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Interactive comment on “Response of ocean phytoplankton community structure to climate change over the 21st century: partitioning the effects of nutrients, temperature and light” by I. Marinov et al.

Anonymous Referee #2

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General Comment:

This article shows how changes in temperature, light and nutrient conditions may affect phytoplankton distribution in a changing world. The authors analyze the model equations of their (and other generic) ocean biogeochemistry and ecosystem models, and they derive first-order approximations for their growth equations that are then used to predict phytoplankton responses to changes in light conditions, temperature and nutrient availability in a changing environment, based on the results of climate simulations. In particular, the paper focuses on the difference in response between

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small phytoplankton and diatoms in 5 different ocean regimes. This paper is a valuable contribution to the marine ecosystem modelling community, where a thorough mathematical understanding of the system of equations used in marine ecosystem models is essential for reasonably realistic projections for ecosystem structure and functioning under various sets of environmental conditions. I fully support its publication in Biogeosciences, after a few revisions, as detailed below.

Specific comments:

1. The use of equations inherent to the model

In this paper, equations inherent to the model are used to construct a “theory”, which is then used to show that the model response agrees with the predictions of its own equations. Obviously, the authors get a rather good agreement between their simulations and their predictions based on a theoretical analysis of their own, underlying model equations. It is not clear to me how the model results could possibly differ from these predictions, and the authors should make this more clear in a revised version of this manuscript.

2 Applicability to real world problems unclear

Uptake kinetic may not be MM: Furthermore, the authors need to discuss whether or not their findings are applicable to other sets of model equations. The representation of phytoplanktonic nutrient uptake as a Michaelis-Menten function is, to my knowledge, still debated. Several authors argue that uptake should be modelled using “optimal uptake kinetics” (Pahlow et al. 2005, Smith & Yamanaka, LO, 2007, Smith et al., MEPS, 2009). While this should not affect the conclusions of this manuscript when the limiting nutrient is considered, the use of optimal uptake kinetics would alter the concentrations of the non-limiting nutrients and is thus likely to modify the nutrient limitation patterns for the different plankton groups.

Parameter values influence conclusions: The dependence of the model results on

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model parameters needs to be debated in more detail. For example, the initial slope of the photosynthesis-irradiance curve α is assumed to be 0.3 for both diatoms and small phytoplankton. Several conclusions of sections 3.3 and 3.4 would have to be modified, were this not the case. An other example is the fact that all phytoplankton groups and even grazing by generic zooplankton have the same temperature dependence (Q10 function of 2), a fact which, to my knowledge, is not confirmed by experimental evidence. And do I interpret the manuscript correctly - it appears that the grazers play only a minor role for future phytoplankton distribution and biomass concentrations? Why? Is this realistic? What about the temperature dependence of respiration?

Individual versus combined effect of changes: In the current version of this manuscript, it is sometimes hard for the reader to link all bits of the puzzle to see what the total effect will be, when all individual contributions are summed up (see also point 5 below, this is also a structural problem). It would be nice to see a clearer synthesis of what is actually predicted for the 'real world ocean': As an example, the authors mention that decreases in nutrients restrict small phytoplankton growth between 45°N and 45°S more than diatom growth, yet there aren't many diatoms at all in this region (Fig. 2), and it is also the region where 'small phytoplankton win' (Fig. 10b). After reading the abstract (page 4566, L14-17), however, I am led to conclude that small phytoplankton will lose in this area. In your Introduction you cite several experimental studies such as Cermeno et al. 2010 show a diatom decline along the AMT line – do these findings agree with your predictions in the different regimes that you specify?

I encourage the authors to let the Discussion section go beyond summarizing the findings of this paper, and put their results into a broader context, discussing some of the points above, and backing up their results with some observational data. Furthermore, some structural changes should be made to increase clarity, see point 5 below.

3 Critical nutrient “hypothesis”

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I think it is exaggerated to suggest that the mechanism proposed by the authors linking critical nutrient concentrations in the ocean to phytoplankton speciation constitutes, in itself, a full-blown “theory”. A theory is a complex set of axioms, rules and derived properties, and it makes a whole range of verifiable predictions, whereas a hypothesis is just one single testable idea, which is more how I interpret this piece of work - “is there a critical nutrient concentration in the ocean?”. I think “theory” should be replaced by “hypothesis” everywhere in this manuscript, so that the dimension of the findings is also reflected in its denomination.

4 Application of the Taylor expansion

Finally, I have some reservations about the way the first order Taylor expansion of the growth rates is used to make projections about the future, without any estimate of the error that is committed through its use. The reader cannot judge whether the use of a first order expansion around the initial state of the system is still valid when changes are compared for periods as large as (2080-2099) – (1980-1999). Have you verified that the Delta terms (ΔI_{par} , ΔT , ΔV_m) are “small deviations from the mean”, as you write? And what is “some initial state” - I assume that you consider the period of 1980-2000 as your initial state? In addition, can you give us an error estimate before you “drop all quadratic and higher terms”? One possibility to do this would be to calculate the second derivative of your function, and evaluate it at the borders of your intervals (present – future state). In mathematical terms, evaluate $f''(c)$ in

$\forall f \in C^1([a, b]), \forall x \in [a, b], \forall x_0 \in [a, b] :$

$$f(x) = f(x_0) + f'(x_0)(x - x_0) + f''(c) \frac{(b-a)^2}{2!}$$

as

$$\exists M < \infty : \Leftrightarrow f''(c) < M$$

At the moment, with no error estimate and no evidence that your environmental changes are “small perturbations”, the reader is left to wonder whether or not your Taylor expansion just works “by chance”.

5 Structure of the manuscript

At present, it takes a little bit too long to read and understand the manuscript. I think that this is partly due to the structure of the paper: I would find it a lot easier to first read all the theoretical work, including Taylor expansions, and the <> relationships, and then, only afterwards, to see all model results and the model-model prediction inter-comparison, together with the division into the different regimes. In the current version of the manuscript, all theoretical sections are concluded by a descriptions of model results, and by the time I focus on the next set of equation manipulations, I have already forgotten what was said about the model results in the section before. Furthermore, I think a table summarizing all the individual effects of temperature, light and nutrients, and showing the total effect resulting from an addition of all three components for the different regimes would be very helpful. In addition, I encourage the authors to use more lists such as the one on page 4577, L5-15 – this makes it easier to understand the conclusions of each sections. Last but not least, I would like to see a link between the experimental findings/model results mentioned in the Introduction on page 4568, L4-17 with the model predictions, discussed in the Discussion section.

Minor comments:

P 4566, L11-22: Not clear what is the overall effect of your 3 different contributions (light, T, nutrients) to the overall effect that climate change will have on small phytoplankton versus diatoms. What are the overall conclusions. Please make this more clear.

P 4566, L15: Confusing – there aren't many diatoms between 45N and 45S that could be influenced. Does this mean that you predict an increase in diatoms between 45N and 45S?

P 4567, L15-17: Your model does not have coccolithophores and they mostly live at temperate and high latitudes, where you have large diatom contributions. Why would you single this phytoplankton group out if you do not discuss them anywhere in your

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manuscript? Btw, neither diatoms nor coccolithophores dominate the majority of the ocean, so see comment below:

P 4567, L18: “these phytoplankton types” - replace by “these or other important phytoplankton types”

P 4568, L21: “each of the three phytoplankton types” - which?

P 4568, L 21: “It is well known.... depending on their half saturation...” I am not sure that we can say that it is well known whether phytoplankton nutrient uptake even follows MM dynamics or not. Reformulate. Could discuss Smith et al. 2009 here.

P 4569, L4569: Why is it important that “level thickness is monotonically increasing”?

P4570, L15: “nitrogen-fixing diazotrophs” - isn’t this a pleonasm?

P4571, L18: Why are the μ_{ref} not in Table 1, and where do they come from? Include a reference. Why are they the same for diatoms and small phytoplankton, as this will influence your calculations/conclusions below (e.g. equation (18))?

P4572, L7: Same here, why are the α values the same for diatoms and small phytoplankton? Include references for where these values come from.

P 4573, L 6: Why is that so? Add reference for temperature dependence of grazing. What is g_x ?

P 4573, L20, 22: Add reference for the “competition theory literature” for K and r strategists.

P 4574, L2: “higher .. growth rates” than who? Do you mean “the highest”?

P 4574, L 15: Reformulate: “Light and temperature...”

P4574, L19-21: “Overall, ...” Can we see this? Where? “over a century” replace by actual years.

P4574, L22: “Model projections...” These figures are not commented at all here, at first

C2213

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mention. Why? Change structure of this section – the figures are actually discussed on page 4575. Not sure Fig. 3 is very illuminating, as you don't focus on the zonal means afterwards in your analysis. I suggest removing this figure and focusing on the analysis of your 5 regimes.

P 4574, L27: Modest changes... How do we know this? Is this realistic?

P 4574, L24: carbon relative abundance – not clear that the text in your bracket makes sense when I look at figure 5g. Surely, small phytoplankton abundance must be (1-diatoms/total phyto)?

P 4575, L4: Wouldn't it be better to first discuss the climate change results and then focus on the impact on μ ?

P 4575, L16: “nutrient functional response” What do you mean here, V_x ? On page 4571, these were called “nutrient limitation terms”.

P 4576, L2: Add space after “ T_f ” in all the terms of equation (10).

P 4576, 11: Estimate how small Δ can be to still be a “small perturbation”.

P 4576, L 18: How have you chosen those different biomes? Reference? Why? Does another selection of biomes (e.g. Longhurst biomes) influence your results?

P 4577, L17: “Let us..” connect this sentence somehow to Fig.1 b,d,f.

P 4577, L 18: “Nutrient functional response”? What do you mean, V_x or $\frac{\partial V_x}{\partial N}$?

P 4577, L 19: “a function of the limiting nutrient” - you only consider N and Fe. In the Mediterranean Sea, all phytoplankton groups are P limited, according to Fig. 1, but you do not consider P-limited areas.

P 4578, L 4: Is that all you say about Fig. 10 here? Furthermore, I find it hard to see how your model results should differ from your predictions, see specific comment above.

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P 4578, L18: Doesn't V_x^N also depend on NH_4 , so that

$$N^{new} = \frac{1}{K^{NH_4}K^{NO_3}}(K^{NH_4}NO_3 + K^{NO_3}NH_4)?$$

P 4579, L 11: “Fig 9 a-d” replace by “Fig. 9 b d”.

P 4579, L6: Can you link your two regimes to the “bloom-regime” and “stress-regime”, as discussed in the literature?

P 4581, L1: Please give temporal scales of your impacts.

P 4581, L 4: Same T_f for all phytos: see specific comment above – this is not necessarily realistic.

P 4581, L21: “confirm prediction”, see specific comment above, how can it not do so?

P 4582, L 18: Refer to your Figure 4 a and b?

P 4583, L 5-13: Cannot see how this should follow from Fig. 8-d. Please reformulate.

P 4583, L 16: “various” - you have only two.

P 4583, L17: “exponential ..” give equation here.

P 4584, L 6: “A close analysis..” of what? “... confirmed by Fig. 8” how?

P 4584, L17: “everywhere” - really?

P 4585, L 5: “Here, ...” Please reformulate, not sure I understand.

P 4586, L 20-23: Do you have validation data for this statement? If so, validate.

P 4587, L 7: “MM type nutrient functional response” - see specific comments

P 4587, L 21: “Temperature dependent...” - can you comment this in the context of findings by Lopez-Urrutia et al., PNAS 2006?

P 4589, L 14: But there aren't that many diatoms between 45S and 45N. How does this influence our observations of the future ocean?

P 4590, L 5: Please be consistent in your notation, see equation (10)

P 4590, L 10,12: Replace “delta” by its symbol as done on page 4576.

P 4590, L 11-12: Justify why this approximation is valid.

P 4595, Table 1: Add μ_{ref} , add references

P 4596, Fig. 1: Label T consistently in all RHS panels

P 4598, Fig. 3: Not sure we need this figure. Caption: “at some point” - specify, “per degree” - latitude?

P 4600 4601: Not sure we need the “Diatoms – small Phytoplankton” plots c,f,i, as they are hardly discussed in the text and almost never referred to. Caption: “All terms” - what do you mean by terms? Titles in a-c have different font size than those of d-i. “day-1” - adjust Latex to get superscript.

Page 4605, Fig. 10: Mention temporal scales applied to get these predictions in your figure caption.

Interactive comment on Biogeosciences Discuss., 7, 4565, 2010.

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