Iron biogeochemistry & the HNLC condition

Philip Boyd
Institute for Marine & Antarctic Studies
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
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

HNLC ocean

Miller et al. 1993
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.
12 mesoscale Fe experiments in > 10 years

Boyd et al. (2007)
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 study.
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-Garcia et al. 2011, Nature)
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 CO$_2$ at the transition from mid-climate states to full ice age conditions.

Jaccard et al. 2013 Science; Martínez-Garcia et al. 2014, Science
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
A model whose phytoplankton have a uniform growth rate, subject only to PO$_4$ 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
Evidence of a dust storm from TOMS Aerosol Index, April 22 -25 1998  NE Pacific

Boyd 2009
Geographical isolation – from sources of aerosol iron

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

Atmospheric Fe flux (mg m$^{-2}$ yr$^{-1}$)

Duce et al. 1991
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

Morel & Price 2003
Surface water iron supplies in the Southern Ocean sustained by deep winter mixing

Alessandro Tagliabue¹,²*, Jean-Baptiste Sallée²,⁴, Andrew R. Bowie⁶, Marina Lévy³,⁴, Sebastiaan Swart²,⁷ and Philip W. Boyd⁸,⁹
Figure 1 | Depths and potential density of the ferricline and its seasonal

Tagliabue et al. 2014
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 SF$_6$ tracer study of iron cycling in unperturbed HNLC waters

Boyd et al. 2005

Time (h) versus depth (m)
Croot et al. 2006
Boyd et al. 2005
New versus regenerated iron

\[ fe \text{ ratio} = \frac{\text{new Fe}}{\text{(new + regen Fe)}} \]
Microbes drive the oceanic ferrous wheel

Boyd & Ellwood
2010
McKay et al. 2005
WHO HAS THE IRON?

Strzepek et al. 2005
GROWTH RATE versus GRAZING MORTALITY

LANDRY et al., 1993

JUNE 1987

GROWTH / OR GRAZING (d⁻¹)

-0.2
0.0
0.2
0.4
0.6
0.8

µ - ALGAL
m - MZOO
Internal cycling of IRON

UPTAKE

2453 to 4055 (e)

>1976 (f)

Biological recycling

GRAZING AND VIRAL LYSIS

Fe Cycle
Voyage, January/February, 2003

Boyd et al. 2005
Aeolian Export (a) 500

Mixed layer

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

2453 to 4055 (e)

>1976 (f)

Lateral advection

0 (d)

Vertical Diffusivity (g) 15±3

PFe Export (h) 216±27 to 548±128

Boyd et al. 2005
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. Nunn¹,²*, Jessica F. Faux³, Anna A. Hippmann⁴, Maria T. Maldonado⁴, H. Rodger Harvey⁵, David R. Goodlett¹, Philip W. Boyd⁶, Robert F. Strzepek⁷

2014 PLoS ONE
+Fe

Nunn et al. 2014
Nunn et al. 2014

Total Peptide Spectral Counts

- PetA
- PetB
- PetC
- PetD
- PetF
- PsaA
- PsaB
- PsaE
- PsaF
- PsaL
- PsbA
- PsbB
- PsbC
- PsbD
- PsbE
- PsbF
- PsbH
- PsbV
- PsbY

+Fe
* up-reg
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**

<table>
<thead>
<tr>
<th>PROCESS</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>increasing Fv/Fm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>decreasing Flavodoxin</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>increasing Flavodoxin</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Opportunism of HNLC organisms

Croot et al. 2001
Thanks Dr. Jim Gower of IOS and NASA
Timescales of responses to iron-enrichment

Opportunism is evident in HNLC waters
\[ L^* = [L1] \text{ minus } [\text{Dfe}] \]

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 sources & sinks

Ecology

Fe chemistry & stable isotopes

Fe Biogeochemistry

SOLAS Dust deposition

Ligands

Omics ‘Geomics’
What sets the depth of the ferricline?

Boyd & Ellwood 2010
Dust distributions over Australia

Mackie et al. 2008
2 distinct dust outflow patterns from Australia

Mackie et al. 2008
Time-series of dust distributions over Australia

Mackie et al. 2008
Air mass trajectories
To follow dust storms

Mackie et al. 2008
Biogeochemistry of iron in Australian dust

Mackie et al. 2008
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