

Modeling phytoplankton traits, trade-offs and biogeography

Stephanie Dutkiewicz

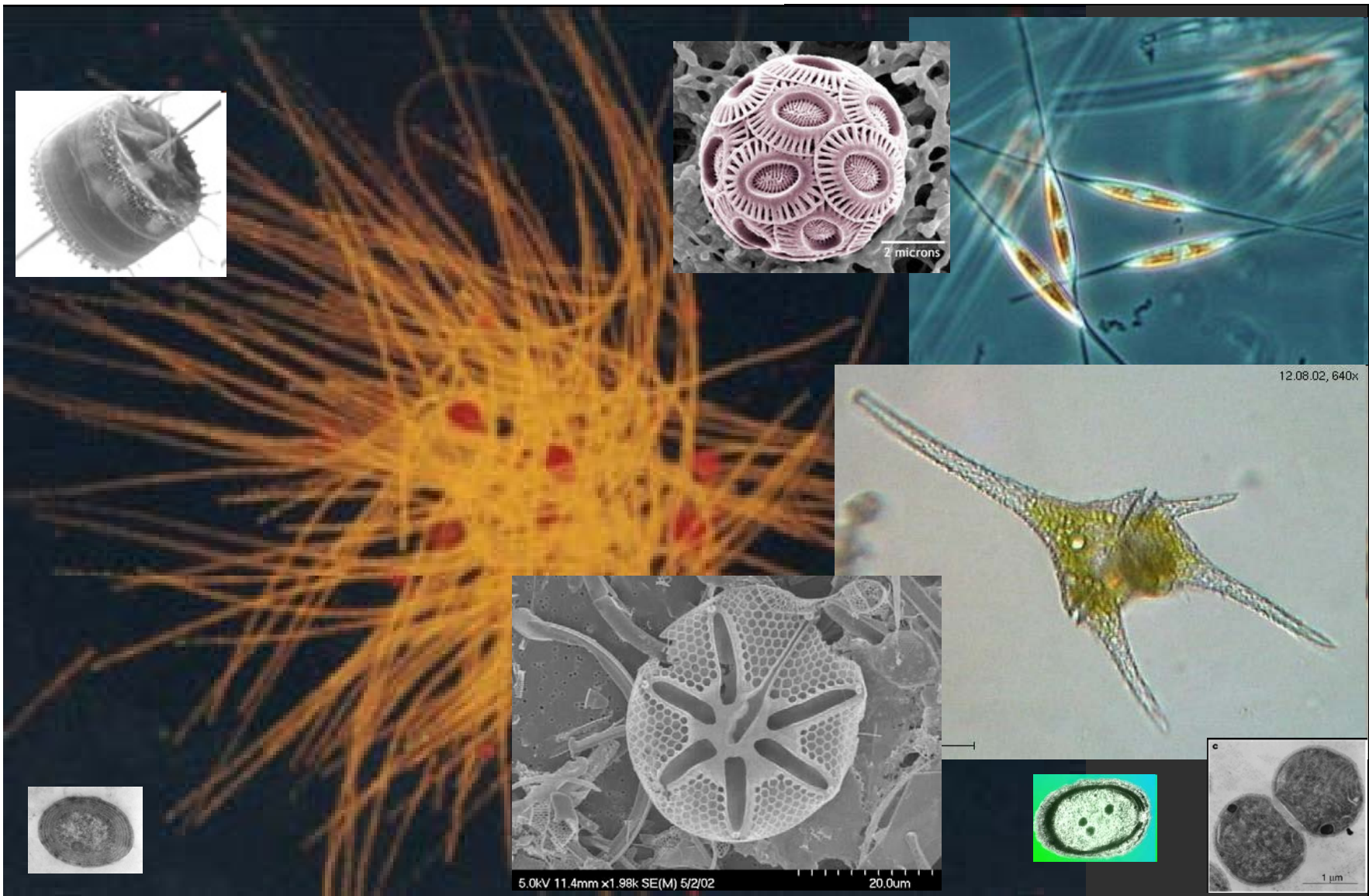
Massachusetts Institute of Technology
Program in Atmospheres, Oceans and Climate

Mick Follows, Anna Hickman¹,

Ben Ward², Fanny Monteiro³, Oliver Jahn, Jason Bragg⁴

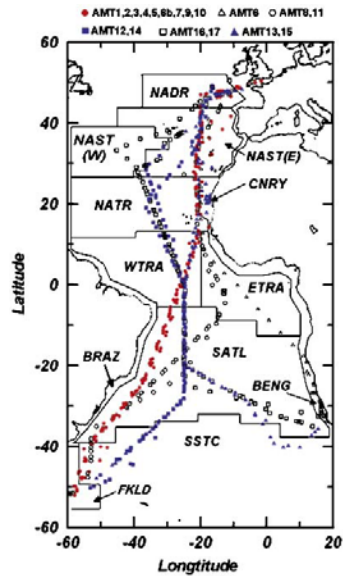
1. Univ. Southampton
2. Ecole Normal Supérieure
3. Univ. Bristol
4. CSIRO, Australia



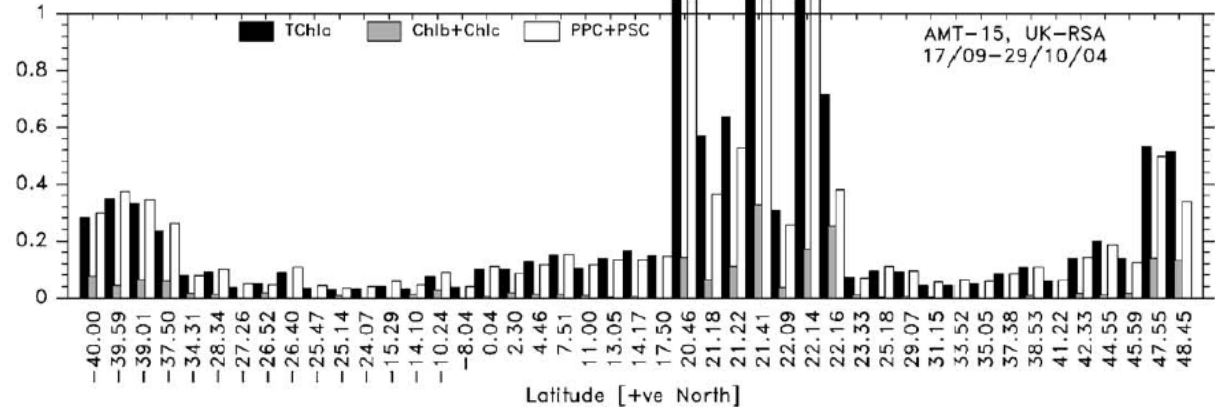


Biogeography: Who lives where?

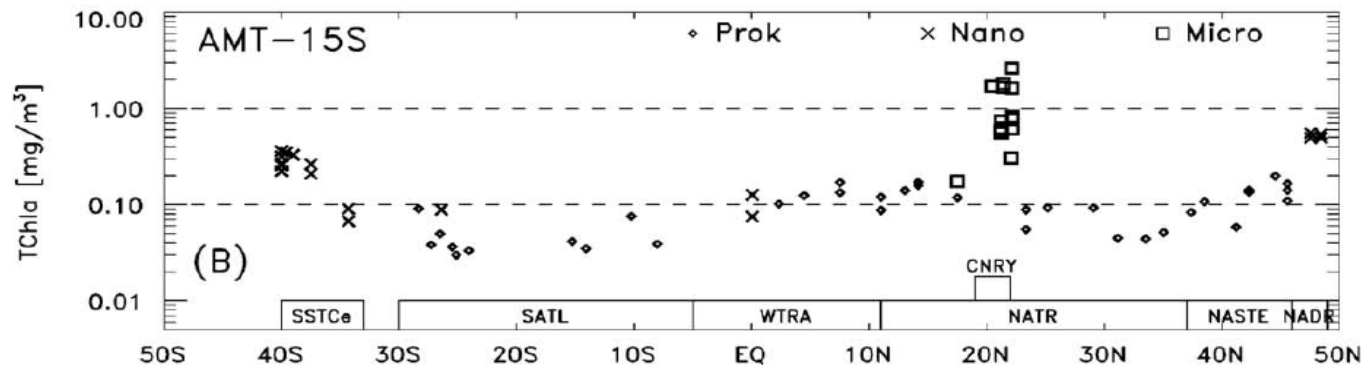
BIOGEOGRAPHY FROM SHIP



AMT15: HPLC Pigments



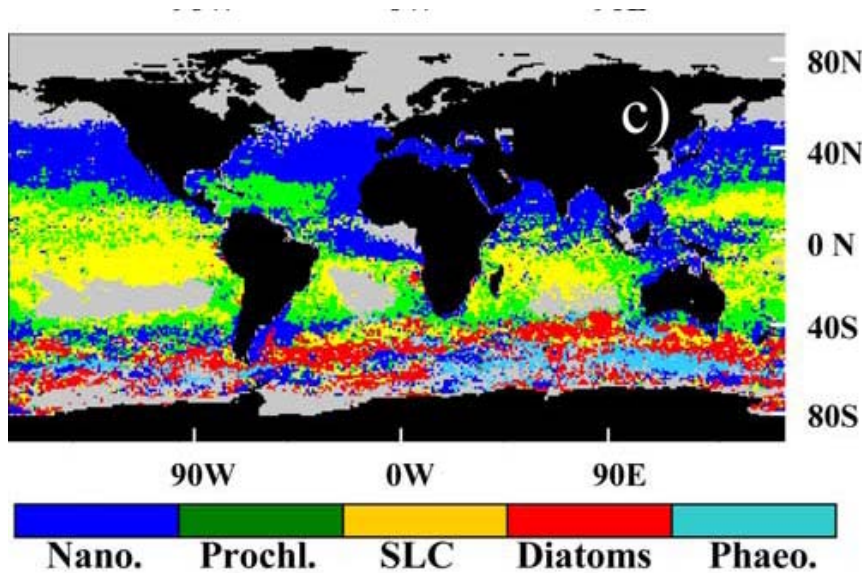
AMT15: Biogeography



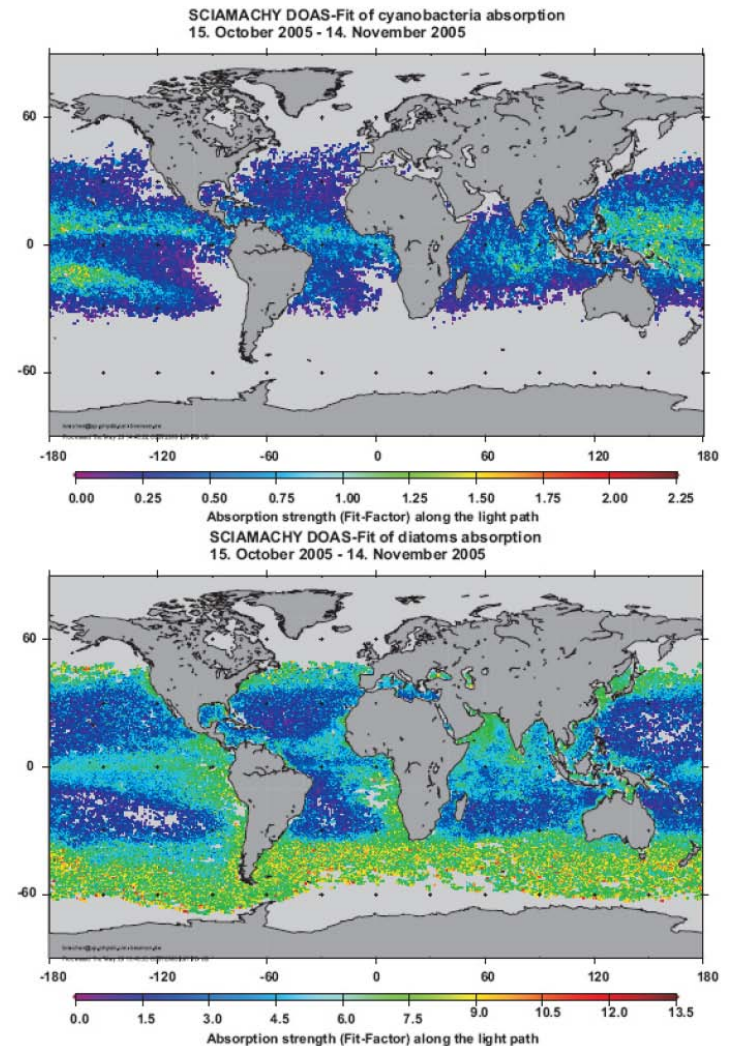
Atlantic Meridional Transect:

Aiken et al, DSR II, 2009

BIOGEOGRAPHY FROM SPACE:



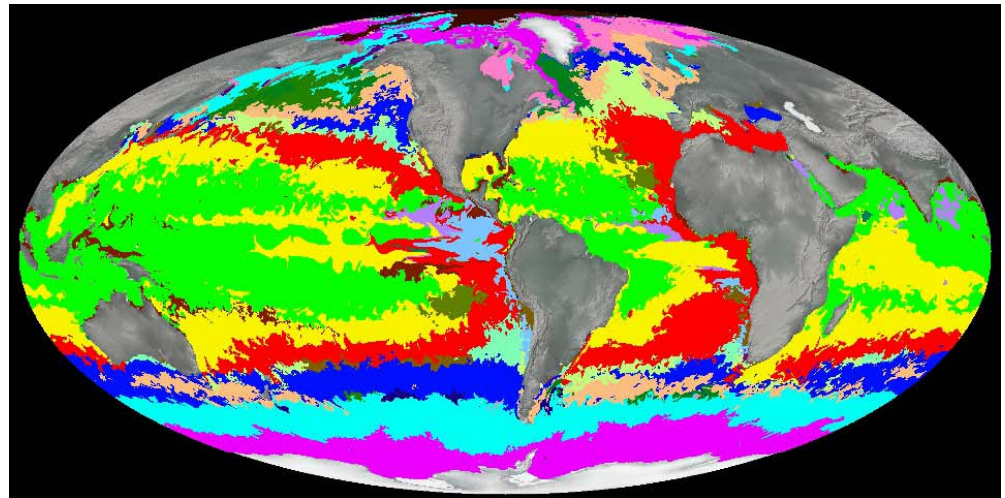
PHYSAT(MODIS): Alvain et al, GBC, 2008



PhytoDOAS(SCIAMACHY):
Bracher et al, BG, 2009

Modeling phytoplankton traits, trade-offs and biogeography

- Biogeography: Who lives where?
- Why do they live there?
- What traits are important?



Model dominant type biogeography

Movie credit: Oliver Jahn, MIT

Modeling phytoplankton traits, trade-offs and biogeography

- Biogeography: Who lives where?
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- What traits are important?

Model needs "trait" information, but also can help us explore the importance of traits

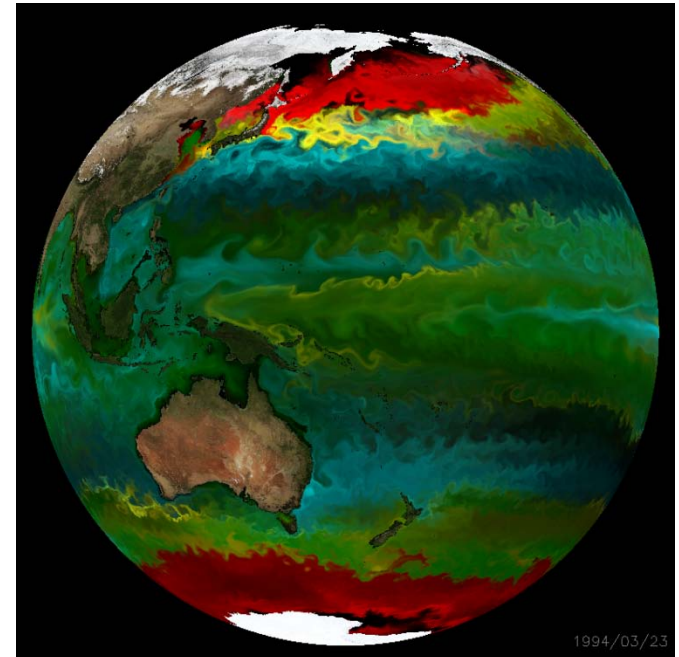
Modeling phytoplankton traits, trade-offs and biogeography

- What traits are important? (Are all traits created equally?)

OUTLINE OF REST OF TALK:

- Introduction to *Prochlorococcus*
- Introduction to model framework
- Series of experiments exploring different traits individually
- Some speculation

Model “functional” biogeography
green/blue: picoplankton;
red/yellow: large
Movie credit: Oliver Jahn, MIT



Prochlorococcus

- cyanobacterium
- one of the most abundant (in terms of cells)
- “model” organism = well studied

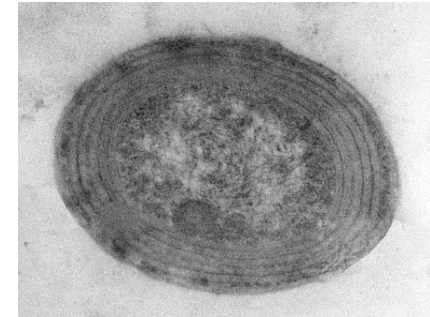
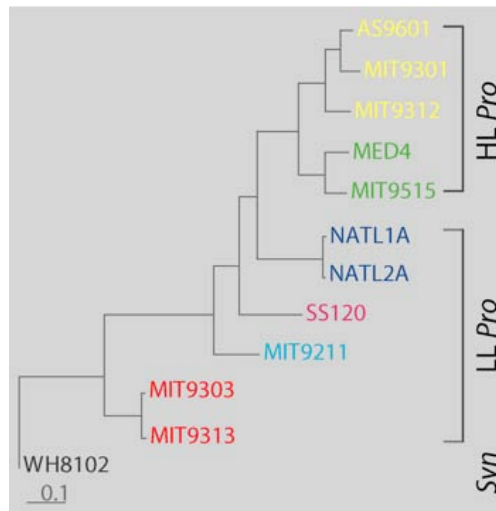


Photo credits:
Partensky Lab

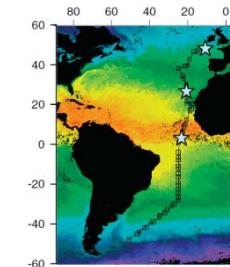
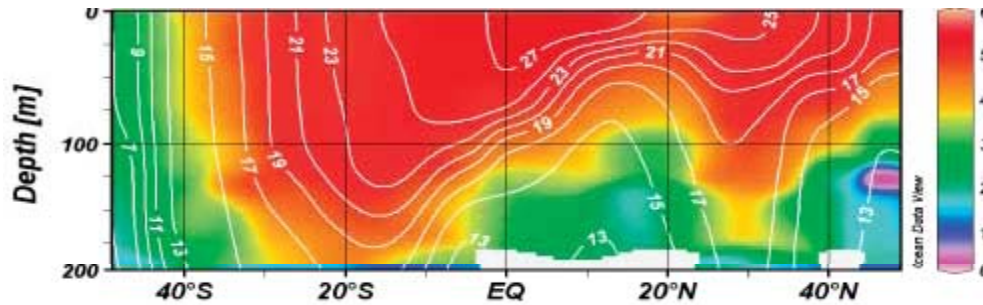


Chisholm Lab

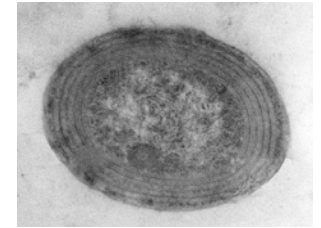


PROCHLOROCOCCUS LIVE WHERE?

AMT13: *Prochlorococcus* (log cell/ml)



Johnson et al,
Science, 2007

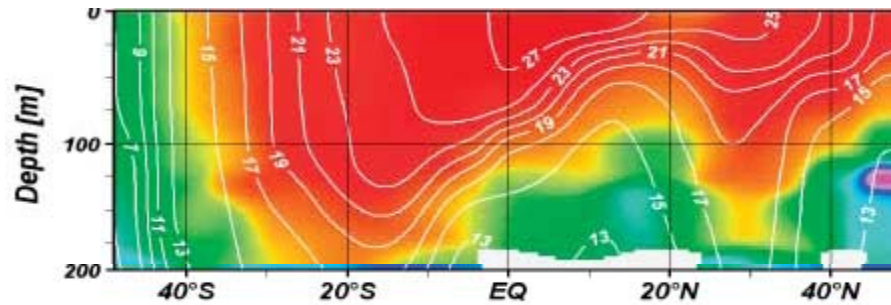


BIOGEOGRAPHY:

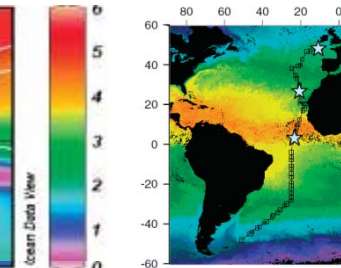
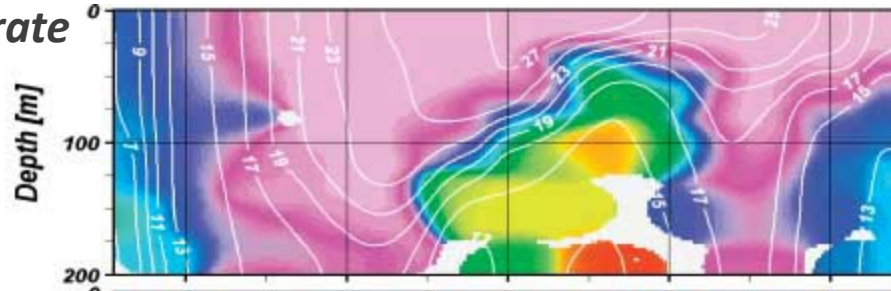
- Low latitudes
- Warm waters

PROCHLOROCOCCUS LIVE WHERE?

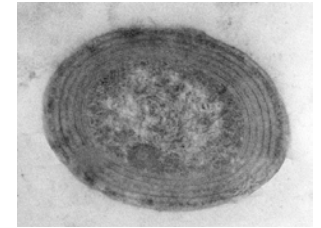
AMT13: *Prochlorococcus* (log cell/ml)



Nitrate



Johnson et al,
Science, 2007

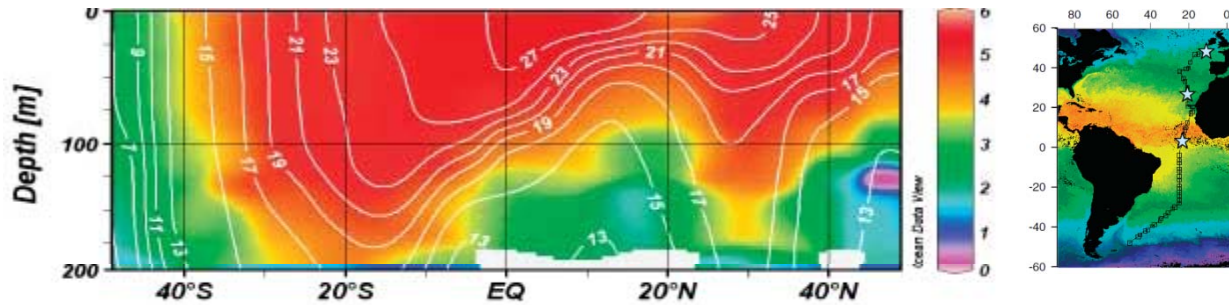


BIOGEOGRAPHY:

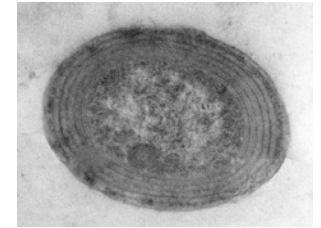
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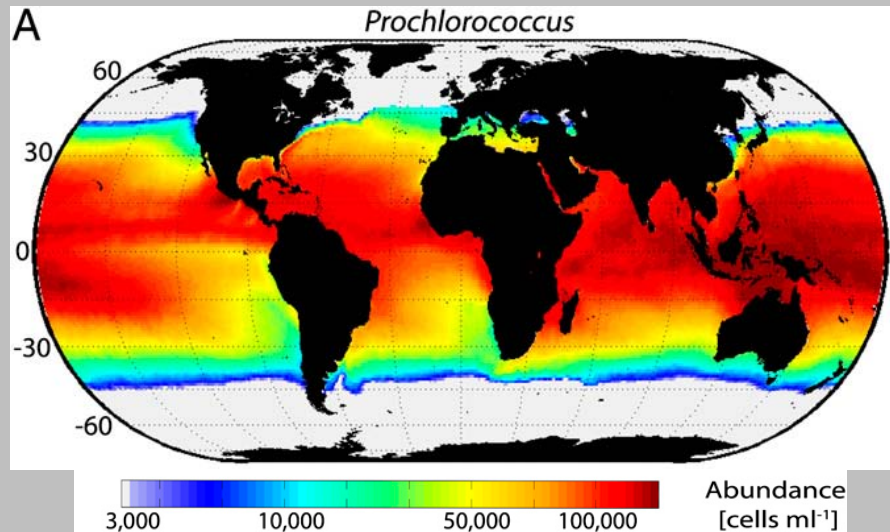


Johnson et al,
Science, 2007



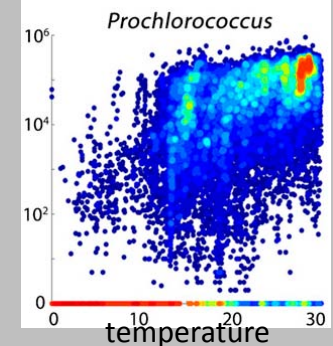
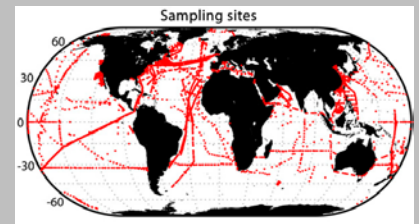
BIOGEOGRAPHY:

- Low latitudes
- Warm waters
- Low nitrate



Flombaum et
al, PNAS, 2013

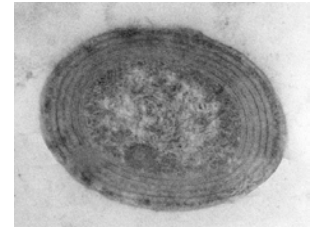
biogeography
constructed by
statistically
from SST, PAR,
nutrients



PROCHLOROCOCCUS TRAITS: **SMALL**



Epifluorescence
microscopy:
Frank Jochem



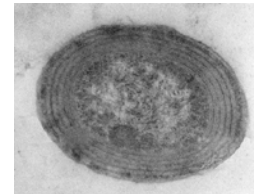
TRAITS

- **small**

Synechococcus



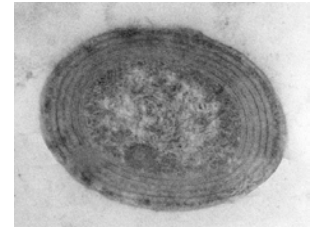
Prochlorococcus



0.5 μ m

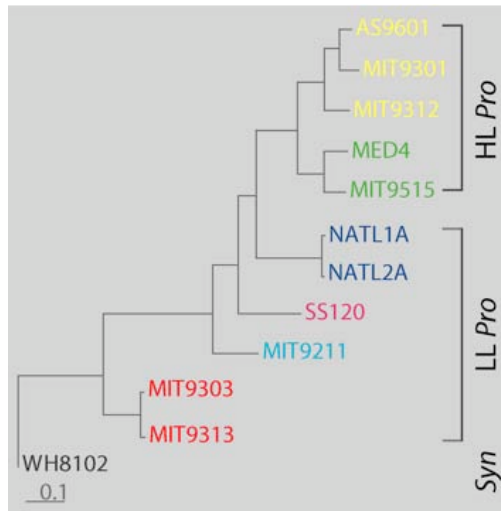
Photo credits:
Partensky Lab

PROCHLOROCOCCUS TRAITS: PIGMENTS

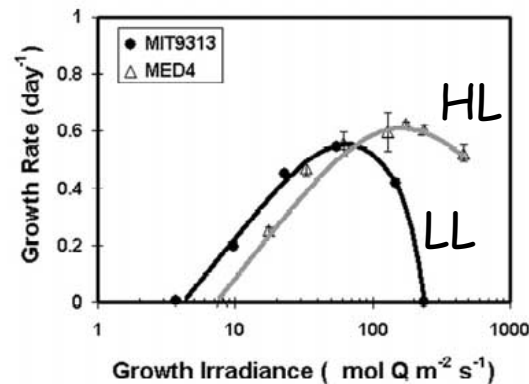


TRAITS

- small
- **unique pigments**

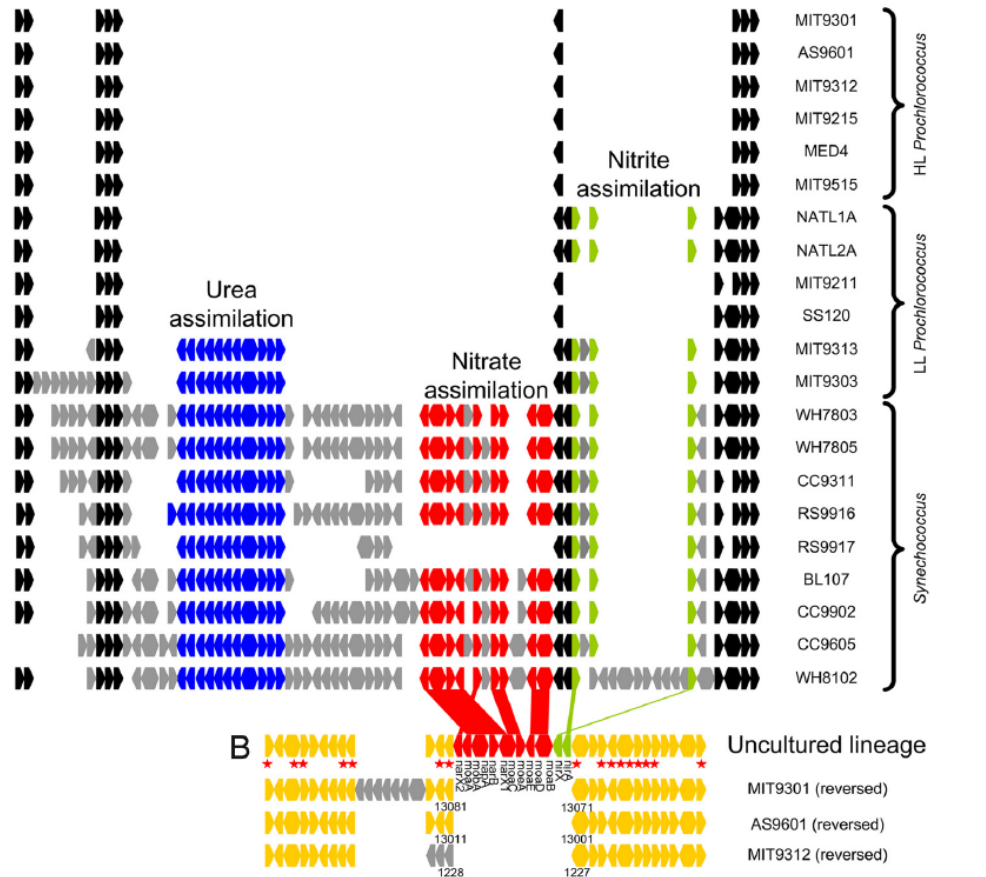


Chisholm Lab

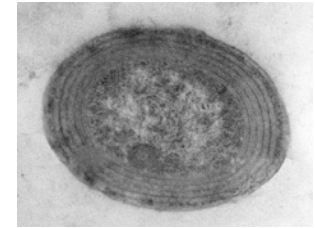


Hess et al, PR, 2001

Nitrogen acquisition genes



cultured Pro

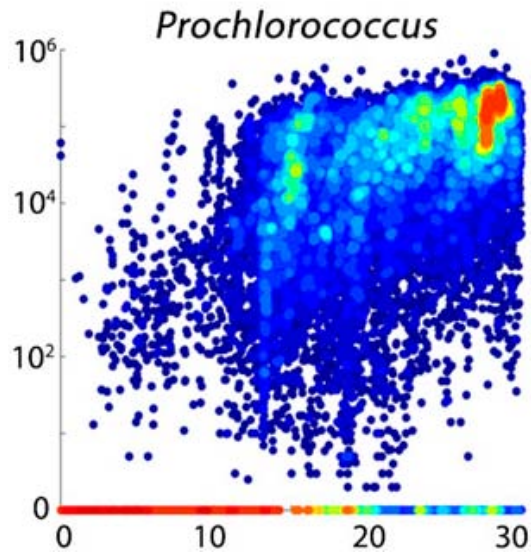
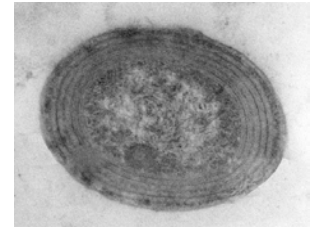


TRAITS

- small
- unique pigments
- **N acquisition**

Martiny et al, PNAS, 2009

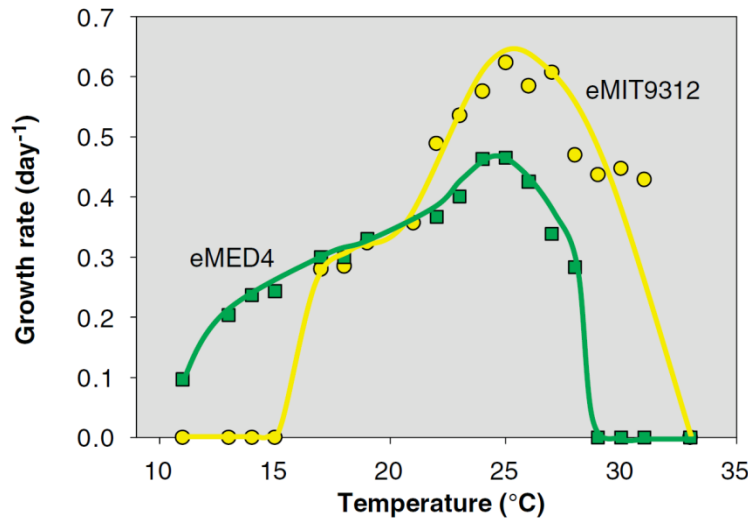
PROCHLOROCOCCUS TRAITS: WARM



temperature

Number of observations	1	5	10	15	20	25	30	35	40	45	50	60	70	80	90	100	200	300	400	500
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15

Flombaum et al, PNAS, 2013

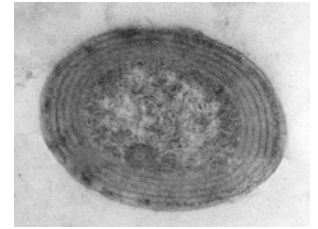


Johnson et al, Science, 2007

TRAITS

- small
- unique pigments
- N acquisition
- warm adapted

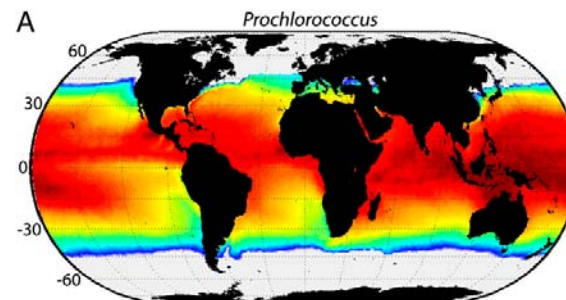
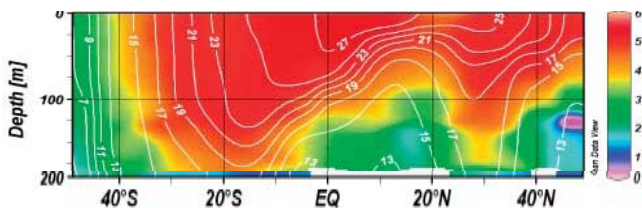
WHICH TRAITS LEAD TO *PROCHLOROCOCCUS* BIOGEOGRAPHY?



Use a numerical model as laboratory to explore which/how many traits important to explain biogeography

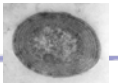
TRAITS

- small
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BIOGEOGRAPHY:

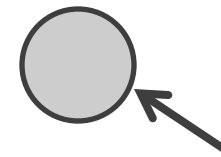
- Low latitudes
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Model description:

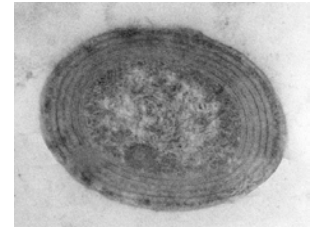


- 3D model circulation (ECCO-GODAE)
- Radiative transfer model, spectral light
- Cycling of N,P,C,Si,Fe,O
- DOM, POM
- Zooplankton grazers
- Phytoplankton types assigned "traits"



generic phytoplankton,
traits added as needed

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



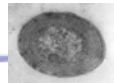
TRAITS

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BIOGEOGRAPHY:

- Low latitudes
- Warm waters
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HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?

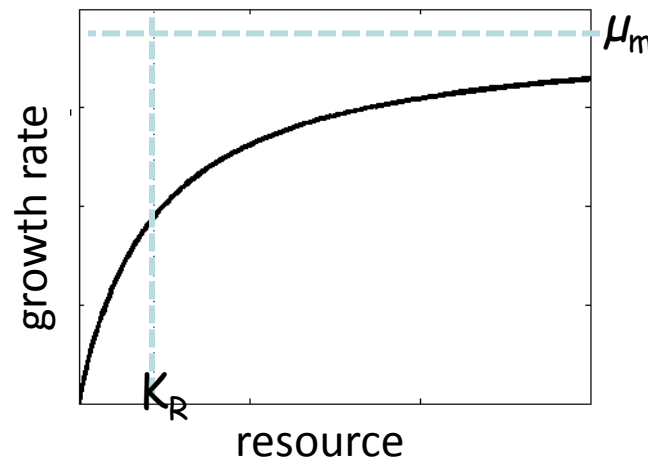


resources limited growth

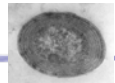
$$\mu_m \frac{R}{R + \kappa_R} P$$

R resource (nutrient, N, Fe, P, Si)

P phytoplankton biomass



HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?

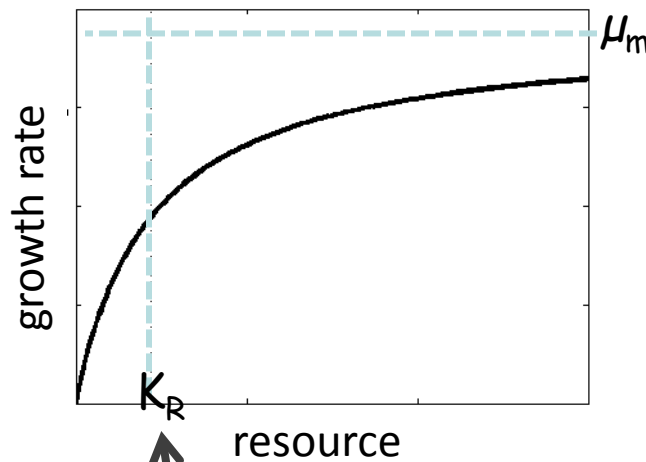


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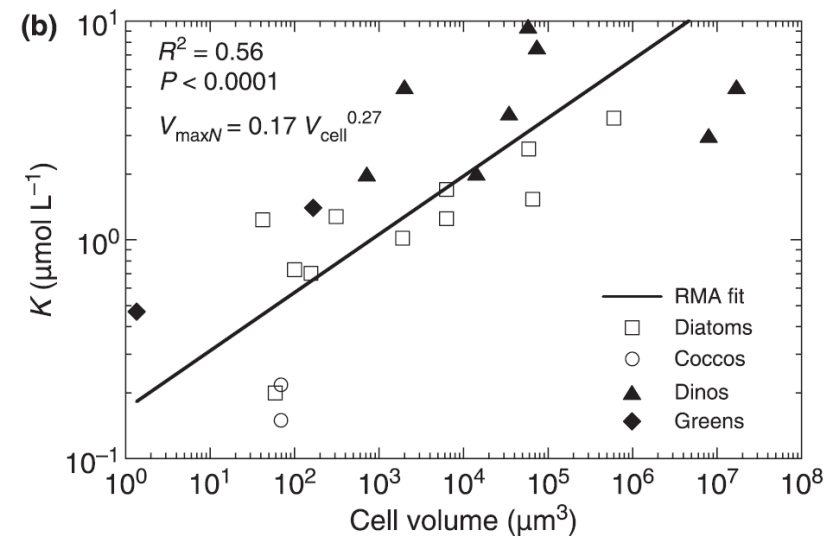
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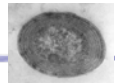


small leads to lower K_R
(see e.g. Aksnes and Egge, MEPS 1991)



Litchman et al,
Ecol Let. , 2007

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?

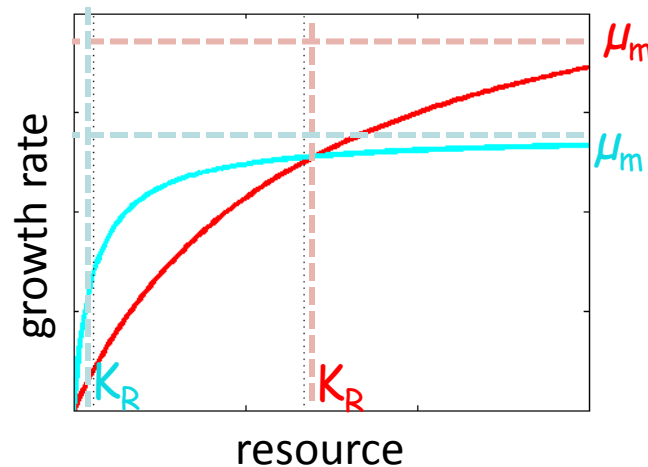


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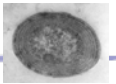
P phytoplankton biomass



r-strategy (opportunist),
grow fast, but require high
nutrients

K-strategy (gleaner), grow
slowly, but grow better at
low nutrients

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



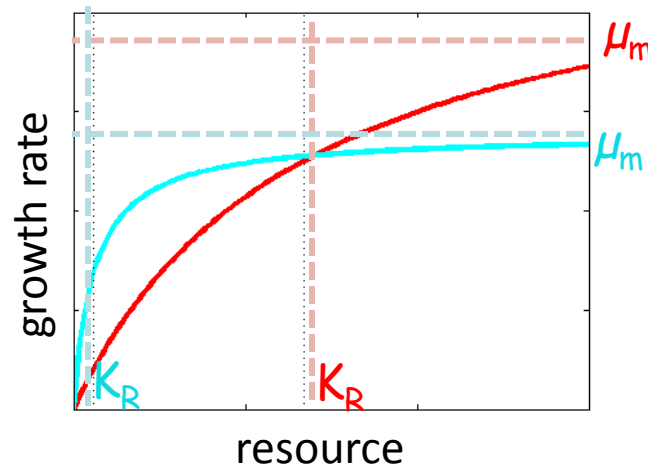
rate change= growth-loss

$$\frac{dP}{dt} = \mu_m \frac{R}{R + \kappa_R} P - MP$$

R resource (nutrient, N, Fe, P, Si)

P phytoplankton biomass

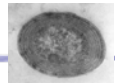
$M(Z, w, m)$ loss (grazing, sinking, etc)



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HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



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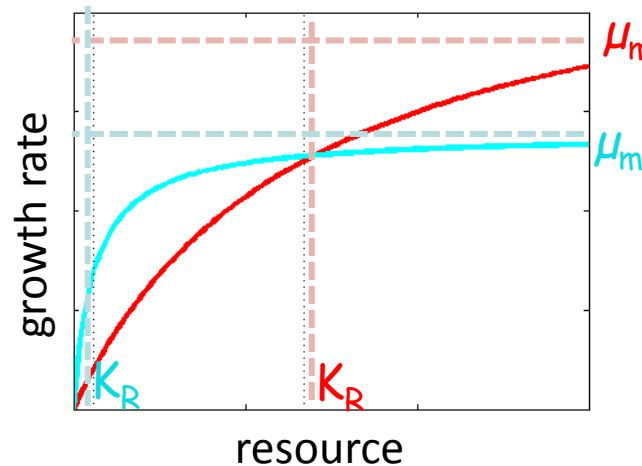
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↓
STEADY STATE:

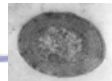
$$R^* = \frac{\kappa_R M}{\mu_m - M}$$

phytoplankton with
lowest R^* favoured

Resource
Competition Theory
(Tilman, 1977)



HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



rate change= growth-loss

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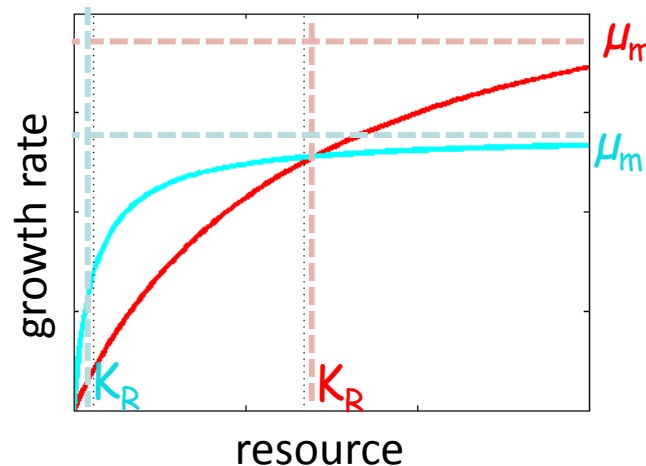
↓
STEADY STATE:

$$R^* = \frac{\kappa_R M}{\mu_m - M}$$

phytoplankton with lowest R^* favoured

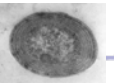
Resource

Competition Theory
(Tilman, 1977)



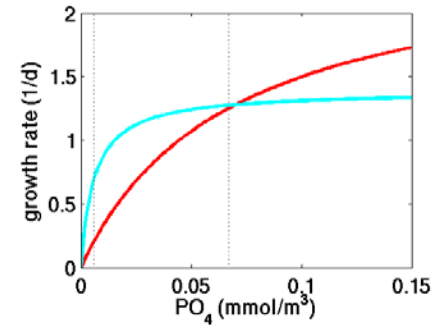
If $R^* < R^*$, **gleaner** wins in steady state conditions

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



$$R^* = \frac{\kappa_R M}{\mu_m - M}$$

$$R^* < R^*$$

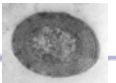


Opportunist
Pro

Pro

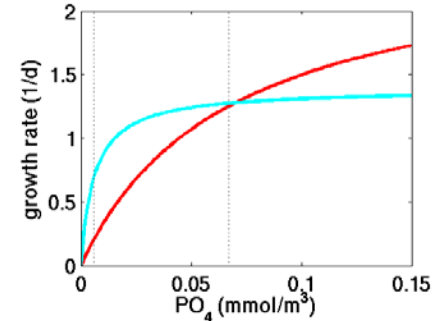
opportunists

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



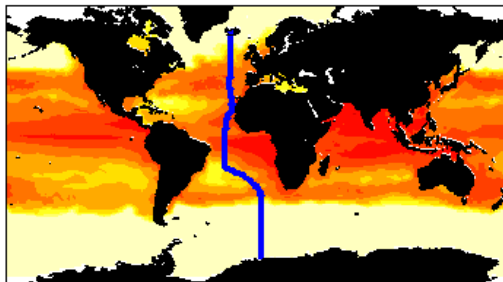
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$$R^* < R^*$$

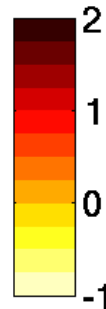


Opportunist
Pro

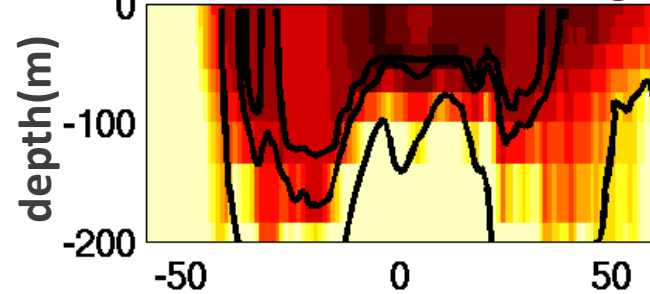
Prochlorococcus-analog



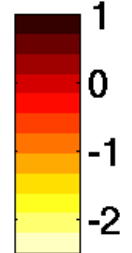
log₁₀
mmolC m⁻²



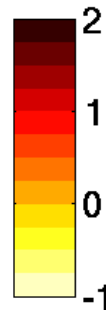
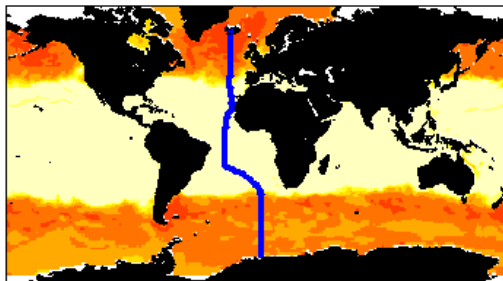
Prochlorococcus-analog



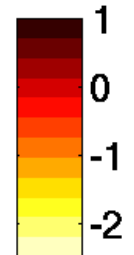
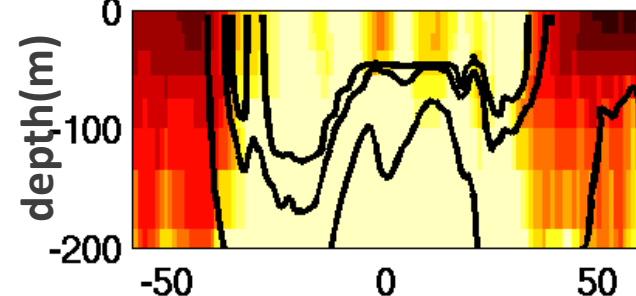
log₁₀
mmolC m⁻³



Opportunist-analog



Opportunist-analog

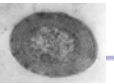


latitude

Pro

opportunists

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



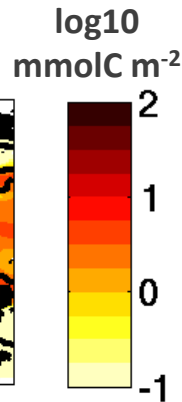
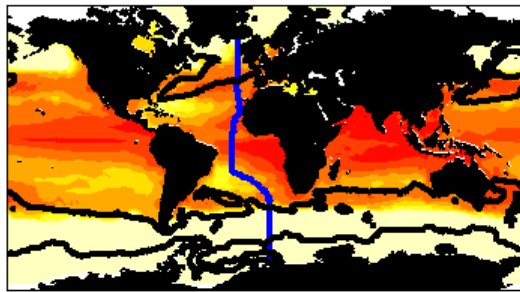
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$$R^* < R^*$$

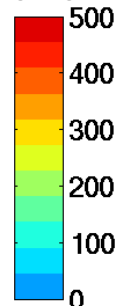
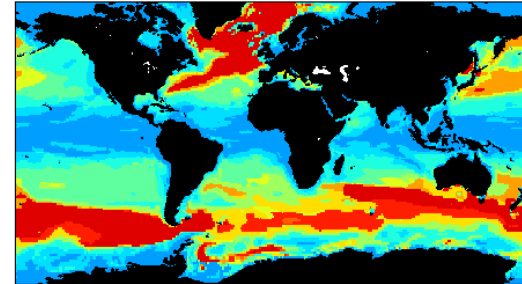
stable environment important

Pro

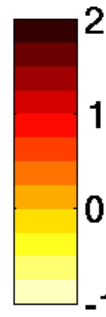
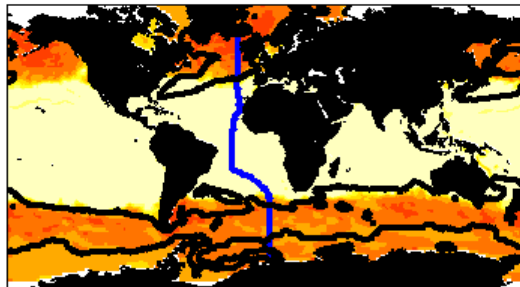
Prochlorococcus-analog



Range of mixed layer depth (m)



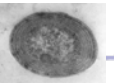
Opportunist-analog



opportunists

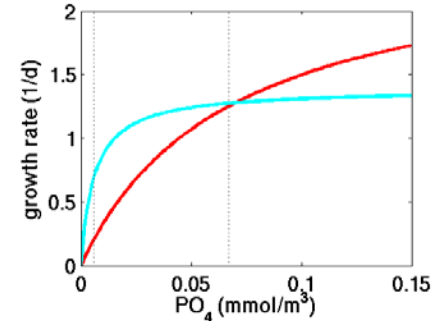
(see e.g. Dutkiewicz et al, *GBC*, 2009)

HOW DOES **SIZE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



$$R^* = \frac{\kappa_R M}{\mu_m - M}$$

$$R^* < R^*$$



Opportunist
Pro

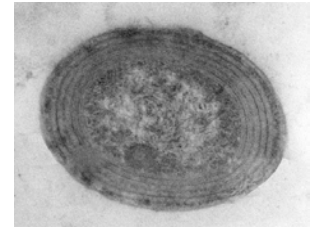
Pro

Having lowest R^* (consequence of their **size**) is an advantage for *Prochlorococcus* in the **stable environments**:

opportunists

Here they draw down nutrients and outcompete others

PROCHLOROCOCCUS TRAITS: PIGMENTS



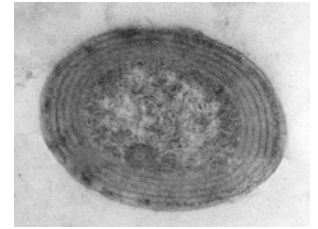
TRAITS

- small
- **unique pigments**
- N acquisition
- warm adapted

BIOGEOGRAPHY:

- Low latitudes
- Warm waters
- Low nitrate

HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?

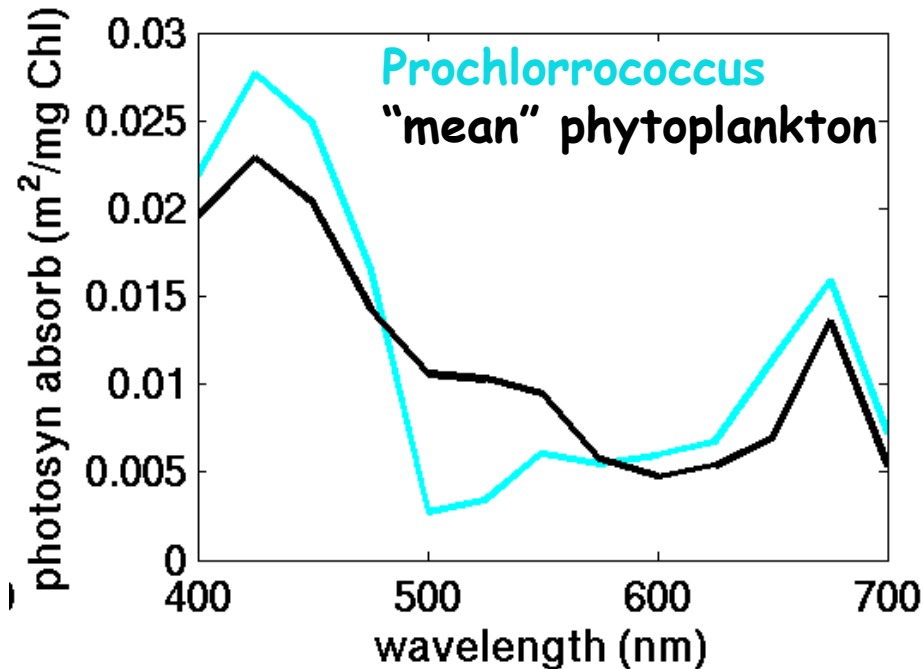


TRAITS

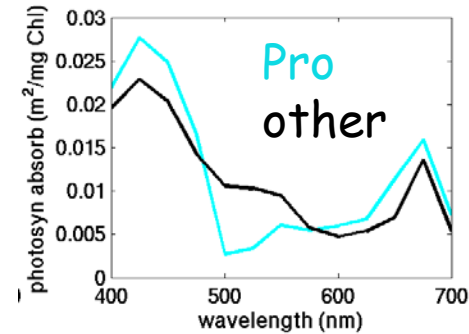
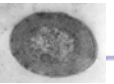
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- Warm waters
- Low nitrate



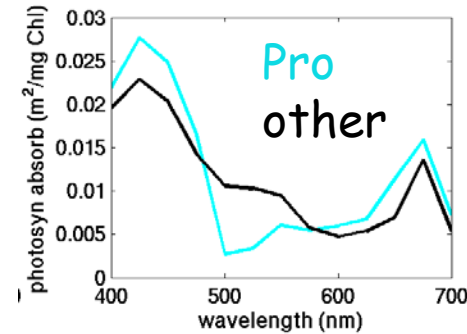
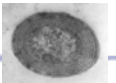
HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



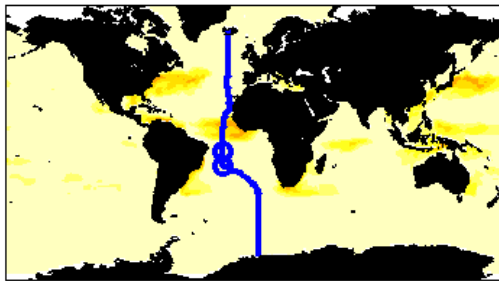
Pro

other

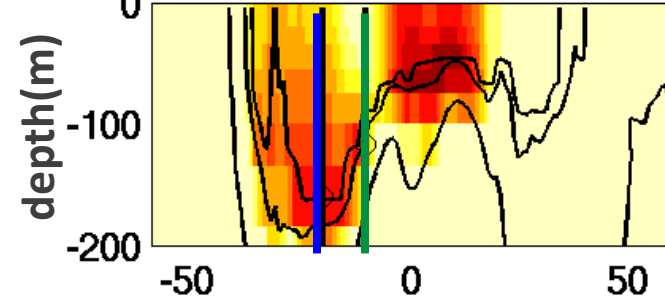
HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



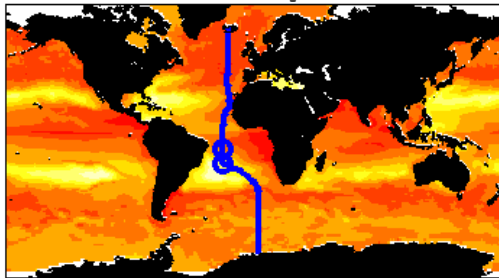
Prochlorococcus-analog



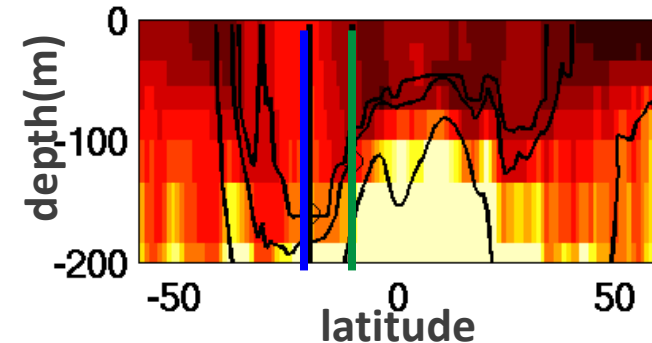
Prochlorococcus-analog



mean spectra



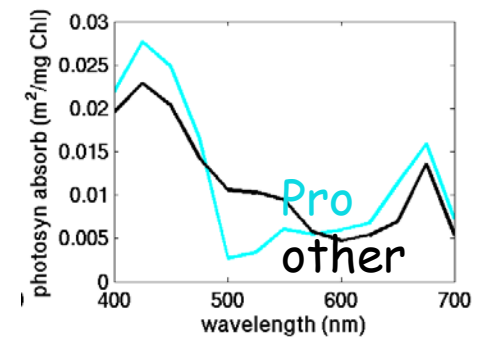
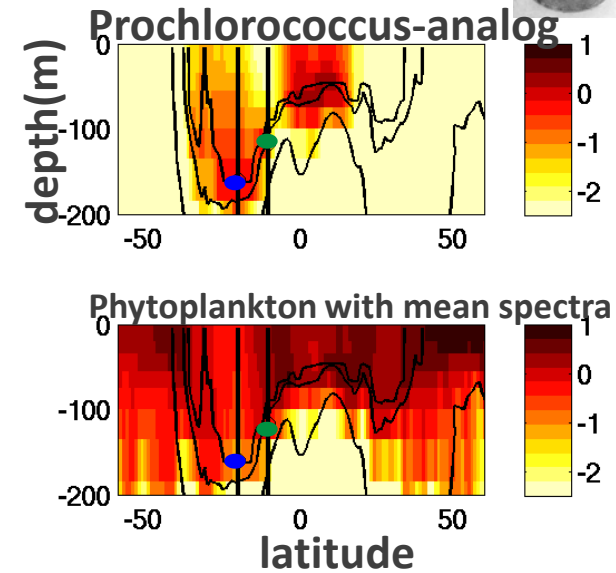
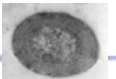
mean spectra



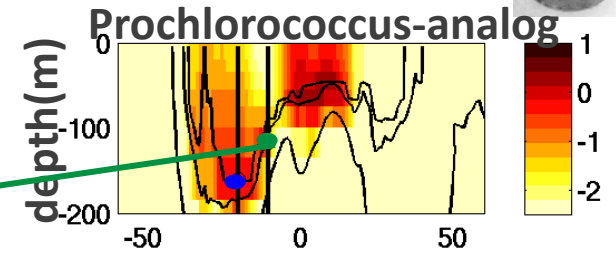
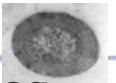
Pro

other

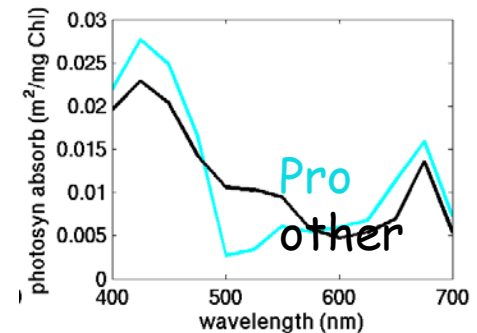
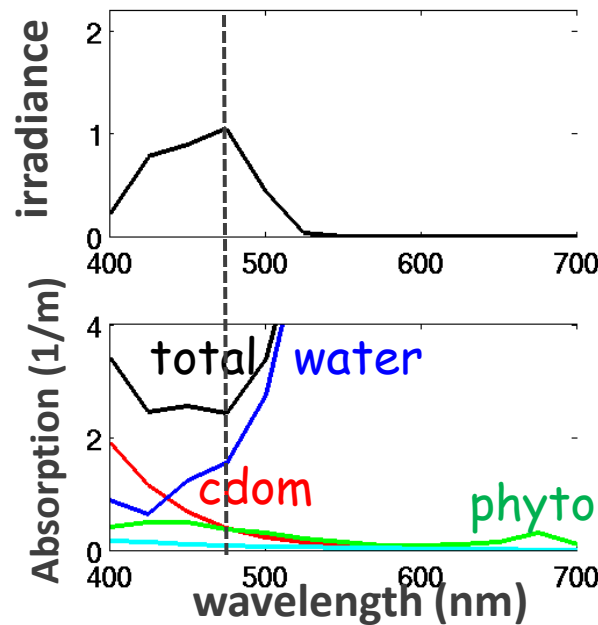
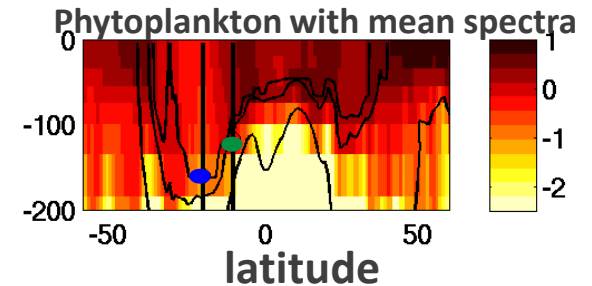
HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



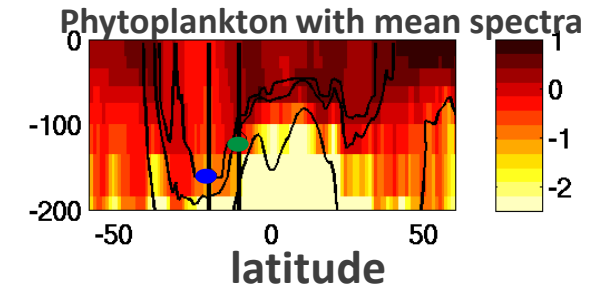
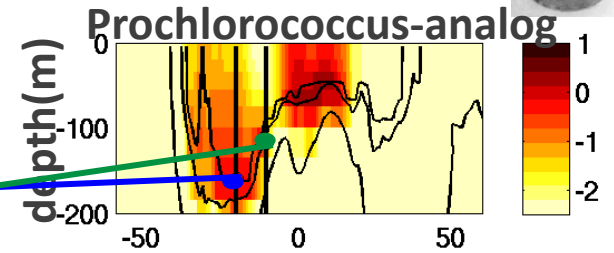
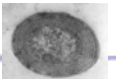
HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



No-Pro location

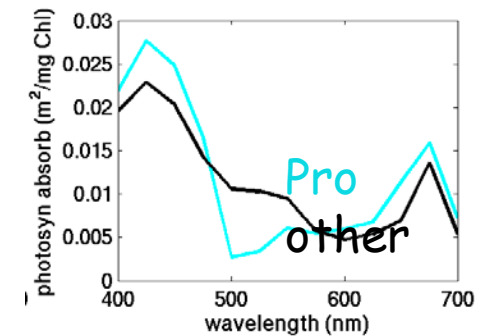
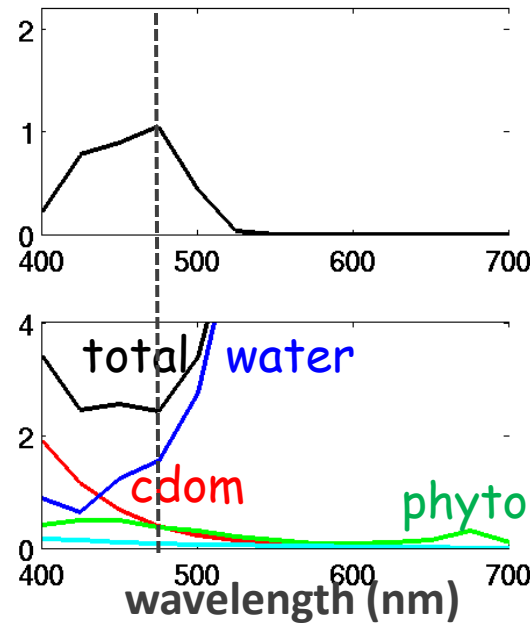
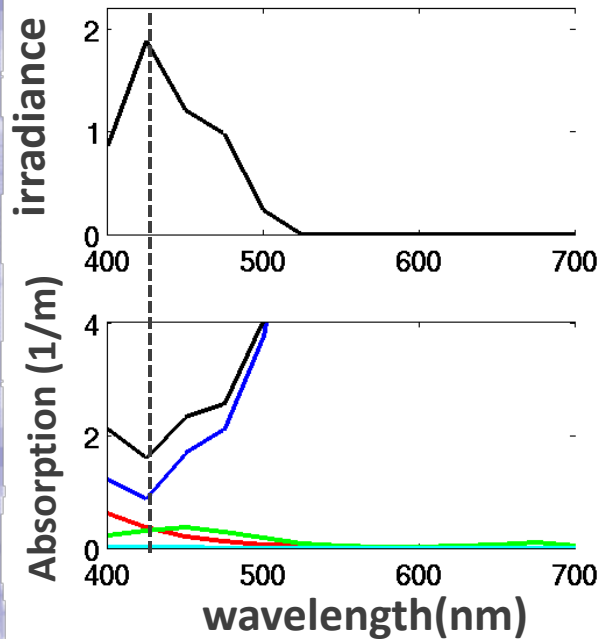


HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?

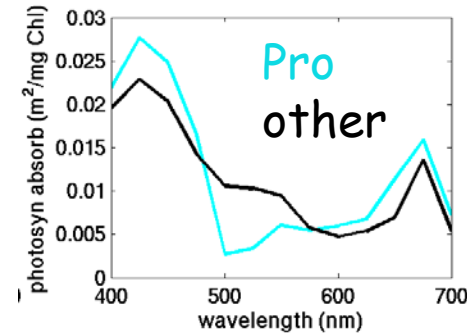
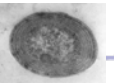


Pro dominated location

No-Pro location



HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



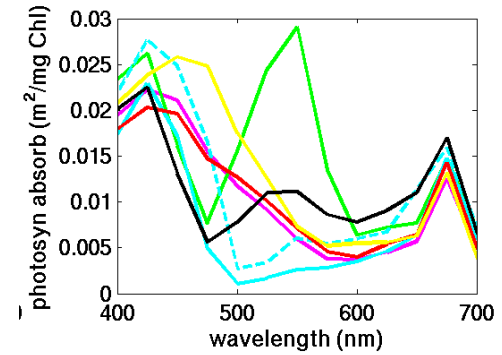
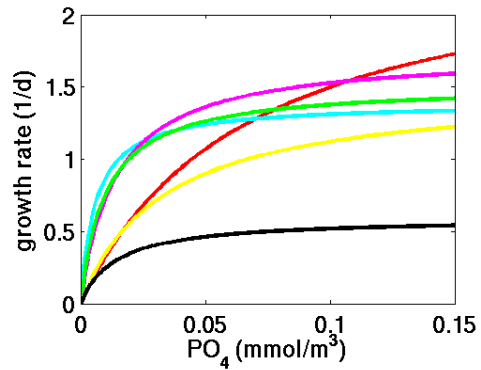
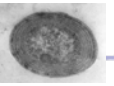
Pro

Absorbing best in blue light is advantageous (or least disadvantageous) in the most oligotrophic regions where organic matter is low.

other

(see e.g. Sathyendranath+Platt, 2007;
Hickman et al, MEPS, 2010)

HOW DO SIZE AND PIGMENTS IMPACT BIOGEOGRAPHY?



Pro

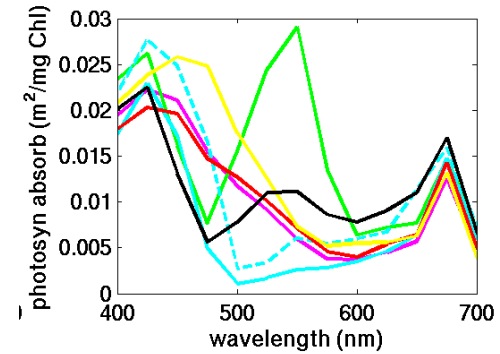
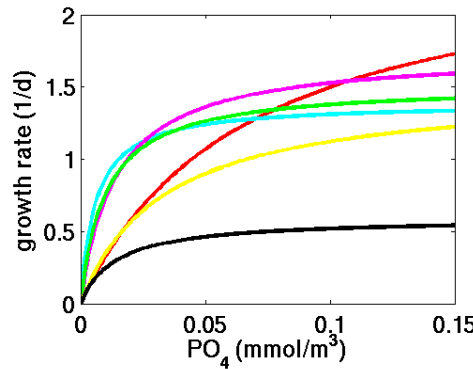
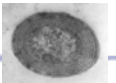
Syn

Pico
euk

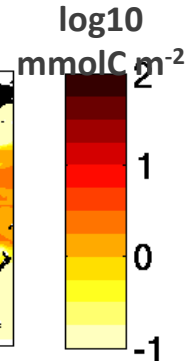
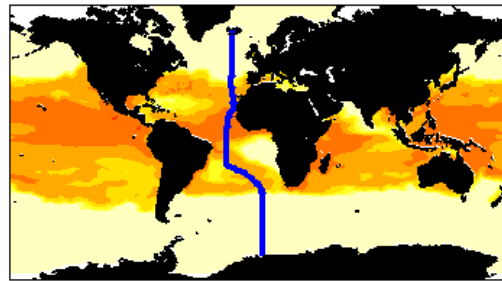
Cocco

diatom

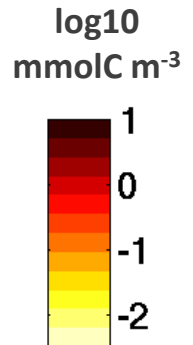
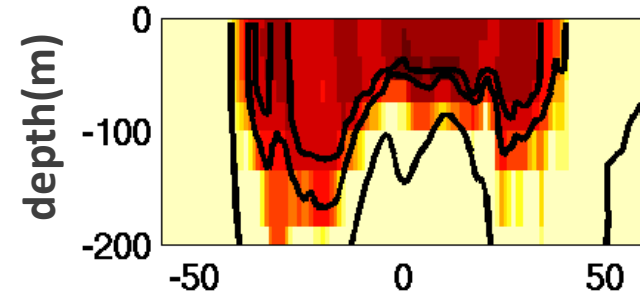
HOW DO SIZE AND PIGMENTS IMPACT BIOGEOGRAPHY?



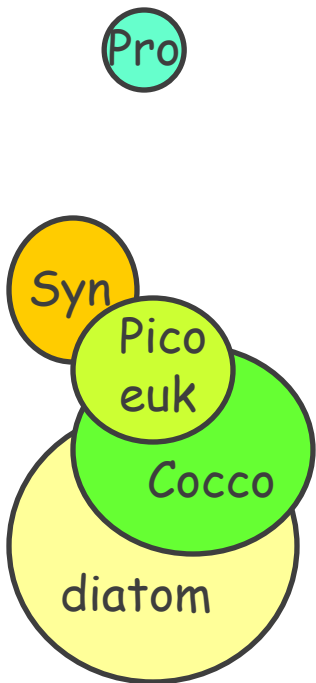
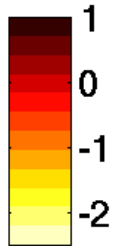
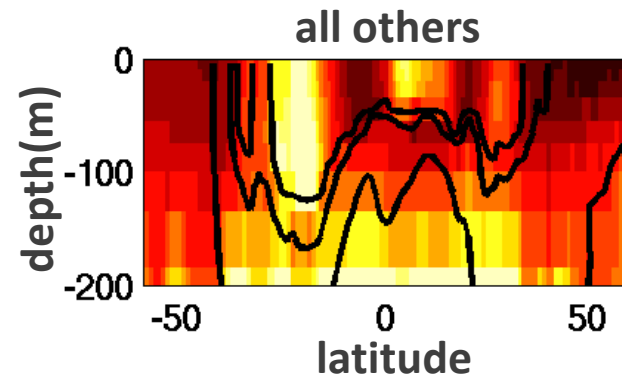
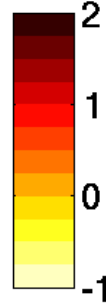
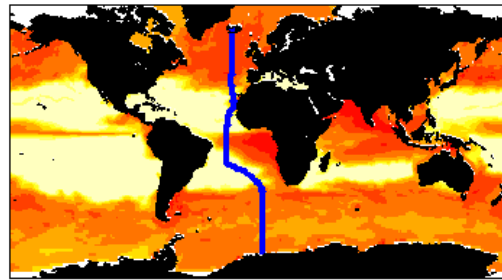
Prochlorococcus-analog



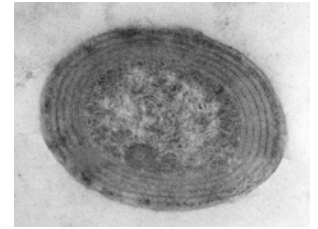
Prochlorococcus-analog



all others



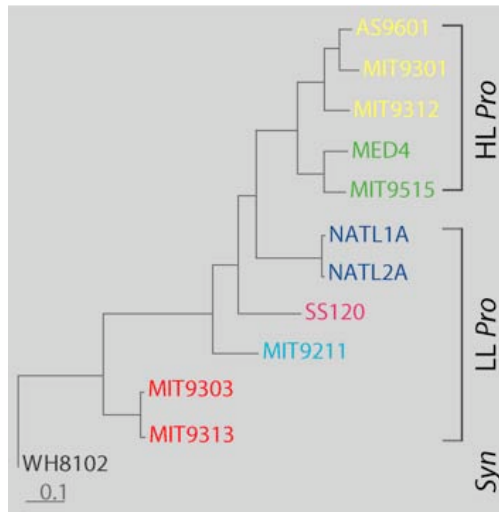
PROCHLOROCOCCUS TRAITS: PIGMENTS



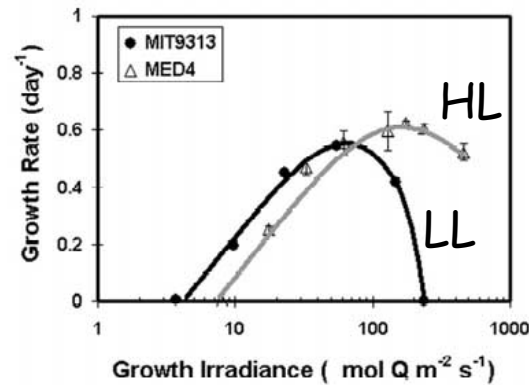
TRAITS

- small
- **unique pigments**
- N acquisition
- warm adapted

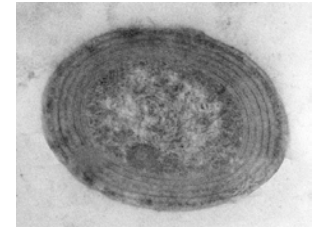
PROCHLOROCOCCUS TRAITS: PIGMENTS



Chisholm Lab



Hess et al, PR, 2001

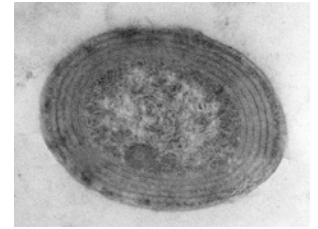
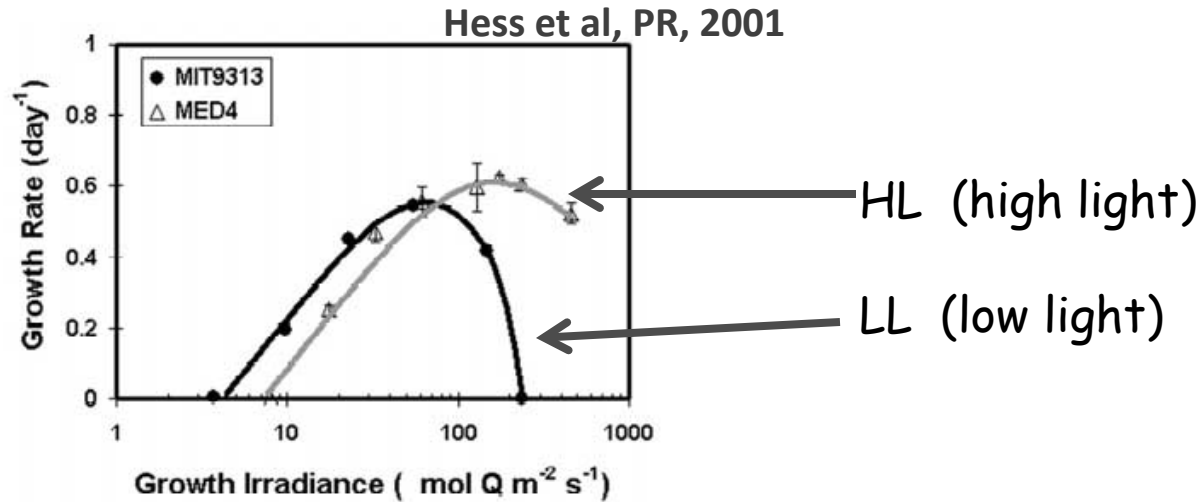


TRAITS

- small
- **unique pigments**
- N acquisition
- warm adapted

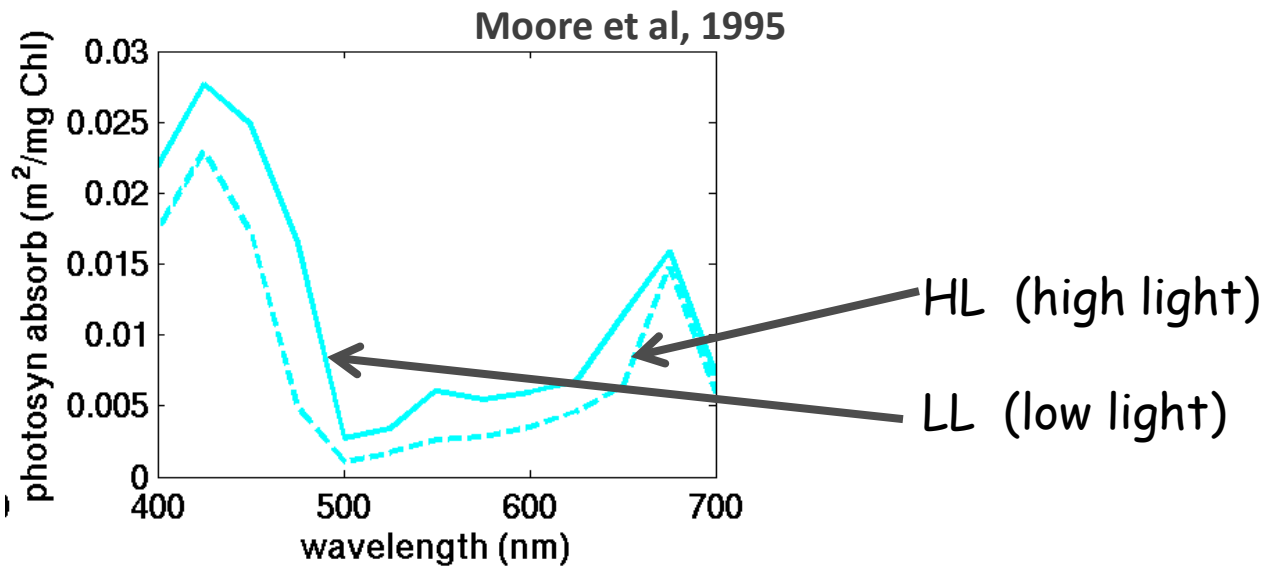
- Different Chl a/b ratios in different "clades"
- Some are strongly photoinhibited

HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



TRAITS

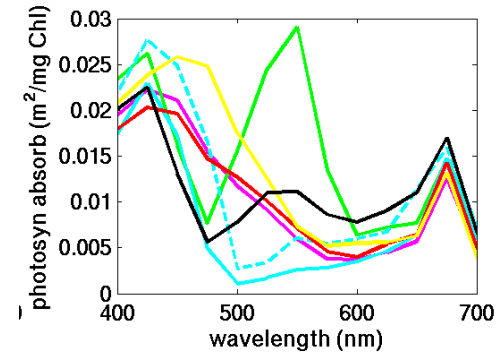
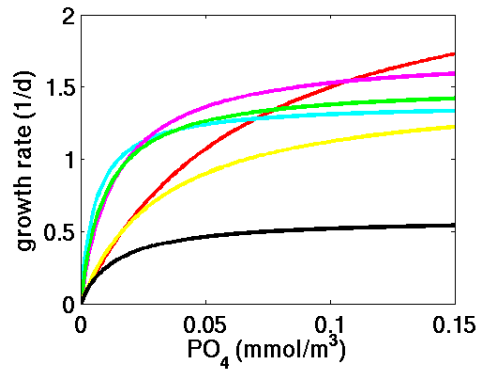
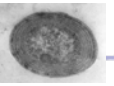
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BIOGEOGRAPHY:

- Low latitudes
- Warm waters
- Low nitrate

HOW DO SIZE AND PIGMENTS IMPACT BIOGEOGRAPHY?



Pro

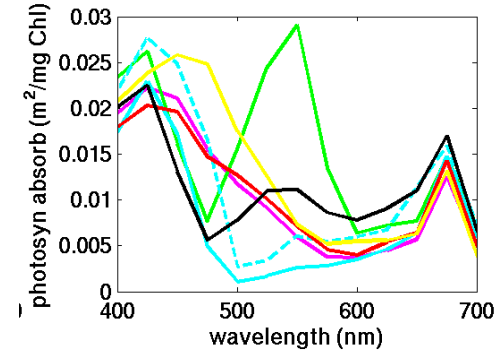
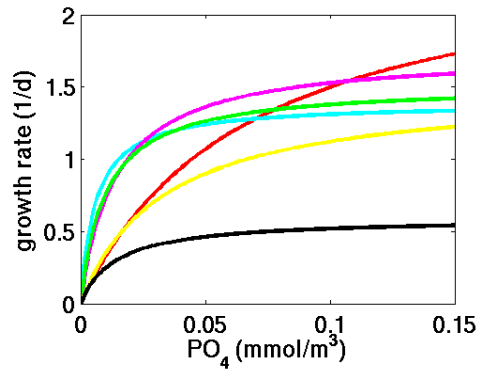
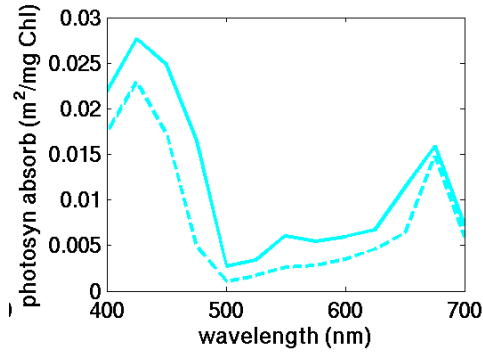
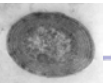
Syn

Pico
euk

Cocco

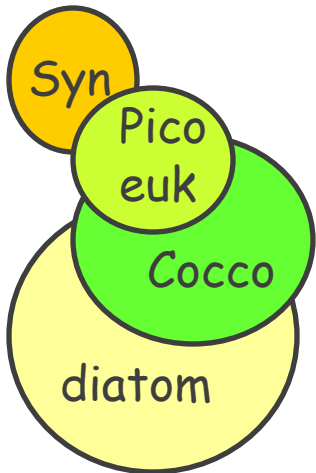
diatom

HOW DO SIZE AND PIGMENTS IMPACT BIOGEOGRAPHY?

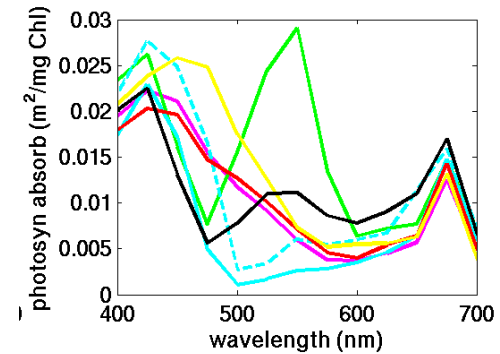
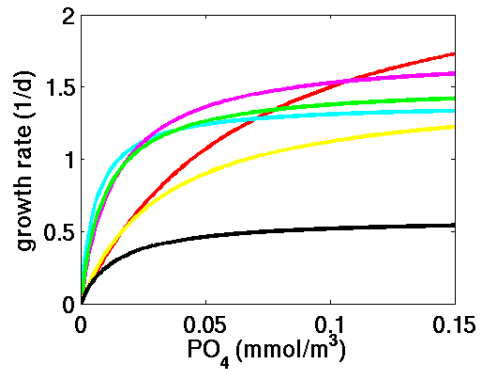
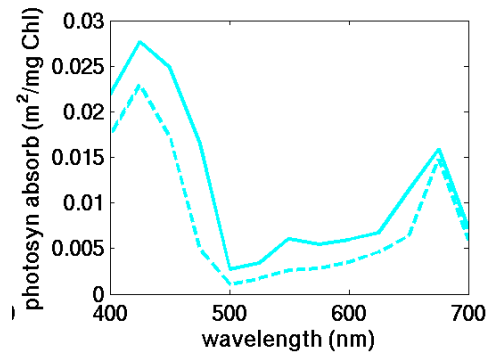
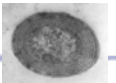


LL
Pro

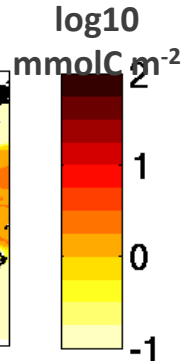
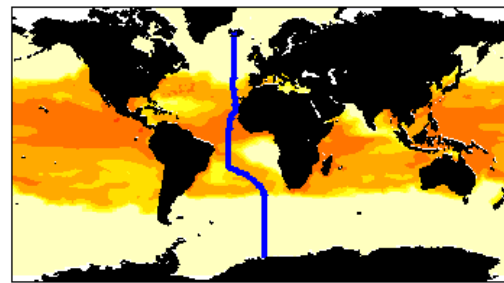
HL
Pro



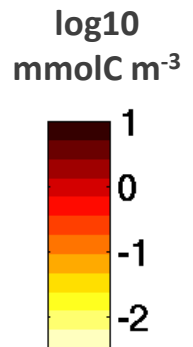
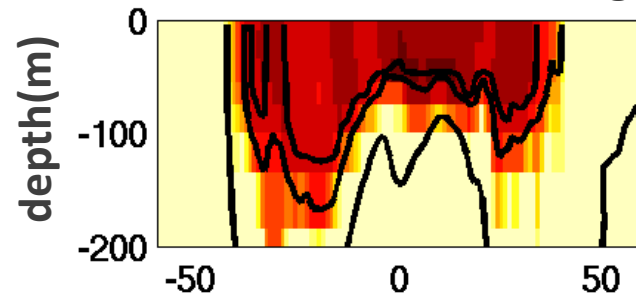
HOW DO SIZE AND PIGMENTS IMPACT BIOGEOGRAPHY?



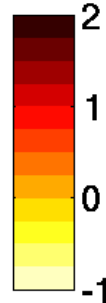
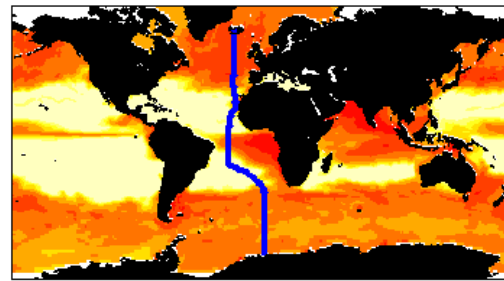
Prochlorococcus-analog



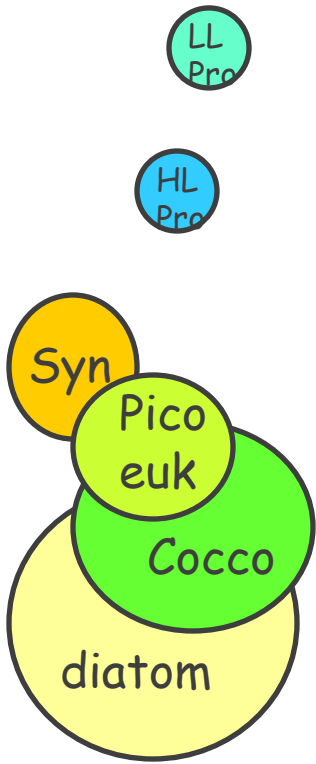
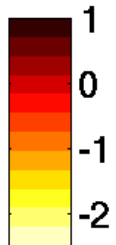
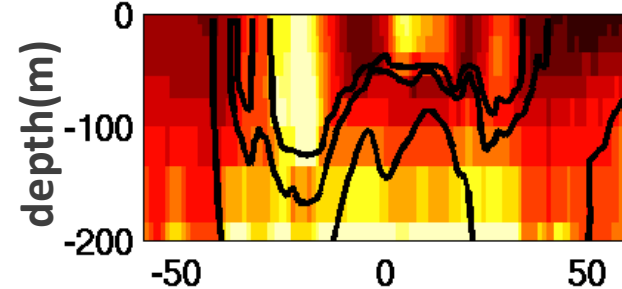
Prochlorococcus-analog



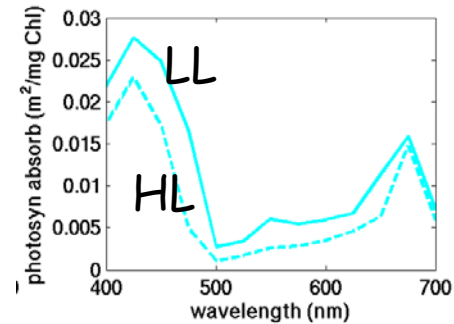
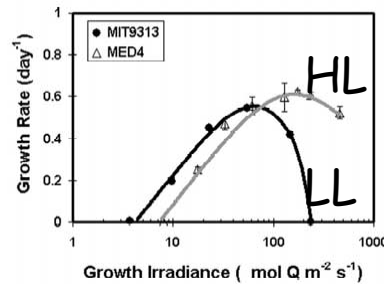
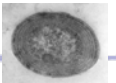
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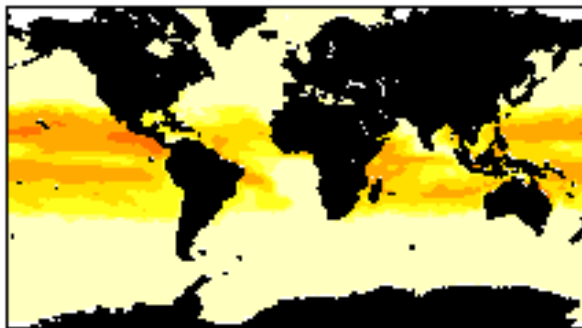
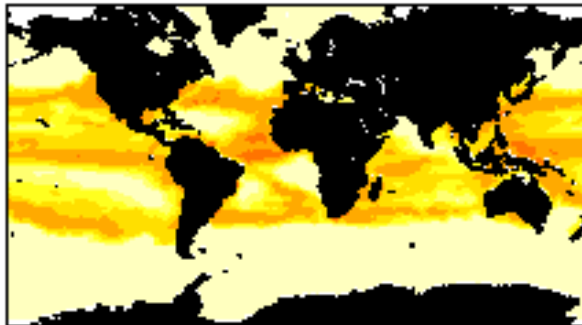
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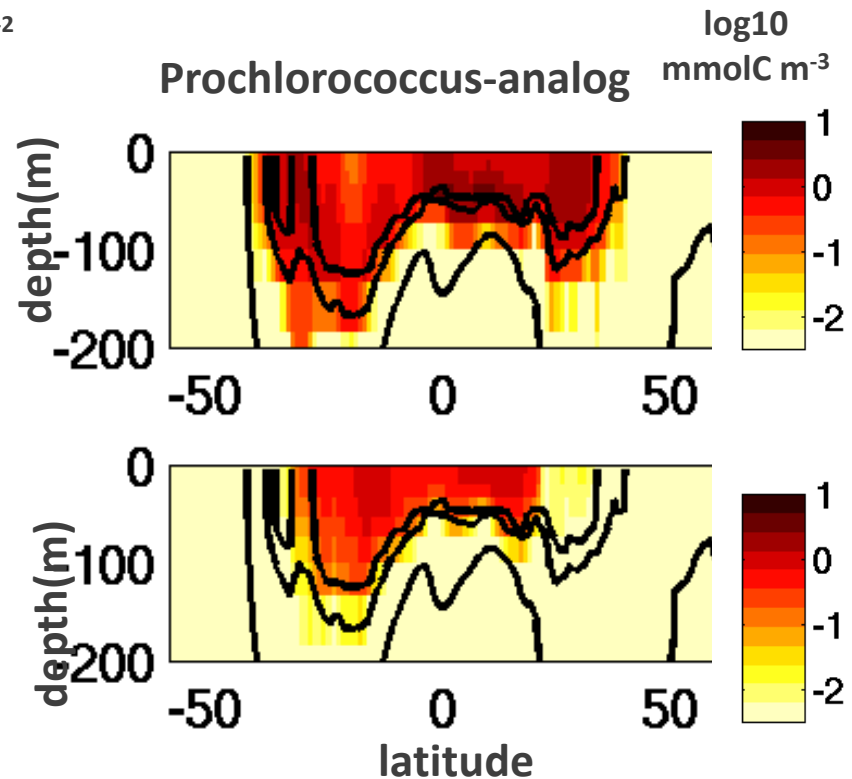
HOW DO PIGMENTS IMPACT BIOGEOGRAPHY?



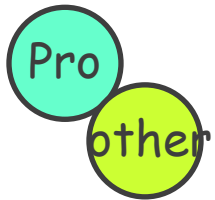
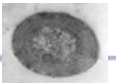
Prochlorococcus-analog



Prochlorococcus-analog



HOW DO PIGMENTS IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?

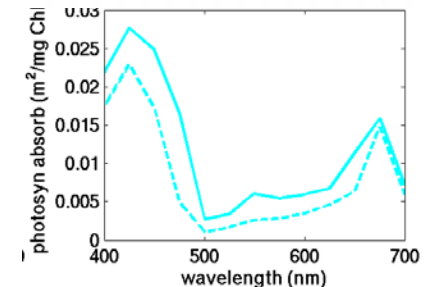
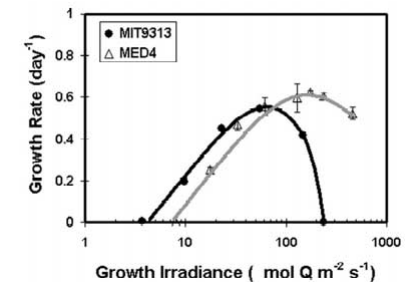
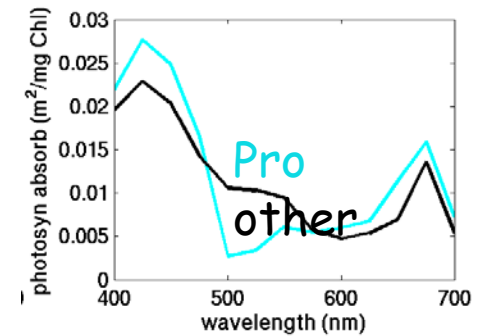


Absorbing best in blue light is advantageous (least disadvantageous) in the most oligotrophic regions where organic matter is low.

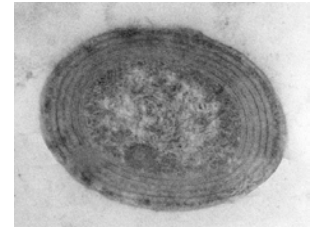


Trade off between absorbing better, but inhibition leads to separate biogeography of clades.

(see e.g. Hickman et al, MEPS, 2010
Sathyendranath+Platt, 2007)



PROCHLOROCOCCUS TRAITS: NITROGEN ACQUISITION

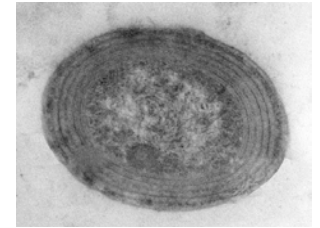
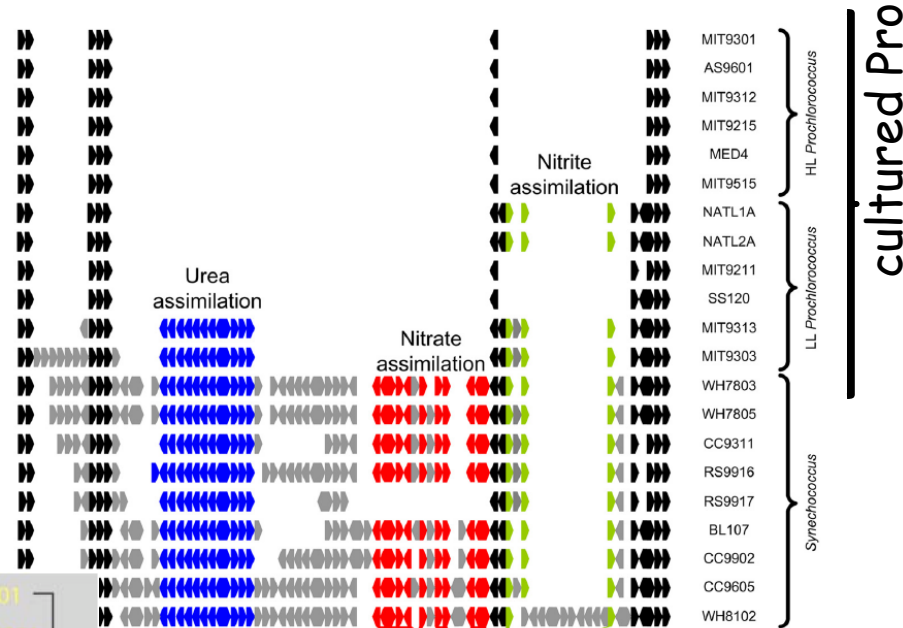


TRAITS

- small
- unique pigments
- **N acquisition**
- warm adapted

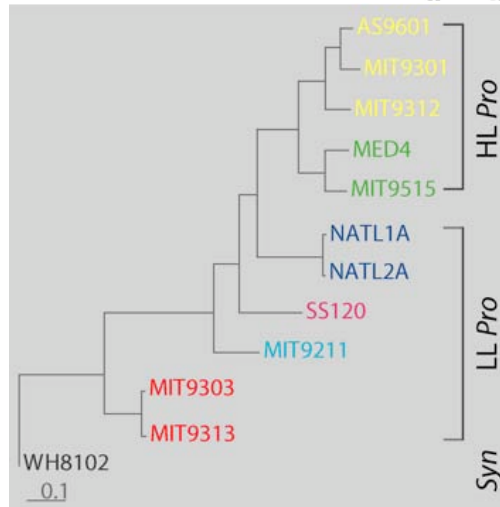
PROCHLOROCOCCUS TRAITS: NITROGEN ACQUISITION

Nitrogen acquisition genes



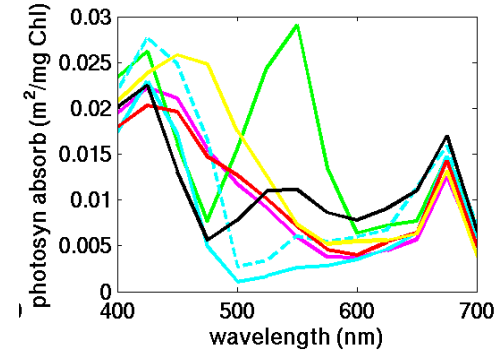
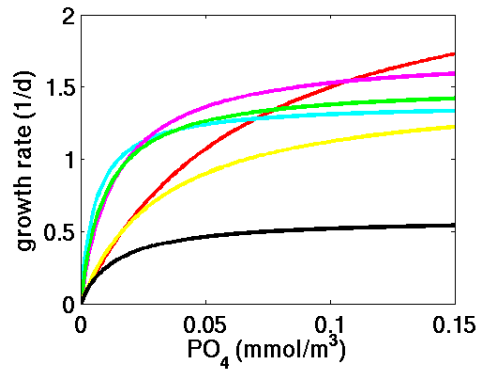
TRAITS

- small
- unique pigments
- **N acquisition**
- warm adapted



Martiny et al, PNAS, 2009

HOW DO SIZE, PIGMENTS, N ACQUISITION IMPACT BIOGEOGRAPHY?

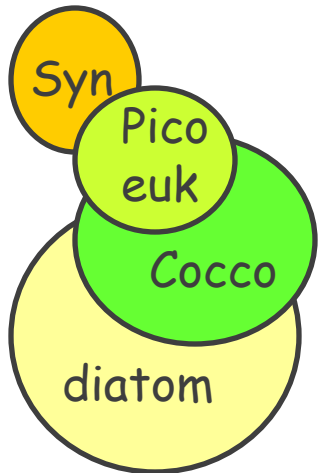


no NO₂/NO₃

HL
Pro

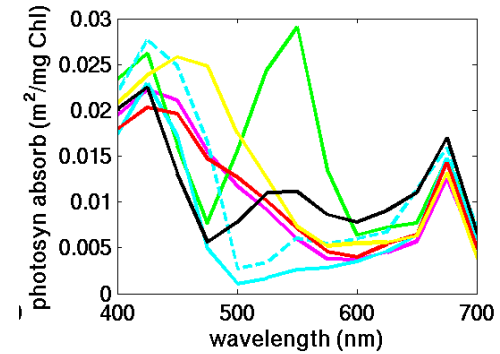
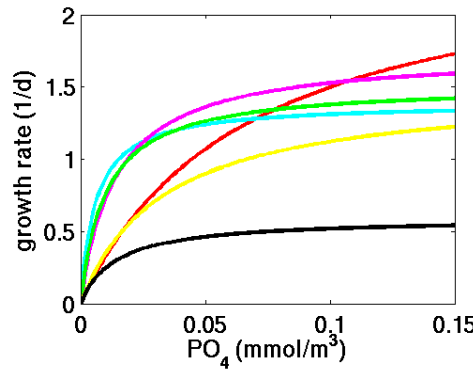
LL
Pro

no NO₃

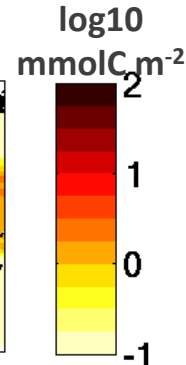


latitude

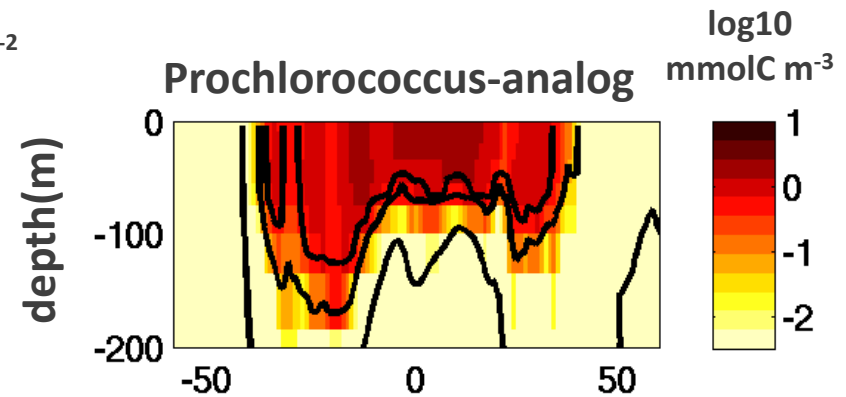
HOW DO SIZE, PIGMENTS, N ACQUISITION IMPACT BIOGEOGRAPHY?



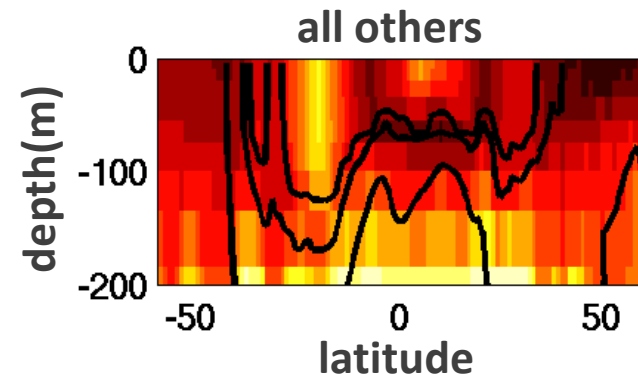
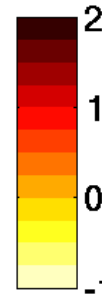
Prochlorococcus-analog



Prochlorococcus-analog



all others



no NO₂/NO₃

HL
Pro

no NO₃

LL
Pro

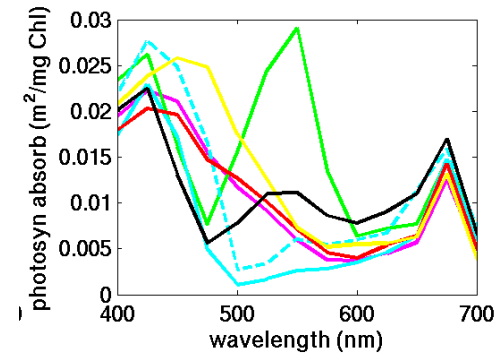
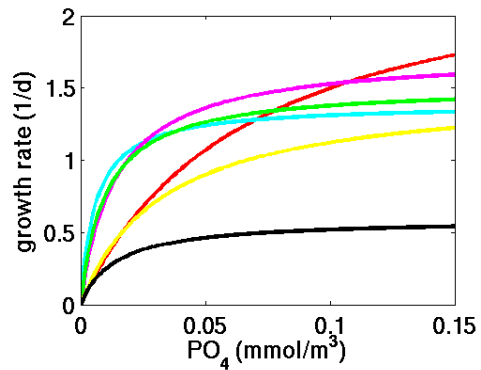
Syn

Pico
euk

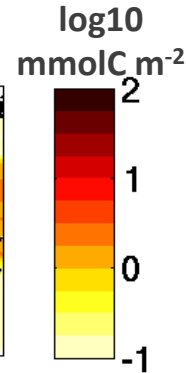
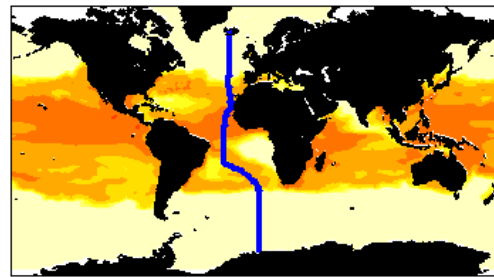
Cocco

diatom

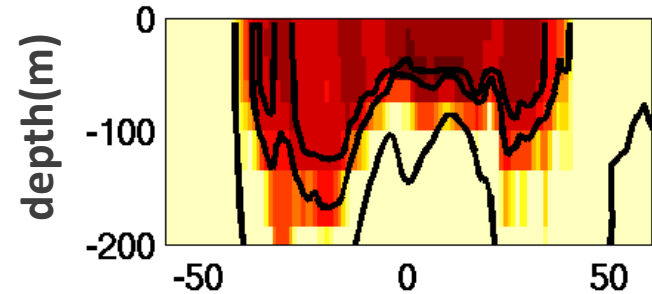
HOW DO SIZE, PIGMENTS, N ACQUISITION IMPACT BIOGEOGRAPHY?



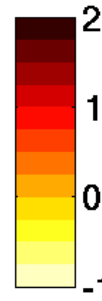
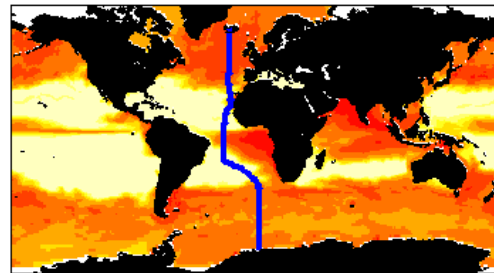
Prochlorococcus-analog



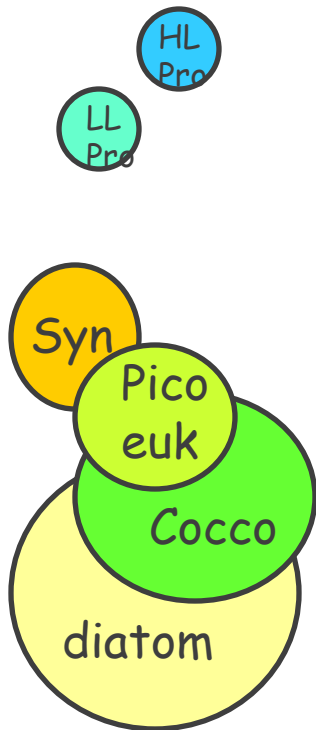
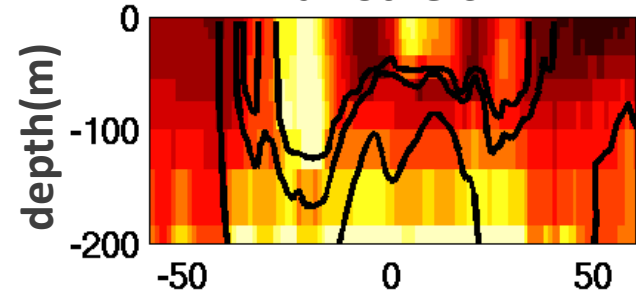
Prochlorococcus-analog



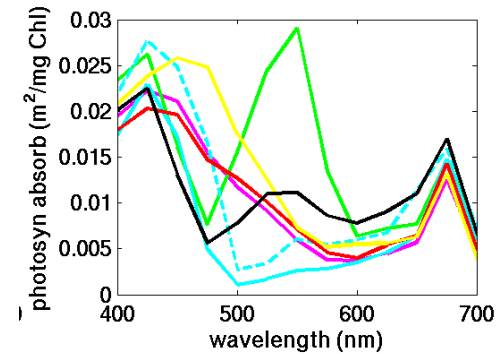
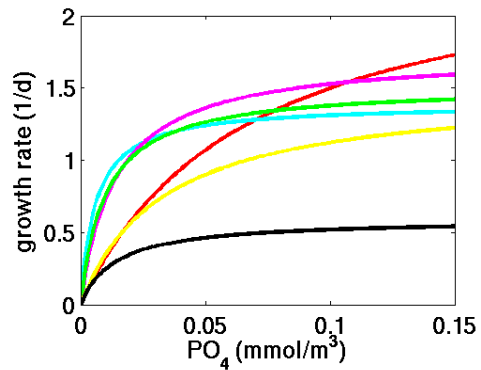
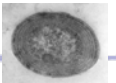
all others



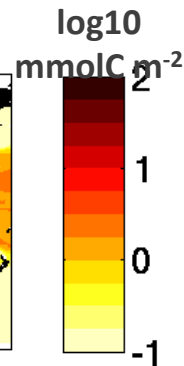
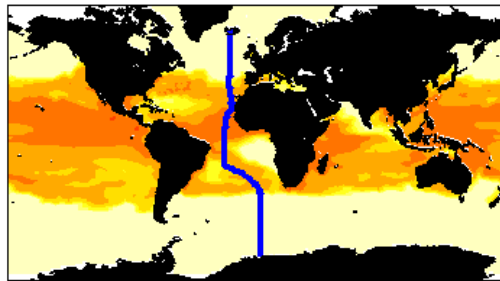
all others



HOW DOES N ACQUISITION IMPACT BIOGEOGRAPHY?

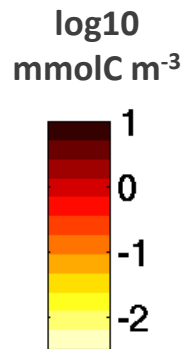
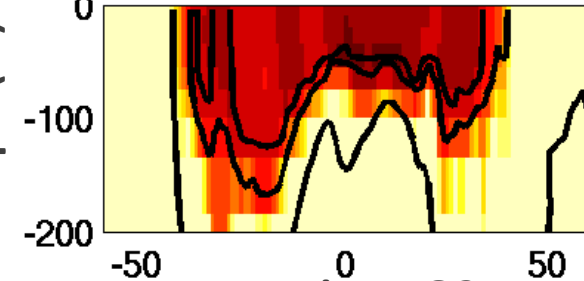


Using NO3



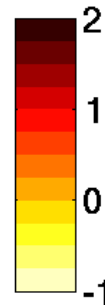
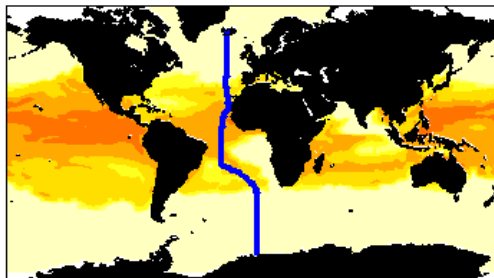
depth(m)

Using NO3

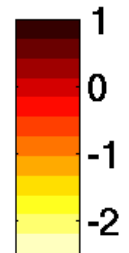
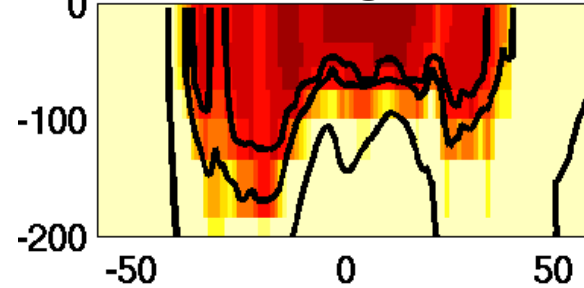


Not using NO3

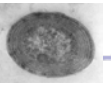
no NO₂/NO₃



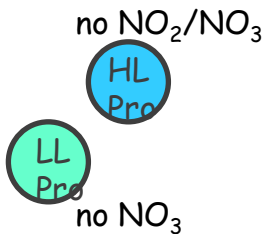
Not using NO3



latitude



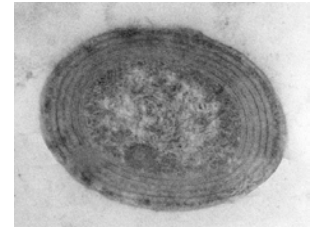
Not being able to assimilate NO_3 (or NO_2) is not "advantage" unless it is a trade-off:



But it is least disadvantageous in the highly oligotrophic stable environments

(see e.g. Bragg et al, PlosOne, 2010)

HOW DOES **TEMPERATURE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



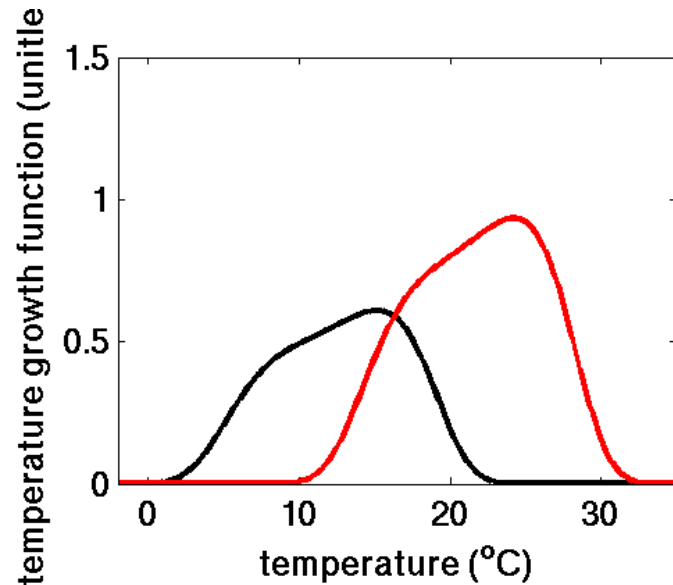
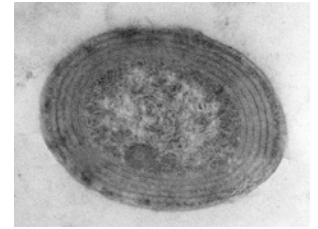
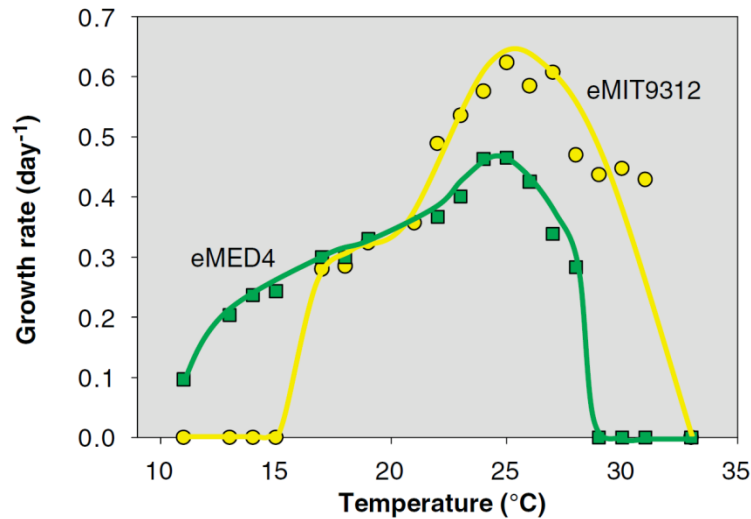
TRAITS

- small
- unique pigments
- N acquisition
- **warm adapted**

BIOGEOGRAPHY:

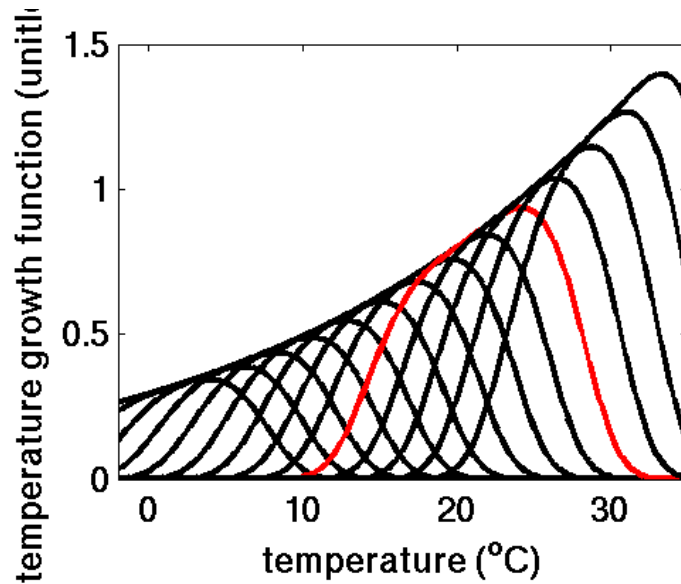
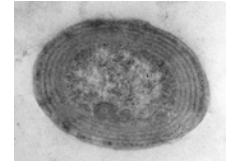
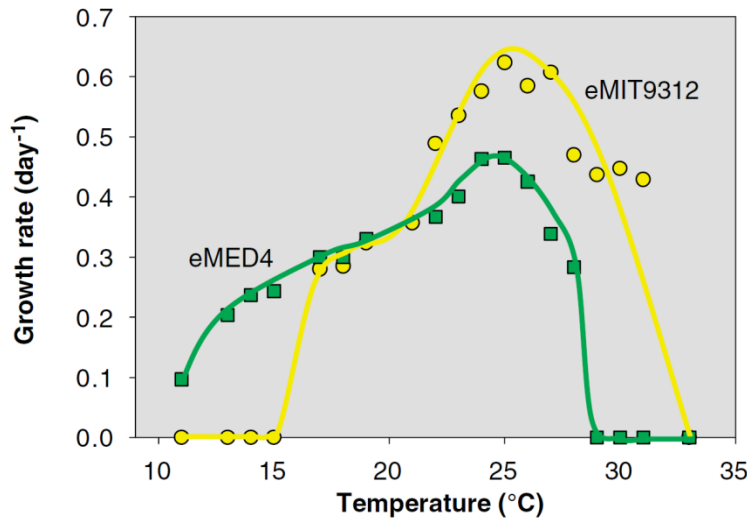
- Low latitudes
- Warm waters
- Low nitrate

HOW DOES **TEMPERATURE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



Growth is function
temperature

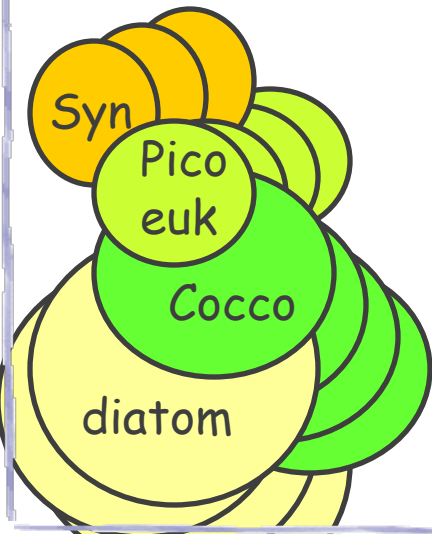
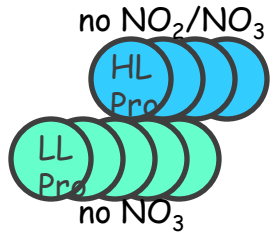
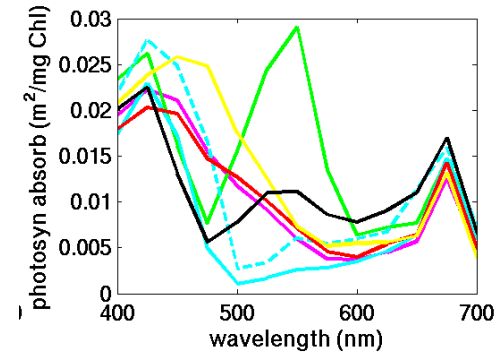
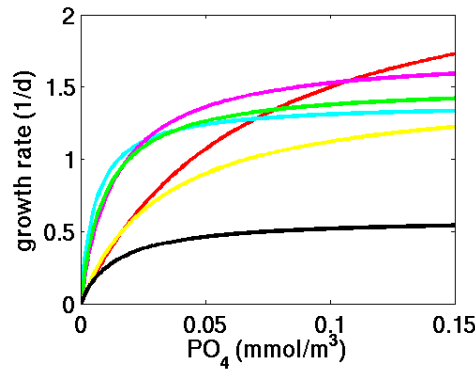
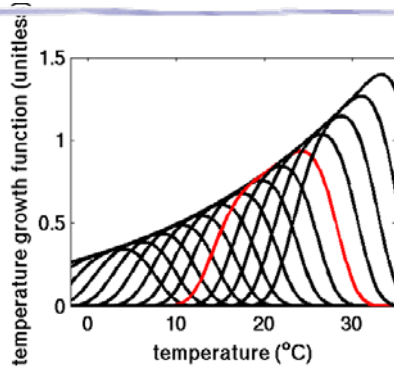
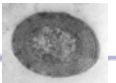
HOW DOES TEMPERATURE IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



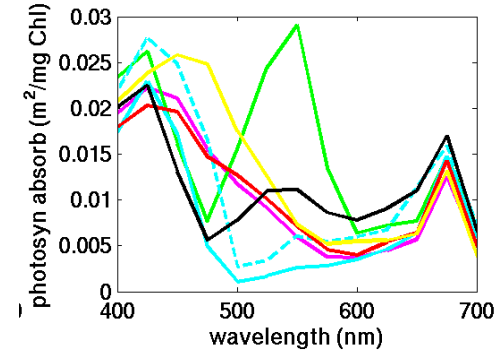
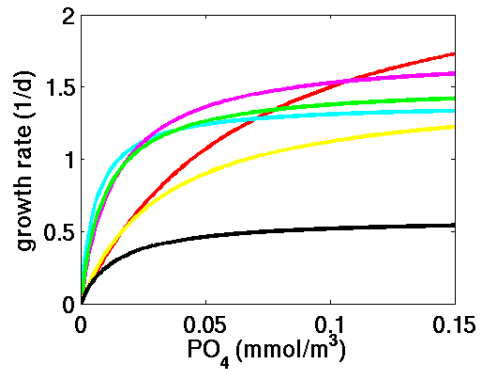
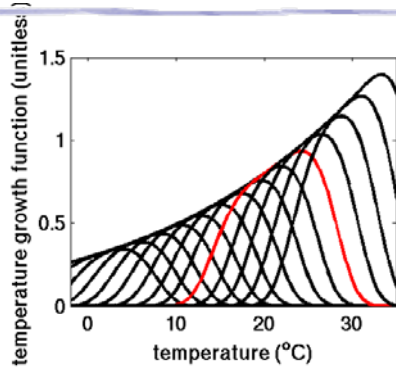
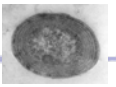
Many *Prochlorococcus*-ecotype analogs each with temperature range:

Which survive?

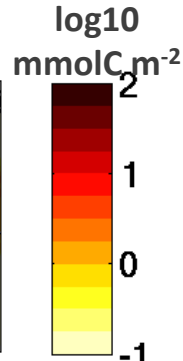
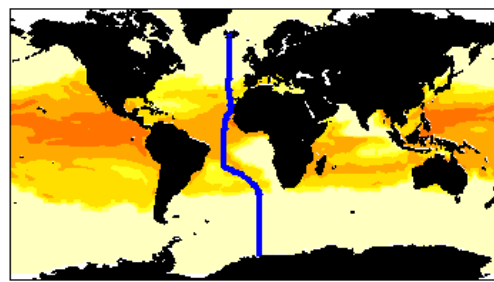
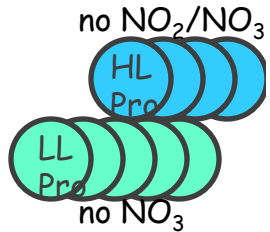
HOW DO TEMPERATURE IMPACT BIOGEOGRAPHY?



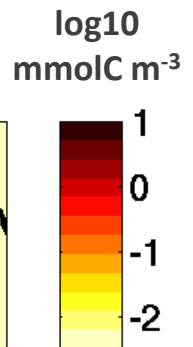
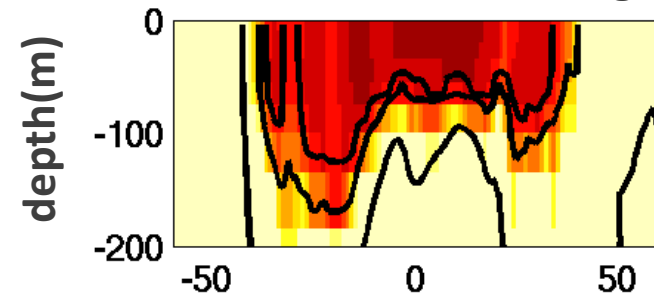
HOW DO TEMPERATURE IMPACT BIOGEOGRAPHY?



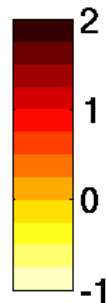
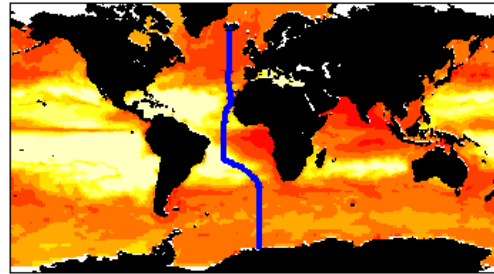
Prochlorococcus-analog



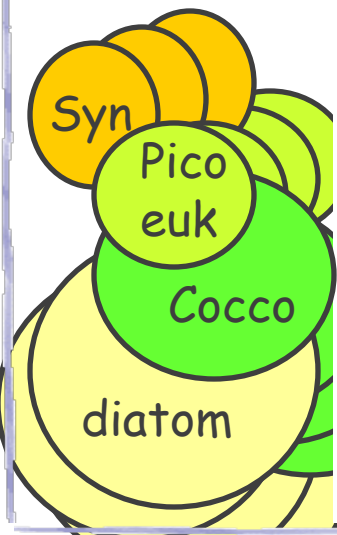
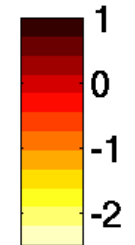
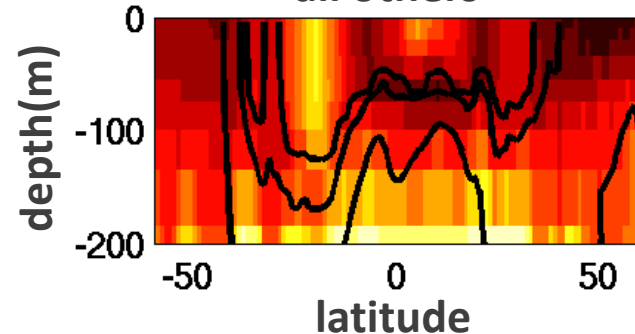
Prochlorococcus-analog



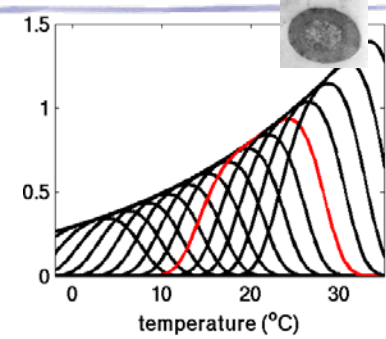
all others



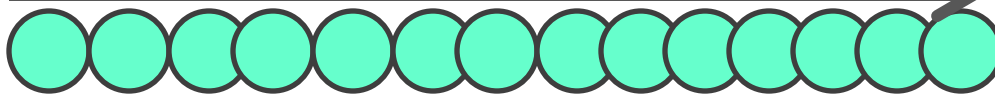
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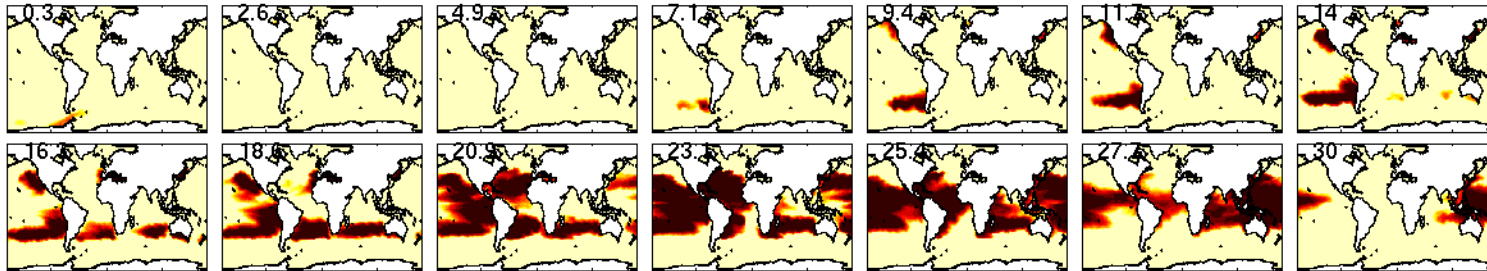
HOW DOES **TEMPERATURE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



Increasing temperature optimum →



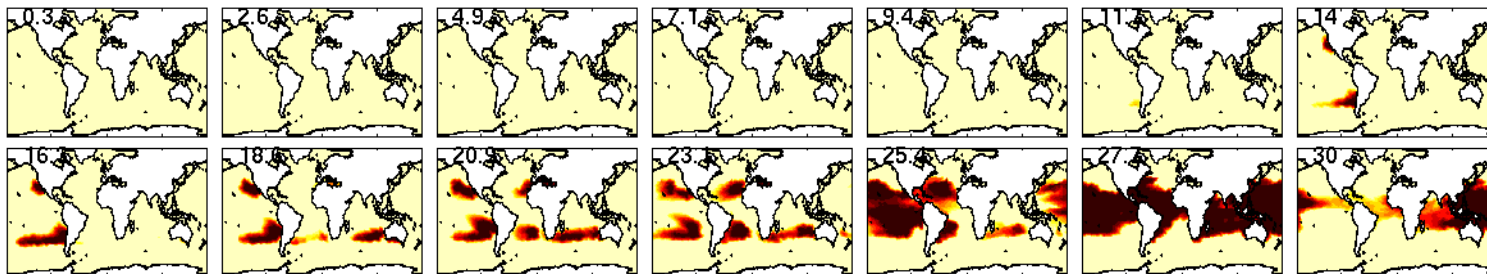
Low Light Pro



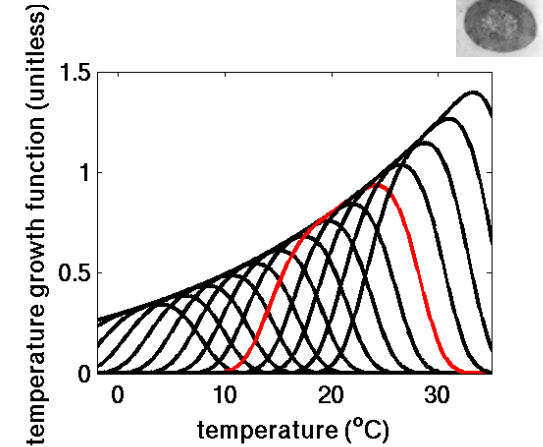
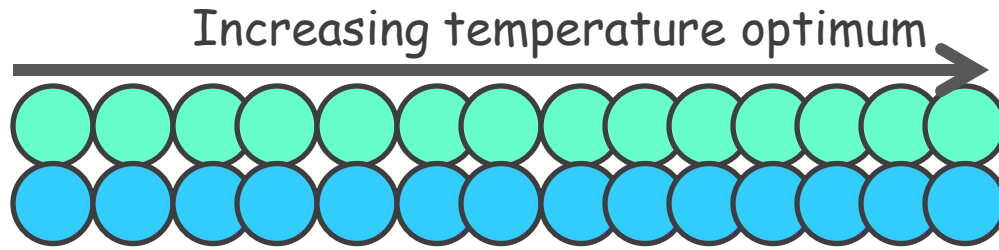
Increasing temperature optimum →



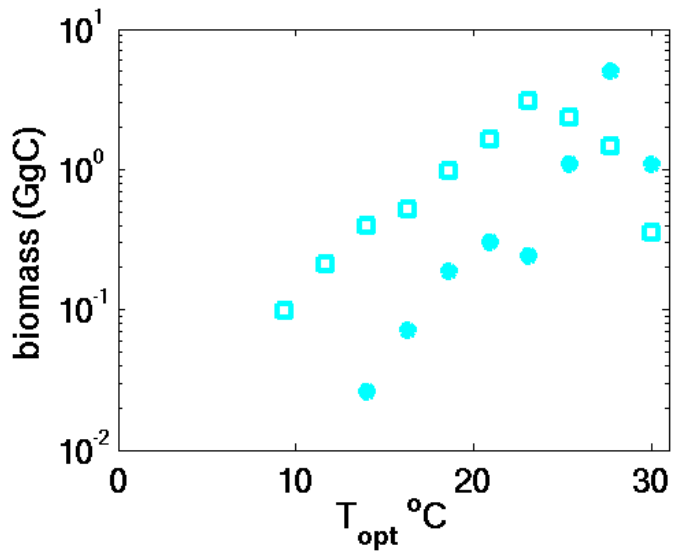
High Light Pro



HOW DOES **TEMPERATURE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



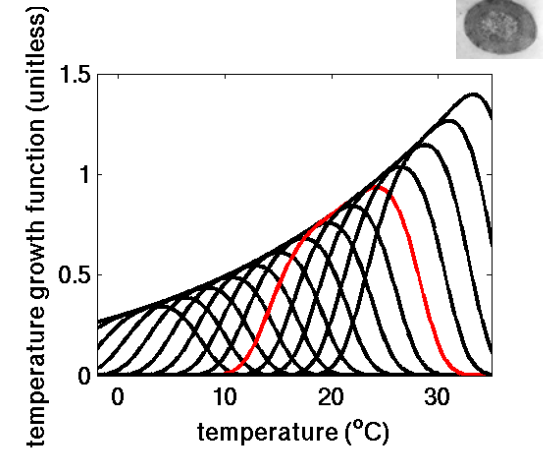
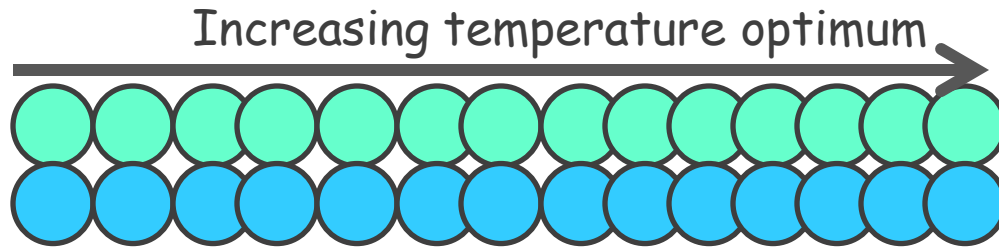
GLOBAL BIOMASS



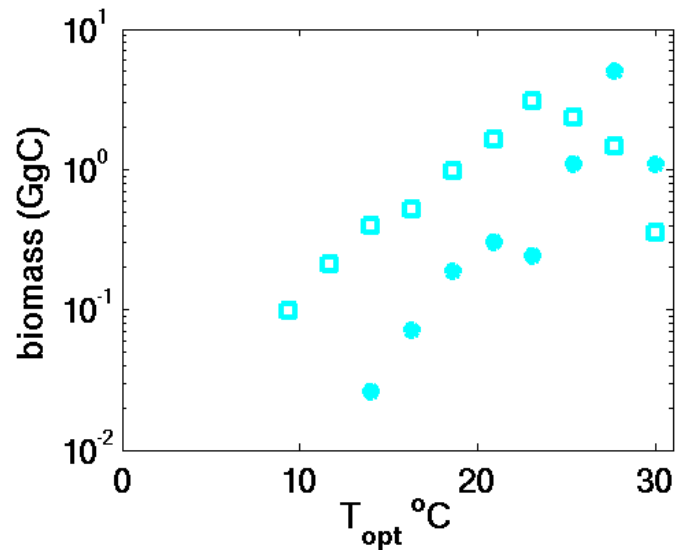
HL Pro *

LL Pro □

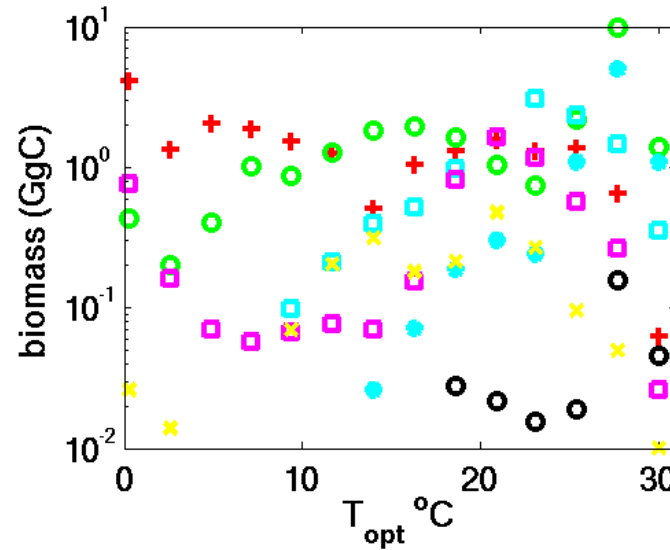
HOW DOES **TEMPERATURE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



GLOBAL BIOMASS

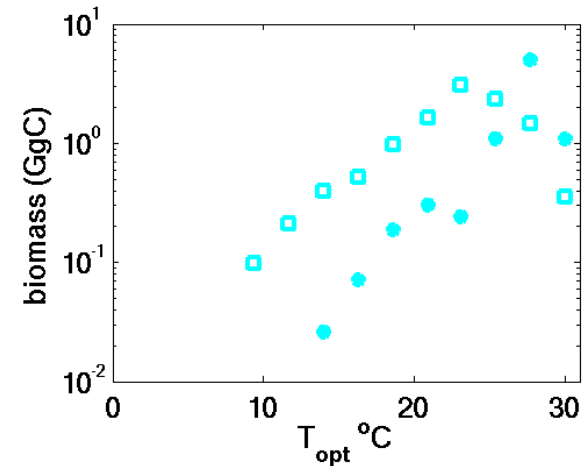
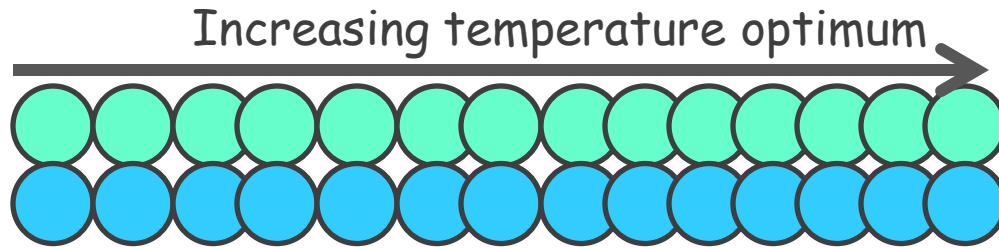


All phytoplankton



HL Pro *
 LL Pro □
 Syn
 Pico Euk
 Coccolith
 Diatom
 Diaz

HOW DOES **TEMPERATURE** IMPACT *PROCHLOROCOCCUS* BIOGEOGRAPHY?



Only warm water adapted clades survive
since no stable, low nutrient, cold regions.

(see e.g. Follows et al, Science, 2010)

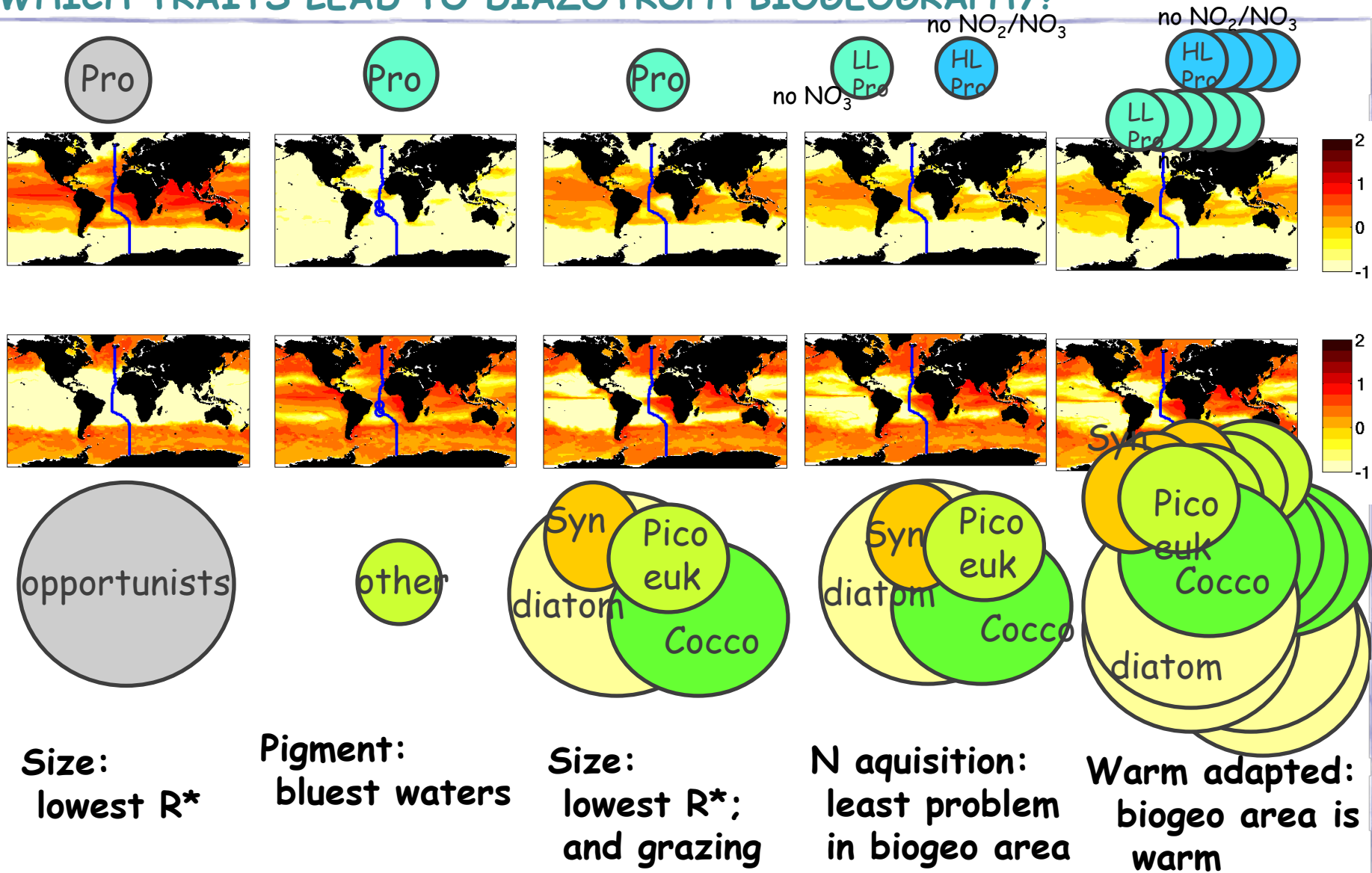
Modeling phytoplankton traits, trade-offs and biogeography

Biogeography: Where do *Prochlorococcus* live?

Why do they live there?

What traits are important for setting the biogeography?
(are all traits created equal?)

WHICH TRAITS LEAD TO DIAZOTROPH BIOGEOGRAPHY?



"First Order" trait:

Size - best competitor for resources in stable environment

How to reduce size?

Loss of genes for least needed "traits"

- additional pigment
- NO₃ assimilation

WHICH TRAITS IMPORANT?

How many traits are needed to explain biogeography?

Which/How many are "first order" traits?

- different for different functional groups?
(e.g. diazotrophs: Dutkiewicz et al 2012)

Are some traits consequence of optimizing another trait?

Though "important", which traits just follow from first order?

- care need when correlating "traits"

Modeling phytoplankton traits, trade-offs and biogeography

Other "traits and trade-offs" being explored in this model framework:

- Other pigments combinations

(see e.g. Hickman et al, MEPS 2010; Hickman poster)

- N_2 fixation (see e.g. Dutkiewicz et al, GBC, 2012; Ward et al., L+O in press)

- Size and grazing pressure

(see e.g. Ward et al, L+O 2012; Ward et al, JP, in revision)

- Trade off for calcification (Fanny Monteiro)

- Zooplankton traits (Fi Prowe)