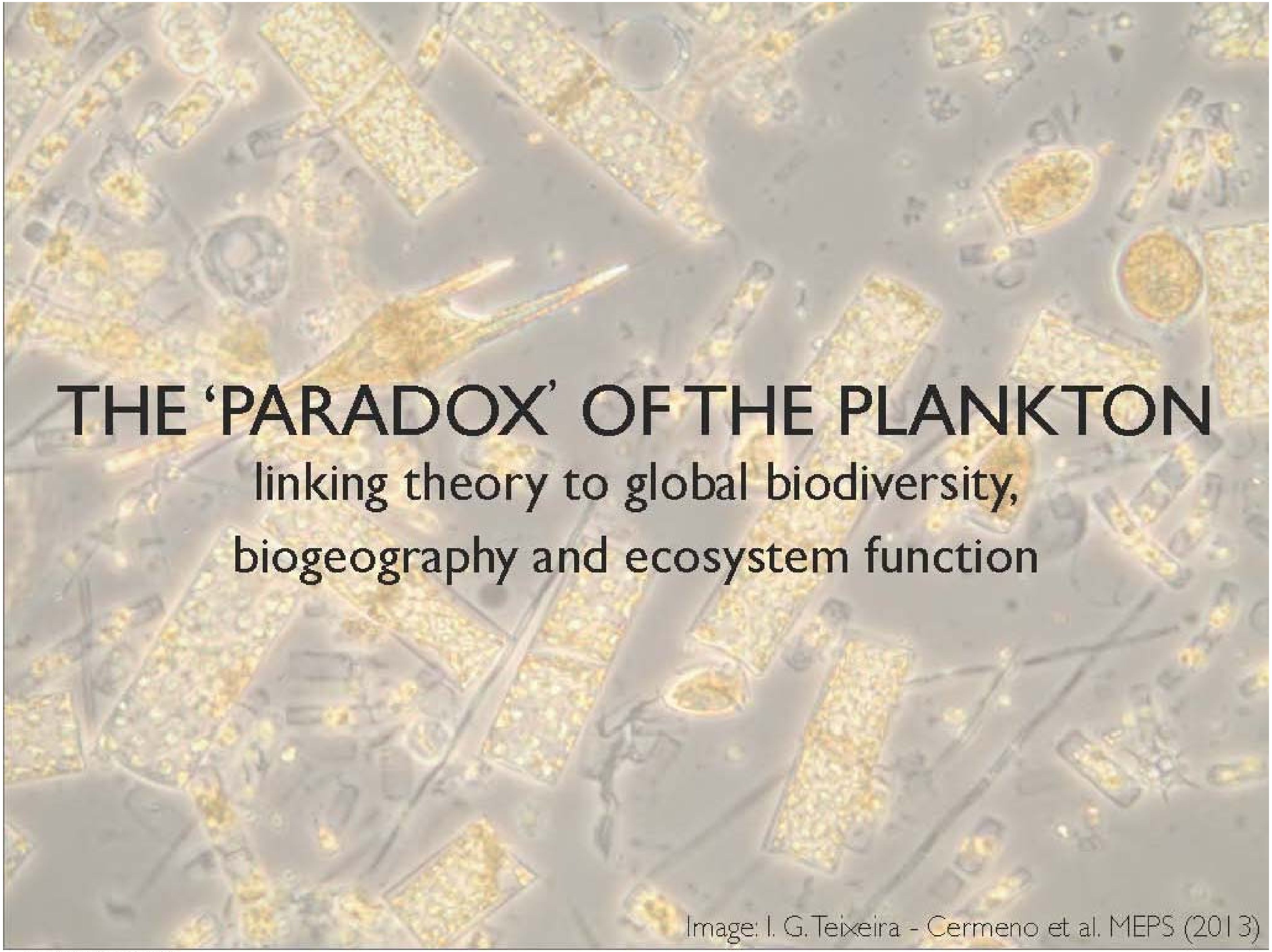

THE 'PARADOX' OF THE PLANKTON

linking theory to global biodiversity, biogeography and ecosystem function

Image: I. G. Teixeira - Cermeno et al. MEPS (2013)

linking theory to global biodiversity, biogeography and ecosystem function

1. Diverse, trait-based models of marine ecosystems - why bother?

2. Maintaining diversity - the 'paradox' and its many solutions

3. Putting it all together - a size-structured plankton community model

4. Taking it apart again - what drives biogeography

5. Conclusions

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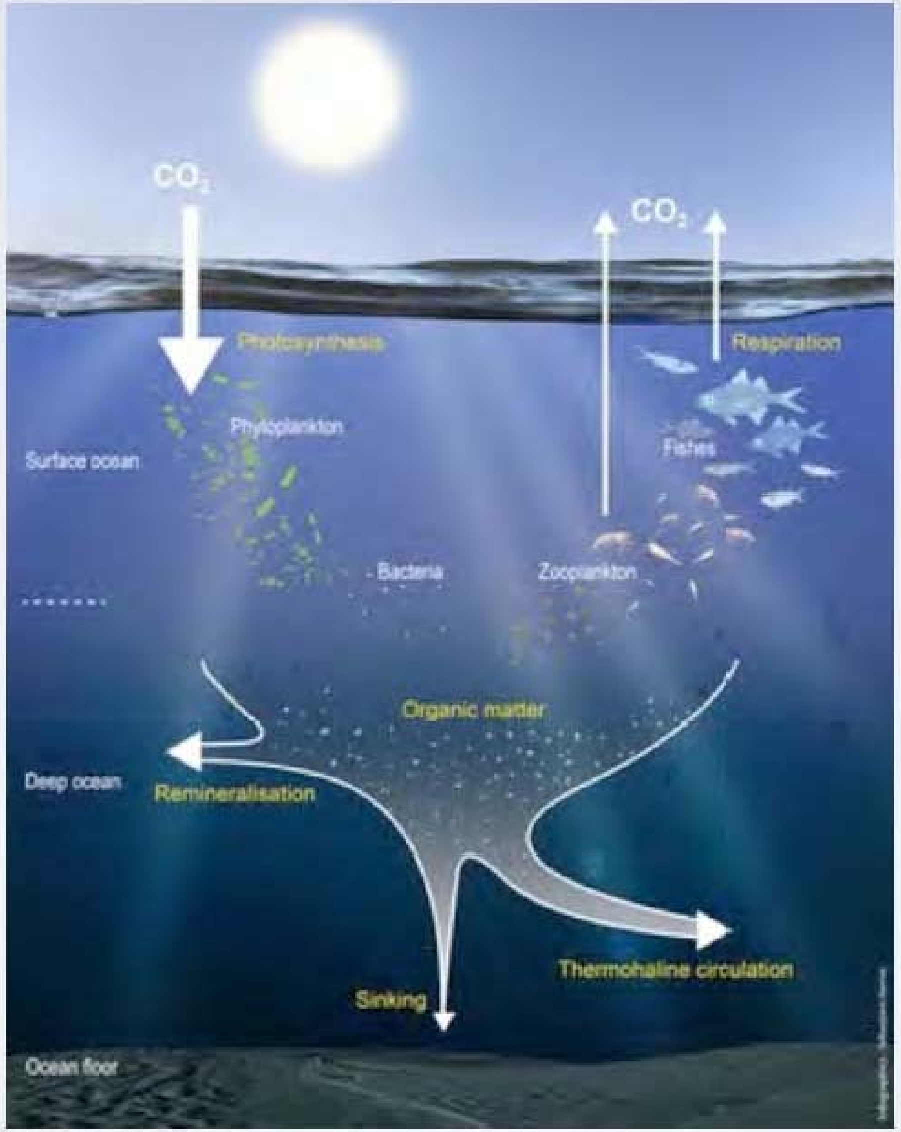
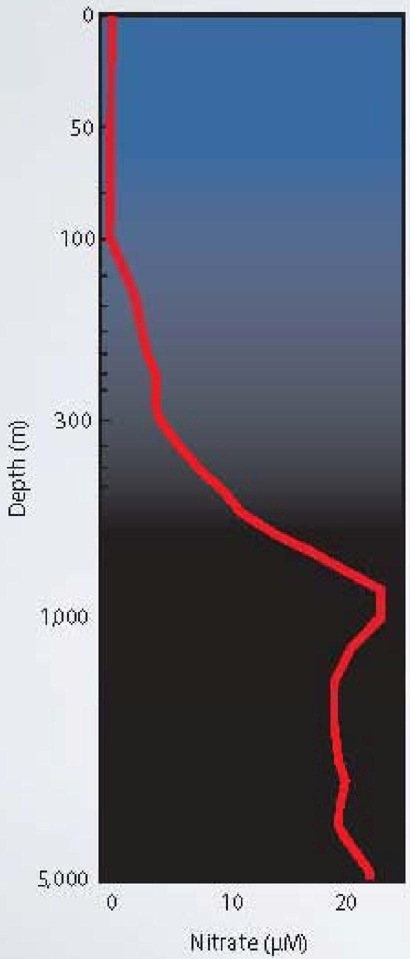
Why include diversity?



Why include diversity?

The biological pump



Nutrient profile attributable to N uptake and particulate sinking

Physical processes tend to destroy gradient

Nutrient restoring models estimate biological production and export by relaxing profiles towards observations

One state variable - very low complexity

Very simple, but lacks flexibility - observed profiles will change

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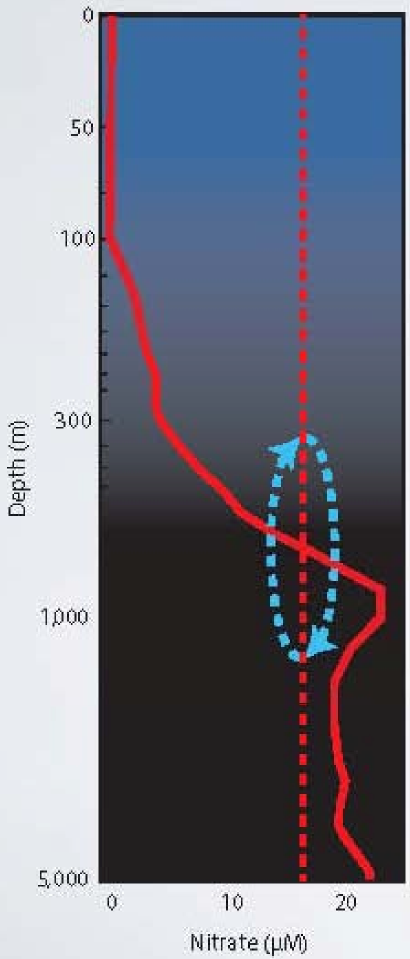
The biological pump



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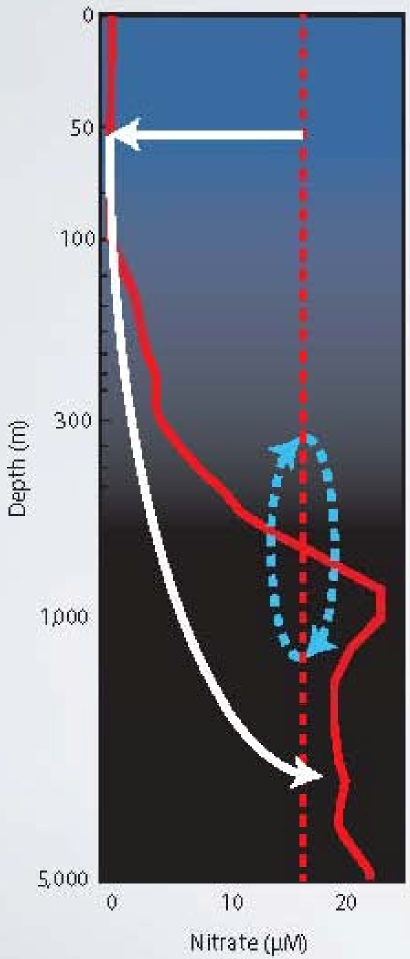

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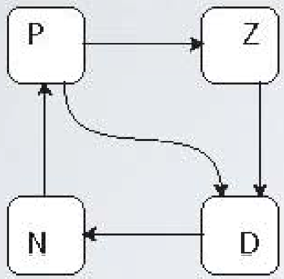
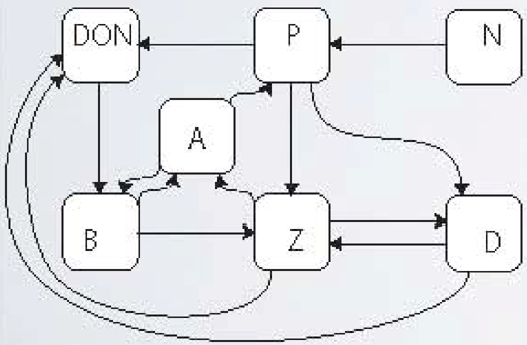
Resolving ecological guilds



More mechanistic - resolving key processes:
- primary production
- grazing
- sinking
- remineralisation



NPZD-type model function set by 'average' traits of communities

Less prone to change than nutrient restoring models,
but shifts in community structure are problematic

With increased complexity comes increased parameter uncertainty

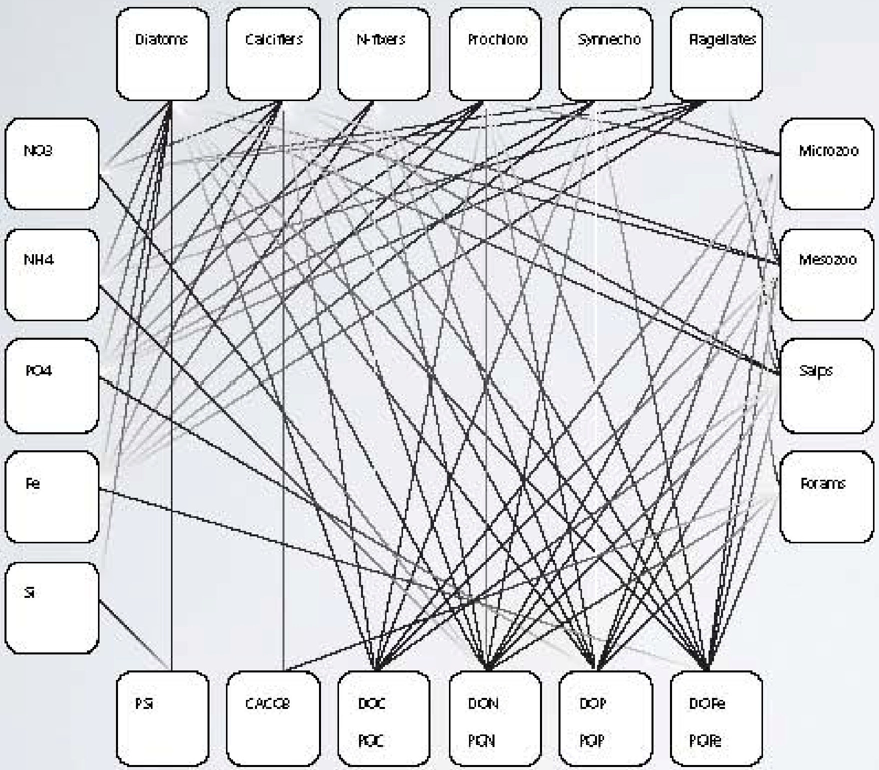
Resolving functional types

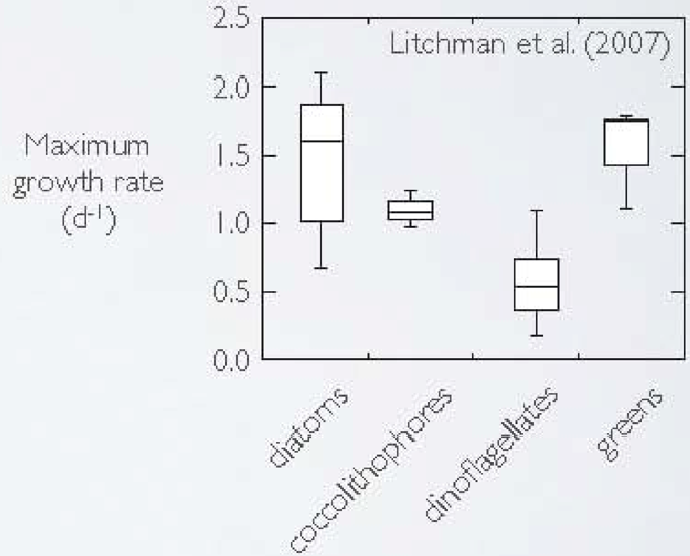
Even more mechanistic
- resolving key functional groups and processes

May require hundreds of empirical parameters

But **PFT models** still based on community averages

Still significant variability of traits within groups

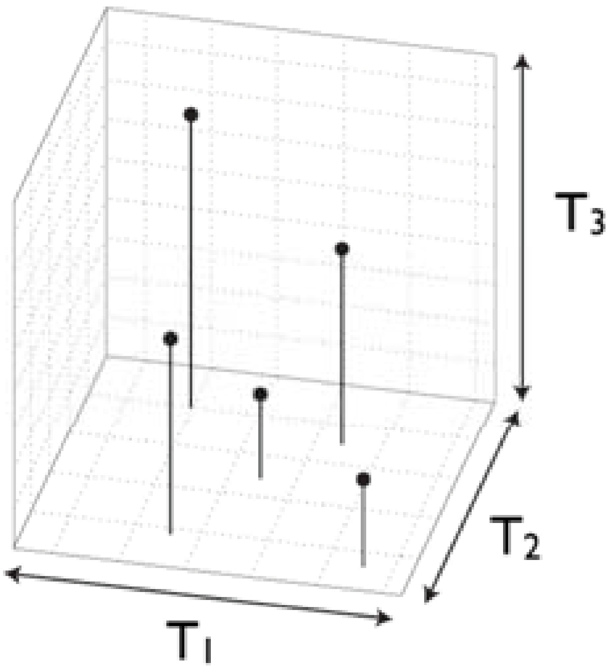




e.g. **~3-fold variation in** μ_{max} within functional groups
can lead to ~**3 orders of magnitude difference in biomass** after 7 days exponential growth

Trait-based models

Everything is everywhere,
but the environment selects



PFT specified individually:
- requires *n* parameters per PFT

Attempt to parameterise diversity

Trait-based approach:
- find trade-offs, ~*n* parameters per trait
- no limit on number of 'species' (in theory)

Attempt to parameterise rules that govern diversity

computational limits

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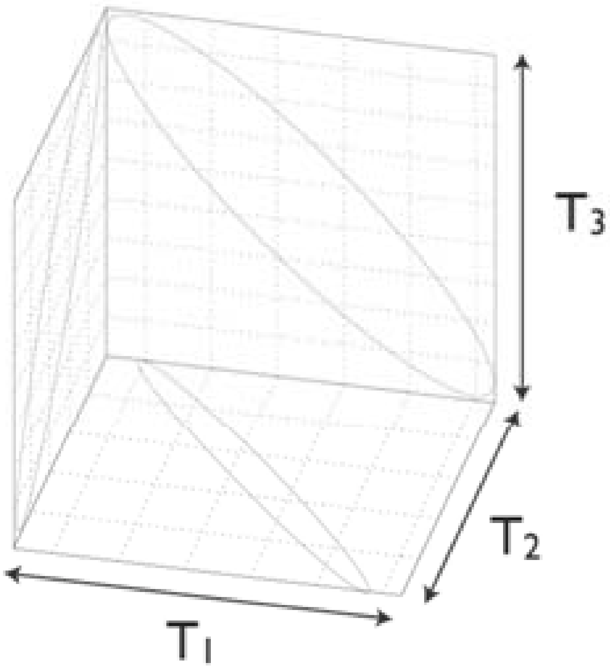

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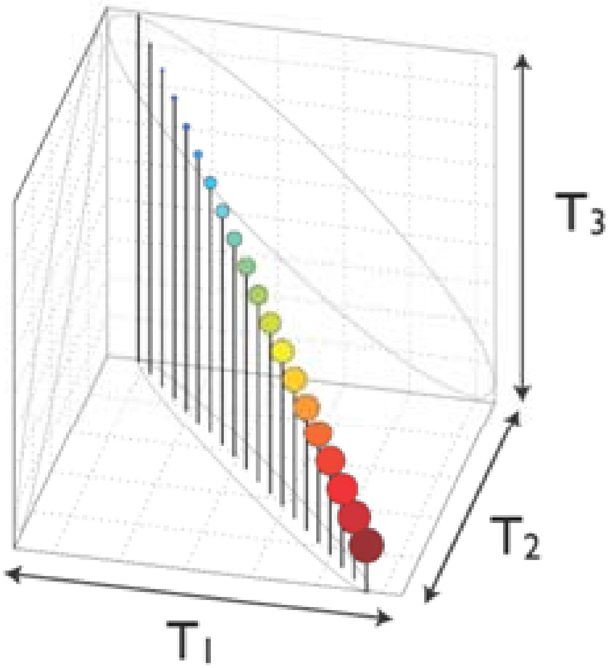

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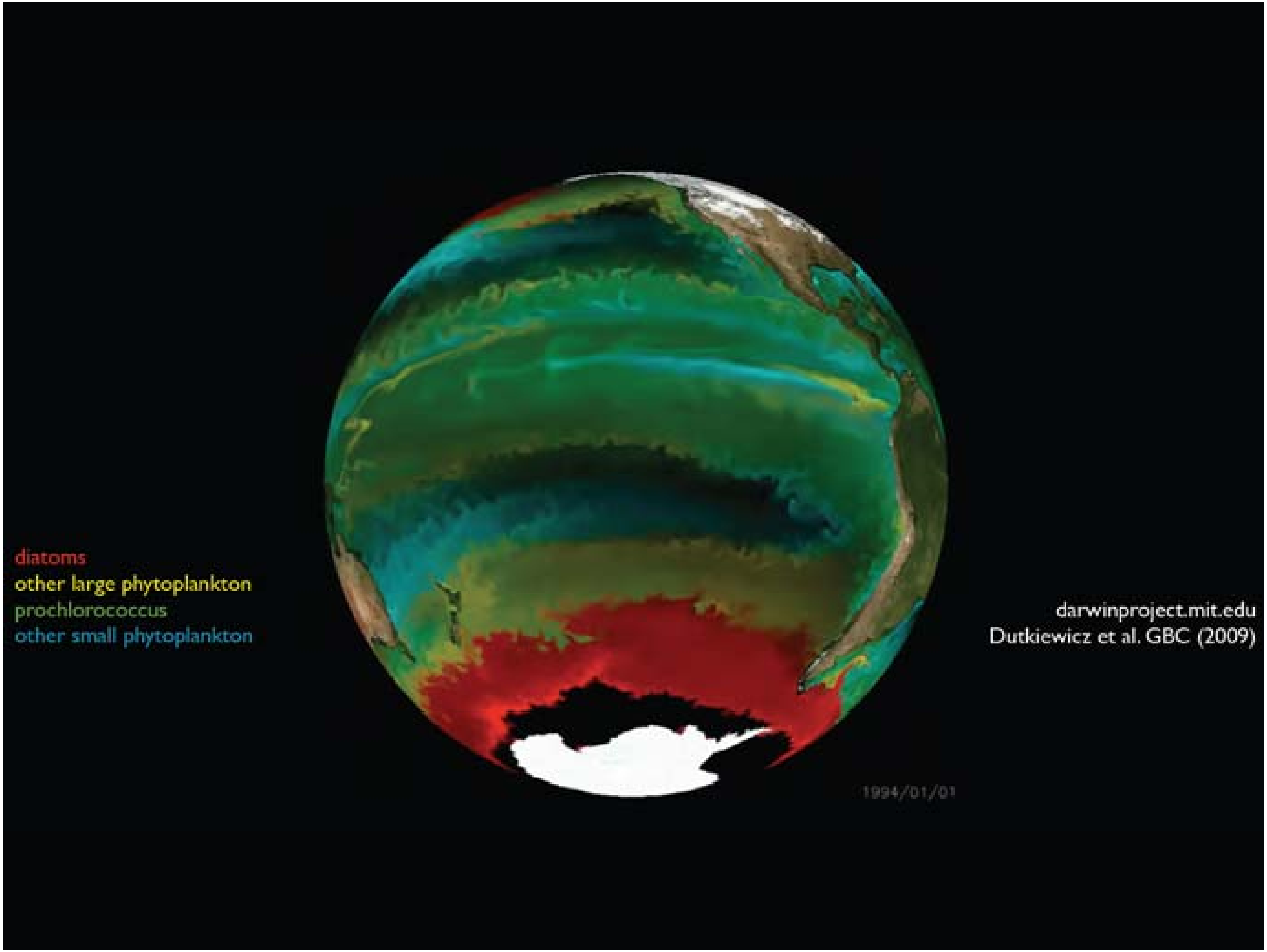
diatoms
other large phytoplankton
prochlorococcus
other small phytoplankton
darwinproject.mit.edu
Dutkiewicz et al. GBC (2009)
1994/01/01

linking theory to global biodiversity, biogeography and ecosystem function

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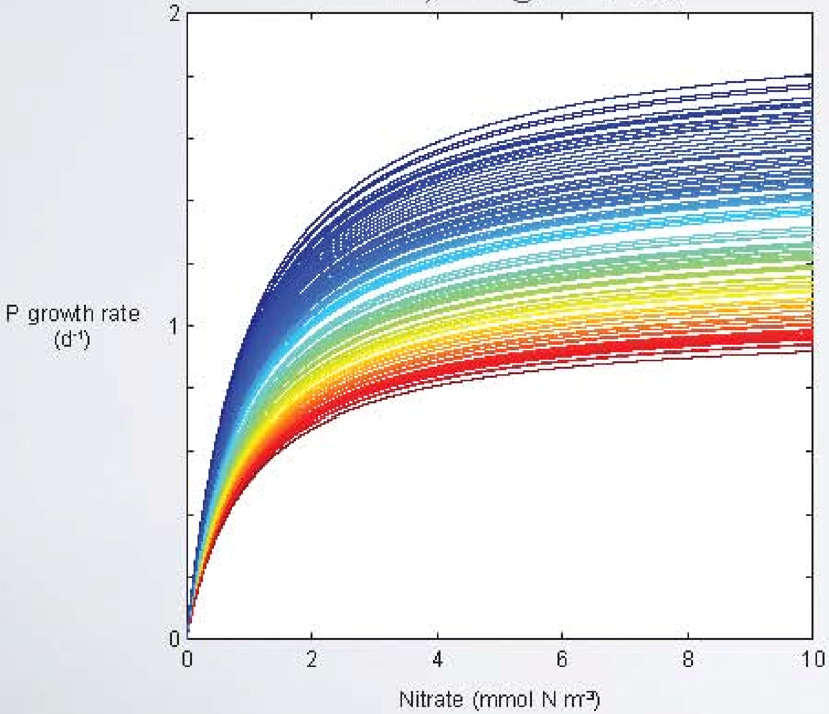
How can so many species coexist in an unstructured environment when competing for the same limited resources?

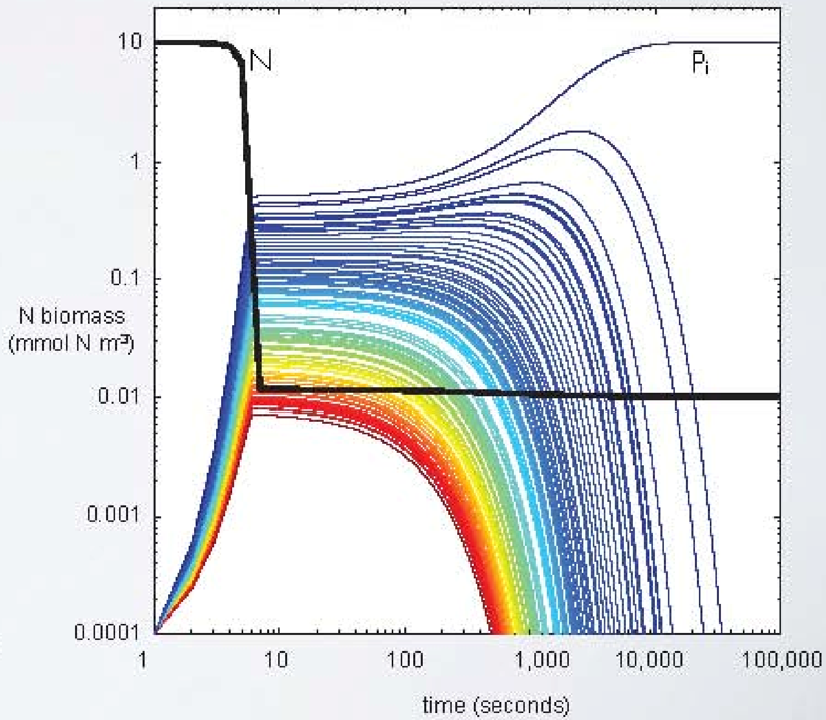
Hutchinson (1961)

$$\frac{1}{P}\frac{dP}{dt} = \mu_{max}\frac{N}{k_N + N} - m$$

100 phytoplankton
with randomly assigned μ_{max}



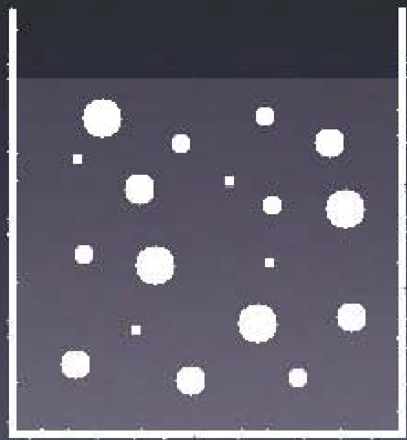
Nutrients drawn down
- only one winner at equilibrium



Resource Competition

$$\frac{dP_i}{dt} = \mu_{max,i} \frac{N}{k_{N,i} + N} P_i - mP_i$$

$$N_{total} = N + \sum_{i=1}^{n} P_i$$



Tilman (1980)

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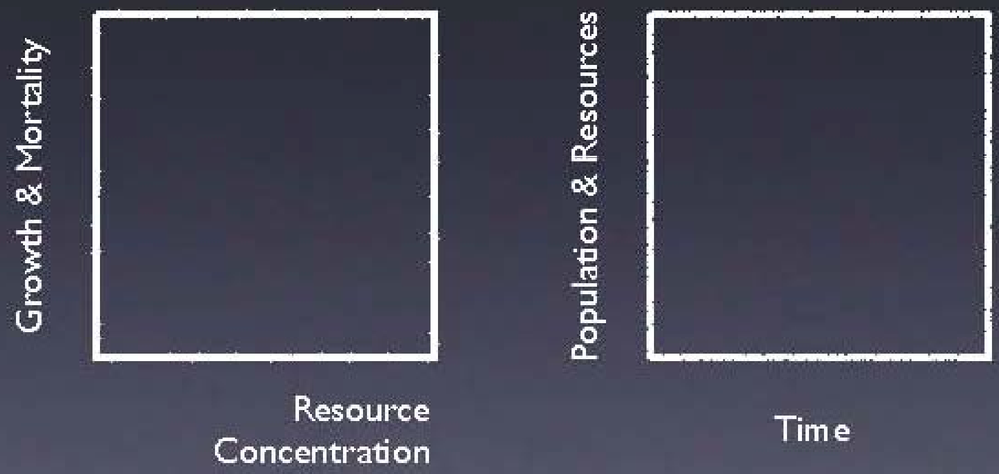

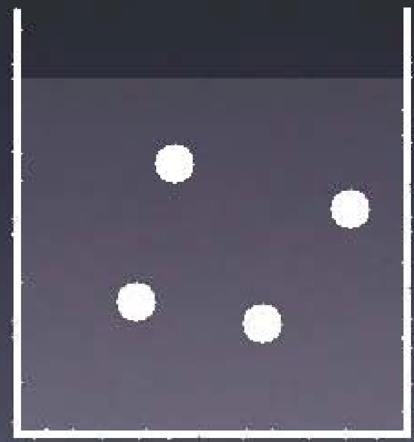

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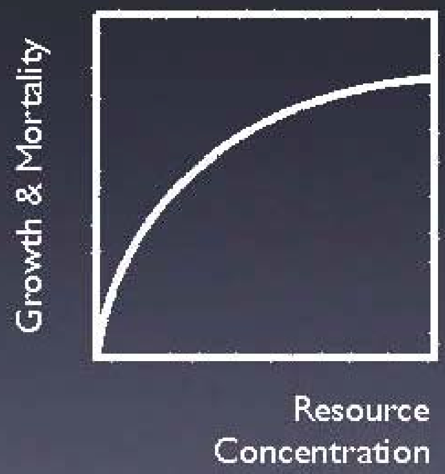

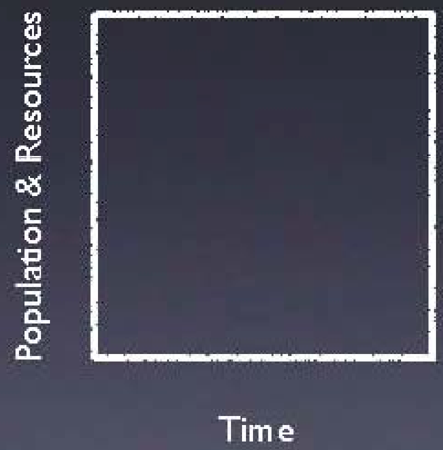

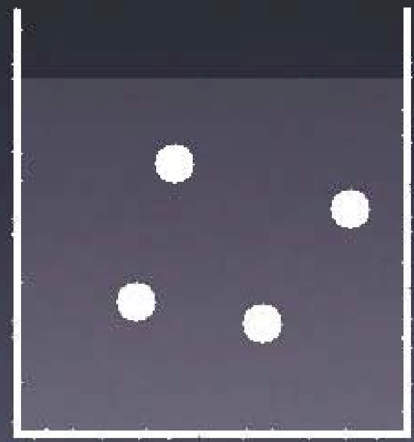

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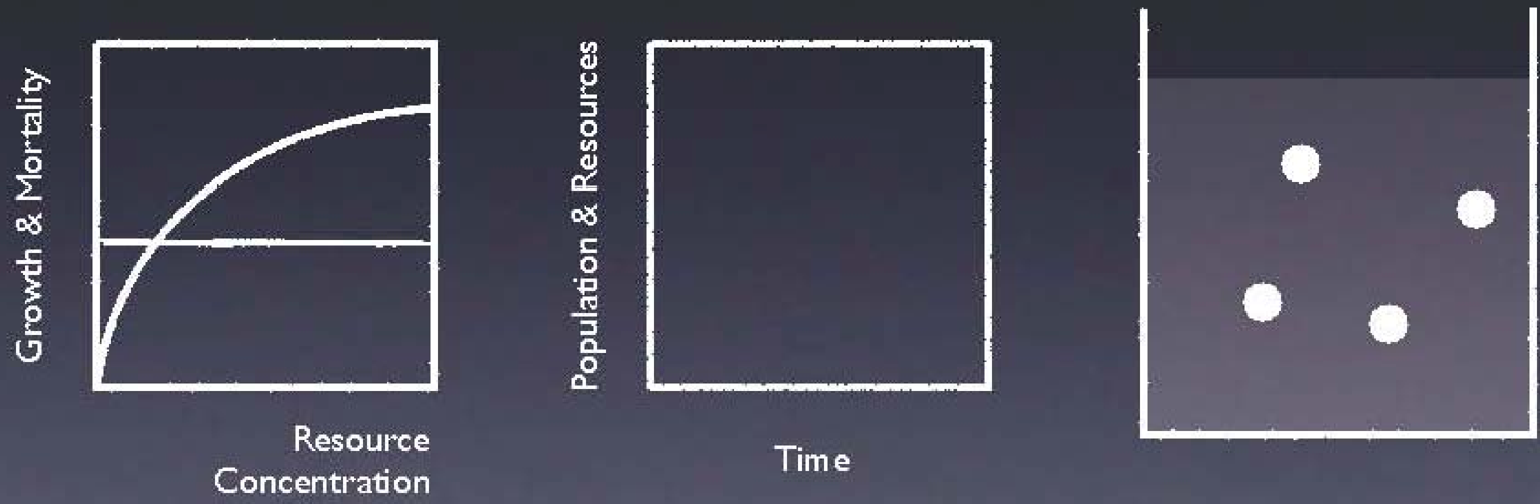

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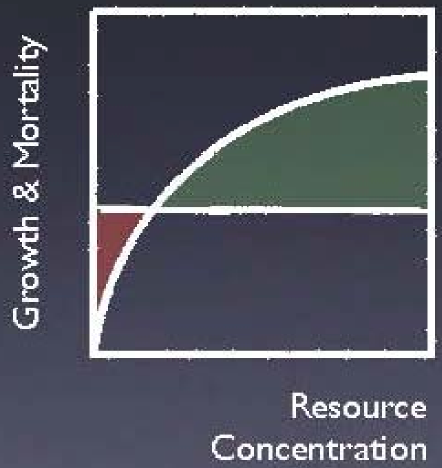

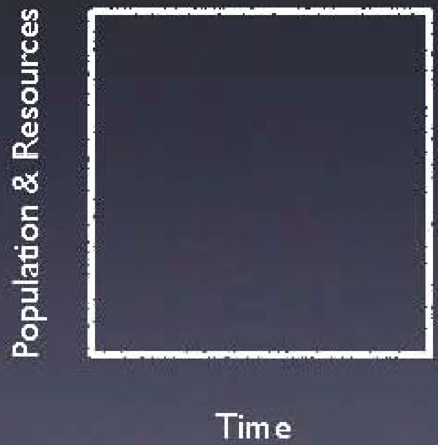

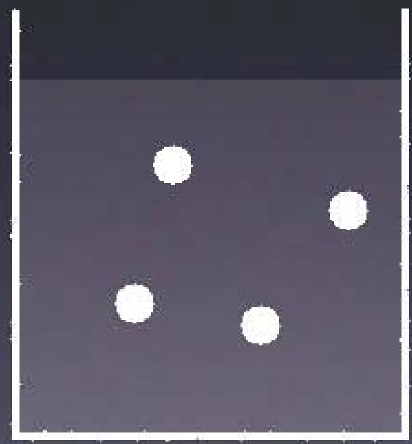

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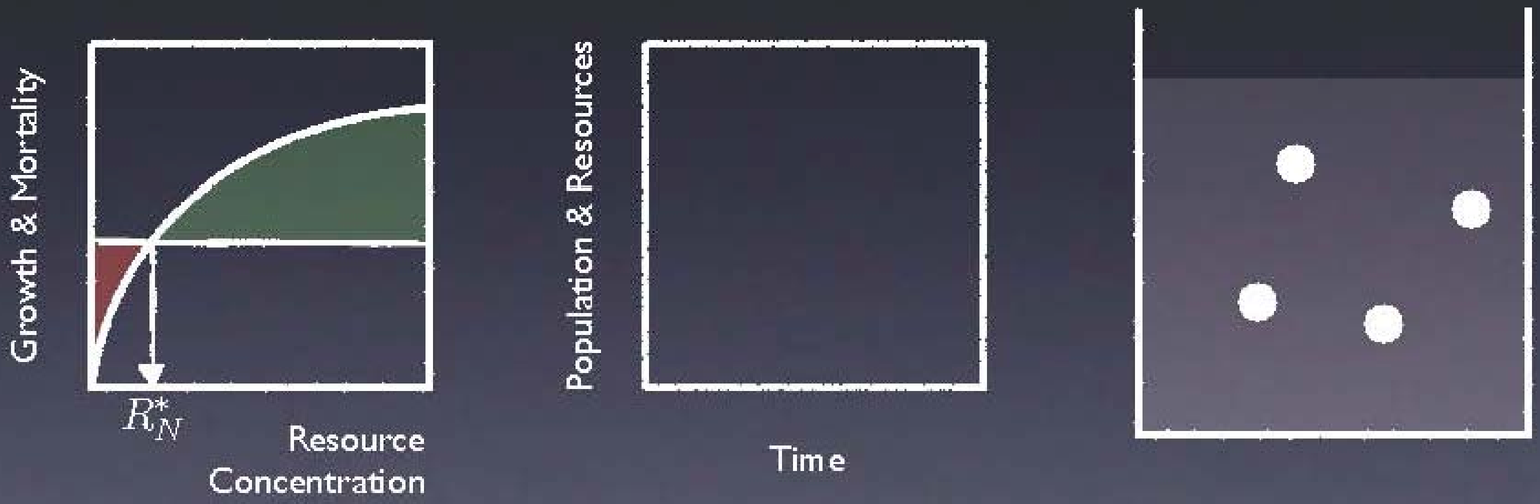

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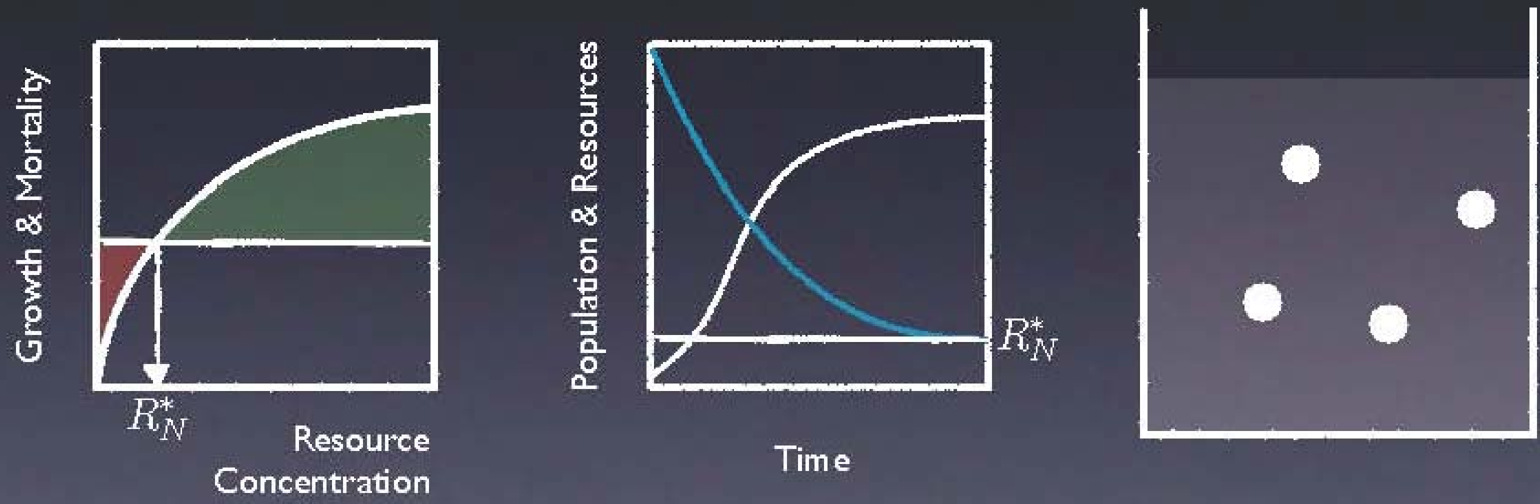
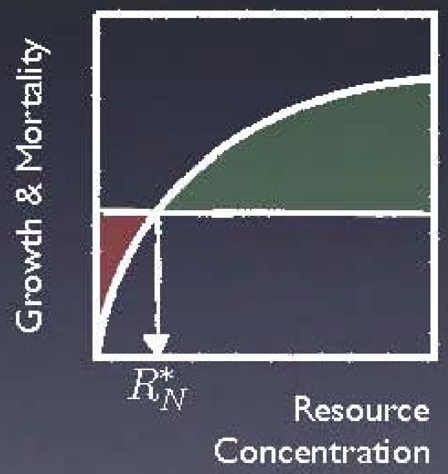
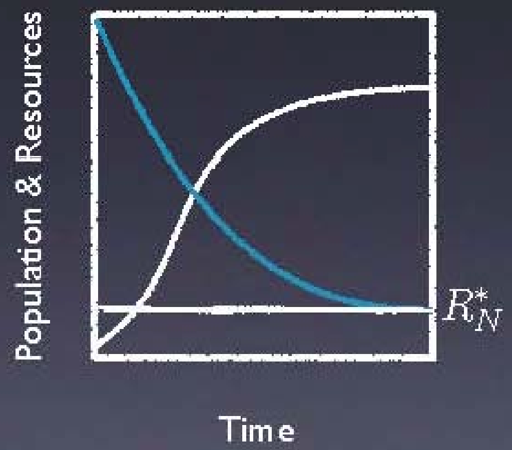


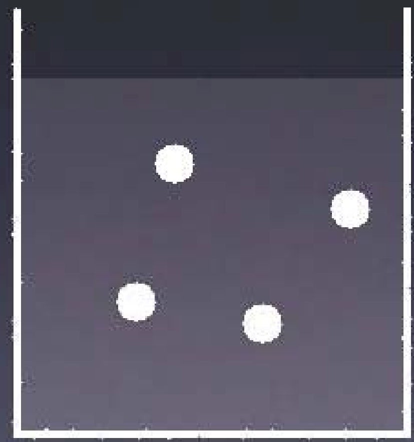
Tilman (1980)

Resource Competition

$$\frac{dP}{dt} = \mu_{max}\frac{N}{k_N + N}P - mP = 0$$







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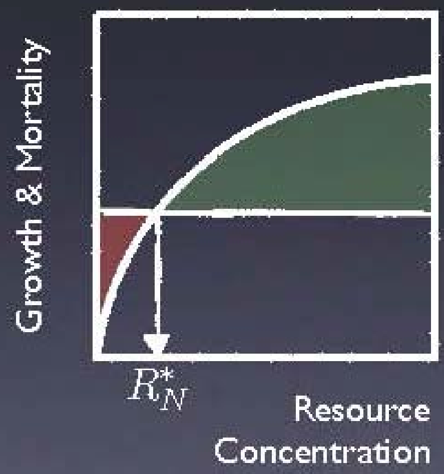
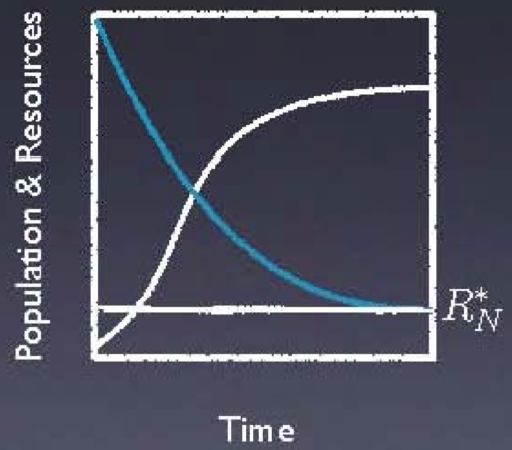
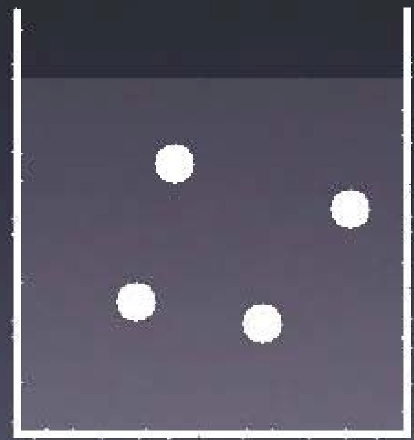


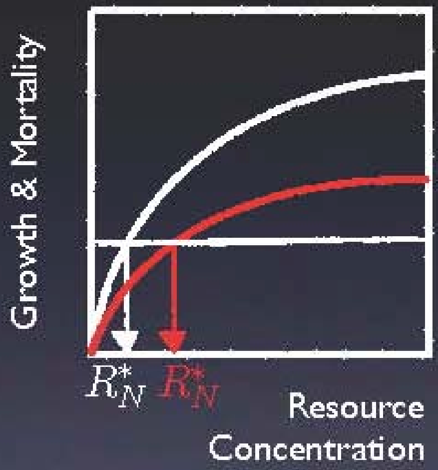


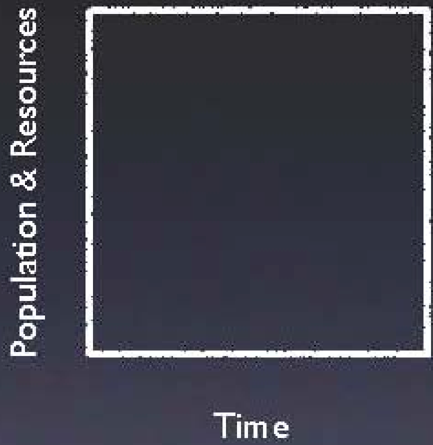


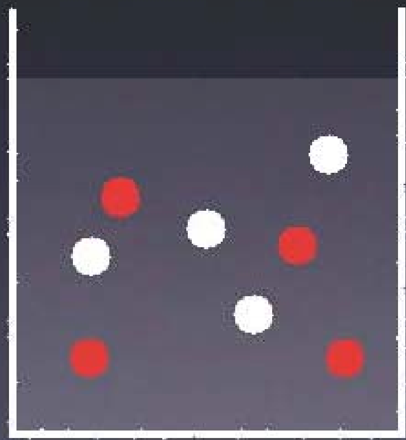
$$R_N^* = \frac{k_N m}{\mu_{max} - m}$$

Tilman (1980)

Resource Competition







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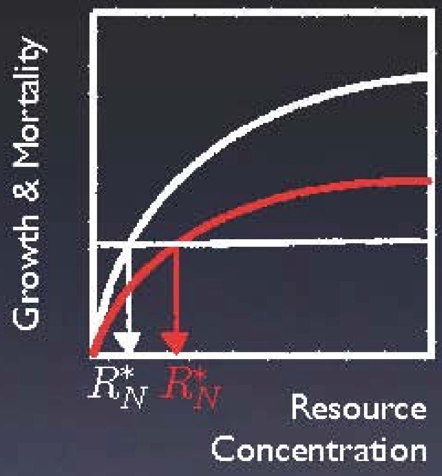

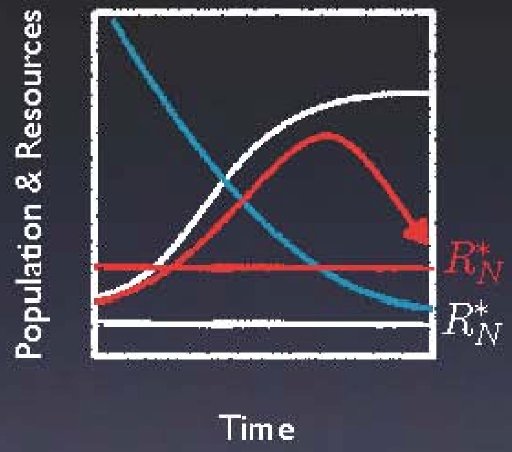

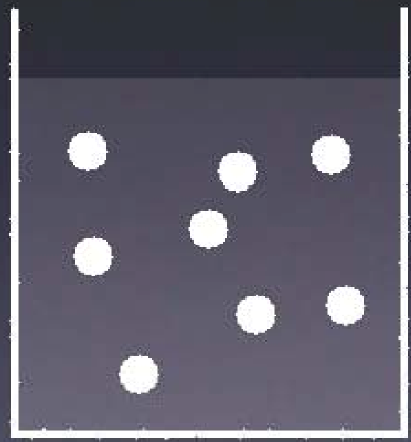

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Tilman (1980)

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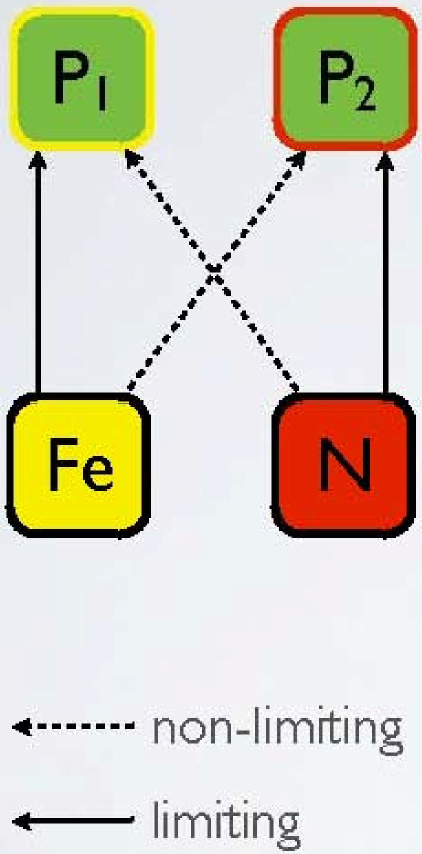
Multiple limiting resources

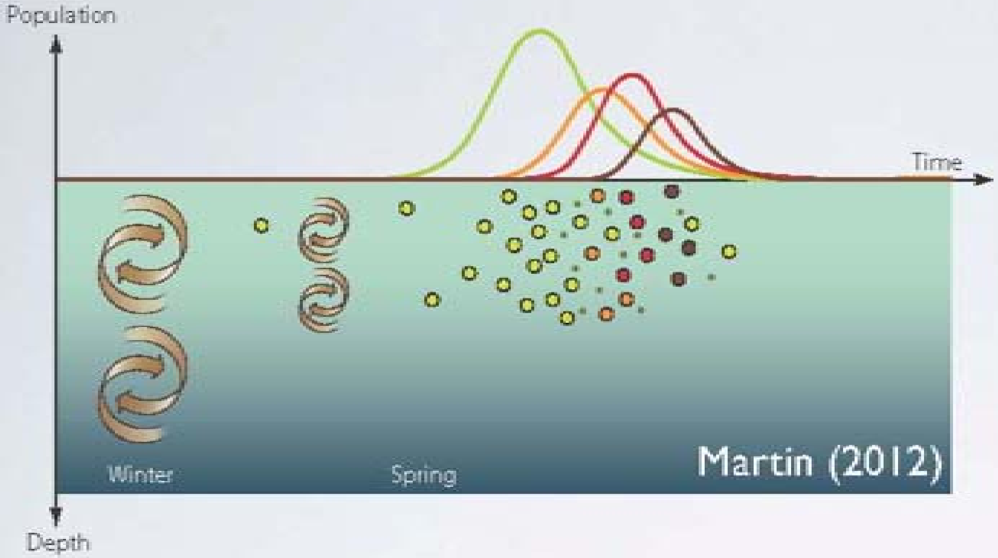


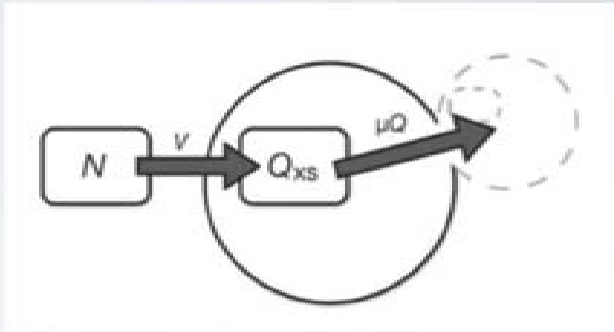
Prochlorococcus - ammonium limited
Synnechococcus - nitrate limited

Diatoms - silicate limited
Other phytoplankton - nitrate limited

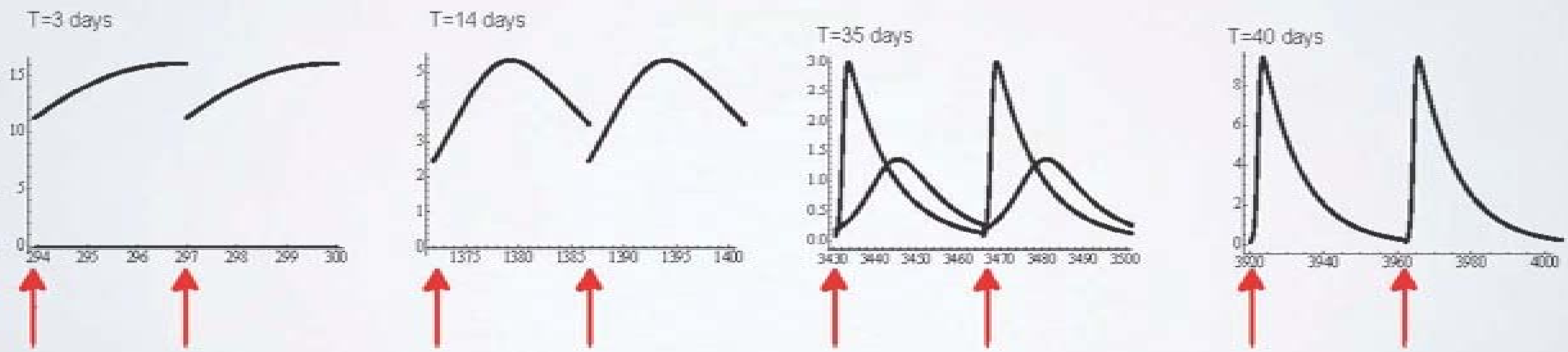
N-fixers - Iron or phosphorus limited
Other phytoplankton - nitrate limited

Growth rate vs. Storage capacity



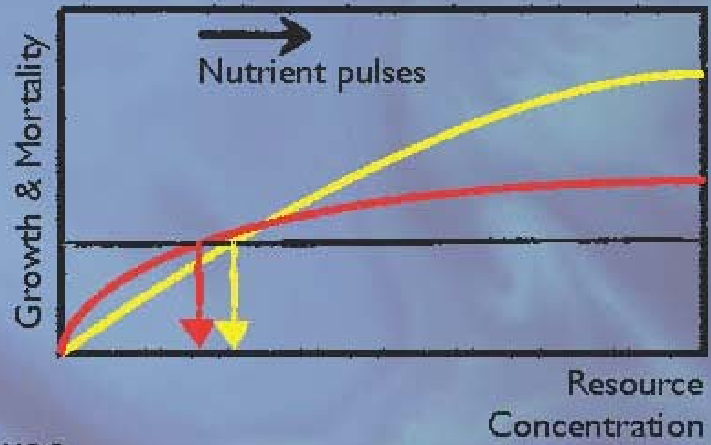


Litchman et al. (2009)

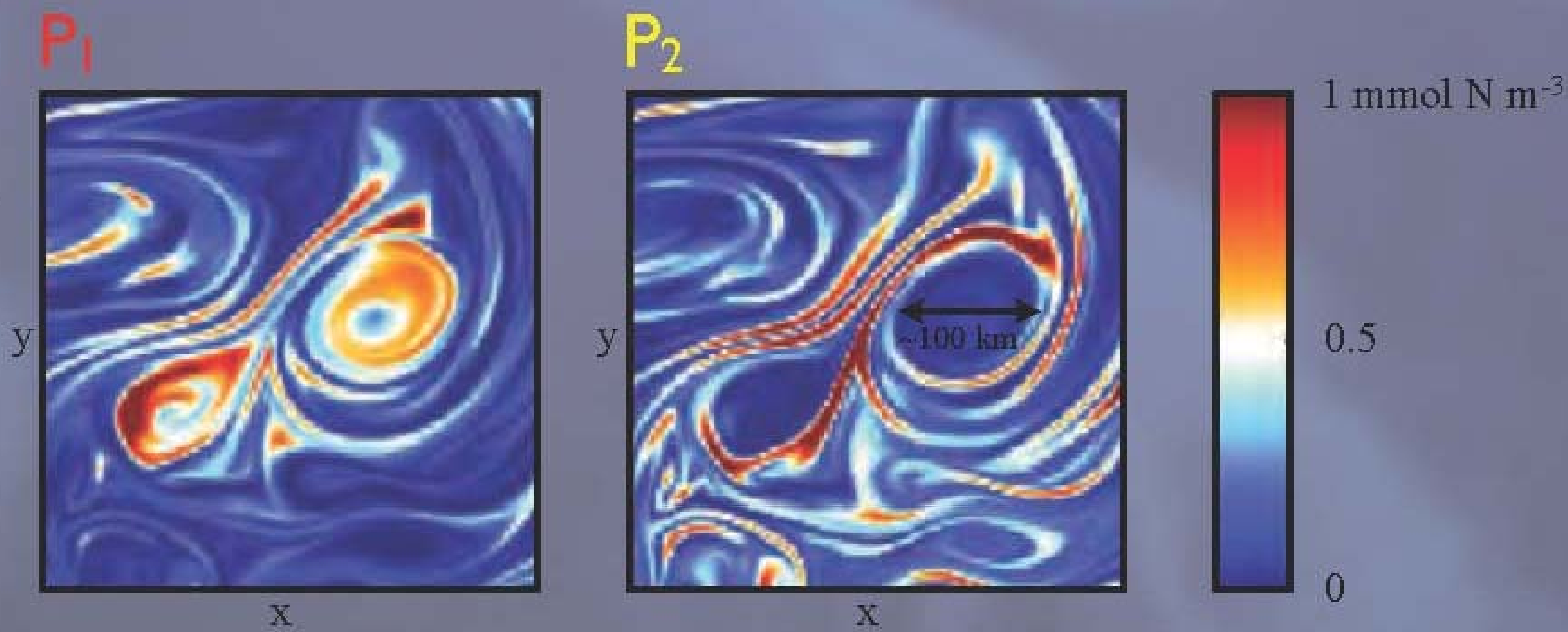


Disturbances must be similar timescale to P growth
- tidal forcing, storms, passage of eddies

Growth rate (r) vs. Nutrient affinity (k)



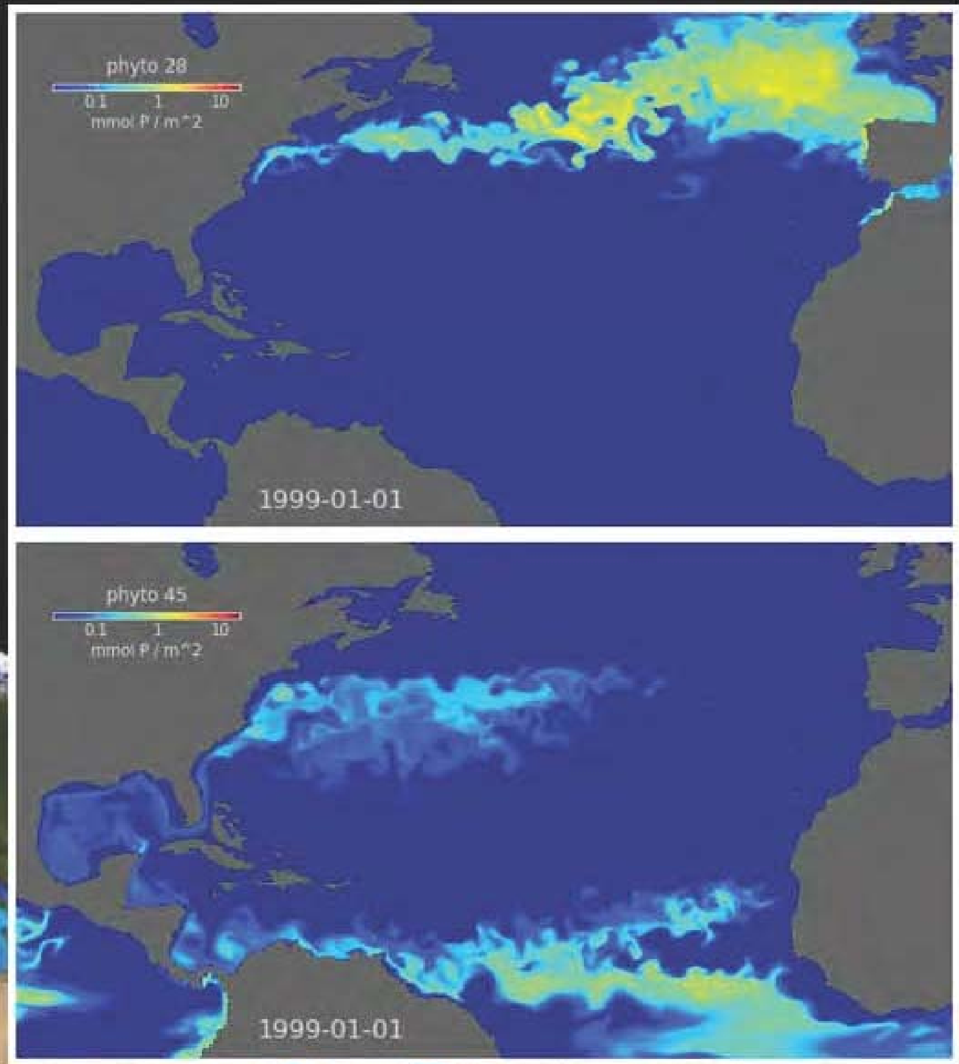
2 species
mutually exclusive at equilibrium

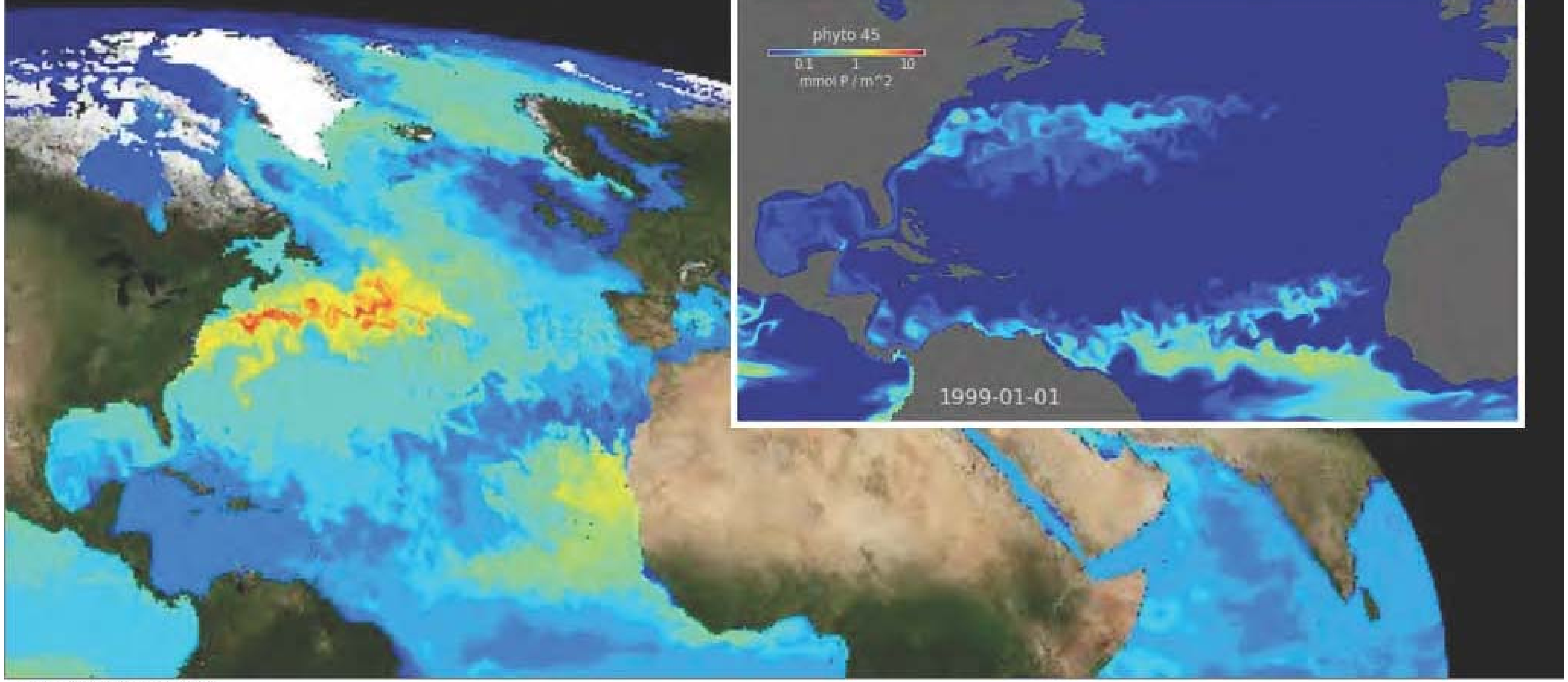


Perruche et al. (2011)

Advection

Barton et al. (2010)

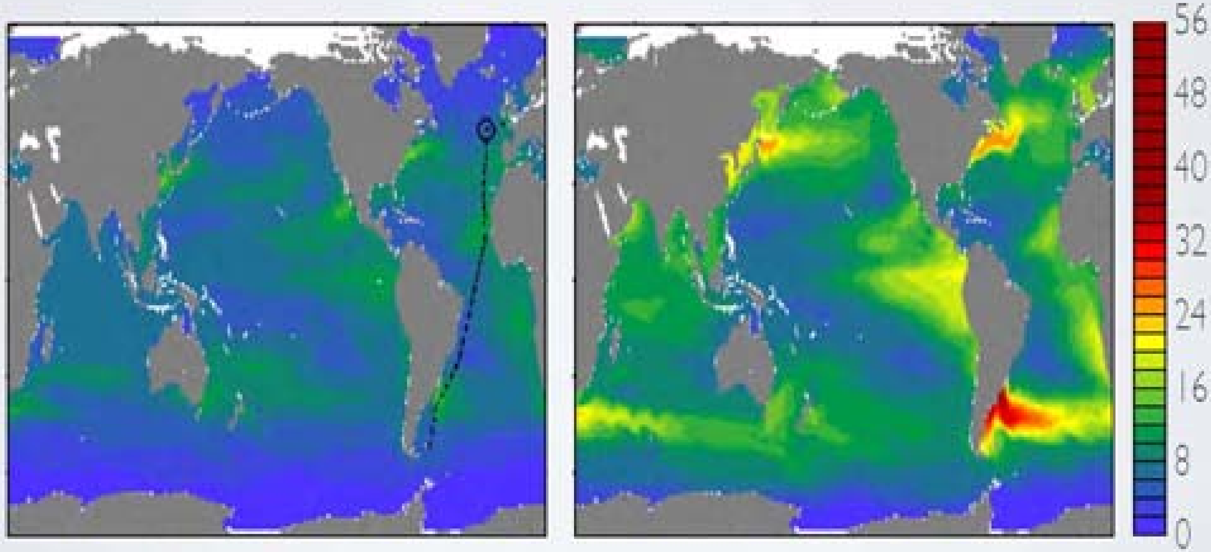




Top-down controls
"kill the winner"

Grazing effort made proportional to prey biomass

keeps most competitive types in check: reduces exclusion



Prowe et al. (2012)

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Why size?

Important functional trait:

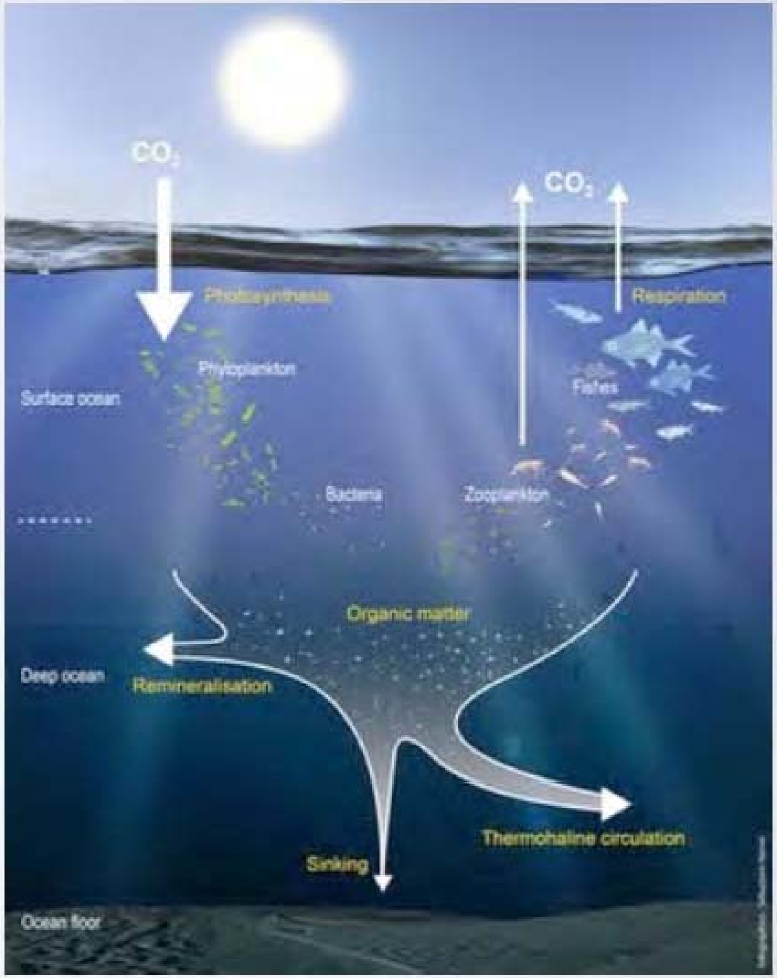
- export
- higher trophic levels

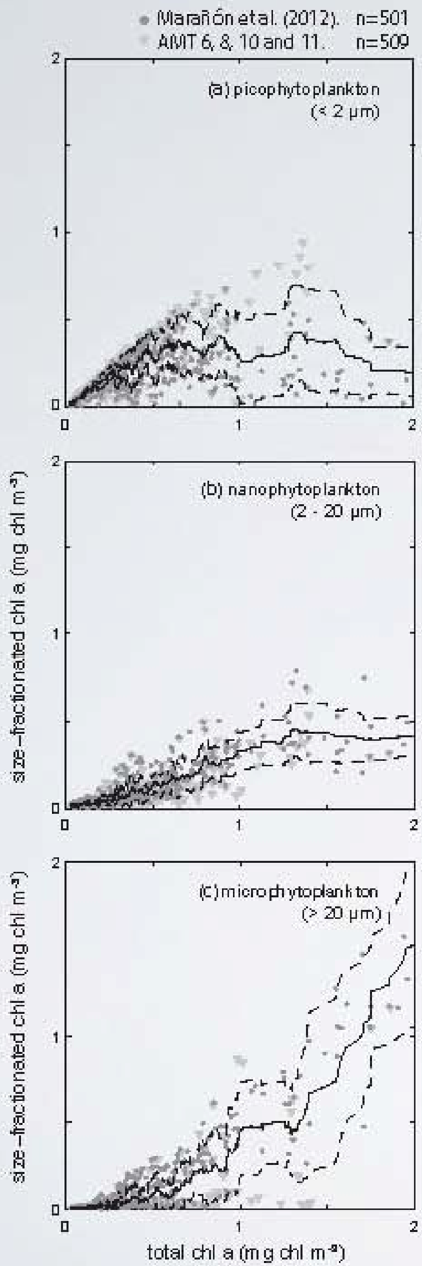
Allometry

Widely observed: in situ/satellite

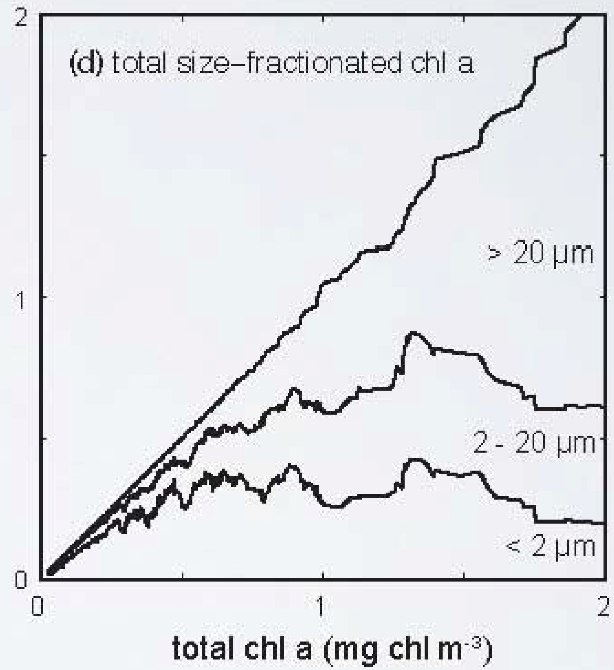
Very clear global organisation...

...driven by environmental factors
that are predicted to change

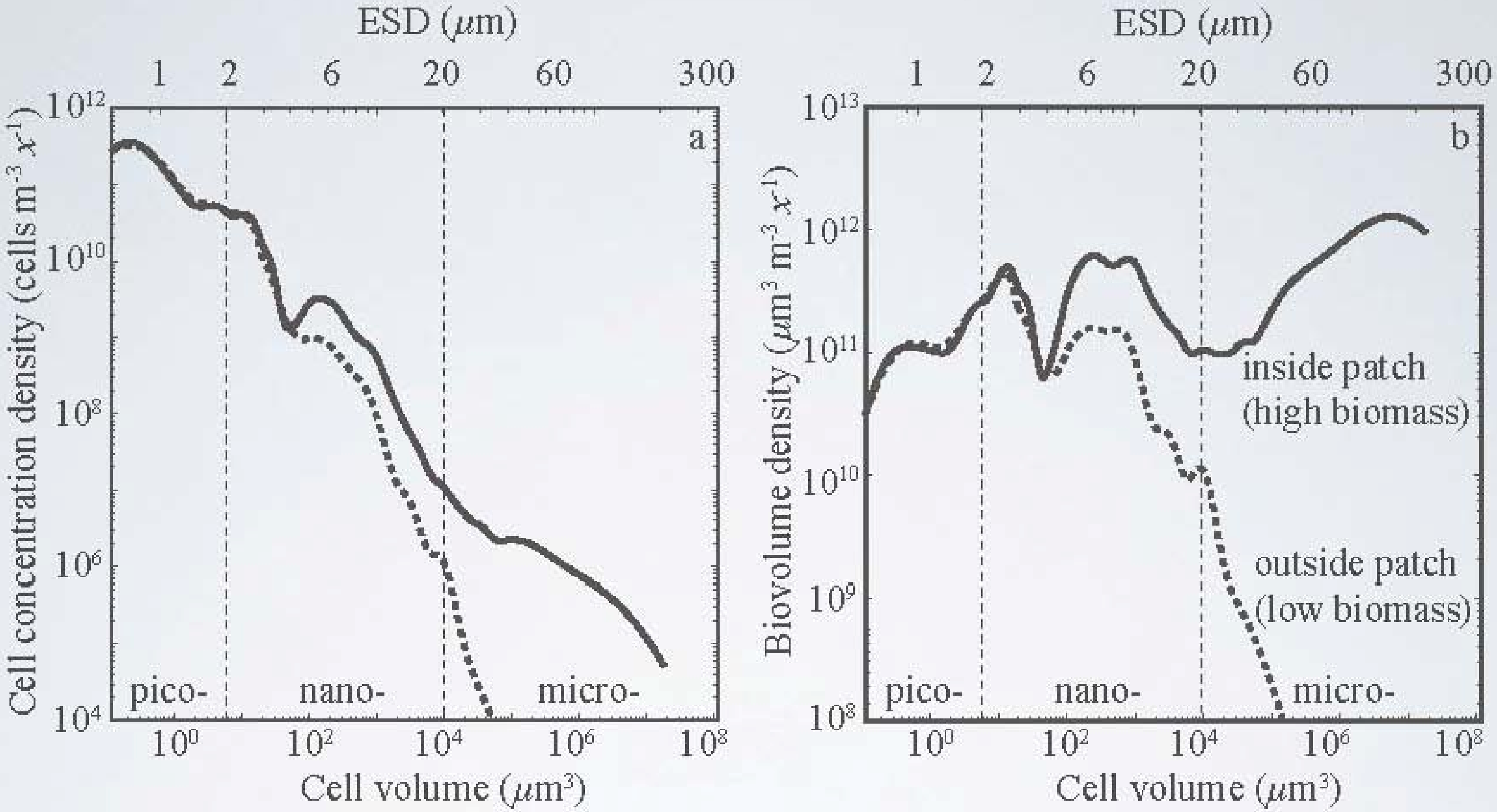




Clear global patterns in size fractionation



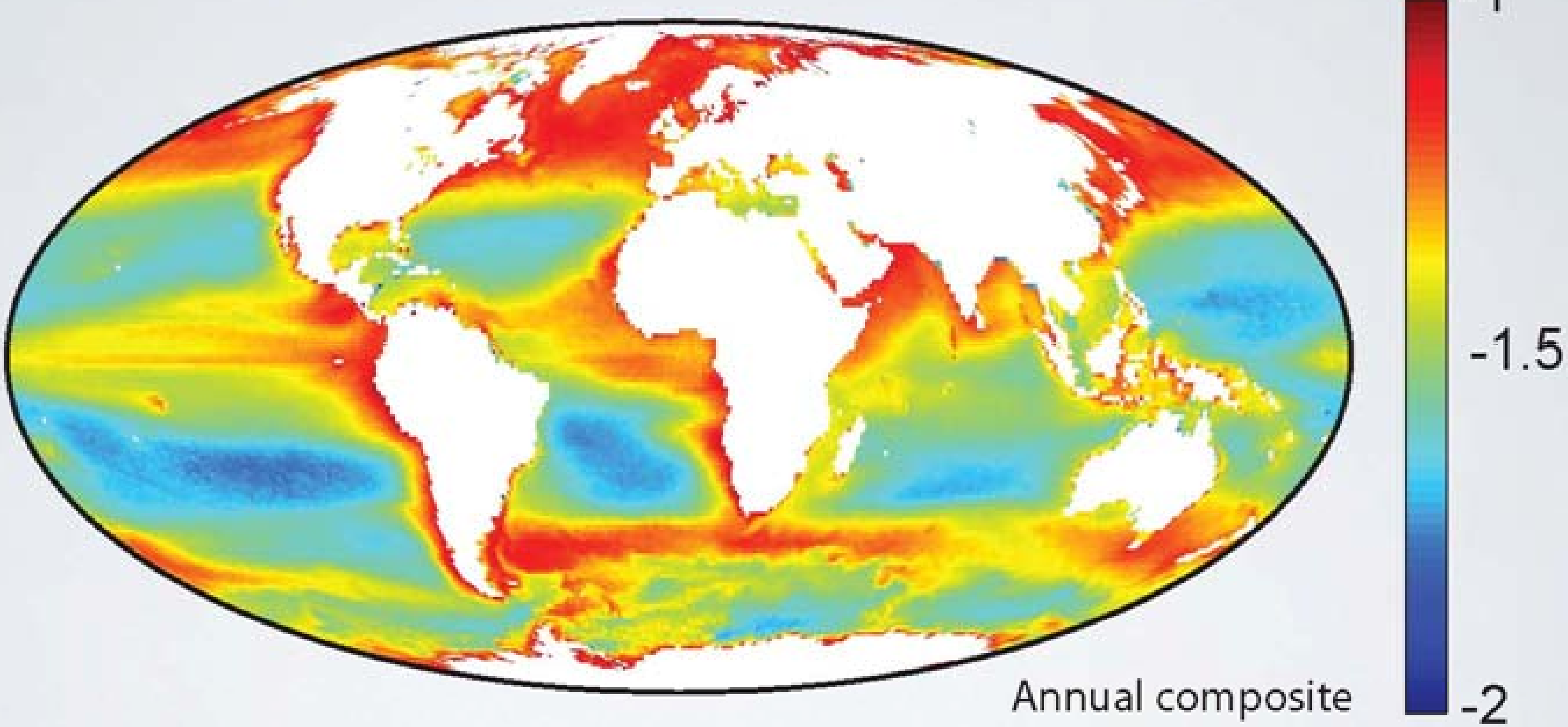
Marañón et al. (2012)
Ward et al. (submitted)



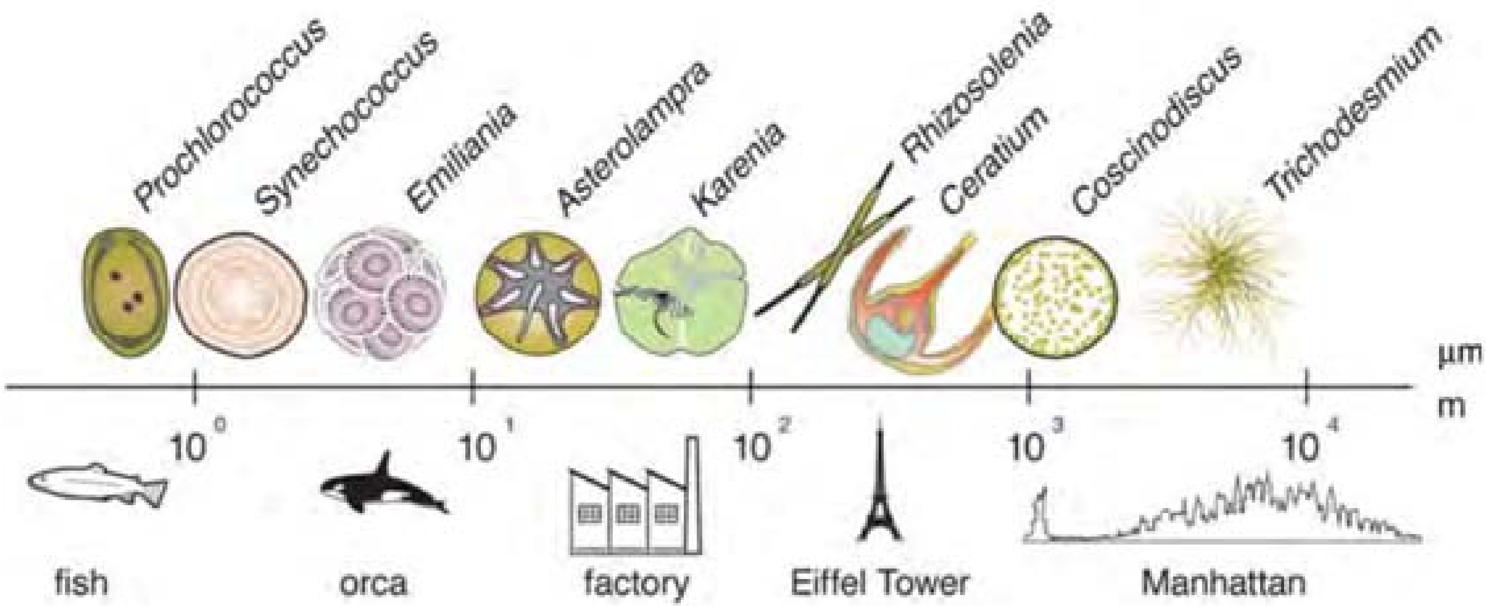
Iron-Ex II Iron Fertilisation

Schartau et al. (2010)

Slope of particle size spectra (plankton in case I waters?)

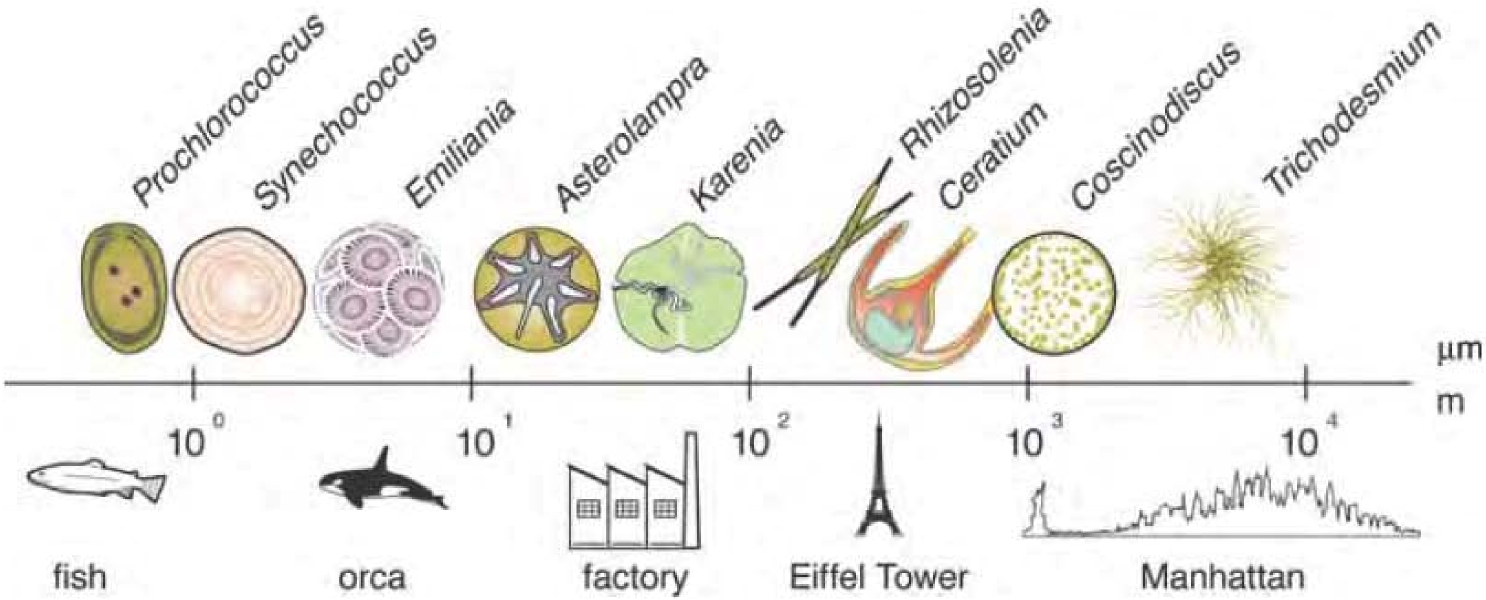


Kostadinov et al. (2010)



Finkel (2010)

James Tyrwhitt-Drake



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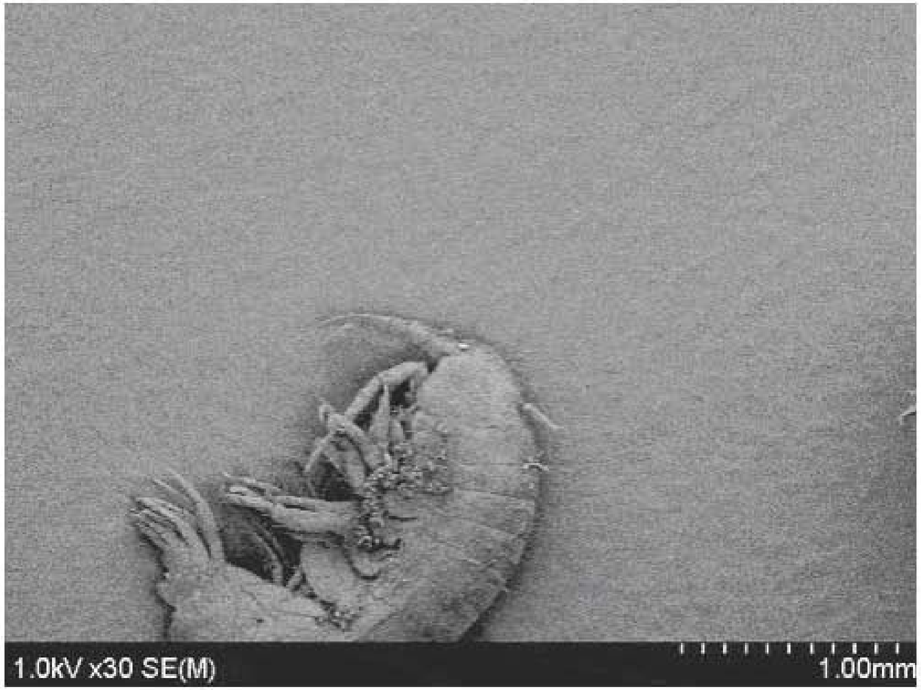
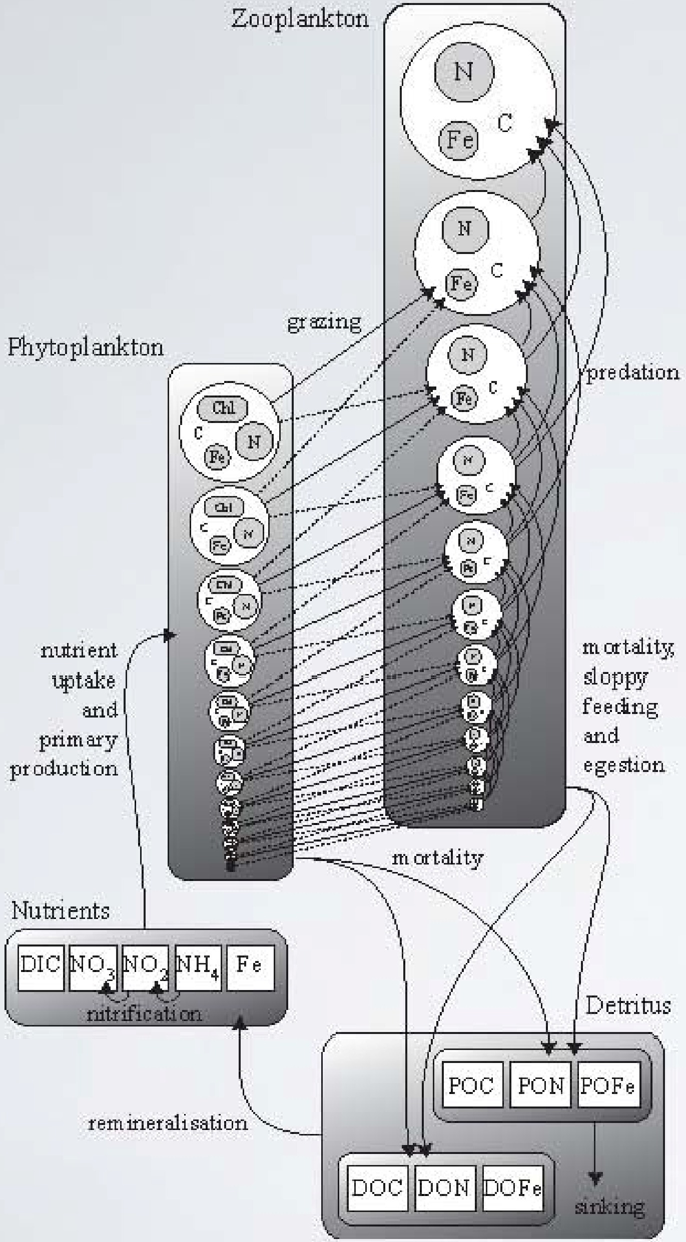


James Tyrwhitt-Drake

Model Structure



n(NPZD) quota model

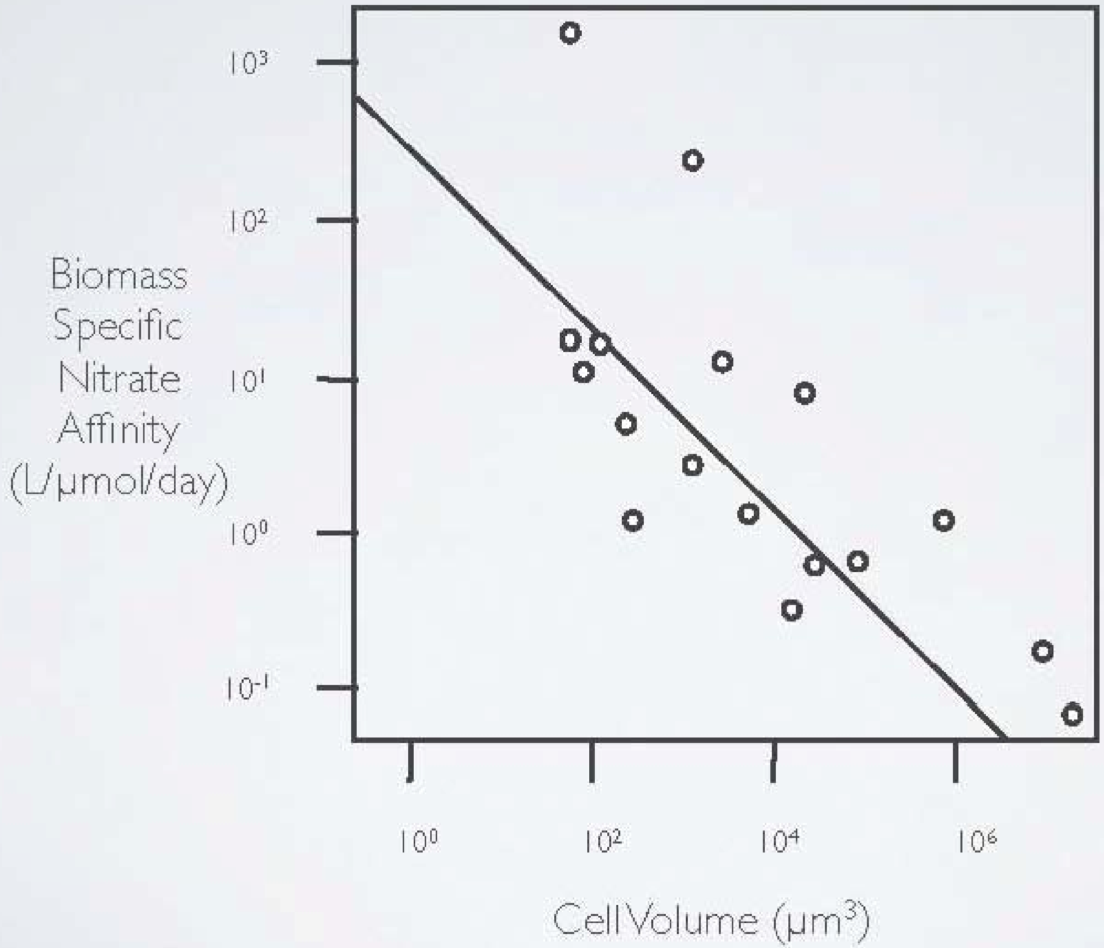
allometric parameterisation
$p=aV^b$

approximately same parametric complexity as similar 2(NPZD) model

~60 biogeochemical parameters
~50 "species"
~300 state variables
(easily scalable)

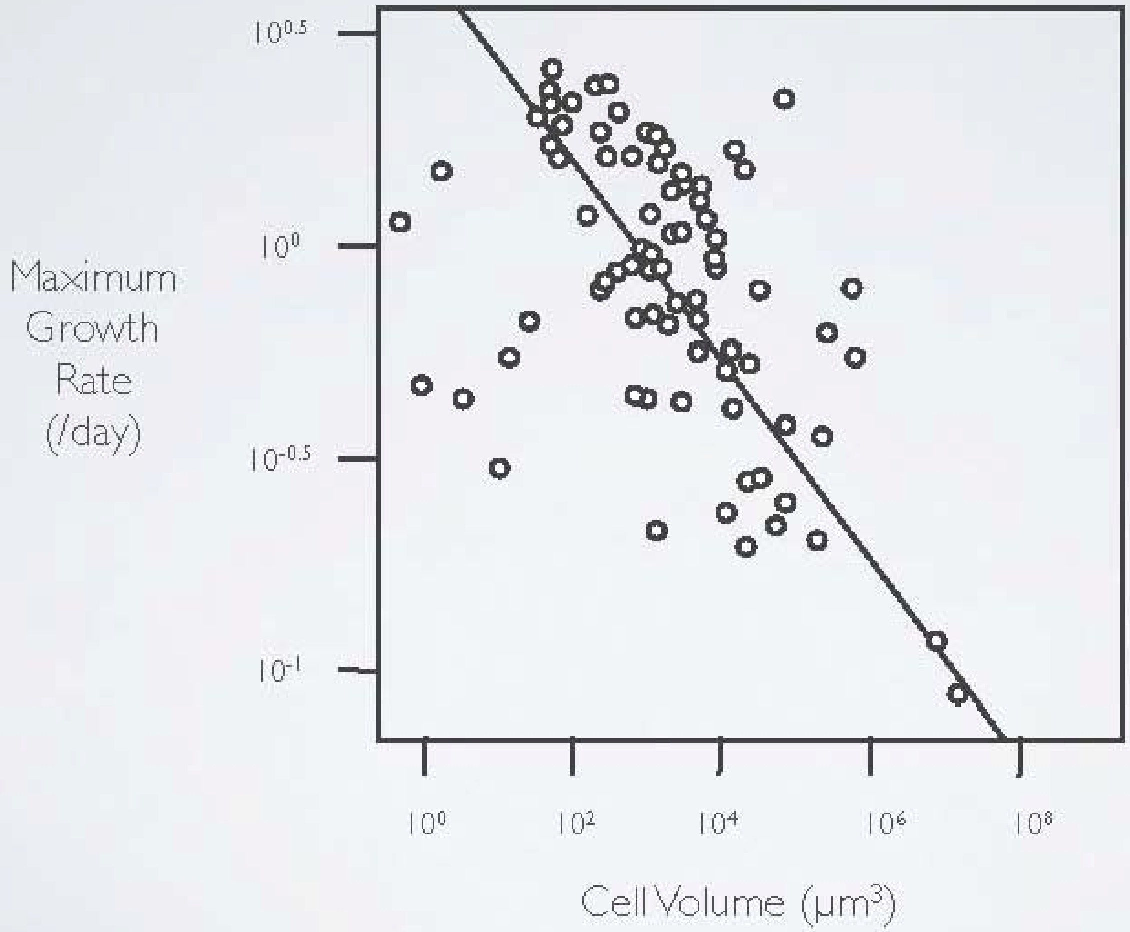
Ward et al. (2012)

Why is the size structure so clear?
I: size dependent traits



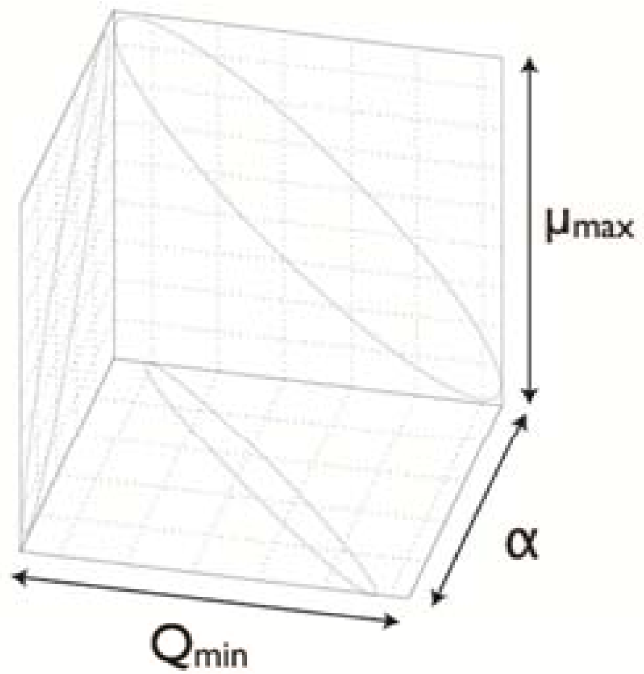
Edwards et al. (2012)

Why is the size structure so clear?
1: size dependent traits

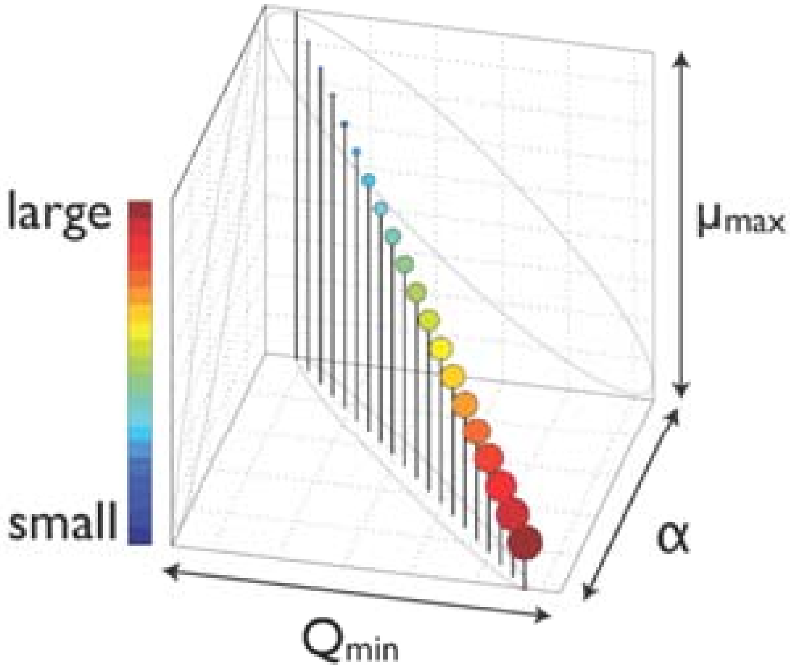


Edwards et al. (2012)

Phytoplankton community size-structure



Phytoplankton community size-structure



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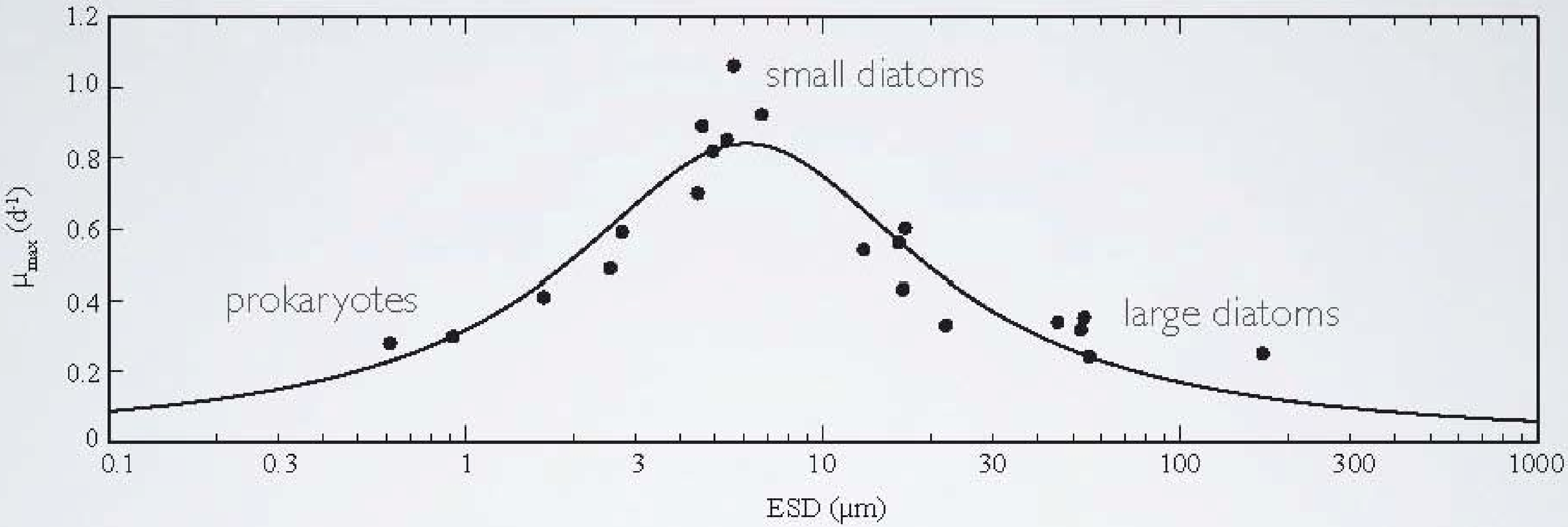
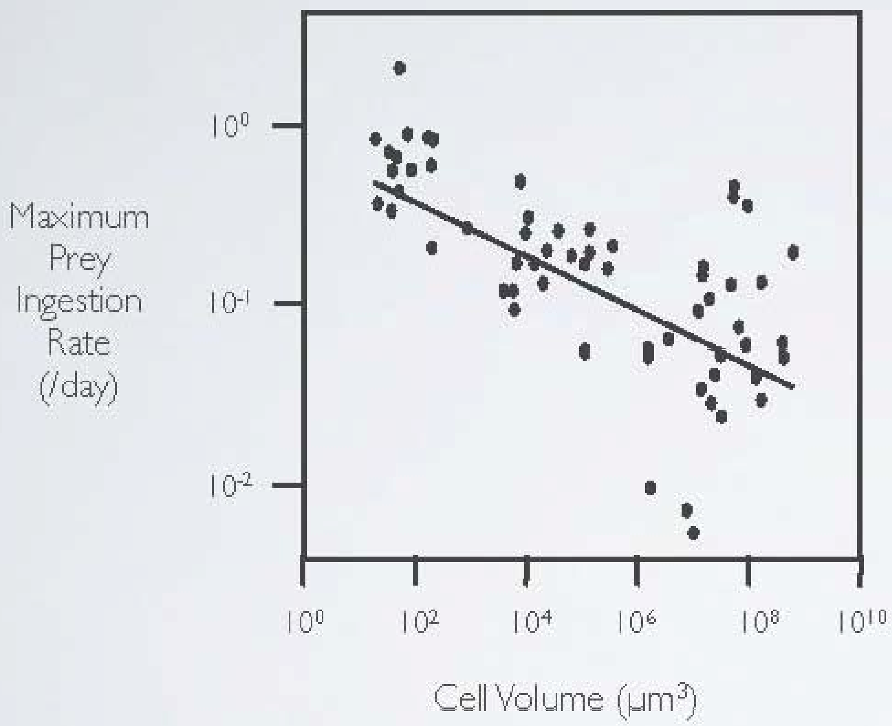
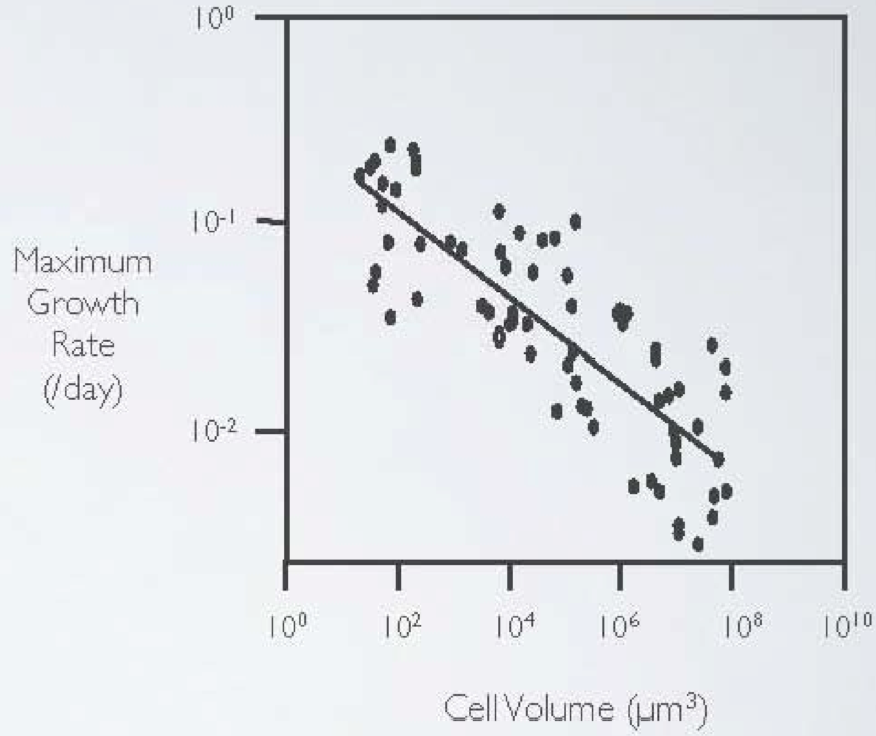


Marañón et al. (2012)

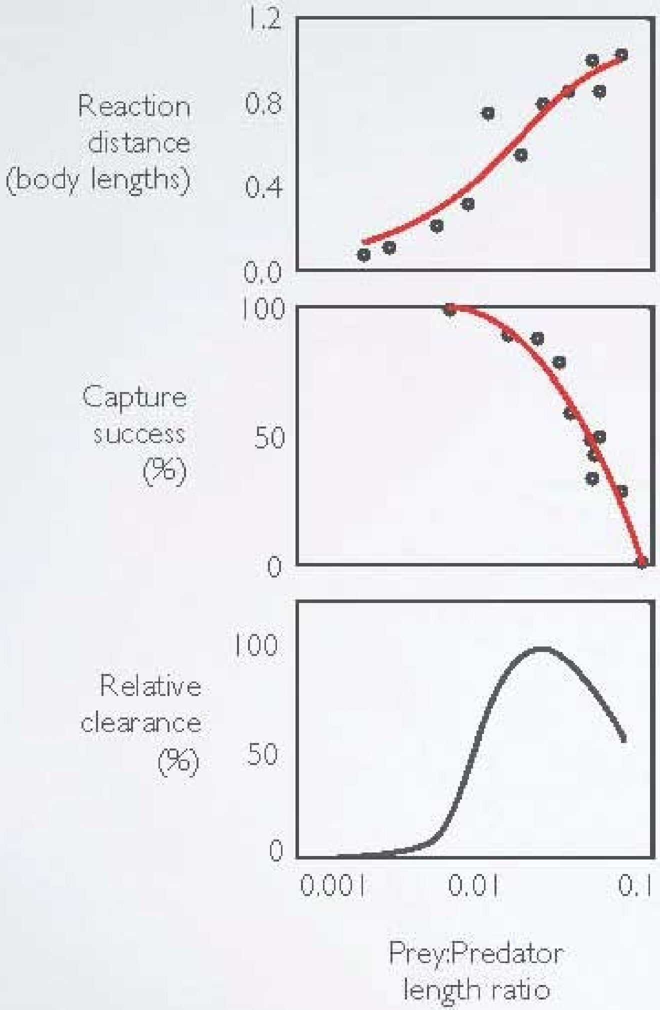
Why is the size structure so clear?
I: size dependent traits



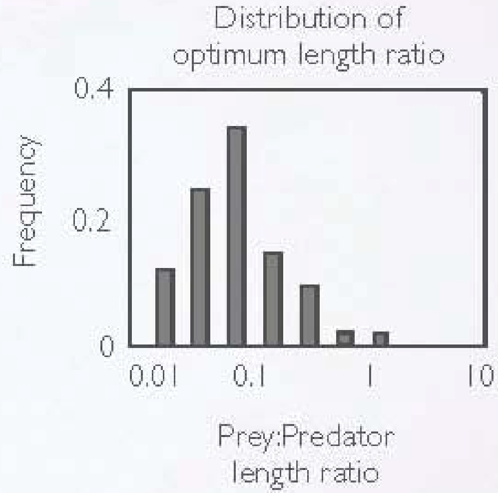


Hansen et al. (1999)

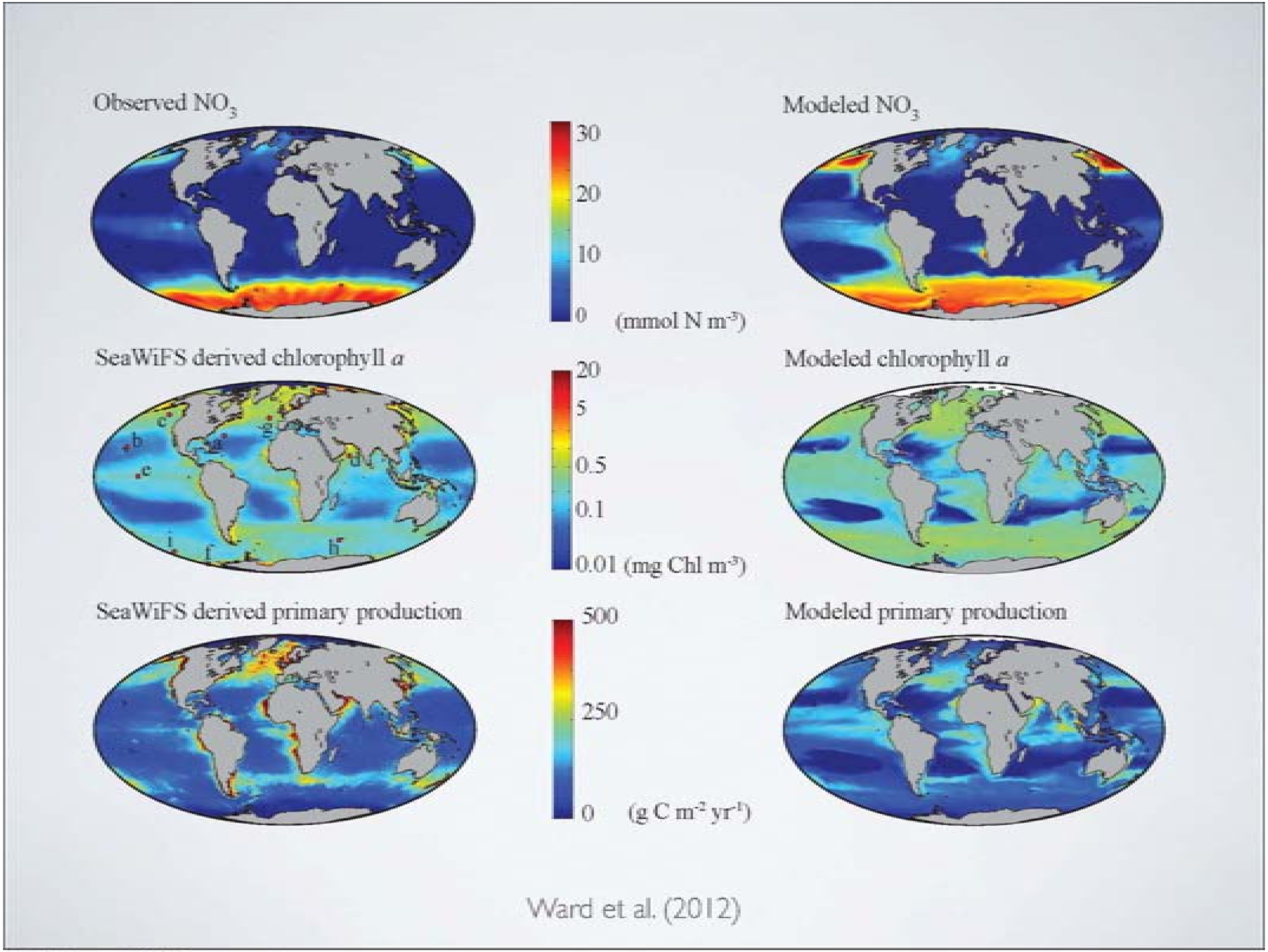
Why are there any big cells?
2: density dependent mortality
(grazing mortality and viral lysis)



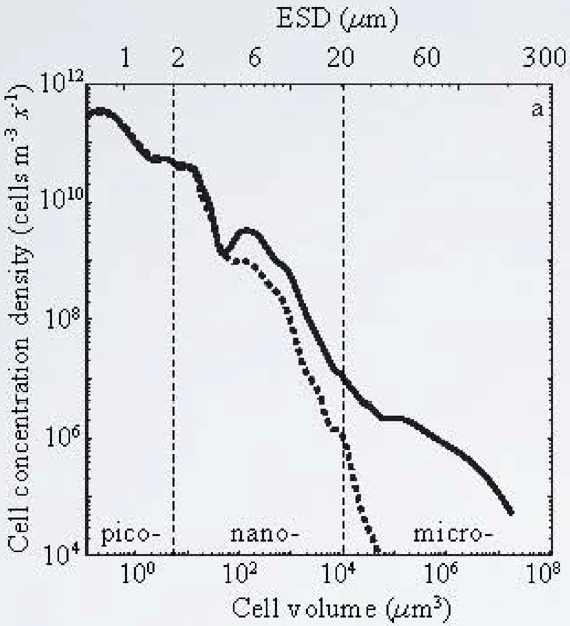
Pieter Bruegel the Elder (1556)

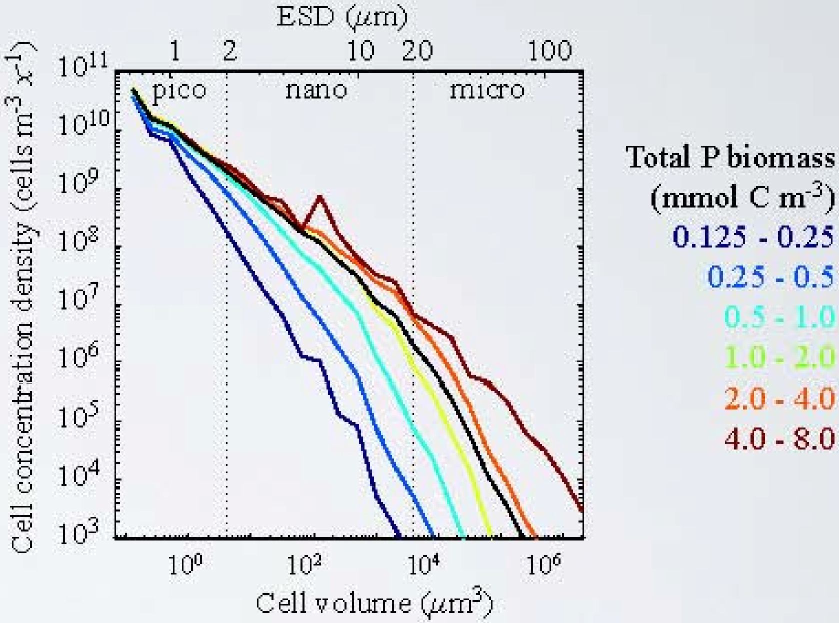


Kiorboe (2008)

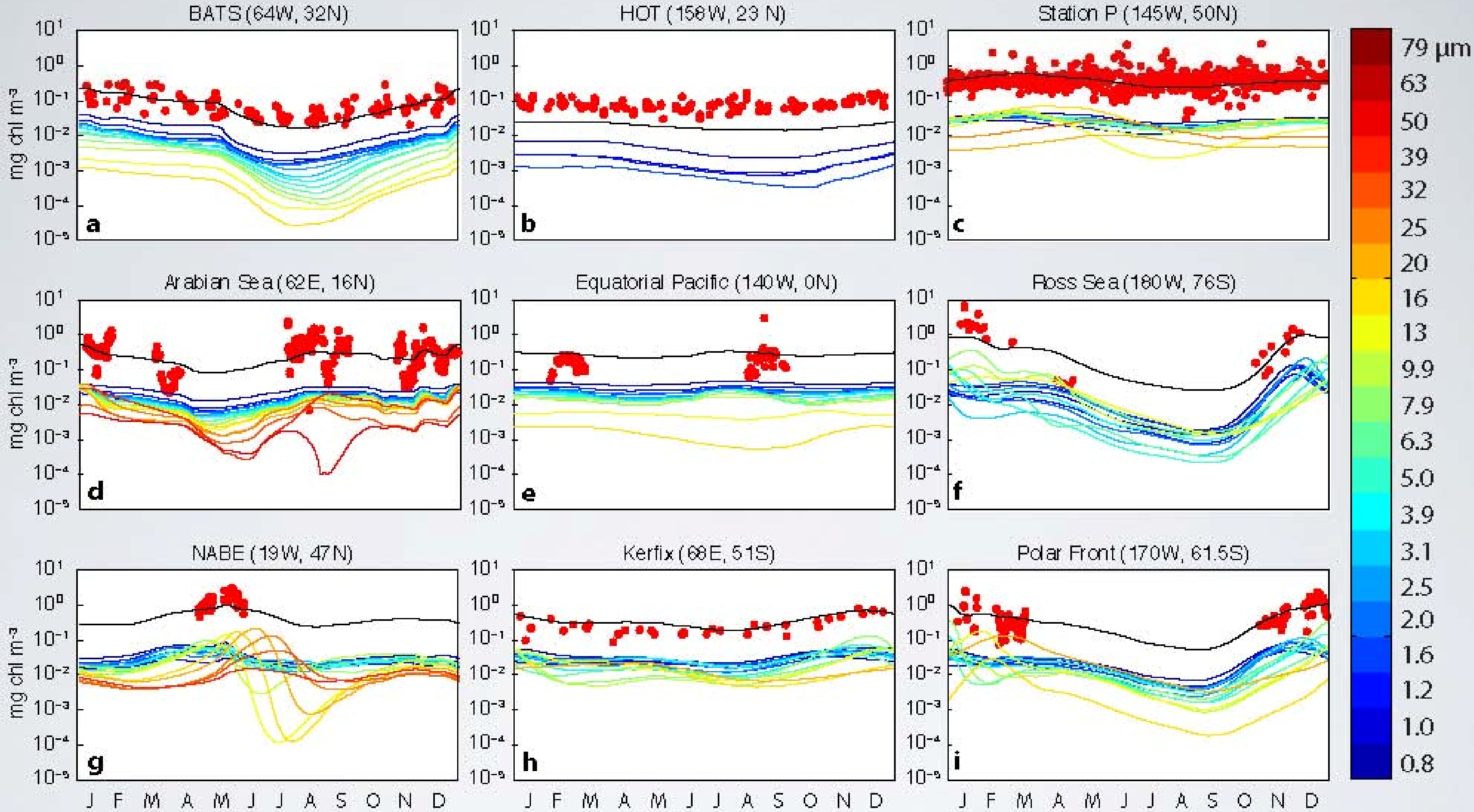


Observed NO_3
Modeled NO_3
30
20
10
0
(mmol N m^{-3})
SeaWiFS derived chlorophyll *a*
Modeled chlorophyll *a*
20
5
0.5
0.1
0.01 (mg Chl m^{-3})
SeaWiFS derived primary production
Modeled primary production
500
250
0
(g C m^{-2} yr^{-1})
Ward et al. (2012)





Schartau et al. (2010)
Ward et al. (2012)



JGOFS Time-series sites

Kleypas & Doney (2001) http://dss.ucar.edu/datasets/ds259.0/
Ward et al. (2012) Limnology & Oceanography

linking theory to global biodiversity, biogeography and ecosystem function

1. Diverse, trait-based models of marine ecosystems - why bother?

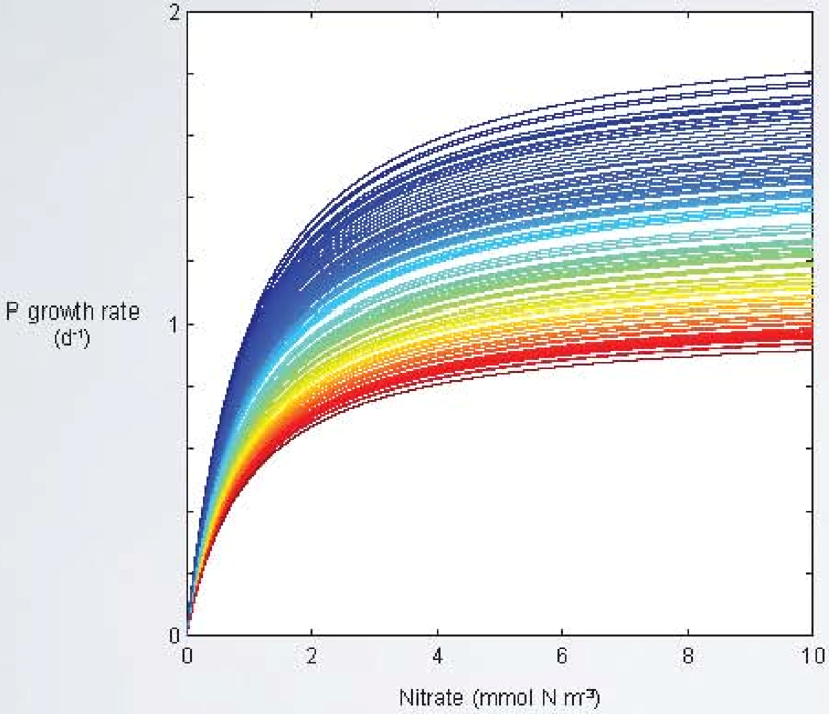
2. Maintaining diversity - the 'paradox' and its many solutions

3. Putting it all together - a size-structured plankton community model

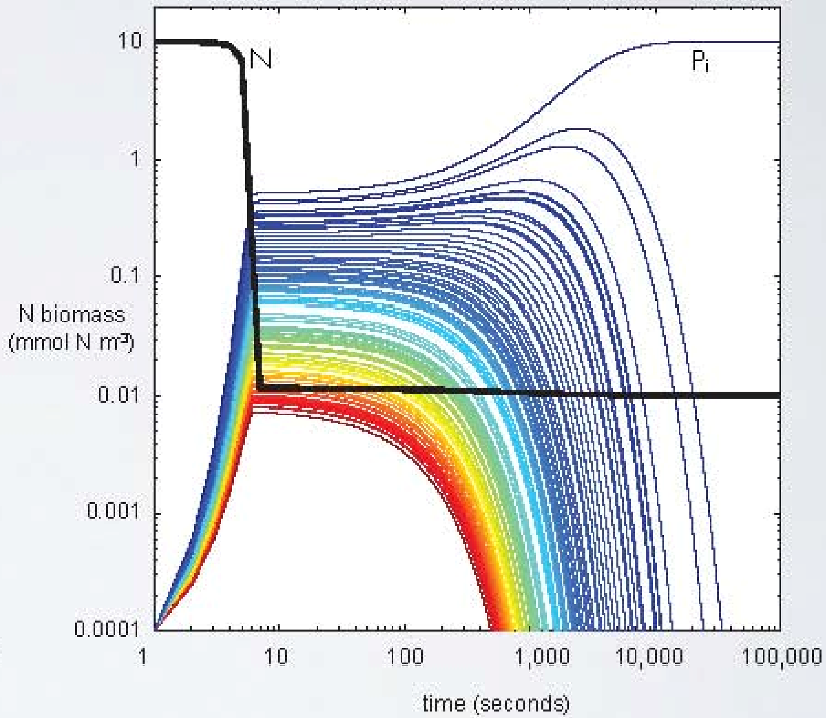
4. Taking it apart again - what drives biogeography

5. Conclusions

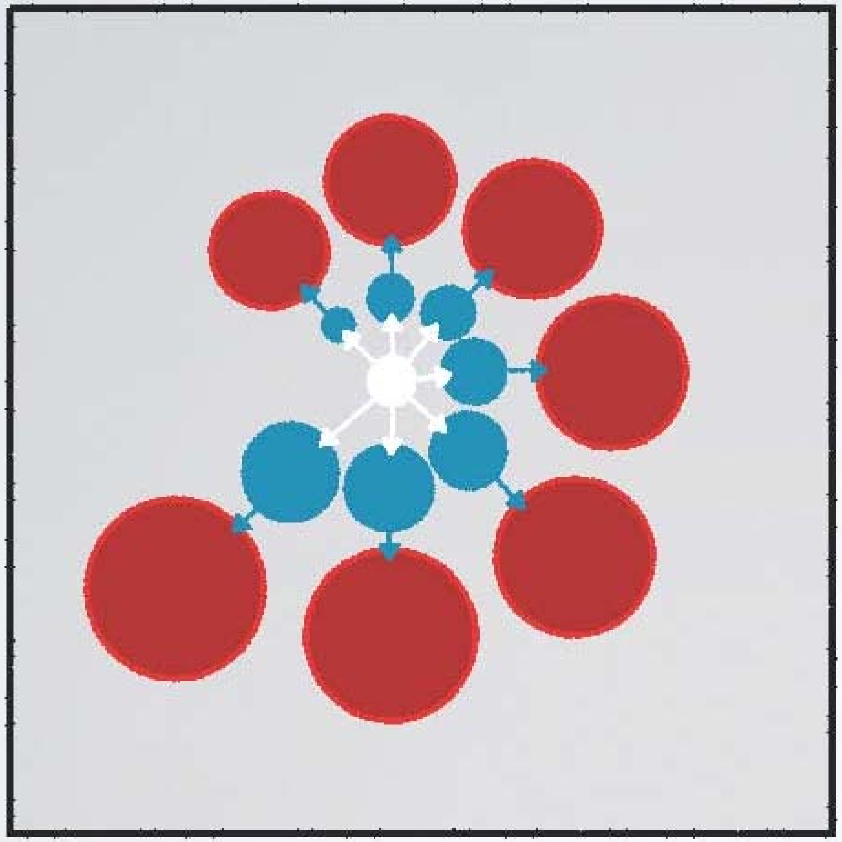
100 different sized phytoplankton

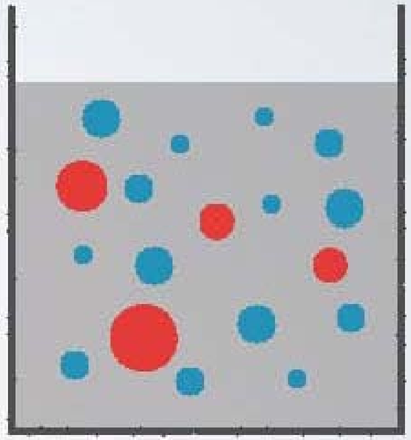


Nutrients drawn down
- only one winner at equilibrium



Why are there any big cells?
Bottom-up vs. Top-down controls





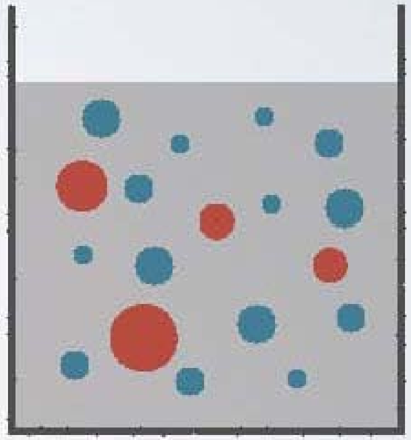
Armstrong (1994)

Why are there any big cells?
Bottom-up vs. Top-down controls

$$\frac{dP_i}{dt} = \mu_{max,i}\frac{N}{k_{N,i}+N}P_i - g_i P_i Z_i - mP_i$$

$$\frac{dZ_i}{dt} = g_i P_i Z_i - \delta Z_i$$

$$N_{total} = N + \sum_{i=1}^{n}(P_i + Z_i)$$



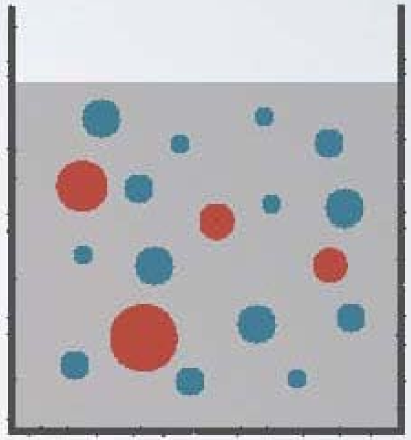
Armstrong (1994)

Why are there any big cells?
Bottom-up vs. Top-down controls

$$R^*_{N,i} = \frac{k_{N,i}(g_i Z_i + m)}{\mu_{max,i} - g_i Z_i - m}$$

$$R^*_{P,i} = \frac{\delta}{g_i}$$

$$R^*_{Z,i} = \frac{1}{g_i}\left(\mu_{max,i}\frac{N}{k_{N,i} + N} - m\right)$$



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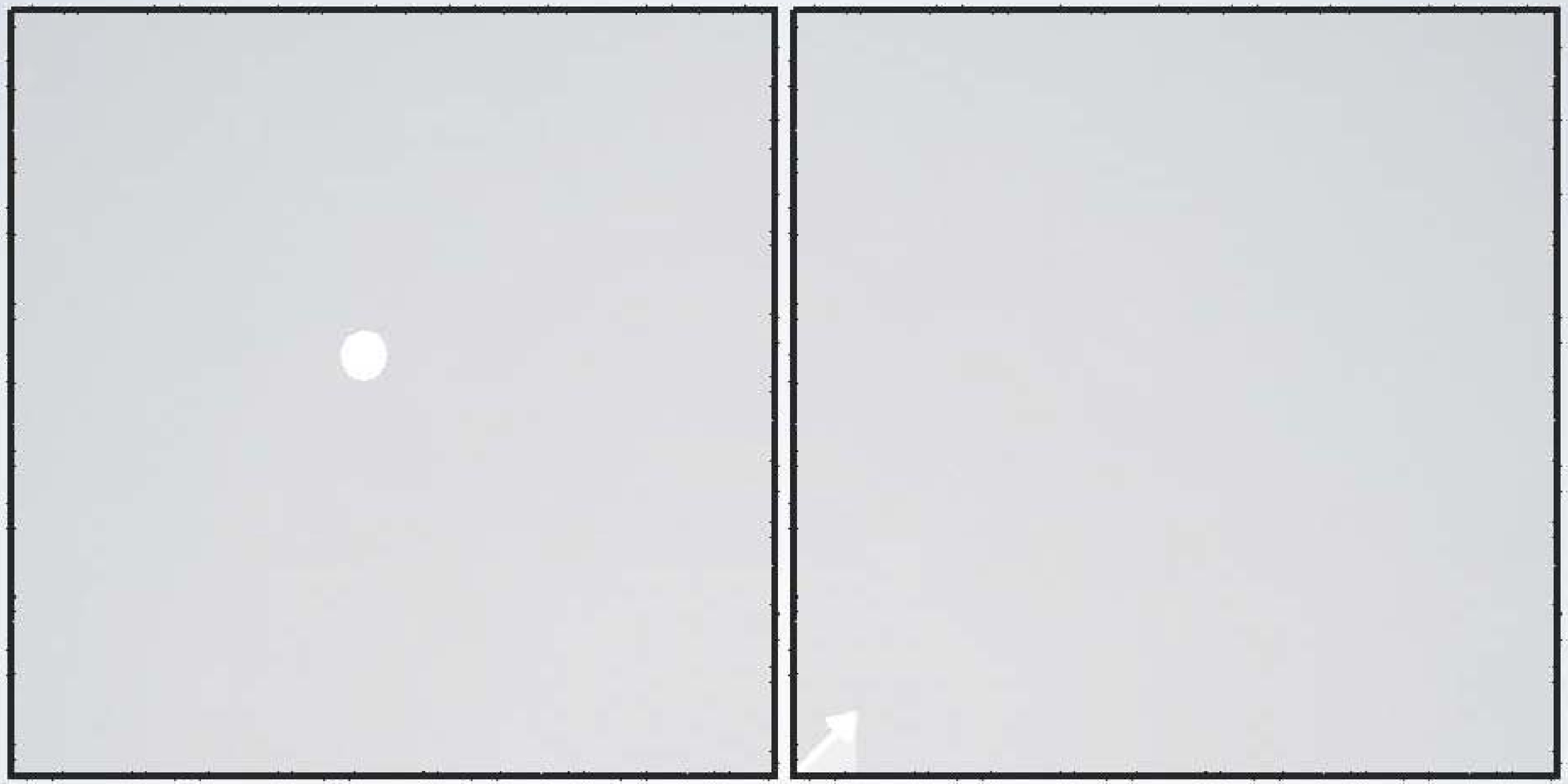

Armstrong (1994)

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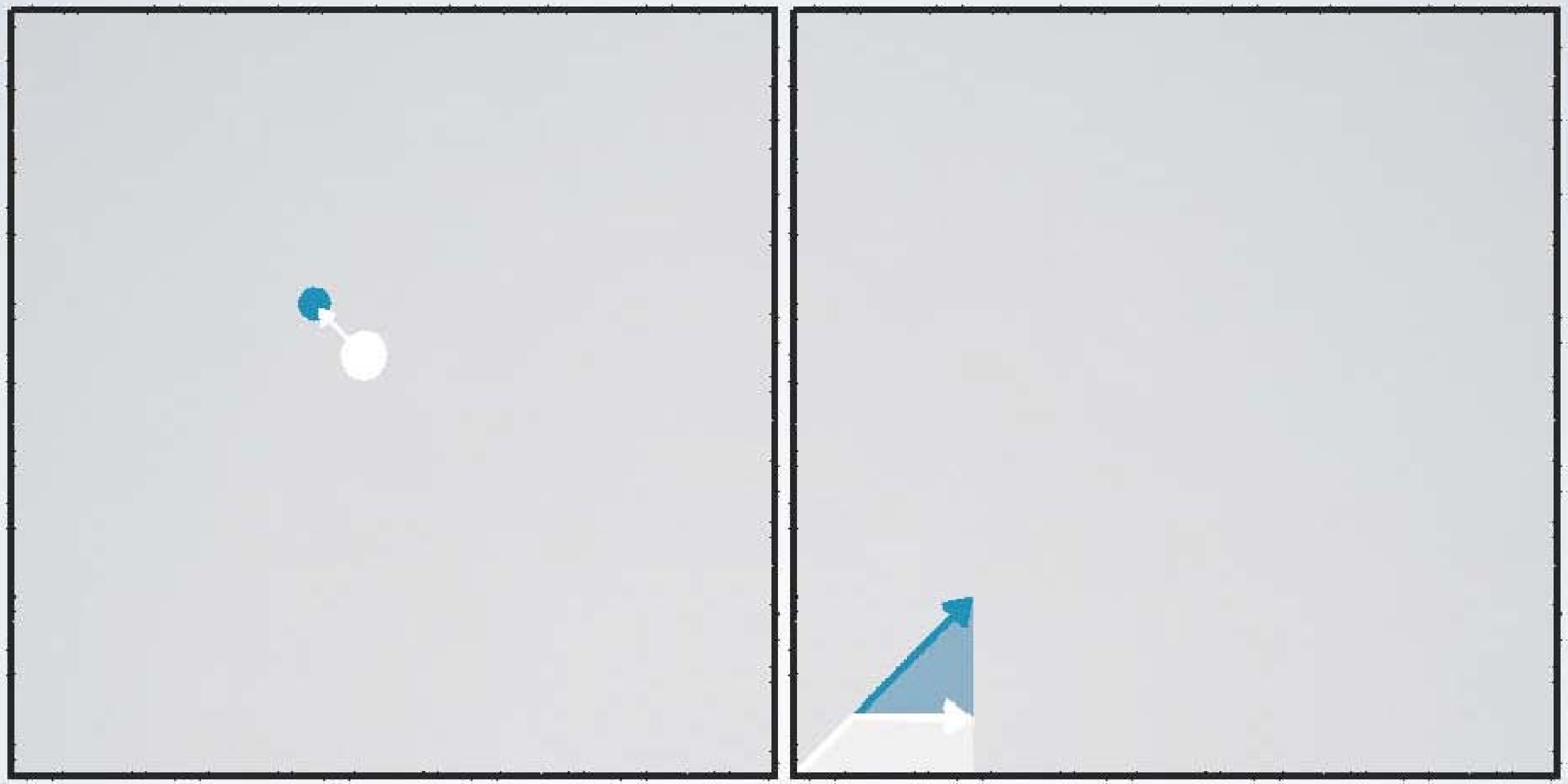
Bottom-up vs. Top-down controls



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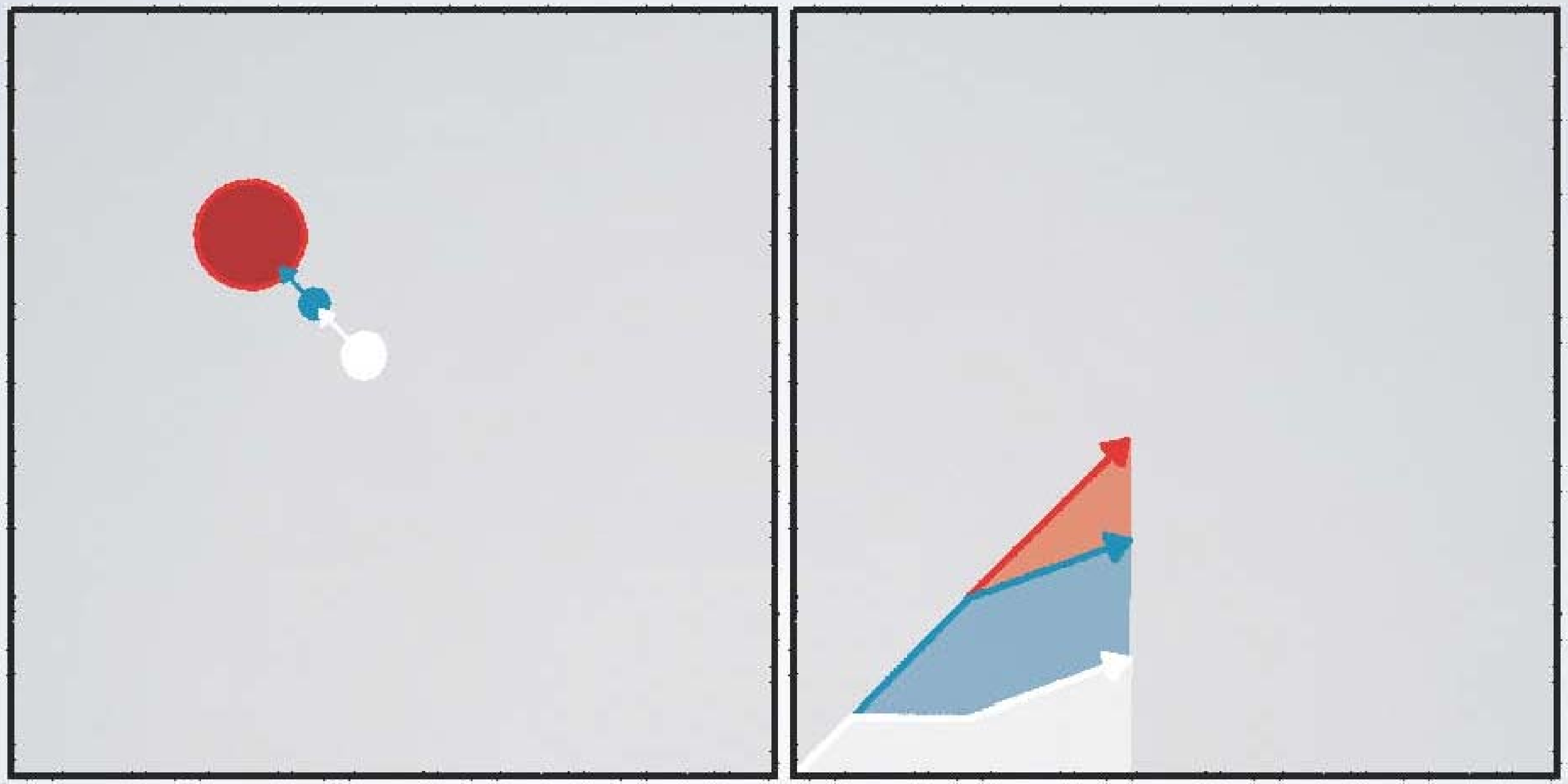
Bottom-up vs. Top-down controls



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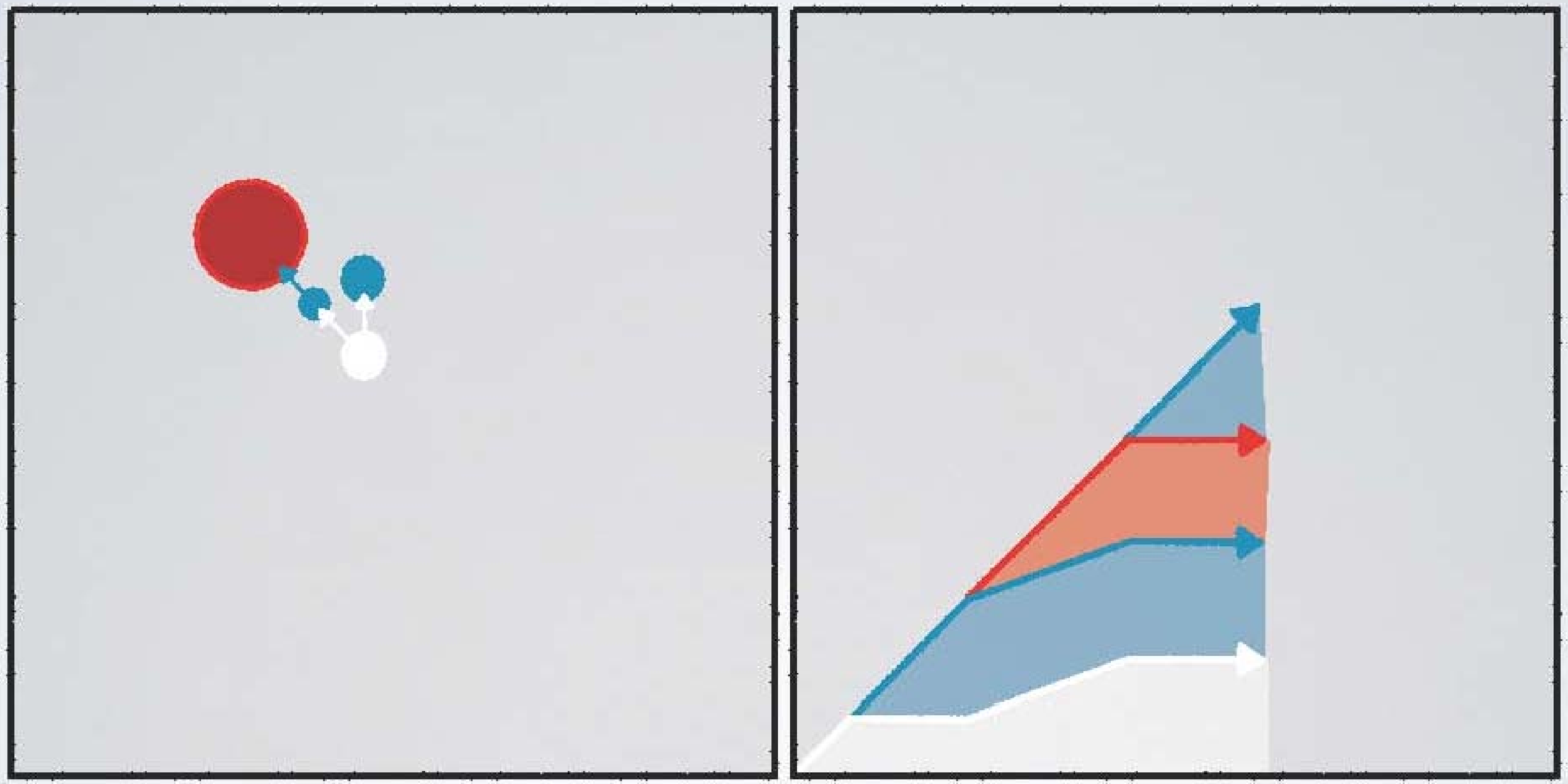

Armstrong (1994)

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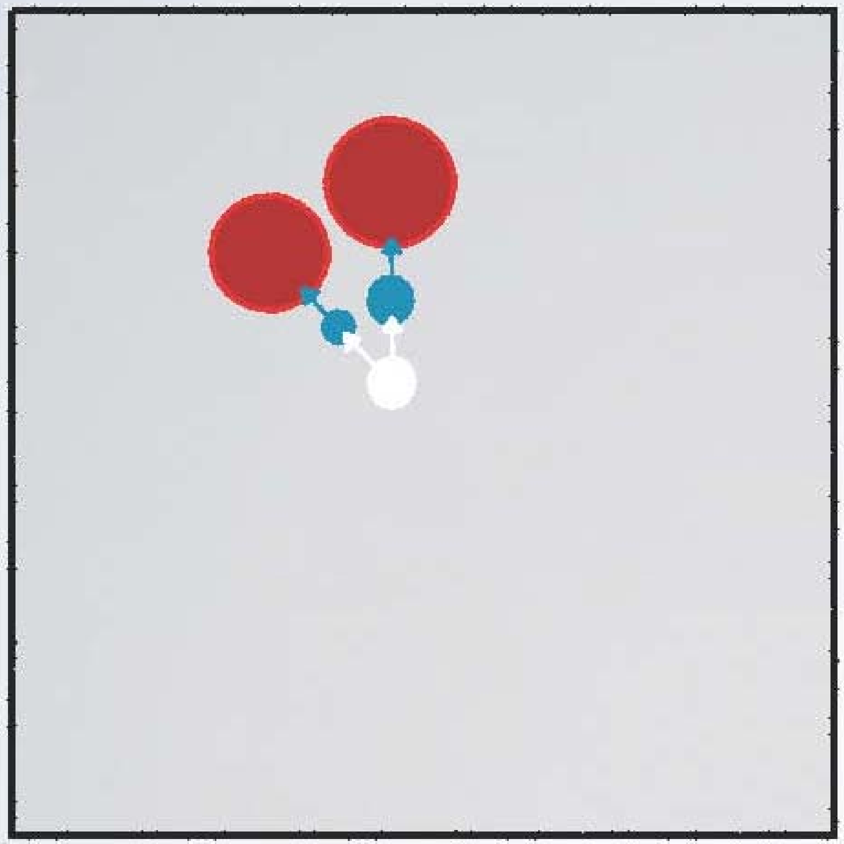
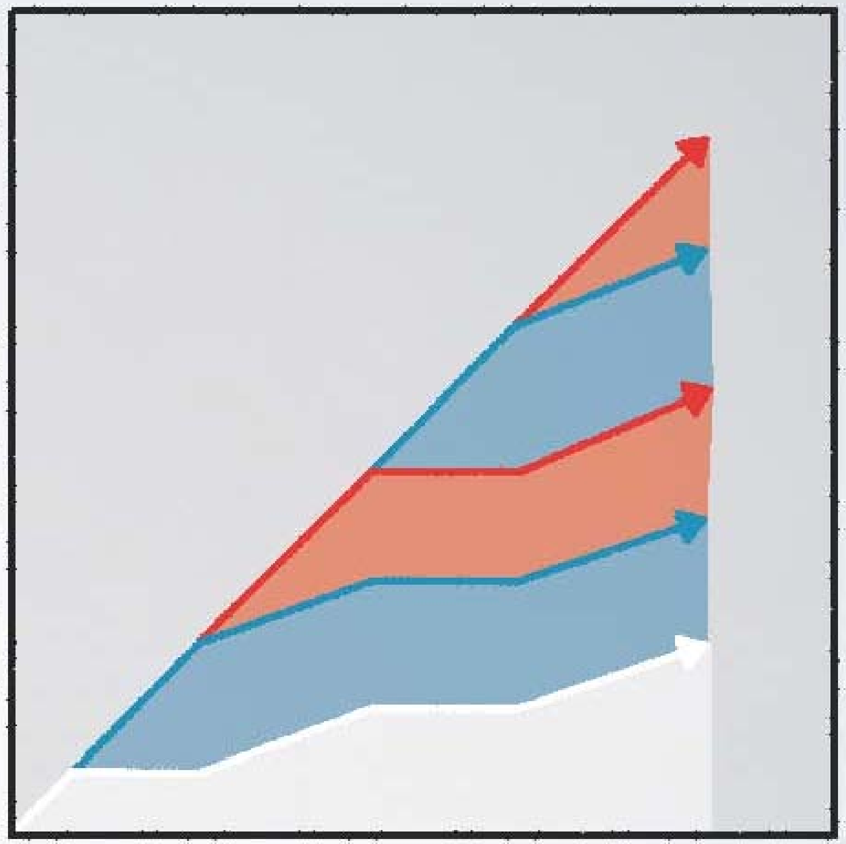
Bottom-up vs. Top-down controls





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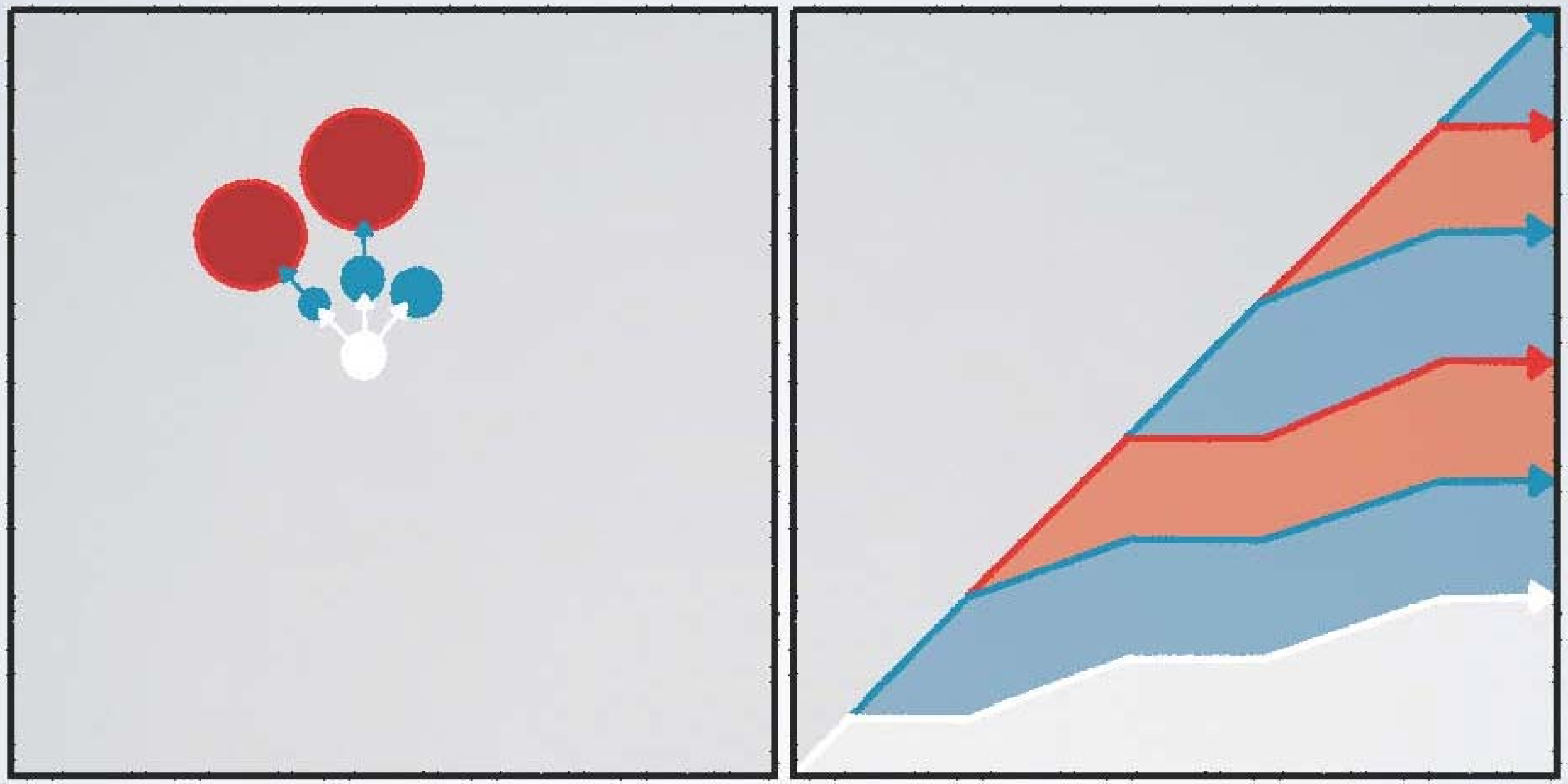

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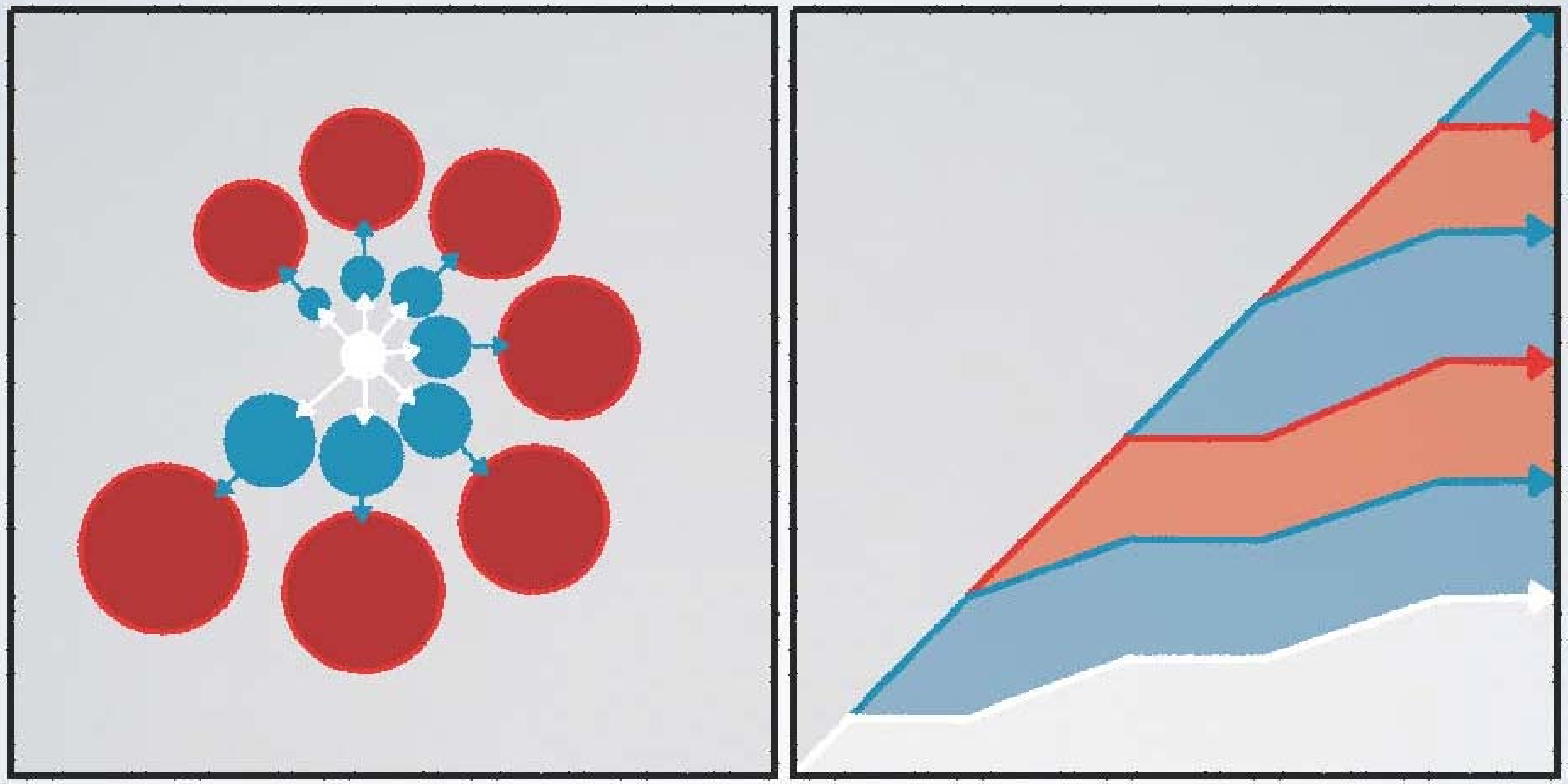

Armstrong (1994)

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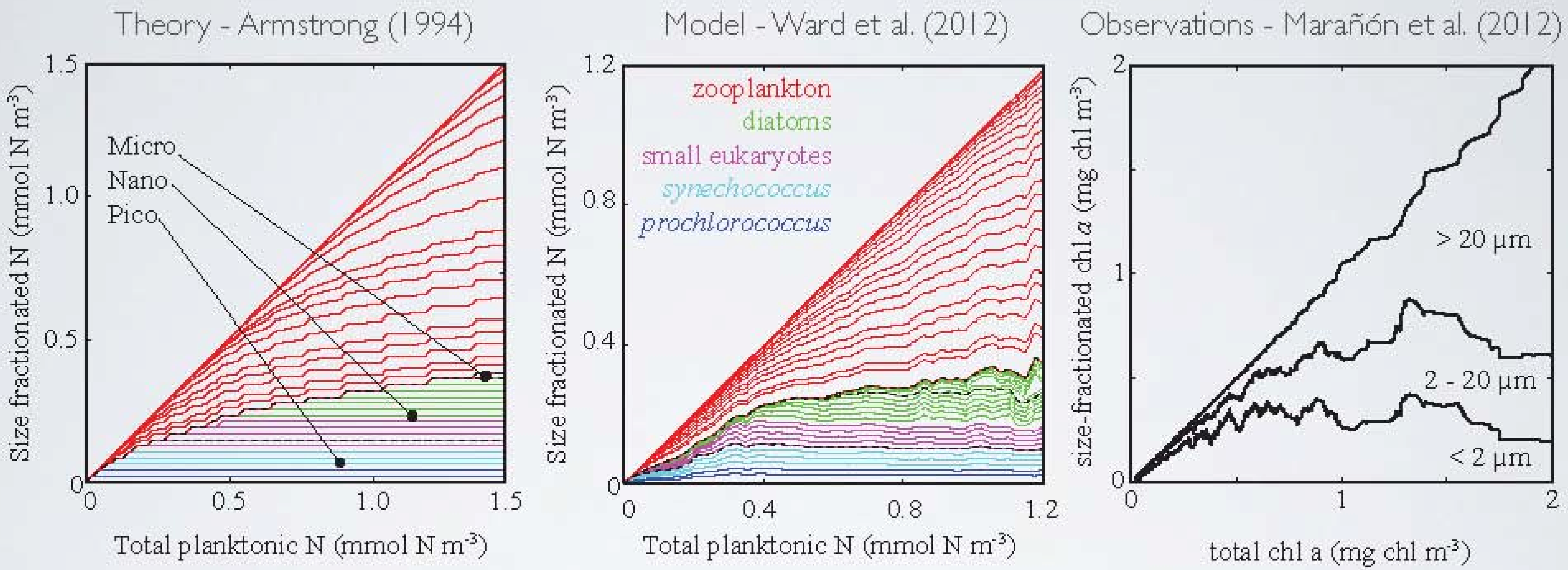
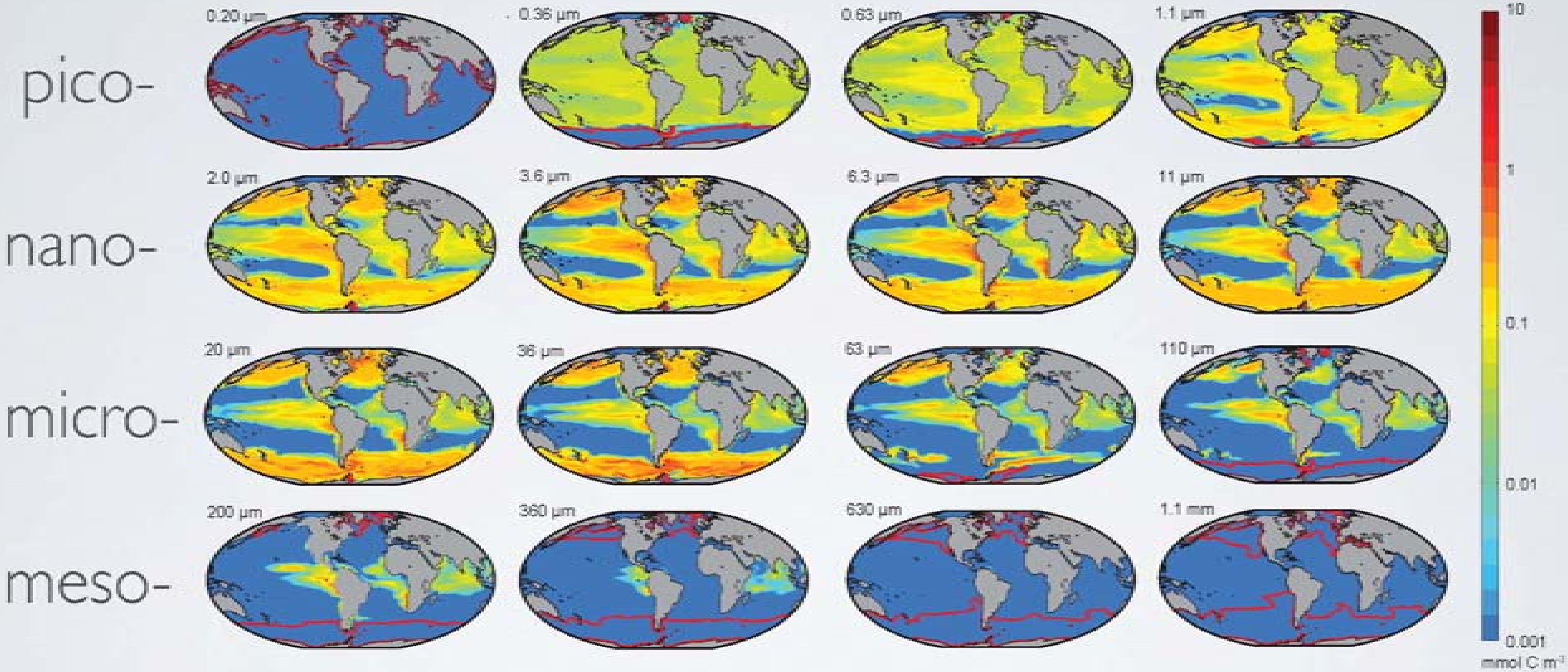
Bottom-up vs. Top-down controls

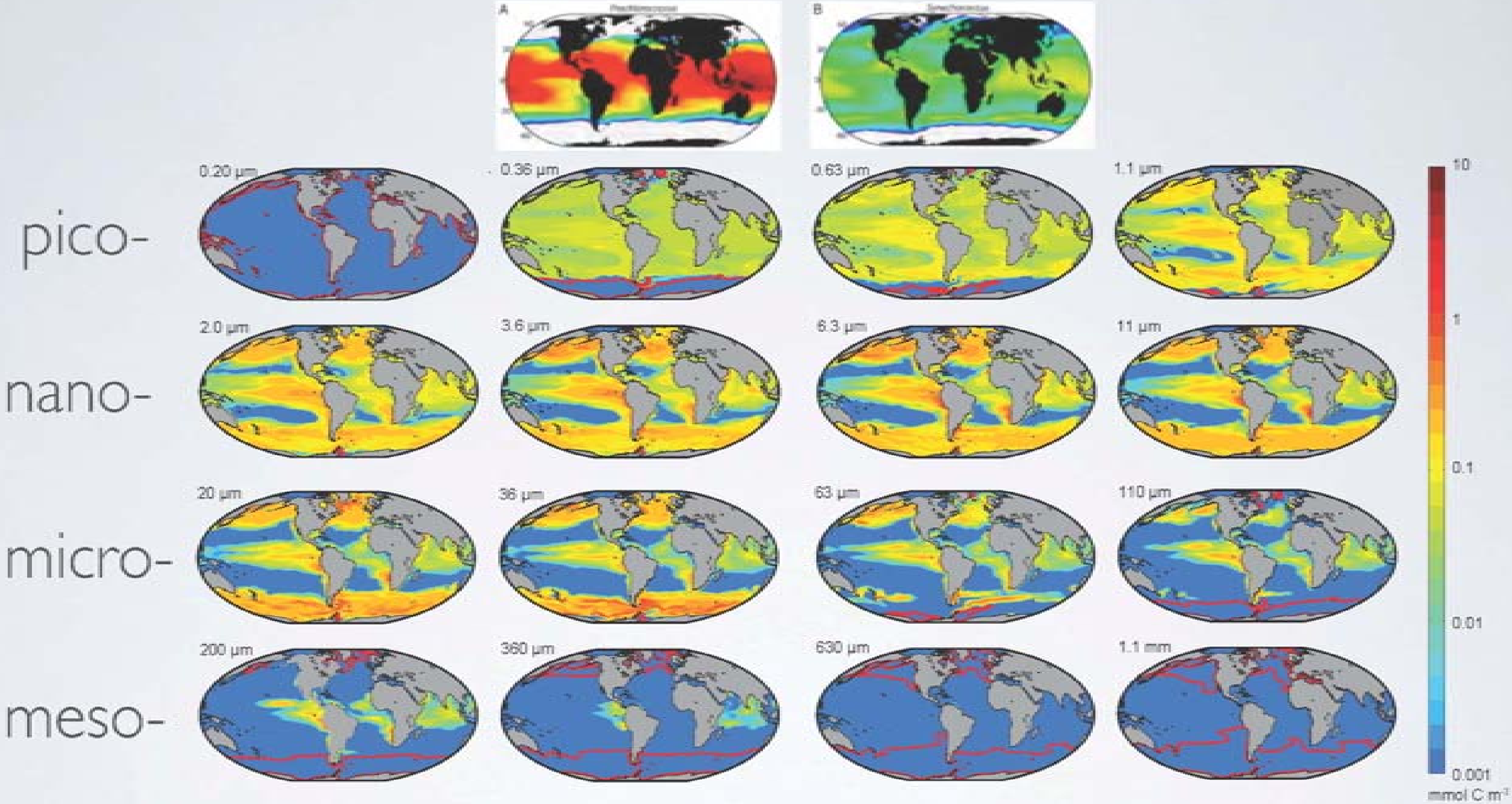


- Top-down controls limit the biomass in each size class
- Bottom-up controls dictate number of size classes, and hence total biomass

Armstrong (1994)

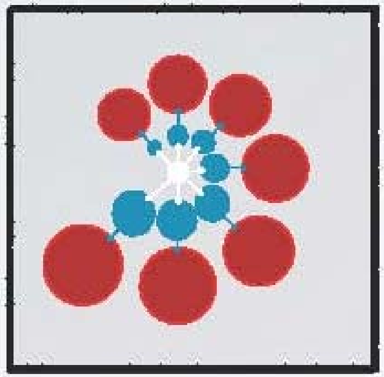

pico-
nano-
micro-
meso-
0.20 µm
0.36 µm
0.63 µm
1.1 µm
2.0 µm
3.6 µm
6.3 µm
11 µm
20 µm
36 µm
63 µm
110 µm
200 µm
360 µm
630 µm
1.1 mm
10
1
0.1
0.01
0.001
mmol C m⁻³

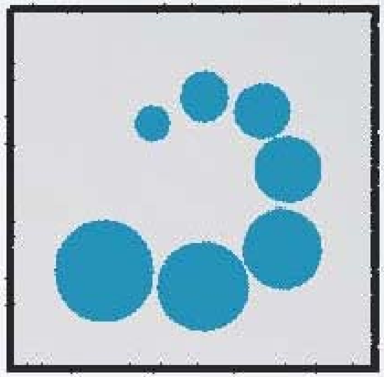
cell density - Flombaum et al. (2013)



Experiment 1:

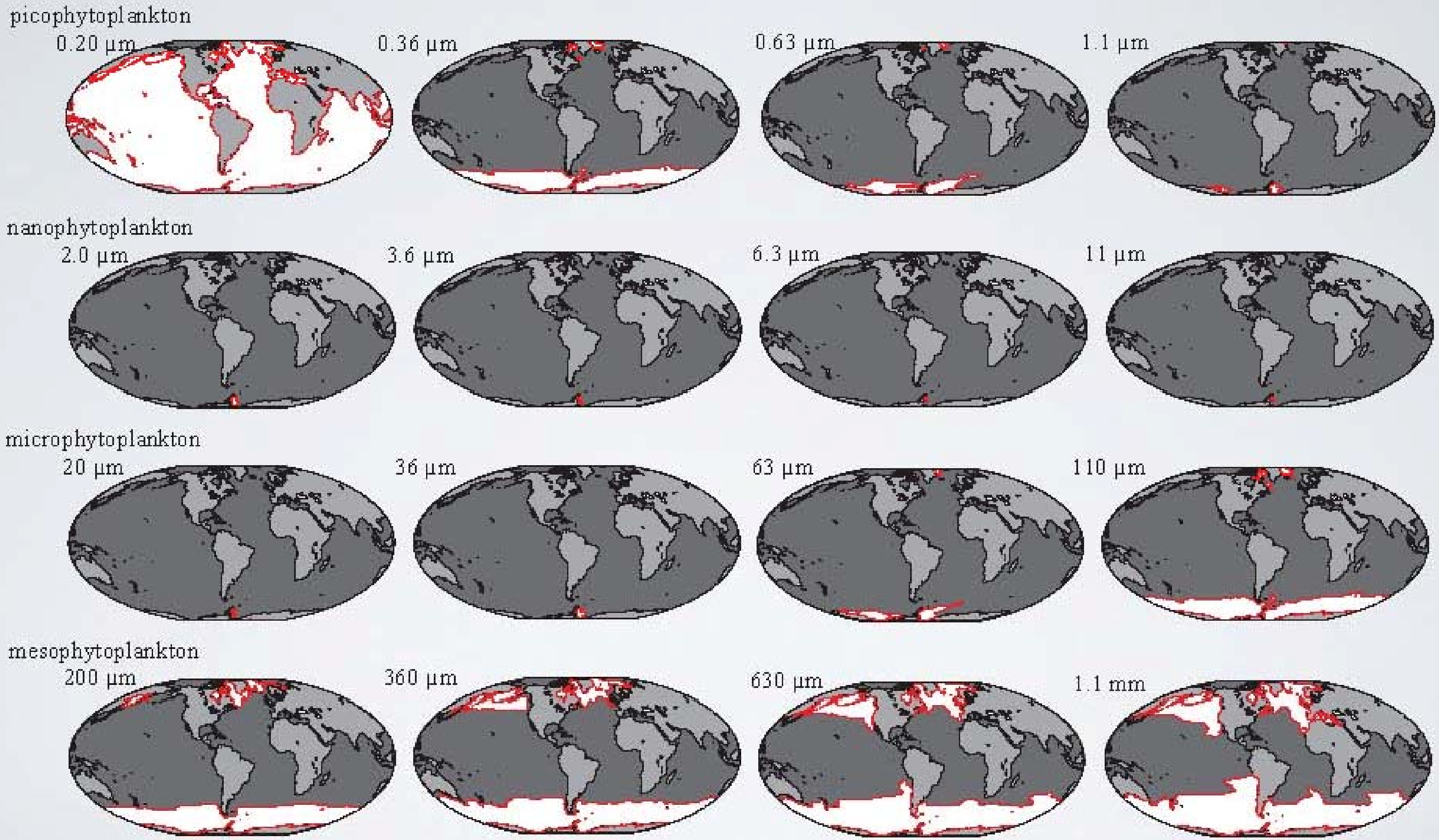
twenty phytoplankton size classes
no nutrient limitation



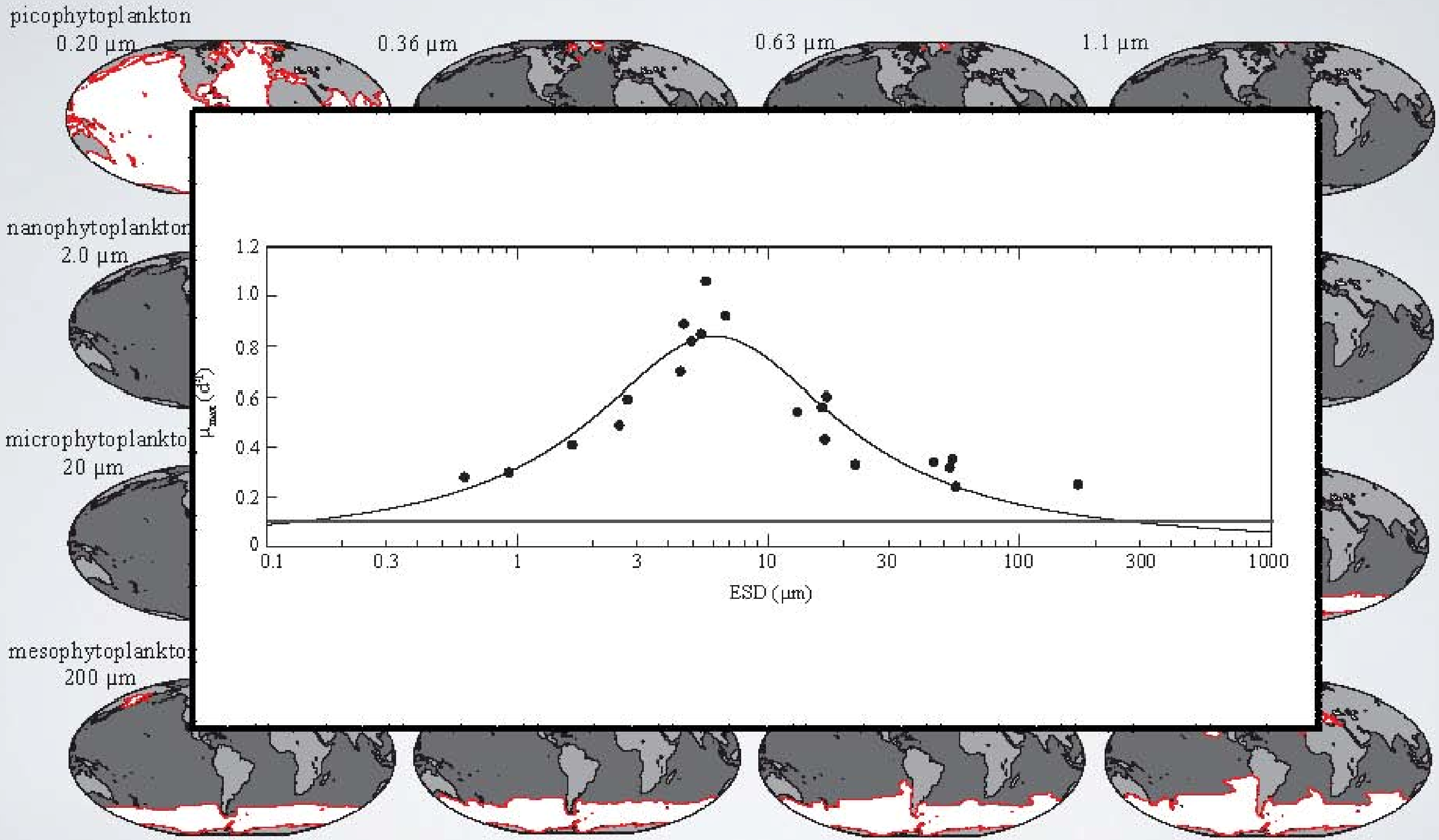


where can phytoplankton live
in absence of competition?

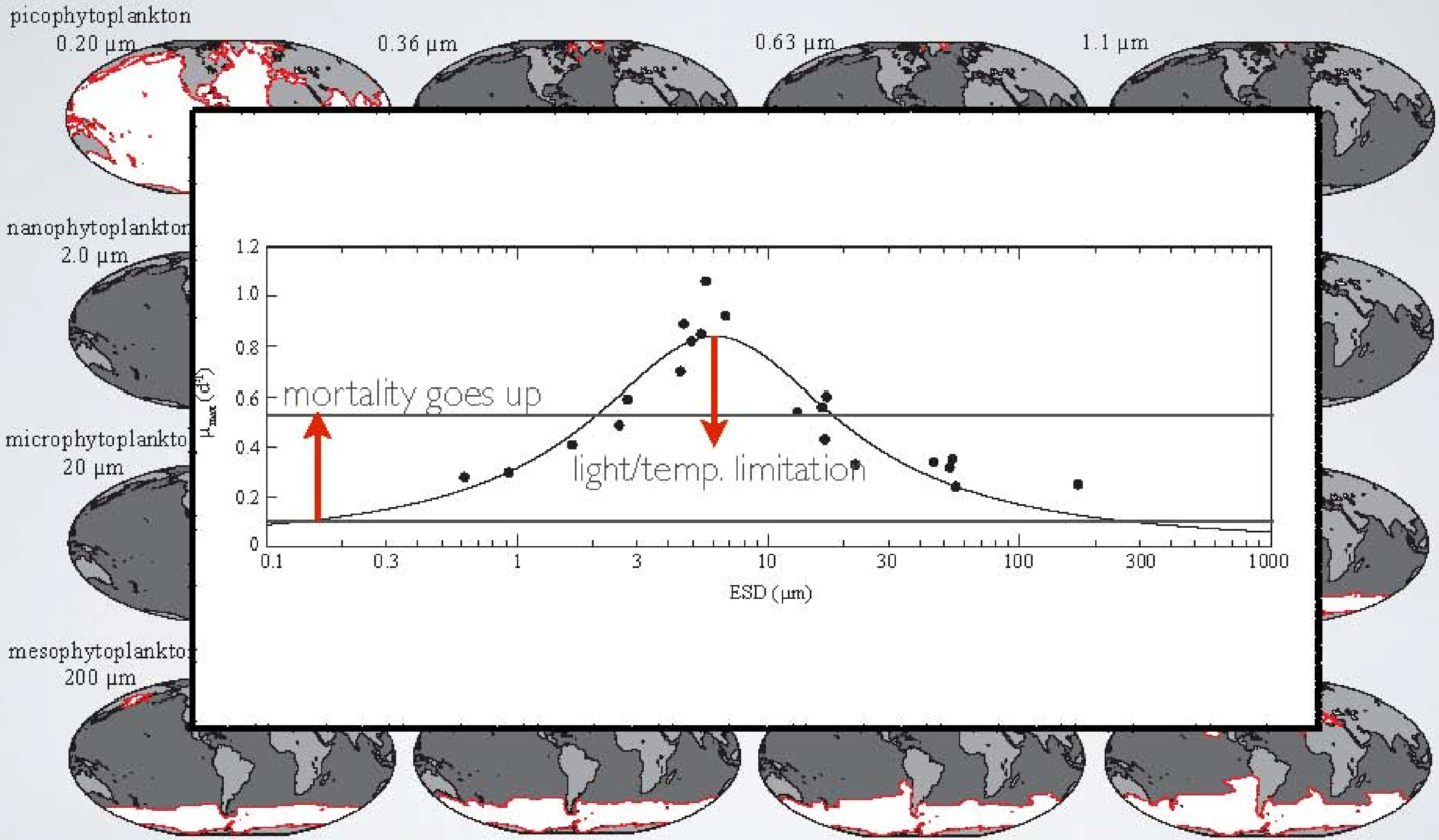
maximum growth rate vs. mortality sets *fundamental niche*



maximum growth rate vs. mortality sets *fundamental niche*



maximum growth rate vs. mortality sets *fundamental niche*



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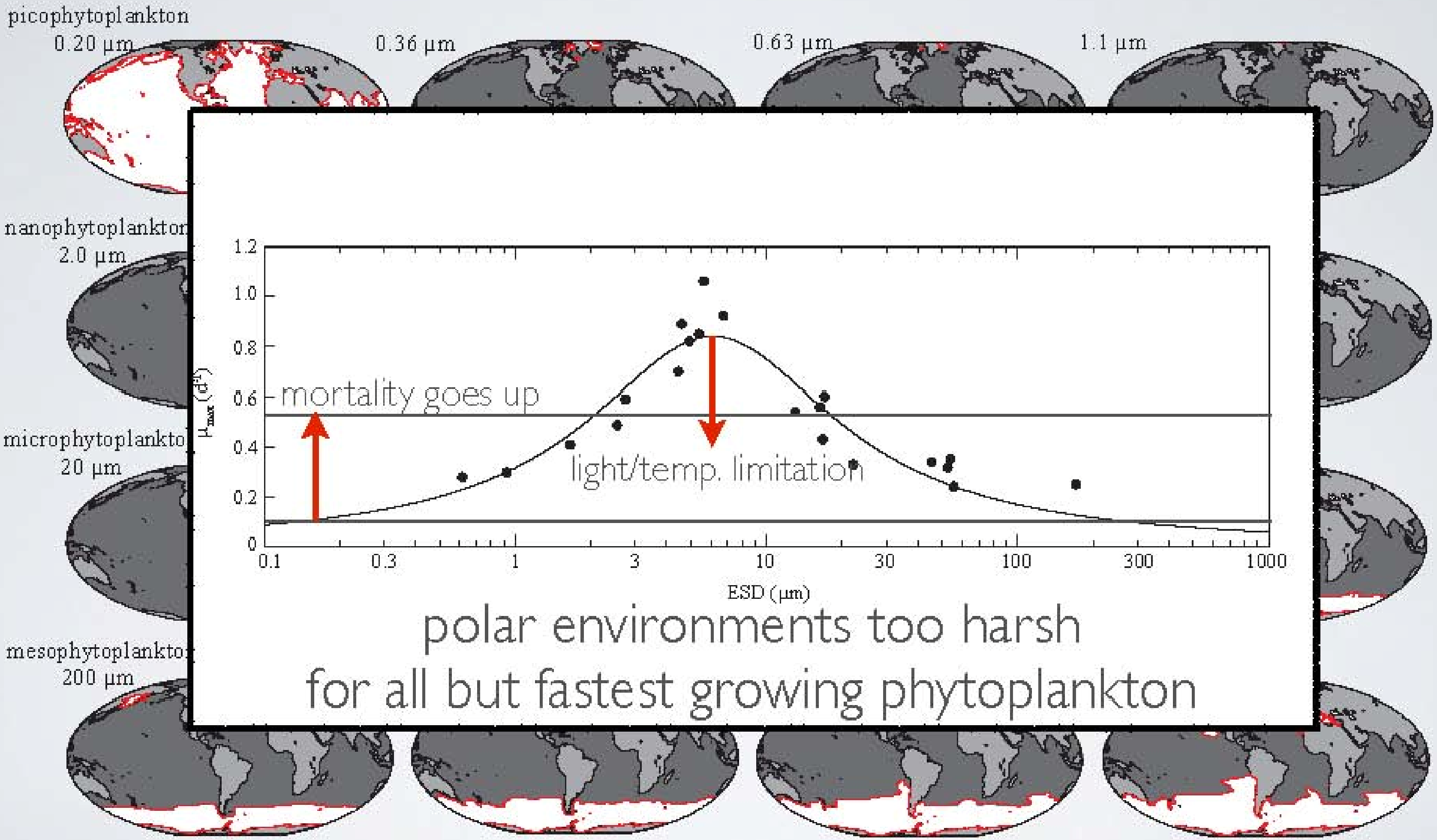
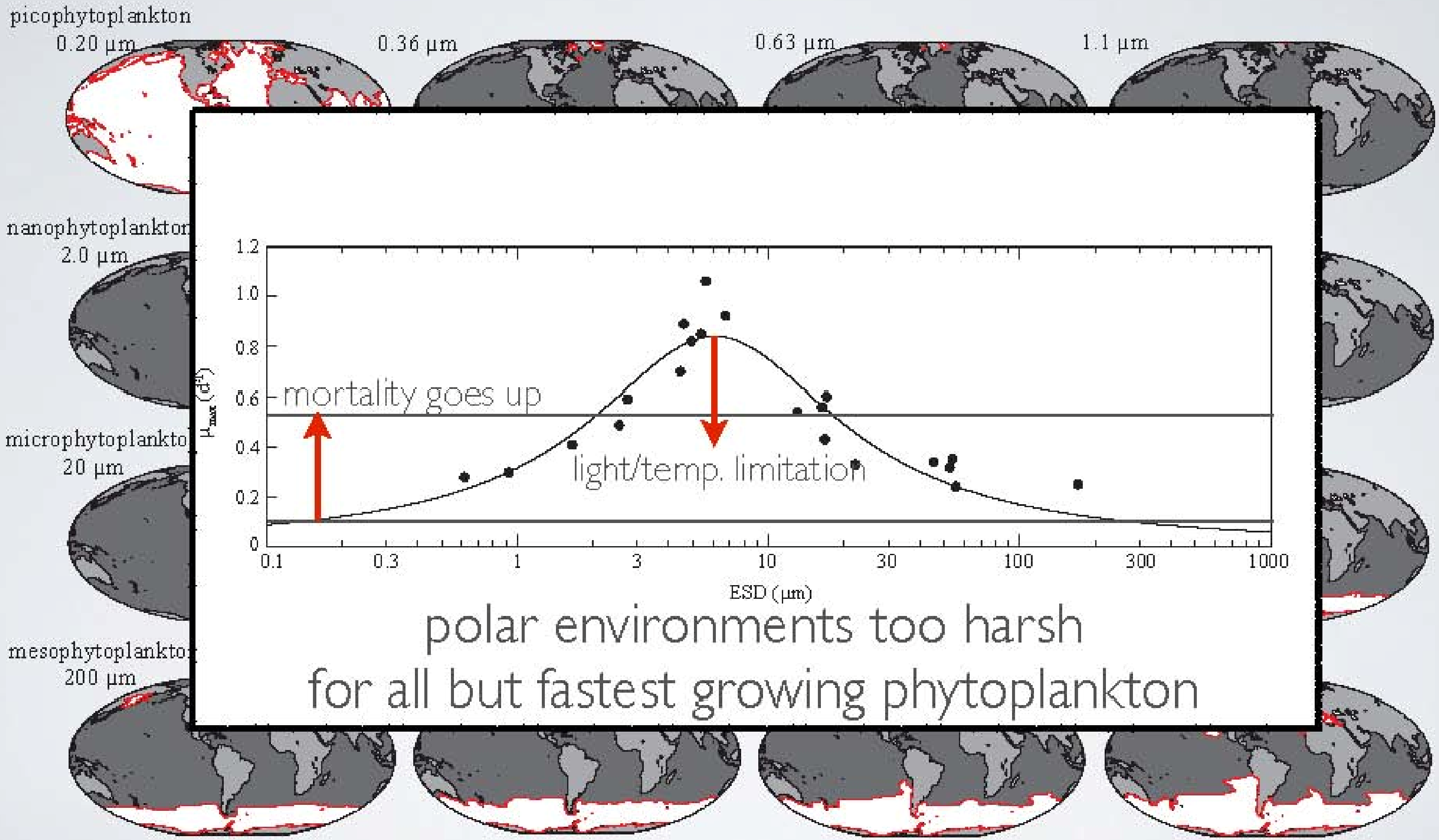
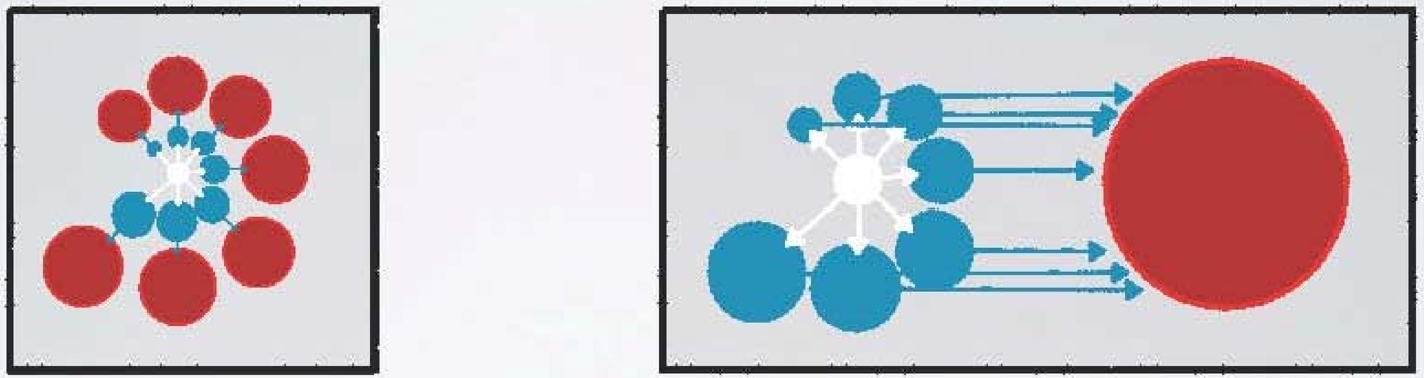


maximum growth rate vs. mortality sets *fundamental niche*



N.B. temp. dependence is identical for all species
(one generic function)

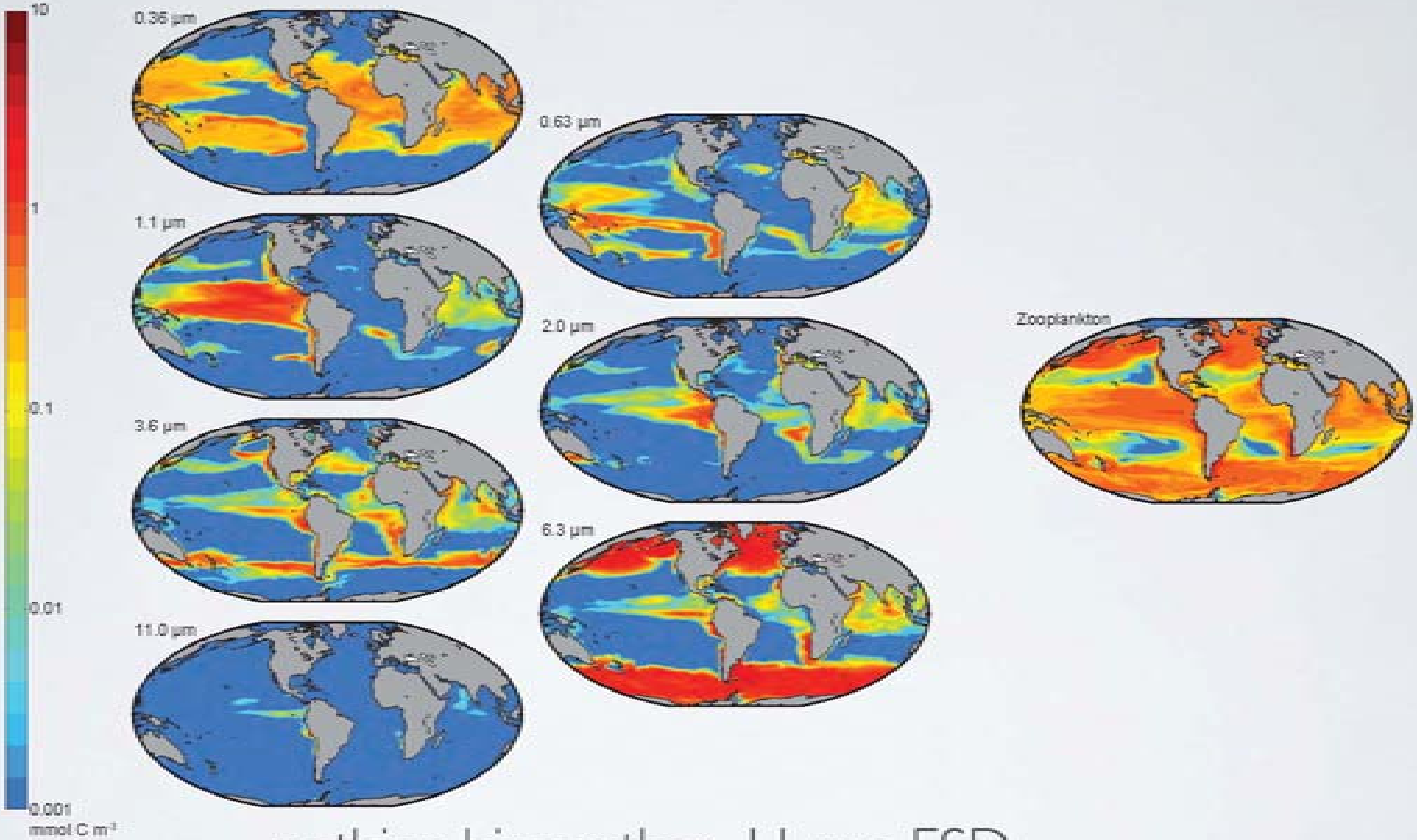
Experiment 2:
twenty phytoplankton size classes
one generic grazer



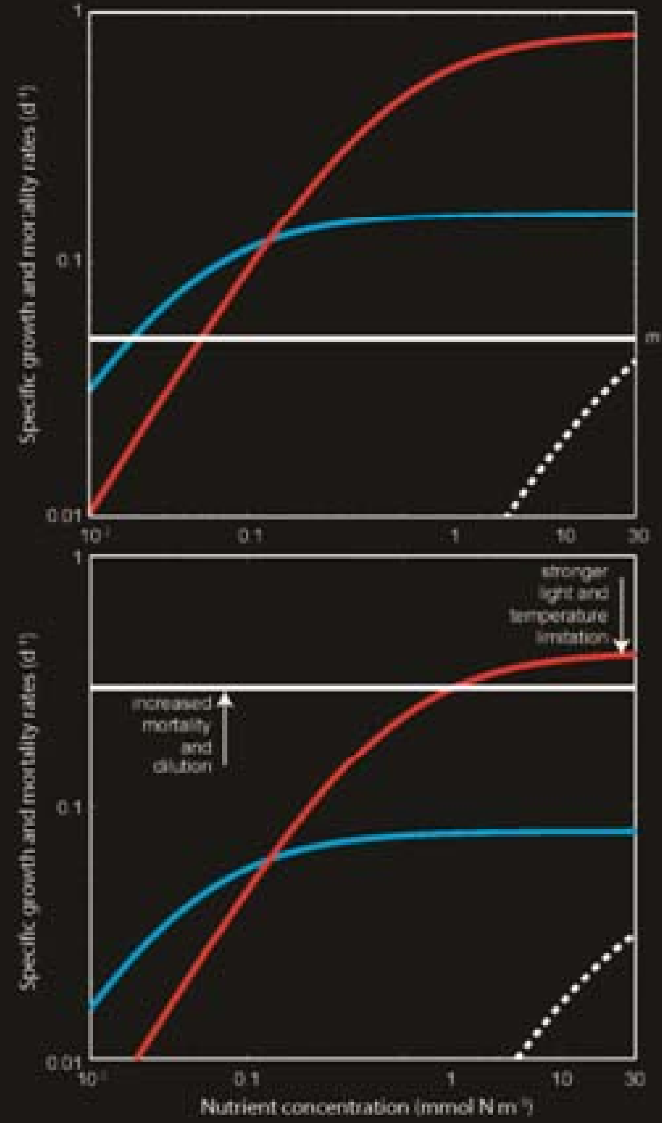
what is the result of competition
in absence of "kill-the-winner"?

but including r-k trade-off
and nutrient storage

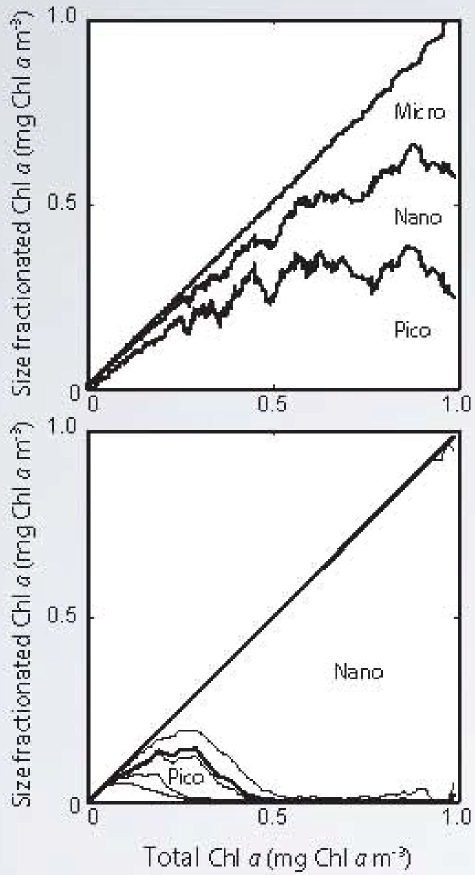
resource competition sets *realised niche*



nothing bigger than 11 µm ESD



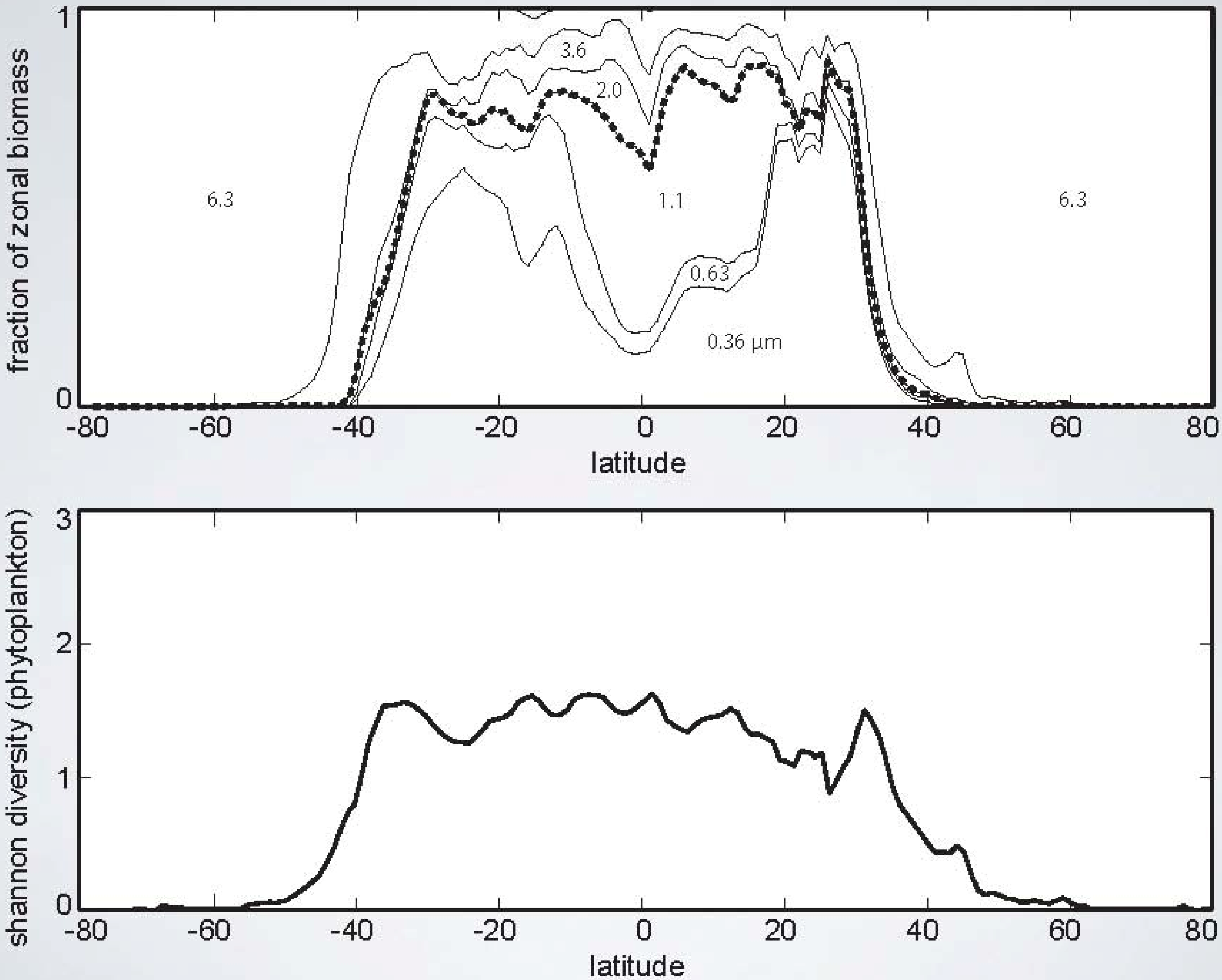
Specific growth and mortality rates (d⁻¹)
m
stronger light and temperature limitation
increased mortality and dilution
Nutrient concentration (mmol N m⁻³)



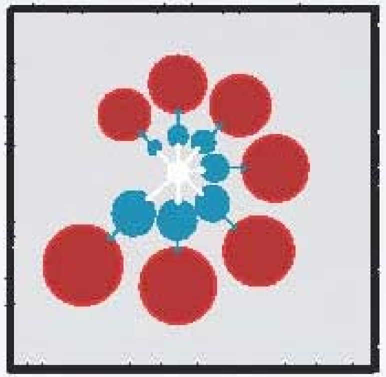
Observations

Model:
20 phytoplankton, 1 zooplankton

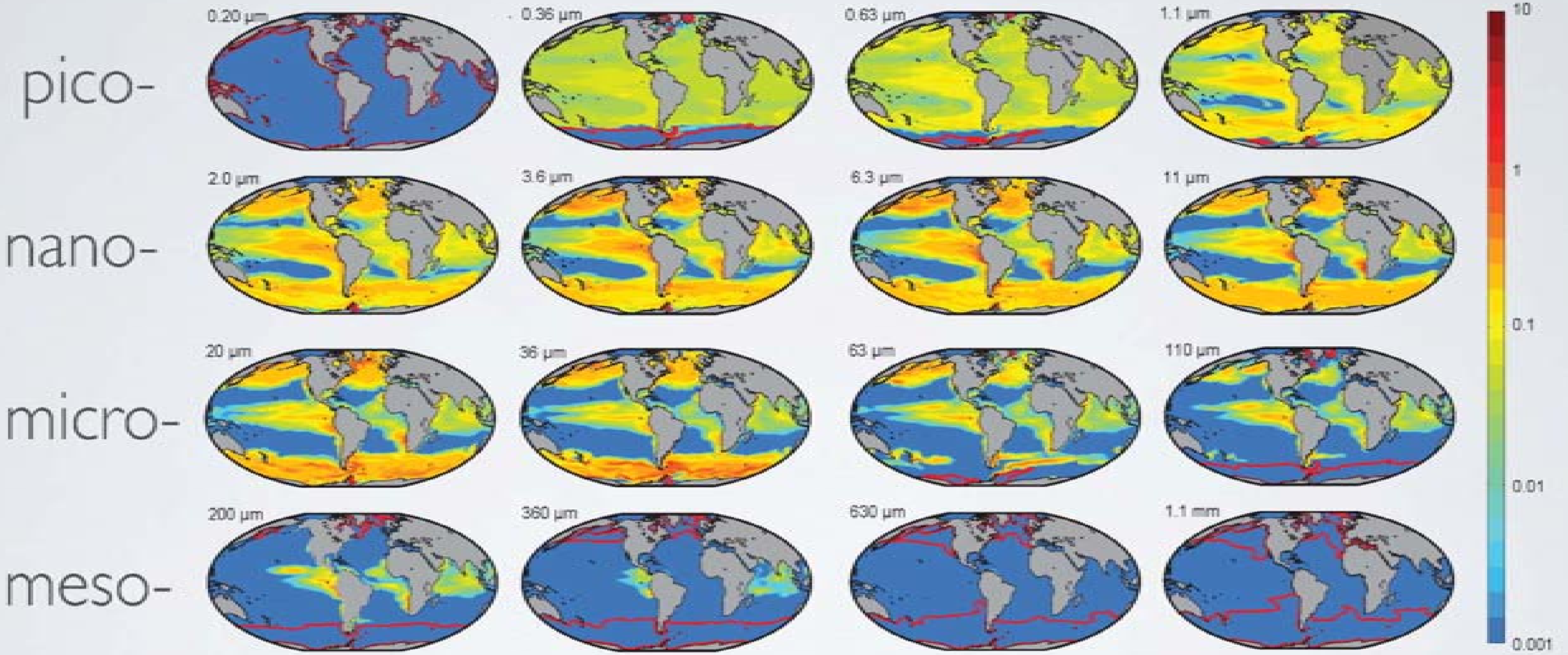
Caveat: relatively low resolution model
might not include time-scales necessary for more coexistence

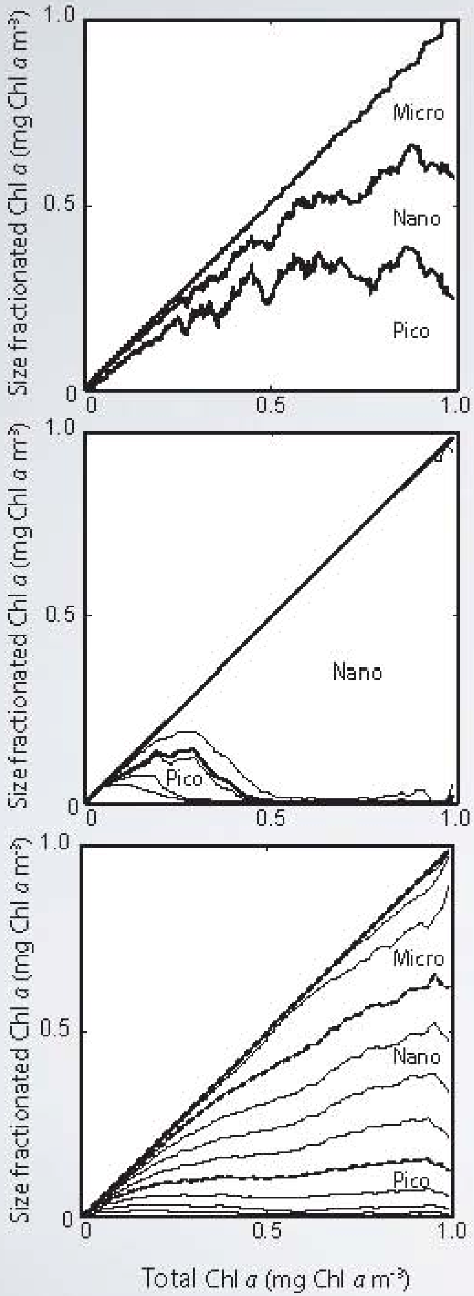

fraction of zonal biomass
1
0
3.6
2.0
6.3
1.1
6.3
0.63
0.36 µm
-80
-60
-40
-20
0
20
40
60
80
latitude
shannon diversity (phytoplankton)
3
2
1
0
-80
-60
-40
-20
0
20
40
60
80
latitude

Experiment 3:
twenty phytoplankton size classes
twenty zooplankton size classes



what is the role of top-down-control
in setting global diversity patterns

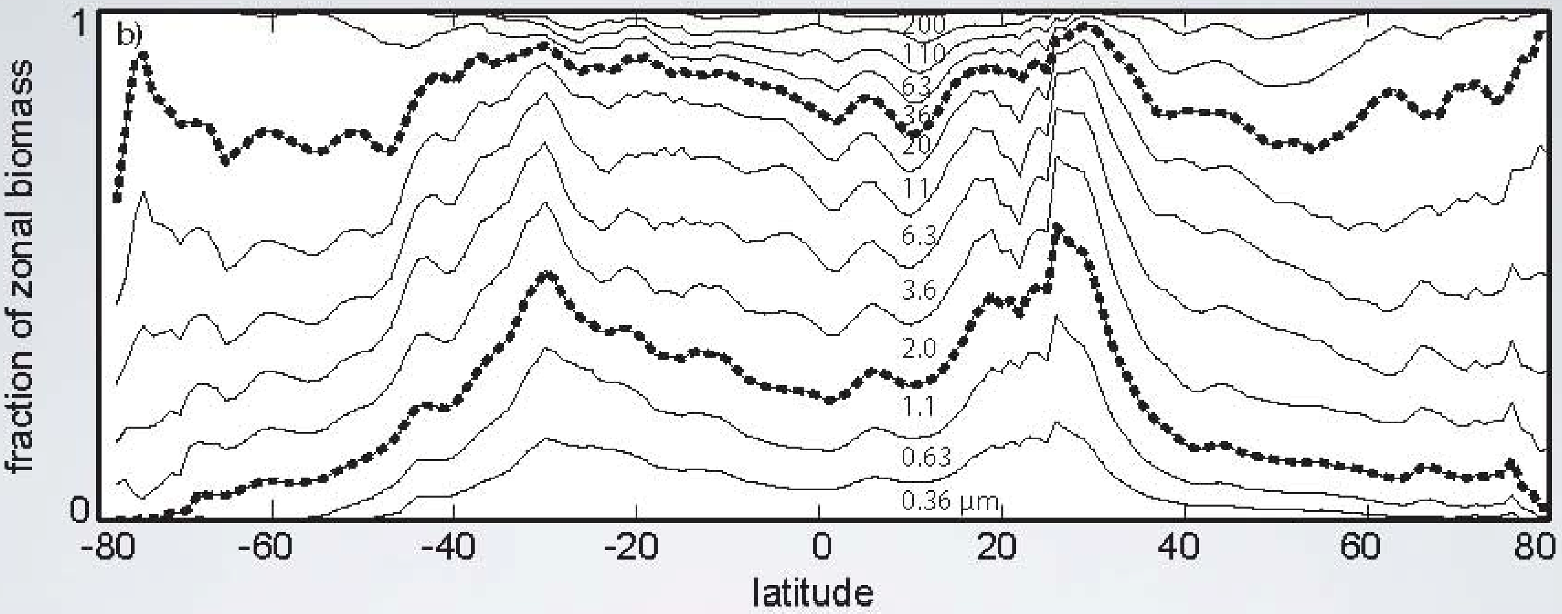

pico-
nano-
micro-
meso-
0.20 µm
0.36 µm
0.63 µm
1.1 µm
2.0 µm
3.6 µm
6.3 µm
11 µm
20 µm
36 µm
63 µm
110 µm
200 µm
360 µm
630 µm
1.1 mm
10
1
0.1
0.01
0.001
mmol C m⁻³



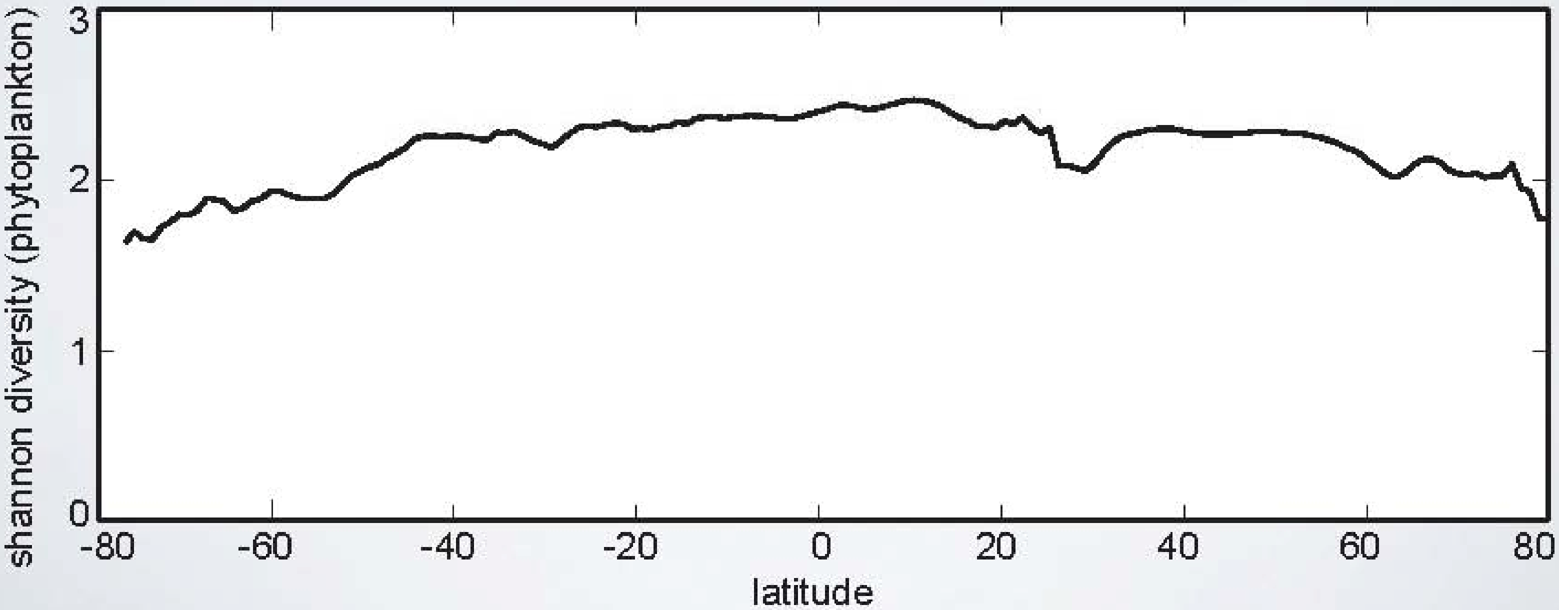
Observations

Model:
20 phytoplankton, 1 zooplankton

Model:
20 phytoplankton, 20 zooplankton



b)
fraction of zonal biomass
200
110
63
36
20
11
6.3
3.6
2.0
1.1
0.63
0.36 µm
latitude



shannon diversity (phytoplankton)
latitude

linking theory to global biodiversity, biogeography and ecosystem function

1. Diverse, trait-based models of marine ecosystems - why bother?

2. Maintaining diversity - the 'paradox' and its many solutions

3. Putting it all together - a size-structured plankton community model

4. Taking it apart again - what drives biogeography

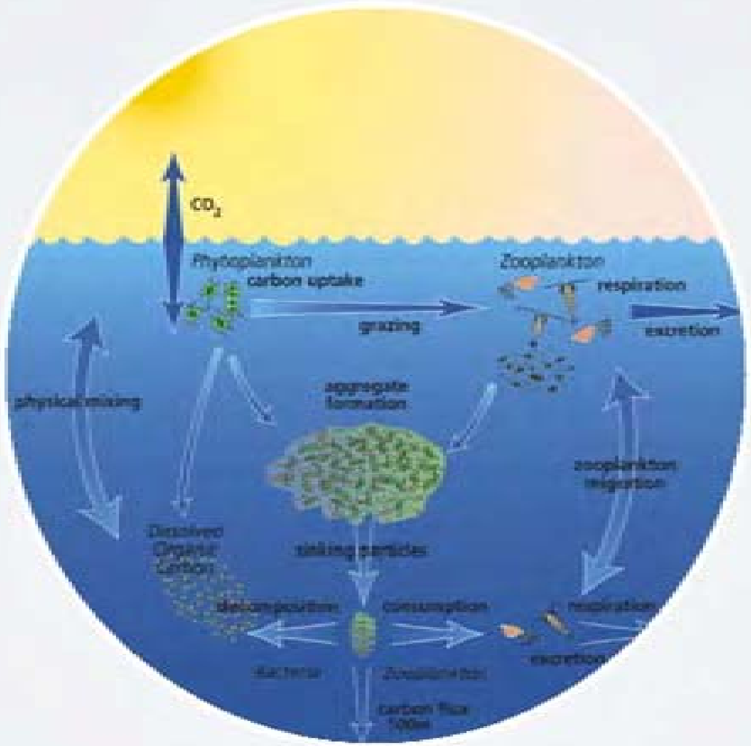
5. Conclusions

The benefits of complexity?

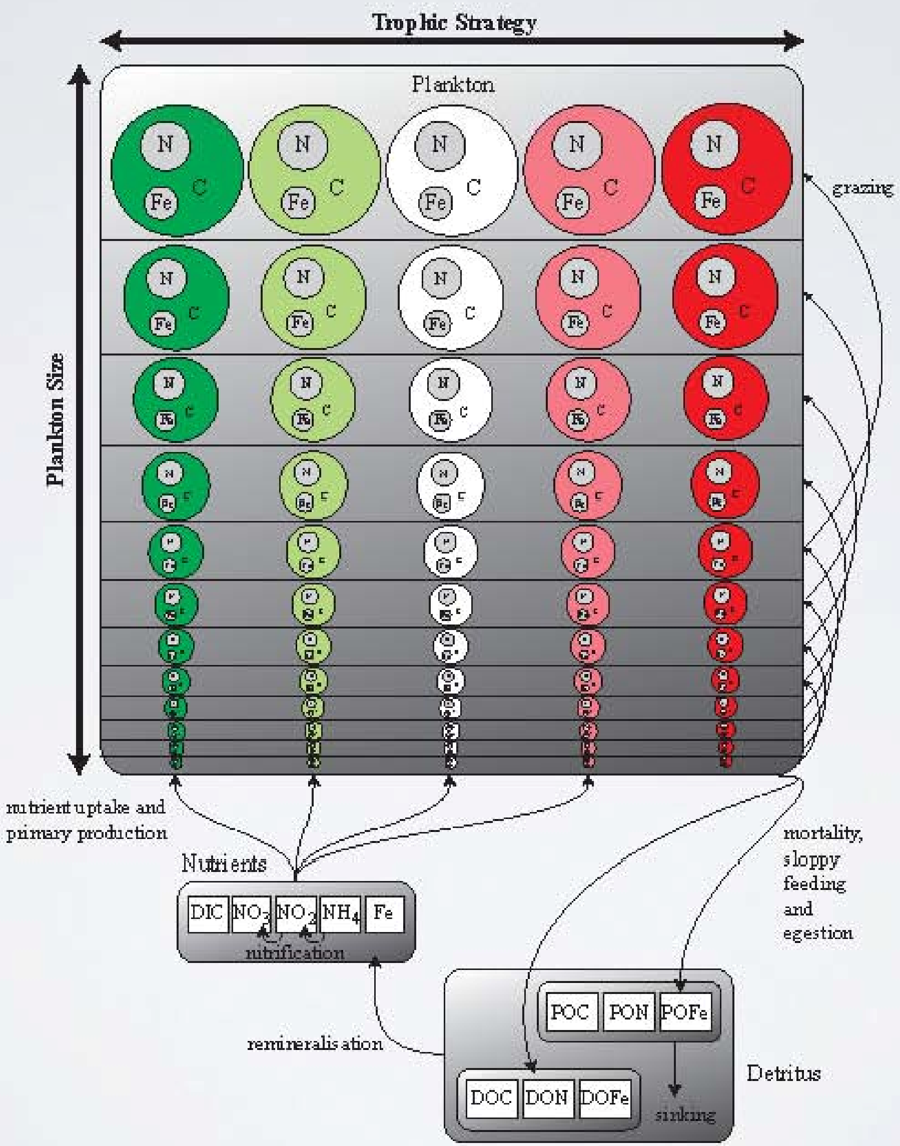
A changing environment may affect
different parts of the community in different ways:

stratification: exclusion of larger cells

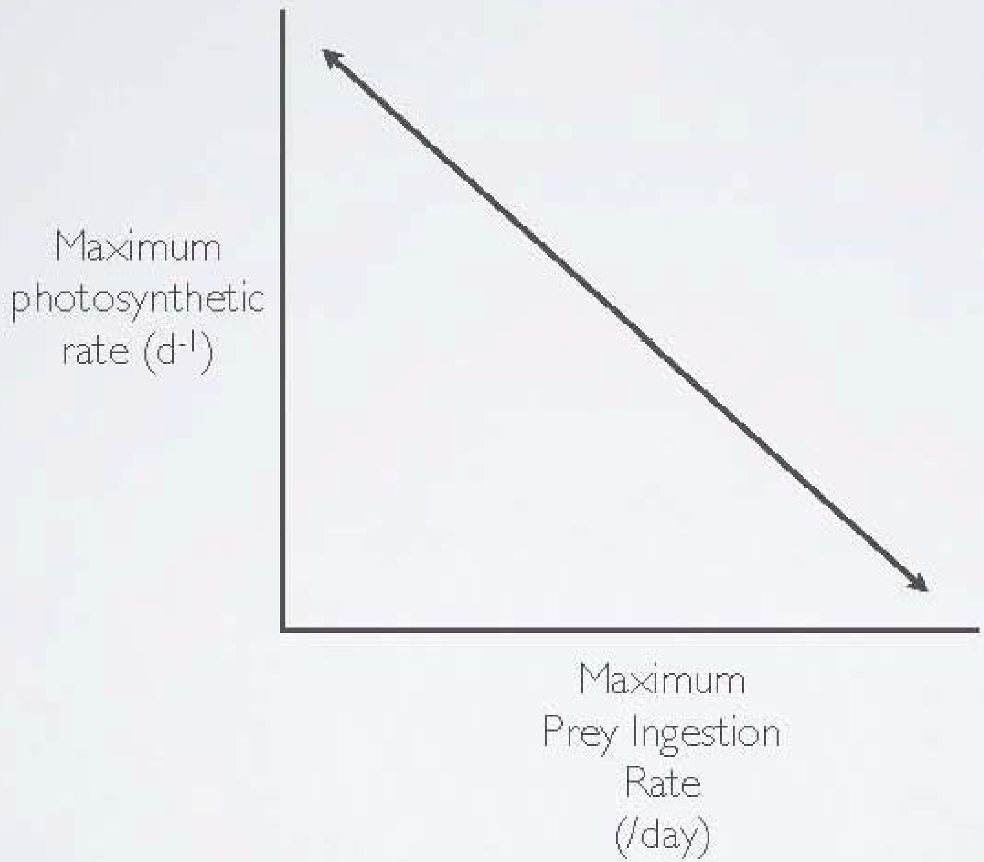
warmer temperatures: increased range of smaller (and larger) cells?



Going beyond the size axis

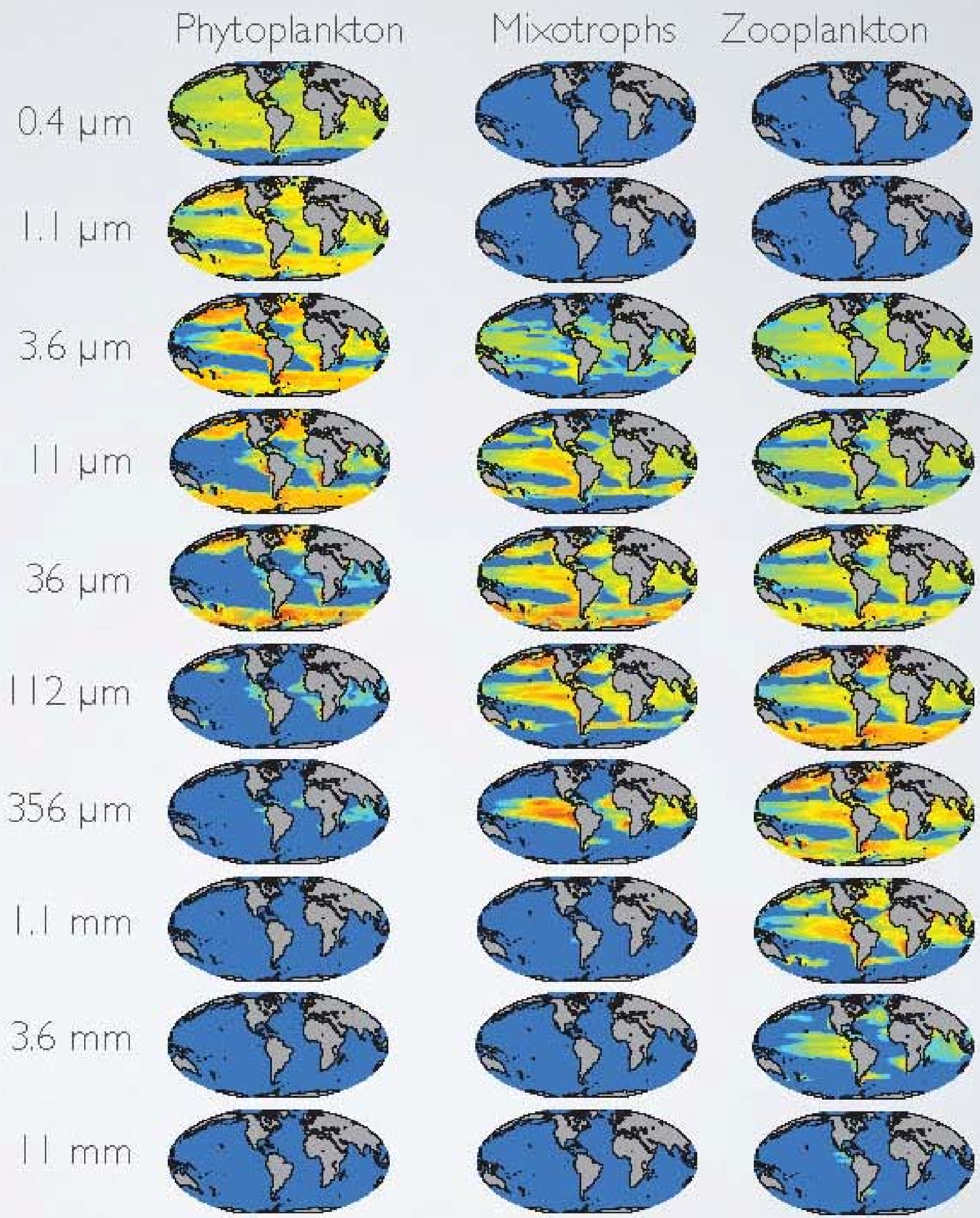


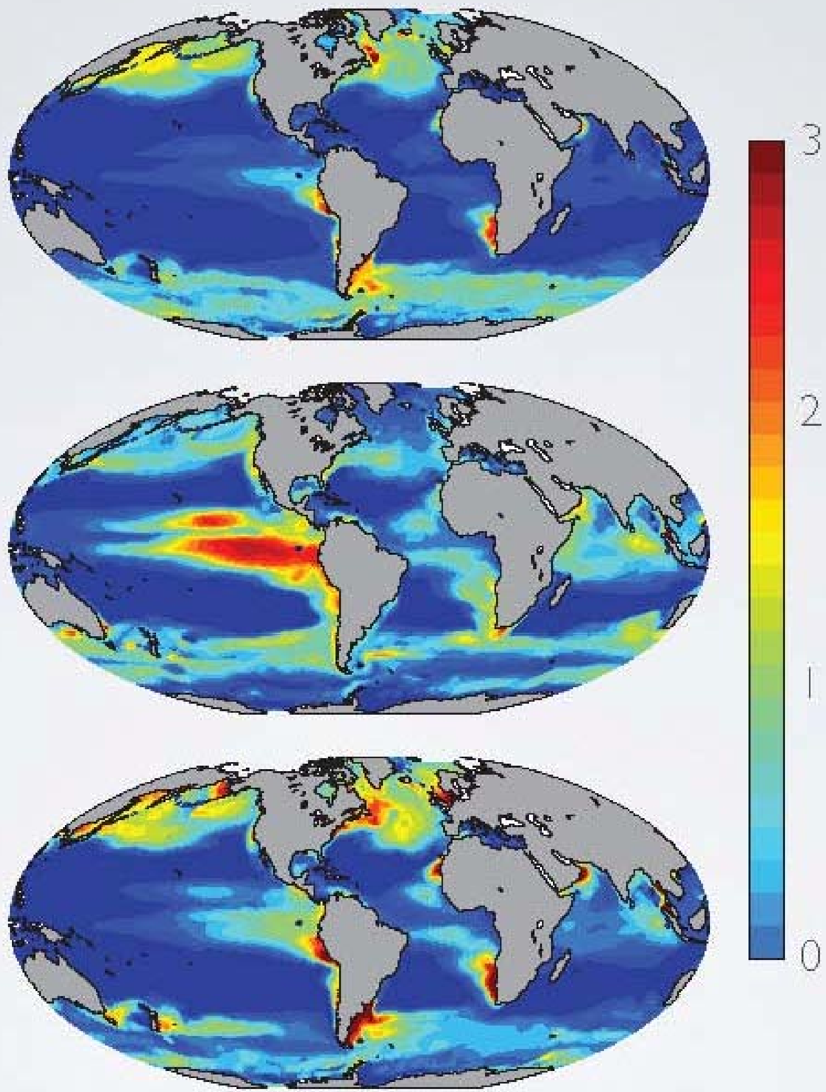
A simple trade-off between autotrophy and heterotrophy



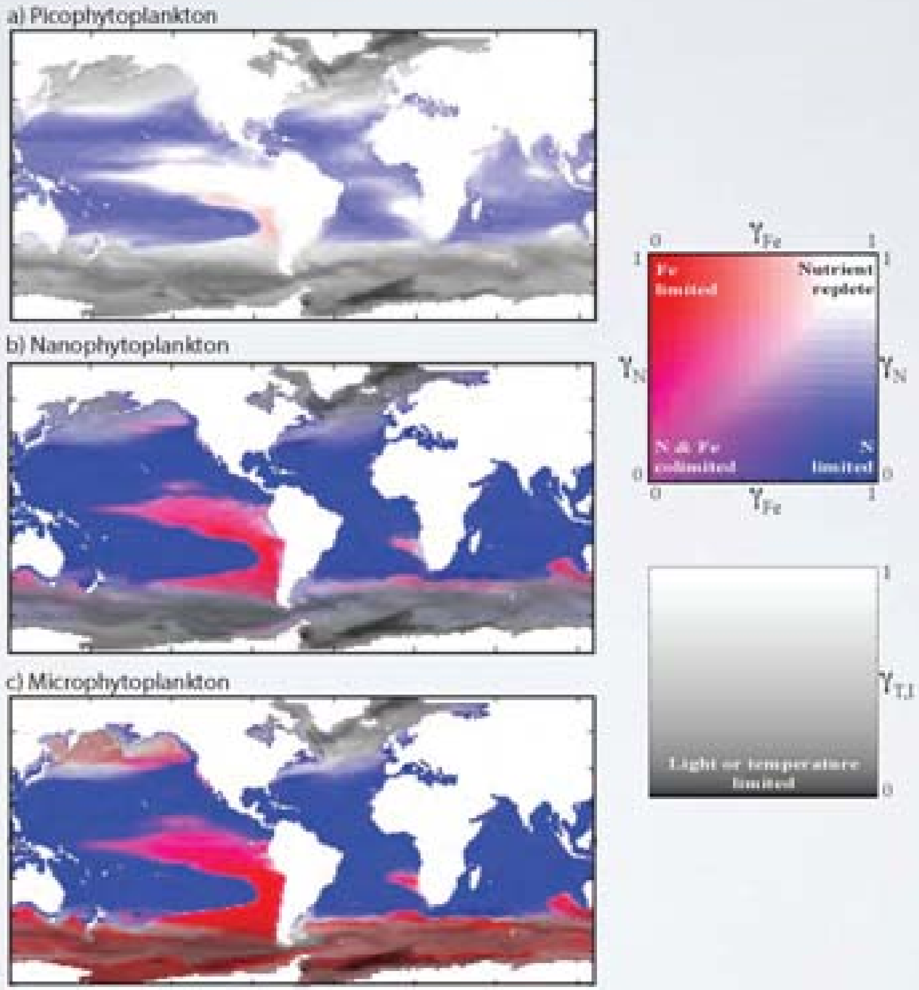
Carbon biomass biogeography

only showing
every other size class

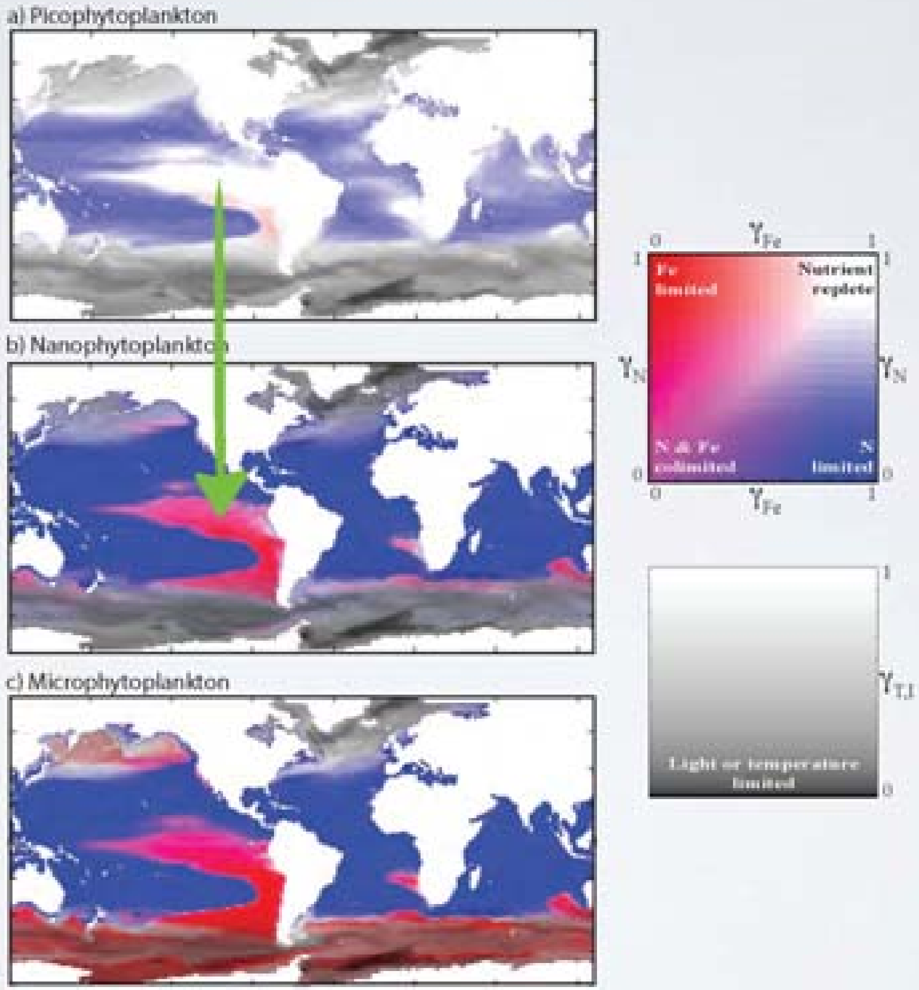



3
2
1
0

Descending the food-chain to find iron?



Descending the food-chain to find iron?



Summary

1. Many solutions to the paradox

2. The challenge is understanding what limits diversity and biogeography

3. Trait-based approaches are ideal because they focus on the "rules"

4. Experiments aimed directly at trade-offs are extremely useful

5. A clear mechanistic concept leads to simpler predictions

Predictions based on a mechanistic model

Running a global climate simulation generates predictions
But driving forces are not always clear
And are subject to uncertainties of scenario

Breaking down model links theory to global patterns,
but mechanisms can be made clear

Predictions can separated from scenarios
 if A, then x, but if B, then y.