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## ***Interactive comment on “Poor correlation between phytoplankton community growth rates and nutrient concentration in the sea” by A. Regaudie-de-Gioux et al.***

### **Anonymous Referee #2**

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This study analyzes the validity of Monod parameterization to account for the relationship between in situ nitrate concentrations and community growth rate. This is a critical issue because classical NPZ models usually adopt this parameterization to represent nutrient-based phytoplankton growth. The objective is scientifically relevant and the manuscript is well written. However, there are some fundamental issues concerning conceptual misunderstanding and methodological biases that preclude recommending this manuscript for publication.

### Main comments

The authors sustain that the dominance of large cells in nutrient rich environments re-

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quires a parameterization different than the classical Monod kinetics. However, a trade-off between half-saturation constant for nutrient uptake ( $K_{\text{sat}}$ ) and maximum growth rate following Monod still would account for these patterns of community size structure. The authors ignore this potential trade-off between  $K_{\text{sat}}$  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. 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. 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  $\text{growth}_{\text{com}}:\text{growth}_{\text{commax}}$ , 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. 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.

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 ( $H_0:b>0$ , where  $b$  is the slope of the regression). However,

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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.

Additional comments:

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. 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?

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

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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.

Page 3. Lines 32-36. The growth rate is a combination of maximum growth and half saturation constant ( $K_{sat}$ ). Having lower  $K_{sat}$  does not necessarily mean growing faster if the maximum growth rate is also lower. This sentence is imprecise.

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.

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.

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.

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.

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).

Page 8. Line 198. Should be relative rather than maximum growth rate.

Page 8. Lines 209-213. Why do not the authors follow this modeling design to show us the difference between NPZD models versus NPjZjD models?

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Page 8. Lines 214-215. This is because they use many more tuning parameters and thus degrees of freedom.

Page 9. Line 228. Should be high maximum nutrient uptake rates.

Page 9. Lines 232-235. Again, this is totally speculative.

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.

Page 10. Lines 271-275. This is not true.  $K_{sat}$  is included in Eq. 3 and  $K_{sat}$  reflects the size structure of the community as well.

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

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