Co-Limitation of Phytoplankton by Light and Multiple Nutrients

Hein de Baar,
Klaas Timmermans, Loes Gerringa, Erik Buitenhuis, Patrick Laan;
Christiane Lancelot, Olivier Aumont, Geraldine Sarthou, Andy Bowie,
Stephane Blain, Paul Worsfold
and many others in European research teams of
MERLIM, CARUSO, IRONAGES

Koninklijk Nederlands Instituut voor Onderzoek der Zee
Royal Netherlands Institute for Sea Research

Europese Unie
European Union
Contents

• Building Blocks for Life
• Concepts of Limitation
• Observations in the Sea
• Growth Experiments
• Ironages
• GEOTRACES (GEOSECS II)
• Summary
Abundance of Chemical Elements

The graph shows the abundance of chemical elements plotted against their atomic numbers on a logarithmic scale. The x-axis represents the atomic number, while the y-axis represents the logarithm of the abundance. Elements are marked with their symbols, such as H for hydrogen, He for helium, and so on. The distribution highlights the relative abundance of elements across the periodic table.
Major Bio-Elements
Abundances versus one million Si atoms

- **Carbon** • $10 \times 10^6$
- **Nitrogen** • $3 \times 10^6$
- **Silicon** • $1 \times 10^6$
- **Phosphorus** • $1 \times 10^4$
- **Iron** • $0.9 \times 10^6$
Metals Abundance & Biological Evolution

<table>
<thead>
<tr>
<th>Metal</th>
<th>Numbers of Atoms Versus 1 Million Si Atoms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mn</td>
<td>9550</td>
</tr>
<tr>
<td>Fe</td>
<td>900000</td>
</tr>
<tr>
<td>Co</td>
<td>2250</td>
</tr>
<tr>
<td>Ni</td>
<td>49300</td>
</tr>
<tr>
<td>Cu</td>
<td>522</td>
</tr>
<tr>
<td>Zn</td>
<td>1260</td>
</tr>
<tr>
<td>Ag</td>
<td>0.49</td>
</tr>
<tr>
<td>Cd</td>
<td>1.61</td>
</tr>
<tr>
<td>Hg</td>
<td>0.34</td>
</tr>
<tr>
<td>Pb</td>
<td>315</td>
</tr>
</tbody>
</table>

**Evolution used abundant metals: essential**

**Low abundant metals no bio-functions: toxic**
Photosynthetic Oxygen Captured in Iron Formations

$4 \text{Fe(II)}_{\text{dissolved}} + 3 \text{O}_2 \rightarrow 2 (\text{Fe}_2\text{O}_3)_{\text{deposit}}$

Dumb algae took away their own iron supply.
2. Concepts of limitation

\[ \frac{\mu}{\mu_{\text{max}}} = \frac{[\text{nutrient}]}{K_{\text{nutrient}} + [\text{nutrient}]} \]


*Emiliania huxleyi* in pristine natural seawater driven into iron limitation by siderophore addition

Timmermans et al., in prep.
Multiple Limitations in Real Ocean

\[
\frac{\mu}{\mu_{\text{max}}} = \left\{1 - \exp\left(\frac{aI}{K_{\text{max}}}\right)\right\}\left\{\frac{[N]}{(K_N + [N])}\right\}\left\{\frac{[P]}{(K_P + [P])}\right\}\left\{\frac{[\text{Fe}]}{(K_{\text{Fe}} + [\text{Fe}])}\right\}\left\{\frac{[\text{Si}]}{(K_{\text{Si}} + [\text{Si}])}\right\}
\]

\text{growth} \quad \text{light} \quad \text{nitrate} \quad \text{phosphate} \quad \text{iron} \quad \text{silicate}

Moreover terms for Mn, Cu, Zn, Co to be included as well !?

- **Caveats**
  - static (steady state) equation applied to dynamic wax and wane of plankton blooms
  - limitations presumed independent while within living cell they are all interacting

de Baar and Boyd (2000) JGOFS Midterm Synthesis Book
Some examples of interactions within the plant cell

- Iron-light co-limitedation
  - electron transfer in photosystems
- Iron essential for nitrate uptake
  - nitrate reductase, nitrite reductase
- Zinc - bicarbonate co-limitedation
  - carbonic anhydrase
3. Observations in the Sea

- Zn and silicate
- Cd and phosphate
- Cu and Ag and silicate
- Fractionations Zn/Cd and Cu/Ag
- Anomalies of major nutrients
Zinc resembles Silicate

North Pacific Ocean
(33°N, 145°W)

Bruland (1980)
Cadmium resembles Phosphate

North Pacific Ocean
(33°N, 145°W)

Bruland (1980)
Improved accuracy of both Cd and PO4 is crucial for further progress.

Global Cd/phosphate dataset for waters >1000m depth.

Open circles deBaar et al. (1994);


Biological function for Cd after all


<table>
<thead>
<tr>
<th></th>
<th>Mn</th>
<th>Fe</th>
<th>Co</th>
<th>Ni</th>
<th>Cu</th>
<th>Zn</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>315</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

carbonic anhydrase

join the Green Party
Silver (Ag) resembles Copper (Cu)

North Pacific Ocean
(18°N, 108°W)

Martin et al. (1983)
Ag has better correlation with Si

Worldwide correlation Ag and Si

Ag/Si ratio increases from $\sim 1.2 \times 10^{-6}$ in Atlantic to $\sim 2.7 \times 10^{-6}$ in Pacific

## Fractionations \( \text{Cu}/\text{Ag} \) and \( \text{Zn}/\text{Cd} \)

<table>
<thead>
<tr>
<th></th>
<th>Group 1b</th>
<th>Group 2b</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \text{Cu}/\text{Ag} )</td>
<td>( \text{Zn}/\text{Cd} )</td>
</tr>
<tr>
<td><strong>Crustal abundance ratio</strong></td>
<td>( \sim 1060 )</td>
<td>( \sim 780 )</td>
</tr>
<tr>
<td><strong>Oceanic waters ratio</strong></td>
<td>( \sim 8 \pm 3 )</td>
<td>( \sim 91 )</td>
</tr>
<tr>
<td><strong>Fractionation factor</strong></td>
<td>( \sim 130 )</td>
<td>( \sim 8.6 )</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>( \text{Mn} )</th>
<th>( 9550 )</th>
<th>( \text{Fe} )</th>
<th>( 900000 )</th>
<th>( \text{Co} )</th>
<th>( 2250 )</th>
<th>( \text{Ni} )</th>
<th>( 49300 )</th>
<th>( \text{Cu} )</th>
<th>( 522 )</th>
<th>( \text{Zn} )</th>
<th>( 1260 )</th>
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<tr>
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<td>( 0.49 )</td>
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<td>( 1.61 )</td>
<td>( \text{Hg} )</td>
<td>( 0.34 )</td>
<td>( \text{Pb} )</td>
<td>( 315 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

First row ‘real biometals’ have shorter ocean residence time than second row ‘abiotic’ metals

(Also differences in inorganic speciation)
Nutrient anomalies \textit{Fragilariopsis kerguelensis} blooms

Fragilariopsis kerguelensis with heavily silicified armor ‘pantzer’
More Fe co-limitations major nutrients

<table>
<thead>
<tr>
<th>Study</th>
<th>Fe-deplete</th>
<th>Fe-replete</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern Ocean (Takeda, 1998)</td>
<td>Si/N = 2.3</td>
<td>Si/N = 0.95</td>
</tr>
<tr>
<td>plankton community</td>
<td>N/P = 12</td>
<td>N/P = 14</td>
</tr>
<tr>
<td>Chaetoceros dichaeta</td>
<td>Si/N = 1.9</td>
<td>Si/N = 0.7</td>
</tr>
<tr>
<td>Nitzschia sp.</td>
<td>Si/N = 2.1</td>
<td>Si/N = 1.2</td>
</tr>
<tr>
<td>California upwelling (Hutcheson, et al., 1998)</td>
<td>Si/N = 1.6</td>
<td>Si/N = 0.8</td>
</tr>
<tr>
<td>plankton community</td>
<td>Si/N = 2.7</td>
<td>Si/N = 1.0</td>
</tr>
<tr>
<td></td>
<td>Si/N = 3.0</td>
<td>Si/N = 1.0</td>
</tr>
<tr>
<td>Uptake by blooms in Ross Sea</td>
<td>Diatoms</td>
<td>Phaeocystis</td>
</tr>
<tr>
<td>Arrigo et al. (1999)</td>
<td>N/P = 9.5</td>
<td>N/P = ~19</td>
</tr>
</tbody>
</table>
Three more recent cases of nitrate anomalies in *Fragilariopsis* blooms

Polarstern 2000
Polarstern 1999
SOIREE 1999
February 1999 SOIREE Nutrient Anomalies: *Fragilariopsis kerguelensis* strikes again

end of bloom season

Nutrients data courtesy Stuart Pickmere, NIWA, New Zealand
Polarstern 1999 survey cruise: NOx/PO4 anomalies at stations dominated by Fragilariopsis
Polarstern (2000) *in situ* Fe enrichment

Bozec, Bakker, de Baar, Thomas, Bellerby and Watson (2003) submitted
### Polarstern (2000) *in situ* Fe enrichment

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Delta C/\Delta P$</td>
<td>82</td>
<td>90 + 5</td>
<td>106</td>
<td></td>
</tr>
<tr>
<td>$\Delta C/\Delta N$</td>
<td>5.9</td>
<td>6.2 + 0.2</td>
<td>6.6</td>
<td></td>
</tr>
<tr>
<td>$\Delta N/\Delta P$</td>
<td>12</td>
<td>14.3 + 0.2</td>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>$\Delta C/\Delta Si$</td>
<td>2.9</td>
<td>5.1 + 0.3</td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>$\Delta Si/\Delta N$</td>
<td>2.1</td>
<td></td>
<td></td>
<td>2.3</td>
</tr>
</tbody>
</table>

- in the patch
- plankton
- community

(Steinberg & Millero, 1998)

Bozec, Bakker, de Baar, Thomas, Bellerby and Watson (2003) submitted
4. Growth Experiments

- Pristine natural seawater medium
- Fragilariaopsis kerguelensis
- Diatoms are Forever
  - light & Fe co-limitation
  - small versus large *Chaetoceros sp.*
- Zn-HCO$_3$ co-limitation *Emiliania huxleyi*
Different forms of Fe in seawater

[FeCO\textsubscript{3}^0] [FeOH\textsuperscript{+}] [Fe(II)\textsubscript{L}] ? [Fe\textsuperscript{2+}] [Fe\textsuperscript{3+}] [Fe(II)\textsubscript{L}] organic complexes

photoreduction

g homicides

[Fe(OH)\textsubscript{2}^+] [Fe(OH)\textsubscript{2}^{2+}]

EDTA dope would disturb all this

Gerringa, de Baar and Timmermans (2000), *Marine Chemistry*, 68, 335-346
Fragilariopsis kerguelensis in natural Antarctic seawater

\[ K_m \text{ Fe}_{\text{diss}} : 0.44 \times 10^{-9} \text{ M} \]
\[ \mu_{\text{max}} : 0.31 \text{ d}^{-1} \]

Timmermans, van der Wagt, de Baar, in prep.
Nutrients Stoichiometry of *Fragilariopsis kerguelensis*

<table>
<thead>
<tr>
<th>Ratio</th>
<th>Southern Ocean</th>
<th>Incubations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fe-deplete</td>
<td>Fe-deplete</td>
</tr>
<tr>
<td>Si : N</td>
<td>7.7</td>
<td>2.5</td>
</tr>
<tr>
<td>N : P</td>
<td>~ 5 ± 1</td>
<td>~ 5 ± 1</td>
</tr>
</tbody>
</table>

Heavily silicified *Frag.kerguelensis* has higher Si/N ratio
**Actinocyclus sp.**

- $K_m \text{Fe}_{\text{diss}}$: $0.98 \times 10^{-9} \text{ M}$
- $\mu_{\text{max}}$: $0.34 \cdot \text{d}^{-1}$
Elemental composition in relation to $\text{Fe}_{\text{diss}}$

mol per liter cell volume

*Actinocyclus* sp.

<table>
<thead>
<tr>
<th>$\text{Fe}_{\text{diss}}$ (x10^-9 M)</th>
<th>Si</th>
<th>N</th>
<th>P</th>
<th>Si : N</th>
<th>N:P</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>18.25</td>
<td>0.69</td>
<td>1.48</td>
<td>27</td>
<td>0.47</td>
</tr>
<tr>
<td>0.45</td>
<td>17.25</td>
<td>0.75</td>
<td>1.50</td>
<td>23</td>
<td>0.50</td>
</tr>
<tr>
<td>0.65</td>
<td>9.88</td>
<td>0.56</td>
<td>1.38</td>
<td>18</td>
<td>0.41</td>
</tr>
<tr>
<td>1.05</td>
<td>5.69</td>
<td>0.59</td>
<td>0.78</td>
<td>10</td>
<td>0.76</td>
</tr>
<tr>
<td>1.85</td>
<td>4.02</td>
<td>0.52</td>
<td>0.52</td>
<td>8</td>
<td>1.00</td>
</tr>
<tr>
<td>3.45</td>
<td>3.66</td>
<td>0.53</td>
<td>0.63</td>
<td>7</td>
<td>0.85</td>
</tr>
<tr>
<td>10.45</td>
<td>2.36</td>
<td>0.61</td>
<td>0.33</td>
<td>4</td>
<td>1.86</td>
</tr>
</tbody>
</table>

Klaas Timmermans et al., in prep.
Light and Fe co-limitation

Chaetoceros brevis

single cells
4 - 6 µm diameter (small)

Timmermans et al. (2001), MEPS 287 - 297.
Chaetoceros dichaeta

*C. dichaeta*

$K_m \text{Fe}_{\text{diss}}: 1.12 \times 10^{-9} \text{ M}$

Chain-forming large cells

Timmermans et al. (2001), MEPS 287 - 297.

---

$\mu (\text{d}^{-1})$

- **Circle**: 20 h light: 4 h dark
- **Filled circle**: 12 h light : 12 h dark

**does not grow at all**

Fe dissolved (x $10^{-9}$ M)
**Open Southern Ocean HNLC species**

Large versus small at optimal light levels

- *C. dichaeta*
  - Chain-forming cells, individual cells
  - 80 µm long, 30 µm width (large)

- *C. brevis*
  - Single cells 4 - 6 µm diameter (small)

C. brevis in its pristine Antarctic seawater
“a wonderful start”
growth rates not affected by Fe additions

Add DFOB siderophore to tie down the iron

*C. brevis*, it works…

...a limitation response

**effect of Fe: restoration of μ**

*C. brevis*, it works.... a limitation response.


- **DFOB (M) addition**
- **µ (d⁻¹)**
- **effect of Fe: restoration of µ**
- **increasing DFOB**
- **decreasing Fe’**

In the Southern Ocean:
Large *C. dichaeta* is mostly Fe-limited except after Fe supply
Small *C. brevis* is never Fe-limited but grazer-controlled

- **ambient dissolved Fe**

- **$K_m$ *C. brevis*:** $0.59 \times 10^{-12}$ M

- **$K_m$ *C. dichaeta*:** $1.12 \times 10^{-9}$ M
Paradigm Shift

• Old Paradigm (Sunda, Swift, Huntsman, 1991)
  - coastal diatom require more Fe than oceanic diatom

• New Paradigm
  - O.K. but third class of large oceanic diatoms having high Fe requirement
  - these large guys are driving export
Emiliania huxleyi

excretes external CaCO3 platelets
Concerted photosynthesis & calcification

- Zn-carbonic anhydrase permits fast use of $[\text{HCO}_3^-]$
- Calcification provides the necessary proton to make $\text{CO}_2$

Buitenhuis, Timmermans and de Baar, Limnol.Oceanogr., in press
Growth on $[\text{HCO}_3^-]$ at 3 different $[\text{Zn}^{2+}]$
Growth on $[\text{Zn}^{2+}]$ at constant $[\text{HCO}_3^-]$
Suitable Equation for co-limitation?

- **A)** Multiply two Monod equations
  - two nutrients act independently on growth rate
- **B)** Minimum nutrient governs growth rate
  - compare \([N]\) with \(K_N\) to select one of two Monod
  - most suitable for independent nutrients
- **C)** Affinity for \([\text{HCO}_3^-]\) depends on \([\text{Zn}^{2+}]\)
  - most suitable concept for Zn-carbonic anhydrase

Which would provide the best fit??

Buitenhuis, Timmermans and de Baar, Limnol.Oceanogr., in press
Multiply two Monod equations

filled circles are data;
open circles are intersect with 3-D model plane

best fit: mean residual on $\mu = 0.018 \text{ day}^{-1}$
Minimum nutrient governs growth rate

filled circles are data;
open circles are intersect with 3-D model plane

best fit: mean residual on $\mu = 0.02 \text{ day}^{-1}$
Affinity for \([\text{HCO}_3^-]\) depends on \([\text{Zn}^{2+}]\)

Filled circles are data; open circles are intersect with 3-D model plane.

Best concept but fit not any better.

Best fit: mean residual on \(\mu = 0.02\) day\(^{-1}\)
5. Iron Resources and Oceanic Nutrients; Advancement of Global Environment Simulations

• Existing ecosystem model Southern Ocean
  - two plankton groups diatoms and nanoplankton
  - limitation by light and four nutrients N, P, Fe, Si
  - successful for Polar Front and for SOIREE
  - (Lancelot et al 2000; Hannon et al 2001)

• Advance to generic global model
  - five bloom-forming groups: diatoms, calcifiers, Phaeocystis, N2-fixers, pico-nano-plankton
  - limitation by light and four nutrients N, P, Fe, Si
  - embedding in Ocean Biogeochemical Climate Models
Control of the carbon cycling in the upper ocean

Planktonic system

High Trophic Levels

POC C:N:P:Si:Fe

Mineralisation

N, P, Si Fe

C Production

T CO₂

Air/sea CO₂ flux

upwelling

POC export

Mineralisation

Intermediate and deep waters

Christian Lancelot, Nice 2003 lecture
Structure of the coupled biological-chemical-physical 1D model

Christianne Lancelot, Nice 2003 lecture
1D SWAMCO-4 results at KERFIX [1993]: moderate diatom bloom and low CO$_2$ sink

Temperature

$\text{fCO}_2$

Air-sea CO$_2$ flux

Prim. Prod/export

Taxon succes.

Iron/Chl $\alpha$

Christiane Lancelot, Nice 2003 lecture
1D SWAMCO-4 results at KERFIX [1993]: Thermodynamic & biological control of air-sea CO2 fluxes

Temperature

\( \rhoCO_2 \)

Primary Productivity/Export

Taxon Succession

Iron/Chl \( a \)

Christiane Lancelot, Nice 2003 lecture
1D SWAMCO-4 results at AESOPS [1996]:
Thermodynamic & biological control of air-sea CO₂ fluxes

Christianne Lancelot, Nice 2003 lecture
PISCES Model by Olivier Aumont: Co-limiting of 4 taxa by 3 nutrients

Example: the Diatoms
6. GEOTRACES (GEOSECS II)
Epoxy-coated stainless steel prototype frame; final type of titanium or carbon fibre, within own clean van
GoFlo with rotating ball valves

NOEX expanding silicone closures

Air tubes link

driver unit pneumatics
Routine deep profiling with ultraclean CTD frame and cable: allows GEOSECS II for trace elements

Geraldine Sarthou, Stephane Blain, Patrick Laan, Klaas Timmermans
October 2003 cruise IRONAGES-3 off West Africa
True and accurate dissolved Fe values still are puzzling.

Certified standard is urgently needed

**Figure 18.** Vertical profiles of dissolved Fe at station 9 (40°N, 23°W) in the Northeast Atlantic Ocean. Duplicate analyses of total dissolved Fe by FIA-CL after acidifying to pH 2 (de Jong *et al.*, 2000) and dissolved Fe by CSV after UV digestion at pH 8 (Boyé, 2000) show good agreement. Also shown is dissolved iron at stations 6 (37°28.9′N, 22°58.7′W) and 8 (42°34.18′N, 23°02.34′W) of Boyé (2000). For comparison dissolved Fe at 47°N, 20°W (Martin *et al.*, 1993a) and 34°N, 13°W (Landing *et al.*, 1995) are also shown. Drafted after Boyé (2000) and Boyé *et al.* (submitted).
Atlantic Fe distribution in Hamburg model

Modelers are ready to go, but lack of good Fe data for validation

Six and Maier-Reimer, European Ironages project modeling
Dust storm on 25th Sept 2000 off Western Africa observed by SeaWiFS satellite

IRONAGES-1 Cruise, Sep 29th – Oct 23rd 2000

Analytical challenge - how to collect, preserve and distribute sea water samples for the preparation of a low level iron in sea water CRM?

Paul Worsfold, Nice 2003 lecture
IRONAGES standard: sampling

- 1000 l HDPE cubic tank
- Filled to 700 l over 8 h
- South Atlantic Ocean, 6.0°S 5.6°W
- Acidified to ~pH 2 using 700 ml Q-HCl
- Homogenised by gentle shaking of tank

Paul Worsfold, Nice 2003 lecture
IRONAGES standard: bottling

- Transfer from tank to clean laboratory using Teflon FEP line and peristaltic pump
- 200 x 1 l LDPE bottles filled in two batches - 160 UoP & 40 NIOZ

Trials underway for:
- homogeneity
- time-series stability
- sample storage

Other bottles sent to 25 worldwide iron laboratories

Paul Worsfold, Nice 2003 lecture
Analytical methods used during the IRONAGES exercise

Laboratories participating in the “Ironcal” workshop, San Antonio, January 2000

Paul Worsfold, Nice 2003 lecture
Laboratory data versus analytical method

Jim Moffett, independent chair

Data courtesy of Andrew Bowie (University of Tasmania, Australia)

Fe concentration (nM)

CSV (DHN)  FI-CL - Fe(II)  FI-CL - Fe(III)  FI - SPEC  ID-ICP-MS  SE-GFAAS  SPE-ICP-MS  Means for each technique  Overall mean

Paul Worsfold, Nice 2003 lecture
Towards GEOTRACES (GEOSECS II)

• Imbalance of ocean sciences
  - plenty modeling of the virtual ocean
    • armchair oceanography: cheap and easy
  - not much real data in real ocean
  - accuracy, certification, calibration is underfunded

• need for certified standards
  • nitrate, phosphate, silicate
  • essential metals Fe, Mn, Zn, Co, Cd
Summary

- Co-limitation is the rule
- Single limiting factor is exceptional
- Southern Ocean nice and simple
  - only light and Fe as two co-limitations
  - only two taxa: diatoms and Phaeocystis
- Oligotrophic central gyres
  - surface waters uncharted for all nutrients
  - NO3, PO4, SiO4 in nanomoles or picomoles?
  - Fe, Mn, Zn, Co, Cu?
  - seasonality of these nutrients?
- New concepts beyond Liebig (1840 !) and M&M (1913 !) are needed
  - dynamics beyond steady state
  - co-limitations beyond single factor
The End

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Our universities and institutes

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Royal Netherlands Institute for Sea Research

Europese Unie
European Union