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Interactive comment on "Marine Phytoplankton Stoichiometry Mediates Nonlinear Interactions Between Nutrient Supply, Temperature, and Atmospheric CO_2" *by* Allison R. Moreno et al.

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We gratefully thank Referee #2 for their time, constructive comments, and suggestions to our manuscript. Below we have a detailed response to each comment posed by Referee #2. We have amended the manuscript in hopes that it will be much improved and our study presented clearer.

Anonymous Referee #2 Received and published: 1 December 2017

Using a "classical" ocean carbon cycle box model and parameterizations of flexible elemental stoichiometry in surface ocean particulate, the authors examine the role of

elemental composition in mediating the response of atmospheric CO2 to ocean temperature change. There is a significantly different sensitivity when the particulate C:P ratio is represented by a "multi-environmental" (Ecological Stoichiometry and temperature dependent) framework compared to a fixed, Redfieldian particulate composition. Most notably, compensation between temperature sensitivity of solubility and biological pumps reduces the sensitivity to subtropical temperature change as well as reversing and enhancing the response to tropical perturbations. Variable elemental composition and phosphorus storage modify the sensitivity of atmospheric pCO2 to the efficiency of phosphate utilization in subtropics and tropics. The key message for is that variable elemental ratios have non-negligible impacts on the ocean's control of atmospheric CO2 and that the temperature sensitivity of solubility and stoichiometrically-mediated biological pumps have some interesting regional dependences.

I enjoyed reading this paper. I found it stimulating and thought provoking. There is a lot going on. The authors combine classical carbon cycle box model with several parameterizations of elemental stoichiometry of the sinking particulate (and/or primary producers). The authors connect cellular scale physiology and global carbon cycle and have used and developed an appropriate framework with which to do so.

My criticism of the paper is that the multi-environmental model is presented very much at face value. The assumptions and construction seem very logical but the choice and constraint of the parameters is by and large opaque. In particular the relationship between the storage component of the multi-environmental model and the Galbraith and Martiny parameterization seems interesting and important but is not really discussed. How important is the storage term in controlling the overall response of the multi-environmental model? It is not at all clear from the manuscript. I feel that some clarification and discussion along these lines is important for the reader.

I found the manuscript very interesting and thought provoking. I had a number of questions, comments and need clarification on certain points which I will detail here. Some are more important than others. While my recommendation is major revision, it

is clarification that I would like to see, not changes to what has been done.

30) The Sarmiento and Toggweiler and contemporary carbon cycle models focused a lot on the sensitivity of atmospheric pCO2 to "high latitude" changes. This isn't discussed here - perhaps there wasn't any as configured? Some comment would be useful and interesting in this regard.

OUR RESPONSE »> In this manuscript, we are focusing our efforts on the potential impacts of the low latitudes. Sarmiento and Toggweiler both found that high latitudes have a big impact on atmospheric pCO2. In no way do we disagree with this seminal work, we simply are trying to bring attention to the importance of low latitude processes as an additional mechanism(s) to consider when predicted biogeochemical feedbacks. We take their original findings into consideration when creating the model. In the box model, fhd, a bidirectional mixing term that ventilates the deep box directly through the high-latitude surface box, has a large impact on the magnitude of atmospheric pCO2. We prescribed the baseline value to be 45.6 Sv in our model but when we increase it to 108 Sv, the change in pCO2 is $\sim$105 ppm for C:P at Redfield proportions. Thus, high-latitude processes clearly have a major impact on ocean and global biogeochemistry. To address this comment in the manuscript, we have added the following: "Although the focus of this study is to determine the impact of low latitudes on pCO2,atm, we point out that at Redfield stoichiometry, pCO2,atm increases by 100 ppm when fhd is increased to 108 Sv from its default value 45.6 Sv.

31) The stoichiometry of sinking particulate and of primary producers is certainly connected but not necessarily the same. The multi-environmental model is founded on primary producer physiology. Perhaps this potential difference should be flagged?

OUR RESPONSE »>We acknowledge that sinking particulate stoichiometry and primary producer stoichiometry can be different in certain regions but overall, it has been found to be reasonably linked (Teng et al. 2014). Thus, we find that this assumption is reasonable to a first order.

Within our paper we have added the following statement, "For certain values of the parameters, the model produced excessive nutrient trapping in the thermocline. In order to dampen the nutrient trapping, we tuned the remineralization depth. Assuming that 25% of the total export is respired in the thermocline with the remaining 75% exported into the deep ocean, produced a better match between the modeled and observed [P] in the thermocline box. Total export is made from both the stoichiometry of sinking particulate and of primary producers, based on Teng et al. (2014) this is a reasonable first order assumption."

32) I would have been interested to see a Droop-style model in the mix as its a relatively common tool - but there is more than enough going on here anyway.

OUR RESPONSE »>We believe that the Galbraith and Martiny (2015) model (nutrient-only model in our study) is qualitatively similar to the Droop model. Thus, we expect the outcome to be very similar (i.e., a direct dependence of C:P on P availability).

33) I very much like the spirit of the multi-environmental model. (Though I find the name a little odd). It accounts for the role of cell size in mediating nutrient affinity and cell composition (contribution of cell wall material). It was not made clear how sensitive the final parameterization or the outcomes of the box model are to the assumed cell size. Nor could I find any information about the cell size assumed (or modeled?) in the simulations.

OUR RESPONSE »>We do not assume that there is a single size characterizing all phytoplankton cells in our model. Instead, cell size is one of the key elements of cell strategy that we model. Smaller cells have greater specific nutrient uptake rates, but their cell wall and membrane occupies a greater fraction of their biomass than larger cells, and thus they have less space (specific to biomass) for investments in either photosynthesis or biosynthesis.

Figure 4 and 5 are meant to illustrate the predictions that our model makes in different environmental conditions. In the original manuscript, these figures showed model

predictions for C:P ratios, biosynthesis investment, and photosynthesis investments. However, in each of these figures, the predicted cell radius is also varying. In order to make the predictions of our model clearer, we have augmented each of Figure 4 and 5 with an additional plot, showing how cell radius varies with environmental conditions.

Our model predicts a strong relationship between nutrient concentrations and cell size. In oligotrophic conditions the model predicts a radius under 1 μm. When resources are abundant the model predicts much larger cells. Our model also predicts a weak, but non-zero dependence of both irradiance and temperature on cell size. Higher irradiances lead to smaller cells (due to a lower requirement for photosynthetic machinery), and there is a non-monotonic, concave relationship between temperature and cell size, which is due to a subtle interaction between biosynthesis efficiency (which varies greatly with T) and size dependent uptake rates.

34) The photosynthesis parameterization and allocation scheme is very reminiscent of Geider's models in spirit and mathematical form. What is the relationship?

OUR RESPONSE »>Our model is very closely related to the multi-compartment photosynthesis model presented in Talmy et al. 2013 (we incorrectly cited Talmy 2014 in the model description, this has been changed to correctly cite this paper). Geider is a co-author of this paper and indeed the modeling framework presented there is very much consistent with the photosynthetic models he has devised throughout his career. We utilized the functional responses which they derived in that paper to represent the allocation of photosynthetic machinery to either light harvesting or carbon fixation. Their model included other compartments (photoprotection and biosynthesis) which were suited to the particular dynamic light environment that they were interested in studying. We use our own parametrization for biosynthesis. Talmy et al. 2013 found that the photoprotection allocation was not a large or greatly changing component of their allocations. We have therefore not included it would complicate our model with little change in our qualitative results.

On the other hand, the decomposition of photosynthesis into light harvesting and carbon fixation components is critical, and makes our model predictions agree much better with experiments studying the variations of C:P or N:P ratios with irradiance. Models that do not have this decomposition predict too large of a decrease in cellular allocations to photosynthesis at high-light levels. In a two compartment model, increases in allocations to carbon fixation cause the overall allocation to light harvesting to have a more mild decrease. The two-compartment treatment also seems more physiologically realistic than a 1-compartment, which only models photosynthetic pigments. Thus we used the functional forms and parameters that were derived (experimentally) in Talmy et al. 2013 for carbon-fixation and light-harvesting. We have added a small amount of text to better clarify the relationship.

35) The statement at line 235 that the "unique maximum of the growth rate occurs for the set of parameters that lead to co-limitation by nutrients, photosynthesis and biosynthesis" is very interesting and intriguing. Is that an emergent property? Is it obvious that it should be this way? I would have liked to hear more about this.

OUR RESPONSE »>It is commonly the case for mathematical models like ours that model the tradeoffs between different allocations of biomass to different physiological functions to have a unique solution with a maximum growth rate. The reason is that if one increases the investment a cell makes in some pool, this will decrease the investments in other pools. Thus, the only way for a cell to increase the photosynthetic rate is to decrease either biosynthesis or nutrient uptake rates, and vice versa. In such cases we generally find a unique solution at which the three rates, μPhoto, μE, and phosphorus are the same. This might be obvious for very simple models, or for people who primarily work using these models. Indeed, the easiest way to see what is going on is to imagine a simpler model with a similar style. For example, if we modeled a cell with fixed radius which is limited by either light or by biosynthesis, then the cell growth rate would be min(μPhoto, μE). If we start with the biosynthesis allocation at 0, the growth rate of the cell will be μE = 0, but μPhoto will be high because of all of

the photosynthesis proteins. As E increases, μE increases, and the cell grows faster. At this time, μPhoto is going down, but this doesn't affect mu. At some value of E, μE = μPhoto (since if E = 1, μPhoto = 0). This point will be the optimal strategy, since further increases in E will cause a switch to limitation by μPhoto, which decreases with increasing E.

We have actually been able to convert the intuitive picture described above into a mathematical proof. Since it does not require much additional space to include it, we have added it to the paper, along with a figure indicating graphically the idea behind the proof.

36) Phosphorus storage seems to be very important. Equation (13) controls a residual storage pool that constrains the parameterized stoichiometry to match the observed relationship between phosphate and particulate stoichiometry, as I understand it. Thus it strongly mirrors the Galbraith and Martiny model of equation (1). For me, some key questions concern this aspect of the model: How significant in the overall control of model stoichiometry is this component? If it dominates, then I could view the multi-environmental model in some way as a combination of the Galbraith and Martiny model with temperature sensitivity. Or does the more mechanistic and detailed physiology have a significant role? Either way, I think the mechanistic model is valuable and interesting but I would like to understand how much the results are driven by the storage of phosphorus. Its important for a number of reasons and I feel that this should be clearly discussed.

OUR RESPONSE »>The impact of the residual pool on the overall size of the P pool is heavily dependent on environmental conditions, varying from a minimum of close to 0% to a maximum of just under 50%, for the combinations of parameter values used in all of our numerical experiments. Over most of the parameter range considered here, the contribution of the residual pool is much more modest, 10-20%. High values occur when phosphorus is available and the temperature is high. In these conditions, ribosomal contributions are decreased, but the residual contribution is high. In cold water,

high P ecosystems, the residual contribution is approximately 25%, and in oligotrophic ecosystems it is close to 0.

Thus, we view the mechanistic/physiological part of the model as being more significant, but it is important to acknowledge that we don't believe that this mechanistic model can on its own explain all of the observations of C:P in the ocean. In particular, it is not possible for the purely mechanistic model to predict the extremely low C:P ratios observed in some ocean regions. This is because the C:P ratio of the biosynthesis apparatus sets a lower limit. Even if we assume that proteins made an even smaller contribution to biosynthesis (which would cause biosynthesis to have a lower C:P), it would still be impossible to match the most extreme observations. If the C:P of the biosynthesis pool was variable or lower, then the contribution of residual pool would be somewhat smaller, but still necessary. (Better understanding the balance between ribosomes and non-photosynthetic proteins is likely a good direction for future research).

In order to make the importance of storage, we have added an additional plot reveals the relative contribution of the storage pool to the total P pool as a function of environmental conditions, with a short discussion.

37) A small thing, but I had to stop and think about equation (1) because [P]o has different dimensions than [P]: the former is a ratio and the latter a concentration. I think it would be much clearer and more appropriate to denote [P]o as in (13), with a symbol in accord with other variables that are ratios.

OUR RESPONSE »>Thank you for noticing this, we have changed the notation so that [P]0 is now (P:C) 0, i.e. the P:C ratio predicted by linear regression at zero P concentration.

38) The box model formulation makes sense; the inclusion of the thermocline reservoir is important for the sensitivity to changes in the subtropical surface. Some small details: how is the carbonate system solved? Is alkalinity fixed or is there an implicit carbonate

pump?

OUR RESPONSE »>Thank you for bringing this to our attention. The nonlinear carbonate system equations are solved using Matlab's fsolve function. We calculated the solubility constants using biome specific salinity and temperature. The solubility constant then is used to break up total carbon into pCO2, bicarbonate and carbonate ions. Total carbon is quantified using the breakdown of carbon ions (pCO2, bicarbonate and carbonate) and alkalinity concentration. Total carbon and its breakdowns (which we keep track of at each time step) are transported laterally to each box through our thermohaline circulation. We have added more detail to our box model design description, to make sure we are clear on how this model is created.

Within our paper we have added these lines to address this comment: "To quantify the breakdown of carbon into these components, we model the solubility pump, using temperature and salinity to determine the partitioning of inorganic carbon among total carbon within a box. The global mean alkalinity is prescribed according to the observed mean ocean values. Our box model simulations various forms of C similar to alkalinity. Biome specific salinity and temperature are used to prescribe the solubility constants of CO2 in seawater and the bromine concentration, which is taken to be proportional to salinity. We use these calculations to determine the pCO2 value at standard pressure (1 atm) within each box. Box specific total carbon is calculated from the pCO2 value, bicarbonate, carbonate and alkalinity concentrations. CO2 cycles through the atmosphere via the air-sea gas exchange fluxes (fah, fas, fat). We used a uniform piston velocity of 5.5 x 10-5 m s-1 to drive air-sea gas exchange (DeVries & Primeau 2009, Follows et al. 2002)."

39) The model doesn't resolve nitrogen, and I would expect that the allocation of nitrogen in proteins and pigments would be an important factor, perhaps more so than phosphorus. Does this actually matter? A comment on this would be helpful.

OUR RESPONSE »>This is an important point that was also raised by reviewer 1(Ref-

eree 1: Response #1). In short, the reason for using P is its role as the ultimate limiting nutrient on long time-scales as well as to simplify the model and avoid an explicit N cycle.

40) Why does temperature affect biosynthesis but not photosynthesis (line 398) imposed from empirical observations? The model description tells us that Q10=2 for temperature dependences, but there is no discussion with regard to photosynthesis. Why this choice?

OUR RESPONSE »>We model photosynthesis as having a Q10=1, which is consistent with physiological studies going back to Shuter 1979 that suggest that photosynthetic efficiency does not depend on temperature over physiologically relevant ranges. The discrepancy between photosynthetic and biosynthetic temperature dependence has traditionally been explained by referring to the differences in the chemistry and physics of the two processes. The electron transport chain relies on quantum mechanical processes, which are unaffected by variations in temperature in a physiologically relevant range. A good reference for this is Devault 1980, Quantum Mechanical Tunneling in Biological Systems. We have added some text to more explicitly explain our choice of temperature dependence parameters for different processes.

41) The discussion of sensitivity to cell radius in lines 400-410 doesn't tell us what is the cell radius (or distribution of) in the model? Is it imposed or modeled (I presume the former but nothing is said in the paper). This should be clear.

OUR RESPONSE »>Cell radius is an emerging property based on the phosphorus concentration, light, and temperature on the cell.

42) Figures 3,4,5 are a bit small and fuzzy when printed.

OUR RESPONSE »>We have fixed these figures so they are clearer.

43) I'd really like to understand how important the storage term is in the overall control of figures 4 and 5. We see the variation in C:P and the relative allocation to biosynthesis

and photosynthesis, but it's not clear how important the latter is to the former.

OUR RESPONSE »>We have included an additional figure as part of our response to an earlier comment about the importance of phosphorus storage.

44) What is the cell size in the box model simulations? Is it imposed? Does it vary? How sensitive are results to r?

OUR RESPONSE »>The cell size varies based on the phosphorus concentration, light, and temperature in each surface box when we are running the multi-environmental stoichiometry. When using the Redfield, nutrient-only and temperature-only stoichiometric models there are not explicit cell sizes but implicit varying ones.

45) The model is P based. However, as is alluded to in the manuscript, nitrogen and iron dynamics are important. Indeed P is found to be the proximal limiting in only a few areas of the global ocean, with N and Fe controlling things locally. So how does this affect the relevance of the model? Wouldn't N and Fe dynamics be more important at the individual scale? Would this (does this) mean that storage is most significant for P:C? Again, understanding the significance of storage for the outcomes here is very important.

OUR RESPONSE »>It is true that phosphorus rarely is a proximal limiting nutrient, whereas nitrogen and iron commonly limit productivity in the short term. However, on long time-scales P is commonly considered the ultimate limiting nutrient and our results are indeed based on long-term equilibrium states. However, it is also clear that the three nutrient cycles have complex interactions both within and outside the cell and we hope to add explicit N and Fe cycles in future iterations of the model.

46) Line 464: "nutirent"

OUR RESPONSE »>We have changed it in the document.

47) The contrasting temperature sensitivities of tropical and subtropical perturbations is very interesting. The dominance of the solubility term in subtropical responses is

ascribed to the "large surface area" of the subtropical region (line 563). I don't think that's true: I think its because the subtropical surface feeds the subtropical thermocline which represents a significant contribution to global water volume. Hence, changes in subtropical solubility have significant leverage. Since tropical waters don't directly feed into any subsurface water mass, they do not have the same leverage. This is why the resolution of the thermocline box is important. The classic Harvardton Bear box models did not resolve the thermocline and so found very low sensitivity to subtropical perturbations relative to 3D circulation models. Resolving the thermocline in the box models brings them into consistency (this was the point of Follows et al, 2002). I thought this was why the authors had chosen the configuration which resolves a thermocline reservoir.

OUR RESPONSE »> The reviewer is correct. The sensitivity of atmospheric CO2 to solubility changes in a box in contact with the atmosphere depends on the volume of the subsurface ocean ventilated from that box and on the degree of air-sea disequilibrium as explained in Follows et al, 2002 and also in DeVries and Primeau 2009. (The disequilibrium effect can be significant for high latitude boxes that have a relatively small surface area and a vigorous exchange rate with deeper water masses). We thank the reviewer for allowing us to clarify the point we were trying to make, which is that because the nutrient supply to the subtropical gyres is dominated by the lateral transport of unused nutrients from the tropical box rather than by vertical exchange, the strength of the biological pump does not scale with the surface area of the subtropical gyre, whereas the volume of the thermocline box very roughly speaking scales as the area of the subtropical box, at least in the limit where the surface area of the tropical box is negligible compare to that of the subtropical box, simply because volume is equal to area times thickness. To make the text clearer and more accurate we have revised it as follows:

The decrease in surface CO2 solubility at high temperatures is sufficient to overcome the increase in export due to higher C:P leading to a positive relationship between

pCO2,atm and subtropical temperatures. It is important to point out that the relative importance of the two competing effect depends critically on the physical circulation of the ocean. Predicted increases in stratification are often invoked as a mechanism that would decrease the vertical supply of nutrients, which one might think would further compensate for the effect of higher C:P. However, the strength of the biological pump in the subtropics is controlled the by lateral transport of nutrients rather than by vertical exchange so that the impact of increasing stratification might not be important. Similarly, it is unclear how increases in stratification might affect the strength of the solubility pump. The sensitivity of pCO2,atm to changes in subtropical surface temperatures depends critically on the volume of the ocean ventilated from the subtropics, i.e. on the volume of the thermocline box in our model. How this volume might change in response to a warming world is a complicated dynamical problem that is beyond the scope of the present work.

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