This study by Zakem et al. uses a global microbial ecosystem model to estimate controls, rates, and abundances of nitrifying microbes (AOA and NOB) in the ocean. Their microbial ecosystem model is based on characteristics of known AOA and NOB communities, which allows predictions of their abundances and rates to emerge in a dynamically consistent way without having to prescribe simple rate functions like most global biogeochemical models. There still seems to be considerable uncertainty in some parameters, which was addressed with an ensemble of model simulations. They use measurements on rates and yields to distinguish the different parameters between AOA and NOB functional types to best estimate their abundances and rates, using three approaches starting with a steady-state 0D model to validate the core microbial model, then with a vertical water column, and finally with a global 3D model. They find that the NH3 and NO2 oxidation rates are mostly consistent in the deep, oxygenated ocean and primarily driven by the export of organic matter to the local system. Global NO2 oxidation rates are slightly lower than NH4 oxidation due to their model predicting NOB are less competitive against phytoplankton relative to AOA. An important finding is that AOA fixes about twice as much carbon mainly due to their higher yield compared to NOB. Their model estimates a global carbon fixation rate of 0.2-0.5 Pg C yr-1 which is a small fraction of global net primary productivity.

Overall I find this to be an important and informative study on global nitrifying microbial communities and their associated rates. I think it was very well written with an ideal balance between a concise technical description and understandable results. The model results and caveats are fairly addressed and discussed. My only minor criticism is that some additional insights and discussion could be provided in the paper (see minor comments below).

Best regards,

Chris Somes

GEOMAR Helmholtz Centre for Ocean Research Kiel

Thank you very much for your careful analysis and constructive feedback, Chris.

Minor Comments:

Figure 4: NPP and Export patterns

It is interesting to me that your global NPP rates are consistent with most estimates whereas the export is on the very high-end of the estimates. I wonder if that has something to do with relatively high nitrification occurring in the euphotic zone.

Good question. In our model, NPP and the export flux are able to be decoupled because of our dynamic remineralization. The decoupling is predominantly controlled by the parameterization of heterotrophic microbes that consume POM and the sinking rate of the POM. So, to first order, nitrification in the euphotic zone does not control this decoupling. Rather, euphotic zone nitrification can be thought of as, predominantly, the “gleaning” of reduced DIN that phytoplankton are otherwise unable to assimilate, mostly when they are partially light-limited towards the base of the euphotic zone. In some dynamic areas, bloom-like conditions can result in abundant DIN supply in the euphotic zone in which case nitrification may coexist with phytoplankton because competitive exclusion has not yet taken place, but this would have a smaller impact on NPP from the fact that phytoplankton would have access to more NO3 than NH4, which has a small energetic cost (reflected in slightly lower uptake kinetics by phytoplankton in the model). In the revised manuscript, we will better explain the controls on the export flux, their uncertainties, and the choices that we make about them in the parameter values.

I'm surprised to see highest NPP and export rates in the Southern Ocean on the annual average, is that consistent with other estimates? If export is overestimated in the Southern Ocean, would that imply NPP might be underestimated in the low latitudes? Does export efficiency (including through the twilight zone) change significantly between low and high latitudes which could alter vertical profile total nitrification rates in different regions?

The high NPP in the S. Ocean is consistent with other published Darwin model estimates. The observations are fairly uncertain there. Stephanie Dukiewicz's work comparing the Darwin ecosystem model output to observed NPP and chlorophyll does suggest: 1. Observations, when they are there, suggest lower productivity in the S. Ocean, and 2. Observations are often missing in that area. (See, for example, Dutkiewicz et al. 2015 *Biogeosci.* Fig. 6 and Dukiewicz et al. 2019 *Nat. Comm* Fig. 1 a and c). Conversely, as you suggest, the model predicts lower productivity in the oligotrophic gyres than observations suggest (see same references/figures). Since export scales with NPP to first order (our Fig. 4b), yes, it changes significantly along latitude following this pattern and yes, it would likely has this same bias when compared to observations (though this is speculation, since our global observations of export are limited). And similarly, nitrification rates could be biased high at high latitudes and low at low latitudes. It would be interesting to do a spatial analysis diving into this, and work on fixing the ever-present problem of how to spread sufficient nutrients into the gyre centers in order to support higher productivity rates there. However, for the purposes of this study, we think the global integrals are still useful estimates. We will include discussion of this model bias, and the uncertainty in S. Oc. NPP in both model and observations, in the revised manuscript.

Lines 317-318: 10-30% of global total

It is intriguing to me that your analysis suggest up to 30% of global nitrification may occur in the euphotic zone. In Figure 3b, it even appears your model is significantly underestimating NO2 oxidation at the base of the euphotic zone. I'm curious about this uncertainty range as I see very little shading around the model lines in Figure 3b.

Thank you for pointing this out. Yes, we realize that our results seem to suggest that there is both huge uncertainty (10-30% of euphotic zone nitrification in 3D) yet very little uncertainty (in 1D). In both models, we vary only the parameters that directly influence the growth and mortality of the nitrifiers (as described in Methods). Because of the dynamic environments in the 3D model, in contrast to the strictly steady state solutions found in 1D, the uncertainty in these parameters results in a much wider range of realized solution space in 3D. However, there is much more uncertainty in the model from other parameters, both in the 1D and 3D configurations. For example, in neither model do we vary the parameters that impact the export flux (i.e. heterotrophic bacteria) or the physical environment, and these parameters would change the depths and intensities of nitrification in both 1D and 3D. Therefore, the mismatch between model and data in the 1D model (Fig. 3) is likely controlled predominantly by this uncertainty that we do not explicitly consider in the ensemble. When we do incorporate this additional uncertainty, the shaded areas become large everywhere, and we lose what we think now is a helpful aspect of interpretability: the fact that abundances and C fixation rates reflect the uncertainty from parameter variations but the nitrification rates remain robust because they are controlled by the export flux. For similar reasons, we did not want to consider all of the uncertainty in all of the ecosystem parameters in the 3D configuration. Also, dealing meaningfully with the full model uncertainty in 3D requires a very involved approach (i.e. 3D ensemble with variation in hundreds of parameters, Monte-Carlo style), which the Darwin-MITgcm configuration has not been designed to do. Thus we took the approach of here relying on an upper estimate of the export flux in order to make the conclusions that we do. We will improve the discussion of the parameter variations and impacts on the solutions (i.e. the 1D vs the 3D uncertainty ranges) in the revised manuscript.

Lines 271-272: “NOB … are higher than AOA … due to anaerobic NO3 reduction”

I find it interesting that the highest NO2 oxidation rates in the global ocean occur near oxygen deficient zones. I wonder how well ODZs are reproduced and how that factors into the uncertainty given the very high rates (I think you mean Fig. 4 c and d instead of Fig. 2 here since I don’t see any indication of oxygen in Fig. 2). For example, I don’t see any hot spot in the Arabian Sea ODZ and there appears to be a hot spot off the North African Eastern Boundary Upwelling System that is not related to export which is typically not anaerobic.

Yes, we consider the ODZs as only qualitatively reproduced, in that anoxic zones form in roughly the right areas (though as you say, missing the Arabian Sea ODZ and having too much O2 depletion in the S. Atlantic). We did not analyze their extent in the model or the mismatch between observations and model. You are correct that this could add uncertainty to our global totals. It would be straightforward and clarifying to calculate the amount of NO2 oxidation in the model ODZs and include that in the analysis in the revised manuscript. Since global NO2 oxidation is lower than NH4 oxidation, we can tell that it has a smaller effect than the higher competitive ability of AOA vs. NOB relative to phytoplankton in the model, but it will still be interesting to quantify. Thank you for this suggestion. Regarding the figures: We did want to point out that Fig. 2 c and d reveal the decoupling between NH4 and NO2 oxidation as well as Fig. 4 c and d, but now we realize that we put that in the wrong place and that Fig. 4 c and d is indeed the right reference for this statement. Thanks for pointing this out.

Section 4.2:

Most global biogeochemical models estimate nitrification based on the amount of particulate organic matter (from export) that remineralizes in each location, which you also acknowledge (lines 147-148) is the main driver of nitrification rates in your model. Thus, I am not completely convinced that global biogeochemical models that do resolve microbial ecosystem functional types cannot provide reliable estimates on global nitrification rates, so perhaps you can be more specific about what you mean by “biogeochemical models that parameterize nitrification using a bulk rate constant do not provide the framework necessary for directly linking laboratory measurements to global-scale dynamics”.

It is true that models with implicit nitrification should in principle be able to estimate deep nitrification rates accurately, if the export flux is estimated accurately. This follows from the conclusions that we make about the steady state nitrification rates and their insensitivity to nitrifier parameters, and we will emphasize this in the text. What we meant by this statement is that the bulk rate constants used in implicit schemes cannot be constrained by the measured values that we use to describe AOA and NOB in the model here. At least, that is our understanding. In contrast, we can use the measured values directly into our parameterization. Therefore, the models with implicit nitrification can get the rates right (if our analysis here is correct that the kinetic parameters don’t matter!), but they don’t help us connect the dots between nitrification rates and associated abundances of organisms, for example, that we would need to start making connections with sequencing datasets. We will revise the statement here to clarify what we mean and emphasize that our results actually support the ability of implicit nitrification schemes to predict nitrification rates.

One important exception is nitrification occurring in the euphotic zone. If possible, perhaps you can provide some insights or recommendations about how global biogeochemical models unable to explicitly resolve microbial functional types could best parameterize this process?

Interesting question. Perhaps there is a way of considering when “excess” reduced DIN exists in the euphotic zone. Primary production (or, phytoplankton growth, if phytoplankton are resolved) could be calculated in two ways: 1. Calculating the potential primary production that would occur if it were only limited by DIN, and 2. Calculating it way it is already being calculated, taking into account limitation by DIN, light, and other nutrients. Then, you could subtract 2 from 1 to give a rate of potential DIN assimilation that isn't being reached because phytoplankton are limited by something else. You would need to take care and also assume that nitrifiers require other nutrients (such as Fe), though at different ratios than phytoplankton relative to DIN uptake. You could then have an implicit rate of euphotic zone nitrification. I think this might work, but it would need to be worked out in a model comparison, and ideally constrained by observations as well. Our euphotic zone estimations still need to be tested with data. We should collaborate.

Section 4.4: "first" (lines 342-344) and "third" (lines 347-350) reasons

These appear to be processes that are more realistically accounted for in your model estimate compared to previous ones. For example, you apply higher yields, but these are supported by recent observations. In my opinion, due to these two processes, this suggests these previous estimates should be considered underestimates or a lower bound more than your estimate here is an overestimate or an upper bound.

We agree that for these reasons some of the previous estimates could be considered underestimates. For example, Bayer et al 2022 do not consider euphotic zone nitrification. But other previous estimates are likely overstimates: Pachiadaki et al 2017, for example, estimated that NOB alone might fix ~1 PgC/yr. It will be helpful to differentiate these two types of previous estimates. The types that can be connected to our present model (such as Bayer et al 2022, because they use the same yields but not a global model with euphotic zone nitrification, and Zhang et al 2020, because they use the same model but lower yields) should be discussed as such.

We still think that we can consider our model as an upper estimate of global nitrifier C fixation, independent of any relationship with previous estimates or models. We think all of the mechanisms considered result in a maximum potential (or a ~10% overestimation in the case of the export flux) of nitrification and C fixation. However, given this comment and the lack of certainty about euphotic zone nitrification rates, we realize that it is not precise to consider it a true upper bound. We have not suggested, even theoretically, that our estimate should include the maximum amount of euphotic zone nitrification possible. We will change the wording from "upper bound" to an "upper estimate" in the revised version.

Lines 345-347: modeled export flux is larger than previous estimates

It is still unclear to me how this error is accounted for in the uncertainty range. Earlier (e.g. line 281) you show that export production occurs between 11-12 Pg C yr-1 in your model. Is it right that your low-end of your uncertainty range for nitrification rates is driven by a model with export production at 11 Pg C yr-1? Or are the low-end rates reduced in some way to explicitly account for the fact the export production is likely too high? Since this is the clear process why your model estimate is providing an upper bound for global nitrification, I think exactly how you account for likely overestimated export production in your uncertainty range should be explicitly described in the main text. On line 149, you state this will be described in section 3.3.4, but I don't find an explicit description of this other than mentioning that export production is larger than other estimates.

We will explain more clearly explain how the error relates to the export flux. We did not change the parameters that impact the export flux directly. The reported range in export in the global model was due to the choice of cutoff to exclude the very high values of export in the coastal grid points (where the model has no skill and makes wildly wrong predictions; lines 152-153). There is a very clear plateau at this total estimate of export, so it is not an arbitrary cutoff (see below plots). So, all global model simulations have the same 12-13 PgC/yr export estimate. The variation in nitrifier parameter values does not change the export. This is confusing, we realize now! We should more clearly explain this in more places, including the caption of the table.

Second, yes, you are right that the low end of our range of global integrals is indeed with respect to this still very high, constant rate of export. We do not attempt to estimate what nitrification rates would be if the export flux is actually lower, so, our results should not be interpreted as providing the full plausible range of global nitrification rates. This is one reason why we wanted to emphasize that our model provides an upper estimate. Conversely, the low end of our range is not particularly useful. We will clarify this in the revised text. Specifically, we will rewrite the paragraph that includes line 149. We will include a more detailed description of how we deal with the export flux (following our responses here and above), and take out the reference to 3.3.4 (we had meant to refer to the detail on the previous estimates themselves, but we can easily do that in both places).

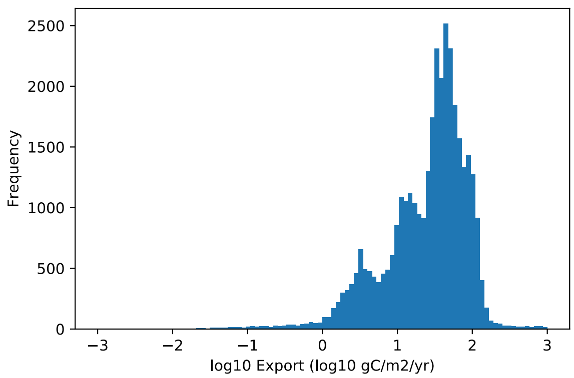

Fig 1. Histogram of export rates at each horizontal grid box in the model.

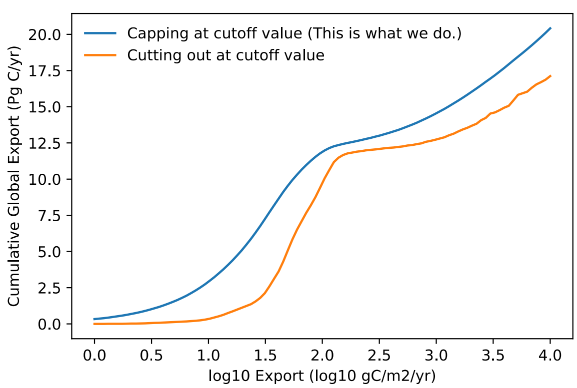

Fig. 2. Calculation of global export (cumulative) with the inclusion of higher and higher rates of export. This shows the clear "plateau" at around 12.5 Pg C/yr. The very high but very sparse areas of export are along the coasts, where the model performance breaks down. The blue line gives the calculation if we assume that there is still some export assumed there. Specifically, if we cut off at 10^3 gC/m2/yr, then we assume that all of the locations with higher export than that all have 10^3 gC/m2/yr. The orange line gives the calculation if we simply neglect all of the higher locations.

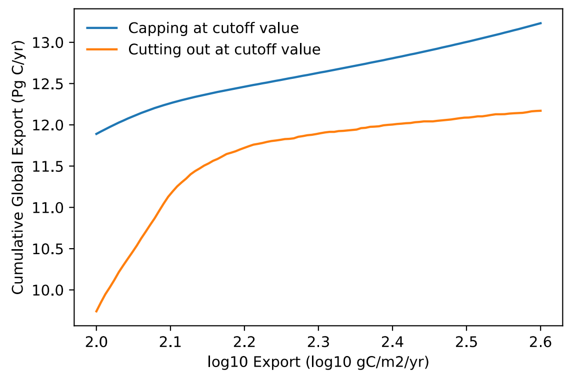

Fig. 3. A zoom in of Fig. 2 highlighting the range in export (12-13 PgC/yr; blue line) at the "plateau". This is the range that we report, and it is the same in all global model simulations with different nitrifier parameter values.

Lines 353-358: comparison with Baltar and Herndl (2019) estimate

It seems to me that comparing your nitrification only estimate with a total deep ocean carbon fixation is a little like comparing "apples to oranges". I'm not familiar with that Baltar and Herndl study, which apparently provides a very large range, so I'm wondering if it is possible to infer a first-order estimate of the nitrification contribution from that study. If you believe that nitrification only accounts for a small fraction of total deep carbon fixation, is there any other specific metabolism you think may be most important to explore next?

Yes, we agree that it is an "apples to oranges" comparison because potentially other metabolisms are responsible for deep C fixation. In the revised version, we'll put the second sentence of this paragraph first, so that at first read it doesn't seem as if we are suggesting that the Baltar and Herndl paper is wrong, but rather, that our studies combined imply that there are unaccounted-for metabolisms. It is a great suggestion to include some specific possibilities, such as sulfate reduction, and we will add this to the revised version.