Disponible en ligne sur
ScienceDirect
www.sciencedirect.com

Elsevier Masson France
EM|consulte
www.em-consulte.com

GEOBIOS

Geobios 43 (2010) 131–149

Original article

Coccolith distribution patterns in surface sediments of Equatorial and Southeastern Pacific Ocean[☆]

Patrons de distribution des coccolithes dans les sédiments de surface de l'océan Pacifique équatorial et sud-oriental

Mariem Saavedra-Pellitero[a,*], José-Abel Flores[a], Karl-Heinz Baumann[b], Francisco-Javier Sierro[a]

[a] *Department of Geology, University of Salamanca, Plaza de la Merced s/n, CP-37008, Salamanca, Spain*
[b] *Department of Geosciences, Universität Bremen, PO Box 330440, 28334 Bremen, Germany*

Received 10 December 2008; accepted 8 September 2009
Available online 24 October 2009

Abstract

This study aims to contribute to a more detailed knowledge of the biogeography of coccolithophores in the Equatorial and Southeastern Pacific Ocean. Census data of fossil coccoliths are presented in a suite of core-top sediment samples from 15°N to 50.6°S and from 71°W to 93°W. Following standard preparation of smear slides, a total of 19 taxa are recognized in light microscopy and their relative abundances are determined for 134 surface sediment samples. Considering the multivariate character of oceanic conditions and their effects on phytoplankton, a Factor Analysis was performed and three factors were retained. Factor 1, dominated by *Florisphaera profunda* and *Gephyrocapsa oceanica,* includes samples located under warm water masses and indicates the occurrence of calcite dissolution in the water column in the area offshore Chile. Factor 2 is related to cold, low-salinity surface-water masses from the Chilean upwelling, and is dominated by *Emiliania huxleyi*, *Gephyrocapsa* sp. < 3 µm, *Coccolithus pelagicus* and *Gephyrocapsa muellerae*. Factor 3 is linked to more saline, coastal upwelling areas where *Calcidiscus leptoporus* and *Helicosphaera carteri* are the dominant species.

© 2009 Elsevier Masson SAS. All rights reserved.

Keywords: Coccolithophores; Surface sediment samples; Biogeography; Equatorial and Southeastern Pacific

Résumé

Cette étude contribue à une meilleure connaissance de la biogéographie des coccolithophoridés dans le Pacifique équatorial et sud-oriental. Une quantification des assemblages de coccolithes fossiles est effectuée dans plusieurs échantillons de sédiments de surface, le long d'un transect 15°N–50.6°S dans une bande longitudinale allant de 71°O à 93°O. Dix-neuf taxons sont identifiés en microscopie optique et leurs abondances relatives calculées pour 134 échantillons. Une Analyse factorielle a été appliquée à l'ensemble des données. Celle-ci permet d'extraire trois facteurs. Le Facteur 1 est dominé par *Florisphaera profunda* et *Gephyrocapsa oceanica* et correspond aux échantillons de sédiments prélevés dans des régions caractérisées par des masses d'eaux chaudes. Le Facteur 1 défini également une région où la dissolution des carbonates a lieu, au large du Chili. Le Facteur 2 est lié à des conditions de basse température et faible salinité des eaux de surface, en relation avec l'upwelling du Chili. Ce facteur reçoit une contribution importante de la part d'*Emiliania huxleyi*, *Gephyrocapsa* sp. < 3 µm, *Coccolithus pelagicus* et *Gephyrocapsa muellerae*. Le Facteur 3, représenté par *Calcidiscus leptoporus* et *Helicosphaera carteri*, correspond à des masses d'eaux à salinité plus élevée, en relation avec l'upwelling côtier.

© 2009 Elsevier Masson SAS. Tous droits réservés.

Mots clés : Coccolithophoridés ; Sédiments de surface ; Biogéographie ; Pacifique équatorial et sud-oriental

---

[☆] Corresponding editor: Emanuela Mattioli.

[*] Corresponding author.
E-mail address: mariemsaavedra@usal.es (M. Saavedra-Pellitero).

0016-6995/$ – see front matter © 2009 Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.geobios.2009.09.004

1. Introduction

The marine pelagic realm is the largest system on our planet, where only a few taxonomic groups and a relatively small number of species are responsible for most of the primary production (Baumann et al., 2004; Rost and Riebesell, 2004). Coccolithophores are a major component of the phytoplankton and the only calcareous primary producers that show a geographically widespread fossil preservation (Stoll and Ziveri, 2002). Accordingly, they can affect the global climatic system since they play a double role in the C cycle: as photosynthetic organisms (organic pump) and as calcite producers (inorganic counter-pump).

Coccolithophores live at different depths in the photic zone owing to their requirement of sunlight for photosynthesis (Winter et al., 1994). Their distribution in the upper water column is influenced by surface oceanic circulation and different parameters such as temperature, salinity, and macro- and micro-nutrient availability. According to their life cycles, coccolithophore cells are surrounded by a coccosphere made of calcite plates (coccoliths) that after death are transported towards the oceanic floor as intact coccospheres or as individual coccoliths in faecal pellets, marine snow, or relatively large aggregate particles (Steinmetz, 1994). Although coccolith assemblages in sediments may be modified by selective destruction or dissolution, and may provide a distorted image of the living communities (Samtleben and Schröder, 1992; Baumann et al., 1999), knowledge about surface sediment distribution is a prerequisite for paleoecological and paleoceanographical studies of Quaternary sediments (Baumann et al., 2000; Boeckel et al., 2006).

Knowledge of the biogeography of coccolithophores is crucial for a better understanding of their biology and environmental preferences. However, only a few comprehensive compilations exist that include broad biogeographical regions and full assemblage studies (McIntyre and Bé, 1967; Okada and Honjo, 1973, 1975; Roth and Coulbourn, 1982; Winter et al., 1994; Ziveri et al., 2004). Okada and Honjo (1973) described the distribution of coccolithophores in the surface waters of the Northern and Central Pacific. They identified 90 species and established six coccolithophorid zones (Subarctic, Transitional, Central North, Equatorial North, Equatorial South and Central South), in which they also traced a vertical zonation within the water column. Their study covered a broad area, the water samples collected from 50°N to 15°S. These findings were included in subsequent studies (Okada and McIntyre, 1977; Winter et al., 1994; Hagino and Okada, 2004). The spatial distribution of living coccolithophores has also been described in the Equatorial current system of the western-central Pacific and in the east Australian current regime (Hagino et al., 2000), and calcareous nannoplankton thanatocoenoses have been investigated in the Pacific seas around Japan (Tanaka, 1991). Nevertheless specifically, there is still a lack of information about the biogeographical distribution of coccolithophores in the Equatorial and southern Pacific.

This study aims to evaluate the distribution patterns of coccolithophorid assemblages in surface sediments and to establish a Holocene biogeographical distribution in the Equatorial and Southeastern Pacific, taking into account that most of the samples are located along one of the largest major eastern boundary currents in the world: the Peru Current (Feldberg and Mix, 2002). This work provides new data that will improve our knowledge about biogeographical coccolithophores distribution already established for the Atlantic and northern Pacific (e.g., Ziveri et al., 2004; Boeckel et al., 2006).

2. Oceanographic settings

The zone of study covers a broad area from the Inter-Tropical Convergence Zone (ITCZ) to almost the Polar Front (between 15°N to 50.6°S; Fig. 1). The intense rainfall that accompanies the ITCZ decreases surface water salinity (Fig. 2), and increases stratification of the upper ocean waters off Panama, Colombia and Ecuador (Strub et al., 1998). Off southern Chile, strong westerly winds are accompanied by important rainfall and continental runoff, which generates a

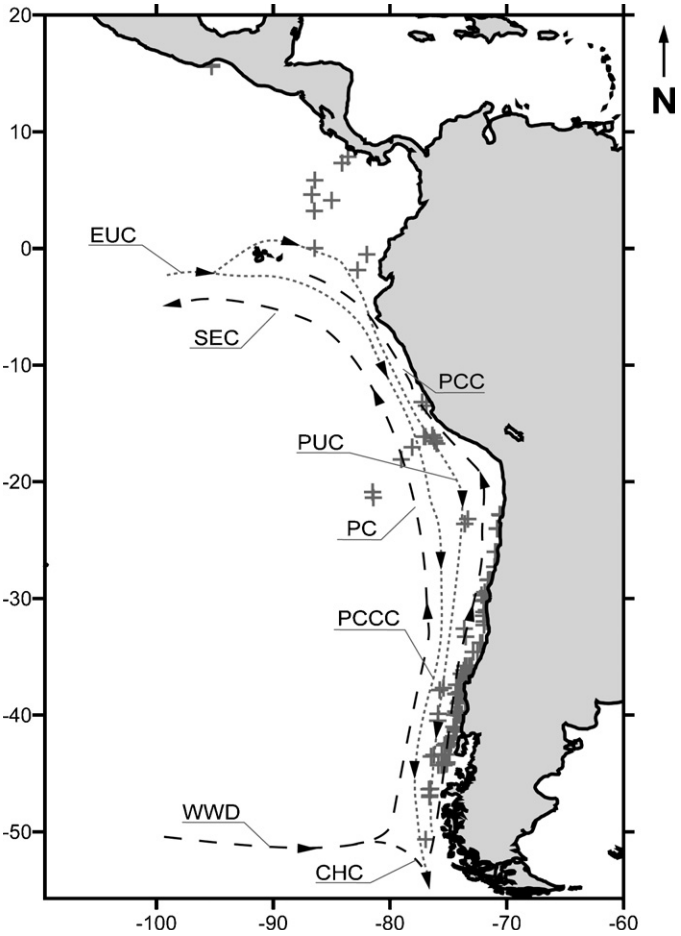


Fig. 1. Region of study and location of the 134 analyzed surface sediment samples (marked with a cross). Major surface and subsurface oceanic circulation patterns in the South Pacific Ocean are indicated (modified from Feldberg and Mix, 2002; Strub et al., 1998). Major surface currents (black dashed lines): West Wind Drift (WWD), Cape Horn Current (CHC), Peru Current (PC), Peru Coastal Current (PCC), and South Equatorial Current (SEC); subsurface currents (dotted lines): Peru-Chile Countercurrent (PCCC), Peru Undercurrent (PUC), and Equatorial Undercurrent (EUC).

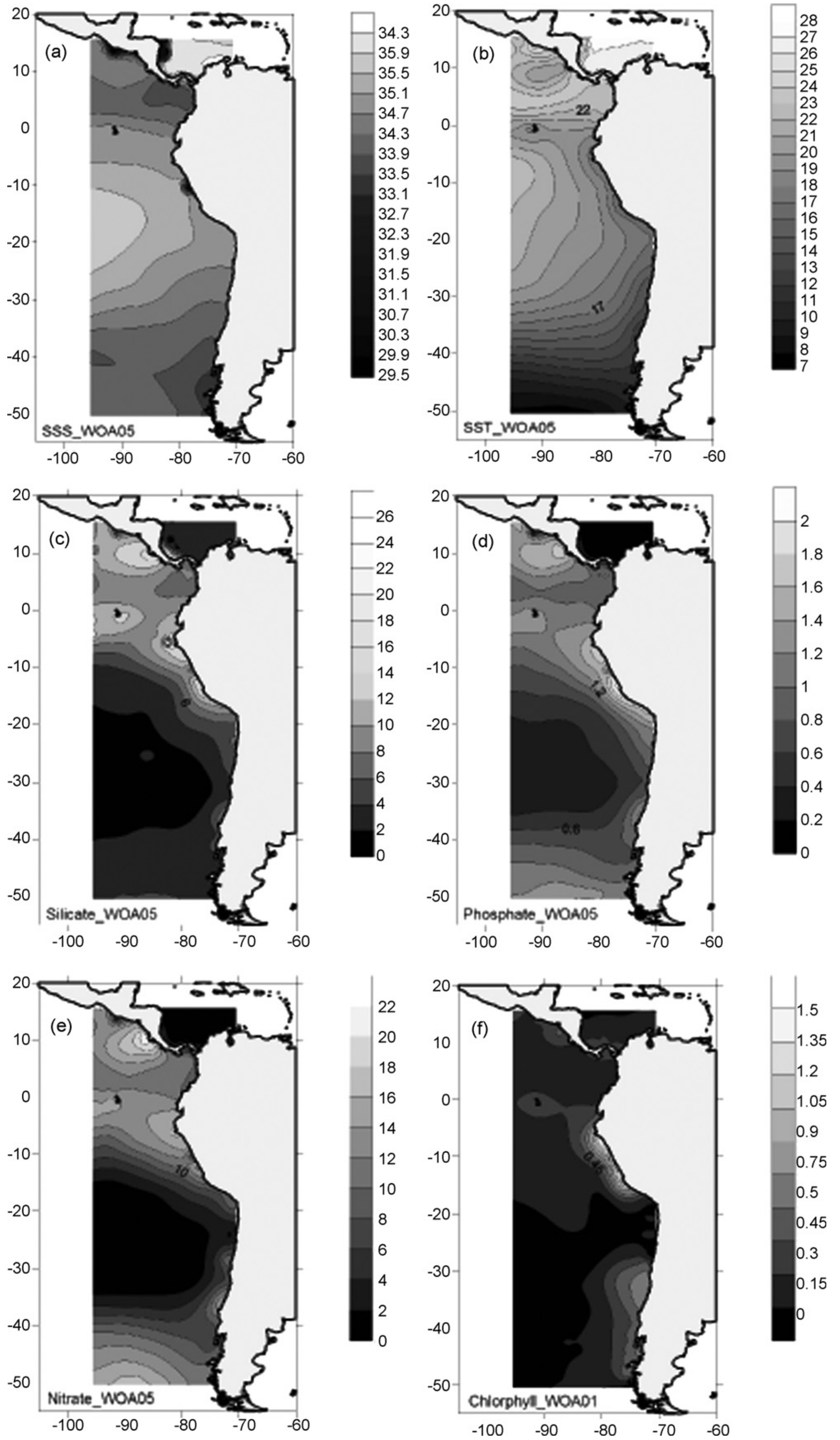


Fig. 2. Physical, chemical and biological variables in the study area: (**a**) mean annual Sea Surface Salinity (SSS, in PSU); (**b**) Sea Surface Temperature (SST, in °C); (**c**) silicate (micromole/l); (**d**) phosphate (micromole /l); (**e**) nitrate (micromole/l); (**f**) chlorophyll concentration (microgram/l) expressed as an average from 0 m to 75 m water depth. Data from the World Ocean Atlas 2005 (Antonov et al., 2006; Garcia et al., 2006; Locarnini et al., 2006) and from the World Ocean Atlas 2001 (Conkright and Boyer, 2002; Levitus, 1982).

tongue of low-salinity water that spreads northward from the fjord region (Strub et al., 1998; Lamy et al., 2002). The Peru Current (PC) is the largest eastern boundary current in the World, and covers the majority of the study area (Fig. 1). Spreading along almost the entire west coast of South America, it is a major stream allowing the exchange of heat and nutrients between high and low latitudes in the Southern Pacific Ocean (Strub et al., 1998). The PC represents the eastern portion of the southern anti-cyclonic subtropical gyre, flowing towards the equator at a speed of ∼2 cm/s between 0 and 100 m depth (Shaffer et al., 1995), with an average transport of 15-20 SV (Wooster and Reid, 1963). Off southern Chile, cool waters from the Antarctic Circumpolar Current/West Wind Drift (WWD) impinge on the continent and form a transition zone between the southward-flowing Cape Horn Current (CHC) and the northward flowing PC. Here, the westerly winds induce important rainfall to the coastal mountains and the Andes, resulting in high fluvial sediment fluxes to the ocean (Lamy et al., 1998a, 2001).

Coastal upwelling driven by southerly winds along the coast of central Chile and Peru brings cold, nutrient-rich waters to the sea surface along the coast of Chile and Peru towards the equator (Wyrtki, 1981; Bryden and Brady, 1985; Strub et al., 1998; Fig. 2). Phytoplankton biomass is high throughout the year in the coastal upwelling system (Rojas de Mendiola, 1981). The sites of high productivity are often associated with capes and adjacent bays off Peru (i.e., at 6°, 9°, 12°, 15°S; Zuta and Guillen, 1970; Rojas de Mendiola, 1981; Thomas et al., 2001) as well as off northern Chile (at 23°, 27°, 30°, 33° and 35–38°S; Strub et al., 1998). A majority of the upwelled waters come from the Poleward Undercurrent (PUC), also known as the Gunther Undercurrent. The PUC is located mainly between depths of 50 m and 300 m, and is especially strong at depths close to 150 m off Peru (Huyer et al., 1991).

Inshore of the Peru Current is the Peru-Chile Countercurrent (PCCC; Fig. 1), a weak and irregular surface current flowing to the south and located approximately 200 km offshore (Huyer et al., 1991). This current transports relatively warm waters southward, and separates the PC from its coastal branch, the Peru Coastal Current (PCC). Close to 5°S, the PC is deflected away from the coast to become part of the South Equatorial Current (SEC; Wyrtki, 1965). Beneath the SEC lies the Equatorial Undercurrent (EUC), which flows eastward across the Pacific at depths of 200–250 m. The upper portion of this current is the source of the 19–24 °C water upwelling along the equator near the Galapagos (Wyrtki, 1981). The lower portion of the current continues eastward, upwelling cold water (11–14 °C) off the coast of Peru (Toggweiler et al., 1991). Both the SEC and EUC contribute to the Equatorial cold tongue, which extends westward to 130°W (Wyrtki, 1965). Further offshore beneath the Peru Current, the PUC is a deeper and slower current flowing southwards, located between 100 m and 400 m depth (Shaffer et al., 1995; Fig. 1). The PUC, which originates in the EUC near the Galapagos Islands, is characterized by cold temperatures, high salinities, and low dissolved oxygen (Wyrtki, 1965; Strub et al., 1998).

3. Material and methods

3.1. Core-top samples

The samples analysed were recovered during three cruises: Genesis IIIRR9702A, NEMO-Me0005A and PUCK: Valparaiso-Talcahuano; 88 of these samples were from multicorers (GeoB 7xxx), while 46 were from boxcores (RR-xx and Me-xx; Appendix B). For the analysis of coccolithophores, the uppermost undisturbed centimetre was sampled from core-tops recovered from depths ranging between 120 m and 4124 m (Fig. 1). The same surface samples have also been used to characterize upwelling and productivity offshore Chile with planktic foraminifera (Mohtadi et al., 2005), and environmental properties with diatoms (Abrantes et al., 2007). The sample distribution is rather patchy, with samples concentrating at intermediate latitudes in eutrophic areas offshore Chile. The temporal resolution of samples is unknown, so it could range from few centuries to several thousand years. However, to provide a general idea about ages a table with sedimentation rates is presented in this work (Table 1). Since almost none of the surface sediments has been dated, the age and sedimentation rates of the sites studied here has to be estimated by extrapolation of adjacent core locations from previous studies (Marchant, 1997; Lamy et al., 1998b, 1999, 2001; Mohtadi and Hebbeln, 2004; Mohtadi et al., 2007; Pena et al., 2008). Sedimentation rates for recent sediments diverge considerably,

Table 1
Sedimentation rates from different regions of the study area calculated with data derived from different works (Marchant, 1997; Lamy et al., 1998b, 1999, 2001; Mohtadi and Hebbeln, 2004; Mohtadi et al., 2007; Pena et al., 2008). Cores in which the first sample dated corresponds to an age older than 10 kyr are marked with an asterisk. Remarks: in core GIK 17748-2, the uppermost 13 cm of the core are missing (Stoffers et al., 1992); in GeoB 3302, sedimentation rates vary between ∼5 and 20 cm/kyr for the Holocene, and in core GeoB 3313 sedimentation rates are on average in the range of 1 m/kyr.

Core	Latitude	Longitude	Latitude total	Longitude total	Depth (m)	Sedimentation rate (m/ka)	Reference
Site ODP 1240	0° 1.31'N	86° 27.76' W	0.02	−86.46	2921	0.04	Pena et al., 2008
GeoB 7112-5	24° 1.99'S	70° 49.41'W	−24.03	−70.82	2507	0.17	Mohtadi and Hebbeln, 2004
GeoB 3375 (*)	27° 28'S	71°15'W	−27.47	−71.25	1947	0.08	Lamy et al., 1998b
GeoB 7139-2	30° 12'S	71° 58.99'W	−30.20	−71.98	3267	0.09	Mohtadi and Hebbeln, 2004
GIK 17748-2	32° 45'S	72° 2'W	−32.75	−72.03	2545	0.09	Lamy et al., 1999 (based on Marchant, 1997)
GeoB 3302 (*)	33° 13'S	72° 06'W	−33.22	−72.10	1498	0.06	Lamy et al., 1999
GeoB 3313	41° 00'S	74° 27'W	−41.00	−74.45	852	1.25	Lamy et al., 2001
GeoB 7186-3	44° 8.96'S	75° 9.49'W	−44.15	−75.16	1169	1.8−4	Mohtadi et al., 2007

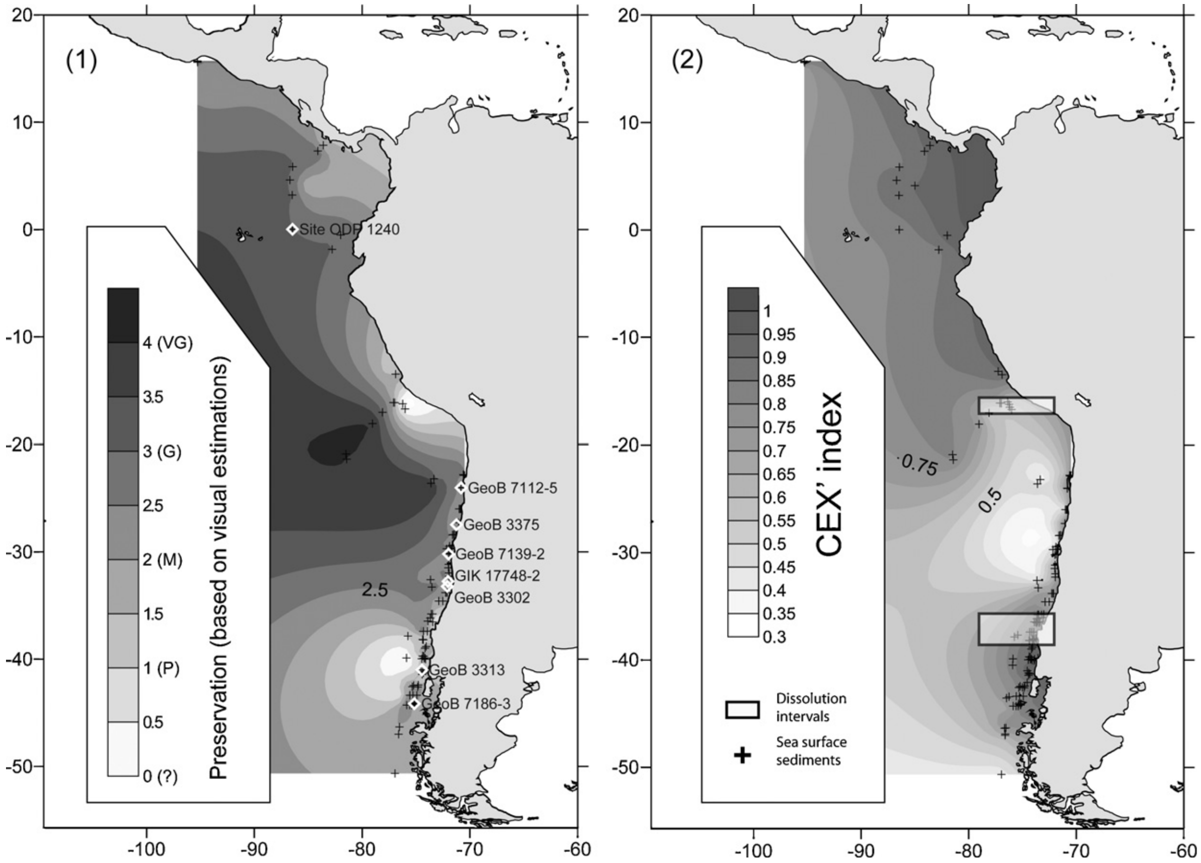


Fig. 3. Preservation contour maps generated with Golden Software Surfer 8® using kriging method: **1**. Distribution map based on a numerical ranking based on Flores and Marino (2002): 4 = "VG" (very good/excellent), 3 = "G" (good), 2 = "M" (moderate), 1 = "P" (poor), 0 = "?" (absence of coccoliths). Core-top samples excluded from the statistical analysis, and samples barren in coccoliths are included in the contour map. Diamonds indicate the location of cores where recent sedimentation rates are known (Table 1); **2**. Distribution map of the CEX' index calculated for each surface-sediment sample considered in this study (excluding dissolution-bearing core-top samples). Main dissolution areas defined in light microscope are indicated with rectangles.

ranging from 0.044 m/kyr at site ODP 1240 (Pena et al., 2008), located on the northern flank of the Carnegie Ridge (0°1.31'N, 86°27.76'W), to 1.8–4 m/kyr at site GeoB 7186–3 (Mohtadi et al., 2007) from the continental slope offshore Chile (44°8.96'S, 75°9.49'W; Fig. 3(1)). These estimations were taken from the age model of different cores based on the youngest ^{14}C AMS datations (although in some cases the first sample dated corresponds to an age older than 10 kyr, e.g., GeoB 3375 or GeoB 3302). Focusing on offshore Chile, where more data are available, the lowest sedimentation rates correspond to the northern flank of the upwelling system (from ~18°S to ~35.5°S) and the highest ones are found in the southern part of the study area. These differences reflect the distinct sedimentation regimes (eolian *versus* fluvial), and point to the increase in dilution due to high terrigenous input from the continent, as already noted by Hebbeln et al. (2000) and Mohtadi et al. (2005).

Different sample preparation techniques have been used by several authors (McIntyre and Bé, 1967; Okada and Honjo, 1973; Backman and Shackleton, 1983; Wei, 1988; Beaufort, 1991; Okada, 1992; Henriksson, 1993; Williams and Bralower, 1995; Andruleit, 1996; Flores and Sierro, 1997; Bollmann et al., 1999; Koch and Young, 2007). The use of different methods may result in biased estimations of nannofossil quantities (Geisen et al., 1999; Bollmann et al., 1999, 2002) and makes difficult to compare results obtained with different techniques (Herrle and Bollmann, 2004; Henderiks and Törner, 2006). Hence the establishment of a worldwide database of surface sediment samples is not easy. To ensure the homogeneity and reproducibility of coccolith counting, the following method was used in this work, specifically completed by auxiliary methodologies of analysis (filtering and the use of SEM). Smear slides were prepared following the procedures of Backman and Shackleton (1983), and Flores and Sierro (1997). Coccolith identification was done using a Leica DMRXE® and a Nikon Eclipse 80i® polarized microscope at a magnification of ×1000, occasionally ×1250, and at least 400 coccoliths per sample were counted.

Carbonate calcium dissolution in the deeper waters can modify the taxonomic composition of recent planktonic microfossil assemblages (Thierstein, 1980), so the location of the present-day lysocline was taken into account in this work. Studies of surface sediments from the South Pacific suggest a present-day Carbonate Compensation Depth (CCD) at ~4500 m depth, and a Carbonate Lysocline (CL) at 3600–3800 m depth (Hebbeln et al., 2000). These data are broadly in accordance with data from other authors and from other regions: southern Pacific (CL: ~3500 m, CCD: ~4100 m;

Broecker and Broecker, 1974; Berger et al., 1976), western Pacific (CL: 3500 m, CCD: 4800 m; Berger et al., 1982), Equatorial Pacific (CL: 3800–4000 m; Thompson, 1976; Farrell and Prell, 1989), and the Peru Basin (CL: 3700 m, CCD: 4300 m; Weber et al., 1995). In our study, all the samples considered were located above the present-day lysocline. Only 3 samples at depths between 3500 m and 4000 m were considered owing to their acceptable coccolith preservation, estimated by means of microscopic observation. Samples located below 4000 m were barren of coccoliths, and were therefore excluded.

A total of 134 core-top samples were studied, but only 96 samples were considered as valid for statistical analysis. 38 samples were excluded owing to the low number of coccoliths (which led to unrealistic percentages in the associations) and to their poor preservation (Fig. 3). In seven of the samples excluded, no coccoliths were detected, and in the remaining 31 the number of coccoliths was lower than 100 coccoliths in 100 fields of view in optical microscope.

3.2. Taxonomy

The identification and taxonomy of the species (Appendix A) mainly follow the work of Jordan and Kleijne (1994) and the subsequent modification of Jordan et al. (2004), although additional considerations from other authors were also taken into account (e.g., the group of *Gephyrocapsa* < 3 µm defined by Flores et al., 1997).

3.3. Dissolution and preservation

The distribution, preservation and accumulation of coccoliths at the sea floor depend on the balance between the biogenic production of $CaCO_3$ in the supersaturated surface waters and its dissolution in the undersaturated deep waters (Farrell and Prell, 1989). First, to determine the preservation degree of coccoliths, a scale based on visual estimations, similar to the one of Flores and Marino (2002), was established considering etching and overgrowth: "VG" = excellent preservation (no evidence of dissolution at all); "G" = good (little or no evidence of dissolution and/or secondary overgrowth of calcite; diagnostic characters fully preserved); "M" = moderate (dissolution and/or secondary overgrowth; partially altered primary morphological characteristics; however, nearly all specimens can be identified at species level); "P" = poor (severe dissolution, fragmentation, and/or secondary overgrowth with primary features largely destroyed; many specimens cannot be identified at species level and/or generic level); and "?" = absence of coccoliths (total dissolution) (Appendix B). A numerical ranking was defined (4 = "VG", 3 = "G", 2 = "M", 1 = "P", 0 = "?"), and a contour map was generated with the Golden Software Surfer 8® using the kriging method. In regard to the preservation conditions of the coccoliths, the core-tops excluded and the barren samples were plotted in order to check their geographical distribution (Fig. 3(1)). Dissolution is an important issue in the study area, especially in the main upwelling sites. A slight modification of a coccolith dissolution index (CEX') was used to estimate the effect of carbonate dissolution on the coccolith assemblages (Boeckel et al., 2006). This index is based on the CEX from Dittert et al. (1999), namely *Calcidiscus leptoporus – Emiliania huxleyi Dissolution Index* = (% *E. huxleyi*) / (% *E. huxleyi* + % *C. leptoporus*). The CEX' index (Boeckel and Baumann, 2004) is a ratio of two coccolithophore species that compares the small and delicate placoliths of *E. huxleyi* and *Gephyrocapsa ericsonii* to strongly calcified coccoliths such as *C. leptoporus*. CEX' = (% *E. huxleyi* + % *G. ericsonii*) / (% *E. huxleyi* + % *G. ericsonii* + % *C. leptoporus*). Carbonate dissolution has a more important effect on small placoliths than on *C. leptoporus*, and hence the ratio of these taxa will change with increasing dissolution. According to Boeckel and Baumann (2004), CEX' values lower than 0.6 coincide with a depositional environment below the calcite lysocline, and hence a CEX' = 0.6 represents a critical boundary. In this work, *Gephyrocapsa* sp. < 3 µm was considered instead of *G. ericsonii*. A contour map with CEX' values was generated with Golden Software Surfer 8® using the kriging method; samples excluded from the statistical analysis were not plotted in this graphic (Fig. 3(2)).

3.4. Distribution maps

Because of the irregularly spaced samples, a kriging method was chosen for the interpolation by using a search ellipse oriented N–S (ratio = 0.85) owing to the fact that most of the samples showed a preferred orientation parallel to the American coast. Broadly, the search ellipse specifies the size of the local neighbourhood in which looking for data (Goovaerts, 1997). Contour maps were generated using Golden Software Surfer 8®. The relative abundances of each taxon were plotted separately. Present-day environmental variables, such as Sea Surface Temperature (SST in °C; Locarnini et al., 2006), Sea Surface Salinity (SSS in PSU; Antonov et al., 2006), Nitrate (micromole/l; Garcia et al., 2006), Phosphate (micromole/l; Garcia et al., 2006), Silicate (micromole/l; Garcia et al., 2006) and Chlorophyll concentrations (microgram/l; Levitus, 1982; Conkright and Boyer, 2002), were obtained from the World Ocean Atlas 2005 and from the World Ocean Atlas 2001 Data Sets, National Oceanographic Data Centre, Washington DC (see http://ingrid.ldgo.columbia.edu/SOURCES/.NOAA/.NODC). The interpolation method was kriging, without any search ellipse. These environmental variables are calculated annually for a 1° latitude and longitude square block. Euclidean distances between each station and World Ocean Atlas database (1° grid) were calculated and the smallest one was chosen. When there were two equal minimum distances, the average was chosen. Diversity in coccolithophores species is generally higher in the upper photic zone than in the lower photic zone, so data from 0 m, 10 m, 20 m, 30 m, 50 m and 75 m were included. An interpolation of data from 0 to 75 m was performed in order to have values every 5 m. An average of the interpolated new data was considered as a reference values (SST, SSS, etc.) at each location corresponding to surface water conditions of living coccolithophores.

3.5. Statistical analyses

Owing to the non-Gaussian distribution observed in the histograms (percentage of the species or group of coccolithophore (x) *versus* number of observations), a log-transformation of $\log(x+1)$ was applied to the dataset to obtain a normal distribution. In the factor analysis, log-transformation amplifies the importance of less abundant species, and thus minimizes the dominance of few abundant species (Mix et al., 1999). Owing to the multivariate character of oceanic conditions and their effects on phytoplankton in the study area, Factor Analysis was applied to the core-top data set generated, including a varimax normalized rotation with the Statistica 7.0® software package (Table 2). Our analysis includes 14 species showing variable abundances from rare to abundant and accounting for 100% of the assemblage, but excluded the reworked species that only appeared rarely (e.g., *Cyclicargolithus floridanus, Discoaster* spp., etc.). The p-values in the marked cells of the correlation table are smaller than 0.05, indicating statistical significance (Table 3). Factor Analysis is a statistical approach that reduces the information brought by an important number of original variables into a smaller set of dimensions (factors) with a minimum loss of information (Hair et al., 1992). In the study area, variables (which are the different stations) are highly correlated each other. By applying Factor Analysis, we can identify how many statistically independent artificial end-members (factors) are there, and which taxa dominate in each factor.

Finally, to investigate the relationship of the factors obtained with different environmental parameters, we examined the Pearson correlation coefficients from a correlation matrix (Statistica 7.0®) between the factor loadings from the factor analysis and some of the environmental variables selected: SST (°C), SSS (PSU), nitrate (micromole/l), phosphate (micromole/l), silicate (micromole/l) and chlorophyll (microgram/l) concentrations.

4. Results

4.1. Dissolution and preservation

Coccolith preservation, resulting from both burial diagenesis and water column dissolution, is shown in Fig. 3(1), illustrating the geographic distribution of the preservation indices based on visual estimations. Observations in LM reveals that the preservation of coccoliths is variable, from heavily dissolved to well preserved, although most of the samples display a moderate preservation. The well-preserved samples are recorded in tropical areas (i.e., samples RR50, RR54, RR60, RR62 or Me07). Poor preservation usually coincides with a very low quantity of coccoliths in the smear slides. Poorly preserved samples are more widespread southwards in the study area. The data concerning coccolith preservation from different samples are given in Appendix B.

Fig. 3(2) shows the effects of dissolution in the water column based on the CEX' index. Two rectangles indicate the areas of poorest preservation and strongest dissolution, where coccoliths are very scarce. It can also be noted that values of the CEX' index (>0.6) are generally high except for some locations offshore Chile coinciding with a moderate-to-good preservation observed in LM, and with relatively low sedimentation rates (0.06–0.17 m/kyr; values from Lamy et al., 1999; Mohtadi and Hebbeln, 2004).

Table 2
Factor scores obtained by the Factor Analysis (including a Varimax normalized rotation) of the 14 most abundant coccolithophore taxa. Bold values are significant at the 0.05 p-level.

	Factor 1	Factor 2	Factor 3
Florisphaera profunda	**2.12**	−0.54	0.32
Calcidiscus leptoporus	−0.46	0.15	**1.93**
Helicosphaera carteri	−1.15	−0.85	**2.03**
Gephyrocapsa oceanica	**2.17**	−0.35	−0.23
Gepyrocapsa muellarae	0.33	**1.07**	0.22
Syracosphaera spp.	−0.43	−0.59	−0.62
Umbilicosphaera spp.	−0.05	−1.19	0.16
Umbellosphaera spp.	−0.45	−0.72	−0.67
Calciosolenia sp.	−0.47	−0.70	−0.72
Coccolithus pelagicus	−1.00	**1.23**	−1.28
Rabdosphaera clavigera	−0.51	−0.72	−0.59
Oolithotus sp.	−0.34	−0.18	−1.18
Emiliania huxleyi	−0.16	**1.59**	0.30
Small *Gephyrocapsa*	0.40	**1.82**	0.32

Bold values indicate the species which define each factor.

Table 3
Correlation table between the first 3 factors and selected average environmental variables (SST, SSS, nitrate, phosphate, silicate and chlorophyll content).

	Factor 1	Factor 2	Factor 3
SSS	**0.45**	**−0.71**	**0.44**
SST	**0.67**	**−0.73**	0.01
Nitrate	**0.32**	−0.02	**−0.37**
Phosphate	**0.53**	−0.16	**−0.41**
Silicate	**0.73**	**−0.50**	**−0.24**
Chlorophyll	−0.05	**0.26**	−0.12

Bold values are significant at $p < 0.05$.

To summarize, the two indices displayed in Fig. 3 show different results. Lower CEX' values (< 0.6) appear from ~20°S to ~34°S and poorer preservations estimated by LM observations occur mainly in two areas, from ~15.5°S to ~17°S and ~39°S to ~41°S. Additionally, the majority of the samples barren in coccoliths due to dissolution are located in areas from ~15.5°S to ~17°S and ~35.5°S to ~39°S.

4.2. Regional distribution of selected species of coccolithophores and their ecological significance

In order to obtain a better overall understanding of the geographical distribution patterns of coccolithophores in the surface sediments of the study area, it is useful to analyse the contour maps generated in this work. The interpolation values of the contour maps should not be taken as absolute values due to the uneven distribution of the samples. A total of 19 taxa were recognized in light microscopy, but we will briefly comment only on the 14 taxa selected for subsequent statistical analysis, from the most abundant to the scarcest taxon. The

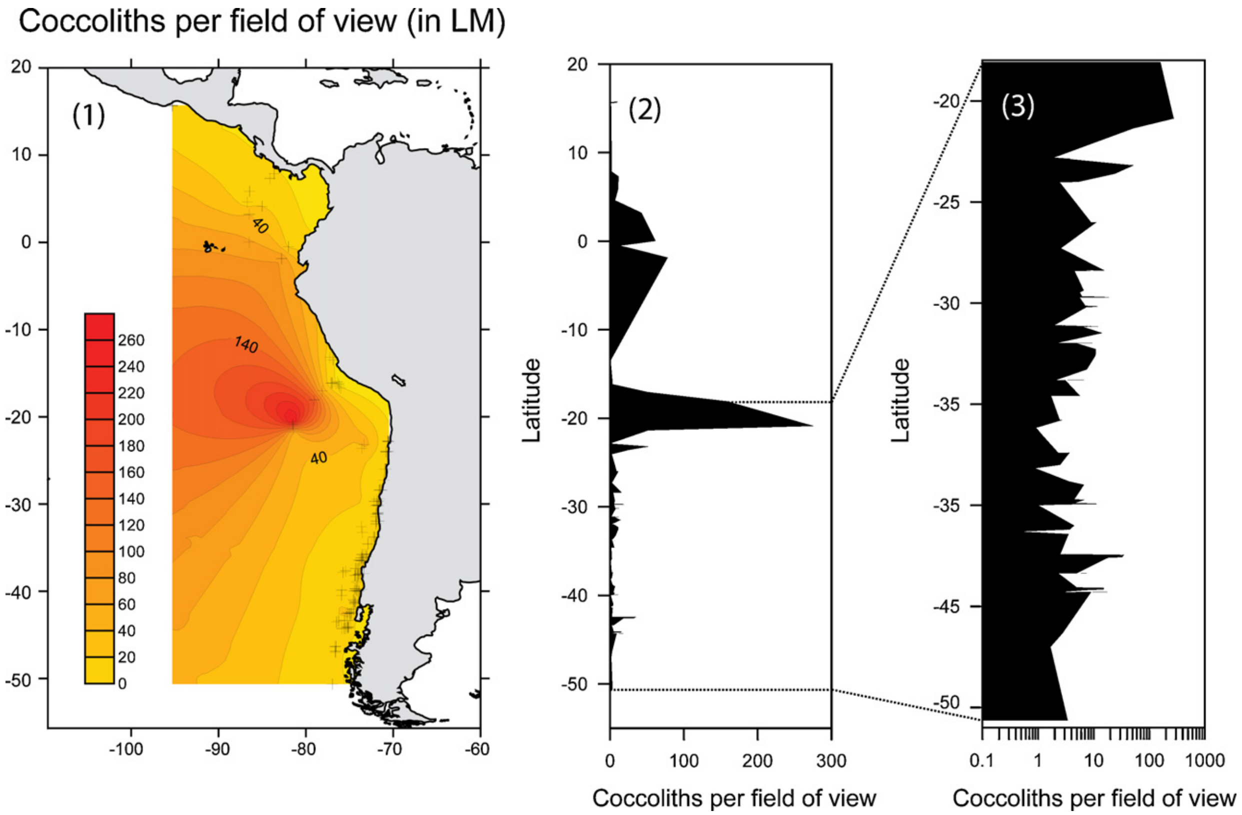


Fig. 4. **1**. Distribution map showing the number of coccoliths per field of view in light microscopy in Equatorial and Southeastern Pacific Ocean; **2**. variations in the number of coccoliths per field of view along a N-S transect of the study area; **3**. Coccoliths per field of view from 18°S to 50.6°S (note the logarithmic scale).

highest concentration of coccoliths based on visual estimation (coccoliths per field of view in LM) is higher in oligotrophic areas and lower offshore Chile, decreasing southward due to the increase in dilution of the biogenic flux (Hebbeln et al., 2000; Mohtadi et al., 2005; Fig. 4).

4.2.1. *Abundant taxa*

The most abundant group is represented by "small" placoliths (average 37.9%), including *Gephyrocapsa* sp. < 3 µm (average 24.1%, maxima 58.2%; Fig. 5(1)) and *E. huxleyi* (average 13.8%, maxima 38%; Fig. 5(2)). Relative abundance values fluctuate and reach maxima off Peru and off Chile in the case of *Gephyrocapsa* sp. < 3 µm and in the subtropical oligotrophic gyre in the case of *E. huxleyi*.

Although *F. profunda* (a species typical of the lower photic zone, LPZ) presents a mean abundance of 16.4% (Fig. 5(3)), its relative abundance fluctuates considerably, reaching a maximum of 58.6% in the Equatorial zone. Its percentage decreases to the south, except for some maxima recorded from 15°S to 16°S and from 21°S to 24°S. Southward ~39°S, this nannolith species becomes very rare in the assemblages.

G. oceanica fluctuates strongly in the study area (with an average of 13.4%), reaching the highest percentages (56.3%) in Equatorial samples. In the coastal upwelling off Chile this species also occurs locally. Its mean abundance is rather low because of its progressive decrease in abundance to the south (Fig. 5(4)).

Calcidiscus leptoporus appears in different oceanic environments (average 12.5%), but maxima (46.2%) are reached from 20° to 50°S, especially close to the Polar Front (Fig. 5(5)). A marked decrease in abundance takes place from 36°S to 44°S.

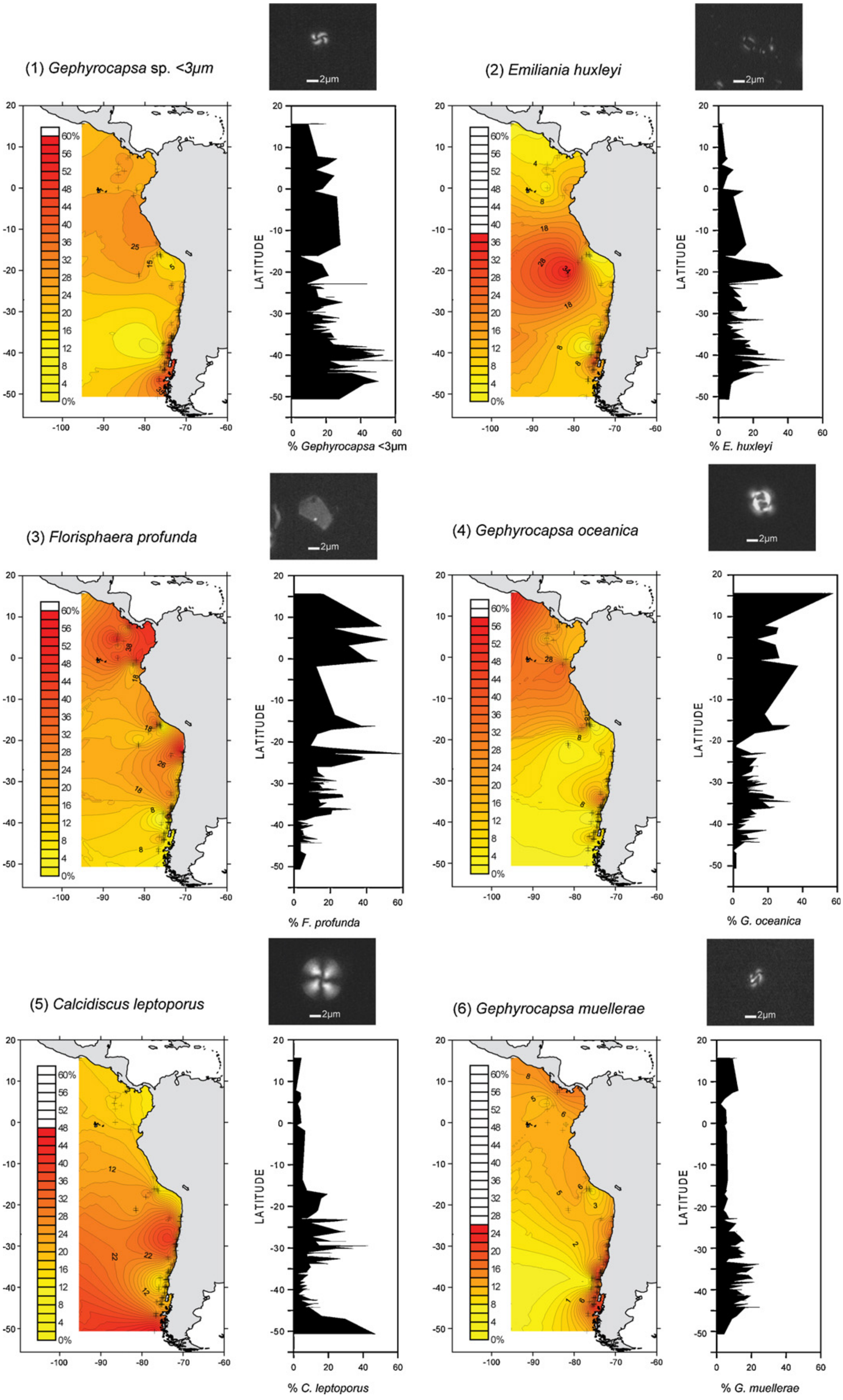
The percentage of *G. muellerae* does not fluctuate much (average 11.8%), but its distribution pattern shows the highest abundances (24.7%) offshore Chile from 25°S, increasing to the south, in cold and high-nutrient upwelled waters (Fig. 5(6)).

4.2.2. *Rare taxa*

Helicosphaera carteri (average 3.8%, maxima 21.1%; Fig. 6(1)) shows a similar distribution with respect to *C. leptoporus* from 25°S to 35°S, where some to the highest values are recorded. This species is not recorded in the subtropical, oligotrophic gyre.

Coccolithus pelagicus is a rare species (1.7% on average), except in the southern part of the Chile upwelling, where maxima of 16.2% are found (Fig. 6(2)). Observations and biometric studies in SEM have indicated that the only subspecies present in this setting is *C. pelagicus* ssp. *braarudii* (temperate form, Geisen et al., 2002) and that there are no specimens of *C. pelagicus* ssp. *pelagicus* (Arctic form, Geisen et al., 2002).

Umbilicosphaera sibogae is the most abundant species of the genus within the studied samples. The presence of *U. foliosa* was confirmed by SEM observations. It occurs in low abundances (average 1%, maxima 6.3%; Fig. 6(3)), but reaches



(1) *Gephyrocapsa* sp. <3µm

(2) *Emiliania huxleyi*

(3) *Florisphaera profunda*

(4) *Gephyrocapsa oceanica*

(5) *Calcidiscus leptoporus*

(6) *Gephyrocapsa muellerae*

Fig. 5. Distribution maps of relative abundance of abundant taxa (range: 0–60%; average < 10%): in the Equatorial and Southeastern Pacific Ocean. **1**. *Gephyrocapsa* sp. < 3 µm; **2.** *Emiliania huxleyi*; **3.** *Florisphaera profunda*; **4.** *Gephyrocapsa oceanica*; **5**. *Calcidiscus leptoporus*; **6.** *Gephyrocapsa muellerae*. On the right of each map a N-S transect with the percentage variations of each taxon and a photograph in LM are shown.

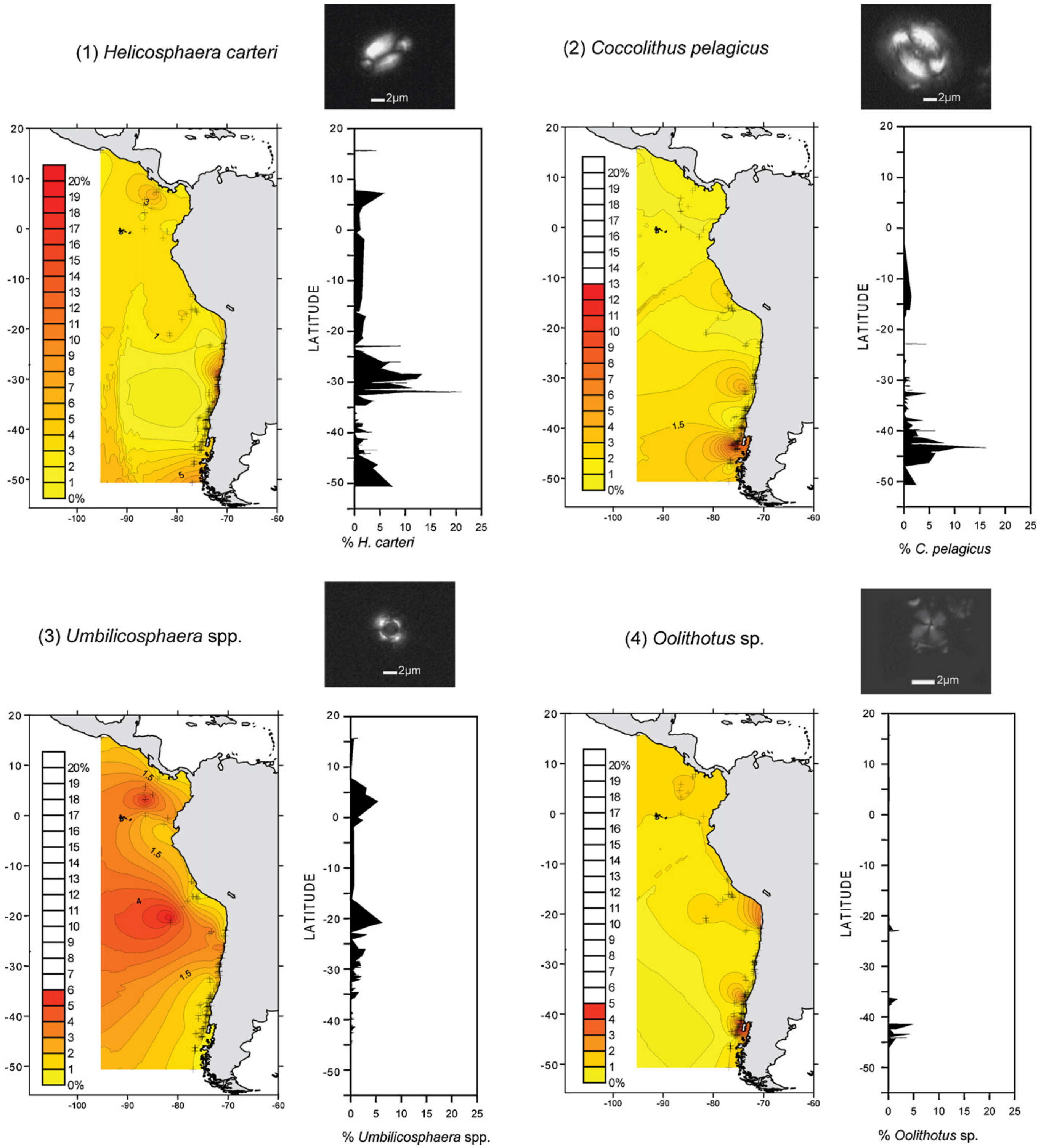


Fig. 6. Distribution map of relative abundance of rare taxa (range: 0-25%; average < 10%): in the Equatorial and Southeastern Pacific Ocean. **1.** *Helicosphaera carteri*; **2.** *Coccolithus pelagicus*; **3.** *Umbilicosphaera* spp.; **4.** *Oolithotus* sp.. On the right of each map a N-S transect with the percentage variations of each taxon and a photograph in LM are shown.

highest percentages in oligotrophic regions. Two sites of relatively high abundance of this taxon are recorded: the first one is located in an area from 1°N to 6°N and 84°W to 91°W, and the second one from 15°S to 25°S and from 79°W, extending westward.

Some other taxa were found with mean relative abundances below 1%. These include *Oolithotus* sp., which is also characteristic of LPZ. This is a delicate species that is rarely recorded in the studied samples (average 0.3%). It reaches the highest values (4.8%) offshore Chile (Fig. 6(4)). Its distribution

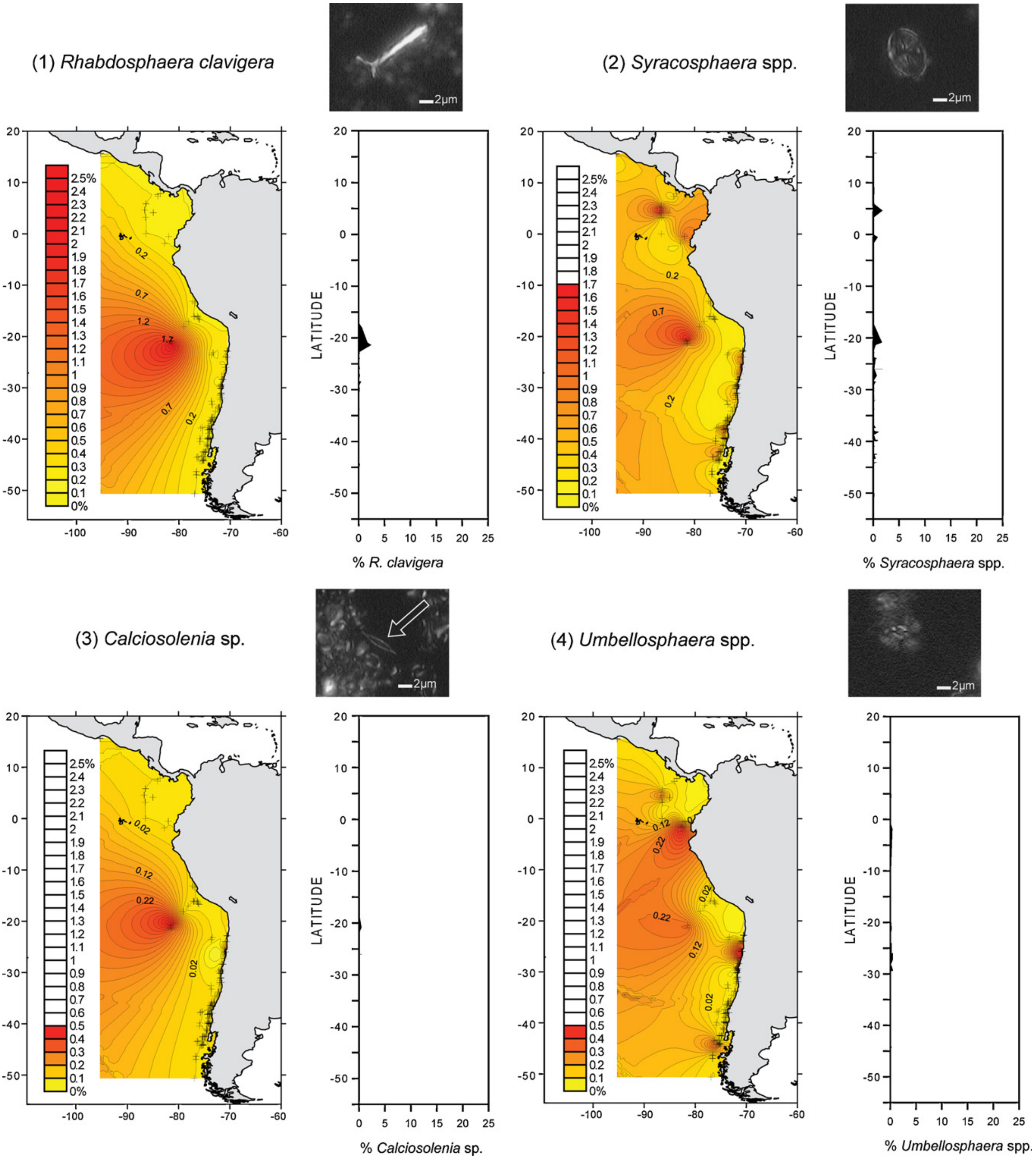


Fig. 7. Distribution map of relative abundance of rare taxa (range: 0-25%; average < 10%): in the Equatorial and Southeastern Pacific Ocean. **1.** *Rhabdosphaera clavigera*; **2.** *Syracosphaera* spp.; **3.** *Calciosolenia* sp.; **4.** *Umbellosphaera* spp. On the right of each map a N-S transect with the percentage variations of each taxon and a photograph in LM are shown.

is restricted to tropical and subtropical areas. *Rhabdosphaera clavigera* appears only in the subtropical oligotrophic gyre (average 0.1%, maximum 2.4%; Fig. 7(1)). *Calciosolenia* sp. shows the same distributional pattern as *R. clavigera*, but it is even more scarce (average 0.01%; maximum 0.5%; Fig. 7(3)). *Syracosphaera* spp. (average 0.2%) reaches its maxima (1.8%) in low productivity zones, mainly located in two areas: from 7°N to 1°S and from 15°S to 23°S (Fig. 7(2)). The presence of some coccoliths of *Syracosphaera* spp. offshore Chile is also recorded. *Umbellosphaera* is a delicate genus that is present in very low percentages (average 0.04%, maximum 0.5%; Fig. 7(4)). SEM observations allowed us to identify fragments

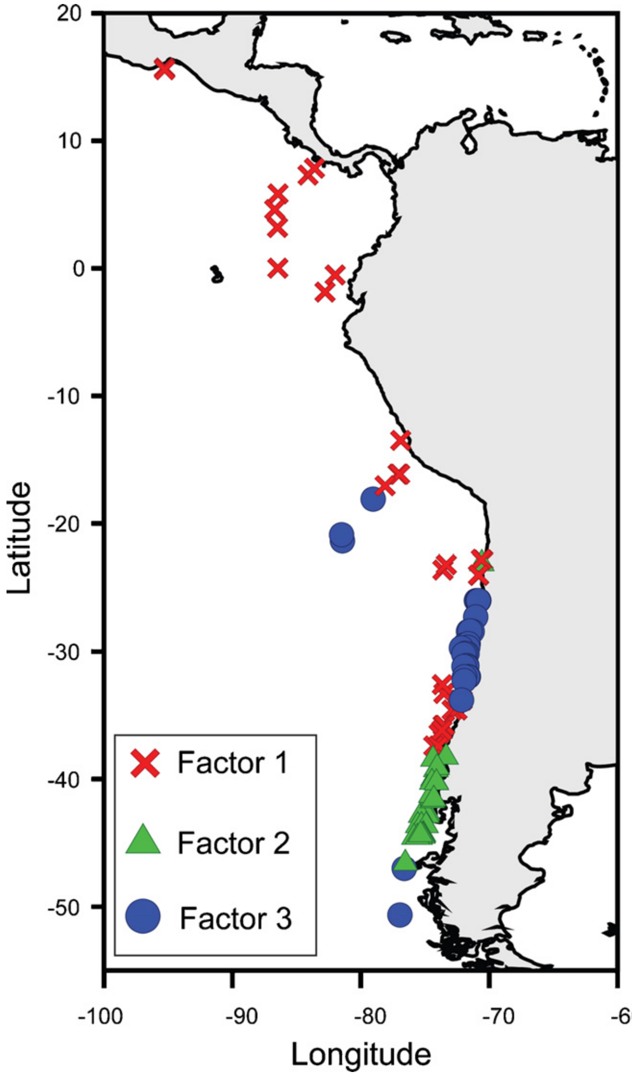


Fig. 8. Dominant factors in the study area as extracted by a Factor Analysis (including a Varimax normalized rotation) of the 14 most abundant coccolithophore taxa (see Table 2 and text for details).

of mainly *U. tenuis* type II coccoliths. Occasionally types III and IV were also found.

4.3. Factor analysis

The Factor Analysis performed in the present dataset retained three factors, together explaining 93.6% of the total variance. The distribution of the dominant factor at each station is shown in Fig. 8. The geographical distribution of dominant factors defines regions linked to different oceanic regimes. For further ecological analysis and interpretation, factors are briefly explained and commented separately below.

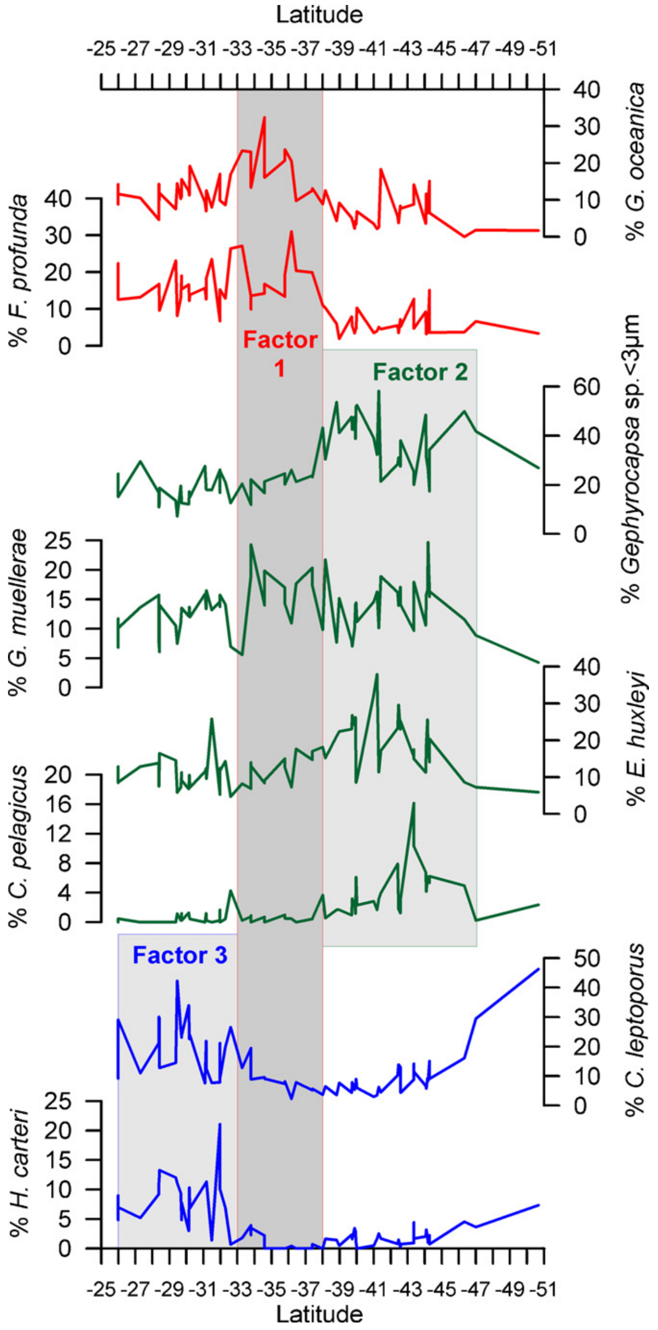


Fig. 9. Percentages of major species that define the three most important factors offshore Chile (from 25°S to 50.6°S). From top to bottom: *Florisphaera profunda* and *Gephyrocapsa oceanica* (factor 1), *Coccolithus pelagicus*, *Emiliania huxleyi*, *Gephyrocapsa muellerae* and *Gephyrocapsa* sp. < 3 µm (factor 2), *Helicosphaera carteri* and *Calcidiscus leptoporus* (factor 3). The dominance of each factor is indicated with grey rectangles and the suggested dissolution area (from 35°S to 38°S), corresponding to the most intense and persistent upwelling activity offshore Chile, is indicated with a darker rectangle.

4.3.1. Factor 1

Two main species contribute to this factor, which explains 31.6% of the total variance: *F. profunda* and *G. oceanica* (Table 2). This factor shows high values in the equatorial/tropical region (from 15°N to 25°S in the study area), linked to warm water conditions, and offshore Chile from ~33°S to 38°S (Fig. 8). Accordingly, the region offshore Chile is a relatively low-temperature and high-nutrient areas in which species typical of warm regions are relatively abundant. This transitional zone has been detected as statistically significant according to factor 1, and separates an area corresponding mainly to factor 3 from an area represented by factor 2 (Figs. 8 and 9). Factor 1 is highly correlated to the silicate content and

SST and, to a lesser extent, to phosphate, SSS and nitrate (Table 3).

4.3.2. *Factor 2*

Gephyrocapsa sp. < 3 µm*, E. huxleyi, C. pelagicus* and *G. muellerae* (Table 2) are the main score species contributing to this factor, which explains 33.9% of the total variance. This factor is strongly anticorrelated to SST and to SSS, and to a lesser extent to silicate content (Table 3). It is dominant off the Chilean upwelling, in the Fjords region (38°S to 47°S, Figs. 8 and 9), in an area where upwelling is prevented due to the yearly onshore blowing winds (Miller, 1976; Strub et al., 1998; Kim et al., 2002), and where low-salinity water masses flow to the North along the southern and central Chilean margin (Kaiser et al., 2005). In this area, dilution is higher in comparison to the northern part offshore the Chilean upwelling.

4.3.3. *Factor 3*

This factor explains 28.2% of the total variance. Its major contributors are *H. carteri* and *C. leptoporus* (Table 2). It predominates from 25° to 33°S (Figs. 8 and 9), a zone of coastal upwelling driven by persistent southeastern winds, resulting in an upward flow of subsurface waters (Shaffer et al., 1995). This factor is also important at two stations south of the study area, where a strong increase in *C. leptoporus* occurs due to the proximity of the South Antarctic Zone region (Gravalosa et al., 2008). This factor is correlated to SSS and anticorrelated to phosphate and nitrate (Table 3).

5. Ecological preferences of the dominant taxa

Concerning the accuracy of the results obtained with factor analysis, it is worth to take into account that the distribution of samples is inhomogeneous, and they are mainly lined up in a N–S direction relatively close to the American coast. Furthermore, preservational factors may control the abundance of species at some stations, mainly in eutrophic environments, owing to the fact that underneath high productive zones degradational processes of organic matter may favour enhanced carbonate dissolution (Boeckel and Baumann, 2004). Factors are commented separately in the following lines.

5.1. *Factor 1*: Florisphaera profunda *and* Gephyrocapsa oceanica

The distribution of *G. oceanica* mirrors warm water masses, as already reported by Brand (1994) and Roth (1994), and also shows a high affinity for fertile waters (Giraudeau, 1992). High abundances of this taxon are located in Equatorial areas where there is a high Primary Productivity (Antoine and Morel, 1996; Abrantes et al., 2007), but its percentage decreases gradually to the South. The local increase in the relative abundance of this taxon in the coastal upwelling of Chile can be explained by the fact that this species is resistant to dissolution, and its relative abundance is passively enhanced by the dissolution of other, more delicate species. Furthermore, *G. oceanica* reacts rapidly to elevated nutrient conditions by an increase in population size (Kleijne et al., 1989).

F. profunda is a lower photic zone inhabitant (Okada and Honjo, 1973). Little is known about the ecology of this species, but it has been reported that its distribution is associated with low-light conditions (Cortés et al., 2001), elevated nutrient contents (Brand, 1994), sea water transparency and/or turbidity (Ahagon et al., 1993), and lower euphotic zone temperature (Okada and Wells, 1997). Fluctuations in *F. profunda* have been used to interpret past changes in the thermocline and nutricline (Molfino and McIntyre, 1990b) and in productivity (Beaufort et al., 1997, 2001). In the study area, *F. profunda* is abundant in the Inter-Tropical Converge Zone, where low SSS and high stratification of the upper ocean waters occur off Panama (Strub et al., 1998). The highest relative abundances have been recorded in the Panama basin, similar to the results of Martínez et al. (2005) in this area. Drops in the abundance of *F. profunda* can be related to a shallower position of the nutricline (Molfino and McIntyre, 1990a, 1990b), especially in areas outside upwelling zones (Fig. 5(3)). This species shows very low abundance values close to 50°S (Fig. 9). In our samples, specimens of *F. profunda* var. *profunda* were recorded as more abundant than the other variety (Okada and Honjo, 1973; Okada and McIntyre, 1977, 1979, 1980; Quinn et al., 2005).

Broadly, high values of factor 1 are recorded in the Equatorial region and in the area from ~33°S to 38°S. However, the high values offshore Chile might be related to intense dissolution in this region, and to the fact that *G. oceanica* and *F. profunda* are robust species (selective preservation). In fact, in the dissolution area from 35.5°S to 39°S important dissolution in the water column has been already inferred on the basis of LM observations (Fig. 3(1)). This area also corresponds to the most intense and persistent upwelling activity in central Chile described by Strub et al. (1998). The interference of carbonate dissolution at the sediment-water interface was already noted with planktonic foraminifera by Mohtadi et al. (2005) from 36°S to 38°S.

5.2. *Factor 2:* Gephyrocapsa *sp. < 3 µm,* Emiliania huxleyi*,* Coccolithus pelagicus *and* Gephyrocapsa muellerae

Confusion is possible in LM between *E. huxleyi* and *Gephyrocapsa* sp. < 3 µm. Both taxa, however, have been grouped as co-occurring in the same factor. In the study area, *Gephyrocapsa* sp. < 3 µm shows affinity for low-salinity and high-nutrient water masses in a region in which upwelling does not occur. *G. ericsonii,* which is here considered as the equivalent of *Gephyrocapsa* sp. < 3 µm, was observed in low-temperature waters (16–20 °C) in the Southern California Bight (Ziveri et al., 1995). Apparently, this taxon does not show preference for a narrow salinity range, although it is limited by nutrients, basically nitrates (Cortés et al., 2001). Boeckel and Baumann (2004) reported that elevated percentages of *G. ericsonii* could be attributed to intermediate-to-low nutrient conditions in surface waters, in agreement with Giraudeau and Bailey (1995), who stated that this species was more abundant in stratified, warm oceanic waters. *E. huxleyi* does not show a clear distribution pattern as *Gephyrocapsa* sp. < 3 µm, because *E. huxleyi* reaches abundance maxima in upwelling and oligotrophic areas, suggesting an adaptation to a wide range of environmental conditions and a cosmopolitan behaviour, already described by many authors (Geitzenauer et al., 1977; Tanaka, 1991; Brand, 1994; Roth, 1994; Winter et al., 1994). Specimens of this species occur in broad temperature ranges from 1 °C to 31 °C, and in a salinity range from 10‰ to 20‰ (Bukry, 1974) and from 40‰ to 45‰ (Winter et al., 1979; Winter, 1982). Recognition of different morphotypes of *E. huxleyi* referred to as Types A, B and C (Young and Westbroek, 1991) was done. The presence of Types A and B in the studied samples has been observed in SEM; conversely Type C was not recorded, probably due to preservational factors. Type C is characterized by coccoliths with small size and shield elements that are well-separated. This morphology is responsible for the susceptibility to dissolution of Type C coccoliths which provide a distinctive delicate appearance to the coccolith (Young and Westbroek, 1991). More detailed morphometric studies are needed for a better understanding of morphological patterns of this species in the study area.

G. muellerae shows a preference for very cold and relatively high productivity water masses off southern Chile, and maxima in abundance of this species appear in the Fjord zone (Fig. 9). This observation is in agreement with Boeckel and Baumann (2004), who recorded this species in association with *Gephyrocapsa* spp. and *C. pelagicus* under elevated nutrient conditions in the Southeastern South Atlantic.

C. pelagicus is recorded in the Chilean upwelling linked to high fertility and low temperature environments (Fig. 9). It is a robust species living within polar and subpolar water masses from the North Atlantic (McIntyre and Bé, 1967; Baumann et al., 2000); it has been generally considered as a cold water proxy (McIntyre and Bé, 1967; McIntyre et al., 1970). It has also been recorded in other upwelling regions, such as the Portuguese shelf (Cachão and Moita, 2000), and off North West Africa (Blasco et al., 1980).

High marine productivity in the region where factor 2 dominates is mainly related to high continental runoff and an important supply of micro-nutrients (basically iron) to coastal regions, and to the delivery of macro-nutrients such as phosphate and nitrate by the ACC (Conkright et al., 1994). These are assumed to be the most important nutrients for coccolithophores (Brand, 1994).

5.3. *Factor 3:* Helicosphaera carteri *and* Calcidiscus leptoporus

In the study area, the contour map of *H. carteri* indicates a weak preference for high salinity, low-nutrient content, owing to the maximum percentages reached in central and north offshore Chile (Figs. 6(1) and 9). We suggest that this species is adapted to mesotrophic watermasses, in agreement with Ziveri et al. (2004). The absence of *H. carteri* in the oligotrophic gyres was also reported by Knappertsbusch (1993) and Ziveri et al. (2004). Ecological preferences of *H. carteri* are rather complex; this has been classically regarded as a coastal taxon and as a marker of high-to-moderate nutrient levels and turbidity (Giraudeau, 1992; Ziveri et al., 1995), but it has been also related to freshwater in the upper layer and hence to low salinity conditions (Colmenero-Hidalgo et al., 2004). The presence of *H. carteri* in upwelling areas was observed in San Pedro Basin (Ziveri et al., 1995) and in Guaymas Basin in the Gulf of California (Ziveri and Thunell, 2000), associated with low to intermediate nutrient concentrations.

Calcidiscus leptoporus presents a fairly similar distribution with respect to *H. carteri* (Figs. 5(5) and 9), and it is dominant in the region of enhanced upwelling offshore Chile, and south of the study area. Some authors did not record any significant correlation between environmental parameters and the abundance of *C. leptoporus* (Renaud and Klaas, 2001), but others have stated that intraspecific groups exhibit geographic and temporal differences that reflect variations in morphotype ecology (Kleijne, 1993; Knappertsbusch et al., 1997; Baumann et al., 2000; Baumann and Sprengel, 2000; Renaud et al., 2002; Quinn et al., 2004; Boeckel et al., 2006). Recent research, combining biometric data and qualitative observations of coccolith ultrastructure, has led to a three-fold division of the extant *Calcidiscus* population (e.g., Young et al., 2003; Quinn et al., 2004), namely *C. quadriperforatus* (large), *C. leptoporus* (intermediate) and *C. leptoporus* (small). They differ in geographical distribution, ecological preferences and perhaps in life cycles (Quinn et al., 2004). Larger coccospheres of *C. leptoporus* are restricted to tropical and subtropical latitudes (McIntyre et al., 1970; Knappertsbusch, 1990; Kleijne, 1993; Knappertsbusch et al., 1997); the intermediate-size morphotype has a more cosmopolitan distribution (Kleijne, 1993; Knappertsbusch et al., 1997) with an affinity for cool, nutrient-poor waters; but the ecology of the small-size form is unclear, as it shows a patchy distribution (Ziveri et al., 2004). In our study area offshore Chile, the intermediate-size morphotype of *C. leptoporus* is the most abundant, but a more exhaustive study is needed to check whether there is any biogeographic significance of the morphotypes of this species. It is worth to note that the three morphotypes of *C. leptoporus* were recently raised to the species rank (Sáez et al., 2003).

Regarding the geographical distribution of factor 3 (Fig. 8), it should be considered that besides the eutrophic conditions in the surface water masses, the composition of coccolithophore assemblages in the core-tops could have been also biased by dissolution processes (Boeckel et al., 2006). In fact, high productivity in the upper water column can generate large amount of organic matter exported to the sediments. Subsequent, degradation of this excess organic matter by organisms which live within the sediment produces CO_2. This metabolic CO_2 contributes to the dissolution of calcite even above the lysocline (Emerson and Bender, 1981; Jahnke et al., 1994; Freiwald, 1995). Values of CEX' index are lower than 0.6 offshore Chile (~20°S to ~34°S). This would lead us to think that the prone-to-dissolution taxa disappeared and dissolution-resistant species record (*H. carteri* and *C. leptoporus*) was enhanced. However, in the area where factor 3 dominates, sedimentation rates are relatively low (0.06–0.17 m/kyr; values from Lamy et al., 1999; Mohtadi and Hebbeln, 2004) as compared to those situated further south in the study area. The organic carbon content in a latitudinal transect from 25°S to 45°S (Hebbeln et al., 2000) is relatively low ($C_{org} < 1.4\%$) in marine sediments, and increases notably around 35°S and 36°S ($C_{org} > 1.8\%$) coinciding with the area where factor 1 dominates offshore Chile (Hebbeln et al., 2000). These measurements allowed us to confirm the border between factor 3 and 1, which marks a transition from an area of moderate-to-high productivity and moderate dissolution rate (in factor 3 moderate-to-good preservation of coccoliths was observed in LM) to an area of high productivity and high dissolution rate, corresponding to factor 1. Hence, we suggest that the *C. leptoporus* and *H. carteri* dominance within factor 3 is depending on paleoenvironmental conditions rather than on dissolution.

5.4. Few notes about rare species: Umbilicosphaera *spp.,* Syracosphaera *spp. and* Rhabdosphaera clavigera

Some rare taxa will not be discussed, owing to their low abundances (i.e., *Umbellosphaera* spp., *Calciosolenia* sp.) or their tendency towards dissolution (i.e., *Oolithotus* sp.). Regarding the rest of rare species, *Umbilicosphaera* spp. is recorded in this work in areas of low primary productivity in tropical and Equatorial areas, where it reaches its highest relative abundances (Fig. 6(3)). *Umbilicosphaera foliosa* and *U. sibogae* were not differentiated in LM in this study, but a dominance of *U. sibogae* over *U. foliosa* was observed in SEM. Ziveri et al. (2004) also considered these two species together, and recorded their highest occurrences at tropical to subtropical latitudes, close to the oligotrophic gyre in the Atlantic. However, these two species may have different ecological preferences: *U. foliosa* shows an affinity for mesotrophic conditions, whereas *U. sibogae* occurs under warmer and oligotrophic waters (Okada and McIntyre, 1979; Ziveri and Thunell, 2000; Boeckel and Baumann, 2004).

In the study area, *R. clavigera* and *Syracosphaera* spp. show both an affinity for nutrient-depleted, tropical-to-subtropical waters located mainly in the subtropical gyre. In oligotrophic areas characterized by well-stratified water masses, K-selected coccolithophore species (e.g., *Rhabdosphaera clavigera*) do not dominate the assemblage but occur in low percentages in assemblages characterized by a high species diversity. Haidar and Thierstein (2001) report that *R. clavigera* proliferates in warm waters depleted in nitrate. Conversely, *Syracosphaera* spp. shows a wider oceanic distribution (Boeckel et al., 2006), although some authors (Young, 1994; Andruleit and Rogalla, 2002) consider this taxon as an indicator of oligotrophic conditions.

6. Summary and conclusions

Our knowledge about coccolithophore biogeography is still limited and rather patchy. Although living and surface-sediment coccolithophore census were intensively studied in the Atlantic and North Pacific, only scattered research was done on coccolithophores in south Equatorial and Southeastern Pacific. This study reports on the different abundance distribution of various coccolithophore taxa in surface sediment samples from 15°N to 50°S and from 71°W to 93°W, with respect to different sea-surface oceanic conditions. It also complements previous research done in the study area using the same surface-samples but different microfossil groups, such as diatoms or planktic foraminifera (e.g., Mohtadi et al., 2005; Abrantes et al., 2007).

Although the exact age of the studied surface-sediment samples cannot be ascertained and may range from few centuries to thousand years, we can assume that the results of this study correspond to a present-day biogeographical distribution of coccolithophores for the study area. Contour distribution maps are produced for 14 taxa. The most abundant taxa, with averages between 60% and 10%, are: *Gephyrocapsa* sp. $< 3\ \mu m$, *F. profunda*, *E. huxleyi*, *G. oceanica*, *C. leptoporus* and *G. muellerae*. Rare taxa also occur, with average relative abundances lower that 10%. These include: *H. carteri*, *C. pelagicus*, *Umbilicosphaera* spp., *Oolithotus* sp., *Syracosphaera* spp., *R. clavigera*, *Calciosolenia* sp. and *Umbellosphaera* spp. SEM observations indicate the presence of *C. pelagicus* ssp. *braarudii* and rule out the presence of *C. pelagicus* ssp. *pelagicus* in the studied samples.

Carbonate dissolution of coccoliths is an important issue in the study area, especially in the main upwelling sites. To estimate it, two different dissolution indices were calculated. Lower CEX' values (< 0.6) appear from ~20°S to ~34°S, and the most important dissolution takes place from ~15.5°S to ~17°S and ~35.5°S to ~39°S, according to LM observations.

Factor Analysis applied to the whole dataset results in three significant factors that are well-related to oceanographic conditions in the study area. Factor 1 comprises the samples located under warm water masses (dominated by *F. profunda* and *G. oceanica*) and defines a dissolution area coinciding with the most intense and persistent upwelling activity offshore central Chile. Factor 2 receives contribution from *E. huxleyi*, *Gephyrocapsa* sp. $< 3\ \mu m$, *C. pelagicus* and *G. muellerae,* which have been related to cold, low-salinity surface water-masses offshore Chile. Factor 3 is linked to a more saline coastal upwelling dominated mainly by *C. leptoporus* and *H. carteri*.

Acknowledgements

B. Boeckel is greatly acknowledged for her assistance and the helpful suggestions that improved the original manuscript. A. Cortina kindly assisted in statistical analyses. The authors wish to thank O. Romero, A. Mix, F. Abrantes, D. Hebbeln and M. Mohtadi for the material supplied. Emanuela Mattioli, Jorijntje Henderiks and an anonymous reviewer are acknowledged for their critical evaluation, constructive opinion and helpful suggestions. This work was funded by Ministerio de Educación y Ciencia Project GRACCIE (CONSOLIDER-INGENIO CSD 2007-00067), by the MEC project CGL2006-10593, the Junta de Castilla y León GR34Project and a MEC FPU Grant (AP-2004-2374) awarded to Mariem Saavedra-Pellitero.

Appendix A

List of the coccolithophore taxa considered in this study.

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

Calciosolenia Gran, 1912 emend. Young et al., 2003

Coccolithus pelagicus (Wallich, 1877) Schiller, 1930

Coccolithus pelagicus ssp. *braarudii* (Gaarder, 1962) Geisen et al., 2000

Coccolithus pelagicus ssp. *pelagicus* (Wallich, 1877) Schiller, 1930

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

Florisphaera profunda Okada and Honjo, 1973

Gephyrocapsa ericsonii McIntyre and Bé, 1967

Gephyrocapsa muellerae Bréhéret, 1978

Gephyrocapsa oceanica Kamptner, 1943

Helicosphaera carteri (Wallich, 1877) Kamptner, 1954

Oolithotus (Cohen, 1964) Reinhardt in Cohen and Reinhardt, 1968

Rhabdosphaera clavigera (Murray and Blackman, 1898)

Syracosphaera Lohmann, 1902

Umbellosphaera Paasche in Markali and Paasche, 1955

Umbilicosphaera Lohmann, 1902

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.geobios.2009.09.004

References

Abrantes, F., Lopes, C., Mix, A., Pisias, N., 2007. Diatoms in Southeast Pacific surface sediments reflect environmental properties. Quaternary Science Reviews 26, 155–169.

Ahagon, N., Tanaka, Y., Ujiié, H., 1993. *Florisphaera profunda*, a possible nannoplankton indicator of late Quaternary changes in sea-water turbidity at the northwestern margin of the Pacific. Marine Micropaleontology 22, 255–273.

Andruleit, H., 1996. A filtration technique for quantitative studies of coccoliths. Micropaleontology 42, 403–406.

Andruleit, H., Rogalla, U., 2002. Coccolithophores in surface sediments of the Arabian Sea in relation to environmental gradients in surface waters. Marine Geology 186, 505–526.

Antoine, D., Morel, A., 1996. Oceanic Primary Production 1. Adaptation of a Spectral Light-Photosynthesis Model in view of application to satellite chlorophyll observations. Global Biogeochemical Cycles 10, 43–55.

Antonov, J.I., Locarnini, R.A., Boyer, T.P., Mishonov, A.V., Garcia, H.E., 2006. World Ocean Atlas 2005. In: Levitus, S. (Ed.), NOAA Atlas NESDIS 61. U.S. Government Printing Office, Washington, D.C.

Backman, J., Shackleton, N.J., 1983. Quantitative biochronology of Pliocene and early Pleistocene calcareous nannofossils from the Atlantic. Indian and Pacific Oceans. Marine Micropaleontology 8, 141–170.

Baumann, K.H., Andruleit, H., Samtleben, C., 2000. Coccolithophores in the Nordic Seas: comparison of living communities with surface sediment assemblages. Deep-Sea Research II: Topical Studies in Oceanography 47, 1743–1772.

Baumann, K.H., Boeckel, B., Frenz, M., 2004. Coccolith contribution to South Atlantic carbonate sedimentation. In: Thierstein, H.R., Young, J.R. (Eds.), Coccolithophores: from molecular processes to global impact. Springer-Verlag, Berlin, pp. 367–402.

Baumann, K.H., Cepek, M., Kinkel, H., 1999. Coccolithophores as indicators of ocean water masses, surface-water temperature, and paleoproductivity-examples from the South Atlantic. In: Fischer, G., Wefer, G. (Eds.), Use of Proxies in Paleoceanography: Examples from the South Atlantic. Springer-Verlag, Berlin, pp. 117–144.

Baumann, K.H., Sprengel, C., 2000. Morphological variations of selected coccolith species in a sediment trap north of the Canary Islands. Journal of Nannoplankton Research 22, 185–193.

Beaufort, L., 1991. Adaptation of the random settling method for quantitative studies of calcareous nannofossils. Micropaleontology 37, 415–418.

Beaufort, L., de Garidel-Thoron, T., Mix, A.C., Pisias, N.G., 2001. ENSO-like forcing on Oceanic Primary Production during the Late Pleistocene. Science 293, 2440–2444.

Beaufort, L., Lancelot, Y., Camberlin, P., Cayre, O., Vincent, E., Bassinot, F., Labeyrie, L., 1997. Insolation cycles as a major control of Equatorial Indian Ocean primary production. Science 278, 1451–1454.

Berger, W.H., Adelseck, C.G., Mayer, L.A., 1976. Distribution of carbonate in surface sediments of the Pacific Ocean. Journal of Geophysical Research 81, 2617–2627.

Berger, W.H., Bonneau, M.C., Parker, F.L., 1982. Foraminifera on the deep-sea floor: lysocline and dissolution rate. Oceanologica Acta 5, 249–258.

Blasco, D., Estrada, M., Jones, B., 1980. Relationship between the phytoplankton distribution and composition and the hydrography in the northwest African upwelling region near Cabo Corbeiro. Deep-Sea Research A: Oceanographic Research Papers 27, 799–821.

Boeckel, B., Baumann, K.-H., 2004. Distribution of coccoliths in surface sediments of the south-eastern South Atlantic Ocean: ecology, preservation and carbonate contribution. Marine Micropaleontology 51, 301–320.

Boeckel, B., Baumann, K.-H., Henrich, R., Kinkel, H., 2006. Coccolith distribution patterns in South Atlantic and Southern Ocean surface sediments in relation to environmental gradients. Deep-Sea Research I: Oceanographic Research Papers 53, 1073–1099.

Bollmann, J., Brabec, B., Cortés, M.Y., Geisen, M., 1999. Determination of absolute coccolith abundances in deep-sea sediments by spiking with microbeads and spraying (SMS-method). Marine Micropaleontology 38, 29–38.

Bollmann, J., Cortés, M.Y., Haidar, A.T., Brabec, B., Close, A., Hofmann, R., Palma, S., Tupas, L., Thierstein, H.R., 2002. Techniques for quantitative analyses of calcareous marine phytoplankton. Marine Micropaleontology 44, 163–185.

Brand, L.E., 1994. Physiological ecology of marine coccolithophores. In: Winter, A., Siesser, W.G. (Eds.), Coccolithophores. Cambridge University Press, Cambridge, pp. 39–49.

Broecker, W.S., Broecker, S., 1974. Carbonate dissolution on the western flank of the East Pacific Rise. In: Hay, W.W. (Ed.), Studies in Pale-Oceanography. Society of Economic Paleontologists and Mineralogists Special Publication, Tulsa, pp. 44–57.

Bryden, H.L., Brady, E.C., 1985. Diagnostic model of the three-dimensional circulation in the upper Equatorial Pacific Ocean. Journal of Physical Oceanography 15, 1255–1273.

Bukry, D., 1974. Coccoliths as paleosalinity indicators-evidence from the Black Sea. Memoirs of the American Association of Petroleum Geologists 20, 353–363.

Cachão, M., Moita, M.T., 2000. *Coccolithus pelagicus*, a productivity proxy related to moderate fronts off Western Iberia. Marine Micropaleontology 39, 131–155.

Colmenero-Hidalgo, E., Flores, J.-A., Sierro, F.J., Bárcena, M.Á., Löwemark, L., Schönfeld, J., Grimalt, J.O., 2004. Ocean surface water response to short-term climate changes revealed by coccolithophores from the Gulf of Cadiz (NE Atlantic) and Alboran Sea (W Mediterranean). Palaeogeography, Palaeoclimatology, Palaeoecology 205, 317–336.

Conkright, M.E., Boyer, T.P., 2002. World Ocean Atlas 2001: Objective Analyses, Data Statistics, and Figures. In: CD-ROM Documentation, National Oceanographic Data Center, Washington, D.C.

Conkright, M.E., Levitus, S., Boyer, T.P., 1994. World Ocean Atlas 1994. NOAA Atlas NESDIS 1, U.S. Department of Commerce, Washington, D.C.

Cortés, M.Y., Bollmann, J., Thierstein, H.R., 2001. Coccolithophore ecology at the HOT station ALOHA. Hawaii. Deep-Sea Research II: Topical Studies in Oceanography 48, 1957–1981.

Dittert, N., Baumann, K.H., Bickert, T., Henrich, R., Kinkel, H., Meggers, H., 1999. Proxies for carbonate dissolution. In: Fischer, G., Wefer, G. (Eds.), Proxies in Paleoceanography: Examples From the South Atlantic. Springer-Verlag, Berlin, pp. 255–284.

Emerson, S., Bender, M., 1981. Carbon fluxes at the sediment-water interface of the deep-sea: calcium carbonate preservation. Journal of Marine Research 39, 139–162.

Farrell, J.W., Prell, W.L., 1989. Climatic change and $CaCO_3$ preservation: an 800,000 year bathymetric reconstruction from the Central Equatorial Pacific Ocean. Paleoceanography 4, 447–466.

Feldberg, M.J., Mix, A.C., 2002. Sea-surface temperature estimates in the Southeast Pacific based on planktonic foraminiferal species; modern calibration and Last Glacial Maximum. Marine Micropaleontology 44, 1–29.

Flores, J.A., Marino, M., 2002. Pleistocene calcareous nannofossil stratigraphy for ODP Leg 177 (Atlantic sector of the Southern Ocean). Marine Micropaleontology 45, 191–224.

Flores, J.A., Sierro, F.J., 1997. Revised technique for calculation of calcareous nannofossil accumulation rates. Micropaleontology 43, 321–324.

Flores, J.A., Sierro, F.J., Francés, G., Vázquez, A., Zamarreño, I., 1997. The last 100,000 years in the western Mediterranean: sea surface water and frontal dynamics as revealed by coccolithophores. Marine Micropaleontology 29, 351–366.

Freiwald, A., 1995. Bacteria-induced carbonate degradation; a taphonomic case study of Cibicides lobatulus from a high-boreal carbonate setting. Palaios 10, 337–346.

Garcia, H.E., Locarnini, R.A., Boyer, T.P., Antonov, J.I., Mishonov, A.V., 2006. World Ocean Atlas 2005. In: Levitus, S. (Ed.), NOAA Atlas NESDIS 61. U.S. Government Printing Office, Washington, D.C, p. 396.

Geisen, M., Bollmann, J., Herrle, J.O., Mutterlose, J., Young, J.R., 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45, 437–442.

Geisen, M., Billard, C., Broerse, A.T.C., Cros, L., Probert, I., Young, J., 2002. Life-cycle associations involving pairs of holococcolithophorid species: intraspecific variation or cryptic speciation? European Journal of Phycology 37, 531–550.

Geitzenauer, K.R., Roche, M.B., McIntyre, A., 1977. Coccolith biogeography from North Atlantic and Pacific surface sediments; a comparison of species distribution and abundances. In: Ramsay, A.T.S. (Ed.), Oceanic Micropaleontology. Academic Press, London, pp. 973–1008.

Giraudeau, J., 1992. Distribution of Recent nannofossils beneath the Benguela system: Southwest African continental margin. Marine Geology 108, 219–237.

Giraudeau, J., Bailey, G.W., 1995. Spatial dynamics of coccolithophore communities during an upwelling event in the Southern Benguela system. Continental Shelf Research 15, 1825–1852.

Goovaerts, P., 1997. Geostatistics for Natural Resources Evaluation. In: Applied Geostatistics Series, Oxford University Press, New York.

Gravalosa, J.M., Flores, J.-A., Sierro, F.J., Gersonde, R., 2008. 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. Marine Micropaleontology 69, 16–25.

Hagino, K., Okada, H., 2004. Floral response of coccolithophores to progressive oligotrophication in the South Equatorial Current, Pacific Ocean. In: Shiyomi, M., Kawahata, H., Koizumi, H., Tsuda, A., Awaya, Y. (Eds.), Global Environmental Change in the Ocean and on Land. TERRAPUB, Tokyo, pp. 121–132.

Hagino, K., Okada, H., Matsuoka, H., 2000. Spatial dynamics of coccolithophore assemblages in the Equatorial Western-Central Pacific Ocean. Marine Micropaleontology 39, 53–72.

Haidar, A.T., Thierstein, H.R., 2001. Coccolithophore dynamics off Bermuda (N. Atlantic). Deep-Sea Research II: Topical Studies in Oceanography 48, 1925–1956.

Hair, J.F., Anderson, R.E., Tatham, R.L., Black, W.C., 1992. Multivariate Data Analysis with Readings. Macmillan Publishing Company, New York.

Hebbeln, D., Marchant, M., Freudenthal, T., Wefer, G., 2000. Surface sediment distribution along the Chilean continental slope related to upwelling and productivity. Marine Geology 164, 119–137.

Henderiks, J., Törner, A., 2006. Reproducibility of coccolith morphometry: Evaluation of spraying and smear slide preparation techniques. Marine Micropaleontology 58, 207–218.

Henriksson, A., 1993. A quick and easy method for estimating absolute abundances of calcareous nannofossils. INA Newsletter 15, 68.

Herrle, J.O., Bollmann, J., 2004. Accuracy and reproducibility of absolute nannoplankton abundances using the filtration technique in combination with a rotary sample splitter. Marine Micropaleontology 53, 389–404.

Huyer, A., Knoll, M., Paluszkiewicz, T., Smith, R.L., 1991. The Peru undercurrent: A study in variability. Deep-Sea Research A: Oceanographic Research Papers 38, 247–271.

Jahnke, R.A., Craven, D.B., Gaillard, J.F., 1994. The influence of organic matter diagenesis on $CaCO_3$ dissolution at the deep-sea floor. Geochimica et Cosmochimica Acta 58, 2799–2809.

Jordan, R.W., Cros, L., Young, J.R., 2004. A revised classification scheme for living haptophytes. Micropaleontology 50, 55–79.

Jordan, R.W., Kleijne, A., 1994. A classification system for living Coccolithophores. In: Winter, A., Siesser, W.G. (Eds.), Coccolithophores. Cambridge University Press, Cambridge, pp. 83–105.

Kaiser, J., Lamy, F., Hebbeln, D., 2005. A 70-kyr sea surface temperature record off southern Chile (Ocean Drilling Program Site 1233). Paleoceanography 20, PA4009, doi:10.1029/2005PA001146.

Kim, J.-H., Schneider, R.R., Hebbeln, D., Müller, P.J., Wefer, G., 2002. Last deglacial sea-surface temperature evolution in the Southeast Pacific compared to climate changes on the South American continent. Quaternary Science Reviews 21, 2085–2097.

Kleijne, A., 1993. Morphology, taxonomy and distribution of extant coccolithophores (calcareous nannoplankton). PhD Thesis, Vrije Universiteit, Amsterdam (unpublished).

Kleijne, A., Kroon, D., Zevenboom, W., 1989. Phytoplankton and foraminiferal frequencies in northern Indian Ocean and Red Sea surface waters. Netherlands Journal of Sea Research 24, 531–539.

Knappertsbusch, M., 1990. Geographic distribution of modern coccolithophorids in the Mediterranean Sea and morphologic evolution of *Calcidiscus leptoporus*. PhD Dissertation, ETH, Zurich.(unpublished).

Knappertsbusch, M., 1993. Geographic distribution of living and Holocene coccolithophores in the Mediterranean Sea. Marine Micropaleontology 21, 219–247.

Knappertsbusch, M., Cortes, M.Y., Thierstein, H.R., 1997. Morphologic variability of the coccolithophorid *Calcidiscus leptoporus* in the plankton, surface sediments and from the Early Pleistocene. Marine Micropaleontology 30, 293–317.

Koch, C., Young, J.R., 2007. A simple weighing and dilution technique for determining absolute abundances of coccoliths from sediment samples. Journal of Nannoplankton Research 29, 67–69.

Lamy, F., Hebbeln, D., Röhl, U., Wefer, G., 2001. Holocene rainfall variability in southern Chile: a marine record of latitudinal shifts of the Southern Westerlies. Earth and Planetary Science Letters 185, 369–382.

Lamy, F., Hebbeln, D., Wefer, G., 1998a. Terrigenous sediment supply along the Chilean continental margin: modern regional patterns of texture and composition. Geologische Rundschau 87, 477–494.

Lamy, F., Hebbeln, D., Wefer, G., 1998b. Late Quaternary precessional cycles of terrigenous sediment input off the Norte Chico, Chile (27.5°S) and palaeoclimatic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 141, 233–251.

Lamy, F., Hebbeln, D., Wefer, G., 1999. High-resolution marine record of climatic change in mid-latitude Chile during the last 28,000 years based on terrigenous sediment parameters. Quaternary Research 51, 83–93.

Lamy, F., Rühlemann, C., Hebbeln, D., Wefer, G., 2002. High- and low-latitude climate control on the position of the southern Peru-Chile Current during the Holocene. Paleoceanography 17. doi:10.1029/2001PA000727.

Levitus, S.E., 1982. Climatological atlas of the world ocean. NOAA Professional Paper 13, U.S. Government Printing Office, Washington D.C.

Locarnini, R.A., Mishonov, A.V., Antonov, J.I., Boyer, T.P., Garcia, H.E., 2006. World Ocean Atlas 2005. In: Levitus, S. (Ed.), NOAA Atlas NESDIS 61. U.S. Government Printing Office, Washington, D.C.

Marchant, M., 1997. Rezente und spätquartäre Sedimentation planktischer Foraminiferen im Peru-Chile Strom. PhD Thesis, Universität Bremen.(unpublished).

Martínez, I., Rincon, D., Yokoyama, Y., Barrows, T., 2005. Foraminifera and coccolithophorid assemblage changes in the Panama Basin during the last deglaciation: Response to sea-surface productivity induced by a transient climate change. Palaeogeography, Palaeoclimatology, Palaeoecology 234, 114–126.

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, M.B., 1970. Modern Pacific Coccolithophorida: a paleontological thermometer. Transactions of the New York Academy of Sciences, Series II 32, 720–731.

Miller, A., 1976. The climate of Chile. In: Schwerdtfeger, W.E. (Ed.), World Survey of Climatology. Climates of Central and South America. Elsevier, Amsterdam, pp. 113–145.

Mix, A.C., Morey, A.E., Pisias, N.G., Hostetler, S.W., 1999. Foraminiferal faunal estimates of paleotemperature: circumventing the no-analog problem yields cool ice age tropics. Paleoceanography 14, 350–359.

Mohtadi, M., Hebbeln, D., 2004. Mechanisms and variations of the paleoproductivity off northern Chile (24°S–33°S) during the last 40,000 years. Paleoceanography 19, doi:10.1029/2004PA001003.

Mohtadi, M., Hebbeln, D., Marchant, M., 2005. Upwelling and productivity along the Peru-Chile Current derived from faunal and isotopic compositions of planktic foraminifera in surface sediments. Marine Geology 216, 107–126.

Mohtadi, M., Romero, O.E., Kaiser, J., Hebbeln, D., 2007. Cooling of the southern high latitudes during the Medieval Period and its effect on ENSO. Quaternary Science Reviews 26, 1055–1066.

Molfino, B., McIntyre, A., 1990a. Nutricline variation in the Equatorial Atlantic coincident with the younger dryas. Paleoceanography 5, 997–1008.

Molfino, B., McIntyre, A., 1990b. Precessional forcing of nutricline dynamics in the Equatorial Atlantic. Science 249, 766–769.

Okada, H., 1992. Use of microbeads to estimate the absolute abundance of nannofossils. INA Newsletter 14, 96–97.

Okada, H., Honjo, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. Deep-Sea Research 20, 355–374.

Okada, H., Honjo, S., 1975. Distribution of coccolithophores in marginal seas along the western Pacific Ocean and in the Red Sea. Marine Biology 31, 271–285.

Okada, H., McIntyre, A., 1977. Modern coccolithophores of the Pacific and North Atlantic oceans. Micropaleontology 23, 1–54.

Okada, H., McIntyre, A., 1979. Seasonal distribution of modern coccolithophores in the western North Atlantic Ocean. Marine Biology 54, 319–328.

Okada, H., McIntyre, A., 1980. Validation of *Florisphaera profunda*, var. *elongata* (2). International Nannoplankton Association Newsletter 2, 81.

Okada, H., Wells, P., 1997. Late Quaternary nannofossil indicators of climate change in two deep-sea cores associated with the Leeuwin Current off Western Australia. Palaeogeography, Palaeoclimatology. Palaeoecology 131, 413–432.

Pena, L.D., Cacho, I., Ferretti, P., Hall, M.A., 2008. El Niño-Southern Oscillation-like variability during glacial terminations and interlatitudinal teleconnections. Paleoceanography 23, PA3101, doi:10.1029/2008PA001620.

Quinn, P.S., Cortés, M.Y., Bollmann, J., 2005. Morphological variation in the deep ocean-dwelling coccolithophore *Florisphaera profunda* (Haptophyta). European Journal of Phycology 40, 123–133.

Quinn, P.S., Sáez, A.G., Baumann, K.H., Steel, B.A., Sprengel, C., Medlin, L.K., 2004. Coccolithophorid biodiversity: evidence from the cosmopolitan species *Calcidiscus leptoporus*. In: Thierstein, H.R., Young, J.R. (Eds.), Coccolithophores, from molecular processes to global impact. Springer-Verlag, Berlin, pp. 299–326.

Renaud, S., Klaas, C., 2001. Seasonal variations in the morphology of the coccolithophore *Calcidiscus leptoporus* off Bermuda (N. Atlantic). Journal of Plankton Research 23, 779–795.

Renaud, S., Ziveri, P., Broerse, A.T.C., 2002. Geographical and seasonal differences in morphology and dynamics of the coccolithophore *Calcidiscus leptoporus*. Marine Micropaleontology 46, 363–385.

Rojas de Mendiola, B., 1981. Seasonal phytoplankton distribution along the Peruvian Coast. In: Richards, F.A.E. (Ed.), Coastal Upwelling. Coastal Estuarine Studies. American Geophysical Union, Washington, pp. 339–347.

Rost, B., Riebesell, U., 2004. Coccolithophore calcification and the biological pump: response to environmental changes. In: Thierstein, H.R., Young, J.R. (Eds.), Coccolithophores: from molecular processes to global impact. Springer-Verlag, Berlin, pp. 99–125.

Roth, P.H., 1994. Distribution of coccoliths in oceanic sediments. In: Winter, A., Siesser, W.G. (Eds.), Coccolithophores. Cambridge University Press, Cambridge, pp. 199–218.

Roth, P.H., Coulbourn, W.T., 1982. Floral and solution patterns of coccoliths in surface sediments of the North Pacific. Marine Micropaleontology 7, 1–52.

Sáez, A.G., Probert, I., Quinn, P.S., Young, J.R., Geisen, M., Medlin, L.K., 2003. Pseudo-cryptic speciation in coccolithophores. Proceedings of the National Academy of Sciences of the United States of America 100, 7163–7168.

Samtleben, C., Schröder, A., 1992. Living coccolithophore communities in the Norwegian-Greenland Sea and their record in sediments. Marine Micropaleontology 19, 333–354.

Shaffer, G., Salinas, S., Pizarro, O., Vega, A., Hormazabal, S., 1995. Currents in the deep ocean off Chile (30°S). Deep-Sea Research I: Oceanographic Research Papers 42, 425–436.

Steinmetz, J.C., 1994. Sedimentation of coccolithophores. In: Winter, A., Siesser, W.G. (Eds.), Coccolithophores. Cambridge University Press, Cambridge, pp. 179–197.

Stoll, H.M., Ziveri, P., 2002. Separation of monospecific and restricted coccolith assemblages from sediments using differential settling velocity. Marine Micropaleontology 46, 209–221.

Strub, P.T., Mesías, J.M., Montecino, V., Ruttlant, J., Salinas, S., 1998. Coastal ocean circulation off Western South America. In: Robinson, R., Brink, K.H. (Eds.), The Global Coastal Ocean. Regional Studies and Syntheses. Wiley and Sons, New York, pp. 273–315.

Tanaka, Y., 1991. Calcareous nannoplankton thanatocoenoses in surface sediments from seas around Japan. Science Reports, Tohoku University. Geology 61, 127–198.

Thierstein, H.R., 1980. Selective dissolution of late cretaceous and earliest tertiary calcareous nannofossils: Experimental evidence. Cretaceous Research 1, 165–176.

Thomas, A.C., Carr, M.E., Strub, P.T., 2001. Chlorophyll variability in eastern boundary currents. Geophysical Research Letters 28, 3421–3424.

Thompson, P.R., 1976. Planktonic foraminiferal dissolution and the progress towards a Pleistocene Equatorial Pacific transfer function. Journal of Foraminiferal Research 6, 208–227.

Toggweiler, J.R., Dixon, K., Broecker, W.S., 1991. The Peru Upwelling and the Ventilation of the South Pacific Thermocline. Journal of Geophysical Research 96, 20467–20497.

Weber, M.E., Wiedicke, M., Riech, V., Erlenkeuser, H., 1995. Carbonate preservation history in the Peru Basin: Paleoceanographic implications. Paleoceanography 10, 775–800.

Wei, W., 1988. A new technique for preparing quantitative nannofossil slides. Journal of Paleontology 62, 472–473.

Williams, J.R., Bralower, T.J., 1995. Nannofossil assemblages, fine fraction stable isotopes, and the paleoceanography of the Valanginian-Barremian (Early Cretaceous) North Sea Basin. Paleoceanography 10, doi:10.1029/95pa00977.

Winter, A., 1982. Paleoenvironmental interpretation of the Quaternary coccolith assemblages from the Gulf of Aqaba (Elat), Red Sea. Revista Española de Micropaleontología 14, 291–314.

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. 161–178.

Winter, A., Reiss, Z., Luz, B., 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat (Aqaba). Marine Micropaleontology 4, 197–223.

Wooster, W.S., Reid, J.L., 1963. Eastern boundary currents. In: Hill, M.N. (Ed.), The Sea. Interscience Publications, New York, pp. 253–280.

Wyrtki, K., 1965. Surface currents of the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Communications Bulletin 4, 271–304.

Wyrtki, K., 1981. An estimate of Equatorial upwelling in the Pacific. Journal of Physical Oceanography 11, 1205–1214.

Young, J.R., 1994. Functions of coccoliths. In: Winter, A., Siesser, W.G. (Eds.), Coccolithophores. Cambridge University Press, Cambridge, pp. 63–82.

Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., Østergaard, J., 2003. A guide to extant coccolithophore taxonomy. Journal of Nannoplankton Research, Special Issue 1.

Young, J.R., Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. Marine Micropaleontology 18, 5–23.

Ziveri, P., Baumann, K.H., Boeckel, B., Bollmann, J., Young, J.R., 2004. Biogeography of selected Holocene coccoliths in the Atlantic Ocean. In: Thierstein, H.R., Young, J.R. (Eds.), Coccolithophores, from molecular processes to global impact. Springer-Verlag, Berlin, pp. 403–428.

Ziveri, P., Thunell, R.C., 2000. Coccolithophore export production in Guaymas Basin, Gulf of California: response to climate forcing. Deep-Sea Research II: Topical Studies in Oceanography 47, 2073–2100.

Ziveri, P., Thunell, R.C., Rio, D., 1995. Export production of coccolithophores in an upwelling region: Results from San Pedro Basin, Southern California Borderlands. Marine Micropaleontology 24, 335–358.

Zuta, S., Guillen, O., 1970. Oceanografía de las Aguas Costeras del Perú. Boletín Instituto del Mar del Perú-Callao 2, 161–323.