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

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Emiliana huxleyi: the most numerically important specie of coccolithophores.

The convergence of 3 biological features renders *Emiliana 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**

Experimental framework.

The mesocosm experiment conducted in Bergen (June 2001).



Nine 11m³ confined water environments. The enclosed atmospheres are artificially maintained under determined values of pCO₂, representing three different conditions of atmospheric pCO₂:

- Futur time (mesocosms n°1,2,3). pCO₂ fixed to ~710 μAtm
- Present time (mesocoms 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.

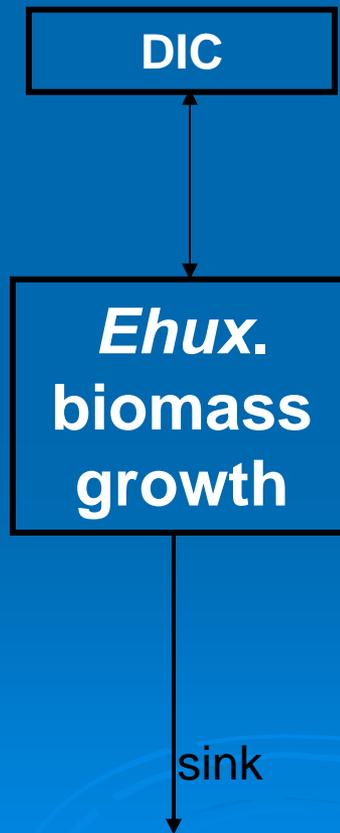
<u>Biological data</u>	<u>Chemical data</u>	<u>Carbon data</u>	<u>Physical data</u>
Phytoplankton species:	Nitrate (mmolN/m ³)	DIC (mmolC/m ³)	Salinity (-)
<i>Emiliana huxleyi</i> (cell/m ³)	Ammonium (mmolN/m ³)	POC(mmolC/m ³)	Temperature (°C)
<i>Micromonas</i> (cell/m ³)	Phosphate (mmolP/m ³)	PIC (mmolC/m ³)	PAR above surface (μmolPhoton/m ² .s)
<i>Synechococcus</i> (cell/m ³)	DOC (mmolC/m ³)	Total Alkalinity (mmol/kgSW)	
Bacteria (part/m ³)	Diss. Oxygen (mmolO ₂ /m ³)	pH (total scale)	
Virus (part/m ³)	TEP (mmolC/m ³)	pCO ₂ Air (μatm)	
		pCO ₂ Water (μatm)	

Challenge of the model:
conjoined representation of *Ehux.* specific processes
involved in the carbon export

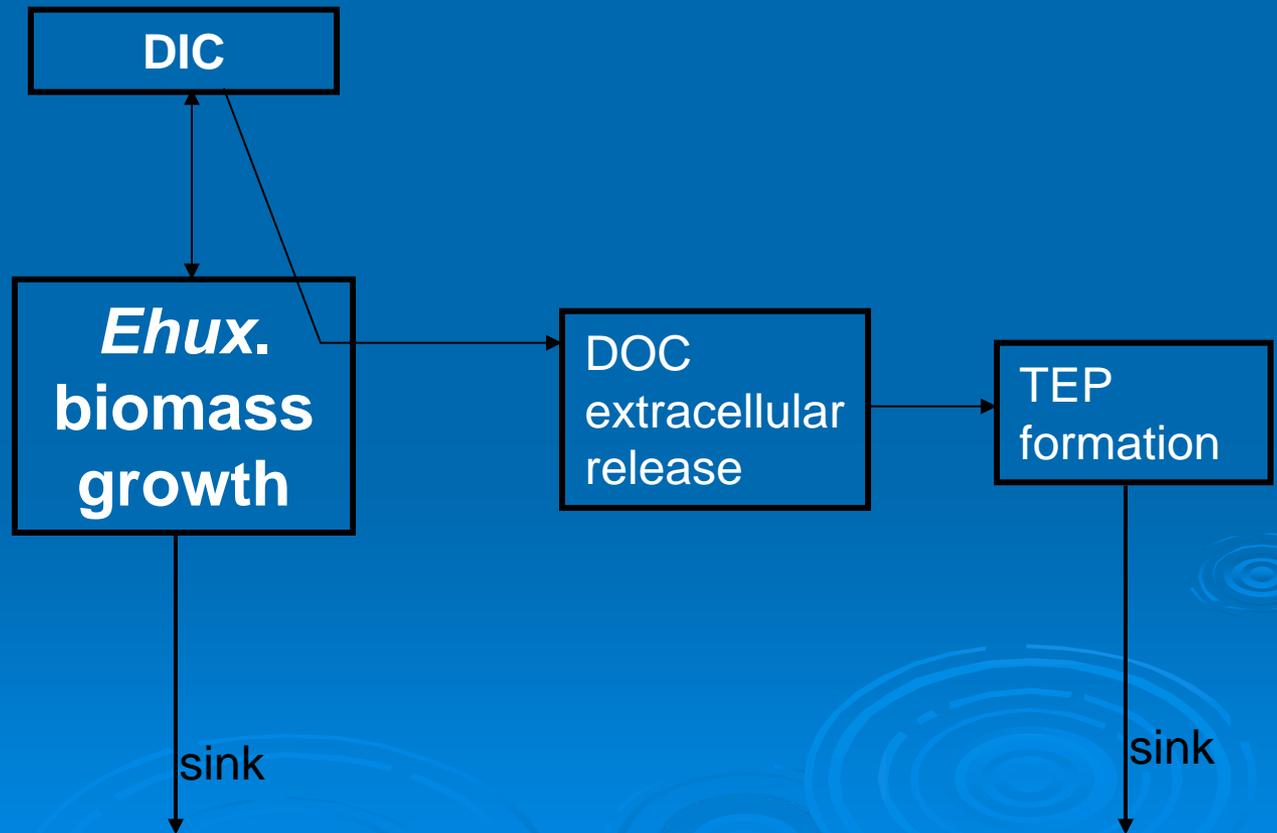
Ehux.
biomass

...

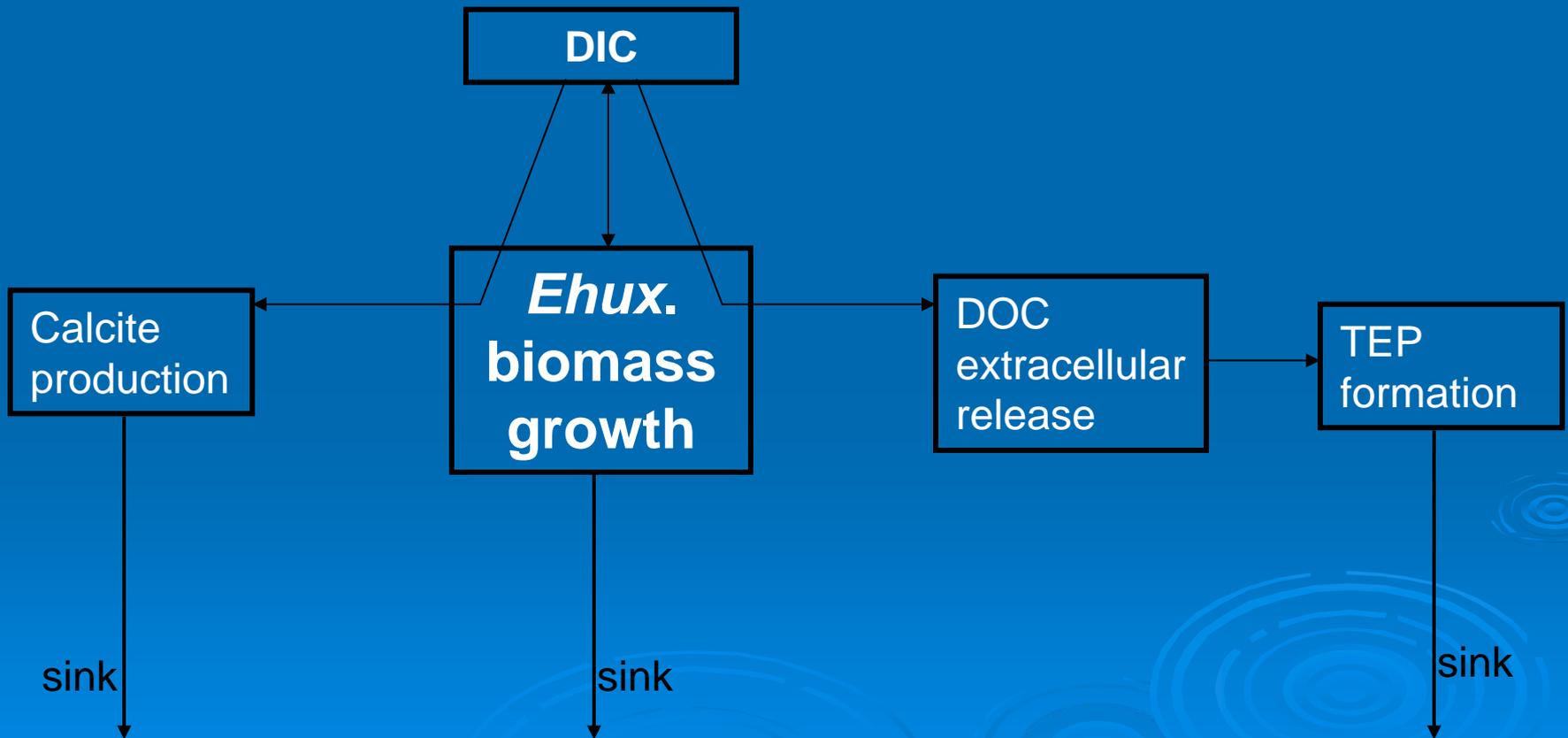
Challenge of the model:
conjoined representation of *Ehux.* specific processes
involved in the carbon export



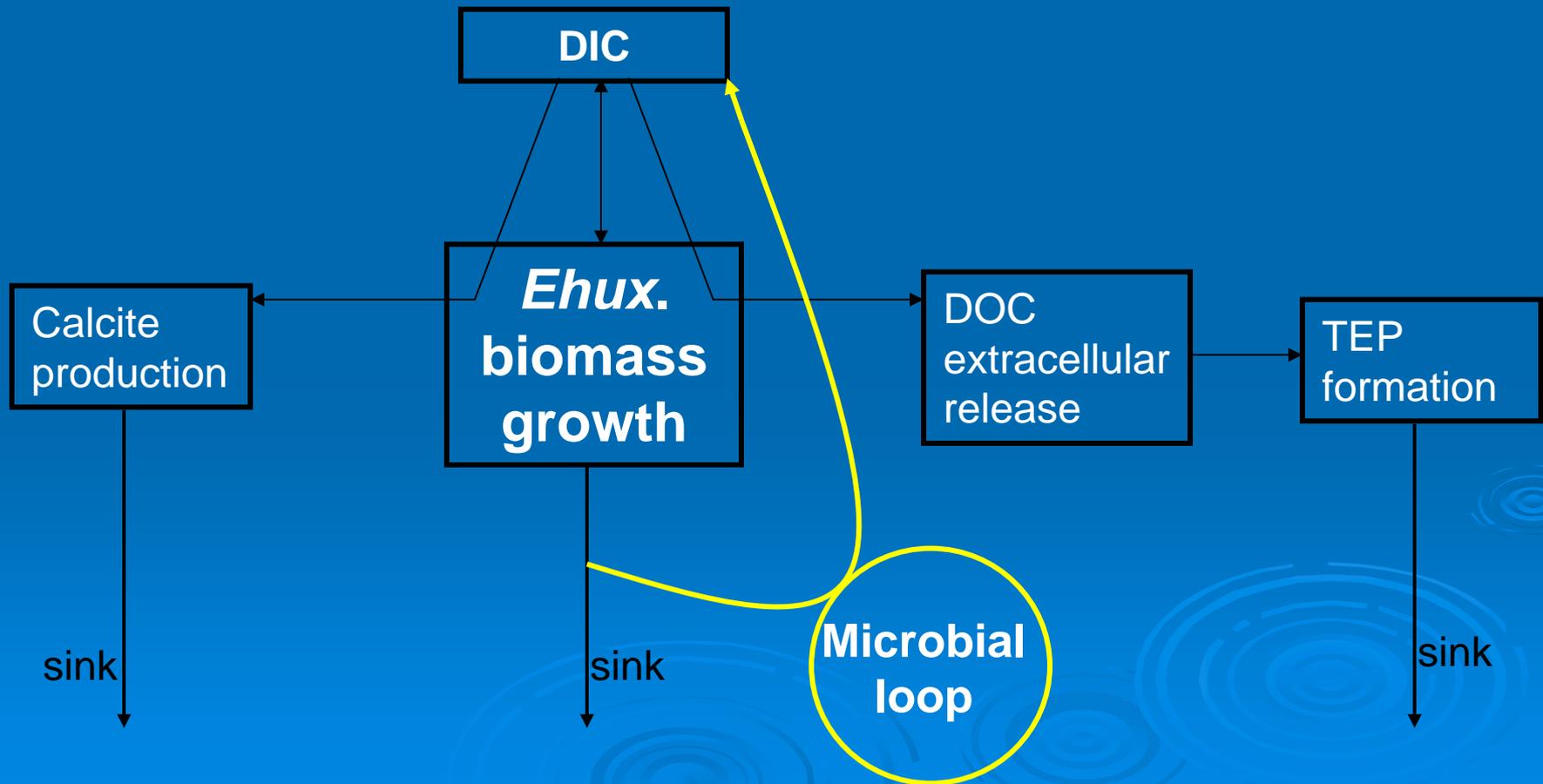
Challenge of the model:
conjoined representation of *Ehux.* specific processes
involved in the carbon export



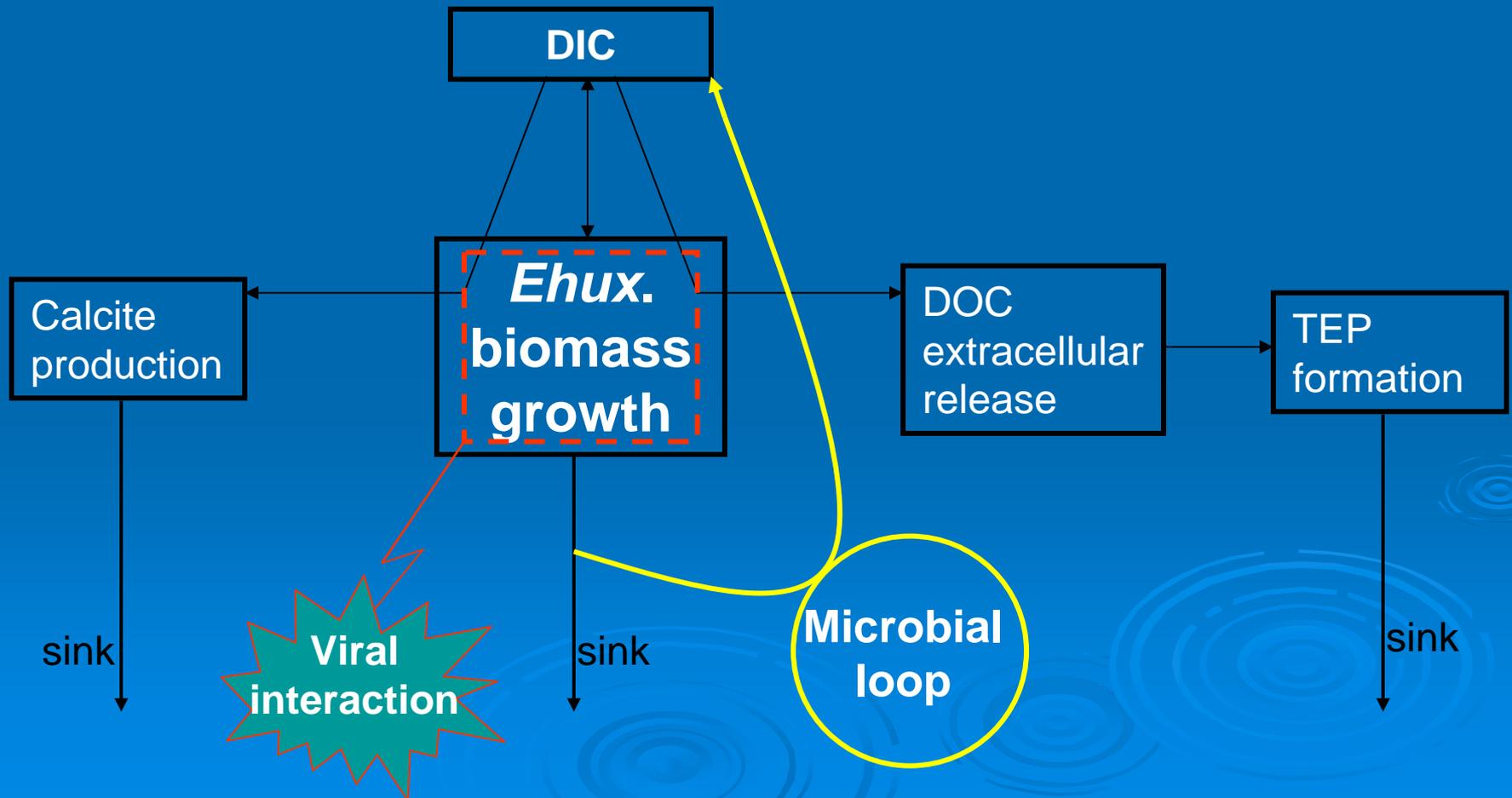
Challenge of the model:
conjoined representation of *Ehux.* specific processes
involved in the carbon export



Challenge of the model: conjoined representation of *Ehux.* specific processes involved in the carbon export



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 *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.

General conception of the model.

- 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.

Mesocosm
enclosed atmosphere

E. huxleyi
CNP

Mesocosm
water column

Mesocosm
bottom

Mesocosm
enclosed atmosphere

E. huxleyi
CNP

attached
Calcite
C

free
Calcite
C

Mesocosm
water column

Mesocosm
bottom

Mesocosm
enclosed atmosphere

E. huxleyi
CNP

Bacteria
CNP

attached
Calcite
C

Labile DOM
CNP

Semi-labile DOM
CNP

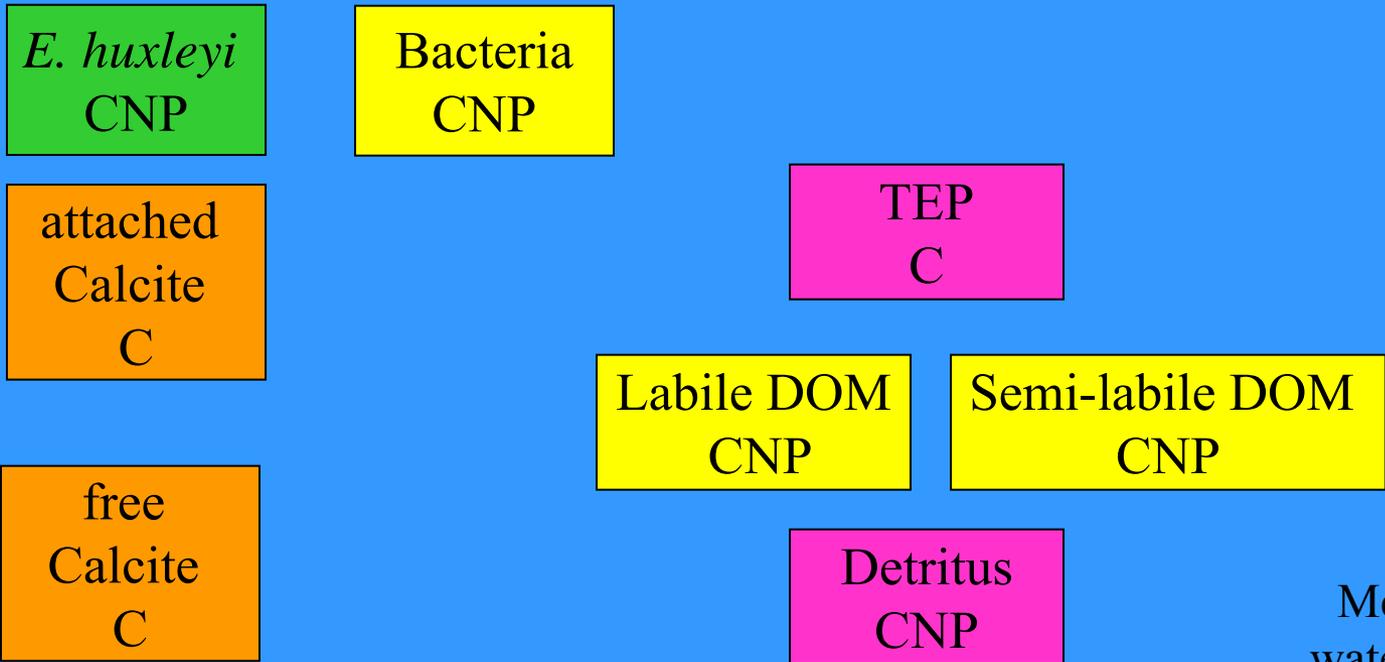
free
Calcite
C

Detritus
CNP

Mesocosm
water column

Mesocosm
bottom

Mesocosm
enclosed atmosphere



Mesocosm
water column

Mesocosm
bottom

Mesocosm
enclosed atmosphere

diss.oxygen
O

DIC
C

Phosphate
P

Nitrate
N

Ammonium
N

E. huxleyi
CNP

Bacteria
CNP

attached
Calcite
C

TEP
C

Labile DOM
CNP

Semi-labile DOM
CNP

free
Calcite
C

Detritus
CNP

Mesocosm
water column

Mesocosm
bottom

Mesocosm
enclosed atmosphere

diss.oxygen
O

DIC
C

Phosphate
P

Nitrate
N

Ammonium
N

Virus

E. huxleyi
CNP

Bacteria
CNP

attached
Calcite
C

TEP
C

Labile DOM
CNP

Semi-labile DOM
CNP

free
Calcite
C

Detritus
CNP

Mesocosm
water column

Mesocosm
bottom

exchanged CO₂
C

Mesocosm
enclosed atmosphere

diss.oxygen
O

DIC
C

Phosphate
P

Nitrate
N

Ammonium
N

Virus

E. huxleyi
CNP

Bacteria
CNP

attached
Calcite
C

TEP
C

Labile DOM
CNP

Semi-labile DOM
CNP

free
Calcite
C

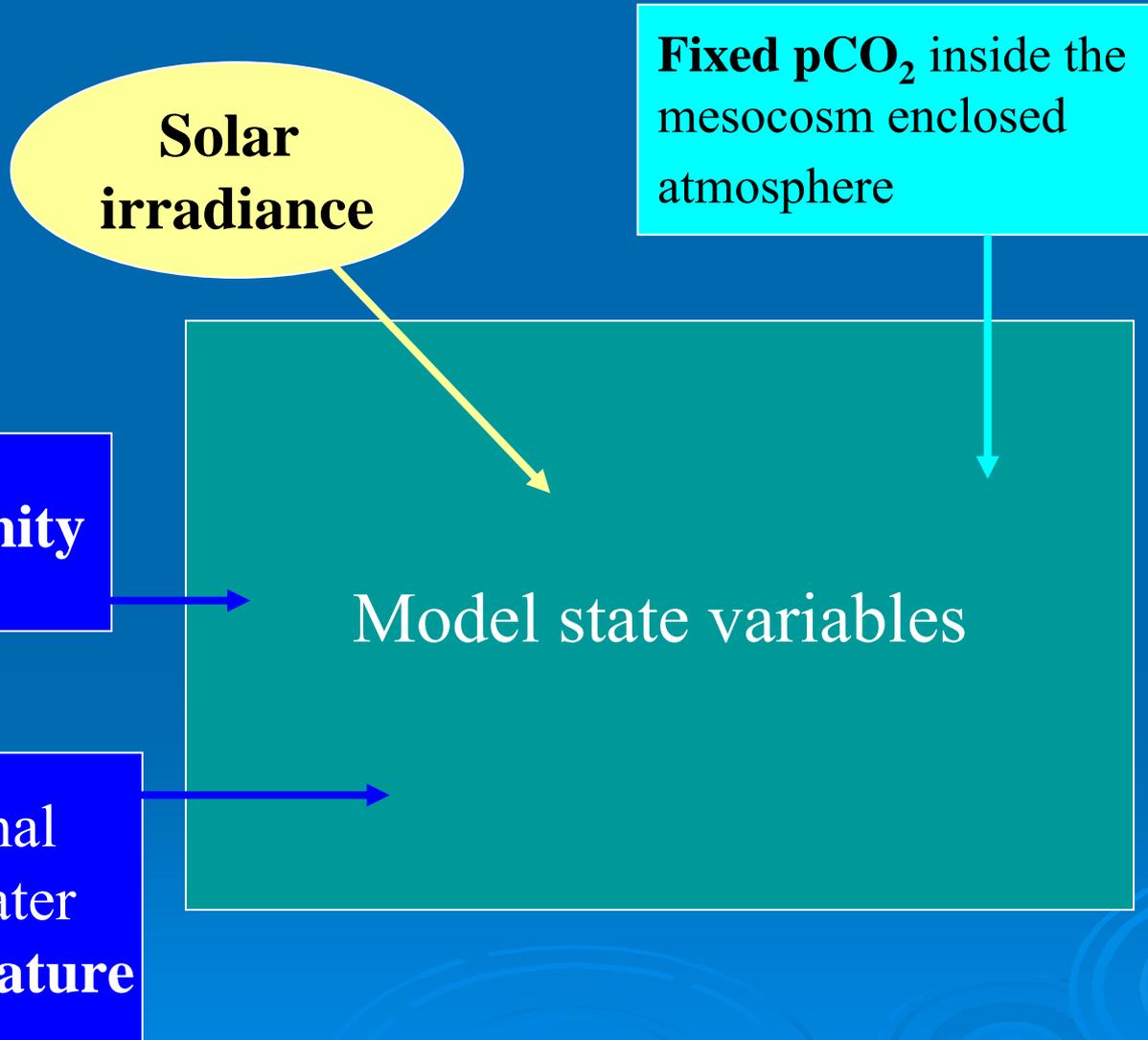
Detritus
CNP

Mesocosm
water column

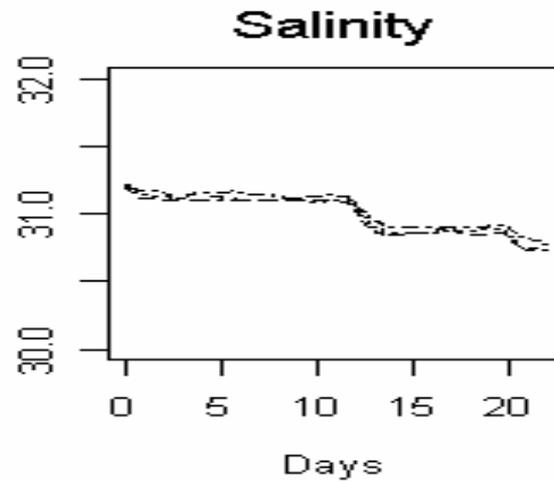
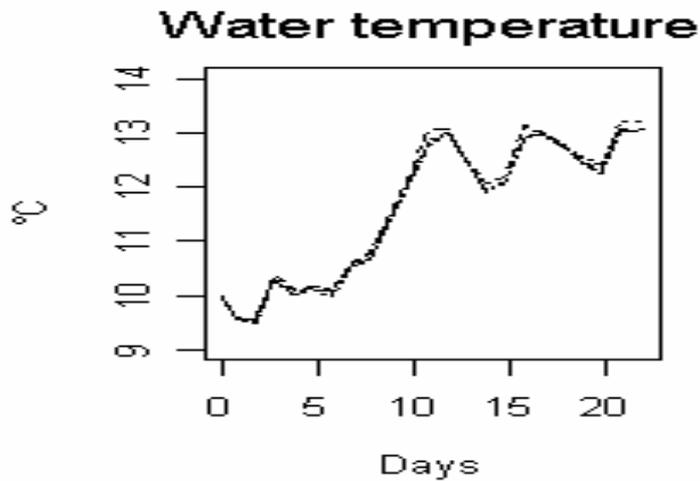
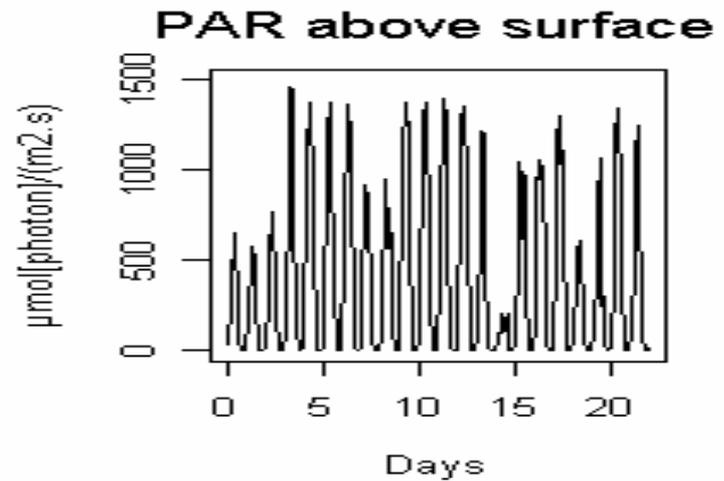
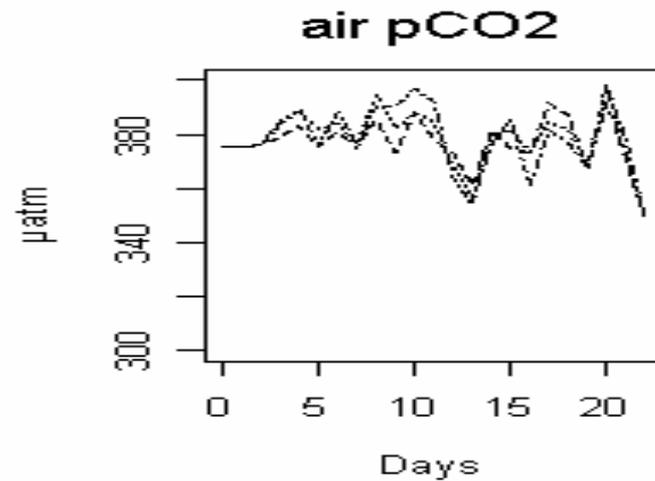
Deposit
CNP

Mesocosm
bottom

Forcing variables.



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.

$$\text{Nit_Uptake} = \text{Rate}_{\text{C_Nit_Uptake}} \cdot \frac{\text{C:N}}{(\text{C:N} + K_{\text{NO}_2})} \cdot \left(\frac{\text{PAR}}{\text{PAR} + K_{\text{PAR}}} \right) \cdot \left(1 + \frac{\text{C:N}}{\text{C:N}_{\text{Min}}} / \frac{\text{C:N}}{\text{C:N}_{\text{Max}}} \right) \cdot E_{\text{hux}_C}$$

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

$$\text{Respiration} = \text{Rate}_{\text{Metabolic}} \cdot E_{\text{hux}_C} + \text{Fract}_{\text{Activity}} \cdot \text{C_Uptake}$$

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

$$\text{Mort}_{E_{\text{hux}_C}} = (\text{Rate}_{\text{Senescence}} + \text{Rate}_{\text{MortVIR}}) \cdot E_{\text{hux}_C}$$

➤ **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

Calcite production.

- 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

$$\text{Calcification} = \text{Ratio}_{\text{Calc:Corg}} \cdot (\text{C_Uptake} - \text{Respiration}) + \text{Rate}_{\text{Calcif}} \cdot \text{Ehux}_C$$

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

$$\text{DOC}_{\text{ExtraRel}} = C_{\text{Uptake}} \cdot (\text{CN}_{\text{Ehux}} / (\text{CN}_{\text{Max}} - \text{CN}_{\text{Ehux}})) \cdot \gamma$$

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

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

$$d\text{TEP}/dt = (\text{Base}_{\text{coagulate}})^2 / (\text{Base}_{\text{coagulate}} + K_{\text{Basecoagulate}}) - \text{TEP}_{\text{sink}}$$

- 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.

$$\text{Prom} = \{ \text{Virus} \cdot (\text{Ehux}_C / \text{Ratio}_{C:\text{Cell}}) \}^{0,5}$$

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

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

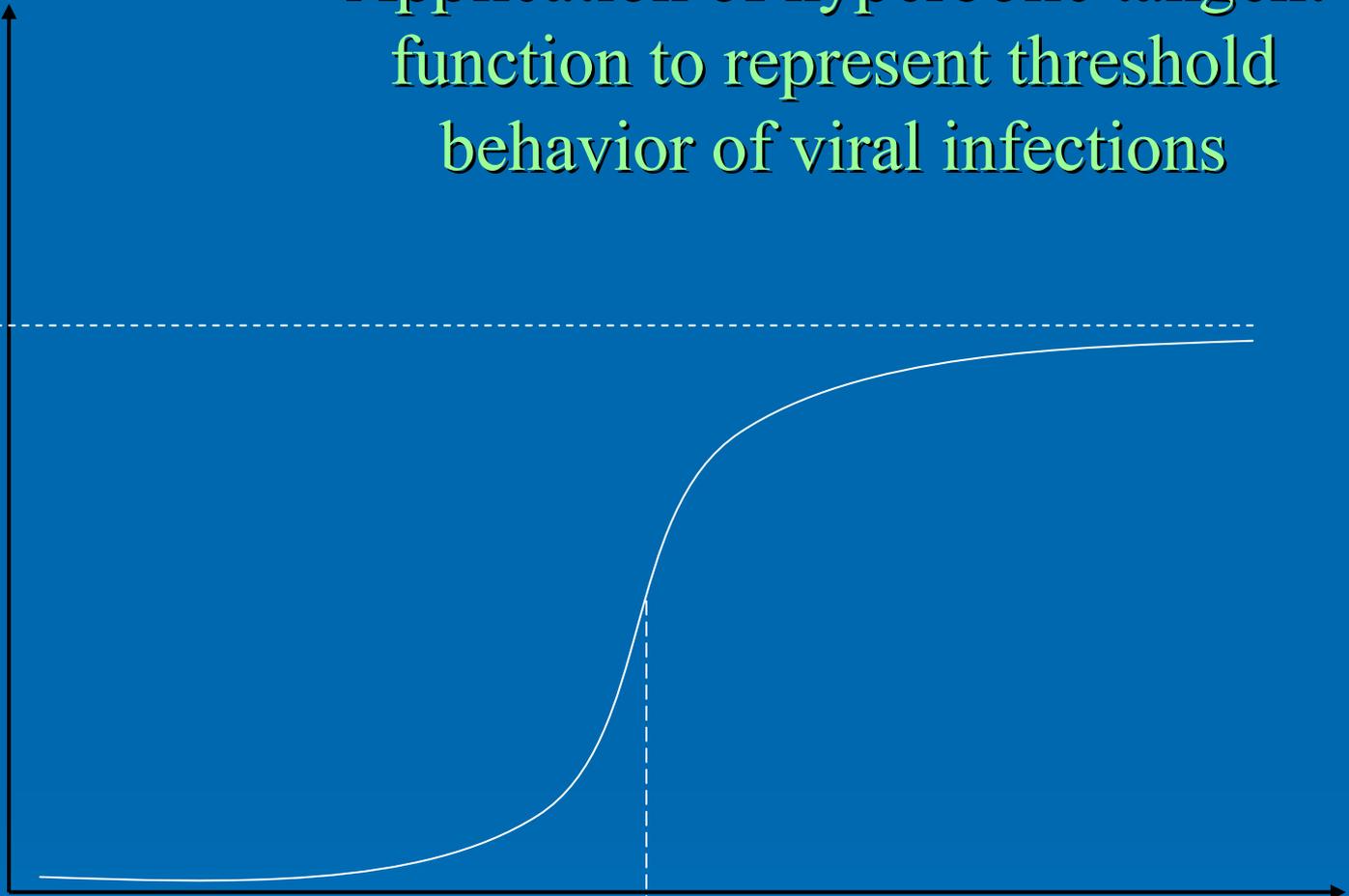
- Dynamics of viruses:

- production by dying infected cells only
- destruction following constant degenerating rate.

Application of hyperbolic tangent function to represent threshold behavior of viral infections

$Mort_{VIR}$
(Mortality rate induced by viruses)

Maximal mortality rate induced by viral lysis



$Prom = Th_{Prom}$
(threshold value of promiscuity)

$Prom$
(Virus-Cell promiscuity)

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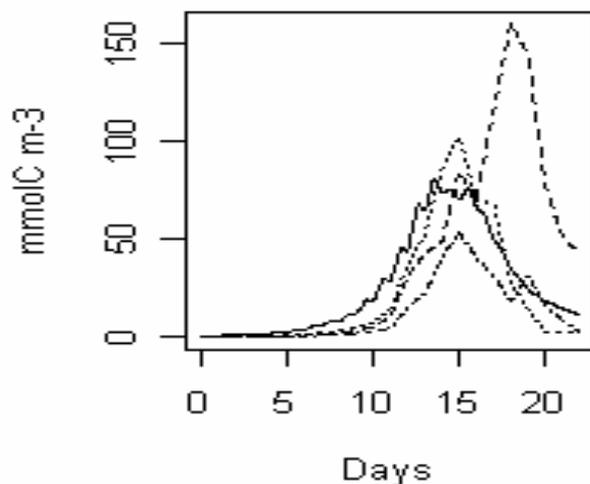
- Dynamics of viruses:
 - production by dying infected cells only
 - destruction following constant degenerating rate.

$$d\text{Virus}/dt = (\text{Release}_{\text{VIR}} \cdot \text{Mort}_{\text{VIR}} \cdot \text{Ehux}_C) - (\text{Rate}_{\text{Vir_Deg}} \cdot \text{Virus})$$

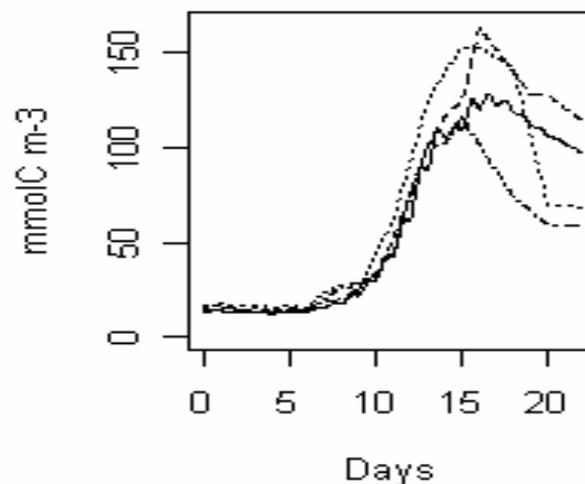
Model results compared to experimental observations.

- Following results only concern mesocosms exposed to present-day atmospheric $p\text{CO}_2$ ($\sim 410 \mu\text{atm}$)
- Observations are given by daily measurements performed on these three present-day mesocosms (nr 4, 5 and 6)

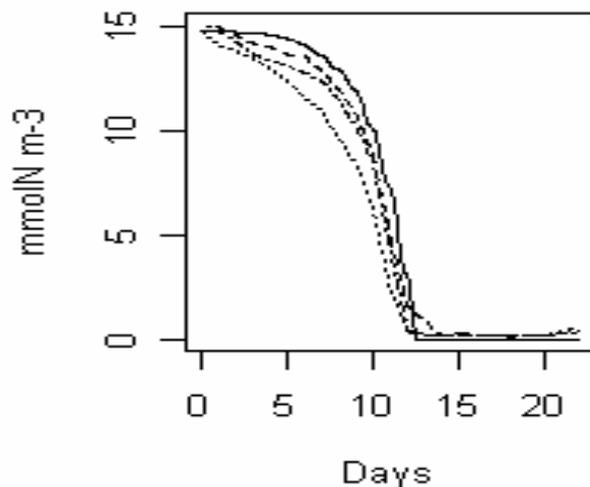
Emiliana carbon biomass



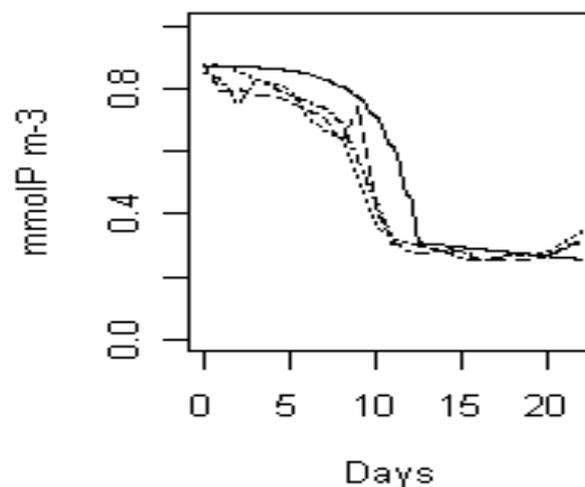
POC



Nitrate

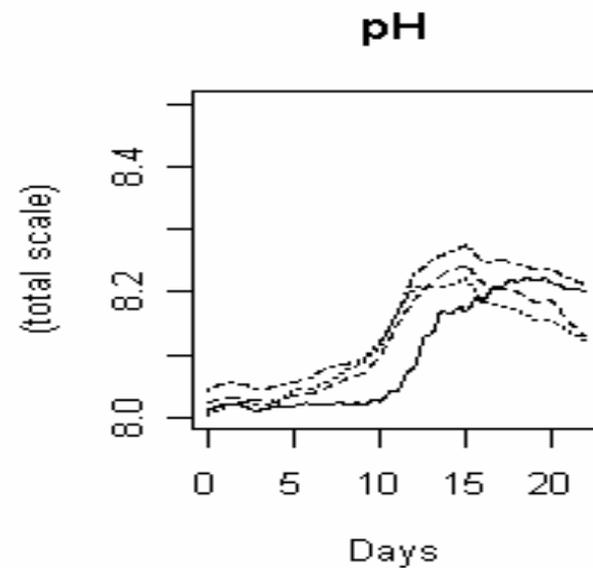
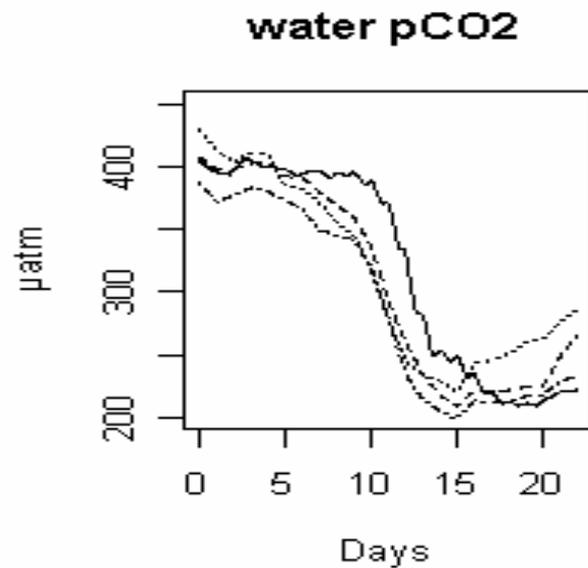
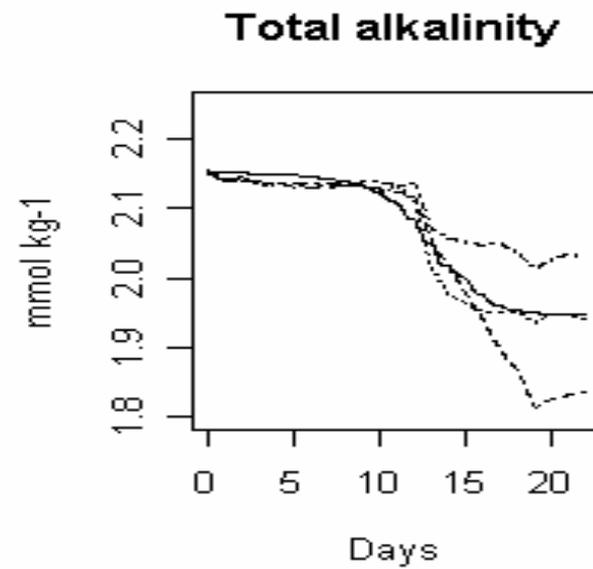
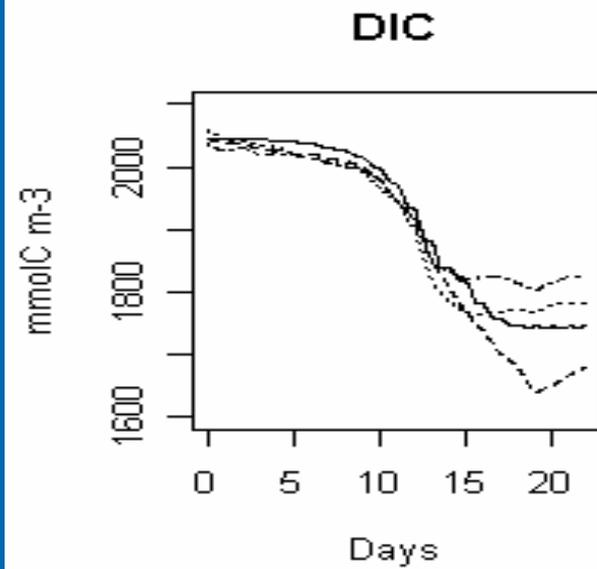


Phosphate



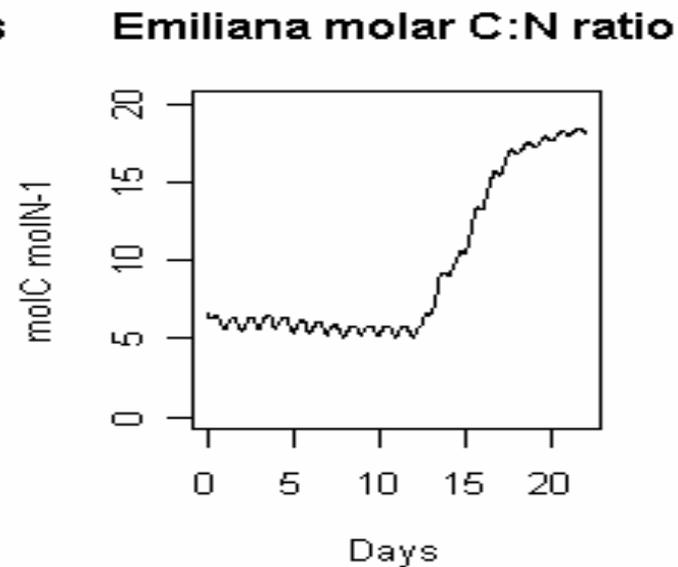
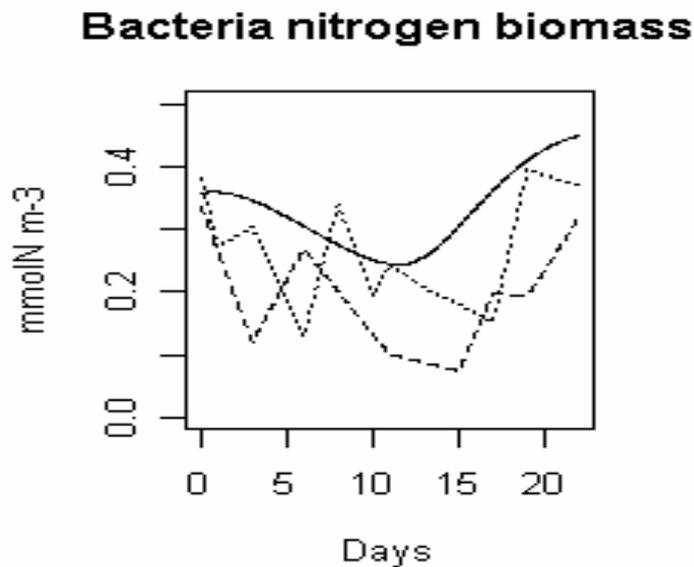
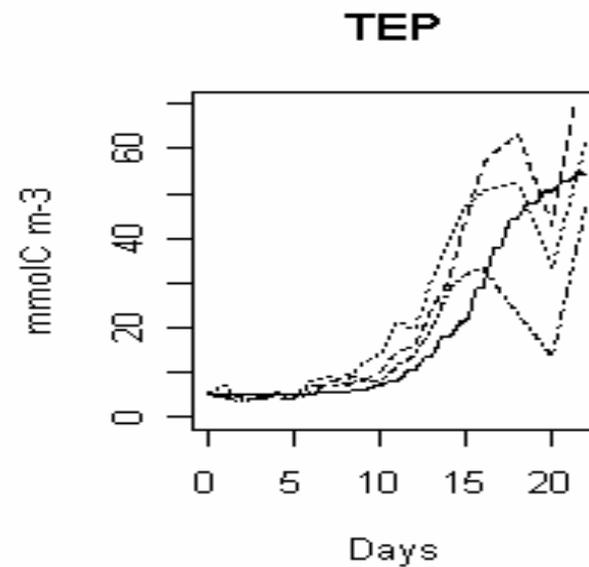
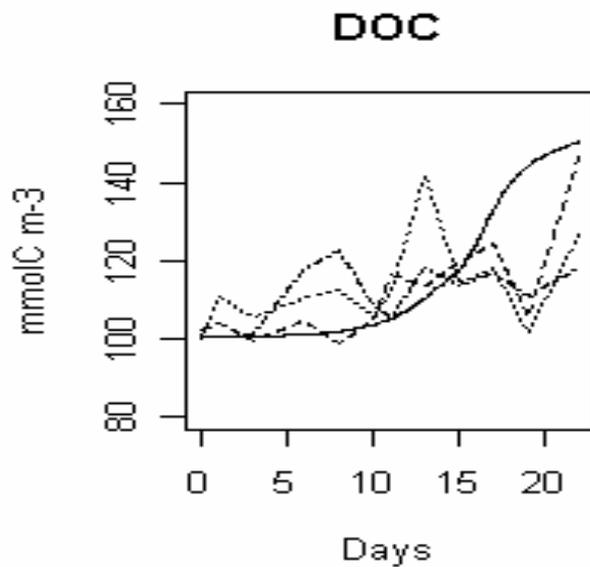
Evolution over the 23 days experiment.

(Continuous line is model. Dotted, dashed, and dashed-dotted lines are respectively mesocosms nr 4, 5, 6.)



Evolution over the 23 days experiment.

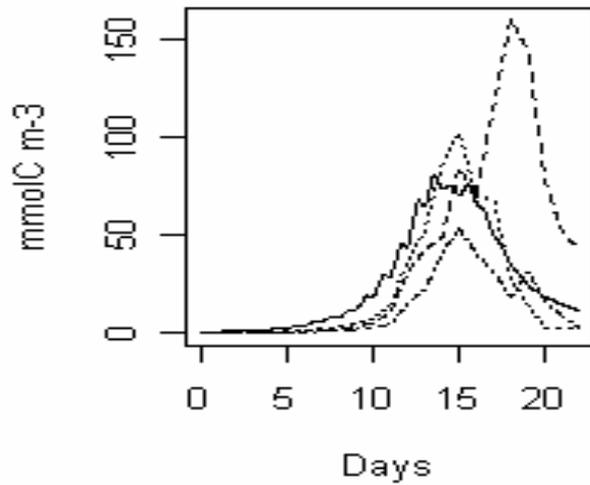
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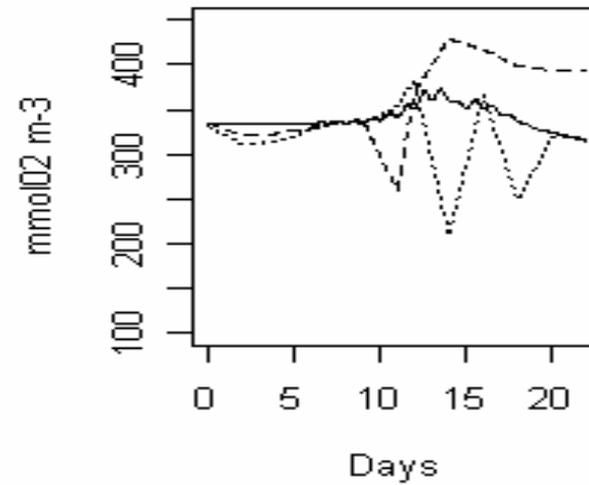
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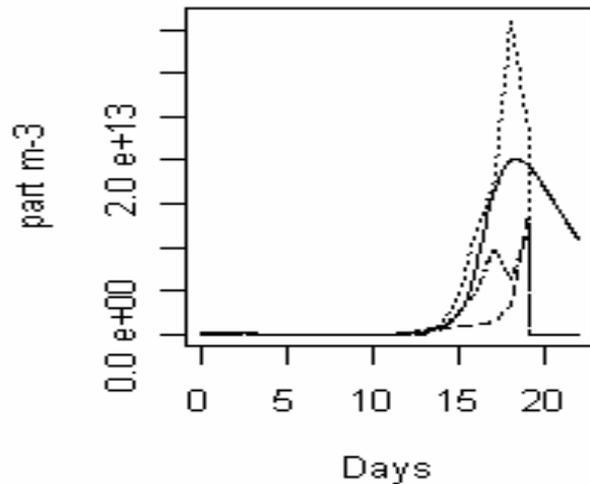
Emiliana carbon biomass



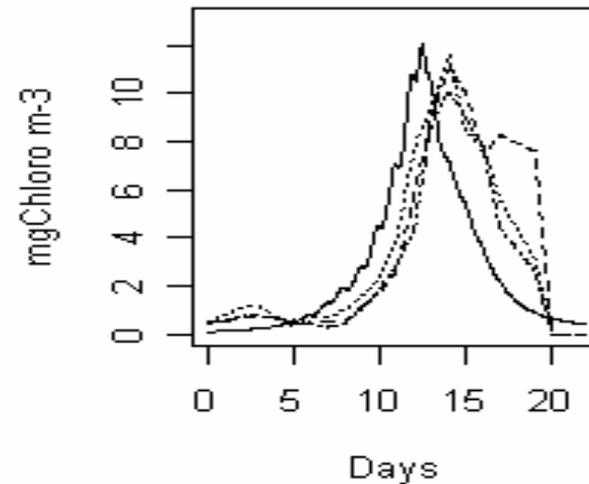
water dissolved Oxygen



Virus



Chl. a

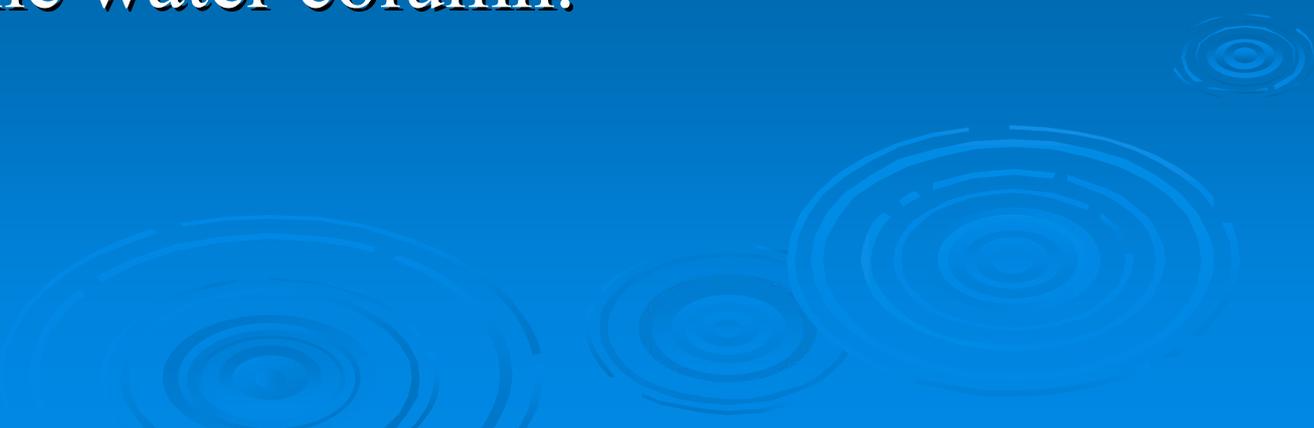


Evolution over the 23 days experiment.

(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 sedimented organic matter.
 - 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 *Emiliana huxleyi* bloom.

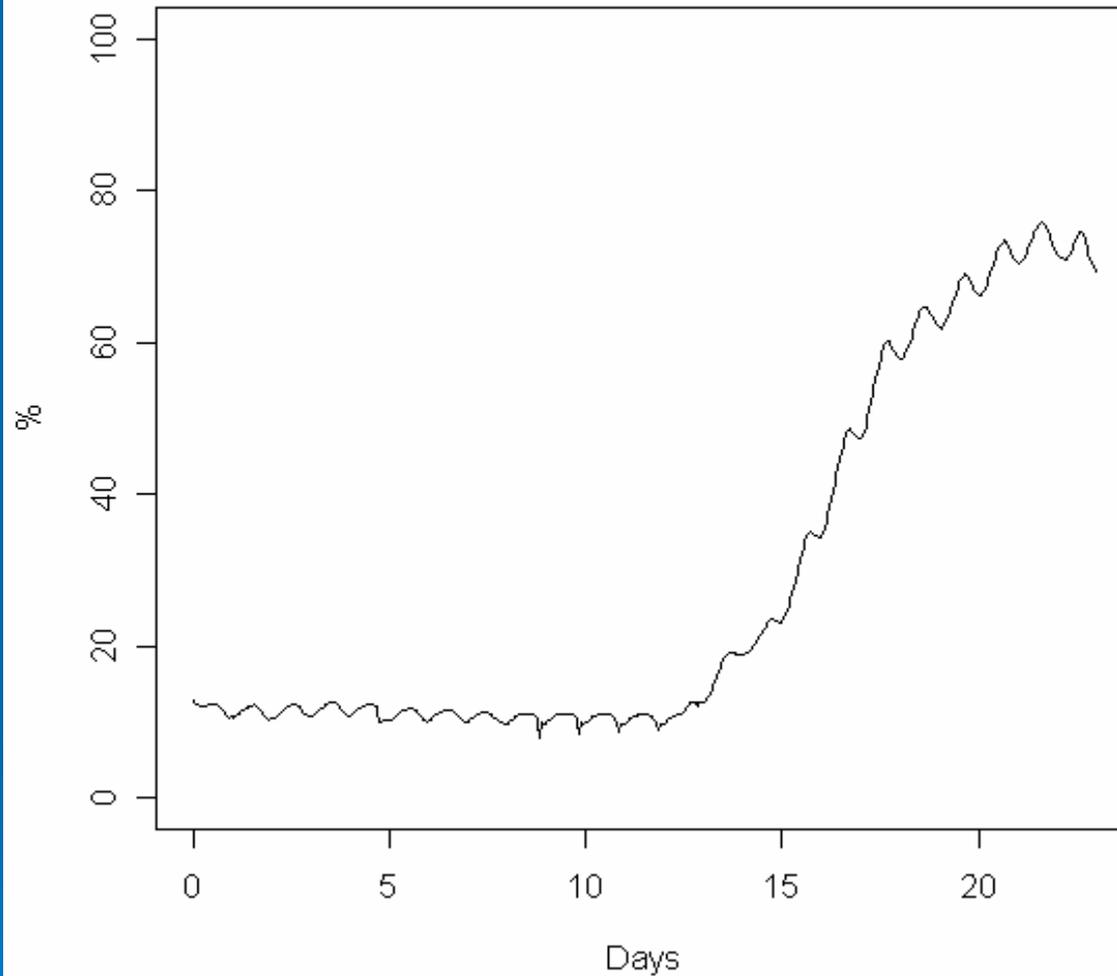


Appreciation of the model.

Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliana 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.).

Percentage of Extracellular Release



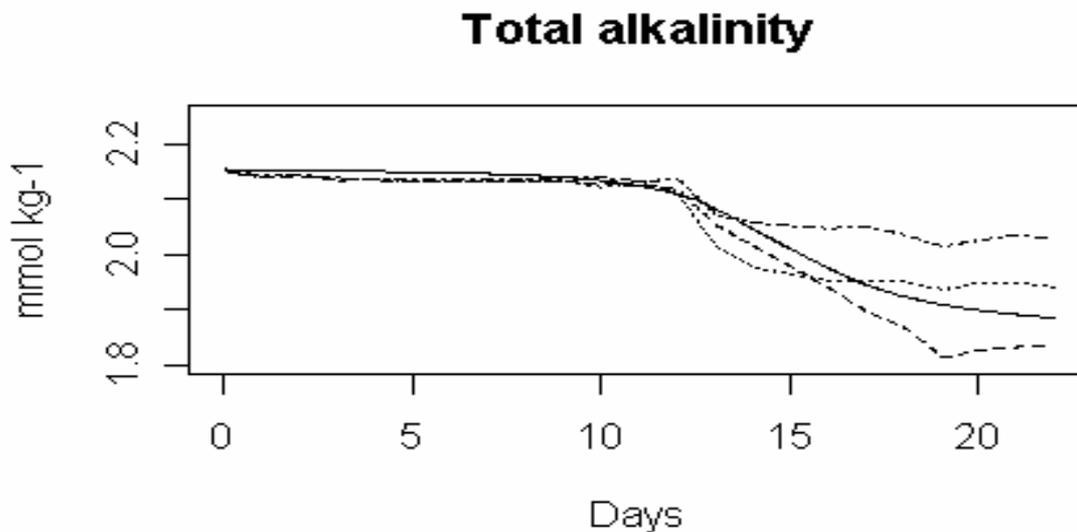
$$\mathbf{P.E.R. (\%) = DOC_{ExtraRel.} / (DOC_{ExtraRel.} + C_{uptake})}$$

Appreciation of the model.

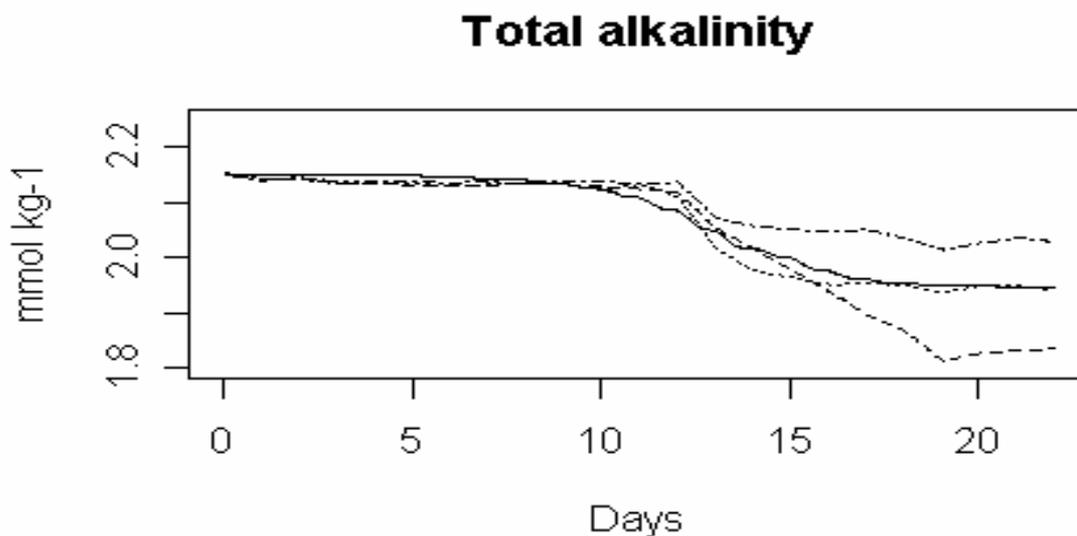
Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliana 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

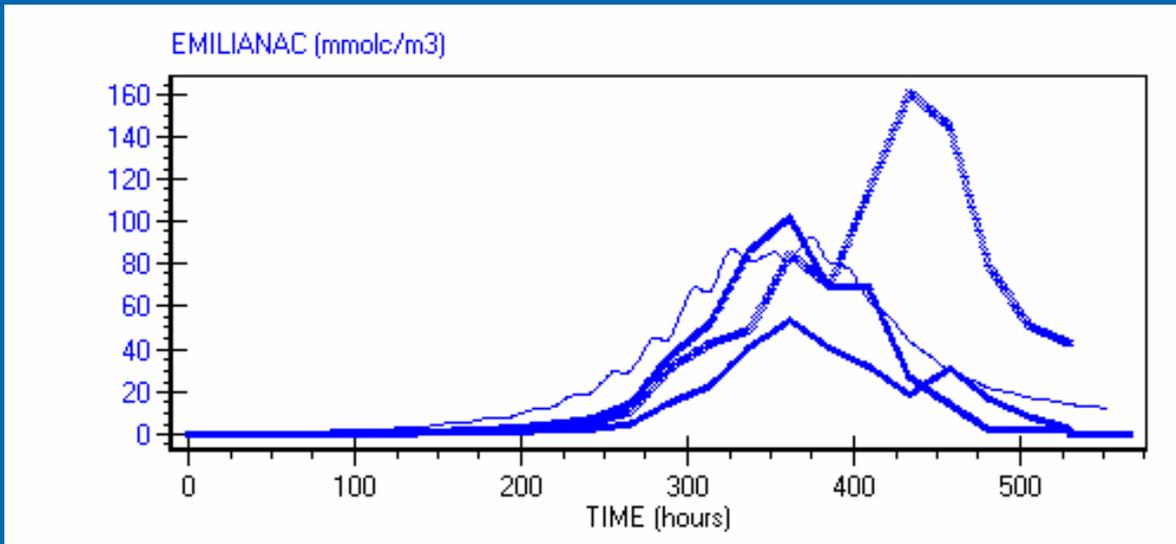


Appreciation of the model.

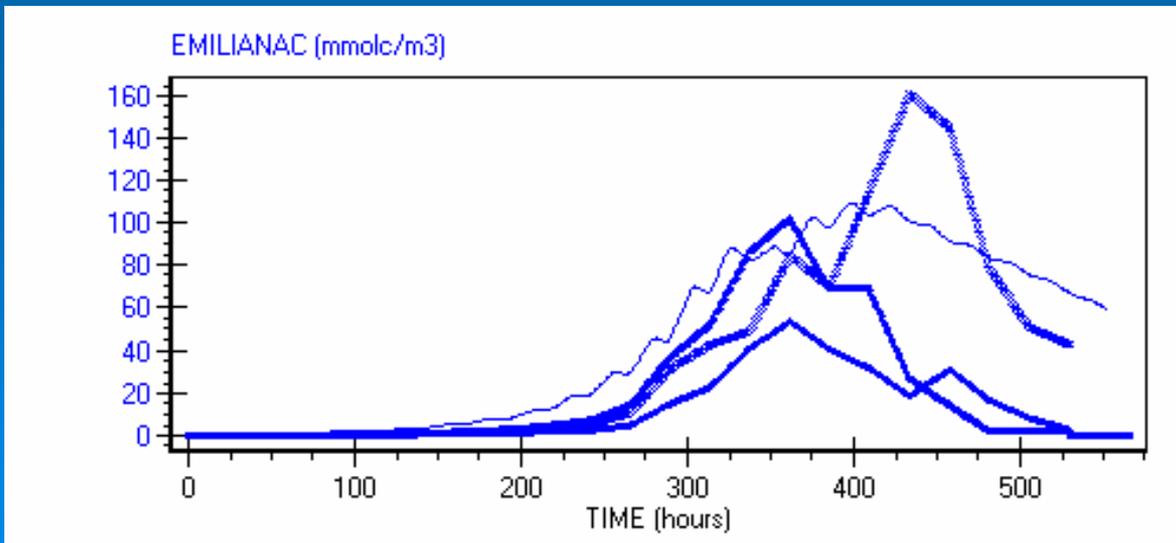
Interesting aspects.

- Convenience of the unbalanced growth to represent *Emiliana 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 *Emiliana 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.

