We would like to thank our reviewers for their insightful comments and suggestions. Both reviewers suggested that we give more discussion to the topic of comparative nutrient-limitation and competition between phytoplankton, and we have added two new figures and extended text to our discussion that highlights the different niches of our diazotrophic population.

Referee #1 also points out that throughout our manuscript, plume communities are often compared to salinity, which does not directly impact the plankton. This is an important point and we do not intend to mislead readers, so we have made several alterations to make this more clear. Salinity in no way interacts with the planktonic communities in our model. However, salinity is a conservative tracer for the physical dilution processes that shape much of the biogeochemistry (and hence ecology) of the Amazon River Plume. Hence it is useful to show the evolution of various populations and rates in the salinity domain.

In a pdf supplement we respond to each of the specific comments of our referees. Please note that all references to our modifications to the manuscript are section and paragraph references to the new manuscript, since we cannot see the formatted version (with line numbers) until after we have submitted this response.

Anonymous Referee #1

Received and published: 8 November 2013

The manuscript "Top-down, bottom-up and physical controls on diatom-diazotroph assemblage growth in the Amazon River Plume" by Stukel et al. uses a regional biogeochemical model to investigate the factors controlling the development of diatomdiazotrophs assemblages (DDA) blooms. The authors find that DDA blooms are associated with prolonged retention time within the silica-rich waters from the Amazon River Plume (ARP) and a reduced grazing pressure.

The study is interesting and deals with important issues related to the controlling factors and fate of DDA that are still poorly understood and, as such certainly deserves publication. On the whole the paper is well written. However, I have some concerns that leave place for improvement:

General comments:

1) The authors claim (page 13933, line 13) that a bottom-up mechanism suggested by Subramaniam et al. (2008) cannot explain the the DDA dominance over UMD. Thus, they hypothesise a top down control that limits UMD growth relative to DDA in lownitrogen mesohaline waters. However, the inter-specific competition for nutrients (see equ. 4 and 8) may well explain DDA dominance over UMD (given enough P and Si, as the authors state on pg 13950 line 27/28) and the successional patterns or competitiveexclusion (page 13952 line 4/7) observed along the ARP.

I suggest that an assessment on how competitive outcomes shape community structure is needed to conclusively differentiate between the contribution of bottom-up and top-down controls.

This is a good suggestion, and we have added an extensive section to our discussion that looks at the relative nutrient-dependencies of each of our phytoplankton taxa across the model domain (last two paragraphs of section 4.1 and new figures 11 and 12). It is important to note, however, that top-down control on a population can exist even while nutrient-limitation structures the diversity of the phytoplankton. Competitive exclusion, in a rigorous sense, is incredibly uncommon amongst pelagic phytoplankton, because (unlike terrestrial and benthic systems) the ocean is dilute. There is no competition for space, but instead the limiting substrates are dissolved nutrients which can never actually be drawn down to zero. Thus, particularly with Monod-type nutrient kinetics, taxa will never be truly excluded by competition with other phytoplankton.

2) Although salinity may be convenient parameter to compare model results with observational data (Subramaniam et al. 2008) the analysis of this parameter promotes the idea that salinity gradients affects directly DDA and mesozooplankotn growth (eg. pg 13947/8). Salinity gradients fail to explain the mechanisms that are at work, and for an in-depth analysis of the controlling factors that promote DDA blooms nutrient gradients should be discussed instead. The authors do recognise that salinity gradients are "coincidental and not causative" however they fail to discuss the "causative" factors. One example is (pg 13947 line16 onwards): the emphasis on DDA growth and mortality rates covariances with salinity distracts the reader from the mechanism controlling the reduction of mesozooplankton biomass that initiates the DDA bloom. The causes of this reduction are not not comprehensively discussed. The authors suggest that physical dilution is playing a role however, the contribution of other factors, such as the decline of diatoms biomass which is in turn ultimately likely related to Si decline, are not discussed. The authors do not provide a comprehensive analysis and enough convincing arguments in support of their conclusion.

The causative mechanisms of DDA bloom formation in our model are discussed thoroughly in sections 3.3 and 4.2. Succinctly:

1) DDA bloom formation results from a decrease in grazing pressure as the diatom bloom weakens further from the river mouth, combined with a low dilution rate which allows time for the DDA bloom to occur.
2) Bloom termination occurs due to Si-limitation at higher salinities. Si-limitation is induced not by biological drawdown, but by physical dilution with low-nutrient oceanic water.

We do not intend to imply that salinity in any way directly affects phytoplankton growth rates – it certainly does not, and in order to decrease the likelihood of such confusion, we have made several clarifications (e.g. last sentence of section 3.2, last sentence of the 4th paragraph of section 3.3, 2nd to last sentence of 4th paragraph of section 3.3). However, we believe that it is valuable to structure our plots as well as much of our discussion around salinity. Salinity is a conservative tracer (in the plume region) for the physical dilution process that dominates much of the biogeochemistry of the plume. Thus showing that a variable co-varies with salinity is not a spurious correlation, but in fact demonstrates that its dominant removal process is physical dilution.

The reviewer is concerned that we focus too much on salinity and physical dilution rather than considering the causes that lead to decreases in diatom biomass. However, the decrease in diatom biomass along float trajectories is predominantly due to physical dilution, which can be best assessed by comparing to salinity (the conservative tracer for this process).

I think that the paper would benefit from from an in-depth discussion of the factors that directly affect community structure and not on spurious correlations with "coincidental" parameters.

We agree that it is important to delineate how the plume evolution along the S gradient structures the nutrient ratios and concentrations, thus we have added an in-depth section looking at community structure throughout the model domain to section 4.2.

However, the primary goal of this manuscript was not to investigate community structure, but to determine when, why, and where DDA blooms form. When addressing this primary question it is important to keep in mind that there is no direct competition between phytoplankton in our model (and likely little direct competition between phytoplankton in the dilute ocean either). Rather phytoplankton interact *only indirectly* by drawing down nutrients and serving as prey for zooplankton. Thus our calculations of growth and grazing rates are a much more direct method of studying bloom determinants than comparing DDA to other phytoplankton taxa.

3) The study is motivated be the important potential role DDA have in enhancing C export. However, this is nowhere discussed and it would be nice to see some discussion on this issue. Also, how do the model results compare to regional N2 fixation rates?

The role of DDA in C export is an incredibly relevant topic, but beyond the scope of this manuscript. In this manuscript we were focused on the ecological, biogeochemical, and physical controls of DDA bloom formation. In a following manuscript we plan to couple this model to an explicit carbon model and a new production model to accurately assess the role of DDA in CO_2 drawdown, new production, and the biological pump.

We have already compared the model's N_2 fixation rates to in situ measurements in sections 3.1 and 3.2. The model does a reasonable job of predicting average N_2 fixation rates, though it does not generate the rare extreme blooms of nitrogen fixers.

Specific Comments:

1) Section 3.3: To investigate the successional patterns along ARP It would be nice to see how nutrients, phytoplankton and zooplankton biomass develop along the float trajectories. I would suggest adding plots of these parameters similarly as done in Fig. 6b for DDA.

We have added these plots.

2) As discussed above, to assess the "causative" factors that control DDA bloom formation Figure 7 and 8 would be more informative if showing parameter variability as a function of Si concentrations, N/P ratios and diatoms concentrations along the lagrangian float trajectories

Since Si, N/P and diatoms do not perfectly co-vary, this would require the generation of significantly more plots, which we feel is largely unnecessary since the two standing stocks that drive these patterns (Si and mesozooplankton) both largely co-vary with salinity.

3) Section 3.4: The authors put a lot of effort in making sensitivity experiments. However the results presented in Figure 9 are very condensed and hard to follow. I would suggest to put more focus on the parameters that are central to the paper (DDA, mesozoopankton, diatoms).

We have added more discussion of the effect of grazers on diatoms and cyanobacteria (middle of the 3rd paragraph of section 3.4).

Most parameters appear insensitive to changes in the phosphate half saturation constant and in phosphate river supply suggests that phosphate concentrations were never limiting phytoplankton growth? How does that compare with observations? I think this merits further discussion.

We have added slightly more discussion of the model's riverine phosphate sensitivity to section 3.4 (end of paragraph 2) and also added a significant section looking at phytoplankton limitations to section 4.1 (last 2 paragraphs).

4) Page 139937 line 10: there is an inconsistency, the term nTheta_L should be is ntheta_L (small caps).

Thank you. Corrected.

5) Table A1: The DDA growth penalty symbols are inconsistent and have been switched?

Thank you. Changed ϑ_S to ϑ_L

Anonymous Referee #2

Received and published: 24 November 2013

In this article the authors explore the reason for the diatom-diazotroph assemblages (DDA) bloom in the Amazon river plume. The authors nicely find that it is not only bottom up pressures (i.e. availability of needed nutrients) that lead to these blooms, but in particular the blooms occur when grazing pressure dips further from the river nutrient loading. Long periods in suitable water is needed as the growth rates are so slow. This combination of effects, and following of Lagrangian particles to elucidate the competing effects is really nice. I do however have some reservation on the document and suggest some improvements.

The major comment I have is:

Though the article makes a point that it concentrates on the DDA, I think it would be a lot better if more attention was given to all the diazotrophs. It is important to consider the results found here in context of the other diaztrophs and the model shows distinct geographic distribution of the 3 types of diazotrophs. The authors make much that their model includes 3 types of diazotrophs while other model usually have just one: this begs the question of how do they all exist in the model: what is special about each that leads it to live where it does. It would be very nice to have a more complete explanation of why each diazotroph exists where it does, which develop blooms and which do not. This could even be done in context of the Lagrangian particles: when/where do other diazotrophs take over; what are the grazing/nutrient pressures on each when there are switches in dominant types. Though the paper can still concentrate on the DDA, knowing more about the other competing species would put these results into better context.

Things that seem to be important to understand: how important is the fact that DDA grow faster when nitrate replete, while other diazotrophs do not? Though the sensitivity experiments have some interest (though see below) it does not test such on/off type switches. What happens if DDA have only one maximum growth rate etc. How important are the different growth rates versus different grazing levels impact the ditributions? How important are the relative assumptions in grazing needs and nutrient needs?

Thank you for these suggestions. We have added a significant new portion to section 4.1 (last two paragraphs) and two new figures (fig. 11 & 12) to address the differences in nutrient-limitation and niches of the five phytoplankton taxa in our model.

We have also added to our discussion of the sensitivity analysis. However, it is not feasible for us to deal with possible alternate constructions of the model (e.g. alternate formulations of nutrient limitation or grazing). We have however tested the effect of having a single maximum growth rate for the DDA (aka no enhanced growth when nitrate is replete). Using a single maximum growth rate (e.g. parameterizing growth rates similarly to UMD or Tricho) of 1.5 d^{-1} (instead of 2.0 when nitrate is replete and 1.0 when growing diazotrophifcally) had relatively little effect on the model when run over a 4 month period. It led to less than a 5% change in basin-wide DDA concentrations, although slightly increased DDA NFix rates contributed to a slight increase in DIN in the mesohaline region and a 20% decrease in DDA concentrations in the mesohaline region.

On more minor points:

- It would be good to have a paragraph in the introduction which gave a fuller description on the three diazotroph types, especially DDA's as they are less well known. This would then connect to the model description and provide an explanation of model choices (e.g. why DDA have two coefficients reducing the maximum growth rate)

We have added a paragraph about DDA to the introduction (3rd paragraph) and also added an explanation in the method about why we gave DDA two growth rates (immediately following eq. 6). (Since the diatom hosts of DDA can be found free-living without their endosymbionts, it is likely that they may behave more like other diatoms during nitrogen-replete conditions.)

- there is very little observations of DDA's blooms: so much of the results here are just "model" - I think a little more attention should be given to this point (a few more sentences).

We have given this point some attention already (e.g. 13% of our conclusion section is devoted to pointing out that the paucity of in situ data left parameterization of the model underconstrained – 5th sentence of conclusions). We do believe this is an incredibly important point however (focused studies are needed!) and have and have added a sentence in section 4.2 (end of paragraph 3) to reiterate this point.

- A matter of taste, but I found the number of acronyms very hard to follow. Since they are not mentioned often it would be less confusing to write out in full ARP, WTNA etc.

We have removed WTNA and fixed our inconsistent abbreviations of *Trichodesmium* and non-diazotrophic diatoms. However, most of our acronyms are used many times (e.g. ARP is used 50 times), so removing them would significantly lengthen the manuscript and also disrupt the flow of many sentences.

- Though I appreciate the sensitivity experiment I have some concerns: 4 months seems very short (though I understand the computational cost) - but would some parameters appear more important in the longer term (e.g. riverine N, P etc). As mentioned before, there is no test on on/off type parameters, or on differences (e.g. if remineralization on N and P were not so different): these could be considerably more sensitive. I find Figure 9 hard to follow, especially given the poor resolution. But it also only looks at gross values - not for instance in changes in distributions and patterns that given the nature of this study may be more important.

The truth is that an entire study could be done on the sensitivity analyses of any particular model (and several such manuscripts have been written). Our goal was to assess which parameters are particularly important and hence need focused laboratory research to measure. We would have liked to run our sensitivity analyses for longer, but it took us a full day of computer time for each four month run – thus running two year sensitivity analyses for each parameter we tested would have taken over 8 months. We have, however, significantly increased our discussion of the sensitivity analysis as well as added some additional notes about model sensitivity that we discovered during initial model tuning.

- Though probably from my own ignorance, I also had some difficulty following the discussion of Figure 10. The authors state that the nutrients separate based on DIP:DIN ratios. I can't quite understand how they see this on the figure. Other comments made on this figure are also a bit difficult to see. I suggest a bit more discussion of what aspects of the figure should be looked at to see these points for those of us with limited understanding of PCA. It would be a pity to lose the insight gained from this analysis.

We have tweaked the PCA section slightly in hopes of making it more intelligible. More importantly, we have added two new paragraphs following the PCA section (and two additional figures), which address the same topic with more traditional approaches.

- line 26: what do you mean by "loading score"

The loadings (or loading scores) of a PCA are the weightings that map the (transformed) data onto each principal component. Basically, if the absolute value of a variable's loading is high, then variability in that variable contributes significantly to that principle component. If the absolute value of the loading is low, the variable does not contribute much to the principle component Variables that have opposite signs are uncorrelated in their projection onto the principle component of interest.

- table 1a: N:P ratio of diaz is repeated twice

Thanks. Corrected.

- why are UMD and DDA "growth penalty" different? (Occam's razor approach would suggest they should be the same).

UMD and DDA have very different biology and growth kinetics. DDA are an endosymbiosis between a diatom host and a diazotrophic cyanobacterium for which it (presumably) creates an ideal habitat niche. In our opinion, Occam's razor would suggest that DDA growing diazotrophically (e.g. supplementing their nitrogen requirements solely through the *Richelia* endosymbiont) would have a growth maximum equal to that of UMD (e.g. in our model $\mu_{small} \times \vartheta_S = \mu_{large} \times \vartheta_{Nif}$). However, since DDA presumably create an ideal niche for *Richelia* it is reasonable to assume that Richelia is outperforming free-living UMD (e.g. $\mu_{large} \times \vartheta_{Nif} > \mu_{small} \times \vartheta_S$). Practically, we found that the trade-off between cyanobacteria and UMD in the oligotrophic gyre was very sensitive to the value of ϑ_S and tuned this parameter to generate realistic distributions of cyanobacteria and UMD. We have added some text to the sensitivity analysis to make this more clear (last paragraph of section 3.4).