

## **Answer to referee #1:**

We thank referee #1 for taking the time to review our manuscript and for his/her valuable comments and suggestions that have significantly improved the quality of our manuscript.

Below, we include our detailed answers to all comments and questions.

## **Answers to general comments (GC):**

### **General Comment #1:**

*Non-grazing mortality – It is not explicitly discussed in the paper as to what the authors consider this to be. Viral lysis is seen as a major mortality pathway for coccolithophore (bloom) communities and so is this what the authors mean by this terminology? How is it parameterised and does it fairly represent viral mortality or (e.g.) programmed cell death? Not representing (or discussing) such a major mortality pathway seems like a limitation of the study, but a necessary limitation due to the uncertainties around viral mortality dynamics and its role in the Southern Ocean. The authors should include viral mortality in their discussion over model limitations, as well as directions for future field observations.*

### **Answer to GC1:**

We thank reviewer for this important comment. While not explicitly stated in the original version of the manuscript, BEC implicitly accounts for the effect of viral lysis in the non-grazing mortality term for its phytoplankton functional types (see Eq. B14 in the original manuscript). According to Moore et al. (2002) “this term [non-grazing mortality] would include losses due to viral lysis [...], as well as internal respiration/degradation, and excretion.” In BEC, the non-grazing mortality rate of phytoplankton scales linearly with their production, i.e. a constant fraction of photosynthetic production is immediately lost due to this term at every time step of integration. We acknowledge that BEC does not represent non-linear increases in losses due to viral lysis towards the end of coccolithophore blooms as suggested in the literature based on observational evidence (see e.g. **Lehahn et al., 2014, Evans et al., 2007, Brussaard et al., 2004**). To better constrain model simulations, future observational studies should investigate whether viral lysis is as important for the termination of coccolithophore blooms in the Southern Ocean, as it has been shown to be e.g. in the North Atlantic (**Lehahn et al., 2014**). To the best of our knowledge, there are only two studies from the Southern Ocean assessing the relative importance of viral lysis and grazing by zooplankton as sinks for phytoplankton biomass, and both point to a minor importance of viral lysis in this ocean region (**Evans et al., 2012, Brussaard et al., 2008**), but unfortunately, none of these studies explicitly assessed their importance for coccolithophore biomass dynamics.

We agree with the reviewer that this process should be included in the discussion of limitations of our study, and we have changed section 5.4 to include the following sentences:

“While the importance of viral lysis has been shown for the termination of coccolithophore blooms in the North Atlantic (e.g. Lehahn et al., 2014, Evans et al., 2007, Brussaard et al., 2004), to the best of our knowledge, there are only two studies from the SO assessing the relative importance of viral lysis and grazing by zooplankton as sinks for phytoplankton biomass, and both point to a minor importance of viral lysis in this ocean region (Evans and Brussaard, 2012; Brussaard et al., 2008). However, none of these studies explicitly assessed the importance for coccolithophore biomass dynamics, which should be investigated in future observational studies.”

### **General Comment #2:**

*Importance of bottom-up and top-down controls – The conclusion that both types of controls need to be considered when examining phytoplankton (and coccolithophore) population dynamics and biogeography is very important point to be made. However, the statement is not limited to the Southern Ocean and is relevant across the full bio- geographical range of coccolithophores.*

### **Answer to GC2:**

We agree with the reviewer that our conclusion that both bottom-up and top-down factors are important when assessing phytoplankton dynamics in general (or diatom and coccolithophore dynamics in particular) is not per-se restricted to the Southern Ocean, but the relative importance of both controls may be regionally varying, an effect which we cannot assess with our Southern Ocean model setup. We thank the reviewer for this comment and include a statement along these lines in the conclusion section:

“Top-down factors are important regulators of phytoplankton biomass dynamics not only in the SO, but globally (Behrenfeld, 2014). Being restricted to the SO by the regional model setup used here, future work with global models should better quantify regional variability in the relative importance of bottom-up and top-down factors in controlling phytoplankton biogeography.”

### **General Comment #3:**

*Coccolithophores/Emiliania huxleyi – Do the authors consider they have parameterised their model to describe the whole coccolithophore community, or rather that they are limited to E. huxleyi dynamics in the Southern Ocean? For this region it is relatively simple as E. huxleyi dominates (to almost monospecific levels depending on latitude). Within the authors recognised limitations, discussion of this point should be considered, especially if there are aspirations to expand such modelling efforts to low- latitude highly-diverse coccolithophore communities.*

*Related to this point, the 400% overestimation of coccolithophore biomass (Pg 19, Lns 25-26) applies to the whole coccolithophore diversity, and in diverse communities would indeed lead to significant issues, however in the E. huxleyi dominated Southern Ocean such issues are far less extreme. There are also numerous estimates of E. huxleyi cell biomass (and even B/C biomass), which are in agreement (and don't vary by 400%).*

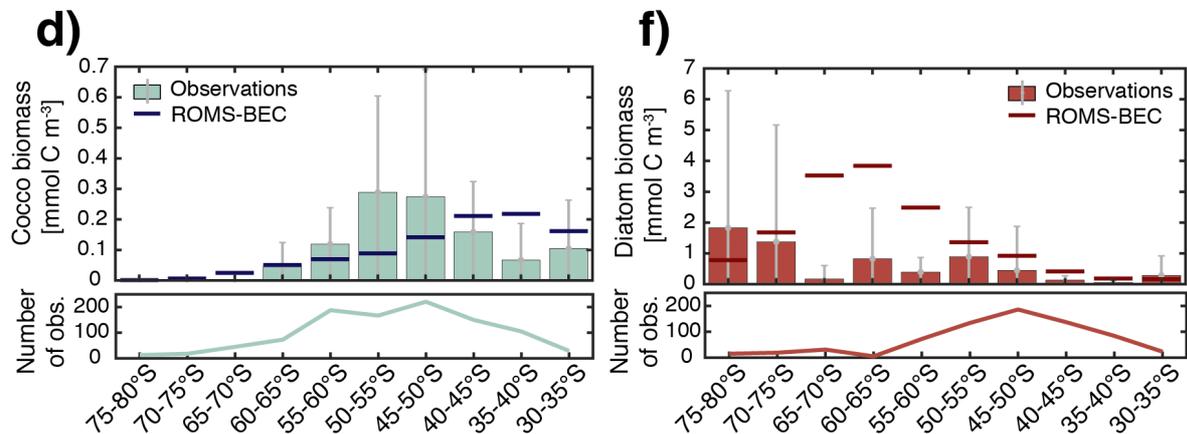
### **Answer to GC3:**

Thank you for this comment. We focused our literature research on *E. huxleyi* literature - the by far most dominant coccolithophore species in our model domain (e.g. **Saavedra-Pellitero et al., 2014**). Parameter values require adjustment when expanding any regional modelling effort to the global scale, as different coccolithophores show a wide range of growth and calcification rates and environmental dependencies (see recent review by **Krumhardt et al., 2017**). With regard to the biomass validation, we have clarified a few points in the manuscript to address the reviewer's comment: We are not, as suggested by the reviewer, overestimating coccolithophore biomass by 400%. This is the uncertainty range (conversion error) obtained when converting cell count observations to carbon biomass, given reported size ranges for *E. huxleyi* (**O'Brien et al., 2013**). Our model estimates of coccolithophore biomass are within this uncertainty of the biomass observations (see updated Fig. 1d in the manuscript, **Fig. R1** below). As stated correctly by the reviewer, the uncertainty is indeed smaller for almost mono-specific coccolithophore communities as present in the Southern Ocean as compared to more diverse communities including a larger size range than *E. huxleyi* alone (see Fig 8b in **O'Brien et al., 2013**).

We have clarified the description of the conversion from cell counts observations to biomass estimates, as well as the calculation of the uncertainty range in the supplementary material in section S1 as follows:

“Based on available information in the literature, each species is first assigned an idealized shape (e.g. sphere for *E. huxleyi*), as well as a mean size (e.g. mean coccosphere diameter for *E. huxleyi*).

Assuming the cytoplasm diameter to be 60% of the coccosphere diameter, we then calculate the mean biovolume of each cell. To get estimates of carbon biomass for each cell, the biovolume is ultimately multiplied with the specific carbon conversion factors from Menden-Deuer and Lessard (2000). The uncertainty range of this conversion is obtained by repeating the conversion using the minimum and maximum reported diameter for each species, respectively, and reporting the uncertainty range in percent of the mean biomass estimate. “



**Figure R1:** Modified version of panel 1d & f in the manuscript with standard deviation of observations added as the grey bars to illustrate variability. We have included this version of the panels in the revised manuscript.

### **Answers to specific comments (SC):**

**SC1:** Pg 1, Ln 16: Please specify ‘Ocean Acidification’ rather than just ‘acidification’.  
Thank you, corrected as suggested.

**SC2:** Pg 1, Ln 22: It is not just the ratio of calcifying to silicifying phytoplankton that is crucial to consider, it is the ratio of calcifying to non-calcifying (organic only) phytoplankton.  
Thank you, corrected as suggested.

**SC3:** Pg 2, Lns 4-5: It should be recognised that all these references are model based estimates rather than field estimates, and also take varying ways to parameterise coccolithophore production. See also pg 19, ln 21 – here it should also be recognised that these low estimates of coccolithophore NPP are derived from model studies with diverse parameterisations of coccolithophore calcification.  
Thank you, we have clarified this part of the introduction. It now reads:

“In comparison, coccolithophores contribute less to biomass ( $\approx 0.04\text{--}6\%$ , Buitenhuis et al., 2013b) and to global NPP ( $0.4\text{--}17\%$ , model-derived estimates using a variety of coccolithophore parametrizations, see O’Brien, 2015; Jin et al., 2006; Moore et al., 2004; Gregg and Casey, 2007a). “

**SC4:** Pg 2, Lns 10-11: Cell densities of  $2.4 \times 10^3$  cells  $\text{mL}^{-1}$  have to be for the Patagonian Shelf bloom and are really (really) high whilst cell densities elsewhere in the Atlantic sector of the SO are much (much) lower. The authors should make it clear that these high numbers are from bloom waters.  
Thank you for pointing this out. We have modified this part of the manuscript accordingly in the introduction:

“In-situ observations confirmed coccolithophore abundances of up to  $2.4 \cdot 10^3$  cells  $\text{mL}^{-1}$  in the Atlantic sector (blooms on the Patagonian Shelf), up to  $3.8 \cdot 10^2$  cells  $\text{mL}^{-1}$  in the Indian sector (Balch

et al., 2016) and up to  $5.4 \cdot 10^2$  cells  $\text{ml}^{-1}$  in the Pacific sector of the SO (Cubillos et al., 2007) with *Emiliania huxleyi* being the dominant species (Balch et al., 2016; Saavedra-Pellitero et al., 2014).“

**SC5:** Pg 3, Ln 14: *Please make clear that zooplankton grazing includes both micro- and macro-zooplankton (rather than just the latter).*

Thank you, we have clarified this as suggested.

**SC6:** Pg 4, Lns 6-7: *‘Coccolithophores grow well at high light intensities and at a range of different temperatures, but have been shown to be light-inhibited at low light levels’ – does this statement fit coccolithophores as a group or just E. huxleyi?*

To the best of our knowledge, the only studies assessing this effect were conducted with *E. huxleyi* (see **Zondervan et al., 2007**, and references therein). We note, however, that the inhibition threshold of  $1 \text{ W m}^{-2}$  is likely of very minor importance for the simulated coccolithophore biogeography, as it represents a very low light level that is not attained in the surface layers during the growing months.

**SC7:** Pg 5, Ln 19: *What is the justification (reference) for using such extremely low carbon to chlorophyll ratios (3 to 5)? These lead to extremely chlorophyll-rich phytoplankton cells whereas ratios are typically 10 to 20 times higher. Are these based on Southern Ocean studies?*

We thank the reviewer for pointing out that we use rather uncommon units in the original manuscript, which may have led to the confusion with regard to the reported carbon-to-chlorophyll values. In fact, we initialize with carbon-to-chlorophyll ratios of 3 and 5 mmol C / mg chl for diatoms and all other phytoplankton types, respectively, admittedly a unit rather uncommon when it comes to reporting carbon-to-chlorophyll ratios in phytoplankton (see e.g. **Thomalla et al., 2017**). These numbers correspond to 36 and 60 mg C / mg chl, respectively, which is in close agreement with the range of ratios suggested by the reviewer and in the literature (**Sathyendranath et al., 2009**, **Thomalla et al., 2017**). We have changed the respective line in section 2.2 of the manuscript to report the ratios in mg C/mg chl, have specified units more clearly, and have added a reference to justify the higher carbon-to-chlorophyll ratio of diatoms compared to the other phytoplankton types (**Sathyendranath et al., 2009**). It now reads:

“Phytoplankton carbon biomass fields are then derived using a constant carbon-to-chlorophyll ratio of  $36 \text{ mg C (mg chl)}^{-1}$  for diatoms and  $60 \text{ mg C (mg chl)}^{-1}$  for all other PFTs (Sathyendranath et al., 2009).”

**Figure 2:** *Colours seem to have changed on panel (a) – blue looks olive green and grey looks to be light green?*

Unfortunately, we cannot identify issues with the color scale in Figure 2 in the published version of the manuscript, and are thus unable to track the origin of this comment.

**SC8:** Pg 14, Ln 4: *extra ‘a’ in this sentence.*

Thank you for pointing out this typo. We deleted the extra “a”.

**SC9:** Pg 20, Ln 30: *A key statement – ‘coccolithophores appear to be of minor importance for global oceanic organic carbon fixation’. Many in situ studies agree with such small contributions to phytoplankton biomass or primary production in the Southern Ocean (including those already cited in the paper: Smith et al., 2017; Charalampopoulou et al., 2016; Poulton et al., 2013; Hinz et al., 2012).*

Thanks for this comment. We have modified this sentence accordingly, and it now states:

“Contributing only a few percent to global NPP, coccolithophores appear to be of minor importance for global oceanic organic carbon fixation, in agreement with previous observational studies from the SO (Smith et al., 2017; Charalampopoulou et al., 2016; Poulton et al., 2013; Hinz et al., 2012). “

**SC10:** Pg 24, Lns 22: *‘Based on our findings, future SO in-situ studies should consider both bottom-up and top-down factors when assessing coccolithophore biogeography in space and time’. This statement should not be limited to just the Southern Ocean.*

Please see answer to GC2 above.

**SC11:** Pg 25, Lns 19 and 22-23: As well as multiple trophic levels (and trophic cascades), what about non-grazing mortality (i.e. viral mortality?). This is not discussed anywhere in the paper and the omission of viral driven population dynamics needs to be addressed in the limitations.

Please see answer to GC1 above.

### Cited literature:

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- Sathyendranath, S., Stuart, V., Nair, A., Oka, K., Nakane, T., Bouman, H., Forget, M.H., Maass, H., Platt, T. (2009). Carbon-to-chlorophyll ratio and growth rate of phytoplankton in the sea. *Marine Ecology Progress Series*, 383, 73–84. <https://doi.org/10.3354/meps07998>
- Thomalla, S. J., Ogunkoya, A. G., Vichi, M., & Swart, S. (2017). Using Optical Sensors on Gliders to Estimate Phytoplankton Carbon Concentrations and Chlorophyll-to-Carbon Ratios in the

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