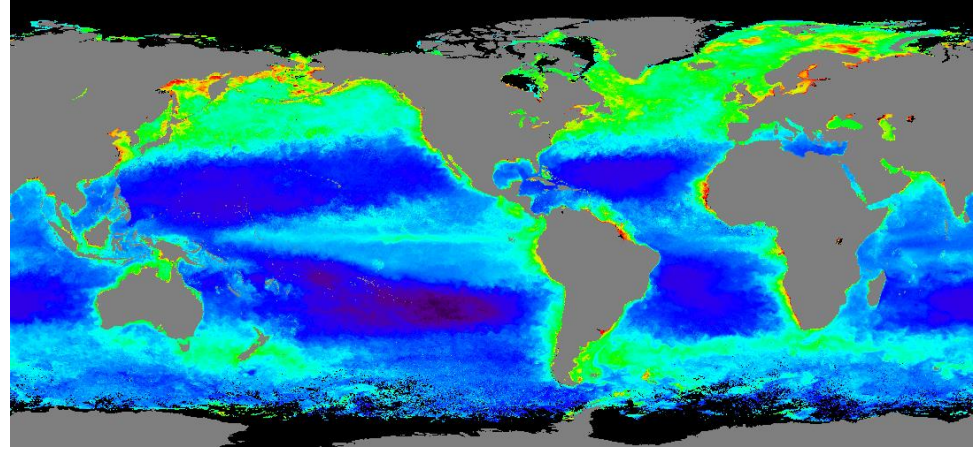
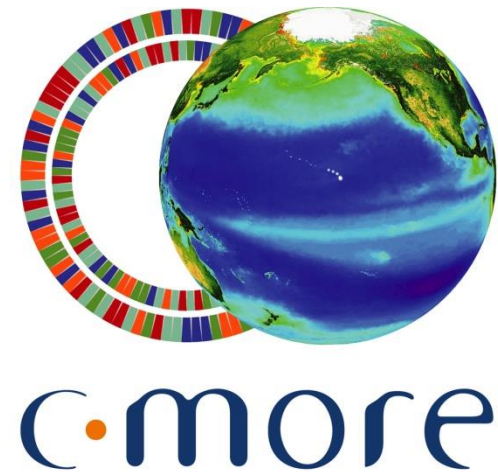


Iron biogeochemistry & the HNLC condition

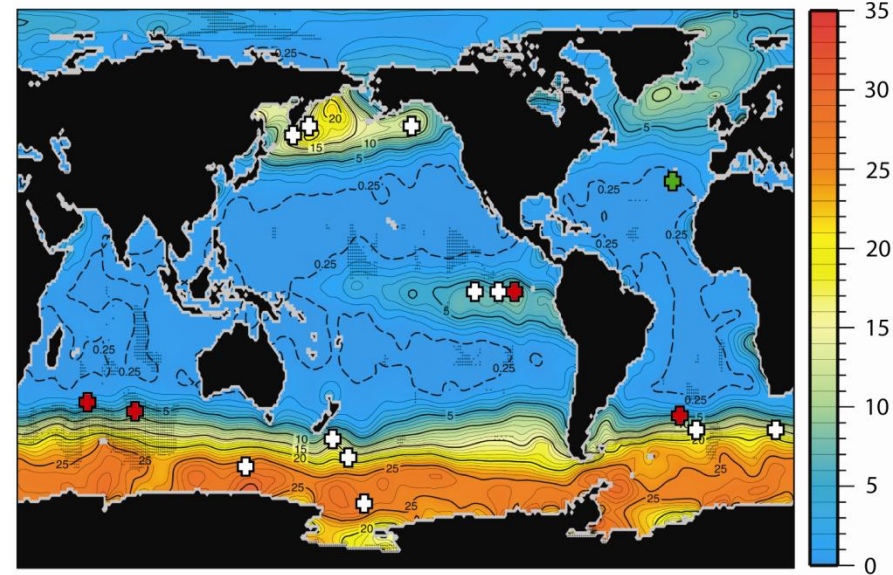


Philip Boyd
Institute for Marine & Antarctic Studies



2014

Outline



HNLC waters – definition and implications

What causes the HNLC condition?

Everyday life in HNLC waters

A closer look at the Southern Ocean

Ready for iron – opportunism by HNLC biota

Iron biogeochemistry

HNLC waters – definition and implications

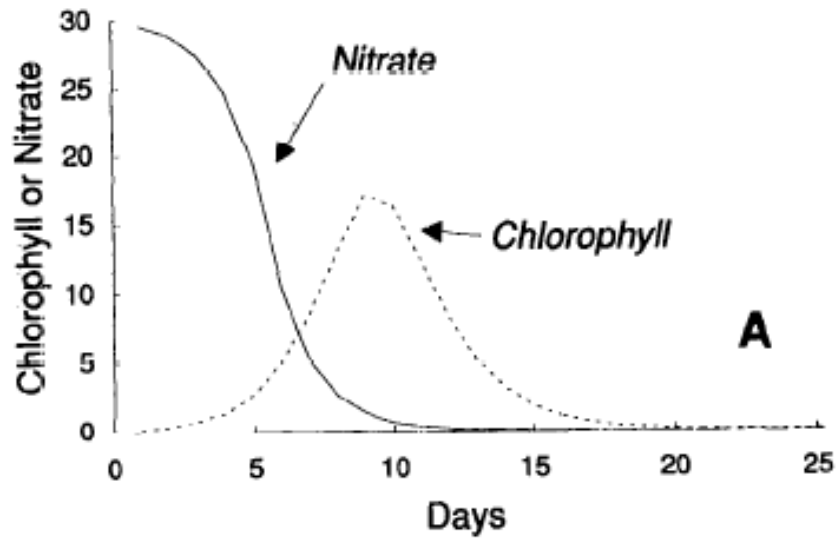
The existence of HNLC waters has long been known...

*Ruud (1930) on a voyage to the whaling grounds
at the ice edge of the Weddell Sea*

**“In contrast to elsewhere, the concentrations of phosphate and nitrate
Proved to be very high....yet throughout the summer the phytoplankton
Was hardly blooming.....”**

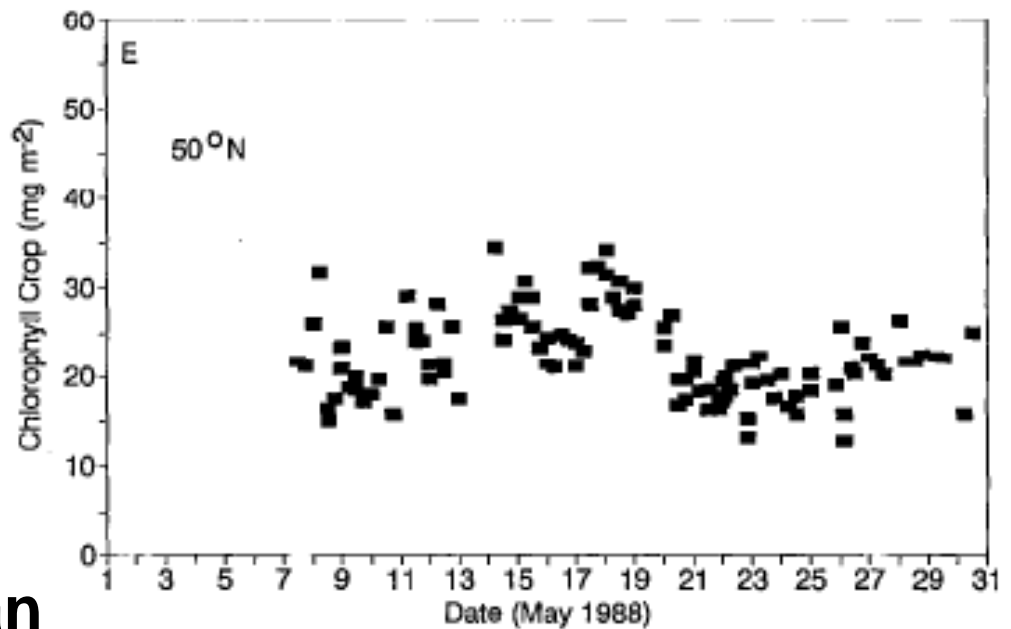
The so-called Antarctic Paradox

Gran (1931) **“Another study seemed to indicate that the growth of diatoms
Is determined by other factors than the concentration of phosphates and nitrates
Besides light and temperature.....”**



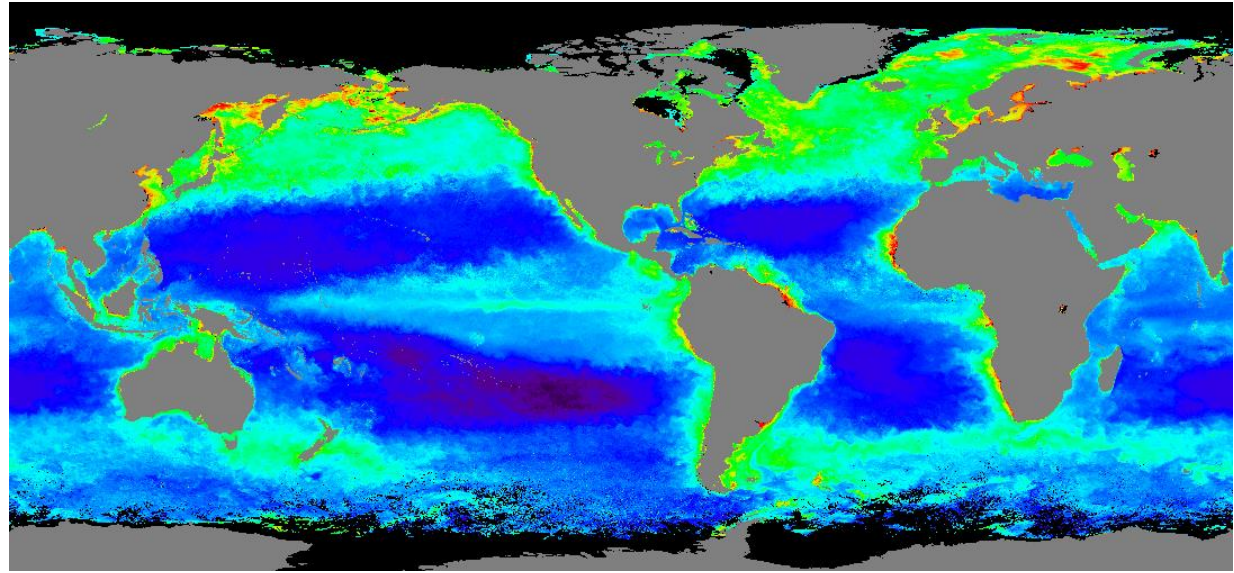
Conventional NO_3 and chlorophyll relationship

SUPER 5 (May 1988)

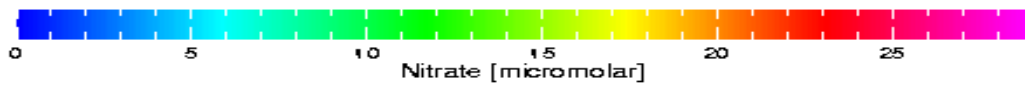
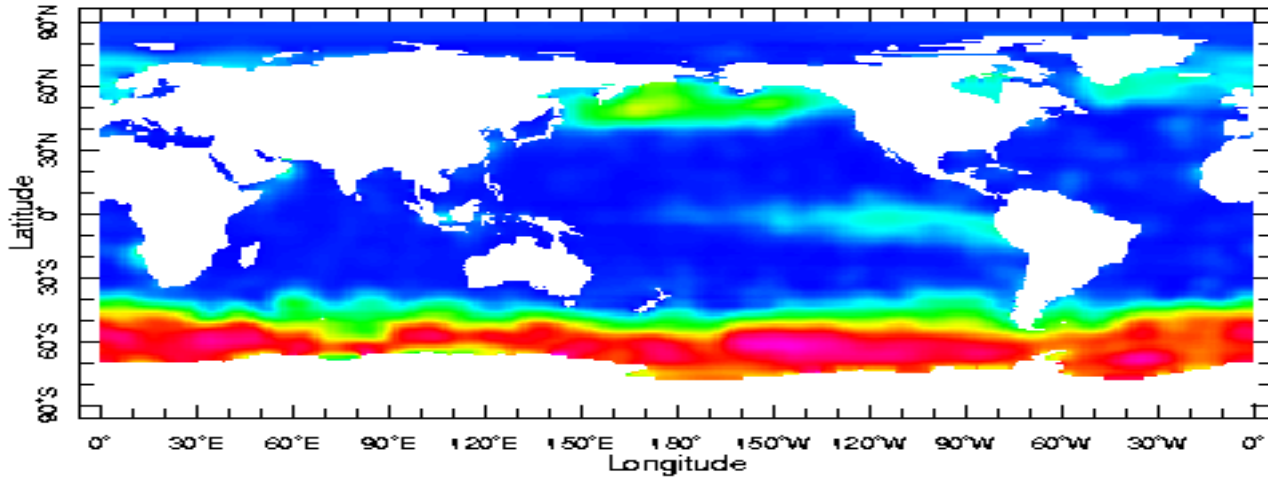


HNLC ocean

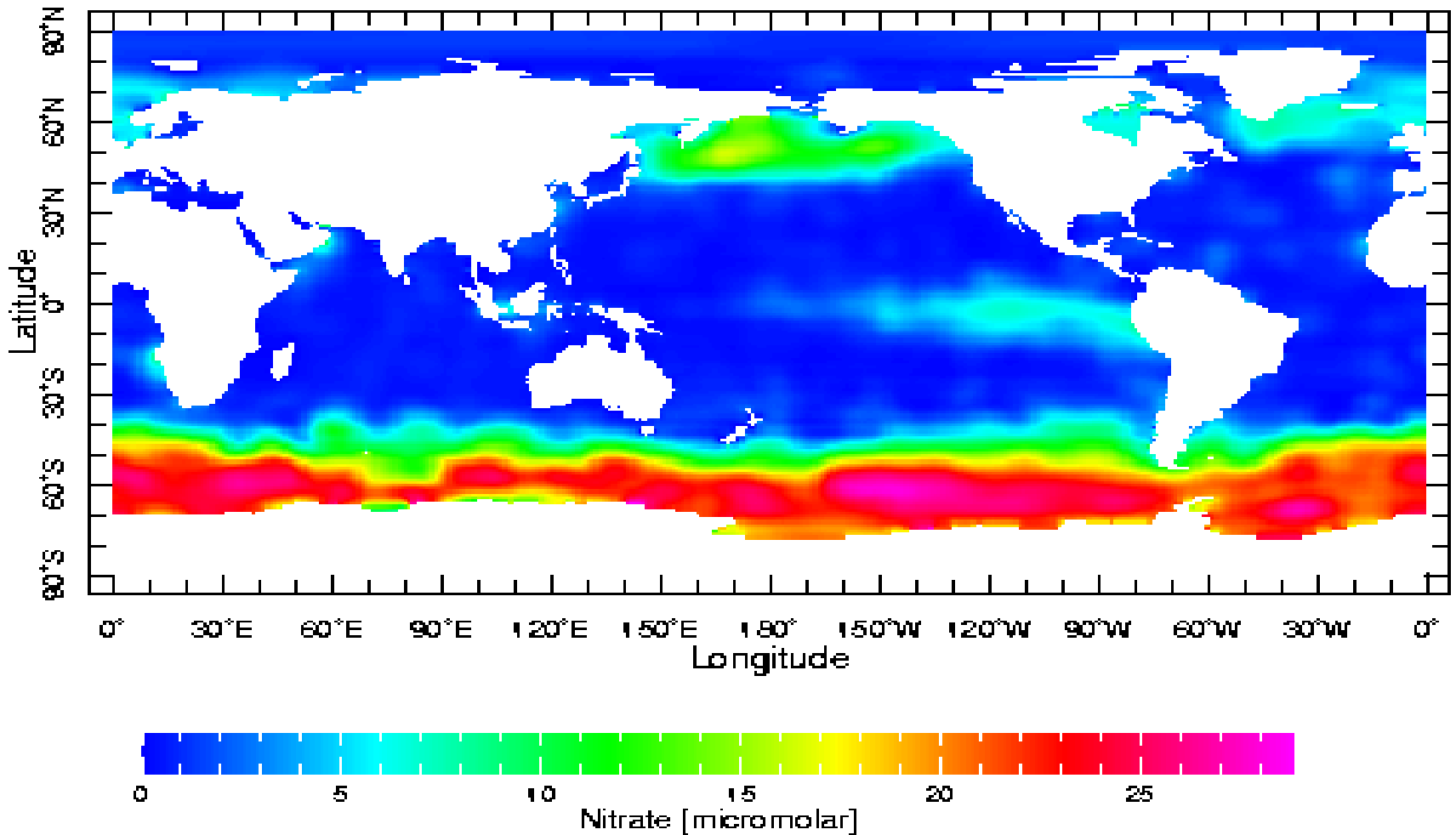
Miller et al. 1993



Courtesy NASA



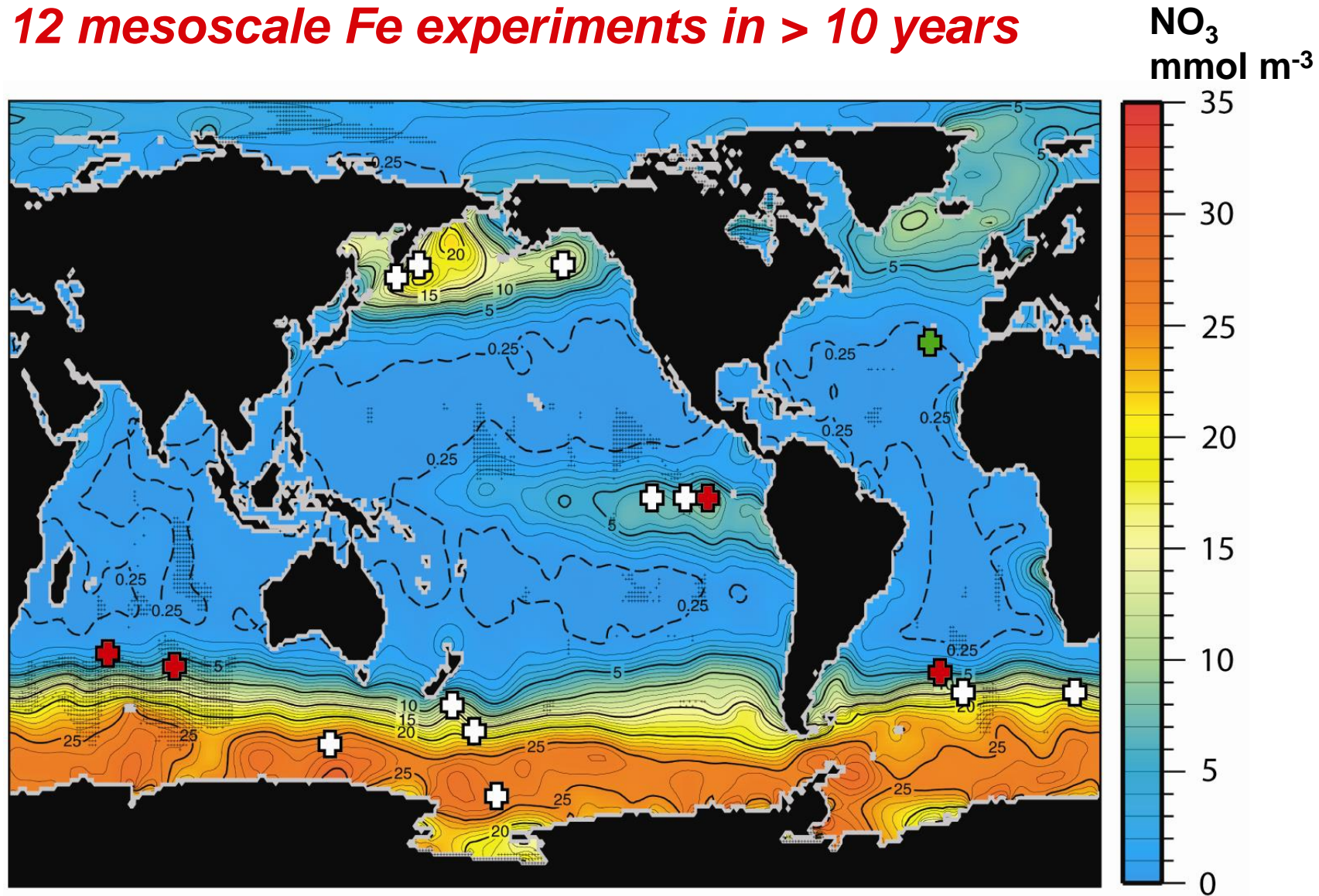
Courtesy NODC



In 1/3 of the ocean, excess plant nutrients are present perennially,
yet paradoxically phytoplankton stocks are at low levels
High Nitrate Low Chlorophyll waters

Courtesy NODC

12 mesoscale Fe experiments in > 10 years

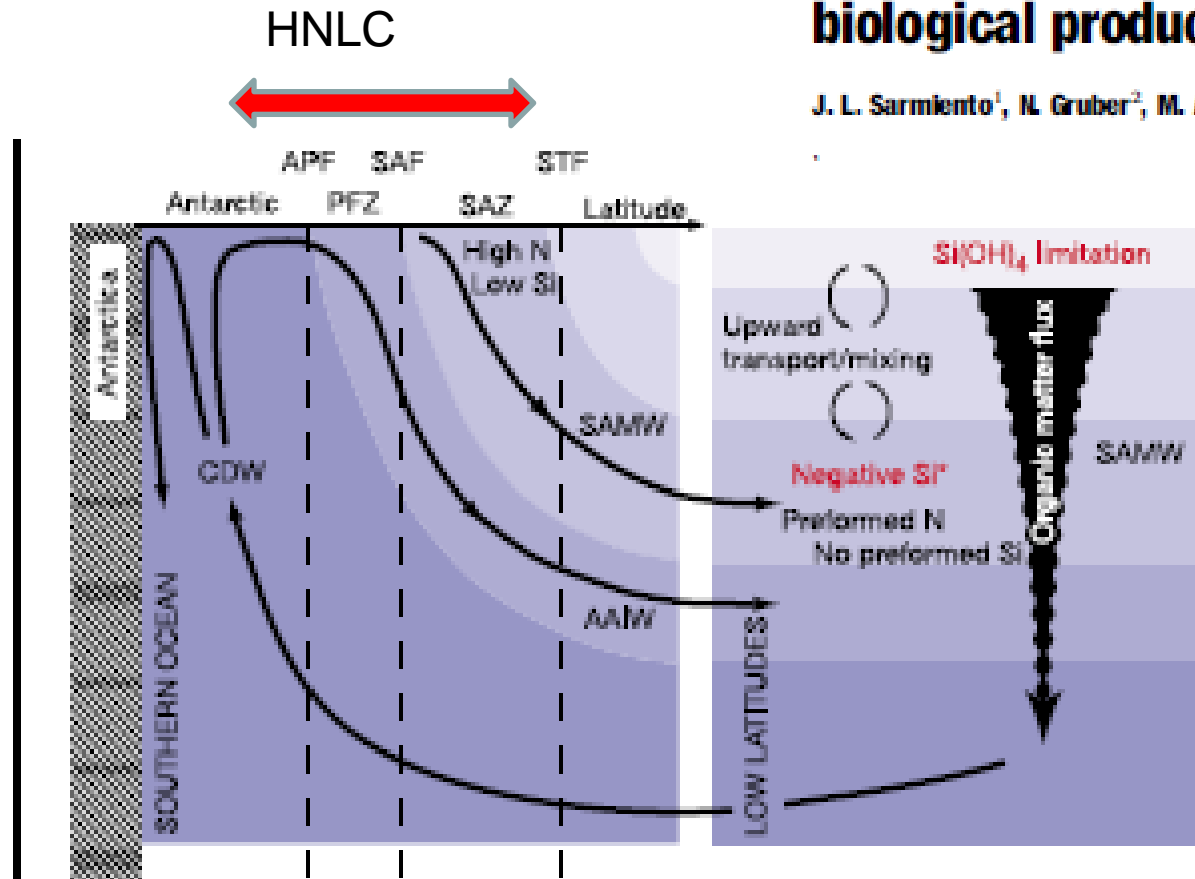


⊕ +Fe (HNLC) ⊕ High Fe ⊕ +Fe (LNLC)

Boyd et al. (2007)

High-latitude controls of thermocline nutrients and low latitude biological productivity

J. L. Sarmiento¹, N. Gruber², M. A. Brzezinski³ & J. P. Dunne⁴



S. Ocean control on thermocline nutrient concentrations

Widespread influence of S. Ocean nutrient supply

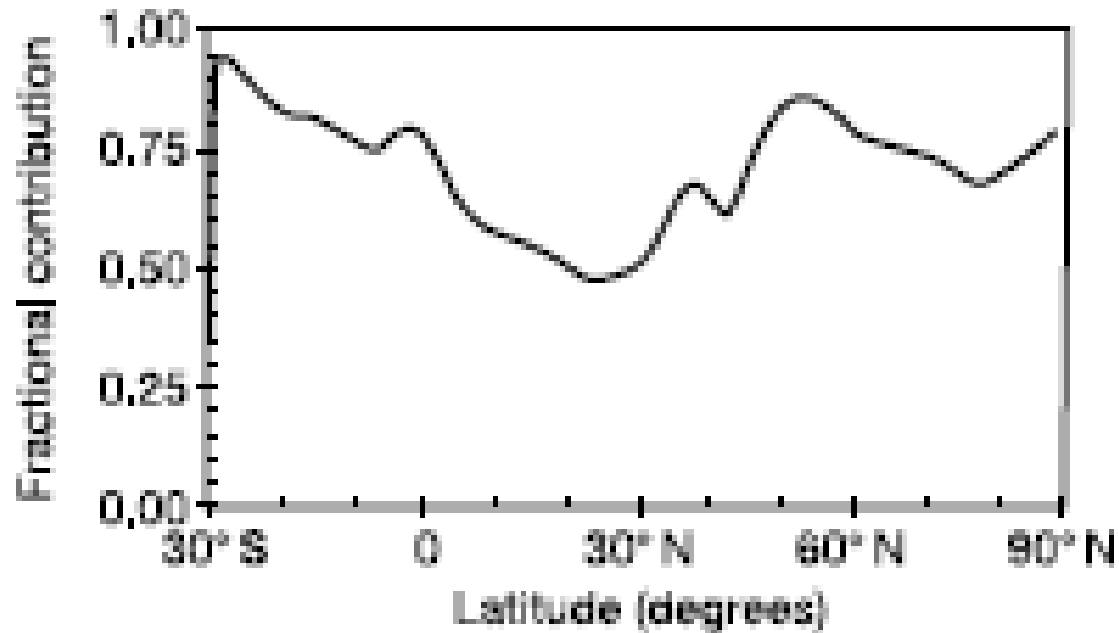
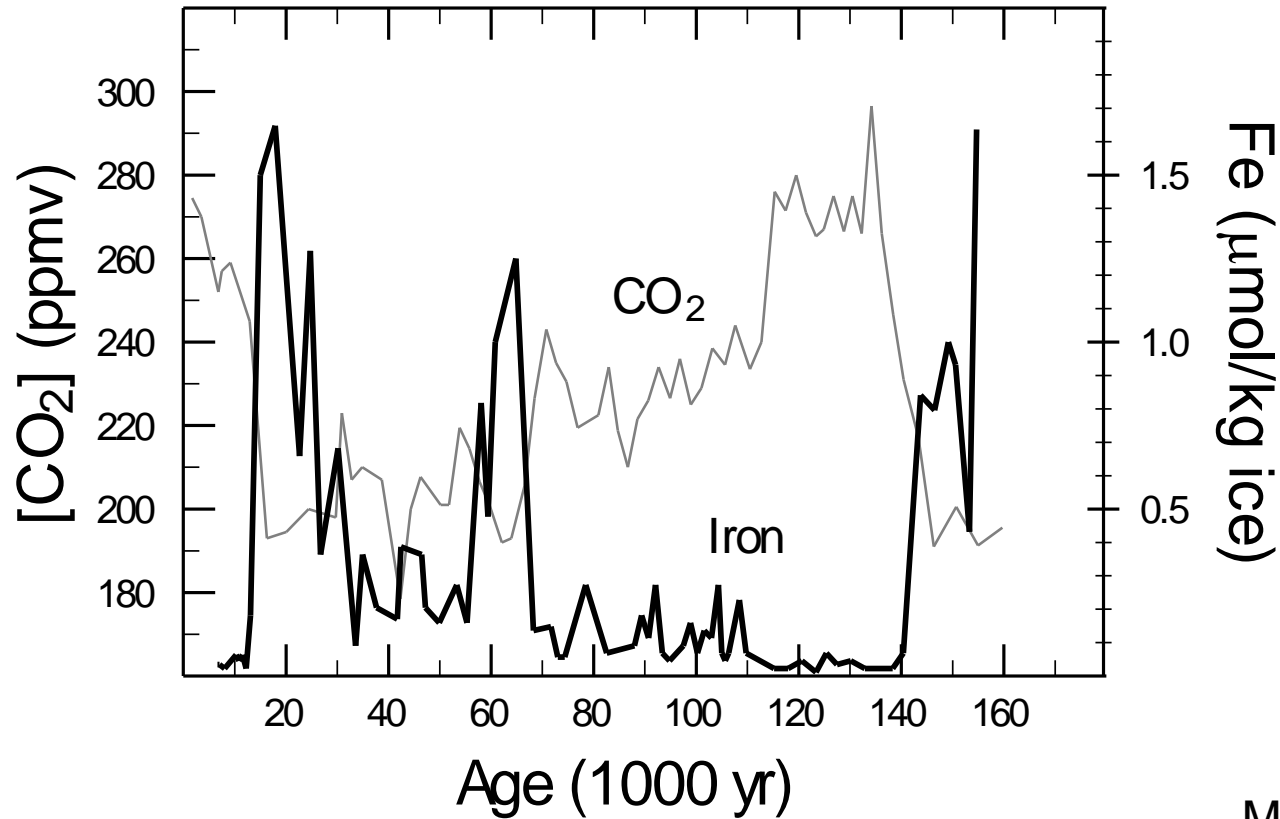


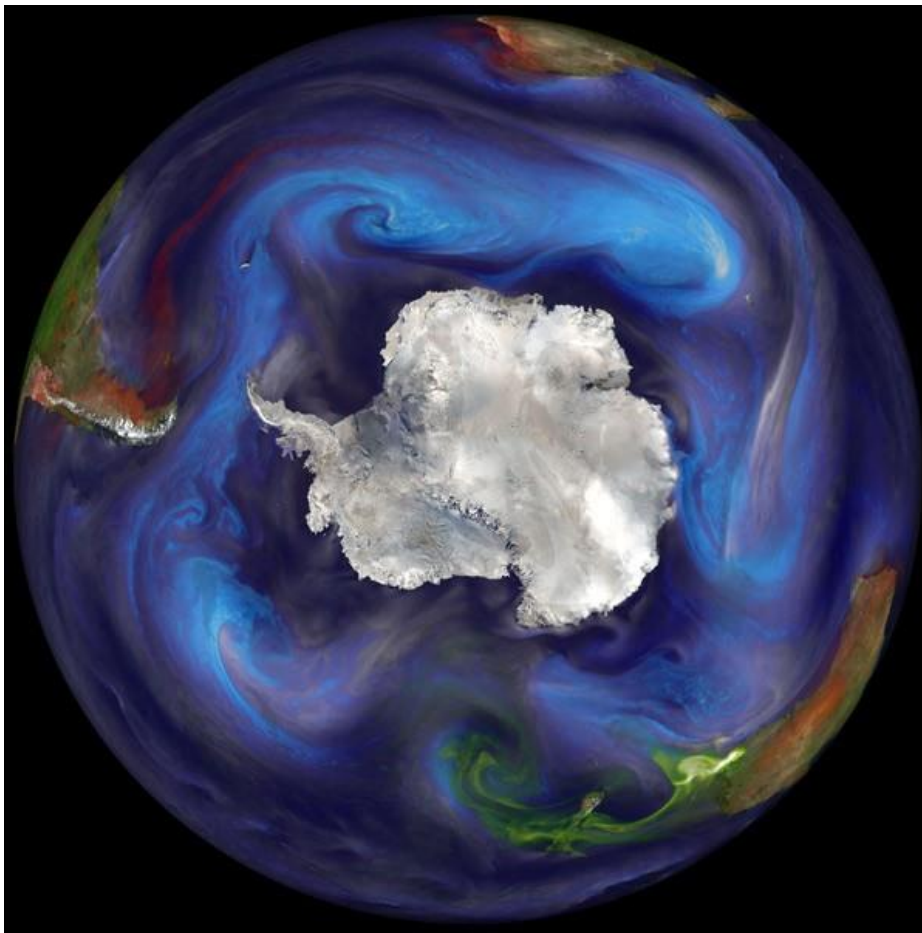
Figure 3 Predicted global zonal mean of the fractional contribution of Southern Ocean nutrient supply to global export production. Data obtained from an ocean biogeochemistry

HNLC waters in the geological past



Martin 1990

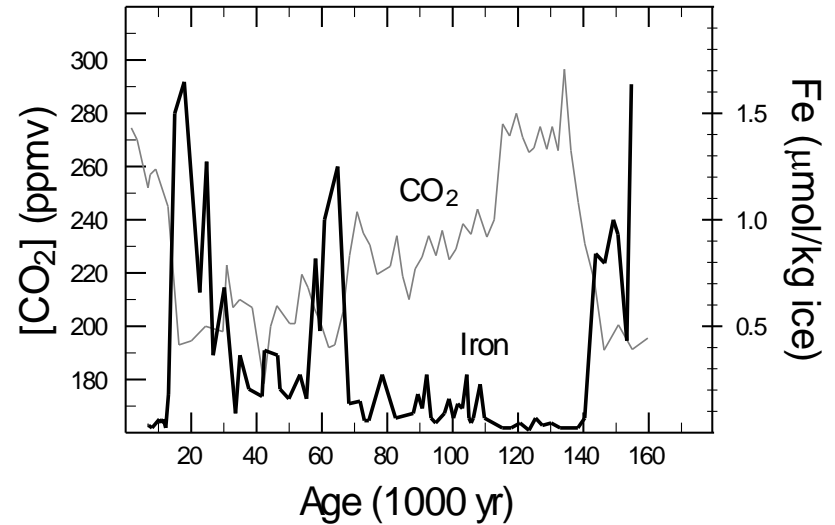
This record has been taken further into the past (4 million years) during recent ODP studies in the Atlantic sector of the Subantarctic S. Ocean (Martínez-García et al. 2011, Nature)



Courtesy Science

Dust supply to the Southern Ocean increases during ice ages, and 'iron fertilization' of the subantarctic zone may have contributed up to 40 ppmv of the decrease (80–100 ppmv) in atmospheric carbon dioxide

A more complex picture of the Ice ages is emerging from cores



Antarctic Zone - reduced POC export

Subantarctic Zone – increased POC export coincident with rising dust fluxes

In the subantarctic, glacial times are characterized by increases in:

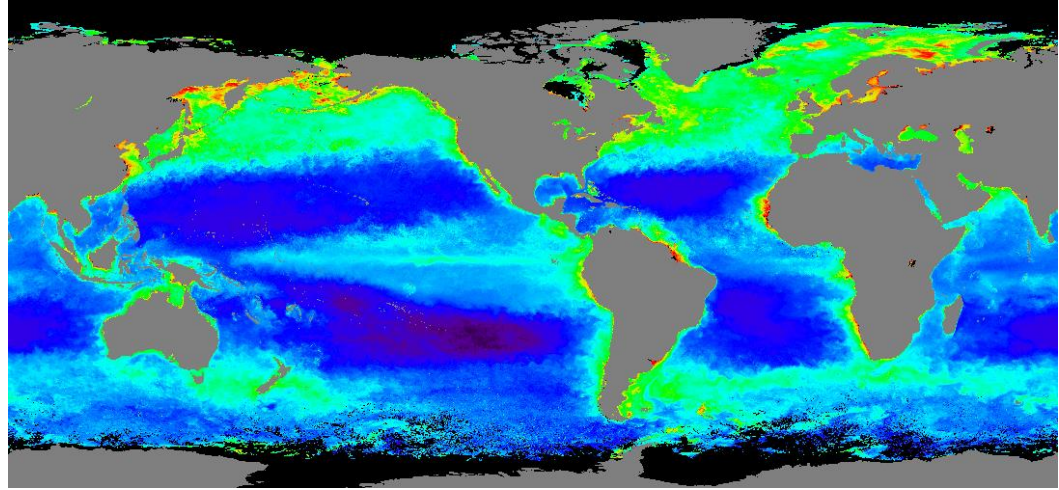
dust flux

productivity

the degree of nitrate consumption

The consequent strengthening of the biological pump can explain the lowering of CO₂ at the transition from mid-climate states to full ice age conditions

What causes
the HNLC condition?



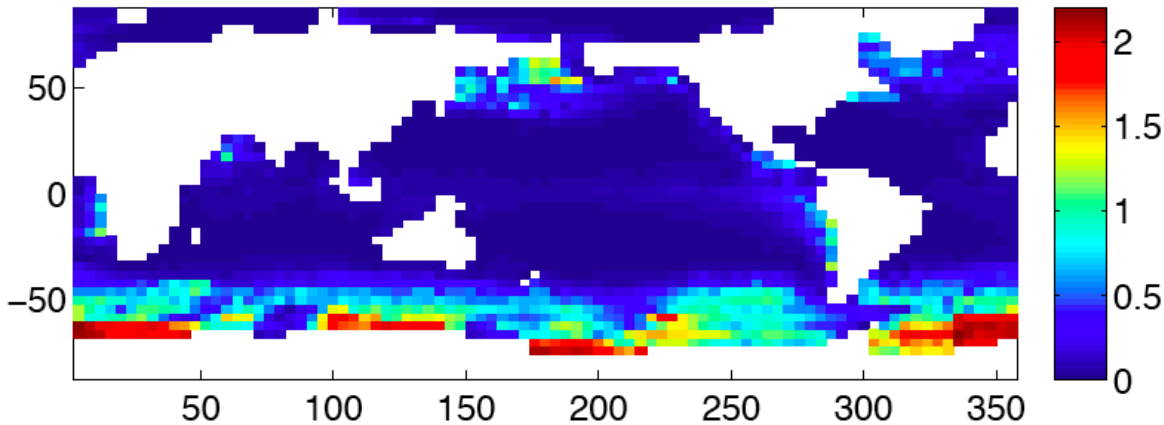
Strength of ocean circulation (Curtis's lecture on Wednesday)

Geographical isolation – from sources of aerosol iron

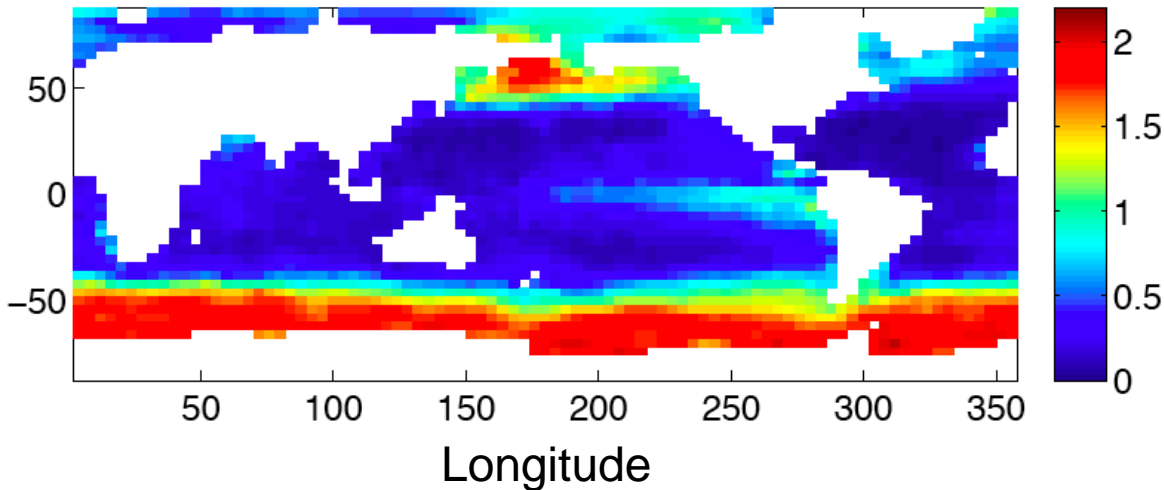
Mismatch between the depth of the ferricline and
nutricline/thermocline

Circulation-PO₄ model

Surface PO₄: Model



Surface PO₄: Climatology

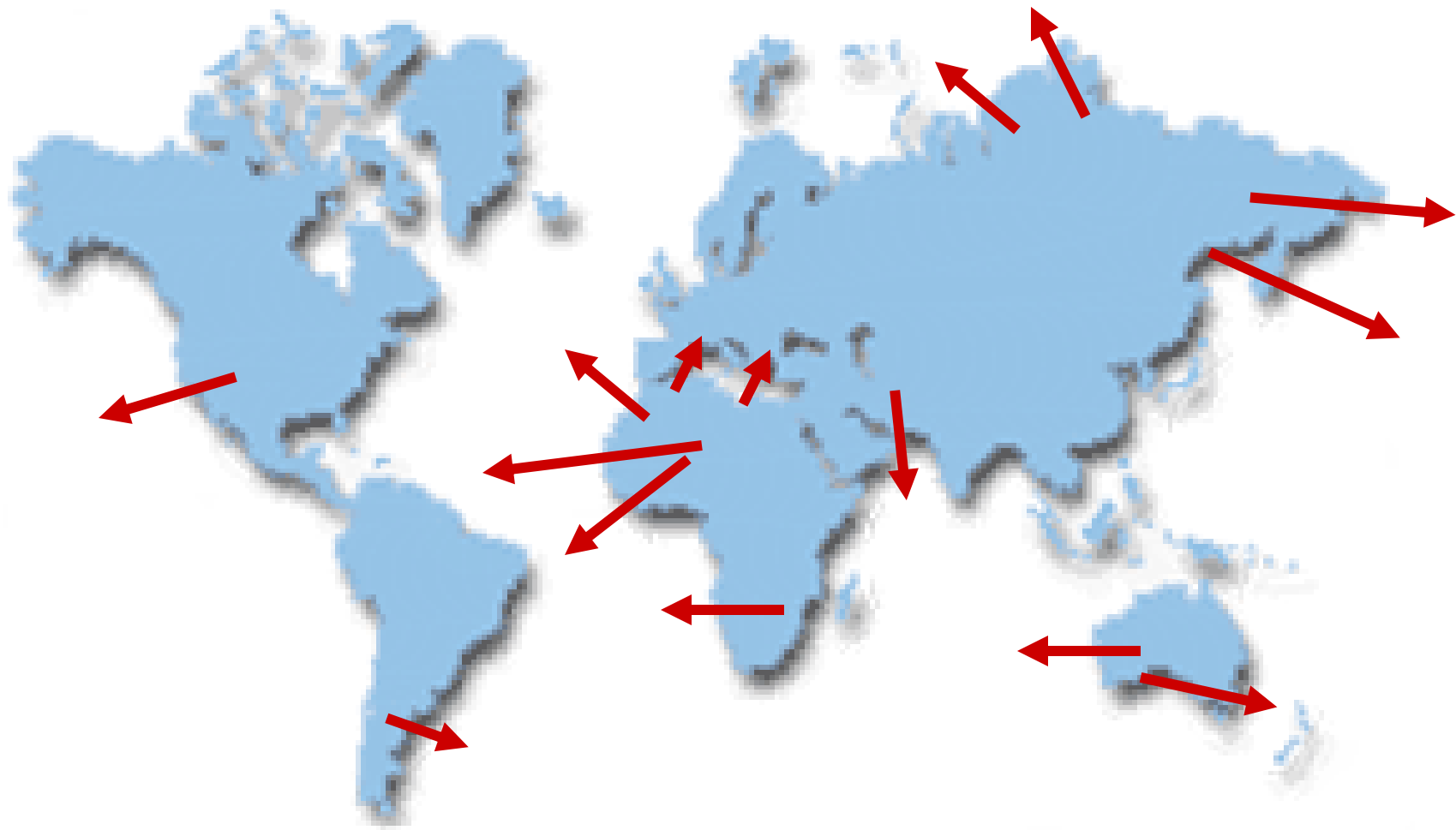


A model whose phytoplankton have a uniform growth rate, subject only to PO₄ limitation produce the observed features, but not their magnitudes.

HNLC regions are at least partly a direct consequence of ocean circulation.

Other limiting factors are important nearly everywhere (all latitudes).

Predominant dust source regions and transport routes

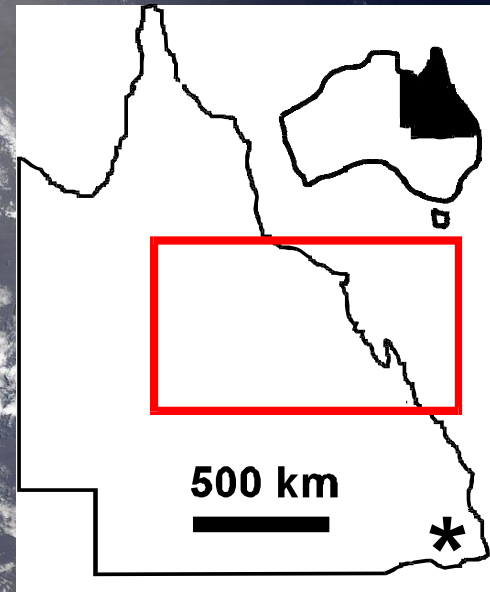
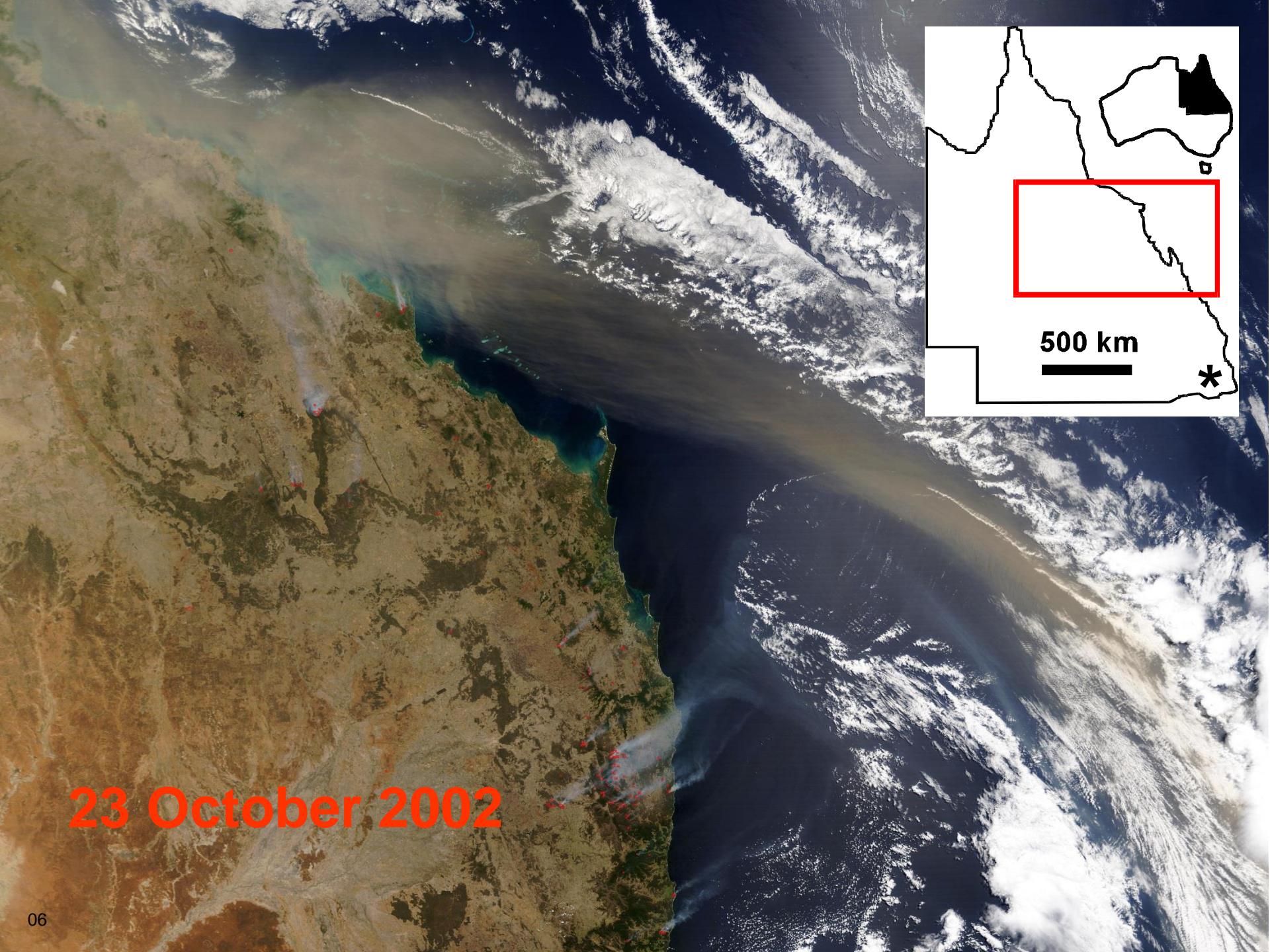


Pye (1987)

Initial uplift of soil in a dust storm

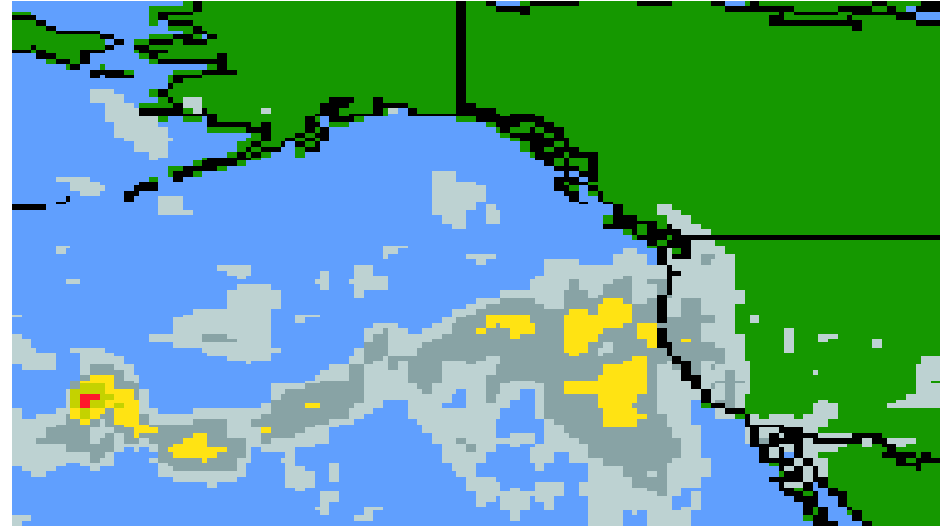
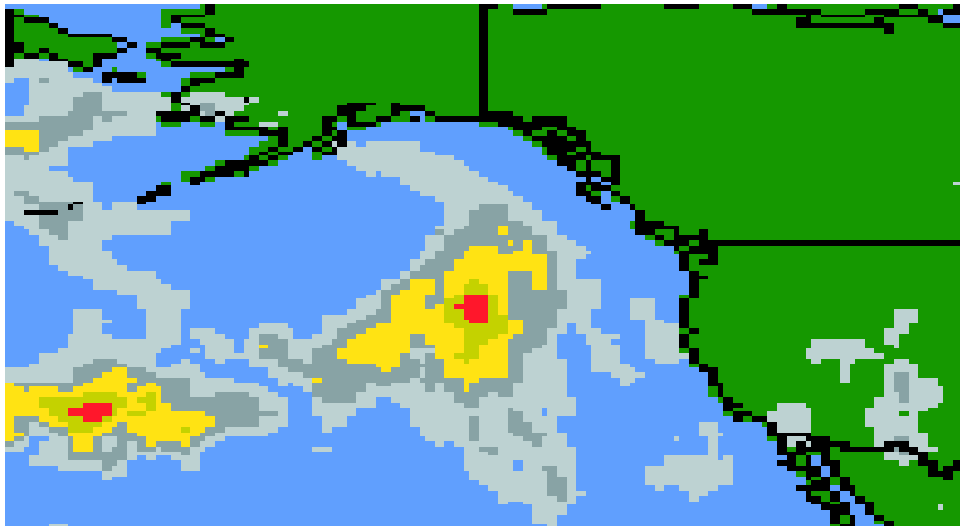
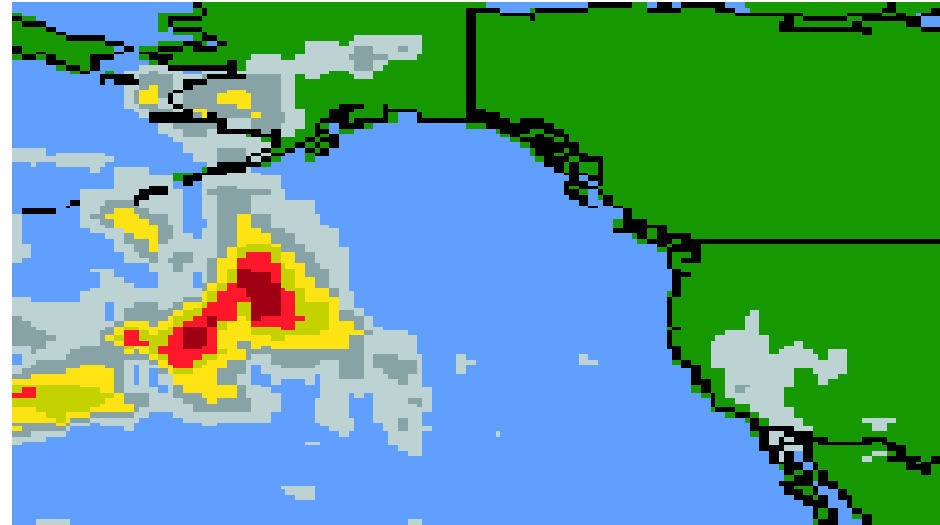
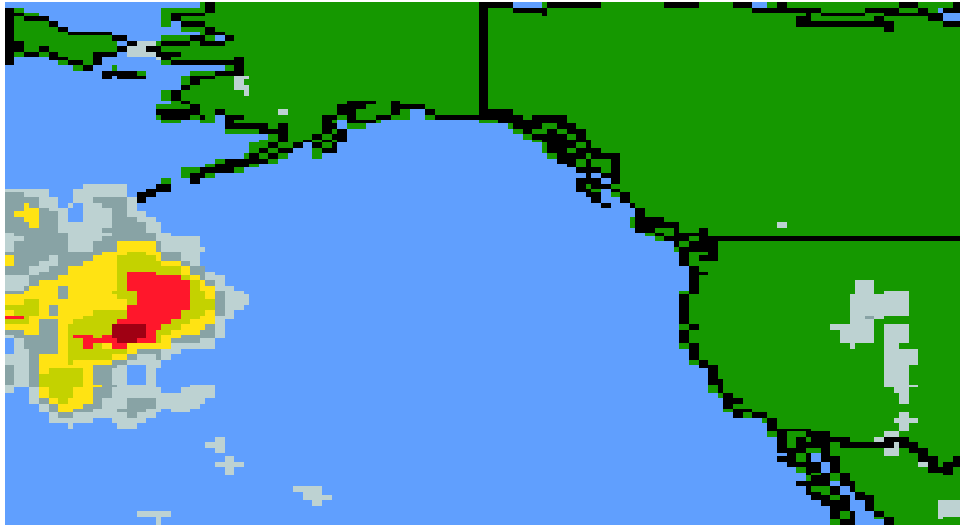


Courtesy McTainsh Australia



23 October 2002

Evidence of a dust storm from TOMS Aerosol Index, April 22 -25 1998 NE Pacific



Geographical isolation – from sources of aerosol iron

1724

Duce and Tindale 1991

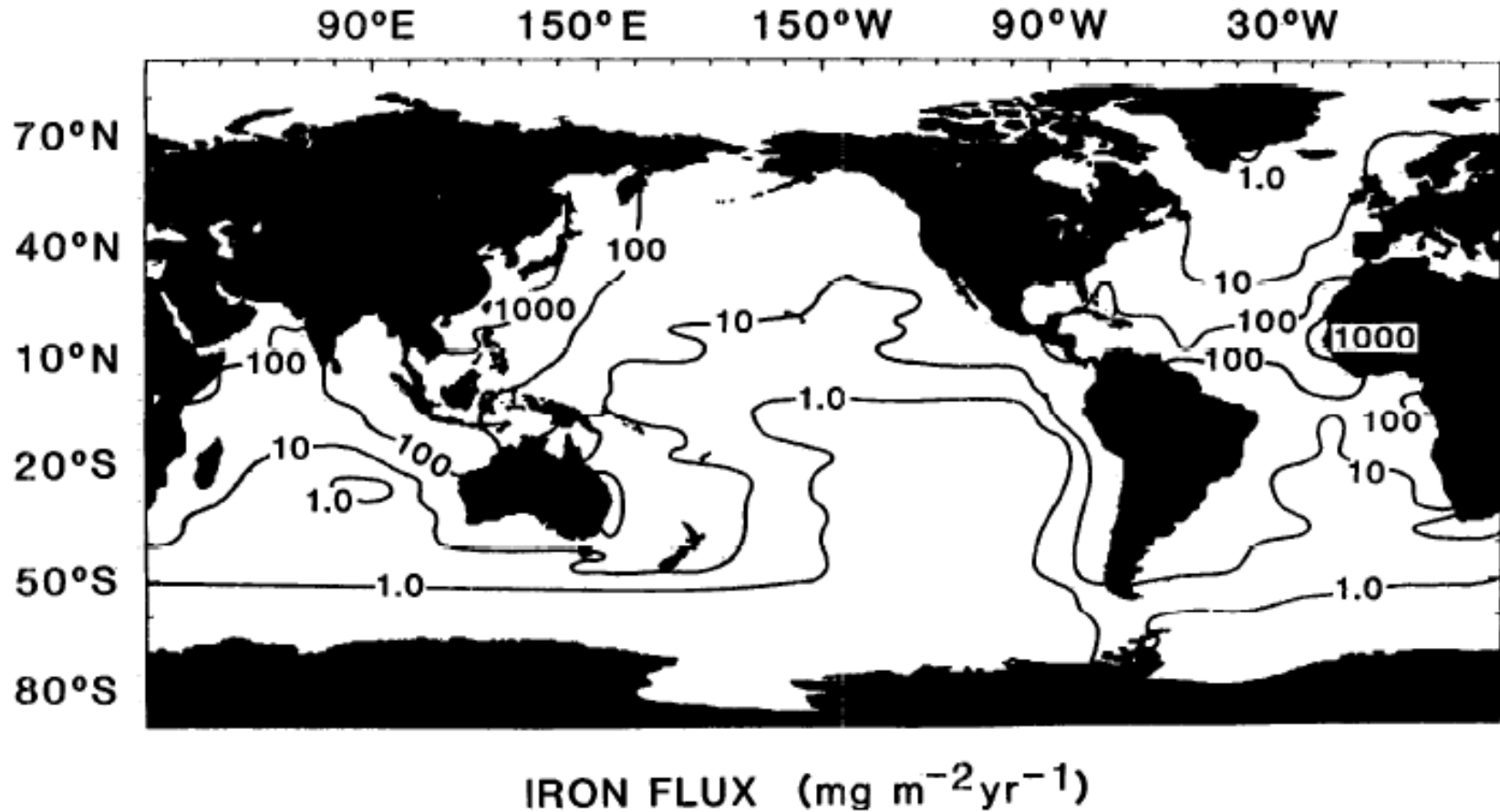
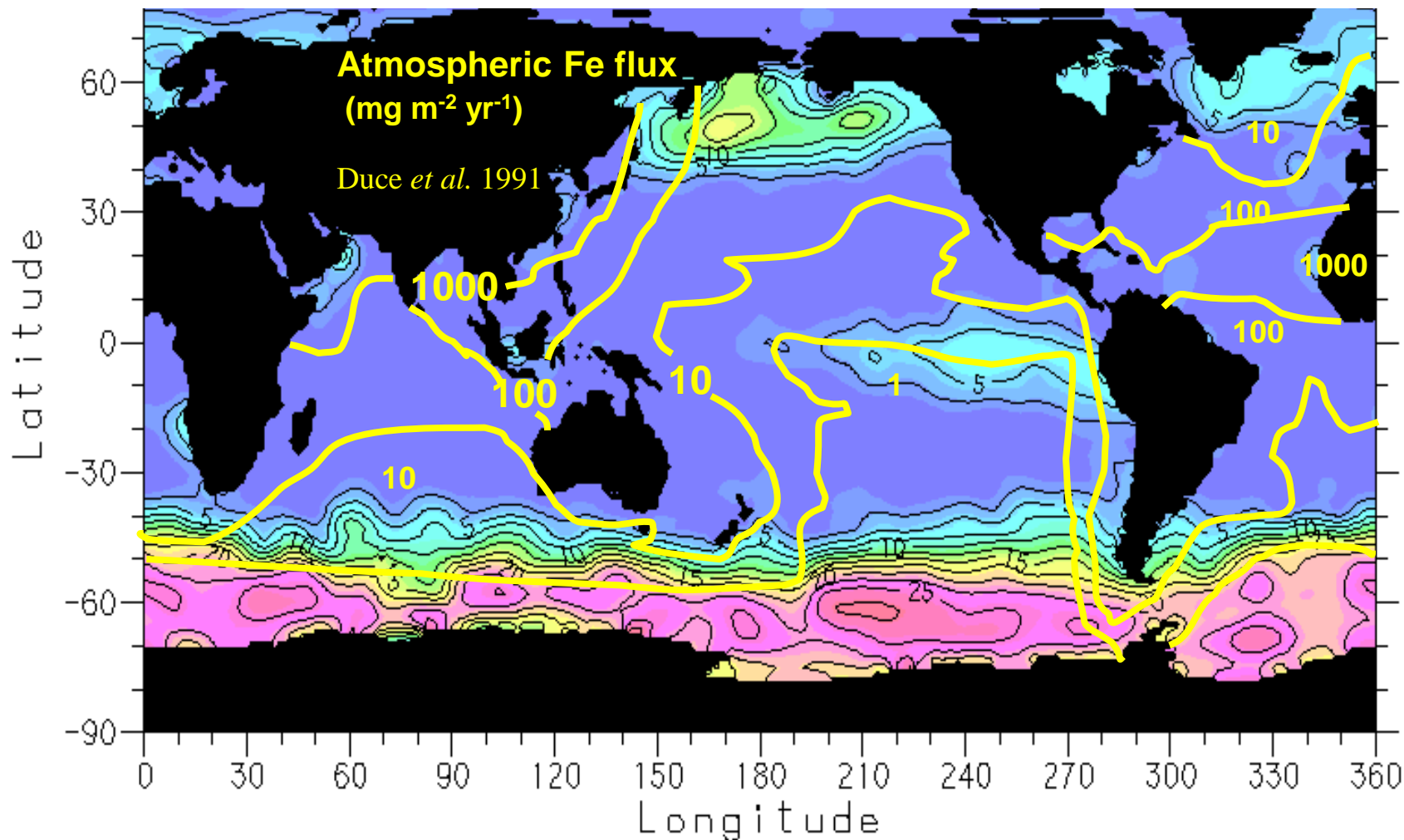


Fig. 8. Calculated flux of total (particulate plus dissolved) Fe from the atmosphere to the ocean (adapted from Donaghay et al. 1991).

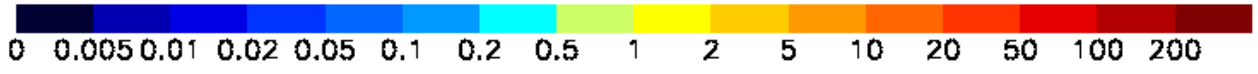
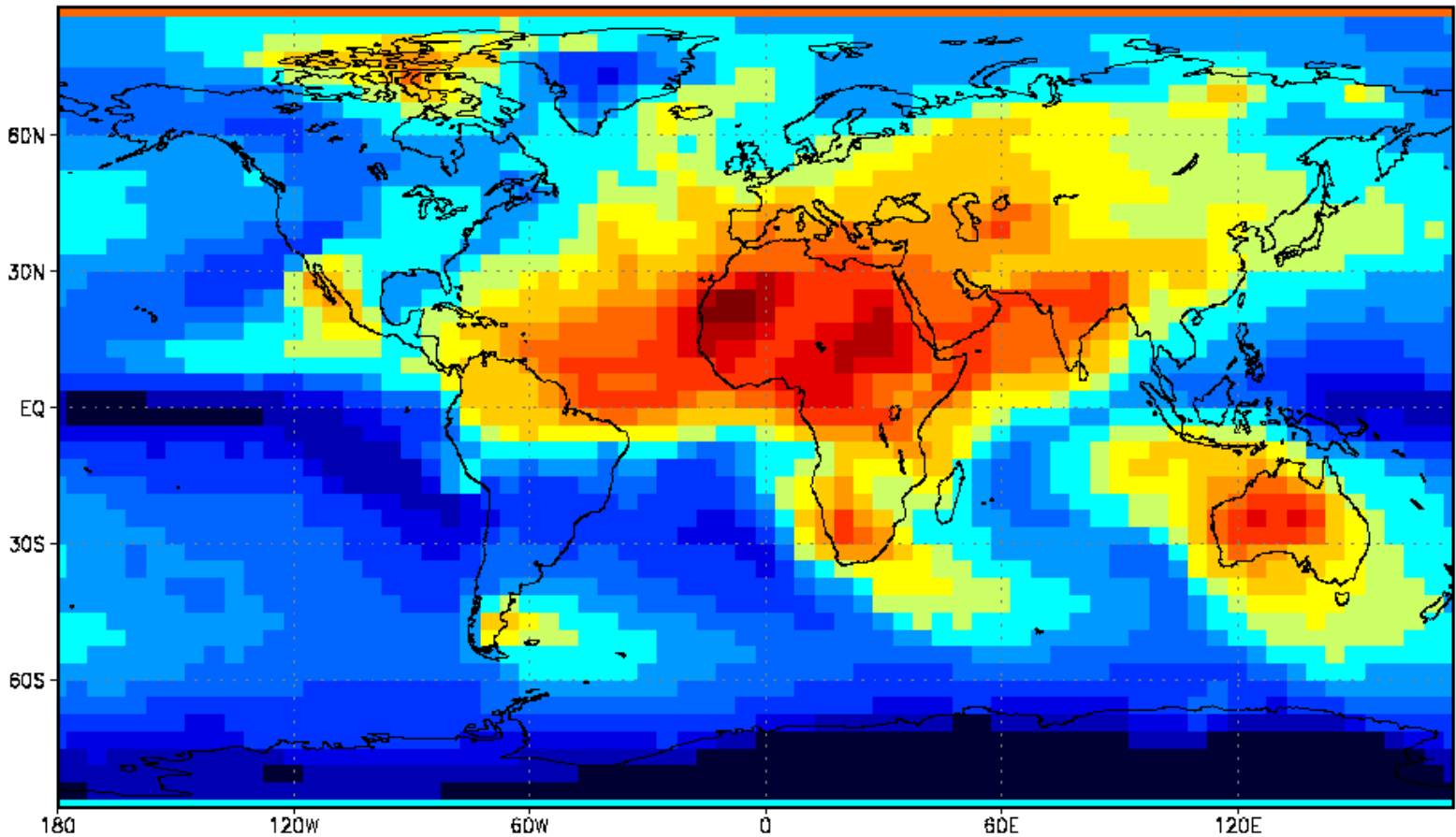
Dust flux overlaid on the NO_3 distribution (μM) in the upper ocean

NOAA world ocean atlas, 1994



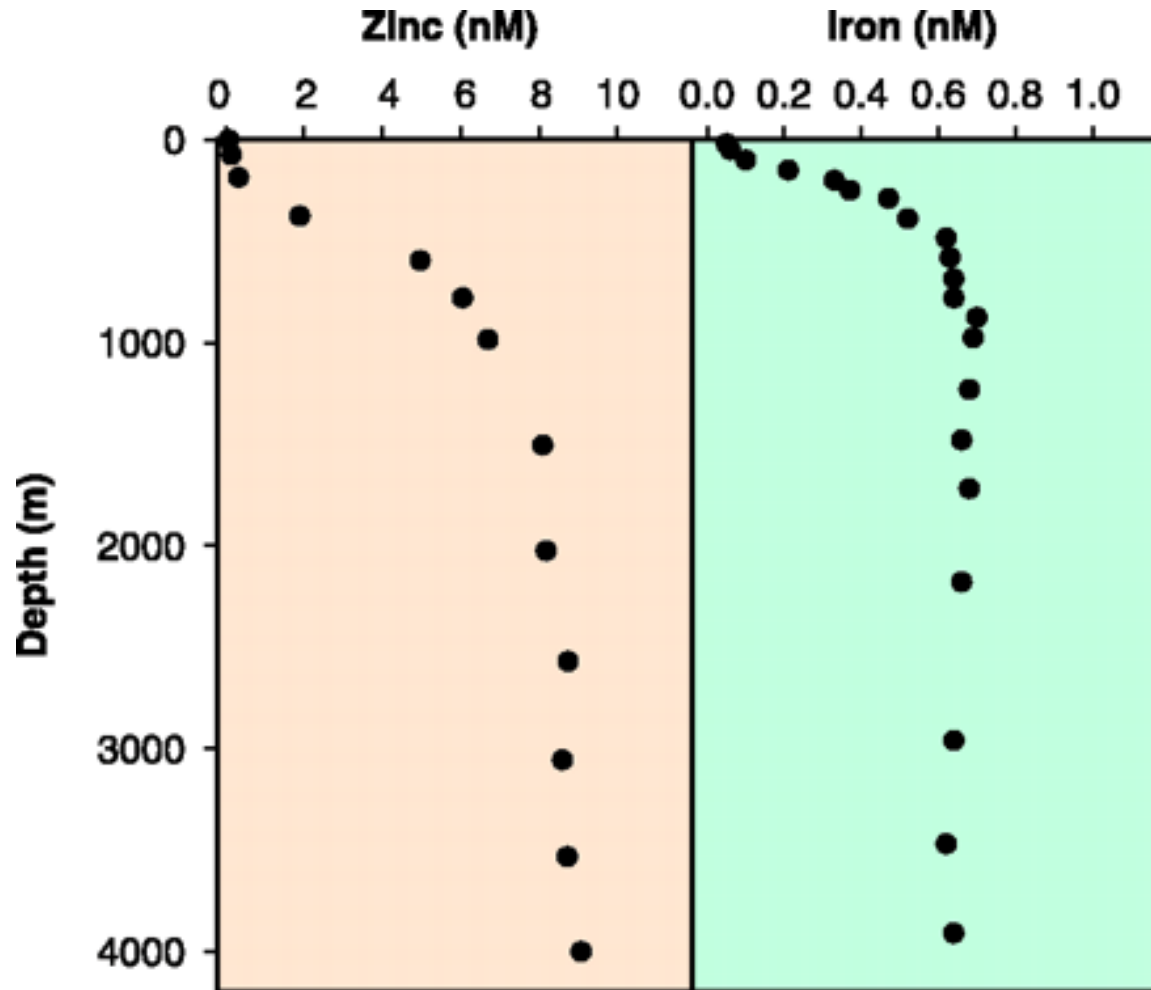
Modelled dust deposition rates

Model Current Dep (g/m²/year)



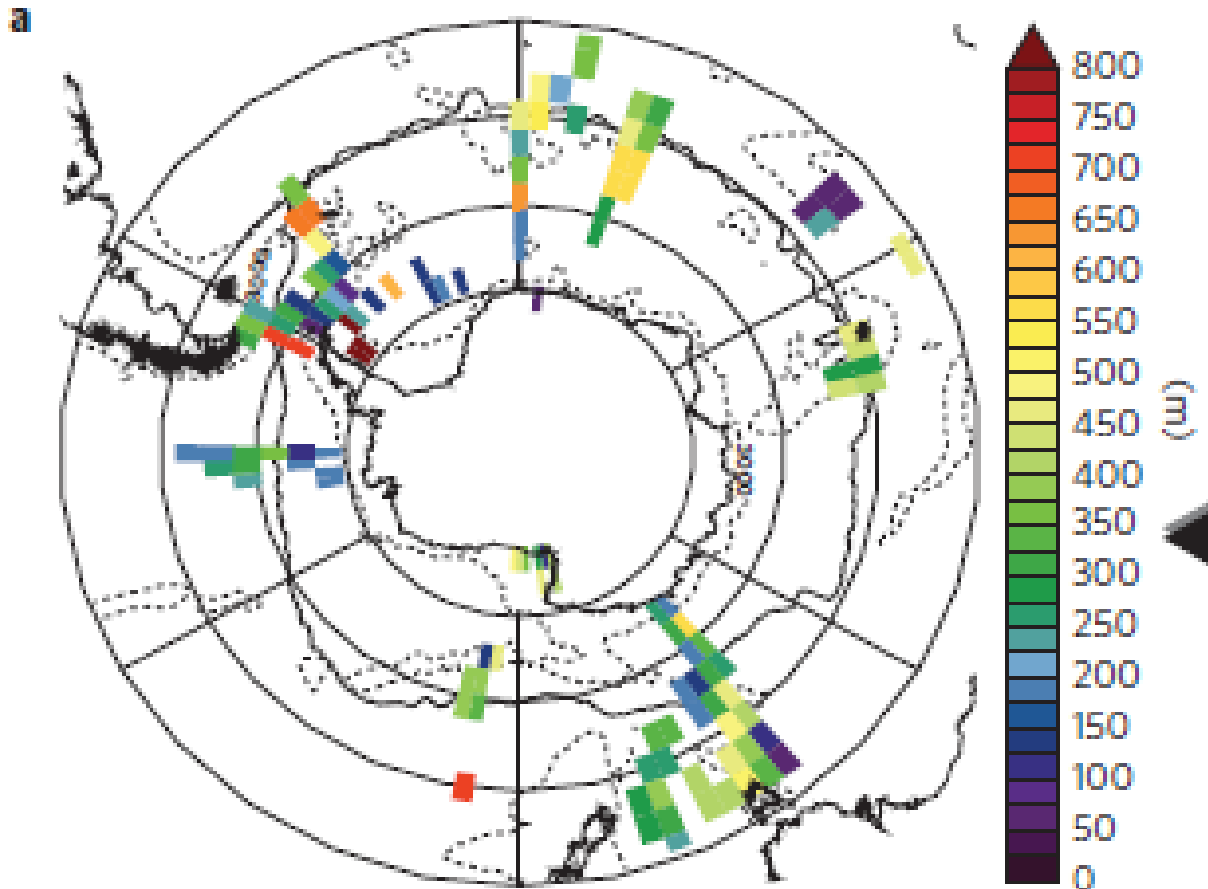
(g m⁻² yr⁻¹) N. Mahowald et al. (1999)

Mismatch between the depth of the ferricline & nutricline/thermocline



Surface water iron supplies in the Southern Ocean sustained by deep winter mixing

Alessandro Tagliabue^{1,2*}, Jean-Baptiste Sallée^{3,4,5}, Andrew R. Bowie⁶, Marina Lévy^{3,4},
Sebastian Swart^{2,7} and Philip W. Boyd^{8,9}



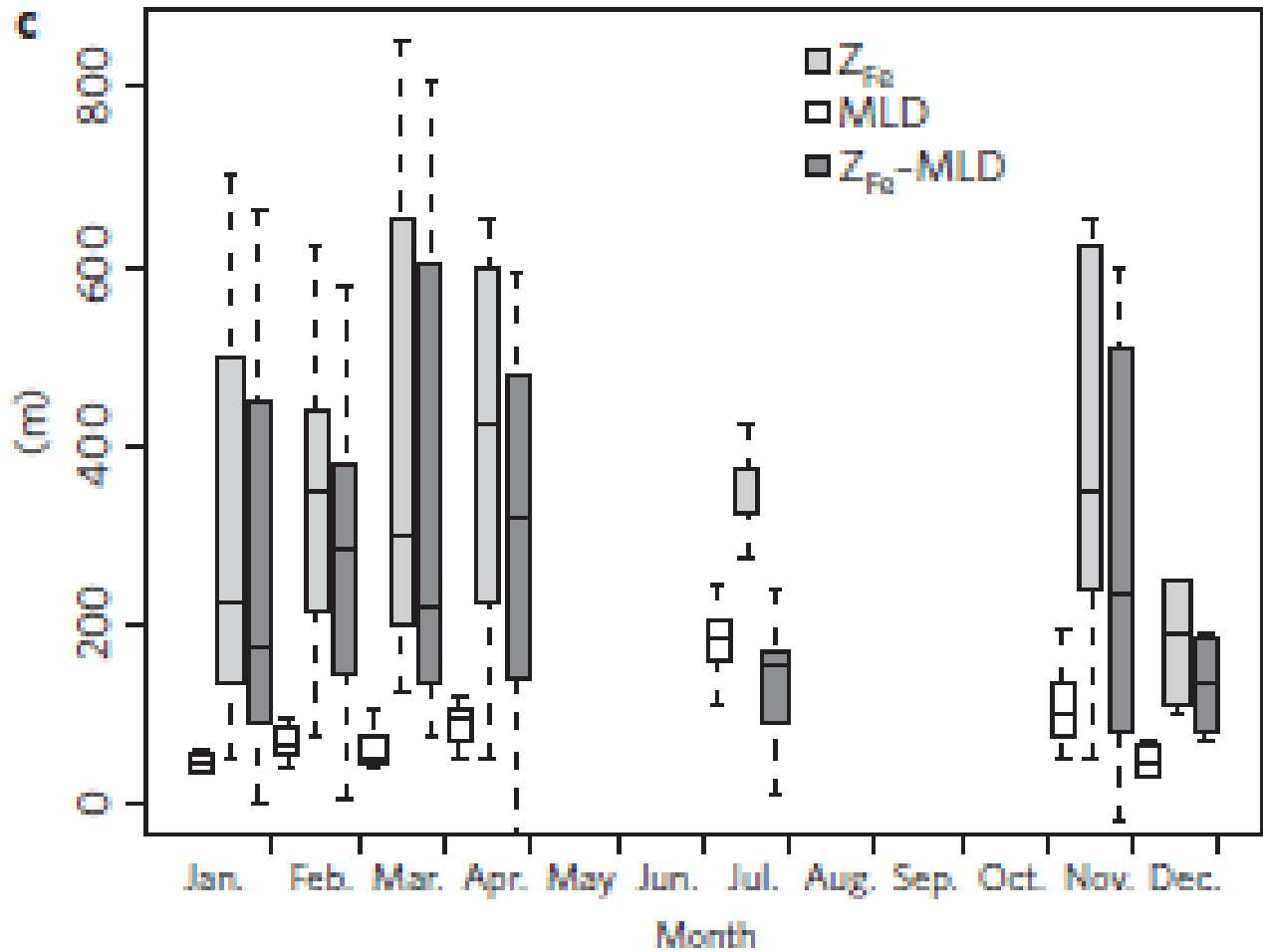
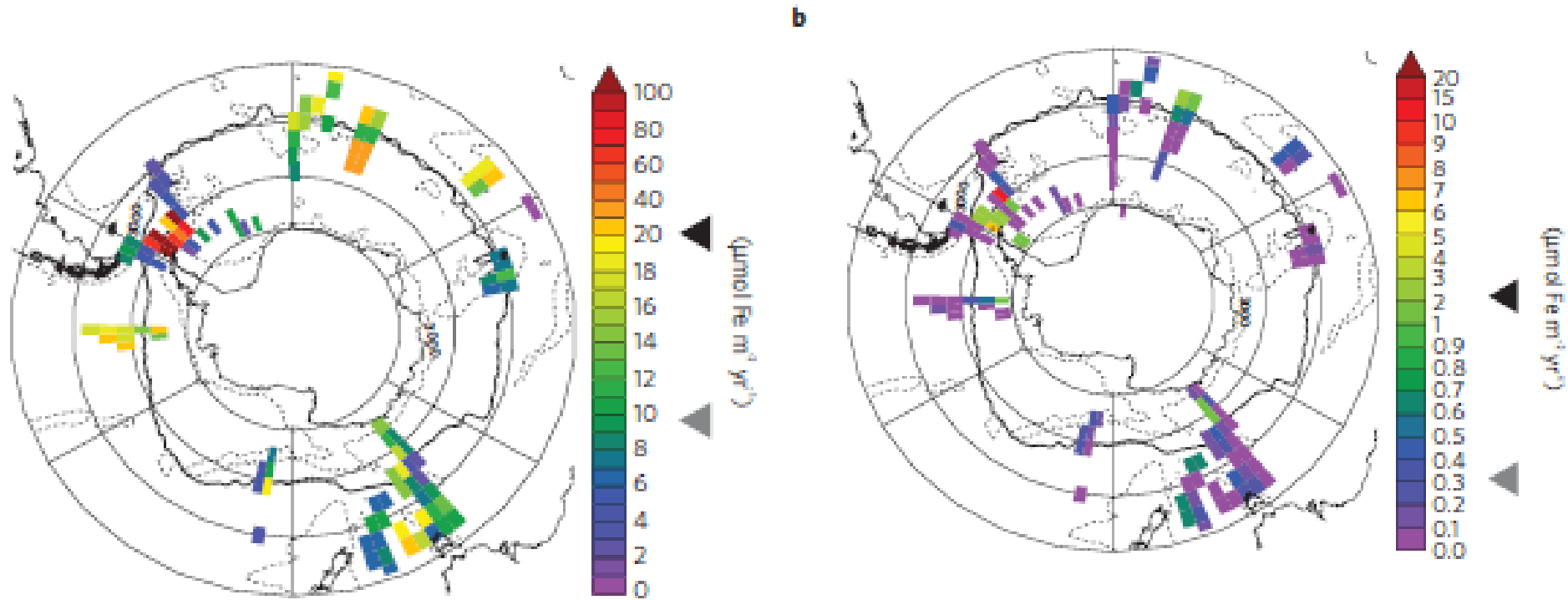
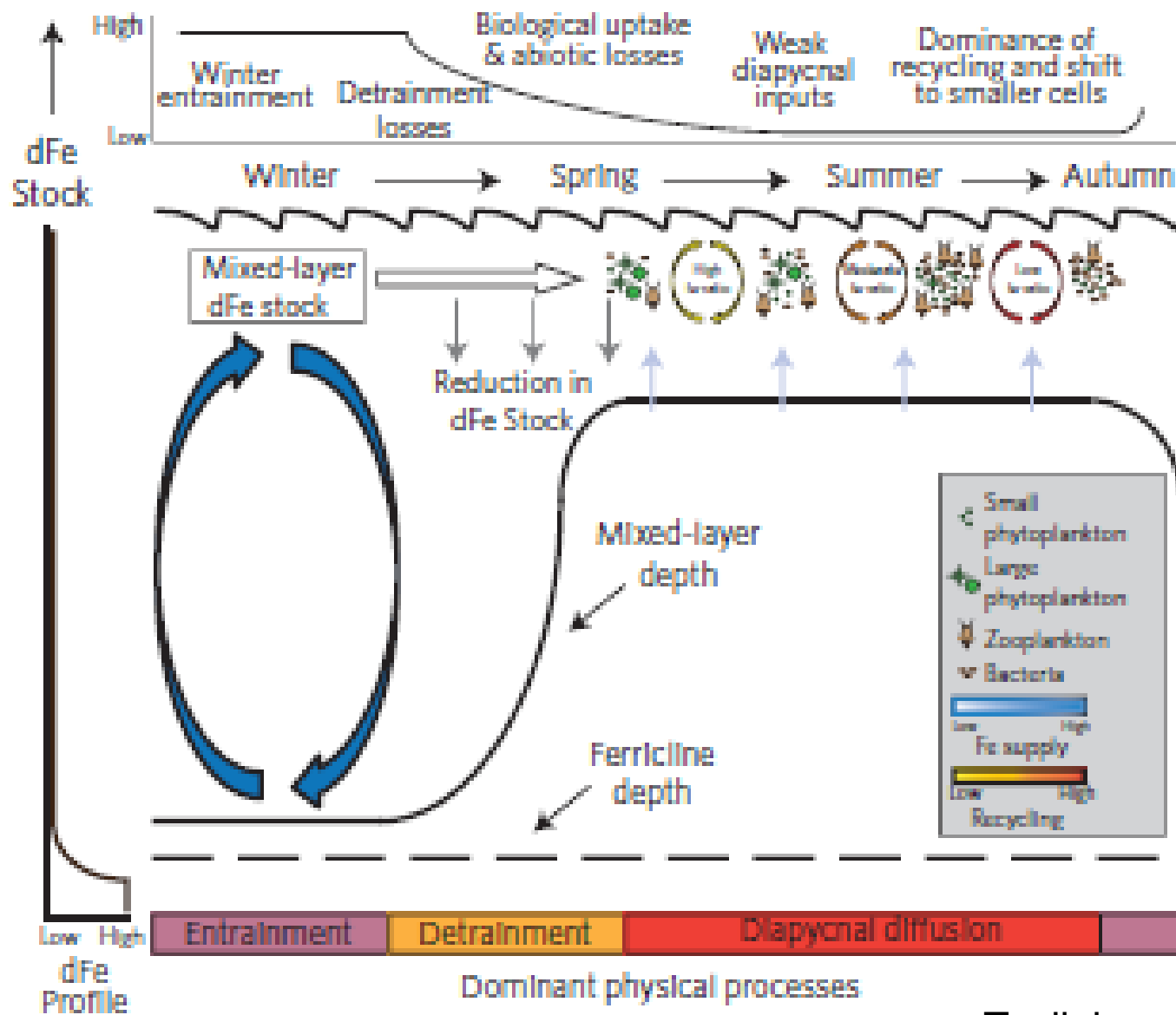


Figure 1 | Depths and potential density of the ferricline and its seasonal

Fe supply from
Winter entrainment
Diapycnal diffusion



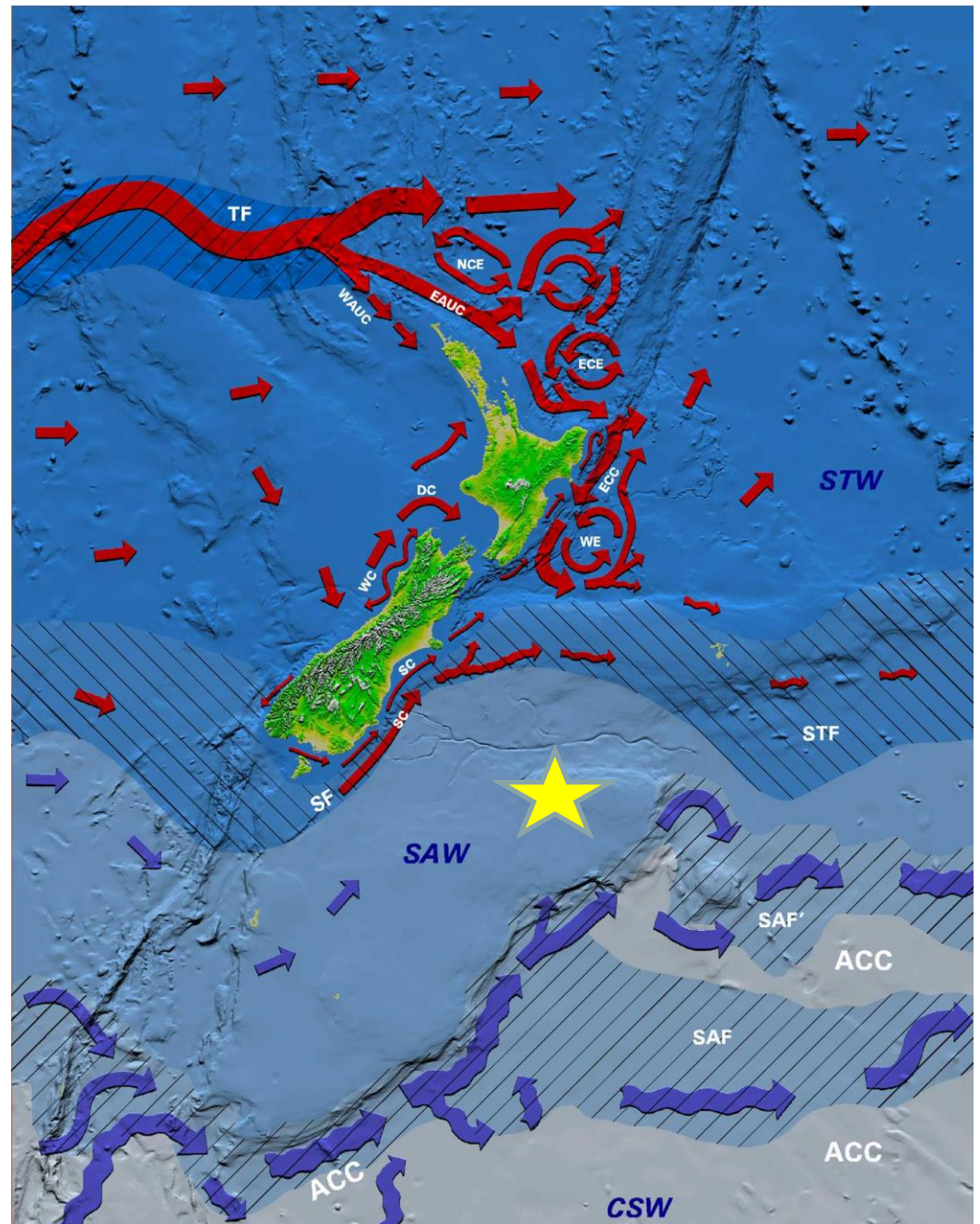


Tagliabue et al. 2014

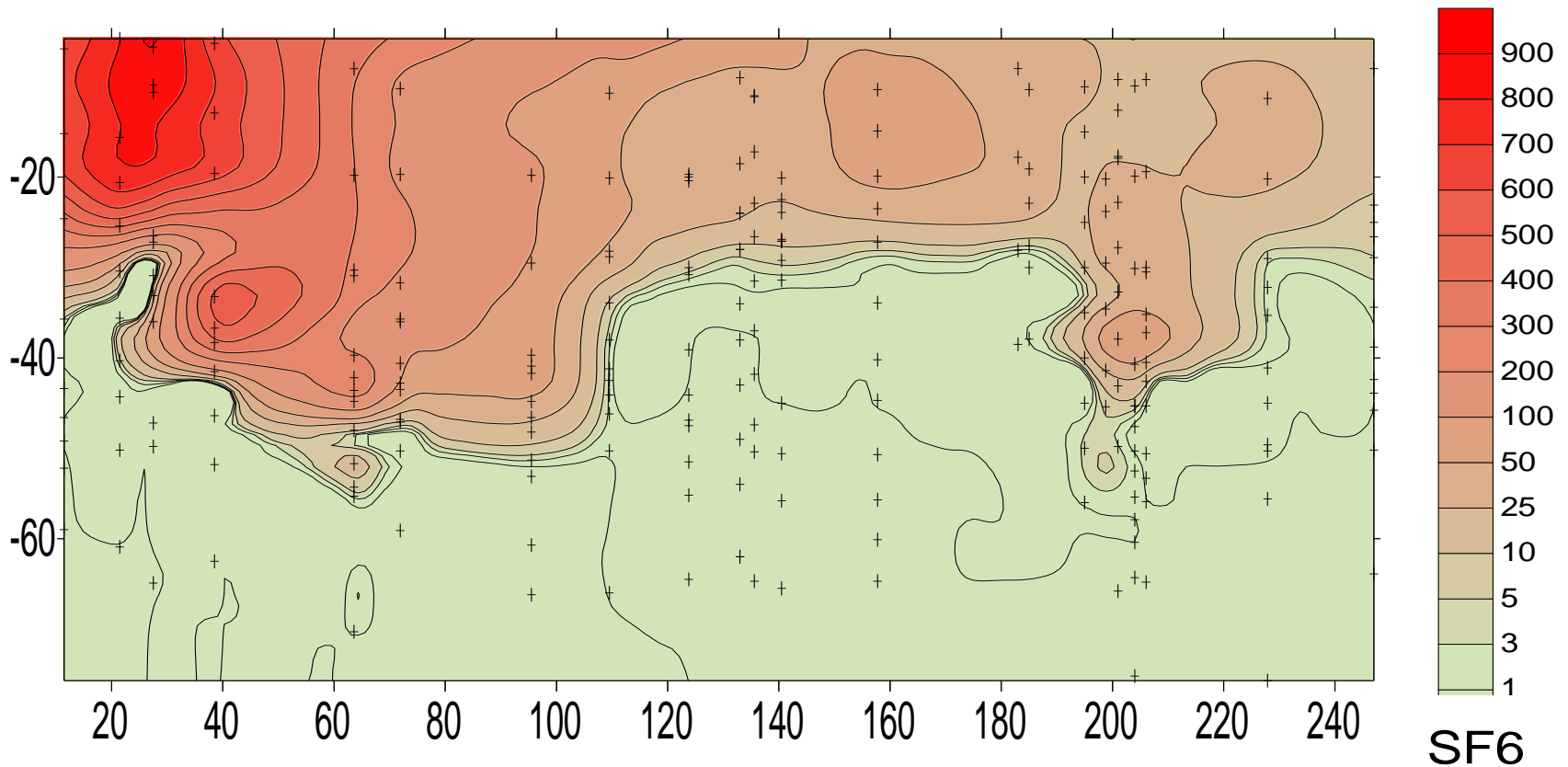
Figure 4 | A schematic representation of the seasonal variability in Southern Ocean Fe cycling. We emphasize seasonal changes in the

Everyday life in
HNLC waters

A case study
FeCycle

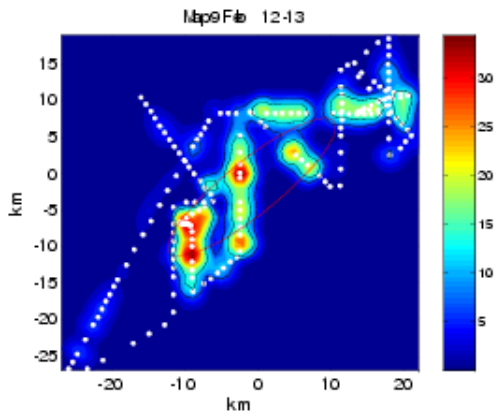
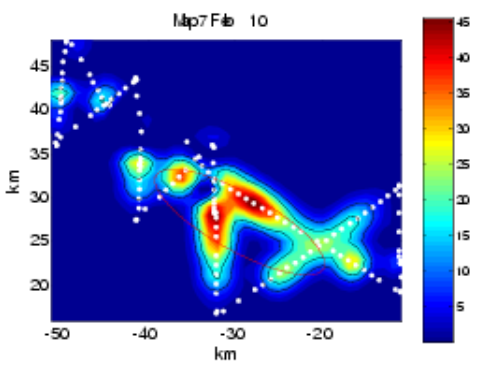
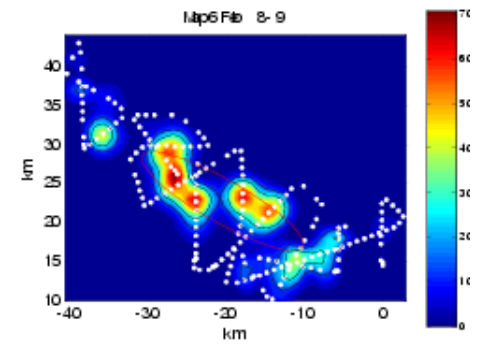
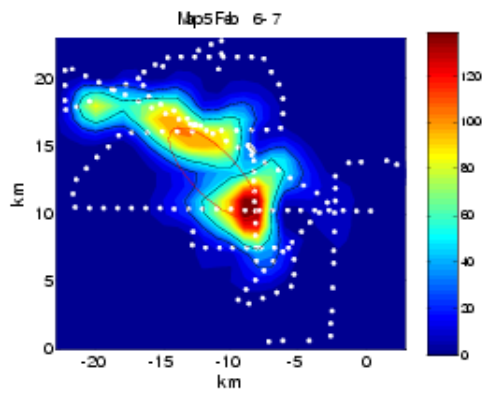
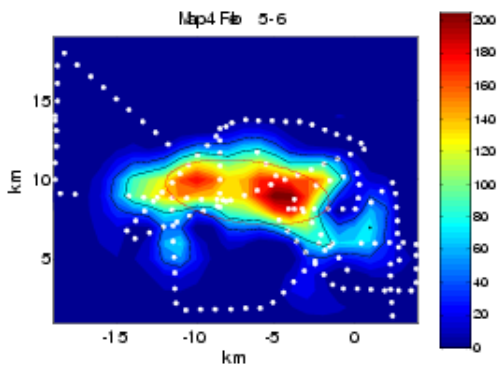
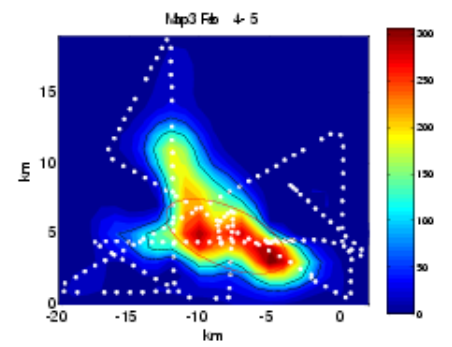
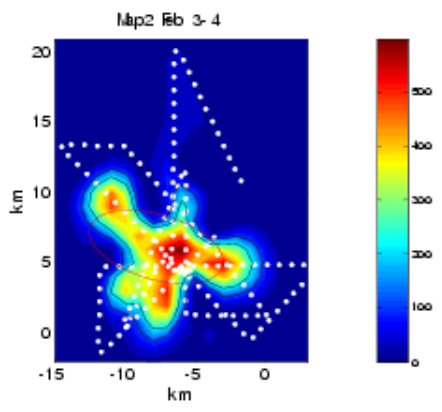
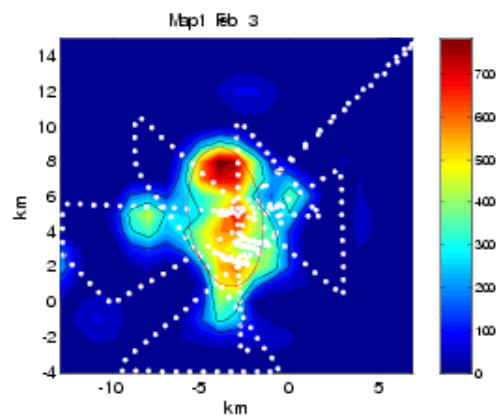


FeCycle - a mesoscale SF₆ tracer study of iron cycling in unperturbed HNLC waters

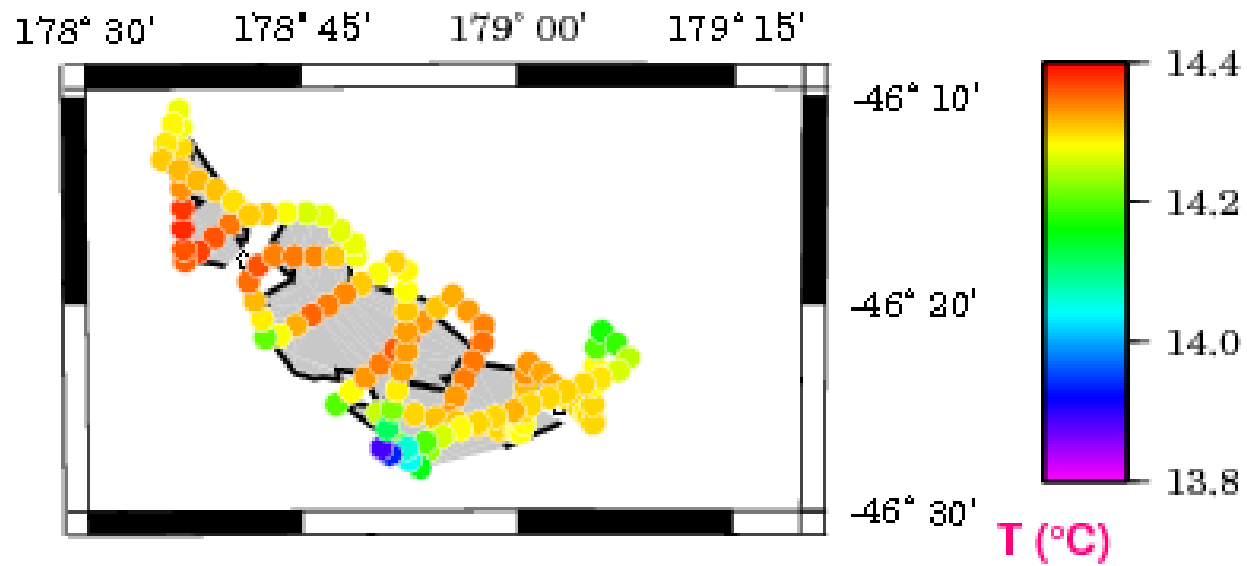
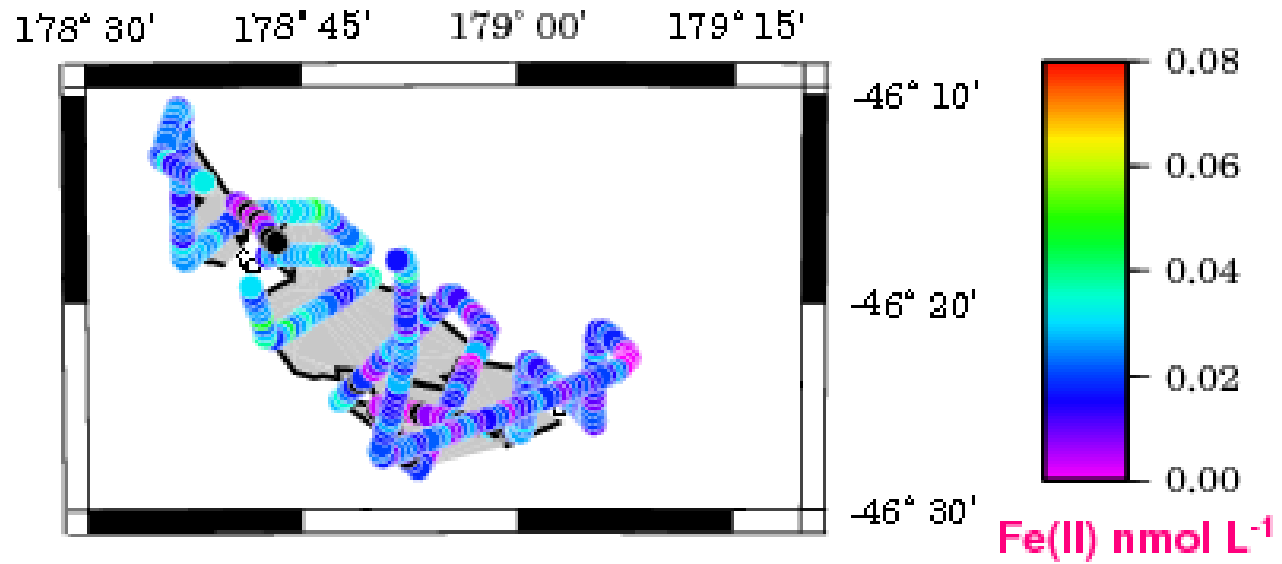


Boyd et al. 2005

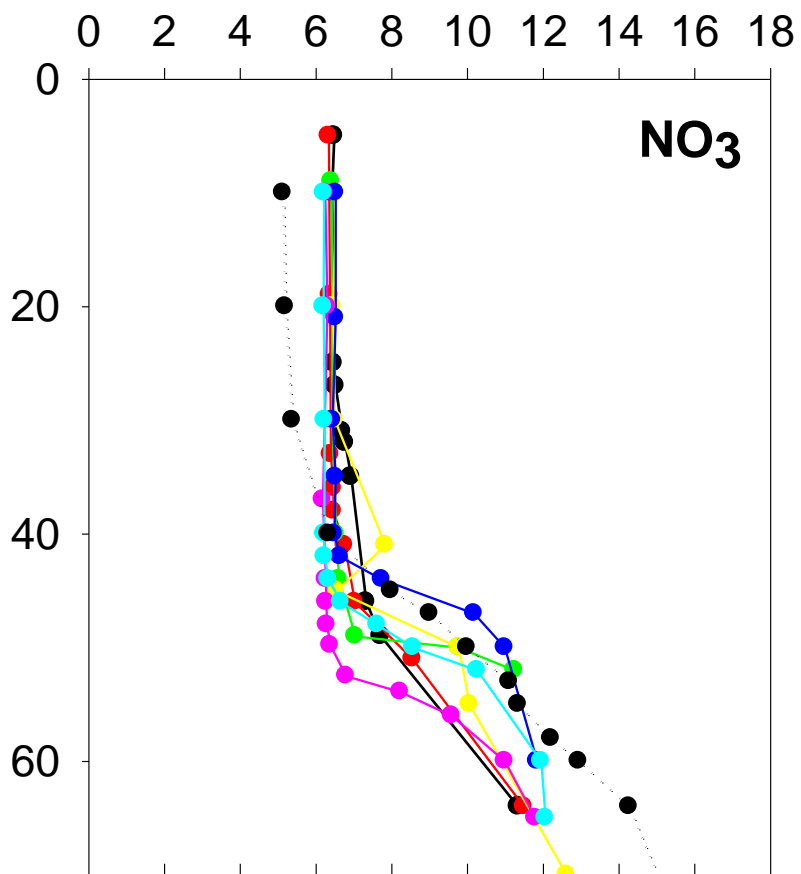
Time (h) versus depth (m)



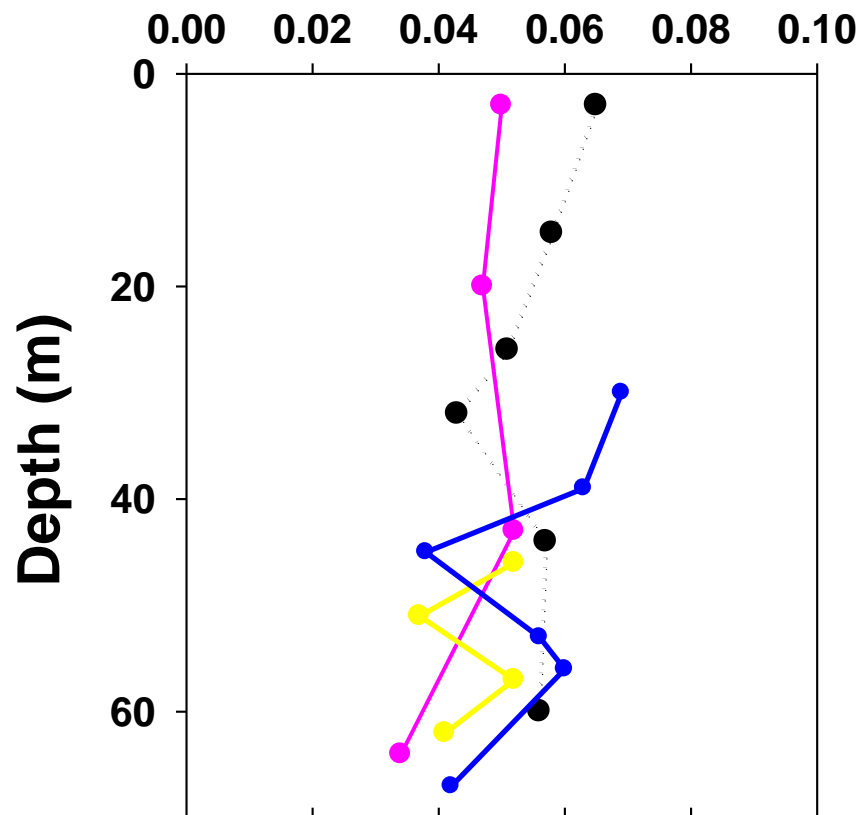
Croot et al. 2006



mmol m⁻³

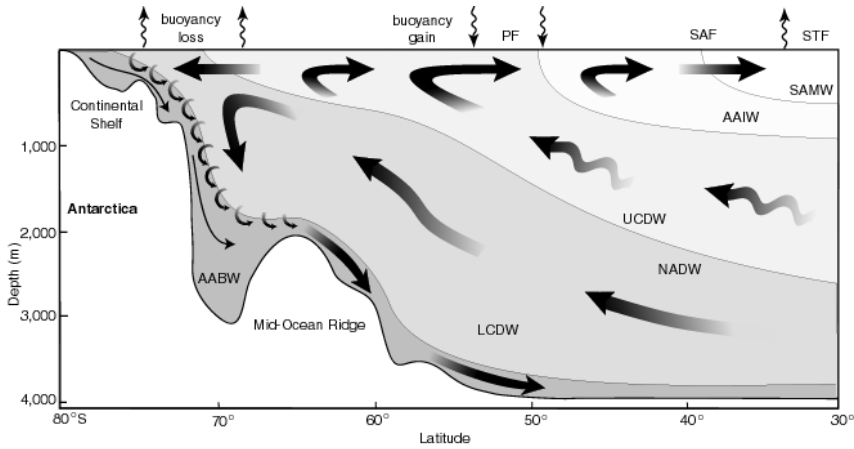


DFe (nmol L⁻¹)

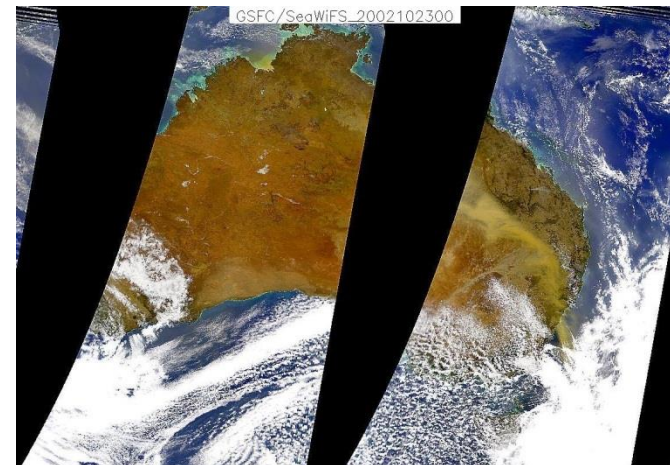


Boyd et al. 2005

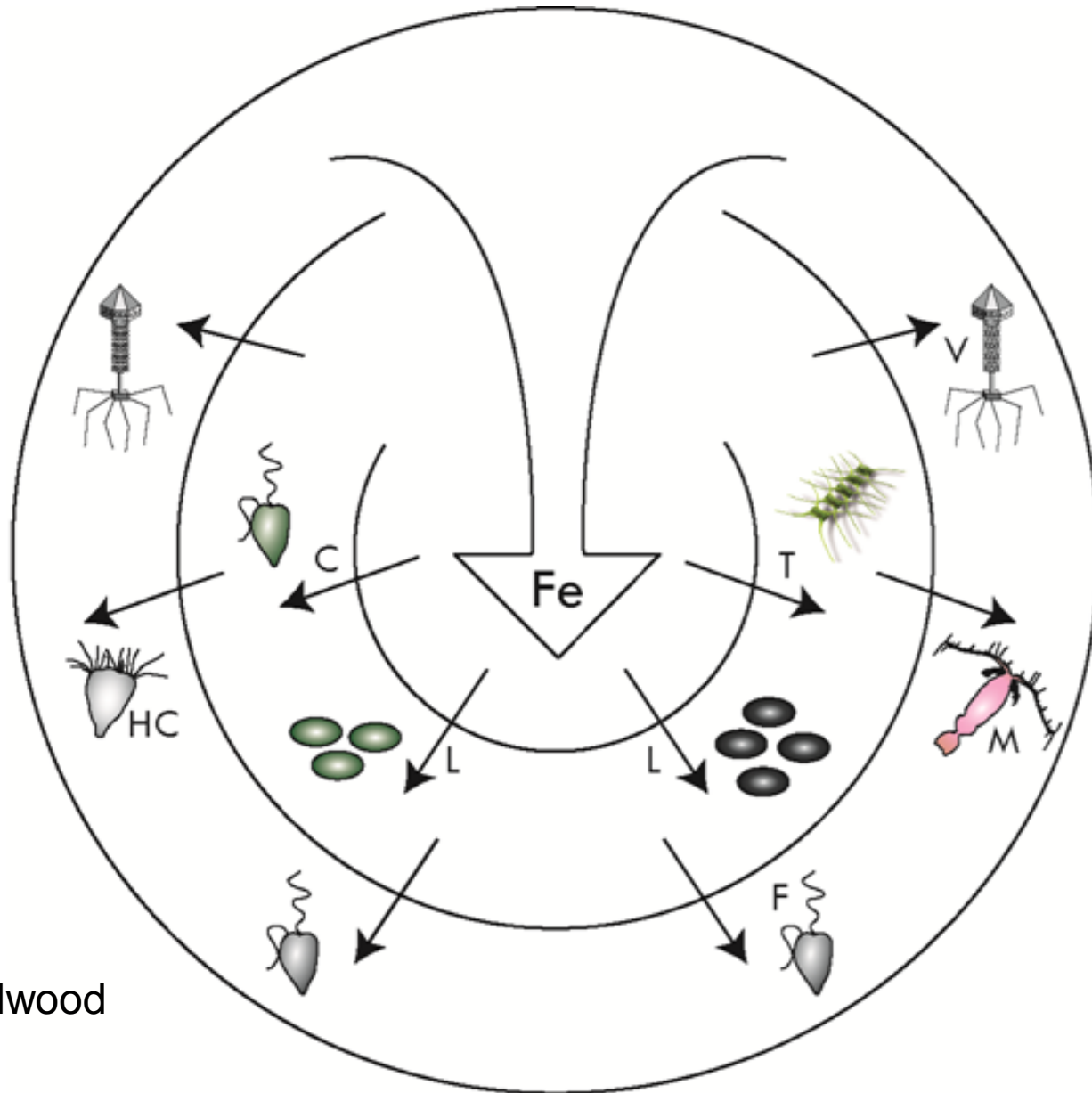
New versus regenerated iron



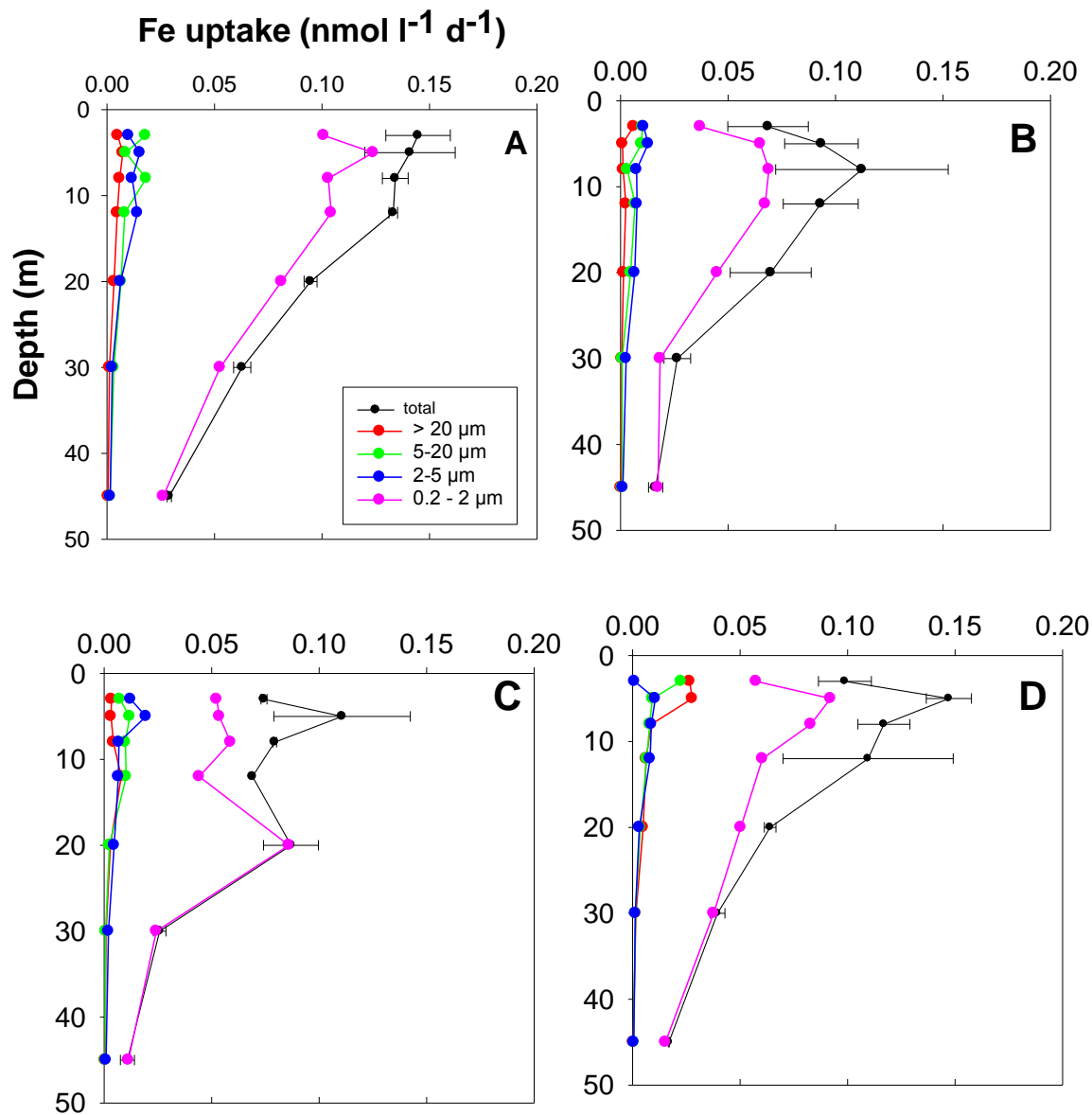
$$fe \text{ ratio} = \text{new Fe} / (\text{new} + \text{regen Fe})$$



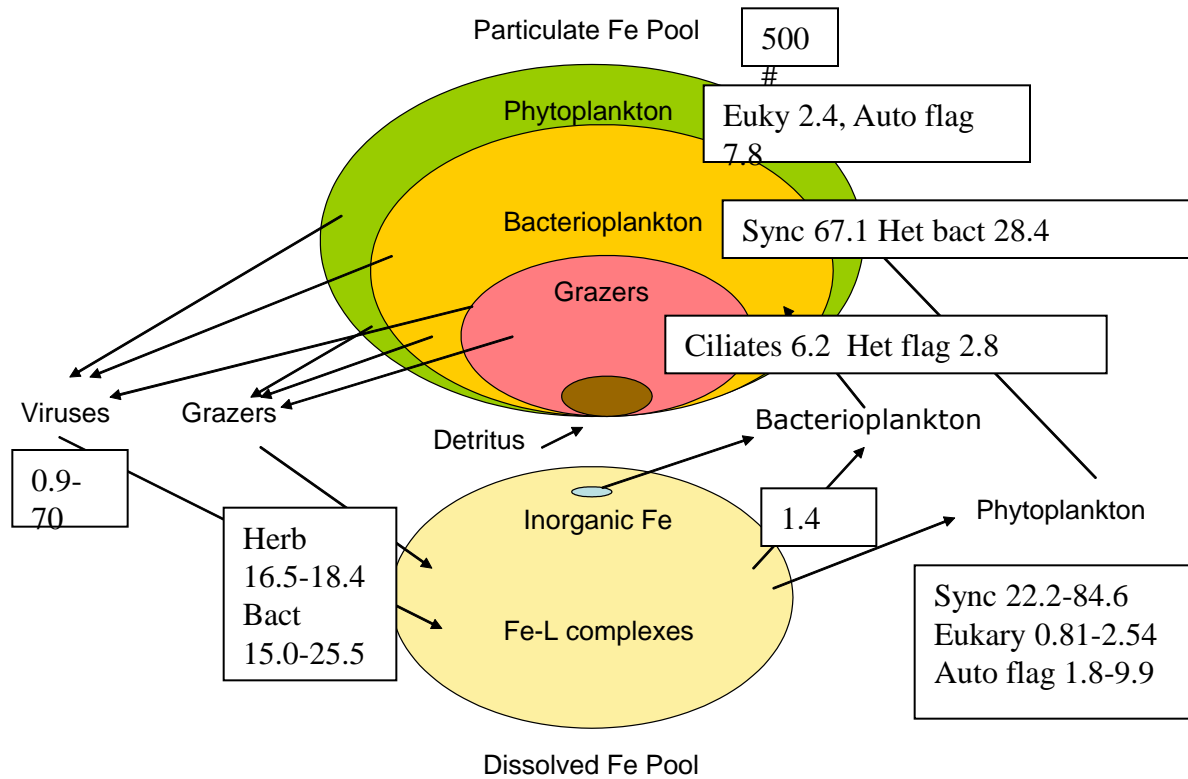
Microbes drive the oceanic ferrous wheel



Boyd & Ellwood
2010

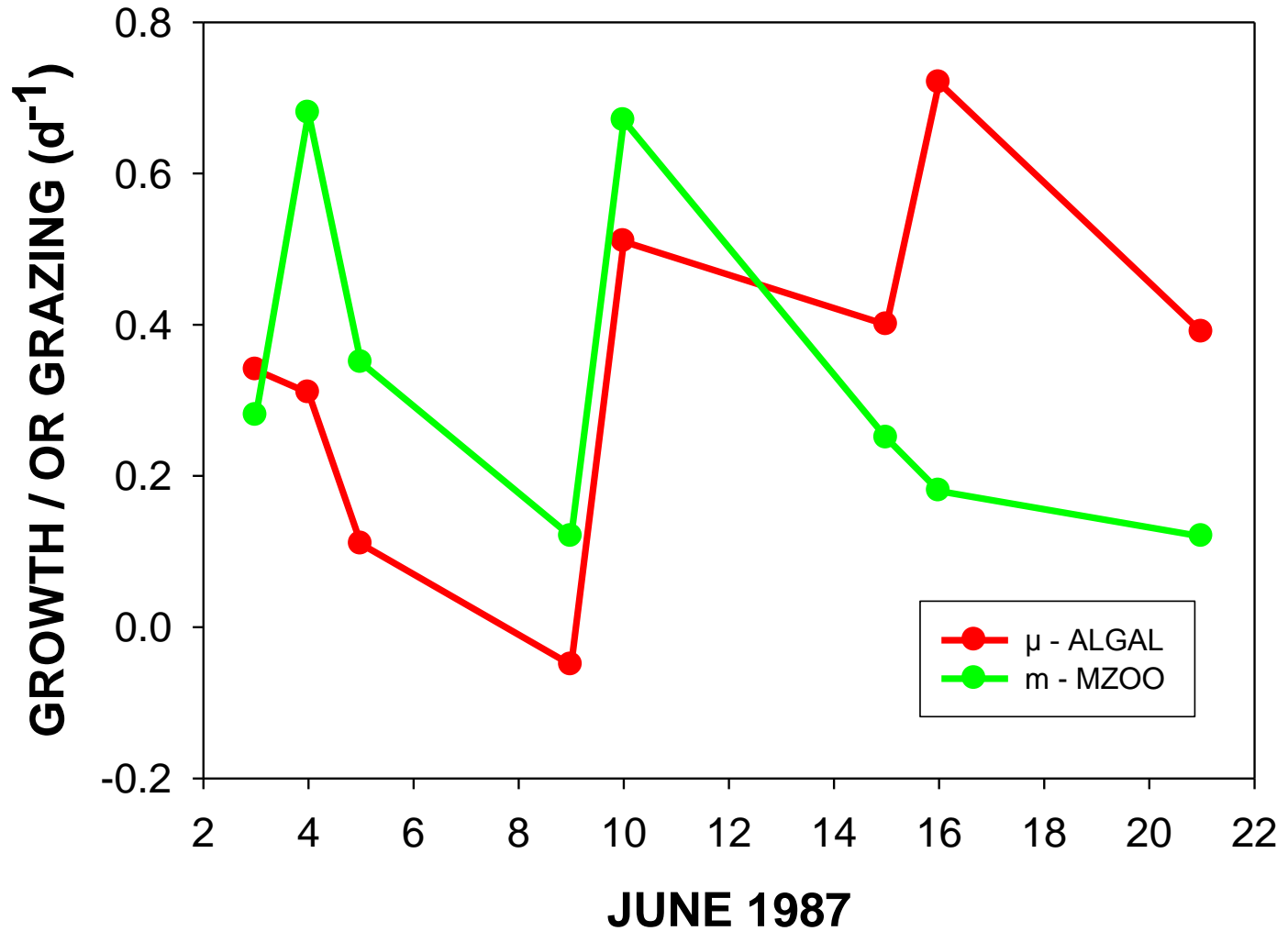


WHO HAS THE IRON?

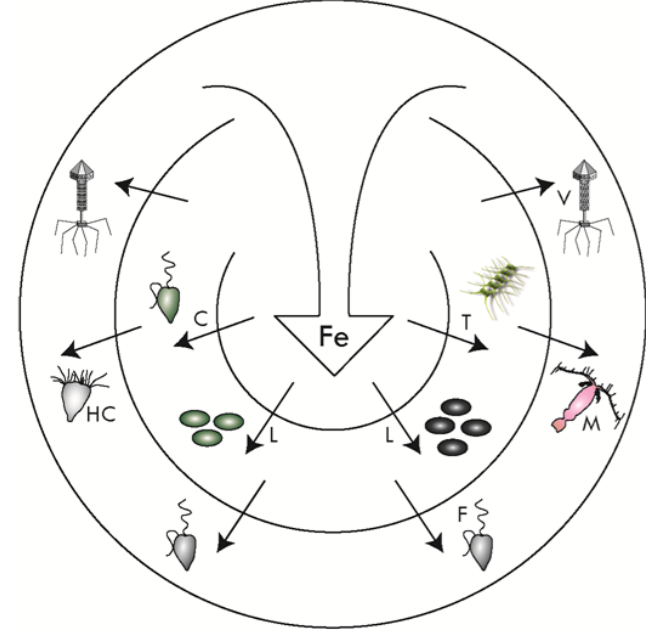


GROWTH RATE versus GRAZING MORTALITY

LANDRY et al., 1993

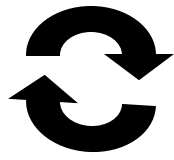


Internal cycling of IRON



UPTAKE

2453 to 4055 (e)



>1976 (f) Biological recycling

GRAZING AND VIRAL LYSIS



Boyd et al. 2005

Aeolian
500 (a)

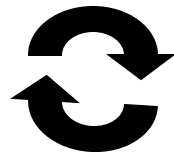


Mixed layer

5 to 50 DFe (b) [$9 \mu\text{mol m}^{-2}$]
450 to 495 PFe (c) [$34 \mu\text{mol m}^{-2}$]

Lateral
advection
0 (d)

2453 to 4055 (e)

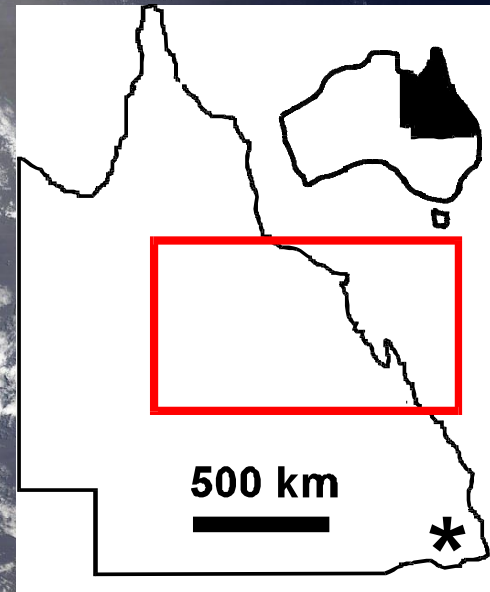
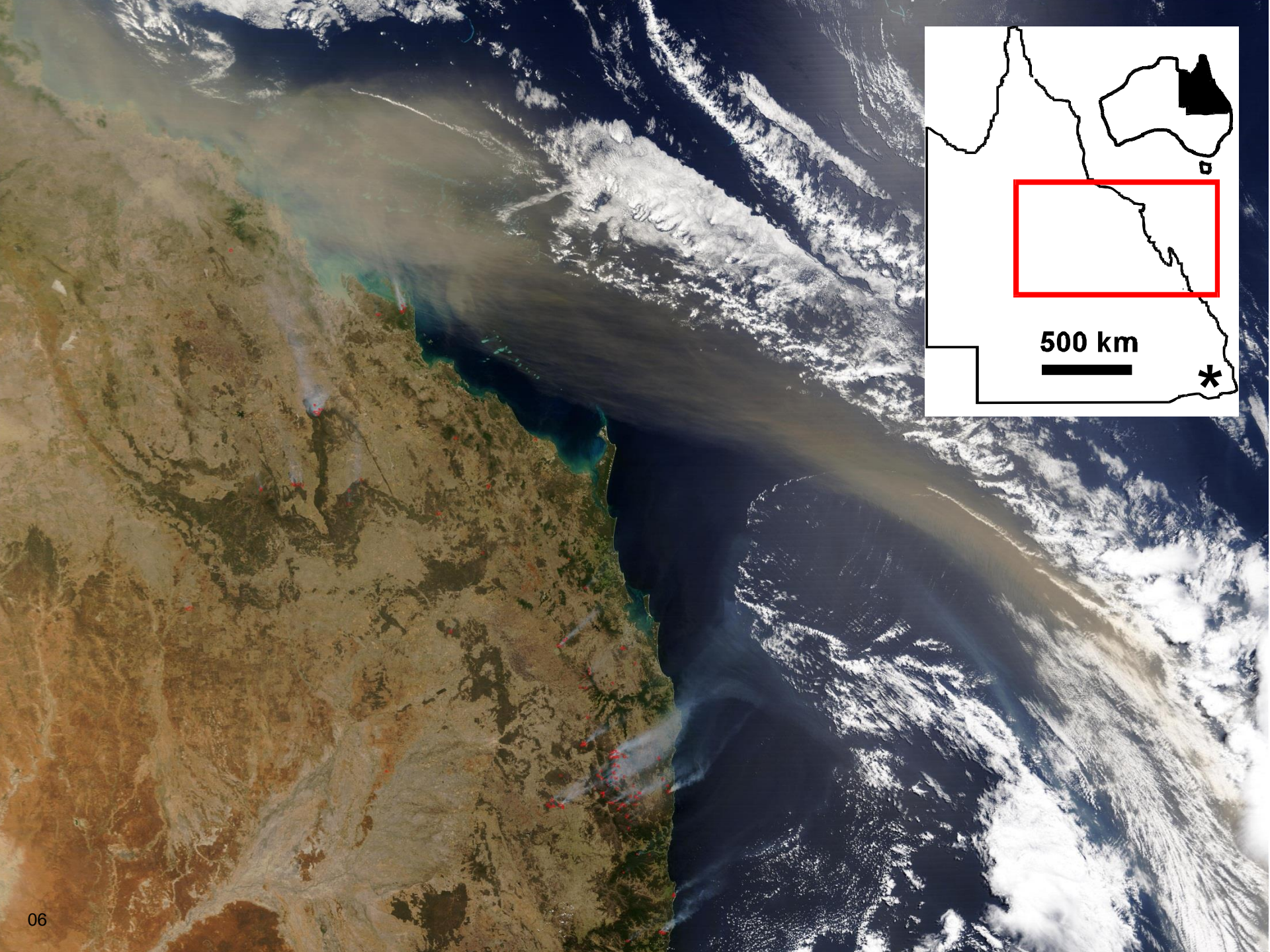


Biological
recycling

>1976 (f)

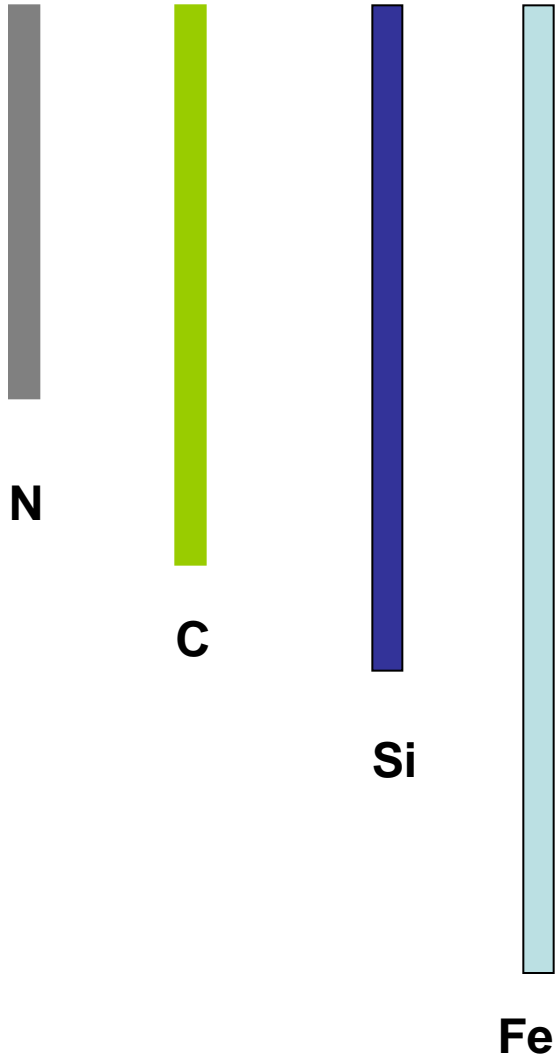
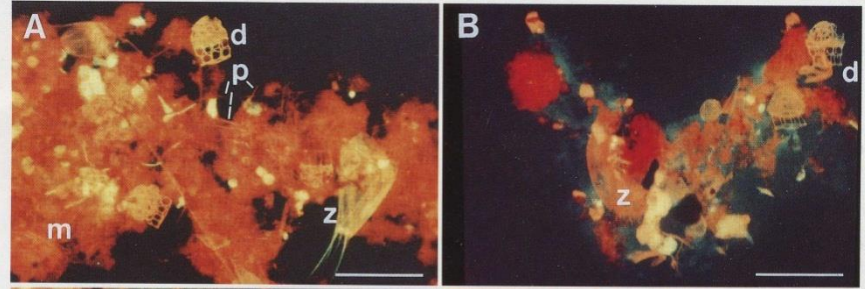
Vertical
Diffusivity (g)
 15 ± 3

PFe Export (h)
 216 ± 27 to 548 ± 128

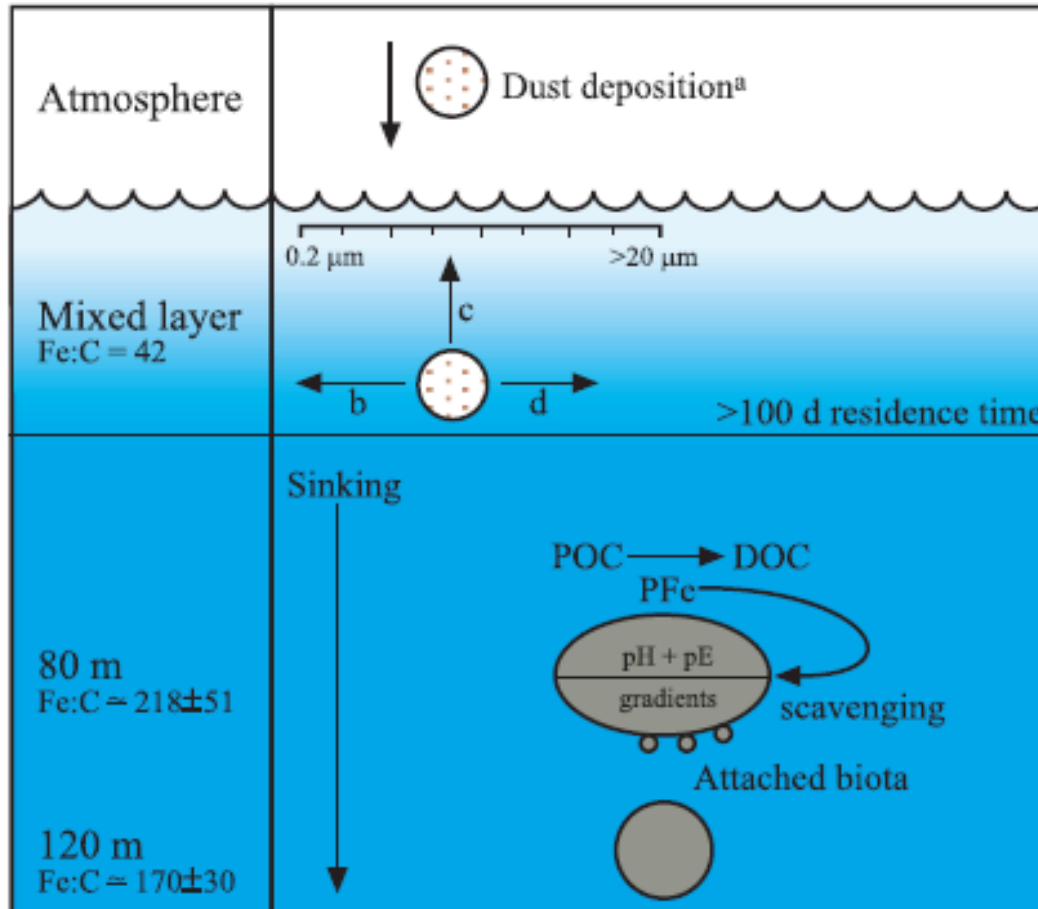


Remineralization length scales

Why is Fe > Si, C, N, P?



Iron's particle reactivity is the main cause



How do phytoplankton cope with
perennially low iron conditions?

Diatom Proteomics Reveals Unique Acclimation Strategies to Mitigate Fe Limitation

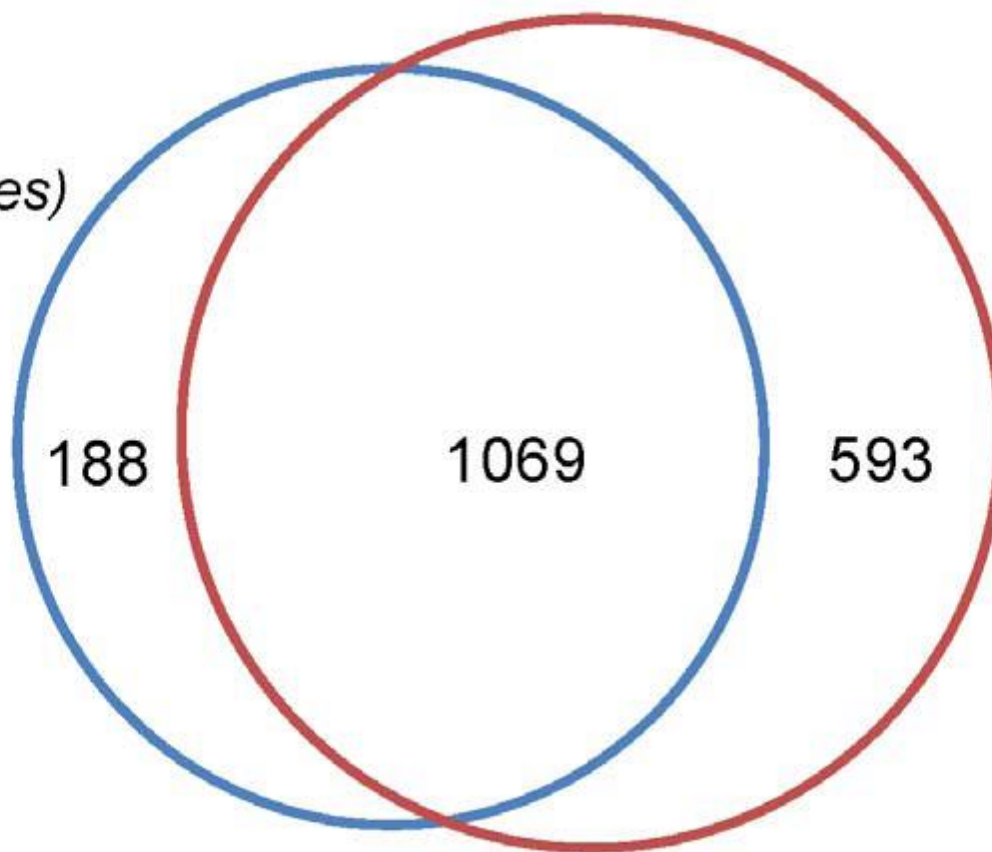
**Brook L. Nunn^{1,2*}, Jessica F. Faux³, Anna A. Hippmann⁴, Maria T. Maldonado⁴, H. Rodger Harvey⁵,
David R. Goodlett¹, Philip W. Boyd⁶, Robert F. Strzepek⁷**

2014 PLoS ONE

Iron replete

1257

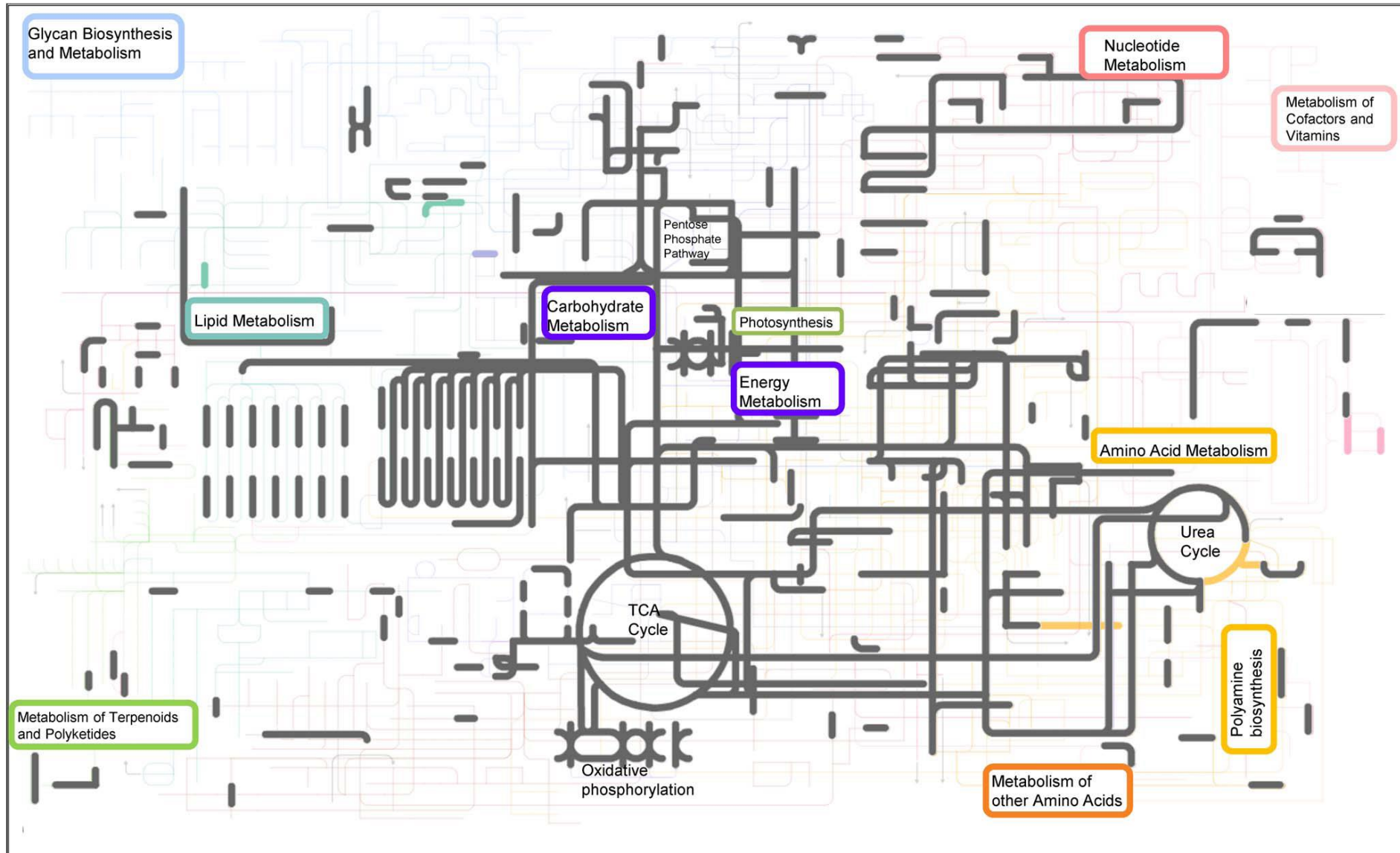
(51 homologues)



Iron deplete

1662

(42 homologues)



+Fe

Nunn et al. 2014

Glycan Biosynthesis and Metabolism

Nucleotide Metabolism

Metabolism of Cofactors and Vitamins

Lipid Metabolism

Carbohydrate Metabolism

Photosynthesis

Energy Metabolism

Amino Acid Metabolism

Urea Cycle

TCA Cycle

Polyamine biosynthesis

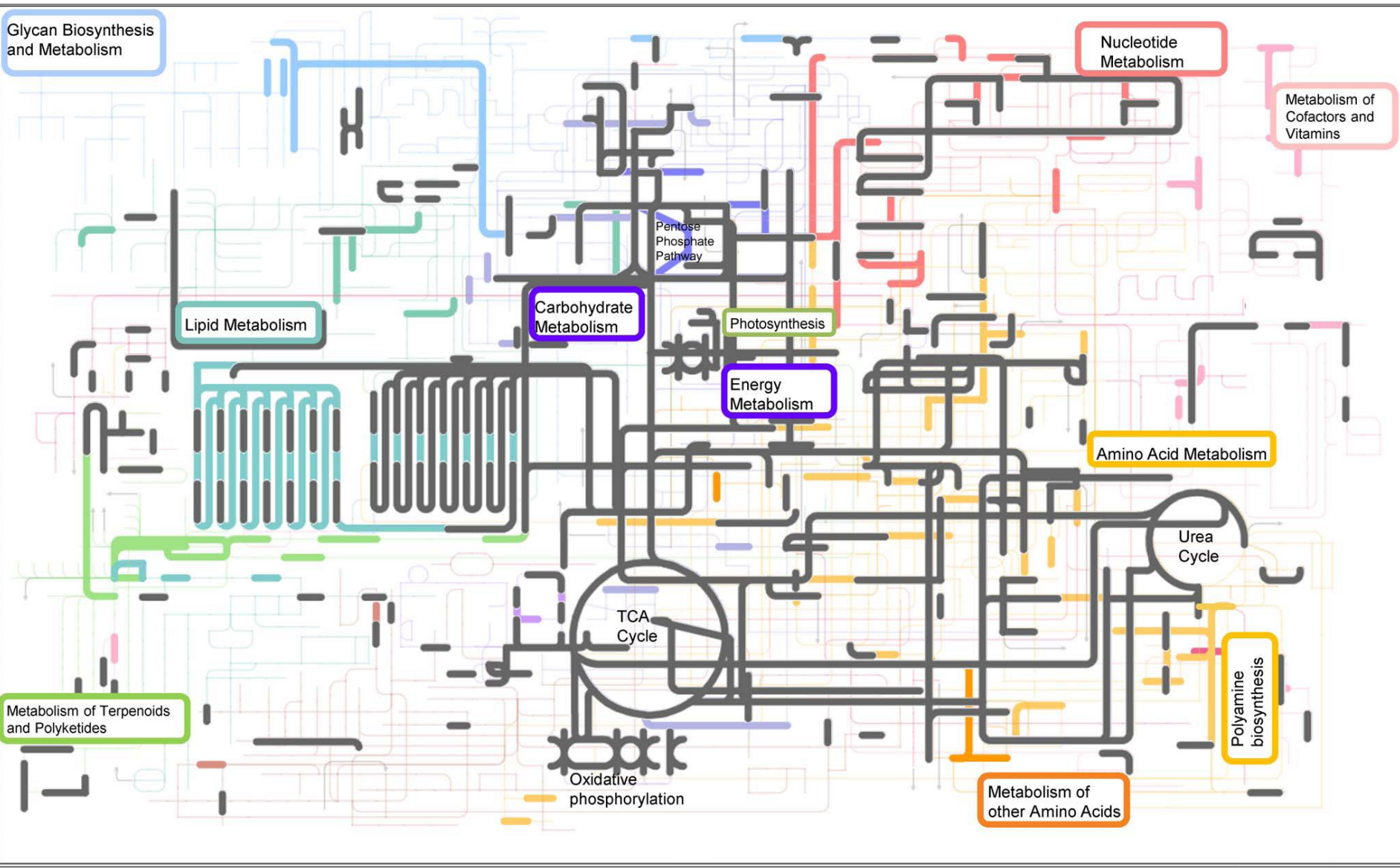
Metabolism of Terpenoids and Polyketides

Oxidative phosphorylation

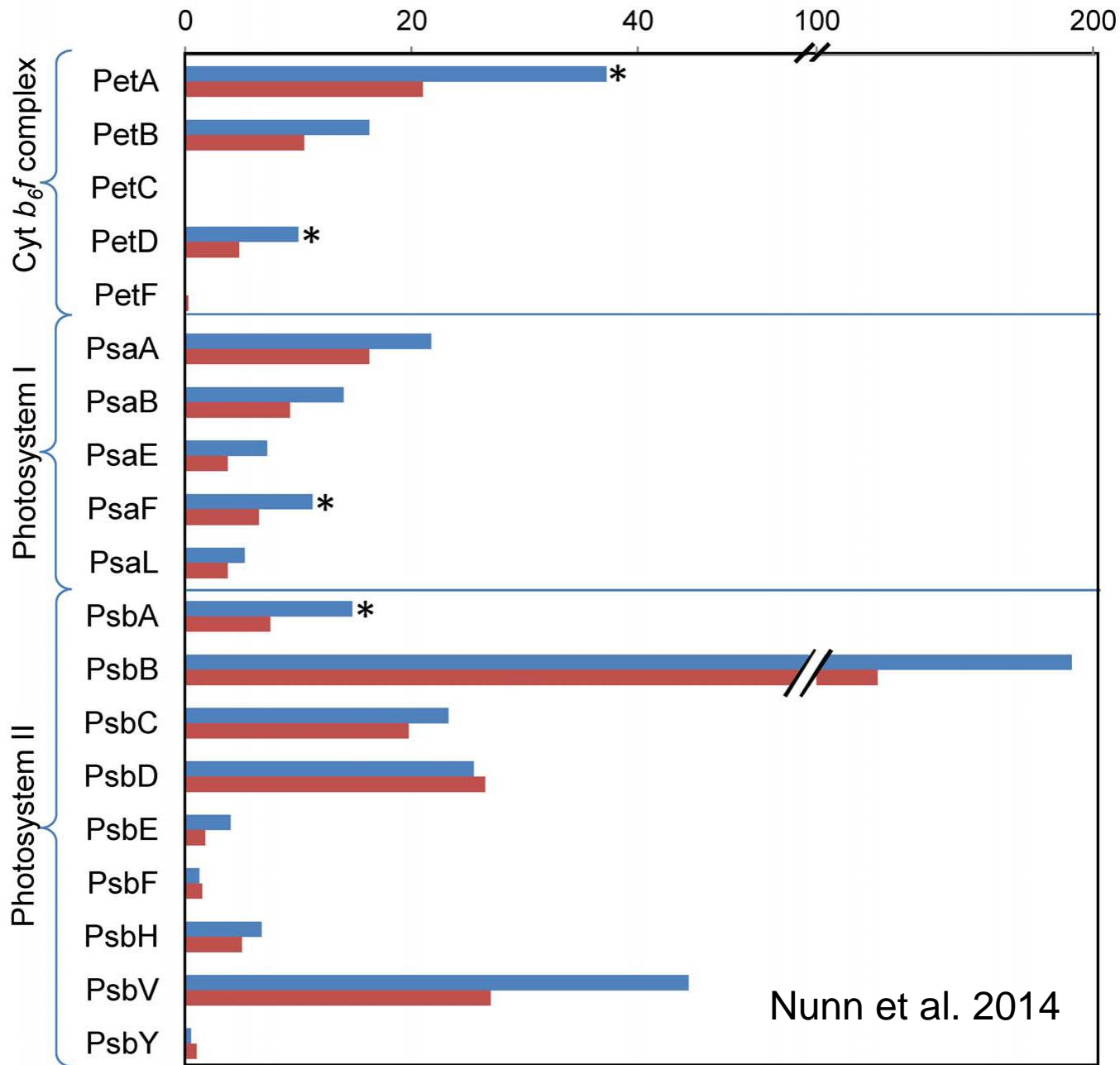
Metabolism of other Amino Acids

-Fe

Nunn et al. 2014

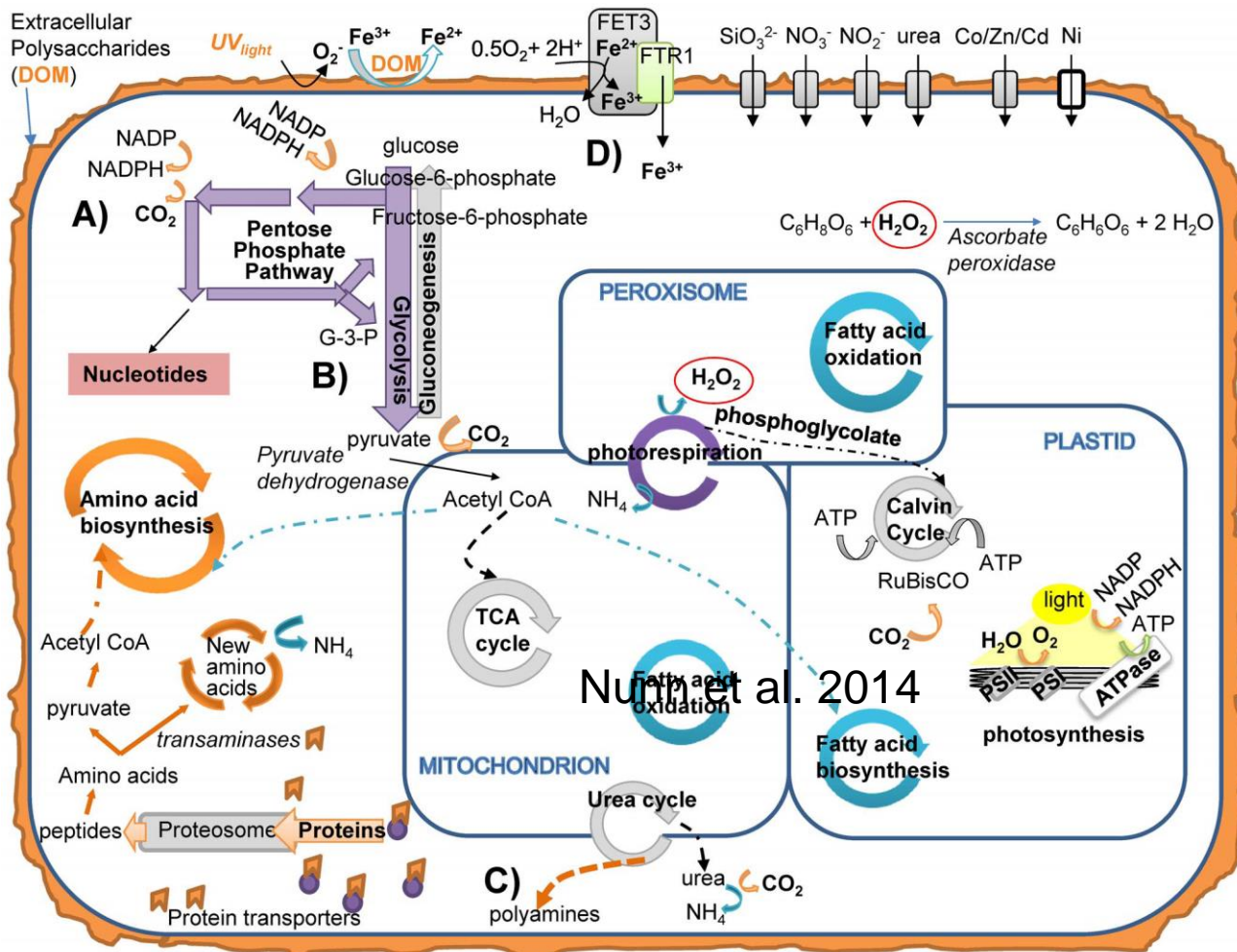


Total Peptide Spectral Counts



+Fe
* up-reg

Nunn et al. 2014



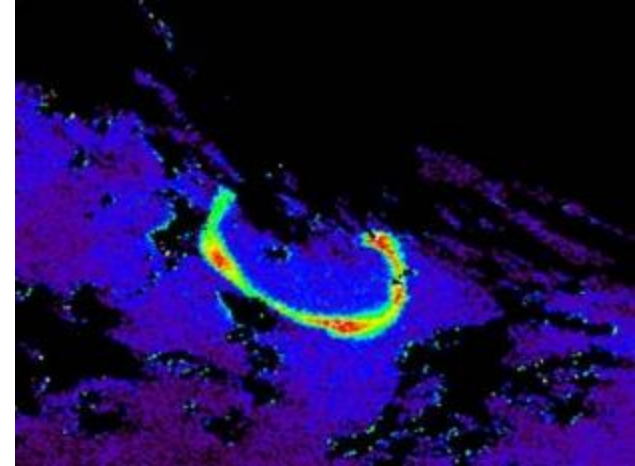
Nunn et al. 2014

In summary – when diatoms are acclimated to Fe limitation
 Proteomics suggest that intracellular N and Fe recycling are used
 To conserve essential resources during mid-exponential growth

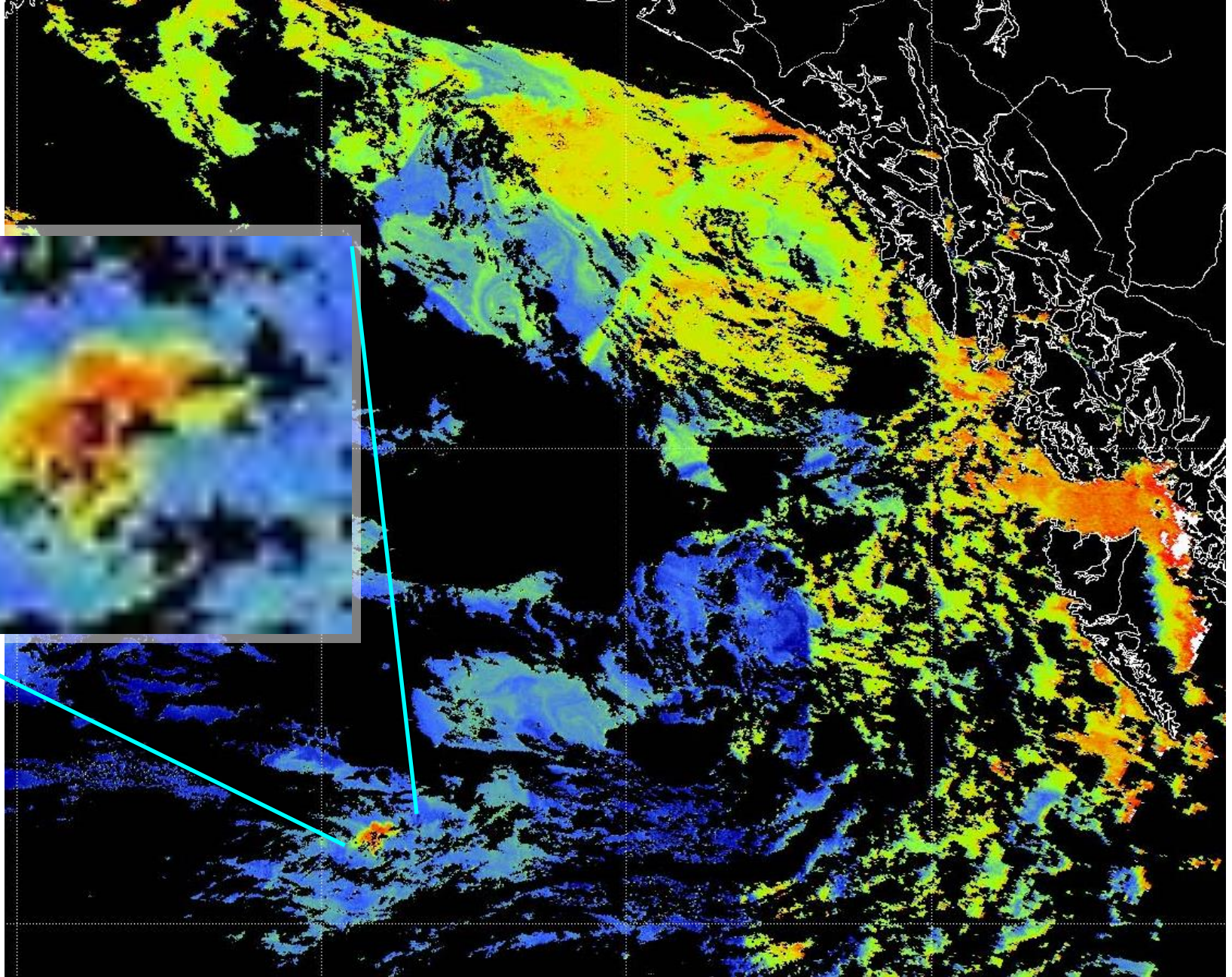
For example – up-regulation of transaminases and proteolytic enzymes
 Allows cells to harvest N from amino-acids

Opportunism of HNLC organisms

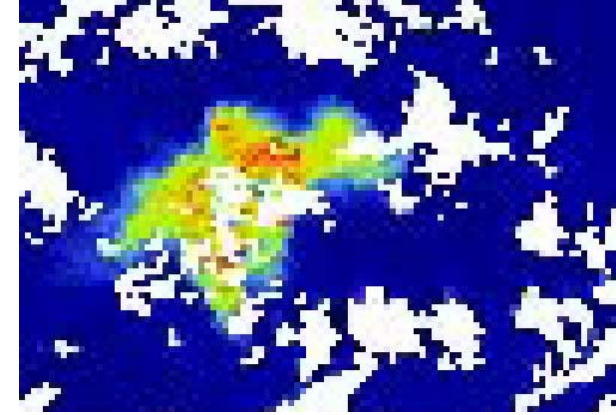
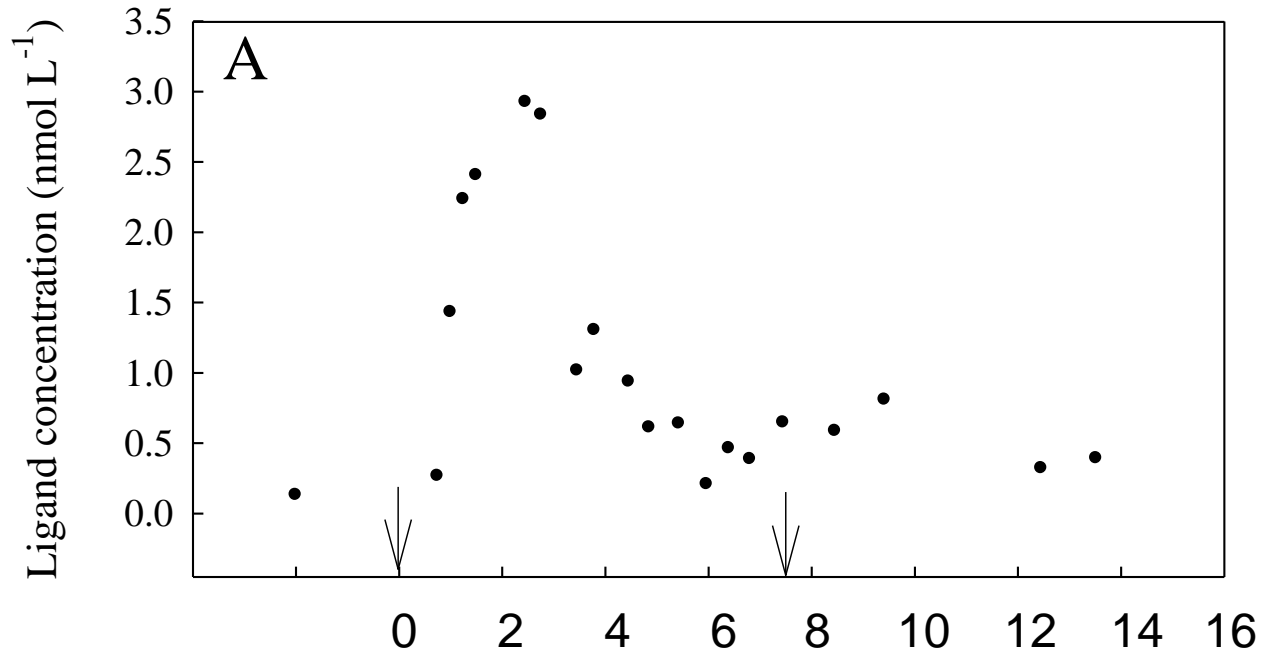
Timescales of responses to iron-enrichment



SOIREEDay	1	2	3	4	5	6	7	8	9	10	11	12	
PROCESS													
increasing Fv/Fm	[Green bar]												
decreasing Flavodoxin				[Green bar]									
increasing Flavodoxin								[Yellow bar]					

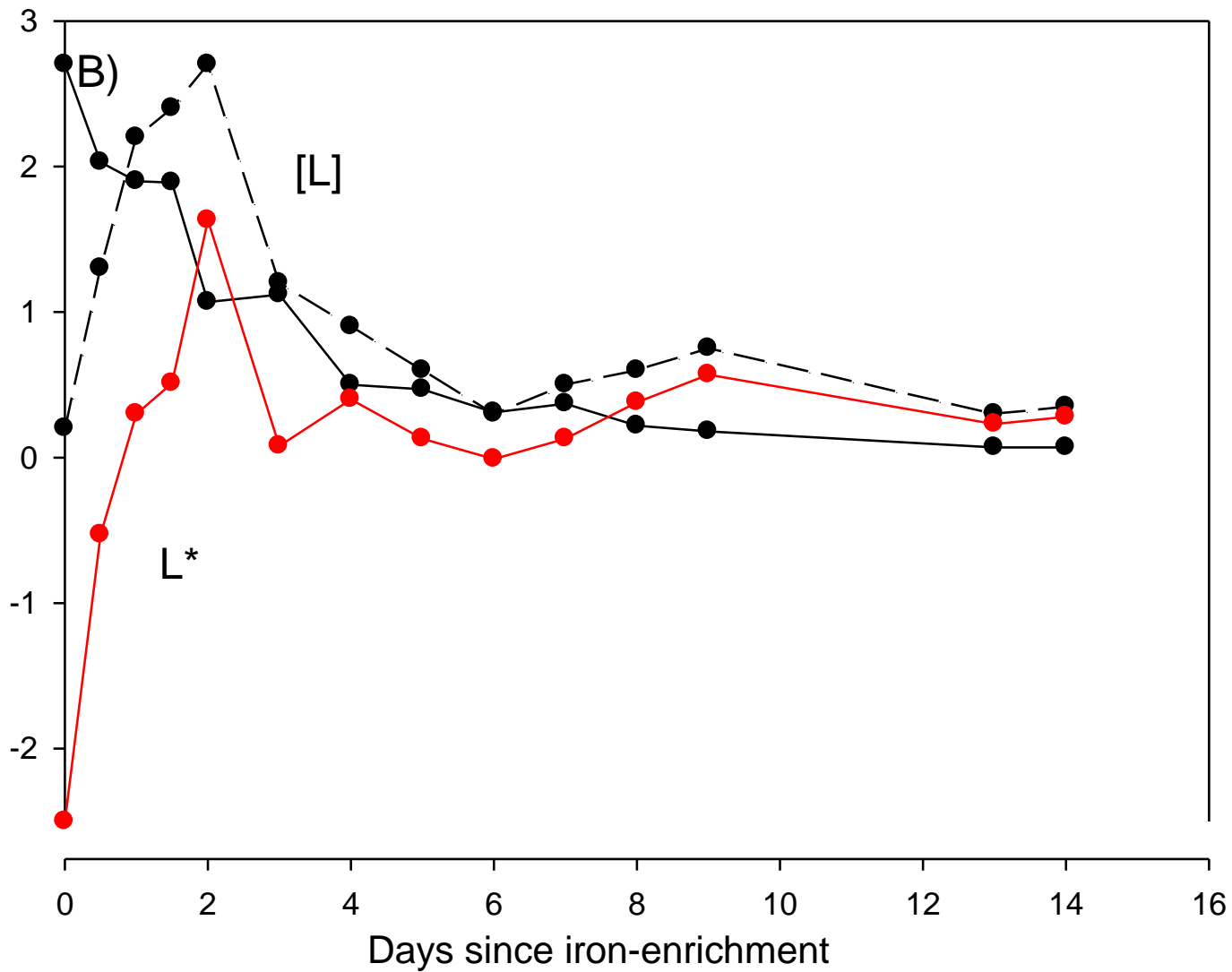


Timescales of responses to iron-enrichment



Adly 2002

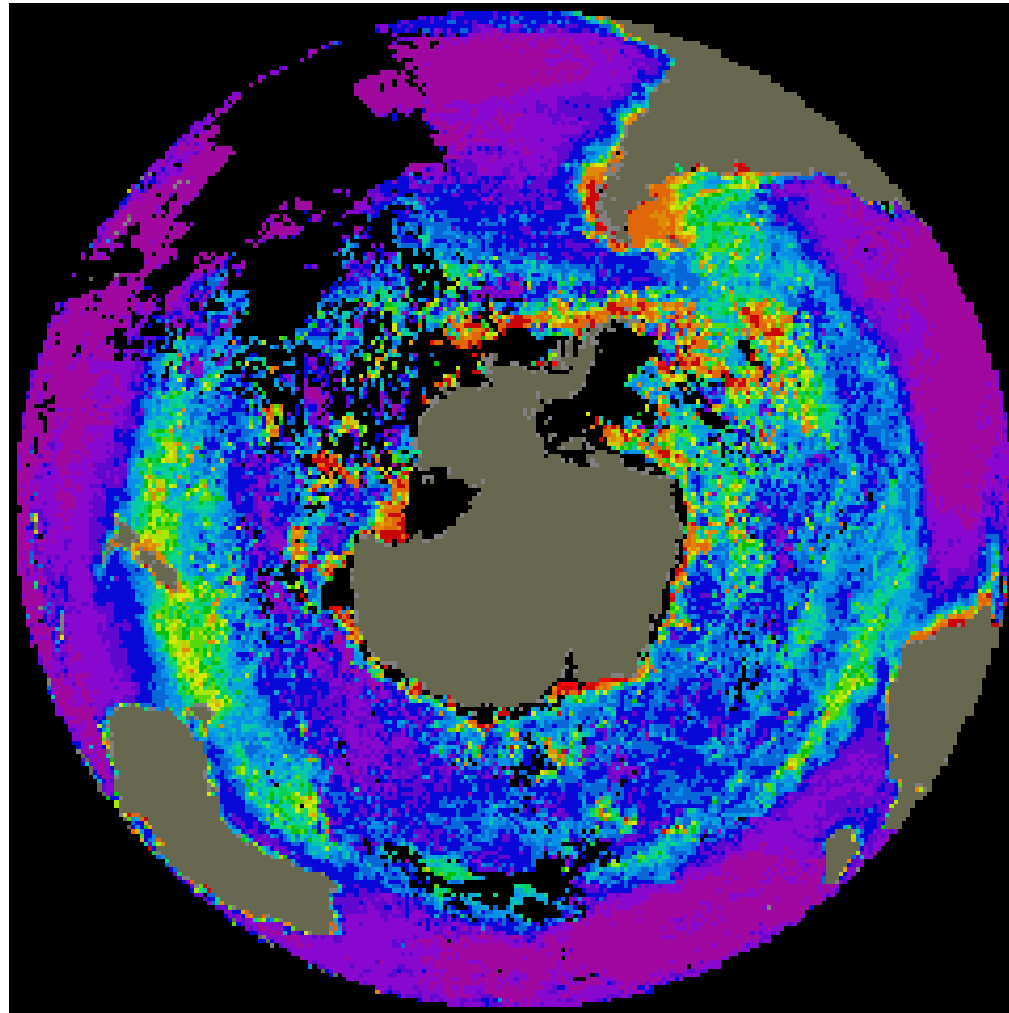
Opportunism is evident in HNLC waters



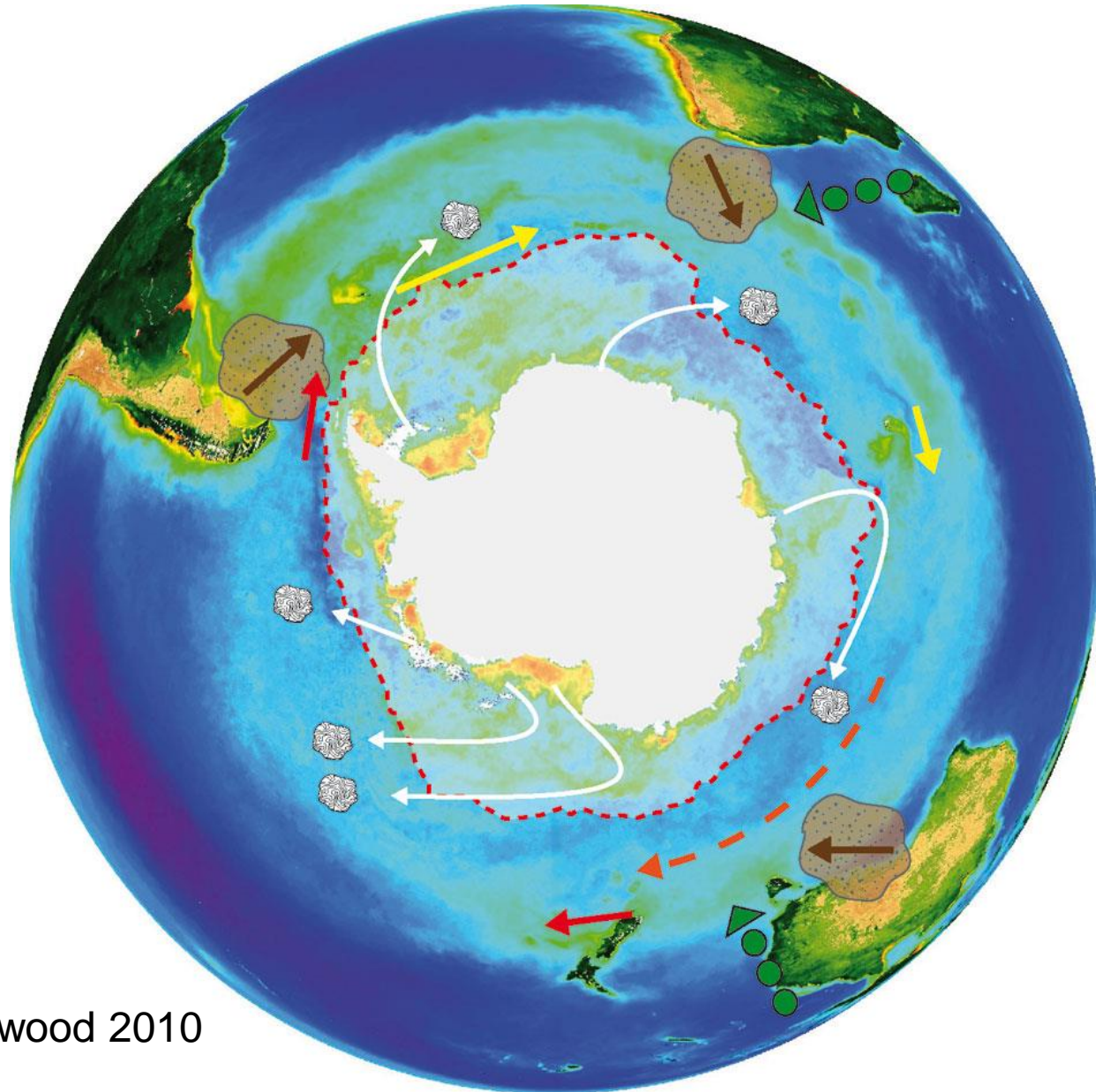
$$L^* = [L1] \text{ minus } [Dfe]$$

Boyd and Tagliabue (submitted)

A closer look at Southern Ocean HNLC 'waters'



> 10 iron supply terms



Boyd & Ellwood 2010

Iron biogeochemistry

C,N,P and
TM stoichiometry

Fe chemistry
& stable isotopes



Fe sources
& sinks

Fe
Biogeochemistry

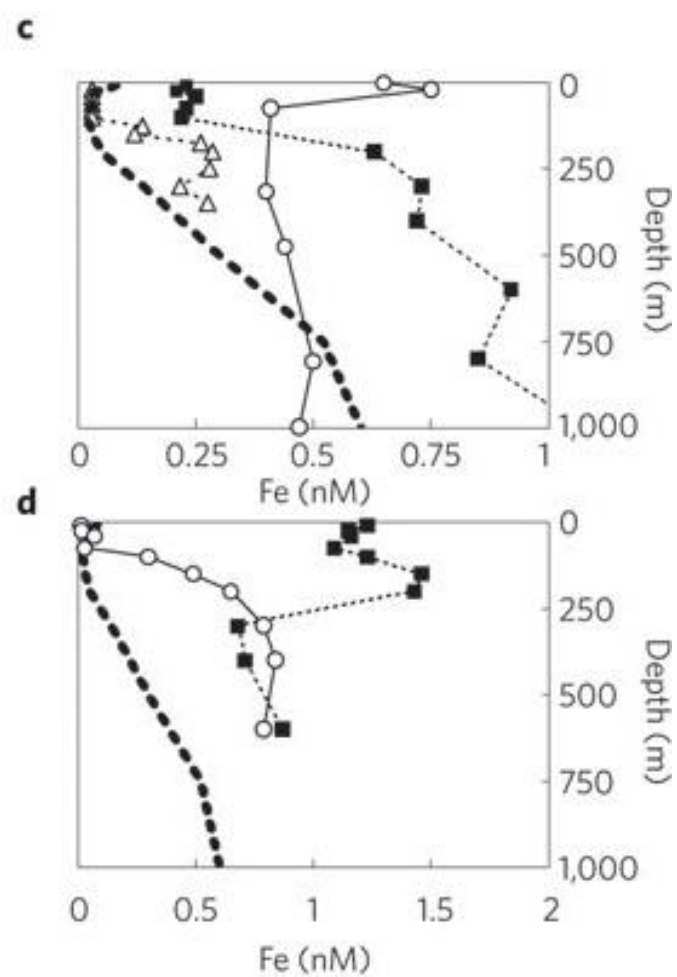
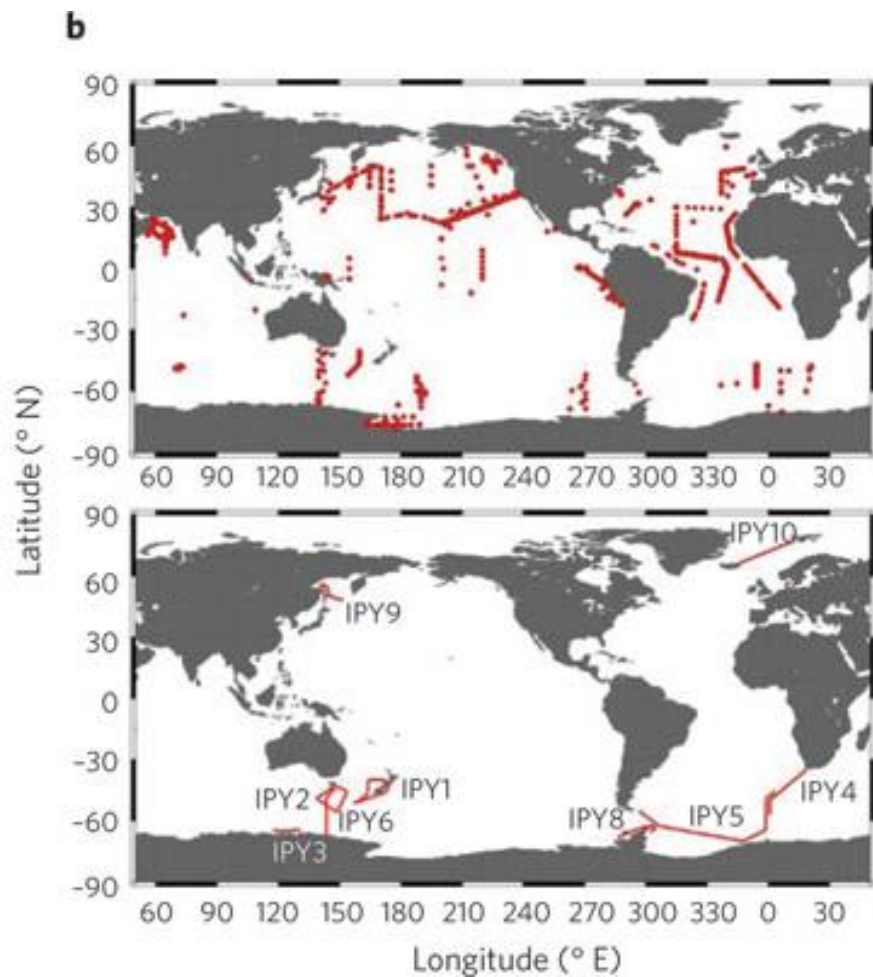
SOLAS
Dust deposition

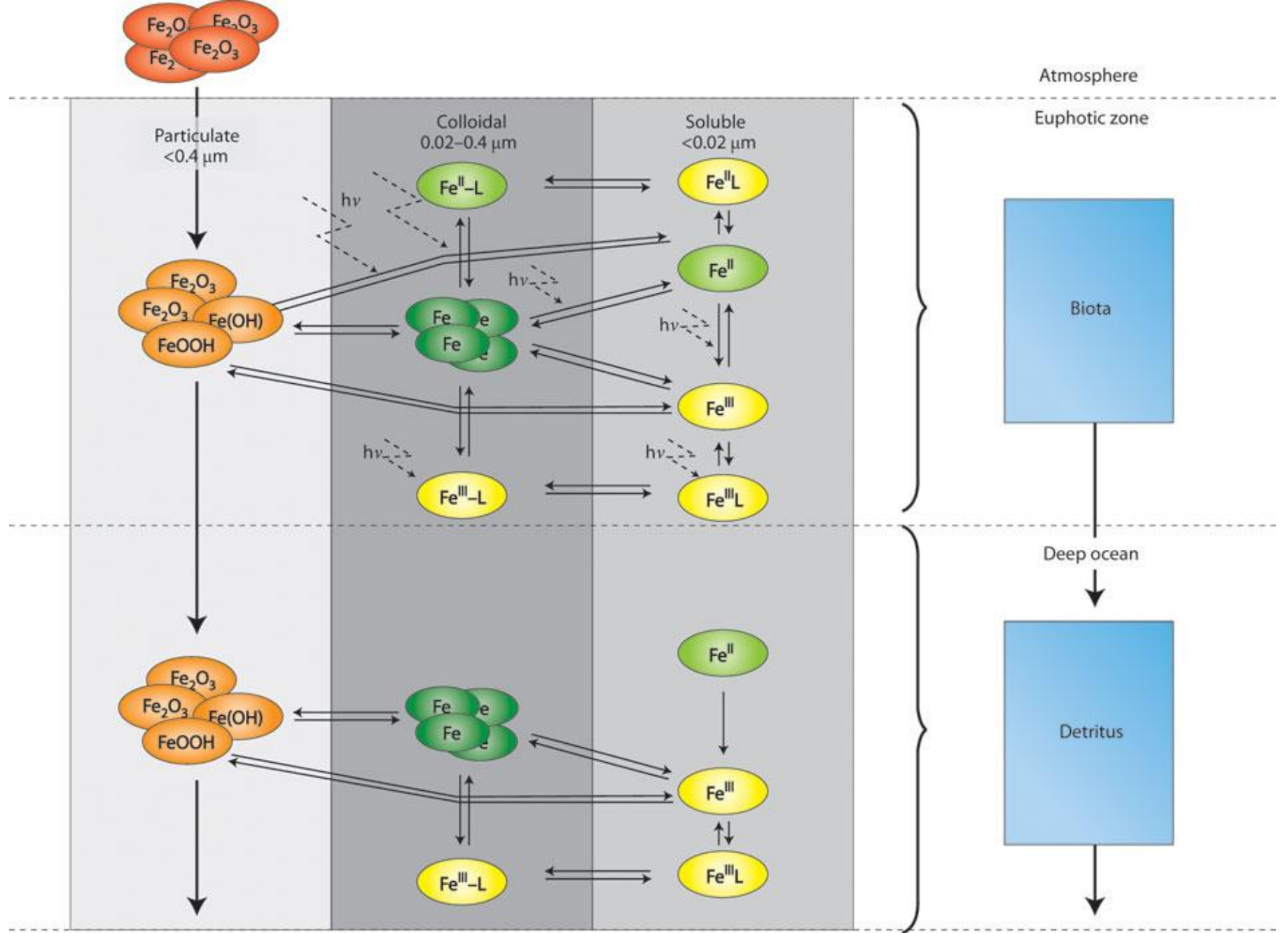
Ecology

Ligands

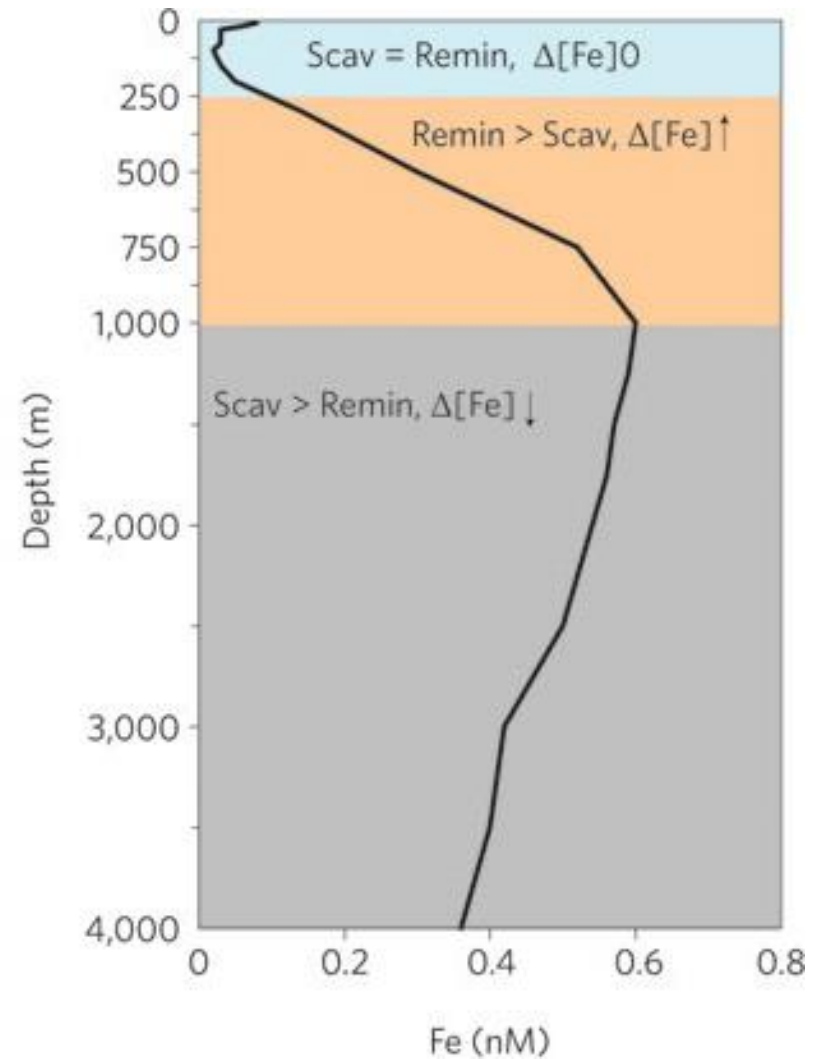
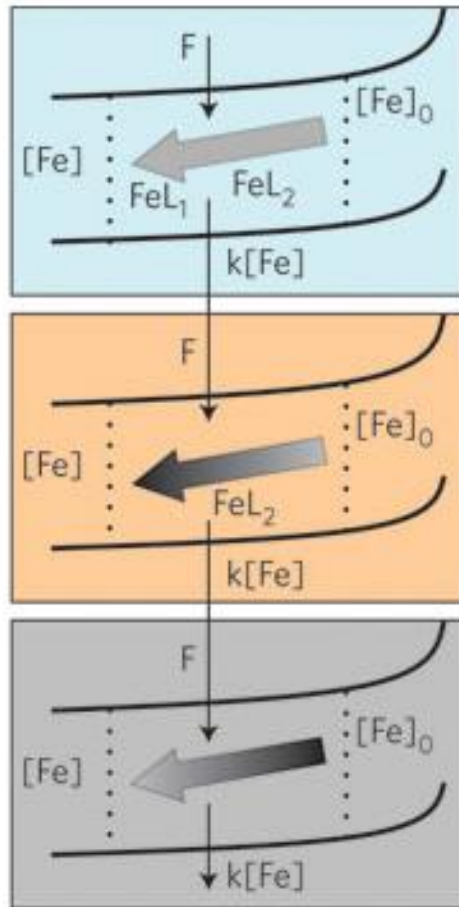
Omics
'Geomics'

GEO TRACES

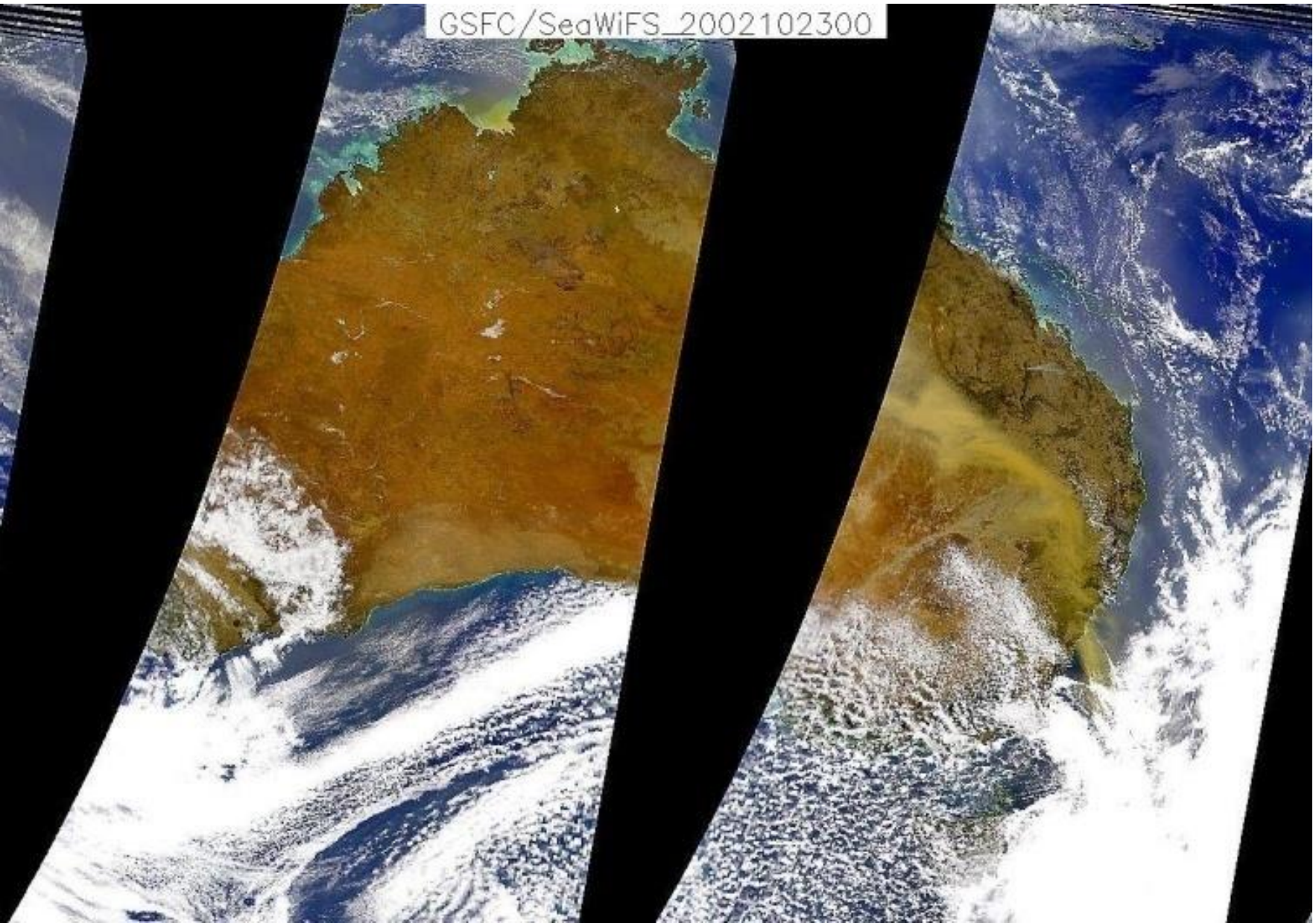




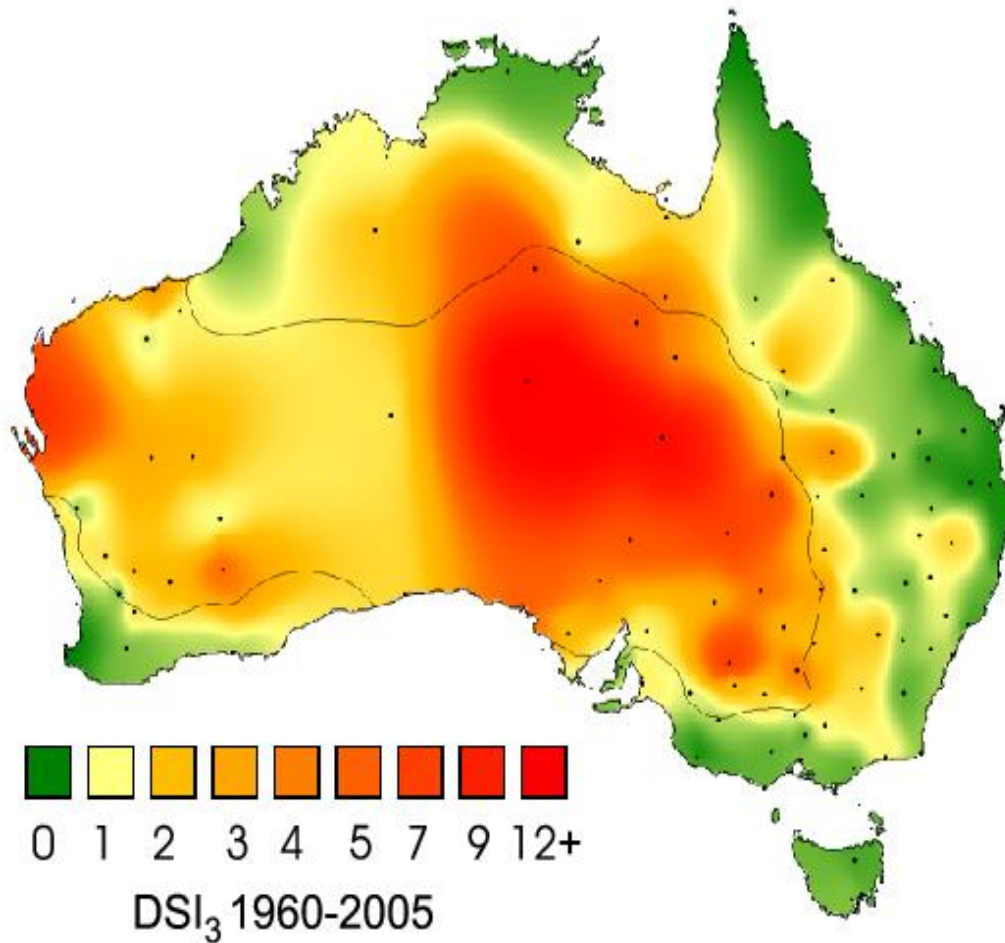
What sets the depth of the ferricline?



Regional Fe biogeochemistry

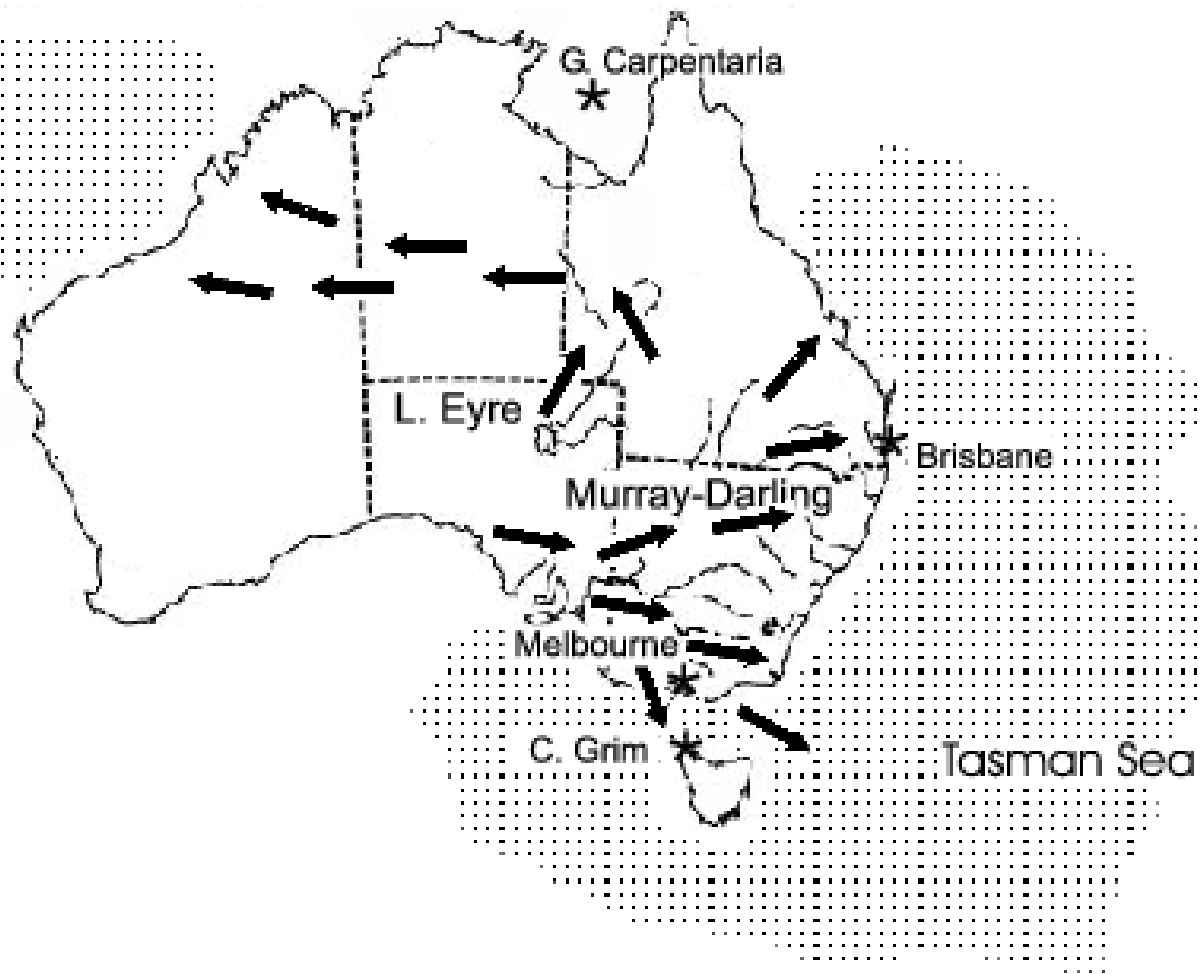


Dust distributions over Australia

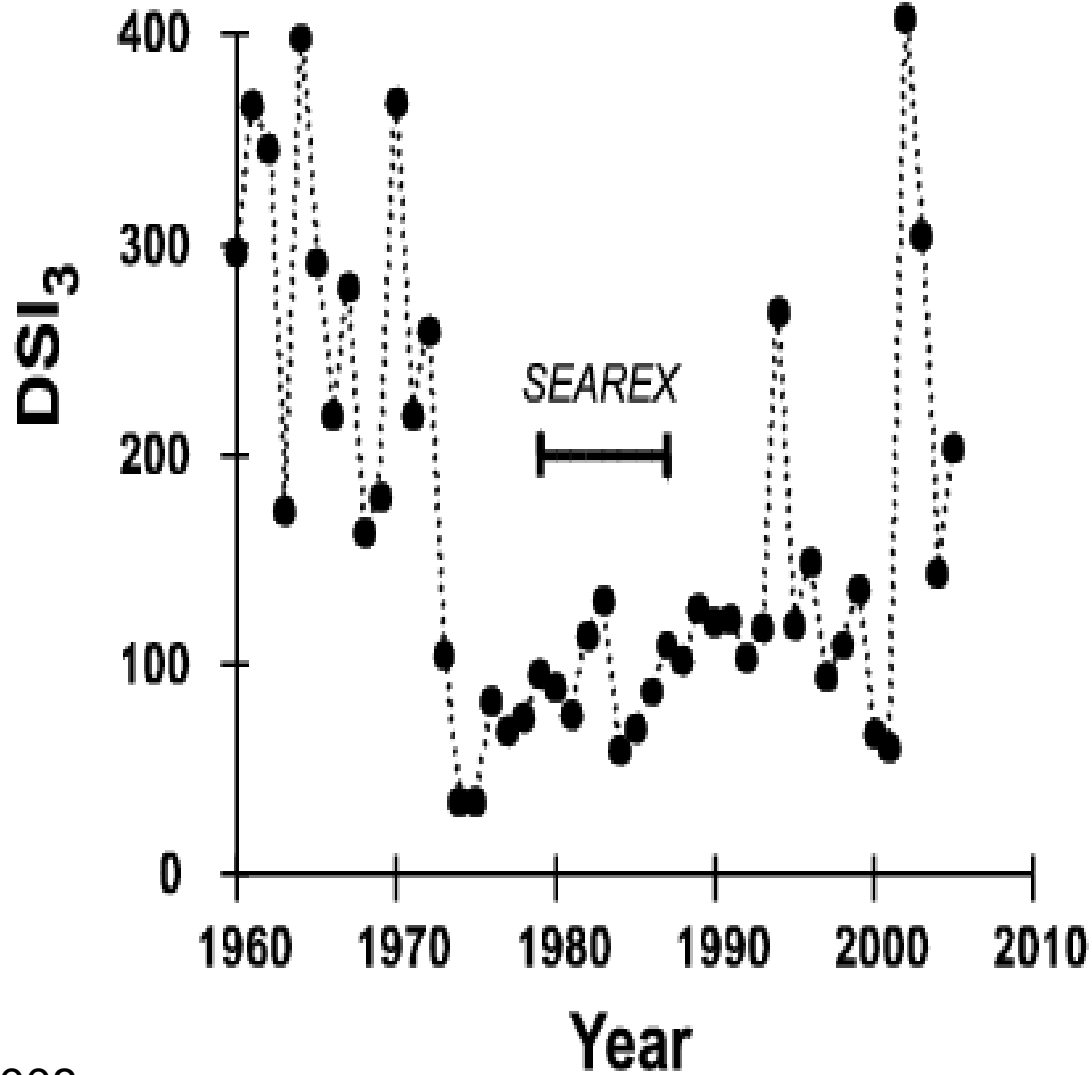


Mackie et al. 2008

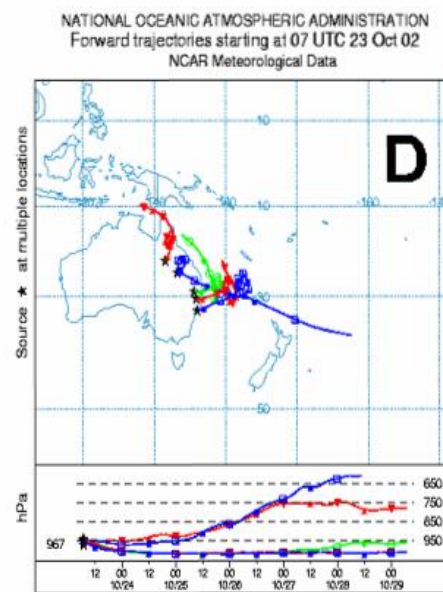
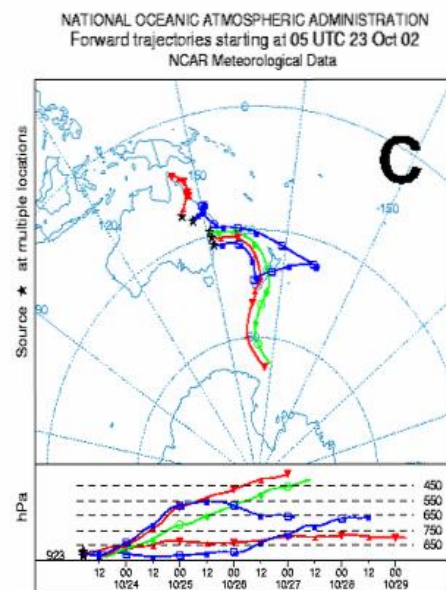
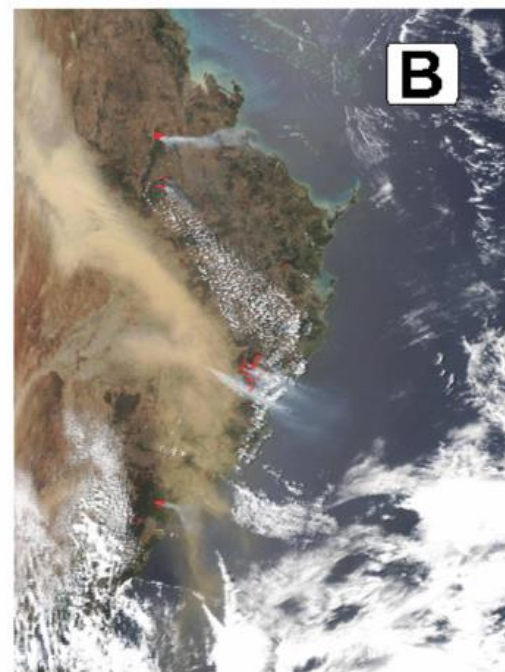
2 distinct dust outflow patterns from Australia



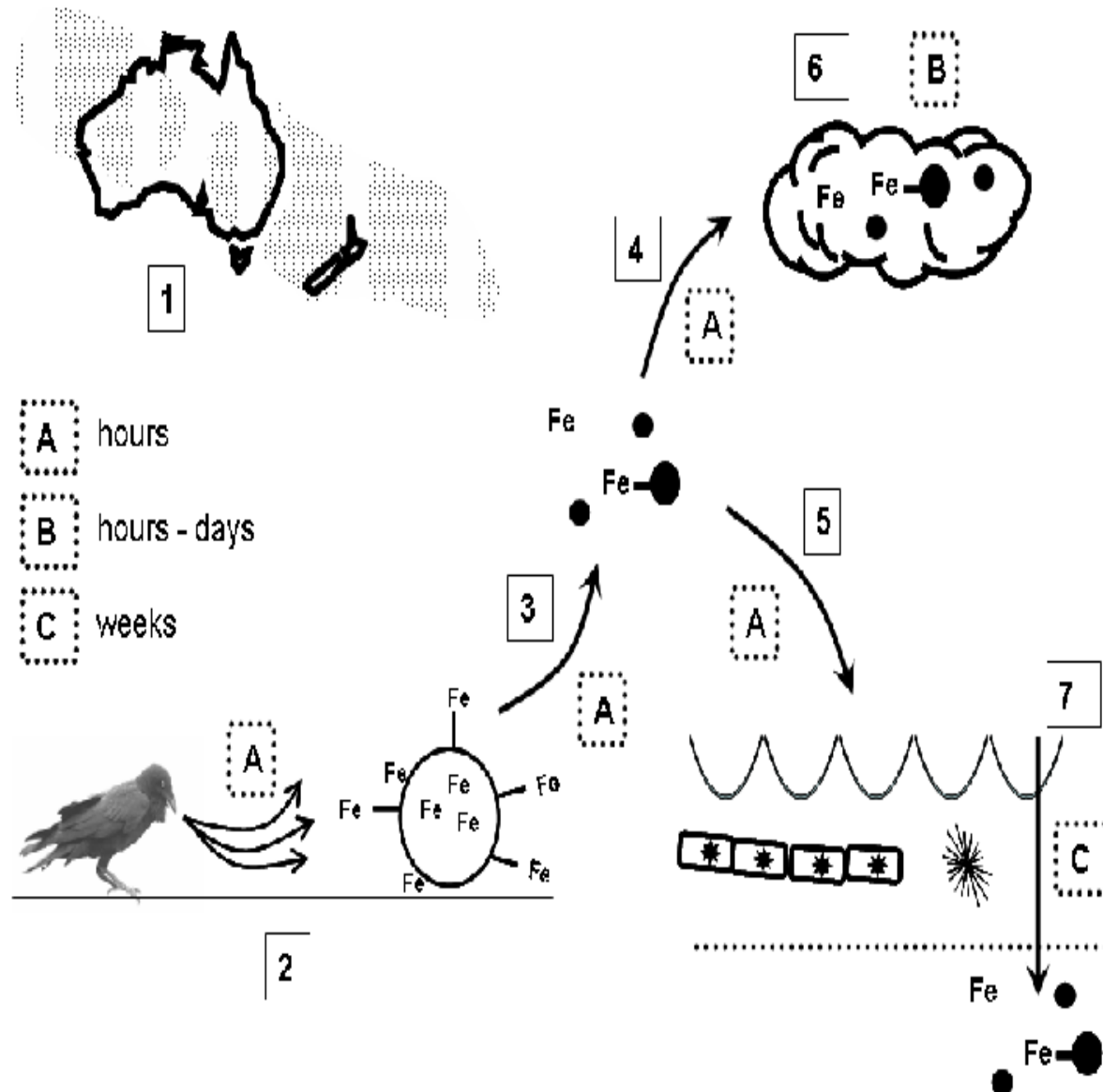
Time-series of dust distributions over Australia



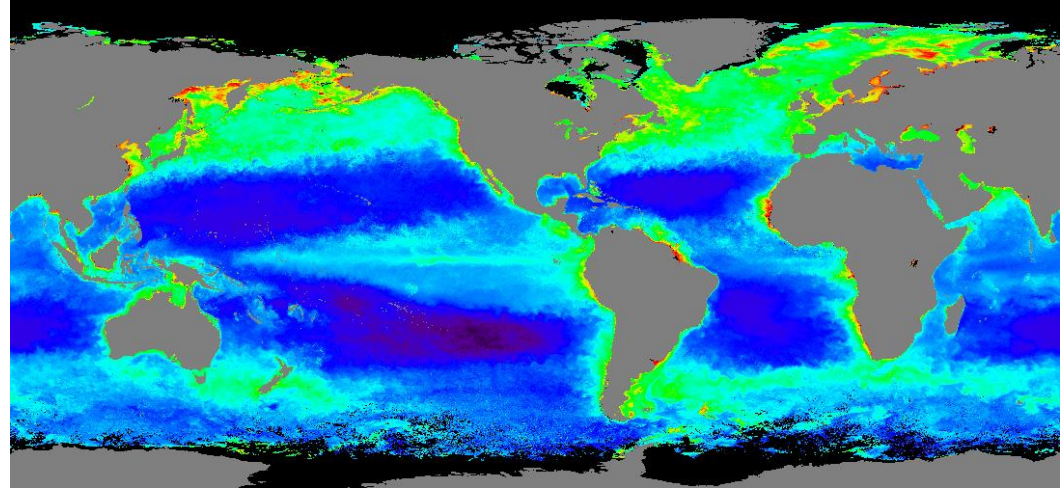
Air mass trajectories To follow dust storms



Biogeochemistry of iron in Australian dust



HNLC Regions of the Ocean



SUMMARY

HNLC waters – 30% OF OPEN OCEAN

Fe SUPPLY largely causes the HNLC condition

Biomass levels in HNLC waters are set by grazing pressure – which in turn resupplies iron

Recycled iron drives most of