



Sea surface distribution of coccolithophores in the eastern Pacific sector of the Southern Ocean (Bellingshausen and Amundsen Seas) during the late austral summer of 2001

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ABSTRACT

Horizontal distributions of coccolithophores were observed in sea surface water samples collected on the RV *Polarstern* between 27 February and 10 April, 2001, in the Pacific sector of the Southern Ocean (Bellingshausen and Amundsen Seas). These samples were analyzed to gain information about the distribution of coccolithophores in relation to the oceanic fronts of the Southern Ocean. A total of fifteen species of coccolithophores were identified, showing cell abundances of up to 67×10^3 cells/l down to 63° S. *Emiliana huxleyi* was the most abundant taxon, always accounting for more than 85% of the assemblage. The second most abundant species was *Calcidiscus leptoporus*, with values lower than 7%. Cell density increases significantly in both the Subantarctic and Polar Fronts (155 and 151×10^3 cells/l, respectively), decreasing abruptly in the intervening Polar Frontal Zone and to the south of the Polar Front. Although temperature at high latitudes is the main factor controlling the biogeographical distribution of coccolithophores, at the regional level (Southern Ocean) the frontal systems, and consequently nutrient distribution, play a crucial role.

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1. Introduction, background and objectives

The Pacific Sector of the Southern Ocean (SO), and in particular the Bellingshausen and Amundsen Seas, is one of the least explored and studied oceanic regions.

The SO is the most extensive High Nutrient–Low Chlorophyll region (HNLC) of the world's oceans, with phytoplankton standing stocks well below the level expected from the nutrient richness of the area (Eynaud et al., 1999). Primary productivity within the Antarctic Circumpolar Current (ACC) is highly variable despite the HNLC conditions (Tréguer and Jacques, 1992). However, phytoplankton blooms have only been observed, both visually and in satellite data, in regions mainly associated with SO fronts (Comiso et al., 1993; Moore and

Abbott, 2000). In the South Atlantic Ocean, the Polar Front (PF) has been reported to be closely associated with elevated levels of primary production (chlorophyll-a) (Van Franeker et al., 2002). Off Southwestern Australia, the occurrence of enhanced chlorophyll levels in the PF has been observed (Banse, 1996). In the South Georgia region, enhanced levels of both primary and secondary production have been observed in the Southern ACC Front (SACCF) (Murphy, 1995; Ward et al., 2002).

The phytoplankton from this ocean has been studied for more than 50 years, but data on living coccolithophores in the SO are limited (Nishida, 1986; Eynaud et al., 1999; Findlay and Giraudeau, 2000). In the western Pacific a poleward decrease in abundance and diversity of coccolithophores was observed in the SO at the same time with decreases in temperature, salinity, nitrate and phosphate. Conversely, high abundances and diversity values was recorded in the Subtropical Front (STF) and Subantarctic Front (SAF) (Findlay et al., 2005). In the Pacific sector of the SO, coccolithophores have been reported to be the major phytoplankton group in the Subantarctic Zone (SAZ), but no living coccolithophores have been recorded south of the PF (Hasle, 1969). Sea surface waters ranging in

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temperature from 0 to 6°C are typified by a monospecific assemblage of *Emiliana huxleyi* (McIntyre et al., 1970).

In the South Atlantic Ocean, the biogeographical extent of coccolithophores is thought to be limited to the south by the 2°C isotherm (McIntyre and Bé, 1967; Verbeek, 1989). The Subantarctic flora in the South Atlantic is mostly *E. huxleyi*. In some cases a monospecific flora of *E. huxleyi* is found in Antarctic waters below the PF (McIntyre and Bé, 1967). South of Africa, in the SO a monospecific assemblage of *E. huxleyi* has been identified polewards of the STF (Verbeek, 1989). Eynaud et al. (1999) identified 38 species in the same area, but south of the PF, only a monospecific assemblage of *E. huxleyi* was found; the species diversity gradually decreases polewards and peaks within the PF and north of the SAF.

In the Australian Sector, the PF is considered to be the southern boundary of coccolithophore occurrence. South of this front, only rare coccolithophores have been observed, all probably transported by surficial currents (Winter et al., 1994). Findlay and Giraudeau (2000) identified five assemblages in this sector with overall abundances and diversities decreasing polewards, and with a minimum temperature for coccosphere production of ~2 °C. Polewards of the Antarctic Divergence (AD) coccolithophores are absent.

The analysis of microfossil assemblages in high-latitude regions is an essential tool to constraining paleoceanographic interpretations (Samtleben et al., 1995a,b). The aim of this study was to investigate the current distribution of coccolithophores in the eastern Subantarctic and Antarctic Pacific sector (Bellingshausen and Amundsen Seas) and their relationships with the frontal systems of the SO, in order to use this information for paleoceanographic reconstructions.

2. Oceanographic setting

The SO, which is the part of the world's oceanic region south of 35°S, accounts for over a quarter of the global ocean's surface (Gille, 1994). It is characterised by a sequence of oceanic fronts with strong flows along them that together form the eastward flowing ACC.

The fronts of the ACC appear as sharp depth changes in the contours of equal temperature and salinity. Different specific temperature and salinity limits characterize each front (Table 2), but the diversity of local conditions often suggests that no single range or gradient is sufficient for unequivocal identification of each front (Holliday and Read, 1998).

The ACC is considered to be the northernmost part of the SO. Despite its great length, the ACC appears to be quite uniform. The northern boundary of the ACC is limited by the STF, which separates the warm saline sub-tropical surface waters from the cold Subantarctic waters (Whitworth and Nowlin, 1987; Strama and Peterson, 1990; Orsi et al., 1995). South of the STF, the surface waters are carried by the ACC around the SO and can be subdivided into Subantarctic and Antarctic waters (Holliday and Read, 1998), delimited by two major fronts: the SAF and the PF (Whitworth and Nowlin, 1987; Orsi et al., 1995; Pollard et al., 2002) (Fig. 1). Both fronts play important roles as biogeographical boundaries (Froneman et al., 1995; Pakhomov et al., 2000). The zone between the STF and the SAF is referred to as the SAZ (Orsi et al., 1995; Pollard et al., 2002) (Fig. 1).

The PF marks the location where Antarctic Surface Water (ASW) moving northward sinks below the Subantarctic Water (SAW) (Deacon, 1933). The PF has both surface and subsurface expressions whose locations do not necessarily coincide (Lutjeharms and Valentine, 1984). Strong gradients in Sea

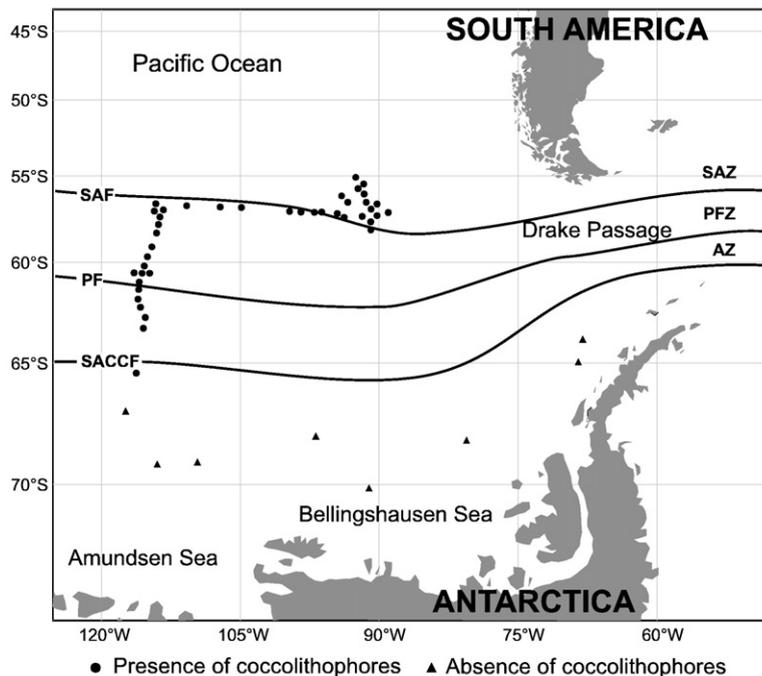


Fig. 1. Study region, oceanographic fronts, and location of water samples. Circles represent samples with the presence of coccolithophores. Triangles represent samples without coccolithophores. SAF: Subantarctic Front, PF: Polar Front, SACCF: Southern ACC Front, PFZ: Polar Front Zone, SAZ: Subantarctic Zone, AZ: Antarctic Zone.

Surface Temperature (SST) mark the surface expression (Deacon, 1933, 1937, Mackintosh; 1946). Occasionally, the PF has a double-front structure (Sievers and Nowlin, 1984; Read et al., 1995; Moore et al., 1999). The area between the SAF and the PF is referred to as the Polar Frontal Zone (PFZ) (Whitworth and Nowlin, 1987; Belkin and Gordon, 1996; Pollard et al., 2002) (Fig. 1). The SACCF lies south of the PF and close to the boundary that separates the ACC from the subpolar regime (Orsi et al., 1995, Holliday and Read, 1998). This SACCF is a controversial feature; whereas for Holliday and Read (1998) and Meredith et al. (2003) it is sometimes well defined in surface waters, for Orsi et al. (1995) it is only appreciable at depth. The Antarctic Zone (AZ) is the area between the APF and the SACCF (Fig. 1). Recent work has defined a possible

new front south of the PF—the Antarctic Ice Boundary Front (AIBF)—a surface and subsurface front related to the position of maximum winter ice coverage (Klyausov, 1993).

3. Materials and methods

3.1. Location and collection

A total of 51 surface-water samples were collected during the ANT-XVIII/5a Expedition aboard the *RV Polarstern* between 27 February and 10 April 2002 (late summer) in the eastern Subantarctic and Antarctic Pacific sector (Bellingshausen and Amundsen Seas), within the area: 55.13°S to 70.18°S latitude and 117.70°W to 68.28°W longitude (Fig. 1; Table 1). Samples were

Table 1
Sample position, date, temperature, salinity, and type of analysis

Sample	Analysis	Latitude (°S)	Longitude (°W)	Date	Temperature (°C)	Salinity psu	Cells/l
1	Semiquantitative	63.95	68.28	27-Feb	2.32	33.85	0
2	Semiquantitative	65	68.75	28-Feb	2.30	33.87	0
3	Semiquantitative	68.35	80.86	02-Mar	1.99	33.53	0
4	Semiquantitative	70.18	91.38	05-Mar	-1.17	32.50	0
5	Semiquantitative	69.21	109.93	13-Mar	0.02	33.55	0
6	Semiquantitative	69.28	114.28	13-Mar	-0.61	33.76	0
7	Quantitative	68.18	97.15	15-Mar	1.10	33.64	0
8	Semiquantitative	67.15	117.7	16-Mar	-0.08	33.74	0
9	Semiquantitative	65.51	116.56	17-Mar	1.35	33.89	7240
10	Quantitative	63.36	115.35	18-Mar	2.50	34.05	62356
11	Quantitative	62.85	115.08	18-Mar	2.87	34.08	82474
12	Quantitative	62.03	116.11	19-Mar	2.50	33.99	66385
13	Semiquantitative	61.96	116.11	19-Mar	2.16	33.99	8574
14	Quantitative	61.33	116.05	19-Mar	2.35	34.02	84871
15	Quantitative	61.25	116.05	19-Mar	2.90	34.05	72097
16	Quantitative	60.61	115.83	20-Mar	3.67	34.10	54066
17	Quantitative	60.61	115.86	20-Mar	3.27	34.11	79872
18	Semiquantitative	60.61	115.61	20-Mar	3.67	34.11	3908
19	Quantitative	60.25	115.7	20-Mar	3.30	34.03	55700
20	Quantitative	59.75	115.35	20-Mar	3.80	34.05	111695
21	Quantitative	59.2	114.88	21-Mar	5.45	34.21	152387
22	Quantitative	58.73	114.6	21-Mar	4.50	34.14	44218
23	Semiquantitative	58.43	114.36	21-Mar	4.54	34.14	2942
24	Quantitative	58.08	114.13	21-Mar	4.54	34.13	38414
25	Quantitative	57.81	114.01	21-Mar	4.50	34.16	91489
26	Quantitative	57	113.55	22-Mar	6.60	34.24	175157
27	Quantitative	56.88	113.46	22-Mar	6.00	34.49	151336
28	Semiquantitative	56.85	113.66	22-Mar	5.78	34.17	1398
29	Quantitative	56.85	111.11	22-Mar	6.00	34.19	179314
30	Quantitative	56.92	107.48	23-Mar	6.50	34.27	66210
31	Quantitative	56.95	105.2	23-Mar	6.50	34.11	115967
32	Quantitative	57.18	99.98	24-Mar	5.96	34.09	89880
33	Semiquantitative	57.22	98.75	24-Mar	5.96	34.13	4880
34	Quantitative	57.18	96.82	25-Mar	5.88	34.02	102434
35	Semiquantitative	57.22	96.77	25-Mar	5.88	34.08	307
36	Quantitative	57.4	94.52	26-Mar	5.95	34.05	125542
37	Semiquantitative	57.37	94.4	26-Mar	5.98	34.16	1625
38	Semiquantitative	57.93	90.9	27-Mar	6.04	34.16	282
39	Semiquantitative	57.63	91.3	28-Mar	5.92	34.05	625
40	Quantitative	57.12	91.02	29-Mar	5.56	34.02	74827
41	Semiquantitative	57.23	91.37	29-Mar	5.94	34.14	2686
42	Semiquantitative	57.25	89.3	30-Mar	6.29	34.20	1586
43	Quantitative	56.57	93.8	02-Apr	6.39	34.07	115722
44	Semiquantitative	56.33	94.18	02-Apr	6.32	34.06	2388
45	Semiquantitative	55.55	91.97	03-Apr	6.89	34.09	1021
46	Quantitative	55.13	92.48	03-Apr	6.79	34.08	70939
47	Quantitative	56.22	91.92	04-Apr	6.59	34.00	57937
48	Semiquantitative	56.58	91.7	04-Apr	5.81	34.19	3193
49	Semiquantitative	55.83	92.58	05-Apr	6.80	34.23	1673
50	Quantitative	57.4	91.25	07-Apr	5.40	34.06	76558
51	Semiquantitative	57.42	91.42	07-Apr	5.24	34.19	4625

taken using the ship's pumping system at 8 m depth. Temperature and salinity data were obtained simultaneously during the cruise by means of the ship's temperature and salinity sensors.

3.2. Preparation techniques and counting procedures

For this study two different types of seawater samples were considered. Exclusively for coccolithophore analyses, 1 l of seawater was prefiltered with a sieve of 41 µm pore size, and then vacuum-filtered through a Millipore® filter (47 mm diameter, 0.1 µm pore size). Taking advantage of a second sampling carried on board for other planktonic organisms, additional samples were examined. In this case, a variable volume of seawater (always more than 8 l) was filtered through a sieve of 41 µm, and then vacuum-filtered through a Millipore® filter (47 mm diameter, 5 µm pore size). Filters were air-dried before storage in plastic Petri dishes.

All samples were examined by light microscopy (1250×) and the abundance of coccolithophores was determined. A piece of the filter (10×10 mm) was mounted between the slide and coverslip with Canada balsam.

Two types of studies were carried out: a quantitative analysis, for the samples filtered at 0.1 µm; and a semi-quantitative analysis, for the samples filtered at 5 µm. In both cases, complete coccospheres were counted (300–350 coccospheres per sample). The abundance of the coccolithophores was expressed in cells/l, based on the volume of the filtered sample and the number of cells per field of view extrapolated to the total sample, using the following formula:

$$N = (n \times S/s)/V, \tag{1}$$

where *N* is the number of cells per liter; *n* the number of cells per field of view; *S* the effective filtration area (mm²)—diameter 45 mm; *s* the surface of a field of view at ×1250 magnification (mm²)—diameter 0.17 mm, and *V* the volume filtered (Eq. (1)).

These analyses were completed with selective Scanning Electron Microscopy observations in order to clarify the taxonomic status of some species.

Additionally, a biometric study of *E. huxleyi* was carried out in 25 samples (4411 coccolith measurements) in order to characterize the dominant morphotypes. Images of 40 randomly chosen fields of view in each sample, and distal

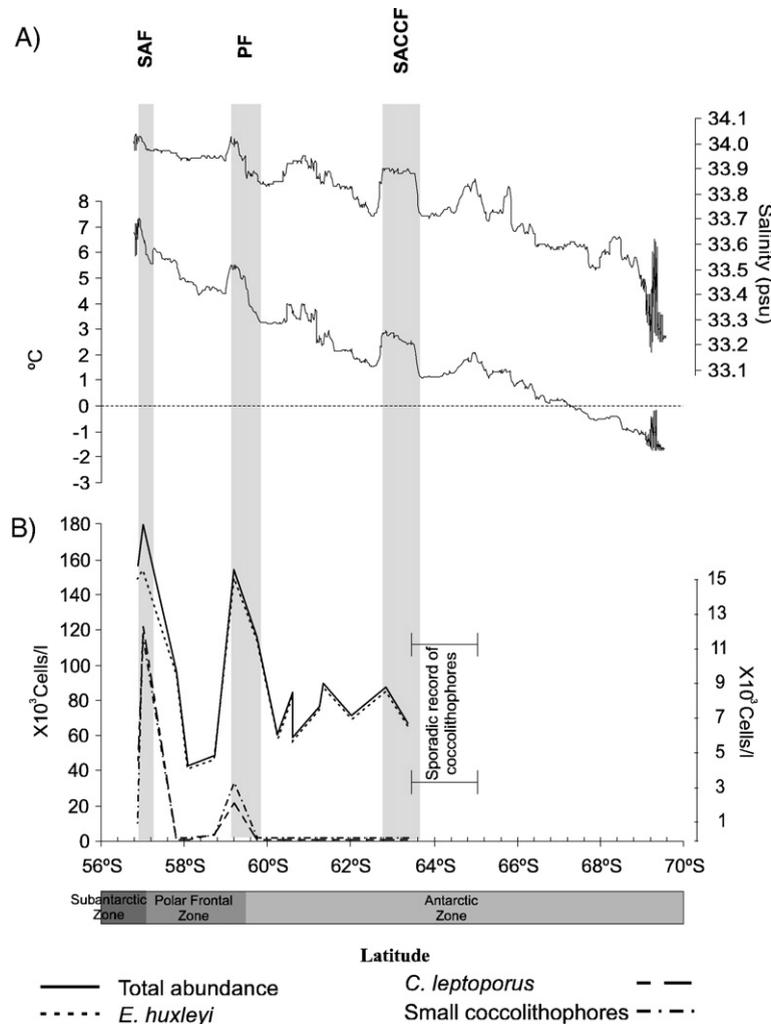


Fig. 2. North–South transect. A) Salinity and sea-surface temperature profiles. B) Abundance of coccolithophores. Right axis: *C. leptoporus* and small coccolithophores. Left axis: Total abundance and *E. huxleyi*.

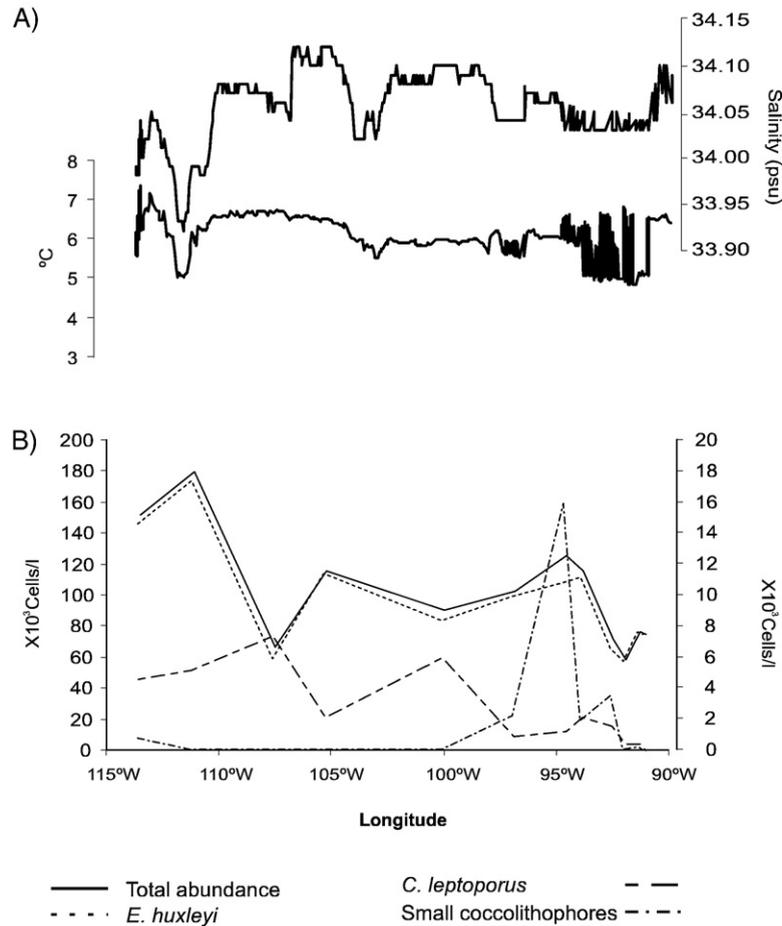


Fig. 3. West–East transect. A) Salinity and sea-surface temperature profiles. B) Abundance of coccolithophores. Right axis: *C. leptoporus* and small coccolithophores. Left axis: Total abundance and *E. huxleyi*.

shield lengths and widths were measured. The images were captured with a Leica DMR XE polarized light microscope, and a Leica DC 250 digital camera, using 1600 \times magnification. Images from several random visual fields of each sample were captured using the Leica QWin Pro software. The resolution of this technique is a tenth of a micron (1 pixel=0.066 μ m).

4. Results

4.1. Hydrography

Samples, as well as SST and salinity data gathered during the cruise, were analyzed on the basis of two transects (Figs. 2

and 3): a North–South transect, samples 8 to 27 (1373 measurements of salinity and temperature); and a West–East transect, samples 27 to 51 (2218 measurements).

The West–East transect showed a temperature interval from 7.35 $^{\circ}$ C to 4.82 $^{\circ}$ C and from 34.04 psu to 33.17 psu in salinity. An abrupt decrease in temperature and salinity is noteworthy west of 110 $^{\circ}$ W. The North–South transect showed variations in temperature from 7.35 $^{\circ}$ C to 1.74 $^{\circ}$ C, and in salinity from 34.04 psu to 33.17 psu. This transect displayed large horizontal gradients in SST and salinity, and they were used to identify the oceanic fronts (Table 2).

The APF in the North–South transect is located between 56.92 $^{\circ}$ S and 57.22 $^{\circ}$ S (between 7.35 $^{\circ}$ C and 5.58 $^{\circ}$ C) with a

Table 2
Criteria for front identification

Front	Definition	Authors	Sectors
Subantarctic (SAF)	Maximum grad T_0 in the range 5 $^{\circ}$ –9 $^{\circ}$ C	Burling (1961)	South of Australia
	Maximum grad T_0 in the range 5.1 $^{\circ}$ –9 $^{\circ}$ C	Lutjeharms and Valentine (1984)	South of Africa
Polar (PF)	Maximum grad T_0 in the range 2 $^{\circ}$ –6 $^{\circ}$ C	Ostapoff (1962)	Indian Ocean
	Grad $T_0 > 2^{\circ}$ C/0.5 $^{\circ}$ latitude	Gordon (1967)	Pacific Ocean
	Grad $T_0 \geq 1.35^{\circ}$ C in 45–65 km latitude	Moore et al. (1999)	Southern Ocean
	Gradient ($^{\circ}$ C km $^{-1}$) 0.03 between the isotherms 3.7 $^{\circ}$ –6.6 $^{\circ}$ C	Eynaud et al. (1999)	Atlantic Ocean
Southern ACC (SACCF)	Grad T_0 1.5 $^{\circ}$ C in 50 km	Meredith et al. (2003)	South Georgia
	$T_0 < 1.3^{\circ}$ C between the SACCF and the SACCB	Ward et al. (2002)	South Georgia

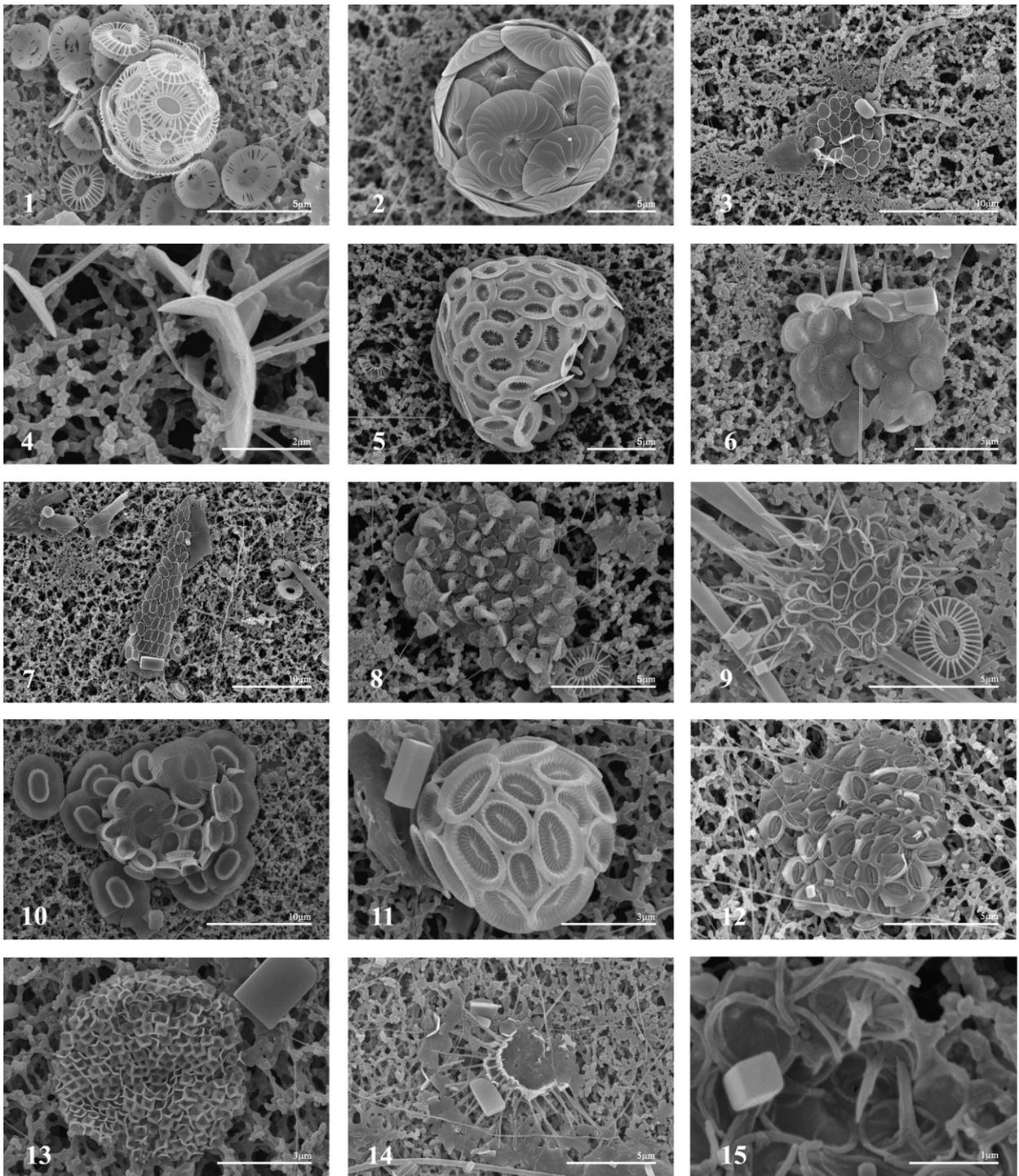
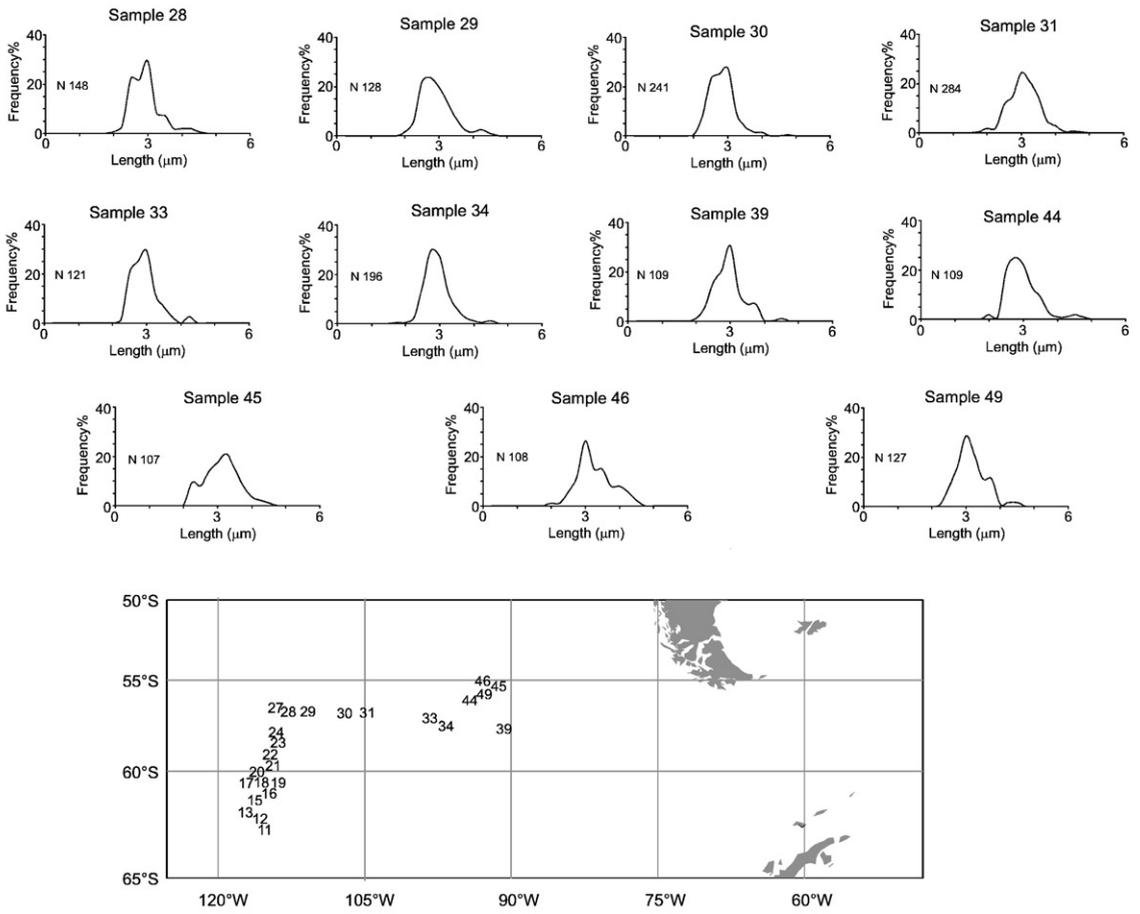


Plate I. Coccoliths and cocsospheres. SEM micrographs have been taken using a HITACHI S-3500N. 1. *Emiliana huxleyi* var. *kleijinae*. Sample 11. 2. *Calcidiscus leptoporus*. Sample 11. 3. *Ophiaster hydroideus*. Sample 15. 4. *Palusphaera vandeli*. Sample 15. 5. *Syracosphaera halldalii*. Sample 15. 6. *Acanthoica quattrosolina*. Sample 11. 7. *Calciopappus caudatus*. Sample 11. 8. *Corisphaera strigilis*. Sample 15. 9. *Wigwamma antarctica*. Sample 16. 10. *Syracosphaera corolla*. Sample 11. 11. *Syracosphaera* cf. *borealis*. Sample 16. 12. *Alisphaera extenta*. Sample 16. 13. *Polycrater galapagensis*. Sample 16. 14. *Papposphaera* sp. Sample 11. 15. *Ophiaster* sp. Sample 11.

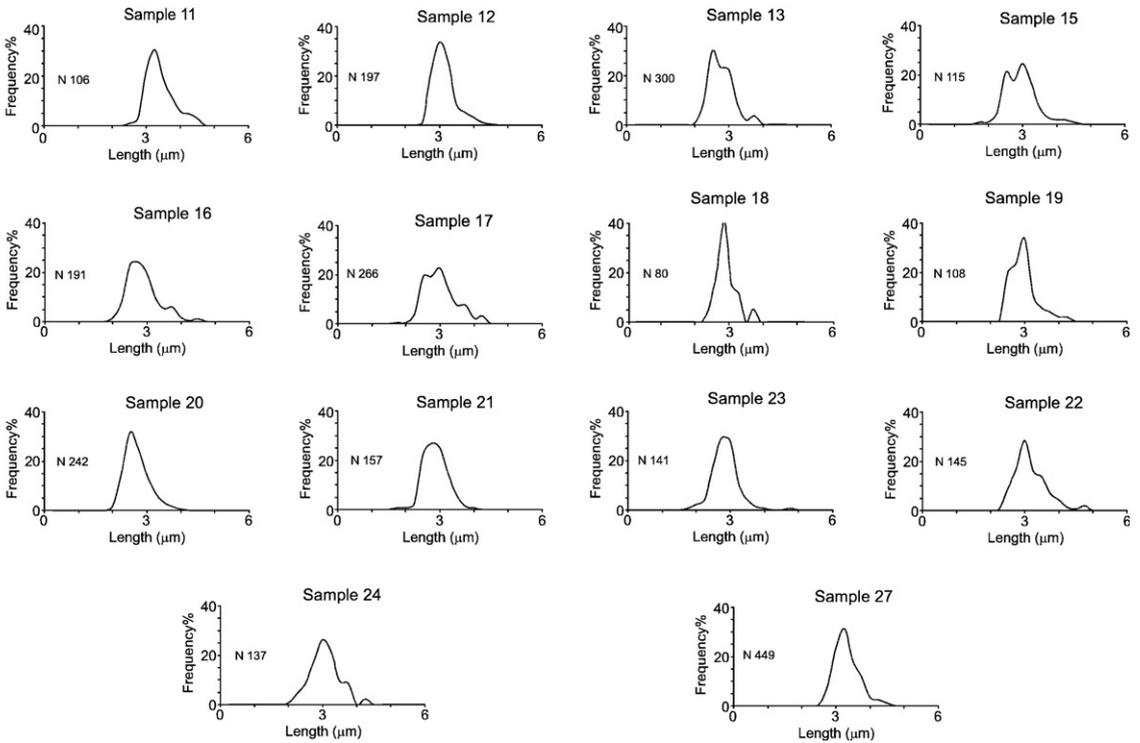
gradient of $0.053\text{ }^{\circ}\text{C km}^{-1}$. The PF in the North–South transect is located between 59.28°S and 59.91°S (between $5.40\text{ }^{\circ}\text{C}$ and $3.27\text{ }^{\circ}\text{C}$) with a gradient of $0.016\text{ }^{\circ}\text{C km}^{-1}$, and

the SACCF is situated between 62.86°S and 63.77°S (between $2.87\text{ }^{\circ}\text{C}$ and $1.14\text{ }^{\circ}\text{C}$) with a gradient of $0.017\text{ }^{\circ}\text{C km}^{-1}$.

A)



B)



4.2. Distribution of coccolithophores.

Analysis of 51 surface-water samples revealed the latitudinal distribution pattern of the coccolithophores through the ocean fronts of the SO within the area investigated. It is remarkable that the number of cells/l increased considerably in the samples of the SAF and the PF, and decreased within the PFZ and south of the PF (Fig. 2).

The samples south of the SACCF, with temperatures between 2.3 °C and –1.2 °C and salinities between 33.9 psu and 32.5 psu, were devoid of coccolithophores.

Samples from the North–South transect showed abundances between 175×10^3 and 38×10^3 cells/l. The highest coccolithophore concentrations ($>150 \times 10^3$ cells/l) were observed within the SAF and the PF. The PFZ and the AZ were characterized by low abundances ($<85 \times 10^3$ cells/l), which contrasts with the high cell densities observed in the SAF and PF. Temperatures associated with samples from the North–South transect were between 6.6°C and 2.2°C, and salinities were between 34.5 psu and 34.0 psu. Coccolithophores disappeared between 65.51°S and 67.15°S, where temperature ranges from 1.35°C to –0.08°C and salinity between 33.89 psu and 33.74 psu.

The West–East transect showed abundances of 179×10^3 cells/l to 58×10^3 cells/l (Fig. 3). The average coccolithophores abundance was 100×10^3 cells/l, with a peak in the SAF. The temperatures associated with these samples ranged between 6.79°C and 5.40°C and salinities between 34.49 psu and 34.00 psu.

Up to fifteen species of coccolithophores were identified in this study (see Taxonomic Appendix). *E. huxleyi* var. *kleijniae* was the most abundant taxon, always accounting for more than 85% of the assemblage (Plate I).

Two assemblages of coccolithophores were established, based on changes in species diversity: Assemblage A was associated with the SAF and the PF, whereas assemblage B was related to the PFZ, the AZ and the SACCF.

4.2.1. Assemblage A

This was dominated by *E. huxleyi* var. *kleijniae*, which often formed more than 85% of the association. *C. leptoporus*, intermediate morphotype, was the second species in abundance, with values lower than 7%. Other identified taxa occurred in very low proportions.

4.2.2. Assemblage B

A monospecific assemblage formed by *E. huxleyi* var. *kleijniae* was linked to the PFZ and to south of the PF.

The presence of fragile taxa, as well as almost pristine forms of *E. huxleyi* allow us to conclude that preservation is good in all analyzed samples.

4.3. Biometric study

A biometric study of *E. huxleyi* coccoliths was performed on 25 samples located at a from between 55°S and 63°S and, between 115°W and 90°W of longitude. This revealed that the length of the distal shield varied from 1.65 to 4.73 µm, the average value being 2.95 µm (Fig. 4). This study indicates that

the populations of *E. huxleyi* exhibit small variations in size along the transects analysed, and peaks of maximum frequency in distal shield lengths within the 2.50 to 3.25 µm interval. No relationships between coccolith size and latitude, temperature or salinity variations were observed (Figs. 2, 3 and 4).

Following the classification of Young and Westbroek (1991), the morphotype of *E. huxleyi* found in all samples corresponds to Type C. This morphotype is characterized by having an average length of the distal shield of 2.8 µm; the elements of the distal shield are well separated; the number of elements is about 28, and the central area is closed. Medlin et al. (1996) consider this type should be considered as a separate variety, recommending the name *E. huxleyi* var. *kleijneae*.

5. Discussion

The high coccolithophore abundance observed in the SAF and PF is related to production, usually associated with a high nutrient supply to surface waters within frontal zones as compared to surrounding oceanic areas (Murphy, 1995; Pollard et al., 1995). Zones with the steepest physical gradients coincide spatially with the highest primary production rates (Van Franeker et al., 2002). The density of coccolithophores in the region decreases polewards. This trend has also been observed by Nishida (1986), Findlay and Giraudeau (2000) in the Australian sector. Eynaud et al. (1999) recorded maximum coccolithophore cell densities to the south of the PF in the Atlantic sector. This distribution of coccolithophorids has been confirmed by Sikes and Volkman (1993), who reported that concentration of alkenones synthesized by *E. huxleyi* decreasing with increasing latitude in Australian sector of SO, at about 60°S. The southernmost sample in which coccolithophores were identified was taken at a latitude of 65.50°S and at a water temperature of 1.35 °C, indicating that the SACCF could be the southernmost boundary of coccolithophore occurrence. Previous studies considered that the PF is the southernmost limit for coccolithophore survival, and that south of this front coccolithophores occur only rarely, probably transported by surficial currents (Verbeek, 1989; Winter et al., 1994, 1999). Although the southernmost samples in this study were filtered through a 5 µm pore size filter, the high coccolithophore abundances found ($60\text{--}80 \times 10^3$ /l) suggest that they were not transported by currents, but were inhabitants of the area.

Temperature seems to be the most important factor limiting coccolithophore distribution in the southernmost locations (no coccolithophores below 1.3 °C), but in the transects studied, nutrient availability controls their abundance.

The highest abundance of coccolithophores occurs within the SAF and the PF. The occurrence of monospecific assemblages of *E. huxleyi* in the PFZ and to the south of the PF indicates that *E. huxleyi* is a species that can grow within a high range of physico-chemical factors, as previously reported by Winter et al. (1994) and Putland et al. (2004). The other species of coccolithophores identified have more restricted habitats. *C. leptoporus*, the second in abundance, and the rest of the species observed were only present in the fronts (SAF and PF).

The total diversity and abundance of coccolithophores recorded in the polar regions of the SO is significantly lower than in the Subarctic (Samtleben et al., 1995a). In the subpolar North Atlantic, coccolithophores often dominate assemblages. Conversely, in the polar regions of the SO, coccolithophores are almost always subordinate to diatoms (Findlay et al., 2005). Towards the north and west the diversity gradually decreases (Samtleben and Schröder, 1992). Generally, a northward decrease in the number of species can be explained by a decrease in surface water temperatures (Samtleben et al., 1995b). In the northern North Atlantic, *E. huxleyi* and *Coccolithus pelagicus* are the most abundant species (Samtleben et al., 1995b). *C. pelagicus* has been found abundant in the water column as far north as 86° (Honjo, 1990). Coccolith assemblages retrieved from sediment cores from the Norwegian Sea and Fram Strait show low diversity and consist almost entirely of *C. pelagicus* and *E. huxleyi*. (Baumann and Matthiessen, 1992). In the Gulf of Alaska the most abundant species is *E. huxleyi* (Booth et al., 1982), also the most abundant coccolithophorid in the subarctic Pacific.

C. pelagicus, which is the dominant species in the subarctic sector of North Atlantic, tolerating temperatures of -1.5°C , was not found at high latitudes in the SO (Winter et al., 1999).

The biometric data are in agreement with previous biometric studies on *E. huxleyi* in the Australian sector of the Antarctic Ocean. Findlay and Giraudeau (2000) indicated that most specimens of *E. huxleyi* collected in the SO, polewards of the STF, belonged to Type C. Previously, McIntyre and Bé (1967) described forms equivalent to this morphotype designating them “cold water” specimens.

Concerning coccolith size, the behaviour of *E. huxleyi* in the past was different than today. Based on data from the Mediterranean and the North Atlantic (Colmenero-Hidalgo et al., 2002), coccoliths $>4\ \mu\text{m}$ were characteristic of glacial sediments while coccoliths with a size $<4\ \mu\text{m}$ are more abundant during the deglaciation and Holocene.

Today, the *E. huxleyi* population in the SO is dominated by a single morphotype: *E. huxleyi* var. *kleijniae*. This suggests that at the high latitudes of the SO *E. huxleyi* var. *kleijniae* is the characteristic morphotype. This morphotype can therefore be considered a cold-water indicator.

6. Conclusions

This study (Bellingshausen and Amundsen Seas) shows that the abundance of coccolithophores in the Southern Ocean increases significantly in the SAF and the PF, and decreases in the PFZ and to the south of the PF. In general, coccolithophore cell density decreases polewards. The southernmost sample in which living coccolithophores were observed was taken at a latitude of 65.50°S and a water temperature of 1.35°C .

Although temperature seems to be the main factor controlling coccolithophore distribution, our results suggest that the dynamics of frontal systems and nutrient availability affect coccolithophore abundances in the region. *E. huxleyi* var. *kleijniae* is the most abundant species in the zone, confirming its cosmopolitan character. The rest of the species, *C. leptoporus* and “small coccolithophores”, are restricted

to the fronts and nutrient content seems to control their presence in the area.

The coccolithophore distribution in this region is not yet well known. Future studies will be essential for better understanding their ecological requirements as well as their relationship with frontal systems in the Southern Ocean, which will facilitate the monitoring of the displacement of these fronts in the past.

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Appendix A. Taxonomic appendix

The taxonomic list comprises all taxa mentioned in the text. Full bibliographic references can be found in Young et al. (2003).

- Acanthoica quattrosproina* Lohmann, 1903
- Alisphaera extenta* Kleijne et al., 2001
- Calcidiscus leptoporus* (Murray and Blackman, 1898) Loebllich and Tappan, 1978
- Calciopappus caudatus* Gaarder and Ramsfjell 1954
- Corisphaera strigilis* Gaarder, 1962
- Emiliana huxleyi* (Lohmann, 1902) Hay and Mohler, 1967
- Ophiaster* sp. Gran, 1912 emend. Manton and Oates, 1983
- Ophiaster hydroideus* (Lohmann, 1903) Lohmann, 1913 emend. Manton and Oates, 1983
- Palusphaera vandellii* Lecal, 1965 emend. R.E. Norris, 1984
- Papposphaera* sp Tangen, 1972
- Polycrater galapagensis* Manton and Oates, 1980
- Syracosphaera* cf. *borealis* Okada and McIntyre 1977
- Syracosphaera corolla* Lecal, 1966
- Syracosphaera halldalii* Gaarder ex Jordan and Green, 1994
- Wigwamma antarctica* Thomsen in Thomsen et al., 1988.

References

- Banse, K., 1996. Low seasonality of low concentrations of surface chlorophyll in the Subantarctic water ring: underwater irradiance, iron, or grazing? Progress in Oceanography 37, 241–291.
- Baumann, K.H., Matthiessen, J., 1992. Variations in surface water mass conditions in the Norwegian Sea: evidence from Holocene coccolith and dinoflagellate cysts. Marine Micropaleontology 20, 129–146.
- Belkin, I.M., Gordon, A.L., 1996. Southern Ocean fronts from the Greenwich meridian to Tasmania. Journal of Geophysical Research 101, 3675–3696.
- Booth, B.C., Lewin, J., Norris, R.E., 1982. Nanoplankton species predominant in the subarctic Pacific in May and June 1978. Deep-Sea Research 29, 185–200.
- Burling, R.W., 1961. Hydrology of circumpolar waters south of New Zealand. New Zealand Department of Scientific Industrial Research 143, 66.
- Colmenero-Hidalgo, E., Flores, J.A., Sierro, F.J., 2002. Biometry of *Emiliana huxleyi* and its biostratigraphic significance in the Eastern North Atlantic Ocean and Western Mediterranean Sea in the last 20000 years. Marine Micropaleontology 46, 247–263.
- Comiso, J.C., McClain, C.R., Sullivan, C.W., Ryan, J.P., Leonard, C.L., 1993. Coastal Zone Color Scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. Journal of Geophysical Research 98, 2419–2451.

- Deacon, G.E.R., 1933. A general account of the hydrology of the South Atlantic Ocean. *Discovery Reports* 7, 177–238.
- Deacon, G.E.R., 1937. The hydrology of the Southern Ocean. *Discovery Reports* 15, 1–124.
- Eynaud, F., Giraudeau, J., Pichon, J.-J., Pudsey, C.J., 1999. Sea-surface distribution of coccolithophores, diatoms, silicoflagellates and dinoflagellates in the South Atlantic Ocean during the late austral summer 1995. *Deep-Sea Research I* (46), 451–482.
- Findlay, C.S., Giraudeau, J., 2000. Extant calcareous nannoplankton in the Australian Sector of the Southern Ocean (austral summers 1994 and 1995). *Marine Micropaleontology* 40, 417–439.
- Findlay, C.S., Young, J.R., Scott, F.J., 2005. Haptophytes: Order Coccolithophorales. In: Scott, F.J., Marchant, H.J. (Eds.), *Antarctic Marine Protists*. Australian Biological Resources Study and Australian Antarctic Division, pp. 276–294.
- Froneman, P.W., McQuaid, C.D., Perissinotto, R., 1995. Biogeographic structure of the microphytoplankton assemblages of the south Atlantic and Southern Ocean during austral summer. *Journal of Plankton Research* 17, 1791–1802.
- Gille, S.T., 1994. Mean sea surface height of the Antarctic Circumpolar Current from Geosat data: method and application. *Journal of Geophysical Research* 99 (C9), 18255–18273.
- Gordon, A.L., 1967. Structure of Antarctic waters between 20°W and 170°W. In: Bushnell, V.C. (Ed.), *Antarctic Map Folio Series, folio 6*. American Geographical Society, New York, p. 10.
- Hasle, G.R., 1969. An analysis of the phytoplankton of the Pacific Southern Ocean: abundance, composition and distribution during the Brategg expedition 1947–1948. *Halvaredets Skr. Science of Royal Marine Biology Research* 52, 168.
- Holliday, N.P., Read, J.F., 1998. Surface oceanic fronts between Africa and Antarctica. *Deep Sea Research I* 45, 217–238.
- Honjo, S., 1990. Particle fluxes and modern sedimentation in the polar oceans. In: Smith, W.O. (Ed.), *Polar Oceanography, vol. II*. Academic Press, New York, pp. 322–353.
- Klyausov, A.V., 1993. On the frontal zone near the northern boundary of sea ice distribution in the Southern Ocean. *Oceanology, English Translation* 33 (6), 727–734.
- Lutjeharms, J.R.E., Valentine, H.R., 1984. Southern Ocean thermal fronts south of Africa. *Deep Sea Research* 31, 1461–1475.
- McIntyre, A., Bé, A.W.H., 1967. Modern Coccolithophoridae of the Atlantic Ocean. Placoliths and Cyrtoliths. *Deep-Sea Research* 14, 561–597.
- McIntyre, A., Bé, A.W.H., Roche, B., 1970. Modern Pacific Coccolithophoridae: a paleontological thermometer. *Transactions of the New York Academy of Science* 32, 720–731.
- Mackintosh, N.A., 1946. The Antarctic Convergence and the distribution of surface temperatures in Antarctic waters. *Discovery Reports* XXIII, 177–212.
- Medlin, L.K., Barker, G.L.A., Campbell, L., Green, J.C., Hayes, P.K., Marie, D., Wrieden, S., Vault, D., 1996. Genetic characterisation of *Emiliania huxleyi* (Haptophyta). *Journal of Marine Systems* 9, 13–31.
- Meredith, M.P., Watkins, J.L., Murphy, E.J., Ward, P., Bone, D.G., Thorpe, S.E., Grant, S.A., Ladkin, R.S., 2003. Southern ACC Front to the northeast of South Georgia: Pathways, characteristics, and fluxes. *Journal of Geophysical Research* 108 (C5), 3162.
- Moore, J.K., Abbott, M.R., Richman, J.G., 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research*, 104, 3059–3073.
- Moore, J.K., Abbott, M.R., 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *Journal of Geophysical Research*, 105, 28709–28722.
- Murphy, E.J., 1995. Spatial structure of the Southern Ocean ecosystem: predator–prey linkages in Southern Ocean food webs. *Journal of Animal Ecology*, 64, 333–347.
- Nishida, S., 1986. Nannoplankton flora in the southern oceans, with special reference to siliceous varieties. *Memoirs of the National Institute Polar Research Special Issue* 40, 56–68.
- Orsi, A.H., Whitworth III, T., Nowlin Jr., W.D., 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Research I* 42, 641–673.
- Ostapoff, F., 1962. The salinity distribution at 200 metres and the Antarctic frontal zones. *Deutsche Hydrographische Zeitschrift* 15, 133–141.
- Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., Froneman, P.W., 2000. Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993, Part 1, Ecological zonation. *Deep-Sea Research I* 47, 1663–1686.
- Pollard, R.T., Read, J.F., Allen, J.T., Griffiths, G., Morrison, A.I., 1995. On the physical structure of a front in the Bellingshausen Sea. *Deep-Sea Research II* 42, 955–982.
- Pollard, R.T., Lucas, M.I., Read, J.F., 2002. Physical controls on biogeochemical zonation in the Southern Ocean. *Deep-Sea Research II* (49), 3289–3305.
- Putland, J.N., Whitney, F.A., Crawford, D.W., 2004. Survey of bottom-up controls of *Emiliania huxleyi* in the Northeast Subarctic Pacific. *Deep-Sea Research I* 51, 1793–1802.
- Read, J.F., Pollard, R.T., Morrison, A.I., Symon, C., 1995. On the southerly extent of the Antarctic Circumpolar Current in the southeast Pacific. *Deep Sea Research II* 42, 933–954.
- Samtleben, C., Schröder, A., 1992. Living coccolithophore communities in the Norwegian–Greenland Sea and their record in sediments. *Marine Micropaleontology* 19, 333–354.
- Samtleben, C., Schäfer, P., Andruliet, H., Baumann, A., Baumann, K.-H., Kohly, A., Matthiessen, J., Schröder-Ritzrau, A., 1995a. Plankton in the Norwegian–Greenland Sea: from living communities to sediment assemblages—an actualistic approach. *Geologische Rundschau* 84, 108–136.
- Samtleben, C., Baumann, C., Schröder-Ritzrau, A., 1995b. Distribution, composition and seasonal variation of coccolithophore communities in the northern North Atlantic. In: Flores, J.A., Sierro, F.J. (Eds.), *5th INA Conference in Salamanca Proceedings*, pp. 219–235.
- Sievers, H.A., Nowlin Jr., W.D., 1984. The stratification and water masses at Drake Passage. *Journal of Geophysical Research* 89 (10), 10,489–10,514.
- Sikes, E.L., Volkman, J.K., 1993. Calibration of alkenone saturation ratios (Uk37) for paleotemperature estimation in cold polar waters. *Geochimica et Cosmochimica Acta* 57, 1883–1889.
- Stramma, L., Peterson, R.G., 1990. The South Atlantic Current. *Journal of Physical Oceanography*, 20, 846–859.
- Tréguer, P., Jacques, G., 1992. Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biology*, 12, 149–162.
- Van Franeker, J.A., van den Brink, N.W., Bathmann, U.V., Pollard, R.T., de Baar, H.J.W., Wolff, W.J., 2002. Responses of seabirds, in particular prions (*Pachyptila* sp.), to small-scale processes in the Antarctic Polar Front. *Deep-Sea Research II* 49, 3931–3950.
- Verbeek, J.W., 1989. Recent calcareous nannoplankton in the Southernmost Atlantic. *Polarforschung*, 59, 45–60.
- Ward, P., Whitehouse, M., Meredith, M., Murphy, E., Shreeve, R., Korb, R., Watkins, J., Thorpe, S., Woodd-Walker, R., Brierley, A., Cunningham, N., Grant, S., Bone, D., 2002. The Southern Antarctic Circumpolar Current Front: physical and biological coupling at South Georgia. *Deep-Sea Research I* 49, 2183–2202.
- Whitworth III, T., Nowlin Jr., W.D., 1987. Water masses and currents of the Southern Ocean at the Greenwich Meridian. *Journal of Geophysical Research* 92 (C6), 6462–6476.
- Winter, A., Jordan, R.W., Roth, P.H., 1994. Biogeography of living coccolithophores in ocean waters. In: Winter, A., Siesser, W.G. (Eds.), *Coccolithophores*. Cambridge University Press, Cambridge, pp. 161–177.
- Winter, A., Elbrächter, M., Krause, G., 1999. Subtropical coccolithophores in the Weddell Sea. *Deep-Sea Research I* 46, 439–449.
- Young, J.R., Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. *Marine Micropaleontology*, 18, 5–23.
- Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., Ostengaard, J., 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue 1*. International Nannoplankton Association, London. 125pp.