

# Coccolithophore assemblage distribution along a temperate to polar gradient in the West Pacific sector of the Southern Ocean (January 2005)

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**ABSTRACT:** We document surface coccolithophore species composition along a N-S transect from New Zealand to the Ross Sea, across the fronts of the Antarctic Circumpolar Current. *Emiliana huxleyi* is the most abundant coccolithophore species throughout, with high concentration in the northernmost samples, in the Polar Frontal Zone and at the Polar Front. Three *E. huxleyi* morphotypes, A, B/C and O were recognized and show different biogeographic distributions along the investigated transect. Coccolithophore distribution appears to be strongly controlled by the location of oceanographic fronts, with minor species (*Calcidiscus leptoporus*, *Syracosphaera* spp., *Acanthoica quattropina*, *Umbellosphaera tenuis*, *Corisphaera strigilis* and other holococcolithophores) largely restricted to the northern Sub-Antarctic Zone, only showing minor occurrence in the southern Sub-Antarctic Zone and being very rare in the Polar Frontal Zone. Our data confirm previous findings and add new information on the biogeography of minor coccolithophore species in relation with oceanographic features. Overall, integration with previous data on the southern extent distribution of *E. huxleyi* showed no significant temporal shifts in the polar dynamic perspective of the species since early observations.

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## INTRODUCTION

Coccolithophores are an important phytoplankton group in the oceans and play a significant role in the carbon cycle. Several studies in different areas of the world oceans described their biogeography, ecology and fine-scale taxonomy. Coccolithophores make an important contribution to phytoplankton in warm oligotrophic areas (McIntyre and Bé 1967; Okada and Honjo, 1973), such as mid-ocean anticyclonic gyres. In such settings, with strong water column stratification, they develop a stratified community along the photic zone (Honjo and Okada 1974). *Emiliana huxleyi*, the most abundant extant coccolithophore species, is known to produce intense blooms at high latitudes, at optimal conditions of high irradiance, high temperatures, shallow mixed layer and reduced grazing (Holligan et al. 1993; Tyrell and Merico 2004).

Early work documented the distribution of coccolithophores at some sites in the South Atlantic and South Pacific, defining their latitudinal and temperature limits poleward (Hasle 1960; 1969; McIntyre and Bé 1967; McIntyre et al. 1970; Nishida 1986). In the last two decades, several authors targeted the specific distribution of coccolithophores along latitudinal gradients in different sectors of the SO (Southern Ocean) and showed a strong response to frontal systems (Hiramatsu and De Dekker 1996; Findlay and Giraudeau 2000; Cubillos et al. 2007; Böckel and Bauman 2008; Mohan et al. 2008; Gravalosa et al. 2008; Patil et al. 2014; Saavedra-Pellitero et al. 2014). The STF (Subtropical Front) as well as all other fronts within the ACC (Antarctic Circumpolar Current) represent important boundaries for the distribution of coccolithophore species.

Linking assemblage composition to the oceanic fronts' position allows tracing shifts (Findlay and Flores 2000; Findlay and

Giraudeau 2002; Fenner and Di Stefano 2004) and imply relations to the climatic variations.

Concern about global climate warming and ocean acidification has raised interest in the fate of coccolithophores and their future biogeographic distribution. In particular, *E. huxleyi* has been targeted as a key species to understand the response of coccolithophores to a changing climate: culture and mesocosm experiments, as well as studies in the natural environment, provided evidence suggesting a calcification response to water chemistry (Cubillos et al. 2007; Beaufort et al. 2011; Horigome et al. 2014). The various morphotypes of *E. huxleyi* are characterized by different coccolith morphology; at least some of these are genetically separated and show distinct though overlapping distribution (Young and Westbroek 1991). Winter et al. (2014), by comparing recent and earlier observations on the southernmost extent, inferred a trend of poleward expansion of *E. huxleyi* distribution in the SO, related to the climatic warming of the last century.

Here we show the sea surface distribution of coccolithophores from New Zealand to the Ross Sea along the cruise track from January 1-5, 2005 providing a quasi-synoptic picture of the investigated transect. We aim to:

- 1) link surface coccolithophore dynamics and latitudinal assemblage shifts with the ACC fronts' position in this area of the SW Pacific, where the PF (Polar Front) is located further South than in other sectors of the SO
- 2) provide additional data on *E. huxleyi* morphotype variation across the ACC fronts

3) constrain the southernmost extent of *E. huxleyi* distribution to the front's location in the SO, also in relation to previous findings in a dynamic oceanographic context.

### OCEANOGRAPHIC SETTING

The SO is an important high-nutrient low-chlorophyll zone of the world ocean, where phytoplankton growth is thought to be limited by the availability of iron in nutrient-replenished surface waters (DeBaar, 1994 among others). The SO is characterized by the eastward flow of the ACC (Antarctic Circumpolar Current), an un-interrupted deep-reaching current that encircles the Antarctic continent.

The ACC is bound to the North by the STF (Subtropical Front), to the South by the Bdy (Southern Boundary): these fronts separate the subantarctic waters of the ACC from the subtropical and subpolar regime, respectively (Orsi et al. 1995). Along the ACC, the main horizontal water transport occurs within restricted regions or fronts, which are characterized by strong surface currents (Nowlin et al. 1977). These fronts represent zonally-continuous bands of large latitudinal density gradients and can be defined through property indicators of water masses, based on the temperature, salinity and oxygen signal at specific depth layers (Orsi et al. 1995).

Although the ACC flow is driven by atmospheric forcing through westerly winds, its path is strongly controlled by bottom topography (Gordon et al. 1978). Steep features, such as oceanic plateaus or ridges, constrain the ACC flow. Therefore the fronts are found at different latitudes around the SO. The overall location of the fronts and their occurrence along the investigated transect are here summarized, from north to south:

- the SAF (Sub Antarctic Front) is defined by a sharp temperature gradient at depths of 300 or 400m (Belkin and Gordon 1996 and Orsi et al. 1995, respectively) and is often characterized by eddies and meanders. Along the path of our transect south of New Zealand (text-fig. 1), the SAF splits in two branches: the NSAF (Northern SAF) corresponds with a thermal gradient in the range 4-7°C at 300 m, while the SSAF (Southern SAF) is associated with a thermal gradient in the range 3-4°C at 300 m. While the NSAF position is stable in time, over the continental slope at the southern edge of the Campbell Plateau, the SSAF position is not controlled by bottom topography and is thus strictly related to the development of meander-features (Budillon and Rintoul 2003; Campanelli et al. 2011).

- the PF (Polar Front) is defined by the subsurface temperature minimum of 2°C at depth above 200m (Orsi et al. 1995) and corresponds to a 2°C gradient in SST. Along our transect, the position of the PF is less constrained by bottom topography and has been found to oscillate by up to 2° of latitude on a seasonal and interannual basis. When the same track has been crossed several times during the same season, the PF has been found shifted South from November to February (table 3 of Budillon and Rintoul 2003; Campanelli et al. 2011). The PF position moved southward by 2° from 1975 to 2005 (Campanelli et al. 2011), probably related to warming of the SO (Gille 2008).

- the sACCf (southern ACC front) is defined by temperatures below 0° at the sub-surface (shallower than 150 m) temperature minimum and by temperatures above 1.8°C within the deeper (>500 m) temperature maximum (Orsi et al. 1995). The sACCf position is stable in time and strictly constrained, in the area of

our transect, by the steep northern flank of the SE Indian / Pacific-Antarctic Ridge.

Within these fronts, the water masses are characterized by more gradual changes in physical properties and can be therefore described as distinct zones (Orsi et al. 1995). From north to south these are:

- the SAZ (Subantarctic Zone) between the STF and the SSAF: in this sector of the Southern Ocean, the SAZ is divided in two parts by the NSAF;
- the PFZ (Polar Frontal Zone) between the SAF and the PF;
- the AZ (Antarctic Zone) from the PF to the Antarctic continent. The sACCf lays within the AZ.

In this sector of the SO south of New Zealand, the AZ south of the Bdy is characterized by the Ross gyre, a cyclonic clock-wise feature driven by the interaction with the westward coastal flow.

### METHODS

#### Sampling

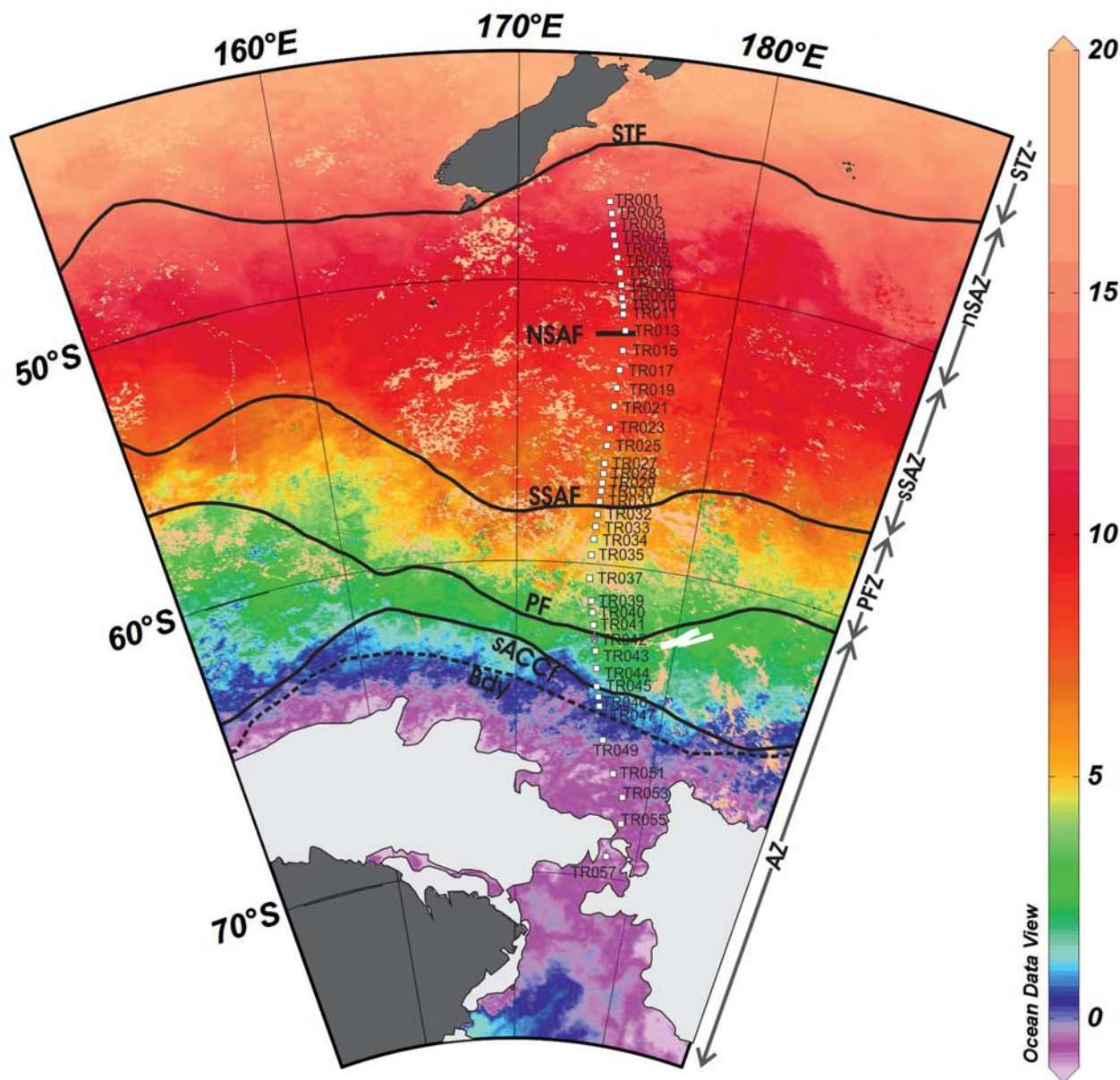
Water samples were collected from the ship's pump (mounted on the hull at approximately 3m water depth and kept running during the transit) during the XX Italian Expedition from New Zealand to Antarctica on board R/V *Italica* (1-5/01/2005, text-fig. 1, PNRA report, 2005). Deeper samples (25, 50, 75, 100, 200m) were collected through a rosette equipped with Niskin bottles at a single station located at 62°26.8'S 174°59.4'E, close to the Polar Front. Depending on particle concentration, a variable amount of seawater (0.5-4 liters) was filtered on cellulose acetate filters, 0.45µm pore size, 47 mm diameter. Filters were oven-dried at 40°C for 4 hours and stored in plastic Petri dishes in the dark. Identification of major phytoplankton groups and specific morphometric analyses on silicoflagellates are discussed in Malinverno et al. (2016) and Malinverno (2010), respectively.

#### Coccolithophore analysis

For coccolithophore counts, a portion of the filter was mounted on a glass slide with a drop of microscope immersion oil and scanned along radial transects with an Olympus BX50 polarized light microscope at 1000x. A total of 16-790 coccospheres and up to 700 coccoliths were enumerated on an area of 4-25mm<sup>2</sup> and 1-30mm<sup>2</sup> respectively, according to their density on the filter.

All counts (n) were converted into cs/L (coccospheres/liter) and cl/L (coccoliths/liter), through correction for the initial volume of seawater (V), effective filtration area (A) and scanned area (a), following the formula: Cs/L = n x A/a x 1/V

SEM (Scanning electron microscope) examinations were performed on 13 selected samples regularly spaced along the studied transect (TR001, 003, 006, 007, 013, 017, 023, 025, 031, 033, 037, 043, 044), aiming for fine scale taxonomy of minor species within the coccolithophore assemblages and identification of *Emiliania huxleyi* morphotypes. One piece of filter was cut and attached to a SEM aluminium stub with bi-adhesive tape and sputter-coater with gold for SEM examination. Samples were analysed with a Vega Tescan SEM at the University of Milano-Bicocca.



TEXT-FIGURE 1

Map of the study area and location of the analyzed surface (white squares) and deeper (grey asterisk) samples. Background colors are SST data (11-micron day 4 km resolution data as obtained from the Giovanni online data system, developed and maintained by the NASA GES DISC. The ACC fronts' location is drawn after Orsi et al. (1995) and adjusted along the cruise track from Campanelli et al. (2011). The different oceanographic zones are indicated on the right side of the map: STZ, Subtropical Zone; nSAZ, northern Subantarctic Zone; sSAZ, southern Subantarctic Zone; PFZ, Polar Frontal Zone; AZ, Antarctic Zone.

Preliminary measurements of *E. huxleyi* coccosphere and coccolith size from 6 of these samples (TR001, 003, 013, 025, 033, 043) and of *Calcidiscus leptoporus* from 3 samples (TR001, 003, 006) were performed through the ImageJ software following the biometric approaches of Triantaphyllou et al. (2010) and Young et al. (2014). Taxonomic identification of minor species followed Young et al. (2003).

## RESULTS

In our section, total coccolithophore abundance ranges from  $5\text{--}137 \times 10^3$  cs/L: highest values were recorded in the northernmost samples close to the STF, in the PFZ and at the PF, while lower values occurred in the SAZ. A total of 14 species were recovered as intact coccospheres along the investigated transect (Table 2). Further 14 species were identified only as free coccoliths.



TABLE 1  
List of sampling stations and geographic coordinates.

Sample	Latitude (°S)	Longitude (°E)
ANTA05 - TR001	46.8102	173.9533
ANTA05 - TR002	47.2848	174.0525
ANTA05 - TR003	47.7065	174.1515
ANTA05 - TR004	48.1587	174.2575
ANTA05 - TR005	48.5497	174.3527
ANTA05 - TR006	48.9428	174.4655
ANTA05 - TR007	49.5498	174.6087
ANTA05 - TR008	49.9973	174.7058
ANTA05 - TR009	50.5052	174.8268
ANTA05 - TR010	50.8732	174.9053
ANTA05 - TR011	51.1255	174.9608
ANTA05 - TR013	51.7030	175.1315
ANTA05 - TR015	52.4558	175.0597
ANTA05 - TR017	53.1882	174.9963
ANTA05 - TR019	53.8375	174.9573
ANTA05 - TR021	54.5020	174.8783
ANTA05 - TR023	55.3113	174.7942
ANTA05 - TR025	55.9168	174.7342
ANTA05 - TR027	56.5632	174.6860
ANTA05 - TR028	56.8970	174.6542
ANTA05 - TR029	57.2352	174.6218
ANTA05 - TR030	57.5597	174.5917
ANTA05 - TR031	57.8835	174.5742
ANTA05 - TR032	58.2607	174.5500
ANTA05 - TR033	58.7528	174.4917
ANTA05 - TR034	59.2597	174.4097
ANTA05 - TR035	59.7338	174.3675
ANTA05 - TR037	60.5005	174.3693
ANTA05 - TR039	61.2592	174.6078
ANTA05 - TR040	61.6523	174.7322
ANTA05 - TR041	62.0495	174.8678
ANTA05 - TR042	62.4373	175.0238
ANTA05 - TR043	62.9057	175.1225
ANTA05 - TR044	63.2928	175.1865
ANTA05 - TR045	63.7243	175.4062
ANTA05 - TR046	64.1615	175.6317
ANTA05 - TR047	64.6742	175.7298
ANTA05 - TR049	65.7498	176.2267
ANTA05 - TR051	66.7605	177.2630
ANTA05 - TR053	67.4645	178.2070
ANTA05 - TR055	68.2930	178.3893
ANTA05 - TR057	69.3753	177.5933

The minor species, as described below, are restricted to the northern part of the SAZ, from 46 to 49.5°S and their abundance is greatly reduced southward, where a nearly monospecific *E. huxleyi* association is present (text-fig. 2).

*E. huxleyi* was the dominant species along the whole latitudinal transect (50 to 100% of coccolithophore assemblage). Coccosphere concentrations were variable ( $4\text{--}70 \times 10^3$  cs/L) in the northern SAZ, more constant ( $20\text{--}50 \times 10^3$  cs/L) in the southern SAZ and showed maximum values in the PFZ, with peak values up to  $140 \times 10^3$  cs/L. Southward of the PF, coccospheres dropped sharply to values  $<10^3$  cs/L between 63.7–64.7°S, then were absent in the southernmost samples, excluding a limited occurrence in a single sample located at 67.7°S. The vertical distribution was observed at one station located at the PF (text-fig. 1): coccolithophores are represented by a monospecific *E. huxleyi* assemblage and their abundance dropped from  $95 \times 10^3$  cs/L in surface waters to  $15\text{--}52 \times 10^3$  cs/L in the upper 100 m; only a few coccospheres were detected at 200m depth (text-fig. 2).

The concentration of coccoliths followed the general trend of coccospheres, but displayed a different ratio of free coccoliths:coccospheres (14–100).

Detailed SEM investigation on the 13 selected samples enabled defining the latitudinal variation in *E. huxleyi* morphotypes. Morphotypes A, B/C and O were separated on the basis of Young et al. (2003) and Hagino et al. (2011). Morphotype O includes all forms with an open central area or with the central area partly covered by an organic membrane following Hagino et al. (2011).

As shown in text-figure 3, morphotype A is present in the northern SAZ, until 51.7°S, where it represents 5–41% of the species; morphotype O is present throughout the whole transect and most abundant in the northern and southern SAZ, where it represents 16–78% of the species, while it decreases in abundance in the PFZ, where morphotype B/C is the dominant form.

Bilayered *E. huxleyi* coccospheres were found throughout the whole section for all three morphotypes. Their concentration was highest in both absolute and relative abundance (10–20% of the total *E. huxleyi* population) in the samples from the nSAZ, rather scarce in the sSAZ, PFZ and AZ but showed increasing relative abundance (25%) in a sample south of the sACCF (text-fig. 4).

Additionally, *E. huxleyi* doublets (Pl. 2, fig. 1), likely representing the division phase, were encountered throughout the section, with peak values up to  $2.8 \times 10^3$  cs/L, but representing on average  $<3\%$  of the total *E. huxleyi* populations.

Within all *E. huxleyi* morphotypes, specimens showing slight over-calcification and/or etching were observed. Slightly over-calcified specimens show a thickening of the tube elements and of the DS elements (Pl. 1, fig. 3): these features were only observed in the two northernmost samples analyzed through SEM. Etching involves mostly the tube elements, which appear separated from the DS elements (Pl. 1, fig. 8), but more severe dissolution can occur, with thinning of the DS elements: in such cases, DS elements are in lower number and sometimes collapsed on the proximal shield (cf. Young 1994). The latter specimens are scarce in samples analyzed through

TABLE 2

List of coccolithophore species recovered along the transect as coccospheres and/or free coccoliths.

Coccolithophore species	Coccospheres	Coccoliths
<i>Acanthoica quattropsina</i> Lohmann, 1903	x	
<i>Coronosphaera binodata</i> (Kamptner 1927) Gaarder in Gaarder and Heimdal 1977		x
<i>C. mediterranea</i> (Lohmann 1902) Gaarder in Gaarder and Heimdal 1977	x	x
<i>Calciosolenia brasiliensis</i> (Lohmann 1919) Young in Young et al. 2003		x
<i>Coccolithus pelagicus</i> (Wallich 1877) Schiller 1930 subsp. <i>pelagicus</i>		x
<i>Corisphaera strigilis</i> Gaarder 1962	x	
<i>Discosphaera tubifera</i> (Murray and Blackman 1898) Ostenfeld 1900		x
<i>Emiliania huxleyi</i> (Lohmann 1902) Hay and Mohler in Hay et al. 1967 - types A, B/C, O	x	x
<i>Florisphaera profunda</i> Okada and Honjo 1973		x
<i>Gladiolithus flabellatus</i> (Halldal and Markali 1955) Jordan and Chamberlain 1993		x
<i>Gephyrocapsa oceanica</i> Kamptner 1943		x
<i>Gephyrocapsa ericsonii</i> McIntyre and Bè 1967	x	x
<i>Helicosphaera carteri</i> (Wallich 1877) Kamptner 1954	x	x
<i>Ophiaster</i> sp. cf. <i>O. hydroideus</i> (Lohmann 1903) Lohmann 1913	x	
<i>Palusphaera vandellii</i> Lecal 1965		x
<i>Rhabdosphaera clavigera</i> Murray and Blackman 1898		x
<i>Scyphosphaera apsteinii</i> Lohmann 1902		x
<i>Syracosphaera borealis</i> Okada & McIntyre 1977	x	x
<i>S. dilatata</i> Jordan et al. 1993		x
<i>S. halldalii</i> Gaarder in Gaarder and Hasle 1971	x	x
<i>S. cf. S. tumularis</i> Sánchez-Suárez 1990		x
<i>S. nana</i> (Kamptner 1941) Okada and McIntyre 1977 - HET and HOL	x	
<i>S. nodosa</i> Kamptner 1941	x	
<i>S. pemma-discus</i> Chang 2013	x	x
<i>S. pulchra</i> Lohmann 1902		x
<i>Umbilicosphaera sibogae</i> (Weber-van Bosse 1901) Gaarder 1970		x
<i>Umbellosphaera tenuis</i> (Kamptner 1937) Paasche in Markali and Paasche 1955	x	x

SEM (below 1%), except for one sample at 43.2°S, where they are more common.

*Calcidiscus leptoporus* ssp. *leptoporus* was the second most abundant taxon. It occurred with greater abundance ( $1\text{--}3 \times 10^3$  cs/L) in the nSAZ, peak values ( $13 \times 10^3$  cs/L) have been recorded at one station located at 49.5°S. It gradually decreased southwards showing low concentration in the sSAZ and sporadic occurrence in the PFZ.

Coccoliths of *C. leptoporus* spp. *leptoporus* ranged from 4.9 to 7.1 µm in diameter, with coccoliths up to 1 µm different in size occurring on the same coccosphere. The number of elements of the DS ranged from 18 to 22, but was as low as 15 on the smallest coccoliths. In the majority of the observed specimens the DS elements were regular, with smoothly curved sutures and anticlockwise imbrication; however, some specimens displayed an irregular growth of some DS elements, which resulted in an irregular pattern of inverse imbrication in the area near the tube (Plate 2 fig. 3, 6). Coccospheres ranged in diameter from 9 to 12 µm, with some coccospheres as large as 15 µm (Pl. 2 fig. 5).

Minor taxa included *U. tenuis* type II (Young et al. 2003) and *Acanthoica quattropsina*, which were present only in the few northernmost samples of the transect (until 48.5°S), holococcolithophores, which are mainly represented by *Corisphaera strigilis* and *Syracosphaera nana* HOL, most abundant in the nSAZ, with sporadic presence in the sSAZ. *Syracosphaera* spp. (mainly *S. borealis*) and *Ophiaster* sp. were most

abundant within the northern and southern SAZ, with a pattern of decreasing abundance southward and sporadic occurrence within the PFZ until the PF. Sporadic occurrences of *Gephyrocapsa ericsonii*, *Helicosphaera carteri* and *Coronosphaera mediterranea* were documented in the nSAZ.

## DISCUSSION

### Total abundance, depth distribution and seasonality of coccolithophores in the SO

In the Southern Ocean, the pattern of total coccolithophore abundance is driven by *E. huxleyi*, which represents 50–100% of the coccolithophore assemblage. Highest abundances occurred in the northernmost samples, in the PFZ and at the PF. Previous data from other locations in the SO showed a similar pattern of maximum concentration in the PFZ and at the PF, where the coccolithophore assemblage was almost monospecific, made by *E. huxleyi*.

In the Pacific Sector, early work by Hasle (1960) showed maximum coccolithophore concentrations (mainly *E. huxleyi*,  $185\text{--}361 \times 10^3$  cs/L) at in the PFZ and PF in December-January; high concentrations were found at the STF ( $552 \times 10^3$  cs/L), the SAF ( $150\text{--}493 \times 10^3$ ) the PFZ and the PF ( $150\text{--}312 \times 10^3$  cs/L) by Gravalosa et al. (2008) in February-April and Saavedra-Pellitero et al. (2014) in November-January. In the Australian Sector, Nishida (1986) showed maximum coccolithophore concentrations at the STF ( $146 \times 10^3$  cs/L) and PF ( $139 \times 10^3$  cs/L) in December-January. Findlay and Giraudeau (2000) found maxi-



imum values ( $163\text{--}199 \times 10^3$  cs/L) at and immediately south of the PF in January and February, while Cubillos et al. (2007) enlightened no significant trend and coccolithophore (*E. huxleyi*) concentrations ranging from  $10$  to  $>100 \times 10^3$  cs/L during several cruises from October to March.

In the Indian Sector, peak values ( $88 \times 10^3$  cs/L) in surface waters coccolithophore concentration occurred in the PFZ (Mohan et al. 2008) in January–March or slightly to the north (Patil et al. 2014) in February.

Finally, in the Atlantic sector, maximum values ( $493 \times 10^3$  cs/L) were recorded at and immediately south of the PF (Eynaud et al. 1999) in February, but much higher values (up to  $800 \times 10^3$  cs/L) have been reported from the Patagonian Shelf and the Scotia Sea when seasonal *E. huxleyi* blooms occur (Holligan et al. 2010; Hinz et al. 2012; Poulton et al. 2013; Balch et al. 2014).

In the SO south of the STF, maximum coccolithophore concentrations are commonly recorded in the upper 50 m of the water column (Findlay and Giraudeau 2000): our data from a single station located at the PF confirmed this pattern, showing maximum concentration at the surface and a drop in the subsurface layers. Therefore, data from the surface waters, as collected through the ship's pump, provide a good tool to monitor the distribution of coccolithophores in relation to oceanographic conditions.

Phytoplankton communities vary in composition and concentration during the summer season in response to limitation by different ecological factors such as light, temperature, nutrient availability and zooplankton grazing (Kopczyńska et al. 2007 among others). During the seasonal phytoplankton production, nutrients are consumed and the surface waters become nutrient-limited in most regions, excluding areas of intense vertical mixing. Seasonal shifts in coccolithophore abundance in the SO have been described by a few authors, which visited the same (or close-by) stations on a seasonal basis or at least twice in the same year. Among these are Hasle (1969) and Nishida (1986), who showed highest coccolithophore concentration in November–early December and decreasing values during Austral summer. Our data, collected in early January 2005, are consistent with observations from areas that were investigated during the same phase of the summer season. Nutrient concentrations, measured three times along the transit from New Zealand to Antarctica (Campanelli et al. 2011), indicated an apparent consumption of phosphates and silicates in particular, from November 2004 to January 2005. Zooplankton concentration was not measured along our transect, but qualitative observation showed the common occurrence of copepods at and southward of the SAF and *Codonellopsis pusilla*, a tintinnid with agglutinated lorica made of *E. huxleyi* B/C coccoliths (Pl. 2, fig. 2), in the PFZ. Their abundance could play a role in regulating the abundance of coccolithophores and other phytoplankton in this area.

#### Biogeography of coccolithophore species: the role of ACC fronts

The coccolithophore assemblage recovered during our survey south of the STF had relatively high diversity, containing up to 14 species, and progressively became monospecific southward. Similar diversity patterns have been documented from other latitudinal transects in the Southern Ocean (as reported in the previous section). Although limited to one season and one transect, our closely-spaced ( $\sim 20^\circ$  latitude) sampling allowed to closely

track the influence of oceanographic features on the distribution pattern of coccolithophore species. In this sector of the SO, the SAF splits in two branches: the northern SAF, being constrained by bottom topography, is located at the southern edge of the Campbell Plateau, while the southern SAF, which is related to the development of meander-features, migrates on a seasonal and interannual basis (Budillon and Rintoul 2003; Campanelli et al. 2011). The surface expression of both branches plays an important role in shaping the coccolithophore distribution.

The coccolithophore assemblage in the SAZ is dominated by *E. huxleyi*, but minor species can make an important contribution in some samples, as described for assemblage C of Findlay and Giraudeau (2000) where minor species make up 17–25 % of the total assemblage. *Calcidiscus leptoporus* is the most important minor species, comprising 3–25% of the total assemblage in the nSAZ and 0.2–4% in the southern sSAZ. Considering the large size and thickness of its coccoliths, as compared with *E. huxleyi*, this species, where present, contributes significantly to the sea-surface carbonate concentration (Malinverno et al. in prep.) and thus likely to carbonate flux to the bottom.

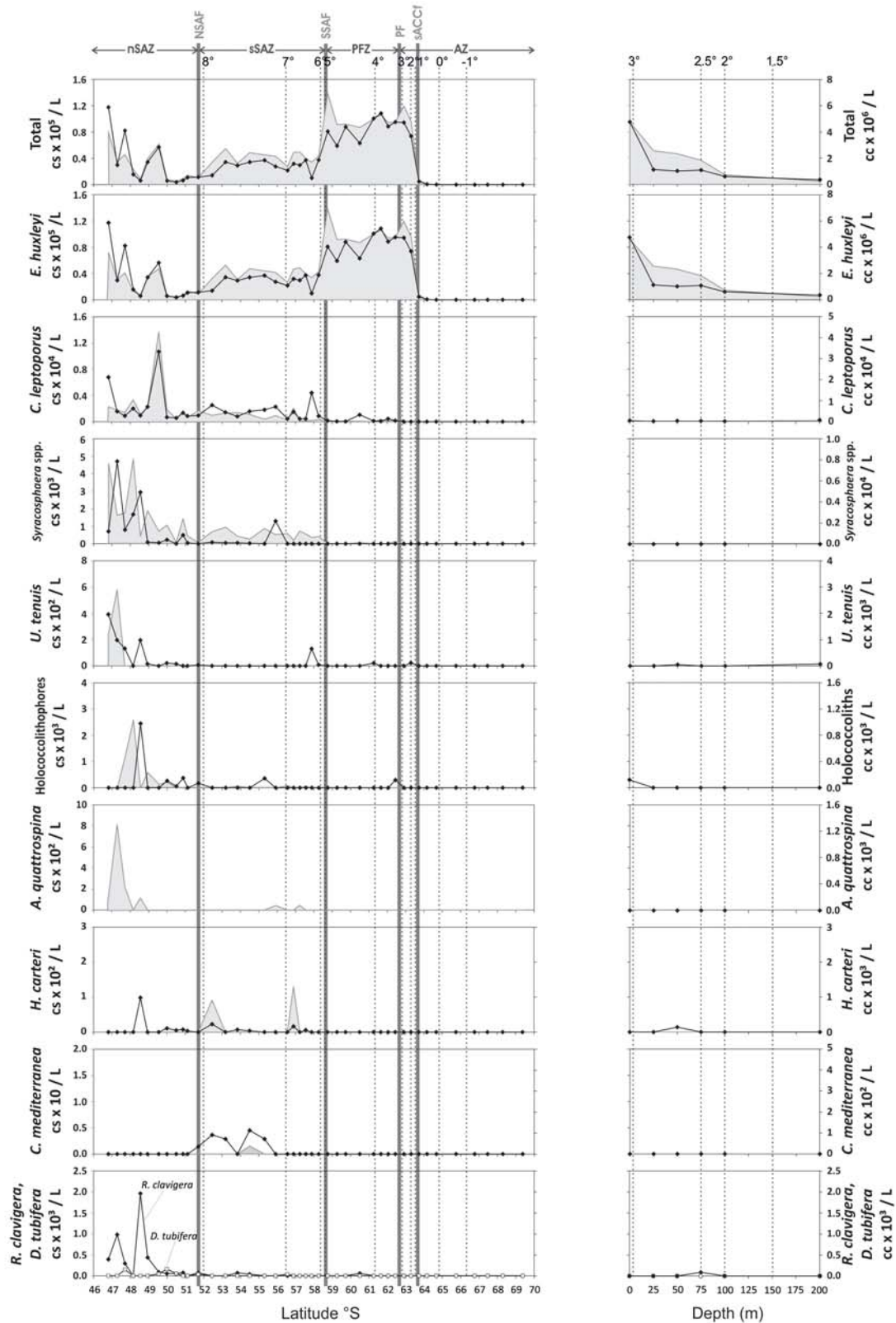
In this region, *C. leptoporus* is represented exclusively by the sub-species *leptoporus* (intermediate morphotype). As also pointed out by Böckel and Bauman (2008), this subspecies occurs south of the STF and is characterized by very small coccoliths, at the lower limit of its size-range: coccoliths as small as  $4.9\mu\text{m}$  can occur with larger ones on the same coccosphere (Pl. 2 fig. 4). If these forms are found as free coccoliths, they could be mis-identified as belonging to the small *C. leptoporus* morphotype. The latter type, identified by Böckel and Bauman (2008) as a significant part of the subtropical assemblage, was not recorded in our samples.

Two minor species, *A. quattropsina* and *U. tenuis*, occurred only in the northernmost samples, close to the STF. *Acanthoica quattropsina* is known to be part of the subtropical assemblage, but its occurrence has already been documented southward into the PFZ (Eynaud et al. 1999). *Umbellosphaera tenuis* is known to occur in the subtropical as well as subantarctic zone, but specimens of type II, as recovered in our samples (Pl. 3 fig. 4), were previously described as typically restricted to the area of the STF (Böckel and Bauman 2008).

Other species belonging to the subtropical assemblage (*Rhabdosphaera* spp., *D. tubifera*, *P. vandellii*, *U. sibogae*, *S. pulchra*) and species from the deep photic zone (*Florisphaera profunda*, *Gladiolithus flabellatus*, *Syracosphaera lamina*) were recorded here only as free coccoliths and were thus probably advected from subtropical waters.

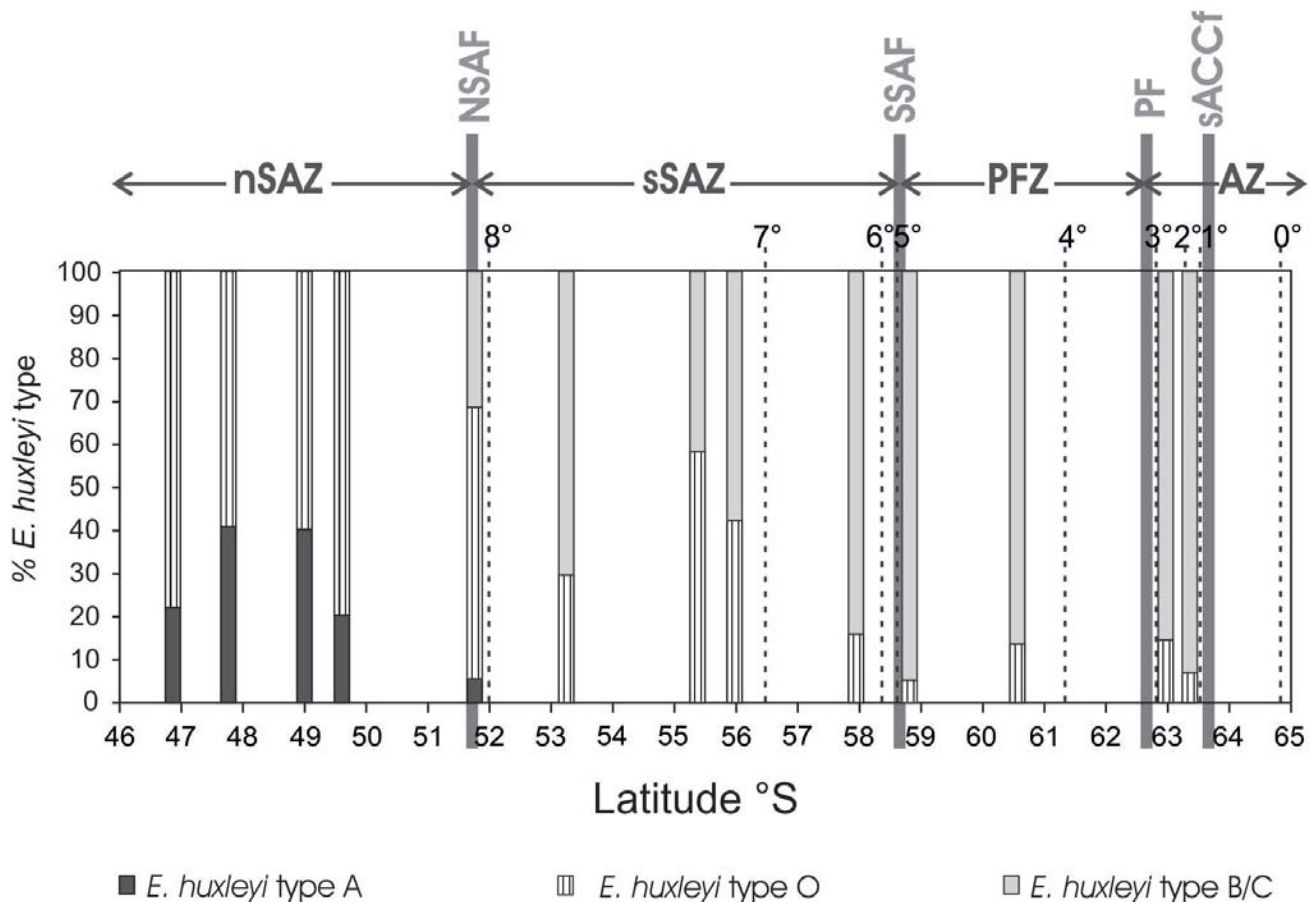
Small species of *Syracosphaera* are known to be abundant in the region of the STF (Böckel and Bauman 2008) and part of the subantarctic assemblage (Eynaud et al. 1999; Findlay and Giraudeau 2000): within the nSAZ we recovered specimens of *S. borealis*, *S. halldalii*, *S. nana* (HET and HOL), *S. nodosa*, *S. ossa*, *S. pemmadiscus* and *Ophiaster* sp., with body coccoliths resembling *O. hydroideus* but lacking antapical link coccoliths. All but one of these species were restricted to the nSAZ, so that the NSAF, corresponding to the sea surface  $8^\circ\text{C}$  isotherm, represents a major boundary to their southern distribution.

In the sSAZ, the only *Syracosphaera* species was *S. borealis*. Interestingly, *Corisphaera strigilis*, recently reported as the holococcolith form of *Syracosphaera hirsuta* (Šupraha et al.



TEXT-FIGURE 2

Total abundance of coccolithophore species (grey area, coccospheres; diamonds, coccoliths) along the transect and at one CTD station at the PF. Fronts' locations are from Campanelli et al. (2011).



TEXT-FIGURE 3

Relative abundance of the different *E. huxleyi* morphotypes at selected stations from SEM counts: dark grey, type A; lines, type O; light grey, type B/C.

2015), was the only holococcolithophore recorded throughout the whole SAZ. Given the close morphological similarity between *S. borealis* and *S. hirsuta* (which was formerly described by Young et al. 2003 as *S. borealis* type II) and the overlapping biogeographic distribution of *S. borealis* and *C. strigilis*, we can speculate that *S. borealis* and *S. hirsuta* represent the subpolar and temperate heterococcolith expression of *C. strigilis*, respectively.

The SSAF represents another major oceanographic boundary, marking the southern limit for minor species (apart from sporadic occurrences of *C. leptoporus* and *S. borealis* southward) and the occurrence of a monospecific and more abundant *E. huxleyi* assemblage (assemblage D of Findlay and Giraudeau 2000).

#### Dynamics of *E. huxleyi* populations across the ACC fronts

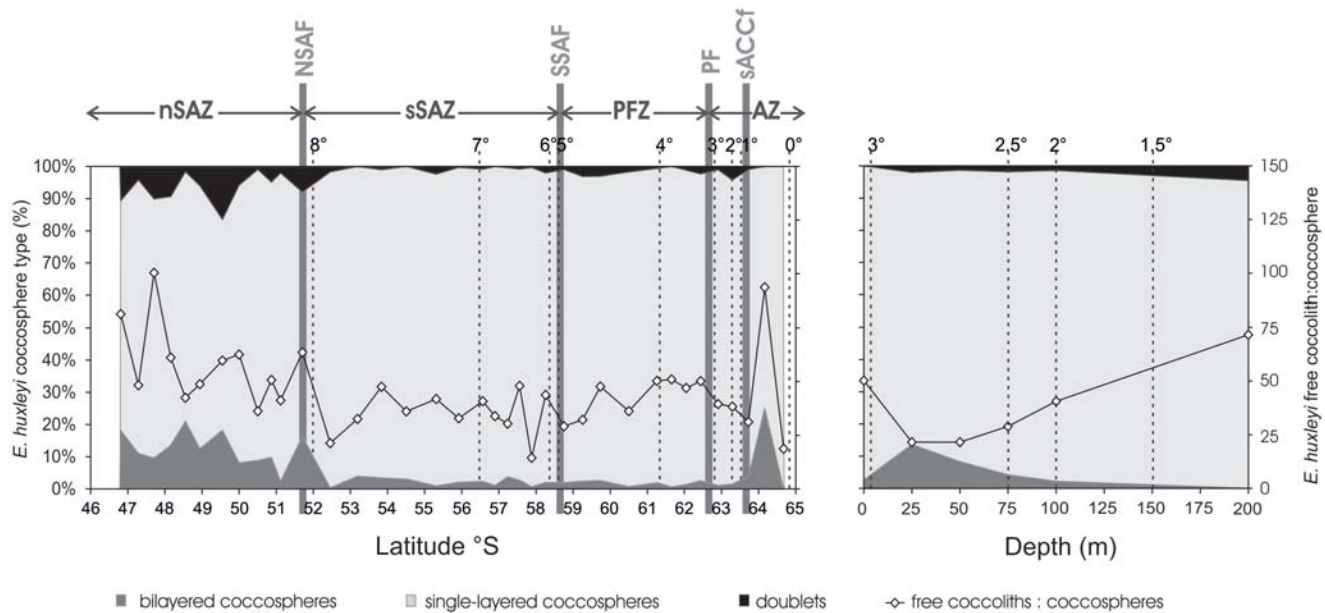
Observations from batch and continuous cultures of *E. huxleyi* showed that limitation by either N or P induce increased coccolith production per cell (Linschooten et al. 1991; Paasche and Burbak 1994; Paasche 1998; 2002; Fritz 1999; Riegman et al. 2000) as growth rate decreases, resulting in bi- and multi-layered coccospheres with up to 60 coccoliths forming

the coccosphere (Balch et al. 1993). However, contrasting effects have been shown for the two limiting nutrients: cells growing under N limitation decrease in size (Müller et al. 2008), increasing the surface to volume ratio and thus nutrient uptake efficiency (Müller et al. 2012), and produce smaller coccoliths (Paasche 1998); in contrast, cells growing under P limitation increase in size (Paasche 2002; Zondervan 2007; Müller et al. 2008) and produce larger coccoliths (Paasche 1998).

Field observation of coccolith overproduction by *E. huxleyi* and formation of multiple layers are common from bloom areas, in particular in the central part and/or later stages of blooms, which are likely nutrient-limited (Fernandez et al. 1993; Balch et al. 1996). However, observations from non-bloom areas are scarce: Böckel and Bauman (2008), studying coccosphere concentration along a transect in the SO, reported increased abundance of bi-layered *E. huxleyi* coccospheres in frontal waters at the STF.

Culture experiments also showed that as cells shift from log-phase to stationary phase following nutrient limitation, coccolith detachment rates increase (Balch et al. 1993; Fritz and Balch 1996; Fritz 1999). This results in an increase in the ratio of free coccoliths:coccospheres from 10-20 for cells growing in





TEXT-FIGURE 4

Relative abundance of single-layered coccospheres (light grey), bi- and multilayered coccospheres (dark grey) and doublets of *E. huxleyi* (black) along with the ratio of *E. huxleyi* free coccoliths:coccospheres (line with diamonds).

log-phase (Paasche 2002) to values up to 200 for cells in stationary phase (Balch et al. 1993).

Observations of free coccolith:coccosphere ratios from natural populations are mostly focused on bloom areas, showing values in the range 10–40 up to >350 in both the North Atlantic (Balch et al. 1991; Fernández et al. 1993; Holligan et al. 1993; van der Wal et al. 1995; Marañón and Gonzáles 1997; Head et al. 1998; Rees et al. 1999, 2002; Lampert et al. 2002; Harlay et al. 2010,) and the Southern Ocean (Holligan et al. 2010; Poulton et al. 2013; Balch et al. 2014). A few observations from non-bloom populations report values of ~10 free coccoliths:coccospheres (Poulton et al. 2010).

In our samples, bilayered coccospheres in the range 0–4% and free coccolith:coccosphere ratio of 20–50 characterized *E. huxleyi* populations throughout the sSAZ and PFZ. In the nSAZ and in one sample south of the PF, the concentration of bilayered coccospheres increased to values >10% and the ratio of free coccoliths:coccospheres rose to values >36 and up to >100. This could lead to the inference that *E. huxleyi* populations from the sSAZ and PFZ represent a similar condition of actively growing cells, while populations from the nSAZ document, at some stations, a later stage of growth. Data of N and P from the same transect (Campanelli et al. 2011) showed levels above limiting values, although a clear draw-down was evident from previous cruises earlier in the season.

Total *E. huxleyi* coccosphere abundance was distinctly higher in the PFZ than in the sSAZ and *E. huxleyi* doublets were most abundant in the PFZ than in the sSAZ, suggesting a higher growth rate there. Separate peaks in doublets' concentration (up to 9–16%) in a few northernmost samples suggests that cells were actively growing at places. Therefore the recorded high

ratio of free coccoliths:coccospheres might indicate the occurrence of an earlier or nearby bloom, from which free coccoliths are advected. The absence of doublets, the high percentage of bilayered cells and the increase in the ratio of free coccolith:coccosphere south of the PF suggests that cells were not actively growing there.

Throughout the transect, free coccoliths were detected as single plates and not in layers, contrary to what was observed in aged cells from cultures (Balch et al. 1993), which might be due to the fact that the preservation of coccoliths layers is unlikely in the natural environment.

#### Biogeography of *E. huxleyi* morphotypes and southernmost occurrence

McIntyre and Bé (1967) revealed the dominance of a cold-water (as opposed to a warm-water) form of *E. huxleyi* in subpolar waters. This form was described and imaged (their plate 6, fig. B) as having flattened (and fewer) DS elements, solid proximal shield and central area closed by a central plate of thin interlocked elements. It corresponds to the cold water form of Nishida (1986), type K of Hiramatsu and De Dekker (1996) and type C of Findlay and Giraudeau (2000). McIntyre and Bé's warm water form corresponds to type A (Young and Westbroek 1991). Following Young et al. (2003), the sub-antarctic form has been described as type B/C and separated, based on coccolith size, from types B and C, which also have lightly calcified DS elements and thus a similar appearance but which are respectively larger or smaller. More recently, Hagino et al. (2011) separated a new type within forms having lightly calcified DS elements, based on the characters of the central area: in type O the central area is open or covered by an organic membrane. Based on re-observation of samples from previous study

and of SEM images from previous publications, Hagino et al. (2011) concluded that *E. huxleyi* type O is extensively distributed also in the SO. However, no details of its latitudinal distribution and its relationship with the other types has been added since.

A shift in dominance between type A and B/C+O at the STF is documented by Hiramatsu and De Dekker (1996) and Findlay and Giraudeau (2000) south of Tasmania, type A disappears south of the SAF, as also shown in Cubillos et al. (2007, their fig. 5, excluding its southward spread into the PFZ in October–November 2004). Similarly, along our transect starting south of the STF, type A represents 5–41% of the species in the nSAZ and is not recorded southward of the NSAF (51.7°S, corresponding to the SAF of Findlay and Giraudeau (2000)). The dominant type in the nSAZ and sSAZ was type O. We included in this type all specimens whose central area is open or covered by an organic membrane. Coccolith morphology within this type were however variable in DS size (2 to 4.1 µm, with large size variability among coccoliths on the same coccosphere), and morphology (variable number of elements, variable elevation of the elements, e.g. Plate 1).

The typical Antarctic form, type B/C, although not recovered in the nSAZ, was abundant in the sSAZ and became the dominant type in the PFZ and in the northernmost AZ. As imaged in Plate 1, figures 5 and 6 of Young et al. (2003), the central area in coccoliths of this type is closed by interlocking elements and the tube elements are well-developed and clearly separated from the distal shield, giving this type a characteristic appearance (our Pl. 1, figs. 9,10). Although Young et al. (2003) defined the DS size range of this type between 3–4 µm, similarly to Gravalosa et al. (2008) we found slightly smaller coccoliths, with average DS length of 2.8 µm ( $n = 32$ ), and coccoliths as small as 2.1 µm occurring along with larger (3 µm) ones on the same coccosphere. Peculiar calcification features, such as the regular closed-grill-like element pattern of the central area (Pl. 1, fig. 11) and the lath-like development of some DS elements (Pl. 1, fig. 12) were observed and may add on the morphological features of this type.

Dissolution morphotypes were observed throughout the transect, but were generally rare (excluding a single station within the nSAZ), as also reported by Cubillos et al. (2007) south of Tasmania, and in contrast with observations of Mohan et al. (2008) which reported dominant type D (dissolution morphotype) in waters of the PF.

The peak in abundance of *E. huxleyi* in the PFZ is close to the southern limit of the species: *E. huxleyi* dropped south of the PF, coinciding with a temperature gradient from 2°C to <1°C, from  $119 \times 10^3$  cs/L to  $7 \times 10^3$  cs/L at 63.7°S, then occurred sporadically and with very low concentration ( $0.2\text{--}0.3 \times 10^3$  cs/L) until 67.4°S at temperatures of -1°C: the latter occurrence was likely related to lateral advection.

The biogeographic extent of coccolithophores and in particular of *E. huxleyi*, the most widespread coccolithophore species, is thought to be limited to the South by the 2°C isotherm (McIntyre and Bé 1967; Verbeek 1989) or the summer 0°C isotherm (McIntyre et al. 1970). Early and recent work addressed the southernmost latitudinal reach of *E. huxleyi* in relation to the ACC fronts and found that *E. huxleyi* was not a common inhabitant of the AZ. Recently, Cubillos et al. (2007) and Winter et al. (2014) proposed a southward expansion of the *E. huxleyi* biogeographic range in recent times (>90s) as compared to ear-

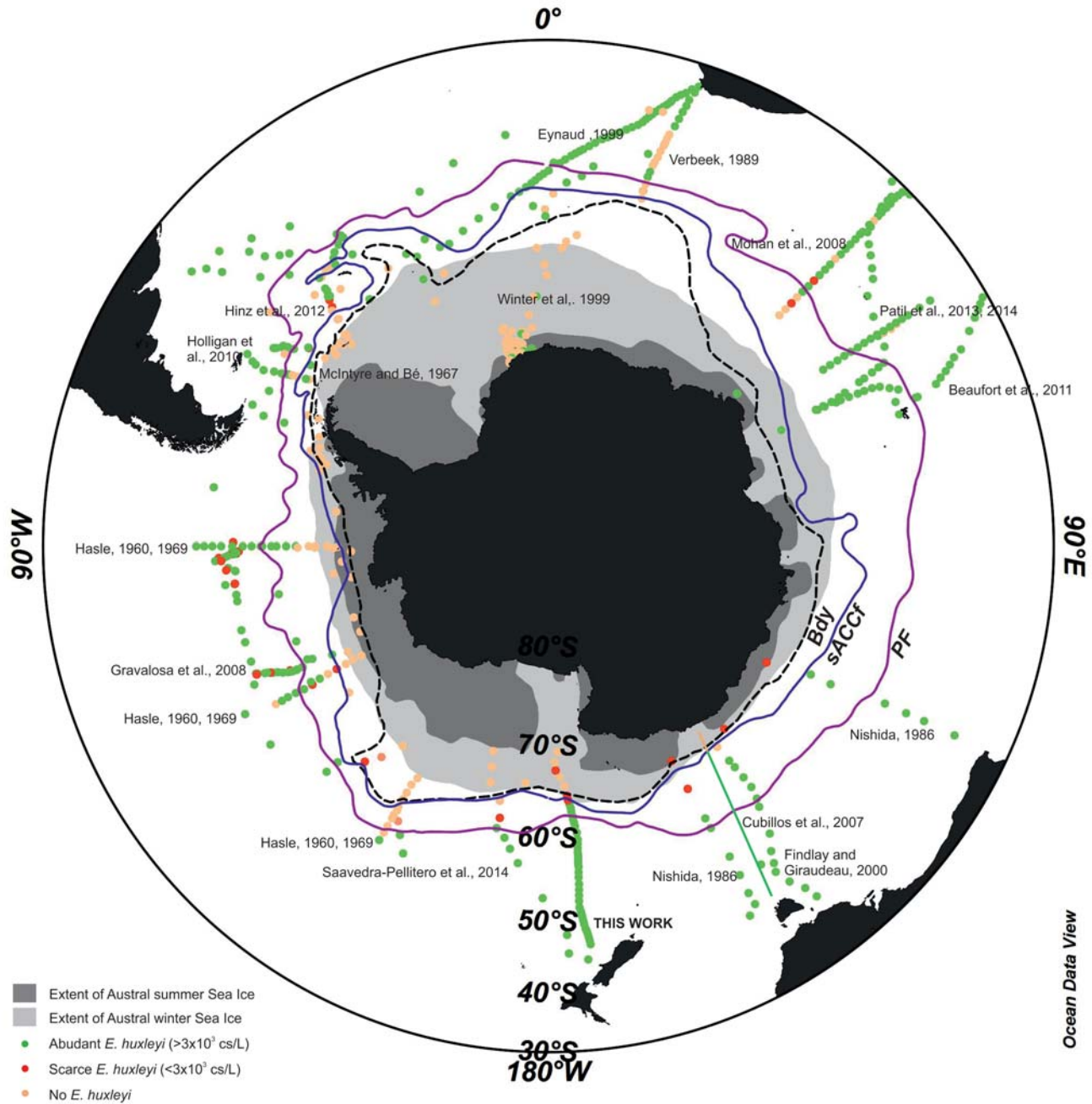
lier observations, reporting the previous absence of *E. huxleyi* in the polar waters south of the PF. Indeed, McIntyre et al. (1970) defined the PF (Antarctic Convergence, 50–55°S) as the southern boundary of the species in the Pacific, but also located such limit at summer sea surface temperature of 0°C (i.e. lower than the 2°C surface temperature that marks the surface expression of the PF) and showed in their figure 1 no samples southward where the species was absent. In contrast, McIntyre and Bé (1967) had reported in their figure 8 the occurrence of *E. huxleyi* down to 60°S in the South Atlantic, south of the PF and reaching the sACCF position. In the recent survey of Holligan et al. (2010) and Hinz et al. (2012) from the same area, no significant latitudinal difference was observed. In order to precisely visualize the southern distribution of *E. huxleyi* from all (pre- and post '90s) previous surveys, we plotted the abundant occurrence, scarce presence ( $<3 \times 10^3$  cs/L) and absence of *E. huxleyi* on a global south-polar projection (text-fig. 5), also adding the standard positions of the PF (Antarctic Convergence), the sACCF and the southern Boundary (Orsi et al. 1995) and the mean winter and summer sea ice coverage. Given the strong latitudinal variations in the ACC fronts' position and seasonal ice extension across the different sectors of the SO, this type of visualization allows to draw strong inferences, which cannot be obtained when the data are plotted on a standard section with fronts' positions fixed at certain latitudes (e.g. Winter et al. 2014). Revisiting early data in this perspective, it is clear that *E. huxleyi* was already present with high abundance to the south of the PF (around 53 to 56°S) back in the '80s and early '90s south of Tasmania, and displayed very low concentration or even absence around the sACCF south of 60°. This pattern is very similar to our findings south of New Zealand, where the position of the sACCF marks the significant drop of *E. huxleyi* abundance. Cubillos et al. (2007) found in the same area south of Tasmania an extended occurrence of *E. huxleyi* down to the sACCF, which is located at 61–64°S (latitude range encompassing the seasonal shift), therefore suggesting a southward expansion as compared to previous records, but coccosphere densities are clearly lower (their fig. 4) southward of 61°S.

In the Pacific, Hasle (1960) described the absence of *E. huxleyi* from polar waters. *E. huxleyi* was abundant at the PF and well south of it into the AZ (although with decreasing abundance, see also her fig. 1) until 64.3°S and until 63.05°S along the transects crossing the eastern Pacific at 90°W and 120°W, respectively, but did not reach further south of the PF in the western Pacific along the transect at 150°W. Recent investigation at overlapping locations in the eastern and western Pacific (Gravalosa et al. 2008 and Saavedra-Pellitero et al. 2014, respectively) revealed indeed a very similar pattern. No significant shifts in the latitudinal distribution of *E. huxleyi* can be therefore inferred, at least in this area.

## CONCLUSIONS

Our survey in surface waters along a transect from New Zealand to the Ross Sea in early January 2005 enabled the definition of a latitudinal succession of coccolithophore species implying the role of the ACC fronts in shaping their distribution.

*E. huxleyi* was the most abundant species throughout the investigated transect. Coccosphere abundance was maximum in the northern samples, in the PFZ and at the PF, in accordance with previous surveys. Coccosphere abundances indicated non-bloom conditions throughout. The abundance of bilayered coccospheres and the free coccoliths:coccosphere ratio pointed



TEXT-FIGURE 5

Compilation of previous data on the southern distribution of *E. huxleyi* plotted on an ortho-polar projection (ODV, Shlitzer 2008). Seasonal sea-ice distribution is from ODV pre-bathymetry and fronts' positions are plotted through the ODV Graphic Object tool: PF = Polar Front, sACCF = Southern ACC Front; Bdy = Southern Boundary.

to actively-growing cells in the sSAZ and PFZ and mature populations, possibly growing under nutrient limitation, at certain locations within the nSAZ and at the southernmost limit of the species' range at the sACCF.

-*E. huxleyi* morphotypes showed a clear latitudinal distribution, with type A restricted to the nSAZ, type O abundant in the nSAZ and sSAZ and scarce in the PFZ and type B/C abundant in the sSAZ and especially in the PFZ.

-Among minor species, *C. leptoporus* ssp. *leptoporus* and *Syracosphaera borealis* are distributed throughout the SAF, with minor occurrence into the PFZ. Given the overlapping distribution of *S. borealis* and *Corisphaera strigilis*, the most abundant *Syracosphaera* and holococcolithophore species, respectively, and the strong similarity between *S. borealis* and *S. hirsuta*, recently found in association with *C. strigilis*, we hypothesize that they represent the life-cycle stages of the same species.



-Other minor coccolithophore species, represented by *Syracosphaera* spp. *U. tenuis*, *A. quattropsina*, *Ophiaster* sp., are restricted to the nSAZ.

-The southernmost extent of coccolithophores is defined by the distribution of *E. huxleyi*: its abundance drops south of the PF but its southern limit of occurrence above  $10^3$  cs/L coincides here with the location of the sACCF and temperatures of  $1^\circ\text{C}$ .

-Although recent work suggested a southward expansion of the *E. huxleyi* latitudinal range after the '90s, re-evaluation of existing distribution data in relation with a dynamic framework of the ACC fronts, showed no significant differences at overlapping locations at least for the Atlantic and Pacific sectors of the SO.

## ACKNOWLEDGMENTS

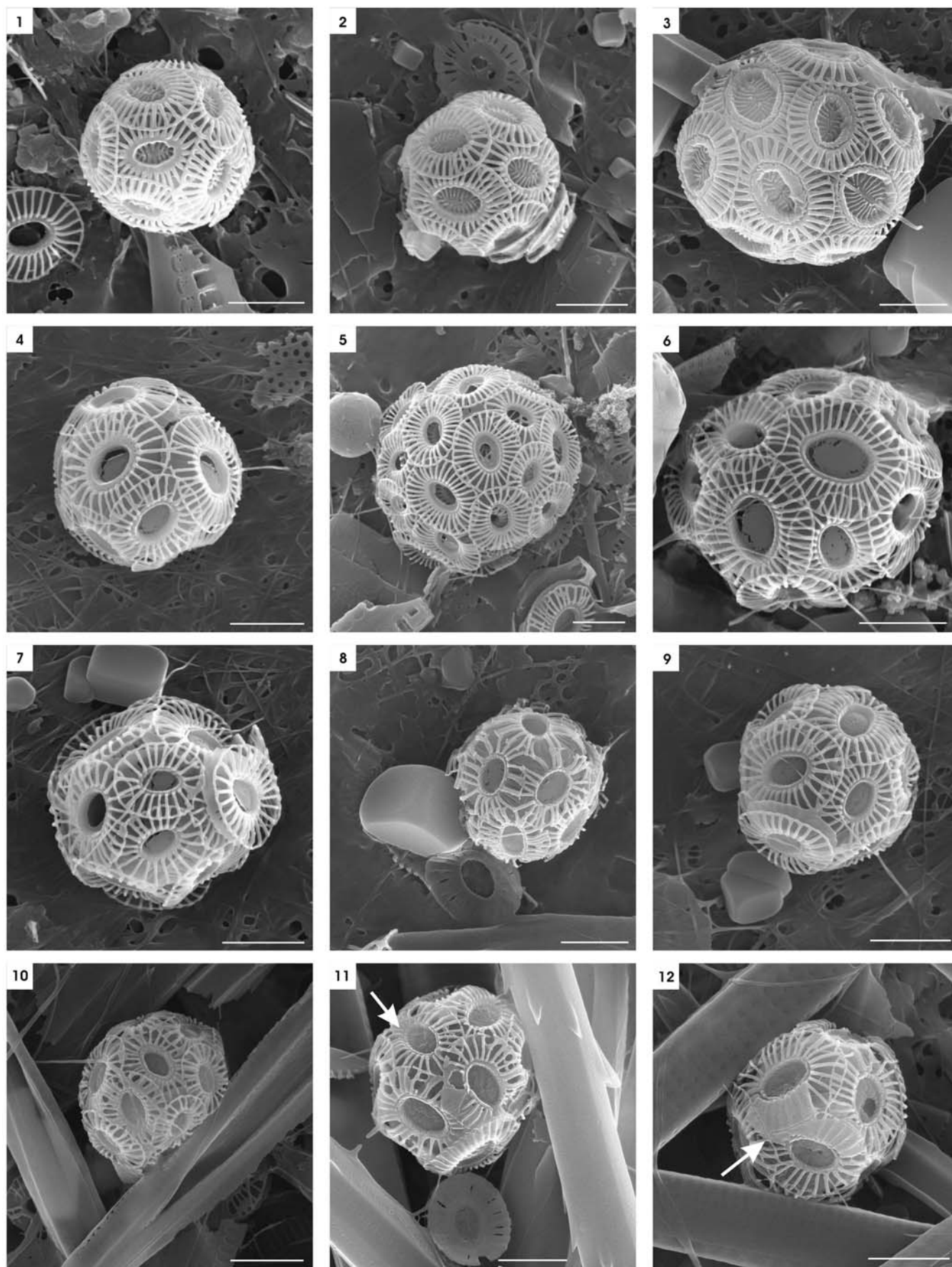
Data and samples for this study were obtained during the XX Italian Antarctic Expedition on board R/V *Italica*. Phytoplankton samples were collected within ABIOLCLEAR Project, financed by the Italian PNRA (Piano Nazionale di Ricerca in Antartide). R. Cristina-Reggiani and P. Gentile are warmly thanked for their assistance in operating the SEM. The manuscript was greatly improved by the critical reviews of Jeremy Young and Kyogo Hagino.

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## PLATE 1

- 1 *E. huxleyi* type A, moderately-calcified tube elements (tr001-06);
- 2 *E. huxleyi*, normal form (TR001-20);
- 3 *E. huxleyi* type A, slightly overcalcified and etched tube elements (TR003-13);
- 4 *E. huxleyi* type O (TR013-54);
- 5 *E. huxleyi* type O, bilayered (TR001-41);
- 6 *E. huxleyi* type O with a few large coccoliths having a large number of DS elements (resembling type B, TR025-01);
- 7 *E. huxleyi* type O with small apical coccoliths and elevated distal shield (resembling type C, TR013-56);
- 8 *E. huxleyi* type O, organic membrane closing the central area and etched DS elements (TR003-20);
- 9 *E. huxleyi* type B/C, typical form with solid central area and tube elements separated from the rim (tr013-61);
- 10 *E. huxleyi* type B/C with solid central area and tube elements separated from the rim (TR033-3);
- 11 *E. huxleyi* type B/C with a regular pattern of elements in the central area (arrow) (TR043-9);
- 12 *E. huxleyi* type B/C with (secondary?) calcification on some of the DS elements, creating a pattern of imbricated tiles (arrow) (TR043-1). Scale bar =  $2\mu\text{m}$ .

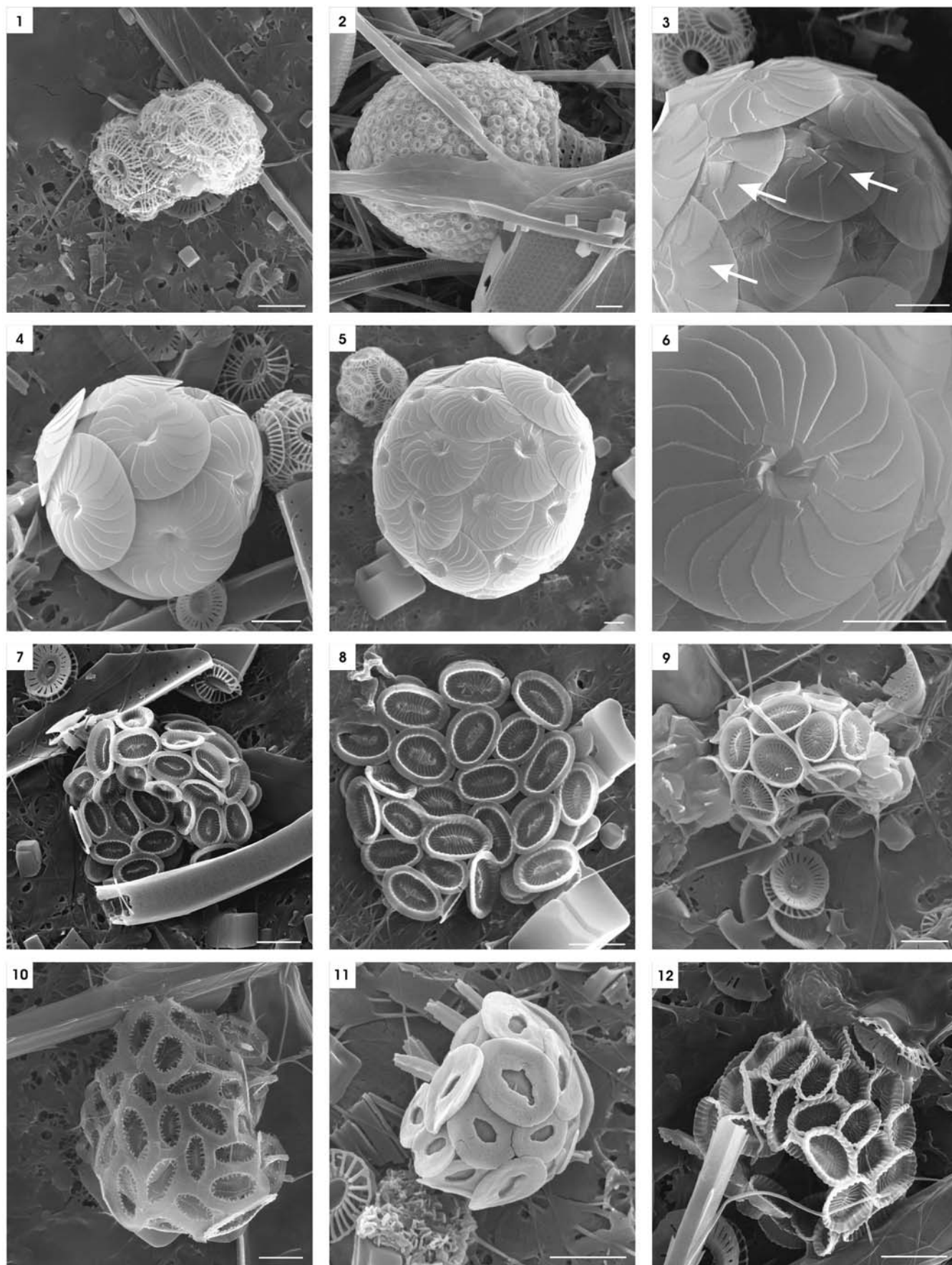


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## PLATE 2

- 1 *E. huxleyi* doublet (TR001-12);
- 2 *Codonellopsis pusilla* tintinnid lorica covered with coccoliths of *E. huxleyi* type B/C (TR033-10);
- 3 *C. leptoporus* spp. *leptoporus* showing irregular imbrication of DS elements (arrows) (TR025-11);
- 4 *C. leptoporus* spp. *leptoporus*, showing coccoliths of different size, 4.8–5.8µm (TR001-38);
- 5 *C. leptoporus* spp. *leptoporus*, large coccosphere (TR013-62);
- 6 *C. leptoporus* spp. *leptoporus*, irregular pattern of some DS elements (TR013-60);
- 7 *Syracosphaera borealis*, showing a more developed axial ridge (TR001-36);
- 8 *Syracosphaera borealis*, showing a more developed axial ridge (TR013-48);
- 9 *Syracosphaera nodosa*, endotheca (TR001-42);
- 10 *Syracosphaera halldalii* (TR003-7);
- 11 *Syracosphaera ossa* with no axial structure and very broad distal flange (TR001-43);
- 12 *Syracosphaera pemma-discus* (TR003-22). Scale bar = 2µm.



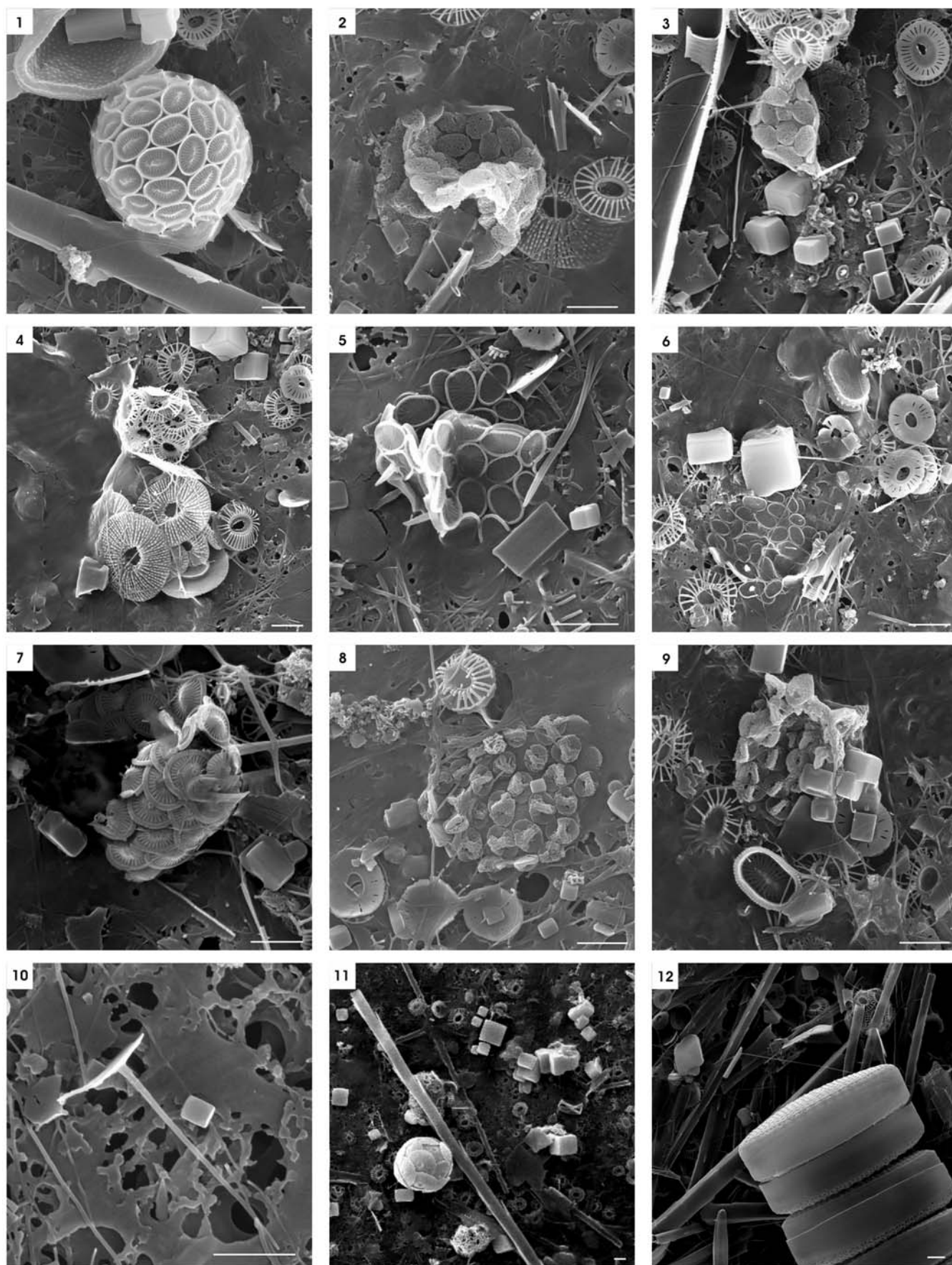


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### PLATE 3

- 1 *Syracosphaera nana* HET (TR001-19);
- 2 *Syracosphaera nana* HOL (TR001-11);
- 3 *S. nana* HOL and undetermined small holococcolithophore, possibly *A. origami* (TR001-26);
- 4 *Umbellosphaera tenuis* type II (TR001-28);
- 5 *Ophiaster* sp. cf. *O. hydroideus* (TR001-29);
- 6 *Ophiaster* sp. cf. *O. hydroideus* (TR001-5);
- 7 *Acanthoica quattropsina* (TR001-47);
- 8 *Corisphaera strigilis* (TR001-40);
- 9 *Corisphaera strigilis* (TR001-22);
- 10 free coccolith of *Palusphaera vandellii* (TR001-7);
- 11 sample view from the nSAZ with *E. huxleyi* coccospheres and coccoliths, *C. leptoporus* (TR001);
- 12 sample view from the PFZ with *E. huxleyi* coccospheres and abundant diatoms (TR043). Scale bar = 2µm.







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