Supplement. Answer to reviewer #1

We thank anonymous referee #1 for the interest he showed in our manuscript and detailed comments that have helped to improve the original version of the manuscript. We have considered all his/her comments and addressed each of his/her concerns below.

R1-Cx: Referee comment, R1-Rx: authors response.

R1-C1: The manuscript documents an annual record of coccolithophore production and coccolith weights/lengths at a Southern Ocean site. The topic is worthy of publication in biogeosciences, and the results will be of potential interest to the wider scientific community.

R1-C2: Line 89: the Southern Ocean is a small area ? – 25% of the global area looks quite significant to me

R1-C3: Line 148: why is this section in the methods ? move regional setting and oceanography to the introduction

R1-C4: Line 235: why unfiltered ? I am not a specialist on sediment traps but it seems odd to use unfiltered seawater. Is there not a risk of contamination?

R1-C5: Lines 357 and 345: “coccolith particle bloom” – since coccoliths are inanimate (just pieces of calcium carbonate) I think the word ‘bloom’ is inappropriate here – use ‘The summer coccolith flux exhibited : : :’

R1-R1: Corrected according to reviewer 1’s suggestion. Now it reads: “coccoliths captured by the traps experienced weight and length…”

R1-R2: The sentence referred by reviewer #1 has been rephrased in order to avoid subjective descriptions of the size of the Southern Ocean. Now it reads: “Despite the fact that the Southern Ocean accounts for about 25% of the global ocean, it contains ~40% of the global ocean inventory of anthropogenic CO₂.”

R1-R3: Corrected according to reviewer 1’ suggestion. In the new version of the manuscript, section “Regional setting and oceanography” has been moved to the introduction (subsection 1.2). Section 1.1 has been titled “1.1. Background and objectives”. Subsections of Material and Methods section have been renumbered accordingly.

R1-R4: The water used to fill the sediment trap cups was unfiltered deep seawater from > 1000m, where the particle abundance is so low that filtering is unnecessary and hard to do without adding more particles than you remove. Moreover, it is important to highlight that the risk of contamination is negligible since the particle levels in sea water are of the order of micrograms per litre while concentration in the trap cups after recovery are of the order of milligrams per litre. This point has been clarified in the new version of the manuscript. The following text has been added in lines 446-449 of the new version of the manuscript with tracked changes:

“Risk of sample contamination by the unfiltered seawater is considered negligible due to the fact that the deep water exhibits low particle abundance and also because particle concentration in sea water is of the order of µg/L while concentration in the trap cups after recovery was of the order of mg/L.”

R1-R5: Corrected according to reviewer 1’s suggestion.
**R1-C6:** Line 548: you mention two factors that possibly explain the changes in calcification. Calcification (i.e. overgrowth) tends to increase with depth in the photic zone, at least in some areas of the world. So in winter it may be that the coccolithophores are sitting deeper and therefore have more calcified coccoliths than in the summer when they are closer to the surface and therefore with lightly calcified coccoliths. Of course this difference in surface vs deeper photic could be related to various parameters (light, nutrients, temperature). Do you have data/images of coccoliths from different photic depths? In Plate 1 you show lightly and heavily calcified coccoliths from the traps – but how do they relate to the surface oceans?

**R1-R6:** We appreciate reviewer 1’s comment. Unfortunately, there is no data available of coccolith weight from different photic depths. Only samples collected by two sediment traps (that were deployed far below the photic zone) and satellite data are available for the study site. Therefore, our current data set precludes the assessment of the relationship between coccolith weight and the depths where the coccolithophore populations developed. In regard to seasonality, no relationship between the overgrowths and a particular period of the annual cycle was observed. This is now clarified in a sentence that has been included in the new version of the manuscript with tracked changes (“lines 674-675”).

**Minor points for correction/consideration**

**R1-C7:** Title and elsewhere: Just a query. Is the use of Australian Sector OK? Naming the sectors after the oceans, like the Atlantic Sector, Pacific Sector and Indian Ocean Sector is fine, but I wonder whether using country names (for sectors and territories) is considered to be geopolitical.

**R1-R7:** We acknowledge the point highlighted by reviewer 1. Indian sector could also be an appropriate term for referring to the study region of this research. Nonetheless, we decided to use the term “Australasian sector of the Southern Ocean” in order to be consistent with the terminology of previous work along the 140°E parallel such as Findlay and Giraudau (2000), Quéguiner (2001), Trull et al. (2001), Sedwick et al. (2008), de Salas et al. (2011), Lannuzel et al. (2011) and many others. Please find the references of the publications mentioned in the previous sentence listed below:


R1-C8: Line 30: Don’t mix z and s verbs. For example, here you use ‘characterized’ and on line 151 ‘summarized’, but on line 35 you use ‘analysed’ and on line 135 ‘fertilisation’. Furthermore, on line 236 you use ‘programmed’ and on line 349 ‘grey’. You need to be consistent, and choose between British English and US English. It looks like you are favouring the former.
R1-R8: Corrected according to reviewer 1’s suggestion. The whole manuscript has been revised and corrected in order to be consistent with the use of British English (i.e. verbs “z” has been replaced by “s” when needed).

R1-C9: Line 45: coccolithophorid vs coccolithophore. Be consistent, and choose one.
R1-R9: Corrected according to reviewer 1’s suggestion. In order to be consistent the word coccolithophorid has been replaced by coccolithophore in the new version of the manuscript.

R1-C10: Line 62: “..some species (but not all) of coccolithophore ..” – please change to ‘some species of (but not all) coccolithophores ..’
R1-R10: Corrected according to reviewer 1’s suggestion.

R1-C11: Lines 71-75: needs to be rewritten, as it doesn’t make sense
R1-R11: The sentence highlighted by reviewer 1 have been deleted following the suggestion of reviewer 2 (See R2-C21).

R1-C12: Line 79: one bracket is missing
R1-R12: Corrected according to reviewer 1’s suggestion.

R1-C13: Line 102: dominantly present -> dominate
R1-R13: Coccolithophores are abundant in the subantarctic waters of the Southern Ocean, but this does not mean that they dominate the phytoplankton communities in terms of numbers or biomass. In order to be more precise, the sentence highlighted by reviewer 1 has been rewritten: “coccolithophores exhibit high concentrations in the Subantarctic Southern Ocean”

R1-C14: Line 115: spares -> sparse
R1-R14: Corrected according to reviewer 1’s suggestion.

R1-R15: Corrected according to reviewer 1’s suggestion.

R1-C16: Line 203: CO2 rich -> CO2-rich
R1-R16: Corrected according to reviewer 1’s suggestion.

R1-C17: Line 253: “After settling 12 hours ..” -> ‘After settling for 12 hours ..’
R1-R17: Corrected according to reviewer 1’s suggestion.

R1-C18: Line 271: by using-> using
R1-R18: Corrected according to reviewer 1’s suggestion.

R1-C19: Line 273: “ ..to the winter ..” -> ‘ ..to winter ..’
R1-R19: Corrected according to reviewer 1’s suggestion.

R1-R20: Since this point has been also mentioned by reviewer 2 (See R2-C55), the text has been modified trying to satisfy both reviewers suggestions. The text now reads: “a Scanning Electron Microscope (SEM)”.

R1-C21: Line 298: “..using a with a Nikon ..” -> ‘.. using a Nikon ..’
R1-R21: Corrected according to reviewer 1’s suggestion.

R1-C22: Line 346: “..should be looked with caution ..” -> ‘should be viewed with caution’
R1-R22: Corrected according to reviewer 1’s suggestion.

R1-C23: Line 358 (and elsewhere) : you need to insert x (times) between the number and the power. For example, 2.2 10 -> 2.2. x 10
R1-R23: Corrected according to reviewer 1’s suggestion. The manuscript has been revised and “x” has been included between the number and the power when absent.

R1-C24: Line 365: Biogenic -> biogenic
R1-R24: Corrected according to reviewer 1’s suggestion.

R1-C25: Line 370: of the species Calcidiscus -> of Calcidiscus
R1-R25: Corrected according to reviewer 1’s suggestion.

R1-C26: Figure 5 (and elsewhere): I realise that ‘liths’ is in common use in presentations, but it is not an official term. Better to use coccoliths.
R1-R26: Corrected according to reviewer 1’s suggestion. The word “liths” has been replaced by coccoliths in the Y-axis of Figure 5. The text has been revised although no inconsistencies were found.

R1-C27: Line 382: tiles? I think you mean 'elements’
R1-R27: PREGUNTAR A Lluïsa Cross The text has been corrected following reviewer 1’s recommendation. The term tiles has been replaced by “tile-like elements”.

R1-C28: Line 384: “Distal shield measures ranged between 2 and 4.35 ..” -> ‘Distal shield ranges from 2.0-4.35 ..’ [use decimal point not comma]
R1-R28: Corrected according to reviewer 1’s suggestion.

R1-C29: Line 424: here you use station 62 S, and before 62 S site – perhaps be consistent in usage
R1-R29: The words site and station are used as synonyms in the text and are used alternatively in order to avoid repetition. Therefore, no changes in the usage of these words have been incorporated in the text.

R1-C30: Line 463: genetical -> genetic
R1-R30: Corrected according to reviewer 1’s suggestion.

R1-C31: Line 550: degrees of calcification -> degree of calcification
R1-R31: Corrected according to reviewer 1’s suggestion.

R1-C32: Line 555: B/C south 50_S -> B/C south of 50_S
R1-R32: Corrected according to reviewer 1’s suggestion.

R1-R33: Corrected according to reviewer 1’s suggestion.

R1-C34: Line 617: absence accompanying in situ -> absence of in situ
R1-R34: Corrected according to reviewer 1’s suggestion.
Additional changes

- Section 3.3, line 674, of the “new version of the manuscript with tracked changes”, the sentence “annual amplitude of the coccolith weight was approximately” has been replaced by “annual amplitude of the **mean** coccolith weight was approximately” in order to be clearer.
- The correlation between Biogenic silica and coccolith fluxes at 2000 m showed in line XX of the first version of the manuscript was the correlation coefficient ($r = 0.86$), not the coefficient of determination ($R^2 = 0.74$). In the new version of the manuscript the coefficient of determination is shown.
- The coccolith length values presented the results listed in section 3.3 of the first version of the manuscript (lines 405-409) corresponded to an earlier version of the data set. The correct values have been included in the new version of the paper. Please note that the seasonal trend remains identical (only there was is a slight variation of the absolute values). Please also note that the calculations made in the discussion regarding the relationship between size and weight in the first paragraph of Section 4.3 are correct. The coccolith length data at 3700 plotted in figure 6 also corresponded to the older version of the dataset. This has been corrected in the new version of the manuscript. Please note that the seasonal trend remains identical.
- Plate I: In the first version of the manuscript the we skipped the letter “d” listing the photos of Plate I. In the new version of the manuscript, this typo has been fixed.
Supplement. Answer to reviewer #2

R2-Cx : Referee comment, R2-Rx: authors response.

R2-C1: General comments.
The calcification of coccolithophores in the high latitude regions is a growing concern as it will have large influence on ocean biogeochemistry and thus climate. The data provides new information on coccolithophore response to varying environmental conditions at Antarctic Zone using sediment traps samples. However, the information provided here can be expressed in a much better way. Sediment trap data from Southern Ocean is difficult to obtain and is therefore a welcome addition to knowledge and needs to be published. Here are some major and minor comments which need to be incorporated in the manuscript.

R2-R1: We sincerely thank reviewer #2 for the careful reading of our manuscript and constructive criticisms and comments that helped to improve the manuscript. The text and figures have been revised and improved accordingly. Next, we briefly summarize the main changes included in the text. A potential explanation behind the formation of secondary crystallizations observed in some of the coccoliths has been included together with the references suggested by the reviewer. Also, in the new version of the manuscript the possible influence of salinity on coccolith morphology is discussed and new references dealing with the impact of temperature in the coccoliths have been included. Moreover, several figures have been improved following reviewer 2’s suggestion: Figure 1 now shows the maximum and minimum sea ice extent during the deployment period; the vertical structure of temperature of the water column in Figure 2 is now plotted with Ocean Data View; several aspects of Figure 3 have been improved following reviewer 2’s comments; and a new figure has been created (Fig. 7) that shows the regression plots between coccolith weight and length. Finally, a throughout revision of the references cited in the manuscript has been performed.

R2-C2: Major comments/changes needed to be done:
1. Authors documented only abundance of coccoliths of E. huxleyi B/C morphotypes in the traps. It is also mentioned that occurrence of other coccolithophores were also documented. Though other coccoliths are in low abundance, it represents changes in the upper oceanic conditions. It is also important to plot a graph of other coccolithophores and discuss what their assemblage indicates.

R2-R2: Due to the very low abundance of other coccolithophore species in the trap samples, authors decided to focus the discussion on total coccolith fluxes because flux plots based on very small counts could be biased and therefore misleading for the reader. However, in compliance with reviewer’s request the fluxes and relative contribution of Emiliania huxleyi, Calcidiscus leptoporus and Gephyrocapsa spp. at both sediment trap depths have been included in the new Supplementary Figure 1. Moreover, the seasonality of these species is now described in the section 3.1 of the results, as well as, discussed at the end of the first paragraph of section 4.2.

R2-C3: 2. The overcalcification of E. huxleyi is documented by few researchers in past few years. But not many papers are published on this. Authors have documented overcalcification on coccoliths retrieved from sediment traps. I assume intact coccospheeres are also documented in the both the sediment traps. In this case, whether authors documented overcalcification on coccospheeres of E. huxleyi? If any information
is available on living coccolithophores in this region, it should be included. It is important to document the overcalcification on E. huxleyi is a natural process and not a part of secondary calcification. So, if extant coccolithophores data is available at/around study site then it should be presented.

R2-R3: We appreciate reviewer 2’s comment on the possible overcalcification of some of the coccoliths captured by the trap. As stated in section “3.2 SEM analyses”, the unusual structures (mainly small spherules deposited on the coccoliths) observed on some of the coccoliths, such as that of the coccoliths shown in Plate I, e.g., is attributed to a secondary recrystallization but not overcalcification. This interpretation is based on the small spherules often present in the coccoliths, particularly on the laths, a feature consistent with a secondary recrystallization and not with overcalcification of the coccoliths during the life cycle of the coccolithophore. Cubillos et al. (2008) undertook a comprehensive analysis of the E. huxleyi morphotypes in the Australian sector of the Southern Ocean along the 140°E meridian (covering the location of the sediment trap station analysed here). According to the former authors the overcalcified forms of Emiliania huxleyi are restricted north of the Polar Front (Subantarctic and Subtropical Zones), and therefore it is unlikely that we register these forms in our traps. Furthermore, the only overcalcified forms reported by Cubillos et al. (2008) correspond to morphotype A, which is characterized by a larger coccoliths than those observed here. Please note that Cubillos et al. (2008) paper is discussed in section 4.3 of the manuscript. Moreover, an explanation about the possible origin of the “small spherules” observed on some coccoliths has been included at the end of section 4.4. of the discussion in order to satisfy reviewer 2’s request.

In regard to the documentation of coccospheres in the trap samples. The number of coccospheres found in the samples was very low due to the low abundance of coccolithophores in the study region. In order to overcome this problem, one could state that concentration used in the SEM preparations could have been increased. However, this was not possible in our particular case due to the large abundance of diatoms at this site which concentration obviously increase with concentration. Please note that the biogenic silica fluxes at the 61ºS site are the arguably the highest ever reported in the world’s ocean. Such high concentration of diatoms greatly hampered the finding of coccospheres under the SEM, that it is the only methodology that allows discriminating between overcalcified and “normal” coccospheres.

R2-C4: 3. Authors often compared diatom assemblage with coccoliths. Plotting a graph of total diatom assemblage vs coccoliths abundance will be useful for understanding changes in the AZ region.

R2-R4: Authors do not completely understand reviewer 2’s request. Total diatom valve and total coccolith fluxes at both sediment trap depths are plotted in figure 5. Only one diatom species is mentioned in the text: Thalassiosirix antarctica. The seasonal succession of diatom species at the 61ºS site is discussed in detail in Rigual-Hernández et al. (2015, JMS) paper that is mentioned in the text. Authors believe that plotting the fluxes and relative abundance of the all the diatom species would be out of the scope of this paper, would not contribute to the discussion and would be misleading for the reader. However, these graphs can be included in the manuscript or in a supplementary figure if the editor considers this information relevant.
R2-C5: 4. A recent study indicates polysaccharides are also responsible for overcalcification of coccolithophores. Authors need to discuss outcomes in more detail and should be cited with recent references.

R2-R5: Corrected according to reviewer 2’s suggestion. A paragraph dedicated to the possible role of the polysaccharides serving as organic scaffold for coccolith formation has been included and new references included and discussed (Gal et al., 2016; Lee et al., 2016) (end of section 4.4)

R2-C6: 5. Authors should be consistent in framing sentences. Some sentences are too large, some are too small. Be consistent in using AZ vs AZ-S, Fe vs. iron, E. huxleyi, vs Emiliania huxleyi etc.

R2-R6: Corrected according to reviewer 2’s suggestions. The whole manuscript has been revised and several sentences have been split into two when possible:
- Line 85 of the new version of the manuscript with tracked changes: a long sentence has been removed.
- Line 86-87: the sentence has been split into two.
- Line 145-146: the sentence has been split into two.
- Line 1096-1098: The introductory sentence of the conclusions section has been split into two and rephrased.

Moreover, the text has been revised for inconsistencies in the use of the terms:
- AZ vs AZ-S, Fe vs. iron, E. huxleyi vs Emiliania huxleyi.
- Fe vs. iron: The term “Fe” has been replaced by “iron” is the new version of the manuscript.
- The term “AZ” has been replaced by “AZ-S” when possible.
- Emiliania huxleyi has been replaced by E. huxleyi when possible.

R2-C7: 6. Since, both sediment traps are located in the 61degS and there is no comparison done with other sediment traps showed in the Fig. 1, it is not necessary to mention “at 61S sediment trap everywhere”

R2-R7: Corrected according reviewer 2’s suggestion. The name of the sampling site has been replaced by synonyms when possible. However, the term 61°S site is still used in the new version of the manuscript when needed.

R2-C8: 7. Authors should crosscheck references very carefully. Many references listed in the text are not reflected in the reference list. Similarly, many references listed in the Reference list are not

R2-R8: Corrected according to reviewer 2’s suggestion. The references listed in the text and in the reference list have been revised. Only a few errors were found and have been corrected in the new version of the manuscript.

R2-C9: mentioned in the text. Genus and species name should appear properly and in italics.
For ex. Line 860- emiliania huxleyi.

**R2-R9:** Corrected according to reviewer 2’s suggestion. The text and references have been thoroughly revised in order to show all species and genus names in italics.

**R2-C10:** Hagino et al. 2011 reference- written in caps

**R2-R10:** Corrected according to reviewer 2’ suggestion.

**R2-C11:** **Minor comments:**

*Line 14-30: The information provided in the abstract can be shifted to the introduction. The abstract should start from Line 31.*

**R2-R11:** We agree with reviewer 2 that the first lines of the abstract could also fit in the introduction. However, we believe that providing a very short rationale of the experiment and highlighting the gaps in the knowledge about the effects of a changing climate in Southern Ocean ecosystems is important to help the non-specialized reader to understand the relevance of our study, thereby potentially reaching a larger audience. Therefore, authors have decided to leave the abstract as it is in the first version of the manuscript.

**R2-C12:** Line 32: In the deep ocean >>> at the Antarctic Zone

**R2-R12:** Corrected according to reviewer 2’s suggestion. Now it reads: “We report here on seasonal variations in the abundance and composition of coccolithophore assemblages collected by two moored sediment traps deployed at the Antarctic Zone south of Australia (2000 and 3700 m depth) for one year in 2001-02.”

**R2-C13:** Line 33: ~2000 >>> 2000

**R2-R13:** Corrected according to reviewer 2’s suggestion.

**R2-C14:** Line 33: and 3700>>> and 3700 respectively

**R2-R14:** In the new version of the manuscript this sentence has been rephrased. As consequence of this change is no need to include the word “respectively”.

**R2-C15:** Line 37: Emiliania huxleyi morphotype B/C>>> E. huxleyi morphotype B/C

**R2-R15:** Corrected according to reviewer 2’s suggestion.

**R2-C16:** Line 38: coccolith assemblage experienced weight and length reduction>>> coccoliths experienced weight and length reduction

**R2-R16:** This sentence had already been corrected following reviewer 1’s suggestion.

**R2-C17:** Line 39: during the summer months>>> during summer months (December-March?)

**R2-R17:** The text has been modified slightly different to that suggested by reviewer 2. Now it reads: “reduction during summer (December – February)”

**R2-C18:** Line 40: at both sediment trap depths>>> at both sediment traps

**R2-R18:** Corrected according to reviewer 2’s suggestion.

**R2-C19:** Line 41: in other southern ocean settings>>> which settings?

**R2-R19:** Corrected according to reviewer 2’s suggestion. Patagonian shelf and Scotia sea are mentioned between brackets in the new version of the manuscript.
Apart from first record, significant outcomes of the study needs to be highlighted here.

The major findings of the investigation are summarized (and numbered) before this sentence. Moreover, in the last sentence of the abstract we clearly explained the importance of our results clearly explaining that our results provide a reference/baseline for evaluation of Southern Ocean coccolithophore responses to changing environmental conditions in the coming decades. Therefore, we believe that the main objectives and outcomes of the study are already mentioned in the text and no more extra information is required.

May not required in the introduction

For example, diatoms can play a prominent role in export of organic matter from the surface ocean, because of their heavy siliceous frustules and capacity for aggregation and rapid sinking facilitates efficient transport of organic carbon (Buesseler, 1998; Smetacek, 1999). Nonetheless, it has also been suggested that this silica-mediated carbon export driven by diatoms may not always reach the ocean interior efficiently (Francois et al., 2002; Lam and Bishop, 2007).” has been removed from the introduction.

Coccolithophores also has the potential >>>> coccolithophores has potential

Despite the fact that the Southern Ocean accounts for about 25% of the global ocean, it contains ~40% of the global ocean inventory of anthropogenic CO2

We believe there must have been a misunderstanding here since Trull et al., 2017 (Biogeosciences) was mentioned in the first version of the manuscript (lines 1097-1099)

Cubillos et al. 2008 or 2007? Cubillos et al. 2008 does not exist. The text has been corrected, now only the citation Cubillos et al., (2007) appears in the text.

Freeman and Lovenduski (2015) not mentioned in the reference list

Corrected according reviewer 2’s suggestion. The reference Freeman and Lovenduski (2015) appears now in the text.

Please see R2-R6 for more details.

Trull et al., 2017 missing in the reference list
R2-R28: As mentioned in a previous comment (R2-R24), we believe that there must have been a misunderstanding here since Trull et al., 2017 did appear in the reference list (lines 1097-1099 of the first version of the manuscript).

R2-C29: Line 138: inferred from one-year record >>> inferred from 10 month record

R2-R29: The sentence has been rephrased and the words “one-year record” replaced by “during ten months”.

R2-C30: Line 139: SOIREE……. Elaborate when using short forms for the first time

R2-R30: Corrected according to reviewer 2’s suggestions.

R2-C31: Line 147: Regional setting and oceanography; and water carbonate chemistry, should be shifted in the introduction under a different sub-heading.

R2-R31: Corrected according to both reviewer 2 and reviewer1’s suggestion. Sections “regional setting and oceanography” is section 1.2 in the new version of the manuscript, while “Water column chemistry in the study region” is now section 1.3.

R2-C32: Line 151... SAACF>>>SACCF

R2-R32: Corrected according to reviewer 2’s suggestion.

R2-C33: Line 151: (SAACF)>>> (SACCF) Fig.1

R2-R33: Corrected according to reviewer 2’s suggestion. Figure 1 in now cited between brackets at the end of the first sentence of section “1.2. Regional setting and oceanography “.

R2-C34: Line 155: upper water column with nutrients (add reference). Similarly for sentences between lines 155-160 (add references)

R2-34: Before the description of the seasonal evolution of water column physical, chemical and biological properties, it is mentioned: “Trull et al. (2001b) summarized the seasonal evolution of water column properties in the study region”. Although we could refer to this cite in each following sentence, authors believe that the text should remain as is now in order to avoid repetition.

R2-C35: Line 155: Chlorophyll-a, vs/ Line 484 chl-a>>> use one style of writing

R2-R35: Corrected according reviewer 2’s suggestion. The term chl-a has been replaced by chlorophyll-a and the text has been revised for inconsistencies.

R2-C36: Line 160:….. in algal biomass occurs within the mixed layer (add reference)

R2-R36: Corrected according reviewer 2’s suggestion. The reference Trull et al. (2001b) has been included.

R2-C37: Line 164: Trull et al. 2001>>> Trull et al. 2001a or Trull et al. 2001b or 2001c??

R2-R37: Trull et al. 2001b is the correct reference here. In the new version of the manuscript the correct reference is specified.

R2-C38: Line 169: Large calanoid copepodies.>>> Copepods and copepodites are different. Copepodites are immature form of copepods. What authors are trying to say? “large Calanoid copepods” or “mainly Calanoid copepodites”??
As highlighted by reviewer 2, copepodites are immature forms of copepods. Zeldis et al. (2001) reported that “The SOIREE site mixed-layer mesozooplankton community was dominated by copepods, with salps and pteropods absent, and euphausiids either absent or very rare (maximum 7 animals m$^{-3}$). The copepod community was numerically dominated by large copepodites (> 1.5mm prosome)...”. Therefore, we believe that the sentence “Mesozooplankton analysis during the SOIREE experiment by Zeldis (2001) indicates that zooplankton community in the study region is dominated by copepods, mainly large calanoid copepodites.” is correct. That is the reason why the sentence has not been modified.

**R2-C39:** Fig. 1. Since author has mentioned that sediment trap location was away from sea ice activity, authors should draw seasonal sea ice zone or winter sea ice limit for the year 2001-2002 in Fig. 1

**R2-R39:** Corrected according to reviewer 2’s suggestion. The winter sea ice limit for August 2001 is now showed in Figure 1. The Figure caption has been adapted accordingly citing the source of the sea ice data represented in Fig. 1. Moreover, the database where this data was obtained is also cited in the new version of the manuscript.

**R2-C40:** Line 180: SACCF- Southern ACC Front >>> SACCF- Southern Antarctic Circumpolar Current Front

**R2-R40:** Corrected according to reviewer 2’s suggestion.

**R2-C41:** Line 193: calcite saturation horizon (CSH) >>> Calcite Saturation Horizon (CSH)

**R2-R41:** Corrected according to reviewer 2’s suggestion.

**R2-C42:** Line 194: CaCO3 compensation depth (CCD) >>> CaCO3 Compensation Depth (CCD)

**R2-R42:** Corrected according to reviewer 2’s suggestion.

**R2-C43:** Fig. 2. Similar to Fig. 1 and Fig. 3, Fig. 2 should be plotted in the Ocean data view and figures should be readable. What does the dotted line indicate in Fig. 2b?

**R2-R43:** Corrected according to reviewer 2’s suggestion. The vertical structure of temperature of the water column has been plotted in Ocean Data view (Fig 2a of the new version of the manuscript). Due to the low number of observations of nutrient concentrations in the study regions, their representation using ODV would require a large interpolation of measurements and the resulting graph would be somewhat misleading for the reader. Therefore, authors have decided to leave the Figure representing silicate and nitrate concentration as it was in the first version of the manuscript (Fig. 2b in the new version of the manuscript).

**R2-C44:** Fig 2 a. legend should contain surface macronutrient concentrations?

**R2-R44:** Only data of the nutrient concentration in the mixed layer is available. This data is data plotted in Figure 2b. In order to be clearer, in the new version of the manuscript it is clarified that the data showed in Figure 2b is representative for the mixed layer.

**R2-C45:** Line 200: (Fig. 3) >>> (Fig. 3a) or (Fig. 3b)

**R2-R45:** Corrected according to reviewer 2’s suggestions. Figure 3b is mentioned in the new version of the manuscript.
R2-C46: Fig. 3. Mark Fig. 3a and Fig 3b; Mark frontal locations, put units for color scale bar, x axis etc. Also, include sampling dots if possible. Mark 1000m sediment trap in fig 3 in different color., as it is mentioned in line 226.

R2-R46: Figure 3 has been corrected according to reviewer 2’s suggestions.

R2-C47: Line 210: Elaborate when appear for the first time

R2-R47: Corrected according to reviewer 2’s suggestions.

R2-C48: Line 211: Tanhua et al. 2008 is missing in the reference list

R2-R48: The reference Tanhua et al. (2008) has been replaced by CARINA group (2011) which appears now in the reference list. The new reference refers to the same data set of that used by Tanhua et al. (2008), i.e. both references are correct.

R2-C49: Line 122: Draw seasonal sea ice zone in Fig. 1

R2-R49: Corrected according to reviewer 2’s suggestion. In the new version of the manuscript the Maximum Winter Sea Ice Extent and Minimum Summer Ice Extent for the study period (August 2001 and February 2002) are represented in Figure 1. The Figure caption has been rewritten accordingly and the dataset from where the sea ice data has been extracted is now cited in the text (Fetterer et al., 2017).

R2-C50: Line 225: for approximately one year>>> for ten months

R2-R50:Strictly speaking the sampled period is 10 months and a half (317 days / 30 day per month = 10.56 months). Authors believe that it is correct to leave the text as it is now because it is specified the number of days sampled between brackets. “The 61°S mooring was equipped with three McLane Parflux time series sediment traps (Honjo and Doherty, 1988) for approximately one year (November 30, 2001 to September 29, 2002, 317 days).”

R2-C51: Line 227: highlight Fig. 3a and 3b

R2-R52: Corrected according to reviewer 2’s suggestion. In the new version of the manuscript both Fig. 3a and 3b are mentioned in the sentence referred by reviewer 2.

R2-C52: Line 231: be consistent in using depths. Either use “~2000” or “2000”, “3800 or 3700

R2-R52: Corrected according reviewer 2’s suggestion. In the new version of the introduction only “2000 m” is used (i.e. not “~2000” used once in the introduction in the first version of the manuscript. Moreover 3800 has been replaced by 3700 following the comments of the reviewer.

R2-C53: Line 283: Emiliania huxleyi>>> E. huxleyi

R2-R53: Corrected according to reviewer 2’s suggestions.

R2-C54: Line 235: why unfiltered seawater used? Won’t it contaminate samples?

R2-R51: A similar question was raised by reviewer 1 (R1-C4). In the new version of the manuscript it has been clarified the reasons why unfiltered seawater was used. In the new version of the manuscript it is stated: “Risk of sample contamination by the unfiltered seawater is considered negligible due to the fact that the deep water is characterized by low particle abundance and also because particle concentration in sea water is of the order of µg/L while concentration in the trap cups after recovery was of the order of mg/L.”
R2-R55: Corrected according to reviewer 2’s suggestion.

R2-C56: Line 286: decantation method outlined by >>> method outlined by
R2-R56: Corrected according to reviewer 2’s suggestion.

R2-C57: Line 287: coated in Gold >>> coated with/using Gold
R2-R57: Corrected according to reviewer 2’s suggestion.

R2-C58: Line 288: please mentioned magnification range (for example 2000-7000x) used during analysis.
R2-R58: Corrected according to reviewer 2’s suggestion. The magnification used during the SEM analysis is specified in the new version of the manuscript (magnification 5000-20000x).

R2-C59: Line 288: Emiliania huxleyi >>> E. huxleyi
R2-R59: Corrected according to reviewer 2’s suggestion.

R2-C60: Line 291: Emiliania huxleyi >>> E. huxleyi
R2-R60: Corrected according to reviewer 2’s suggestion.

R2-C61: Line 293: Emiliania huxleyi >>> E. huxleyi
R2-R61: Corrected according to reviewer 2’s suggestion.

R2-C62: 293-294: Emiliania huxleyi coccoliths into morphotypes >>> Emiliania huxleyi into different morphotypes
R2-R62: Corrected according to reviewer 2’s suggestion.

R2-C63: Line 298: using a with a Nikon >>> using a Nikon
R2-R63: Corrected according to reviewer 1 and 2’s suggestions.

R2-C64: Line 319: sea surface temperature (SST) already elaborated in line 153
R2-R64: Corrected according to reviewer 1 and 2’s suggestions.

R2-C65: Line 320: Sea Surface Temperature Analysis >>> SST Analysis
R2-R65: Corrected according to reviewer 1 and 2’s suggestions.

R2-C66: Line 323: SST variations >>> Sea Surface variations
R2-R66: This change has not been incorporated because the authors wanted to refer specifically to Sea Surface Temperatures (SST) not Sea Surface variations in general.

R2-C67: Line 326: Photosynthetically active radiation (PAR) >>> Photosynthetically Active Radiation (PAR)
R2-R67: Corrected according to reviewer 2’s suggestion.

R2-C68: Line 327: particulate inorganic carbon (PIC) >>> Particulate Inorganic Carbon (PIC)
R2-R68: Corrected according to reviewer 2’s suggestion. Moreover, in the caption of figure 4, the names Photosynthetically Active Radiation and Particulate Inorganic Carbon have been replaced by their acronyms, i.e. PAR and PIC.

R2-C69: Fig. 4. Authors have mentioned March as a late summer months in the line 158. In this case, the shaded area should also include March

R2-R69: The sentence highlighted by reviewer 2 has been corrected. In the new version of the manuscript, it reads: “By late summer-early autumn (March) SST ranges between 2 and 3 °C”

R2-C70: Line 341: particulate inorganic carbon (PIC)>>> PIC

R2-R70: Corrected according to reviewer 2’s suggestion.

R2-C71: Line 342-346- It is important................................. Trull et al., 2017)>>> already mentioned before

R2-R71: Reviewer 2 is right, the fact that the satellite algorithm used to detect PIC is not reliable in Antarctic waters is mentioned in the introduction as well. Nonetheless, authors believe it is important to mention this point again in the caption of Figure 4 in order reinforce this idea and to make the reader aware that the PIC satellite data presented in that figure should be viewed with caution.

R2-C72: Line 347: particulate organic carbon (POC)>>> POC; Calcium Carbonate (CaCO3)>>> CaCO3

R2-R72: Corrected according to reviewer 2’s suggestion.

R2-C73: Fig. 5. Please check scale bars. 2x109 appeared twice on left side.; in the first figure only 109 appeared. Is it 1x109?. Put same scale in both figures. Mark Figure 5a and 5b.

R2-R73: Corrected according to reviewer 2’s suggestion. A decimal has been included in the all the labels of axis of Figure 5 in order to avoid the number repetition highlighted by reviewer 2. Moreover, now axis in both figures have the same scale. Finally, the axis titles have been corrected as they were wrongly named in the first version of the manuscript.

R2-C74: Fig. 5. What is the reason diatom valve flux remained almost constant at 2000 and 3700 but there is an increase in diatom flux during February and March. Please explain.

R2-R74: Differences in the magnitude of fluxes between the upper and deeper trap are most likely due to small differences in the source area of the particles collected by each trap, the so-called statistical funnel (discussed in section 4.1). This statistical funnel increases with depth and therefore it is expected some variability between the fluxes captured by each trap. This is clarified in the new version of the manuscript where it is stated: “The slightly different seasonal pattern observed at both sampling depths (Fig. 5) is mainly attributed to the fact that the area of the ocean from which the particles have been produced increases with depth (Siegel and Deuser, 1997) (863-865 of the new version of the manuscript with tracked changes).

R2-C75: Line 370-372: which Calcidiscus leptoporus species? Small or intermediate? Which time of sampling month these species are documented?
**R2-R75**: *Calcidiscus leptoporus* coccoliths were not divided into size classes during the LM microscopy analysis. Therefore, in the new version of the manuscript it is specified “sensu lato” after the species name. Relative abundances of this species can be found in Table 1. Moreover, in the new version of the manuscript the fluxes and relative abundance of this species have been plotted in supplementary Figure 1, are described in the results section “3.1 Seasonal dynamics of coccolith export fluxes” and discussed in discussion section “4.2 Seasonal dynamics of the calcareous and siliceous phytoplankton fluxes”. Please also note that due to the low abundance of this species in the samples and to its similar seasonal pattern to that of *E. huxleyi*, *C. leptoporus* data does not provide any relevant contribution to the discussion. That is the main reason why initially this data was not included in the first version of the manuscript and also why the information of this species is included as supplement.

**R2-C76**: Line 383: distal shields partially missing, may be due to >>>> distal shield partially missing, due to

**R2-R76**: Corrected according to reviewer 2’s suggestion. The sentence has been rephrased to: “…partially missing, mainly due to the slender and delicate structure of the laths”.

**R2-C77**: Line 384: 2 to 4.35>>>> 2 to 4.35

**R2-R77**: Corrected according to reviewer 1 and 2’ suggestion.

**R2-C78**: Line 394: (2.3 and 2.1 pg/coccolith)>>>> (2.3 ±..., and 2.1±..., pg/coccolith)

**R2-R78**: Corrected according to reviewer 2's suggestion. The standard deviation is now showed in all the coccolith mass values provided in section “3.3 Coccolith weight and length changes”

**R2-C79**: Lien 396: (down to 1.6 and 1.9 pg at 2000 and 3700m, respectively)>>>> (down to 1.6±..., and 1.9±..., pg/coccolith at 2000 and 3700m)

**R2-R79**: Corrected according to reviewer 2's suggestion. The standard deviation is now showed in all the coccolith mass values provided in section “3.3 Coccolith weight and length changes”

**R2-C80**: Line 399: Average annual coccolith weight at the 61S traps>>>>it is already mentioned that both traps are located at AZ-S, at 61S, just mentioned depths. Similarly at Line 433, at the 61S site>> study site. Similarly correct changes at line 446 and elsewhere

**R2-R80**: Corrected according to reviewer 2’s suggestion. The name of the station 61ºS site has been replaced when possible in the text. Please not that some time specifying the station is needed, such as in line 446 of the first version of the manuscript. Here we make a comparison with data from other station 47ºS site in the subantarctic zone, and therefore, specifying the name of out sampling site is needed. Please see also R2-R7.

**R2-C81**: Line 405-406: what makes *E. huxleyi* coccolith change their lengths in early spring to summer discuss under discussion. Please refer Bollmann et al paper.

**R2-R81**: Authors believe that reviewer 2 refers to Bollman and Herrle (2007, EPSL) paper where a close relationship between the length of *E. huxleyi* coccoliths and salinity is described. We appreciate reviewer 2’s comment and in the new version of the manuscript the possible effect of Sea Surface Salinity (SSS) on the observed coccolith weight and length variability is discussed (lines 966-971 of the corrected version of the manuscript with tracked changes). Moreover, SSS data for the 61ºS site was obtained
from the World Ocean Atlas and is presented in section “2.5 Satellite imagery, meteorological and oceanographic data” of the new version of the publication.

R2-C82: Line 410-412: If possible, plot graphs of correlation
R2-R82: Corrected according to reviewer 2’s suggestion. A new Figure (Fig. 7) has been included in the new version of the manuscript showing the regression plots between E. huxleyi coccolith weight and length.

R2-C83: Line 422: South of the Polar Front>>> South of the PF
R2-R83: Corrected according to reviewer 2’s suggestion.

R2-C84: Line 422: include recent studies carried out in the Southern Ocean such as, Patil et al., 2017, Saavedra Pellitero et al, Malinverno et al.,
R2-R84: Corrected according to reviewer 2’s suggestion. The references suggested by reviewer 2 have been incorporated in the new version of the manuscript.

R2-C85: Line 426: Buesseler et al., 2007 reference is not in the reference list
R2-R85: Corrected according to reviewer 2’s suggestion.

R2-C86: Line 435: What author mean by “coccolith particle bloom”? 
R2-R86: The term “coccolith particle bloom” has been replaced by “the period of enhanced coccolith flux” in order to be clearer.

R2-C87: Line 450: use either AZ or AZ-S
R2-R87: Corrected according to reviewer 2’s suggestion. The term AZ has been replaced by AZ-S in the new version manuscript when required.

R2-C88: Line 463: general variability they found between>>> general variability found between
R2-R88: Corrected according to reviewer 2’s suggestion.

R2-C89: Line 463: please differentiate morphological differences between Morphotypes A, B/C, var. huxleyi and var. aurorae. E. huxleyi morphotype C is usually less calcified morphotype of E. huxleyi usually found in the AZ. What are the probable reasons for absence of morphotype C in sediment trap samples?
R2-R89: Corrected according to reviewer 2’s suggestion. A description of the other morphotype found in our study region (morphotype A) has been included in section 3.2 of the new version of the manuscript with tracked changes (lines 636-656). As stated in the first version of the manuscript (Lines 463-4365), morphotype A has been documented to be genetically different than morphotype B/C. Based on this observation, Cook et al. (2011) associated these two morphologies with two varieties defined as E. huxleyi var. huxleyi and E. huxleyi var. aurorae, respectively. The text has been rephrased in order to be clearer (see line 804 of the new version of the manuscript with tracked changes). Findlay and Giraudeau (2000, Mar Mic) and Cubillos et al. (2011) analysed samples from a transect along the 140ºE meridian, where our 61ºS sediment trap was deployed. Findlay and Giraudeau (2000) did report E. huxleyi morphotype C in their samples, Young et al. (2003) reviewed their classification of E. huxleyi morphotypes and revised Type C specimens from the Antarctic Ocean documented by Findlay and Giraudeau (2000) to be Type B/C. This is mentioned in Young et al. (2003), Hagino et al. (2005, Mar Mic) and
Cubillos et al. (2007). So the fact that morphotype C has not been previously reported in our study region further supports our observations.

R2-C90: Plate 1: I don’t agree with all six images belonging to morphotype B/C. Plate 1b, e, looks like morphotype C. Plate 1g is unrecognizable due to overcalcification. Authors can follow Young et al., 2003 atlas for differentiating E. huxleyi morphotypes.

R2-R90: Authors did follow Young et al. (2003) classification, in fact, one of the co-authors (Lluïsa Cros) co-authored the Atlas referred to by reviewer 2. Authors believe that the different morphologies observed in the coccoliths are just variations within an E. huxleyi B/C population. Morphotype B/C exhibits a similar morphology to types B and C (Young et al. 2003) but it is intermediate in size. However, coccolith size was considered of limited value in discriminating morphotypes by Cubillos et al. (2007) based on the large variability in size of the coccoliths on the same coccospheres. This is now clearly explained in the paper (Lines 646-656). It is also worth noting that Young et al. (2003) revised the morphotype described as C in our study area by Findlay and Giraudou (2000) and redefined it as Type B/C.

R2-C91: Line 508: Silicate and/or Fe>>> Silicate and/or iron
R2-R91: Corrected according to reviewer 2’s suggestion.

R2-C92: Line 522, line 535: Tagliabue et al., 2014. Year of publication missing in the reference list
R2-R92: We believe there has been a misunderstanding because the year of the publication (2014) is mentioned was in line 1074 of the first version of the manuscript.

R2-C93: Line 533: the part of the Emiliania huxleyi>>> the part of the E. huxleyi
R2-R93: Corrected according to reviewer 2’s suggestion.

R2-C94: Line 598: Trull et al., 2001>>> Trull et al., 2001a or 2001b or 2001c?
R2-R94: Corrected according to reviewer 2’s suggestion. The reference of Trull et al. 2001b is not specified in the text.

R2-C95: Line 623: both traps (2.5 pg at 2000m to 2.6 pg at 3700)>>> both traps (2.5±... pg at 2000m to 2.6±... at 3700m)
R2-R95: Since the annual coccolith weights are already mentioned in the results section and later on in the discussion (section 4.5 Calcium carbonate content of Emiliania huxleyi coccoliths), the annual coccoliths weights have been removed here in order to avoid repetition.

R2-R96: Corrected according to reviewer 2’s suggestion.

R2-C97: Line 655: E. huxleyi morphotype B/C is more weakly calcified than other morphotypes>>> I am not convinced with this. E. huxleyi morphotype C is more weakly calcified than B/C. It can be written as >> E. huxleyi morphotype B/C is weakly calcified than A if authors want to tell extent of calcification.

R2-R97: In order to be clearer, the sentence highlighted by reviewer 2 has been rephrased. Now it reads” Since E. huxleyi morphotype B/C is considered to be geographically restricted to the Southern Ocean (Cubillos et al., 2007; Cook et al., 2013)
we limit the comparison of our results to studies reporting this morphotype conducted only in the Southern Ocean.“ (lines 1052-1053).

**R2-C98:** Line 676, 682: *Salter et al. (2014) missing in the reference list*

**R2-R98:** Corrected according to reviewer 2’s suggestion. The reference is now listed in the new version of the manuscript.

**R2-C99:** Line 679, 683: *Rembauville et al. missing in the reference list*

**R2-R99:** Corrected according to reviewer 2’s suggestion. The reference is now listed in the new version of the manuscript.

**R2-C100:** Line 698: *Analysis of the sediment trap materials* >>> *analysis of two sediment trap material*

**R2-R100:** This sentence has been rephrased “Analysis of the materials captured by two sediment traps deployed…”. Moreover, this sentence has been split into two following reviewer 2’s suggestion R2-C6.
Coccolithophore populations and their contribution to carbonate export during an annual cycle in the Australian sector of the Antarctic Zone

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Abstract

The Southern Ocean is experiencing rapid and relentless change in its physical and biogeochemical properties. The rate of warming of the Antarctic Circumpolar Current exceeds that of the global ocean, and the enhanced uptake of carbon dioxide is causing basin-wide ocean acidification. Observational data suggest that these changes are influencing the distribution and composition of pelagic plankton communities. Long-term and annual field observations on key environmental variables and organisms are a critical basis for predicting changes in Southern Ocean ecosystems. These observations are particularly needed, since high-latitude systems have been projected to experience the most severe impacts of ocean acidification and invasions of allochthonous species.

Coccolithophores are the most prolific calcium carbonate producing phytoplankton group, playing an important role in Southern Ocean biogeochemical cycles. Satellite imagery has revealed elevated particulate inorganic carbon concentrations near the major circumpolar fronts of the Southern Ocean, that can be attributed to the coccolithophore Emiliania huxleyi. Recent studies have suggested changes during the last decades in the distribution and abundance of Southern Ocean coccolithophores. However, due to limited field observations, the distribution, diversity and state of coccolithophore populations in the Southern Ocean remain poorly characterized.
We report here on seasonal variations in the abundance and composition of coccolithophore assemblages collected by two moored sediment traps deployed at the Antarctic Zone south of Australia (2000 and 3700 m depth) for one year in 2001-02. Additionally, seasonal changes in coccolith weights of *E. huxleyi* populations were estimated using circularly polarised micrographs analysed with *C-Calctia* software. Our findings indicate that (1) coccolithophore sinking assemblages were nearly monospecific for *E. huxleyi* morphotype B/C in the Antarctic Zone waters in 2001-2002; (2) coccoliths captured by the traps experienced weight and length reduction during summer (December – February); (3) the estimated annual coccolith weight of *E. huxleyi* at both sediment traps (2.11 ± 0.96 and 2.13 ± 0.91 pg at 2000 m and 3700 m) was consistent with previous studies for morphotype B/C in other Southern Ocean settings (Scotia Sea and Patagonian shelf); (4) coccolithophores accounted for approximately 2-5% of the annual, deep-ocean CaCO3 flux. Our results are the first annual record of coccolithophore abundance, composition and degree of calcification in the Antarctic Zone. They provide a baseline against which to monitor coccolithophore responses to changes in environmental conditions expected for this region in coming decades.

**Key words:** Southern Ocean, Antarctic Zone, coccolithophores, coccolith weight, sediment traps.

1. Introduction

1.1. Background and objectives

The rapid increase in atmospheric CO2 levels since the onset of the industrial revolution is modifying the environmental conditions of marine ecosystems in a variety of ways. The enhanced greenhouse effect, mainly driven by increased atmospheric CO2 levels, is causing ocean warming (Barnett et al., 2005), shallowing of mixed layer depths (Levitus et al., 2000) and changes in light penetration and nutrient supply (Bopp et al., 2001; Rost and Riebesell, 2004; Sarmiento et al., 2004b; Deppeler and Davidson, 2017). Moreover, the enhanced accumulation of CO2 in the ocean is giving rise to changes in the ocean carbonate system, including reduction of carbonate ion concentrations and lowering of seawater pH. Most evidence suggests that the ability of many marine calcifying organisms to form carbonate skeletons and shells may be reduced with increasing seawater acidification including some species of (but not all). coccolithophores.
corals, pteropods and foraminifera (e.g. Orr et al., 2005; Moy et al., 2009; Lombard et al., 2010; Beaufort et al., 2011; Andersson and Gledhill, 2013). Since phytoplankton are extremely sensitive to global environmental change (Litchman et al., 2012) all predicted changes in marine environmental conditions are likely to modify the abundance, composition and distribution of phytoplankton communities.

Changes in the relative abundances of major phytoplankton functional groups are likely to influence ocean biogeochemistry and ocean carbon storage, with feedbacks to the rate of climate change (e.g. Boyd and Newton, 1995; Boyd et al., 1999; Falkowski et al., 2004; Cermeño et al., 2008). The precipitation and sinking of CaCO$_3$ by coccolithophores has the potential for complex contributions to carbon cycling. Carbonate precipitation removes more alkalinity than dissolved inorganic carbon from surface waters, thereby acting to increase pCO$_2$ in surface waters (the so-called carbonate counter pump, e.g. Zeebe, 2012). On the other hand, ballasting by carbonates appears to increase transfer of organic carbon to the ocean interior (Armstrong et al., 2002; Klaas and Archer, 2002). On seasonal timescales the counter pump contribution dominates (Boyd and Trull, 2007), but more complex interactions can occur over longer timescales as a result of changing extents of carbonate dissolution in sediments, including the possibility that enhanced calcite dissolution in the Southern Ocean contributed to lower atmospheric CO$_2$ levels during glacial maxima (Archer and Maier-Reimer, 1994; Sigman and Boyle, 2000; Ridgwell and Zeebe, 2005).

The Southern Ocean is a critical component of the Earth’s ocean–climate system and plays a pivotal role in the global biogeochemical cycles of carbon and nutrients (Sarmiento et al., 2004a; Anderson et al., 2009). Despite the fact that the Southern Ocean accounts for about 25% of the global ocean, it contains ~40% of the global ocean inventory of anthropogenic CO$_2$ (Khatiwala et al., 2009; Takahashi et al., 2009; Frölicher et al., 2015), and it exports nutrients to more northern latitudes ultimately supporting ~75% of the ocean primary production north of 30°S (Sarmiento et al., 2004a). Model projections suggest that the reduction in the saturation state of CaCO$_3$ will reach critical thresholds sooner in cold, high-latitude ecosystems such as the Southern Ocean (Orr et al., 2005; McNeil and Matear, 2008; Feely et al., 2009). Therefore, calcifying organisms living in these regions will be the first to face the most severe impacts of ocean acidification.

In view of the rapid changes in climate and other environmental stressors presently occurring in the Southern Ocean, a major challenge facing the scientific community is to
predict how phytoplankton communities will reorganize in response to global change. In this regard, two main aspects of the distributions of coccolithophores are emerging. Firstly, coccolithophores exhibit high concentrations in the Subantarctic Southern Ocean, a feature termed by Balch et al. (2011) as the “Great Calcite Belt” based on satellite reflectance estimates of PIC abundances. Although importantly the PIC accumulations are significantly less than those that arise in the North Atlantic, and the satellite algorithm is not reliable in Antarctic waters, where it badly overestimates PIC abundances (Balch et al., 2016; Trull et al., 2017). Secondly, recent studies suggest that the magnitude and geographical distribution of *E. huxleyi* blooms may be experiencing significant and rapid changes. Cubillos et al. (2007) and Winter et al. (2014) postulated that *E. huxleyi* has expanded its ecological niche south of the Polar Front in the recent decades. Contrastingly, Freeman and Lovenduski (2015) suggested an overall decline in Southern Ocean PIC concentrations using satellite records between 1998 and 2014. The explanation of these contrasting results may lie in the methodologies applied. While shipboard surface water observations provide a highly detailed picture of a given ecosystem, they are very sparse, only represent a snapshot in time, and can easily miss blooms of any given species. The satellite PIC signal has the great advantage of large-scale and repeated coverage, but can miss subsurface populations (e.g. Winter et al., 2014) and be mimicked by the spectral characteristics of other scattering sources, such as microbubbles (Zhang et al., 2002), glacial flour (Balch et al., 2011), and noncalcifying organisms such as *Phaeocystis antarctica* (Winter et al., 2014), a colonial prymnesiophyte algae very abundant in high latitude systems of the Southern Ocean (e.g. Arrigo et al., 1999; Arrigo et al., 2000). Notably the PIC algorithm performs particularly poorly in Antarctic waters (Balch et al., 2016; Trull et al., 2017)

For these reasons, year-round field observations of areas representative of key Southern Ocean regions are essential to determine the current state of coccolithophore communities and to develop baselines against which long-term trends can be detected. Moreover, a better understanding of coccolithophore distribution, ecology and seasonal dynamics is required to improve our interpretations of the sedimentary record and our models of biogeochemistry. Sediment traps are a direct method to collect data about calcareous and siliceous micro and nanoplanckton. Traps allow the monitoring of seasonal and annual variability of plankton export, document species successions, and help to determine the specific role of microplankton species in the biological and carbonate
pumps. The autonomous collection capacity of sediment traps is particularly useful in the remote Southern Ocean, where inaccessibility and harsh working conditions prevent year-round ship-based sampling.

We present here the first record of composition, abundance, and seasonality of coccolithophore assemblages in the Antarctic Zone of the Southern Ocean, collected by two deep ocean sediment traps deployed on a single mooring during 10 months south of Australia at the site of the Southern Ocean Iron Release Experiment (SOIREE), near 61°S, 140°E (Boyd et al., 2000a). Moreover, we report weight and length measurements on *E. huxleyi* coccoliths, assessing the impact of seasonally varying environmental parameters on *E. huxleyi* coccoliths. That provides a baseline of coccolith dimensions for the populations living in this region. All the above information is needed for monitoring coccolithophore responses, if any, to changing environmental conditions in the Antarctic Zone south of Australia during coming decades.

1.2 Regional setting and oceanography

The southern Antarctic Zone (AZ-S; Parslow et al., 2001) is delimited in the north by the southern branch of the Polar Front (PF) and in the south by the southern front of the Antarctic Circumpolar Current (SACC) (Fig. 1). Trull et al. (2001b) summarised the seasonal evolution of water column properties in the study region. The intense heat loss of surface waters during winter decreases Sea Surface Temperature (SST) to values < 1°C, resulting in strong vertical convection. Winter mixing extends to depths of about 120 m, replenishing the upper water column with nutrients. Chlorophyll-α levels during winter are negligible throughout the region due to the reduced solar radiation and the deep, continuous vertical mixing. During summer, increasing solar radiation warms the surface ocean and a seasonal thermocline forms (Fig. 2). By late summer-early autumn (March) SST ranges between 2 and 3 °C. Considerable nutrient depletion associated with a moderate increase in algal biomass occurs within the mixed layer (Trull et al., 2001b).

Nonetheless, due to the limited sampling of the study region, the timing of the summer nutrient minimum is not well constrained by the available data (Trull et al., 2001b). Silicate exhibits the strongest summer draw-down of all the macronutrients, reaching ~30% of its winter values (Fig. 2; Trull et al., 2001b), mainly due to diatom growth and subsequent biogenic silica export to the deep sea (Rigual-Hernández et al., 2015a). The low algal biomass accumulation in the region is attributed to the very low iron levels (0.1-
0.2 nM; Boyd et al., 2000a; Sohrin et al., 2000). Mesozooplankton analysis during the SOIREE experiment by Zeldis (2001) indicates that zooplankton community in the study region is dominated by copepods. Grazing pressure was low (<1% of the phytoplankton standing stock removed per day) and, therefore, is thought not to play an important role in the control of the micro-phytoplankton (primarily diatom) stocks, but nanoflagellate grazer abundances were significant and were likely to have regulated smaller phytoplankton abundances (Hall and Safi, 2001).

Figure 1. Annual mean sea surface temperature map (World Ocean Atlas; Locarnini et al., 2013) of the Australian sector of the Southern Ocean, showing the position of the main frontal and zonal systems (adapted from Orsi et al., 1995) and the location of the 61°S, 54°S and 47°S sediment trap stations (inverted triangles). Abbreviations: STF = Subtropical Front, SAZ = Subantarctic Zone, SAF = Subantarctic Front, PFZ = Polar Frontal Zone, PF = Polar Front, AZ = Antarctic Zone, SACCF = Southern Antarctic Circumpolar Current Front, SB = Southern Boundary, Max WSI = Maximum Winter Sea Ice Extent (August 2001) and Min SSI = Minimum Summer Sea Ice Extent (February 2002) (Fetterer et al., 2017).
Figure 2: (a) Seasonal variation in the vertical structure of temperature (°C) between January 2001 and December 2002 for the 61°S site from the World Ocean Atlas 2009 (Locarnini et al., 2010). (b) Summary of seasonal evolution of macronutrient concentrations (silicate and nitrate) in the mixed layer at the 61°S site taken from the WOCE SR3 transects between 1993 and 1996 (modified from Trull et al., 2001b).

1.3 Water carbonate chemistry in the study region

Calcite solubility increases at higher pressures and lower temperatures, so that dissolution increases with depth in the water column. Based on downward changes in the calcite dissolution rate, two critical depth horizons can be distinguished: the Calcite Saturation Horizon (CSH) that can be defined as the depth at which the water becomes undersaturated with respect to calcite (i.e. where $\Omega_{\text{calcite}} = 1$); and the CaCO$_3$ compensation depth (CCD), the depth at which the rate of calcite rain from the upper water column equals the dissolution rate. Figure 3 shows carbonate concentrations [CO$_3^{2-}$] and calcite saturation ($\Omega_{\text{calcite}}$) for the WOCE SR03 2001 transect between Antarctica and Tasmania along the 140°E meridian as estimated by Bostock et al. (2011). In the AZ-S waters south of Tasmania, the CSH and CCD occur at 3000 and 3700 m, respectively (Fig. 3). Therefore, the location of sediment traps at the 61°S site allows for the assessment of dissolution changes, if any, of coccolithophore assemblages between the two critical dissolution depth horizons: the CSH and CCD. Notably, both progressive uptake of anthropogenic CO$_2$ and increased upwelling of naturally CO$_2$-rich deep waters over the past 20 years is leading to shallowing of these features (Pardo et al., 2017).
Figure 3. Cross section of the mooring location in comparison to regional seafloor bathymetry, carbonate concentrations [CO$_3^{2-}$] and calcite saturation ($\Omega_{\text{calcite}}$) for WOCE transect SR03 2001 from Bostock et al. (2011), who calculated them from the Dissolved Inorganic Carbon (DIC) and alkalinity in the CARINA database (CARINA, 2011). The location of the transects is shown on the map on the right top. $\Omega_{\text{calcite}} = 1$ contour is highlighted with a red line to show the approximate depth of the CSH across the transect.

2. Material and Methods

2.1 Sediment trap experiment

As part of the SAZ collaborative research program (Trull et al., 2001c), a sediment trap experiment was carried out at the 61°S site (60° 44.43’S; 139° 53.97’E) in the Australian sector of the southern Antarctic Zone within the region where the Southern Ocean Iron Release Experiment (SOIREE) was conducted (Boyd et al., 2000a). The 61°S site is characterized by weak currents with a mean eastward geostrophic surface velocity of approximately 0.03 ± 0.02 m s$^{-1}$ (Trull et al., 2001b). The site is north of the Seasonal Sea-Ice Zone (Massom et al., 2013; Rigual-Hernández et al., 2015a) and remote from any known iceberg pathway (Gladstone et al., 2001).
The mooring was equipped with three McLane Parflux time series sediment traps (Honjo and Doherty, 1988) for approximately one year (November 30, 2001 to September 29, 2002, 317 days). The traps were located at 1000, 2000 and 3700 m below the surface in a water column of 4393 m (Figures 3a and 3b). Each trap was provided with 21 cups. Sampling intervals were synchronized between traps and in order to resolve the seasonal flux cycle ranged from 8 days (in austral summer) to 55 days in austral winter. No samples were recovered from the shallowest trap owing to equipment malfunction and, therefore, only results for the 2000 and 3700 m traps are presented here. Each trap was paired with an Aanderaa current meter and temperature sensors. The 250 ml collection cups were filled with a buffered solution of sodium tetraborate (1 g L⁻¹), sodium chloride (5 g L⁻¹), strontium chloride (0.22 g L⁻¹), and mercury chloride (3 g L⁻¹) in unfiltered, deep (> 1000 m) seawater from the region. Risk of sample contamination by the unfiltered seawater is considered negligible due to the fact that the deep water exhibits low particle abundance and also because particle concentration in sea water is of the order of µg/L, while concentration in the trap cups after recovery was of the order of mg/L.

The two deeper traps completed their collection sequence as programmed, providing continuous time-series for a year. Due to the low particle fluxes during the winter, insufficient material remained for phytoplankton analysis of cup 1 from the 2000 m trap and cups 1, 2, 19, 20 and 21 from the 3700 m trap (Table 1).

2.2 Sample processing and coccolithophore counting procedure

The sediment trap cup contents were washed through a 1 mm sieve after recovery and then divided into 10 aliquots using a rotary splitter (McLane, Inc.). A description of the analytical procedures for estimation of geochemical fluxes is provided in Trull et al. (2001a) and Rigual-Hernández et al. (2015a). One aliquot was used for siliceous and calcareous micro- and nano-plankton analyses. Each fraction for plankton analysis was refilled with distilled water to 40 ml, from which 10 ml was subsampled and buffered with a solution of sodium carbonate and sodium hydrogen carbonate (pH 8) and kept refrigerated for calcareous nanoplankton analysis. Samples for coccolithophore analysis were prepared following the methodology of Flores and Sierro (1997). In short, 300 µl were extracted with a micropipette and dropped onto a glass Petri dish previously filled with a buffered solution and with a cover slip on its bottom. After settling for 12 hours, the buffer solution was removed using short strips of filter paper placed at the edge of the
dish. Then, the cover slip was left to dry completely and mounted on a glass slide using Canada balsam. Coccoliths were identified and counted using a Nikon Eclipse 80i polarized light microscope at 1000× magnification. A minimum of 400 coccoliths were counted in each sample. Coccospheres occurred in much lower numbers than loose coccoliths in these preparations. The coccolith counts were transformed into daily fluxes of specimens m⁻² d⁻¹ following the formula:

\[ F = \frac{N \times \frac{A}{n} \times \frac{a}{d} \times V \times S}{T} \]

where “\(F\)” is the daily coccolith flux, “\(N\)” the number of coccoliths, “\(A\)” the total area of a Petri dish, “\(n\)” the number of fields-of-view analysed, “\(a\)” the area of a single field of view, “\(V\)” the dilution volume, “\(S\)” the split of the cup, “\(d\)” the number of days of collection and “\(T\)” the aperture area of the sediment trap.

Since the sediment trap collection period was shorter than a full calendar year, an estimate of the annual coccolith flux of the 2000 m trap was calculated. This estimate takes into account the fact that the unsampled days occurred in winter when particle fluxes were low, and were obtained using the flux for the last winter cup (#21 in 2002) to represent mean daily fluxes during the unobserved interval. Due to the lack of samples corresponding to winter 2002 for the 3700 m sediment trap record, the annualization of the coccolith fluxes for this trap was made based only on the samples with available data. Therefore, the annualized and annual flux data for the 3700 m trap presented in Table 1 should be used with caution.
Table 1: Daily export fluxes of total mass flux, calcium carbonate (CaCO₃), particulate organic carbon (POC), diatom valves and coccoliths registered at the 61°S site from November 2001 through October 2002. Mass fluxes listed as zero were too small to measure (<1 mg).

### 2.3 SEM analysis

As the resolution of the light microscope is insufficient to differentiate *E. huxleyi* morphotypes, the samples of the 2000 m trap record were analysed using a Scanning Electron Microscope (SEM). Glass cover-slips were prepared following the method outlined by Flores and Sierro (1997). The dried cover-slips were mounted on aluminium stubs and coated with gold. An EVO HD25 SEM (Carl Zeiss) was used to determine the morphotype of *E. huxleyi* coccoliths found in the samples (magnification 5000-20000x). Due to the large abundance of diatom valves and the scarcity of coccoliths in the samples, a compromise between number of identified coccoliths and time spent had to be reached. Therefore, a target minimum of thirty *E. huxleyi* coccoliths per sample were identified.

The taxonomic concepts of Young and Westbroek (1991), Young et al. (2003), Cubillos...
et al. (2007) and Hagino et al. (2011) were followed to classify the *E. huxleyi* coccoliths into **different** morphotypes.

### 2.4 C-Calcita analyses

The glass slides used for coccolith counts were also analysed for coccolith mass and size measurements using a Nikon Eclipse LV100 POL polarised light microscope equipped with circular polarization and a Nikon DS-Fi1 8-bit colour digital camera. Calibration images were performed on an apical rhabdolith of the genus *Acanthoica* collected by a sediment trap at the 47°S site (46°48′S, 142°6′E), located in the Australian sector of the Subantarctic Zone. Camera parameters and microscope light settings were maintained constant throughout the imaging session. Depending on coccolith concentration, between 13-28 random fields of view per sample were photographed. The images were then analysed by the image processing software C-Calcita (Fuertes et al., 2014). The output files for single *E. huxleyi* coccoliths were visually selected. Length and weight measurements were automatically performed by C-Calcita software. A total of 2328 coccoliths were analysed with a minimum of 50 coccoliths per sample. For more methodological details see Fuertes et al. (2014).

An estimated range of annual contributions of coccoliths to total CaCO$_3$ export was calculated for the 2000 m trap record by multiplying the coccolith flux of each sampling interval by the maximum and minimum standard deviations of coccolith weight values measured on each sample. Then, the minimum and maximum estimates of coccolith-CaCO$_3$ fluxes for each sampling interval (i.e. cup) were used to estimate the minimum and maximum annual contribution of coccoliths to total carbonate following the same procedure as for the annual coccolith fluxes.

### 2.5 Satellite imagery, meteorological and oceanographic data

Weekly mean SST$_t$ for the 2001-2002 interval were obtained from the NOAA Optimum Interpolation SST Analysis database (Reynolds et al., 2002). Seasonal SST variation range was low, with maximum SSTs of 2.94 °C observed during March 2002 and minimum of 0.12 °C, in early October 2002. SST variations mirrored changes in the vertical structure of the water column temperature profile (Fig. 4) that displayed vertical homogeneity of the water column in autumn and winter and a seasonal thermocline during the austral summer (Fig. 2b).
Sea surface salinity (SSS) climatology for the study site was obtained from the NOAA World Ocean Atlas 2005 (Antonov et al., 2006). SSS exhibited very low seasonal variability with values ranging between 33.7 and 33.9 psu.

Photosynthetically Active Radiation (PAR), monthly chlorophyll-α concentration and Particulate Inorganic Carbon (PIC) concentration estimates were obtained from NASA’s Giovanni program (Acker and Leptoukh, 2007) (Fig. 4) for the region: 130°E, 62.5°S, 150°E, 59.5°S. Chlorophyll-α concentration was low throughout the year (ranging from 0.07 to 0.30 mg m⁻³) and in line with previous observations in the study region (Trull et al., 2001b). Algal biomass responded rapidly to the solar radiation increase in September 2001 and reached its highest levels in November 2001 (Fig. 4). Chlorophyll-α concentration declined throughout the summer, reaching negligible values in autumn and winter (i.e. from March to August 2002). Satellite-derived PIC concentration exhibited a clear seasonal pattern similar to that of the chlorophyll-α with peak concentrations in November (up to 0.003 mol m⁻³) and values below detection limit in winter (Fig. 4).
Figure 4: (a) Satellite-derived SST (°C), PAR (Einstein m$^{-2}$ d$^{-1}$), chlorophyll-$a$ concentration (mg m$^{-3}$) and PIC concentration (mol m$^{-3}$) for the period November 2001 to September 2002. It is important to note that satellite PIC concentration estimates have been reported to be biased for high latitudes systems of the Southern Ocean where the satellite algorithm is thought to produce overestimates (Balch et al., 2016; Trull et al., 2017). Therefore PIC data presented here should be viewed with caution. (b) Temporal variability of the total mass, CaCO$_3$, and POC the < 1mm fraction at 2000 and 3700 m water depth from November 2001 through to November 2002 at the 61°S site (Rigual-Hernández et al., 2015a). Grey strips represent summer.

3. Results
3.1 Seasonal dynamics of coccolith export fluxes

Coccolith fluxes showed a pronounced seasonal pattern at both sediment trap depths, roughly following the chlorophyll-\(a\) dynamics in the surface layer with maximum fluxes during the austral summer and minima during winter (Fig. 4 and 5). The summer coccolith flux exhibited a bimodal distribution with a major peak registered in early January (2.2 x 10^9 coccoliths m^{-2} d^{-1} at 2000 m) and a secondary maximum recorded in mid-February (9.8 x 10^8 coccoliths m^{-2} d^{-1}). Coccolith flux was low in autumn and winter (down to ~7 x 10^7 coccoliths m^{-2} d^{-1}). Coccolith fluxes in the deeper trap (3700 m) followed a similar pattern to that in the 2000 m trap with a delay of about one sampling interval.

The fluxes of all biogeochemical components were closely correlated (Table 2 in Rigual-Hernández et al., 2015a). Coccolith fluxes at both traps were broadly in line with biogenic particle fluxes estimated by Rigual-Hernández et al. (2015a) showing strongest correlations with biogenic silica (\(R^2 = 0.74\) at 2000 m and \(R^2 = 0.71\) at 3700 m), followed by PIC (\(R^2 = 0.62\) at 2000 m and \(R^2 = 0.47\) at 3700 m) and POC (\(R^2 = 0.56\) at 2000 m and \(R^2 = 0.41\) at 3700 m).

Coccolithophore sinking assemblages captured by the traps were nearly monospecific, with an overwhelming dominance of \(E. huxleyi\) that represented >99% of the annual coccolith sinking assemblage at both trap depths. Background concentrations of \(Calcidiscus leptoporus\) (sensu lato), Gephyrocapsa spp. and Helicosphaera spp. were also registered, together representing 0.6% and 0.3% of the coccolith assemblage at 2000 and 3700 m, respectively, of the total annual coccolith fluxes (Table 1). The seasonal changes in the coccolithophore species flux and relative abundance can be found in Supplementary Figure 1. The seasonal pattern of \(C. leptoporus\) and \(Gephyrocapsa\) spp. followed that of \(E. huxleyi\) with peak values during the summer and minima during winter. The numbers of coccospheres found in the samples were negligible in both sediment trap records.
Figure 5: Seasonal variation of total coccolith and diatom valve flux at the 2000 and 3700 m sediment traps at the 61°S site. Grey strips represent summer.

3.2 SEM analyses

*Emiliania huxleyi* coccoliths correspond to morphotype B/C, having proximal shields slightly wider than the distal ones and with a central area usually filled by several (usually 5 to 11) flat, wide and thin tile-like elements (see Plate 1, image a). Distal shields of several are partially missing, most likely due to the slender and delicate structure of the laths. Distal shield measures ranged between 2 to 4.35 µm in the samples recovered from the 2000 m sediment trap. The coccoliths captured by the traps were clearly different than those of morphotype A which is the other morphotype that has been reported in the Australian sector of the Southern Ocean (Cubillos et al., 2007). Morphotype A has a central area composed of curved elements (Young et al., 2003) and its distal shields elements are often straight or concave (Cubillos et al., 2007) and more robust than those of B/C (Young et al., 2003). Since the size of the coccoliths has been reported to vary...
significantly on the same coccosphere, coccolith size was not used as a discriminatory
feature to differentiate between morphotypes following Cubillos et al. (2007).

It is conspicuous that most of the coccoliths display a morphology which is
compatible with a secondary recrystallisation. Small spherules like recrystallisations are
present on these coccoliths, especially on the laths (Plate 1, images c-f). However, some
coccoliths, mostly from cup 10 (February) have no spherules covering them (Plate 1,
images a and b). Aside from this sample, no relationship between the morphology of the
coccoliths and collection time was found. These coccoliths present very thin slender laths
(usually from 20 to 26) and wider central areas than the coccoliths having spherules.

3.3 Coccolith weight and length changes

Average coccolith weight at both sediment trap depths exhibited a clear seasonal
pattern with high values (2.28 ± 1.16 and 2.09 ± 0.80 pg/coccolith at 2000 m and 3700
m, respectively) at the onset of the coccolithophore productive period in early spring,
followed by a pronounced decrease (down to 1.65 ± 0.63 and 1.88 ± 0.63 pg at 2000 m
and 3700 m, respectively) in approximately January – early February. Average coccolith
weight followed a gradual increasing trend from approximately mid-February into winter,
reaching values up to 2.71 ± 1.20 pg in August 2002 at 2000 m and up to 2.43 ± 1.00 in
May at 3700 m, respectively. Average annual coccolith weight was 2.11 ± 0.96 and 2.13
± 0.91 pg at 2000 and 3700 m, respectively. The annual amplitude of the mean coccolith
weight was approximately 1 pg at 2000 m and 0.9 pg at 3700 m. The lower annual
amplitude exhibited by the coccolith assemblages captured at the 3700 m trap is attributed
to the lower sampling duration at that depth over the winter season.

Mean coccolith length was greatest in early spring 2001 (2.54 ± 0.44 and 2.55 ±
0.46 µm at 2000 and 3700 m, respectively), followed by a decrease in early summer
(down to 2.35 ± 0.43 and 2.44 ± 0.41 µm at 2000 and 3700 m, respectively) (Fig. 6). From
late February coccolith length increased again reaching the highest values of the record
in winter 2002 (up to 2.71 ± 0.42 and 2.64 ± 0.41 µm at 2000 and 3700 m, respectively).
Seasonal variations of coccolith length and weight exhibited a strong correlation
at both depths (R² = 0.84, n = 20 at 2000 m; R² = 0.61, n = 16 at 3700m), indicating a
clear, dependable relationship between the two variables (Fig. 7).
Figure 6: Mean and standard deviation of coccolith weight and length over the sediment trap deployment period at 2000 m and 3700 m at the 61°S site. The red solid line represents a 3-point running average. Grey strips represent summer.

Figure 7: Regression plots between *E. huxleyi* coccolith mass (pg) and length (µm) at the 2000 m (a) and 3700 m (b) sediment traps.

4. Discussion

4.1 Origin, magnitude and composition of the coccolithophores

Since there is a current debate about the potential expansion of *E. huxleyi* populations south of the PF during recent decades (Cubillos et al., 2007; Saavedra-
Pellitero et al., 2014; Winter et al., 2014; Malinverno et al., 2015; Patil et al., 2017), it is important to evaluate the likely origins of the sinking coccolith assemblages collected at station 61°S. This assessment is particularly needed in the case of deep-moored, sediment-trap experiments because the source area of the particles collected by the traps can be as wide as hundreds of square kilometres (Buesseler et al., 2007).

Several lines of evidence strongly suggest that the coccolithophore fluxes registered by the traps were produced in waters of the Antarctic Zone. Firstly, the mooring was deployed in a quiescent area of the AZ-S (Trull et al., 2001b), between the stronger flows associated with the southern branch of the PF and the SACCF (Fig. 1). The relatively weak currents around the sediment trap location greatly reduce the area of likely origins of the particles intercepted by the traps, i.e. the statistical funnel (Siegel and Deuser, 1997; Siegel et al., 2008). Moreover, the large magnitude of the coccolith export fluxes at both depths, plus the long duration of the period of enhanced coccolith flux (about 3 months), rule out the likelihood of a transient lateral transport event (e.g., transport by mesoscale eddies) of a coccolithophore bloom produced in more northerly latitudes. Lastly, the composition of the biogeochemical fluxes and diatom assemblages collected by the traps are characteristic of AZ waters (Rigual-Hernández et al., 2015a), further supporting the idea that the coccolithophores captured by the traps were produced close to the site. All this clearly indicates that in 2001 *E. huxleyi* was an established member of the phytoplankton communities of the Antarctic Zone to the south of Australia.

The annual coccolith export to the deep ocean at the 61°S site (1.03 x 10^{11} coccoliths m^{-2} yr^{-1}) is one sixth that registered by Wilks et al. (2017) (6.5 x 10^{11} coccolith m^{-2} yr^{-1}) in the SAZ waters (station 47°S; Fig. 1) north of the study site. The lower abundance of coccolithophores at the *sampling* site is most likely due to the negative effects of low temperature and low light levels on coccolithophore growth (Paasche, 2002; Boyd et al., 2010), but important also is the competitive advantage of diatoms over coccolithophores in the silicate-rich waters of the AZ-S. The lower coccolithophore production in the AZ-S is also reflected in the lower carbonate export at this site, i.e. 6 g m^{-2} yr^{-1} versus 10-13 g m^{-2} yr^{-1} at the 47°S site (Rigual-Hernández et al., 2015b; Wilks et al., 2017). The non-proportional latitudinal change in coccolith and carbonate fluxes (i.e., sixfold versus twofold changes, respectively) is most likely due to variations in the contribution of heterotrophic calcifiers (i.e. foraminifers and pteropods) to total carbonate export. There are also differences in the carbonate content per coccolith of the
cocco lithophore species and the morphotypes of *E. huxleyi* dwelling in each zonal system. Indeed, mean coccolith weight can vary up to two orders of magnitude between small species such as *E. huxleyi* (2-3.5 pg) and large and heavily calcified taxa such as *Coccolithus pelagicus* (~150 pg) (Giraudeau and Beaufort, 2007). Intraspecific size variability is also common in most cocco lithophore species, mainly due to growth variations driven by different environmental factors and by genotypic variability (e.g. Knappertsbusch et al., 1997; Poulton et al., 2011).

Based on the significant genetic variability found between Southern Ocean populations of morphotypes A and B/C, Cook et al. (2011) classified these morphotypes as *E. huxleyi* var. *huxleyi* and *E. huxleyi* var. *aurorae*, respectively. Since only morphotype B/C had been reported at and south of the Antarctic Polar Front, Cook et al. (2013) concluded that the rapid drop in water temperature occurring at the Antarctic Polar Front may act as an open-ocean barrier to gene flow between these the two Southern Ocean *E. huxleyi* morphotypes/varieties. The nearly monospecific coccolith assemblages of *E. huxleyi* morphotype B/C collected by the 61°S site traps (Plate 1) are consistent with those studies and supports the idea that the physiological differences in light-harvesting pigments of morphotype B/C compared to other *E. huxleyi* varieties (Cook et al., 2011) may represent a critical ecological advantage in the cold and low-light waters of the AZS south of Australia.
Plate 1: SEM photos showcasing the different morphologies of *Emiliania huxleyi* morphotype B/C coccoliths found in the sediment traps of the 61°S site. Scale bars = 1 μm.

### 4.2 Seasonal dynamics of the calcareous and siliceous phytoplankton fluxes

The eight-day sampling resolution during spring and summer enabled us to monitor the detailed temporal dynamics of phytoplankton fluxes at the 61°S site. Comparison of satellite-derived PIC and chlorophyll-a concentrations for the study region with coccolith fluxes registered by the sediment trap suggests a time lag of about two months between their surface maxima and peak coccolith fluxes registered by the shallower trap (Fig. 4). Therefore, the growth phase of the *E. huxleyi* bloom probably took place between October and December 2001, a period characterised by very low SSTs (0.1-0.9 °C). It was before development of any significant stratification in the upper water column (Fig. 2b and 4a). These observations indicate that the very cold temperatures (near 0°C) and strong mixing of the water column in the Antarctic waters during spring are not an impediment for the development of an *E. huxleyi* bloom. The very low *C. leptoporus* and *Gephyrocapsa* spp. fluxes throughout the annual cycle suggest that the environmental conditions of the AZ-S must represent an ecological limit of these species. Peak fluxes of

Con formato: Fuente: Cursiva
$C.\ leptoporus$ and $Gephyrocapsa$ spp at both sediment traps coincide with those of $E.\ huxleyi$ indicating that the summer solar irradiance increase is the main factor stimulating coccolithophore growth irrespectively of the species. The onset of seasonal increase in coccolithophore arrivals in the traps occurred at the same time as that of diatoms, suggesting a rapid response of both phytoplankton groups to enhanced light levels. Although both coccolith and diatom fluxes exhibited a pronounced and nearly parallel increase throughout December (Fig. 5), coccolith fluxes peaked one week later than those of diatoms. A similar succession was observed in late summer, when coccoliths displayed a secondary flux maximum, one sampling interval later (8 days) than that of diatoms (Fig. 5). These observations agree with the bloom-dynamics scheme proposed by Barber and Hiscock (2006) (the so-called coexistence theory), in that neither phytoplankton group seems to outcompete the other during the development of the bloom. Interestingly, diatoms seem to decline earlier than coccolithophores, a feature often (but not always) observed in other parts of the world ocean (e.g. Margalef, 1978; Holligan et al., 1983; Lochte et al., 1993; Sieracki et al., 1993; Thunell et al., 1996; Balch, 2004). Indeed, a recent study of the phenological characteristics of coccolithophore blooms by Hopkins et al. (2015) concluded that they often follow those of diatoms in many regions, the sequencing driven by increasing stabilization and/or nutrient depletion (mainly silicate and/or iron, and possibly also favoured by associated increase of carbonate saturation; Merico et al, 2004) of the surface layer. The slightly different seasonal pattern observed at both sampling depths (Fig. 5) is mainly attributed to the fact that the area of the ocean from which the particles have been produced increases with depth (Siegel and Deuser, 1997). Lack of nutrient and mixed-layer-depth measurements during the sediment trap deployment precludes us from establishing robust links between changes in physical and chemical parameters in the upper water column and the observed phytoplankton succession. Nonetheless, some shipboard observations of mixed-layer properties from years previous to the sediment trap deployment (Fig. 2; Trull et al., 2001b) can provide some insight about the mechanisms driving the phytoplankton succession. Macronutrient measurements indicate that, although considerable nutrient draw-down often occurs by mid-summer, the AZ-S waters never reach potentially limiting concentrations (i.e. below 10 µM) of silicate, nitrate or phosphate (Fig. 2a; Trull et al., 2001b). Thus, macronutrient limitation was not a likely driver of the observed phytoplankton succession at the 61°S site traps. Iron levels in the AZ-S, on the other hand, are low year-round (0.1-0.2 nM;
Boyd et al., 2000b; Sohrin et al., 2000) and exhibit clear seasonality in the AZ (Tagliabue et al., 2014). So, iron availability does represent a potential driver for the observed phytoplankton succession. Indeed, laboratory experiments have shown that *E. huxleyi* has lower minimum iron requirements for growth than oceanic diatoms (Brand et al., 1983; Muggli and Harrison, 1997). This physiology likely provides an ecological advantage over diatoms in the later stages of the spring-summer bloom, when most iron has been stripped from the mixed layer.

In regard to the mechanism underlying the second diatom-coccolith succession observed at both depths in February (Fig. 5), it is possible that a vertical mixing event – as frequently reported in the AZ (e.g. Brzezinski et al., 2001) – supplied waters rich in iron and macronutrients to the euphotic zone, resetting the phytoplankton succession. Alternatively, the part of the *E. huxleyi* populations accumulated at or just above the nutricline may have increased using the iron moved by diapycnal diffusion through the pycnocline (Tagliabue et al., 2014). Their deposition in February could have been triggered by a drop of the light levels (Fig. 4). This second hypothesis is also consistent with the following observations: (1) the presence of a sub-surface chlorophyll-a maximum in the study region during spring and summer (Parslow et al., 2001; Trull et al., 2001b); (2) reports of high *E. huxleyi* cell accumulations associated with the nutricline in other settings of the world ocean (Beaufort et al., 2008; Henderiks et al., 2012) and (3) peak annual sedimentation in late February of the diatom *Thalassiothrix antarctica* (Rigual-Hernández et al., 2015a), a typical component of the “shade flora” (Kemp et al., 2000; Quéguiner, 2013). Further sampling and taxonomic analysis of the vertical distributions of phytoplankton in the AZ-S south of Australia are required to assess these hypotheses.

### 4.3 Seasonal variability in coccolith calcification

Two main factors have been proposed as driving seasonal changes in coccolith weights of *E. huxleyi*: a seasonal shift in the dominant morphotypes/ecotypes — each with a different degree of calcification (Poulton et al., 2011) — and the physiological response of a given morphotype to the seasonal variation of environmental parameters (e.g. Smith et al., 2012; Meier et al., 2014). SEM analysis of the sediment trap samples revealed that only morphotype B/C, *sensu* Young et al. (2003), thrives in the AZ-S waters south of Tasmania. That is consistent with a report by Cubillos et al. (2007) of dominance of B/C south of 50°S. Therefore, a seasonal shift in the dominant morphotype can be ruled out.
out in respect to changing coccolith weight. The observed decrease in coccolith weight
could have been caused by a change in coccolith calcification or reduction in coccolith
dimensions. Young and Ziveri (2000) showed that coccolith weight is approximately
linearly correlated to the cube of coccolith length. Applying that, the decrease in length
by 7.5% (a reduction to 92.5%) observed from the pre-bloom to the summer bloom in the
2000 m traps (i.e. difference in minimum coccolith lengths in cups 5 and 8) corresponds
to a coccolith weight loss of 21% (0.925^3 \approx 0.79). That is similar to the observed weight
reduction in the 2000 m trap between the pre-bloom and summer bloom coccolith
assemblages (16.2 - 27.6%, respectively Fig. 6). When the linear correlation between
coccolith length and weight proposed by Young and Ziveri (2000) is also applied to the
3700 m trap coccoliths, the predicted reduction of coccolith weight between the pre-
bloom and bloom assemblages is 12%. That is again very similar to the reduction in
coccolith weight observed in the E. huxleyi coccoliths intercepted by the 3700 trap (10%).
It is strongly suggested that the seasonal changes in coccolith weight at the 61°S site were
mainly driven by changes in coccolith length and were not due to significant changes in
their degrees of calcification.

Laboratory, mesocosm and field studies have shown that multiple environmental
factors including irradiance, temperature, salinity, macronutrient concentrations and iron
availability affect coccolith formation by E. huxleyi cells (e.g. Paasche, 2002; Zondervan,
2007; Langer and Benner, 2009; Feng et al., 2017). Since calcification in E. huxleyi is a
light-dependent process (Paasche, 1999, 2002), the observed decrease in coccolith weight
during summer in both traps was somewhat unexpected. Some field experiments have
shown that calcification in coccolithophores can occur at low light levels, or even in the
absence of light (e.g. van der Wal et al., 1994). However, it is often reduced compared to
that at higher irradiance levels (Zondervan, 2007).

In terms of temperature effects, Saruwatari et al. (2016) described a decrease in
coccolith size with increasing temperature cultivating E. huxleyi strains (morphotype B/C,
strains MR57N and MR70N) from the Bering and Chukchi Seas. However, comparison
of our results with those of Saruwatari et al. (2016) should be done with great caution due
to two reasons. Firstly, the E. huxleyi coccolithophores living in the Arctic seas most
likely correspond to a different ecotype than those dwelling in the AZ waters, and
therefore they may potentially exhibit different physiological responses to water
temperature changes. Secondly, the SST range in our study site was remarkably lower (0
- 3°C) than that used by Saruwatari et al. (2016) in their cultures (5 - 20°C). These
limitations make drawing inferences from Saruwatari et al. (2016) difficult. Feng et al. (2017), on the other hand, showed that optimal temperature for calcification of *E. huxleyi* cells retrieved in the Southern Ocean (morphotype A, strain NIWA1108) was ~20°C, while temperatures below 10°C resulted in a dramatic reduction of calcification rates and severe malformations of coccoliths, such as incomplete distal shield elements. Although *E. huxleyi* morphotype B/C found at the 61°S site likely represents an ecotype more tolerant to low temperatures than morphotype A (Cubillos et al., 2007; Cook et al., 2013), the frequent variations in the structure of the coccoliths (e.g. incomplete distal shield elements; Plate 1) captured by the traps suggest some degree of low-temperature stress. Despite the important role of temperature in coccolithophore growth (Paasche, 2002), enhanced summer SSTs may lead to an increase in coccolith weight, a response opposite to that observed at both traps. Therefore, it is unlikely that seasonal SST variations at the 61°S are behind the observed variability in coccolithophore weight.

Bollmann and Herrle (2007) identified a close relationship between changes in SSS (gradient from 33 to 38) and the length of *E. huxleyi* coccoliths using a global compilation of core top and plankton samples. However, based on the almost negligible annual variability in SSS (values ranging between 33.7 to 33.9 psu) in the study region, salinity most likely did not play a significant role on the observed seasonal variability in coccolith morphology observed in our traps.

In regard to the possible impact of macronutrient concentrations on coccolith weight, both nitrate and phosphate are known to have a pronounced effect on coccolith calcite content and morphology (Zondervan, 2007). However, as mentioned previously, none of these macronutrients reach limiting concentrations throughout the annual cycle in the AZ-S (Fig. 2; Trull et al., 2001b), and, therefore, their influence in the calcification of coccolithophores is likely to be low or negligible.

On the other hand, low iron levels have been reported to have a pronounced negative effect on CaCO\(_3\) production by *E. huxleyi* cells (Schulz et al., 2004), so it represents a candidate driver of seasonal changes in coccolith weight. During winter, deep water mixing re-stocks the mixed layer with iron (Tagliabue et al., 2014). As soon as light levels become sufficient for photosynthesis in early spring, phytoplankton rapidly develops under non-limiting concentrations of macro- and micronutrients. These favourable conditions for coccolithophore growth could explain the heavier and larger coccoliths registered in early December (Fig. 6). As the phytoplankton bloom develops,
the dissolved iron stock is rapidly depleted in the photic zone possibly resulting in a size
and weight reduction of coccoliths of the already substantial *E. huxleyi* populations. From
late summer throughout autumn, some recycling of iron in the upper water column by
increasing summer populations of zooplankton feeding on the bloom (Tagliabue et al.,
2014), coupled with increasing light levels and the continued shallowing of the mixed
layer, would allow coccolithophores to produce again longer and heavier coccoliths (Fig.
6).

Iron-limitation, therefore, represents the most likely environmental driving factor
for the seasonal variability in coccolith weight and length of *E. huxleyi* assemblages at
the 61°S site. However, we note again that the absence of *in situ* measurements of
chemical and physical parameters of the water column, means that control of coccolith
weight by varying iron availability in the AZ-S remains an hypothesis needing validation
by future studies.

4.4 Effects of calcite dissolution on the sinking coccolith assemblages

The similar average annual coccolith weight registered at both traps indicates that
negligible coccolith dissolution occurs at meso- and bathypelagic depths in the AZ-S
south of Australia. That is despite the fact that coccolith sinking assemblages captured by
the deeper trap were exposed to potentially intense dissolution after crossing the CSH
(located at 3000 m in the study region; Fig. 2). The similar coccolith values observed at
both depths can be attributed to the formation of algal and faecal aggregates in the mixed
layer that include fine mineral particles (Passow and De La Rocha, 2006) and provide
protection against dissolution. They also facilitate rapid transport of the coccoliths down
through the water column. The aggregate-formation hypothesis is supported by the
findings of Closset et al. (2015) who estimated that sinking rates at the 61°S site were, at
least 213 m d^-1 during the productive period, a value consistent with the sinking rates of
algal and/or faecal aggregates (Turner, 2002, 2015).

Despite not finding increased dissolution with water depth between 2000 and 3700
m, it is possible that coccoliths experienced some carbonate dissolution before reaching
the traps. Milliman et al. (1999), suggested that the same biological processes that
facilitate aggregate formation and flocculation, such as ingestion, digestion and egestion
by grazers, may be responsible for significant carbonate dissolution at epipelagic depths
(i.e. depths shallower than 800-1000 m. Indeed, the negligible amounts of coccospheres
found in both traps, together with the high sinking velocities, suggest that grazing could
have been an important influence on export. That is supported by findings of Ebersbach
et al. (2011) in the PFZ north of our study location. They documented that an important
fraction of the particles sinks from the mixed layer as faecal aggregates. On the other
hand, the small spherules often observed on the coccoliths captured by the traps suggest
some degree of coccolith dissolution followed by remineralisation. We speculate that
some of the coccoliths captured by the traps could have experience partial dissolution in
the upper water column leading to the exposure of their organic coccolith scaffold (Gal
et al., 2016; Lee et al., 2016) to the environment. It is possible that salts dissolved in the
water column subsequently precipitated over this scaffold structures resulting in the
formation of the recrystallised structures observed in some coccoliths (Plate I, e.g.).
However, the available data are insufficient to evaluate the impact of carbonate
dissolution in the upper water column and processes leading to secondary recrystallisation
in the coccoliths.

4.5 Calcium carbonate content of *Emiliania huxleyi* coccoliths

A broad range of calcite contents for *E. huxleyi* coccoliths (1.4 - 7.0 pg) has been
proposed in the literature (e.g. Young and Ziveri, 2000; Beaufort, 2005; Holligan et al.,
2010; Poulton et al., 2011). The differences in these estimates are most likely due to
variability in the amount of coccolith calcite between morphotypes and to the varied
methodological biases associated with the three main approaches for estimating coccolith
mass: morphometrics, regression and birefringence. Since *E. huxleyi* morphotype B/C is
considered to be geographically restricted to the Southern Ocean (Cubillos et al., 2007;
Cook et al., 2013) we limit the comparison of our results to studies conducted only in the
Southern Ocean reporting this morphotype.

Average annual coccolith quotas at both trap depths at the 61°S site (2.11 ± 0.96
and 2.13 ± 0.91 pg per coccolith at 2000 m and 3700 m, respectively) are almost identical
to that estimated by Holligan et al. (2010) (2.20 ± 0.60 pg; morphotype B/C) in the Scotia
Sea using a regression line between the number of coccoliths against PIC. Moreover, our
estimates are slightly higher, but with a considerable overlap in the ranges of coccolith
weight, than those estimated by Poulton et al (2011) for the *E. huxleyi* morphotype B/C
populations found in Patagonian shelf waters (1.40 ± 0.6 pg). The greater standard
deviation of our data is most likely due to the time periods compared. While the average
coccolith weight estimated for our traps reflects an integration of the annual variability in
coccolith weight, the shipboard observations by Poulton et al. (2011) provide a snapshot
of the summer coccolithophore populations, that likely exhibit lower coccolith size and, thus, variability.

Because our coccolith weight estimates are similar to those of Poulton et al. (2011) and Holligan et al. (2010), we can estimate the fractional contribution of coccolithophores to total carbonate production in the AZ-S south of Australia. Coccolithophores account for approximately 2-5% of the annual deep-ocean CaCO3 fluxes at mesopelagic depths at the 61°S site. The contribution of coccolithophores to the annual CaCO3 budget in the AZ-S south of Australia is similar to the estimate by Salter et al. (2014) for the macronutrient-rich, but iron deficient M6 site in the Indian sector of the AZ (12%) and remarkably lower than an estimate for the iron-fertilised station A3 over the central Kerguelen Plateau (85%; Rembauville et al., 2016). Due to the different methodologies for estimating coccolithophore contributions to carbonate production, comparison of our results with these other studies should be treated with caution. While only whole coccoliths were counted for our calculation, therefore providing a conservative estimate, Salter et al. (2014) and Rembauville et al. (2016) estimated the weight of the < 20 µm fraction using inductively coupled plasma-atomic emission spectrometry. That approach often results in overestimates of the coccolith contribution to bulk carbonate content.

There can be non-negligible contributions of non-coccolith fragments to the fine fraction (Giraudeau and Beaufort, 2007). Despite the biases associated with both methodologies, the general trend appears clear: the fractional contributions of coccolithophores to bulk carbonate export are lower in the iron-limited waters of the AZ compared to those in naturally iron-fertilised settings of the Southern Ocean. These findings underscore the secondary role of this phytoplankton group in the biological carbon pumps (both the inorganic carbon and carbonate counter pumps) south of the PF where non-calcifying phytoplankton - mainly diatoms and Phaeocystis - largely control the biologically-mediated CO2 exchange between the ocean and the atmosphere.

Conclusions

Analysis of the materials captured by two sediment traps deployed at the 61°S site allowed for the characterization and quantification of coccolith assemblages in Australian sector of the Antarctic Zone. The data presented here provide a baseline of the state of coccolithophore populations in this region against which future changes can be assessed. More specifically, our study has shown the following:
• Coccolithophores were a consistent member of the phytoplankton communities of the Antarctic Zone south of Australia in year 2001. Coccolithophore assemblages in this region are monospecific being composed almost entirely of *Emiliania huxleyi* morphotype B/C. This observation supports the hypothesis that the physiological differences in light-harvesting pigments of morphotype B/C (or *E. huxleyi* var. *aurorae*), compared to other Southern Ocean *E. huxleyi* varieties (Cook et al., 2011), may represent an ecological advantage in the cold, low-light and iron-limited environment of the Antarctic Zone.

• The onset of the coccolithophore productive period took place at the same time as that of diatoms, indicating that neither phytoplankton group outcompetes the other during the development of the bloom. We speculate that the diatom-coccolithophore succession observed during the peak phase of the productive period could result from the lower minimum iron requirements for growth of *E. huxleyi*, a feature that may confer a competitive advantage over diatoms.

• A decrease in coccolith weight and size during the summer months was observed at both sediment trap depths. After assessing the potential influence of several environmental parameters, increasing iron limitation seems to be the most likely candidate to drive this change. This hypothesis, however, will need to be validated in future field and laboratory culture experiments with morphotype B/C.

• The similar weight of *E. huxleyi* coccolith assemblages captured by the 2000 and 3700 m sediment traps indicates that negligible coccolith dissolution occurs during transit through meso- and bathypelagic depths in the study region. This is most likely due to a rapid transport of the coccoliths in algal and/or faecal aggregates.

• Coccolith weight values calculated for both sediment trap records using a birefringence-based approach were similar to previous estimates of *E. huxleyi* morphotype B/C in other Southern Ocean settings using regression and morphometric methods (Holligan et al., 2010; Poulton et al., 2011, respectively).

• Coccolithophore fluxes at the 61°S site account for only 2-5% of the annual deep-ocean CaCO3 fluxes, suggesting that heterotrophic calcifiers must represent the main biogenic carbonate producer in the AZ-S south of Australia.

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Supplements

Supplementary Figure 1: Seasonal variation of flux and relative abundance of the main coccolithophore species captured by the 2000 and 3700 m trap: (a) *Emiliania huxleyi*, (b) *Calcidiscus leptoporus* and (c) *Gephyrocapsa* spp.

References


