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IAEA
International Atomic Energy Agency

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2 - 10 November 2009

Marine Mosaics: Emerging Patterns of Nitrogen Fixation in the Oceans

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USC
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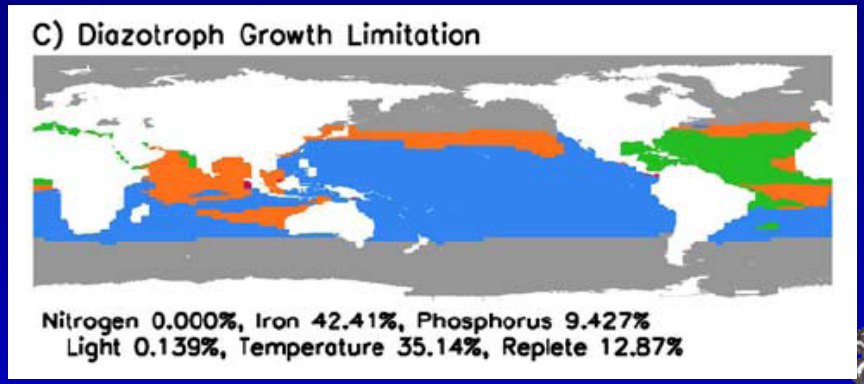
Marine Mosaics: Emerging Patterns of Nitrogen Fixation in the Oceans

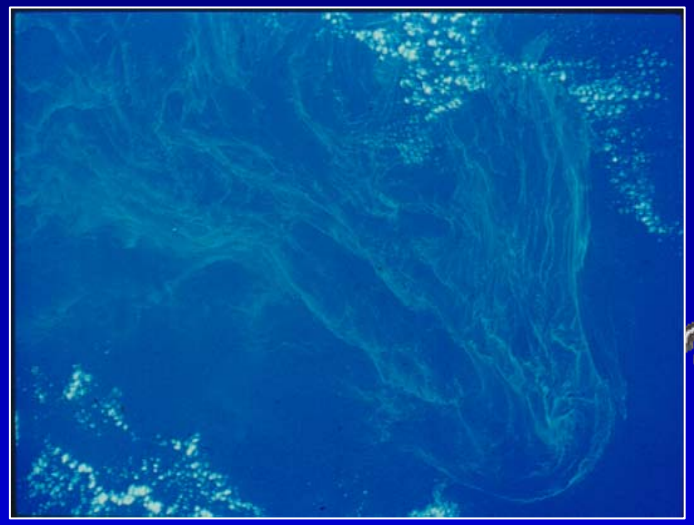


Douglas G. Capone
University of Southern California

With special thanks to Eric Webb & Jill Sohm

What I will cover

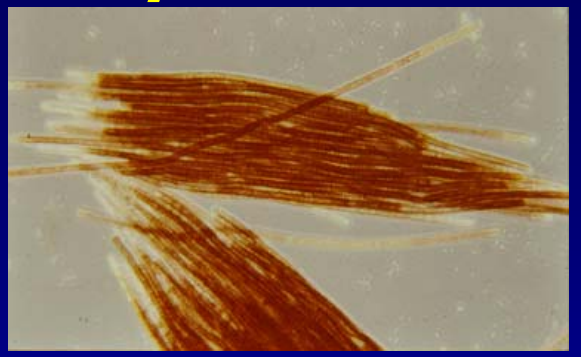
- *Some background*
  - *Diazotrophic groups*
  - *Historical timeline*
- *Emergent interbasin distribution patterns*
  - *Diazotrophs and N_2 fixation*
- *Nutrient distributions/ controls & forcings*
- *Diagnostics for limitation/ stress*
- *Spatial patterns of geochemically inferred N_2 fixation*



Space Shuttle picture of a*Trichodesmium* bloom in the Capricorn Channel

➢ Potential Human/ Climate change impacts

Functional Groups of Marine Diazotrophs (adapted from Falcowski)



- ***Filamentous/ non-heterocycstous***
  - ***Trichodesmium*** **and close relatives**
- ***Diazotrophic diatom associations*** **- DDAs**
  - ***Richelia/ Hemiaulus- (het 1,2,3)***
- **Coccoid cyanobacteria**
  - **Groups a,b,c (Waterbury)**

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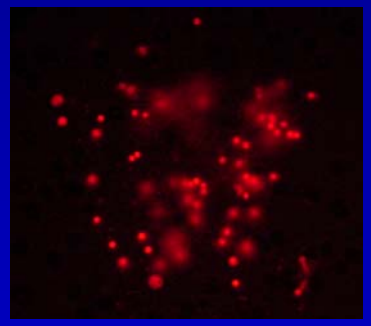
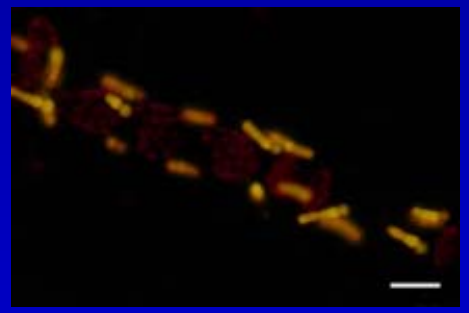
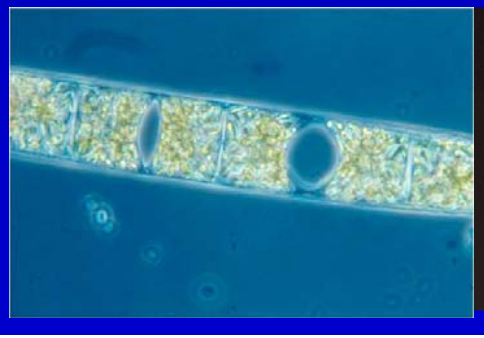
- **Bacterioplankton-**
  - **α & γ proteobacteria**
- **Other sources**
  - **Archaea, deep sea**



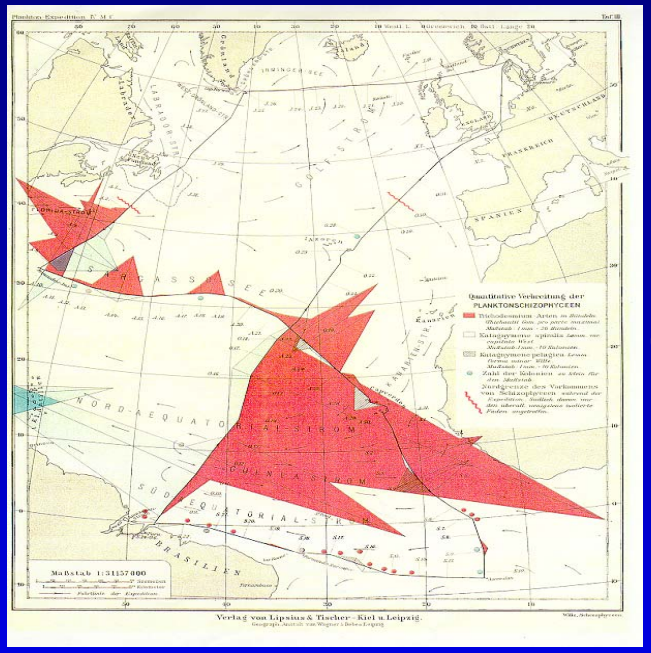


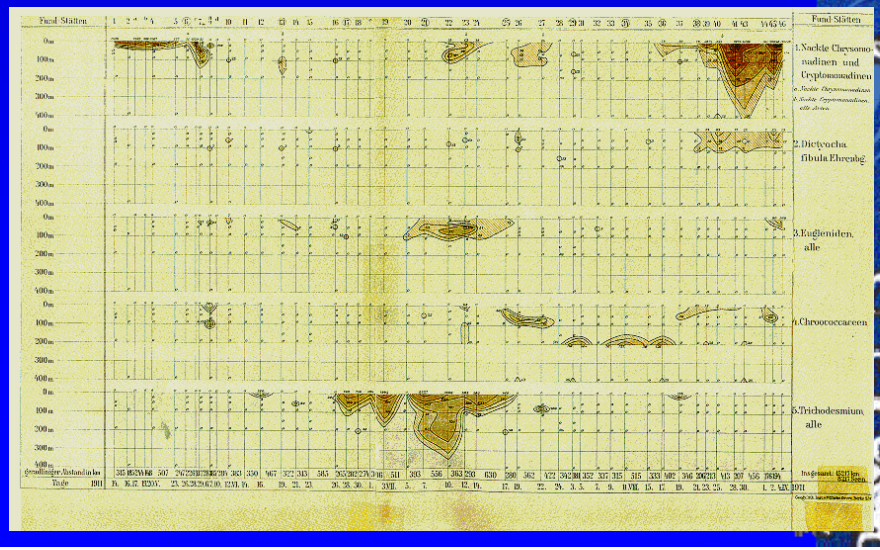


Historical Timeline

- Late 1800-1970s
  - Early phycological observations
- 60's - $^{15}N_2$ uptake
  - Dugdale et al.
- 70's – C_2H_2 reduction
  - Ranging surveys
  - Limited importance?
    - (Capone & Carpenter 1982)
- Late 80's
  - Geochem re-eval
- Early 2000-
  - Infusion of molec- Zehr

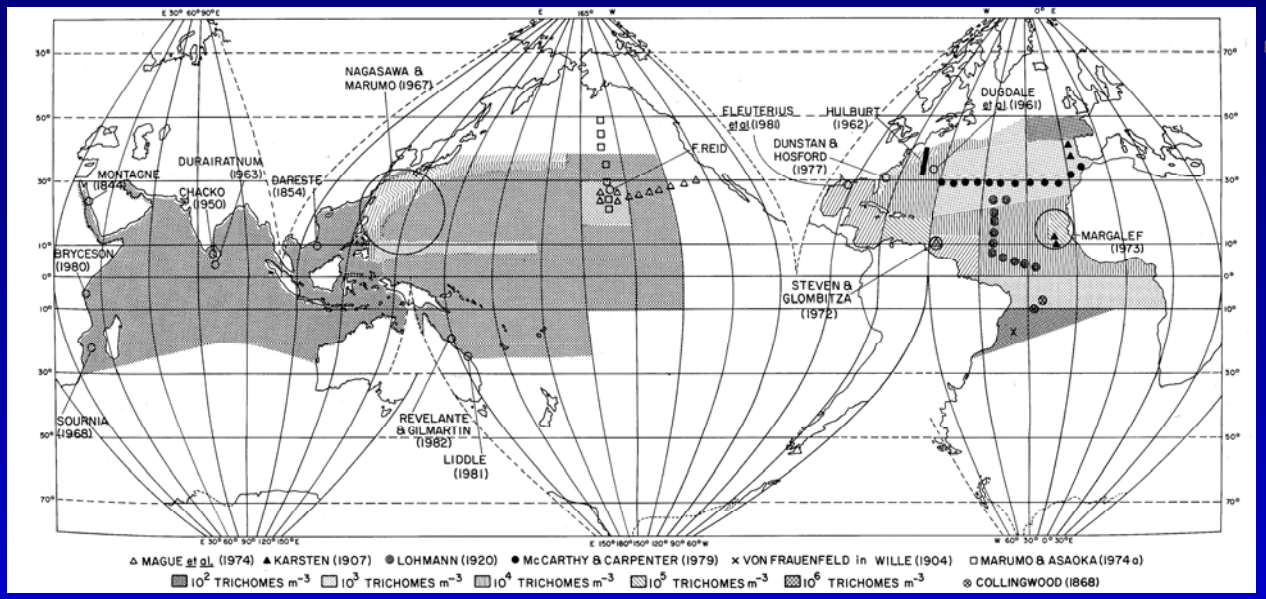
Willie 1904



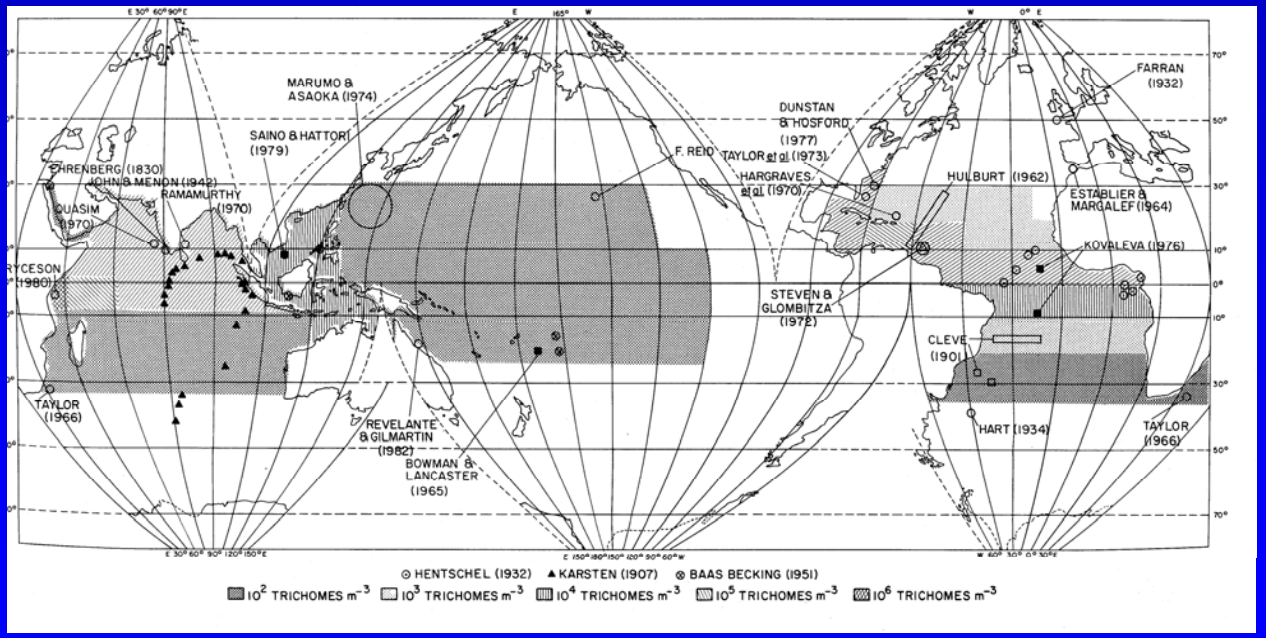


Carpenter 1983- compiled phycological surveys

Northern hemi-sphere summer

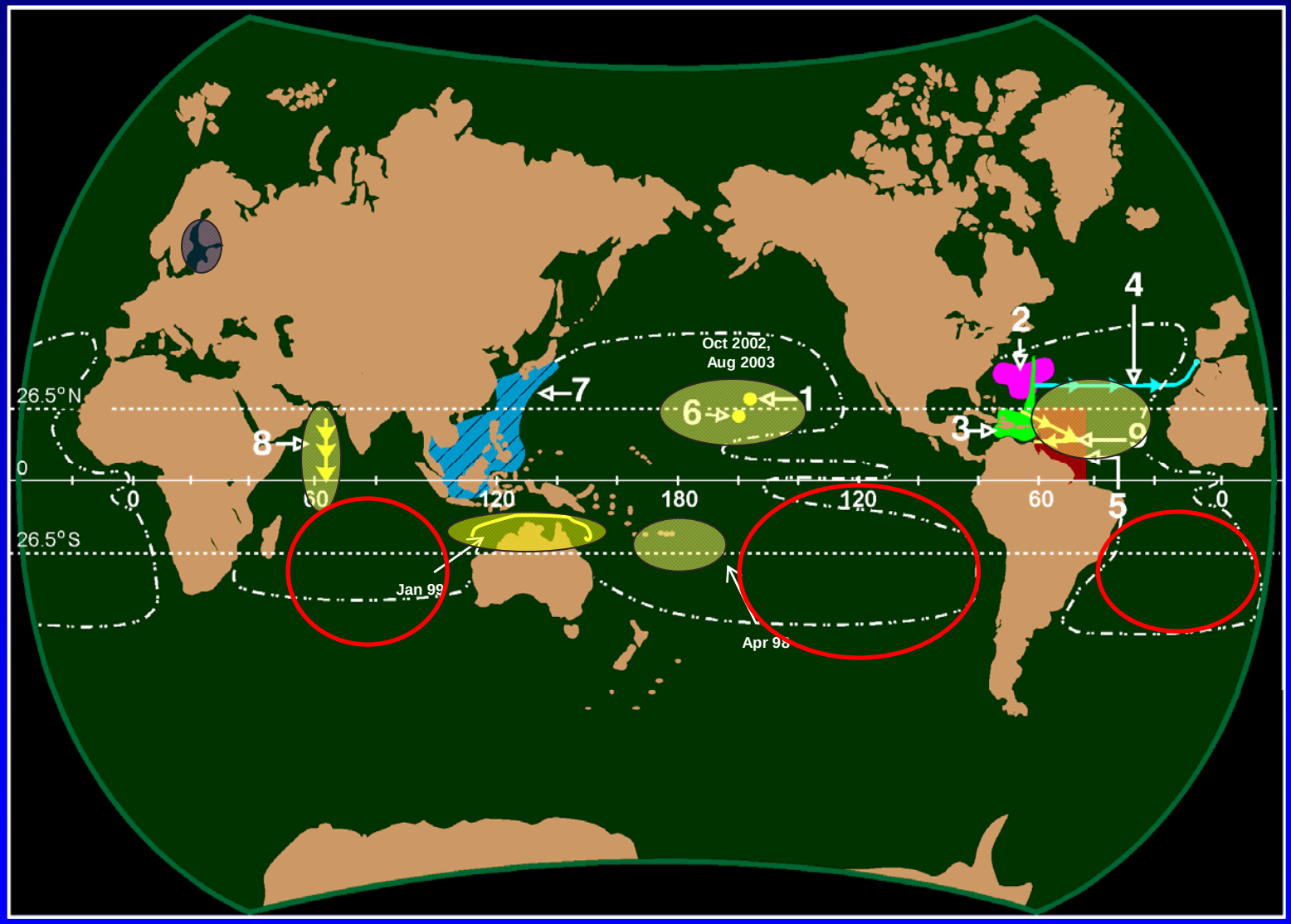


Northern hemi-sphere winter



Density zones

Field efforts in late 70-90s- largely N. Atlantic: most of oligotrophic ocean were not sampled



Renewed Motivation

Michaels et al. 1996;
Gruber et al. 1997

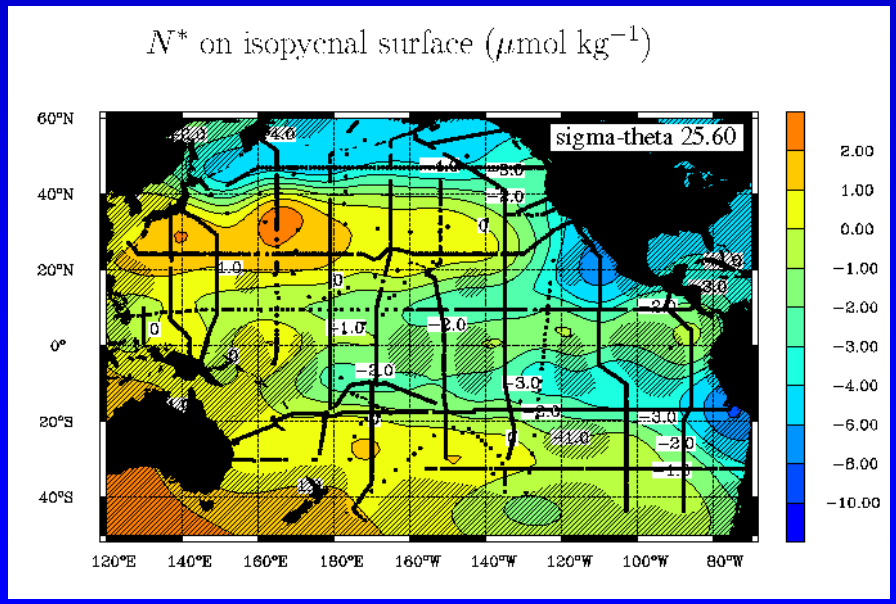
N* Anomalies:

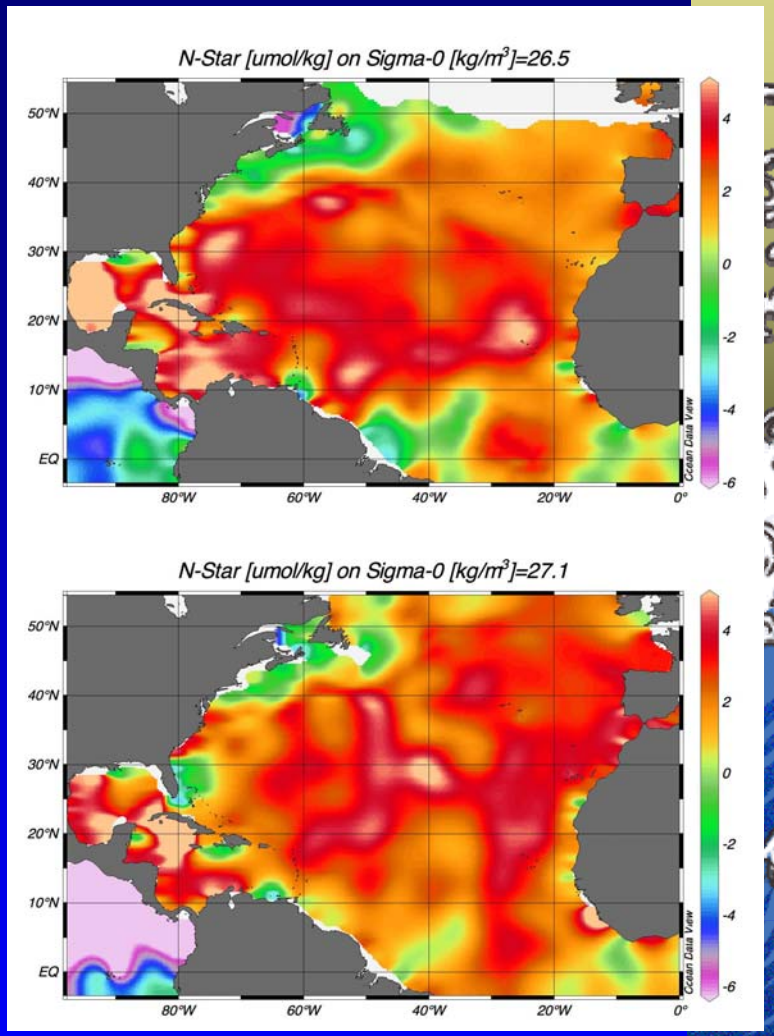
Redfield C:N:P: 106:16:1

$$N^* = [N] - 16[P]$$

+N* = N regen in excess of Redfield
(Diazotroph biomass N:P > 16)

-N* = preferential N loss
(e.g. due to denitrification)





Interbasins Comparisons

- *Conventional biomass measures*
  - *(microscopic density, chlorophyll)*
- *Rate measurements*
  - *($^{15}N_2$ uptake, C_2H_2 reduction)*
- *nifH qPCR densities of select groups*

N. Atlantic work

Carpenter et al. 2004

High densities of Trichodesmium in western *Tropical N Atlantic*

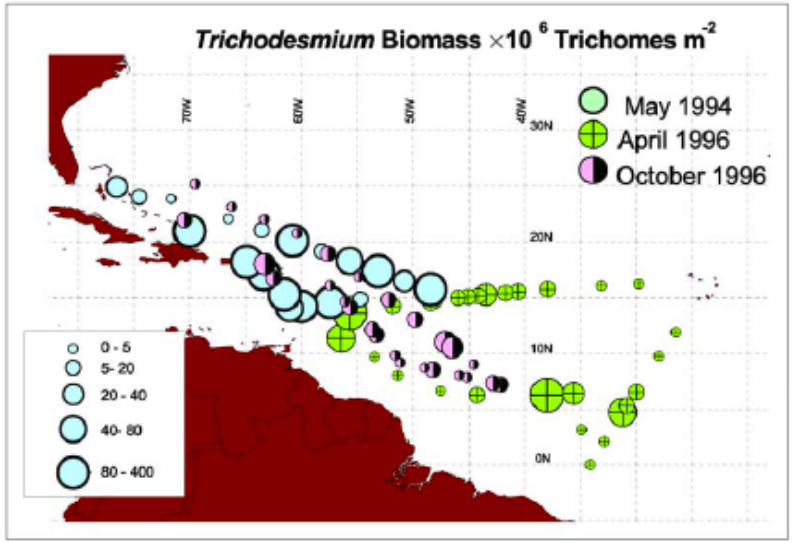
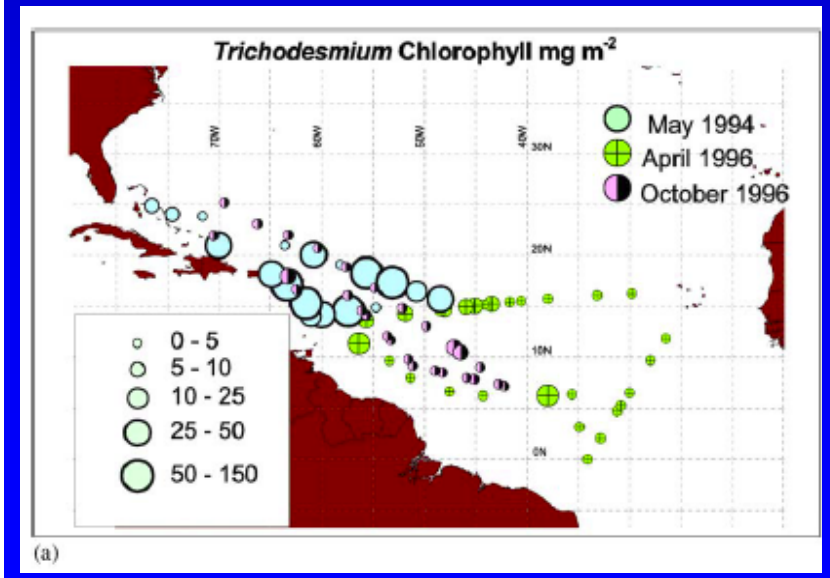
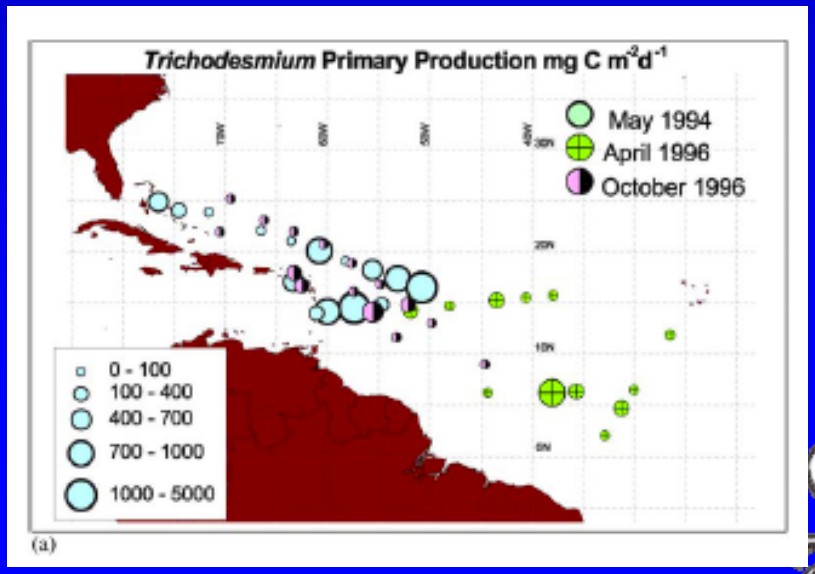


Fig. 4. Depth integrated trichome standing crop for all three cruises.

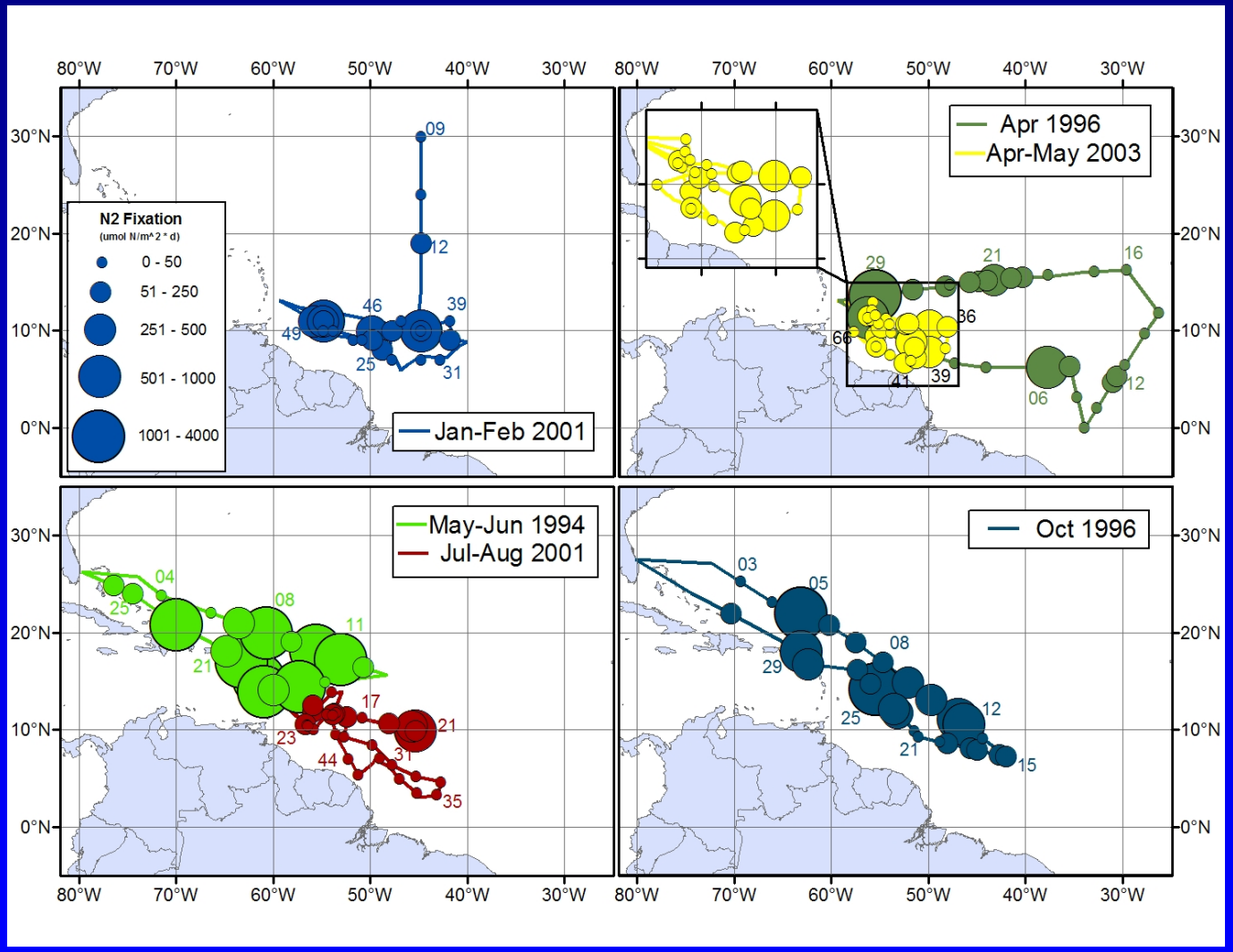




Trichodesmium N_2 Fixation:

Highly variable in time and space – But can be substantial

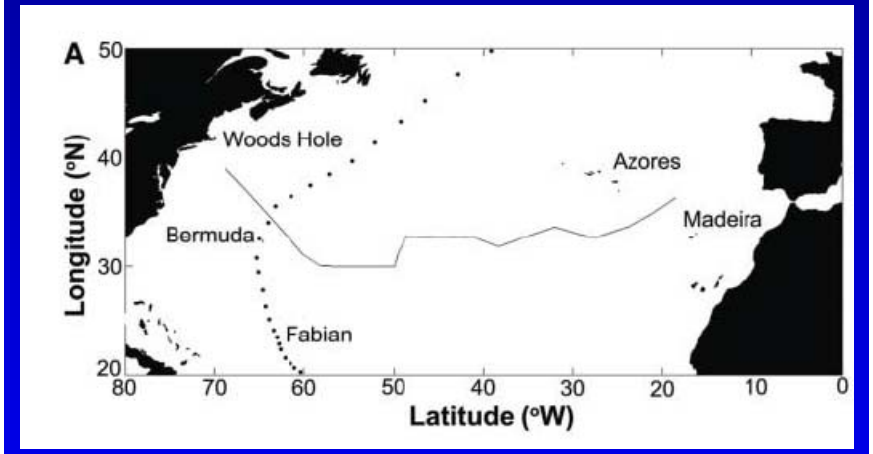
~240 µmol N/m² * d - comparable to vertical NO_3 flux

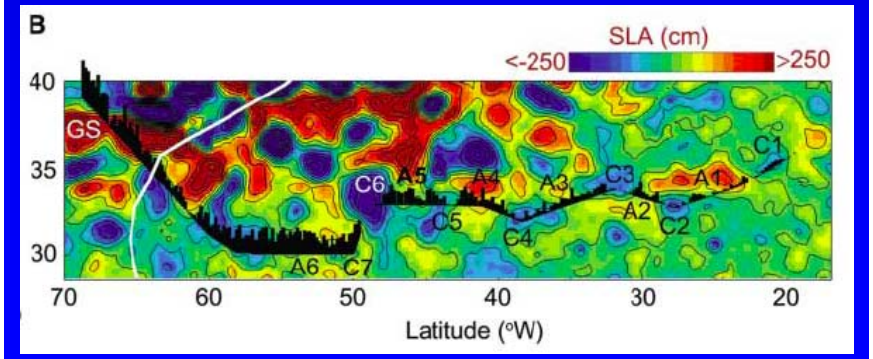


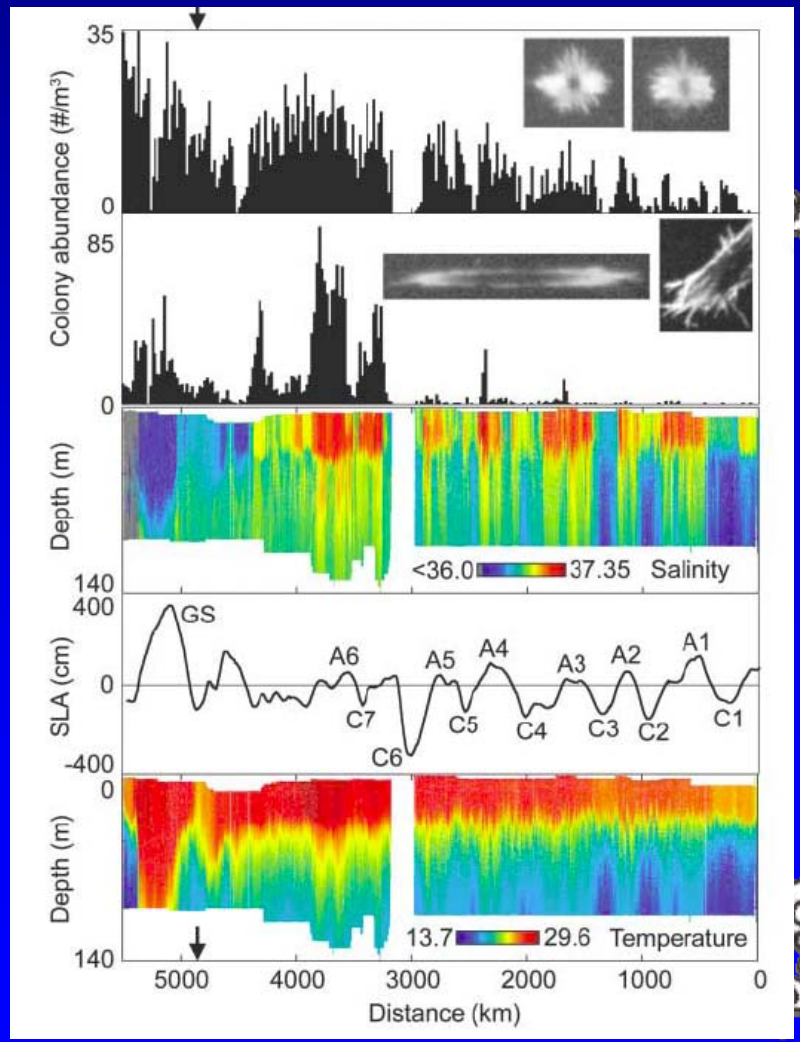
Capone et al. 2005, Global Biogeochemical Cycles

Davis & McGillicuddy 2006- Science
Video Plankton Recorder

Sept 2003: East-west gradient @ 30°N







Voss et al. 2004 GRL

Bulk N_2 fixation (μmol N m^{-2} d^{-1})

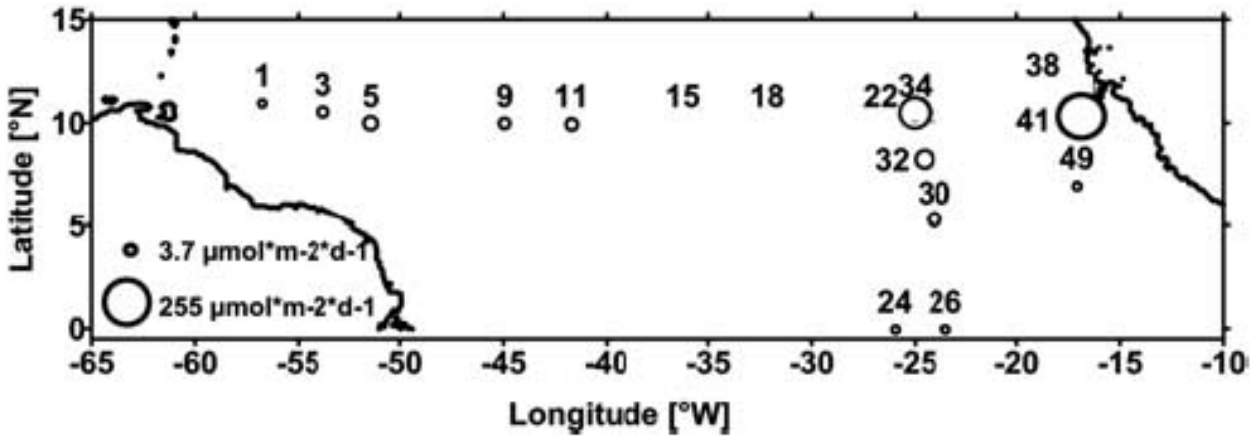


Figure 1. Station map and nitrogen fixation (circles). Circle size is linearly proportional to the N-fixation rate. At stations 15, 18, 22, and 38 no surface values were measured and no depth integration carried out.

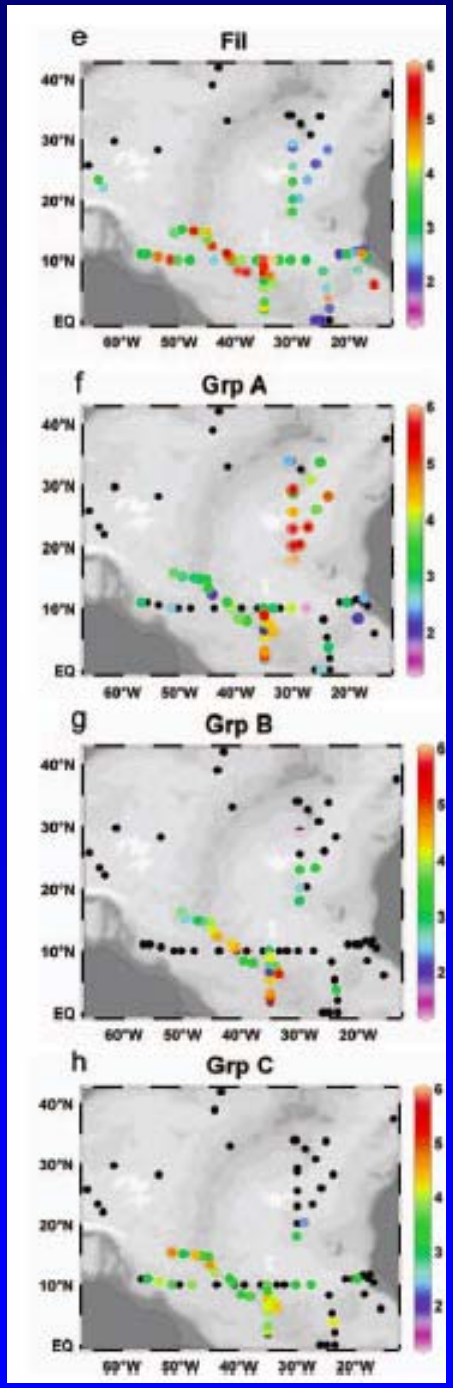
Oct- Nov 2002

Langlois et al. 2008 AEM

N. Atlantic
4 cruises
nifH copies/ L

Distribution of diazotrophs qPCR

"Filamentous forms most abundant"
57- 73% of clones

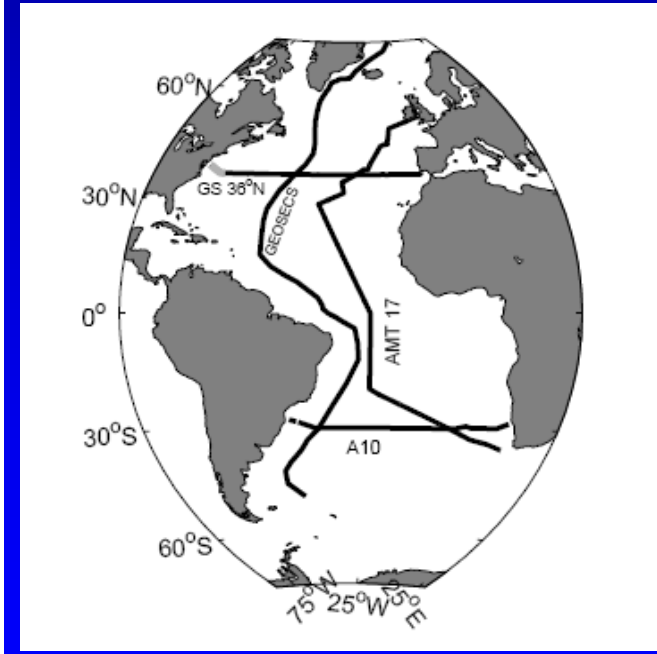


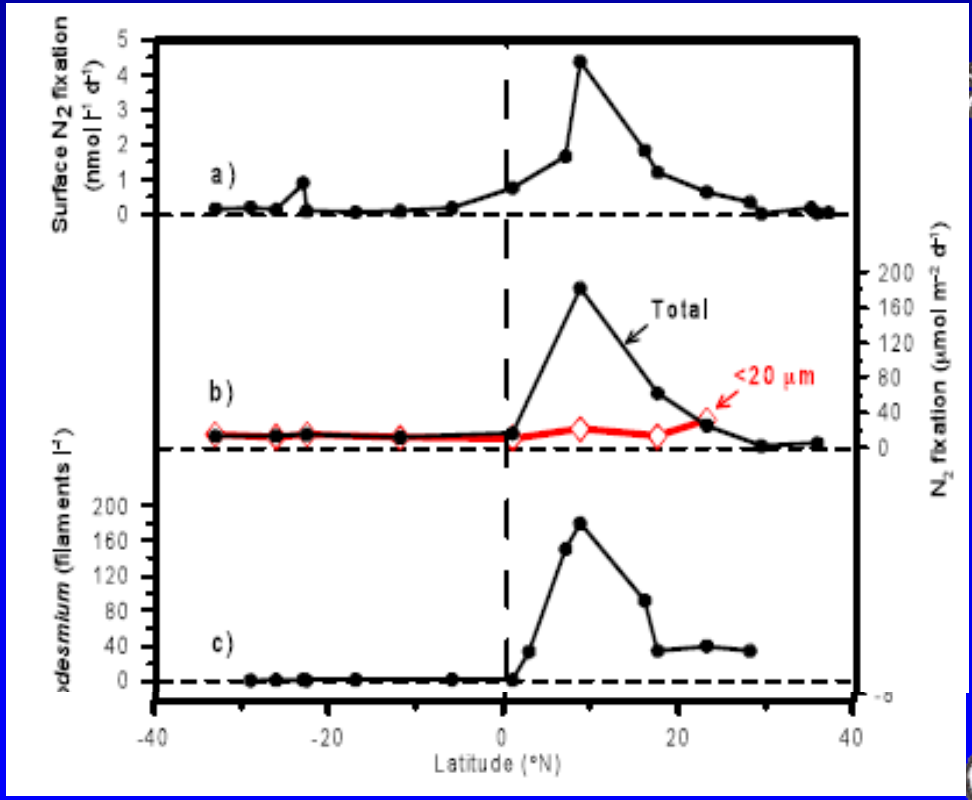
M Moore et al. in press

Nature GeoSciences

Atlantic Inter-basin trends

Atlantic Meridional Transect 17





Shifting gears: N. Pacific

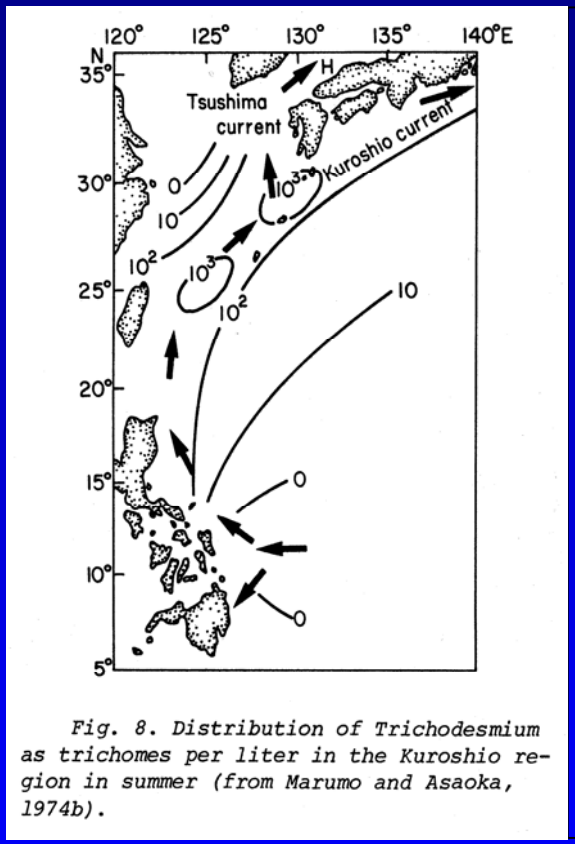


Fig. 8. Distribution of Trichodesmium as trichomes per liter in the Kuroshio region in summer (from Marumo and Asaoka, 1974b).

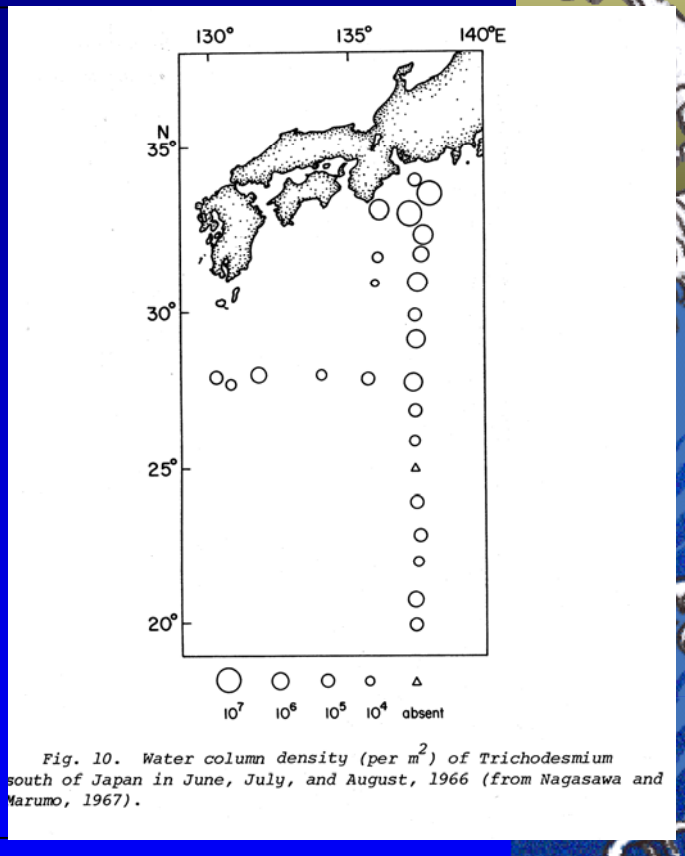


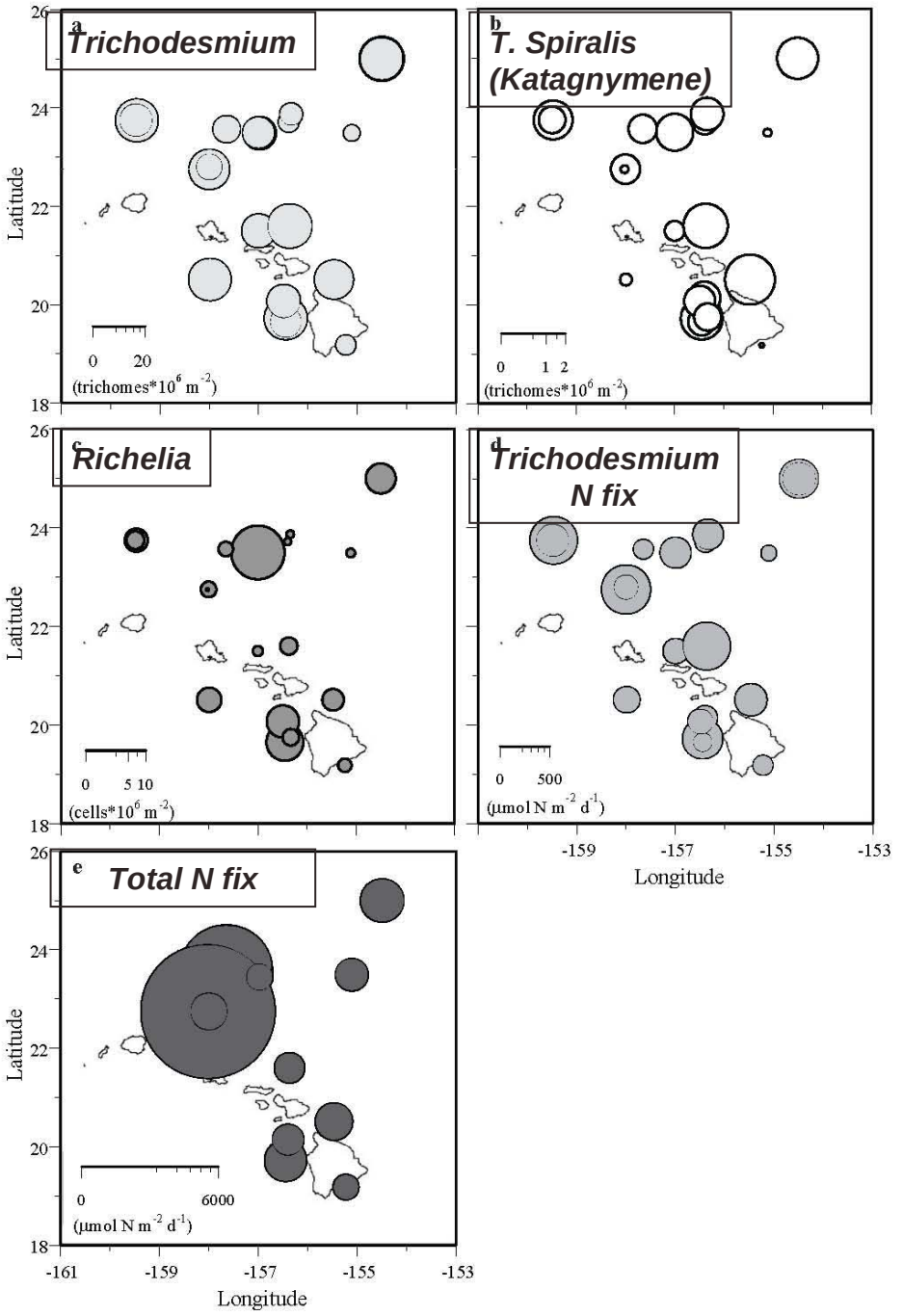
Fig. 10. Water column density (per m^2) of Trichodesmium south of Japan in June, July, and August, 1966 (from Nagasawa and Marumo, 1967).

Early observational data-
high Tricho densities near island landmasses

Sohm et al. in prep.

Biocomplexity Cruise
Sep-Oct 2002
Vicinity of Hawaiian Islands

Appreciable densities-
but clearly other sources of N_2 fixation

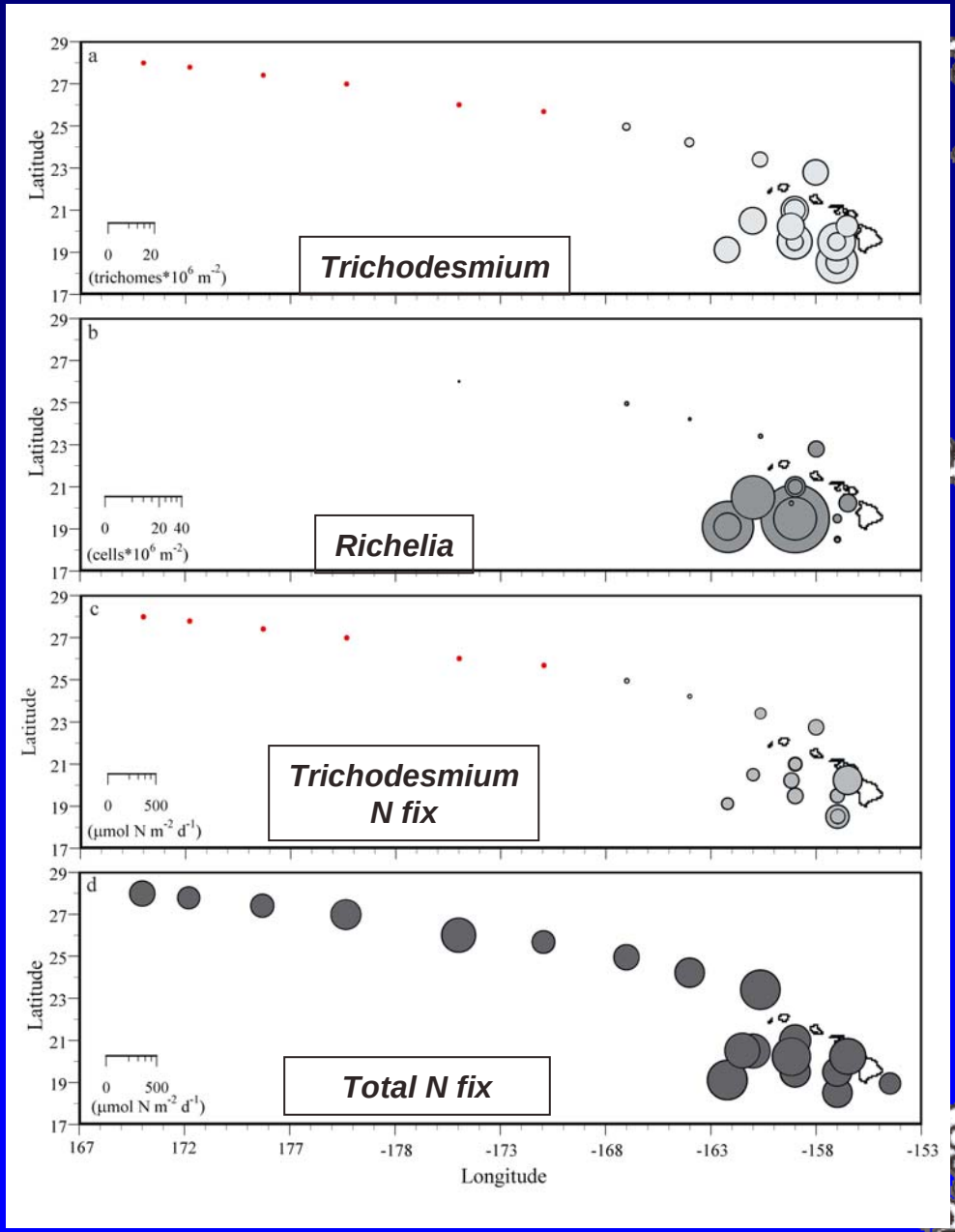


Sohm et al. in prep.

Biocomplexity Cruise Jun-Jul 2003

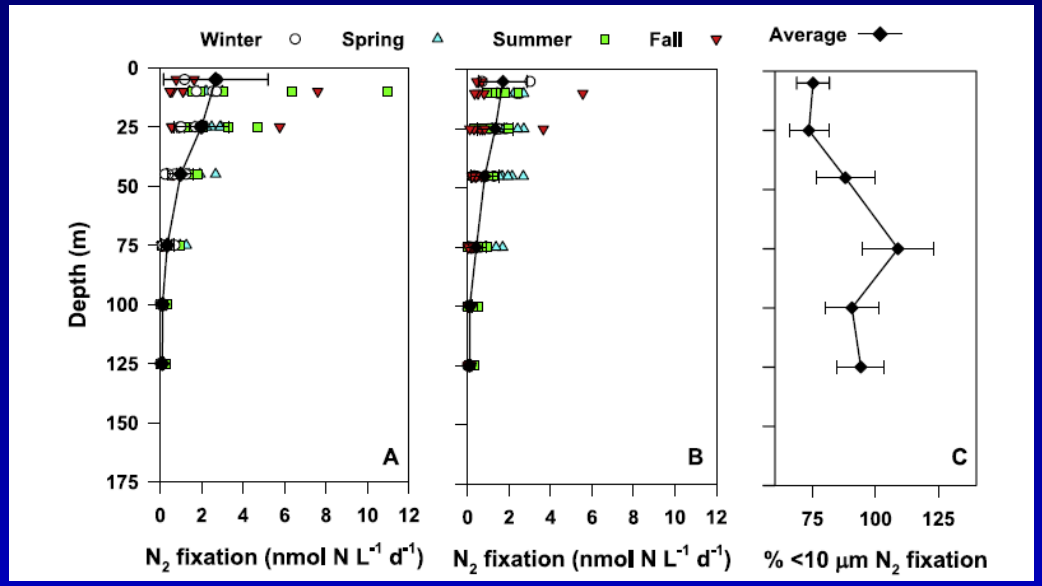
Filamentous, DDA forms rare west of the Hawaiian Islands.

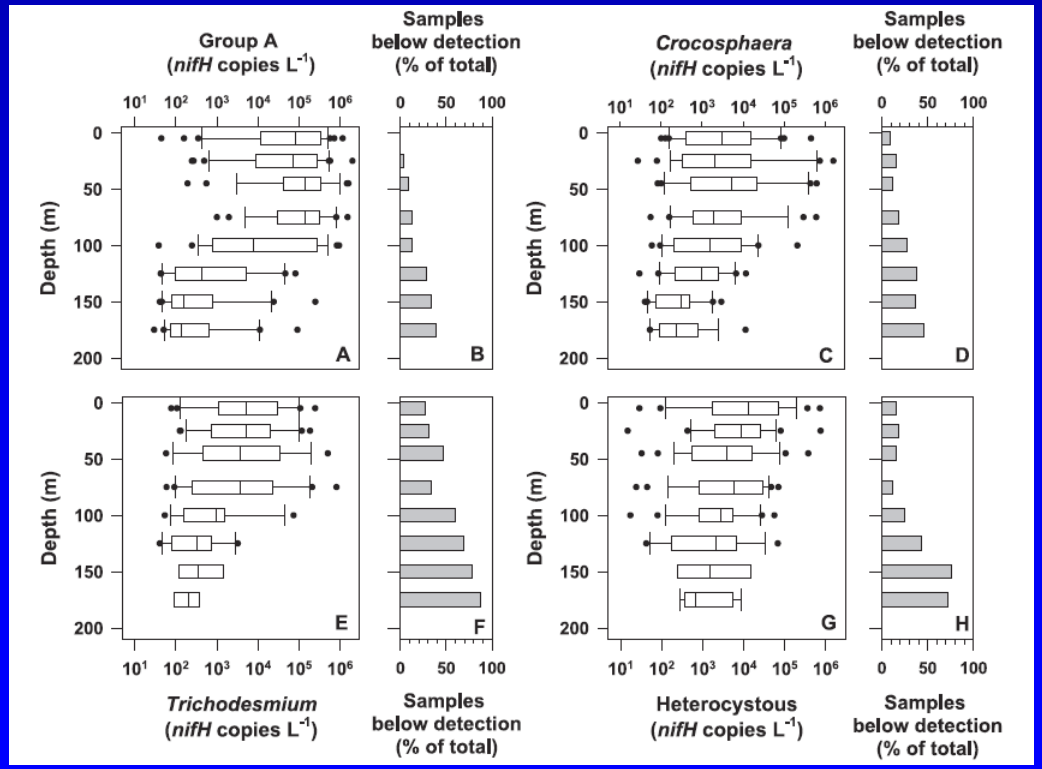
Other significant contributors to N_2 fixation



Church et al. 2009 ALOHA- north of Oahu

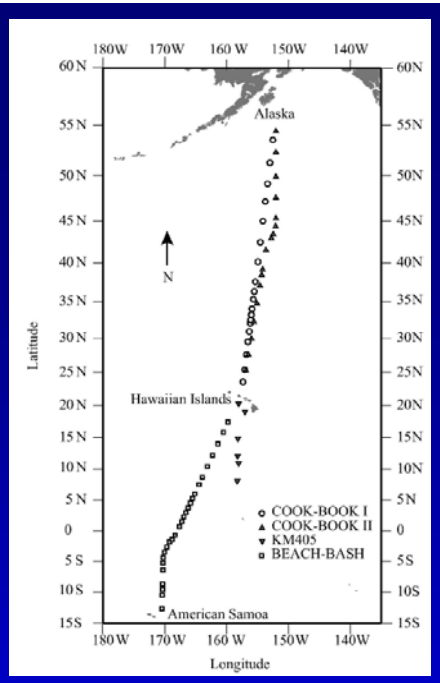
Type A cyanos- dominant at ALOHA

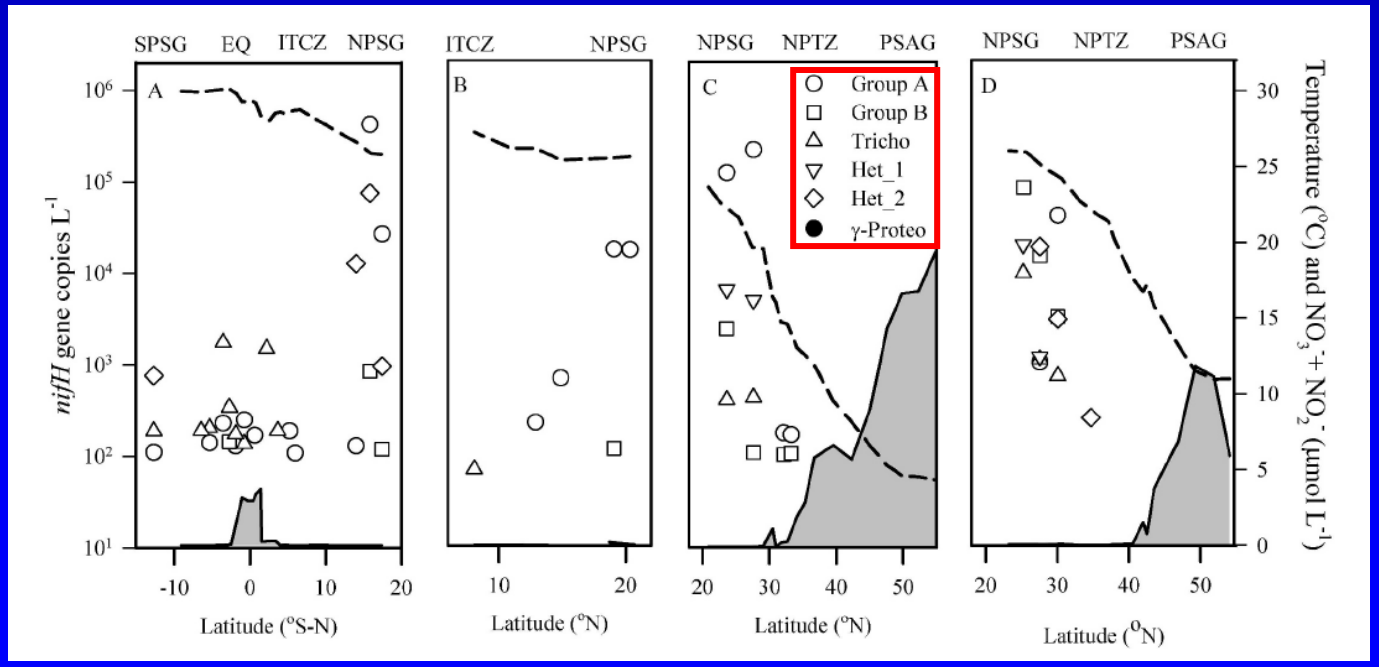




Church et al. 2008
L & O, 4 cruises,
N. Pacific

"Group A cyanos most abundant"





Note: Het 1& Het 2 are heterocystous symbionts – e.g. Richelia)

Bonnet et al. 2008

J Murray cruise 2006

N_2 fixation

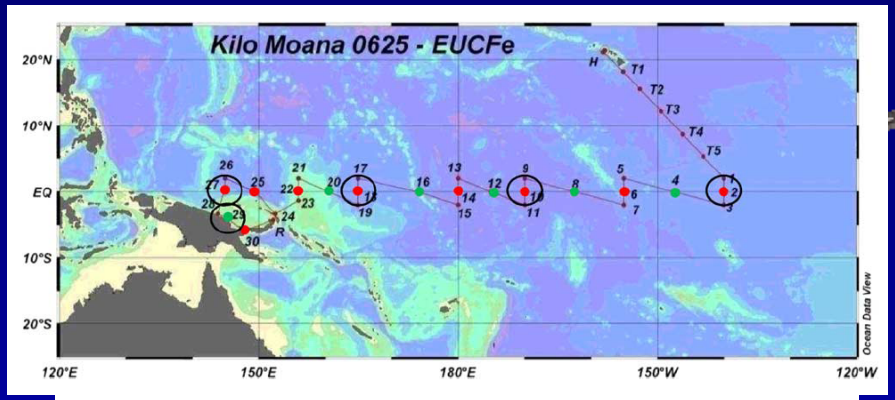
(nmol N/ L* d)

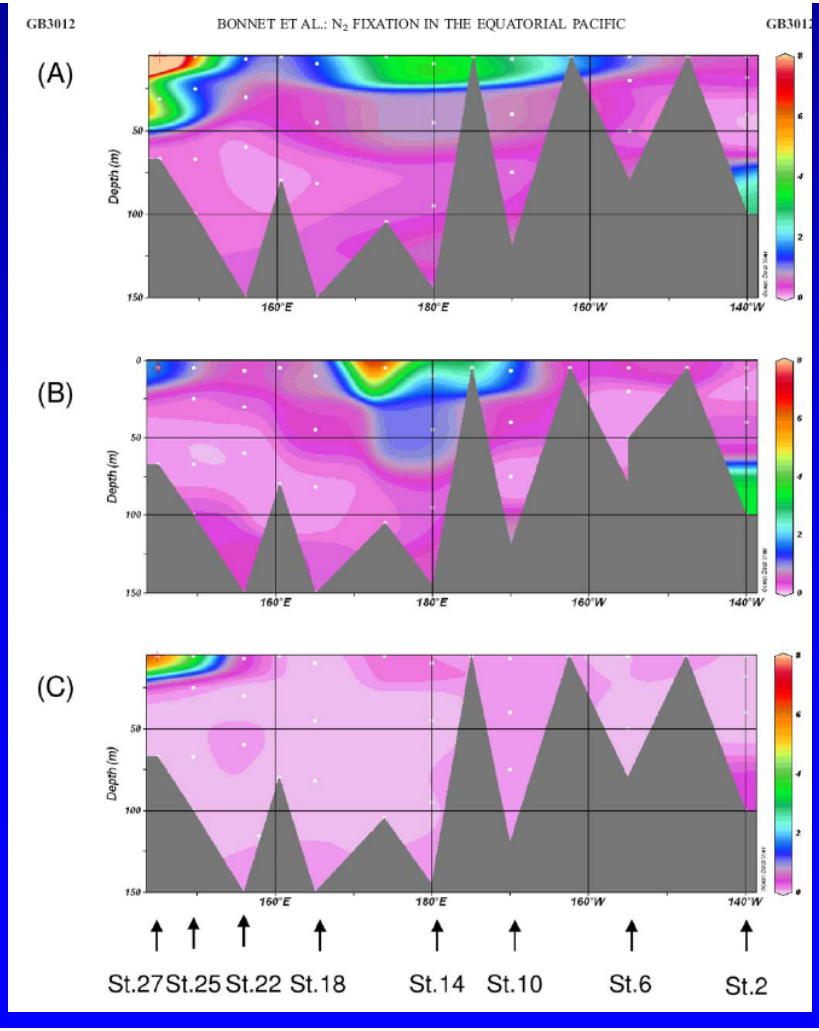
in:

bulk water (A)

< 10 μm (B)

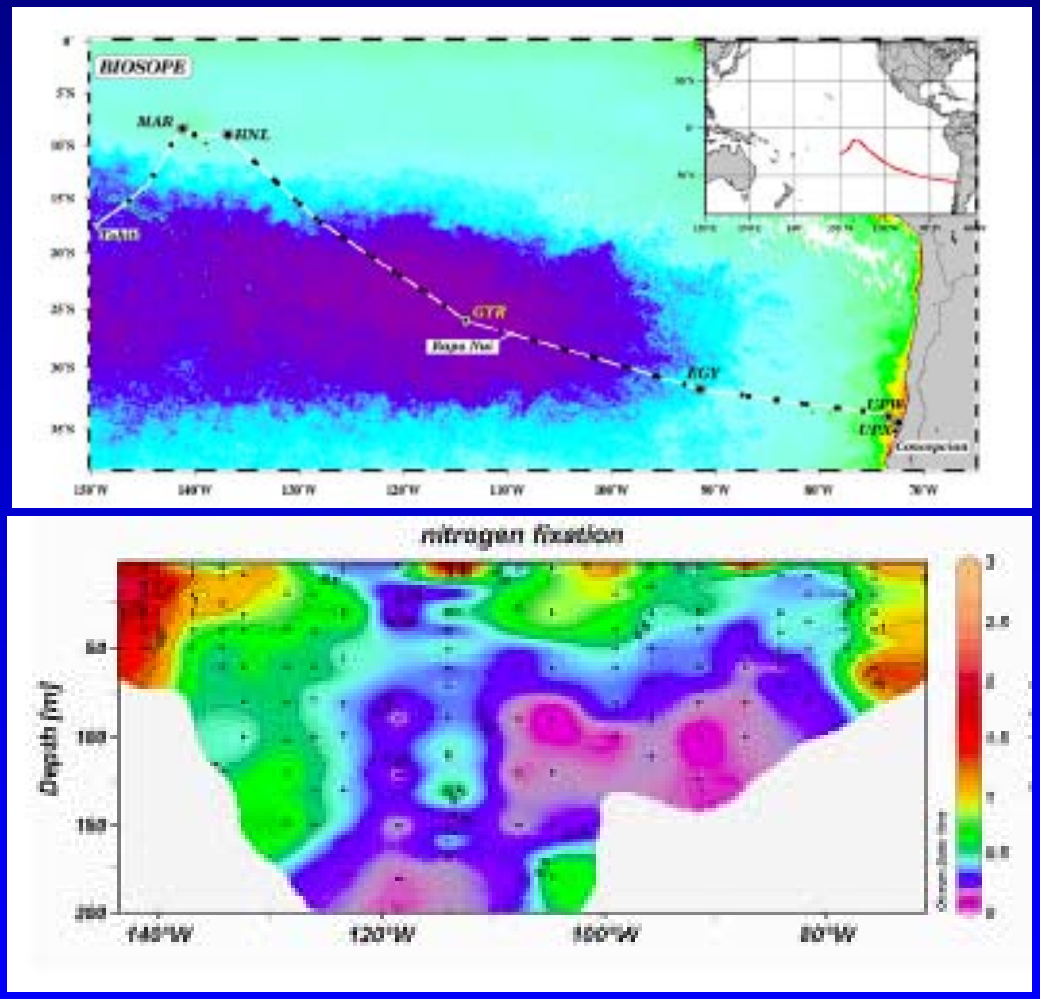
> 10 μm (C)





Raimbault et al. 2008 Biogeoscience
South Pacific Gyre

Very low rates in core of gyre 30 μmol $m^{-2}d^{-1}$

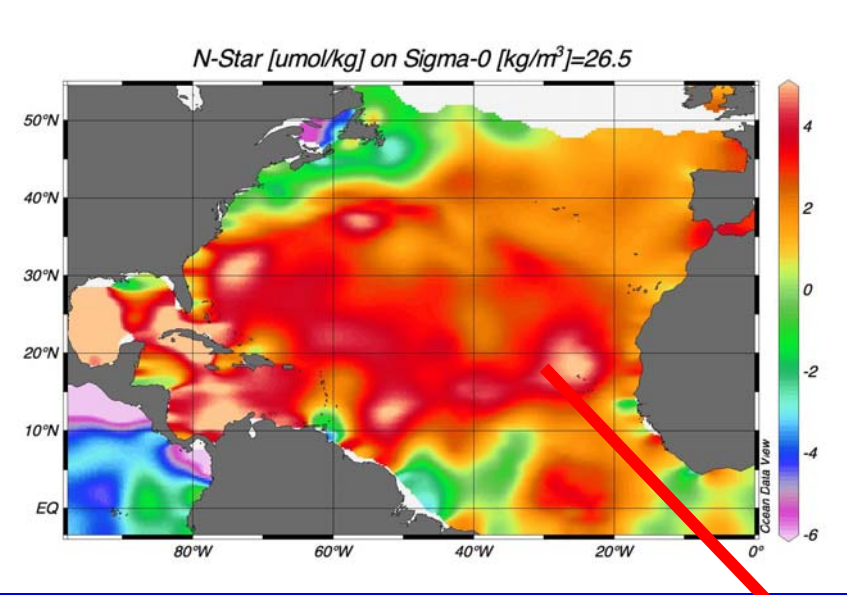


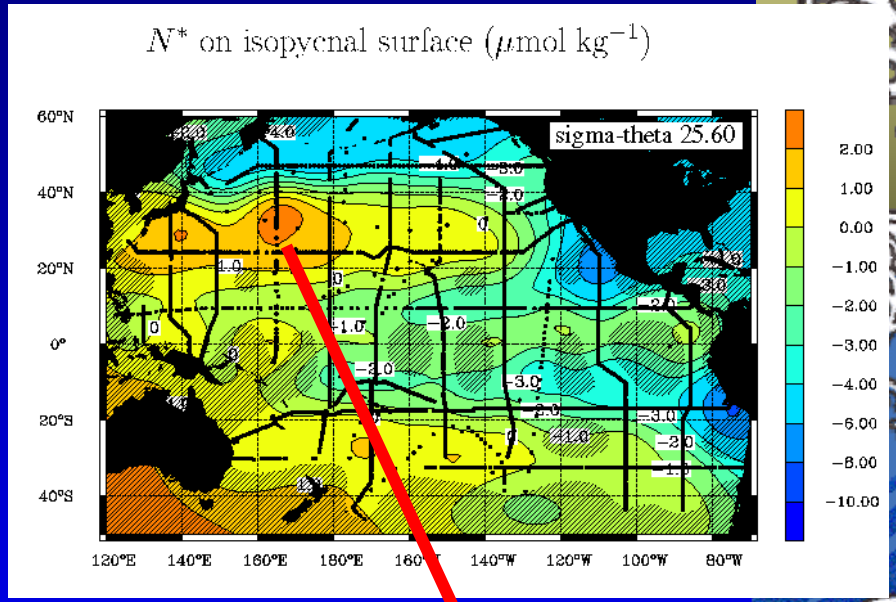
N_2 fixation (nmol N/ L* d)

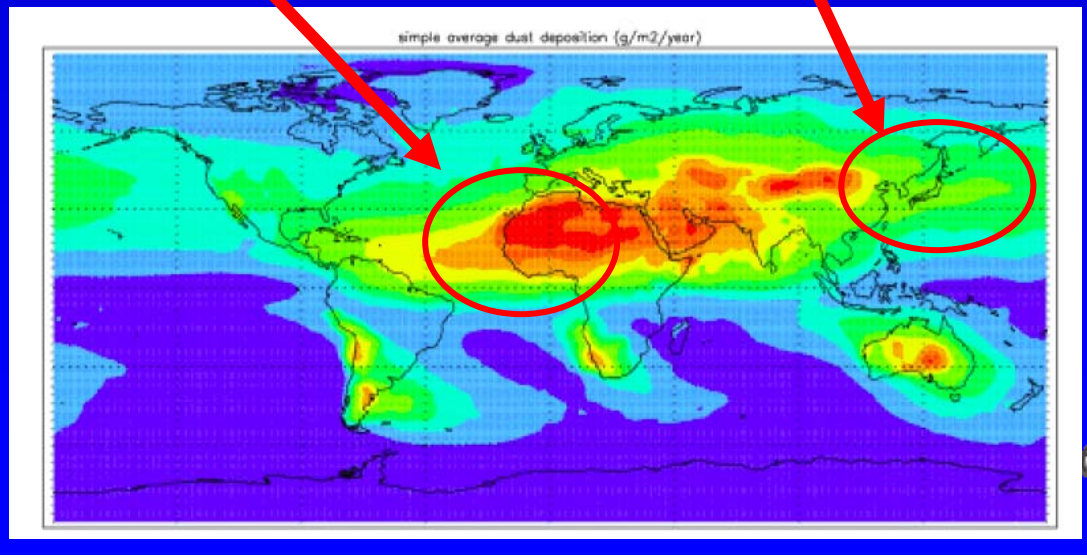
Factors Potentially Limiting Marine N_2 Fixation

- ***Physical:***
  - ***light (photoautotrophs)***
  - ***temperature***
  - ***stability (mixing)***
- ***Chemical:***
  - ***Nutritional: Fe, P, Si, Mo, other metals, CO_2***
  - ***N:P ratio***
  - ***Inhibition: O_2, combined N***
  - ***Organics (heterotrophs)***

With advent of N*- it did not escape notice that the greatest N* anomalies are in areas of greatest dust flux

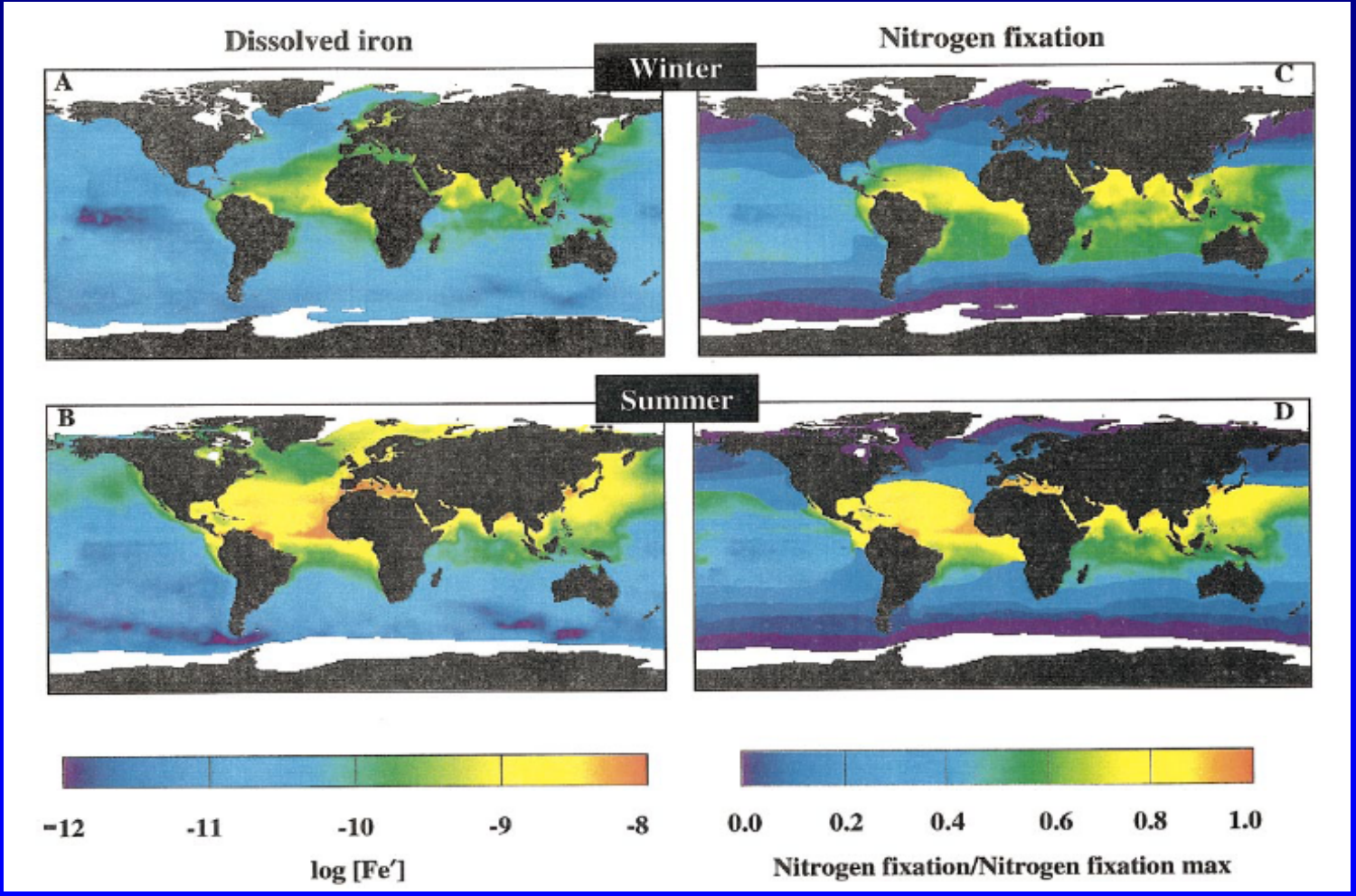






Mahowald et al. GBC 2005 Dust depo maps

Berman-Frank et al. 2001
Limnol & Oceanogr.



Wu et al. *2000 (Ed Boyle lab) Nature*

w/ higher dust flux & [Fe] in the Atlantic –

N. Atlantic driven to P limitation w/r to N_2 fixation

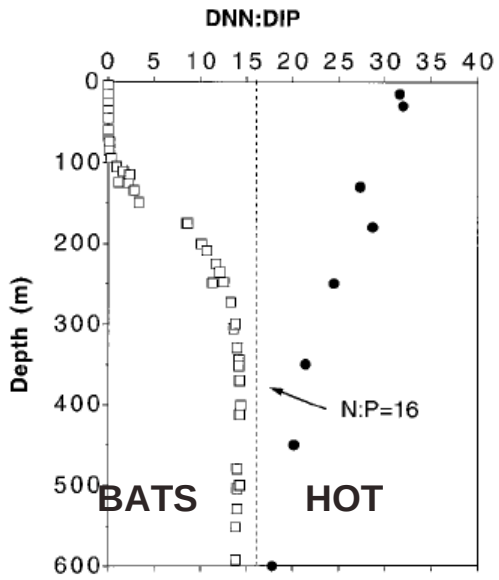


Fig. 2. Vertical profiles of N:P molar ratios in the Sargasso Sea near Bermuda (31.67°N, 64.17°W) (●) and in the Pacific near Hawaii (HOT USJGOFS Web site at hahana.soest.hawaii.edu) (□).

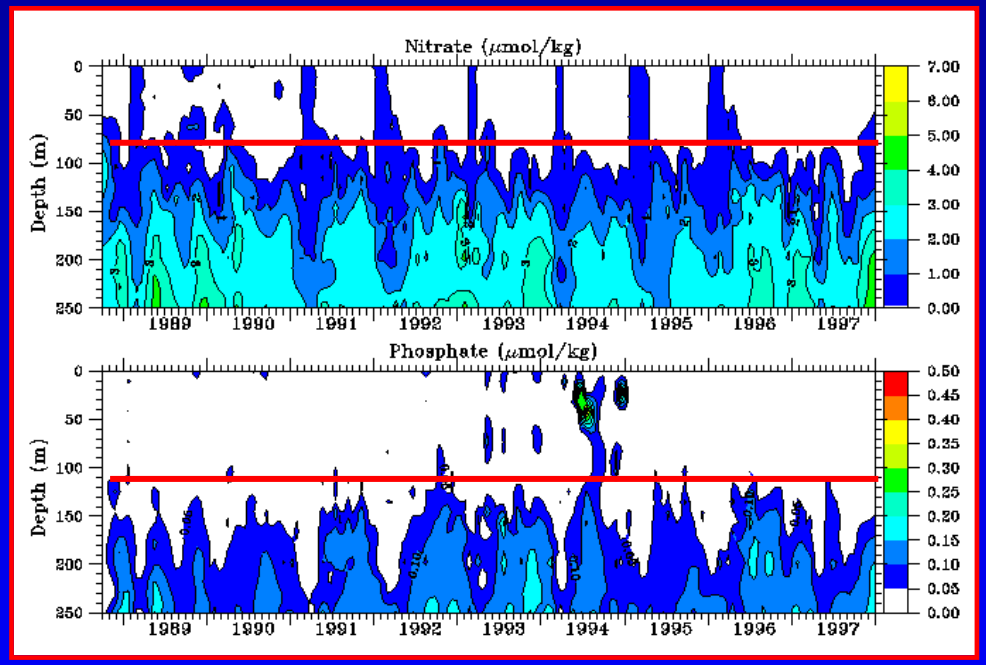
Table 1. A comparison of euphotic zone biogeochemical parameters between North Atlantic and North Pacific gyres.

Parameters (units)	Sargasso Sea	Pacific near Hawaii
DIP (nM)	0.48 ± 0.27*	13 ± 2†; 9–40‡
TDN (nM)	4512 ± 430	5680 ± 620‡
TDP (nM)	75 ± 42	222 ± 14‡
TDN:TDP	60 ± 7	26 ± 3
Eolian Fe flux (μmol Fe m^{-2} day^{-1}) (*20*)	0.2–0.8	0.08–0.16
N_2 fixation rate (mmol N m^{-2} $year^{-1}$)	72§	31–51‖

*Average DIP between 26° and 31°N in the surface waters of the Sargasso Sea in March 1998. †North Pacific near Hawaii (22.9°N, 158.0°W) in November 1998. ‡North Pacific near Hawaii at station ALOHA during 1991–97 (*23*). §Based on isopycnal N* distribution and water age (*21*). ‖Based on a variety of independent estimates including nitrogenase activity by acetylene reduction method, *Trichodesmium* abundance, N:P mass balance, and ^{15}N isotope balance (*23*).

N Atlantic- BATS

BATS seasonal nutrients:
Nitracline
Well above phosphacline



Wu et al. 2001 Science

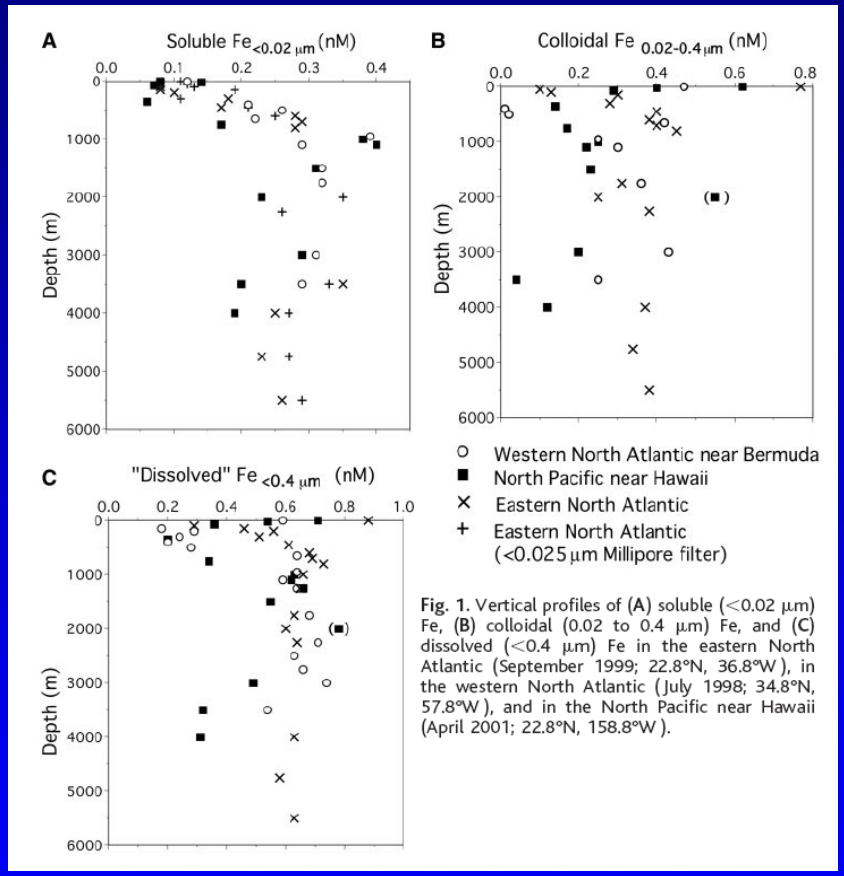
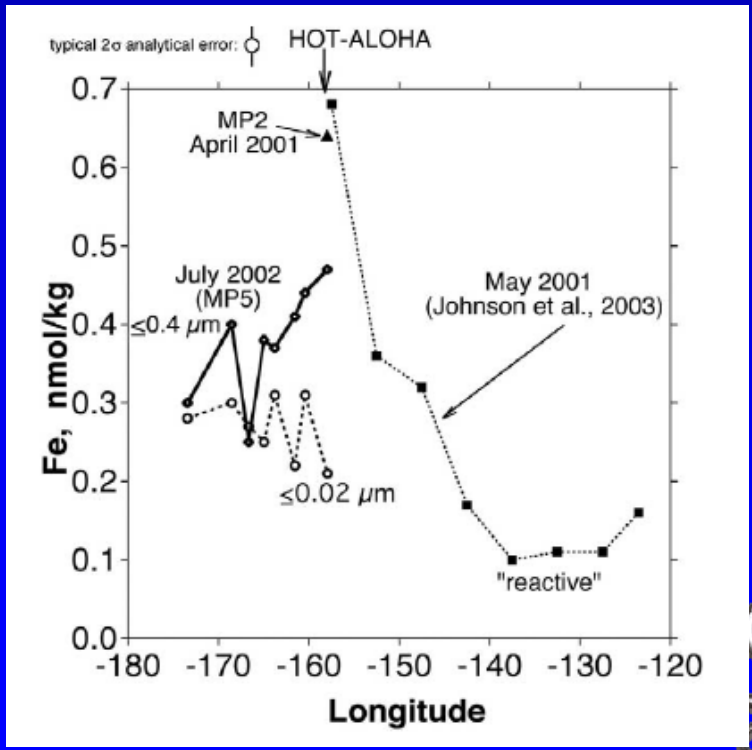


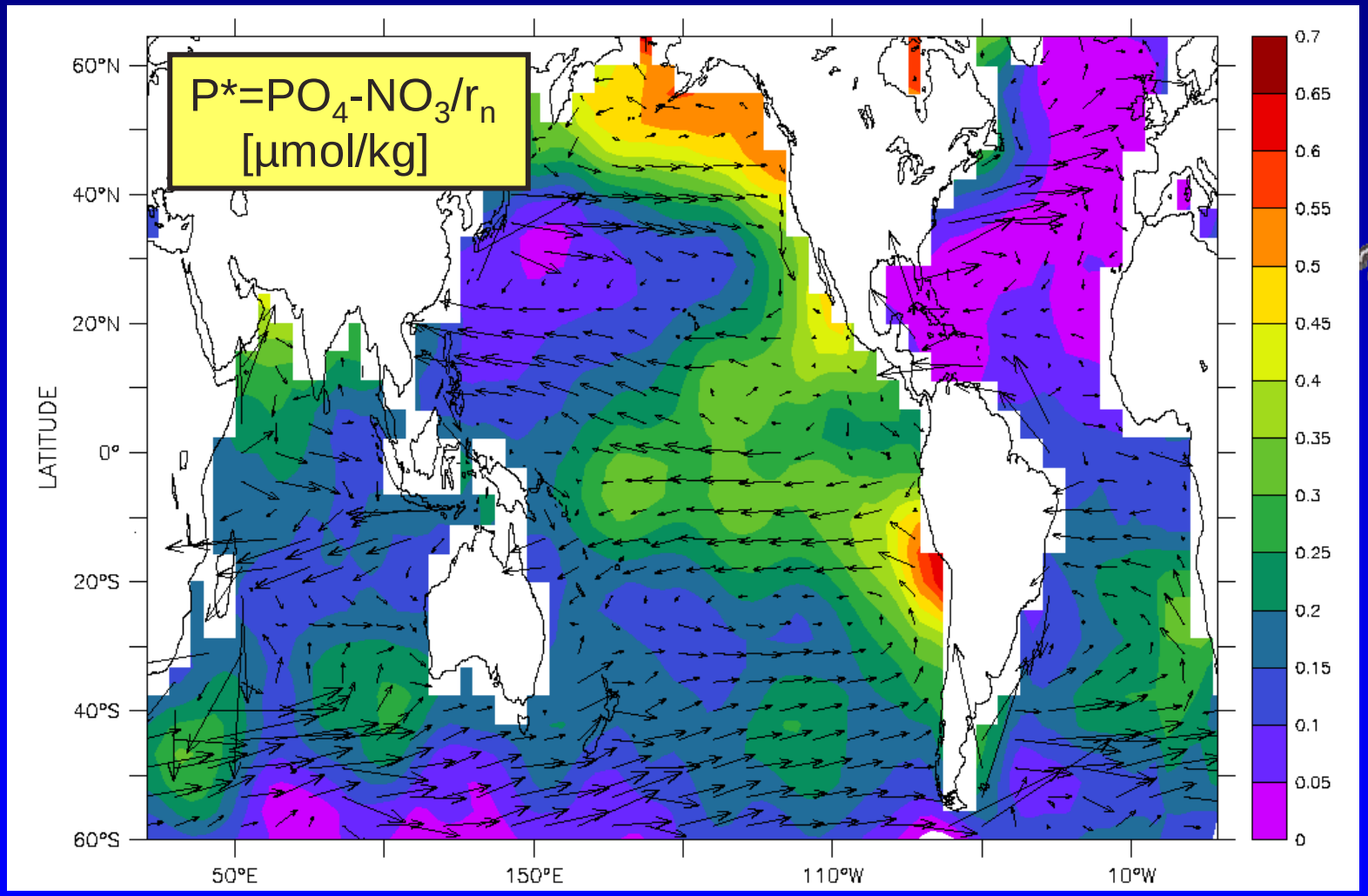
Fig. 1. Vertical profiles of (A) soluble (<0.02 μm) Fe, (B) colloidal (0.02 to 0.4 μm) Fe, and (C) dissolved (<0.4 μm) Fe in the eastern North Atlantic (September 1999; 22.8°N, 36.8°W), in the western North Atlantic (July 1998; 34.8°N, 57.8°W), and in the North Pacific near Hawaii (April 2001; 22.8°N, 158.8°W).

Boyle et al. 2005



Climatological P* (0-100 m)

Deutsch et al., 2007, Nature World Ocean Atlas [2001] + GCM



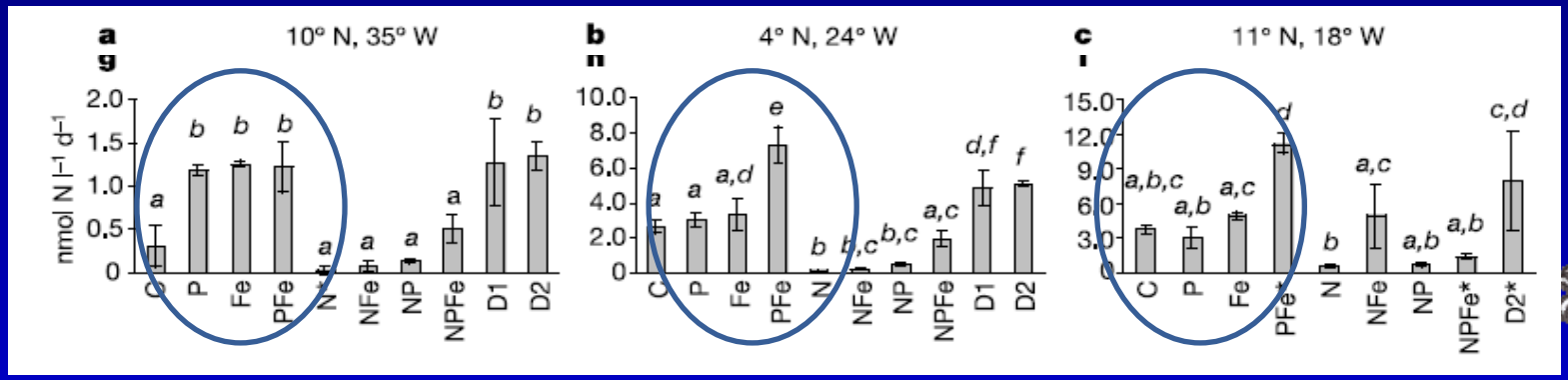
Diagnostics for limitation of N_2 Fixation

- *Bioassays*
- *N:P:Fe biomass ratios*
- *Correlations with N_2 fixation*
- *Uptake kinetics, turnover of inorganic P*
- *Alkaline phosphatase/ ELF*
- *isiB- iron stress/ flavodoxin gene*

Bioassays of N_2 fixation ($^{15}N_2$ uptake)- not clear

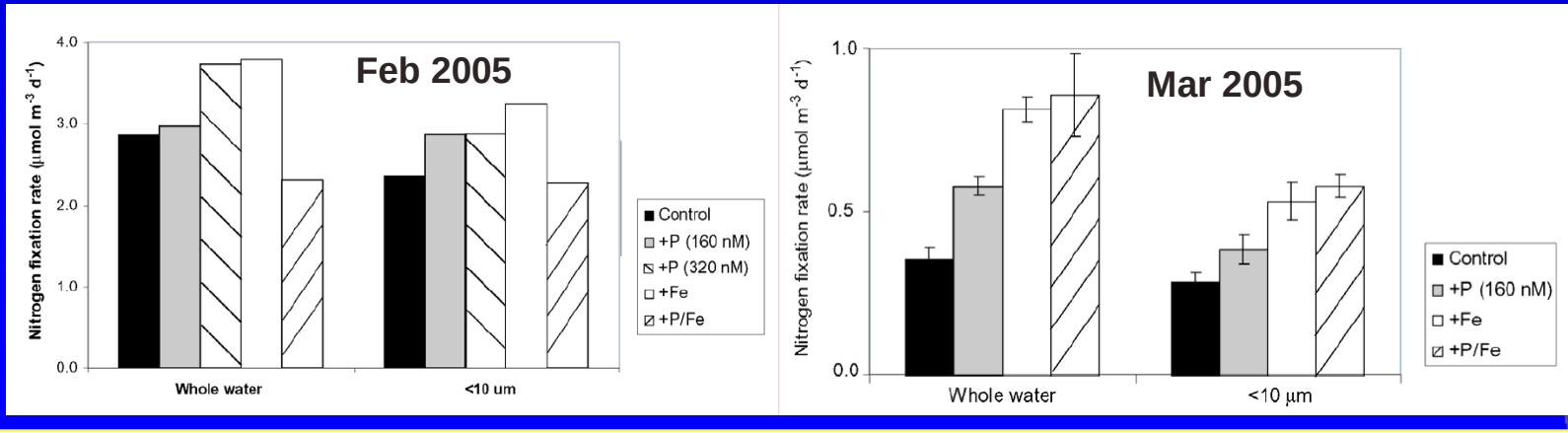
Mills et al., 2004, Nature

Eastern tropical N Atlantic: Evidence of co-limitation



Grabowski et al. Aq. Microbial Ecol. 2008

N. Pacific Gyre- ALOHA

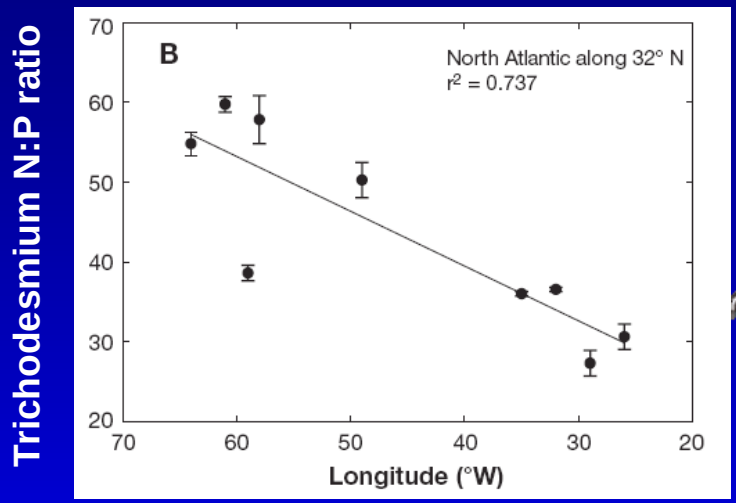


Zehr et al. 2007- @ ALOHA- no P effect on diazotroph activity, growth or gene expression

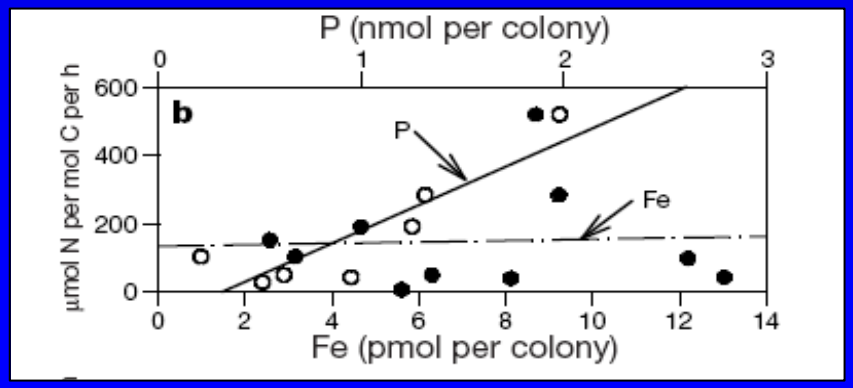
Some of our evidence supports a more severely P limited N Atlantic w/r to N_2 fixation

- *Krauk et al. 2006*

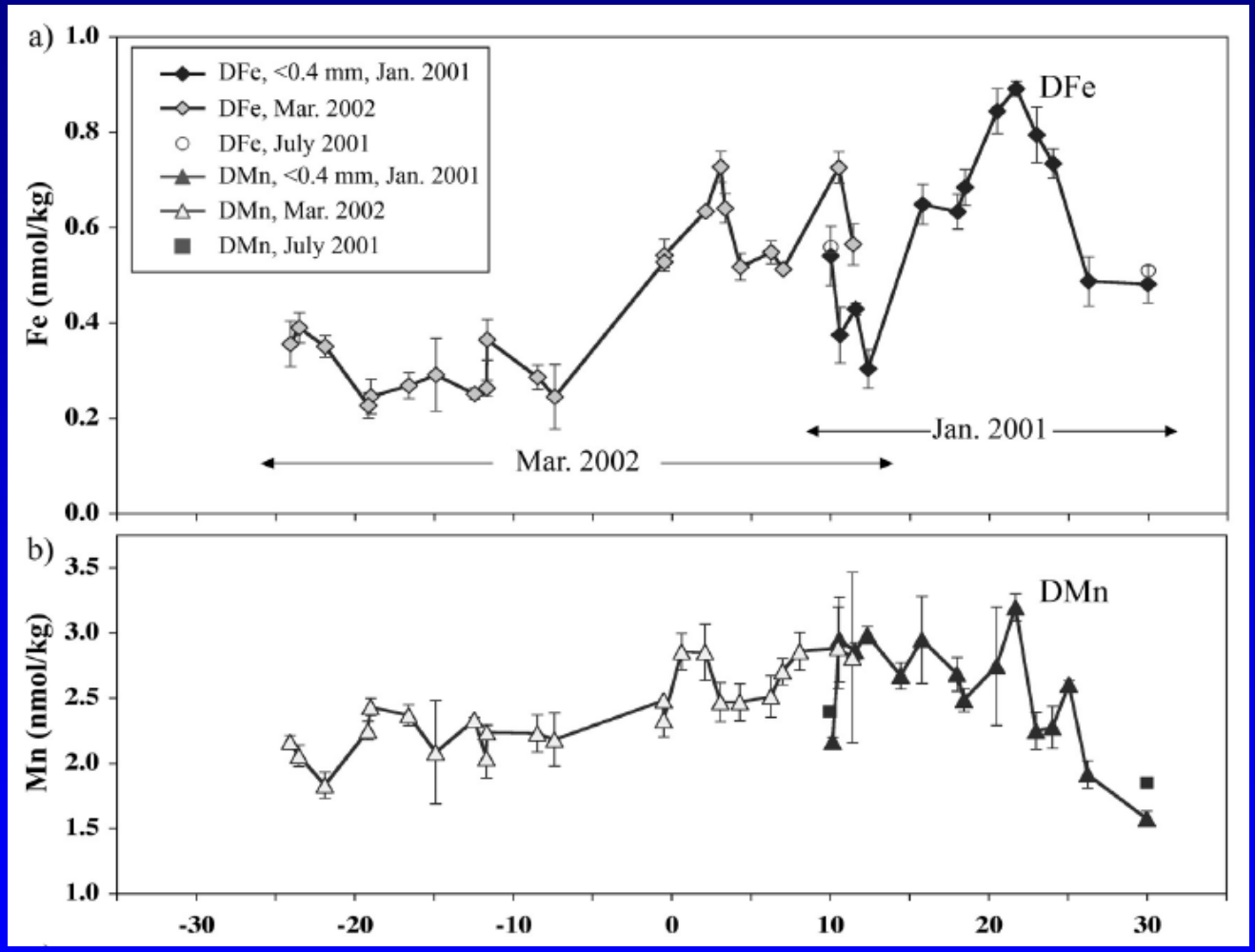
  Mar. Ecol. Prog. Series
  - *N:P ratios of* Trichodesmium
  - *Highest in the western N. Atlantic relative to Pacific*



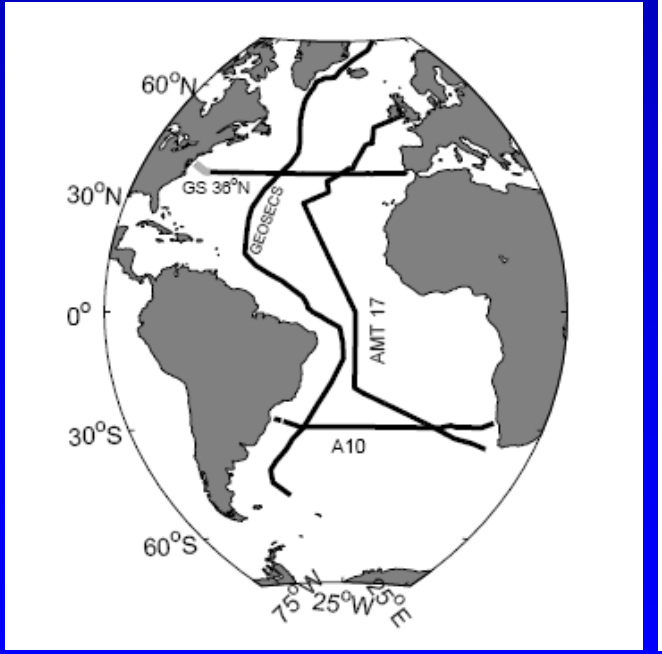
- *Sanudo-Wilhelmy et al. Nature 2001*
  - *Trichodesmium nitrogenase activity correlation with cell P, not cell or dissolved Fe in tropical N. Atlantic*

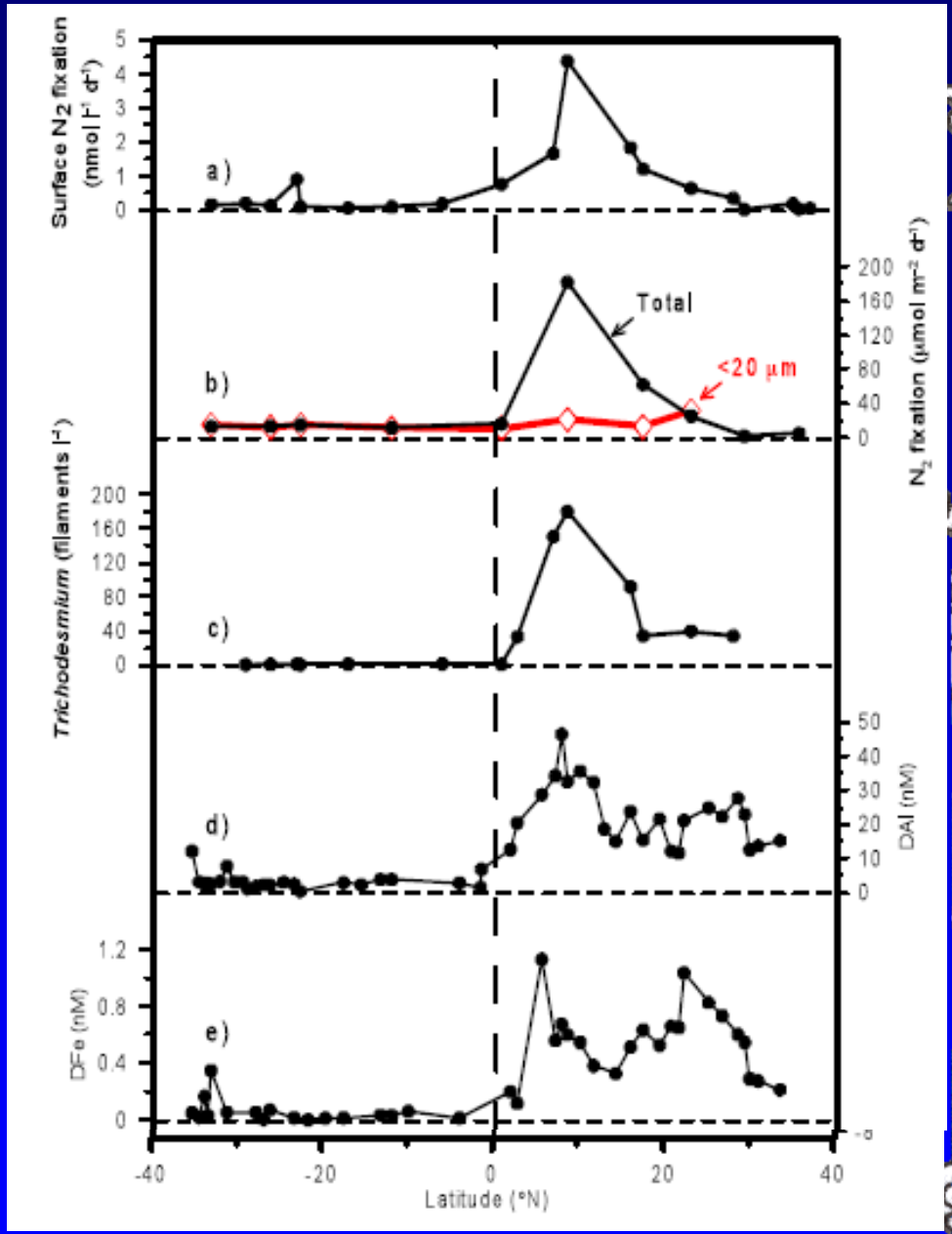


Bergquist et al. 2006
Atlantic transects



M. Moore et al. in press Nature GeoSciences

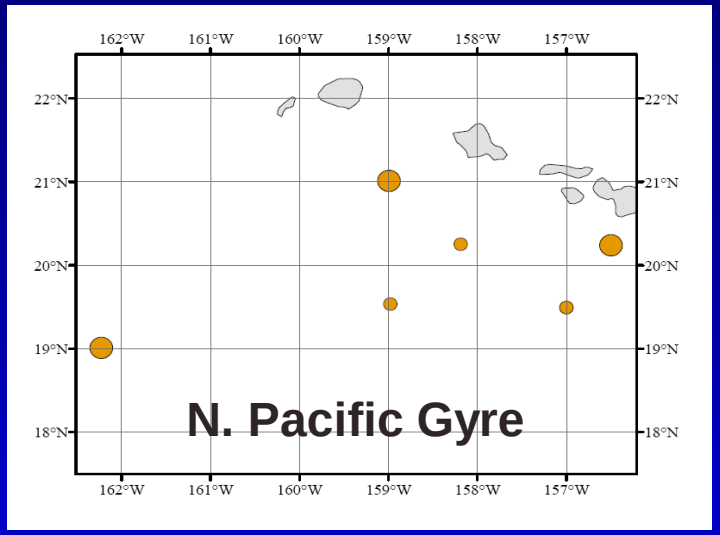


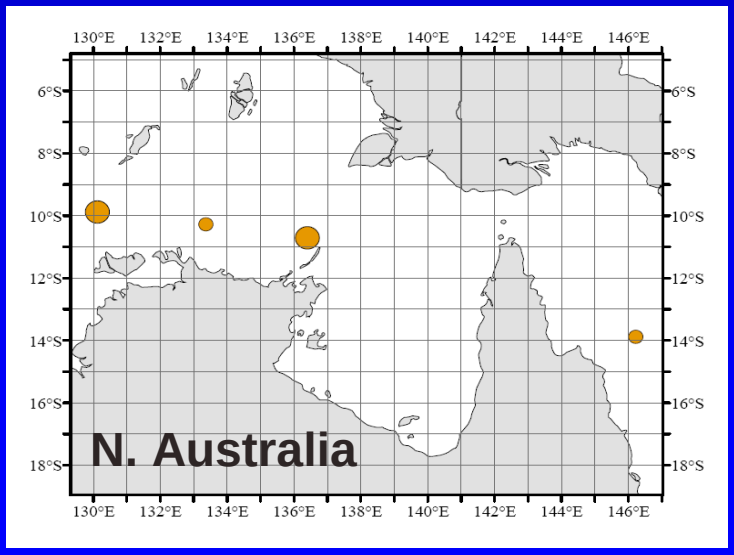


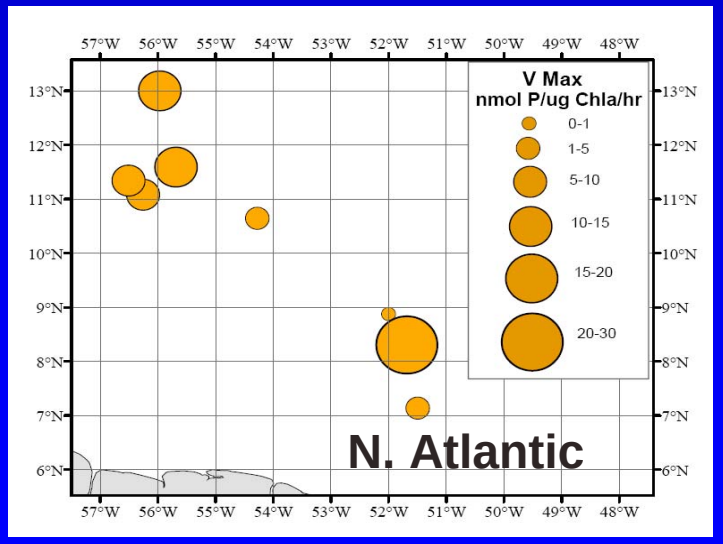
Sohm, Mahaffey & Capone, 2008, L & O

Kinetics of phosphate uptake:

V_{max} for DIP uptake by Tricho colonies consistently higher in N. Atlantic *Trichodesmium* populations





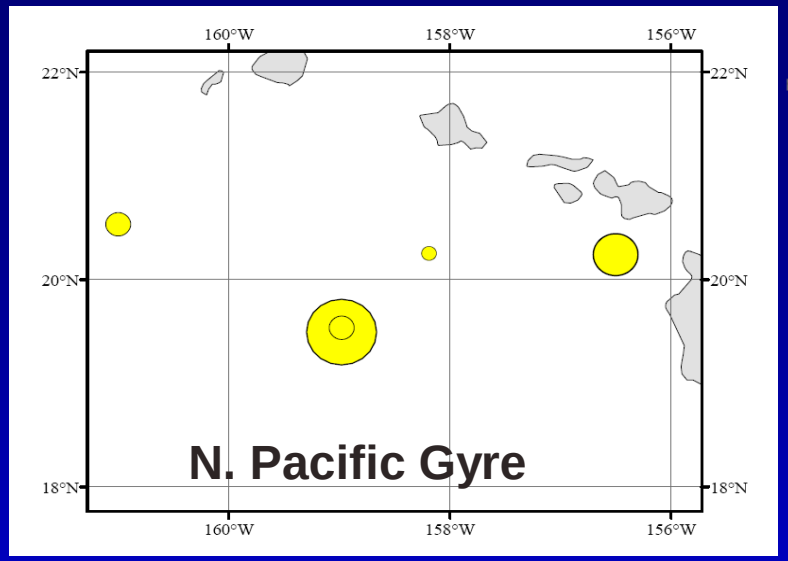


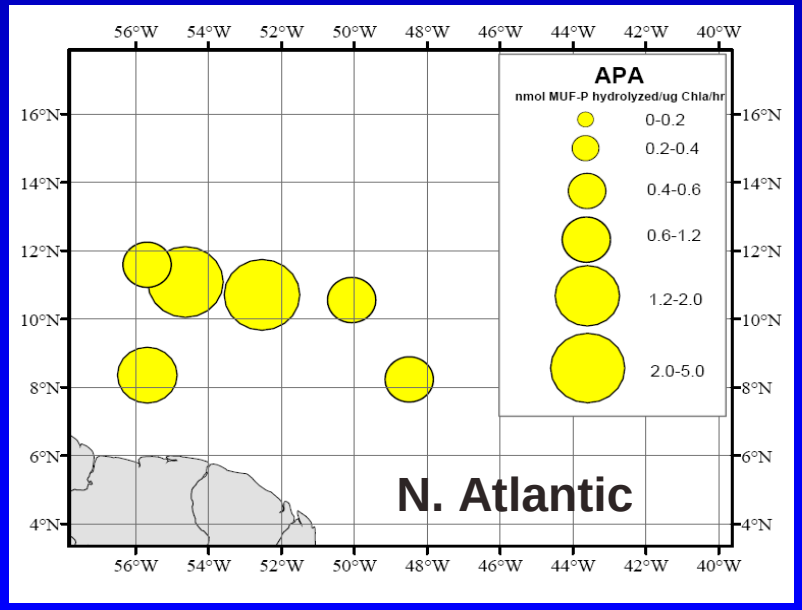
Sohm, Mahaffey & Capone, 2008, Limnol. & Oceanog.

Alkaline phosphatase activity (APA):

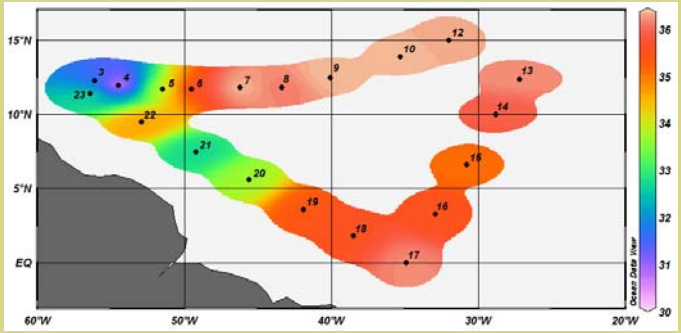
Allows plankton to utilize dissolved organic P pool

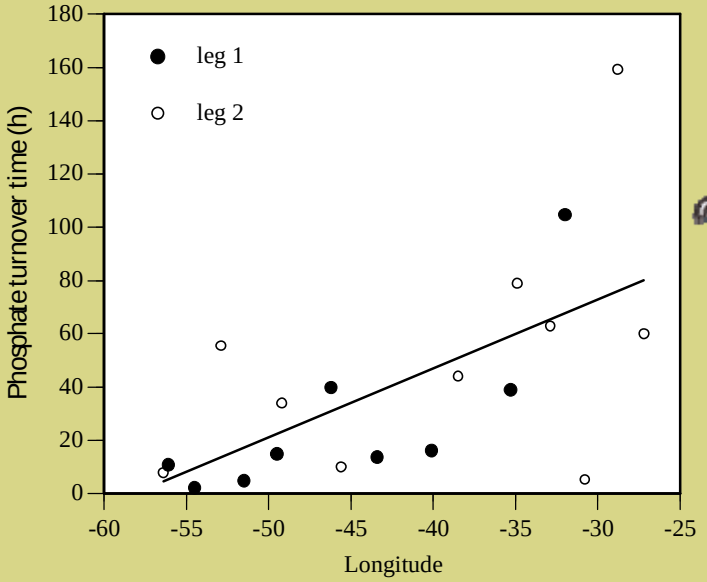
High APA is generally indicative of severe P limitation

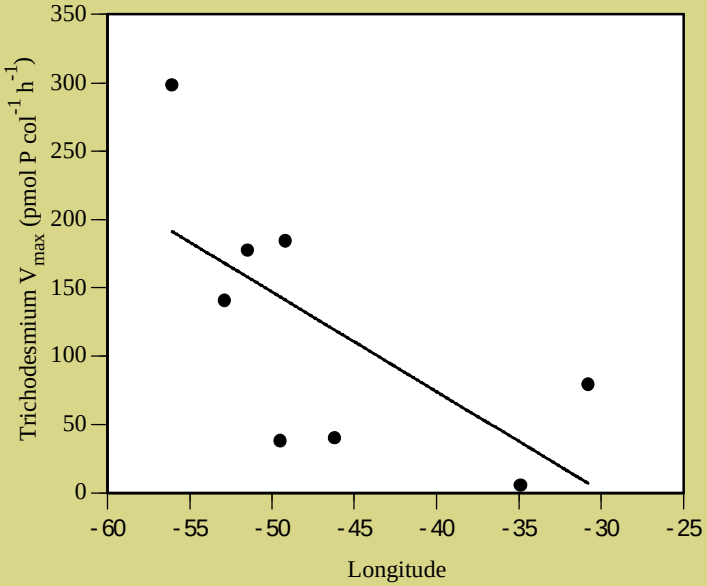




Sohm & Capone, submitted
Global Biogeochemical Cycles





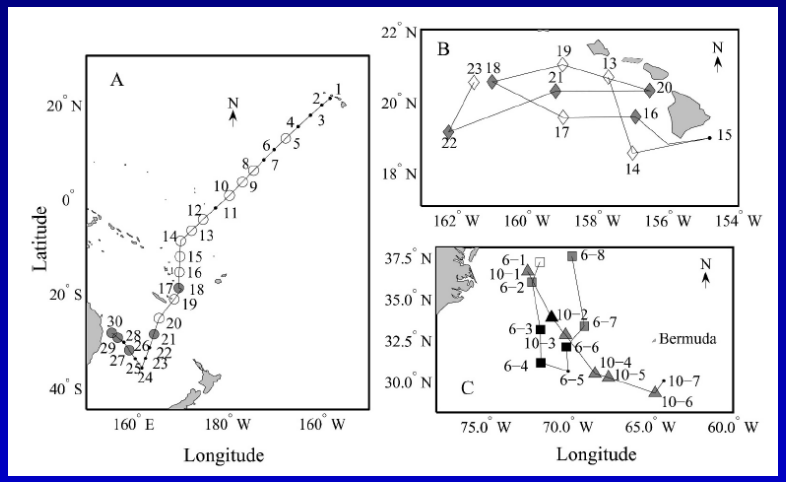


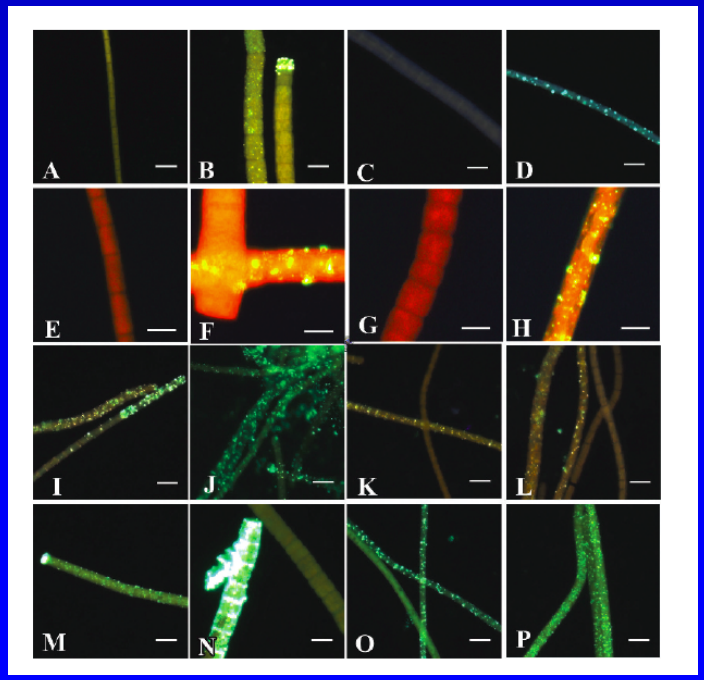
Western side of basin

- Higher V_{max} for P uptake
- Higher bulk P pool turnover

Hynes et al. 2008 Limnol & Oceanogr

Enzyme linked fluorescence-alkaline phosphatase (semi-quantitative)





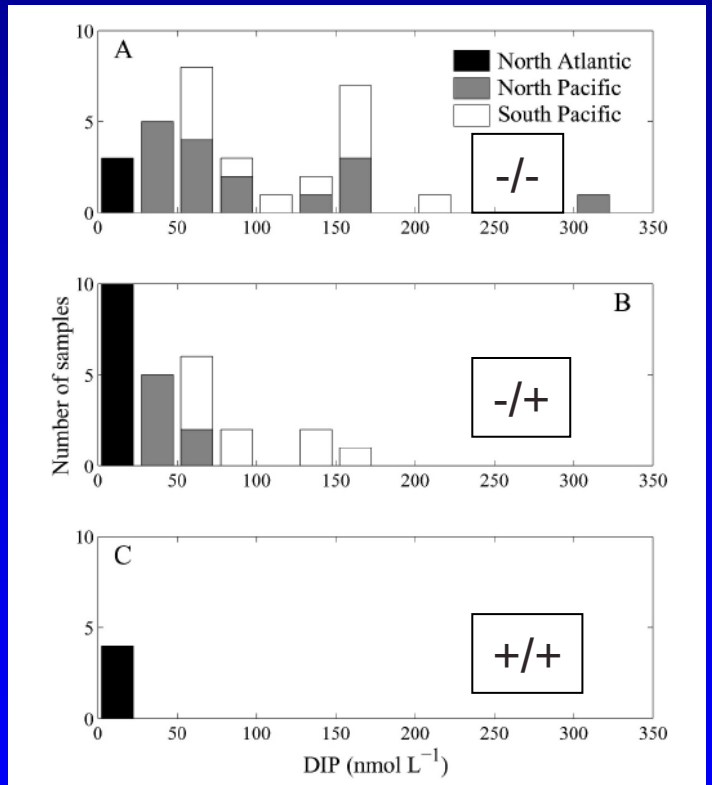
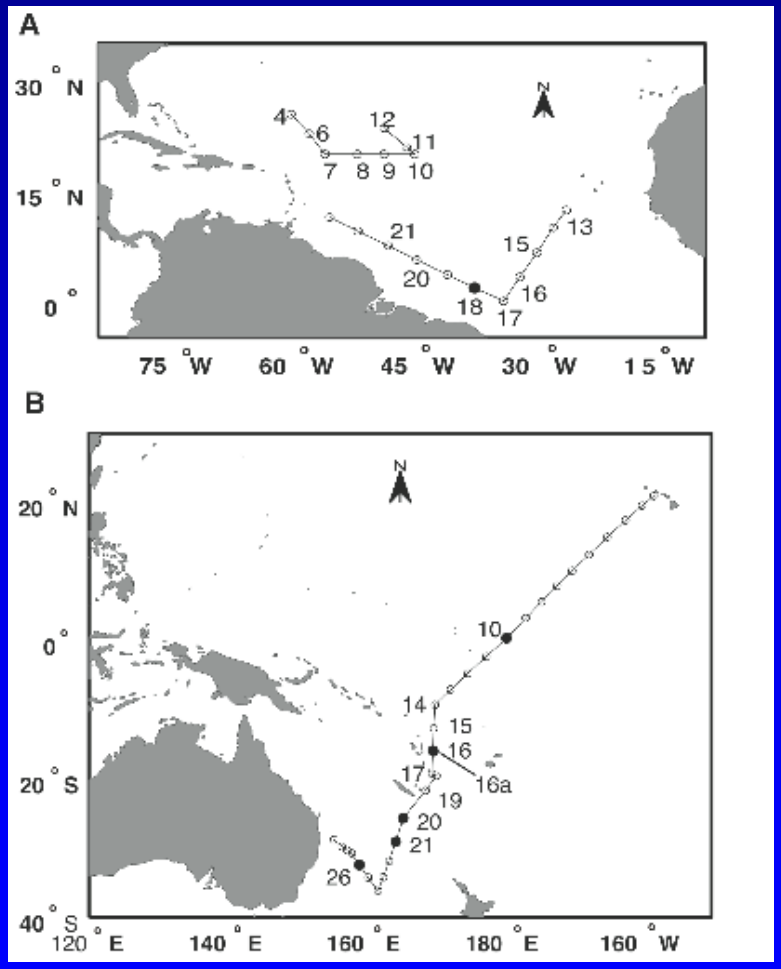
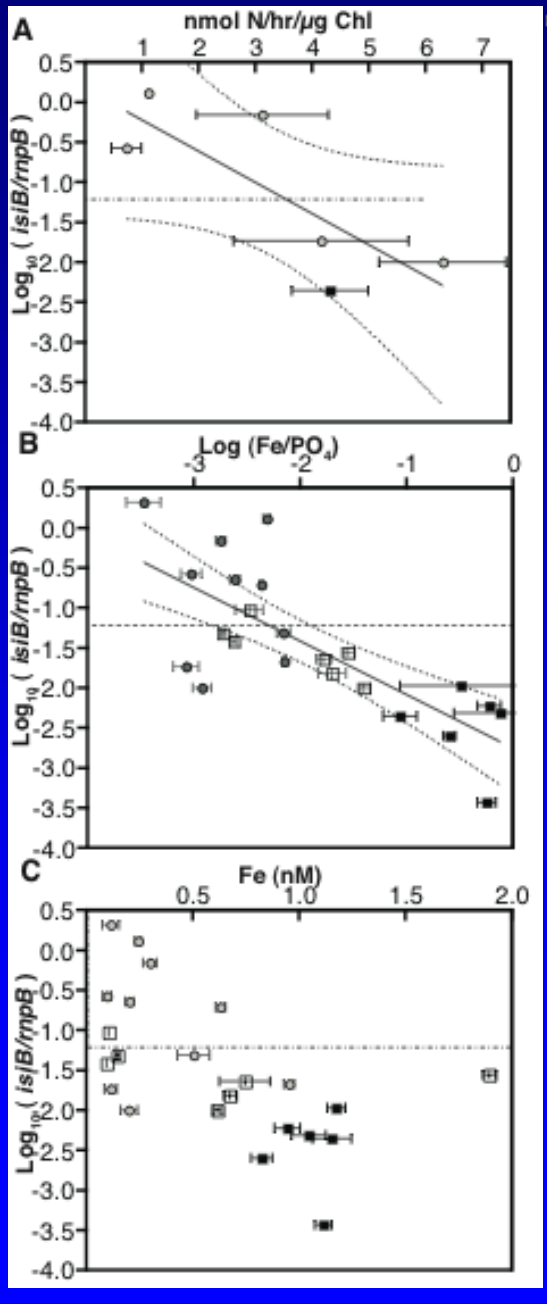


Fig. 5. Histogram of binned surface DIP concentrations (nmol L^{-1}) separated by ELF label ratings: (A) '− −', (B) '+ −', (C) '+ +'. Colors represent ocean basin: North Atlantic (black), North Pacific (gray), and South Pacific (white). Bin width is 25 nmol L^{-1}.

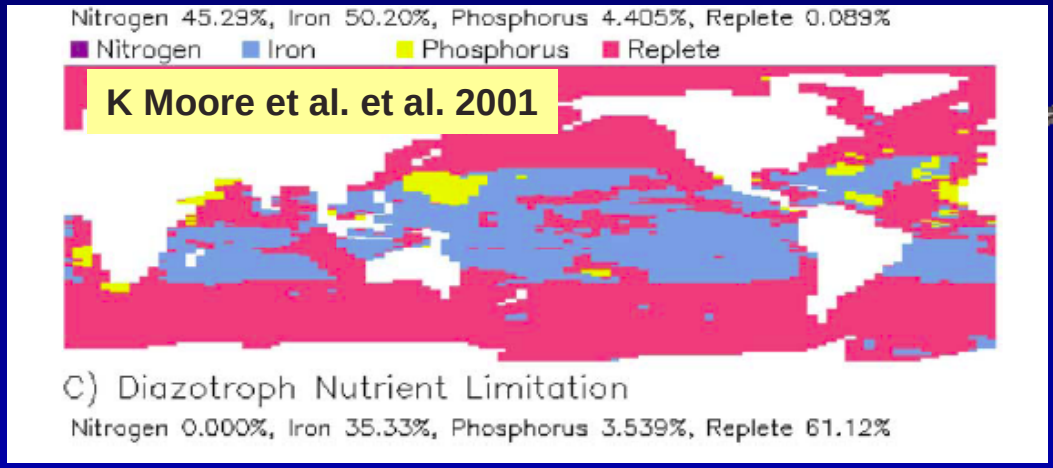
Chapell et al. manuscript

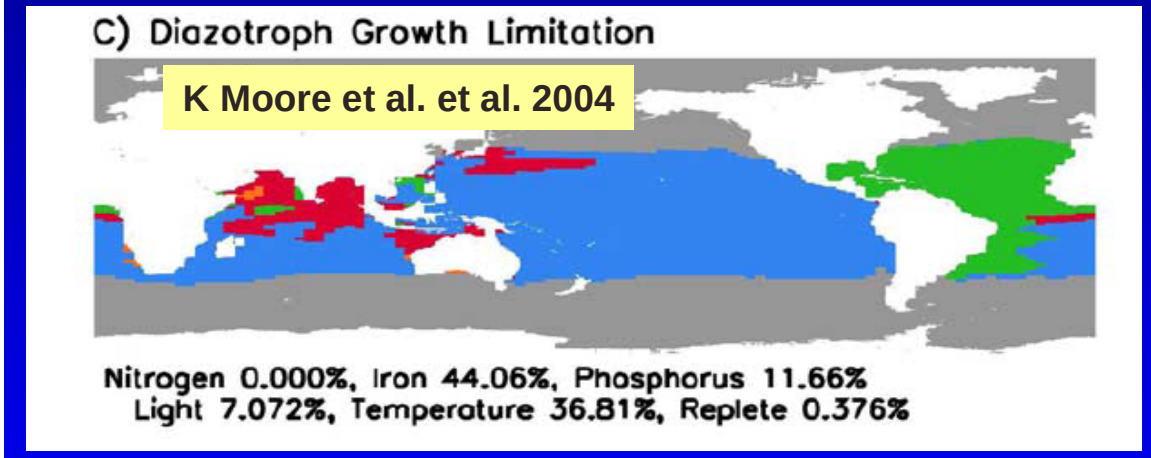
isiB- photosynthetic flavodoxin expression

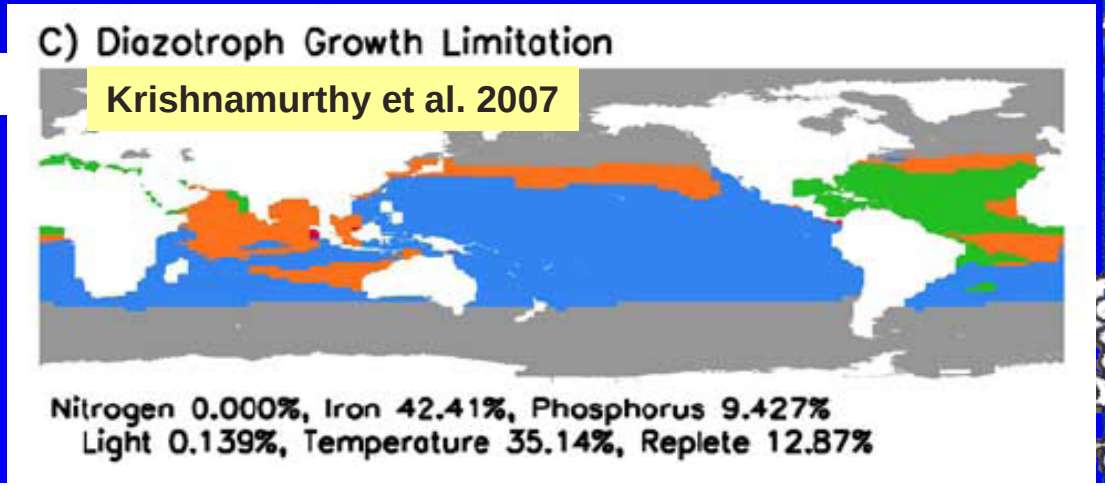




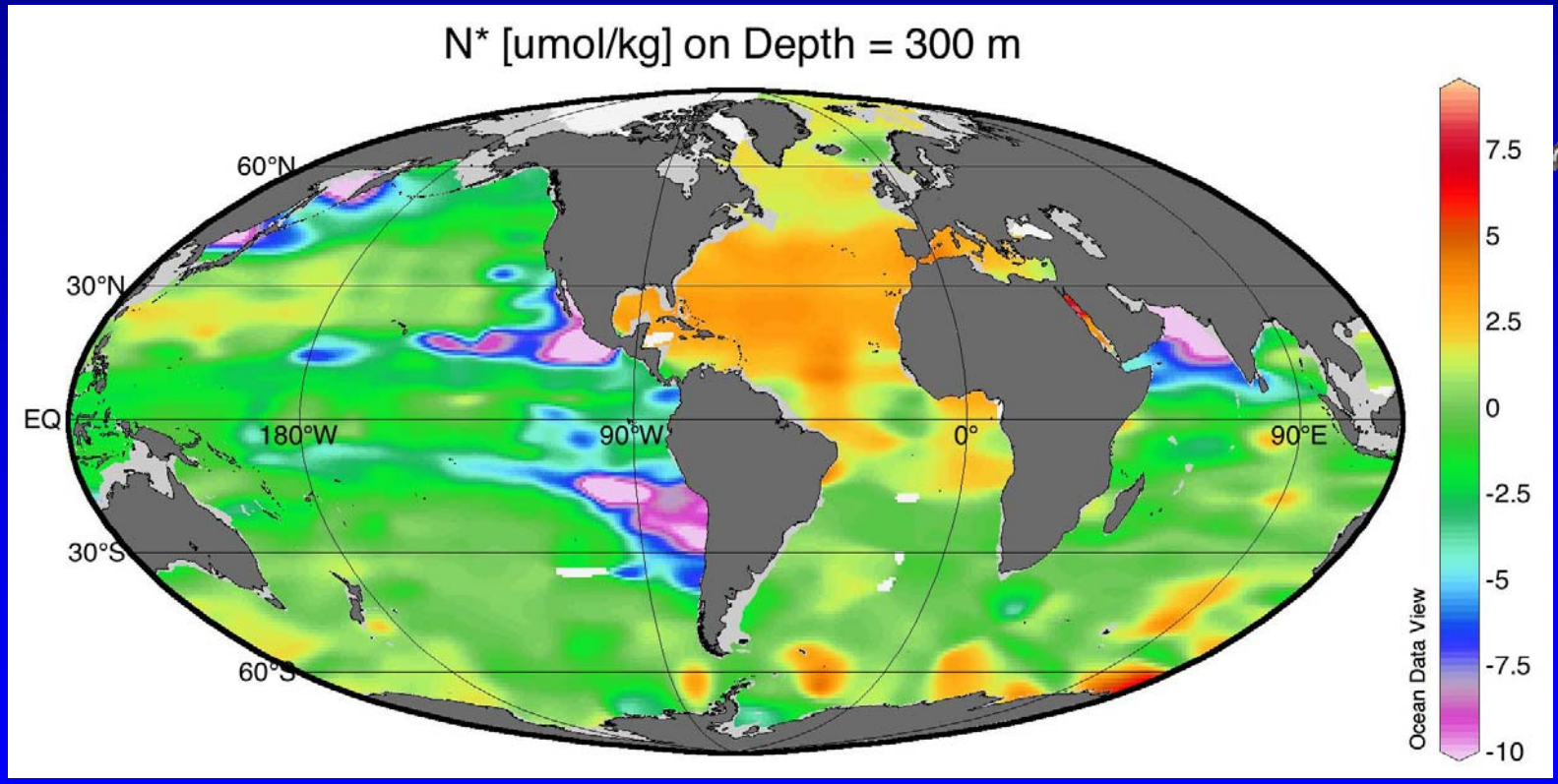
Emerging mosaics of limiting factors for diazotrophs





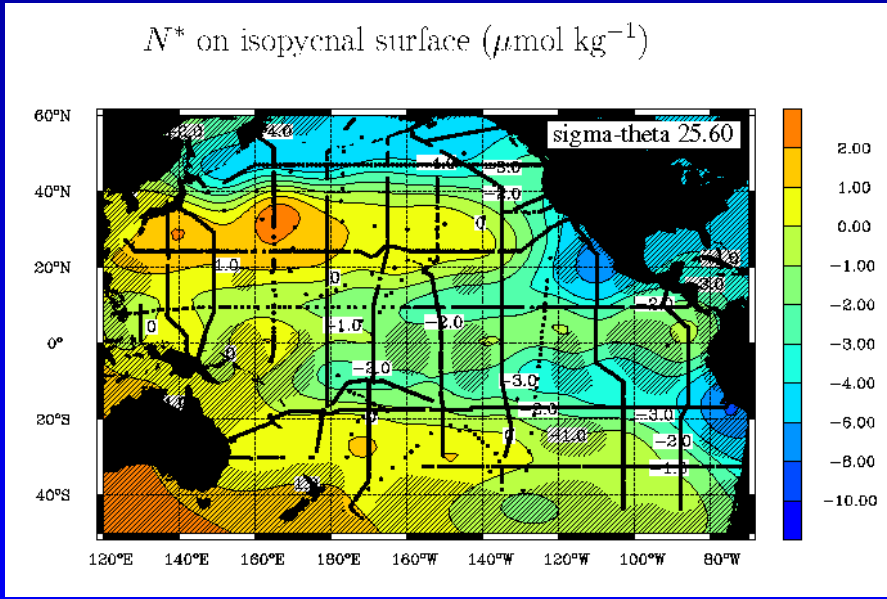


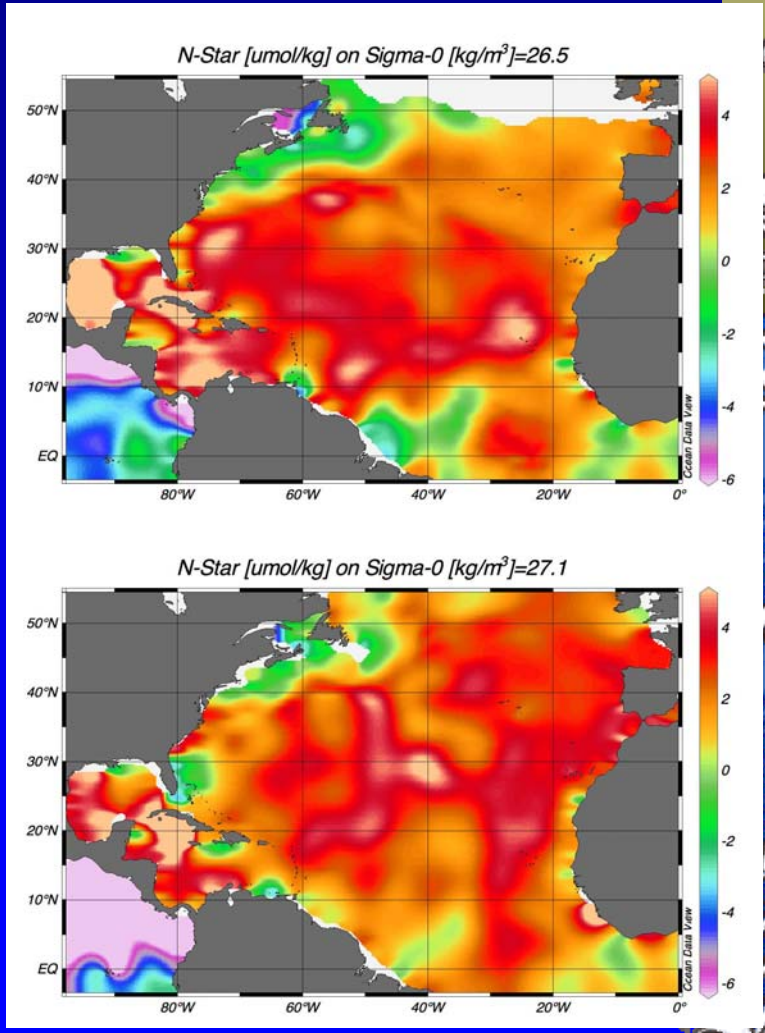
N*- Suggests Hot Spots of N_2 Fixation- e.g. Atlantic
Pacific- Hard to say w/ denitrification zones



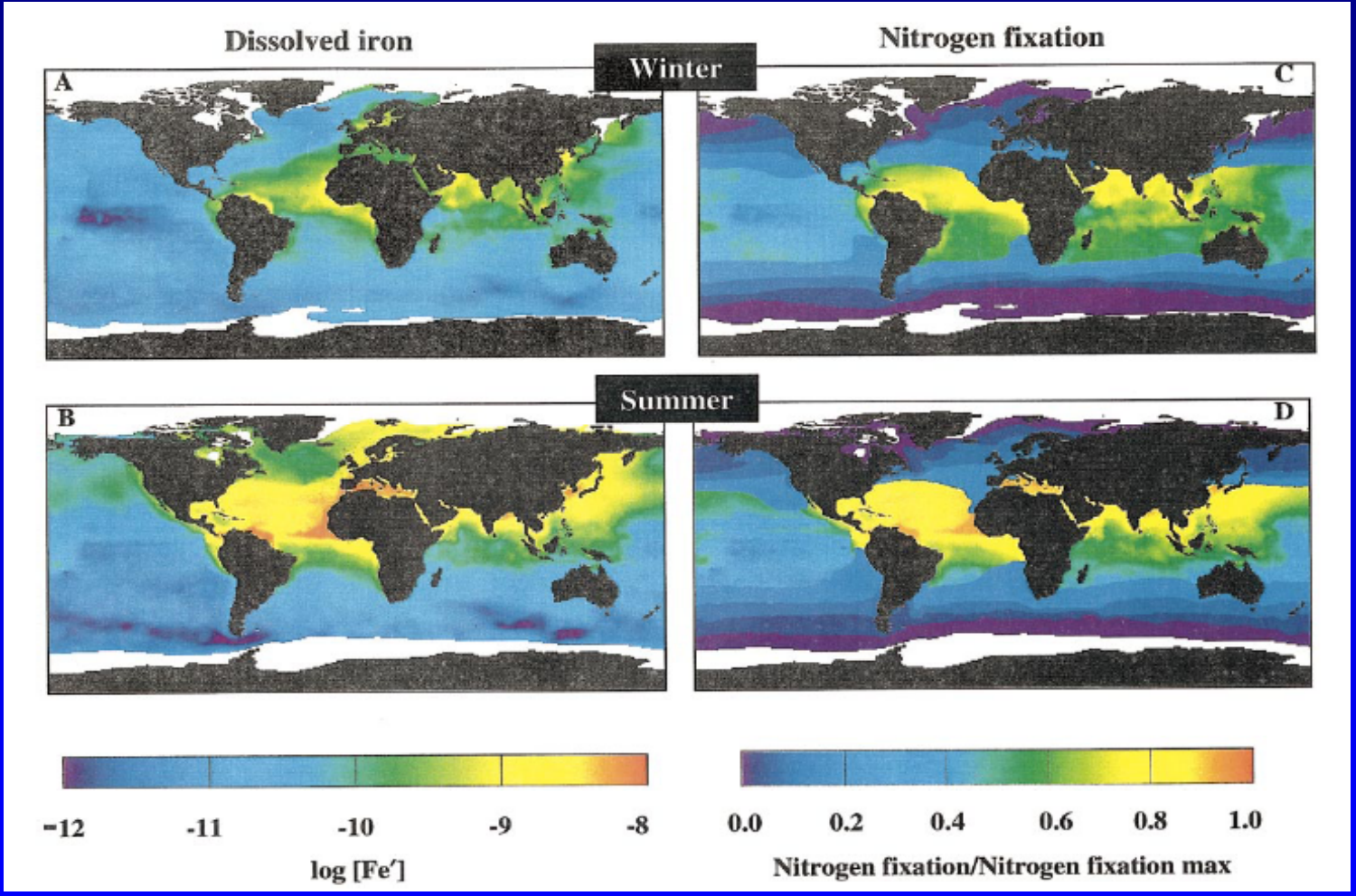
$N^* = 0.87([NO_3^-] - 16[PO_4^{3-}] + 2.9)$ (Gruber & Sarmiento 1997)

Global Patterns of N_2 Fixation



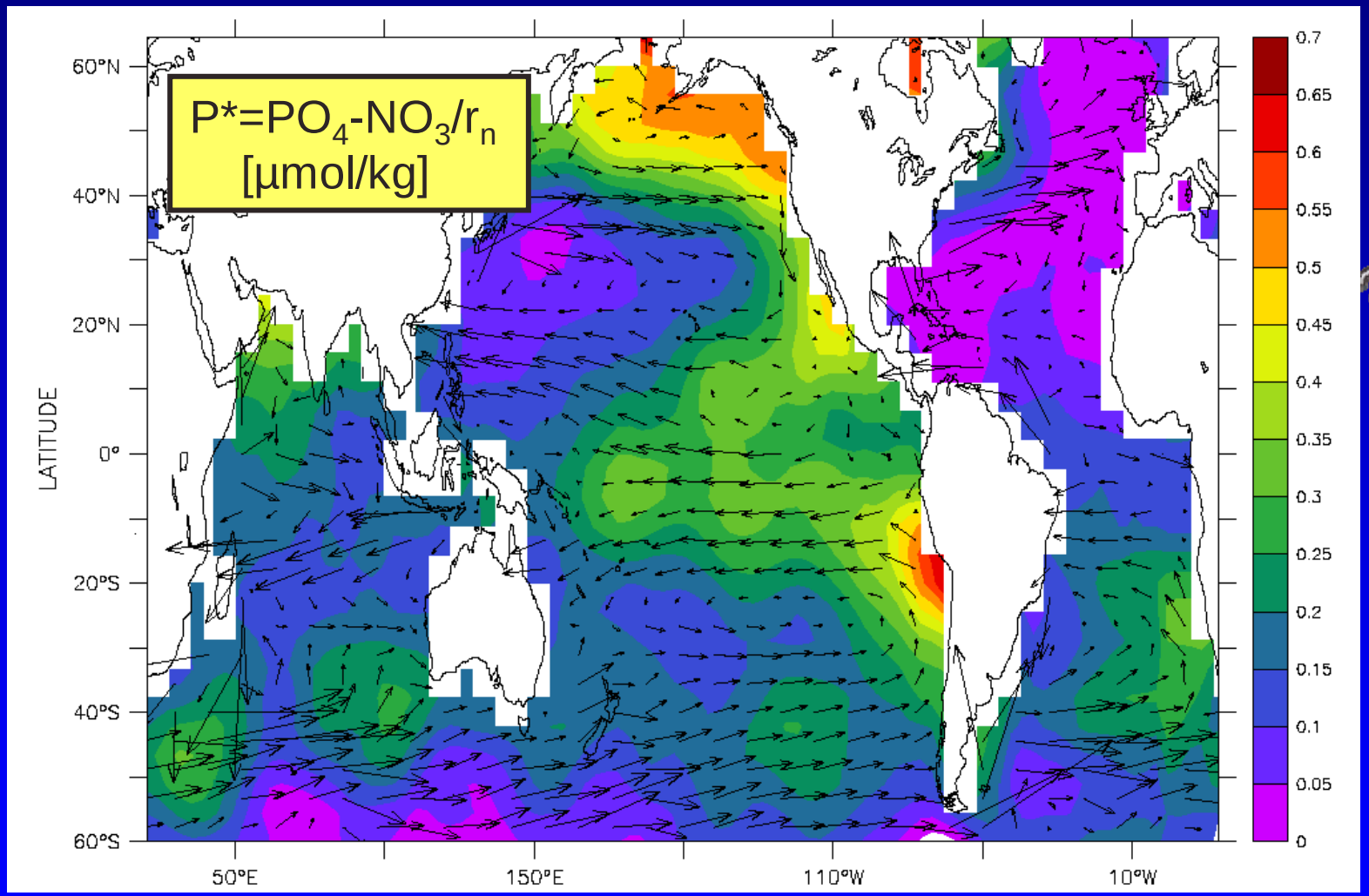


Berman-Frank et al. 2001
Limnol & Oceanogr.

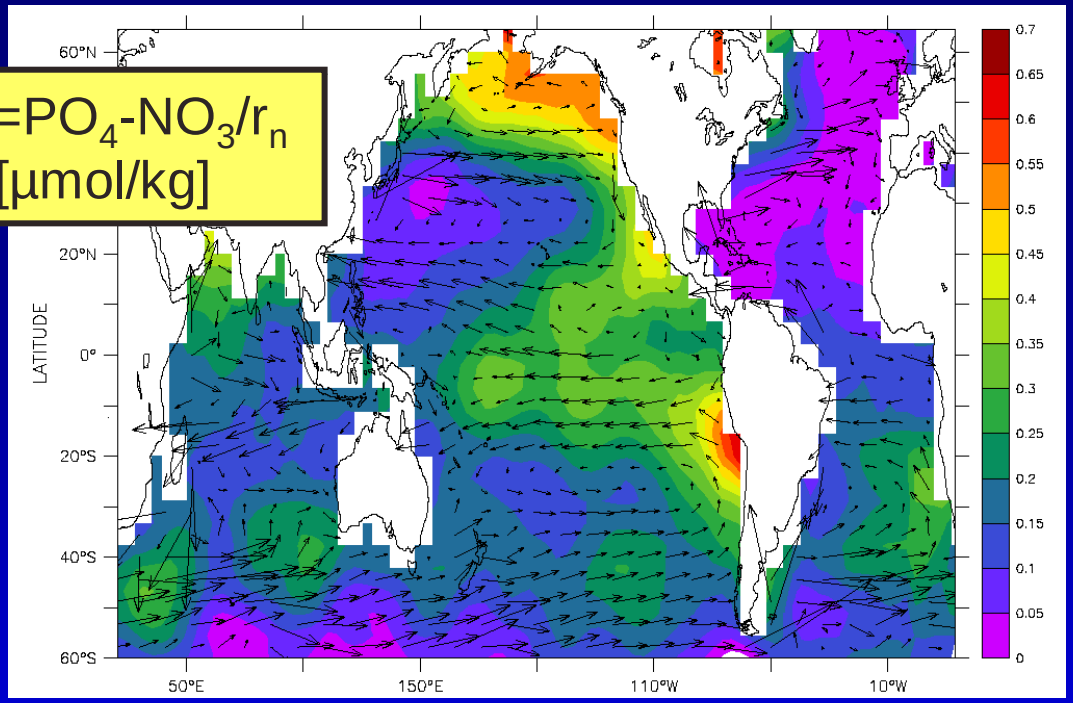


Climatological P* (0-100 m)

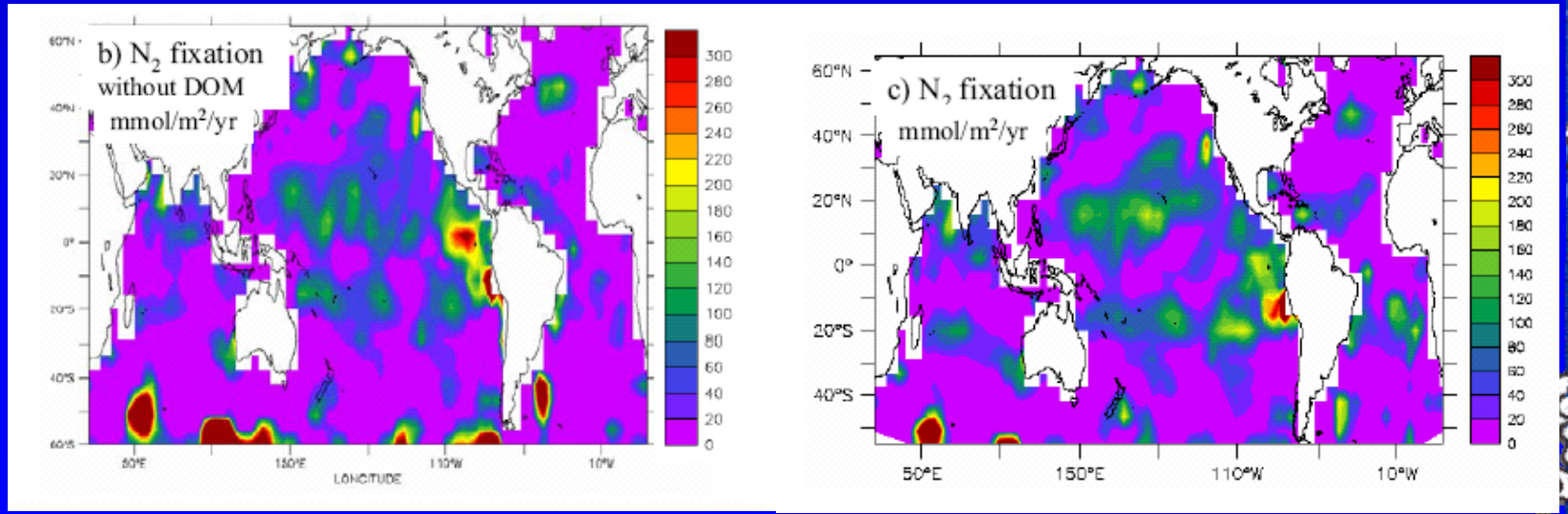
Deutsch et al., 2007, Nature World Ocean Atlas [2001] + GCM



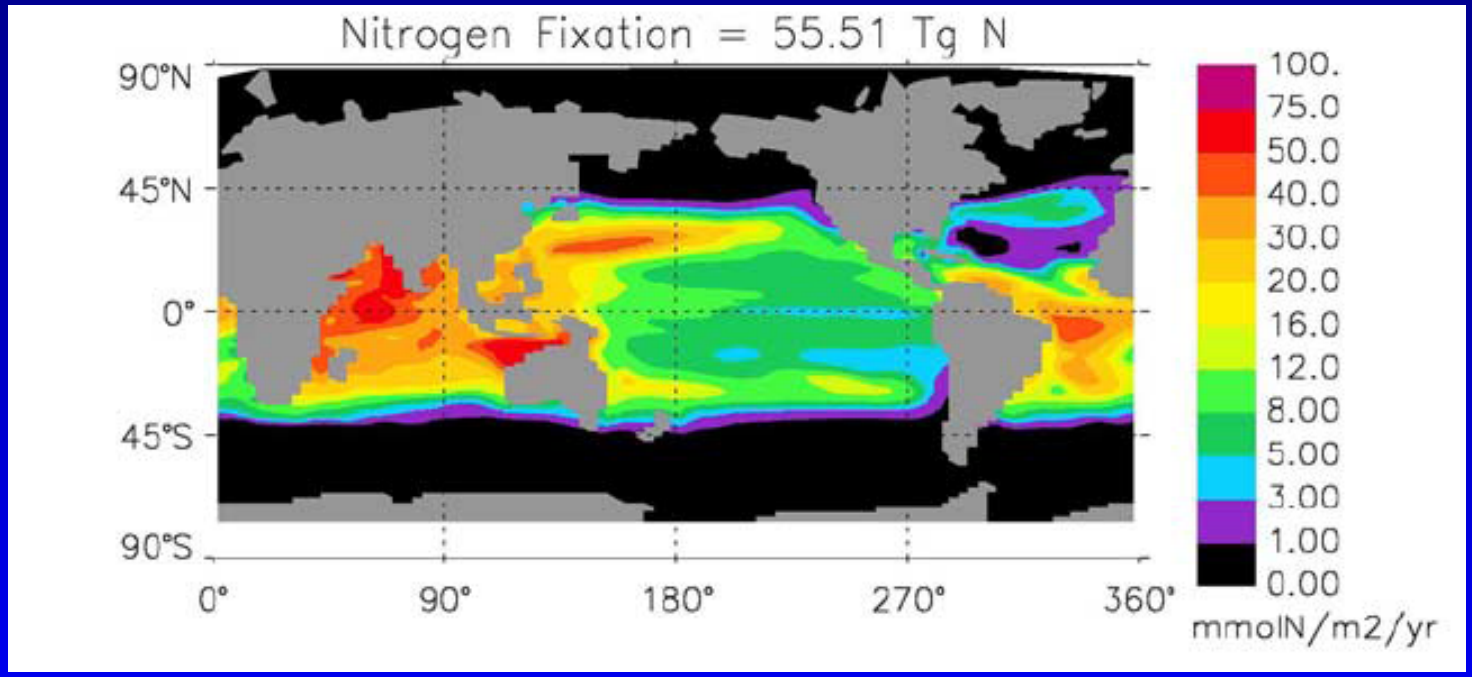
$P^* = PO_4 - NO_3/r_n$ [µmol/kg]



Deutsch et al., 2007, 140 Tg y^{-1}, Pacific & sub-tropics

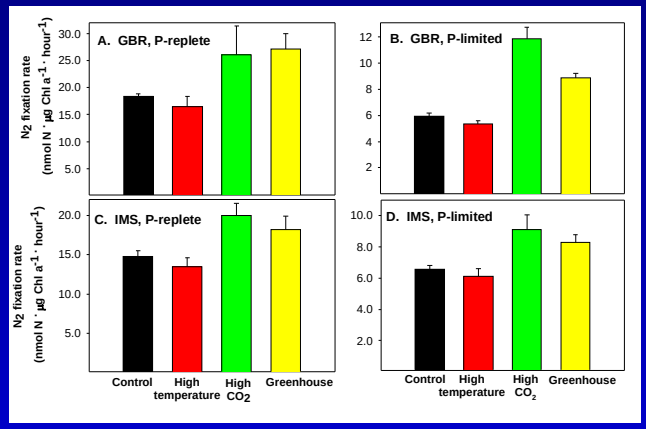


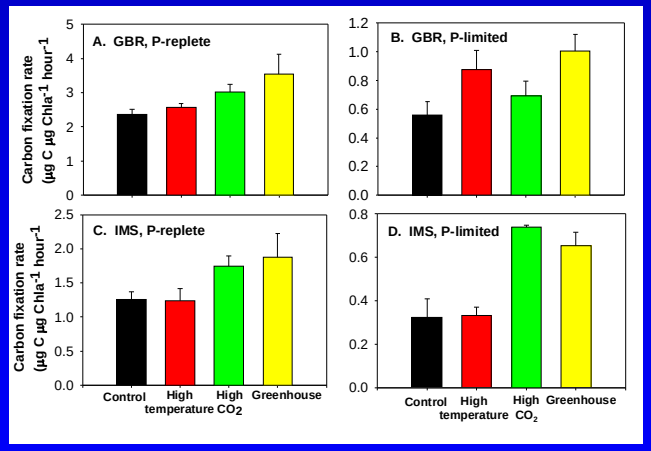
Moore et al. 2004, S. Atlantic, W. Pacific, Arabian Sea



Human/ Climate Change Impacts

- *Surface temperature*
  - *Direct enzymological effect*
  - *Increased stratification-nutrients*
  - *Migration to higher latitutdes (Breitbarth)*
- *Shifts in dust delivery*
- *Ocean chem*
  - *CO_2 increase-stimulates N_2 fixation*
  - *pH- ??*
  - *Increasing atm N deposition*
- *Diazotroph diversity*





Recap

- ***Dominant Diazotrophs***
  - Trichodesmium *dominant diazotroph in N. Atlantic*

    relative to S. Atlantic and N. Pacific
  - *Type A coccoid cyanobacteria appear dominant in No. Pacific Gyre*
- ***Primary Limiting Factors for N_2 fixation***
  - *N. Atlantic severely P limited*
  - *No. & So. Pacific Gyre, So. Atl. tend towards Fe limitation*
- ***Do these nutrient trends define diazotroph distributions?***
  - *Need e.g. uptake kinetic work with coccoids*
- ***Conflicting patterns of geochemically infered global distribution***

Acknowledgements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Students, postdocs and assistants: the folks that make things happen!

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Sergio Sanudo-Wilhelmy


Claire Mahaffey


Juliette Finzi

Robert Hamersley

Angie Knapp


Rebecca Shipe


Jay Burns

Jill Sohm

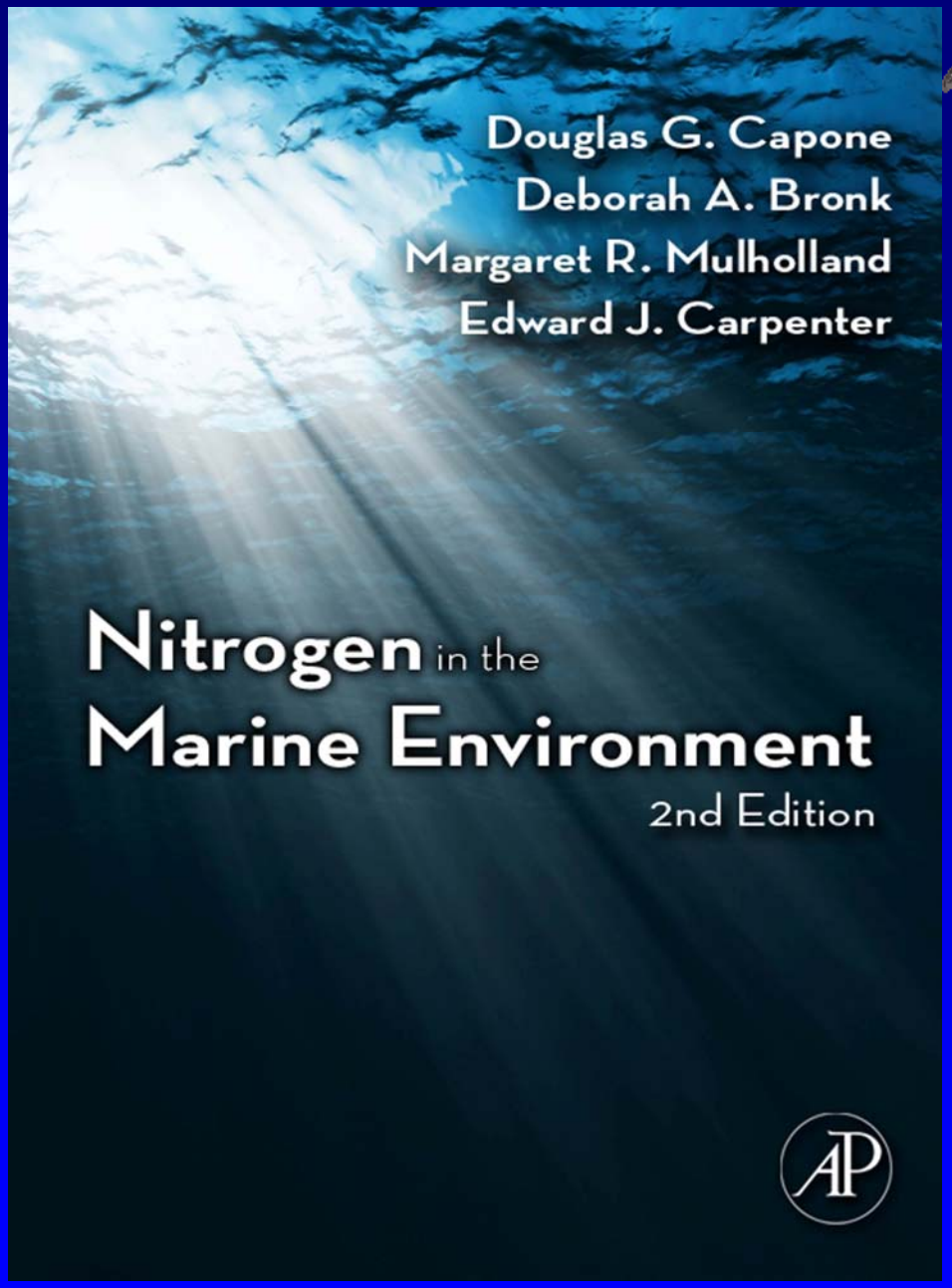

Ian Hewson


Sophie Bonnet

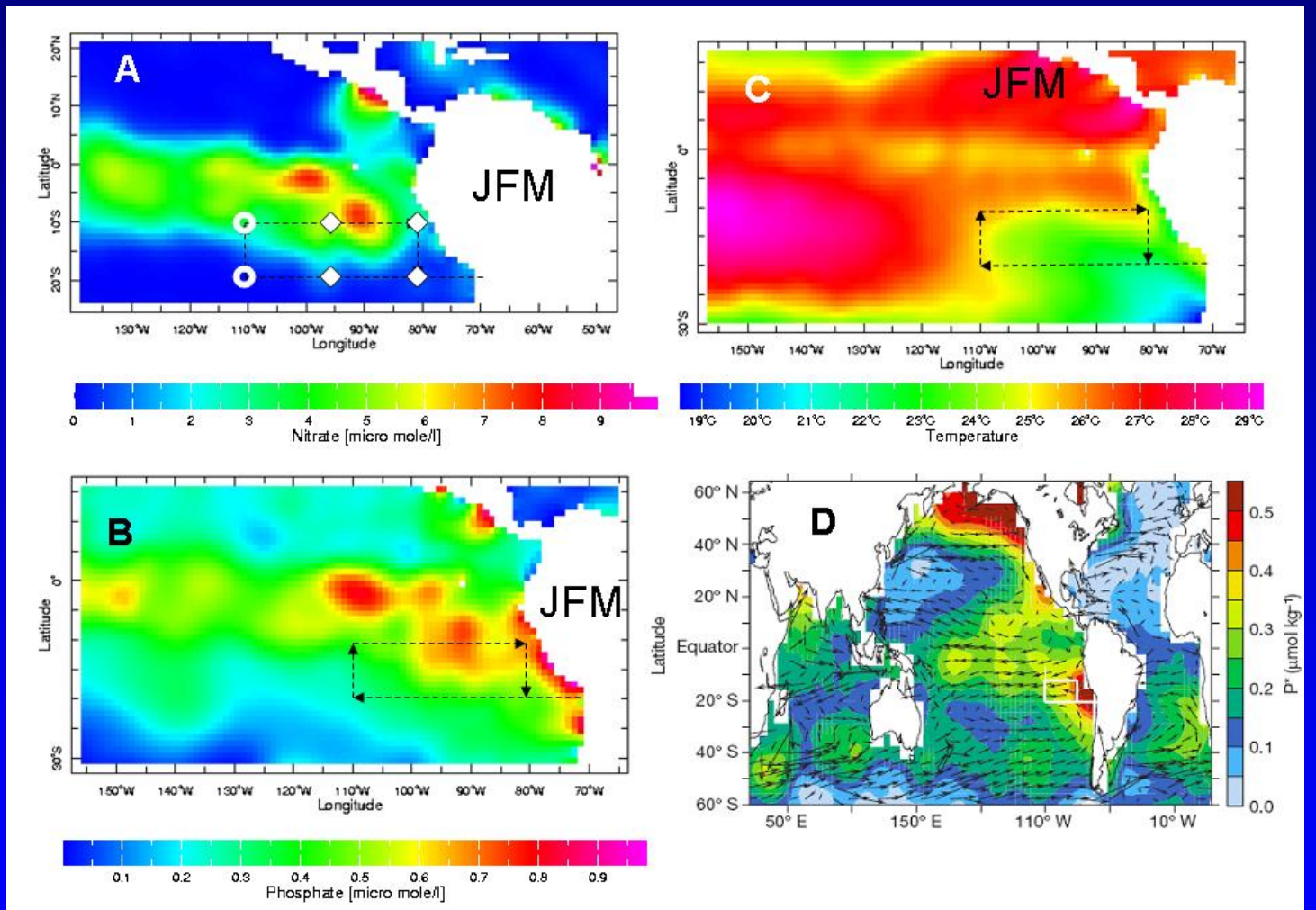

Troy Gunderson


The End
(for now…..)

Commercial moment: Now at your local newsstand!



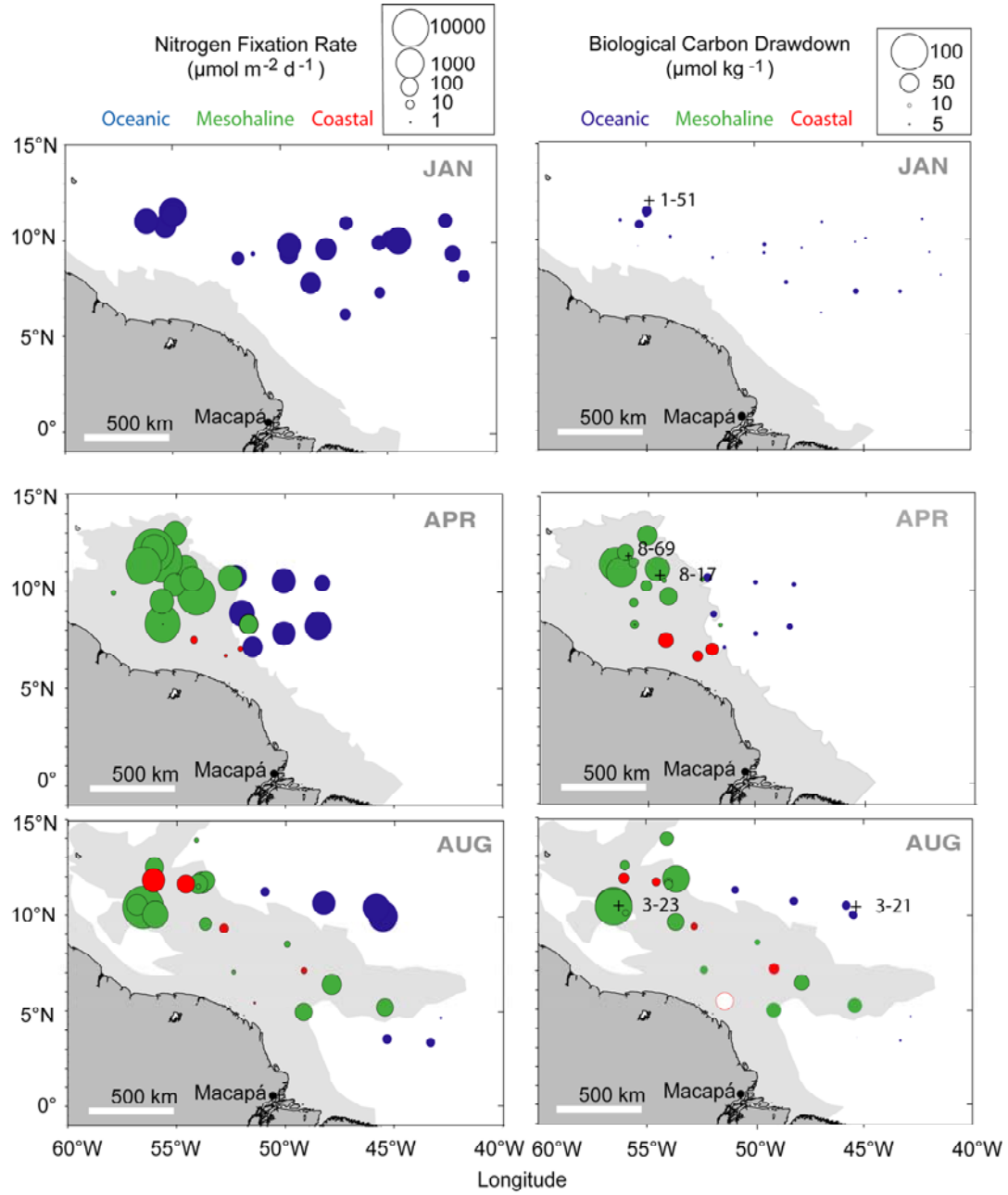
Testing the Hypothesis



Moore et al. in press Nature Geosciences

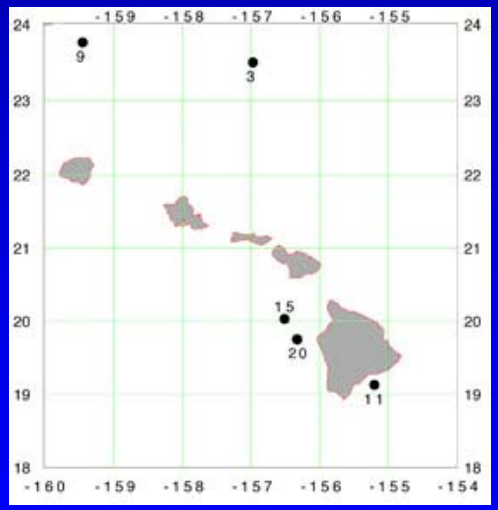
Table 1. Estimates of N inputs to the open Atlantic and global ocean.

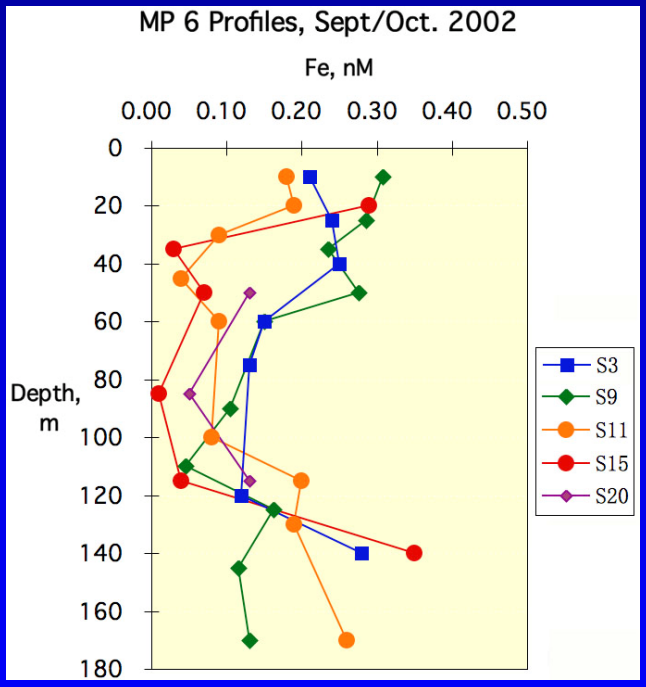
Process	Method	Value (10^{11} mol N y^{-1})	Ref
North Atlantic N_2 fixation	Scaled direct biological rates for *Trichodesmium*	16	17
"	N* accumulation in thermocline	20	11
"	N* accumulation in thermocline[¶]	4 (7)	19
Whole Atlantic N_2 fixation	P* flux convergence	14	3
Net N* increase in Atlantic overturning circulation	N* divergence in upper limb between 30°S and 36°N[†]	11 ± 3	This study
"	Deep water N* distribution combined with NADW formation rate[‡]	15 ± 4	This study
Global N_2 fixation	P* flux convergence	100	3


Nitrogen Fixation Rate
(μmol m-2 d-1)
10000
1000
100
10
1
Oceanic
Mesohaline
Coastal
Biological Carbon Drawdown
(μmol kg-1)
100
50
10
5
Oceanic
Mesohaline
Coastal
JAN
APR
AUG
1-51
8-69
8-17
3-23
3-21
500 km
Macapá
15°N
10°N
5°N
0°
60°W
55°W
50°W
45°W
40°W
Longitude

Boyle lab- Biocomplexity data

- N. Pacific Fe limited

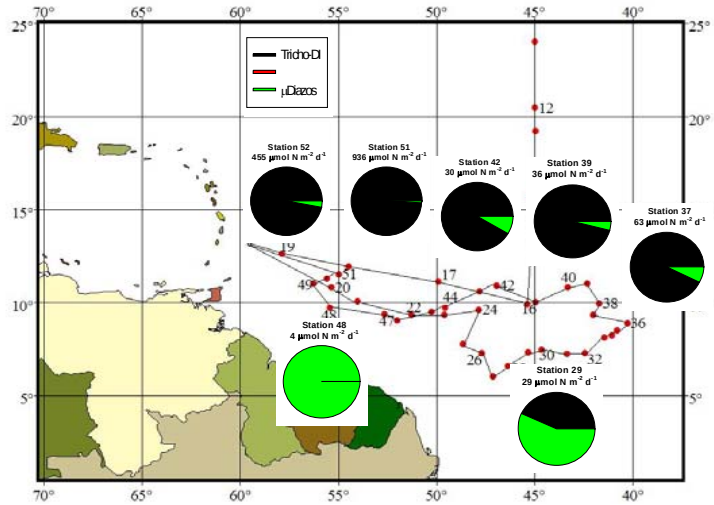




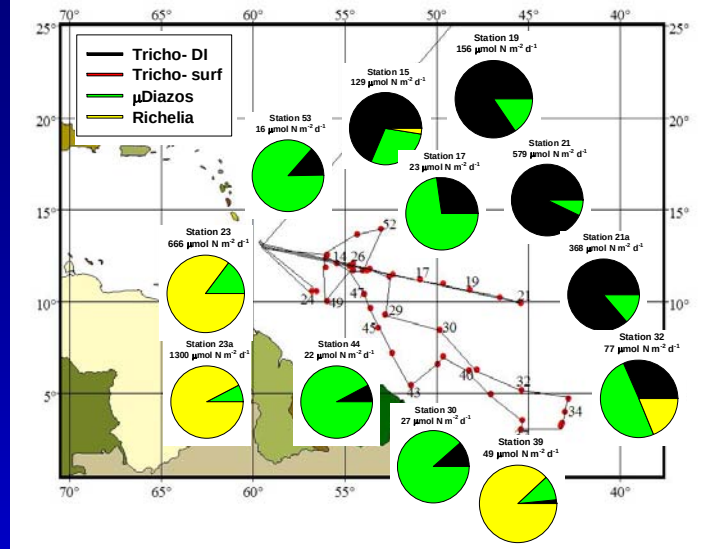
Possibilities

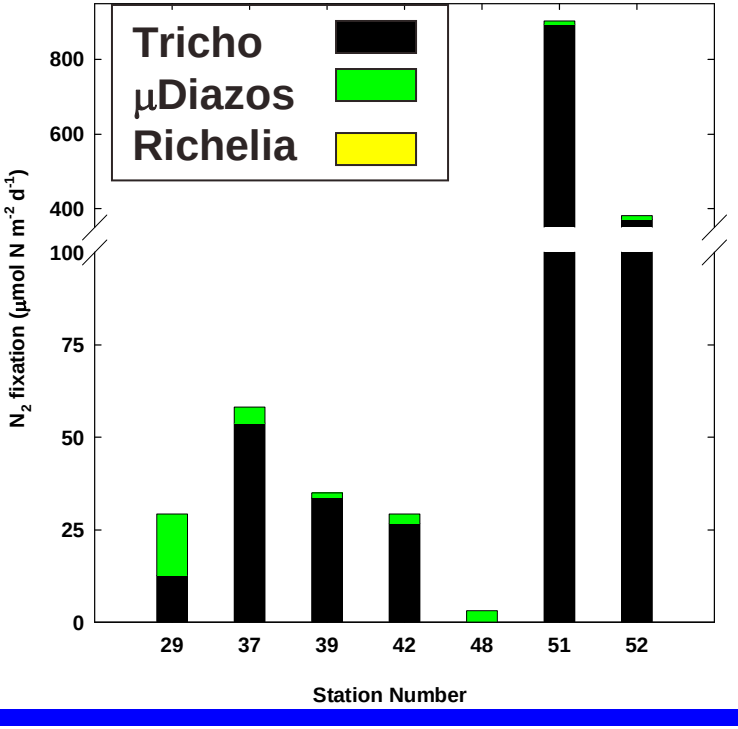
- ***Overestimation of removal:***
  - ***i.e. Denitrification (broadly defined)***
  - ***Anammox consumes "recycled" N- NO_3 consump in OMZs 50 % of prior estimates- Lam et al. submitted***
- ***Underestimation of inputs***
  - ***Other sources in the upper euphotic zone***
    - ***e.g. pico/ nanoplankton***
  - ***In the deep sea below the euphotic zone?***
    - ***Holl & Montoya 2006- NO_3 effects***
  - ***Low levels at higher latitudes-***
    - ***Needoba et al. 2007, Holl et al. 2007***
- ***The "Deutsch" solution: Inputs proximal to removal (OMZs)?***
  - ***N fix can respond over shorter time scales to N:P variability***

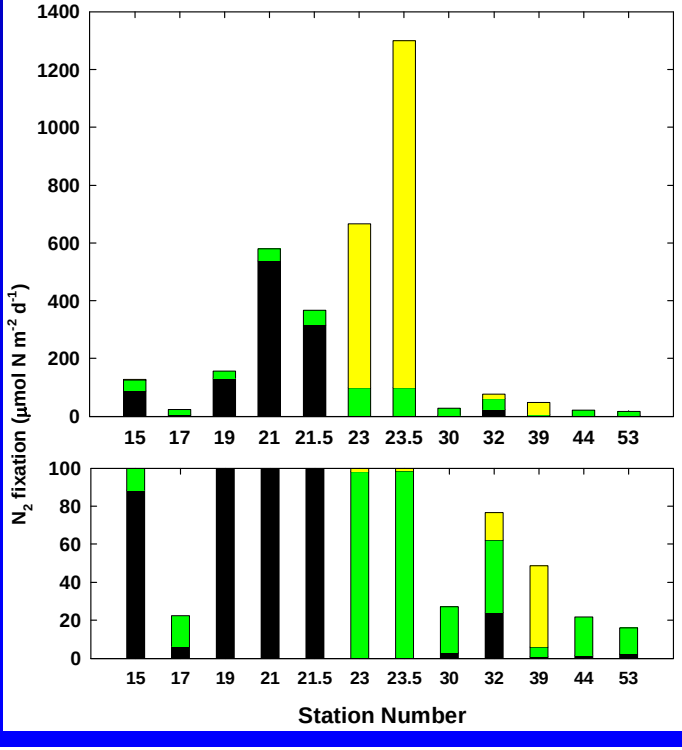
Winter Tropical N.W. Atlantic Summer



MP 01







Foster et al. 2008

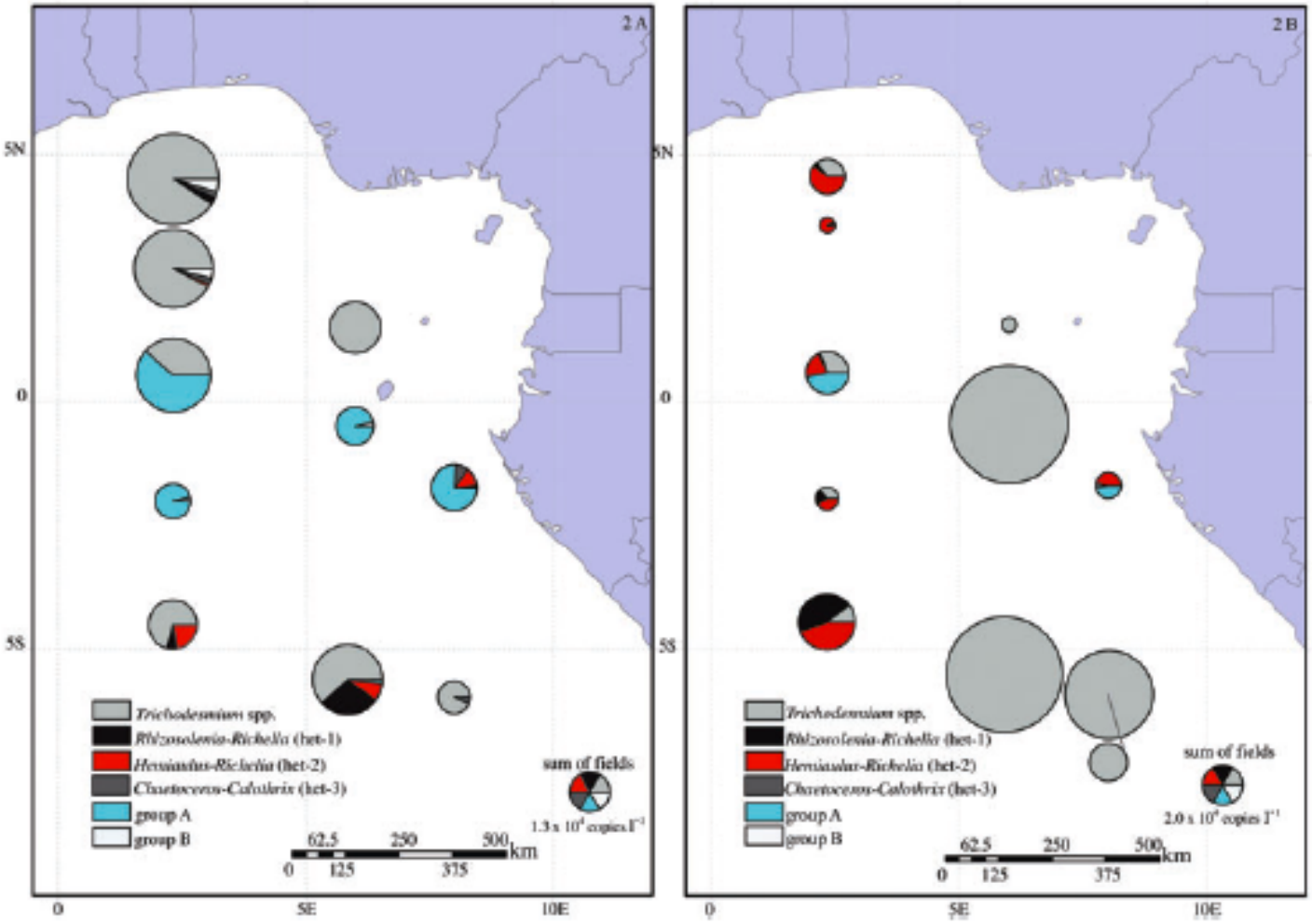
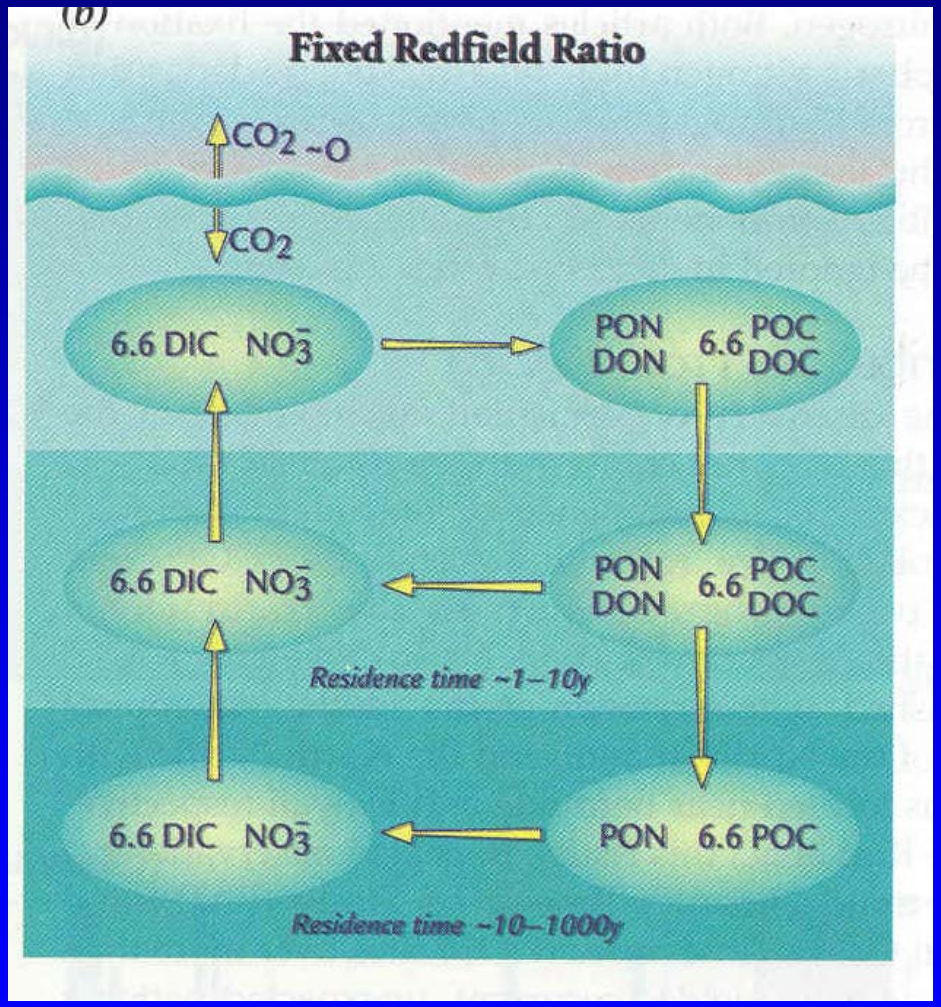


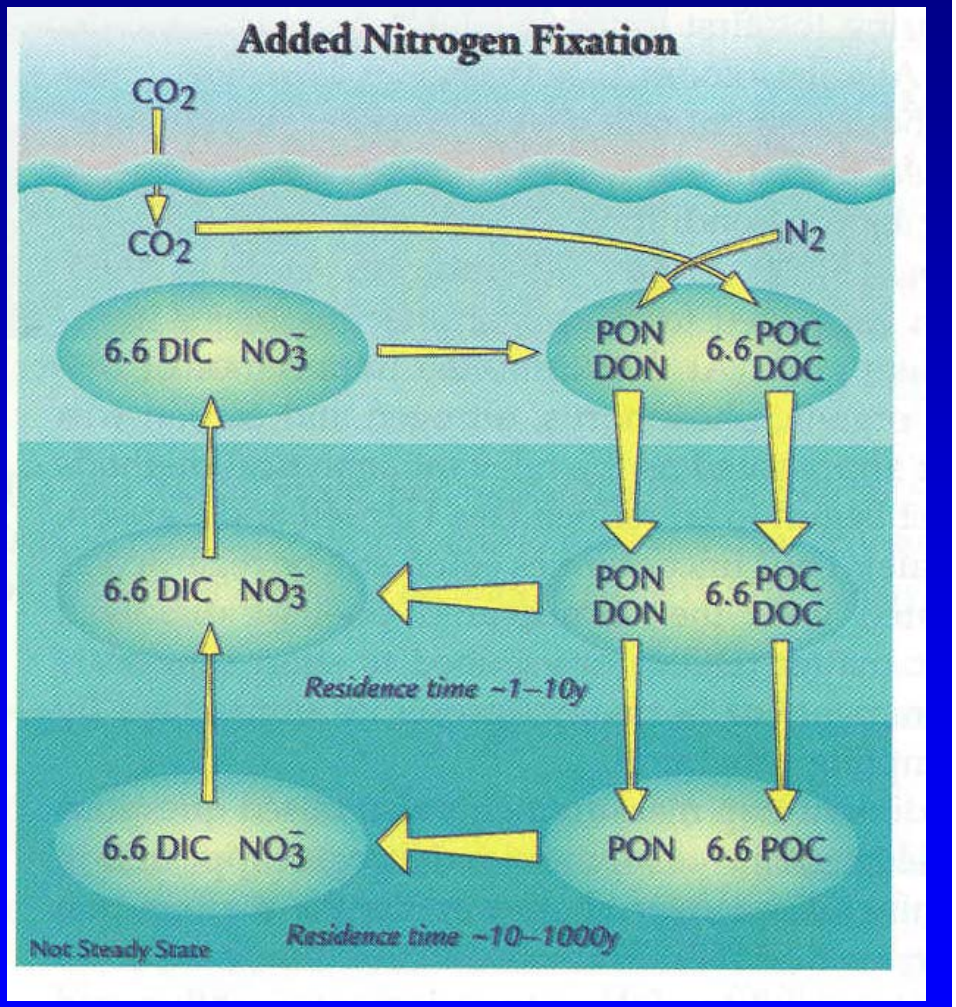
Fig. 2. Results from q PCR assays from surface samples collected in the Gulf of Guinea in June 2007.
A. The abundance of *nifH* gene copies l^{-1} from q PCR assays.
B. Results from the q RT-PCR assays for determining *nifH* gene expression (cDNA *nifH* copies l^{-1}).
Note that since only daytime samples were retrieved, group B was not included in the transcript abundance analyses.

Conundrum Status

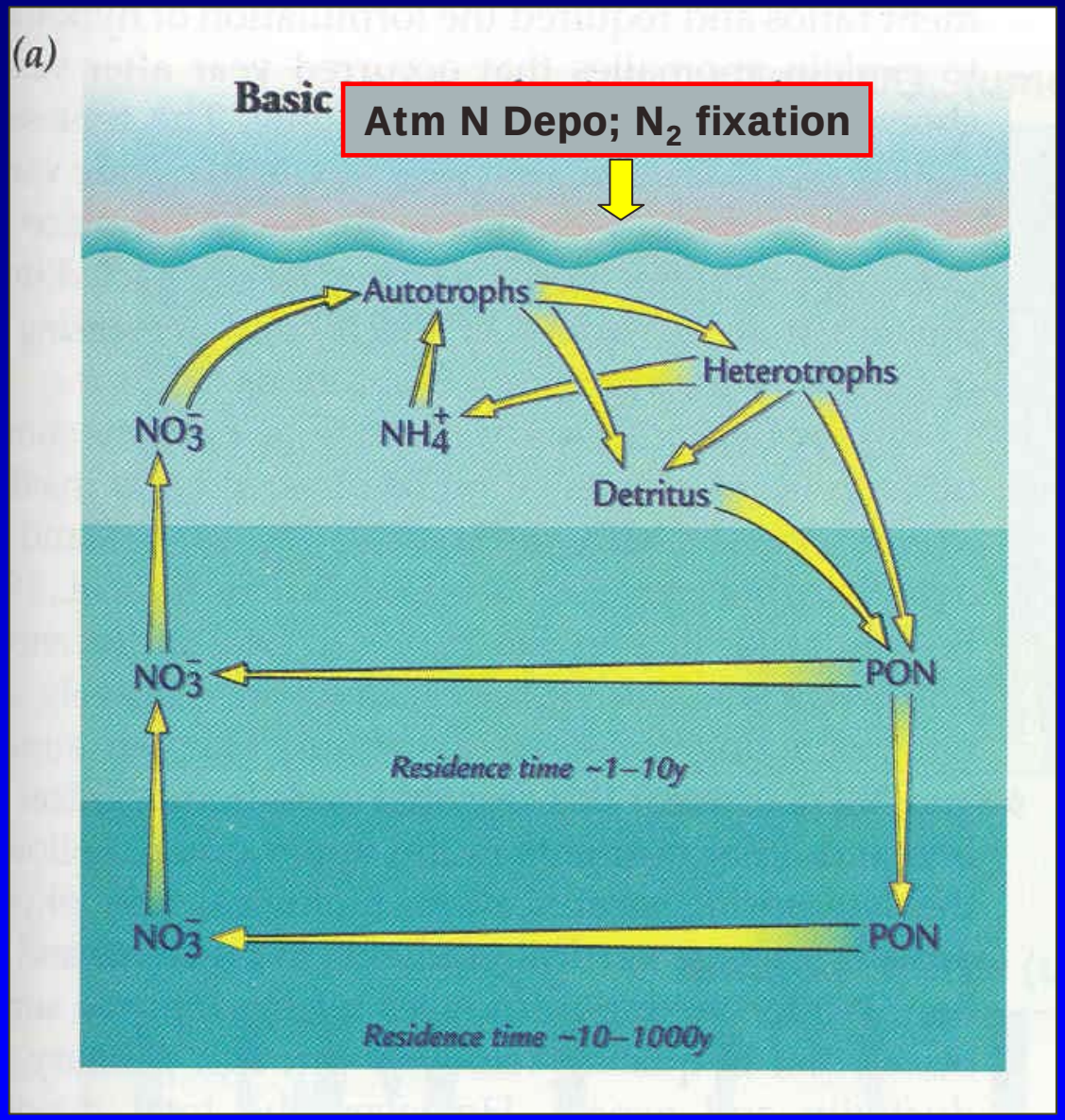
- *Several Independent lines of evidence suggest N_2 fixation is occurring at significant rates in waters affected by N loss processes*
  - several independent geochem estimates
  - biological assays
  - nif genes
  - remote sensing
- *Solution to coupling of N Fix and NO_3 consumption w/ OMZs*
  - *More field data needed to verify*
- *Potential areas for Fe fertilization/ C sequestration*
- *New conundrum- what N* and P* tell us about the distribution of N_2 Fixation in the Ocean*

Recent Motivation: N_2 fixation provides a pathway for atmospheric CO_2 uptake in the open ocean





Redfield C:N:P: 106:16:1


(a)
Basic
Atm N Depo; N_2 fixation
Autotrophs
Heterotrophs
NO_3^-
NH_4^+
Detritus
NO_3^-
PON
Residence time ~1–10y
NO_3^-
PON
Residence time ~10–1000y