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Interactive comment on "The distribution, dominance patterns and ecological niches of plankton functional types in Dynamic Green Ocean Models and satellite estimates" *by* M. Vogt et al.

Anonymous Referee #1

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.... Summary: ....

In this paper, the authors compare phytoplankton functional type (pPFT) dominance patterns in four Dynamic Green Ocean Models (DGOMs) and two satellite-based pPFT algorithms. They also estimate realized ecological niches of pPFTs and use them to calculate the probability of pPFT dominance as a comparison metric for all models/algorithms. This study is interesting because of its potential to analyze how realized ecological niches of pPFTs may help explain the very different patterns of dominance and coexistence revealed by DGOMs and satellite-based pPFT algorithms. However,

the paper in its current form does not take full advantage of that potential. Its main focus is on the description of differences in annual and monthly global patterns of pPFT dominance, which unfortunately is not used to derive any new conclusions as to why such large differences occur. I cannot recommend publication of this manuscript before the authors make some major revisions. Below I list my major concerns and some detailed comments.

.... Major concerns: ....

1. What is the main research question of this study?

While the results are very well described, there is not enough relevant discussion on the importance of these results. Currently, it is difficult to see what the main goal of the paper really is because of seemingly many aims presented in the abstract and introduction, and a coincident lack of relevant conclusions. The abstract suggests there are three aims: (1) to compare spatial and temporal representation of pPFTs in four DGMS and two satellite pPFT algorithms, (2) to investigate mean dominance patterns, (3) and to estimate realized ecological niches of pPFTs. On the other hand, the introduction suggests that the aim is to (1) compare phytoplankton biogeographies in the models and to (2) use the concept of the ecological niche to understand how phytoplankton are implemented in current DGOMs. In your Conclusions, there are only two sentences relevant to these aims.

An apparent conclusion is that better resolved phenology and succession is needed for models. But do the results of this study really suggest that? There is not one time series shown in this paper and the only monthly results are shown in 3-month intervals. In fact, the authors themselves admit in the caveats of the study that a higher resolution of data is needed to study these aspects. Please justify how this framework could be suitable for deriving conclusions on phenology and seasonal succession, or remove these statements.

I would like to see all aims described more consistently in the paper. More importantly, it is necessary to state what these aims contribute to and how. Please be explicit about the motivation and specific problem being addressed in this study. It seems that the paper tries to address two very large important issues at the same time: (1) evaluation of model pPFT biogeography, and (2) understanding different phytoplankton implementations in DGOMs and satellite-based algorithms. But the discussion of these issues is very general and not well linked to the presented results. It is difficult to follow how your results contribute to solving these issues.

2. Evaluation of pPFT biogeography

The authors do a good job in describing and comparing the monthly and annual patterns of biomass/dominance in DGOMs and satellite algorithms. I agree with the authors that dominance patterns are more robust than relative biomass in both DGOMs and satellite-based estimates, and are thus a good comparison metric. This is a valuable contribution. However:

I would like to know how these results compare to several previous similar dominance comparisons of PFT models and/or PFT satellite-algorithms such as in Sinha et al. (2010), Brewin et al. (2011), Gregg and Casey (2007).

I suggest rewriting parts of the discussion section. There is a very large section 4.1. which mixes up reasons for discrepancies in model and satellite estimates of pPFT biogeographies with their implications for carbon export and phytoplankton phenology and succession. Most of this discussion is based on previous findings and is weakly related to any new results presented here. Such a review of spatial and temporal biases in satellite and model biogeographies already identified in many previous publications (mostly cited here) belongs to the introduction but is out of place in the Discussion, unless placed specifically in the context of the results from Section 3.

I would insist that the authors are consistent in treating satellite algorithm estimates either as observations to validate model results against, or as independent but also model estimates to compare with. Currently, "satellite estimates" are used interchange-

ably with "observations", but are not actually treated as data for ground-truthing the models (and rightly so).

A large portion of the introduction talks about means of validating DGOMs using new available distribution data and data on important traits enabling a systematic model evaluation effort. However, none of the results presented in this study take advantage of those resources. Why is that? If the focus of the paper is to evaluate pPFT biogeography, have you not considered using the MAREDAT data in the context of this paper?

3. Probability of dominance

I wonder why you needed to model the probability of pPFT dominance of the four models and two satellite algorithms in order to characterize their ecological niches. Wouldn't it be sufficient and more accurate to map the model dominant pPFTs as color-coded points in a coincident SST-NO3 niche space? Or is there so much scatter that no general patterns would be seen? If that's the case, then the calculated probabilities of dominance are indeed useful, but not for satellites. Dominance patterns for the two satellite algorithms shown in Fig. 5 are likely misleading since the GAM captures only around 40% of original deviance. Also, patterns seen in Fig. 4 are patchy and maybe ecologically unrealistic (e.g. tiny areas of diatom dominance inside large areas of nano dominance), and they are thus difficult to interpret in a meaningful way.

I cannot see how patterns shown in Fig. 4 and Fig. 5 can be used to advance our understanding of model pPFT implementations, which seemed to be the aim of the paper. Can the differences in realized niches in DGOMs be related to their respective growth dynamics compared in Table 4? It seems to me that a two-element ecological niche in GAM might be too simplistic to really increase our mechanistic understanding of the model differences, as was done for example in Hashioka et al. (2012).

On another note, it is interesting to see that you can explain so much more variability in model dominance than in satellite estimates. Does this mean that DGOMs are too simplistic because majority of their deviance is explained by only 2-3 niche descriptors? Or does it mean that satellite estimates are not necessarily ecologically realistic because they cannot be coupled to observed nutrient and SST fields?

The similarity report for this manuscript points at a recent publication by Palacz et al. (2013) which uses a similar ecological niche framework to correct for unrealistic diatom dominance patterns in HNLC regions in NOBM - another dynamic pPFT model. Some of their results should be very relevant to your discussion on differences in modeling biomass and dominance patterns.

4. Coexistence of PFTs

The difference in simulating coexistence patterns in models and satellite-based algorithms is a very interesting issue that could be explored further in this paper. Is it possible to use the ecological niche approach to increase our understanding of why there is so little coexistence between pPFTs in the dynamic models? The authors discuss the role of fixed stoichiometry and number of pPFTs but what about the information on ecological traits of PFTs mentioned in the introduction? I was expecting some discussion on how your realized niches reflect (or not) the results published by Litchman and Klausmeier, 2008; Buitenhuis et al., 2010; Thomas et al., 2012; Edwards et al., 2012.

Can your ecological niche approach be used to improve model trait parameterizations to allow for greater coexistence? I expect that the paper puts forward some recommendations on how this could be done in the future.

5. Effects of model MLD formulations.

Sinha et al. (2010) concluded that the choice of circlulation model used for coupling strongly affected the global annual pPFT distribution patterns in PlankTOM5.2 due to differences in mixing intensity. Coupling to NEMO resulted in lower mixing which favoured mixed phytoplankton at the expense of larger silicifiers. Mixing is also an important factor in characterizing the niche of calcifiers, as indicated for example by Balch

et al. (2004) (not cited) in his extended Margalef mandala. This is also clearly shown in your Fig. 7 when you compare the PlankTOM5.2 and Alvain et al. coccolithophore deviance explained for niche models with and without MLD.

In Appendix B1 of this paper, authors point out that neither model shows a good fit to observations of MLD, and that MLD is underestimated. I would like to see a discussion on how the findings of Sinha et al. (2010) might affect the robustness of your ecological niche model and results interpretation. Are the MLD estimates very different in the 4 models considered? Could the inaccuracy in simulating MLD explain the large differences between model and satellite dominance patterns in the high latitude areas?

.... Detailed comments: ....

Page 3 line 27 to page 4 line 1: I don't see how you can derive any conclusions about phytoplankton succession and phenology. Please replace this statement with a more adequate conclusion.

Page 6, line 23: The authors claim they build on the results of Sailley et al. (2013) and Hashioka et al. (2012). How is that done exactly?

Page 6. line 25: What do you mean by "understand how phytoplankton are implemented"? The niche analysis is rather descriptive and in my view does not enhance understanding of model mechanisms. Please be more specific about the aims and see my comments on the general goal of the paper.

Pages 7 to 10: A large portion (if not all) of subsections 2.1 and 2.2 could be moved to the appendix or to the supplement. Most of the information is available in other publications. Section 2.3 is very informative and gives a sufficiently good basis to understand the methodology.

Page 9, line 9: Table 4 should actually be labelled as Table A1.

Page 11, paragraph 2: What about the recent PhytoDOAS estimates of coccolithophore biomass distributions in Sadeghi et al. (2012), which are neither limited to one PFT nor to bloom conditions? There is no need to include these results here but they should at least be cited, and included in the discussion on evaluation of calcifier biogeographies in your models.

Page 12, line 14: Used for what?

Page 13, line 7: Is this the most recent study to confirm this claim? To my knowledge, most in situ observations would reveal very low concentrations of many pPFTs even when a single group is dominant. You can see that in field estimates under different conditions from subtropical gyres (e.g. BATS, HOTS), equatorial upwelling regions (Equatorial Biocomplexity cruises) and in the North Atlantic (e.g. North Atlantic Bloom Experiment). Does the MAREDAT PFT atlas not confirm this claim as well?

Page 14, lines 1-2: Has MLD been used as such a proxy in a niche analysis before? Can you provide a reference for that? Why didn't you use photosynthetically available radiation as a more direct proxy for light? Have you checked if MLD and PAR are strongly correlated in your models?

Page 14, line 4: Does surface mean the respective top layer from each model in this study? Or is it a fixed depth interval, e.g. from 0 to 10 m? Please specify.

Page 14, lines 8-12: For a similar discussion on including/excluding iron as a niche descriptor, take a look at Palacz et al. (2013).

Page 15, lines 1-2: I'm confused by the phrase "observed dominance was then modelled". Do you call the calculated probability the "observed" one? If it's because you use the WOA nutrient and SST fields, then this is still misleading because you don't use any pPFT field data to create the GAM model. Please find an alternative name for this metric.

Page 15, last paragraph: Please provide a more comprehensive description of the probability map generation procedure than is currently here. It is not known which NO3, SST and MLD fields (model or WOA) where used for which part of the analysis.

How was the most likely dominant group determined?

Page 18, line 9: Do you mean satellite estimates or field observations? Please see one of my general comments on referring to satellite estimates consistently.

Page 18, line 11: Which observations? From satellites or from the field? If the latter, please include citation.

Page 19, lines 1-3: I really cannot see how this study can tell anything new about phytoplankton succession and phenology. Even if you looked at relative biomasses instead of dominances, the temporal and spatial scales are very crude. The studies of Bopp et al. (2005) and Hashioka et al. (2012) were a lot more suitable to derive such conclusions.

Page 19, lines 24-27: I would like to know how well the GAM fits represent model simulations. A 65% deviance explained does not mean that there are no biases in certain regions of the niche space. I recommend that you create a new table in which you can compare the fits for annual and monthly (at least months used in Fig. 3) means of both models and satellites. Also, consider moving Fig. 7 into the main body of the paper because it is very informative in the context of validating your approach, and not just as a sensitivity study.

Page 20, paragraph 1: I agree that it makes sense to drop MLD to explain general annual patterns but I would not discard it when analyzing patterns of dominance on higher spatial and temporal resolution. However, Fig. 7 suggests that the effect of MLD could be quite significant in explaining deviance for coccolithophores and coexistence categories. if you decide to focus more on the general lack of coexistence in the DGOMs, then it could be wise to keep the MLD as an additional niche descriptor.

Page 20, line 3: Have you actually checked the correlation between MLD and SST and NO3 on a pixel by pixel basis? I imagine it is easy to make a test to support your claim.
Page 20, lines 20-25: This is such an interesting and rather novel result. Why don't you

discuss the potential reasons for the difference in modeling coexistence? Coexistence is currently not mentioned once in the discussion.

Page 21, line 21: should be Fig. 4d and not 4c

Page 23, lines 1-20: If I understand correctly, the authors suggest that overestimated diatom dominance (with respect to satellites) is due to smaller number of pPFTs and fixed stoichiometries in the DGOMs. However, two models that represent calcifiers or nitrogen fixers explicitly do not show any more coexistence than the other two. Rather, they shift the dominance to another group. The question is: how do you evaluate that result to conclude that this advances model development? From the paper, I cannot conclude which model scheme provides a more realistic dominance/coexistence pattern.

Page 24: In lines 1-2 the authors suggest they will discuss reasons for model-satellite differences in diatom dominance. However, the subsequent paragraph does not say anything about these reasons. The implications of these differences on carbon export estimates are very interesting but aren't they largely based on conclusions from previous studies? Please make it clear what is the contribution of this paper in this context.

Page 25, lines 23-26: Isn't this statement in conflict with what is later said about coccolithophores in paragraph 1 on page 27?

Page 26, lines 1-12: I'm not convinced that there is a need to review these results here. So why is it important to compare patterns of dominance/coexistence on annual scales?

Page 27, paragraph 1: Gregg and Casey (2007) confirm these interpretations using a limitted data set of in situ observations. A recent study by Sadeghi et al. (2012) may also be useful as an independent global estimate of coccolithopore biomass. Palacz et al. (2013) also discuss how coccolithophores in PFT models compare to estimates

from various satellite algorithms and some limited field measurements. Please consider discussing your results in the context of those findings.

Page 28, lines 19-27: I agree that you cannot draw conclusions about temporal or spatial variability and seasonal succession. Yet, most of the previous subsection was devoted to such a discussion. The use of available high resolution satellite or model estimates of niche descriptors such as temperature, light and nutrients would be adequate considering that your goal was to simplify the model to interpret the ecological niches in the models, and not to generate true observed patterns. Even though your current analysis takes observed inputs, it does not simulate true observed PFT dominance because it uses model outputs to fit the GAM. Also, except for nitrate, all other niche descriptors identified here are available at high resolution from satellites. Palacz et al. (2013) for example showed that you can capture patterns of relative biomass distributions in a PFT model using a similar ecological niche approach without including nitrate as a predictor.

Page 29, lines 9-11: Which other predictor variables have you tested? Shouldn't you include those predictors to bring the model and satellite fits in GAMs closer together to make a more reasonable comparison of dominance patterns?

Conclusions: Except for the first two sentences, these conclusions do not reflect what was done in the paper. The first two sentences are a rather descriptive summary of the dominance patterns and niche analysis from the paper. The remainder of this section describes future work but does not say how this particular study can have any impact on that work (except for the part on skill metrics). Moreover, this text is largely repeated from the introduction. I recommend rewriting this section to make it more relevant to what the paper is actually about.

Table 1 & 2: They are a bit messy. Please move some of the explanations into the table caption, i.e. that diatoms are equivalent to silicifiers. Or that small phytoplankton are equivalent to pico and nanophytoplankton.

Table 4: What is the meaning of questions marks next to Ksio4 in the PISCES column? Please delete or explain in the figure caption. Avoid using superscript notation for such long expessions as in the CCSM-BEC column. These formulas will be illegible in the final version. Can't you rewrite the formula using a "2ˆ(...)" notation as you do for "exp" instead of "eˆ"?

Fig. 5: The use of colors is very counter-intuitive. Consider reversing the colors or choose an alternative colormap which will associate higher probability with warmer colors.

Fig. 6: I guess the model chlorophyll is also "surface" and not "depth-integrated" or "depth-averaged". Please specify the depth range corresponding to these estimates.

Fig. 7: Very informative figure. Insert space inside "combinationsas" in line 2 of caption. Fig. 7 should really be Figure C1. However, I would recommend including this figure in the main body of the paper.

Appendix A: What is the purpose of having this appendix? Was Table 4 meant to be included in the main text? If so, then it makes no sense to refer to that table in a 2-line appendix. If Table 4 was meant to be in the Appendix, then it should be called Table A1. Either remove Appendix A or change the label of present Table 4.

In all figure captions, consider specifying whether the dominance patterns are based on original model and satellite estimates, or whether they were simulated by the GAM.

.... References included in the review but not cited in the manuscript: ....

Balch, W. M.: Re-evaluation of the physiological ecology of coccolithophores, in: Coccolithophores. From Molecular Processes to Global Impact, edited by: Thierstein, H. R. and Young, J. R., Springer, Berlin, 165–190, 2004.

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Palacz, A. P., John, M. A. St., Brewin, R. J. W., Hirata, T., and Gregg, W. W.: Distribution of phytoplankton functional types in high-nitrate, low-chlorophyll waters in a new diagnostic ecological indicator model, Biogeosciences, 10, 7553-7574, doi:10.5194/bg-10-7553-2013, 2013.

Sadeghi, A., Dinter, T., Vountas, M., Taylor, B. B., Altenburg-Soppa, M., Peeken, I., and Bracher, A.: Improvement to the PhytoDOAS method for identification of coccolithophores using hyper-spectral satellite data, Ocean Sci., 8, 1055–1070, doi:10.5194/os-8-1055-2012, 2012.

Sinha, B., Buitenhuis, E. T., Quéré, C. L., and Anderson, T. R.: Comparison of the emergent behavior of a complex ecosystem model in two ocean general circulation models, Prog. Oceanogr., 84, 204–224, doi:10.1016/j.pocean.2009.10.003, 2010.

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