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Pacific Southern Ocean coccolithophore-derived particulate inorganic carbon (PIC): A novel comparative analysis of in-situ and satellite-derived measurements

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Abstract.

Polar plankton communities are already experiencing the impact of ocean acidification and global warming. Coccolithophores are the main type of calcifying phytoplankton in the Southern Ocean (SO) and they play a key role in the carbon cycle through the production of particulate organic, and inorganic carbon (PIC). Coccolithophores account for most of the optical PIC backscattering in the sea, so remote sensing is potentially an excellent monitoring tool. However, in situ measurements in the SO are sparse in space and time due to the harsh weather conditions.

Here, we combine micropalaeontology and remote-sensing to evaluate critical discrepancies between coccolithophore and satellite-derived PIC in the Pacific SO in non-bloom conditions. Plankton samples were collected from two latitudinal transects: from New Zealand to Antarctica (December 2004-January 2005) and across the Drake Passage (February-March 2016). Coccolithophore species specific PIC estimates were compared, based on 1) Scanning Electron Microscope cocolith morphometric analyses and 2) remote sensing PIC values acquired from NASA's Ocean Color Web service. Considering that the SO is the cloudiest region on Earth (which limits the amount of satellite data available), in-situ and satellite-derived PIC datasets show very good agreement in both transects, particularly in the Subantarctic and Polar Front zones. *Emiliania huxleyi* morphogroup B substantially contributes to the sea-surface PIC content south of the Subantarctic Front in both transects, whereas *E. huxleyi* types A, A overcalcified, and other taxa (e.g. *Calcidiscus leptoporus*), only contribute to coccolithophore PIC in the northernmost stations.

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Of particular interest are strong peaks in satellite-derived PIC south of the Polar Front, which do not show up in the coccolithophore data. We suggest that the high reflectance signal from this southernmost region (which could have been initially attributed to coccolithophores) may be due to the prevalence of small opal particles or unknown highly reflective particles (such as *Phaeocystis* aggregations or suspended sediment). Our observations highlight the importance of satellite products for estimating global PIC levels, while emphasizing the critical need for validation through field samples. This work contributes to our understanding of coccolithophore PIC dynamics in the "data desert" Pacific SO, offering valuable insights for both remote sensing applications and the broader field of marine science.

1 Introduction

Coccolithophores are a major component of calcifying phytoplankton communities in the Southern Ocean (SO) (e.g. Saavedra-Pellitero et al., 2014; Saavedra-Pellitero et al., 2019; Malinverno et al., 2015; Charalampopoulou et al., 2016; Rigual Hernández et al., 2020a) and play an important and complex role in the carbon cycle through the production of particulate inorganic carbon (PIC) and particulate organic carbon (POC) (e.g. Rost and Riebesell, 2004; Salter et al., 2014). These haptophyte algae produce an external covering (coccosphere) of interlocking calcite platelets (coccoliths). This process decreases the alkalinity of surface waters, thereby reducing the uptake of CO_2 from the atmosphere into the surface ocean, thus acting in opposition to carbon sequestration by the biological carbon pump (Rost and Riebesell, 2004). Previous work has suggested that calcification during blooms of the coccolithophore *Emiliania huxleyi*, aka *Gephyrocapsa huxleyi* (Bendif et al., 2023), might alter the air-sea flux of CO_2 (e.g. Harlay et al., 2010; Shutler et al., 2013), although to date, the impact of this has mostly only been explored on a limited regional basis (e.g. Balch et al., 2016).

Since the early days of satellite-based colour measurements of the oceans, large coccolithophore blooms have been visible as highly reflective regions in satellite images (e.g. Holligan et al., 1983). Coccolithophores, and their detached coccoliths, are strongly optically active and notably affect the optical budget of the surface ocean, and can thus be seen from space using satellite remote sensing (Smyth et al., 2002; Tyrrell and Taylor, 1996). Coccolithophores are responsible for most of the optical PIC backscatter in the ocean; the other, larger PIC particles associated with foraminifera and pteropods provide negligible backscatter per unit mass and therefore have minimal optical impact (Balch et al., 1996). In general, detached coccoliths account for 10-20 % of the light backscattered from the sea under non-bloom conditions, whereas under bloom conditions it can be more than 90 % (Balch et al., 1991; Balch et al., 1999). The strong scattering properties of the coccolithophores and the associated PIC lead to enhanced reflection in the entire visible spectrum (400-700 nm). Gordon et al. (2001) and Balch et al. (2005) developed algorithms to estimate the PIC concentration in the surface layer of the water column from the radiance emanating from the water. The relationship between inherent optical properties and the resultant light fields is well understood (e.g. Mitchell et al., 2017). The difficulty lies in understanding the combined effects of different in-water constituents on the inherent optical properties, and ultimately, the underwater light fields. While there have been many advances in this area (e.g.

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Babin et al., 2003a; Babin et al., 2003b; Devred et al., 2006), there will always be some error in calculating these relationships. For example, some authors have shown that satellite ocean-colour-based PIC estimates did not match in situ (ship-based) observations and that satellite-derived PIC can be overestimated in Antarctic waters (e.g. Holligan et al., 2010; Trull et al., 2018). One potential source of error is that aquamarine waters characterized by high reflectance of light can also be caused by suspended sediment and even opal particles, such as fragments of diatom frustules (e.g. Broerse et al., 2003).

Satellite data has played a key role in showing the importance of the increasing *E. huxleyi* blooms in the world's oceans (e.g. Balch et al., 1991; Iida et al., 2002; Siegel et al., 2007; Neukermans et al., 2018; for further citations see review in Balch and Mitchell, 2023). This is relevant for monitoring changes at a global scale and to detect seasonal patterns as well as interannual variations (e.g. Smyth et al., 2004; Winter et al., 2014; Rigual-Hernández et al., 2020a) or trends, with the ultimate goal of feeding information into models for climate projections in the context of global warming and ocean acidification (e.g. Neukermans et al., 2018; Krumhardt et al., 2019). Recent concerns about climate change and ocean acidification pointed to *E. huxleyi* as a target cosmopolitan species to understand the biological response. Expansion or reduction of the biogeographic range, changes in coccolith calcification and preservation are possible responses that were observed in water and sediment samples. The high-latitude distribution of *E. huxleyi* has undergone a recent poleward expansion in both the northern (Rivero-Calle et al., 2015) and southern hemisphere (Cubillos et al., 2007; Winter et al., 2014). However, data from the SO is rather limited and there are not enough in situ measurements to unravel the complex dynamic relationships between *E. huxleyi* distribution and the frontal dynamics of the Antarctic Circumpolar Current (ACC). Significant zonal differences are shown in the relationship between coccolithophore data and ACC frontal positions across the different sectors of the SO, but no strong evidence of recent expansion on a circumpolar scale has been identified (Malinverno et al., 2015).

The band of high reflectance and elevated PIC waters observed in the SO between 30°- 60° S during Austral summer, known as "the Great Calcite Belt", has been linked to a region of increased seasonal concentration of coccolithophores (Balch et al., 2011; Balch et al., 2016). Comparisons of in situ and remote sensing measurements of PIC have been undertaken in the Atlantic and Indian sectors of the SO for coccolithophore bloom conditions (e.g. Balch et al., 2014; Balch et al., 2016; Poulton et al., 2011). Nonetheless, this type of comparison is very limited in specific areas of the globe (such as the vast Pacific sector of the SO) but also in non-bloom coccolithophore conditions. This is partially due to the fact that available coccolithophore concentrations are sparse in space and time in the SO. Most of the subpolar studies focus on coccospheres, whilst there are scarce data on free coccoliths (Mohan et al., 2008).

Changes in the calcification of *E. huxleyi* coccoliths have been shown in sub-Antarctic waters, (Cubillos et al., 2007), with different morphotypes representing the genotypic response to different water chemistry. Beaufort et al. (2011) and Horigome et al. (2014) point to an environmental control on different calcification of *E. huxleyi*. Several estimates of coccolith-PIC exist: estimation of coccolith-mass from coccolith volume calculated from coccolith-size (Young and Ziveri, 2000; Beuvier et al.,

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2019) or estimation of coccolith-calcite mass through calibration of its birefringence signal at the light microscope (Beaufort, 2005; Bollmann, 2014; Fuertes et al., 2014). Direct comparisons between coccolith-PIC and sea surface water scattering in the SO have targeted areas of coccolithophore bloom (Holligan et al., 2010; Poulton et al., 2011; Balch et al., 2014; Oliver et al., in press) but so far this has not been undertaken for non-bloom areas.

Here, we calculate the contribution of *E. huxleyi* and minor coccolithophore species to sea surface PIC along two latitudinal transects across the ACC fronts, a New Zealand transect and a Drake Passage transect, where coccosphere concentrations are below $1.3x10^5$ and $1.5x10^5$ cells/L, respectively corresponding to non-bloom to outer bloom conditions (Poulton et al., 2011). Our aims are: 1) to define the contribution of the different coccolithophore species to PIC in surface waters, 2) to assess the degree of calcification of the different *E. huxleyi* morphotypes along the transect and 3) to assess the source of high reflectance in the Antarctic Zone, south of the Southern ACC Front, along our investigated transect.

2 Oceanographic setting, phytoplanktonic communities, and study area

The SO is a high-nutrient, low-chlorophyll area in the Southern Hemisphere (e.g. De Baar et al., 1995) that connects all the main oceans through the strong and eastward flowing ACC. In the SO, there are a number of oceanographic fronts characterized by increased horizontal transport and rapid changes in water properties (Orsi et al., 1995; Klinck and Nowlin, 2001). The ACC is bounded by the Subtropical Front (STF) in the north, which separates it from the warmer and saltier waters of the subtropics, and its southern edge is marked by the Southern Boundary, which separates it from subpolar cold, silicate-rich waters (Orsi et al., 1995). Although the ACC flow is mostly driven by the westerly winds, the position of the fronts varies spatially and seasonally and it is also controlled by steep topographic features, such as oceanic plateaus or ridges (Gordon et al., 1978). South of the STF, the Subantarctic Front (SAF) separates the Subantarctic Zone (SAZ) and the Polar Frontal Zone (PFZ) (Fig. 1). The location of the SAF is indicated by a strong thermal gradient and by the rapid descent of a salinity minimum associated with the Antarctic Intermediate Water, from the surface in the PFZ (S<34 ‰) to depths greater than 300 m in the SAZ (S<34.20 ‰) (Orsi et al., 1995; Whitworth, 1980). South of the SAF, the prominent Polar Front (PF) separates the PFZ and the Antarctic Zone (AZ). The PF represents the northernmost extent of the 2°C isotherm at 200 m depth and corresponds to a 2°C gradient in sea surface temperature (Orsi et al., 1995). The Southern ACC Front is characterized by temperatures below 0°C at the minimum temperature in the sub-surface (<150 m) and above 1.8°C at the maximum temperature at depths >500 m (Orsi et al., 1995). A more detailed description of the property indicators at each SO front can be found in Orsi et al. (1995).

Coccolithophores dominate the SO phytoplankton communities, especially in the SAZ, where they reach relatively high numbers and diversity (e.g. Gravalosa et al., 2008; Saavedra-Pellitero et al., 2014; Malinverno et al., 2015; Charalampopoulou et al., 2016; Saavedra-Pellitero et al., 2019; Rigual Hernández et al., 2020a). On the other hand, diatoms and other siliceous microfossils dominate south of the PF (e.g. Saavedra-Pellitero et al., 2014; Malinverno et al., 2016; Cárdenas et al., 2018). The

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coccolithophore abundance and diversity in the Drake Passage drastically drop from north to south, with the oceanographic fronts appearing to act as ecological boundaries (Saavedra-Pellitero et al., 2019), whereas the total coccolithophore abundance is highest in the PFZ south of New Zealand (Malinverno et al., 2015). Similar marked shifts at the SAF and PF in coccolithophore number, community composition, and diversity occurring were also previously noted in other sectors of the SO (e.g. Mohan et al., 2008; Gravalosa et al., 2008; Saavedra-Pellitero et al., 2014; Balch et al., 2016; Charalampopoulou et al., 2016) and are in accordance with previous observations in both transects (Malinverno et al., 2015; Saavedra-Pellitero et al., 2019). In particular, the PF (Drake Passage) and the Southern ACC Front (New Zealand transect) constitute natural sharp barriers marked by a clear drop in the number of *E. huxleyi*, which often is the only species found in the PFZ and almost always or only occurs here as B morphogroup (type B/C and O). Furthermore, a general southwards decreasing trend in *E. huxleyi* mass, linked to a latitudinal trend from more calcified *E. huxleyi* (A morphogroup) to weakly calcified morphotypes (B morphogroup), was already recorded across the Drake Passage (Saavedra-Pellitero et al., 2019).

3 Materials and methods

3.1 Sampling considerations and morphometrics

3.1.1 The New Zealand transect

Fifty-eight surface water samples were collected from the ship's pump of the R/V Italica (at ca. 3 m water depth) from 46.81°S to 69.98°S during the XX Italian Expedition from New Zealand to Antarctica (31st December 2004- 6th January 2005). Details on sample locations, sampling volume, coccolithophore and coccolith counts can be found in Malinverno et al. (2015).

From these samples we selected a total of 13 samples for Scanning Electron Microscope (SEM, Vega Tescan at the University of Milano-Bicocca) morphometric analyses of *E. huxleyi* as being representative of the different *E. huxleyi* populations from the various biogeographic zones across the ACC (Fig. 1). For each sample, 30-50 images of *E. huxleyi* free coccoliths and coccospheres were collected as encountered during filter scanning (377 images in total, Table 1S in Supplementary Material). Distal shield length and width, tube thickness, and number and thickness of distal shield elements were manually measured using the ImageJ software (Schneider et al., 2012) in micrometers (µm) using the scalebar of the SEM images (Fig. 2).

3.1.2 The Drake Passage transect

Nineteen water samples were collected on a transect at the western end of the Drake Passage (55.44°S to 61.75°S) during Polarstern Expedition PS97 from 24th February 2016 to 5th March 2016 (Fig. 1). These selected plankton samples were obtained using a rosette sampler with 24×12 L Niskin bottles (Ocean Test Equipment Inc.) attached to a CTD Seabird

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SBE911plus device (Lamy, 2016). The bottles were fired by a SBE32 carousel and just the shallowest samples, from 5, 10 and 20 m water depth, were considered in this work.

A total of 203 images of *E. huxleyi* coccospheres were taken from the samples in the Drake Passage while scanning the filters within the SEM (Table 2S in Supplementary Material). Coccoliths were measured using the Coccobiom2 macro (Young, 2015) in the software programme Fiji, an image processing package based on ImageJ (Schindelin et al., 2012). Measurements were made in micrometers (µm), based on the scale bar of the SEM images. Note that they were scaled to 100% with a Coccobiom2 SEM calibration of 1.09 and the specific magnification.

3.2 Coccolithophore PIC estimates

Species-specific coccolith-PIC (in pMol) was estimated following the volume calculation of Young and Ziveri (2000)

$$PIC = (2.7 \times Ks \times L^3) \div 100 \qquad \text{[equation 1]}$$

where:
2.7 = density of calcite;
Ks = species-specific shape factors, as provided by Young and Ziveri (2000) and modified for *E. huxleyi* according to the degree of calcification obtained for each morphotype (see Table 1);
L = coccolith mean length from measurements in the case of *E. huxleyi*. For minor species, we considered the averaged coccolith length provided by Young and Ziveri (2000).
100 = molecular weight of calcite

Measurements of the distal shield diameters of *Calcidiscus leptoporus* the second most abundant species, that is significantly larger than *E. huxleyi*, were made on different samples offshore New Zealand, corresponding to the highest abundances of this taxa (Table 1 and Table 3S in Supplementary Material). The coccolith-PIC contribution for each sample was calculated by applying the obtained species-specific calcite quota to the abundances of species and morphotype (i.e., coccospheres/L) from Malinverno et al. (2015) and Saavedra-Pellitero et al. (2019). In the New Zealand transect, the single / double coccolith layers were considered in the estimates (Table 1S in Supplementary Material), while in the Drake Passage transect, where this information was not available, an average was considered based on own observations (Table 1 and Table 4S in Supplementary Material).
We also calculated the relative tube width' in *E. huxleyi* as a size-independent index to estimate the degree of calcification in this taxa following a modification of the index proposed by Young et al. (2014) (Fig. 2):

$$Relative\ tube\ width' = (2 \times tube\ width) \div coccolith\ length \qquad \text{[equation 2]}$$

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3.3 Satellite-derived PIC data

Daily, 8-daily and monthly L-3 MODIS-derived PIC values (mol m^{-3}) (NASA Ocean Biology Processing Group, 2022, 2023a) with a spatial resolution of 4 km, covering both the sampling period and the geographical extent of each transect, were acquired from NASA's Ocean Color Web service as individual netCDF files for each timestamp. The date ranges of each PIC period are summarised in Table 2.

Daily, 8-daily (going forward, referred to as weekly) and monthly values of PIC were extracted for all sampling locations in both transects (Figures 1S and 2S in Supplementary Material). Processing of the PIC data was done with a Python script that used NetCDF4 and other libraries commonly used for data analysis such as Pandas. The PIC data processing was done in JASMIN Notebook Service (https://jasmin.ac.uk/).

One limitation of optical remote sensing products is that they cannot provide a reliable signal under cloudy conditions. Combined with other conditions that interfere with the detection of water-leaving radiances (NASA Ocean Biology Processing Group, 2023a), daily PIC grids have a high number of missed observations, or gaps, which prevent us from getting daily satellite-derived PIC values of the sampling dates for most sample locations in both transects. Based on this fact, weekly and monthly satellite-derived PIC values were therefore used in the analysis.

3.4 Statistical analysis

A principal component analysis (PCA) was performed on the *E. huxleyi* morphometric dataset (including samples from both transects) using PAST™ software version 4.13 (Hammer et al., 2001). The morphometric data considered here were: coccolith length, coccolith width (minor), distal shield element (or T-element) width, number of T-elements and tube width measurements. The main aim of the PCA is to find hypothetical components that account for the maximum variance in the multivariate dataset (Davis, 1986; Legendre and Legendre, 1998; Harper, 1999). These components are linear combinations of the original variables (Hammer et al., 2001). The first Principal Component explains the highest variance, followed by the subsequent components which explain the next largest variances. All the measurements were log-transformed prior to the PCA to avoid skewness.

4 Results

4.1 Coccolith-PIC versus satellite-derived PIC

Emiliania huxleyi is clearly the dominant species in the coccolithophore assemblage of the Pacific SO (Malinverno et al., 2015; Saavedra-Pellitero et al., 2019) with abundances of $1.4 * 10^5$ coccospheres/L right south of the SAF in the New Zealand transect

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and 1.5* 10^5 coccospheres/L in the Chilean SAZ (PS97/034-2) and it is also the main contributor to sea-surface PIC (Figs. 3 and 4). *Calcidiscus leptoporus* (mostly *Calcidiscus leptoporus* ssp. *leptoporus*) is the second most abundant species and makes significant contributions to the coccolithophore PIC at certain locations (up to 1.4* 10^4 cells/L in the New Zealand transect and 1.4* 10^3 cells/L in the Drake Passage, Figs. 3 and 4) (Malinverno et al., 2015; Saavedra-Pellitero et al., 2019). *Calcidiscus leptoporus* generally represents on average 13.4% of the total coccolithophore PIC in the New Zealand transect and 3.8% in the Drake Passage, but can occasionally reach maximum PIC contributions of 57.5% (at the TR007 station, in the SAZ) and of 23.3% (at the PS97/038-1 in the PFZ) (Fig. 5).

A minor contribution from less abundant or rare species occurs just in the northern SAZ of both transects, where diversity is higher (for species list see Malinverno et al., 2015; Saavedra-Pellitero et al., 2019), with a poleward decreasing trend and almost no contribution south of the SAF (Fig. 5). *Emiliania huxleyi* is solely responsible for almost all of the coccolith-PIC in the PFZ, but its contribution decreases at the PF (in the Drake Passage) or Southern ACC Front (in the New Zealand transect, ca. 63.7°S) and south of it.

Weekly and monthly MODIS-derived PIC at the sampling locations consistently overestimate PIC values by a factor of 2 to 5 with respect to in-situ values calculated from coccolith mass in the New Zealand transect (Fig. 3) and by occasionally an order of magnitude in the Drake Passage (Fig. 4). Apart from the discrepancy in absolute values (and considering that there are already inherent variations in the weekly compared to the monthly PIC estimates), there is a relatively good agreement in the latitudinal satellite and coccolith-PIC trends in the SAZ and PFZ.

However at the PF (ca. 60°S in the Drake Passage) or to the south of it (ca. 62.5°S in the New Zealand transect), the satellite- and the coccolith-PIC estimates became decoupled, with high reflectance but no coccolithophores in the AZ.

4.2 Morphometries and mass estimates of *Emiliania huxleyi*

Emiliania huxleyi consist of different morphotypes that show a different and partly overlapping distribution along both latitudinal transects (Malinverno et al., 2015; Saavedra-Pellitero et al., 2019). Type A is mostly restricted to the northern SAZ, but it is occasionally present in the PFZ in the Drake Passage (Figs. 3, 4) and it is the only type within morphogroup A in this study. Morphotypes belonging to the *E. huxleyi* morphogroup B (which includes morphotypes B, B/C, C and O) are present in the SAZ and the PFZ, but they disappear south of the PF.

Morphometric measurements on coccoliths of *E. huxleyi* from the selected samples show that the length of types A, B/C-C and O overlap in both transects (Fig. 6). In the Drake Passage, coccolith lengths range from 2.86 to 3.96 µm, with a mean average of 3.49 µm for A type (including normal and overcalcified specimens), 2.87 to 4.11 µm for B type, 2.2 to 3.98 µm for B/C-C types, 2.42 to 4.16 µm for O type, and an average of 2.98 µm for morphogroup B. In the New Zealand transect,

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maximum axes range from 2.25 to 3.59 µm, with an average of 2.95 µm for *E. huxleyi* A type, 1.95 to 3.62 µm for B/C-C types, 2.07 to 4.14 µm for O type, and an average of 2.87 µm for morphogroup B.

Figure 5 provides a latitudinal overview of morphometric data compared to the (averaged) degree of calcification. In the New Zealand transect there are no significant changes in coccolith lengths except for a wide scatter of values characterizing the size class distribution of each sample. This feature reflects the large variability in coccoliths size as observed on coccoliths from a single coccosphere (Fig. 2e). However, in the Drake Passage transect, *E. huxleyi* coccoliths are notably larger offshore of Chile (Fig. 6a).

Emiliania huxleyi masses calculated in the New Zealand transect range from 0.61 to 2.93 pg with an average of 1.47 pg per coccolith belonging to the morphogroup A, and from 0.36 to 2.86 pg, with an average of 1.15 pg per placolith from morphogroup B (Fig. 3c). In the Drake Passage the masses per coccolith for morphogroup A are almost double than in the New Zealand transect, varying between 1.4 pg and 6.3 pg, with an average of 3 pg. The placolith masses in morphogroup B range from 0.6 to 3.7 pg with a mean of 1.4 pg across the Drake Passage (Fig. 4c). Note that this data is shown in Figures 3 and 4, but the coccolith-PIC was calculated in this work using equation 1 and the average lengths mentioned in Table 1. The coccolith-PIC estimated for *E. huxleyi* are generally lower in the New Zealand transect (average morphogroup A: 0.021 pmol and B: 0.013 pmol) than in the in the Drake Passage (average morphogroup A: 0.034 pmol and B: 0.014 pmol).

We observed that some coccoliths are clearly overcalcified (see Figure 5 for an example), with a thick inner tube (up to 0.7 µm in sample PS97/018-1) that extends into the central area. Specimens belonging to the morphogroup A show a higher degree of calcification than those belonging to morphogroup B, resulting not only in a thicker inner tube but also in thicker distal shield T elements. The overcalcified coccospheres co-occur with normally-calcified ones but they are restricted to the northernmost samples (Fig. 6). The relative tube width' (an index for calcification; Young et al., 2014), calculated using equation 2, varies from 0.08 to 0.22 in morphogroup A and from 0.06 to 0.18 in B for the New Zealand transect. Values are higher in the Drake Passage, ranging from 0.04 to 0.41 for *E. huxleyi* morphogroup A, and from 0.02 to 0.19 for morphogroup B.

The variation in the degree of calcification (calculated using equation 2) is higher within each sample than along the New Zealand transect (Fig. 3b), although overcalcified specimens (relative tube width' >0.22), typically represented by type A, occur in the northernmost samples (Fig. 6b). Averaged relative tube width' shows increased values not only in the SAZ offshore New Zealand, but also around 54 °S and in the PFZ (Fig 6b), which points to a certain degree of variation in the calcification within morphotypes BC/C and O. A more marked N-S decrease in the relative tube width' values is observed in the Drake Passage with notably higher values offshore of Chile (Figs. 3b and 6a), where relatively large and heavily calcified type A coccospheres are present.

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To better characterize *E. huxleyi* morphotypes in the study area we performed a PCA of the log-transformed morphometric data. The first component, related to the tube width, explains 79.9% of the variance, and the second, related to length as well as width (and to a lesser extent distal shield element width and number of T-elements), accounts for 11.5% (Fig. 7).

5. Discussion

5.1 PIC variability in the SAZ and PFZ

In the studied transects, the calculated coccolith-PIC and the satellite-derived PIC trends show quite good agreement in the SAZ and PFZ, but there is a strong discrepancy in the AZ. Here we discuss potential factors influencing water-leaving radiance in each of these areas.

The fact that satellite-derived data show consistently higher numbers than coccolith-PICs (Figs. 3 and 4) could be either due to an overestimation of the satellite PIC values or to an underestimation of the species specific coccolith-PIC (i.e., coccolith-calcite quotas). Additionally, the fact that the difference between satellite PICs and in situ values in the Drake Passage transect is larger than in the New Zealand transect can be in part attributed to the fact that detached coccoliths (on top of coccospheres) were only considered in the estimates for the New Zealand transect. Part of the disparity can be attributed to the different spatial scale, considering the image pixel area vs. the discrete sampling. However, the fact that the overall trends are the same in this region and that in situ measurements agree with the remote sensing data, could suggest that there is a satellite bias linked to the algorithm (which could be easily adjusted for the region north of the SO). We are aware that the MODIS/Aqua Ocean Color was re-processed in 2022 (NASA Ocean Biology Processing Group, 2023a) to incorporate updates in instrument calibration, new ancillary sources and algorithm improvements but the validation of the PIC measurements is based just on a very low number of in-situ measurements compared to other products (e.g., 1347 in situ measurements for Chlorophyll a and just 42 for PIC, all of them in the Atlantic Ocean; NASA Ocean Biology Processing Group, 2023c, 2023b) .

The SAZ and PFZ are generally characterized by moderate coccolithophore concentration with limited contribution from other biogenic particles (Figs. 3 and 4) (Malinverno et al., 2016; Saavedra-Pellitero et al., 2019). Given that *E. huxleyi* is the dominant species in both transects and the most important contributor to pelagic PIC, we focused on its abundance, morphotype distribution and calcite weight. Coccolith-PIC calculated in this study for *E. huxleyi* are generally in agreement with the calcite content per coccolith obtained by Poulton et al. (2011) along the Patagonian Shelf and by Rigual Hernández et al. (2020a) in the Australian & New Zealand sectors of the SO (see Tables 1 in those papers). Our PIC *E. huxleyi* estimates seem generally higher than the estimates by Charalampopoulou et al. (2016) off southern Chile (0.015 pMol per coccolith) and across the rest of Drake Passage (< 0.009 pMol).

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On the other hand, our values are slightly lower than those obtained through the birefringence method SYRACO, an automated system of coccolith recognition (SYstème de Reconnaissance Automatique de COccolithes) in the same latitudinal range (e.g. Beaufort et al., 2011) and notably lower than Saavedra-Pellitero et al. (2019) across the Drake Passage using circularly polarised light plus the C-Calcita software developed by Fuertes et al. (2014) (Fig. 8a). In order to explore this difference, we calculated PICs in the Drake Passage using Saavedra-Pellitero et al. (2019) mass estimates for the same samples, considering an average mass of 4.64 pmol for *E. huxleyi* (n = 796, standard deviation = 2.53) but without distinguishing different morphotypes (Fig. 8b). The mass per coccolith of *E. huxleyi* using C-Calcita in the Drake Passage is 2.8 times higher than in this work (mean of 1.66 pg in this work). We then used this factor to calculate the potential contribution of the rest of the coccolithophore taxa (see Figure 8). Both N-S coccolith mass and PIC trends mirror each other, but the C-Calcita-derived PICs tend to overestimate satellite values, except in a couple of locations. This can be attributed to the calibration of the coccolith thickness within the software C-Calcita, which has been improved in recent years with the use of a calcite wedge instead of a calcareous spine (e.g. Guitián et al., 2022). The differences in PIC could also be due to the fact that we are comparing in situ values to monthly averages, and also smoothing data by considering averaged values when estimating coccolith-PICs (especially length and number of coccoliths per coccosphere). In addition, sampling at slightly different times of the year may also have an influence on the PIC values determined (Rigual Hernández et al., 2018; Rigual-Hernández et al., 2020a, b). An increase in coccolith weight and size within morphotype B/C from December to August (but also from December to March) was observed at a sediment trap station deployed at 61°S in the Australian sector of the SO south of Tasmania (Rigual Hernández et al., 2018). Variations in light intensity in the mixed layer and increasing iron limitation were seen as the most likely drivers of this change. This could explain differences in the carbonate masses of different transects.

Our measurements on selected samples along the New Zealand transect, and across the Drake Passage show: (a) differences in calcification among the various *E. huxleyi* morphotypes, being very evident in type A (Figs. 3 b-c, 4 b-c, 5, and 7), (b) a wide scatter of relative tube width' within morphotypes and within each sample, especially marked in the New Zealand transect (Figs. 4b, 7) and (c) a slight decreasing trend in coccolith size and degree of calcification across the Drake Passage (Figs. 3b, 5a), which is not observed in the New Zealand transect. This suggests that environmental forcing does not significantly impact the degree of calcification but it clearly controls the distribution of *E. huxleyi* morphotypes (which are genetically-based, Bendif et al., 2023) and thus indirectly impacts on the coccolith mass variation. This could also explain the southwards decreasing trend in calcification in the Drake Passage due to the fact that the relatively large and heavily calcified type A coccospheres are present in the northern SAZ. The PCA performed on the *E. huxleyi* morphometric dataset shows that those heavily calcified type A coccospheres occupy a relatively restricted ecological niche offshore of Chile (Fig. 7).

In general, we find a different pattern than Balch et al. (2014), who determined coccolith-quotas in the center of a coccolithophore bloom in the Patagonian Shelf (Atlantic Ocean) ranging from 0.008 to 0.017 pg per coccolith by comparing automated coccolith-counts with in-situ PIC. In the context of other observations, the coccolith quotas calculated by Balch et

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al. (2014) are relatively low and show a much greater variation within a limited region. Given the above evidence in two different transects of the SO and sampling 11 years apart, we assume that with our approach, our coccolith-PIC calculations do not underestimate actual sea surface PIC concentration. We attribute the discrepancy between the coccolithophore in-situ and satellite-derived PIC to overestimation of the algorithm in the SO, due to the limited number of data points used for the calibration.

5.2 Assessing potential biases in PIC estimates for the AZ

In the AZ (south of about 62.5°S in the New Zealand transect and about 60°S in the Drake Passage), high reflectance is detected by remote sensing but it is not associated with a coccolithophore bloom (Figs. 3 and 4). Concentration of *E. huxleyi*, which show maximum numbers in the PFZ at the New Zealand transect and moderate values in the Drake Passage, drops southward of this location (Malinverno et al., 2016), at the Southern ACC Front and the PF.

Satellite data show the different impact of ACC fronts on the distribution of *E. huxleyi* (Holligan et al., 2010): in the Drake Passage, where the fronts are strictly constrained by topography, *E. huxleyi* is bounded by the PF to the south (Saavedra-Pellitero et al., 2019), while in the eastern Scotia Sea, where the ACC fronts are broadly separated, *E. huxleyi* spreads between the PF and the Southern ACC Front (Holligan et al., 2010; Poulton et al., 2011; Poulton et al., 2013). This pattern also emerges from the compilation by Malinverno et al. (2016), which shows that the Southern ACC Front marks the southern boundary in different ocean sectors.

Occasional occurrences of *E. huxleyi* south of the Southern ACC Front have been documented south of Tasmania and in the Weddell sea in certain years by conventional micropalaeontological observations (e.g. Winter et al., 1999; Cubillos et al., 2007) as well as in the Australian sector of the SO and in the Scotia Sea using surface reflectance data only (Holligan et al., 2010; Winter et al., 2014). However, in the present work, *E. huxleyi* is constrained by the Southern ACC Front corresponding to a sea surface temperature of 1°C in the New Zealand transect.

The magnitude and spectral characteristics of water-leaving radiance detected by satellites are influenced by the inherent properties of the optically active constituents. These include: (1) light scattering by PIC, other biogenic particles or lithogenic material (e.g. Bi et al., 2023) as well as (2) light absorption by phytoplankton biomass (i.e., chlorophyll-a concentration) and dissolved organic matter (e.g. Reynolds et al., 2001; Ferreira et al., 2009). The strong correlation between high values of water-leaving radiance and high *E. huxleyi* PIC concentrations has been successfully proved in bloom areas (e.g. Gordon et al., 1988; Balch et al., 2005; Holligan et al., 2010; Balch et al., 2011; Balch et al., 2014; Balch and Mitchell, 2023; Oliver et al., in press). However, not all bright waters are caused by *E. huxleyi* blooms, as shown by Broerse et al. (2003) in the Bering Sea, Balch et al. (2007) in the Gulf of Maine, and Daniels et al. (2012) in the Bay of Biscay. Suspended particles, which include either

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reworked coccoliths, lithogenic material or empty diatom frustules, could be responsible for high values of water-leaving radiance, at least in nearshore regions (Broerse et al., 2003; Balch and Mitchell, 2023).

The occurrence of bright waters along the studied transects should theoretically be constrained by the position of the PF/ Southern ACC Front. Malinverno et al. (2015; 2016) showed a significant shift in the community composition from carbonate to silica-dominated microfossils in the New Zealand transect at the Southern ACC Front. Coccolithophores disappear south of the Southern ACC Front, and the composition of the siliceous phytoplankton changes from a dominance of large diatoms (*Fragilariopsis kerguelensis*) in the north to a dominance of small diatoms (such as the cold adapted *Fragilariopsis cylindrus*) in the south, with a notable increase in spiny silicoflagellates (e.g., *Stephanocha speculum* var. *coronata*) and small siliceous plankton (Parmales, Archaeomonads) (Malinverno et al., 2016) (Fig. 9). The diatoms present have not yet been studied in the exact same water samples collected during PS97 Expedition. However, the abundance of subfossil diatoms in surface sediments in the Drake Passage shows an increase south of the PF, along with an increase in the relative abundance of siliciclastics and in biogenic opal (Cárdenas et al., 2018). *Fragilariopsis kerguelensis* appears to dominate up to the Southern ACC Front, and *F. cylindrus* is found south of this front, in colder waters of the Drake Passage (Cárdenas et al., 2018). Although opal particles have a much lower refractive index than calcite (Balch, 2009; Costello et al., 1995), we suggest that the high abundance of small opal particles observed could explain the observed high scattering of these waters at least in the New Zealand transect (Figs. 1, 3, 4). Alternative sources of high reflectance in the SO considered by other authors include microbubbles (mostly during storms), floating loose ice or high concentrations of other particulate matter such as glacial flour (especially close to the Antarctic continent) or *Phaeocystis* blooms (Balch et al., 2011; Balch, 2018; Balch and Mitchell, 2023).

5.3 *Emiliania huxleyi* morphotypes

The PCA performed on the *E. huxleyi* morphometric dataset in particular reveals a Type A overcalcified morphotype that is highly distinct from the other morphotypes (Fig. 6). This morphotype has also been previously observed in the coastal waters of the eastern South Pacific and in the open ocean (Beaufort et al., 2011; Von Dassow et al., 2018; Saavedra-Pellitero et al., 2019). However, it should be noted that type A overcalcified in this work includes the moderately calcified, robustly calcified and extremely heavily calcified A morphotypes described by Diaz-Rosas et al. (2021). Coccospheres of *E. huxleyi* classified by Diaz-Rosas et al. (2021) as extremely heavily calcified R/hyper-calcified and/or A-CC morphotypes (with complete overgrowth of the coccolith central area but without fusion of distal shield elements) occasionally occurred offshore of Chile in samples closest to the coastline (see an example in Figure 6). In the Southern Hemisphere, these extremely heavily calcified morphotypes were only previously observed at the Pacific border of southern Patagonia (in the Archipelago Madre de Dios Fjord area) and in the Northern Hemisphere, in Norwegian fjords (e.g. Young et al., 2014). Diaz-Rosas et al. (2021) suggested that the R/hyper-calcified morphotype has a marginal ecological niche preference compared to moderately calcified types A and A-CC. Therefore the few specimens of *E. huxleyi* type A overcalcified (i.e. heavily calcified looking in between the

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R/hyper-calcified and/or A-CC morphotypes by Diaz-Rosas et al. (2021)) observed in this work, and by Saavedra-Pellitero et al. (2019) in the Drake Passage, could be attributed to different niches overlapping offshore of Chile.

The normal type A specimens show a moderate range of variation in tube width, comparable to type O, but smaller than B, B/C-C, with type C having the thinnest tube width. The distal shield element width and the number of T-elements of the different specimens are closely related to the length and width measured (Fig. 7) as they are all indicators of coccolith size. There is broader variation in coccolith size (length and width) within morphogroup B compared to morphogroup A, which is more restricted. Suchéras-Marx et al (2022) pointed out that *E. huxleyi* coccolith size is limited by the cell diameter because heterococcoliths are produced intracellularly and are extruded later on. Interestingly, specimens of *E. huxleyi* type A in the New Zealand transect are notably smaller than those offshore of Chile, which we link to local adaptations, seasonality and even ecological interactions such as predation (e.g. Monteiro et al., 2016; Hansen et al., 1996).

However, the coccolithophore assemblages in the PFZ and south of it are monospecific, which is also known from other areas of the SO (e.g. Charalampopoulou et al., 2016), and consist almost entirely of *E. huxleyi* morphogroup B. The mean placolith length of *E. huxleyi* morphogroup B (including types B, B/C-C, and O) in both transects is very similar (Drake Passage: 2.98 µm, New Zealand: 2.87 µm) and agrees well with the corresponding B/C measurements of Charalampopoulou et al. (2016) in samples retrieved in 2009 in the Drake Passage (2.8 µm). Still, our averaged values are slightly lower than the mean length estimated by Poulton et al. (2011) on the Patagonian Shelf (3.25±0.40 µm). This could be due to the fact that Poulton et al. (2011) did not distinguish between types B and O (i.e. they were merged into B/C), which are typically larger coccoliths than B/C (Fig. 6) and could have contributed to increase the averaged length. The length range for types B/C-C (Drake Passage: 2.2 to 3.98 µm, New Zealand: 1.95 to 3.62 µm) agrees quite well with the range reported by Cook et al. (2011) for cultured B/C strains (2.65 to 4.80 µm) and is in the range of sizes presented by Charalampopoulou et al. (2016) for the Drake Passage (1.8 to 5.5 µm). The fact that we record lower values is simply a matter of taxonomical considerations regarding the overlapping morphotypes B, B/C, C and O, visually represented in Figure 6.

The different taxonomic considerations of *E. huxleyi* by various studies make it difficult to compare and combine data, especially in light of recent advances in the field. Given the dominance of this taxa in the SO, a key area for global warming and ocean acidification studies, the efforts of the scientific nannofloral community should focus on a more uniform classification of *E. huxleyi* morphotypes. However, differentiation and recognition of the various morphotypes plays only a minor role in the calculation of the total coccolithophorid PIC, as observed in other areas of the SO (e.g. Rigual Hernández et al., 2020a, b). The changes in masses within the B morphotype (with types B/C-C, C, O) in the two transects are negligible in the PIC calculation, while a differentiation into morphogroups A and B has an influence on the calculation of the PIC. However, specimens of *E. huxleyi* belonging to morphogroup A only occur in the northern areas of both transects, where they play a role together with the PIC input from other massive species such as *C. leptoporus* (Fig. 5). Overall, the changes in total coccolith-

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PIC in the study area are caused by the abundance and occurrence within the entire coccolithophore community. The relative contribution of the different *E. huxleyi* morphogroups to the coccolith-PIC in the SO deserves further exploration in light of the rapid development of remote sensing algorithms and recent evolution of machine learning approaches for PIC estimates.

6 Conclusions/Summary

The comparison between particulate inorganic carbon (PIC) derived from satellite data and in situ coccolithophore-based estimates in two transects of the Pacific sector (separated in time and space) provides an invaluable ground truth benchmark for the study of coccolithophores at high latitudes. Based on our data the following conclusions can be drawn:

1) We found out that satellite-derived PIC values and coccolith-PIC trends are in good agreement in the Subantarctic Zone (SAZ) and Polar Front Zone (PFZ). However, remote sensing tends to overestimate PIC values, which we link to a certain bias in the algorithm due to the limited number of measurements used for the validation of the PIC calibration (all of them in the Atlantic ocean). This could be potentially adjusted for in the Southern Ocean and specifically for the study area.

2) A striking observation is the decoupling of satellite-derived PIC and coccolith-PIC estimates at and to the south of the Polar Front (PF), particularly in the Antarctic Zone (AZ). Despite having high reflectance values, no coccolithophores were observed in this area. We hypothesize that the high satellite-derived PIC values in the AZ could be due to the high abundance of small opal particles.

3) *Emiliania huxleyi* is the predominant coccolithophore species contributing the most to the sea-surface PIC in the New Zealand transect (mainly sampled in 2005) and as well as in the Drake Passage (sampled in 2016). *Calcidiscus leptoporus* may occasionally contribute significantly to the PIC contributions at certain locations, whereas the rest of the coccolithophore taxa contribute only marginally to the PIC in the studied areas.

4) *Emiliania huxleyi* consists of different morphotypes, which have different, partly overlapping geographical distributions. The relatively massive Type A occurs in the northern SAZ and occasionally in the PFZ of the Drake Passage, while specimens of the less calcified morphogroup B (which includes Types B, B/C, C and O) occur in the SAZ and the PFZ of both transects, but disappear drastically south of the PF. But neither the slightly different carbonate masses nor the southward changes in morphotype composition have a decisive influence on the coccolithophore-derived PIC, which is only determined by the amount of *E. huxleyi* in this area.

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5) The satellite-derived and coccolith-PIC discrepancy we observed in this work emphasizes the importance of in situ measurements and highlights the need for further investigation to fully understand the factors influencing water-leaving radiance and the reliability of remote sensing estimates, especially south of the PF.

Future research should focus on refining satellite algorithms to improve the accuracy of PIC estimates and better understand the dynamics of coccolithophore communities in the Pacific sector of the Southern Ocean (especially compared to the Atlantic and Indian sectors). Such efforts will enhance our understanding of carbon cycling and its impact on marine ecosystems in this key high latitude region.

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Data Availability Statement

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The authors confirm that the data from which the findings of this study are available within the article Supplementary Materials and are stored in the data repository https://pangaea.de/

Author contributions

The study was designed by EM, MSP and KHB. EM and NMV carried out the morphometric measurements and classified the specimens of *E. huxleyi*. EM and MSP calculated coccolith-PICs, plotted the data and wrote an earlier version of the manuscript. N B-J and HL provided remote sensing data for the study area, and were actively involved in the discussion of the findings as well as in the writing of the paper. All authors approved the submitted version.

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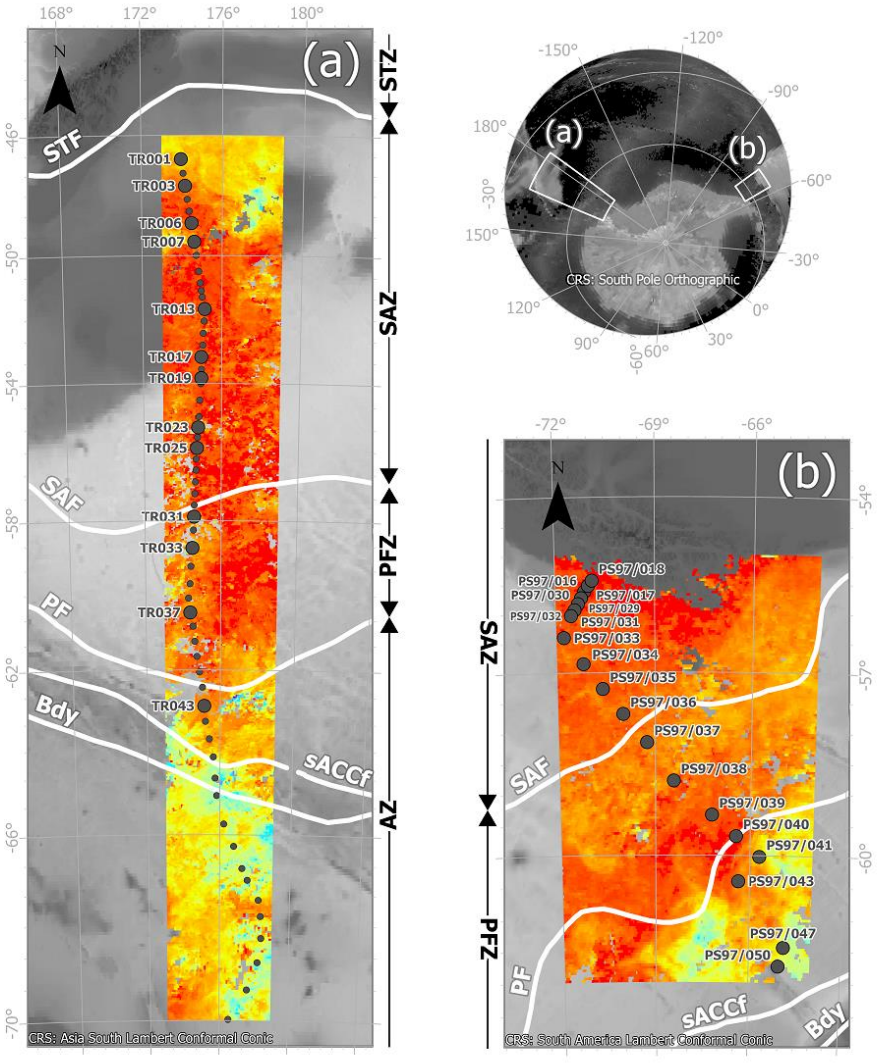

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765 **Figure 1: Study area showing the location of the water samples retrieved from (a) the New Zealand transect, collected during the**
766 **XX Italian Expedition from New Zealand to Antarctica on board R/V Italica (December 2004-January 2005) and (b) the Drake**
767 **Passage transect, collected during Polarstern Expedition PS97 across the Drake Passage (February-March 2016). The maps show**
768 **satellite-derived PIC values (NASA Ocean Biology Processing Group 2022) corresponding to (a) monthly mean over January 2005**
769 **and (b) monthly mean over February and March 2016, overlain on a bathymetry background (GEBCO Compilation Group, 2022).**
770 **White lines indicate the ACC fronts (Orsi and Harris, 2019), from north to south these are: SAF (Subantarctic Front), PF (Polar**
771 **Front), sACCf (Southern ACC Front) and BDy (Southern Boundary). The Southern Ocean zones are labeled on the side of each**
772 **map: STZ, Subtropical Zone; SAZ, Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone.**
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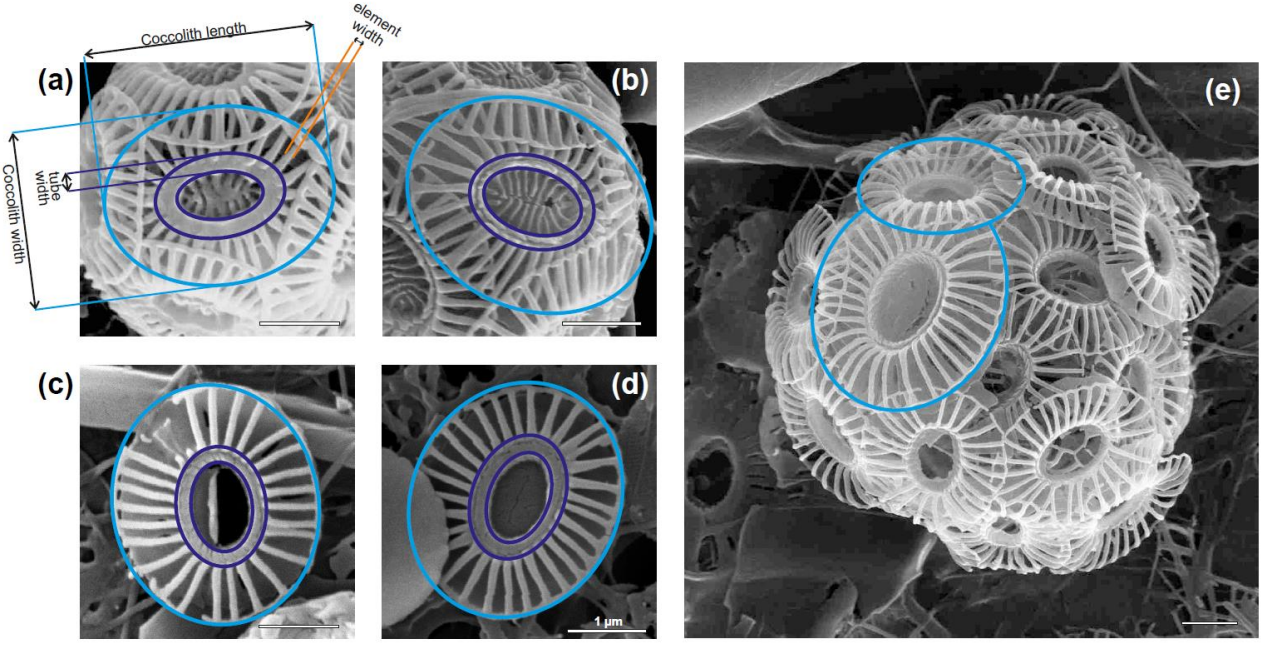

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776 **Figure 2: Parameters measured in *E. huxleyi* coccoliths (a, b) type A and (c, d, e) type O in plankton samples from the New Zealand**
777 **transect. Note the coccolith size variation in (e) within the same coccosphere.**
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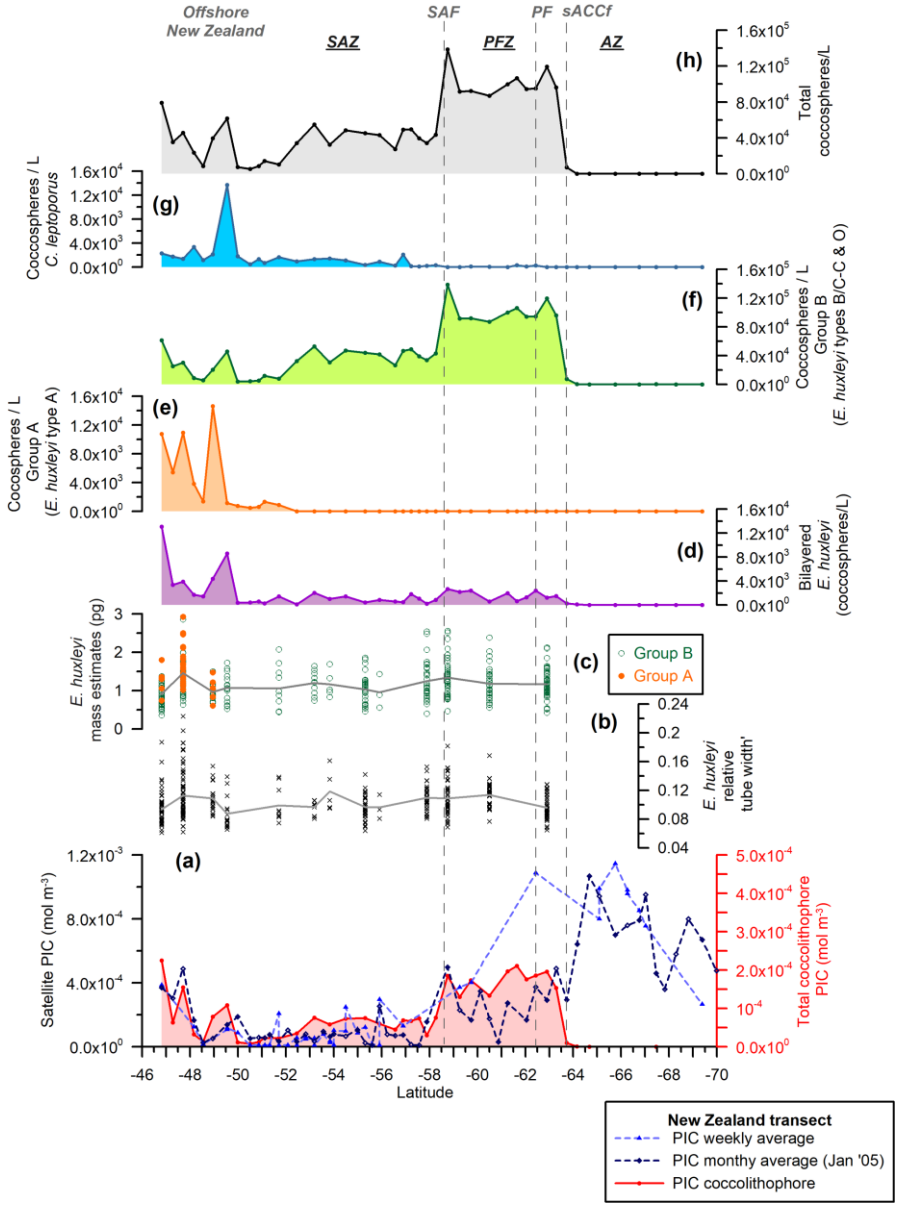

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782 **Figure 3: New Zealand transect showing (a) satellite-derived PIC values (NASA Ocean Biology Processing Group, 2022)**
783 **corresponding to a monthly average (January 2005, dark blue dashed line with diamonds), weekly average (electric blue dashed**
784 **line with triangles) and estimated total coccolithophore PIC (red line with dots), all in mol m^{-3}, (b) *E. huxleyi* relative tube width'**
785 **(average in gray), (c) *E. huxleyi* coccolith mass estimates (pg) (average in gray), (d) number of bilayered *E. huxleyi* (coccospheres/L),**
786 **(e) number of *E. huxleyi* morphogroup A (coccospheres/L), (f) number of *E. huxleyi* morphogroup B (coccospheres/L), (g) number**
787 **of *Calcidiscus leptoporus* (coccospheres/L), (h) Number of total coccolithophores (coccospheres/L) (Malinverno et al., 2015).**
788 **Vertical dashed lines indicate some of the ACC fronts (Orsi and Harris, 2019): SAF (Subantarctic Front), PF (Polar Front) and**
789 **sACCf (Southern ACC Front). The Southern Ocean zones are labeled as SAZ (Subantarctic Zone), PFZ (Polar Frontal Zone) and**
790 **AZ (Antarctic Zone).**

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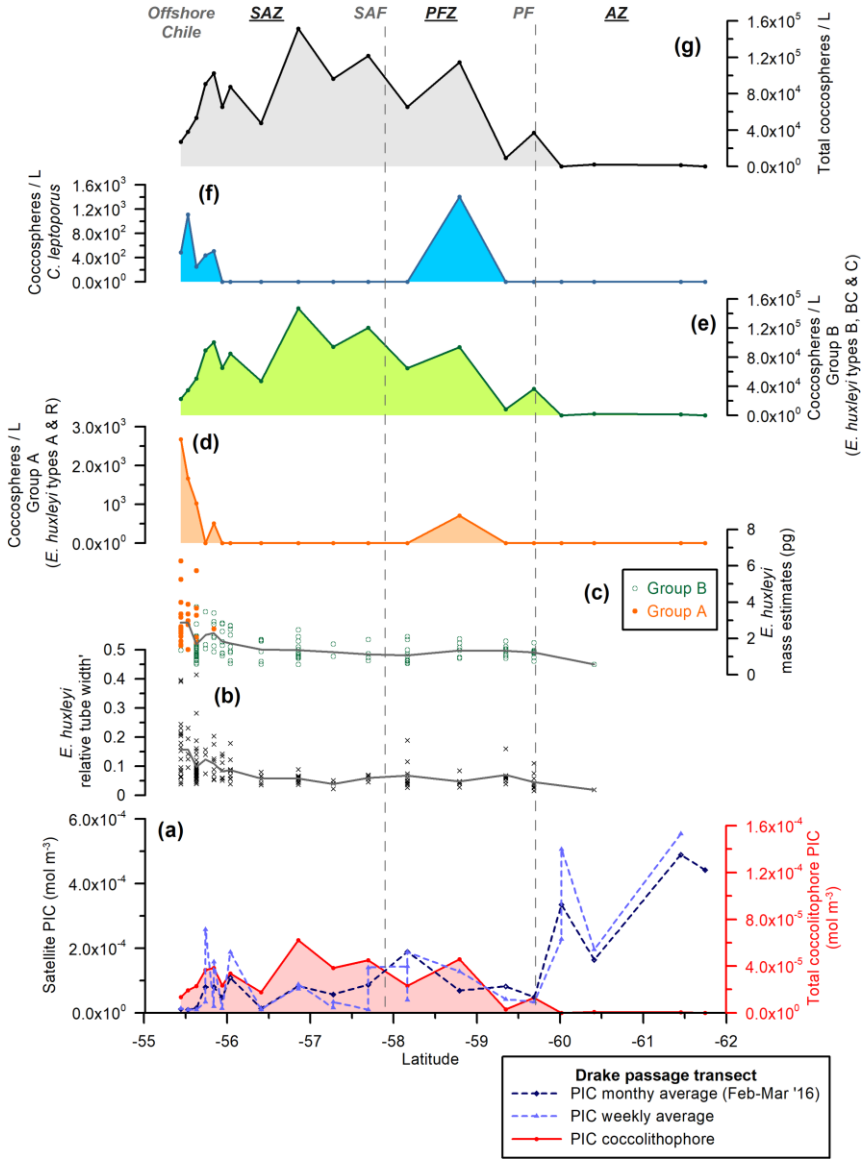

Figure 4: Drake Passage transect showing (a) satellite-derived PIC values (NASA Ocean Biology Processing Group, 2022) corresponding to a monthly average (February and March 2016, dark blue dashed line with diamonds), weekly average (electric blue dashed line with triangles) and estimated total coccolithophore PIC (red line with dots), all in mol m^{-3}, (b) *E. huxleyi* relative tube width' (average in gray), (c) *E. huxleyi* coccolith mass estimates (pg) (average in gray), (d) number of *E. huxleyi* morphogroup A (coccospheres/L), (e) number of *E. huxleyi* morphogroup B (coccospheres/L), (f) number of *Calcidiscus leptoporus* (coccospheres/L), (g) Number of total coccolithophores (coccospheres/L) (Saavedra-Pellitero et al., 2019).
Vertical dashed lines indicate some of the ACC fronts (Orsi and Harris, 2019): SAF (Subantarctic Front) and PF (Polar Front). The Southern Ocean zones are labeled as SAZ (Subantarctic Zone), PFZ (Polar Frontal Zone) and AZ (Antarctic Zone).

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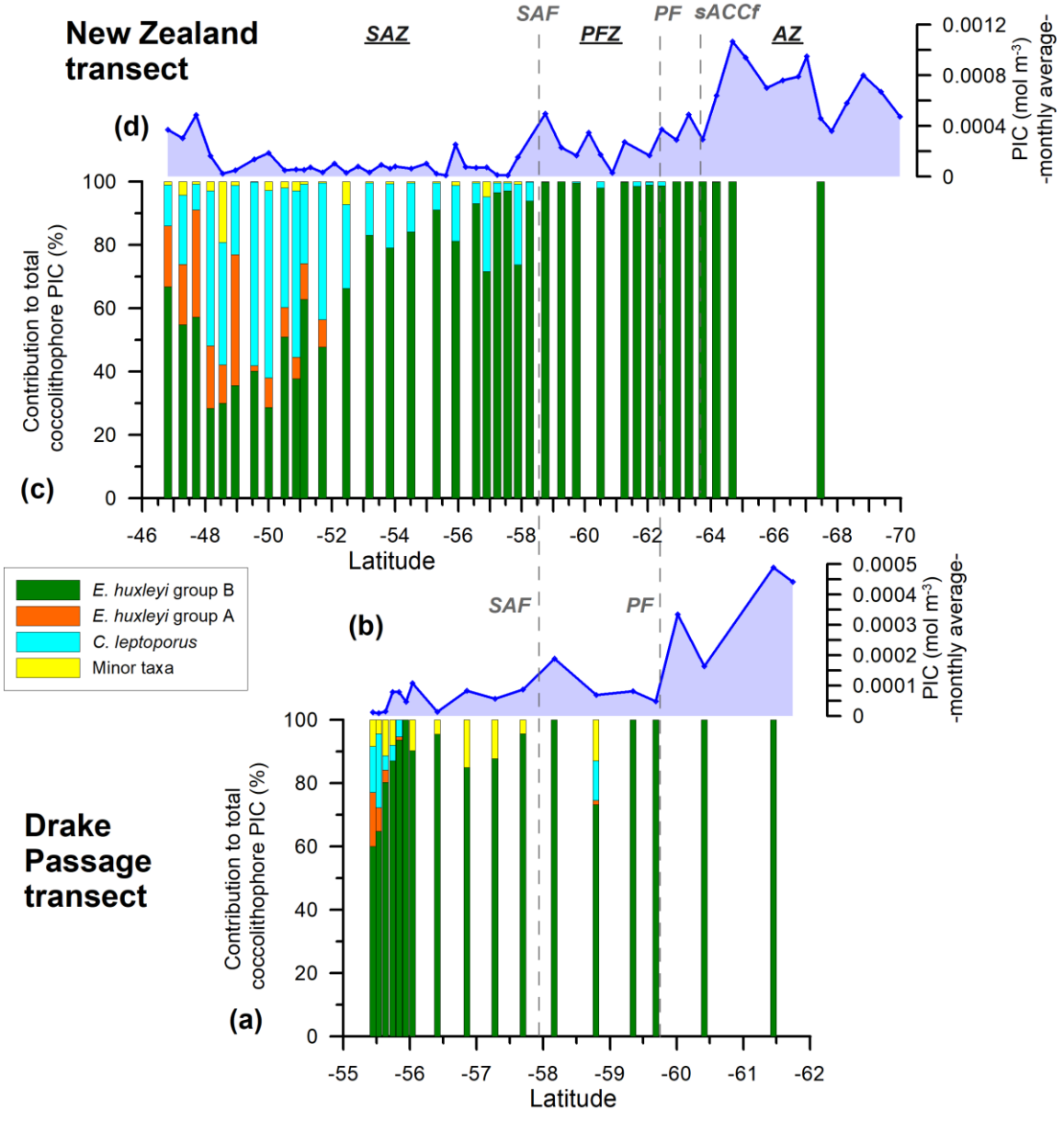

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804 **Figure 5: New Zealand and Drake Passage transects showing (a, c) the relative PIC contribution of the different nannofloral taxa**
805 **(*E. huxleyi* morphogroups A and B, *Calcidiscus leptoporus* and minor species) to the estimated coccolithophore PIC; (b, d) satellite-**
806 **derived PIC values (NASA Ocean Biology Processing Group 2022) corresponding to a monthly average (February and March 2016,**
807 **dark blue line with diamonds) in mol m^{-3}. Vertical dashed lines indicate some of the ACC fronts (Orsi and Harris, 2019): SAF**
808 **(Subantarctic Front) and PF (Polar Front). The Southern Ocean zones are labeled as SAZ (Subantarctic Zone), PFZ (Polar Frontal**
809 **Zone) and AZ (Antarctic Zone).**
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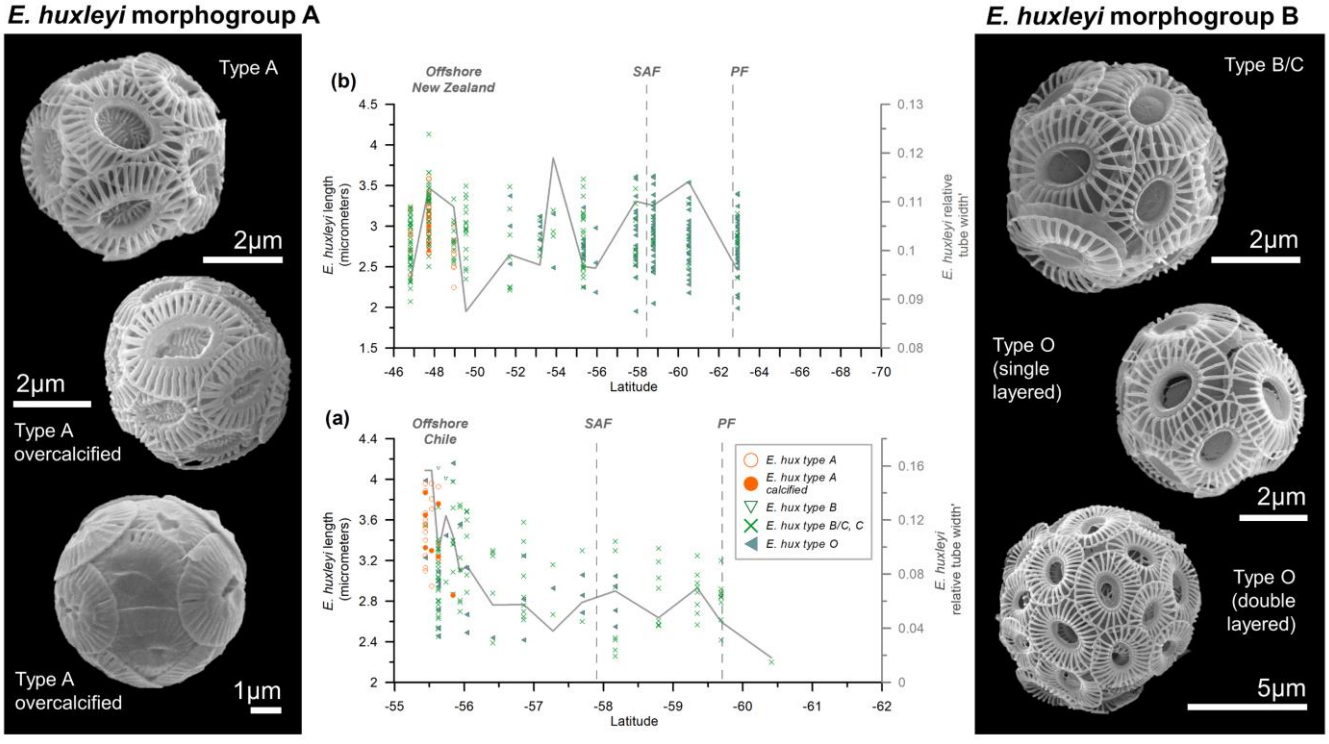

Figure 6: *Emiliania huxleyi* length (in µm) (indicated with different symbols depending on the type, and different colors depending on the morphogroup) and averaged relative tube width' (gray line) in (a) the Drake Passage and (b) New Zealand transects. On the left-hand side: pictures of coccospheres of *E. huxleyi* type A (within the morphogroup A) showing different degrees of calcification and on the right-hand side pictures of type B/C as well as type O belonging to the morphogroup B. All the coccospheres are from the New Zealand transect, except for the left bottom one, which was retrieved offshore of Chile.

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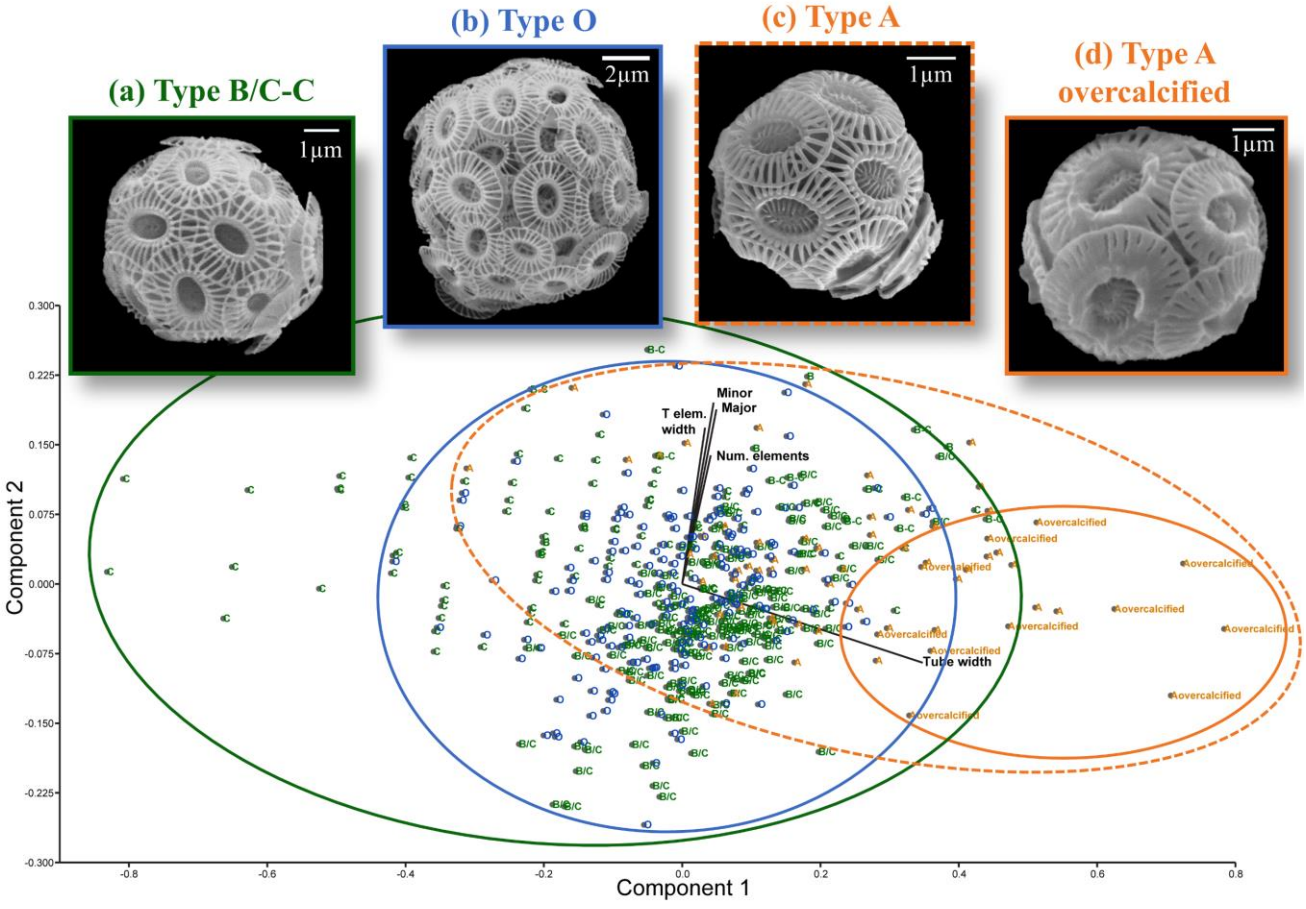

Figure 7: Principal component analysis (PCA) of the *E. huxleyi* morphometric dataset (including samples from both transects), log-transformed. This includes the coccolith length (major), the coccolith width (minor), the distal shield element width, the number of T-elements and the tube width measurements. Each coccolith measured has been labeled with its morphotype: A, A overcalcified (both in orange), B, B/C-C (both in green) and O (in blue). All the SEM pictures of coccospheres are from samples retrieved in the Drake Passage transect except for (c), which is from the New Zealand transect.

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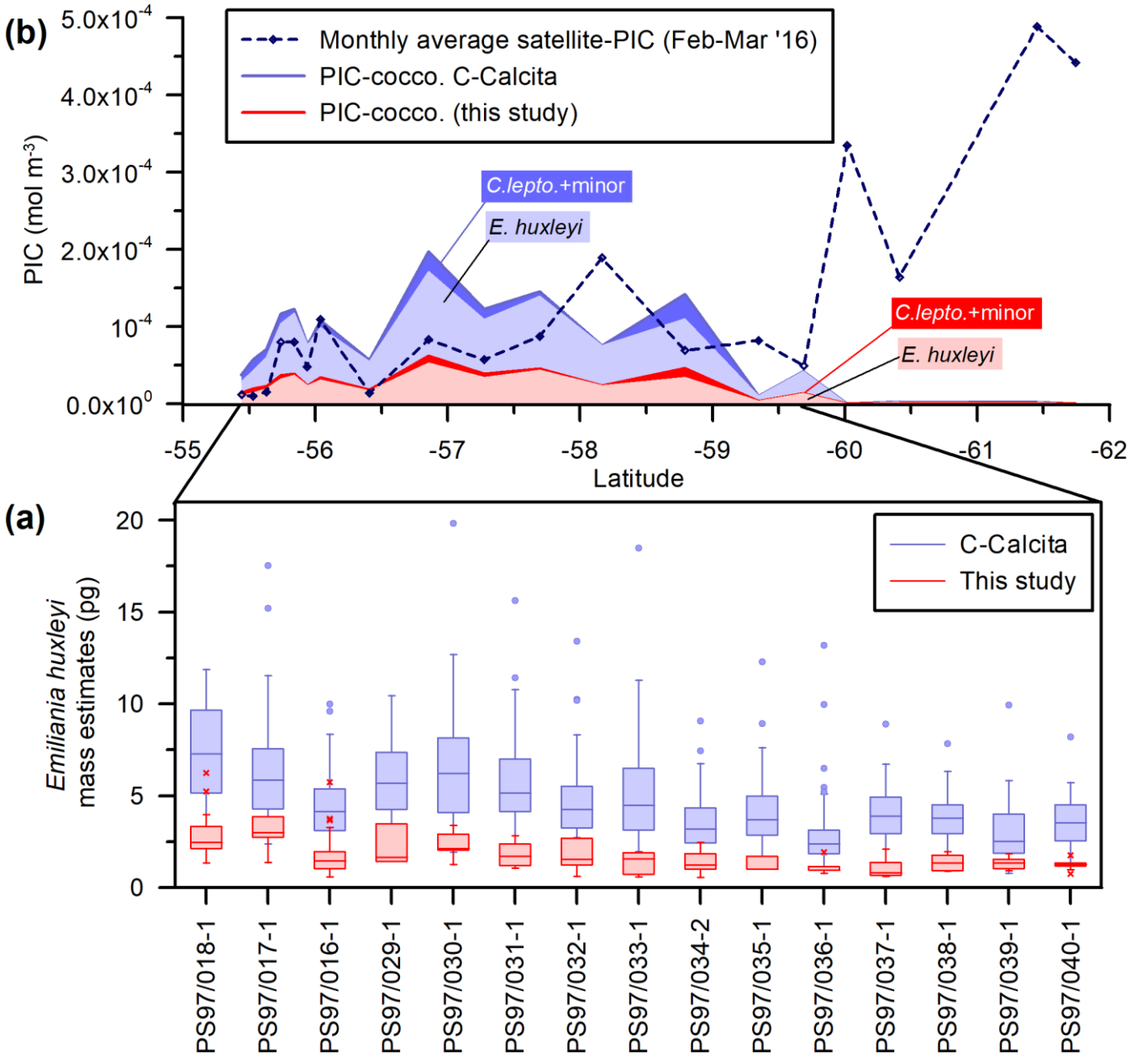

Figure 8: Drake Passage latitudinal transect showing (a) coccolith mass estimates box plots (in pg): in red for this study (outliers are indicated with "x") and blue for Saavedra-Pellitero et al. (2019) (outliers are indicated with a dot); (b) monthly average satellite-derived PIC values (dark blue dashed line with diamonds) and estimated coccolithophore PIC (all in mol m^{-3}). Contributions of different coccolith taxa have been indicated (*C.lepto.* = *Calcidiscus leptoporus*).

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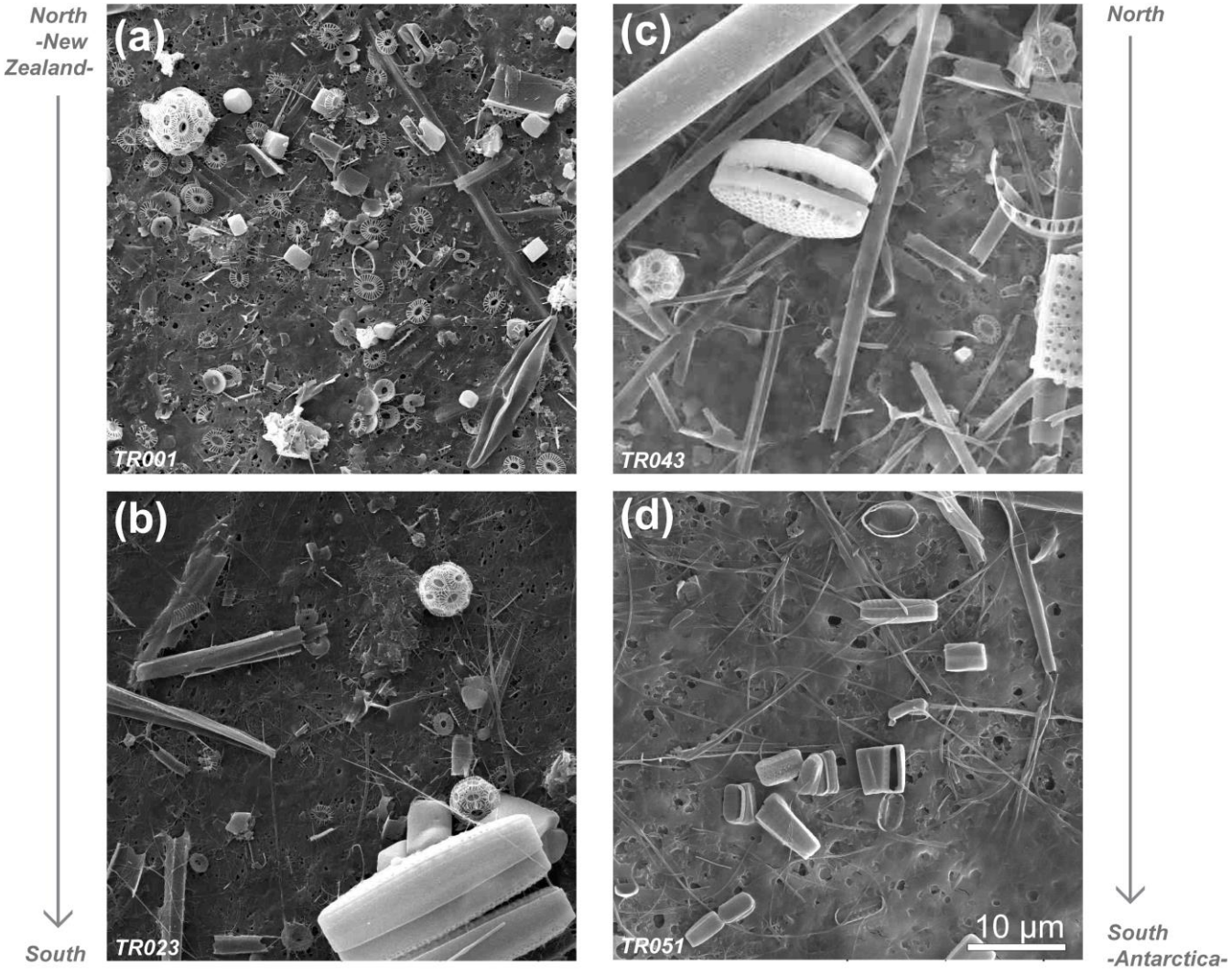

Figure 9: SEM pictures of samples retrieved in the Subantactic Zone (a, b) and south of the Polar Front (c, d) in the New Zealand transect.

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Table 1: Length, Ks and number of coccoliths per coccosphere used in this work for the New Zealand transect and the Drake Passage transect. (*) Indicates an average of the number of coccoliths per coccosphere.

Coccolithophore species	Length (µm) New Zealand	Length (µm) Drake passage	Source	Ks	Source	Number of coccoliths per coccoshere N. Zealand	Number of coccoliths per coccoshere Drake P.	Source
Calcidiscus leptoporus* spp. *leptoporus	5	5	This work (biometries offshore N. Zealand)	0.08	Young and Ziveri (2000)	15	15	Kleijne (1993)
***Emiliania huxleyi group* A (average value)**	2.95	3.49	This work	0.03	This work	15 single layered, 35 double layered	25 (*)	This work (own observations)
***Emiliania huxleyi* A overcalcified**				0.04	Young and Ziveri (2000)			
***Emiliania huxleyi* A (normal)**				0.02	Young and Ziveri (2000)			
***Emiliania huxleyi* group B (average value)**	2.87	2.98	This work	0.02	Young and Ziveri (2000)			
***Emiliania huxleyi* B-B/C-C**				0.02	Young and Ziveri (2000)			
***Emiliania huxleyi* O**				0.015	This work			
Gephyrocapsa muellerae	3.9	3.9	Young and Ziveri (2000)	0.05	Young and Ziveri (2000)	15	15	Samtleben & Schroder (1992)
***Syracosphaera* spp.**	2.2	5.5	Young and Ziveri (2000)	0.03	Young and Ziveri (2000)	25	25	Okada & McIntyre (1977)
Minor taxa			Young and Ziveri (2000)		Young and Ziveri (2000)			Yang & Wei (2003)

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Table 2. Summary of PIC time resolution and span. (**) The first 8-day period of each year always begins with January 1, the second with January 9, the third with January 17, etc. The final "8-day" composite of each year comprises only five days in non-leap years (27 - 31 December) or six days in leap years (26 - 31 December) (NASA Ocean Biology Processing Group, 2018).

Transect	**Drake passage transect**		**New Zealand transect**	
File time period	Time span	Num. of files	Time span	Num. of files
Daily timestamp	15-02-2016 / 05-03-2016	20	22-12-2004 / 06-01-2005	16
8-daily (**) timestamp	10-02-2016 / 12-03-2016	4	26-12-2004 / 08-01-2005	2
Monthly timestamp	01-12-2004 / 31-01-2005	2	01-02-2016 / 31-03-2016	2