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ARTÍCULO

ASSESSMENT OF BEST DATA SET FOR STATISTICAL ANALYSIS OF COCCOLITHOPHORE DISTRIBUTION IN THE ARGENTINEAN CONTINENTAL MARGIN

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Abstract. Coccolithophore thanatocoenosis from 33 surface sediment samples in the Argentinean Continental Margin were analyzed. *Emiliania huxleyi*, the most ubiquitous species in today's ocean, occurs at relative abundances higher than 60% and tends to obscure the variations in abundance of less-represented species. This study aims to compare two intensively used counting methods in coccolithophore studies, *i.e.*, including and excluding *E. huxleyi* from the data set, and thus compare which of both methodologies better reflects the known oceanographic conditions in the area. In the two data sets, species abundances were converted to percentages and Cluster Analysis were performed. The result including *E. huxleyi* reveals two groups (A and B) separated by compositional Euclidean distance of 12.8. Group A is restricted to the southeastern area (near Malvinas Islands) and is dominated by *Gephyrocapsa muellerae* (> 56%). Group B is dominated by *E. huxleyi* (> 93%) and is distributed into two areas: in the southwest (near Tierra del Fuego) and the north (between 40 °S–47 °S). The result excluding *E. huxleyi* also shows two groups (A' and B') distant to a compositional Euclidean distance of 15.8. Group A' has both a southern and northern distribution, whereas Group B' is present only in the northern area. These two groups cannot be explained by the relation between the coccolithophore taxa dominance and the surface oceanographic conditions. Our results indicate that the inclusion of *E. huxleyi* is the most appropriate approach since it seems to better correlate with the known oceanographic regime in the Argentinean Continental Margin.

Key words. Calcareous nannoplankton. Counting methodology. Data analysis. Surface sediment. Southwest Atlantic Ocean.

Resumen. EVALUACIÓN DEL MEJOR CONJUNTO DE DATOS PARA EL ANÁLISIS ESTADÍSTICO DE LA DISTRIBUCIÓN DE COCOLITOFÓRIDOS EN EL MARGEN CONTINENTAL ARGENTINO. Se analizó la tanatocenosis de cocolitofóridos en 33 muestras de sedimentos superficiales del Margen Continental Argentino. *Emiliania huxleyi*, especie actual más ubicua, se encuentra en abundancias relativas superiores al 60% y tiende a ocultar las variaciones de especies menos representadas. El objetivo de este estudio es comparar dos métodos de conteo de uso intensivo, *i.e.*, incluir y excluir *E. huxleyi* del conjunto de datos y así comparar cuál de ambas metodologías refleja mejor las condiciones oceanográficas. En los dos conjuntos de datos, las abundancias de los taxones se convirtieron en porcentajes y se realizaron Análisis de Agrupamiento. El resultado que incluye *E. huxleyi* revela dos grupos (A y B) separados por una distancia euclidiana de 12,8. El grupo A, restringido a la zona sureste (cerca de las islas Malvinas), está dominado por *Gephyrocapsa muellerae* (> 56%). El grupo B, dominado por *E. huxleyi* (> 93%), se distribuye en dos áreas: suroeste (cerca de Tierra del Fuego) y norte (entre 40 °S–47 °S). El resultado que excluye a *E. huxleyi* muestra dos grupos (A' y B') a una distancia euclidiana de 15,8. El grupo A' tiene una distribución sur y norte, mientras que el grupo B' está presente en el norte. Estos dos agrupamientos no pueden explicarse por la relación entre la dominancia de los cocolitofóridos y las condiciones oceanográficas superficiales. Nuestros resultados indican que la inclusión de *E. huxleyi* es el enfoque más apropiado ya que parece correlacionarse mejor con el régimen oceanográfico conocido en el Margen Continental Argentino.

Palabras clave. Nanoplancton calcáreo. Metodología de conteo. Análisis de datos. Sedimentos superficiales. Océano Atlántico Sudoeste.

COCCOLITHOPHORES, phytoplankton belonging to division Haptophyta and class Prymnesiophyceae, are one of the most important primary producers of the oceans (Young *et al.*, 2003). A distinctive feature of these algae is the presence of calcified scales, the coccoliths, which form a major component of pelagic carbonate oozes and are abundant in sea-floor sediments above calcite compensation depth. Isolated coccoliths can preserve the major compositional characteristics of the overlying photic-zone communities due to protected and accelerated sedimentation inside fecal pellets or marine snow (Steinmetz, 1994). Coccolithophores are present in a wide range of marine environments ranging from tropical to subpolar latitudes. Biogeography of living coccolithophores responds sensitively to changes in environmental parameters but there is still much discussion as to which conditions control the vertical and horizontal distributions (Winter *et al.*, 1994). However, their diversity and distribution in the photic zone seem to be affected by surface oceanic circulation and parameters such as sea surface temperature, salinity and nutrient availability (Winter & Siesser, 1994; Ziveri *et al.*, 2004). Based on those observations, coccolith assemblages in surface sediment have been used as proxies to monitor variations in paleoceanographic conditions (*e.g.*, Brand, 1994; Winter & Siesser, 1994; Saavedra-Pellitero *et al.*, 2013).

Knowledge of the spatial distribution of living coccolithophores is crucial to understand their biology and environmental preferences. Significant biogeographic contributions of modern coccolithophores in the Atlantic Ocean have been made by McIntyre & Bé (1967) and Okada & McIntyre (1977, 1979). McIntyre & Bé (1967) established a latitudinal biogeographical nannoplankton zonation based on temperature ranges and assemblage differences. The four floral zones (tropical, subtropical, transitional, and subantarctic or subarctic) are typified in the warmest and coldest by the dominance of one or more key species. The transitional flora, which is localized in the ACM, is characterized by the dominance of placoliths such as *Gephyrocapsa ericsonii*, *Emiliania huxleyi* and *Calcidiscus leptoporus*, and lesser amounts of *Coccolithus pelagicus*. However, these latitudinal zonations do not consider the influence of coastal currents, eddies and upwelling, concealing species-specific biogeography. Mostajo (1986) analyzed coccoliths in sediment samples from the Southwest Atlantic Ocean including the ACM and identified the Subtropical, Transitional and Subantarctic water masses *sensu* Boltovskoy (1970). Besides, she defined the boundaries of the Confluence Zone (= Convergence) for summer and winter. More recently, Boeckel *et al.* (2006) analyzed the coccolith composition of sediment samples from the South Atlantic and the Southern Ocean concerning to different environmental parameters. According to them, coccolith distribution is related to the nutricline and thermocline position.

In most studies dealing with the distribution of modern coccolithophores, *Emiliania huxleyi* was found to be the dominant species (*e.g.*, Okada & McIntyre, 1979; Baumann *et al.*, 2008; Saavedra-Pellitero & Baumann, 2015). In addition, *Emiliania huxleyi* has a wide biogeographic range, being the most ubiquitous coccolithophore in today's oceans. In subarctic and subantarctic waters *E. huxleyi* constitutes almost 100% of the coccolithophore assemblage (McIntyre & Bé, 1967) and tends to overlap the relative abundance fluctuations of other less common taxa. As a result, for ecological interpretations and paleoceanographic reconstructions, some studies chose to remove *E. huxleyi* from quantitative analysis (*e.g.*, Giraudeau, 1992; Giraudeau & Rogers, 1994; Boeckel *et al.*, 2006), whereas other studies decided to include it (*e.g.*, Boeckel & Baumann, 2004; Saavedra-Pellitero *et al.*, 2013). However, whereas the exclusion of *E. huxleyi* seems to be a smart decision to highlight distribution patterns from other less represented but stenotopic species in the assemblages, the impact of its exclusion from the data sets had never been tested. This situation encouraged us to test which data set better correlates with known oceanographic conditions in the ACM, prior to focusing our studies on the environmental parameters controlling its distribution and reconstructing paleoceanographic conditions in the fossil record.

The main goal of this study is to compare two different counting methodologies –including and excluding *E. huxleyi*– by defining two data sets from a same sample set from the ACM (40 °S–55 °S and 66 °W–55 °W) and explain which of both methodologies better reflects the known oceanographic conditions. This study is an important prerequisite for future paleoecologic and paleoceanographic studies in sediments from the ACM, since it will allow the comparison between fossil (Pleistocene–Holocene) and recent assemblages with a high degree of confidence.

OCEANOGRAPHIC SETTING

The South Atlantic Ocean plays a particular role in the thermohaline circulation and water mass distribution, making it an important region of nutrient exchange. The South Atlantic Ocean is dominated by three water zones

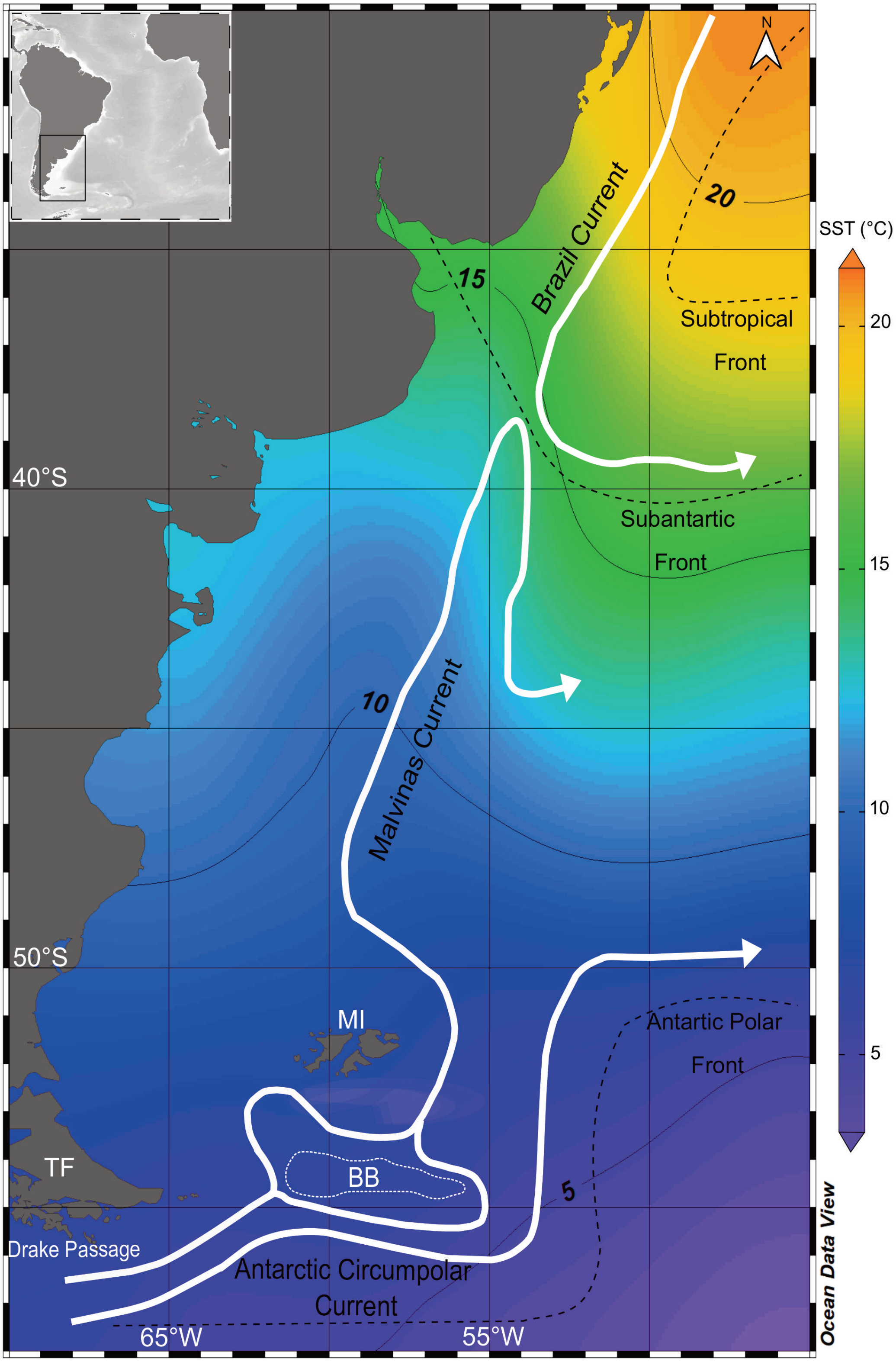

Figure 1. Upper ocean circulation and Sea Surface Temperature (SST in °C, Boyer *et al.*, 2013) annual average at 0 m in the southwestern Atlantic Ocean. Currents are indicated with a white line, according to Piola & Matano (2017) and Hernandez-Molina *et al.* (2010), and isotherms with a black line. Oceanographic fronts are indicated with a dash line according to Peterson & Stramma (1991). Legend for the physiographic reference points, in alphabetical order: **BB** - Burdwood Bank, **MI** - the Malvinas Islands, **TF** - Tierra del Fuego. Plotted with Ocean Data View (ODV) software version 5.1.7 (Schlitzer, 2015).

divided by three oceanographic fronts: Subtropical Front, Subantarctic Front and Antarctic Polar Front (Peterson & Stramma, 1991) (Fig. 1). The Subtropical Zone is distinguished by warm, salty and poor-nutrient waters. To the south is the Subantarctic Zone, where the ACM is located, which is characterized by an abrupt decline in salinity and temperature of surface waters. The Antarctic Polar Zone is dominated by waters with very high nutrient content and sea surface temperature lower than 10 °C.

In the Southwestern Atlantic Ocean, the ACM is a highly significant region in the oceanographic-climatic system (Violante *et al*., 2017). The ACM, one of the largest continental margins on Earth, has different environments (shelf, slope, submarine canyons and rise) and the oceanic circulation is characterized by the opposing flows and confluence between the Malvinas and the Brazil currents (Matano *et al*., 2010) (Fig. 1). The MC is a narrow branch of the ACC with a northward flow along the continental slope of Argentina near 34–38 °S. It is characterized by cold (T< 15 °C) and “fresh” waters (S< 34.2 PSU). This current is highly homogenous and barotropic, thus it has less thermohaline stratification than waters of tropical or subtropical origin (Matano, 1993; Piola & Matano, 2017; Violante *et al*., 2017). Most of the ACC water flowing eastward in the northern Drake Passage loops northward to form the MC. A portion of the upper flow deflects northward west of the Burdwood Bank and the remainder of the northern ACC deflects northward across a gap located east of the Burdwood Bank. Both branches of the MC rejoin to the north of the bank (Piola & Matano, 2017). In the northern portion of the Drake Passage, the mean annual surface temperature of the MC is around 4 °C and increases northward up to 16°C where the currents separate from the continental boundary. The MC percolates over the shelf influencing the regional ecosystems (Piola *et al*., 2010). At 38°S, this current collides with the tropical-warm (T> 20 °C) and salty waters (S> 36 PSU) of the BC flowing towards the south along the Brazilian continental margin, originating a highly dynamic frontal zone: the BMC (Gordon, 1989; Piola & Matano, 2017). The encounter of MC and BC generates a sharp horizontal and vertical gradient in temperature, salinity, density and nutrient content (Gordon, 1989; Peterson & Stramma, 1991; Bianchi *et al*., 1993; Piola & Matano, 2001; Matano *et al*., 2010). As a result of increased upper-water column stability and nutrient availability, the BMC is a region of high primary productivity and major sink for atmospheric CO_2 (Feely *et al*., 2001). The BMC shows spatial and seasonality fluctuation characterized by an equatorward (poleward) displacement of the front during austral winter (summer) (Boltovskoy, 1981; Mostajo, 1986).

MATERIALS AND METHODS

During three expeditions on board the A.R.A. Austral oceanographic vessel, from September 2017 to October 2018; 33 sea-floor sediment samples were obtained from the ACM. According to the locations, stations were grouped in three geographic areas: north area (40 °S to 47 °S and 55 °W to 60 °W), southeast area (53 °S to 54 °S and 61 °W to 64 °W, near the Malvinas Islands), and southwest area (55 °S and 65 °W, near Tierra del Fuego) (Fig. 2, Tab. 2). The samples were obtained from gravity core or box corer and the uppermost centimeter of comparatively undisturbed sediment column was sampled.

AMS ^{14}C dates were performed on six samples from gravity and box cores, with the intention of having a better age control of the three different station areas investigated. Dating was conducted on picked planktonic foraminifera *Globigerina bulloides* (d’Orbigny, 1826). The analysis was carried out at DirectAMS Radiocarbon Dating Service, Washington, USA. AMS ^{14}C ages were converted to calendar years using CALIB 7.8.2 software (Stuiver & Reimer, 1993), Marine20 calibration curve (Heaton *et al*., 2020) and no ΔR. In addition, age and sedimentation rates from other sites were estimated from the adjacent core locations. Numerous box and multicores in the vicinity of the samples positions exhibit relatively continuous late Quaternary sedimentation rates in which top sediments are allocated to Holocene (based on AMS ^{14}C dates on planktic foraminifera, total organic carbon and alkenones, *e.g.*, Benthien & Muller, 2000; Vink, 2004; Mollenhauer *et al*., 2006; Ruhlemann & Butzin, 2006). From the apparently coeval deposition of these sediments, we infer that transport processes occurred due to rapid advection in the upper water column (Benthien & Muller, 2000; Mollenhauer *et al*., 2006). Sedimentation rates of ~13 cm per 1,000 years can be inferred for the Holocene hemipelagic sediments at a water depth of ~2,000 m (Mollenhauer *et al*., 2006).

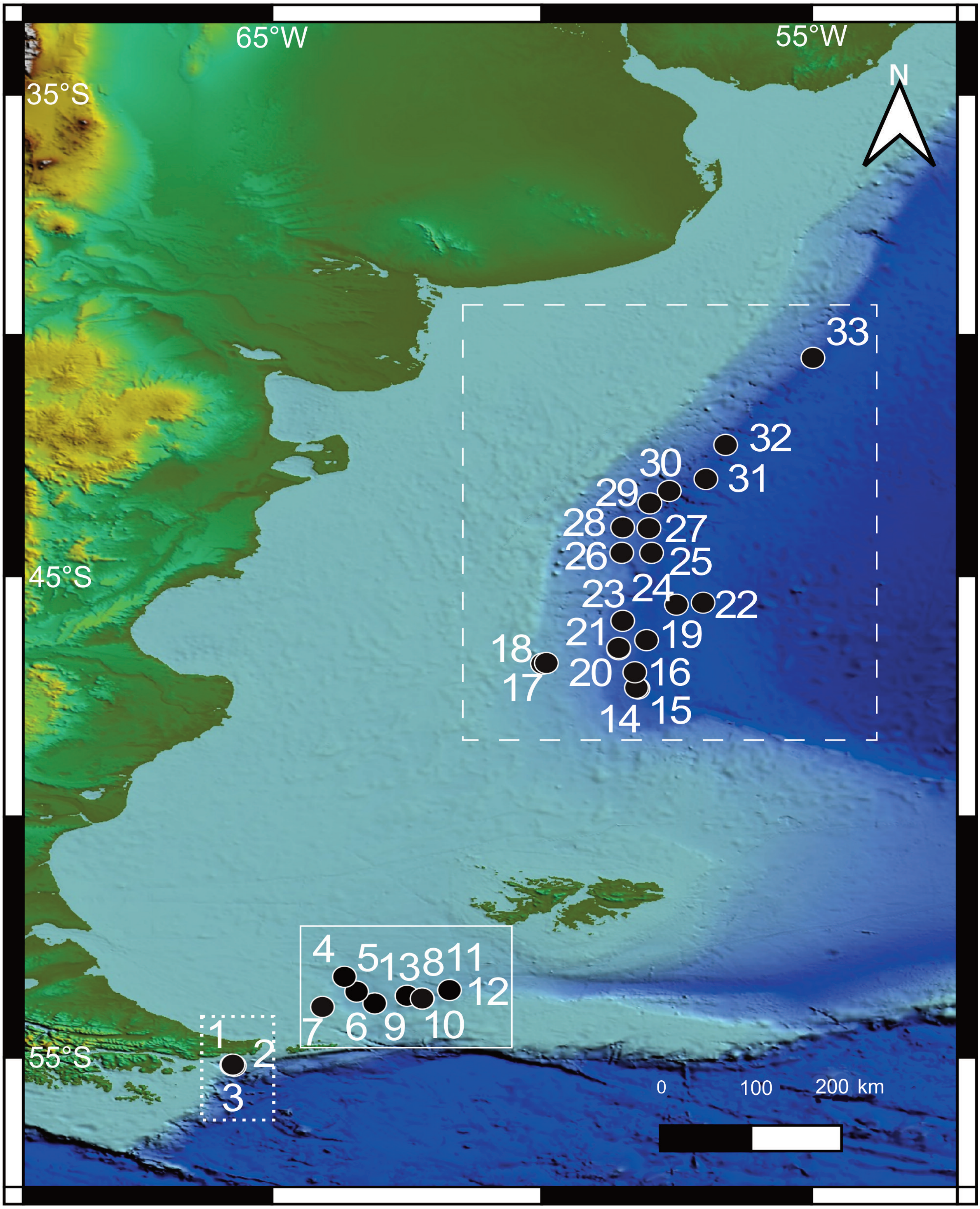

Figure 2. Map of Argentinean Continental Margin with site number locations. The three station areas are indicated with rectangles: north area (dash line), southeast area (continuous line) and southwest area (dotted line). Exact positions are indicated in Table 2. Plotted with GMRT data (Ryan *et al.*, 2009).

Sample preparation and coccolithophore counting

The 33 samples were prepared for study under a polarized light microscope using a modification of the Standard Gravity Settling Technique of Bramlette & Sullivan (1961). In each case, 0.10 to 0.12 g of wet sediment was mixed in 10 ml of mineral water with the addition of hydrogen peroxide and hexametaphosphate. This solution was ultrasonically treated for 30 seconds to facilitate disaggregation of coccoliths from the sediment. After 30 seconds, 200 µl of the suspension was mounted on a cover slide and affixed with Norland 61 optical adhesive. Coccolith observation was done using a Leica DM750 P microscope at 1,000x magnification. The preservational state of the coccoliths was examined under microscope. Samples are deposited and curated in the Y-TEC Laboratory of Biostratigraphy Micropaleontological Repository under the acronym YT.RMP_N. and numbers 000006.1 to 000006.35.

For the two data sets (including and excluding *E. huxleyi*) at least 300 coccoliths were counted on an arbitrarily chosen transect, using the same sample set. This counting effort represents a 95% confidence of recording any species with a relative abundance of 1% (Thierstein *et al.*, 1977), ensuring that most of the species were included (exceeds 99% *sensu* Fatela & Taborda, 2002). Absolute abundance (coccoliths per field of view) was calculated for each sample. For a qualitative control, in the data set including *E. huxleyi*, after reaching 300 specimens, additional 150 fields of view were examined to identify any species present in the sample. Those species were not included in the Cluster Analysis.

Coccoliths of *Gephyrocapsa,* which are smaller than 3 µm and hard to identify due to their tiny size, were grouped under the name of *Gephyrocapsa* spp. small. Systematic criteria in this study follow Hine & Weaver (1998), Young *et al.* (2003), Jordan *et al.* (2004) and the online Nannotax Catalog (www.nannotax.org).

Coccolith dissolution index and Shannon diversity index

Carbonate calcium dissolution in deep waters can modify the taxonomic composition of recent coccolithophore assemblages making difficult to conduct biogeographic and paleoecological reconstructions (Thierstein, 1980). To estimate the effect of carbonate dissolution on the coccolith assemblages, the preservation index, CEX', from Boeckel & Baumann (2004) was applied. This index is based on the CEX from Dittert *et al.* (1999), namely *Calcidiscus leptoporus* - *Emiliania huxleyi* Dissolution Index. The CEX' index (Boeckel & Baumann, 2004) is a ratio that compares the small and delicate placoliths of *E. huxleyi* and *Gephyrocapsa ericsonii* to strongly calcified coccoliths such as *C. leptoporus*:

$$\text{CEX}'=[\textit{E. huxleyi}\,(\%)+\textit{G. ericsonii}\,(\%)]/[\textit{E. huxleyi}\,(\%)+\textit{G. ericsonii}\,(\%)+\textit{C. leptoporus}\,(\%)]$$

Carbonate dissolution has more effect on small placoliths than on robust ones and hence, the ratio of these taxa will change with increasing dissolution. According to Boeckel & Baumann (2004), a CEX' value lower than 0.6 indicates a depositional environment below the calcite lysocline. In this study, *Gephyrocapsa* spp. small (< 3 µm) was considered instead of *G. ericsonii*.

H' was used to measure the species diversity in each sample. This value varies from 0, when the communities have a single taxon, to higher values when communities have more taxa with an equitable number of individuals. H' was performed with Past 4.02 (Hammer *et al.*, 2001).

Statistical methods

Coccolith assemblages are composed of species that appear frequently (common species), and others with very low frequency (rare species). Clifford & Stephenson (1975) considered that the probability of occurrence of a rare species in a sample is very small and therefore the co-occurrences lack of a spatial pattern. Thus, it is not possible to link them to habitat requirements because they occur randomly. Owing to these features, before the statistical analysis, species with an abundance less than 1% of the total specimens in all samples were considered rare species and were eliminated in both data sets, focusing on the variations of the most abundant taxa.

For the statistical treatment of both data sets, coccolithophore relative abundances were expressed as percentages, as are known in Aitchison's composition (Aitchison, 1986). The percentages of composition are relative values adding up to 100; thus, there is a statistical dependence and spurious correlations between percentages. Aitchison (1986, 1999) proposed log-ratios strategy to break the dependences. Application of this strategy in coccolithophore studies can be found in Monechi *et al.* (2000) and Buccianti & Esposito (2004).

In order to compare the two counting methodologies, two hierarchical Cluster Analysis were performed. One widely used clustering algorithm is Ward's method, which attempts to generate clusters to minimize the within-cluster variance. For each cluster, the means for all the variables are computed. Next, for each object, the squared Euclidean distance to the cluster means is calculated. These distances are summed for all the objects. This variance is a weighted squared distance between cluster centre. However, Euclidean distance is not appropriate for compositional data because it is not perturbation invariant and not sub-compositionally dominant. Therefore, to adapt Ward's method, data matrices were re-expressed using the *clr* as proposed by Martín-Fernández *et al.* (1998) and Aitchison *et al.* (2000).

The *clr* is isometric and was calculated with the following equation:

$$clr(x) = (\ln x1/g(x), \ln x2/g(x), \ldots \ln xd/g(x)) = (z_1, z_2, \ldots, zd), \text{ where } g(x) = \sqrt[d]{\prod_1^d x_i}$$

where *d,* is the component number in the composition, *clr (x)* and *z* are the raw percentages and transformed value, respectively, for samples in rows and species in column matrix data, with the geometric mean *g(x)* of all components in the composition serving as the common divisor for each row.

Null values were replaced using multiplicative replacement strategy with 0.1% (Martín-Fernández *et al.*, 2003) before transformation to avoid division by 0, as recommended by Aitchison (1986). Clusters were identified with the geometric mean of species distribution after the closure operation was applied (the center in compositional words). Besides, the *clr* variances of each species within the group were computed.

Cluster Analysis and *clr* transformation were performed with Past 4.02 (Hammer *et al.*, 2001).

Institutional abbreviations. A.R.A., Austral, Armada de la República Argentina Austral, Argentina; **Y-TEC,** Yacimientos Petrolíferos Fiscales Tecnología, Berisso, Argentina; **YT.RMP_N.,** Yacimientos Petrolíferos Fiscales Tecnología, Repositorio Micropaleontológico, Nanofósiles.

Oceanic abbreviations. ACM, Argentinean Continental Margin; **ACC,** Antarctic Circumpolar Current; **BC,** Brazil Current; **BMC,** Brazil-Malvinas Confluence; **MC,** Malvinas Current.

Indices, statistical and dating abbreviations. AMS ^{14}C, Accelerator mass spectrometry radiocarbon; **BP,** before present; **CEX** and **CEX',** *Calcidiscus leptoporus* - *Emiliania huxleyi* Dissolution Index; ***clr,*** centered log-ratio transformation; ***H',*** Shannon diversity index.

RESULTS

Radiocarbon dating

The six calibrated AMS ^{14}C ages obtained from sea-floor samples indicate Late Holocene/Recent sediments for the three investigated station areas (Tab. 1). Ages are given in ^{14}C radiocarbon and calendar years BP.

TABLE 1 – Accelerator mass spectrometry radiocarbon dates and calibrated ages obtained on six sea-floor sediment samples.

Site number	Sample	Direct AMS Code	^{14}C Radiocarbon age ± 1 σ error		Calendar age BP ± 1 σ error	
3	Geo0_GC8	D-AMS 044169	811	± 23	124–428	276 ± 152
8	Geo01_BC11	D-AMS 044170	806	± 21	120–425	272.5 ± 152.5
13	Geo01_GC16	D-AMS 044171	978	± 18	300–528	414 ± 114
21	Geo02_GC22	D-AMS 044172	2729	± 23	2110–2412	2261 ± 151
14	Geo02_GC24	D-AMS 044173	2848	± 22	2286–2614	2450 ± 164
25	Geo02_GC30	D-AMS 044174	1983	± 21	1268–1512	1390 ± 122

TABLE 2 – Coccolith abundance chart including *Emiliania huxleyi*, with sites location, water depth samples, field of views and preservation (G, Good). The asterisk indicates taxa found after counting but not included in any of the quantitative analysis.

Site number	Station	Sample	Longitude	Latitude	Depth (m)	Field of views	Preservation	*Calcidiscus leptoporus*	*Coccolithus pelagicus braarudii*	*Coccolithus pelagicus pelagicus*	*Emiliania huxleyi*	*Gephyrocapsa muellerae*	*Gephyrocapsa oceanica*	*Gephyrocapsa* spp. small	*Helicosphaera carteri*	*Helicosphaera princei*	*Helicosphaera wallichii*	*Pontosphaera japonica*	*Pontosphaera multipora*	*Rhabdophaera clavigera*	*Syracosphaera pulchra*	*Syracosphaera* sp.	*Umbellosphaera tennuis*	*Umbilicosphaera sibogae*	Reworked	Total specimens	Richness	Absolute Abundance = Coccoliths/Field of view	Shannon index (H´)	CEX´
1	Geo0_GC09	YT.RMP_N.000006.2	-65,7458	-55.1572	866	47	G	36	1	1	267	24	2	8	12	4							3		3	361	10	8	0,98	0,88
2	Geo0_GC10	YT.RMP_N.000006.3	-65,6978	-55.1722	951	14	G	12	*		359	12		14	*	2	*						*		*	399	8*	29	0,45	0,97
3	Geo0_GC08	YT.RMP_N.000006.1	-65,7252	-55.149	841	13	G	30	2	1	295	19		4	2	6							3			362	9	28	0,76	0,91
4	Geo01_GC03	YT.RMP_N.000006.25	-63,6582	-53.3244	440	70	G	19			220	117		8	2	5	1						3		2	377	8	5	1,05	0,92
5	Geo01_GC04	YT.RMP_N.000006.26	-63,4325	-53.6318	563	150	G	13			265	190	1	24	1	4							1		2	501	8	3	1,02	0,96
6	Geo01_GC05	YT.RMP_N.000006.27	-63,097	-53.8768	573	32	G	9	*		180	129		6		1							3			328	7*	10	0,93	0,95
7	Geo01_GC08	YT.RMP_N.000006.28	-64,066	-53.95	135	130	G	40		1	371	55	2	45	1	8	1						5		4	533	10	4	1,05	0,91
8	Geo01_BC11	YT.RMP_N.000006.30	-62,2242	-53.7764	440	16	G	4	*		158	256	*	18									*		*	436	7*	27	0,86	0,98
9	Geo01_BC12	YT.RMP_N.000006.31	-62,2182	-53.7766	439	15	G	3			81	250	1	*		*							1		*	336	7*	22	0,64	0,96
10	Geo01_BC13	YT.RMP_N.000006.32	-62,2167	-53.7777	435	12	G	4		1	60	278		13	*	*									*	356	7*	30	0,68	0,95
11	Geo01_BC14	YT.RMP_N.000006.33	-62,2178	-53.7763	440	14	G	1		*	55	278		18	*										*	352	6*	25	0,65	0,99
12	Geo01_GC15	YT.RMP_N.000006.34	-61,7118	-53.6	678	6	G	4		*	153	160		15	1	*										333	7*	56	0,92	0,98
13	Geo01_GC16	YT.RMP_N.000006.35	-62,4991	-53.7188	490	5	G	7			127	205	1	4	*	*	*								*	344	8*	69	0,82	0,95
14	Geo02_GC24	YT.RMP_N.000006.11	-58,2471	-47.321	2455	3	G	3		*	339	3	3		1	1			*				*		*	350	9*	117	0,19	0,99
15	Geo02_GC25	YT.RMP_N.000006.12	-58,2182	-47.3371	2620	2	G	10	*	1	336	1	*		*	2		*					3		*	353	10*	177	0,25	0,97
16	Geo02_GC26	YT.RMP_N.000006.13	-58,2775	-47.0004	2601	2	G	5	*	*	330	2	*		*	1		*		*		*	*		*	338	12*	169	0,13	0,99
17	Geo02_GC18	YT.RMP_N.000006.5	-59,9165	-46.808	782	3	G	5		*	290	9		*	1	*										305	7*	102	0,24	0,98
18	Geo02_GC19	YT.RMP_N.000006.6	-59,9889	-46,8214	732	6	G	4			336	9		1	1	2						4	2			359	8	60	0,35	0,99
19	Geo02_GC23	YT.RMP_N.000006.10	-58,0592	-46,3331	3060	2	G	11	*	*	327	1	2	4	*	2	*	*		*		*	2			349	14*	175	0,33	0,97
20	Geo02_GC21	YT.RMP_N.000006.8	-58,5758	-46.5215	2379	2	G	4	*	1	280	3			*	*							2			290	8*	145	0,19	0,99
21	Geo02_GC22	YT.RMP_N.000006.9	-58,5773	-46.4945	2378	3	G	9		*	310	4	*		*	1							*	1		325	9*	108	0,23	0,97
22	Geo02_GC27	YT.RMP_N.000006.14	-57,5058	-45.5971	3420	3	G	14	*	2	397	1	4	2	1	1		*		*			5			427	9	142	0,37	0,97
23	Geo02_GC20	YT.RMP_N.000006.7	-58,5021	-45.9319	2589	3	G	4	*	*	332	7			*	1								*		344	8*	115	0,18	0,99
24	Geo02_GC28	YT.RMP_N.000006.15	-57,012	-45,5557	3478	4	G	9	*	*	322	5	8	5	*	1							1	*		351	11*	88	0,41	0,97
25	Geo02_GC30	YT.RMP_N.000006.17	-57,967	-44,5202	2756	2	G	9	*	*	463	7	7	*	*	1						*	3	*	*	490	12*	245	0,29	0,98
26	Geo02_GC31	YT.RMP_N.000006.18	-58,5198	-44.5198	1957	2	G	5	*	*	477	7	7	1	*	1						*	1		*	499	11*	250	0,25	0,99
27	Geo02_GC32	YT.RMP_N.000006.19	-58,5033	-43.9908	2256	2	G	5	*		377	1	*		*	1					1		1	*	*	386	10*	193	0,14	0,99
28	Geo02_GC29	YT.RMP_N.000006.16	-58,0158	-44.007	2425	2	G	12	*	*	446	1	*	1	1	3		*		*			1	*	*	465	13*	233	0,22	0,97
29	Geo02_GC33	YT.RMP_N.000006.20	-57,9975	-43.4928	2324	2	G	8	*	2	386	6	1		*	2	*					*	1	*	*	406	12*	203	0,27	0,98
30	Geo02_GC34	YT.RMP_N.000006.21	-57,6395	-43.2348	2298	2	G	10	*	*	332	2	*	3	*	*				*	*			*	2	349	12*	174	0,22	0,97
31	Geo02_GC35	YT.RMP_N.000006.22	-56,9603	-42.9867	3436	3	G	13			321	14	3		*	2		*		1			2	*	2	358	10*	119	0,46	0,96
32	Geo02_GC36	YT.RMP_N.000006.23	-56,5943	-42.279	2657	3	G	5	*	2	416	9	*	3	1	*	*	*			*		1		5	442	13*	146	0,26	0,99
33	Geo02_GC37	YT.RMP_N.000006.24	-54,977	-40.4713	2756	2	G	5	*		300	5	2	1	1	*		*			*		*	1	1	316	12*	158	0,26	0,98

Coccolithophore assemblages in the ACM

All the samples contain coccoliths and a total of 21 taxa were identified in both data sets (Tabs. 2, 3). Taxa are listed alphabetically with full citations in the Taxonomic Appendix. The most abundant coccolith taxa are *E. huxleyi* (77.54% average), *Gephyrocapsa muellerae* (16.53% average), *Calcidiscus leptoporus* (2.65% average) and *Gephyrocapsa* spp. small (1.58% average) (Fig. 3). Pre-Quaternary taxa, which occurred sporadically (*Chiasmolithus* spp., *Helicosphaera sellii*, *Reticulofenestra pseudoumbilicus*, *Sphenolithus moriformis*, *Watznaueria* spp.), were found in 22 samples and grouped as 'Reworked'. Absolute abundance (coccoliths per field of

TABLE 3 – Coccolith abundance chart, excluding *Emiliania huxleyi*.

Site number	Field of views	***Calcidiscus leptoporus***	***Calciosolenia brasiliensis***	***Ceratholithus cristatus***	***Coccolithus pelagicus braarudii***	***Coccolithus pelagicus pelagicus***	***Gephyrocapsa muellerae***	***Gephyrocapsa oceanica***	***Gephyrocapsa*** spp. small	***Helicosphaera carteri***	***Helicosphaera hyalina***	***Helicosphaera princei***	***Helicosphaera wallichii***	***Pontosphaera multipora***	***Rhabdophaera clavigera***	***Syracosphaera*** sp.	***Umbellosphaera irregularis***	***Umbellosphaera tenuis***	***Umbilicosphaera sibogae***	Total specimens	Absolute abundance = Coccoliths/Field of view
1	150	315			2	2	138		21	13		62	1			3		19		576	4
2	150	212			3		119		40	6		30	1					13		424	3
3	66	162			4	3	99		20	10		31				2		22		353	5
4	300	130				3	304	3	30	12		15				1		23		521	2
5	300	56					440	1	14	4		9				1		13		538	2
6	150	32					472		11	2		2						6		525	4
7	450	105			2	2	103	5	32	7		24	7			1		20	1	309	1
8	20	3					316					1								320	16
9	22	4					315		13			2						1		335	15
10	15	3					327		12									1		343	23
11	22	5					315		7											327	15
12	11	15					323		13	1								3		355	32
13	14	6					314		4	1										325	23
14	150	274			1	1	95	1	25	6		21	4	1		2		12	2	445	3
15	63	240			1	2	47	2	8	2		31	1					10	1	345	5
16	150	290			3	1	53	14	8	17		54	1		1	5		5	6	458	3
17	300	257			2	1	131	1	10	11		23				1			1	438	1
18	300	203			2		130	6		6		10	2					1		360	1
19	63	250			10		58	16	18	12		23	4		5	2		11	3	412	7
20	150	396			2	3	110	8	22	19		40	1			2		6	2	611	4
21	150	364			5	1	86	16	18	17	2	44	2					4	7	566	4
22	53	300	1		3	5	27	27	14	20		83	3		2	5		3	15	508	10
23	66	181			3	5	152	13	22	7	1	26				3		7	3	423	6
24	85	254			2	2	17	20	22	12		35	2		5	2	4	23	13	413	5
25	49	310			6	3	32	21	11	16		33			2	2		10	7	453	9
26	49	237			3	1	77	13	19	3	1	24					2	19	2	401	8
27	65	256			6		43	13	13	7		30				3	1	24		396	6
28	60	300			1	2	33	16	15	7		35	3			1	1	29	4	447	7
29	56	290			4	5	39	5	7	9	1	38	1			2		18	4	423	8
30	62	301			7		32	12	11	2		18	1			2	1	17	3	407	7
31	57	239		1	2		31	17	15	7	1	19			3	2	3	42	8	390	7
32	69	260			10	2	37	19	12	8	4	18	1		1	4	2	28	1	407	6
33	62	229			1	1	41	20	19	10	1	27	1		5	6	2	19	12	394	6

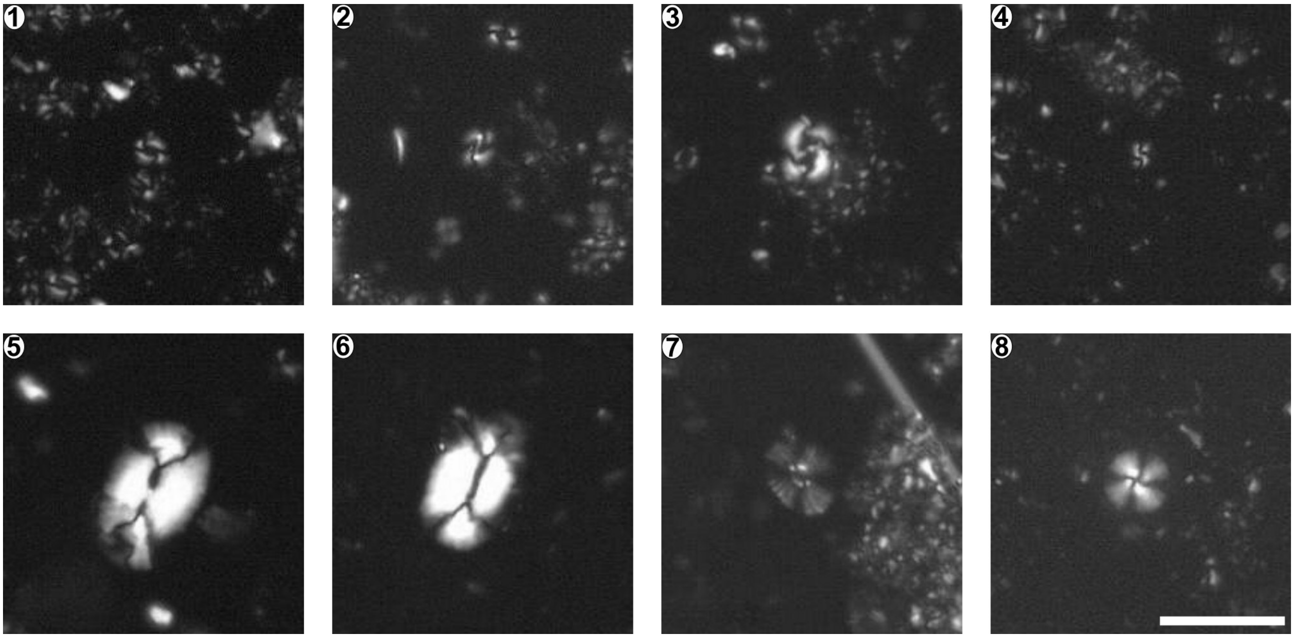

Figure 3. Coccolithophore species considered for the Cluster Analysis with both data sets. **1,** ***Emiliania huxleyi***, sample **YT.RMP_N.000006.12**; **2,** ***Gephyrocapsa muellerae***, sample **YT.RMP_N.000006.13**; **3,** ***Gephyrocapsa oceanica***, sample **YT.RMP_N.000006.16**; **4,** ***Gephyrocapsa*** spp. small, sample **YT.RMP_N.000006.19**; **5,** ***Helicosphaera carteri***, sample **YT.RMP_N.000006.28**; **6,** ***Helicosphaera princei***, sample **YT.RMP_N.000006.11**; **7,** ***Umbellosphaera tenuis***, sample **YT.RMP_N.000006.23**; **8,** ***Calcidiscus leptoporus***, sample **YT.RMP_N.000006.12**. Scale bar: 10 μm.

view) and richness showed the same trend: highest values in the northern sites and decreasing towards the south. H’ values range between 0.13 and 1.05 with highest values at the southern sites and lowest values at the northern sites.

In all the samples, coccolith preservation is good. High CEX’ index values, all over 0.6 (min= 0.88, max= 0.99), indicate that dissolution is not significant. In almost all the samples, *E. huxleyi* is the dominant species except for a group located in the southeast area (which is dominated by *G. muellerae*). The ubiquitous *E. huxleyi* exhibits the highest abundance in the northern sites (> 90%) and minimum in the southeastern sites (≈ 15%).

Accordingly, maximum percentages of *G. muellerae* are recorded at the southeastern sites, close to the Malvinas Islands (60%–70%). The distribution of *Gephyrocapsa* spp. small basically concurs with the *G. muellerae* trend. It shows the highest percentages (mean 3.4%) at the southern sites and, conversely, the minimum values (< 1%) at the northern sites. *Calcidiscus leptoporus* is especially abundant at the southwestern sites, near Tierra del Fuego (mean 7%), and less abundant at the southeastern and northern sites (≈ 2%).

Cluster Analysis

Clusters Analysis were based on taxa with abundances greater than 1%. In the data set including *Emiliania huxleyi*, only four taxa meet that criterion (*Calcidiscus leptoporus*, *E. huxleyi*, *Gephyrocapsa muellerae* and *Gephyrocapsa* spp. small) (Tab. 4.1); whereas in the data set excluding *E. huxleyi*, seven taxa had abundances greater than 1% (*C. leptoporus*, *G. muellerae*, *G. oceanica*, *Gephyrocapsa* spp. small, *Helicosphaera carteri*, *H. princei* and *Umbellosphaera tenuis*) (Tab. 4.2).

The dendrogram based on the data set including *E. huxleyi* shows two well-defined groups (A and B) distant to a compositional Euclidian distance of 12.8 (Fig. 4.1). Group A, composed of nine samples (sites 4–6 and 8–13), lies in the southeast area and is dominated by *G. muellerae* (> 56%). Group B, composed of 24 samples, is distributed in two geographical areas: in the southwest and in the north, and is dominated by *E. huxleyi* (> 93%) (Fig. 5.1).

The dendrogram based on the data set excluding *E. huxleyi*, shows two groups (A’ and B’) separated with a compositional Euclidean distance of 15.8 (Fig. 4.2). Group A’, composed of 14 samples, spans through the southern sites and one northern site (sites 1–13 and 14, respectively).

TABLE 4 – Relative abundances of the taxa used in the Cluster Analysis. 1) Data set including *Emiliania huxleyi*. 2) Data set excluding *Emiliania huxleyi*.

1

Site number	***Calcidiscus leptoporus*** **(%)**	***Emiliania huxleyi*** **(%)**	***Gephyrocapsa muellerae*** **(%)**	***Gephyrocapsa*** spp. small (%)
1	10,7	79,7	7,2	2,4
2	3,0	90,4	3,0	3,5
3	8,6	84,8	5,5	1,1
4	5,2	60,4	32,1	2,2
5	2,6	53,9	38,6	4,9
6	2,8	55,6	39,8	1,9
7	7,8	72,6	10,8	8,8
8	0,9	36,2	58,7	4,1
9	0,9	24,2	74,8	0,1
10	1,1	16,9	78,3	3,7
11	0,3	15,6	79,0	5,1
12	1,2	46,1	48,2	4,5
13	2,0	37,0	59,8	1,2
14	0,9	98,2	0,9	0,1
15	2,9	96,7	0,3	0,1
16	1,5	97,8	0,6	0,1
17	1,6	95,3	3,0	0,1
18	1,1	96,0	2,6	0,3
19	3,2	95,3	0,3	1,2
20	1,4	97,5	1,0	0,1
21	2,8	95,9	1,2	0,1
22	3,4	95,9	0,2	0,5
23	1,2	96,7	2,0	0,1
24	2,6	94,4	1,5	1,5
25	1,9	96,6	1,5	0,1
26	1,0	97,3	1,4	0,2
27	1,3	98,3	0,3	0,1
28	2,6	97,0	0,2	0,2
29	2,0	96,4	1,5	0,1
30	2,9	95,7	0,6	0,9
31	3,7	92,1	4,0	0,1
32	1,2	96,1	2,1	0,7
33	1,6	96,5	1,6	0,3

2

Site number	***Calcidiscus leptoporus*** **(%)**	***Gephyrocapsa muellerae*** **(%)**	***Gephyrocapsa oceanica*** **(%)**	***Gephyrocapsa*** spp. small (%)	***Helicosphaera carteri*** **(%)**	***Helicosphaera princei*** **(%)**	***Umbellosphaera tenuis*** **(%)**
1	55,4	24,3	0,1	3,69	2,29	10,9	3,34
2	50,4	28,3	0,1	9,51	1,43	7,14	3,09
3	47	28,8	0,1	5,81	2,9	9	6,39
4	25,1	58,8	0,58	5,8	2,32	2,9	4,45
5	10,4	81,9	0,19	2,61	0,74	1,68	2,42
6	6,09	89,8	0,1	2,09	0,38	0,38	1,14
7	35,5	34,8	1,69	10,8	2,36	8,11	6,76
8	0,93	98,4	0,1	0,1	0,1	0,31	0,1
9	1,19	93,8	0,1	3,87	0,1	0,6	0,3
10	0,87	95	0,1	3,49	0,1	0,1	0,29
11	1,52	95,9	0,1	2,13	0,1	0,1	0,1
12	4,22	90,8	0,1	3,65	0,28	0,1	0,84
13	1,84	96,3	0,1	1,23	0,31	0,1	0,1
14	63,1	21,9	0,23	5,76	1,38	4,84	2,76
15	70,6	13,8	0,59	2,35	0,59	9,12	2,94
16	65,8	12	3,17	1,81	3,85	12,2	1,13
17	59,3	30,2	0,23	2,31	2,54	5,31	0,1
18	57	36,5	1,68	0,1	1,6	2,81	0,28
19	64,4	14,9	4,12	4,64	3,09	5,93	2,84
20	65,9	18,3	1,33	3,66	3,16	6,66	1
21	66,3	15,7	2,91	3,28	3,1	8,01	0,73
22	63,3	5,7	5,7	2,95	4,22	17,5	0,63
23	44,4	37,3	3,19	5,39	1,72	6,37	1,72
24	66,3	4,44	5,22	5,74	3,13	9,14	6,01
25	71,6	7,39	4,85	2,54	3,7	7,62	2,31
26	60,5	19,6	3,32	4,85	0,77	6,12	4,85
27	66,3	11,1	3,37	3,37	1,81	7,77	6,22
28	69	7,59	3,68	3,45	1,61	8,05	6,67
29	71,4	9,61	1,23	1,72	2,22	9,36	4,43
30	76,6	8,14	3,05	2,8	0,51	4,58	4,33
31	64,6	8,38	4,59	4,05	1,89	5,14	11,4
32	68,06	9,68	4,97	3,14	2,09	4,71	7,33
33	62,74	11,23	5,47	5,2	2,74	7,39	5,2

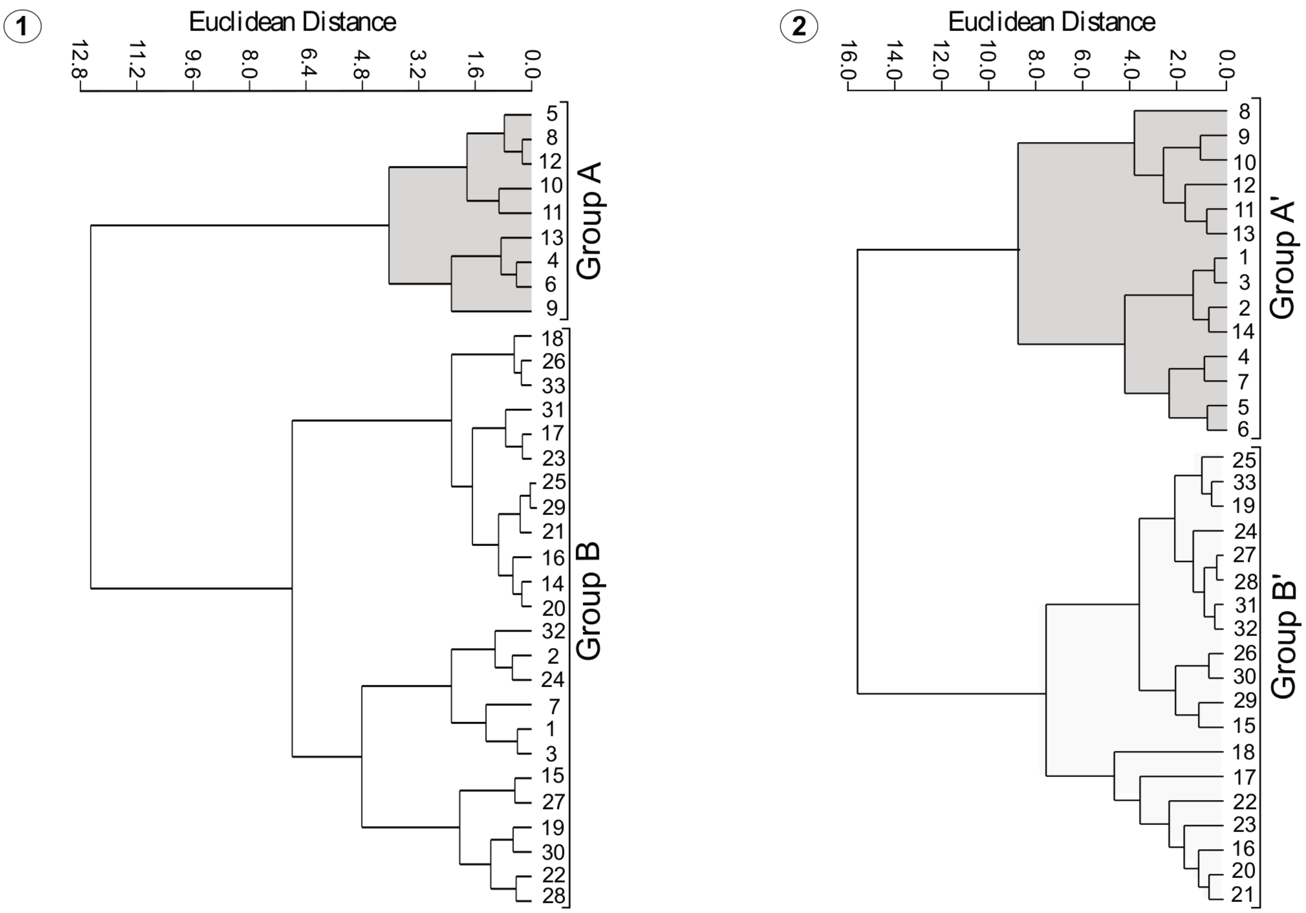

Figure 4. Dendrograms obtained from the Cluster Analysis (Ward method adapted to compositional data). **1,** Data set including ***E. huxleyi***. **2,** Data set excluding ***E. huxleyi***.

Group B′, composed of 19 samples, corresponds to the northern sites. The most abundant species in these groups are *C. leptoporus* and *G. muellerae*, showing no preference for one or the other group. Both are dominant in some sites of the group A′ and in some sites of the group B′ (Fig. 5.2).

DISCUSSION

Coccolithophore preservation

Previous to compare the two counting methods, is essential to identify if coccolith assemblages are affected by dissolution. Therefore, some qualitative and quantitative indices have been made. In all the samples, observations in light microscope reveal well-preserved coccoliths. The data concerning coccolith preservation from different samples are given in Table 2.

High CEX′ index values, all over 0.6, indicate that dissolution is not significant. Nevertheless, it is important to be careful with the results of this dissolution index, which is based on differential dissolution, because it can be influenced by the different ecological affinities of the species. In the ACM, coccolithophore assemblages tend to be *E. huxleyi*-monospecific northward and this could be linked to environmental conditions that influenced the ecological preferences of coccoliths. In this area, the CEX′ index served as a mere approximation, suggesting an integrated approach combining different dissolution proxies is necessary. However, Bickert & Wefer (1996) suggested that present-day lysocline of calcite in the South Atlantic Ocean is at ≈ 4,000 meters. All samples included in this study were above that depth (Tab. 2).

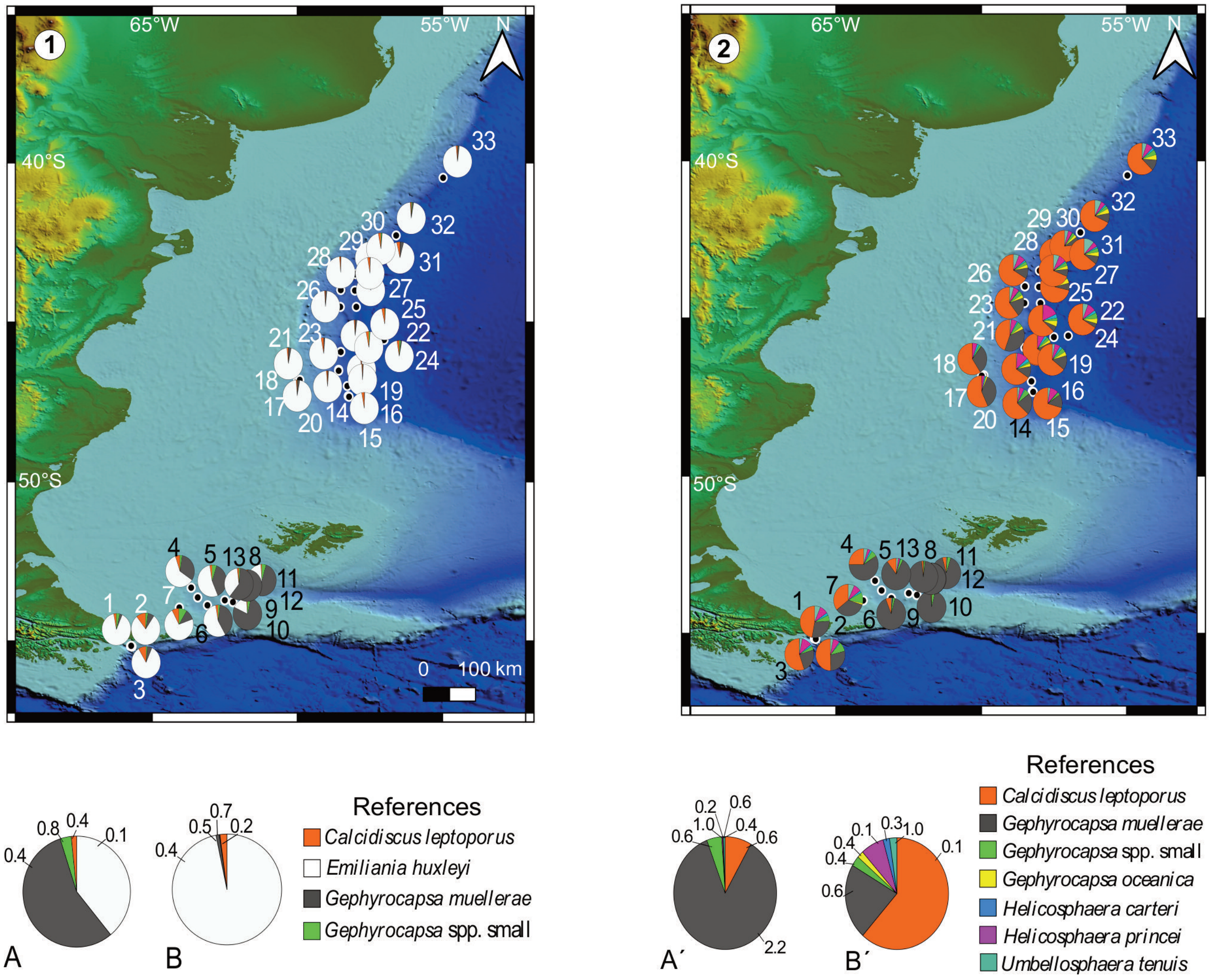

Figure 5. Maps of the Argentinean Continental Margin showing pie-charts depicting coccolith taxa and spatial distribution of assemblages. **1,** Data set including ***E. huxleyi***. **2,** Data set excluding ***E. huxleyi***. A and A' in black sites numbers; B and B' in white sites numbers. Pie-charts A, B and A', B' are the center of assemblages, the numbers indicate the *clr* variances. Plotted with GMRT data (Ryan *et al.*, 2009).

Coccolithophore assemblages and Cluster Analyses

Emiliania huxleyi is the only species present in all assemblages and, in most of them, is also the dominant one. Its highest abundance occurs in the north and in the southwest area. *Emiliania huxleyi* is adapted to a wide range of environmental conditions and has a cosmopolitan distribution (Winter & Siesser, 1994). This species occurs under a broad salinity and temperature range, although its highest abundances are at water temperatures of < 23 °C (Winter *et al.*, 1979; Haidar & Thierstein, 2001). Brand (1994) reported high abundances of *E. huxleyi* in nutrient-rich environments such as subtropical central gyres edges, upwelling regions and along continental margins. Boeckel *et al.* (2006) observed that *E. huxleyi* exhibits highest abundances in sediments from Brazil, Uruguay and the Argentinean Continental Margin (> 80%). Indeed, present day records of *E. huxleyi* blooms have been studied along the ACM by Poulton *et al.* (2011, 2013) and Balch *et al.* (2014). These intense and regular high-reflectance blooms have been observed during the austral summer along the ACM shelf break and slope, and are enhanced to permanent high-chlorophyll zone (Romero *et al.*, 2006; Rühlemann & Butzin, 2006; Matano *et al.*, 2010; Poulton *et al.*, 2011, 2013).

If *E. huxleyi* is excluded from the data set, *C. leptoporus* (mean 46.45%) and *G. muellerae* (mean 34.82%) become the most abundant species, each dominating different oceanographic areas: *C. leptoporus* is abundant at the southwestern sites and at the northern sites, whereas *G. muellerae* dominates the assemblages at the southeastern sites. *Calcidiscus leptoporus* is a cosmopolitan species but is a typical component of the cold-water floras (McIntyre & Bé, 1967; Mostajo, 1986). Opinions about nutrient requirements are diverse, and possibly it could be related to the presence of different morphotypes (Knappertsbusch *et al.*, 1997), which have not been considered, as it is out of the scope of this study. In the southeastern Atlantic Ocean, *C. leptoporus* was associated with intermediate and low nutrient conditions in surface waters (Boeckel & Baumann, 2004).

Regarding *G. muellerae*, Holligan *et al.* (2010) and Charalampopoulou *et al.* (2016), reported that this species is characteristic in the south of the Malvinas Islands and shows a preference for very cold and relatively high productivity water masses. Likewise, *Gephyrocapsa* spp. small delineates the same trend of *G. muellerae*, being abundant under elevated nutrient conditions (Okada & McIntyre, 1977; Saavedra-Pellitero *et al.*, 2010; Martínez-Sánchez *et al.*, 2019).

Several environmental parameters are regulating the complex ecosystem in which coccolithophores live. Some variables of the photic zone, such as temperature, salinity, water column stratification and nutrient concentrations, can be related to the underlying surface sediment assemblages. In other words, coccolith sediment assemblages represent the average sea surface environmental conditions of the last few hundred years in the area. As more stenotopic species are represented in those assemblages, a more accurate interpretation of the environmental conditions will be possible. *Emiliania huxleyi* proved to have high tolerance to a wide range of environmental conditions and is extremely abundant in the studied area. The exclusion of this species from statistical analysis might allow to better identify geographical distribution patterns of less represented, but stenotopic species; or as the environmental parameters build up a very complex and synergetic ecosystem, the exclusion of *E. huxleyi* might also represent a loss of information.

The studied area is restricted to the Subantarctic water mass (*sensu* Mostajo, 1986), although sea surface temperature difference between the northern and southern sites is about 12 °C. In the northern portion of the Drake Passage it is about 4 °C and increases northward up to 16 °C, where the currents separate from the shelf break. However, the distribution of the coccolithophore assemblages seems to be controlled by other contrasting oceanographic features such as nutrient availability or salinity, and not by the temperature gradient. Satellite chlorophyll-*a* observations indicate that the shelf break and slope have a high nutrient concentration (Romero *et al.*, 2006; Franco *et al.*, 2008). Numerical and analytical models suggest that these high concentrations are associated with interactions between the Malvinas Current and the bottom topography, which creates upwelling systems (Piola & Matano, 2017).

The dendrogram obtained from the Cluster Analysis including *E. huxleyi* shows two groups (A and B) and revealed a good constraint between the occurrence and distribution of species and oceanographic features. Group A, which is dominated by *G. muellerae,* is confined to the southeast area. Piola & Matano (2017) suggest that most of the water of ACC loops northward to form the MC and a portion deflects northward west off the Burdwood Bank. In this area, where the MC curve to the east, samples are dominated by *G. muellerae* (group A). As mentioned above, *G. muellerae* shows a good correlation with cool and nutrient-rich environments (Boeckel *et al.*, 2006). Additionally, Matano & Palma (2008) and Miller *et al.* (2011) postulated and verified, using simplified models, that the upwelling might be associated with frictionally driven intrusions of the MC onto the shelf. Matano *et al.* (2010) observed that this area, where the samples are dominated by *G. muellerae*, is one of the regions of largest cross-shelf exchanges. Accordingly, bathymetry data revealed that these sites are located near the 200 m isobath, where the MC loops. In consequence, elevated percentages of *G. muellerae* could be attributed to nutrient-rich waters in this active upwelling region. Group B, which is dominated by *E. huxleyi*, includes the southwestern and northern sites of the ACM. *Emiliania huxleyi*, an opportunistic species, is also abundant in upwelling areas (Brand, 1994). Accordingly, it seems that these two groups could be explained by competition between *G. muellerae* and *E. huxleyi* along nutrient-rich surface waters, where *G. muellerae* exhibit a better response.

The dendrogram obtained from the Cluster Analysis excluding *E. huxleyi* shows two groups (A' and B') which cannot be explained by the dominance of the species that compose the assemblages at these sites, neither by the oceanographic regimen.

In the ACM, the distribution of the coccolithophore assemblages seems to be related to surface nutrient availability and this parameter is probably reflected by the ecological competition between the most abundant species, *E. huxleyi* and *G. muellerae*. Further analysis is required to better understand the relation between the oceanographic regime in the ACM and coccolith assemblages, but the exclusion of *E. huxleyi* from these analyses will incur in an important loss of information.

CONCLUSIONS

We tested which of the most used data sets showed clusters that could be explained by known oceanographic conditions in the ACM. The data set including *E. huxleyi* formed a grouping that is geographically well defined and could be explained by enhanced upwelling in the ACM, whereas the data set excluding *E. huxleyi* showed a grouping not entirely geographically defined, that could be barely explained by the sea surface temperature gradient. In addition, the remarkably low number of other species in the ACM, in relation to *E. huxleyi* and *G. muellerae*, could limit the use of the commonly applied counting methods, excluding *E. huxleyi*. According to the known oceanographic regime and models for the ACM, the most appropriate method for paleoecological and paleoceanographic reconstructions based on recent coccoliths is to consider the assemblage including *E. huxleyi*. This comparison of counting methods is a helpful prerequisite for a better understanding of the present-day environment influences on the coccoliths spatial distribution in the MCA, that will allow us to extrapolate this information in paleoceanographic reconstructions.

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