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

B. Ausín[1,2] (blanca.ausin@erdw.ethz.ch), D. Zúñiga[3,4,5] (diana.zuniga@uvigo.es), J.-A. Flores[1] (flores@usal.es), C. Cavaleiro [4,5,6] (catarina.cavaleiro@ipma.pt), M. Froján[3] (mariafrojan@iim.csic.es), N. Villacieros-Robineau[7] (nvrobineau@gmail.com), F. Alonso-Pérez[3] (fernando@iim.csic.es), B. Arbones[3] (belen@iim.csic.es), C. Santos [4,5,6,8] (celia.neto@ipma.pt), F. de la Granda[9] (francisco.delagranda@bsh.de), C. G. Castro[3] (cgcastro@iim.csic.es), F. Abrantes[4,5](fatima.abrantes@ipma.pt), T. Eglinton[2] (timothy.eglinton@erdw.ethz.ch), E. Salgueiro[4,5](emilia.salgueiro@ipma.pt)

[1]Departamento de Geología, Universidad de Salamanca, Salamanca, 37008, Spain
[2]Department of Earth Sciences, ETH Zurich, Zurich, 8092, Switzerland
[3] Instituto de Investigaciones Marinas (IIM), Consejo Superior de Investigaciones Científicas (CSIC), Vigo, E-36208, Spain
[4] Div. Geologia e Georecursos Marinhos, Instituto Português do Mar e da Atmosfera (IPMA), Lisbon, 1749-077, Portugal
[5] CCMAR - Centre of Marine Sciences, Universidade do Algarve, Faro, 8005-139, Portugal
[6] MARUM, Center for Marine Environmental Sciences, Bremen, 28359, Germany
[7]Laboratoire d´Oceanographie et du Clima, Université Pierre et Marie Curie, Paris, 75005, France
[8]Alfred Wegener Institute, Helmholtz Center for Polar and Marine Sciences, Bremerhaven, D-27570, Germany
[9]Federal Maritime and Hydrographic Agency, Hamburg, 20359, Germany

Correspondence to: Blanca Ausín (blanca.ausin@erdw.ethz.ch)

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 coccolithophore 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 coccolithophore 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 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 coccolithophore 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

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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 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.

Keywords: extant coccolithophore ecology, coccolith, Iberian margin, coastal upwelling, water column

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 abundance of calcareous nannofossils 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; 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

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et al., 2013; Guerreiro et al., 2014), being scarce for northern locations (Abrantes and Moita, 1999; Moita, 2001). In this context, we present a yearlong dataset of living coccolithophores 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 analyzing 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). 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 (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; 42º05´ N; 8º56´ W, 75 m water depth), and one further 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

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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, Bakun's 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 and coccolith 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. 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. Excluding barren samples, at least 500 coccoliths per sample and all the coccospheres (i.e. coccolithophores) encountered during this process (ranging from 100 to 300) were counted and identified using a polarized light microscope at ×1000 magnification. Consequently, species with a relative abundance > 2% could be detected with a confidence limit of 99.5% for the coccolith data set, and within a confidence limit range of 90%-99.5% for the coccosphere data set (Fatela and Taborda, 2002).

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 coccolithophore, 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 coccolithophores, 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* group' (Flores et al., 1999). Distinct morphotypes of the species *Coccolithus pelagicus* were classified according to coccolith size criteria (*C. pelagicus* ssp. *braarudii* (> 10 µm) and *C. pelagicus* ssp. *pelagicus* (< 10 µm)) following Parente et al. (2004). Non-extant species of calcareous nannofossils were counted as

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"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.

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 RAIA station was affected by resuspension of coccoliths from the underlying sediments, which may also 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 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, Bakun's upwelling index, and both Minho River and Douro River discharges. For each variable, three different temporal resolutions were considered averaging the available data corresponding to: the sampling date, the sampling day plus two days before, and the sampling day plus four days before. Barren samples were excluded from the ordination analyses and only major coccolithophore species (those with a relative abundance > 2 % in at least 2 samples and whose confidence limit of detection is > 90% in this study) were considered. After significant variables were identified via backward procedure, CCA was performed. Ordinations were performed with 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 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-} 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 homogenously characterized by colder waters (< 13 ^{0}C) with salinity values < 35.8 and higher nutrient concentration (0.3–0.5 μM of HPO_4^{2-} and 2.5–5 μM of NO_3^-). The outer-shelf station

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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 in 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 x10^6 cells L^{-1} in September 2011 (Fig. 3a). At the CALIBERIA outer-shelf station, diatom abundances were much lower reaching a maximum of ~200 x10^3 cells L^{-1} during the second upwelling period (March–June 2012).

4.3 Total coccolithophore and coccolith absolute abundances

In general, coccolithophore 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, coccolithophore 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).

At CALIBERIA outer-shelf station, coccolithophore absolute abundance ranged between 0−3x10^5 cells L^{-1} (Fig. 3c). Higher cell densities occurred during spring and summer months between 10−50 m depth, reaching maximum numbers in March 2012 (Fig. 3c). On the contrary, coccolithophore 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 6x10^7 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 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 outer-shelf station, 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).

Distributions of total both coccolithophore and coccolith abundances within each station are in general agreement. One exception is found in March 2012 at both stations, when the maximum of coccolithophores does not have a counterpart in the

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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 coccolithophore abundance.

4.4 Major assemblage composition

Assemblages of both forms, coccolithophores 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 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 5x10^5 cells L^{-1}, being more abundant in March and June 2012 at 10 m, similarly to small *Gephyrocapsa* group (up to ~4x10^4 cells L^{-1}) (Fig. 6). *G. oceanica* (up to ~8x10^3 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 (~5x10^3 cells L^{-1}) at 50 m. *Syracosphaera* spp. and *C. leptoporus* were present in November, the former at 10 (1x10^3 cells L^{-1}) and the latter at 50 m water depth (1.5x10^4 cells L^{-1}) (Fig. 6). *C. mediterranea* shows higher density (3x10^4 cells L^{-1}) in June 2012 at 10 m and lower abundances in February and March. Coccolith and coccolithophore 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).

4.6. Outer-shelf temporal variability in species absolute abundance

At the CALIBERIA outer-shelf station, *E. huxleyi* (up to 2x10^5 cells L^{-1}) was much more abundant during the upwelling regime (Fig. 7). Small *Gephyrocapsa* group (up to 1.75x10^5 cells L^{-1}) and *G. oceanica* (up to 1.4x10^5 cells L^{-1}) showed their highest abundance in March 2012, with the latter dominating at greater depths. *F. profunda* (up to 5x10^4 cells L^{-1}) only appeared during winter, mostly between 50−100 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 (2x10^4 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 at and 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. Yet, coccoliths showed a wider vertical distribution (Fig. 7). Coccoliths of *G. oceanica* were much more abundant during the upwelling regime if compared with coccolithophores of the same species.

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¶
Species absolute abundance and spatial and temporal variability¶
At the RAIA onshore station, *E. huxleyi* ranged between 2x10^4 and 5x10^6 coccoliths/L. It was more abundant in July at 10 m, similarly to small *Gephyrocapsa* (up to~1x10^6 coccoliths/L) and *G. oceanica* (up to~0.8x10^6 coccoliths/L), 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) 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), small *Gephyrocapsa* (up to 0.8x10^6 coccoliths/L), and *G. oceanica* (up to 0.2x10^6 coccoliths/L) were much more abundant during the upwelling regime, with the latter dominating at greater depths (Fig. 5).

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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 CCA$_{CALIBERIA}$ model explained 51 % of the constrained inertia (i.e. variance) in the coccolithophore 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. 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 to 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 coccolithophore 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 coccolithophores drastically drops below 50 m water depth, possibly due to rapid zooplankton grazing and coccolithophore disaggregation into coccoliths.

Total abundance of both, coccolithophores and coccoliths, were higher at the outer-shelf station if 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

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contributors to Chl *a* values in the study area. On the contrary, 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 coccolithophores to better explain primary productivity patterns at the NW Iberian continental margin.

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

At the inner-shelf station, total coccolithophore 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 unfavorable 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 favored 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 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 coccolithophore abundance (Figs. 2f and 3d).

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

At the outer-shelf site, coccolithophore 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 coccolithophore maximum in March 2012 at both stations, summer coccolithophore 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 four year weekly−sampled data set. On the other hand, the coccolithophore 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

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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

Both the coccolithophore and coccolith major assemblages were mainly represented by *E. huxleyi*, 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 coccolithophore assemblage, in the water column of RAIA station, discussion on coccolithophore ecology will be uniquely based on the coccolithophore 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 favorable 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 week 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., 2014). Its highest abundance coincides with maximum Chl *a* values and higher nutrient content (Figs. 2g-i and 7), suggesting rapid response to nutrient availability (Guerreiro et al., 2013). This is supported by comparison of the temporal distribution of *G. oceanica* coccolithophores and coccoliths. Water column conditions during the upwelling regime in July-November and May-June indicate ongoing relaxation of the upwelling event; at those times, only coccoliths of *G. oceanica* are present, indicating an ongoing or already terminated decay of the species population (Cachão and Oliveira, 2000). On the contrary, in March, only coccolithophores 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 (Figs. 7), 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 been widely used to qualify and quantify past productivity variations in many oceanic regions (e.g. Beaufort, 1996;

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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. 8). Considering that the influence of Duero and Minho River discharges is limited to the fist 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 consequence of their common temporal occurrence during the winter months. Contrary to the expected, 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.

Syracosphaera 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) 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 close to the shore (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 further offshore in November 2011 (Figs. 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 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) describes *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; Silva et al., 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.

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 nannoplankton as primary

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producers in the study area and suggest 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 coccolithophore abundance, contrary to that of diatoms, with an increase in both coccolithophore and coccolith abundances towards the outer shelf where the water column was characterized by relatively more oligotrophic conditions. Even so, temporal variability in coccolithophore 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 coccolithophore 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 favorable winds promote optimal conditions for coccolithophore growth. We found higher coccolithophore 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 regime and low productivity conditions. The assemblage composed by *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.

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

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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

Acknowledgements

The authors want to thank the Captain and crew of the RV 'Mytilus (CSIC)'. This work was funded by the EXCAPA project (10MDS402013PR) funded by Xunta de Galicia, and CALIBERIA project supported the coccolithophore analysis (PTDC/MAR/102045/2008 from Fundação para a Ciência e a Tecnologia -Portugal- and COMPETE/FEDER -FCOMP-01-0124-FEDER-010599). Project CGL2015-68459-P from Ministerio de Economía y Competitividad also contributed to the founding of this study. B.A. was supported by a FPU grant (AP2010-2559) of the Ministry of Education of Spain and by an ETH Zurich Postdoctoral Fellowship from the Swiss Federal Institute of Technology in Zurich (ETHZ). D.Z. was funded by a postdoctoral fellowship (Plan I2C) from Xunta de Galicia (Spain). F.G. was funded by RAIA.co (0520_RAIA.co_1_E). N. V-R. was funded by Isabel Barreto Program (Xunta de Galicia, Spain). M.F. (BI/PTDC/MAR/102045/2008/2010-016), C.S. (BI/ PTDC/MAR/102045/2008/2010-022) and C.C. (BI/PTDC/MAR/102045/2008/2011-027) were supported by CALIBERIA project. E.S. was funded by a postdoctoral fellowship (SFRH/ BPD/111433/2015) from FCT and from Plurianual/Estratégico project (UID/Multi/04326/2013).

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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 (outer-shelf)	$3x10^5$	Summer regime, colder and more nutrient waters
	This study	Portuguese Margin	RAIA (inner shelf)	$2x10^5$	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

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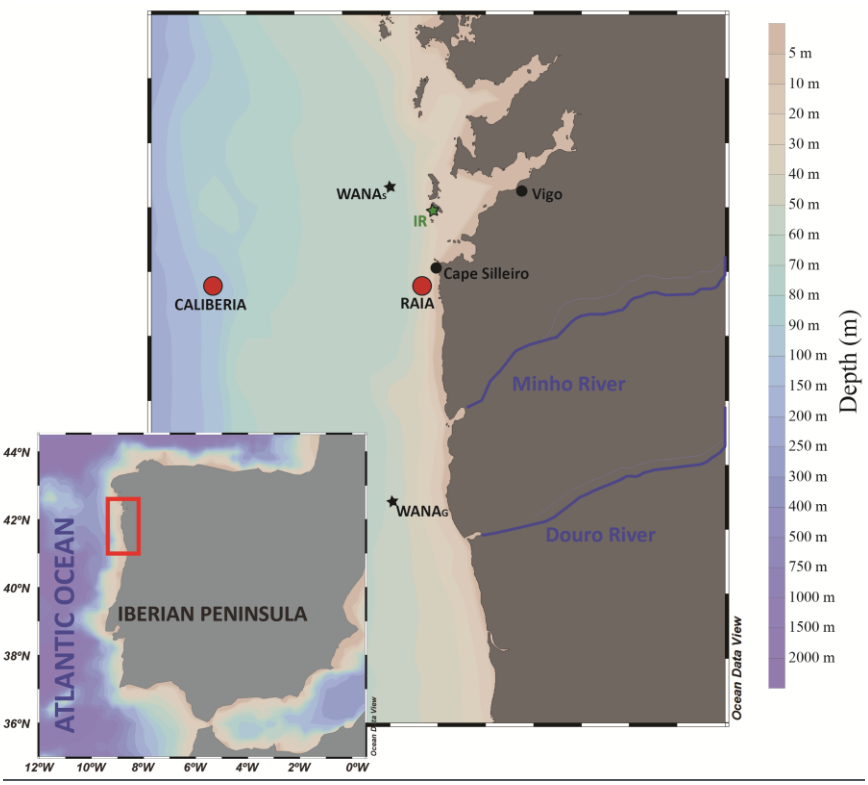

Figure 1. Map of the NW Iberian Margin showing CALIBERIA and RAIA stations. Location of Cíes meteorological station (IR, in green), and WANA hindcast reanalysis points WANA$_S$ and WANA$_G$ (black stars) from which irradiance and wave data were respectively obtained (Zúñiga et al. 2016).

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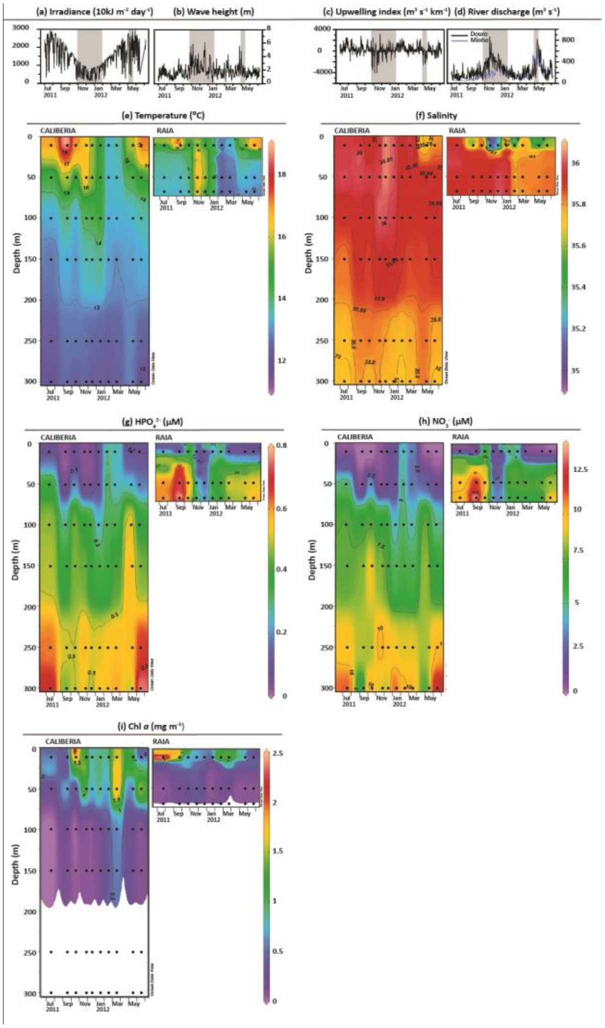

Figure 2. Environmental conditions for the studied period. Available data on a) irradiance, b) wave height, c) Bakun's upwelling index, and d) discharges by Minho (blue) and Douro (black) Rivers (Zúñiga et al., 2016; 2017). Grey and white bars represent downwelling and upwelling periods, respectively, 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.

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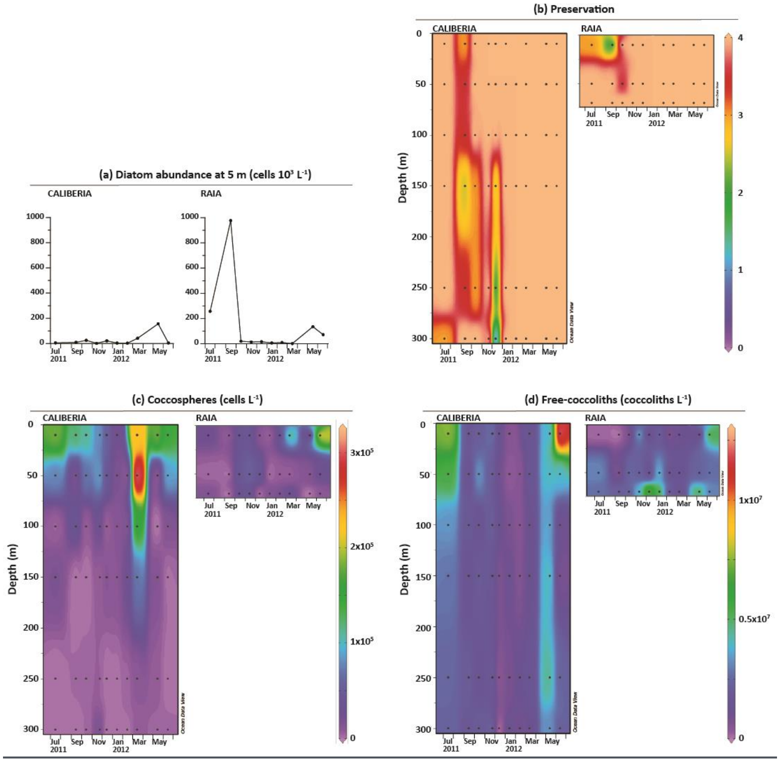

Figure 3. a) Diatom absolute abundance (cells 10^3 L^{-1}) at 5 m at CALIBERIA (this study) and RAIA (Zúñiga et al., 2017); b) Preservation of coccolithophore samples; and temporal and vertical distribution of the total number of c) coccolithophores (cells L^{-1}) and d) free-coccoliths (coccoliths L^{-1}), 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.

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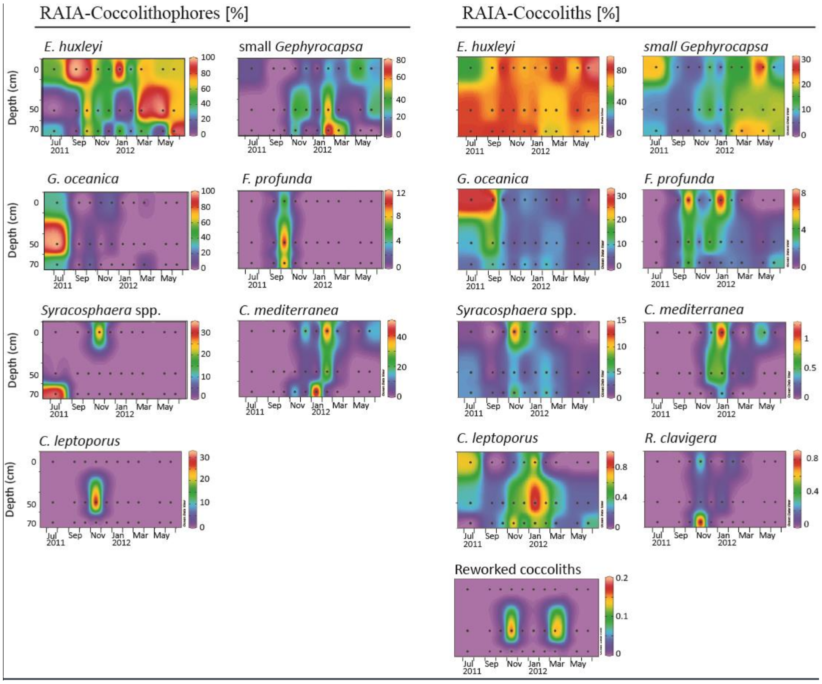

<u>Figure 4. Relative abundance (%) of major species of coccolithophores (left panel) and coccoliths (right panel) in RAIA station. Black dots represent the sampling month and depth. Note that each color bar has been scaled to the maximum and minimum values of its corresponding species.</u>

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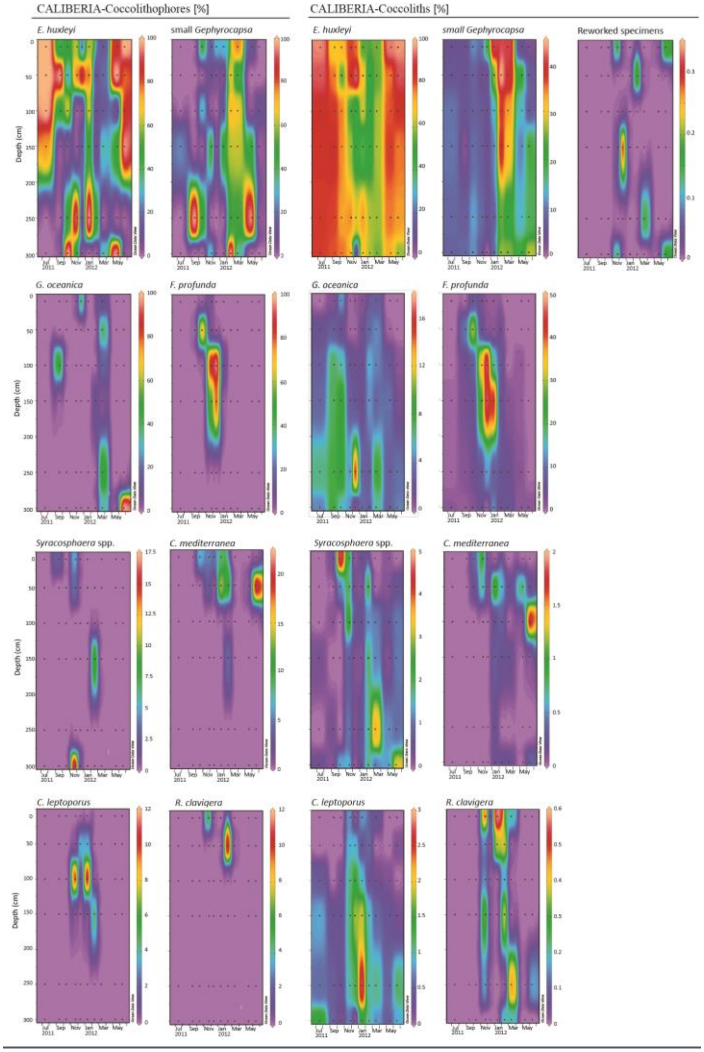

Figure 5. Relative abundance (%) of major species of coccolithophores (left panel) and coccoliths (right panel) in CALIBERIA station. Black dots represent the sampling month and depth. Note that each color bar has been scaled to the maximum and minimum values of its corresponding species.

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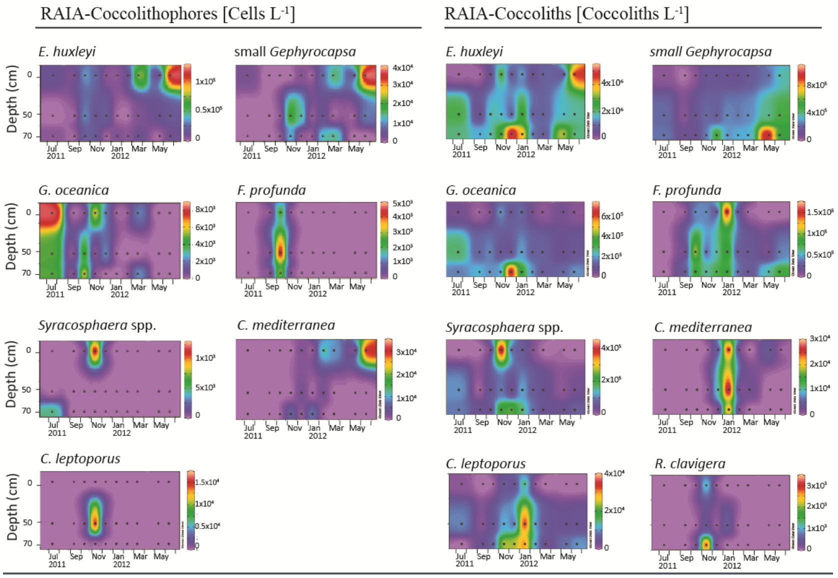

Figure 6. Absolute abundance of major species of coccolithophores (left panel, given in Cells L^{-1}) and coccoliths (right panel, given in coccoliths L^{-1}) in RAIA station. Black dots represent the sampling month and depth. Note that each color bar has been scaled to the maximum and minimum values of its corresponding species.

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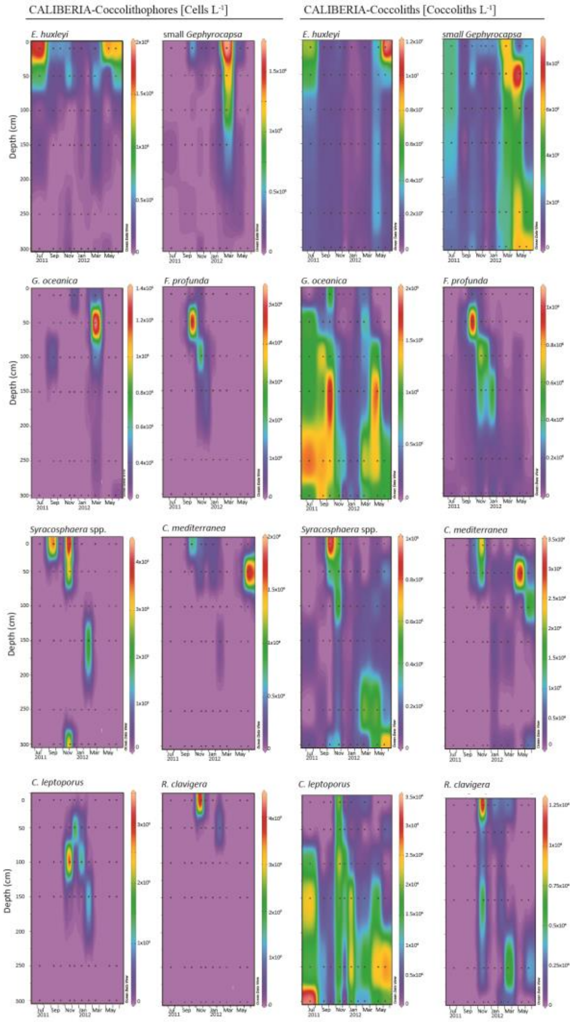

Figure 7. Absolute abundance of major species of coccolithophores (left panel, given in Cells L^{-1}) and coccoliths (right panel, given in coccoliths L^{-1}) in CALIBERIA station. Black dots represent the sampling month and depth. Note that each color bar has been scaled to the maximum and minimum values of its corresponding species.

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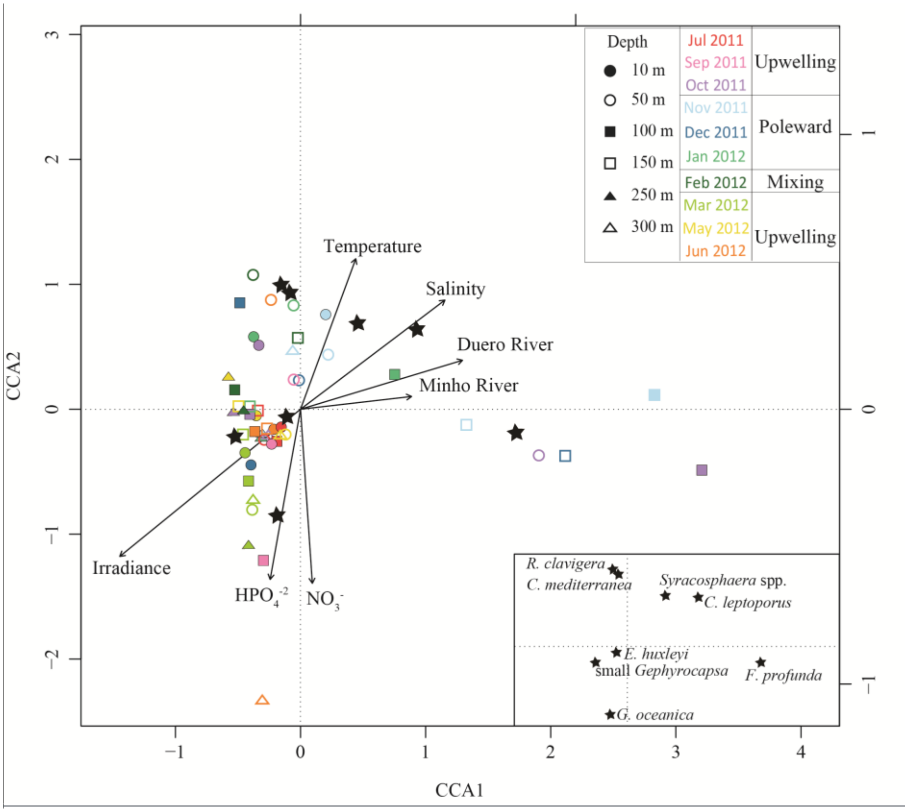

Figure 8. Ordination graph for the first two axes of the CCA for CALIBERIA datasets. The species scores are represented by stars and environmental variables by arrows. Samples are shown through colored symbols according to their sampling month and depth.

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List of relevant changes made in the manuscript:

- In this new version, we base our interpretations in coccolithophore ecology on the coccolithophore data set, instead of the coccolith data set, a point that was raised by the fourth reviewers. *Results*, *discussion*, and *conclusions* sections have been modified accordingly.
- We have re-organized and restructured text.
- We have also produced new figures and reorganized them according to the reviewers' suggestions.

We want to thank Mário Cachão for his thoroughly revision of this manuscript, which we find relevant and constructive. We have reviewed our manuscript following his suggestions and made the appropriate changes whenever possible.
Here, we address the three main concerns Cachão raises on our Manuscript.

1. Although authors refer to our paper of the
Liths/Spheres model to justify (and well) to keep both data sets separately, the manuscript often refers to coccolithophore abundances based on coccolith abundances and not cell(coccosphere) abundances which may induce the reader (specially the biologically driven reader) in error. Thus, this paper should be mainly dealing with coccosphere abundances. Coccolith data should be used to complement and compare to the cell counts (the model L/S cannot be applied because the sampling was performed monthly) and not the other way around as this paper does;

We decided to use the coccolith species data set in the previous version because:

i) a previous exploratory analyses showed that temporal distribution of coccolithophore species and their corresponding coccoliths was very similar (of course they differed in their vertical distribution since rarely coccospheres make it to the seafloor).

ii) the confidence limits for the detection of minor species was better if using the coccolith data set, which allowed higher statistical significance when performing statistical analyses, but also the consideration of more deeper samples in the CCA (since at greater depths some samples where barren for coccospheres but not for coccoliths, and barren samples have to be removed from CCA) enriching this analyses. According to Fatela and Taborda (2002; Fig. 2), the detection of a minor species (here considered to be < 2% of the total assemblage) is performed at a confidence level of 100% when counting 500 specimens (i.e. coccolith data set); and it is of 90%-100% when counting 100-300 specimens (i.e. coccosphere data set). The latter is in any case a reasonable confidence limit too, which has proven to be valuable and informative, even when only identifying a maximum of 100 coccospheres per sample by polarized light microscopy (e.g. Bai et al., 2014; Sun et al., 2014).

But in summary, we agree with Cachão and the other reviewers that ecological inferences have to be based on the coccosphere data set. Therefore, we base interpretations about coccolithophore species ecology (section 5.2. of the manuscript) on the coccosphere data set in this new version. We still present and interpret the coccolith data set to provide additional information on other matters that cannot be assessed by using the coccosphere data set (i.e. resuspension events).

2. The authors do not consider the existence of the species Gephyrocapsa muellerae. Possibly this species was integrated into the small Gephyrocapsa group but this is nor referred. I find this a critical point to accept this paper since it compromises the conclusions based on gephyrocapsids and misses important ecological inferences. I attribute this to the fact that coccolith counts were performed with only x1000 magnification.
In addition SEM should also be used to complement taxonomic identifications namely with other coccolithophore taxa difficult to identify only by optical microscopy.

The species *Gephyrocapsa muellerae* was indeed considered, identified, and counted, separately from small *Gephyrocapsa* group, and was being shown (and still is) along with other minor species in Supplementary Figure S3. For this reason, ecological inferences with small *Gephyrocapsa* group have to be discarded since they are not possible.

Despite *G. muellerae* shows very low abundance, we do not think it is due to the use of x1000 magnification. Counts in our lab are always produced with such magnification and *G. muellerae* is always identified without any difficulty, as the Reviewer may know well. The main author of this manuscript and also co-author J.A Flores have used that objective in other numerous studies in which *G. muellerae* is ofen identified as one of the major species. Besides, due to the importance of this species as paleoecological indicator, special care is always placed when identifying potential *G. muellerae*. But in any case, if small *Gephyrocapsa* can be identified and differentiated from *E. huxleyi*

with x1000, *G. muellerae* (which is larger, > 3-3.5 um) can too, being differentiated from similar Gephyrocapsids.
It is worth mentioning that at the beginning of this study 9 well-preserved and diverse samples from different months were scrutinized by Scanning Electronic Microscope for exploratory analyses of preservation, species presence, and picture collection. Nevertheless, not a single coccosphere of *G. muellerae* was found.

Minor concern. The presence of C. pelagicus ssp. pelagicus as coccoliths may derive from reworking. However it can also be specimens from the lower end of the C. pelagicus ssp. braarudi morphotype (under current revision). Because the authors don't refer the classification criteria it is difficult to distinguish which might be the case.

Clasification of *C. pelagicus* ssp*. pelagicus* was made according to size criteria (< 10 µm) (e.g. Parente et al., 2004, and references therein) and it is now stated in the text. Specimens of *C. pelagicus* were measured with the calibrated scale (reticule) placed into one eyepiece of the microscope. No other detailed morphometric analyses were undertaken since that is other study itself formulated to respond other questions and that should be conducted differently. Only one coccosphere of this subspecies was found (in CALIBERIA-March-2012 at 100 m) by optic microscope. None was found within the 9 samples observed with SEM, although these samples were mostly from 10-50 m depth, and coccoliths of *C. pelagicus ssp. pelagicus* were mostly found in deeper waters.
We cannot really tell if these are either reworked specimens or from the lower end of the *C. pelagicus* ssp. *braarudi* morphotype. Nevertheless, two notions might suggest the later:
1.- Distribution of *C. pelagicus ssp. pelagicus* does not match with the few reworked specimens identified in both CALIBERIA and RAIA.
2.- As stated in the manuscript "*. C. pelagicus ssp. pelagicus* spp., and *Coccolithus pelagicus* ssp. *braarudii* showed similar distributions". This might suggests they are both the same species. However, this information has been deleted from this final version since interpretation of coccolithophore ecology is now based on coccolithophore data set, instead of coccolith data set, and only major species are discussed.

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Further explanation for some minor comments (point by point) can be found in the next pages, which is the previous version of the manuscript commented by the Reviewer.
Required minor changes in bibliography, terminology, equations, etc. have been done following Cachão's comments. Therefore, related comments have been deleted in such file.

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

Blanca Ausín[1,2], D. Zúñiga[3,4,5], Jose-Abel Flores[1], Catarina Cavaleiro[4,5,6], María Froján[3], Nicolás Villacieros-Robineau[7], Fernando Alonso-Pérez[3], Belén Arbones[3], Celia Santos[4,5,6,8], Francisco de la Granda[9], Carmen G. Castro[3], Fátima Abrantes[4,5], Timothy I. Eglinton[2], Emilia Salgueiro[4,5]

[1]Departamento de Geología, Universidad de Salamanca, Salamanca, 37008, Spain
[2]Department of Earth Sciences, ETH Zurich, Zurich, 8092, Switzerland
[3]Instituto de Investigaciones Marinas (IIM), Consejo Superior de Investigaciones Científicas (CSIC), Vigo, E-36208, Spain
[4]Div. Geologia e Georecursos Marinhos, Instituto Português do Mar e da Atmosfera (IPMA), Lisbon, 1749-077, Portugal
[5]CCMAR - Centre of Marine Sciences, Universidade do Algarve, Faro, 8005-139, Portugal
[6]MARUM, Center for Marine Environmental Sciences, Bremen, 28359, Germany
[7]Laboratoire d´Oceanographie et du Clima, Université Pierre et Marie Curie, Paris, 75005, France
[8]Alfred Wegener Institute, Helmholtz Center for Polar and Marine Sciences, Bremerhaven, D-27570, Germany
[9]Federal Maritime and Hydrographic Agency, Hamburg, 20359, Germany

Correspondence to: Blanca Ausín (blanca.ausin@erdw.ethz.ch)

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.

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 January, winter mixing conditions were also detected with the water column being characterized by colder (< 13 ^{0}C) and less 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 crop

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.

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* (u ~ 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 ng 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 $\mathrm{CCA}_{\mathrm{CALIBERIA}}$ 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. profundus* is 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 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 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, $\text{CCA}_{\text{CALIBERIA}}$ 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, [illegible]monstrated 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., 2006). 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., 2006; 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 coccolithophores 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

Acknowledgements

The authors want to thank the Captain and crew of the RV 'Mytilus (CSIC)'. This work was funded by the EXCAPA project (10MDS402013PR) funded by Xunta de Galicia, and CALIBERIA project supported the coccolithophore analysis (PTDC/MAR/102045/2008 from Fundação para a Ciência e a Tecnologia -Portugal- and COMPETE/FEDER -FCOMP-01-0124-FEDER-010599). Project CGL2015-68459-P from Ministerio de Economía y Competitividad also contributed to the founding of this study. B.A. was supported by a FPU grant (AP2010-2559) of the Ministry of Education of Spain and by an ETH Zurich Postdoctoral Fellowship from the Swiss Federal Institute of Technology in Zurich (ETHZ). D.Z. was funded by a postdoctoral fellowship (Plan I2C) from Xunta de Galicia (Spain). F.G. was funded by RAIA.co (0520_RAIA.co_1_E). N. V-R. was funded by Isabel Barreto Program (Xunta de Galicia, Spain). M.F. (BI/PTDC/MAR/102045/2008/2010-016), C.S.

(BI/ PTDC/MAR/102045/2008/2010-022) and C.C. (BI/PTDC/MAR/102045/2008/2011-027) were supported by CALIBERIA project. E.S. was funded by a postdoctoral fellowship (SFRH/ BPD/111433/2015) from FCT and from Plurianual/Estratégico project (UID/Multi/04326/2013).

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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
	Cachao et al., 2000	Portuguese Margin	Northwest (Oporto)	$2.7x10^5$	Winter regime, upwelling conditions, and local runoff
	Silva etal., 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
	Cachao 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

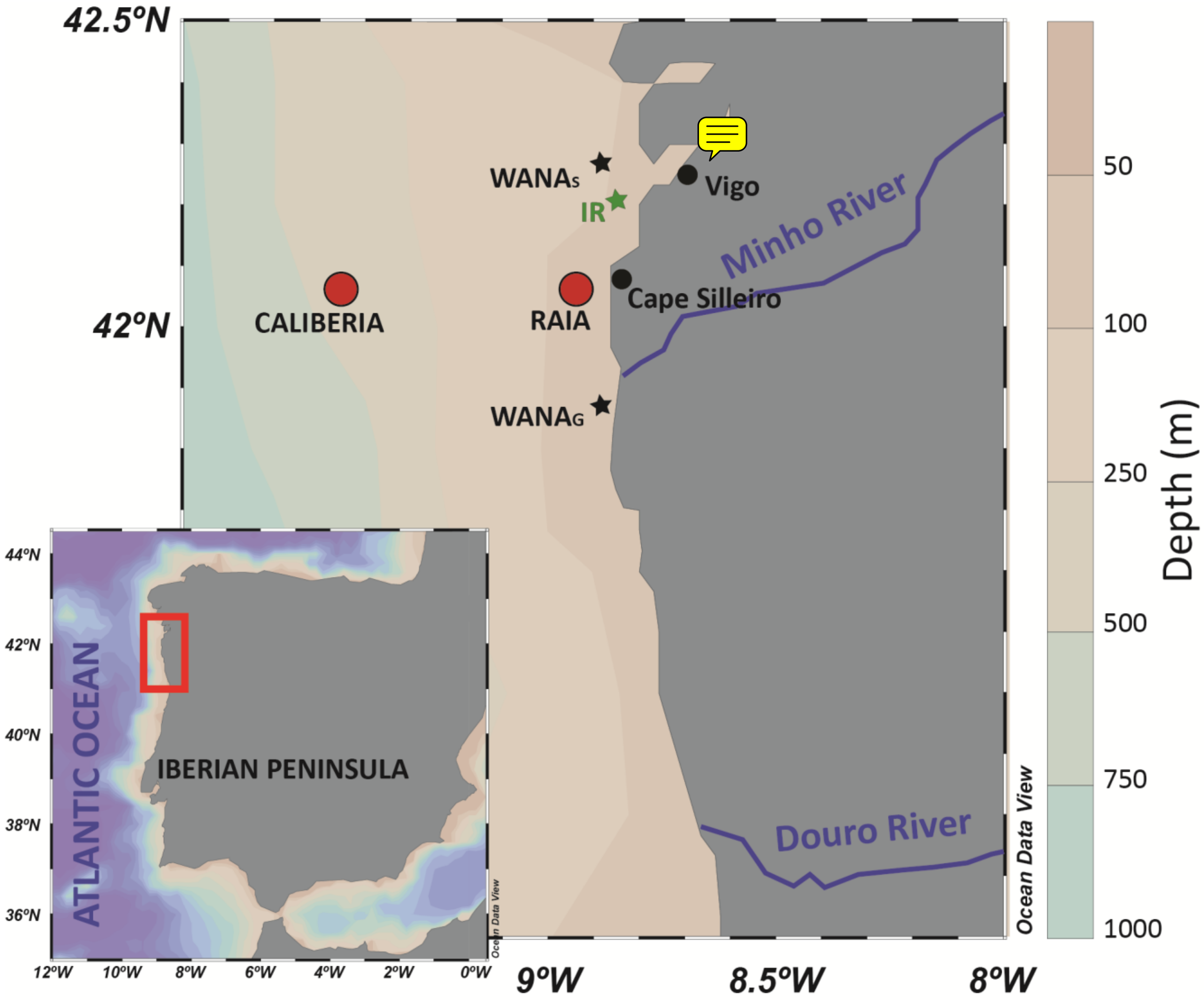


Figure 1. Map of the NW Iberian Margin showing CALIBERIA and RAIA stations. Location of Cíes meteorological station (IR, in green), and WANA hindcast reanalysis points WANAS and WANAG (black stars) from which irradiance and wave data were respectively obtained (Zúñiga et al. 2016). Modified from Zúñiga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

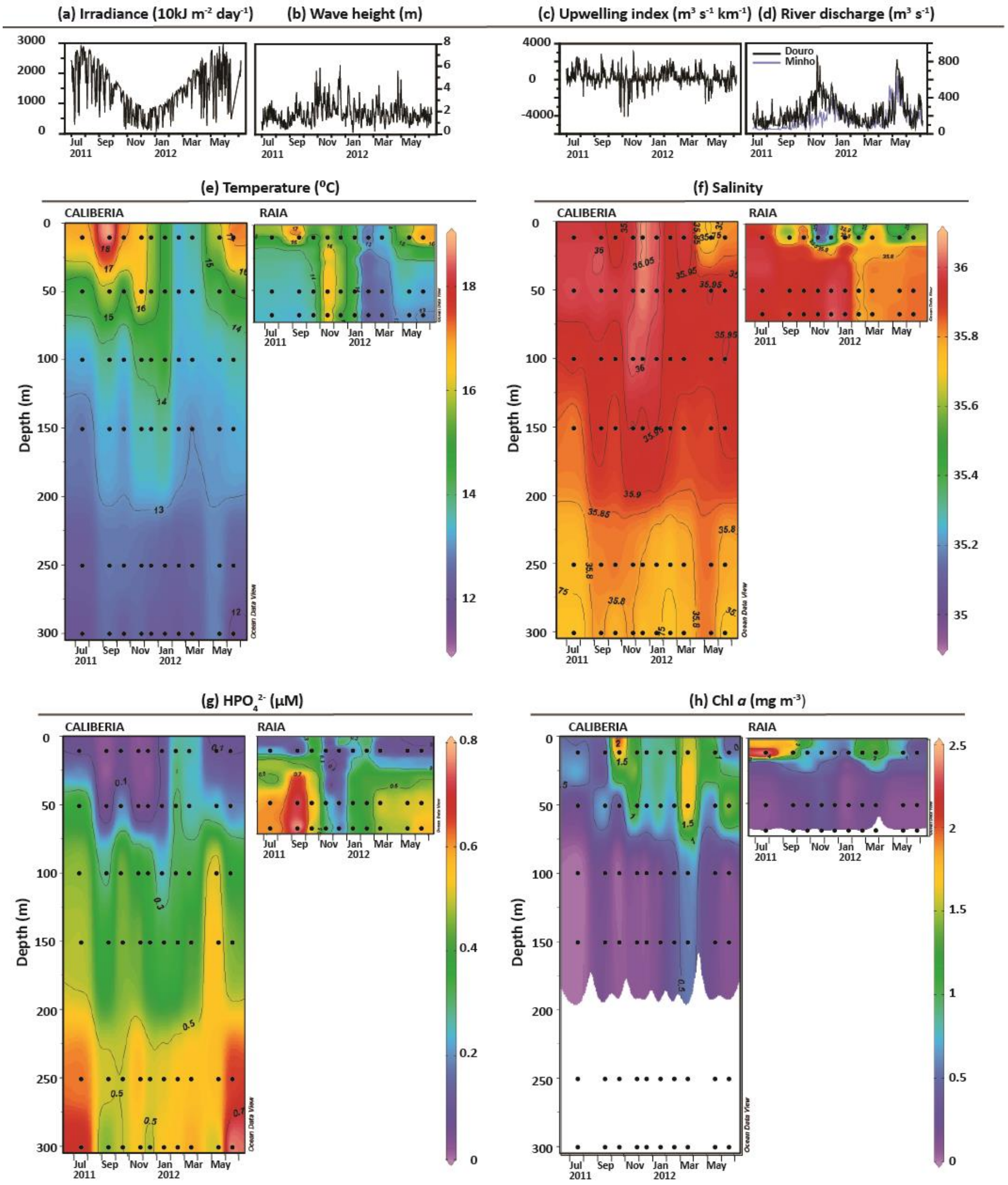
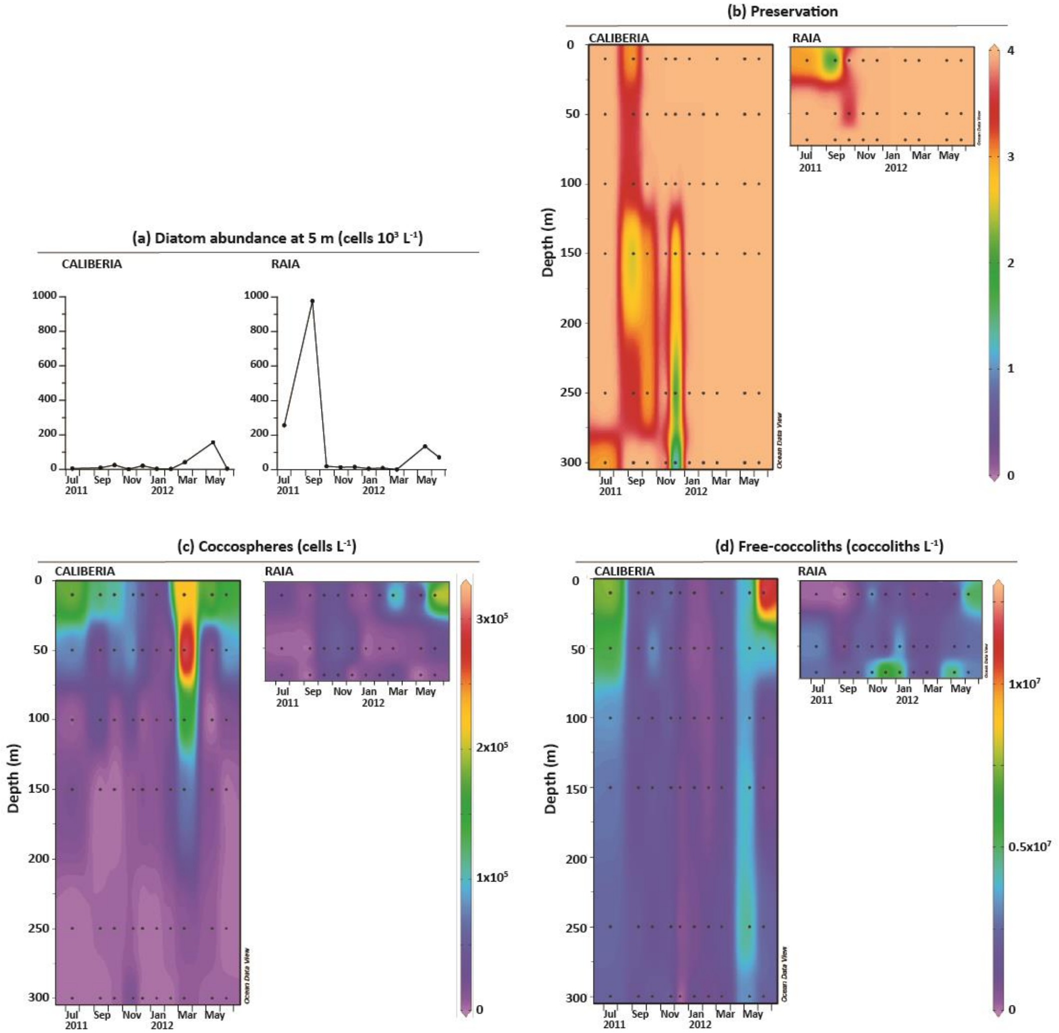


Figure 1. Environmental conditions for the studied period. Available data on a) irradiance, b) wave height, c) upwelling index, and d) discharges by Minho (blue) and Douro (black) Rivers (Zúñiga et al., 2016; 2017). Temporal and vertical distribution of e) temperature, f) salinity, g) HPO_4^{2-}, and h) Chl *a* at CALIBERIA and RAIA stations. Black dots represent collected water samples for coccolithophore analyses.

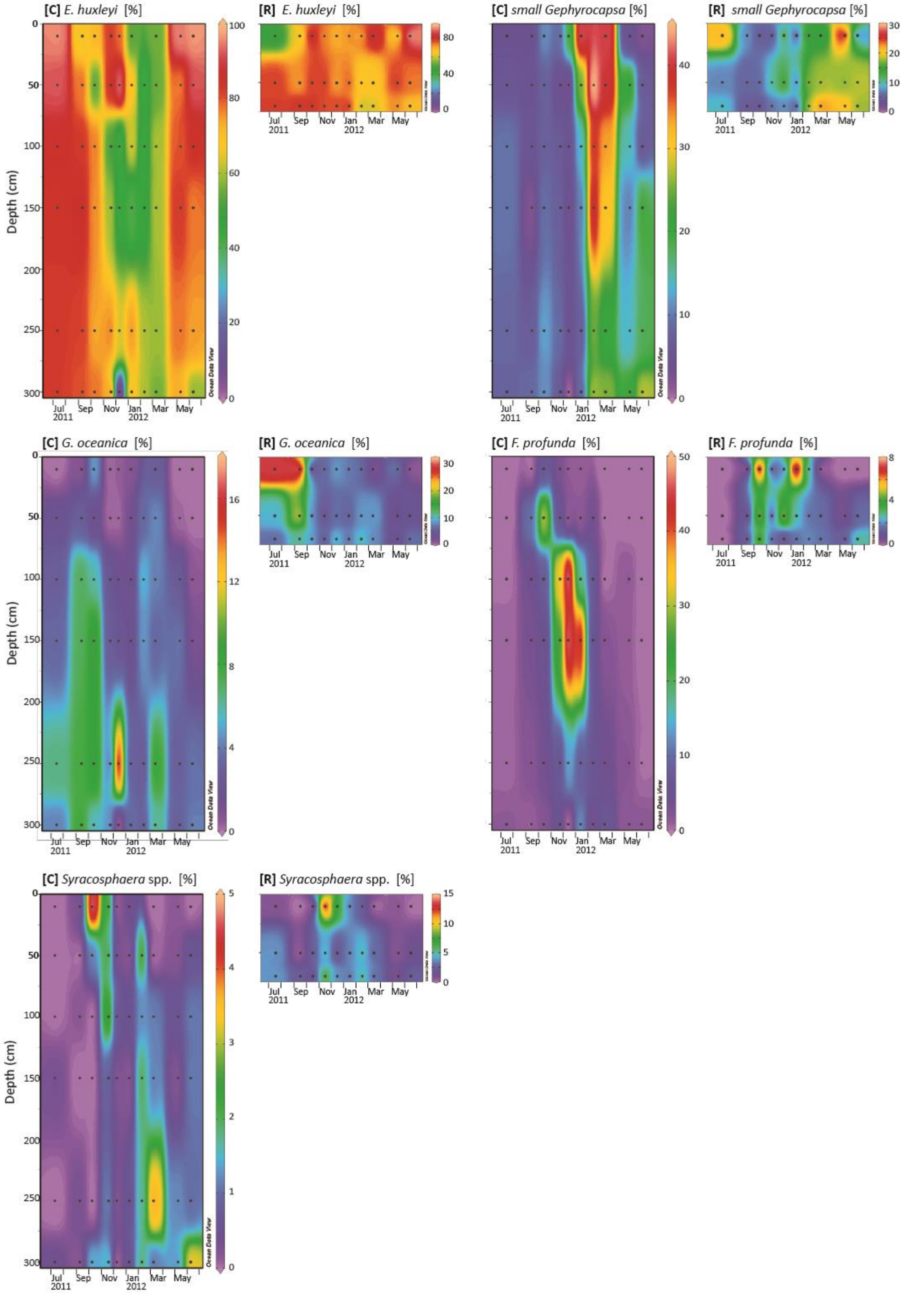

(a) Diatom abundance at 5 m (cells 10^3 L^{-1})

(b) Preservation

(c) Coccospheres (cells L^{-1})

(d) Free-coccoliths (coccoliths L^{-1})

Figure 3. a) Diatom absolute abundance (cells L^{-1}) at 5 m at CALIBERIA (this study) and RAIA (Zúñiga et al., 2017); b) Preservation of coccoliths through time and depth; c) temporal and vertical distribution of the total number of free-coccoliths (coccoliths L^{-1}) and d) coccospheres (cells 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.



[C] *E. huxleyi* [%]

[R] *E. huxleyi* [%]

[C] *small Gephyrocapsa* [%]

[R] *small Gephyrocapsa* [%]

[C] *G. oceanica* [%]

[R] *G. oceanica* [%]

[C] *F. profunda* [%]

[R] *F. profunda* [%]

[C] *Syracosphaera* spp. [%]

[R] *Syracosphaera* spp. [%]

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.

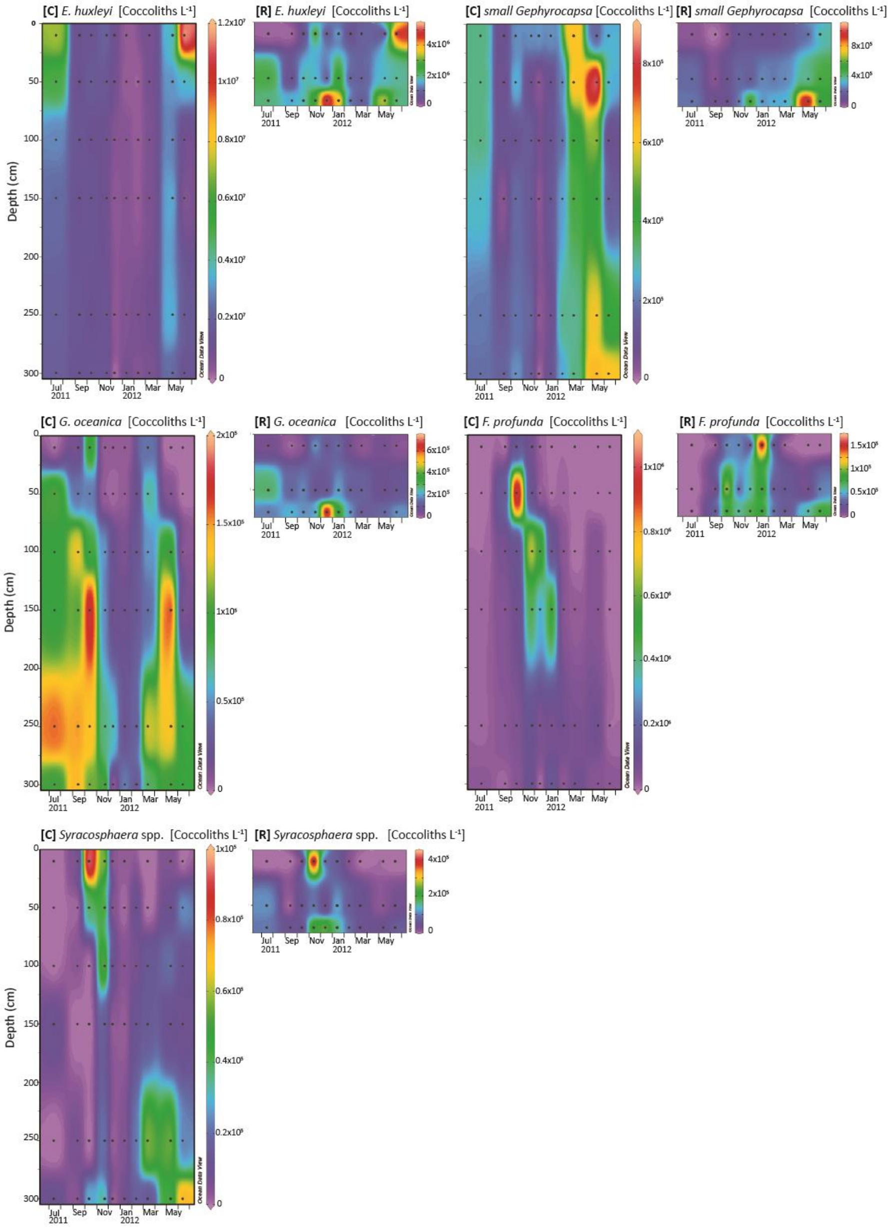


Figure 5. Absolute abundance of major coccolithophore species. Temporal and vertical distribution of the absolute abundance of major species of coccoliths (coccoliths L^{-1}) as in Figure 4.

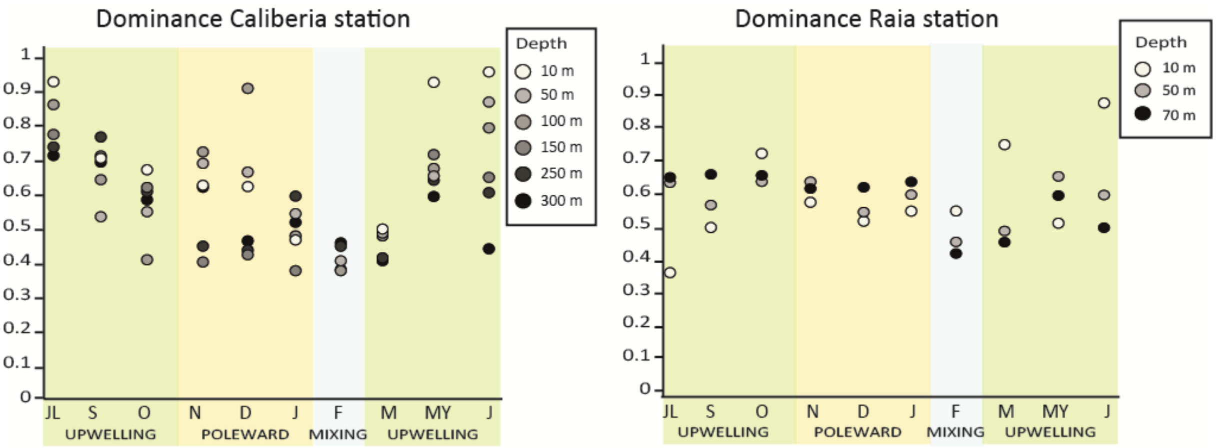


Figure 6. Species dominance at CALIBERIA (left panel) and RAIA (right panel), during the upwelling, Iberian Poleward Current (IPC), and mixing periods.

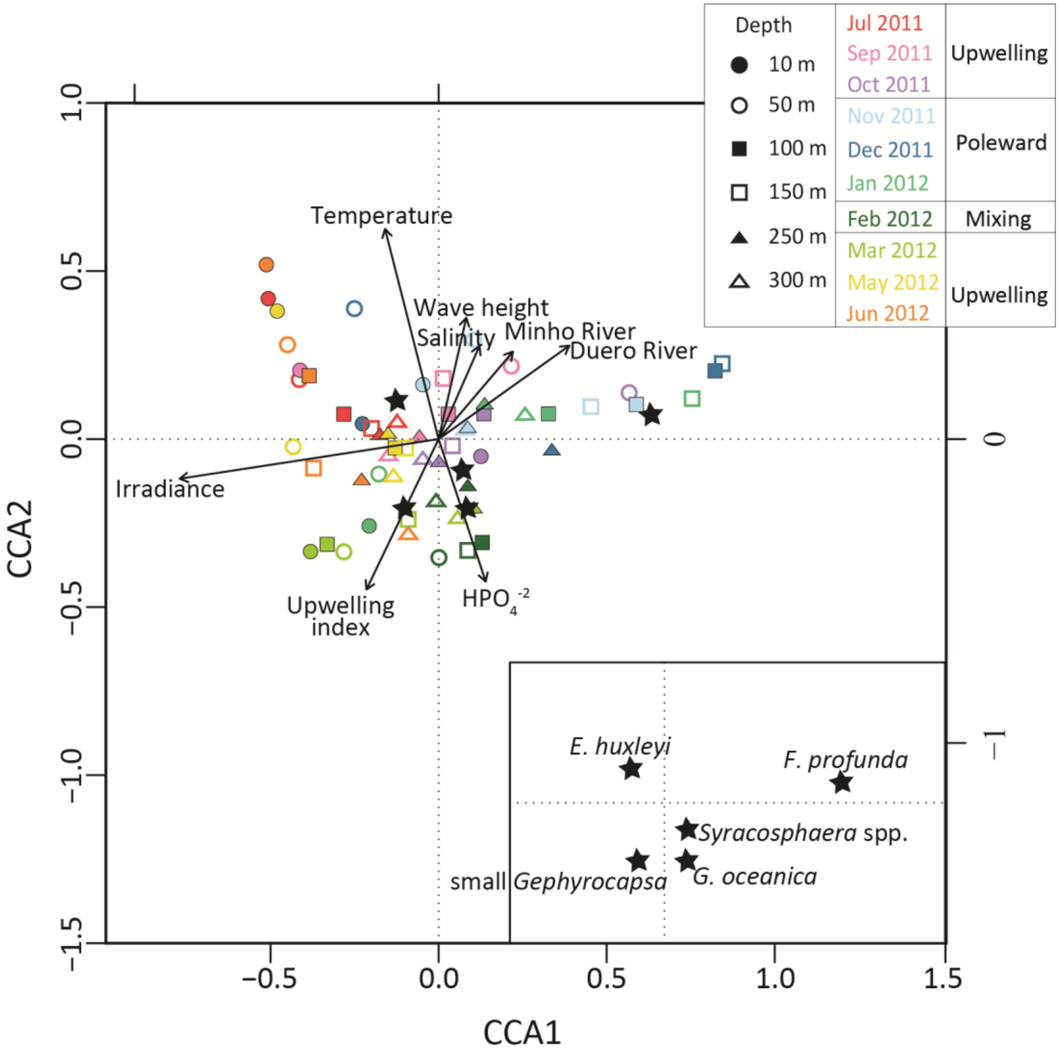


Figure 7. Ordination graph for the first two axes of the CCA for CALIBERIA datasets. The species scores are represented by stars and environmental variables by arrows. Samples are shown through colored symbols according to their sampling month and depth.

We want to thank Reviewer #2 for their convenient comments and suggestions, which helped to improve our manuscript. Discussion point by point and explanation of main changes can be found here.

Reviewer 2

I would also suggest alterations to some of the figures. It makes more sense to me to group figures by station, instead grouping both stations together for each variable. For example, I kept flipping between all the figures to compare variables at one station. It would be easier to interpret if all variables were plotted next to each other for a station, if that is possible. For me, it is less valuable to have the data from the two stations plotted next to each other. Also, I suggest changing the color scale/greyscale on figures 6 and 7 because similar shades are impossible to distinguish from one another.

We have kept Fig. 3 as it was (comparing total abundances and % between stations) so it illustrates the discussion, in which differences and similarities between stations are discussed. The rest of the figures have been altered so species distributions are plotted by stations as the Review suggests. Discussion about diversity has been deleted so Figure 6 has been deleted too.

3.2 Coccolithophore analysis: How many total cells and/or field of view were quantified per sample? The authors refer to the confidence limits based on the number of species-level counts. What were these? What was the confidence level of the total coccolithophore count?
Samples were counted considering 500 coccoliths per sample, and all the coccospheres encountered during that process were considered as well. The total number of identified coccospheres ranges from 100 to 300 per sample. We refer the reader to Fatela and Taborda (2002), where Fig. 2 can be used to calculate confidence limits. Based on this, we know that a species with just 2% of relative abundance in the sample can be detected at a confidence level of 100% in a counting based on 500 coccoliths. For coccospheres, the confident limit is ranges from 90% to 100% in a count ranging from 100 to 300 coccospheres.
This information relative to confidence levels of both coccosphere and coccolith counts has been added to the new version.
In any case, and in order to infer ecology of coccolithophores, we use and interpret in this new version the coccosphere data set. We still present and interpret the coccolith data set to provide additional information on other matters (i.e. resuspension events).

Diatom analysis: Zuniga et al 2017 citation does not have year in reference list. Corrected.
How many total diatom cells were counted, and what is the uncertainty associated with these counts? This does not appear to be presented in Zuniga 2017.
At least 500 diatom cells were counted in each sample. Therefore, species with just 1% of relative abundance in the sample can be detected with a confidence limit of 99.5%.

Statistical analysis- Were these analyses performed only on the coccolith data? If so, the language needs to make this clear. For example, is n the total number of individuals, or total number of coccoliths? What affect might diversity in coccolith production among species have on equating coccoliths with community composition? I would like to see some discussion of this. Is it common to use coccolith composition as a proxy for species composition? Does coccolith composition accurately reflect species composition? Reference to equation 2: is this your equation 2, or are you referring to an equation 2 in Hammer et al. 2001? The equation syntax is unclear. If the calculation is made by adding the squared fractional abundance of each species, shouldn't this be represented by a sigma symbol?

We have gotten rid of Diversity analyses since they did not provide too much information and in any case we did not need them to support our interpretations.

Results: 4.1 Environmental conditions: Why is phosphate the only nutrient reported? Nitrate and silicic acid have a much larger impact on coastal production, and are likely important in determining coccolithophore growth or their ability to competition with other phytoplankton groups.

Coccolithophores utilize phosphate and nitrate, but not silicic acid. We did not plot nitrate for two main reasons:

1.-All nutrients were considered in the initial variable selection prior to CCA, as stated in the text, but variable selection only pointed at HPO_4^{-2} *as being significant to explain coccolith variability, and rejected* NO_3^-, (and also $Si(OH)_4$, although this was expected). *Therefore, we preferred not to show data that was not going to be included in the discussion.*

2.-Nitrate shows the same temporal and spatial variability as phosphate, although different absolute values.

In any case, Nitrate has been presented now for those readers that might wonder about its distribution and concentration.

4.3 Coccolith absolute abundance Line 24 "suggesting that their disaggregation takes places right after the cells die"- I would not expect to find many suspended coccolithophores (or any other phytoplankton) in 2-5 L of seawater collected below the euphotic zone/mixed layer. This does not necessarily mean that cells "disaggregate" right after they die, although it is a possibility. By disaggregate do the authors mean lose their coccoliths? The terminology is unclear. Intact coccospheres are probably mostly transported below the euphotic zone in larger particles, which were not sampled in this study. Alternatively, intact coccospheres may sink below the mixed layer at specific times of the bloom cycle that are unlikely to be resolved by monthly observations. Either way, I don't think this study can really resolve the fate of coccospheres due to the sampling methods used (i.e. filtering small volumes of seawater). Line 30 again refers to disaggregation. Is this a common term when referring to coccolithophore cells? Cells are not aggregates. To me, disaggregation involves organic particles like marine snow. What do the authors mean by "mature" when referring to a bloom? Is this the bloom peak, or the decline? More precise language would be helpful.

By "disaggregate", we mean the coccosphere, which is composed by imbricated coccoliths. We made clear in the text that is the coccosphere the one that disaggregates in coccoliths, not the cell itself, although this is a common term when referring to coccospheres. By mature we mean "in a developed stage", although this term is no longer used in this new version.

4.6 Diversity: Dominance figures: I cannot distinguish the difference between 50, 100, and 150 grey tones. Also, 250 and 300 m both appear to be black to me. Cannot see a clear or consistent relationship between dominance and depth, although it may be obscured by the similar grey tones. In many cases, the deeper depths have higher dominance than the shallower samples, opposite of statement page 7, line 29.

This figure is not needed anymore and has been deleted.

4.7 CCA: How was upwelling index incorporated into this dataset? Was the index number from the day of sampling used, the week-long cumulative value, or a monthly average? A randomly selected value on any day of the month wouldn't necessarily reflect the time scale or ecologically relevant physical processes. These probably occur on a weekly time-scale (I think, though I am not familiar with that specific system). Similarly, how were wave-height and river discharge data incorporated? These influences leading to the community sampled that day.

Initial upwelling data consisted on 4 measurements per day (each one every 6 hours). The final data incorporated in the CCA was the mean value for the 4 measurements of each corresponding sampling day. For river discharge, only one measurement per day was available, so the corresponding value for the specific sampling day was the one included in the CCA. Initial wave-height data consisted in 24 measurements per day, one measurement per hour. Similarly to the upwelling index, the average for the sampling day was calculated and incorporated in the CCA.

In a previous exploratory analysis, we calculated the mean values of each of the studied variables for 3 days (two days before the sampling day), and also for 5 days (4 days before the sampling day). CCA for both 3-day and 5-day data set explained much less variance in the coccolith data set. Considering this, along with the evidence in literature that supports that coccolithophores respond rapidly to the environmental changes in this region and elsewhere, we decided to use the 1-day data set (sampling day).

Why is March characterized as "upwelling"? According the figure 1, the water column appears similarly mixed/mixing as February. I am confused by what could cause the CCA second axis, where upwelling index forcing is on the negative axis and water temperature on the positive, even though water temperature is highest during the months classified as "upwelling". The major separation of samples along this second axis seems to be primarily defined by the February-March period when the water column was well-mixed and surface waters were cold.

This is because during the sampling day corresponding to March there was upwelling, while this did not occur during February. Despite similar conditions in the water column can be observed for both months, they were caused by winter mixing in February and by upwelling in March. What it is plotted in figure 2c is –Qx (- Upwelling index), this is now indicated in this new version.

Regarding the placement of Syracosphaera on the ordination, its variation does not appear to be explained by these axes, so there is little you can say about it. The ordination does a good job explain variation between the others though.

Indeed, we could not say too much about *Syracosphaera* based on the ordination. However, the new CCA performed using the coccosphere data set relates this species with higher salinity and temperature, something that might be indicating its preference for the subtropical ENACW carried by the ICP in autumn, (and not necessarily for higher temperature and salinity *per se*.) This is now discussed in the new version.

Discussion 5.1 The title of this section should be changed to reflect the abundance measurement that this study is based on, since productivity was not measured. 5.1.1

Changed

Line 4: Is there a citation for this statement ("no vertical flux of coccoliths nor coccospheres is observed at those times")

There is not, because this is based on what we observe on Figures 3d. (i.e. no coccoliths nor coccospheres presence above 75 m that could explain this maxima at 70 m by in-situ production).

Line 16: I think the wording in this sentence should be changed, since productivity was not measured.

5.1.2 Line 19: Again, should refer to abundance, not productivity. Changed.

Line 20: "donwelling" typo. Corrected.

Page 10, line 15: "Yet, our outcomes highlight that both species are unambiguously linked to the upwelling regime and high primary production." Again, since production was not measured, there is no direct link to production in the dataset presented.

This statement is based upon the assumption (which in turn is a well-known fact for this region) that upwelling periods in the study area are linked to higher primary productivity. Still, we are aware that we did not measured primary productivity and that is not entirely correct to establish such a direct link between these two species and higher PP at the daily time scale. Nevertheless, this statement is made in the context of the use of fossil coccoliths of these species preserved in marine sediments as paleoenvironmental indicators. At the temporal resolution that marine sediments offer, increases in these two species would indicate persistent upwelling conditions and therefore it can be expected and assumed that productivity was higher at those times.

First of all, we want to thank Reviewer #3 for their in-depth review that has helped to improve our manuscript. We have modified it whenever possible, while discussion on point by point and explanation of main changes can be found here.

Other major concerns relate to the identification based only on polarized light microscopy, without more powerful scanning electron microscopy used to supplement this technique. Their interpretation of some ecological associations could particularly be affected by this. In particular, they appear not able to distinguish well enough within the Noelaerhabdaceae (Emiliania, Gephyrocapsa, . . .). They may well be able to distinguish large-vs-small Gephyrocapsa's, but probably not intermediate species (G. muellerae). We did distinguish *E. huxleyi* from *G. aperta* and *G. ericsonii*, even the coccospheres! *G. aperta* and *G. ericsonii* were lumped together and merged within the group "small *Gephyrocapsa*", following a general approach based upon the assumption that they are influenced by the same ecological conditions. And we do distinguish the intermediate species *G. muellerae*!, which was also shown in the Supplementary pictures. All these species are mentioned in the Appendix, and shown in independent figures.
Counts and classification of coccolithophores in our lab are always performed by polarized light microscope. Although the use of SEM can facilitate coccolithophore classification, our access to those resources is (as for many other groups) costly and therefore very limited, and in any case the use of polarized light microscopy is a well-established approach used by many other research groups (e.g. Ferreira and Cachão, 2005; Bai et al., 2014; Sun et al., 2014; Balestra et al., 2017; Bonomo et al., 2017).

In the case of Emiliania huxleyi, their approach ignores that great morphological, physiological, phylogeographical, and genomical differences. It is now well demonstrated that different morphotypes seem to have contrasting ecological associations, and it has been recently demonstrated that the genomes of offshore and coastal E. huxleyi may show major differences. These differences within the species or species-complex can especially complicate patterns in upwelling systems, where different types may be observed. I would much prefer that they include an SEM analysis at morphotype level of E. huxleyi and other Noelaerhabdaceae. Another problem – which in fact is one of the most interesting aspects of the paper – is the uncoupling of coccolith and coccosphere patterns. In some near-bottom samples this appears to be due to resuspension of coccoliths from the sediment, but even excluding that, the coupling is not close. If they did a graph of free coccolith vs coccosphere abundances they would probably see this. That means that inferences about ecological associations of coccolithophores may be different if coccospheres or coccoliths are examined. Of course, they do mention that part of this might be due to the stage of a "bloom" that is observed (so free coccoliths may be sampled when the major bloom phase was missed). Would there be any way to combine these two data sets for a more complete picture? That would be interesting. All this is discussed below in detail in three related comments.

The English language use in the Abstract needs refinement and extensive editing. Done.

Minor comments: "For the first time . . ." This isn't necessary. Deleted.

"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" . "on the contrary" is redundant to "despite", and not sure what is being contrasted to. Corrected.

Introduction, lines 27-30, and later. It isn't clear that one would expect that studies in the southern Iberian coast at about latitude 39-40N would not be reflect patterns at 42N. How different are oceanographic patterns and processes at in the Northwest and Southwest Iberian coasts? There is a bit too much emphasis trying to sell the study based on this particular site not having been studied much for coccolithophores before, but that doesn't sell it in and of itself (and I think the study is interesting enough without forcing this issue).

There are several features that make the NW Iberian Margin interesting for the study of coccolithophore distribution and different from the SW Iberian Margin. 1.- Its proximity to the Minho River mouth. 2.-It is next to the Rias Baixas, a region that is the target zone of dozens of studies itself due to its related specific processes. 3.-Its distance to the Strait of Gibraltar, from which the different branches of Mediterranean Outflowing Water outflow, which strongly impacts column water dynamics in the SW part, not so strongly in the NW part. 4.-Its distance to the Gulf of Cadiz, source of reworked coccoliths in the SW part (Ferreira et al., 2008). Nevertheless, we believe the vast majority of the readers interested in this paper will be aware of such oceanographic differences, but in any case, we have rephrased it according to the Reviewer comment since certainly that was not the point we wanted to make anyways.

p. 4, line 8: "Upwelling index". So we don't have to go look up which Zúñiga used, please say Bakun upwelling index (well known index). Corrected.

Comment on 3.2 Coccolithophore analyses: All identification seems to have been done only with polarizing microscopy, not electron microscopy. They reference identification guide of Young et al. 2003, but that guide is based almost exclusively on scanning electron microscopy. I am not clear to know to what degree polarizing microscopy is sufficient for species-level identification, and where the limits are, partially as I am not that experienced with polarized microscopy identification.

Polarized light is widely used in many oceanographic, also for this region (e.g. Cachão et al., 2000; Ferreira and Cachão, 2005; Balestra et al., 2017), and also in most paleontological studies based on coccolithophores and nannofossils. Coccolith identification by polarized light is very easy and straight-forward, not that much for coccosphere identification, which can be time consuming and less straight-forward. We acknowledge that the use of Scanning Electronic Microscope is more precise for coccosphere classification. Unfortunately, we do not have access to those resources to undertake such task and make the most of this material. It has to be kept in mind that most of the interpretation deals with general temporal coccolithophore abundance patterns, and for that only the total coccosphere abundance is needed. Inferences on coccolithophore ecology are only discussed in the last section 5.2., for which counts of coccolithophores at the species level are used in this new version.

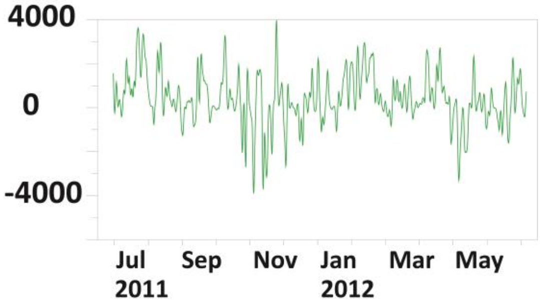
Regarding confidence levels, and following Fatela and Taborda (2002; Fig. 2), the detection of a minor species (here considered to be < 2% of the total assemblage) is performed at a confidence level of 100% when counting 500 specimens (i.e. coccolith data set); and it is of 90%-100% when counting 100-300 specimens (i.e. coccosphere data set). The latter is in any case a reasonable confidence limit too (even the lower one), and other studies based on a maximum count of 100 coccospheres have been proven to provide valuable and useful information (e.g. Bai et al., 2014; Sun et al., 2014).

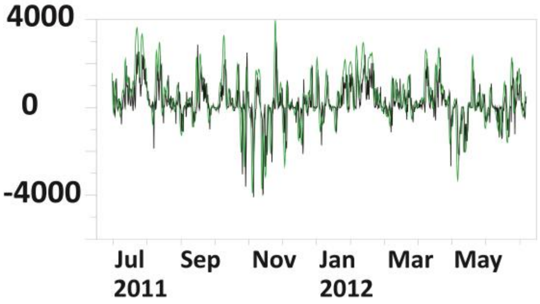
Section 4.1. The text description of oceanographic processes seems a little bit disconnected from what is shown in the graphs. For instance, in 2C I do see that from July to Oct 2011, upwelling favorable winds seemed to dominate, considering the Bakun upwelling index. By February 2012, there were large periods of upwelling-favorable winds, but I wouldn't say they continued through

June of that year, as there were substantial periods of downwelling favorable winds in April-May and the end of June. It might be nice to overlay 8-day and 30-day running means for the indices in 2c.

We refer the reader to a previous work for a better visualization (since our figures are limited by the width of the station figures) and identification of oceanographic processes associated to the shown oceanic conditions occurring in the area during the sampling days (Zúñiga et al., 2016).

We have produced a 3- and a 4-point moving average smoothing spline for the Bakun Upwelling Index. Below is shown the 4-point moving average in green (higher than 4 the resolution is very poor and some important events are lost). But its overlap with our 2c figure does not favor an easier visualization of the processes, not event taking this figure individually and making it bigger.





In statistical analyses, the upwelling index averaged for several days prior to sampling should be used, as it takes several days for upwelling to develop when favorable winds blow (so winds have to blow for at least a few inertial periods/days). We did so in an exploratory analyses. We calculated the mean values of each of the studied variables for 3 days (two days before the sampling day), and also for 5 days (4 days before the sampling day). First, we incorporated these three data sets to the variable selection, which suggested the use of averaged data from the sampling day. Second, and to make sure that possible collinear effects among the three different temporal resolutions of a certain variable were not guiding variable selection, we also performed exploratory CCAs with each set of temporal resolution. CCA for both 3-day and 5-day data set explained less variance in the coccolith data set. Considering this, we decided to use the 1-day data set (sampling day).

While I see clearly the correspondence between Fig. 2e and the statement “Finally, during February, winter mixing conditions were also detected with the water column being characterized by colder (< 13 â ¸Aˇr C) and more saline (< 35.8) waters”, February doesn’t seem to be especially salty compared to the rest of the time series in Fig. 2f. In fact it is less salty than January. Corrected.

Saying the patterns in Chl-a were comparable between CALIBERIA and RAIA stations (lines 2-3) also seems not to correspond to Fig. 2h. The highest concentrations of Chl-a were found in July in RAIA (>2 mg m-3), were also high in September (>1 mg m-3), while values in Caliberia were low (<1 mg m-3) in July and Sept 2011. January surface (10 m) levels were comparatively low at RAIA but moderate in CALIBERIA. . . Certainly… we corrected this.

The uncoupling between abundances of free coccoliths and coccospheres makes me question the strategy of basing coccolithophore diversity patterns on free coccoliths, rather than on coccospheres. Dicussed above. How do the authors define "bloom"? This needs to be more clear. For the "deeper blooms" that the authors attribute to wave-mediated resuspension of sediments, I would have thought they would mention at least one other evidence supporting this conclusion. If those blooms are from resuspension of sedimented coccolithophores, wouldn't they be dominated by free coccoliths and not complete coccospheres? On p. 6 lines 24-25 they say "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". Indeed, the deep coccolith max at RAIA station during Nov.-Jan. is not matched by a deep max of coccospheres. These "deeper blooms" are indeed dominated by coccoliths (actually there are not coccospheres at that depth at those times), but this confusion most likely derive from the broad and imprecise use we made of the term "bloom". We have corrected that and also clarified in the text when we mean coccospheres and when we mean coccoliths.

"Our results show that freshwater lenses advected to RAIA station have negligible influence on coccolithophore productivity" The authors did not observe that in one year of study, but that doesn't mean influence is always negligible. Rephrased.

p. 9, lines 19-20 "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". I have two problems with this: First, what is "coccolithophore productivity"? Productivity is often most strictly used to refer to a rate (e.g., primary productivity in g C m-3 day-1 or g C m-2 day-1), though less precisely the word is sometimes used to refer to patterns of biomass or organism abundance. Here I am not sure if they are referring to coccosphere or coccolith abundance, which follow somewhat distinct patterns, and they certainly aren't talking about a rate. They show one example why it is often better to use the more strict sense: They have an increase in coccoliths during winter at the onshore station that they attribute to re-suspension, not to production, so coccolith abundance does not necessarily reflect coccolithophore productivity on smaller temporal and spatial scales. Second, I don't see where they show "increasing five orders of magnitude". Their highest reported abundance of coccospheres is 3x105 cells ml-1. They have not defined their detection limit. I doubt they could easily detect 3x101 cells ml-1 (there would be 6-15 total coccospheres per filter, on average, and they would have to count the whole filter to be able to detect those, not just a "random piece"). It seems more possible they could have documented a "five orders of magnitude" change in the numbers of coccoliths, but again we need to know what their detection limit and minimum abundance seen was. The term "coccolithophore productivity" has been replaced in the text by coccolithophore abundance, a more correct term for what we mean. We have clarified through the text when we are referring to coccoliths and when to coccospheres. Finally, we have deleted the orders of magnitude to avoid confusion.

p. 9, lines 22-23: "This affinity of coccolithophores for summer stratified conditions during the upwelling season was already observed by Silva" Wasn't this already observed much earlier? Seems that more generally it was a pattern already recognized by the review of Margalef in 1978. Indeed, but we mean it for the regional (the Iberian Margin), not global context.

p. 10, lines 5-16. I have some difficulty with the discussion of the environmental affinities of E. huxleyi. This species seems to be everywhere outside the poles, mostly representing 50%-100% of coccolithophore communities (though occasionally lower percentages). Morphological, phylogenetic, genomic, and physiological studies now seem to suggest there may be quite different ecotypes with different sets of adaptations. Work by Young and Beaufort and later others (e.g. Cubillos et al. 2007; Cook et al. 2011, Hendriks et al. 2012; Poulton et al.; Smith et al. 2012) have identified different morphotypes (A, B, B/C, O, etc.) which seem to display different oceanographic distributions. Hagino et al. and Bendif et al. have shown that different haplotypes seem to be to be associated with different water temperatures. Read et al. (2013) showed that there could be major genomic differences, and von Dassow et al. (2015) showed that much of the genome content differences related to coastal/productive vs offshore/low latitude origins. So it does not surprise me at all that studies could find contrasting ecological associations of E. huxleyi, when all of these morphological, phenotypic, physiological, and genomic variants are grouped together. I think there is much more information in the non-E. huxleyi species, like G. oceanica, small Gephyrocapsa, and Florisphaera. This caveat should be properly discussed. Further, the study would really benefit from incorporating electron microscopy analyses, to be able to distinguish the different morphotypes of E. huxleyi, as they have been observed to show very different ecological patterns. Detailed morphometric analyses were not undertaken for two main reasons: First, and unfortunately, we do not have access to (nor the resources to access) a SEM; second, a morphometric study is other investigation itself formulated to respond other questions and that should be conducted differently. Although we do not doubt of the usefulness of genome analyses, we do not see how these can be essential or a requisite to provide the key information we need to answer our research questions (i.e. How are coccolithophore and coccolith abundance patters in the NW Iberian Margin? What can we say about their inner-shelf and outer-shelf temporal variability in relation to seasonality and/or diverse oceanographic processes?). *E. huxleyi* is the dominant species (based on its relative abundance), something common in many other studies. But its temporal variability should not be assessed by looking at its relative abundance. The later just informs on the assemblage composition, but tells nothing about its temporal variability. *E. huxleyi* temporal variability must be assessed by looking at its absolute abundance, where indeed a distinct seasonal signal is observed, and therefore a clear link with the environmental conditions can be established (i.e. preference for upwelling regime conditions). A detailed study on the different *E. huxleyi* morphotypes would certainly provide some information on their relationship with the environmental variables. Nevertheless, such specific research question is out of the scope of this paper.

p. 11, lines 30-31: “Our results highlight the role of coccolithophores as significant primary producers in the study area, being strongly correlated with higher values of Chl a” I am not sure they have justified to go from a correlation between coccolithophore abundance and Chl-a concentrations to considering that coccolithophores are major primary producers in this area. Most of the coccolithophores all the time were either E. huxleyi (typically 5 μm diameter cells) or small Gephyrocapsa (even smaller!). Abundances of 1x105 cells L-1 do not mean very high biomass when talking about 3-5 μm diameter cells. I would be more convinced if they had used an estimation of cell carbon (based perhaps on volumes from Young & Ziveri 2000 and C:volume estimates from other studies) and a reasonable carbon:chl-a ratio, to show what range of phytoplankton biomass they might represent. Also, the correlation is never explicitly analyzed, as far as I can tell.

We agree such statement is too categorical and that we cannot establish such correlation. We have therefore rephrased to hypothesize that according to our results, higher coccolithophore abundances also occur along with periods characterized by high Chl-a concentrations, something that might indicate that this phytoplankton group can be contributing to some extent to higher Chl-a concentrations. We believe this is an important point to make, since coccolithophores are generally an overlooked group when exploring the contribution of different phytoplanktonic groups to Chl-a values.

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We want to thank Reviewer #4 two for their comments and suggestions, and we have changed our manuscript accordingly whenever possible. Discussion point by point and explanation of main changes can be found here.

General comments: The manuscript reads well, but I have a hard time fully grasping its message. Thus, the paper may contribute to the understanding of the coccolithophore ecology of the NW Iberian coast, but just after a couple of clarifications. In particular, I am not fully convinced that usage of both coccosphere and coccolith counts is appropriate to infer the made conclusions. To my knowledge coccolith numbers never equals coccosphere numbers in water samples for several reasons. Those are, (a) dramatically different numbers of coccoliths/sphere for different species, (b) the occurrence of multilayered coccospheres, e.g. in E. huxleyi, and (c) the preservation potential of the different coccolith types that result in selective preservation, (d) the occurrence of faecal pellet gracers, just to name a few. What is the meaning of single liths in the water column, how do they get there, what is the influence of zooplankton grazing on their occurrences, and how far can they been transported, etc.? Further usage of the coccolith data would at least need an intense discussion on this issue!

Indeed, and as already discussed for the other reviewers, we use and interpret the coccosphere data set in this new version in order to avoid these issues and to correctly address coccolithophore ecology.

Furthermore, what is the total number of coccospheres identified per sample that statistically was not significant to ensure a correct estimation of the abundance of even the five majority species and species groups? Most of the information given is limited to the five major species/groups, so that minority species would not been included anyway. My main suggestion is thus to exclude coccolith data from the interpretation and focus only on the reasonably acceptable coccosphere counts!

According to Fatela and Taborda (2002; Fig. 2), the detection of a minor species (here considered to be < 2% of the total assemblage) is performed at a confidence level of 100% when counting 500 specimens (i.e. coccolith data set); and it is of 90%-100% when counting 100-300 specimens (i.e. coccosphere data set). The latter is in any case a reasonable confidence limit too. This information relative to confidence levels of both coccosphere and coccolith counts has been added to the new version.
We agree with Reviewer #4 and the other reviewers that ecological inferences have to be based on the coccosphere data set. Therefore, we base interpretations about coccolithophore species ecology (section 5.2. of the manuscript) on the coccosphere data set in this new version.

The authors state that the results highlight the role of coccolithophores as significant primary producers in the study area, which contrast the occurrence of diatoms. If at all, such a statement can only been made on coccosphere numbers, should include information on other phytoplankton, and would also have to consider a similar rang of diatom data. Corrected

I also would recommend using the term “bloom” in a different way, neither as representative of the standing crops of coccolithophores nor as a term for coccoliths! It should be a large, temporary colony of coccolithophores (=coccospheres) or of coccolithophore species. Thus, I would name only the occurrence in May 2012 at CALIBERA station as a bloom event. Corrected.

Apart from this terminology issues, I would like to see a discussion on the reasons both for Type A and Type B “blooms”, if the coccoliths will still be used. Their differences are mentioned but that’s it. And if the “deeper blooms” are based on wave-mediated resuspension of sediments, this for sure is something different. But if this is an assemblage composed of resuspended coccoliths, it should be composed of species accumulated in the sediment. But to me it is not clear, if this is the case. It simply is not specfied here! We believe we did explain this in the text. This is the reason why we treat both data sets (coccospheres and coccoliths) separately, so we can assess processes that differentially affect coccoliths that are already deposited on the underlying sediments and coccospheres (which rarely make it to the sea floor). This “deep blooms” as we referred to them in the previous version (we have eliminated that term from the employed terminology) were and still are explained and discussed in this version.

It is mentioned in the oceanographic setting that down-welling favourable conditions and a decrease in primary productivity occurred during autumn and winter (October to March– April). However, the peak occurrence of coccospheres is during March 2012, at the end of a slight cooling of the upper water column. Is this an unexpected “upwelling” event or are similar events known from this area at this time of the year?

In the oceanographic setting we explain the seasonal oceanography of the study area in general terms. We refer the reviewer to the paper by Zuñiga et al. (2016), where a monthly time series of the conditions of the water column can be found for RAIA station from 2008 to 2012. As described in their work for this long time-series: ¨…*from January to March-April, the water column was thermally homogeneized (_14 °C) and characterized by high nitrate levels (4–6 mmol kg_1) due to the winter mixing and river runoff. Subsequently, the transitional phase from winter to the upwelling season was marked by the spring bloom episode, as registered in* ***March 2008, April 2011 and March 2012***”. Therefore March is as a transitional month between both the winter and the upwelling regime, and similar events like the one identified in our Manuscript are likely to occur during this periods. “*During these spring transition periods, the development of sea surface thermal stratification due to incipient solar heating, jointly with the up-welled of nutrient rich subsurface waters, caused by the establishment of northerly winds, trigger the increase of Chl a levels in the water column*”.

However, apart from the temperature signal, this event seems to have only minor impact on the other parameters. Nutrients just slightly increase from close to zero to just 0.3 µM HPO42-. Is this due also for the other available nutrients described in the methods? Indeed, as shown in the new figure. It would important to add other nutrients, since, e.g. off Bermuda increasing coccolithophore abundances coincide with the seasonal advection of nitrate-rich but phosphate-poor waters to the euphotic zone (Haidar and Thierstein 2001). Thus, taking phosphate as a representative of all nutrients could hamper the ecological interpretation of the species.

We did not plot nitrate for two main reasons:
1.-All nutrients were considered in the initial variable selection prior to CCA, as stated in the text, but variable selection only pointed at HPO_4^{-2} *as being significant to explain coccolith variability, and rejected* NO_{3-}, (and also $Si(OH)_4$, although this was expected)*. Therefore, we preferred not to show data that was not going to be included in the discussion.*
2.-Nitrate shows the same temporal and spatial variability as phosphate, although different absolute values.
In any case, Nitrate has been presented now for those readers that might wonder about its distribution and concentration. As coccolithophores utilize phosphate and nitrate, but not silicic acid, do not show the latter.

Actually, the discussion in chapter 5.2 species by species is a bit boring and rather superficial to me (and is based on coccolith data, of course). It mainly confirms previous interpretations of the species and “just” defines assemblages that may be used as local proxy indicators. I would discuss the CCA much more (if not based on coccolith data).

We use the coccosphere species abundance data in these new version to address such issues and have tried to discuss species in more detail.
However, we believe the CCA has to be used to make more apparent relationships that both are and are not that obvious for the human eye from the simple visualization of the species distribution, but its interpretation must be made based on the background we already have on the species. This is, just because a CCA locates a species close variable *X*, that does not mean there is a causal relationship between them. Therefore, such interpretations have to be made with caution without trespassing the boundaries of the statistical possibilities. In our case, CCA seems to indicate coccolithophore-environmental relationships that have been found by other authors already, and does not reveal any striking/new feature, so we discuss this accordingly. Nevertheless, the new CCA performed using the coccosphere data set relates *Syracosphaera* spp. species with higher salinity and temperature, something that might be indicating its preference for the subtropical ENACW carried by the ICP in autumn, (and not necessarily for higher temperature and salinity *per se*.) This is now discussed in the new version. For other species, the same conclusions as in the previous version can be made since their location in relation to the environments on the bi-plot is still the same.

I have also problems with the figures. Actually, I don't like this colourful tiny way of presentation and would favour similar graphs limited to grey scale! And since the data are described station by station, I would plot the information for each station together. We would also like any journal to provide a page per figure, but this is never the case. There is a lot of data to present, and their size can be changed just by using the pdf zoom tools. Regarding colours, we used the default colour scale provided by ODV, with which most readers are already familiarized, and which helps to visualize the data. Figures can be also visualized in grey scale simply by printing them in black and white (and this works for both physical printing and virtual pdf printing). We are afraid the opposite (greyscale to colours) is not possible.

We have kept Fig. 3 as it was (comparing total abundances and % between stations) so it illustrates the discussion, in which differences and similarities between stations are discussed, but the rest of the figures have been altered so species distributions are plotted by stations as the Review suggests.

I would also recommend adding the oceanographic currents to figure 1. And Wind is often mentioned in the text, but no data is shown nor is there any further information given. At least some general or schematic information should be given in Figure 1 as well! There is still some controversy about the Portugal Coastal Current (PCC) and its existence, for which co-authors of this Manuscript do not have a single and agreed opinion. This is the reason why it is not mentioned either in the oceanographic settings. Actually, it is not necessary for the discussion. Winds are explained in the text, but we don't think it is necessary to plot their arrows in the figure; besides they change in seasonal terms so this would lead to two separated (and unnecessary figures). Winds are mentioned because the upwelling occurring is this region is wind-driven upwelling. So whenever we mention the wind it is another way to refer to the upwelling (and its forcing mechanism).

Specific comments: Page 1, l. 30: "group" not in italics. Corrected.

Page 1, l. 34: Please specify which relevant information you mean. It is specified in the next 5 lines.

Page 2, l. 20: Those upwelling systems are generally named as Eastern Boundary Upwelling Ecosystems (EBUEs; Fréon et al., 2009). Added.

Page 3: Chapter 2, Oceanographic setting – I would merge this together with the chapter 4.1, which would allow pointing to "unexpected oceanographic events". We think the reader will appreciate an introduction to the study area, this is why this section goes right after the introduction.

Page 4, l. 25: Young et al. (2003) not in reference list. Corrected.

Page 5: Chapter 4.1 is not always clear to me. Sometimes the statements are only for RAIA station, sometimes for both. Please clarify. The text description in the text and what i got fromm the figures seems to be not fully the same! Corrected.

Page 5: Chapter 4.2 is not needed if the data is already published. Only RAIA data is already published, not CALIBERIA.

Page 8, l. 17: Data from Ferreira and Cachao come from an estuary and coccolith data is at the same range (up to 4.8 x105 coccoliths/l) at the RAIA station! Added.

Page 10, l. 5 ff.: Is there anything known on E. huxleyi morphotypes for this region. The discussion of the environmental affinities of E. huxleyi would need further information on morphotypes, which may have different adaptations. In other areas such as off SW-Africa, distinct differences in the occurrences of morphotypes have been observed (Henderiks et al. 2012, Mar.Ecol.Prog.Ser. 448).

E. huxleyi morphotypes would certainly provide some information on their relationship with the environmental variables. Nevertheless, such specific research question is out of the scope of this paper and such morphological analyses are certainly not essential or a requisite to provide the key information we need to answer our research questions (i.e. How are coccolithophore and coccolith abundance patters in the NW Iberian Margin? What can we say about their inner-shelf and outer-shelf temporal variability in relation to seasonality and/or diverse oceanographic processes?).

Page 11, l. 5 ff.: I am a bit worried about these minor species. So far nothing has been presented on these and information is only given in the supplement. Again, this information seems to be based only on coccolith data, but seems also been limited in a statistical sense. Otherwise please introduce information on the species earlier.

We presented both their relative and their absolute abundance in the Supplementary files so everybody can see these results, and they are presented on page 7. L21-23. We did not comment too much on these because they were not included in the CCA (relative abundance was not > 2% in at least 2 samples). Simply describing their abundance was, as mentioned by the Reviewer, a bit boring, so we decided to give this information to the reader in the form of figures in case anybody was further interested. As aforementioned, the ecological interpretations at the species level in this new version are based on coccosphere data set and not the coccolith data set, but information on minor species is still included in the Supplementary material.

Fatela, F., Taborda, R.: Confidence limits of species proportions in microfossil assemblages, Marine Micropaleontology, 45, 169-174, 2002.
Zúñiga, D., Villacieros-Robineau, N., Salgueiro, E., Alonso-Pérez, F., Rosón, G., Abrantes, F., Castro, C.G.: Particle fluxes in the NW Iberian coastal upwelling system: Hydrodynamical and biological control, Continental Shelf Research, 123, 89-98, 2016.