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

L. Perrin et al.

lpelod@locean-ipsl.upmc.fr

Dear Editors,

We have read and considered the comments made by reviewer 2 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. In particular, the overall clarity of the manuscript will be improved, including shortening the text, improving grammar/syntax, and decreasing the number of figures

and tables in the main text by moving part of them to the supplementary material. 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 only values will be described in the text of the manuscript.

General comments:

1) Emiliania huxleyi and not coccolithophores in general. We have made changes throughout the text to avoid referring to E. huxleyi as a model for coccolithophores in general.

2) The deep niche focus was chosen for two reasons: (1) little is known about E. huxleyi growth in these low-nutrient, low-light conditions despite the fact that they could represent a non-negligible portion of the global E. huxleyi population, and; (2) the BIOSOPE transect is unique in the breadth of physical and chemical parameters measured, which makes our joint experimental/modeling exercise easier. We do acknowledge, however, that we might have missed the relevance of our work for other environments including the cold, dark and nutrient-poor Arctic and Antarctic. We will explain the relevance of our findings to environments other than the deep ecological niche in a revised manuscript.

3) The main message of our work is that batch experiments coupled to simple physiological modeling can help interpret environmental controls on distributions of coccolithophore populations in the ocean. We agree that this needs clarification and the subordination of the BIOSOPE deep niche approach to this overall message needs to be better stated in the manuscript. Once this message is delivered more clearly than in the original submission, we have to stress that the BIOSOPE deep niche was chosen for the reasons explained above. The deep niche study chosen to apply our approach is the best possible field situation based on the available published datasets of chemical and physical properties. Figures and Tables will be reorganized as stated in the first paragraph of this reply.

4) We agree that depending on the light cycle, the amount of light available for the cell (light dose) will be different. This point and the specification of the L:D cycle will be added to the text and discussed in addition to the intensity of irradiance.

8) We agree that the possibility of organic nutrient utilization needs to be discussed with reference to the oligotrophic environment of the South Pacific Gyre. What is interesting is that the physiological parameters constrained by our model, which considers only inorganic nutrients, result in a depth of the potential growth rate that coincides with that DCM and the maximum number of coccolithophore cell counts in the GYR station of the BIOSOPE transect. We therefore conclude that either organic nutrients are not used significantly, or if they are used, the pattern of their distribution in the water column mimics that of inorganic nutrients. We cannot exclude this second possibility although from the correspondence between the modeling and the in situ vertical distribution of coccolithophore cells and chlorophyll, it is very likely that inorganic nutrients play the predominant role in controlling the vertical position of the coccolithophores. This will be added to the discussion section.

Specific comments:

Ln 18: The word "ecosystem" is not used in a correct way. We will change this part of the sentence and add the reason why coccolithophores are important for organic carbon and mineral export.

Ln 18-19: We will change this sentence as recommended.

Ln 30: We will change this sentence to "…metabolism and behavior in a low light and low nutrients environment of the ocean".

Ln 38-39: This will be changed as recommended.

Ln 40-41: We will briefly mention the other factors that influence the ocean-atmosphere CO_2 fluxes.

Ln 42-43: We will be more specific in saying that the mentioned factors influence the

PIC:POC ratio of coccolithophores but not of the whole phytoplankton community.

Ln 44: This will be specified in this sentence.

Ln 47: The sentence will be added as recommended.

Ln 60: The term "discovered" will be changed to "observed". Deep photic zone (low light) communities of coccolithophores have been observed in the North and Central Pacific at least since the work of Okada and Honjo (1973).

Ln 62: We agree that the sentence is not correct and needs to be changed. Nitrate and phosphate have actually their 'clines' around the same depth throughout the transect. We need to specify that the nitracline and the phosphacline were observed around 200 m at the GYR station (in the middle of the South Pacific Gyre), but of course this depth is not the same along the transect as both nitracline and phosphacline are shallower at the extremities of the gyre.

Ln 114: We chose to work with a surface strain from the BIOSOPE transect because no E. huxleyi strains were isolated inside the gyre at 200 m depth. This is a limitation of our study that we will mention.

Ln 120-123: A model of the PAR daily cycle at the date and the coordinates of the GYR station was used to calculate the L:D cycle (Figure 1). This was between 14:10 and 12:12 along the whole transect. Thus, the 12:12 cycle used in our experiments is representative of the in situ situation. This point will be specified in the manuscript.

Ln 159: Nutrients were measured on a Seal Analytical auto-analyzer model AA3. Here is the relevant link: http://www.seal-analytical.com/Products/AA3HRAutoAnalyzer/tabid/59/language/en-US/Default.aspx

Ln 168-170: POP was measured as the difference between the total particulate phosphorus and the particulate inorganic phosphorus. Both were analyzed using a Seal Analytical 3 auto-analyzer after some different analytical steps summarized in the paper of Labry et al. (2013). At one step filters were hydrolyzed using a HCl solution, so

filters were not fumed. We will specify these points in the manuscript.

Ln 189: It is N-uptake. The relevant symbol will be changed to Nup to be in accordance with the Droop model. However, nutrient uptake and nutrient fixation are equivalents in the Monod theory because nutrients are assimilated as soon as they are taken up.

Ln 192-194: True, as noticed by the first reviewer as well, we actually made an error 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 in the manuscript) and the text that describes this point. This will entail only a minor difference in the model results because the C/N ratios for the control experiments are near the Redfield ratio: for example the C/N ratio for the control NO3 experiment of Langer et al. (2013) was 5.72.

Ln 202-205: We need to be clearer about these two different methods to determine cell volume and surface area. Cell volume (or surface area) were calculated for the experiment of Langer et al. (2013) because of the lack of measurements, while cell volume was directly measured in the experiment presented in this manuscript and reported in the "experimental" part of the "Materials and methods".

Ln 214: We will change "NO3 and PO4" to "N and P" to avoid confusion.

Ln 216: We will change the nutrients notation in the text because of the existing confusion between nutrient N and nitrogen N. We will refer to nutrients in general with the letter R, to the nutrient nitrogen with the letter N and to nutrient phosphate with the letter P.

Ln 243: (see answer to previous comment). We will change the notation for the half saturation constants for nutrient uptake: KN is the constant for nitrate uptake, KP is the constant for phosphate uptake and KR is the generalized constant for nutrient uptake. Same thing for the nutrient quotas, e.g. QN/P, that will be referred to as QR.

Ln 250-251: We mean nutrient cellular quota.

Ln 269, 279, 288, 306: We will remove these sub-headings.

Ln 293: We will express ratios as C:P and C:N when revising the manuscript

Ln 379-381: True and as specified in the general comments of this review, we need to be more careful when we talk about E. huxleyi and coccolithophores as a group. Of course this work gives us new insights for the species E. huxleyi and maybe for other Isochrysidales or Noelaerhabdaceae but undoubtedly not for all coccolithophore species.

Ln 409: This sentence will be rephrased.

Ln 442: We will change "for decreasing phosphate than for decreasing nitrate" to " for phosphate limitation than for nitrate limitation".

Ln 447: We will modify this sentence making it clear that Zondervan (2007) is almost entirely based on E. huxleyi results.

Ln 452-460: As in general comment, the light dose will be added to the text in order to improve the comparison and because of the importance of the light dose and not only the light intensity. Only Feng et al. (2008) used a 12:12 L:D cycle, but the other mentioned studies Rokitta and Rost (2012), Trimborn et al., (2007) and Zondervan et al. (2002) used a 16:8 L:D cycle. We will change this paragraph to be more specific and avoid comparing experiments with very different L:D cycle experiments.

Ln 463-465: We will rephrase this sentence as recommended to be clearer on the species-specific relation between coccolith size and coccosphere size and to take into account the fact that the PIC quota per coccolith could be estimated by the size of coccoliths but that the PIC per coccosphere depends on the number of coccoliths per cell.

Ln 467, 476, 483: These sub-sections will be deleted to avoid repetition of the discussion.

Ln 561: This sentence will be rephrased. Other sources of nitrogen might include organic nitrogen, although based on the modeling results (see answer to comment 8, above) we think that inorganic nitrogen dominates over organic nitrogen.

Ln 573: We will add some comparisons and references in the revised text, especially papers of Laws (2013) and Selph et al. (2011) which evaluate and estimate respectively in situ growth rates considering the mortality of phytoplankton due to grazing. Consequently, their estimation of growth rate will be lower than the net growth rate ad need to be compared carefully with our estimation. In the legend of figure 13B, the red triangles are the coccolithophore data from Litchman et al. (2007) (black points are the data of Marañón et al., 2013). This will be specified in the legend.

References

Feng, Y., Warner, M. E., Zhang, Y., Sun, J., Fu, F.-X., Rose, J. M. and Hutchins, D. A.: Interactive effects of increased pCO2, temperature and irradiance on the marine coccolithophore Emiliania huxleyi (Prymnesiophyceae), Eur. J. Phycol., 43(1), 87–98, doi:10.1080/09670260701664674, 2008.

Labry, C., Youenou, A., Delmas, D. and Michelon, P.: Addressing the measurement of particulate organic and inorganic phosphorus in estuarine and coastal waters, Cont. Shelf Res., 60, 28–37, doi:10.1016/j.csr.2013.04.019, 2013.

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

Laws, E. A.: Evaluation of In Situ Phytoplankton Growth Rates: A Synthesis of Data from Varied Approaches, Annu. Rev. Mar. Sci., 5(1), 247–268, doi:10.1146/annurev-marine-121211-172258, 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.1461-0248.2007.01117.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.

Okada, H. and Honjo, S.: The distribution of oceanic coccolithophorids in the Pacific, Deep Sea Res. Oceanogr. Abstr., 20(4), 355–374, doi:10.1016/0011-7471(73)90059-4, 1973.

Rokitta, S. D. and Rost, B.: Effects of CO2 and their modulation by light in the life-cycle stages of the coccolithophore Emiliania huxleyi, Limnol. Oceanogr., 57(2), 607–618, doi:10.4319/lo.2012.57.2.0607, 2012.

Selph, K. E., Landry, M. R., Taylor, A. G., Yang, E.-J., Measures, C. I., Yang, J., Stukel, M. R., Christensen, S. and Bidigare, R. R.: Spatially-resolved taxon-specific phytoplankton production and grazing dynamics in relation to iron distributions in the Equatorial Pacific between 110 and 140°W, Deep Sea Res. Part II Top. Stud. Oceanogr., 58(3–4), 358–377, doi:10.1016/j.dsr2.2010.08.014, 2011.

Trimborn, S., Langer, G. and Rost, B.: Effect of varying calcium concentrations and light intensities on calcification and photosynthesis in Emiliania huxleyi, Limnol. Oceanogr., 52(5), 2285–2293, doi:10.4319/lo.2007.52.5.2285, 2007.

Zondervan, I., Rost, B. and Riebesell, U.: Effect of CO2 concentration on the PIC/POC ratio in the coccolithophore Emiliania huxleyi grown under light-limiting conditions and different daylengths, J. Exp. Mar. Biol. Ecol., 272(1), 55–70, doi:10.1016/S0022-0981(02)00037-0, 2002.
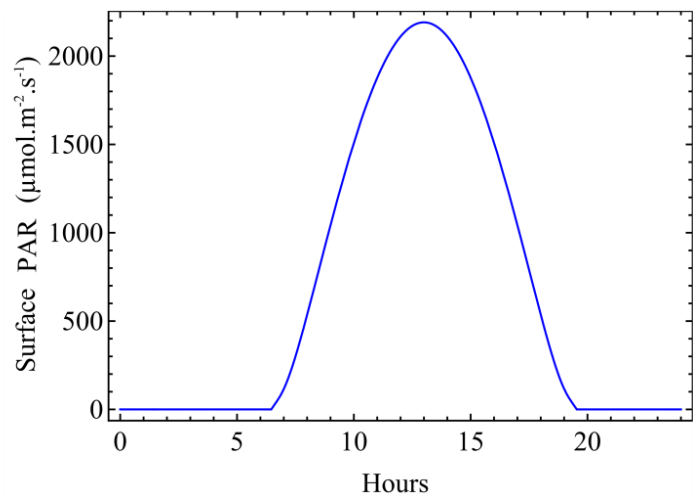
Fig. 1. L :D cycle calculated for the GYR station at the sampling day.

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