

Interactive comment on “Marine Phytoplankton Stoichiometry Mediates Nonlinear Interactions Between Nutrient Supply, Temperature, and Atmospheric CO₂” by Allison R. Moreno et al.

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We gratefully thank Referee #1 for their time, constructive comments, and suggestions to our manuscript. Below we have a detailed response to each comment posed by Referee #1. We have amended the manuscript in hopes that it will be much improved and our study presented clearer.

Anonymous Referee #1 Received and published: 7 November 2017

Variability in marine phytoplankton stoichiometry can lead to differences in carbon export to the deep ocean. This manuscript expands on previous models (mainly Galbraith

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and Martiny, 2015 and Yvon-Durocher et al., 2015) to further our understanding of how various environmental factors lead to changes in phytoplankton stoichiometry. The authors show how incorporating factors, such as temperature, light, and phosphorus concentrations, are able to model variations across the global ocean that would otherwise be lost in more mainstream models using fixed C:P ratios. The manuscript overall nicely lays out the difference modeling approaches taken and how they ultimately change the effect on carbon export in the global ocean. I want to point out that I am not a modeler and therefore cannot assess the math presented to its full extend, but I am a biogeochemist and can provide a critique on the science presented in this manuscript. I believe this manuscript should be published with the revisions I have outlined below.

1) My first issue with the manuscript in general is the lack of nitrogen. The ocean overall is nitrogen limited and it is a bit worrisome that it is never mentioned. Why was nitrogen left out? There must be a reason, and including a sentence or two to explain why it has been left out would be sufficient without having to incorporate it into the models.

OUR RESPONSE >> This is a very important point and the reviewer comments make it clear that the justification of using P as a representative of nutrient availability needs to be clarified in our manuscript. The underlying reason for picking P rather than N is linked to ideas outlined by Tyrrell, 1999. On long time-scales, P is commonly considered the ultimate limiting nutrient whereas N is only limiting productivity and export on short time-scales. On long time-scales, nitrogen fixation/denitrification will presumably adjust the N inventory. Our modeling is focused on long term steady-state outcomes and we would like to avoid issues associated with modeling the N cycle (like getting N-fixation and denitrification rates correct). Thus, we chose to use P as a representative for nutrient availability. However, we do recognize that the reality may be more complex and hope to add an explicit nitrogen (and Fe) cycle in the future.

We have amended the manuscript to address this concern: “Phosphorus is used to represent the role of nutrient availability in controlling stoichiometry and C export. We chose this over N to avoid having to include a parameter rich N cycle. Furthermore, P

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rather than N is commonly regarded as the ultimate limiting nutrient (Tyrrell 1999) and thus P availability represents the long-term steady-state biogeochemical equilibrium."

2) My second issue is the inclusion of iron and iron deposition. It is mentioned several times throughout the manuscript and honestly seems to be thrown in haphazardly. Even calling the one region the iron-limited upwelling zone does not really make sense. I do not disagree that these regions are distinct from the subtropical gyres, but there needs to be another way to separate them. The simplest thing to do would be to remove all talk of iron and iron deposition as it does not add anything to the manuscript. If you choose though to leave it in, there needs to be more discussion and also a few references as there are currently none. I have listed below each mention of iron and have provided some input should you choose to include it.

OUR RESPONSE »>We agree with the reviewer on this point and realize that the references to Fe limitation are confusing. Thus, we have removed the labeling of iron-limited regions in the manuscript. Now, we only introduce the concept of iron limitation in the discussion as a factor contributing to setting surface macronutrient concentrations in tropical ecosystems.

3) My third issue is how phospholipids have been defined and treated within the model. The decision to functionally treat phospholipids with the storage pool needs to be justified or expanded upon as it is currently not clear. As the authors state, phospholipids are localized within the cellular membrane (defined in the model as a functional pool) and not as energy storage molecules as suggested in the text. Lipids associated with energy storage, localized within intracellular lipid droplets, are generally non-phosphorus, highly reduced, and non-polar (see Levitan et al 2014 "Remodeling of intermediate metabolism in the diatom *Phaeodactylum tricornutum* under nitrogen stress"). This raises the question of how the authors have defined the storage pool, is it defined as utilized by organisms for energy storage or is it only in the sense that "this is a pool where some phosphorus is stored within the cell?"

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OUR RESPONSE »> We agree that this can be confusing. Due to the similarity in behavior of P-lipids and P-storage (no other types of storage molecules like lipids or carbohydrates are considered here), they were treated as the same in the model to save parameters. To address this issue, we have attempted to clarify this issue in the manuscript.

The manuscript now reads as follows: "Phytoplankton can substitute sulfoquinovos-diacylglycerol (SQDG) for phospholipids in their cell membranes under low P conditions (Van Mooy et al., 2009). Similarly, P storage molecules are also regulated by P availability. Thus, we here assume that phospholipids and P-storage exhibit the same behavior and thus model-wise treated as one pool."

4) L34: First mention of iron-limited tropical upwelling region. Again, I would honestly remove "iron-limited" and just call the region the tropical upwelling region. These regions become macronutrient limited as well once you leave the immediate upwelling zone so its deceiving to just focus on iron. It is also known that the Southern Ocean is iron limited, so, again, it is deceiving to focus on iron in the upwelling regions when there are other regions that are iron limited.

OUR RESPONSE »>As stated in #2, we agree with this point and have changed the description of the tropical box as suggested.

5) L46: add "ppm" after approximately 46

OUR RESPONSE »>We changed this in the document.

6) L70: add "et al." after Durocher

OUR RESPONSE »>We changed this in the document.

7) L76-85: Remove iron-stressed and iron-limited. The sentence "Iron deposition in the tropical upwelling. . ." is not correct. There is actually very little iron deposition to the tropics, the North African dust plume deposits iron to the tropical Atlantic but that is the one example (see Jickells et al 2005 "Global Iron Connections Between

Desert Dust, Ocean Biogeochemistry, and Climate"). Iron is upwelled along the coasts in these areas along with macronutrients, but it is incorrect to call that iron deposition.

OUR RESPONSE »>We have removed iron-stressed and iron-limited from this section. Iron limitation will now only be referenced in the discussion.

Within our paper we have added the following sentence to address this comment, "Iron limitation is commonly thought to control [P] in the tropical upwelling regions (Moore et al., 2004; Raven and Falkowski, 1999) and the degree of nutrient drawdown has a strong impact on predicted (and observed) C:P in phytoplankton. This environmental control on C:P leads to highly non-linear controls on pCO₂,atm whereby increased export in the tropics leads to increasing pCO₂,atm."

8) L111-115: Questions 1 and 2 seem redundant, please remove question 1 or give more detail if it is in fact different from question 2.

OUR RESPONSE »>We recognize the confusion seen between the two research questions. The first is to determine the influence of cellular allocation strategies based on different environmental conditions (nutrients, temperature, and multi-environmental) on stoichiometric ratios. The second is to determine the influence of changing environmental conditions such as phosphorus concentrations and temperature on each stoichiometric model. In order to address this confusion, we have clarified the first question to include cellular allocation strategies.

Within our paper we have changed the research questions to read as follows: "We will explicitly address the following research questions: (1) How does environmental variability influence marine phytoplankton cellular allocation strategies and in turn the stoichiometric ratio? (2) What are the effects of changing environmental conditions on stoichiometric ratios, carbon export, and pCO₂,atm?, and (3) What is the influence of the environmental gradients among the three major surface biomes on carbon export and pCO₂,atm?"

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9) L135: Where in the water column are you taking the phosphorus concentration?

OUR RESPONSE »> Phosphorus concentrations are prescribed within each box and then the model is run to steady state. The tropical and subtropical surface boxes extend down to a depth of 100 m, the high latitude surface box extends down to 1000 m, the thermocline box extends from a depth of 100 m down to a depth of 1000 m, and the deep box extends down to a depth of 4000 m. For the use of phosphorus within our multi-environmental stoichiometric model we use the concentration in the respective surface box.

10) L207: add "et al." after Daines

OUR RESPONSE »>We changed this in the document.

11) L212: add "et al." after Daines

OUR RESPONSE »>We changed this in the document.

12) L213: Expanding on the phospholipid justification, can you explain more why you choose a zero contribution for phospholipids? Although non-P substitutes can reduce the phosphorus incorporated into P-lipids, observations suggest non-zero quantities remain. For example, 1.3 +/- 0.6% P uptake in the P-limited Sargasso are incorporated into phospholipids (Van Mooy et al 2009 – mentioned in next correction) and phospholipids make up approximately 5% of particulate organic P in the P-limited eastern Mediterranean (Popendorf et al 2011 "Gradients in intact polar diacylglycerolipids across the Mediterranean Sea are related to phosphate availability"). Might it be more appropriate to have two distinct P-lipid/total cellular P values for high and low phosphorus regions?

OUR RESPONSE»>We do in no way intend to imply that cells do not include P-lipids. Please see #3 for a detailed response to this point.

13) L215-216: For phospholipid substitution, a more appropriate reference would be Van Mooy et al 2009 "Phytoplankton in the ocean use non-phosphorus lipids in re-

sponse to phosphorus scarcity" instead of Van Mooy et al 2006.

OUR RESPONSE »>We have added the Van Mooy et al. 2009 reference.

14) L228: add "et al." after Daines

OUR RESPONSE »>We changed this in the document.

15) L282: . . .that underlies the subtropical gyres and equatorial upwelling regions (labeled M), and deep waters. . .

OUR RESPONSE »>We changed this is in the document.

16) L314: "Iron limitation is implicitly simulated through its control on the tropical [P]. . ." – how does iron control phosphorus concentrations? This is not clear in the manuscript and I personally have not come across any such research stating such. Again, if you are going to keep iron in the manuscript please provide references of where you have gotten the information and expand on the explanation of how you can make this justification.

OUR RESPONSE »>Iron was removed from the manuscript and only discussed briefly in the discussion section.

17) Table 2: Please switch the columns so that Range of fhd (sv) is first and references is second (will be consistent with Table 1).

OUR RESPONSE »>We have switched the column to be consistent with Table 1.

18) L350: "This set of experimental runs was intended to capture the effects of changing levels of iron deposition. . ." – Again, talking about iron deposition in these tropical up-welling regions does not make sense and as you have not provided references I would just remove it all together. This experiment wanted to test the sensitivity of pCO₂ to nutrient availability, I believe that is a good enough reason and there is no need to mention iron limitation.

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OUR RESPONSE »>We agree with this reviewer that and have removed this reference to Fe limitation.

19) L377: Change variables to variable

OUR RESPONSE »>We changed this in the document.

20) L379: Remove "iron stressed"

OUR RESPONSE »>We changed this in the document.

21) Figures 6 and 10: I really like these figures and think you could include more in the discussion about the implications of how global temperatures will affect export. It is a nice way to tie your work with large scale impacts on biogeochemical cycles and reiterate the importance of the study.

OUR RESPONSE »>We completely agree this with observations. We hope to expand on the potential implications of global temperatures effect on export based on findings.

22) L477: add "the" before data

OUR RESPONSE »>We changed this in the document.

23) L589: remove iron-limited

OUR RESPONSE »>We changed this in the document.

24) L596: remove "iron deposition or"

OUR RESPONSE »>We changed this in the document.

25) L600: remove sentence "This observation suggests that pCO₂ may have a complex link: : :". You honestly have not shown anything to do with iron delivery and its link to pCO₂, there is nothing included in the model that I saw and again have provided zero references about iron deposition

OUR RESPONSE »>We agree with the reviewer, it has been removed from the docu-

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ment. Instead, we linked it to macronutrient availability.

26) L650: remove "thus"

OUR RESPONSE »>We changed this in the document.

27) L674: remove "which might be influenced by increased atmospheric iron deposition,"

OUR RESPONSE »>We changed this in the document.

28) L680: change separating to separate

OUR RESPONSE »>We changed this in the document.

29) References: There are a few references that are not mentioned in the manuscript. A couple are about iron cycling and I am curious if and where they were originally included and also possibly had more of an explanation associated with them of why you link iron to phosphorus? Cunningham and John 2017 Moore 2004 Raven and Falkowski 1999 Also, please move Van Bogelen and Neidhardt 1990 and Van Mooy et al 2008 references to after the Toseland et al 2013 reference

OUR RESPONSE »>We apologize for the missing use of these references. This has been fixed in the manuscript.

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