Biogeosciences

Biogeosciences Editorial Office

Dear Co-Editors-in-Chief and Associate Editor,

Please find attached the revised version of our manuscript "*Poor correlation between phytoplankton community growth rates and nutrient concentration in the sea*" (bg-2014-439) to be considered as a review manuscript. We have carefully considered the constructive comments by the reviewer 2 in preparing the revised version of the manuscript. We have thoroughly revised the original version to address all the comments raised by the reviewers.

In particular, we discussed in detail about the limitation of our results considering the iron limitation from HNLC zone and the methodology bias for oligotrophic waters. We discussed also about the use of trade-offs between K_s and μ_{max} in modeling. We added new results of phytoplankton community growth rates data calculated from another methodology (primary production and standing stocks).

We believe, that as a result of these changes, the manuscript is now much improved relative to that originally submitted, and hope that you would find it now acceptable for publication in *Biogeosciences*.

Sincerely,

Dr. Aurore Regaudie-de-Gioux

Actions taken to accommodate the comments by the Reviewer 1

Reviewer #1*: This paper addresses whether natural phytoplankton communities follow Monod's model when growing to conclude it does not follow it because changes in the community composition and size structure.*
The paper is highly relevant as it implies the need to change phytoplankton growth parameterization in NPZD models. Or at least in those that consider phytoplankton as a whole. Even for models with several species it is important to understand if they reproduce something similar to a community in the range of sizes. It is interesting to observe that the fact that a community does not grow like one species has been overlooked for so long time. With phytoplankton accounting for half of the planets primary production this is an important result. The paper is simple, generally well written and illustrated

   Comments: We thank the reviewer for his/her comment and his/her positive feedback on our manuscript.

Actions taken to accommodate the comments by the Reviewer 2

Reviewer #2: *The authors sustain that the dominance of large cells in nutrient rich environments requires a parameterization different than the classical Monod kinetics. However, a tradeoff between half-saturation constant for nutrient uptake (Ksat) and maximum growth rate following Monod still would account for these patterns of community size structure. The authors ignore this potential trade-off between Ksat and max growth in the schematic representation shown in Fig. 1. From a theoretical perspective, it is unlikely that this species' configuration (shown in Fig. 1) can be maintained in a simple competition model.*

   Comments: We agree with the reviewer that the parameterization of phytoplankton growth and size without a trade-off between Ksat and max_growth is counterintuitive from a theoretical perspective based on simple competition models. Indeed, many models (e.g. Darwin model) are "forced" to use this trade-off otherwise small phytoplankton would outcompete large phytoplankton in the whole ocean (unless other constrains like top-down differences are introduced). So we agree with the reviewer that the species configuration in our Fig. 1 cannot maintain species coexistence in a competition model but the problem is that this theoretical perspective is in contrast with the empirical evidence on the size dependence of Ksat and max_growth. Indeed, much of our ms deals with this incoherence between competition theory and empirical data. The most up-to-date compilations on the size dependence of Ksat and max-growth do not reveal the existence of a trade-off between these two variables, so it is hard to embrace the theoretical requirements in a simple competition model. Edwards et al. (2012, doi:10.4319/lo.2012.57.2.0554.) found that Ksat increases with increasing cell size and V_{max} and μ_{max} decrease with increasing size. Our Fig. 1 is just a (simplified) representation of the empirical evidence collected so far and we agree that it is

counterintuitive from a theoretical perspective based only on bottom-up competition, but we cannot force empirical data to fit theoretical models, we believe it should be the other way round.

In our ms, in our Fig. 6 we do indeed analyse two different configurations of the Monod model that are close to the comment of the reviewer. In the first one we parameterize max_growth as a unimodal function of cell size (in line with some recent experimental data, Marañon et al. 2013, doi: 10.1111/ele.12052) in Fig. 6A and in Fig. 6B we parameterize our model with the trade-off the reviewer points out. As we discuss, both parameterizations lead to a Monod-like dependence of community growth rate, in contrast with what is observed from empirical data.

Actions: Following this reviewer comment, we now discuss in detail the uncertainties due to this trade offs, in particular we also note the implications that the recent empirical data have on our understanding of the trade-offs and how recent reviews have found "no mechanistic foundation for a trade-off conflict between the half-saturation coefficient and the maximum specific uptake rate." (Fiksen et al. 2013, doi:10.4319/lo.2013.58.1.0193).

Discussion section now reads:
"Many models (e.g. Darwin model) use a trade-off between K_s and μ_{max}—some organisms grow fast at high nutrient concentrations (high V_{max} or μ_{max}) and others may be better competitors at low nutrient concentrations with low K_s. Without this trade-off, small phytoplankton would outcompete large phytoplankton in the whole ocean unless other constrains are introduced (e.g. top-down differences). Although this trade-off would maintain species coexistence in a competition model, this theoretical perspective is in contrast with the empirical evidence on the size dependence of K_s and μ_{max}. Indeed, the most up-to-date compilations on the size dependence of K_s and μ_{max} do not reveal the existence of a trade-off between these two variables. Edwards et al. (2012) found that K_s increases with increasing cell size and V_{max} and μ_{max} decrease with increasing size. Furthermore, Fiksen et al. (2013) were unable to identify any mechanistic trade-off conflicts between K_s and V_{max}. In this work, we decided to parameterize empirical phytoplankton growth rate and size (Fig. 1) without accounting the trade-off between K_s and μ_{max} considering that recent empirical data do not reveal its existence."

Reviewer #2: *The authors suggest the possibility of size-differential grazing (page 3, lines 37-39), but this is only a speculation: the papers cited do not provide a quantification of this effect nor do the authors test it in their analysis.*

Comments: We agree with the reviewer. We did not expect to affirm the size-differential grazing but that could explain why large phytoplankton species dominate in productive ecosystems. In this work, we did not expect to quantify the size-differential grazing effect.
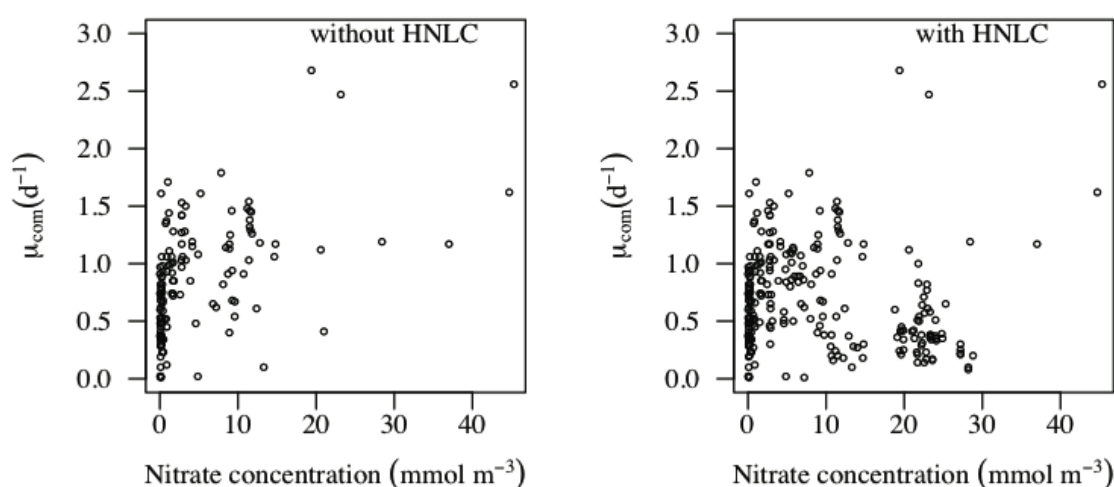
Actions: We change this sentence.

Introduction section now reads:
"Indeed, large phytoplankton communities seem to dominate in productive ecosystems thanks to their physical and chemical capacities to escape to zooplankton grazing (Irigoien et al., 2004; Irigoien et al., 2005)."

Reviewer #2: *Indeed, the resulting relationship between community growth rate and nitrate concentration shown in Fig. 1 (right panel) could be easily obtained by incorporating additional limitation terms (i.e. iron limitation) in Equation 3. The latter is the most parsimonious accounting for the low growth rate observed at high nitrate concentrations. Following the argument stated above, it is interesting to see that the ratio growth_com:growth_commax, which is equivalent to the nutrient limitation term S/(S+K) follows Monod (Fig. 3C), but it does not community growth rate. This is probably because factors other than nitrate concentration limited phytoplankton growth rate. I would suggest the authors to include iron limitation in their model formulation and test this possibility.*
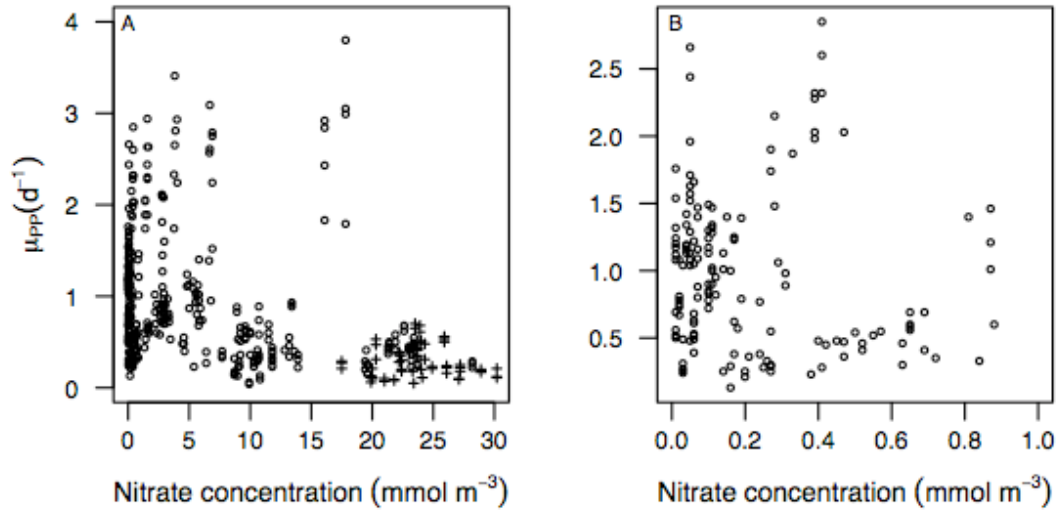
Comments: We would like to thank the reviewer for highlighting the iron limitation statement. We agree indeed that iron limitation needs to be included in our model formulation. By the fact, we consider that iron limitation is already included in our model formulation (Eq. 3) in S/S+K considering that a Monod kinetic is observed between μ_{rel} and nutrient concentration and that iron is part of the oceanic nutrient.

We revised in detail the in situ community growth rates and we observed that 110 data from the total 242 data were from HNLC regions. We observed indeed that when the data from HNLC zones were removed, the relationship between in situ community growth rates and nitrate concentration is closer to a Monod kinetic than considering the whole dataset although it does not perfectly fit.

For planktonic community at low nitrate concentrations (<1M), community growth rates are partly free from iron limitation (i.e. other nutrients are more probably more limiting) and still showed a lack of Monod kinetic with nitrate concentration. We agree with the reviewer that those data may be biased and overestimated as highlighted in Latasa et al. (2013). We will discuss about this methodological bias in the ms.

Although the community growth rates at low nitrate concentrations (<1M) have to be taken with caution, we observed that in situ community growth rates estimated from primary production and standing stocks do not significantly respond either to nitrate concentration by a Monod kinetic. Crosses represent phytoplankton communities of

Chen and Liu (2010) Table A2 sampled in HNLC regions (High-Nutrient, Low-Chlorophyll) and circles represent the rest of the phytoplankton communities from Table A2 dataset.

We observed so that using another method than the dilution experiment as ^{14}C primary production, the in situ phytoplankton community growth rate does not respond to nitrate concentration following a Monod kinetic.

   Actions: We now discuss in the manuscript about the iron limitation. We will discuss also in detail about the bias that can induce the dilution experiment under low nutrient concentration. Furthermore, we will present the in situ phytoplankton community growth rates estimated from primary production and standing stocks in the manuscript.

Methods section now reads:
"If the in situ community growth rate (μ_{com}) responds to the nutrient concentration following Monod's equation, we could formulate:

$$\mu_{com} = \frac{S}{S + K_s} \mu_{com\_max}$$

   (1)
Where S is the nutrient concentration (e.g. nitrate, phosphate, silicate, iron and so on) and K_s is the half-saturation constant for that nutrient."
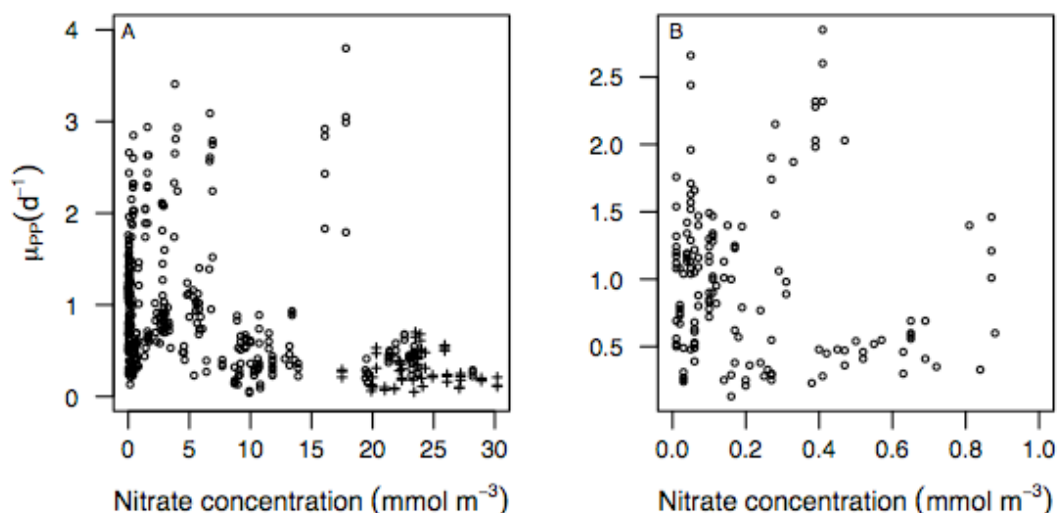
Discussion section now reads:
"The lack of significant response following a Monod kinetic may be explained by factors other than nitrate concentration limiting phytoplankton community growth rate. Indeed, we observed that from the total 242 in situ phytoplankton community growth rate data, 110 were from High Nutrient-Low Chlorophyll (HNLC) oceanic regions and so under iron limitation. If the data from HNLC zones are removed from our analysis, we observe that the relationship between phytoplankton community growth rate and nitrate concentration is closer to follow a Monod kinetic than considering the whole

dataset ($R^2 = 0.43$, $p < 0.05$). The iron limitation may partly explain for a part the lack of Monod kinetic between the in situ phytoplankton community growth rate and nitrate concentration presented here. However, we observed that in situ phytoplankton community growth rate does not respond to nutrient concentration following a Monod kinetic at nutrient concentrations below 1 μmol L^{-1} although these data do not correspond to iron-limited HNLC regions. The estimation of phytoplankton growth rate by dilution experiments in the most oligotrophic regions may be biased and have to be taken with caution. Indeed, Latasa et al. (2014) explained that most of the studies determining phytoplankton growth rate from dilution experiment presented regression slopes between apparent phytoplankton growth rate and dilution different from zero when the null hypothesis to be tested in dilution experiment should be the positive slope (b<0) and not a null slope (b=0). Latasa and co-workers believed that a proportion of the experiments with non-significant regressions were disregarded eliminating ecological situations of low growth and grazing. This may result in an overestimation of phytoplankton growth rates.

Although the presented patterns from dilution experiments have to be taken with caution considering the iron limitation at high nutrient concentration and the possible overestimation of phytoplankton growth rate at low nutrient concentration, we observed similar results from in situ phytoplankton community growth rate determined by another methodology. Indeed, we analysed the response of the in situ phytoplankton community growth rate calculated from primary production and standing stocks (Chen and Liu 2010) and nitrate concentration (Fig. 6). As we observed for the dilution experiment, the in situ phytoplankton community growth rate does not respond to nitrate concentration following a Monod kinetic both considering and excluding data from HNLC zones ($R^2 = 0.17$, $p < 0.05$ and $R^2 = 0.06$, $p < 0.05$ respectively). This result confirms our previous observation of the lack of Monod kinetic between in situ phytoplankton community growth rate and nutrient concentration. Unfortunately, the primary production data did not have been analysed under nutrient amended and the maximum growth rate could not have been estimated."

Figure section now reads:
"**Figure 6**. Relationships between in situ community growth rates (μ_{PP}, d^{-1}) estimated from primary production and standing stocks and nitrate concentration (A) from 0 to 40 mmol m^{-3} and (B) from 0 to 1 mmol m^{-3} from Chen and Liu (2) Table A2 dataset. Crosses represent phytoplankton communities of Table A2 sampled in HNLC regions (High-Nutrient, Low-Chlorophyll) and circles represent the rest of the phytoplankton communities from Table A2 dataset."

Reviewer #2: *The problem is not Monod formulation; the problem is using Monod with only one nutrient limitation if we are to test global ocean data. Droop model in this context would lead to the same issues.*

Comments: The reviewer implies that our ms tries to "confront" Monod vs Droop models, but we are not. We agree with the reviewer that Droop model would lead to the same issues. Community growth rates are expected to follow a Monod or Droop kinetic (Monod and Droop models have similar kinetics following a Michaelis-Menten kinetic) regardless of the nutrient limiting the community growth rate. Using Monod (or Droop) with only one or more nutrient limitation, the response is expected to be the same, a Michaelis-Menten kinetic.

Reviewer #2: *It is really surprising that community growth rates are relatively constant across such a wide range of nitrate concentrations (i.e. Fig. 3). Even in the most oligotrophic low nitrate environments, phytoplankton growth rates seem to be quite similar to those reported for high nutrient environments. Part of these results could arise from methodological bias in growth rate estimation with the dilution technique (see Latasa 2014). According to Latasa (2014): " The null hypothesis to be tested in dilution experiments should be the positive slope (H0:b>0, where b is the slope of the regression). However, in most studies, the null hypothesis is implicitly assumed to be b=0. Summarizing data from the literature, Dolan et al. (2000) noted that, when reported, between 6% and 66% of the experiments in each study do not yield grazing rates statistically different from zero, i.e., the slope of the regression between apparent phytoplankton growth and dilution were not different from zero at the 0.05 confidence level. It is very likely that this proportion is higher because experiments with non-significant slopes often are not published......Thus, a further implication of discarding experiments with non-significant regressions is to eliminate ecological situations of low growth and grazing and results in an overestimation of phytoplankton growth rates". This methodological bias represents a major issue questioning the validity of core data used in this study to test the performance of different parameterizations for nutrient kinetics and community growth rate. Thus, at high nitrate concentrations additional factors might be limiting phytoplankton growth. On the other size, at low nitrate concentrations methodological biases might overestimate phytoplankton community growth. None of these fundamental questions are even commented in the manuscript.*

Comments: We would like to thank the reviewer for highlighting this important point. We agree that we should discuss in detail about the methodological bias involved by the dilution experiment under low nutrient concentration and that our results should be taken as a rough guide. However, we observed similar results from in situ phytoplankton community growth rate determined by another method than the dilution experiment. Indeed, we analysed the response of the in situ phytoplankton community growth rate calculated from primary production and standing stocks (Chen and Liu 2010) and nitrate concentration. As for the dilution experiment, the in situ phytoplankton community growth rate does not respond to nitrate concentration following a Monod kinetic considering or not data from HNLC zones. This result confirms our previous observation of the lack of Monod kinetic between in situ

phytoplankton community growth rate and nutrient concentration.

Action: We now discuss in detail about the methodological bias caused by the dilution experiment under low nutrient concentration and we expose new results of the response of in situ phytoplankton community growth rate estimated by another method to nutrient concentration.
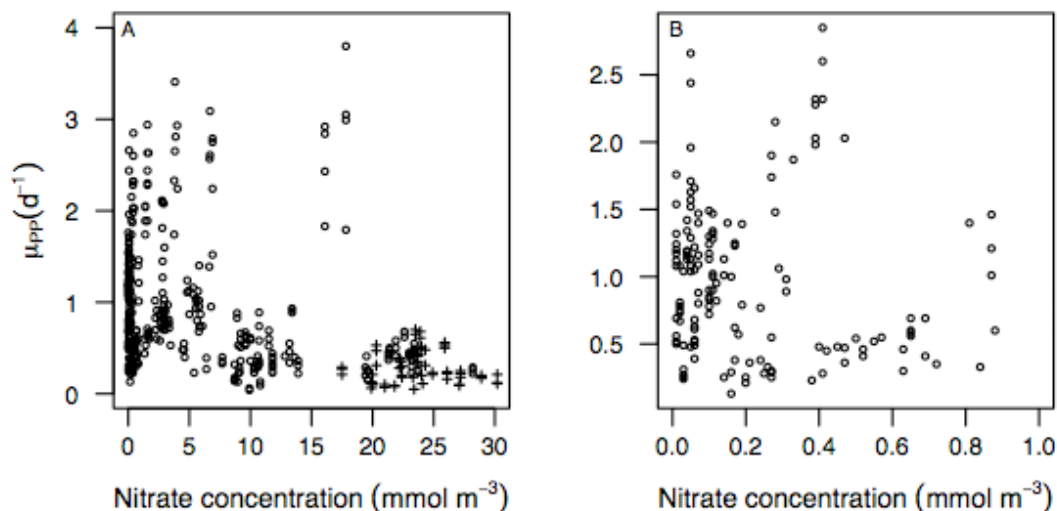
Discussion section now reads:
"The estimation of phytoplankton growth rate by dilution experiments in the most oligotrophic regions may be biased and have to be taken with caution. Indeed, Latasa et al. (2014) explained that most of the studies determining phytoplankton growth rate from dilution experiment presented regression slopes between apparent phytoplankton growth rate and dilution different from zero when the null hypothesis to be tested in dilution experiment should be the positive slope (b<0) and not a null slope (b=0). Latasa and co-workers believed that a proportion of the experiments with non-significant regressions were disregarded eliminating ecological situations of low growth and grazing. This may result in an overestimation of phytoplankton growth rates.
Although the presented patterns from dilution experiments have to be taken with caution considering the iron limitation at high nutrient concentration and the possible overestimation of phytoplankton growth rate at low nutrient concentration, we observed similar results from in situ phytoplankton community growth rate determined by another methodology. Indeed, we analysed the response of the in situ phytoplankton community growth rate calculated from primary production and standing stocks (Chen and Liu 2010) and nitrate concentration (Fig. 6). As we observed for the dilution experiment, the in situ phytoplankton community growth rate does not respond to nitrate concentration following a Monod kinetic both considering and excluding data from HNLC zones ($R^2 = 0.17$, $p < 0.05$ and $R^2 = 0.06$, $p < 0.05$ respectively). This result confirms our previous observation of the lack of Monod kinetic between in situ phytoplankton community growth rate and nutrient concentration. Unfortunately, the primary production data did not have been analysed under nutrient amended and the maximum growth rate could not have been estimated."
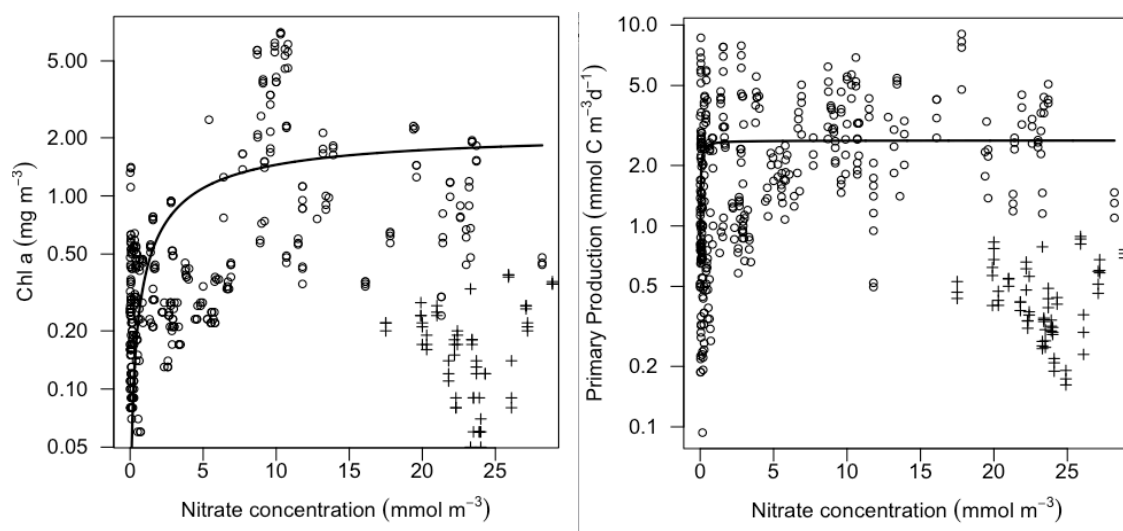
Figure section now reads:
"**Figure 6**. Relationships between in situ community growth rates (μ_{PP}, d^{-1}) estimated from primary production and standing stocks and nitrate concentration (A) from 0 to 40 mmol m^{-3} and (B) from 0 to 1 mmol m^{-3} from Chen and Liu (2) Table A2 dataset. Crosses represent phytoplankton communities of Table A2 sampled in HNLC regions (High-Nutrient, Low-Chlorophyll) and circles represent the rest of the phytoplankton communities from Table A2 dataset."

Reviewer #2: *Page 2. Lines 23-25. The main conclusion of the manuscript (i.e. community growth rate response to nutrient concentration following Monod must not be used) is not justified. First, the Monod parameterization has been used to simulate spatial and temporal variability in total Chla and primary production rate with great success.*

Comments: As explained previously, we were able to analyse the response of in situ phytoplankton community growth rate estimated by primary production and standing stocks to nitrate concentration. We observed a similar result than with growth rate data from dilution experiment. Indeed, the in situ phytoplankton community growth rate estimated from PP and standing stocks did not respond to nitrate concentration following a Monod kinetic including or not data from HNLC regions.

From the same dataset, we analysed the response of in situ primary production and in situ Chla to nitrate concentration. We observed that PP and Chla do respond indeed to nitrate concentration following a Monod kinetic when data from HNLC were excluded. Although our results are in accordance with the reviewer comment (Monod parameterization of Chla and PP), we can observe that the phytoplankton community growth rate (evaluated by two different methods) did not respond to nitrate concentration following a Monod kinetic. The Monod parameterization of PP and Chla doesn't seem to give a good representation of the in situ phytoplankton community growth rate response to nutrient concentration. We are suggesting so in our ms that a Monod parameterization where the Ksat and growth_max parameterizations are different for different functional groups would be better to represent the whole phytoplankton community and would result in a significant improvement of the models.

Actions: We present now the relationship between in situ phytoplankton community growth rate estimated by primary production and standing stocks and nitrate concentration and we discuss the results.
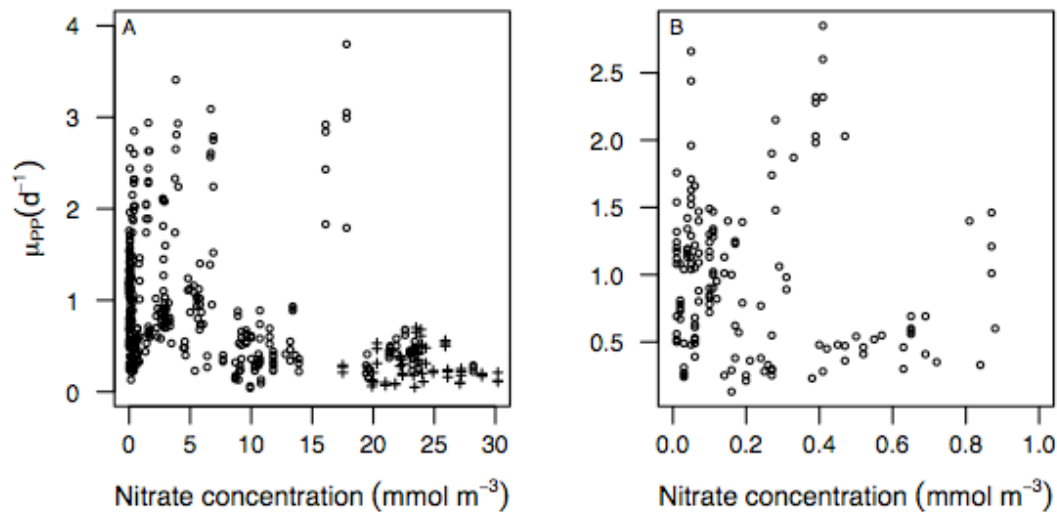
Discussion section reads now:
"Although the presented patterns from dilution experiments have to be taken with caution considering the iron limitation at high nutrient concentration and the possible

overestimation of phytoplankton growth rate at low nutrient concentration, we observed similar results from in situ phytoplankton community growth rate determined by another methodology. Indeed, we analysed the response of the in situ phytoplankton community growth rate calculated from primary production and standing stocks (Chen and Liu 2010) and nitrate concentration (Fig. 6). As we observed for the dilution experiment, the in situ phytoplankton community growth rate does not respond to nitrate concentration following a Monod kinetic both considering and excluding data from HNLC zones ($R^2 = 0.17$, $p < 0.05$ and $R^2 = 0.06$, $p < 0.05$ respectively). This result confirms our previous observation of the lack of Monod kinetic between in situ phytoplankton community growth rate and nutrient concentration. Unfortunately, the primary production data did not have been analysed under nutrient amended and the maximum growth rate could not have been estimated."

Figure section now reads:
"**Figure 6**. Relationships between in situ community growth rates (μ_{PP}, d^{-1}) estimated

from primary production and standing stocks and nitrate concentration (A) from 0 to 40 mmol m^{-3} and (B) from 0 to 1 mmol m^{-3} from Chen and Liu (2) Table A2 dataset. Crosses represent phytoplankton communities of Table A2 sampled in HNLC regions (High-Nutrient, Low-Chlorophyll) and circles represent the rest of the phytoplankton communities from Table A2 dataset."

Reviewer #2: *Second, if the authors are implicitly suggesting that Droop parameterization is better, then they should repeat the modeling experiment with it to prove it. Otherwise, what equation should be used?*

Comments: Our expectations in our ms were not to reject Monod model either to suggest that Droop parameterization is better. Indeed, we are suggesting that a Monod parameterization where the Ksat and growth_max parameterizations are different for different functional groups would be better and would result in a significant improvement of the models. The Monod kinetic used for the NPZ/NPZD models is not necessarily correct to represent the whole phytoplankton population growth rate. The solution we propose is to use size-dependent (or functional group dependent) nutrient limitation curves (based on Monod or alike), as we show this would lead to a pattern similar to that observed with in-situ data.

It is important to highlight that we are criticizing the use of a single Monod equation for the whole community, the use of different equations (based on Monod or alike) for different phytoplankton compartments that capture the size-dependent differences would be our recommendation

Reviewer #2: *Page 3. The argumentation stated in the first two paragraphs of Introduction is not strictly correct according to current ecophysiological evidence. Field and experimental data clearly show that high-nutrient environments attain higher productivities (sensu stricto primary production rate per unit photosynthetic biomass) than oligotrophic systems. According to the authors and references provided, the observation that large organisms dominate in high-nutrient environments supports the idea that phytoplankton growth rate in these environments is relatively low, yet, their elaboration is based on the erroneous consideration that larger cells grow at a lower rate than cyanobacteria or picoeuk.*

Comments: Field and experimental data show indeed that high-nutrient environments attain higher productivities but they do not necessarily show that phytoplankton species composing those environments attain higher growth rates. As we show in our Fig. 3 and Fig. 6, the most up-to-date compilation of field data on phytoplankton community growth rates in the ocean (both from the dilution method and ^{14}C production per unit of biomass) do not support the assertion that high-nutrient environments attain higher growth rates. We agree with the reviewer that this result is counterintuitive. We also disagree with the reviewer assertion that we are erroneously considering that larger cells grow at a lower rate than picoeukaryotes. Indeed, empirical data do not support that larger cells have higher growth rates than picoeukaryotes, at most, and as we discuss in our Fig. 7 the response is unimodal, with mid-sized cells having the highest growth rates. We are just exposing observations and results that have been published in the past and accepted by the scientific community.

Reviewer #2: *Page 3. Lines 32-36. The growth rate is a combination of maximum growth and half saturation constant (Ksat). Having lower Ksat does not necessarily mean growing faster id the maximum growth rate is also lower. This sentence is imprecise.*

Comments: We agree with the reviewer that the growth rate is a combination of maximum growth rate and Ksat. Lower Ksat does not necessarily mean growing faster but in the specific context of our sentence "*Small phytoplankton species have low half-saturation constants that allow them to uptake nutrients at a faster rate than larger cells and to dominate in nutrient limited conditions (Eppley et al., 1969; Aksnes and Egge, 1991; Hein et al. 1995).*", we referred here to small phytoplankton species that are characterized by high growth rate at low nutrient concentration due to their low Ksat. Undoubtedly, the maximum growth rate of small phytoplankton species is higher than for large phytoplankton species.

Action: We will change the corresponding sentence.

Introduction section now reads:
"Small phytoplankton species have low half-saturation constants and high maximum

growth rates that allow them to uptake nutrients at a faster rate than larger cells and to dominate in nutrient limited conditions (Eppley et al., 1969; Aksnes and Egge, 1991; Hein et al. 1995)."

Reviewer #2: *Page 3. Line 37-39. I agree that size-differential grazing pressure partially account for the patterns of community size structure, but to what extent? The papers cited do not provide a quantification of this effect nor do the authors test it in their analysis.*

       Comments: We did not expect to quantify the effect of size-differential grazing pressure but just to find a possible explanation of why large phytoplankton may be dominant in high productive ecosystems. It would have been very interesting to quantify this effect in our study, however the in situ data that we used here did not provide any zooplankton grazing data.

Reviewer #2: *Page 5, Line 97. "For simplicity, only one nutrient (nitrogen) was considered to be limiting" This consideration is not valid if data from HNLC regions were included. If so, Equation 3 should include the iron limitation term.*

       Comments: We agree with the reviewer and we already consider that the iron limitation is included in our Eq. 3, into the S/S+K term. Our model is incomplete as it is the case of most models which are only a simplified representation of nature. We can notice here that excluding data from HNLC regions where iron is limiting, our model can explain why the in situ phytoplankton community growth rates do not respond to nitrate concentration following a Monod kinetic.
The reviewer seems to be neglecting our most important claim and it is that using a very simple model including only one nutrient limitation term with Monod like responses to nutrient limitation for each size class, we reach the (counterintuitive) conclusion that community rate does not follow Monod like behaviour. We agree that adding more variables (e.g. other limiting nutrients), the model will be more complex and introduce further "noise", and the prediction would differ even more from a Monod kinetic.

Reviewer #2: *Page 5. Lines 111-113. This is not strictly correct. The community growth rate should be an emergent property of an explicit competition model setup.*

       Comments: We are not referring to a specific model here. Indeed, we believe that for a given moment in time, the community growth rate is the average of the growth rates of all the cells in a community. This must be true for both models and empirical data. We do agree with the reviewer that in a model, the community growth rate is an emergent property but the definition of how it would be calculated for a given moment in time is correct.

Reviewer #2: *Page 6. Lines 137-141. This is the reason why the authors need to use Droop model as well and compare the outcome with Monod. As far as I understand, Equation 6 is still Monod model.*

Comments: The reviewer implies that our ms tries to "confront" Monod vs Droop models, but we are not. Community growth rates are expected to follow a Monod or Droop kinetic (Monod and Droop models have the same kinetics following a Michaelis-Menten kinetic) regardless of the nutrient limiting the community growth rate. Using Monod (or Droop) with only one or more nutrient limitation, the response is expected to be the same, a Michaelis-Menten kinetic.

The Droop model has been used on our simulation (Eq. 6). Indeed, Droop model is:

$u = Q*\mu$ where u is the specific uptake rate, Q is the cell nutrient content and μ is the specific growth rate.

Reviewer #2: *Page 7. Lines 177-179. It is surprising that the authors correct for the potential effect of temperature but, for simplicity, they consider that only one nutrient limited growth (Page 5 Lines 97-98).*

Actions: We discuss in the new ms version the iron limitation effect on the phytoplankton community growth rate.

Discussion section now reads:

"The lack of significant response following a Monod kinetic may be explained by factors other than nitrate concentration limiting phytoplankton community growth rate. Indeed, we observed that from the total 242 in situ phytoplankton community growth rate data, 110 were from High Nutrient-Low Chlorophyll (HNLC) oceanic regions and so under iron limitation. If the data from HNLC zones are removed from our analysis, we observe that the relationship between phytoplankton community growth rate and nitrate concentration is closer to follow a Monod kinetic than considering the whole dataset ($R^2 = 0.43$, $p < 0.05$). The iron limitation may partly explain the lack of Monod kinetic between the in situ phytoplankton community growth rate and nitrate concentration presented here."

Reviewer #2: *Page 8. Line 198. Should be relative rather than maximum growth rate.*

Comments: We meant "(community growth rate) in relation to its maximum growth rate" that is equivalent to μ_{rel}. We will rephrase the sentence to avoid any confusion.

Action: We change the corresponding sentence.

Discussion section now reads:

"However, for the relative reproductive rates, the Monod model is a good characterization of community dynamics"

Reviewer #2: *Page 8. Lines 209-213. Why dis not the authors follow this modeling design to show us the difference between NPZD models versus NPjZjD models?*

Comments: Our goal here is not to compare NPZD models but to inform about the use of Monod kinetic in models when they consider the same response of phytoplankton community growth rate to nutrient concentration than the phytoplankton

species composing this community, that is following a Monod kinetic.

Reviewer #2: *Page 8. Lines 214-215. This is because they use many more tunning parameters and thus degrees of freedom.*

> **Comments**: We thank the reviewer for his/her comment.
> **Action**: We can add this explanation too to our sentence.

Discussion section now reads:
"This is well in line to the findings of Friedrichs et al. (2006; 2007) that observed that complex models with multiple phytoplankton functional groups fit better the available data than the simpler models. This is mainly due to the use of many tuning parameters and thus degrees freedom."

Reviewer #2: *Page 9. Line 228. Should be high maximum nutrient uptake rates.*

> **Comments**: We thank the reviewer for his/her comment.
> **Action**: We change the corresponding sentence.

Discussion section now reads:
"Several studies have shown that the high surface area to volume (S:V) ratio of small phytoplankton species result in high maximum nutrient uptake rates and low K_s and may explain why small phytoplankton species dominate in natural nutrient-limited ecosystems (Eppley et al., 1969; Aksnes and Egge, 1991; Hein et al., 1995)."

Reviewer #2: *Page 9. Lines 232-235. Again, this is totally speculative.*

> **Comments**: We agree with the reviewer that our statement is speculative. Indeed, the corresponding sentence specified "seem to": "Conversely, large phytoplankton species seem to dominate in productive and well-mixed ecosystems (Irwin et al., 2006) due to their physical and chemical capacities to escape to zooplankton grazing (Irigoien et al., 2004; Irigoien et al., 2005) and due to upward motion increasing their residence time in upper layer against their tendency to sink (Li, 2002; Rodríguez et al., 2001)." We did not attempt here to confirm any assumptions.

Reviewer #2: *Page 9. Lines 246-249. The authors use Monod to reject Monod. The authors should test the alternative possibility using Droop model, perhaps assuming as they have done so far that intracellular quotas are size dependent.*

> **Comments**: Again, the reviewer seems to assume that our intention is to reject Monod although we are not doing so. We are just favoring a parameterization of Monod, with different Ksat and u_max for different functional groups.

Reviewer #2: *Page 10. Lines 271-275. This is not true. Ksat is included in Eq. 3 and Ksat reflects the size structure of the community as well.*

Comments: We thank the reviewer for his/her comment.
Action: We revise now the corresponding paragraph.

Discussion section now reads:
"Although community growth rates did not respond to nutrient concentration following Monod kinetics, the in situ and simulated μ_{com_rel} did (Fig.s 3B, 5B). The μ_{com_rel} is exempted from the effects of temperature, light and community composition. The K_s and $\mu_{com\_rel\_max}$ were quite similar between the in situ ($K_s = 0.16 \pm 0.02$ and $\mu_{com\_rel\_max} = 0.99 \pm 0.02$) and predicted ($K_s = 0.11 \pm 0.01$ and $\mu_{com\_rel\_max} = 0.98 \pm 0.01$) μ_{com_rel}. So when the community growth rate depends only on nutrient concentration, the response of the community growth rate to nutrient variation follows the predicted Monod kinetic."

Reviewer #2: *Figure legends. Figure 2. There is no trade-off in these nutrient uptake-growth curves!*

Comments: We thank the reviewer for his/her comment and we agree with him/her.
Action: We now change the corresponding sentence.

Figures section now reads:
"**Figure 2**. Functional forms of (A) normalized biomass spectrum (NBSS) and (B) phytoplankton species growth rate to nutrient concentration. (B) Simple allometric equations are indicated by the size range from small (thinnest lines) to large (thickest lines) size species. (A) The solid line represents the linear regression."