Climate and the regulation of the marine N cycle

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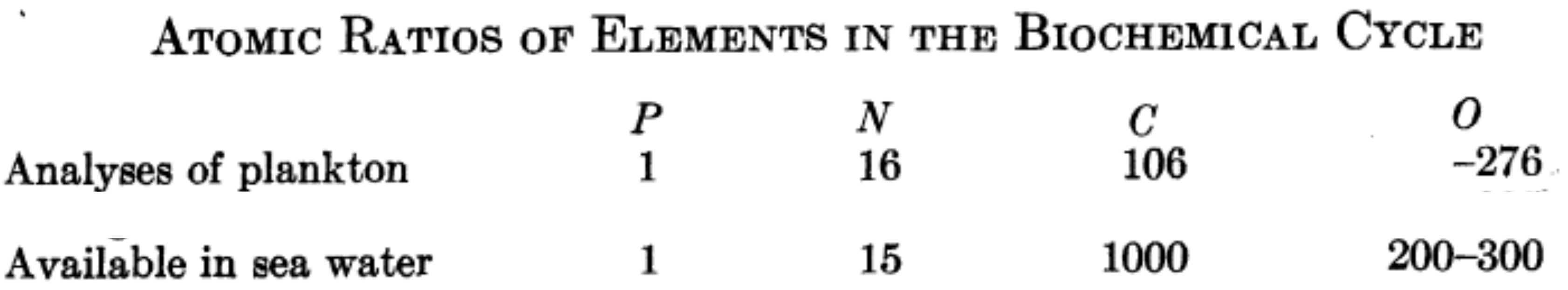
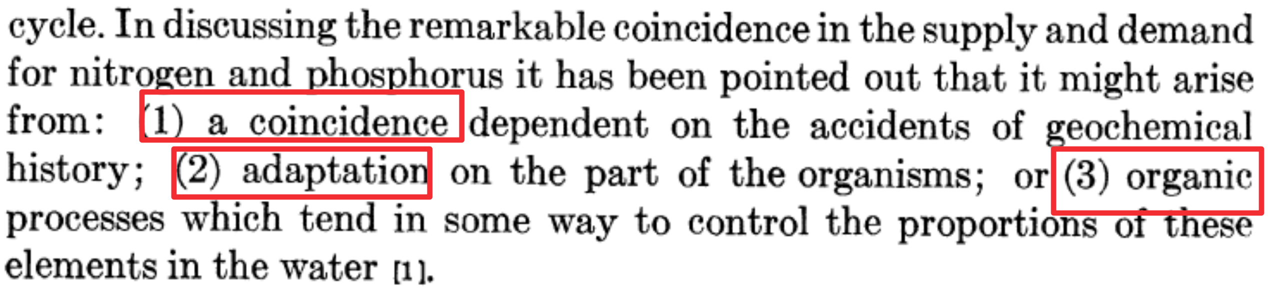
Acknowledgements
Tom Weber (PhD student/Postdoc), Tim Devries (Postdoc)
NSF, Gordon and Betty Moore Foundation

Foundations



ATOMIC RATIOS OF ELEMENTS IN THE BIOCHEMICAL CYCLE

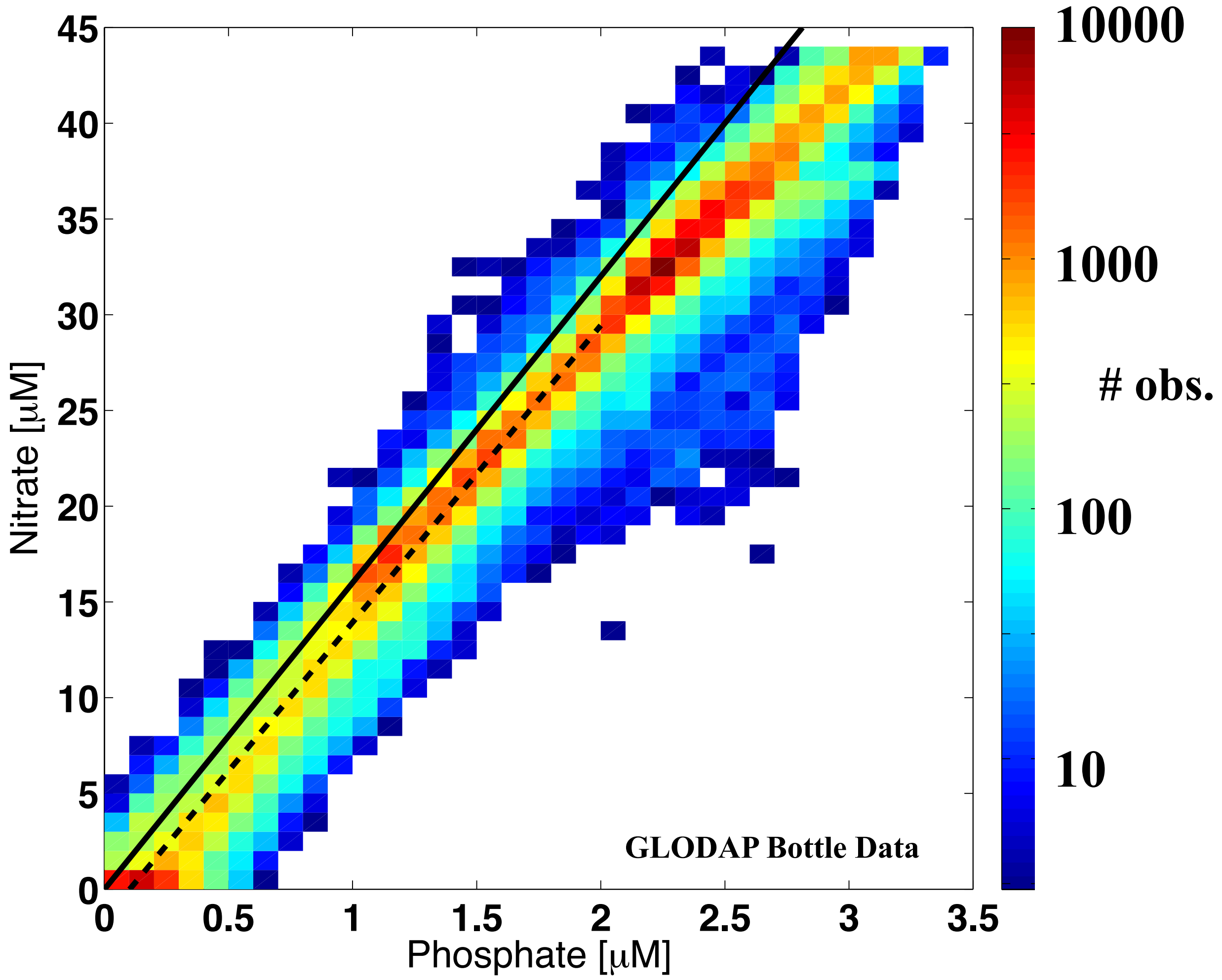
	P	N	C	O
Analyses of plankton	1	16	106	–276
Available in sea water	1	15	1000	200–300



cycle. In discussing the remarkable coincidence in the supply and demand for nitrogen and phosphorus it has been pointed out that it might arise from: (1) a coincidence dependent on the accidents of geochemical history; (2) adaptation on the part of the organisms; or (3) organic processes which tend in some way to control the proportions of these elements in the water [1].

A.C. Redfield [1958]

A Modern View

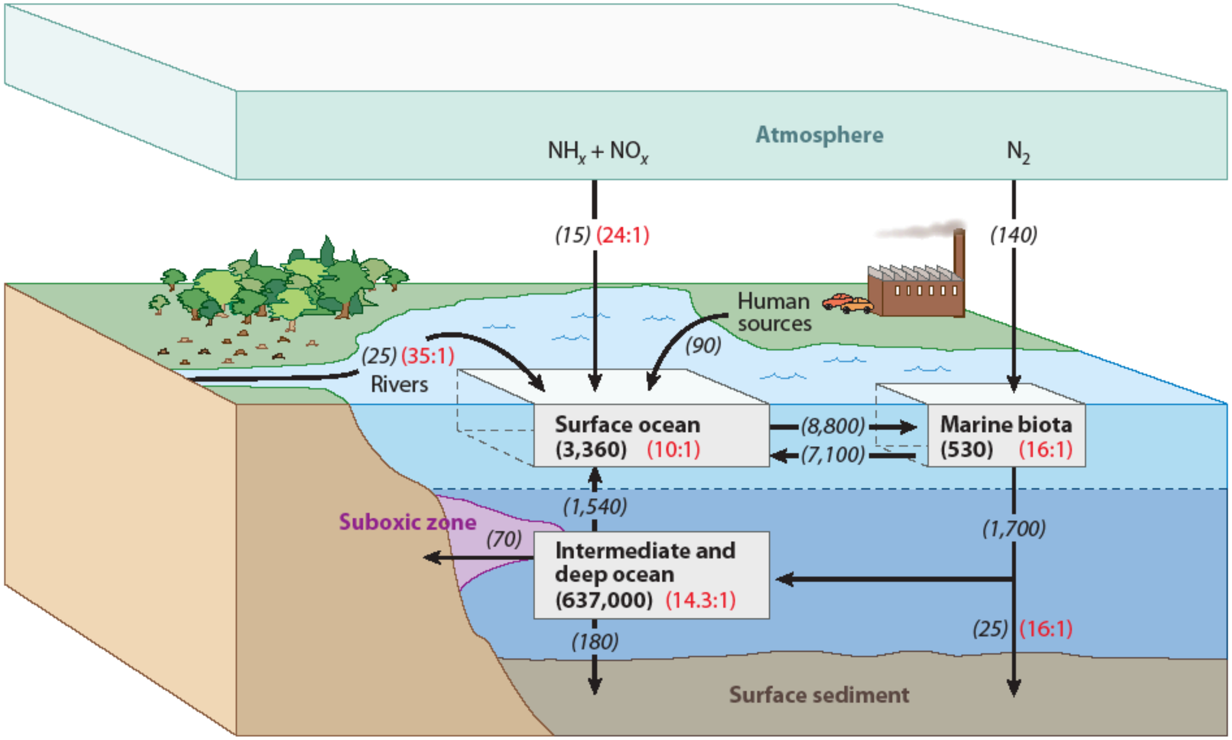


NO_3 and PO_4 are among best correlated properties of ocean (r^2=0.98)

Slope = 16:1, same as mean biomass, R_o, suggesting a universal stoichiometry.

Global reservoirs of NO_3 (ΣN) and PO_4 (ΣP) have a slightly lower ratio, $\Sigma N:\Sigma P=14.3$.

Ocean N and P Cycles



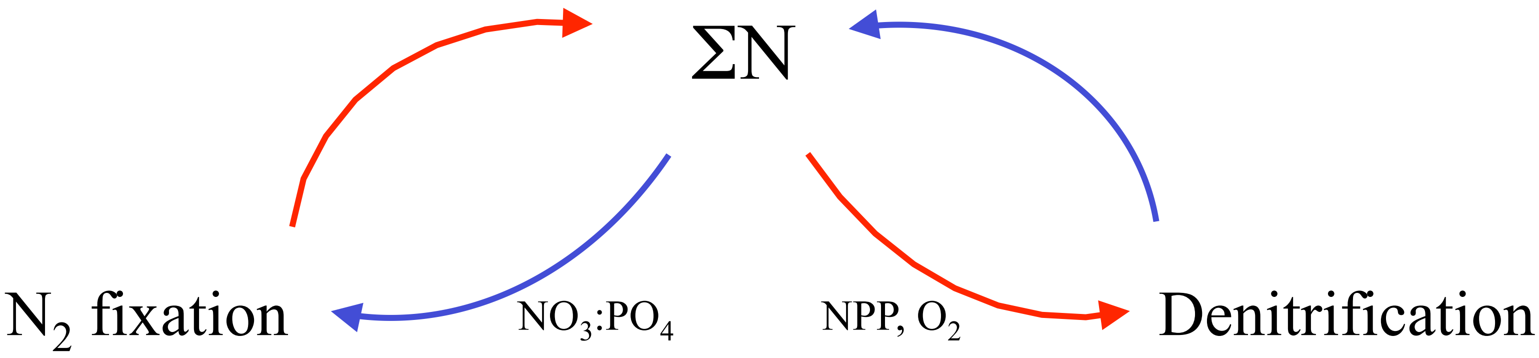
Deutsch and Weber [2012]
Annual Reviews of Marine Science

P reservoir (ΣP): geologically controlled slow turnover (~50ky).

N reservoir (ΣN): biologically controlled fast turnover (~2ky).

ΣN:ΣP not directly reflected in any major input/output.

N cycle as Biological Stabilizer



ΣN

N_2 fixation

$NO_3:PO_4$

NPP, O_2

Denitrification

<u>Source feedback:</u>
Physiological cost of N_2 fixation reduces competitive advantage when N is plentiful

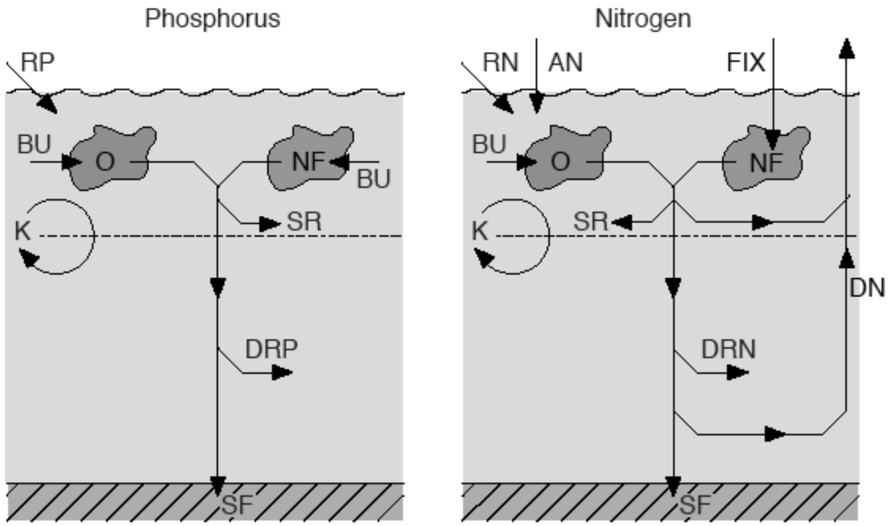
Redfield [1958]

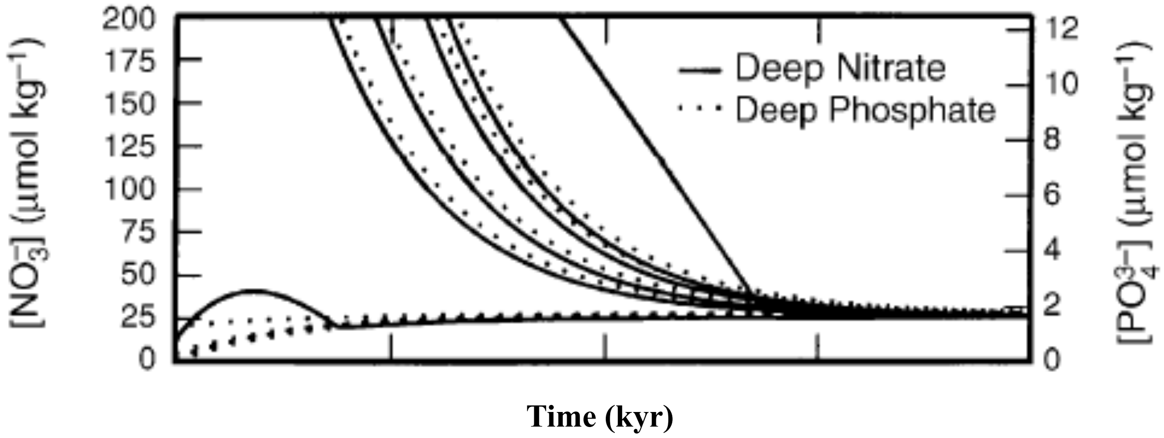
<u>Sink feedback:</u>
Increased productivity expands suboxic zones, increases denitrification

Codispoti [1989]

Biogeochemical Feedbacks

A simple model





Tyrrell [1999], Lenton + Klausmeier [2007]

Assumptions:

1)Diazotrophs need P, but not N.

2)Cost is slower growth rate ($\mu_F<\mu_o$).

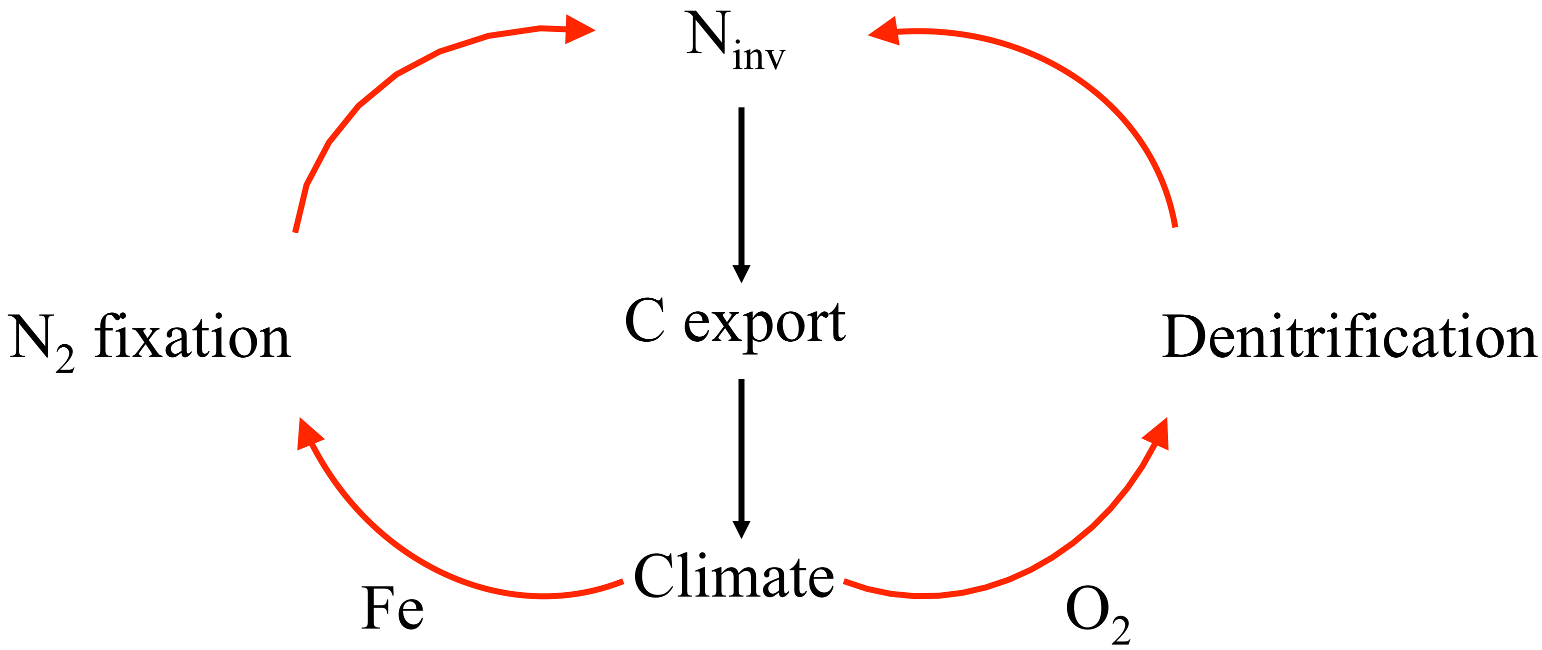
Outcomes:

1) N inventory (ΣN) Diazotrophs growth rate handicap

2) N inventory (ΣN) ~ Denitrification rate

Both factors climate driven and poorly known.

N cycle as Climate Amplifier?



N_{inv}

N_2 fixation

C export

Denitrification

Climate

Fe

O_2

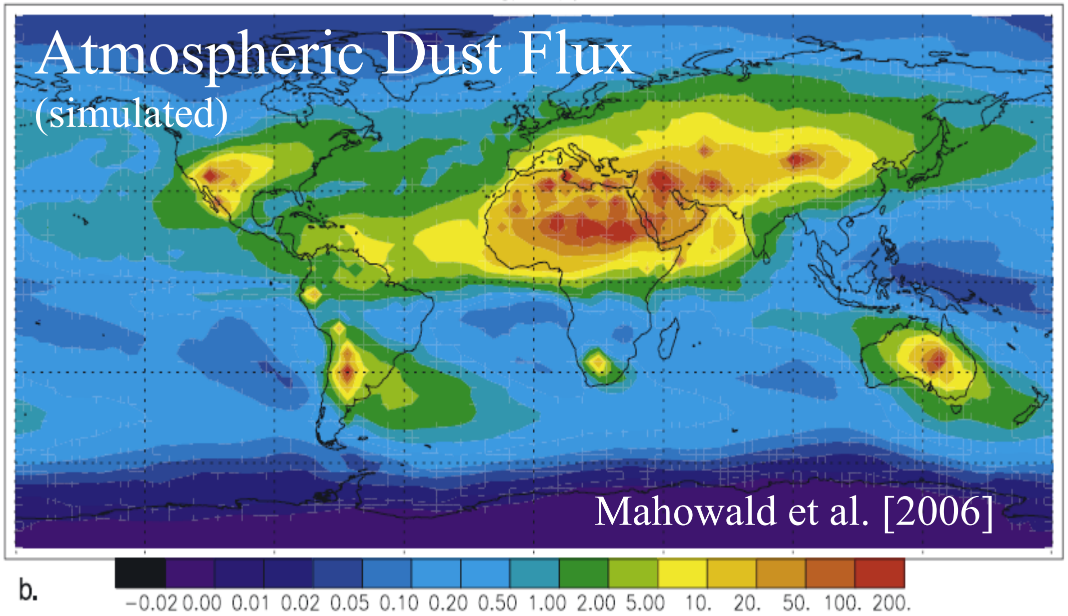
Source forcing:
N_2 fixation Fe intensive
Favored by cold/dry
climate?

Falkowski [1997]
Broecker + Henderson [1998]

Sink forcing:
Anoxia more widespread
in warm climates

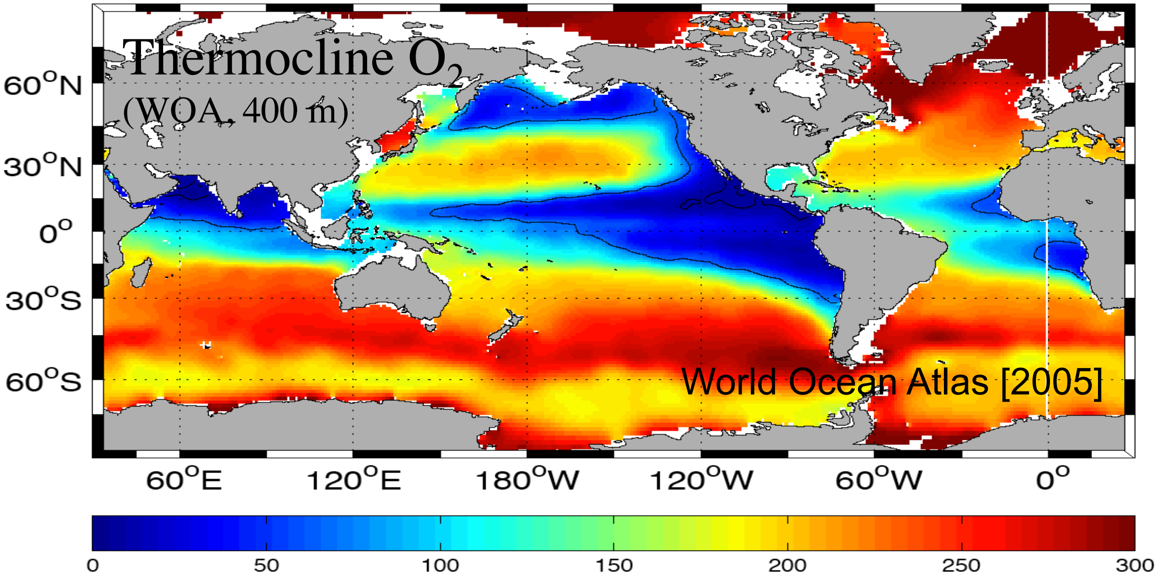
Altabet et al. [1995]
Ganeshram et al. [1995]

Climate forcing: Dust and O_2



Iron supply largely from atmospheric dust deposition.

N2 fixation
Atl >> Pac



Anoxic zones closely linked to water mass age.

Denitrification
Pac >> Atl

Unknowns and Debates

Key Uncertainty:

Rates and/or environmental controls poorly known
→ Hard to evaluate its response to climate

Questions:

Denitrification: How fast is it?

N_2 Fixation: What regulates the distribution?

What are the implications for N cycle dynamics?

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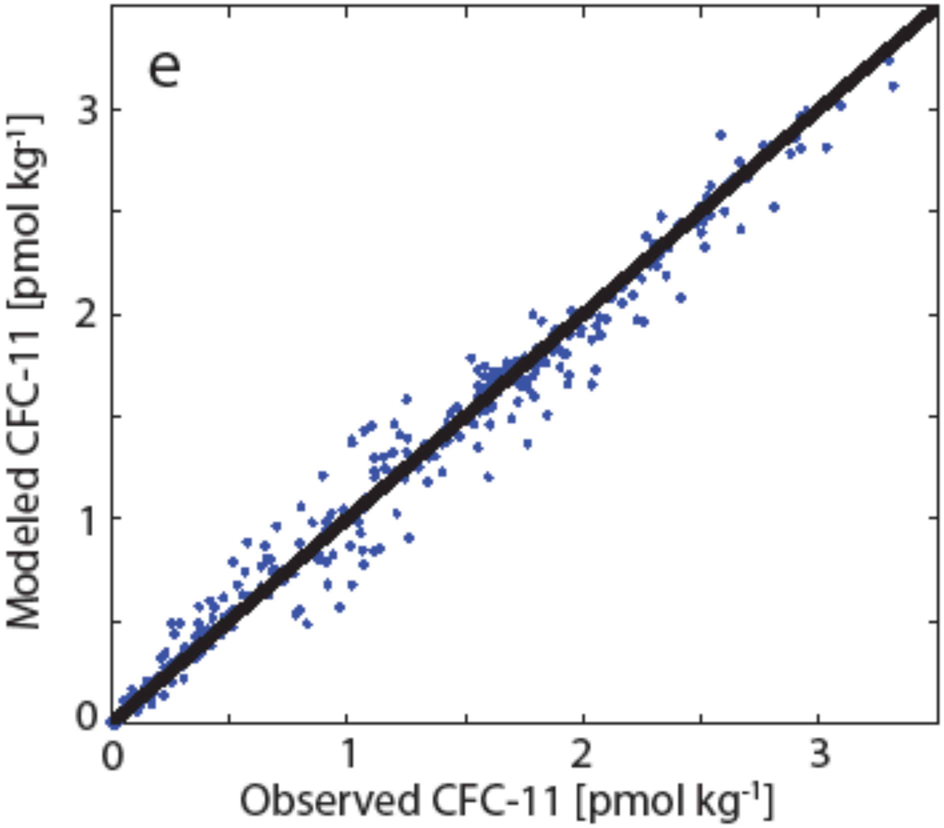
Ocean Model: Circulation



Circulation Model

Coarse resolution (2-4^{o}) GCM
Observed surface forcing
Linearized momentum eqns.
Optimal fit to T, S, ^{14}C
DeVries and Primeau [2011]

Added constraint for CFCs (for ventilation of anoxic zones).

DeVries et al. [2011]
Nature Geoscience

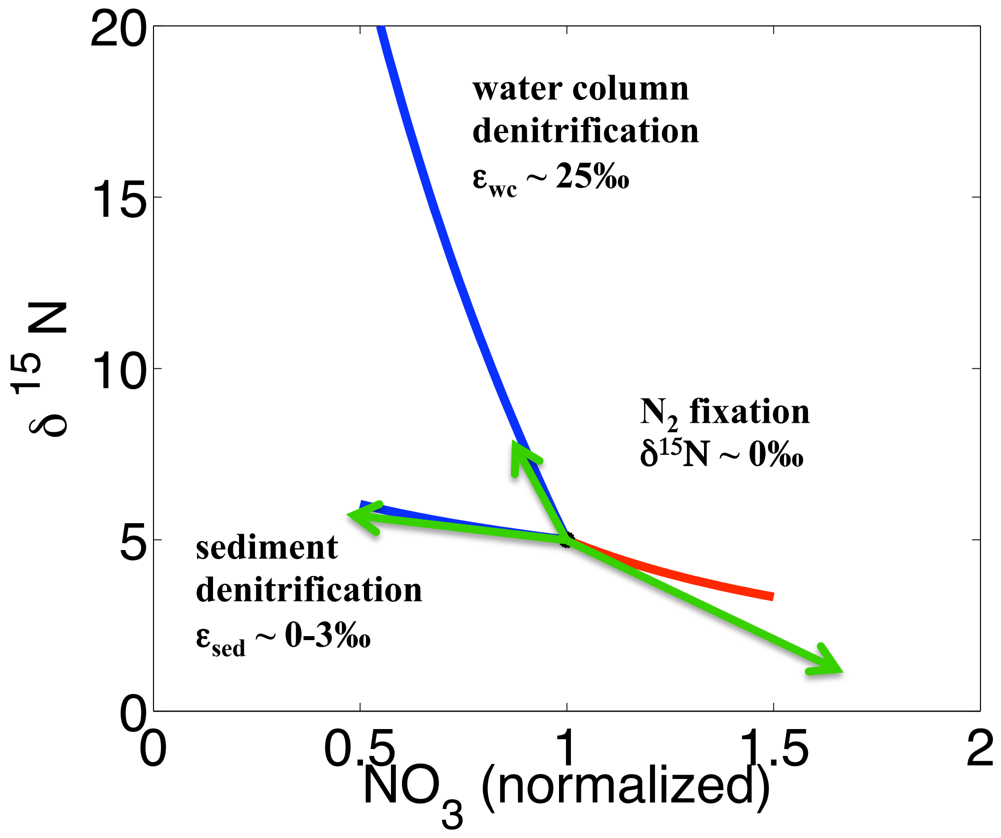
Tracer Constraints

Constraints on N budget:

$$N^* = \left[NO_3^-\right] - 16\left[PO_4^{3-}\right]$$

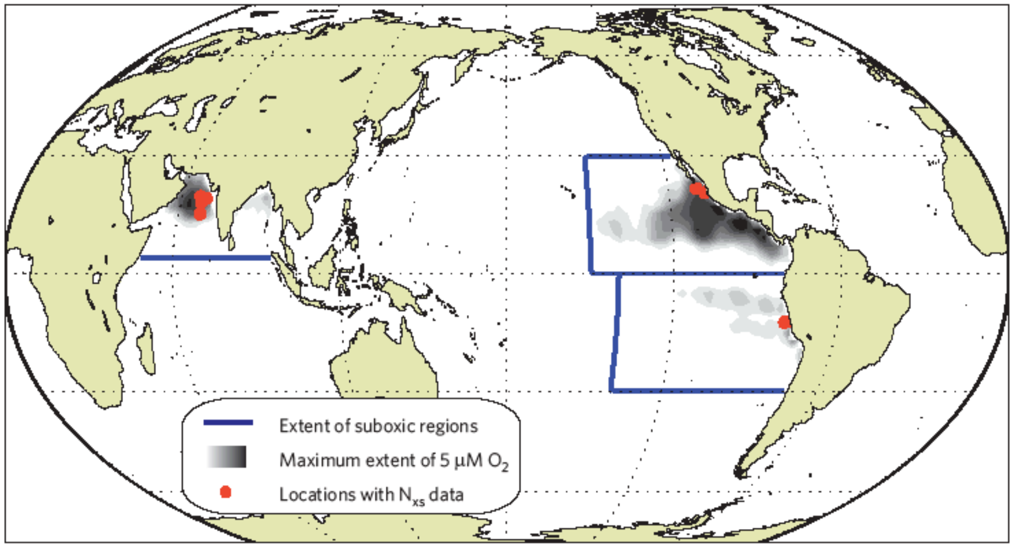
$$\delta^{15}N = \left(\frac{{}^{15}N / {}^{14}N}{R_{air}} - 1 \right) \cdot 1000$$

$$N_2^{xs} = \left({}^{N_2}\!/_{Ar} - {}^{N_2}\!/_{Ar_{ref}} \right) * N_2^{sat}$$



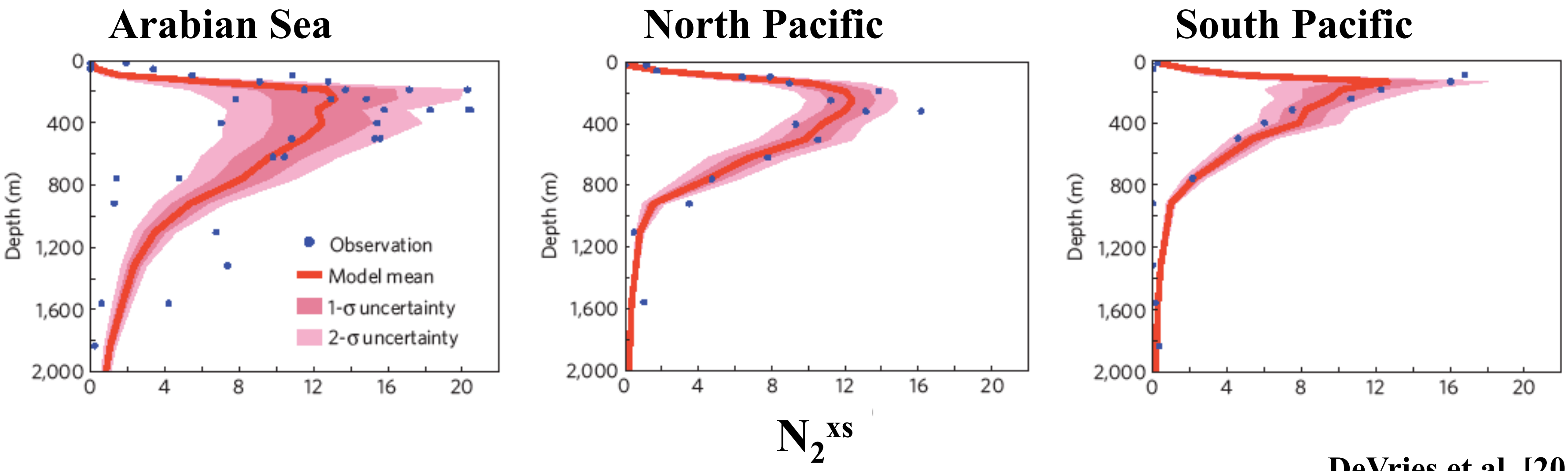
The use of multiple tracers gives combination of regional and global constraints on the major fluxes.

Data: N_2



Denitrification rates and spatial distribution fit to observed N_2 profiles in probabilistic simulations.

Global rates 60-70 Tg/yr

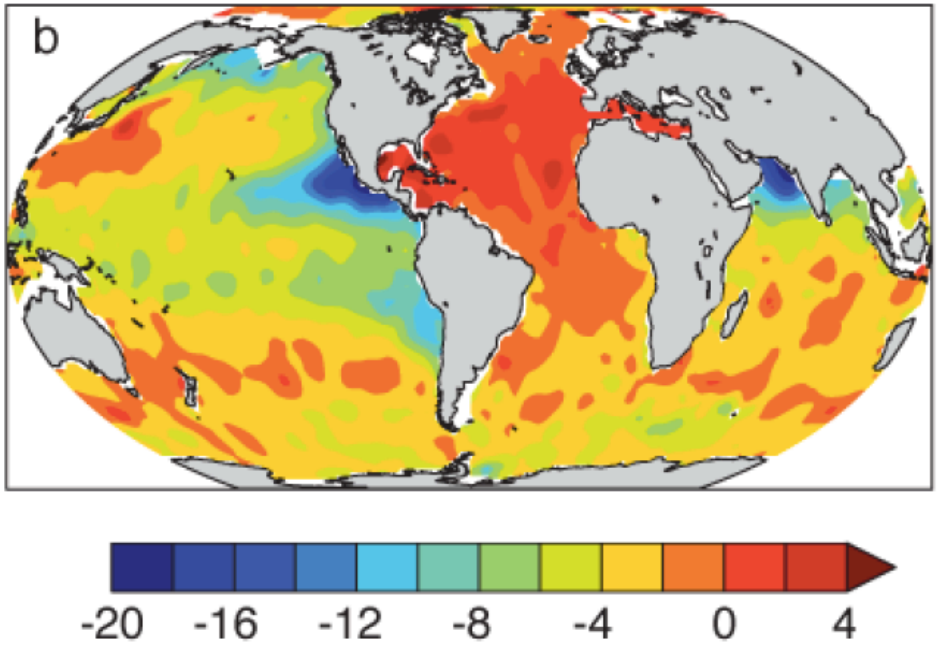


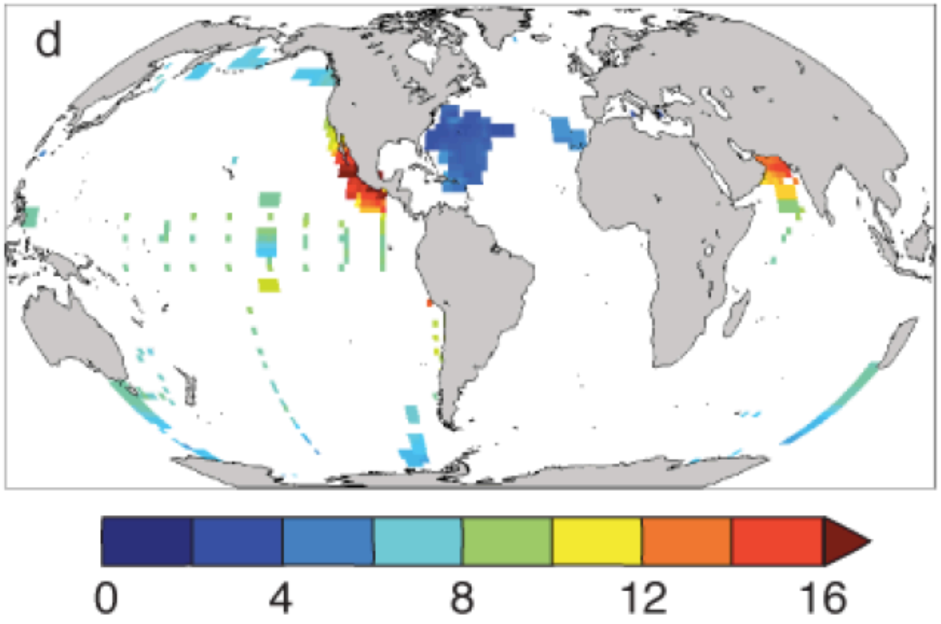
DeVries et al. [2011]
Nature Geoscience

Data: N*, δ^{15}N

$$N^* = \left[NO_3^-\right] - 16\left[PO_4^{3-}\right]$$

$$\delta^{15}N = \left(\frac{{}^{15}N / {}^{14}N}{R_{air}} - 1 \right) \cdot 1000$$



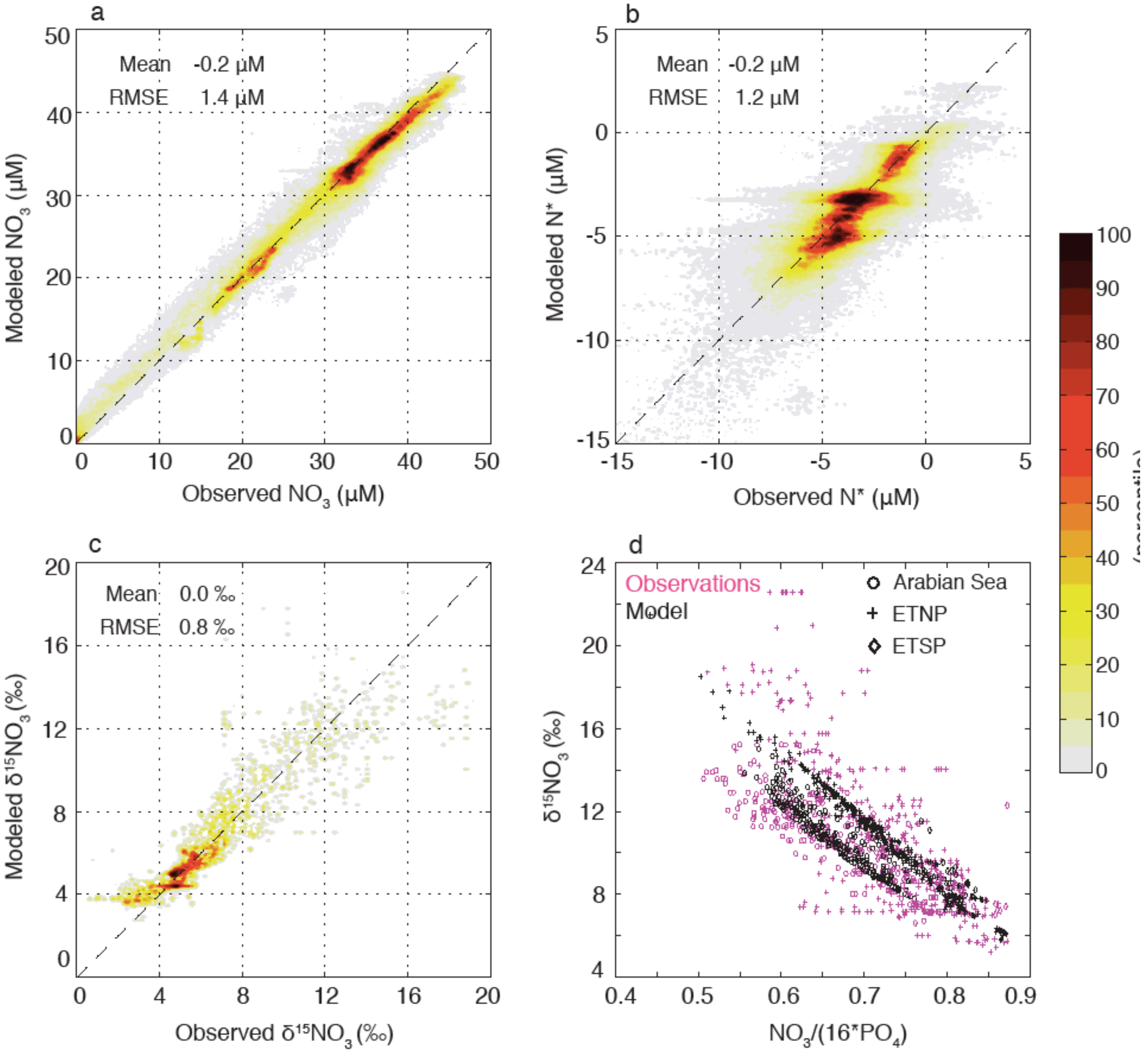


Data is dense
Constraint mostly regional

Data is sparse
Constraint mostly global

DeVries et al. [2013]
Biogeoscience

Model vs data

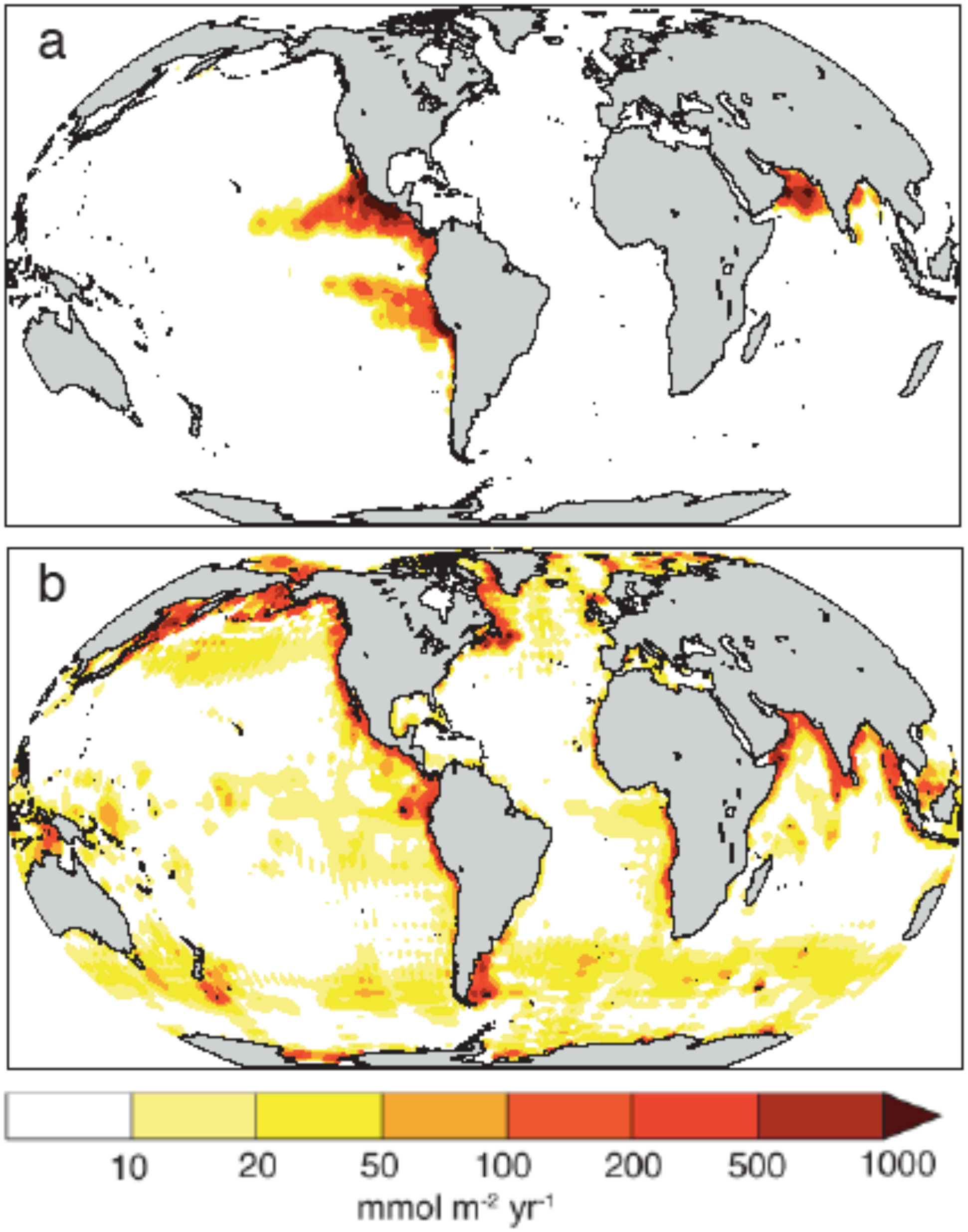


Model captures most of the variation in all tracer observations.

Largest biases in deep N*, probably from particle flux model.

DeVries et al. [2013]
Biogeoscience

Global Denitrification



Water Column Rates

Range: 50-77 Tg/yr
Compatible with N_2 results

Sedimentary Rates

Range: 71-168 Tg/yr
Smaller than previous estimates

→ Balanced budget likely

DeVries et al. [2013]
See also Eugster and Gruber [2013]

Unknowns and Debates

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Questions:

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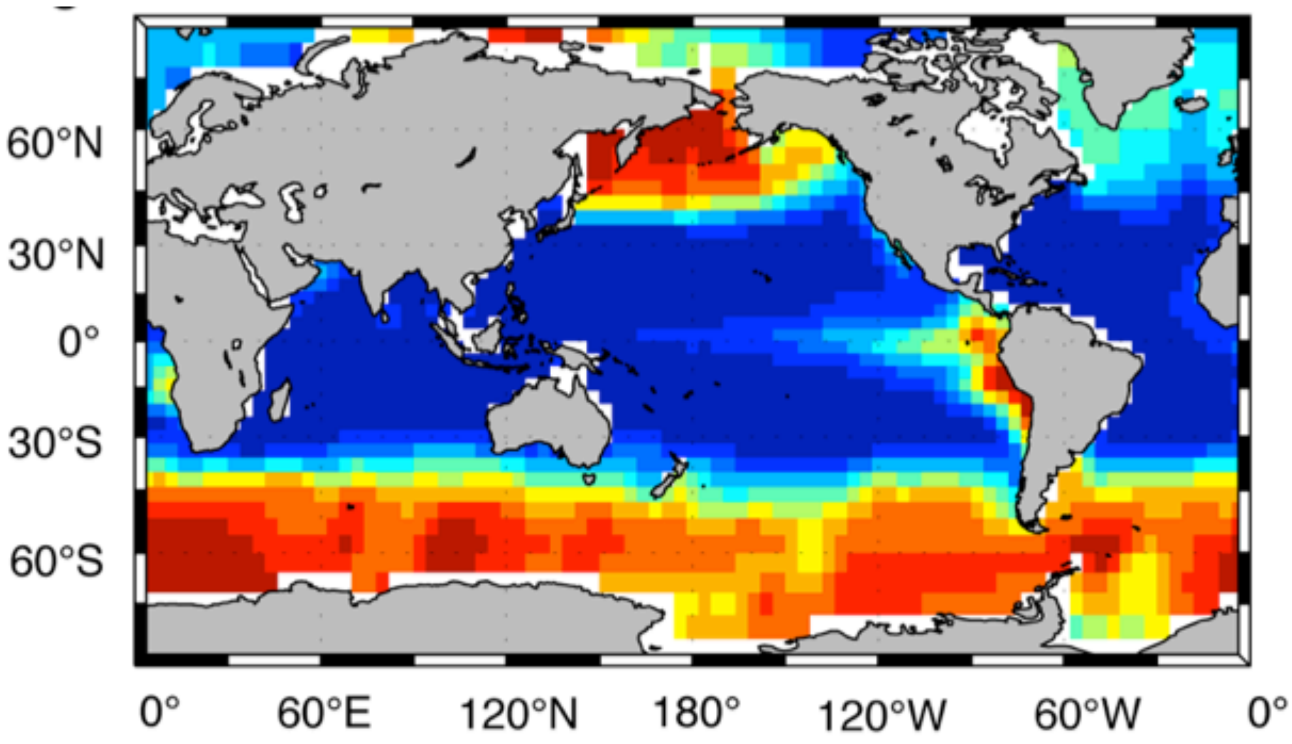
Model: Circulation + Ecosystem

Simulated Surface PO_4



Ecosystem Model

Two plankton types (diazotrophs + non-diaz.)

Plankton growth rates
~ Light, Temp, Fe

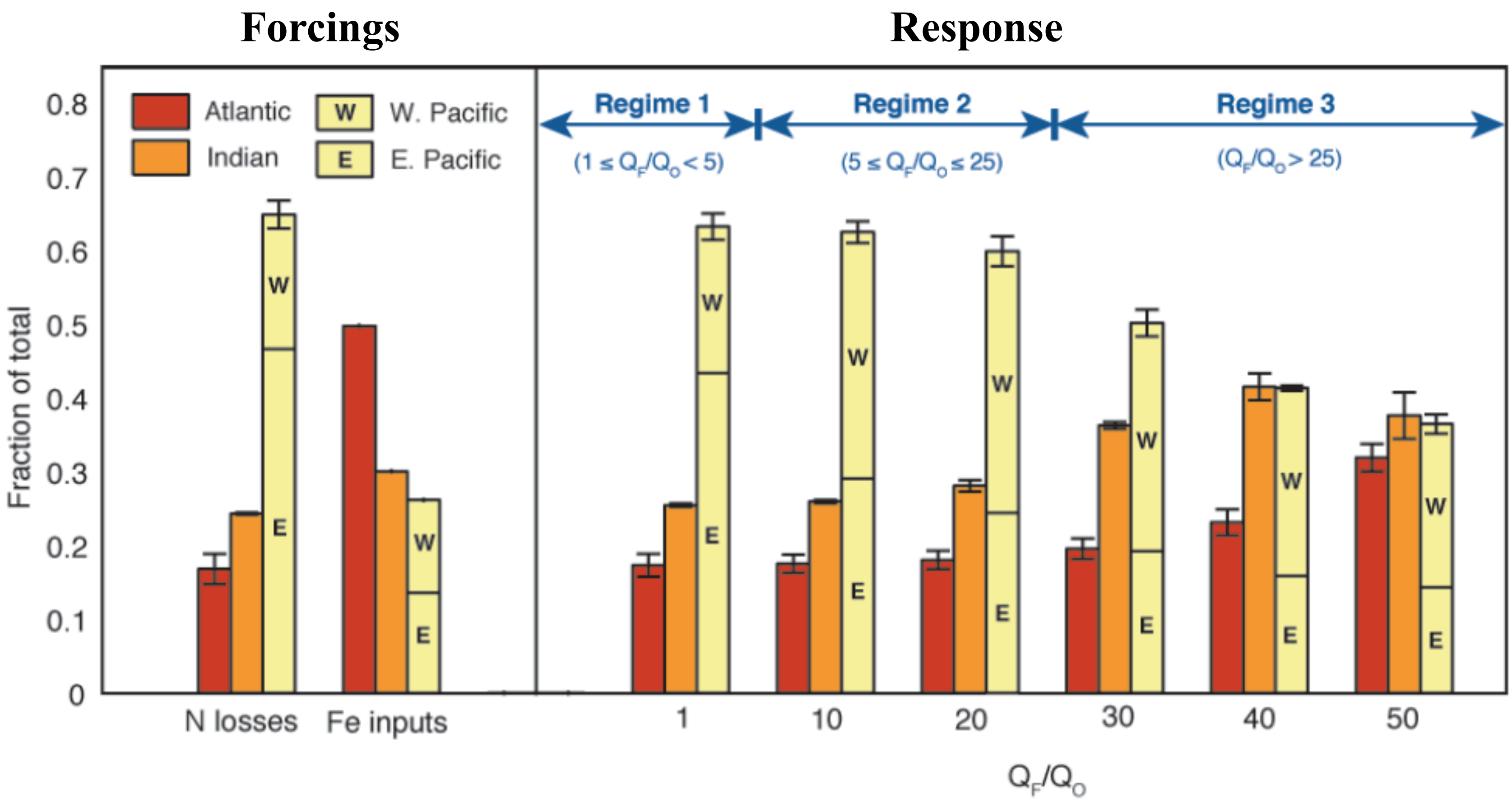
Sinking particle flux
~ $z^{-\alpha}$

Fit to surface PO_4 data

Empirically based denitrification rates.

Approach: 1) Manipulate plankton traits
2) Determine implications for observable tracers
3) Test underlying assumptions re: traits.

Limitation regimes



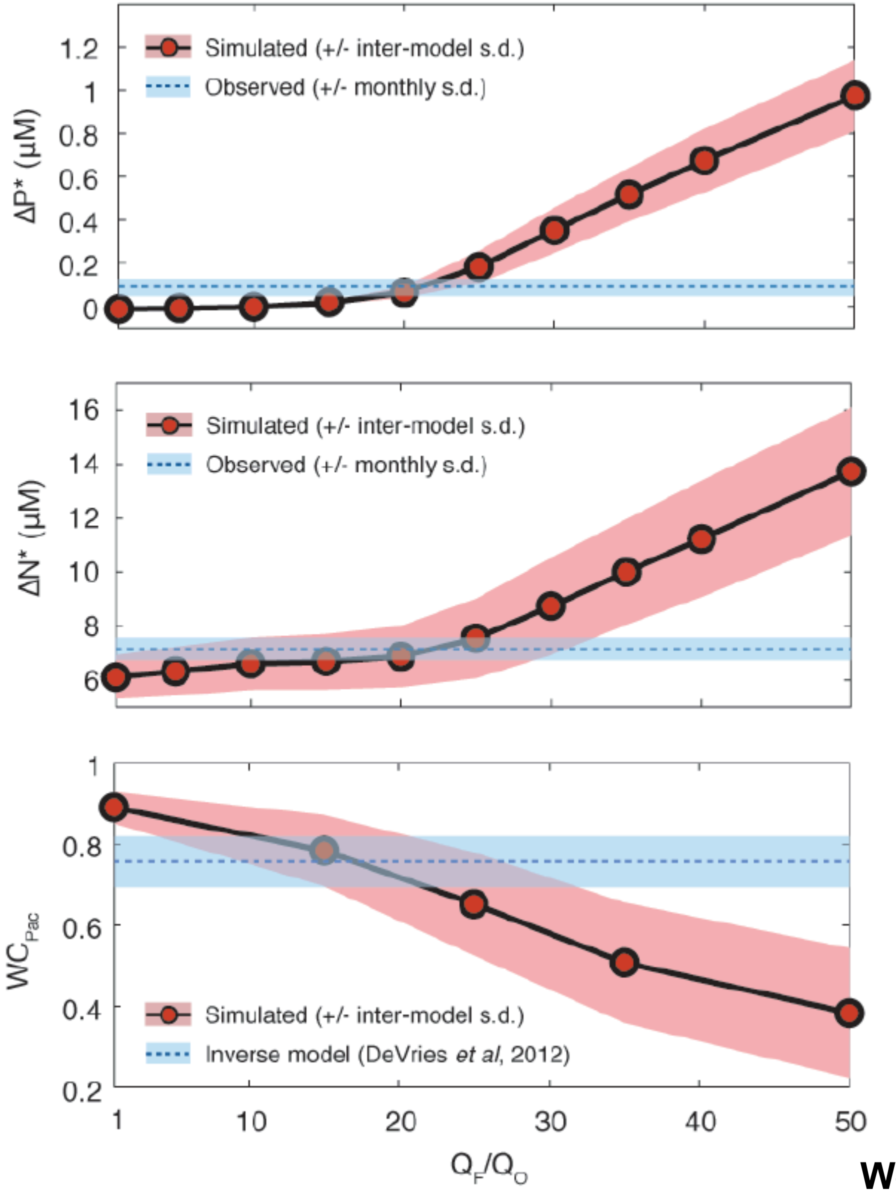
Diazotroph Fe limitation governed by cellular Fe:P quota (Q_F/Q_o)

At low Fe limitation, N_2 Fixation looks like denitrification.

As Fe limitation increases it looks gradually more like dust deposition.

Weber and Deutsch [in review]

Which regime are we in?



Surface excess PO_4
Pacific-Atlantic

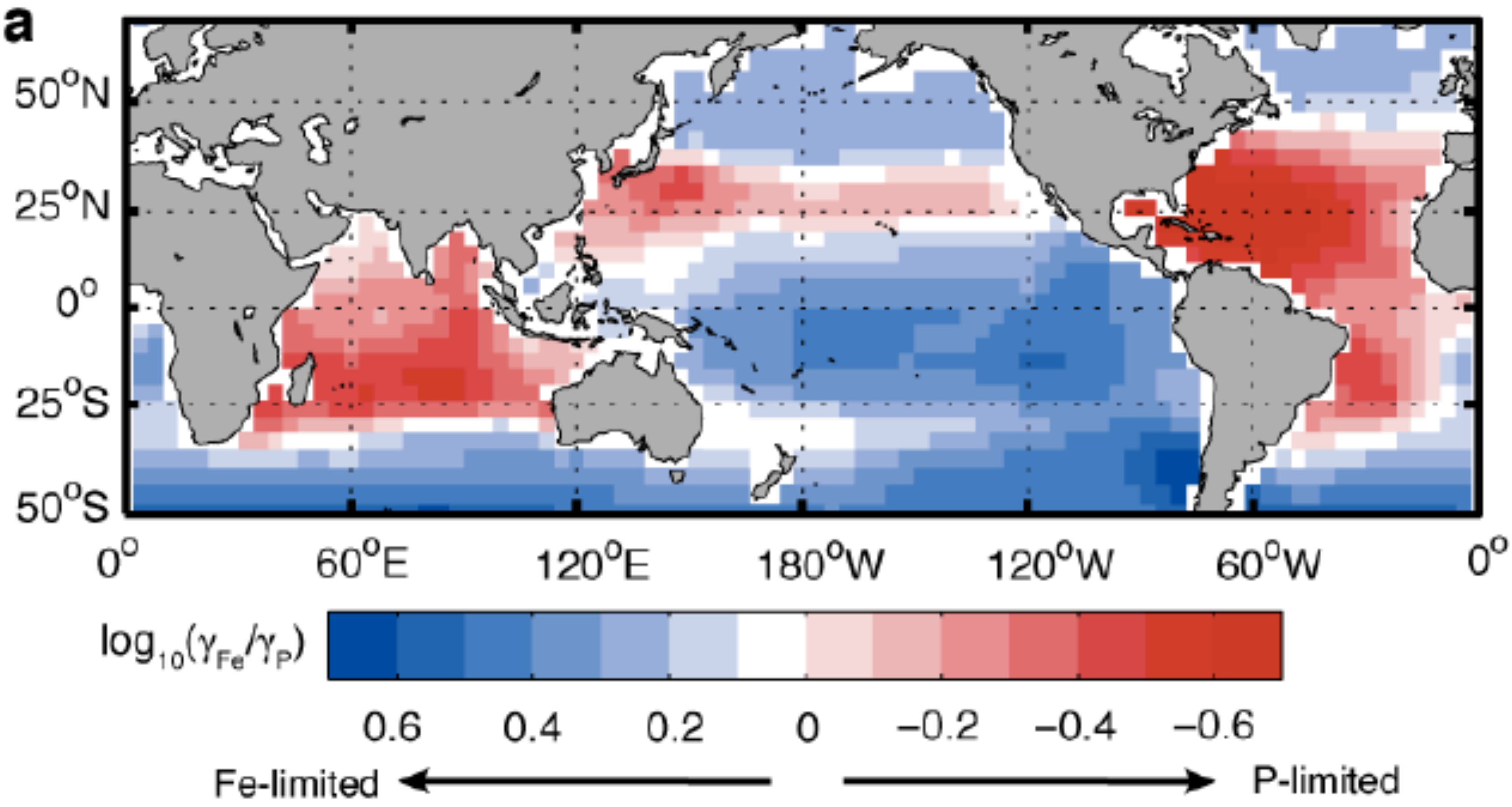
Thermocline NO_3
deficit
Pacific-Atlantic

Denitrification rate
Pac./(Pac.+Ind.)

All these data constraints (and more) are best matched in the intermediate Fe limitation regime (Regime 2).

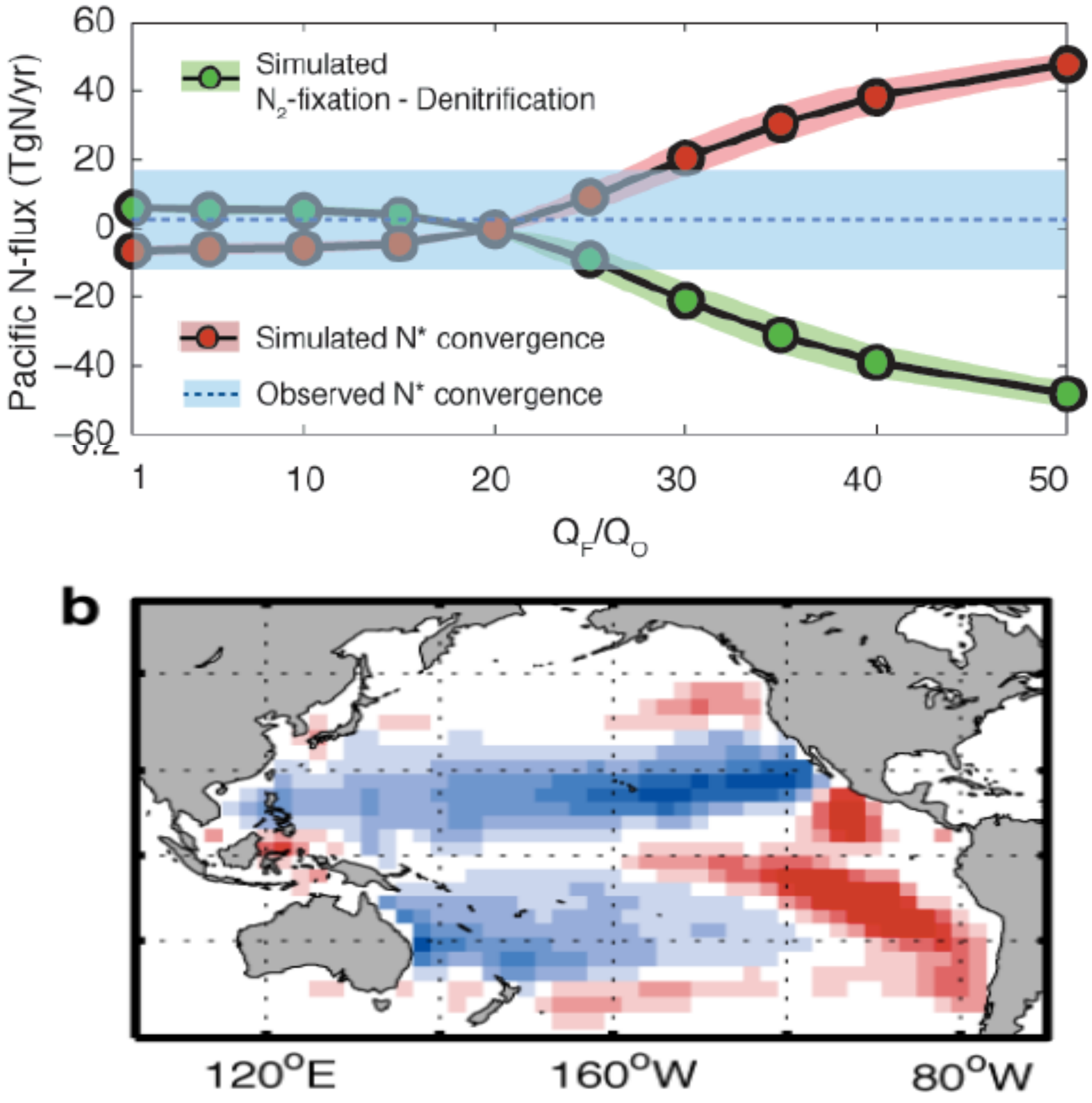
Weber and Deutsch [in review]

Regime 2: Local Fe limitation



Weber and Deutsch [in review]

Regime 2: Basin P limitation



In regime 2, the basin scale rates are very nearly balanced and cross-basin transport of N deficits is small, consistent with data.

Fe fertilization of Fe-limited diazotrophs does not change total budget.

→ Basin scale fixation is limited by generation of excess P.

Weber and Deutsch [in review]

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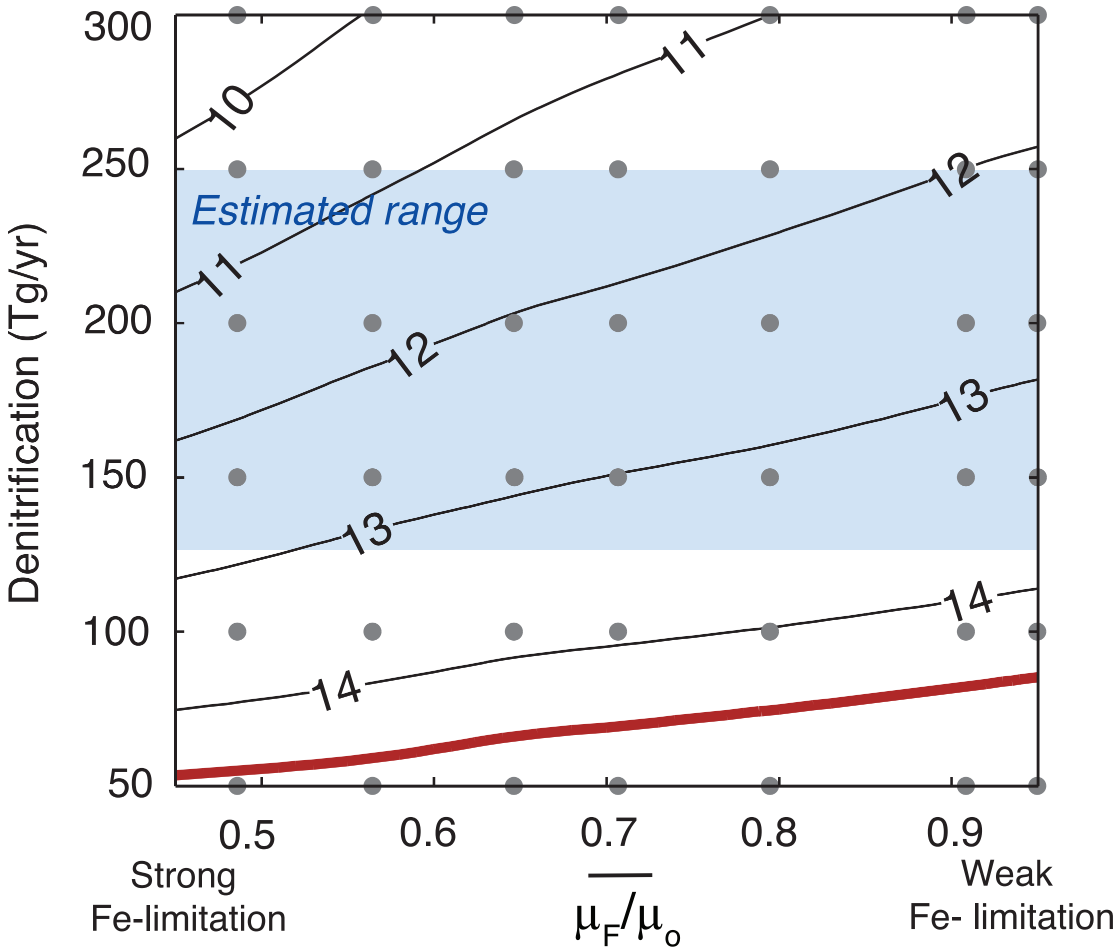
Global ΣN:ΣP



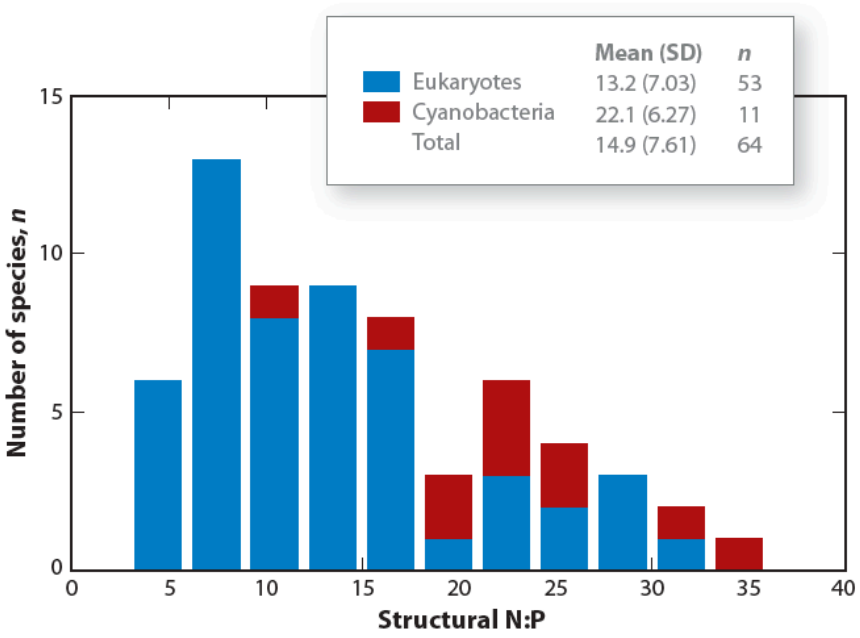
Steady State ΣN:ΣP reflects the global NO_3:PO_4 ratio needed to allow N_2 fixers to balance prescribed N losses.

For observed denitrification rates global N:P ratio well below the true value, and NO_3 deficit twice what is observed.

→ Something is still missing!

Weber and Deutsch [2012]

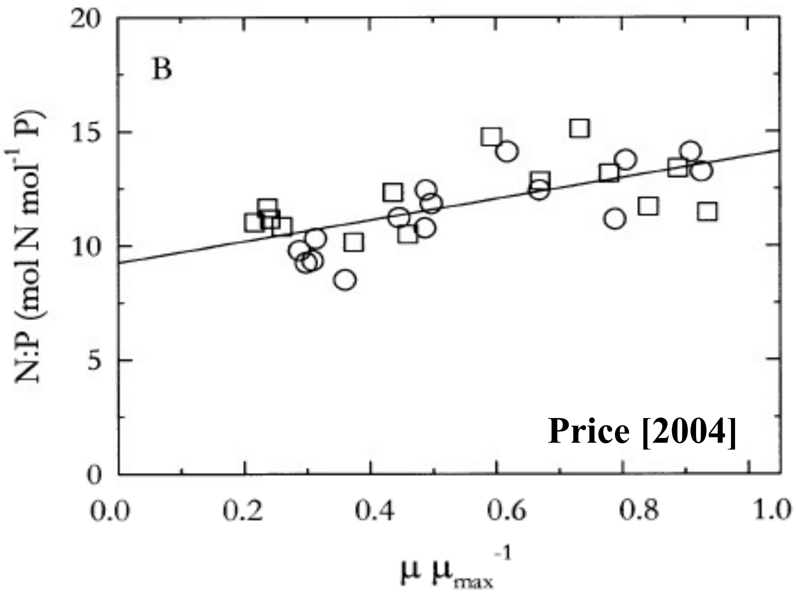
Stoichiometric Diversity



		Mean (SD)	*n*
🟦	Eukaryotes	13.2 (7.03)	53
🟥	Cyanobacteria	22.1 (6.27)	11
	Total	14.9 (7.61)	64

Inter-species (phylogenetic) variations under ‘ideal’ growth conditions.

→ Evolution

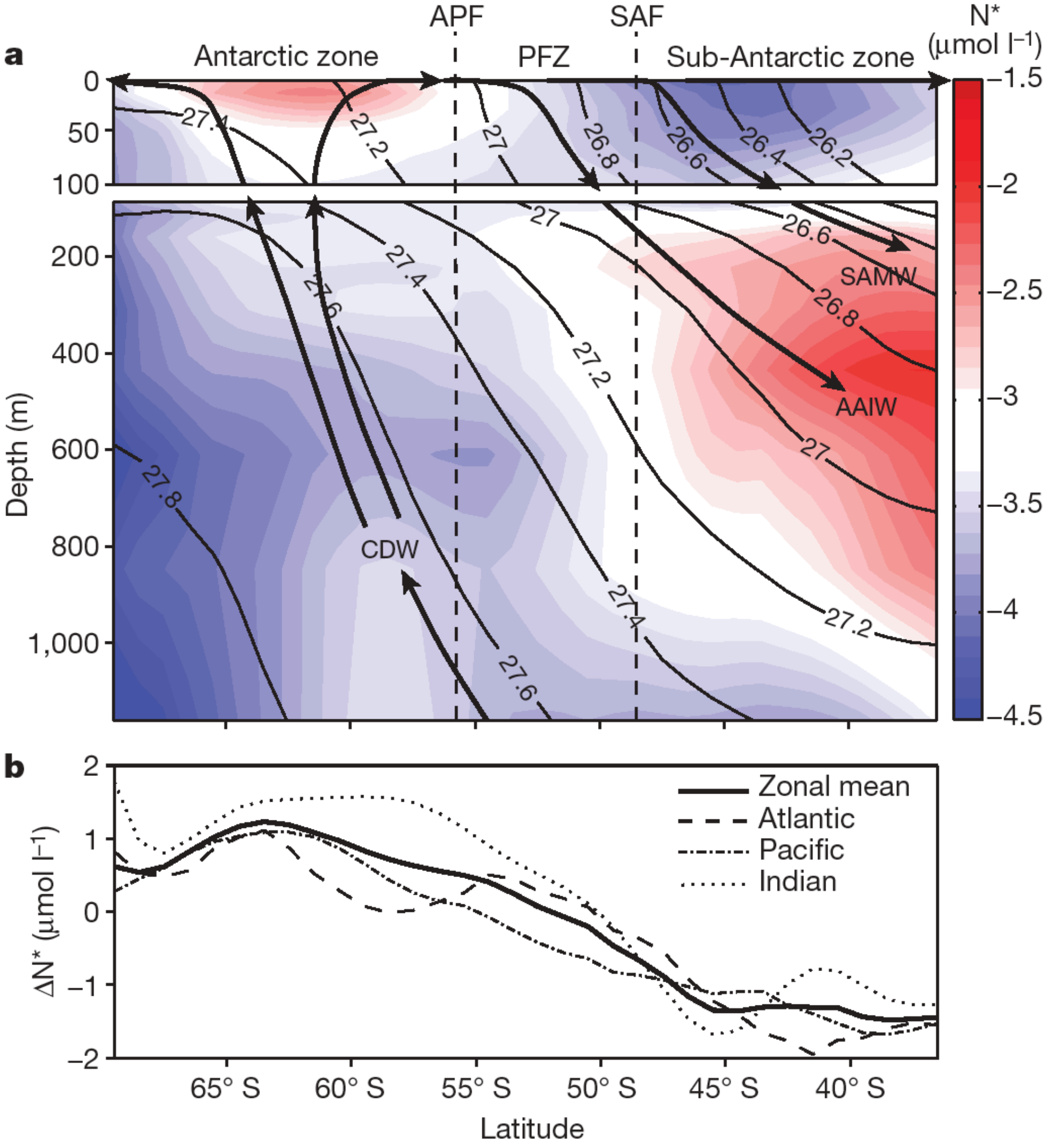


Price [2004]

Intra-species (phenotypic) variations under different environmental conditions.

→ Acclimation

Observed N:P Patterns



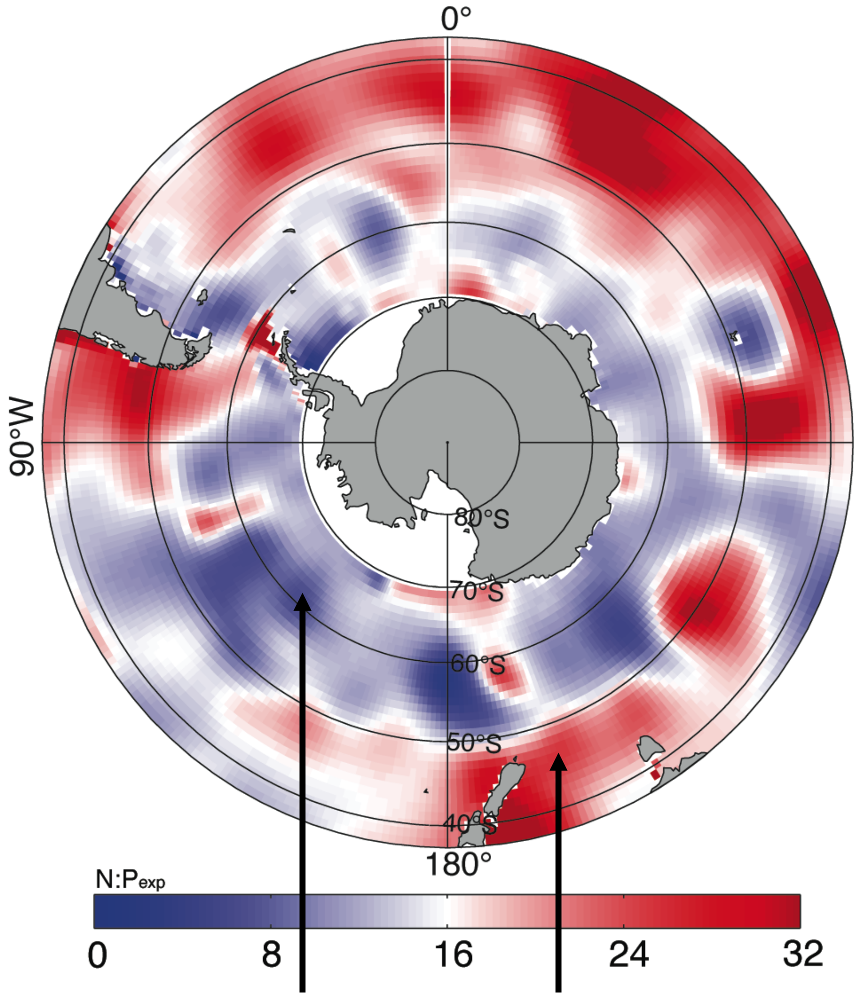
Southern Ocean N* has large-scale gradients along pathways of meridional overturning.

Similar patterns observed independently in all basins → structure is robust.

Suggests low N:P export in Antarctic Zone and high N:P export in Subantarctic.

Weber and Deutsch [2010]
Nature

Diagnosing N:P export



Antarctic:
Low N:P
Export

Subantarctic:
High N:P
Export

The actual N:P of plankton estimated by transport convergence of NO_3 and PO_4 independently.

The inferred N:P ratio of export has a large-scale pattern with wide variation (>2x).

Weber and Deutsch [2010]

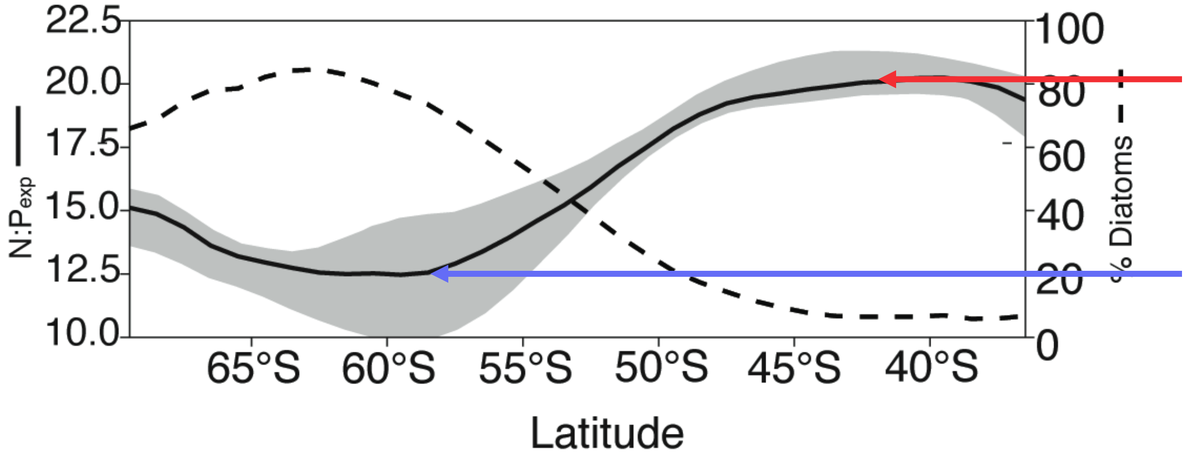
Biogeography and N:P

Correlation of N:P with possible sources of variability

	Zonal ($n = 35$)	1° × 1° ($n = 11{,}408$)	Expected relationship	
			Direction	N/P range
Community composition*	−98	−50	Negative	10–31
Light (mixed layer average)	62	19	Negative	7–41
Summertime growth rate†	86	39	Negative	8–45‡
[Fe]	72	22	Positive	9–14
Temperature	89	38	Positive	20–25

Community composition (% diatoms) diagnosed from Si export fluxes.

$$R_o = -9.6\,\phi_{diat} + 20.4$$

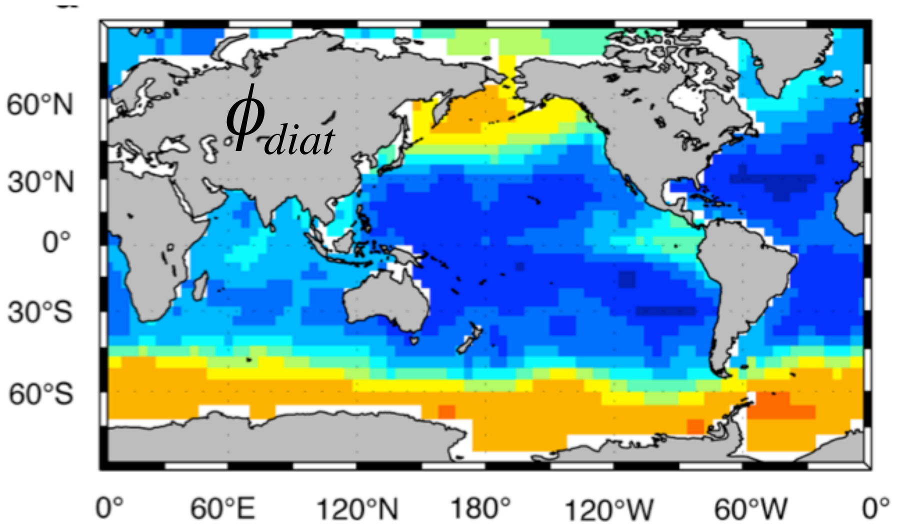


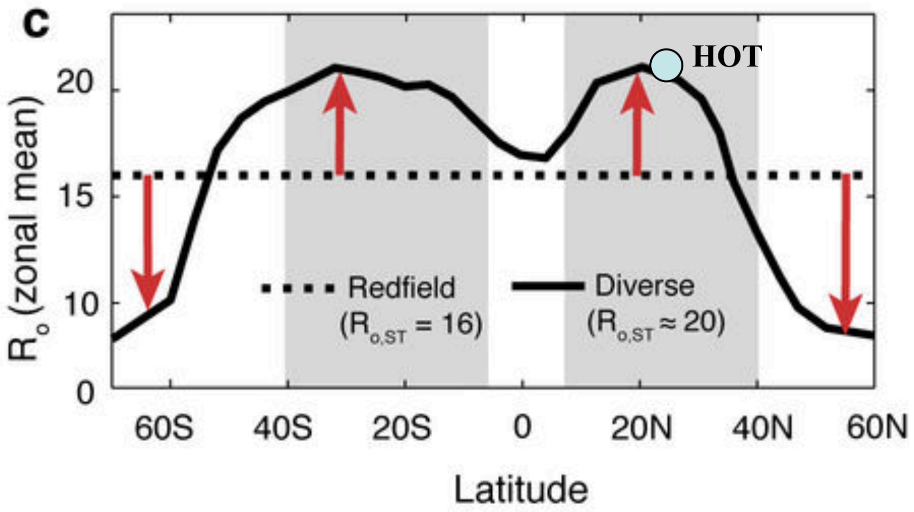
Other Plankton: High N/P

Diatoms: Low N/P

Weber and Deutsch [2010]

Variable Stoichiometry





Extrapolate relationship from Southern Ocean to world:

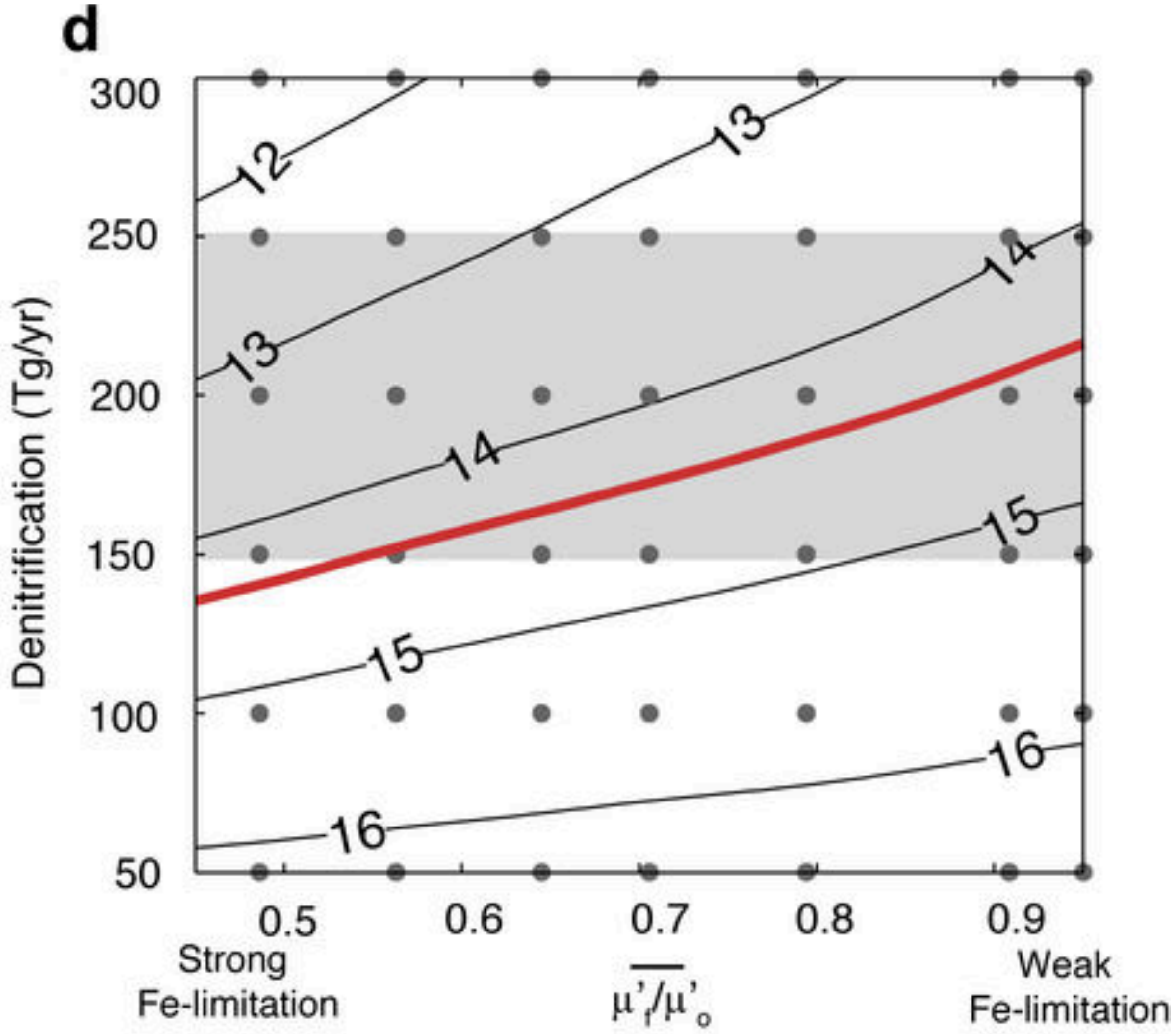
$$R_o = -9.6\,\phi_{diat} + 20.4$$

Constrain global mean export to have a 16:1 ratio

$$\frac{\int R_o J_{ex}(P)\,dA}{\int J_{ex}(P)\,dA} = 16$$

Weber and Deutsch [2012],
c.f. Martiny et al. [2013]

Diversity sustains N

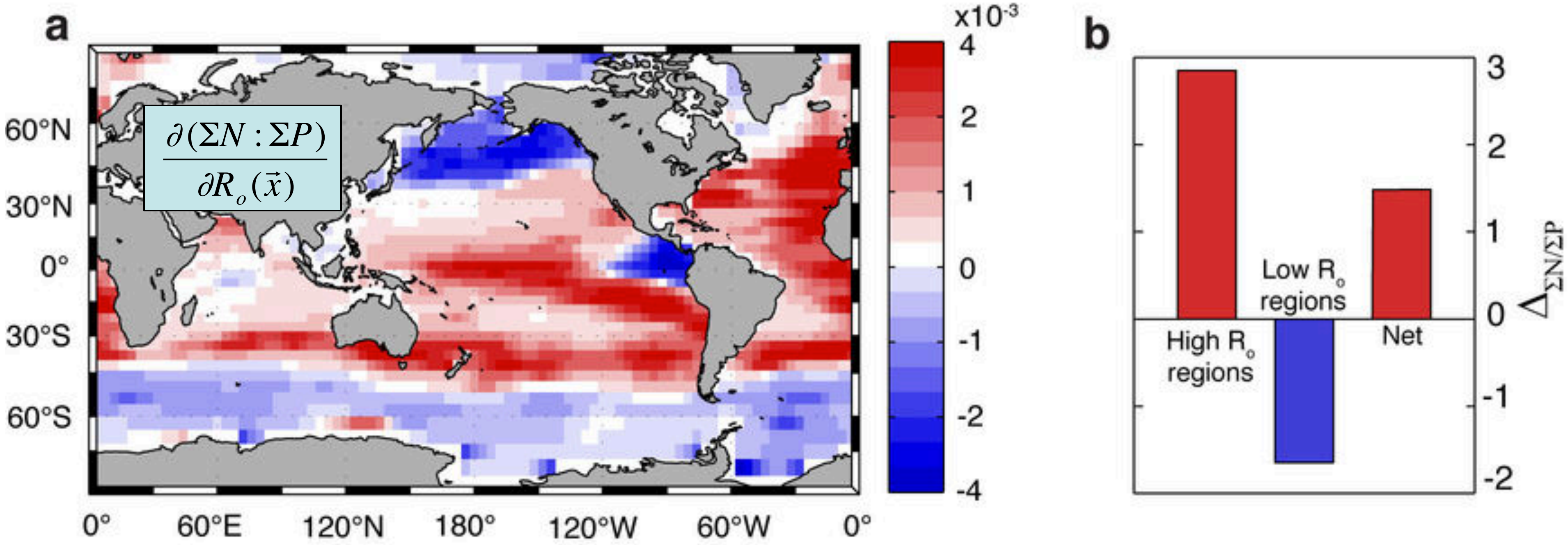


Large-scale diversity of plankton N:P ratios is essential to explain the ocean's ΣN:ΣP ratio.

Strong Fe limitation and/or high denitrification rates still pose a problem.

Weber and Deutsch [2012]

Global Teleconnections



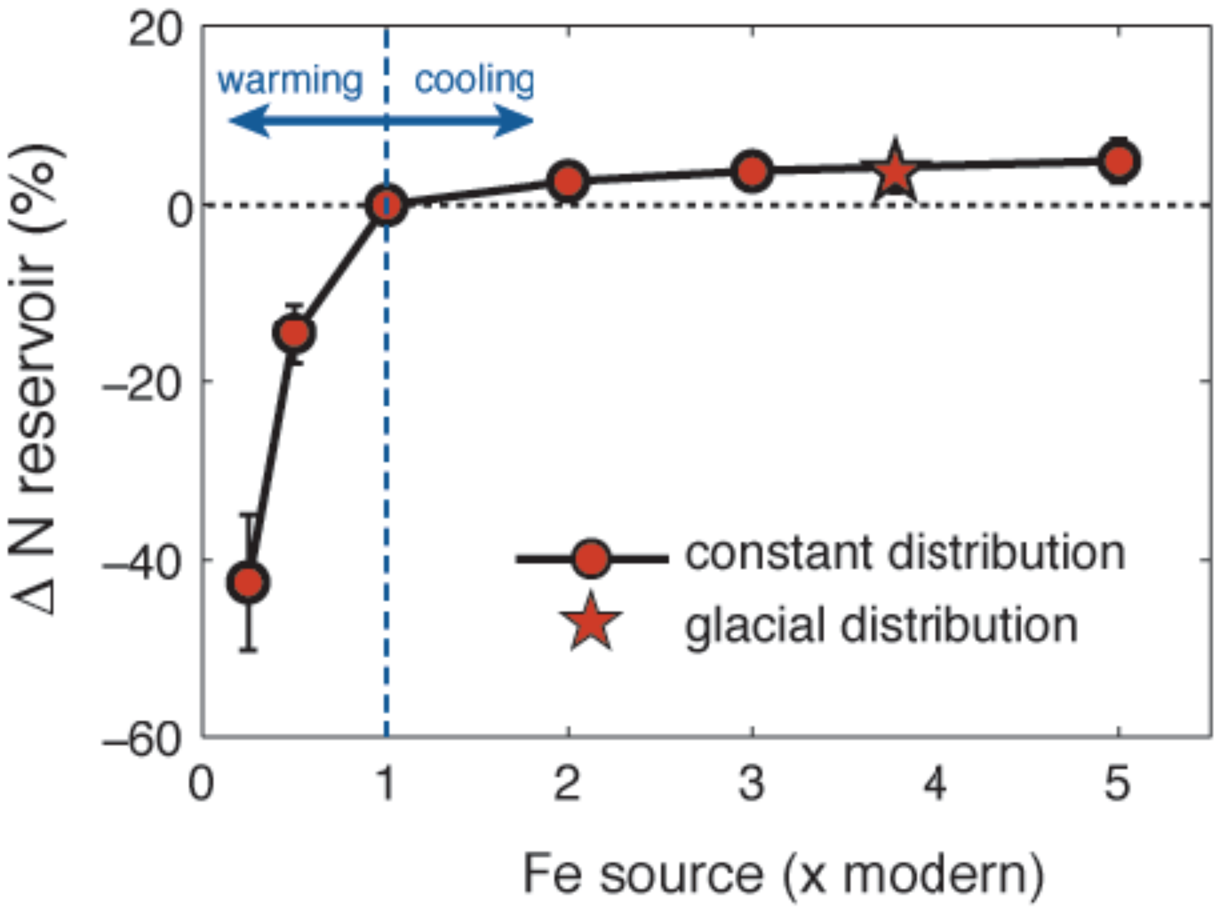
The ecological niche of diazotrophs is determined not only by local competition but also be remote plankton communities.

The influence of these regions must be communicated by ocean circulation.

Weber and Deutsch [2012]

Response to Dust Forcing

Intermediate Fe limitation (Regime 2)



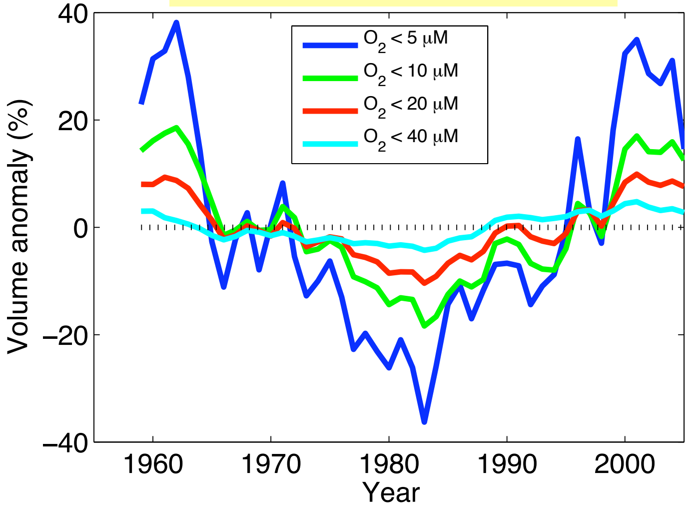
N inventory shows weak response to Fe increase (glacial), but a strong response to Fe decrease (future?).

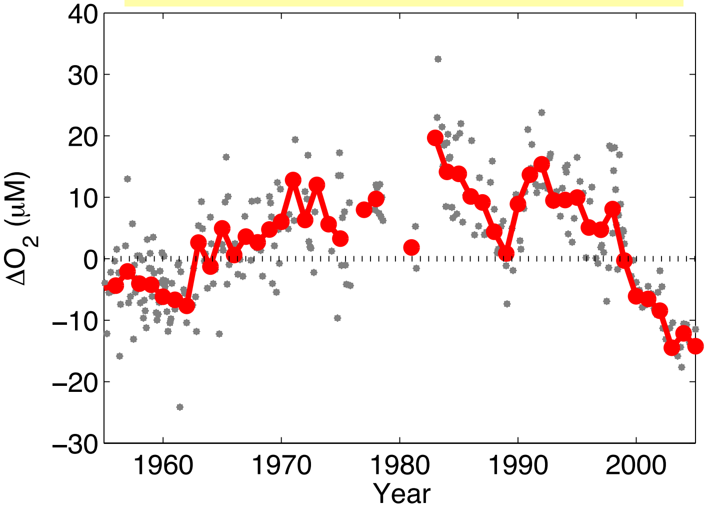
Response to Circulation

Simulations (GCM)

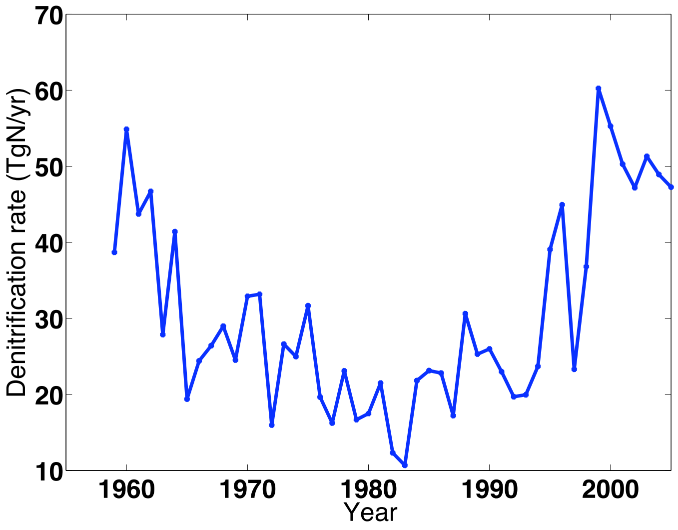
Observations (CalCOFI)

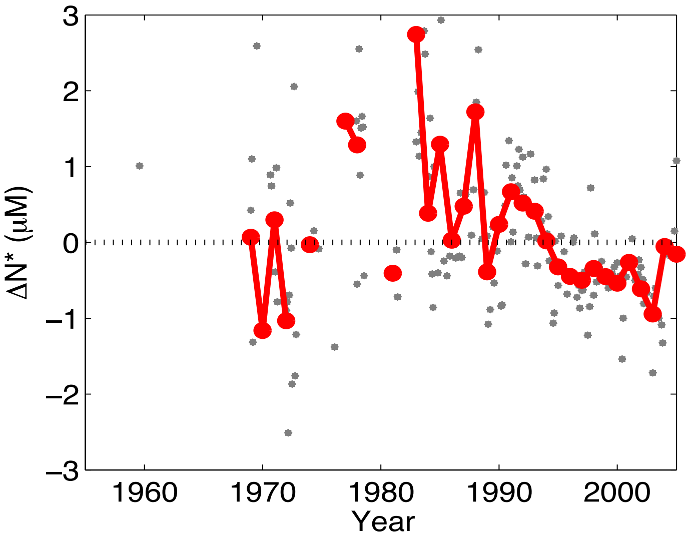
O_2 cycle





N cycle

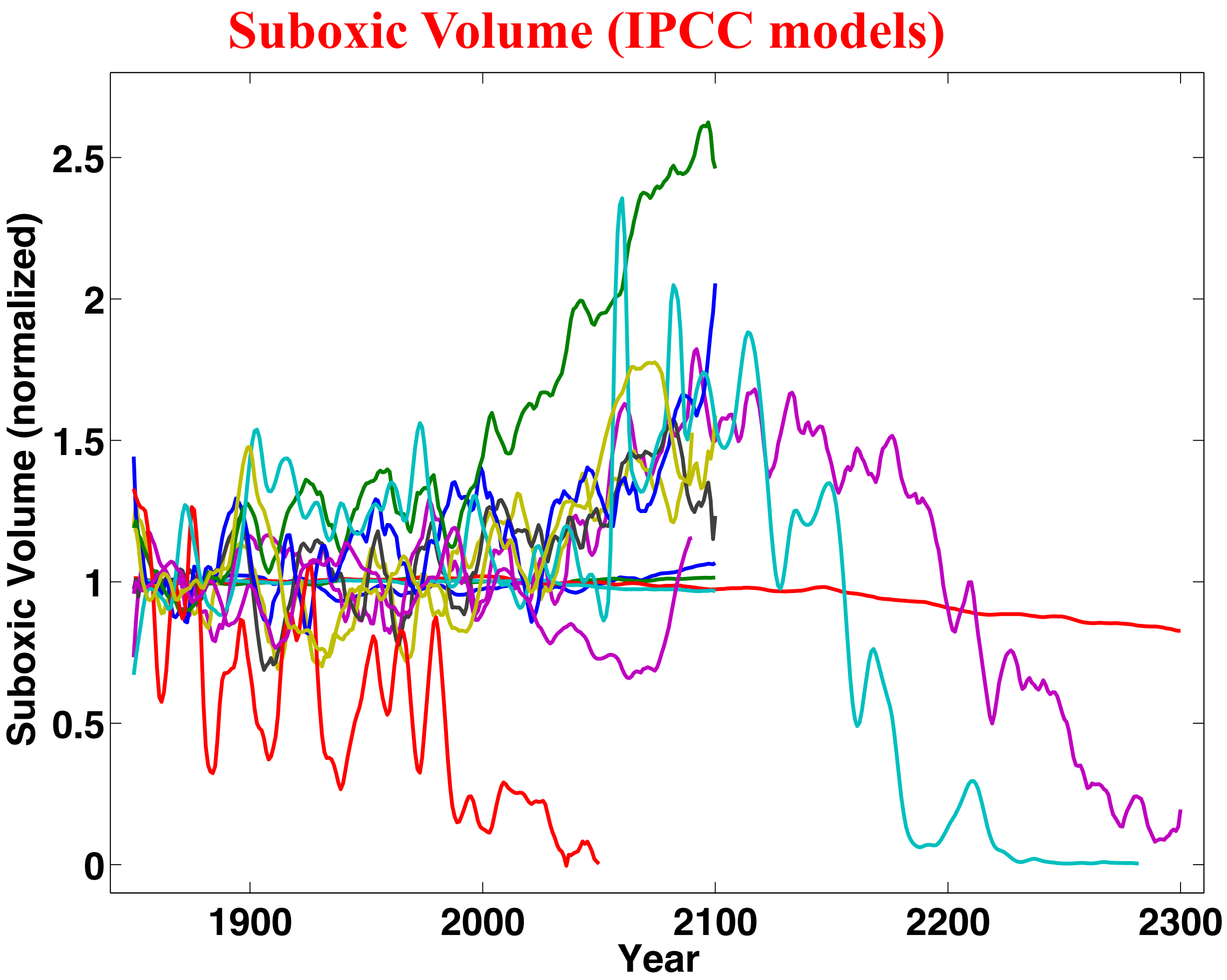




Large decadal variations in simulated anoxic zones explain observed time series in Eastern North Pacific. Driven by climate variability (PDO).

Deutsch et al. [2011]

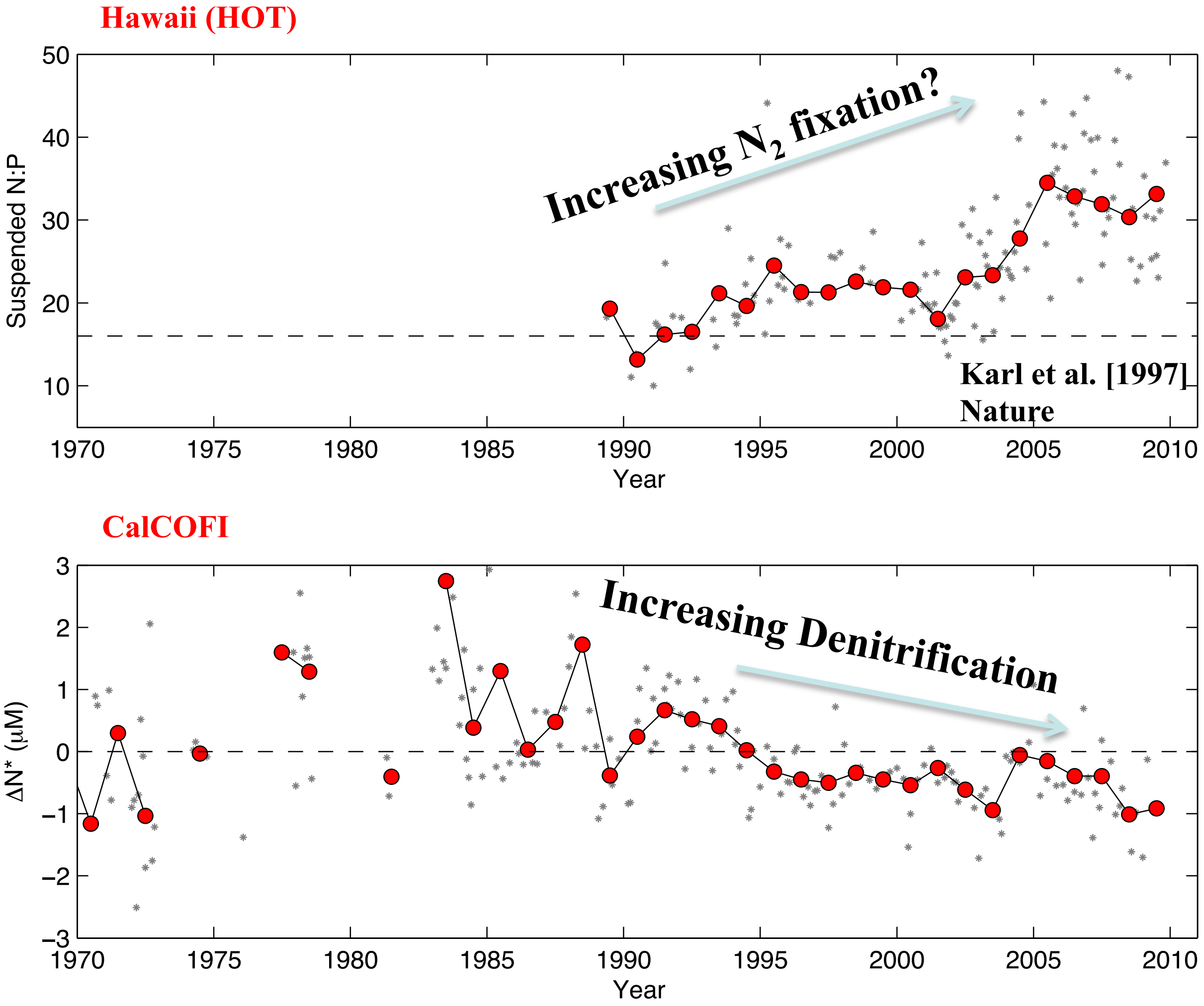
Suboxic Volume Changes



State-of-the-art Earth System Models predict wildly different suboxic zones.

The only agreement is on likelihood of large changes.

Denitrification vs N_2 fixation


Hawaii (HOT)

CalCOFI

Karl et al. [1997]
Nature

1) **Coincidence?**

2) **Evidence of feedback?**

3) **A common forcing?**

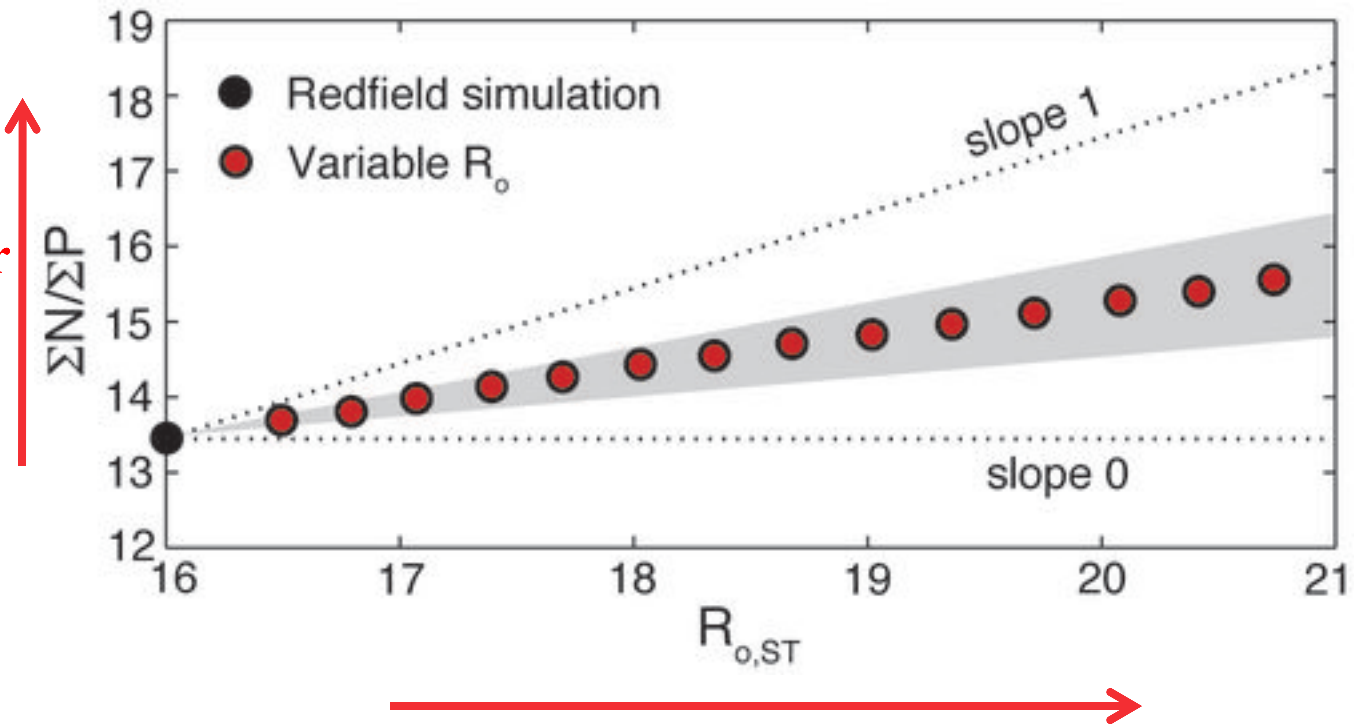
Deutsch and Weber [2012]
Annual Reviews of Marine Science

Conclusions

- Limits to N fixation are scale-dependent: local Fe limitation, but basin P limitation.
- Plankton stoichiometric diversity is important to the regulatory feedbacks in N cycle. So are the pathways of nutrient supply.
- Long-term N cycle appears to be approximately balanced, but climate-forced changes in N budget and N limitation appear strong on decadal time scales.

Sensitivity to Diversity

Increasing N reservoir

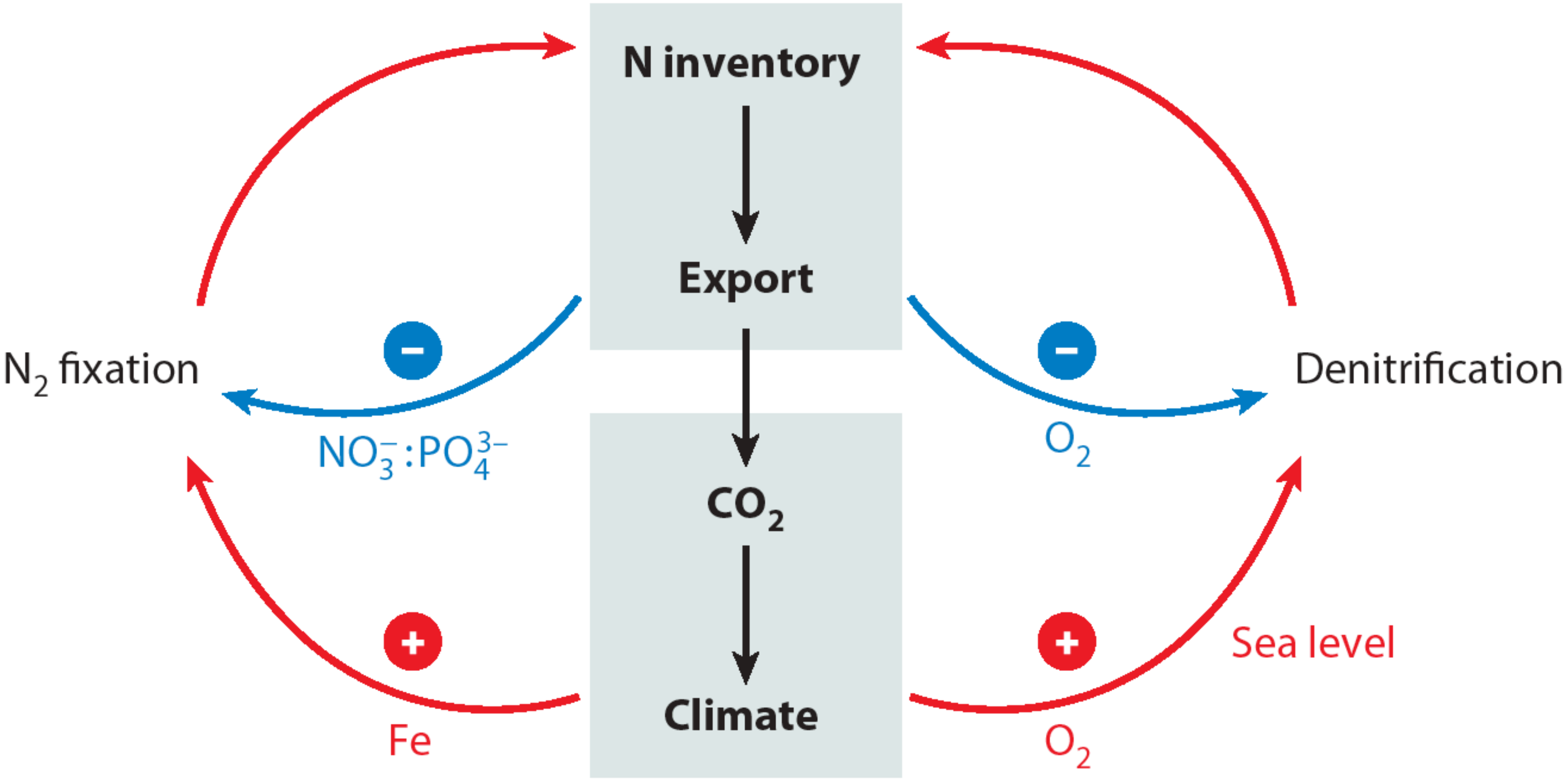


Increasing diversity of plankton N:P

Increasing diversity of plankton N:P raises the ocean ΣN:ΣP ratio, but only by <50% of $R_{o,ST}$

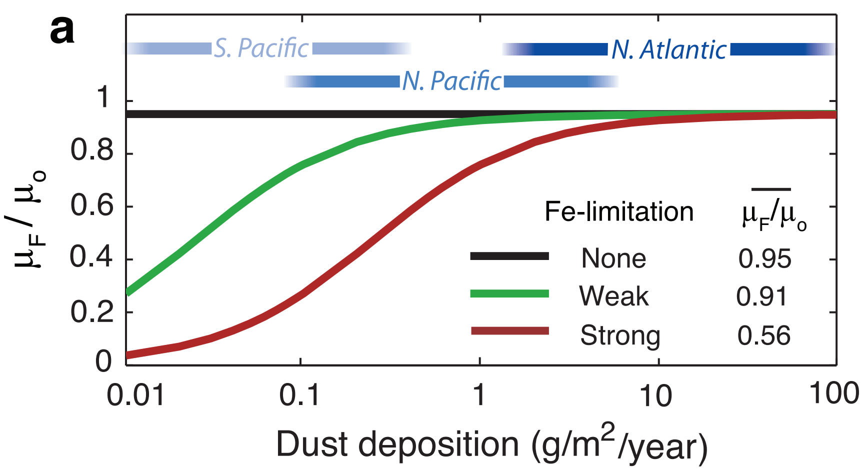
Nitrogen Cycle

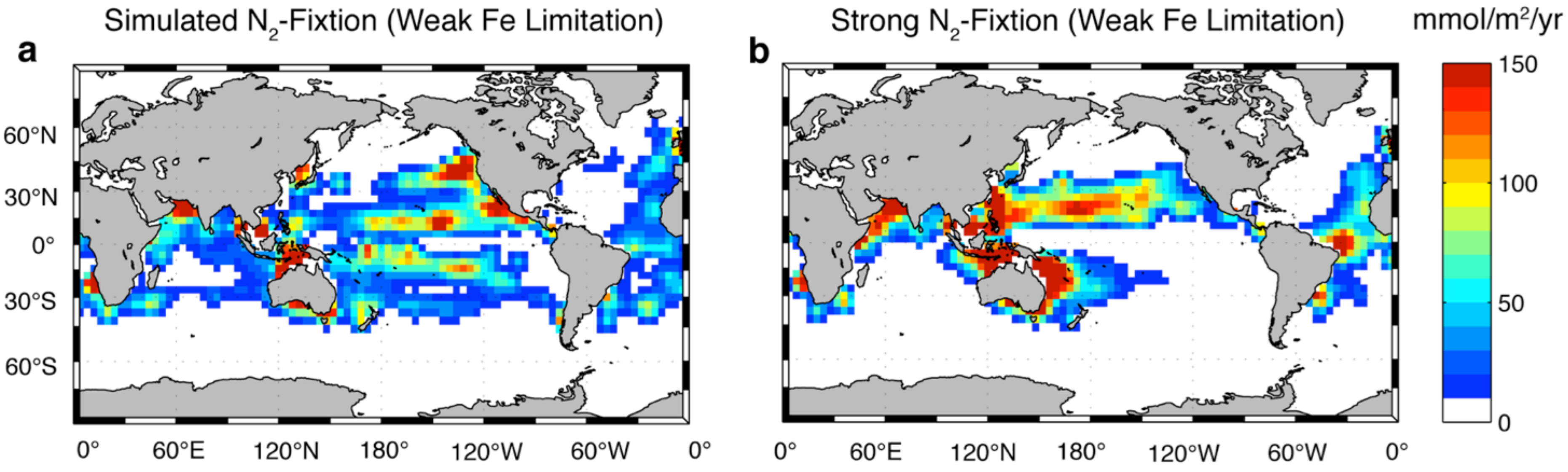
Biological homeostat or Climate amplifier?



Deutsch and Weber [2012]
Annual Reviews of Marine Science

N_2 fixation – Fe limitation





Hypoxic sensitivity

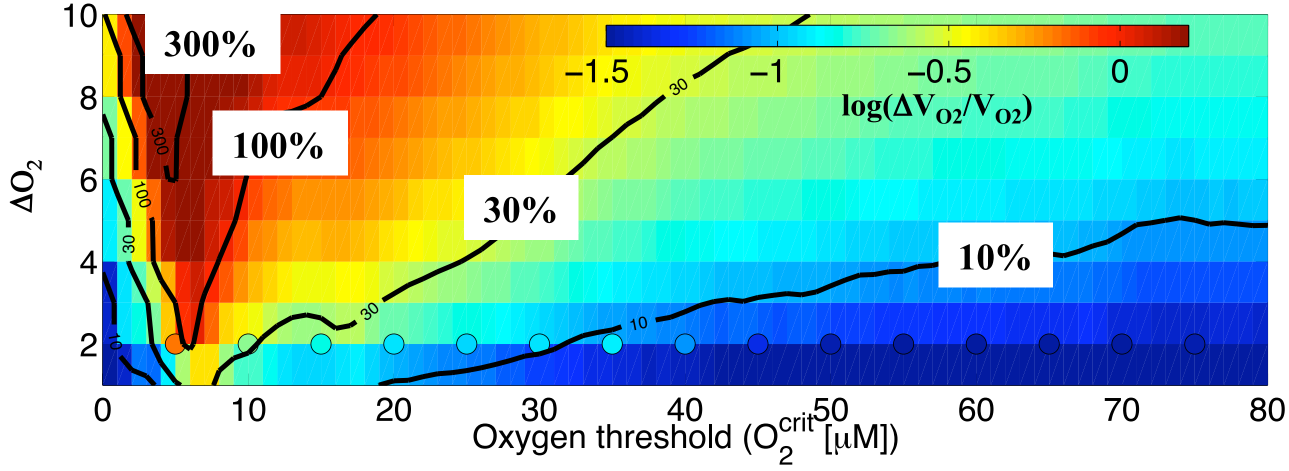
$$\Delta V_{O2} = \frac{\partial V_{O2}}{\partial O_2^{crit}} \overline{\Delta O}_2$$

Change in volume (predicted)

Derivative of histogram (observed)

Global O_2 anomaly (assumed)

Normalized change in hypoxic volume ($\Delta V_{O2}/V_{O2}$)



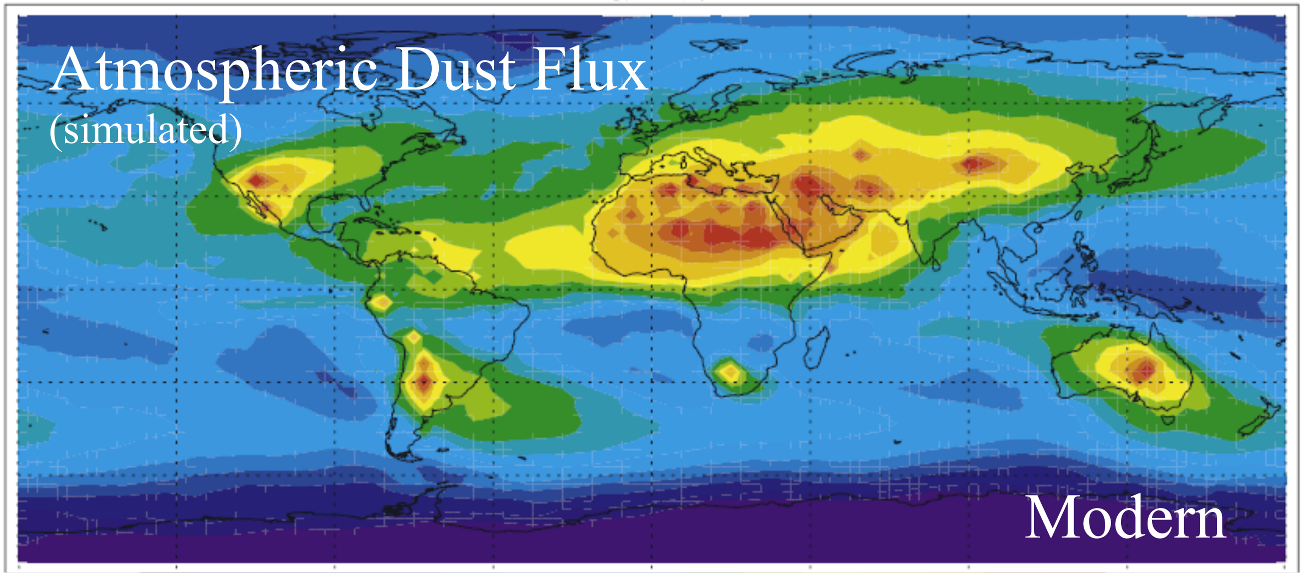
The sensitivity of hypoxic volumes can be predicted from data alone.

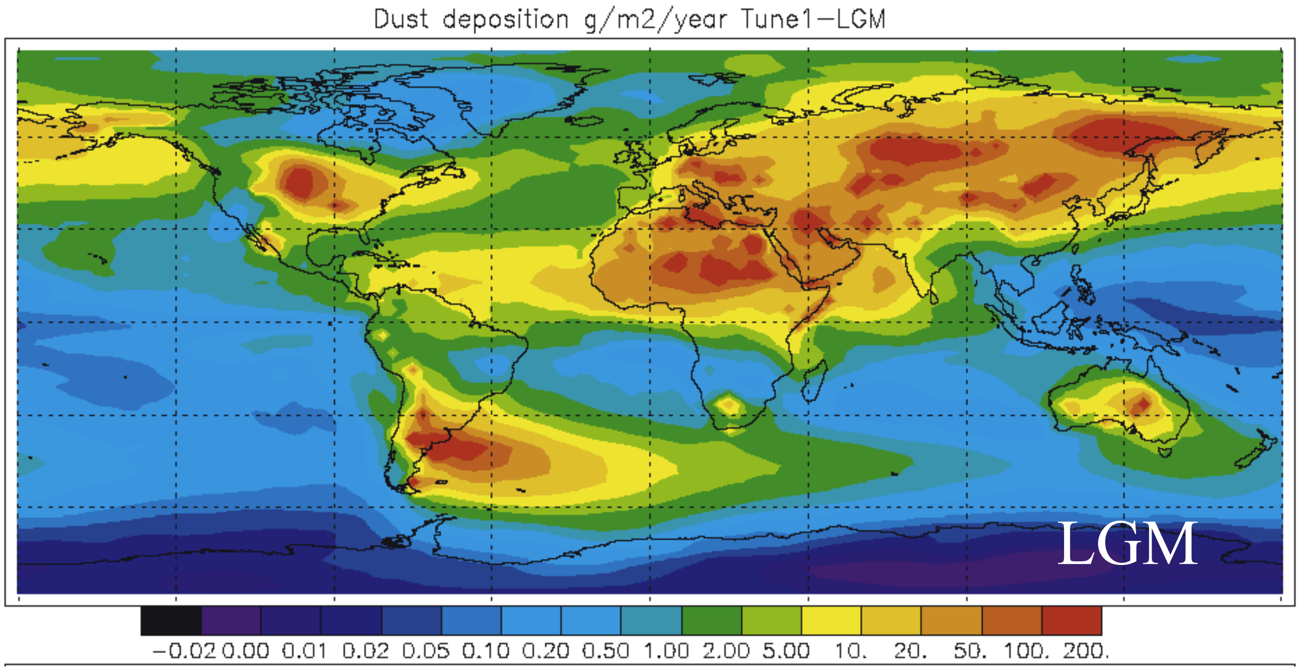
It increases rapidly with decreasing O_2 threshold.

Model simulations (dots) consistent with this simple prediction.

Deutsch et al. [2011]
Science

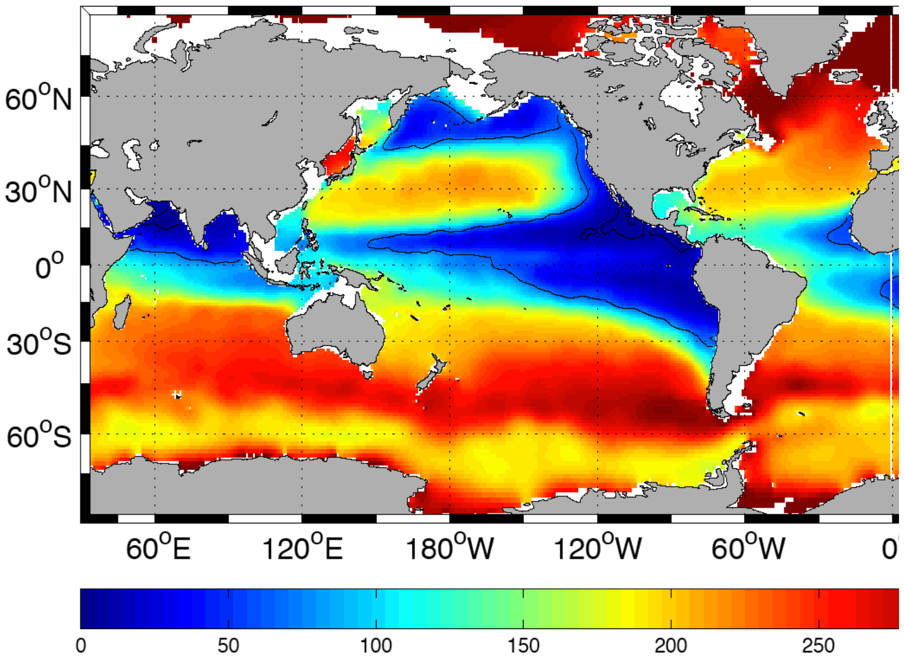
Climate forcing: Fe





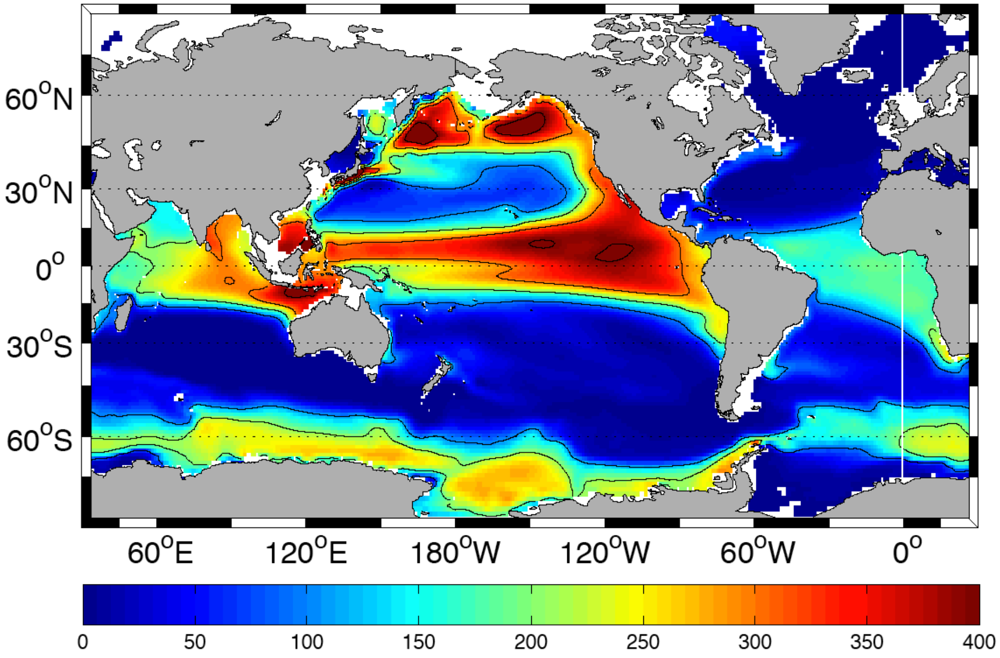
Climate forcing: O_2

Observed O_2 [μM] @400 m



World Ocean Atlas [2005]

Simulated Ideal Age [yr] @400 m



ECCO Circulation

Warming ocean may increase anoxia.
Solubility decreases, Stratification increases.

Conclusions

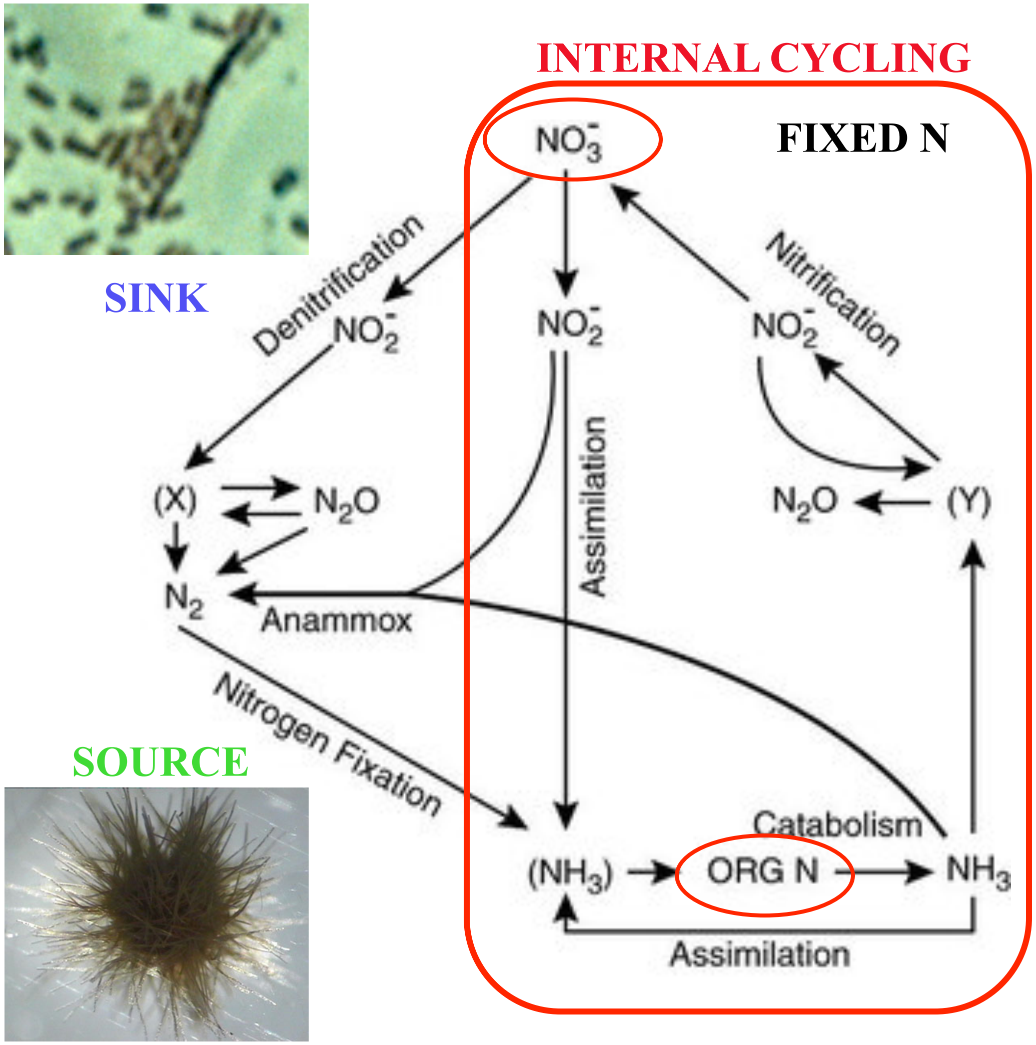
- Variation of plankton stoichiometry across biomes is essential to maintaining the N inventory of the ocean.

- Ocean circulation damps (but does not erase) the effect of metabolic diversity by communicating its effects over large scales. N_2 fixing plankton “feel” the mean.

- Subtle variations in climate yield large fluctuations in denitrification and provide a useful test case for the strength of N cycle feedbacks on decadal time scales.

- The oceanic nutrient ratio (ΣN:ΣP) is a powerful constraint on biogeochemical models.

N vs P cycles



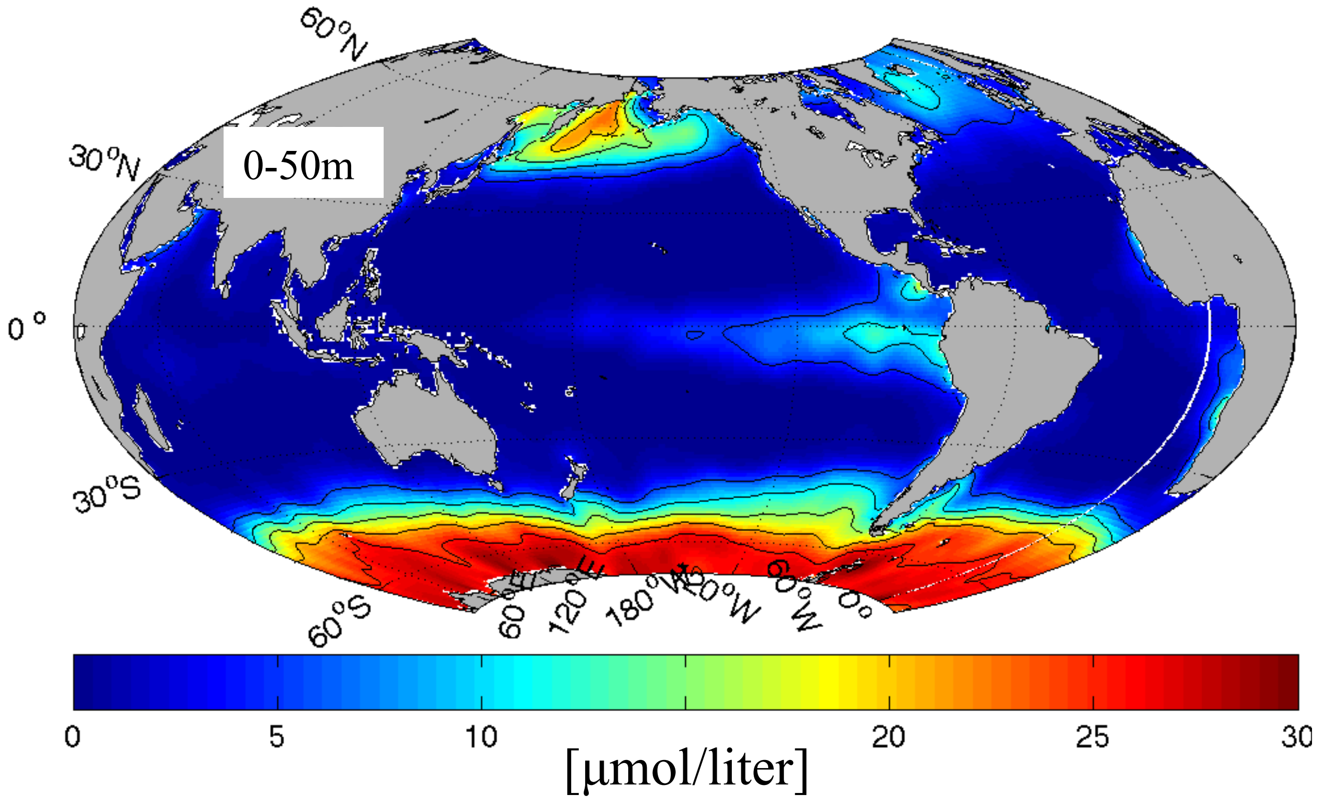
P reservoir (ΣP): geologically controlled slow turnover (~50ky).

N reservoir (ΣN): biologically controlled fast turnover (~2ky).

ΣN:ΣP not directly reflected in any major input/output.

Nitrogen and the Carbon Pump

Annual mean surface [NO_3^-]



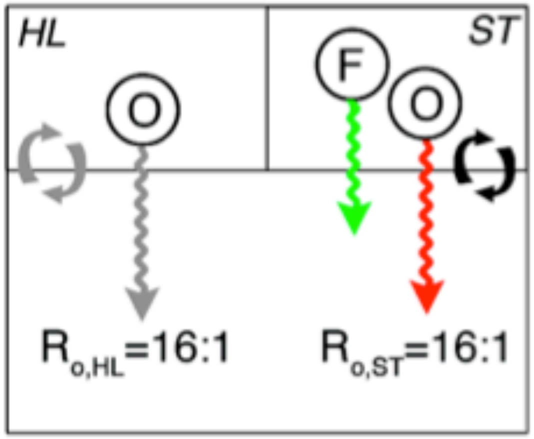
Changes in biological carbon storage can occur via changes in:

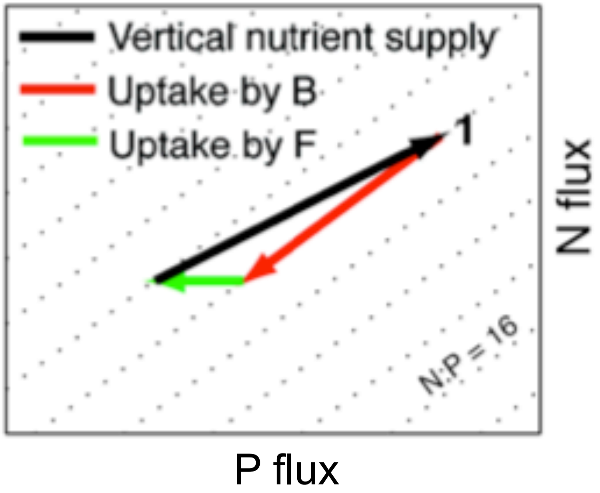
1) Nutrient reservoir (low latitudes)
2) Nutrient utilization (high latitudes)

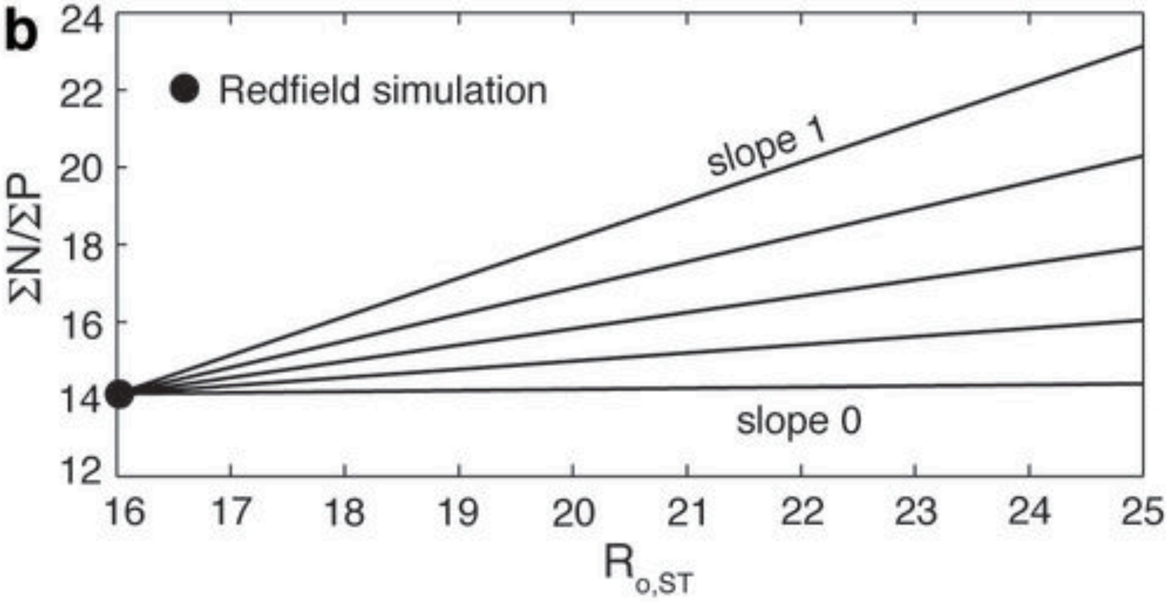
But what regulates the Nitrogen inventory?

The Role of Circulation

1) No lateral circulation, No plankton diversity



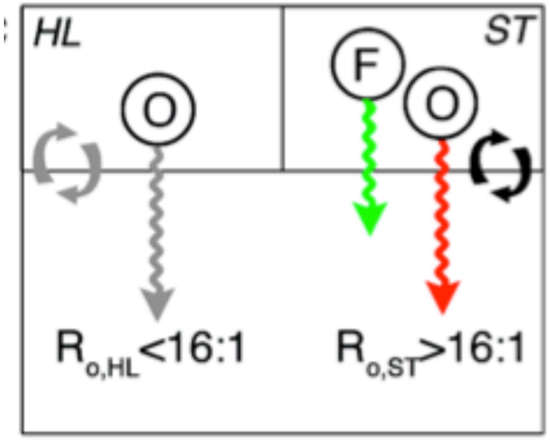


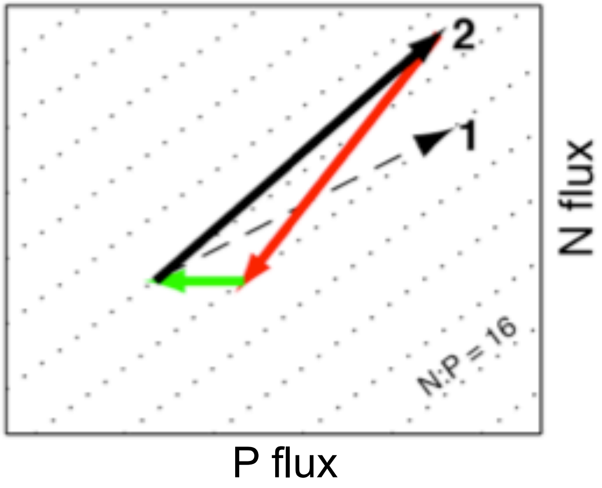


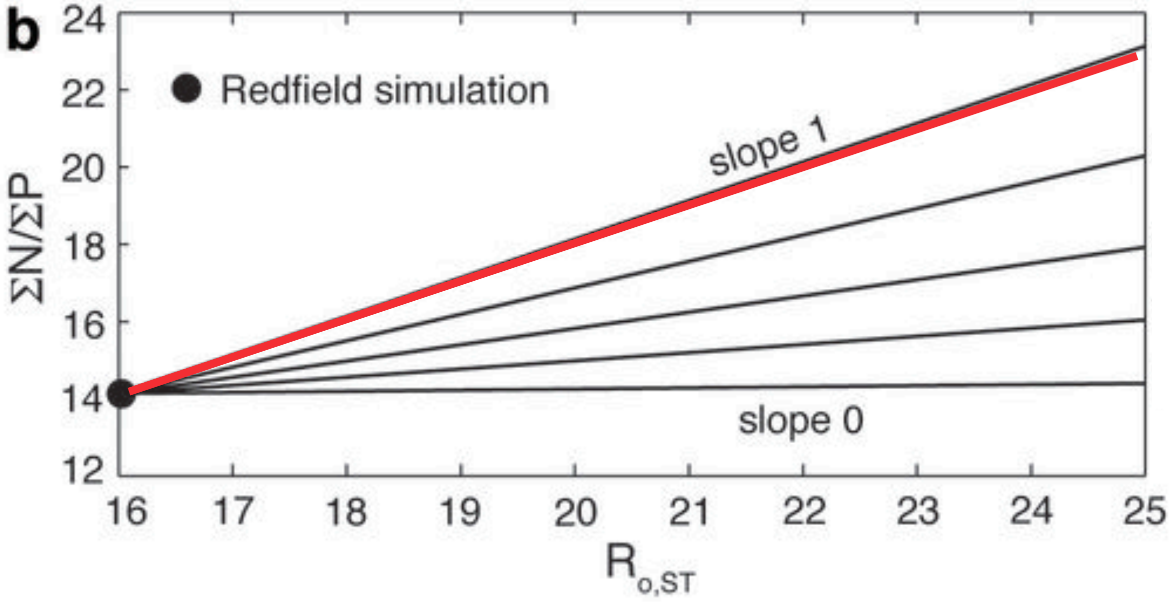
The ocean ΣN:ΣP falls below Ro, due to the need to balance denitrification with N_2 fixation.

The Role of Circulation

2) No lateral circulation, Plankton N:P diversity





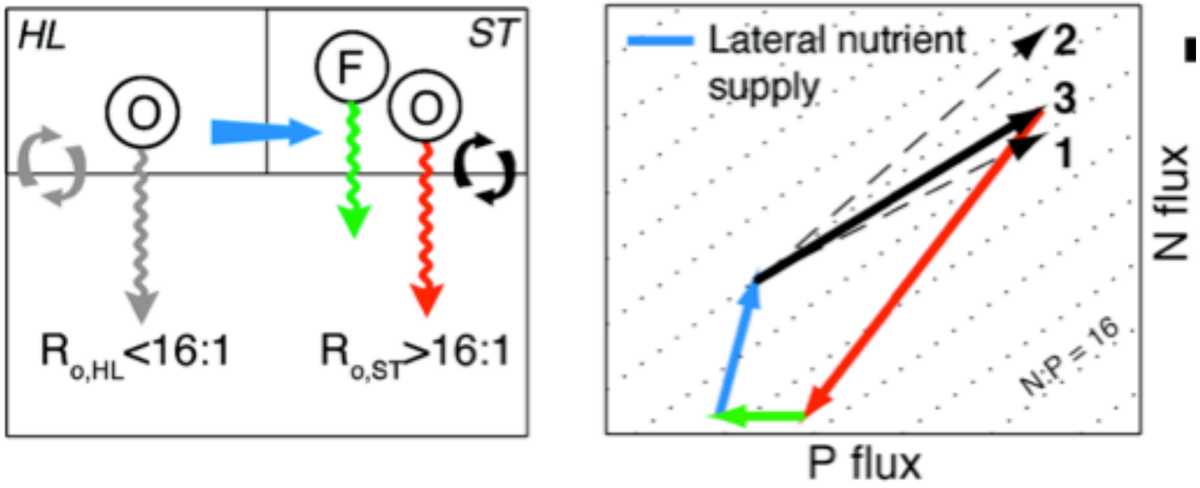


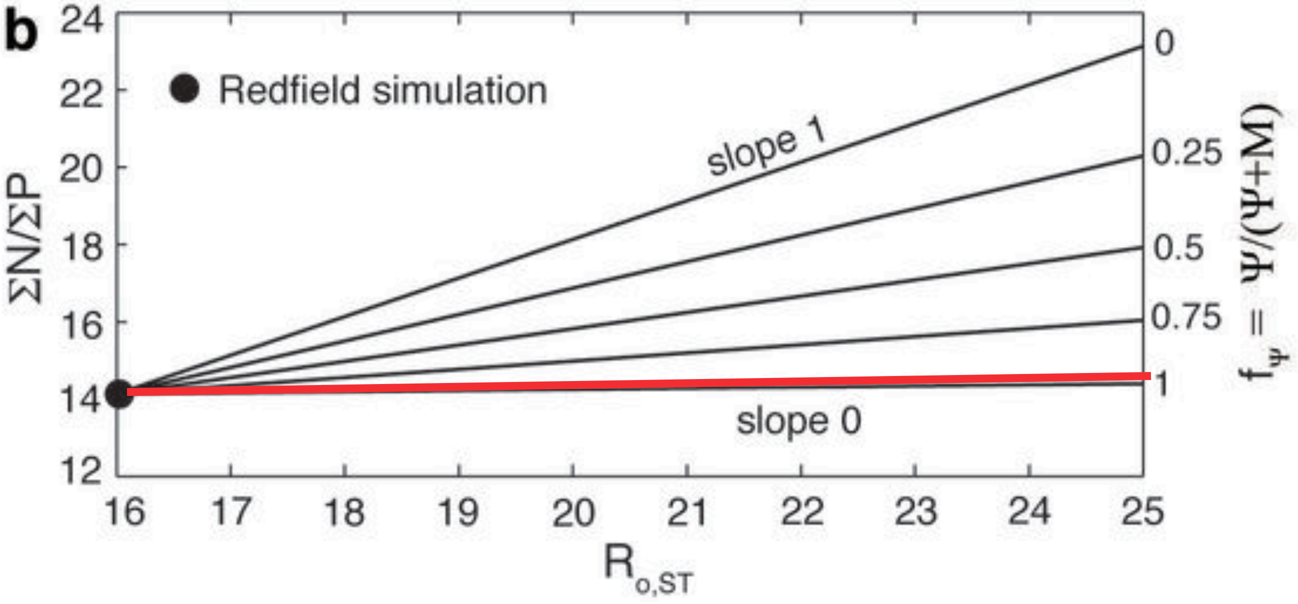
As the N:P of subtropical plankton increases, the ocean ΣN:ΣP rises by the same amount.

The diazotroph niche is determined only by the deep nutrient supply and local competition.

The Role of Circulation

3) Lateral circulation, Plankton N:P diversity

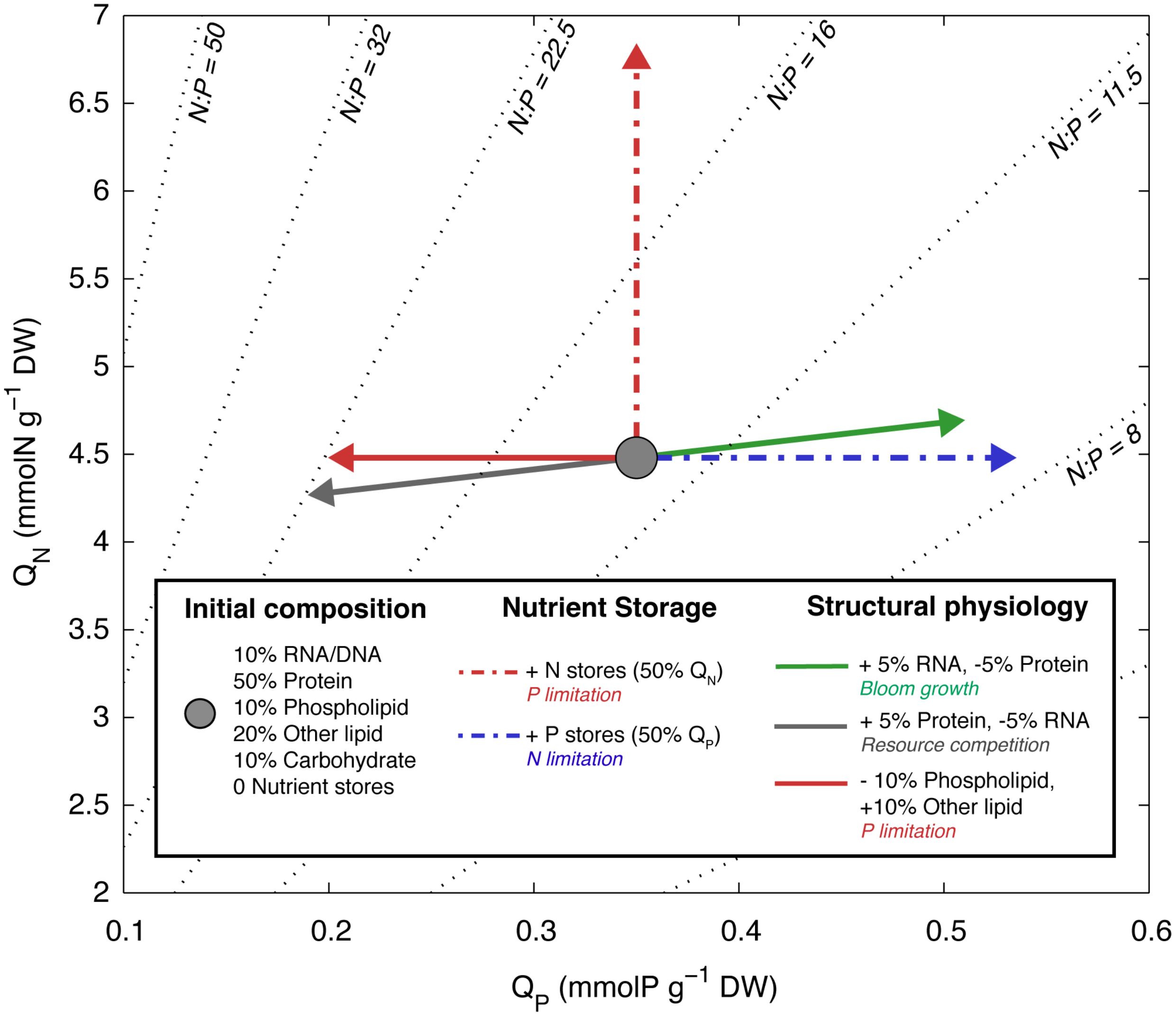




When lateral circulation is strong, diazotrophs "feel" the N:P demand of remote communities.

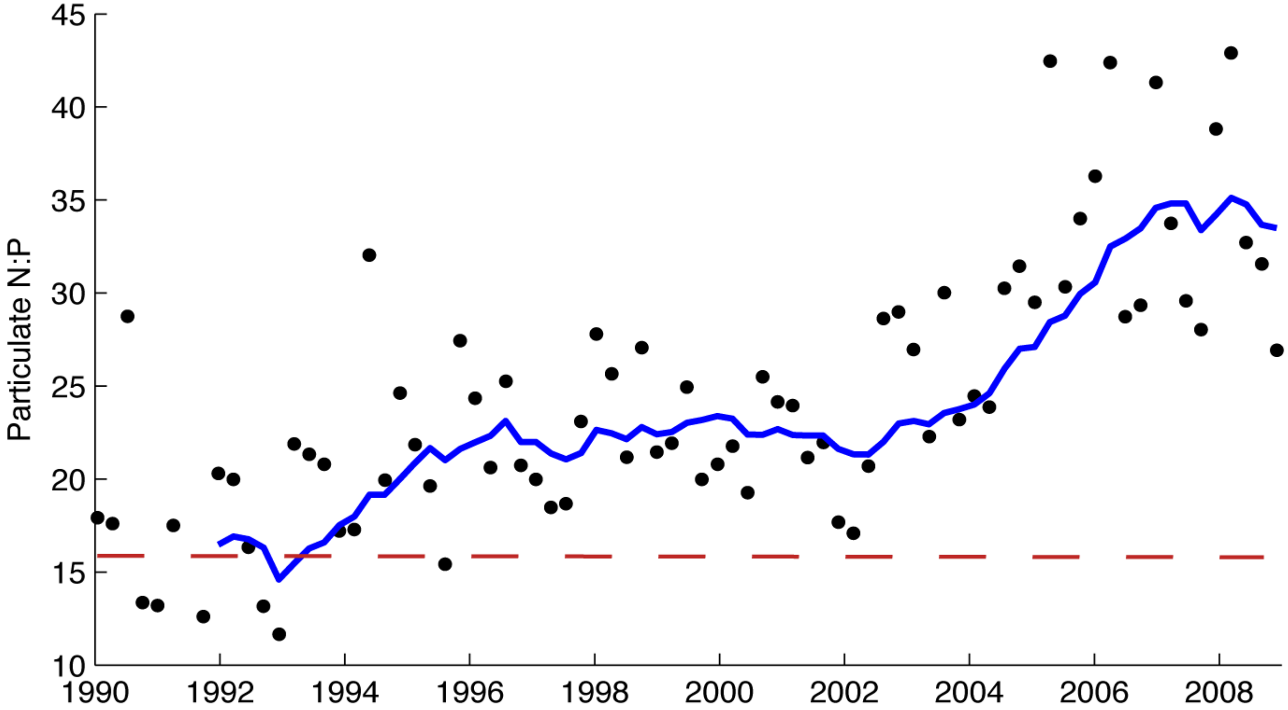
In the limit, ΣN:ΣP is independent of plankton diversity.

Sources of Variability



Low Latitude N/P

Hawaii Ocean Time-series



Sensitivity: diatom