**Biogeosciences
Discussions**

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

D. Aksnes (Referee)

dag.aksnes@bio.uib.no

This study aims to improve the understanding of how species stoichiometric emerges from the interplay between environment and cell physiology. This is approached by simulation and use of a model that is assembled from previous published models on nutrient uptake (Armstrong 2008) and protein expression (Bonachela et al. 2011). In contrast to previous studies, the authors avoid the use of optimality assumptions or assumptions concerning dependencies between quotas. That is fine. Instead, what is considered to be, simple and plausible physiological mechanisms makes the foundation for the study.

My main concern is too what extent the assumed mechanisms are plausible, i.e. reflects reality. Thus I am not convinced that "Our model contributes to the understanding

of the global cycles of oceanic nitrogen and phosphorus. . ..". I have the following questions concerning the mechanistic content of the model:

1. The choice of their sub model on nutrient uptake appears ad hoc and the rationale for the choice is lacking. This sub model (Eq. 3-4) is the approximate relationship that Armstrong (2008) derived. Why use the approximate equation instead of the exact solution, i.e. the quadratic expression?

2. The parameters K_N and K_P have been denoted the "standard half-saturation coefficients" in the present study. If I understand this correctly these half saturation coefficients are not those measured/reported in standard bulk experiments, but rather the coefficients that are defined according to the concentration at the cell surface. How are these concentrations measured and how are these coefficients affected by processes involved in the uptake?

3. Furthermore, the parameters K_N and K_P are according to Fiksen et al. (2013, their Eq. 13a), composite parameters that include quantitites such as the fraction of the surface that are covered with uptake sites (which is determined by the number of the uptake proteins and the size of the cell), the handling time/rate of an uptake site, the site radius, and the molecular diffusion coefficient. It appears to me that the mechanism of the uptake model would be more plausible by substituting K_N and K_P by the mechanism that determine these coefficients. It seems that the relevant parameters needed for this are already part of their model (Table 3 and the Appendix).

4. The result of Berg and Purcell (1977), that the uptake rate is not proportional to the number of uptake proteins, appears important for the present study. It is not evident that this important mechansim is contained in the present model and this needs to be clarified.

5. The recent study of Fiksen et al (2013) reviews several nutrient uptake models that have been proposed including those of Armstrong (2008) and Bonachela et al. (2011). Several issues raised in this review appear relevant for the present study. E.g. the error

that is associated with the use of the approximate nutrient uptake model that they have assumed.

6. It is unclear to me how the protein expression (Eq. 7) was derived. Is it derived from "first principles" or is it an assumed convenient mathematical expression? In case of the last, to what extent are the expectations from the model subject to this and other choices made by the authors.

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 Sea Res I 55:1311-1317.

Bonachela J.M.Raghib M, Levin SA. 2011. Dynamic model of flexible phytoplankton nutrient uptake. PNAS 108:20633-20638.

Berg HC, Purcell 1977. Physics of chemoreception. Biophys. J. 20:193-219

Fiksen Ø, Follows MJ, Aksnes DL. 2013. Trait-based models of nutrient uptake in microbes extend the Michaelis-Menten framework. Limnol. Oceanogr. 58:193-202

Interactive comment on Biogeosciences Discuss., 10, 3241, 2013.

C936