# Response to Reviewer #1

We thank the reviewer for their careful reading of the manuscript, and constructive suggestions. Below, the original comments of the reviewer are quoted verbatim, and our responses are provided right after each comment.

*"General comments*
*The manuscript describes three variants (FS, IA, and DA) in a biogeochemical model (FABM-NflexPD) coupled with a hydrodynamical model (GOTM). It clearly describes the differences between a fixed stoichiometry (FS) to more complex variants considering a dynamic acclimation (DA) and an instantaneous acclimation (IA).*
*Based on an idealized set up, the response of each model variant to irradiance and temperature is studied. Results show that adding higher complexity to the model creates differences in the model output that cannot be negligible. It is an interesting manuscript related to the scope of the journal and model development.*
*Overall, this manuscript presents an interesting approach to understand the dynamics of adding a flexible stoichiometry. However, the authors pose two objectives for this manuscript that are not fully addressed, so it is suggested that more discussion is added to fully address the objectives specified. It is also necessary that the authors specify why they used an NPD model instead of the NPZD model available from the FABM library. Moreover, I think the manuscript is lacking a more extensive discussion (or conclusions) about the novelty of this work, which could be done by, for example, extending the discussion (or conclusions) to explain why this work is relevant, given the model development is interesting but there is not a comparison to observations. Under the idealized set up of the different model variants created in this work and without comparison to observations, the authors should clearly state the applicability of their work and why it is important to have an IA variant considered in further biogeochemical modeling research.*
*This manuscript is within the standards of excellence of the journal, but the authors should address the comments suggested here."*
Response: we will extend the discussion to better communicate how the objectives are met, novelty of the work, applicability of the model and reasons to consider acclimation in biogeochemical modeling research. Regarding not having used an NPZD scheme, but an NPD scheme: indirect effects of zooplankton make it difficult to understand the direct effects of including acclimative mechanisms, please see our detailed response below to the comment for L450-454 in the Discussion section.

*"Specific comments*
*Introduction*
*L29 It is mentioned that acclimation models are now commonly used, but only Geider's model is included. Could it be added a couple more examples apart from Geider's paper?"*
Response: We will mention a few additional examples. We also realized that the example given for constant N:C and variable Chl:C ratio should not be Moore et al., (2002), where N:C was variable, but Moore et al. (2004), we will correct this.

*“L34-35 In the sentence ‘Models that account for variations in cellular composition are indeed more likely to provide more realistic estimates of phytoplankton biomass and biogeochemical fluxes’. Can it be briefly explained how are estimates provided more realistic based on the variable cellular ratios?”*
Response: we will explain that the estimates of the models with variable cellular composition become more realistic specifically with respect to comparison against in situ and satellite observations and biosynthesis, and consequently the drawdown of nutrients.

*“L38 clones/types – what is the meaning of this? Could it be specified what are clones/types?”*
Response: we will specify that these are ‘phytoplankton functional types or clones’.

*“L42 ... ‘response to changes in resource environment’ ... - please describe what those resources are.”*
Response: we will specify the resources as mineral nutrients and light.

*“L48-54 Please add the units of Q, fv, fA, and the Chl:C.”*
Response: we will add units for $Q$ [molN/molC] and $\theta$ (gChl/molC) and specify that $f_V$ and $f_A$ are dimensionless.

*“L59-60 What is short-term in this case? Please specify.”*
Response: we will specify that here short-term refers to hours to days.

*“L84-85 ‘Compared to the FS variant, do the results differ sufficiently to justify the additional complexities introduced by the IA variant?’ - I think this is an interesting question to set as an objective of this study. However, it is not fully addressed in this work (see further comments in the conclusion section). If the FS model provides significantly different results than the IA model, is that a justification to add further complexity to models? Under an idealised setup and with no comparison to observations, how can you tell that the differences found are answering to your question? Because of the obvious differences between FS and IA stated in section 1.4, it is expect that the results of the simulation will differ between both approaches. I suggest this question to be rephrased, as it is hard to justify IA over FS when there’s no comparison to observations, which would help the manuscript better ground the differences found. Also, add more about the answer to your objective (ii) in the discussion and conclusion section (see below comments for those sections).”*
Response: thanks for this careful observation. Although earlier work have provided ample evidence for the improved realism of variable cellular composition models as explained in the previous paragraphs of our introduction, without any comparison against observation data, we indeed cannot defend in the current study that the performance of the IA variant is better than the FS variant, which the objective (ii) itself implies presumptively by ‘.. to justify the additional complexities introduced by the IA variant’. In the revised manuscript, we simplified this objective as: ‘compared to the FS variant, do the results of the IA variant differ substantially?’. We will also mention that while answering these questions, we aimed at gaining mechanistic understanding of the dynamics driving the difference between the model estimates. Please see below for our response to the specific comments for the discussion and conclusion sections.

*“Model description*
*L128 Which mechanisms mentioned in the Introduction is this referring to? I am not sure to what section of the introduction to look. Could it be specified which section? Or mention those mechanisms in L128.”*
Response: We are referring to the section 1.2 in the introduction. We will refer to this section and mention these mechanisms explicitly.

*“L142, eq. 10 – Please describe what Qo is and reference where it is defined (Table 3).”*
Response: we will describe Qo and other intermediate terms appearing in the equation, referring to tables where they are defined.

*“L177 – Please describe what nutrient affinity is in this section.”*
Response: We will introduce the definitions for nutrient affinity, and what affinity and maximum nutrient uptake rate represent.

*“L203 – Add reference at the end of the sentence (Table 3).”*
Response: will do.

*“L248 – The sinking rate value was based on observations? Please say where was that value obtained from.”*
Response:we will indicate here that the value is chosen arbitrarily for this idealized setup to induce a downward vertical flux, and that in reality the sinking rates of detritus depends on the average size and density of detritus particles being modelled and displays a vast range (Guidi et al., 2008).

*“L254 – Mention the other meteorological variables assumed as constant.”*
Response: we will mention that the constant meteorological variables are wind speed, air pressure, humidity, cloud cover.

*“Results*
*L287 – can the authors extend the explanation about the effect of DIN depletion? Are the DIN depletion differences the only reason for the differences between Ln (FS) and fc (IA + DA)?”*
Response: in fact, differences between the $L_N$ (FS) and $f_C$ of the acclimative variants cannot be reduced to the differences in DIN because of the structural differences between how these quantities are computed, although they both serve in representing nutrient limitation of growth, thus they are functionally equivalent. But the incomplete depletion of DIN as simulated by the FS variant, and the high sensitivity of the Monod function (Eq.15) to the nutrients at low concentrations are the reasons for the $L_N$ values being not too low. This contrasts with the $f_C$ of IA and DA being close to zero, owed to $f_V$ being close to its maximum value of 0.5 and $Q$ being close to the subsistence quota, $Q_0$ (see Eq.11). We will extend our explanation accordingly (please see also our response to the comment for L312-313).

*“L291 – In the contour plot for the net growth rate, it looks as if FS has higher values during the spring bloom in comparison to IA and DA.”*

Response: thanks for noticing this, our statement does not apply for growth rate, but for nutrient uptake rate. We will reformulate this sentence accordingly. However FS attaining higher growth rates during the spring bloom indeed deserves some explanation: this is mainly caused by the lower whole cell chlorophyll respiration cost, $R_{Chl}$ of the FS variant than those of the IA and DA variants in the surface layers during winter/spring. Observing that $R_{Chl}$ is scaled from the chloroplast-specific $\hat{R}_{Chl}$based on $f_C$ (Eq. 25), the lower $R_{Chl}$ is a result of fixed $f_C$ of the FS variant (computed based on prescribed $f_V$ and $Q$) being lower than the $f_C$ of the acclimative variants (computed based on variable $f_V$ and $Q$) in the surface layers during spring (Fig. R1.1a, where the $f_C$ and $L_N$ of the FS variants are both shown, whereas in the manuscript, only the $L_N$ of the FS variant was shown. In the revised manuscript, we will use the version shown here). It should be noted that, when the chloroplast size of the FS variant is assumed to be variable like the IA and FS variants, but based on the nutrient limitation term, $L_N$ as described in Appendix B (Fig.R1.1b, note that now $f_C$=$L_N$), $R_{Chl}$becomes higher at the surface layers, and as a result, net growth rate, $\mu$ shrinks, and is not any longer higher than those of the IA and DA variants, as shown below in Fig.R1.1c,d). We will explain these in the revised manuscript, and extend Figs. 7 and B2 with the panels c-d in Fig.R1.1, respectively

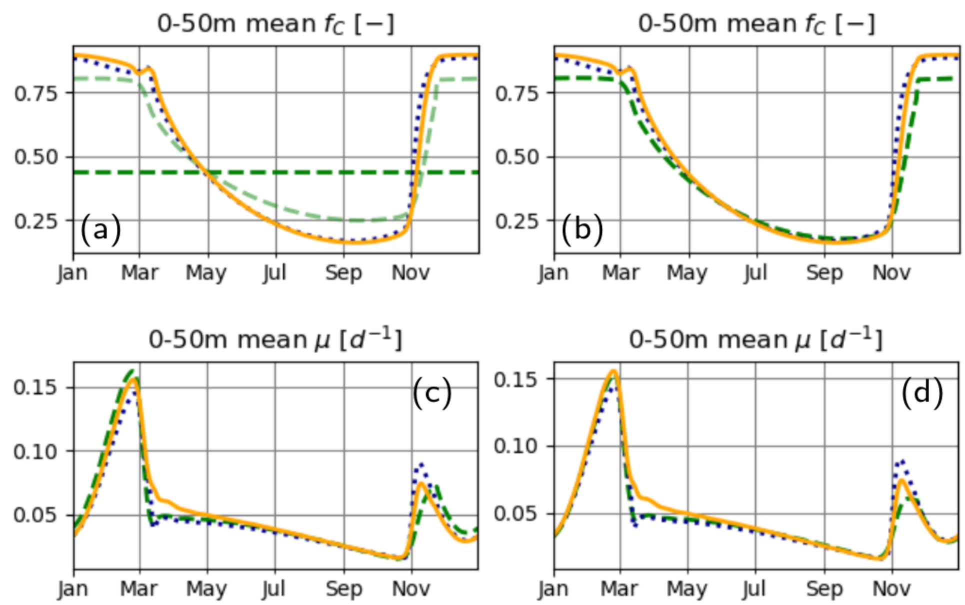


Figure R1.1. Upper 50 m average (a-b) $f_C$ [-] (and $L_N$ [-] for FS) and (c-d) $\mu$ [d-1], as simulated by IA (fine-dashed dark blue line), DA (continuous orange line), (a, c) default FS (dashed green line; in panel a, $L_N$ is shown with pale dashed green line. Note that in the Fig.7c of the original version of the manuscript, the prescribed $f_C$ was not shown, and only $L_N$ was shown) and (b, d) FS with variable chloroplast size (as described in Appendix B).

*“L300 – Which sensitivity experiment?”*

Response: these results were not shown, we will indicate this at the end of the sentence.

*"L304-305 – saying 'before the onset of winter mixing' is vague. Do the authors mean one day before, the week before? I suggest it is specified which day/date this is. Moreover, it is confusing to see how 'substantially' higher are the values of DIN for the FS variant in comparison to IA and DA variants. To avoid confusion, please also specify what the DIN values are for the FS, IA, and DA variants before (insert date here) the onset of winter mixing. I can see there are differences during the summer period for DIN, but is that a substantial difference? Beware of the adjectives used if there is not a quantitative comparison."*

Response: we will mention `early November' for the onset of winter mixing and refer to Fig.7a. In the parenthesis L305, we will specify the exact DIN concentrations estimated by each variant on the date the minimum concentrations are reached). Relevantly, recognizing the ambiguity in references to both times of the year and quantities in the contour plots, we will include an additional figure that shows the vertical profiles at different times of the year (exemplified for a summer profile in Fig. R1.2.

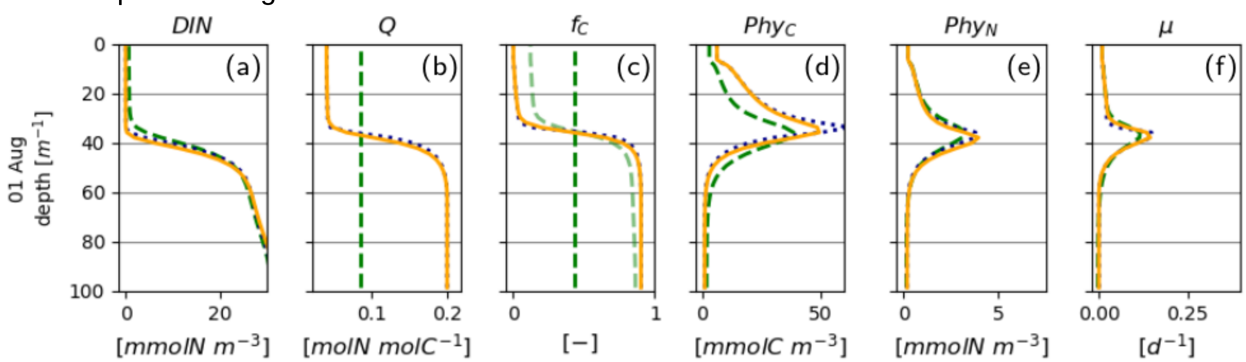


Figure R1.2. Summer (as represented by August, 1st) vertical distribution of (a) DIN [mmolN $m^{-3}$], (b) phytoplankton *Q* [molN $molC^{-1}$], (c) resources available for carbon fixation, $f_C$ [-] (and $L_N$ [-] for FS, shown with the pale green dashed-line), (d) $Phy_C$ [mmolC m−3], (e) $Phy_N$ [mmolN $m^{-3}$], and (f) $\mu$ [$d^{-1}$], as simulated by the FS (dashed green line), IA (fine-dashed dark blue line) and DA (continuous orange line) variants.

*"L312-313 – the differences between Ln (FS) and fc (IA, DA) are large to be only explained by small differences in the DIN during the summer period. Could the authors give a thought to that difference and explain it in a short sentence?"*

Response: Differences in DIN at the near-surface are stronger (e.g., minimum concentrations reached by FS and IA/DA variants are 0.005 vs 0.7 mmolN $m^{-3}$, respectively) than suggested by the top 50m averages shown in Fig.7c. Besides, as explained above in response to the comment on L287, the Monod function is strongly sensitive to the DIN at low concentrations. We will mention these as an extended explanation. We also realized that the last sentences in this paragraph can be potentially confusing therefore we will remove them.

*"L316 – Please describe more the differences between FS and IA, DA during the spring bloom. FS reaches a higher PhyC in March than IA and DA."*

Response: We agree that the differences between the FS and acclimative variants during spring and summer need to be better explained. Although the net growth rate estimated by FS variant becomes slightly higher those estimated by the acclimative variants (as explained above in response to comment to L291), differences in $Phy_C$ are greater. The main reason for this discrepancy is the decoupling of $Phy_C$ and $Phy_N$ in the acclimative variants vs. their constant proportionality as determined by the prescribed *Q*. As shown in Fig.7b, during winter and spring, *Q* of the acclimative variants become much larger than the constant *Q* of FS (computed as the biomass-weighed spatio-temporal averages of the *Q* estimated by the IA variant, see Table 3). This, in turn, translates into much higher concentrations of $Phy_C$ as estimated by FS, compared to those estimated by the acclimative variants, despite the fact that the $Phy_N$ concentrations are similar among the model variants. Although this was hinted by the Fig.4d-f, a direct comparison of top 50m average concentrations, as shown in Fig. R1.3b below makes this clearer. The critical dependence of $Phy_C$ of the FS variant to the prescribed value of *Q* was more clearly illustrated by a sensitivity experiment we conducted, where the FS variant was run with twice the default value of *Q*. This results in a dramatic reduction of simulated $Phy_C$ (Fig.R1.3d) without much difference in other quantities like DIN (not shown), $Phy_N$ and $\mu$ (Fig.R1.3e-f). In the revised manuscript, we will explain the differences in FS and acclimative variants along these lines, extend Fig.7 with $Phy_N$ and will mention the experiment with doubled constant *Q*, and possibly include the resulting equivalent of Fig.7 in an additional appendix.

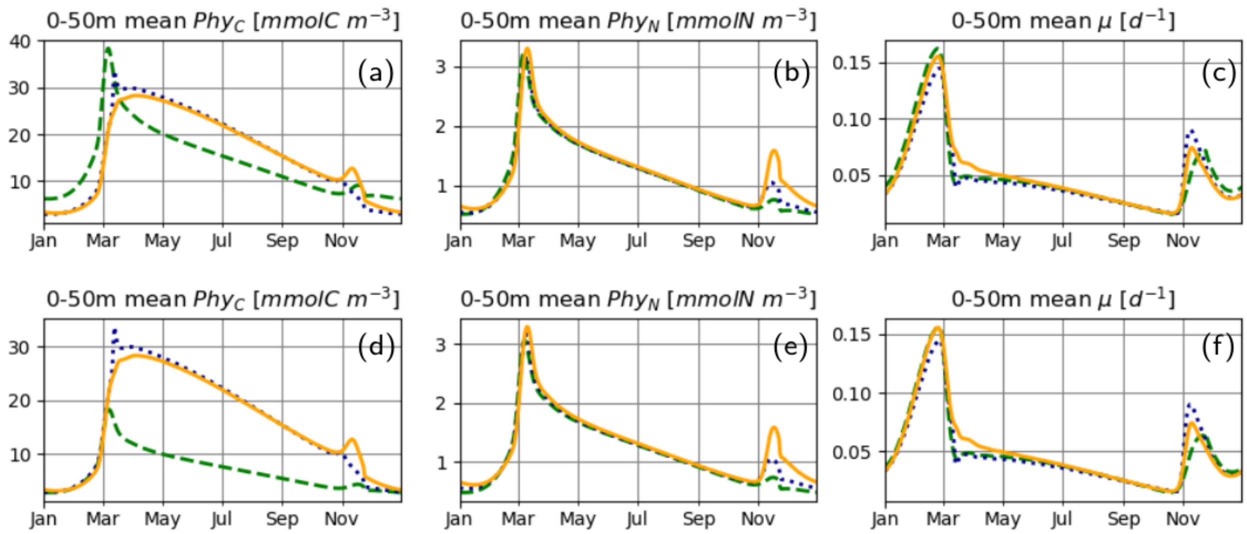


Figure R1.3. Upper 50 m average (a,d) $Phy_C$ [mmolC m$^{-3}$], (b,e) $Phy_N$ [mmolN m$^{-3}$], and (c,f) $\mu$ [d$^{-1}$], as simulated by IA (fine-dashed dark blue line), DA (continuous orange line), (a-c) default FS (dashed green line) and (d-f) FS with doubled constant Q.

*"Discussion*
*L344-352 – the discussion in this paragraph mainly focuses in 3-D models, but this work considers a 1-D approach. For L349-350, the authors mention 'Recent applications of these models in 3D setups with realistic forcings (Kerimoglu et al., 2017; Pahlow et al., 2020) have indicated that accounting for acclimation enhances the ability of models to reproduce field observations.' I suggest to also giving examples of 1-D models that have been developed with flexible stoichiometry (photo-acclimation) and have been compared to simpler variants and have been a better fit for field observations."*
Response: Response: we will point to such examples (e.g., Christian, 2005; Ayata et al., 2013; Chen & Smith, 2018), including our own study that recently appeared (Anugerahanti et al., 2021, which was previously cited as 'in prep.'). Here we will also mention the utility of 1D setups in examining the behavior of model components in a cost-effective way (as was suggested in the next comment on the L365).

*“L365 – If computational costs were nearly negligible for the different variants in this work, adding a further state variable (e.g. zooplankton, phosphorus, etc) would have made the model more realistic and it would have been interesting to look at further biogeochemical processes in each of the variants and how they respond to the complexities added. I would suggest adding some thoughts in this paragraph about the importance of a 1-D model in terms of time- and space-effectiveness when referring to computational costs and to mention why not more state variables were added or if that is part of future work.”*
Response: in this study, we chose a minimal setup for the sake of achieving a better understanding of the direct effects of the flexibilities involved in phytoplankton growth and nutrient uptake, and how these are modeled. As we explained below (in response to the comment on L450-454) in detail, inclusion of other food web components like zooplankton would make the model analysis substantially more difficult, and potentially inconclusive. We agree also that it is worth mentioning that computationally efficient 1-D setups are valuable environments by virtue of capturing the vertical structure of resource gradients, which has a determining role in functioning of the marine and aquatic systems. We will mention this in the context of earlier 1D studies regarding the phytoplankton acclimation (see our response to the previous comment on the L344-352). We had explained why phosphorus is not included in a paragraph in section 4.4, which we will reformulate this paragraph to make things more clear. Considering the comment below on the L416-419, we will include here the future plans of including P in the model in future work, and the relevance of this extension.

*“L387-388 ‘However, improvements in these specific aspects typically result in greater discrepancies in other aspects, such as the timing of the spring bloom, or winter concentrations of nutrients and phytoplankton.’ - Was a different tuning of parameters tried? In Table 3, from the papers the authors used, how was it decided, which value to use? Was it a mean of all the estimates or different phytoplankton species? Could it have been a better tuning for the FS variant without facing higher discrepancies in the output? I suggest that in the caption of Table 3 it is specified about how that data was obtained from those two papers and mention in this section of the discussion if different parameterisations were tried and what issues were encountered. Currently, it sounds as if the higher discrepancies due to tuning are only an idea and not something proven.”*
Response: In Table 3, the parameters were chosen as typical values from within the previously published range of values without particular reference to species, which we will clarify in the caption. We have extensively investigated the effects of parameters, but reporting of these results would be outside the scope of the current work. In fact, the observation stated in L387-388 was based on our work in tuning the FS and IA models against the observations in two oceanic sites, which we presented in a study that recently appeared (Anugerahanti et al., 2021), which was previously cited as `Anugerahanti et al’ (‘in prep’ was omitted). Implications of particular choice of parameters, and investigating the behavior of models under different environmental conditions (which we have also partially explored, as hinted in L362-X) remain to be open questions, which we will mention explicitly.

*“L416-419 – Comparing to N:P ratios it is hard in this manuscript as the model does not include P. I suggest including more discussion about how the different variants would affect the N:P*

*ratio even if P is not a state variable in the model. This could be phrased as future work if the authors have interest in a follow-up for the N:P ratio."*
Response: We agree that discussing the N:P is difficult within the context of the present work, and while it is indeed the case that we are intending to address the N:P in a follow-up work, a discussion of this issue would be a source of distraction here. The statement here was regarding the qualitative role of acclimation in resource limitation. We will revise this sentence without particular reference to the N:P ratio, but will mention the plans on including P in a future study in a more fitting paragraph in section 4.4 (see our response above to the comment on L365).

*"L450-454 – Why was the NPZD model not used for this manuscript? Zooplankton is relevant for phytoplankton growth, especially in a location such as the one chosen in this manuscript, where seasonal changes are relevant. I think that there should be a strong justification as to why the NPZD model available from the FABM library was not used. How would the results be expected to change with an explicit zooplankton in each variant?"*
Response: As mentioned above, we chose a minimal setup in this study for being able to concentrate on the direct effects of the flexibilities involved in phytoplankton growth, and how these are described in models. Including zooplankton would have introduced indirect effects and complicate the model analysis. While being interesting and relevant in a broader context which we partially would like to address in follow-up work, having to deal with these intricacies would make it difficult to achieve our objectives of the current study. It is worth noting that the IA model can be comfortably coupled to a zooplankton module, based on our experience (Anugerahanti et al., in preparation). Coupling to zooplankton, in turn, would allow investigating how these bottom-up effects propagate through the food-web, and influence the ecosystem functions in a cost-effective way. We mentioned these in the extended discussion. We will mention these in this paragraph.

*"Overall, I think there should be a paragraph added with more discussion about the objectives set in this manuscript. Where the objectives fully addressed in this work?"*
Response: We believe that the stated objectives were addressed in this work, especially after revising the second objective following the suggestion of the reviewer, as explained above. The differences between the model variants are extensively discussed already in section 4.2. Therefore, we do not see the need for a repeated discussion on whether the objectives are met.

*"Conclusions*
*L472-479 – It is not necessary to mention again that information as it is clearly stated in the introduction and model description sections."*
Response:  we intended to provide here a wrap-up, but agree with the reviewer that it is too repetitive in its current form. Therefore we will condense this part.

*"For the conclusion, can the authors conclude more in terms of the objectives of the manuscript (section 1.4)? How do the authors justify the IA model without comparing it to observations and under an idealised set up? It is better or just different? If this is discussed in more detail in the*

*discussion section as suggested, then adding a couple of sentences about this in the conclusions would create a good closure for the manuscript."*
Response: As explained above, in the current study, we cannot argue that the IA model is better, but we show that it is substantially different, and as such, we will have fully met the second objective (in its revised form). However, we agree that a closure with reference to the specific objectives would indeed be good. We will revise the second paragraph accordingly.

*"Code availability – Please add the Zenodo link in this section."*
Response: we will add the Zenado link.

*"Technical corrections*
*Table 1 – in the Expansion/Value column, first row, do you mean* $Phyto^2_N$ *or* $Phyto_N$*?"*
Response: $Phy^2_N$ as typed is correct, as this is a quadratic mortality term (see the units of m in Table 1).

*"L127-132 – please be consistent with the quotation marks when you mention each model variant."*
Response: we will include the missing quotation marks.

*"Table 2 – What are the blank spaces representing?"*
Response: in fact there are no blank spaces: for instance Eq.(5) in the second row applies to all 3 variants. However this is indeed not clear when the vertical lines are not shown. In the revised manuscript, we will include the vertical lines if allowed by the journal, otherwise we will write equations for each column.

*"Table 2 – For dimensionless variables, please write 'dimensionless' instead of a hyphen"*
Response: we considered this suggestion, however we are concerned that this will just lead to unnecessary crowding of the tables and figures. According to the International System of Units (SI), the recommended unit for dimensionless quantities is 'one', but we think this can be even more confusing than the hyphen. At the end, given the clarifications in the caption, we are convinced that there is no room for confusion anyway, therefore would like to keep the hyphen.

*"Table 2 – for the units with (**), it is inconsistent to put gChl mol C-1. Table 2 caption states that they are in gChl gC-1."*
Response: gChl gC-1 is used only for presentation (eg in figures). But apparently this note in the caption leads to confusion, therefore we will remove it.

*"Table 2 – Why are there Equations being named in the middle of the columns? Such as Eq. 14, Eq. 18, Eq. 26, Eq. 11 and the last NA? If they correspond to both IA and DA, please specify it in each column. Otherwise, it is fairly confusing."*
Response: yes, the referred equations apply to IA and DA, but we understand the concern. If allowed by the journal formatting requirements, we will include vertical border lines, otherwise we will specify equations for each column.

*“L237 – The authors mention Eq. 23 and Eq. 17, is this correct? I think instead of Eq. 23, it should be Eq. 28. Please correct me if I am wrong.”*
Response: you are right, the correct reference should be Eq.28. In fact, the correct reference for the equation needing I should be Eq. 22 and not Eq.17. We will correct these.

*“L243 – n2 = 17m. Missing the n (greek letter).”*
Response: we will include it.

*“L274 – Fig 4 h-i instead of Fig 3 h-i.”*
Response: will do.

*“L282 – Fig 5 e-f, h-i instead of Fig 5 e-f, h-j”*
Response: will do.

*“L283 – Is it Fig 5 j-l instead of Fig 5 n-o? Fig 5 n-o is for light limitation.”*
Response: yes, we should have referred to panels j-l

*“Figure 5 caption – for dimensionless variables/parameters, write ‘dimensionless’ instead of a hyphen."*
Response: as indicated in our response above to the comment for Table 2, we would like to keep the hyphen.

*“Figure 6 – subplot (4,3,7) – change (h) for (g).”*
Response: thank you, we will change it.

*“Appendix A, L501 – subscripts for growth and Q should be a multiplication (last term in Eq. A1).”*
Response: will correct this.

We would like to thank the reviewer again for their very careful reading and patiently helping us in eliminating technical errors.

**References:**


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