

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

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

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

23
24 Referee #1 (V. Smetacek)

25 victor.smetacek@awi.de

26 The Southern Ocean (SO) plays a key role in the ocean carbon cycle hence efforts to model its
27 past, current and possible future impact on atmospheric CO₂ levels are most worthy of
28 discussion in a broad forum. This general rule applies particularly to this paper because the
29 authors are prominent members of the ocean modelling community. Their message is that
30 adding more zooplankton grazers, in this case , "large, slow-growing crustacean zooplankton",
31 to a global ocean biogeochemistry model produces phytoplankton biomass levels in the SO
32 closer to values obtained from satellite imagery. An earlier model without the additional
33 zooplankton components gave unrealistically high summer phytoplankton biomass values in the
34 SO. This is a logical conclusion: plant biomass will go down if the growth rate is kept constant
35 but the grazing pressure increased. From this straight-forward balance equation the authors
36 conclude that grazing rate rather than iron supply is responsible for the low chlorophyll
37 concentrations in the Southern Ocean. Since this generalisation would bring the great HNLC
38 debate of the 1990s - is it light, iron or grazing that controls productivity? - back to square one, it
39 is necessary to review the arguments for the case made here in order to help clear up what is
40 probably widespread confusion in the community regarding the extent of iron limitation in HNLC
41 regions and the capabilities of biogeochemical models to deal with the issue.

42 Comment only – no reply needed.

1 A number of questions arose in my mind whilst reading the manuscript to which I could not find
2 the answers in the manuscript and supplementary information. If the issues have been
3 considered they should be mentioned prominently in the main text. If, on the other hand, one
4 or more of these issues has not been considered, then the text will need to be rewritten in the
5 appropriate places and the conclusions modified accordingly.

6 **Comment only – no reply needed.**

7 Question 1: Since phytoplankton biomass is equated with chlorophyll concentrations throughout
8 the text, I would like to know whether the following factors that affect its variability have been
9 considered and how: a) Latitudinal variation in mixed layer depth, b) increasing C/Chl ratios with
10 declining iron supply.

11 a) Mixed layer depth (MLD) The “phytoplankton biomass” of interest to food web and carbon
12 cycle studies is the integrated stock per area of water column (in mg or g chlorophyll or carbon
13 m⁻²) and not just the concentration. The difference between concentration (obtained from
14 discrete measurements) and stock (obtained from integrating discrete values for the mixed
15 layer) is highlighted by the differences in chlorophyll yields between the OIF experiments SEEDS
16 I in the Subarctic Pacific and EIFEX in the SO: >20 mg Chl m⁻³ and 3 mg Chl m⁻³ respectively.
17 However, the mixed layer during SEEDS I was only 10 m deep but 100 m during EIFEX, so the
18 standing stocks were 200 and 300 mg Chl m⁻² respectively. As others have fallen into the MLD
19 dilution trap before (e.g. de Baar et al. 2005), I refer to Smetacek and Naqvi (2008) and the
20 comments to Smetacek et al. (2012) where the issue has been explained in detail. Reference to
21 the effect of MLD on phytoplankton biomass is given only in Lines 9-12 of page 17 but the MLD
22 values used in the model need to be explained explicitly in the text and, where appropriate, in
23 the legends.

24 Only concentrations are referred to in this paper and the model results are compared with
25 satellite images that measure concentration in the upper few metres. How the effects of much
26 deeper MLDs in the SO as compared to the N. Pacific and N. Atlantic have been taken into
27 account needs to be highlighted in the text and legend of figure 4.

28 MLD is explicitly produced by the dynamic ocean physical model (NEMO) based on the local
29 atmospheric conditions as represented in forcing data from the ECMWF re-analysis. We clarified
30 this in the text. More importantly, MLD is identical in both the PlankTOM10 and PlankTOM6
31 simulations, and thus the differences between these two models can only be attributed to the
32 ecosystem structure. We focus here on surface concentrations because we are trying to explain
33 the surface differences between the North and South as observed via satellite Chl data. We
34 clarified in Fig. 4 and throughout the paper that we report the surface concentration for Chl and
35 biomass for the top model box (10 m). These surface conditions reflect the internal dynamics of
36 mixing created by changes in MLD. We further enhanced the results and discussion to mention
37 the role of MLD in the Northern and Southern hemisphere.

38 The new text reads as:

39 Methods Section 2.4 (p. 7, lines 37-38): “The model resolves 30 vertical levels, with a 10 m depth
40 resolution in the upper 100 m. NEMOV3.1 calculates vertical diffusion explicitly and represents
41 eddy mixing using the parameterisation of Gent and McWilliams (1990). **The model thus
42 generates its own mixed-layer dynamics and associated mixing based on local buoyancy fluxes
43 and winds.**”

1 Results Section 3.3 (p. 9, lines 38-47): “The failure of PlankTOM6 to reproduce the observed low
2 Chl concentration in the Southern Ocean during summer is further highlighted in Fig. 10, which
3 shows the seasonal cycle of mean Chl for the Northern Hemisphere and the Southern Ocean,
4 where it is most pronounced. In PlankTOM6, the seasonal cycle in the North and South are very
5 similar, with the slightly lower concentrations in Southern Ocean during summer caused by a
6 slightly deeper summer time mixed-layer depth (29m compared to 19m). In contrast in
7 PlankTOM10, the seasonal cycle of Chl in the South is flatter and concentrations are always
8 below those in the North, as in the observations. As PlankTOM6 and PlankTOM10 have identical
9 physical environments (including mixed-layer depth), the North-South differences are entirely
10 due to ecosystem structure. “

11 Discussion Section 4 (p. 12, line 41 to p.13 line 7): “Our results indicate that zooplankton grazing
12 exerts an important control on Southern Ocean Chl. This propagates through to influence
13 phytoplankton biomass. Indeed, the North/South ratio of phytoplankton biomass at surface is
14 greater in PlankTOM10 (1.62) compared to PlankTOM6 (1.18), very close to the modelled
15 North/South ratio of Chl. The difference between the PlankTOM10 and PlankTOM6 also persists
16 through depth until about 300 m. Because of these marked differences, it is clear that the
17 representation of global biogeochemical cycles in ocean models is influenced by the ecosystem
18 structure. In both PlankTOM6 and PlankTOM10, the mesozooplankton and macrozooplankton
19 faecal pellets aggregate into the same large, fast-sinking particle pool, thus limiting the effect of
20 different size classes of zooplankton on carbon export. To distinguish the effects of different
21 food web structures on export production, a wider spectrum of particle size classes sinking at
22 different speeds are needed (e.g. Kriest; 2002). In addition, an improved vertical dynamics of the
23 mesopelagic zone, together with the enhanced representation of zooplankton dynamics in the
24 present study would allow further exploration of the interactions between iron fertilisation,
25 grazing, and mixed-layer dynamics, which have led to large differences among ocean iron
26 fertilization experiments (Smetacek and Naqvi 2008; Boyd et al. 2008). “

27 In the model, meso- and macrozooplankton biomass is derived from 200 m vertical net tows and
28 then converted to concentration in the 200 m water column (lines 12 ,Äi 15, page 12).
29 Phytoplankton concentrations should be treated in an equivalent fashion but for the MLD and
30 not a standard depth as for zooplankton. It is likely that the differences in surface chlorophyll
31 concentrations between satellite and model will reduce further when this effect is considered.

32 Please note that in the model results, meso- and macrozooplankton biomass are presented for
33 the surface ocean only, as is phytoplankton concentration, and thus all biomass metrics are
34 consistent. Zooplankton biomasses are not derived from vertical net tows, but rather produced
35 in situ by the model based on the growth and loss term equations presented in the
36 Supplementary Material. Only the observed meso- and macrozooplankton biomasses presented
37 in Figure 3 (panels d and f) are based on tows. We had already noted in the text that when
38 comparing the observations with the model, the depth difference in the sampling method can
39 explain a factor of 1.5 to 2.0 in biomass. Given the uncertainty in the data and the large regional
40 spread in observed zooplankton biomass, it would bring little additional information to scale the
41 data for the purpose of Figure 3 and could introduce additional errors. Instead, we have now
42 explained the difference in the figure caption directly. Everywhere else throughout the
43 manuscript only surface biomass is discussed. We now explain in the discussion (Section 4, see
44 response above) why we do not analyse more the fluxes to depth and interactions with MLD any
45 further, which we intend to present in a subsequent analysis that will require further
46 development of the particulate sinking dynamics in the model.

1 New text to Section 2.1 (p. 4, lines 28-30): “The PFT biomasses are produced by the model for
2 each grid box based on the growth and loss term equations presented in Supplementary
3 Material.”

4 New text caption of Figure 3 reads (p.25, lines 17-21): “All data are for the surface, generally
5 corresponding to the mixed layer, except for observed Chl, which is seen by satellite over one
6 optical depth, and observed mesozooplankton and macrozooplankton, which are from depth-
7 integrated tows and may underestimate surface concentrations (by a factor 1.5-2; see text).”

8 b) Chlorophyll-biomass ratios Chlorophyll synthesis is one of many biochemical pathways that
9 are limited by iron deficiency. Providing iron to phytoplankton leads to increased production of
10 this pigment and C/chl ratios can drop two to threefold with only a marginal increase in
11 biomass, an effect which is particularly apparent in diatoms. So chlorophyll concentrations are
12 an unreliable proxy for phytoplankton biomass because they can vary so much between iron-
13 limited and iron-replete conditions. The ratio (Chl/C) has been considered as a determinant of
14 growth rate in the model but I could not ascertain whether the “phytoplankton biomass” based
15 on chlorophyll in the SO was also corrected for this variable. This would exacerbate the
16 chlorophyll problem by increasing the real, carbon-based biomass.

17 Indeed the ratio Chl/C varies as a function of Fe, as does the phytoplankton biomass. This is fully
18 considered in the model, and was clarified in the text:

19 Methods Section 2.1 (p. 5, lines 3-5): “Phytoplankton PFT growth rates are also limited by light
20 and inorganic nutrients (P, N, Si, and Fe) using a dynamic photosynthesis model that represents
21 the two-way interaction between photosynthetic performance and Fe/C and Chl/C ratios
22 (Buitenhuis et al. 2013a).”

23 We now make an explicit link between Chl and phytoplankton biomass in the Discussion, which
24 confirms that the North/South differences in Chl are also present in phytoplankton biomass (see
25 new text in Section 4, 4th paragraph, mentioned above).

26 Question 2 Why only 3 zooplankton PFTs? What would the model results look like if a fourth
27 zooplankton PFT that included the salps was introduced: micro-feeding, fast-growing, large
28 zooplankton? Put in another way, why stop at the third category of zooplankton? They have
29 many more PFTs than phytoplankton. Salps are relevant because their stocks have been
30 increasing in the SO over the past decades concomitant with a krill decline (Atkinson et. al.
31 2004) so it is possible that a replacement is taking place with consequences for SO productivity.
32 Salps differ from the category of zooplankton added here (slow-growing macrozooplankton) in
33 that they have short generation times because they can produce individual animals by budding
34 in the course of a day to weeks depending on temperature and presumably food supply. Their
35 inclusion might lead to complete grazing down of the phytoplankton because nothing is known
36 about the checks and balances on their population size. Since they swim, feed and breathe
37 simultaneously it should be possible to model their grazing efficiency fairly easily using threshold
38 values (particle concentration at which they starve, multiply, etc.) from the literature. If the data
39 have not been collected yet, the model results could be used to generate interest in this
40 question.

41 It would be very interesting to have additional zooplankton and we are working on new model
42 versions that explicitly include pteropods, foraminifera and salps. However, these are
43 substantial additions to the model that require a lot of time (one researcher and one PhD
44 student are working full time on this new model version). The model version presented here
45 with 3 zooplankton is the simplest model that succeeds in reproducing the North/South ratio in

1 Chl, which is already an advance compared to previous models and which we deem worthy of a
2 publication on its own, i.e. each addition of a PFT to the model must be fully understood and
3 evaluated by the scientific community before proceeding to further additions. We added in the
4 conclusion that the addition of further zooplankton compartments could result in even more
5 realistic horizontal distribution of Chl.

6 The additional text in the discussion Section 4 (p.13 lines 11-13) reads: “In addition, the model
7 does not include several other ecosystem pathways known to play an important role, such as
8 viral lysis (Evans et al., 2009), and the zooplankton representation does not include salps,
9 pteropods, and auto- and mixotrophic dinoflagellates. The nano- and microzooplankton are also
10 combined into a single compartment.”

11 Question 3: Has iron recycling due to zooplankton grazing been considered in the model? The
12 authors refer to “the dynamics of the SO zooplankton community” as being a more important
13 determinant of low summer phytoplankton biomass than iron limitation. They mention that
14 trophic cascades within the zooplankton have been built into the model but there is no mention
15 of recycling of the limiting nutrient, in this case iron, by the zooplankton, i.e. a feedback loop
16 which would stimulate net production. At the end of the abstract and in the conclusions one is
17 reminded that zooplankton make fast-sinking faecal pellets and carry out vertical migration,
18 implying that the more zooplankton, the more vertical flux and carbon sequestration. So, in
19 today’s times it might be a good thing to have zooplankton around because they sink carbon, a
20 few decades ago, before collapse of the traditional commercial fisheries, zooplankton were
21 good because they made fish food. Since the zooplankton category introduced here are long-
22 lived, their food supply would have to be sustainable, so one wonders what percentage of the
23 faecal pellets produced sinks out of the mixed layer. If all were to sink out, the surface layer
24 would soon be depleted of essential elements and the grazers would starve; so the category
25 introduced here only evolved because most of its wastes are recycled in the surface layer. Salps
26 on the other hand are roving grazers that can afford to let their wastes sink behind them. This is
27 just to mention a few complications that arise when attempting to model the impact of
28 zooplankton and nekton on the biogeochemistry of the surface layer.

29 Yes, iron recycling due to zooplankton grazing is considered in the model. We now specify this in
30 the Methods Section 2.1 (p. 4, lines 35-38): “The model includes full cycles of carbon (C), oxygen
31 (O₂), and phosphorus (P), which are assimilated and released by biological processes at a
32 constant ratio of 122:172:1 (Anderson and Sarmiento, 1994). Phytoplankton and particulate
33 organic matter have a variable Fe/C ratio, while zooplankton and bacteria have a fixed ratio of
34 $2e^{-6}$, which is lower than the minimum phytoplankton Fe/C ratio (Schmidt et al. 1999).
35 Zooplankton and bacteria release excess iron. The model also includes a full cycle of silica (Si)
36 and calcite (CaCO₃) as in Maier-Reimer (1993), and simplified cycles for Fe and nitrogen (N).”
37 Our iron model is parameterised according to Aumont and Bopp (2006), and it successfully
38 reproduces the changes in surface Chl concentration following iron enrichment as noted in
39 Section 3.4.3.”

40 For the representation of faecal pellets, see the text we added to Discussion Section 4 (p. 12,
41 lines 28-43), as explained above.

42 General comments In order to continue improvement of biogeochemical models by exploring
43 the impact of zooplankton dynamics on ecosystem structure and functioning, it will be necessary
44 to develop a framework of interactions based on the evolutionary ecology of the
45 phytoplankton/zooplankton relationship. Unfortunately this has not received the attention it
46 deserves for various reasons (see Smetacek et al. 2004, Smetacek 2012), in particular, because

1 the necessary, dependable, quantitative information is still lacking. To my mind this can only
2 come from studies carried out in situ because enclosures of any sort will hamper the
3 zooplankton and nekton. Furthermore, comprehensive measurement programmes of the same
4 body of water will be necessary to study rates and processes within functioning ecosystems.
5 Perturbing the system under study in order to identify shifts in the mechanisms would enhance
6 the value of the information gained from sustained measurements of the same water mass. The
7 whole-lake experiments carried out in the 1970s in the USA and Canada brought unsuspected
8 trophic cascades into focus: Lakes changed their colour depending on the presence or absence
9 of predatory fish. “Were it not for whole lake experiments, limnology would be where bio-
10 oceanography is today, firmly entrenched in the bottom-up paradigm. It follows that bio-
11 oceanography could be where limnology is today if more dedicated in situ experiments are
12 carried out by the scientific community” (comments in Smetacek et al 2012). Could removal of
13 the whales, that once lived sustainably from krill biomass equivalent to double the global
14 commercial fish catch, have had an effect on SO chlorophyll concentrations? Such hypotheses
15 could be tested with ocean iron fertilization (OIF) experiments that have proven themselves as
16 the equivalent of whole-lake experiments in the sea.

17 We would welcome this kind of experimental data to provide mechanistic information on the
18 phytoplankton/zooplankton interactions. We added a reference to Smetacek et al. 2004 in the
19 conclusions Section 5 (1st paragraph).

20 All ocean iron fertilization (OIF) experiments carried out so far have shown that iron addition led
21 to a substantial increase in the photosynthetic efficiency index (Fv/Fm) and remained higher for
22 many weeks inside the fertilized patch than values measured concomitantly in surrounding iron-
23 limited water. These results, bolstered with direct measurements of iron concentrations and
24 various types of bottle experiments have unequivocally shown that phytoplankton growth rates
25 in HNLC areas are limited by the iron supply. The conclusion of this paper: that zooplankton
26 grazing rather than iron controls phytoplankton biomass build up would imply, framed in John
27 Martin’s iron hypothesis, that fluctuations in the grazer populations were responsible for
28 climate cycles. This is probably not what the authors mean so the wording of their concluding
29 remarks needs to be properly qualified rather than presented in a simplistic sweeping
30 statement.

31 Please refer to Section 4 last paragraph which covered much of the qualified language that is
32 called for in this comment. We have now moved this paragraph to the end of the Conclusions,
33 where it has more weight and visibility. It reads: “Our results on the important role of grazing do
34 not contradict the results on the importance of Fe-fertilisation as highlighted in Fe enrichment
35 experiments (Boyd and al., 2007), because additional Fe would trigger further growth provided
36 that Fe were initially below an optimal concentration (Blain et al., 2007). However, our results
37 suggest that low Fe concentrations by themselves are insufficient to account for the very low Chl
38 levels observed in the Southern Ocean HNLC region in summer, and that differences in
39 zooplankton trophic and community structure, and concomitant grazing dynamics play an
40 important role in controlling phytoplankton blooms and maintaining very low Chl levels in that
41 region. Although previous studies emphasised the role of phytoplankton community structure
42 (Arrigo et al., 1999) and mixed layer dynamics for nutrient supply and demand (Platt et al.,
43 2003a;Platt et al., 2003b) in ocean biogeochemical cycles, our analysis makes it clear that it is
44 important to consider the whole pelagic ecosystem, including the zooplankton, when studying
45 and predicting ecosystem responses to Fe (or any essential nutrient) fertilisation. This complex
46 interplay has received less attention than either the drivers of primary production or the

1 representation of Fe cycling in global biogeochemical modelling. Our results suggest that
2 representing zooplankton interactions more explicitly would improve the representation of
3 biogeochemistry – climate interactions. “

4 While we do not want to imply that zooplankton grazing is responsible for glacial-interglacial
5 CO₂ variations, we note here that the current consensus is that iron fertilisation caused no more
6 than 1/3 of the observed glacial-interglacial atmospheric CO₂ variations and that global
7 biogeochemistry models still fail to reproduce the other 2/3 of the observed atmospheric signal.
8 Therefore there are clearly important issues to resolve in the next generation of global
9 biogeochemical models. We cannot show here whether zooplankton had an influence on
10 atmospheric CO₂ levels on millennial time scales, but we cannot rule it out given their
11 importance in determining the vertical flux and regional distribution of carbon in the ocean.

12 Nevertheless, the improved model presented here clearly demonstrates that increasing
13 zooplankton PFTs is an important way to nudge biogeochemical models closer to reality. The
14 last sentences of the Conclusions focus on the possible outcome of ocean iron fertilization (OIF):
15 “Assessments of the impact of such geoengineering will be unreliable, at least until the full
16 ecosystem response including the grazing pathways (Landry et al., 1997) and the relationship to
17 deep water carbon export (Smetacek et al., 2012) can be reproduced with models, which could
18 be used to make quantitative predictions”. The authors are putting the cart before the horse
19 here: OIF experiments are the most reliable way of achieving the assessments called for here. So
20 far only puddles of a few weeks’ duration have been studied. Larger, longer-term experiments
21 are needed to assess the impact of higher trophic levels on ocean biogeochemistry. The ensuing
22 model would then permit one to extrapolate from the experimental scale to the really large-
23 scale of relevance to the global carbon cycle, should this be deemed necessary.

24 Indeed, OIF may be the most reliable, but they are local in time and space by nature. The only
25 way to make a large-scale assessment of the quantitative potential of purposeful Fe-fertilisation
26 is to use models to scale up the observations. We have specified in the conclusion Section 5 (p.
27 13, line 45) that our comment on the role of models refer to making quantitative predictions
28 “over large areas”.

29 References

30 Smetacek, V. Making sense of ocean biota: How evolution and biodiversity of land organisms
31 differ from that of the plankton. J. Biosci. 37, 589-607, DOI 10.1007/s12038- 012-9240-4, 2012
32 Smetacek, V., Assmy, P., Henjes, J.: The role of grazing in structur- ing Southern Ocean pelagic
33 ecosystems and biogeochemical cycles, Antarctic Science 16: 541-558, 2004 Smetacek, V. and
34 Naqvi, S.W.A.: The next generation of iron fertilization experiments in the Southern Ocean. Phil
35 Trans. R. Soc. A 366, 3947-3967, 2008.

37 Anonymous Referee #2

38 This is a very interesting modelling study demonstrating that grazing by various zooplankton
39 functional types (PFTs) could have an important role in controlling primary production in high
40 nitrate-low chlorophyll regions. The authors provide a new model that includes
41 macrozooplankton as an additional heterotrophic plankton type and conclude that trophic
42 cascades induced by macrozooplankton predation on mesozooplankton could control
43 phytoplankton growth in the Southern Ocean. This challenges the present interpretation of
44 dominating processes and will certainly stimulate follow up studies. Thus, the manuscript is

1 timely and relevant. It is generally well written and easy to follow, although some clarifications
2 are required in the methods. Some relevant improvements are nevertheless necessary regarding
3 the suggested role of macrozooplankton. The study potentially underestimates the role of
4 microzooplankton grazing which in turn has implications for the role of macrozooplankton.

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

10 Although our model simulations underestimates the biomass of protozooplankton, we think the
11 results would still be unchanged even if the biomass of protozooplankton and their grazing of
12 phytoplankton were higher in the model. This is because the main reason why the addition of
13 macrozooplankton leads to important trophic cascade with a large influence on phytoplankton
14 biomass is that the growth rate of macrozooplankton is much slower than that of proto- and
15 mesozooplankton (see Figure 2). This was highlighted in our sensitivity study presented in Figure
16 9 (of the submitted manuscript), where we showed that the slow growth rate of the largest
17 zooplankton was the largest single factor controlling the size of the North/South ratio in Chl. In
18 the specific response below we explain how we have clarified this finding in the text.

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

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

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

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

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

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

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

25 p 11938, line 20: "of" missing.

26 corrected

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

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

37 The text now reads (Introduction, p.3, lines 9-14): "Fewer studies have examined the role of
38 different zooplankton PFTs in global ocean biogeochemistry, even though there are zooplankton
39 physiological datasets (e.g. Hirst and Bunker, 2003; Straile, 1997). The simulation of
40 phytoplankton biomass was improved in published studies when more mechanistic
41 parameterisations of zooplankton dynamics constrained by observations were included in a
42 global model (Buitenhuis et al., 2006; Buitenhuis et al., 2010). Similarly, the seasonal cycle of
43 phytoplankton (Aita et al. 2003) and the open-ocean oxygen depletion (Bianchi et al. 2013) were
44 improved when the influence of zooplankton vertical migration was included in global
45 biogeochemical models. The choice of the grazing formulation in particular was found to

1 influence phytoplankton diversity (Prowe et al., 2012;Vallina et al., 2014b) and the resulting
2 food web dynamics (Sailley et al., 2013;Vallina et al., 2014a), and to have implications for energy
3 flow to higher trophic levels (Stock et al., 2014).

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

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

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

19 We added new text to the Discussion (Section 4, p. 13, lines 11-13): “In addition, the model does
20 not include some ecosystem pathways such as viral lysis (Evans et al., 2009), and the
21 zooplankton representation does not include salps, pteropods, and auto- and mixotrophic
22 dinoflagellates. The nano- and microzooplankton are also combined into a single compartment.”

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

24 Now specified in the legend of figure 1 (p. 25, lines 4-6): “The arrows show grazing fluxes by
25 protozooplankton (purple), mesozooplankton (red), and macrozooplankton (green). Only fluxes
26 with weighing factors above 0.1 are shown (Table 3). “

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

31 We have done nearly 500 sensitivity tests during the development of this model. The
32 parameters that influenced the results on the North/South ratio the most are those that are
33 presented in the paper, namely the presence (or not) of macrozooplankton and their grazing
34 rate. Hence these are the sensitivity studies that are detailed in Figure 9 and 10 (of the
35 submitted text) and discussed in the text (Results Section 3.4.1 and 3.4.2). Parameters that
36 influenced the growth and loss of phytoplankton had little influence in comparison. We now
37 noted in the text, Section 2.4 (p. 8, lines 1-2) “A series of sensitivity tests are presented for the
38 model parameters that influence the key results the most.” Also, average Chl/C ratios are fairly
39 accurately known, and are well represented by the model; it’s the variation of θ_{\max} between
40 different PFTs for which there is relatively little data.

41 p 11942, line 29: The procedure to define the nutrient limiting parameters for phytoplankton is
42 very unclear. For instance, was zooplankton biomass, abundance or grazing used to examine co-
43 variation? All PFT or selected PFT? What is meant by “magnitude of limiting parameters” of

1 zooplankton PFTs? In addition, I thought phytoplankton (growth?) is parameterized here. This
2 chapter needs serious improvement.

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

10 Section 2.1 (p. 5, lines 17-21): “We used a two-step approach to define the nutrient limitation
11 parameters, which are not well constrained by observations. Firstly, we assigned initial PFT-
12 specific half-saturation values to each phytoplankton PFT based on literature-derived values,
13 using the value for a similar-sized PFT when PFT-specific information was not available. We then
14 examined the covariation of surface Chl concentration with the limiting nutrient concentrations
15 as shown in Figure 3, and adjusted the magnitude of the half-saturation parameters of
16 phytoplankton PFT to approximately fit the observations, keeping the ratios of k-half values
17 between phytoplankton PFTs approximately the same as the initial ratios. With this approach,
18 we use the observed k-half values as an initial starting point but tune the model to match the
19 emerging properties highlighted in Figure 3.

20 Section 2.1 (p.5, line 46 to p. 6 line 2): The half-saturation parameters of zooplankton grazing
21 rates were initially set to a constant value of $20 \mu\text{mol C L}^{-1}$ for zooplankton PFTs and $60 \mu\text{mol C L}^{-1}$
22 for bacteria, based on the relationship between metabolic rates and body volume of Hansen et
23 al. (1997). We used the same approach as for nutrient limitation of the phytoplankton PFTs, and
24 adjusted the half-saturation parameters for grazing based on the observed covariations
25 between surface Chl concentrations and zooplankton biomass (Fig 3). The selected set of
26 parameter values that approximately fit the observed covariations in Figure 3 is reported in
27 Table 2. “

28 p 11944: Table 3: What was the scientific basis for the weighing factors? For instance, grazing on
29 Phaeocystis is hampered by its size (at least colonies); so, what justifies weighing them similar to
30 mixed phytoplankton? In addition, considering that Phaeocystis was considered to be colonial,
31 why is this species grazing loss by microzooplankton weighted similar to that of small
32 flagellates? The table further suggests that protozooplankton has a higher preference for
33 colonial Phaeocystis than meso- and macrozooplankton. This does not make sense to me. I
34 would like understand the rationale behind this weighing. Moreover, protozooplankton is a
35 diverse group including a number of heterotrophic dinoflagellates that prey on large plankton
36 such as diatoms and have a high contribution to grazing losses in productive systems (Calbet
37 2008). The weighing, however, suggest a focus on flagellates/ciliates as major grazers of
38 microzooplankton. This might strongly influence the model results and I wonder whether the
39 model will be able to depict the apparent shift in dominating trophic pathways in low and high
40 nutrient regimes. Finally, the legend should also clearly indicate whether grazer or prey biomass
41 was weighted. The table suggests links between trophic groups that are not depicted in Fig 1.

42 The weighing factors are generally based on predator-prey size ratio. The assignment of
43 weighing factors faces two types of difficulty. First, as the reviewer mentions, some PFTs are
44 diverse and the behaviour within PFT may not be fully homogeneous. Second, there are few
45 data to guide the preferences that would be applicable at the global scale. However through
46 multiple sensitivity tests made while developing the model, we found that the weighing factors

1 influenced primarily the biomass of the prey and predators, but had little influence on their
2 geographic distribution. Because weighing factors are relatively arbitrary, we have tried to limit
3 the number of changes we applied to the absolute minimum, and to use the resulting model
4 biomass as presented in Table 4 to determine the size of the relative preference among PFTs for
5 each grazer. We have not further adjusted the preference to the specificities of Phaeocystis
6 because they are not the main focus of our analysis, the role of the mucus in Phaeocystis colony
7 as a protection from grazing is unclear (particularly for protozooplankton), and we tried to keep
8 the number of changes apart from overall size considerations to a minimum. A specific focus on
9 Phaeocystis could explore this aspect in further detail. We expanded the text in Section 2.1 (p. 6,
10 lines 9-11) to include: “The weighing factors influenced primarily the biomass of the prey and
11 predators, but had little influence on their geographic distribution. We thus used the model
12 results on biomass (Table 4) to guide the size of the relative preferences among PFTs for each
13 grazer. “

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

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

17 We added a clarification on this correction. We do not have an exact value for the fraction of the
18 grazing on mesozooplankton that is accounted by macrozooplankton, but in total grazing
19 accounts for 2/3 to 3/4 of the mortality of mesozooplankton (Hirst and Kiorboe, 2002). The new
20 text reads (Section 2.1, p. 6, lines 22-25): “This correction preserves the temperature-
21 dependence of mortality, but it recognises that explicit grazing by macrozooplankton already
22 takes place in the model, which does not represent the grazing by other organisms (e.g. salps,
23 fish larvae). In total, grazing accounts for 2/3 to 3/4 of the mortality of mesozooplankton (Hirst
24 and Kiorboe, 2002).“

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

28 (Note this comment refers to page 11948 rather than 11944). We have deleted this sentence as
29 it is not needed in the context of our paper, and we can only speculate on possible explanations
30 for the observed trends in growth rates among phytoplankton PFTs here. It is sufficient for this
31 paper to show that we have observations for each PFT and to use these observations to
32 parameterise the model.

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

37 We added a figure comparing the PlankTOM10 and PlankTOM6 zonal mean biomass for the
38 main phytoplankton and zooplankton PFTs (new Figure 9), and added the model statistics for
39 PlankTOM6 to Table 4. The following corresponding text was added in Section 3.3 (p. 9, lines 33-
40 37): “The models are generally similar also in their representation of the distribution of biomass
41 among phytoplankton PFTs, with most of the biomass being in picophytoplankton in both
42 models (Fig. 9 and Table 4). However, PlankTOM6 allocates more biomass to protozooplankton
43 compared to PlankTOM10, though PlankTOM6 is still at the low end of observed concentrations
44 (Table 4). “

1 A comparison between modelled and observed biomass is presented in Table 4, which shows
2 that protozooplankton biomass in PlankTOM10 is underestimated both in absolute value and in
3 the relative fraction of zooplankton biomass. Mesozooplankton are slightly underestimated in
4 biomass but are within the observed range for the relative fraction, while macrozooplankton is
5 within the observed range in absolute value and slightly overestimates the relative fraction.
6 Metrics of the data-model bias are also presented in Figures 3 and 8. There are not enough
7 observations of carbon content of zooplankton biomass to show meaningful maps of
8 observations for the three zooplankton groups. For mesozooplankton, where the largest
9 database exist (see Buitenhuis et al. 2006 Figure 4), most of the data are in the Northern
10 Hemisphere. Thus a comparison with observations is not helpful here where we focus on
11 North/South ratio. We added a general comment on the functionality of the model as a whole in
12 Section 3.2 (p. 9 lines 16-23): “The marine ecosystem as a whole appears to function
13 realistically: Mesozooplankton grazing on phytoplankton is somewhat overestimated relative to
14 the 5.5 Pg/y estimated by Calbet 2001, so they have taken over the role of principal herbivores.
15 Possibly the faster turnover rates of small copepods are overrepresented in the observational
16 data on mesozooplankton, leading to a trophic position of mesozooplankton somewhat too low
17 in the foodchain. Export production, phytoplankton biomass and metazoan zooplankton
18 biomass are realistic in the model, leading to realistic seasonal cycles, but the regenerated part
19 of primary production is underestimated, concomitant with low protozooplankton biomass,
20 which impacts the model on shorter timescales of days.”

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

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

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

30 We added in Section 4 (p. 12, lines 5-6) “and several regional discrepancies exist between
31 observed and modelled biomass and fluxes” but did not go into the specifics as a detailed model
32 evaluation at the regional scale is beyond the scope of this manuscript. Our manuscript already
33 contains quantitative and qualitative information on those regions that are characterised by a
34 higher model-data misfit (e.g. Figures 3, 4, 6, 7, 8, and Table 4). Our focus here is on the use of
35 the controlled model experiments between PlankTOM10 and PlankTOM6 to highlight the role of
36 grazing for Southern Ocean phytoplankton biomass.

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

42 We think the model overestimates macrozooplankton grazing in the tropical Pacific, and thus it
43 underestimates mesozooplankton biomass compared to observations. This leads to an
44 insufficient grazing pressure by mesozooplankton on phytoplankton, and consequently to an
45 overestimation of surface Chl (as shown in Fig. 4). This is the same mechanism that explains the

1 North/South Chl ratio that is discussed here. The challenge for models will be to find the right
2 balance among zooplankton so that all key regions are well represented. We argue in this
3 response that macrozooplankton need to be incorporated because their growth rate is much
4 slower than those of other zooplankton, and thus their grazing pressure during summer is
5 greatly influenced by their winter concentrations. We added a reference to the importance of
6 this timing difference in the discussion (Section 4, end of second paragraph).

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

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

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

28 We have added a new figure showing the trophic cascades discussed in the text (new Figure 13).
29 We do not think that the underestimation of protozooplankton has a large influence on the
30 results because their growth rate is relatively close to that of mesozooplankton (compared to
31 the difference in growth rate between meso and macrozooplankton, see Table 1). What causes
32 the important trophic cascades that we see in PlankTOM10 is the fact that macrozooplankton
33 grow much more slowly than mesozooplankton and microzooplankton. Thus their maximum
34 grazing pressure can occur later in the growing season, which has a larger influence on the
35 phytoplankton biomass. This is shown in our set of sensitivity tests discussed in Section 3.4.1
36 and 3.4.2 in relation with Figure 9 (in the submitted text), where we show that when the top
37 grazers in PlankTOM10 is represented as macrozooplankton (e.g. with slow growth rate), the
38 North/South ratio in Chl is preserved no matter how the rest of the ecosystem looks.

39 Further evidence that the underestimation of protozooplankton biomass is not a serious issue
40 comes from new Figure 9 which compares the zonal mean concentration of phytoplankton and
41 zooplankton biomass between PlankTOM6 and PlankTOM10. The Figure shows that
42 protozooplankton biomass in PlankTOM6 is 2.5 times higher than in PlankTOM10, and falls
43 within the range of observations (Table 4). Yet PlankTOM6 overestimates summer Chl biomass
44 in the Southern Ocean. We added a sentence to the discussion (Section 4, p. 12, lines 25-27) to
45 make this clear. It reads: "Although PlankTOM6 simulates some degree of trophic cascade with
46 the presence of two zooplankton PFTs, our sensitivity tests presented in Fig. 11 show that the

1 difference in growth rates between the two zooplankton PFTs is too small to impact the
2 phytoplankton significantly. “
3 We are planning a number of improvements to our model that we hope will help elucidate the
4 limitations of the current analysis. We mentioned this in the Discussion (Section 4, p. 13, lines
5 17-18): “The effect of further ecosystem model developments will be explored in follow-up
6 studies.”