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***Interactive comment on “A mathematical
modelling of bloom of the coccolithophore
Emiliana huxleyi in a mesocosm experiment” by
P. Joassin et al.***

P. Joassin et al.

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Dear reviewer,

We do thank you for the time you spent to read our manuscript. Your comments will indubitably help us to improve our work. Here below, you will find our answers to all your comments taken one by one.

Reviewer: “The discussion tends to focus on whether the data fits the observations of this particular experiment.”

The referee is right saying that an important part of the manuscript is devoted to the comparison of model results with the observations. We found indeed this validation

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exercise crucial and obligatory before applying the model to other pCO₂ conditions or to other environments. Indeed, the diversified data set collected in the frame of this mesocosm experiment really gives a unique opportunity to test mathematical formulations, usually used or not, to represent key processes characterizing *Emiliana huxleyi* dynamics: calcification, primary production, extra-excretion, TEP formation. The good matching of model results with interconnected observations provided all by the same experience constitutes a positive appreciation of the adequacy of these formulations used to represent the mentioned processes. This demonstrated also the coherence of the experimental data set. A lot of mathematical formulations presented in the manuscript are new and thus need to be tested before using the model to understand for instance the impact of changes pCO₂ on *Emiliana huxleyi* dynamics. For instance, the model proposes for a first time the representation of particular processes such the enhancing of cellular mortality due to viral lysis in confined environments. Till now, there was no investigation about the necessity to include such process in order to correctly represent an experimentally induced bloom. Concerning this aspect, the model gives a solid conclusion, demonstrating that the enhanced mortality due to viral lysis should not be ignored in confined environments. Beside this viral aspect, the model does bring clarification to the global dynamics of coccolithophores by demonstrating that an unbalanced growth in carbon and nitrogen is duly needed to reproduce the temporal decoupling between DIC and DIN uptakes. This learning is actually one of the most important elements of the conclusion and so far, all the models of coccolithophores use balanced growth model only representing nitrogen cycling (e.g; Tyrell and Taylor, 1996). In this study we have quantified (by estimating the *Emiliana huxleyi* extra-excretion) the importance of the unbalancing between carbon and nitrogen. We will clarify these points in the paper by adding a paragraph in the introduction, highlighting more clearly model objectives.

It must also be recalled that this mesocosm experiment had offered a unique diversified data set to test conjointly several formulations about cellular processes. In our knowledge, this is the first time that a dynamic model of coccolithophores disposes of such a

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diversified data set to be calibrated. Indeed, alkalinity and DIC data allow for instance the validation of the representation of the calcification process. Data on DOC, DIC and TEP allow the validation of the representation of DOC extra-excretion and TEP formation. Nitrate, Ammonium and phosphate data allow testing the formulation of inorganic nutrients uptakes by coccolithophores. Data on DIC, nutrients and chlorophyll allow assessing the uncoupling of carbon and nitrogen dynamics. All these mathematical formulations were revealed to be consistent with the whole set of observations. This global approach singularises our model as far as the validation of existing models of coccolithophores dynamics may be quite crude. Indeed, the validation of many models including coccolithophores resides only in satellite-derived concentrations in chlorophyll or phytoplankton abundances. In those cases, the absence of data for alkalinity, DIC, PIC and DOC does not allow testing formulations concerning calcification or TEP production.

Finally, it should be noted that we did not limit our discussion to the analysis of the matching between model results and observations. We used the model in order to provide carbon and nitrogen budgets. These flows have not been measured and the model provided quantification for them (see figure nr.6 in the manuscript). Doing so, the model showed the presence of 3 to 4 particular periods in the bloom chronology. This section is in the discussion.

Reviewer: “I think these choices are defensible for this particular experiment, but one should be very aware that they leave some important aspects untested. Among these is the balance between nutrient competition and predatory loss of Ehux relative to other phytoplankton in general, and relative to other flagellates in the same size class in particular. With no grazing control on bacterial biomass, the model probably has no steady state with mineral nutrient limited bacterial growth rate. This probably gives an internal feedback loop where Ehux production of labile DOC increases stimulates bacterial competition for mineral nutrients. Whether this is realistic or not is not discussed.”

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Giving the fact that experimentalists affirm that the rapid end of the *Emiliana huxleyi* bloom in the mesocosm was due to virus attack and that the grazing was not a significant mortality cause, the model will not go through an explicit representation of grazers. Also, the mortality term related to the mortality of *Emiliana huxleyi* not due to virus action is a lumped representation of natural lyses and grazing. We have clarified this point in the manuscript where the model structure is described.

Reviewer: Competition between Ehux and other flagellates in the same size class in particular.

The development of phytoplankton groups other than *Emiliana huxleyi* occurred in the beginning of the experiment in some mesocosms. These groups are *Micromonas* and *Synechococcus*. The most important bloom is the one of *Micromonas*. This group realised a bloom which was observed and measured through the *Micromonas* enumeration. However, available data of phosphate and nitrate showed that the impact of this bloom on nutrients stocks is not significant (these data are presented in section 3). For instance, the nitrate profile remains quasi flat at the time of the *Micromonas* bloom. The chlorophyll time-series only manifest a slight increase during the *Micromonas* bloom, reaching values 10 times lower than the chlorophyll peak caused by the *Emiliana huxleyi* bloom.

It should be noted that initializing the model after these two early blooms was not a solution to avoid the eventual side-step due to these bloom. If the model started at day 10, the time given to the simulation is not enough to leave the coccolithophores blooming in phase with the observations. Indeed, it should be recalled that we are using an unbalanced growth model in carbon and nitrogen and thus, time is needed for the C/N ratio to adapt leading *Emiliana huxleyi* to bloom. This delay is totally in agreement with the observations. We have clarified why we did not explicitly model the other phytoplankton bloom in the manuscript in the section devoted to the description of model structure.

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Reviewer: The whole data set is used for fitting, i.e. there is no validation part of this work;

You are right saying that parameters have been calibrated in order to reproduce all the available data. We can say that our calibrated parameters remain in the range found in the literature models (e.g. Paasche, 2002; Tyrrell & Taylor, 2006); with these parameters, model results remain in the range of the three replicates. Microbial loop parameters (bacteria, labile and semi-labile DOC and DON) as well as POM (POC, PON) dynamics parameters have been taken unchanged from the work of Anderson and Williams (1998) (see our bibliography). These parameters set have been found able to simulate the microbial loop dynamics in mesocosms (e.g. Van Den Meersche et al., 2004) and in real sites such as the Ligurian Sea (e.g. Raick et al., 2005) and the Black Sea (Gregoire et al., 2008). We essentially focused our calibration efforts on the parameters associated to the dynamics of *Emiliania huxleyi*. The calibrated parameters values are totally in the range proposed by Paasche (2002). Other parameters concern innovating formulations like the ones describing the enhanced mortality due to viral lysis. These parameters are calculated with the relevant data from the three replicates of present-day pCO₂ mesocosms. An ideal validation exercise would have required testing the model in mesocosm with totally different initial conditions. Unfortunately, it was not possible.

Reviewer: What is not clear to me is whether the model picks up effects of the CO₂-treatments. There is only one simulation presented, the one for present-day CO₂. While one may claim that the model picks up main features of the bloom dynamics, it seems that no claim is made for the model's ability to predict effects of changing CO₂;

The model has only been tested in present-day pCO₂ conditions. It will be tested in high pCO₂ conditions in the future. Prior to appreciate the reaction of the model in particular pCO₂ conditions, one should appreciate the capacity of the model to represent *Emiliania huxleyi* dynamics and to take into account the specific conditions imposed by

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the mesocosm environment. This requirement motivated the consideration of particular process like the enhanced *Emiliana huxleyi* mortality due to viral lysis in a confined environment. Actually, the present work does not intend to focus its discussion on the predictive capabilities of the model but focuses on the gathering in the same conceptual structure of formulations representing such different processes like primary production, calcification and TEP production. A good matching of the model results with the data of the present-day pCO₂ conditions should be underlined as it reflects the coherence of the mesocosm experimental data set and the reliability of the formulations used. Beyond that first stage, the model may be suitable for further applications in higher pCO₂ conditions.

Reviewer: If this work is published, it is likely to be used as a module, more or less uncritically used to incorporate Ehux into larger plankton models. My main worry with this is not the model itself, but more the discussion which tends to focus on whether the data fits the observations of this particular experiment, more than on the shortcomings and limitations if this model is coupled into more complete models. I would strongly recommend inclusion of at least some of these caveats in the discussion.

The present model has been derived from mesocosm environment. It is not sure at all whether the model can be taken unchanged for being applied in real conditions. It will for sure require some adaptations but what we propose can be a good starting point. As already said, all the data collected during this mesocosm experiment were really unique and ideal in order to test mathematical formulations of processes associated to *Emiliana huxleyi* dynamics. Also, to our opinion, the major outputs of this work are:

- 1) A mathematical formulation of biogeochemical processes associated to *Emiliana huxleyi* development (calcification, primary production, extra-excretion).
- 2) Biogeochemical parameters that can be used as starting values in real oceanic conditions.

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3) State variables that need to be used to represent *Emiliana huxleyi* dynamics. Indeed, it was found necessary to describe *Emiliana huxleyi* by its carbon and nitrogen contents. In addition, the model shows that the Ca:C ratio of *Emiliana huxleyi* is almost unchanged during the experiment ranging between 0.55 and 0.57. This means that if the model is applied in environment where calcite does not dissolve, it is not necessary to explicitly represent the attached and detached calcite. This point has been clarified in the text in the discussion.

4) An understanding of biogeochemical cycling during the experiment as provided by our budget calculation (see section discussion)

These model outputs have been clearly listed in the discussion.

Reviewer: English language in the title does not seem perfect;

We modify the title and a lot of editing corrections have been brought to the manuscript.

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