Ocean Science
Discussions

Is coccolithophore distribution in the Mediterranean Sea related to seawater carbonate chemistry?

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Abstract

The Mediterranean Sea is considered a "hot-spot" for climate change, being characterized by oligotrophic to ultra-oligotrophic waters and rapidly changing carbonate chemistry. Coccolithophores are considered a dominant phytoplankton group in these waters. As a marine calcifying organism they are expected to respond to the ongoing changes in seawater CO_2 systems parameters. However, very few studies have covered the entire Mediterranean physiochemical gradients from the Strait of Gibraltar to the Eastern Mediterranean Levantine Basin. We provide here an updated state of knowledge of the coccolithophore distribution in the Mediterranean Sea and relate this to a broad set of in situ measured environmental variables. Samples were taken during the Meteor (M84/3) oceanographic cruise in April 2011, between 0–100 m water depth from 28 stations. Total diatom, dinoflagellate and silicoflagellate cell concentrations are also presented. Our results highlight the importance of seawater carbonate chemistry, especially CO_3^{2-}, in unraveling the distribution of heterococcolithophores, the most abundant coccolithophore life phase. Holo- and hetero-coccolithophores respond differently to environmental factors. For instance, changes in heterococcolithophore assemblages were best linked to the combination of $[CO_3^{2-}]$, pH, and salinity ($\rho = 0.57$) although salinity might be not functionally related to coccolithophore assemblage distribution. Holococcolithophores, on the other hand, were preferentially distributed and showed higher species diversity in oligotrophic areas (Best fit, $\rho = 0.32$ for nutrients), thriving in nutrient depleted waters. Clustering of heterococcolithophores revealed three groups of species sharing more than 65 % similarities. These clusters could be assigned to the eastern and western basins, and deeper layers (below 50 m), respectively. In addition, the species *Gephyrocapsa oceanica, G. muellerae* and *Emiliania huxleyi* morphotype B/C are spatially distributed together and trace the influx of Atlantic waters into the Mediterranean Sea. The results of the present work emphasize the importance of considering holo- and hetero-coccolithophores separately when analyzing changes in species assemblages and diversity. Our findings clearly show that

coccolithophores are a dominant phytoplankton group in the entire Mediterranean Sea; they have life stages that are expected to respond differently to the variability in seawater carbonate chemistry and nutrient concentrations.

1 Introduction

Marine phytoplankton constitutes about 1–2 % of the global biomass among primary producers (Falkowski, 1994); however, it contributes to ~ 46 % of the primary production in a global scale (Field et al., 1998). Coccolithophores represent ~ 10 % of global phytoplankton biomass (Tyrrell and Young, 2009). They play an important role in biogeochemical cycles, contributing to both the organic and inorganic carbon pumps through photosynthesis and calcification, being calcification the main process controlling PIC : POC (rain ratio). For instance, in the eastern Mediterranean Sea, they are the main contributor to the inorganic carbon pump ($CaCO_3$ production and flux) throughout the year (Knappertsbusch, 1993; Ziveri et al., 2000; Malinverno et al., 2003).

Most studies looking at coccolithophore assemblages and distribution take into account parameters such as nutrients, PAR, temperature, salinity, oxygen (i.e. Young, 1994; Ziveri et al., 1995; Hagino et al., 2000; Takahashi and Okada, 2000; Haidar and Thierstein, 2001; Cortés et al., 2001; Ignatiades et al., 2009). Only recently, parameters related to the seawater carbonate system have been considered due to their importance for calcification and the ongoing and projected changes directly related to the rapidly increasing atmospheric $p\text{CO}_2$. Carbonate chemistry parameters have been suggested as drivers of: coccosphere morphology modification in field samples (Beaufort et al., 2008; Triantaphyllou et al., 2010; Beaufort et al., 2011), of *Emiliania huxleyi* blooms (Merico et al., 2006) and of changes in coccolithophore assemblage composition (Charalampopoulou et al., 2011). Although it is not clear why coccolithophores calcify, calcification is a key physiological energy spending process (Brand, 1994; Balch, 2004) that changes the carbonate chemistry of their surrounding media.

Therefore, the availability of the necessary resources for carrying out calcification should facilitate coccolithophore's growth in the ocean.

The Mediterranean Sea provides an ideal ground to explore the factors controlling coccolithophore distribution because of the well known large gradient in physicochemi-
5 cal parameters. It has a negative fresh-water balance with evaporation exciting precip-itation and surface water temperature, salinity, TA, CO_3^{2-} increase towards the eastern basin. The Mediterranean Sea is one of the most nutrient-poor regions of the global ocean (Dugdale and Wilkerson, 1988), with a trophic status ranging from mesotrophic in the northwest to extremely oligotrophic in the east (Krom et al., 1991; Berman et al.,
10 1984; Berland et al., 1988; Yacobi et al., 1995; Psarra et al., 2000). The spatial diversi-fication of the phytoplankton community structure along an east–west transect shows that dinoflagellates and coccolithophores dominate in the eastern basin and diatoms in the western basin (Ignatiades et al., 2009). Ocean acidification, warming and changes in nutrient availability are expected to significantly alter primary production rates, as
15 well as the overall plankton community structure. Studies on coccolithophores distri-bution in the Mediterranean Sea are mostly regional (Dimiza et al., 2008; Malinverno et al., 2003), loosing part of the above mention gradients. Additionally, when a west to east transect was sampled (Knappertsbusch, 1993; Ignatiades et al., 2009) carbonate chemistry parameters were not. Thus comparisons between the different basins are
20 scarce and the influence of carbonate chemistry parameters on actual coccolithophore assemblages remains therefore uncertain.

The present work investigates the regional and vertical distribution of living coccol-ithophores in the Mediterranean Sea with respect to in situ measured environmental parameters and with attention to those of the carbonate chemistry. It provides an up-
25 to-date state of the coccolithophore assemblage's composition and distribution in the Mediterranean Sea, with a basin resolution that has not been assessed before, and along physical and chemical gradients.

2   Material and methods

2.1   Hydrography and phytoplankton

A detailed water sampling was conducted during the M84-3 cruise from 6 to 28 April 2011 on board the R/V *Meteor* (Tanhua, 2013; Tanhua et al., 2013a). Here we investigate a subset of 81 samples from 28 stations collected between 0 and 100 m water depth. Figure 1 shows the location of all sampled stations during the cruise trajectory. Samples were taken using a SeaBird carousel (24 Niskin bottles) Rossette connected to a SeaBird SBE911 plus CTD-O_2 sensor. Samples collected at < 1 m water depth were obtained by filling a 5 L plastic container with surface water. Sampling depths and the bottle data can be found in: http://cdiac.ornl.gov/ftp/oceans/CLIVAR/Met_84_3_Med_Sea/.

Between 1.5 and 4.5 L of water were gently filtered onto acetate cellulose membranes (Millipore, 0.45 µm pore size, 47 mm diameter). Membrane filters were oven dried at 40 °C for ∼ 12 h and stored in sealed Petri dishes. A portion of each filter was placed on aluminum stubs and gold coated using an EMITECH K550X sputter coater. The quantification and identification of the main phytoplankton groups and coccolithophore species were performed by JEOL-JSM 6300 and ZEISS-EVO MA10 scanning electron microscopes (SEM). 5–15 mm transects on the filter, corresponding to an average of 2.3 mL of seawater were observed at 3000X and phytoplankton groups quantified as coccolithophores, diatoms, dinoflagellates and silicoflagellates. Coccolithophore species were identified, and their absolute and relative abundances counted. In samples with very few coccospheres a larger filter portion was observed in order to quantify a minimum of 100 cells (a maximum number of 420 cells were counted). Lower (C_L) and upper (C_U) confidence intervals at 95 % significance were estimated following Bollmann et al. (2002). For a 100 cell count these were: $C_L = 82$, $C_U = 102$ and for a 420 cell count: $C_L = 382$, $C_U = 422$. Cell densities (number of cell L^{-1} seawater) were

calculated. *Emiliania huxleyi* was sub-classified into morphotypes according to Young et al. (2003).

For each sample the Shannon–Wiener diversity index (H') was calculated for hetero-coccolithophores and holococcolithophores. These two groups were treated separately because they represent two different stages of a coccolithophore's life cycle, and taxonomy between the two does not always account for it.

2.2 Environmental parameters

A detailed protocol of all measured environmental variables can be found in Tanhua et al. (2013a). In situ salinity, temperature and oxygen data were determined by CTD (described in Sect. 2.1). Overall data accuracies were: 0.002 °C for temperature and 0.003 for salinity. Macronutrients (phosphate and nitrate and silicate concentrations) were measured on-board with a QuAAtro auto-analyzer from SEAL analytics. The following protocols from SEAL analytics were followed: NO_3 (Method No. Q-068-05 Rev. 4), PO_4^{-3} (Method No. Q-031-04 Rev. 2) and Si (Method No. Q-066-05 Rev. 3). The nutrient analytical error was determined on 5–7 sample replicates taken at selected stations. The error is: for nitrate 0.08 μmol kg^{-1}, phosphate 0.007 μmol kg^{-1} and silicate 0.10 μmol kg^{-1}.

The carbonate system was characterized by measuring dissolved inorganic carbon (DIC), pH and total alkalinity (TA). DIC content was measured coulometrically using a SOMMA (Single-Operator Multi-Metabolic Analyzer) system. The precision of the analysis is ± 0.6 μmol kg^{-1} and the accuracy is 2.5 μmol kg^{-1}. pH was measured by double-wavelength spectrophotometry, and it is reported at 25 °C on the total scale. The reproducibility of the pH measurements was 0.0012. TA was analyzed following a double end point potentiometric technique. The precision of the TA measurements was 0.1 μmol kg^{-1}. More details about the CO_2 analysis and quality control are presented in Álvarez et al. (2013). Using as input conditions atmospheric pressure and 25 °C and as output conditions in situ temperature and pressure, we calculated the in situ conditions for other CO_2 related variables from pH and total alkalinity (TA) for

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the first 100 m water column. Calculations were performed using the program CO2Sys (Lewis and Wallace, 1998). Equilibrium constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987) were chosen, Álvarez et al. (2013). Input temperature and pressure were 25 °C and 0 dbar respectively.

5   A characterization of the upper 100 m environmental parameters is shown in Fig. 2; the profiles for the complete water column at a higher spatial horizontal resolution and a full description of the physicochemical setting are presented in Tanhua et al. (2013b); Álvarez et al. (2013) in this OS special issue.

2.3   Statistical analyses

10 The E-PRIMERv.5 package was used for the following analyses: (1) the BIOENV routine, which computes a rank correlation between the elements of similarity matrices for environmental parameters and biological data, was run to detect the combined changes in environmental parameters and species distribution among stations. The routine examines all possible combinations of environmental variables and gives the

15 "best fit" (highest Spearman rank correlation coefficient, ρ) of environmental variables explaining changes in biological communities. This test was performed for all heterococcolithophore and holococcolithophore species contributing > 2 % to the total assemblage of each group. Before running the routine, we checked for mutual correlation among environmental variables and selected a subset of them for this routine. These

20 were: salinity, temperature, oxygen, pH, partial pressure of carbon dioxide ($p\mathrm{CO_2}$), and the concentrations of bicarbonate ion ($\mathrm{HCO_3^-}$), carbonate ion ($\mathrm{CO_3^{-2}}$), nitrate+nitrite and phosphate. (2) Hierarchical Cluster Analyses by group average. These were performed for heterococcolithophore and holococcolithophore species. *Emiliania huxleyi* morphotype A was removed of the data set used to run the cluster analyses. This was

25 done to emphasize our results on overall community composition and not on *E. huxleyi* that largely dominated the assemblages in our samples. When clusters among species were detected, pair wise Spearman correlations were performed using the

software SPSSv18 to assess the environmental parameters influencing changes in each species abundance.

For the analyses performed by E-PRIMER software, the biological data was transformed in logarithmic scale $\log(1 + x)$ to avoid overemphasizing the dominant species.
Environmental data were standardized ($-\text{mean} \cdot \text{STD}$) to bring data into a comparable scale. Similarity matrices were created for biological and environmental data. For the biological data the Bray–Curtis similarity coefficient was used to examine similarity between each sample's pair. Euclidean distances were used to create the environmental data matrix. Pair wise Spearman correlations were performed on the basis of non-transformed non-standardized data.

3 Results

3.1 Main phytoplankton community

The overall total phytoplankton cell density, including diatoms, dinoflagellates, silicoflagellates and coccolithophores, was increasing westwards the Mediterranean Sea, with maximum densities at Gibraltar Strait. This is in agreement with the satellite-derived chlorophyll *a* concentration at a date approximating the sampling period (Fig. 1). Coccolithophores were the most abundant phytoplankton group during the sampling, relative to diatoms, dinoflagellates and silicoflagellates. They were present in great numbers in all the main Mediterranean basins and accounted for 68 to 99 % of phytoplankton. Dinoflagellates reached only an average of 2 % (maximum of 5 %). Diatoms, although present in all studied basins, displayed low concentrations in the eastern Mediterranean. They were on average 6 % (maximum 25 %) of total phytoplankton. Silicoflagellates (*Dictyocha spp.*) accounted in average for 1 % of phytoplankton (maximum 9 %). Figure 3 shows the distribution of the first three phytoplankton groups in the Mediterranean transect. A species present mostly at low cell densities was the xanthophyta *Meringosphaera mediterranea*.

3.2 Heterococcolithophores and holococcolithophores

A total of 70 coccolithophore species in heterococcolithophore life stage and 45 in the holococcolithophore stage were recorded (see Appendix A). The majority of the quantified cells were in the heterococcolithophore phase. The species *Emiliania huxleyi* largely dominated the coccolithophore counts in all stations except for station # 319 (at the center of the Tyrrhenian basin), where *Corisphaera gracilis* and *Rabdosphaera clavigera* were the dominant species.

The results from the Spearman's rank correlation based routine (BIOENV) suggest that the heterococcolithophore distribution was best linked to a combination of CO_3^{2-}, pH, and salinity with $\rho = 0.566$ (Table 1). Holococcolithophores were preferentially distributed in low nutrient–high pH seawaters. ($\rho = 0.328$, Table 2) and were almost absent at 100 m.

Single Spearman correlations for the species that were clustered together reveal that their distribution can be better explained by seawater carbonate chemistry parameters; for instance, species that were mostly abundant at eastern stations thrived in waters with higher $[CO_3^{2-}]$ and pH and in the surface. Some of these species were negatively correlated to phosphate concentrations and only *D. tubifer* showed a high positive correlation with temperature. Finally, *F. profunda* and *G. flabellatus* were correlated to $[NO_3 + NO_2]$ and negatively with temperature. Table 3 shows these results.

When clustering all the species within the heterococcolithophore life stage, 3 groups were identified sharing more than 65 % similarities. Figure 4 presents the results of further clustering the species with high similarities. The distribution of these species along the east–west transect (stations with black labels in Fig. 1) that includes the stations in the Levantine, Ionian (excluding 307–309), Tyrrhenian (excluding 319), Algerian, Alborean and Gibraltar regions shows that the three groups are distinctively distributed in the Mediterranean Sea (Figs. 5, 6 and 7). The first group comprises species that were more abundant in the eastern stations: *U. tenuis, D. tubifera, P. vandelii, S. pulchra, R. clavigera,* and *S. protrudens* (*R. xyphos* was very close to this cluster but similarity

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was less than 60 %). *P. vandelii* however was patchily distributed all along the transect. The second group includes *E. huxleyi* Type B/C and the *Gephyrocapsa* species: *G. ericsonii, G. muellerae* and *G. oceanica*. A third group was formed by *Florisphaera profunda* and *Gladiolithus flabellatus*, being closely related to *A. robusta* and *H. carteri* (the last two with similarities below 60 %). The species in the latter group were almost restricted to depths below 50 m, with higher abundances at 100 m, and were patchily present from the Algerian to the Levantine basins. Clustering analysis for the holococolith phase did not reveal any pattern in the species composition among the different samples.

In the first 50 m water column, heterococcolithophore and holococcolithophore species diversity index (H') changed slightly in the W–E transect. Although correlations between H' and the longitude of the sample sites (° E) were rather weak, the trend was opposite for the two life stages. For instance, heterococcolithophore diversity tended to decrease towards the east ($\rho = -0.35$, $p = 0.004$) while holococcolithophore species diversity tended to increase W–E ($\rho = 0.41$; $p = 0.001$) (Fig. 8). H' index at 100 m was often zero for both groups being on average 0.3 for holococcolithophores, that are mostly present at surface, and 1.3 for heterococcolithophores.

From the five morphotypes proposed by Young et al., 2003 (A, B, B/C, C, and R) only morphotypes A and B/C were observed in Mediterranean waters. The latter restricted to the western region.

4 Discussion

4.1 Main phytoplankton community

Although picoplankton can seasonally dominate phytoplankton assemblages in the Mediterranean Sea (Decembrini et al., 2009; Yacobi et al., 1995), previous studies have often suggested that coccolithophores are one of the most abundant phytoplankton groups in this sea, in both, eastern (e.g. Gotsis-Skretas et al., 1999; Malinverno

et al., 2003; Ignatiades et al., 1995, 2009; Rabitti et al., 1994; Ziveri et al., 2000), and western basins (e.g Barlow et al., 1997; Barcena et al., 2004). We present a quantitative analysis of the abundance of different phytoplankton groups at a basin scale. This study documents the dominance of coccolithophores in the phytoplankton community (Fig. 3), including the ultra-oligotrophic eastern region where nutrients concentrations fell below detection limits. Dinoflagellates, although present in all studied basins at low concentrations, were more abundant in the Aegean stations, at Sardinia channel ($< 3 \times 10^3$ cells L^{-1}) and at Gibraltar ($< 1 \times 10^4$ cells L^{-1}). Similar concentrations have been reported in previous studies (e.g. Ignatiades et al., 2009). Silicoflagellates were almost absent at 100 m and more abundant at surface waters of the Tyrrhenian Sea, with cell densities up to 6.7×10^3 cells L^{-1}. Diatoms were preferentially distributed in the higher nutrients, colder, less saline and with lower [CO$_3^{2-}$] waters of the western Mediterranean Sea at maximum cell density of 1.6×10^3 cells L^{-1} (Fig. 3). Even though only reached at the Gibraltar Strait, the highest cell density of coccolithophores was 1–2 orders of magnitude higher than for the other phytoplankton groups. According to the so called Margalef's Mandala (Margalef, 1978) phytoplankton succession would depend on nutrient concentrations and turbulence. Temporal changes in phytoplankton abundances are also often referred as light–nutrients controlled features (Sverdrup, 1953). In this study, however, the dominance of coccolithophores over other phytoplankton groups was clear in all the basins, including the Gibraltar strait, where nitrate and phosphate were available and silicate concentrations were above the half saturation constant for diatoms (Ks_Si: 3.46–4.97 μM, Leblanc et al., 2003; 3.9 ± 5.0 μM, Sarthou et al., 2005; or 0.8–2.3 μM, Nelson et al., 1976) and we could have expected the community to be dominated by fast growing phytoplankton. In the interior of the Mediterranean [Si] was probably too low (often below 1.0 μmol kg^{-1}) to support large diatom populations, except for the deeper layers (100 m) of the Ionian and Levantine basin which ranged from 0.8–1.4 μmol kg^{-1}. Egge and Aksnes (1992) observed that at Si values lower than 0.6 μM *Emiliania huxleyi* outcompeted the otherwise dominant *Skeletonema costatum*. For the dataset here presented, nutrients variability alone does

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not explain the dominance of coccolithophores during April 2011, at least not directly. However, a threshold in nutrient concentrations, below which coccolithophores would perform better than other groups in a competitive scenario; would affect their populations. A possible phosphate limitation for other phytoplankton groups (notice the high N/P ratios in both the eastern and western basins as well as in the Gibraltar Strait) cannot be ruled out of explaining coccolithophore dominance over other groups. Turbulence does not account for it neither, since coccolithophores dominated in regions were water density was homogeneous thought the first 100 m as well as in regions where isoclines can be distinguished (e.g. see salinity and temperature profiles from Fig. 2). We suggest that the relative success of coccolithophores over diatoms, dinoflagellates and silicoflagellates during April 2011 in all Mediterranean Sea basins, can be due to a combination of environmental parameters rather than nutrients and turbulence alone. For instance, heterococcolithophore distribution was related to carbonate system parameters (Table 1) as we will discuss in the following section, where alternative explanations are also discussed.

4.2 Heterococcolithophores and holococcolithophores

Coccolithophores have a heteromorphic life cycle with diploid cells producing heterococcoliths and haploid cells producing holococcoliths. Nothing is know about the effects of the ongoing climate change and ocean acidification on this life stage and the impacts on their distribution. Carbonate chemistry parameters are only recently sampled and considered when looking in general at coccolithophore assemblages and distribution. Although it is not conclusive why coccolithophores calcify, calcification is an energy consuming process for coccolithophores (Brand, 1994; Balch, 2004), maintained by natural selection through millions of years. It is therefore plausibly that the availability of the necessary resources for carrying out calcification should facilitate coccolithophore's growth in the ocean. In this context, it is important to understand how marine calcifying organisms could respond to the rapidly accumulation of atmospheric pCO$_2$ and their interaction with ocean's carbonate chemistry (Kroeker et al., 2013). It has been shown

in culture experiments that during calcification, *Emiliania huxleyi*, the most abundant living coccolithophores, utilized seawater CO_3^{2-}, resulting in particulate inorganic carbon; while during photosynthesis, they consume CO_2 and produce particulate organic carbon (for details see Zeebe and Wolf-Gladrow, 2001). Even further, coccolithophore sensitivity to CO_2 is different among species and strains (Langer et al., 2006, 2009). These differences, as pointed out by Rost et al. (2008) could imply that changes in the carbonate system might have profound effects on phytoplankton species assemblages and succession. Finally, the carbonate system parameters might be critical, but under-looked, to solve the coccolithophore distribution patterns.

Our findings documented that during the time of the M84/3 cruise heterococcolithophore distribution was best linked to $[CO_3^{2-}]$, pH, and salinity ($\rho = 0.566$; Table 1). The single abiotic parameter that best grouped heterococcolithophore assemblages in a manner consistent with the sampling locations was $[CO_3^{2-}]$. Nevertheless, the robustness of the relationships described by correlations and the causal mechanisms behind them should be pursued by other ways (e.g. by experiments, theoretical analysis) (Austin, 2002 and references therein).

Although coccolithophores preferentially use HCO_3^- for their intracellular calcification within a calcifying vesicle (Mackinder et al., 2010) at alkaline pH values CO_3^{2-} is the major carbon source for $CaCO_3$ and we can assume the uptake of both HCO_3^- and CO_3^{2-} (Ziveri et al., 2012). In the Mediterranean Sea, CO_3^{2-} increases gradually towards the east. Thus, it is possible that those species thriving in the eastern basins utilize comparatively more CO_3^{2-} than those that prosper in the western Mediterranean. Using a compilation from world-wide plankton samples and sediments spanning the last 40k years, Beaufort et al. (2011) recorded significant correlations between coccolith mass belonging to the family Noelaerhabdaceae (genera *Emiliania, Gephyrocapsa* and *Reticulofenestra*) with $[CO_3^{2-}]$ and $[HCO_3^2]$. They argue that differentially calcified species are distributed in the ocean according to the ocean's carbonate chemistry. Modeling studies also highlighted the importance of $[CO_3^{2-}]$ for coccolithophore distribution, as

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observed by Merico et al. (2006); *Emiliania huxleyi* blooms in the Baltic Sea coincide with periods of high $[CO_3^{2-}]$.

Changes in pH are concomitant with changes in the ratio between bicarbonate and carbonate ions. This makes difficult to disentangle which parameter of the carbonate system could affect coccolithophore populations. Under laboratory culture conditions, *Emiliania huxleyi* calcification is sensitive to low pH and bicarbonate, while photosynthesis and growth is sensitive to low pCO_2 (Balch et al., 2013) and the coccolith morphogenesis in *Calcidiscus leptoporus* is hampered by pCO_2 and no other parameter of the carbonate chemistry (Langer and Bode, 2011). How will these responses translate to a community scale in the ocean? Charalampopoulou et al. (2011) found that the coccolithophore species distribution between the North Sea and the Atlantic Ocean related to pH and irradiance. In this study, pCO_2, one of the parameters considered to run the BIOENV routine, was not part of the best fitting variables to explain coccolithophore distribution patterns. This might be an indication that, during the time of the study there was no evident pCO_2 limitation of photosynthesis in the observed species. Mimicking the experimental design of the above mentioned culture experiments into a mesocosm scale could help elucidating how will the different effects of carbonate chemistry modification on coccolithophore's physiology and morphology shape the community.

Salinity, even if one of the environmental variables that optimized the best fitting combination of variables explaining the biological data, might not be crucial in controlling heterococcolithophore distribution since experimental evidence (Brand, 1984) indicates strain specific differences that allow *Emiliania huxleyi* to survive at a wide salinity range. *E. huxleyi* has been found in oceanographic regions characterized by very diferent salinities (reviewed by Tyrrell et al., 2008). Furthermore, heterococcolithophores isolated from the Mediterranean Sea (CODENET collection) were maintained at salinities of 32–33 with non-observed adverse effects (Probert and Houdan, 2004). Overall, we suggest CO_3^{2-} and pH as functionally related important variables in explaining heterococcolithophore distribution in the Mediterranean Sea.

In contrast to what was shown for heterococcolithophores, CO_3^{2-} appears not to be relevant to holococcolithophore distribution. Instead, they were preferentially distributed in low nutrient – high pH seawaters ($\rho = 0.328$, Table 2) typical of the surface (upper 50 m) Mediterranean waters but almost absent at deeper depths (100 m). Although considering the two life stages as single species of a homogeneous group, Ignatiades et al. (2009) hypothesized NO_3^- and PO_4^{3-} as factors that could be controlling their distribution form the Gulf of Lions to the Levantine basin. It should be noticed that in this study phytoplankton cell counts were performed using an inverted microscope, a method that is alleged to underestimate coccolithophore counts, especially of the smaller and low-calcified species (O'Brien et al., 2013; Bollmann et al., 2002). Holococcolithophores were, in general present in all samples collected in Mediterranean surface waters but almost absent at 100 m. Higher abundances in very oligotrophic waters of the Mediterranean Sea have been reported before (Kleijne, 1991, 1992). Cros and Estrada (2013), reported on the environmental preferences of the holococcolithophores being upper photic zone, nutrient depleted waters. They linked the observed segregation to a differentiation of ecological niches. Dimiza et al. (2008) observed that holococcolithophores around the Andros Island were more abundant in surface waters together with some heterococcolithophore species such as *Rabdosphaera clavigera*. The lower ρ obtained in the BIOENV analysis for holococcolithophores (Table 3) might be due to the lack, in the statistical analysis, of an important parameter (e.g. irradiance, zooplankton grazing) not measured during this study.

Another feature that was different between the coccolithophore life stages is the development of species assemblages. Holococcolithophore species did not form different assemblages along the Mediterranean Sea (no species clustering with high similarities in abundance and distribution). Interestingly, during this haploid life stage the different species seem to behave as a homogeneous group, exploiting a similar ecological niche. On the contrary, three heterococcolithophore clusters were identified whose species shared more than 65 % similarities (Fig. 4). The first group comprises species that were more abundant in the eastern stations: *U. tenuis, D. tubifera, P. vandelii, S.*

pulchra, R. clavigera, and *S. protrudens*. The second group includes *E. huxleyi* Type B/C and the *Gephyrocapsa* species*: G. ericsonii, G. muellerae* and *G. oceanica*. A third group was formed by *Florisphaera profunda* and *Gladiolithus flabellatus*. Most of the species in these clusters have been found to share an ecological niche in other studies:

5 *U. tenuis, D. tubifera, S. pulchra and R. clavigera* have been considered typical in oligotrophic warm waters and/or surface water species (Okada and Honjo, 1973; Okada and McIntyre, 1977, 1979; Nishida, 1979; Ziveri et al., 2000; Haidar and Thierstein, 2001; Malinverno et al., 2003; Ziveri et al., 2004 for *Syracosphaera* spp.; Triantaphyllou et al., 2004). The gephyrocapside species have been considered typical of eutrophic

10 areas (Kleijne et al., 1989; Broerse et al., 2000) with lower density, lower salinity and higher temperature (Takahashi and Okada, 2000; Knappertsbusch, 1993). Finally, *F. profunda* and *G. flabellatus* are widely recognized depth euphotic zone species, often living below the 100 m depth (Okada and Honjo, 1973; Boeckel et al., 2006); and are controlled by the dynamics of the nutricline and thermocline (Molfino and McIntyre,

15 1990; Triantaphyllou et al., 2004). Both species were an important component below the 50 m; with highest abundances around 100 m, where fluorescence data (not shown) locate the deep chlorophyll maximum. The positive correlation with $[NO_3 + NO_2]$ support the previous observations. However, the negative correlation with temperature obtained reflects the fact that nutrients are generally linked to deep mixing and colder waters,

20 not a negative effect on the species. For instance, higher abundances of *F. profunda* have been observed in sediments underneath relatively warmer and stratified surface waters with a deep nutricline (Boeckel et al., 2006).

The clustering of coccolithophore species resembles those proposed by Young (1994): umbelliform group such as *Umbellosphaera tenuis*, found in nutrient-depleted

25 waters; a second group of placolith-bearing cells such as *Emiliania huxleyi* or *Gephyrocapsa* spp. found in coastal or mid-ocean upwelling regions and a last group, composed of floriform cells, such as *Florisphaera profunda*, associated with deep photic-zone assemblages in low to mid-latitudes. We would add in his first group the Rabdolith bearing species as well as some *syrocosphaera* species widely associated to oligotrophic

(Ziveri et al., 2004) surface waters (Malinverno et al., 2003) and cluster them together in our study. As Balch (2004) suggested when referring to this species grouping proposed by Young, "it is likely that the three groups of coccolithophores show differences in their growth strategies which ultimately would relate to their natural abundance".

Heterococcolithophores and holococcolithophores also displayed opposite trends in species diversity (Fig. 8). However the weak correlation obtained between the diversity index H' and the longitude of the sample site should be notice. Giving the taxonomical problems between the two life stages (see Sect. 2.1) considering the two as a single group would lead to the overestimation of the number of species, affecting H'. Future work on the topic discriminating between the two life stages would be necessary in order to clarify the trends here suggested.

Overall, distribution patterns and their relation with environmental parameters are different between the holo- and hetero-coccolithophore life phases. This is probably the result of a different physiology and reveals that the two phases are exploiting different ecological niches. Differences in the morphology and ecology of the two life phases enable the species to survive under a wider range of environmental conditions and could imply a wider distribution range or its seasonal lasting. For instance, blooms of *Emiliania huxleyi* in heterococcolith phase can end by viral attacks (Martínez et al., 2007; Vardi et al., 2012) to which the haploid phase (i.e. holococcolithophores) can resist (Frada et al., 2008, 2012): therefore, the occurrence of haploid individuals would serve as new starting point in case of viral attack to the heterococcolith phase. Another factor that could have affected the results here presented is zooplankton grazing: although generally, zooplankton grazing does not drive *E. huxleyi* blooms to an end (Nejstgaard et al., 1997), their effect on smaller populations could be more important. Possibly important factors that were not addressed in our study are zooplankton grazing and irradiance. Therefore, their contribution to the control of the observed distribution of holo- and heterococcolith life phase cannot be ruled out.

Atlantic waters (AW), with a winter salinity around 36.515 (Rohling, 2009), enter the Mediterranean Sea through the Gibraltar Strait. In its eastwards pathway, the surface

water increases in salinity, TA, temperature and decreases in nutrient concentrations. The modified Atlantic waters (MAW) in the western Mediterranean mainly follows a cyclonic circulation starting along the North African coast eastwards, as the Algerian current. The main part of it flows into the Tyrrhenian Sea (Tanhua et al., 2013b and references therein). Therefore, if there are species that arrive within AW (but whose optimal environment is not typical of eastern Mediterranean waters), the Tyrrhenian Sea could still host them.

During April 2011, the distribution of the species *Gephyrocapsa oceanica*, *G. muellerae* and the morphotype B/C of the species *Emiliania huxleyi* was highly and negatively correlated with salinity. We have argued that salinity constrain to coccolithophore distribution is not critical. A high correlation with this parameter might just reflect the carry-over of a different species assemblage in a different water mass. *Gephyrocapsa oceanica*, *G. muellerae* and the morphotype B/C of the species *Emiliania huxleyi* were mostly present until, $\sim 10°$ E, after the Sardinian channel and in the Tyrrhenian Sea. They are all present in Atlantic waters (Ziveri et al., 2004; McIntyre and Bé, 1967) and have been reported before for western Mediterranean waters (e.g. Cros and Fortuño, 2002; Knappertsbusch, 1993 the latter only for *Gephyrocapsa* spp). The morphotype B/C of *E. huxleyi* has been associated to cold (Hagino et al., 2005; Mohan et al., 2008), nutrient-rich ($> 10 \mu$mol nitrate kg^{-1}) waters with low calcite saturation states. These characteristics can be found in Atlantic waters but are lost very soon in the Mediterranean Sea. Knappertsbusch (1993) related *G. oceanica* to surface Atlantic waters' influence given the highly negative correlation with salinity. Here we propose *Gephyrocapsa oceanica, G. muellerae* and *Emiliania huxleyi* morphotype B/C as tracers for AW influx into the Mediterranean.

5 Conclusions

Our results highlight the importance of seawater carbonate chemistry, especially [CO$_3^{2-}$], in unraveling the distribution of heterococcolithophores, the most abundant

coccolithophore life stage. In contrast, holococcolithophore distribution was mainly linked to oligotrophic conditions. This correlation can be due to competitive advantages under such conditions, but this hypothesis remains to be tested.

Environmental parameters that drive the observed patterns in distribution and assemblage composition of the haploid and diploid life phases of coccolithophores (holo and hetero-coccolithophore) differ. Our results emphasize the importance of considering holo- and hetero-coccolithophores separately when analyzing changes in species assemblages and diversity, and the impacts of acidification on coccolithophores.

The actual distribution of the species *Gephyrocapsa oceanica, G. muellerae* and *Emiliania huxleyi* morphotype B/C could serve as tracers for AW influx into the Mediterranean.

References

Álvarez, M., Sanleón-Bartolomé, H., Tanhua, T., Mintrop, L., Luchetta, A., Cantoni, C., Schroeder, K., and Civitarese, G.: The CO_2 system in the Mediterranean Sea: a basin wide perspective, Ocean Sci. Discuss., 10, 1447–1504, doi:10.5194/osd-10-1447-2013, 2013.

Austin, M. P.: Spatial prediction of species distribution: an interface between ecological theory and statistical modelling, Ecol. Model., 157, 101–118, 2002.

Bach, L. T., Mackinder, L. C., Schulz, K. G., Wheeler, G., Schroeder, D. C., Brownlee, C., and Riebesell, U.: Dissecting the impact of CO_2 and pH on the mechanisms of photosynthesis and calcification in the coccolithophore Emiliania huxleyi, New Phytol., 199, 121–134, doi:10.1111/nph.12225, 2013.

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Balch, W. M.: Re-evaluation of the physiological ecology of coccolithophores, in: Coccolithophores – From Molecular Processes to Global Impact, edited by: Thierstein, H. and Young, J. R., Springer, Berlin, 165–190, 2004.

Barcena, M. A., Flores, J. A., Sierro, F. J., Perez-Folgado, M., Fabres, J., Calafat, A., and Canals, M.: Planktonic response to main oceanographic changes in the Alboran Sea (Western Mediterranean) as documented in sediment traps and surface sediments, Mar. Micropaleontol., 53, 423–445, 2004.

Barlow, R. G., Mantoura, R. F. C., Cummings, D. G., and Fileman, T. W.: Pigment chemotaxonomic distributions of phytoplankton during summer in the western Mediterranean, Deep-Sea Res. Pt. II, 44, 833–850, doi:10.1016/S0967-0645(96)00089-6, 1997.

Beaufort, L., Couapel, M., Buchet, N., Claustre, H., and Goyet, C.: Calcite production by coccolithophores in the south east Pacific Ocean, Biogeosciences, 5, 1101–1117, doi:10.5194/bg-5-1101-2008, 2008.

Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E. M., Ruiz-Pino, D., Metzl, N., Goyet, C., Buchet, N., Coupel, P., Grelaud, M., Rost, B., Rickaby, R. E. M., and de Vargas, C.: Sensitivity of coccolithophores to carbonate chemistry and ocean acidification, Nature, 476, 80–83, 2011.

Berland, B. R., Benzhitski, A. G., Burlakova, Z. P., Georgieva, L. V., Izmestieva, M. A., Kholodov, V. I., and Maestrini, S. Y.: Conditions hydrologiques estivales en Mediterranee, repartition du phytoplankton et de la matiere organique, Oceanol. Acta, SP, 9, 163–177, 1988.

Berman, T., Townsend, D. W., El Sayed, S. Z., Trees, G. C., and Azov, Y.: Optical transparency, chlorophyll and primary productivity in the Eastern Mediterranean near the Israeli Coast, Oceanol. Acta, 7, 367–372, 1984.

Boeckel, B., Baumann, K. H., Henrich, R., and Kinkel, H.: Coccolith distribution patterns in South Atlantic and Southern Ocean surface sediments in relation to environmental gradients, Deep-Sea Res. Pt. I, 53, 1073–1099, doi:10.1016/j.dsr.2005.11.006, 2006.

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

Brand, L. E.: The salinity tolerance of forty-six marine phytoplankton isolates, Estuar. Coast. Shelf S., 18, 543–556, 1984.

Brand, L. E.: Physiological ecology of marine coccolithophores, in: Coccolithophores, edited by: Winter, A. and Siesser, W. G., Cambridge University Press, 39–49, 1994.

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Interactive Discussion

Broerse, A. T. C., Brummer, G.-J. A., and Van Hinte, J. E.: Coccolithophore export production in response to monsoonal upwelling off Somalia (northwestern Indian Ocean), Deep-Sea Res. Pt. II, 47, 2179–2205, 2000.

Charalampopoulou, A., Poulton, A. J., Tyrrell, T., and Lucas, M. I.: Irradiance and pH affect coccolithophore community composition on a transect between the North Sea and the Arctic Ocean, Mar. Ecol.-Prog. Ser., 431, 25–43, 2011.

Cortés, M. Y., Bollman, J., and Thierstein, H. R.: Coccolithophore ecology at the HOT station Aloha, Hawaii, Deep-Sea Res. Pt. II, 48, 1957–1981, 2001.

Cros, L. and Estrada, M.: Holo-heterococcolithophore life cycles: ecological implications, Mar. Ecol.-Prog. Ser., 492, 57–68, 2013.

Cros, L. and Fortuno, J.-M.: Atlas of northwestern Mediterranean coccolithophores, Sci. Mar., 66, 7–182, 2002.

Decembrini, F., Caroppo, C., and Azzaro, M.: Size structure and production of phytoplankton community and carbon pathways channelling in the Southern Tyrrhenian Sea (Western Mediterranean), Deep-Sea Res. Pt. II, 56, 687–699, 2009.

Dickson, A. G. and Millero, F. J.: A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media, Deep-Sea Res., 34A, 1733–1743, 1987.

Dimiza, M. D., Triantaphyllou, M. V., and Dermitzakis, M. D.: Vertical distribution and ecology of living coccolithophores in the marine ecosystems of Andros Island (Middle Aegean Sea) during late summer 2001, Hellenic Journal of Geosciences, 43, 7–20, 2008.

Dugdale, R. C. and Wilkerson, F. P.: Nutrient sources and primary production in the eastern Mediterranean, Oceanol. Acta, Special Issue, 9, 179–184, 1988.

Egge, J. K. and Aksnes, D. L.: Silicate as regulating nutrient in phytoplankton competition, Mar. Ecol.-Prog. Ser., 83, 281–289, 1992.

Falkowski, P. G.: The role of phytoplankton photosynthesis in global biogeochemical cycles, Photosynth. Res., 39, 235–258, 1994.

Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P. G.: Primary production of the biosphere: integrating terrestrial and oceanic components, Science, 281, 237–240, 1998.

Frada, M., Probert, I., Allen, M. J., Wilson, W. H., and De Vargas, C.: The "Cheshire Cat" escape strategy of the coccolithophore Emiliania huxleyi in response to viral infection, P. Natl. Acad. Sci. USA, 105, 15944–15949, 2008.

Frada, M. J., Bidle, K. D., Probert, I., and de Vargas, C.: In situ survey of life cycle phases of the coccolithophore Emiliania huxleyi (Haptophyta), Environ. Microbiol., 14, 1558–1569, 2012.

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Gotsis-Skretas, O., Pagou, K., Moraitou-Apostolopoulou, M., and Ignatiades, L.: Seasonal horizontal and vertical variability in primary production and standing stocks of phytoplankton and zooplankton in the Cretan Sea and the Straits of the Cretan Arc (March 1994–January 1995), Prog. Oceanogr., 44, 625–649, 1999.

Hagino, K., Okada, H., and Matsuoka, H.: Spatial dynamics of coccolithophore assemblage in the Euatorial Western-Central Pacific Ocean, Mar. Micropaleontol., 39, 53–72, 2000.

Hagino, K., Okada, H., and Matsuoka, H.: Coccolithophore assemblages and morphotypes of Emiliania huxleyi in the boundary zone between the cold Oyashio and warm Kuroshio currents off the coast of Japan, Mar. Micropaleontol., 55, 19–47, 2005.

Haidar, A. T. and Thierstein, H. R.: Coccolithophore dynamics off Bermuda (N. Atlantic), Deep-Sea Res. Pt. II, 40, 1925–1956, 2001.

Ignatiades, L., Georgopoulos, D., and Karydis, M.: Description of the phytoplanktonic community of the oligotrophic waters of the SE Aegean Sea (Mediterranean), Mar. Ecol.-P. S. Z. N. I., 16, 13–26, 1995.

Ignatiades, L., Gotsis-Skretas, O., Pagou, K., and Krasakopoulou, E.: Diversification of phytoplankton community structure and related parameters along a large-scale longitudinal east–west transect of the Mediterranean Sea, J. Plankton Res., 31, 411–428, 2009.

Kleijne, A.: Holococcolithophorids from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean, Mar. Micropaleontol., 17, 1–76, 1991.

Kleijne, A.: Extant Rhabdosphaeraceae (coccolithophorids, class Prymnesiophyceae) from the Indian Ocean, Red Sea, Mediterranean Sea and North Atlantic Ocean, ScriptaGeol., 100, 1–63, 1992.

Kleijne, A., Kroon, D., and Zevenboom, W.: Phytoplankton and foraminiferal frequencies in northern Indian Ocean and Red Sea surface waters, Neth. J. Sea Res., 24, 531–539, 1989.

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

Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M., and Gattuso, J. P.: Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming, Glob. Change Biol., 19, 1884–1896, doi:10.1111/gcb.12179, 2013.

Krom, M. D., Kress, N., Brenner, S., and Gordon, L.: Phosphorous limitation of primary productivity in the Eastern Mediterranean Sea, Limnol. Oceanogr., 36, 424–432, 1991

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Interactive Discussion

Langer, G. and Bode, M.: CO_2 mediation of adverse effects of seawater acidification in Calcidiscus leptoporus, Geochem. Geophy. Geosy., 12, 1–8, doi:10.1029/2010GC003393, 2011.

Langer, G., Geisen, M., Baumann, K.-H., Kläs, J., Riebesell, U., Thoms, S., and Young, J. R.: Species-specific responses of calcifying algae to changing seawater carbonate chemistry, Geochem. Geophy. Geosy., 7, Q09006, doi:10.1029/2005GC001227, 2006.

Langer, G., Nehrke, G., Probert, I., Ly, J., and Ziveri, P.: Strain-specific responses of *Emiliania huxleyi* to changing seawater carbonate chemistry, Biogeosciences, 6, 2637–2646, doi:10.5194/bg-6-2637-2009, 2009.

Leblanc, K., Quéguiner, B., Garcia, N., Rimmelin, P., and Raimbault, P.: Silicon cycle in the NW Mediterranean Sea: seasonal study of a coastal oligotrophic site, Oceanol. Acta, 26, 339–355, 2003.

Lewis, E. and Wallace, D. W. R: Program Developed for CO_2 System Calculations ORNL/CDIAC-105. Carbon Dioxide Information Analysis CentreOak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee, 1998.

Mackinder, L., Wheeler, G., Schroeder, D., Riebesell, U., and Brownlee, C.: Molecular mechanisms underlying calcification in coccolithophores, Geomicrobiol. J., 27, 585–595, doi:10.1080/01490451003703014, 2010.

Malinverno, E., Ziveri, P., and Corselli, C.: Coccolithophorid distribution in the Ionian Sea and its relationship to eastern Mediterranean circulation during late fall to early winter 1997, J. Geophys. Res., 108, 8115, doi:10.1029/2002JC001346, 2003.

Margalef, R.: Life-forms of phytoplankton as survival alternatives in an unstable environment, Oceanol. Acta, 1, 493–509, 1978.

Martinez, J. M., Schroeder, D. C., Larsen, A., Bratbak, G., and Wilson, W. H.: Molecular dynamics of Emiliania huxleyi and cooccurring viruses during two separate mesocosm studies, Appl. Environ. Microb., 73, 554–562, 2007.

McIntyre, A. and Be', A. W. H.: Modern coccolithophoridae of the Atlantic Ocean. 1. Placoliths and cyrtoliths, Deep-Sea Res., 14, 561–597, 1967.

Mehrbach, C., Culberson, C. H., Hawley, J. E., and Pytkowitcz, R. M.: Measurements of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure, Limnol. Oceanogr., 18, 897–907, 1973.

Merico, A., Tyrrell, T., and Cokacar, T.: Is there any relationship between the phytoplankton seasonal dynamics and the carbonate system?, J. Marine Syst., 59, 120–142, 2006.

Coccolithophore distribution in the Mediterranean Sea

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Mohan, R., Mergulhao, L. P., Guptha, M. V. S., Rajakumar, A., Thamban, M., AnilKumar, N., Sudhakar, M., and Ravindra, R.: Ecology of coccolithophores in the Indian sector of the Southern Ocean, Mar. Micropaleontol., 67, 30–45, 2008.

Molfino, B. and McIntyre, A.: Precession forcing of nutricline dynamics in the equatorial Atlantic, Science, 249, 766–769, 1990.

Nejstgaard, J. C., Gismervik, I., and Solberg, P. T.: Feeding and reproduction by Calanus finmarchicus, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore Emiliania huxleyi, Mar. Ecol.-Prog. Ser., 147, 197–217, 1997.

Nelson, D. M., Goering, J. J., Kilham, S. S., and Guillard, R. R. L.: Kinetics of silicic acid uptake and rates of silica dissolution in the marine diatom Thalassiosira pseudonana, J. Phycol., 12, 246–252, 1976.

Nishida, S.: Atlas of Pacific nannoplanktons, News Osaka, Micropaleont, 3, 1–31, 1979.

Okada, H. and McIntyre, A.: Modern coccolithophores of the Pacific and North Atlantic Oceans, Micropaleontology, 23, 1–55, 1977.

Okada, H. and McIntyre, A.: Seasonal distribution of modern coccolithophores in the western North Atlantic Ocean, Mar. Biol., 54, 319–328, 1979.

O'Brien, C. J., Peloquin, J. A., Vogt, M., Heinle, M., Gruber, N., Ajani, P., Andruleit, H., Arístegui, J., Beaufort, L., Estrada, M., Karentz, D., Kopczyńska, E., Lee, R., Poulton, A. J., Pritchard, T., and Widdicombe, C.: Global marine plankton functional type biomass distributions: coccolithophores, Earth Syst. Sci. Data, 5, 259–276, doi:10.5194/essd-5-259-2013, 2013.

Probert, I. and Houdan, A.: The laboratory culture of coccolithophores, in: Coccolithophores: From Molecular Processes to Global Impact, edited by: Thierstein, H. R. and Young, J. R., Springer, Germany, 217–250, 2004.

Psarra, S., Tselepides, A., and Ignatiades, L.: Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability, Prog. Oceanogr., 46, 187–204, 2000.

Rabitti, S., Bianchi, F., Boldrin, A., Da Ros, L., Socal, G., and Totti, C.: Particulate matter and phytoplankton in the Ionian Sea, Oceanol. Acta, 17, 297–307, 1994.

Rohling, E. J., Abu-Zied, R., Casford, J. S. L., Hayes, A., and Hoogakker, B. A. A.: The marine environment: present and past, in: The Physical Geography of the Mediterranean, edited by: Woodward, J. C., Oxford University Press, ISBN: 978-0-19-926803-0, 33–67, 2009.

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Rost, B., Zondervan, I., and Wolf-Gladrow, D. A.: Sensitivity of phytoplankton to future changes in ocean carbonate chemistry: current knowledge, contradictions and research directions, Mar. Ecol.-Prog. Ser., 373, 227–237, 2008.

Sarthou, G., Timmermans, K. R., Blain, S., and Treguer, P.: Growth physiology and fate of diatoms in the ocean: a review, J. Sea Res., 53, 25–42, 2005.

Sverdrup, H. U.: On conditions for the vernal blooming of phytoplankton, ICES J. Mar. Sci., 18, 287–295, 1953.

Takahashi, K. and Okada, H.: Environmental control on the biogeography of modern coccolithophores in the southeastern Indian Ocean offshore of Western Australia, Mar. Micropaleontol., 39, 73–86, 2000.

Tanhua, T.: Repeat hydrography in the Mediterranean Sea – Cruise No. M84/3 – 5 April–28 April 2011, Istanbul (Turkey)–Vigo (Spain), METEOR-Berichte, M84/3, 48 pp., DFG-Senatskommission für Ozeanographie, doi:10.2312/cr_m84_3, 2013.

Tanhua, T., Hainbucher, D., Cardin, V., Álvarez, M., Civitarese, G., McNichol, A. P., and Key, R. M.: Repeat hydrography in the Mediterranean Sea, data from the *Meteor* cruise 84/3 in 2011, Earth Syst. Sci. Data, 5, 289–294, doi:10.5194/essd-5-289-2013, 2013a.

Tanhua, T., Hainbucher, D., Schroeder, K., Cardin, V., Álvarez, M., and Civitarese, G.: The Mediterranean Sea system: a review and an introduction to the special issue, Ocean Sci., 9, 789–803, doi:10.5194/os-9-789-2013, 2013b.

Triantaphyllou, M. V., Ziveri, P., and Tselepides, A.: Coccolithophore export production and response to seasonal surface water variability in the oligotrophic Cretan Sea (NE Mediterranean), Micropaleontology, Advances in the biology, ecology and taxonomy of extant calcareous nannoplankton, 50, 127–144, 2004.

Triantaphyllou, M., Dimiza, M., Krasakopoulou, E., Malinverno, E., Lianou, V., and Souvermezoglou, E.: Seasonal variation in Emiliania huxleyi coccolith morphology and calcification in the Aegean Sea (Eastern Mediterranean), Geobios., 12th Meeting of the International Nannoplankton Association, Lyon 2008, 43, 99–110, 2010.

Tyrrell, T. and Young, J. R.: Coccolithophores, in: Encyclopedia of Ocean Sciences, 2nd edn., edited by: Steele, J. H., Turekian, K. K., and Thorpe, S. A., Academic Press, San Diego, US, 3568–3576, 2009.

Tyrrell, T., Schneider, B., Charalampopoulou, A., and Riebesell, U.: Coccolithophores and calcite saturation state in the Baltic and Black Seas, Biogeosciences, 5, 485–494, doi:10.5194/bg-5-485-2008, 2008.

Vardi, A., Haramaty, L., Van Mooy, B. A., Fredricks, H. F., Kimmance, S. A., Larsen, A., and Bidle, K. D.: Host-virus dynamics and subcellular controls of cell fate in a natural coccolithophore population, P. Natl. Acad. Sci. USA, 109, 19327–19332, 2012.

Yacobi, Y., Zohary, T., Kress, N., Hecht, A., Robarts, R., Waiser, M., Wood, A., and Li, W.: Chlorophyll distribution throughout the southern Mediterranean in relation to the physical structure of the water mass, J. Mar. Syst., 6, 179–190, 1995.

Young, J. R.: Functions of coccoliths, in: Coccolithophores, edited by: Winter, A. and Siesser, W. G., Cambridge University Press, 63–82, 1994.

Young, J., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., and Østergaard, J.: A guide to extant coccolithophore taxonomy, J. Nannoplankton Res. (Spec Issue), 1, 1–125, 2003.

Zeebe, R. E. and Wolf-Gladrow, D.: CO_2 in Sea Water: Equilibrium, Kinetics, Isotopes, Elsevier Oceanography Series, 65, Amsterdam, 2001.

Ziveri, P., Thunell, R. C., and Rio, D.: Seasonal changes in coccolithophore densities in the Southern California Bight during 1991–1992, Deep-Sea Res. Pt. I, 42, 1881–1903, 1995.

Ziveri, P., Rutten, A., de Lange, G., Thomson, J., and Corselli, C.: Present-day coccolith fluxes recorded in central eastern Mediterranean sediment traps and surface sediments, Palaeogeogr. Palaeocl., 158, 175–195, 2000.

Ziveri, P., Baumann, K. H., Böckel, B., Bollman, J., and Young, J. R.: Present day coccolithophore biogeography in the Atlantic Ocean, in: Coccolithophores: From Molecular Processes to Global Impact, edited by: Thierstein, H. R. and Young, J. R., Springer Verlag, 2004.

Ziveri, P., Thoms, S., Probert, I., Geisen, M., and Langer, G.: A universal carbonate ion effect on stable oxygen isotope ratios in unicellular planktonic calcifying organisms, Biogeosciences, 9, 1025–1032, doi:10.5194/bg-9-1025-2012, 2012.

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Table 1. Rho values (ρ) for the best Spearman's rank correlations for all possible combinations between the environmental parameters explaining patterns in heterococcolithophores assemblages. On the left, the number of variables taken into account; on the right, description of the variables and the highest ρ values for the rank correlations at a given number of variables. In the first row, the ρ value for each variable is shown in decreasing order of contribution to explain changes in the biological data. Only $\rho > 0.2$ are shown.

Number of variables	Variables (ρ)
1	CO_3^{2-} (0.551); pH (0.498); pCO$_2$ (0.397); PO_4^{3-} (0.358); $NO_3^- + NO_2^-$ (0.328); Salinity (0.310); O$_2$ (0.226);
2	CO_3^{2-} Salinity (0.563)
3	**CO_3^{2-} pH, Salinity (0.566)**
4	CO_3^{2-} pH, PO_4^{3-}, Salinity (0.565)
5	CO_3^{2-} pH, pCO$_2$, PO_4^{3-}, Salinity (0.539)
6	CO_3^{2-} pH, pCO$_2$, PO_4^{3-}, Salinity, Temperature (0.517)
7	CO_3^{2-} pH, pCO$_2$, PO_4^{3-}, Salinity, O$_2$, Temperature (0.507)
8	All (0.491)

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Table 2. Rho values (ρ) for the best Spearman's rank correlations for all possible combinations between the environmental parameters explaining patterns in holococcolithophores assemblages. Only $\rho > 0.2$ are shown. Description as in Table 1.

Number of variables	Variables (ρ)
1	$NO_3^- + NO_2^-$ (0.275); PO_4^{3-} (0.236); pH (0.214); pCO_2 (0.204);
2	$NO_3^- + NO_2^-$ pH (0.327)
3	$\mathbf{NO_3^- + NO_2^-}$ $\mathbf{PO_4^{3-}}$, **pH** **(0.328)**
4	$NO_3^- + NO_2^-$ pH, O_2, Salinity (0.311)
5	$NO_3^- + NO_2^-$ PO_4^{3-}, pH, O_2, Salinity (0.311)
6	$NO_3^- + NO_2^-$ PO_4^{3-}, pH, pCO_2, O_2, Salinity (0.299)
7	$NO_3^- + NO_2^-$ PO_4^{3-}, pH, pCO_2, O_2, Salinity, Temperature (0.283)
8	All (0.275)

Table 3. Three highest Spearman's correlation (ρ) results for each of the species belonging to the observed clusters with the environmental parameters. Preferential depth and distribution along the west to east transect is described. Number of samples taken into account for the analysis is also shown (N). Significance levels were 0.000 in all cases.

Species	Varible (r, N)			Preferential depth	Distribution
E. huxleyi Type B/C	Salinity (−0.691; 81),	CO_3^{2-} (−0.685; 73),	pH (−0.616; 73)	0–100 m	W
G. ericsonii	Salinity (−0.805; 81),	CO_3^{2-} (−0690; 73),	pH (−0.576; 73)	Above 50 m	W
G. oceanica	CO_3^{2-} (−0.833; 73),	Salinity (−0.803; 81),	pH (−0.731; 73)	0–100 m	W
G. muellerae	CO_3^{2-} (−0.835; 73),	Salinity (−0.830; 81),	pH (−0.707; 73)	0–100 m	W
U. tenuis	CO_3^{2-} (0.626; 73),	pH (0.605; 73),	PO_4^{3-} (−0.551; 74)	Above 50 m	E
R. clavigera	CO_3^{2-} (0.727; 73),	pH (0.701; 73),	PO_4^{3-} (−0.546; 74)	Above 50 m	E
D. tubifer	pH (0.600; 73),	Temperature (0.597; 81),	CO_3^{2-} (0.541; 73)	Above 50 m	E
S. pulchra	pH (0.551; 73),	CO_3^{2-} (0.528; 73),	PO_4^{3-} (−0.399; 74)	0–100 m	E
S. protrudens	pH (0.557; 73),	CO_3^{2-} (0.489; 73),	PO_4^{3-} (−0.450; 74)	Above 50 m	E
F. profunda	$NO_3^- + NO_2^-$ (0.637; 81),	Temperature (−0.553; 81),	pH (−0.468; 73)	Below 50 m	W–E
G. flabellatus	$NO_3^- + NO_2^-$ (0.583; 81),	Temperature (−0.522; 81),	O_2 (−0.481; 73)	Below 50 m	W–E

Table A1. Coccolithophore species list. Heterococcolithophores.

Family Calciosoleniaceae	Kamptner, 1937
[1] *Anoplosolenia brasiliensis*	(Lohmann, 1919); Deflandre, 1952
[2] *Calciosolenia murrayi*	Gran, 1912
Family Coccolithaceae	Poche, 1913
[3] *Calcidiscus leptoporus*	(Murray and Blackman, 1898); Loeblich and Tappan, 1978
[4] *Hayaster perplexus*	(Bramlette and Riedel, 1954); Bukry, 1973
[5] *Pleurochrysis carterae*	(Braarud and Fagerland, 1946); Christensen, 1978
[6] *Umbilicosphaera sibogae*	(Weber-Van Bosse, 1901); Gaarder, 1970
[7] *U. sibogae*	(Kamptner, 1963; ex Kleijne, 1993) Geisen in Sáez et al., 2003
[8] *U. hulburtiana*	Gaarder, 1970
Family Helicosphaeraceae	Black, 1971
[9] *Helicosphaera carteri*	(Wallich, 1877) Kamptner, 1954
[10] *H. pavimentum*	Okada and McIntire, 1977
Family Noelaerhabdaceae	Jerkovic, 1970
[11] *Emiliania huxleyi*	(Lohmann, 1902) Hay and Mohler, in Hay et al., 1967 var. *huxleyi*
[12] *Gephyrocapsa ericsonii*	McIntire and Be', 1967
[13] *G. ornata*	Heimdal, 1973
[14] *G. oceanica*	Kamptner, 1943
[15] *G. muellerae*	Bréhéret, 1978
[16] *Reticulofenestra parvula*	(Okada and McIntyre, 1977) Biekart, 1989
Family Papposphaeraceae	Jordan and Young, 1990
[17] *Papposphaera lepida*	Tangen, 1972
Family Pontosphaeraceae	Lemmermann, 1908
[18] *Pontosphaera japonica*	(Takayama, 1967) Nishida, 1971
[19] *Scyphosphaera apsteinii*	Lohmann, 1902
Family Rhabdoaphaeraceae	Ostenfeld, 1899
[20] *Acanthoica biscayensis*	Kleijne, 1992
[21] *A. quattrospina*	Lohmann, 1903
[22] *Algirosphaera cucullata*	(Lecal-Schlauder, 1951) Young, Probert and Kleijne, 2003
[23] *Algiropsphaera robusta*	(Lohmann, 1902) Norris, 1984
[24] *Anacanthoica acanthos*	(Schiller, 1925) Deflandre, 1952
[25] *C. lecaliae*	Kleijne, 1992
[26] *Discosphaera tubifer*	(Murray and Blackman, 1898) Ostenfeld, 1900
[27] *Palusphaera vandeli*	Lecal, 1965
[28] *Rhabdosphaera clavigera*	Murray and Blackman, 1898 var. *clavigera*
[29] *R. clavigera*	(Lohmann, 1902) Kleijne and Jordan, 1990 var. *stylifera*
[30] *R. xiphos*	(Deflandre and Fert, 1954); Norris, 1984

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Table A1. Continued.

Family Syracosphaeraceae	Lemmermann, 1908
[31] *Alisphaera capulata*	Heimdal, in Heimdal and Gaarder, 1981
[32] *A. extentata*	(Kamptner, 1941) Kleijne, R. W. Jordan, Heimdal, Samtleben, A. H. L. Chamberlain and Cros, 2002
[33] *A. gaudi*	(Kamptner, 1941) Kleijne, Jordan, Heimdal, Samtleben, Chamberlain and Cros, 2002
[34] *A. unicornis*	Okada and McIntire, 1977
[35] *Calciopappus caudatus*	Gaarder and Ramsfjell, 1954
[36] *C. rigidus*	Heimdal, 1981
[37] *Coronosphaera binodata*	(Kamptner, 1927) Gaarder, in Gaarder and Heimdal, 1977
[38] *C. mediterranea*	(Lohmann, 1902) Gaarder and Heimdal, 1977
[39] *Michaelsarsia adriaticus*	(Schiller, 1914) Manton et al., 1984
[40] *M. elegans*	Gran, 1912, emend. Manton et al., 1984
[41] *Ophiaster formosus*	Gran, 1912
[42] *Ophiaster hydroideus*	Gran, 1912
[43] *Syracosphaera ampliora*	Okada and McIntire, 1977
[44] *S. anthos*	(Lohmann, 1912) Jordan and Young, 1990
[45] *S. bannockii*	(Borsetti and Cati, 1976) Cros et al., 2000
[46] *S. borealis*	Okada and McIntire, 1977
[47] *S. corolla*	(Lecal, 1966)
[48] *S. delicata*	Cros et al., 2000
[49] *S.dilatata*	(Heimdal, in Heimdal and Gaarder, 1981) Jordan, Kleijne and Heimdal, 1993
[50] *S. histrica*	Kamptner, 1941
[51] *S. lamina*	Lecal-Schlauder, 1951
[52] *S. marginoporata*	Knappertsbusch, 1993
[53] *S. molischii*	Schiller, 1925
[54] *S. nana*	(Kamptner, 1941); Okada and McIntyre, 1977
[55] *S. nodosa*	Kamptner, 1941
[56] *S. noroitica*	Knappertsbusch, 1993
[57] *S. ossa*	(Lecal, 1966); Loeblich and Tappan, 1968
[58] *S. pirus*	Halldal and Markali, 1955
[59] *S. prolongata*	Gran, 1912, ex Lohmann, 1913
[60] *S. protrudens*	Okada and McIntyre, 1977
[61] *S. pulchra*	Lohmann, 1902
[62] *S. rotula*	Okada and McIntire, 1977
[63] *Syracosphaera sp. type D*	sensu Kleijne, 1993
[64] *S. tumularis*	Sánchez-Suárez, 1990
[65] *Syracospahaera* sp.	
Family Umbellosphaeroideae	Kleijne, 1993
[66] *Umbellosphaera tenuis*	(Kamptner, 1937); Paasche, in Markali and Paasche, 1955
[67] *F. profunda*	Okada and Honjo, 1973
[68] *Gladiolithus flabellatus*	(Halldal and Markali, 1955) Jordan and Green, 1994
[69] *Polycrater galapagensis*	Manton and Oates, 1980
[70] *Ceratolithus cristatus*	Norris, 1965

Table A2. Coccolithophore species list. Holococcolithophores.

[1] *Acanthoica quattrospina*	Cros et al., 2000
HOL = sp. aff Sphaerocalyptra	
[2] *Anthosphaera fragaria*	Kamptner, 1937, emend. Kleijne, 1991
[3] *A. lafourcadii*	(Lecal, 1967); Kleijne, 1991
[4] *A. periperforata*	Kleijne, 1991
[5] *Anthosphaera* sp. Type A	Cros and Fortuno, 2002
[6] *Anthosphaera* sp. Type C	Cros and Fortuno, 2002
[7] *Calcidiscus leptoporus* HOL	(Murray and Blackman, 1898) Loeblich and Tappan, 1978
[8] *C. leptoporus* ssp. quadriperforatus HOL	Kamptner (1937) Geisen et al., 2002
[9] *Calicasphaera concava*	Kleijne, 1991
[10] *Calyptrolithina divergens*	(Halldal and Markali, 1955) Heimdal, 1982
[11] *C. divergens f. tuberosa*	(Heimdal, in Heimdal and Gaarder, 1980) Heimdal, 1982
[12] *C. multipora*	(Gaarder, in Heimdal and Gaarder, 1980) Norris, 1985
[13] *Calyptrolithophora papillifera*	(Halldal, 1953) Heimdal, in Heimdal and Gaarder, 1980
[14] *Calyptrosphaera cialdii*	Borsetti and Cati, 1976
[15] *C. dentata*	Kleijne, 1991
[16] *C. heimdalae*	Norris, 1985
[17] *C. sphaeroidea*	Schiller, 1913
[18] *Coccolithus pelagicus*	Gaarder, 1962
ssp. *braarudii* HOL = *Crystallolithus braarudii*	
[19] *Corisphaera gracilis*	Kamptner, 1937
[20] *C. strigilis*	Gaarder, 1962
[21] *C. tyrrheniensis*	Kleijne, 1991
[22] *Corisphaera* sp.	Kleijne, 1991
[23] *Coronosphaera mediterranea*	(Kamptner, 1941) Heimdal in Heimdal and Gaarder, 1980
HOL *gracillima*-type = *Calyptrolithophora gracillima*	

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Table A2. Continued.

[24] *Coronosphaera mediterranea*	Kamptner, 1937
HOL hellenica type = *Zygosphaera hellenica*	
[25] *Gliskolithus amitakarenae*	Norris, 1985 orthog. Emend. Jordan and Green, 1994
[26] *Helicosphaera carteri*	(Kamptner, 1937) Deflandre, 1952
HOL = *Syracolithus catilliferus*	
[27] *Helladosphaera cornifera*	(Schiller, 1913) Kamptner, 1937
[28] *Homozygosphaera arethusae*	(Kamptner, 1941) Kleijne, 1991
[29] *H. spinosa*	(Kamptner, 1941) Deflandre, 1952
[30] *H. triarcha*	Halldal and Markalii, 1955
[31] *Homozygosphaera vercellii*	Borsetti and Cati, 1979
[32] *Poricalyptra gaarderae*	(Borsetti and Cati, 1967) Kleijne, 1991
[33] *Poritectolithus*	sp. 2 of Cros and Fortuño, 2002
[34] *Sphaerocalyptra adenensis*	Kleijne, 1991
[35] *S. quadridentata*	(Schiller, 1913) Deflandre, 1952
[36] *Sphaerocalyptra*	sp. 1 of Cros and Fortuño, 2002
[37] *Sphaerocalyptra*	sp. 3 of Cros and Fortuño, 2002
[38] *Sphaerocalyptra*	sp. 6 of Cros and Fortuño, 2002
[39] *Syracolithus schilleri*	(Kamptner, 1927) Loeblich and Tappan, 1963
[40] *Syracolithus* sp. type A	Kleijne (1991)
[41] *Syracosphaera anthos*	(Schiller, 1925) Kamptner, 1937
HOL = *Periphyllophora mirabilis*	
[42] *Syracosphaera bannockii*	(Borsetti and Cati, 1976) Heimdal, 1982
HOL = *Zygosphaera bannockii*	
[43] *Syracosphaera pulchra*	Lohmann, 1902
HOL oblonga type = *Calyptrosphaera oblonga*	
[44] *Syracosphaera pulchra*	Kamptner, 1937
HOL pirus type = *Calyptrosphaera pirus*	
[45] *Zygosphaera amoena*	Kamptner, 1937

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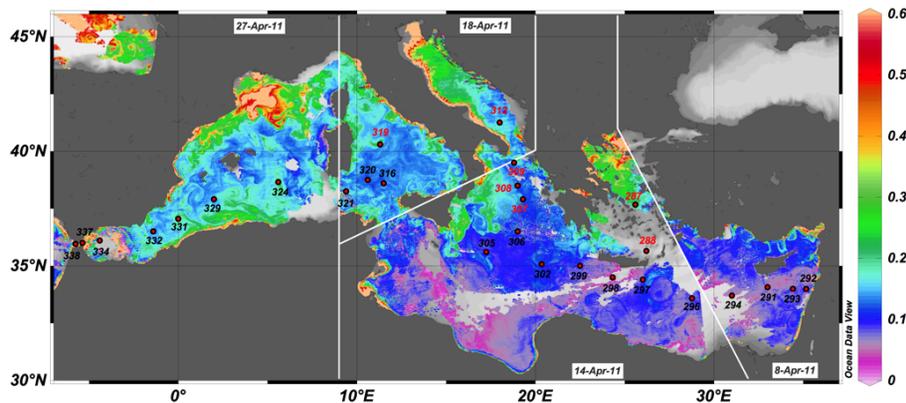
Fig. 1. Sampling stations presented in this study collected during the M84-3 research cruise. Superimposed are the images of chlorophyll (mgC m^{-3}) at an approximate date of the sampling period in the different basins. The transect shown in the following figures includes the stations labeled in black.
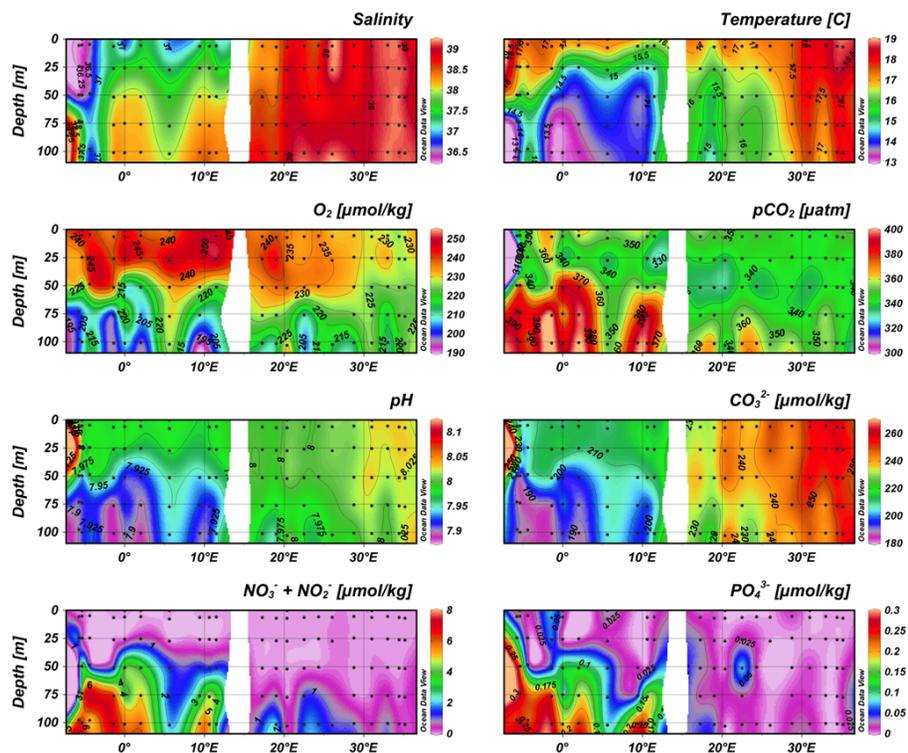
Fig. 2. Environmental parameters at sampling stations for surface waters during the M84-3 cruise.
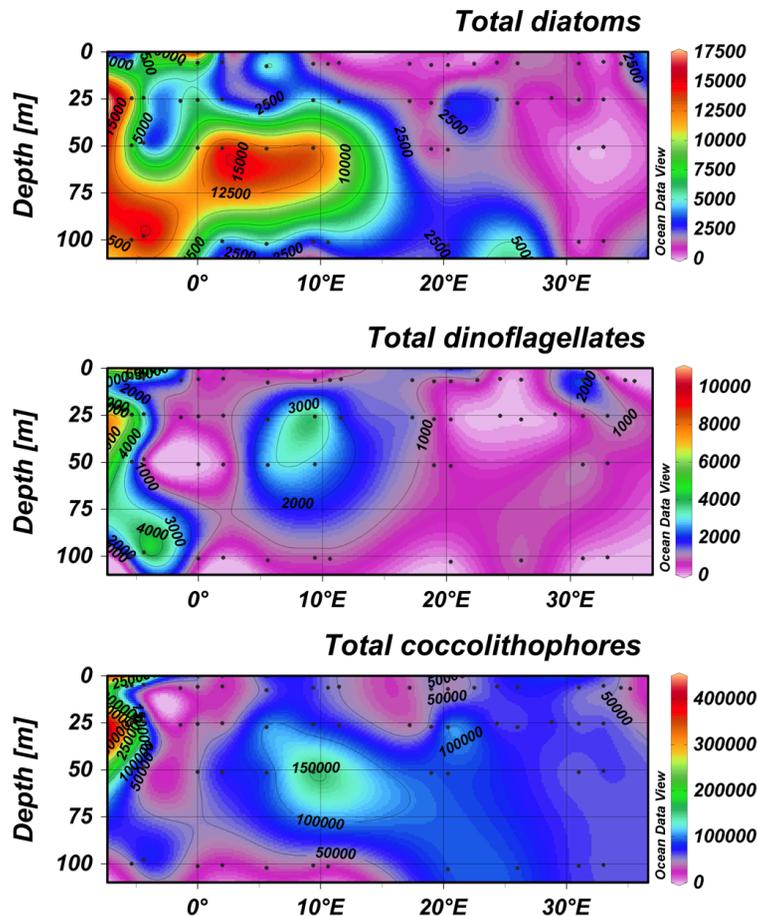
Fig. 3. Distribution of diatoms (upper panel), dinoflagellates (middle panel) and total coccolithophores (lower panel) in a west to east transect along the Mediterranean Sea (black labelled stations in Fig. 1).

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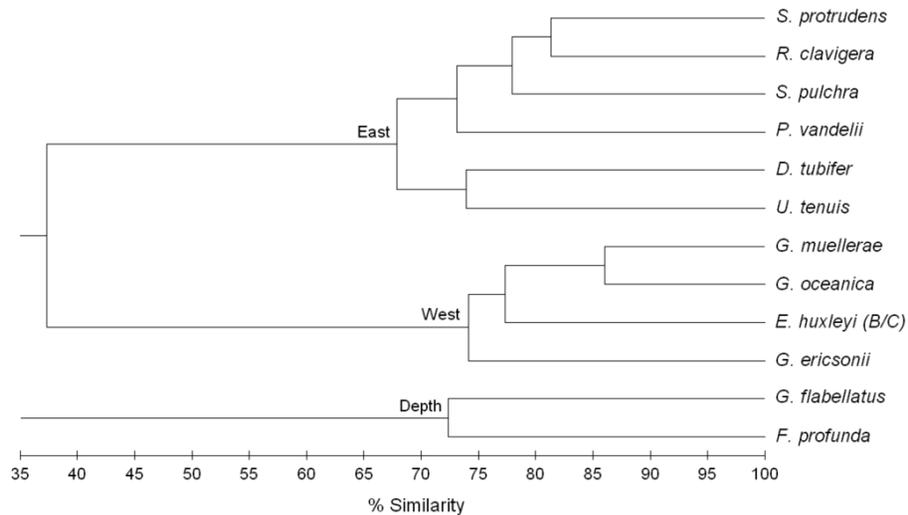
Fig. 4. Hierarchical cluster for the heterococcolithophores species that shared more than 65 % similarity in their abundance and distribution patterns.
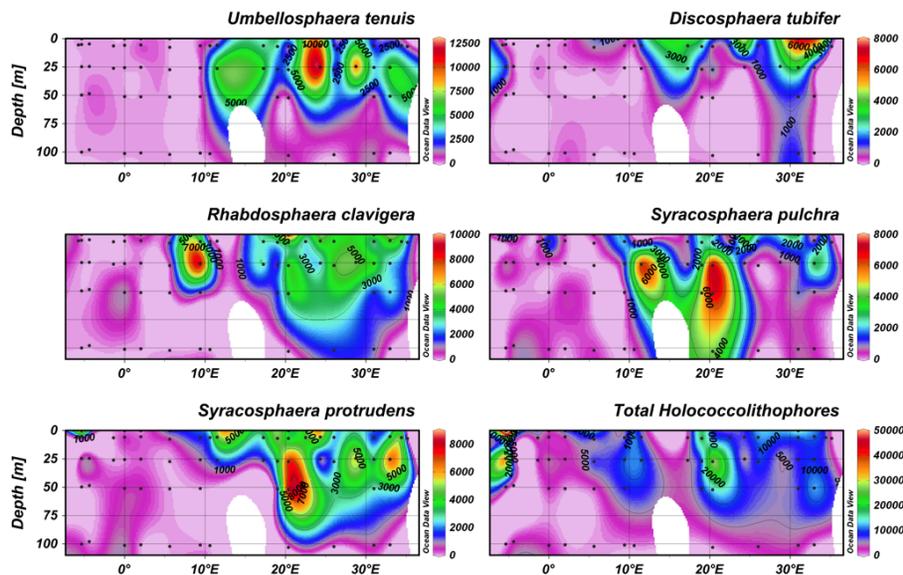
Fig. 5. Distribution, along a west to east transect, of the heterococcolithophore species forming the cluster comprised mainly by "eastern Mediterranean species". Holococcolithophores as a group is added in the bottom right panel.
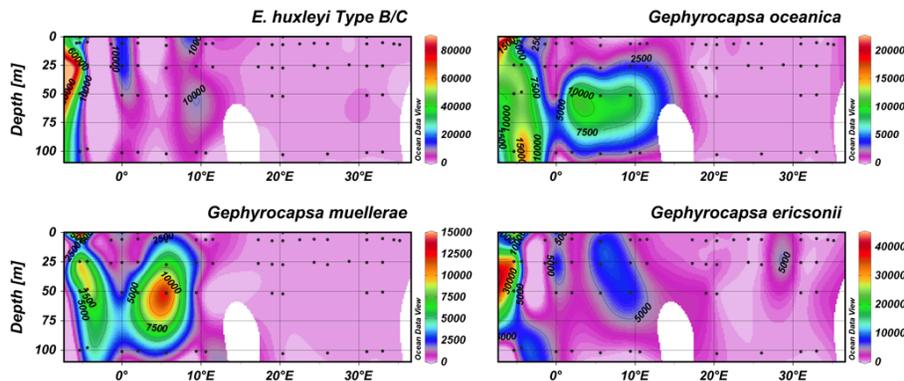
Fig. 6. Distribution, along a west to east transect, of the heterococcolithophore species forming the cluster comprised mainly by "western Mediterranean species".

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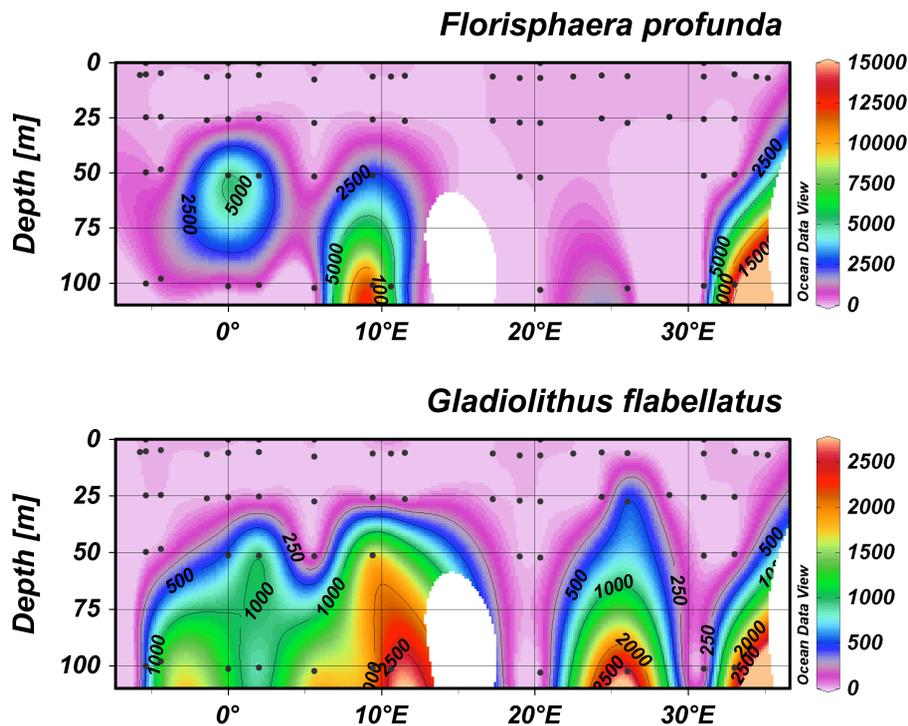
Fig. 7. Distribution, along a west to east transect, of the heterococcolithophore species forming the smallest of the observed clusters comprised exclusively by deep photic zone species.
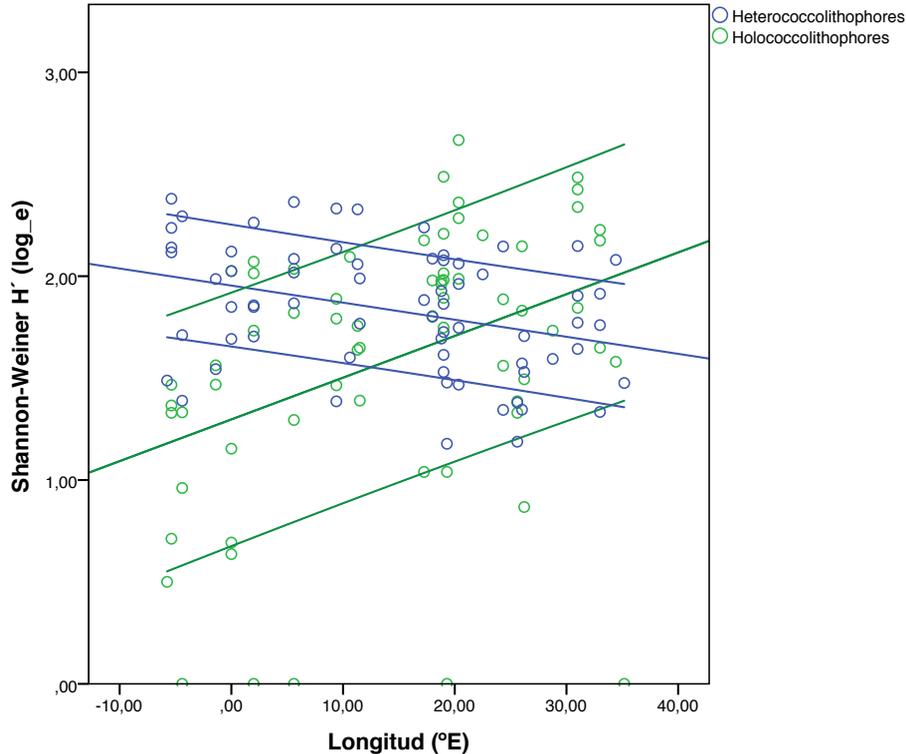
Fig. 8. Shannon–Weiner diversity index considering all samples until 50 m for heterococcolithophores (blue) and holococcolithophores (green). Bands represent 1α confidence interval. A higher index, or higher uncertainty in correctly guessing the "next species" that would be sampled, is representative of a more diverse community.