

Interactive comment on “Growth of the coccolithophore *Emiliana huxleyi* in light- and nutrient-limited reactors: relevance for the BIOSOPE deep ecological niche of coccolithophoresbatch” by L. Perrin et al.

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Dear Editors,

We have read and considered the comments made by reviewer 1 to our manuscript. We found these comments pertinent and think they will improve the manuscript. In the following we detail our responses to specific questions and are prepared to implement these corrections/changes should the article be accepted for publication in Biogeosciences.

Answers to main comments:

C1

1) We agree with this comment and we will merge some figures and add a supplementary part for tables and/or figures that are not indispensable in the text. Figures 1, 8, 10, 11, 12 and table 3 will be placed in a supplementary material. Figures 5 and 6 will be merged such as figures 13 and 14. Table 5 will be removed and values will be described in the text of the manuscript.

2) As the reviewer points out, our physiological model can be applied to datasets other than the Langer et al. (2013) dataset and the dataset we obtained with our own batch experiments. In our opinion Langer et al. (2013) is the best dataset available for our modeling exercise because sampling for measurement of medium and cellular chemical composition was done with a high frequency in this experiment. We hope our approach will also be used with other datasets in the future. However, we chose not to include other datasets in the present manuscript because this would have significantly increased the length of the manuscript without adding much in terms of the new modeling method proposed. We think that the modeling we present is strong enough to support our conclusions on the environmental controls on *E. huxleyi* distribution in the deep ecological niche of South Pacific Gyre.

3) We will improve the language and make the text more concise. The sub-sections 4.1.1 to 4.1.3 will be deleted from the manuscript.

Answers to additional comments:

1) The change will be implemented as recommended.

2) The change will be implemented as recommended.

3) This will be changed to “a poorly known but potentially important ecosystem for coccolithophores”.

4) The change will be implemented as recommended.

5) The change will be implemented as recommended.

C2

6) It is true that we did not specify that we only added nitrate and phosphate to the medium and that we did not add the NH_4Cl indicated in the reference medium in order to avoid the problem of multiple nitrogen sources. This will be explained in the revised text.

7) We agree with this comment and will state in the revised text that prior to experiments cells were only acclimated to temperature, light and carbon chemistry conditions, but not to low nutrients. Acclimation to low nutrient concentrations is not possible in a batch approach, because acclimation presupposes constant conditions. The central feature of a batch culture, by contrast, is that nutrient concentrations change over the course of the experiment.

8) The change will be implemented as recommended.

9) Samples were always taken in the afternoon between noon and 4pm, and always in the same sampling order. Each culture bottle sampling operation took approximately 45 min, preventing samples from different bottles from being taken at the same time. However, each analytic value was averaged over the three replicates. This will be specified.

10) This is correct and the statement about coccolith width measurements will be removed.

11) We will mention that the error for pH measurements is 0.02 pH units.

12) We will mention that the conversion from the concentration of Ca to particulate inorganic carbon (PIC) is based on a 1:1 stoichiometry between Ca^{2+} and PIC. i.e. all the calcium in the filters is considered to originate from calcium carbonate (Fagerbakke et al., 1994).

13) It is true that we made a mistake on this point. The C/N ratio for the nitrate uptake calculation is not necessary for this calculation because the PON data are available for the control experiments. To correct this point we will change the Monod plot (Fig. 7)

C3

and the part in the text that describes this point. This will entail only minor difference in the model results because the C/N ratios for the control experiments were near the Redfield ratio: for example the C/N ratio for the control NO_3 experiment of Langer et al. (2013) was 5.72.

14) To clarify notation, we propose to use KR for nutrients in general, KN for the nitrate half-saturation constant and KP for the phosphate half-saturation constant.

15) The change will be implemented as recommended

16) This is an interesting comment. In fact, we would like to be less assertive in the revised manuscript with regards to P-limitation being attained in the low-light PO_4 -limited culture. We propose to discuss the following hypotheses:

(1) P-limitation was not attained in the low light and low PO_4 experiment. The cells were P-limited. This can be inferred from a) the POP quota, which is lower than that of the control; b) the POP:POC ratio (POC:POP), which is also lower (higher) than that of the control; c) a deviation of the growth curve from exponential growth starting on day 16 (out of 19) at the very latest. While a decline in POP quota is an early sign of limitation, the decline in growth rate is a late appearing sign, indicating severe limitation. The cessation of cell division (stationary phase) is merely the last stage in the process of becoming P-limited over the course of a batch culture.

(2) Cells used another source of phosphorus such as organic phosphorus. However, no other sources of phosphorus other than the added phosphate were present in the culture medium except possible organic sources present in the initial seawater. If organic phosphorus sources were available in the medium, cells in the high light low PO_4 experiment would not have been expected to reach the stationary phase. This hypothesis is not rejected but seems not to be the reason for this absence of a stationary phase.

17) We made a mistake in calculating the magnitude of the error bar which is in fact

C4

smaller than we thought; we will thus remove this sentence.

18) The change will be implemented as recommended.

19) We mention the Leonardos and Geider (2005) experiment because it is the only experiment to our knowledge where nutrient- and light co-limitation was carried out. We will mention that this experiment was carried out with a non-calcifying strain.

20) We will change the sentence to "...to ensure that changes in the carbonate system were within a minimal range (< 10% except for the P-limited experiment where the DIC change were 12 and 13%; Table 1)".

21) This sentence will be rephrased according to comment 16.

22) The change will be implemented as recommended.

23) As mentioned in main comment 3, these sub-sections will be removed from the manuscript.

24) We will modify this sentence in order to be clearer: "According to Gregg and Casey (2007) the key to their success in the global oceans is to find areas where nutrients and light are low enough to inhibit growth of diatoms and chlorophytes, but where there is sufficient vertical mixing to prevent excessive their sinking losses or where they can find nutrients at depth under low illumination levels."

25) We agree that there is a contradiction and propose to modify the relevant sentence. In fact, in stratified, sunlit portions of the upper ocean, coccolithophore blooms occur after diatom blooms have depleted the nutrients. This advantage over diatoms in nutrient-depleted waters is a consequence of the greater affinity for nutrients of coccolithophores. Overall, coccolithophores have an advantage in low nutrient and low light compared to diatoms and chlorophytes (Balch, 2004; Gregg and Casey, 2007). This explains their development in the low-light, low-nutrient waters in some regions of the ocean (Beaufort et al., 2008; Haidar and Thierstein, 2001; Jordan and Winter, 2000).

C5

26) This sentence will be changed and was actually not clear. What we wanted to say is that phosphate measurements in the depth range 0-100 m in the GYR station of the BIOSOPE transect were always above 0.1 micromoles per litre, which suggests that PO₄-limiting conditions are not attained in this water column (Moutin et al., 2008).

27) The sentence is confusing and will be simplified.

28) A short discussion of grazing and vertical export as parameters that contribute to defining the distribution of coccolithophore populations will be included in the revised manuscript.

29) The sentence in question will be split into two.

30) We need to modify this sentence. While it is not possible to obtain reliable half-saturation constants for nutrient uptake in a batch experiment (a chemostat experiment is necessary), other parameters such as the maximum growth rates and maximum uptake rates can indeed be estimated in a batch experiment. As far as we know the only literature found to estimate the half-saturation constant for nutrient uptake for *E. huxleyi* using a batch culture is from Eppley et al. (1969). However, we think that the transient character of batch cultures makes the determination of half-saturation constants very difficult. We propose to circumvent this difficulty by modeling the batch experiments with a simple Droop model that enables us to extract information on nutrient affinity (the half saturation constant) from the transient results of the batch experiment

31) Reference to the final revised version of Beaufort et al. (2008) will be made.

32) POC: PON and POC:POP will be reported and the decimal point will be used instead of the comma in the final manuscript.

References

Balch, W. M.: Re-evaluation of the physiological ecology of coccolithophores, in *Coccolithophores*, edited by P. D. H. R. Thierstein and D. J. R. Young, pp. 165–190, Springer Berlin Heidelberg, 2004.

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Beaufort, L., Couapel, M., Buchet, N., Claustre, H. and Goyet, C.: Calcite production by coccolithophores in the south east Pacific Ocean, *Biogeosciences*, 5, 1101–1117, 2008.

Eppley, R. W., Rogers, J. N. and McCarthy, J. J.: Half-Saturation Constants for Uptake of Nitrate and Ammonium by Marine Phytoplankton, *Limnol. Oceanogr.*, 14(6), 912–920, doi:10.4319/lo.1969.14.6.0912, 1969.

Fagerbakke, K. M., Haldal, M., Norland, S., Heimdal, B. R. and Båtvik, H.: *Emiliana huxleyi*. Chemical composition and size of coccoliths from enclosure experiments and a Norwegian fjord, *Sarsia*, 79(4), 349–355, doi:10.1080/00364827.1994.10413566, 1994.

Gregg, W. W. and Casey, N. W.: Modeling coccolithophores in the global oceans, *Deep Sea Res. Part II Top. Stud. Oceanogr.*, 54(5–7), 447–477, doi:10.1016/j.dsr2.2006.12.007, 2007.

Haidar, A. T. and Thierstein, H. R.: Coccolithophore dynamics off Bermuda (N. Atlantic), *Deep Sea Res. Part II Top. Stud. Oceanogr.*, 48(8–9), 1925–1956, doi:10.1016/S0967-0645(00)00169-7, 2001.

Jordan, R. W. and Winter, A.: Assemblages of coccolithophorids and other living microplankton off the coast of Puerto Rico during January–May 1995, *Mar. Micropaleontol.*, 39(1–4), 113–130, doi:10.1016/S0377-8398(00)00017-7, 2000.

Langer, G., Oetjen, K. and Brenneis, T.: Coccolithophores do not increase particulate carbon production under nutrient limitation: A case study using *Emiliana huxleyi* (PML B92/11), *J. Exp. Mar. Biol. Ecol.*, 443, 155–161, doi:10.1016/j.jembe.2013.02.040, 2013.

Litchman, E., Klausmeier, C. A., Schofield, O. M. and Falkowski, P. G.: The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level, *Ecol. Lett.*, 10(12), 1170–1181, doi:10.1111/j.1461-

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0248.2007.011117.x, 2007.

Marañón, E., Cermeño, P., López-Sandoval, D. C., Rodríguez-Ramos, T., Sobrino, C., Huete-Ortega, M., Blanco, J. M. and Rodríguez, J.: Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use, *Ecol. Lett.*, 16(3), 371–379, doi:10.1111/ele.12052, 2013.

Riegman, R., Stolte, W., Noordeloos, A. A. M. and Slezak, D.: Nutrient uptake and alkaline phosphatase (ec 3:1:3:1) activity of *Emiliana huxleyi* (PRYMNESIOPHYCEAE) during growth under N and P limitation in continuous cultures, *J. Phycol.*, 36(1), 87–96, doi:10.1046/j.1529-8817.2000.99023.x, 2000.

Interactive comment on *Biogeosciences Discuss.*, doi:10.5194/bg-2016-196, 2016.

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