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Interactive comment on "A model for variable phytoplankton stoichiometry based on cell protein regulation" *by* J. A. Bonachela et al.

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Dear Editor,

Please find below the reply to the second referee report for the paper "A model for variable phytoplankton stoichiometry based on cell protein regulation", of which we are the authors.

Note that some of the additions made in response to referee #1 have been updated/modified in order to accommodate the manuscript to the feedback of the two referees in a coherent way.

Response:

We want to thank referee #2 for calling our attention to cell size, because we may have not made enough effort to explain its role in the model.

Size appears in key parts of the uptake sub-model. It is explicitly present in the form of the effective half-saturation constant (Eqs.(5) and (6)) and sets the maximum number of uptake proteins through the relative absorbing area (Eq.(A4)). Size is also implicitly present in many of the parameters, as many cell traits scale with size (for instance, maximum and minimum quotas. Thus, cell size sets limits to the response of the cell to environmental changes and imposes interactions between the N and P uptake sites, which compete for space, especially in the co-limitation region.

Concerning the generality of the conclusions, note that there is an extensive bibliography ranging across a wide spectrum of species and sizes that supports qualitatively the uptake regulatory process as it is modeled here. That literature includes, for instance, *Ankistrodesmus falcatus*, *Asterionella formosa*, *Euglena gracilis*, *Scenedesmus sp.* (Gotham and Rhee a and b), or *Thalassiosira pseudonana* (McCarthy and Goldman, 1979), whose size is one or two orders of magnitude larger than that used in this paper.

As explained in the manuscript, there are several possible reasons for a cell of *any* size to up-regulate the number of proteins for low nutrient concentration. For instance, increasing the number of these transporters also helps increase the number of successful encounters between nutrient ion and the cell as the absorbing area also grows. Importantly, the dynamic character of the number of uptake proteins can provide a mechanism for the cell to reach more easily that regime in which, as referee 1 points out, the number of proteins is not important anymore. This has been also remarked in other articles, including the one the referee cites. Concretely, in (Armstrong,2008):

"In Eq. (19) [equation presenting an effective half saturation constant similar to the one

we use in our manuscript]*, an increase in porter density n would shift the half-saturation constant away from porter limitation and toward diffusion limitation, which is what one would intuitively expect."*

An increase in the number of proteins would suffice for Eqs.(5) and (6) in the manuscript to reach, combined to Eqs.(3) and (4), the well-known result for diffusion limitation: $V = 4\ \pi D_X r_c [X]$, regardless of cell size. On the other hand, larger cells will have different maximum/minimum quota values and, therefore, will react differently than small cells to the same environments.

As a final remark on the importance of cell size, we want to point out that we are at this moment addressing the referee's question about testing the model for a wide range of r. Specifically, we are working to implement our model at a global level, using a large number of initial species, in order to test if our model is able to replicate the global patterns of stoichiometry observed in the ocean. Thus, one of the interesting questions to be addressed will be how cells of different sizes react to different, realistic environments. We hope this new project will answer the referee's question, among others.

Following the comments and suggestions by referee #2 (also in accordance to comments by referee #1), we have modified the manuscript to stress the importance of size in our model. Specifically, to the additions mentioned in the reply to referee #1:

1. In the new sub-section "The role of size", in the Discussion:

   "The parameter values used in this paper correspond to a generic Synechococcus phytoplankton strain. This parametrization has allowed us to compare, at least qualitatively, the obtained results with a large variety of experimental articles available in the literature.

A strength of our model is that it is based on physiological mechanisms that could be parametrized for a range of different phytoplankton species, regardless of the size. Cell radius is explicitly present in Eqs.(5) and (6). These expressions are the result of an approximation (Armstrong, 2008; Bonachela et al. 2011) that has proven to work well for both small and large phytoplankton cell sizes (Armstrong, 2008), while the dynamic equations for the number of uptake sites (or V_{max}) introduce an effective dependence on size intended to compensate for the coarser performance expected for intermediate sizes. For instance, this expression predicts improved uptake abilities for small cells when it is formulated in terms of a normalized maximum uptake rate, V_{max}/r_c^2 (Armstrong, 2008) (see (Armstrong, 2008, Fiksen et al. 2013) for a more detailed study on the performance of the "non-regulation" version of these expressions with respect to size). The dynamics for protein regulation facilitates the description of two well-known extreme results using one single expression: if we use Eq.(5) with Eq.(4) (alternatively, Eq.(6) with Eq.(3)), the resulting form for V becomes independent of the number of uptake sites for scarce nutrient conditions, while the large nutrient concentration extreme provides the maximum uptake rate measured in typical (bulk) experiments. These two cases are usually referred to as diffusion and kinetic limitation regimes (see (Bonachela et al, 2011) for a mathematical derivation, and references therein). This limits remain valid regardless of cell size.

In addition, cells of different sizes have different physiological ranges (e.g. different Q_{max} and Q_{min}) and, therefore, react differently to similar environmental changes. For small cells with high surface area to volume ratios, physiological regulation of uptake protein dynamics should impact nutrient uptake rates through changes in absorbing area (Eqs.(9) and (10)). However, larger organisms tend to become limited by diffusion more easily and, therefore, the number of uptake proteins may become less important (Pasciak and Gavis, 1974; Armstrong, 2008) (see above). Nonetheless, uptake regulation has been observed

across a wide spectrum of species and sizes. For instance, the focal species in the classic studies by McCarthy and Goldman (McCarthy and Golman, 1979) or Gotham and Rhee (Gotham and Rhee, 1981a,b) include Ankistrodesmus falcatus, Asterionella formosa, Euglena gracilis, Scenedesmus sp., and Thalassiosira pseudonana; the radii of these species can be up to two orders of magnitude larger than the value we used in this paper (see table 3).

Uncertainty about the relationship between cell size and uptake protein regulation or cell stoichiometry could be addressed through additional empirical and modeling studies. From the empirical point of view the experimental test we propose above could be repeated using several species of different sizes. From the theoretical perspective, one possible approach could follow the approach of (Fiksen et al. 2013). This approach would apply two versions of our model –one with protein regulation and one without– across a continuum of cell sizes. Such a study would reveal the dependence of cellular stoichiometry on cell size. The comparison of both the experimental and theoretical studies could provide important insight into protein and stoichiometry regulation across taxa."

2. And, in Conclusions:

   "Crucially, these physiological ranges scale with cell size, which also induces competition between the N and P uptake proteins for space at the cell membrane. The effects of cell size are particularly relevant for the extent of nutrient co-limitation."

Fig.1, as the referee points out, just collects the broad trends observed in the literature using schematic plots. To improve clarity, we have changed the caption, which now starts:

"Qualitative plot of the patterns for growth rate μ and quotas Q observed in the experi-

mental literature"

Also, the meaning of "symmetric" is clarified using the caption of Fig.2b, referred to in the sentence that the referee points out:

"The use of an identical functional form for the dependence of growth on the limiting quota imposes a symmetry of the Q versus w plots around the optimal input ratio (the symmetry between N and P quotas mentioned in the text)."

Concerning the sentence in page 3245, line 21 highlighted by the referee ("Regulation of protein production is the key mechanism underlying the dynamics of the population"), we have to clarify that we refer exclusively to our model, in which we focus on those processes to explain the emergent stoichiometry of an isolated population in a controlled environment. In a more realistic scenario, other physiological factors (e.g. temperature or light dependence) and ecological interactions should be added to our description. To avoid misunderstandings, we have modified the sentence, which now reads:

"We focus our model on regulation of protein production as a key mechanism underlying the dynamics of the population. Thus, we include explicit equations for the regulation of nutrient uptake proteins."

Finally, we have included the missing symbols for the number of uptake proteins for N and P in the table. We thank the referee for pointing that out.

References:

Armstrong, RA 2008. Nutrient uptake rate as a function of cell size and surface transporter density: A Michalis-like approximation to the model of Pasciak and Gavis. Deep

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