Marine microplankton functional groups

- Physiology
- Ecology & biogeography
- Biogeochemical implications
- Climate change
The oldest photosynthetic organisms on Earth

Oxygenic photosynthesis
light + water

Global implications of functional groups
Photosynthesis contributed to the expansion and to increase the body size of mammals.
Marine microplankton functional groups

• Physiology
• Ecology & biogeography
• Biogeochemical implications
• Climate change
**Functional group:** individuals or species that fulfill a function within the ecosystem (ecological, trophic, biogeochemical).

**Microbial plankton:**
- Microalgae
  - Picoplankton (Prochlorococ-Synechoc-picoeu)
  - Diatoms
  - Nitrogen fixers (cyanobacteria)
  - Calcifiers (cocolitofóridos, forams)
  - Mixotrophs (flagellates)
  - DMS producers (some phytoplankton?)
- Remineralizers (heterotrophic bacteria)
Microbial plankton:

-Marine microalgae

(50 % global primary production)
(1% global photosynthetic biomass)
Microbial plankton:
- Marine microalgae
- Remineralizers

Remineralize organic matter that convert into mineral nutrients which become available to photoautotrophs
**Functional group:** individuals or species that fulfill a function within the ecosystem (trophic, biogeochemical).

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Prokaryotic

Eukaryotic
Microbial plankton:
- Microalgae

**Picoplankton**

![Graph showing the relationship between nitrogen concentration (R) and uptake rate (V). The equation for the uptake rate is given as $V = V_{max} \frac{R}{R + K}$. The graph compares uptake rates for Diatoms and Picoplankton. The saturation constant ($K_{sat}$) and maximum uptake rate ($V_{max}$) are indicated.]
Nutrient acquisition

Catalysis (conversion of nutrients into biomass)

Phytoplankton growth

Microbial plankton:
- Microalgae

Picoplankton

Very low half saturation constant (Ksat)
Microbial plankton:
- Microalgae

**Picoplankton**

The fate of phytoplankton biomass:
1) sinking  
2) export to higher trophic levels  
3) microbial loop and remineralization
Microbial plankton:
- Microalgae

**Picoplankton**

+ stratification $\rightarrow$ - nutrients $\rightarrow$ + picoplankton (in relative terms)
Microbial plankton:
- Microalgae

**Diatoms**

50% ocean primary production and dominate export

Anywhere as long as there are nutrients + Si
Diatoms vs. Silicate

Competitive superior in unstable environments where nutrients enter intermittently.
Microbial plankton:
- Microalgae
  **Diatoms**

If nutrient limitation extends for too long like in subtropics
Fig. 7.19. The phytoplankton mandala of Margalef that summarises conceptually the role of forcing (gradients in nutrient supply and turbulence) in determining phytoplankton species and size composition (reprinted with permission from Margalef R (1997) Our biosphere. In: Kinne O (ed) Excellence in Ecology. Ecology Institute, Oldendorf)
Modelling analysis showing the main distribution of phytoplankton functional groups: Prochlorococcus (green), nanoflagellates (orange), diatoms (red) and other large phyto (yellow).

Microbial plankton:
- Microalgae
  Diatoms

The fate of phytoplankton biomass:
1) sinking  2) export to higher trophic levels
3) microbial loop and remineralization
Nitrogen fixation (bacteria):

\[ \text{N}_2 + 8\text{H}^+ + 8\text{e}^- + 16\text{ATP} \rightarrow 2\text{NH}_3 + \text{H}_2 + 16\text{ADP} + 16\text{Pi} \]

Energetically COSTLY (it requires 16ATP to catalyze the reaction)

Microbial plankton:
- Microalgae
  
  Nitrogen fixers

Nitrogen is the \textbf{most limiting nutrient} in the sea, yet the atmosphere is plenty of N$_2$. 
Nitrogen fixation:
\[ \text{N}_2 + 8\text{H}^+ + 8\text{e}^- + 16\text{ATP} \rightarrow 2\text{NH}_3 + \text{H}_2 + 16\text{ADP} + 16\text{Pi} \]

High Fe requirements

Fe-protein

MoFe-protein

ADP-AlF\(_4^-\)
Asp-129 [4Fe:4S]
P-cluster
FeMo-cofactor

Nitrogenase
Most of nitrogen fixation happens in subtropical waters where nitrate concentration is very low.

It is worth investing chemical energy to oxidize N2 and outcompete other phytoplankton.

**Fe limitation**
(Fe is supplied to the ocean through dust deposition from continental land masses)
Nitrogen fixation represents a **NEW SOURCE OF NITROGEN** to the system and thus has the potential to increase the capacity of the ocean to absorb atmospheric CO₂ and store in the deep ocean for long-term.

The **fate** of phytoplankton biomass:
1) **sinking**  
2) **export to higher trophic levels**  
3) microbial loop and **remineralization**
Precipitate calcium carbonate:
\[ \text{Ca}^{2+} + 2\text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{H}_2\text{O} + \text{CO}_2 \]

Microbial plankton:
- Microalgae
  Calcifiers
Coccoliths reflect the light which is detected by using satellites Moderate Resolution Imaging Spectroradiometer (MODIS) Coastal Zone Color Scanner (CZCS) & SeaWiFS Moderate Resolution Imaging Spectroradiometer (MODIS)
Fig. 7.19. The phytoplankton mandala of Margalef that summarizes conceptually the role of forcing (gradients in nutrient supply and turbulence) in determining phytoplankton species and size composition (reprinted with permission from Margalef R (1997) Our biosphere. In: Kinne O (ed) Excellence in Ecology. Ecology Institute, Oldendorf)
Microbial plankton:
- Microalgae

Flagellates - mixotrophs

They possess photosynthetic machinery and thus are difficult to identify under the microscope.

High bacterivory by the smallest phytoplankton in the North Atlantic Ocean (contributes 30-90% bacterivory)
Fig. 7.19. The phytoplankton mandala of Margalef that summarises conceptually the role of forcing (gradients in nutrient supply and turbulence) in determining phytoplankton species and size composition (reprinted with permission from Margalef R (1997) Our biosphere. In: Kinne O (ed) Excellence in Ecology. Ecology Institute, Oldendorf)
Gaia Theory of Earth’s self-regulation

Plancton microbiano:
- Algas fotosintéticas

Productores de DMS

Phytoplankton biomass and primary production
Marine microbial functional groups in a food web

Silica
CO2
vulcanism & rock weathering

Export all calcifiers

N2 fixers
DMS
mixotrophy
DOM
bacteria
recycling

phyto

CO2
all
N
fixers

?]

zoo

Nutrients

Export

Export

Export

Lisocline

Organic matter + CaCO3 + Silica

Upper ocean

Deep ocean sediments
Marine microbial functional groups in a food web
Diatoms & coccolithophores are the most important phytoplankton groups in terms of carbon export and sequestration in the deep marine sediments.

Mineral skeletons and cell size size

Calcium carbonate pump
\[ \text{Ca}^{2+} + 2\text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{H}_2\text{O} + \text{CO}_2 \]
The nutricline depth serves as an index of nutrient supply.
Projection of the empirical relationship between the C/D-ratio and the nutricline depth into a Ocean General Circulation Model to predict future changes in the distribution of diatoms and coccolithophores in the Atlantic Ocean.

The cccos expand their distribution with respect to diatoms towards temperate latitudes.

This represents a positive feedback in the climate system – the ocean will decrease its potential to store atmospheric carbon dioxide aggravating the climate problem.
Glacial/interglacial fluctuations of diatoms and coccoss
Evolution of the nitrogen cycle and its influence on the biological sequestration of CO_2 in the ocean

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Elevated consumption of carbon relative to nitrogen in the surface ocean

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The role of nutricline depth in regulating the ocean carbon cycle

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Contributed by Paul G. Falkowski, November 10, 2008 (sent for review October 7, 2008)
An example of evolutionary success: reconstructing the evolutionary history of marine diatoms
Part 1. Diversity dynamics of marine diatoms using the fossil record

Part 2. Detecting shifts in marine diatom diversification using time-calibrated molecular phylogenies
Diatom productivity in broad regions of the oceans such as the equatorial Pacific is limited by the availability of silicic acid.


Diatoms vs. Silicate

The silica cycle in the ocean

Continental inputs

$F_{R_{\text{gross}}}$ = 7.3

Estuaries

$F_{R_{\text{net}}}$ = 5.8

Rivers:

$F_{R_{\text{gross}}} = 6.2$ (dissolved silica) + 1.1 (dissolvable biogenic silica) = 7.3 Tmol Si year$^{-1}$

Ocean

$F_{D_{\text{surface}}}$ = 135

Aeolian inputs

$F_{A}$ = 0.5

Surface mixed layer

$F_{D_{\text{deep}}}$ = 26.2

Sediments

$F_{S_{\text{rain}}}$ = 78.8

Hydrothermal inputs

$F_{H}$ = 0.6

$F_{D_{\text{benthic}}}$ = 72.5

$F_{F_{\text{net deposit}}}$ = 6.3

Controls on opal burial in marine sediments

A deviation from the steady-state – for instance by increasing the supply of silicic acid to the ocean – will lead to an increase in the rate of opal burial to maintain the conditions of steady-state.

OPAL ACCUMULATION RATE IN MARINE SEDIMENTS CAN BE USED AS A PROXY FOR ADDITIONS OF SILICIC ACID TO THE OCEAN
Hypothesis 1. Hypothesis based on competition for silicate. Like the diatoms, radiolarians, which are ameboid protozoa, also require silicic acid to build their mineral skeletons.

H1: Competition for silicic acid between diatoms and radiolarians explains the rise of diatoms over the Cenozoic.

Diatoms are competitively superior for silicic acid with respect to the radiolarians

Hypothesis 1. Hypothesis based on competition for silicate. Like the diatoms, radiolarians, which are ameboid protozoa, also require silicic acid to build their mineral skeletons.

*This hypothesis does not require additional inputs of silicic acid to the ocean – (the partitioning of available silicate among siliceous plankton serves to explain their evolutionary trajectories).*
**Hypothesis 2.** The second hypothesis states that increased inputs of silicic acid to the ocean facilitated the evolutionary success of diatoms.

First hypothesis is based on **BIOLOGY** (competition for available silicic acid) whereas this second hypothesis is based on **GEOLOGY**.

These are not mutually exclusive possibilities but as far as we know, so far NO TEST HAS BEEN MADE TO explore the second one.
A global database of microfossil occurrences reported by the Ocean Drilling Program (ODP) and the Deep Sea Drilling Project (DSDP)

‘NEPTUNE database’
‘NEPTUNE database’

- **Diversity** of diatoms and radiolarians through time using sampling standardized techniques. (the number of samples increases towards recent times)

- Summed Common Species Occurrence Rate, **SCOR** (index of global dominance or geographic expansion).

  \[
  \text{SCOR} = \sum_{y=1}^{n} \frac{Y_{ij}}{n_j} \quad Y \text{ number of sites in which a given species is present in a time bin} \\
  \text{ } \quad n \text{ total number of sites in the time bin}
  \]

- We compiled data of **opal accumulation rate** in marine sediments >> proxy for additions of silicic acid to the ocean.

  - If the rise of diatoms is driven by enhanced inputs of silicic acid to the ocean, then we should see parallel changes in the rate of opal accumulation in marine sediments.
The striking similarity of these curves suggests that the diversity of diatoms and radiolarians could be controlled by secular changes in the availability of silicic acid.
SCOR: global expansion of siliceous plankton
Enhanced inputs of silicic acid to the ocean could stimulate the expansion of diatoms.
There are two main sources of silicic acid to the ocean:

1) Continental weathering fluxes

2) Volcanism – remained relatively constant throughout the late Cenozoic era.
Lithium is a trace element in rocks
Li is hosted **only** in silicate minerals - Potential to track silicate weathering

**Inputs Li**: rock weathering & volcanism

\[ \delta^7\text{Li}_w = \sim 23\% \]
\[ \delta^7\text{Li}_v = \sim 8.3\% \]

**Outputs Li**: adsorption of dissolved Li to secondary clays which removes \( ^6\text{Li}_{sw} \) preferentially and thus increases \( \delta^7\text{Li} \) in seawater (\( \delta^7\text{Li}_{sw} \)) -- **reverse weathering**

Continental erosion represents the main source of secondary clays to the ocean. Thus, **an increase in \( \delta^7\text{Li}_{sw} \) reflects enhanced rates of continental erosion.**

This isotope is removed preferentially during reverse weathering which increases \( ^7\text{Li} \) in seawater.
$\delta^7\text{Li}_{SW}$ during the Cenozoic era recorded in the calcium carbonate test of planktic foraminifera

Continental weathering and the rise of marine diatoms

Rises of diatom diversity and SCOR correlate with periods of enhanced continental weathering - linking the Cenozoic evolution of marine diatoms to the erosion of continents
1. Increases the areal extent for rock weathering

2. Steep slopes shift the weathering regime: from transport-limited to weathering-limited. (i.e. more nutrients transported to the ocean)
Glaciers transport silica-rich lithogenic particles that enter the surface ocean.
Glaciers transport silica-rich lithogenic particles that enter the surface ocean.
Five groups were selected for the present study:

- Thalassiosirales
- Bacillariales
- Chaetocerales
- Rhizosoleniales
- Coscinodiscales

We can estimate rates of net diversification rates from time-calibrated molecular phylogenies.

1) widespread distribution
2) well represented in the fossil record
3) sequences available in GenBank
4) biogeochemical relevance

100 sequences of the 18S rRNA
**BEAST v1.7.4.**

BEAST is a program for Bayesian MCMC analysis of molecular sequences. Assuming a relaxed molecular clock model.

## Calibration points

<table>
<thead>
<tr>
<th>Genera/Species</th>
<th>Calibration point</th>
<th>Calibration date</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chaetoceros</td>
<td>34 – 36 my</td>
<td>Minimum age*</td>
<td>Neptune database</td>
</tr>
<tr>
<td>Rhizosolenia</td>
<td>93 – 90 my</td>
<td>Fixed age^</td>
<td>Sinninghe-Damsté et al., 2004</td>
</tr>
<tr>
<td>Skeletonema</td>
<td>37 – 39 my</td>
<td>Minimum age</td>
<td>Neptune database</td>
</tr>
<tr>
<td>S. grethae ATL, PAC</td>
<td>3.1 – 3.3 my</td>
<td>Fixed age</td>
<td>Coates et al., 1992</td>
</tr>
<tr>
<td>T. weissflogii ATL, PAC</td>
<td>3.1 – 3.3 my</td>
<td>Fixed age</td>
<td>Coates et al., 1992</td>
</tr>
<tr>
<td>Coscinodiscus</td>
<td>44 – 48 my</td>
<td>Minimum age</td>
<td>Neptune database</td>
</tr>
</tbody>
</table>

*Minimum age first observation of the genus in the geological record

^Fixed age well dated origination of a genotype
We used the TreePar/LASER/MEDUSA packages to estimate the diversification rates based on a Yule model and a birth-death model.

The program calculates which trees are more similar to the original one using the AIC and then estimates the rates of diversification.

Fig. 5. Tree notation. (Left) An example of a tree that evolved under the birth-death shift process. The sampled species are denoted with a solid circle. (Right) The corresponding sampled tree with root edge. The labels $l$ and $r$ are suppressed on most branches for clarity.
MEDUSA package:

diversification rate of different lineages from an analysis of 10,000 phylogenetic trees

5,000 trees identify a shift in diversification around 80 m.y.
The combined effects of enhanced nutrient supply and oceanic turbulence, which provide the adequate conditions for the growth and expansion of marine diatoms.
The combined effects of enhanced nutrient supply and oceanic turbulence, which provide the adequate conditions for the growth and expansion of marine diatoms.