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

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Abstract. For the first time a systematic investigation of the coccolithophore ecology based on the spatial and temporal variability in their abundance and distribution through the water column was performed for the NW Iberian coastal upwelling system. From July 2011 to June 2012 monthly sampling at different water depths was conducted at two stations located along the 42º N parallel.

Total coccolithophore abundances were higher at the offshore station where warmer and nutrient−depleted waters favoured coccolithophore rather than diatom blooming, the other phytoplankton group that is known to be dominant at the onshore location.

In seasonal terms, coccolithophore blooms were registered at both stations during upwelling seasons, coinciding with high irradiance levels and generally in conjunction with stratified and nutrient−poor conditions in the water column, but also when colder and nutrient−rich subsurface waters upwelled onto the continental shelf. On the contrary, despite minimum abundances were generally found during downwelling periods, unexpectedly high coccolithophore abundances were registered in subsurface waters at the onshore station. This finding was only explained if strong storms during downwelling periods favoured resuspension processes, thus remobilizing deposited coccoliths from surface sediments, and hence hampering the identification of the autochthonous coccolithophore community structure.

Major composition of coccolithophore assemblages at both locations was dominated by *Emiliania huxleyi*, small *Gephyrocapsa group*, *Gephyrocapsa oceanica*, *Florisphaera profunda*, and *Syracosphaera* spp. Ecological preferences of the different taxa were assessed by exploring the relationships between environmental conditions and temporal and vertical variability in coccolithophore abundance. Our findings will provide relevant information in regards to the use of fossil coccolithophore assemblages in marine sediment records to infer environmental conditions in the past, which is of particular relevance in Paleoceanography. *E. huxleyi* and the small *Gephyrocapsa* group are proposed as proxies for the upwelling regime and high primary production. Conversely, *F. profunda* is suggested as a proxy for the downwelling regime and low productivity conditions. Finally, the assemblage composed by *Syracosphaera pulchra*, *Coronosphaera mediterranea*, and *Rhabdosphaera clavigera* may be used as a useful indicator of the presence of warm and nutrient−poor southerly waters conveyed by the Iberian Poleward Current.

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. Molfino and McIntyre, 1990), primary productivity (e.g. Beaufort et al., 1997; Beaufort et al., 2001), and CO_2 (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, upwelling plumes, etc., 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 their fossil abundance 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 Iberian−Canary Upwelling System, 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; Sánchez-Goñi et al., 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 the first yearlong dataset of living coccolithophores based on monthly sampling at several depths at two different stations (one onshore and one offshore) across the NW Iberian margin. This study aims to characterize spatial and temporal variability in coccolithophore productivity as a response to the environmental conditions.

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Our findings will further contribute to infer different paleoceanographic patterns of the NW Iberian coastal upwelling system by analyzing fossil coccolithophore assemblages.

2 Oceanographic setting

Our 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). 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). On the contrary, 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 favorable 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., 2002b; 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; Dias et al., 2002b; 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 favors a decrease in temperature that promotes a well homogenized mixed layer of cold and nutrient−rich waters (Álvarez-Salgado et al., 2003; Castro et al., 2006).

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; 42º05´ N; 8º56´ W, 75 m water depth), and one offshore (52.8 km from the coastline) located at the outer continental shelf (CALIBERIA station; 42º05´ N, 9º23´ 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 dried. Additionally, diatom abundance was determined at 5 m water depth by depositing between 10 and 50 mL in composite sedimentation chambers for observation through an inverted microscope. Sample preparation and analyses for diatom abundance determination are described in detail in Zúñiga et al. (2017). Inorganic nutrients were measured by segmented flow analysis with Futura-Alliances autoanalyzers following Hansen and Grassoff (1983) and pigment extract fluorescence was performed to estimate final Chl *a* concentrations with a Turner Designs fluorometer calibrated using pure Chl *a* (Sigma) (for details, see Zúñiga et al., 2016).

Data of regional irradiance, wave height, upwelling index, and river discharge from July 2011 to June 2012 presented in Zúñiga et al. (2016; 2017) were used in this study to evaluate the influence of physical forcing on coccolithophore abundance and variability (Figs. 2a−d).

3.2 Coccolithophore analyses

A random piece of filter was cut and mounted on a slide and rendered transparent with a few drops of immersion oil. At least 500 coccoliths per sample and all the coccospheres encountered during this process were counted and identified using a polarized light microscope at ×1000 magnification. Estimation of the abundance of rare species (those whose relative abundance was < 2 % in the first count) was refined in a second count considering 20 fields of view per sample. General preservation of coccoliths and coccospheres was determined in every sample based on visual criteria as barren, very poor, poor, moderate, and good following Flores and Marino (2002), and converted into a numerical scale from 0 for barren samples to 4 for good general preservation.

Following Cachão and Oliveira (2000), data sets of free−coccoliths and coccospheres were studied separately. The relative abundance (%) and the absolute abundance (given in coccoliths L^{-1} and cells L^{-1}, for coccoliths and coccospheres, respectively) of each species were calculated for all samples. Absolute abundance (A) was calculated by Eq. (1):

$$A = (C\ a) / (N\ V\ n)$$

where C is the number of coccoliths or coccospheres, N is the number of visual fields considered; V is the volume of the filtered water (mL); *a* is the area of the filter; and *n* is the area per visual field.

Species were classified following Young et al. (2003). *Gephyrocapsa* specimens smaller than 3 µm (*G. aperta* and *G. ericsonii*) were lumped together as 'small *Gephyrocapsa*' (Flores et al., 1999). Non extant species of calcareous nannofossils were counted as "reworked specimens". These belong to older stratigraphic levels and have generally been affected by resuspension and secondary transport by rivers or deep currents (Ferreira et al., 2008), indicating an allochthonous environmental signal.

Total number of coccospheres identified per sample was not statistically significant to ensure a correct estimation of the abundance of both majority and minority species (Fatela and Taborda, 2002). Consequently, only total number of coccospheres was considered and discussed in this study, while assessment of temporal variability and abundance of coccolithophore species is based on the coccolith data set.

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 dataset given that the composition of the coccolithophore assemblage at RAIA station was affected by allochthonous sources (see Sect. 5.1.1.). Ecological relationships were assessed as a function of the distance among them on an ordination graph. Akaike's information criterion (AIC) was applied in a prior ordination analyses to identify the model with the minimum number of environmental variables that, being statistically significant, explained the maximum inertia (i.e. variance in the coccolithophore data). Initially, eleven explanatory variables were considered: temperature, salinity, NO_3^-, HPO_4^{2-}, $Si(OH)_4$, particulate organic carbon (POC), irradiance, wave height, upwelling index, and both Minho River and Douro River discharges. After significant variables were identified via backward procedure, CCA was performed. Barren samples and all the species that do not show a relative abundance greater than 2 % in at least two samples were excluded from the ordination analyses. Ordinations were performed with the "vegan" package v.2.3. (Oksanen et al., 2016) for R (R Core Team, 2015).

In order to evaluate coccolithophore diversity at both stations, the species dominance was measured for each sample using PAST software (Hammer et al., 2001), based on Eq. (2):

$$Dominance = sum((ni/n)^2)$$

where n is the total number of individuals and n_i is number of coccoliths of taxon *i*.

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−March to 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. 2c). On the other hand, from November to January, downwelling favorable 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 2f). Since November till December, anomalously warmer (14−16 ^{0}C), saltier (>35.8), and nutrient−poor (~0.1 μM of HPO_4^{2-}) waters conveyed by the IPC were distinguished (Figs. 2e−g). Finally, during February, winter mixing conditions were also detected with the water column being characterized by colder (< 13 ^{0}C) and more saline (< 35.8) waters with higher nutrient concentration (0.5−0.3 µM of HPO_4^{2-}). Even though warmer and nutrient−poor waters characterized the offshore station, the temperature distribution in the upper layer revealed seasonal patterns similar to the onshore station with comparable Chl *a* concentrations (Fig. 2e−h).

4.2 Diatom abundance

Diatom abundances at 5 m water depth at the RAIA onshore station have been previously discussed by Zúñiga et al. (2017). These peak during the upwelling periods and reach a maximum of ~1 x10^6 cells L^{-1} in September 2011 (Fig. 3a). At the CALIBERIA offshore station, diatom abundances were much lower reaching a maximum of ~200 x10^3 cells L^{-1} during the second upwelling period (March−June 2012).

4.3 Coccolith absolute abundance and coccosphere standing crops

All taxa identified and counted at both stations are listed in Appendix A.

In general, coccolithophore preservation varied from moderate to good (Fig. 3b), allowing identification of nearly all (moderate preservation) or all specimens (good preservation) at species level. At RAIA onshore station, coccosphere absolute abundance was generally very low, except during March and June 2012 at 10 m water depth reaching 1x10^5 and 2x10^5 cells L^{-1}, respectively (Fig. 3c). Coccolith absolute abundance ranged between 0 and 6x10^6 coccoliths L^{-1} (Fig. 3d). Minimum values were registered in July and September 2011 and February 2012 at 10 m. Coccolith minima in September 2011 coincides 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 offshore station, coccosphere absolute abundance ranged between 0−3x10^5 cells L^{-1} (Fig. 3c). Higher values occurred during spring and summer months between 10−50 m depth, reaching maximum numbers in March 2012 (Fig. 3c). On the contrary, coccosphere abundances dropped to minimum levels during winter. Coccolith absolute abundance ranged between 0 and 1.25x10^7 coccoliths L^{-1} (Fig. 3d) with maximum abundances in July 2011 (~7.5x10^6 coccoliths L^{-1}) and June 2012 (~1.25x10^7 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).

The number of coccospheres drastically drops below 50 m water depth at both stations, suggesting that their disaggregation takes places right after the cells die. Comparison of coccolith and coccosphere distributions within each station show two types of coccolithophore blooms. One type was represented by an increase in coccosphere abundance and very low abundance of coccoliths (Type A for short) in September 2011, October 2011 and March 2012 at CALIBERIA, and in March 2012 at RAIA. The other type (Type B) was characterized by an increase in the abundance of both coccospheres and coccoliths, occurring in July 2011, May 2012, and June 2012 at CALIBERIA, and in June 2012 at RAIA. Contrary to Type A blooms, Type B blooms indicate ongoing disaggregation of coccospheres and therefore are expected to represent a more mature bloom.

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4.4 Coccolithophore assemblage

Relative abundances of major coccolithophore species are shown in Fig. 4. *E. huxleyi* was the dominant species, representing an annual average of 60 % and 70 % of the total assemblage at RAIA onshore and CALIBERIA offshore stations, respectively, and achieving percentages higher than 90 % at both stations during the upwelling regime. Other major species were small *Gephyrocapsa* (up to 25 % at RAIA and 40% at CALIBERIA stations), *Gephyrocapsa oceanica* (up to 30% at RAIA and 10% at CALIBERIA stations sampling sites), *Florisphaera profunda* (up to 7 % at RAIA and 40 % at CALIBERIA stations), and *Syracosphaera* spp. (mainly *S. pulchra*, up to 13 % at RAIA and 4 % at CALIBERIA sites). Coccolithophore species that did not exceed 2 % of relative abundance (minor species) in more than one sample were not considered for further analysis (Figs. S1 and S2, supplementary material). Reworked specimens did not exceed 0.2 % of relative abundance for any sample.

4.5 Species absolute abundance and spatial and temporal variability

At the RAIA onshore station, *E. huxleyi* ranged between $2x10^4$ and $5x10^6$ coccoliths L^{-1}. It was more abundant in July at 10 m, similarly to small *Gephyrocapsa* (up to~ $1x10^6$ coccoliths L^{-1}) and *G. oceanica* (up to~ $0.8x10^6$ coccoliths L^{-1}), and it showed a relative maximum during December 2011−January 2012 at 70 m (Fig. 5). *F. profunda* was present during winter at all depths and in May−June 2012 at 70 m water depth. Its highest density (~$1.5x10^5$ coccoliths L^{-1}) occurred in January at 10 m water depth. *Syracosphaera* spp., *Calcidiscus leptoporus*, and *Coccolithus pelagicus* ssp. *braarudii* showed similar distributions, being more abundant below 50 m water depth during the winter months (Fig. S3).

At the CALIBERIA offshore station, *E. huxleyi* (up to $1x10^6$ coccoliths L^{-1}), small *Gephyrocapsa* (up to $0.8x10^6$ coccoliths L^{-1}), and *G. oceanica* (up to $0.2x10^6$ coccoliths L^{-1}) were much more abundant during the upwelling regime, with the latter dominating at greater depths (Fig. 5). *F. profunda* (up to $1x10^6$ coccoliths L^{-1}) only appeared during winter between 50−100 m water depth, while *Syracosphaera* spp. abounded during October−November 2011 and March−June 2012 between 250−300 m water depth, coexisting with *Coronosphaera mediterranea*, and *Rhabdosphaera clavigera* in November 2011 at 10 m water depth (Fig. 5, S1 and S3). Some minor species like *C. leptoporus* were present throughout the studied period, while *C. pelagicus* ssp. *braarudii* appeared mostly during summer, between 100−300 m water depth, and *Coccolithus pelagicus* ssp. *pelagicus* showed a rather patchy distribution (Fig. S3).

4.6 Diversity

At RAIA onshore site, species dominance showed intermediate values for almost the whole studied period (Fig. 6). Maximum variability was registered at 10 m water depth where highest values were recorded during the upwelling regime. On the other hand, at CALIBERIA offshore station, dominance varied both spatially and seasonally, showing a clear decreasing pattern with depth and registering maximum values during the upwelling seasons.

4.7 CCA

The $CCA_{CALIBERIA}$ model explained 54 % of the total inertia in the coccolithophore data. The first canonical axis (CCA1) explained 60 % of this constrained variance and was mostly related to the negative gradient of irradiance, and to the positive gradients of both Douro River and Minho River discharges (Fig. 7). 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 upwelling index. *E. huxleyi* was linked to the upwelling regime samples (June−July) and showed a positive relationship with temperature. Small *Gephyrocapsa* was also related to the upwelling regime (March) but, unlike *E. huxleyi,* linked to increasing upwelling index and HPO_4^{2-}. *F. profunda* was associated to the downwelling regime samples and presented a negative relationship with irradiance. *G. oceanica* was related to HPO_4^{2-} and mainly linked to samples below 50 m water depth. Finally, *Syracosphaera* spp. is related to samples representing intermediate conditions between downwelling− and upwelling−favorable conditions (November 2011 –January 2012).

5 Discussion

5.1 Coccolithophore productivity patterns 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 was 2 orders of magnitude higher than that found by Ferreira and Cachão (2005) for the SW Iberian margin. Unfortunately, very few studies quantify the occurrence of free−coccoliths in the water column, limiting comparison with other regions.

Total coccolithophore abundances were higher at the offshore station if compared with the coastal site (Fig. 3c, and 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. Type A blooms agree with higher Chl *a* values and low diatom abundances offshore in October 2011 and March 2012 (Figs. 2h and 3c). This demonstrates that under more (but not extreme) oligotrophic conditions this phytoplankton group out-competes diatoms (Baumann et al., 2005; Gregg and Casey, 2007), and suggests coccolithophores can possibly be significant contributors to Chl *a* values in the study area. On the contrary, at the onshore 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 (Figure 2h and 3d). These results point to the need of considering coccolithophores to better explain primary production patterns at the outer NW Iberian continental margin. Contrary to Type A blooms, Type B blooms differ significantly between both stations, and thus coccolithophore variability at the onshore and the offshore locations is discussed separately.

5.1.1 Onshore temporal variability of coccolithophore abundance: the influence of coastal processes

At the onshore station, total coccolithophore productivity presented maximum values during both upwelling and downwelling regimes, and except for the blooms in March and June (Type A and B, respectively), coccolith maxima occurred close to the seafloor (75 m). However, no vertical flux of coccoliths nor coccospheres is observed at those times. These unexpected results during autumn−winter, when environmental conditions are unfavorable for coccolithophore growth, can only be explained by the existence of an allochthonous source of coccoliths at the inner continental shelf. Further support for an allochthonous source comes from these "deeper blooms" composition (i.e. November−January and May), with many more taxa than the typical bloom−forming *E. huxleyi* and small *Gephyrocapsa* group recurrently dominating in productive conditions (Tyrrell and Merico, 2004) (Fig. 6). Simultaneously, large increases in wave height are observed (Fig. 2d), that is, high−energy wave−driven processes could have favored the 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 CCA to be applied to the RAIA data set. Guerreiro et al. (2013) have observed a rapid increase in coccolithophore production at the onshore shelf of the central Iberian margin influenced by a nutrient−rich buoyant plume resulting from intense river runoff. Alternatively, our results show that freshwater lenses advected to RAIA station have negligible influence on coccolithophore productivity.

5.1.2 Offshore temporal variability in coccolithophore abundance: seasonal dynamics in coccolithophore productivity

At the offshore site, coccolithophore productivity was seasonally modulated, increasing five orders of magnitude during the summer/upwelling regime and decreasing drastically during the winter/donwelling periods. Except for the Type A bloom in March 2012, summer coccolithophore blooms were associated with high irradiance levels and relaxation of northerly winds during summer, conditions that promoted water column stratification and nutrient depletion (Fig. 2). 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 four year weekly−sampled data set. On the other hand, the Type A bloom found 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 3). Indeed, despite the general association of coccolithophores with weak upwelling and nutrient depletion, our results show that these phytoplankton group may follow diverse life strategies, as demonstrated for this region by Guerreiro et al. (2013).

5.2 Coccolithophore ecology and potential as paleoenvironmental indicators

The coccolithophore assemblage was mainly represented by *E. huxleyi*, small *Gephyrocapsa*, *G. oceanica*, *F. profunda*, and *Syracosphaera* spp. at both stations. The other 15 taxa (Appendix A) were minor species, and their relative and absolute abundances and distribution are shown in the Supplementary material (Figs. S1−S4). Aiming at assessing ecological preferences of coccolithophores in order to explore their potential as proxy of environmental changes in regional oceanographic reconstructions, the discussion is limited to those taxa whose abundance in the water column is reflected in the underlying sediments and/or in the sediment records from the study region.

E. huxleyi dominated the assemblage throughout the studied period regardless of the environmental conditions, but its abundance appeared highly related to the upwelling regime (Fig. 2c and 4). Along with small *Gephyrocapsa*, *E. huxleyi* is responsible for the seasonal and vertical gradient observed in the species dominance, most notably offshore (Fig. 6), dominating the assemblage during the upwelling seasons at shallow depths. These results are 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), where both taxa are proposed as indicators of higher productivity. Interestingly, $CCA_{CALIBERIA}$ relates both taxa to the upwelling regime samples, but also emphasizes a connection of the bloom of small *Gephyrocapsa* with persistent northerly winds occurring during spring when cold and 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 favorable winds relax (Fig. 7). This contradicts findings by Silva et al. (2008), who associated *E. huxleyi* and small *Gephyrocapsa* to spring and summer blooms, respectively. Yet, our outcomes highlight that both species are unambiguously linked to the upwelling regime and high primary production.

G. oceanica was related to nutrient−rich waters below 50 m (Fig. 5), as evidenced by the CCA biplot (Fig. 7). Its higher abundance at the onshore station agreed with previous studies, which identify *G. oceanica* as a component of the lower limit of the photic zone (LPZ) in coastal settings (Baumann and Boeckel, 2013), and relate this species 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., 2014). Such affinity for coastal environments is imprinted in the sedimentary record, as demonstrated by Guerreiro et al. (2015) through the study of surface sediment samples from the central Portuguese margin.

F. profunda was related to the downwelling regime and deeper waters (Figs. 5), in agreement with its classical definition as a LPZ inhabitant (Okada and Honjo, 1973; Molfino and McIntyre, 1990). Since Molfino and McIntyre (1990) pointed to the inverse relationship of *F. profunda* with productivity in the upper photic zone (UPZ), its relative abundance in fossil records has become widely used to qualify and quantify past productivity variations in many oceanic regions (e.g. Beaufort, 1996; Beaufort et al., 1997; Beaufort et al., 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 analyses for CALIBERIA supports this interpretation, relating *F. profunda* to deeper and downwelling regime samples (Fig. 7) at more oceanic locations in the study area. Conversely, and contrary to the expected, its abundance was not linked to deeper but to shallow waters at the onshore station (Fig. 5). 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.

Syracosphaera spp. is a major component during autumn (Fig. 5), in agreement with (Beaufort and Heussner (2001). In spite of previous work (Guerreiro et al., 2015) has suggested that its imprint in the underlying sediments may be underrepresented 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 and in both onshore (Silva et al., 2008) and 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; Silva et al., 2009; Moita et al., 2010) as a tracer for ENACW of subtropical origin (Fiúza, 1983). Except for *H. carteri*, this assemblage was observed offshore in November 2011 (Figs. S1 and S3), when the upper water column was characterized by warmer, saltier and nutrient−poor waters compared to the onshore station (Fig. 2). Although further research is required to assess its preservation in the fossil record, our results broaden its geographical extent as a potential proxy for ENACW of subtropical origin conveyed northward by the IPC. Indeed, this assemblage coexists with *C. leptoporus* (Fig. S3), a tracer of nutrient−depleted water masses of subtropical origin in the study area (Silva et al., 2008; Guerreiro et al., 2014). These authors also pointed to *C. leptoporus* as a typical late−winter representative, a notion that contrasts with its wide vertical and temporal distribution in this study. These differences might be attributed to the existence of morphotypes (intermediate and large), which were not discerned in this study. Silva et al. (2008) observed both forms coexisting during the upwelling regime, but only the intermediate morphotype was observed in winter.

Minor species *C. pelagicus* ssp. *braarudii* and *C. pelagicus* ssp. *pelagicus* have received substantial attention in the western Iberian margin in relation to their potential as indicators of surface water dynamics (Cachão and Moita, 2000; Parente et al., 2004; Narciso et al., 2006a). Nevertheless, little has been documented about their abundance in the water column. Offshore, *C. pelagicus* ssp. *braarudii* appeared at and below 100 m depth (Fig. S3) with absolute abundances in agreement with those found in previous studies (Cachão and Moita, 2000). It seems to be related to the upwelling regime, supporting its affinity for upwelling favorable conditions (Narciso et al., 2006). On the other hand, *C. pelagicus* ssp. *pelagicus* shows no clear affinity for a specific season, temperature or depth range in this study (Fig. S3). Nevertheles, high abundances of this subspecies in sediment cores retrieved off W Iberia are strongly correlated with influxes of subpolar waters in the region during extremly cold conditions (stadials) (Parente et al., 2004; Narciso et al., 2006b; Amore et al., 2012; Palumbo et al., 2013).

6 Conclusions

This paper reports on the first assessment of the temporal and spatial variability of coccolithophore species abundance and vertical distribution in the NW Iberian coastal upwelling system. Our results highlight the role of coccolithophores as significant primary producers in the study area, being strongly correlated with higher values of Chl *a* at the outer Iberian margin continental shelf. Indeed, an onshore−offshore gradient was observed in coccolithophore abundance, contrary to that of diatoms, with an increase in coccolithophore abundance towards the outer shelf where the water column was characterized by relatively more oligotrophic conditions. Even so, temporal variability in coccolithophore abundance differs between stations. Onshore, coastal processes like strong stormy events were found to resuspend coccoliths from the underlying sediments, masking the autochthonous coccolithophore assemblage in the water column and hampering interpretation of their ecology. Offshore, the variability in coccolithophore abundance is modulated by the seasonal upwelling−downwelling regime. Most coccolithophore blooms were observed during spring−summer when high irradiance levels and upwelling favorable winds promotes optimal conditions for coccolithophore growth. We found that coccolithophore blooming occurred mostly under stratified and nutrient−poor conditions, but also when the cold and nutrient−rich ENACW upwelled onto the continental shelf.

This information on coccolithophore ecology will 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. Especially in offshore locations, far from the influence of coastal hydrodynamic processes, increases in the absolute abundance of *E. huxleyi* and the small *Gephyrocapsa* group might be indicators of higher productivity generated by upwelling conditions. Conversely, *F. profunda* is proposed as a proxy for the downwelling regime and low productivity conditions. The assemblage composed by *S. pulchra*, *C. mediterranea*, and *R. clavigera* may be used as an indicator of the presence of warm and nutrient−poor southerly waters conveyed by the IPC.

Appendix A. Taxonomic list of the identified species. Their presence at each station is noted by x.

Taxon	CALIBERIA	RAIA
Braarudosphaera bigelowii (Gran & Braarud 1935)	x	x
Coronosphaera mediterranea (Lohmann, 1902)	x	x
Calcidiscus leptoporus (Murray & Blackman 1898)	x	x
Coccolithus pelagicus ssp. *braarudii* (Gaarder 1962)	x	x
Coccolithus pelagicus (Wallich 1877) Schiller 1930 ssp. *pelagicus*	x	x
Discosphaera tubifera (Murray & Blackman, 1898)	x	
Emiliania huxleyi (Lohmann 1902)	x	x
Florisphaera profunda (Okada & Honjo 1973)	x	x
Gephyrocapsa aperta Kamptner 1963	x	x
Gephyrocapsa ericsonii McIntyre & Bé 1967	x	x
Gephyrocapsa muellerae Bréhéret 1978	x	x
Gephyrocapsa oceanica Kamptner 1943	x	x
Gladiolithus flabellatus (Halldal & Markali 1955)	x	
Helicosphaera spp., (mainly *H. carteri* (Wallich 1877))	x	x
Oolithotus fragilis (Lohmann 1912)	x	x
Pontosphaera spp. Schiller 1925	x	x
Rhabdospahera clavigera Murray & Blackman 1898	x	x
Scyphosphaera apsteinii Lohmann, 1902	x	x
Syracosphaera spp. (mainly *S. pulchra*, Lohmann 1902)	x	x
Umbellosphaera spp., (mainly *U. tenuis* (Kamptner 1937))	x	x
Umbilicosphaera sibogae (Weber-van Bosse 1901)	x	x

Competing interests. The authors declare that they have no conflict of interest

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Table 1. Maximum coccolithophore abundance (cells L^{-1}) reported in this study, in other works from the Iberian Margin and in major upwelling areas in the Atlantic Ocean.

	Reference	Oceanic region	Region	Maximum cells L^{-1}	Environmetal conditions
Iberian Margin	This study	Portuguese Margin	CALIBERIA (offshore)	3x10^{5}	Summer regime, colder and more nutrient waters
	This study	Portuguese Margin	RAIA (onshore)	2x10^{5}	Summer regime, warmer and oligotrophic waters
	Cachão et al. (2000)	Portuguese Margin	Northwest (Oporto)	2.7x10^{5}	Winter regime, upwelling conditions, and local runoff
	Silva et al. (2008)	Portuguese Margin	Central West Lisbon Bay	2x10^{3}	Declining phase of the upwelling event
	Guerreiro et al. (2013)	Portuguese Margin	Central West (Cape Carvoeiro)	1.5x10^{5}	Winter regime, upwelling conditions but decreasing nutrient content, river discharge
	Abrantes and Moita (1999)	Portuguese Margin	Southwest (Cape Saint Vicent)	3x10^{4}	Summer regime, warmer waters
	Cachão et al. (2000)	Portuguese Margin	Southwest (Cape Saint Vicent)	8.4x10^{4}	Winter regime, upwelling conditions
Other major upwelling areas in the Atlantic Ocean	Abrantes et al. (2002)	North Atlantic	NW Africa	5x10^{3}	Local upwelling
	Kinkel et al. (2000)	Equatorial Atlantic	Equatorial upwelling	3×10^{6}	Upwelling conditions
	Giraudeau et al. (1993)	South Atlantic	Benguela	4.6×10^{5}	Low turbulence and low nutrient content
	Mitchell-Innes and Winter (1987)	South Atlantic	South Africa (Cape Peninsula)	2×10^{6}	Declining phase of the upwelling event

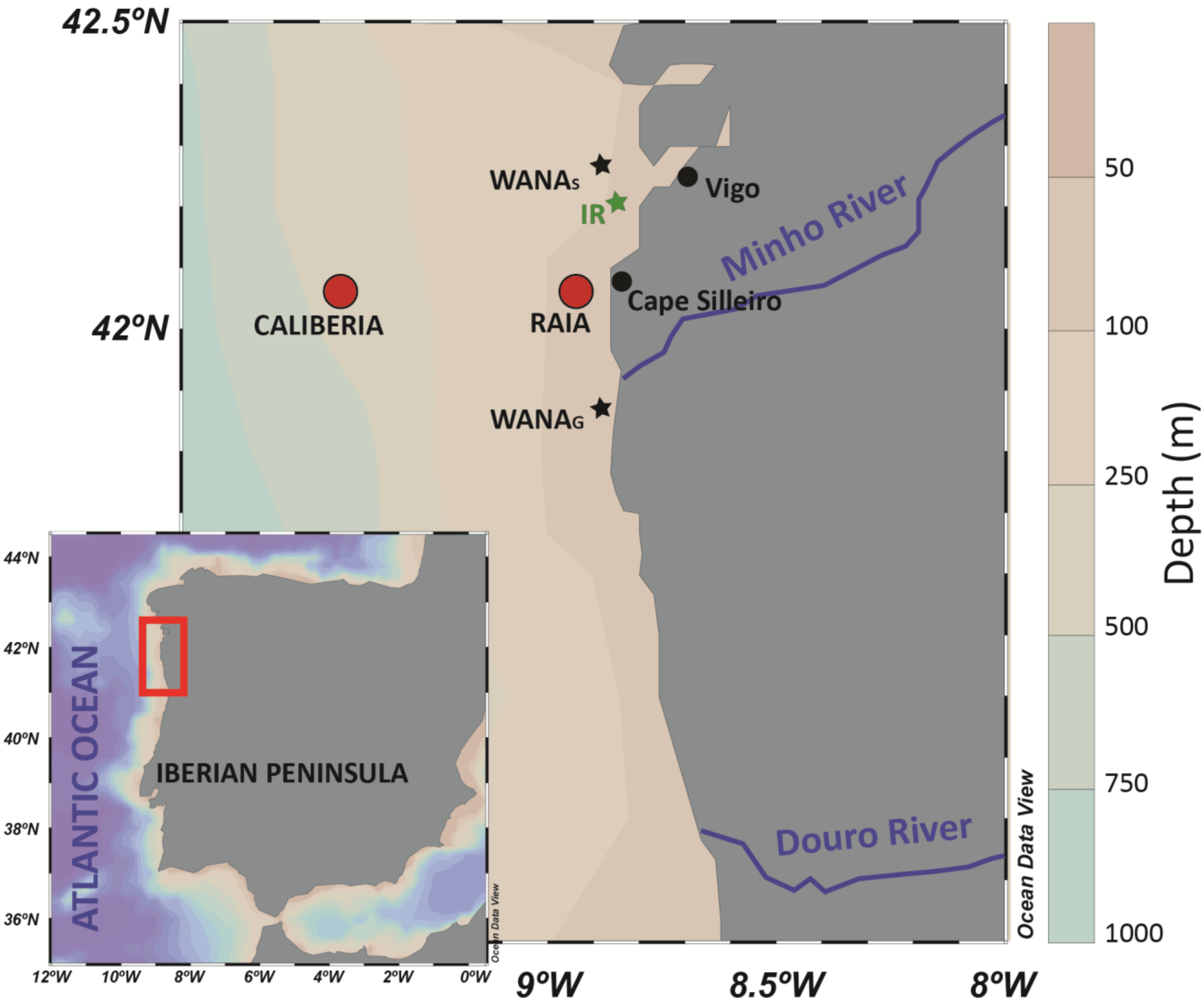

Figure 1. Map of the NW Iberian Margin showing CALIBERIA and RAIA stations. Location of Cíes meteorological station (IR, in green), and WANA hindcast reanalysis points WANAS and WANAG (black stars) from which irradiance and wave data were respectively obtained (Zúñiga et al. 2016). Modified from Zúñiga et al. (2016).

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Discussion started: 3 July 2017

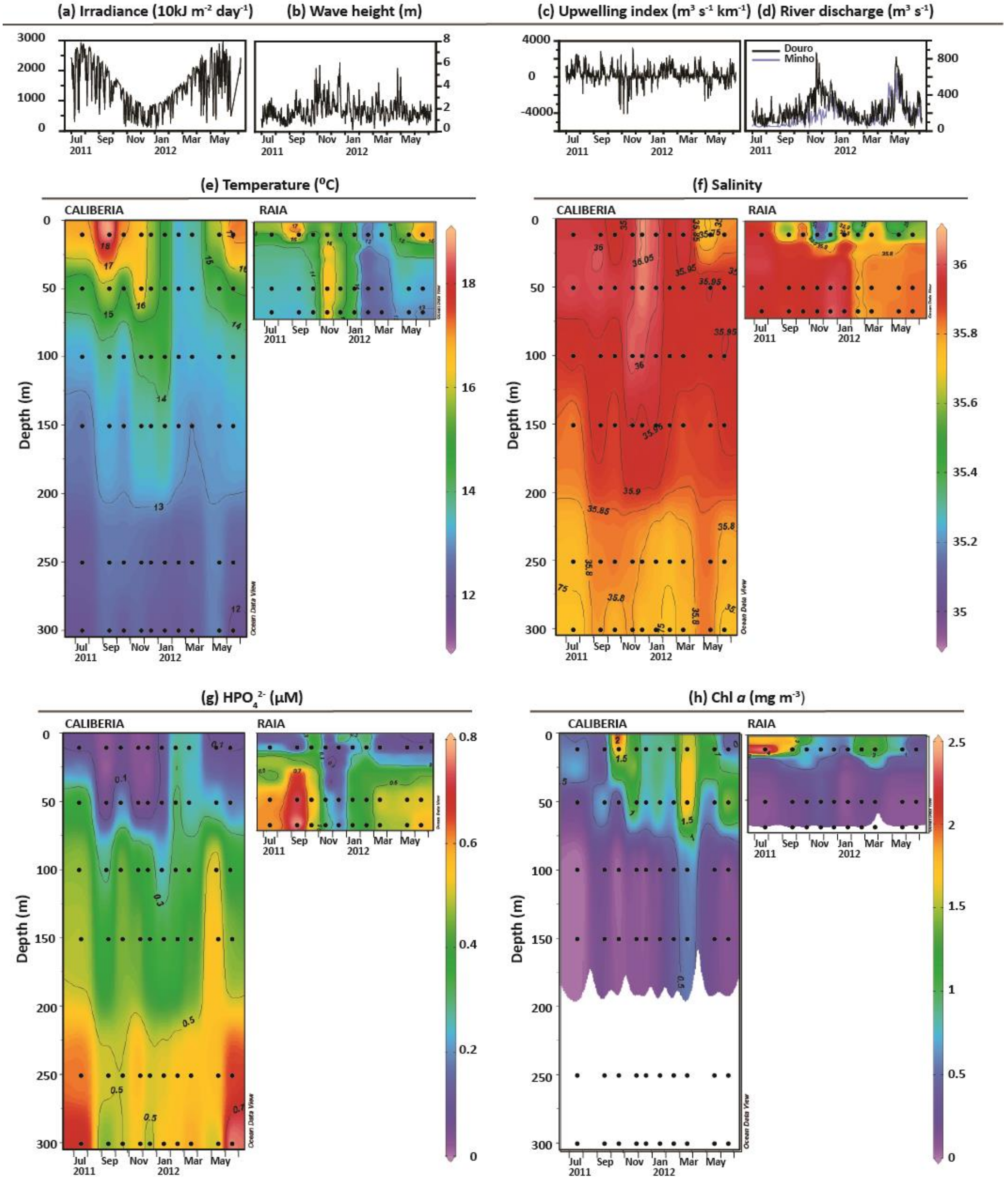

Figure 2. Environmental conditions for the studied period. Available data on a) irradiance, b) wave height, c) upwelling index, and d) discharges by Minho (blue) and Douro (black) Rivers (Zúñiga et al., 2016; 2017). Temporal and vertical distribution of e) temperature, f) salinity, g) HPO_4^{2-}, and h) Chl *a* at CALIBERIA and RAIA stations. Black dots represent collected water samples for coccolithophore analyses.

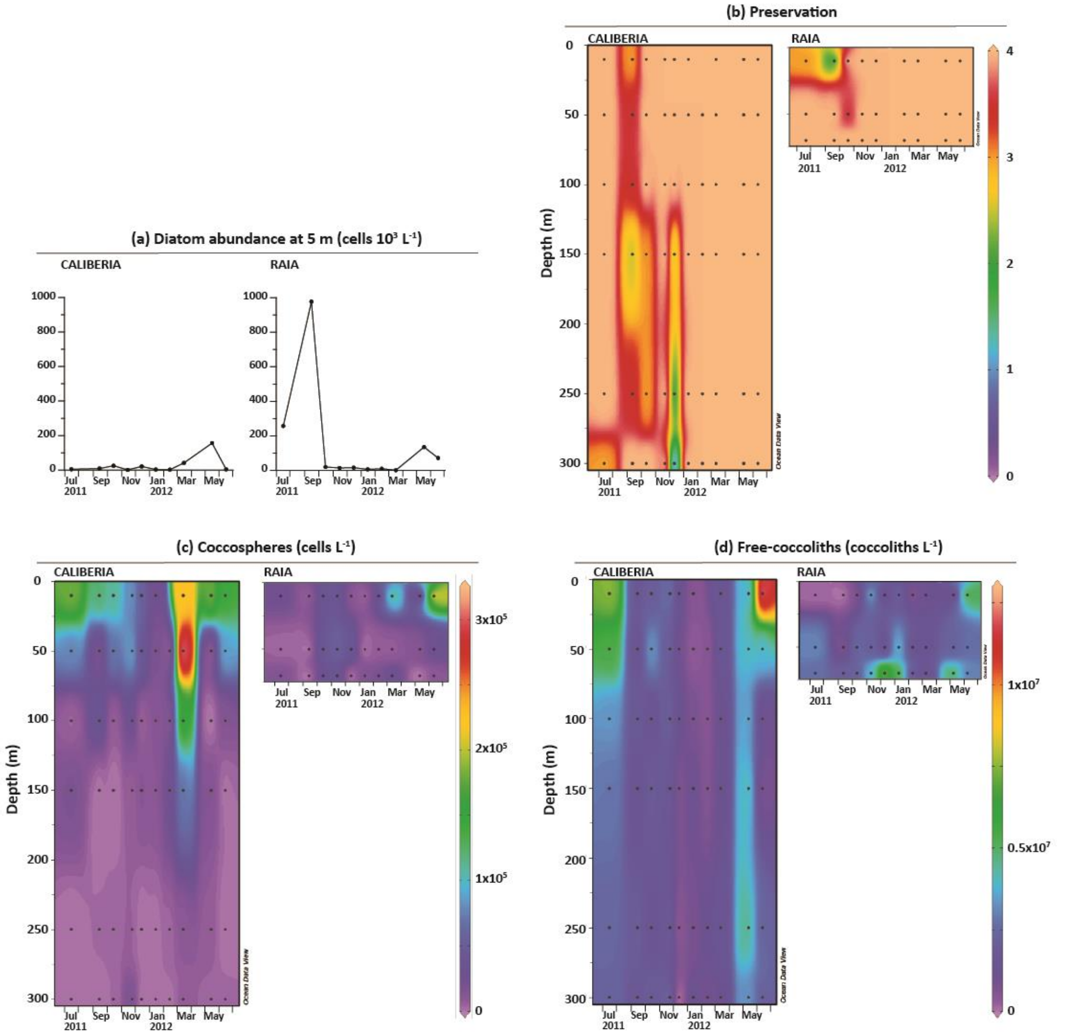

Figure 3. a) Diatom absolute abundance (cells 10^3 L^{-1}) at 5 m at CALIBERIA (this study) and RAIA (Zúñiga et al., 2017); b) Preservation of coccolithophore samples; and temporal and vertical distribution of the total number of c) coccospheres (cells L^{-1}) and d) free-coccoliths (coccoliths L^{-1}), at CALIBERIA and RAIA stations. Black dots represent the sampling month and depth. See text for conversion of numeric values in preservation color bar to the corresponding qualitative preservation.

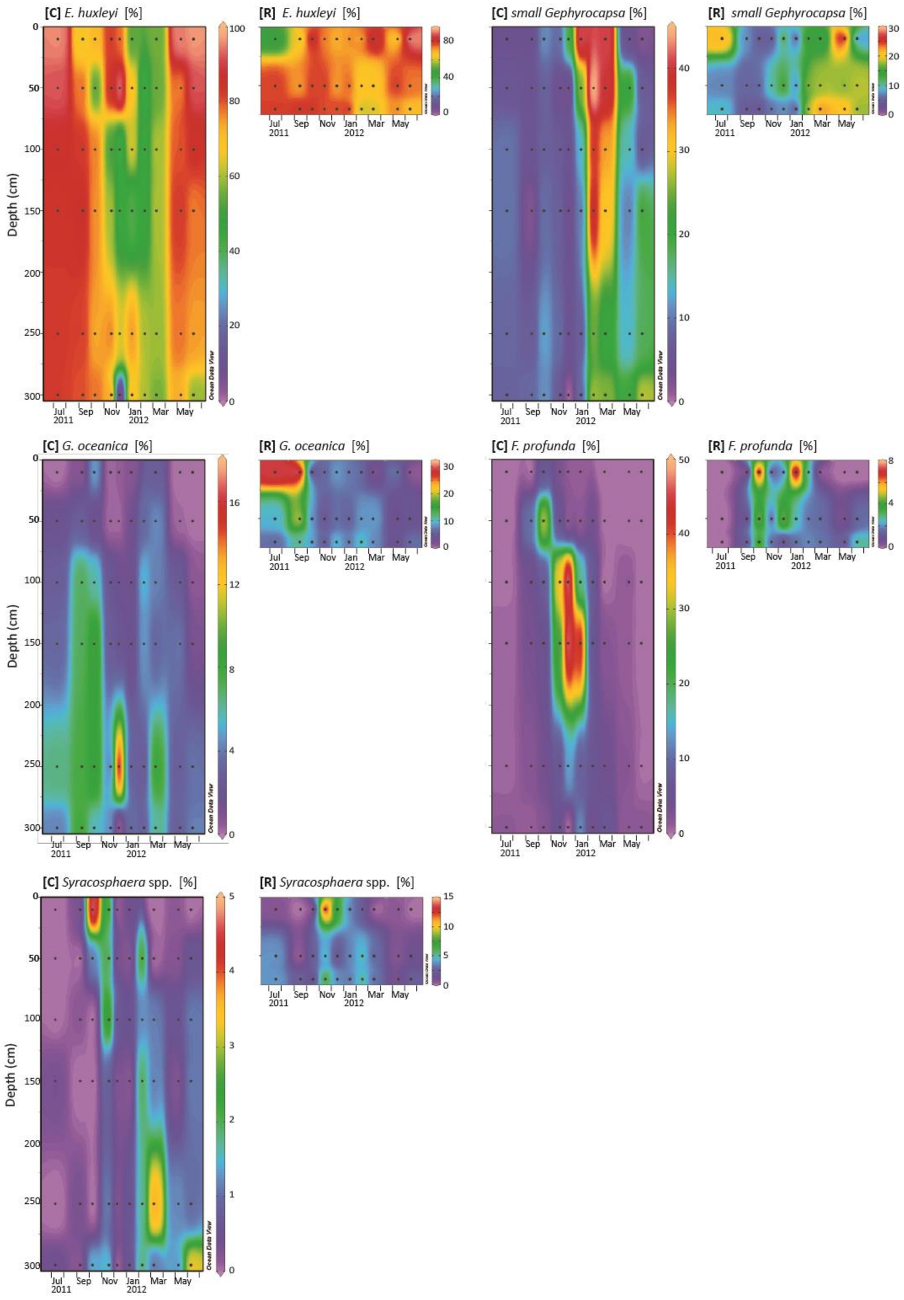

Figure 4. Relative abundance of major coccolithophore species. Temporal and vertical distribution of the relative abundance of major species of coccoliths (%) at CALIBERIA (indicated by [C]) and RAIA (indicated by [R]) stations. Black dots represent the sampling month and depth. Note that each color bar has been scaled to the maximum and minimum values of its corresponding species.

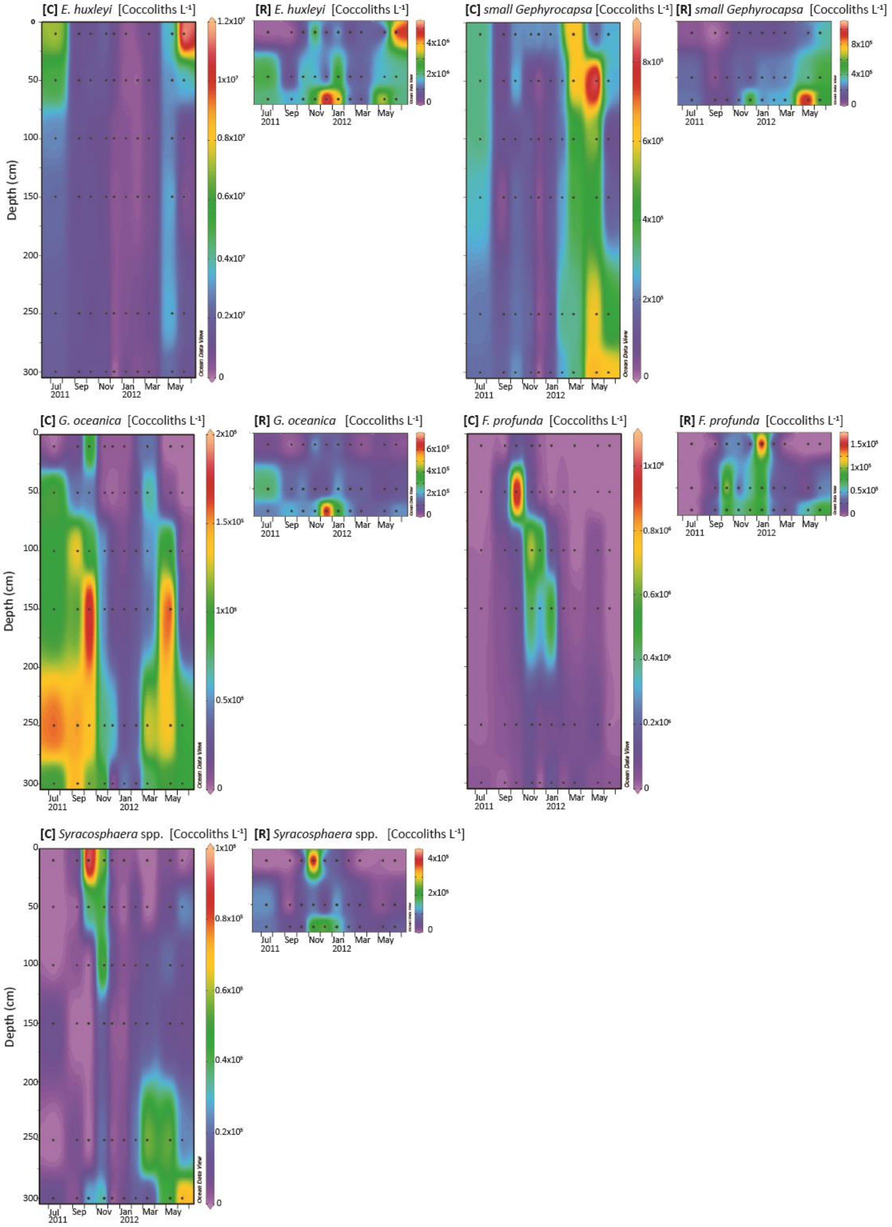

Figure 5. Absolute abundance of major coccolithophore species. Temporal and vertical distribution of the absolute abundance of major species of coccoliths (coccoliths L^{-1}) as in Figure 4.

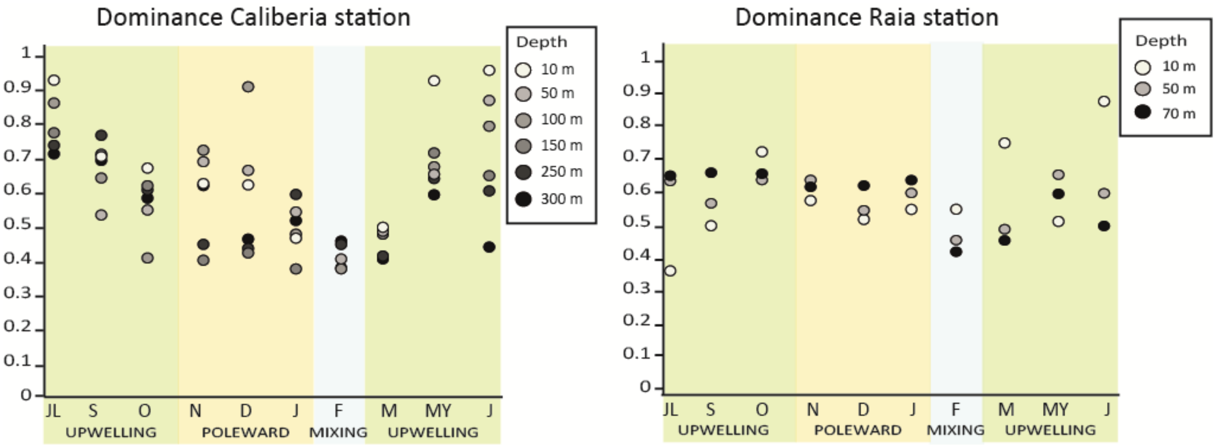

Figure 6. Species dominance at CALIBERIA (left panel) and RAIA (right panel), during the upwelling, Iberian Poleward Current (IPC), and mixing periods.

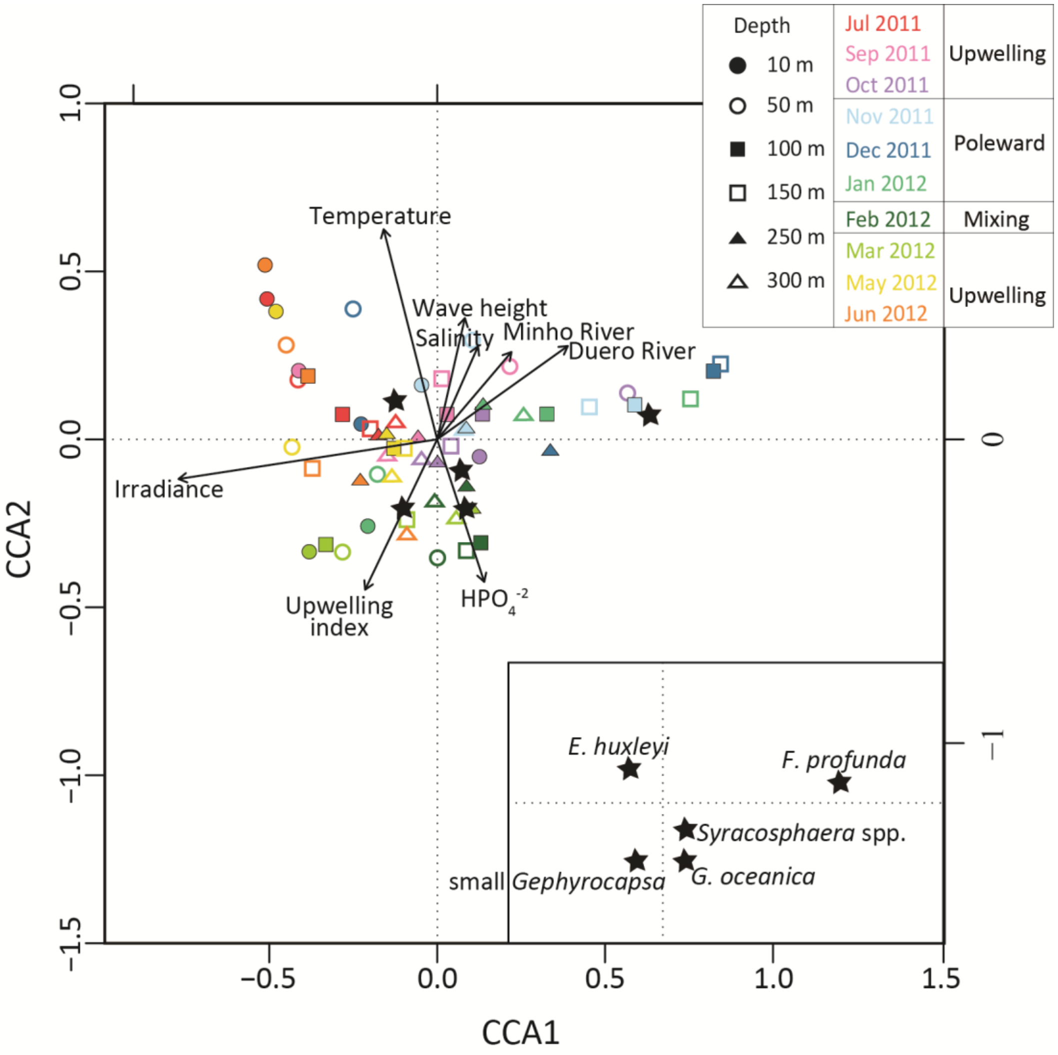

Figure 7. Ordination graph for the first two axes of the CCA for CALIBERIA datasets. The species scores are represented by stars and environmental variables by arrows. Samples are shown through colored symbols according to their sampling month and depth.

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