Marine Micropaleontology 109 (2014) 1–20

Contents lists available at ScienceDirect

Marine Micropaleontology

journal homepage: www.elsevier.com/locate/marmicro

Research paper

Biogeographic distribution of living coccolithophores in the Pacific sector of the Southern Ocean

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ARTICLE INFO

Article history:
Received 16 June 2013
Received in revised form 25 February 2014
Accepted 2 March 2014
Available online 12 March 2014

Keywords:
Coccolithophores
Southern Ocean
Depth
Front
Ecology

ABSTRACT

This paper adds to a series of studies addressing the distribution of living coccolithophores in the Southern Ocean (SO). We investigated plankton samples collected during *RV Polarstern* cruise ANT-XXVI/2 (from 27th November 2009 to 27th January 2010) along a broad E–W transect in the Pacific sector of the SO during austral summer. One hundred and fifty samples from twenty-nine stations were collected from the upper 150 m of the water column. Both coccoliths and coccospheres per sample were counted separately using a scanning electron microscope (SEM). The highest abundances of $640 \cdot 10^3$ coccospheres/l were reached close to the Subtropical Front (STF) and increases in the numbers of coccospheres and coccoliths were found both at the Subantarctic Front (SAF) and the Polar Front (PF). However, the numbers decrease southward until almost a monospecific assemblage and sporadic record of *Emiliania huxleyi* (types B/C and C) south of the PF. Thirty-three coccolithophore species, including sixteen species found as isolated coccoliths, were identified of which *E. huxleyi* is clearly the most dominant coccolithophore taxon in the studied samples. Two main coccolithophore assemblages were established coincident with areas bounded by the oceanographic fronts: the Polar Front Zone (PFZ) and Subantarctic Zone (SAZ). In the upper photic zone of the SAZ, *Acanthoica quattrospina*, *Calcidiscus leptoporus*, *Coccolithus pelagicus* (sensu lato) HOL, *E. huxleyi* type A, *Ophiaster* spp. and *Syracosphaera* spp. among others were found. The PFZ was characterized by a reduced number of species, i.e., *Calciopappus caudatus*, *E. huxleyi* types B, B/C and C, as well as *Pappomonas* spp. and *Papposphaera* spp. The sea surface temperature measured in situ was the most prominent factor influencing coccolithophore diversity, distribution and assemblage compositions in the Pacific sector of the SO during austral summer. Coccolithophore biogeography in the study area showed marked differences with the northern high latitudes; the reduced presence of the cold water species *Coccolithus pelagicus*, abundant in the (sub) Arctic region, and the dominance of *E. huxleyi* type B/C and C in the SO contrasts with the dominance of *E. huxleyi* types A and B in the North Atlantic. Findings such as these cover existing gaps in an unexplored area of the SO as well as supporting previous research performed in neighboring areas. The current coccolithophore numbers and assemblage distribution in relation to the frontal dynamics of the SO provide valuable information for potential future paleoceanographic reconstructions.

1. Introduction

Coccolithophores, phytoplankton belonging to the division Haptophyta (Young and Bown, 1997; Young et al., 2003) are one of the most important producers of marine carbonate in the pelagic realm (Westbroek et al., 1993). Their distribution and diversity in the photic zone are affected by surface oceanic circulation and therefore by different parameters such as sea surface temperature (SST), sea surface salinity (SSS) and nutrient availability. Coccolithophores are present in a wide range of marine environments, from tropical to subpolar regions (Winter et al., 1994; Ziveri et al., 2004). Recent concerns about climate change and the effects of rising surface ocean temperatures and possibly increasing ocean acidification on marine organisms have triggered an increasing interest in coccolithophore ecology (e.g., Beaufort et al., 2008, 2011; Charalampopoulou et al., 2011). It is currently not known how coccolithophore populations may adapt to proposed changes in their environment if at all. However geographical shifts in the occurrences of coccolithophore species and assemblage compositions have been observed already (e.g., Cubillos et al., 2007; Winter et al., 2013). Thus, detailed knowledge of coccolithophore spatial variations, assemblage composition, and production are needed. Although general aspects of coccolithophore biogeography and habitat are known from taxonomic surveys of the plankton and of bottom sediments in various oceans (e.g., Winter et al., 1999; Andruleit et al., 2000; Gravalosa et al., 2008; Ho et al., 2012), little work has been

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http://dx.doi.org/10.1016/j.marmicro.2014.03.003
0377-8398/

done on absolute numbers of single species relative to ecological parameters in natural populations. Records on coccolithophores from the surface waters of the Pacific sector of the Southern Ocean (SO) have been comparatively scarce so far.

Therefore the lateral and vertical coccolithophore compositions along a broad E–W transect of the SO were examined qualitatively and quantitatively. In addition, the complex relationship between coccolithophore taxa and environmental conditions was revealed by multivariate analysis. Comparison and combination of our results with living coccolithophore studies carried out in different sectors of the SO were performed. Although plankton assemblages from the photic zone only provide snap-shot insights into the living communities, they provide essential information on the occurrence and distribution of the species, and the ecology of different taxa. This is a prerequisite for the application of coccolithophores and their remains (organic and inorganic) in paleoceanographic reconstructions.

2. Material and methods

One hundred and fifty samples were obtained from 29 stations during the expedition ANT-XXVI/2 from 27th November 2009 to 27th January 2010 (Punta Arenas, Chile – Wellington, New Zealand) on board the *R/V Polarstern* within the area 44.8°S to 68.7°S and 80.1°W to 174.5°E (Fig. 1). For the study of the coccolithophore assemblages, 2 l of water were taken using a Rosette sampler with 24 × 12 l Niskin bottles (Ocean Test Equipment Inc.) attached to a conductivity–temperature–depth (CTD) device. The bottles were fired by an SBE carousel (SBE32). To survey the water column, a Seabird SBE 9plus sensor (Seabird Electronics Inc.) was used (Gersonde et al., 2011). Seawater samples were taken at different water depths (surface to deep) for precise multi-purpose oceanographic research and 4 to 7 samples per station were collected for coccolithophore studies from 10 to 150 m depth (Table 1).

2.1. Techniques for the preparation and identification of coccolithophore taxa

The samples were filtered through cellulose nitrate filters (0.45 μm pore size) onboard. The filters were dried in an oven at ~40 °C during 24 h and stored in Petri dishes. Once on land a small piece of the filter (<1 cm^2) was cut out, fixed on an aluminum stub and sputtered with gold/palladium. Coccolithophore assemblages were examined with Zeiss DSM 940A scanning electron microscope (SEM) at magnifications of 3000×, and 5000× when required.

Identification of species followed the taxonomic guide of Young et al. (2003) as well as the revised classification of Jordan et al. (2004) and www.nannotax.org. We distinguished four different morphotypes of *Emiliania huxleyi* in the study area. These are type A (*huxleyi*, Plate Ia), type B (*pujosiae*, Plate Ib), type B/C (Plate Ic) and type C (*kleijneae*, Plate Id). We have not separated *E. huxleyi* type O, a new morphotype based on molecular genetic studies recently described by Hagino et al. (2011). Specimens of this type could have been incorporated into B, B/C and/or C morphotypes in this research. *Emiliania huxleyi* type C and type B/C coccoliths look very similar; both types have delicate distal shield elements and a central area opened or covered by a thin plate (Young et al., 2003). Even though they have different sizes (type C, 2.5–3.5 μm and type B/C, 3–4 μm, Young et al., 2003), classification of the specimens was occasionally hindered by overlapping size ranges.

Coccospheres and coccoliths were counted in transects across the filter area separately; we counted a minimum of 400 coccoliths and 200 coccospheres per sample whenever possible. All the sampling points were considered when plotting the number of coccospheres/l and coccoliths/l. However, stations with less than 50 coccospheres or less than 100 coccoliths were excluded when plotting the percentages of the different species. Also we only show the coccosphere numbers and percentages for selected species in this work. In addition the presence or absence of diatoms was indicated based on SEM visual observations. When present, a semi-quantitative assessment at a magnification of

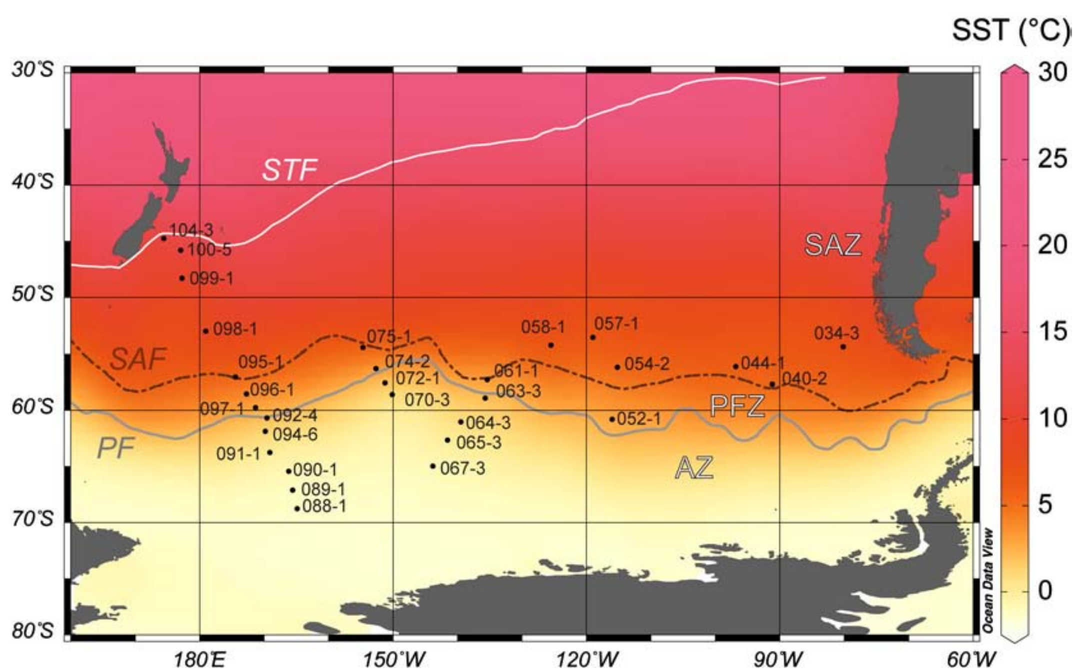


Fig. 1. Sea surface temperature (°C) annual average at 0 m depth in the study area and location of the ANT-XXVI/2 CTD stations plotted with Ocean Data View (ODV) software version 4.5. The different oceanographic fronts are indicated as follows: Subtropical Front (STF) with a white line, Subantarctic Front (SAF) with a brown dashed line and Antactic Polar Front (PF) with a gray line, according to Orsi et al. (1995). The areas between the fronts are referred to as Subantarctic Zone (SAZ), Polar Front Zone (PFZ) and Antarctic Zone (AZ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3000× was done as follows: 0 = low (few specimens per several fields of view), 1 = intermediate (at least one specimen per field of view) and 2 = high (many specimens per field of view). Contour maps were generated with Golden Software Surfer® using the kriging method for

Table 1.
Sampling location of studied plankton samples, numbers of total coccospheres/l, and coccoliths/l as well as in situ sea surface temperature (SST), salinity (SSS) and fluorescence data.

Station	Latitude	Longitude	Sampling depth (m)	Total coccosph./l	Total coccoliths/l	SST (°C)	SSS (psu)	Fluorometer
PS75/034-3	54.37°S	80.09°W	10	61,399	1,067,896	5.68	34.07	0.00
			20	30,830	1,142,585	5.69	34.07	0.00
			40	52,838	619,722	5.63	34.07	0.00
			75	17,082	614,538	5.42	34.09	0.01
PS75/040-2	57.65°S	91.14°W	10	58,352	834,952	4.30	34.06	0.15
			20	22,813	361,596	4.49	34.10	0.15
			40	26,901	863,450	4.59	34.12	0.16
			60	39,268	1,182,797	4.50	34.11	0.16
			75	27,127	328,374	4.49	34.11	0.16
			100	2375	144,036	4.38	34.10	0.16
			150	39,777	587,717	4.20	34.08	0.16
PS75/044-1	56.09°S	96.78°W	10	30,830	692,443	5.32	34.10	0.04
			20	63,770	1,156,156	5.32	34.10	0.04
			40	72,493	938,376	5.29	34.10	0.04
			60	35,407	522,073	5.10	34.13	0.04
			100	10,068	196,844	5.07	34.13	0.04
PS75/052-1	60.77°S	115.98°W	22	69,930	1,273,959	3.33	33.97	0.07
			40	70,379	882,265	3.30	33.97	0.07
			60	133,323	1,609,706	3.19	33.96	0.07
			100	77,591	1,069,517	2.85	33.98	0.04
PS75/054-2	56.15°S	115.13°W	20	493,508	4,893,347	6.83	34.10	0.04
			40	320,249	4,568,793	6.82	34.10	0.04
			60	380,279	5,831,896	6.77	34.09	0.04
			100	125,438	3,628,748	5.50	34.09	0.04
PS75/057-1	53.53°S	118.91°W	20	171,398	2,323,904	7.46	34.05	0.04
			40	161,054	3,054,286	7.45	34.05	0.06
			60	149,951	2,174,634	7.42	34.05	0.06
			100	4567	627,060	5.84	34.19	0.04
PS75/058-1	54.21°S	125.44°W	10	23,938	701,510	8.08	34.08	0.05
			20	54,434	1,785,997	8.08	34.08	0.06
			40	81,187	1,132,678	8.05	34.10	0.06
			60	45,069	499,056	8.09	34.17	0.05
			100	4858	218,457	6.71	34.29	0.03
PS75/061-1	57.22°S	135.39°W	20	266,969	2,039,013	4.61	33.90	0.05
			40	303,323	2,622,362	4.59	33.90	0.07
			55	155,025	3,741,535	4.56	33.89	0.08
			100	10,180	918,674	3.44	33.96	0.06
			150	1975	137,623	3.25	33.98	0.04
PS75/063-3	58.9°S	135.62°W	20	120,316	2,995,603	2.81	33.96	0.07
			40	125,798	1,438,465	2.72	33.97	0.07
			55	118,218	2,310,417	2.49	33.97	0.07
			100	3961	125,243	0.07	34.06	0.03
PS75/064-3	61.01°S	139.46°W	20	710	3550	0.54	33.85	0.09
			40	0	9009	0.50	33.84	0.09
			60	0	0	0.45	33.84	0.09
			100	800	6399	-1.05	33.95	0.03
			150	0	4368	-0.45	34.22	0.03
PS75/065-3	62.6°S	141.51°W	20	0	1453	0.20	33.81	0.12
			40	796	0	−0.07	33.81	0.13
			60	1179	3537	−0.08	33.81	0.10
			100	0	3537	−1.17	33.86	0.07
			150	0	17,989	−1.66	33.96	0.03
PS75/067-3	64.97°S	143.8°W	20	0	3879	−0.46	33.85	0.10
			40	0	5100	−0.55	33.85	0.14
			60	0	2108	−0.58	33.85	0.11
			100	0	2872	−1.39	33.89	0.05
			150	0	0	−0.60	34.27	0.03
PS75/070-3	58.58°S	150.07°W	20	0	875	1.21	34.04	0.05
			40	0	827	0.67	34.05	0.06
			55	0	0	0.47	34.09	0.06
			100	0	839	−1.44	34.19	0.03
			150	0	2264	−0.43	34.34	0.03
PS75/072-1	57.56°S	151.22°W	20	0	24,771	1.56	33.92	0.10
			35	0	5610	1.11	33.94	0.09
			60	982	8835	−0.63	34.01	0.03
			100	1022	24,531	0.13	34.12	0.03
			150	0	26,992	0.47	34.18	0.03

(continued on next page)

Table 1. (*continued*)

Station	Latitude	Longitude	Sampling depth (m)	Total coccosph./l	Total coccoliths/l	SST (°C)	SSS (psu)	Fluorometer
PS75/074-2	56.24°S	152.65°W	20	153,684	4,182,845	4.66	33.85	0.06
			40	72,857	1,677,895	4.02	33.85	0.11
			60	79,239	2,669,292	2.78	33.88	0.06
			100	11,976	975,969	1.86	34.00	0.03
			150	6253	760,892	1.60	34.05	0.03
PS75/075-1	54.43°S	154.64°W	20	393,967	9,033,582	7.72	33.91	0.09
			50	34,109	3,194,214	6.67	33.92	0.15
			65	18,391	2,514,624	6.31	33.97	0.09
			100	5311	701,031	4.46	33.99	0.05
			150	1734	311,664	4.27	34.00	0.03
PS75/088-1	68.73°S	164.8°W	20	0	15,677	−0.67	33.64	0.30
			40	0	2141	−0.98	33.74	0.33
			60	0	6330	−1.72	34.23	0.09
			100	0	0	−1.19	34.33	0.03
			150	0	0	0.04	34.49	0.03
PS75/089-1	67.08°S	165.54°W	20	0	0	−0.50	33.73	0.31
			40	0	0	−1.50	34.04	0.14
			60	0	4520	−1.75	34.23	0.04
			100	0	2606	−1.46	34.29	0.04
			150	0	1130	−0.27	34.45	0.03
PS75/090-1	65.41°S	166.16°W	20	0	0	0.03	33.77	0.17
			40	0	957	0.02	33.77	0.20
			60	0	0	−1.74	34.21	0.10
			100	0	0	−1.53	34.29	0.03
			150	0	0	0.20	34.51	0.03
PS75/091-1	63.69°S	169.07°W	20	0	2113	0.51	33.38	0.09
			35	0	814	−0.52	33.50	0.12
			60	0	15,647	−1.49	33.95	0.04
			100	1130	0	−0.56	34.15	0.03
			150	0	10,027	1.04	34.45	0.03
PS75/094-6	61.82°S	169.75°W	10	2906	5812	2.00	33.43	0.12
			20	0	0	2.00	33.43	0.13
			35	2199	35,184	1.85	33.45	0.14
			60	846	72,796	−1.09	33.77	0.03
			100	8629	283,534	−0.61	33.92	0.03
			150	1018	50,902	1.18	34.20	0.03
PS75/092-4	60.67°S	169.5°W	20	106,539	5,140,603	3.98	33.83	0.07
			40	156,676	2,894,612	3.95	33.83	0.07
			60	38,385	1,366,579	3.51	33.83	0.09
			100	15,547	1,314,692	2.47	33.87	0.03
			150	17,374	1,076,395	2.42	33.94	0.03
PS75/097-1	59.7°S	171.35°W	10	312,074	3,239,131	4.06	33.83	0.09
			20	273,742	2,442,062	4.06	33.83	0.09
			40	351,038	3,989,870	4.05	33.83	0.09
			60	114,686	2,292,431	3.51	33.86	0.09
			80	2669	551,223	2.08	33.88	0.05
			100	14,382	830,057	2.00	33.90	0.04
			150	10,724	732,831	1.89	33.94	0.03
PS75/096-1	58.55°S	172.7°W	10	147,990	2,185,302	5.13	33.91	0.03
			20	163,885	1,815,000	5.13	33.91	0.03
			40	198,032	2,315,776	5.12	33.91	0.04
			60	140,071	1,937,651	5.03	33.90	0.04
			80	54,960	786,272	3.92	33.96	0.05
			100	6415	510,709	3.60	33.96	0.04
			150	7343	771,030	3.12	33.98	0.03
PS75/095-1	57.02°S	174.43°W	20	72,367	1,004,802	6.28	33.97	0.03
			40	77,751	871,128	6.26	33.97	0.03
			60	69,044	939,620	6.05	33.98	0.04
			80	86,931	799,930	4.81	33.99	0.05
			150	2560	542,755	4.04	34.02	0.03
PS75/098-1	52.96°S	179.01°W	20	170,180	8,076,962	9.15	34.29	0.04
			45	260,450	4,235,000	8.98	34.35	0.05
			60	284,085	3,799,781	8.96	34.37	0.05
			100	20,223	699,363	8.08	34.36	0.03
			150	1866	246,326	8.01	34.45	0.03
PS75/099-5	48.26	177.27°E	10	384,414	3,858,313	10.80	34.16	0.04
			20	169,848	1,266,251	9.96	34.19	0.04
			40	261,846	542,504	8.81	34.25	0.04
			60	178,778	238,978	7.97	34.25	0.04
			100	3942	324,818	7.25	34.29	0.03
			150	0	1053	7.09	34.29	0.03
PS75/100-5	45.76	177.15°E	11	143,681	8,461,655	13.22	34.21	0.04
			20	162,574	8,302,251	12.63	34.22	0.05
			40	452,011	9,684,859	11.81	34.23	0.05
			60	195,456	2,494,135	9.22	34.23	0.04
			100	3666	314,049	7.81	34.25	0.03
			150	0	187,039	7.47	34.32	0.03

Table 1. (*continued*)

Station	Latitude	Longitude	Sampling depth (m)	Total coccosph./l	Total coccoliths/l	SST (°C)	SSS (psu)	Fluorometer
PS75/104-3	44.77	174.53°E	10	552,758	4,326,080	12.02	34.25	0.04
			20	642,472	5,509,821	11.95	34.26	0.06
			40	230,186	4.1E + 07	9.66	34.30	0.05
			60	1806	420,901	10.16	34.64	0.03
			100	2837	230,734	9.47	34.61	0.03
			150	2838	218,542	8.75	34.55	0.03

each of the species found and Ocean Data View software version 4.5 (Schlitzer, 2011).

2.2. Species diversity

We calculated the Shannon–Wiener index (H′) using the Paleontological Statistics (PAST™) software version 2.14 (Hammer et al., 2001) with the following equation: $H' = -\sum_{i=1}^{S} \frac{ni}{N} \ln \frac{ni}{N}$, where n_i is the number of individuals in species *i*; *S* is the number of taxa, and *N* is the total number of all individuals.

H′ varies from 0 for communities with only a single taxon to high values for communities with many taxa, each with few individuals.

2.3. Statistical analysis

In order to synthesize the information provided by the empirical coccolithophore counts, an R-mode Factor Analysis was applied to the % abundances of all the species, including a varimax normalized rotation with the Statistica data analysis software system version 7. As mentioned before, samples with less than 50 coccospheres were excluded from the initial database; therefore just 70 samples were considered for the Principal Component Analysis (PCA). Prior to the PCA a log-transformation of log(x + 1) was performed, where x represents the percentage of the coccolithophore species, and was applied to the dataset to obtain a normal distribution. This transformation amplified the importance of less abundant species, and minimized the dominance of few abundant species (Mix et al., 1999), in our case *E. huxleyi*.

For the PCA 14 species or groups of coccolithophores were considered. Owing to the fact that individual trends observed were similar, holococcolithophores (HOL) and *Syracosphaera* species were combined together. However contrary to this, *E. huxleyi* morphotypes (A, B and B/C + C) were regarded as different groups for the same reason. A correlation matrix between coccolithophore factor scores derived from the PCA and the CTD in situ measurements (SST, SSS and fluorescence) was performed to assess quantitatively the relationship between these environmental parameters and the coccolithophore factors.

3. Oceanographic setting

The SO plays an important role in the climate system due to its influence in the meridional overturning circulation (e.g., Marshall and Speer, 2012) and in the global carbon cycle (e.g., Fischer et al., 2010). The Antarctic Circumpolar Current (ACC) is the most important current in this region, which is furthermore characterized by the occurrence of distinct fronts, where rapid changes in water properties occur over a short distance (Klinck and Nowlin, 2001). The ACC flows eastward driven by the intense Southern Hemisphere westerly winds connecting all major oceans (Orsi et al., 1995). The mean ACC sea surface temperatures range from −1 to 5 °C, depending on the time of year and location. The mean SSS decreases poleward, in general, from 34.9 at 40°S to 34.7 psu at 65°S. The northern boundary of the ACC is defined by the Subtropical Front (STF; Clifford, 1983; Hofmann, 1985; Orsi et al., 1995), usually found between 35°S and 45°S. Here the average SST changes from about 12 °C to 7 to 8 °C and salinity decreases from greater than 34.9 to 34.6 psu or less. The distinct fronts and surface water mass regimes separated by the fronts south of the STF have been called, from north to south (Whitworth, 1980): Subantarctic Zone (SAZ), Subantarctic Front (SAF), Polar Frontal Zone (PFZ), Polar Front (PF) and Antarctic Zone (AZ; Orsi et al., 1995; Figs. 1 and 2). The position of the fronts varies spatially, steered occasionally by regional topographic features, and also fluctuates seasonally. North of the SAF, average SST is generally greater than 4 °C, while south of the PF, average SST is less than 2 °C (Orsi et al., 1995; Klinck and Nowlin, 2001). South of the PF, sea ice forms and melts seasonally, with large consequences for ocean physics and biology (Marshall and Speer, 2012).

The CTD-rosette deployed at the ANT-XXVI/2 stations provided vertical water column profiles of SST, SSS, fluorescence (reflecting chlorophyll *a* concentrations; Gersonde et al., 2011). Data displayed in Fig. 2 is based on in situ measurements performed every meter on a vertical CTD cast. SST varies between 13.4 °C and −1.8 °C, SSS between 34.6 psu and 33.4 psu and fluorescence between 0 and 0.38 for the sampling points considered in this study.

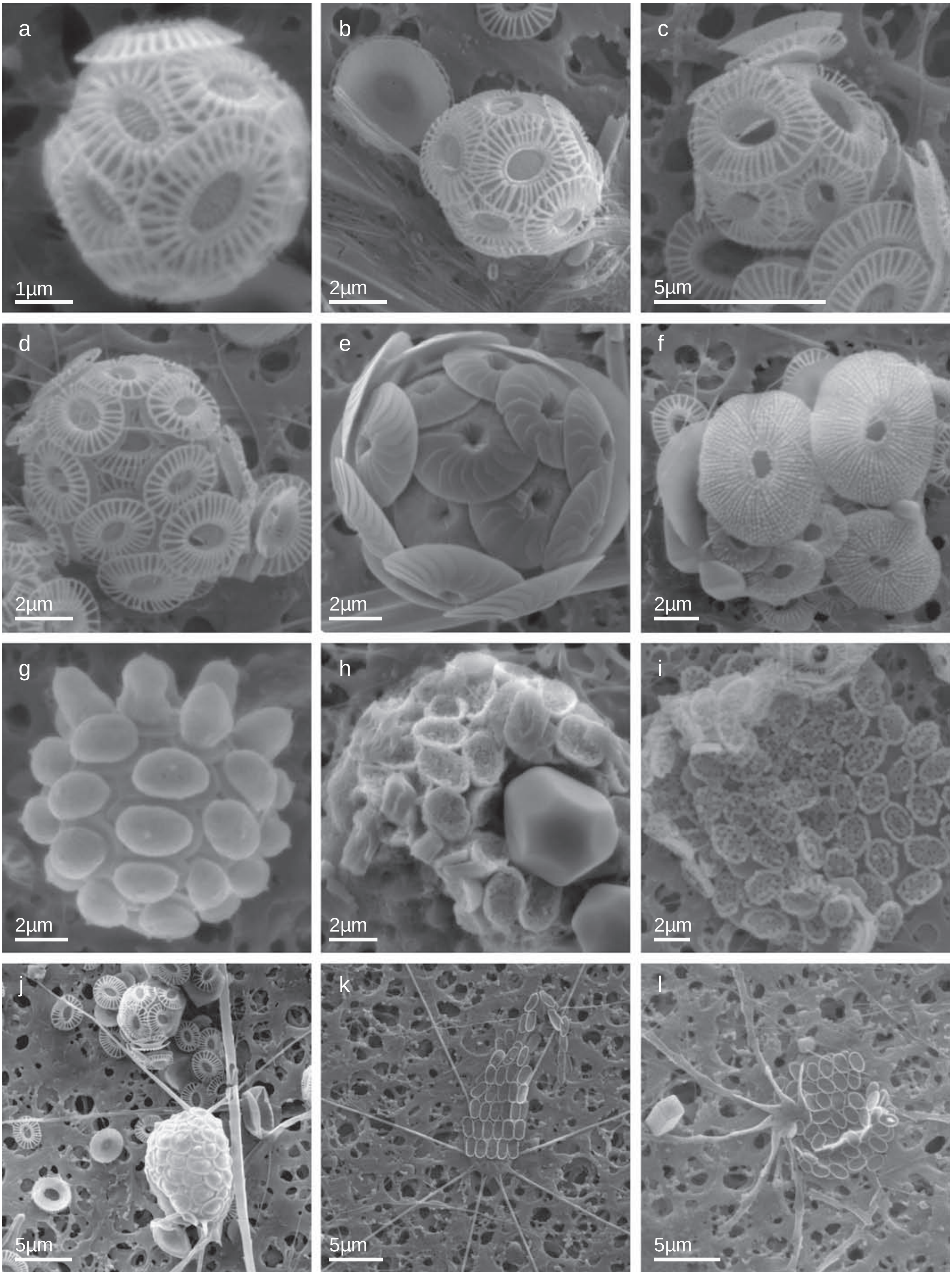
The SAF and the PF were crossed several times along the cruise track. According to the criteria for the surface water characteristics north and south of the surface ocean fronts given by Orsi et al. (1995), the SAF was recognized between stations PS75/052-1 and 054-2, PS75/058-1 and PS75/061-1, PS75/097-1 and PS75/096-1; the PF between stations PS75/061-1 and PS75/063-3, PS75/072-1 and PS75/074-2, PS75/092-4 and PS75/094-6, as indicated in Figs. 1 and 2.

4. Results

4.1. Distribution of coccolithophores

The analysis of the 150 water samples displayed both the highest coccolithophore numbers at the upper surface (<60 m water depth) as well as a definite latitudinal distribution pattern of the coccoliths and coccospheres with shifts in the numbers occurring at the oceanic fronts. Sharp increases in the coccolithophore numbers can be clearly followed along the PF ranging from 126 · 10^3 coccospheres/l and 2996 · 10^3 coccoliths/l in the east (station PS75/063-3) to 157 · 10^3 coccospheres/l and 5141 · 10^3 coccoliths/l in the west of the study area (station PS75/092-4, Fig. 3). The highest numbers of coccolithophores with 642 · 10^3 coccospheres/l at 20 m depth (Fig. 3, Table 1) and with 41495 · 10^3 coccoliths/l at 40 m depth were observed in the western South Pacific close to the STF at station PS75/104-3. Increments in the total number of coccospheres and coccoliths are also observed when crossing the SAF (e.g., 303 · 10^3 coccospheres/l and 394 · 10^3 coccospheres/l at stations PS75/061-1 and PS75/075-1) although they are not as evident as in the case of the PF, especially regarding station PS75/095-1 where there is a drop in the values (87 · 10^3 coccospheres/l, see Fig. 3). Coccolithophore barren samples were observed at all the depths in the southernmost and coldest locations; e.g., PS75/067-3, PS75/070-3, PS75/088-1, PS75/089-1, PS75/090-1. However, the highest diatom numbers have been recorded in the uppermost 60 m of the water column at those stations and generally south of the PF (Fig. 3).

Although the detached coccolith numbers are higher (Table 1), the distribution patterns displayed by total coccosphere numbers and total coccolith numbers are similar, and there is a significant correlation between them ($R^2 = 0.68$, Fig. 4).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4.2. Coccolithophore species

We identified 33 different species of coccolithophores, including 16 species only found as isolated coccoliths (see Table 2). The difference in the numbers of coccospheres and coccoliths is due to the high diversity observed in the genus *Syracosphaera* (e.g., at the stations PS75/058-1, PS75/100-5 and PS75/104-3). Detached coccoliths may have been transported; therefore we will focus on the number of coccospheres. We will comment on the most significant coccolithophore species.

4.2.1. Distribution of E. huxleyi morphotypes

Quantitatively, *E. huxleyi* is the most abundant taxon in the Pacific SO, occurring at up to $482.4 \cdot 10^3$ coccospheres/l (at station PS75/054-2). *Emiliania huxleyi* is the only species present at all the stations except in the southernmost coccolithophore-barren samples. So far, five different morphotypes of *E. huxleyi* have been well established (types A, B, B/C, C, R; Young et al., 2003) and at least three of them are genetically distinct (Schroeder et al., 2005; Cook et al., 2011). The presence of malformed *E. huxleyi*, morphotype D, with irregular shaped "T" elements observed by some authors in the SO (e.g., Verbeek, 1989; Findlay and Giraudeau, 2000; Cubillos et al., 2007; Mohan et al., 2008) was not observed in our study.

Emiliania huxleyi type C is the most abundant morphotype, with a maximum of $466.8 \cdot 10^3$ coccospheres/l at 20 m depth at the station PS75/054-2 (Fig. 5b). It is present in all the samples (maximum of 98.1% and minimum of 47.2% in the coccosphere database, Fig. 6b), except south of the PF, where coccolithophores are only sporadically recorded. In addition, *E. huxleyi* type B/C (maxima of 22%, Fig. 6c) displays a comparable distribution pattern, but with lower numbers i.e., maximum of $57.3 \cdot 10^3$ coccospheres/l at PS75/075-1 at 20 m depth (Fig. 5b, c). Both types, B/C and C, clearly dominate the coccolithophore assemblage in the study area, with an average of 89.1%. The coccolith numbers of these two morphotypes are higher than the numbers of coccospheres. *Emiliania huxleyi* type B is present at locations south of the SAF, but it shows a different distribution pattern to that of *E. huxleyi* types B/C and C. Morphotype B displays a maximum abundance of 2.4% (Fig. 6d) and $4.1 \cdot 10^3$ coccospheres/l at station PS75/099-5 at 20 m depth (Fig. 5d). *Emiliania huxleyi* type A is geographically restricted to the westernmost SAZ locations of the study area, reaching $15.8 \cdot 10^3$ coccospheres/l at station PS75/100-5 at 40 m depth and 4.8% at 60 m depth (Figs. 5e and 6e). The coccospheres of this morphotype are rather compact and their coccoliths are more robust than other *E. huxleyi* types. Therefore not many detached coccoliths or collapsed coccospheres were found. Overcalcified specimens of *E. huxleyi* type A were observed, but not separated into a different group because of its rare occurrence.

4.2.2. Distribution of other coccolithophore taxa

According to their lateral and vertical distribution patterns all other taxa can also be roughly assigned to the different oceanographic areas. In the upper surface of the SAZ, *Ophiaster* spp., *C. leptoporus* and *Syracosphaera* spp. are the predominant coccolithophore taxa. *Ophiaster* spp. (the majority of the specimens belong to *Ophiaster hydroideus*, Plate Il) displays a restricted occurrence in the SAZ offshore New Zealand where they reached a maximum of $153.2 \cdot 10^3$ coccospheres/l (at station PS75/099-5). Here the coccolithophore assemblage is composed of up to 85.7% of *Ophiaster* spp. at water depths shallower than 60 m (Fig. 7b). *Calcidiscus leptoporus* (Plate Ie) occurred north of the SAF and represents a maximum abundance of 67.6% at station PS75/058-1. However, due to the high coccolithophore concentration in the western south Pacific, maximum numbers of $42.7 \cdot 10^3$ coccospheres/l (Fig. 7c) are found at 20 m depth station PS75/104-3. While coccospheres are restricted to the uppermost 60 m of the water column, coccoliths are also found at deeper locations.

Fourteen species belonging to the genus *Syracosphaera* have been recorded in the study area (Table 2 and Taxonomical appendix) with relative coccosphere abundance up to 7.4%. *Syracosphaera* spp. (see Plate IIf–k) only occur in the SAZ with concentrations of $11.99 \cdot 10^3$ coccospheres/l at station PS75/100-5 (20 m depth, Fig. 7d). Less abundant coccolithophore species dwelling in the SAZ include *Umbellosphaera tenuis*, *Acanthoica quattrospina*, *Calyptrosphaera* aff. *C. papillifera* and *Coccolithus pelagicus* (sensu lato). *U. tenuis* (Plate If), defined as tropical to subtropical species (e.g., McIntyre and Bé, 1967; Okada and McIntyre, 1977, 1979), is only present in one SAZ station offshore New Zealand in the uppermost 20 m of the water column. *Umbellosphaera tenuis* type IV appears with a relative abundance of 6.9% and with $11.2 \cdot 10^3$ coccospheres/l at 20 m at station PS75/100-5. The presence of *A. quattrospina* in the Pacific sector of the SO during austral summer was previously noted by Hasle (1960) at ~57°S. In our study area, only coccospheres of *A. quattrospina* (Plate Ij) were observed adding up to 5.8% and $9.9 \cdot 10^3$ coccospheres/l at station PS75/099-5 (20 m). This species is present only in the uppermost 60 m of the water column and it is also restricted to the northernmost locations, in the westernmost SAZ.

Holococcolithophores reach maximum abundances of 4.8% and $26.7 \cdot 10^3$ coccospheres/l at shallow depths (uppermost 60 m) close to New Zealand (i.e., stations PS75/100-5 and PS75/104-3). The species *Calyptrolithophora* aff. *C. papillifera* (Plate Ih) and *C. pelagicus* (sensu lato) HOL (Plate Ii) were found, although the heterococcolith-bearing phase of *C. pelagicus* (sensu lato) was not reported.

Other taxa found in the SAZ, with maximum coccosphere abundances below 3%, are *Algirosphaera cucullata* (2.2% and $12.1 \cdot 10^3$ coccospheres/l, Plate Ig), *Palusphaera* spp. (1.3% and $5 \cdot 10^3$ coccospheres/l) and *Gephyrocapsa muellerae* (0.5% and $0.8 \cdot 10^3$ coccospheres/l, Plate IIe). There are also sporadic records of *Helicosphaera carteri* (Plate IIk), *Umbilicosphaera sibogae* and *Michaelsarsia* spp. Although some authors noted the presence of *Gephyrocapsa oceanica* in the southernmost Atlantic and Indian oceans (e.g., Verbeek, 1989; Eynaud et al., 1999; Mohan et al., 2008), we neither found *G. oceanica* nor *Gephyrocapsa ericsonii* in our study area.

Our data showed the presence of *Calciopappus caudatus* at 44.7°S (SST 12 °C), but also further to the south at colder temperatures, e.g., at 100 m at station PS75/054-2 (SST 5.5 °C). *Calciopappus caudatus* reached its maximum in the eastern Pacific sector of the SO (8.7%). It shows a broad distribution in the SAZ and PFZ, but also in the water column ranging from 0 to 100 m depth, which indicates a species habitat deeper than the other coccolithophores. There were $12.8 \cdot 10^3$ coccospheres/l at station PS75/098-1 at 60 m depth (Fig. 7e). Other coccolithophore taxa dwelling in the PFZ are *Papposphaera* spp. and *Pappomonas* spp. (types 1 and 2 were reported, accounting for 2.8% and reaching $10.7 \cdot 10^3$ coccospheres/l, Plate IIa–c).

5. Ecological analysis and discussion

5.1. Diversity indices

In general, the highest numbers of coccolithophores occurred at stations with the highest diversity (Figs. 3 and 8). However, these highest numbers are basically restricted to the uppermost 60–100 m and progressively decrease with depth, while Shannon–Wiener diversity index

Plate I. (a) *Emiliania huxleyi* type A, sample PS75/100-5 at 20 m depth, (b) *Emiliania huxleyi* type B, sample PS75/074-2 at 60 m depth, (c) *Emiliania huxleyi* type B/C, sample PS75/034-3 at 10 m, (d) *Emiliania huxleyi* type C, sample PS75/034-3 at 10 m depth, (e) *Calcidiscus leptoporus*, sample PS75/075-1 at 65 m depth, (f) *Umbellosphaera tenuis* type IV, sample PS75/100-5 at 20 m depth, (g) *Algirosphaera cucullata*, sample PS75/104-3 at 20 m depth, (h) *Calyptrolithophora* aff. *C. papillifera*, sample PS75/099-5 at 40 m depth, (i) *Coccolithus pelagicus* (sensu lato) HOL, sample PS75/104-3 at 20 m depth, (j) *Acanthoica quattrospina*, sample PS75/075-1 at 20 m depth, (k) *Calciopappus caudatus*, sample PS75/044-1 at 60 m depth, (l) *Ophiaster hydroideus*, sample PS75/099-5 at 20 m depth.

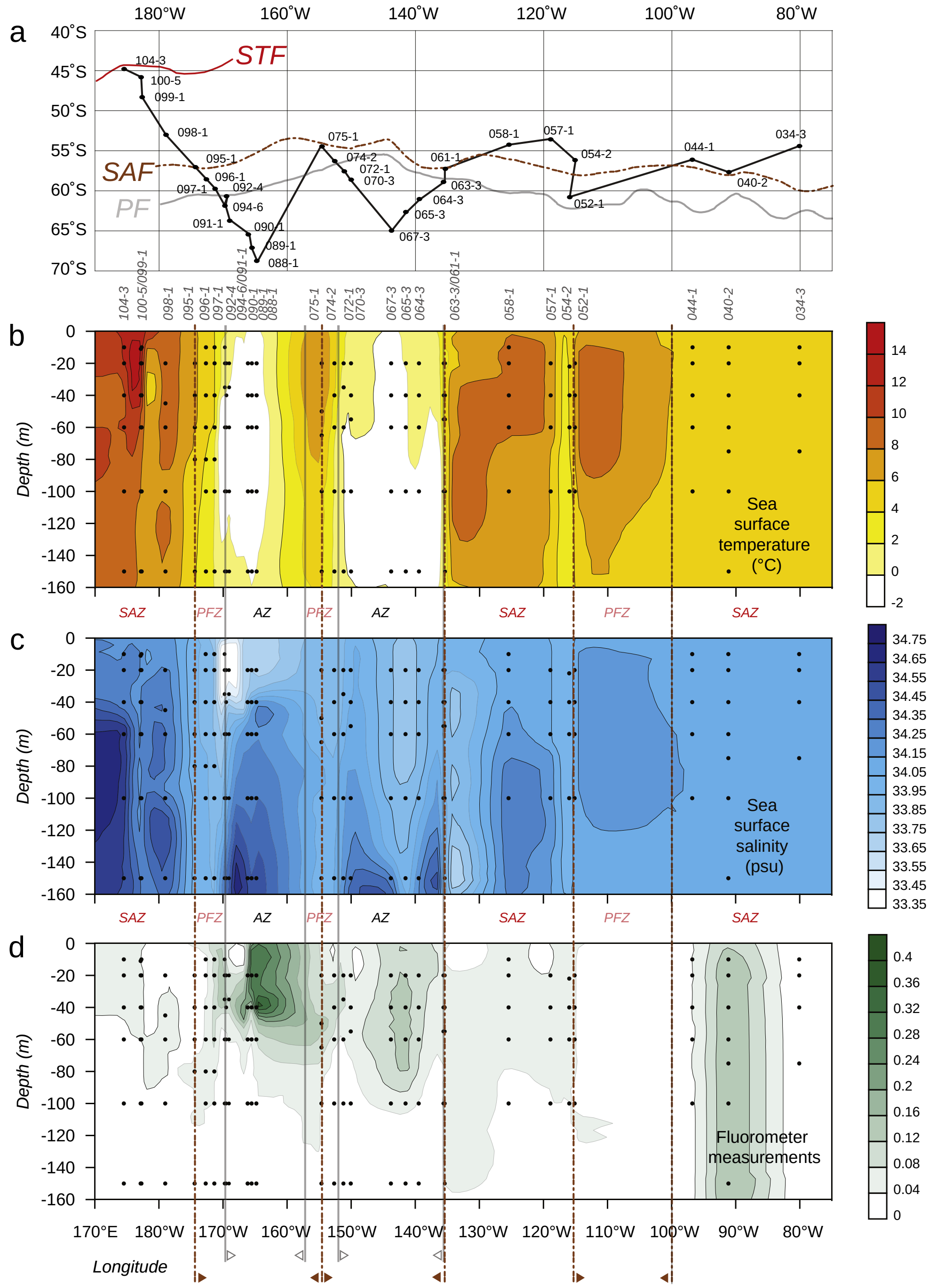


Fig. 2. (a) Location of the ANT-XXVI/2 CTD stations studied, (b) sea surface temperature, (c) sea surface salinity and (d) fluorescence profiles from 80.1°W to 174.5°E up to a depth of 160 m. Black dots indicate sampling points. The different oceanographic fronts (according to Orsi et al., 1995) are indicated as STF—red line, SAF—brown dashed line, PF—gray line, and arrowheads point southward. The areas between the fronts are referred to as Subantarctic Zone (SAZ), Polar Front Zone (PFZ) and Antarctic Zone (AZ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(H′) values are more constant for the uppermost 150 m at each station. Shannon–Wiener index is higher for coccoliths as for coccospheres, although both display a very similar distribution pattern. Diversity of coccolithophores varies according to the areas bounded by the different oceanographic fronts. The SAZ is characterized by a high diversity ($1.3 \leq H' \geq 0.8$) and the PFZ displays a lower diversity ($0.8 < H' > 0$). The AZ shows extremely low diversity with just a sporadic record of *E. huxleyi*; this area is characterized by very low numbers of coccoliths and coccospheres and high abundance of diatoms (Figs. 3b and 8).

5.2. Statistical analysis

An R-mode PCA was performed in the log-transformed % coccosphere dataset and retained three factors, which account for 95.1% of the total variance. Factor 1 explains 61.21% of the variance and is characterized by *E. huxleyi* types B/C and type C. *Ophiaster* spp. are the main contributor to the Factor 2, explaining 19.04% of the variance. Factor 3 in which the important species are *C. caudatus* and *C. leptoporus* (Table 3) accounts for 14.82% of the variance. The

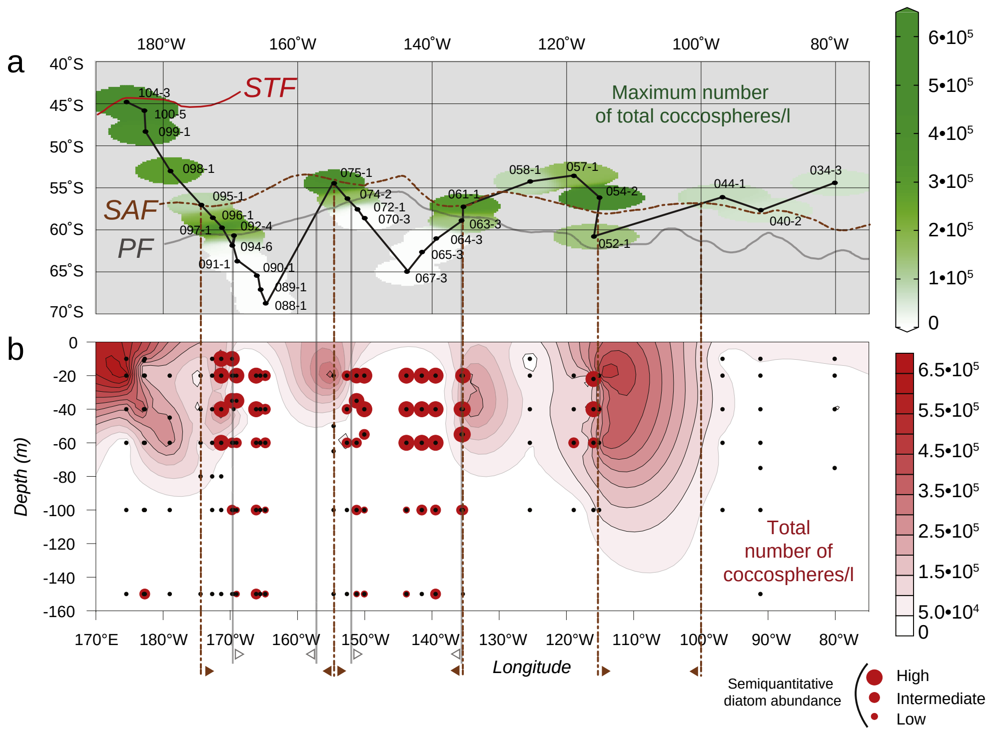


Fig. 3. (a) Location of the ANT-XXVI/2 CTD stations studied and maximum number of coccospheres/l and per station, (b) longitudinal transect showing the total number of coccospheres/l for the uppermost 150 m of the water column; black dots indicate sampling points and red dots indicate the semiquantitative estimation of the diatom abundance ranging from low = small dots to high = big dots. The different oceanographic fronts (according to Orsi et al., 1995) are indicated as STF—red line, SAF—brown dashed line, PF—gray line, and arrowheads point southward.

distribution of the dominant factor at each sampling point portrays the frontal regime zonation (Fig. 9). Factor 1 clearly dominates in the PFZ and in the easternmost stations of the study area, which means that *E. huxleyi* types B/C and C are widespread in the Pacific sector of the SO, except for the areas north of the SAF, where the coccolithophore diversity increases. On the other hand, Factor 2 reaches its highest loadings in the SAZ off New Zealand and Factor 3 north of the SAF, at stations PS75/057-1 and PS75/058-1.

To better characterize these factors, a correlation matrix between the factor loadings and the CTD in situ measurements (SST, SSS and fluorescence) was performed. The Pearson correlation coefficients indicate that Factor 1 is anticorrelated to SST (−0.68) and SSS (−0.65) and Factor 2 is correlated to SST (0.63) and SSS (0.60). However the rest of the coefficients are rather low (Table 4).

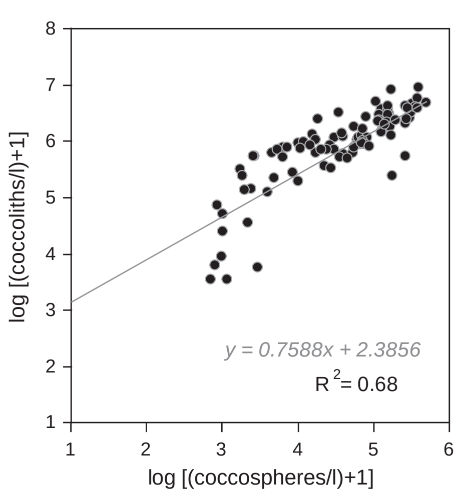


Fig. 4. Number of total coccospheres/l versus number of total coccoliths/l (both log-transformed) and corresponding linear regression equation.

5.3. Ecological interpretation of the assemblages

Detailed studies of the coccolithophore communities in the surface ocean (<150 m) of the SO revealed good correlations between the occurrence and distribution of species and morphotypes of *E. huxleyi* and oceanographic features. Frontal systems were identified as areas of abrupt change in both absolute numbers (Figs. 10a, 11) and community composition of coccolithophores (Fig. 10b). Oceanographic fronts control the diversity and the coccolithophore distribution in the Pacific sector; in particular the PF constitutes a natural sharp barrier which marks a drop in diversity, number of coccospheres, and number of coccoliths. In the study area, elevated numbers of coccospheres and coccoliths have been observed at the SAF and PF (Fig. 11). However, a general decrease took place poleward, as has already been previously noted (e.g., Winter et al., 1994), until almost monospecific assemblages of *E. huxleyi* south of the PF (Fig. 10b), agreeing with Gravalosa et al. (2008), Charalampopoulou (2011) and Winter et al. (2013). Frontal systems have been described as high biological productivity regions (e.g., Murphy, 1995; Bracher et al., 1999; Pollard et al., 2002; Patil et al., 2013). High coccolithophore densities along the SO fronts would be related to physical accumulation of particulate matter and nutrients in areas of convergence (e.g., Franks, 1992) or to more favorable conditions associated with the front itself (e.g., Laubscher et al., 1993) as suggested for the increased phytoplankton biomass at the SAF and PF in the Atlantic sector (Whitehouse et al., 1996). Maxima in chlorophyll *a* concentration were recorded at the southernmost locations (Fig. 2d) coincident with high abundances of diatoms south of the PF (Fig. 3). However, chlorophyll *a* sharp increases were not observed at the SAF and PF, which suggest that the dynamics of the fronts had more influence over the coccolithophore assemblages during the 2009–2010 austral summer than over the diatoms. Future quantitative analyses of

Table 2.
Summary of the numbers of coccolithophore species and morphotypes in the investigated plankton samples. Subantarctic Zone (SAZ) refers to the area between Subtropical Front (STF) and Subantarctic Front (SAF), Polar Front Zone (PFZ) between the SAF and the Antarctic Polar Front (PF) and the Antarctic Zone (AZ) south of the PF. The presence of each species has been indicated with "+" and with "−" if it is occasional. The maximum number of coccoliths/l, coccospheres/l and relative coccosphere abundances recorded in the study area is also indicated. (*) The species *Wigwamma antarctica* was observed, outside of the counts.

Coccolithophore species and morphotypes	STF / SAZ	SAF / PFZ	PF / AZ	Max coccoliths/l	Max coccosph./l	Max coccosph. (%)
Acanthoica quattrospina	+				$9.9 \cdot 10^3$	5.8
Algirosphaera cucullata	+				$12.1 \cdot 10^3$	2.2
Calcidiscus leptoporus	+			$1932.3 \cdot 10^3$	$42.7 \cdot 10^3$	67.6
Calciopappus caudatus	+	+		$56.9 \cdot 10^3$	$12.8 \cdot 10^3$	8.7
Coccolithus pelagicus (sensu lato) HOL, *Calyptrolithophora* aff. *C. papillifera*	+				$26.7 \cdot 10^3$	4.8
Emiliania huxleyi type A	+			$46.2 \cdot 10^3$	$15.8 \cdot 10^3$	4.8
Emiliania huxleyi type B	+	+		$1118.7 \cdot 10^3$	$4.1 \cdot 10^3$	2.4
Emiliania huxleyi type B/C	+	+	−	$8441.3 \cdot 10^3$	$57.3 \cdot 10^3$	22.0
Emiliania huxleyi type C	+	+	−	$28476.7 \cdot 10^3$	$466.8 \cdot 10^3$	98.1
Gephyrocapsa muellerae	+			$0.9 \cdot 10^3$	$0.8 \cdot 10^3$	0.5
Helicosphaera carteri	+			$0.9 \cdot 10^3$		
Michaelsarsia spp.	−			$6.2 \cdot 10^3$		
Ophiaster spp.	+				$153.2 \cdot 10^3$	85.7
Palusphaera spp.	+				$5 \cdot 10^3$	1.3
Pappomonas spp., *Papposphaera* spp.	+	+	−		$10.7 \cdot 10^3$	2.8
Syracosphaera spp.: *S. borealis, S. castellata, S. corolla, S. delicata, S. dilatata, S. florida, S. halldalii, S. histrica, S. molischii, S. nana, S. ossa, S. prolongata, S. tumularis, S. type J*	+			$610.2 \cdot 10^3$	$11.99 \cdot 10^3$	7.4
Umbellosphaera tenuis	+			$69.3 \cdot 10^3$	$11.2 \cdot 10^3$	6.9
Umbilicosphaera sibogae	+			$0.5 \cdot 10^3$		
Wigwamma antactica (*)						

different plankton groups performed in exactly the same samples from the SO would be recommended for better understanding of phytoplankton ecological patterns at high latitudes and their relationship with the different fronts. This is interesting to note since *E. huxleyi* is the dominant species in both, north and south high latitudes, and also many of the subordinate species occur in the northern realm as well as in the SO. One of the few exceptions concerns *C. pelagicus* (sensu lato) which is nearly absent in the south, whereas it is a common part of the coccolithophore assemblage of the Nordic Seas (e.g., Baumann et al., 2000).

Comparison of the number of total coccospheres to the basic environmental variables measured in situ (SSS, fluorescence) did not display any significant relationship except for the maximum number of coccospheres and SST measurements ($R^2 = 0.68$, Fig. 10c). Generally, the observed coccolithophore numbers are in agreement with the findings of previous research done in different areas of the SO, such as the Drake Passage (Charalampopoulou, 2011), the Australian sector (Nishida, 1986; Findlay and Giraudeau, 2000; Cubillos et al., 2007), the Pacific sector (Hasle, 1960; Gravalosa et al., 2008, Fig. 11), the Atlantic sector (Eynaud et al., 1999; Holligan et al., 2010), and the Indian sector (Mohan et al., 2008). However, there are marked differences with regard to the occurrence of coccolithophores in rather comparable environments of the Northern Hemisphere. The maximum number of total coccolithophores recorded in the study area during austral summer is much lower than the numbers recorded in boreal spring/summer in northern high latitudes, which have been shown to easily reach numbers on the order of $1000 \cdot 10^3$ coccospheres/l in the Bering Sea (Harada et al., 2012) and $10{,}000 \cdot 10^3$ coccospheres/l in the Norwegian–Greenland Sea (Samtleben et al., 1995).

Although coccolithophore diversity is lower in polar regions than in the tropics, a number of species dwell there (e.g., Manton et al., 1977; Thomsen, 1981; Brand, 1994) as shown by the "moderate" SO coccolithophore diversity values. Coccolithophore Shannon–Wiener diversity values in the Pacific sector of the SO are comparable to the Indian sector (Mohan et al., 2008) and Drake Passage (Charalampopoulou, 2011) indices. However, coccolithophore diversity in the SO is still lower than that observed at northern high latitudes, e.g., in the Norwegian Sea (Charalampopoulou et al., 2011).

Our data showed a general decreasing trend in coccosphere numbers and coccolithophore diversity from the STF towards Antarctica, which we related with the strong latitudinal SST gradient and the frontal dynamics of the Pacific sector of the SO. The remarkable low number of extant coccolithophores, specially of *E. huxleyi*, south of the PF (Figs. 11 and 12) could limit the use of one of the most commonly applied organic geochemical SST proxy, i.e., the alkenone paleothermometry, due to the fact that alkenones would be below the detection limit in the AZ (e.g., Ho et al., 2012).

Different coccolithophore assemblages could be established based on the species diversity, number of coccospheres, and PCA results. Future examination of coccolithophore assemblages and number of coccospheres/coccoliths preserved in the SO sedimentary record will help to recognize the location of the different frontal regimes and will potentially facilitate monitoring the displacement of the oceanic fronts in the past. We will comment on the most significant coccolithophore species present in the SAZ and PFZ from north to south in our study area.

5.3.1. The coccolithophore assemblage of the SAZ

The highest coccolithophore diversity as well as the highest coccolithophore numbers are recorded in the SAZ and can be linked to warm water conditions. This is also suggested by the high correlation of Factor 2 loadings with SST (Table 4).

Emiliania huxleyi, the most common coccolithophore species, dominates the communities in the SO. Different *E. huxleyi* morphotypes were previously reported from environmentally diverse regions related to distinct water masses (e.g., McIntyre and Bé, 1967; Okada and Honjo, 1973; Hiramatsu and De Deckker, 1996; Findlay and Giraudeau, 2000; Beaufort et al., 2008; Cook et al., 2011; Henderiks et al., 2012). The robust morphotype A appeared as a scarce species in the SAZ in agreement with some of the plankton data collected off Tasmania (Cubillos et al., 2007). According to those authors, *E. huxleyi* type A was present in the SAZ during 2005–2006 austral summer but its distribution changed regarding previous years, when it reached locations south of the PF. The central and eastern Pacific SO were barren of *E. huxleyi* type A, supporting the coccolithophore studies performed by Charalampopoulou (2011) in transects from the continental shelves of Chile and the Falkland Islands southward. In contrast, morphotype A of *E. huxleyi* dominates in the North Atlantic and the Norwegian coastal waters (e.g., van Bleijswijk et al., 1991). *Emiliania huxleyi* type A was replaced in the Pacific SO by the very rare *E. huxleyi* type B south of the SAF and the clearly dominant and weakly calcified types B/C and C poleward.

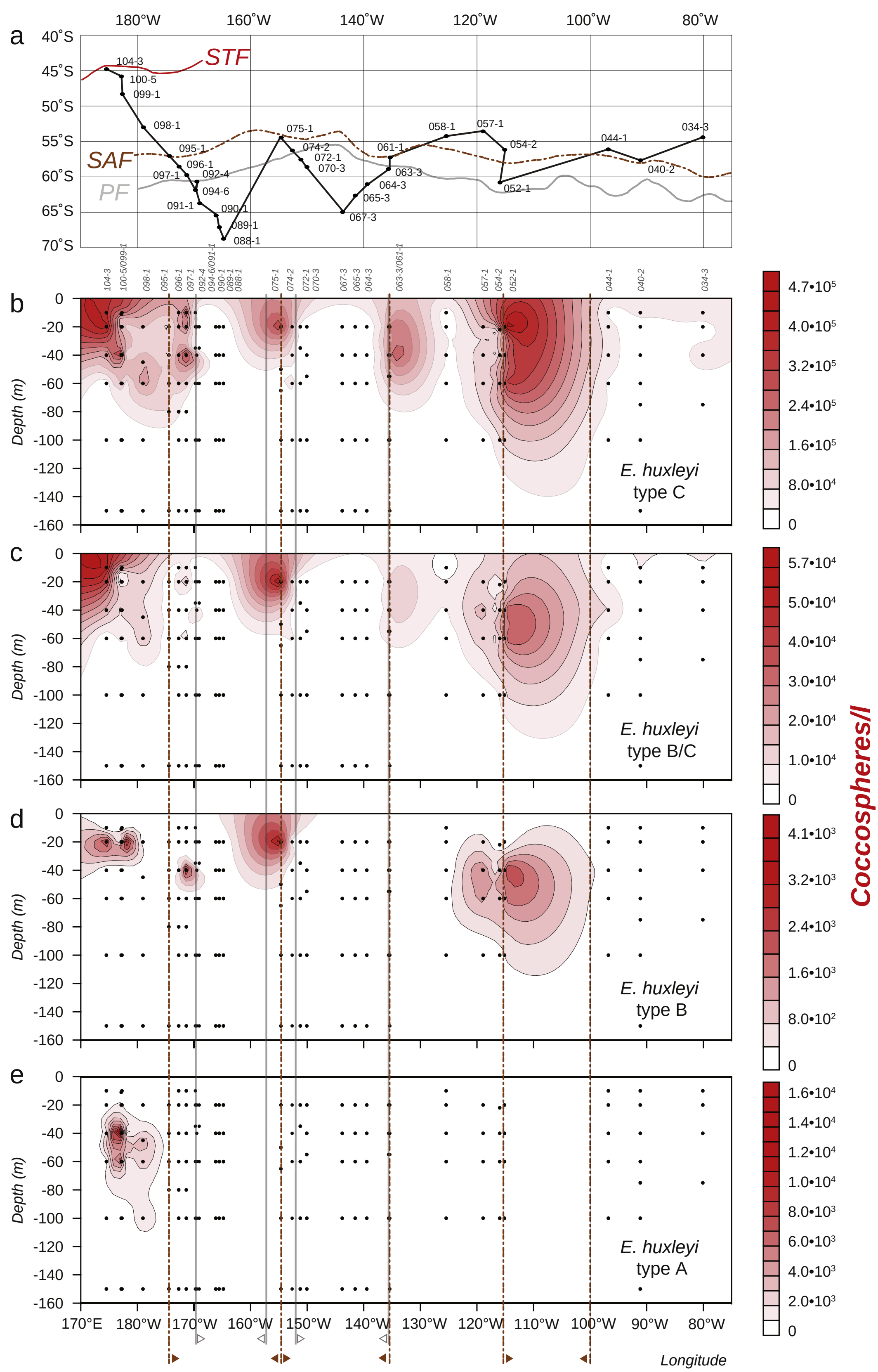


Fig. 5. (a) Location of the ANT-XXVI/2 CTD stations studied and longitudinal transects showing coccospheres/l of (b) *Emiliania huxleyi* type C, (c) *Emiliania huxleyi* type B/C, (d) *Emiliania huxleyi* type B and (e) *Emiliania huxleyi* type A for the uppermost 150 m of the water column. Station numbers are indicated and oceanographic fronts are given as well (STF—red line, SAF—brown dashed line, PF—gray line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The dominance of *O. hydroideus* in the northern SAZ contrasts with the very low relative abundances recorded in the Australian sector of the SO (Findlay and Giraudeau, 2000) and in the Norwegian–Greenland Sea (Samtleben and Schröder, 1992). *Ophiaster hydroideus* dwells in the

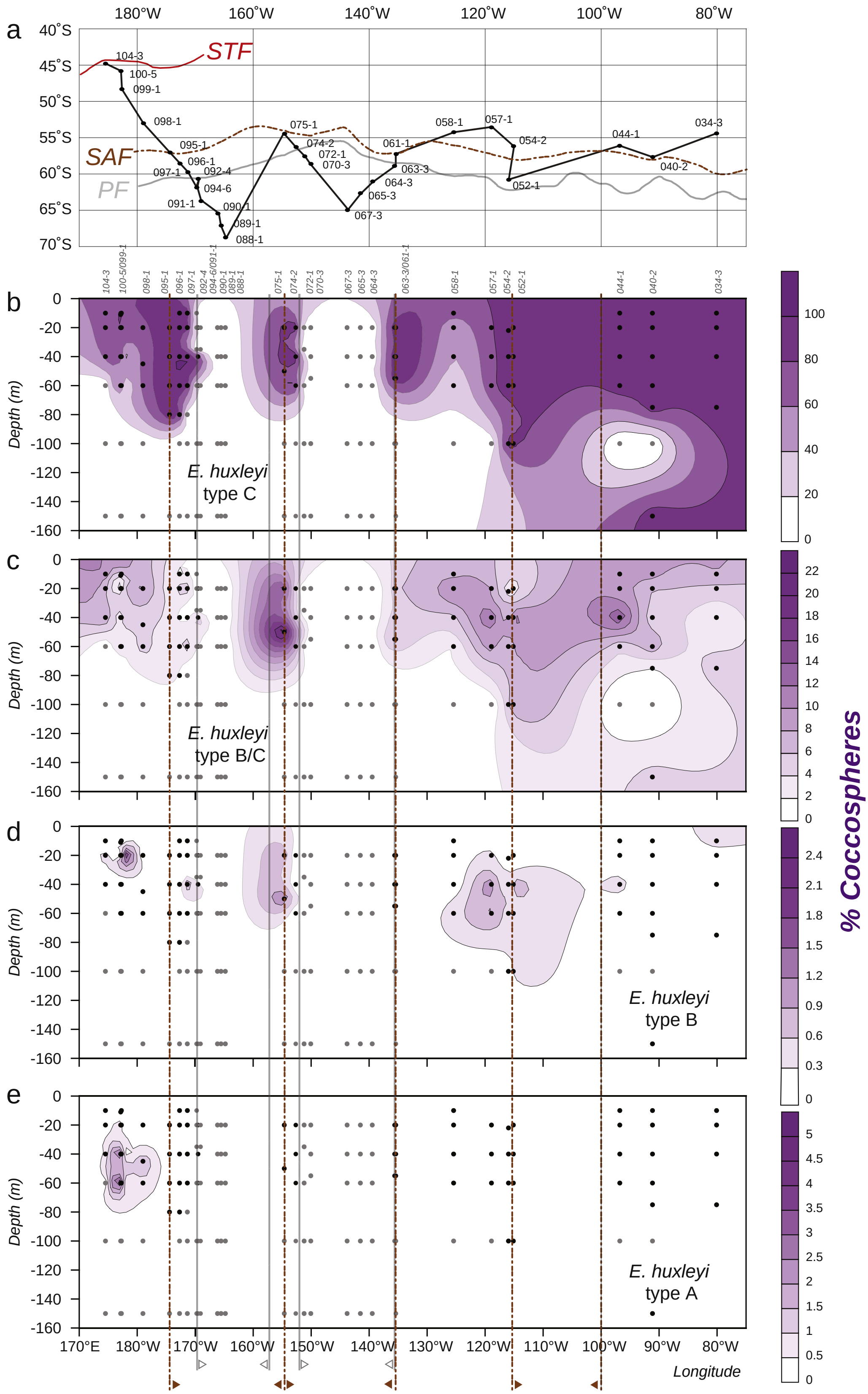


Fig. 6. (a) Location of the ANT-XXVI/2 CTD stations studied and longitudinal transects showing relative abundances of (b) *Emiliania huxleyi* type C, (c) *Emiliania huxleyi* type B/C, (d) *Emiliania huxleyi* type B and (e) *Emiliania huxleyi* type A for the uppermost 150 m of the water column. Back dots indicate sampling points and gray dots indicate points with low number of coccospheres (<50) which were excluded when calculating species percentages. Station numbers are indicated and oceanographic fronts are given as well (STF—red line, SAF—brown dashed line, PF—gray line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

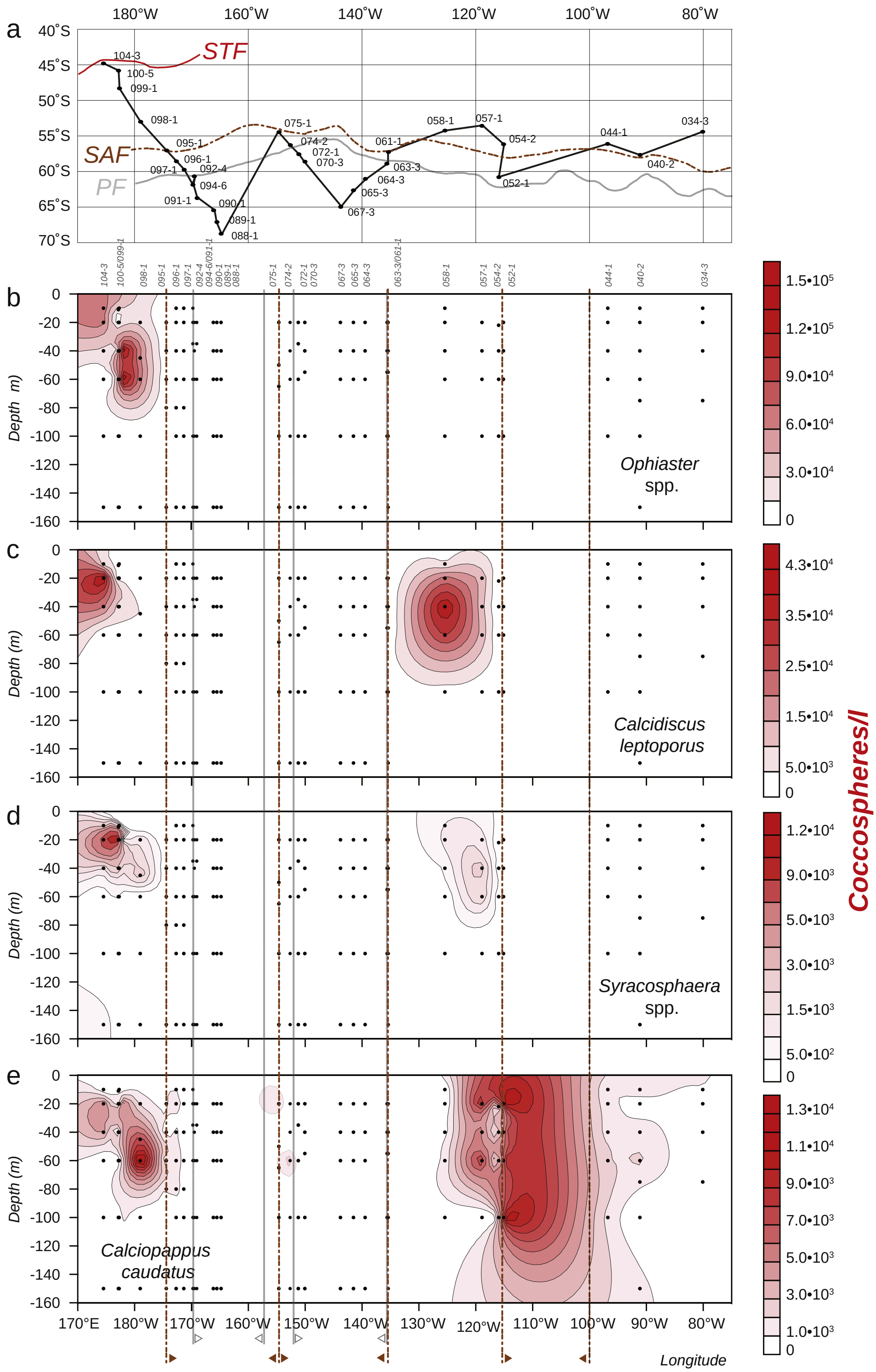
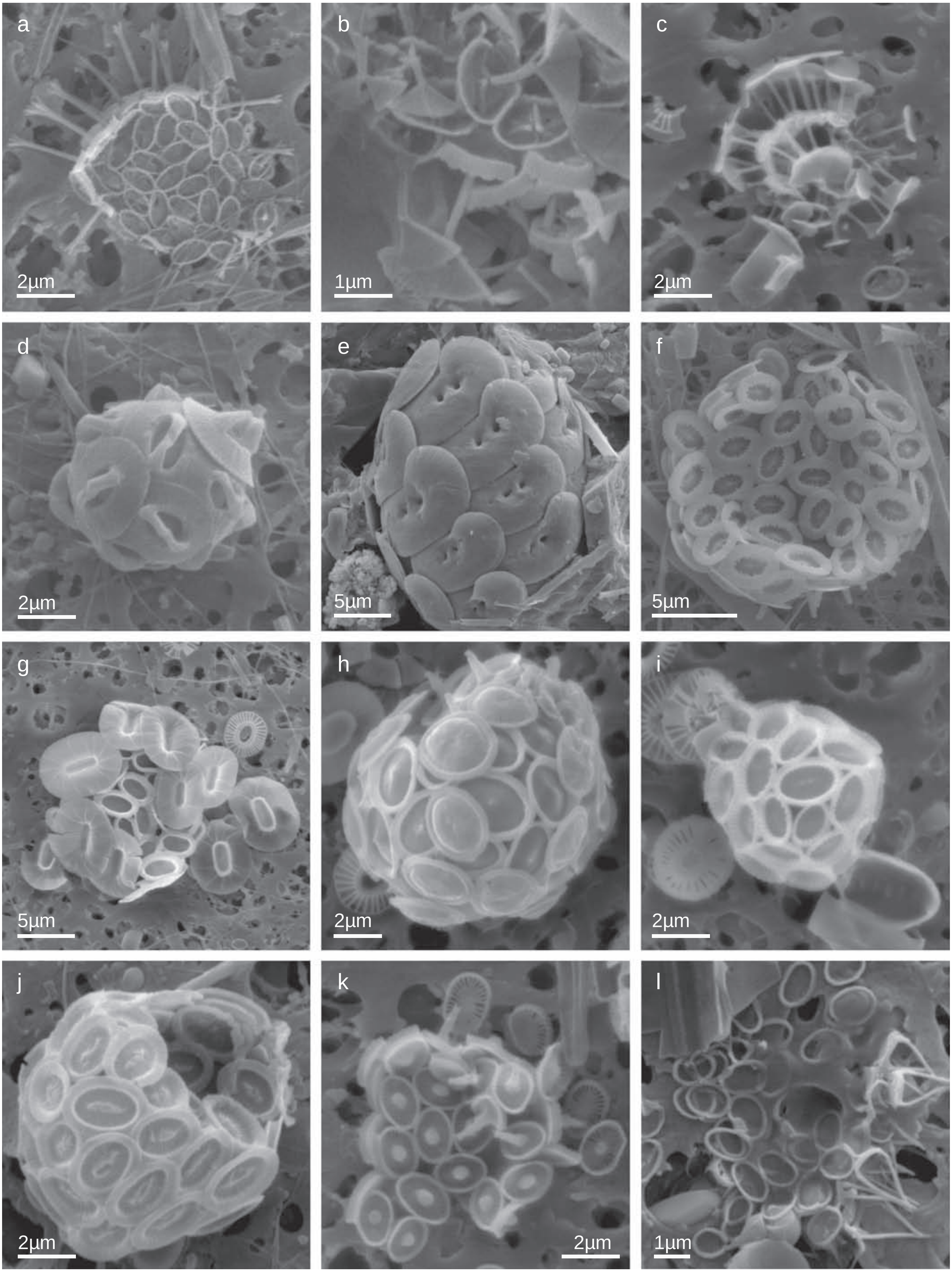


Fig. 7. (a) Location of the ANT-XXVI/2 CTD stations studied and longitudinal transects showing coccospheres/l of (b) *Ophiaster* spp., (c) *Calcidiscus leptoporus*, (d) *Syracosphaera* spp. and (e) *Calciopappus caudatus* for the uppermost 150 m of the water column. Station numbers are indicated and oceanographic fronts are given as well (STF—red line, SAF—brown dashed line, PF—gray line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

upper photic zone, agreeing with the observations from Hagino et al. (2000) in the equatorial Pacific, although this species lives dominantly in the middle–lower photic zone (e.g., Jordan and Chamberlain, 1997; Cros, 2001; Haidar and Thierstein, 2001).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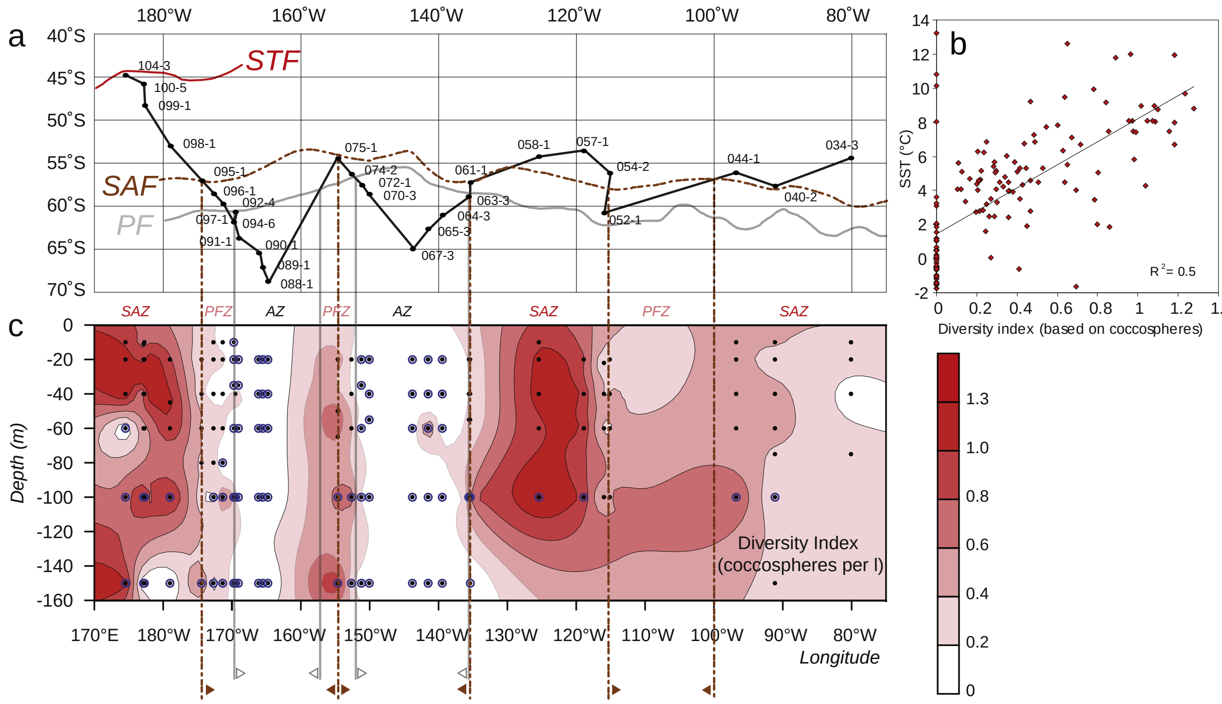

Fig. 8. (a) Location of the ANT-XXVI/2 CTD stations studied, (b) Shannon–Wiener index (H′) based in coccospheres/l database versus sea surface temperature (SST, in °C) measured in situ, (c) H′ based in coccospheres/l database contour map. Black dots indicate sampling points and color circles indicate points with low number of coccospheres (<50) which were excluded when calculating species percentages. Station numbers are indicated and oceanographic fronts are given as well (STF—red line, SAF—brown dashed line, PF—gray line). The areas between the fronts are referred to as Subantarctic Zone (SAZ), Polar Front Zone (PFZ) and Antarctic Zone (AZ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Even if there are differences with the northern high latitudes, there are also similarities. This happens with the genus *Syracosphaera*, of which *Syracosphaera pulchra* was first recorded in the subantarctic Pacific (Hasle, 1960). Later, Findlay and Giraudeau (2000) and Charalampopoulou (2011) found a series of different *Syracosphaera* species in the SO, even south of the STF. We noted almost all those cited *Syracosphaera* taxa in the Pacific sector of the SO and we even added a few more. A comparable highly diverse *Syracosphaera* assemblage has also been recorded from the cold-water of the southeast Greenland margin (Balestra et al., 2004).

The reduced presence of *C. pelagicus* (sensu lato) in the study area and its dominance in the North Hemisphere constitutes a notable north–south difference. *Coccolithus pelagicus* is one of the few cold-adapted species which dominates coccolithophore assemblages in the (sub) Arctic regions (e.g., Samtleben and Schröder, 1992; Andruleit, 1997; Baumann et al., 2000; Balestra et al., 2004). Even if surface polar water masses from the SO would constitute a reasonable habitat for this species, already Hasle (1960) noted that neither *C. pelagicus* nor its holococcolith-bearing phase *C. pelagicus* HOL (formerly *Crystallolithus hyalinus*) were recorded in the Pacific SO. However we observed few specimens of *C. pelagicus* (sensu lato) HOL in the SAZ, in agreement with Nishida (1979).

We did not find any *C. leptoporus* coccosphere or coccoliths south of the SAF in the Pacific sector of the SO. However occurrences of this species, even poleward the SAF, were observed in the Australian SO sector (Findlay and Giraudeau, 2000) and Indian SO sector (e.g., Mohan et al., 2008). Due to the fact that the rest of the coccolithophore taxa restricted to the SAZ in our study area occur in very low proportions (i.e., *A. quattrospina*, *A. cucullata*, *G. muellerae*, *H. carteri*, *Michaelsarsia* spp., *Paluspһaera* spp., *U. tenuis* and *U. sibogae*) we will not comment further on them. In any case the SAZ assemblage distribution pattern can be observed in Fig. 12.

5.3.2. The coccolithophore assemblage in the PFZ

Both the diversity and the number of coccolithophores notably decreased south of the SAF (note the anticorrelation of Factor 1 loadings with SST). The members of the PFZ assemblage are also occurring in the SAF, but reached higher latitudes (Table 2, Fig. 12).

A reduced number of species constitute the PFZ assemblage, with *E. huxleyi* type B/C and type C dominating. The higher number of detached coccoliths of types B/C and C with respect to the number of coccospheres types B/C and C can be explained by the fact that specifically, these coccoliths are quite delicate and coccospheres tend to collapse easily. Detached *E. huxleyi* types B/C and C coccoliths could come from the external layer of multi-layered coccospheres whose presence has been observed. Different authors observed that type C or type B/C (terminology varies according to authors) are widespread in all the sectors of the SO (e.g., Findlay and Giraudeau, 2000; Cubillos et al., 2007; Gravalosa et al., 2008; Mohan et al., 2008; Holligan et al., 2010; Charalampopoulou, 2011). *Emiliania huxleyi* type B was not previously recorded in the SO (e.g., Findlay and Giraudeau, 2000; Cubillos et al., 2007; Mohan et al., 2008) and was just found in the Northern Hemisphere (Cook et al., 2011) reaching high percentages in the Northeast Atlantic and North Sea (e.g., van Bleijswijk et al., 1991; Young and Westbroek, 1991; Holligan et al., 1993). This fact would suggest that the few specimens of *E. huxleyi* type B observed in our

Plate II. (a) *Pappomonas* sp., sample PS75/058-1 at 60 m depth, (b) *Papposphaera* cf. *obpyramidalis*, sample PS75/063-3 at 20 m depth, (c) *Papposphaera lepida*, sample PS75/100-5 at 20 m depth, (d) *Gephyrocapsa muellerae*, sample PS75/058-1 at 60 m depth, (e) *Helicosphaera carteri*, sample PS75/104-3 at 100 m depth, (f) *Syracosphaera halldalii*, sample PS75/057-1 at 40 m depth, (g) *Syracosphaera corolla* (formerly *Gaarderia corolla* (Lecal) Kleijne, 1993), sample PS75/098-1 at 45 m depth, (h) *Syracosphaera* sp., sample PS75/100-5 at 10 m depth, (i) cf. *Syracosphaera* sp., sample PS75/100-5 at 20 m depth, (j) *Syracosphaera* cf. *borealis*, sample PS75/044-1 at 20 m depth, (k) *Syracosphaera* cf. *castellata*, sample PS75/100-5 at 20 m depth, (l) *Wigwamma antarctica*, sample PS74/104 at 100 m depth.

Table 3.
Factor Score matrix obtained by the Factor Analysis (including a Varimax normalized rotation) of the 14 most abundant coccolithophore taxa. Bold values indicate the species which define each factor.

	Factor 1	Factor 2	Factor 3
Calcidiscus leptoporus	−1.29	−0.19	**3.01**
Emiliania huxleyi type A	−0.07	−0.19	−0.63
Emiliania huxleyi type B	0.00	−0.63	−0.15
Emiliania huxleyi types B/C, C	**3.05**	1.29	0.94
Calciopappus caudatus	0.33	−0.87	**0.75**
Gephyrocapsa muellerae	−0.05	−0.58	−0.39
Syracosphaera spp.	−0.28	−0.11	−0.01
Ophiaster spp.	−1.32	**3.03**	−0.46
Acanthoica quattrospina	−0.24	−0.05	−0.29
Papposphaera spp.	0.16	−0.33	−0.63
Umbellosphaera tenuis	0.04	−0.37	−0.73
Algirosphaera cucullata	−0.11	−0.35	−0.46
Palusphaera spp.	−0.08	−0.43	−0.46
Holococcolithophores	−0.13	−0.22	−0.50

Table 4.
Correlation matrix between the 3 factors and environmental variables (SST, SSS and fluorescence) measured in situ. Marked correlations are significant at $p < 0.05$.

	Factor 1	Factor 2	Factor 3
SSS	−0.68	0.63	0.18
SST	−0.65	0.60	0.18
Fluorometer	0.19	−0.25	0.02

study area might actually be large-sized *E. huxleyi* type B/C. In any case, there is a noteworthy north–south variation in coccolith size in the study area which should be taken into account in future studies.

The north–south trend from *E. huxleyi* morphotype A to B/C recorded in the study area was also observed in other SO sectors (Findlay and Giraudeau, 2000; Cubillos et al., 2007; Mohan et al., 2008) and neighboring areas (e.g., Charalampopoulou, 2011). Although it has been suggested that the decrease in *E. huxleyi* calcification would be related to the effect of diminishing carbonate ion concentrations and calcite saturation state in the SO, Cubillos et al. (2007) linked it with a shift in dominance of one ecotype over another, corroborated later on by Cook et al. (2011). In the Northern Hemisphere, Hagino et al. (2005) observed a comparable south–north trend consisting of a replacement of *E. huxleyi* type A in the warm Kuroshio Current regime by *E. huxleyi* types B and C in the cold Oyashio current regime. Later, Hagino et al. (2011) re-examined the morphology of *E. huxleyi* in some of the samples used by Okada and Honjo (1973) and Hagino et al. (2005) and found a new morphotype based on molecular genetic studies. According to Hagino et al. (2011) type O, characterized by an open central area, dominates in the North Pacific Subarctic Gyre and its adjacent seas and it is extensively distributed in the SO. We consider that *E. huxleyi* type O is very similar to types B, B/C and C in size and shield characteristics; specifically when the central area of type O coccoliths is covered by an organic membrane or when coccoliths of types B, B/C and C have lost their central plate. Our study could therefore be biased by the inclusion of type O within other *E. huxleyi* morphotypes and a future re-examination of our plankton samples may help to better assess type O cold-water bipolar geographic distribution (Hagino et al., 2011). From our findings the main difference observed between north and south high latitudes regarding *E. huxleyi* is the dominance of distinct morphotypes, types B/C and C predominate in the SO while types A and B reach their highest percentages in (sub) Arctic regions. The lightly calcified and distinctive *E. huxleyi* morphotypes B/C and C (referred to as C, var. *kleijneae* or more usually B/C according to different authors) are widespread in all sectors of the SO and were found to be by far the dominant coccolithophore in the Pacific sector. However, *E. huxleyi* type B/C is not only restricted to the SO, recently Henderiks et al. (2012) found this morphotype to be occasionally dominant coccolithophore species at specific stages of the phytoplankton succession in the Benguela upwelling system (SE Atlantic).

Balestra et al. (2004) observed that *C. caudatus* showed major abundance at the stations close to the southeast Greenland shore characterized by rather low SST (2–3 °C). This may suggest that this species has affinity for cold-water masses. However, our findings in the Pacific SO indicate a preference for warmer waters in subpolar regions. The ecological factors that control the middle–lower photic zone distribution of *C. caudatus* in the water column are still not clear (Samtleben et al., 1995; Hagino et al., 2005).

Species of the family Papposphaeraceae (basically the genus *Pappomonas*, but also *Papposphaera* and *Wigwamma*) are present north

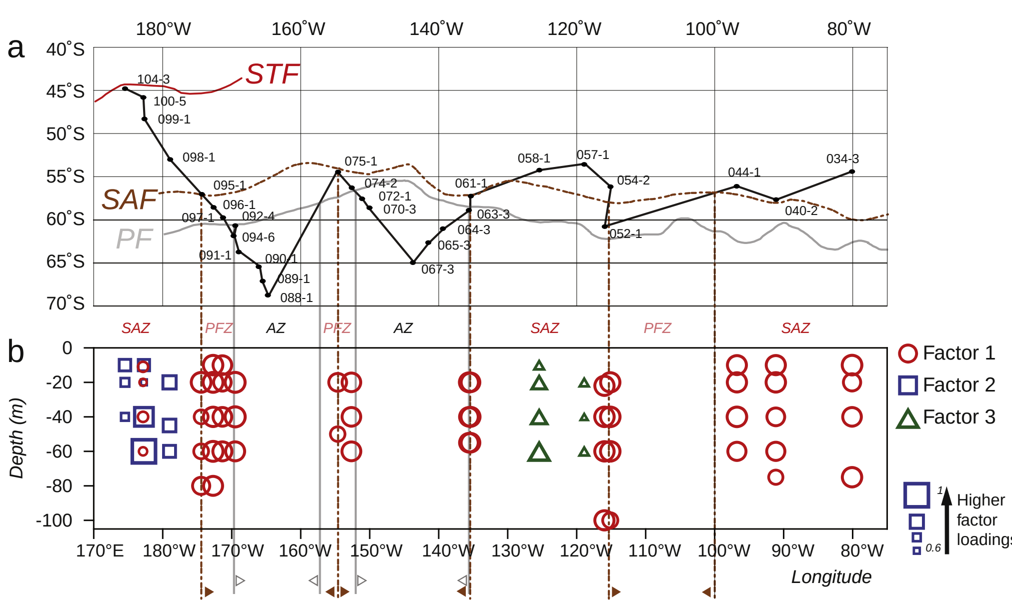

Fig. 9. (a) Location of the ANT-XXVI/2 CTD stations studied and (b) dominance of the factors indicated with circles (Factor 1), squares (Factor 2) and triangles (Factor 3) for the uppermost 100 m of the water column (characterization of each factor is displayed in Tables 3 and 4). Station numbers are indicated and oceanographic fronts are given as well (STF—red line, SAF—brown dashed line, PF—gray line). The areas between the fronts are referred to as Subantarctic Zone (SAZ), Polar Front Zone (PFZ) and Antarctic Zone (AZ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

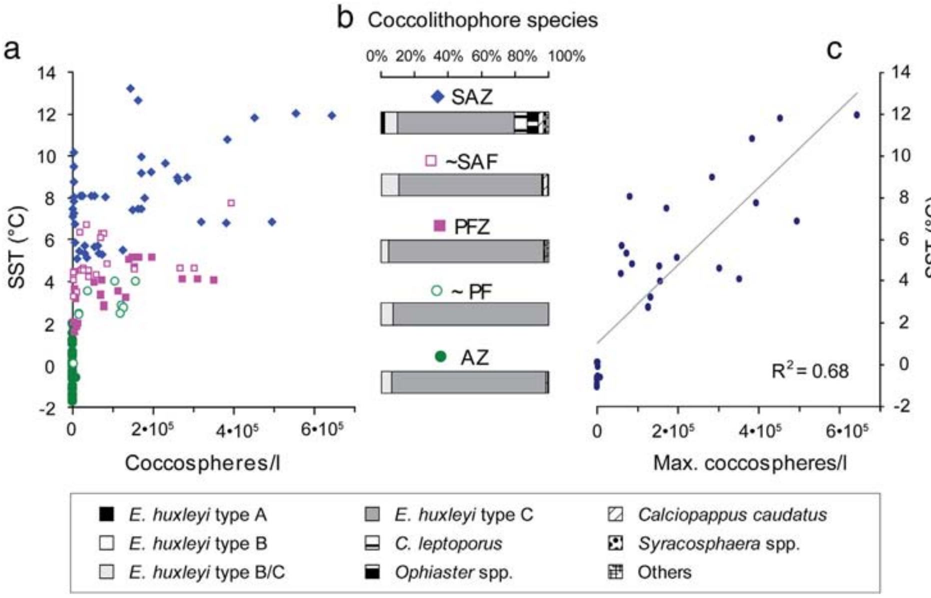

Fig. 10. (a) Number of coccospheres/l (all depths) versus sea surface temperature (SST, in °C) measured in situ; filled green circles correspond to samples located in the Antarctic Zone (AZ), empty green circles to samples located close to the Polar Front (PF), filled pink squares to samples located in the Polar Front Zone (PFZ), empty pink squares to samples located in the Subantarctic Front (SAF), and filled blue diamonds to samples located in the Subantarctic Zone (SAZ); (b) mean relative coccosphere abundance for the AZ, PF, PFZ, SAF and SAZ including *Emiliania huxleyi* (types A, B, B/C and C), *Calcidiscus leptoporus*, *Ophiaster* spp., *Calciopappus caudatus*, *Syracosphaera* spp., and other coccolithophore species; (c) maximum number of total coccospheres/l per station versus SST measured in situ.

of the PF. In fact some studies have demonstrated that they dwell in the SO at higher latitudes (e.g., Findlay and Giraudeau, 2000) and also in the Norwegian–Greenland Sea (Samtleben and Schröder, 1992). It has been suggested that species of the Papposphaeraceae family might be mixotrophic (Garrison and Thomsen, 1993; Marchant and Thomsen, 1994) which would provide them with an advantage over autotrophic coccolithophores for enduring at low light intensities and dark winters in polar waters (Charalampopoulou, 2011).

6. Conclusions

The distribution of the number of coccospheres analyzed in 150 samples obtained during austral summer of 2009–2010 in the Pacific sector of the Southern Ocean (SO, from 44.8°S to 68.7°S and from 80.1°W to 174.5°E) reflects the present-day dynamics of the oceanographic fronts. Based on our data the following conclusions can be drawn:

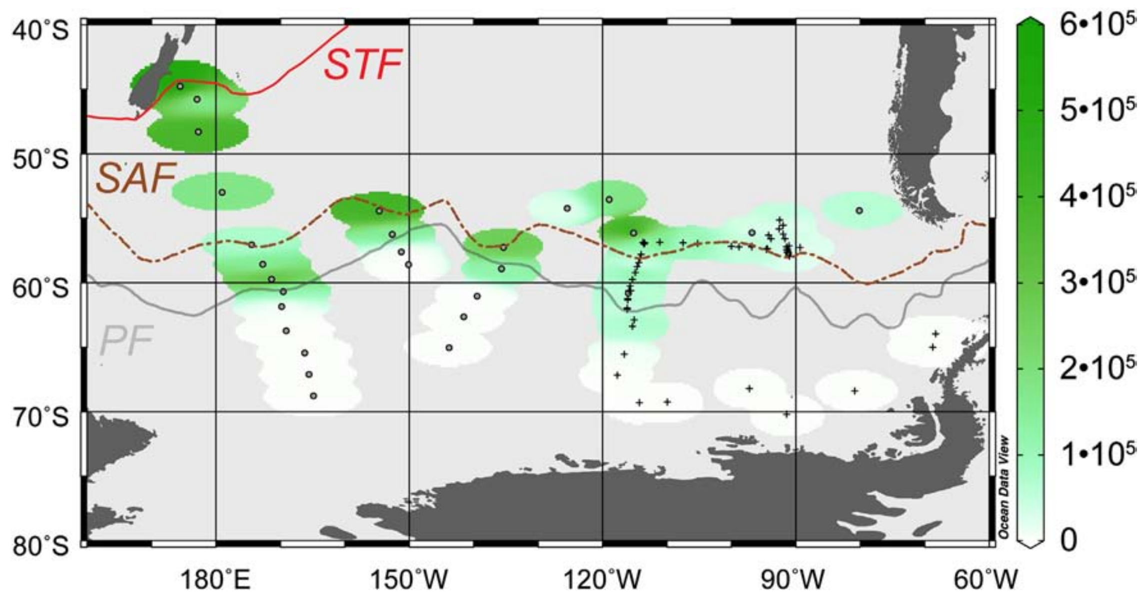

Fig. 11. Number of coccospheres/l at shallow depths (8 m to 22 m depth) plotted with Ocean Data View, ODV software version 4.5. ANT-XXVI/2 CTD coccolithophore data (indicated with circles) has been merged with ANT-XVIII/5a coccolithophore surface-water samples (indicated with crosses) retrieved during late austral summer 2002 (Gravalosa et al., 2008). Oceanographic fronts are given (STF—red line, SAF—brown dashed line, PF—gray line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

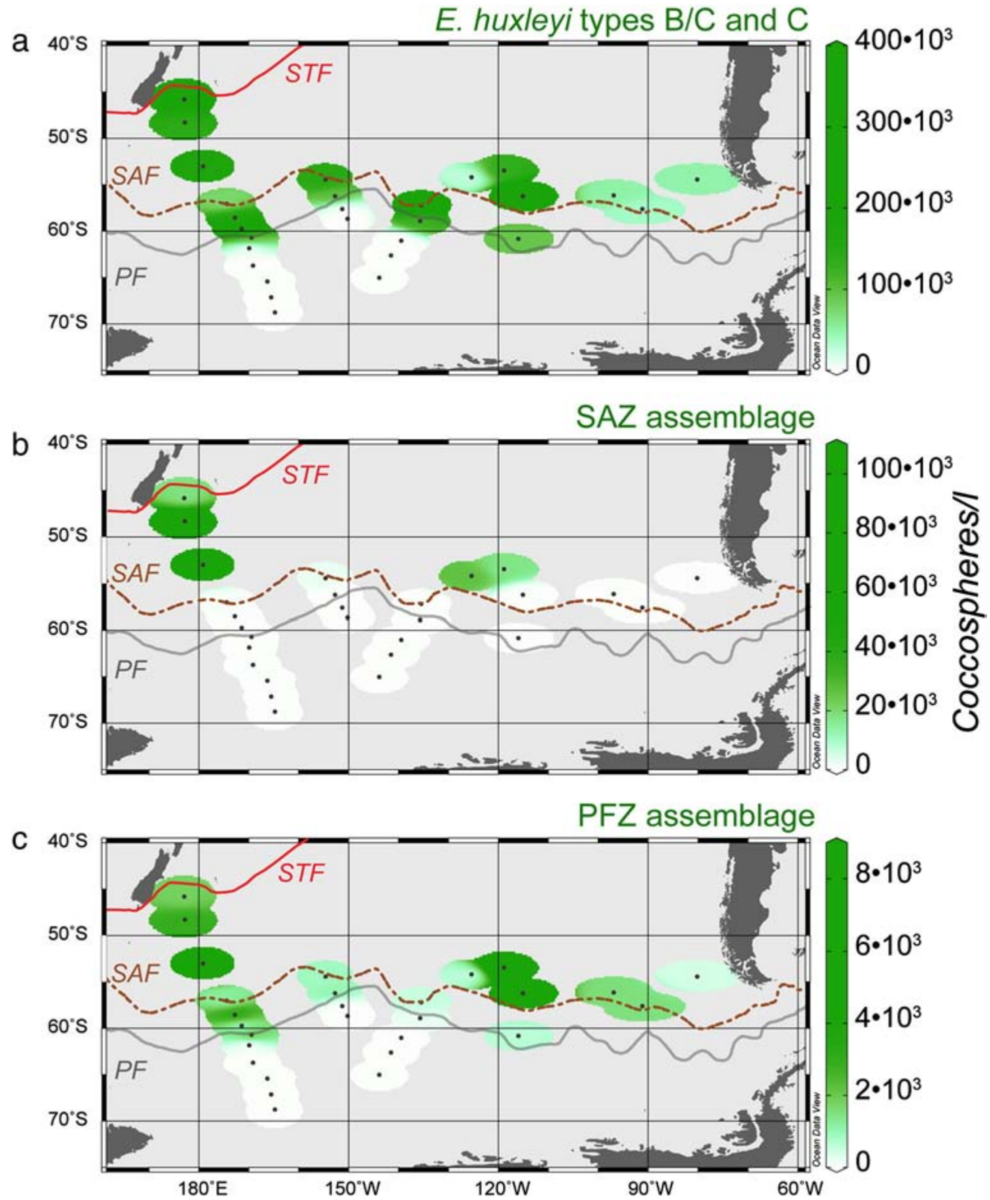

Fig. 12. (a) Location of the ANT-XXVI/2 CTD stations showing the uppermost 65 m average of coccosphere numbers for (a) *E. huxleyi* types B/C and C, (b) *E. huxleyi*-free SAZ assemblage (i.e., *Acanthoica quattrospina*, *Algirosphaera cucullata*, *Calcidiscus leptoporus*, *Coccolithus pelagicus* (sensu lato) HOL, *Calyptrolithophora* aff. *C. papillifera*, *Gephyrocapsa muellerae*, *Ophiaster* spp. *Palusphaera* spp., *Syracosphaera* spp., *Umbellosphaera tenuis*) and (c) *Emiliania huxleyi*-free PFZ assemblage (i.e., *Calciopappus caudatus*, *Pappomonas* spp., *Papposphaera* spp.). Oceanographic fronts are indicated (STF—red line, SAF—brown dashed line, PF—gray line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(1) Maximum numbers of $640 \cdot 10^3$ coccospheres/l occur close to the STF and increases in the numbers of coccospheres and coccoliths have also been observed at both the SAF and the PF. However, the numbers decrease southward until almost a monospecific and sporadic record of *E. huxleyi* (types B/C and C) south of the PF. The very low numbers recorded south of the PF would indicate that interpretations of alkenone results are probably limited in such high latitudes.

(2) Most of the coccolithophore species, except of *C. caudatus* which was present down to 100 m, are restricted to the uppermost 60 m of the water column. Here, the sea surface temperature is the most prominent factor influencing the coccolithophore diversity, distribution, and assemblage compositions in the Pacific sector of the SO.

(3) Thirty-three different species of coccolithophores, including 16 species found as isolated coccoliths, were identified. Although *E. huxleyi* is clearly the most dominant taxa in the Pacific SO, different coccolithophore assemblages were distinguished for the PFZ and for the SAZ. In the upper photic zone of the SAZ, *A. quattrospina*, *C. leptoporus*, *C. pelagicus* (sensu lato) HOL, *E. huxleyi* type A, *Ophiaster* spp. and *Syracosphaera* spp. among others were found. The PFZ was characterized by a reduced number of species, i.e., *C. caudatus*, *E. huxleyi* types B, B/C and C, as well as *Pappomonas* spp. and *Papposphaera* spp.

(4) The coccolithophore biogeography at southern high latitudes notably differs from the northern ones. The reduced presence of the cold water species *C. pelagicus* (sensu lato), abundant in the (sub) Arctic region, and the dominance of *E. huxleyi* types B/C and C in the SO contrasting with the dominance of *E. huxleyi* types A and B in the North Atlantic constitute noteworthy differences. Nevertheless, the current coccolithophore numbers and assemblage distribution in relation to the frontal dynamics of the SO provide

valuable information for potential future paleoceanographic reconstructions.

Taxonomical appendix

List of the coccolithophore taxa considered in this study. Identification generally followed Young et al. (2003), in which full reference can be found (HOL - holococcolithophore).

Acanthoica quattrospina Lohmann, 1903

Algirosphaera cucullata Lecal-Schlauder, 1951

Calcidiscus leptoporus (Murray and Blackman, 1898) Loeblich & Tappan, 1978

Calciopappus caudatus Gaarder & Ramsfjell 1954

Calyptrolithophora papillifera (Halldal 1953) Heimdal, in Heimdal & Gaarder 1980, ?=*S. histrica* HOL

Coccolithus pelagicus (Wallich 1877) Schiller 1930

Emiliania huxleyi (Lohmann, 1902) Hay & Mohler in Hay et al., 1967

Emiliania huxleyi type A

Emiliania huxleyi type B

Emiliania huxleyi type B/C

Emiliania huxleyi type C

Gephyrocapsa muellerae Bréhéret, 1978

Helicosphaera carteri (Wallich, 1877) Kamptner, 1954

Michaelsarsia Gran in Murray & Hjort, 1912 emend. Manton et al., 1984

Ophiaster Gran 1912 emend. Manton & Oates 1983

Palusphaera Lecal 1965 emend. Norris 1984

Pappomonas Manton & Oates 1975

Papposphaera Tangen 1972

Syracosphaera Lohmann, 1902

(including *S. borealis*, *S. castellata*, *S. corolla*, *S. delicata*, *S. dilatata*, *S. florida*, *S. halldalii*, *S. histrica*, *S. molischii*, *S. nana*, *S. ossa*, *S. prolongata*, *S. tumularis*, *S. type J*)

Umbellosphaera tenuis (Kamptner, 1937) Paasche in Markali and Paasche, 1955

Umbilicosphaera sibogae (Weber van Bosse, 1901) Gaarder, 1970

Wigwamma antarctica Thomsen in Thomsen et al., 1988

Acknowledgments

Lluïsa Cros is acknowledged for her suggestions and her valuable help in species identification. We are grateful to Ric Jordan and two anonymous reviewers for their constructive comments. *R/V Polarstern* officers and crew are thanked for their help during ANT-XXVI/2 Expedition. Samples were supplied through the assistance of the Alfred Wegener Institute for Polar and Marine Research. This work was funded by the Spanish "Programa Nacional de Movilidad de Recursos Humanos del Plan Nacional de I+D+i 2008–2011" and specifically by the MEC Postdoc grant (EX2009-0177) awarded to Mariem Saavedra-Pellitero.

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