Trace element bioavailability to communities in natural systems.

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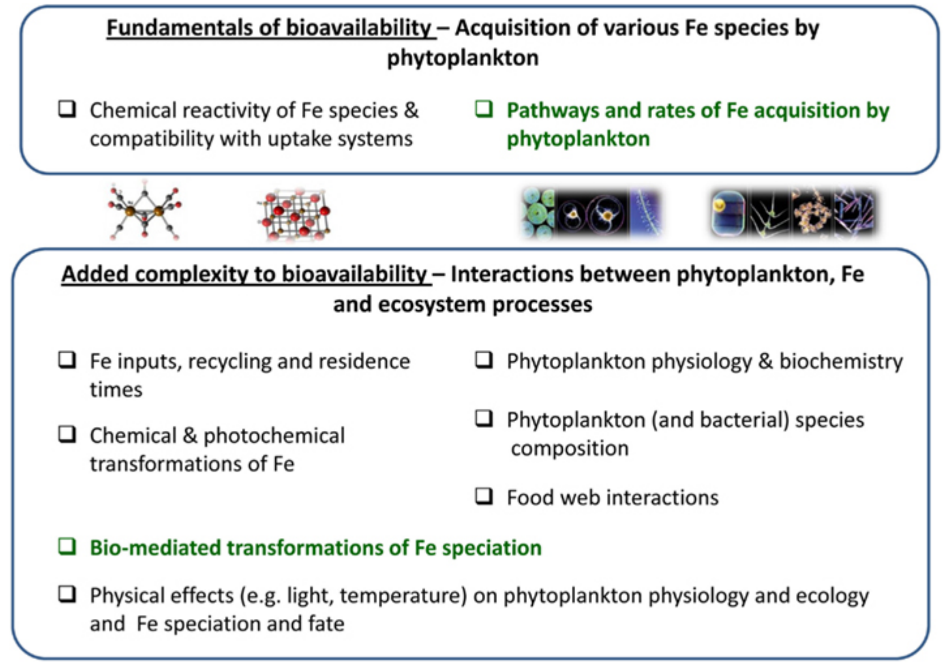
Introduction: what do we mean by 'bioavailability'?

'Bioavailability':

Multiple concepts operating at multiple time/space scales



Shaked and Lis 2012 *Frontiers*

Consider trace element 'bioavailability' in a broad system context, e.g. including:

Kinetics of uptake, overall availability versus requirements, nutrient limitation, circulation

Availability as a function of nutrient – biota feedbacks at system scales

Nutrient – Biota interactions

'It is a recognized principle of ecology that the interactions of organisms and environment are reciprocal. The environment not only determines the conditions under which life exists, but the organisms influence the conditions prevailing in their environment.'

Alfred Redfield (1958)

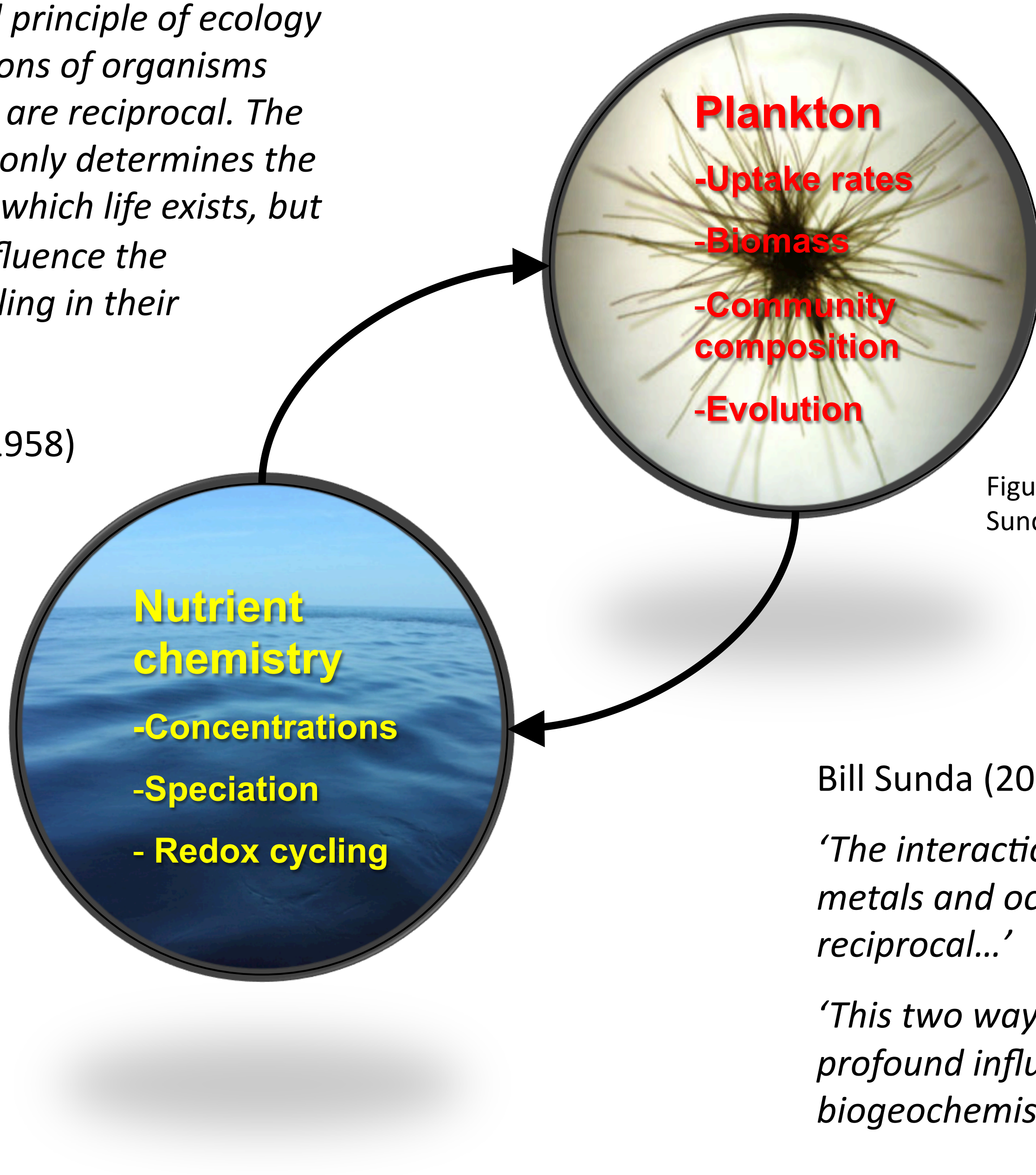


Figure after Sunda 2012

Bill Sunda (2012):

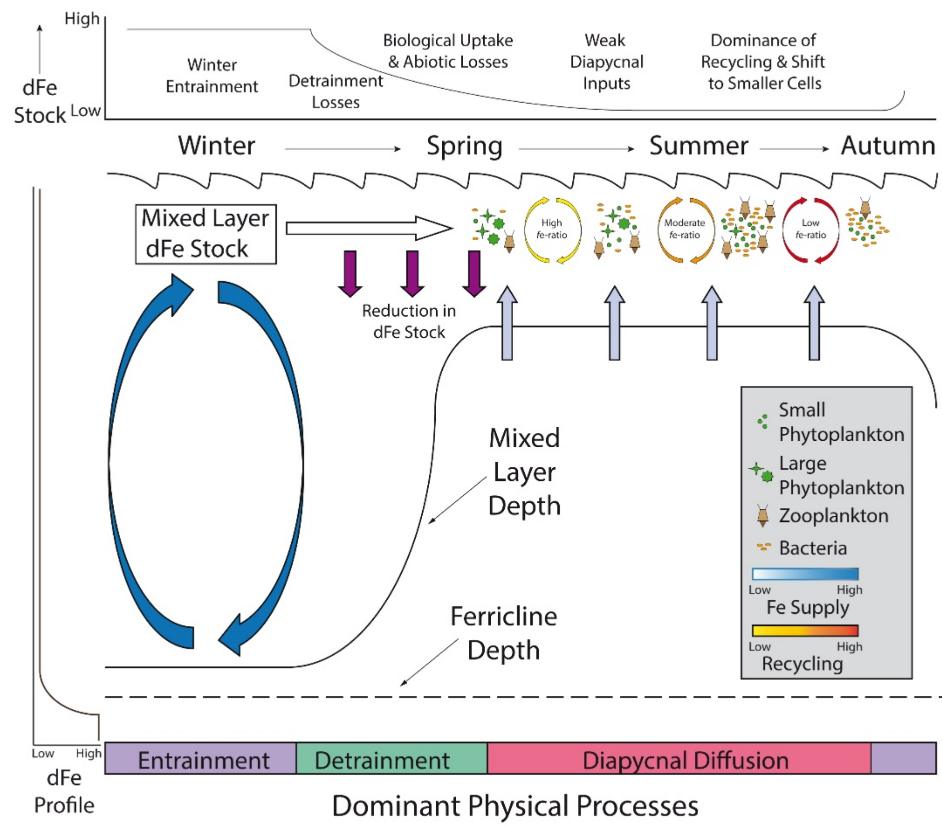
'The interactions between trace metals and ocean plankton are reciprocal…'

'This two way interaction… has a profound influence on the biogeochemistry of the ocean…'

Introduction: bioavailability as dynamic emergent system property

Bioavailability of a nutrient will be dynamic function of multiple system characteristics

Questions need to be considered in the context of appropriate spatio-temporal scales



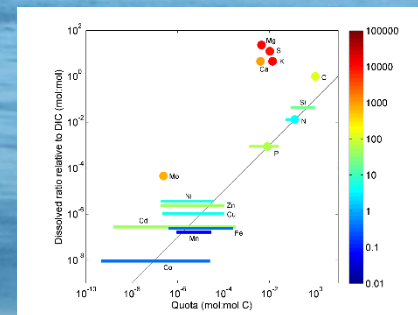
Tagliabue et al. (2014) *Nature Geo.*

Overview

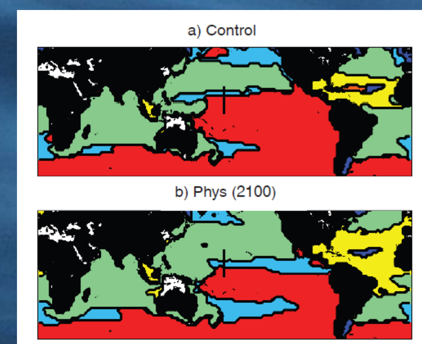
i) Whole ocean perspective: enriched versus unenriched metals

ii) Regional (~basin) scale: feedbacks and provinces

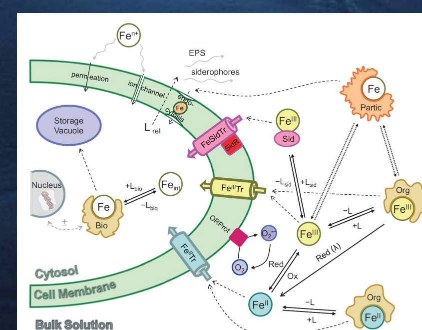
iii) Local-cellular scales: kinetics and complexities



Moore et al. 2013

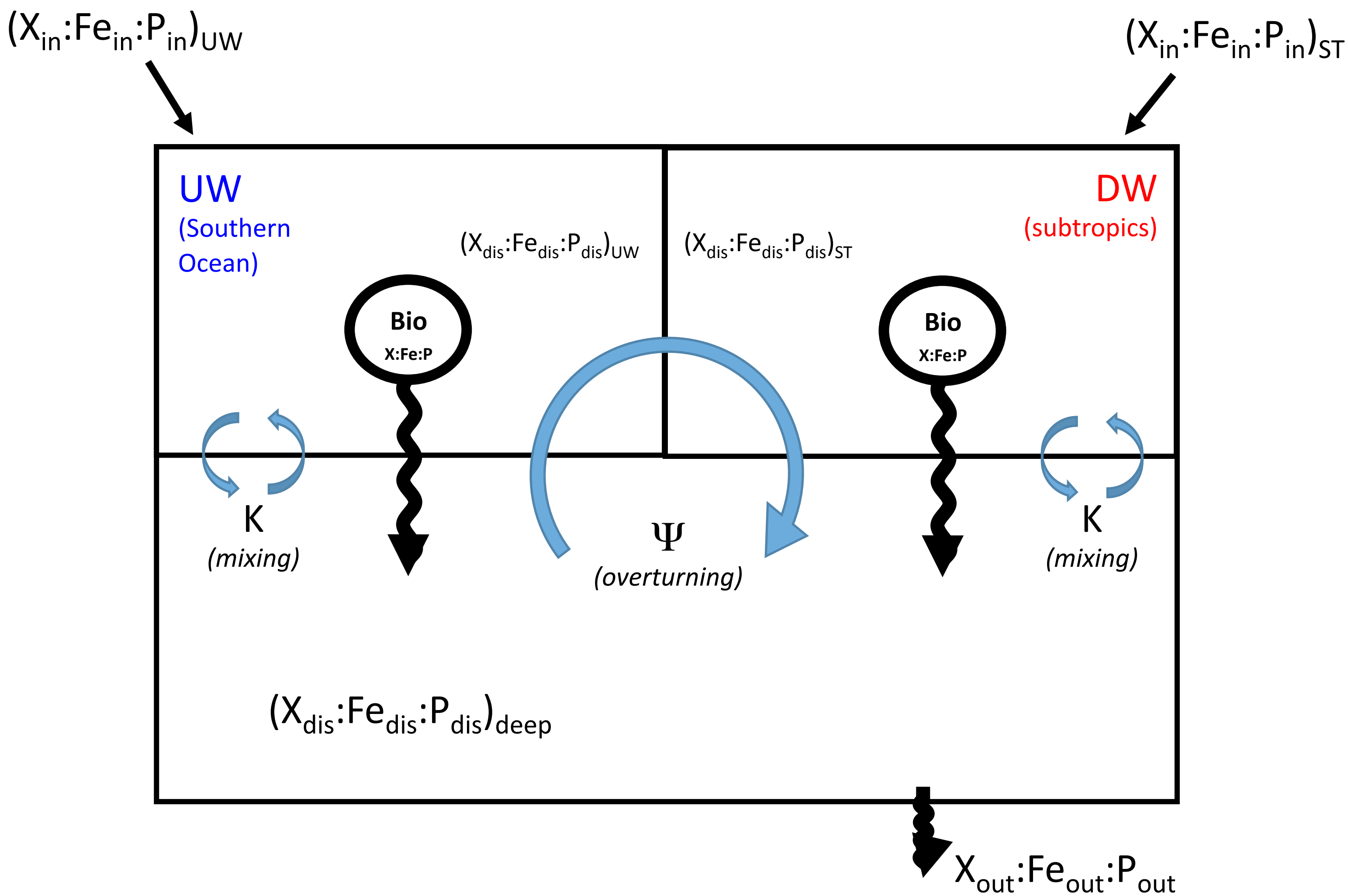


Dutkeiwicz et al. 2014



Hassler et al. 2011

Drivers of a multi-nutrient ocean



Based on: *Broecker 1971; Whitfield 1981; Tyrrell 1999; Parekh et al. 2004; Weber and Deutsch 2012*

i) Largest scales: oceanic inventories

Trace metals have differential availability (relative to biological demands) within the modern ocean

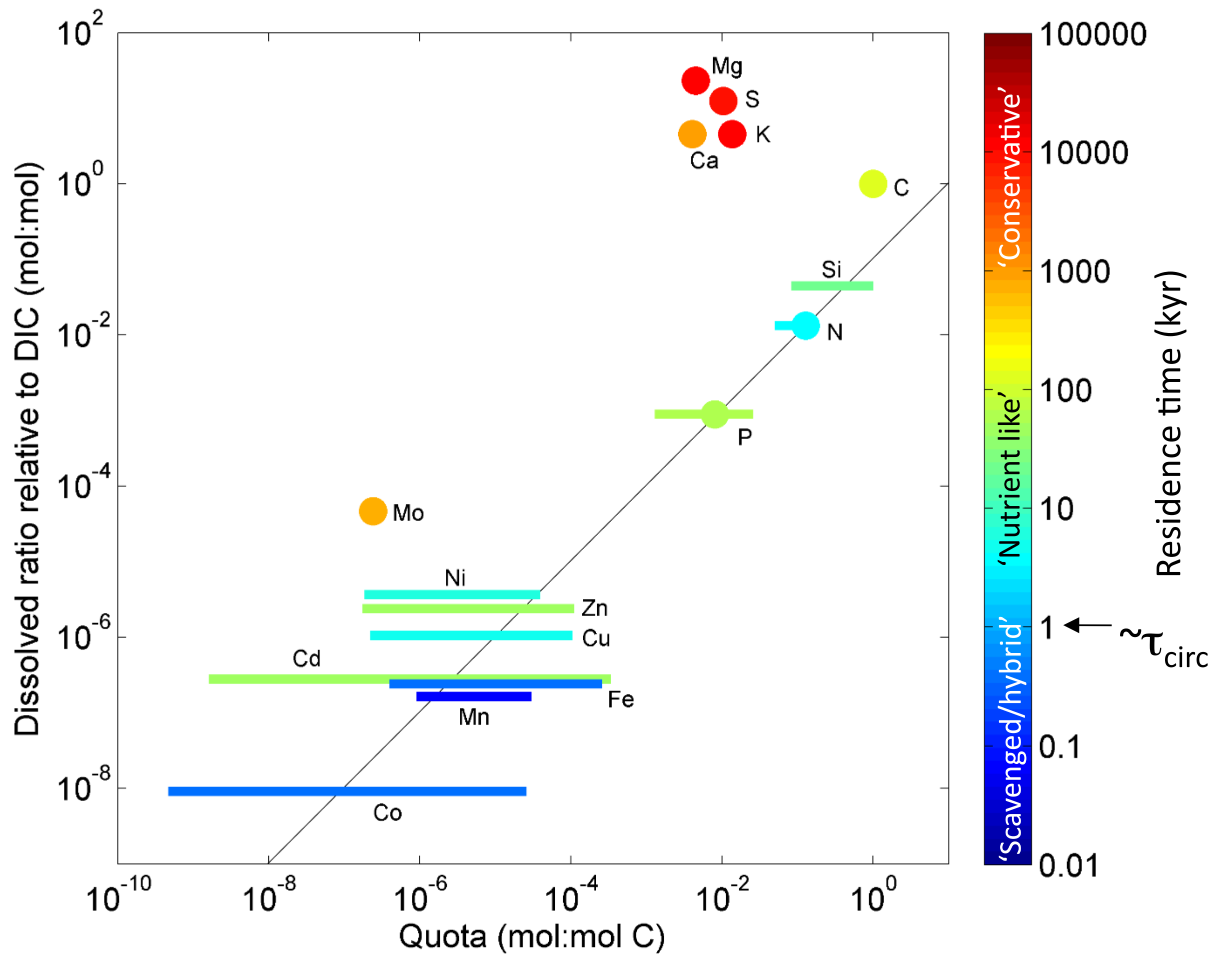


Figure adapted from Moore et al. (2013) *Nature Geo.*

'…you conveniently ignore all that stoichiometric variability…'

(Gideon Henderson, GEOTRACES mtg., London, Dec 2015)

Recognise it and embrace it… (e.g. *Sarmiento et al. 2004 Nature; Weber and Deutsch 2012 Nature; DeVries and Deutsch 2014 Nature Geo.; Galbraith and Martiny 2015 PNAS*)

i) Largest scales: oceanic inventories

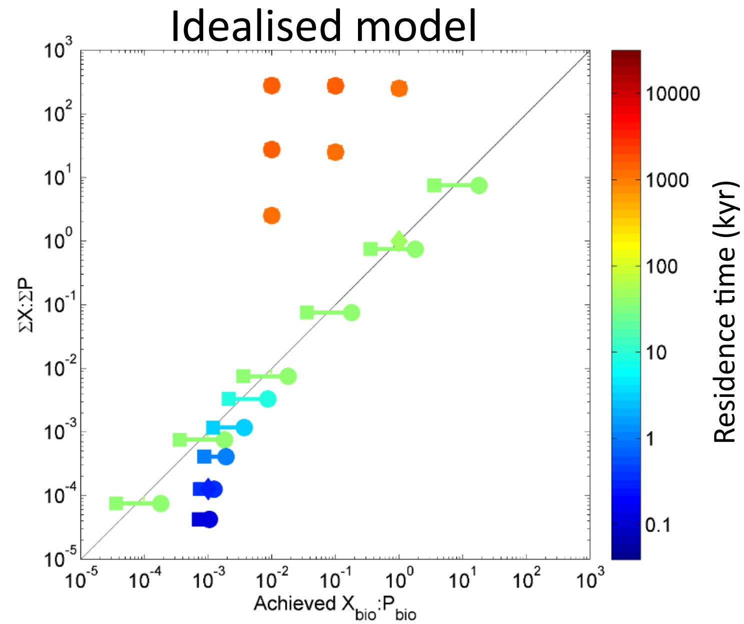
Driving factors for nutrient 'X' include:

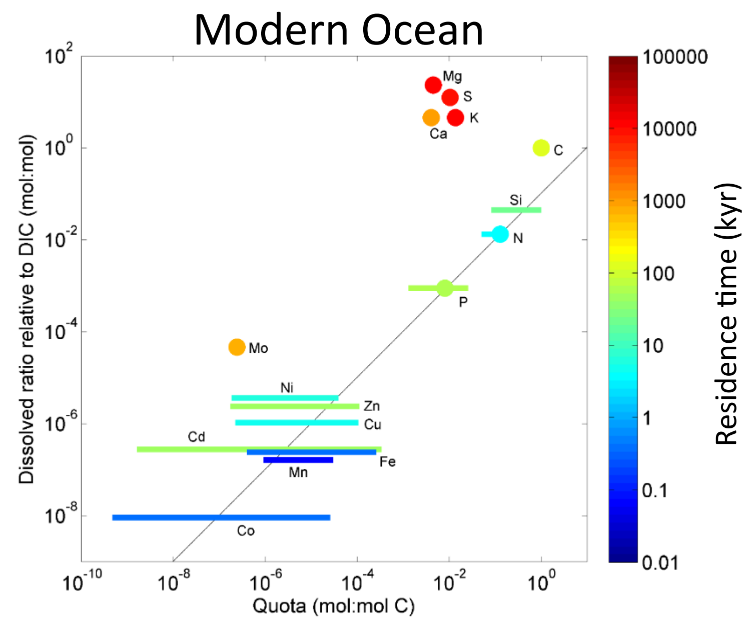
1) Stoichiometry of input relative to other nutrients* (i.e. $X_{in}:P_{in}$)

2) Loss/burial* (both 'abiotic' and biotic)

3) *Minimum* and *maximum* biological stoichiometry, i.e. $(X_{bio}:P_{bio})_{min}$ and $(X_{bio}:P_{bio})_{max}$

*See e.g. *Broecker 1971; Whitfield 1981*

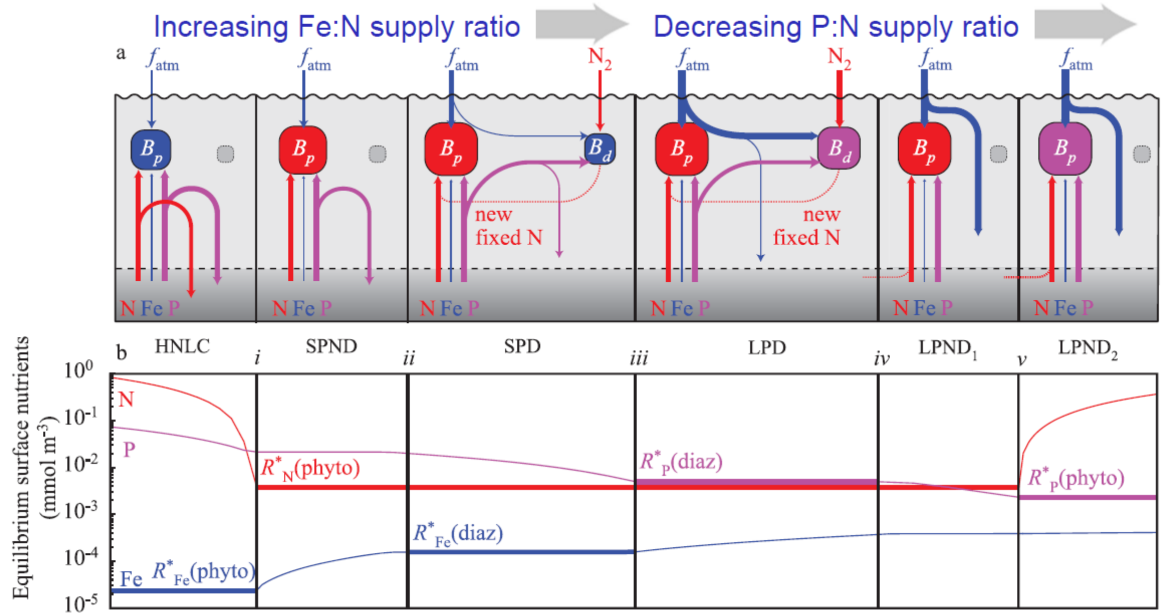




ii) Province scale: nutrient-biota feedbacks and *R**

Resource ratio framework (Tilman 1982) provides a conceptual basis for interpreting multi-nutrient – biota interactions.

Within regimes individual nutrients can both limit and be controlled by individual microbial 'types'.



Ward et al. (2013) L&O

Limiting nutrient dictated by *ratios of nutrient supply* relative to microbial requirements (*demand*)

R* (the equilibrium nutrient concentration) is a function of ecosystem characteristics

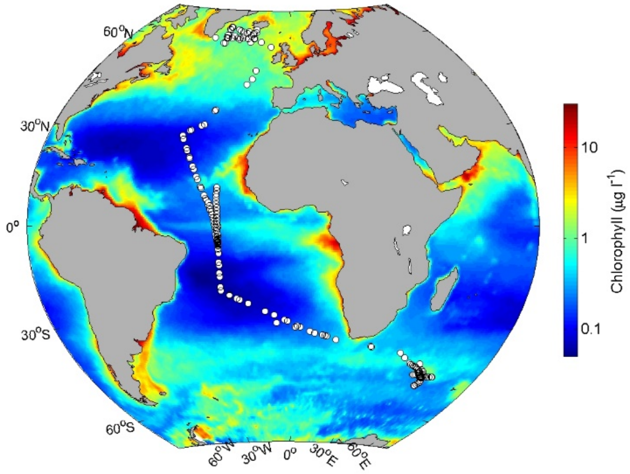
Biotic standing stock, is a function of limiting nutrient supply

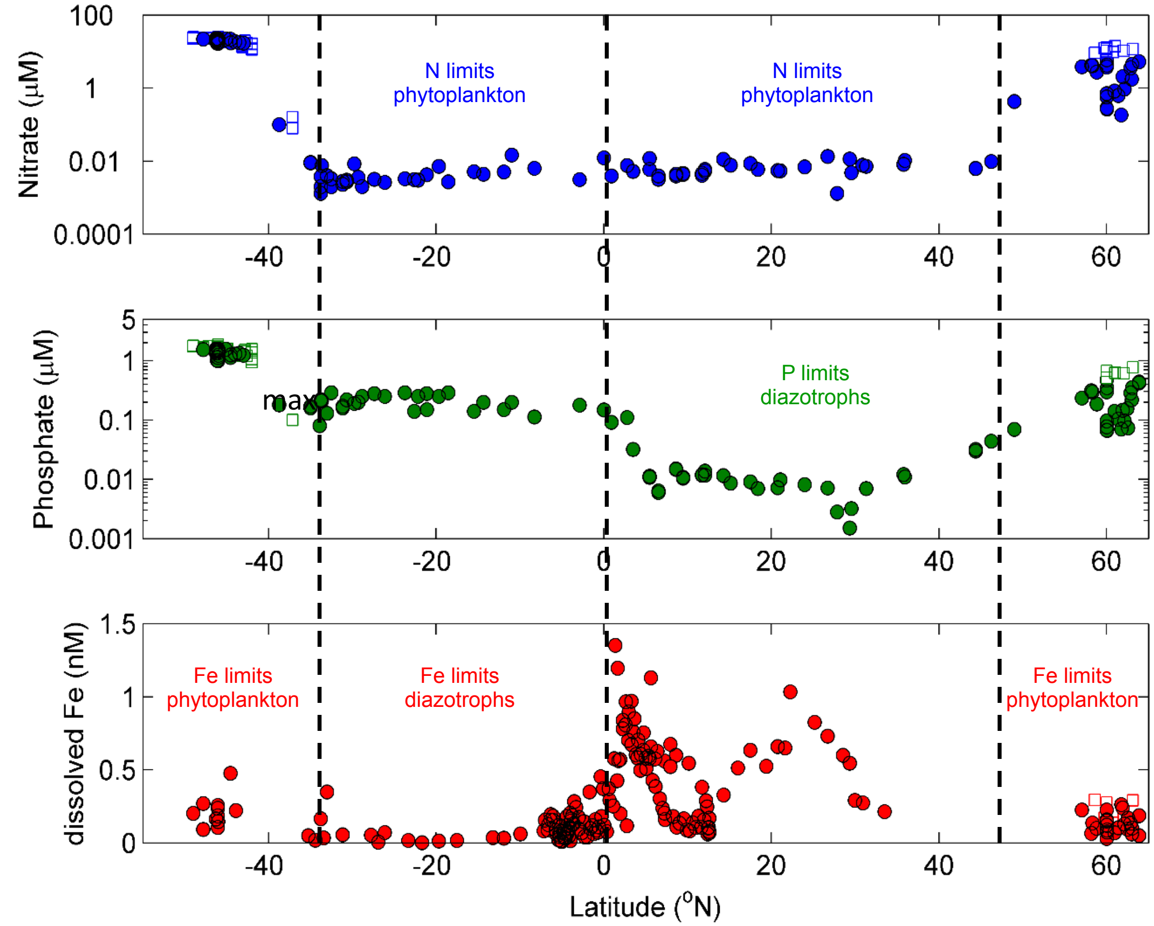
$$R^* = \frac{Half\ stauration\ const.}{\frac{Max\ growth\ rate}{mortality} - 1}$$

$$Biomass = \frac{Supply\ rate}{mortality}$$

See e.g. Dutkiewicz et al. (2009) GBC; Dutkiewicz et al. (2012) GBC; Ward et al. (2013) L&O.

ii) Province scale: nutrient-biota feedbacks





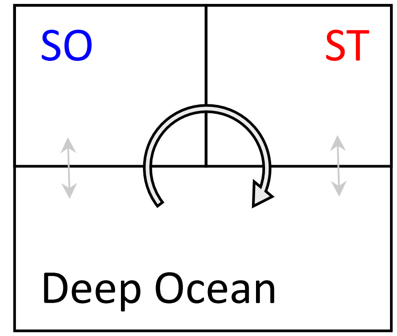
Three principal limiting nutrients clearly delineate 4 'biogeochemical provinces' in the Atlantic Ocean.

UK GEOTRACES
micronutrient cycles and paleoproxies in the ocean

Dutkeiwicz et al. 2009; 2012 GBC; Moore et al. 2009 Nature Geo.; Sohm et al. 2011 Nature Rev. Micro.; Ward et al. 2013 L&O; Schlosser et al. 2014 PNAS

Two regimes: Fe and 'P'

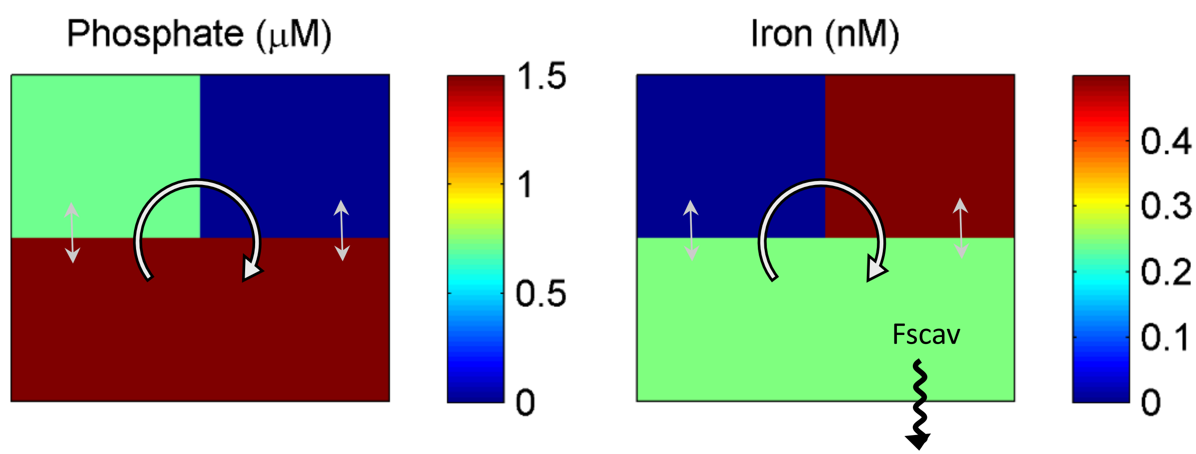
Back to simple framework



Schematic circulation

The 'macronutrient' ('P') becomes limiting in downwelling surface box

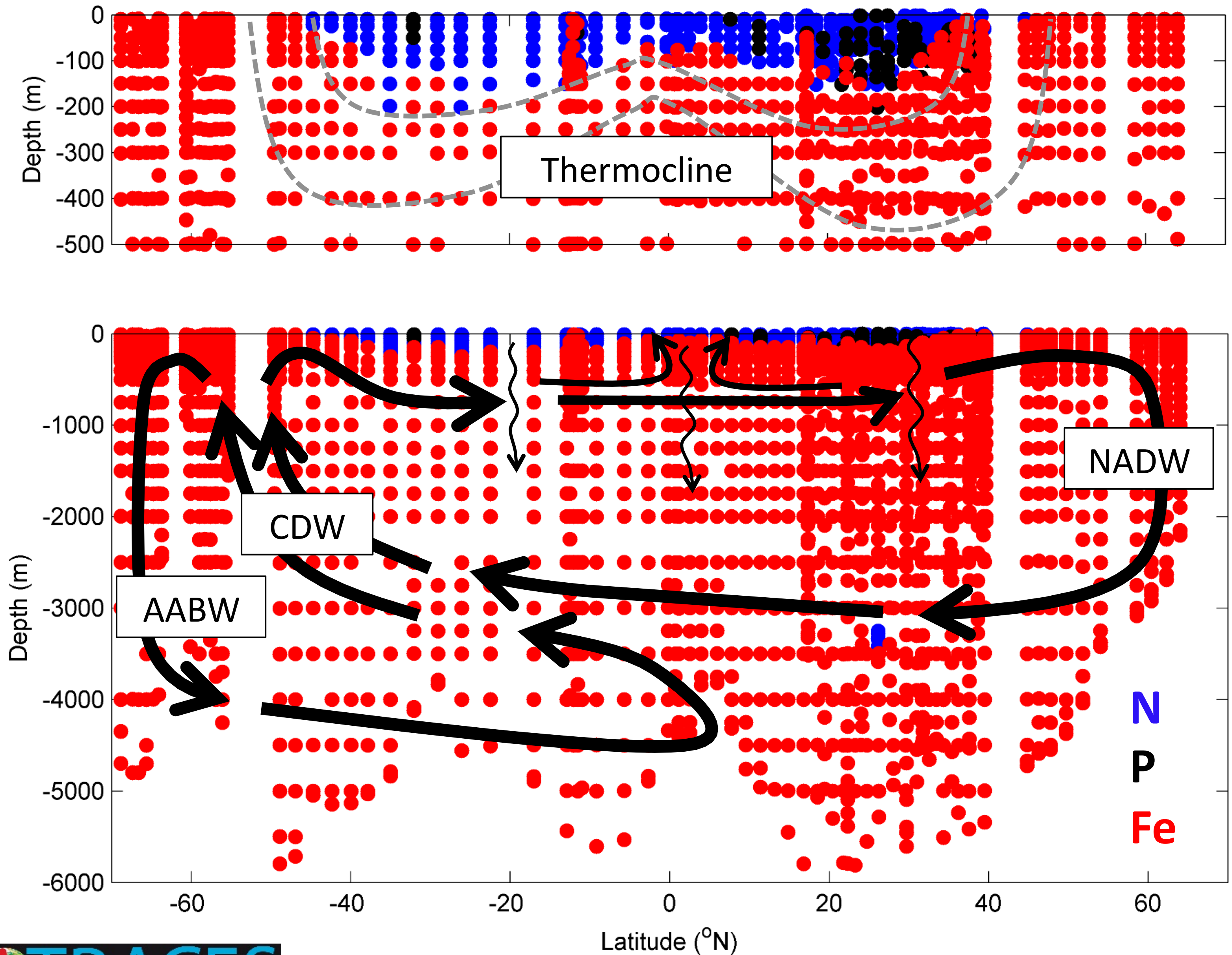
The scavenged nutrient ('Fe') becomes limiting in upwelling surface box



Upwelling is a key driver of iron limitation:

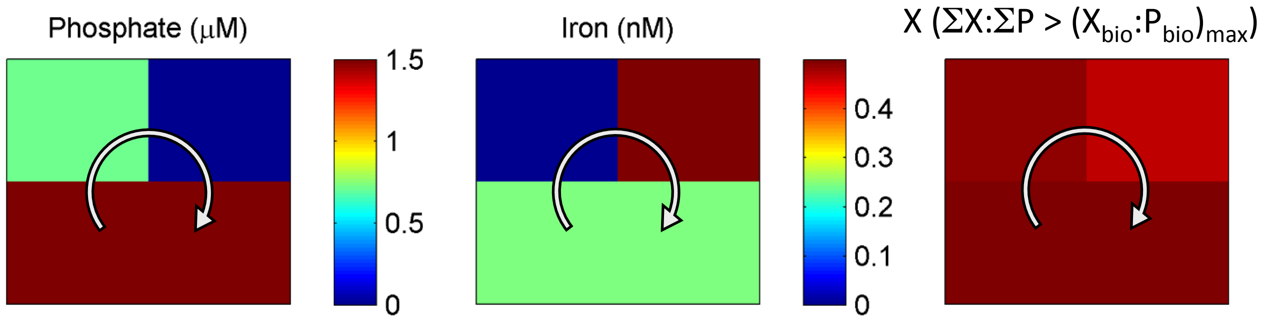
e.g. Eastern Equatorial Pacific *(Martin et al. 1994 Nature);* Southern Ocean *(Boyd et al. 2000 Nature);* Coastal Upwelling regions *(Hutchins and Bruland 1998 Nature)*

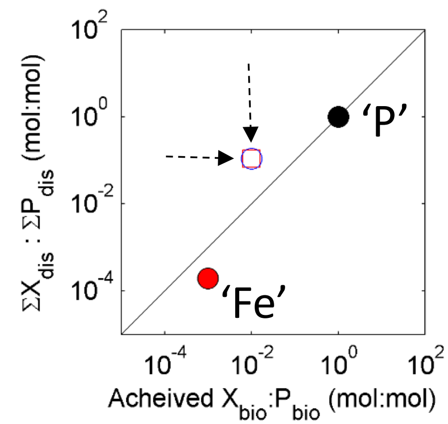
Relative nutrient deficiency



Moore (In review) Phil. Trans. R. Soc. A.

Add in a third 'non-limiting' element 'X'





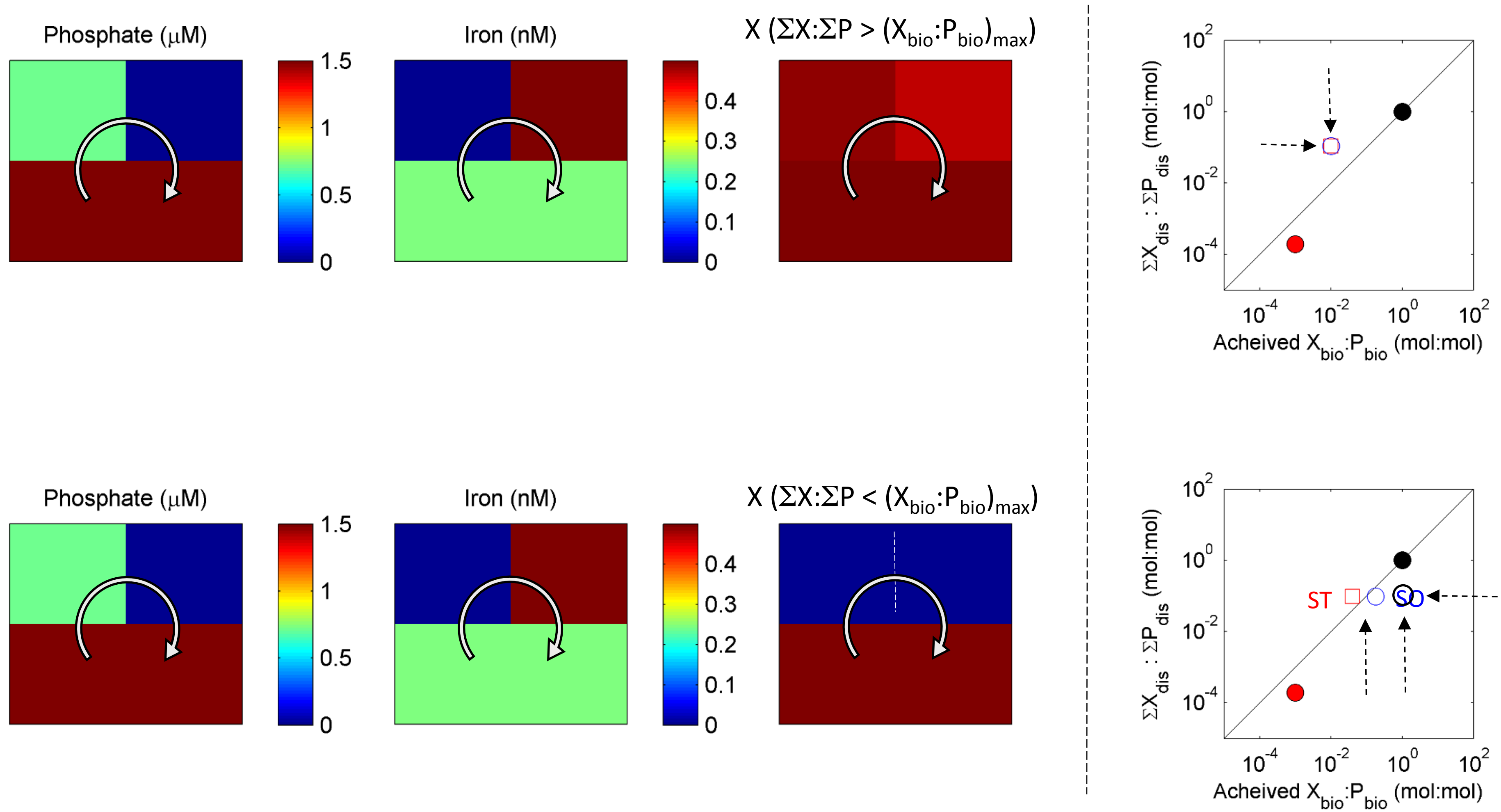
Where:

ΣX = total inventory of X

ΣP = total inventory of P

Moore, Bernardello and Martin *In prep.*

Add in a third ‘non-limiting’ element ‘X’

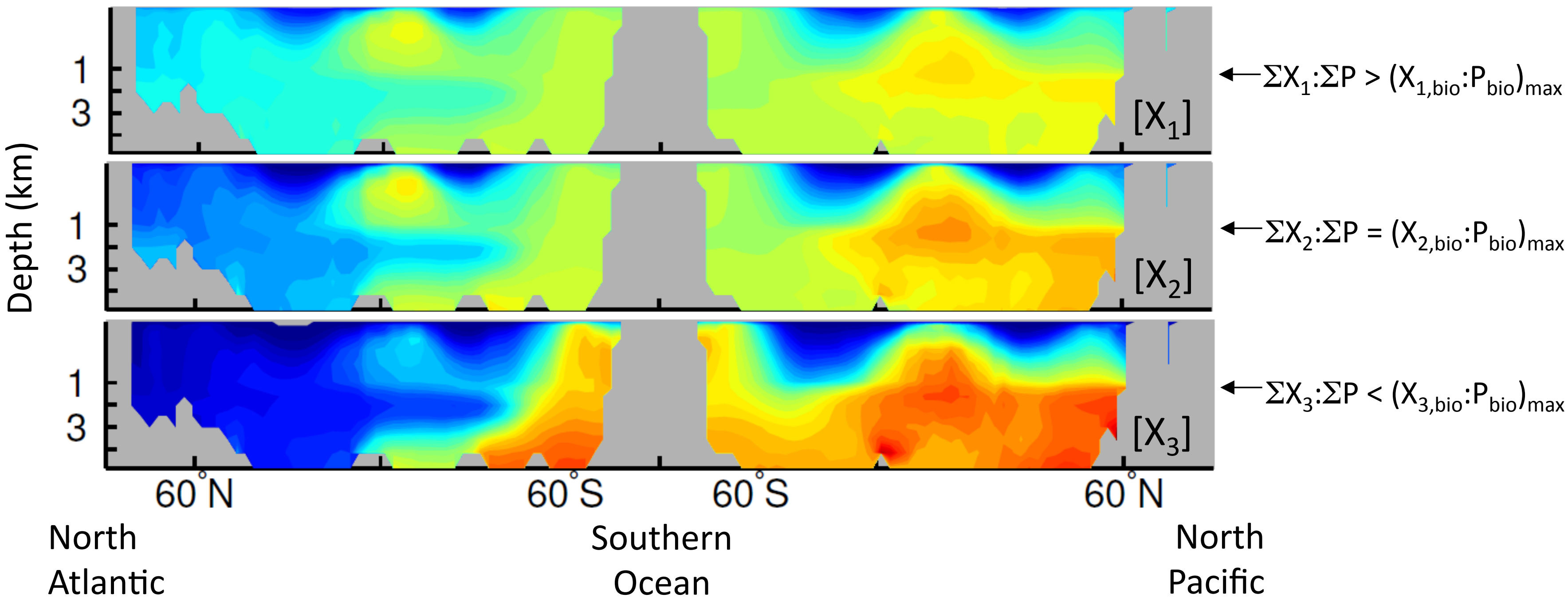


Biouptake influences downstream availability

⇒ *stoichiometry **and** circulation can be key drivers*

Moore, Bernardello and Martin *In prep.*

Nutrient 'X' : plastic stoichiometry, set inventories



Embracing *stoichiometric plasticity*:

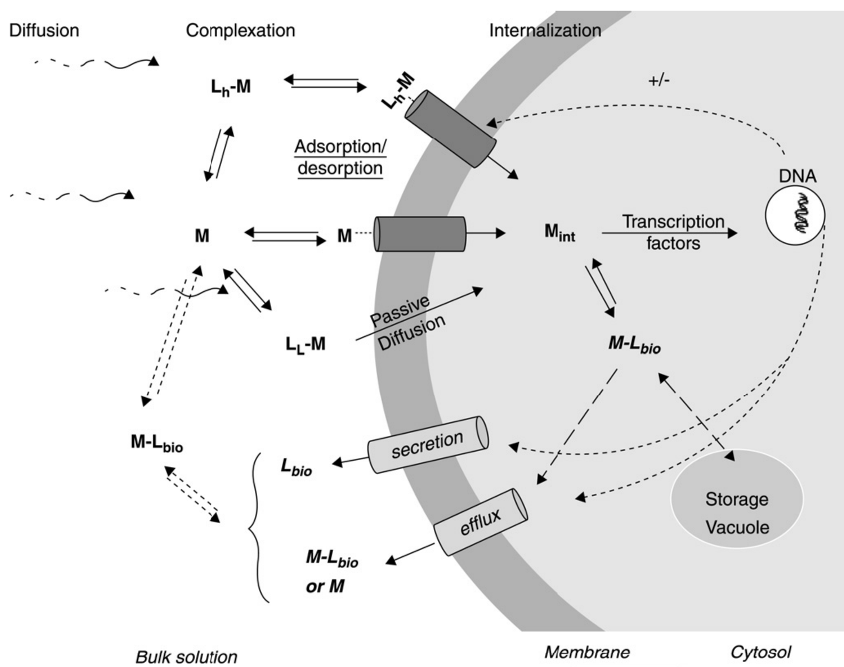
changes in a single characteristic can produce a range of 'nutrient like' distributions within a realistic circulation*

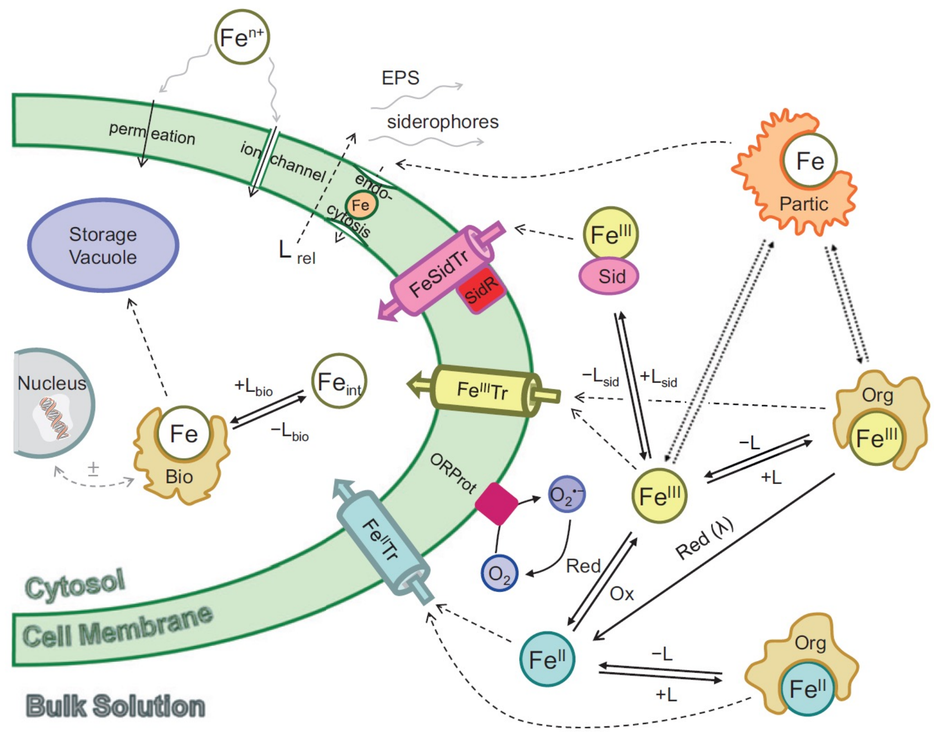
Moore, Bernardello and Martin *In prep.*
(as inspired by presentations of Little, Vance et al. at London mtg. 2015)

*MITgcm 2.8deg

iii) Cellular – local community scales

Multiple, complex (and interacting) processes control trace element uptake at the community – cellular scales



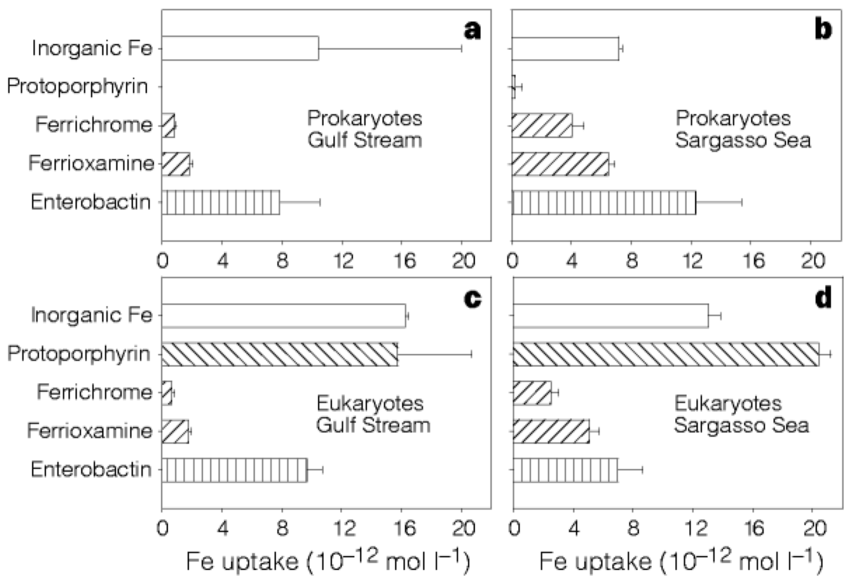


Worms et al. 2006 *Biochimie*

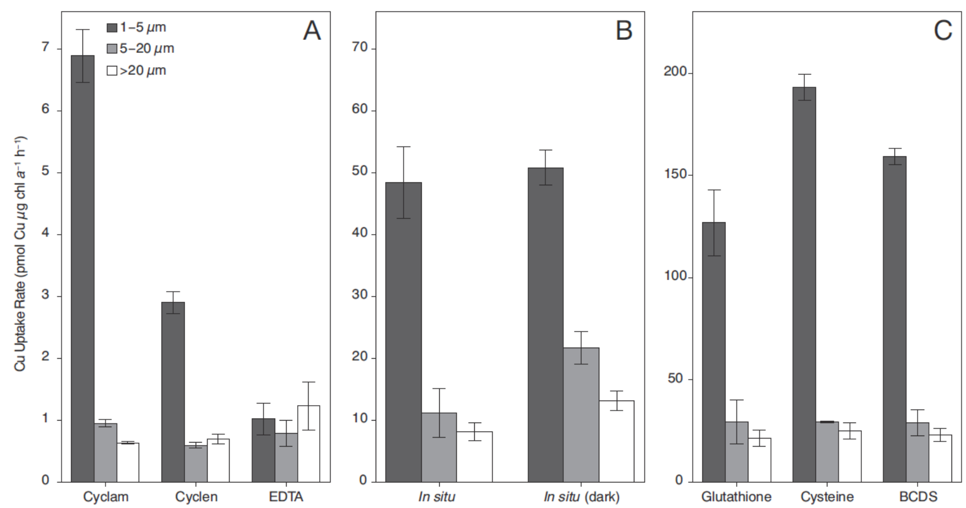
Hassler et al. 2011 *PNAS*

Uptake kinetics

Uptake kinetics are a function of both **chemical** (*e.g. ligands, redox*) and **biological** (*e.g. cell size, transport systems*) characteristics



Hutchins et al. 1999 *Nature*



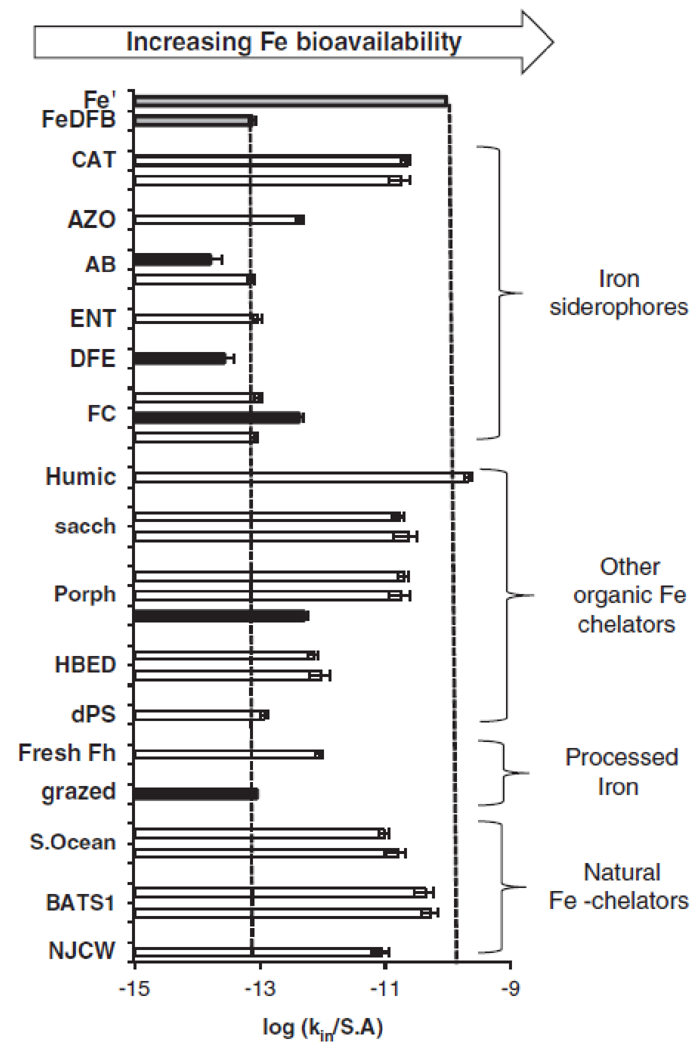
Semeniuk et al. 2015 *Mar. Chem.*

Uptake kinetics

Synthesis faces 'significant challenges in terms of quantitative extrapolation to systems outside of the experimental framework…'

(Shaked and Lis 2012 Frontiers)

i.e. how do we place the complex uptake kinetics into a framework which is tractable within dynamic natural systems?



Lis et al. 2015 *ISME*

Some open questions

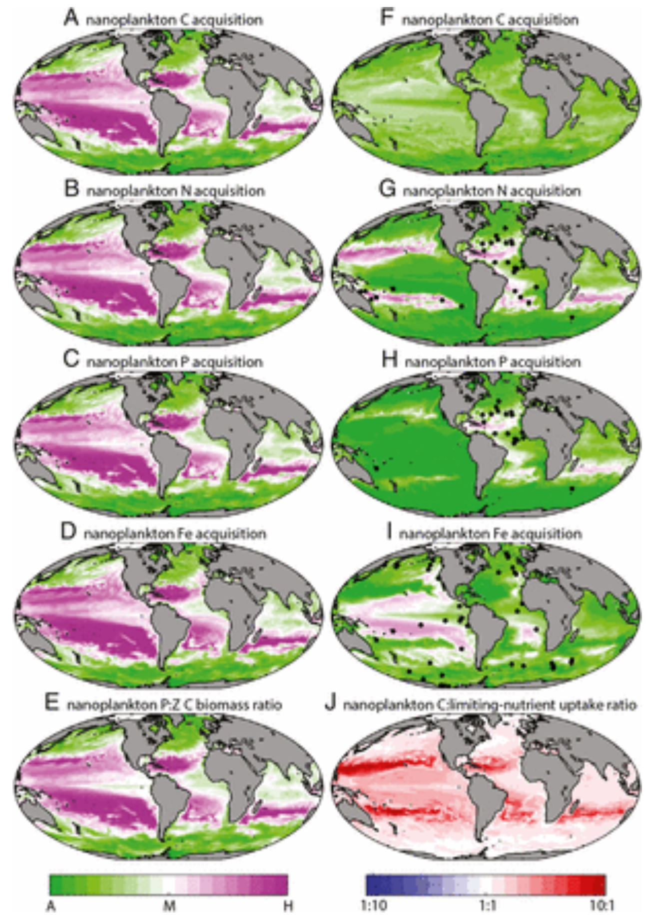
What 'modes' of metal (M) uptake dominate in different natural systems?

How does this relate to M limitation?

What about competition for uptake sites? *(e.g. Sunda and Huntsman 1998 L&O; Cullen et al. 2003 L&O)*

What about M (and non-metal) 'co-limitation'? *(Saito et al. 2008 L&O; Arrigo 2005 Nature; Bertrand et al. 2015 PNAS)*

Mixotrophy? *(Ward and Follows 2016 PNAS)*



Ward and Follows 2016 PNAS

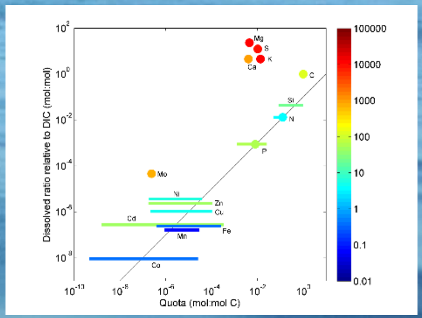
e.g. can the 'R*' concept be generalised to multiple trace-metals with interacting uptake kinetics?

Conclusions

Bioavailability is a dynamic emergent property of the natural system…

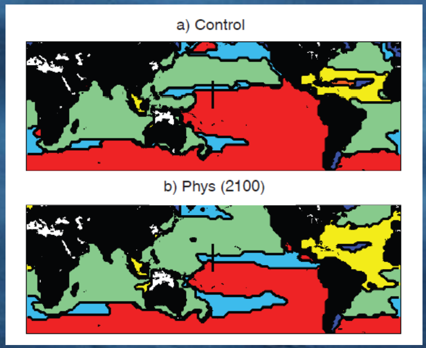
Questions are thus scale related:

What sets overall differential availability of trace metals versus requirements over long timescales?
e.g. inputs, outputs, bio-stoichiometry (evolution), feedbacks



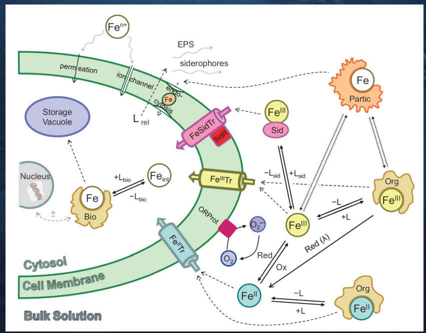
Moore et al. 2013

What controls the differential availability of trace metals at multiple spatio-temporal scales within the modern ocean?
e.g. spatially variable inputs, geochemistry (scavenging), circulation, feedbacks (biouptake and flexible stoichiometry)



Dutkeiwicz et al. 2014

What controls bioavailability (and bio-demand) at cellular-community scales?
e.g. ligand characteristics, exchange kinetics, community structure (and related feedbacks)



Hassler et al. 2011


Thanks for listening!