

We sincerely thank both reviewers for their insightful comments on our manuscript, which have greatly helped to clarify our findings. The main changes made to our manuscript include:

- The addition of three new figures illustrating the findings. New Figure 9 compares the PlankTOM10 and PlankTOM6 zonal mean biomass for the main phytoplankton and zooplankton PFTs and provides further background information on their differences; New Figure 10 shows the seasonal cycle in surface Chl in the North and South Pacific oceans and shows to which extent the modelled Chl seasonality in PlankTOM10 are closer to the observations than that those of PlankTOM6; New Figure 13 shows the biomass of phytoplankton and the three zooplankton in the North and South Pacific Ocean in the two models to illustrate the effect of the timing of zooplankton grazing on phytoplankton discussed in the text.
- We clarified a number of model results that were highlighted by the two reviewers, namely: our use of Chl and biomass, which is now more precise in the text, with a more extensive analysis of how grazing influences biomass; that our model does include its own representation of mixed-layer dynamics, and thus it represents the vertical dilution effects that are present in the ocean; and more explanation and rationale for the choices of model parameters.
- We extended the discussion of the limitations of our modelling analysis, but also explained more clearly why we think the model is adequate to study the role of macrozooplankton grazing, in spite of the model shortcoming.

Please find below our reply (in blue) along with the new text (in red). The original comments (in black) are also copied for clarity.

Anonymous Referee #2

This is a very interesting modelling study demonstrating that grazing by various zooplankton functional types (PFTs) could have an important role in controlling primary production in high nitrate-low chlorophyll regions. The authors provide a new model that includes macrozooplankton as an additional heterotrophic plankton type and conclude that trophic cascades induced by macrozooplankton predation on mesozooplankton could control phytoplankton growth in the Southern Ocean. This challenges the present interpretation of dominating processes and will certainly stimulate follow up studies. Thus, the manuscript is timely and relevant. It is generally well written and easy to follow, although some clarifications are required in the methods. Some relevant improvements are nevertheless necessary regarding the suggested role of macrozooplankton. The study potentially underestimates the role of microzooplankton grazing which in turn has implications for the role of macrozooplankton.

The relative contribution of the different heterotrophic PFTs depends the strengths of the trophic linkage between auto- and heterotrophic PFTS which is represented in the model by weighing factors. As outlined in the detailed comments below, I have some problems with the weighing within the microzooplankton group. Heterotroph dinoflagellates are an important grazer in the polar ocean and their role appears to be underestimated.

Although our model simulations underestimates the biomass of protozooplankton, we think the results would still be unchanged even if the biomass of protozooplankton and their grazing of phytoplankton were higher in the model. This is because the main reason why the addition of

macrozooplankton leads to important trophic cascade with a large influence on phytoplankton biomass is that the growth rate of macrozooplankton is much slower than that of proto- and mesozooplankton (see Figure 2). This was highlighted in our sensitivity study presented in Figure 9 (of the submitted manuscript), where we showed that the slow growth rate of the largest zooplankton was the largest single factor controlling the size of the North/South ratio in Chl.

Another cause for the underestimation of microzooplankton grazing may result from the underestimation of the biomass. The authors compare the geographical distribution of phytoplankton PFTs in models and the field; this is omitted for heterotrophic groups and only global averages are presented. As it looks like, however, there are larger geographic differences in some regions. Most important microzooplankton biomass in the Southern ocean appears to be underestimated which likely has important implications in the relative consumption rates of primary production by the different heterotrophic PFTs.

We think the underestimation is associated primarily with the lack of an explicit representation of semi-refractory DOC in our model leading to an underestimation of bacterial biomass, a primary food source for protozooplankton. We have incorporated new figures and additional elements to the discussion to better explain our results and in particular to explain why we think the results are still valid even with the underestimation of protozooplankton. Please see the reply to the specific comments below for details of the changes done in the manuscript.

Underestimation of protozooplankton in the Southern Ocean would tend to lead to higher phytoplankton biomass in the Southern Ocean, so it is not a realistic explanation for the high North/South ratio of Chl. We therefore conclude that despite the model shortcomings it is fit to address the questions we pose. We are working on improving the DOC compartment of our model but this is a major task. Its effect on bacteria, protozooplankton and more generally on recycling will be the topic of a follow up analysis.

In addition, the manuscript would greatly profit the presentation of model data/field data regarding the stock sizes of the different auto- and heterotrophic PFTs and their growth/grazing rates in the northern and southern ocean. The conclusion that trophic cascades induced by high stocks of macrozooplankton enable phytoplankton blooms in the north and their lack in the south prevents bloom formation is based on these data. However, this is not shown at all. I further miss some representation of how modelled data on the processes reflects real observations.

We have added new Figures 10 and 13 to illustrate this point better in the manuscript. New Figure 10 shows the seasonal cycle in surface Chl in the North and South Pacific oceans and highlights the differences in the two hemispheres, which are clear in both SeaWiFS Chl and the seasonal Chl estimate of PlankTOM10. In contrast, PlankTOM6 has a similar seasonal Chl cycle in the two hemispheres. This figure shows to which extent the modelled Chl seasonality in PlankTOM10 are closer to the observations than that those of PlankTOM6. New Figure 13 shows the biomass of phytoplankton and the three zooplankton in the North and South Pacific Ocean in the two models to illustrate the effect of the timing of zooplankton grazing on phytoplankton discussed in the text (second paragraph of the Discussion).

Specific comments Introduction: p 11938, line 5: The terms small and large zooplankton need to be better defined. Are microzooplankton or small copepods included in the small plankton? Their ecology and function in the ecosystem is very different. On the other hand recycling is also a function of feeding by large zooplankton (particularly of omnivorous zooplankton in the post-spring bloom period (see Banse 1995).

We have clarified the use of 'small' and 'large' throughout the Introduction. The grouping of different types of zooplankton is detailed in the Methods (section 2.1, 1st paragraph). With three zooplankton PFTs only, we had to define what the functional behaviour of each PFT would be. We named the three PFTs based on sizes of organisms (i.e. proto-, meso-, and macrozooplankton), but we recognise that classes to which groups such as the copepods belong may span more than one size class. Unfortunately we cannot represent this level of complexity in our current model, but further developments could incorporate spectra of sizes. Extract of the text from Section 2.1: "protozooplankton (e.g. heterotrophic flagellates and ciliates), mesozooplankton (predominantly copepods), and crustacean macrozooplankton (euphausiids, amphipods, and others, called 'macrozooplankton' for simplicity".

p 11938, line 20: "of" missing.

corrected

p 11939, line 8: The is very descriptive. Examples of the inclusion of zooplankton functional types are not given (what are the "few examples"). The role of zooplankton is only very generally described; what are the insights gained from the inclusion of zooplankton and which PFTs were included, so far? What are the important interactions? It is left open what the more explicit representation should be and what are the expected important clues are.

We have split this paragraph in two and re-ordered the text to clarify our modelling strategy. The first paragraph now clearly highlights where improvements in zooplankton led to improved representation of biogeochemical cycles in global models, and includes two additional examples (i.e. Aita et al. 2003 and Bianchi et al 2013). The second paragraph discusses the role of zooplankton mechanistically, and explains why additional research on zooplankton is needed.

The text now reads (Introduction paragraphs 3 & 4): "Fewer studies have examined the role of different zooplankton PFTs in global ocean biogeochemistry, even though there are some data sets on zooplankton traits (e.g. Hirst and Bunker, 2003; Straile, 1997). The simulation of phytoplankton biomass was improved when more mechanistic parameterisations of zooplankton dynamics constrained by observations were included in a global model (Buitenhuis et al., 2006; Buitenhuis et al., 2010). Similarly, the seasonal cycle of phytoplankton (Aita et al. 2003) and the open-ocean oxygen depletion (Bianchi et al. 2013) were improved when the influence of zooplankton vertical migration was included in a model in global biogeochemical models. The choice of the grazing formulation in particular was found to influence phytoplankton diversity (Prowe et al., 2012; Vallina et al., 2014b) and the resulting food web dynamics (Sailley et al., 2013; Vallina et al., 2014a), and to have implications for energy flow to higher trophic levels (Stock et al., 2014).

Zooplankton can influence the fate of exported materials through several processes, including grazing, repackaging of organic matter in faecal pellets, and vertical migrations in the mesopelagic layer (e.g. Stemmann et al., 2000). Furthermore, there are important interactions among grazing, nutrient cycles, and environmental conditions as was shown in studies based on regional models and observations in the equatorial Pacific (Landry et al., 1997; Price et al., 1994), North Pacific (Frost, 1991), the Atlantic (Daewel et al., 2014; Steinberg et al., 2012) and the Southern Ocean (Banse, 1995; Bishop and Wood, 2009). The importance of grazing was also highlighted during iron enrichment experiments (Henjes et al., 2007; Latasa et al., 2014), in part explaining why some experiments led to increased carbon export and others did not (Martin et al., 2013). Thus, a more explicit representation of different zooplankton PFTs in global models could provide important clues for the functioning of marine biogeochemistry. "

Methods: p 11941, line 3: Hetero- and mixotrophic dinoflagellates could play an important role as grazers in polar ecosystems (Calbet 2008). Is this group included in the protozooplankton?

Heterotrophic dinoflagellates are included in the protozooplankton, but there is no representation of mixotrophic dinoflagellates.

We added new text to the Discussion (Section 4, 4th paragraph): “In addition, the model does not include some ecosystem pathways such as viral lysis (Evans et al., 2009), and the zooplankton representation does not include salps, pteropods, and auto- and mixotrophic dinoflagellates. The nano- and microzooplankton are also combined into a single compartment.”

p 11941, line 5: The different coloring of lines in Figure 1 needs explanation.

Now specified in the legend of figure 1: “The arrows show grazing fluxes by protozooplankton (purple), mesozooplankton (red), and macrozooplankton (green). Only fluxes with weighing factors above 0.1 are shown (Table 3). “

p 11942, line 20: In some cases too little data was available to parameterize the model (e.g., Chl_a/C ratio), so that other more arbitrary solutions were used. I would like to know whether authors considered a sensitivity analysis to evaluate the potential error inherent in the model output caused by the lack of data.

We have done nearly 500 sensitivity tests during the development of this model. The parameters that influenced the results on the North/South ratio the most are those that are presented in the paper, namely the presence (or not) of macrozooplankton and their grazing rate. Hence these are the sensitivity studies that are detailed in Figure 9 and 10 (of the submitted text) and discussed in the text (Results Section 3.4.1 and 3.4.2). Parameters that influenced the growth and loss of phytoplankton had little influence in comparison. We now noted in the text, Section 2.4 (1st paragraph) “A series of sensitivity tests are presented for the model parameters that influence the key results the most.” Also, average Chl/C ratios are fairly accurately known, and are well represented by the model; it’s the variation of θ_{\max} between different PFTs for which there is relatively little data.

p 11942, line 29: The procedure to define the nutrient limiting parameters for phytoplankton is very unclear. For instance, was zooplankton biomass, abundance or grazing used to examine co-variation? All PFT or selected PFT? What is meant by “magnitude of limiting parameters” of zooplankton PFTs? In addition, I thought phytoplankton (growth?) is parameterized here. This chapter needs serious improvement.

We re-wrote this section to explain more clearly what we did, in particular separating the explanation of limitation parameters for phytoplankton PFTs from that of limitation parameters of zooplankton PFTs. Essentially, we tuned the k-half values for nutrient limitation in the phytoplankton growth equations and for food limitation in the zooplankton growth equations to approximately match the observed co-variation with Chl shown in Figure 3, which is an emerging property of the model. The biggest text changes are reported below, but note that the text was clarified throughout section 2.1:

Section 2.1, 6th paragraph: “We used a two-step approach to define the nutrient limitation parameters, which are not well constrained by observations. Firstly, we assigned initial PFT-specific half-saturation values to each phytoplankton PFT based on literature-derived values, using the value for a similar-sized PFT when PFT-specific information was not available. We then examined the covariation of surface Chl concentration with the limiting nutrient concentrations as shown in Figure 3, and adjusted the magnitude of the half-saturation parameters of

phytoplankton PFT to approximately fit the observations. Adjustments were made by keeping the ratios of k-half values between phytoplankton PFTs approximately constant. With this approach, we use the observed k-half values as an initial starting point but tune the model to match the emerging properties highlighted in Figure 3.

Section 2.1, 9th paragraph: The half-saturation parameters of zooplankton grazing rates were initially set to a constant value of 20 $\mu\text{mol C L}^{-1}$ for zooplankton PFTs and 60 $\mu\text{mol C L}^{-1}$ for bacteria, based on the relationship between metabolic rates and body volume of Hansen et al. (1997). We used the same approach as for nutrient limitation of phytoplankton PFT, and adjusted the half-saturation parameters for grazing based on the observed covariation between surface Chl concentrations and zooplankton biomass (Fig 3). The selected set of parameter values that approximately fit the observed covariation in Figure 3 is reported in Table 2. “

p 11944: Table 3: What was the scientific basis for the weighing factors? For instance, grazing on Phaeocystis is hampered by its size (at least colonies); so, what justifies weighing them similar to mixed phytoplankton? In addition, considering that Phaeocystis was considered to be colonial, why is this species grazing loss by microzooplankton weighted similar to that of small flagellates? The table further suggests that protozooplankton has a higher preference for colonial Phaeocystis than meso- and macrozooplankton. This does not make sense to me. I would like understand the rationale behind this weighing. Moreover, protozooplankton is a diverse group including a number of heterotrophic dinoflagellates that prey on large plankton such as diatoms and have a high contribution to grazing losses in productive systems (Calbet 2008). The weighing, however, suggest a focus on flagellates/ciliates as major grazers of microzooplankton. This might strongly influence the model results and I wonder whether the model will be able to depict the apparent shift in dominating trophic pathways in low and high nutrient regimes. Finally, the legend should also clearly indicate whether grazer or prey biomass was weighted. The table suggests links between trophic groups that are not depicted in Fig 1.

The weighing factors are generally based on predator-prey size ratio. The assignment of weighing factors faces two types of difficulty. First, as the reviewer mentions, some PFTs are diverse and the behaviour within PFT may not be fully homogeneous. Second, there are few data to guide the preferences that would be applicable at the global scale. However through multiple sensitivity tests made while developing the model, we found that the weighing factors influenced primarily the biomass of the prey and predators, but had little influence on their geographic distribution. Because weighing factors are relatively arbitrary, we have tried to limit the number of changes we applied to the absolute minimum, and to use the resulting model biomass as presented in Table 4 to determine the size of the relative preference among PFTs for each grazer. We have not further adjusted the preference to the specificities of Phaeocystis because they are not the main focus of our analysis, the role of the mucus in Phaeocystis colony as a protection from grazing is unclear (particularly for protozooplankton), and we tried to keep the number of changes apart from overall size considerations to a minimum. A specific focus on Phaeocystis could explore this aspect in further detail. We expanded the text in Section 2.1 (second to last paragraph) to include: “The weighing factors influenced primarily the biomass of the prey and predators, but had little influence on their geographic distribution. We thus used the model results on biomass (Table 4) to guide the size of the relative preferences among PFTs for each grazer. “

We corrected Fig. 1 to represent the links in Table 3.

p 11944, line 25: The reduction in the temperature related mortality of mesozooplankton by a factor of 2 needs explanation.

We added a clarification on this correction. We do not have an exact value for the fraction of the grazing on mesozooplankton that is accounted by macrozooplankton, but in total grazing accounts for 2/3 to 3/4 of the mortality of mesozooplankton (Hirst and Kiorboe, 2002). The new text reads (Section 2.1, last sentence): “This correction preserves the temperature-dependence of mortality, but it recognises that explicit grazing by macrozooplankton already takes place in the model, which does not represent the grazing by other organisms (e.g. salps, fish larvae). In total, grazing accounts for 2/3 to 3/4 of the mortality of mesozooplankton (Hirst and Kiorboe, 2002).”

Results p 11944, line 18: The influence of eco-evolutionary determinants such as reproductive strategy on growth needs explanation. Fig 2 provides empiric maximal growth rates and, therefore, I cannot follow why life cycle strategies should play a role.

(Note this comment refers to page 11948 rather than 11944). We have expanded the text to provide a clearer explanation of our hypothesis. Here we can only speculate on possible explanations for the observed trends. We do not know for sure what are the causes and we hope this result may trigger more research and discussions. We added further explanations in Section 3.1 as follows: “From these relationships, we conclude that the observed phytoplankton growth rates may be more influenced by eco-evolutionary determinants (e.g. reproduction strategies, responses to ecological niche availability) than by environmental physical constraints (e.g. diffusion rates across cell walls). If physical constraints played a predominant role, growth would decrease with size because the surface to volume ratio is larger in smaller organism, as observed within heterotrophic PFTs.”

p 11949, line 26; p 11950, line 12: I miss an evaluation of how well the modeled distribution of micro-, meso- and macrozooplankton compares to observations. As it looks like, there are important differences in all 3 groups regarding the global distribution. Annual mean biomass of the different PFTs should also be presented for the PlankTOM6 model.

We added a figure comparing the PlankTOM10 and PlankTOM6 zonal mean biomass for the main phytoplankton and zooplankton PFTs (new Figure 9), and added the model statistics for PlankTOM6 to Table 4. The following corresponding text was added in Section 3.3 (first paragraph): “The models are generally similar also in their representation of the distribution of biomass among phytoplankton PFTs, with most of the biomass being in picophytoplankton in both models (Fig. 9 and Table 4). However, PlankTOM6 allocates more biomass to protozooplankton compared to PlankTOM10 though PlankTOM6 is still at the low end of observed concentrations (Table 4).”

A comparison between modelled and observed biomass is presented in Table 4, which shows that protozooplankton biomass is underestimated both in absolute value and in the relative fraction of zooplankton biomass. Mesozooplankton are slightly underestimated in biomass but are within the observed range for the relative fraction, while macrozooplankton is within the observed range in absolute value and slightly overestimates the relative fraction. Metrics of the data-model bias are also presented in Figures 3 and 8. There are not enough observations of carbon content of zooplankton biomass to show meaningful maps of observations for the three zooplankton groups. For mesozooplankton, where the largest database exist (see Buitenhuis et al. 2006 Figure 4), most of the data are in the Northern Hemisphere. Thus a comparison with observations is not helpful here where we focus on North/South ratio.

p 11952, line 19: “range of observations” Observations of what, biomass or grazing or growth rate?

We refer here to the observed growth rate, as shown in Figure 2 and Table 1. This was clarified in the text (Section 3.4.2, second line).

Discussion: p 11955, line 1: In their results, the authors do not compare the geographical distribution of heterotrophic PFTs with observations. Here, some discrepancies exist, for instance in the underestimation of microzooplankton biomass in the Southern Ocean, the underestimation of mesozooplankton biomass in upwelling and tropical areas or the global pattern of macrozooplankton distribution.

We added in Section 4 (line 4-5) “**and several regional discrepancies exist between observed and modelled biomass and fluxes**” but did not go into the specifics as a detailed model evaluation at the regional scale is beyond the scope of this manuscript. Our manuscript already contains quantitative and qualitative information on those regions that are characterised by a higher model-data misfit (e.g. Figures 3, 4, 6, 7, 8, and Table 4). Our focus here is on the use of the controlled model experiments between PlankTOM10 and PlankTOM6 to highlight the role of grazing for Southern Ocean phytoplankton biomass.

p. 11955, line 12: Following the same argument of top down control for the Southern Ocean, this does not apply for the tropical Pacific in which according to the model results micro- and macrozooplankton are abundant, but not mesozooplankton. However, data of Moriarty and O’Brian (2013) shows also higher mesozooplankton in this area. What is the difference between the areas and mechanisms then?

We think the model overestimates macrozooplankton grazing in the tropical Pacific, and thus it underestimates mesozooplankton biomass compared to observations. This leads to an insufficient grazing pressure by mesozooplankton on phytoplankton, and consequentially to an overestimation of surface Chl (as shown in Fig. 4). This is the same mechanism that explains the North/South Chl ratio that is discussed here. The challenge for models will be to find the right balance among zooplankton so that all key regions are well represented. We argue in this response that macrozooplankton need to be incorporated because their growth rate is much slower than those of other zooplankton, and thus their grazing pressure during summer is greatly influenced by their winter concentrations. We added a reference to the importance of this timing difference in the discussion (Section 4, end of second paragraph).

p. 11955, line 14-23: This refers to results (seasonal development) which are not shown. However, they seem to be important for the interpretation of the results and might therefore be presented. With regard to the importance of the conclusions about the role of macrozooplankton, one wonders why the data/model output shown is largely limited to Chl_a. It would be interesting to see the different autotroph/heterotrophic stocks and related rates (as for instance, grazing rates by the different heterotrophic PFTs, loss rates of the different autotrophic PFTs) and how these compare to in-situ estimates.

We have now added a figure showing the seasonal cycle of the model phytoplankton and zooplankton (new Figure 13), and a figure comparing the seasonal cycle of Chl to SeaWiFS (new Figure 10). These figures illustrate the comments that were already in the text (Section 4, second paragraph). The paper already presents an extensive comparison between model results and observations wherever possible at the large scale. Additional comparisons would not bring much further insights. It is clear that the model has limitations and many discrepancies with observations can be found, particularly at the regional level. Nevertheless the controlled model experiments between PlankTOM10 and PlankTOM6 are informative to highlight the role of grazing for Southern Ocean phytoplankton biomass.

p. 11956, line 9 following: For me, the underestimation of microzooplankton biomass and the weighing of prey preferences is an important issue to be discussed here. Microzooplankton grazing is a considerable larger loss rate than other zooplankton grazing, and its underestimation has likely a strong influence on the role of macrozooplankton top down control. Why is no modelling data presented regarding the trophic cascades?

We have added a new figure showing the trophic cascades discussed in the text (new Figure 13). We do not think that the underestimation of protozooplankton has a large influence on the results because their growth rate is relatively close to that of mesozooplankton. What causes the important trophic cascades that we see in PlankTOM10 is the fact that macrozooplankton grow much more slowly than mesozooplankton and microzooplankton. Thus their maximum grazing pressure can occur later in the growing season, which has a larger influence on the phytoplankton biomass. This is shown in our set of sensitivity tests discussed in Section 3.4.1 and 3.4.2 in relation with Figure 9 (in the submitted text), where we show that when the top grazers in PlankTOM10 is represented as macrozooplankton (e.g. with slow growth rate), the North/South ratio in Chl is preserved no matter how the rest of the ecosystem looks.

Further evidence that the underestimation of protozooplankton biomass is not a serious issue comes from new Figure 9 which compares the zonal mean concentration of phytoplankton and zooplankton biomass between PlankTOM6 and PlankTOM10. The Figure shows that protozooplankton biomass in PlankTOM6 is 2.5 times higher than in PlankTOM10, and falls within the range of observations (Table 4). Yet PlankTOM6 overestimates summer Chl biomass in the Southern Ocean. We added a sentence to the discussion (Section 4, end of second paragraph) to make this clear. It reads: “Although there is some trophic cascade also in PlankTOM6 with the presence of two zooplankton PFTs, our sensitivity tests presented in Fig. 11 show that the difference in growth rates between the two zooplankton is too small to impact phytoplankton significantly. “

We are planning a number of improvements to our model that we hope will help elucidate the limitations of the current analysis. We mentioned this in the Discussion (Section 4, last sentence): “The effect of further ecosystem developments will be explored in a follow-up study.”