Spatial and temporal variability in coccolithophore abundance and distribution in the NW Iberian coastal upwelling system

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Abstract. A systematic investigation of the spatial and temporal variability in coccolithophore abundance and distribution through the water column of the NW Iberian coastal upwelling system was performed. From July 2011 to June 2012, monthly sampling at various water depths was conducted at two parallel stations located at 42°N.

Total coccosphere abundance was higher at the outer-shelf station, where warmer, nutrient-depleted waters favoured coccolithophore rather than phytoplanktonic diatom blooms, which are known to dominate the inner-shelf location.

In seasonal terms, higher coccosphere and coccolith abundances were registered at both stations during upwelling seasons, coinciding with high irradiance levels. This was typically in conjunction with stratified, nutrient-poor conditions (i.e. relaxing upwelling conditions). However, it also occurred during some upwelling events of colder, nutrient-rich subsurface waters onto the continental shelf. Minimum abundances were generally found during downwelling periods, with unexpectedly high coccolith abundance registered in subsurface waters at the inner-shelf station. This finding can only be explained if strong storms during these downwelling periods favoured resuspension processes, thus remobilizing deposited coccoliths from surface sediments, and hence hampering the identification of autochthonous coccolithophore community structure.

At both locations, the major coccolithophore assemblages were dominated by Emiliania huxleyi, small Gephyrocapsa group, Gephyrocapsa oceanica, Florisphaera profunda, Syracosphaera spp., Coronosphaera mediterranea, and Calcidiscus leptoporus. Ecological preferences of the different taxa were assessed by exploring the relationships between environmental conditions and temporal and vertical variability in coccosphere abundance. These findings provide relevant information for the use of fossil coccolith assemblages in marine sediment records, in order to infer past environmental conditions, of particular importance for Paleoceanography. Both E. huxleyi and the small Gephyrocapsa group are proposed as proxies for the upwelling regime with a distinct affinity for different stages of the upwelling event: E. huxleyi was associated with warmer, nutrient-poor and more stable water column (i.e. upwelling relaxation stage) while the small Gephyrocapsa group was linked to colder waters and higher nutrient availability (i.e. early stages of the upwelling event), similarly to G. oceanica. Conversely, F. profunda is suggested as a proxy for the downwelling regime and low-productivity conditions. The assemblage composed

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by Syracosphaera pulchra, Coronosphaera mediterranea, and Rhabdosphaera clavigera may be a useful indicator of the presence of subtropical waters conveyed northward by the Iberian Poleward Current. Finally, C. leptoporus is proposed as an indicator of warmer, saltier, and oligotrophic waters during the downwelling/winter regime.

1 Introduction

Coccolithophores are a group of marine calcifying phytoplankton with worldwide distribution in modern oceans. These microscopic algae are one of the main contributors to biogenic sediments by the production of calcite plates, named coccoliths, which form their outer shell, the coccosphere. Environmental conditions within the photic zone determine coccolithophore productivity, assemblage composition, and spatial distribution. Thus, fossil coccolith records recovered from sedimentary archives are extensively used to reconstruct past variability of surface water dynamics (e.g. McIntyre, 1967), nutricline position (e.g. Molino and McIntyre, 1990), primary productivity (e.g. Beaufort et al., 1997; Beaufort and Heussner, 2001), and CO² (e.g. Stoll et al., 2002), among others. In the modern ocean, different coccolithophore assemblages are broadly distributed according to five biogeographic regions, each of them characterized by specific water masses (McIntyre and Bé, 1967). However, local processes such as eddies, jets and upwelling plumes can determine a much wider variety of assemblages whose ecology and relationships with the local environmental conditions cannot be extrapolated elsewhere (Baumann et al., 2005). Hence, extensive understanding on the regional ecology of coccolithophores in modern ocean waters is crucial to correctly interpret abundance of calcareous nanofossils in marine sediment records to infer environmental conditions and productivity variations in the past.

The Atlantic Iberian Margin is located at the northern part of the Canary Eastern Boundary Upwelling Ecosystem, one of the four major coastal upwelling systems of the world’s oceans (Fraga, 1981; Fiúza, 1983; Arístegui et al., 2009). It is a preferred location for paleoceanographic investigations due to high sedimentation rates, which allow studying marine records at sub-millennial scale. Furthermore, the combination of fluvial inflow from several rivers and a narrow continental shelf allows for the study of land–ocean interaction processes (Sánchez-Goñi et al., 1999, 2002). Fossil coccolith records are being extensively used for climatic reconstructions along the western Iberian Margin (Parente et al., 2004; Flores et al., 2010; Incarbona et al., 2010; Amore et al., 2012; Palumbo et al., 2013). However, the few existing studies characterizing living coccolithophore community, distribution, abundance, and ecology in the water column are mostly based on central and southern areas (Cachão and Moita, 2000; Cachão et al., 2000; Ferreira and Cachão, 2005; Silva et al., 2008; Moita et al., 2010; Guerreiro et al., 2013; Guerreiro et al., 2014), being scarce for northern locations (Abrantes and Moita, 1999; Moita, 2001). In this context, we present a year-long data set of coccospheres and free coccoliths based on monthly sampling at several depths at two different stations (one on the inner shelf and one on the outer shelf) across the NW Iberian Margin. This study aims to characterize spatial and temporal variability in coccolithophore abundance as a response to local and regional environmental processes. These findings will further contribute to infer different paleoceanographic patterns of the NW Iberian coastal upwelling system by analysing fossil coccolith assemblages.

2 Oceanographic setting

The sampling sites (RAIA and CALIBERIA stations; Fig. 1) were located in the NW Iberian coastal upwelling system. Large-scale oceanographic processes in this area are marked by a strong seasonal pattern, mostly determined by the regional atmospheric circulation. Generally, the semi-permanent Azores High displaces northward during spring–summer seasons (April to September/October), promoting northerly winds blowing over the continental shelf and inducing offshore Ekman transport (Fiúza, 1983; Alvarez et al., 2011). Accordingly, upwelling of subsurface, cold, and nutrient-rich Eastern North Atlantic Central Water (ENACW) occurs, leading to high primary production (Fraga, 1981; Tenore et al., 1995; Figueiras et al., 2002). In contrast, during autumn and winter (October to March/April), the Azores High weakens and migrates southward while the Icelandic Low intensifies. In this context, southerly wind regime is accompanied by downwelling favourable conditions and a consequent decrease in primary productivity. Strong southwesterly winds at this time might also induce highly energetic storms that can lead to wave-driven mobilization of fine sediments from mid-shelf depths (Dias et al., 2002a; Vitorino et al., 2002; Oberle et al., 2014). During these periods, fluvial discharges from Minho and Douro rivers, located south, can contribute terrestrial sediments to the study area (Dias et al., 2002a, b; Zúñiga et al., 2016). Oceanographically, from October to January, the region is affected by the presence of the Iberian Poleward Current (IPC), which flows northwards and transports relatively warm, saline and nutrient-poor waters to our study site (Haynes and Barton, 1990; Castro et al., 1997; Álvarez-Salgado et al., 2003, and references therein; Peliz et al., 2005; Relvas et al., 2007). Later on, the winter cooling in February–March favours a decrease in temperature that promotes a well homogenized mixed layer of cold and nutrient-rich waters (Castro et al., 1997; Álvarez-Salgado et al., 2003).
3 Material and methods

3.1 Sea water samples collection and environmental data

Sea water samples were collected at two stations: one close to the coast (4.1 km from the coastline) located off Cabo Silleiro (RAIA station; 42°05′N; 8°56′W, 75 m water depth), and one further offshore (52.8 km from the coastline) located at the outer continental shelf (CALIBERIA station; 42°05′N, 9°23′W; 350 m water depth). Continuous CTD–SBE911 profiles were recorded at both stations to measure temperature and salinity through the water column. Sampling was conducted monthly on board R/V Mytilus from July 2011 to June 2012 (except August and April). Water column samples were obtained from selective rosette 10 L PVC Niskin bottles at 10, 50, and 70 m water depth at RAIA station and at 10, 50, 100, 150, 250, and 300 m water depth at CALIBERIA sampling site. Seawater samples were used for analyses of coccolithophore and diatom assemblages, and determination of both inorganic nutrients (NO$_3^-$, HPO$_4^{2-}$, Si(OH)$_4$) and chlorophyll a (Chl a) concentrations. For coccolithophore analyses, a seawater volume between 2 and 5 L was filtered through a cellulose filter of 0.45 µm pore size by using a vacuum pump. Then, each filter was stored in plastic Petri dishes and rendered transparent with a few drops of immersion oil. A random piece of filter was cut and mounted on a slide by resuspension and secondary transport by rivers or deep to older stratigraphic levels and have generally been affected by resuspension and secondary transport by rivers or deep
Figure 2. Environmental conditions for the studied period. Available data on (a) irradiance, (b) wave height, (c) Bakun’s upwelling index, and (d) discharges by Minho (blue) and Douro (black) rivers (Zúñiga et al., 2016, 2017). Grey and white bars represent downwelling and upwelling periods, respectively, based on upwelling index and biogeochemical data presented and interpreted in Zúñiga et al. (2016, 2017). Temporal and vertical distribution of (e) temperature, (f) salinity, (g) HPO$_4^{2-}$, (h) NO$_3^-$, and (i) Chl a at CALIBERIA and RAIA stations. Black dots represent collected water samples for coccolithophore analyses.
currents (Ferreira et al., 2008), indicating an allochtonous environmental signal.

3.3 Statistical analysis

Evaluation of ecological similarities among coccolithophore species and their relationship with the environmental conditions was performed using a canonical correspondence analysis (CCA). The analysis was only implemented for the CALIBERIA station data set given that RAIA station was affected by resuspension of coccoliths from the underlying sediments, which may also have affected coccolithophore distribution in the water column (see Sect. 5.1.1). Ecological relationships were assessed as a function of the distance among the species and the variables on an ordination graph. Akaike’s information criterion (AIC) was applied in prior ordination analysis to identify the model with the minimum number of environmental variables that, being statistically significant, explained the maximum inertia (i.e. variance among the species and the variables on an ordination graph). After significant variables were identified via backward procedure, CCA was performed. Ordinations were performed using the “vegan” package v.2.3. (Oksanen et al., 2016) for R (R Core Team, 2015).

4 Results

4.1 Environmental conditions and associated physical processes during sampling

Environmental conditions at RAIA station from November 2008 to June 2012 have been previously assessed in detail by Zúñiga et al. (2016). For the period considered in this study, northerly winds occurred from July to November 2011, and from February to May/June of 2012, with the water column being characterized by the upwelling of cold, more saline and nutrient-rich ENACW on the NW Iberian Margin, principally at the inner continental shelf where the presence of these upwelled waters at shallower depths were strongly linked to Chl a maxima (Fig. 2i). On the other hand, from November to January, and part of May, downwelling favourable winds and low irradiance levels were also accompanied by high wave heights and consecutive Minho and Douro river discharges, as shown by the presence of less saline water lenses at the surface layer (Fig. 2d and f). From November to December, anomalously warmer (14–16 °C), saltier (> 35.8), and nutrient-poor (< 0.1 µM of HPO$_4^{2-}$ and < 2.5 µM of NO$_3^-$) waters conveyed by the IPC were distinguished (Figs. 2e–h). Finally, during February, winter mixing conditions were also detected with the water column being homogeneously characterized by colder waters (< 13 °C) with salinity values < 35.8 and higher nutrient concentrations (0.3–0.5 µM of HPO$_4^{2-}$ and 2.5–5 µM of NO$_3^-$). The outer-shelf station was generally characterized by warmer and more nutrient-poor waters. Yet the temperature and nutrient distribution in the upper layer revealed similar seasonal patterns in both stations, and the influence of less saline lenses from river discharges was also observed at the outer-shelf station in May (Figs. 2e–h). Chl a concentrations were of the same order in both stations, although its temporal variability differed markedly and coupling between stations only occurred from March to May (Fig. 2i).

4.2 Diatom abundance

Diatom abundances at 5 m water depth at the RAIA inner-shelf station have been previously discussed by Zúñiga et al. (2017). These peak during the upwelling periods and reach a maximum of ~ 1 × 10$^6$ cells L$^{-1}$ in September 2011 (Fig. 3a). At the CALIBERIA outer-shelf station, diatom abundances were much lower, reaching a maximum of ~ 200 × 10$^3$ cells L$^{-1}$ during the second upwelling period (March–June 2012).

4.3 Total coccosphere and coccolith absolute abundances

In general, coccosphere and coccolith preservation varied from moderate to good (Fig. 3b), allowing identification of nearly all (moderate preservation) or all specimens (good preservation) at species level.

4.3.1 Coccolithophore standing crops

At RAIA inner-shelf station, coccosphere absolute abundance was generally very low, except during March and June 2012 at 10 m water depth reaching 1 × 10$^5$ and 2 × 10$^5$ cells L$^{-1}$, respectively (Fig. 3c). At CALIBERIA outer-shelf station, coccosphere absolute abundance ranged between 0 and 3 × 10$^5$ cells L$^{-1}$ (Fig. 3c). Higher cell densities occurred during spring and summer months between 10 and 50 m depth, reaching maximum numbers in March 2012 (Fig. 3c). In contrast, coccosphere abundances dropped to minimum levels during winter.

4.3.2 Coccolith absolute abundance

At RAIA inner-shelf station, coccolith absolute abundance ranged between 0 and 6 × 10$^7$ coccoliths L$^{-1}$ (Fig. 3d). Minimum values were registered between July and October.
2011 and February–May 2012 at 10 m. Coccolith minima in September 2011 coincide with poor sample preservation but also maxima in diatom abundance. Maximum values were observed in December 2011 and January 2012 at 70 m, and June 2012 at 10 m.

At CALIBERIA outer-shelf station, coccolith absolute abundance ranged between 0 and $1.25 \times 10^7$ coccoliths L$^{-1}$ (Fig. 3d) with maximum abundances in July 2011 ($\sim 7.5 \times 10^6$ coccoliths L$^{-1}$) and June 2012 ($\sim 1.25 \times 10^7$ coccoliths L$^{-1}$) at 10 m water depth, decreasing gradually through the fall season (October and November 2011), and dropping to minimum values in winter (December 2011–March 2012).

Distributions of total both coccosphere and coccolith abundances within each station are in general agreement. One exception is found in March 2012 at both stations, when the maximum of coccospheres does not have a counterpart in the coccolith signals. Another exception to this general agreement occurs from November to January at RAIA station, when higher coccolith abundances at 70 m depth are not reflected by the coccosphere abundance.

4.4 Major assemblage composition

Assemblages of both forms, coccospheres and coccoliths, showed the same major composition at both stations (Figs. 4 and 5). *E. huxleyi* was the dominant species, being present through the whole studied period, and achieving percentages higher than 90 % of both forms during the upwelling regime. The second major taxa was the small *Gephyrocapsa* group, which reached its highest relative abundance from February
to May at both stations. Other major species were *Gephyrocapsa oceanica*, *Florisphaera profunda*, *Syracosphaera* spp. (mainly *S. pulchra*), *Coronosphaera mediterranea*, *Calcidiscus leptoporus*, and, to a small extent, *Rhabdosphaera clavigera* in only two samples of CALIBERIA station. Reworked coccolith specimens did not exceed 0.3 % of relative abundance for any sample (Figs. 4 and 5). Other minor species and taxa identified and counted are listed in Appendix A.

**4.5 Inner-shelf temporal variability in species absolute abundance**

At the RAIA inner-shelf station, *E. huxleyi* ranged between 0 and $5 \times 10^5$ cells L$^{-1}$, being more abundant in March and June 2012 at 10 m, similarly to small *Gephyrocapsa* group (up to $\sim 4 \times 10^4$ cells L$^{-1}$) (Fig. 6). *G. oceanica* (up to $\sim 8 \times 10^3$ cells L$^{-1}$) reached its maximum in July at 10 m depth, but it abounded at and below 50 m water depth. *F. profunda* was present in October at all depths, reaching its highest density ($\sim 5 \times 10^3$ cells L$^{-1}$) at 50 m. *Syracosphaera* spp. and *C. leptoporus* were present in November, the former at 10 (1 $\times 10^3$ cells L$^{-1}$) and the latter at 50 m water depth (1.5 $\times 10^4$ cells L$^{-1}$) (Fig. 6). *C. mediterranea* shows higher density (3 $\times 10^4$ cells L$^{-1}$) in June 2012 at 10 m and lower abundances in February and March. Coccolith and coccosphere distribution were found to differ significantly, especially at and below 50 m water depth. For instance, all major species showed relative maxima in coccoliths L$^{-1}$ from November to January at 70 m water depth (Fig. 6).
Figure 5. Relative abundance (%) of major species of coccospheres (a) and coccoliths (b) in CALIBERIA station. Black dots represent the sampling month and depth. Note that each colour bar has been scaled to the maximum and minimum values of its corresponding species.
4.6 Outer-shelf temporal variability in species absolute abundance

At the CALIBERIA outer-shelf station, E. huxleyi (up to $2 \times 10^5$ cells L$^{-1}$) was much more abundant during the upwelling regime (Fig. 7). The small Gephyrocapsa group (up to $1.75 \times 10^5$ cells L$^{-1}$) and G. oceanica (up to $1.4 \times 10^5$ cells L$^{-1}$) showed their highest abundance in March 2012, with the latter dominating at greater depths. F. profunda (up to $5 \times 10^4$ cells L$^{-1}$) only appeared during winter, mostly between 50 and 100 m water depth, while Syracosphaera spp. abounded in September and, similarly to R. clavigera, November 2011 at 10 m. C. mediterranea shows its highest density ($2 \times 10^4$ cells L$^{-1}$) in June 2012, and lower abundances during October–November 2011 within the first 50 m. C. leptoporus appeared from November to January and at below 50 m water depth.

Except for G. oceanica and C. leptoporus, temporal distribution of coccolithophore species at the outer-shelf station were broadly mimicked by their corresponding coccoliths, although coccoliths showed a wider vertical distribution (Fig. 7). Coccoliths of G. oceanica were much more abundant during the upwelling regime if compared with coccospheres of the same species. Coccoliths of Syracosphaera spp. coexisted with those of C. mediterranea and R. clavigera in November 2011 at 10 m water depth (Fig. 7). Coccoliths of C. leptoporus were present throughout the studied period at and below 100 m depth, and only appeared in the first 50 m during November–December.

4.7 CCA

The first canonical axis (CCA1) of the CCACALIBERIA model explained 51% of the constrained inertia (i.e. variance) in the coccosphere data and was mostly related to the negative gradient of irradiance, and to the positive gradients of salinity and both Douro River and Minho River discharges (Fig. 8). The second canonical axis (CCA2) explained 22% of the constrained variance and showed a positive gradient with temperature and a negative relationship with HPO$_4^{2-}$ and NO$_3^-$, E. huxleyi was linked to the upwelling regime samples (June and July) and showed a positive relationship.
with temperature. The small *Gephyrocapsa* group was also related to the upwelling regime during March but, unlike *E. huxleyi*, linked to higher nutrient content. *F. profunda* was associated with the downwelling regime samples and presented a negative relationship with irradiance. *G. oceanica* was related to nutrients and mainly linked to samples below 50 m water depth. *Syracosphaera* spp., *C. mediterranea*, and *R. clavigera* are all associated with the poleward regime samples (November 2011–January 2012), positively related to temperature and negatively associated with nutrients. *C. leptoporus*, which is located next to the latter species, shows a positive relationship with salinity and temperature, and a negative one with nutrient content and irradiance.

5 Discussion

5.1 General patterns in coccolithophore and coccolith abundance in the NW Iberian Margin

This work represents the first year-long investigation of variability in coccolithophore abundance and distribution in the NW Iberian coastal upwelling system. On the one hand, maximum coccosphere abundance at both stations was comparable to maximum values reported for other northern, central, and southern locations along the Portuguese Margin and other major upwelling systems (Table 1). On the other hand, coccolith abundance in RAIA station was the same order of magnitude as that found by Ferreira and Cachão (2005) for an estuary in the SW Iberian Margin. Unfortunately, very few studies quantify the occurrence of free coccoliths in the water column, limiting comparison with other regions.

At both stations, the number of coccospheres drastically drops at below 50 m water depth, possibly due to rapid zooplankton grazing and coccolithophore disaggregation into coccoliths.

Total abundances of both coccospheres and coccoliths were higher at the outer-shelf station compared with the inner-shelf site (Figs. 3c, d), as previously stated by other studies based on water column and surface sediment samples recovered along longitudinal transects off the Portuguese coast (Abrantes and Moita, 1999; Cachão et al., 2000; Moita, 2001) and as inferred from Table 1. Higher cell densities agree with higher Chl $a$ values and low diatom abundances further offshore in October 2011 and March 2012 (Figs. 2i and 3a, c). This suggests that under more (but not extreme) oligotrophic conditions this phytoplankton group can out-compete diatoms (Baumann et al., 2005; Gregg and Casey, 2007), and possibly be significant contributors to Chl $a$ values in the study area. In contrast, at the inner-shelf station where upwelling is more intense, the entrance of cold and nutrient-rich waters favors diatoms proliferation at times of maximum Chl $a$, as recorded in July and September 2011. These results point to the need of considering coccolithophore and coccolith abundance in the NW Iberian Margin

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Figure 7. Absolute abundance of major species of coccospheres (a, given in cells L$^{-1}$) and coccoliths (b, given in coccoliths L$^{-1}$) in CALIBERIA station. Black dots represent the sampling month and depth. Note that each colour bar has been scaled to the maximum and minimum values of its corresponding species.
ithophores to better explain primary productivity patterns at the NW Iberian continental margin.

5.1.1 Inner-shelf temporal variability of coccosphere and coccolith abundance: the influence of coastal processes

At the inner-shelf station, total coccosphere abundance presented maximum values during the upwelling season. By contrast, coccolith maxima were also observed during the downwelling regime, close to the seafloor (75 m). Given that environmental conditions at those times were unfavourable for coccolithophore growth and that no coccoliths nor coccospheres are observed above this depth to explain possible vertical settling, the existence of an allochthonous source of coccoliths (i.e. laterally transported from nearby locations) or resuspension of coccoliths from underlying sediments is proposed to explain these results. Further support for coccolith resuspension comes from the composition of the coccolith assemblage at those times (i.e. November–January and May), counting on many more taxa than the typical bloom-forming *E. huxleyi* and small *Gephyrocapsa* group (Fig. 6) recurrently dominating in productive conditions (Tyrrell and Merico, 2004). Simultaneously, large increases in wave height were observed (Fig. 2b), that is, high-energy wave-driven processes could have favoured resuspension of coccoliths from the underlying sediments. Our data are in agreement with Zúñiga et al. (2016), who studied downward CaCO$_3$ fluxes at the same location and concluded that calcareous shelled organisms had to be remobilized from surface sediments during the highly hydrodynamic downwelling periods. As a consequence, discernment between autochthonous and allochthonous coccolithophore signals in the water column was not possible for these periods, preventing application of CCA to the RAIA data set. Guerreiro et al. (2013) have observed a rapid increase in coccolithophore production at the inner shelf of the central Iberian Margin influenced by a nutrient-rich buoyant plume resulting from intense river runoff. However, our results give no conclusive evidence as to whether freshwater lenses advected to RAIA station influenced the total coccosphere abundance (Figs. 2f and 3d).

5.1.2 Outer-shelf temporal variability in coccosphere and coccolith abundance: the influence of seasonal dynamics

At the outer-shelf site, coccosphere and coccolith abundances were seasonally modulated, showing higher values during the summer/upwelling regime and decreasing drastically in abundance during the winter/downwelling periods. Except for the coccosphere maximum in March 2012 at both stations, summer coccosphere and coccolith maxima were associated with high irradiance levels and relaxation of northerly winds during summer, conditions that promoted more stable water column and nutrient depletion (Figs. 2 and 3c). This affinity of coccolithophores for summer stratified conditions during the upwelling season was already observed by Silva et al. (2008) in Lisbon Bay, from a 4-year weekly-sampled data set. On the other hand, the coccosphere maximum in March 2012 occurred under completely different environmental conditions: cold and nutrient-rich waters characteristic of the onset of the upwelling season (Figs. 2 and 3c). Indeed, despite the general association of coccolithophores with weak upwelling and nutrient depletion, our results show that these phytoplankton groups may follow diverse life strategies, as demonstrated for this region by Guerreiro et al. (2013).

5.2 Coccolithophore ecology and potential as paleoenvironmental indicators

Both the coccosphere and coccolith major assemblages were mainly represented by *E. huxleyi*, the small *Gephyrocapsa* group, *G. oceanica*, *F. profunda*, *Syracosphaera* spp., *C. mediterranea*, and *C. leptoporus* at both stations. Given that resuspension events were found to mask the composition of the coccolith assemblage, and therefore to possibly influence the coccosphere assemblage, in the water column of RAIA station, discussion on coccolithophore ecology will be uniquely based on the coccosphere data set from CALIBERIA station.

*E. huxleyi* was the dominant species throughout the studied period regardless of the environmental conditions (Fig. 7). Higher cell densities of *E. huxleyi*, as well as the small *Gephyrocapsa* group, appeared highly related to the upwelling regime, in agreement with other studies carried out in the central Iberian Margin and other coastal upwelling regions (Ziveri et al., 1995; Baumann et al., 2008; Silva et al., 2008; Guerreiro et al., 2013; Narciso et al., 2016), where both taxa are proposed as indicators of productive periods. Despite this common affinity for the upwelling regime, temporal variability of their absolute abundance and the CCA (Figs. 7 and 8) also emphasize a connection of the small *Gephyrocapsa* group with spring samples, when colder and more nutrient-rich ENACW waters upwelled on the shelf. In contrast, *E. huxleyi* was related to warmer and nutrient-poor waters during summer stratification when upwelling favourable winds relaxed (Zúñiga et al., 2017). Silva et al. (2008) also found both taxa were linked to the upwelling season, and noticed a preferential development of *E. huxleyi* during very weak upwelling events, although in spring and late summer. Yet, our outcomes highlight that both species are unambiguously linked to the upwelling regime.

*G. oceanica* was related to nutrient-rich waters below 50 m, as evidenced by the CCA bi-plot (Figs. 7 and 8). This species is regarded as a component of the lower limit of the photic zone in coastal settings (Baumann and Boeckel, 2013), and has been related to relatively nutrient-rich coastal waters in the SW Iberian Margin (Ferreira and Cachão, 2005; Silva et al., 2008; Guerreiro et al., 2013; Guerreiro et al.,...
Apart from 2010) as a tracer for ENACW of subtropical origin (Fiuza, (Cachão et al., 2000; Silva et al., 2008, 2009; Moita et al., 2010) as a tracer for ENACW of subtropical origin (Fiúza, Cachão et al., 2000; Silva et al., 2008, 2009; Moita et al., 2010). In contrast, in March, only coccospheres of G. oceanica are present, indicating new growth of cells of this species (Cachão and Oliveira, 2000).

F. profunda was related to the downwelling regime and deeper waters (Fig. 7 and 8), in agreement with its classical definition as a LPZ inhabitant (Okada and Honjo, 1973; Molfino and McIntyre, 1990). Since Molfino and McIntyre (1990) pointed out the inverse relationship of F. profunda with productivity in the upper photic zone (UPZ), its relative abundance in fossil records has been widely used to qualify and quantify past productivity variations in many oceanic regions (e.g. Beaufort, 1996; Beaufort et al., 1997, 2001; Grelaud et al., 2012), including the Atlantic Iberian Margin (Incarbona et al., 2010; Palumbo et al., 2013; Marino et al., 2014). Indeed, the ordination analysis for CALIBERIA supports this interpretation, relating F. profunda to deeper and downwelling regime samples (Fig. 8). Considering that the influence of Duero and Minho River discharges is limited to the first 10 m of the water column (Fig. 2f), the proximity of F. profunda to these environmental variables in the bi-plot is only interpreted as a consequence of their common temporal occurrence during the winter months. Contrary to expectation, coccolith abundance of F. profunda was not linked to deeper but to shallow waters at the inner-shelf station (Fig. 6). This fact supports coccolith remobilization from surface sediments at the inner continental shelf from October to January, preventing further interpretation of the coccolithophore ecology close to the coast during that period.

Syracosphera spp. (mainly S. pulchra) is a major component during autumn (Fig. 7), in agreement with Beaufort and Heussner (2001). In spite of previous work (Guerreiro et al., 2015) suggesting that its imprint in the underlying sediments may be under-represented owing to selective dissolution of delicate coccoliths, several studies propose that this genus can dominate the water column assemblage in the study area in occasional periods – both close to the shore (Silva et al., 2008) and in open ocean conditions (Guerreiro et al., 2014). In this regard, S. pulchra along with Helicosphaera carteri, C. mediterranea, and R. clavigera constitute a minority but persistent late summer–autumn assemblage in the S and SW Iberian coast that has been proposed by previous authors (Cachão et al., 2000; Silva et al., 2008, 2009; Moita et al., 2010) as a tracer for ENACW of subtropical origin (Fiúza, 1983). Apart from H. carteri, this assemblage was observed further offshore in November 2011 (Fig. 7), when the upper water column was characterized by warmer, saltier, and nutrient-poor waters if compared to the inner-shelf station (Fig. 2), and as emphasized by the CCA (Fig. 8). A similar assemblage including these three species has been observed in the Central North Atlantic Ocean and was related to warm and oligotrophic waters (Narciso et al., 2016). Although further research is required to assess its preservation in the fossil record, our results broaden the geographical extent of this assemblage as a potential proxy for ENACW of subtropical origin conveyed northward by the IPC.

This assemblage coexists with C. leptoporus, which is also present in the following winter months at and below 50 m water depth (Fig. 7). In a study of the vertical distribution of extant coccolithophores, Baumann et al. (2008) describe C. leptoporus as a deep-dwelling species, along with F. profunda. This species has shown broad tolerance to environmental conditions and has been related to warm and oligotrophic waters (Giraudeau, 1992; Silva et al., 2013) as well as to colder, fresher, and eutrophic waters (Baumann et al., 2016), in this and other regions. In this study, CCA points to a clear relationship of C. leptoporus with saltier, warmer, and poor-nutrient waters, and low levels of irradiance (Fig. 8). These results are in good agreement with previous works in the study area (Silva et al., 2008, 2009; Guerreiro et al., 2014), where C. leptoporus is regarded as a tracer of nutrient-depleted water masses of subtropical origin in the study area, suggesting a strong regional hydrographic control on its distribution.

Figure 8. Ordination graph for the first two axes of the CCA for CALIBERIA data sets. The species scores are represented by stars and environmental variables by arrows. Samples are shown through coloured symbols according to their sampling month and depth.
6 Conclusions

This paper reports on the assessment of the temporal and spatial variability and distribution of coccolithophore and coccolith abundances in the NW Iberian coastal upwelling system. Our results highlight the role of calcareous nanoplanckton as primary producers in the study area and suggest that this group might be a potential contributor to higher Chl a values at the outer Iberian Margin continental shelf. A coastal–offshore gradient was observed in coccosphere abundance, contrary to that of diatoms, with an increase in both coccosphere and coccolith abundances towards the outer shelf where the water column was characterized by relatively more oligotrophic conditions. Even so, temporal variability in coccosphere and coccolith abundances differs between stations. At the inner shelf, coastal processes like strong stormy events were found to resuspend coccoliths from the underlying sediments, masking the autochthonous coccolith assemblage in the water column and hampering interpretation of their ecology. Further offshore, the variability in coccosphere and coccolith abundance is modulated by the seasonal upwelling–downwelling regime. Higher abundances of both forms were observed during spring–summer, when high irradiance levels and upwelling favourable winds promote optimal conditions for coccolithophore growth. We found that higher coccosphere and coccolith abundance occurred mostly under more stratified and nutrient-poor conditions, but also when the cold and nutrient-rich ENACW upwelled onto the continental shelf.

This information on coccolithophore distribution and temporal variability might be of great use to qualitatively interpret coccolith fossil records in terms of past dynamics of the upper water column and thus to monitor large-scale modes of surface oceanic circulation along the NW Iberian Margin, but more specifically in locations far from the influence of coastal hydrodynamic processes. Increases in the absolute abundance of both E. huxleyi and the small Gephyrocapsa group in the fossil record are proposed as indicators of upwelling periods and therefore persistent northerly winds. Despite their common affinity for the upwelling regime, distinct ecological preferences were found between both taxa and attributed to their affinity for different stages of the upwelling event: E. huxleyi was linked to upwelling relaxation conditions (i.e. more stable, warmer and nutrient-poor water column) while the small Gephyrocapsa group was associated with early stages of the upwelling event (i.e. colder waters and higher nutrient availability), similarly to G. oceanica. Conversely, F. profunda is proposed as a proxy for the downwelling/winter regime. The assemblage composed of S. pulchra, C. mediterranea, and R. clavigera may be used as a tracer of the hydrographic influence of the IPC, which carries warmer and nutrient-poor southerly waters. More broadly, C. leptoporus is proposed as an indicator of warmer, saltier, and oligotrophic waters during the downwelling/winter regime.

Data availability. The coccolithophore data set is available from the corresponding author upon request. The environmental data set is part of ongoing research and will be equally accessible after the aforementioned investigation is completed.
### Table A1. Taxonomic list of the identified species. Their presence at each station is denoted by ×.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>CALIBERIA</th>
<th>RAIA</th>
</tr>
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<tbody>
<tr>
<td><em>Braarudosphaera bigelowii</em> (Gran and Braarud, 1935)</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Coronosphaera mediterranea</em> (Lohmann, 1902)</td>
<td>×</td>
<td>×</td>
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<tr>
<td><em>Calcidiscus leptoporus</em> (Murray and Blackman, 1898)</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Coccolithus pelagicus</em> ssp. <em>braarudii</em> (Gaarder, 1962)</td>
<td>×</td>
<td>×</td>
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<tr>
<td><em>Coccolithus pelagicus</em> (Wallich, 1877) Schiller, 1930 ssp. <em>pelagicus</em></td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Discosphaera tubifera</em> (Murray and Blackman, 1898)</td>
<td>×</td>
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</tr>
<tr>
<td><em>Emiliania huxleyi</em> (Lohmann, 1902)</td>
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<td>×</td>
</tr>
<tr>
<td><em>Florisphaera profunda</em> (Okada and Honjo, 1973)</td>
<td>×</td>
<td>×</td>
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<tr>
<td><em>Gephyrocapsa aperta</em> Kamptner, 1963</td>
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<td>×</td>
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<tr>
<td><em>Gephyrocapsa ericsonii</em> McIntyre and Bé, 1967</td>
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<td>×</td>
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<tr>
<td><em>Gephyrocapsa muellerae</em> Bréhéret, 1978</td>
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<td>×</td>
</tr>
<tr>
<td><em>Gephyrocapsa oceanica</em> Kamptner, 1943</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Gladiolithus flabellatus</em> (Halldal &amp; Markali, 1955)</td>
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<td></td>
</tr>
<tr>
<td><em>Helicosphaera</em> spp. (mainly <em>H. carteri</em> (Wallich, 1877))</td>
<td>×</td>
<td>×</td>
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<tr>
<td><em>Oolithotus fragilis</em> (Lohmann, 1912)</td>
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<td></td>
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<tr>
<td><em>Pontosphaera</em> spp. Schiller, 1925</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Rhabdospahera clavigera</em> Murray and Blackman, 1898</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Scyphosphaera apsteinii</em> Lohmann, 1902</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Syracosphaera</em> spp. (mainly <em>S. pulchra</em>, Lohmann, 1902)</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Umbillosphaera</em> spp. (mainly <em>U. tenuis</em> (Kamptner, 1937))</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td><em>Umbilicosphaera sibogae</em> (Weber-van Bosse, 1901)</td>
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</table>
Competing interests. The authors declare that they have no conflict of interest.

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