Climate and the regulation of the marine N cycle

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## Atomic Ratios of Elements in the Biochemical Cycle

<table>
<thead>
<tr>
<th></th>
<th>P</th>
<th>N</th>
<th>C</th>
<th>O</th>
</tr>
</thead>
<tbody>
<tr>
<td>Analyses of plankton</td>
<td>1</td>
<td>16</td>
<td>106</td>
<td>-276</td>
</tr>
<tr>
<td>Available in sea water</td>
<td>1</td>
<td>15</td>
<td>1000</td>
<td>200–300</td>
</tr>
</tbody>
</table>

In discussing the remarkable coincidence in the supply and demand for nitrogen and phosphorus it has been pointed out that it might arise from: 

1. **a coincidence** dependent on the accidents of geochemical history; 
2. **adaptation** on the part of the organisms; or
3. **organic** processes which tend in some way to control the proportions of these elements in the water.

A.C. Redfield [1958]
NO$_3$ and PO$_4$ are among best correlated properties of ocean ($r^2=0.98$)

Slope = 16:1, same as mean biomass, $R_o$, suggesting a universal stoichiometry.

Global reservoirs of NO$_3$ ($\Sigma N$) and PO$_4$ ($\Sigma P$) have a slightly lower ratio, $\Sigma N: \Sigma P=14.3$. 
Ocean N and P Cycles

P reservoir ($\Sigma P$): geologically controlled slow turnover (~50ky).

N reservoir ($\Sigma N$): biologically controlled fast turnover (~2ky).

$\Sigma N : \Sigma P$ not directly reflected in any major input/output.

Deutsch and Weber [2012]
Annual Reviews of Marine Science
N cycle as Biological Stabilizer

Source feedback:
- Physiological cost of \( \text{N}_2 \) fixation reduces competitive advantage when N is plentiful

Redfield [1958]

Sink feedback:
- Increased productivity expands suboxic zones, increases denitrification

Codispoti [1989]
Biogeochemical Feedbacks
A simple model

Assumptions:
1) Diazotrophs need P, but not N.
2) Cost is slower growth rate ($\mu_F < \mu_o$).

Outcomes:
1) N inventory ($\Sigma N$) Diazotrophs growth rate handicap
2) N inventory ($\Sigma N$) $\sim$ Denitrification rate

Both factors climate driven and poorly known.

Tyrrell [1999], Lenton + Klausmeier [2007]
N cycle as Climate Amplifier?

Source forcing:
$\text{N}_2$ fixation Fe intensive
Favored by cold/dry climate?

Falkowski [1997]
Broecker + Henderson [1998]

Sink forcing:
Anoxia more widespread in warm climates

Altabet et al. [1995]
Ganeshram et al. [1995]
Climate forcing: Dust and $O_2$

Iron supply largely from atmospheric dust deposition.
- N2 fixation
  - Atl $\gg$ Pac

Anoxic zones closely linked to water mass age.
- Denitrification
  - Pac $\gg$ Atl
Unknowns and Debates

Key Uncertainty:

Rates and/or environmental controls poorly known
→ Hard to evaluate its response to climate

Questions:

Denitrification: How fast is it?

$N_2$ Fixation: What regulates the distribution?

What are the implications for N cycle dynamics?
Unknowns and Debates

Key Uncertainty:

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Denitrification: How fast is it?

N₂ Fixation: What regulates the distribution?

What are the implications for N cycle dynamics?
Ocean Model: Circulation

Circulation Model

Coarse resolution (2-4°) GCM
Observed surface forcing
Linearized momentum eqns.
Optimal fit to T, S, \(^{14}\)C
DeVries and Primeau [2011]

Added constraint for CFCs
(for ventilation of anoxic zones).

DeVries et al. [2011]
Nature Geoscience
Tracer Constraints

Constraints on N budget:

\[ N^* = \left[ NO_3^- \right] - 16 \left[ PO_4^{3-} \right] \]

\[ \delta^{15}N = \left( \frac{^{15}N}{^{14}N} \right) \cdot R_{\text{air}} - 1 \cdot 1000 \]

\[ N_{2}^{xs} = \left( \frac{N_2}{Ar} - \frac{N_2}{Ar_{\text{ref}}} \right) \cdot N_2^{sat} \]

The use of multiple tracers gives combination of regional and global constraints on the major fluxes.
Denitrification rates and spatial distribution fit to observed $N_2$ profiles in probabilistic simulations.

Global rates 60-70 Tg/yr

DeVries et al. [2011]
*Nature Geoscience*
Data: $N^*$, $\delta^{15}N$

$$N^* = \left[ NO_3^- \right] - 16 \left[ PO_4^{3-} \right]$$

$$\delta^{15}N = \left( \frac{^{15}N}{^{14}N} \cdot R_{air} - 1 \right) \cdot 1000$$

Data is dense
Constraint mostly regional

Data is sparse
Constraint mostly global

DeVries et al. [2013]
Biogeoscience
Model vs data

Model captures most of the variation in all tracer observations.

Largest biases in deep N*, probably from particle flux model.

DeVries et al. [2013]
*Biogeoscience*
Global Denitrification

**Water Column Rates**

Range: 50-77 Tg/yr
Compatible with N\textsubscript{2} results

**Sedimentary Rates**

Range: 71-168 Tg/yr
Smaller than previous estimates

→ Balanced budget likely

DeVries et al. [2013]
See also Eugster and Gruber [2013]
Unknowns and Debates

Key Uncertainty:

Rates and/or environmental controls poorly known
  → Hard to evaluate its response to climate

Questions:

Denitrification: How fast is it?

$N_2$ Fixation: What regulates the distribution?

What are the implications for N cycle dynamics?
Model: Circulation + Ecosystem

**Ecosystem Model**

- Two plankton types (diazotrophs + non-diaz.)
- Plankton growth rates \( \sim \text{Light, Temp, Fe} \)
- Sinking particle flux \( \sim z^{-\alpha} \)
- Fit to surface \( \text{PO}_4 \) data
- Empirically based denitrification rates.

**Approach:**
1) Manipulate plankton traits
2) Determine implications for observable tracers
3) Test underlying assumptions re: traits.
Diazotroph Fe limitation governed by cellular Fe:P quota ($Q_F/Q_0$)
At low Fe limitation, $N_2$ Fixation looks like denitrification.
As Fe limitation increases it looks gradually more like dust deposition.

Weber and Deutsch [in review]
Which regime are we in?

All these data constraints (and more) are best matched in the intermediate Fe limitation regime (Regime 2).

Weber and Deutsch [in review]
Regime 2: Local Fe limitation

Weber and Deutsch [in review]
Regime 2: Basin P limitation

In regime 2, the basin scale rates are very nearly balanced and cross-basin transport of N deficits is small, consistent with data.

Fe fertilization of Fe-limited diazotrophs does not change total budget.

→ Basin scale fixation is limited by generation of excess P.

Weber and Deutsch [in review]
Unkowns and Debates

Key Uncertainty:

Rates and/or environmental controls poorly known
⇒ Hard to evaluate its response to climate

Questions:

Denitrification: How fast is it?

$\text{N}_2$ Fixation: What regulates the distribution?

What are the implications for N cycle dynamics?
Steady State $\Sigma N : \Sigma P$ reflects the global $\text{NO}_3: \text{PO}_4$ ratio needed to allow $\text{N}_2$ fixers to balance prescribed N losses.

For observed denitrification rates global N:P ratio well below the true value, and $\text{NO}_3$ deficit twice what is observed.

→ Something is still missing!

Weber and Deutsch [2012]
Stoichiometric Diversity

Inter-species (phylogenetic) variations under ‘ideal’ growth conditions.

→ Evolution

Intra-species (phenotypic) variations under different environmental conditions.

→ Acclimation
Southern Ocean N* has large-scale gradients along pathways of meridional overturning.

Similar patterns observed independently in all basins \(\rightarrow\) structure is robust.

Suggests low N:P export in Antarctic Zone and high N:P export in Subantarctic.
Diagnosing N:P export

The actual N:P of plankton estimated by transport convergence of NO$_3$ and PO$_4$ independently.

The inferred N:P ratio of export has a large-scale pattern with wide variation (>2x).

Weber and Deutsch [2010]
Biogeography and N:P

Correlation of N:P with possible sources of variability

<table>
<thead>
<tr>
<th></th>
<th>Zonal (n = 35)</th>
<th>1° × 1° (n = 11,408)</th>
<th>Expected relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community composition*</td>
<td>-98</td>
<td>-50</td>
<td>Negative</td>
</tr>
<tr>
<td>Light (mixed layer</td>
<td>62</td>
<td>19</td>
<td>Negative</td>
</tr>
<tr>
<td>average)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summertime growth rate†</td>
<td>86</td>
<td>39</td>
<td>Negative</td>
</tr>
<tr>
<td>[Fe]</td>
<td>72</td>
<td>22</td>
<td>Positive</td>
</tr>
<tr>
<td>Temperature</td>
<td>89</td>
<td>38</td>
<td>Positive</td>
</tr>
</tbody>
</table>

Community composition (% diatoms) diagnosed from Si export fluxes.

\[
R_o = -9.6 \phi_{diat} + 20.4
\]

Other Plankton: High N/P

Diatoms: Low N/P

Weber and Deutsch [2010]
Variable Stoichiometry

Extrapolate relationship from Southern Ocean to world:

\[ R_o = -9.6 \phi_{diat} + 20.4 \]

Constrain global mean export to have a 16:1 ratio

\[
\frac{\int R_o J_{ex}(P) \, dA}{\int J_{ex}(P) \, dA} = 16
\]

Weber and Deutsch [2012], c.f. Martiny et al. [2013]
Large-scale diversity of plankton N:P ratios is essential to explain the ocean’s ΣN:ΣP ratio.

Strong Fe limitation and/or high denitrification rates still pose a problem.

Weber and Deutsch [2012]
The ecological niche of diazotrophs is determined not only by local competition but also by remote plankton communities. The influence of these regions must be communicated by ocean circulation.

Weber and Deutsch [2012]
Response to Dust Forcing

Intermediate Fe limitation (Regime 2)

N inventory shows weak response to Fe increase (glacial), but a strong response to Fe decrease (future?).
Response to Circulation

Large decadal variations in simulated anoxic zones explain observed time series in Eastern North Pacific. Driven by climate variability (PDO).

Deutsch et al. [2011]
Suboxic Volume Changes

State-of-the-art Earth System Models predict wildly different suboxic zones.

The only agreement is on likelihood of large changes.
Denitrification vs N₂ fixation

1) Coincidence?
2) Evidence of feedback?
3) A common forcing?

Deutsch and Weber [2012]
Annual Reviews of Marine Science
Conclusions

- Limits to N fixation are scale-dependent: local Fe limitation, but basin P limitation.
- Plankton stoichiometric diversity is important to the regulatory feedbacks in N cycle. So are the pathways of nutrient supply.
- Long-term N cycle appears to be approximately balanced, but climate-forced changes in N budget and N limitation appear strong on decadal time scales.
Increasing diversity of plankton N:P raises the ocean $\Sigma N: \Sigma P$ ratio, but only by <50% of $R_{o,ST}$.
Nitrogen Cycle
Biological homeostat or Climate amplifier?

Deutsch and Weber [2012]
Annual Reviews of Marine Science
$N_2$ fixation – Fe limitation

![Graph showing dust deposition and $\mu_F/\mu_o$ ratio](image)

- Fe-limitation $\mu_F/\mu_o$:
  - None: 0.95
  - Weak: 0.91
  - Strong: 0.56

![Simulated $N_2$-Fixion Maps](image)

- Simulated $N_2$-Fixion (Weak Fe Limitation)
- Strong $N_2$-Fixion (Weak Fe Limitation)

**Estimated range**

- Reducing $N_2$-fixation
- Increasing $N_2$-fixation

**Latitude**

- 60S  40S  20S
- 0  20N  40N  60N

**Dust deposition (g/m$^2$/year)**

- 0.01  0.1  1  10  100

**Denitrification (Tg/yr)**

- 50  100  150  200  250  300

- $\mu_F/\mu_o$
- 0.5  0.6  0.7  0.8  0.9

**Fe-limitation**

- Weak
- Strong
Hypoxic sensitivity

\[ \Delta V_{O_2} = \frac{\partial V_{O_2}}{\partial O_{2}^{\text{crit}}} \Delta O_2 \]

- Change in volume (predicted)
- Derivative of histogram (observed)
- Global \(O_2\) anomaly (assumed)

The sensitivity of hypoxic volumes can be predicted from data alone.

It increases rapidly with decreasing \(O_2\) threshold.

Model simulations (dots) consistent with this simple prediction.

Deutsch et al. [2011]

*Science*
Climate forcing: Fe

Atmospheric Dust Flux (simulated)

Modern

Dust deposition g/m²/year Tunel–LGM

LGM
Climate forcing: $O_2$

Warming ocean may increase anoxia.
Solubility decreases, Stratification increases.
Conclusions

• Variation of plankton stoichiometry across biomes is essential to maintaining the N inventory of the ocean.

• Ocean circulation damps (but does not erase) the effect of metabolic diversity by communicating its effects over large scales. $\text{N}_2$ fixing plankton “feel” the mean.

• Subtle variations in climate yield large fluctuations in denitrification and provide a useful test case for the strength of N cycle feedbacks on decadal time scales.

• The oceanic nutrient ratio ($\Sigma \text{N}:\Sigma \text{P}$) is a powerful constraint on biogeochemical models.
N vs P cycles

**P reservoir (ΣP):**
- Geologically controlled
- Slow turnover (~50ky).

**N reservoir (ΣN):**
- Biologically controlled
- Fast turnover (~2ky).

**ΣN:ΣP** not directly reflected in any major input/output.
Nitrogen and the Carbon Pump

But what regulates the Nitrogen inventory?

Changes in biological carbon storage can occur via changes in:

1) Nutrient reservoir (low latitudes)
2) Nutrient utilization (high latitudes)
The Role of Circulation

1) No lateral circulation, No plankton diversity

The ocean $\Sigma N: \Sigma P$ falls below $R_o$, due to the need to balance denitrification with $N_2$ fixation.
The Role of Circulation

2) No lateral circulation, Plankton N:P diversity

As the N:P of subtropical plankton increases, the ocean $\Sigma N:\Sigma P$ rises by the same amount.

The diazotroph niche is determined only by the deep nutrient supply and local competition.
The Role of Circulation

3) Lateral circulation, Plankton N:P diversity

When lateral circulation is strong, diazotrophs “feel” the N:P demand of remote communities.

In the limit, $\Sigma N: \Sigma P$ is independent of plankton diversity.
Sources of Variability
Low Latitude N/P

Hawaii Ocean Time-series

Particulate N:P

Sensitivity: diatom

![Graph showing sensitivity to diatom with three methods: Method 1 (red), Method 2 (blue), and Method 3 (green). The graph plots $\Sigma N/\Sigma P$ against $R_{o,ST}$ with a slope of 1 and a horizontal line at a slope of 0.]