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Biogeosciences Discussions

Coccolithophore biodiversity controls carbonate export in the Southern Ocean

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Abstract

Southern Ocean waters are projected to undergo profound changes in their physical and chemical properties in the coming decades. Coccolithophore blooms in the Southern Ocean are thought to account for a major fraction of the global marine calcium carbonate ($CaCO_3$) production and export to the deep sea. Therefore, changes in the composition and abundance of Southern Ocean coccolithophore populations are likely to alter the marine carbon cycle, with feedbacks to the rate of global climate change. However, the contribution of coccolithophores to $CaCO_3$ export in the Southern Ocean is uncertain, particularly in the circumpolar Subantarctic Zone that represents about half of the areal extent of the Southern Ocean and where coccolithophores are most abundant. Here, we present measurements of annual $CaCO_3$ flux and quantitatively partition them amongst coccolithophore species and heterotrophic calcifiers at two sites representative

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of a large portion of the Subantarctic Zone. We find that coccolithophores account for a major fraction of the annual $CaCO_3$ export with highest contributions in waters with low algal biomass accumulations. Notably, our analysis reveals that although *Emiliania huxleyi* is an important vector for $CaCO_3$ export to the deep sea, less abundant but larger species account for most of the annual coccolithophore $CaCO_3$ flux. This observation contrasts with satellite remote sensing images that mostly reflect *E. huxleyi* blooms as a result of its higher cell abundance and detachment of its relatively small liths. It appears likely that the climate-induced migration of oceanic fronts will initially result in the poleward expansion of large coccolithophore species increasing $CaCO_3$ production. However, subantarctic coccolithophore populations will eventually diminish as acidification overwhelms those changes. Overall, our analysis emphasizes the need for species-centred studies to improve our ability to project future changes in phytoplankton communities and their influence on marine biogeochemical cycles.

1. Introduction

The emissions of carbon dioxide (CO_2) into the atmosphere by anthropogenic industrial activities over the past 200 years are inducing a wide range of alterations in the marine environment (Pachauri et al., 2014). These include ocean warming, shallowing of mixed layer depths, changes in nutrient supply to the photic zone, and decreasing carbonate-ion concentrations and pH of the surface ocean, a process known as ocean acidification (Rost and Riebesell, 2004; Stocker et al., 2014). In particular, ocean acidification poses a major global-scale risk for marine calcifying organisms because the decline in the saturation state of carbonate minerals in seawater makes the biological precipitation of carbonate difficult and increases the dissolution rates of their shells or skeletons (Gattuso and Hansson, 2011). Owing to their moderate alkalinity and cold temperatures, Southern Ocean waters are projected to become undersaturated with respect to aragonite no later than 2040 and to calcite by the end of the century (Cao and Caldeira, 2008; McNeil and Matear, 2008; Shadwick et al., 2013). Since such thresholds will be reached sooner in polar regions, Southern Ocean ecosystems have been proposed as bellwethers for prospective impacts of ocean acidification on marine organisms at mid and low latitudes (Fabry et al., 2009).

Coccolithophores are a major component of phytoplankton communities in the Southern Ocean, particularly in its northern-most province, the Subantarctic Zone, where

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they often exhibit maximum abundances and diversity (e.g. Gravalosa et al., 2008; Saavedra-Pellitero et al., 2014; Malinverno et al., 2015; Charalampopoulou et al., 2016). Coccolithophores play an important and complex role in the Southern Ocean carbon cycle (Salter et al., 2014). On the one hand, the production of calcite platelets (termed coccoliths) decreases the alkalinity of surface waters thereby reducing the atmospheric uptake of CO_2 from the atmosphere into the surface ocean. On the other hand, the production of organic matter through photosynthesis, and its subsequent transport to depth in settling particles, enhances carbon sequestration via the biological carbon pump (Volk and Hoffert, 1985). Additionally, due to their high density and slow dissolution, coccoliths act as an effective ballast for organic matter, increasing organic carbon sequestration depths (Buitenhuis et al., 2001; Boyd and Trull, 2007; Ziveri et al., 2007). Therefore, changes in the abundance, composition and distribution of coccolithophores could have an extensive impact on ocean nutrient stoichiometry, carbon sequestration, and nutrition for higher trophic levels in the Southern Ocean (Deppeler and Davidson, 2017).

The remoteness and vastness of the Southern Ocean, together with the inherent temporal and spatial variability of pelagic ecosystems, hampers accurate characterization and quantification of Southern Ocean phytoplankton communities. Advances in satellite technology and modelling algorithms have allowed a circumpolar and year-round coverage of the seasonal evolution of major phytoplankton functional groups within the Southern Ocean (e.g. Alvain et al., 2013; Hopkins et al., 2015; Rousseaux and Gregg, 2015). In particular, satellite reflectance observations have been used to quantitatively estimate coccolithophore Particulate Inorganic Carbon (PIC) concentrations throughout the Southern Ocean. These satellite estimates suggest apparent high PIC values during summer near the major Southern Ocean fronts attributed to coccolithophores (Balch et al., 2011; Balch et al., 2016). This band of elevated reflectance and PIC that encircles the entire Southern Ocean was termed the "Great Calcite Belt" by these authors. However, recent research (Trull et al., 2018) indicates that satellite ocean-colour-based PIC estimates could be unreliable, particularly in Antarctic waters where they erroneously suggests high PIC abundances. Shipboard observations, on the other hand, provide a detailed picture of phytoplankton community composition and structure, but are dispersed, both temporally and geographically, and provide rather heterogenous data in terms of taxonomic groups investigated, and the sampling scales and methodologies used

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(e.g. Kopczynska et al., 2001; de Salas et al., 2011; Poulton et al., 2013; Patil et al., 2017, among others). *In situ* year-round monitoring of key strategic regions is critically needed to establish baselines of phytoplankton community composition and abundance and to validate and improve ocean biogeochemical models (Rintoul et al., 2012). This information is also essential if we are to detect possible climate-driven changes in the structure of phytoplankton communities that could influence the efficiency of the biological carbon pump, with consequent feedbacks to the rate of deep-water carbon sequestration and global climate change (Le Quéré et al., 2007; Deppeler and Davidson, 2017).

Here, we document coccolithophore and carbonate particle fluxes collected over a year by four sediment trap records deployed at two strategic locations of the Australia and New Zealand sectors of the Southern Ocean considered representative of a large portion of the SAZ. Our measurements provide coccolith mass estimates of the main coccolithophore species and quantitatively partition annual carbonate fluxes amongst coccolithophore species and heterotrophic calcifiers. We find that coccolithophores are a major vector for $CaCO_3$ export out of the mixed layer and that the largest contribution to $CaCO_3$ export is not from the most abundant species *Emiliania huxleyi* but rather from larger coccolithophores species with substantially different physiological traits (e.g. *Calcidiscus leptoporus*). Our results emphasize the urgent need for diagnostic fitness response experiments on other coccolithophore species aside from *E. huxleyi* (e.g. Feng et al., 2017) in order to be able to be able to predict the impacts of anthropogenically induced changes in Southern Ocean ecosystems and biological carbon uptake mechanisms.

2. Material and methods

2.1 Oceanographic setting

The SAZ alone accounts for more than half of the Southern Ocean area (Orsi et al., 1995) and represents a transitional boundary between the warm, oligotrophic waters of the subtropical gyres to the north and the cold, silicate-rich waters south of the Polar Front (PF). The SAZ is arguably the largest high nutrient, low chlorophyll (HNLC) province in the world's ocean and is central to the linkages between the ocean–atmosphere CO_2 exchange and climate. The deep winter convection in the SAZ, which

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that exceeds 400 m, results in the formation of a high-oxygen water masses known as Subantarctic Mode and Antarctic Intermediate Waters that connect the upper and lower limbs of the global overturning circulation (Sloyan and Rintoul, 2001a, b). The formation of these water masses are responsible for the sequestration of a large fraction of anthropogenic CO_2 (Sabine et al., 2004), with an estimated 1 Gt C yr^{-1} transported to intermediate depths annually (Metzl et al., 1999). Macronutrient concentrations display pronounced seasonal changes in the SAZ with fully replete levels during winter to substantial depletion during summer, particularly for silicate (Dugdale et al., 1995; Rintoul and Trull, 2001; Bowie et al., 2011). Phytoplankton community in the subantarctic zone is dominated by pico- and nanoplankton including cyanobacteria, coccolithophores and autotrophic flagellates with lower abundances of diatoms than polar waters south the Polar Front (Chang and Gall, 1998; Kopczynska et al., 2001; de Salas et al., 2011; Rigual-Hernández et al., 2015b; Eriksen et al., 2018).

2.2 Field experiments

Here we report on the coccolithophore and biogeochemical fluxes collected over a year at the Australian Southern Ocean Time Series (SOTS) observatory (Trull et al., 2010) and the New Zealand Subantarctic Mooring (SAM) site (Nodder et al., 2016) (Fig. 1). The SOTS observatory is located in the abyssal plane of the central SAZ approximately 530 km southwest of Tasmania (46° 56' S, 142° 15' E) within an anti-cyclonic gyre in a region characterized by weak circulation (Trull et al., 2001; Herraiz-Borreguero and Rintoul, 2011). SOTS was equipped with three vertically moored, conical time-series sediment traps (McLane Parflux Mk 7G-21) placed at ~1000, 2000 and 3800 m depth between August 2011 until July 2012. The physical, chemical and biological parameters of SOTS site are regarded as representative for large portion of the Indian and Australian sectors of the SAZ (~90°E and 140°E; Trull et al., 2001). The SAM site is located in the Bounty Trough in in the subantarctic waters south east of New Zealand (46°40'S, 178' 30°E) and was equipped with conical, time-incremental sediment trap (McLane PARFLUX Mk7G-21) placed at 1500 m depth, with samples used in the present study collected between November 2009 until November 2010. The SAM site is considered to be representative of a wide area of the northern sector of the SAZ off eastern New Zealand, approximately 171°E to 179°W and 45 to 47°S (Law et al., 2014; Fig. 1). Full details of the field experiments from these two localities in the Australian and New

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165 Zealand sectors of the SAZ can be found in Trull et al. (2001) and Nodder et al. (2016),
166 respectively.

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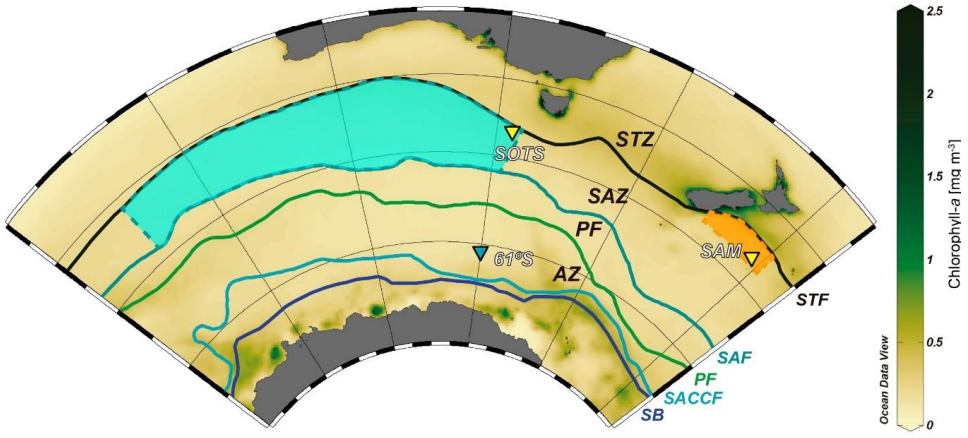

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169 **Figure 1**: Chlorophyll-*a* composite map of the Australian-New Zealand sector of the
170 Southern Ocean (July 2002 to July 2012) from the MODIS Aqua Sensor showing the
171 location of the sediment trap moorings sites: SOTS, 61°S and SAM. The regions for
172 which the SOTS and SAM sites are representative are marked with light blue and orange
173 areas, respectively. Abbreviations: Subtropical front - STF, Subantarctic Zone – SAZ,
174 Subantarctic Front - SAF, Polar Frontal Zone - PFZ, Polar Front - PF, Antarctic Zone –
175 AZ, Southern Antarctic Circumpolar Current Front – SACCF, southern boundary of the
176 ACC – SB. Oceanic fronts after Orsi et al. (1995).

177 **2.3 Sample processing**

178 In short, the recovered trap bottles were refrigerated upon recovery and then
179 allowed to settle. The sample slurry was then wet-sieved through a 1 mm screen in the
180 case of SOTS (no attempt to extract zooplankton "swimmers" was made for the <1 mm
181 fraction analysed here) and through a 200 µm sieve to remove "swimmers" for the SAM
182 site. The remaining fraction was then split using a McLane wet sample divider; the SOTS
183 samples were subdivided into one tenth aliquots while one fifth splits were made for the
184 SAM samples. For the SOTS samples, a total of 55 samples were processed for calcareous
185 nannoplankton analysis. The one-tenth splits dedicated to phytoplankton analysis were
186 further subdivided into four aliquots with the McLane splitter. One aliquot was used for

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calcareous nannoplankton analysis and the remaining three were kept refrigerated for biomarker and non-calcareous microplankton analyses. In the case of the SAM samples, the one-fifth aliquots were further subdivided into five subsplits, and one of those was used for calcareous nannoplankton analysis. Two different types of glass slides per sample were prepared. The first preparation was used for the estimation of coccosphere and calcareous dinocyst (calcispheres of thoracosphaerids) fluxes and for coccolith imaging. A volume ranging between 1000 and 5000 µl of the raw sample was mounted on a glass slide using Canada balsam following Flores and Sierro (1997). This technique produces random settling of the coccoliths for microscopic identification and enumeration. The second type of glass slide was prepared following a modified protocol for non-destructive disintegration of aggregates modified from Bairbakhish et al. (1999). The objective of this chemical treatment is to reduce biases in the coccolith flux estimations associated with the presence of different types of aggregates and coccospheres (Bairbakhish et al., 1999). In brief, 2000 µl were extracted from the aliquot for calcareous nannoplankton analysis and then treated with a solution comprising 900 µl sodium carbonate and sodium hydrogen carbonate, 100 µl ammonia (25%) and 2000 µl hydrogen peroxide (25%). The sample was agitated for 10 seconds every 10 minutes and this process was repeated over an hour. Then, the reaction was stopped with catalase enzyme and samples were allowed to settle for at least 48 hours before preparation on microscope slides. pH controls indicate that the solution kept pH levels near 9, therefore precluding coccolith dissolution. Finally, trap samples were mounted on microscope slides following the same decantation method as used for the first type of glass slides (i.e. Flores and Sierro, 1997).

2.4 Determination of $CaCO_3$ fluxes

A detailed description of the geochemical analytical procedures for the SOTS samples is provided in Trull et al. (2001) and Rigual-Hernández et al. (2015a) while more detailed procedures of the SAM trap can be found in Nodder et al. (2016). In short, for the SOTS site three of the one tenth splits were filtered onto 0.45 pore size filters. Then the material was removed from the filter as a wet cake of material**,** dried at 60°C, and ground in an agate mortar. This material was used to determine the total mass and composition of the major components of the flux. Particulate inorganic Carbon (PIC) content was measured by closed system acidification with phosphoric acid and coulometry. For the SAM site, one-fifth split was analysed for elemental calcium (Ca)

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concentration using ICP-MS techniques. The samples were oven-dried, digested in nitric/hydrochloric acid and then analysed according to the methods under US EPA 200.2. Ca was used to estimate $CaCO_3$ content in the samples assuming a 1:1 molar ratio in $CaCO_3$.

2.5 Quantification and characterization of coccolithophore sinking assemblages

Qualitative and quantitative analyses of coccospheres and coccoliths were performed using a Nikon Eclipse 80i polarised light microscope at 1000 x magnification. The taxonomic concepts of Young et al. (2003) and the Nannotax website (Young et al., 2019) were used. A target of 100 coccospheres and 300 coccoliths was established; however, owing to the pronounced seasonality in coccolithophore export, there were some periods with very low abundance of coccospheres in the samples and therefore the target of 100 coccospheres was not always met. Coccosphere and coccolith species counts were then transformed into daily fluxes after Rigual Hernández et al. (2018).

2.6 Determination of coccolith mass and size

Birefringence and morphometric methods are the two most commonly used approaches for estimating the calcite content of isolated coccoliths. The circularly-polarized light-microscopy-based technique (Fuertes et al., 2014) is based on the systematic relationship between the thickness of a given calcite particle (in the thickness range of 0 - 1.55 mm) and the first-order polarization colours that it displays under polarized light (Beaufort, 2005; Beaufort et al., 2014; Bolton et al., 2016). The advantages of this approach are that: (i) it directly measures complete coccoliths with no assumptions regarding their shape or thickness and (ii) it allows for quantification of calcite losses associated with missing parts or etching of the coccoliths. Disadvantages of this technique are the errors associated with the coccolith-calcite calibration and their consequent effect on the coccolith mass estimates (Fuertes et al., 2014; González Lemos et al., 2018). The morphometric approach, on the other hand, allows better taxonomic identification of the coccoliths and has smaller errors in the length measurements (~0.1 to 0.2 μm; Poulton et al. 2011). However, this method does not allow direct measurement of coccolith thickness and assumes identical shape and width proportions for all specimens of the same species, among other uncertainties (see Young and Ziveri, 2000 for a review). Since the two

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methods have different associated errors (Poulton et al., 2011), we applied both approaches to our coccolith flux data in order to obtain two independent estimates of the fractional contribution of coccolithophores species to total carbonate export in the SAZ.

For the birefringence-based approach, a minimum of 50 coccoliths of each of the main coccolithophore species were imaged using a Nikon Eclipse LV100 POL light microscope equipped with circular polarisation and a digital camera (Nikon DS-Fi1 8-bit colour). The only exception was *E. huxleyi* for which coccolith mass values had already been estimated in all the same samples at high resolution by Rigual-Hernández et al. (under review). For the minor components of the flux assemblage, a lower number of coccoliths were measured (Table 1). A photograph of the same apical rhabdolith of the genus *Acanthoica* was taken and used for calibration at the beginning of each imagining session during which microscopy light and camera settings were kept constant. A different number of fields of view of multiple samples representative of different seasons were photographed until the target number of coccoliths for each species was reached. Photographs were then analysed by the image processing software C-Calcita. The output files for single coccoliths were visually selected and classified into the lowest possible taxonomic level. Length and weight measurements were automatically determined by C-Calcita software. Morphometric measurements of all the species are summarized in Table 1. For further methodological details see Fuertes et al. (2014) and Bolton et al. (2016).

The second approach consisted of performing morphometric measurements on the coccoliths followed by the estimation of their coccolith mass assuming a systematic relation between length and thickness (Young and Ziveri, 2000). Young and Ziveri (2000) proposed that the calcite content of a given coccolith could be estimated using the following formula:

$$\text{Coccolith calcite (pg)} = 2.7 \times k_s \times l^3$$

where 2.7 is the density of calcite ($CaCO_3$; pg μm^3), "k_s" is a shape constant that varies between species and morphotypes and whose value is based on the reconstruction of coccolith cross profiles and "l" is the distal shield length (DSL). In order to undertake coccolith measurements on the same coccoliths used for the birefringence-based approach, we employed the distal shield length values measured by C-Calcita using circularly polarized light instead of morphometric measurements on Scanning Electron Micrographs (SEM) as made in Young and Ziveri (2000).

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Since coccolith distal shield length (DSL) has been reported to be systematically underestimated using cross-polarized light microscopy (e.g. D'Amario et al., 2018), we evaluated the possible errors in the DSL measurements made by C-Calcita. For this assessment, we measured 40 detached coccoliths of *C. leptoporus* under the SEM from samples of the SOTS sediment traps using the image processing software Image-J. Average DSL measurements under the SEM were then compared with those made by C-Calcita on 40 randomly selected *C. leptoporus* coccoliths. The average coccolith length obtained with the SEM analysis (6.37 ± 1.02, n = 40) was ~ 4% shorter than that estimated with C-Calcita (6.62 ± 1.47, n = 40). Therefore, we assumed the error for the DSL measurements with circularly polarized light is < 5%. For the k_s value of each taxa, data from the literature were (Table 1). *E. huxleyi* assemblages in the SAZ are composed of a mixture of five different morphotypes: A, A overcalcified, B, B/C and C, each of which is characterized by different shape factors (k_s). Since k_s is not available for all the morphotypes found in the SAZ and it is not possible to differentiate between morphotypes in our light microscopy images, we used the mean shape factor constant for *E. huxleyi* (i.e. k_s = 0.0275) to provide a range of coccolith mass estimates for this species (Table 1 and Fig. 4).

2.7 Calculation of annual estimates

Since the trap collection periods encompassed a period shorter than a calendar year, annual estimates of coccolith and $CaCO_3$ fluxes had to be estimated. For the SOTS site, a total of 336 days were sampled for the 1000 and 2000 m traps and 338 days for the 3800 m. Since the unobserved interval occurred in winter, the missing sampling period was filled using an average flux value of the winter cups (first and last trap bottles). In the case of the SAM trap, the number of samples available for $CaCO_3$ and calcareous nannoplankton analyses was different, covering a period of 313 and 191 days respectively. Since gaps were quasi-equally distributed along the time series, annual fluxes were estimated by filling the gaps in the record with average fluxes calculated from the available data. The estimated range of the annual contribution of coccolithophores to total $CaCO_3$ export at the SOTS and SAM traps was calculated by multiplying the coccolith flux of each species in each sampling interval by its average coccolith weight values obtained with the birefringence and morphometric techniques.

3. RESULTS

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3.1 Magnitude and seasonality of coccolithophore fluxes

Annualized coccolith fluxes were similar at the SOTS three trap depths, with 8.6, 7.3 and 8.6 x 10^{11} liths m^{-2} yr^{-1} at 1000, 2000 and 3800 m respectively, and about three times larger than those of the SAM site (3.0 x 10^{11} liths m^{-2} yr^{-1}). The contribution of intact coccospheres to the total coccolith export was low at both sites, with annual coccosphere fluxes two orders of magnitude lower than coccolith fluxes at SOTS (3.5, 3.3 and 1.8 x 10^{9} coccospheres m^{-2} yr^{-1} at 1000, 2000 and 3800 m, respectively) and SAM (2.2 x10^{9} coccospheres m^{-2} yr^{-1}).

Both coccolith and coccosphere fluxes displayed a marked seasonality that followed the general trend of algal biomass accumulation in the surface waters at the SOTS and SAM sites (Fig. 2). Coccolith fluxes at 1000 m started to increase in early October and remained above the threshold of 1 x 10^{9} coccoliths m^{2} d^{-1} until mid-April, i.e. approximately eight months (Fig. 2). Three maxima were recorded during the period of high coccolith export: October-early November 2011 (4 x 10^{9} coccoliths m^{2} d^{-1}), late December 2011 (9 x 10^{9} coccoliths m^{2} d^{-1}) and March 2012 (4 x 10^{9} coccoliths m^{2} d^{-1}). Coccolith fluxes of the main coccolithophore species generally followed the similar seasonal pattern to that of the total coccolith flux (Supplementary figure 1) and are not discussed further. Coccolithophore fluxes registered by the 2000 and 3800 m sediment traps followed a generally similar seasonal pattern to those of the shallower trap at the SOTS site (Fig. 2). At SAM, coccolith fluxes exhibited a strong seasonality with peak fluxes in early January 2010 (up to 6 x 10^{9} coccoliths m^{2} d^{-1}) and a secondary peak in August 2010 (3 x 10^{9} coccoliths m^{2} d^{-1}). Coccosphere fluxes at both sites displayed maximum fluxes during the austral summer and minima during winter; however maximum coccosphere export peaks did not always match those of coccolith export (Fig. 2).

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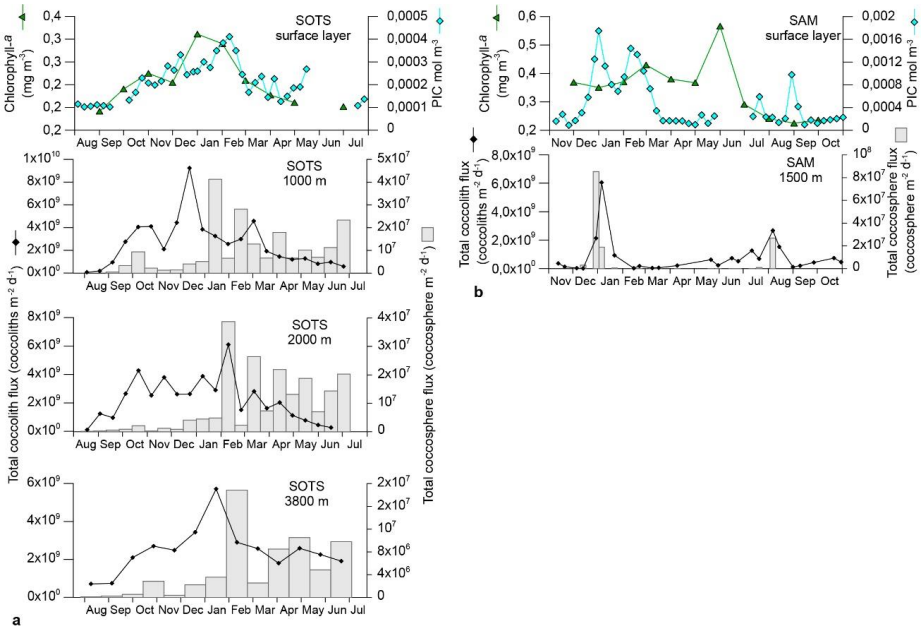

Figure 2: Satellite-derived chlorophyll-*a* and Particulate Inorganic Carbon (PIC) concentration in the surface layer and total coccolith and coccosphere fluxes registered by the sediment traps at the SOTS (a), SAM (b) and 61°S sites (c, Rigual Hernández et al., 2018). Coccosphere fluxes are not available for the 61°S site.

3.2. Coccolithophore assemblage composition

Coccolith sinking assemblages were overwhelmingly dominated by *Emiliania huxleyi* for all sediment trap records analysed (Fig. 3a). At the SOTS site, the annualized integrated relative contribution of *E. huxleyi* decreased slightly with depth, comprising 88% of the total coccolithophore assemblage at 1000 m, 82% at 2000 m and 80% at 3800 m. Secondary components of the coccolith sinking assemblage were *Calcidiscus leptoporus* (*sensu lato*) (6.7, 10.2 and 9.7% at 1000, 2000 and 3900 m, respectively), *Heliscosphaera carteri* (1.4, 2 and 1.4%) and small *Gephyrocapsa* spp. (< 3 µm) (1.4, 1.5 and 4.4%). Background concentrations (≤ 1%) of *Calciosolenia* spp., *Coccolithus pelagicus*, *Gephyrocapsa muellerae*, *Gephyrocapsa oceanica*, *Gephyrocapsa* spp. (> 3 µm), *Syracosphaera pulchra*, *Syracosphaera* spp., *Umbellosphaera tenuis* (*sensu lato*), and *Umbilicosphaera sibogae* were also registered. At the SAM site, *E. huxleyi* accounted for 83% of the annualized coccolith flux, with subordinate contributions of *C. leptoporus* (12.2%) and *Gephyrocapsa* spp. (< 3 µm) (1.5%). Background concentrations (< 1%) of

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361 *Calciosolenia* spp., *G. oceanica*, *Gephyrocapsa* spp. (> 3 µm), *H. carteri*, *Syracosphaera*
362 spp., *U. sibogae* and *U. tenuis* were observed.

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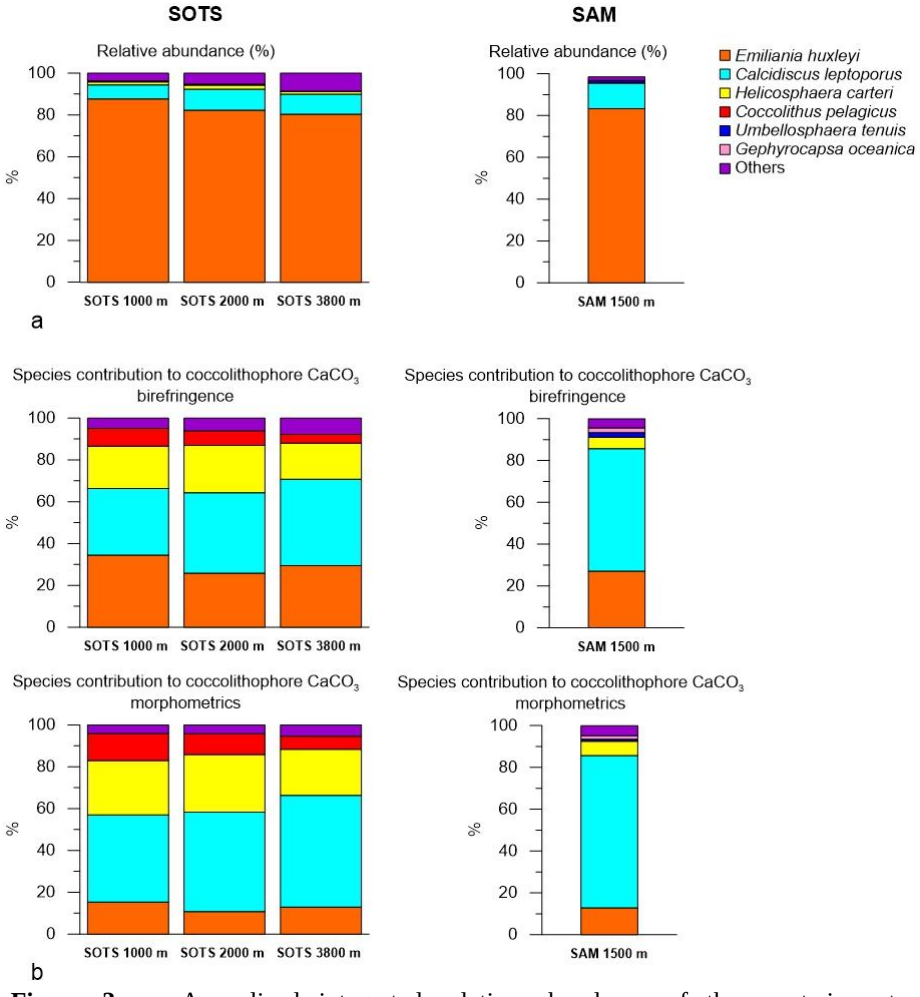

364 **Figure 3: a**. Annualized integrated relative abundance of the most important
365 coccolithophore species in the SOTS and SAM sediment trap records. **b**. Fractional
366 contribution of coccolithophore species to total coccolithophore $CaCO_3$ in the SOTS and
367 SAM sediment traps.

368 **3.3 Calcite content per species**

369 Coccolith length and mass for all species measured using birefringence and
370 morphometric techniques are provided in Table 1. Overall, the average coccolith mass
371 estimates for the coccolithophore species at SOTS and SAM sites using both approaches

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372 are within the range of values in the published literature. The Noelaerhabdaceae family
373 members, *G. oceanica* and *Gephyrocapsa* spp., display almost identical mass values with
374 both approaches (Fig. 4). In contrast, substantial discrepancies are identifiable for *C.*
375 *pelagicus*, *C. leptoporus*, *H. carteri* and *U. sibogae*, for which coccolith mass estimates
376 are about two-fold greater using morphometrics than with the birefringence approach.
377 The range of annual contributions of coccolithophores to carbonate is illustrated in Figure
378 5.

Species and morphotypes	Type of measurement	n	Length (µm) Average	Length (µm) SD	Mass $CaCO_3$ (pg) Average	Mass $CaCO_3$ (pg) SD	k_s	Crystal units types	References
Calcidiscus leptoporus	Birefrigence	210	6.39	1.49	33.65	21.11	-	V and R	
	Morphometrics	210	6.39	1.49	66.23	53.28	0.080		1
	Literature estimates	-	4.3-9.6		22.6-125.2		0.061-0.105		1,2
Coccolithus pelagicus	Birefrigence	54	13.28	1.14	170.90	32.33	-	V and R	
	Morphometrics	54	13.28	1.14	387.96	99.64	0.060		1
	Literature estimates	-	8.5-13.5		99.5-398.6		0.051 - 0.060		1,2,3
Emiliania huxleyi	Birefrigence	12842	2.78	0.57	2.64	1.43	-	R	
	Morphometrics	12842	2.78	0.57	0.99-2.64 (1.81)*	0.60-1.60	0.015-0.04 (0.0275)*	(V-unit vestigial)	
E. huxleyi type A	Literature estimates	-	3-4		1.50 - 3.50		0.02		1,4,5
E. huxleyi type A o/c	Literature estimates	-	3.5		4.6		0.04		1
E. huxleyi type B/C	Literature estimates	-	1.8-5.5		0.3-3.5		0.015		5,6,7
E. huxleyi type B	Literature estimates	-	3.5-5		2.30 - 6.81		0.02		1,5
Gephyrocapsa oceanica	Birefrigence	51	5.87	0.62	26.70	5.64	-	R	
	Morphometrics	51	5.87	0.62	28.14	8.97	0.050	(V-unit vestigial)	
	Literature estimates	-	5-5.35		16.9-25.7		0.050-0.062		1,2
Gephyrocapsa spp.	Birefrigence	10	4.03	0.59	9.00	2.51	-	R	
	Morphometrics	10	4.03	0.59	9.33	3.84	0.050	(V-unit vestigial)	1
	Literature estimates	-	-	-	-		-		
Helicosphaera carteri	Birefrigence	64	11.20	1.12	100.10	20.34	-	V and R	
	Morphometrics	64	11.20	1.12	194.95	56.45	0.050		1
	Literature estimates	-	9.1-10		135-142.8		0.050-0.070		1,2
Syracosphaera pulchra	Birefrigence	81	6.77	1.09	17.77	6.80	-	V, R and T	
	Morphometrics	81	6.77	1.09	26.94	11.16	0.030		1
	Literature estimates	-	2.7-6		13.5-16.5		0.027-0.083		1,2,4
Umbellosphaera tenuis	Birefrigence	54	6.42	0.99	15.69	5.02	-	R	
	Morphometrics	54	6.42	0.99	11.45	4.61	0.015		1
	Literature estimates	-	5-6		8.7-23.9		0.015-0.071		1,2
Umbilicosphaera sibogae	Birefrigence	6	7.76	1.81	27.14	11.07	-	V and R	
	Morphometrics	6	7.76	1.81	78.93	51.38	0.055		1
	Literature estimates	-	4.1-6	-	16-35		0.055-0.086		1,2

379 **Table 1**: Coccolith mass estimates of the main coccolithophore species found at the SOTS
380 and SAM sites using birefringence (C-Calcita) and morphometrics. Additionally, length
381 and mass estimates from the literature are also listed for most species. References: (1)
382 Young and Ziveri (2000), (2) Beaufort and Heussner (1999), (3) Samtleben and Bickert
383 (1990), (4) Poulton et al. (2010), (5) Poulton et al. (2011), (6) Holligan et al. (2010) and
384 (7) Charalampopoulou et al. (2016). * coccolith mass range obtained applying the
385 minimum and maximum k_s values for *E. huxleyi* found in the literature (i.e. 0.015 and
386 0.04, respectively).

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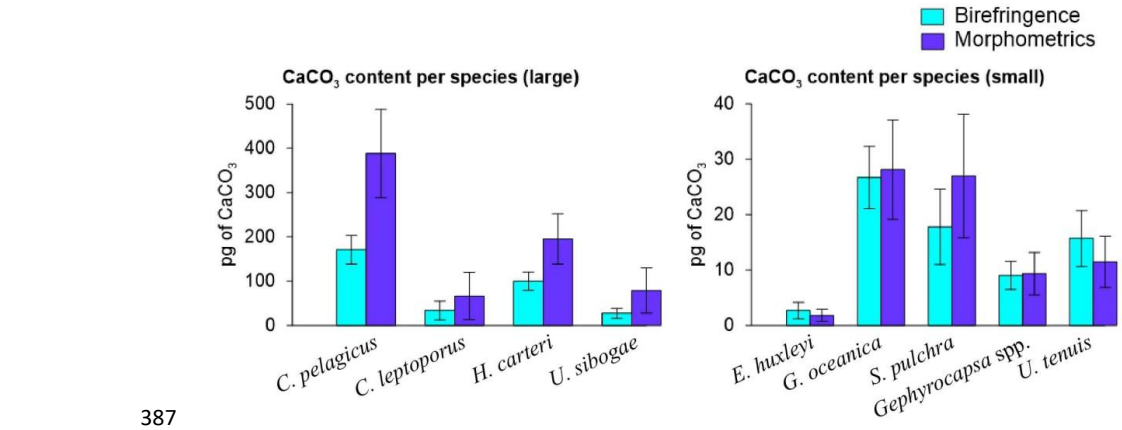

Figure 4: Average and standard deviation of the coccolith mass estimates of the most important coccolithophore species captured by the SOTS and SAM sediment traps using birefringence (C-Calcita) and morphometric approaches. For *E. huxleyi*, the morphometric-based coccolith mass estimate was calculated by applying a mean shape factor constant (k_s) value estimated from the range of all the morphotypes found at the SAZ (i.e. k_s = 0.0275, Table 1).

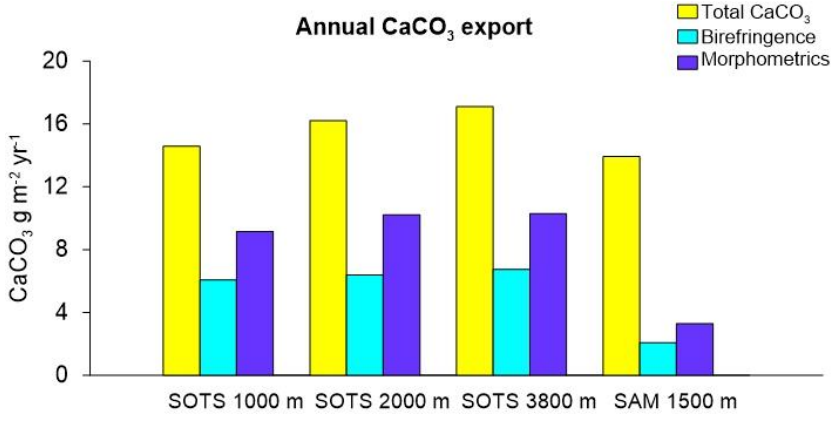

Figure 5: Inorganic carbon ($CaCO_3$) fluxes of coccolith calcite estimated using birefringence (C-Calcita) and morphometric approaches for the SOTS and SAM sites.

4. Discussion

4.1 Coccolithophore phenology in the SAZ: satellite versus sediment trap records

Total coccolith flux seasonality at the SOTS site shows good congruence with satellite-derived PIC in the surface layer, with both parameters suggesting enhanced

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coccolithophore productivity between October and March (austral mid-spring to early autumn; Fig. 2a). Interestingly, substantial coccosphere export (> 1 x 10^7 coccospheres m^2 d^{-1}) does not occur until January indicating that coccolith and coccosphere export are not tightly coupled in the subantarctic waters south of Australia. Two different processes could be invoked to explain the mismatch between coccolith and coccosphere fluxes at this site. Firstly, *E. huxleyi*, the dominant coccolithophore species in the Southern Ocean, is able to produce coccoliths rapidly (up to three coccoliths per hour; Paasche, 1962; Balch et al., 1996) and shed the excess of coccoliths into the surrounding water under certain environmental conditions (Paasche, 2002). Although the coccolith shedding rate of *E. huxleyi* increases linearly with cellular growth rate (Fritz and Balch, 1996; Fritz, 1999), the tiny size and low weight of detached coccoliths allow them to remain in the upper water column long after cell numbers have begun to decline. It follows that high concentrations of detached coccoliths do not necessary imply a proportional abundance of coccospheres in the surface layer (Tyrrell and Merico, 2004; Poulton et al., 2013) or in the traps. Additionally, a substantial fraction of the coccospheres produced in the surface layer may experience substantial mechanical breakage by zooplankton before reaching the trap depths. Indeed, previous studies in the subantarctic waters south of Tasmania demonstrated that microzooplankton grazing pressure is sufficient to remove up to 82% of primary production in mid-summer (Pearce et al., 2011) and most of the particles exported out the mixed layer during the productive period occur in the form of faecal aggregates (Ebersbach et al., 2011). Therefore, it is highly likely that: (i) the intensity of coccosphere export registered by the traps is influenced by grazing pressure in the surface layer, and (ii) that the impact of grazing on coccolithophores varies throughout the year (Calbet et al., 2008; Lawerence and Menden-Deuer, 2012; Quéguiner, 2013).

In contrast, seasonal variations in satellite-derived PIC concentration and coccolith fluxes at SAM show some discrepancies not observed at SOTS. While maximum PIC concentrations in the surface layer and coccolith and coccosphere fluxes co-occur in December and January (austral early to mid-summer), satellite-derived PIC suggests a secondary maximum in February-early-March not recorded by the trap (Fig. 2b). One possibility is that the satellite secondary maximum is not coccoliths. The higher chlorophyll-a levels at the SAM site (Fig. 2) suggests that other phytoplankton groups, such as diatoms, are more abundant than in the subantarctic waters south of Tasmania. Empty and broken diatom valves have been suggested to display similar spectral characteristics than those of coccolithophore blooms (Broerse et al., 2003; Tyrrell and

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435 Merico, 2004; Winter et al., 2014). Therefore, the second peak in satellite-derived PIC
436 could have been caused by a senescent diatom bloom. This hypothesis is likely since
437 diatom blooms in the SAZ are known to develop early in the productive season (Rigual-
438 Hernández et al., 2015b) and rapidly decay following the depletion of silicate and/or iron
439 stocks in the surface layer (Lannuzel et al., 2011). However, no secondary late summer
440 maximum was observed in biogenic silica fluxes in the SAM. Another possible
441 explanation is a contribution to the satellite record from lithogenic material. Fully
442 resolving causes of mismatches between *in-situ* and satellite PIC estimates is not
443 achievable for the SAM site (nor more broadly for the Southern Ocean; Trull et al., 2018).
444 A second difference between the SAM and SOTS sites is that maximum annual
445 coccosphere export occurred one week earlier than maximum coccolith fluxes at SAM,
446 (Fig. 2). The different seasonalities between the sites suggest that different export
447 mechanisms may operate. The formation of rapidly sinking algal aggregates by diatoms
448 is known to scavenge particles they have collided with and increase particle sinking
449 (Alldredge and McGillivary, 1991; Passow and De La Rocha, 2006), thus the formation
450 of such rapid-sinking aggregates could potentially facilitate the preservation of
451 coccospheres early in the productive season at the SAM site. However, the lack of
452 accompanying *in situ* information on plankton community structure in the study region
453 precludes the assessment of these hypotheses.
454 Despite the uncertainties involved in our interpretations, the overall picture that
455 emerges from our comparison of satellite and sediment trap flux data is that the duration
456 of the coccolithophore bloom based on ocean-colour-based PIC concentrations most
457 likely provides an over-estimation of the coccolithophore productive season. Our
458 observations motivate caution in describing coccolithophore phenology solely based on
459 satellite-derived PIC concentrations (e.g. Hopkins et al., 2015).
460

461 **4.2 Magnitude and composition of subantarctic coccolithophore assemblages**

462 Annual coccolith export across the major zonal systems of the Australian sector
463 of the Southern Ocean exhibits a clear latitudinal gradient, with maximum fluxes at the
464 SAZ (8.6 x 10^{11} liths m^{-2} yr^{-1}) and eight-fold lower fluxes in the polar waters of the AZ
465 (1.0 x 1011 liths m-2 yr-1; Rigual-Hernández et al., 2018). Coccolithophore species
466 occurrence documented by our subantarctic sediments traps are consistent with previous
467 reports on coccolithophore assemblage compositions in the surface layer (Findlay and

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Giraudeau, 2000; Saavedra-Pellitero et al., 2014; Malinverno et al., 2015; Chang and Northcote, 2016) and sediments (Findlay and Giraudeau, 2000; Saavedra-Pellitero and Baumann, 2015) and are more diverse than those found in the AZ (Rigual Hernández et al., 2018). The southward decline in coccolithophore abundance and diversity is most likely due to the decrease in sea-surface temperature (SST) and light availability moving poleward (Charalampopoulou et al., 2016; Trull et al., 2018). In particular, the close relationship between temperature and growth rates has been demonstrated in a range of coccolithophore species and strains (Buitenhuis et al., 2008), and seems to be a critical, if not the most important, control on the biogeographical distribution of coccolithophore species in the Southern Ocean (Trull et al., 2018). This pronounced latitudinal change in coccolithophore assemblage composition contrasts with the little longitudinal variability between the subantarctic SOTS and SAM sites (Fig. 3). These observations underscore the role of circumpolar fronts as natural physical barriers for plankton species distribution in the Southern Ocean (Medlin et al., 1994; Boyd, 2002; Cook et al., 2013).

Notably, the rare occurrence of the cold-water species *Coccolithus pelagicus* at the SOTS and SAM sites contrasts with the high contribution of *C. pelagicus* to the living coccolithophore communities in the subpolar and polar waters of the North Atlantic and North Pacific oceans, where it is often the second most abundant species after *E. huxleyi* (McIntyre and Bé, 1967; Baumann et al., 2000; Broerse et al., 2000a; Broerse et al., 2000b; Ziveri et al., 2000). This important difference in species composition between Northern and Southern hemisphere subpolar ecosystems could have important implications in the calibration of the satellite PIC signal in the Southern Ocean. A recent study by Trull et al. (2018) comparing satellite and shipboard observations identified a substantial over-estimation of coccolithophore PIC in the Southern Ocean waters by the NASA satellite ocean-colour-based PIC algorithm. Since satellite reflectance observations are mainly calibrated against Northern Hemisphere PIC results (Balch et al., 2011; Balch et al., 2016), we speculate that differences in the coccolithophore assemblage composition, and particularly, differences in *C. pelagicus* numbers, could contribute to the over-estimation of PIC concentrations by the satellite PIC algorithm in the Southern Ocean. Indeed, the scaling of reflectance (in satellite images) to PIC (in ocean) is very dependent on coccolith area:mass ratios (Gordon and Du, 2001; Balch et al., 2005). *Coccolithus pelagicus* has remarkably heavier and thicker coccoliths (100-400 pg per coccolith; Table 1) than *E. huxleyi* (~3 pg per coccolith), i.e. about 100 times heavier. However, the average coccolith area of *C. pelagicus* is only about ten times greater than

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that of *E. huxleyi*. Thus, this lack of proportional relationship between area and mass between these species should be taken into consideration when calibrating the satellite signals of coccolithophore-related PIC in the Southern Ocean.

4.3 Coccolith calcite content of subantarctic coccolithophore species

Multiple methodological biases associated with each of the methods used for estimating coccolith calcite content (i.e. birefringence, morphometrics) could be invoked to explain the different estimates observed for some of the species (see Young and Ziveri, 2000; Fuertes et al., 2014 and references therein). However, the fact that these discrepancies vary greatly across species suggests that the composition of the crystal-units of the coccoliths could be the most important factor causing these differences. All the heterococcoliths of the species analysed are mainly composed of either V- or R-calcite crystal units or a combination of both (Young et al., 2003; Table 1). R units are characterized by sub-radial c-axes that are reasonably well measured by the birefringence technique, but, the almost vertical optical axes of the V units (Young, 1992; Young et al., 1999) make the same thickness less birefringent (Fuertes et al., 2014). Thus, it is likely that differences in the birefringence properties of the R and V units could be responsible for the different estimates provided by the two approaches. This is supported by our results which show coccolith mass estimates of those species composed of R units, such as *G. oceanica* and *Gephyrocapsa* spp. exhibit almost identical values with both techniques (Table 1). In contrast, those species with coccoliths composed by a combination of R and V units, such as *C. pelagicus*, *C. leptoporus*, *H. carteri* and *U. sibogae*, display divergent mass estimates between approaches. The case of *E. huxleyi* is more complex due to the large intraspecific genetic variability that results in substantial differences in the profile and degree of calcification between specimens (Young and Ziveri, 2000). Our birefringence mass estimate for *E. huxleyi* (2.67 ± 1.49 pg) is less than one picogram lower than the mean range value calculated with the morphometric technique (i.e. 1.81 ± 1.10 pg with an average k_s value of all the morphotypes found at the SAZ, i.e. $k_s = 0.0275$), but identical to the maximum (2.64 ± 1.60 pg; using $k_s = 0.04$). These results suggest a reasonably good consistency between techniques for *E. huxleyi*.

Taking into consideration all the above, it is likely that the coccolith mass of some species is underestimated by the birefringence technique, and therefore, the fractional contribution of coccolithophores to total PIC using this approach should be taken as a conservative estimate. Since both methods for estimating calcite content have inherent

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uncertainties, the range of values provided by both techniques is used here as an approximation of the fractional contribution of coccolithophores to total annual $CaCO_3$ export to the deep sea in the Australian and New Zealand sectors of the SAZ.

4.4 Contribution of coccolithophores to carbonate export in the Australian-New Zealand sectors of the Southern Ocean

The magnitude of the total PIC export in the subantarctic waters was similar between the SOTS and SAM sites (range 14-17 g m^{-2} yr^{--1}), and thus slightly above the global average (11 g m-2 yr-1; Honjo et al., 2008). Our estimates indicate that coccolithophores are major contributors to $CaCO_3$ export in the Australian and New Zealand waters of the SAZ, accounting for 40-60% and 15-25% of the annual $CaCO_3$ export, respectively (Fig. 5). Heterotrophic calcifiers, mainly planktonic foraminifera (Salter et al., 2014), must therefore account for the remainder of the annual $CaCO_3$ export at both sites. Previous work on foraminifera fluxes in our study regions allows an approximate estimate of the contribution of foraminifera to total $CaCO_3$ flux that can be used to assess the validity of our estimates. Combining counts of foraminifera shells (King and Howard, 2003) with estimates of their average shell weights (20-40 µg per shell depending on size; Moy et al., 2009) suggests contributions of 1/3 to 2/3 of planktonic foraminifera to the total $CaCO_3$ flux in the Australian SAZ (Trull et al., 2018). In the subantarctic waters south of New Zealand, Northcote and Neil (2005) estimated that planktonic foraminifera accounted for about 78-97% of the total $CaCO_3$. Thus estimations of the contribution of heterotrophic calcifiers to total carbonate in both study regions are in reasonable agreement with our coccolithophore $CaCO_3$ estimates at both sites. The lower contribution of coccolithophores to $CaCO_3$ export at the SAM site in comparison with that of SOTS may be explained by differences in the ecosystem structure between sites. Algal biomass accumulation in the surface waters of the SAM region (average chlorophyll-*a* concentration between 2002 and 2018 is 0.31 mg m^{-3}) is substantially higher than that at SOTS (0.23 mg m^{-3}). We speculate that the higher abundance of non-calcareous phytoplankton (e.g. diatoms) in the subantarctic waters south of New Zealand could simultaneously reduce coccolithophore biomass through resource competition (Quéré et al., 2005; Sinha et al., 2010) while stimulating foraminifera growth (Schiebel et al., 2017). The combination of both factors could be responsible for the lower coccolithophore productivity at the SAM site despite similar total $CaCO_3$ export. Assuming that both the SOTS and SAM sites can be considered

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representative of a broad longitudinal swath of the SAZ south of Australia and New Zealand (ca. 1% of areal extent of the global ocean), the coccolithophore $CaCO_3$ export in these two regions together account for approximately 0.4 T C_{inorg}mol yr^{-1}. This value represents approximately 1% of the global annual PIC export to the deep ocean (Honjo et al., 2008) and underscores the notion that the high nutrient low-chlorophyll waters of the circumpolar SAZ should not be taken as indicative of low biological activity or export.

Our results indicate that although *E. huxleyi* overwhelmingly dominates the coccolithophore sinking assemblages at both study sites, other species with lower relative contribution but substantially heavier coccoliths are more important contributors to the annual coccolithophore $CaCO_3$ export budget (Fig. 3). Particularly relevant is the case of *C. leptoporus* that despite its relatively low abundance (~ 10% of the annual assemblage at both sites; Fig. 3), it accounts for between 30-50% and 60-70% of the annual coccolithophore-$CaCO_3$ export at the SOTS and SAM sites, respectively (Fig. 3). Similarly, other species with heavy coccoliths, such as *H. carteri* and *C. pelagicus*, are important contributors to the annual coccolithophore PIC export to the deep sea (up to ~30% and ~10% of the annual coccolithophore PIC, respectively) despite their low annual relative abundance (<2% at both sites) (Fig. 3). These results serve as an important reminder that it is often not the most abundant species, but rather the largest coccolithophore species that account for the greatest contribution to coccolithophore $CaCO_3$ production and export (Young and Ziveri, 2000; Baumann et al., 2004; Daniels et al., 2016).

The important contribution made by the coccolithophore community in setting the magnitude of carbonate production and export to the deep sea is evidenced when we compare the coccolith and total $CaCO_3$ fluxes of the SOTS sediment trap with those deployed in the AZ along the 140°E meridian (Fig. 1). Although both total and coccolithophore $CaCO_3$ export decrease with increasing latitude these changes are largely uneven. While total $CaCO_3$ decreases two-fold from the SAZ to the AZ, coccolithophore $CaCO_3$ export decreases 28-fold (Supplement Figure 2). This lack of proportional latitudinal change can be attributed to two main factors. First, subantarctic coccolithophore populations are diverse and relatively rich in species with large and heavy coccoliths such as *C. leptoporus* or *H. carteri* that account for a large fraction of the annual carbonate production and export. South of the PF, assemblages become monospecific, or nearly monospecific, dominated by the small and relatively lightly

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calcified *E. huxleyi*. Second, latitudinal variations in the abundance of heterotrophic calcifiers (mainly foraminifera but also pteropods) must play a major role in modulating the observed variations in $CaCO_3$ export. In particular, our data suggests that the fractional contribution of heterotrophic calcifiers to $CaCO_3$ production increases from ~40-60 % in the Australian SAZ to up to 95% in the AZ (Rigual Hernández et al., 2018). This pattern is consistent with previous shipboard and sediment trap studies that reported higher abundances of planktonic foraminifera at the PFZ and AZ compared to that of the SAZ in the Australian sector (King and Howard, 2003; Trull et al., 2018). Controls on the biogeographic distribution of foraminifera species are complex and beyond the scope of this paper, however, we provide a few observations. Both temperature and diet are critical factors controlling the spatial distribution of planktonic foraminifera species. In particular, the lower temperatures south of the SAF seem to favour the development of *Neogloboquadrina pachyderma* sin. and *Turborotalita quinqueloba* as indicated by the high abundance of these species in the PFZ (> 80% of the annual integrated flux for both species together; King and Howard, 2003). Additionally, the dramatically different algal communities dwelling in each zonal system may also play a role in planktonic foraminifera species distributions. In particular, diatoms can account for a major part of the diet of some foraminifera species, including *N. pachyderma* (Schiebel and Hemleben, 2017). Therefore, it is likely that the preferential grazing on diatoms of some foraminifera species may play an important role in the increase of foraminifera $CaCO_3$ production moving poleward.

4.5 Future predictions of coccolithophore community response to environmental change in the subantarctic zone

The response of *E. huxleyi* to environmental change has been extensively studied in laboratory experiments (Meyer and Riebesell, 2015; Müller et al., 2015; Feng et al., 2017) and the available information is sufficient to propose possible changes of its niche and calcification in the Southern Ocean, as discussed in detail in Trull et al. (2018). Due to the ubiquity and abundance of *E. huxleyi*, the ecophysiology of this species is often regarded as typical of all coccolithophores. However, *E. huxleyi* is rather different from most other coccolithophore species in that its physiological adaptations place it in the upper limit of the r-K ecological gradient of these organisms (i.e. an opportunistic species), while most of the other species are located at the opposite end of the spectrum

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(i.e. conservative or K-selected species) (Probert and Houdan, 2004). Our results demonstrate that *E. huxleyi* plays an important, but not dominant role in $CaCO_3$ export, with other species such as *C. leptoporus, H. carteri* or *C. pelagicus* making a larger contribution to the annual $CaCO_3$ export in the SAZ (Fig. 3). Therefore, it is of critical importance to evaluate how these other biogeochemically important coccolithophore species will respond to projected climate-induced changes in the Southern Ocean. Here, we now assess the response of large coccolithophore species to projected changes in temperature and carbonate chemistry, that have been highlighted among the most important environmental stressors expected to impact Southern Ocean coccolithophore physiological rates (Müller et al., 2015; Charalampopoulou et al., 2016; Feng et al., 2017; Trull et al., 2018).

The Southern Ocean is warming rapidly (Gille, 2002; Böning et al., 2008), largely due to the southward migration of the ACC fronts (Sokolov and Rintoul, 2009). Only between 1992 and 2007 the position of Southern Ocean fronts shifted by approximately 60 km to the south (Sokolov and Rintoul, 2009) and this trend is expected to continue throughout the next century (Rintoul et al., 2018). Therefore, it is likely that any further southward migration of ACC fronts will be coupled with an expansion of subantarctic coccolithophore species towards higher latitudes. The poleward expansion of *E. huxleyi* geographic range has already been suggested in the Southern Ocean (Cubillos et al., 2007; Winter et al., 2014; Charalampopoulou et al., 2016) and it also appears to be occurring in the North Atlantic (Rivero-Calle et al., 2015). Given the important contribution of large subantarctic coccolithophore species to $CaCO_3$ export, the expansion of their ecological niche could result in a substantial increase in $CaCO_3$ production and export in the Southern Ocean. However, this may not be the future scenario for the SAZ southeast on New Zealand, where bathymetry strongly controls the location of ocean fronts (Fernandez et al., 2014; Chiswell et al., 2015). If the fronts are bathymetrically 'locked', then the SAZ will not expand in areal extent, although the region is still predicted to undergo significant physical, biogeochemical and biological changes (Law et al., 2017) that will have likely flow-on effects on coccolithophore productivity and export (Deppeler and Davidson, 2017).

The available carbonate chemistry manipulation experiments with *C. leptoporus* have come to different conclusions. While some studies identified an increase in coccolith malformations with increasing CO_2 concentrations (Langer et al., 2006; Langer and Bode, 2011; Diner et al., 2015), another study (Fiorini et al., 2011) reported no changes in the

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calcification of *C. leptoporus* at elevated pCO_2. Interestingly, *C. leptoporus* did not experience changes in its photosynthesis rates over the tested CO_2 range in any of the aforementioned studies. The most likely explanation for the different results between the studies is a strain-specific variable responses to changing carbonate chemistry (Diner et al., 2015). Strain-specific variability in response to changing carbonate chemistry has been previously reported in other coccolithophores, such as *E. huxleyi* (Langer et al., 2009; Müller et al., 2015), and therefore it is likely that this also occurs in other species. Given the fact that Southern Ocean fronts act as barriers for species distributions and gene flows (Medlin et al., 1994; Patarnello et al., 1996; Thornhill et al., 2008; Cook et al., 2013), it is possible that the subantarctic *C. leptoporus* populations exhibit a different ecophysiology than those used in the above mentioned laboratory experiments. Prediction of the responses of *H. carteri* and *C. pelagicus* is even more challenging due to the lack of experiments testing the response of these species to changing seawater carbonate chemistry. The only available insights in the response of one of these species to ocean acidification are found in the fossil record. Both Gibbs et al. (2013) and O'Dea et al. (2014) reconstructed the evolution of *C. pelagicus* populations during the Palaeocene-Eocene Thermal Maximum (PETM), a period arguably regarded as the best geological approximation of the present rapid rise in atmospheric CO_2 levels and temperatures. These studies concluded that *C. pelagicus* most likely reduced its growth rates and calcification during this period. This limited number of studies suggest that the ongoing ocean acidification in the Southern Ocean could potentially have a negative impact on the physiological rates of *C. leptoporus* and *C. pelagicus* while the effect on *H. carteri* is unknown. Physiological response experiments (e.g. Müller et al., 2015) with Southern Ocean strains of *C. leptoporus*, *H. carteri* and *C. pelagicus* are, therefore, urgently needed to be able to quantify the effect of projected changes in oceanic conditions in the SAZ on their physiological rates and consequent effects on carbon cycling in the Southern Ocean.

Our synthesis suggests opposing influence of environmental stressors on subantarctic coccolithophore populations. Poleward migration of fronts will likely increase coccolithophore $CaCO_3$ production in the Southern Ocean, while changes in carbonate chemistry speciation will reduce growth rates of subantarctic coccolithophores. It seems possible that coccolithophores will initially expand southward as waters warm and fronts migrate, but then eventually diminish as acidification overwhelms those changes.

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Author contributions

TWT, SDN, DMD and LN planned and performed the field experiment. ARH led the coccolithophore study and performed sample processing and microscopy and image analyses. AMB and ARH performed SEM analyses. ARH and SN preformed numerical analyses. ARH wrote the paper with feedback from all authors.

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Competing interests

The authors declare no competing interests.

Data Availability

Morphometric data of major coccolithophore species generated during the current study are listed in Table 1, while species relative abundance and species fluxes (plotted in Supplement Figure 1) will be publicly available through the Australian Antarctic Data Centre (link to be included before publication).

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