A mathematical model of bloom of the coccolithophore *Emiliania huxleyi* in a mesocosm experiment.

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*Emiliania huxleyi*: the most numerically important specie of coccolithophores.

The convergence of 3 biological features renders *Emiliania huxleyi* to be one of the major actors involved in the oceanic carbon export:

- Oceanwide distributed phytoplankton producing large blooms
- Calcifying algal
- Production of TEP
Nine 11m³ confined water environments. The enclosed atmospheres are artificially maintained under determined values of pCO2, representing three different conditions of atmospheric pCO2:
• Future time (mesocosms n°1,2,3). pCO2 fixed to ~710 µAtm
• Present time (mesocosms n°4,5,6). pCO2 fixed to ~410 µAtm
• Glacial past time (mesocosms n°7,8,9). pCO2 fixed to ~190 µAtm
### Data set used in the model.

<table>
<thead>
<tr>
<th>Biological data</th>
<th>Chemical data</th>
<th>Carbon data</th>
<th>Physical data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton species:</td>
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<tr>
<td><em>Emiliania huxleyi</em></td>
<td>Nitrate (mmolN/m³)</td>
<td>DIC (mmolC/m³)</td>
<td>Salinity (-)</td>
</tr>
<tr>
<td>(cell/m³)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Micromonas</em></td>
<td>Ammonium (mmolN/m³)</td>
<td>POC (mmolC/m³)</td>
<td>Temperature (°C)</td>
</tr>
<tr>
<td>(cell/m³)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Synechococcus</em></td>
<td>Phosphate (mmolP/m³)</td>
<td>PIC (mmolC/m³)</td>
<td>PAR above surface (µmolPhoton/m².s)</td>
</tr>
<tr>
<td>(cell/m³)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacteria (part/m³)</td>
<td>DOC (mmolC/m³)</td>
<td>Total Alkalinity (mmol/kgSW)</td>
<td></td>
</tr>
<tr>
<td>Virus (part/m³)</td>
<td>Diss. Oxygen (mmolO₂/m³)</td>
<td>pH (total scale)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TEP (mmolC/m³)</td>
<td>pCO₂ Air (µatm)</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>pCO₂ Water (µatm)</td>
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</table>
Challenge of the model: conjoined representation of *Ehux*. specific processes involved in the carbon export
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- DIC
- *Ehux*. biomass growth
- sink
Challenge of the model: conjoined representation of *Ehux*. specific processes involved in the carbon export

- DIC
- *Ehux*. biomass growth
- DOC extracellular release
- TEP formation
- sink
- sink
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Challenge of the model: conjoined representation of *Ehux*. Specific processes involved in the carbon export.
General conception of the model.

- Zero dimensional model involving 26 state variables.

- Description of Carbon, Nitrogen and Phosphorous cyclings through \textit{Ehux}. biomass and the microbial loop.

- The microbial loop includes representations of bacterial biomass and dissolved organic matter (DOM).

- DOM is divided into two pools: labile and semi-labile.

- Balanced model for bacterial biomass growth.
DIC and total alkalinity are explicitly represented. Dissolved CO$_2$ and pH are computed from DIC and total alkalinity.

Consideration of two forms for particulate inorganic carbon (PIC): attached to cells and free (detached coccoliths).

Application of specific constant sinking speeds to all particulate matters: $Ehux.$, free PIC, detritus and TEP.

The model does not consider the degradation of the organic sediment.

The model considers CO$_2$ molecular diffusion across the air-water interface.
E. huxleyi
CNP

attached Calcite C

free Calcite C

Mesocosm enclosed atmosphere

Mesocosm water column

Mesocosm bottom
Mesocosm enclosed atmosphere

Mesocosm water column

Mesocosm bottom

E. huxleyi
CNP

attached Calcite C

free Calcite C

Bacteria CNP

Labile DOM CNP

Semi-labile DOM CNP

Detritus CNP
Mesocosm enclosed atmosphere

- E. huxleyi CNP
- Bacteria CNP
- Attached Calcite C
- Free Calcite C
- Labile DOM CNP
- Semi-labile DOM CNP
- TEP C
- Detritus CNP

Mesocosm water column

Mesocosm bottom
Mesocosm enclosed atmosphere

- **Virus**
  - *E. huxleyi* CNP
  - Attached Calcite C
  - Free Calcite C

- **Bacteria** CNP
  - Dissolved Oxygen O
  - DIC C
  - Phosphate P
  - Nitrate N
  - Ammonium N

- **Labile DOM CNP**
- **Semi-labile DOM CNP**
  - TEP C

- **Detritus CNP**

Mesocosm water column

Mesocosm bottom
Forcing variables.

Solar irradiance

External sea water

Salinity

Fixed pCO₂ inside the mesocosm enclosed atmosphere

Model state variables

Temperature
Evolution of forcing variables measured over the 23 days experiment.
Formulation of *Ehux*. particular processes.

- Algal growth
- Phosphorous uptake
- Calcite production
- DOM exudation and DOC extracellular release
- TEP formation
- Enhanced cellular mortality due to viral lysis
Algal growth.

- **Unbalanced growth model**: DIN and DIC uptakes are decoupled. Cellular C:N molar ratio is variable. Cellular N:P molar ratio is fixed. Ammonium is assimilated preferentially to nitrate.

- **Respiration**: sum of metabolic respiration (proport. to biomass) and respiration induced by cellular activity (proport. to DIC uptake)

\[
\text{Respiration} = \text{Rate}_{\text{Metabolic}} \cdot Ehx_C + \text{Fract}_{\text{Activity}} \cdot C_{\text{Uptake}}
\]

- **Mortality**: sum of mortality caused by cellular senescence (constant rate) and losses of cells caused by viral lysis (variable rate).

\[
\text{Mort}_{Ehx_C} = (\text{Rate}_{\text{Senescence}} + \text{Rate}_{\text{MortVIR}}) \cdot Ehx_C
\]

- **No grazing** is considered.
Phosphorous uptake.

- *Ehux.* uses both:
  - organic phosphorous (labile and semi-labile DOP)
  - and inorganic phosphorous (DIP)

- DIP is assimilated preferentially to DOP
In the frame of the experimental observations, the *Ehux* calcifying activity is mainly considered like a structural cellular requirement.

Combination of two terms:
- Major term based on *Ehux* primary production
- Minor term based on *Ehux* carbon biomass

Calcification = \( \text{Ratio}_{\text{Calc:Corg}} \cdot (\text{C}_{\text{Uptake}} - \text{Respiration}) + \text{Rate}_{\text{Calcif}} \cdot \text{Ehux}_C \)
DOM exudation and DOC extracellular release.

- **DOM exudation.** Combination of:
  - a passive leakage consisting of labile materials (DOC, DON and DOP)
  - an active DOC extracellular release

- **DOC extracellular release:**
  - linked to carbon overconsumption
  - enhanced when algal growth is sustained under low nutrients availability conditions

\[
DOC_{\text{ExtraRel}} = C_{\text{Uptake}} \cdot \left( \frac{CN_{Ehux}}{(CN_{\text{Max}} - CN_{Ehux})} \right) \cdot \gamma
\]
TEP formation.

- TEP formation strongly linked to DOC extracellular release.

- A fraction of DOC extracellular release consists of acidic polysaccharides supporting coagulating properties, making precursors of TEP

\[
\text{Base}_{\text{coagulate}} = \text{Fract}_{\text{AcidicPolysacch}} \cdot \text{DOC}_{\text{ExtraRel}}
\]

\[
\frac{d\text{TEP}}{dt} = \left(\text{Base}_{\text{coagulate}}\right)^2 / \left(\text{Base}_{\text{coagulate}} + K_{\text{Basecoagulate}}\right) - \text{TEP}_{\text{sink}}
\]

- The model does not include aggregating properties of TEP.
- The model considers TEP is not involved in bacterial loop.
Enhanced cellular mortality due to viral lysis.

- Promiscuity between cellular hosts and viral infectious agents is used as epidemic index.

\[ \text{Prom} = \{ \text{Virus} \cdot (E_{hux}C/Ratio_{C:Cell}) \}^{0.5} \]

- Supplementary term added to cellular mortality rate representing lysis induced by viral attack.

\[ \text{Mort}_{\text{VIR}} = \{ \tanh[I((\text{Prom}/\text{Th}_{\text{Prom}})-1)] - \tanh[-I] \} \cdot \{\text{Mort}_{\text{VIRmax}} / (1 - \tanh[-I]) \} \]

- Dynamics of viruses:
  - production by dying infected cells only
  - destruction following constant degenerating rate.
Application of hyperbolic tangent function to represent threshold behavior of viral infections

\[ \text{Prom} = \text{Th}_{\text{Prom}} \]

(Mortality rate induced by viral lysis)

Maximal mortality rate induced by viral lysis

Prom (Virus-Cell promiscuity)
Enhanced cellular mortality due to viral lysis.

- Promiscuity between cellular hosts and viral infectious agents is used as epidemic index.

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\]

- Dynamics of viruses:
  - production by dying infected cells only
  - destruction following constant degenerating rate.

\[
\frac{d\text{Virus}}{dt} = (\text{Release}_{\text{VIR}} \cdot \text{Mort}_{\text{VIR}} \cdot E_{\text{lux}_C}) - (\text{Rate}_{\text{Vir}\_\text{Deg}} \cdot \text{Virus})
\]
Model results compared to experimental observations.

- Following results only concern mesocosms exposed to present-day atmospheric pCO$_2$ (~410 µatm)

- Observations are given by daily measurements performed on these three present-day mesocosms (nr 4, 5 and 6)
Evolution over the 23 days experiment.

(Continuous line is model. Dotted, dashed, and dashed-dotted lines are respectively mesocosms nr 4, 5, 6.)
Evolution over the 23 days experiment.
(Continuous line is model. Dotted, dashed, and dashed-dotted lines are respectively mesocosms nr 4, 5, 6.)
Evolution over the 23 days experiment.

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Evolution over the 23 days experiment.
(Continuous line is model. Dotted, dashed, and dashed-dotted lines are respectively mesocosms nr 4, 5, 6.)
Appreciation of the model.
Aspects to be improved.

- The model does not consider any diagenetic process in the sediments.

- The model does not consider any aggregating process in the water column.
Appreciation of the model.
Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliania huxleyi* bloom.
Appreciation of the model.
Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliania huxleyi* bloom.

- Good representation of TEP formation via the DOC extracellular release.

  * Importance of an accurate representation of the DOC extracellular release.

  * Check with the Percentage of Extracellular Release quotient (P.E.R.).
P.E.R. (%) = \( \frac{\text{DOC}_{\text{ExtraRel.}}}{\text{DOC}_{\text{ExtraRel.}} + C_{\text{uptake}}} \)
Appreciation of the model.
Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliania huxleyi* bloom.
- Good representation of TEP formation via the DOC extracellular release.
- Better representation of calcification in the final phase of bloom (limited nutrient conditions).
Representation of calcification based only on algal carbon biomass

Representation of calcification based on primary production and algal carbon biomass
Appreciation of the model.
Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliania huxleyi* bloom.

- Good representation of TEP formation via the DOC extracellular release.

- Better representation of calcification in the final phase of bloom (limited nutrient conditions).

- Model suitable for experimental application conducted in confined sea water environment by considering virus-cell interaction.
Extinction of *Emiliania huxleyi* bloom

With consideration of enhanced mortality due to viral lyses.

Without considering any action of viruses

Thin line is model, thick lines are observations.
Thank you for your attention.