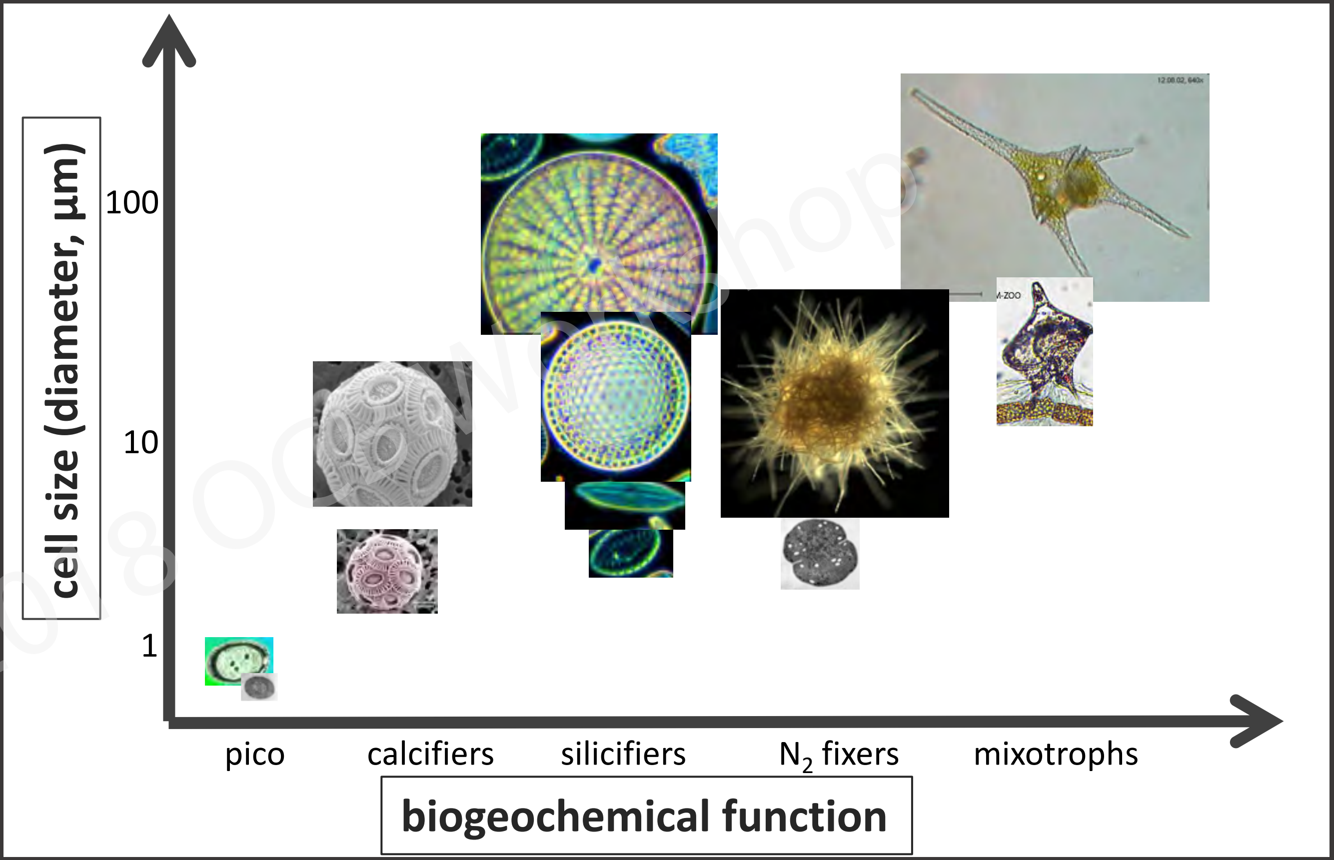
Ecosystem:
phytoplankton, zooplankton



Movie credit: Oliver Jahn and Mick Follows

What is the state of the art?

Diverse phytoplankton communities



OUTLINE

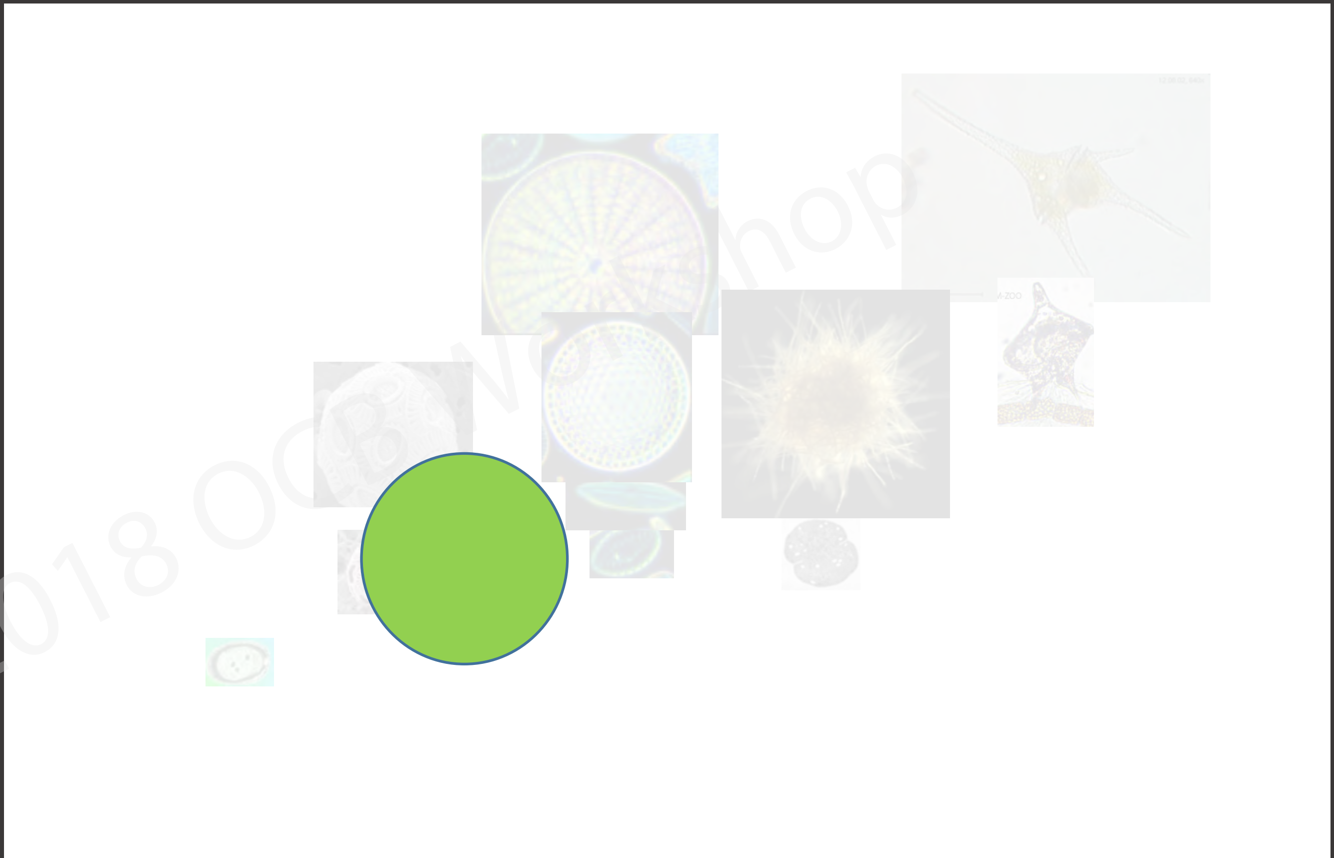
Global 3-D biogeochemical, ecosystem models

- What is state of the art in terms of diversity?

What is the state of the art?

Global 3-D biogeochemical, ecosystem models

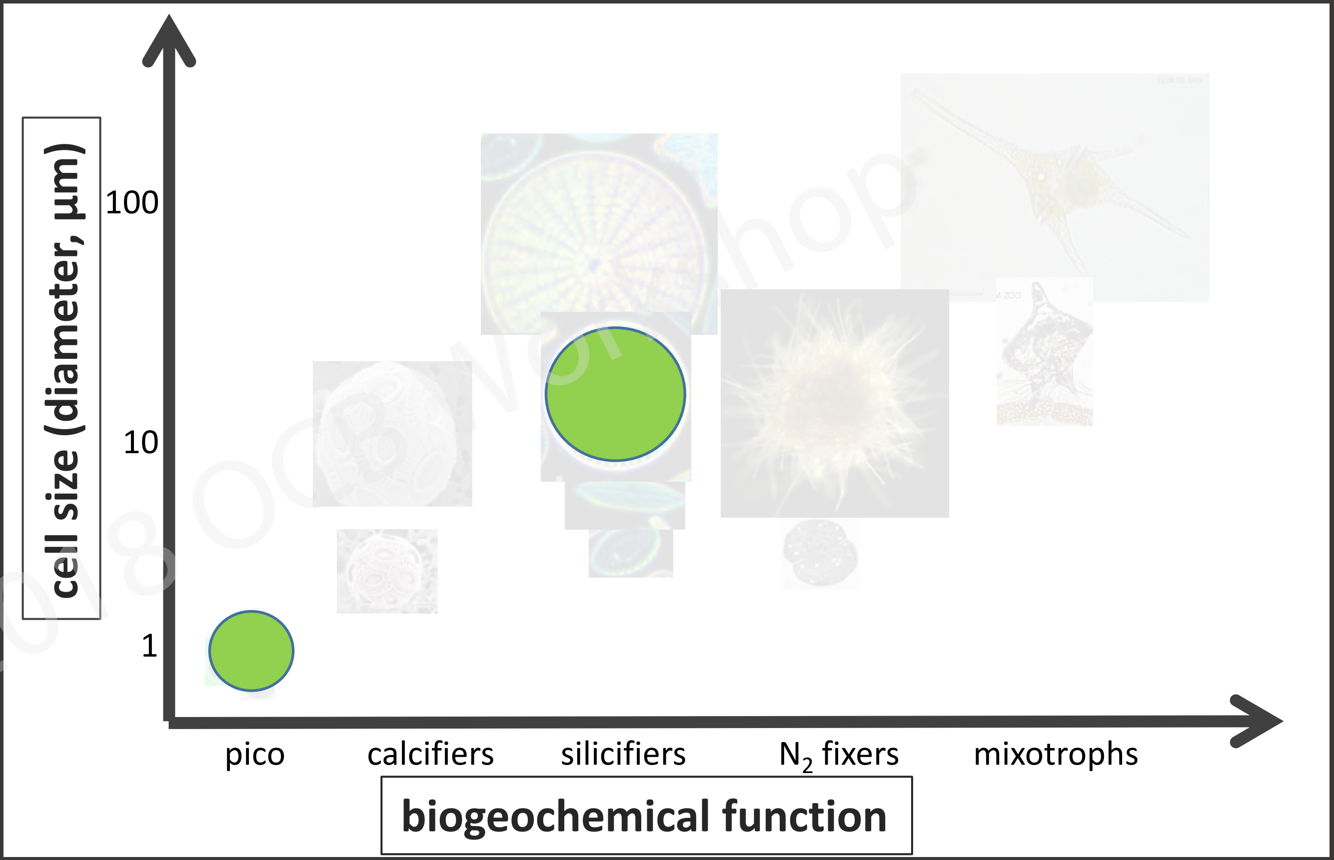
e.g. *Six and Maier-Reimer, GBC, 1996.*



What is the state of the art?

Global 3-D biogeochemical, ecosystem models

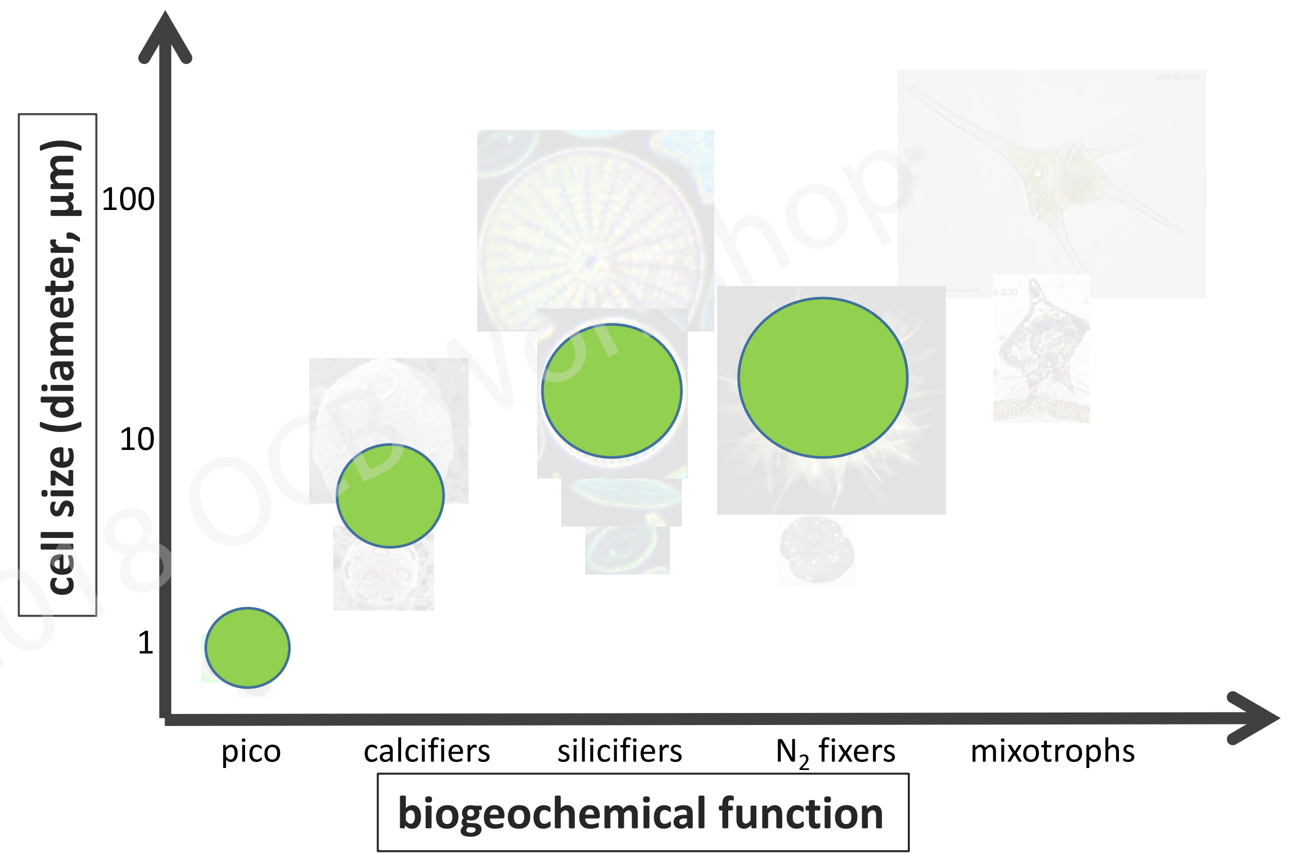
e.g. *Chai et al, 2002; Moore et al, 2002; Aumont et al, 2005; Dutkiewicz et al., 2005*



What is the state of the art?

Global 3-D biogeochemical, ecosystem models

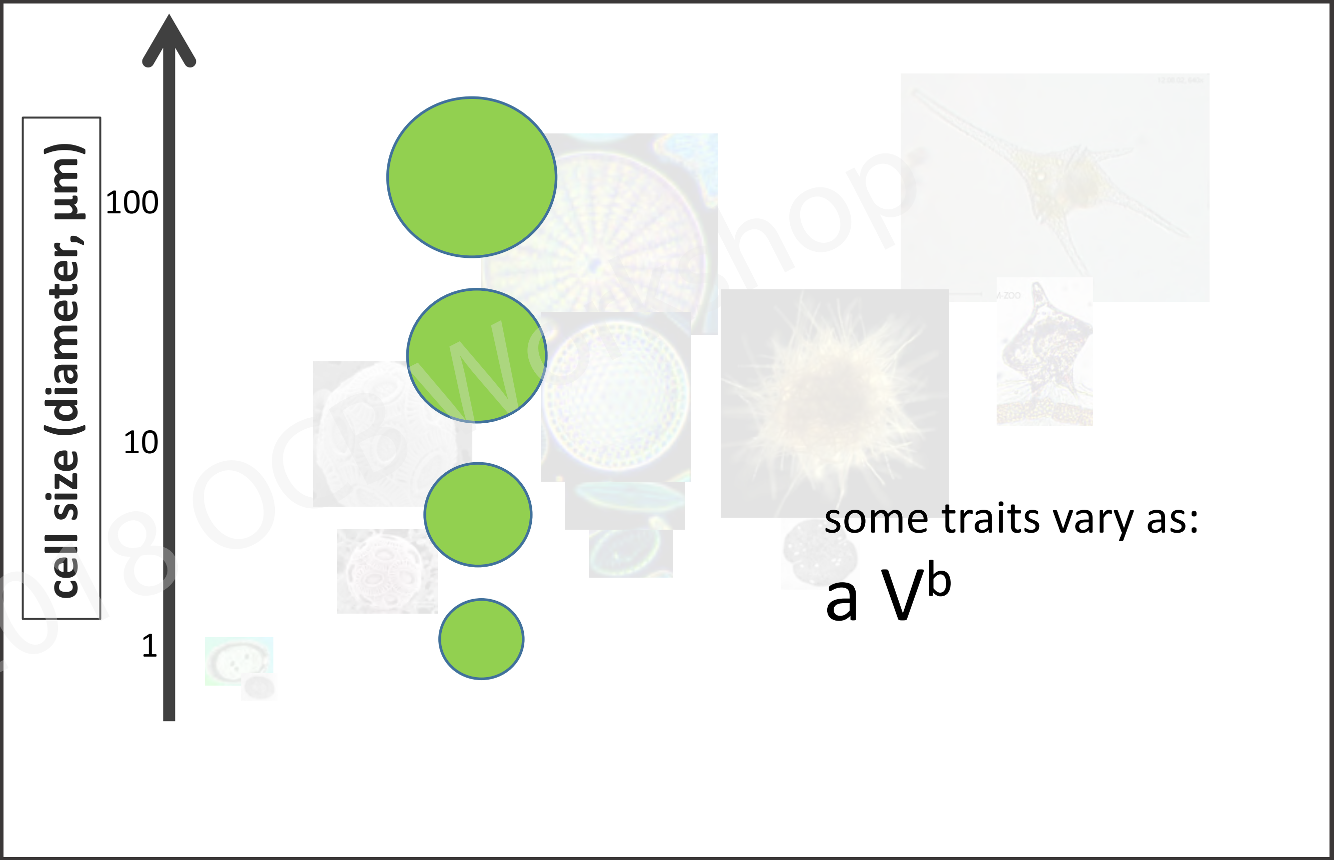
e.g. *Gregg et al, 2003; LeQuere et al 2005; Aumont et al, 2014; Dutkiewicz et al 2015*



What is the state of the art?

Global 3-D biogeochemical, ecosystem models

e.g. *Ward et al, L&O 2012*



some traits vary as:

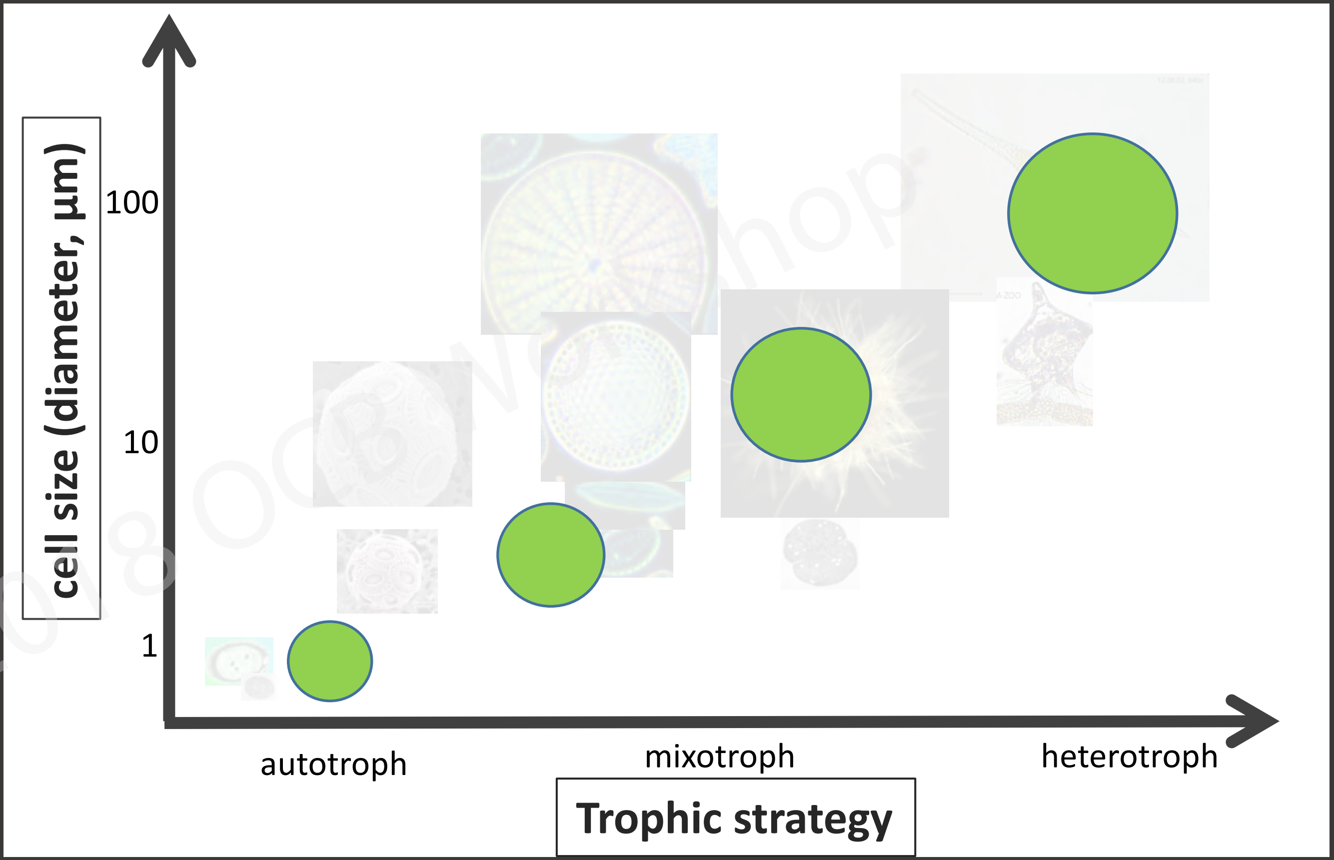
$a\ V^b$

Following from 0-D models: Moloney and Fields, 1991; Armstrong, 1994; Baird et al, 2007

What is the state of the art?

Global 3-D biogeochemical, ecosystem models

e.g. *Ward et al, PNAS, 2016*



What is the state of the art?

Global 3-D biogeochemical, ecosystem models

Current models have range of complexity, including:

- only a 2 or a handful functional types (many climate models)

- many types with more complex ecosystems
  - set traits (e.g. Ward et al, L&O, 2012
  - random assignment of traits

(e.g. Follows et al, Science 2007;
Coles et al, Science, 2017)

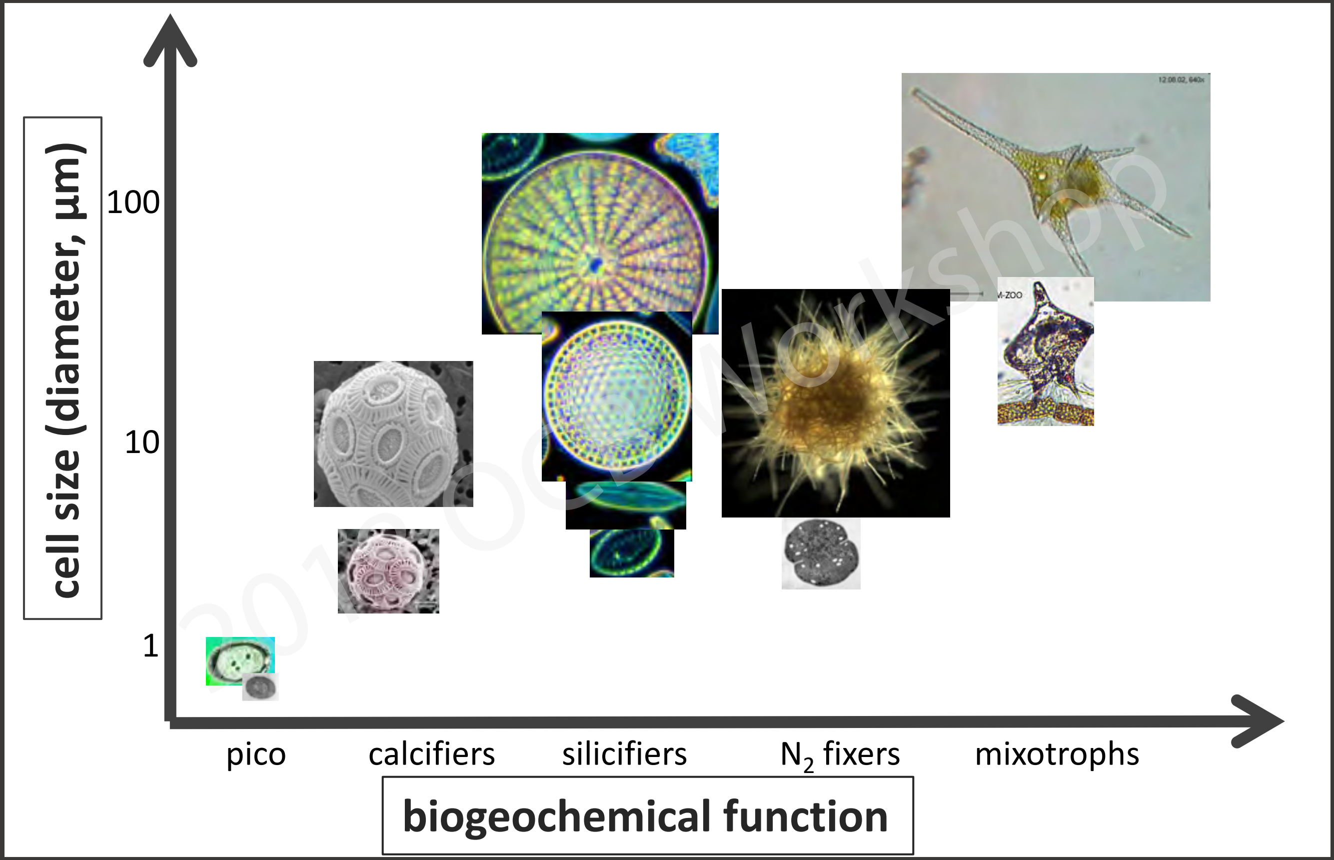
OUTLINE

Global 3-D biogeochemical, ecosystem models

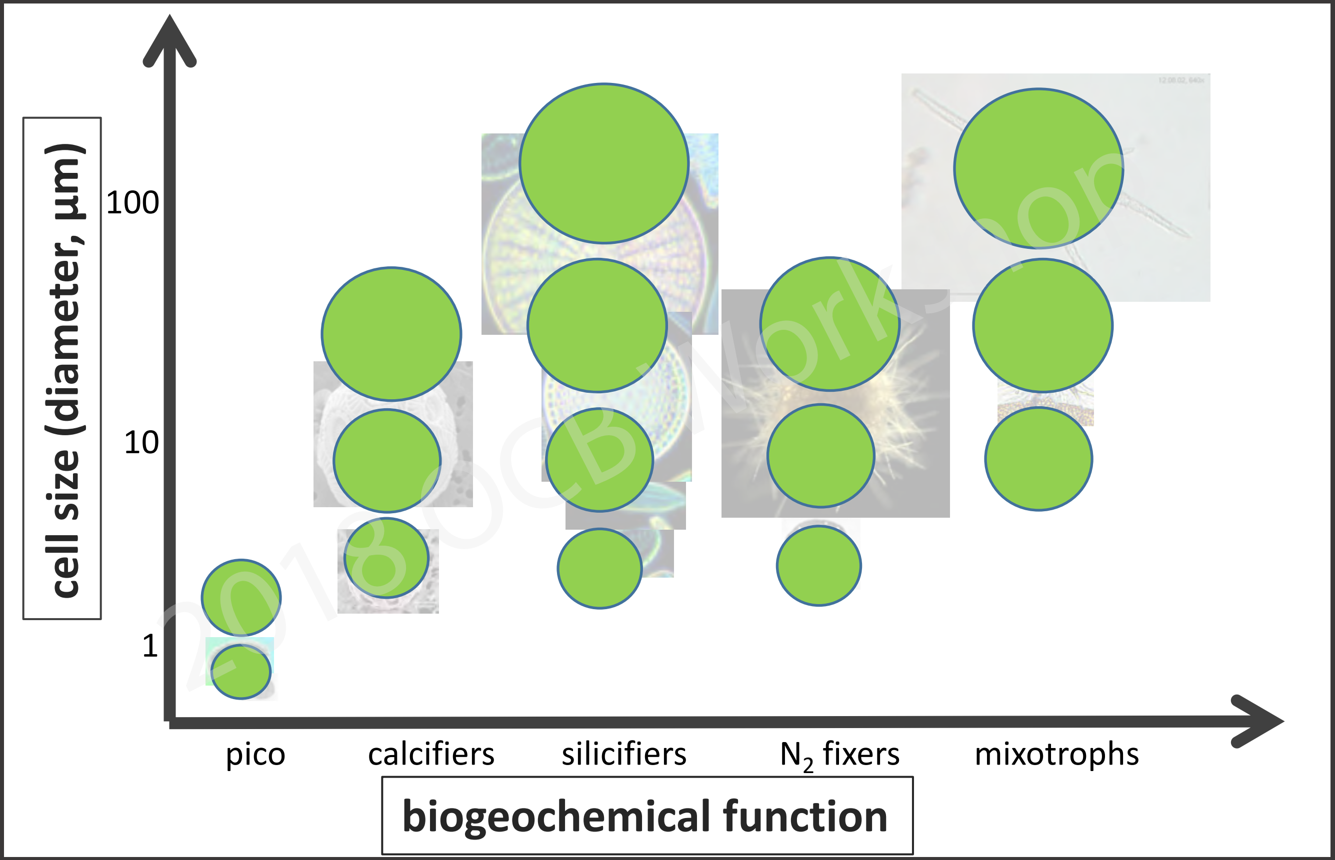
- What is state of the art in terms of diversity?

- Why including physiological diversity matters:
  - Example 1: size classes within functional groups
  - Example 2: trophic strategy
  - Example 3: symbiosis

PHYSIOLOGICAL DIVERSITY MATTERS



EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS



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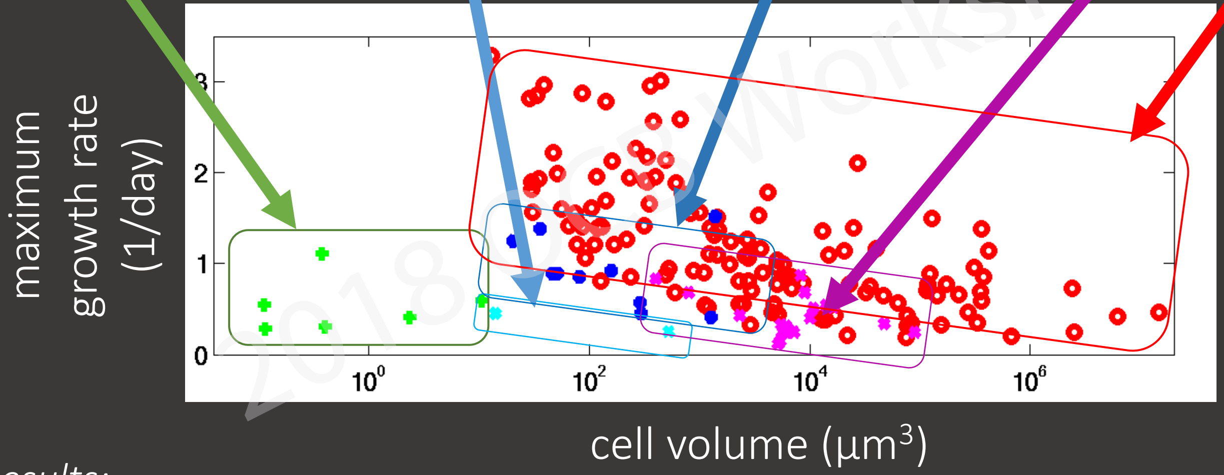


Change in slope for pico-phytoplankton:
deLong et al, PNAS, 2010
Kempes et al, PNAS, 2012
Maranon et al, Ecol. Let., 2013

Cost of Nitrogen Fixation:
Fu et al, J Phy, 2005
Goebel et al, J Phy, 2008
Inomura et al, ISME, 2016

Cost of Calcification:
Anning et al, JMR, 1996; Raven and Crawfurd, MEPS, 2012; Brownlee et al, 2004; Monteiro et al, Science Advances, 2016

Mixotrophy
Litchman et al, Ecol Let, 2007:

Diatoms:
Raven et al, Bio Rev, 1983

$a V^b$

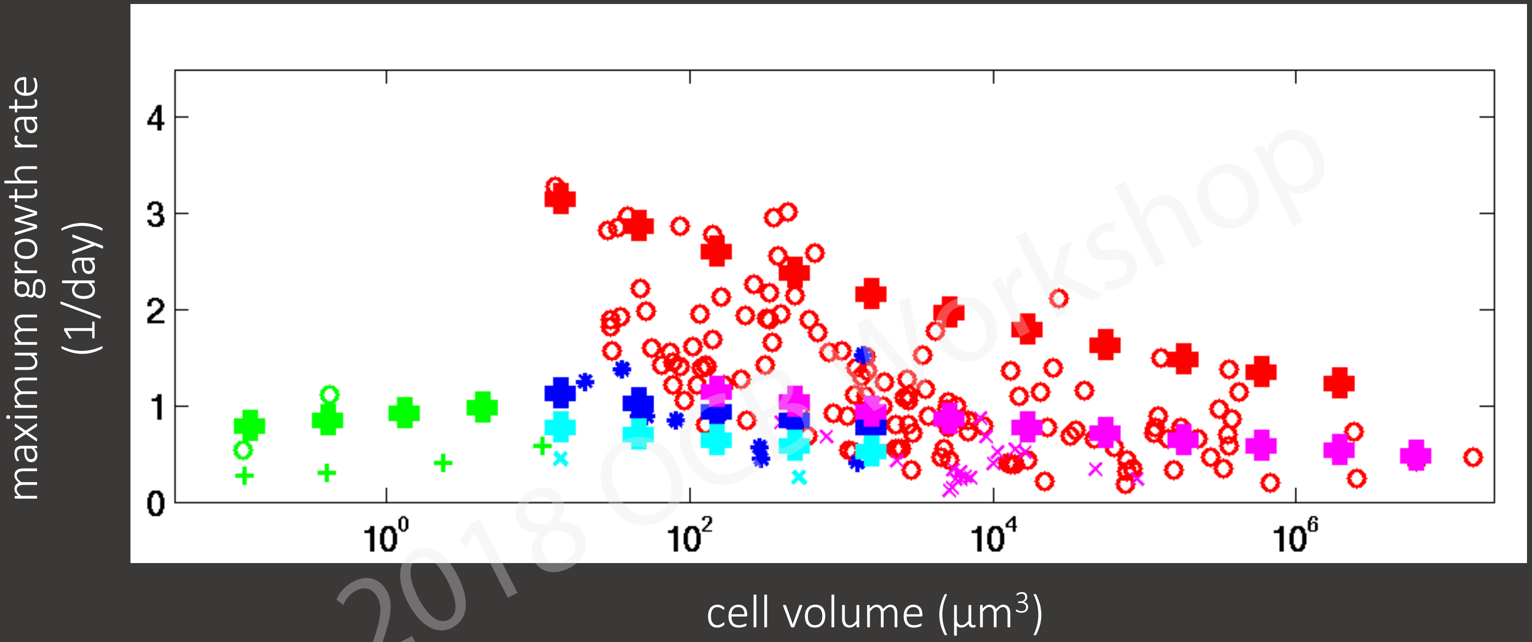
Laboratory Results:
Tang, 1995;
Maranon et al 2013;
Sarthou et al 2005;
Buitenhuis et al, 2008

pico-phytoplankton
diazotroph
coccolithophore
diatom
dinoflagellate

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

small symbols are observations,
bolder crosses are model organisms

aV^b



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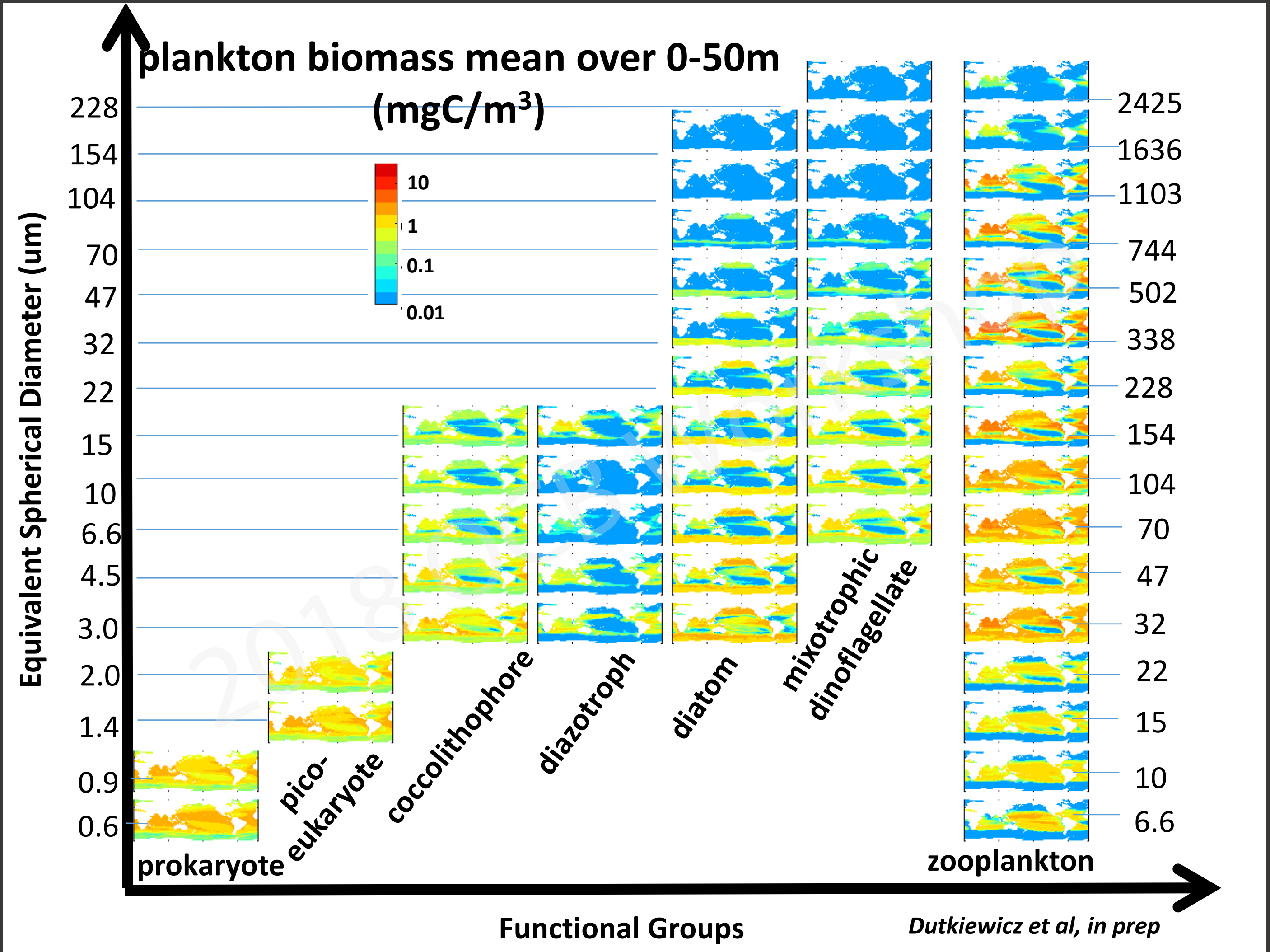
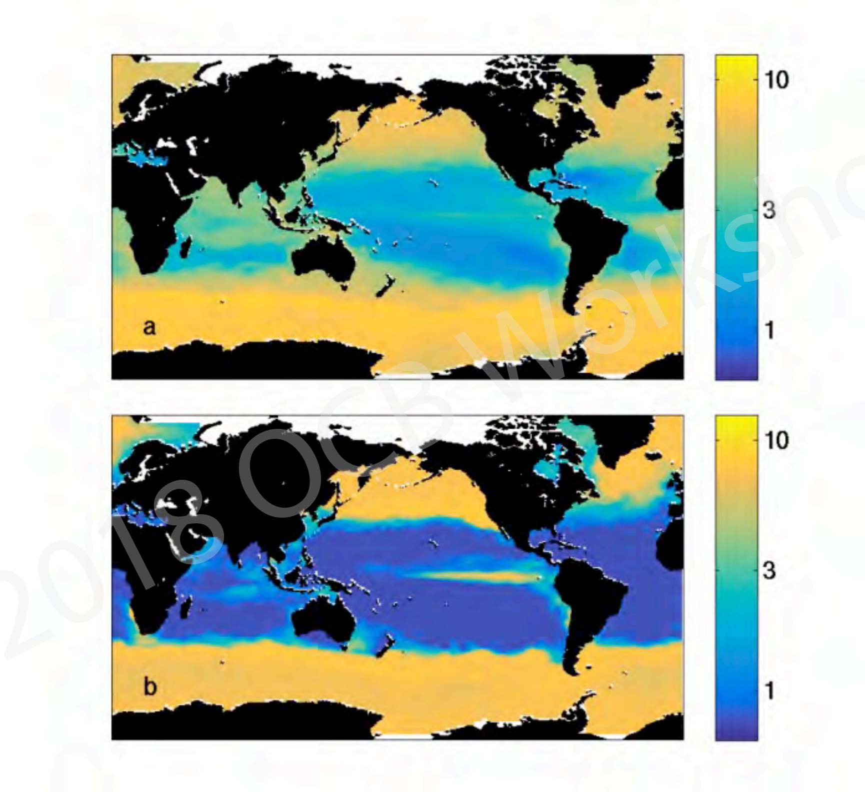


Dutkiewicz et al, in prep

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

mean equivalent spherical diameter (um)



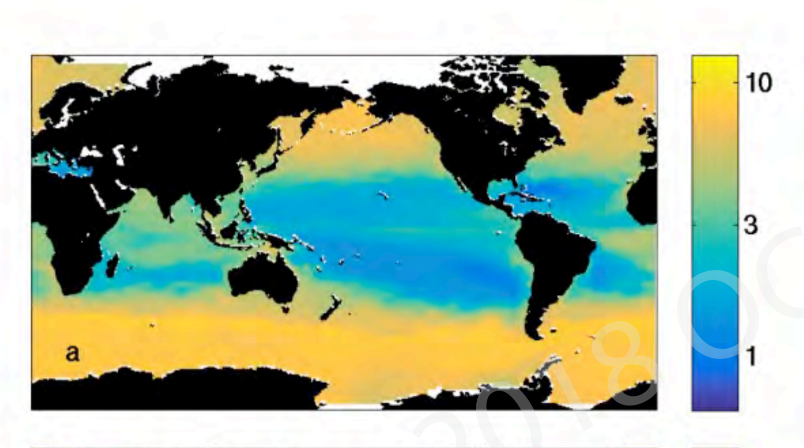
Simulation with size classes within functional groups

More traditional PFT model, with 2 functional types and 1 zooplankton

Treguer et al, Nat Geo, 2018

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

present day biomass weighted mean cell diameter (um)



Dutkiewicz et al, in prep

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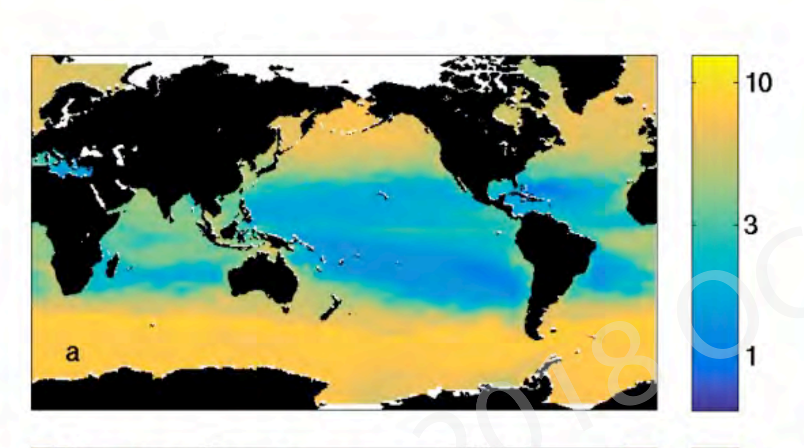


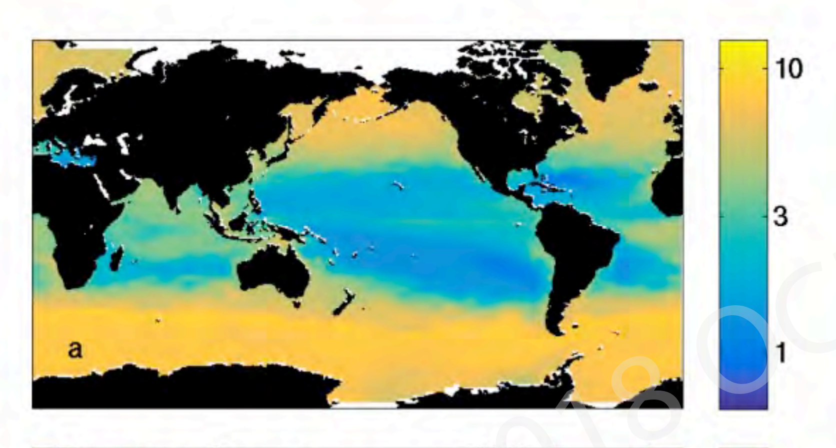
"Business as usual" climate change scenario:

- Warmer waters
- Increased stratification
- Alterations to circulation

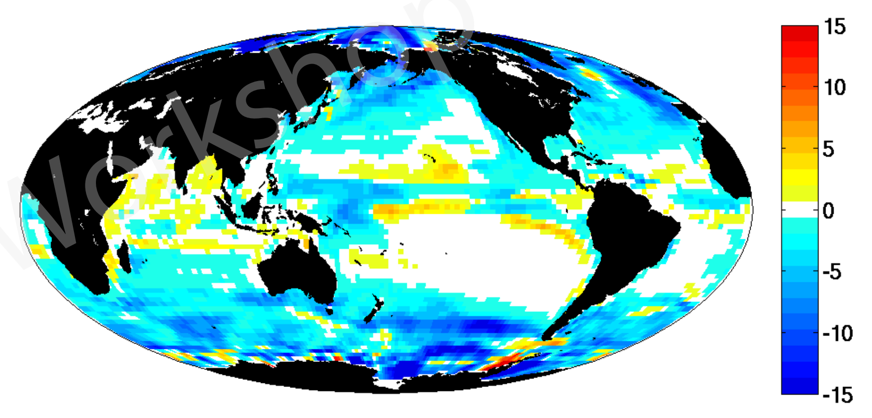
Dutkiewicz et al, in prep

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

present day biomass weighted mean cell diameter (um)



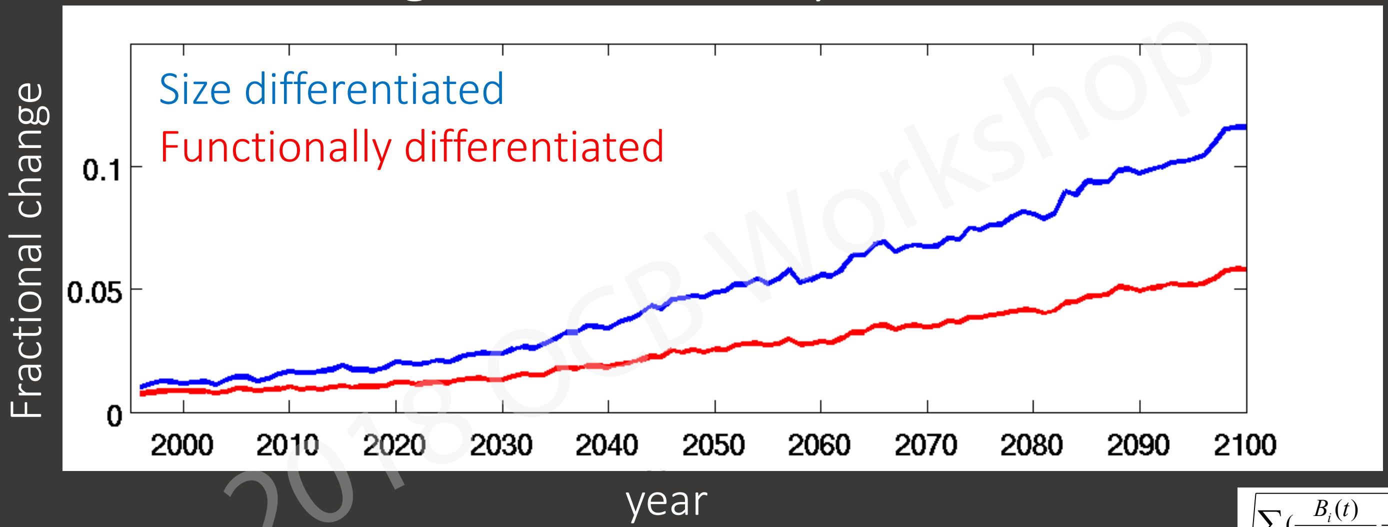
change in cell diameter (um)
(2100 – 1860)



- Trend towards smaller cells with lower nutrient supply
- Global average decrease of 2um by 2100
- In some regions >10um decrease

Dutkiewicz et al, in prep

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS



Change in Community Structure

$$\sqrt{\sum\left(\frac{B_i(t)}{\sum_i B_i(t)} - \frac{B_i(t=0)}{\sum_i B_i(t=0)}\right)^2}$$

B is biomass in group

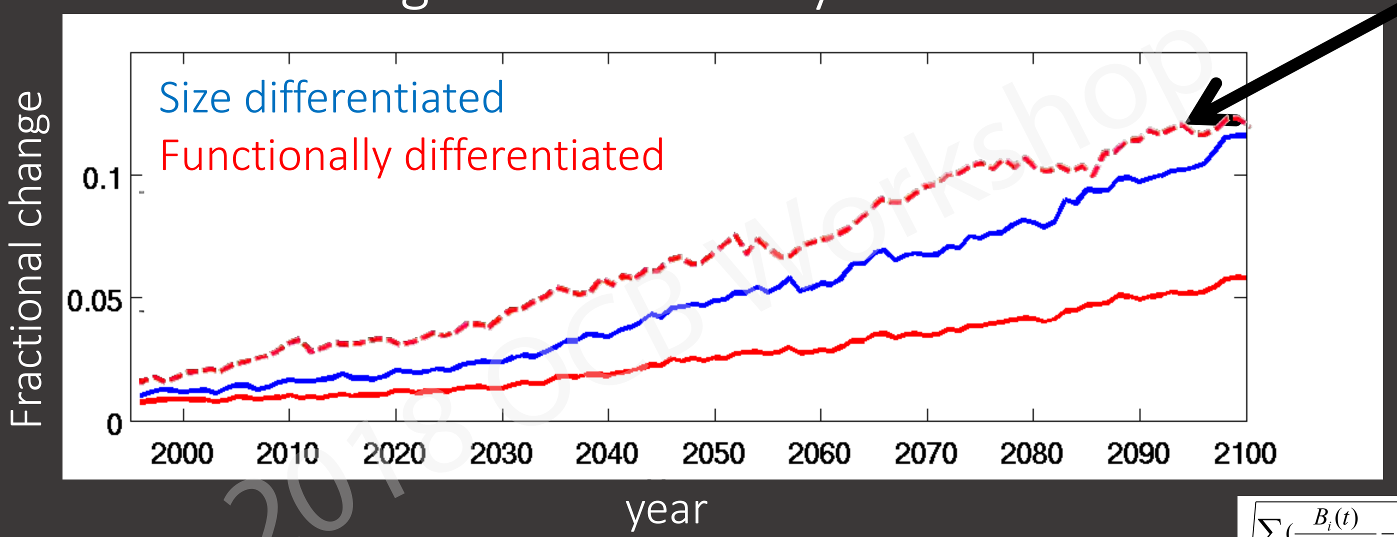
0= community is same as pre-industrial

1= community is completely different to pre-industrial

Dutkiewicz et al, in prep

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

Change in Community Structure



classical PFT model, with 2 P and 1 Z

$$\sqrt{\sum\left(\frac{B_i(t)}{\sum_i B_i(t)}-\frac{B_i(t=0)}{\sum_i B_i(t=0)}\right)^2}$$

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Dutkiewicz et al, in prep

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

Climate Change Scenario:

- decrease in mean cell size; large in some regions (with consequences for higher trophic levels)
- size distribution changes ≠ functional change
- including only functional diversity over-estimates functional changes (with consequences for export and feedback to climate system)

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

Climate Change Scenario:

- decrease in mean cell size; large in some regions
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- including only functional diversity over-estimates functional changes
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What would happen if we included evolution?

EXAMPLE 2: TROPHIC STRATEGY

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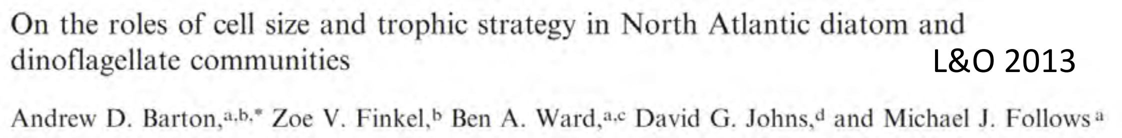
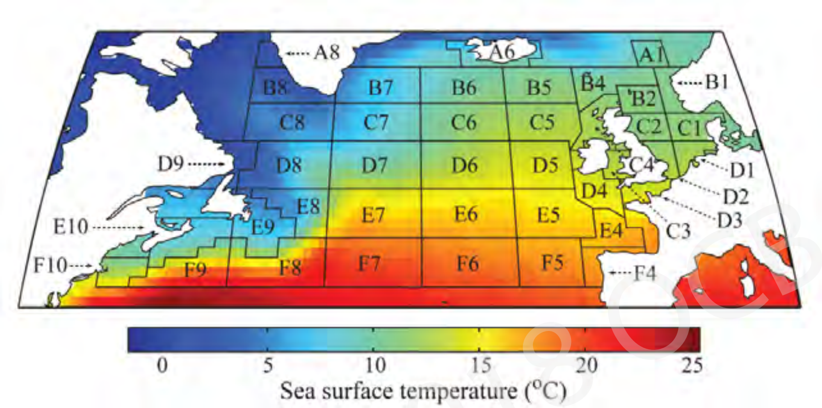
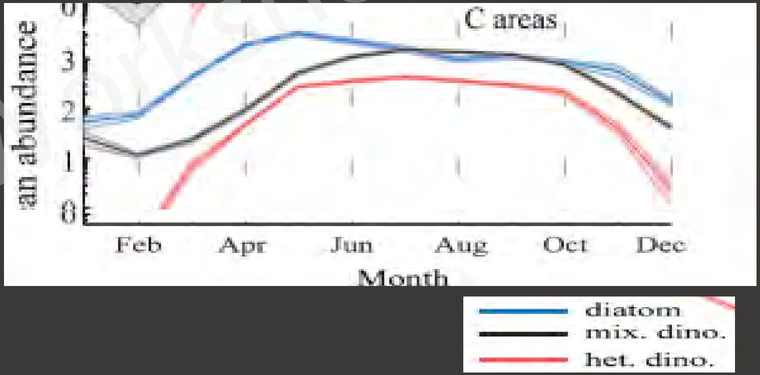

On the roles of cell size and trophic strategy in North Atlantic diatom and dinoflagellate communities

L&O 2013

Andrew D. Barton,[a,b,*] Zoe V. Finkel,[b] Ben A. Ward,[a,c] David G. Johns,[d] and Michael J. Follows[a]

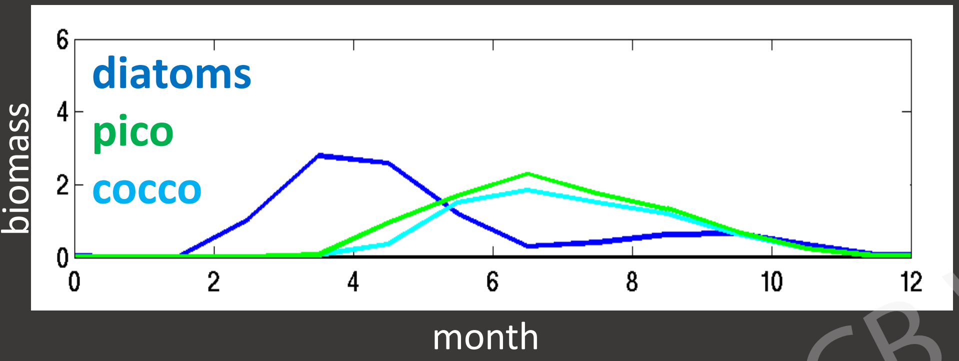


Continuous Plankton Recorder (CPR) data



EXAMPLE 2: TROPHIC STRATEGY

Simulation without mixotrophy



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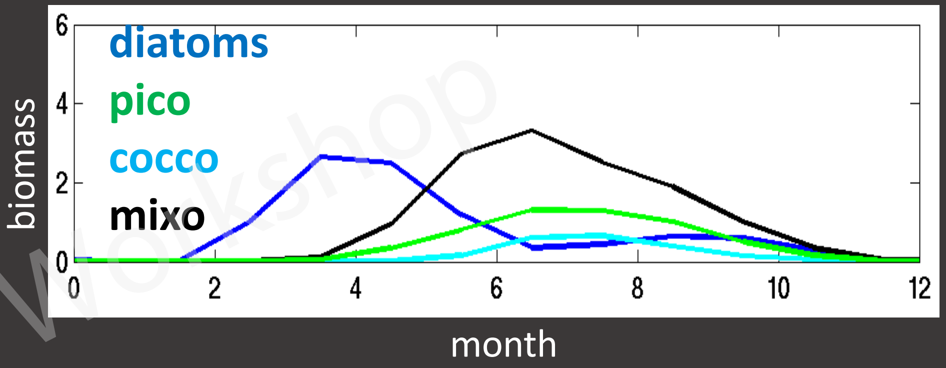

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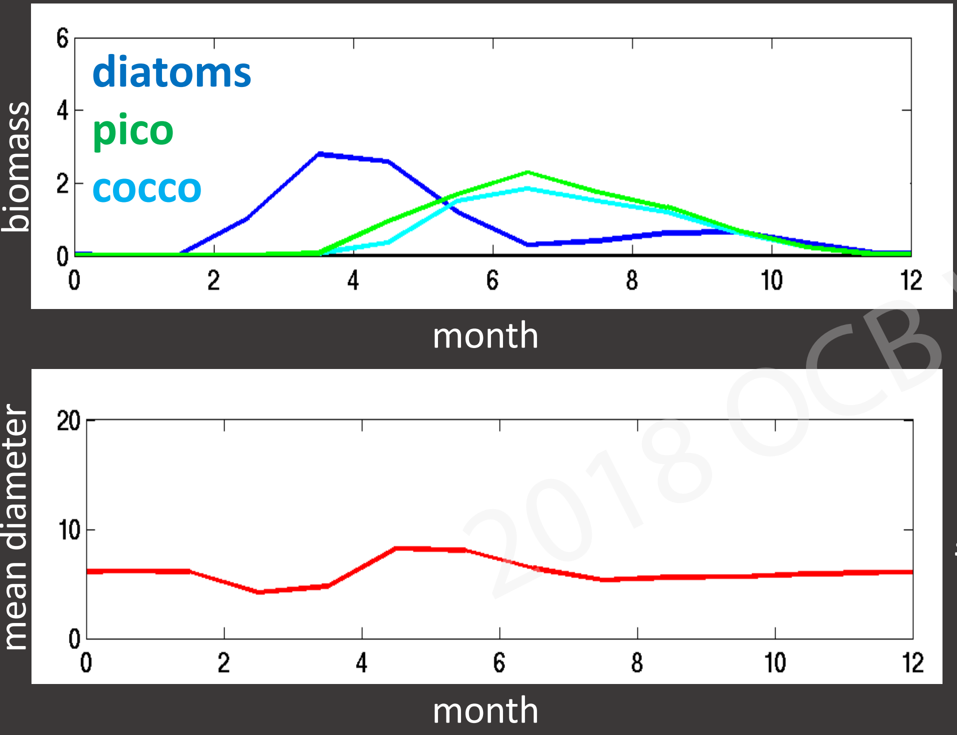
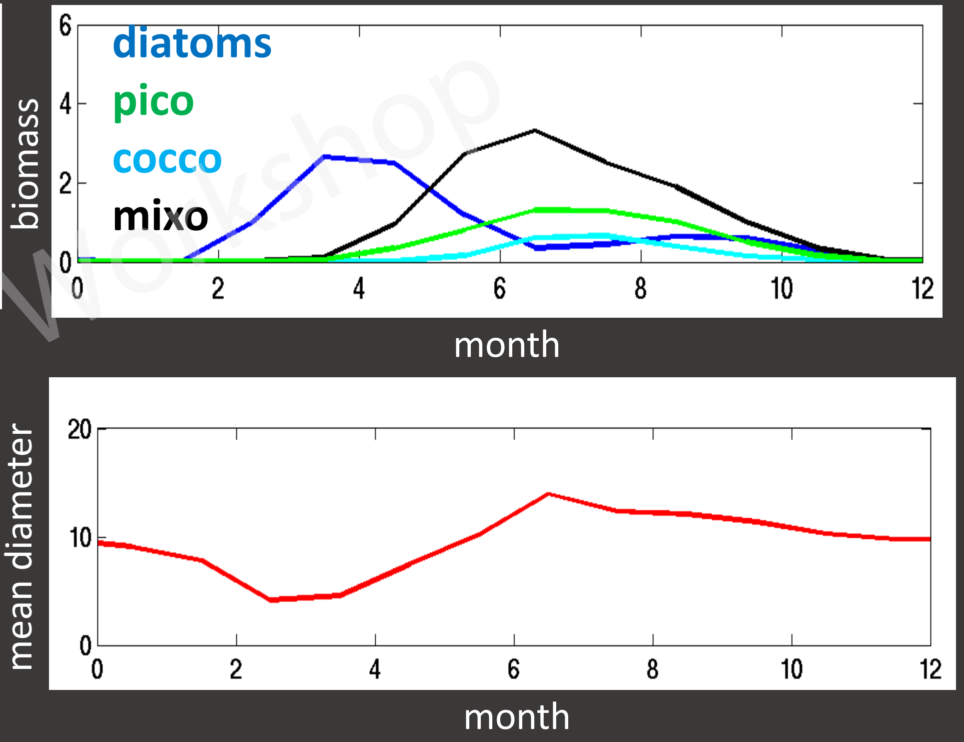
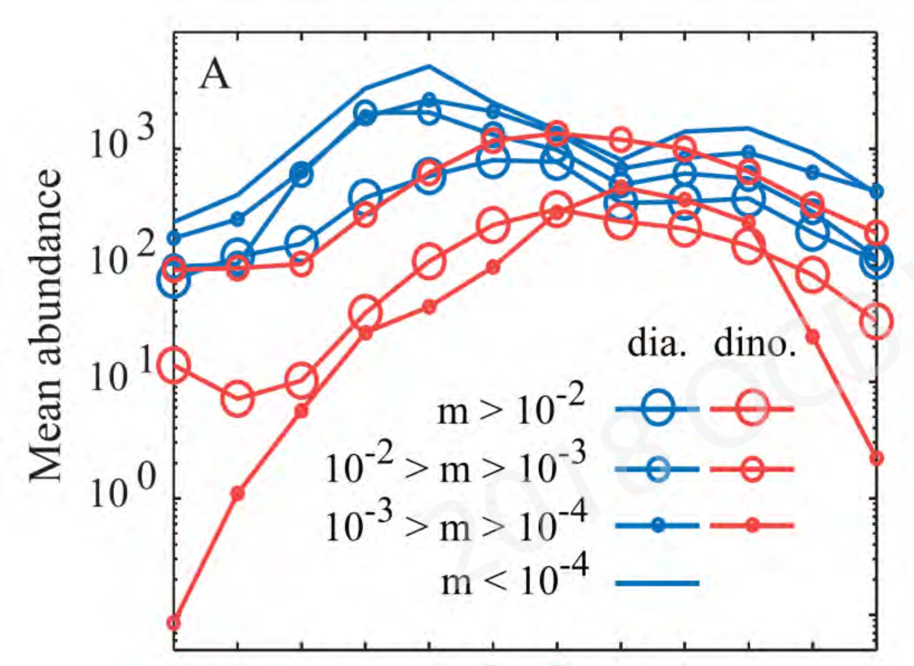


Simulation with mixotrophy



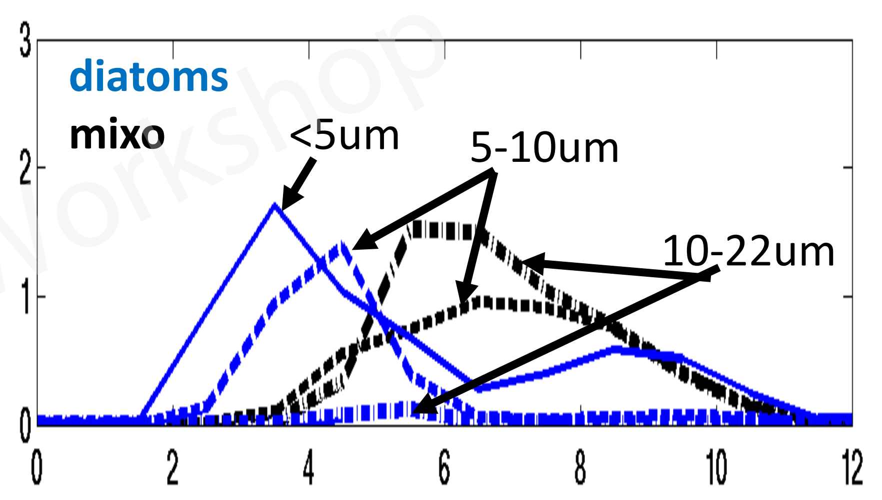
EXAMPLE 2: TROPHIC STRATEGY

CPR OBSERVATIONS



Barton et al, L&O, 2013

Simulation with mixotrophy



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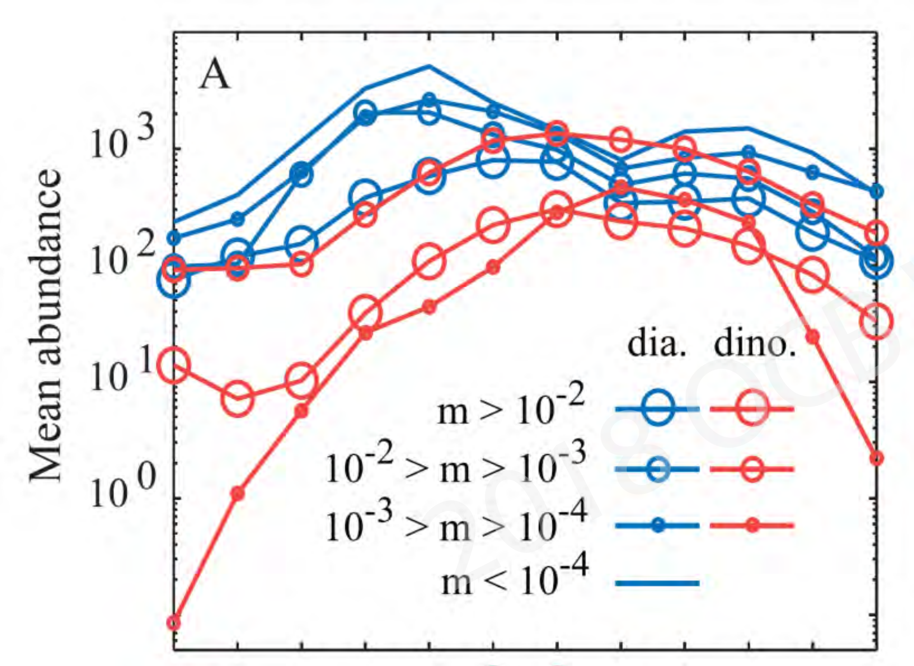

Barton et al, L&O, 2013

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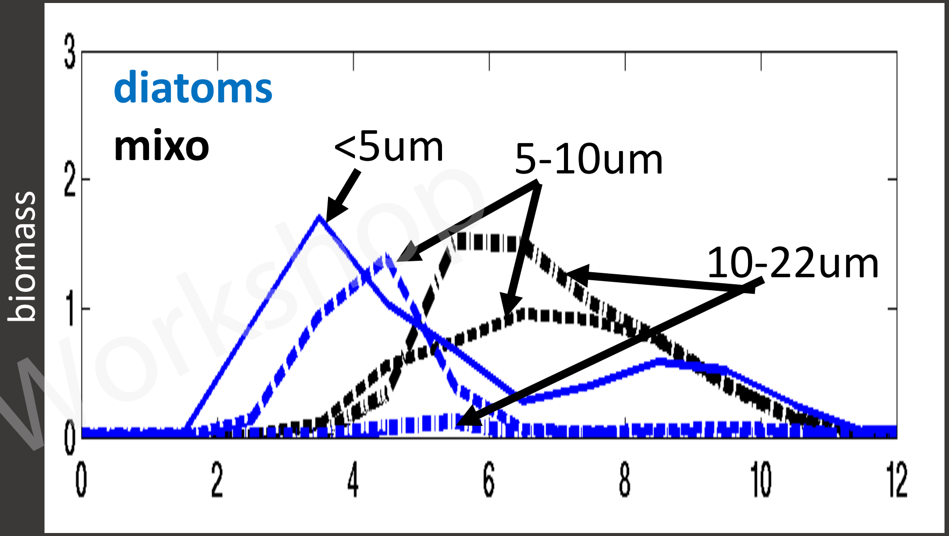

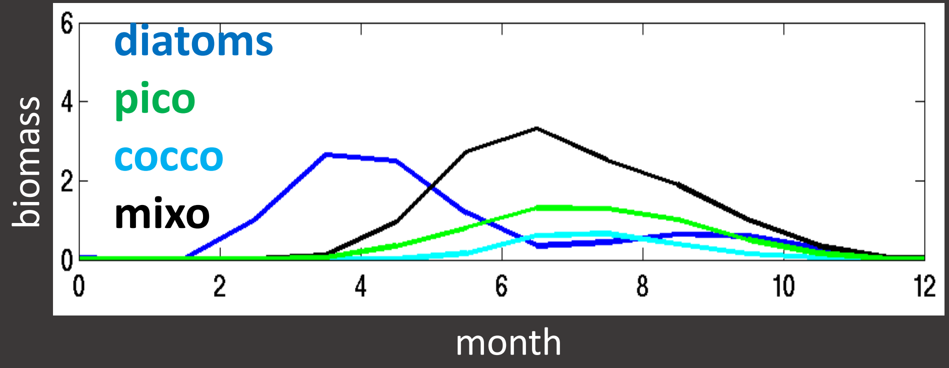

EXAMPLE 2: TROPHIC STRATEGY

Including mixotrophy:

- allows for larger cells to survive
  (with consequences for higher trophic levels and carbon export – see Ward and Follows, PNAS, 2016)
- it also changes the seasonal timing of the largest size
  (with consequences for higher trophic levels)
- allows laboratory to understand timing of size/functional distributions

EXAMPLE 3: SYMBIOISIS

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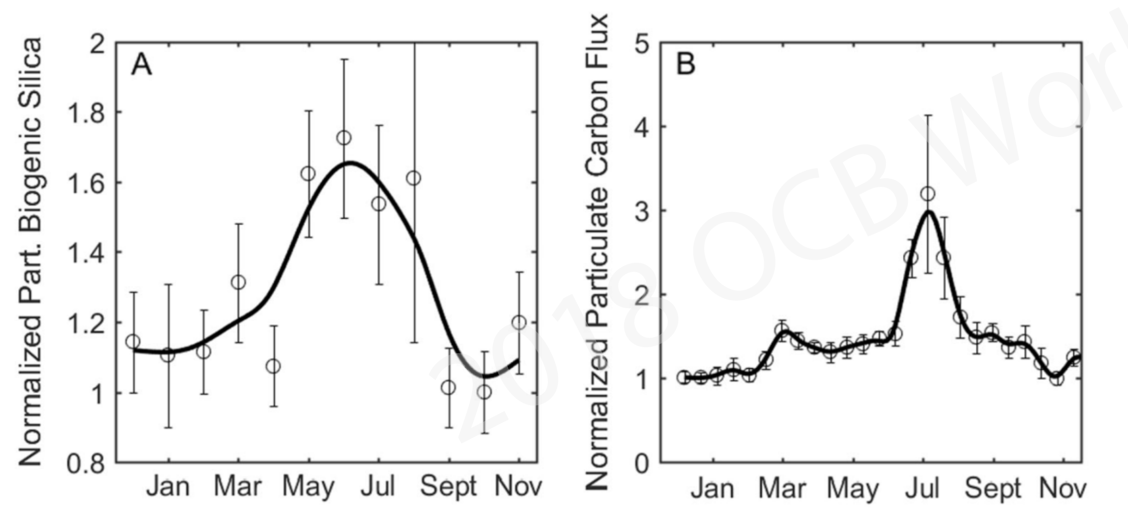
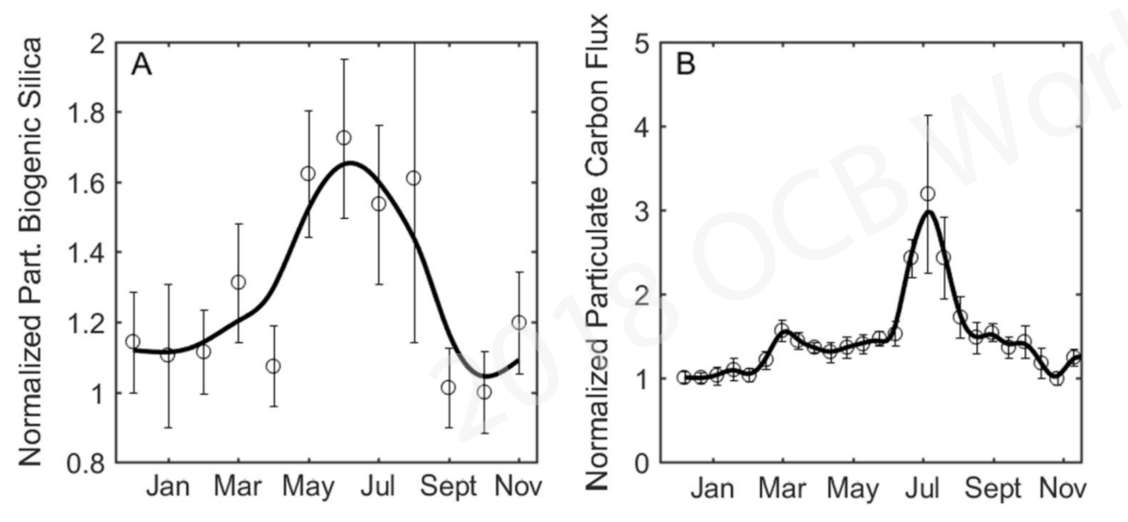


Follett et al, ISME J, 2018

Station Aloha
Observations

EXAMPLE 3: SYMBIOISIS

Station Aloha
Observations



Follett et al, ISME J, 2018

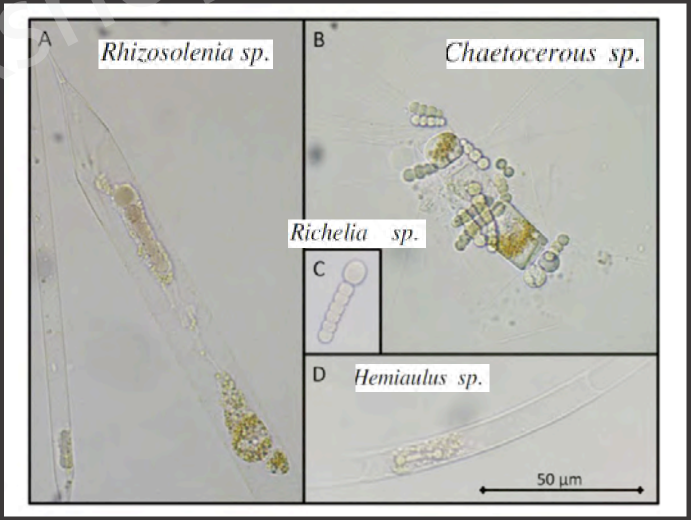
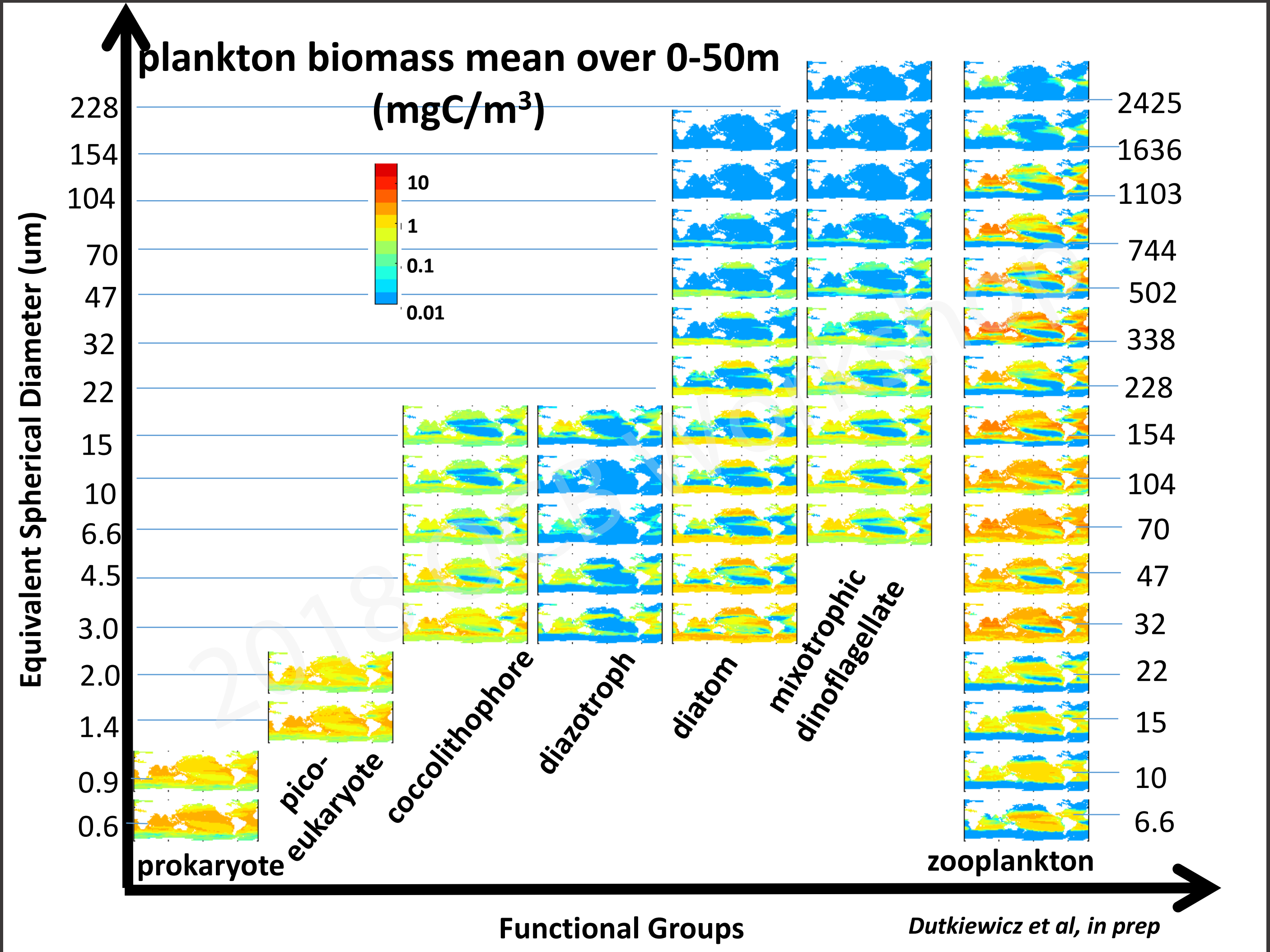


Photo: Chris Follett

EXAMPLE 3: SYMBIOISIS



Dutkiewicz et al, in prep

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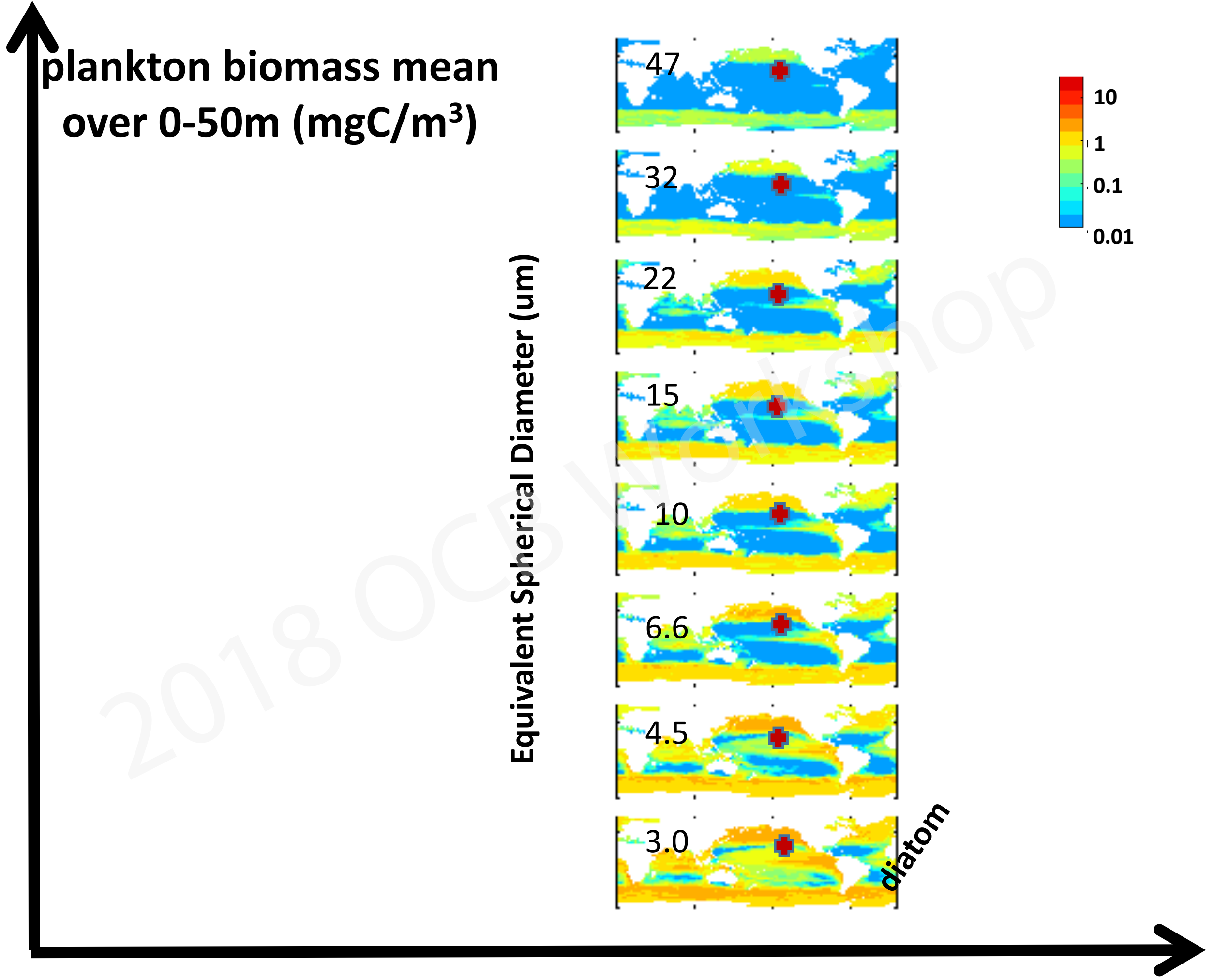


plankton biomass mean over 0-50m (mgC/m^3)

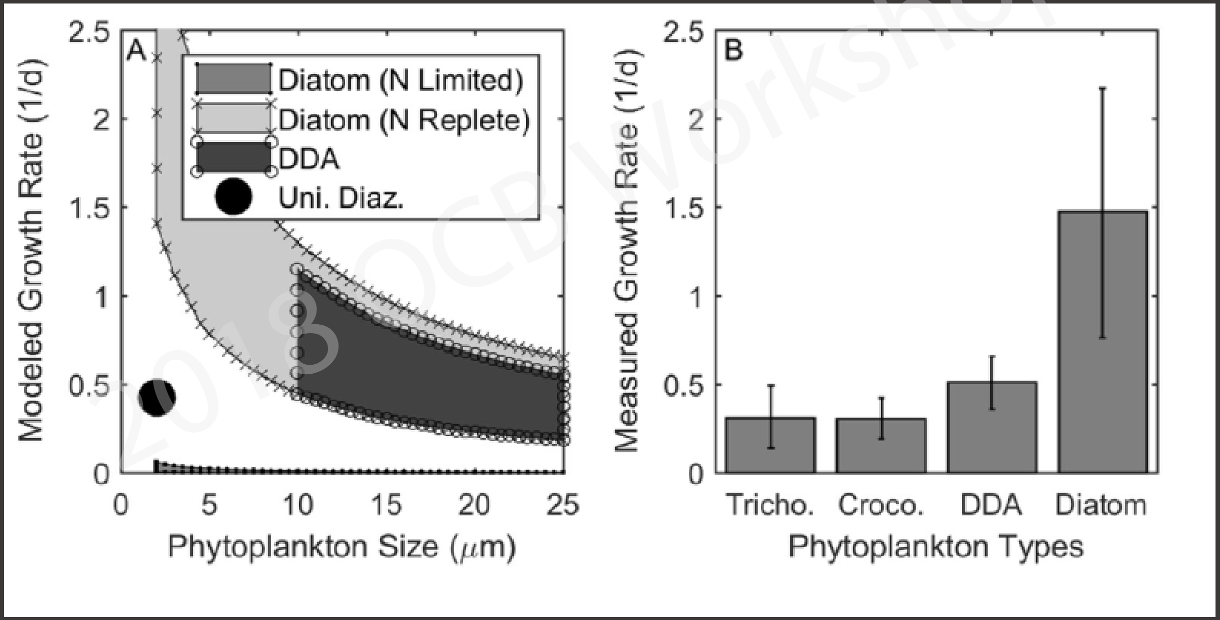
Dutkiewicz et al, in prep

EXAMPLE 3: SYMBIOISIS

Seasonal resource conditions favor a summertime increase in North Pacific diatom–diazotroph associations

Christopher L. Follett[1] · Stephanie Dutkiewicz[1] · David M. Karl[2,3] · Keisuke Inomura[1] · Michael J. Follows[1]

ISME Journal, 2018



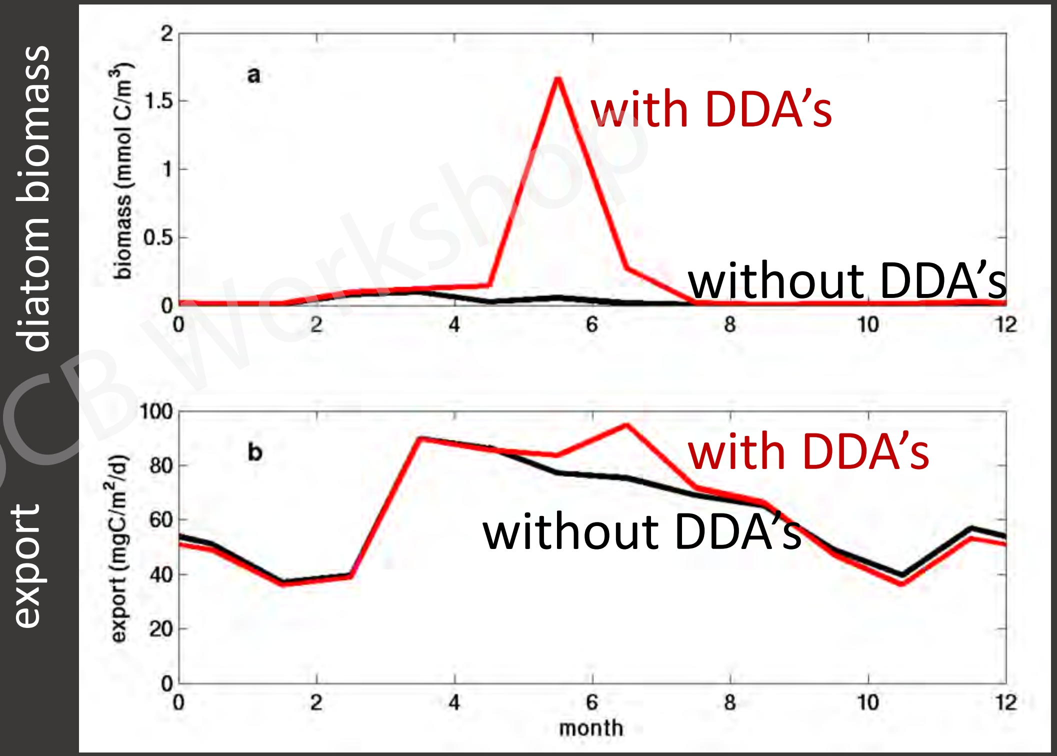
EXAMPLE 3: SYMBIOISIS

Treguer et al, Nat Geo, 2018

EXAMPLE 3: SYMBIOISIS

Large diatoms exist in oligotrophic regions due to symbiosis with nitrogen fixers,

With consequences to food web and carbon export



Treguer et al, Nat Geo, 2018

Note: this includes non-negative interactions
- see also poster by B.B. Cael

SUMMARY

The next generation of ecosystem models need to include diversity of physiological strategies:

- in order to obtain more realistic size structuring
- to capture the appropriate shifts in communities with climate change

- and consequences for higher trophic levels and carbon export

OUTLINE

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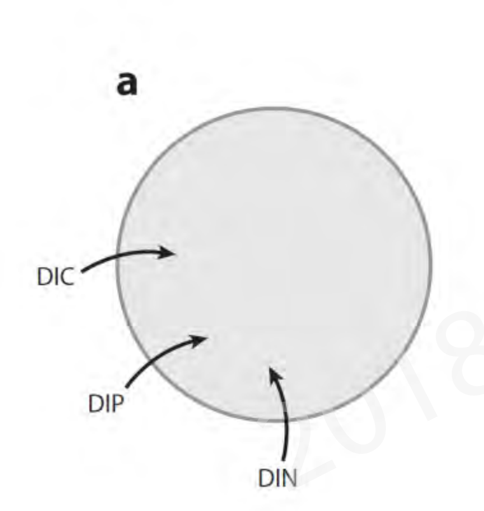
- What is state of the art in terms of diversity?

- Why including physiological diversity matters?
  - some examples

- Other aspects of physiological parameterization
  - flexible stoichiometry
  - treatment of multiple limiting factors

What is the state of the art?

Monod Kinetics
(fixed cell quotas)



C:N:P:Fe ~ 120:16:1:1e-3

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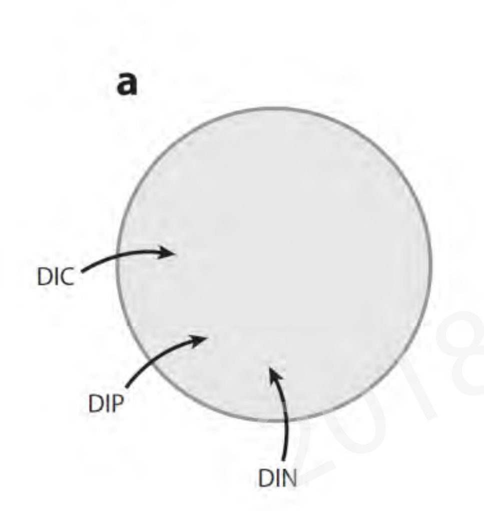


C:N:P:Fe ~ 120:16:1:1e-3

Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter

Adam C. Martiny[1,2], Chau T. A. Pham[1], Francois W. Primeau[1], Jasper A. Vrugt[1,3], J. Keith Moore[1], Simon A. Levin[4] and Michael W. Lomas[5]*†

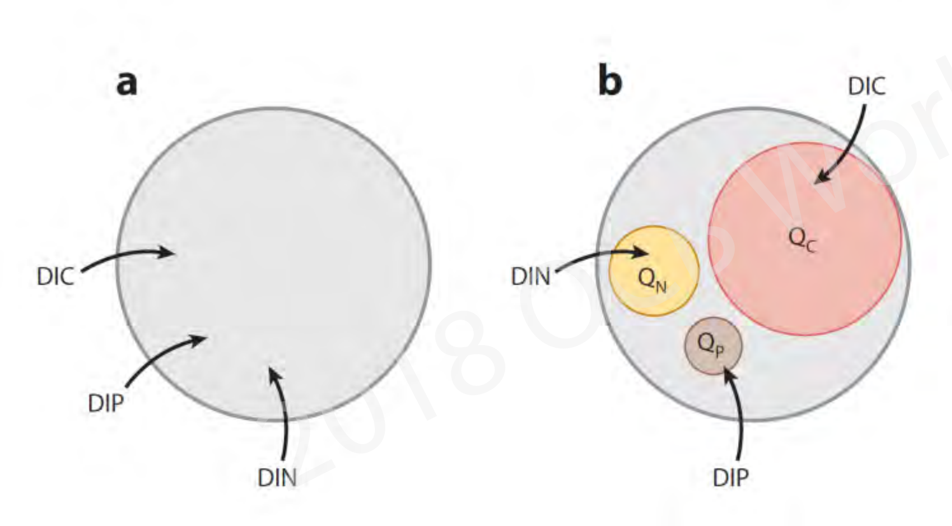
Nat Geo 2013

C:N:P ~ 195:28:1 subtropics
137:18:1 warm upwelling
78:13:1 polar

What is the state of the art?

Monod Kinetics
(fixed cell quotas)

Droop/Caperon Kinetics
(variable cell quotas)



Droop (1968), Caperon
stoichiometry function of
environment

Shuter, 1979, Geider et al 1998,
Pahlow 2005:
stoichmetry function of
cell attributes

Several 3-D model include flexible Fe and Si,
but few have full flexible C:N:P

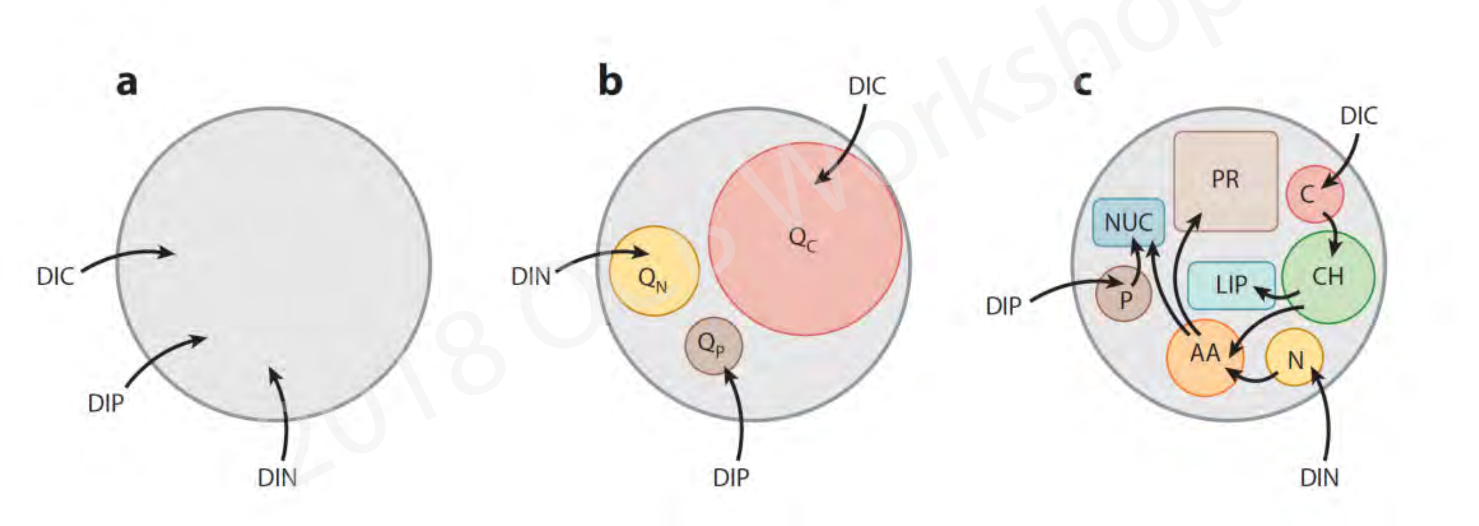
Though see Chai-Te Chien’s poster

What is the state of the art?

Monod Kinetics
(fixed cell quotas)

Droop/Caperon Kinetics
(variable cell quotas)

Macromolecular
Approach



Follows and Dutkiewicz, Ann Rev Mar Sci, 2011

What is the state of the art?

<u>Single cell approach</u>:

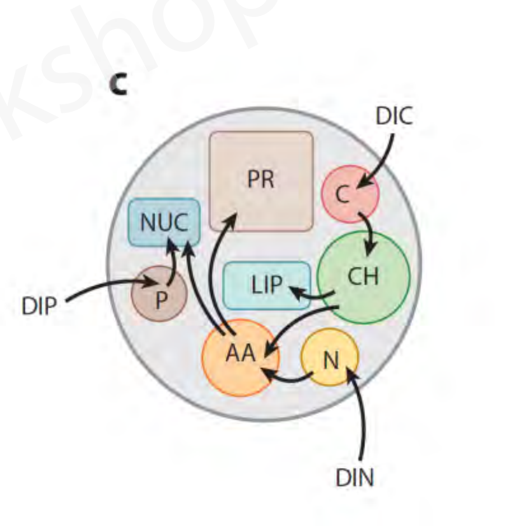
- Inomura et al, ISME, 2016
- Inomura et al, in prep

- See posters:
  Anne-Willem Omta
  B.B. Cael

<u>Inclusion in 3-D model</u>:

Kei Inomura (post-doc UW) including this as parameterization in 3-D model

Macromolecular Approach



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What is the state of the art?

Growth rate:

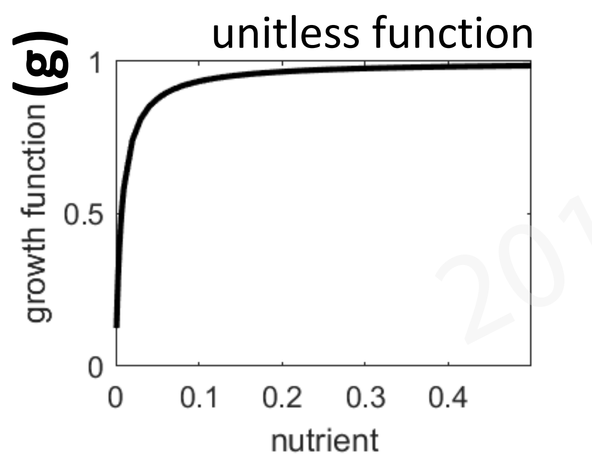
$$\mu = \mu_{max} f(N, P, Fe, I, T, \ldots)$$

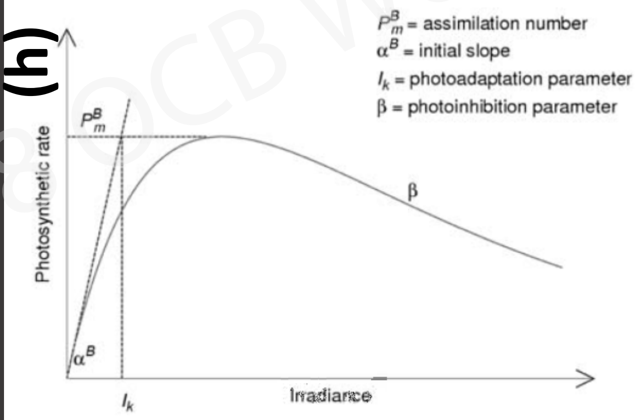
What is the state of the art?

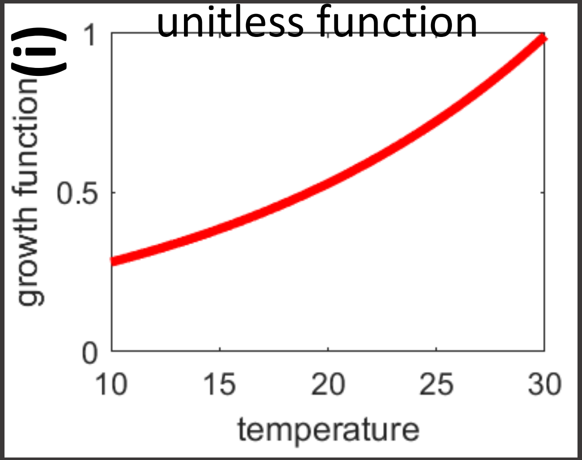
Growth rate:

$$\mu = \mu_{max} f(N, P, Fe, I, T, \dots)$$

$$= \mu_{max}\ \mathrm{min(g(N,P,Fe))}\ \ \mathrm{h(I)}\ \ \ \mathrm{i(T)}$$







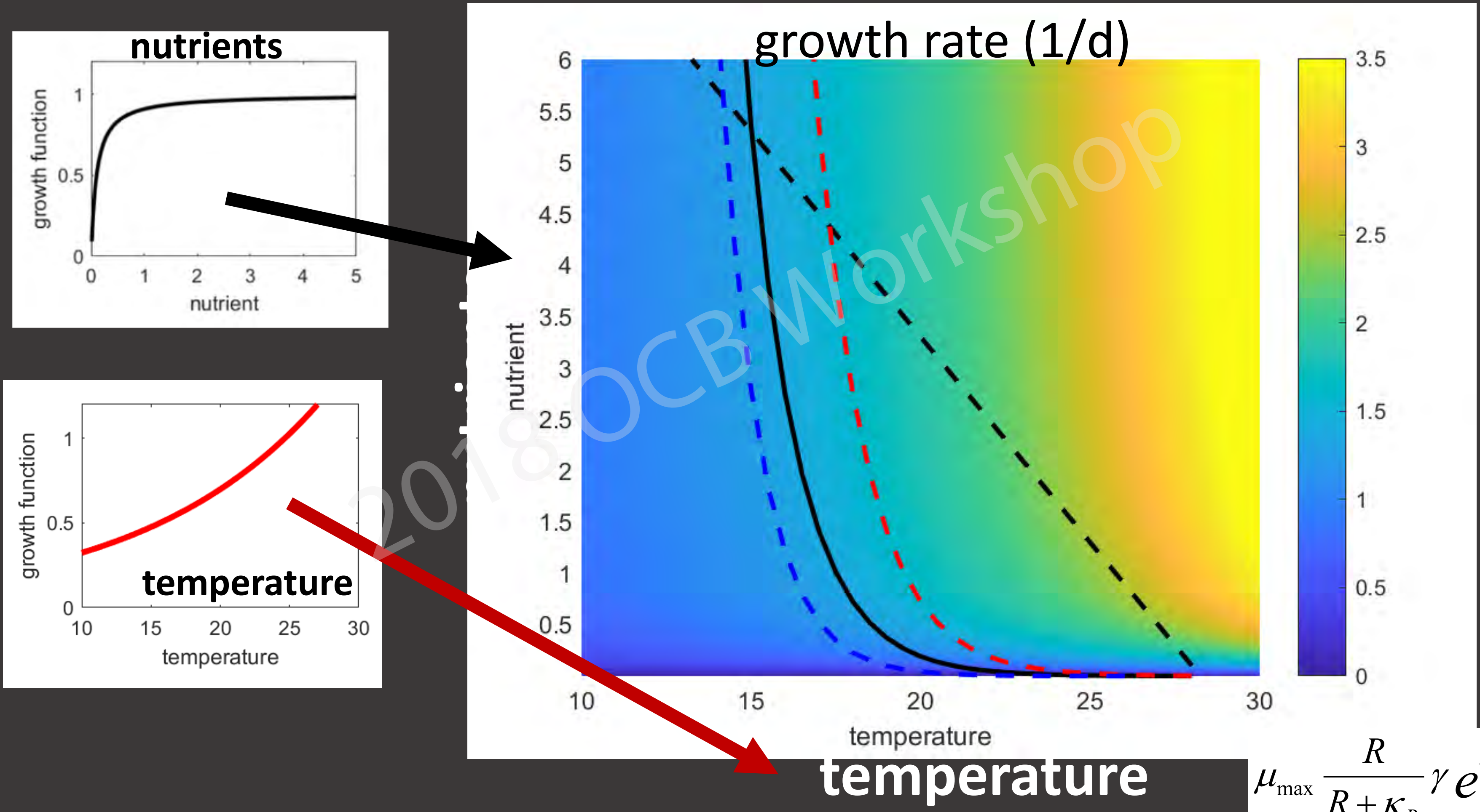
What is the state of the art?

Growth rate:

$$\mu = \mu_{max} f(N, T, \ldots)$$

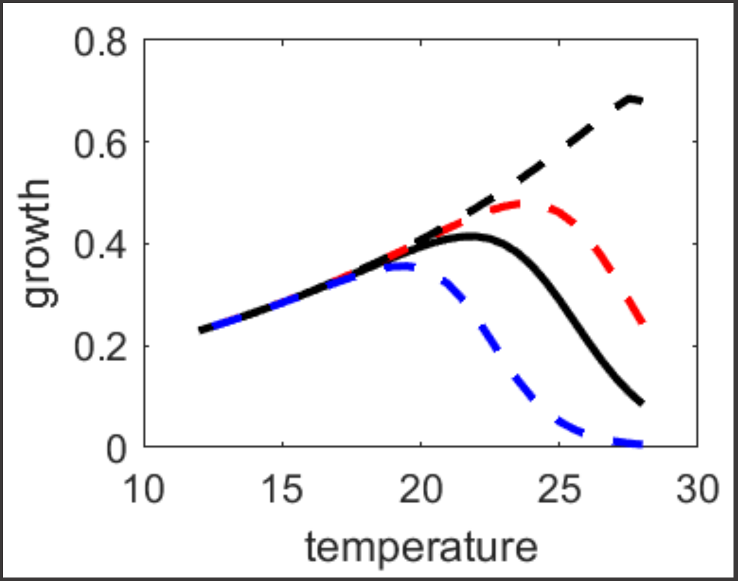
What is the state of the art?

growth as function of nutrients and temperature

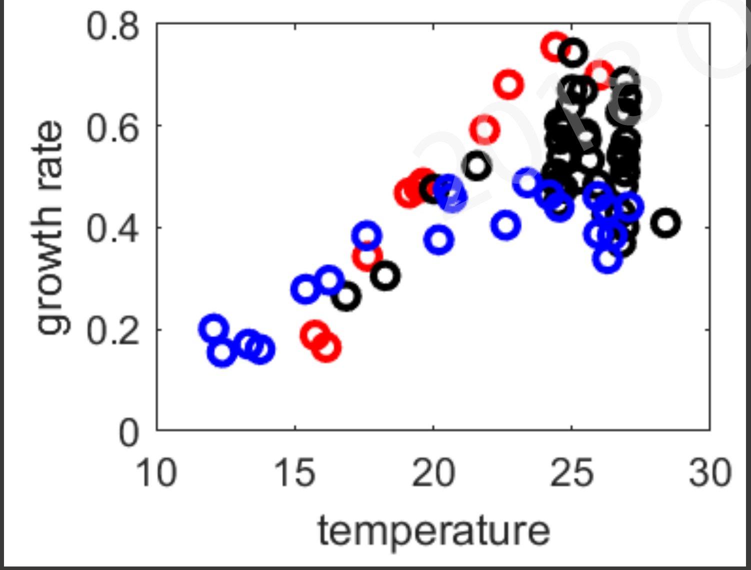


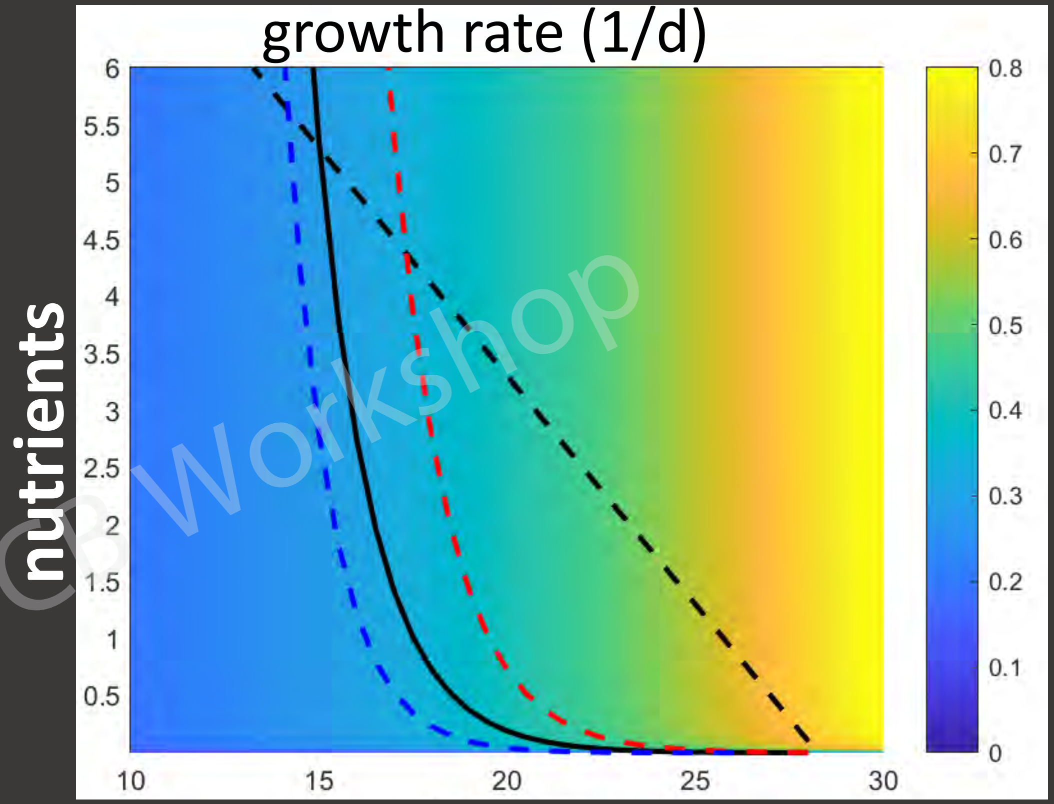
$$\mu_{\max}\frac{R}{R+\kappa_R}\gamma\, e^{AT}$$

growth as function of nutrients and temperature



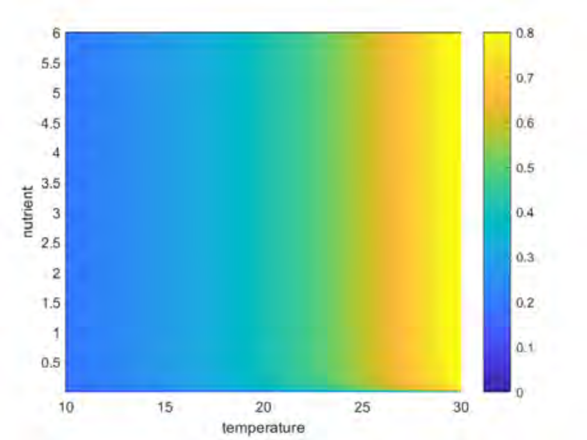
observed Pro growth rates in North-East Pacific

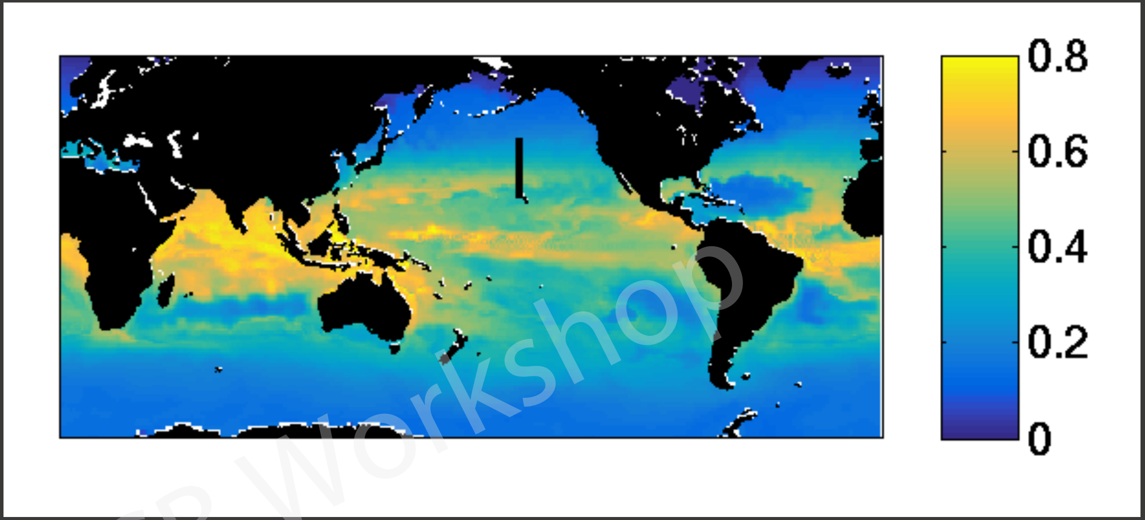




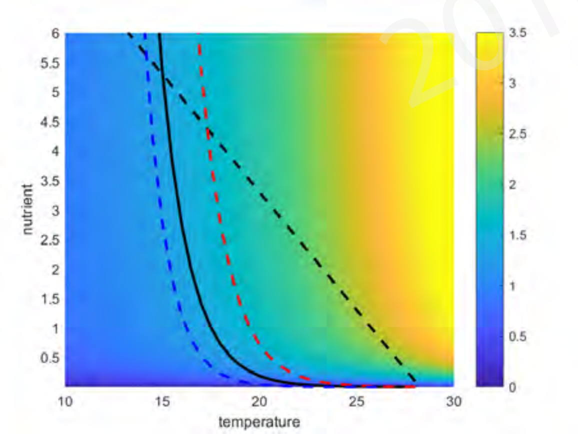
$$\mu_{\max}\frac{R}{R+\kappa_R}e^{-AT}$$

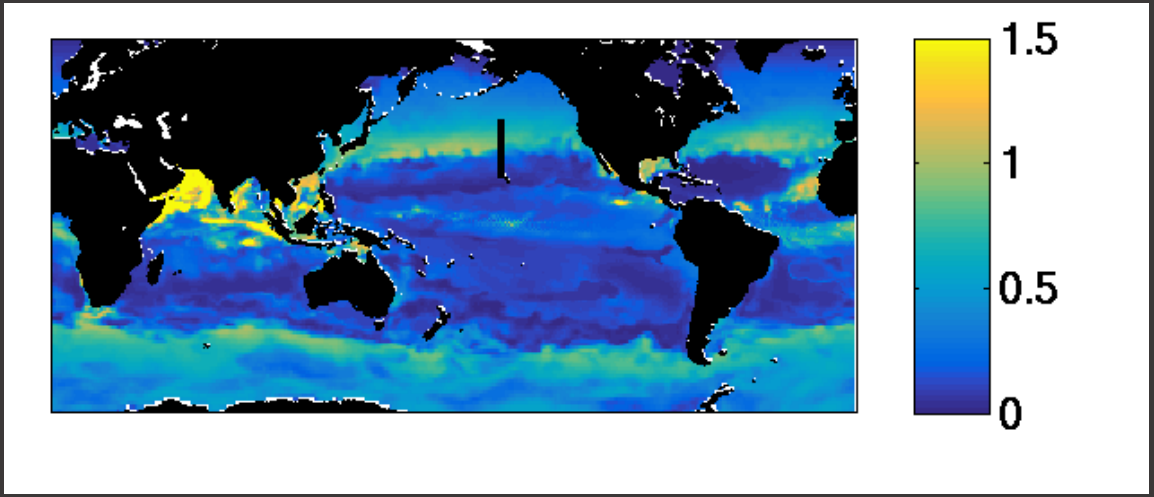
Numerical model results: annual mean *Prochlorococcus* growth rates (1/d)





5um Diatom growth rates (1/d)





SOME QUESTIONS

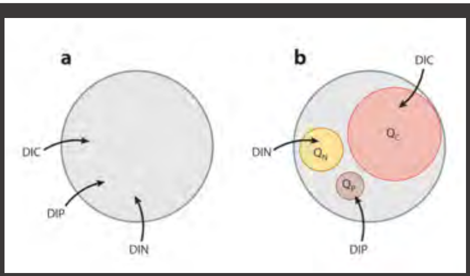
What should the next generation of 3-D ecosystem models include:

- Variable stoichiometry? How?

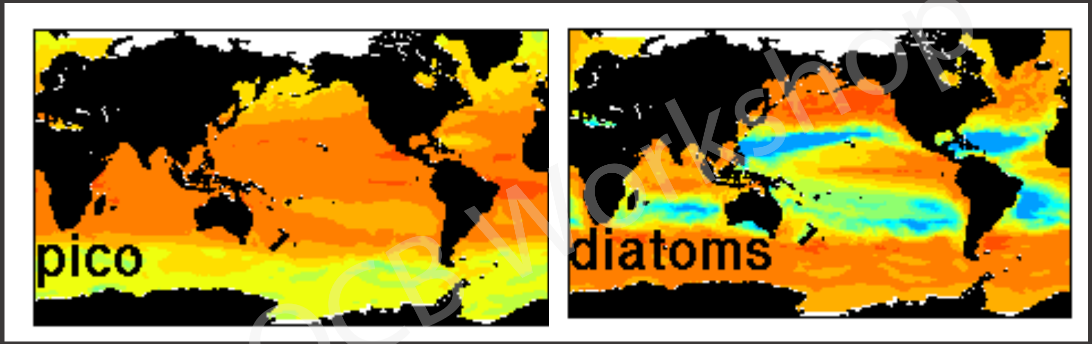
- Better representation of multiple limiting factors?
    - what laboratory/field studies do we need?
    - how universal are "planes" of multiple response functions

- Inclusion of more physiological diversity (e.g. mixotrophy, symbiosis)
    - but how much? do we know enough?

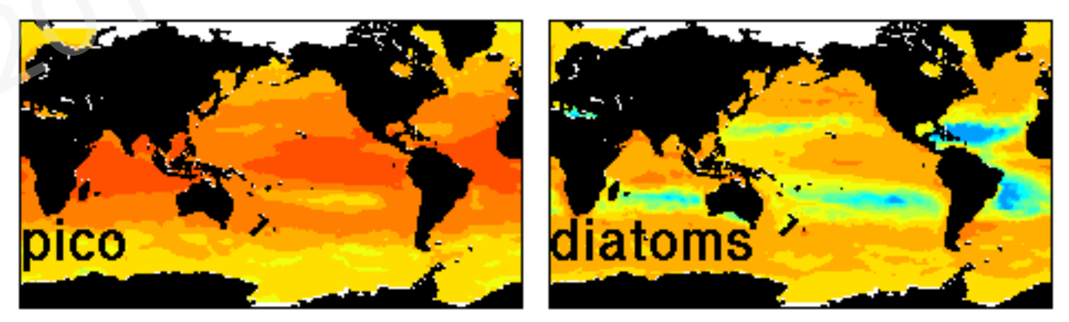
What is the state of the art?



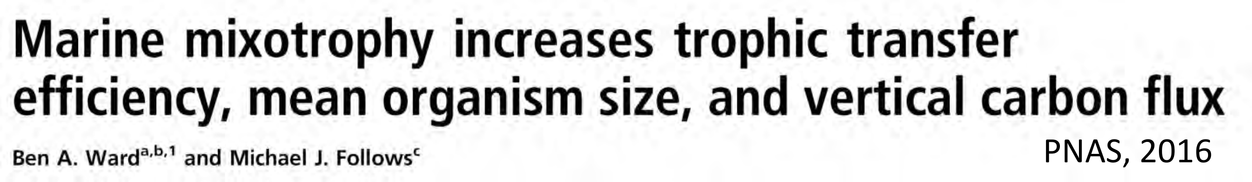
Monod Kinetics
(fixed cell quotas)



Droop/Caperon Kinetics
(variable cell quotas)



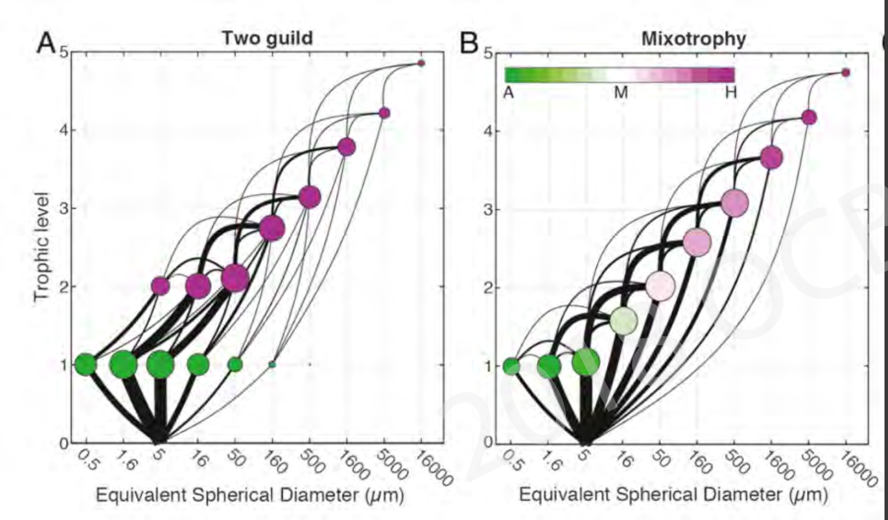
EXAMPLE 2: TROPHIC STRATEGY



Marine mixotrophy increases trophic transfer efficiency, mean organism size, and vertical carbon flux

Ben A. Ward[a,b,1] and Michael J. Follows[c]

PNAS, 2016



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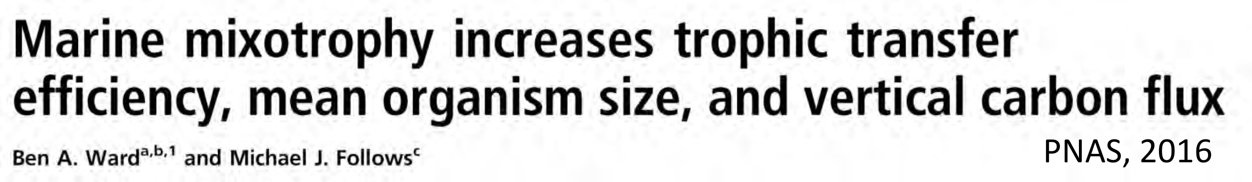

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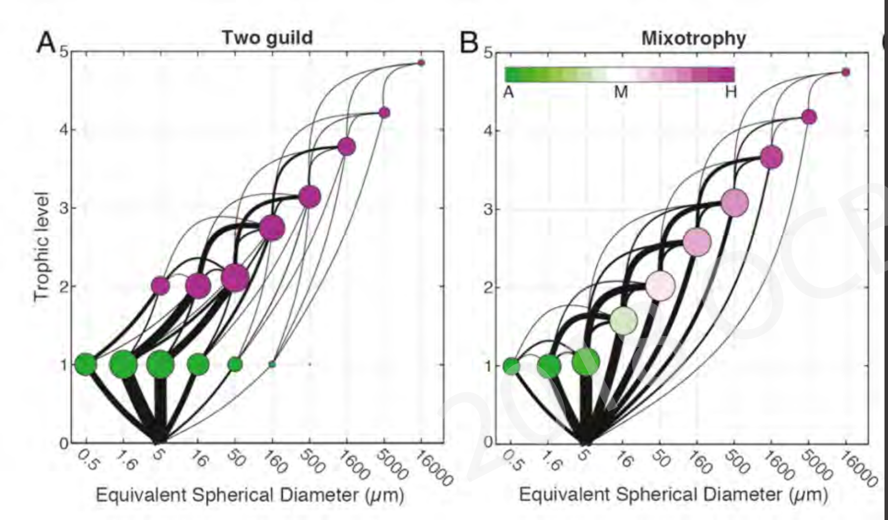

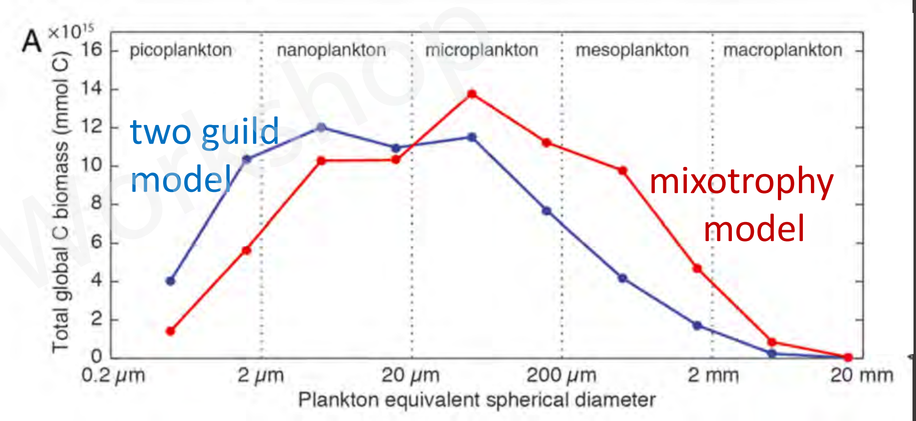

two guild model

mixotrophy model

- mixotrophy allows for larger cells; more realistic size distribution
- and increases the carbon export

What is the state of the art?

Phylogenetic Diversity in the Macromolecular Composition of Microalgae

Zoe V. Finkel[1]*, Mick J. Follows[2], Justin D. Liefer[1], Chris M. Brown[3], Ina Benner[1], Andrew J. Irwin[4]

PlosOne 2016

Observation of Macromolecular Pools