"Response of ocean phytoplankton community structure to climate change over the 21st century: partitioning the effects of nutrients, temperature and

light",

by I. Marinov, S.C. Doney and I.D. Lima.

Responses to Anonymous Referee 2 Comments:

Please find referee comments in regular font, and our responses in Bold letters underneath. I am attaching a pdf version of the improved paper, where these changes have been made to the text and are shown in color. Naturally, line numbers in referee comments are from the previous manuscript version. In my responses (in bold) I refer sometimes to page numbers from my new manuscript (pdf version attached).

Specific comments from Reviewer:

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 model parameters needs to be debated in more detail. For example, the initial slope of the photosynthesis-irradiance curve alpha 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"

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

5 Structure of the manuscript

Our Response:

- Our response to these comments are modifications throughout the text (detailed under Minor Comments below) and the addition of 1.5 extra pages to the Discussion (see the last 2 pages of the manuscript) addressing these directly.

- In response to point 1 above "I find it hard to see how model results should differ from our predictions" we have added (top of page 17, new manuscript) "It is encouraging that the predictions from the linearized perturbation analysis are consistent with the results from the fully prognostic CCSM simulations. This suggests that other factors that could influence the prognostic simulations (e.g., lateral advection, multi-stressors, grazing) are of second order importance."

- In response to point 5 above, we have rearranged the Discussion section and have simplified the theoretical discussions, particularly the introductions to theoretical sections 3.2 and 3.3.

- In response to point 3 above, we have replaces Critical nutrient theory with Critical nutrient hypothesis throughout the text.

- In response to point 2 above we have modified and lengthened our Discussion section to discuss: the role of grazers and different temperature dependencies for phytoplankton and zooplankton for future phytoplankton distribution; the assumption of Michaelis-Menten (as opposed to Optimal Nutrient Uptake kinetics); putting the results into a broader context of observations and potential future satellite predictions.

- We have added a set of new references, in particular those related to the temperature dependency of grazing versus growth; references related to Optimal Uptake kinetics;

references related to new satellite studies of size-spectra (which might be used to confirm our hypothesis.

Pages 23-24 in the text now read:

"Our critical nutrient hypothesis applies to the large areas of the ocean where both small phytoplankton and diatoms are limited by the same nutrient and is based on a Michaelis-Menten representation for nutrient limitation of photosynthesis. To what extent do our findings apply to other models and to the real ocean? Preliminary analysis suggests that the critical nutrient hypothesis also holds in a completely different ecosystem model (GFDL TOPAZ, Dunne et al. in prep). Generalizations of the present work to a broader class of models will be addressed in follow up work, but a couple of initial observations follow.

One question that needs to be addressed further is the role of grazers for future phytoplankton distribution. In our model temperature affects phytoplankton growth and grazing rates equally. However, stronger temperature dependence for heterotrophic processes (such as zooplankton growth) than for autotrophic processes (phytoplankton growth) has been predicted in the context of the metabolic theory of ecology by Lopez-Urrutia et al. (2006). This effect might result in phytoplankton escaping zooplankton grazing at low temperatures where zooplankton perform poorly, perhaps allowing frequent algal blooms to develop in polar regions (Rose and Caron, 2008; Lopez-Urrutia, 2008). The opposite should be true in low latitudes. Furthermore, this mis-match might contribute to a larger impact of increasing temperature on high latitude phytoplankton biomass compared to our present model predictions, and to a smaller impact of increasing temperature on phytoplankton are more active."

This work shows clearly that the equation forms specified in GCMs for nutrient limitation and photosynthetic nutrient uptake influence significantly the behavior of the system under environmental or climate change scenarios. Several authors argue that phytoplankton nutrient uptake should be modeled using "optimal uptake kinetics" (OU) (Pahlow et al. 2005, Smith and Yamanaka 2007, Smith et al. 2009) rather than as the Michaelis-Menten (MM) function used in this study. Replacing MM with OU alters the control simulation and the concentrations of non-limiting nutrients. Unlike MM kinetics, the OU theory predicts direct nutrient dependence for the maximum growth μ_{ref} and for the apparent half saturation coefficient K_x^N . While the type of analysis presented here can clearly be applied to OU kinetics, the derivative of growth as a function of nutrient (and Eq. 12b) will change. Further work needs to be done to understand how this might change our conclusions.

Recent modeling studies (Bopp et al., 2005), laboratory and field data (Jin et al., 2006, Cermeno et al., 2009) have suggested an increase in the relative abundance of small phytoplankton in low and midlatitudes with enhanced stratification. Our model results agree with this (small phytoplankton relative abundance increases in all biomes except for the Southern hemisphere subpolar), but our analysis points out that (a) climate change can have opposite implications for absolute and relative contributions of small phytoplankton to the total biomass and (b) changes in the absolute values of biomass are mechanistically more meaningful than relative changes. For example, in the 45°S-45°N biome climate change results in both (1) a larger drop in the small phytoplankton biomass than in diatom biomass - as predicted by the mechanistically meaningful critical nutrient hypothesis – and (2) a relative increase in small phytoplankton biomass, mathematically simply a consequence of small phytoplankton having much larger background biomass in this area. We suggest that both absolute and relative changes in phytoplankton be recorded and analyzed in future climate change studies. Our work suggests that a deeper theoretical understanding of the basic ecological equations used in global models might help us predict future ecological and biogeochemical climatedriven shifts and point to critical processes that need targeted observations. Mapping phytoplankton community composition and its temporal variability from satellite and insitu measurements is essential for validating our critical nutrient hypothesis and model results and generally for forecasting the evolution of ocean ecology and carbon cycle. A number of investigators have developed algorithms to estimate phytoplankton functional types (e.g., Uitz et al., 2006, Alvain et al, 2008; Uitz et al., 2010) and size structure (e.g. Kostadinov et al., 2009, 2010; Mouw and Yoder, 2010) from satellite data. We suggest that satellite estimates of interannual variability in size structure can provide a potential test for our proposed "critical nutrient hypothesis". One idea would be to compare the variability in small and large phytoplankton at locations where plankton variability is primarily due to nutrient changes, both in areas where nutrients are lower and where nutrients are higher than critical values."

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.

Added for clarification:

"Climate driven changes in nutrients, temperature and light have regionally varying and sometimes counterbalancing impacts on phytoplankton biomass and structure, with nutrients and temperature dominant in the 45°S-45°N band and lighttemperature effects dominant in the marginal sea-ice and subpolar regions. As predicted, decreases in nutrients inside the 45°S-45°N "critical nutrient" band result in diatom biomass decreasing more than small phytoplankton biomass."

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?

We changed "limit more strongly" to "decrease more strongly" for clarity. Also we included the following additional summary statement: "Overall, decreases in nutrients dominate the ecological response inside the 45°S-45°N "critical nutrient" band, with diatom biomass decreasing more than small phytoplankton biomass."

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

Rewrote the paragraph to discuss diatoms and small phytoplankton only, the main groups discussed in the paper:

"Diatoms, a phytoplankton group with siliceous tests, are thought to (a) be better at exporting carbon to the deep ocean and (b) be grazed less efficiently than nano or picophytoplankton. By contrast, small (nano or pico) phytoplankton are lighter and sink less readily than diatoms, so they tend to be associated with higher surface recycling of inorganic nutrients and carbon and less efficient carbon transport to the deep. Any future changes in the relative contribution of these or other important phytoplankton types to the total ocean biomass could thus have a significant impact on elemental stoichiometry, ocean biogeochemistry, and ocean carbon"

P 4567, L18: "these phytoplankton types" - replace by "these or other important phytoplankton types" **Corrected**

P 4568, L21: "each of the three phytoplankton types" - which? **Corrected**.

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. **Text now reads:**

"Laboratory and field incubation studies demonstrate that different phytoplankton species drawdown nutrients with greater or lesser efficiency. This can be expressed using nutrient half saturation (*K*) values, with (lower *K*) phytoplankton drawing down nutrients more efficiently in the stratified low latitudes." Smith et al. and OU kinetics discussed in the Discussion section, page 24 top paragraph.

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

Not important indeed for this paper since we don't discuss depth variation, but generally important for models, just means levels are closely spaced at the surface for better resolution. Removed "monotonically increasing" and added "25 vertical levels with enhanced vertical resolution in the upper compared to the deep ocean"

P4570, L15: "nitrogen-fixing diazotrophs" - isn't this a pleonasm? **Wanted this to be extra clear for the readers.**

P4571, L18: Why are the μref 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))?

I have corrected Table 1 to include these terms. This was assumed for simplicity, µref values come from Geider et al. 1998. We have added reference in the text.

P4572, L7: Same here, why are the *alpha* values the same for diatoms and small phytoplankton? Include references for where these values come from. This was assumed for simplicity (and our state of knowledge does not allow us quite yet to make a better assumption), alpha values, just like μref values come from

Geider et al. 1998. We have added reference in the text.

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

This is assumed for simplicity, added explanation for gx. Moore et al. 2004.

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

Reference added.

P 4574, L2: "higher .. growth rates" than who? Do you mean "the highest"? **Yes, correct, "the highest". Corrected.**

P 4574, L 15: Reformulate: "Light and temperature...." Cannot find this is the text.

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

Corrected to actual years in text. No, we cannot really see it, but there is not enough room for an extra figure.

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

Moved around paragraphs, kept Fig 3 as it is the only figure in the paper that summarizes the effects of climate change on the system. This figure allows for direct comparison to previous work reported in the literature (e.g. Sarmiento et al. GBC 2004).

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

Corrected to read: "Climate driven changes in biomass are partly driven by changes in specific growth rates, as suggested by similarities in the respective large scale patterns in the 45°S-45°N domain and parts of the Southern Ocean. Areas where the patterns strongly diverge (e.g., north of 45°N for diatoms) are areas where grazing (and to a lesser degree linear mortality and aggregation) have first order importance."

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)?

Definition clarified in the text.

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

Correct, moved around paragraphs.

P 4575, L16: "nutrient functional response" What do you mean here, V*x*? On page 4571, these were called "nutrient limitation terms".

For consistency, we now use the term "nutrient functional response" throughout the text.

P 4576, L2: Add space after "Tf" in all the terms of equation (10). Corrected here and in the appendix.

P 4576, 11: Estimate how small ! 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? Several different approaches have been proposed in the literature for constraining biomes, Longhurst's being one example. The biome definitions used here (marginal ice, subpolar, torpical/subtropical) are certainly influenced by Longhurst's work and that of others (e.g., Sarmiento et al., 2004) but are also based on the different domains resulting from the critical nutrient theory discussed later on in the manuscript. Currently we are pursuing a more in-depth analysis of climate change effects on biome areal extent and location, but this analysis is beyond the scope of the present manuscript and will be the topic on it's own for a future paper. We have rearranged this paragraph for clarity.

P 4577, L17: "Let us.." connect this sentence somehow to Fig.1 b,d,f. Ok, changed this phrase to: "We start by noticing that small phytoplankton and diatoms are limited by the same nutrient over most of the global ocean (Fig 1b,d,f)"

P 4577, L 18: "Nutrient functional response"? What do you mean, Vx or *frac*"Vx"N? **Vx**.

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.

Correct. The same theory applies to P-limited areas, but there was not enough space here for us to cover P limitation, which is less important in our global model relative to the others nutrients. We have added text to the manuscript noting that Plimitation may be important on a regional basis and that the same basic analysis framework would apply. (lines 9-10, page 12 in the text)

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.

Rewrote completely/lengthened our discussion of Figure 10, and have moved it now to after Equation (17).

P 4578, L18: Doesn't V Nx also depend on NH4, so that Nnew = 1

KNH4KNO3 (KNH4NO3 + KNO3NH4)?

Yes, correct. I am disregarding for now the dependence of NO_{3critical} on NH4 (made this clear in the text). In truth, I don't know yet how to include this dependence in NO_{3critical} in a simple way (the formulation is rather complicated in this model), but I've been thinking about it lately and hope to address this in a future paper. From what I can see so far, NH4 brings only a small correction to NO_{3critical} - the large scale picture presented here holds for sure, without this correction.

P 4579, L 11: "Fig 9 a-d" replace by "Fig. 9 b d". Corrected.

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

Interesting suggestion, I will keep this in mind for future work as we haven't thought yet of climate change response in terms of those two regimes.

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

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

We agree with the reviewer that assuming the same temperature response function for all phytoplankton is a simplification, but one that is probably reasonable at this point in time given the relatively limited state of knowledge about the temperature responses of open-ocean phytoplankton species and the level of sophistication of the global climate-ecosystem models.

P 4581, L21: "confirm prediction", see specific comment above, how can it not do so? Of course. Better phrasing is that "equations give us intuition about what to look for/how to interpret figures."

P 4582, L 18: Refer to your Figure 4 a and b? **Yes, done.**

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

P 4583, L 16: "various" - you have only two. **Changed.**

P 4583, L17: "exponential .." give equation here. **Done**

P 4584, L 6: "A close analysis.." of what? "... confirmed by Fig. 8" how? Corrected: A close analysis of Eq. 12a shows ...

P 4584, L17: "everywhere" - really? Yes, we mean that N/(N+K) is a decreasing function of K. K is larger for diatoms.

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.

The phrase "We note conceptual agreement with Agawin et al. (2000) and Moran et al. (2010), who experimentally noticed shifts in the total community to smaller sizes with an increase in temperature" added after Equation 25. Addressed also in the Discussion section, page 24, paragraph starting with line 16 onward.

P 4587, L 7: "MM type nutrient functional response" - see specific comments We have added a comment on this topic as a separate paragraph in the Discussion section on page 24 as follows:

"Several authors argue that phytoplankton nutrient uptake should be modeled using "optimal uptake kinetics" (OU) (Pahlow et al. 2005, Smith and Yamanaka 2007, Smith et al. 2009) rather than as the Michaelis-Menten (MM) function used in this study. Replacing MM with OU alters the control simulation and the concentrations of non-limiting nutrients. Unlike MM kinetics, the OU theory predicts direct nutrient dependence for the maximum growth μ_{ref} and for the apparent half saturation coefficient K_x^N . While the type of analysis presented here can clearly be applied to OU kinetics, the derivative of growth as a function of nutrient (and Eq. 12b) will change. Further work needs to be done to understand how this might change our conclusions."

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

We now comment on this in a separate paragraph towards the end of the paper (page 23, line 23) as follows:

"One question that needs to be addressed further is the role of grazers for future phytoplankton distribution. In our model temperature affects phytoplankton growth and grazing rates equally. However, stronger temperature dependence for heterotrophic processes (such as zooplankton growth) than for autotrophic processes (phytoplankton growth) has been predicted in the context of the metabolic theory of ecology by Lopez-Urrutia et al. (2006). This effect might result in phytoplankton escaping zooplankton grazing at low temperatures where zooplankton perform poorly, perhaps allowing frequent algal blooms to develop in polar regions (Rose and Caron, 2008; Lopez-Urrutia, 2008). The opposite should be true in low latitudes. Furthermore, this mis-match might contribute to a larger impact of increasing temperature on high latitude phytoplankton biomass compared to our present model predictions, and to a smaller impact of increasing temperature on phytoplankton biomass in low latitudes where zooplankton are more active."

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?

Interesting point, and I think the answer to this is related to my discussion (in Section 3.5 and in the Discussion section) on the distinction between relative versus absolute changes in diatoms or small phytoplankton. If in the low latitudes we only had small phytoplankton we

would simply say as our conclusions that "small phytoplankton concentration decreases with climate change". However, the presence of diatoms changes the situation; such that the relative drop in diatoms (relative to their small overall contribution to the phytoplankton pool) is larger than the relative drop in small phytoplankton. We therefore notice, in agreement with others, that in low latitudes there is "an increase in the relative contribution of small phytoplankton" (relative to diatoms),

Discussion text (page 24) now reads:

"Recent modeling studies (Bopp et al., 2005), laboratory and field data (Jin et al., 2006, Cermeno et al., 2009) have suggested an increase in the relative abundance of small phytoplankton in low and midlatitudes with enhanced stratification. Our model results agree with this (small phytoplankton relative abundance increases in all biomes except for the Southern hemisphere subpolar), but our analysis points out that (a) climate change can have opposite implications for absolute and relative contributions of small phytoplankton to the total biomass and (b) changes in the absolute values of biomass are mechanistically more meaningful than relative changes. For example, in the 45°S-45°N biome climate change results in both (1) a larger drop in the small phytoplankton biomass than in diatom biomass - as predicted by the mechanistically meaningful critical nutrient hypothesis – and (2) a relative increase in small phytoplankton biomass, mathematically simply a consequence of small phytoplankton having much larger background biomass in this area. We suggest that both absolute and relative changes in phytoplankton be recorded and analyzed in future climate change studies."

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

P 4590, L 10,12: Replace "delta" by its symbol as done on page 4576. **Done**

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

Added to the main text (middle of page 10 in the new manuscript) and Appendix before Eq. A3: "We use a standard Taylor series expansion of the specific growth rate (Eq. 2) around some initial state ... As is customary, we retain the first order (linear) terms in the expansion, dropping higher order quadratic terms (e.g. ΔT_f^2 , $\Delta T_f \Delta I_{par}$) which tend to be considerably smaller than the first order perturbations."

P 4595, Table 1: Add μref , add references Added μref to table. Value taken from the Geider growth model (Geider 1998).

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

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

Corrected caption.

Kept Fig 3 as it is the only figure in the paper that summarizes the effects of climate change on the system. This figure allows for direct comparison to previous work

reported in the literature (e.g. Sarmiento et al. GBC 2004).

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.

Corrected "All terms" to "contributions", font size in titles, and "days⁻¹" (caption for Figure 5). Added references to diatom-small phytoplankton column (e.g., line 6 page 10 and line 23, page 14).

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

Figure 10 was redrawn to clarify the comparison of the Earth System Model output and the critical nutrient hypothesis results; see new Figure 10 below. The caption was rewritten as well as follows:

Figure 10. (a) Critical nutrient hypothesis. Green areas: $N \le N_{critical}$ and hypothesis predicts that small phytoplankton specific growth rates should change more with nutrient change than diatom growth rates. Light blue areas: $N > N_{critical}$ and diatom growth rates should change more than small phytoplankton growth rates. Dark blue areas: no theoretical prediction possible as diatoms and small phytoplankton are limited by different nutrients (e.g., diatoms are Si limited while small phyto are N limited in W Pacific). Area separation based on point-by-point comparisons of surface limiting nutrient (NO₃ or Fe or PO₄) values with the corresponding critical nutrient value calculated from Eq. 17 in the text. (b) Climate model results. Green areas: Model regions where small phytoplankton growth rates change more than diatom growth rates in response to nutrient perturbations $\left|\Delta \mu_{sp}^{nutr}\right| > \left|\Delta \mu_{diat}^{nutr}\right|$. Light blue areas: diatom growth rates change more $\left|\Delta \mu_{diat}^{nutr}\right| > \left|\Delta \mu_{sp}^{nutr}\right|$. $\Delta \mu_{sp}^{nutr}$ terms calculated as linear trends for the 1980-2100 period (as in Figures 6,7,8). The critical nutrient hypothesis predicts well the model results; green and light blue areas in (a)

coincide nicely with green and light blue areas in (b), respectively.

a. Critical nutrient hypothesis



b. Model results: Phytoplankton response to nutrient changes

