Physiological diversity matters: a modelling perspective

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Acknowledgments:
Ben Ward
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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

Physiological diversity matters: a modelling perspective
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

Physiological diversity matters: a modelling perspective
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
Global 3-D biogeochemical, ecosystem models

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

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

What is the state of the art?

Physiological diversity matters: a modelling perspective
What is the state of the art?

Global 3-D biogeochemical, ecosystem models

e.g. Ward et al, PNAS, 2016

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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)
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

Physiological diversity matters: a modelling perspective
EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

Physiological diversity matters: a modelling perspective
EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

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

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;

Mixotrophy
Litchman et al, Ecol Let, 2007:

Diatoms:
Raven et al, Bio Rev, 1983

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

Mixotrophy
Litchman et al, Ecol Let, 2007:

Diatox:
Raven et al, Bio Rev, 1983

pico-phytoplankton
diazotroph
coccolithophore
diatom
dinoflagellate

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EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

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Tang, 1995;
Maranon et al 2013;
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EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

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EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

Simulation with size classes within functional groups

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

mean equivalent spherical diameter (um)

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

Physiological diversity matters: a modelling perspective
EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

present day biomass weighted mean cell diameter (um)

“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

Size differentiated
Functionally differentiated

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

- Size differentiated
- Functionally differentiated

0 = community is same as pre-industrial
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\[
\sqrt{\frac{\sum B_i(t)}{\sum B_i(t) - \sum B_i(t = 0)^2}}
\]

B is biomass in group

classical PFT model, with 2 P and 1 Z

EXAMPLE 1: SIZE CLASSES WITHIN FUNCTIONAL GROUPS

Physiological diversity matters: a modelling perspective
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)
Climate Change Scenario:

- decrease in mean cell size; large in some regions
  (with consequences for higher trophic levels)

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- including only functional diversity over-estimates functional changes
  (with consequences for export and feedback to climate system)

What would happen if we included evolution?
EXAMPLE 2: TROPHIC STRATEGY

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EXAMPLE 2: TROPHIC STRATEGY

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

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

Simulation with mixotrophy

Physiological diversity matters: a modelling perspective
EXAMPLE 2: TROPHIC STRATEGY

Simulation without mixotrophy

Simulation with mixotrophy

Physiological diversity matters: a modelling perspective
EXAMPLE 2: TROPHIC STRATEGY

CPR OBSERVATIONS

Simulation with mixotrophy

Barton et al, L&O, 2013
EXAMPLE 2: TROPHIC STRATEGY

Physiological diversity matters: a modelling perspective

Simulation with mixotrophy

Barton et al, L&O, 2013

Biogeochemical Cycling 2018 OCB Workshop
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

Physiological diversity matters: a modelling perspective
EXAMPLE 3: SYMBIOISIS

Station Aloha Observations

*Follett et al, ISME J, 2018*

Physiological diversity matters: a modelling perspective
EXAMPLE 3: SYMBIOISIS

Physiological diversity matters: a modelling perspective

Station Aloha Observations

Follett et al, ISME J, 2018

Photo: Chris Follett
EXAMPLE 3: SYMBIOISIS

Physiological diversity matters: a modelling perspective
EXAMPLE 3: SYMBIOISIS

Physiological diversity matters: a modelling perspective

Dutkiewicz et al, in prep
EXAMPLE 3: SYMBIOISIS

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

Christopher L. Follett¹ · Stephanie Dutkiewicz¹ · David M. Karl²³ · Keisuke Inomura¹ · Michael J. Follows¹
ISME Journal, 2018

Physiological diversity matters: a modelling perspective
EXAMPLE 3: SYMBIOISIS

Physiological diversity matters: a modelling perspective

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

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

Treguer et al, Nat Geo, 2018
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
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
  - 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
What is the state of the art?

Monod Kinetics
(fixed cell quotas)

C:N:P:Fe \(\sim 120:16:1:1e-3\)

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

Adam C. Martiny\(^1,2\), Chau T. A. Pham\(^3\), 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 \(\sim 195:28:1\)  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:
stoichiometry 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

What is the state of the art?

Single cell approach:
- Inomura et al, ISME, 2016
- Inomura et al, in prep

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

Inclusion in 3-D model:
Kei Inomura (post-doc UW)
including this as parameterization
in 3-D model
Global 3-D biogeochemical, ecosystem models

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What is the state of the art?

Growth rate:

$$\mu = \mu_{max} f (N, P, Fe, I, T, ...)$$
What is the state of the art?

Growth rate:

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

$$= \mu_{max} \min(g(N, P, Fe)) \ h(I) \ i(T)$$
What is the state of the art?

Growth rate:

\[ \mu = \mu_{max} f(N, T, ...) \]
growth as function of nutrients and temperature

\[ \mu_{\text{max}} \frac{R}{R + \kappa_R} \gamma e^{\alpha T} \]

What is the state of the art?

Physiological diversity matters: a modelling perspective
growth as function of nutrients and temperature

\[
\mu_{\text{max}} \frac{R}{R + \kappa_R} e^{-\alpha T}
\]
Numerical model results: annual mean *Prochlorococcus* growth rates (1/d)

5um Diatom growth rates (1/d)
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\textsuperscript{a,b,1} and Michael J. Follows\textsuperscript{c}  

PNAS, 2016
Marine mixotrophy increases trophic transfer efficiency, mean organism size, and vertical carbon flux

Ben A. Ward and Michael J. Follows

PNAS, 2016

EXAMPLE 2: TROPHIC STRATEGY

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

Physiological diversity matters: a modelling perspective
What is the state of the art?

Phylogenetic Diversity in the Macromolecular Composition of Microalgae

Zoe V. Finkel¹ *, Mick J. Follows², Justin D. Liefer¹, Chris M. Brown³, Ina Benner¹, Andrew J. Irwin⁴

PlosOne 2016

Observation of Macromolecular Pools

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