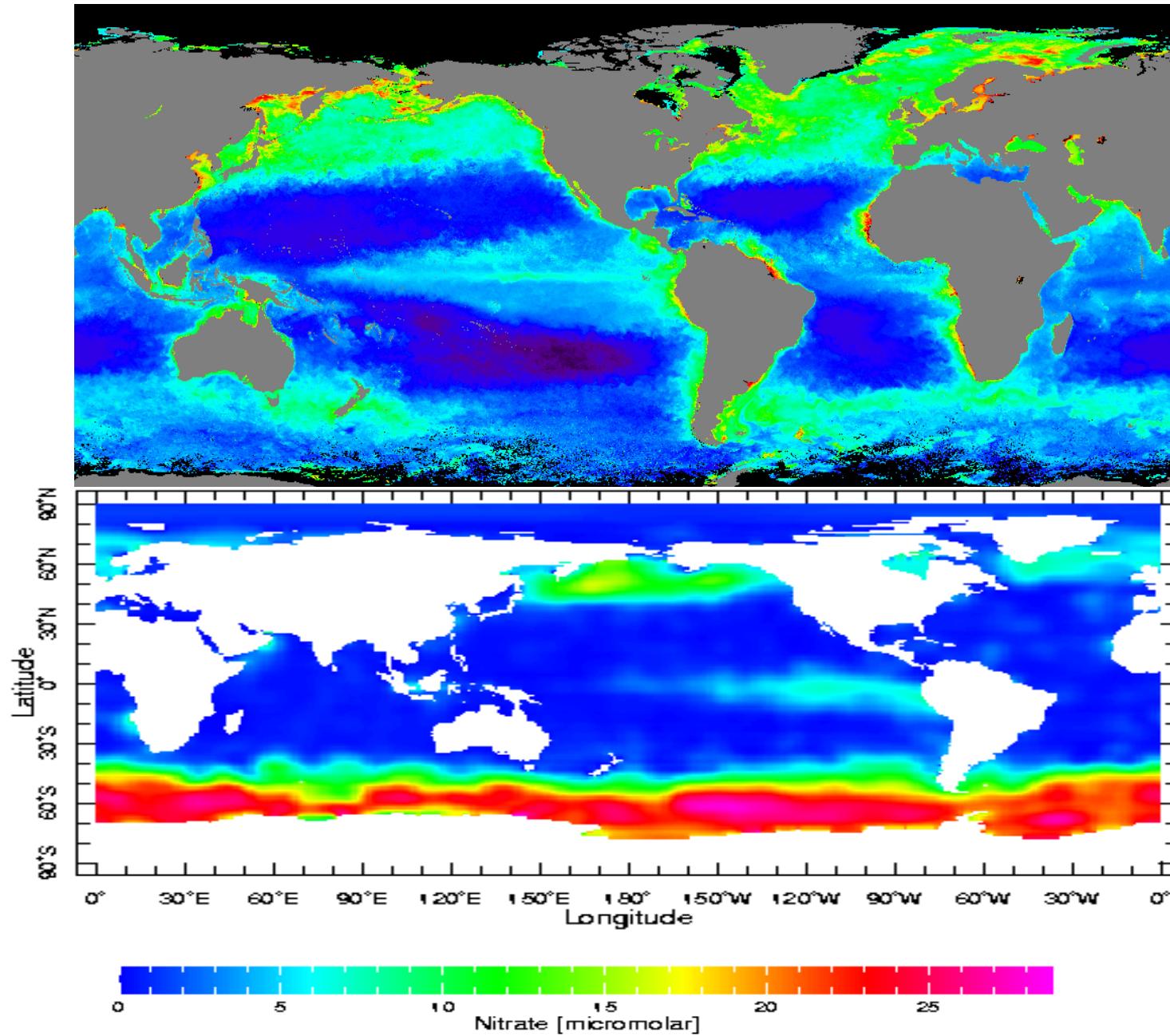
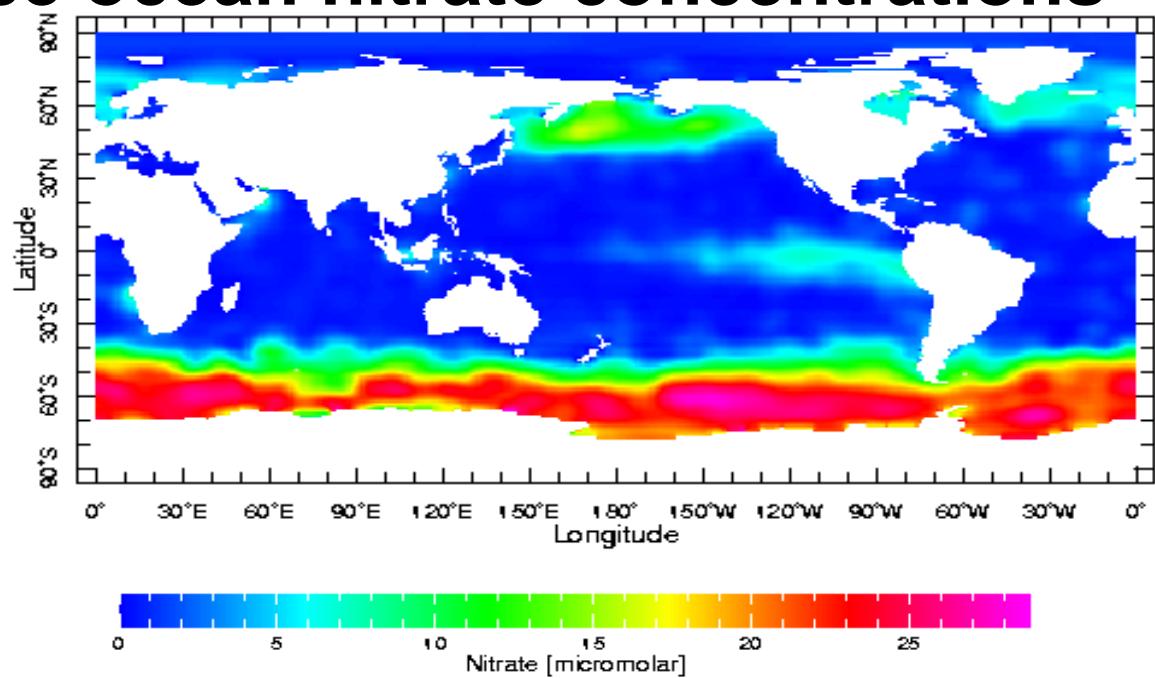


# High Nutrient Low Chlorophyll Ecosystems



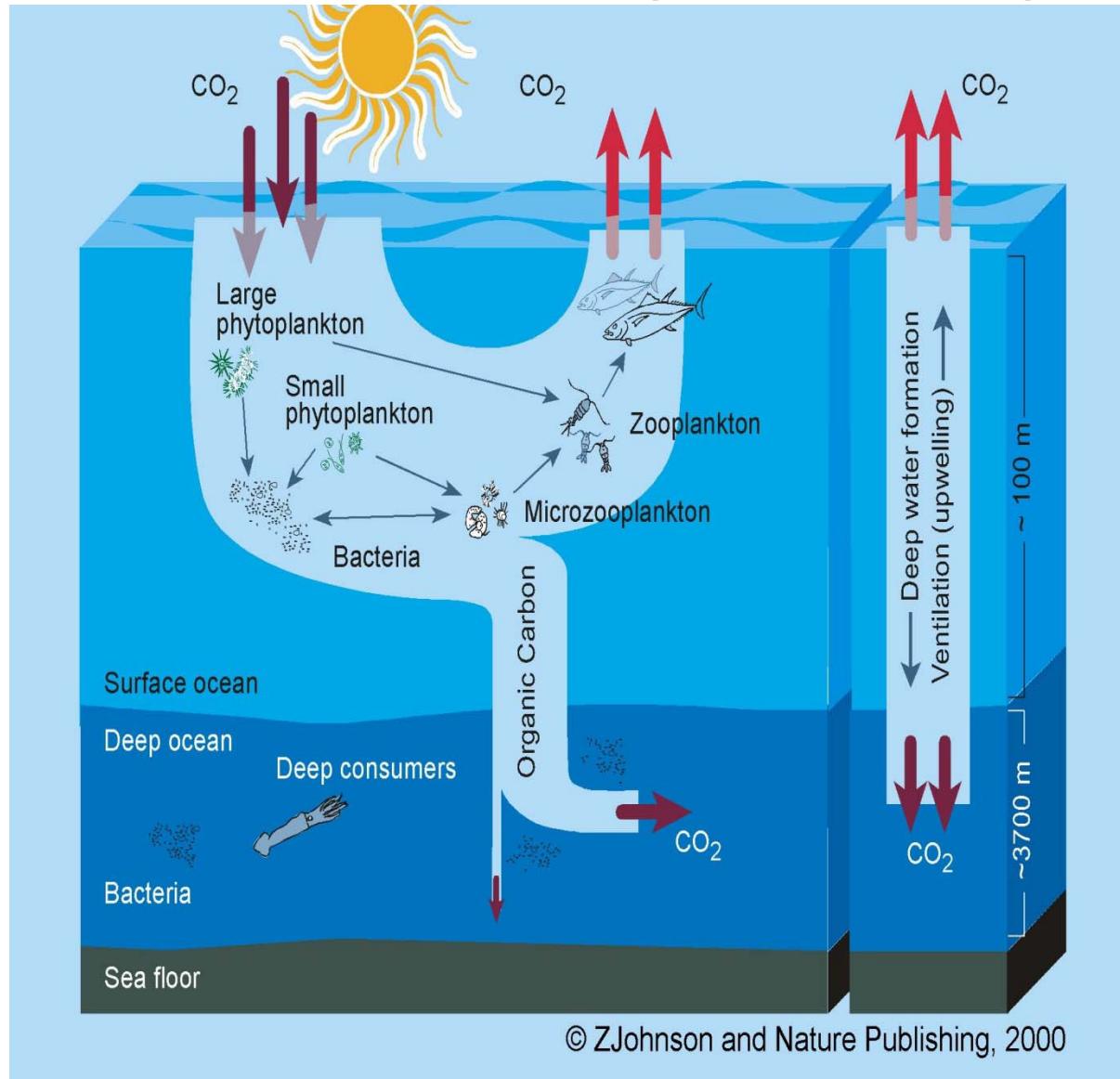
# Average surface ocean nitrate concentrations

In ~1/3 of the ocean, excess nutrients are perennially available yet phytoplankton biomass is relatively low.

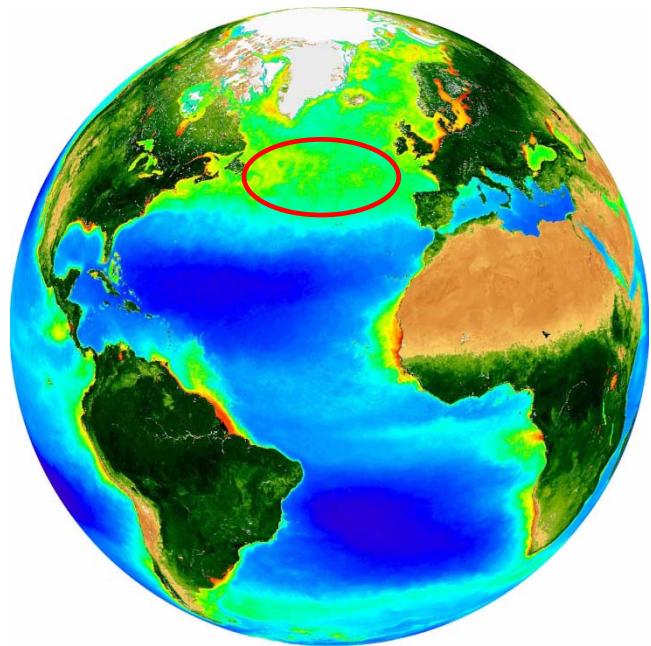


Such regions are termed High Nitrate Low Chlorophyll (HNLC) waters

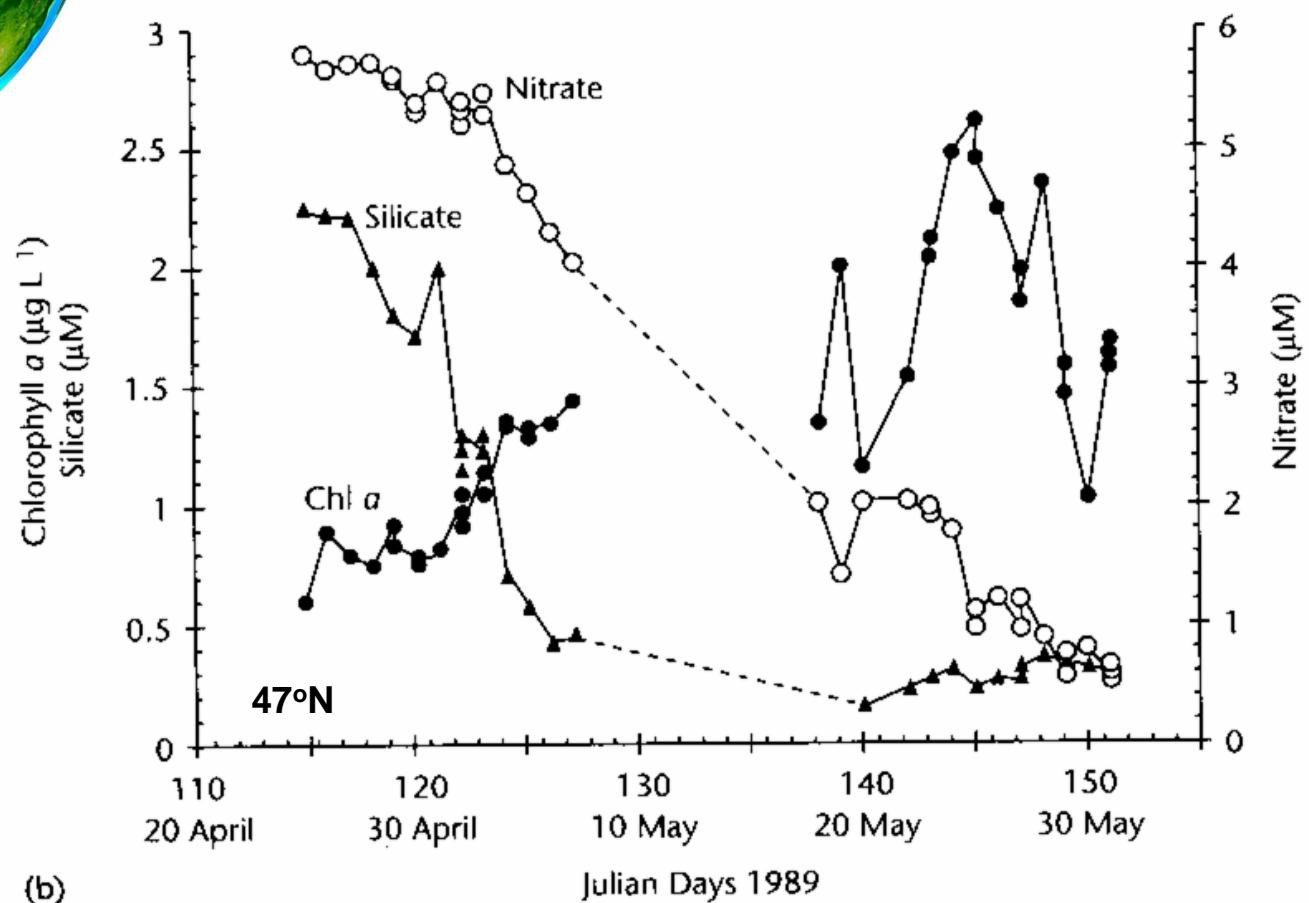
# Whatever factors limit complete utilization of nutrients in HNLC regions have important consequences on the functioning of the biological pump



**Such processes limit new production and thus ultimately export of carbon to the deep sea.**



## North Atlantic Spring Bloom



(b)

# Subarctic North Pacific

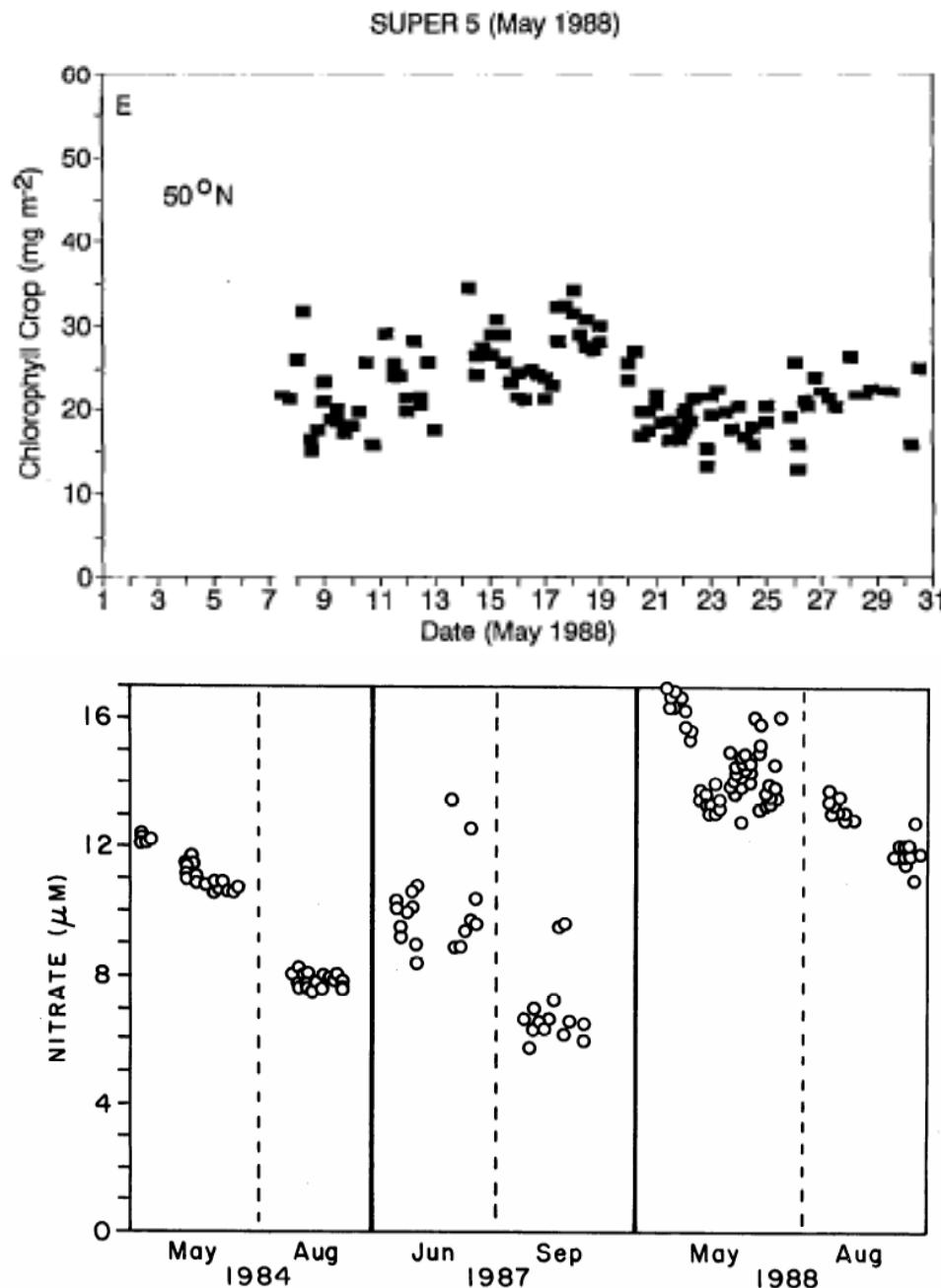
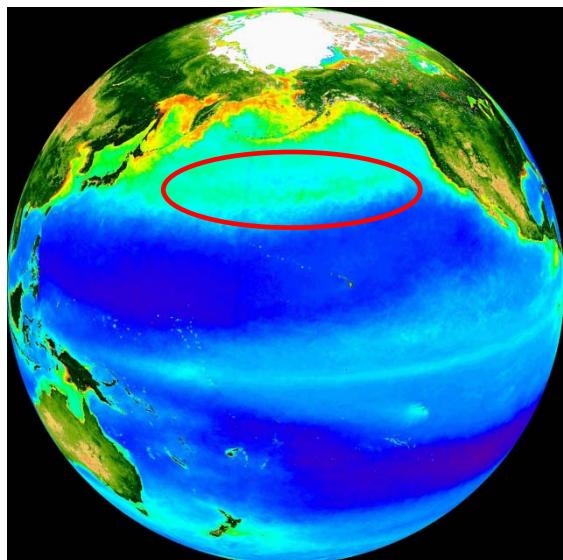
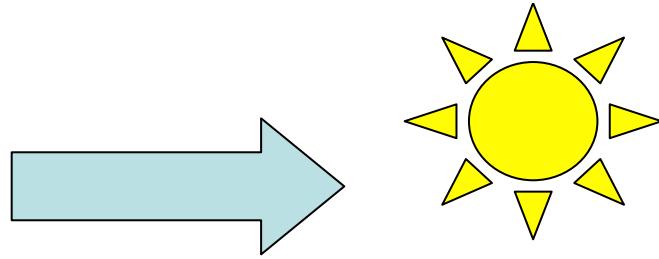


Fig. 7. Interannual variation in  $\text{NO}_3$  concentration as seen during three spring and summer cruises.

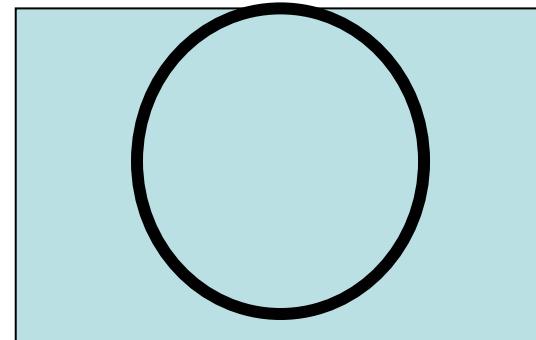
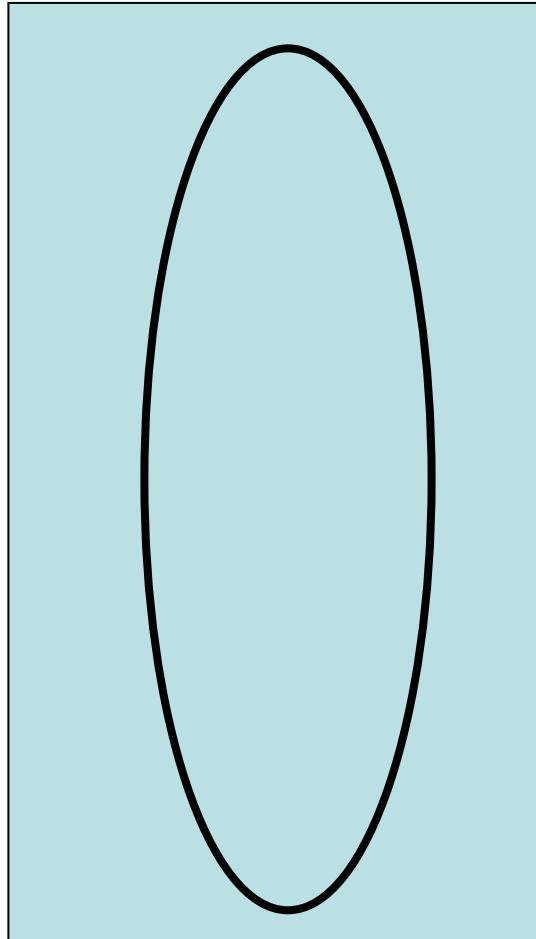
# What limits the accumulation of phytoplankton in large regions of the oceans?

- H1: Phytoplankton growth is limited by light (due to deep mixing)
- H2: Plankton biomass is kept low by vigorous predation
- H3: Nitrate uptake is inhibited by uptake of ammonium
- H4: Phytoplankton growth is limited by availability of specific nutrients



**H1: Deep mixing results  
in light limited growth**

DEEP  
MIXED  
LAYER



SHALLOW  
MIXED LAYER

**Remember the Critical Depth?**

# Sverdrup and the critical depth

Sverdrup (1953)

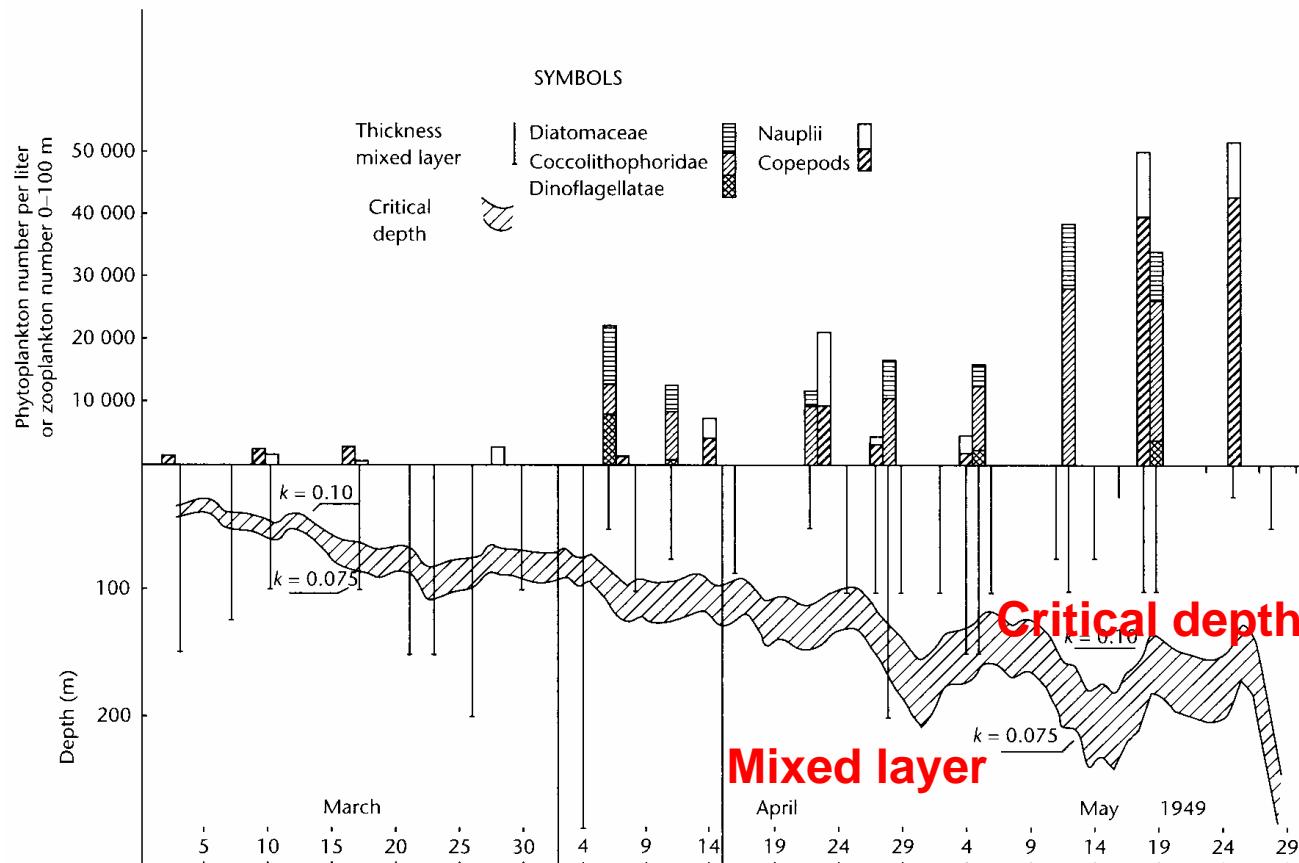
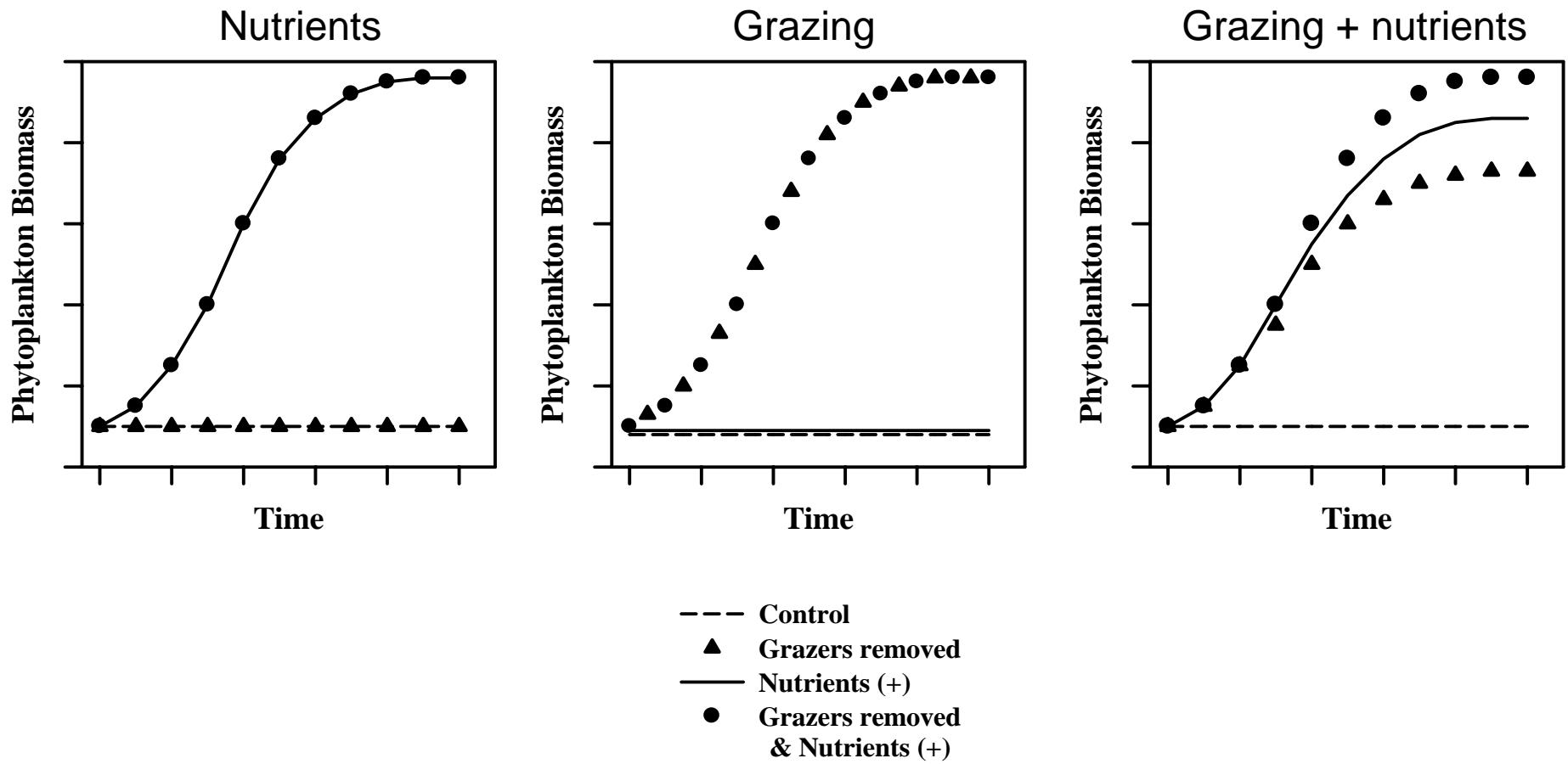


Fig. 1.4 Data for 1949 from Weathership "M" (66°N, 2°E) showing the relationship between the approximate critical depth (shading between approximate  $k$  values of 0.075 and 0.10) and mixing depth. Phytoplankton counts increased in April–May, when critical depth exceeded the mixing depth. While these data are crude, the observation set has never been duplicated. (After Sverdrup 1953.)

Cold temperatures and high winds often results in very deep mixing in Southern Ocean; however, the Subarctic North Pacific and Equatorial Pacific typically do not mix as deep (<120 m) as other systems that experience regular nutrient drawdown.

Conclusion: although light limitation may be important in some HNLC systems, light alone is insufficient to explain lack of seasonal nitrate drawdown.

# Three possible scenarios of factors limiting the accumulation of phytoplankton biomass



## H2: Food web control of plankton biomass--grazers keep biomass cropped to low levels, allow nutrients to accumulate

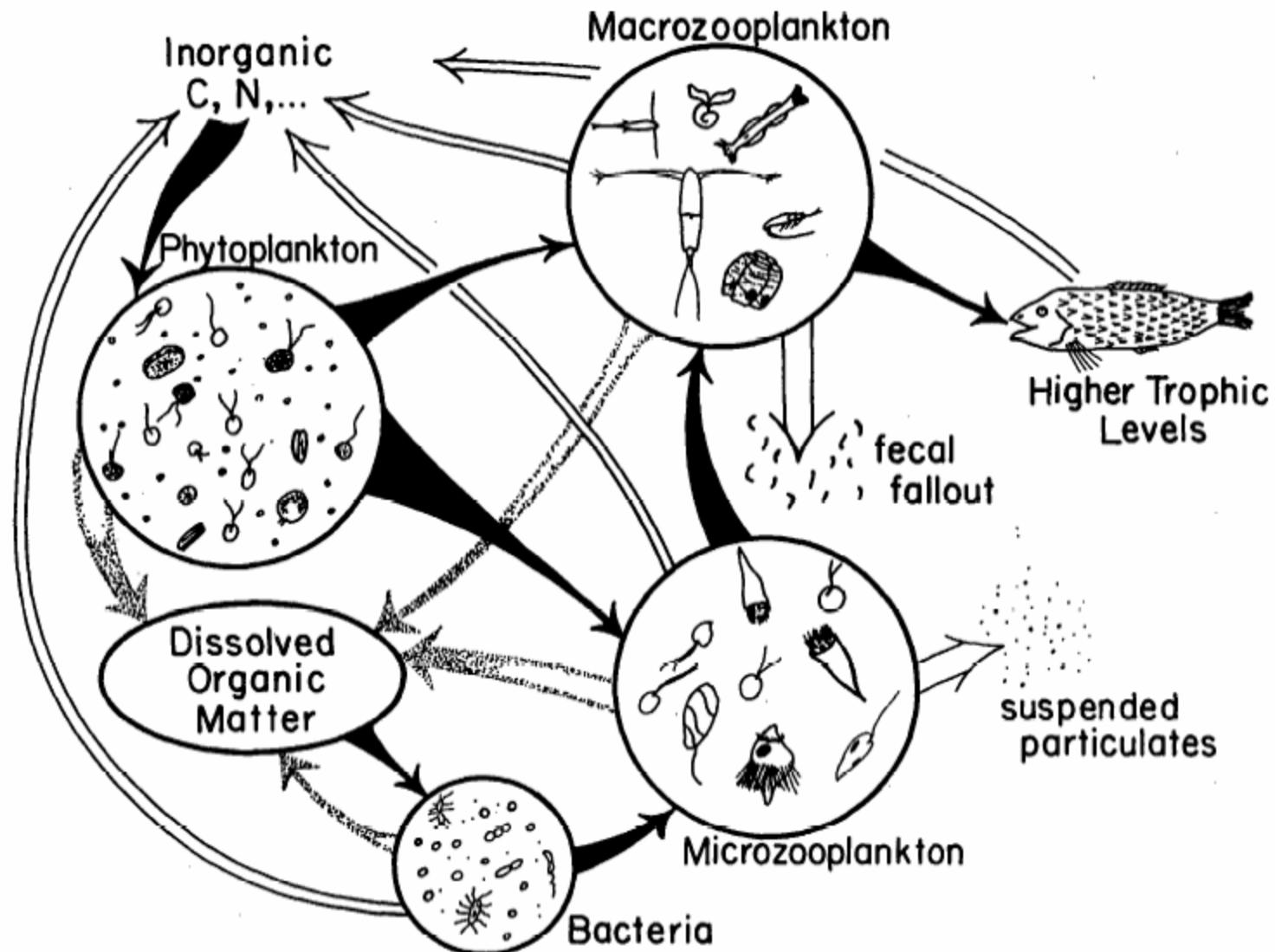
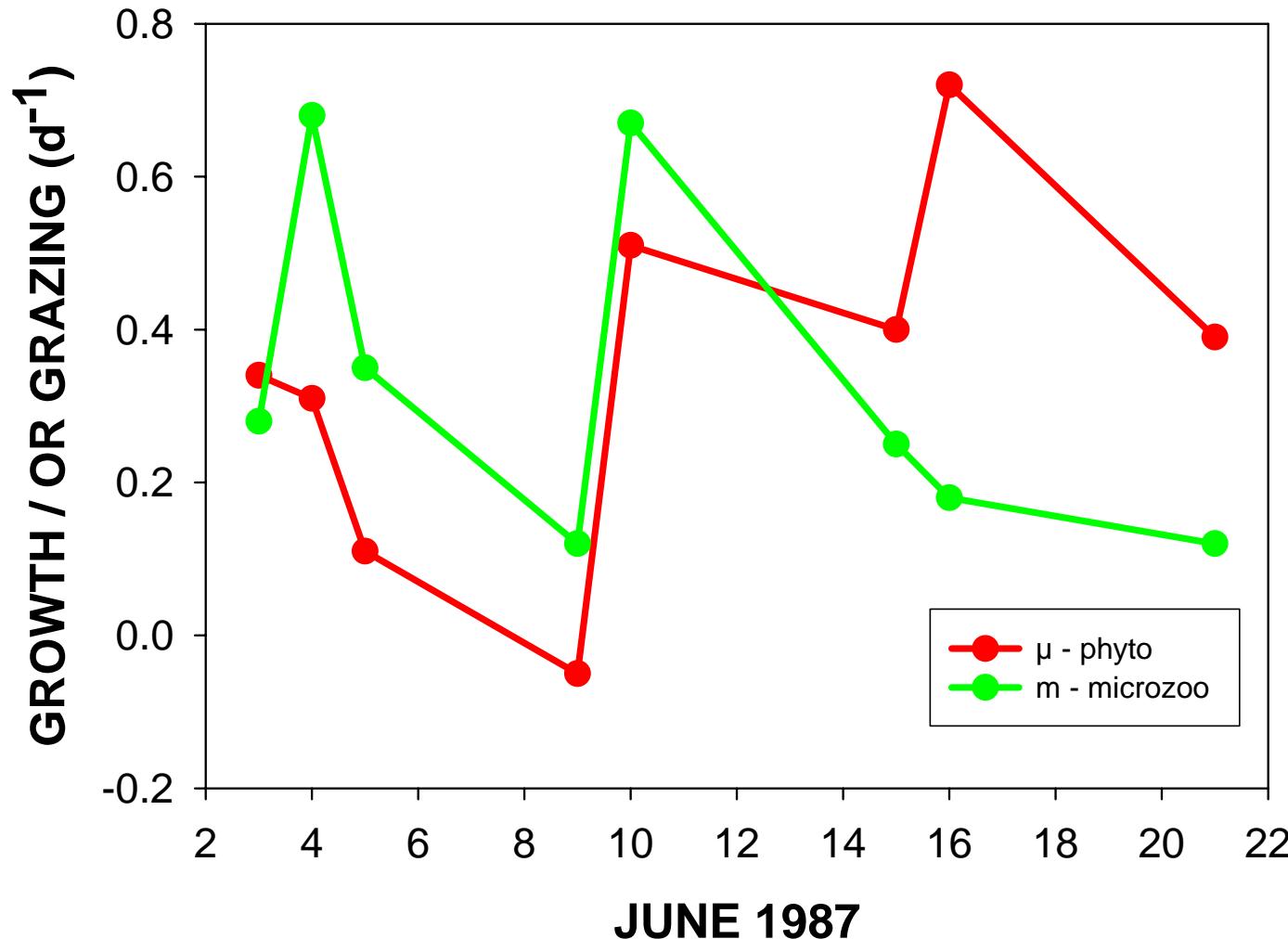


Fig. 4. Diagram of principal food-web connections in the subarctic Pacific. Black arrows—consumption; white arrows—regeneration processes; stippled arrows—transfers to dissolved organic pool.

## Tightly coupled growth and grazing

LANDRY et al. (1993)



In the subarctic North Pacific and Eastern Equatorial Pacific,  
strong evidence supporting micrograzer control of algal biomass.

Remember:

Production = growth rate \* biomass

$$P = \mu B$$

If grazers reduce biomass, production decreases (unless growth rates increase). Thus, grazing can directly limit production.

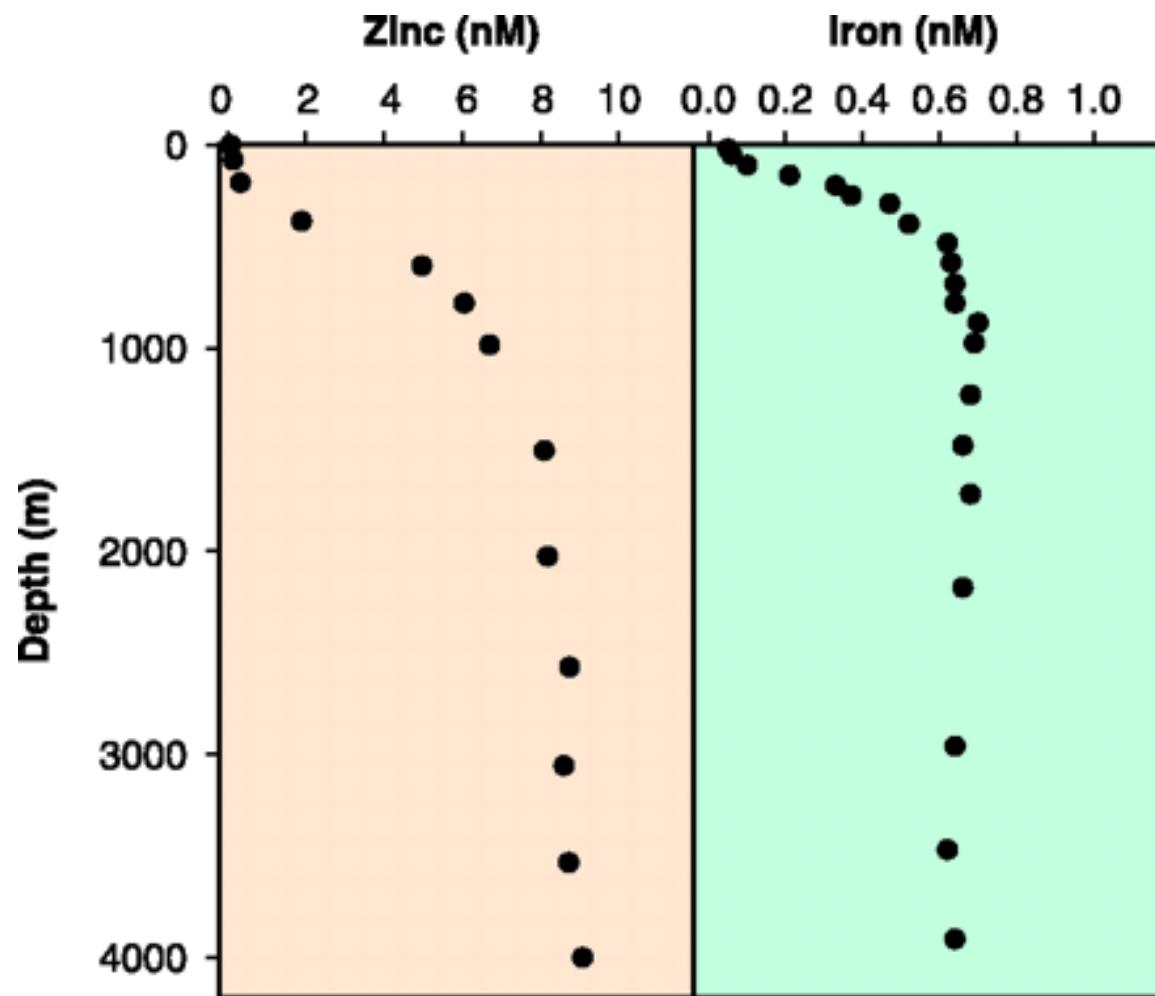
# The case for Iron

- Iron is essential for life: required for synthesis of chlorophyll, component of cytochromes (electron transport chain), needed for nitrate utilization (nitrate reductase), essential for N<sub>2</sub> fixation (nitrogenase).
- Iron is highly insoluble in oxygenated seawater; readily precipitates.
- In regions far removed from continental shelves primary Fe input occurs via atmospheric deposition and upwelling.
- In areas of active upwelling, demand for Fe is elevated; however, many of these regions are also far removed from terrestrial Fe sources.

# Various metals essential to life demonstrate nutrient like distributions in the oceans

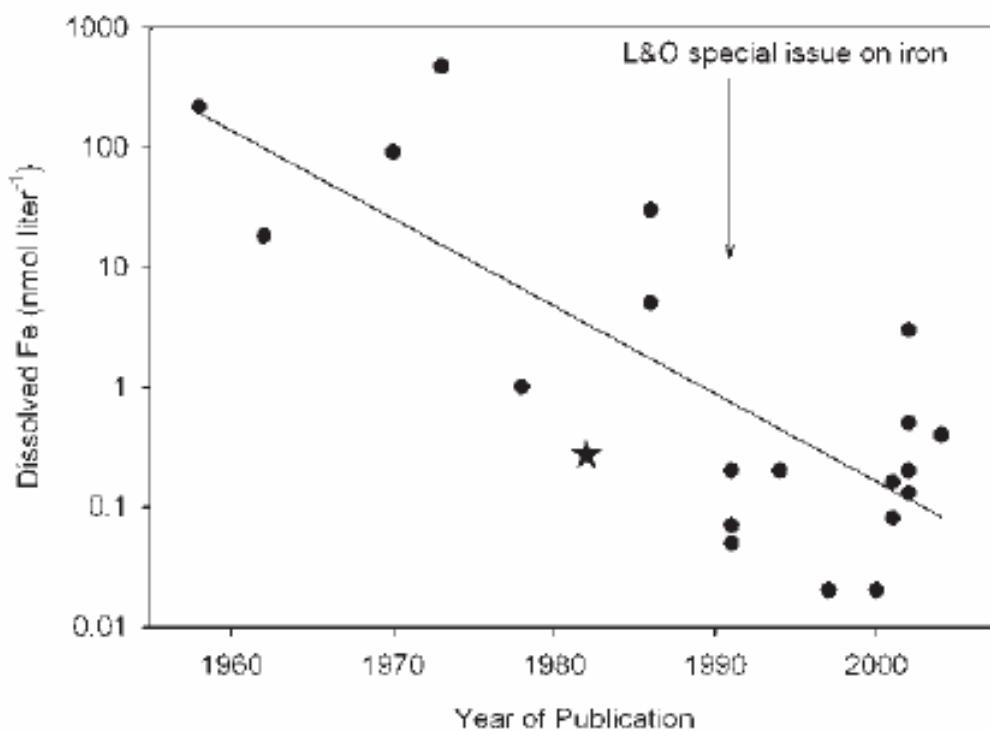
Surface depletion due to algal uptake; increasing concentrations increase through remineralization

In many HNLC regions, upper ocean concentrations of Fe <0.1 nM



From Morel and Price [2003]

**Figure 2.** Total dissolved Fe concentrations in marine waters reported by papers published in *L&O* since 1958. The star is Fitzwater et al. (1982), which has been cited 307 times.



**Obtaining accurate measurements of Fe concentrations in the open ocean have plagued oceanographers for many years.**

## Iron concentrations throughout the world's oceans measured by John Martin's group at Moss Landing Marine Labs

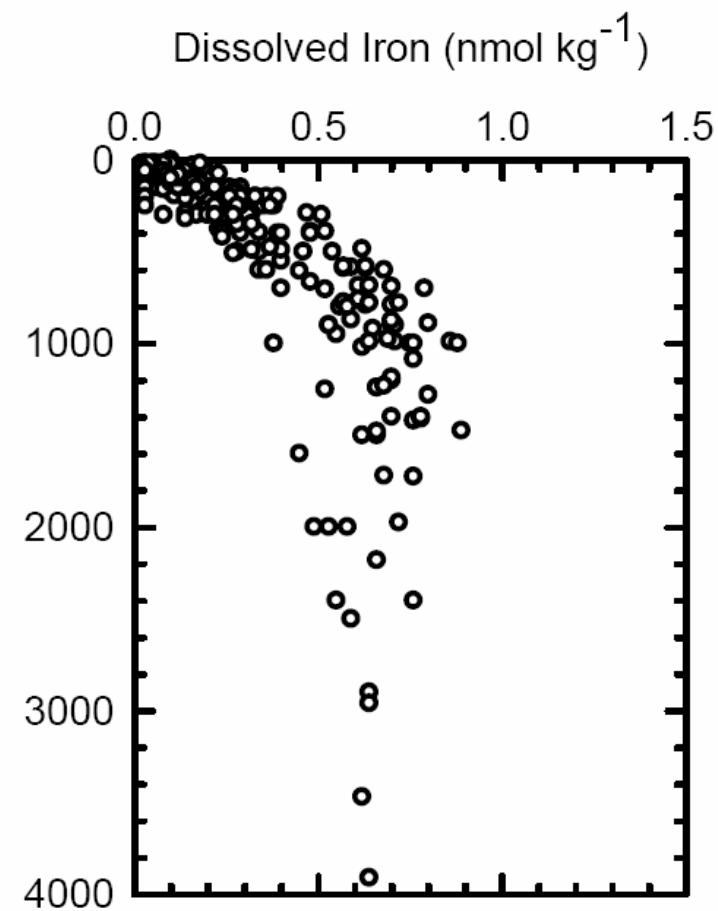
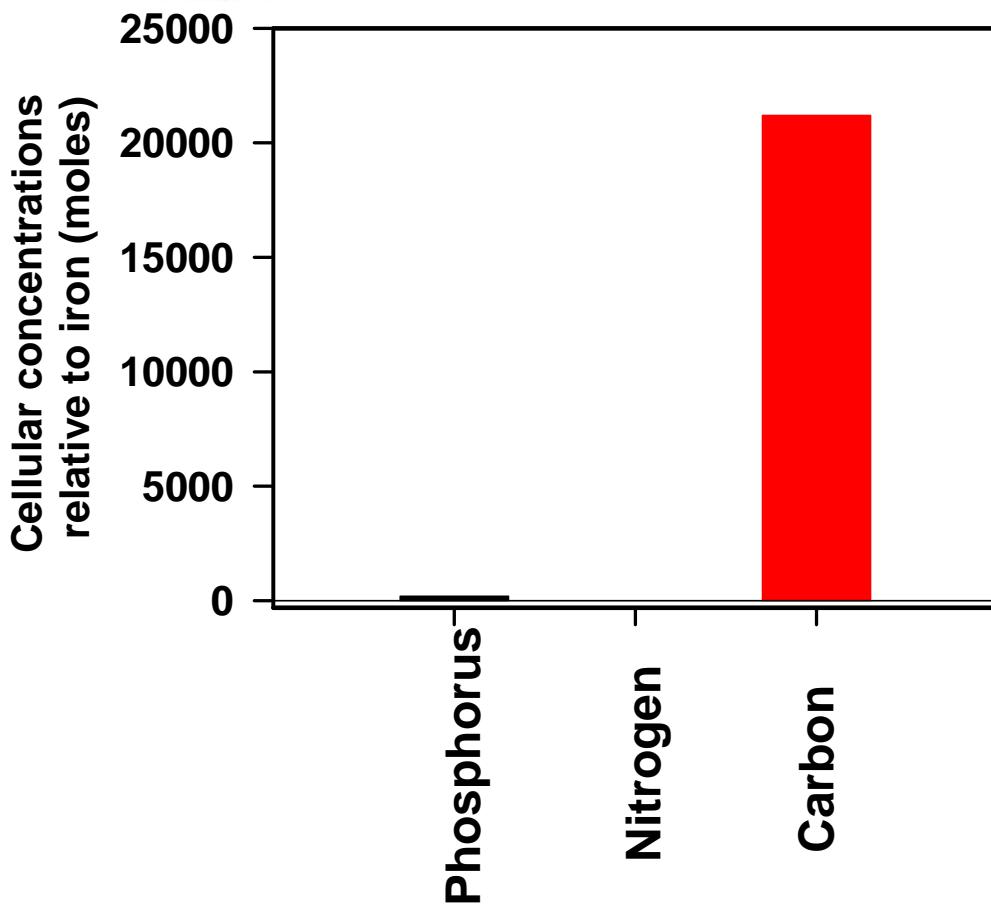


Figure courtesy K. Johnson (MBARI)



A little bit of  
Fe goes a  
long way...



## GENERAL PURPOSE

**20-10-20**

(For Continuous Liquid Feed Programs)

### Guaranteed Analysis

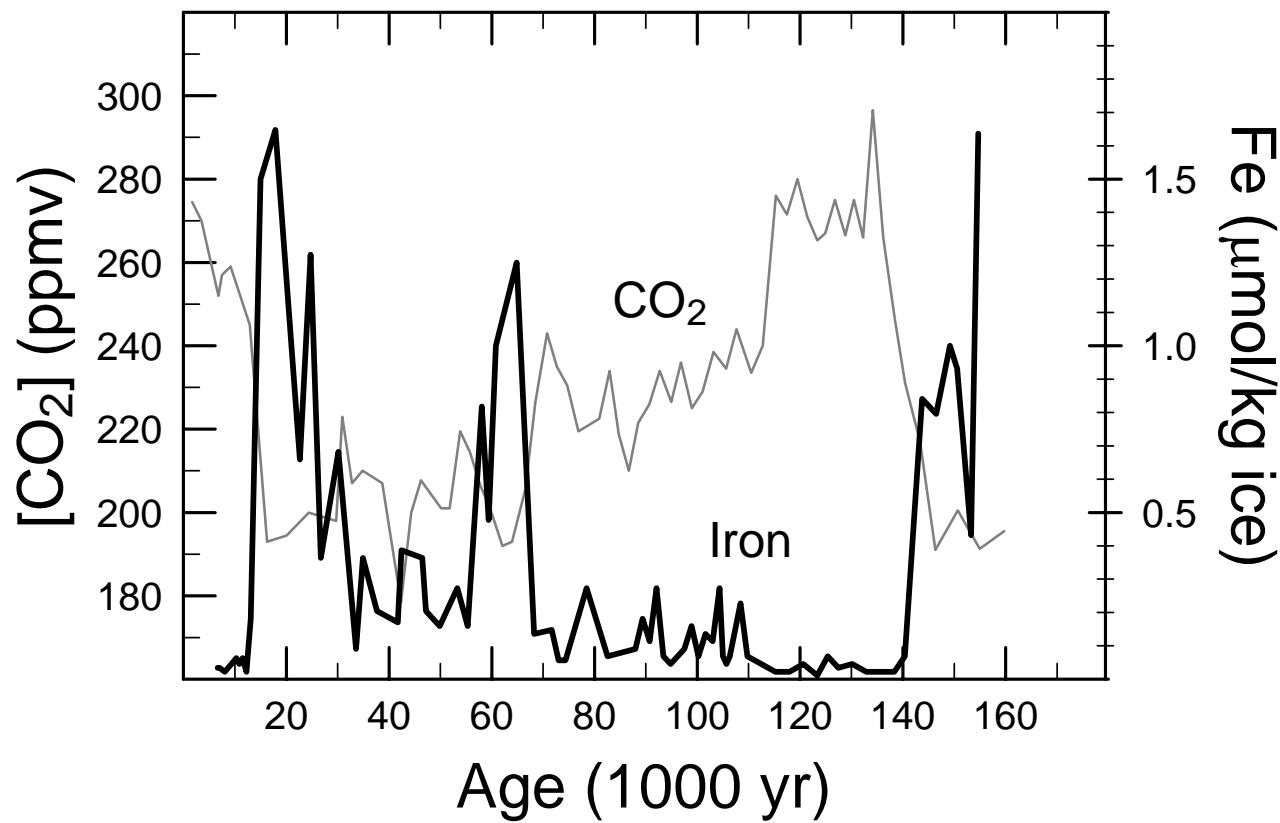
F1143	
Total nitrogen (N) .....	.20%
7.77% ammoniacal nitrogen	
12.23 % nitrate nitrogen	
Available phosphate ( $P_2O_5$ ) .....	.10%
Soluble potash ( $K_2O$ ) .....	.20%
Magnesium (Mg) (Total) .....	0.05%
0.05% Water Soluble Magnesium (Mg)	
Boron (B) .....	0.0068%
Copper (Cu) .....	0.0036%
0.0036% Chelated Copper (Cu)	
Iron (Fe) .....	0.05%
0.05% Chelated Iron(Fe)	
Manganese (Mn) .....	0.025%
0.025% Chelated Manganese (Mn)	
Molybdenum (Mo) .....	0.0009%
Zinc (Zn) .....	0.0025%
0.0025% Chelated Zinc (Zn)	

Derived from: ammonium nitrate, potassium phosphate, potassium nitrate, magnesium sulfate, boric acid, copper EDTA, manganese EDTA, iron EDTA, zinc EDTA, sodium molybdate. Potential acidity: 487 lbs. calcium carbonate equivalent per ton.

**Phytoplankton biomass:**

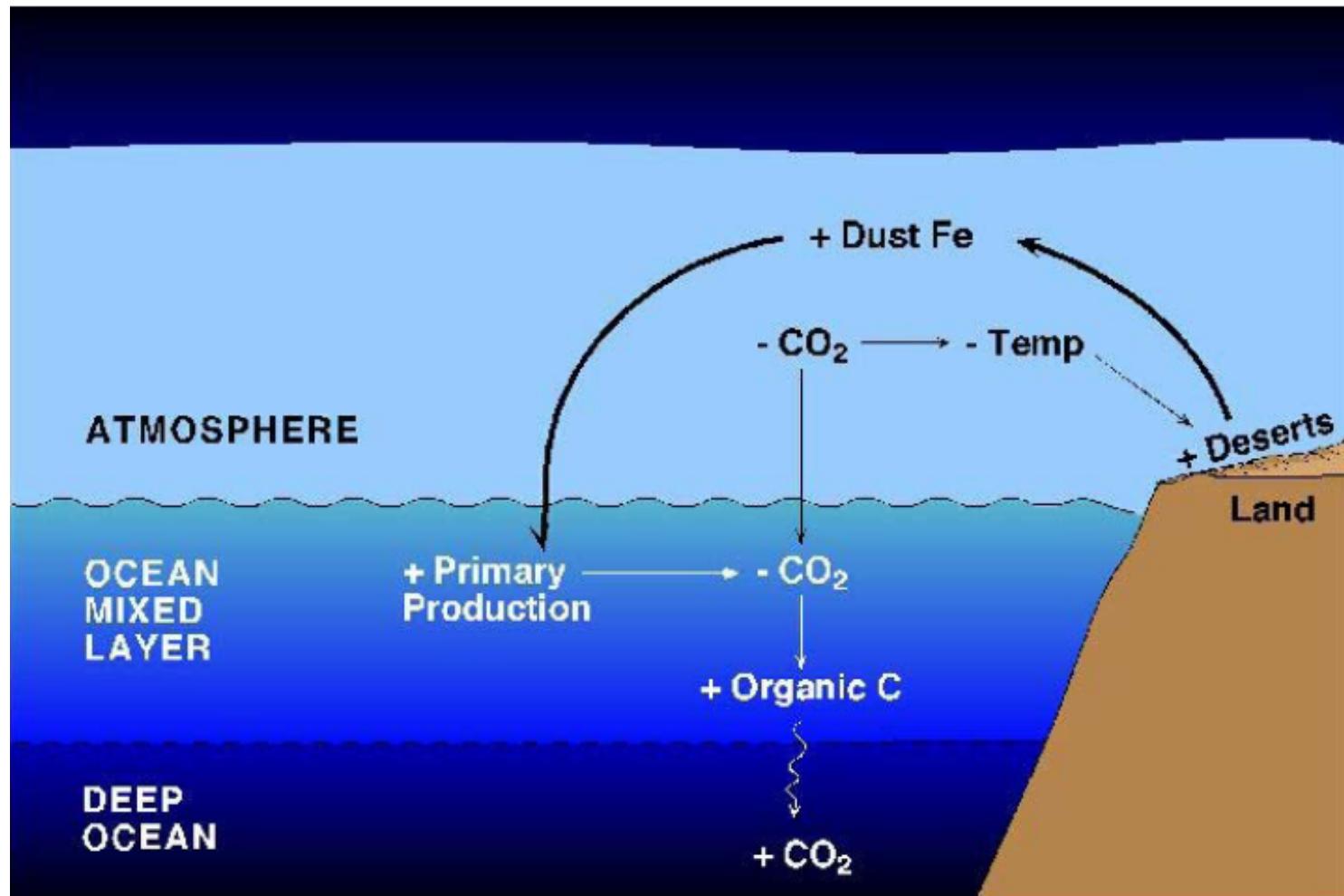
**106C : 16N : 1P : 0.005Fe**

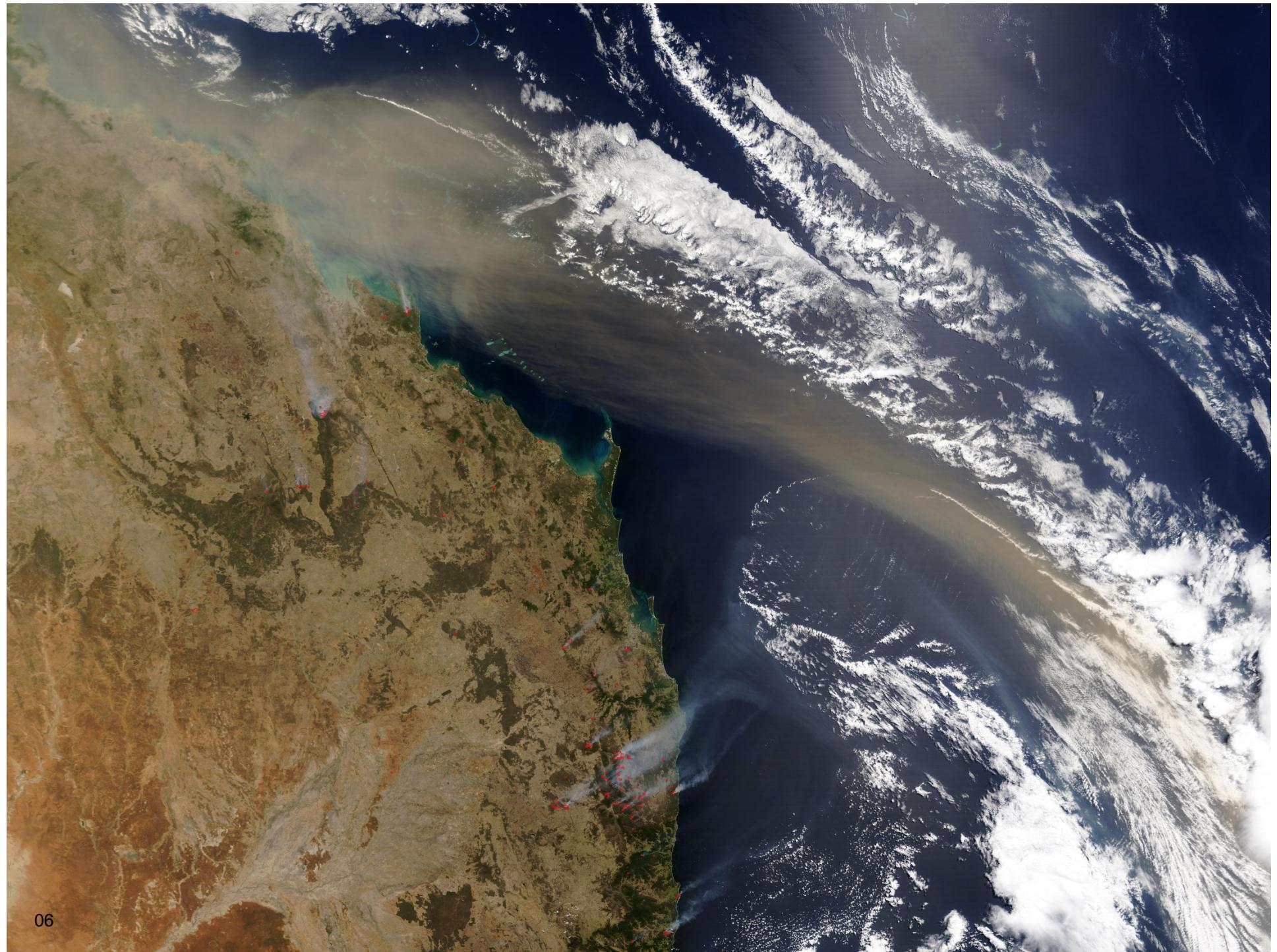
**There is evidence suggesting that changes in Fe supply influence atmospheric CO<sub>2</sub>**



**Glacial-interglacial variations in CO<sub>2</sub> demonstrate inverse relationships to the availability of iron in seawater**

## The “Iron Hypothesis”, John Martin, MLML





06

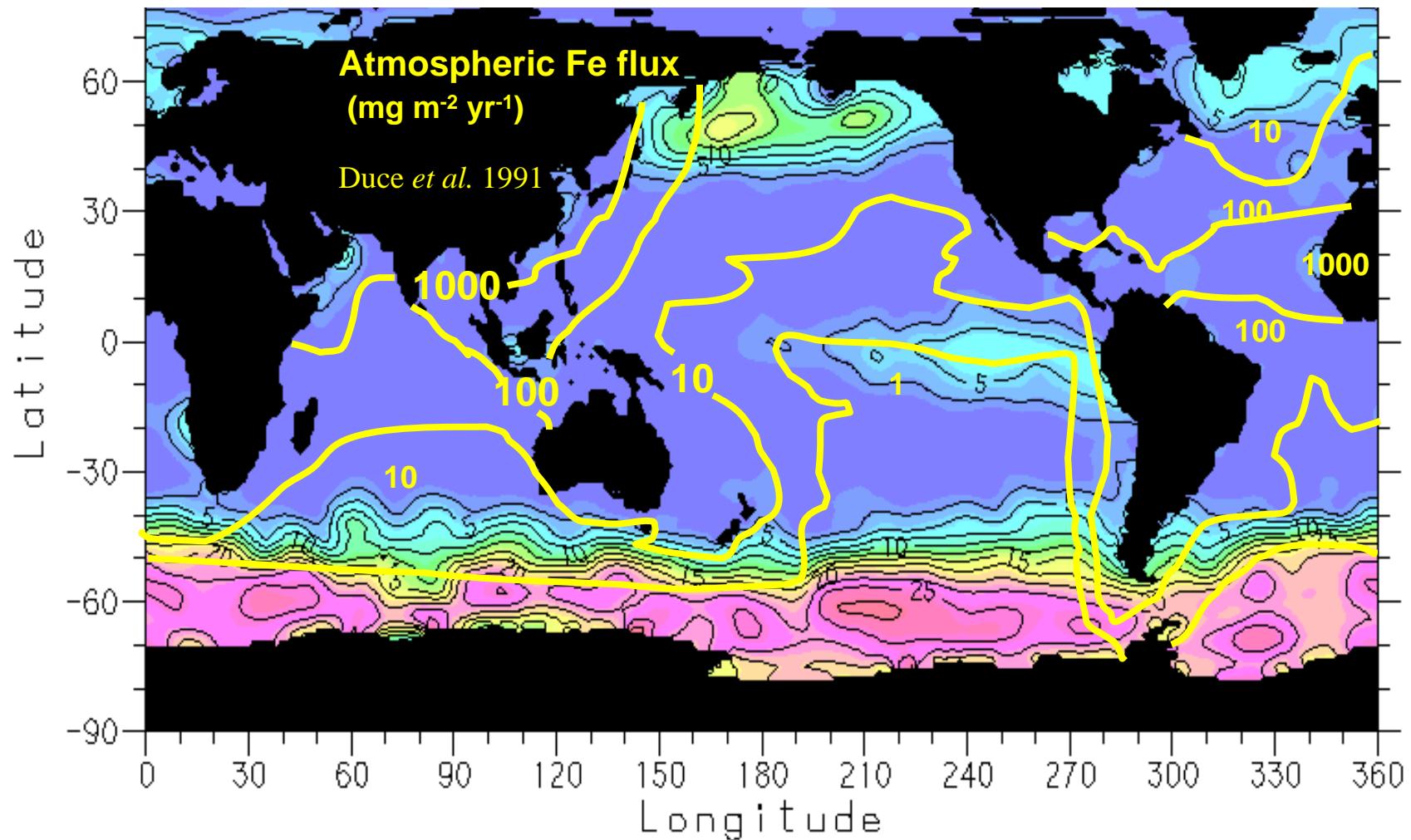
# Dust source regions and transport routes

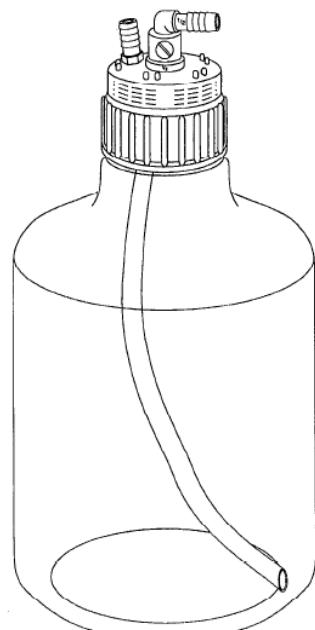
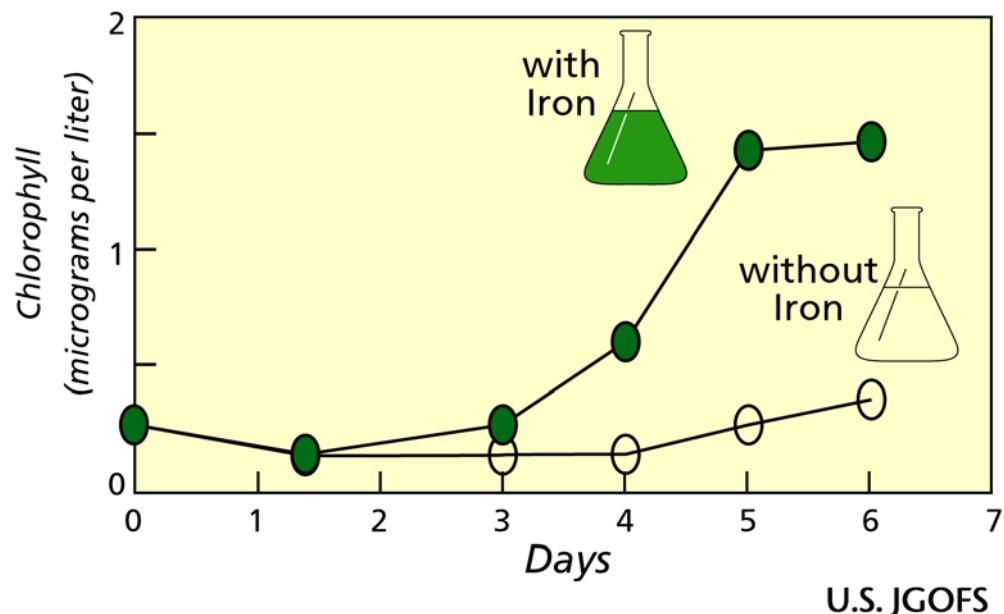


Pye (1987)

# Dust flux overlaid on the $\text{NO}_3$ distribution ( $\mu\text{M}$ ) in the upper ocean

NOAA world ocean atlas, 1994





**Experiments  
done in carboys  
and bottles  
confirmed that  
phytoplankton  
growth was  
limited by Fe**

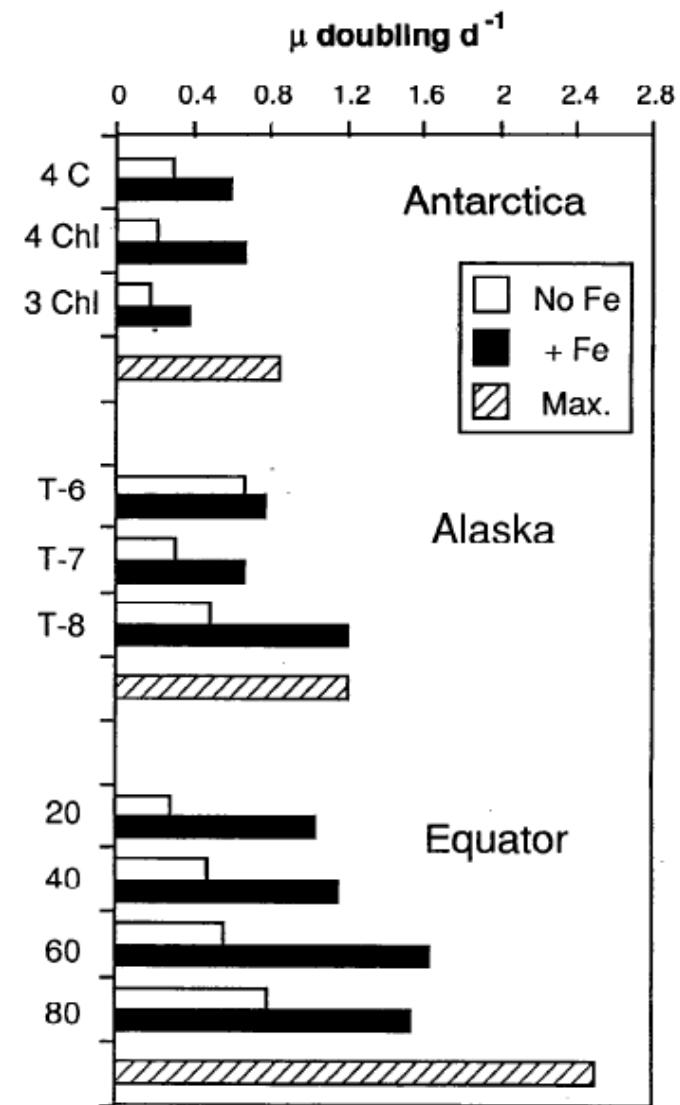
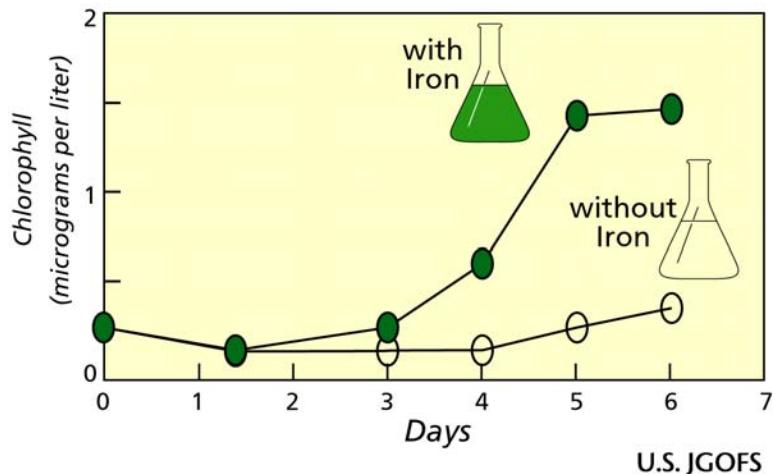


Fig. 7. A comparison of doubling rates from the Antarctic, Gulf of Alaska, and equatorial Pacific with and without added Fe (data from Table 2); theoretical maxima for various temperatures are also shown.

Martin et al. (1990)



Bottle experiments demonstrated increases in Chl by the addition of iron; however, there were concerns about what might have been missed...exclusion of large grazers, sinking, mixing, etc.

*Limnol. Oceanogr.*, 36(8), 1991, 1793–1802  
© 1991, by the American Society of Limnology and Oceanography, Inc.

### The case for iron

**John H. Martin, R. Michael Gordon, and Steve E. Fitzwater**  
Moss Landing Marine Laboratories, Moss Landing, California 95039

*Limnol. Oceanogr.*, 35(3), 1990, 772–775  
© 1990, by the American Society of Limnology and Oceanography, Inc.

Does iron really limit phytoplankton production in the offshore subarctic Pacific?

*Karl Banse*

School of Oceanography, WB-10  
University of Washington  
Seattle 98195

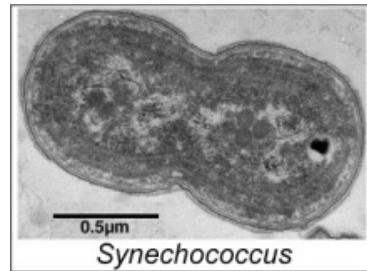
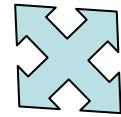
*Limnol. Oceanogr.*, 35(3), 1990, 775–777  
© 1990, by the American Society of Limnology and Oceanography, Inc.

**THE RESULTS OF  
BOTTLE  
EXPERIMENTS  
MADE A BIG  
SPLASH –  
BUT NOT  
EVERYONE WAS  
CONVINCED...**

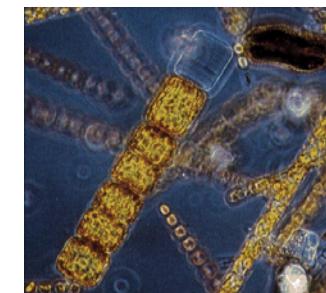
Yes, it does: A reply to the comment by Banse

- Bottle experiments indicated that the addition of iron shifted the phytoplankton assemblage from small cells (subject to tight grazing) to large cells (diatoms) that grow rapidly, consume nutrients, and sink.
- But was this due to a bottle effect? Exclusion of grazers....

No iron controls

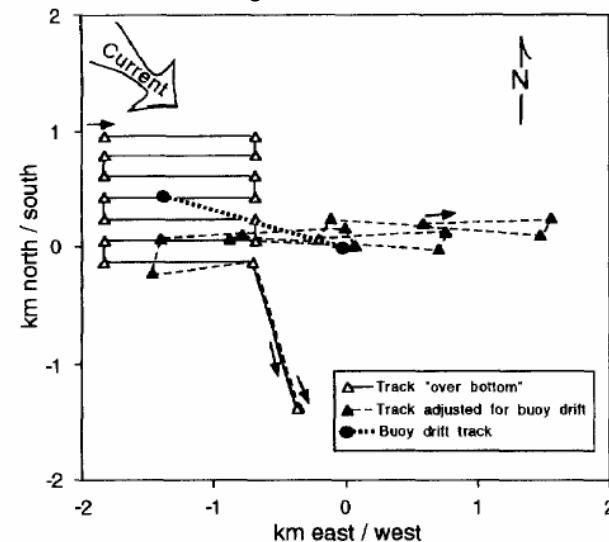
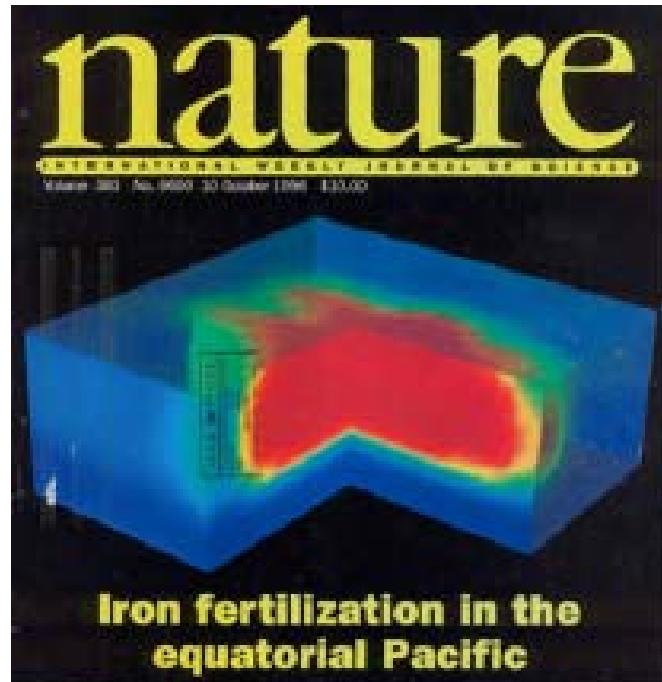


+Fe

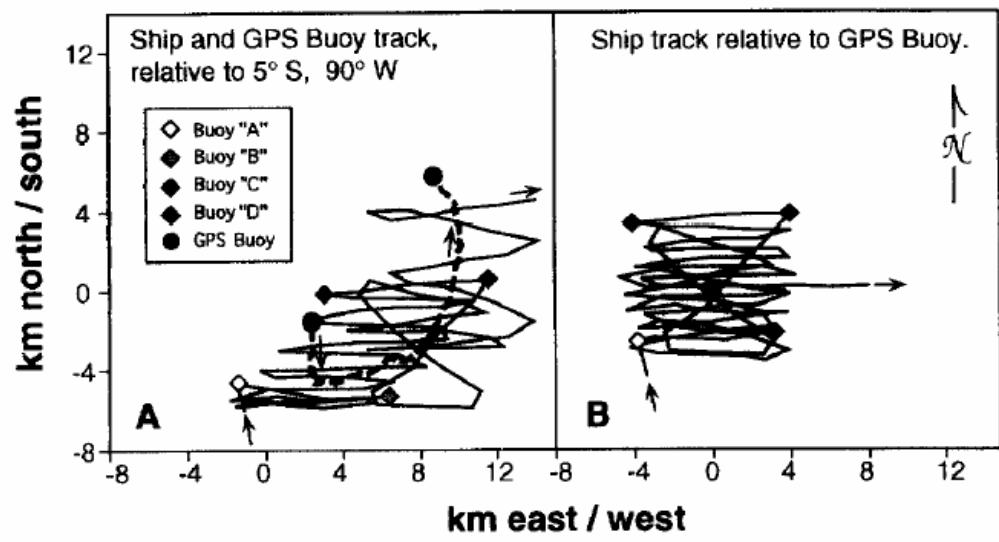


# Solution: Mesoscale (100s of km) enrichment experiments to examine community level responses to iron.

Iron added as acidic iron sulfate. The inert tracer SF<sub>6</sub> is added along with iron.



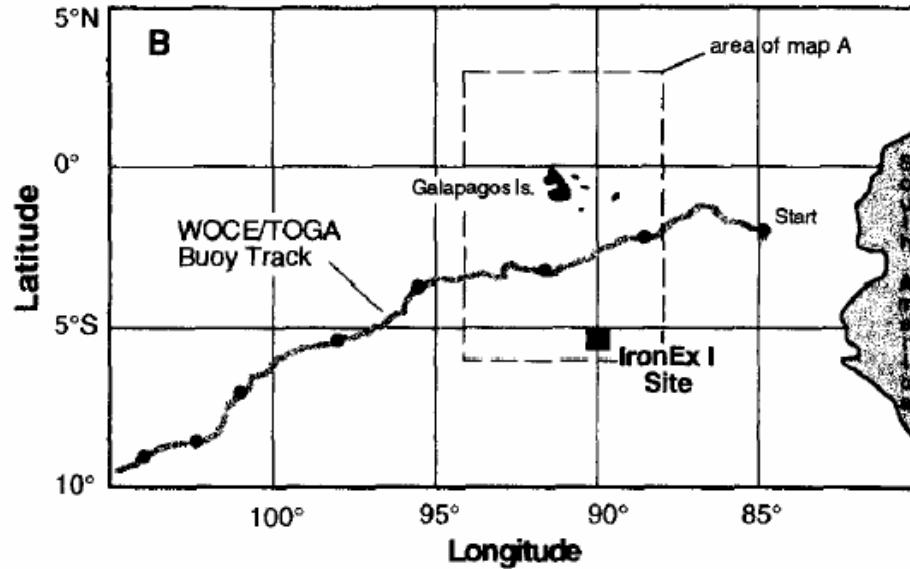
Cartesian coordinate system



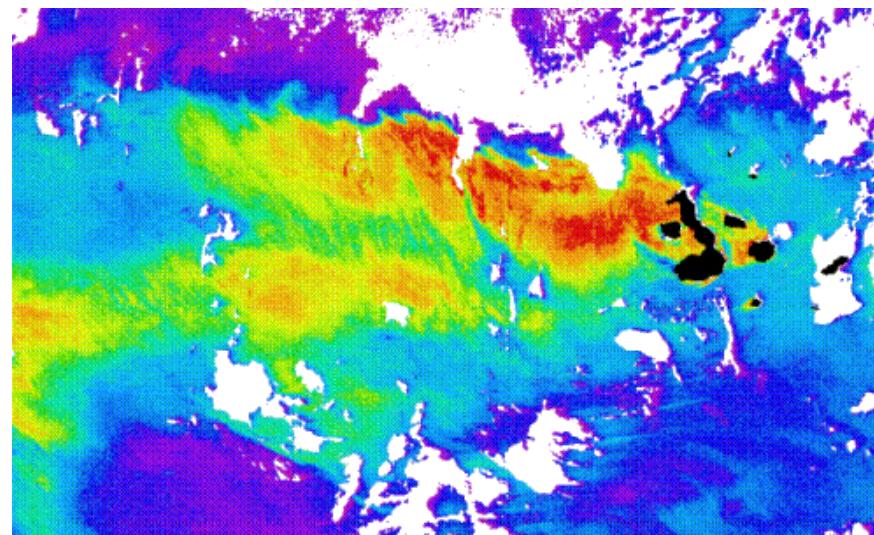
Lagrangian system following drogues

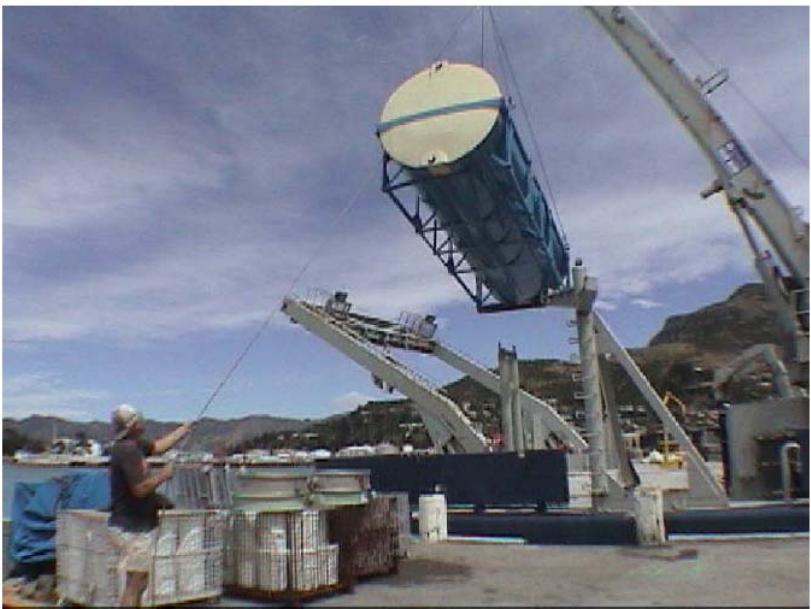


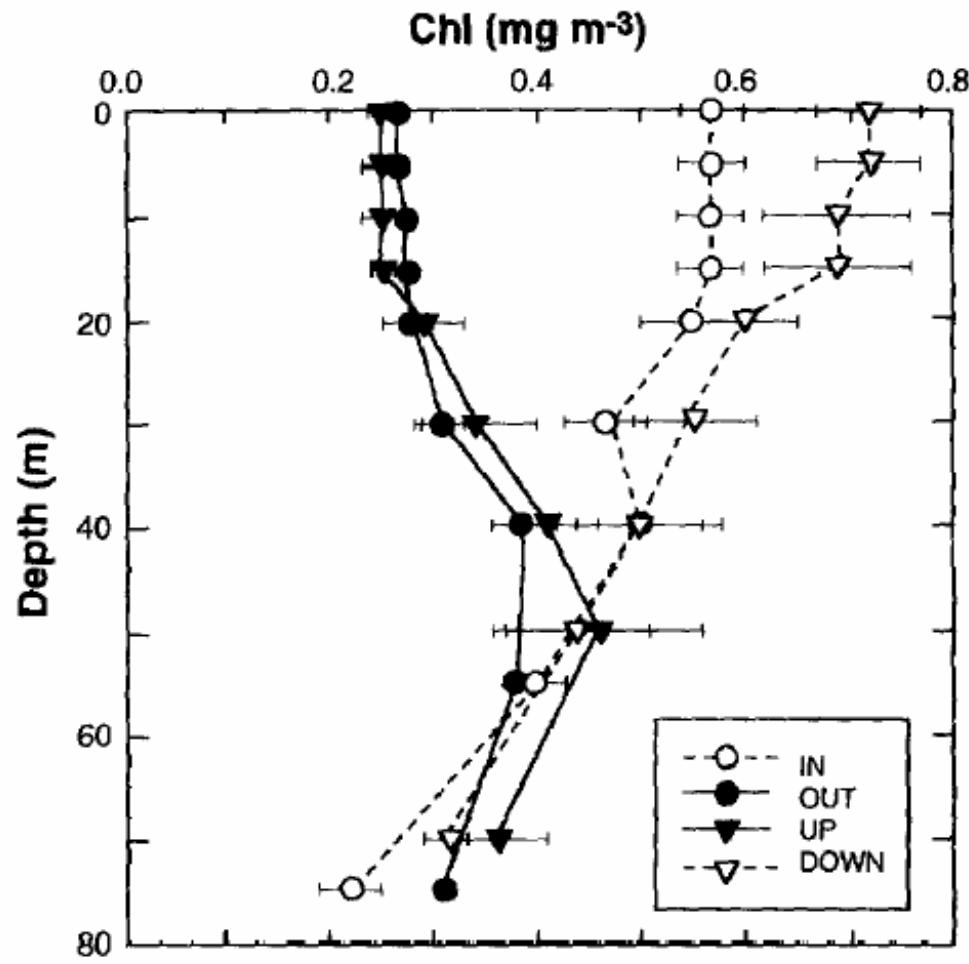
**IronEX I: 1993, Equatorial Pacific near Galapagos Islands.** 443 kg of Fe into a 64 km<sup>2</sup> patch. Initial Fe concentrations ~0.1 nM, final target Fe concentration was 4 nM. Added 17,500 L of 0.5 M Fe solution (pH 2.0). A separate batch of 2000 L of SF6 was mixed into the iron solution.



Coale et al. (1994)





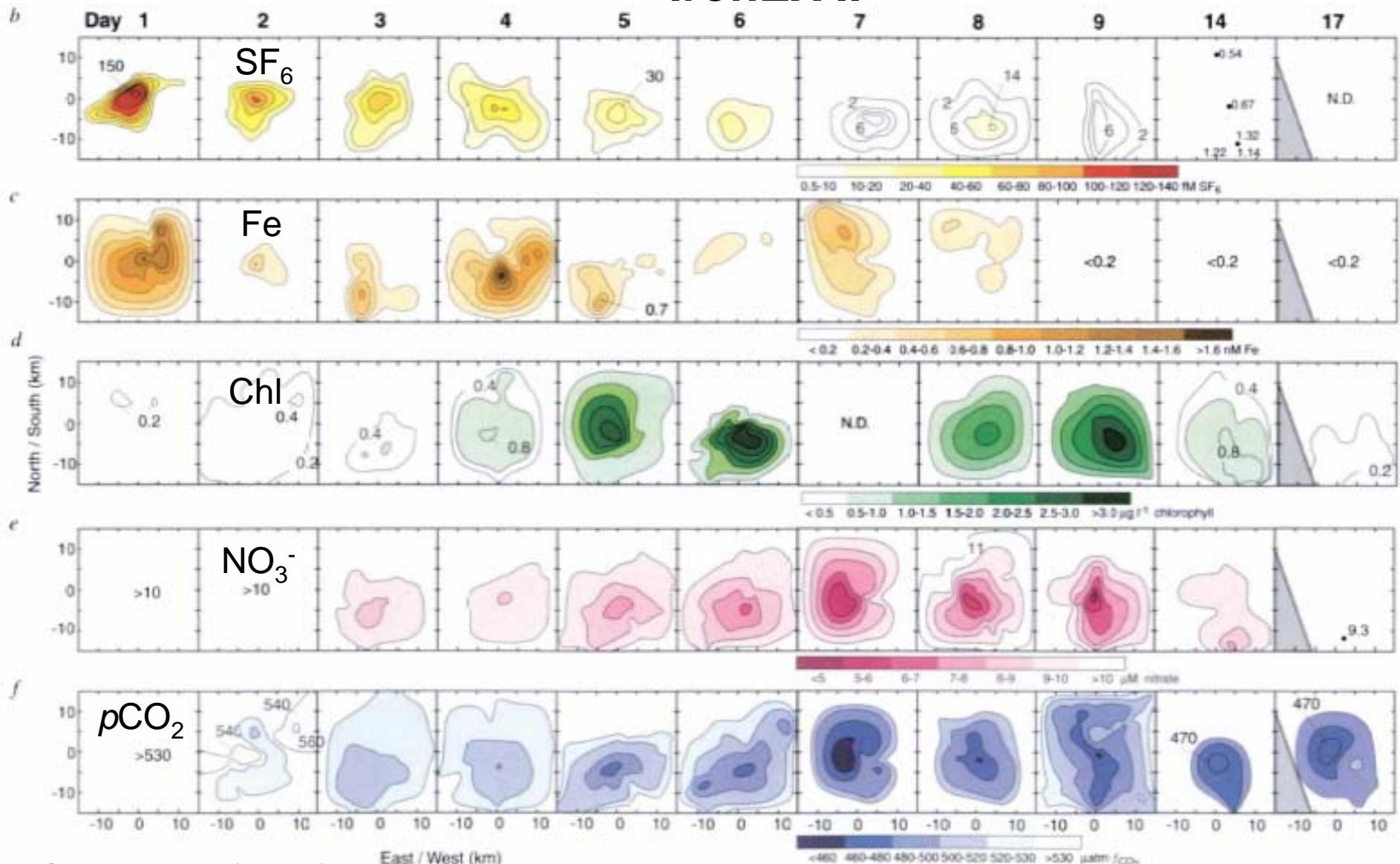


Coale et al. (1998)

Fe concentrations downstream of the Galapagos Islands (in the island plume) were  $\sim 1$  nM.

**IronEX I:** Chl concentrations enriched in the patch and downstream of natural Fe source (Galapagos Islands). However, only weak drawdown of nitrate observed over course of experiment...perhaps Fe is not the only limiting nutrient? Grazing? After day 4, the patch subducted beneath a low salinity front.

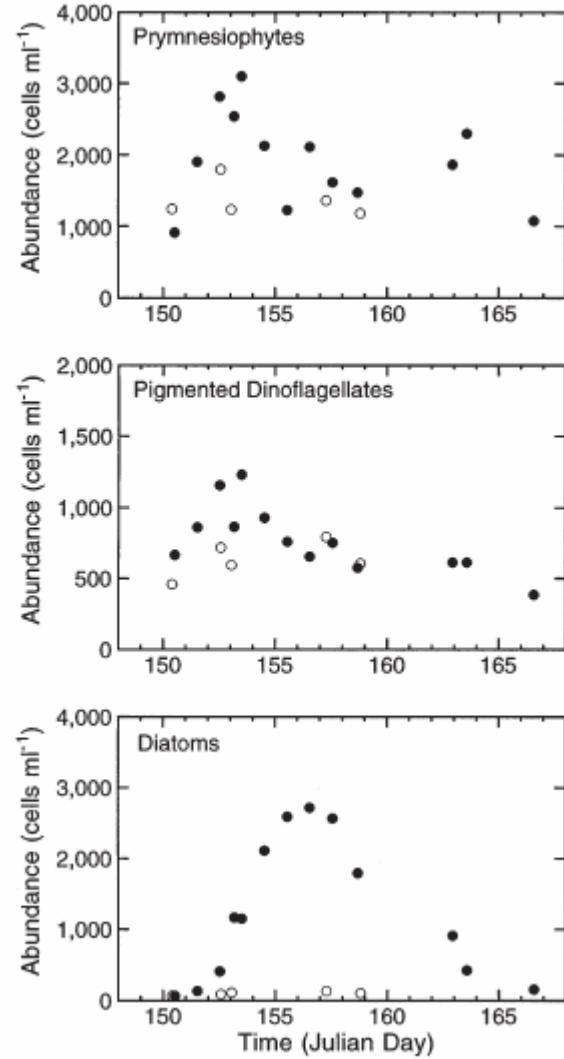
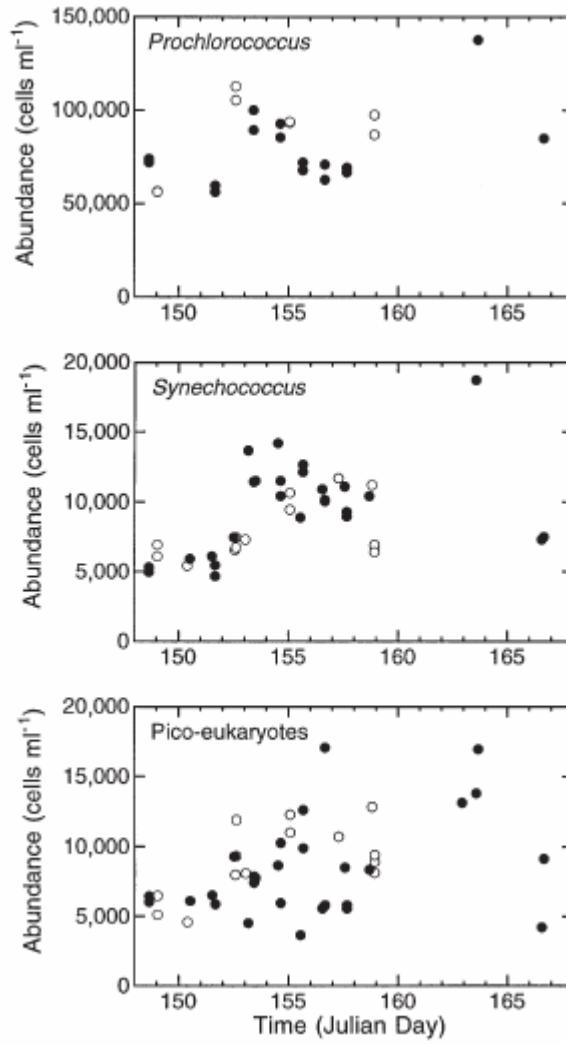
# IronEX II



Coale et al. (1996)

June 1995, Equatorial Pacific; 225 kg Fe in 72 km<sup>2</sup>; Day 1 Fe concentrations ~2 nM. Fe added again on days 3 and 7 (to bring surface water concentrations to ~1 nM)

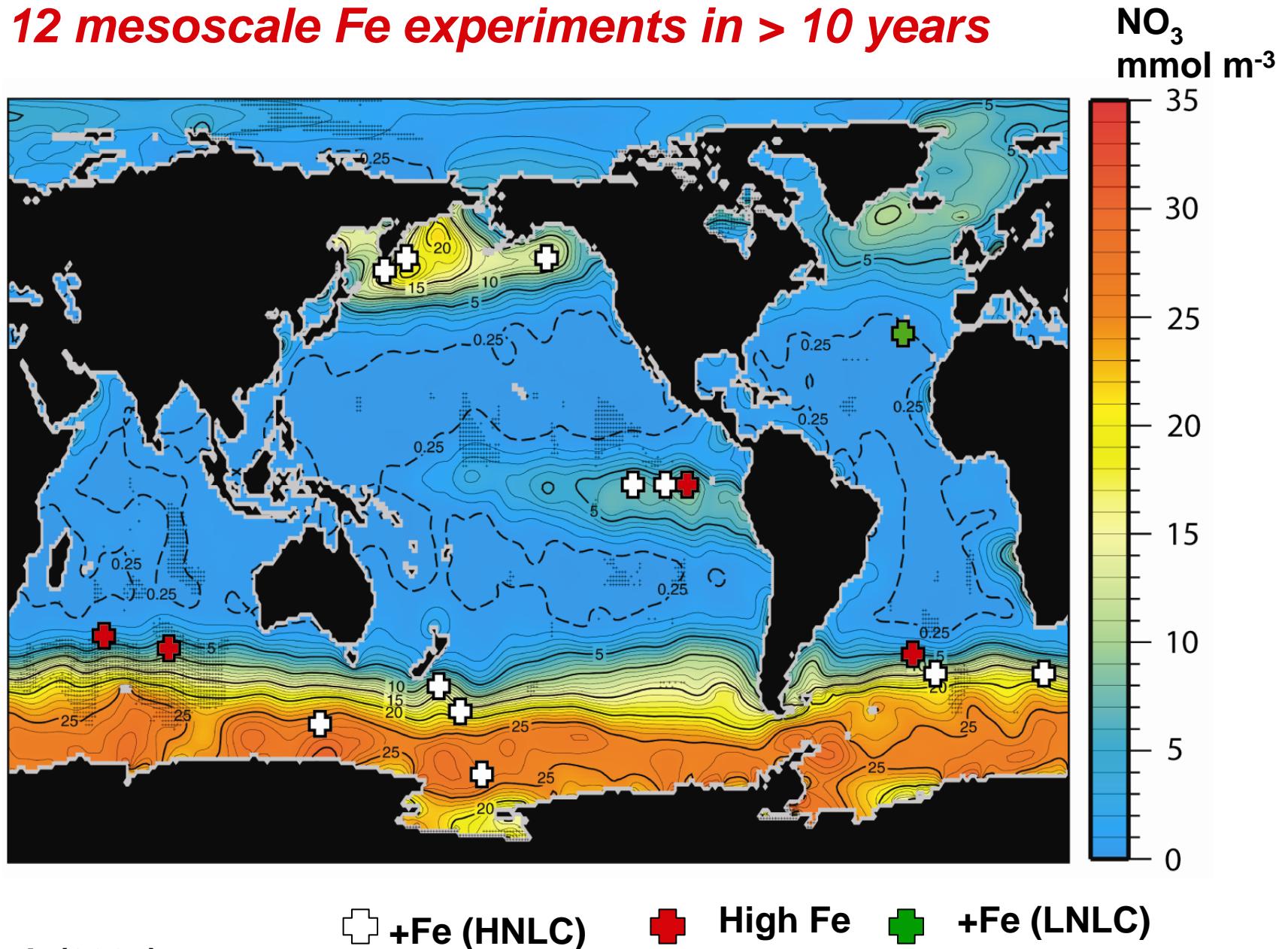
# IRONEX II: Equatorial Pacific June 1995; a shift from cyanobacteria to diatoms



**The increase in Chl  
within the Fe  
seeded patch  
appear largely  
driven by growth  
of diatoms  
(85-fold increase in  
abundance).**

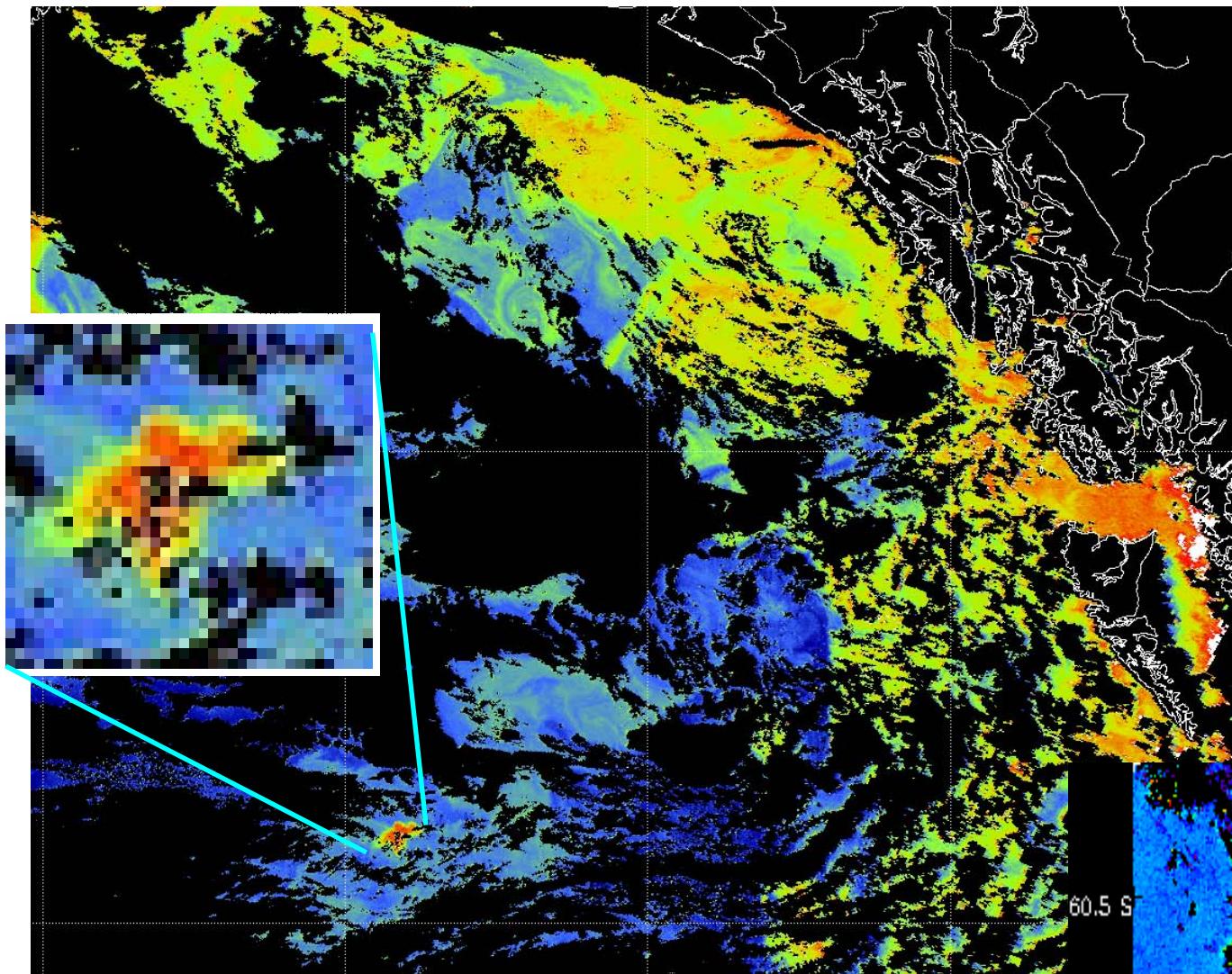
Landry et al. (2000)

## *12 mesoscale Fe experiments in > 10 years*



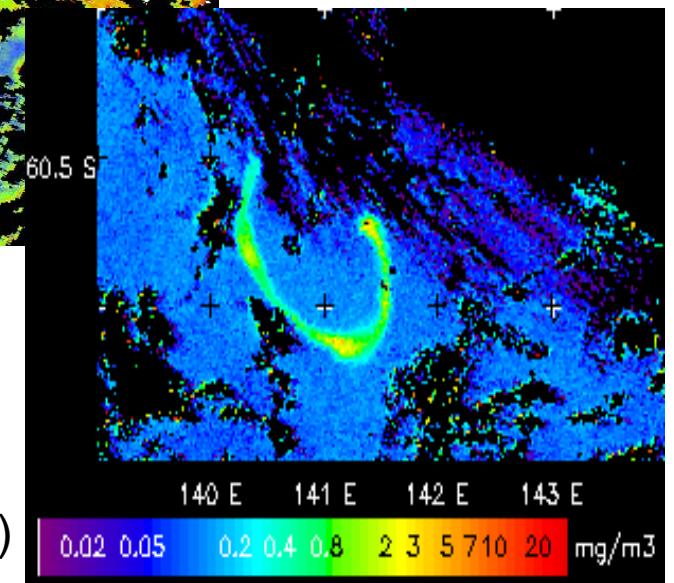
Boyd et al. (2007)

The resulting blooms are large enough to be viewed from space

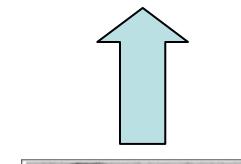
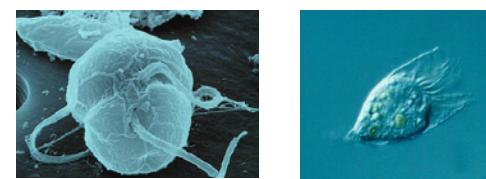
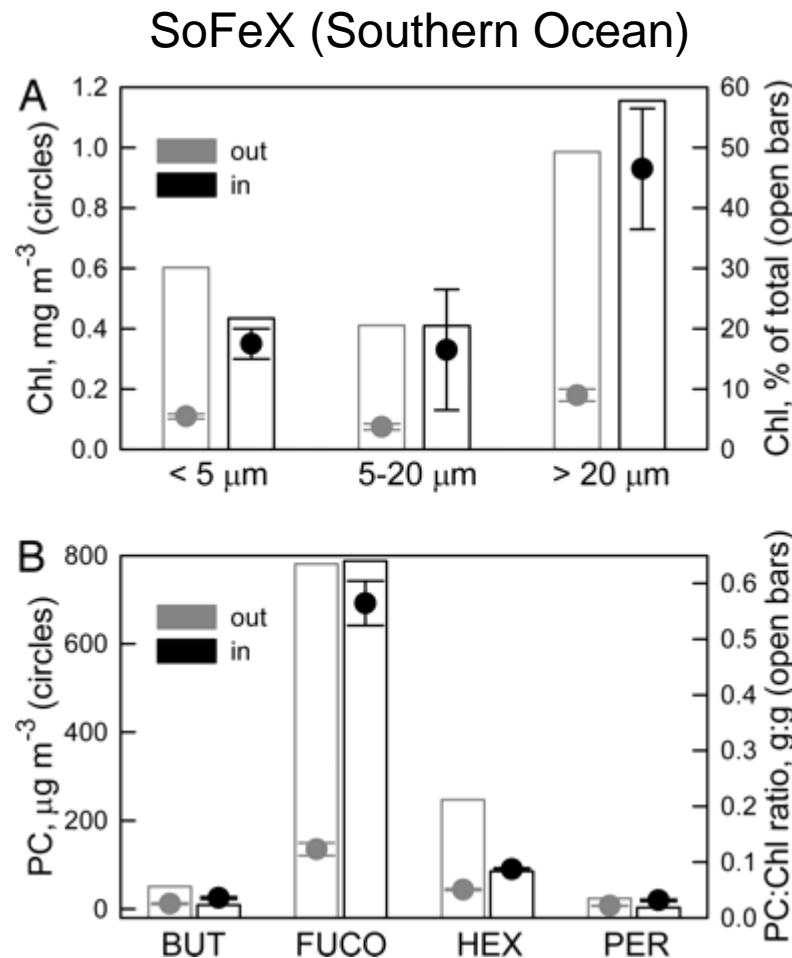


SERIES (Subarctic North Pacific)

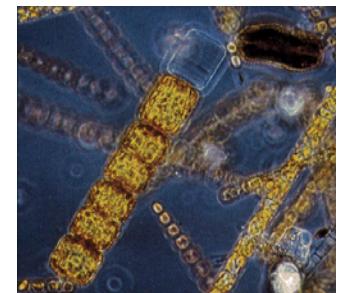
SOIREE (Southern Ocean)



- One of the major findings from these open ocean Fe enrichment experiments was that specific components of the phytoplankton community increased in biomass following the addition of Fe.



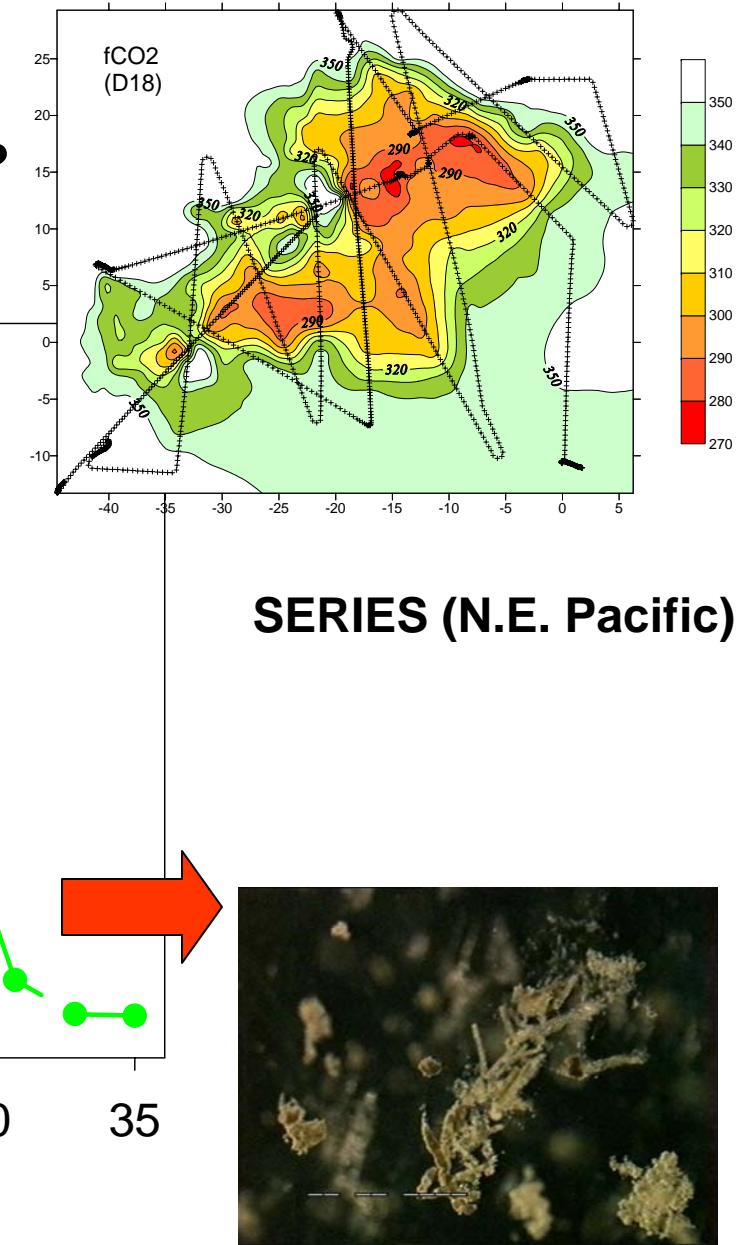
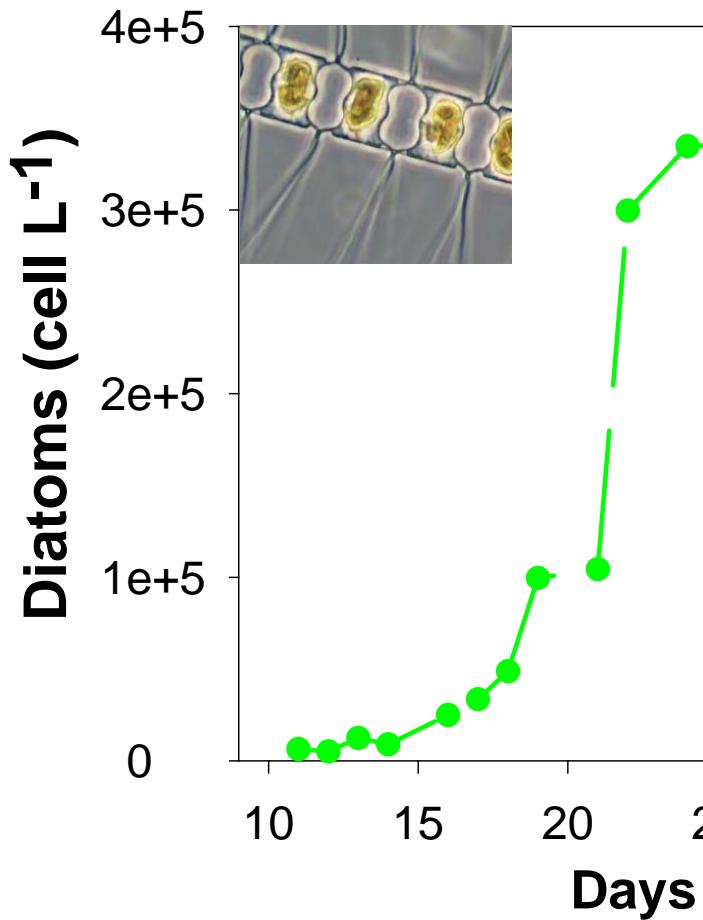
No iron



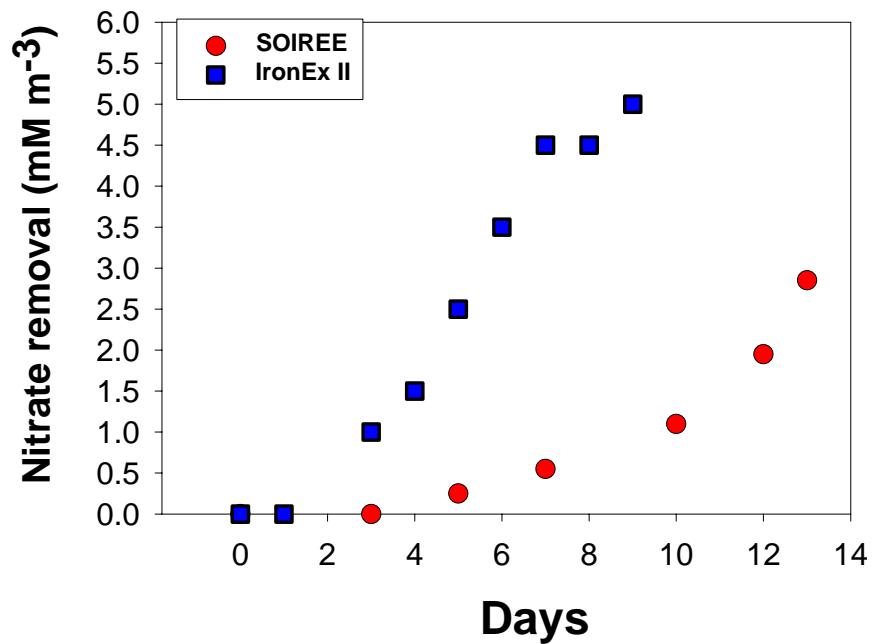
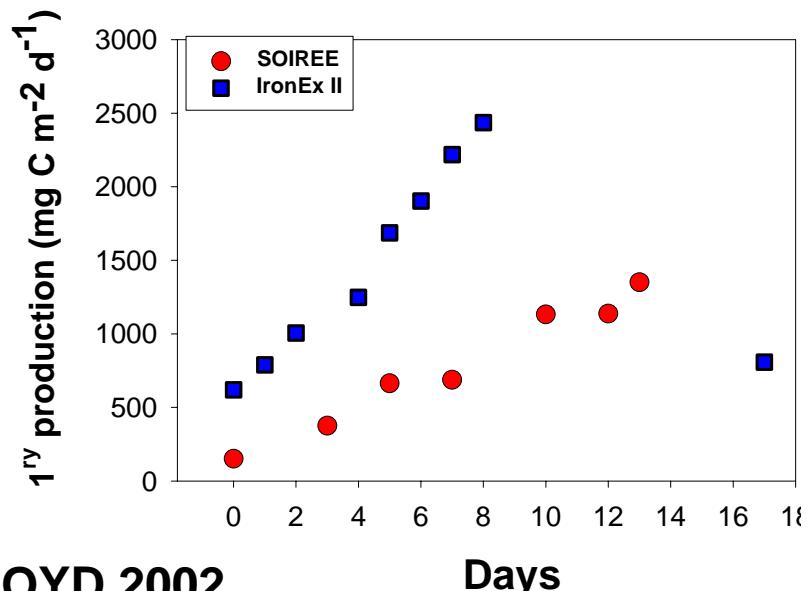
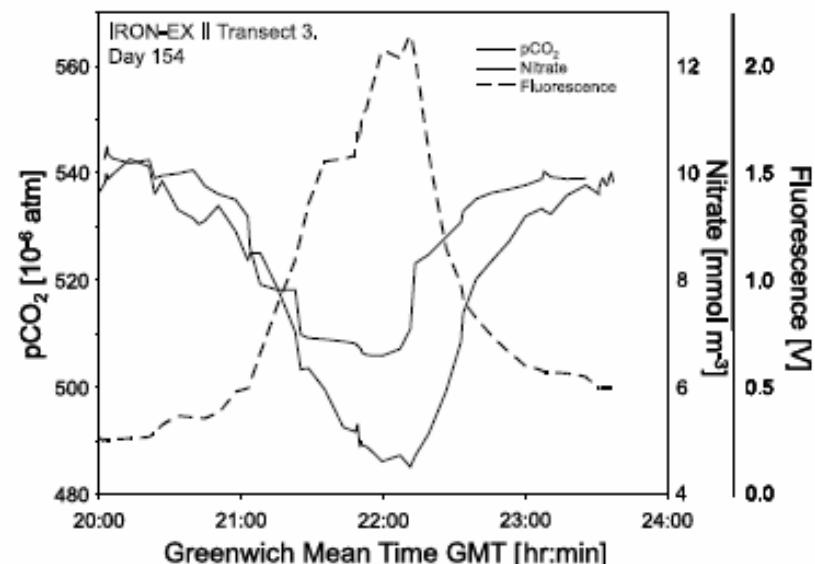
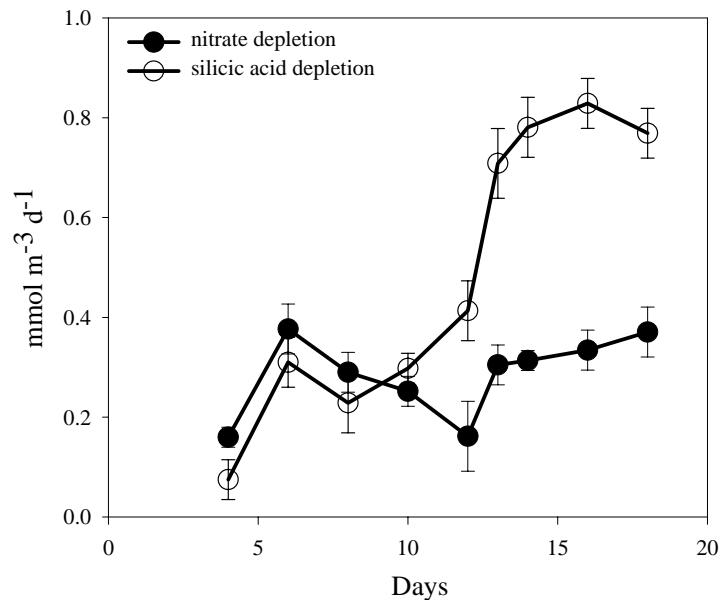
Iron

??  
↑

# Diatoms grow rapidly, then disappear?

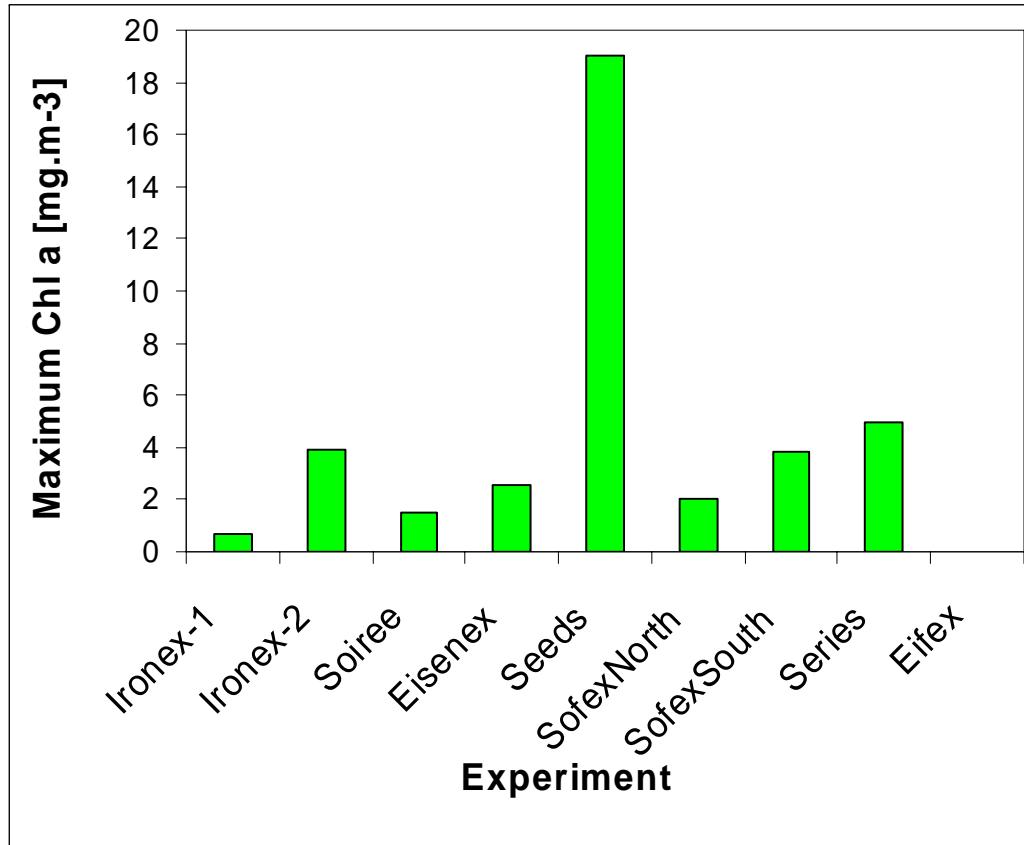


# Iron supply impacts many aspects of phytoplankton processes and ocean biogeochemistry

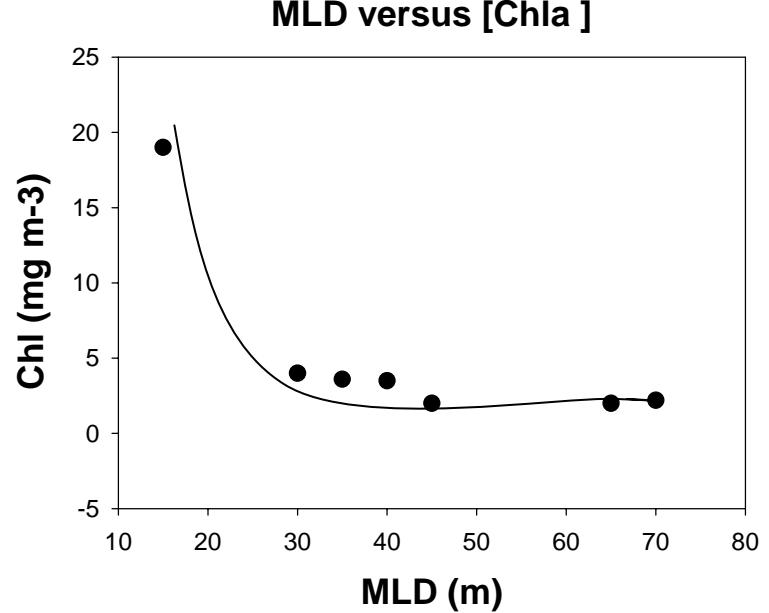


BOYD 2002

# A wide range in bloom signatures



De Baar et al. 2005

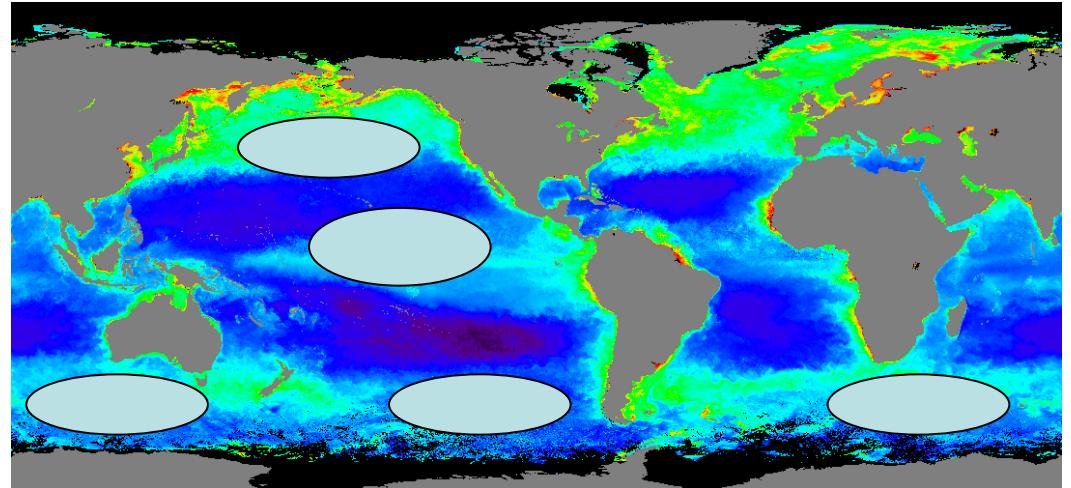


## The HNLC condition-lessons learned from large scale manipulation experiments

- HNLC conditions are maintained by low Fe supply which suppresses phytoplankton growth and biomass production.
- Low concentrations of Fe appear to favor smaller cells (picoplankton).
- Growth of dominant picoplankton also suppressed by Fe supply but to a lesser extent than larger, rarer cells.
- Active microzooplankton grazing keeps picoplankton biomass low and relatively invariant, providing a highly regenerative upper ocean (rapid  $\text{NH}_4^+$  cycling).

# HNLC Regions of the Ocean

## SUMMARY



***HNLC waters – 30% OF OPEN OCEAN***  
***IRON SUPPLY causes the HNLC condition***  
***But some regions are also influenced by light,  
Grazing or silicic acid supply***  
***Biomass levels in HNLC waters are set by  
Grazing pressure – which in turn resupplies iron***

Seeding a bloom and studying its development has provided important information on plankton control of biogeochemistry