

INTERPLAY BETWEEN ECOSYSTEM STRUCTURE AND IRON AVAILABILITY IN A GLOBAL MARINE ECOSYSTEM MODEL

Stephanie Dutkiewicz

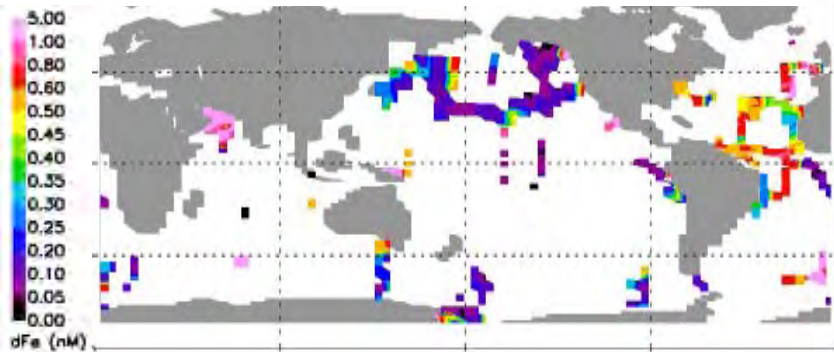
Fanny Monteiro, Mick Follows,
Jason Bragg

Massachusetts Institute of Technology
Program in Atmospheres, Oceans and Climate

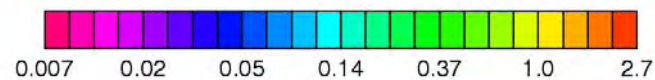
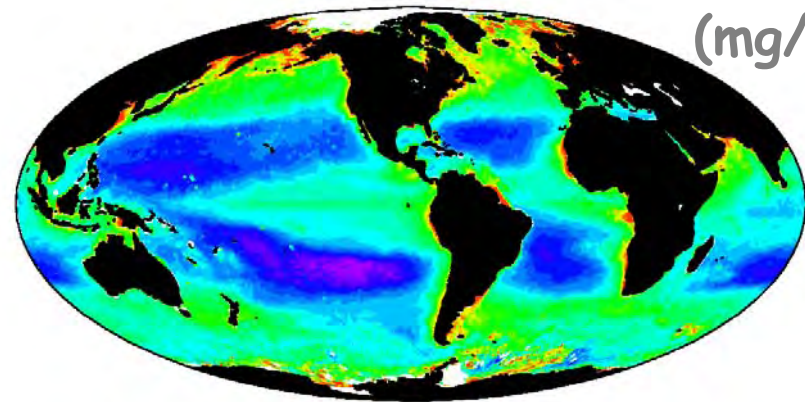


MOTIVATION

Observations of Iron (nM) (from Moore+Braucher, BG, 2008)



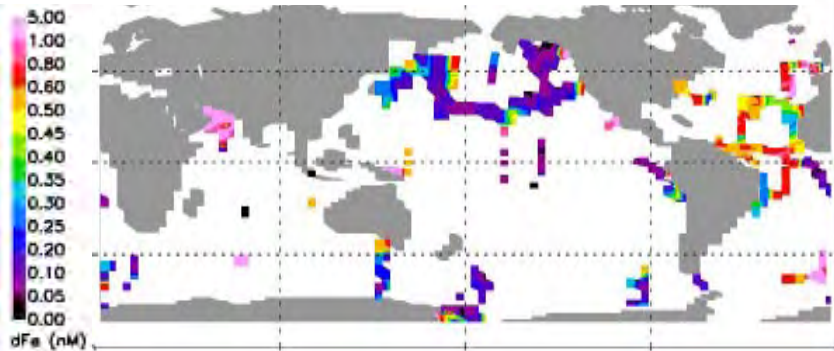
how does iron sets ecosystem structure and biomass?



MOTIVATION: interplay between iron and ecosystem

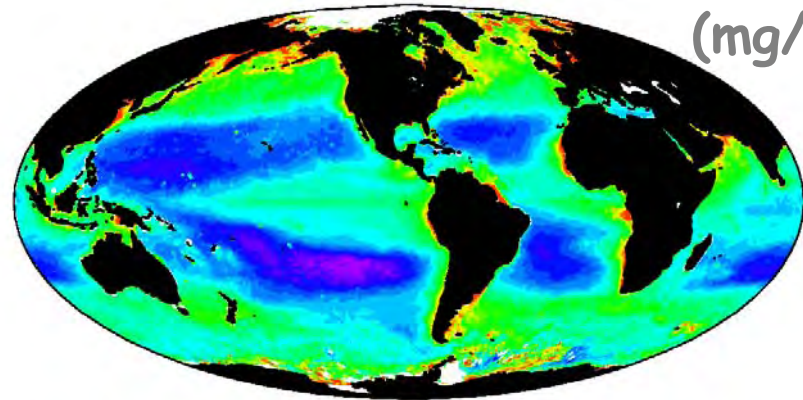
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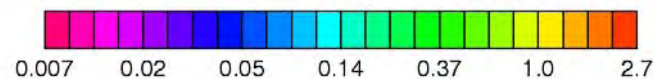


how does iron sets ecosystem structure and biomass?

SeaWiFS Chl a
(mg/m³)



how does community affect iron concentrations ?

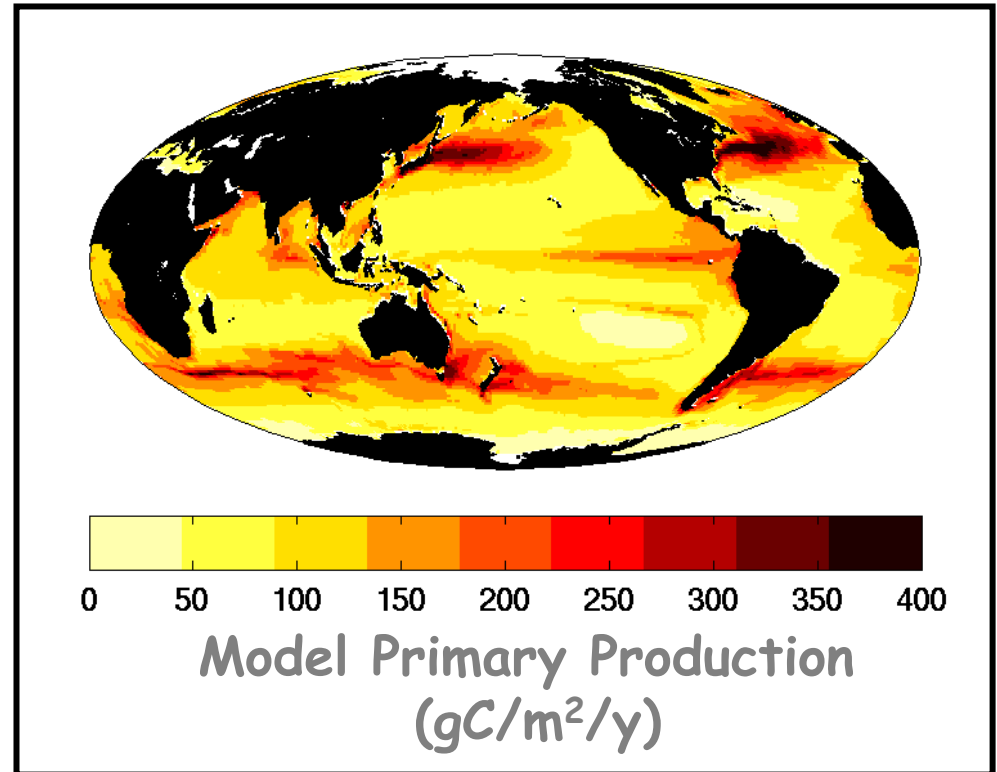


OUTLINE OF TALK

- model description: physical/biogeochemistry/ecosystem
- control experiment results
- theory: resource competition
- use theory to understand sensitivity experiments
 - changing iron availability (solubility)
 - phytoplankton physiology parameters
- summary

MODEL DESCRIPTION

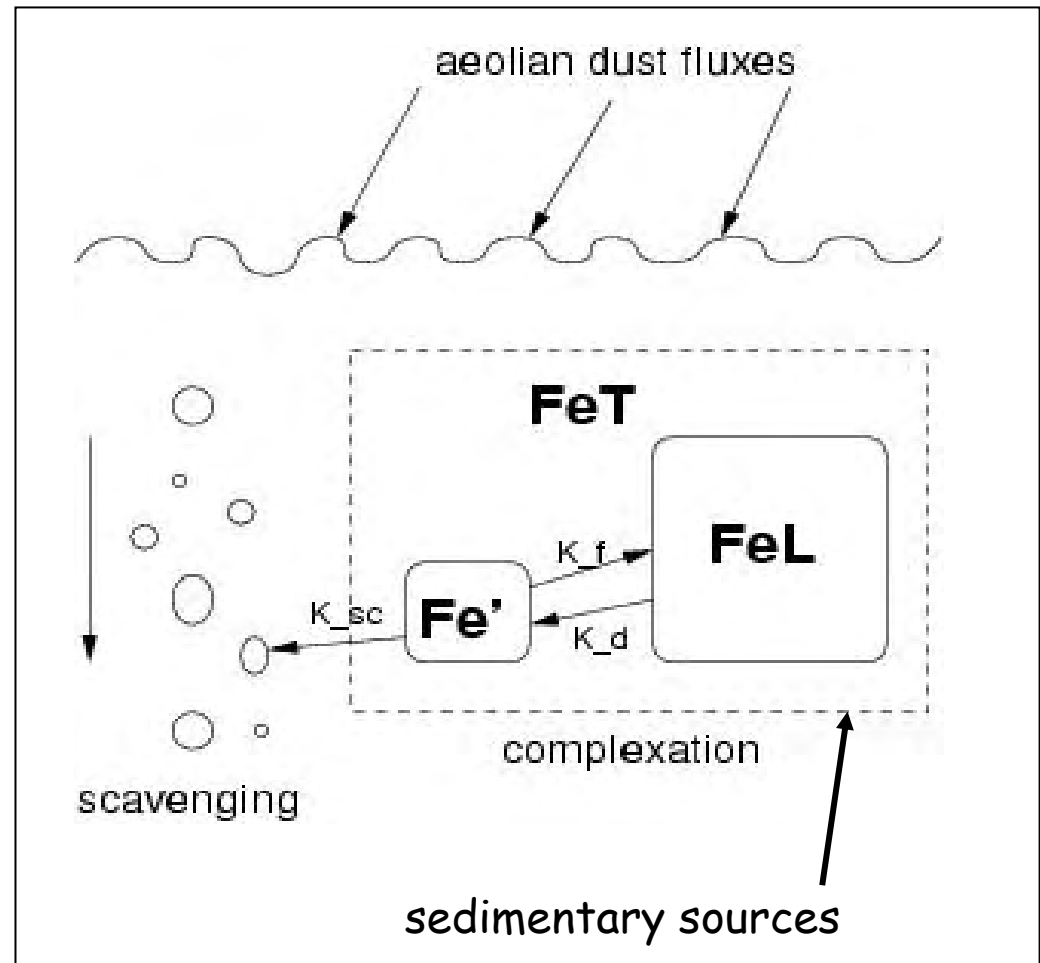
- 3-D MIT ocean general circulation model (Marshall et al, JGR 1997)
- global $1^\circ \times 1^\circ$ horizontal, 22 levels in vertical (10m-500m)
- physics: ECCO state estimates (Wunsch+Heimbach, Physica D 2007)
- biogeochemistry: N,P,Si,Fe
- ecosystem: phytoplankton
zooplankton
(Follows et al, Science, 2007;
Dutkiewicz et al, GBC, 2009)
- Results:
tenth year annual mean



MODEL DESCRIPTION

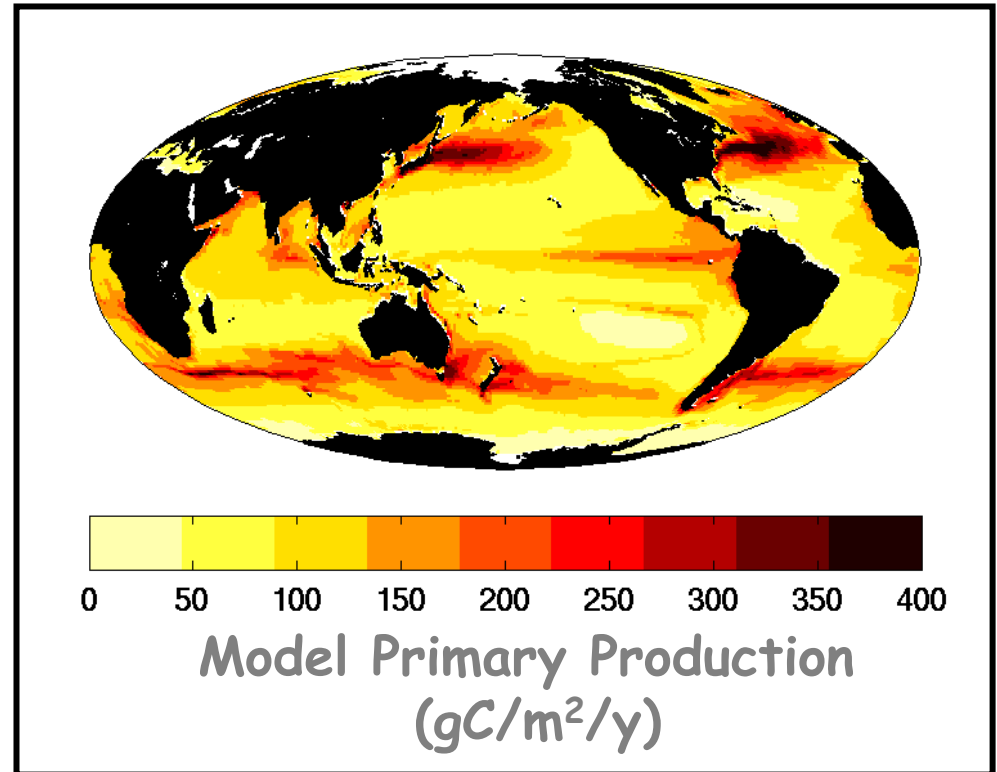
IRON PARAMETERIZATION:

- based on Parekh et al 2004/2005 (GBC)
- uniform ligand
- only free iron scavenged
- iron scavenging proportional sinking particulate matter
- sedimentary source proportional to sinking matter (Elrod et al, GRL 2004)
- variable solubility of aeolian dust (Luo et al, GBC 2008)



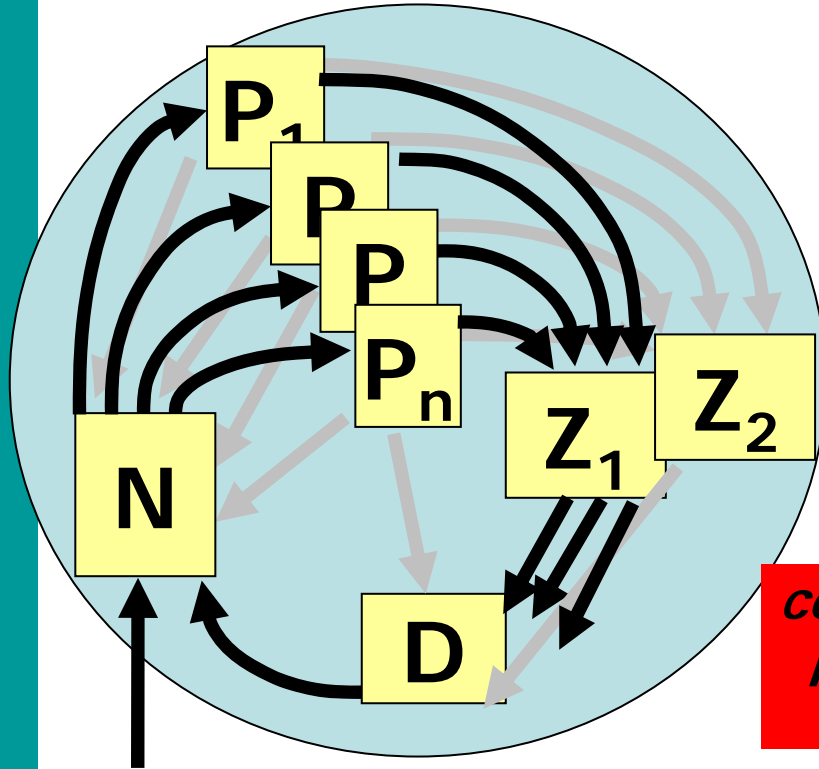
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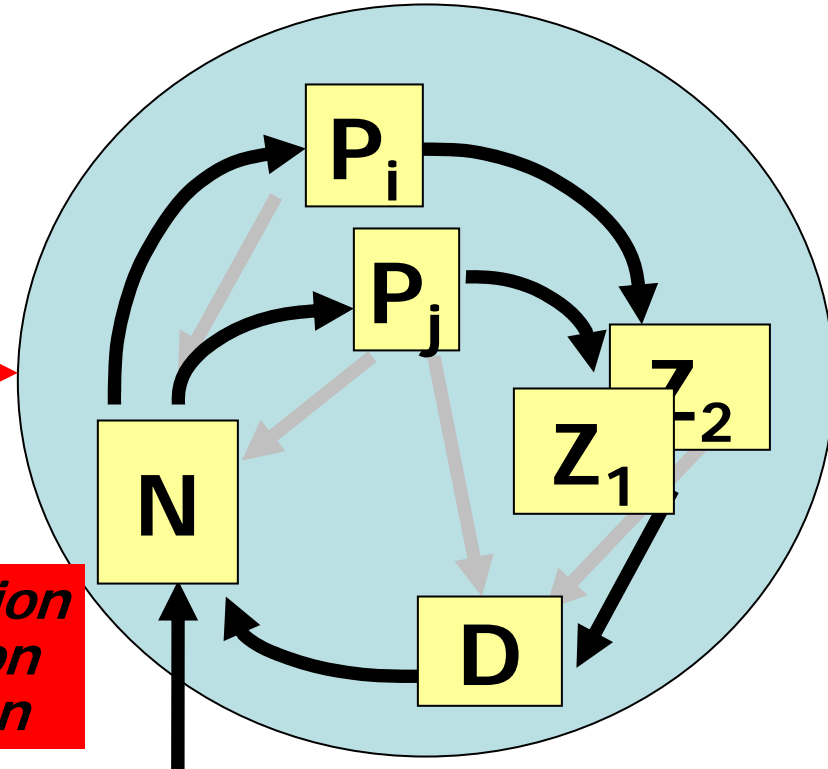
*genetics and
physiology*



*physical and
chemical
environment*

ECOSYSTEM MODEL:

Follows et al, Science, 2007;
Dutkiewicz et al, GBC, 2009



**competition
predation
selection**

- n could be 100's
- here reduced to 9 representative for computational reasons

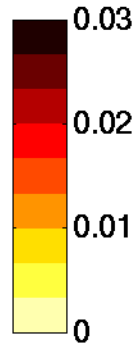
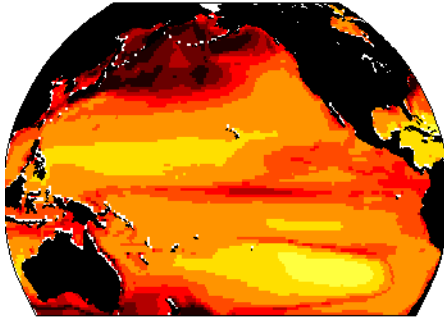
MODEL RESULTS: CONTROL EXPERIMENT

Iron solubility: variable, following Luo et al, GBC 2008

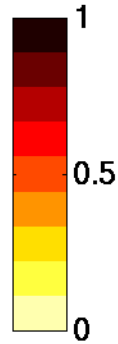
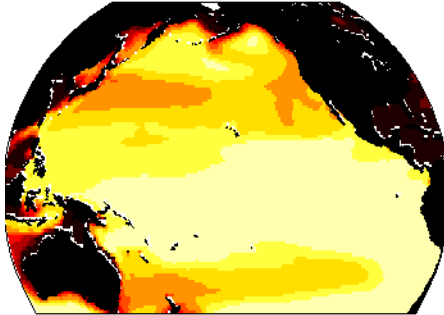
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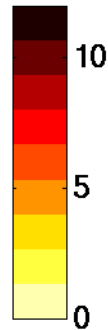
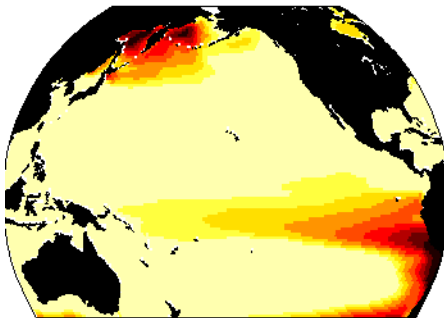
biomass
($\mu\text{M P}$)



dFe
(nM Fe)

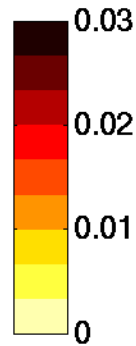
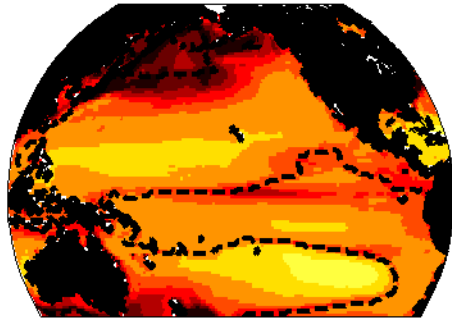


NO3
($\mu\text{M N}$)



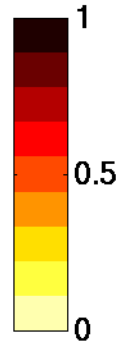
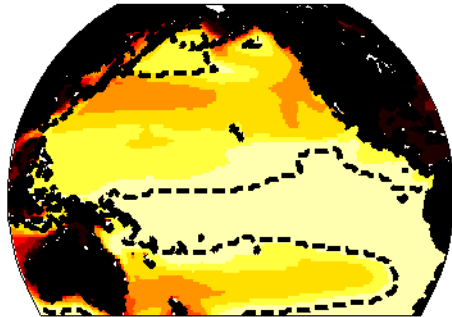
MODEL RESULTS: CONTROL EXPERIMENT

biomass
($\mu\text{M P}$)



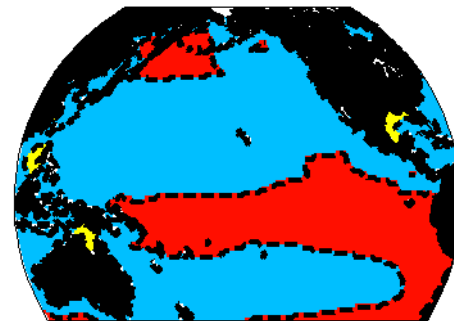
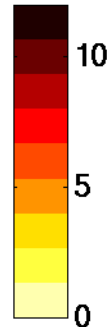
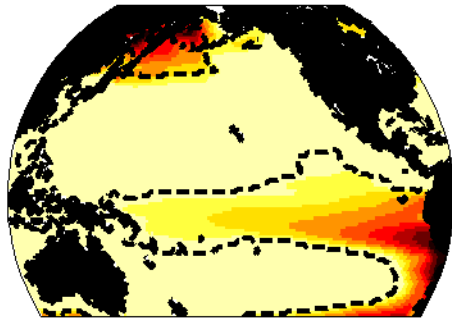
Iron solubility: variable, following Luo et al, GBC 2008

dFe
(nM Fe)



biomass is limited by different nutrients in different regions

NO₃
($\mu\text{M N}$)

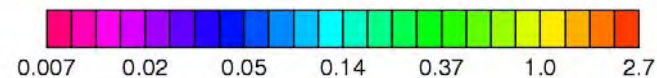
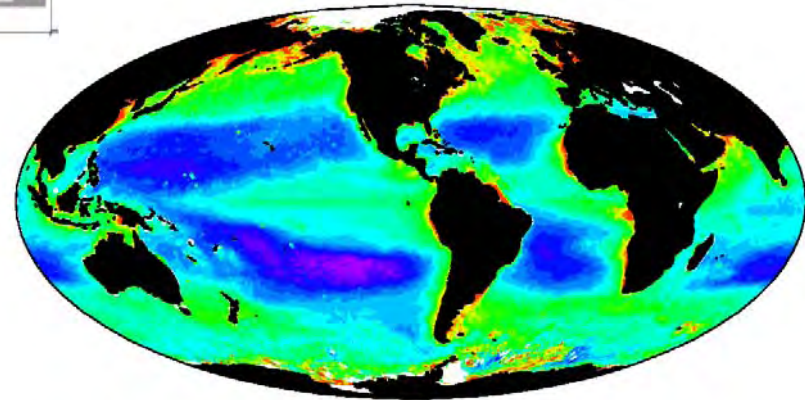
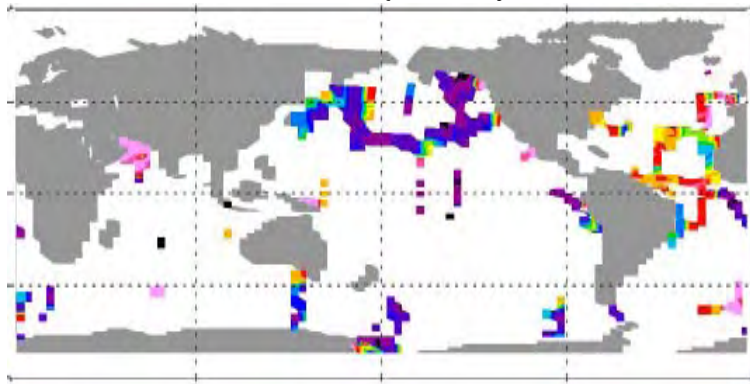


limiting nutrient

dashed line is boundary between nitrogen and iron limited regions

MOTIVATION: interplay between iron and ecosystem

Use this model as a **"laboratory"** to explore the interplay between the ecosystem and iron: sensitivity experiments



but first look at a theory that can help us understand the system better

RESOURCE COMPETITION THEORY

Tilman 1977, 1982

RESOURCE COMPETITION THEORY

Tilman 1977, 1982

$$\frac{\partial P}{\partial t} = \mu \frac{N}{N + \kappa_N} P - mP$$
$$\frac{\partial N}{\partial t} = -\mu \frac{N}{N + \kappa_N} P + S$$

N -> nutrient

P -> phytoplankton

$\mu(T, I)$ -> growth

$m(Z, w)$ -> loss

S -> nutrient source

κ_N -> nutrient half saturation

$$0 = \frac{\partial P}{\partial t} = \mu \frac{N}{N + \kappa_N} P - mP$$

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STEADY STATE:

$$\bar{P} = \frac{S}{m}$$

$$\bar{N} = \frac{\kappa_N m}{\mu - m} = R^*$$

$$0 = \frac{\partial P}{\partial t} = \mu \frac{N}{N + \kappa_N} P - mP$$

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STEADY STATE:

$$\bar{P} = \frac{S}{m}$$

$$\bar{N} = \frac{\kappa_N m}{\mu - m} = R^*$$

- Phytoplankton biomass not set by physiology
- Concentration of limiting nutrient set by physiology and loss terms
- Function of top down and bottom up controls
- Organisms with lowest R^* excludes others

RESOURCE COMPETITION THEORY

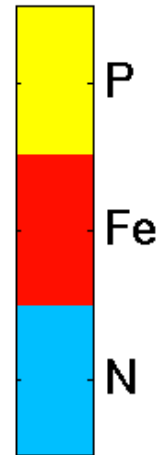
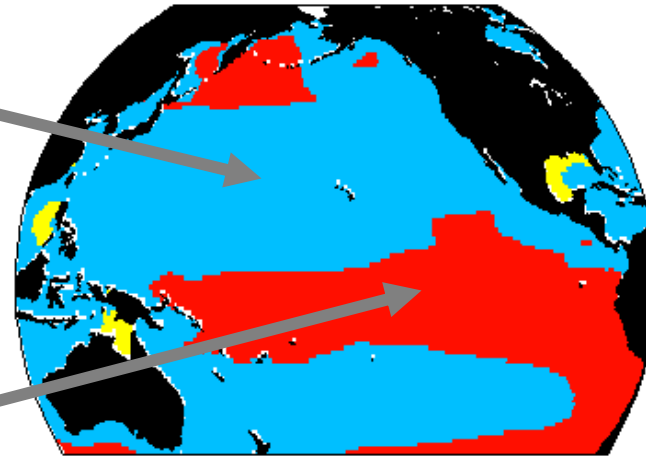
Tilman 1977, 1982

$$\bar{P} = \frac{S_N}{m}$$

$$\bar{N} = \frac{\kappa_N m}{\mu - m} = R_N^*$$

N=nitrogen

limiting nutrient



$$\bar{P} = \frac{S_{Fe}}{m}$$

$$\bar{Fe} = \frac{\kappa_{Fe} m}{\mu - m} = R_{Fe}^*$$

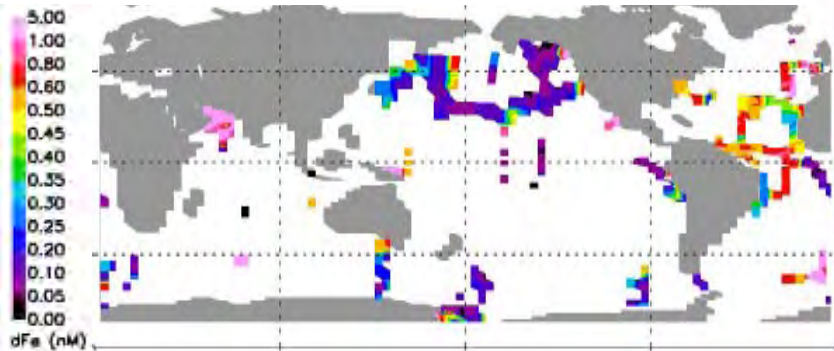
In our model:

theory works for most limiting nutrient,
works best in relatively stable regions
(Dutkiewicz et al, GBC, 2009)

MOTIVATION: interplay between iron and ecosystem

Observations of Iron (nM)

(from Moore+Braucher, BG, 2008)



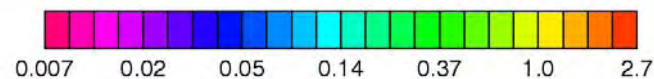
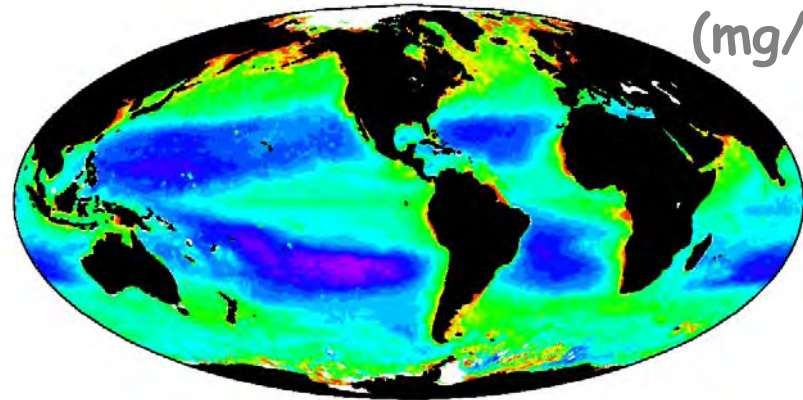
how does iron sets ecosystem structure and biomass?

$$\bar{P} = \frac{S_{Fe}}{m}$$

$$\bar{Fe} = \frac{\kappa_{Fe} m}{\mu - m}$$

how does community affect iron concentrations ?

SeaWiFS Chl a
(mg/m³)



MODEL RESULTS: SENSITIVITY EXPERIMENTS

Look at differences between simulations:

- 1) 1% and 4% iron solubility: no diazotrophs
- 2) 1% and 4% iron solubility: include diazotrophs
- 3) control and experiment where K_{fe} non-diazotrophs halved
- 4) control and experiment where K_{fe} diazotrophs halved

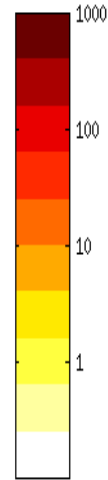
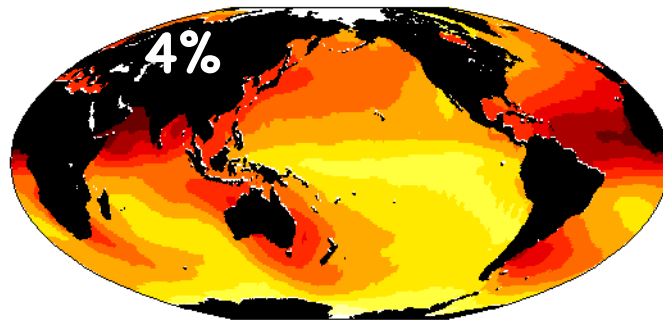
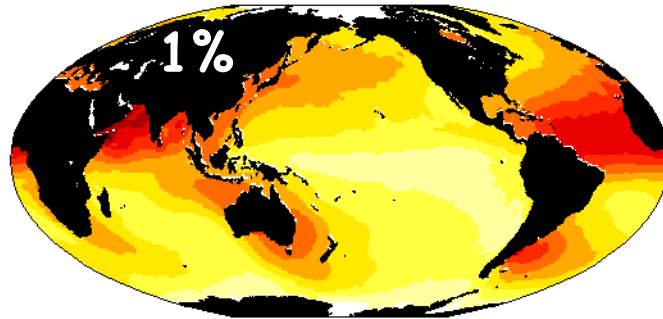
$$\bar{P} = \frac{S_{Fe}}{m}$$

$$\bar{Fe} = \frac{K_{Fe}m}{\mu - m}$$

MOTIVATION

Assumption about solubility of Aeolian iron dust

Soluble Aeolian Iron Dust Flux ($\mu\text{mol Fe}/\text{m}^2/\text{y}$)



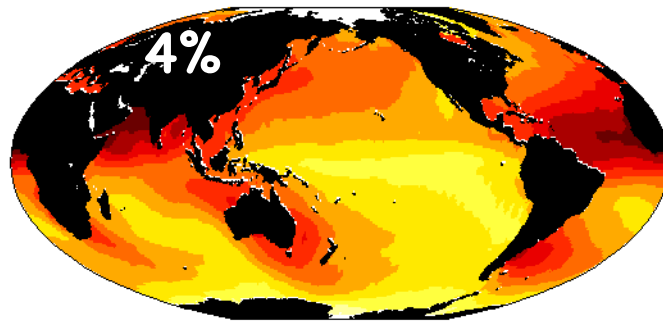
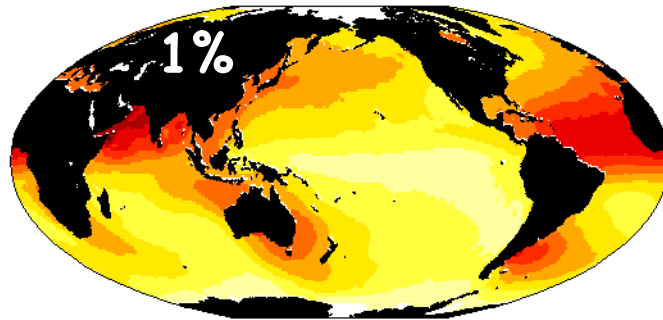
iron solubility measured
to range from <1% to 80%

Uniform solubility
(using dust estimates of
Luo et al., JGR 2003)

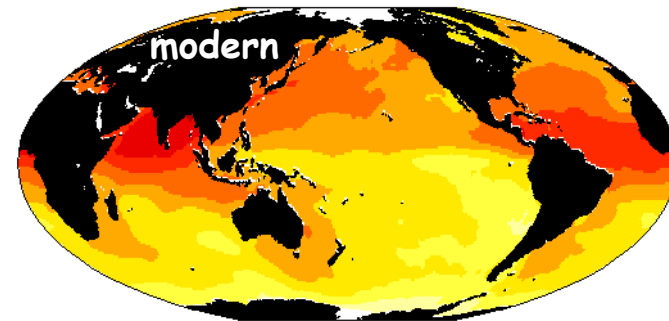
MOTIVATION: AN ASIDE...

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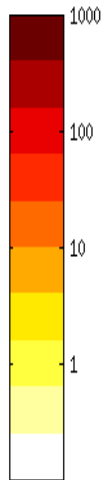
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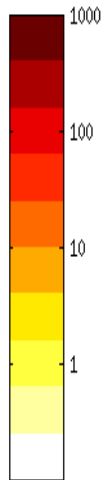
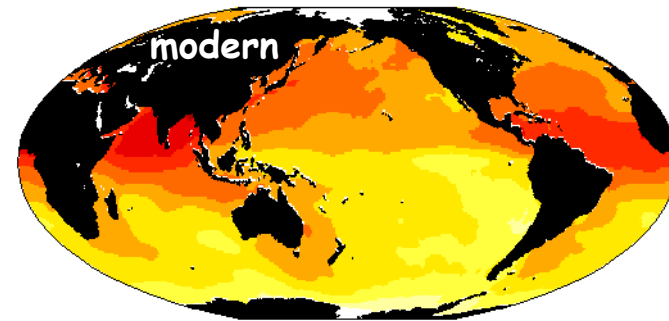
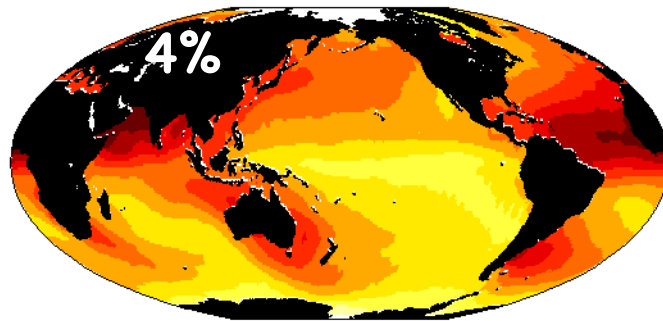
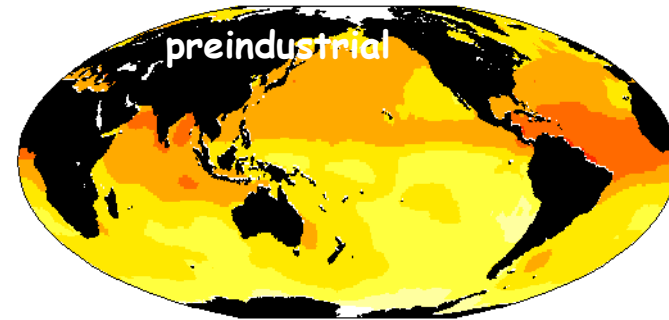
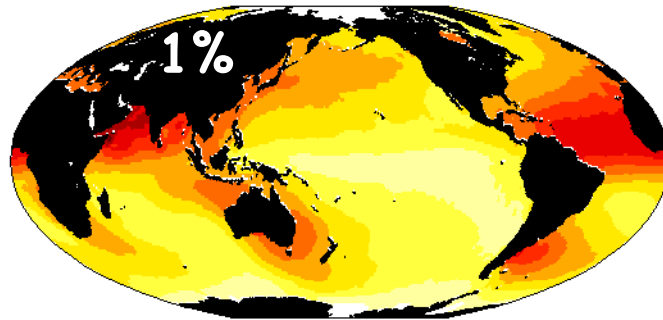
Variable solubility
(Luo et al., GBC 2008)



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Uniform solubility
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Variable solubility
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MODEL RESULTS: SENSITIVITY EXPERIMENTS (1)

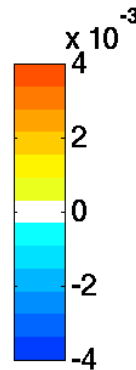
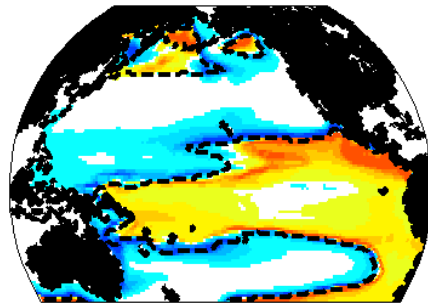
Difference between simulations (4%-1%): no diazotrophs

2.5% increase in primary production

(comparable to 3.5% with 10 times iron, Moore et al, GBC 2004

2% preindustrial to modern, Krishnamurthy et al, GBC 2009)

diff in biomass
($\mu\text{M P}$)



positive=increase
with increased
iron solubility

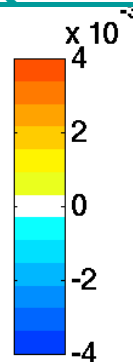
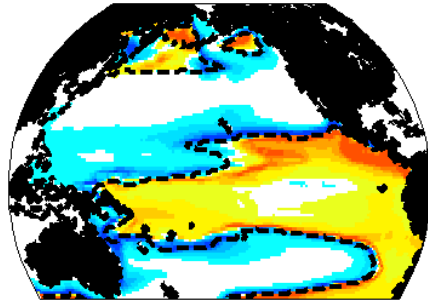
dashed line is boundary between nitrogen and iron limited regions

**Can we understand the spatial pattern
from resource competition theory?**

MODEL RESULTS: SENSITIVITY EXPERIMENTS (1)

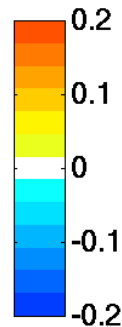
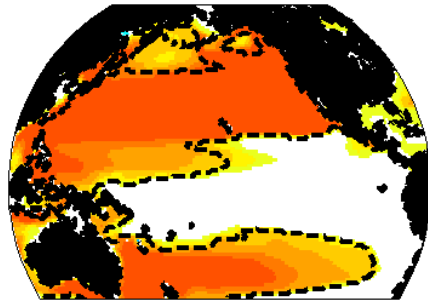
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diff in biomass
($\mu\text{M P}$)

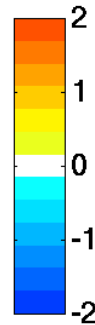
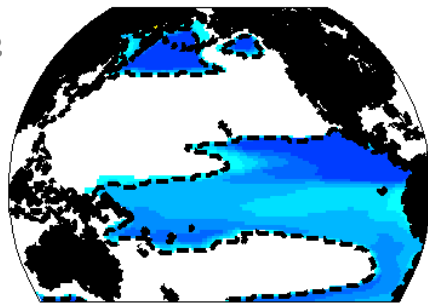


positive=increase
with increased
iron solubility

diff in iron
(nM P)



diff in nitrate
($\mu\text{M P}$)

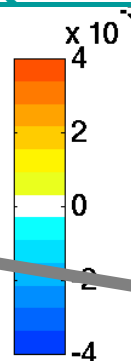
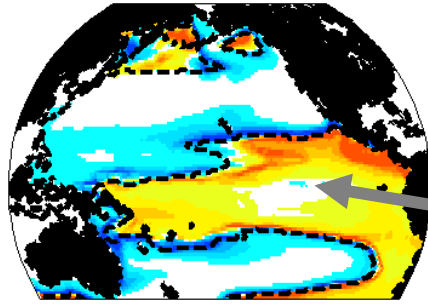


dashed line is boundary between nitrogen and iron limited regions

MODEL RESULTS: SENSITIVITY EXPERIMENTS (1)

Difference between simulations (4%-1%): no diazotrophs

diff in biomass
($\mu\text{M P}$)

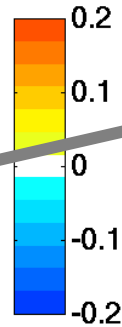
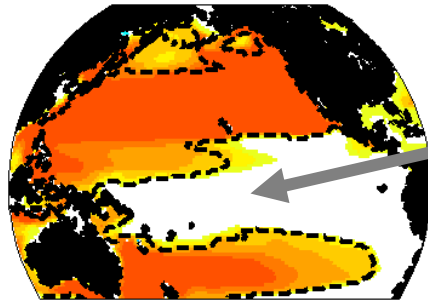


- increase in iron availability leads to increase biomass in iron limited regions

$$\bar{P} = \frac{S_{Fe}}{m}$$

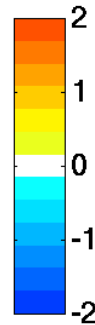
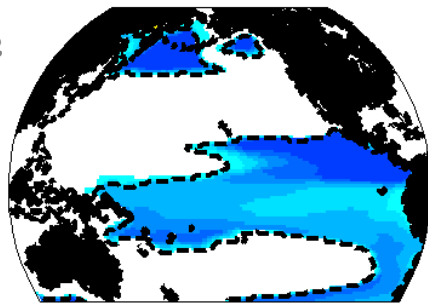
$$\bar{Fe} = \frac{\kappa_{Fe} m}{\mu - m} = R_{Fe}^*$$

diff in iron
(nM Fe)



- no change to phytoplankton physiology, so no change to iron concentration

diff in nitrate
($\mu\text{M N}$)



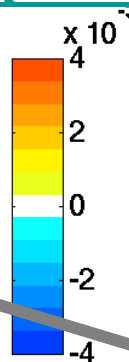
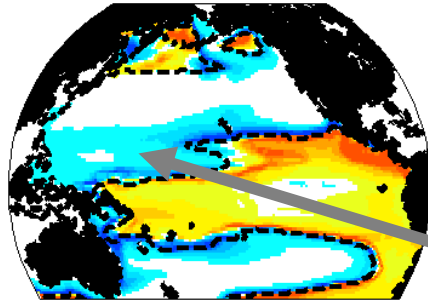
- additional nitrate consumed by increased biomass

dashed line is boundary between nitrogen and iron limited regions

MODEL RESULTS: SENSITIVITY EXPERIMENTS (1)

Difference between simulations (4%-1%): no diazotrophs

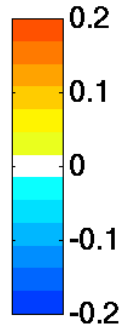
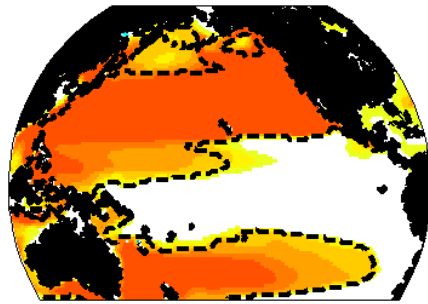
diff in biomass
($\mu\text{M P}$)



• decreased supply of nitrogen leads to decreased biomass in nitrogen limited regions

(Dutkiewicz et al, GBC, 2005, Williams+Follows, DSR, 1998)

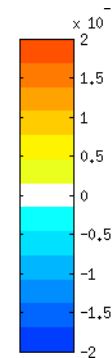
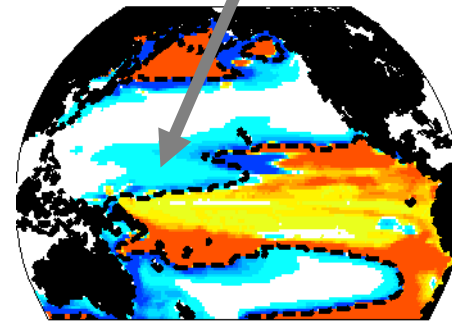
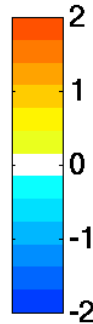
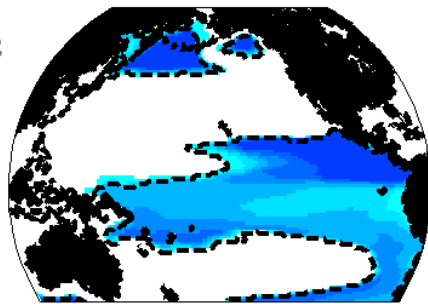
diff in iron
(nM Fe)



$$\bar{P} = \frac{S_N}{m}$$

$$\bar{N} = \frac{\kappa_N m}{\mu - m} = R_N^*$$

diff in nitrate
($\mu\text{M N}$)



diff in source of nitrate
($\mu\text{M N/s}$)

dashed line is boundary between nitrogen and iron limited regions

MODEL RESULTS: SENSITIVITY EXPERIMENTS

Look at differences between simulations:

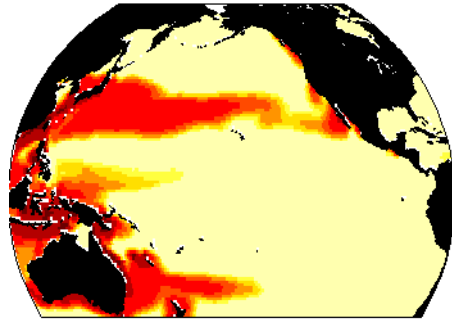
- 1) 1% and 4% iron solubility: no diazotrophs
- 2) 1% and 4% iron solubility: include diazotrophs
- 3) control and experiment where K_{fe} non-diazotrophs halved
- 4) control and experiment where K_{fe} diazotrophs halved

$$\bar{P} = \frac{S_{Fe}}{m}$$

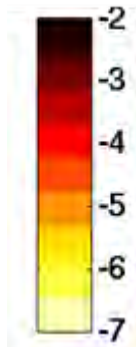
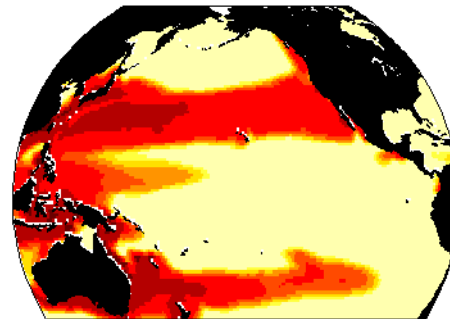
MODEL RESULTS: SENSITIVITY EXPERIMENTS (2)

Difference between simulations (4%-1%): **with** diazotrophs

diazotrophs 1%
log ($\mu\text{M P}$)



diazotrophs 4%
log ($\mu\text{M P}$)



with increased iron availability, increased region where diazotrophs can exist, total nitrogen fixation increases 15%

diazotrophs exist where:

- 1) Non-diazotrophs are nitrogen limited
- 2) AND iron is sufficient

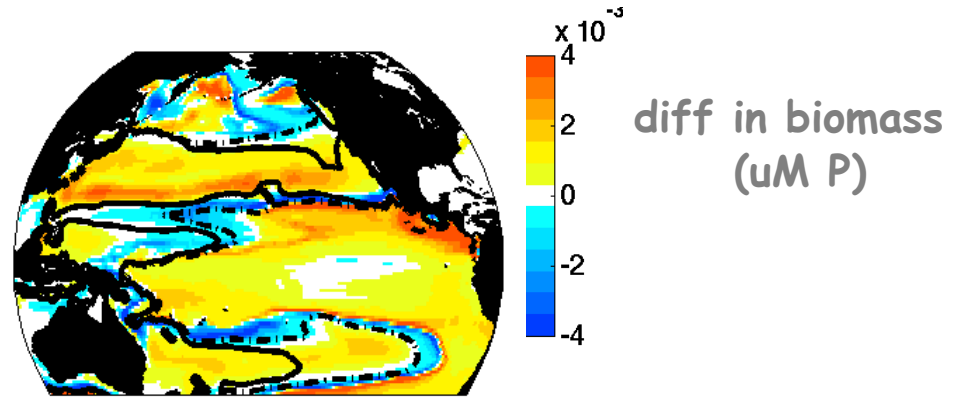
(Monteiro et al, in prep, 2009)

50% increase with 10 times iron flux
(Moore et al, GBC 2004)

35% increase with LGM over modern dust
(Moore and Doney, 2007)

MODEL RESULTS: SENSITIVITY EXPERIMENTS (2)

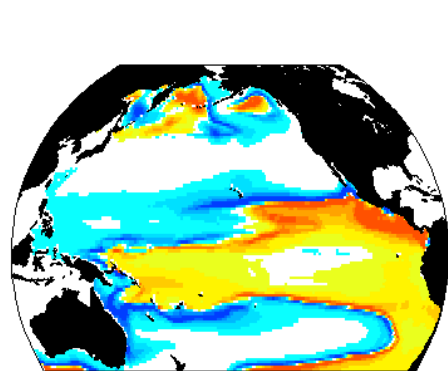
Difference between simulations (4%-1%): **with** diazotrophs



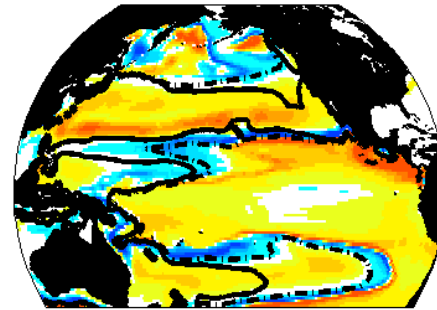
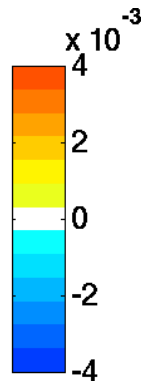
solid line: region of diazotrophs 1%
dashed line: region of diazotrophs 4%

MODEL RESULTS: SENSITIVITY EXPERIMENTS (2)

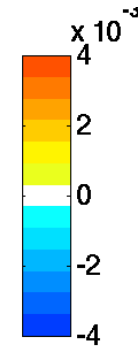
Difference between simulations (4%-1%): **with** diazotrophs



diff in biomass
WITHOUT diazotrophs
($\mu\text{M P}$)



solid line: region of diazotrophs 1%
dashed line: region of diazotrophs 4%



diff in biomass
($\mu\text{M P}$)

- region where diazotrophs and non-diazotrophs co-exist
- non-diazotrophs are nitrogen limited
- diazotrophs are iron limited
- need more complex theory here

RESOURCE COMPETITION THEORY

including 2 phytoplankton types and 2 nutrients

This is set of equations for region where diazotrophs and other phytoplankton co-exist

$$\frac{\partial P_1}{dt} = \mu_1 \frac{N}{N + \kappa_{N1}} P_1 - m_1 P_1$$

$$\frac{\partial P_2}{dt} = \mu_2 \frac{Fe}{Fe + \kappa_{Fe2}} P_2 - m_2 P_2$$

$$\frac{\partial N}{\partial t} = -\mu_1 \frac{N}{N + \kappa_{N1}} P_1 + S_N$$

$$\frac{\partial Fe}{\partial t} = -\mu_1 \frac{N}{N + \kappa_{N1}} R_1 P_1 - \mu_2 \frac{Fe}{Fe + \kappa_{Fe2}} R_2 P_2 + S_{Fe}$$

N → nitrogen

Fe → iron

P_1 → non-diazotroph

P_2 → diazotroph

$\mu_{1/2}(T, I)$ → growth

$m_{1/2}(Z, w)$ → loss

$S_{N/Fe}$ → nitrogen or iron source

$\kappa_{N/Fe}$ → N or Fe half saturation

$R_{1/2}$ → Fe:P ratio

Assume diazotrophs grow slower, lower K and higher Fe:P

RESOURCE COMPETITION THEORY

including 2 phytoplankton types and 2 nutrients

Steady state solution for region where diazotrophs and other phytoplankton co-exist

$$\begin{aligned} \bar{P}_1 &= \frac{S_N}{m_1} \\ \bar{P}_2 &= \frac{S_{Fe}}{R_2 m_2} - \frac{m_1}{m_2} \frac{R_1}{R_2} \bar{P}_1 = \frac{1}{R_2 m_2} (S_{Fe} - R_1 S_N) \\ \bar{P}_1 + \bar{P}_2 &= \frac{S_N}{m_1} \left(1 - \frac{m_1}{m_2} \frac{R_1}{R_2}\right) + \frac{S_{Fe}}{R_2 m_2} \\ \bar{N} &= \frac{\kappa_{N1} m_1}{\mu_1 - m_1} = R_N^* \\ \bar{Fe} &= \frac{\kappa_{Fe2} m_2}{\mu_2 - m_2} = R_{Fe}^* \end{aligned}$$

N → nitrogen

Fe → iron

P_1 → non-diazotroph

P_2 → diazotroph

$\mu_{1/2}(T, I)$ → growth

$m_{1/2}(Z, w)$ → loss

$S_{N/Fe}$ → nitrogen or iron source

$\kappa_{N/Fe}$ → N or Fe half saturation

$R_{1/2}$ → N:P ratio

MODEL RESULTS: SENSITIVITY EXPERIMENTS (2)

Difference between simulations (4%-1%): **with** diazotrophs

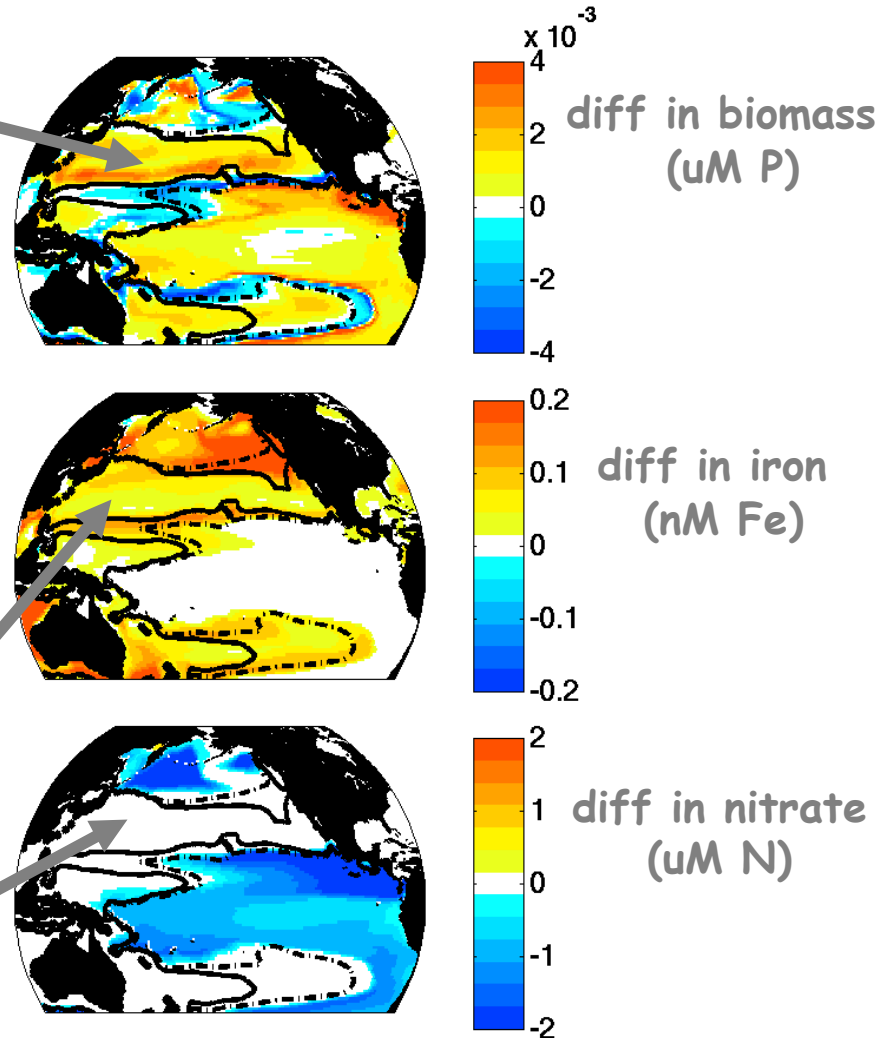
- biomass increases with increasing availability of iron, AND
- source of nitrogen increases with increased diazotrophs

$$\bar{P}_1 + \bar{P}_2 = \frac{S_N}{m_1} \left(1 - \frac{m_1}{m_2} \frac{R_1}{R_2}\right) + \frac{S_{Fe}}{R_2 m_2}$$

$$\bar{Fe} = \frac{\kappa_{Fe2} m_2}{\mu_2 - m_2} = R_{Fe}^*$$

$$\bar{N} = \frac{\kappa_{N1} m_1}{\mu_1 - m_1} = R_N^*$$

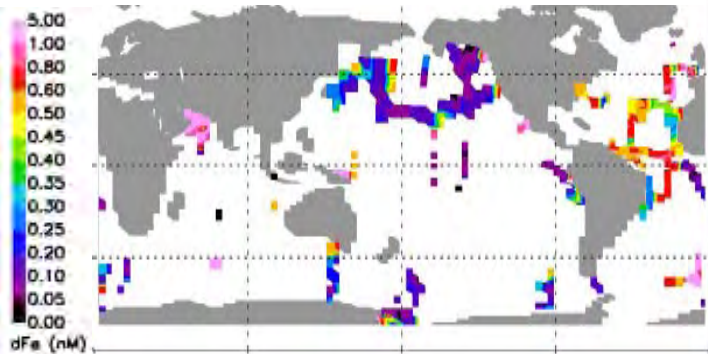
- Diazotroph (sort of) control iron
- Non-diazotrophs control nitrogen and there is no change



solid line: region of diazotrophs 1%
dashed line: region of diazotrophs 4%

MOTIVATION: interplay between iron and ecosystem

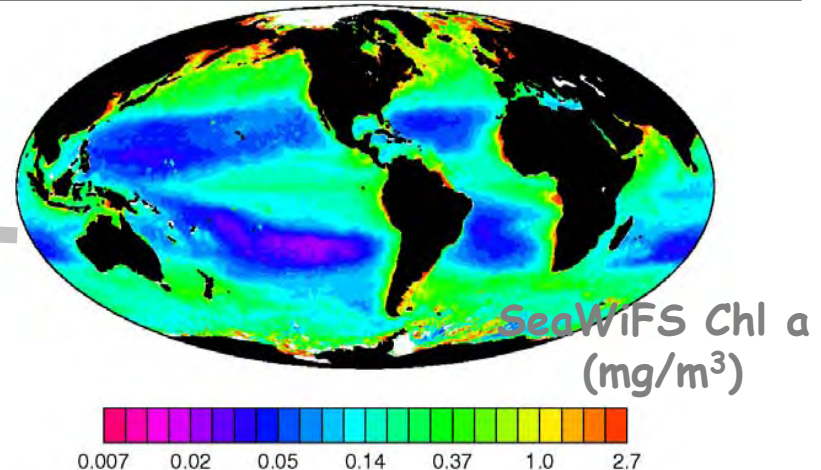
Observations of Iron (nM)
(from Moore+Braucher, BG, 2008)



iron sets ecosystem structure
and concentrations

- increased availability of iron leads to:
- increased biomass in iron limited regions
 - increased regions of nitrogen fixation and increased biomass in those regions
 - increased biomass leads to decreased lateral nitrogen supply, and reduced biomass in some regions

how does community affect iron concentrations?



MODEL RESULTS: SENSITIVITY EXPERIMENTS

Look at differences between simulations:

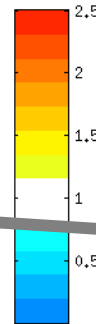
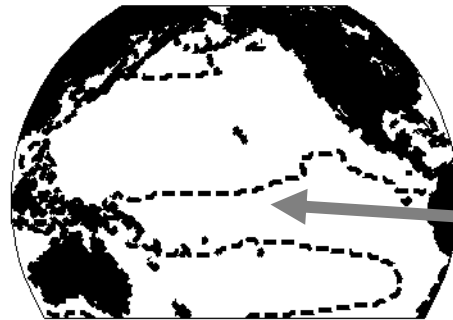
- 1) 1% and 4% iron solubility: no diazotrophs
- 2) 1% and 4% iron solubility: diazotrophs
- 3) control and experiment where K_{fe} non-diazotrophs halved
- 4) control and experiment where K_{fe} diazotrophs halved

$$\overline{Fe} = \frac{K_{Fe} m}{\mu - m}$$

MODEL RESULTS: SENSITIVITY EXPERIMENTS (3)

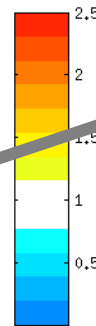
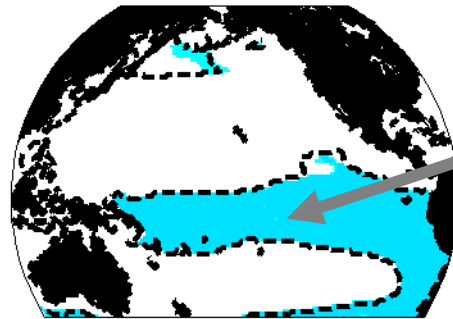
Compare with simulation where **non-diazotrophs** K_{fe} halved

$\frac{\text{Biomass}_{\text{sensitivity}}}{\text{Biomass}_{\text{control}}}$



- no change to supply, so no change in biomass

$\frac{\text{Iron}_{\text{sensitivity}}}{\text{Iron}_{\text{control}}}$



- half K_{fe} , leads to halving iron concentration

$$\bar{P}_1 = \frac{S_{Fe}}{m_1}$$
$$\bar{Fe} = \frac{\kappa_{Fe} m_1}{\mu_1 - m_1} = R_{Fe}^*$$

dashed line is boundary between nitrogen and iron limited regions

MODEL RESULTS: SENSITIVITY EXPERIMENTS

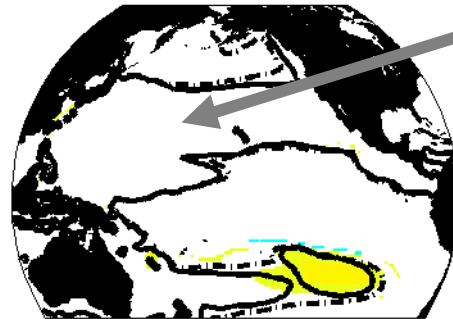
Look at differences between simulations:

- 1) 1% and 4% iron solubility: no diazotrophs
- 2) 1% and 4% iron solubility: include diazotrophs
- 3) control and experiment where K_{fe} non-diazotrophs halved
- 4) control and experiment where K_{fe} diazotrophs halved

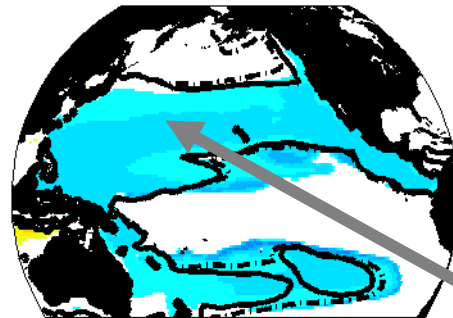
MODEL RESULTS: SENSITIVITY EXPERIMENTS (4)

Difference between simulations where **diazotrophs** K_{fe} halved

$\frac{\text{Biomass}_{\text{sensitivity}}}{\text{Biomass}_{\text{control}}}$



$\frac{\text{Iron}_{\text{sensitivity}}}{\text{Iron}_{\text{control}}}$



- no change to supply, so mostly no change in biomass

$$\bar{P}_1 + \bar{P}_2 = \frac{S_N}{m_1} \left(1 - \frac{m_1}{m_2} \frac{R_1}{R_2}\right) + \frac{S_{Fe}}{R_2 m_2}$$

$$\bar{Fe} = \frac{\kappa_{Fe2} m_2}{\mu_2 - m_2} = R_{Fe}^*$$

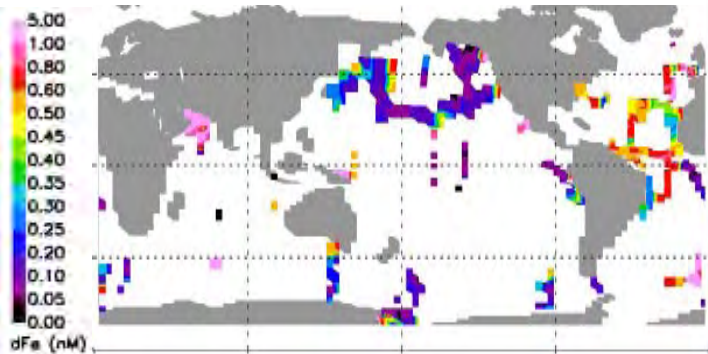
$$\bar{N} = \frac{\kappa_{N1} m_1}{\mu_1 - m_1} = R_N^*$$

solid line: region of diazotrophs control
dashed line: region of diazotrophs half K_{fe}

- half K_{fe} , leads to halving iron concentration
- region where diazotrophs exist increases, since R_{fe}^* decreases

SUMMARY: interplay between iron and ecosystem

Observations of Iron (nM)
(from Moore+Braucher, BG, 2008)



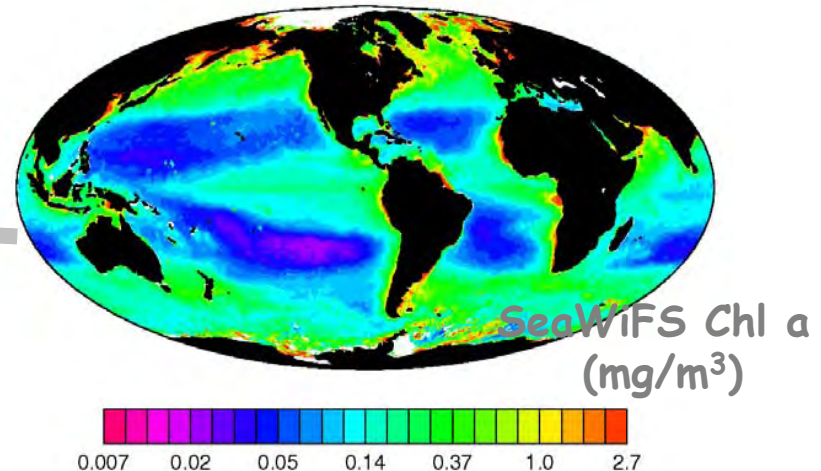
iron sets ecosystem structure
and concentrations

change in source of iron leads to:

- increased biomass in iron limited regions
- increased regions of nitrogen fixation and increased biomass in those regions
- increased biomass leads to decreased lateral nitrogen supply, and reduced biomass in some regions

community affect iron concentrations:

- change in phytoplankton physiology leads to change in iron concentration (but only where iron is limiting that phytoplankton)
- diazotroph physiology control where nitrogen fixation can occur



SUMMARY

- There is a strong link between ecosystem and iron cycling that can be understood through resource competition
- The **source of iron** is critical in determining:
 - total biomass of phytoplankton over much of the tropical Pacific
 - amount and region of nitrogen fixing in the sub-tropical Pacific
- The physiology and grazing of phytoplankton communities can largely regulate the **iron concentration** over much of the Pacific
 - non-diazotrophs where iron is main limiting nutrient
 - diazotrophs where others are nitrogen limited AND $Fe > R_{Fe}^*$
- From modelling perspective: we need to understand supply better before we can get ecosystems right, but also we need to get ecosystems right before we can get iron concentration right!

<http://darwinproject.mit.edu>

SUMMARY

- There is a strong link between ecosystem and iron cycling that can be understood through resource competition

simple 0-D theoretical system

$$\frac{\partial N}{\partial t} = -\mu \frac{N}{N + \kappa_N} P + S$$
$$\frac{\partial P}{dt} = \mu \frac{N}{N + \kappa_N} P - mP$$

includes advection
and diffusion
remineralization etc

3-D simulation equations (for i nutrients and j phytoplankton)

$$\frac{\partial N_i}{\partial t} = -\mu(T, I) \min\left(\frac{N}{N + \kappa_N}, \frac{PO_3}{PO_3 + \kappa_{PO_3}}, \frac{Fe}{Fe + \kappa_{Fe}}\right) P_j + S_{Ni}$$
$$\frac{\partial P_j}{dt} = \underbrace{\mu(T, I)}_{\text{growth function of temperature and light}} \underbrace{\min\left(\frac{N}{N + \kappa_N}, \frac{PO_3}{PO_3 + \kappa_{PO_3}}, \frac{Fe}{Fe + \kappa_{Fe}}\right)}_{\text{nutrient limitation minimum function of several nutrients}} P_j - \underbrace{mP_j - \text{sinking} - \text{grazing}}_{\text{more complex loss terms}} + S_{Pj}$$

growth function
of temperature
and light

nutrient limitation
minimum function
of several nutrients

more complex
loss terms

SUMMARY

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SUMMARY

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- The **source of iron** is critical in determining:
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 - amount and region of nitrogen fixing in the sub-tropical Pacific

$$S_{Fe} = \text{advect} + \text{diffusion} + S_{aeolian} + S_{sed} - \text{scavenging} + \text{remineralization}$$

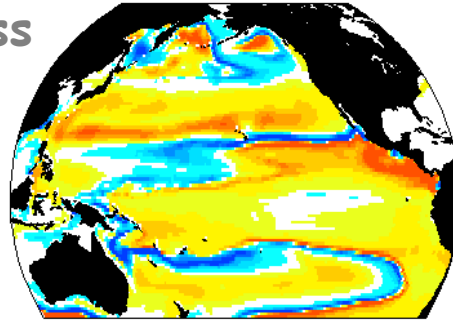
$$S_{Fe} = -\nabla \cdot (\vec{u}^* Fe) + \nabla \cdot (K \nabla Fe) + \alpha F_{aeolian} + F_{sed} - k_{scav} Fe' + r_{dofe} DOFe + r_{pofe} POfe$$

ADDITIONAL SENSITIVITY EXPERIMENTS

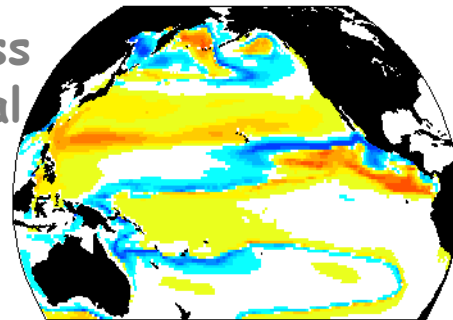
Change in assumption of iron solubility -> source of iron

positive=increase
with increased
iron source

difference in biomass
4%-1% solubility

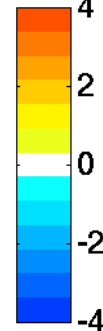


difference in biomass
modern-preindustrial

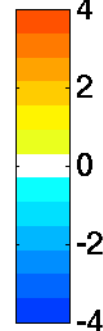


$\mu\text{M P}$

$\times 10^{-3}$

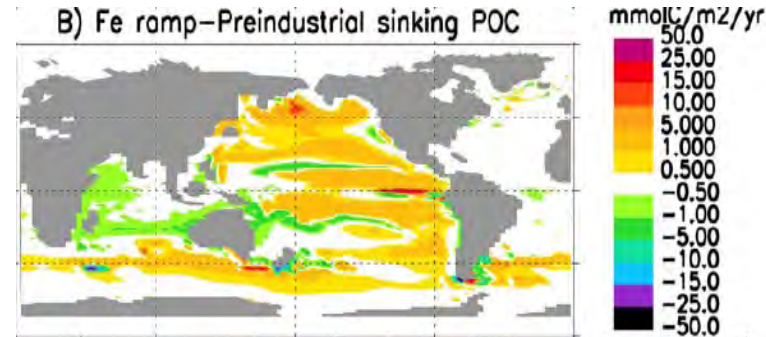


$\times 10^{-3}$



POC difference: modern versus
preindustrial dust

(from Krishnamurthy et al, GBC 2009)



SUMMARY

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$$S_{Fe} = \text{advect} + \text{diffusion} + S_{aeolian} + S_{sed} - \text{scavenging}$$

$$S_{Fe} = -\nabla \cdot (\vec{u}^* Fe) + \nabla \cdot (K \nabla Fe) + \alpha F_{aeolian} + F_{sed} - k_{scav} Fe'$$

GAPS IN OUR KNOWLEDGE: how to model iron chemistry, in particular solubility and ligand

SUMMARY

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 - non-diazotrophs where iron is main limiting nutrient
 - diazotrophs where others are nitrogen limited AND $Fe > R_{Fe}^*$

GAPS IN OUR KNOWLEDGE: physiological parameters of phytoplankton (e.g. K_{fe})

SUMMARY

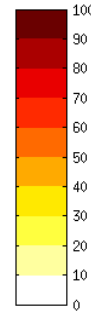
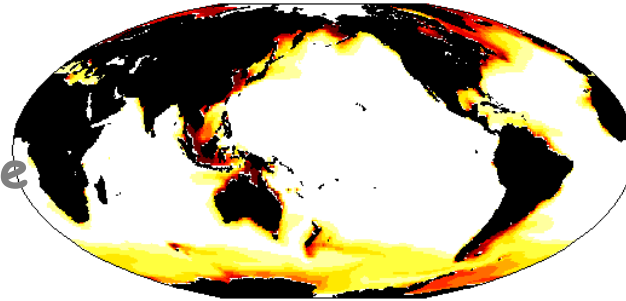
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<http://darwinproject.mit.edu>

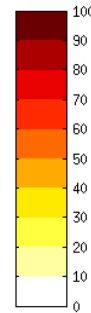
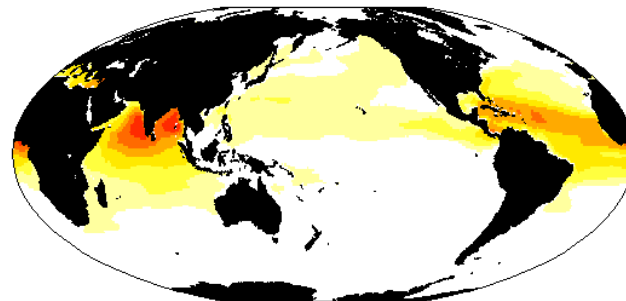
IRON SOURCES

$$\text{Total dissolved iron: } Fe = Fe_{\text{sedimentary}} + Fe_{\text{dust}} + Fe_{\text{remineralization}}$$

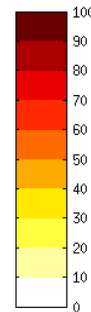
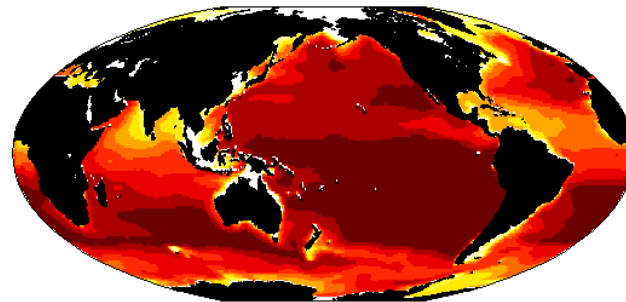
% iron from
sedimentary source



% iron from
aeolian source



% iron from
remineralization



**MODEL
RESULTS**

(compare to
Aumont et al, GBC, 2003
who found 73% from
regenerated)

IRON PARAMETERIZATION

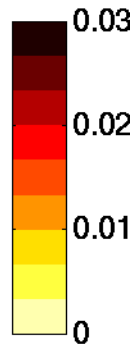
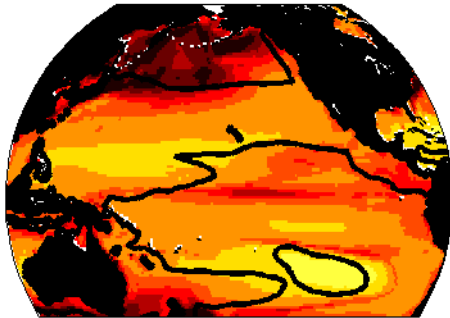
	LANL	MIT	PRINCETON	STANFORD SIMPLE	STANFORD COMPLEX	UCLA
Reference	Moore et al, 2004	Parekh et al, 2004	Friedrichs et al, 2007	Tagliabue and Arrigo, 2005	Tagliabue and Arrigo, 2006	Moore et al, 2004
Iron pools transported	Total dissolved iron (Fe_T)	Total dissolved iron (Fe_T)	Total dissolved Iron (Fe_T)	Total dissolved Iron (Fe_T)	Fe(II), Fe(III), Fe(III)La, Fe(III)Lb, Fe(III)s	Total dissolved Iron (Fe_T)
Bioavailable iron	Fe_T	Fe_T	Fe_T	Fe_T	Fe(II), Fe(III), Fe(III)Lb	Fe_T
Ligand(s)	None	One ligand $L_T = 1nM$	None	None	Two ligands Lb= 0.6, La 2nM	None
Ligand(s) binding strength	None	$\beta = 10^5 (\mu M^{-1})$	None	None	$\beta Lb = 10^{6.12} (\mu M^{-1})$ $\beta La = 10^{5.32} (\mu M^{-1})$	None
Iron scavenging	Scav rate: 0.12 yr^{-1} Increase: [Fe]>0.6nM Decrease:[Fe] <0.5nM	Only free iron, Fe' , scavenged at rate 10^{-3} d^{-1} everywhere	2 nd order scavenging of Fe_T of $50 \text{ m}^3 \text{ mol}^{-1} \text{ d}^{-1}$	None	Free inorganic Fe (Fe(II) and Fe(III)) scavenged at 10^{-3} d^{-1} everywhere	Scavenging rate: 0.12 yr^{-1} Increase: [Fe]>0.6nM Decrease: [Fe] <0.5nM
Back scavenging	None	None	None	None	None	None
Photochemistry	None	None	None	None	Yes	None
Natural dust deposition	Mahowald et al (2003)	Mahowald et al (2003)	Ginoux et al (2001)	Southern Ocean direct Fe deposition*	Southern Ocean direct Fe deposition*	Luo et al., 2003
% Fe soluble	2%	2%	2%	N/A	N/A	2%
Sedimentary source	Yes, depth<900m	None	Yes, variable	None	Yes, including shelf	Yes, no shelf

Maltrud et al, in preparation
(Atmospheric CO₂ reduction from iron fertilization: a model intercomparison study)



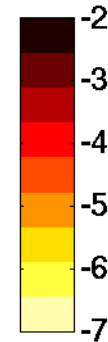
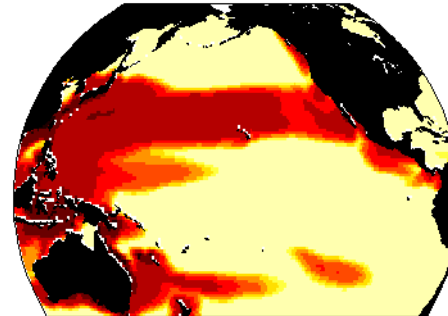
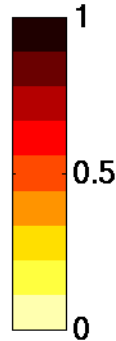
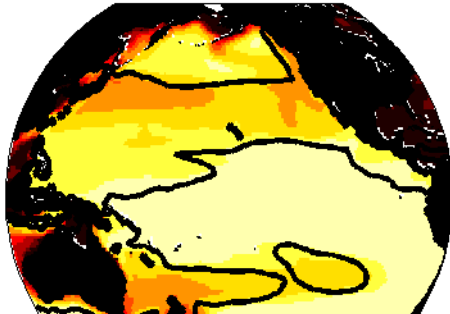
MODEL RESULTS: CONTROL EXPERIMENT

biomass
($\mu\text{M P}$)



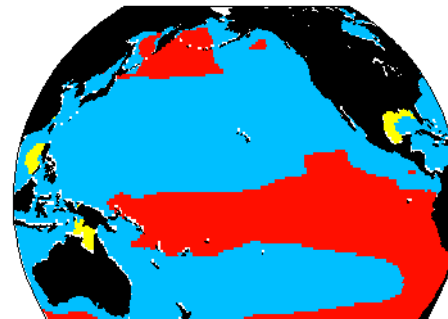
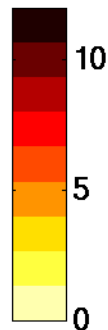
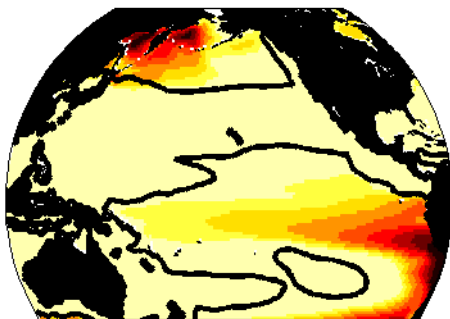
Where do diazotrophs exist?

dFe
(nM Fe)



diazotrophs
log
($\mu\text{M P}$)

NO₃
($\mu\text{M N}$)

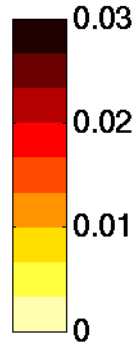
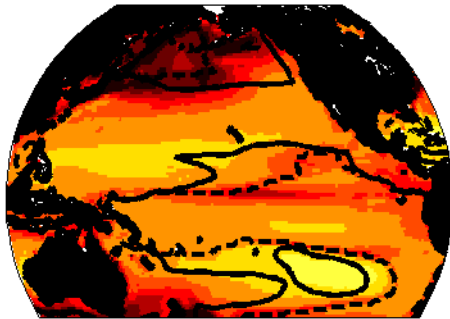


limiting
nutrient

solid line region of diazotrophs

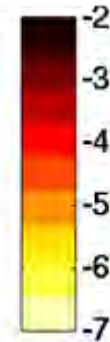
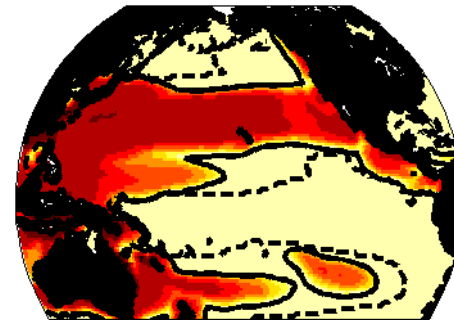
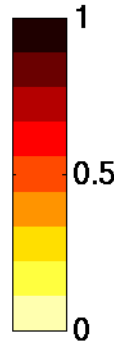
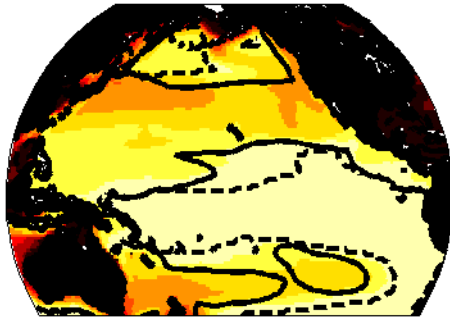
MODEL RESULTS: CONTROL EXPERIMENT

biomass
($\mu\text{M P}$)



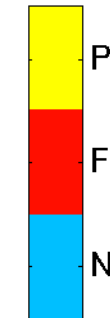
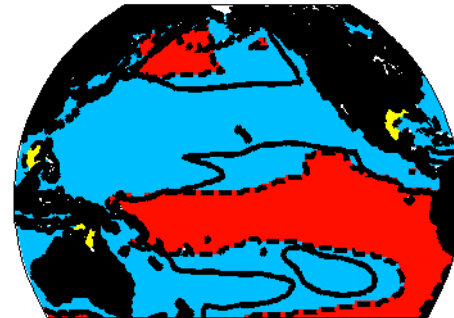
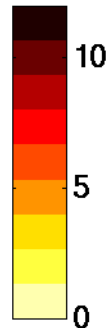
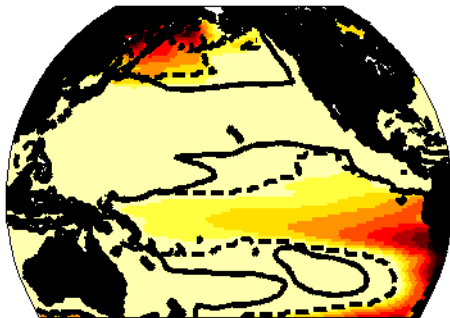
diazotrophs exist where:
 1) Non-diazotrophs are nitrogen limited
 2) AND iron is sufficient ($>R_{fe}^*$)
 (Monteiro et al, in prep, 2009)

dFe
(nM Fe)



diazotrophs
log
($\mu\text{M P}$)

NO₃
($\mu\text{M N}$)



limiting
nutrient

dashed line boundary between nitrogen and iron limited regions; solid line region of diazotrophs

simple 0-D theoretical system

$$\frac{\partial N}{\partial t} = -\mu \frac{N}{N + \kappa_N} P + S$$

$$\frac{\partial P}{dt} = \mu \frac{N}{N + \kappa_N} P - mP$$

3-D simulation equations (for i nutrients and j phytoplankton)

$$\frac{\partial N_i}{\partial t} = -\mu(T, I) \min\left(\frac{N}{N + \kappa_N}, \frac{PO_3}{PO_3 + \kappa_{PO_3}}, \frac{Fe}{Fe + \kappa_{Fe}}\right) P_j + S_{Ni}$$

$$\frac{\partial P_j}{dt} = \underbrace{\mu(T, I)}_{\text{growth function of temperature and light}} \underbrace{\min\left(\frac{N}{N + \kappa_N}, \frac{PO_3}{PO_3 + \kappa_{PO_3}}, \frac{Fe}{Fe + \kappa_{Fe}}\right)}_{\text{nutrient limitation minimum function of several nutrients}} P_j - \underbrace{mP_j - \text{sinking} - \text{grazing}}_{\text{more complex loss terms}} + S_{Pj}$$

growth function
of temperature
and light

nutrient limitation
minimum function
of several nutrients

more complex
loss terms

The Darwin Project

MODEL DEVELOPMENT

- inclusion of diverse diazotrophs (Fanny Monteiro)
- different absorption spectrum/pigments (Anna Hickman)
- radiative transfer code (Watson Gregg)
- size-based trade-offs (Stephanie Dutkiewicz, Chris Kempes)
- mixotrophy/predation (Ben Ward)
- quota based model (Ben Ward)
- high resolution simulation (Oliver Jahn)

<http://darwinproject.mit.edu>

Sensitivity experiments to see:

- 1) how important iron parameterization is on model community structure and iron concentrations
(e.g. Moore and Braucher, BG, 2008; Krishnamurthy et al, GBC, 2009)**

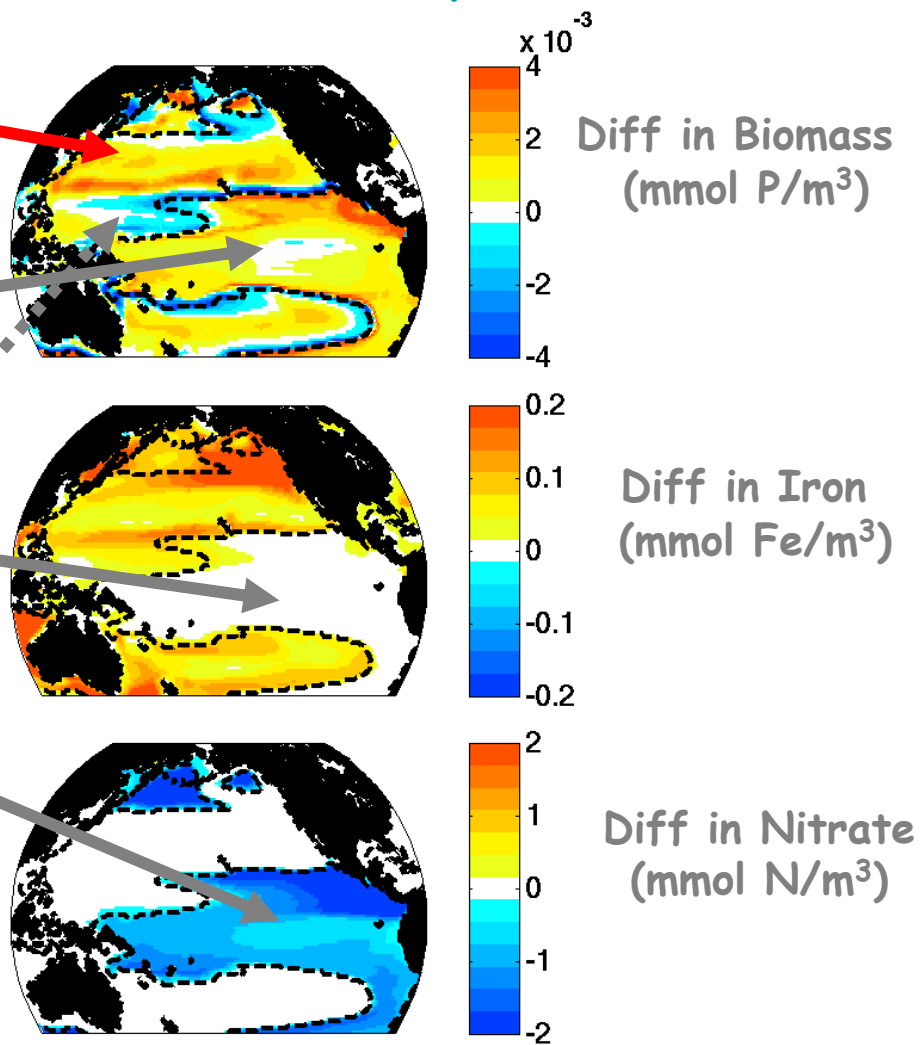
- 2) such experiments can help us understand the linkage between community structure and biogeochemical cycling:**
 - to what extent does iron supply control phytoplankton communities in the Pacific?
(e.g. diazotrophs: Moore and Doney, GBC 2007)
and in turn**
 - to what extent do phytoplankton communities control iron concentrations?**

MODEL RESULTS: SENSITIVITY EXPERIMENTS (2)

Difference between simulations (4%-1%): **with** diazotrophs

BUT WHAT IS HAPPENING HERE?

- increase in iron supply leads to increase biomass in iron limited regions
- no change to phytoplankton physiology, so no change to iron concentration
- additional nitrate consumed by increased biomass
- leads to lower supply to nitrogen limited region



dashed line is boundary between nitrogen and iron limited regions

MOTIVATION

Change in assumption of availability of iron

Effect on primary production and biomass:

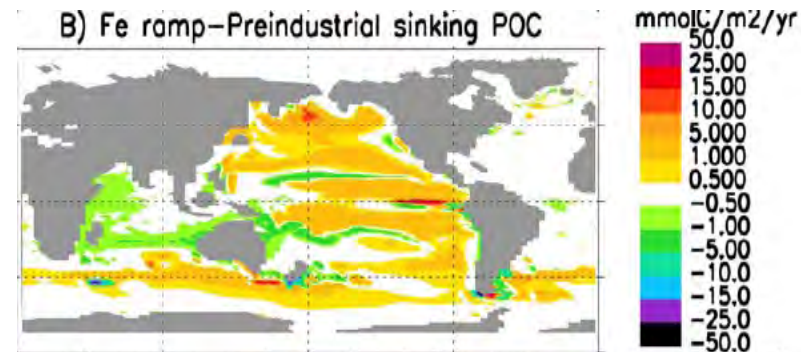
- increased iron availability -> increase in PP
- PP increased 3.5% with 10 times iron flux (Moore et al, GBC 2004)
- PP increased 2% preindustrial to modern (Krishnamurthy et al, GBC 2009)

Effect on Nitrogen fixing:

- increased iron availability -> increased N₂ fixing
- 50% increase with 10 times iron flux (Moore et al, GBC 2004)
- 35% increase with LGM over modern dust (Moore and Doney, 2007)

POC difference: modern versus preindustrial dust

(from Krishnamurthy et al, GBC 2009)



MODEL DESCRIPTION

- ecosystem usually run with 100's of phytoplankton types (and several simulations run to form ensemble)
- but here for computational reasons we reduce to 9 representative types, which fall into the "functional groups":

diatoms, other large, small, *Prochlorococcus*, diazotrophs

