Coccolithus pelagicus, a productivity proxy related to moderate fronts off Western Iberia

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Abstract

The traditional interpretation of *Coccolithus pelagicus* as a cold water proxy is examined based on its distribution patterns in the water column off the Portuguese coast (using data from eleven cruises) and in Holocene surface sediment samples and Quaternary cores from the same region.

Coccolithus pelagicus is common in the Portuguese upwelling system, an area where surface waters are predominantly of subtropical origin. Although revealing an affinity for low temperature upwelled waters, the species was found in waters up to 18°C associated with riverine plume and shelf-break fronts. *C. pelagicus* seemed to consistently occupy a particular ecological niche, between other phytoplankton groups, related to moderate turbulence conditions combined with nutrient availability. From this behaviour, it is proposed that *C. pelagicus* can be used as a tracer of the periphery of areas of enhanced productivity.

Coccolithus pelagicus preferences for fronts of moderate temperature and salinity gradients are tentatively used to explain particular features of its sedimentary record. The repeated increase of *C. pelagicus* in thanatocoenoses (surface sediment assemblages) close to three river mouths, on the Portuguese shelf, are interpreted as a positive response to the development of riverine plumes. On the other hand, inconsistencies in the correlation between sea surface cooler-glacial and warmer-interglacial isotope stages and the relative abundance pattern of *C. pelagicus* during the Late Quaternary, as registered in two Galicia Bank piston cores (42°N), are tentatively explained in terms of shifts in the extent of the outer limit of the local palaeoproductivity belt off the Iberian Peninsula. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Coccolithus pelagicus (Wallich) Schiller is one of the most readily identified extant coccolithophore species, both as coccospheres from water column samples and as coccoliths from sediment samples (Fig. 1). It forms the largest (8–16 µm) and most robust coccoliths of any common species and so has

an exceptionally high preservation potential. So, it ought to be easy to apply our understanding of its ecological behaviour, based on laboratory and biogeographic data, to its occurrence in the sedimentary record. The species stratigraphic record, as a common component of calcareous nannofossil assemblages, covers practically the entire Cainozoic (~65 Ma, FO in subzone NNTp2C of Varol 1998), so its present day ecological and oceanographic meaning may be traceable back to the Lower Palaeocene (Danian).

Coccolithus pelagicus has a complex life cycle with

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Fig. 1. Scanning electron microscope images of coccospheres of *Coccolithus pelagicus* (Wallich) Schiller, 1930: (A) water column specimen from Sines (SW off Portugal). (B) Upper Pliocene specimen from Pombal (central western Portugal).

two distinct phases (Parke and Adams, 1960): a motile holococcolith-bearing phase, originally described as *Crystallolithus hyalinus* Gaarder and Markali (= *C. pelagicus* f. *hyalinus* in Jordan and Kleijne, 1994) and a non-motile heterococcolith-bearing phase (= *C. pelagicus* f. *pelagicus* in Jordan and Kleijne, 1994). The motile phase was not recognised in either the sediments or the water column samples and so this paper deals only with the latter phase, which will be referred to as *Coccolithus pelagicus* for simplicity.

Living *Coccolithus pelagicus* is mainly known from North Atlantic subpolar and polar water masses (McIntyre and Bé, 1967), particularly in the Arctic influenced Greenland Sea (Andrulleit, 1997). Together with *Papposphaera sagittifera*, this species characterises a “polar group” occurring in surface waters of both the warmer Norwegian current and the colder East Greenland Current (Samtleben et al., 1995). Blooms of this species can persist for several weeks (Winter et al., 1994) with described maximum concentrations reaching over 10^6 cells l^{-1} , as reported from the West coast of Ireland, during early Summer (Milliman, 1980). Its presence in the water column was also reported from coastal areas off South Africa in both the Atlantic and Indian Oceans and from southern Australia (Winter et al., 1994).

Coccolithus pelagicus is well represented in cold waters at temperatures ranging from -1.7 to $15^{\circ}C$

(Okada and McIntyre, 1979; Winter et al., 1994). The optimum growth conditions for the species have been established between 2 and $12^{\circ}C$ (Okada and McIntyre, 1979). Therefore, *C. pelagicus* is widely used as a palaeotemperature proxy for cold waters in palaeoceanographic studies: as a qualitative/semi-quantitative parameter (McIntyre et al., 1970; Raffi and Rio, 1981), in transfer functions (Geitzenauer et al., 1976; Giraudeau and Pujos, 1990) and in factorial analysis (Haq, 1980). Shifts in its relative abundance in the total nannofossil assemblage and in the assemblage of placoliths (e.g. *Reticulofenestra pseudumbilicus*) were used to detect cyclic climatic variations, during the late Miocene (Beaufort and Aubry, 1990; Beaufort, 1994).

Coccolithus pelagicus has also been used as an indicator for nutrient enrichment of the surface oceanic waters (McIntyre and Bé, 1967; Rahman and Roth, 1990; Roth, 1994). Since temperature and nutrient content in surface waters are strongly covariant, unresolved questions include: when and how does each of these factors influence *C. pelagicus* development?

Resolving these questions may help us to understand the reason(s) underlying the recent restriction of *Coccolithus pelagicus* to the northernmost North Atlantic and to the shelf waters of upwelling areas (Blasco et al., 1980; Estrada, 1984; Mitchell-Innes

Table 1

Synoptic table of the cruises and sampling characteristics from which data on *Coccolithus pelagicus* was retrieved for the present work

Cruises	Institutions and vessels	Water column sampling and phytoplankton counting procedure	Sampling area
CICLOSI—August 85 CICLOSI—November 85 CICLOSI—January 86 CICLOSI—March 86 AREAS 87—April 87	IPIMAR R/V Noruega	At each station, samples from different depths were integrated volumetrically to represent a 100 m water column. Sampling depths: 0, 5, 10, 20, 30, 40, 50, 75, 100 m.	Lat.: 36°10'–41°50' N Long.: 7°30'–10°30' W
CECIRXIII—August 87	IH R/V Almeida Carvalho	Water samples from different depths down to 75 m were counted individually. Sampling depths: 0, 5, 10, 20, 30, 40, 50, 75 m.	10 days repeated coverage of a transect at 41°05' N; range: 8°42'–9°45' W
CECIRXVI—December 89		Water samples from different depths were counted individually and mathematically integrated to represent a 100 m water column. Depths: 5, 20, 30, 50, 75, 100 m (CECIR XVI) and 5, 10, 20, 30, 40, 50, 75 (SARAS 91).	Lat.: 37°10'–39°45' N Long.: 8°50'–11°50' W Lat.: 36°–40°40' N Long.: 8°55'–11° W
SARAS91—September 91	IPIMAR		
FAR2V—July 1990 FAR3V—July 1991 FAR4V—July 1992	R/V Noruega	Sampling depth: 20 m	Lat.: 36°30'–41°50' N Long.: 7°30'–10° W

and Winter, 1987; Giraudeau and Rogers, 1994; Wells and Okada, 1997). Roth (1994) documented an asymmetrical high and middle northern latitude distribution for *C. pelagicus* in surface sediments of the eastern and western Pacific Ocean margins although the species is also reported from surface sediments from southern latitudes (approx. 40–60°S) by Roth and Berger (1975). From middle latitude northeastern Atlantic areas, a decrease in abundance of *C. pelagicus* was also noticed from the Pliocene to the Pleistocene, being generally less frequent after the Plio-Pleistocene transition (Backman, 1984), especially after 1.25 Ma (Su, 1996). Similarly, *C. pelagicus* was quite common in the Pliocene of the western Mediterranean but practically disappeared during the Plio-Pleistocene transition (Rio et al., 1990). It never re-colonised this area in spite of several low temperature intervals during the Quaternary, as stressed by Gard (1989). These shifts may be a consequence of: (1) change in palaeoecological preferences with time (evolutionary signal); (2) the presence of morpho-

gically indistinguishable placoliths deriving from ecologically distinct entities (Raffi and Rio, 1981); (3) the fact that the real meaning of this heterococcolith-bearing phase is related to other (palaeo)ecological requirements such as nutrient levels or competition (Gard, 1989); (4) distinct operating modes of ocean circulation; or (5) perhaps reflects a complex interplay of all these factors.

In this paper the distribution, frequency and dynamics of *Coccolithus pelagicus* in the Atlantic waters of the Iberian upwelling system are presented. These evidences are used to interpret its sedimentary record in surface sediment assemblages and Quaternary time series off the Portuguese coast. The ecological behaviour and palaeoecological interpretation of this species at its ecological limit are discussed.

2. Study area

The Atlantic coast of the Iberian Peninsula is the

Fig. 2. (A) Map of the study region where it is indicated the area of water column sampling (light grey), the location of the Galicia Bank, IFREMER piston cores N3KF21 and N3KF24 and the area of the surface sediment stations (dark grey-(S)). (B) Detailed location of the surface sediment stations (S) along three sections parallel to the coastline, offshore Porto.

northern limit of the upwelling area associated with the North Atlantic anticyclonic gyre (Woster et al., 1976) and is a hydrographically complex region characterised by the confluence of different water masses (Fiúza, 1984; Rios et al., 1992; Fiúza et al., 1998) and currents (Frouin et al., 1990; Haynes and Barton, 1990; Dias et al., 1996; Fiúza et al., 1998). Along the Portuguese coast, the wind regime induces seasonal upwelling with different patterns along the coast, determined by coastal morphology, the continental shelf/upper slope bathymetry and local winds (Fiúza, 1983). During winter, there is normally a cold water band along the coast, due to net surface heat loss of shallow coastal waters (Fiúza, 1984).

North–south differences in river discharges can give rise to temporary or seasonal structures such as sediment and nutrient laden river plumes and, to a superficial lens of lower salinity to the north of the Nazaré canyon (Silva, 1992). Several surveys carried out during the last decades off the West Iberian coast have shown large scale meridional variations of phytoplankton assemblages in the shelf region (Estrada, 1984; Moita, 1993a,b).

In a coastal upwelling region such as this area, phytoplankton assemblages may be positioned along a trophic axis related to decaying turbulence and nutrient availability (Margalef, 1978). In the upwelling core species with maximum growth rates predominate

(mostly diatoms), contrasting with assemblages in offshore nutrient-poor stratified waters, which are dominated by taxa with lower growth rates (notably dinoflagellates). Coccolithophores appear to occupy an intermediate ecological position between those two groups (Estrada and Blasco, 1985).

3. Material and methods

3.1. Water column

Water column results are based on data from eleven cruises off the Portuguese coast during four seasons, between 1985 and 1992 (Table 1). These cruises, by the R/V *Noruega* from the Institute of Fisheries and Marine Research (IPIMAR) and R/V *Almeida Carvalho* from the Portuguese Hydrographic Institute (IH), had the general objective of improving knowledge of planktonic communities in the Portuguese area of the upwelling system. Variable sampling strategies were used, reflecting the specific cruise purposes. For this study, data from nearly 700 stations were used (Fig. 2).

Temperature values were obtained by measurements with a NBIS Mk IIIB CTD or a SEACAT-SBE19 CTD during CECIR and FAR cruises, respectively, or from reversing thermometers coupled to Nansen bottles during the others. Nutrients were measured on a Technicon Autoanalyser, according to the methods given by Technicon (1977).

Phytoplankton samples were preserved with hexamethylenetetramine buffered formalin to a final concentration of 2% (Thronsen, 1978). Subsamples of 100 ml were allowed to settle for three days. Cells were identified and counted by the Utermohl technique (Hasle, 1978) using a Zeiss IM35 inverted microscope with phase contrast and brightfield illumination. A magnification of $\times 160$ was used to enumerate the *Coccolithus pelagicus* cells and other large coccolithophore species (*Helicosphaera carteri*, *Calcidiscus leptoporus*, *Umbicosphaera sibogae*, *Syracosphaera pulchra*, *Coronosphaera mediterranea*, *Scyphosphaera apsteinii*, etc.) in alternate transects of the whole bottom chamber.

During the first set of cruises (CICLOS I-IV and AREAS87) composite samples representing 100 m depth water column (or less in shallow areas) were

counted (Table 1): water samples from each depth were mixed in proportion to the extent of the water column they represented (Venrick, 1978). For the other cruises, samples from each depth were counted separately and a mathematical integration of the sampled water column has been performed in order to obtain results comparable with the previous data sets. Counts of individual samples have also been used to analyse the distribution of *Coccolithus pelagicus* in the water column.

To obtain a consistent geographic synthesis of the *Coccolithus pelagicus* distribution, the Portuguese shelf was divided into half-degree latitude (30 nautical miles) squares. The frequency of presence and the mean densities were recalculated within each square (Fig. 13) using data from cruises CICLOS I-IV, AREAS, CECIR XVI and SARAS91, since they sampled the entire coast and the uppermost water column.

3.2. Sediments

Two different sets of sediment samples were studied, Holocene surface sediment coccolith assemblages and Pleistocene coccolith assemblages (Table 2). For comparison of these two data sets, we found the following taphonomic concepts useful. *Coccolith thanatocoenoses* refers to the uppermost surface sediment coccolith assemblages, reflecting a cumulative process of coccolithophore development in the water column followed by *post-mortem* coccolith transfer to the bottom. *Coccolith taphocoenoses* refers to permanent buried assemblages in the sediment (below reworking by endobenthonic organisms). In general, the taphocoenoses have lower diversity coccoliths than thanatocoenoses due to post-burial early diagenesis; on the other hand, thanatocoenoses can still be subjected to reworking by resuspension and mixture by bioturbation.

Holocene thanatocoenoses were sampled from the Portuguese inner-shelf off Porto (Table 2, Fig. 2A and B) in the “West Douro silty-clay unit” (Drago et al., 1994) by the IH. This silty-clay unit was formed from fine-grained sediment transported by the rivers Douro, Ave and Cávado to the inner shelf (Fig. 2B). This unit was selected since the homogeneous nature of its sediments suggest uniform bottom hydrodynamic conditions, and because of the almost complete absence of

Table 2

Location and characteristics of sediment samples used in the present work

Data type	Location	Characteristics
Present day thanatocoenoses	Lat.: 41°10'–41°30'N; Long.: ~9°00' W	Distance to shore: 15–20 km Water depth: 70–90 m
Quaternary taphocoenoses	N3KF21: 42°08,7'N; 12°10,2'W N3KF24: 42°07,9'N; 11°57,3'W	250 cm core thickness. Isotope stages 1–11? Isotope stages 1–3

reworking (Cachão, 1993). Here, 72 samples were collected along three traverses, parallel to shore, separated by one nautical mile (Fig. 2B). Samples were collected by a “SmithMcIntyre” dredger device, representing a mean sediment thickness of 20 cm, as part of the IH program SEPLAT.

A second set of samples was retrieved from two piston cores located south of the Galicia Bank (NORESATLANTE III, IFREMER), provided by the IH (Fig. 2A). Samples were taken at 5 cm inter-

vals for the upper 50 cm of sediment and at 10 cm intervals for the next 50–250 cm. Core N3KF21 provided a condensed section to approximately 400 ka (oxygen isotope stage 11?). Core N3KF24 had a higher sedimentation rate and yielded a detailed time series to about 50 ka (oxygen isotope stage 3). Age determination and isotope stage interpretations are from Fatela (1995).

Coccolithus pelagicus data were obtained by counting 300 large (>3.5 µm) coccoliths. The

Fig. 3. Distribution of (A) of sea surface temperature (°C) (shaded areas indicate upwelling centers) and (B) *Coccolithus pelagicus* (cells l⁻¹) integrated in the water column (0–100 m), during CICLOS I cruise, August 1985.

Fig. 4. Distribution of (A) of sea surface temperature (°C) and (B) *Coccolithus pelagicus* (cells l^{-1}) integrated in the water column (0–100 m), during CICLOS II cruise, November 1985.

data are given as percentage abundances. *Emiliana huxleyi* and other small placoliths were excluded from these counts being evaluated separately when present. Coccolith evaluations were performed on permanently mounted smear slides, with a polarising microscope (Leitz ORTHOLUX II POL-BK) at $\times 1250$ magnification. Rippled smear slides were used to obtain gradients of coccolith concentration. Small portions of sediment were rippled by spreading (with the moderate friction of a toothpick) directly on a cover glass, and then mounted with a synthetic balsam cement. In order to obtain fields with a more or less homogeneous coccolith distribution, fields with no large placoliths or with placolith overlapping were rejected. Diversity was optimised by counting at each time the maximum possible number of distinct morphotypes per field of view.

4. Results

4.1. Species distribution in the water column

4.1.1. Cruises description

CICLOS I: During summer 1985, the colder waters present inshore and closely spaced isotherms parallel to the coastline (Fig. 3A) indicate the occurrence of upwelling off the NW and SW coasts (Moita, 1993b). *Coccolithus pelagicus* was almost absent from the upwelled waters north of Lisbon but was well represented in the SW upwelling system (Fig. 3B). Off Cape S. Vicente upwelling, colder waters from 150 m rose to the surface and flowed southeast (Fig. 3A). *Coccolithus pelagicus* densities varied between 10 and 1500 cells l^{-1} and the species was absent from the upwelling centre itself but was found bordering it.

CICLOS II: This cruise was carried out at the end of the upwelling season, when southerlies alternating

Fig. 5. Distribution of (A) of sea surface temperature ($^{\circ}\text{C}$) and (B) *Coccolithus pelagicus* (cells l^{-1}) integrated in the water column (0–100 m), during CICLOS III cruise, January 1986.

with northerlies caused downwelling during most of the cruise. The isotherms are still parallel to the coastline but with a low gradient between inshore and offshore waters (Fig. 4A). *Coccolithus pelagicus* abundances ranged between 20 and 1000 cells l^{-1} , with the highest densities in two stations in the Nazaré—Peniche area (Fig. 4B), outside the diatom peak and between cold inshore and warmer offshore waters. In the southern coast, *C. pelagicus* was widespread and abundances reached 300 cells l^{-1} adjacent to Cape S. Vicente.

CICLOS III: Despite the occurrence of two northerly wind events during this winter cruise, the outline of the upwelling process was not recognised or was masked by the winter convection. A longshore cold water band was developed (Fig. 5A). According to Fiúza (1984), this is a common feature during winter, since shallow coastal waters cool faster. On the western coast, there was a shallow temperature

gradient between coastal and offshore waters until 150 m depth. On the southern coast, a zonal front appears to have been formed between inshore and offshore stations. On the western coast this front seems to have been much weaker, and probably was located offshore of the sampled area. In these conditions the distribution of *Coccolithus pelagicus* was very patchy and scarce (reaching 160 cells l^{-1}) (Fig. 5B). The species was almost absent on the NW coast while in the south, its maxima values were observed in the front.

CICLOS IV: This spring cruise was carried out under northerlies, with an upwelling episode higher than the events observed during the summer cruise CICLOS I. The location of the upwelling is visible from the isotherms that tend to run parallel to the coastline along the innershelf (Fig. 6A). The water column was almost vertically mixed along the entire coast (Fig. 6D, F). On the NW shelf, a low salinity

Fig. 6. Distribution of (A) of sea surface temperature ($^{\circ}\text{C}$), (B) surface salinity and (C) *Coccolithus pelagicus* (cells l^{-1}) integrated in the water column (0–100 m), during CICLOS IV cruise, March 1986. Vertical distribution of (D) temperature ($^{\circ}\text{C}$), (E) salinity and (F) density (σ_t , kg m^{-3}), at the section offshore Peniche ($39^{\circ}15'\text{N}$), during March 1986.

lens, displaced offshorewards to the south of Porto (Fig. 6B, E), induced weak stratification in the uppermost 50 m, as observed off Peniche (Fig. 6D–F). *Coccolithus pelagicus* was found bordering this lens, both inshore and offshore of it, and was blooming in several stations (blooms are considered as more than 10^3 cells l^{-1}), reaching 4000 cells l^{-1} (Fig. 6C).

AREAS 87: During this spring cruise the sea surface temperature was about 3°C higher than during the CICLOS IV (Fig. 6A, Fig. 7A) and the water column was thermal stratified (Fig. 6D, Fig. 7D). On the NW coast this stratification was enhanced nearcoast by several river plumes (Fig. 7B, E and F). *Coccolithus pelagicus* was found in low densities, although reaching 2,000 cells l^{-1} on the outer side of the salinity front off Peniche (Fig. 7C).

CECIR XVI: During winter 1989, the distribution of *Coccolithus pelagicus* was patchy, with the highest densities (400 cells l^{-1}) confined to the upwelling

centre off cape S. Vicente, as on other occasions (Fig. 8A). The species presents a distinctly different pattern from that of *Calcidiscus leptoporus* and *Umbilicosphaera sibogae* (Fig. 8B and C), which normally occupy warmer offshore waters (see SARAS 91 cruise, below). Physical data are not yet accessible by the IH.

SARAS 91: During this early autumn cruise carried out at the end of the upwelling season, the sea surface temperature data revealed a front on the SW coast (Fig. 9A). This structure probably originated from the confluence of offshore warmer and saltier waters with the coastal upwelled waters. *Coccolithus pelagicus* occurred on the inner side of the front, although in low densities (Fig. 9B). In contrast, a community of other coccolithophores including *Calcidiscus leptoporus* (Fig. 9C), *Discosphaera tubifera* and *Umbilicosphaera sibogae* occupied the warmer offshore waters. A transect parallel to the front (Fig. 10)

Fig. 7. Distribution of (A) of sea surface temperature ($^{\circ}\text{C}$), (B) surface salinity and (C) *Coccolithus pelagicus* (cells l^{-1}) integrated in the water column (0–100 m), during AREAS 87 cruise, April 1987. Vertical distribution of (D) temperature ($^{\circ}\text{C}$), (E) salinity and (F) density (σ_t , kg m^{-3}), at the section offshore Peniche ($39^{\circ}15'\text{N}$), during April 1987.

shows that *C. pelagicus* was more common along the thermocline, particularly in the area of the persistent upwelling centre off Cape S. Vicente (37°N), and was totally absent in surface waters warmer than 18.5°C (Fig. 10A, B).

CECIR XIII: This cruise recorded an upwelling event at $41^{\circ}05'\text{N}$, by sampling the same transect between 19th and 27th of August 1987. Coastal wind stress data obtained before and during the sampling period and the general physical conditions during the cruise are described in Silva and Moita (1993). Fig. 11A reveals an offshore displacement of isotherms as a consequence of a north wind event that began on 22nd August. After the 25th, there was a wind relaxation, this gave rise to an onshore motion of the inner part of the upwelling front (15°C isotherm). The upwelling event that started on 22nd

August induced diatom development, probably in response to an increase in turbulence and nitrate enrichment (silicate concentrations remained above $10\text{ }\mu\text{M}$ before and during the upwelling event) (Fig. 11D). Diatoms were distributed inside the upwelling front following both the offshore displacement of the isotherms and the onshore movement of the inner part of the front after the 25th. Small dinoflagellates and coccolithophores such as *Calcidiscus leptoporus* and *Helicosphaera carteri* were the main components of phytoplankton assemblages in the warmer offshore waters (Fig. 11C). Even before the upwelling event, *Coccolithus pelagicus* was present along the $15\text{--}17^{\circ}\text{C}$ thermal front, with densities above 50 cells l^{-1} , between the diatoms and the offshore community. During the upwelling peak *C. pelagicus* abundances increased and moved offshore, tracking the thermal

Fig. 8. Distribution of (A) *Coccolithus pelagicus*, (B) *Calcidiscus leptoporus* and (C) *Umbilicosphaera sibogae* (cells l^{-1}) integrated in the water column (0–100 m), during CECIR XVI cruise, December 1989.

Fig. 9. Distribution of (A) of sea surface temperature (°C), (B) *Coccolithus pelagicus* and (C) *Calcidiscus leptoporus* (cells l^{-1}) integrated in the water column (0–100 m), during SARAS 91 cruise, September 1991.

Fig. 10. Vertical distribution of (A) *Coccolithus pelagicus* (cells l⁻¹) and (B) temperature (°C) at the alongside section (C) during SARAS 91 cruise, September 1991.

front (Fig. 11A and B). The maximum densities (1,000 cells l⁻¹) were reached on the 26th August (Fig. 11B, Fig. 12B). The species increased at midshelf by about one order of magnitude in two days (Fig. 11B). That corresponds, following Reynolds (1989), to replication rates that reached 1.15 or 1.44 div day⁻¹ considering, respectively, the station in the section with maximum density or the mean species densities in the section (Fig. 11E). In the water column the species was mainly distributed in the pycnocline/nitrocline, at midshelf (Fig. 12A and B).

4.1.2. Overview of *Coccolithus pelagicus* distribution

The mean abundance and the frequency of presence of *Coccolithus pelagicus* along the Portuguese coast are synthesised in Fig. 13. These data show that the species is more abundant in the area north of Lisbon despite being more persistent in SW coastal waters (Fig. 13B and C). Although *C. pelagicus* occurs in low densities (below 500 cells l⁻¹), the maxima observed in the distribution of the mean abundance mainly reflect the species densities during spring and autumn (Figs. 4B, 6C, 7C and 9B).

The species is mostly present in shelf waters, up to 80 km offshore, extending northwards and offshore-wards to approximately 130 km in the regions of Setúbal and Nazaré/Figueira da Foz (Fig. 3B). The pattern

north of Lisbon reflects the species distribution during spring cruises, bordering salinity fronts (Figs. 6 and 7). Along the SW coast, the highest densities of *Coccolithus pelagicus* were observed in the Cape S. Vicente region reflecting the species relation to this important and persistent upwelling centre. *C. pelagicus* was not detected in oceanic waters to the west of 11°W, however, the outmost areas were sampled only once.

Coccolithus pelagicus is present in 60% of the samples in the coastal waters off Caminha but is most consistently present to the south of the Nazaré canyon, a region characterised by a higher influence of warmer and saltier waters of subtropical origin. Maximum frequencies of *C. pelagicus* were observed near cape S. Vicente, extending north and offshore towards the region of Setúbal. In this region, the distribution pattern can be related to the persistency of upwelling at the cape and to the convergence of offshore warmer and saltier waters with the coastal waters, as observed during the SARAS 91 cruise.

Table 3 summarises the seasonal variability of *Coccolithus pelagicus* observed during the cruises. The species was found in higher densities during spring, also showing the highest variability (STD = 366) during this season. The mean and maximum densities tend to decrease through the year, reaching the lowest values during winter. During summer and

Fig. 11. Space–time distribution of temperature and phytoplankton (integrated in the water column, 0–75 m), during the repeated coverage of a cross-shelf section at $41^{\circ}05'\text{N}$ during CECIR XIII cruise, summer 1987 (Silva and Moita, 1993). The 200 m line indicates the shelf break position. (A) temperature ($^{\circ}\text{C}$) at 5 m where the shaded areas indicate the upwelling core (dark grey) and the upwelling front (light grey). (B) *Coccolithus pelagicus* (cells l^{-1}), where the shaded are indicate densities higher than 50 cells l^{-1} . (C) *Helicosphaera carteri* plus *Calcidiscus leptoporus* (cells l^{-1}), integrated in the water column, where the shaded area indicate densities higher than 100 cells l^{-1} . (D) Diatoms (log cells l^{-1}), where the shaded area indicates more than 10,000 cells l^{-1} . (E) Changes in the *C. pelagicus* densities during the upwelling event considering: (squares) the maxima densities in the front (integrated in a 75 m water column); (circles) the integrated densities in the overall cross-shore section (36 km) (each station was previously integrated in the water column of 75 m). Replication rates per day = r .

autumn, the maximum densities are of the same order of magnitude.

The relationship of *Coccolithus pelagicus* with the thermohaline characteristics of surface waters during the upwelling season was studied by using individual (non-integrated) depth data obtained during three different cruises carried out along the Portuguese

coast in consecutive years (FAR cruises) and during the development of an upwelling event (CECIR XIII). The maximum concentrations (Fig. 14) were observed between salinities of 35.7 and 35.9, in the coldest temperatures registered ($>10^3$ cells l^{-1} between 13 and 14.5°C and 0.5×10^3 cells l^{-1} between 13 and 16°C). The species developed very close to the

Fig. 12. Cross-shelf vertical distribution of (A) Nitrate (μM) and (B) *Coccolithus pelagicus* (cells l^{-1}) at the $41^{\circ}05'\text{N}$ section, during CECIR XIII cruise, on the 26th August 1987.

segment that characterise the ENAWst water mass, the main source of upwelling on the Portuguese coast (Fiúza, 1984).

4.2. Sedimentary record of *Coccolithus pelagicus*

4.2.1. Surface sediment data

For the “West Douro silty-clay unit” offshore Porto, a sedimentation rate of 0.57 cm/year was determined on the top 35 cm by ^{210}Pb dating (Drago et al., 1994). Accordingly, the upper 20 cm of surface sediments records more or less 35 years of coccolithophore development.

The relative abundance of *Coccolithus pelagicus* determined along three sections of sediment samples retrieved from this shelf area (Fig. 2B), displayed a more or less regular pattern (Fig. 15A). The species relative abundance shifted from 1.4 to 7.6% with some consistency along the three sections. In each of the sections, higher values are aligned with the mouths of rivers Douro, Ave and Cávado. Although precision for each count is near the total range of variability (for 95% level of significance from a Poisson distribution), the trend can easily be perceived (Fig. 15B). By contrast, a similar robust species, *Calcidiscus leptoporus*, does not display this trend, showing instead a relatively uniform distribution along the sampled sections (Fig. 15C and D).

4.2.2. Piston core data

In order to determine possible meaningful changes in the relative frequency of *Coccolithus pelagicus* in coccolith taphocoenoses, for the Upper Pleistocene–

Holocene time interval, two piston cores from the Galicia Bank were studied (Fig. 2, Table 2). High resolution core N3KF24 (Fig. 16), revealed a pronounced *C. pelagicus* percentage decrease in late isotope stage 3 (from 20–30 to $<10\%$), with a moderate occurrence during stage 2 and in the first half of stage 1 (reaching 15%). From this point ($\sim$ the last 5000 years) to the present day, *C. pelagicus* practically disappears ($<2\%$) from the sedimentary record of the Galicia Bank, being replaced by other species, such as *Calcidiscus leptoporus*. The same trend can be recognised in the top (upper 10 cm) of the lower resolution core N3KF21, in which *C. pelagicus* reveals a clear drop, from around 30% to less than 5% (Fig. 16).

Low relative frequency values of *Coccolithus pelagicus* were also registered during isotope stages 5 and 9–11?, while a clear increase in the relative frequency of this species was registered during isotope stages 3 and 7.

In Fig. 16, the relative abundances of *Coccolithus pelagicus* and *Calcidiscus leptoporus* are presented and the correlation coefficient (r) between them was estimated. These two species were selected for comparison due to their similar degree of resistance to dissolution and to their distinct present day biogeographies. Our data show a change in their relative behaviour. In the N3KF21 time series, the uppermost four samples show antivaration ($r_{\text{Cp/Ci}} = -0.35$). During the isotope stage interval 3–7 the relative abundances of the two species more or less follow each other ($r_{\text{Cp/Ci}} = 0.8$) while during stages 8–11? they show almost no correlation ($r_{\text{Cp/Ci}} = 0.19$). For the N3KF24 time series this effect also occurs. During

Fig. 13. (A) Sampling statistics: *c* is the number of cruises which covered each square (August 1985, November 1985, January 1986, March 1986, April 1987, December 1989, September 1991; *n* is the number of stations sampled in each square and used in calculations. (B) Mean densities of *Coccolithus pelagicus* where each square has a side of 30 nautical miles. (C) Squared mesh representation of the frequency of presence of *C. pelagicus* (percentage of the samples in which the species occurs).

Table 3

Seasonal variation of *Coccolithus pelagicus* densities (cells l^{-1}) on the coast of Portugal (two cruises per season). Mean = mean densities for all sampled stations in each season; Maximum = maximum density registered for each season

	Spring	Summer	Autumn	Winter
Considered cruises:	CICLOS III, AREAS 87	CICLOS I, CECIR XIII	CICLOS II, SARAS 91	CICLOS III, CECIR XVI
Maximum (cells l^{-1})	4000	1540	1200	263
Mean (cells l^{-1})	105	51	29	15
Stand. Dev. (cells l^{-1})	366	141	113	37
Number of stations	207	161	117	138

isotope stage 1, their relative trends are rather different, showing a pronounced increase in *C. leptoporus* followed by an almost immediate drop in *C. pelagicus* ($r_{Cp/Cl} = -0.64$). During isotope stage 2 the correlation is positive ($r_{Cp/Cl} = 0.63$) while during upper isotope stage 3 there is no correlation ($r_{Cp/Cl} = 0.08$).

5. Discussion

5.1. Present day variability of *Coccolithus pelagicus*

Coccolithus pelagicus is a frequent species in Portuguese waters experiencing seasonal variability: the species is found throughout the upwelling season (spring to early autumn), with maximum densities (>1000 cells l^{-1}) mainly during spring, and minima

during winter (Table 3). It is almost absent from a lens of lower salinity that occupies the shelf to the north of the Nazaré canyon during spring and summer, a pattern also followed by other coccolithophores such as *Emiliana huxleyi* (Moita, 1993b; Moita, unpublished data). To the north of Porto, where surface waters reach the lowest temperatures, *C. pelagicus* is also rare. The persistency of the species in this region (Fig. 13C) is mainly due to occurrences observed during a single cruise (CICLOS I, summer 1985) (Fig. 3B). Further north, *C. pelagicus* has only once been recorded from the Galician waters (Estrada, 1984) which may in part be related to low densities of *C. pelagicus* in that region.

The consistent occurrence of *Coccolithus pelagicus* in the southern surface waters off Portugal, which are modified waters of subtropical origin, was not expected since it is generally characterised in the North Atlantic as a subarctic cold water species (Winter et al., 1994). The species does, however, occur in other upwelling areas of both the northern and southern Atlantic. *C. pelagicus* was first directly related to an upwelling region (off NW Africa) by Blasco et al. (1980) but it had been listed as a common species for the region by Margalef (1973). The distribution pattern off north-western Africa was similar to that off the Portuguese coast; the species was not very abundant, and occurred mostly in shelf waters, where it was rather widely distributed (Blasco et al., 1980). It occurs here with other coccolithophore species such as *Emiliana huxleyi*, *Helicosphaera* spp. and *Syracosphaera* spp. in a well-defined area, between the areas rich in diatoms and dinoflagellates (Margalef and Estrada, 1981; Estrada and Blasco, 1985).

In the Benguela upwelling system, the species was reported in surface sediments, dominating the Recent

Fig. 14. Abundance of *Coccolithus pelagicus* (cells l^{-1}) observed during summer cruises (August 1987 and July 1990–1992 plotted over a T/S diagram. The solid line indicates ENACWst as defined by Fiúza (1984); Fiúza et al. (1998).

Fig. 15. (A) *Coccolithus pelagicus* and (C) *Calcidiscus leptoporus* relative abundances along three shore-parallel sections off Porto (see Fig. 2) and location of the Douro, Ave and Cávado river mouths and of the Douro submarine canyon. Mean coccolith numbers (in 300 counts) for the three sections with 95% significance level (vertical bars) from the Poisson distribution of (B) *C. pelagicus* and (D) *C. leptoporus*. The *C. leptoporus* data are plotted as a control to eliminate the possibility that the *C. pelagicus* distribution is diagenetic in origin.

taphocoenoses in two distinct areas associated with the northern and the southern Benguela upwelling regimes (Giraudeau et al., 1993) and in the water column (Giraudeau and Rogers, 1994). It was also reported in specific coastal currents off South Africa in both the Atlantic and Indian oceans (Mitchell-Innes and Winter, 1987; Winter et al., 1994). Based on the occurrence of *Coccolithus pelagicus* off western Tasmania (Hallegraeff, 1984) and around New Zealand (Burns, 1975) it is also interpreted as reflecting coastal upwelling conditions by Wells and Okada (1997). However, to date, there are no records of living *C. pelagicus* south of the subtropical front in the southern oceans (Findlay, 1998, personal communication). Winter et al. (1994) attribute rare records of this species in the Southern Hemisphere of the Pacific Ocean to sparse sampling near the major continental coastlines.

Water column data obtained during months of stronger upwelling along the Portuguese coast showed an affinity of *Coccolithus pelagicus* maxima not only with the upwelling source water, the ENAWst water mass (Fiúza, 1984; Fiúza et al., 1998) (Fig. 14), but also with the lowest temperatures observed. *C. pelagicus* has previously been described as living in waters of -1.7 to $+15^{\circ}\text{C}$ with an optimal temperature range of 2 – 12°C (Okada and McIntyre, 1979; Winter et al., 1994). The present data enlarge these ranges. During a moderate upwelling event off Portugal, the species apparently reached replication rates up to $1.44 \text{ div day}^{-1}$, in a temperature range of 15 – 19°C , or $1.15 \text{ div day}^{-1}$, in a temperature range of 16.5 – 17.5°C (Fig. 11A, B and E). Off the Iberian Peninsula, the optimal conditions for the species development (more than 500 cells l^{-1}) were found up to 16°C , while living conditions can be expanded

Fig. 16. Quaternary time series for *Coccolithus pelagicus* (full triangles) and *Calcidiscus leptoporus* (open squares) for piston cores NORES-TLANTE III N3KF321 and N3KF24. YD = Younger Dryas event (10,700 BP); LGM = Last Glacial Maximum (17,800 BP). Isotope stages and time events from Fatela (1995).

up to 18°C (Fig. 14). In the Benguela upwelling system the species seems to develop in similar conditions since the mean surface temperature ranges from 12 to 17°C off the Namibian coast and between 14 and 16°C off the South African coast (Giraudeau and Rogers, 1994). Baumann (personal communication, 1997) refers to having found few *C. pelagicus* (but only as coccoliths) in plankton samples from 17°N, in SST > 20°C. Even considering that in the Iberian and other upwelling systems the species probably is near its ecological limit (compared with densities up to 10^6 cells l^{-1} in N-Atlantic waters), the new temperature ranges and the fact that *C. pelagicus* was observed several times at abundances above 1000 cells l^{-1} dilutes its use as a “cold water proxy”.

Off the Portuguese coast, in the water column, higher densities of *Coccolithus pelagicus* were associated with the presence of salinity fronts and with the confluence of water bodies such as upwelling fronts or flows. As shown in Figs. 6B, 7B, 9B and 12B, *C. pelagicus* appeared bordering the upwelling induced thermal fronts and associated with the pycnocline/nitrocline, but declined in the upwelling cores and in lower salinity water bodies. The species was never

observed in stratified oceanic waters, notwithstanding the rare sampling coverage of that area (Fig. 13A). These results suggest that along the western Iberian coast *C. pelagicus* occupies a niche between the coastal upwelled and well mixed waters (characterised by the dominance of diatoms) and the offshore stratified warmer and saltier waters (rich in coccolithophores such as *Calcidiscus leptoporus*, *Discoisphaera tubifera* or, during winter, *Umbilicosphaera sibogae*). Based on these data it seems that *C. pelagicus* has a higher requirement for nutrient availability combined with conditions of moderate turbulence, than those other coccolithophore species. Turbulence should be an important factor to maintain *C. pelagicus* in the photic layer since otherwise it would sink relatively fast from the photic zone as it is non-motile and its coccospheres are heavily calcified. Young (1994) estimated for these cells an excess density of about $\Delta\rho = 0.5$ g cm^{-3} and sinking rates of 7–8 m/day.

We often observed a tendency for *Coccolithus pelagicus* to occur in the convergence of different water bodies. By the end of summer, a frontal area can be formed by the confluence of coastal waters with warmer and saltier offshore surface waters that

Fig. 17. Interpretative ecological niche of *Coccolithus pelagicus* on fronts of moderate intensity, between turbulent nutrient enriched and more stratified low productive waters.

probably form a poleward flow, as described to exist along the Iberian slope during autumn and winter (Frouin et al., 1990; Haynes and Barton, 1990). As noted above those waters are relatively rich in *Calcidiscus leptoporus*, *Discosphaera tubifera* and *Umbilicosphaera sibogae* (members of the subtropical and tropical coccolithophore biogeographic assemblages of Winter et al., 1994). *C. pelagicus* was distributed along the shoreward side of the front (Fig. 9). Also, during spring, off the NW coast, higher *C. pelagicus* concentrations (in some cases >1000 cells l^{-1}) were observed bordering a shallow lens of reduced salinity (Fig. 6B). At the NW corner of the Iberian Peninsula, at Cape Finisterre, *C. pelagicus* was also found in the convergence of different water bodies by Estrada (1984). She included *C. pelagicus* in a component assemblage together with other coccolithophores such as *Helicosphaera carteri* and *Deutschlandia anthos*, a diatom, *Navicula* sp. and the silicoflagellate *Dictyocha speculum*.

The affinity of *Coccolithus pelagicus* for frontal areas can also be invoked to explain the peculiar present day distribution of the species in the North Atlantic (see Roth, 1994, Fig. 3; Winter et al., 1994, Fig. 3), occupying a particular extended niche between two oceanic domains: one characterised by more stratified subtropical waters with greater coccolithophore diversity, brought northwards as the North Atlantic Current (between 46 and 50°N, Pollard and Pu, 1985), and another by northern more turbulent and nutrient rich polar waters, fertile in diatoms (Baumann and Matthiessen, 1992; Winter et al., 1994). This may

be further complicated by other aspects such as the restriction of diatom development due to silica depletion (Margalef, 1986; Young, 1996; personal communication). However, silica depletion was not observed during CECIR XIII off Porto (see Results) nor in the Norwegian–Greenland Sea (K.H. Baumann, personal communication, 1997). Another plausible explanation may be the seasonal competition between *E. huxleyi* and *C. pelagicus* with the former developing preferentially during spring and summer (Station BRAVO in Okada and McIntyre, 1979).

McIntyre et al. (1970) first addressed the question of the restriction of *Coccolithus pelagicus* in the Antarctic region, inferring that the development of a strong Antarctic front, between subtropical and subpolar water masses, thermally suppressed the ecological niche of this species. Sediment data from Houghton (1993) also indicates that this species is practically absent from the strong frontal diatom-dominated region of the Dogger Bank (southern North Sea), increasing in abundance towards the NW margin of the North Sea where North Atlantic waters seasonally carry coccolithophores into this area. So, sharp fronts may be invoked to explain *C. pelagicus* restriction, while our data suggest that moderate fronts may provide the right balance between nutrient concentrations, turbulence and temperature leading to its preferential development. These conditions could be defined as intermediate between those that lead to diatom development and those that allow the establishment of a diversified coccolithophore community (Fig. 17).

5.2. *Coccolithus pelagicus* record from the late Pleistocene to Recent

The previous model for the ecological behaviour of *Coccolithus pelagicus* can be tentatively applied to our surface sediment and piston core data from the Portuguese occidental margin. The relative abundance of *C. pelagicus* in sediments, expressed as percentages, cannot be directly compared with the species densities in the water column. Instead, the results are used as a proxy for the species development relative to other coccolithophores, during a more or less extended interval of time.

Marked changes in the abundance of *Coccolithus pelagicus* coccoliths relative to the total coccolith thanatocoenoses ($>3.5\ \mu\text{m}$) were found in the three sections along the Portuguese Northwest Continental margin (Figs. 2 and 15). *C. pelagicus* frequency consistently rises, $\times 3$ – 4 fold near the position of three river mouths: Douro, Ave and Cávado (Fig. 15). This feature, in such a small area could not be directly related to the presence of any known localised oceanographic (steady currents, local cold water gyres or upwelling centres) or geomorphologic (canyons or bottom rises) structures. Moreover, processes such as winnowing by river mouth associated currents would not be able to selectively accumulate *C. pelagicus* placoliths without also concentrating other dissolution resistant placoliths, such as those of *Calcidiscus leptoporus*. In fact, neither a similar pattern nor a meaningful trend was found for this last species (Fig. 15). Contamination by river discharges of fossil *C. pelagicus* coccoliths can be ruled out since the drainage basins of the rivers are on Palaeozoic granitic and metamorphic basements. Indeed, coccolith thanatocoenoses from the northern Portuguese shelf are characterised by the almost complete absence of reworked forms in the shelf area, when compared with other sectors further south (Cachão, 1993, 1995). This is due to the larger width and bottom stability of the northern shelf, and to the absence of strong bottom currents such as the Mediterranean outflow, which clearly affects the shelf off Algarve, the south region of Portugal (Ambar and Howe, 1979; Ambar, 1982), inducing coccolith thanatocoenoses with more than 30% of reworking forms (mainly Eocene and Miocene forms, Cachão, 1993, JNICT MAR/743/90 project unpublished report). None of

these features were recognised on the northern innermost shelf off Porto.

Having excluded sorting and reworking as causal effects, the preferential development of *Coccolithus pelagicus* is, thus, directly related to river discharge. This seems to meet the above idea of *C. pelagicus* being favoured in frontal areas, in this case associated with river plumes. Already Pujos (1992) had referred to the tendency of *C. pelagicus* to increase in frequency during intervals of maximum river discharge off the Cabo Verde Islands. These were characterised by the author as low salinity periods related with interglacial stages. *C. pelagicus* frequency values were found to be negatively covariant with estimated palaeosalinities, for the last 700 ka (op. cit.). In accordance to our data, this pattern may be re-interpreted not in terms of a direct dependence of *C. pelagicus* from salinity, but as a consequence of oceanic saline fronts of riverine origin.

Our data from piston cores N3KF21 and N3KF24 revealed a pronounced decrease in the percentage of *Coccolithus pelagicus* off the Galicia Bank, during the Holocene (isotope stage 1) (Fig. 16). By contrast, Gard (1989) and Baumann and Matthiessen (1992) showed that this species increased its abundance further north, during the Holocene. If *C. pelagicus* had simply disappeared from Iberian latitudes, during late stage 1, to be exclusively confined to the northern areas of the North Atlantic Ocean this could be interpreted as a consequence of a global warming of the middle latitude surface ocean. Since *C. pelagicus* is still living in the surface waters of the Iberian shelf (even increasing its frequency southwards, at least to $36^{\circ}30'\text{N}$), the referred reduction of this species percentage around the Galicia Bank is difficult to attribute to an increase in sea surface temperature. Instead, the present day confinement of *C. pelagicus* to the innershelf or to the shelf break of Iberia is probably related to changes in local palaeoceanographic conditions (e.g. upwelling intensity). These changes in productivity conditions from last glacial stage to interglacial stage 1, offshore the Iberian Margin, seem to agree with earlier conclusions of Abrantes (1991) based on the diatom record and organic carbon content. This author demonstrated that a westward shift and progressive intensification of the coastal upwelling system off Portugal during stage 3, culminating in stage 2, was followed by a marked decrease

in upwelling intensity during Early Holocene. However, these proxies do not exactly reflect the same (palaeo) productivity signal, as a close comparison between the two time series shows. Diatoms allow the estimation of the magnitude/strength of the palaeoproductivity area while *C. pelagicus* responds to the outer thermal and productivity front of the upwelled waters.

A similar trend of a progressive eastward confinement of *Coccolithus pelagicus* was recorded by Pujos (1985) in the Equatorial Pacific Ocean during the Pleistocene. *C. pelagicus* disappeared from the Siqueiros area (106°W) and from most DSDP Leg 85 sites (130°W) at 2.0 and 1.7 Ma, respectively, but only much latter (0.8 Ma) from the Galapagos area (86°W). It persists until the present day record at DSDP Leg 85 Site 571 (03°59,84'N; 114°08,53'W). Site 571 is currently influenced by upwelling (op. cit.) which seems to corroborate the occurrence of this species in the Atlantic Ocean associated with upwelling systems.

Relatively low percentages of *Coccolithus pelagicus* (similar to present day ones) were also registered during the last interglacial isotope stage 5 (Fig. 16). Probably a drop in the general palaeoproductivity associated with an increase in the global sea surface temperature can explain this trend (Seibold and Berger, 1996). However, the rise in the isotope stage 7 and the drop during the 9–11? isotope interval can probably be related to local changes in palaeoproductivity. So, lower percentages of this species during warm interglacial stages 1, 5 and 9–11? (but not 3 and 7) may be interpreted as a consequence of a weaker influence over the Galicia Bank of upwelled waters, whether locally generated or extended from the W Iberian margin, and/or to a higher influence of southern stratified, saltier and warmer waters. These water masses first brought eastward by the (palaeo)-Azores current system were then pushed northward as a surface current along the outerslope and upper slope off the west coasts of Portugal and Spain, as currently occurs during the winter months (Frouin et al., 1990; Rios et al., 1992). These waters are responsible for the presence off the Iberian Peninsula of warm water species such as *Calcidiscus leptoporus*, *Discosphaera tubifera*, *Umbilicosphaera sibogae* and *Umbilicosphaera tenuis*. Accordingly, during isotope stages 2–4 and 7, the productivity

area along the western Iberia probably extended further west than at the present day, allowing *C. pelagicus* to better be represented in coccolithophore communities over the Galicia Bank.

Covariation intervals between *Coccolithus pelagicus* and *Calcidiscus leptoporus* on N3KF21 and N3KF24 are considered induced artefacts due to changes in other species relative abundances. During these covariation periods (a broad isotope interval 3–7 in N3KF21 and with particular expression during isotope stage 2 in N3KF24) the border between the two species biogeographic domains was probably locked above the Galicia Bank and, so, their relative variations would be maintained. Antivariation intervals must indicate that their abundances changed in opposite directions since it is not possible to create this effect by changing the abundance of other species. Since, in present day conditions, *C. pelagicus* is confined to the shelf area while *C. leptoporus* is better represented in offshore waters, these species opposite behaviour is interpreted as reflecting a shift of the border of the two domains, in offshore or inshore directions. For instance, N3KF24 shows that the anti-variation trend between these two species seems to have started earlier (0.6 m below) than the interpreted 3–2 isotope limit. With the exception of small shifts, *C. pelagicus* keeps more or less constant during most of the middle section of this core with a small trend to increase at the upper part of the isotope stage 2 and lower part of isotope stage 1. Approximately, around the estimated stratigraphic location for the Younger Dryas event, the earlier trend inverts and *C. pelagicus* becomes less common on the Galicia Bank.

This interpretation of the *Coccolithus pelagicus* record may add some other (palaeo) oceanographic applications (as moderate front tracer ?) to its use. What may be lost in linear palaeotemperature estimations may be gained in terms of a better understanding of general ocean circulation patterns. Can these particular (palaeo) oceanographic conditions help to explain the virtual absence of this species from the Mediterranean area at the present day and during the Pleistocene? Also, is it a coincidence that at approximately the same time (during stage 1), *C. pelagicus* disappeared in both hemispheres from Atlantic oceanic areas at latitudes 42°N (Galicia Bank) and 42°S (Core RC 8-39 in Gard, 1989) a trend which seems to have started earlier, during the transition of isotope

stage 3 to stage 2? Alternatively, what changed in the Atlantic Ocean circulation to constrain *C. pelagicus* in the subarctic region during warm isotope stage 5 (Gard, 1989) while allowing its present day development in this area (McIntyre and Bé, 1967)?

From our data it is plausible to infer a cyclic constraint of *Coccolithus pelagicus* to areas closer to continental margins, related to the onshore confinement of a particular set of turbulence and nutrient availability conditions. It is also possible that this constraint may have followed a more general trend of migration of the productive belt of the Northern Atlantic Ocean towards Greenland, during the Holocene. If this is true then *C. pelagicus* may be used as a proxy of the location of the outer limits of productivity enhanced areas. Bukry (1980) showed earlier that in the eastern Pacific Ocean, during the late Miocene–Pleistocene interval, the species abundance pattern does not follow a latitudinal gradient, being restricted instead to what can be interpreted as upwelling induced cold water paths more or less parallel to shore.

6. Conclusion

The traditional interpretation of *Coccolithus pelagicus* as a typical species of the subarctic coccolithophore province in the Atlantic Ocean needs to be modified since it occurs consistently in the Iberian upwelling system, part of the northern Atlantic anticyclonic gyre. The presence of *C. pelagicus* off Iberia and other areas such as the northwestern and southwestern Africa, suggests that this species has an affinity for upwelling areas when at its ecological limit of occurrence.

The interpretation of *Coccolithus pelagicus* as a proxy of low (polar to subpolar) (palaeo)temperature conditions does not fully explain the distribution patterns observed at the Western Iberian Margin. In this upwelling system, where the species is frequently observed in waters of subtropical origin, although related with the lowest temperatures, *C. pelagicus* optimum living and maximum temperatures can be extended to 16 and 18°C, respectively, in agreement with temperatures of other Atlantic upwelling systems. *C. pelagicus* dynamics in the water column suggest that its niche may be associated with moderate

fronts of different origins, including thermal (upwelling), haline (lens of reduced salinity or riverine plumes), and the confluence of distinct water bodies.

The establishment of this species as a front tracer, on the outer limits of areas where nutrient availability is enhanced and turbulence is moderate, provides an interpretation for the increased abundances of *Coccolithus pelagicus* in the present day sedimentary record of the Portuguese north-western Continental Margin, beneath riverine plumes.

Similarly, changes in palaeoproductivity conditions interpreted as a result of expansions and contractions of the outer limits of influence of the upwelled waters offshore the Iberian Margin, can explain the record of *Coccolithus pelagicus* during the Upper Quaternary, across several isotope stages. For instance, a marked relative abundance drop of *C. pelagicus* from the last glacial maximum until the present is in agreement with a decrease in palaeoproductivity.

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