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Biogeosciences Discussions

Interactive comment on "Overlooked runaway feedback in the marine nitrogen cycle: the vicious cycle" *by* A. Landolfi et al.

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We thank the referees for their thoughtful reviews and constructive comments that can improve the clarity and quality of the manuscript.

REFEREE #1

Comment: : I liked the central idea of this paper. It's an interesting concept and, to some degree, the sensitivity studies are a nice way to illustrate it. It's short and to the point. I feel that the presentation and some details of the execution could be improved; at present they are distracting and, for me, detract from the central message which

is interesting and seems robust. I feel that the central message is interesting but the presentation and model illustrations need some work.

We thank the reviewer for her/his generally positive evaluation and will concentrate more on the central message and thereby make the presentation more concise.

Comment: My itemized comments and questions below outline these concerns: 1. On that note, in discussing the N2 fixation pattern of the (slightly confusingly named) "CONTROL" simulation (p. 8910, lines 5-6) the authors remark that it is in close agreement with the inferences of Deutsch (2007). This reads as if the authors believe this to be a good thing, whereas current evidence suggests that the inferred N2 fixation patterns of Deutsch et al (2007), based on the divergence of the tracer P*, are rather implausible. See for example the compiled observations of Breitbarth and LaRoche (2005) and the more recent compilation of Luo et al (2012 - the MAREDAT compilation). Mills and Arrigo (2010) explain how variable elemental ratios in the phytoplankton can lead to this difficulty of interpreting P* divergence.

Answer: We thank referee 1 for pointing out the newly available database (Luo et al. 2012) on the global distribution of diazotrophs and associated fixation rates. Unfortunately, for the reason of very limited data coverage in the equatorial Pacific the Luo et al. database does not provide constraints on the validity of the Deutsch et al. 2007 hypothesis. Future updates of this database, as envisaged by Luo et al., will largely contribute to the current debate on the geographical location of N inputs by N2 fixation.

In our paper, however, we don't make any assumption regarding the current geographical distribution of N2 fixers. The main aim of our paper, is to investigate

potential implications of the conceptual model of high P* levels providing an ecological niche for N2 fixation. This relates to the interpretation of Deutsch et al. (2007), but also to underlying assumptions used in many global biogeochemical model parameterizations of N2 fixation. In the revised version of the manuscript we will emphasize this point more clearly. We will also point out more explicitly that we do not regard the "CONTROL" simulation, which agrees best with the Deutsch et al. findings and, which we will rename "BASELINE" simulation, as the most realistic simulation.

Our sensitivity analysis shows that if a tight spatial coupling between N2 fixation and denitrification occurs, as implied by Deutsch et al. 2007, then the conditions for a vicious cycle emerge and the balance of the marine N inventory is at risk. Our analysis suggests that there are factors, such as the combination of iron limitation and DOM dynamics, which can prevent this spatial coupling and avoid the vicious cycle and the resulting N loss. From the tropical/subtropical oxygen data distribution we infer that these factors must be currently at work to prevent the vicious cycle from occurring at large scales in the present ocean (Fig. 5d of the BGD version).

Comment: 2. The 150 year timescale of the model runs is rather too short for a manuscript which discusses the large-scale biogeochemical balance in the nitrogen cycle. There a strong transient in 3 of the 4 model runs but eventually P* must settle down on a global scale. How can we be sure this isn't just an initial transient because the initial conditions of the experiments don't match the system being integrated? In the case of the runaway feedback would we eventually see a global build up of P*? Why isn't the excess P used up somewhere else? I feel that at least one case should have been run for thousands of years to see what the long term development is? Its hard for me to clearly envisage what the final state would be and this model is certainly coarse enough to integrate for much longer timescales. If possible I feel that all cases

should be integrated for at least a millenium. The Atlantic and Pacific basins are not communicating very much on this centennial timescale. I find the short integrations a significant concern as it muddies the waters considerably when talking about global balance/imbalance.

Answer: We agree with the reviewer that the sensitivity simulations investigated here all display some transient behavior and that they will eventually reach some steady state with a constant nutrient inventory and P* distribution. However, current coarse-resolution ocean circulation models such as the model used in our study, which can be integrated for thousands of years without using up excessive computational resources, do still have many deficiencies and accordingly display substantial deviations from observed nutrient and oxygen distributions (Kriest et al., 2012). Issues of particular relevance in the tropical oceans are the "nutrient trapping" problem, i.e. an excessive remineralization of nutrients in the eastern tropical Pacific (see Aumont et al. 1999) and the general difficulty of simultaneously simulating realistic distributions of excess P in all ocean basins (Somes et al., 2010). These model deficiencies enforce a decision between considering an equilibrium solution, which deviates substantially from observed conditions or considering a transient solution, which is still close to the observed nutrient and oxygen distributions. Here we opt for the latter alternative, because we want to investigate the feedback effects linking nitrogen fixation and denitrification in action. Equilibrium solutions would not allow comparing net nitrogen losses resulting from different parameterisations, but only allow the indirect quantification of feedback effects via different nutrient inventories.

The reviewer is right to say that P* is expected to increase. Given a constant phosphate inventory in our model, declining nitrate inventories compared to initial (observed) conditions are consistent with an increasing P* inventory. In

fact, it has been observed in equilibrium model runs with similar biogeochemical models (but in a different physical setting) that nitrate inventories do not recover and continued to decrease. To give an example we show mean ocean nitrate and P* (Fig. 1 in rebuttal; A. Oschlies, unpublished data) from a 10,000 years spin up of the Kiel version of the UVic earth system model (Keller et al., 2012). Starting from WOA09 nutrient fields a sharp decline of the NO3 concentrations is observed over the first 1000 years. After a slight recovery, the mean NO3 concentration settles into a steady state, which, is far from the initial condition. That there is only a slight recovery is due to the fact that the growing P* can only trigger N2-fixation in surface waters. Obviously most of the additional P* has no effect, basically since it is stored away into the interior of the ocean. While eventually all model solutions in the typically dissipative models will reach a steady state, an active vicious cycle is best diagnosed in its transient state. Given the relatively short time scales on which oxygen minimum zone water connect with the upwelling regions (Glessmer et al., 2009), and the relatively short timescales of the proposed feedback cycles, we think that our approach of sensitivity simulations starting from observed biogeochemical tracer distributions is robust.

We find that the vicious cycle is independent of the model deficiencies or parameter settings. The vicious cycle is merely the result of the stoichiometric imbalance between the amount of NO3 used up in the denitrification process versus the amount of N gained from N2 fixation. Denitrification uses 120 moles of nitrate per mole of phosphorus for Redfield organic matter and even higher NO3 is needed for organic matter with higher N:P. Instead, only 16 moles of nitrogen (per mole phosphorus) are gained during N2 fixation. Thus, denitrification naturally leads to more NO3 loss than N gained. This holds for any realistic organic matter stoichiometry. As the amount of NO3 needed for denitrification of organic matter is related to its C and N content (see RNloss equation in the manuscript) a net N loss is observed also considering higher N:P elemental ratio of diazotrophs. This means that N2 fixation cannot compensate for N

losses if the fixation-derived organic matter is remineralised via denitrification. Independent support comes from the large drifts of the N inventory from initial conditions observed over millennial timescale simulations (eg. Moore and Doney 2007, Schmittner et al., 2008). We will improve the description of the vicious cycle in the text to prevent any confusion.

Comment: 3. The choice of a low temperature cutoff for diazotroph growth may be convenient, and may not really matter for the key point of this paper, but I think it serves to continue to promote the idea that this is a real physical limitation. While Trichodesmium may not grow at lower temperatures, diazotrophy is certainly possible witnessed, for example, by the activity of other nitrogen fixers in the Baltic. See, for example, Staal et al (2003) for a discussion. So, I do feel that this temperature limitation is a bit of a hack which, though perhaps not critical to this message, promotes the use of an unrealistic parameterization.

Answer: We agree with the reviewer that the fixation of N2 is not intrinsically inhibited by low temperatures (Sohm et al. 2011). Infact a recent modeling study (Monteiro et al. 2011) suggested that the restriction of diazotroph to tropical and subtropical regions is the outcome of nutrient resource competition with non-fixing phytoplankton rather than of temperature control itself. However, optimum growth temperatures in laboratory and field experiments are well documented (eg. Moisander et al. 2010, Breitbarth et al. 2007). Differences in optimal growth temperature appear to be related to the diverse strategies adopted by the diazoptophic groups to protect nitrogenase from oxygen inactivation (Stal, 2009). High oxygen solubility at low temperatures, as in the Baltic Sea, impose alternative strategies, such as the build up of heterocysts, to maintain anoxic conditions within the N2 fixing cell (Stal, 2009). We will comment on the problems associated with the model's temperature limitation in the revised

version and modify Figure 1 of the manuscript accordingly.

Comment: 4. Even in the "most realistic" case, the simulated nitrogen fixation distribution does not capture key features of the observed compilations (e.g. Luo et al 2012) where there is intense diazotrophic activity in the tropical and subtropical Atlantic. Is this to do with the short integration times and transients in the N cycle? Is it to do with the physical resolution?

Answer: Our model does not fully reproduce the observed distribution of N2 fixers in the North Atlantic. We do not think that this is related to the short integration times or the coarse resolution of the grid. Rather, we think that this deficiency is due to the underlying assumption in this, and other model parameterisations of the ecological niche of diazotrophs (and also in the estimate of Deutsch et al. 2007): According to these, the principal control at work is that slowly growing diazotrophs have an advantage over ordinary phytoplankton only in high-P* areas. Reproducing the observed distribution of N2 fixers has been a major challenge in fully prognostic biogeochemical models (eg. Coles and Hood 2007, Moore & Doney 2007). In the standard assumptions used to parameterize the ecological niche of diazotrophs in current models as well as in the observational estimate of Deutsch et al. (2007), N additions via N2 fixation activity tend to reduce the diazotrophs' niche by leading to P limitation. Partial fixes to this problem have been suggested by increasing phosphorus remineralization rates relative to nitrogen by a factor of two and/or by diazotrophic DOP uptake in regional models (eg. Coles and Hood 2007). These fixes however, do not seem to be sufficient to reproduce observed patterns of nitrogen fixation in our global biogeochemical model. Further work to improve this aspect of our model is currently under way and will be published elsewhere. It is likely that an improved representation of N2 fixation in the North Atlantic would, in the global average, enhance the spatial decoupling of N2 fixation from denitrification sites further and thereby reduce the potential for the occurrence of a vicious cycle. This is in support of our main conclusions and will be discussed in more detail in the revised version of the manuscript.

Comment: 5. I felt that the abstract and the progression of the text dont do the spirit of article justice. The abstract seemed a bit too "abstract" to tell what was coming. I think a more straightforward and concise description of the feedback mechanism and influence of decoupling would have let me know where the manuscript was going and I would have been able to appreciate more quickly the idealized experiments, rather than having the light come on half way through the paper.

Answer: Thank you for pointing out the deficiencies of the abstract. We will rewrite the abstract accordingly in the revised manuscript.

REFEREE #2 K. J. MOORE

Comment: I found this to be an interesting paper, even though I disagree with the authors' main conclusion that a “vicious cycle” is possible, where increased N fixation above the major water column denitrification zones can lead to accelerating net N loss for the oceans. I believe the paper should be published in BG after some revision and modification. The vicious cycle disappears in the simulation presented when a parameterized iron limitation is added to the model along with advective transport of semi-labile DOM. Both additions make the model more realistic, with respect to what we know about the real ocean, particularly the eastern tropical Pacific. I would suggest even shifting the emphasis of the paper from the vicious cycle to the importance of these two factors for correctly simulating the marine N cycle.

Answer: We thank the reviewer K. Moore for his very constructive and insightful comments that will help to improve the final version of the manuscript. Additional figures have been prepared that will be included in the revised manuscript.

We agree with the reviewer that in the real ocean numerous factors work against the persistent operation of a vicious cycle. Theoretically, however, the stoichiometry of nitrate consumption during denitrification of organic matter leads to a net loss of fixed nitrogen whenever remineralization of newly fixed organic nitrogen occurs via denitrification in suboxic waters. For Redfield stoichiometry, the vicious cycle can start in any water column where more than 1/7th of the newly fixed organic nitrogen is remineralized via denitrification. Our Figure 5d shows areas where, according to oxygen distributions from the World Ocean Atlas, the Martin particle flux curve and the assumption of Redfield organic matter, an onset of the vicious cycle is possible.

Factors that help to avoid operation of the vicious cycle in our model simulations are iron limitation and DOM dynamics, which appear to make the model more realistic and contribute to a spatial decoupling of N sources and sinks. In the revised paper we will more explicitly acknowledge this apparent advance in the model's degree of realisms. However, without a better mechanistic understanding of the controls of diazotrophy, we are reluctant to focus too much on these model improvements and rather prefer to leave the emphasis of the paper on the potential action of the vicious cycle in relation to the spatial coupling of N sources and sinks. In this regard our findings represent a very new perspective on the stabilizing feedbacks of the marine N cycle. Our results contrast the common understanding that decoupling N inputs from N losses may drive the oceanic fixed N inventory away from steady-state. For example N2 fixation is thought to be able to compensate for N losses as long as iron limitation does

not limit its activity (eg. Codispoti et al. 1989, Falkowski et al. 1997, Moore and Doney et al 2007) or if non-Redfield nutrient utilization occurs (Mills and Arrigo 2010). However, our results suggest that factors such as iron limitation of diazotrophic activity help to avoid large-scale operation of a vicious cycle that would lead to substantial loss of fixed marine nitrogen.

Comment: 1. The lack of an explicit iron cycle is a real weakness of the model. The static parameterization of iron limitation is also problematic, in that it does not allow for important feedbacks that could influence the N cycle dynamics. For example, increasing export above the denitrification zones, would lead to increased scavenging loss for sub-surface iron, ultimately reducing iron inputs to surface waters and providing a negative feedback on the export production. Also, the prescribed iron limitation is likely too weak, and would vary in the real ocean no a number of factors including upwelling rates, among other factors. In the ocean biogeochemical model that I utilize, the CESM-BEC model (Moore et al., 2004), the growth rates of the diazotrophs are reduced by 50% in the equatorial upwelling zone (compared with the factor of 0.8 reduction used here for diazotrophs), but off the equator iron limitation reduces the growth rates even more to 20-30% of the maximum. The paper assumes a 50% reduction in growth for the non-diazotrophs, while our model would predict similar reductions for the small phytoplankton, but even large reductions for diatoms. Thus, the iron impacts on N fixation are likely significantly underestimated in their IRON case.

Answer: We do agree with the reviewer that an explicit model of iron biogeochemistry would be desirable. However, our choice of not having an explicit iron cycle in our biogeochemical model stems from the large complexities and uncertainties associated with the iron cycle that include solubility, bioavailability, particle scavenging and complexation by ligands (eg. Boyd & Ellwood 2010). However, even our simple and pragmatic parameterization of iron limitation

in not static as it allows for some feedbacks on the N cycle. Concerning the example described by the reviewer, the increased export above denitrification zones would lead to a reduction of PO4 concentrations relative to WOA PO4 concentrations. This in turn would "switch on" the model's iron limitation and thereby reduce growth rates of both ordinary phytoplankton and diazotrophs, mimicking iron limitation and providing a negative feedback on export production.

In order to explore the sensitivity of our results to the prescribed iron limitation, we have set up an experiment varying the degree of growth rate limitation. We find that a reduction of the iron constraint of the diazotrophs growth rate from 0.8 (as used in the IRON experiment) to 0.5, as suggested by the reviewer, results in a N inventory decrease of 6.4% instead of 5% over 150 years. Thus, the magnitude of the N loss is sensitive to the degree of decoupling of N2 fixation from denitrification induced by iron limitation in support of our conclusions. We will add this finding to the corresponding 'Results' section of the revised manuscript.

Comment: 2. There are additional factors that I think should work against the vicious cycle in the real ocean. Additional detail on the model structure in the methods section and appendix would help clarify the significance of some of these factors. One factor is the export efficiency of different phytoplankton groups. Is there any difference in export efficiency between diazotrophs and non-diazotrophs in the model? I would expect that a shift towards increasing N fixation in the upwelling zone at the expense of diatoms, would significantly decrease the export ratio, even if total production were increasing. Given the positive buoyancy of Trichodesmium species, the export of efficiency of diazotrophs may even be lower than other small phytoplankton species.

Answer: We thank the reviewer for bringing up this interesting point, which we neglected in the first version of our manuscript. In the present model the export efficiency between diazotrophs and non-diazotrophs is the same. However, previous experiments (not shown) revealed that a reduced export efficiency of diazotrophs resulted in increased export rates of ordinary phytoplankton. In the upwelling regions above the OMZs the remineralization of N2-fixation derived N stimulated export production by non-fixing phytoplankton. Thus, any inputs of new nitrogen by diazotrophs, eg. as DON, must have remineralization time-scales that allow the advection of the newly fixed nitrogen away from the OMZ to reduce the potential for a vicious cycle. We will add this information to the Methods section.

Comment: 3. A second point related to the N fixation seen in their simulations above the denitrification zones is whether it is realistic for diazotrophs to comprise a significant fraction of the community in upwelling zones. I would think that the diazotrophs would be largely outcompeted by faster growing phytoplankton, unless the subsurface denitrification had completely stripped out DIN. What percentage of the community do diazotrophs make up in terms of production and export in these simulations, and how does this vary spatially?

Answer: We added a new figure (see Fig. 2 of rebuttal) to show that the model's diazotrophs may contribute up to 40% of total production in the upwelling regions where surface NO3 is not completely drawn down. Co-existence of diazotrophs with non-fixing phytoplankton in regions where NO3 is not completely drawn down is favored in our model by the use of a Holling type III grazing function (Prowe et al. 2011). We will include this information in the revised version of the manuscript.

Comment: 4. Given the high nitrate concentrations in the upwelling regions, the diazotrophs present would likely be obtaining much of their N through DIN uptake, rather than through N fixation (Holl and Montoya, 2005). Thus, the potential for N fixation to increase export into the OMZs would be greatly reduced. How is N uptake partitioned between DIN and fixation in the model, and what are the relative fractions from each source in different regions?

Answer: As correctly indicated by the reviewer, in regions where NO3 is present N2 fixers take up NO3 rather than fixing N2 (see Fig. 3 of rebuttal). In our model, this is however a small percentage relative to their total production (mmol N/m3/y) in regions of elevated activity (Fig. 4 of rebuttal). This issue will be discussed in more detail and shown in a new figure. However, the vicious cycle may persist also if N2 fixers obtain much of their N through NO3 uptake. The vicious cycle will persist as long as any N2-fixation derived organic matter will be remineralized via denitrification within an OMZ (Fig. 1c of the BGD version). Organic matter production by ordinary phytoplankton will eventually stop when surface waters become NO3 depleted (Fig. 1b of the BGD version). Instead, organic matter production by diazotrophs can persist under such conditions being unaffected by NO3 limitation (Fig. 1c of the BGD version).

Comment: 5. The total denitrification and N fixation in these simulations are very low compared to the observational estimates. Some discussion of this fact and its causes should be added to the paper. Figure 4 should include a panel with the observed OMZ thickness in the corrected WOA data. The simulated thickness, particularly in the CONTROL simulation appears too thick relative to the observations. How much of a role does this play in the vicious cycle?

Answer: The N2 fixation estimates of the DOM run (180 TgN/y) compare well with

the very recent current global extrapolations of direct measurements (1̃77 TgN/y) (Grosskopf et al. 2012) and lie in the upper range of the traditional geochemical estimates (135 ± 50 TgN/y) (Gruber, 2004). Current global-ocean estimates of denitrification vary between 200-400TgN/y (Gruber 2005, Codispoti et al. 2001). These estimates include sedimentary denitrification that is thought to comprise at least half of total denitrification (Somes et al. 2010, Altabet et al. 2007). As our model does not comprise sedimentary denitrification our simulated water column denitrification estimates (10-25 Tmol N/y = 180 - 350 TgN/y) lie in the upper range of the observational estimates. Elevated model denitrification rates are associated with errors in simulating oxygen fields that result in larger and thicker OMZ relative to observations (Fig. 5. of rebuttal. This figure, where we added WOA data OMZ thickness as suggested by K. Moore, will substitute Fig 4 in the revised version of the manuscript.). This is a common problem in global coupled biogeochemical circulation models (eg. Gnanadesikan et al. 2002) that is found to be mostly related to the deficient representation of the equatorial current system (Dietze and Loptien, submitted 2012).

The vicious cycle is merely the result of the stoichiometric imbalance between the amount of NO3 used up in the denitrification equation versus the amount of inorganic N gained from the remineralization of organic matter derived from N2 fixation. Thus, remineralization of organic matter via denitrification naturally leads to more NO3 loss than inorganic N gained for any realistic organic matter stoichiometry. An improved model circulation should result in a more realistic oxygen distribution and reduced expansion of the OMZs. This latter would favor oxygenic remineralization relative to denitrification resulting in a somewhat reduced potential for the vicious cycle to occur. Nevertheless, the ongoing expansion of tropical OMZs (Stramma et al., 2008) has to be considered if we are to predict the evolution of the N cycle in a highly changing environment.

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Fig. 1. Nitrate (upper panel) and P* (lower panel) concentrations (mmol/m3) for 10,000 year sin-up of the Earth Sytem Climate Model, UVic version 2.9, (Keller at al. 2012).

Fig. 2. Average NO3 concentrations (mmol NO3 / m3) in the surface (upper 50m) for (a) CONTROL and (b) IRON simulations. Contribution of diazotrophs to total autotrophic production (%) in (c) CONTROL and (d) IRON simulations. Black contour represents the 0.02 mmol NO3 / m3 isoline.

Fig. 3. NO3 uptake of diazotrophs (mmolN/m2/y) in the (a) CONTROL (b) IRON and (c) DOM simulations. DOP uptake (mmolP/m2/y) in the (d) DOM simulation.

Fig. 4. Fraction of diazotroph NO3 uptake relative to their total N uptake (%) in (a) CONTROL (b) IRON and (c) DOM simulations. Fraction of DOP uptake (%)

relative to total P uptake in the (d) DOM simulation.

Fig. 5. Average thickness (m) of the low O2 water layer (lower than 5 mmol/m3) in the WOA (a) and CONTROL simulation (b). Panel (b) and (c) are thickness changes of the (b) IRON and (c) DOM simulations relative to the CONTROL simulation. Thickness changes are in units (m) with negative numbers denoting reductions relative to the CONTROL simulation.

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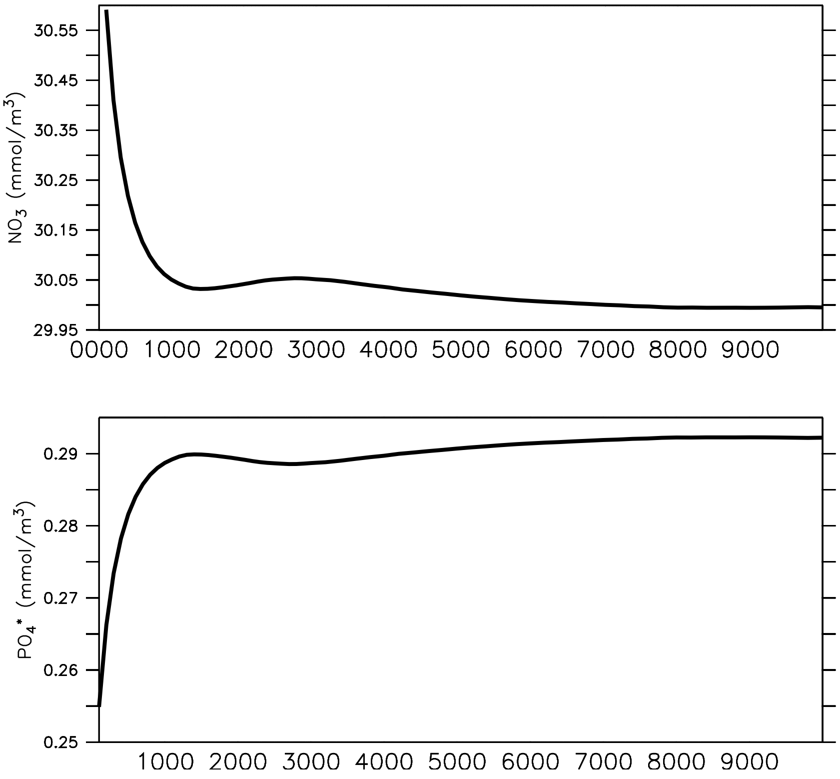
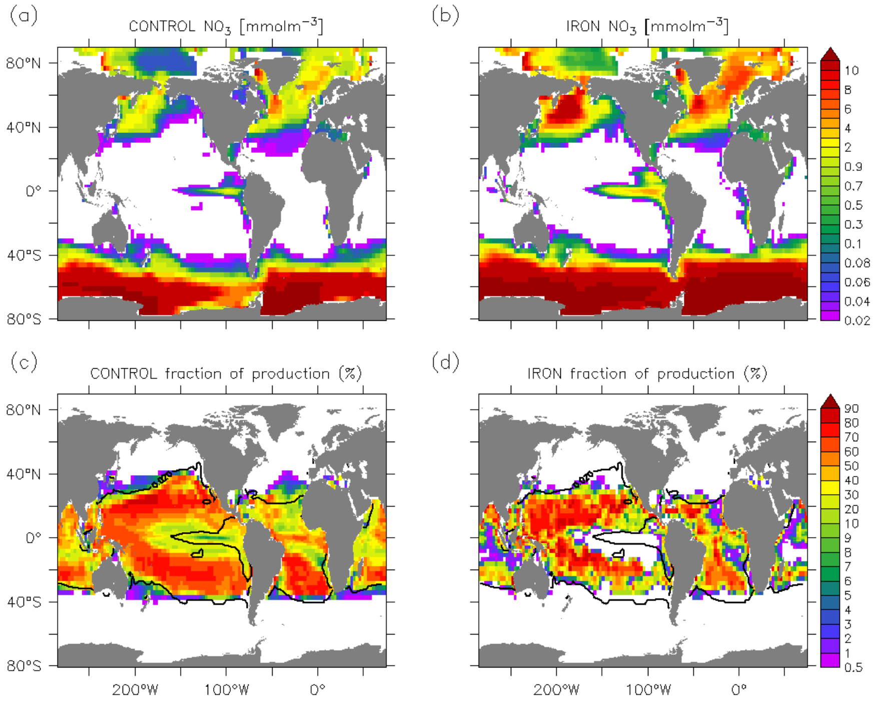


Fig. 1. Nitrate (upper panel) and P* (lower panel) concentrations (mmol/m3) for 10,000 year sin-up of the Earth Sytem Climate Model, UVic version 2.9, (Keller at al. 2012)



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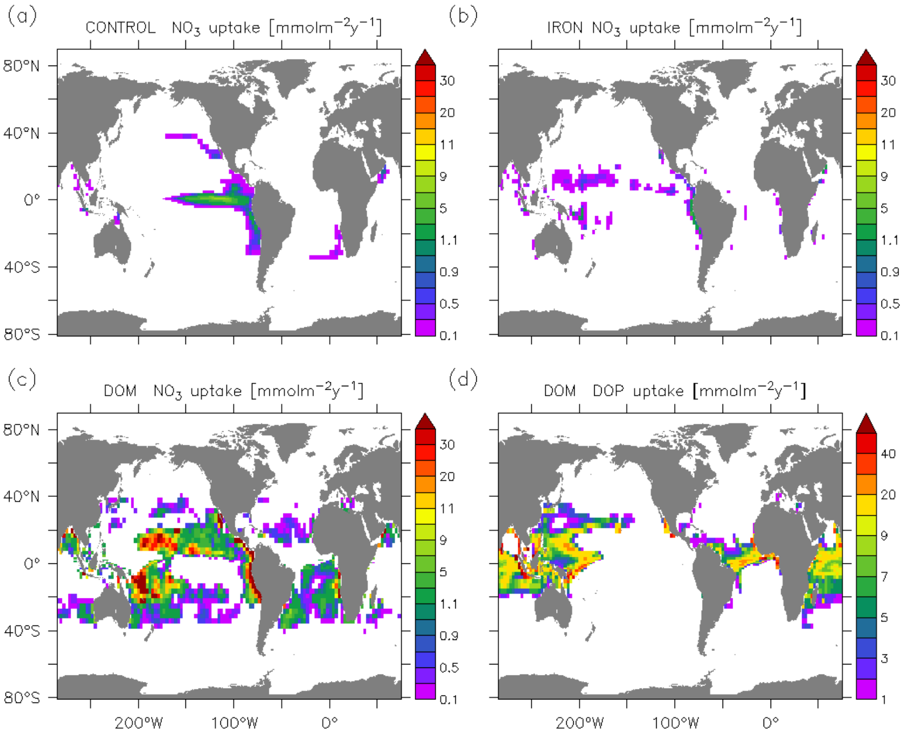

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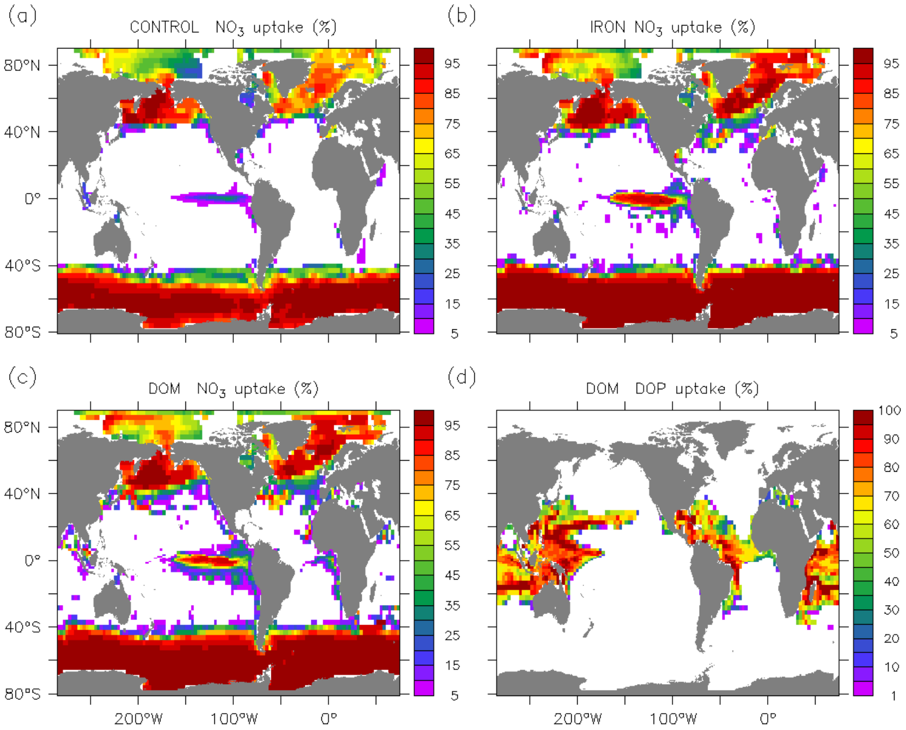

Fig. 4. caption in text

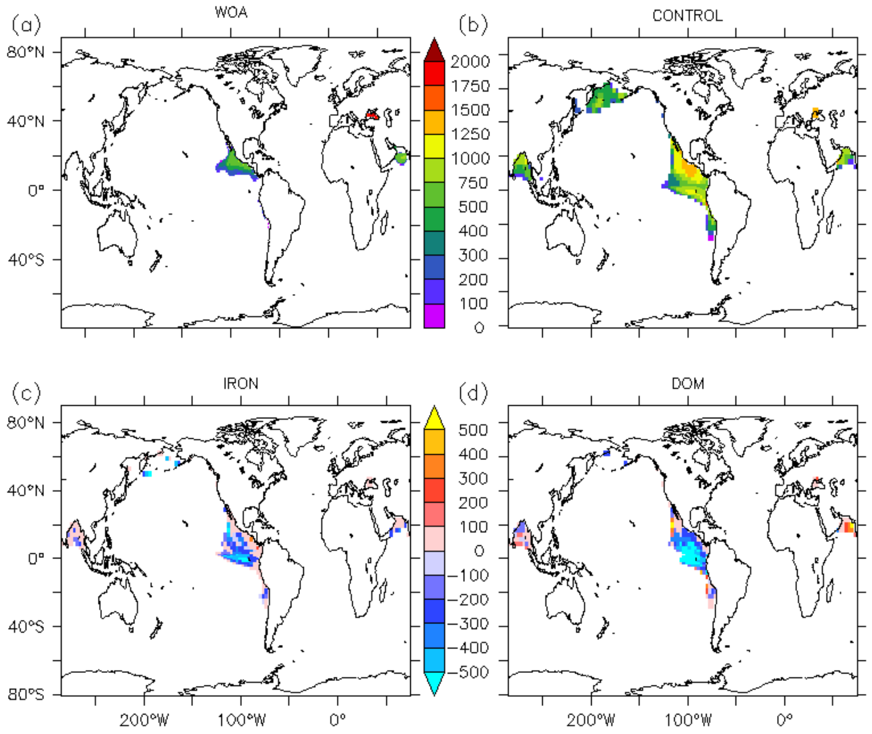

Fig. 5. caption in text