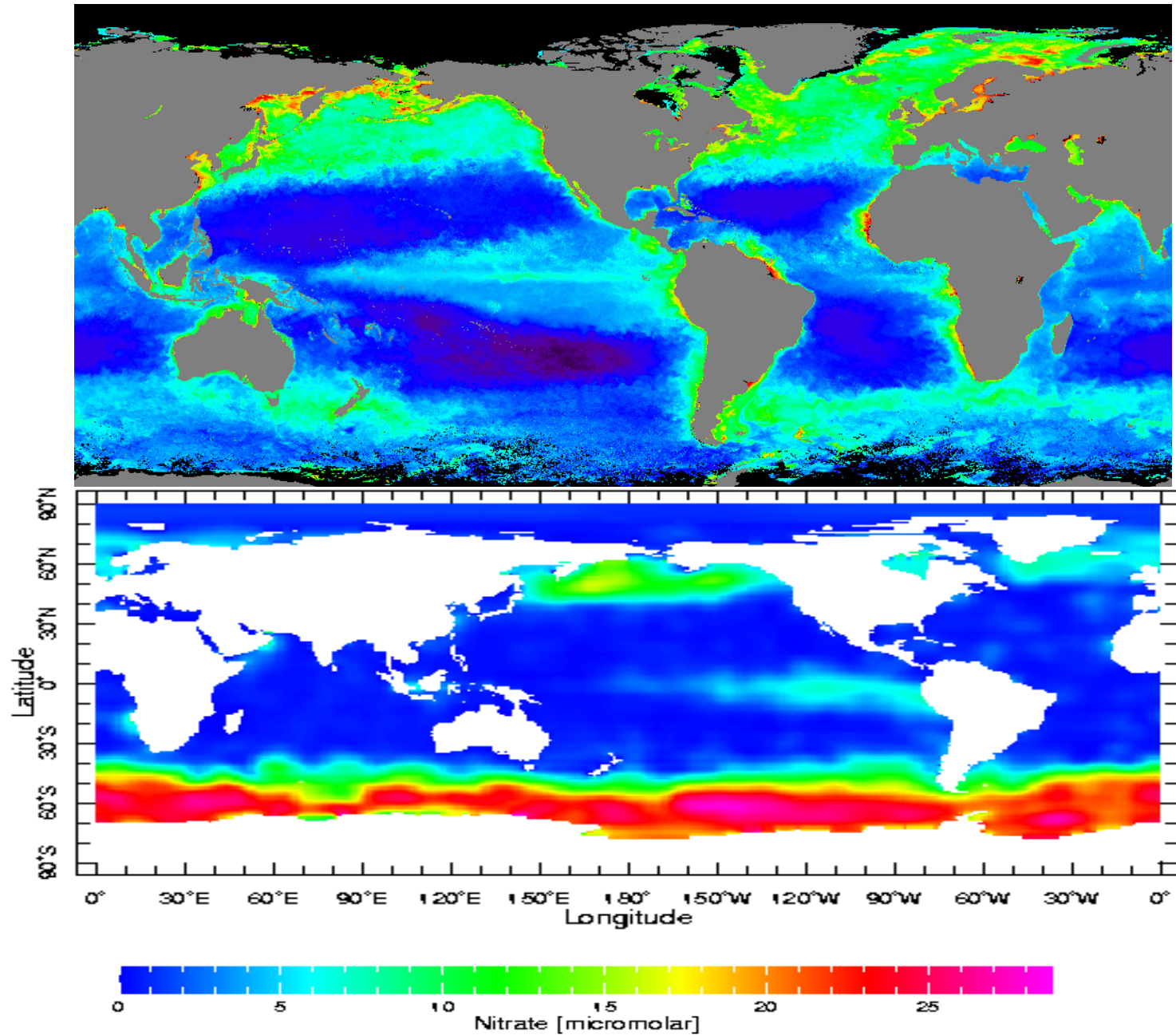


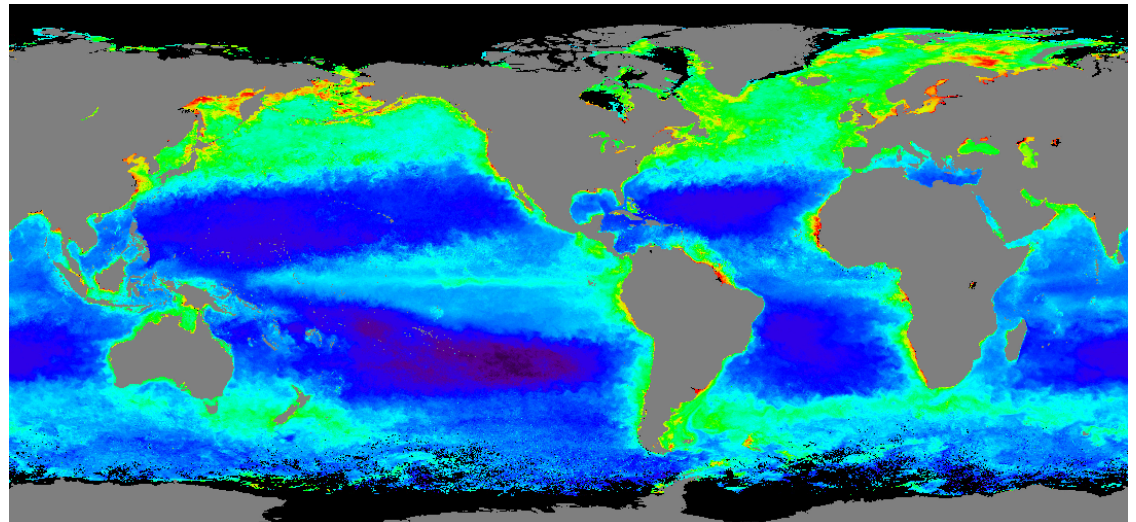
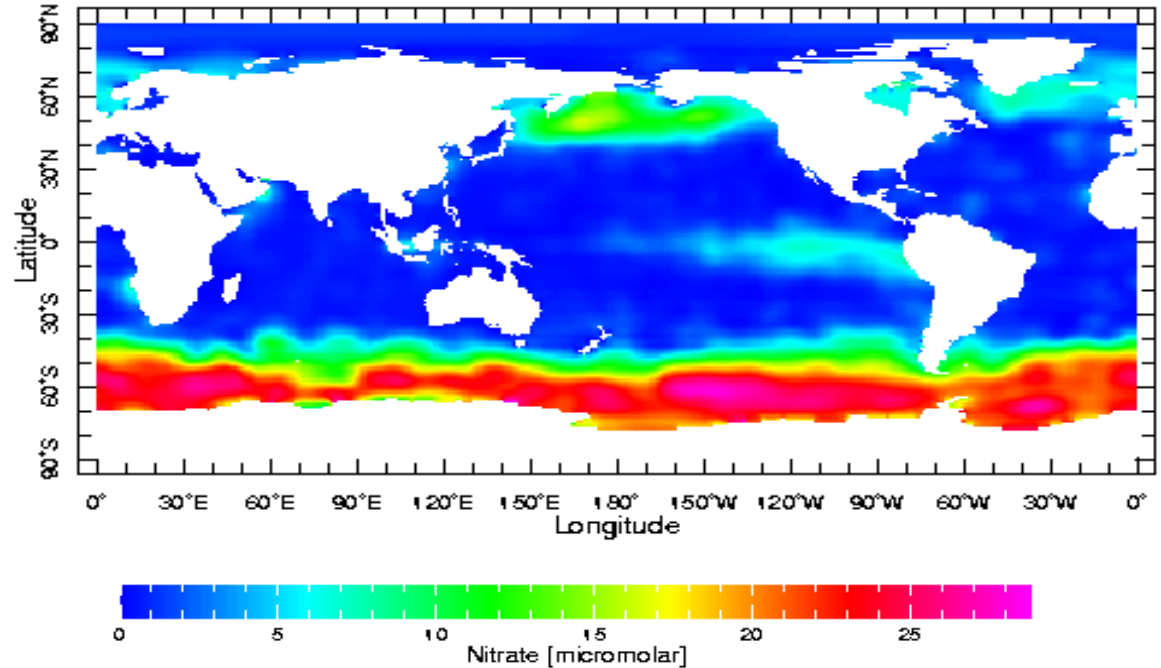
High Nutrient Low Chlorophyll Ecosystems



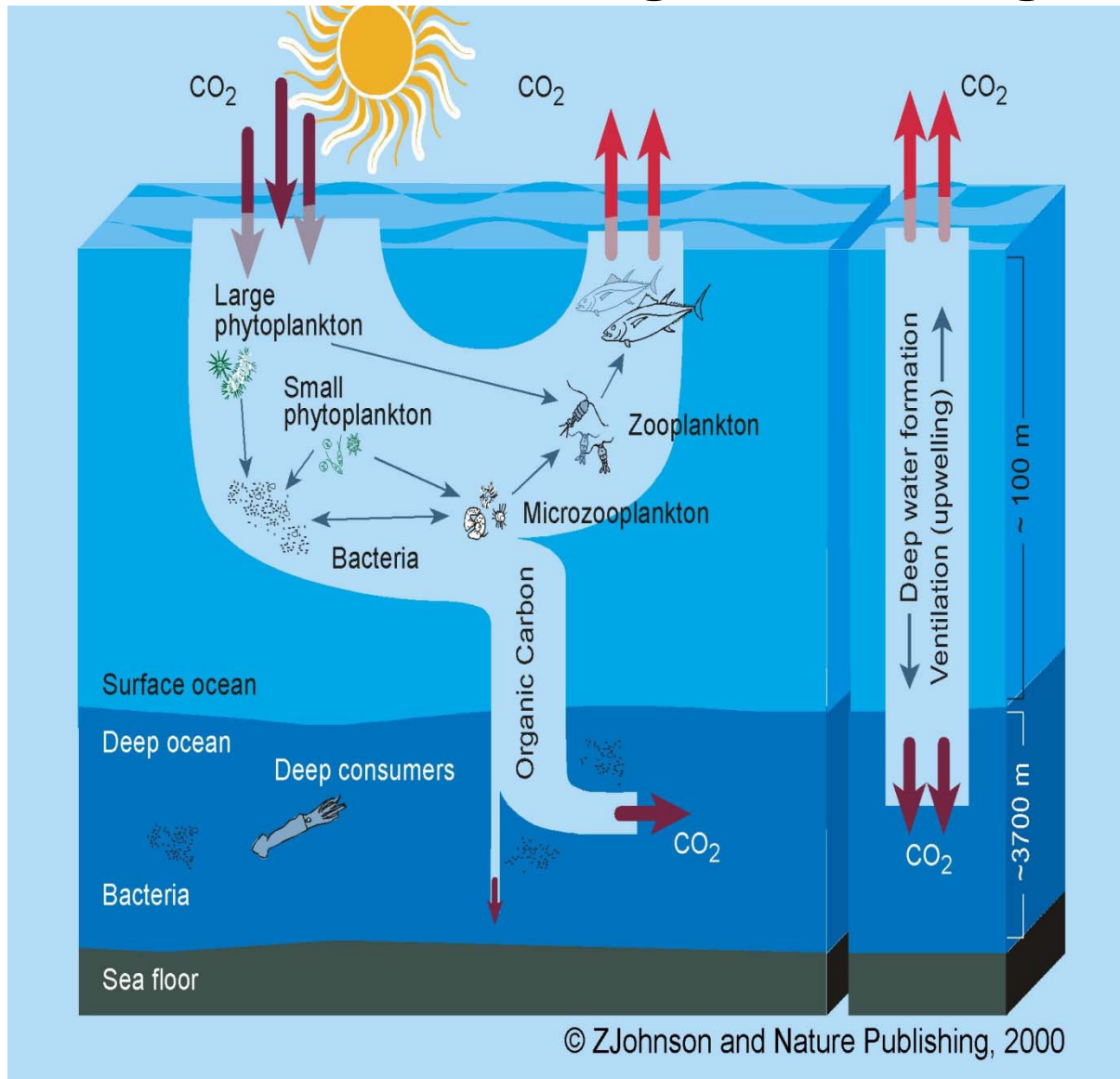
Average surface ocean nitrate concentrations

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

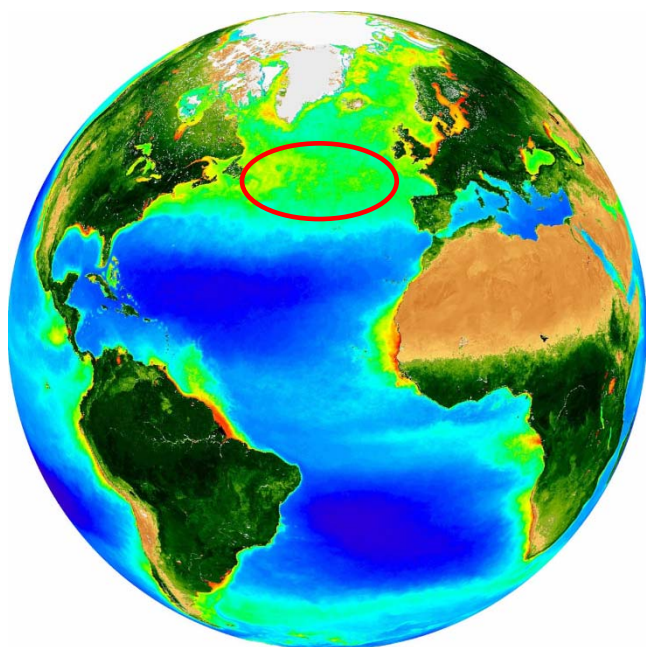
Such regions are termed High Nitrate Low Chlorophyll (HNLC) waters



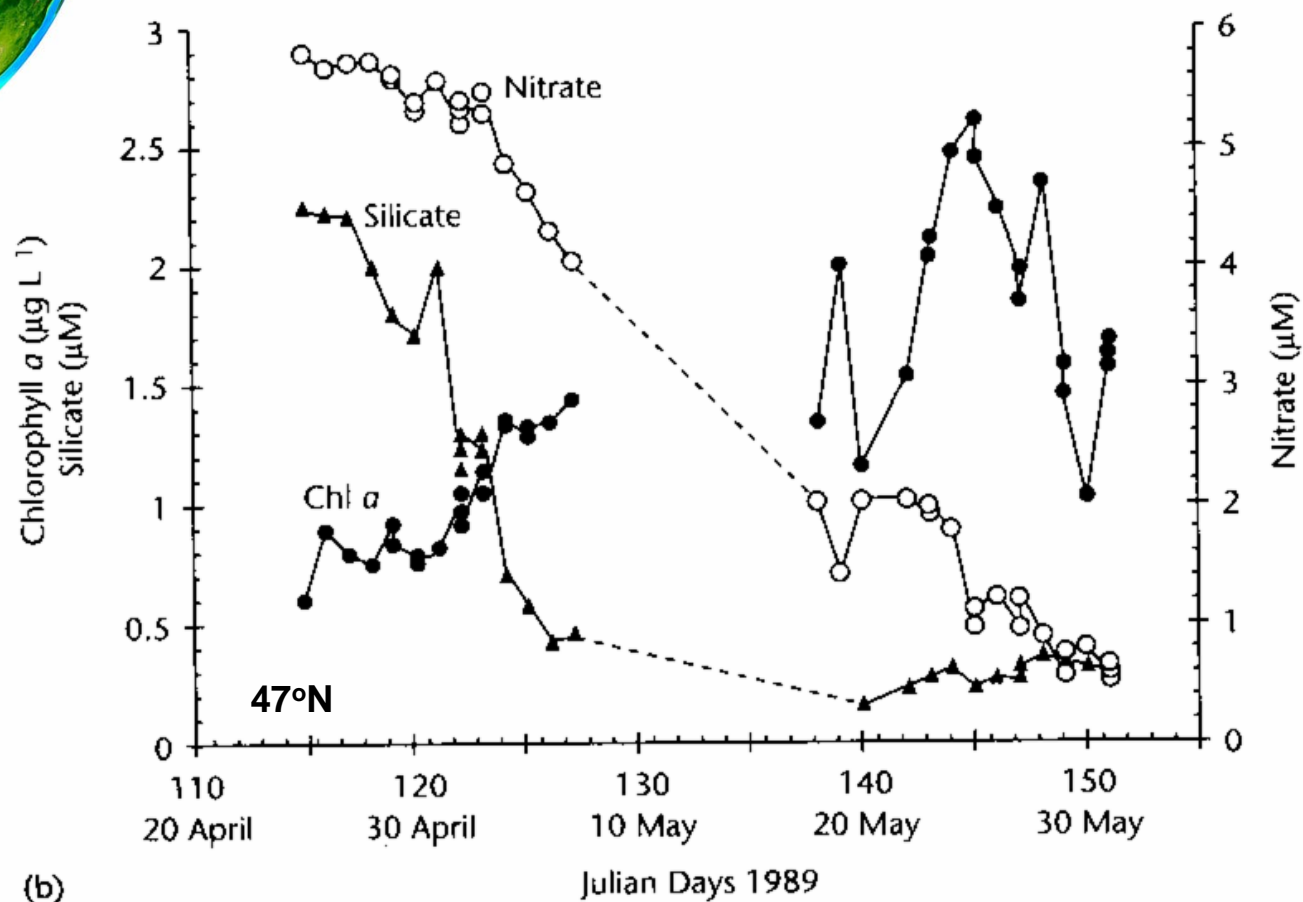
Whatever factors limit complete utilization of nutrients in HNLC regions have important consequences on the functioning of the biological pump



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



North Atlantic Spring Bloom



(b)

Subarctic North Pacific

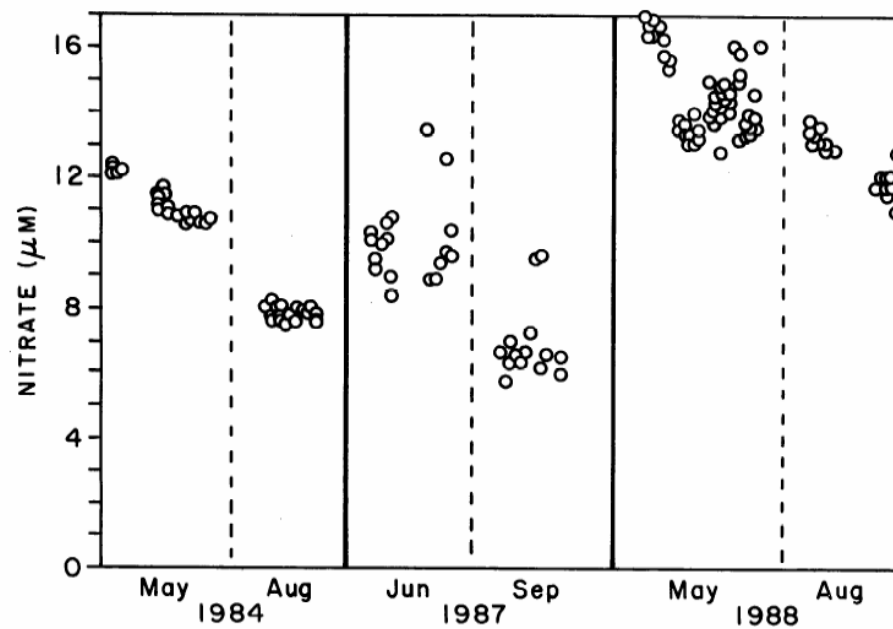
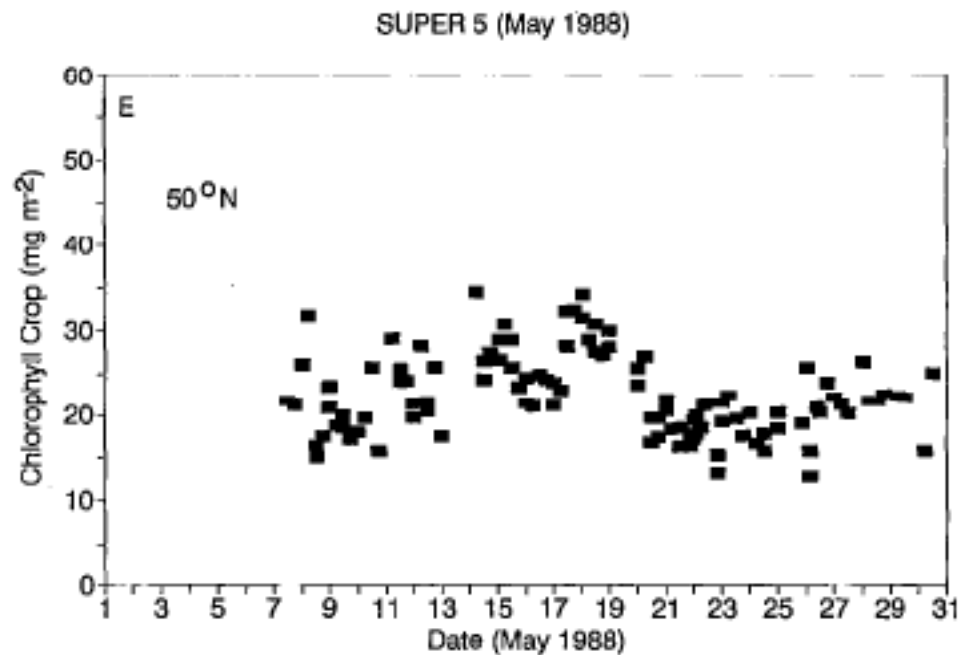
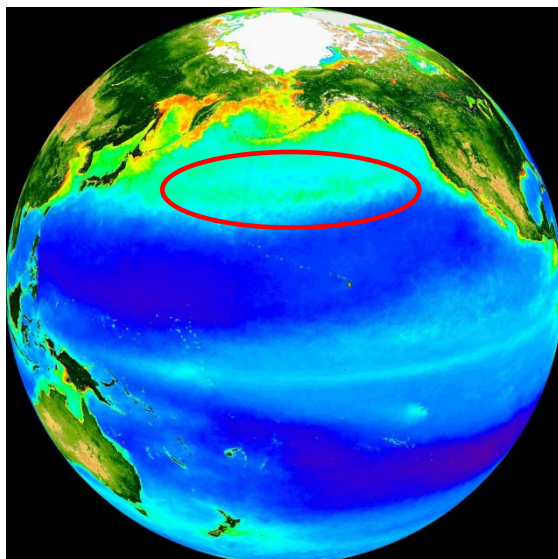
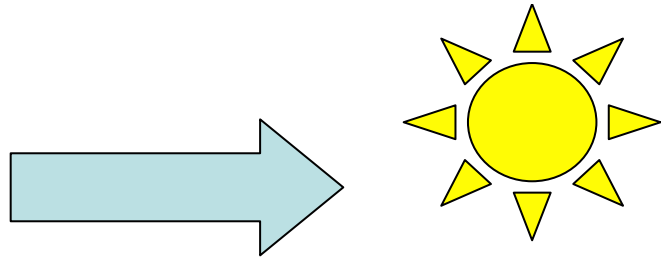


Fig. 7. Interannual variation in NO₃ concentration as seen during three spring and summer cruises.

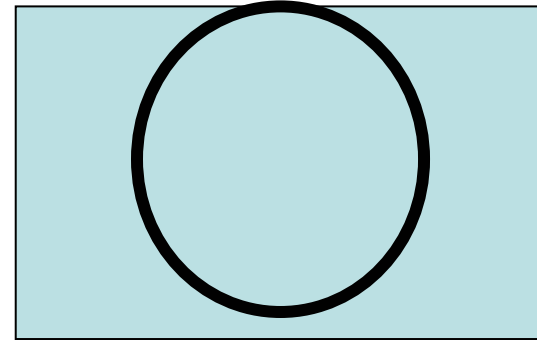
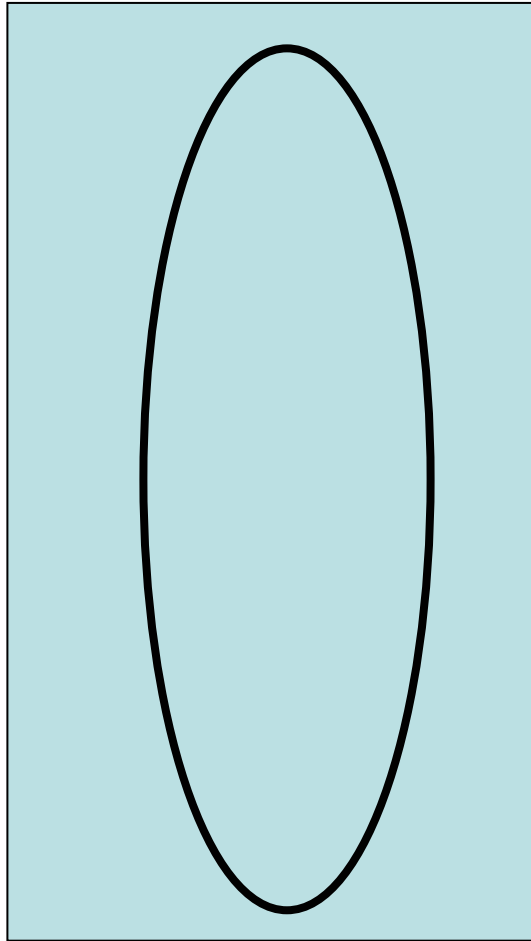
What limits the accumulation of phytoplankton in large regions of the oceans?

- 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)

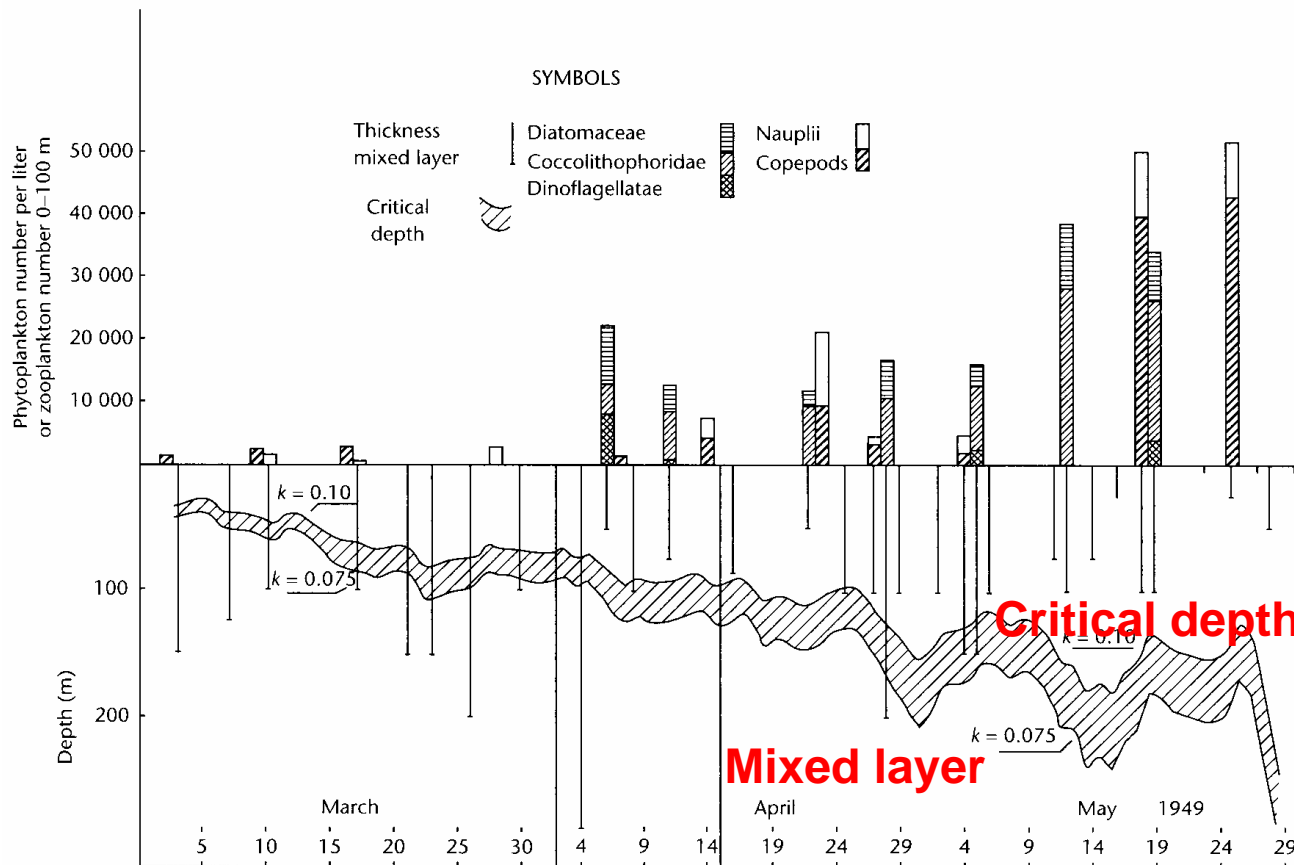
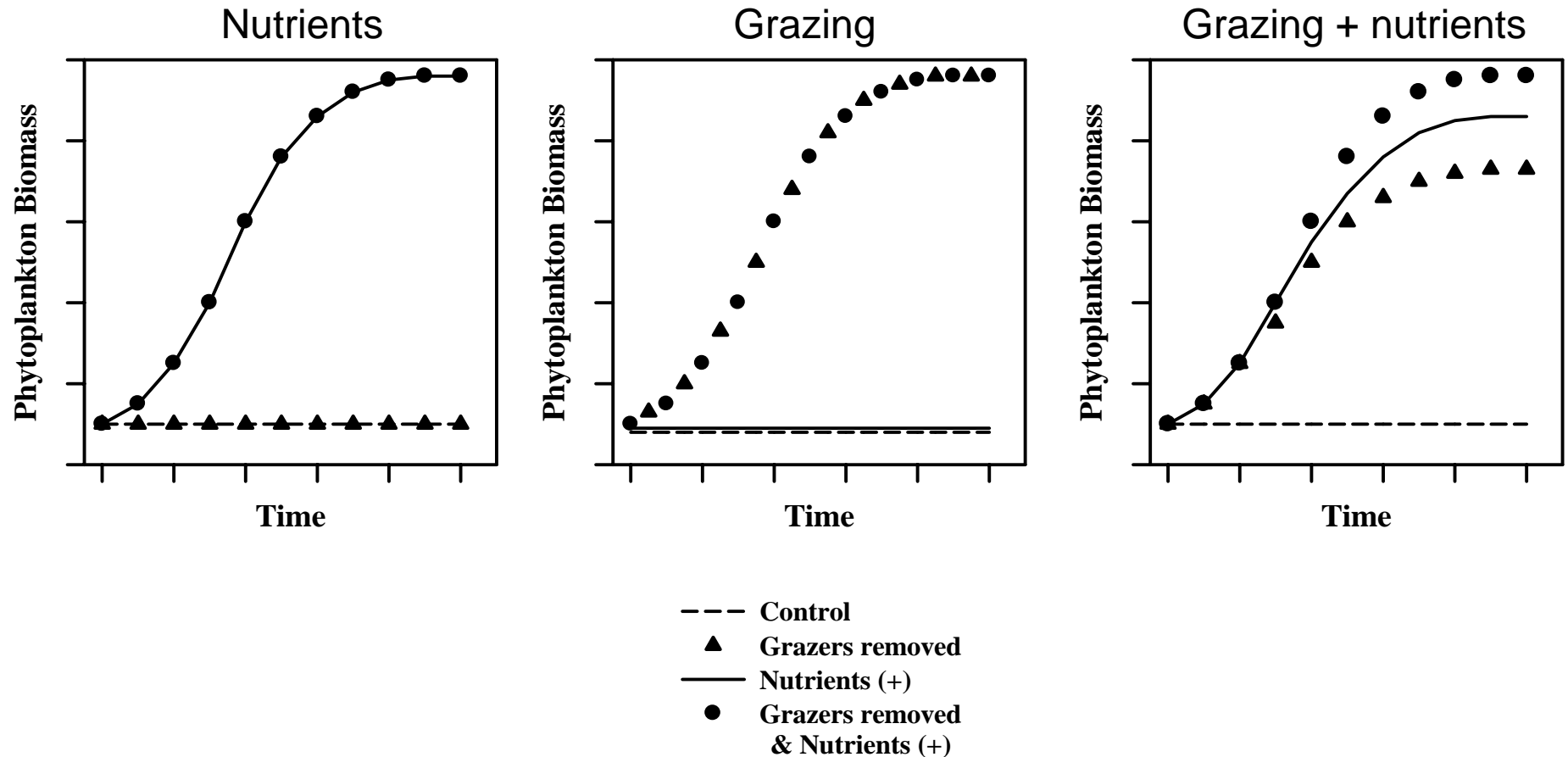


Fig. 1.4 Data for 1949 from Weather ship "M" (66°N, 2°E) showing the relationship between the approximate critical depth (shading between approximate k values of 0.075 and 0.10) and mixing depth. Phytoplankton counts increased in April-May, when critical depth exceeded the mixing depth. While these data 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

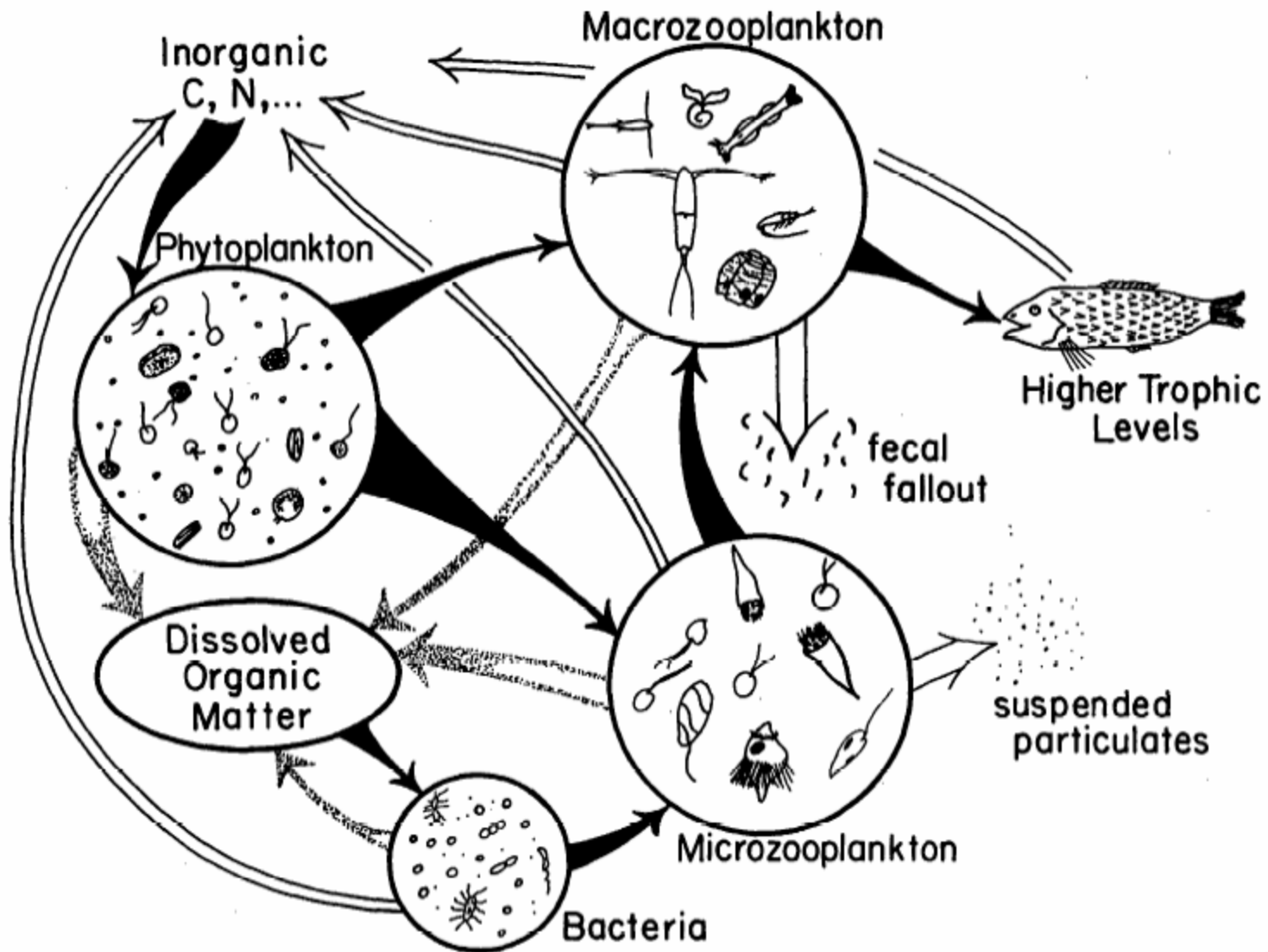
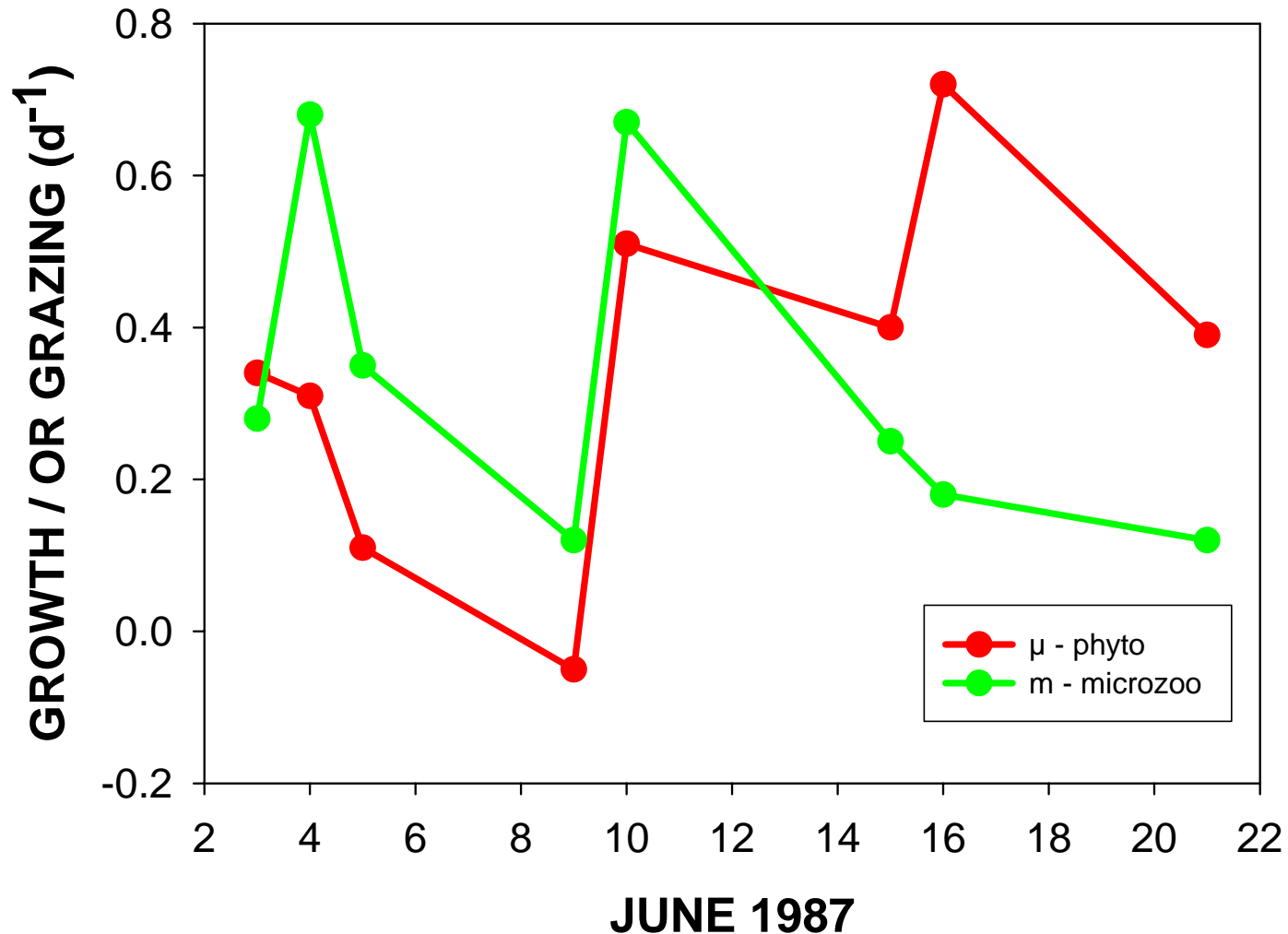


Fig. 4. Diagram of principal food-web connections in the subarctic Pacific. Black arrows—consumption; white arrows—regeneration processes; stippled arrows—transfers to dissolved organic pool.

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.

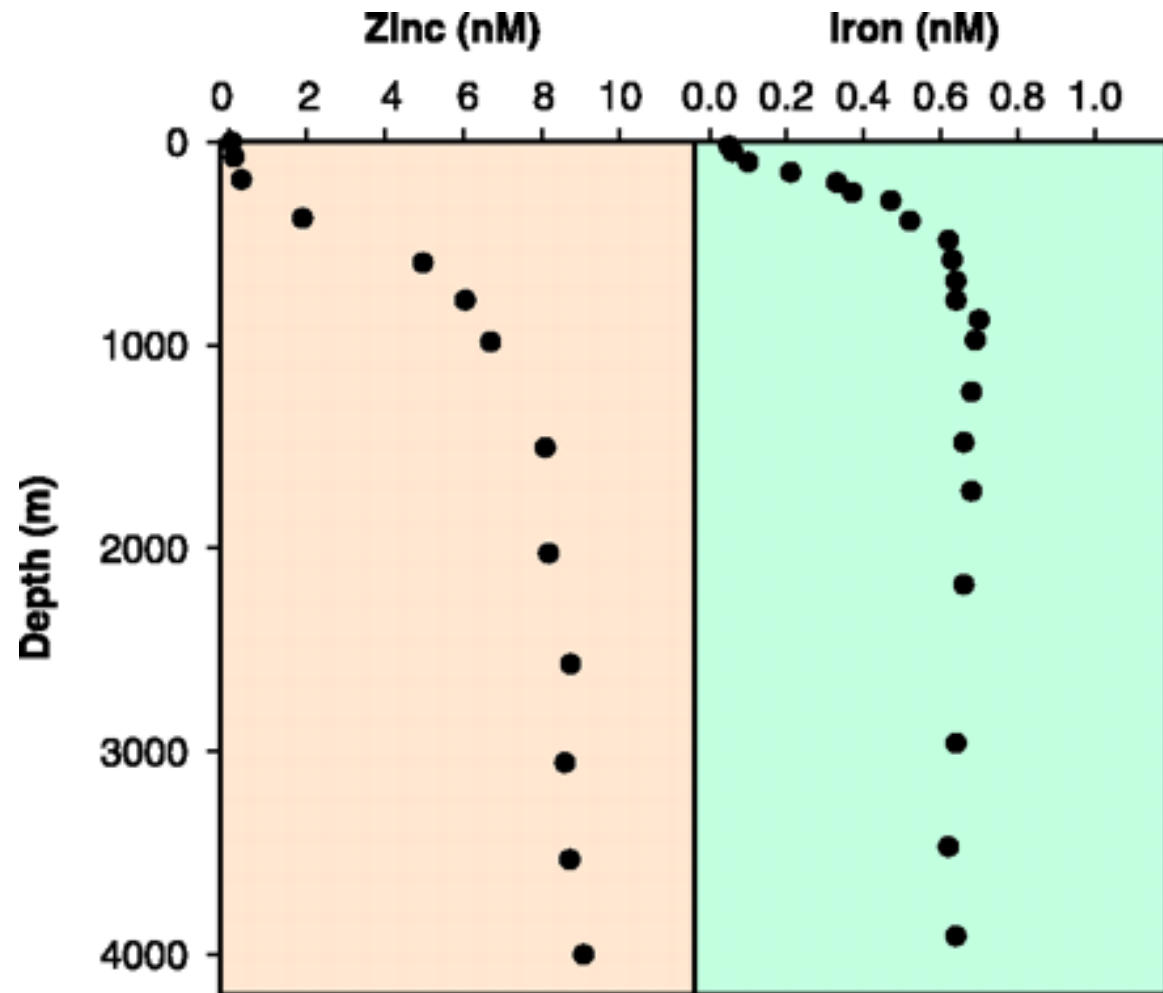
The case for Iron

- 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_2 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

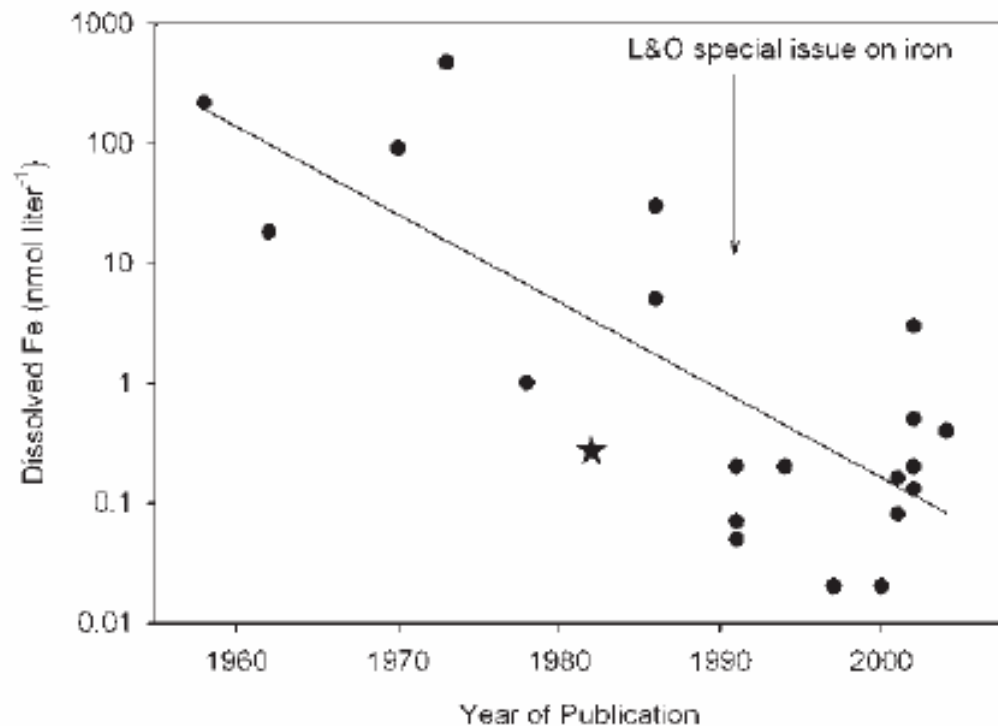
Surface depletion
due to algal
uptake;
increasing
concentrations
increase through
remineralization

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

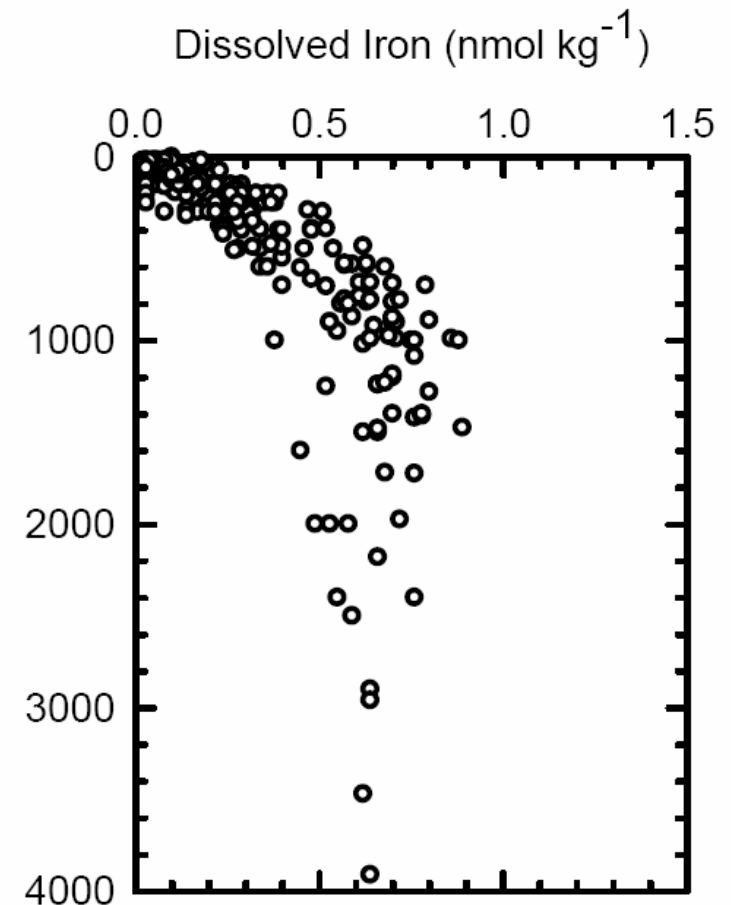
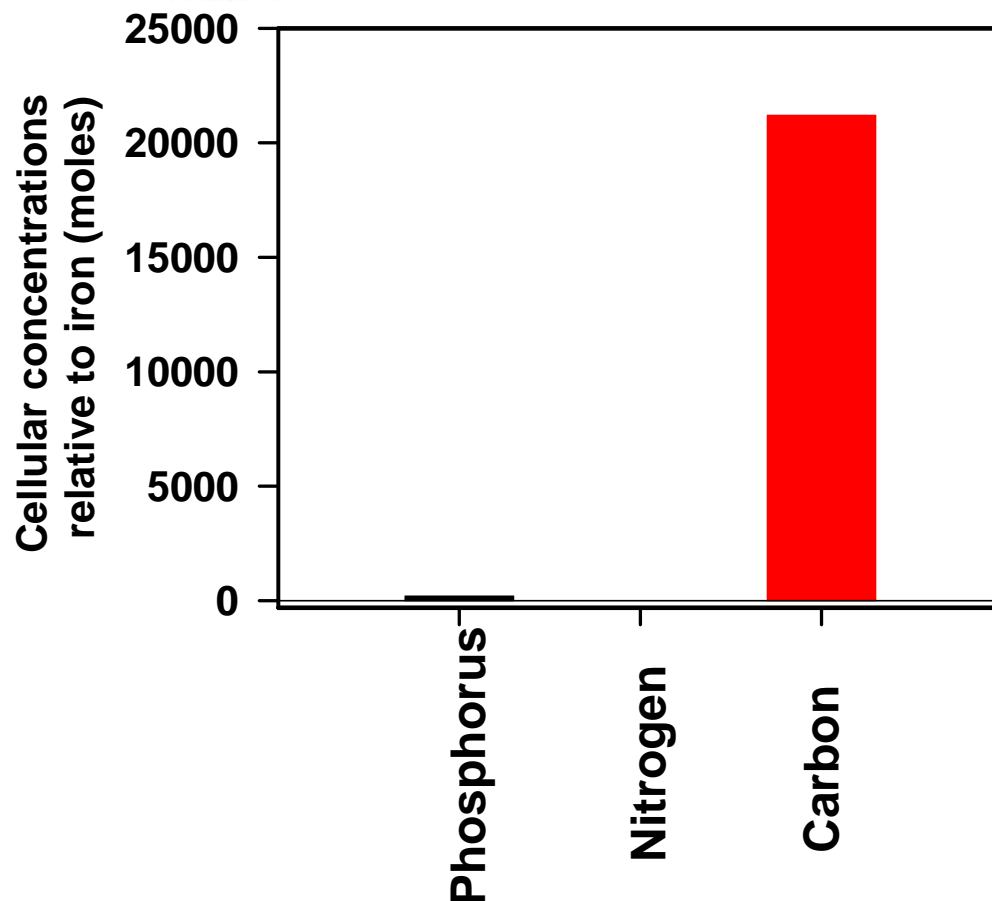


Figure courtesy K. Johnson (MBARI)



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



GENERAL PURPOSE

20-10-20

(For Continuous Liquid Feed Programs)

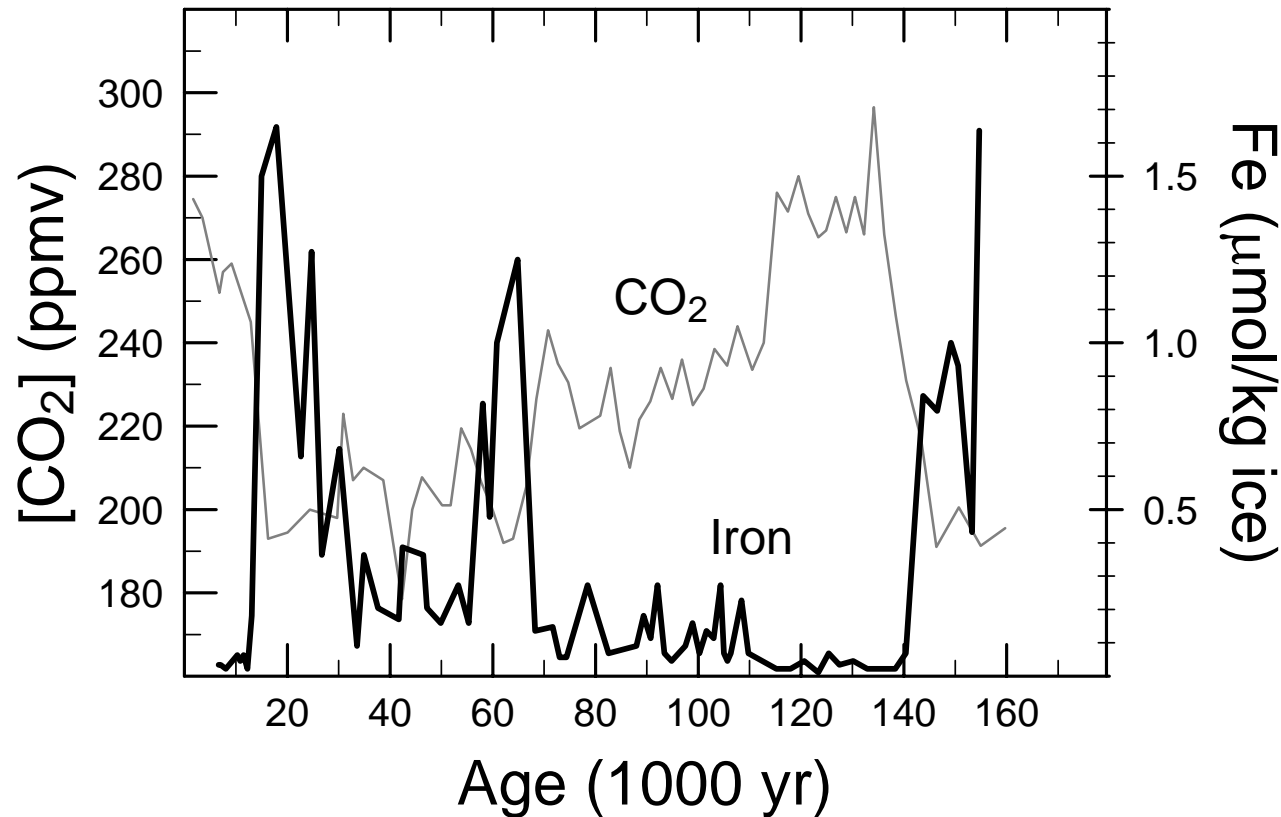
Guaranteed Analysis	F1143
Total nitrogen (N)	20%
7.77% ammoniacal nitrogen	
12.23 % nitrate nitrogen	
Available phosphate (P ₂ O ₅)	10%
Soluble potash (K ₂ O)	20%
Magnesium (Mg) (Total)	0.05%
0.05% Water Soluble Magnesium (Mg)	
Boron (B)	0.0068%
Copper (Cu)	0.0036%
0.0036% Chelated Copper (Cu)	
Iron (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:

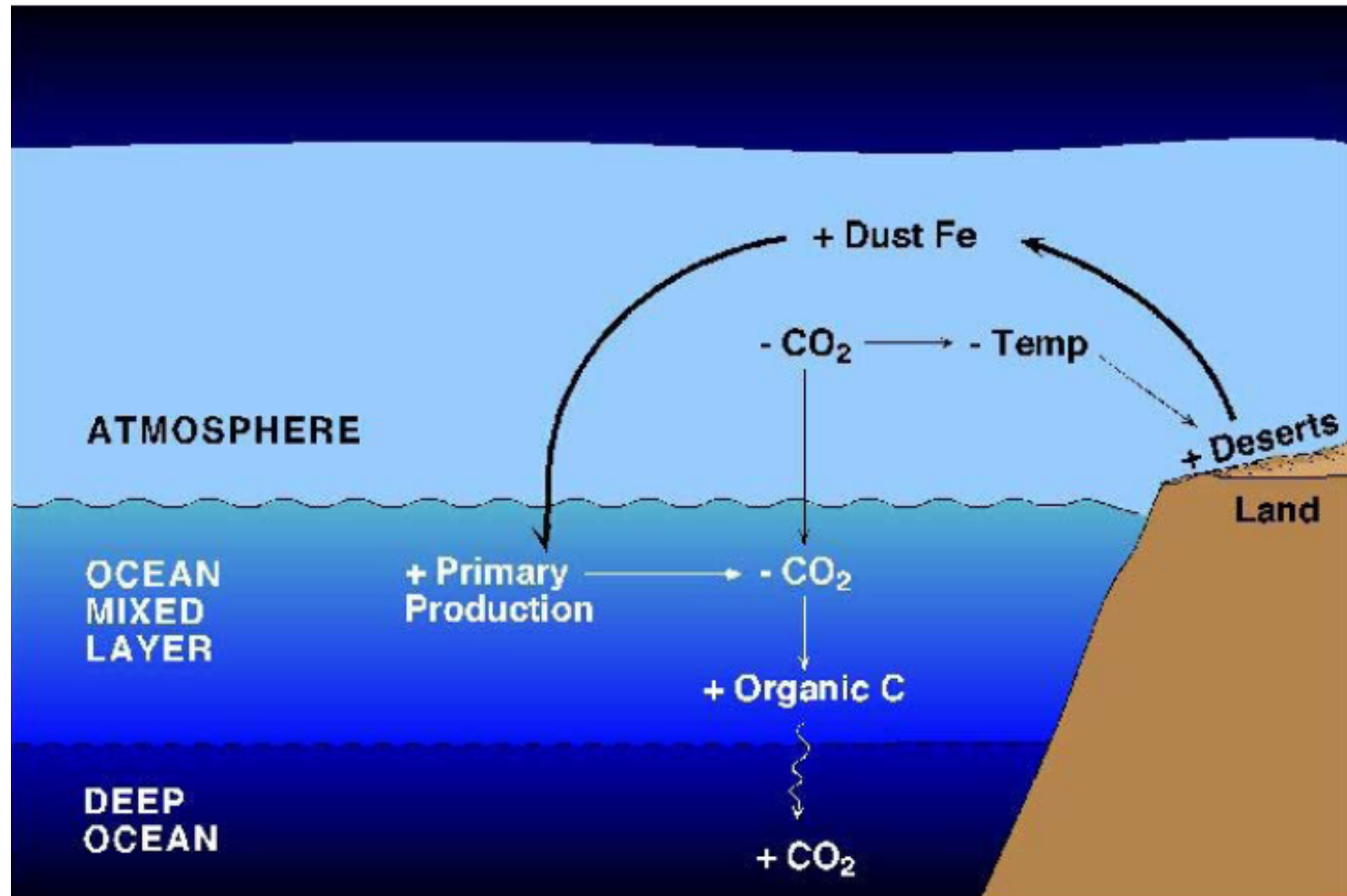
106C : 16N : 1P : 0.005Fe

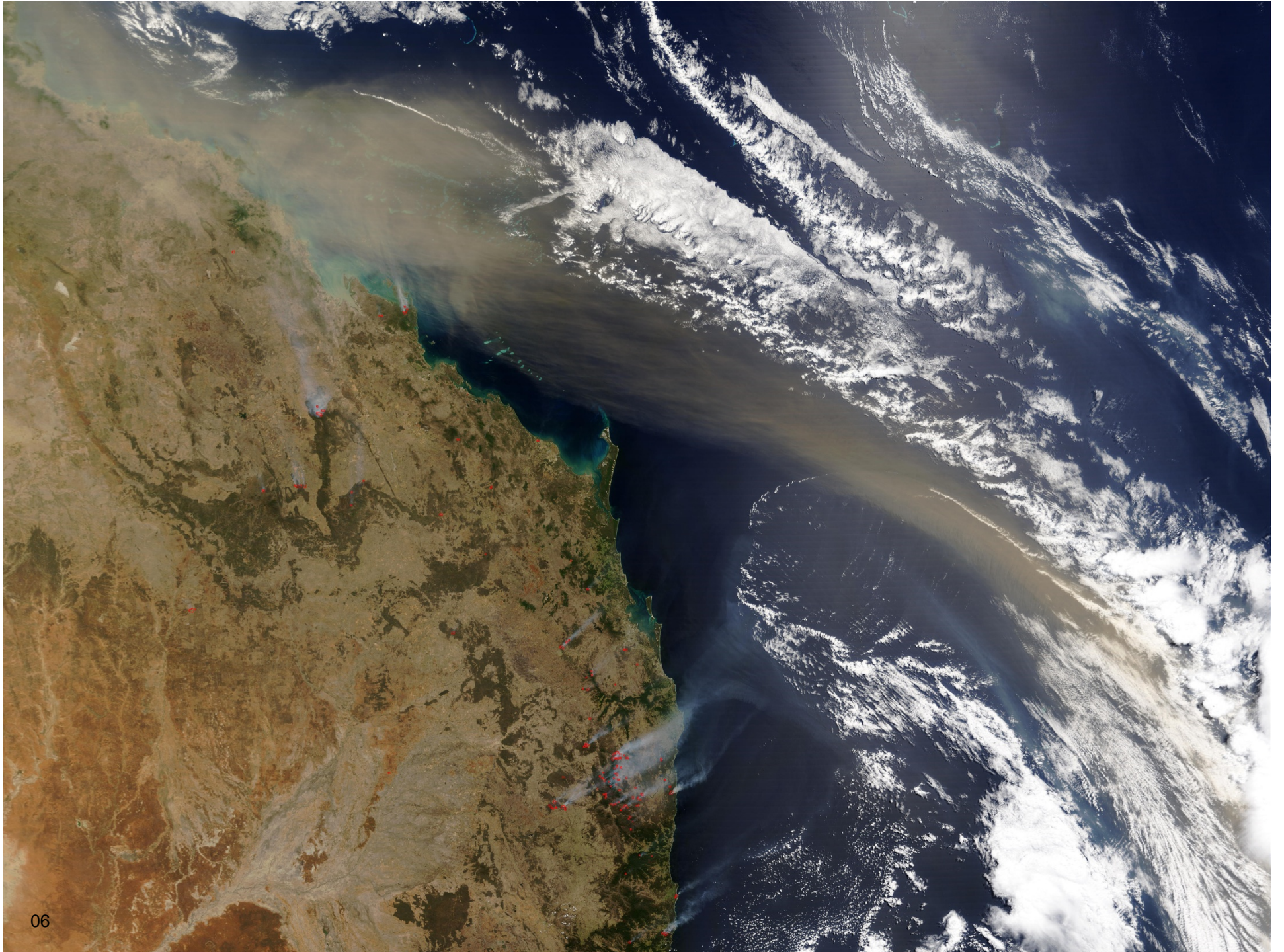
There is evidence suggesting that changes in Fe supply influence atmospheric CO₂



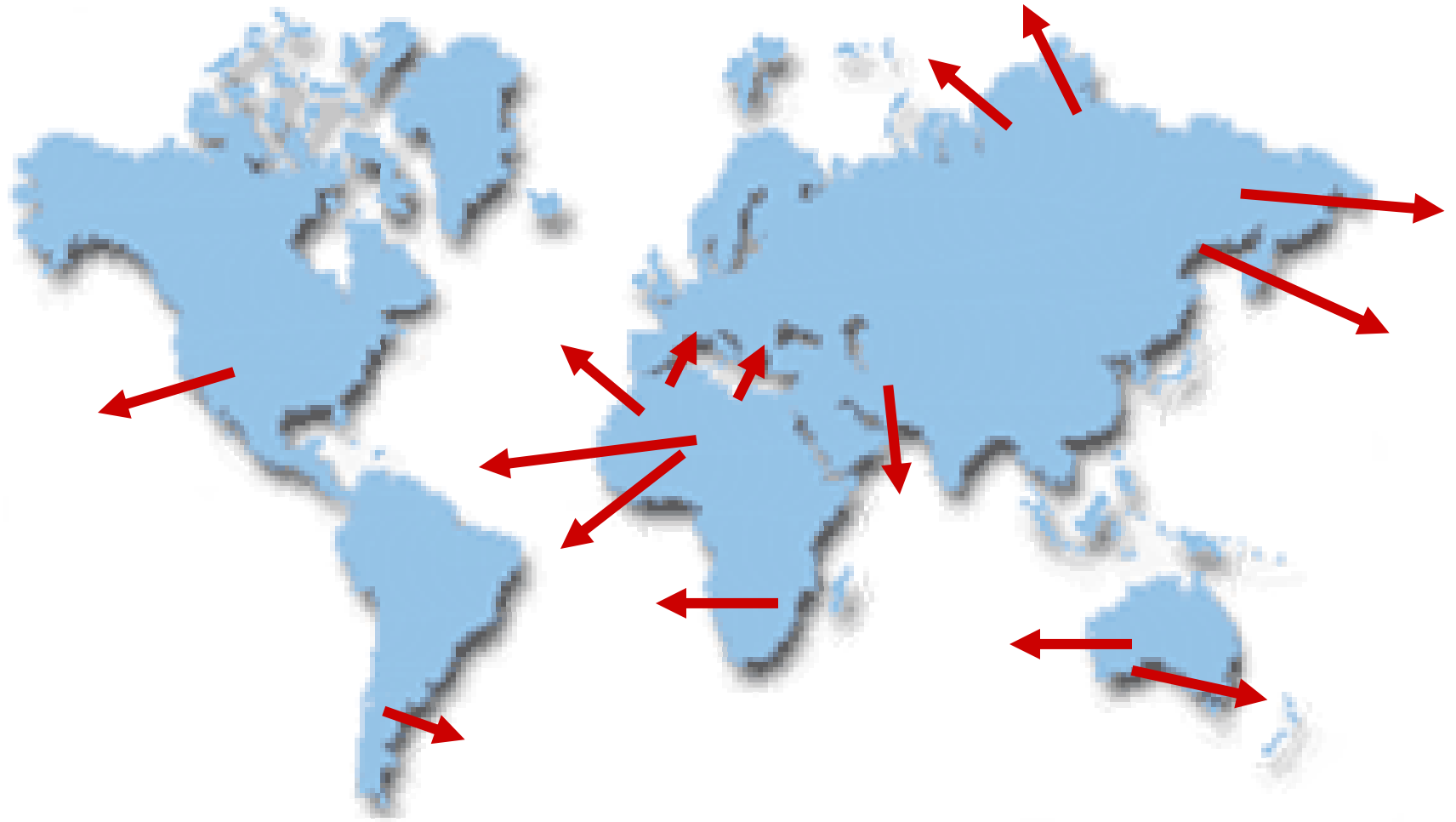
Glacial-interglacial variations in CO₂ demonstrate inverse relationships to the availability of iron in seawater

The “Iron Hypothesis”, John Martin, MLML





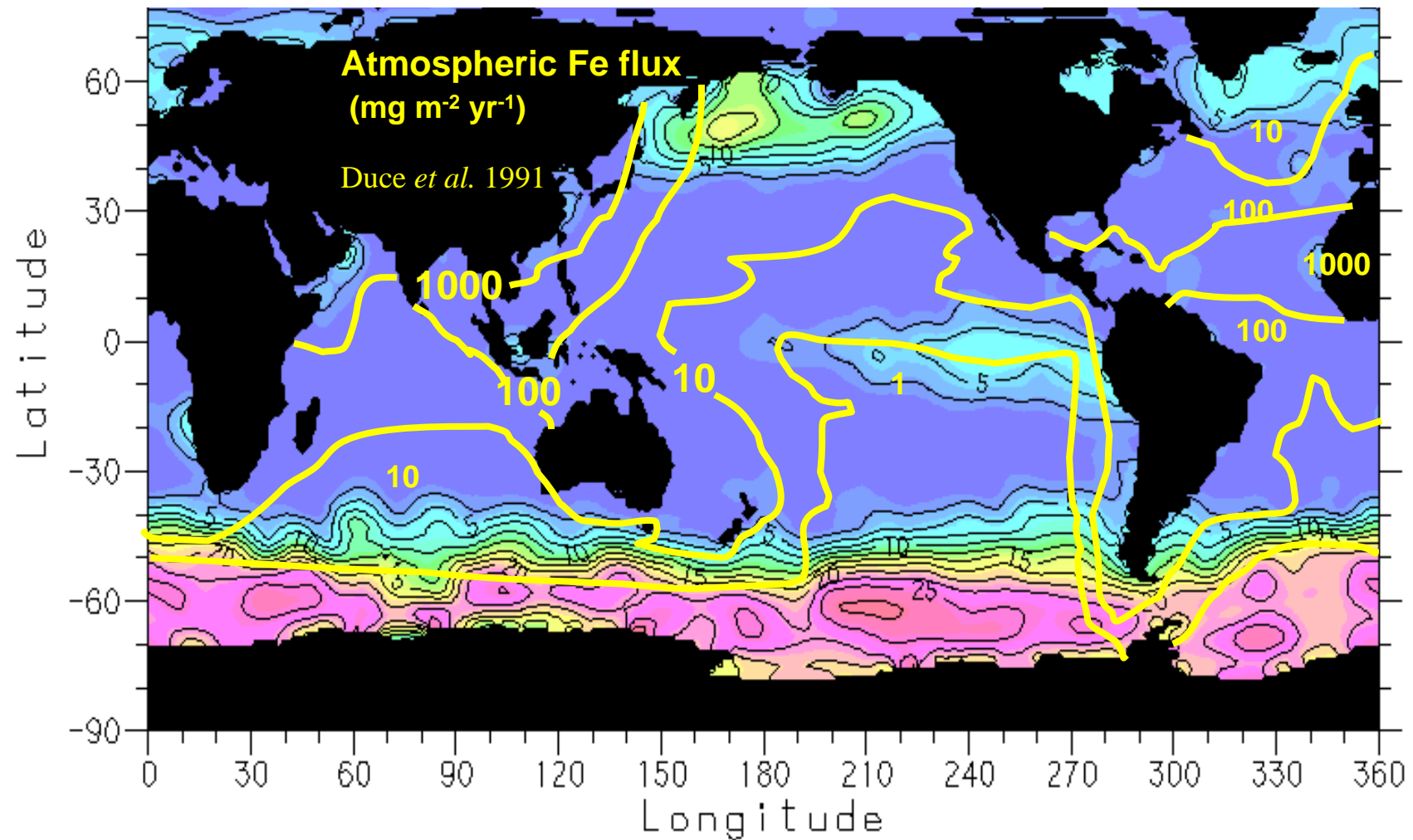
Dust source regions and transport routes

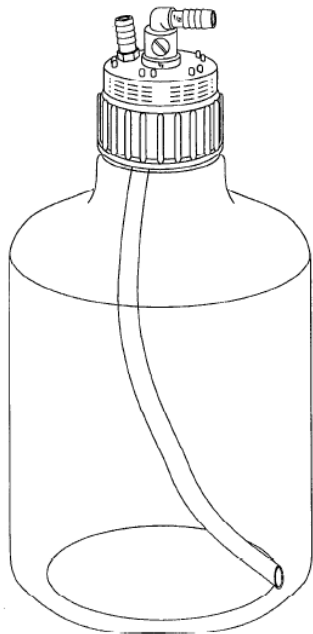
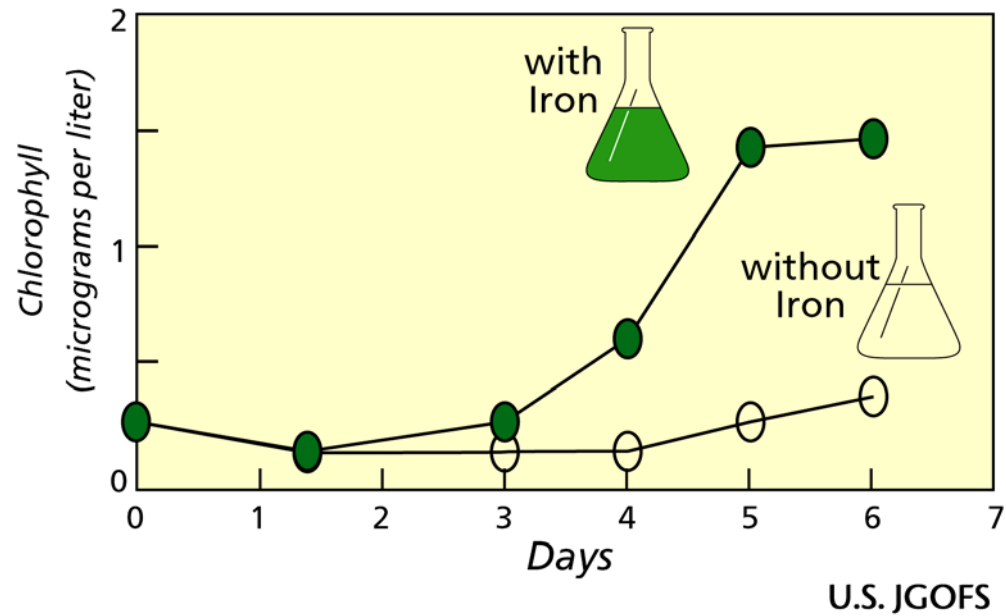


Pye (1987)

Dust flux overlaid on the NO_3 distribution (μM) in the upper ocean

NOAA world ocean atlas, 1994





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

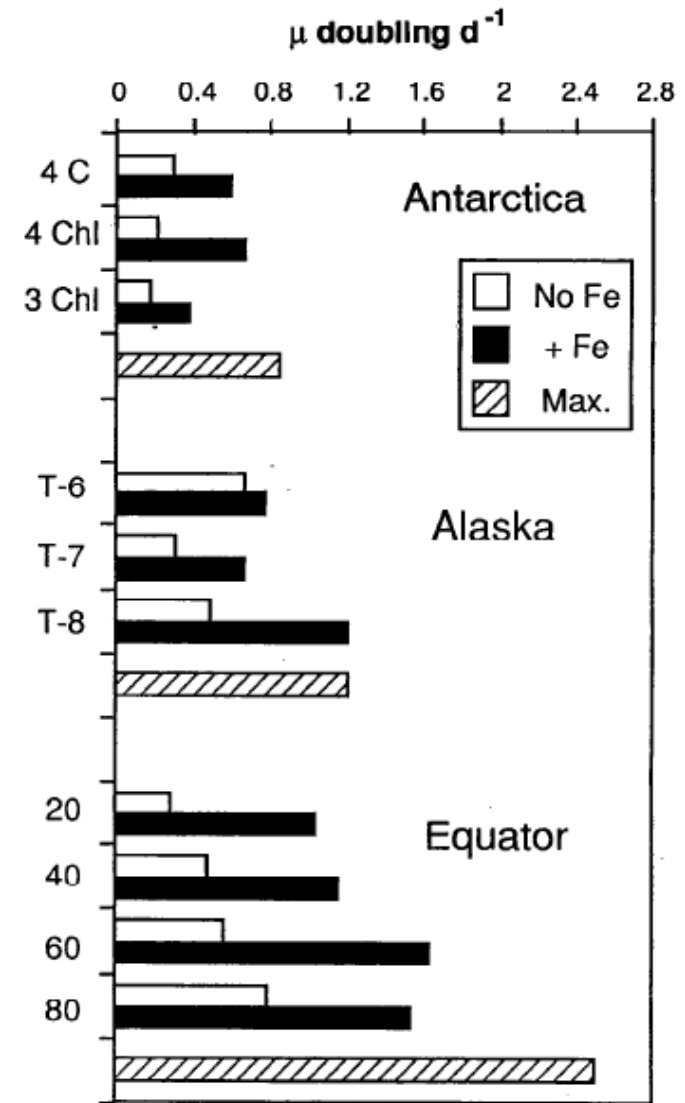
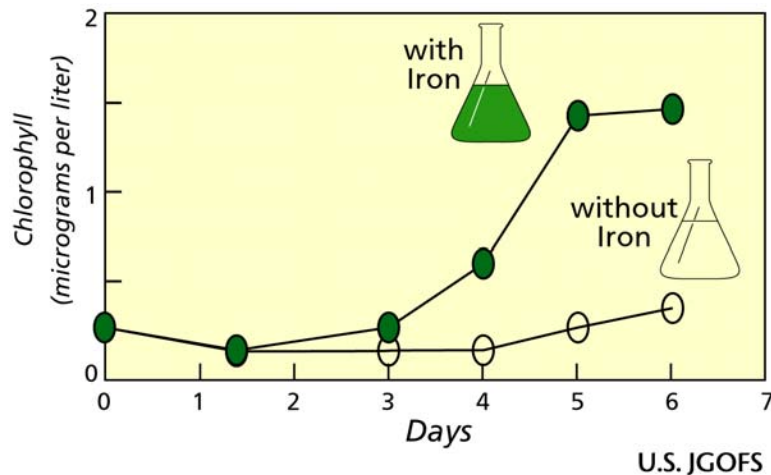


Fig. 7. A comparison of doubling rates from the Antarctic, Gulf of Alaska, and equatorial Pacific with and without added Fe (data from Table 2); theoretical maxima for various temperatures are also shown.

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

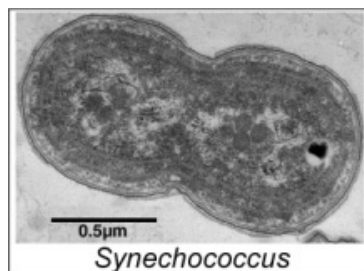
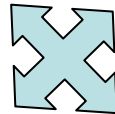
Limnol. Oceanogr., 35(3), 1990, 775–777
 © 1990, by the American Society of Limnology and Oceanography, Inc.

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

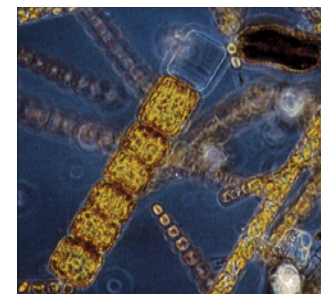
Yes, it does: A reply to the comment by Banse

- 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

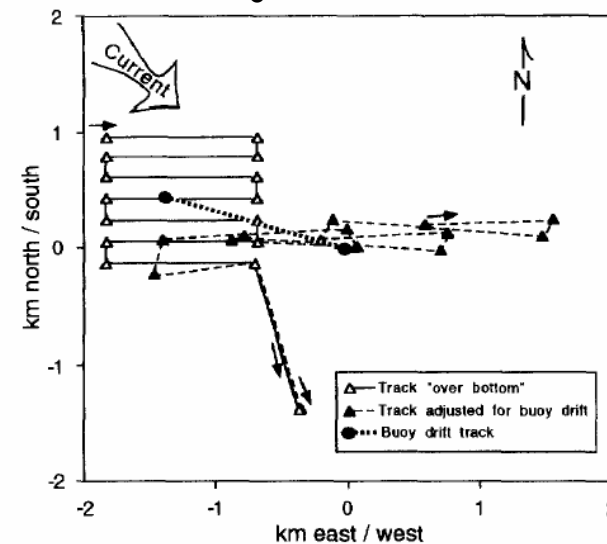
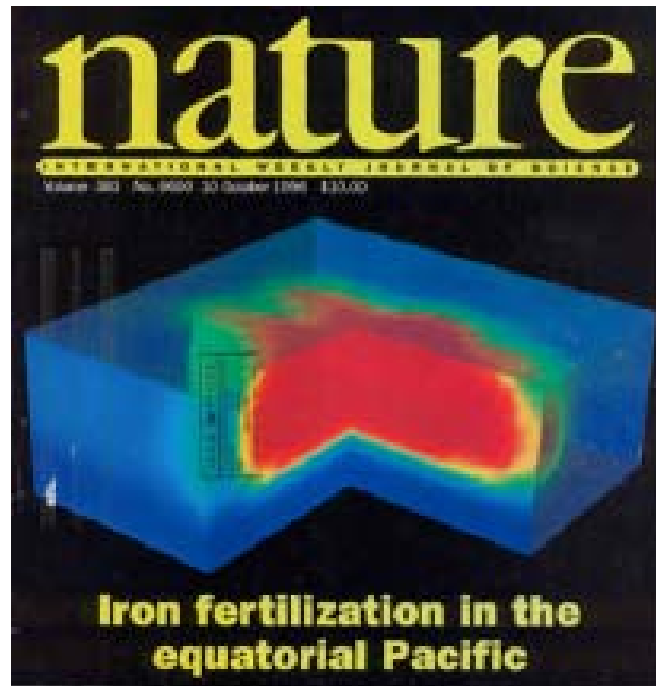


+Fe

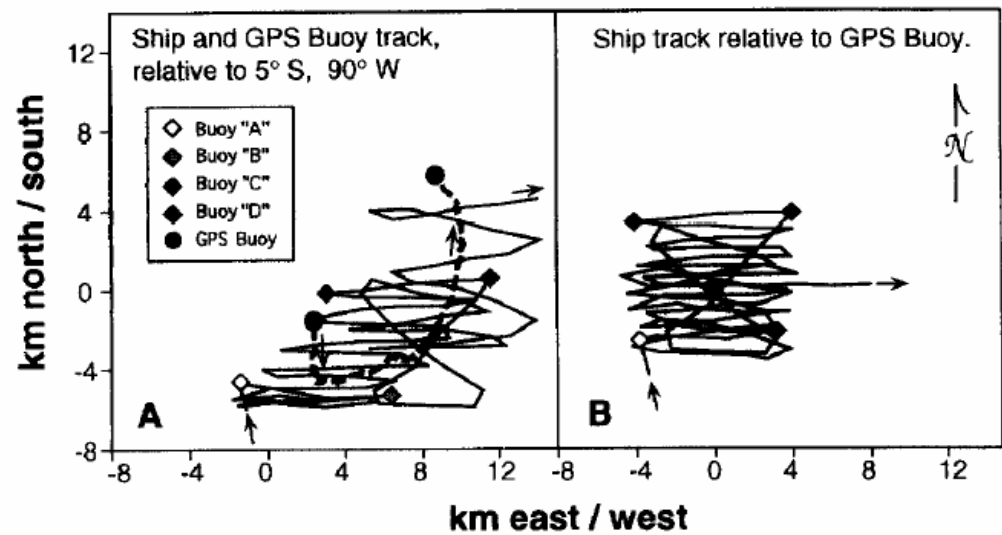


Solution: Mesoscale (100s of km) enrichment experiments to examine community level responses to iron.

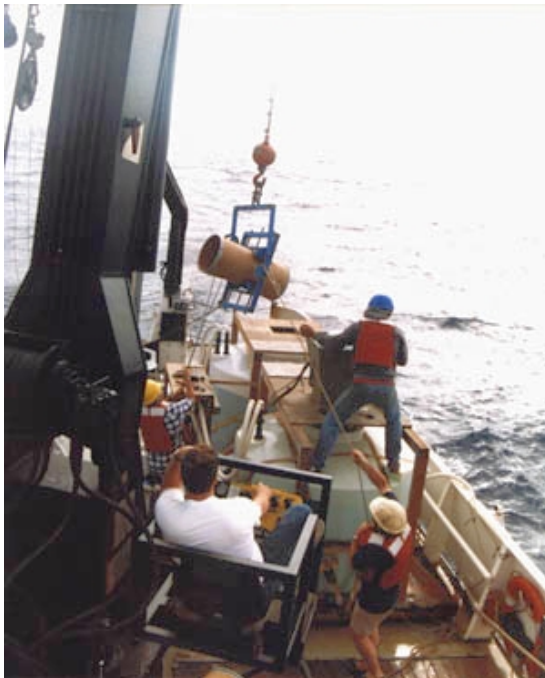
Iron added as acidic iron sulfate. The inert tracer SF_6 is added along with iron.



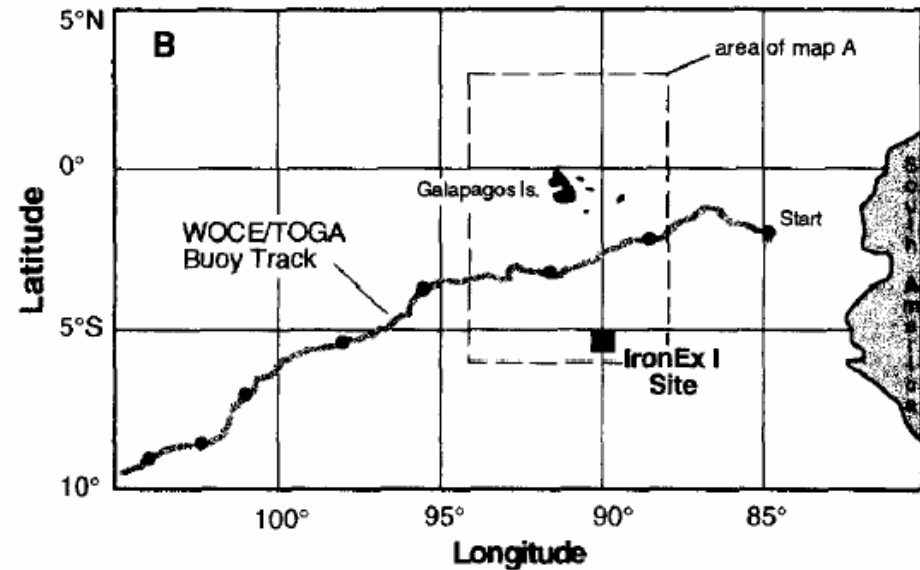
Cartesian coordinate system



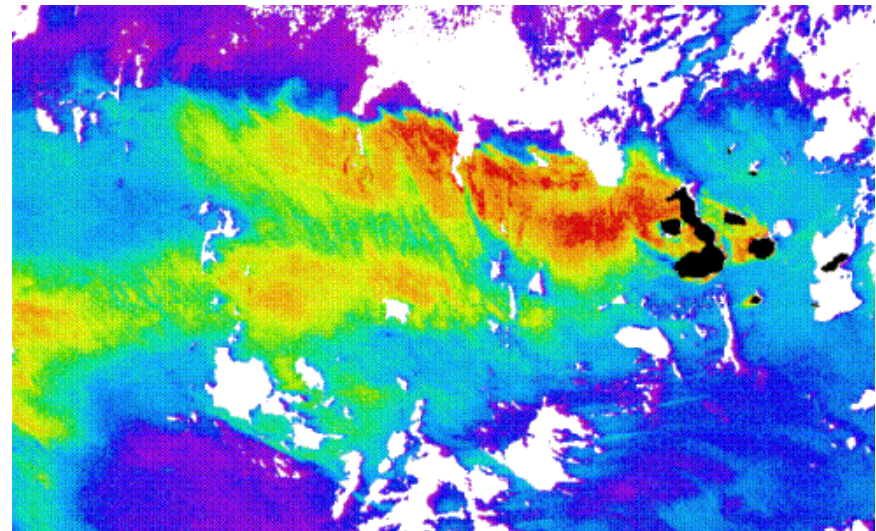
Lagrangian system following drogues

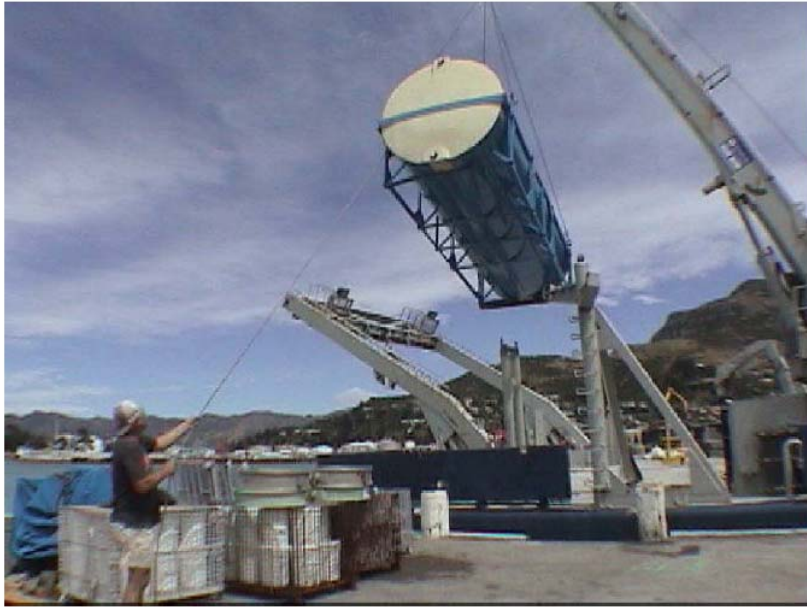


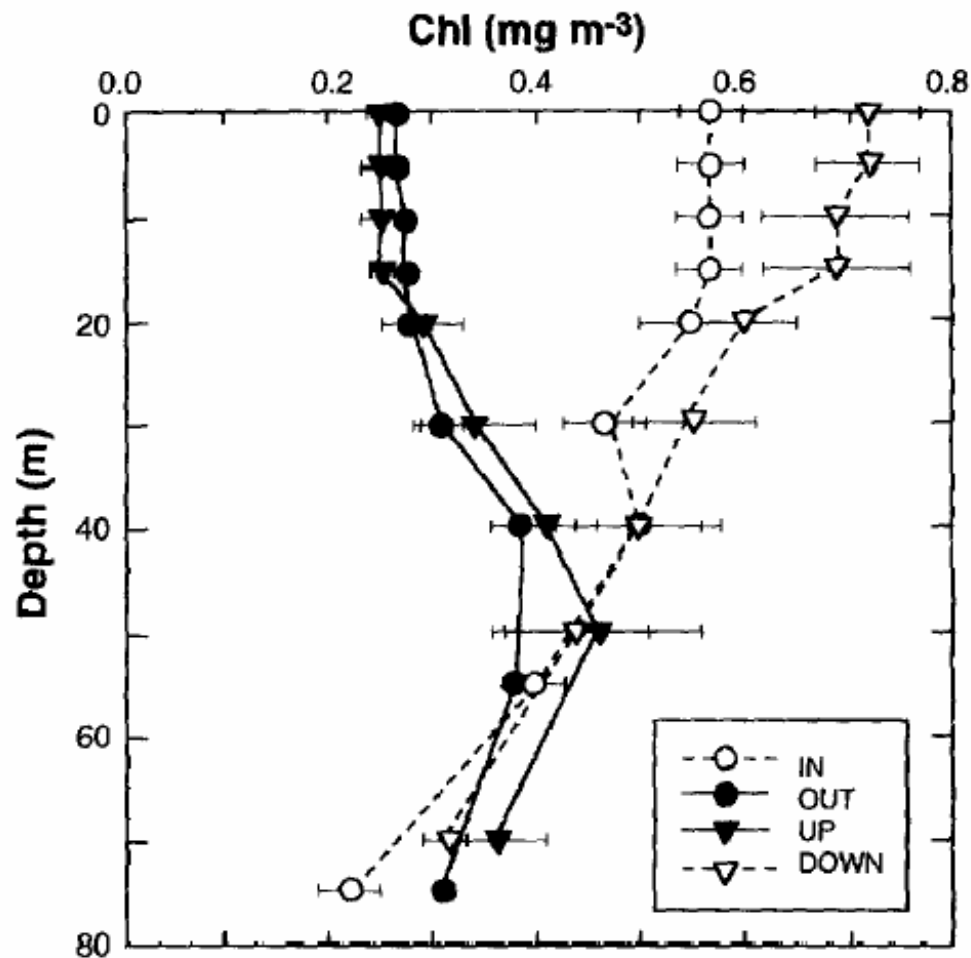
IronEX I: 1993, Equatorial Pacific near Galapagos Islands. 443 kg of Fe into a 64 km² patch. Initial Fe concentrations ~0.1 nM, final target Fe concentration was 4 nM. Added 17,500 L of 0.5 M Fe solution (pH 2.0). A separate batch of 2000 L of SF₆ was mixed into the iron solution.



Coale et al. (1994)





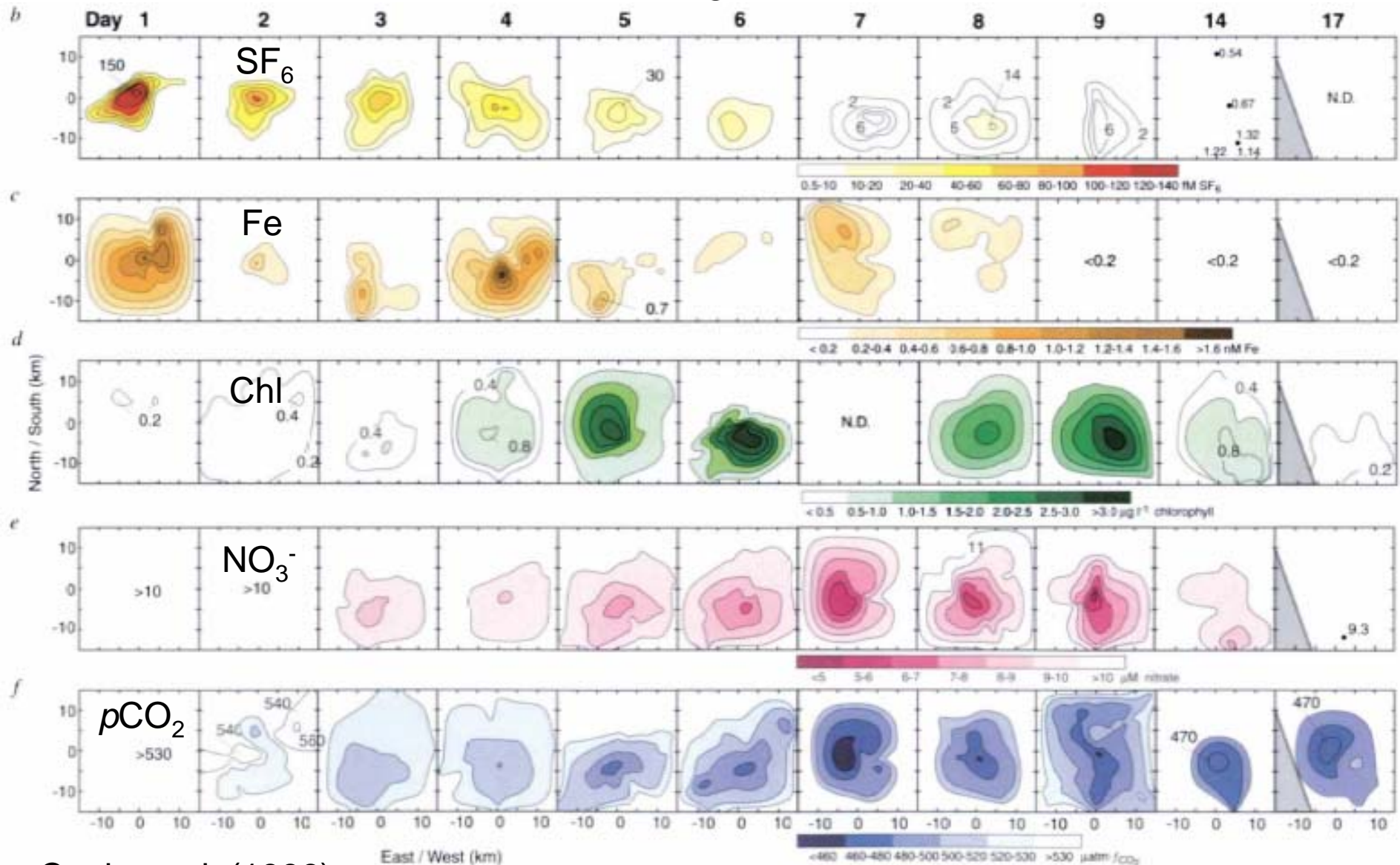


Coale et al. (1998)

Fe concentrations downstream of the Galapagos Islands (in the island plume) were ~ 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.

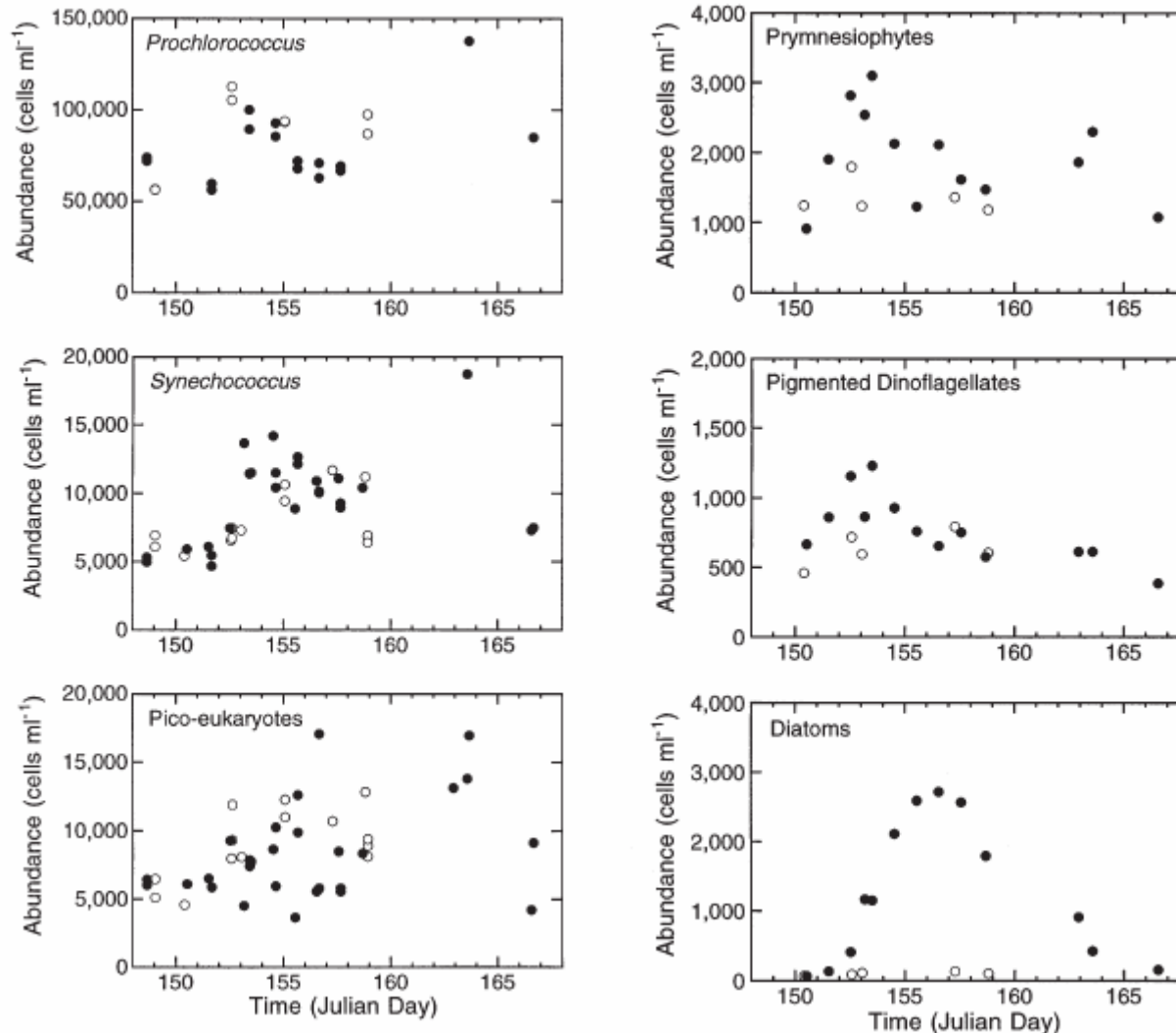
IronEX II



Coale et al. (1996)

June 1995, Equatorial Pacific; 225 kg Fe in 72 km²; Day 1 Fe concentrations ~2 nM. Fe added again on days 3 and 7 (to bring surface water concentrations to ~1 nM)

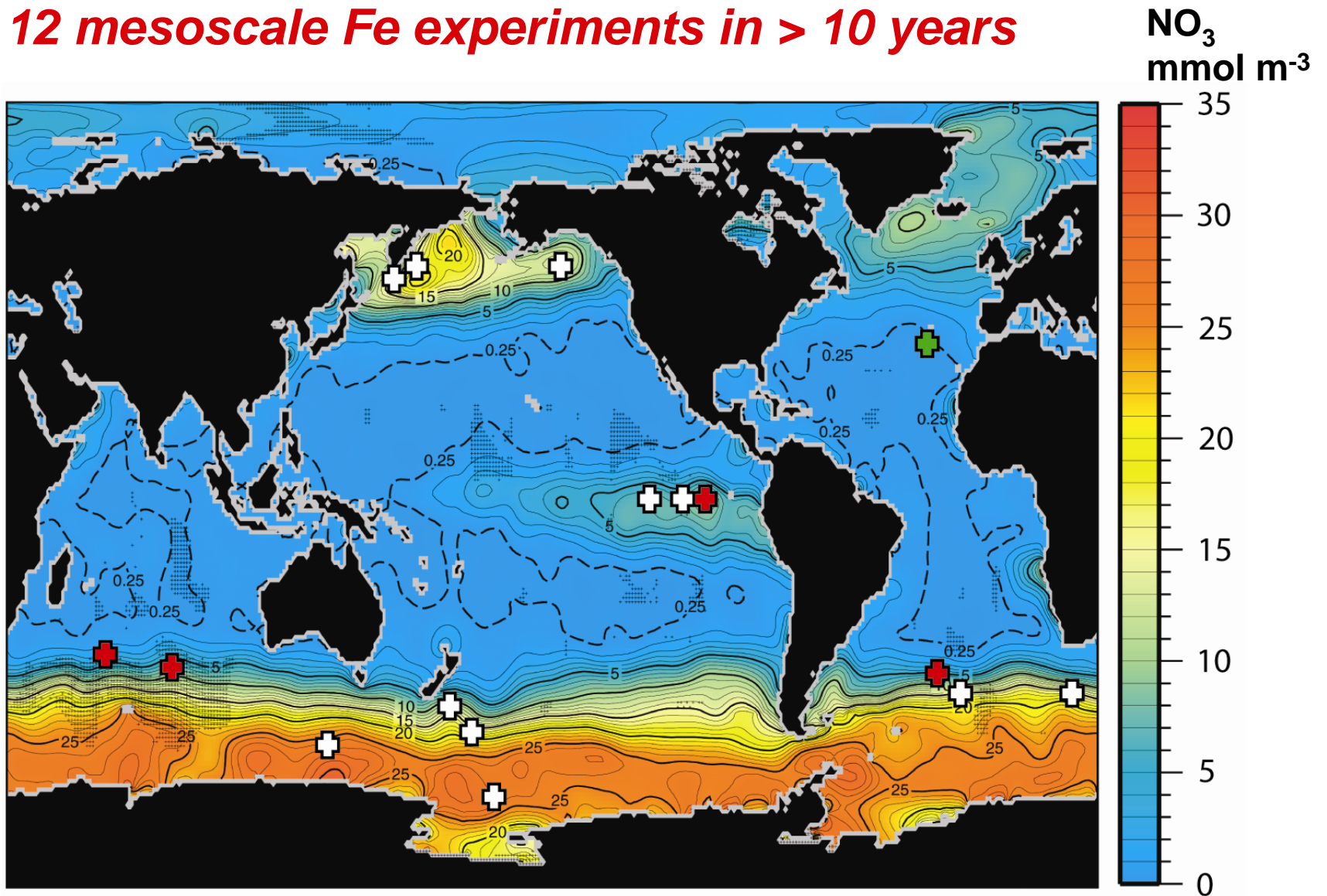
IRONEX II: Equatorial Pacific June 1995; a shift from cyanobacteria to diatoms



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)

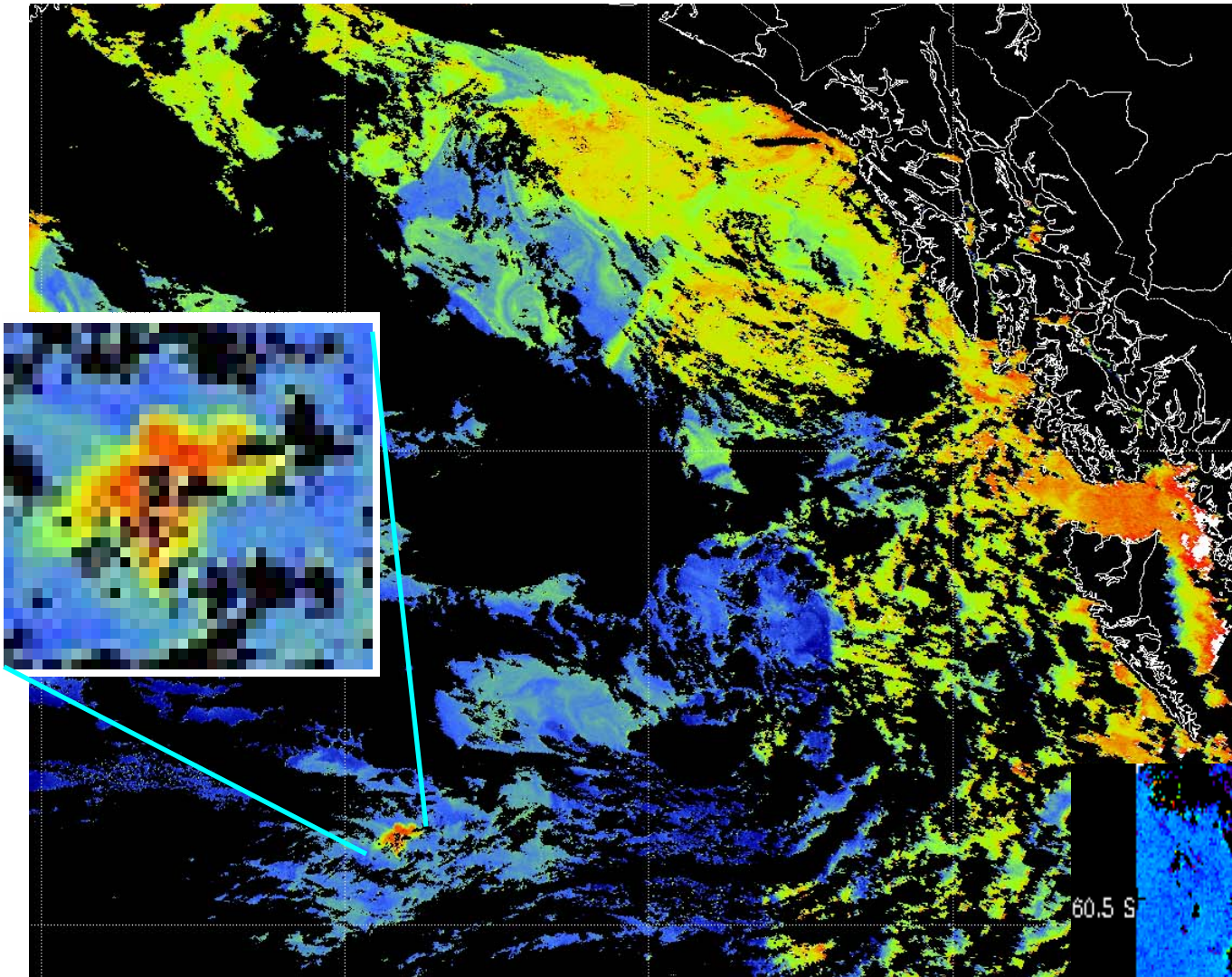
12 mesoscale Fe experiments in > 10 years



⊕ +Fe (HNLC) ⊕ High Fe ⊕ +Fe (LNLC)

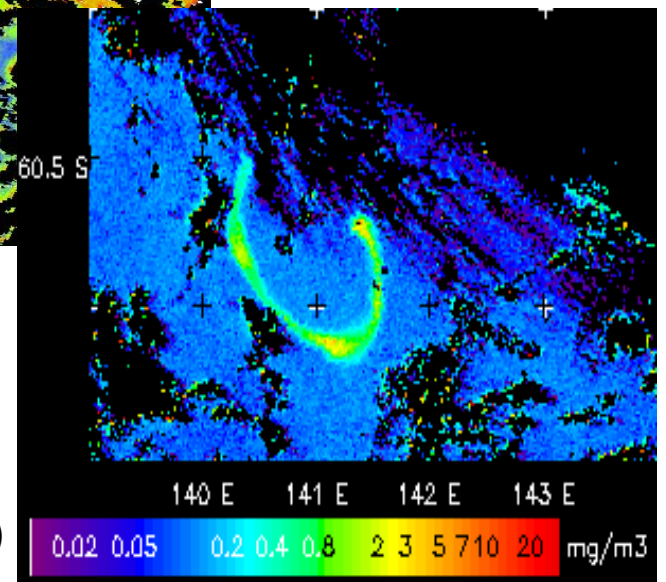
Boyd et al. (2007)

**The
resulting
blooms are
large
enough to
be viewed
from space**



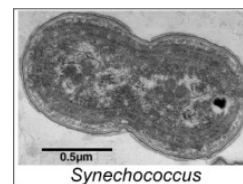
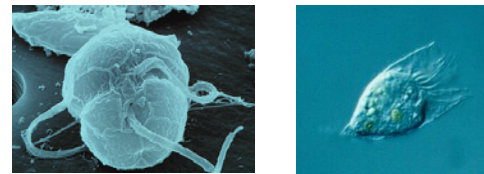
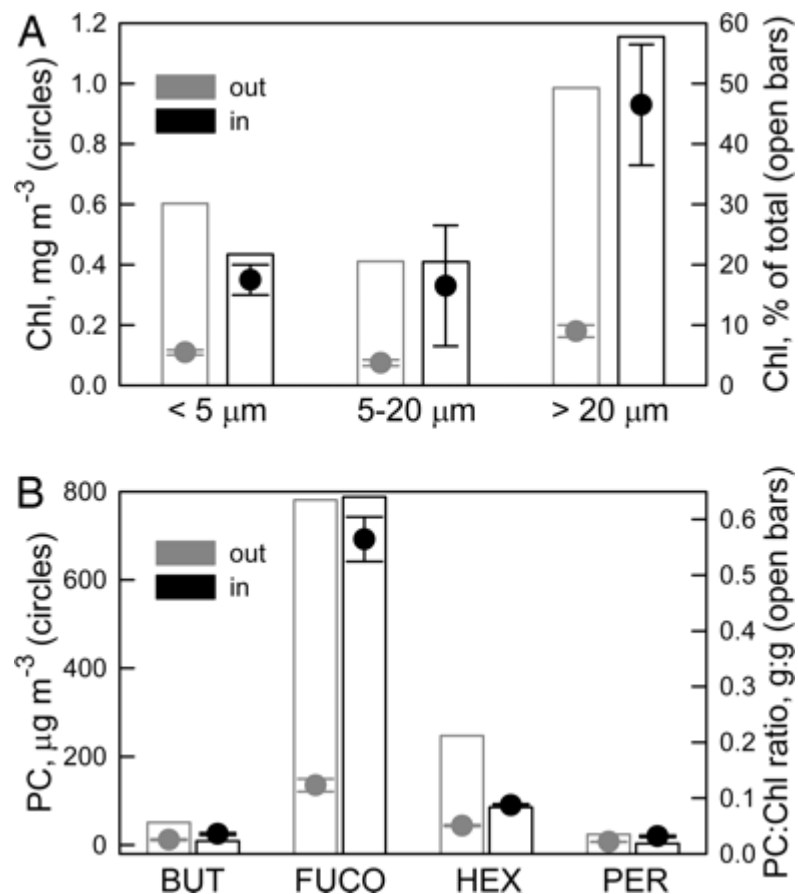
SERIES (Subarctic North Pacific)

SOIREE (Southern Ocean)

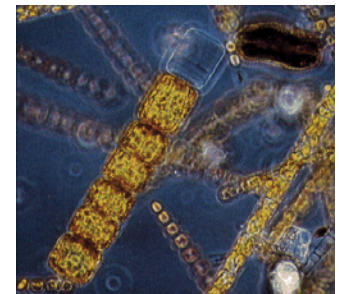


- One of the major findings from these open ocean Fe enrichment experiments was that specific components of the phytoplankton community increased in biomass following the addition of Fe.

SoFeX (Southern Ocean)



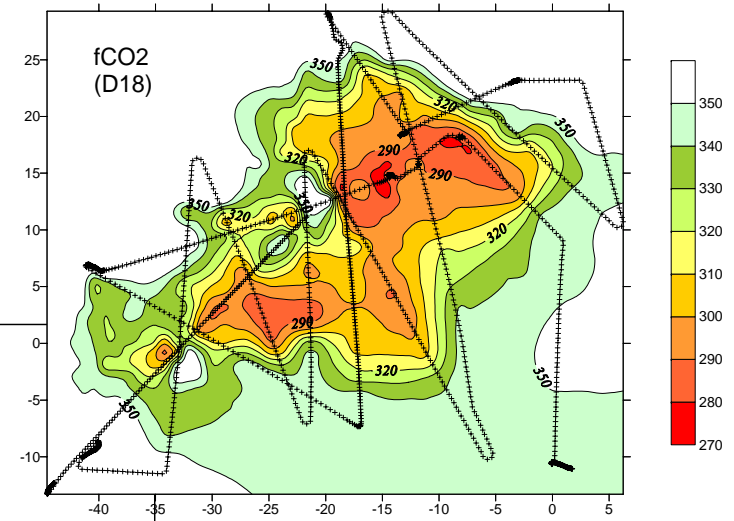
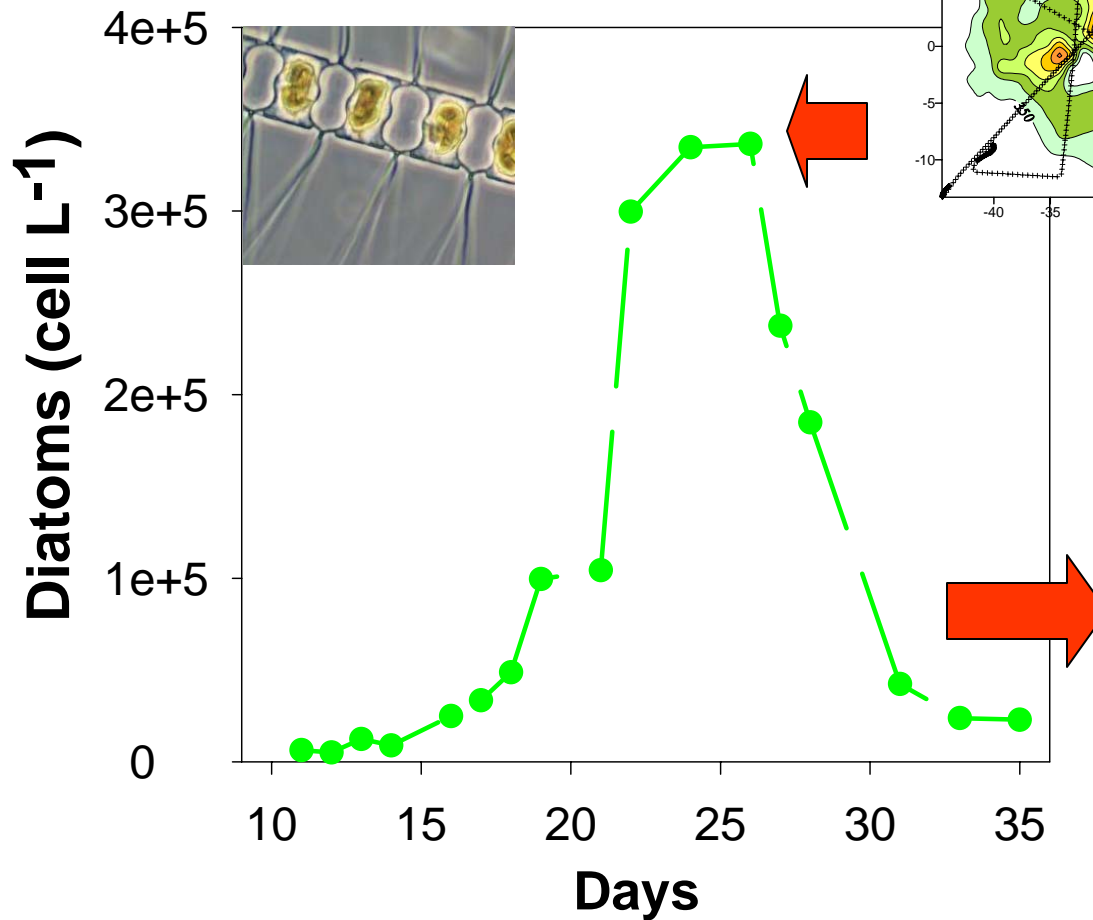
No iron



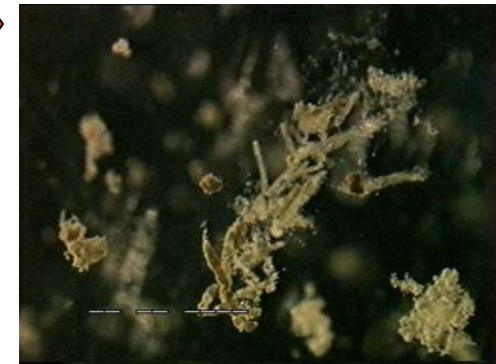
Iron

??

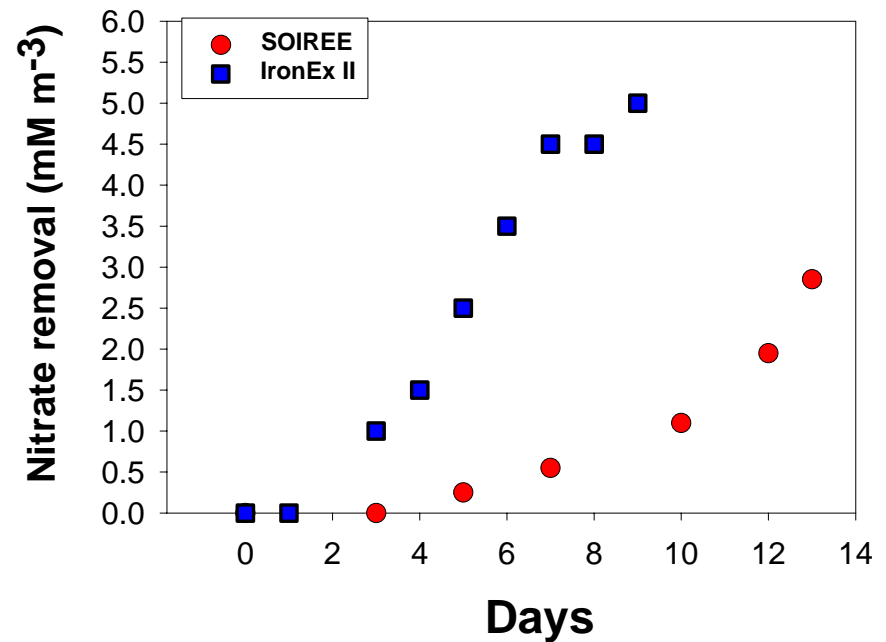
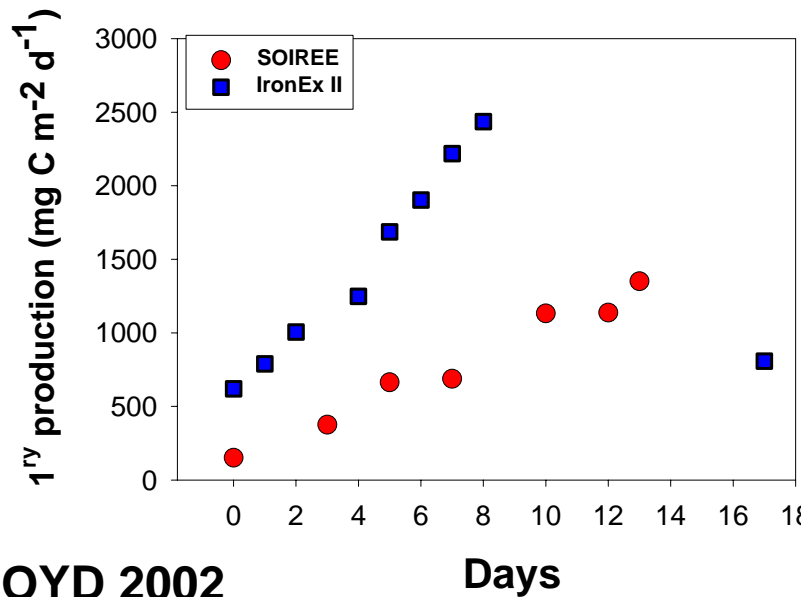
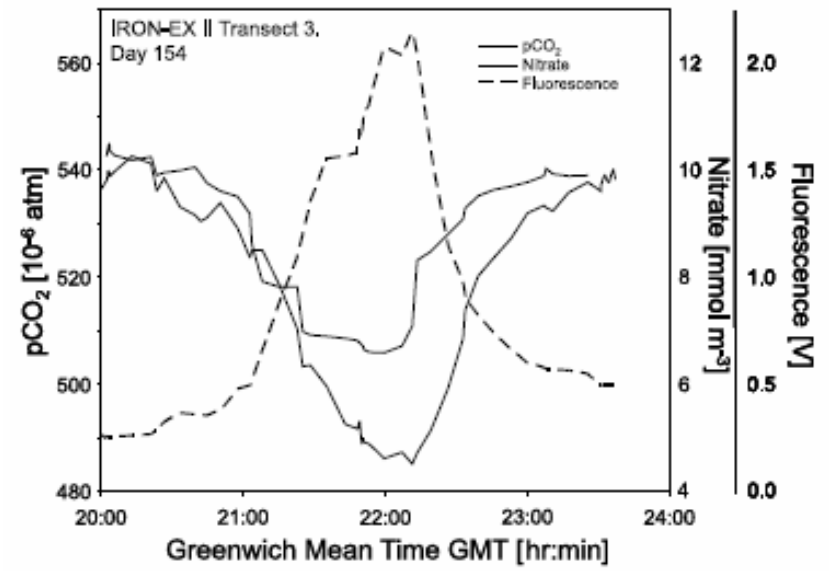
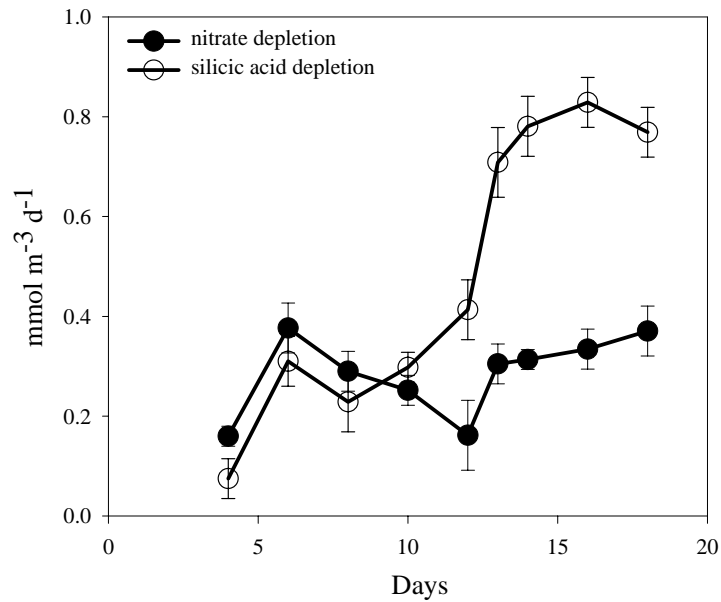
Diatoms grow rapidly, then disappear?



SERIES (N.E. Pacific)

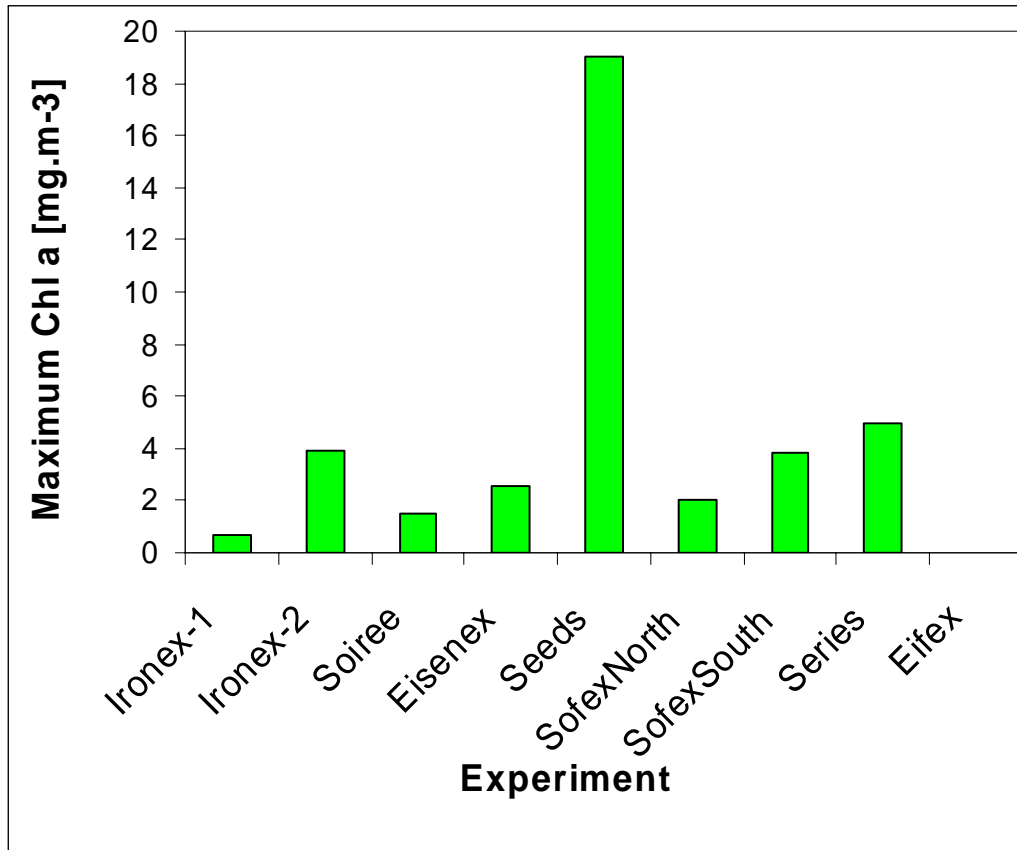


Iron supply impacts many aspects of phytoplankton processes and ocean biogeochemistry

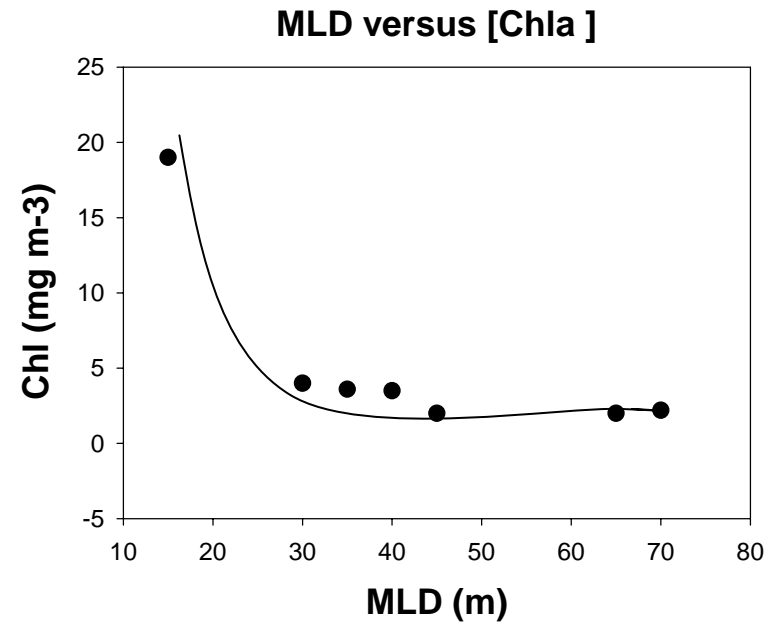


BOYD 2002

A wide range in bloom signatures



De Baar et al. 2005

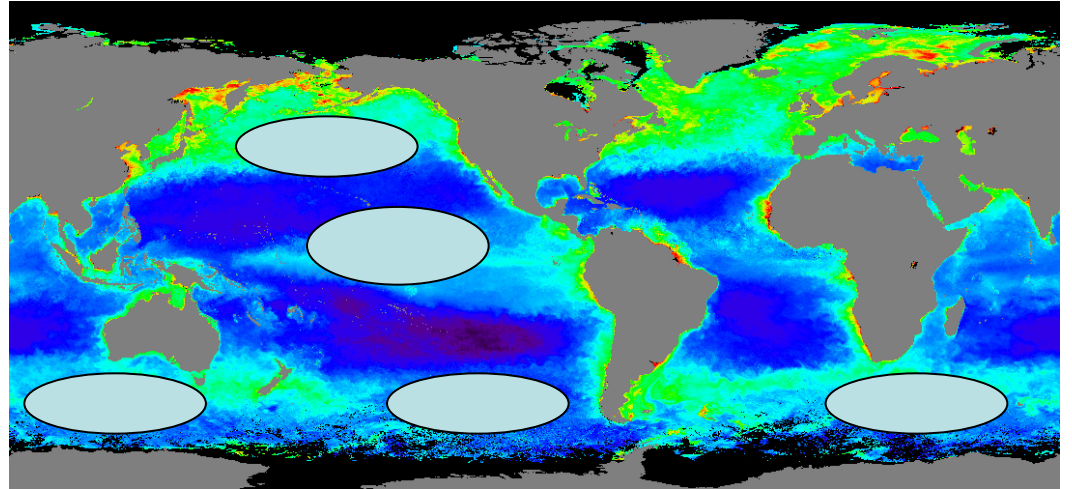


The HNLC condition-lessons learned from large scale manipulation experiments

- 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 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***