Light, Nutrients (including iron) and Primary Productivity

John J. Cullen

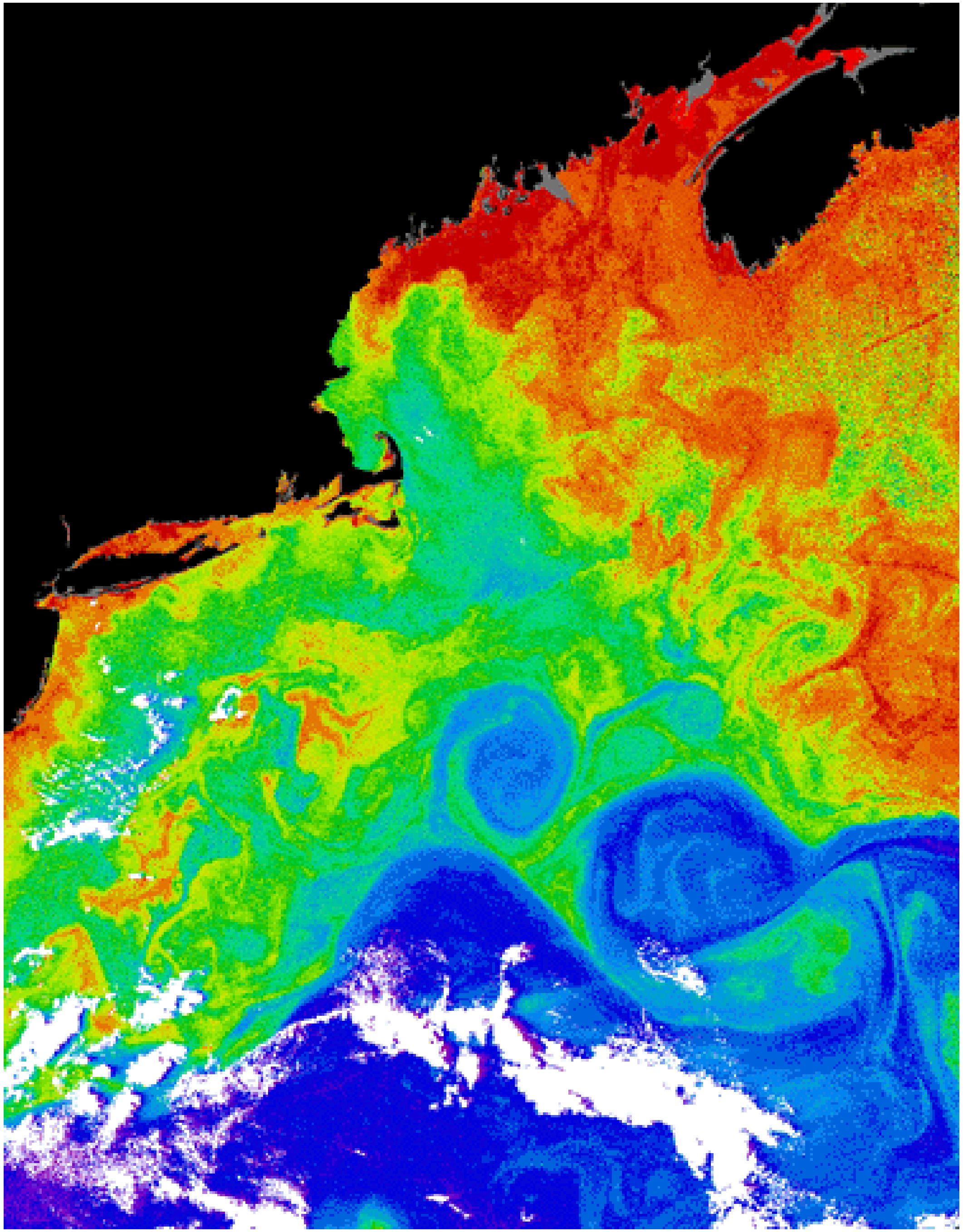
Department of Oceanography, Dalhousie University
Halifax, Nova Scotia, Canada B3H 4R2

2014 C-MORE Summer Training Course
“Microbial Oceanography:
Genomes to Biomes”

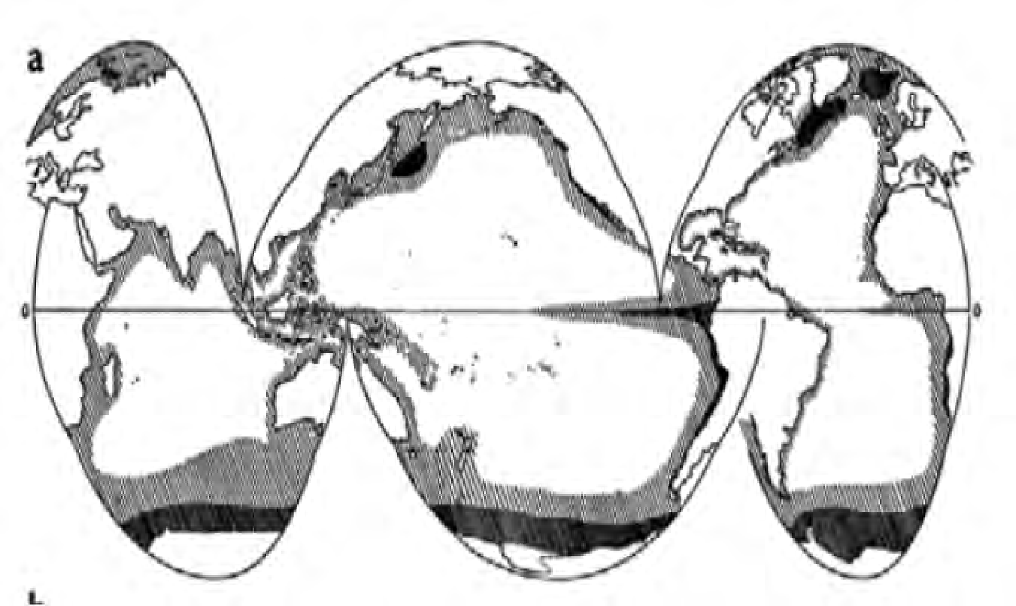
IMAGE: *NASA Goddard Space Flight Center*

Productivity in the ocean depends on light and nutrients

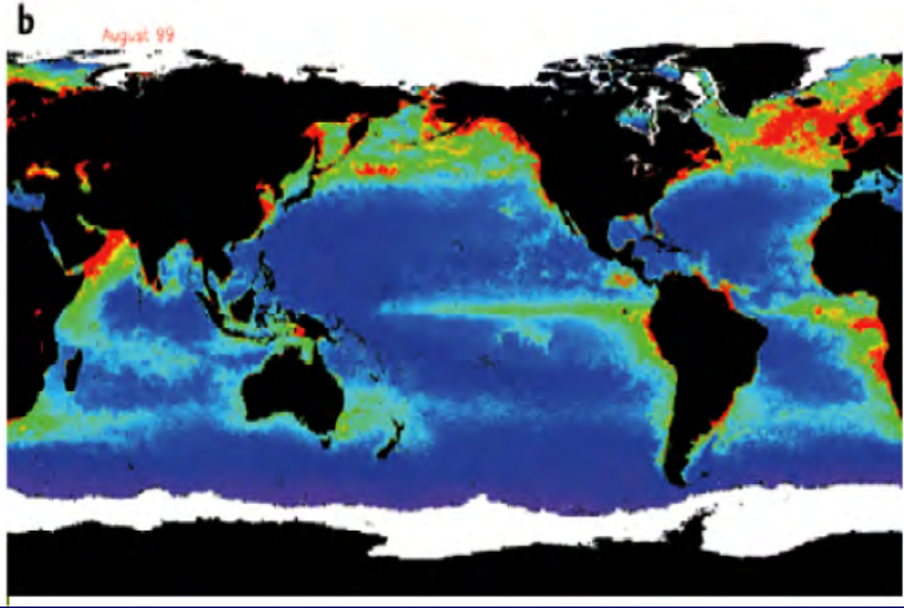
The major nutrients are N and P



Physical processes have a major influence



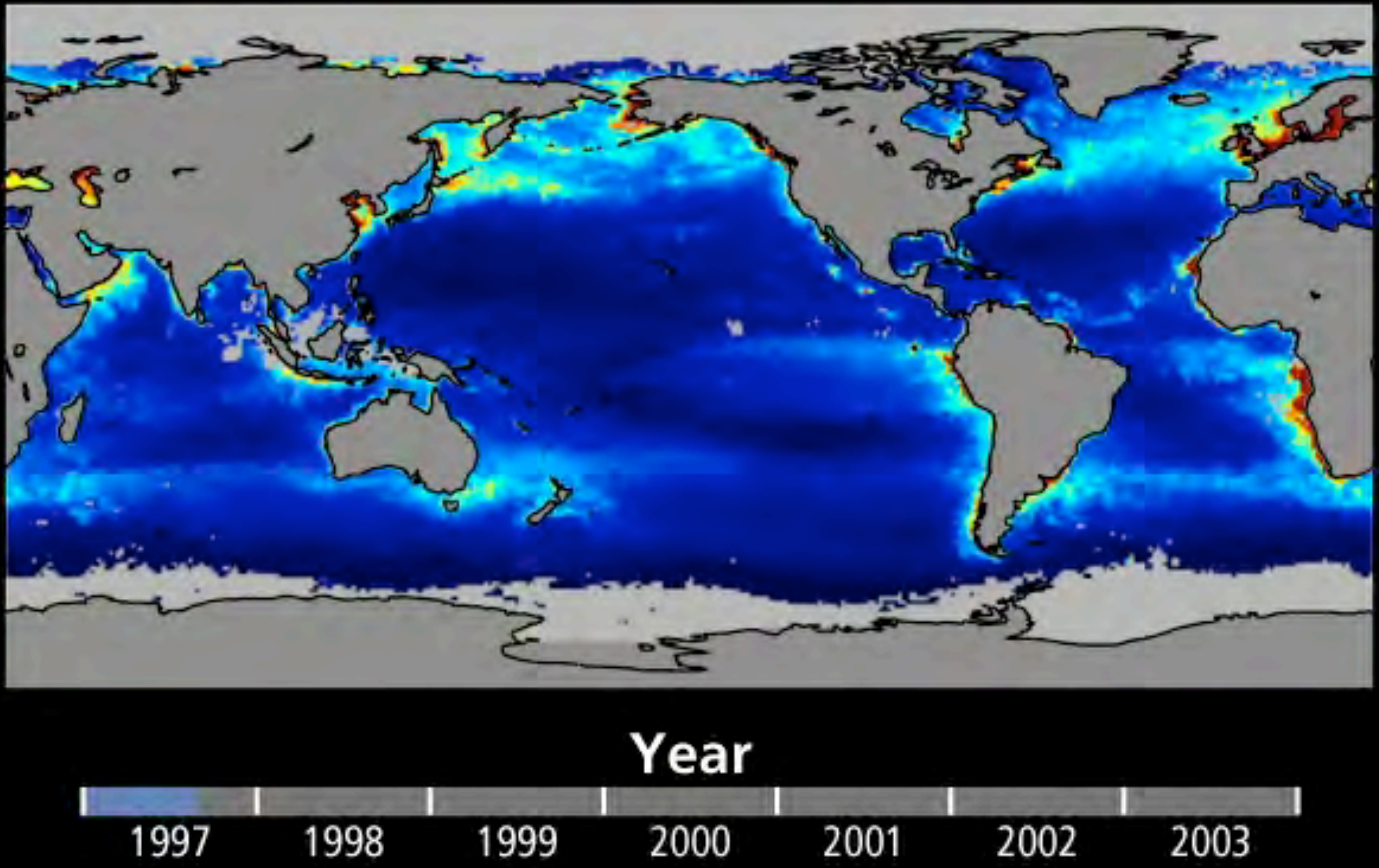
Sverdrup's (1955) map of productivity based on vertical convection, upwelling and turbulent diffusion



Global productivity estimated from remote sensing (Falkowski et al. 1998).

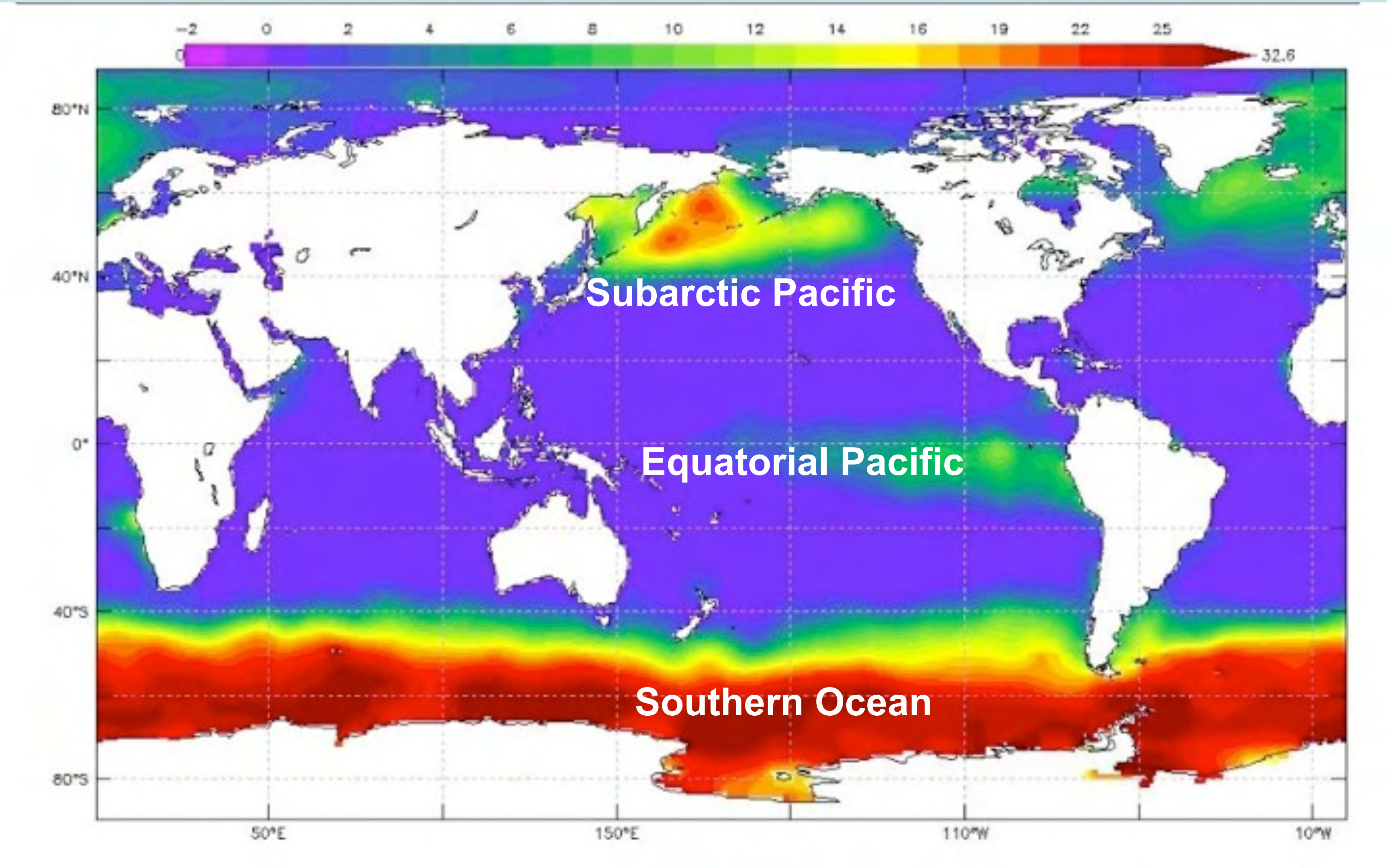
As presented by John McGowan (Oceanography Mag., 2004)

Global productivity from SeaWiFS ocean color (NASA/GSFC)



Incomplete utilization of nutrients:
HNLC = High Nutrient Low Chlorophyll Waters

Concentration of nitrate at the surface (µmol kg^{-1})

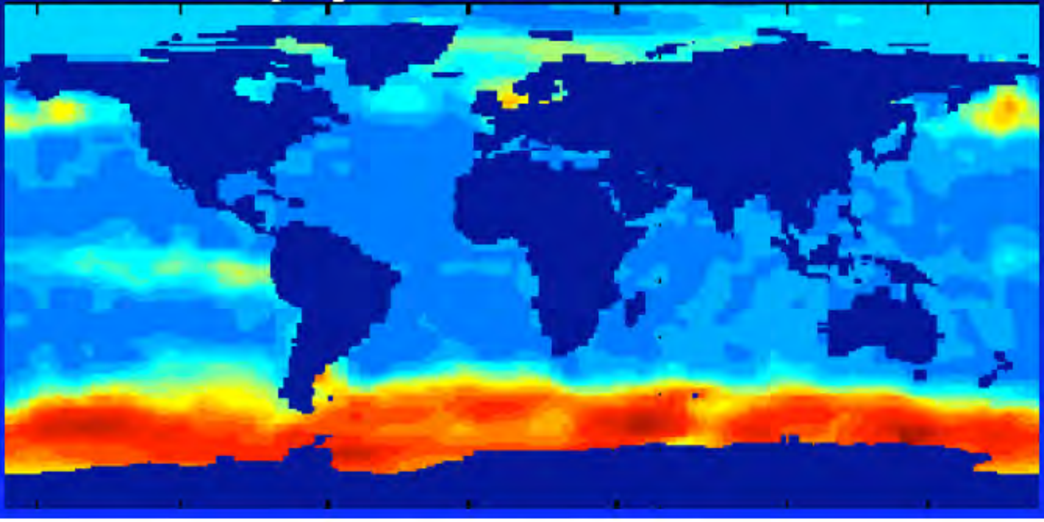


Subarctic Pacific

Equatorial Pacific

Southern Ocean

High-nutrient, Low-chlorophyll waters are associated with low iron flux



Nitrate
Concentration

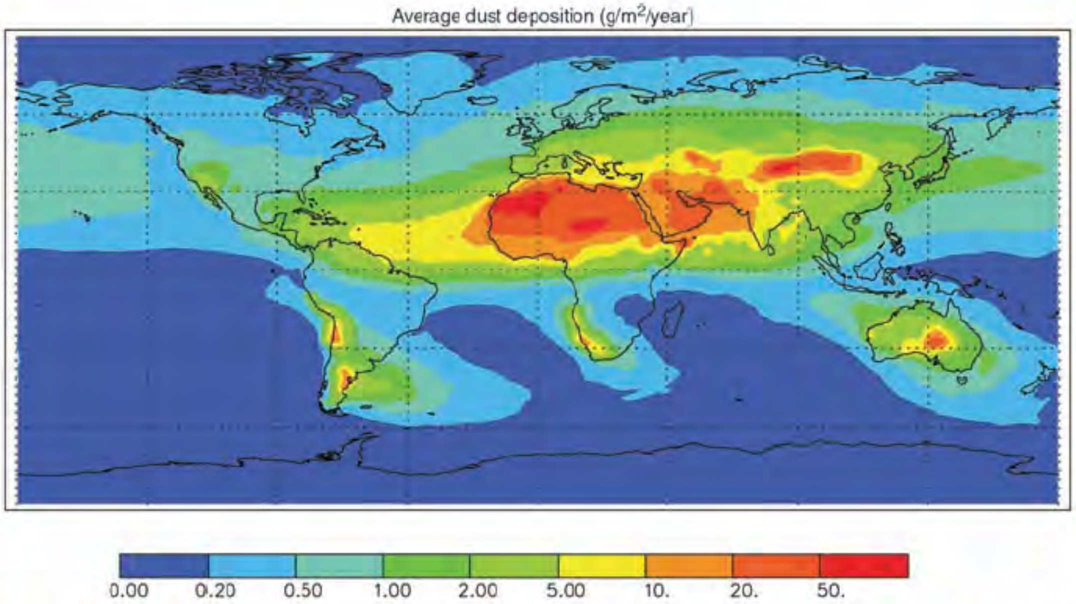


Fig. 2. Dust fluxes to the world oceans based on a composite of three published modeling studies that match satellite optical depth, in situ concentration, and deposition observations (*11*, *14*, *15*).

Jickells et al.

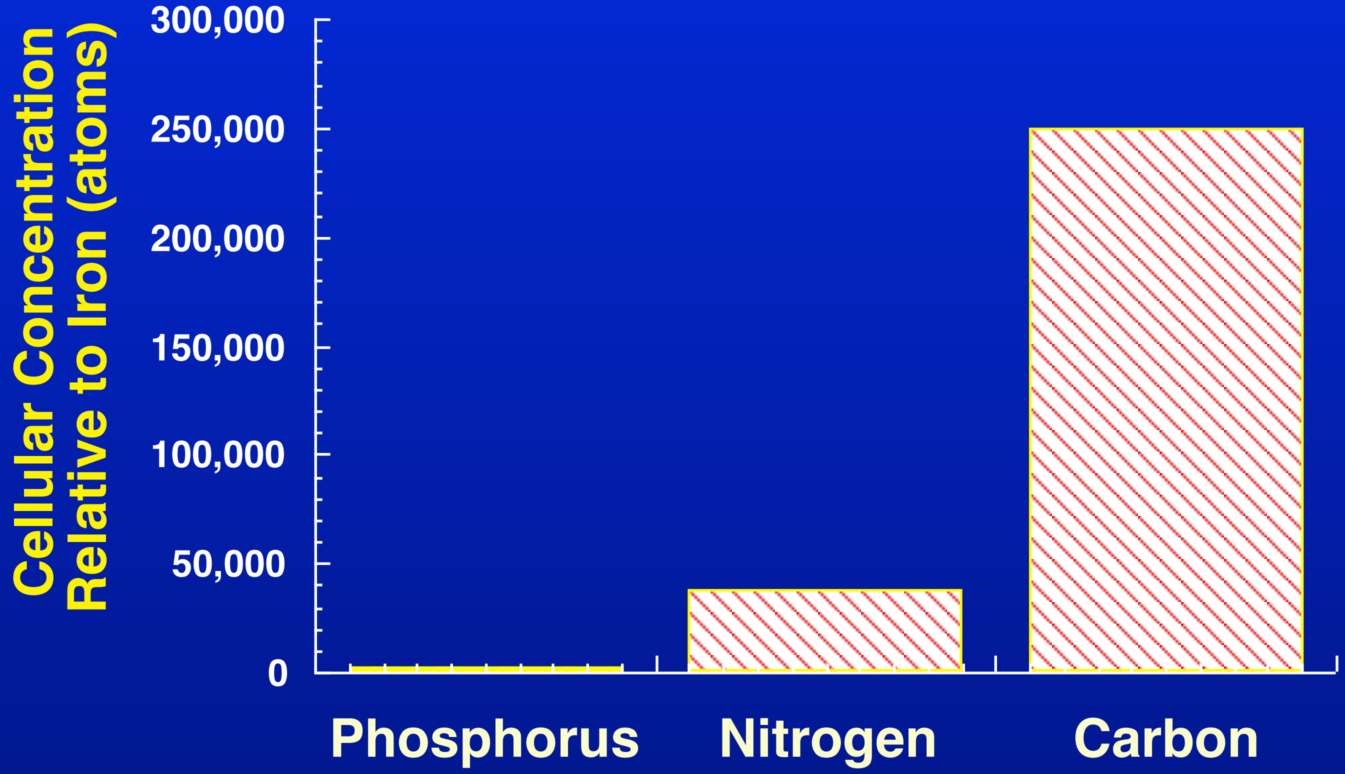
1 APRIL 2005 VOL 308 SCIENCE

Iron is an important nutrient, required in trace amounts

Required for:

- synthesis of chlorophyll
- utilization of nitrate
- nitrogen fixation

A little bit of iron can support a lot of plant material



But…

Iron is not very soluble in seawater, so it was long thought to be a potential limiting nutrient

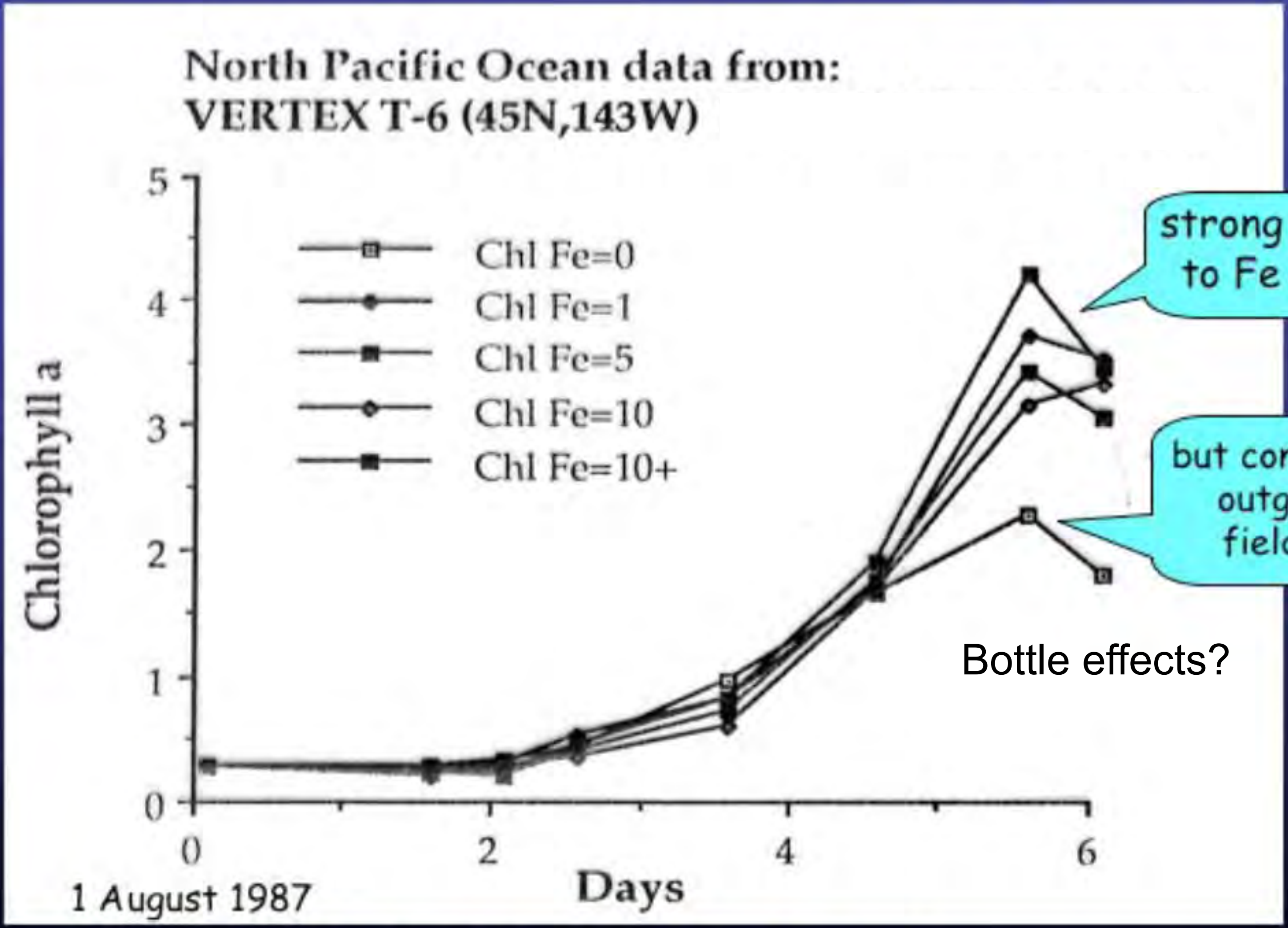
However…

Very difficult to measure without contamination

So…

Little progress was made until the 80’s

Subarctic North Pacific, August 1987



strong response to Fe addition

but control also outgrowing field value

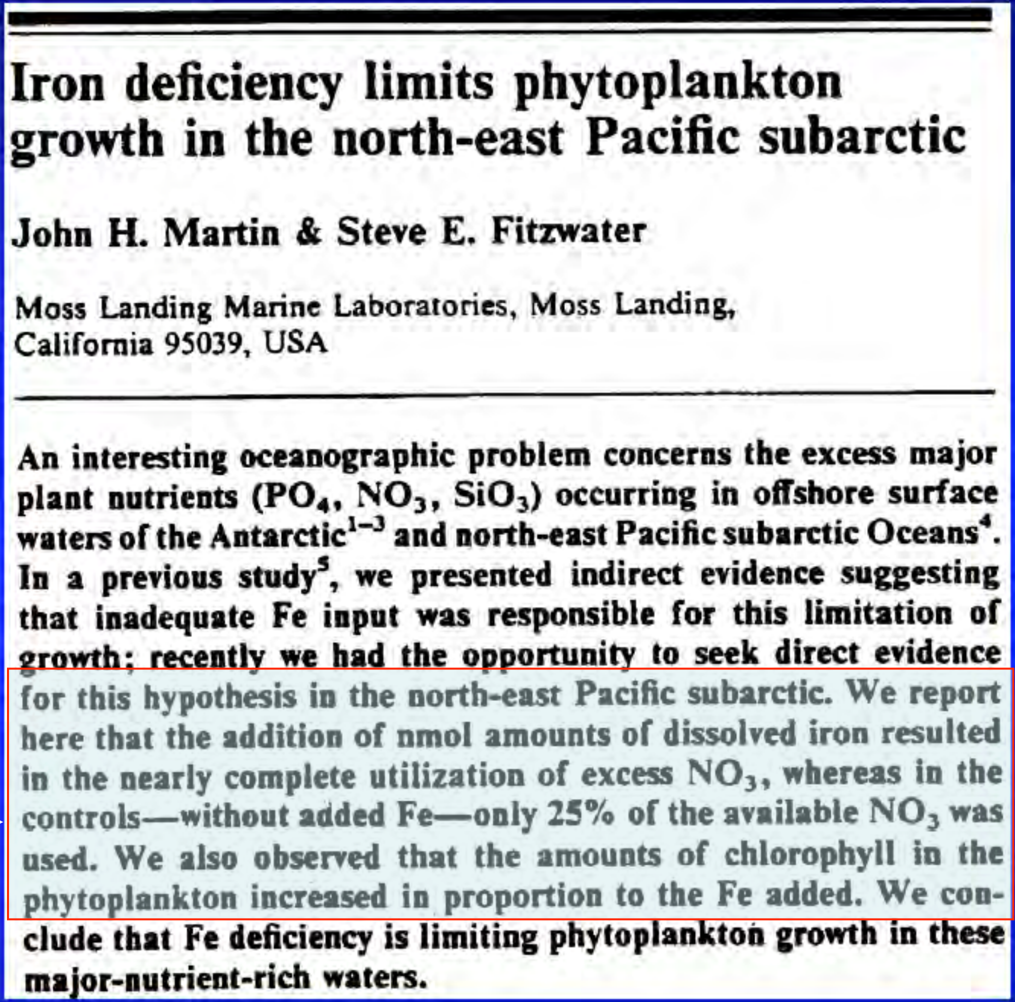
Bottle effects?

1 August 1987

....as shown in Paris by John Martin in September 1987

Martin and Fitzwater (1988) *Nature*, **331**, 341-343.

1988



Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic

John H. Martin & Steve E. Fitzwater

Moss Landing Marine Laboratories, Moss Landing,
California 95039, USA

An interesting oceanographic problem concerns the excess major plant nutrients (PO_4, NO_3, SiO_3) occurring in offshore surface waters of the Antarctic[1–3] and north-east Pacific subarctic Oceans[4]. In a previous study[5], we presented indirect evidence suggesting that inadequate Fe input was responsible for this limitation of growth; recently we had the opportunity to seek direct evidence for this hypothesis in the north-east Pacific subarctic. We report here that the addition of nmol amounts of dissolved iron resulted in the nearly complete utilization of excess NO_3, whereas in the controls—without added Fe—only 25% of the available NO_3 was used. We also observed that the amounts of chlorophyll in the phytoplankton increased in proportion to the Fe added. We conclude that Fe deficiency is limiting phytoplankton growth in these major-nutrient-rich waters.

The “Iron Hypothesis” gains prominence

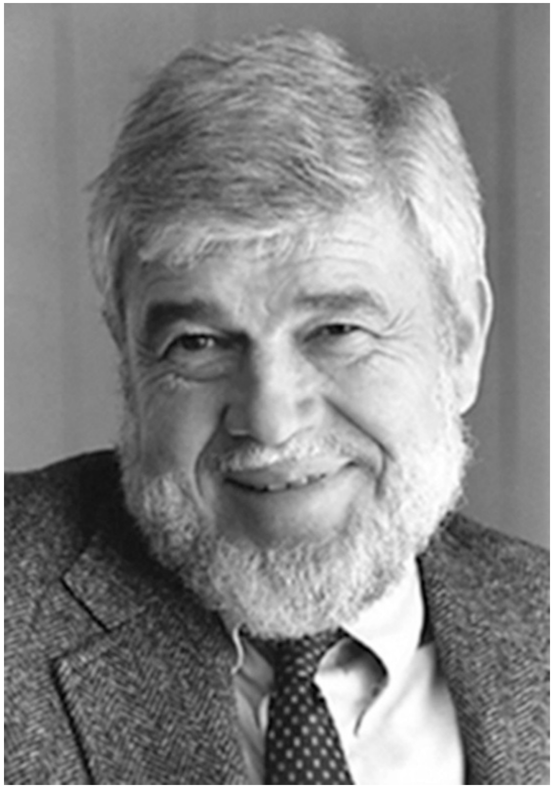
Nature 331 p341-343 1988

PALEOCEANOGRAPHY, VOL.5, NO.1, PAGES 1-13

GLACIAL-INTERGLACIAL CO_2 CHANGE: THE IRON HYPOTHESIS

John H. Martin

Moss Landing Marine Laboratories
Moss Landing, California



Abstract. Several explanations for the 200 to 280 ppm glacial/interglacial change in atmospheric CO_2 concentrations deal with variations in southern ocean phytoplankton productivity and the related use or nonuse of major plant nutrients. An hypothesis is presented herein in which arguments are made that new productivity in today's southern ocean (7.4×10^{13} g yr^{-1}) is limited by iron deficiency, and hence the phytoplankton are unable to take advantage of the excess surface nitrate/phosphate that, if used, could result in total southern ocean new production of $2\text{-}3 \times 10^{15}$ g C yr^{-1}. As a consequence of Fe-limited new productivity, Holocene interglacial CO_2 levels (preindustrial) are as high as they were during the last interglacial (≈ 280 ppm). In contrast, atmospheric dust Fe supplies were 50 times higher during the last glacial maximum (LGM). Because of this Fe enrichment, phytoplankton growth may have been greatly enhanced, larger amounts of upwelled nutrients may have been used, and the resulting stimulation of new productivity may have contributed to the LGM drawdown of atmospheric CO_2 to levels of less than 200 ppm. Background information and arguments in support of this hypothesis are presented.

Martin’s “Iron Hypothesis” had support in the record of global climate change

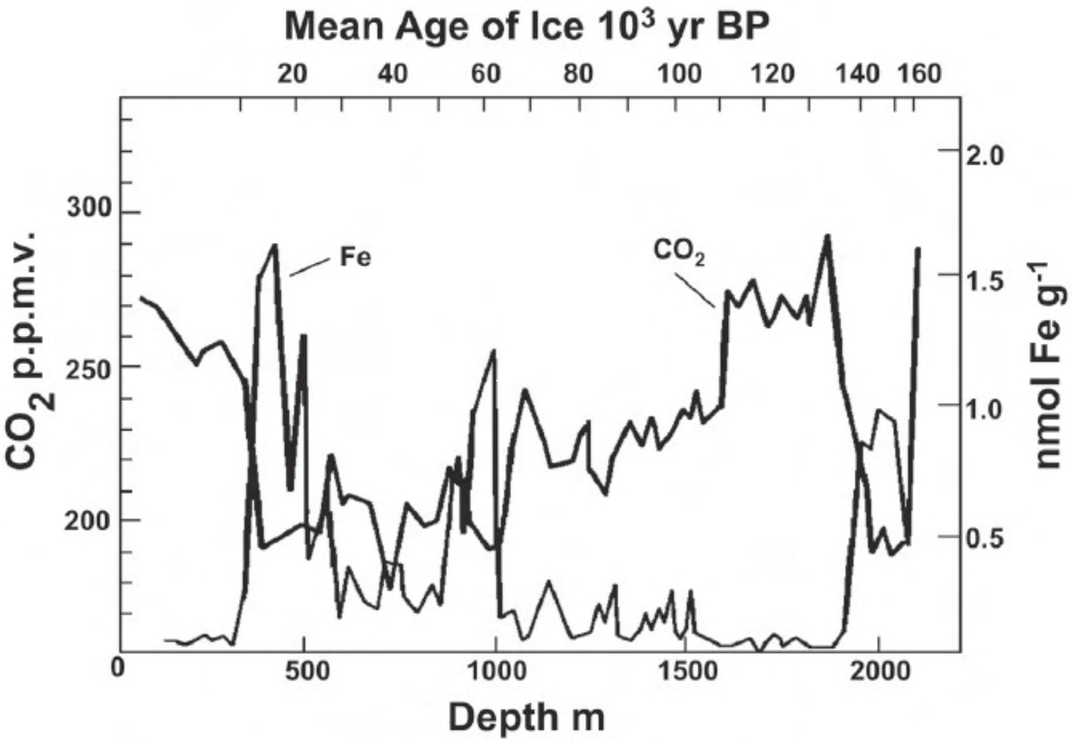
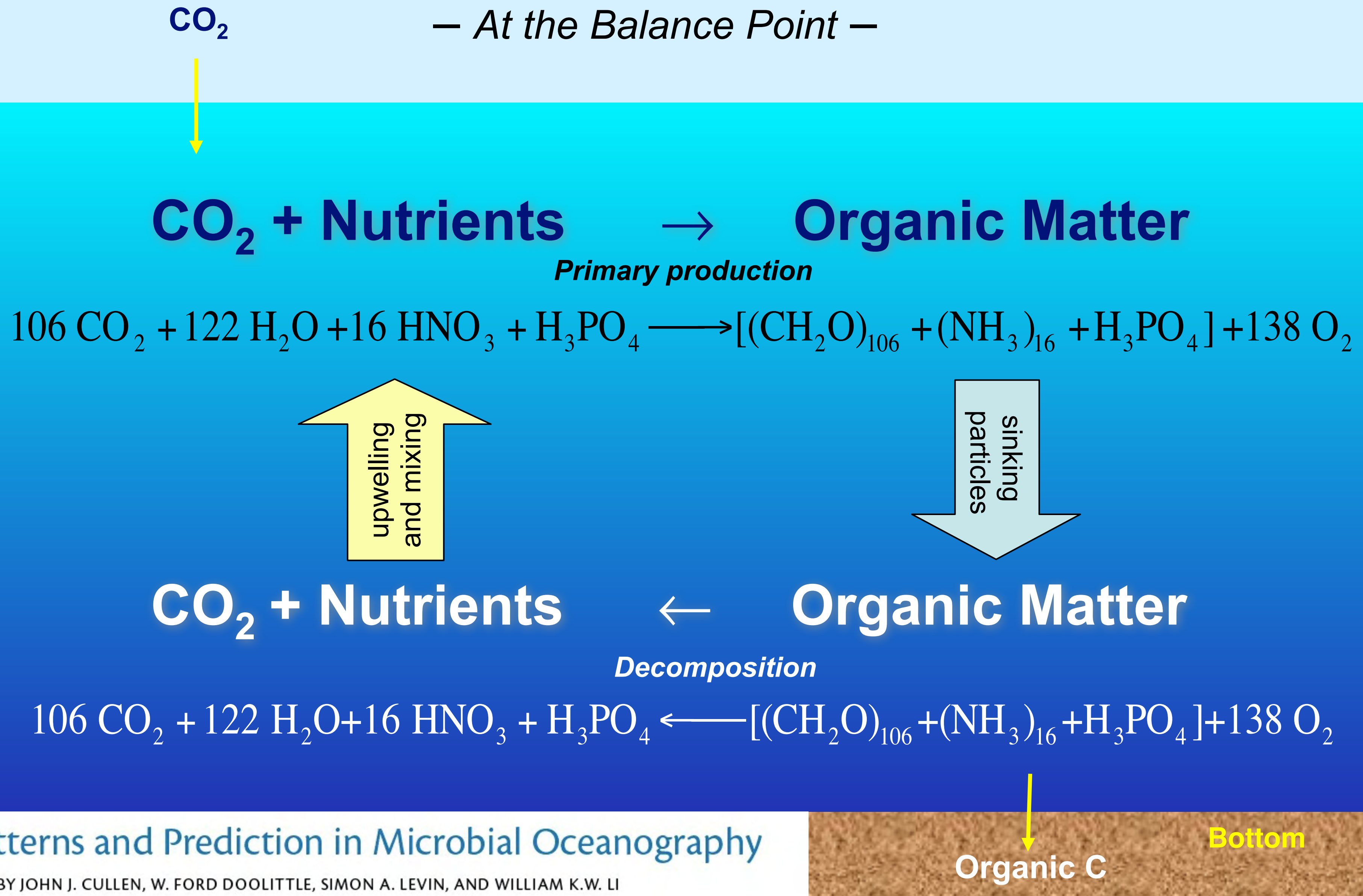


Figure 2. Relationship between Fe and CO_2 concentrations from the Vostok ice cores. *After Martin (1990b)*

From Strong et al., Oceanography, 2009

Ocean Cycle of Life and Death

– At the Balance Point –



CO_2

CO_2 + Nutrients → Organic Matter

Primary production

$$106\ CO_2 + 122\ H_2O + 16\ HNO_3 + H_3PO_4 \longrightarrow [(CH_2O)_{106} + (NH_3)_{16} + H_3PO_4] + 138\ O_2$$

upwelling and mixing

sinking particles

CO_2 + Nutrients ← Organic Matter

Decomposition

$$106\ CO_2 + 122\ H_2O + 16\ HNO_3 + H_3PO_4 \longleftarrow [(CH_2O)_{106} + (NH_3)_{16} + H_3PO_4] + 138\ O_2$$

Organic C

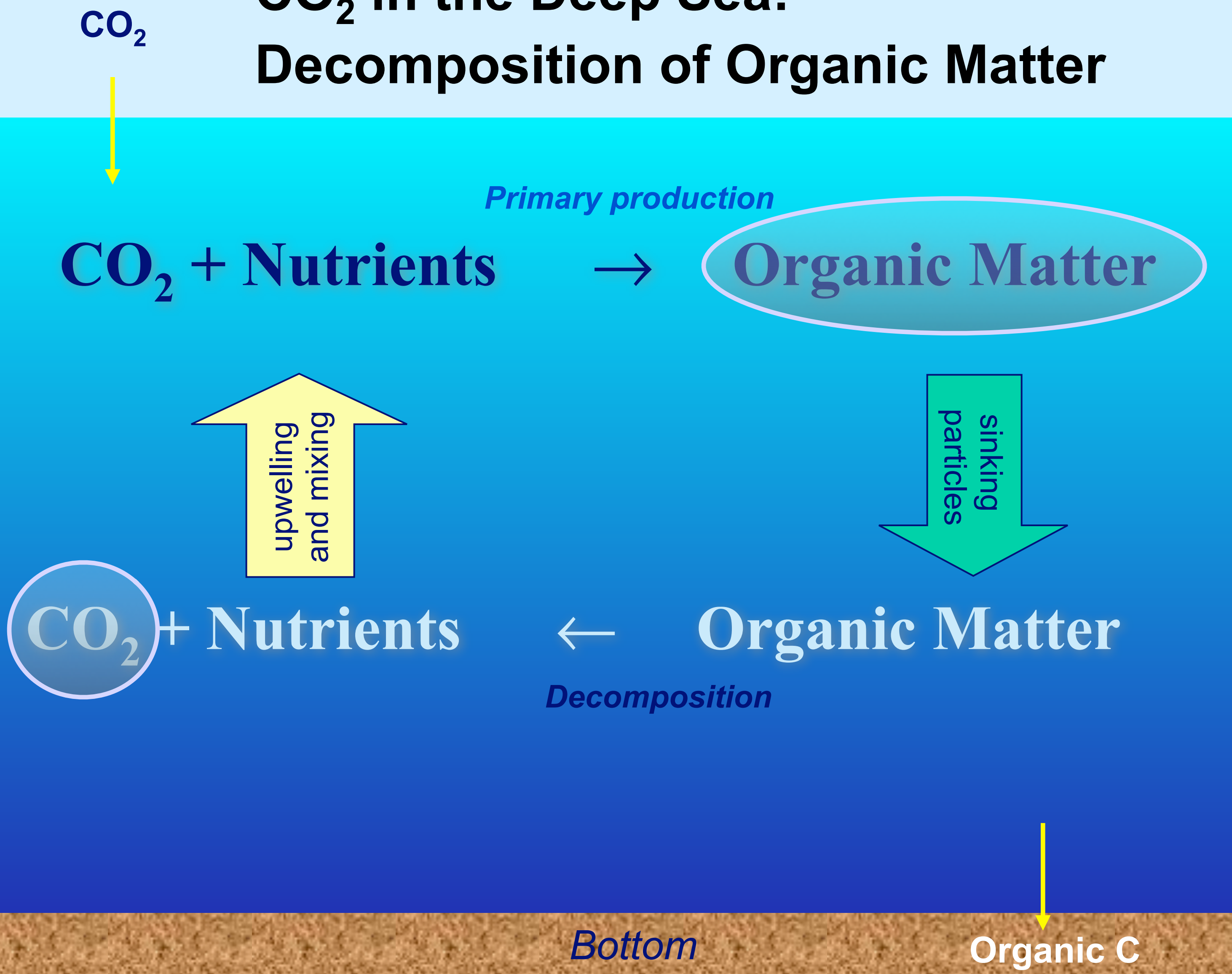
Bottom

Patterns and Prediction in Microbial Oceanography

BY JOHN J. CULLEN, W. FORD DOOLITTLE, SIMON A. LEVIN, AND WILLIAM K.W. LI

Oceanography Magazine, 2007, Figure 1

Biological Reason for Elevated CO_2 in the Deep Sea: Decomposition of Organic Matter



CO_2

Primary production

CO_2 + Nutrients → Organic Matter

upwelling and mixing

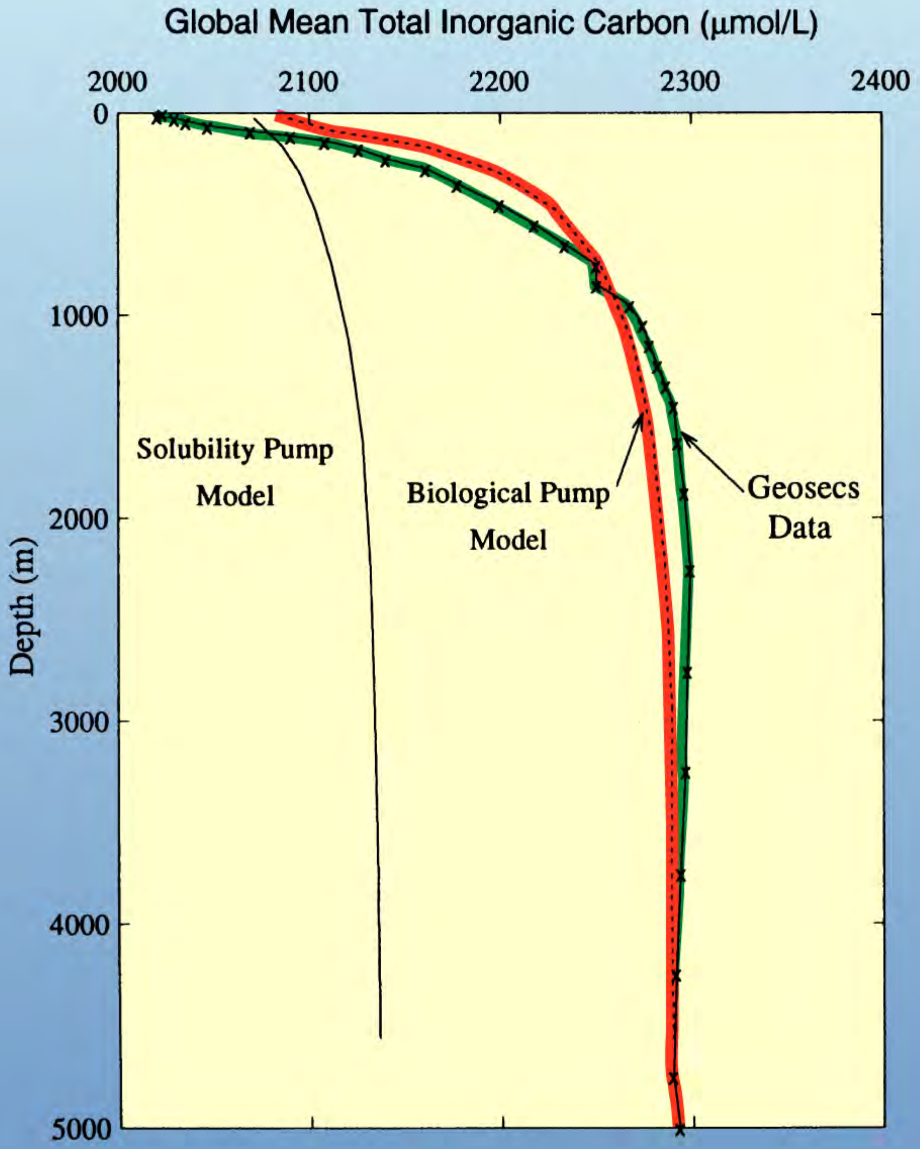
sinking particles

CO_2 + Nutrients ← Organic Matter

Decomposition

Bottom

Organic C



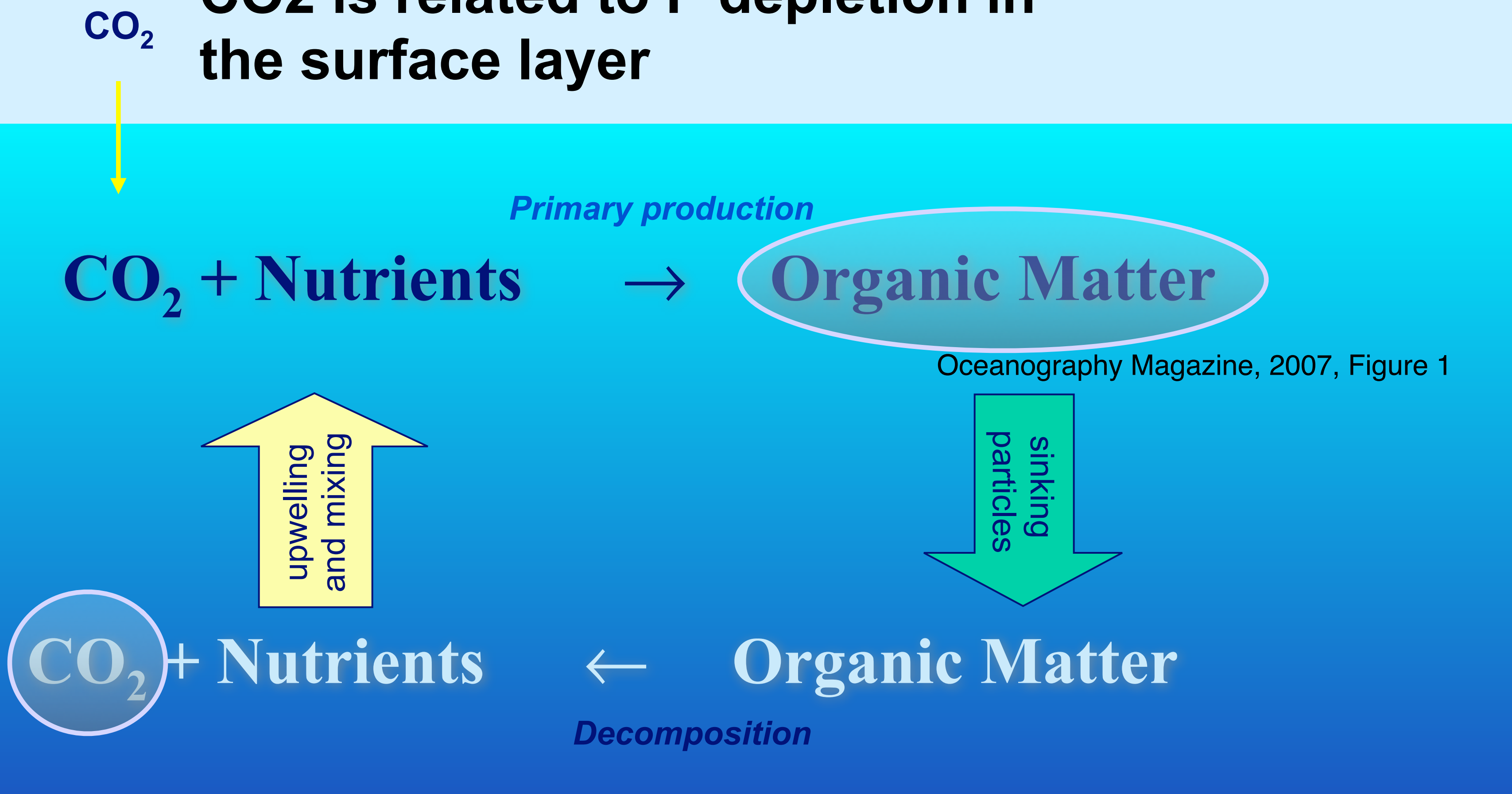
Murnane and Sarmiento

CO_2 is elevated in the deep ocean
because nutrients are depleted at the surface
and regenerated at depth

from a slide by Dave Karl

Cullen C-MORE 2013

The magnitude of the biologically mediated deep accumulation of CO2 is related to P depletion in the surface layer



CO_2

Primary production

CO_2 + Nutrients → Organic Matter

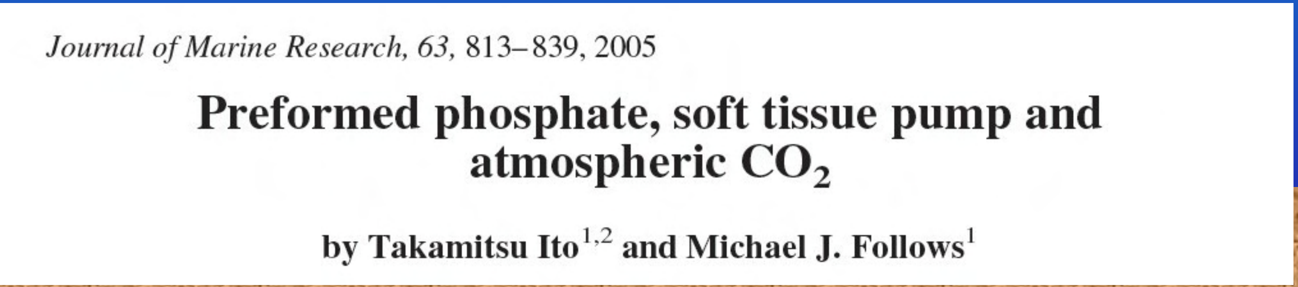
Oceanography Magazine, 2007, Figure 1

upwelling and mixing

sinking particles

CO_2 + Nutrients ← Organic Matter

Decomposition



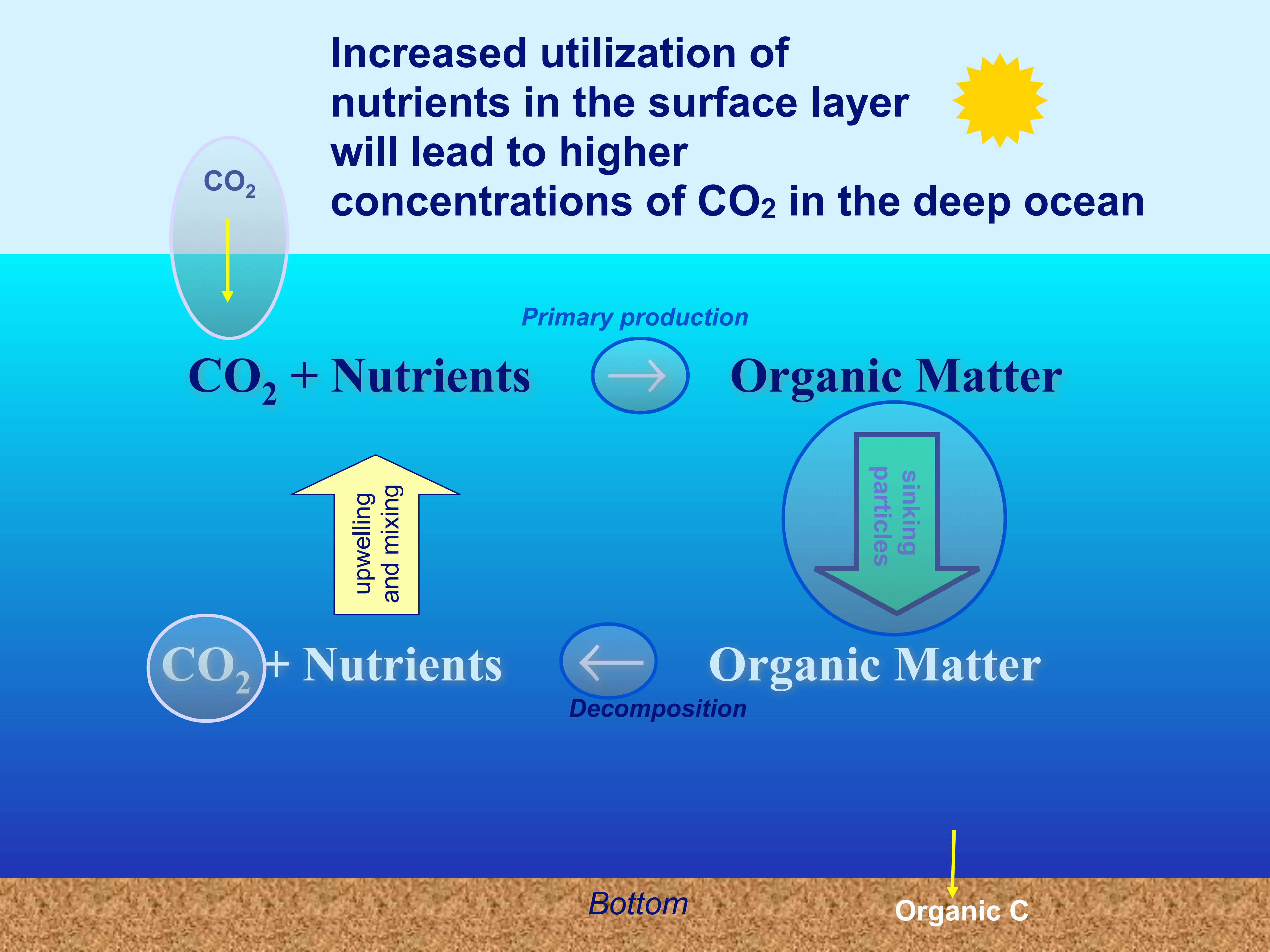
Journal of Marine Research, 63, 813–839, 2005

Preformed phosphate, soft tissue pump and atmospheric CO_2

by Takamitsu Ito[1,2] and Michael J. Follows[1]

Organic C

Increased utilization of nutrients in the surface layer will lead to higher concentrations of CO_2 in the deep ocean



“give me half a tanker of iron, and I will give you the next ice age”

… John Martin

Over beer, on the Redfield patio, Woods Hole Oceanographic Institution, July 1988

May 20, 1990

First surge of publicity

SCIENCE/TECHNOLOGY

Adding Iron to Ocean Makes Waves As Way To Cut Greenhouse CO_2

Approach would increase biological activity and thus CO_2 uptake, but some contend it could impede policies to reduce CO_2 emissions

Rudy Baum, C&EN San Francisco

tant of the greenhouse gases, which also include methane and chlorofluorocarbons (C&EN, March 13, 1989, page 25). A significant increase in the concentration of CO_2 in the atmosphere since the beginning of the Industrial Revolution, because of burning fossil fuels and, more recently, widespread deforestation, has led to fears of possibly dramatic and, at least in the short term, large-

es were primarily responsible for the decrease in CO_2 during ice ages, and several ocean/atmosphere models have been developed in the past decade to account for the change. These models incorporate the notion of a "biological pump"—photosynthetic uptake of CO_2 by the chlorophyll-containing marine microorganisms known as phytoplankton, and subsequent removal of carbon

Professor touts sea flora to curb global warming

By Kirby Moss
American-Statesman Staff

For two years, a University of

tilizers such as phosphate, nitrate and iron, Heller said.

Although he does no research, he has brought together scientists

Algae seen as cure for warming

Continued from B1

lieve, as does Heller, that pumping iron particles into the water could yield an underwater forest.

And if that experiment were suc-

Pumping up algae to fight greenhouse effect

OPINION

Manipulation of ocean dangerous

By Rodney M. Fujita, Ph.D.
Special to the American-Statesman

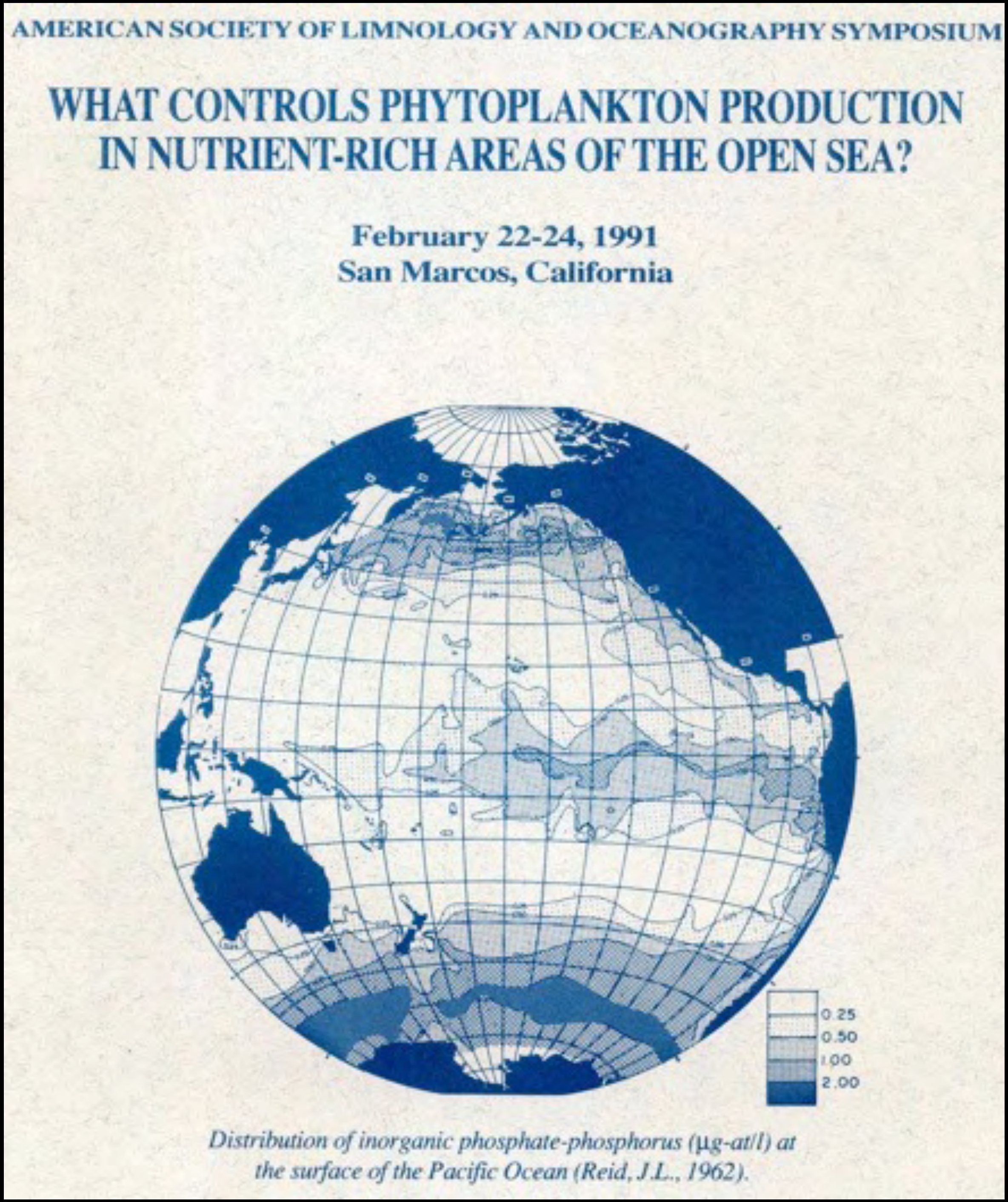
PUBLIC FORUM

An Aug. 7 *American-Statesman* story ("Professor touts sea flora to curb global warming") discussed a proposal that the oceans be fertilized with iron and other nutrients in order to stimulate enormous blooms of marine plants. Professor Adam Heller and some other scientists believe that this is a promising way to remove carbon dioxide from the atmosphere and thus limit the rate and extent of global warming due to the greenhouse effect. This proposal and Heller's comments raise a number of environmental concerns.

cies must be eaten by larger animals that produce heavy fecal pellets, which transport the carbon to the deep sea. Fertilization can drastically change the kinds of plants that grow in the sea, with no guarantee that they will be the right kinds. Changes in plant species can also result in changes in animal populations, with the result that the large plant populations stimulated by fertilization might remain in the surface waters.

As they are eaten and decompose, the carbon that they took up will be released into the water and into the atmosphere. These changes in species composition would have important and unpredictable effects on marine ecosystems.

Heller also claims that because humans have disrupted natural systems, it does not make sense to treat them as pristine. Although it is regrettably true that pristine natural systems are rare, this does not mean that human disruptions can always be corrected with more human intervention. Prevention of pollution is always more certain to protect the environment and the quality of human life than are attempts to manage pollutants once they have been discharged. The root causes of global warming are fossil fuel combustion and the destruction of temperate and tropical forests. These human activities are



AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY SYMPOSIUM

WHAT CONTROLS PHYTOPLANKTON PRODUCTION IN NUTRIENT-RICH AREAS OF THE OPEN SEA?

February 22-24, 1991
San Marcos, California

Distribution of inorganic phosphate-phosphorus (µg-at/l) at the surface of the Pacific Ocean (Reid, J.L., 1962).

February 1991

Scientists tackle the issue head-on

1991 Consensus Resolution: Synopsis

- Research — ***YES***
- Geoengineering — ***NO***

The ocean geoengineering controversy has lived on

Ocean Fertilization

Science, Policy, and Commerce

BY AARON L. STRONG, JOHN J. CULLEN, AND SALLIE W. CHISHOLM

ABSTRACT. Over the past 20 years there has been growing interest in the concept of fertilizing the ocean with iron to abate global warming. This interest was catalyzed by basic scientific experiments showing that iron limits primary production in certain regions of the ocean. The approach—considered a form of "geoengineering"—is to induce phytoplankton blooms through iron addition, with the goal of producing organic particles that sink to the deep ocean, sequestering carbon from the atmosphere. With the controversy surrounding the most recent scientific iron fertilization experiment in the Southern Ocean (LOHAFEX) and the ongoing discussion about restrictions on large-scale iron fertilization activities by the London Convention, the debate about the potential use of iron fertilization for geoengineering has never been more public or more pronounced. To help inform this debate, we present a synoptic view of the two-decade history of iron fertilization, from scientific experiments to commercial enterprises designed to trade credits for ocean fertilization on a developing carbon market. Throughout these two decades there has been a repeated cycle: Scientific experiments are followed by media and commercial interest and this triggers calls for caution and the need for more experiments. Over the years, some scientists have repeatedly pointed out that the idea is both unproven and potentially ecologically disruptive, and models have consistently shown that at the limit, the approach could not substantially change the trajectory of global warming. Yet, interest and investment in ocean fertilization as a climate mitigation strategy have only grown and intensified, fueling media reports that have misconstrued scientific results, and conflated scientific experimentation with geoengineering. We suggest that it is time to break this two-decade cycle, and argue that we know enough about ocean fertilization to say that it should not be considered further as a means to mitigate climate change. But, ocean fertilization research should not be halted: if used appropriately and applied to testable hypotheses, it is a powerful research tool for understanding the responses of ocean ecosystems in the context of climate change.

236 *Oceanography* Vol.22, No.3


PLANKTOS
Multi-Benefit Bio-Remedies for the Climate's Carbon Ills

Where most CO2 can go and rightfully should be


Save the Earth ... and Get Rich!

This pioneering R&D company has big plans that Wall Street hasn't heard about yet – and it is nothing less than solving the gravest environmental threat facing the world today.
Their innovative technology for helping big corporations comply with the Kyoto Protocol could generate $300 million in new revenues within the next 12 months – sending the share price soaring!


ENVIRONMENT

Haida group dumps man behind ocean fertilization

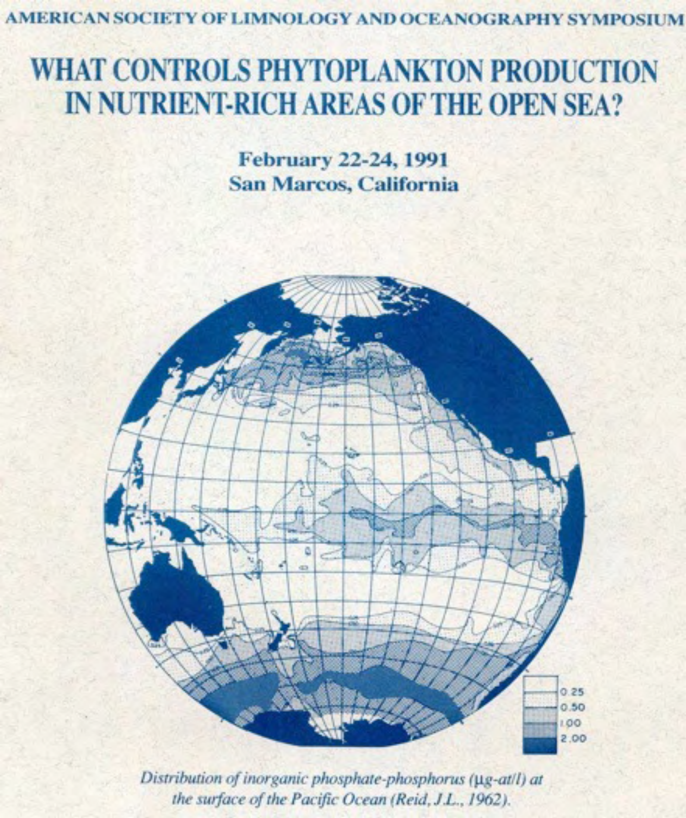
MARK HUME
VANCOUVER — The Globe and Mail
Published Thursday, May. 23 2013, 9:50 PM EDT
Last updated Thursday, May. 23 2013, 9:59 PM EDT

Russ George has been dumped by the small Haida organization for which he designed a controversial ocean fertilization project last year.

In a statement released on Thursday, Haida Salmon Restoration Corp. (HSRC) said it has "removed" Mr. George as a director of the company. "In addition, the HSRC has terminated Mr. George's employment as an officer of the corporation," it states.

Today's topic is the science.

Focus on microbial ecology



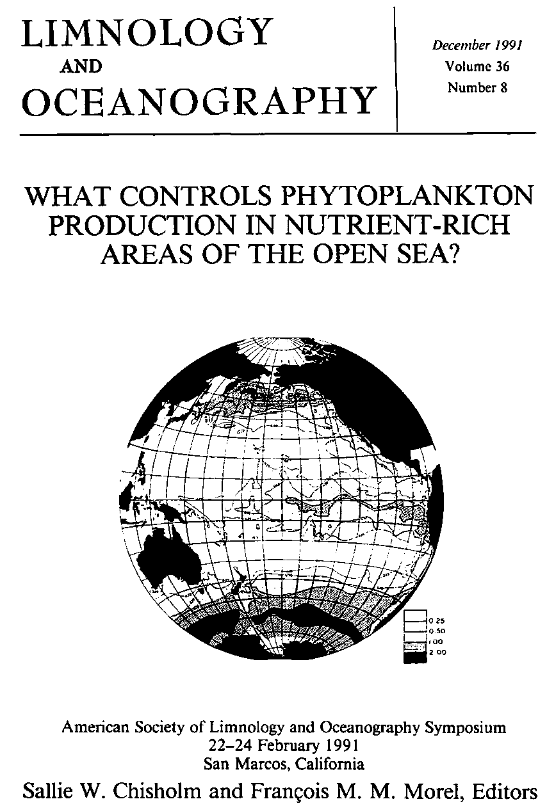
AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY SYMPOSIUM

WHAT CONTROLS PHYTOPLANKTON PRODUCTION IN NUTRIENT-RICH AREAS OF THE OPEN SEA?

February 22-24, 1991
San Marcos, California

Distribution of inorganic phosphate-phosphorus (µg-at/l) at the surface of the Pacific Ocean (Reid, J.L., 1962).

During the symposium



LIMNOLOGY AND OCEANOGRAPHY

December 1991
Volume 36
Number 8

WHAT CONTROLS PHYTOPLANKTON PRODUCTION IN NUTRIENT-RICH AREAS OF THE OPEN SEA?

American Society of Limnology and Oceanography Symposium
22–24 February 1991
San Marcos, California
Sallie W. Chisholm and François M. M. Morel, Editors

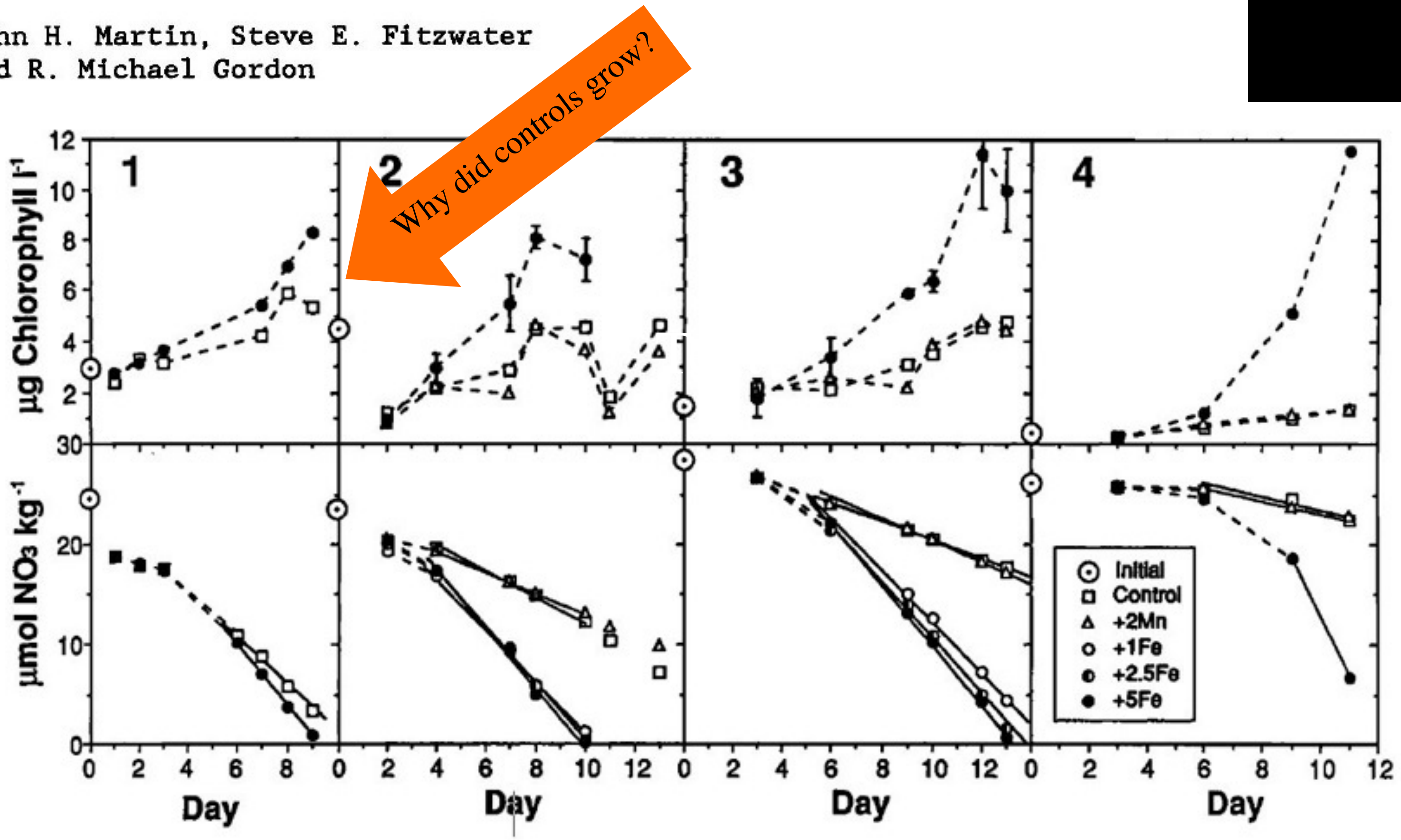
In the special issue and
other papers published in the early
1990’s

Limitations of bottle experiments were recognized

GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 4, NO. 1, PAGES 5-12, MARCH 1990

IRON DEFICIENCY LIMITS PHYTOPLANKTON GROWTH
IN ANTARCTIC WATERS

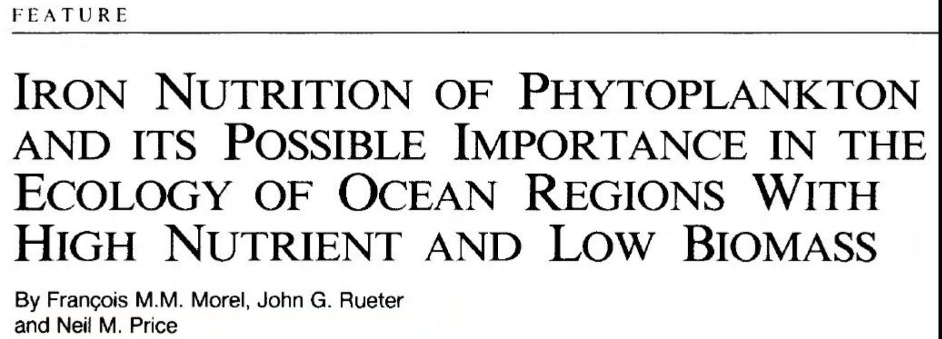
John H. Martin, Steve E. Fitzwater
and R. Michael Gordon



Why did controls grow?

Fig. 2. Chlorophyll and nitrate concentrations versus experiment day at Stations 1 to 4 (see Figure 1) with added Fe or Mn versus control. Station 2 and 3 chlorophyll values for the three samples with added Fe were averaged; means and standard deviations are shown. Solid lines in nitrate figures are from Table 1 linear regressions.

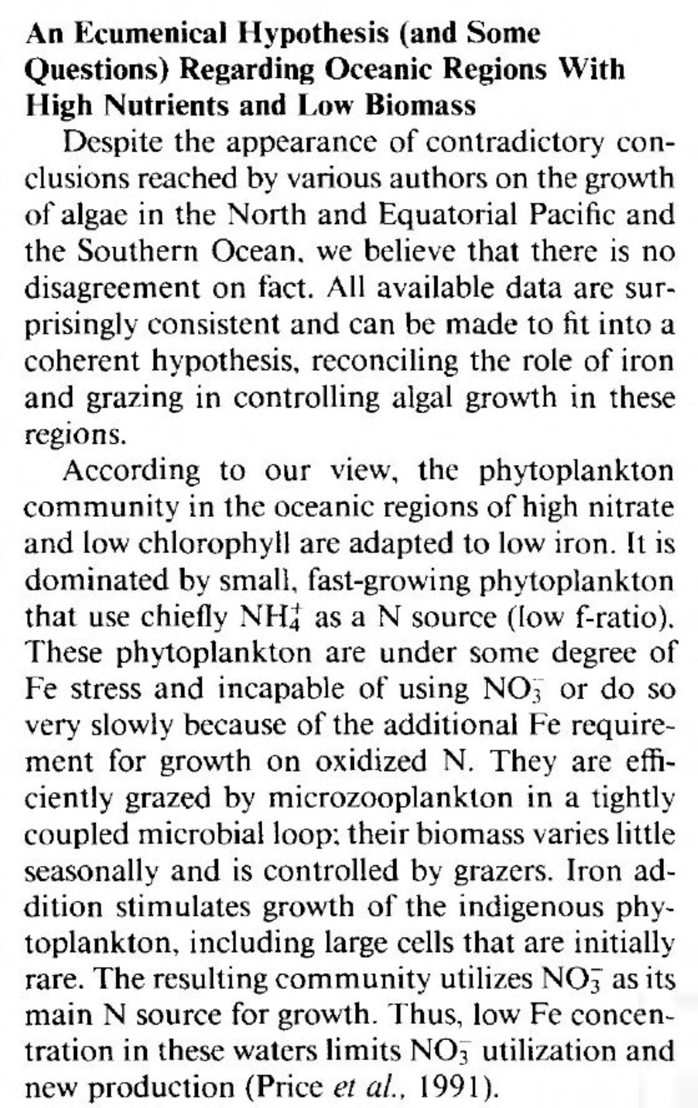
The “Ecumenical Iron Hypothesis” was developed quickly



FEATURE

IRON NUTRITION OF PHYTOPLANKTON AND ITS POSSIBLE IMPORTANCE IN THE ECOLOGY OF OCEAN REGIONS WITH HIGH NUTRIENT AND LOW BIOMASS

By François M.M. Morel, John G. Rueter
and Neil M. Price



An Ecumenical Hypothesis (and Some Questions) Regarding Oceanic Regions With High Nutrients and Low Biomass

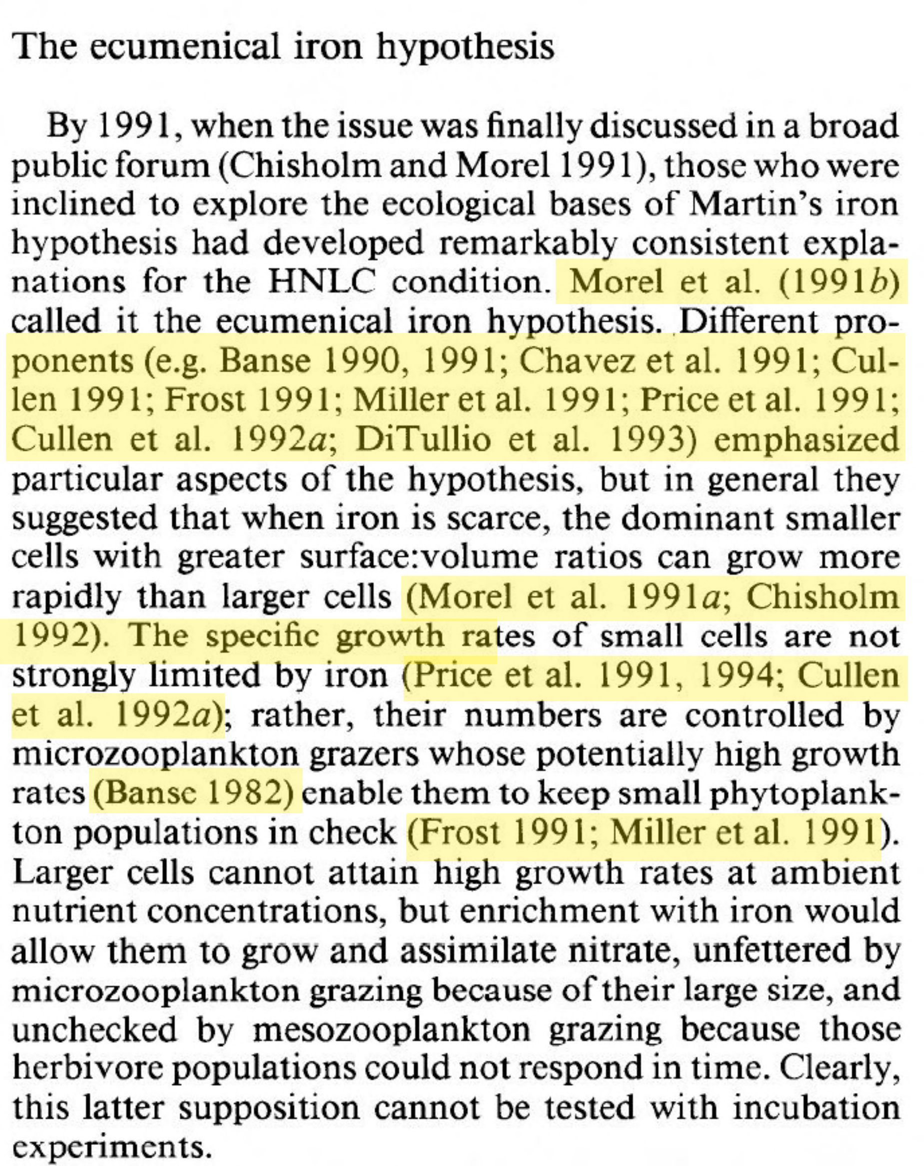
Despite the appearance of contradictory conclusions reached by various authors on the growth of algae in the North and Equatorial Pacific and the Southern Ocean, we believe that there is no disagreement on fact. All available data are surprisingly consistent and can be made to fit into a coherent hypothesis, reconciling the role of iron and grazing in controlling algal growth in these regions.

According to our view, the phytoplankton community in the oceanic regions of high nitrate and low chlorophyll are adapted to low iron. It is dominated by small, fast-growing phytoplankton that use chiefly NH_4^+ as a N source (low f-ratio). These phytoplankton are under some degree of Fe stress and incapable of using NO_3^- or do so very slowly because of the additional Fe requirement for growth on oxidized N. They are efficiently grazed by microzooplankton in a tightly coupled microbial loop; their biomass varies little seasonally and is controlled by grazers. Iron addition stimulates growth of the indigenous phytoplankton, including large cells that are initially rare. The resulting community utilizes NO_3^- as its main N source for growth. Thus, low Fe concentration in these waters limits NO_3^- utilization and new production (Price *et al.*, 1991).

Morel, F. M. M., J. G. Rueter, and N. M. Price (1991), *Oceanography Mag.*, *4*, 56-61.

Many biological oceanographers drew similar conclusions

…I don’t think that the original hypotheses were far off the mark

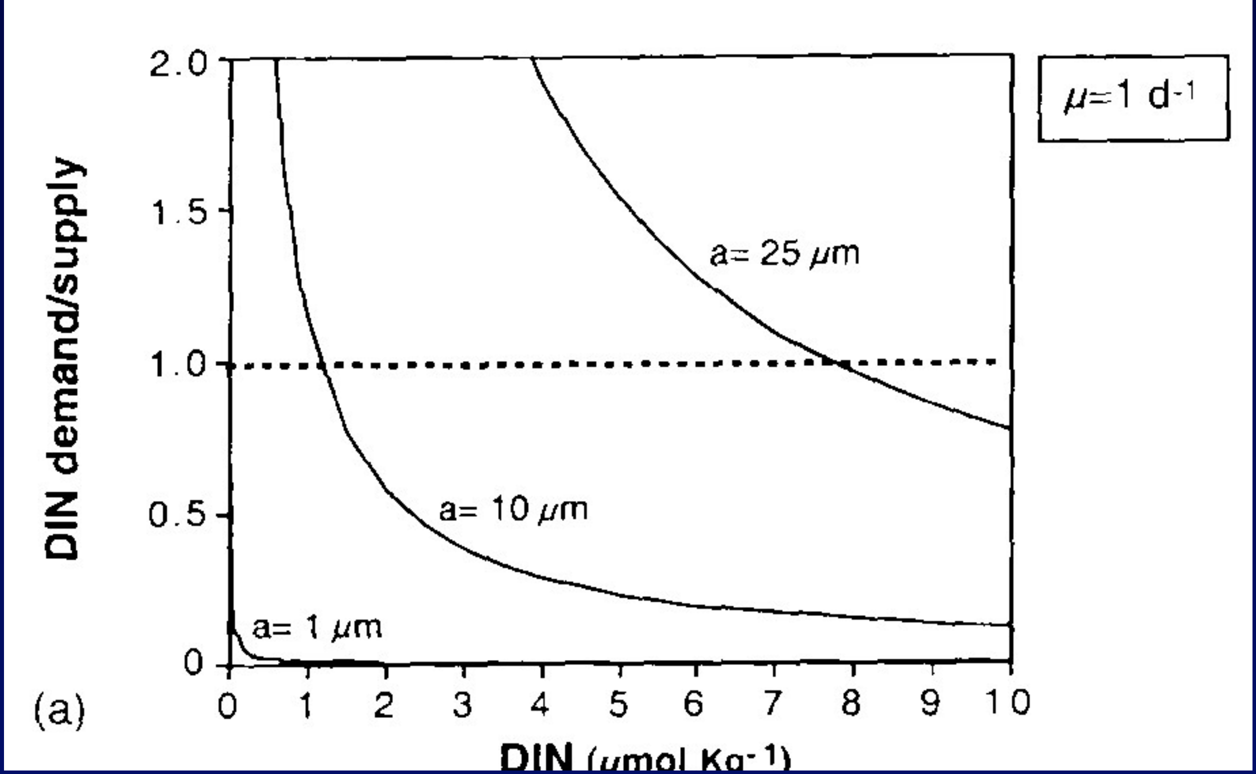


The ecumenical iron hypothesis

By 1991, when the issue was finally discussed in a broad public forum (Chisholm and Morel 1991), those who were inclined to explore the ecological bases of Martin’s iron hypothesis had developed remarkably consistent explanations for the HNLC condition. Morel et al. (1991*b*) called it the ecumenical iron hypothesis. Different proponents (e.g. Banse 1990, 1991; Chavez et al. 1991; Cullen 1991; Frost 1991; Miller et al. 1991; Price et al. 1991; Cullen et al. 1992*a*; DiTullio et al. 1993) emphasized particular aspects of the hypothesis, but in general they suggested that when iron is scarce, the dominant smaller cells with greater surface:volume ratios can grow more rapidly than larger cells (Morel et al. 1991*a*; Chisholm 1992). The specific growth rates of small cells are not strongly limited by iron (Price et al. 1991, 1994; Cullen et al. 1992*a*); rather, their numbers are controlled by microzooplankton grazers whose potentially high growth rates (Banse 1982) enable them to keep small phytoplankton populations in check (Frost 1991; Miller et al. 1991). Larger cells cannot attain high growth rates at ambient nutrient concentrations, but enrichment with iron would allow them to grow and assimilate nitrate, unfettered by microzooplankton grazing because of their large size, and unchecked by mesozooplankton grazing because those herbivore populations could not respond in time. Clearly, this latter supposition cannot be tested with incubation experiments.

Cullen, J. J. (1995), Status of the iron hypothesis after the open-ocean enrichment experiment, *Limnology and Oceanography*, *40*, 1336-1343.

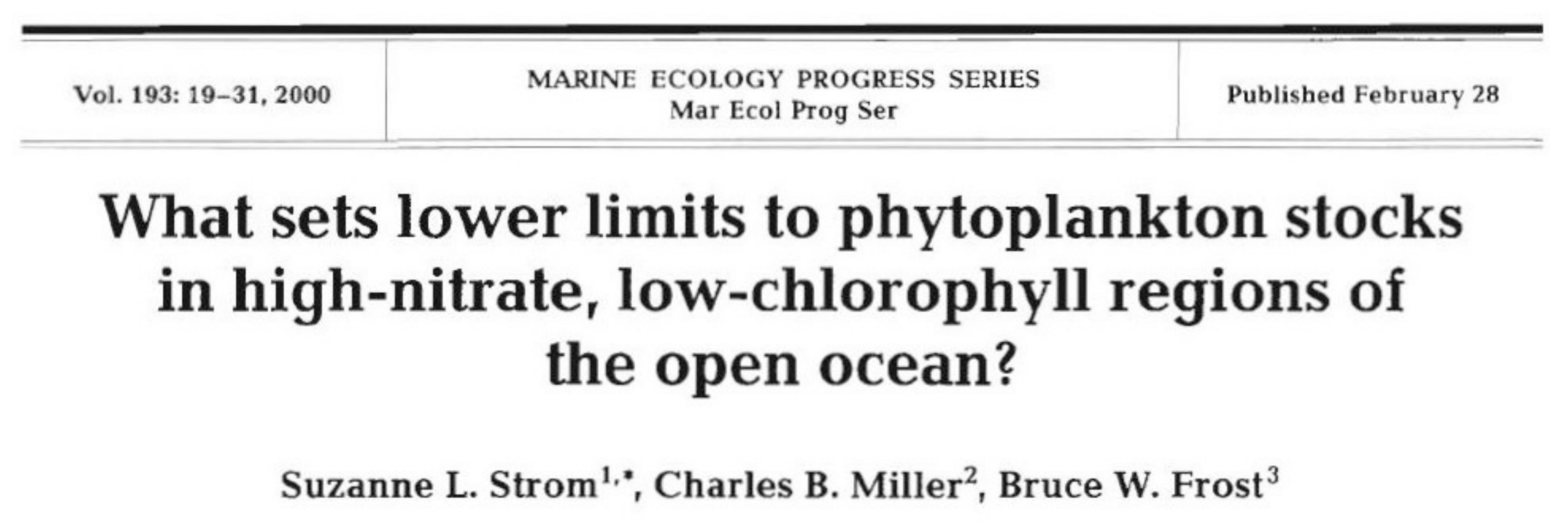
Cell size matters: bigger cells have lower surface:volume and thus require higher concentrations of nutrients to grow at the same rage as smaller cells



Riebesell U, Wolf-Gladrow DA (2002) Supply and uptake of inorganic nutrients. In: Williams PJL, Thomas DN, Reynolds CS (eds) Phytoplankton Productivity. Carbon Assimilation in Marine and Freshwater Ecosystems. Blackwell, Oxford, p 109-140

See also: Chisholm, S.W., 1992. Phytoplankton size. In P.G. Falkowski, A. Woodhead (Eds.), Primary Productivity and Biogeochemical Cycles in the Sea (pp. 213-238). New York: Plenum.

Cell size matters: smaller cells are grazed by protozoa that can reproduce very rapidly and control prey populations



Vol. 193: 19–31, 2000

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published February 28

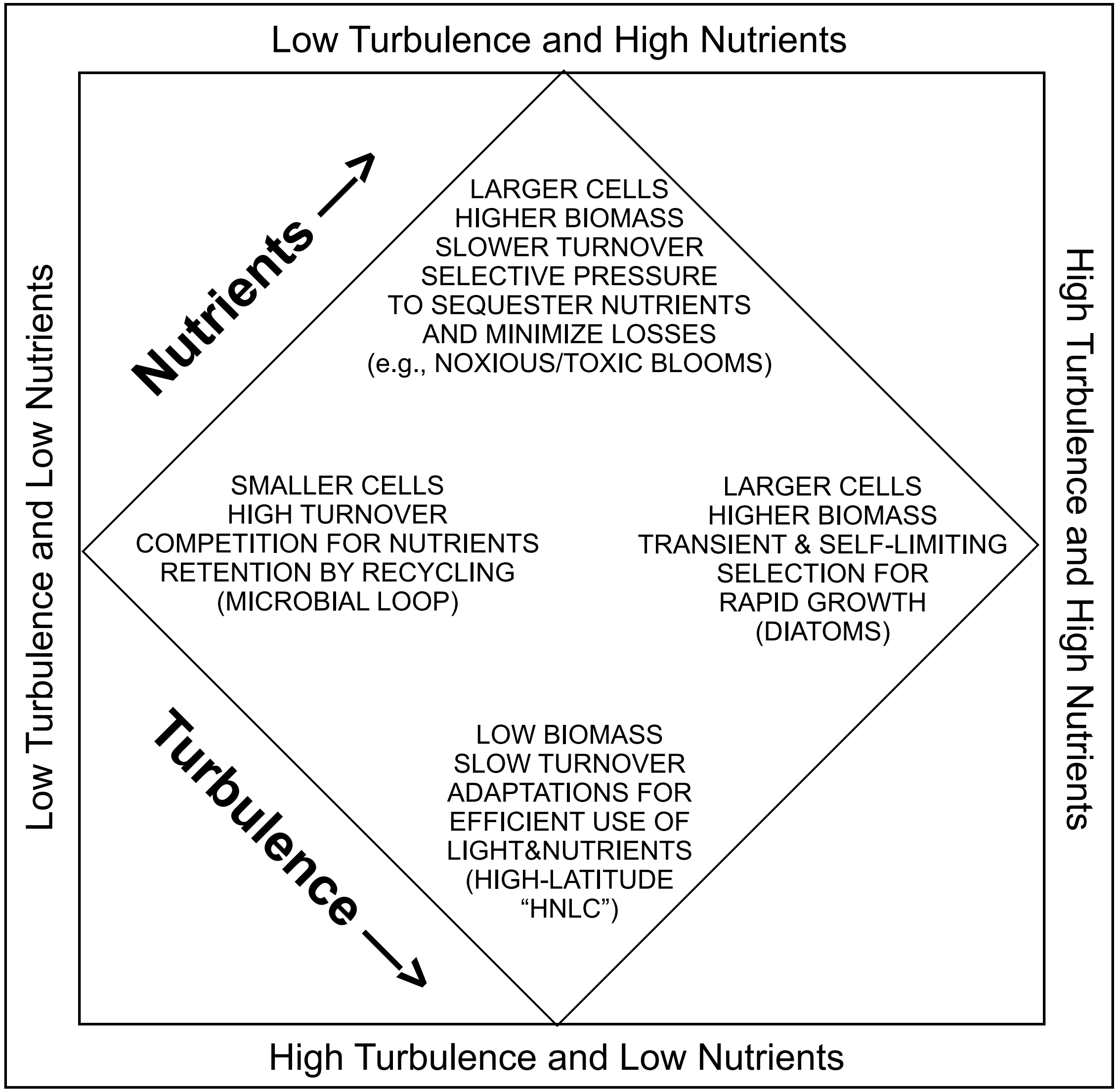
What sets lower limits to phytoplankton stocks in high-nitrate, low-chlorophyll regions of the open ocean?

Suzanne L. Strom[1,*], Charles B. Miller[2], Bruce W. Frost[3]

See also:

Banse K (1992) Grazing, temporal changes of phytoplankton concentrations and the microbial loop in the open sea. In: Falkowski PG, Woodhead AD (eds) Primary Productivity and Biogeochemical Cycles in the Sea, Vol 43. Plenum, New York, p 409- 440

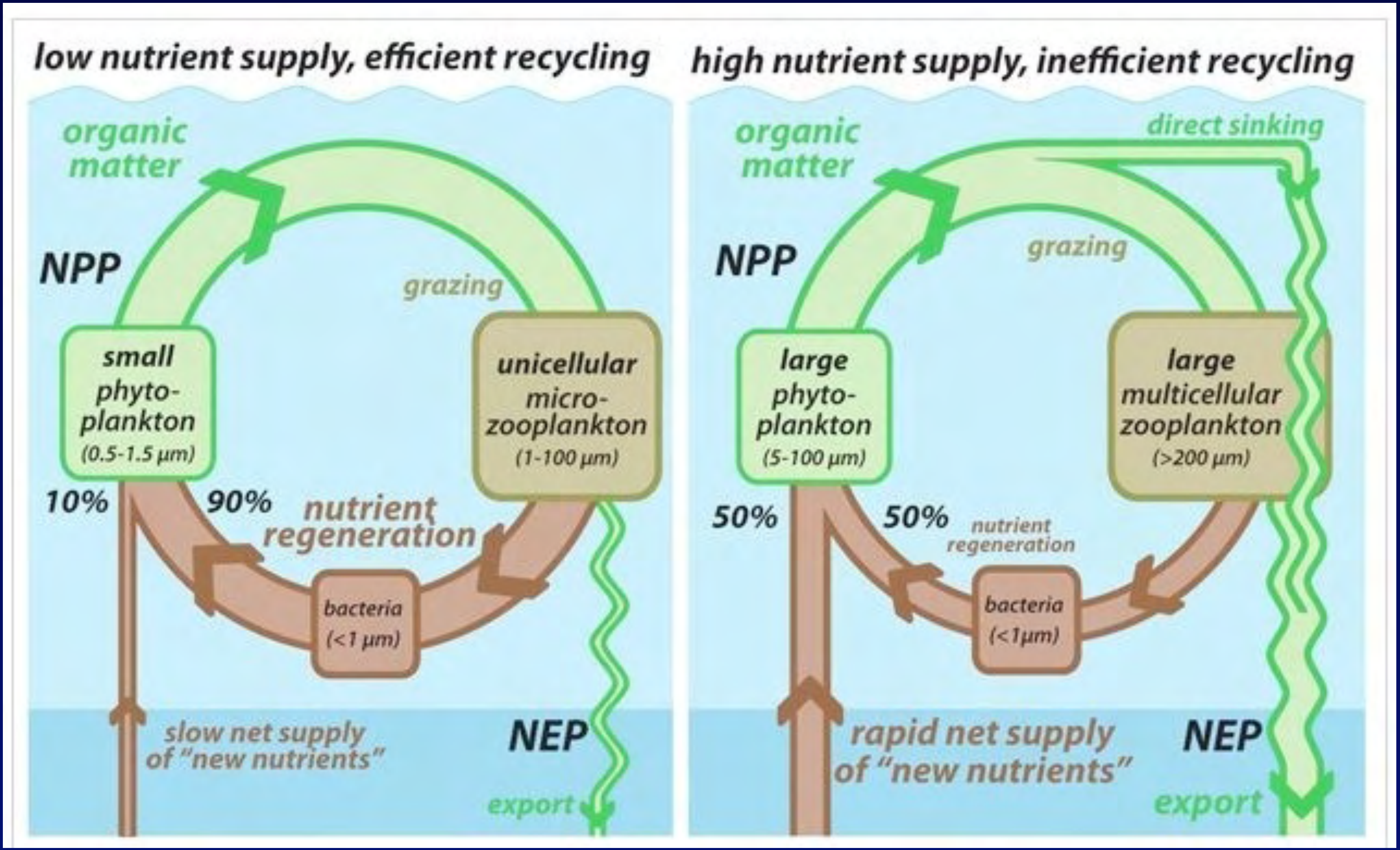
Event-Scale Forcing —>
<— Succession



Potential for Production and Export —>

Cullen et al. 2002, The Sea

Sustained release from iron limitation could reimpose the low nutrient condition, still limited by the rate of supply of new nutrients, but with lower residual N and P

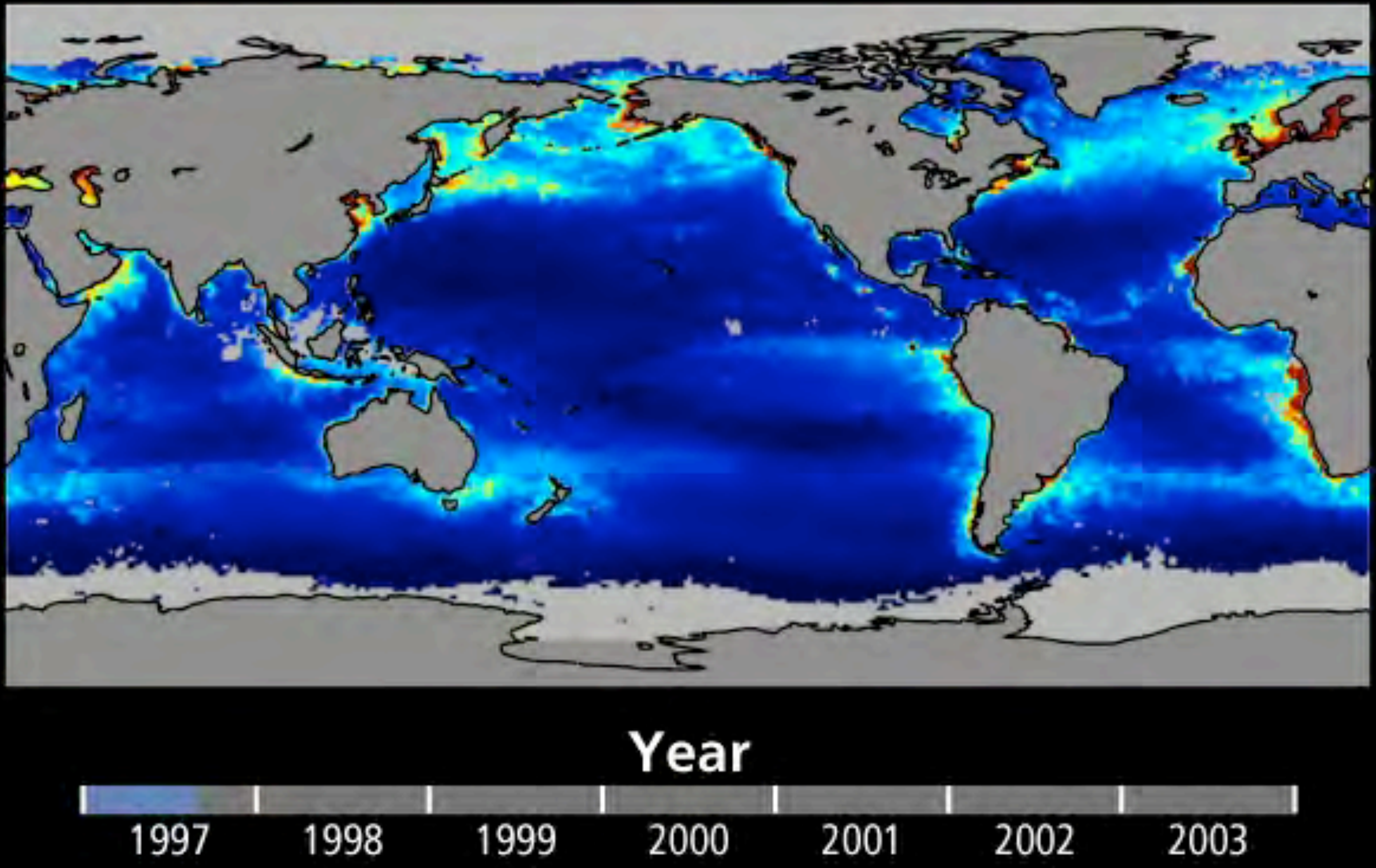


Citation: Sigman, D. M. & Hain, M. P. (2012) The Biological Productivity of the Ocean: Section 1. *Nature Education Knowledge* 3(10):21

http://www.nature.com/scitable/knowledge/library/the-biological-productivity-of-the-ocean-section-70631104

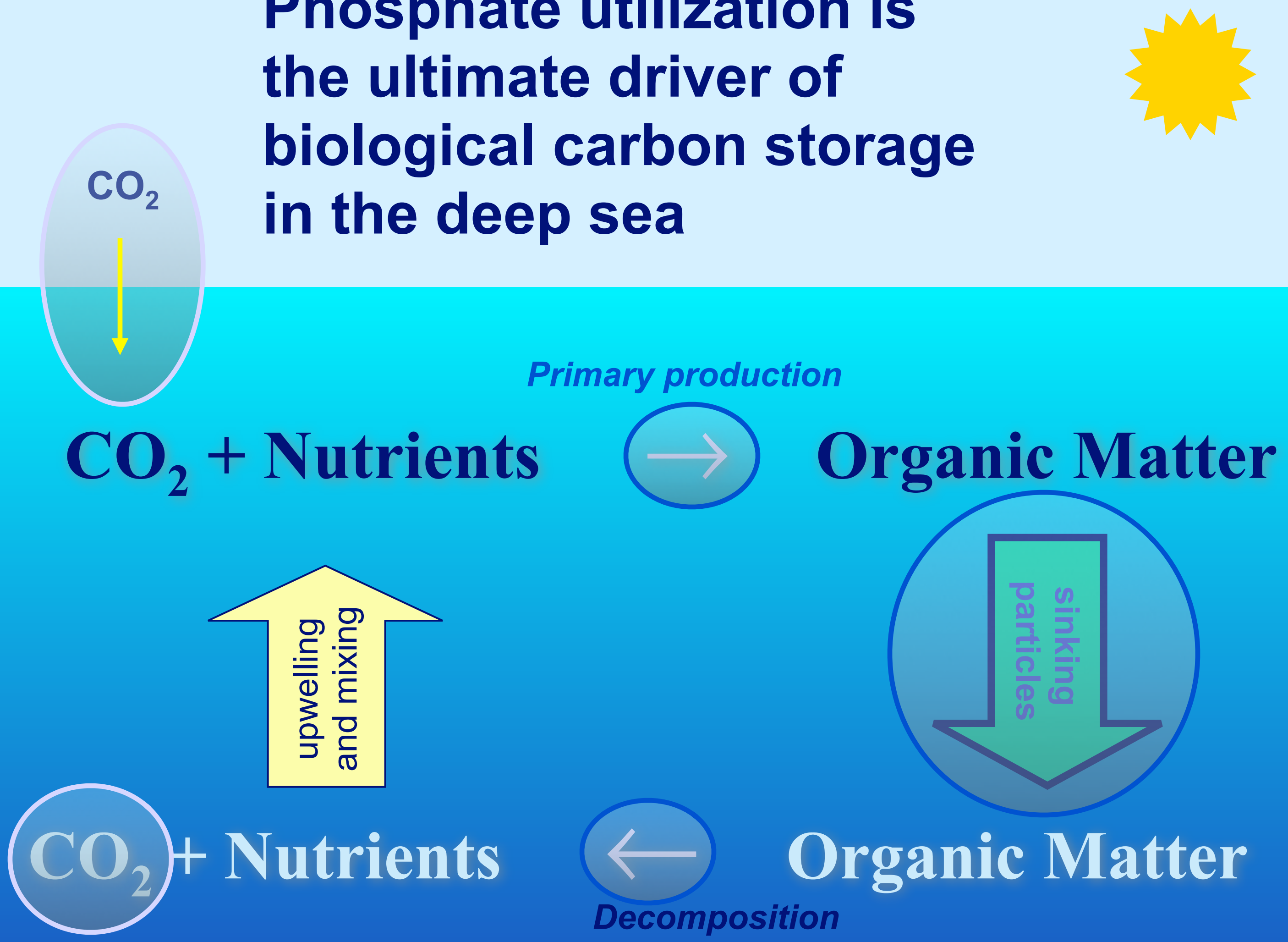
John Cullen: C-MORE 2011

Do the patterns still make sense?



Global productivity from SeaWiFS ocean color (NASA/GSFC)

Phosphate utilization is the ultimate driver of biological carbon storage in the deep sea



CO_2

Primary production

CO_2 + Nutrients → Organic Matter

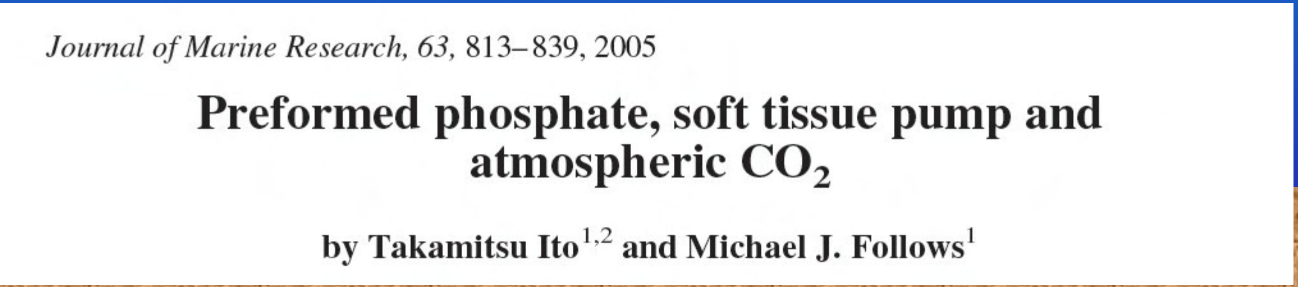
upwelling and mixing

sinking particles

CO_2 + Nutrients ← Organic Matter

Decomposition

Organic C

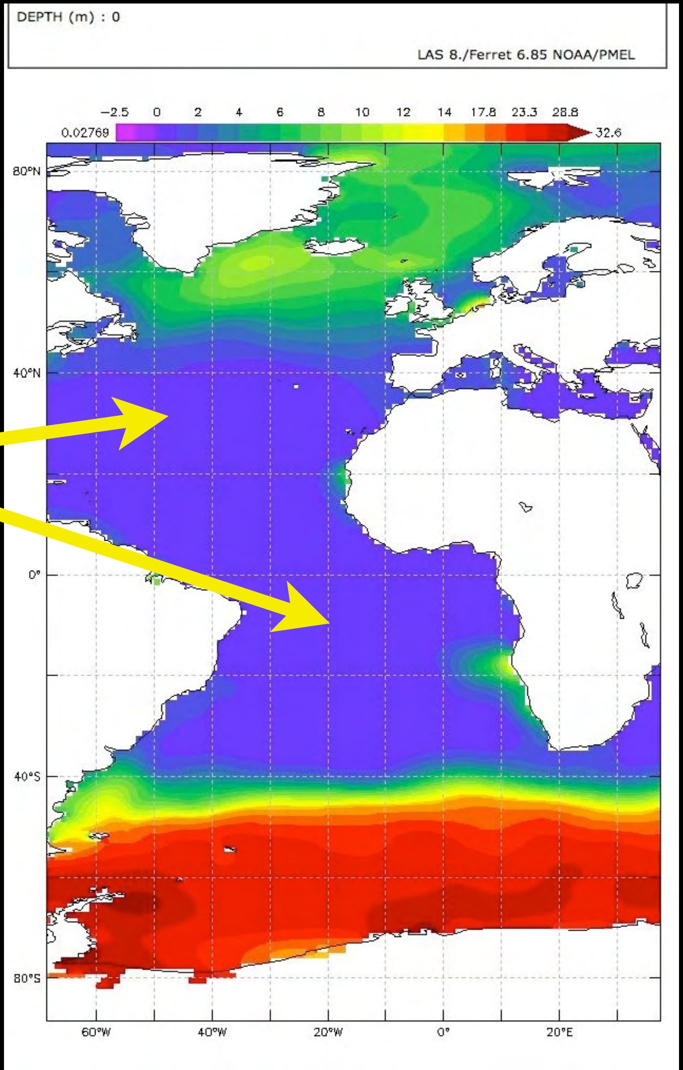


Journal of Marine Research, 63, 813–839, 2005

Preformed phosphate, soft tissue pump and atmospheric CO_2

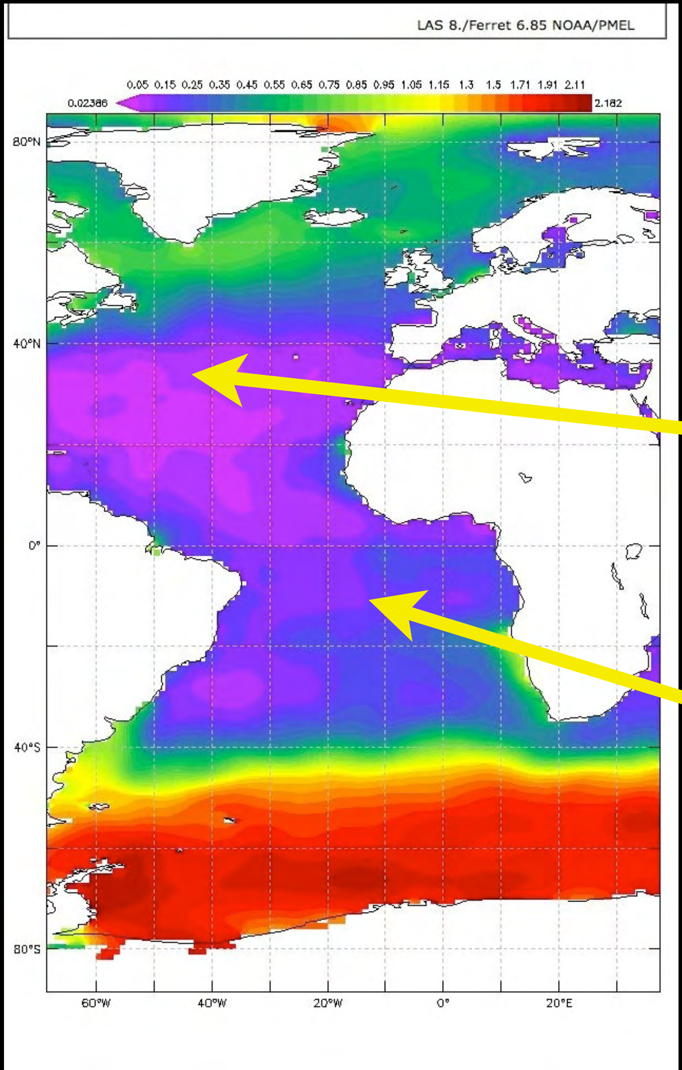
by Takamitsu Ito[1,2] and Michael J. Follows[1]

Surface Nitrate



Really
Low

Surface Phosphate



Really
Low

Not so
Low!

nature geoscience

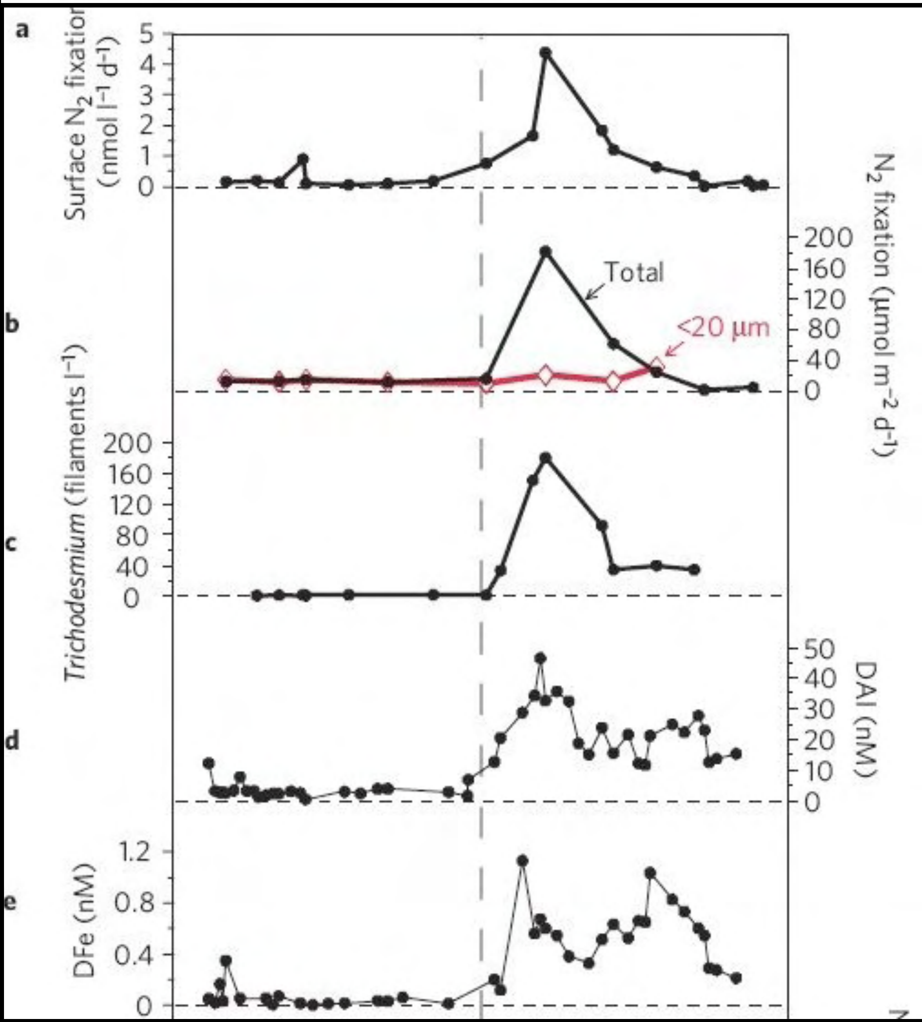
LETTERS

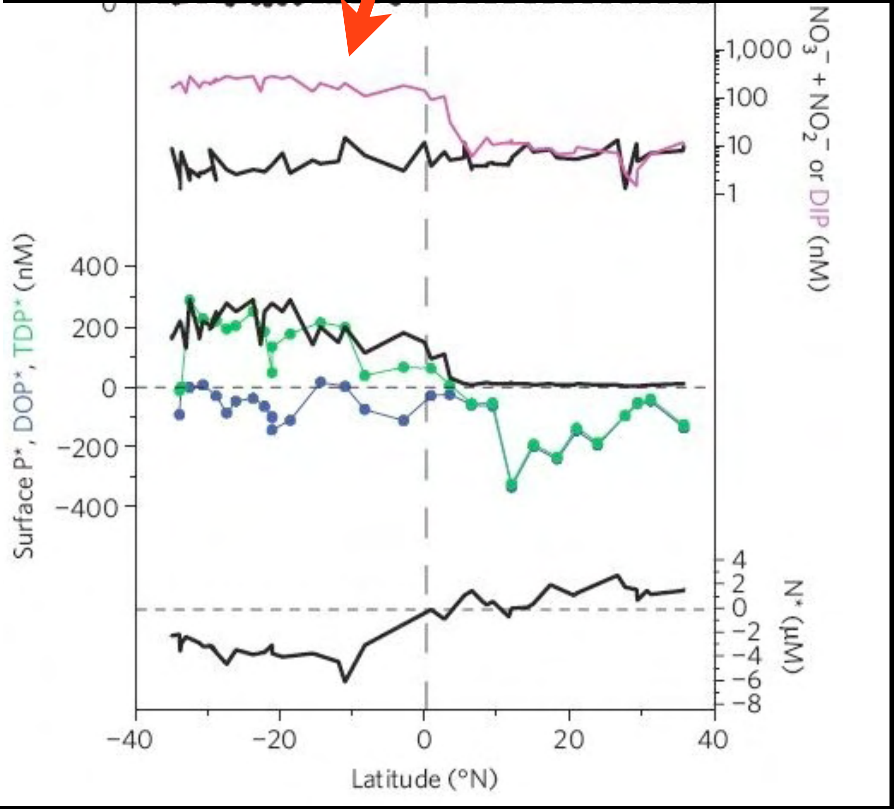
Large-scale distribution of Atlantic nitrogen fixation controlled by iron availability

C. Mark Moore[1,2]*, Matthew M. Mills[3], Eric P. Achterberg[2], Richard J. Geider[1], Julie LaRoche[4], Mike I. Lucas[5], Elaine L. McDonagh[2], Xi Pan[2], Alex J. Poulton[2], Micha J. A. Rijkenberg[2], David J. Suggett[1], Simon J. Ussher[6] and E. Malcolm S. Woodward[7]

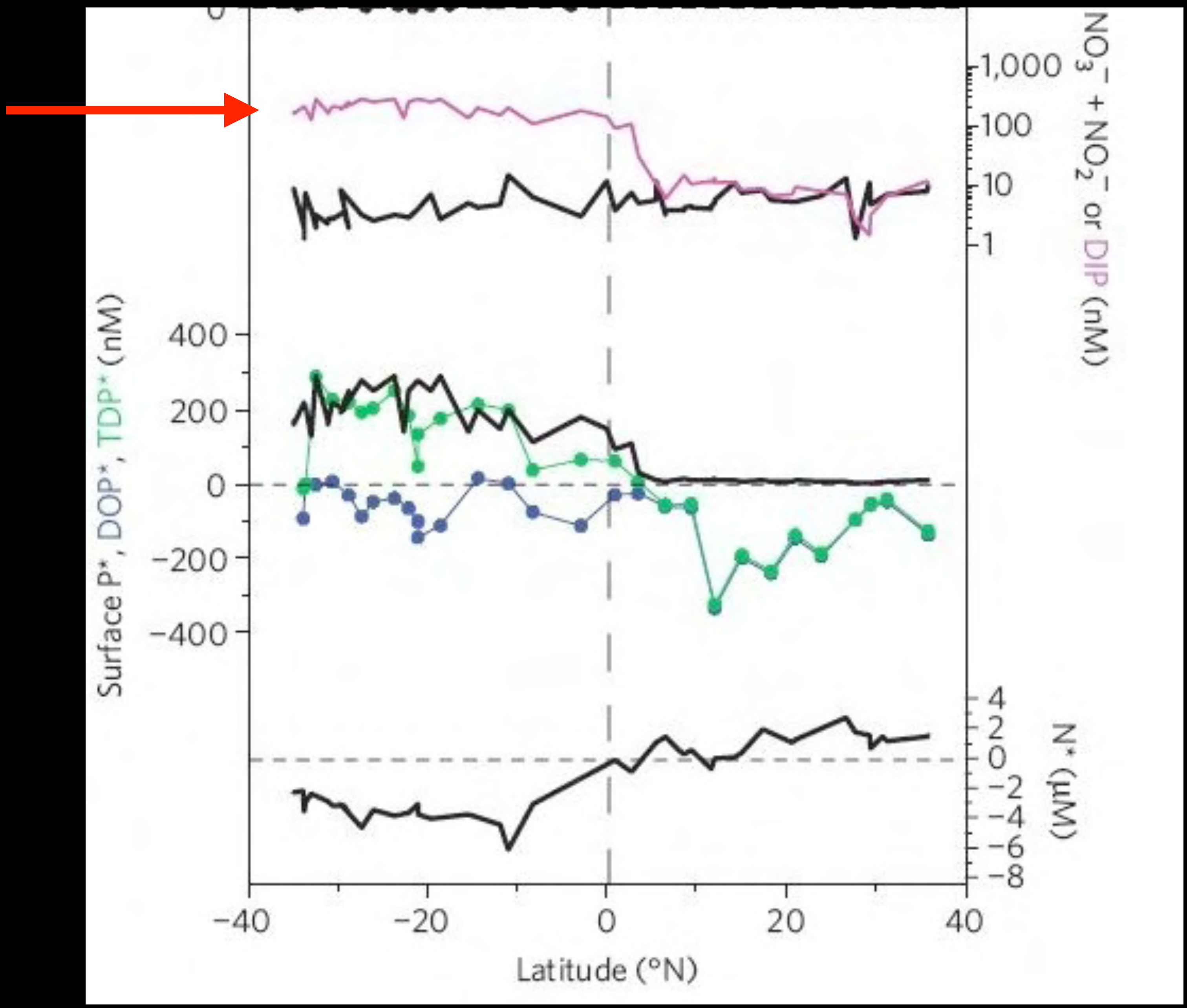
Interpretation from measurements:

Phosphate is not drawn down in the south Atlantic because N-fixation is limited by the supply of iron



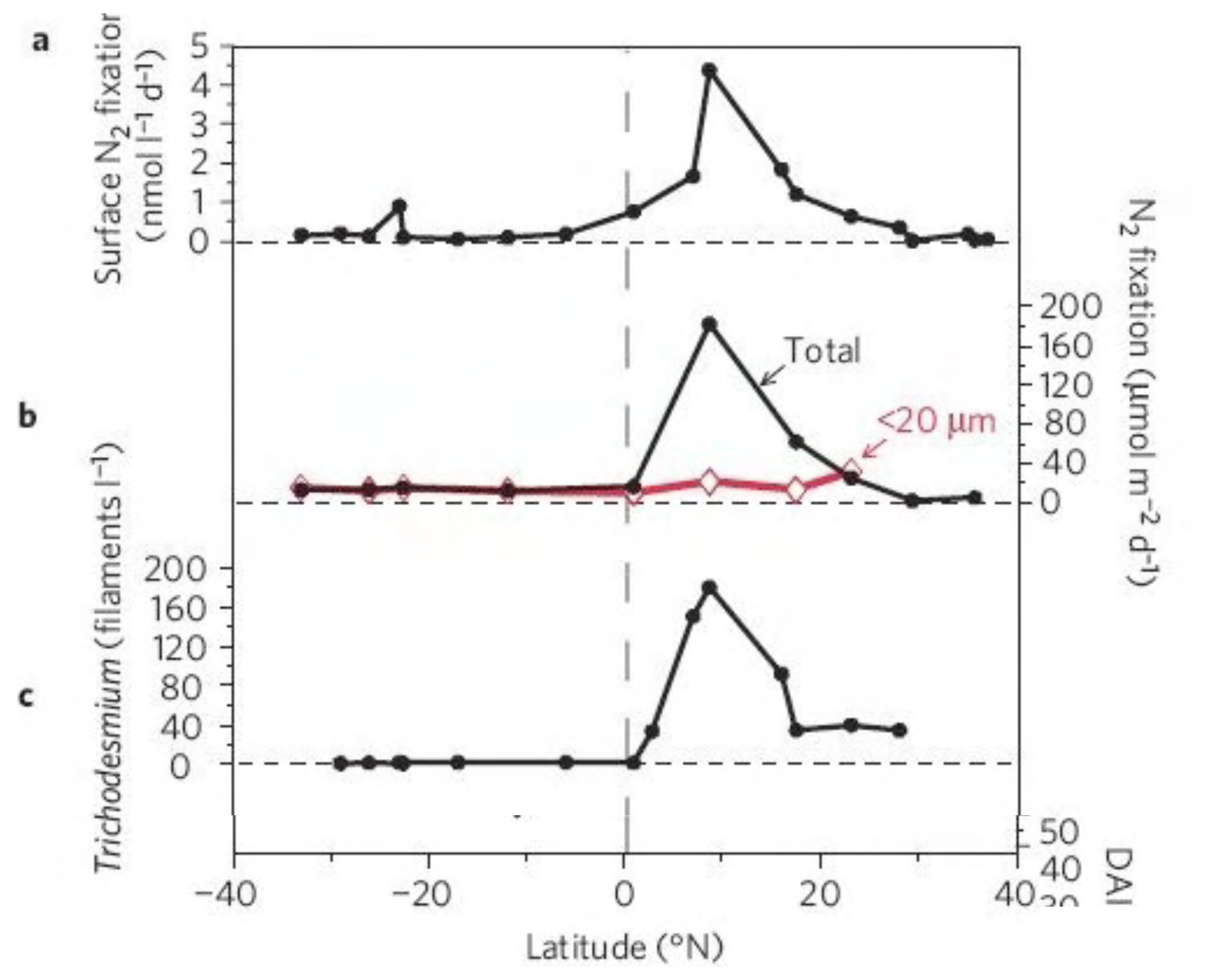


A pretty big deal



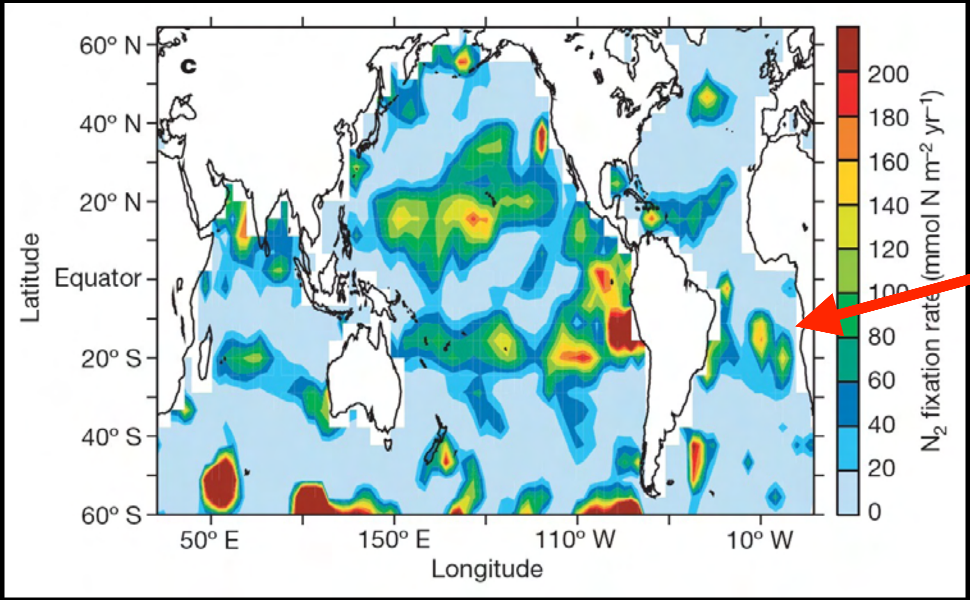
What is the N-fixation rate in the South Atlantic?

Measurements suggest it is very low



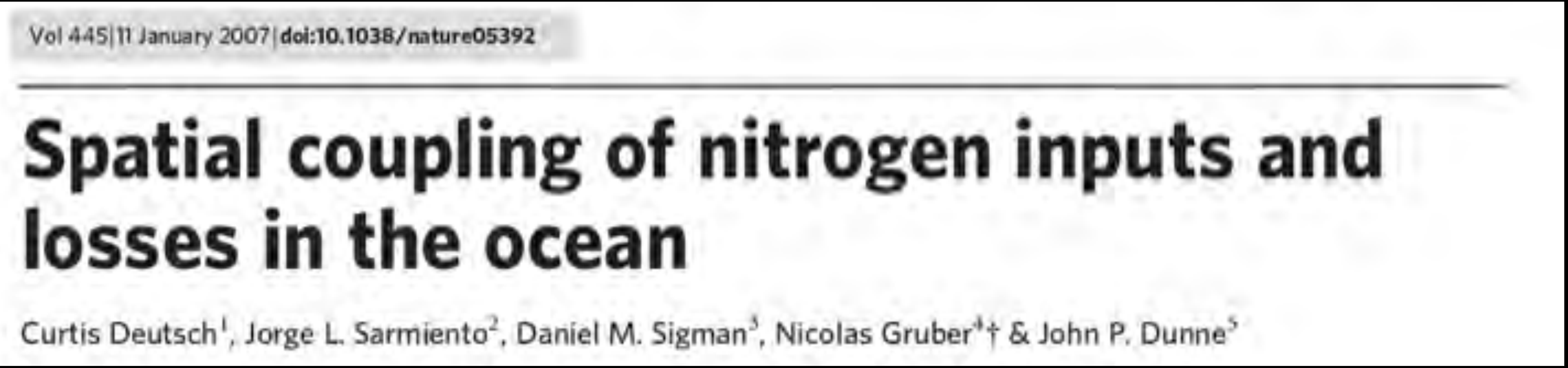
What is the N-fixation rate in the South Atlantic?

Model results are not so categorical



Deutsch et al. Nature 2007

Diagnostic Model



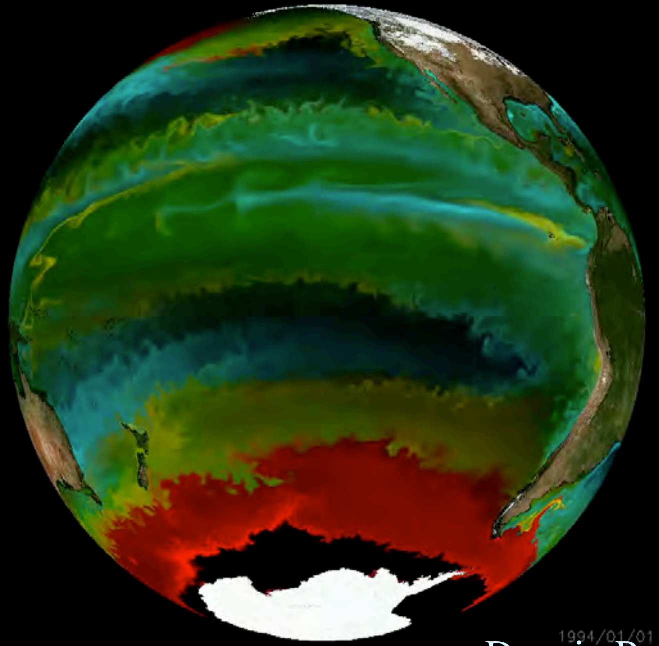
Vol 445 | 11 January 2007 | doi:10.1038/nature05392

Spatial coupling of nitrogen inputs and losses in the ocean

Curtis Deutsch[1], Jorge L. Sarmiento[2], Daniel M. Sigman[3], Nicolas Gruber[4]† & John P. Dunne[5]

What is the N-fixation rate?

Prognostic models



Darwin Project:
Mick Follows (MIT) and colleagues

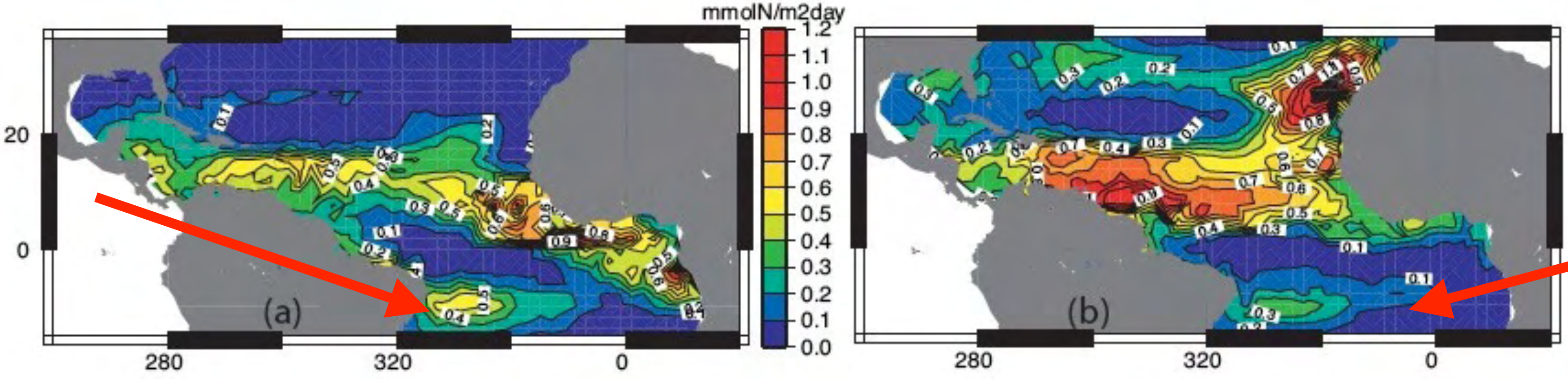
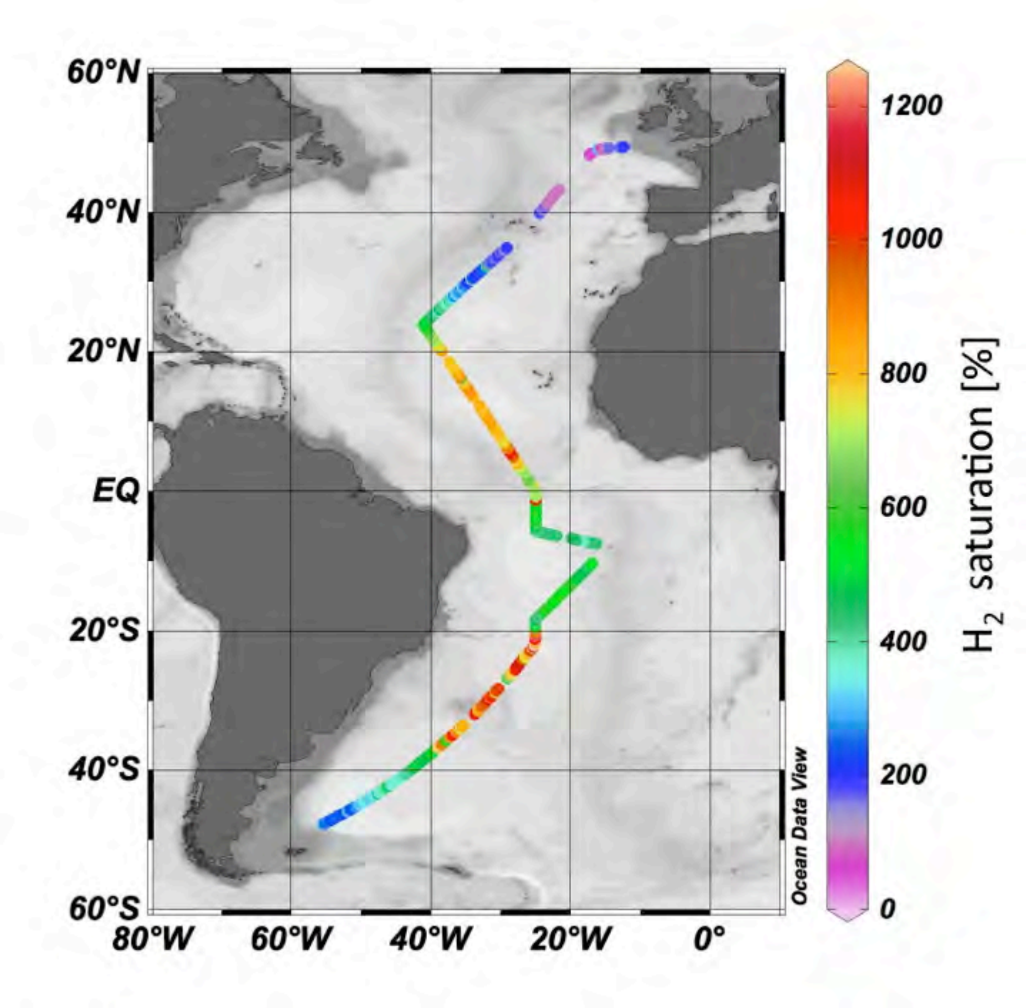


Fig. 3. Surface nitrogen fixation rates for **(a)** spring (April) and **(b)** fall (August) are shown for the NSTAR run.

Coles and Hood Biogeosciences 2007

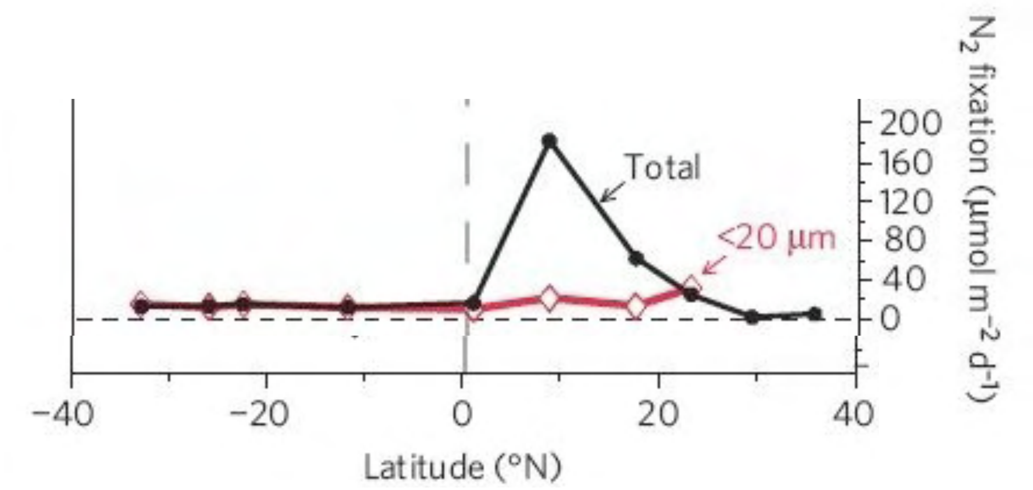
Can measurements of hydrogen provide clues?



$$N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16\ Pi$$

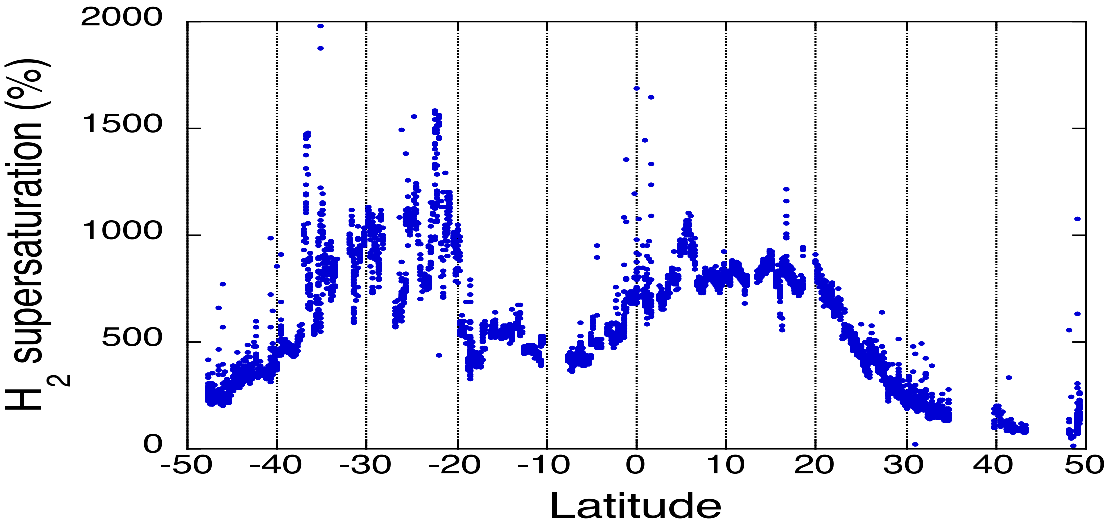
R. Moore et al., JGR Oceans, in review

Rate measurements

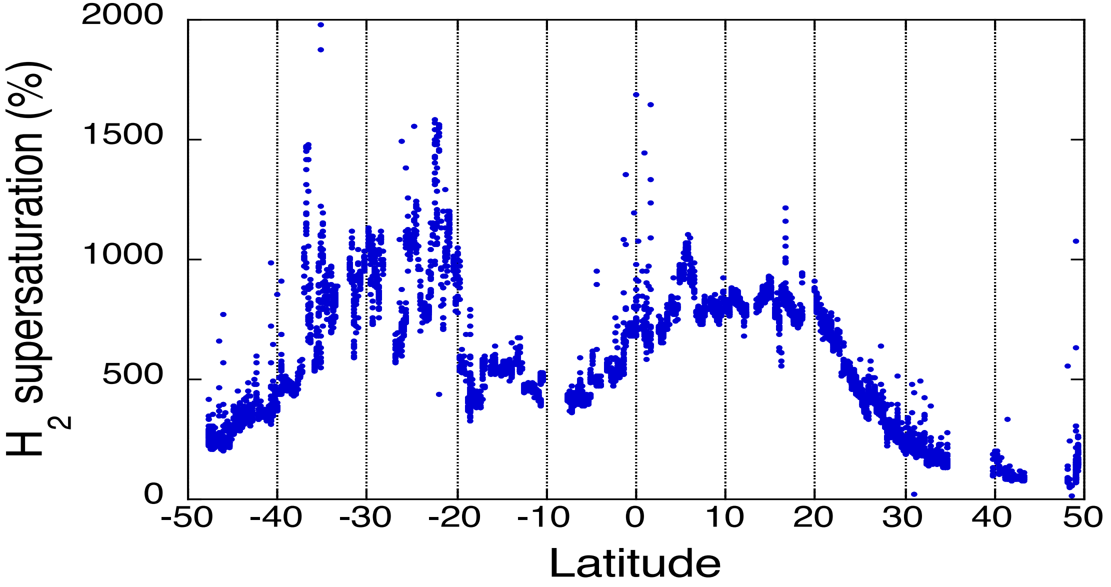


C.M. Moore et al., 2009

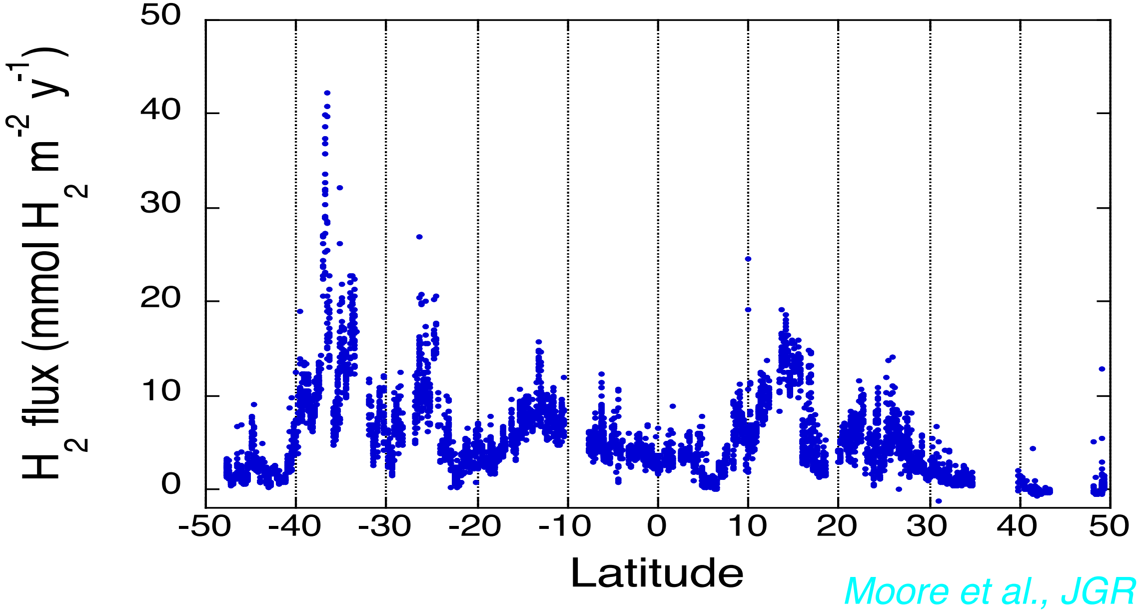
Hydrogen supersaturation



R.M. Moore et al., JGR Oceans, in review

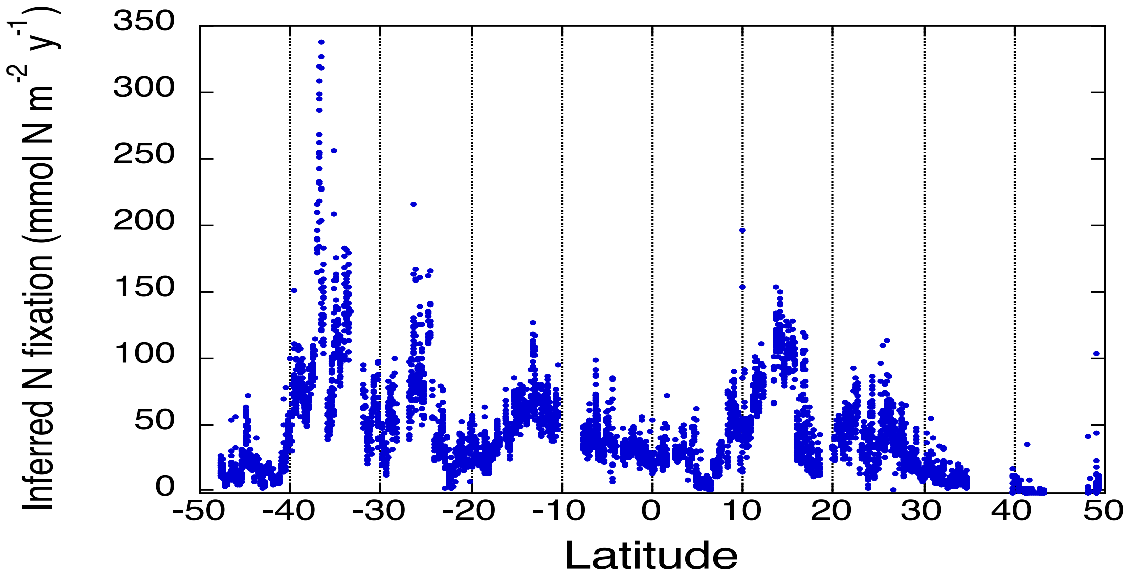


Hydrogen supersaturation

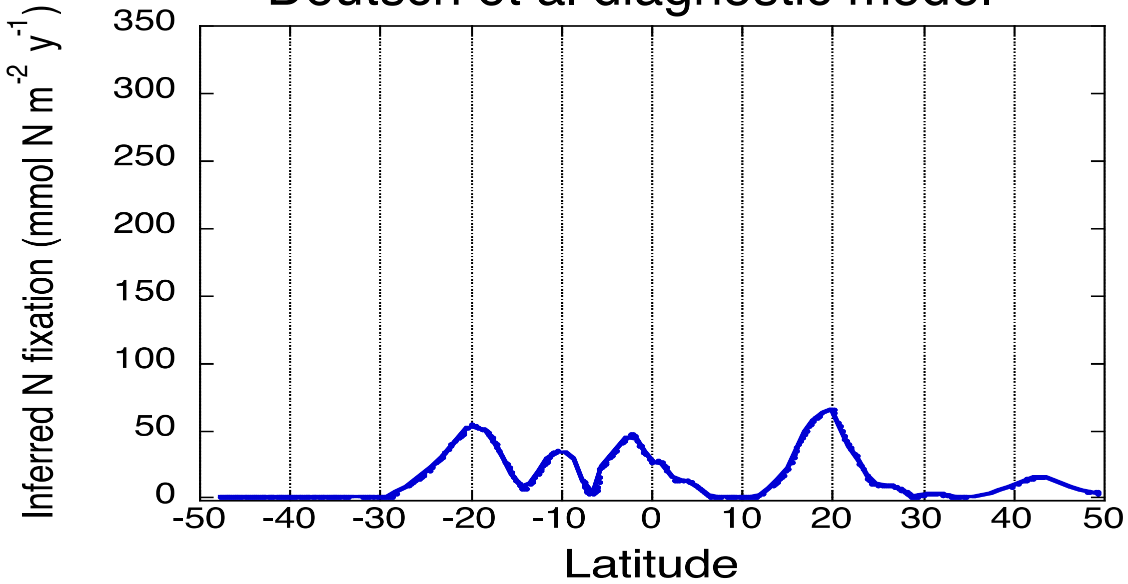


Hydrogen flux to atmosphere

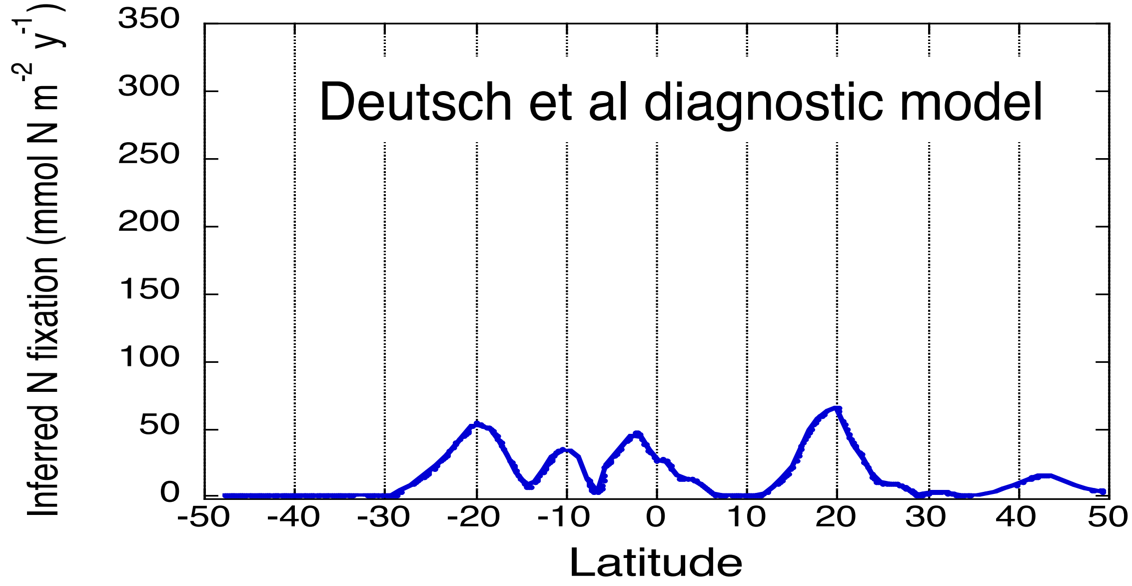
Moore et al., JGR Oceans, in review

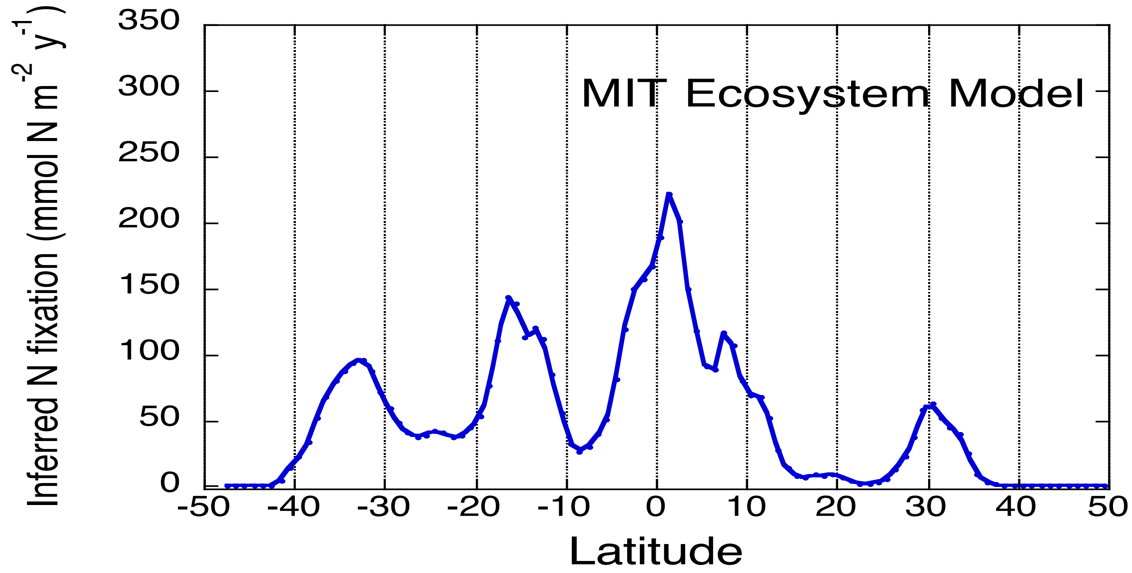


N fixation inferred from H2 flux

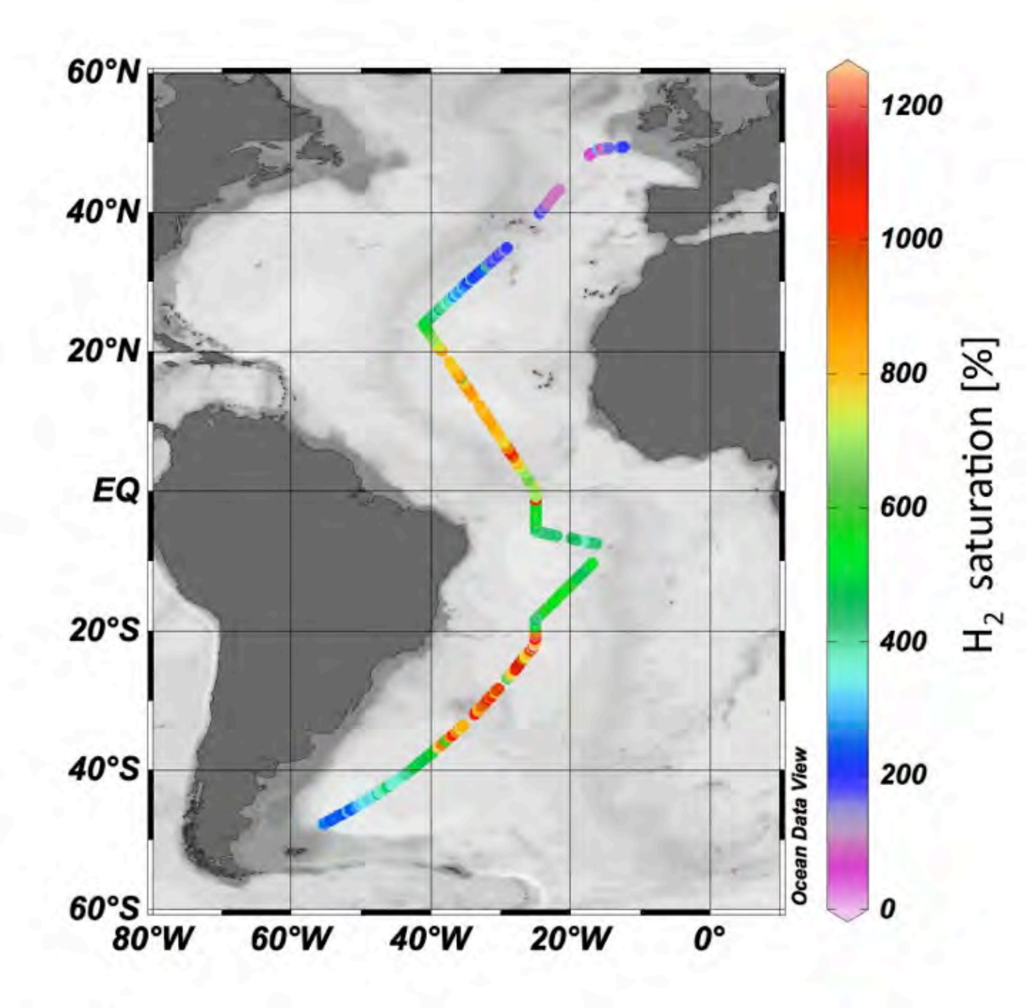


Deutsch et al diagnostic model


Deutsch et al diagnostic model
Inferred N fixation (mmol N m^{-2} y^{-1})
350
300
250
200
150
100
50
0
-50
-40
-30
-20
-10
0
10
20
30
40
50
Latitude


MIT Ecosystem Model
Inferred N fixation (mmol N m^{-2} y^{-1})
350
300
250
200
150
100
50
0
-50
-40
-30
-20
-10
0
10
20
30
40
50
Latitude

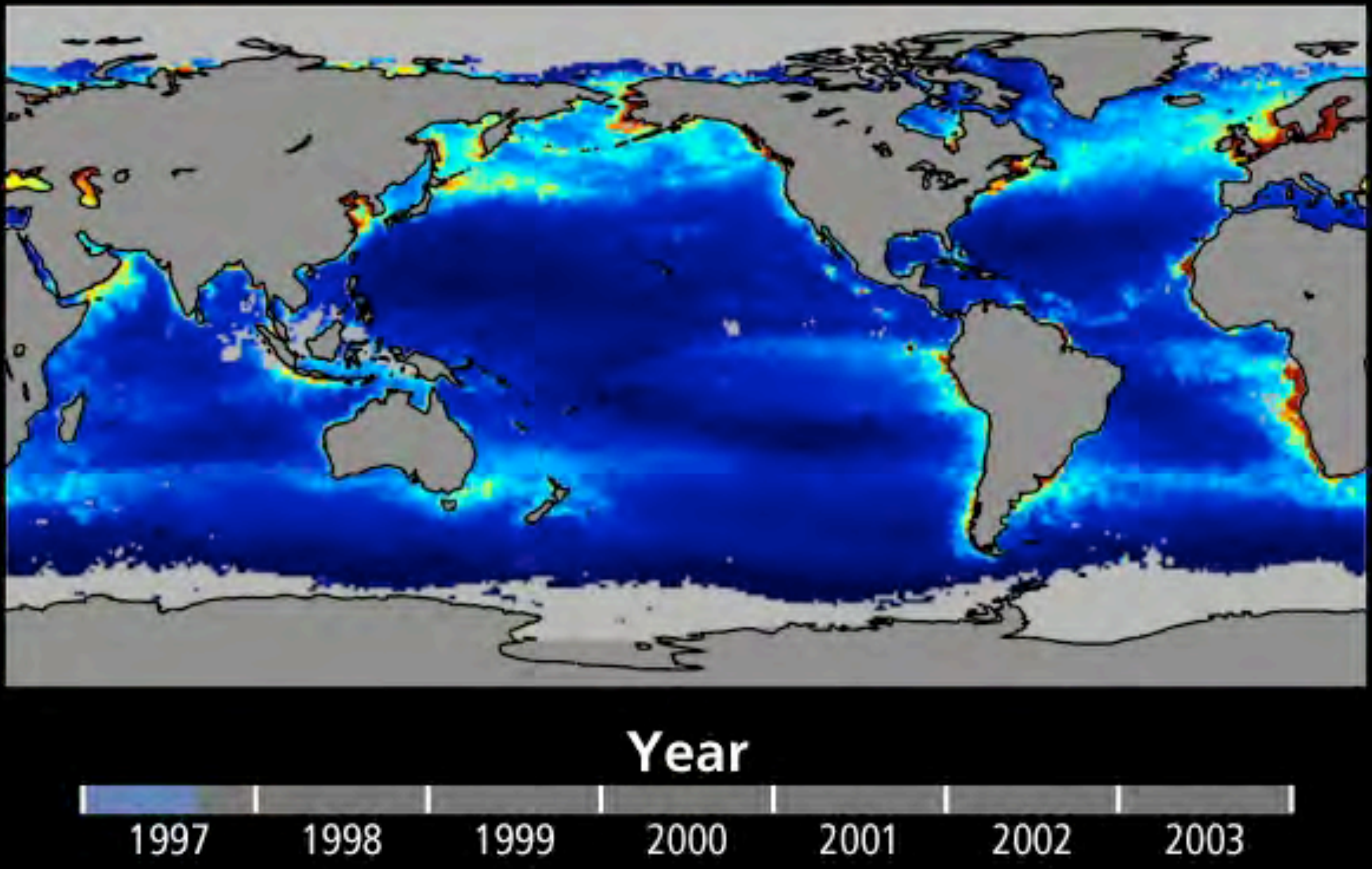
Can measurements of hydrogen provide clues?



$$N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16\ Pi$$

R. Moore et al., JGR Oceans, in review

Do the patterns still make sense?



Global productivity from SeaWiFS ocean color (NASA/GSFC)