



Interactive comment on “Contrasting juxtaposition of two paradigms for diazotrophy in an Earth System Model of intermediate complexity” by Ulrike Löptien and Heiner Dietze

Andreas Oschlies

aoschlies@geomar.de

Received and published: 11 April 2020

Publisher’s note: the content of this comment was adjusted on 2 April 2024 after approval of the BG co-editors-in-chief since some formulations were inappropriate.

Comments by Andreas Oschlies, Chia-Te Chien, Wolfgang Koeve, Angela Landolfi, Markus Pahlow, Friederike Prowe and Christopher Someš

General comments:

Printer-friendly version

Discussion paper

The authors of this manuscript, Ulrike LÖptien and Heiner Dietze, are colleagues of our research group. Because the manuscript of LÖptien and Dietze (2020) addresses important scientific questions and to ensure that comments based on the knowledge built in our research group are used in a scientifically most productive way, we collectively decided to also respond publicly so that the authors and other interested readers may consider whether to take these into account in future work on this topic.

The manuscript discusses two interesting ideas, called paradigms by LÖptien and Dietze (2020), on the controls of marine diazotrophs. It specifically contrasts frequently used earlier ideas on bottom-up controls with less prominent ones on top down controls by grazing. Unfortunately, the study fails to deliver on the goals set out in the abstract and introduction. It nevertheless calls for a concerted and perhaps overdue effort to examine the impact of grazing formulations on the simulated distribution and activity of diazotrophs, the importance of which was also indicated by the sensitivity experiments reported by Wang et al. (2019). LÖptien and Dietze (2020) deserve credit for pointing this out clearly at the onset. Their approach of selecting passive switching by fixed grazing preferences of a linear grazing function can represent one first step (but note that the linear grazing function employed in eq.8 in LÖptien and Dietze (2020) appears different from the Holling-type II grazing function used by Keller et al. (2012)). Major control is exerted also by the shape of the grazing function and by active switching (Prowse et al., 2012; Vallina et al., 2014). Some of the studies cited in the current contribution (Schmittner et al., 2008; Somes et al., 2010; Landolfi et al., 2013) use sigmoidal grazing functions. Other studies explicitly avoid different grazing preferences on diazotrophs and ordinary phytoplankton (Monteiro et al., 2010; Weber and Deutsch, 2014). Interestingly, the prognostic CESM model used in the Wang et al. (2019) study employs grazing preferences higher for diazotrophs than for diatoms, i.e. contrary to the results obtained for the GRAZ and REF experiments of LÖptien and Dietze (2020). A more in-depth discussion of the treatment of grazing of diazotrophs in models is required, beyond qualitative statements like ‘one assumption often implicitly incorporated . . . is selective grazing’ (l.54-55).

[Printer-friendly version](#)[Discussion paper](#)

The second paradigm of the study, called ‘low-P demands’ paradigm, also deserves a more careful investigation. There is, to our knowledge, no evidence for half-saturation constants for phosphate uptake being smaller in diazotrophs than in ordinary phytoplankton (e.g. Monteiro et al., 2010), as assumed as key mechanism in the OLIGO simulation. Line 60-63 states “The idea is that diazotrophs outcompete ordinary phytoplankton under P-depleted conditions because they can allocate more P to intracellular P-uptake machinery. The underlying physiological explanation is that diazotrophs presumably need less P to build their N-uptake machinery, which is already taken care of by the nitrogen-fixation machinery (which is known not to need so much P).” We are not aware of any observational evidence for this physiological explanation. Subsistence P (and also N) quotas estimated by Pahlow et al. (2013, Table 2) for *Trichodesmium* sp. were higher than for non-diazotrophic species and explained by the N and P requirements of the N₂-fixation apparatus and consistent with a lower P use efficiency in diazotrophs during N₂ fixation (Raven, 2012). It should be noted that the ‘low-P demands’ paradigm is not the mechanism that leads to the success of diazotrophs in P-depleted regions as investigated in different model settings (Pahlow et al., 2013, Landolfi et al., 2015), where the ability to access N via N₂ fixation (and not P) allows diazotrophs to allocate more N (and not P) to acquire P.

An important aspect the authors neglect to discuss is feedbacks with denitrification, which can strongly impact patterns and rates of N₂ fixation in the model and may respond differently under their different “paradigms”, e.g. by different partitioning of newly fixed N into lateral and vertical export routes. In this respect it is important to know whether global NO₃ and thus N₂ fixation are in steady-state at the end of the tuning experiments run for 2000 years (line 151). Several studies have shown that a 2000yr spin up is short for global ocean tracers to reach steady state (e.g., Wunsch and Heimbach, 2008) and may be too short particularly for the nitrogen fixation and denitrification rates to reach equilibrium (Kriest and Oschlies, 2015).

The authors claim that their study is designed to constrain the envelope of model re-

sponses (l.69), but fail to provide an estimate of this constrained envelope. In particular the projections of diazotrophy under climate change presented at the end of the manuscript deserve estimates of uncertainty regarding their representativeness of the two ‘paradigms’. Instead of focusing on differences in the sign-of-change for the two ‘paradigms’, the authors need to provide evidence that these differences are significant at the ‘paradigm’ level. Such an analysis could develop quite naturally from the parameter perturbation experiments carried out earlier in the manuscript. To prepare for such an analysis, the choice of model runs that aim to implement the two paradigms should be explained and justified in more detail. Implementation of the ‘selective grazing’ paradigm varies the growth penalty of diazotrophs and the relative grazing preferences on diazotrophs and ordinary phytoplankton. The tuned parameters reveal that grazing preferences in the GRAZ simulation differ less between diazotrophs and ordinary phytoplankton than they do in the REF run. Does this mean that REF is a more extreme case of the grazing paradigm than experiment GRAZ itself? Temperature dependencies of diazotrophs and ordinary phytoplankton remain different in all three configurations. With temperatures often correlating with surface nutrients, this may well map on the degree of OLIGO in all model configurations. It might help to illustrate how growth and grazing rates vary for a typical range of environmental conditions.

The conclusion that “the development of a reliable model must be preceded by additional in-situ observations” (l.70) does not hold up to closer scrutiny and surely should not be interpreted as to stop model development until more or better data are available. In contrast, model development can actually point to those measurements that would be most valuable in reducing uncertainties. In particular, it remains unclear how the authors can justify the conclusion that more observations of biomass of diazotrophs are needed, rather than, for example, measurements of nitrogen fixation.

The conclusion that more observations are required before reliable models can be developed is even more difficult to understand when considering that the authors base their results entirely on the model-derived N₂-fixation estimate of Wang et al. (2019)

instead of available observations of N₂ fixations. Moreover, the Wang et al. (2019) estimate is based on a circulation model and partially inconsistent assumptions about elemental ecological stoichiometry. In particular, denitrification is, in the model of Wang et al. (2019) computed from modeled DON and DIN and observed (not modelled) oxygen concentrations. Wang et al. (2019) show that different model configurations they tested vary considerably in the simulated N₂ fixation (their Fig. S4) and admit that the imperfect agreement with direct measurements of nitrogen fixation does not permit the identification of the one parameterization that is most realistic. Löptien and Dietze (2020) base their conclusions on the comparison with one model realization of Wang et al. (2019). It is important to know whether their conclusions would still hold if real data were used in the model assessments. Since its publication, the Luo et al. (2012) data base has been enhanced, particularly by adding new observations in the Pacific Ocean (e.g. Knapp et al., 2016; Landolfi et al., 2018).

The authors announce ‘far reaching implications of both paradigms’ in the context of climate change projections and the assessment of geoengineering options (l. 66ff), but fail to show implications of differing N₂-fixation parameterizations on marine carbon uptake, warming projections, the efficacy of climate engineering options, or any related aspect in a quantitative manner. Given the small differences in projected N₂-fixation (Fig. 3b) for the two ‘paradigms’ (compared, e.g., with the uncertainty range of published N₂-fixation estimates), more solid evidence needs to be provided to support the bold statement regarding ‘far reaching implications’.

In summary, the manuscript fails to deliver on the goals set out in the abstract and introduction. It confirms that model configurations can be designed that show similar patterns for the present state of the ocean, but diverge under global warming (Löptien and Dietze, 2019). The manuscript raises several important issues, a careful investigation of which is desired and would be a scientifically very useful contribution to a better understanding of the controls of marine nitrogen fixation. The results are expected to deserve the additional work that is likely needed. In its current form, this manuscript

does not seem to have reached the degree of sophistication expected for a significant scientific step forward.

Individual comments:

I.6 the adjective phosphorous should be replaced by the noun phosphorus.

I.11 the call for more measurements of cyanobacteria biomass is not substantiated by the findings reported in the manuscript. Presumably, measurements of fixation rates would be much more beneficial.

I.14-15, The logic of this argument is difficult to follow. What matters for phytoplankton is what is dissolved in seawater rather than in the atmosphere. There is much more inorganic carbon dissolved in seawater than is N₂.

I.21-22 Some reference for "Paleo-record suggest balanced by denitrification" would be useful here. The Altabet et al. (2002) study cited does not discuss the Holocene, perhaps Altabet (2007) would be better?

I.40. It is not so much the energetic cost of breaking the triple bond of N₂ (which is very similar to that of reducing NO₃ to NH₄), but mostly the cost of getting rid of O₂ that would otherwise destroy the enzyme nitrogenase (Grosskopf and LaRoche, 2012).

I.56. Selective grazing 'paradigm' need more careful description. The statement of 'implicitly incorporation' is not really true, see e.g. the early explicit discussion in Moore et al. (2001).

I.99 Presumably, this is a typo and units should be $\mu\text{mol m}^{-3}$ (also in Table 1).

I.102, eq. 2: there is an error in this equation. Presumably, the final term should read "max(0,(exp(T/Tb)-2.6))"

I.115, eq. 8. It should be mentioned that zooplankton also grazes on itself and on detritus, making the prey switching algorithm in the model a little more complex than suggested here. In addition, presenting the equation in this form does not make clear

that this is a Holling-type II functional response after Fasham et al. (1990). We unfortunately only now noticed that there was a typo in eq. 27 of Keller et al. (2012), which should read $\Theta = \phi_{P_O} P_O + \phi_{P_D} P_D + \dots + K_{Grazed}$ as it is coded correctly in the UVic 2.9 version of Keller et al. (2012).

I.122 The map of indirectly estimated N₂ fixation should not be called ‘observations’

I.127 it should be made clear that the term ‘outperformance’ used here is only valid with respect to a model-derived estimate of N₂ fixation by Wang et al. (2019). In this regard, it would be helpful to clarify the very different model structure and parameterizations used in Wang et al. (2019), particularly with respect to stoichiometry and grazing formulations. When assessing the quality of the model, it would be better to use a model-data misfit as metric, i.e. observations of N₂ fixation and/or observations of biogeochemical tracer distributions. It would be interesting to see how different the different model configurations behave with respect to real data.

I.132, eq. 9. This metric does not seem to be area/volume weighted. Is this OK?

I.136 Some more explanation would be useful as to why a second metric was introduced to exclude solutions with low biomass of diazotrophs. Would these still have yielded a good fit to the model-derived N₂ fixation target?

I.147 Disregarding differences in the volume-weighted RMS errors of nutrient concentrations because they are smaller than the corresponding global standard deviations of the observations appears to rely on a very conservative criterion that does not necessarily rule out statistical significance of the differences. What would be the result of the same criterion applied to nitrogen fixation?

I.152. ‘hindcasting historical conditions’ is unclear. Presumably, what is meant is ‘preindustrial’?

I.157 It is not clear why the data compiled by Luo et al. (2012) are too sparse to allow for comparison with observations. For example, Paulsen et al. (2017) or Dutkiewicz

et al. (2014; 2015) used the Luo et al. (2012) data base to calibrate their model, Monteiro et al. (2010) used direct measurements in their investigation of controls on global patterns of nitrogen fixation as well. While the spatial and temporal coverage of the data in Luo et al. (2012) is far from optimal, it may still serve as a useful constraint. Why not use model-data misfits of these direct measurements rather than resorting to an indirect model-derived estimate? What is the correlation between the Luo et al. (2012) (or its Landolfi et al. 2018 update with a lot more data added for the Pacific Ocean, including those obtained as part of the SFB 754 work at Kiel) with the Wang et al. (2019) estimate?

I.171 why not compare also with Luo et al. (2012) fixation rates?

I.173. “the simulated distribution of diazotrophs based on OLIGO is more realistic than in GRAZ. The biomass of diazotrophs in GRAZ is apparently too low.” Given the very low optimized half-saturation constant for PO₄ and the ability of model diazotrophs to take up NO₃, the niche of diazotrophs may have expanded towards the niche otherwise occupied by oligotrophic non-fixing small phytoplankton. What is the percentage of NO₃ uptake relative to the total N uptake in diazotrophs in OLIGO? And what is the contribution of diazotrophs to total biomass and total production in OLIGO?

I.177ff. An interesting result shown in Fig. 1 and Fig. 2 is that both OLIGO and GRAZ do not simulate any N₂ fixation nor diazotrophs in the Bay of Bengal, which agrees much better with recent measurements (Löscher et al., 2020) than the notoriously high (and probably unrealistic) N₂ fixation rates simulated by most current ESMs, including the REF simulation. Only at the end of the Results section do the authors say that both model formulations show an onset of N₂ fixation in the Bay of Bengal in the middle of the 21st century (without showing any results or providing quantitative information). More information could turn this into a scientifically very useful result.

I.192-195 It would be interesting to understand why these ratios differ among the different models. Is this because of different surface nutrients, because of different grazing

pressures or because of different parameters of the diazotrophs?

I.200ff. This is an interesting result that the model is much more sensitive to parameter variations in the GRAZ configuration than in the OLIGO configuration (and presumably the REF configuration?). What is the reason for this different sensitivity? It would be helpful to make use of the results of the perturbed parameter simulations in Fig. 3 to get a more quantitative impression of the robustness of the results, e.g. by showing results of transient runs for all ensemble members that yield a cost function of some narrow range around the optimum of GRAZ and OLIGO (and REF?), respectively. A more detailed analysis might help to constrain the envelope of model responses, as claimed at the end of the introduction.

I.205 This is an interesting result that should be explored in more detail.

I.216 ff. This is an expected effect of global warming that has been discussed extensively in the literature, also with respect to its potential impact on biogeochemical cycles. References to respective papers should be included here to give proper credit.

References:

Altabet, M. A., M. J. Higginson, and D. W. Murray. The effect of millennial-scale changes in Arabian Sea denitrification on atmospheric CO₂. *Nature*, 415, 159–162, 2002.

Altabet, M. A. Constraints on oceanic N balance/imbalance from sedimentary 15N records. *Biogeosciences*, 4, 75–86, 2007.

Dutkiewicz, S., B. A. Ward, J. R. Scott, and M. J. Follows. Understanding predicted shifts in diazotroph biogeography using resource competition theory. *Biogeosciences*, 11, 5445–5461, 2014.

Dutkiewicz, S., A. E. Hickman, O. Jahn, W. W. Gregg, C. B. Mouw, and M. J. Follows. Capturing optically important constituents and properties in a marine biogeochemical and ecosystem model. *Biogeosciences*, 12, 4447–4481, 2015.

Fasham, M. J. R., H. W. Ducklow, and S. M. McKelvie. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research*, 48, 591–639, 1990.

Grosskopf T., and J. LaRoche. Direct and indirect costs of dinitrogen fixation in *Crocospaera watsonii* WH8501 and possible implications for the nitrogen cycle. *Frontiers in Microbiology*, 3, 2012.

Keller, D. P., A. Oschlies, and M. Eby. A new marine ecosystem model for the University of Victoria earth system climate model. *Geoscientific Model Development*, 5, 1195–1220, 2012.

Knapp, A. N., K. L. Casciotti, W. M. Berelson, M. G. Prokopenko, and D. G. Capone. Low rates of nitrogen fixation in eastern tropical south pacific surface waters. *Proceedings of the National Academy of Sciences*, 113, 4398, 2016.

Kriest I., and A. Oschlies. MOPS-1.0: towards a model for the regulation of the global oceanic nitrogen budget by marine biogeochemical processes. *Geoscientific Model Development*, 8, 2929–2957, 2015.

Landolfi, A., H. Dietze, W. Koeve, and A. Oschlies. Overlooked runaway feedback in the marine nitrogen cycle: the vicious cycle. *Biogeosciences*, 10, 1351–1363, 2013.

Landolfi, A., P. Kähler, W. Koeve, and A. Oschlies. Global marine N₂ fixation estimates: From observations to models. *Frontiers in Microbiology*, 9, 2112, 2018.

Löptien, U., and H. Dietze. Reciprocal bias compensation and ensuing uncertainties in model-based climate projections: Pelagic biogeochemistry versus ocean mixing. *Biogeosciences*, 16, 1865–1881, 2019.

Löptien, U., and H. Dietze. Contrasting juxtaposition of two paradigms for diazotrophy in an earth system model of intermediate complexity. *Biogeosciences Discussions*, 2020:1–16, 2020.

[Printer-friendly version](#)[Discussion paper](#)

Löscher, C. R., W. Mohr, H. W. Bange, and D. E. Canfield. No nitrogen fixation in the Bay of Bengal? *Biogeosciences*, 17, 851–864, 2020.

Monteiro, F. M., M. J. Follows, and S. Dutkiewicz. Distribution of diverse nitrogen fixers in the global ocean. *Global Biogeochemical Cycles*, 24, GB3017, 2010.

Moore, J. K., S. C. Doney, J. A. Kleypas, D. M. Glover, and I. Y. Fung. An intermediate complexity marine ecosystem model for the global domain. *Deep Sea Research Part II*, 49, 403–462, 2001.

Paulsen, H., T. Ilyina, K. D. Six, and I. Stemmler. Incorporating a prognostic representation of marine nitrogen fixers into the global ocean biogeochemical model HAMOCC. *Journal of Advances in Modeling Earth Systems*, 9, 438–464, 2017.

Prowe, A. F., M. Pahlow, S. Dutkiewicz, M. Follows, and A. Oschlies. Top-down control of marine phytoplankton diversity in a global ecosystem model. *Progress in Oceanography*, 101, 1–13, 2012.

Raven, J. A. Protein turnover and plant RNA and phosphorus requirements in relation to nitrogen fixation. *Plant Science*, 188-189, 25–35, 2012.

Schmittner, A., A. Oschlies, X. Giraud, M. Eby, and H. Simmons. A global model of the marine ecosystem for long-term simulations: Sensitivity to ocean mixing, buoyancy forcing, particle sinking, and dissolved organic matter cycling. *Global Biogeochemical Cycles*, 19, 2005.

Somes, C. J., A. Schmittner, E. D. Galbraith, M. F. Lehmann, M. A. Altabet, J. P. Montoya, R. M. Letelier, A. C. Mix, A. Bourbonnais, and M. Eby. Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochemical Cycles*, 24, 2010.

Vallina, S. M., B. A. Ward, S. Dutkiewicz, and M. J. Follows. Maximal feeding with active prey-switching: A kill-the-winner functional response and its effect on global diversity and biogeography. *Progress in Oceanography*, 120, 93–109, 2014.

[Printer-friendly version](#)[Discussion paper](#)

Weber T., and C. Deutsch. Local versus basin-scale limitation of marine nitrogen fixation. *Proceedings of the National Academy of Sciences*, 111, 8741–8746, 2014.

Wunsch C., and P. Heimbach. How long to oceanic tracer and proxy equilibrium? *Quaternary Science Reviews*, 27, 637–651, 2008.

Interactive comment on Biogeosciences Discuss., <https://doi.org/10.5194/bg-2020-96>, 2020.

BGD

Interactive
comment

Printer-friendly version

Discussion paper