



1 **Coccolithophore populations and their contribution to carbonate export during an**
2 **annual cycle in the Australian sector of the Antarctic Zone**

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13 **Abstract**

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

23 Coccolithophores are the most prolific calcium carbonate producing phytoplankton
24 group, playing an important role in Southern Ocean biogeochemical cycles. Satellite
25 imagery has revealed elevated particulate inorganic carbon concentrations near the major
26 circumpolar fronts of the Southern Ocean, that can be attributed to the coccolithophore
27 *Emiliania huxleyi*. Recent studies have suggested changes during the last decades in the
28 distribution and abundance of Southern Ocean coccolithophores. However, due to limited
29 field observations, the distribution, diversity and state of coccolithophore populations in
30 the Southern Ocean remain poorly characterized.



31 We report here on seasonal variations in the abundance and composition of
32 coccolithophore assemblages collected by two moored sediment traps deployed in the
33 deep ocean (~2000 and 3700 m) in the Australian sector of the Antarctic Zone for one
34 year in 2001-02. Additionally, seasonal changes in coccolith weights of *E. huxleyi*
35 populations were estimated using circularly polarized micrographs analysed with *C-*
36 *Calcita* software. Our findings indicate that (1) coccolithophore sinking assemblages
37 were nearly monospecific for *Emiliania huxleyi* morphotype B/C in the Antarctic Zone
38 waters in 2001-2002; (2) coccolith assemblages experienced weight and length reduction
39 during the summer months; (3) the estimated annual coccolith weight of *E. huxleyi* at both
40 sediment trap depths (2.11 ± 0.96 and 2.13 ± 0.90 pg at 2000 m and 3700 m) was
41 consistent with previous studies for morphotype B/C in other Southern Ocean settings;
42 (4) coccolithophores accounted for approximately 2-5% of the annual, deep-ocean CaCO_3
43 flux. Our results are the first annual record of coccolithophore abundance, composition
44 and degree of calcification in the Antarctic Zone. They provide a baseline against which
45 to monitor coccolithophorid responses to changes in environmental conditions expected
46 for this region in coming decades.

47

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

50

51 **Introduction**

52 The rapid increase in atmospheric CO_2 levels since the onset of the industrial
53 revolution is modifying the environmental conditions of marine ecosystems in a variety
54 of ways. The enhanced greenhouse effect, mainly driven by increased atmospheric CO_2
55 levels, is causing ocean warming (Barnett et al., 2005), shallowing of mixed layer depths
56 (Levitus et al., 2000) and changes in light penetration and nutrient supply (Bopp et al.,
57 2001; Rost and Riebesell, 2004; Sarmiento et al., 2004b; Deppeler and Davidson, 2017).
58 Moreover, the enhanced accumulation of CO_2 in the ocean is giving rise to changes in the
59 ocean carbonate system, including reduction of carbonate ion concentrations and
60 lowering of seawater pH. Most evidence suggests that the ability of many marine
61 calcifying organisms to form carbonate skeletons and shells may be reduced with
62 increasing seawater acidification including some species (but not all) of coccolithophores,
63 corals, pteropods and foraminifera (e.g. Orr et al., 2005; Moy et al., 2009; Lombard et al.,



64 2010; Beaufort et al., 2011; Andersson and Gledhill, 2013). Since phytoplankton are
65 extremely sensitive to global environmental change (Litchman et al., 2012) all predicted
66 changes in marine environmental conditions are likely to modify the abundance,
67 composition and distribution of phytoplankton communities.

68 Changes in the relative abundances of major phytoplankton functional groups are
69 likely to influence ocean biogeochemistry and ocean carbon storage, with feedbacks to
70 the rate of climate change (e.g. Boyd and Newton, 1995; Boyd et al., 1999; Falkowski et
71 al., 2004; Cermeño et al., 2008). For example, diatoms can play a prominent role in export
72 of organic matter from the surface ocean, because of their heavy siliceous frustules and
73 capacity for aggregation and rapid sinking facilitates efficient transport of organic carbon
74 (Buesseler, 1998; Smetacek, 1999), although this silica-mediated carbon export may not
75 reach the ocean interior efficiently (Francois et al., 2002; Lam and Bishop, 2007). The
76 precipitation and sinking of CaCO_3 by coccolithophores also has the potential for
77 complex contributions to carbon cycling. Carbonate precipitation removes more
78 alkalinity than dissolved inorganic carbon from surface waters, thereby acting to increase
79 pCO_2 in surface waters (the so-called carbonate counter pump, e.g. (Zeebe, 2012), but
80 ballasting by carbonates appears to increase transfer of organic carbon to the ocean
81 interior (Armstrong et al., 2002; Klaas and Archer, 2002). On seasonal timescales the
82 counter pump contribution dominates (Boyd and Trull, 2007), but more complex
83 interactions can occur over longer timescales as a result of changing extents of carbonate
84 dissolution in sediments, including the possibility that enhanced calcite dissolution in the
85 Southern Ocean contributed to lower atmospheric CO_2 levels during glacial maxima
86 (Archer and Maier-Reimer, 1994; Sigman and Boyle, 2000; Ridgwell and Zeebe, 2005).

87 The Southern Ocean is a critical component of the Earth's ocean-climate system
88 and plays a pivotal role in the global biogeochemical cycles of carbon and nutrients
89 (Sarmiento et al., 2004a; Anderson et al., 2009). Despite its relatively small area (~25%
90 of the global ocean), the Southern Ocean contains ~40% of the global ocean inventory of
91 anthropogenic CO_2 (Khaliwala et al., 2009; Takahashi et al., 2009; Frölicher et al., 2015),
92 and it exports nutrients to more northern latitudes ultimately supporting ~ 75% of the
93 ocean primary production north of 30°S (Sarmiento et al., 2004a). Model projections
94 suggest that the reduction in the saturation state of CaCO_3 will reach critical thresholds
95 sooner in cold, high-latitude ecosystems such as the Southern Ocean (Orr et al., 2005;
96 McNeil and Matear, 2008; Feely et al., 2009). Therefore, calcifying organisms living in
97 these regions will be the first to face the most severe impacts of ocean acidification.



98 In view of the rapid changes in climate and other environmental stressors presently
99 occurring in the Southern Ocean, a major challenge facing the scientific community is to
100 predict how phytoplankton communities will reorganize in response to global change. In
101 this regard, two main aspects of the distributions of coccolithophores are emerging.
102 Firstly, coccolithophores are dominantly present in the Subantarctic Southern Ocean, a
103 feature termed by Balch et al. (2011) as the “Great Calcite Belt” based on satellite
104 reflectance estimates of PIC abundances. Although importantly the PIC accumulations
105 are significantly less than those that arise in the North Atlantic, and the satellite algorithm
106 is not reliable in Antarctic waters, where it badly overestimates PIC abundances (Balch
107 et al., 2016; Trull et al., 2017). Secondly, recent studies suggest that the magnitude and
108 geographical distribution of *E. huxleyi* blooms may be experiencing significant and rapid
109 changes. Cubillos et al. (2008) and Winter et al. (2014) postulated that *E. huxleyi* has
110 expanded its ecological niche south of the Polar Front in the recent decades.
111 Contrastingly, Freeman and Lovenduski (2015) suggested an overall decline in Southern
112 Ocean PIC concentrations using satellite records between 1998 and 2014. The
113 explanation of these contrasting results may lie in the methodologies applied. While
114 shipboard surface water observations provide a highly detailed picture of a given
115 ecosystem, they are very sparse, only represent a snapshot in time, and can easily miss
116 blooms of any given species. The satellite PIC signal has the great advantage of largescale
117 and repeated coverage, but can miss subsurface populations (e.g. Winter et al., 2014) and
118 be mimicked by the spectral characteristics of other scattering sources, such as
119 microbubbles (Zhang et al., 2002), glacial flour (Balch et al., 2011) and noncalcifying
120 organisms such as *Phaeocystis antarctica* (Winter et al., 2014), a colonial
121 prymnesiophyte algae very abundant in high latitude systems of the Southern Ocean (e.g.
122 Arrigo et al., 1999; Arrigo et al., 2000). Notably the PIC algorithm performs particularly
123 poorly in Antarctic waters (Balch et al., 2016; Trull et al., 2017)

124 For these reasons, year-round field observations of areas representative of key
125 Southern Ocean regions are essential to determine the current state of coccolithophore
126 communities and to develop baselines against which long-term trends can be detected.
127 Moreover, a better understanding of coccolithophore distribution, ecology and seasonal
128 dynamics is required to improve our interpretations of the sedimentary record and our
129 models of biogeochemistry. Sediment traps are a direct method to collect data about
130 calcareous and siliceous micro and nanoplankton. Traps allow the monitoring of seasonal
131 and annual variability of plankton export, document species successions, and help to



132 determine the specific role of microplankton species in the biological and carbonate
133 pumps. The autonomous collection capacity of sediment traps is particularly useful in the
134 remote Southern Ocean, where inaccessibility and harsh working conditions prevent year-
135 round ship-based sampling.

136 We present here the first record of composition, abundance, and seasonality of
137 coccolithophore assemblages in the Antarctic Zone of the Southern Ocean, a record
138 inferred from one-year records from two deep ocean sediment traps deployed on a single
139 mooring south of Australia at the site of the SOIREE ocean iron fertilisation experiment
140 near 61°S, 140°E (Boyd et al., 2000a). Moreover, we report weight and length
141 measurements on *E. huxleyi* coccoliths, assessing the impact of seasonally varying
142 environmental parameters on *E. huxleyi* coccoliths. That provides a baseline of coccolith
143 dimensions for the populations living in this region. All the above information is needed
144 for monitoring coccolithophore responses, if any, to changing environmental conditions
145 in the Antarctic Zone south of Australia during coming decades.

146

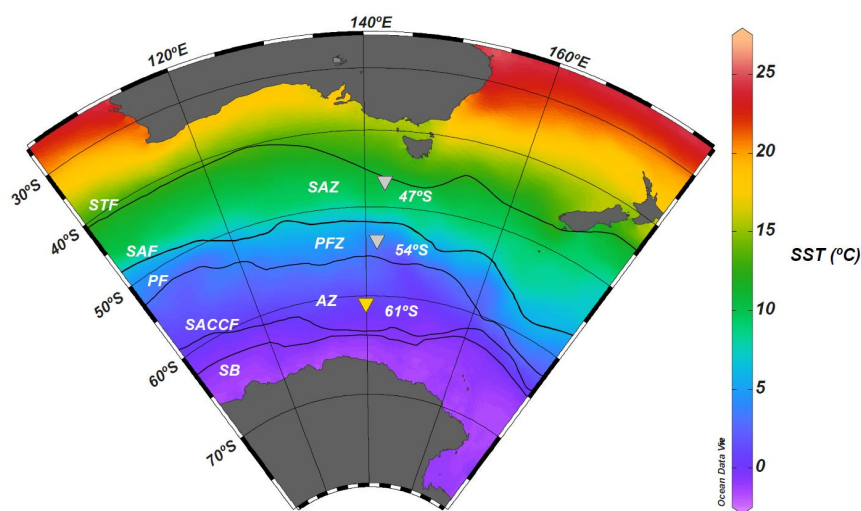
147 2. Material and Methods

148 2.1 Regional setting and oceanography

149 The southern Antarctic Zone (AZ-S; Parslow et al., 2001) is delimited at the north
150 by the southern branch of the Polar Front (PF) and at the south by the southern front of
151 the Antarctic Circumpolar Current (SAACF). Trull et al. (2001b) summarized the
152 seasonal evolution of water column properties in the study region. The intense heat loss
153 of surface waters during winter decreases Sea Surface Temperature (SST) to values <
154 1°C, resulting in strong vertical convection. Winter mixing extends to depths of about
155 120 m, replenishing the upper water column with nutrients. Chlorophyll-*a* levels during
156 winter are negligible throughout the region due to the reduced solar radiation and the
157 deep, continuous vertical mixing. During summer, increasing solar radiation warms the
158 surface ocean and a seasonal thermocline forms (Fig. 2). By late summer (March) SST
159 ranges between 2 and 3 °C. Considerable nutrient depletion associated with a moderate
160 increase in algal biomass occurs within the mixed layer. Nonetheless, due to the limited
161 sampling of the study region, the timing of the summer nutrient minimum is not well
162 constrained by the available data (Trull et al., 2001b). Silicate exhibits the strongest
163 summer draw-down of all the macronutrients, reaching ~30% of its winter values (Fig. 2;
164 Trull et al., 2001), mainly due to diatom growth and subsequent biogenic silica export to



165 the deep sea (Rigual-Hernández et al., 2015a). The low algal biomass accumulation in the
166 region is attributed to the very low iron levels (0.1-0.2 nM; Boyd et al., 2000a; Sohrin et
167 al., 2000). Mesozooplankton analysis during the SOIREE experiment by Zeldis (2001)
168 indicates that zooplankton community in the study region is dominated by copepods,
169 mainly large calanoid copepodites. Grazing pressure was low (<1% of the phytoplankton
170 standing stock removed per day) and, therefore, is thought not to play an important role
171 in the control of the micro-phytoplankton (primarily diatom) stocks, but nanoflagellate
172 grazer abundances were significant and were likely to have regulated smaller
173 phytoplankton abundances (Hall and Safi, 2001).

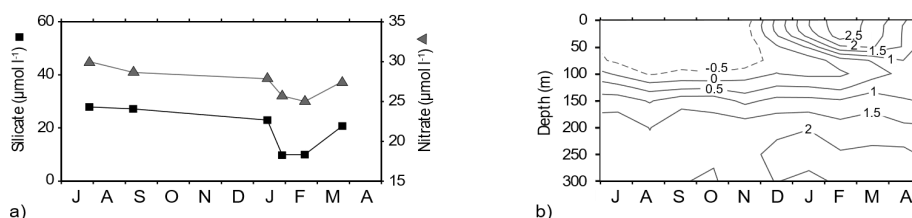


174

175 **Figure 1.** Annual mean sea surface temperature map (World Ocean Atlas; Locarnini et
176 al., 2013) of the Australian sector of the Southern Ocean, showing the position of the
177 main frontal and zonal systems (adapted from Orsi et al., 1995) and the location of the
178 61°S, 54°S and 47°S sediment trap stations (inverted triangles). Abbreviations: STF -
179 Subtropical Front, SAZ - Subantarctic Zone, SAF - Subantarctic Front, PFZ - Polar
180 Frontal Zone, PF - Polar Front, AZ - Antarctic Zone, SACCF - Southern ACC Front and
181 SB - Southern Boundary.



182



183 **Figure 2:** (a) Summary of seasonal evolution of macronutrient concentrations (silicate
184 and nitrate) at the 61°S site taken from the WOCE SR3 transects between 1993 and 1996
185 (modified from Trull et al., 2001b) (b) Seasonal variation in the vertical structure of
186 temperature ($^{\circ}\text{C}$) between June 2001 and April 2002 for the 61°S site from the World
187 Ocean Atlas 2009 (Locarnini et al., 2010).

188

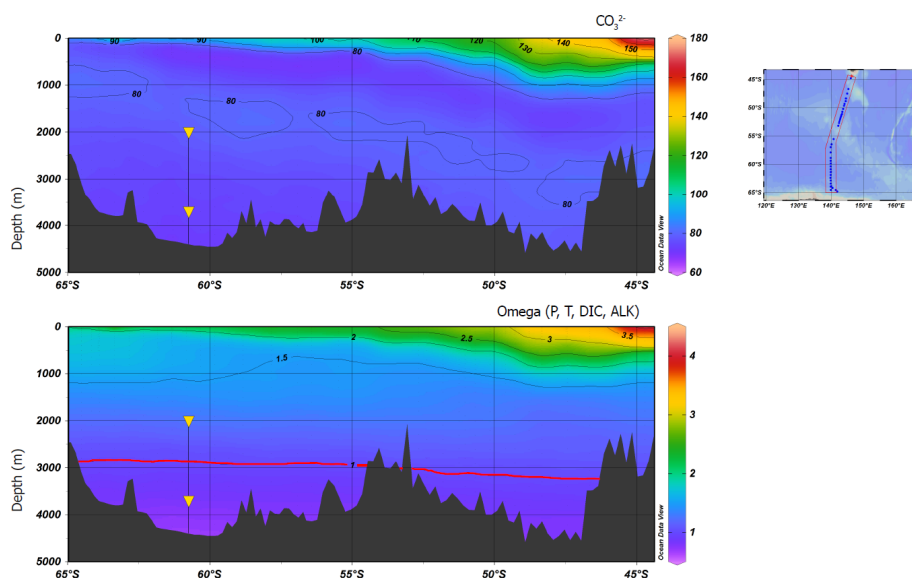
189 2.2 Water carbonate chemistry

190 Calcite solubility increases at higher pressures and lower temperatures, so that
191 dissolution increases with depth in the water column. Based on downward changes in the
192 calcite dissolution rate, two critical depth horizons can be distinguished: the calcite
193 saturation horizon (CSH) that can be defined as the depth at which the water becomes
194 undersaturated with respect to calcite (i.e. where $\Omega_{\text{calcite}} = 1$); and the CaCO_3
195 compensation depth (CCD), the depth at which the rate of calcite rain from the upper
196 water column equals the dissolution rate. Figure 3 shows carbonate concentrations [CO_3^{2-}
197] and calcite saturation (Ω_{calcite}) for the WOCE SR03 2001 transect between Antarctica
198 and Tasmania along the 140°E meridian as estimated by Bostock et al. (2011). In the AZ-
199 S waters south of Tasmania, the CSH and CCD occur at 3000 and 3700 m, respectively
200 (Fig. 3). Therefore, the location of sediment traps at the 61°S site allows for the
201 assessment of dissolution changes, if any, of coccolithophore assemblages between the
202 two critical dissolution depth horizons: the CSH and CCD. Notably, both progressive
203 uptake of anthropogenic CO_2 and increased upwelling of naturally CO_2 rich deep waters
204 over the past 20 years is leading to shallowing of these features (Pardo et al., 2017)

205



206



207 **Figure 3.** Cross section of the mooring location (only 2000m and 3700m sediment traps
208 are represented) in comparison to regional seafloor bathymetry, carbonate concentrations
209 [CO_3^{2-}] and calcite saturation (Ω_{calcite}) for WOCE transect SR03 2001 from Bostock et al.
210 (2011), who calculated them from the DIC and alkalinity in the CARINA database
211 (Tanhua et al., 2008). The location of the transects is shown on the map on the right top.
212 $\Omega_{\text{calcite}} = 1$ contour is highlighted with a red line to show the approximate depth of the
213 CSH across the transect.

214

215 2.3 Sediment trap experiment

216 As part of the SAZ collaborative research program (Trull et al., 2001c), a sediment
217 trap experiment was carried out at the 61°S site (60° 44.43'S; 139° 53.97'E) in the
218 Australian sector of the southern Antarctic Zone within the region where the Southern
219 Ocean Iron Release Experiment (SOIREE) was conducted (Boyd et al., 2000a). The 61°S
220 site is characterized by weak currents with a mean eastward geostrophic surface velocity
221 of approximately $0.03 \pm 0.02 \text{ m s}^{-1}$ (Trull et al., 2001b). The site is north of the Seasonal
222 Sea-Ice Zone (Massom et al., 2013; Rigual-Hernández et al., 2015a) and remote from any
223 known iceberg pathway (Gladstone et al., 2001).

224 The 61°S mooring was equipped with three McLane Parflux time series sediment
225 traps (Honjo and Doherty, 1988) for approximately one year (November 30, 2001 to
226 September 29, 2002, 317 days). The traps were located at approximately 1000, 2000 and



227 3700 m below the surface in a water column of 4393 m; Figure 3b). Each trap was
228 provided with 21 cups. Sampling intervals were synchronized between traps and in order
229 to resolve the seasonal flux cycle ranged from 8 days (in austral summer) to 55 days in
230 austral winter. No samples were recovered from the shallowest trap owing to equipment
231 malfunction and, therefore, only results for the 2000 and 3800 m traps are presented here.
232 Each trap was paired with an Aanderaa current meter and temperature sensors. The 250
233 ml collection cups were filled with a buffered solution of sodium tetraborate (1 g L^{-1}),
234 sodium chloride (5 g L^{-1}), strontium chloride (0.22 g L^{-1}), and mercury chloride (3 g L^{-1})
235 in unfiltered, deep seawater from the region. The two deeper traps completed their
236 collection sequence as programmed, providing continuous time-series for a year. Due to
237 the low particle fluxes during the winter, insufficient material remained for phytoplankton
238 analysis of cup 1 from the 2000 m trap and cups 1, 2, 19, 20 and 21 from the 3700 m trap
239 (Table 1).

240

241 **2.4 Sample processing and coccolithophore counting procedure**

242

243 The sediment trap cup contents were washed through a 1 mm sieve after recovery
244 and then divided into 10 aliquots using a rotary splitter (McLane, Inc.). A description of
245 the analytical procedures for estimation of geochemical fluxes is provided in Trull et al.
246 (2001a) and Rigual-Hernández et al. (2015a). One aliquot was used for siliceous and
247 calcareous micro- and nano-plankton analyses. Each fraction for plankton analysis was
248 refilled with distilled water to 40 ml, from which 10 ml was subsampled and buffered
249 with a solution of sodium carbonate and sodium hydrogen carbonate (pH 8) and kept
250 refrigerated for calcareous nannoplankton analysis. Samples for coccolithophore analysis
251 were prepared following the methodology of Flores and Sierro (1997). In short, 300 μl
252 were extracted with a micropipette and dropped onto a glass Petri dish previously filled
253 with a buffered solution and with a cover slip on its bottom. After settling 12 hours, the
254 buffer solution was removed using short strips of filter paper placed at the edge of the
255 dish. Then, the cover slip was left to dry completely and mounted on a glass slide using
256 Canada balsam. Coccoliths were identified and counted using a Nikon Eclipse 80i
257 polarized light microscope at 1000 \times magnification. A minimum of 400 coccoliths were
258 counted in each sample. Coccospheres occurred in much lower numbers than loose
259 coccoliths in these preparations. The coccolith counts were transformed into daily fluxes
260 of specimens $\text{m}^{-2} \text{d}^{-1}$ following the formula:



261

262

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

263

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

268

269 Since the sediment trap collection period was shorter than a full calendar year, an
270 estimate of the annual coccolith flux of the 2000 m trap was calculated. This estimate
271 takes into account the fact that the unsampled days occurred in winter when particle fluxes
272 were low, and were obtained by using the flux for the last winter cup (#21 in 2002) to
273 represent mean daily fluxes during the unobserved interval. Due to the lack of samples
274 corresponding to the winter 2002 for the 3700 m sediment trap record, the annualization
275 of the coccolith fluxes for this trap was made based only on the samples with available
276 data. Therefore, the annualized and annual flux data for the 3700 m trap presented in
Table 1 should be used with caution.



61_2000		Sampling period	Length	Total Mass Flux	CaCO ₃			POC		Diatoms	Coccolithophore flux	Relative abundance		
Cup	mid point	days		mg m ⁻² d ⁻¹	mg m ⁻² d ⁻¹	%	mg m ⁻² d ⁻¹	%	10 ⁶ valves m ⁻² d ⁻¹	10 ⁶ coccoliths m ⁻² d ⁻¹	<i>E. huxleyi</i>	<i>C. leptoporus</i>	Other	
1	nov. 30, 2001	8	48	14	30	0.7	1.5	2.2	9	2.5	98.8	1.2	0.0	
2	dic. 08, 2001	8	78	17	22	1.7	2.2	82	2.7	98.5	1.3	0.2		
3	dic. 16, 2001	8	326	62	19	6.9	2.1	82	2.7	98.5	1.3	0.2		
4	dic. 24, 2001	8	509	140	28	6.4	1.3	85	8.2	99.5	0.5	0.0		
5	ene. 01, 2002	8	1151	44	4	26.9	2.3	408	12.3	99.8	0.2	0.0		
6	ene. 09, 2002	8	1069	170	16	14.8	1.4	200	22.3	99.8	0.2	0.0		
7	ene. 17, 2002	8	656	60	9	11.3	1.7	159	9.2	99.3	0.7	0.0		
8	ene. 25, 2002	8	702	38	5	11.0	1.6	296	8.4	99.3	0.7	0.0		
9	feb. 02, 2002	8	666	39	6	12.0	1.8	184	5.4	98.8	1.2	0.0		
10	feb. 10, 2002	8	595	24	4	8.2	1.4	295	6.0	99.5	0.5	0.0		
11	feb. 18, 2002	8	534	20	4	6.2	1.2	149	9.8	99.0	0.5	0.5		
12	feb. 26, 2002	8	524	19	4	4.7	0.9	152	5.0	100.0	0.0	0.0		
13	mar. 06, 2002	8	586	15	3	6.9	1.2	120	6.4	99.8	0.2	0.0		
14	mar. 14, 2002	8	285	11	4	3.2	1.1	71	2.0	99.8	0.2	0.0		
15	mar. 22, 2002	8	290	7	3	3.2	1.1	66	2.0	97.6	1.0	1.5		
16	mar. 30, 2002	8	263	8	3	2.6	1.0	87	0.9	99.2	0.8	0.0		
17	abr. 08, 2002	10	264	7	3	2.2	0.8	97	1.3	98.1	1.9	0.0		
18	may. 08, 2002	50	130	5	4	1.2	1.0	47	0.8	99.8	0.2	0.0		
19	jun. 29, 2002	54	65	2	4	0.7	1.0	10	0.7	98.8	0.8	0.4		
20	ago. 22, 2002	55	56	2	4	0.8	1.5	19	0.9	99.5	0.2	0.2		
21	sep. 29, 2002	20	42	2	4	0.5	1.3	6	0.9	98.0	2.0	0.0		
Annualised values				232	17	7.4	3.3	1.4	67	2.8				
Annual flux				85 g m ⁻² y ⁻¹	6 g m ⁻² y ⁻¹		1.2 g m ⁻² y ⁻¹		24 10 ⁶ valves m ⁻² y ⁻¹	1.03 10 ¹¹ coccoliths m ⁻² y ⁻¹	99.4	0.5	0.1	

61_3700		Sampling period	Length	Total Mass Flux	CaCO ₃			POC		Diatoms	Coccolithophore flux	Relative abundance		
Cup	mid point	days		mg m ⁻² d ⁻¹	mg m ⁻² d ⁻¹	%	mg m ⁻² d ⁻¹	%	10 ⁶ valves m ⁻² d ⁻¹	10 ⁶ coccoliths m ⁻² d ⁻¹	<i>E. huxleyi</i>	<i>C. leptoporus</i>	Other	
1	nov. 30, 2001	8	38	9	23	0.4	1.1	1.1	-	-	-	-	-	
2	dic. 08, 2001	8	31	9	28	0.4	1.2	-	-	-	-	-	-	
3	dic. 16, 2001	8	99	29	30	1.4	1.4	4	1.3	-	-	-	-	
4	dic. 24, 2001	8	231	59	26	1.4	0.6	12	5.5	99.3	0.5	0.2		
5	ene. 01, 2002	8	873	87	10	17.3	2.0	118	11.6	99.8	0.2	0.0		
6	ene. 09, 2002	8	1157	154	13	19.8	1.7	479	15.9	100.0	0.0	0.0		
7	ene. 17, 2002	8	828	166	20	9.4	1.1	354	20.0	100.0	0.0	0.0		
8	ene. 25, 2002	8	490	34	7	6.4	1.3	169	11.0	99.8	0.2	0.0		
9	feb. 02, 2002	8	491	32	6	6.5	1.3	385	4.6	100.0	0.0	0.0		
10	feb. 10, 2002	8	419	19	4	6.0	1.4	281	4.2	99.8	0.2	0.0		
11	feb. 18, 2002	8	584	36	6	6.2	1.1	254	15.9	99.1	0.7	0.2		
12	feb. 26, 2002	8	581	31	5	5.2	0.9	238	12.2	100.0	0.0	0.0		
13	mar. 06, 2002	8	849	23	3	7.6	0.9	326	15.0	99.8	0.2	0.0		
14	mar. 14, 2002	8	369	18	5	3.3	0.9	44	6.6	99.2	0.8	0.0		
15	mar. 22, 2002	8	218	8	4	2.6	1.2	32	6.6	99.5	0.2	0.2		
16	mar. 30, 2002	8	258	10	4	2.5	1.0	43	6.8	99.3	0.7	0.0		
17	abr. 08, 2002	10	257	9	3	2.3	0.9	32	4.8	99.5	0.2	0.2		
18	may. 08, 2002	50	118	5	4	1.2	1.0	8	1.2	99.8	0.0	0.2		
19	jun. 29, 2002	54	0	0	4	0.0	1.0	-	-	-	-	-		
20	ago. 22, 2002	55	0	0	4	0.0	1.0	-	-	-	-	-		
21	sep. 29, 2002	20	0	0	4	0.0	1.0	-	-	-	-	-		
Annualised values				188	17	9	2.3	1.2	62	3.3				
Annual flux				69 g m ⁻² y ⁻¹	6 g m ⁻² y ⁻¹		0.9 g m ⁻² y ⁻¹		23 10 ⁶ valves m ⁻² y ⁻¹	1.20 10 ¹¹ coccoliths m ⁻² y ⁻¹	99.7	0.2	0.1	

277 **Table 1:** Daily export fluxes of total mass flux, calcium carbonate (CaCO₃), particulate
 278 organic carbon (POC), diatom valves and coccoliths registered at the 61°S site from
 279 November 2001 through October 2002. Mass fluxes listed as zero were too small to
 280 measure (<1 mg).

281

282 2.5 SEM analysis

283 As the resolution of the light microscope is insufficient to differentiate *Emiliania*
 284 *huxleyi* morphotypes, the samples of the 2000 m trap record were analysed using
 285 Scanning Electron Microscopy. Glass cover-slips were prepared following the
 286 decantation method outlined by Flores and Siero (1997). The dried cover-slips were
 287 mounted on aluminium stubs and coated in gold. A EVO HD25 SEM (Carl Zeiss) was
 288 used to determine the morphotype of *Emiliania huxleyi* coccoliths found in the samples.
 289 Due to the large abundance of diatom valves and the scarcity of coccoliths in the samples,
 290 a compromise between number of identified coccoliths and time spent had to be reached.
 291 Therefore, a target minimum of thirty *Emiliania huxleyi* coccoliths per sample were
 292 identified. The taxonomic concepts of Young and Westbroek (1991), Young et al. (2003),



293 Cubillos et al. (2007) and Hagino et al. (2011) were followed to classify the *Emiliana*
294 *huxleyi* coccoliths into morphotypes.

295

296 **2.6 C-*Calcita* analyses**

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

310 An estimated range of annual contributions of coccoliths to total CaCO₃ export
311 was calculated for the 2000 m trap record by multiplying the coccolith flux of each
312 sampling interval by the maximum and minimum standard deviations of coccolith weight
313 values measured on each sample. Then, the minimum and maximum estimates of
314 coccolith-CaCO₃ fluxes for each sampling interval (i.e. cup) were used to estimate the
315 minimum and maximum annual contribution of coccoliths to total carbonate following
316 the same procedure as for the annual coccolith fluxes.

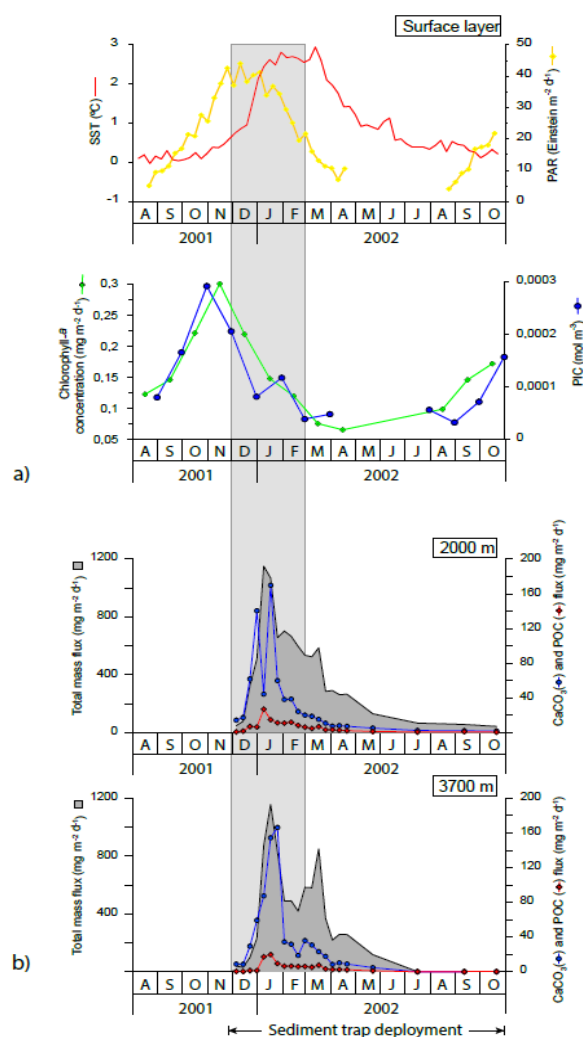
317

318 **2.7 Satellite imagery, meteorological and oceanographic data**

319 Weekly mean sea surface temperatures (SST) for the 2001-2002 interval were
320 obtained from the NOAA Optimum Interpolation Sea Surface Temperature Analysis
321 database (Reynolds et al., 2002). Seasonal SST variation range was low, with maximum
322 SSTs of 2.94 °C observed during March 2002 and minimum of 0.12 °C, in early October
323 2002. SST variations mirrored changes in the vertical structure of the water column
324 temperature profile (Fig. 4) that displayed vertical homogeneity of the water column in
325 autumn and winter and a seasonal thermocline during the austral summer (Fig. 2b).



326 Photosynthetically active radiation (PAR), monthly chlorophyll-*a* concentration
327 and particulate inorganic carbon (PIC) concentration estimates were obtained from
328 NASA's Giovanni program (Acker and Leptoukh, 2007) (Fig. 4) for the region: 130°E,
329 62.5°S, 150°E, 59.5°S. Chlorophyll-*a* concentration was low throughout the year (ranging
330 from 0.07 to 0.30 mg m⁻³) and in line with previous observations in the study region (Trull
331 et al., 2001b). Algal biomass responded rapidly to the solar radiation increase in
332 September 2001 and reached its highest levels in November 2001 (Fig. 4). Chlorophyll-
333 *a* concentration declined throughout the summer, reaching negligible values in autumn
334 and winter (i.e. from March to August 2002). Satellite-derived PIC concentration
335 exhibited a clear seasonal pattern similar to that of the chlorophyll-*a* with peak
336 concentrations in November (up to 0.003 mol m⁻³) and values below detection limit in
337 winter (Fig. 4).
338



339

340 **Figure 4:** (a) Satellite-derived SST ($^{\circ}\text{C}$), photosynthetically active radiation (Einstein m^{-2}
 341 d^{-1}), chlorophyll-*a* concentration (mg m^{-3}) and particulate inorganic carbon (PIC)
 342 concentration (mol m^{-3}) for the period November 2001 to September 2002. It is important
 343 to note that satellite PIC concentration estimates have been reported to be biased for high
 344 latitudes systems of the Southern Ocean where the satellite algorithm is thought to
 345 produce overestimates (Balch et al., 2016; Trull et al., 2017). Therefore PIC data
 346 presented here should be looked with caution. (b) Temporal variability of the total mass,
 347 calcium carbonate (CaCO_3) and particulate organic carbon (POC) the $< 1\text{mm}$ fraction at
 348 2000 and 3700 m water depth from November 2001 through to November 2002 at the
 349 61°S site (Rigual-Hernández et al., 2015a). Grey strips represent summer.



350

351 **3. Results**

352

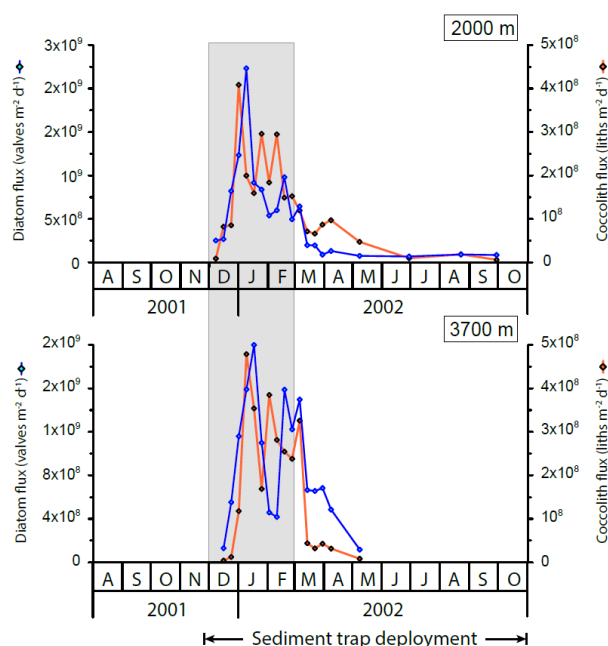
353 **3.1 Seasonal dynamics of coccolith export fluxes**

354 Coccolith fluxes showed a pronounced seasonal pattern at both sediment trap
355 depths, roughly following the chlorophyll-*a* dynamics in the surface layer with maximum
356 fluxes during the austral summer and minima during winter (Fig. 4 and 5). The summer
357 coccolith particle bloom exhibited a bimodal distribution with a major peak registered in
358 early January ($2.2 \cdot 10^9$ coccoliths $\text{m}^{-2} \text{d}^{-1}$ at 2000 m) and a secondary maximum recorded
359 in mid-February ($9.8 \cdot 10^8$ coccoliths $\text{m}^{-2} \text{d}^{-1}$). Coccolith flux was low in autumn and winter
360 (down to $7.5 \cdot 10^7$ coccoliths $\text{m}^{-2} \text{d}^{-1}$). Coccolith fluxes in the deeper trap (3700 m) followed
361 a similar pattern to that in the 2000 m trap with a delay of about one sampling interval.

362 The fluxes of all biogeochemical components were closely correlated (Table 2 in
363 Rigual-Hernández et al., 2015a). Coccolith fluxes at both traps were broadly in line with
364 biogenic particle fluxes estimated by Rigual-Hernández et al. (2015a) showing strongest
365 correlations with Biogenic silica ($R^2 = 0.86$ at 2000 m and $R^2 = 0.71$ at 3700 m), followed
366 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
367 and $R^2 = 0.41$ at 3700 m).



368 Cocolithophore sinking assemblages at the 61°S site were nearly monospecific,
369 with an overwhelming dominance of *E. huxleyi* that represented >99% of the annual
370 coccolith sinking assemblage at both trap depths. Background concentrations of the
371 species *Calcidiscus leptoporus*, *Gephyrocapsa* spp. and *Helicosphaera* spp. were also
372 registered, together representing 0.6% and 0.3% at 2000 and 3700 m, respectively, of the



373 total annual coccolith fluxes (Table 1). The numbers of coccospheres found in the samples
374 were negligible in both sediment trap records.

375 **Figure 5:** Seasonal variation of total coccolith and diatom valve flux at the 2000 and 3700
376 m sediment traps at the 61°S site. Grey strips represent summer.

377

378 3.2 SEM analyses

379

380 *Emiliania huxleyi* coccoliths correspond to morphotype B/C, having proximal
381 shields slightly wider than the distal ones and with a central area usually filled by several
382 (usually 5 to 11) flat, wide and thin tiles (see Plate 1, image a). Several coccoliths present
383 distal shields partially missing, may be due to the slender and delicate structure of the
384 laths. Distal shield measures ranged between 2 to 4,35 μm in the samples recovered from
385 the 2000 m sediment trap. It is conspicuous that most of the coccoliths display a
386 morphology which is compatible with a secondary recrystallization. Small spherules like
387 recrystallizations are present on these coccoliths, especially on the laths (Plate 1, images
388 c-f). However, some coccoliths, mostly from cup 10 (February) have no spherules



389 covering them (Plate 1, images a and b). These coccoliths present very thin slender laths
390 (usually from 20 to 26) and wider central areas than the coccoliths having spherules.

391

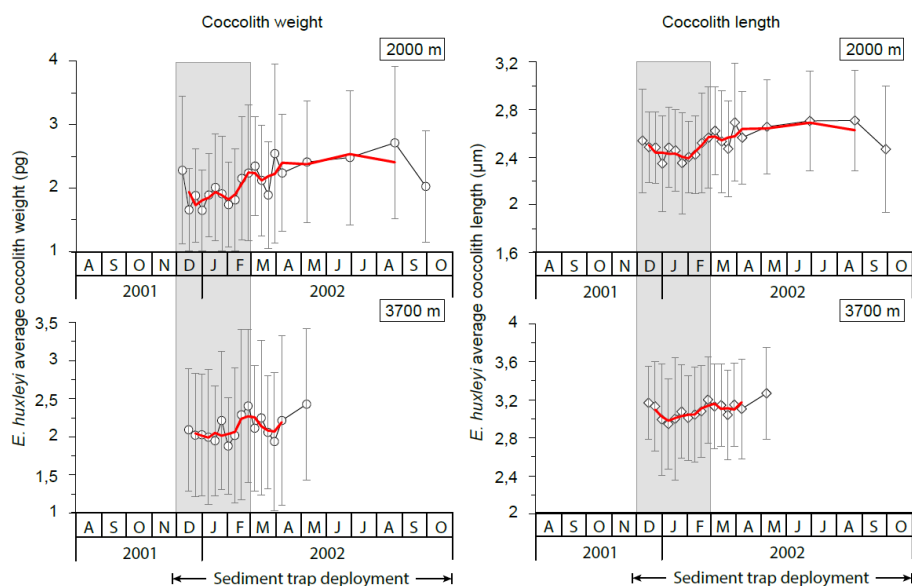
392 **3.3 Coccolith weight and length changes**

393 Average coccolith weight at both sediment trap depths exhibited a clear seasonal
394 pattern with high values (2.3 and 2.1 pg/coccolith at 2000 m and 3700 m, respectively) at
395 the onset of the coccolithophorid bloom in early spring, followed by a pronounced
396 decrease (down to 1.6 and 1.9 pg at 2000 m and 3700 m, respectively) in approximately
397 late January – early February. Average coccolith weight followed a gradual increasing
398 trend from approximately mid-February into winter, reaching values up to 2.7 pg in
399 August 2002 at 2000 m and up to 2.43 in May at 3700 m, respectively. Average annual
400 coccolith weight at the 61°S traps was 2.11 ± 0.96 and 2.13 ± 0.90 pg at 2000 m and 3700
401 m, respectively. The annual amplitude of coccolith weight was approximately 1 pg at
402 2000 m and 0.5 pg at 3700 m. The lower annual amplitude exhibited by the coccolith
403 assemblages captured at the 3700 trap is attributed to the lower sampling duration at that
404 depth over the winter season.

405 Mean coccolith length was greatest in early spring 2001 (3.1 and 3.2 μm at 2000
406 and 3700 m, respectively), followed by a decrease in early summer (down to 2.8 and 2.9
407 μm at 2000 and 3700 m, respectively) (Fig. 6). From late February coccolith length
408 increased again reaching the highest values of the record in winter 2002 (up to 3.2 and
409 3.3 μm at 2000 and 3700 m, respectively).

410 Seasonal variations of coccolith length and weight exhibited a strong correlation
411 at both depths ($R^2 = 0.84$, $n = 20$ at 2000 m; $R^2 = 0.61$, $n = 16$ at 3700m), indicating a
412 clear, dependable relationship between the two variables.

413



414

415 **Figure 6:** Mean and standard deviation of coccolith weight and length over the sediment
 416 trap deployment period at 2000 m and 3700 m at the 61°S site. The red solid line
 417 represents a 3-point running average. Grey strips represent summer.

418

419 **4. Discussion**

420 **4.1 Origin, magnitude and composition of the coccolithophores**

421 Since there is a current debate about the potential expansion of *E. huxleyi*
 422 populations south of the Polar Front during recent decades (Cubillos et al., 2007; Winter
 423 et al., 2014), it is important to evaluate the likely origins of the sinking coccolith
 424 assemblages collected at station 61°S. This assessment is particularly needed in the case
 425 of deep-moored, sediment-trap experiment because the source area of the particles
 426 collected by the traps can be as wide as hundreds of square kilometres (Buesseler et al.,
 427 2007).

428 Several lines of evidence strongly suggest that the coccolithophore fluxes
 429 registered by the traps were produced in waters of the Antarctic Zone. Firstly, the mooring
 430 was deployed in a quiescent area of the AZ-S (Trull et al., 2001b), between the stronger
 431 flows associated with the southern branch of the PF and the SACCF (Fig. 1). The
 432 relatively weak currents around the sediment trap location greatly reduce the area of likely
 433 origins of the particles intercepted by the traps, i.e. the statistical funnel (Siegel and



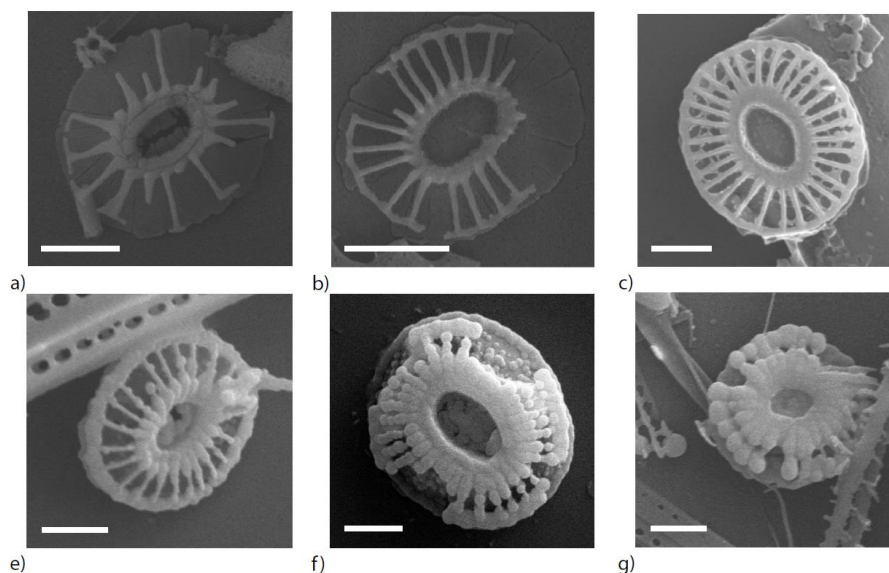
434 Deuser, 1997; Siegel et al., 2008). Moreover, the large magnitude of the coccolith export
435 fluxes at both depths, plus the long duration of the “coccolith particle bloom” (about 3
436 months), rule out the likelihood of a transient lateral transport event (e.g., transport by
437 mesoscale eddies) of a coccolithophore bloom produced in more northerly latitudes.
438 Lastly, the composition of the biogeochemical fluxes and diatom assemblages collected
439 by the traps are characteristic of AZ waters (Rigual-Hernández et al., 2015a), further
440 supporting the idea that the coccolithophores captured by the traps were produced close
441 to the site. All this clearly indicates that in 2001 *E. huxleyi* was an established member of
442 the phytoplankton communities of the Antarctic Zone to the south of Australia.

443 The annual coccolith export to the deep ocean at the 61°S site (1.03×10^{11}
444 coccoliths $\text{m}^{-2} \text{yr}^{-1}$) is one sixth that registered by Wilks et al. (2017) (6.5×10^{11} coccolith
445 $\text{m}^{-2} \text{yr}^{-1}$) in the SAZ waters (station 47°S; Fig. 1) north of the study site. The lower
446 abundance of coccolithophores at the 61°S site is most likely due to the negative effects
447 of low temperature and low light levels on coccolithophore growth (Paasche, 2002; Boyd
448 et al., 2010), but important also is the competitive advantage of diatoms over
449 coccolithophores in the silicate-rich waters of the AZ. The lower coccolithophore
450 production in the AZ is also reflected in the lower carbonate export at this site, i.e. 6 g m^{-2}
451 y^{-1} versus $10\text{-}13 \text{ g m}^{-2} \text{y}^{-1}$ at the 47°S site (Rigual-Hernández et al., 2015b; Wilks et al.,
452 2017). The non-proportional latitudinal change in coccolith and carbonate fluxes (i.e.
453 sixfold versus twofold changes, respectively) is most likely due to variations in the
454 contribution of heterotrophic calcifiers (i.e. foraminifers and pteropods) to total carbonate
455 export. There are also differences in the carbonate content per coccolith of the
456 coccolithophore species and the morphotypes of *E. huxleyi* dwelling in each zonal system.
457 Indeed, mean coccolith weight can vary up to two orders of magnitude between small
458 species such as *E. huxleyi* (2-3.5 pg) and large and heavily calcified taxa such as
459 *Coccolithus pelagicus* (~150 pg) (Giraudeau and Beaufort, 2007). Intraspecific size
460 variability is also common in most coccolithophore species, mainly due to growth
461 variations driven by different environmental factors and by genotypic variability (e.g.
462 Knappertsbusch et al., 1997; Poulton et al., 2011).

463 Recognizing the significant genetical variability they found between Southern
464 Ocean populations of morphotypes A and B/C, Cook et al. (2011) classified these
465 morphotypes as *E. huxleyi* var. *huxleyi* and *E. huxleyi* var. *aurorae*, respectively. Since
466 only morphotype B/C had been reported at and south of the Antarctic Polar Front, Cook
467 et al. (2013) concluded that the rapid drop in water temperature occurring at the Antarctic



468 Polar Front may act as an open-ocean barrier to gene flow between these the two Southern
469 Ocean *E. huxleyi* morphotypes/varieties. The monospecific coccolith assemblages of *E.*
470 *huxleyi* morphotype B/C collected by the 61°S site traps (Plate 1) are consistent with those
471 studies and supports the idea that the physiological differences in light-harvesting
472 pigments of morphotype B/C compared to other *E. huxleyi* varieties (Cook et al., 2011)
473 may represent a critical ecological advantage in the cold and low-light waters of the AZ
474 south of Australia.
475



476

477 **Plate 1:** SEM photos showcasing the different morphologies of *Emiliana huxleyi*
478 morphotype B/C coccoliths found in the sediment traps of the 61°S site. Scale bars =1
479 μm .

480

481 4.2 Seasonal dynamics of the calcareous and siliceous phytoplankton fluxes

482 The eight-day sampling resolution during spring and summer enabled us to
483 monitor the detailed temporal dynamics of phytoplankton fluxes at the 61°S site.
484 Comparison of satellite-derived PIC and Chl-*a* concentrations for the study region with
485 coccolith fluxes registered by the sediment trap suggests a time lag of about two months
486 between their surface maxima and peak coccolith fluxes registered by the shallower trap
487 (Fig. 4). Therefore, the growth phase of the *E. huxleyi* bloom probably took place between



488 October and December 2001, a period characterized by very low SSTs (0.1-0.9 °C). It
489 was before development of any significant stratification in the upper water column (Fig.
490 2b and 4a). These observations indicate that the very cold temperatures (near 0°C) and
491 strong mixing of the water column in the Antarctic waters during spring are not an
492 impediment for the development of an *E. huxleyi* bloom.

493 The onset of seasonal increase in coccolithophore arrivals in the traps occurred at
494 the same time as that of diatoms, suggesting a rapid response of both phytoplankton
495 groups to enhanced light levels. Although both coccolith and diatom fluxes exhibited a
496 pronounced and nearly parallel increase throughout December (Fig. 5), coccolith fluxes
497 peaked one week later than those of diatoms. A similar succession was observed in late
498 summer, when coccoliths displayed a secondary flux maximum, one sampling interval
499 later (8 days) than that of diatoms (Fig. 5). These observations agree with the bloom-
500 dynamics scheme proposed by Barber and Hiscock (2006) (the so-called coexistence
501 theory), in that neither phytoplankton group seems to outcompete the other during the
502 development of the bloom. Interestingly, diatoms seem to decline earlier than
503 coccolithophores, a feature often (but not always) observed in other parts of the world
504 ocean (e.g. Margalef, 1978; Holligan et al., 1983; Lochte et al., 1993; Sieracki et al., 1993;
505 Thunell et al., 1996; Balch, 2004). Indeed, a recent study of the phenological
506 characteristics of coccolithophore blooms by Hopkins et al. (2015) concluded that they
507 often follow those of diatoms in many regions, the sequencing driven by increasing
508 stabilization and/or nutrient depletion (mainly silicate and/or Fe, and possibly also
509 favoured by associated increase of carbonate saturation; Merico et al, 2004) of the surface
510 layer.

511 Lack of nutrient and mixed-layer-depth measurements during the sediment trap
512 deployment precludes us from establishing robust links between changes in physical and
513 chemical parameters in the upper water column and the observed phytoplankton
514 succession. Nonetheless, some shipboard observations of mixed-layer properties from
515 years previous to the sediment trap deployment (Fig. 2; Trull et al., 2001b) can provide
516 some insight about the mechanisms driving the phytoplankton succession. Macronutrient
517 measurements indicate that, although considerable nutrient draw-down often occurs by
518 mid-summer, the AZ-S waters never reach potentially limiting concentrations (i.e. below
519 10 µM) of silicate, nitrate or phosphate (Fig. 2a; Trull et al., 2001b). Thus, macronutrient
520 limitation was not a likely driver of the observed phytoplankton succession at the 61°S
521 site traps. Iron levels in the AZ-S, on the other hand, are low year-round (0.1-0.2 nM;



522 Boyd et al., 2000b; Sohrin et al., 2000) and exhibit clear seasonality in the AZ (Tagliabue
523 et al., 2014). So, iron availability does represent a potential driver for the observed
524 phytoplankton succession. Indeed, laboratory experiments have shown that *E. huxleyi* has
525 lower minimum Fe requirements for growth than oceanic diatoms (Brand et al., 1983;
526 Muggli and Harrison, 1997). This physiology likely provides an ecological advantage
527 over diatoms in the later stages of the spring-summer bloom, when most iron has been
528 stripped from the mixed layer.

529 In regard to the mechanism underlying the second diatom-coccolith succession
530 observed at both depths in February (Fig. 5), it is possible that a vertical mixing event –
531 as frequently reported in the AZ (e.g. Brzezinski et al., 2001) – supplied waters rich in
532 iron and macronutrients to the euphotic zone, resetting the phytoplankton succession.
533 Alternatively, the part of the *Emiliania huxleyi* populations accumulated at or just above
534 the nutricline may have increased using the iron moved by diapycnal diffusion through
535 the pycnocline (Tagliabue et al., 2014). Their deposition in February could have been
536 triggered by a drop of the light levels (Fig. 4). This second hypothesis is also consistent
537 with the following observations: (1) the presence of a sub-surface chlorophyll-a
538 maximum in the study region during spring and summer (Parslow et al., 2001; Trull et
539 al., 2001b); (2) reports of high *E. huxleyi* cell accumulations associated with the nutricline
540 in other settings of the world ocean (Beaufort et al., 2008; Henderiks et al., 2012) and (3)
541 peak annual sedimentation in late February of the diatom *Thalassiothrix antarctica*
542 (Rigual-Hernández et al., 2015a), a typical component of the “shade flora” (Kemp et al.,
543 2000; Quéguiner, 2013). Further sampling and taxonomic analysis of the vertical
544 distributions of phytoplankton in the AZ south of Australia are required to assess these
545 hypotheses.

546

547 **4.3 Seasonal variability in coccolith calcification**

548 Two main factors have been proposed as driving seasonal changes in coccolith
549 weights of *E. huxleyi*: a seasonal shift in the dominant morphotypes/ecotypes — each
550 with a different degrees of calcification (Poulton et al., 2011) — and the physiological
551 response of a given morphotype to the seasonal variation of environmental parameters
552 (e.g. Smith et al., 2012; Meier et al., 2014). SEM analysis of the 61°S sediment trap
553 samples revealed that only morphotype B/C, *sensu* Young et al. (2003), thrives in the AZ-
554 S waters south of Tasmania. That is consistent with a report by Cubillos et al. (2007) of
555 dominance of B/C south 50°S. Therefore, a seasonal shift in the dominant morphotype



556 can be ruled out in respect to changing coccolith weight. The observed decrease in
557 coccolith weight could have been caused by a change in coccolith calcification or
558 reduction in coccolith dimensions. Young and Ziveri (2000) showed that coccolith weight
559 is approximately linearly correlated to the cube of coccolith length. Applying that, the
560 decrease in length by 7.5% (a reduction to 92.5%) observed from the pre-bloom to the
561 summer bloom in the 2000 m traps (i.e. difference in minimum coccolith lengths in cups
562 5 and 8) corresponds to a coccolith weight loss of 21% ($0.925^3 \approx 0.79$). That is similar to
563 the observed weight reduction in the 2000 m trap between the pre-bloom and summer
564 bloom coccolith assemblages (16.2 - 27.6%, respectively Fig. 6). When the linear
565 correlation between coccolith length and weight proposed by Young and Ziveri (2000) is
566 also applied to the 3700 m trap coccoliths, the predicted reduction of coccolith weight
567 between the pre-bloom and bloom assemblages is 12%. That is again very similar to the
568 reduction in coccolith weight observed in the *E. huxleyi* coccoliths intercepted by the
569 3700 trap (10%). It is strongly suggested that the seasonal changes in coccolith weight at
570 the 61°S site were mainly driven by changes in coccolith length and were not due to
571 significant changes in their degrees of calcification.

572 Laboratory, mesocosm and field studies have shown that multiple environmental
573 factors including irradiance, temperature, macronutrient concentrations and iron
574 availability affect coccolith formation by *E. huxleyi* cells (e.g. Paasche, 2002; Zondervan,
575 2007; Langer and Benner, 2009; Feng et al., 2017). Since calcification in *E. huxleyi* is a
576 light-dependant process (Paasche, 1999, 2002), the observed decrease in coccolith weight
577 during summer in both traps was somewhat unexpected. Some field experiments have
578 shown that calcification in coccolithophores can occur at low light levels, or even in the
579 absence of light (e.g. van der Wal et al., 1994). However, it is often reduced compared to
580 that at higher irradiance levels (Zondervan, 2007).

581 In terms of temperature effects, Feng et al. (2017) showed that optimal
582 temperature for calcification on *E. huxleyi* cultures (morphotype A, strain NIWA1108)
583 was ~20°C, while temperatures below 10°C resulted in a dramatic reduction of
584 calcification rates and severe malformations of coccoliths, such as incomplete distal
585 shield elements. Although *E. huxleyi* morphotype B/C found at the 61°S site likely
586 represents an ecotype more tolerant to low temperatures than morphotype A (Cubillos et
587 al., 2007; Cook et al., 2013), the frequent variations in the structure of the coccoliths (e.g.
588 incomplete distal shield elements; Plate 1) captured by the traps suggest some degree of
589 low-temperature stress at the 61°S site. Despite the important role of temperature in



590 coccolithophore growth (Paasche, 2002), enhanced summer SSTs may lead to an increase
591 in coccolith calcification, a response opposite to that observed at both traps. Therefore,
592 it is unlikely that seasonal SST variations at the 61°S are behind the observed variability
593 in coccolithophore weight.

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

600 On the other hand, low iron levels have been reported to have a pronounced
601 negative effect on CaCO₃ production by *E. huxleyi* cells (Schulz et al., 2004), so it
602 represents a candidate driver of seasonal changes in coccolith weight. During winter, deep
603 water mixing re-stocks the mixed layer with iron (Tagliabue et al., 2014). As soon as light
604 levels become sufficient for photosynthesis in early spring, phytoplankton rapidly
605 develops under non-limiting concentrations of macro- and micronutrients. These
606 favourable conditions for coccolithophore growth could explain the heavier and larger
607 coccoliths registered in early December (Fig. 6). As the phytoplankton bloom develops,
608 the dissolved iron stock is rapidly depleted in the photic zone possibly resulting in a size
609 and weight reduction of coccoliths of the already substantial *E. huxleyi* populations. From
610 late summer throughout autumn, some recycling of iron in the upper water column by
611 increasing summer populations of zooplankton feeding on the bloom (Tagliabue et al.,
612 2014), coupled with increasing light levels and the continued shallowing of the mixed
613 layer, would allow coccolithophores to produce again longer and heavier coccoliths (Fig.
614 6).

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

621

622 **4.4 Effects of calcite dissolution on the sinking coccolith assemblages**



623 The similar average annual coccolith weight registered at both traps (2.5 pg at
624 2000 m to 2.6 pg at 3700 m) indicates that negligible coccolith dissolution occurs at meso-
625 and bathypelagic depths in the AZ south of Australia. That is despite the fact that
626 coccolith sinking assemblages captured by the deeper trap were exposed to potentially
627 intense dissolution after crossing the CSH (located at 3000 m in the study region; Fig. 2).
628 The similar coccolith values observed at both depths can be attributed to the formation of
629 algal and faecal aggregates in the mixed layer that include fine mineral particles (Passow
630 and De La Rocha, 2006) and provide protection against dissolution. They also facilitate
631 rapid transport of the coccoliths down through the water column. The aggregate-
632 formation hypothesis is supported by the findings of Closset et al. (2015) who estimated
633 that sinking rates at the 61°S site were, at least 213 m d⁻¹ during the productive period, a
634 value consistent with the sinking rates of algal and/or faecal aggregates (Turner, 2002;
635 Turner, 2015).

636 Despite not finding increased dissolution with water depth between 2000 and 3700
637 m, it is possible that coccoliths experienced some carbonate dissolution before reaching
638 the traps. Milliman et al. (1999) suggested that the same biological processes that
639 facilitate aggregate formation and flocculation, such as ingestion, digestion and egestion
640 by grazers, may be responsible for significant carbonate dissolution at epipelagic depths
641 (i.e. depths shallower than 800-1000 m. Indeed, the negligible amounts of coccospheres
642 found in both traps, together with the high sinking velocities, suggest that grazing could
643 have been an important influence on export. That supported by findings of Ebersbach et
644 al. (2011) in the PFZ north of 61°S. They documented that an important fraction of the
645 particles sinks from the mixed layer as faecal aggregates. However, the available data are
646 insufficient to evaluate the impact of carbonate dissolution in the upper water column.

647

648 **4.5 Calcium carbonate content of *Emiliana huxleyi* coccoliths**

649 A broad range of calcite contents for *E. huxleyi* coccoliths (1.4 - 7.0 pg) has been
650 proposed in the literature (e.g. Young and Ziveri, 2000; Beaufort, 2005; Holligan et al.,
651 2010; Poulton et al., 2011). The differences in these estimates are most likely due to
652 variability in the amount of coccolith calcite between morphotypes and to the varied
653 methodological biases associated with the three main approaches for estimating coccolith
654 mass: morphometrics, regression and birefringence. Since *E. huxleyi* morphotype B/C is
655 more weakly calcified than other morphotypes (Young and Ziveri, 2000) and considered
656 to be geographically restricted to the Southern Ocean (Cubillos et al., 2007; Cook et al.,



657 2013) we limit the comparison of our results to studies conducted only in the Southern
658 Ocean.

659 Average annual coccolith quotas at both trap depths at the 61°S site (2.11 ± 0.96
660 and 2.13 ± 0.90 pg per coccolith at 2000 m and 3700 m, respectively) are almost identical
661 to that estimated by Holligan et al. (2010) (2.20 ± 0.60 pg ; morphotype B/C) in the Scotia
662 Sea using a regression line between the number of coccoliths against PIC. Moreover, our
663 estimates are slightly higher, but with a considerable overlap in the ranges of coccolith
664 weight, than those estimated by Poulton et al (2011) for the *E. huxleyi* morphotype B/C
665 populations found in Patagonian shelf waters (1.40 ± 0.6 pg). The greater standard
666 deviation of our data is most likely due to the time periods compared. While the average
667 coccolith weight estimated for our traps reflects an integration of the annual variability in
668 coccolith weight, the shipboard observations by Poulton et al. (2011) provide a snapshot
669 of the summer coccolithophore populations, that likely exhibit lower coccolith size and,
670 thus, variability.

671 Because our coccolith weight estimates are similar to those of Poulton et al. (2011)
672 and Holligan et al. (2010), we can estimate the fractional contribution of coccolithophores
673 to total carbonate production in the AZ south of Australia. Coccolithophores account for
674 approximately 2-5% of the annual deep-ocean CaCO_3 fluxes at mesopelagic depths at the
675 61°S site. The contribution of coccolithophores to the annual CaCO_3 budget in the AZ
676 south of Australia is similar to the estimate by Salter et al. (2014) for the macronutrient-
677 rich, but iron deficient M6 site in the Indian sector of the AZ (12%) and remarkably lower
678 than an estimate for the iron-fertilized station A3 over the central Kerguelen Plateau
679 (85%; Rembauville et al., 2016). Due to the different methodologies for estimating
680 coccolithophore contributions to carbonate production, comparison of our results with
681 these other studies should be treated with caution. While only whole coccoliths were
682 counted for our calculation, therefore providing a conservative estimate, Salter et al.
683 (2014) and Rembauville et al. (2016) estimated the weight of the $< 20 \mu\text{m}$ fraction using
684 inductively coupled plasma-atomic emission spectrometry. That approach often results in
685 overestimates of the coccolith contribution to bulk carbonate content. There can be non-
686 negligible contributions of non-coccolith fragments to the fine fraction (Giraudeau and
687 Beaufort, 2007). Despite the biases associated with both methodologies, the general trend
688 appears clear: the fractional contributions of coccolithophores to bulk carbonate export
689 are lower in the iron-limited waters of the AZ compared to those in naturally iron-
690 fertilized settings of the Southern Ocean. These findings underscore the secondary role



691 of this phytoplankton group in the biological carbon pumps (both the in organic carbon
692 and carbonate counter pumps) south of the PF where non-calcifying phytoplankton -
693 mainly diatoms and *Phaeocystis* – largely control the biologically-mediated CO₂
694 exchange between the ocean and the atmosphere.

695

696 **Conclusions**

697

698 Analysis of the sediment trap materials captured at the 61°S site allowed for the
699 characterization and quantification of coccolith assemblages in Australian sector of the
700 Antarctic Zone, providing a baseline of the state of coccolithophore populations in this
701 region against which future changes can be assessed. More specifically, our study has
702 shown the following:

- 703 • Coccolithophores were a consistent member of the phytoplankton communities of the
704 Antarctic Zone south of Australia in year 2001. Coccolithophore assemblages in this
705 region are monospecific being composed almost entirely of *Emiliana huxleyi*
706 morphotype B/C. This observation supports the hypothesis that the physiological
707 differences in light-harvesting pigments of morphotype B/C (or *E. huxleyi* var.
708 *aurorae*), compared to other Southern Ocean *E. huxleyi* varieties (Cook et al., 2011),
709 may represent an ecological advantage in the cold, low-light and iron-limited
710 environment of the Antarctic Zone.
- 711 • The onset of the coccolithophore productive period took place at the same time as that
712 of diatoms, indicating that neither phytoplankton group outcompetes the other during
713 the development of the bloom. We speculate that the diatom-coccolithophore
714 succession observed during the peak phase of the productive period could result from
715 the lower minimum iron requirements for growth of *E. huxleyi*, a feature that may
716 confer a competitive advantage over diatoms.
- 717 • A decrease in coccolith weight and size during the summer months was observed at
718 both sediment trap depths. After assessing the potential influence of several
719 environmental parameters, increasing iron limitation seems to be the most likely
720 candidate to drive this change. This hypothesis, however, will need to be validated in
721 future field and laboratory culture experiments with morphotype B/C.
- 722 • The similar weight of *E. huxleyi* coccolith assemblages captured by the 2000 and 3700
723 m sediment traps indicates that negligible coccolith dissolution occurs during transit



724 through meso- and bathypelagic depths in the study region. This is most likely due to
725 a rapid transport of the coccoliths in algal and/or faecal aggregates.

- 726 • Coccolith weight values calculated for both sediment trap records using a
727 birefringence-based approach were similar to previous estimates of *E. huxleyi*
728 morphotype B/C in other Southern Ocean settings using regression and morphometric
729 methods (Holligan et al., 2010; Poulton et al., 2011, respectively).
- 730 • Coccolithophore fluxes at the 61°S site account for only 2-5% of the annual deep-
731 ocean CaCO₃ fluxes, suggesting that heterotrophic calcifiers must represent the main
732 biogenic carbonate producer in the AZ south of Australia.

733

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