surface ocean solas lower atmosphere study

Dinitrogen fixation above/IN Oxygen Minimum Zones

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Contributing authors
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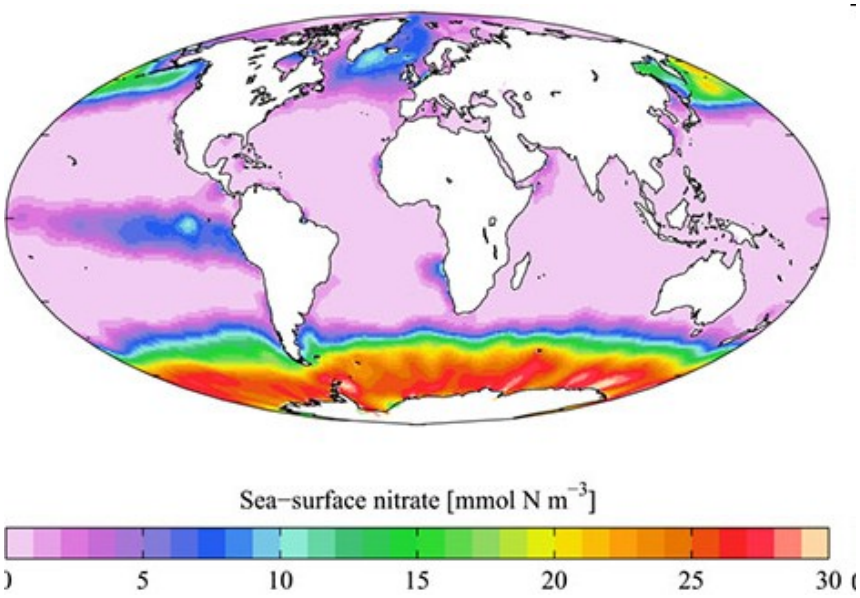
NITROGEN : A CRITICAL NUTRIENT IN THE OCEAN

- Nitrogen is essential for life
  - protein synthesis (enzymes → major metabolic processes)
  - photosynthesis (constituant of chlorophyll, light collection…)

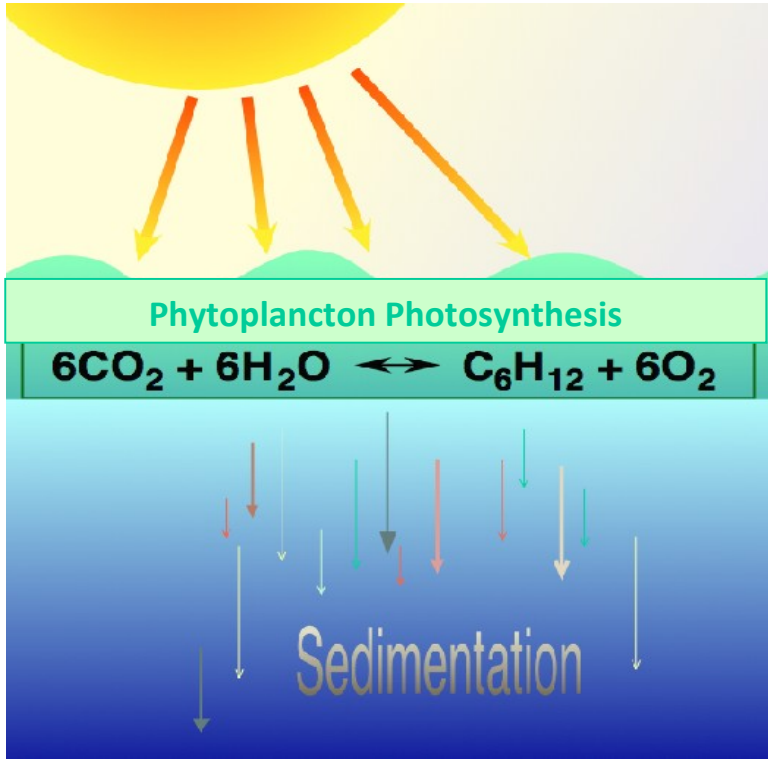
- The surface ocean is mostly depleted in nitrate



NITROGEN : A CRITICAL NUTRIENT IN THE OCEAN

- Nitrogen often limits the efficiency of the biological carbon pump

Carbon sequestration → about 30% of human C02 emissions



Primary Production 45 x 1015 g C.yr-1 (IPCC)

NITROGEN INVENTORY IN THE OCEAN

Species	Mean conc. euphotic zone (mmol m^{-3})	Mean conc. aphotic zone (mmol m^{-3})	Oceanic inventory (Tg N)
Nitrate, NO_3^{-} [a]	7	31	5.8×10^5
Nitrite, NO_2^{-} [b]	0.1	0.006	160
Ammonium, NH_4^{+} [c]	0.3	0.01	340
Dissolved Organic N, *DON* [d]	6	4	7.7×10^4
Particulate Organic N, *PON* [e]	0.4	0.01	400
Nitrous oxide, N_2O [f]	0.01	0.04	750
Fixed Nitrogen [g]			6.6×10^5
Nitrogen gas, N_2 [h]	450	575	1×10^7

Is this N2 form available for phytoplankton?

Gruber (2008)

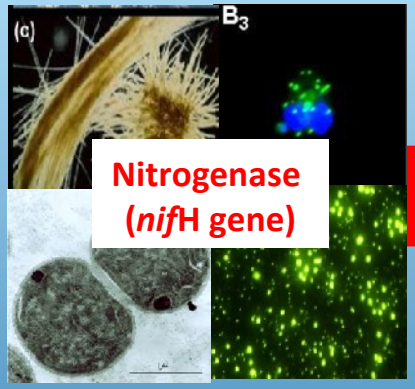
YES → ONLY SOME PROKARYOTES → DINITROGEN FIXATION

Global N2 Fixation
100 - 120 x 1012 g N.yr-1

Atmosphere

Water column

N2 + 8H + + 8e- → 2 NH3 + H2

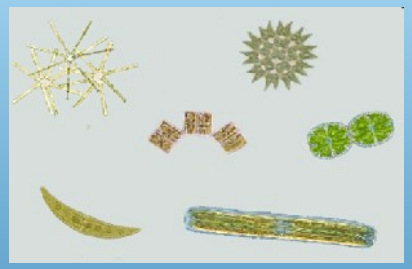


High ecological advantage in NO3-depleted waters

'New' N

Sustains up to 50% 'new' PP

Karl et al., (1997)



?

Higher trophic Levels

Thermocline

BUT

High Fe requirements
High ATP
O2 inhibition

≥ NO3- diffusion
Capone et al., (2005)
Bonnet et al., (2011)

Exported organic matter

N2 fixation

$N_2 + 8H^+ + 8e^- \rightarrow 2\,NH_3 + H_2$

Denitrification

$NO_3^- \rightarrow NO_2^- \rightarrow NO + N_2O \rightarrow N_2$

Anammox

$NH_4^+ + NO_2^- \rightarrow N_2 + 2H_2O$.

DINITROGEN FIXATION → MAJOR EXTERNAL SOURCE OF N

But global N budget not balanced

N SOURCES

N SINKS

Process	Codispoti *et al.*[a]	Galloway *et al.*[a,b]	Gruber[a]
		Sources (Tg N yr^{-1})	
Pelagic N_2 fixation	117	106	120 ± 50
Benthic N_2 fixation	15	15	15 ± 10
River input (DON)	54	18[c]	35 ± 10
River input (PON)	36	30	45 ± 10
Atmospheric		33	50 ± 20
Total sources		202	265 ± 55
		Sinks (Tg N yr^{-1})	
Organic N export	1		
Benthic denitrification	300		180 ± 50
Water column denitrification	150	1[illegible]	65 ± 20
Sediment Burial	25	16	25 ± 10
N_2O loss to atmosphere	6	4	4 ± 2
Total sinks	482	342	275 ± 55

Under-estimation?

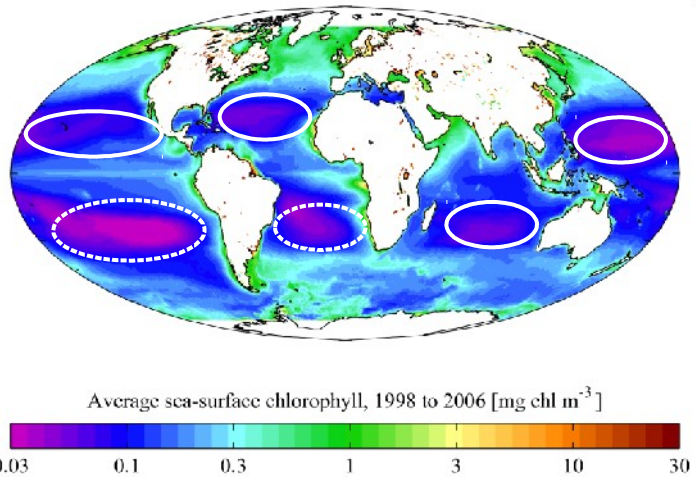
N-gain

Over-estimation?

N-loss

Gruber (2008)

GLOBAL N2 FIXATION REVISED UPWARD (x 300 in 20 years!!!)

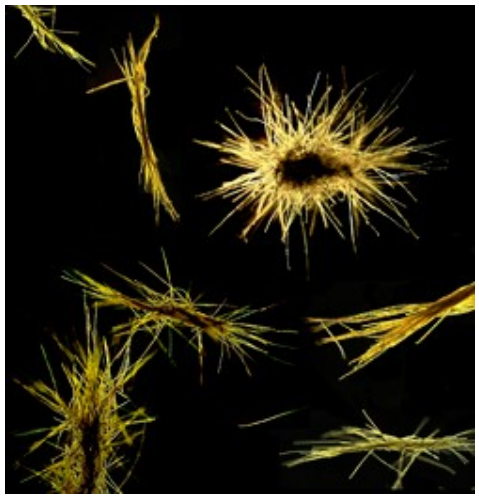


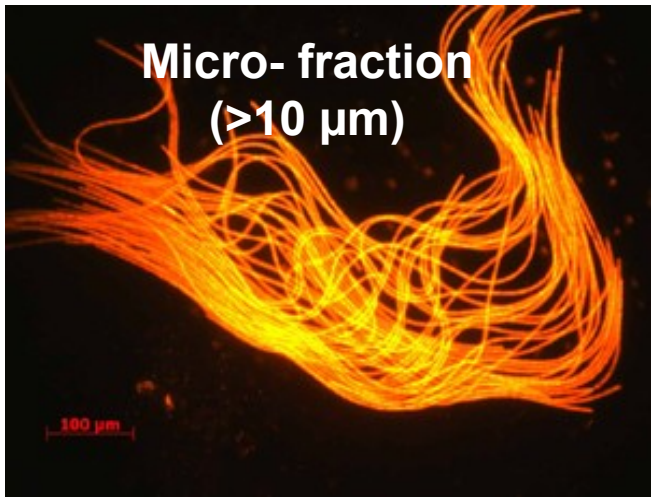
Conventional wisdom regarding N2 fixation:

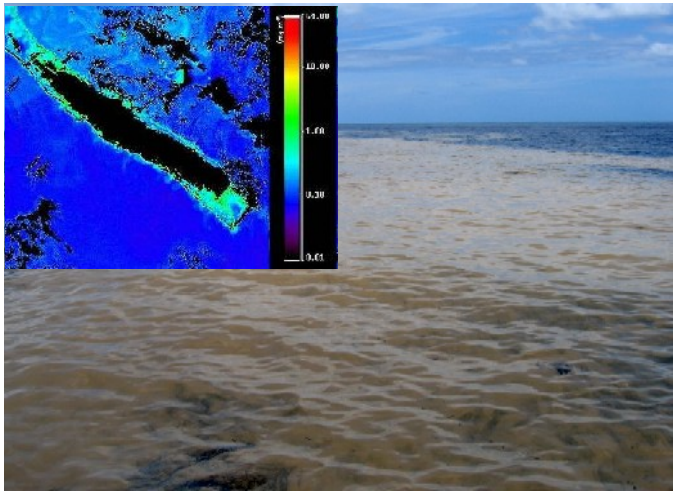
- **Warm oligotrophic waters (22-27°C)**
- **Stability water column**
- **Undetectable [nitrates]**

$N \equiv N$

(e.g. Karl et al., 2002)







Trichodesmium spp.

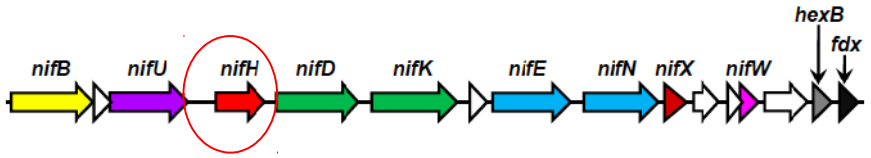
Marine Nationale

MOLECULAR TECHNIQUES → 'NEW' DIAZOTROPHS DISCOVERED

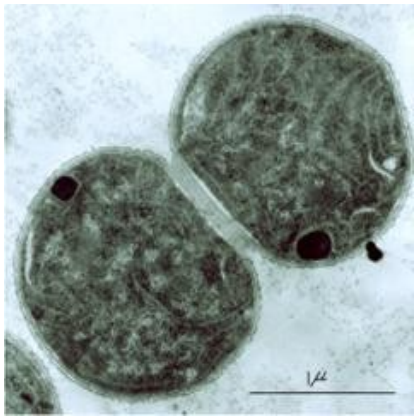
Unicellular cyanobacteria fix N_2 in the subtropical North Pacific Ocean

Jonathan P. Zehr*, John B. Waterbury†, Patricia J. Turner*, Joseph P. Montoya‡, Enoma Omoregie*, Grieg F. Steward*, Andrew Hansen§ & David M. Karl§

Zehr et al., (2001, Nature)



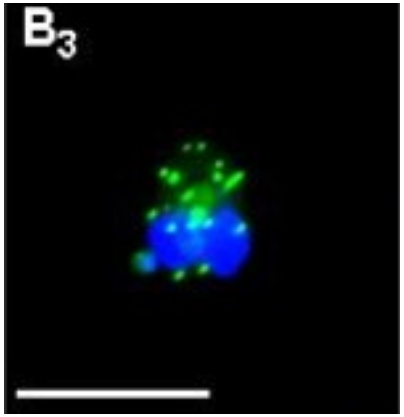
Nano- (2-10 µm)



Crocosphaera watsonii (Groupe B)

Image from Zehr et al. (2001)

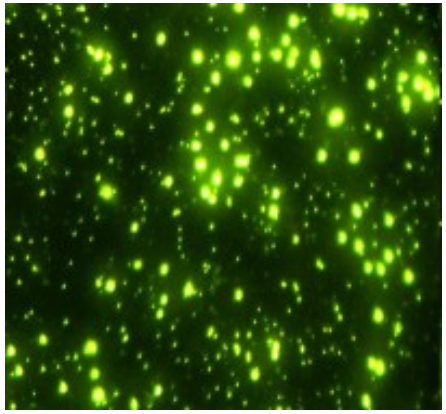
Pico (0.2-2 µm)



Uncultivated Group e A

Image from Bonnet et al., (2009) – I. Biegala

Pico (0.2-2 µm)



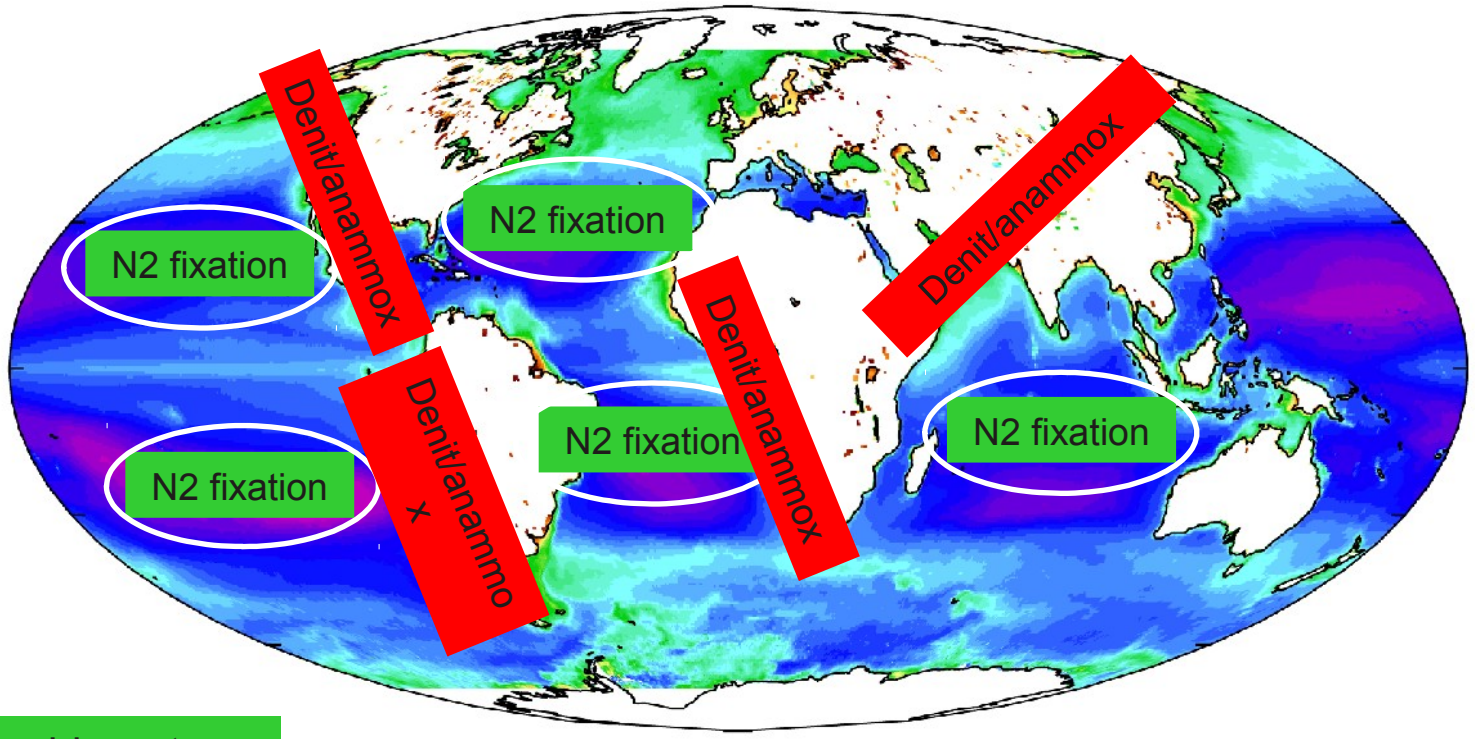
Het. bacteria

→ Account for 50-80% of N2 fixation rates in the tropical North and South Pacific

(Montoya et al., 2004; Bonnet et al., 2009; Halm et al., 2011…)

NEW ORGANISMS… ‘NEW’ ECOLOGICAL NICHES…?

Conventionnal view: spatial decoupling between **gains** and **losses** of N

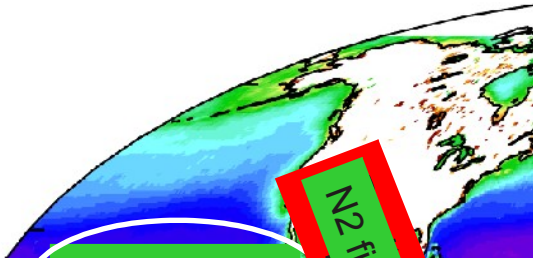


Oligotrophic waters
High T°C / low

OMZ (upwelling zones)
Low T°C / high

We look for N2 fixation where we expect it to happen…

GEOCHEMICAL STUDIES → SPATIAL COUPLING GAINS AND LOSSES?

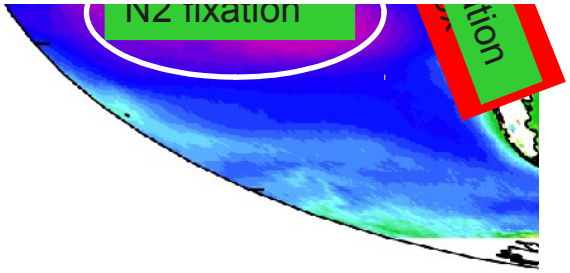


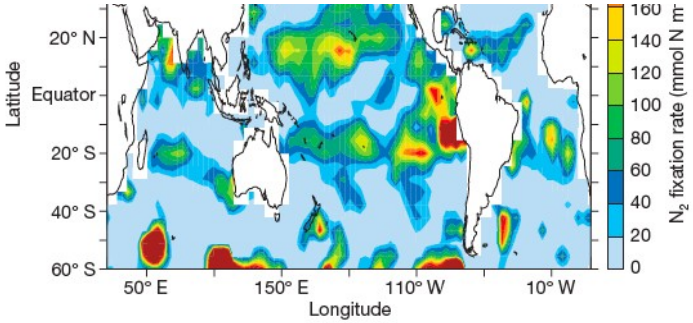
Vol 445 | 11 January 2007 | doi:10.1038/nature05392 nature

ARTICLES

Spatial coupling of nitrogen inputs and

Do µmolar levels of NO3- preclude N2 fixation to occur above OMZs?

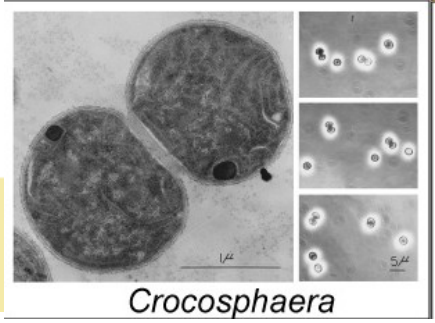




N2 Fixation

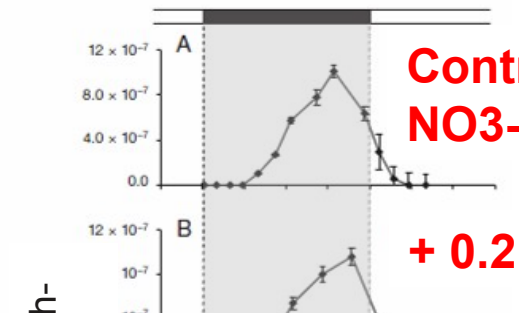
Deustch et al., (2007, Nature)

Crocosphaera watsonii WH8501
Crocosphaera watsonii WH0003


Crocosphaera

N2 FIXATION INHIBITED BY HIGH [NO3-]?

Culture experiments to reproduce increasing [NO3-] gradients

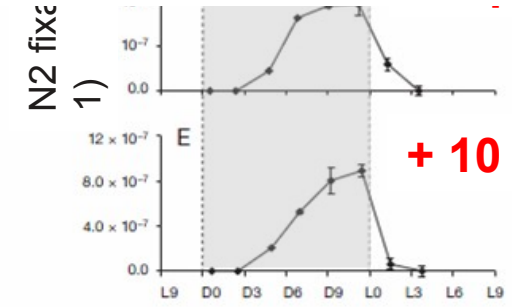


Control: 0 NO3-

+ 0.2 µM NO3-

Increasing [NO3-]

0.2 TO 10 µM [NO3-] DO NOT EXCLUDE N2 FIXATION IN CULTURE

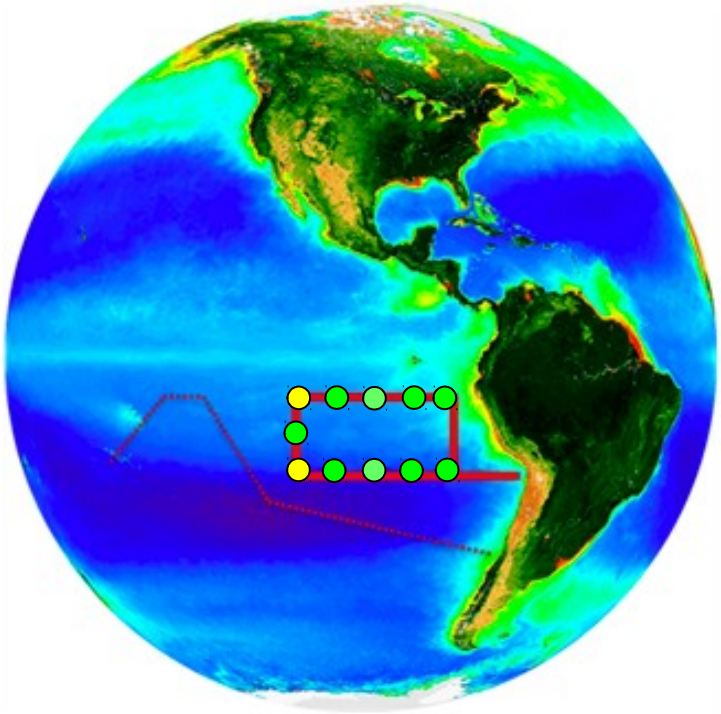


+ 10 µM NO3-

Time (24h)

Dekaezemacker & Bonnet, (2011

WHAT ABOUT ON THE FIELD? (Pacific cruises Feb. 2010 & 2011)



- Drifting traps/stations
- Fixed traps (14 months)

OBJECTIVE

Quantitative analysis of N2 fixation above the OMZ off Peru/Chile

→ **Isotopic studies/molecular biology** (small time/space scale)

→ **Geochemical approach (traps + waters column)** (higher time/space scale)

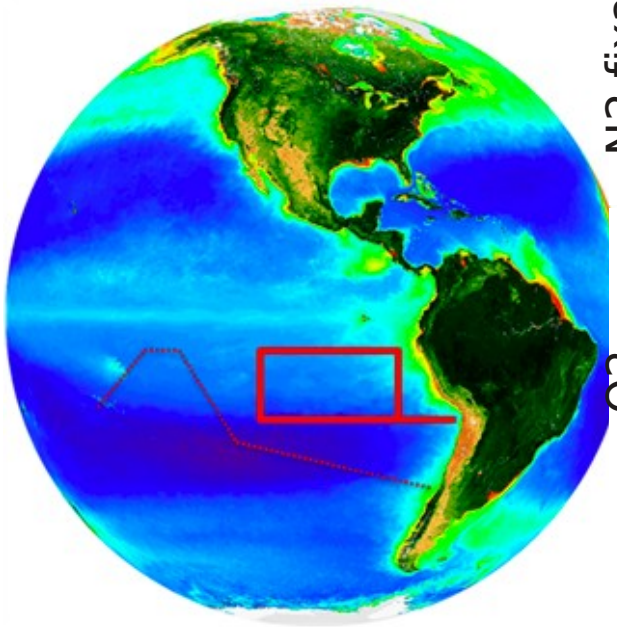
ETSP project (NSF) - PI: D.G. Capone, A. Knapp, W. Berelsen

French part: Humboldt-Fix project (INSU/LEFE) - PI: S. Bonnet

Ph.D Julien Dekaezemacker

QUANTIFICATION OF N2 FIXATION RATES (15N2 LABELLING METHOD)

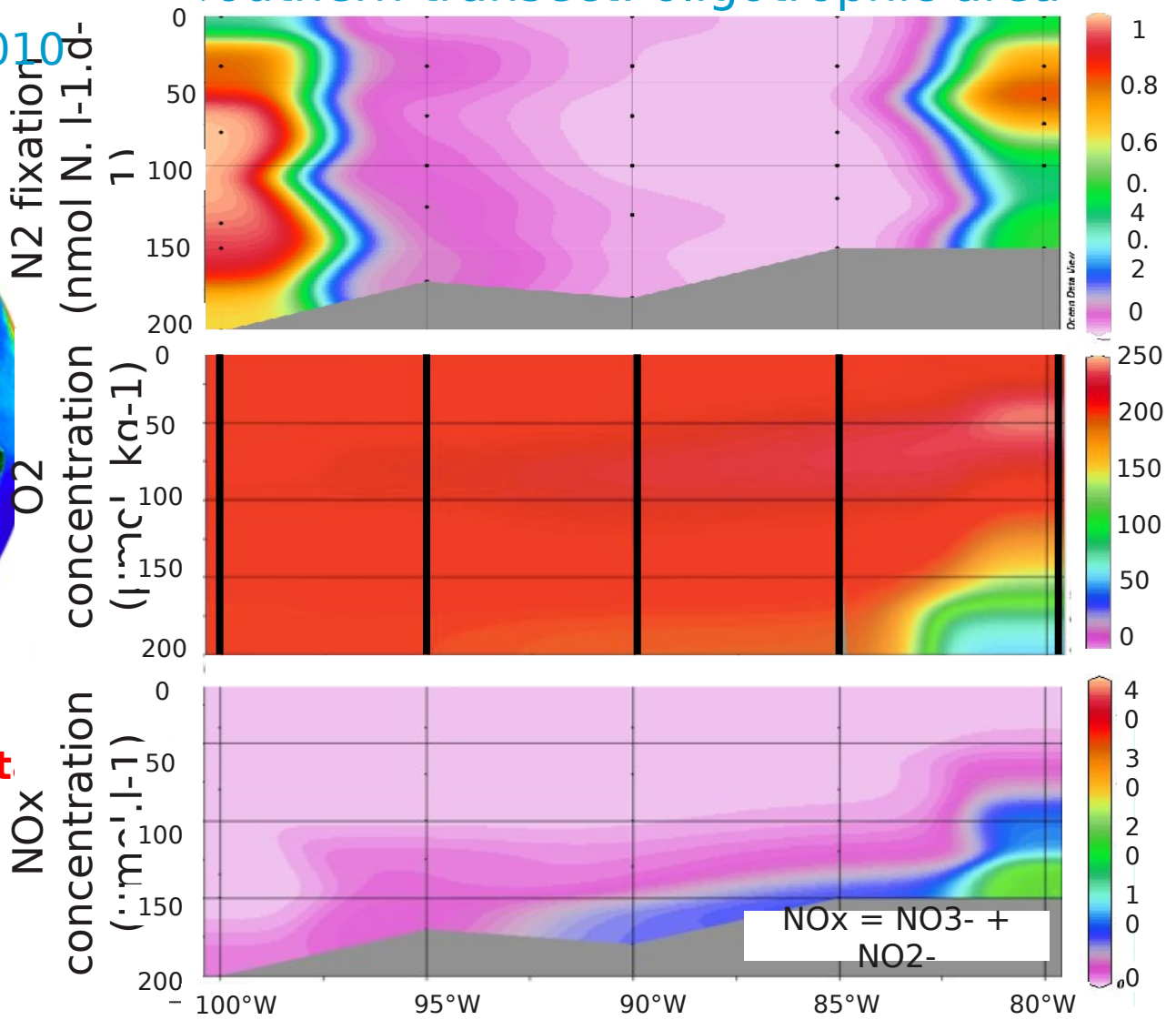
ETSP cruise, February 2010



Consistent with recent dat
BIOSOPE cruise

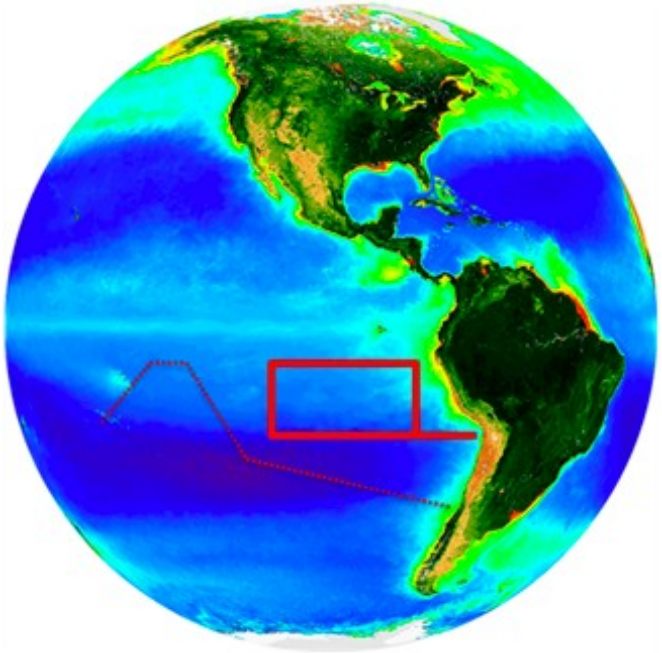
Raimbault & Garcia (2008)
Moutin *et al*. (2008)
&
Halm et al., (2011)

Southern transect: oligotrophic area



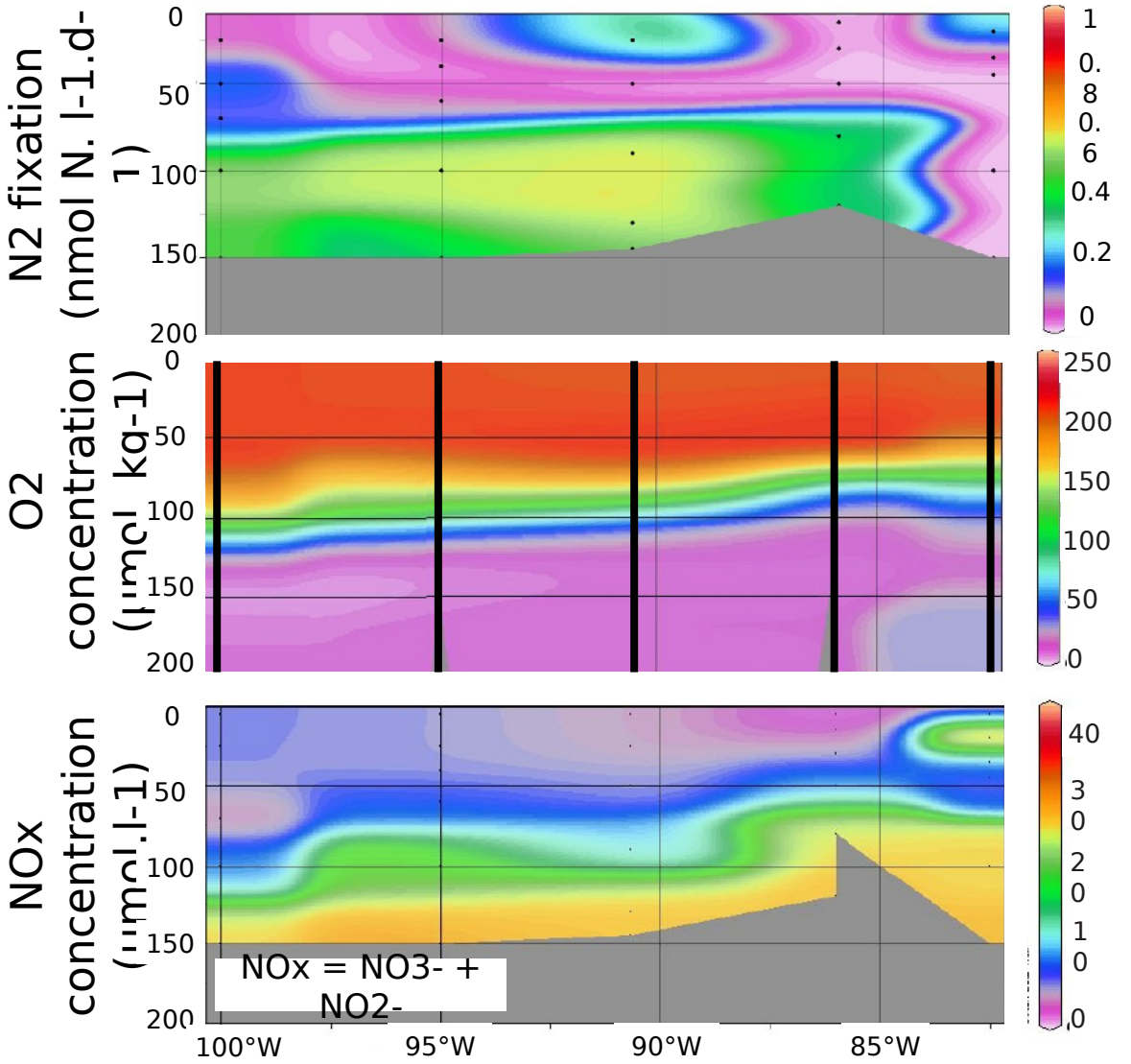
QUANTIFICATION OF N2 FIXATION RATES (15N2 LABELLING)

ETSP cruise, February 2010



N2 fixation is possible in NO3-rich areas Maximum at the oxycline

Northern transect



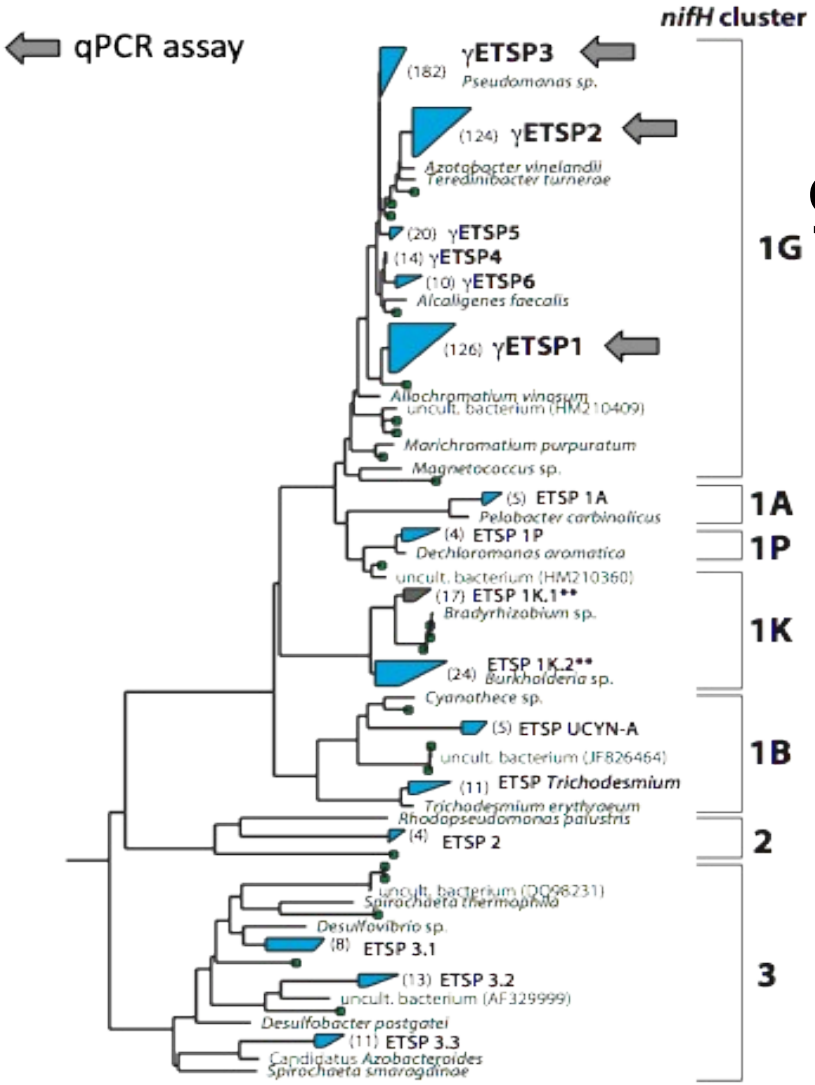
INTEGRATED RATES AND COMPARISON WITH OTHER BASINS

Location	Areal rates (µmol N.m-2.d-1)	Source
Tropical North Pacific	69	Dore et al., 2002
Tropical Atlantic	86	Goering et al., 1966
Arabian Sea	35-99	Capone et al., 1998
Tropical Atlantic	24-140	Voss et al., 2004
Eastern Tropical North Pacific	520	Montoya et al., 2004
Equatorial Pacific	18-358	Bonnet et al., 2009
ETSP Gyre	12-190	Halm et al., 2011
ETSP Coastal OMZ	7-190	Fernandez et al., 2011
Eastern Tropical South Pacific Oligotrophic area HNLC area (above OMZ)	 0-148 7-53	This study

Same order of magnitude than in subtropical gyres

→ need to be taken into account into global N budgets

DIAZOTROPHS DIVERSITY?



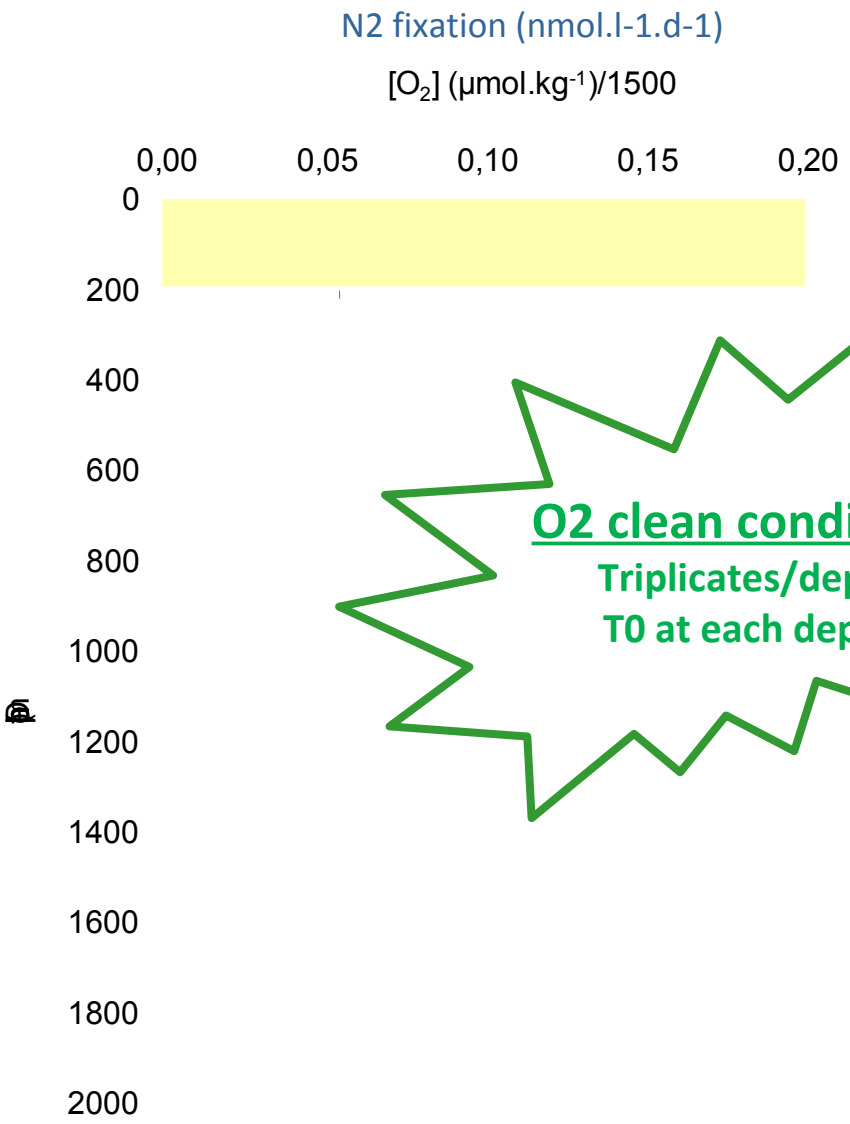
97% of total sequences (heterotrophic bact.)

3% of total sequences (cyanobacteria)

Almost exclusively heterotrophic Bacteria (in accordance with Fernandez et al., 2010)

Data from Zehr group UCSC (K. Turk-Kubo)

N2 FIXATION IN THE APHOTIC ZONE?



O2 clean conditions

Triplicates/depth

T0 at each depth

N2 fixers also active in the aphotic zone

⇩

Integrated rates in the aphotic zone = 2 x rates in the euphotic zone

⇩

Need to be taken into account in N budgets as well

FIRST CONCLUSIONS

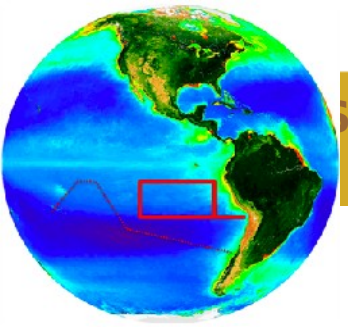
- **Is N2 fixation is possible in denitrified NO3-rich waters? Yes**

OMZ → IDEAL ECOLOGICAL NICHE FOR N2 FIXERS?

- Low [02] concentrations (less inhibition nitrogenase)
- High bioavailable [Fe2+] (Moffett et al., 2007) due to reductive conditions

- **N2 fixation is performed almost exclusively by heterotrophic bacteria**

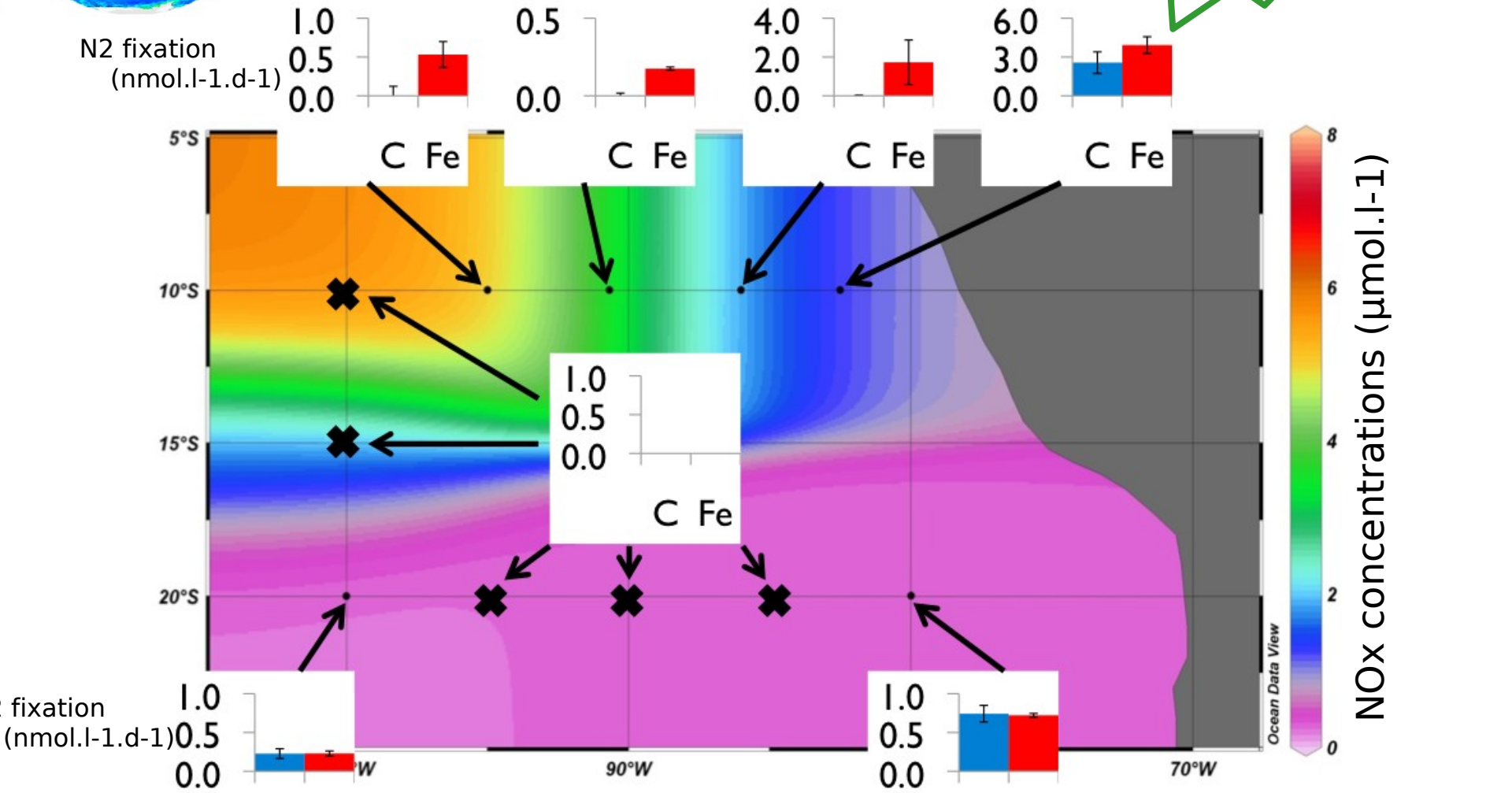
Unkown organisms → What control their activity?



SURFACE Fe ADDITION EXPERIMENTS (+ 3 nM)

El Niño year (February 2010)

Trace Metal Clean conditions



- **Fe stimulates N2 fixation in HNLC waters**

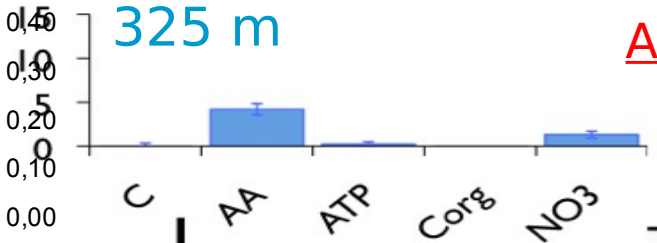
Dekaezemacker et al., (in prep)

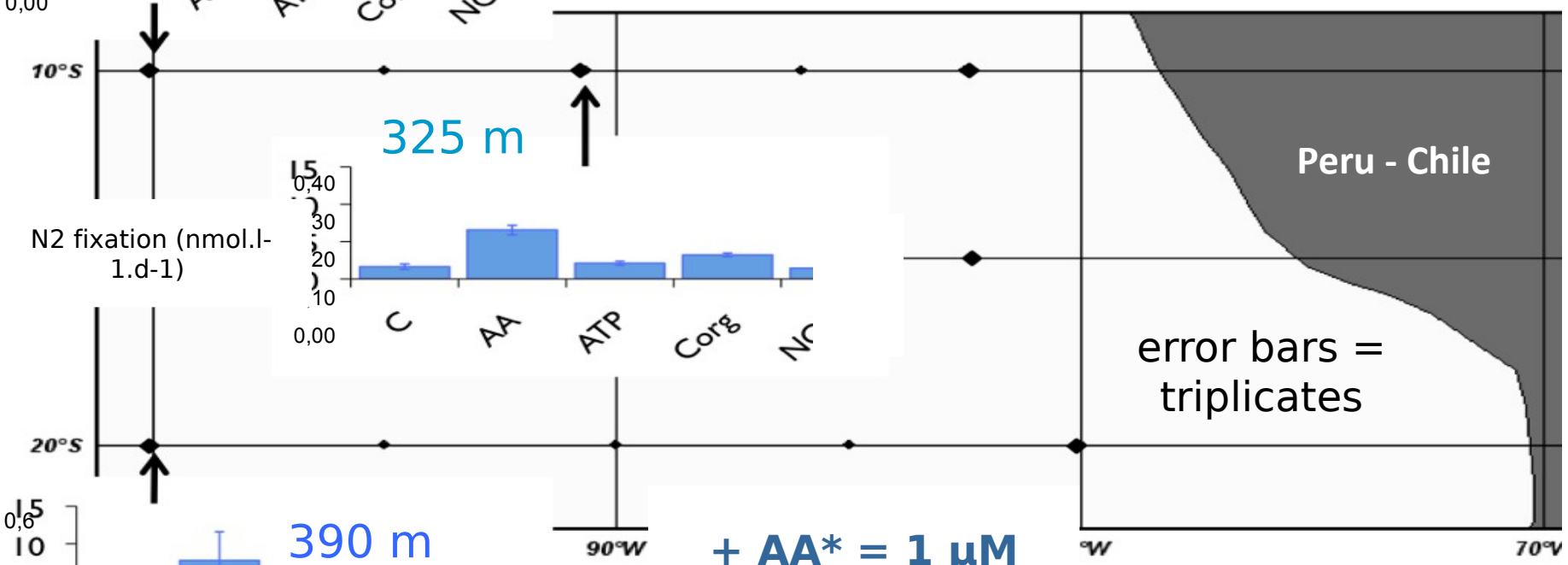
ORG. NUTRIENTS ADDITIONS IN THE CORE OF THE OMZ

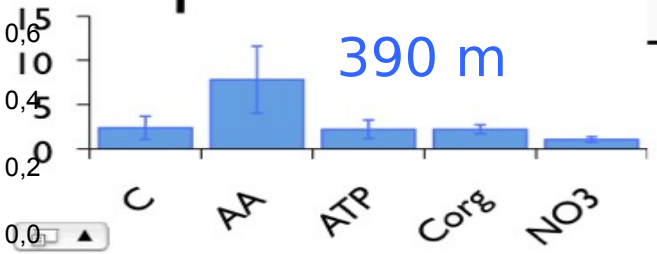
La Nina year (March 20110)

O2 Clean conditions

Ambiant OMZ [NO3-]≈40 µM







+ AA* = 1 µM
+ ATP = 1 nM
+ Corg* = 1 µM
+ NO3- = 8 µM

*** AA: Amino acids**
*** Corg = organic carbon**

- **AA stimulate N2 fixation at open ocean stations**

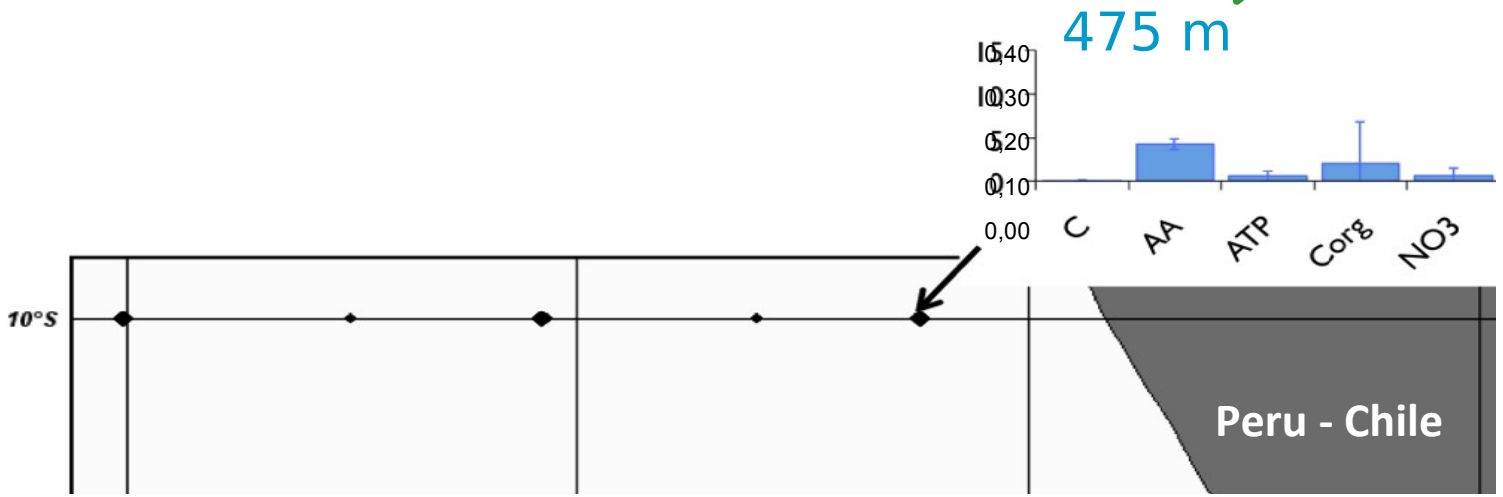
Bonnet et al., (in prep)

ORG. NUTRIENTS ADDITIONS IN THE CORE OF THE OMZ

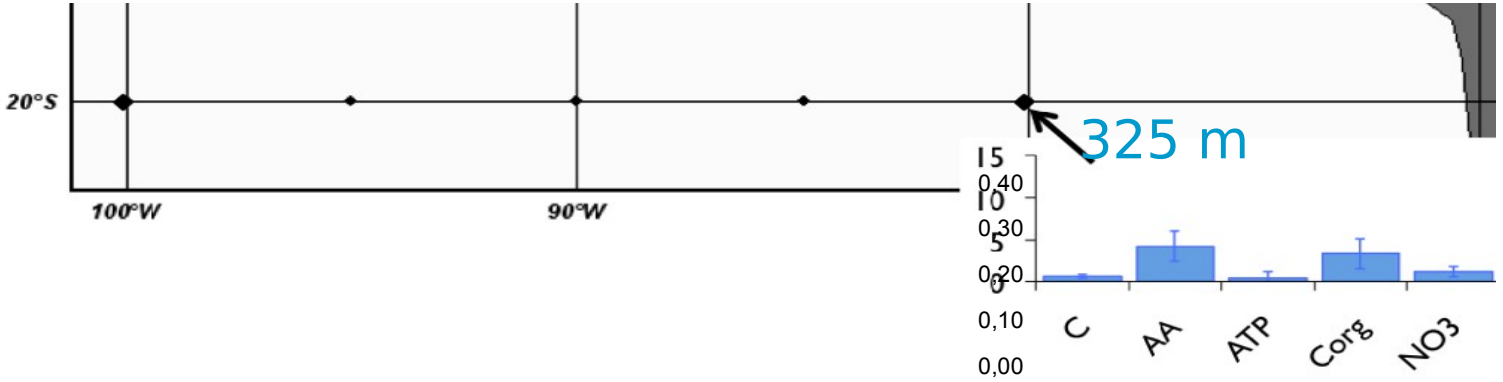
La Nina year (March 20110)

O2 Clean conditions

Ambiant [NO3-]≈40 µM

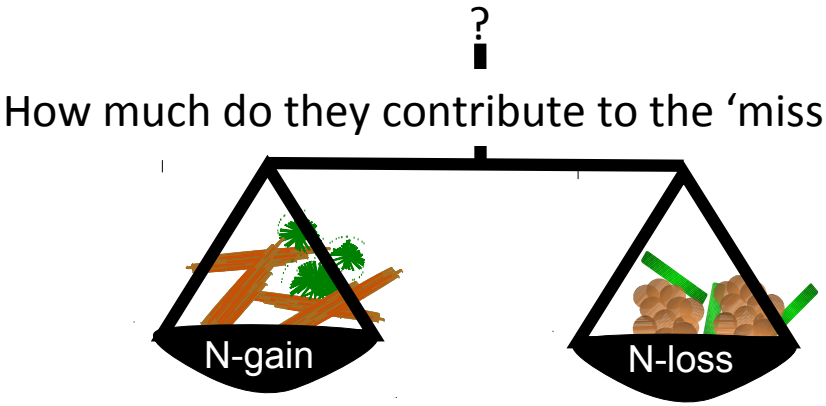


- **AA and Corg stimulate N2 fixation close to the coast**



CONCLUSIONS

Need to take into accounts these new sources of N2 fixation into global N budgets and models → OMZs extension

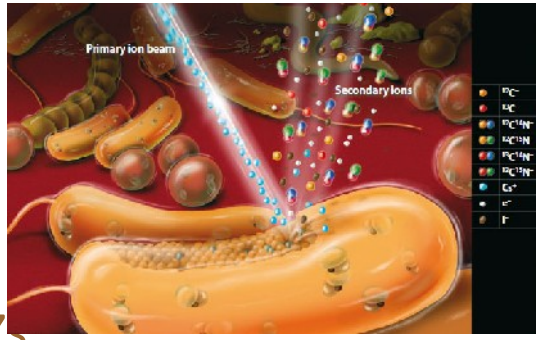


We need to go further

- Seasonal variability ?
- Coupling of gain/loss at high space resolution

→ AMOP project (SOLAS) (A. Paulmier, V. Garcon, C. Maes, B. Dewitte)

→ German et US cruises coming in Peru/Mexican OMZs



NanoSIMS

METHODOLOGICAL ISSUES: DO THEY CONTRIBUTE TO THE MISSING N?

surface ocean solas lower atmosphere study

SOLAS workshop on N2 fixation - February 2012, Kiel, Germany (J. LaRoche, W. Mohr)

We under-estimate N2 fixation with the 15N2 labelling technique

We need to use and define new protocols (5N2 saturated seawater)

International Council for Science
SCOR
Scientific Committee on Oceanic Research

SCOR Working Group proposal submitted

'The reassessment of marine dinitrogen fixation methodology and measurements'

Chairs: J. Laroche, L. Stal

13 countries, more than 20 institutions

AKNOWLEDGEMENTS

J. Dekeazemacker, D.G. Capone, A. Knapp, K. Turk, J.P. Zehr, R. Harmersley, O. Grosso, T. Moutin