



## Coccolithophore and benthic foraminifera distribution patterns in the Gulf of Cadiz and Western Iberian Margin during Integrated Ocean Drilling Program (IODP) Expedition 339



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### ABSTRACT

For the first time during an Integrated Ocean Drilling Program (IODP) Expedition (Exp. 339, Mediterranean Outflow) water samples for living coccolithophore distributions and mudline samples for coccoliths, benthic foraminifera, and geochemical analyses in the underlying surface sediments were collected. In total, 14 water samples (from 5 to 20 m water depth) and 7 mudline samples were gathered at the drill sites. Coccolithophore distributions show spatial variations in species diversity. In particular, assemblages that characterize the Western Iberian Margin differ from those in the Gulf of Cadiz, indicative of oceanographic and environmental controls on the community in the upper ocean (0–20 m depth). Comparison of the living assemblages to those in surface sediments shows differences in the presence of some species, suggesting the influence of post deposition sedimentary processes. Other factors such as the season of sampling and the limited sampling depth may also have a role in the differences recorded. Benthic foraminiferal assemblages seem to be primarily determined by source, quantity and quality of available food. Sites in the Gulf of Cadiz are bathed by Mediterranean Outflow Water (MOW) and characterized by a considerable amount of advected food particles. Elevated epibenthic foraminifera exploit this niche, while arborescent epifaunal and infaunal taxa thrive on food particles falling out of MOW. The combined data suggest different flow speeds and settling of MOW suspension load in the Gulf of Cadiz. In contrast, assemblages from the Western Iberian Margin located farthest from or outside of MOW are determined by local export productivity and mirror trophic conditions in the surface waters. Both assemblages reveal variation in the composition at intermediate and deep water depths along the southern and western Iberian Margins with distance from the Strait of Gibraltar.

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### 1. Introduction

Integrated Ocean Drilling Program (IODP) Expedition 339 took place from November 2011 to January 2012 in the Gulf of Cadiz and off western Iberia (North East Atlantic) to explore the effects of Mediterranean Outflow Water (MOW) on North Atlantic circulation and climate (Expedition 339 Scientists, 2012; Hernández-Molina et al., 2013, 2014a, 2014b). The Iberian Margin and the Gulf of Cadiz are key areas for studying paleoceanographic and paleoclimatic variability because

high sedimentation rates allow environmental reconstructions at millennial-to-centennial time scales (Shackleton et al., 2000; Expedition 339 Scientists, 2012; Hernández-Molina et al., 2013; Hodell et al., 2013, 2015). Moreover, the western and southern sections of the Iberian Peninsula's Atlantic coast are part of an active seasonal upwelling system and changes to this system over time have been studied using different paleo-proxies to investigate climate related changes in regional ocean productivity (Wooster et al., 1976; Fiúza et al., 1998; Soares and Dias, 2006 and references therein; Salgueiro et al., 2010; Amore et al., 2012; Palumbo et al., 2013; Maiorano et al., 2015).

Coccolithophores are one of the most abundant phytoplankton groups playing a major role in marine primary production and in the

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oceanic carbon cycle since the Mesozoic (Winter and Siesser, 1994). Understanding of modern coccolithophore ecology and diversity in conjunction with data from core top sediments is important for assessing the quality and accuracy of the information preserved in the sedimentary record and enables their use as paleoceanographic proxies (Baumann et al., 2005 and references therein). Foraminifers are a significant component of marine benthic communities and one of the longest and most intensively studied microfossil groups (Sen Gupta, 2003; Murray, 2006 and references therein). Due to their abundance in every marine and estuarine environment and excellent potential of their shells for fossil preservation, many attempts have been made to develop proxy methods for paleoenvironmental reconstruction using foraminifera (Jorissen et al., 2007 and reference therein). Recently, Schönfeld (2002a) proposed a proxy method for the reconstruction of bottom current strength based on abundance patterns of epibenthic foraminifera occupying elevated substrates along the pathway of the MOW in the Gulf of Cadiz and along the SW Iberian Margin (Schönfeld, 2002b; Rogerson et al., 2011).

For the first time during an IODP Expedition, water samples were collected along with mudline samples at each drill site (IODP Expedition 339). Here we evaluate calcareous nannoplankton and benthic foraminifera assemblages in these samples in combination with salinity, water temperature, water isotopes ( $\delta^{18}\text{O}$ ,  $\delta\text{D}$ ), inorganic nutrients (nitrate  $\text{NO}_3$ , phosphate  $\text{PO}_4$ ; data from World Ocean Atlas – WOA13), Apparent Oxygen Utilization (AOU; data from WOA13), Total Organic Carbon (TOC) and Total Nitrogen (TN) concentrations of bulk sediment samples.

The coccolithophore (collected in the upper 20 m of the water column) and coccoliths in the mudline samples can be used to reconstruct surface water conditions (photic zone), whereas benthic foraminifera can be used for reconstructing conditions of intermediate and bottom water masses, in particular for the amount of food supplied to the bottom (export productivity) and oxygenation. This data-set allows us to characterize the distribution and ecology of the two groups as well as their preservation in the seafloor sediments along the Western and Southern Iberian Margin. As part of the research goals of IODP Expedition 339, the produced data-sets will provide site-specific information on ecology and taphonomy for microfossil-based paleoceanographic and paleoclimatic reconstructions.

## 2. Oceanographic setting

Surface water circulation along the West Iberian Margin is influenced by two major current systems that transport surface water masses from west to east across the Atlantic: the North Atlantic Current (NAC) extending to the north of the Iberian Peninsula; and the Azores Current (AC) south of Iberia (Saunders, 1982; Pollard and Pu, 1985; Barton, 2001; Peliz et al., 2005). As the AC flows eastwards, branches of this current smoothly loop northward of Portugal, eventually reaching into the Portugal Current (PC) and southward into the Canary Current (CC). Both currents flow equatorward along the Portuguese and the NW African Margins (Saunders, 1982; Barton, 2001). Beneath the near-surface equatorward flow of the PC and CC currents, the Iberian Poleward Current (IPC) can be recognized traveling northward at about 300–400 m water depth, opposite to the general circulation and closely bound to the continental slope (Fig. 1).

In the Gulf of Cadiz, circulation patterns are dominated by water mass exchange through the Strait of Gibraltar. This exchange is driven by the highly saline and warm Mediterranean Outflow Water (MOW) near the bottom and the turbulent, less saline, cool-water mass of Atlantic water at the surface. Regionally the water masses that characterize the area are: the surface Atlantic water (SAW); the eastern North Atlantic central water (ENACW); the modified Antarctic intermediate water (AAIW); the North Atlantic deep water (NADW); and the MOW (Serra et al., 2010; Rogerson et al., 2012; Louarn and Morin, 2011). In the Gulf of Cádiz, the MOW flows between 500 and 1400 m below sea

level (m.b.s.l.) with a velocity close to  $300 \text{ cm s}^{-1}$  at the Strait of Gibraltar and  $\sim 80\text{--}100 \text{ cm s}^{-1}$  at the latitude of Cape San Vicente (Hernández-Molina et al., 2011, 2013). The investigated sites are influenced by different current regimes (Table 1). Between April and October, the northward displacement and strengthening of the Azores high pressure cell causes strong northerlies and upwelling along the shelf of the Iberian Margin (Fiúza et al., 1998; Sousa and Bricaud, 1992; Sánchez and Relvas, 2003) while surficial circulation patterns in the Gulf of Cadiz are largely wind-driven during these periods (García Lafuente et al., 2008). The IPC develops at this time and a cold and nutrient-rich coastal water mass forms along the Iberian Margin, stimulating primary productivity (Wooster et al., 1976). In contrast, during fall-winter the winds often switch to westerlies leading to the occurrence of downwelling over the shelf and the surfacing of the IPC (Vitorino et al., 2002; Guerreiro et al., 2014). Surface circulation reverses and northward transport occurs down to 1500 m depth (Relvas et al., 2007). This water is warm and nutrient-poor and associated with the weaker south-westerlies and down-welling (Smyth et al., 2001). However, upwelling of a smaller magnitude than during spring/summer, produced by northerly winds blowing across the shelf, can also occur in the autumn or winter (Relvas et al., 2007; de Castro et al., 2008).

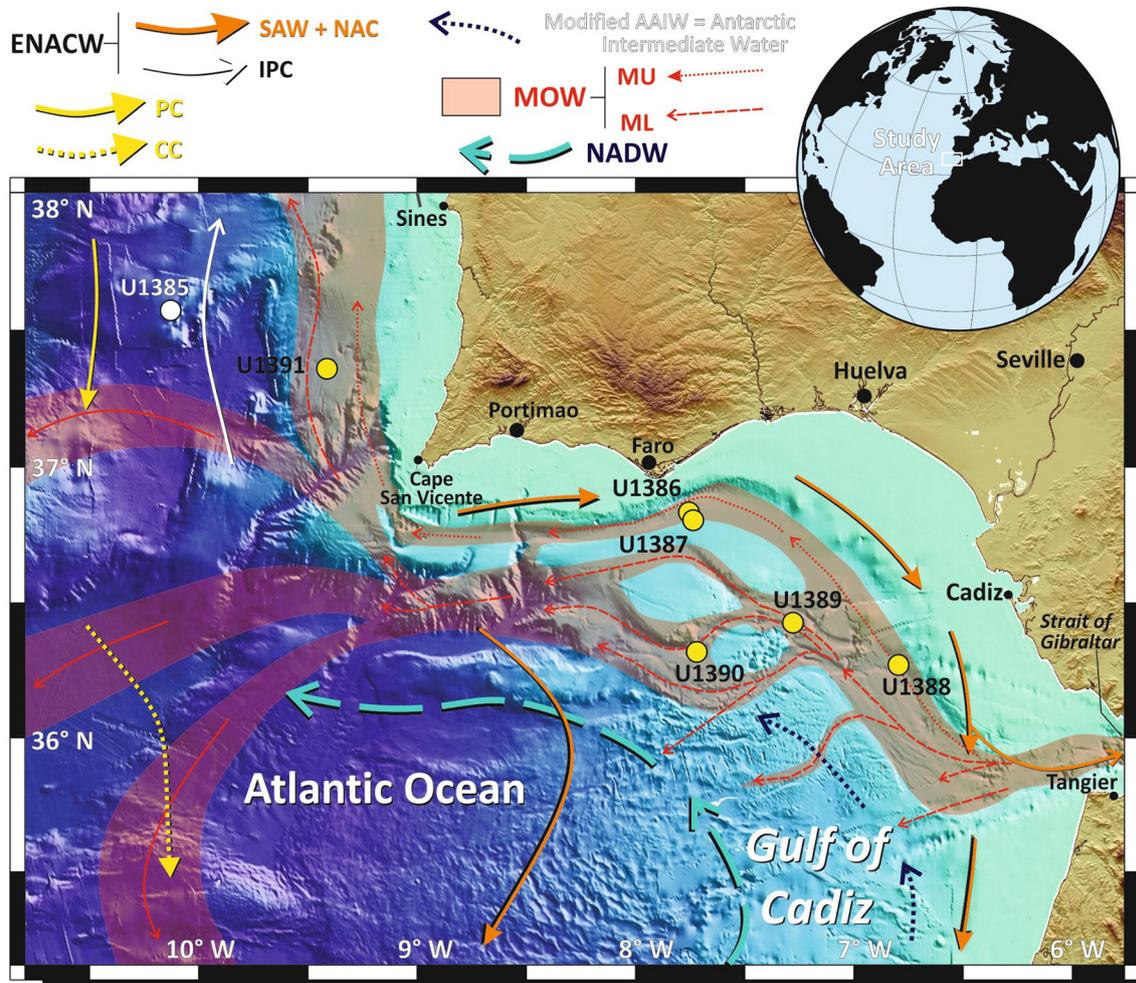
## 3. Material and methods

### 3.1. Water-column and mudline samples

Water samples for coccolithophore and geochemical analyses were acquired between December 2011 and January 2012 at the various drill sites of IODP Expedition 339. In total, 14 samples from 7 stations were collected (Table 1). Water samples were taken at 5 and 20 m depth with a 5 liter niskin bottle. At each station the underlying surface sediments, represented by the mudline samples at the top of the first core, were also gathered. Mudline samples represent the unconsolidated sediment layer at the sediment-water interface. They were collected at the boreholes of the different sites where the uppermost core (called the mudline core) recovered a good sediment/water interface. In total 7 mudline samples were acquired for coccolithophore, foraminifera, and geochemical analyses (Table 1). The top fluffy sediment/water material from the core was emptied out of the core liner into a clean bucket, from which the samples were pipetted out, oven-dried and stored in sterile plastic bags for future analyses.

### 3.2. Hydrography and geochemical sample processing

Temperature (T) and salinity were measured at the same time as the water sampling using a thermometer and a refractometer, respectively, on board the drillship *JOIDES Resolution* (Table 1). Water temperature at the mudline sediment surface of each hole was measured using the APC temperature tool APCT-3 located in the piston core cutting shoe (Stow et al., 2013) (Table 1). A small portion of the bottom water was also stored in 50 ml Teflon vials and kept refrigerated for  $\delta^{18}\text{O}$  and  $\delta\text{D}$  analyses. Isotope measurements on the water samples were performed on board and onshore using a Picarro L2130-I Analyzer. For some drill sites, it wasn't possible to perform the isotopic analyses. In these cases, we have inferred the respective values from Voelker et al. (2015), (indicated with an asterisk in Table 1). On the mudline samples, TOC and TN were measured at the University of California Santa Cruz (UCSC), using a Carlo Erba elemental analyzer connected to an isotope ratio mass spectrometer (EA-IRMS; Iso-Prime). Reproducibility for these samples is  $\pm 0.13 \text{ wt\%}$  for TOC and  $\pm 0.001 \text{ wt\%}$  for TN. Additional data on AOU (García et al., 2014a) and  $\text{NO}_3$  and  $\text{PO}_4$  concentrations (García et al., 2014b) were selected from the World Ocean Atlas (WOA13) and extracted with Ocean Data View (ODV) software (Schlitzer, 2014) (Table 1). These data were weight averaged from a grid of  $1^\circ$  longitude by  $1^\circ$  latitude, and represent mean values of every December month from 1955 to 2012.



**Fig. 1.** Superficial, intermediate, deep-water circulation and geographic location of the studied sites. Bottom water masses and ocean currents shown as ENACW = eastern North Atlantic central water; NAC = North Atlantic Current; AC = Azores Current; PC = Portugal Current; CC = Canary Current; IPC = Iberian Poleward Current; SAW = surface Atlantic water; NADW = Northeast Atlantic deep water; AAIW = Antarctic intermediate water mass. (modified from Hernandez-Molina, 2014)

### 3.3. Coccolithophore sample processing and analysis

For coccolithophore analysis, 2 l of sea water were immediately filtered on board onto cellulose acetate filters (47 mm diameter, 0.45  $\mu\text{m}$  pore-size), using a low-vacuum filtration system. Filters were oven dried and stored in petri-dishes. The mudline sediment samples were prepared for coccolith assemblage analysis using a combined dilution/filtering technique as described by [Andruleit \(1996\)](#). Data presented in this paper are based on absolute quantitative analyses performed on water and sediment samples, using a Zeiss Axio-phot Polarised Light Microscope at a magnification of 1560 $\times$ . Selected samples were also qualitatively analyzed onshore by a scanning electron microscope (SEM HITACHI S-3500N) to assess the preservation state of the assemblages. Coccolithophore species abundance (cells/l) was calculated following [Jordan and Winter \(2000\)](#) by scaling up the raw counts from a known scanned area. The formula used was:

$$A = N * S/V \quad (1)$$

where N is the number of cells of a species on the whole piece of filter; S, the scaling factor (area of the whole filter to area of scanned filter piece), V, the volume of the water filtered (liters) and A, the absolute abundance of the species in cells/l.

For the mudline samples the counts have been expressed in terms of specimen abundance per gram of dry sediment (total coccolith concentration) as follows:

$$\text{Number of coccoliths in 1 g of sediment} = F \times C/A \times W \quad (2)$$

where F is the filtration area ( $\text{mm}^2$ ); C, the number of counted coccoliths; A, the counted area ( $\text{mm}^2$ ); W, sediment weight (grams). In the water and sediment samples, coccolithophore/coccolith species with low concentrations were grouped together at the genus level. Reworked coccoliths in the mudline samples were also counted in order to evaluate the relationship between sediment transport and deep and bottom water dynamics and characteristics. Taxonomy for identification follows [Young et al. \(2003\)](#) and [Jordan et al. \(2004\)](#). The recognized taxa in the water and mudline samples are listed in Appendix A and a summary of existing information on ecology is given in Appendix B. Total (absolute) coccolithophore/coccolith abundances in the water and sediment samples are displayed in [Table 1](#).

#### 3.3.1. Statistical analysis in the water column

In order to explore colinearity among the initial environmental variables, a multicorrelation analyses was performed. Variables were first checked for unimodal distribution. None of them, nor their  $\log_{10}$  transformation, showed unimodal distribution, and therefore Spearman correlation was performed.

**Table 1**  
Site names, depths, longitude and latitude, temperature, salinity,  $\delta^{18}\text{O}$ ,  $\delta\text{D}$ ,  $\text{PO}_4$  (from WOA),  $\text{NO}_3$  (from WOA), AOU (from WOA), TOC, TN, C:N ratio, sedimentation rates of the sites, water masses, standing crop of coccolithophores and total coccolith abundances, for each site.

Site	Water-mudline depths (m)	Long	Lat	Date of sampling	T (°C)	S (g kg <sup>-1</sup> )	$\delta^{18}\text{O}$ ‰	$\delta\text{D}$ ‰	$\text{PO}_4$ (μmol/l)	$\text{NO}_3$ (μmol/l)	AOU (ml/l)	TOC (Wt%)	TN (Wt%)	C:N	Sedimentation rates of the sites	Water masses	Standing crop (cells/l)	Coccoliths/g
U1385	5	37°34.285'N	10°7.562'W	11/25/2011	18.4	36.5	0.28	1.71	0.35	0.88	−0.07					AC, PC, CC, IPC	1.87E + 04	
	20	37°34.285'N	10°7.562'W	11/25/2011	18.3	36.5	0.74	3.33	0.35	1.13	−0.09						2.19E + 04	
	2598	37°34.285'N	10°7.562'W	11/25/2011	3.6	36	0.16	0.36				3.10	0.52	5.96	17.2 cm/ka Hodell et al., 2015	NADW		8.14E + 08
U1386	5	36°49.685'N	7°45.321'W	11/29/2011	18.5	37	0.99	4.87	0.29	1.88	−0.12					SAW, ENACW, AAIW	2.80E + 04	
	20	36°49.685'N	7°45.321'W	11/29/2011	18.5	37	0.80*	6.00*	0.26	2.45	−0.16					MOW	4.53E + 04	
	561.9	36°49.685'N	7°45.321'W	11/29/2011	13.1	37.5	0.84	5.75				3.25	0.51	6.36	19 cm/ka Kaboth et al., 2015			4.19E + 08
U1387	5	36°48.321'N	7°43.1321'W	12/8/2011	18.2	36.5	1.02	7.30	0.29	1.90	−0.12					SAW, ENACW, AAIW	3.11E + 04	
	20	36°48.321'N	7°43.1321'W	12/8/2011	18.2	36.5	0.86	6.52	0.26	2.48	−0.16					MOW	6.18E + 04	
	559.1	36°48.321'N	7°43.1321'W	12/8/2011	13.1	36	0.80*	6.00*				3.23	0.53	6.09	16.4 cm/ka Singh et al., 2015			2.69E + 08
U1388	5	36°16.142'N	6°47.648'W	12/18/2011	17.6	37	1.10	6.67	0.26	2.63	−0.10					SAW, ENACW, AAIW	6.69E + 04	
	20	36°16.142'N	6°47.648'W	12/18/2011	17.6	37	1.30	7.22	0.22	2.70	−0.13					MOW	8.05E + 04	
	663	36°16.142'N	6°47.648'W	12/18/2011	n/a	37	0.82	6.36				3.33	0.50	6.66	>36–60 cm/ka Stow et al., 2013			7.43E + 05
U1389	5	36°25.515'N	7°16.683'W	12/25/2011	17.9	37	1.22	6.71	0.29	2.02	−0.11					SAW, ENACW, AAIW	7.41E + 04	
	20	36°25.515'N	7°16.683'W	12/25/2011	17.8	37	1.01	6.43	0.25	2.64	−0.16					MOW	5.52E + 04	
	644	36°25.515'N	7°16.683'W	12/25/2011	13.4	36	0.80*	6.00*				3.63	0.58	6.26	30 cm/ka Stow et al., 2013			1.69E + 08
U1390	5	36°19.110'N	7°43.078'W	1/2/2012	17.9	37	1.07	7.36	0.29	1.92	−0.12					SAW, ENACW, AAIW	8.72E + 04	
	20	36°19.110'N	7°43.078'W	1/2/2012	17.8	37	1.17	7.98	0.26	2.50	−0.16					MOW	6.79E + 04	
	992	36°19.110'N	7°43.078'W	1/2/2012	13.1	36	0.80*	6.00*				3.70	0.62	5.97	81 cm/ka Stow et al., 2013			4.26E + 07
U1391	5	37°21.5322'N	9°24.6558'W	1/8/2012	16.4	37	0.73	4.90	0.42	1.16	−0.07					SAW, ENACW, AAIW	6.48E + 04	
	20	37°21.5322'N	9°24.6558'W	1/8/2012	16.2	37	0.75*	4.00*	0.41	1.46	−0.10					MOW	1.04E + 05	
	1073	37°21.5322'N	9°24.6558'W	1/8/2012	11.4	36	0.67	4.72				3.82	0.62	6.15	33 cm/ka Stow et al., 2013			3.12E + 07

\* Note the \* in  $\delta^{18}\text{O}$  and  $\delta\text{D}$  means that the values are inferred from Voelker et al. (2015).

In order to assess the relationship between coccolithophore taxa and the environmental conditions, a canonical correspondence analysis (CCA) was performed. Only those taxa with relative abundances >2% in more than two samples were used for the ordination analysis. Additionally, coccolithophore percentages were first square-root-transformed to stabilize their variances. Akaike's information criteria (AIC) were used in a first CCA to identify a model that, based on the minimum number of statistically significant variables, explained the maximum variance in the coccolithophore data. Statistical analyses were performed with R software (R Core Team, 2015), using the "vegan" package for ordination analyses (Oksanen et al., 2016).

### 3.4. Benthic foraminifer analyses

Mudline samples were quantitatively evaluated for live and dead assemblages of benthic foraminifera. IODP Sites U1385–U1386 and U1389–U1391 are represented by mudline samples from one borehole while U1387 by holes A and B. No mudline sample suitable for foraminiferal analysis was recovered from IODP Site U1388. Rose Bengal was added to the mudline samples immediately after recovery to identify benthic foraminifera alive at the time of sampling (Murray and Bowser, 2000; Schönfeld, 2012). After a staining time of several hours, samples were washed over 125 and 63  $\mu\text{m}$  sieves and dried. The dried residue was split into size fractions 63–125  $\mu\text{m}$  and >125  $\mu\text{m}$ , and all stained benthic foraminifera >125  $\mu\text{m}$  were picked, identified and counted (Table 2). Taxonomy of benthic foraminifera follows Jones (1994), Schönfeld (1997, 2002b), Mendes et al. (2012) and Holbourn et al. (2013). The standing stock of benthic foraminifera is expressed as two indices for comparison to previous studies, number of specimens per 10  $\text{cm}^3$  (Schönfeld, 1997, 2002a) and number of specimens per 50  $\text{cm}^2$  (Nardelli et al., 2010; Phipps et al., 2012). Both indices apply the inner diameter of 67 mm of the core liners (and thus recovered cores) used in IODP Expedition 339 (Stow et al., 2013). To estimate the sediment volume, a minimum sediment thickness of 2 cm has been inferred from infaunal microhabitats for the mudline samples (see Discussion section).

## 4. Results

### 4.1. Hydrological and geochemical data

The temperature of the surface water samples recovered during the sampling period ranged between 16.2 and 18.5  $^{\circ}\text{C}$  and are represented in Table 1. Sea surface salinity data are similar at all sites and show values between 36.5 and 37.0  $\text{g kg}^{-1}$ .  $\delta^{18}\text{O}$  values of the surface water samples range between 0.3 and 1.3‰ (SMOW), and  $\delta\text{D}$  values range between 1.71 and 7.98‰ (SMOW).

$\text{NO}_3$  is 1.98  $\mu\text{mol/l}$  on average and ranges between 0.88 and 2.70  $\mu\text{mol/l}$  and  $\text{PO}_4$  concentration shows a smaller range, between 0.22 and 0.42  $\mu\text{mol/l}$ , with an average value of 0.30  $\mu\text{mol/l}$  (data from WOA13). AOU ranges between  $-0.07$  and  $-0.16$  ml/l. All the values are reported in Table 1.

Bottom water temperatures measured at each site at the time of drilling vary between 3.6 and 13.4  $^{\circ}\text{C}$  (Stow et al., 2013). IODP Site U1385, shows the lowest temperature, while all other sites are bathed by MOW and show bottom water temperatures >10  $^{\circ}\text{C}$ . Salinity at the seafloor shows a slightly larger range than surface waters with values from 36.0 to 37.5  $\text{g kg}^{-1}$ .  $\delta^{18}\text{O}$  values range between 0.16 and 0.82‰ (SMOW), and  $\delta\text{D}$  values between 0.36 and 6.36‰ (SMOW). TOC values of the bulk mudline sediment range between 3.1 and 3.8 wt%. Sites U1385–U1388 show values <3.3 wt% while values >3.6 wt% characterize U1389–U1391 (Table 1). TN values are fairly uniform and vary between 0.5 and 0.62 wt%. Similar to TOC, Sites U1389–U1391 reveal higher TN values. TOC and TN show a strong positive correlation ( $R^2 = 0.84$ ), and C/N ratios show a small range between 5.96 and 6.66.

### 4.2. Living coccolithophore communities: abundances and distributions.

A total of 31 species were recognized in the samples (Appendix A). In the Gulf of Cadiz, the maximum total abundance was found at Site U1391 ( $10.4 \times 10^4$  cells/l) at 20 m water depth while the minimum was found in the Iberian Margin at Site U1385 ( $1.87 \times 10^4$  cells/l) (Table 1). In general, concentrations show higher values at the deeper sites (U1389, U1390, U1391) as well as at Site U1388 at the Gibraltar Gateway. Site U1385 shows the lowest values of all water samples at both depths. Absolute and relative coccolithophore abundances from all the stations and depths are plotted in Fig. 2. The assemblages are dominated by *Emiliania huxleyi* (values were from  $\sim 1 \times 10^4$  and up to  $\sim 6 \times 10^4$  cells/l). *E. huxleyi* abundances drive the observed pattern of total coccolithophore distribution at stations U1385 through U1389. Other important taxa are *Gephyrocapsa* spp. (here represented in majority by the species *G. oceanica*; see Appendix B) reaching  $\sim 0.16 \times 10^4$  cells/l at Site U1388, and the small placoliths group with the highest abundances both at 5 and 20 m at Sites U1390 and U1391 ( $2.5 \times 10^4$ – $3.5 \times 10^4$  cells/l). The holococcolithophore group reaches  $\sim 1 \times 10^4$  cells/l at Site U1391 (20 m depth). The two species *Calcidiscus leptoporus* and *Coccolithus pelagicus* are present with very low values at all the sites. *Syracosphaera* spp. is present in all the stations except U1385 at both depths. *Helicosphaera* spp. is rare in all stations. The warm water taxa group (in this study consisting of *Rhabdosphaera* spp., *Umbellosphaera* spp., and *Coronosphaera* spp. as supported by the statistical analysis see Fig. 3) is present with abundances on the order of  $\sim 0.25 \times 10^4$  at all the sites except U1385 where it has lower abundances (on the order of  $\sim 0.007 \times 10^4$ ) at both 5 and 20 m.

#### 4.2.1. Statistical analyses applied to surface water samples

Table 3 shows the multicorrelation between variables. High Spearman's correlation coefficients ( $\rho$ ) and associated  $p$ -values between water isotopes ( $\delta^{18}\text{O}$ ,  $\delta\text{D}$ ) and inorganic nutrients ( $\text{NO}_3$ ,  $\text{PO}_4$ ) indicate strong and significant linear correlations between them. The initial CCA based on the AIC considered the following variables: T, S,  $\delta\text{D}$ ,  $\delta^{18}\text{O}$ ,  $\text{NO}_3$ ,  $\text{PO}_4$  and AOU. Via a forward selection procedure, it identified T,  $\delta\text{D}$ ,  $\delta^{18}\text{O}$ , and  $\text{NO}_3$  as the minimum variables, statistically significant at the 95% level, required to explain the maximum inertia (variance) in the coccolithophore assemblages of the water column. The CCA bi-plot diagram (Fig. 3) illustrates the relationship between coccolithophore taxa, explanatory variables, sites and sample depths as a function of the distance between them. The model based on these four environmental variables explained 50.1% of the total inertia in the coccolithophore data. Of the explained inertia (50% of total inertia) the first canonical axis (CCA1) explains 74% and CCA2 explains 19% (i.e. 93% together), and therefore only these two axes are considered. CCA1 is negatively and strongly correlated with T, while CCA2 shows a positive relationship with  $\text{NO}_3$ ,  $\delta\text{D}$  and  $\delta^{18}\text{O}$ , in that order. Nevertheless, it has to be highlighted that the nutrient data represent an average of nutrient concentration from every December between 1955 and 2012 for each studied station (data from WOA13). Such data might not necessarily represent the nutrient conditions in the water column for the specific sampling period, and therefore must be interpreted with caution.

#### 4.3. Coccolith assemblages in surface sediment samples

Absolute and relative coccolith abundances are shown in Fig. 4a and b, with values ranging between  $\sim 8 \times 10^8$  (Site U1385) and  $\sim 0.074 \times 10^8$  (Site U1388) coccoliths/g. The coccoliths recorded in the surface sediments are in general well preserved. However, at Site U1388, where the lowest abundances were recorded, just *C. pelagicus* subsp. *pelagicus*, *C. leptoporus* and reworked coccoliths were recognized. *E. huxleyi* abundances vary between  $0.3 \times 10^8$  and  $1.83 \times 10^8$  coccoliths/g. *Syracosphaera* spp. are rare in the surface sediment while *Helicosphaera* spp. is recorded in all the sediment samples with a mean value of  $0.13 \times 10^8$  coccoliths/g. *C. leptoporus* and *C. pelagicus* subsp. *pelagicus*

Table 2

Census counts of stained benthic foraminifera assumed alive at the time of sampling. Vaguely stained shells are indicated separately.

Site Reliability of staining	U1385B		U1386B		U1387A + B		U1389C		U1390C		U1391B	
	Certain	Uncertain	Certain	Uncertain	Certain	Uncertain	Certain	Uncertain	Certain	Uncertain	Certain	Uncertain
Total no. foraminifera	23	2	37	7	17	8	8	2	51	4	18	3
Total no. agglutinated foraminifera	19	0	9	0	4	2	1	0	25	0	0	0
Total no. hyaline foraminifera	3	2	26	7	11	6	7	2	24	4	18	3
Total no. miliolid foraminifera	1	0	2	0	2	0	0	0	2	0	0	0
% agglutinated foraminifera	76		20		24		10		45		0	
% hyaline foraminifera	20		75		68		90		51		100	
% miliolid foraminifera	4		5		8		0		4		0	
Number of taxa	7	1	16	5	16	7	7	1	17	4	9	3
Standing stock (per 10 cm <sup>3</sup> ; sediment thickness 3 cm)	2.2	0.2	3.5	0.7	1.6	0.8	0.8	0.2	4.8	0.4	1.7	0.3
Standing stock (per 10 cm <sup>3</sup> ; sediment thickness 2 cm)	3.3	0.3	5.2	1.0	2.4	1.1	1.1	0.3	7.2	0.6	2.6	0.4
Standing stock (per 50 cm <sup>2</sup> )	32.6	2.8	52.4	9.9	24.1	11.3	11.3	2.8	72.2	5.7	25.5	4.2
% stained shells of stained + unstained assemblage	6.7		1.3		1.5		0.2		21.4		5.4	
Agglutinated												
<i>Astrorhiza granulosa</i>	4											
<i>Marsipella cylindrica</i>					1				10			
<i>Marsipella cf. elongata</i>			7		1							
<i>Reophax dentaliniformis</i>									1			
<i>Reophax scorpiurus</i>					1	2						
<i>Reophax spiculifer</i>					1							
<i>Rhizammina algaeformis</i>							1		2			
<i>Rhizammina sp.</i>	14								2			
<i>Saccorhiza ramosa</i>	1								10			
<i>Veleroninoides scitulus</i>			2									
Hyaline												
<i>Amphicoryna scalaris</i> – microsphere			1	1								
<i>Astrononion tumidum</i>											1	
<i>Brizalina dilatata</i>									1			
<i>Bulimina alazanensis</i>	1											
<i>Bulimina marginata</i>			3	1	1	1			1			
<i>Bulimina mexicana</i>											5	
<i>Cassidulina laevigata</i>					1							
<i>Chilostomella oolina</i>			2	1	2	1						
<i>Epistominella exigua</i>	1											
<i>Globobulimina affinis</i>			2		1							
<i>Globocassidulina subglobosa</i>			3					1				
<i>Globulina sp.</i>											1	
<i>Gyroldina lamarckiana</i>								1	2			
<i>Gyroldinoides soldanii</i>		2			1						1	
<i>Hanzawaia concentrica</i>									1			1
<i>Hyalinea balthica</i>			1			1				1		
<i>Laevidentalina aphelis</i>			1									
<i>Lenticulina gibba</i>					1							
<i>Lenticulina inornata</i>								1				
<i>Melonis barleeanum</i>			6	1				2	2	6	1	2
<i>Melonis pompilioides</i>										1		
<i>Nonionella turgida</i>										1		
? <i>Planorbulina variabilis</i>			1									
<i>Pullenia quinqueloba</i>			1									
? <i>Pullenia sp.</i>									1			
<i>Pyrulina angusta</i>	1											
<i>Pyrulina fusiformis</i>												1
<i>Pyrulina sp. 1</i>					1							
<i>Robertinoides bradyi</i>							1					
<i>Siphogenerina columellaris</i>									1		1	
<i>Siphonina tubulosa</i>					1			1	6			1
<i>Trifarina bradyi</i>										1	1	
<i>Uvigerina hollicki</i>			1		1							
<i>Uvigerina mediterranea</i>			1	2				1	4		5	1
<i>Uvigerina peregrina</i>							1					
<i>Uvigerina spp.</i>				1			1					
<i>Valvulineria complanata</i>			3		1							
Miliolid												
<i>Bilocolinella labiata</i>					1							
<i>Miliolinella subrotunda</i>									1			
<i>Pyrgo murrhina</i>									1			
<i>Quinqueloculina seminula</i>			2									
<i>Triloculina tricarinata</i>	1				1							

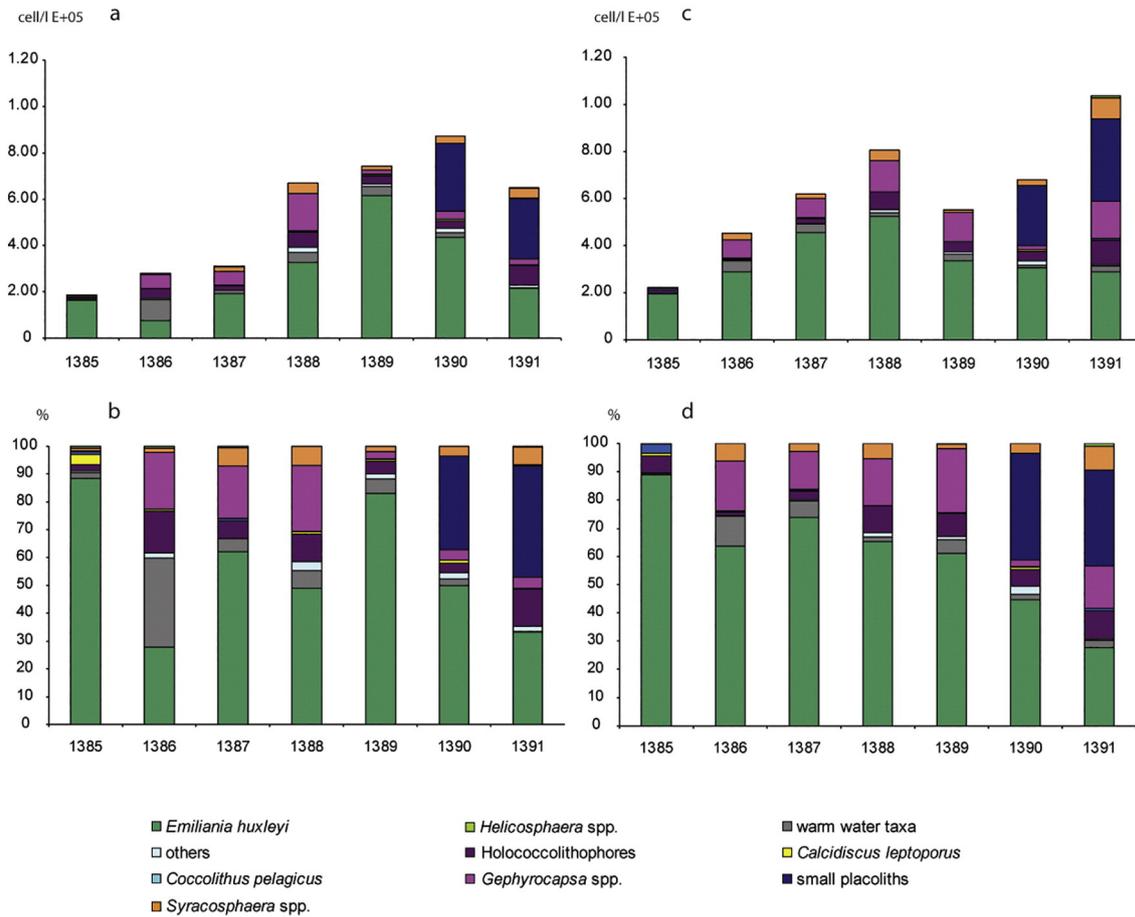


Fig. 2. a) Coccolithophore taxa distribution (coccol/l) at 5 m of depth at the different sites; b) percentages of the coccolithophore taxa distribution at the different sites at 5 m of depth; c) coccolithophore taxa distribution (coccol/l) at 20 m of depth at the different sites; d) percentages of the coccolithophore taxa distribution at the different sites at 20 m of depth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

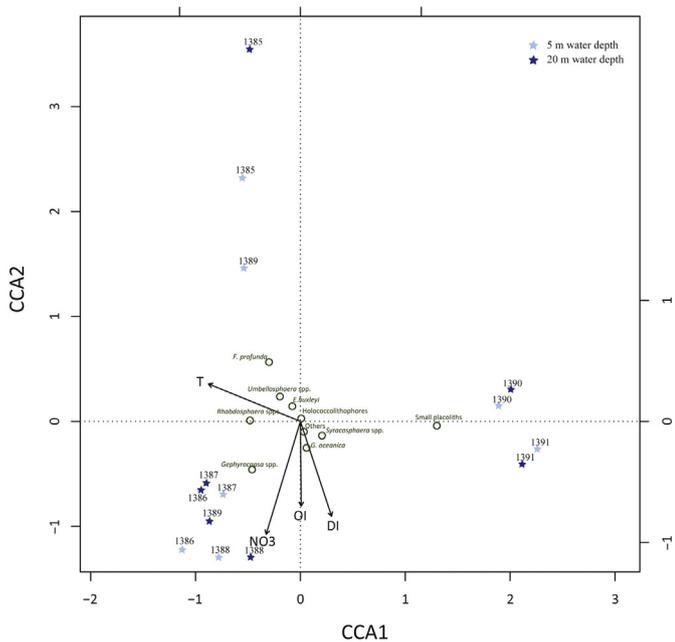


Fig. 3. Ordination bi-plot diagram for the first two axes of the CCA. Gray circles stand for the score species, while explanatory variables are represented by gray circles and environmental variables by arrows. Samples are represented by colored stars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and subsp. *azorinus* are present with mean values on the order of  $\sim 0.2 \times 10^8$  coccoliths/g, in all the mudline samples. *C. pelagicus* subsp. *braarudi* is present with lower values and is found just at Sites U1385, U1386 and U1391. The small placoliths group has been found only at Sites U1385, U1386 and U1387 with values on the order of  $0.9 \times 10^8$  coccoliths/g. *Gephyrocapsa* spp., has a mean value on the order of  $0.5 \times 10^8$  coccoliths/g but it is absent in Sites U1388 and U1391. The warm water taxa and the holococcolithophore group are present in low abundances at all the sites. Reworked coccoliths are of Paleocene and Cretaceous age and occur at all stations. In Fig. 5, the relative abundances of the three *C. pelagicus* subspecies are shown. *C. pelagicus* subsp. *braarudi* is present just at Sites U1385, U1391 and U1386. At the other sites, *C. pelagicus* subsp. *pelagicus* and *C. pelagicus* subsp. *azorinus* are

Table 3

Spearman's multicorrelation. Correlation coefficients ( $\rho$ ) are shown for paired variables. Strong and significant correlations are marked in bold.

	T	S	$\delta^{18}\text{O}$	$\delta\text{D}$	$\text{NO}_3$	$\text{PO}_4$	AOU
T	1	<b>-0.62*</b>	-0.44	-0.42	<b>-0.6*</b>	0.46	0.11
S		1	0.56	0.36	0.51	-0.41	-0.26
$\delta^{18}\text{O}$			1	<b>0.8**</b>	<b>0.76**</b>	<b>-0.74**</b>	-0.45
$\delta\text{D}$				1	<b>0.58**</b>	-0.54	-0.48
$\text{NO}_3$					1	<b>-0.97**</b>	<b>-0.72**</b>
$\text{PO}_4$						1	<b>0.71**</b>
AOU							1

\* Statistical significance at 95% level.

\*\* Statistical significance at 99% level.

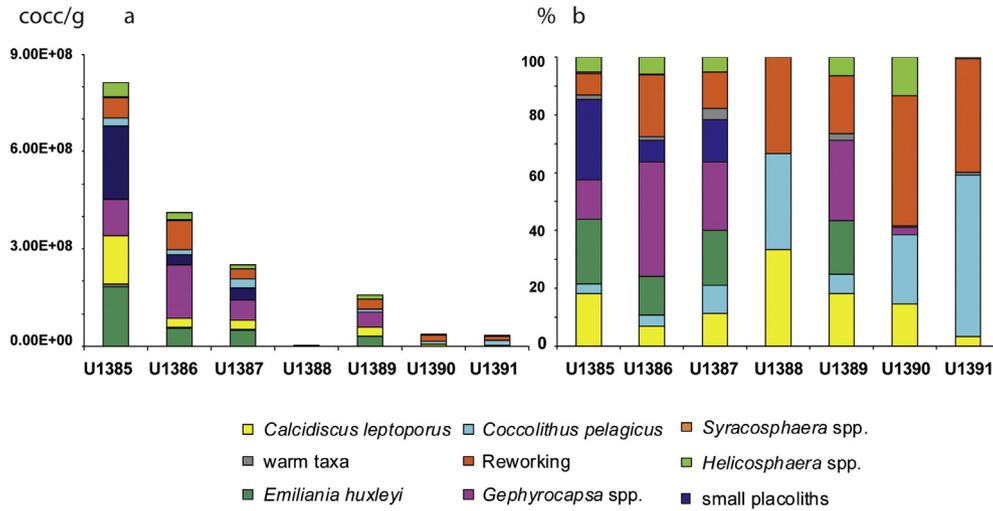


Fig. 4. a) Coccolith taxa distribution (cocc/g) at the different sites and, b) percentages of the coccolith taxa distribution at the different sites in the mudline samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

commonly present, except in U1388 where just *C. pelagicus* subsp. *pelagicus* occurs.

4.4. Living benthic foraminiferal assemblages

Census counts of stained benthic foraminifera are presented in Table 2. In some cases, difficulties arose from weak staining, thus we have listed these specimens separately. The number of recovered stained shells varies between 10 and 55, and result in standing stock numbers of 1–8 specimens per 10 cm<sup>3</sup> and 14–78 specimens per 50 cm<sup>2</sup>. With the remarkable exception of Hole U1390C (21% stained shells), stained

foraminiferal shells make up only a minor portion (1–5%) of the assemblages. 10 agglutinating, 37 hyaline and 5 miliolid taxa have been identified. Except for Hole U1385B, where arborescent agglutinating foraminifera dominate, all sites show hyaline species as the most abundant. In the Gulf of Cadiz, agglutinating foraminifera are common whereas they are absent at the western Iberian Margin Site U1391. Miliolids are generally scarce or absent in all samples.

The living assemblage of Hole U1385B mostly consists of the agglutinating astrorhizid taxa *Rhizammina* sp., *Astrorhiza granulosa*, and *Saccorhiza ramosa*. Holes U1386B and U1387A/B contain a diverse fauna with particularly high abundances of intermediate (*Melonis*

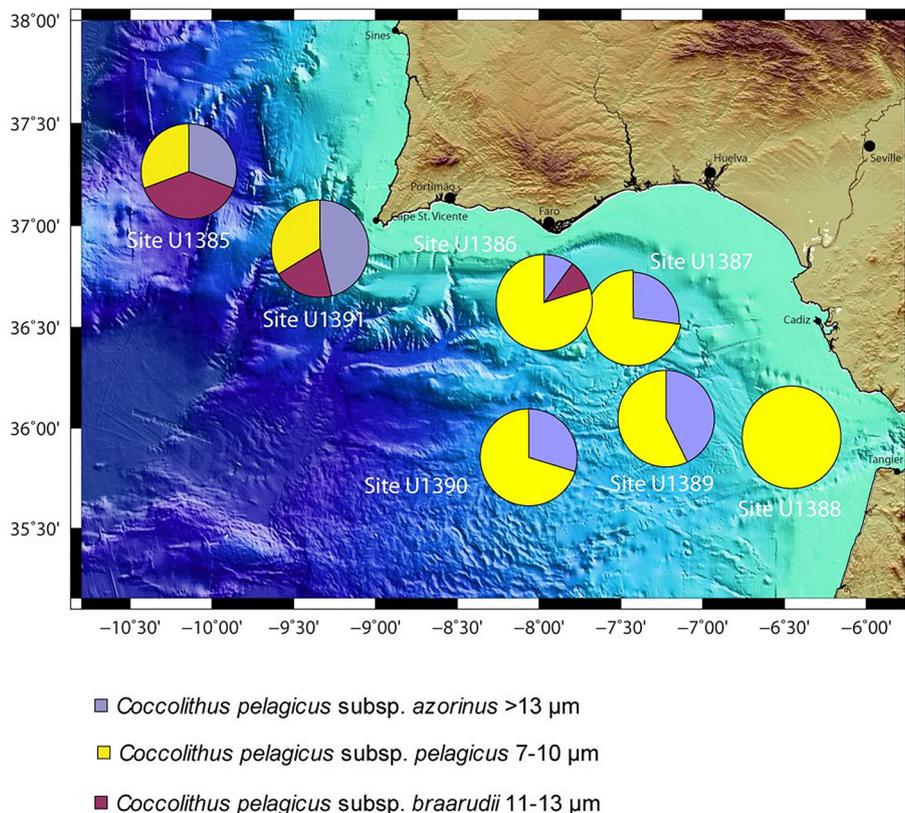


Fig. 5. Relative percentage of the three *Coccolithus pelagicus* subspecies at the different sites in the mudline samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*barleeanum*) and deep (*Bulimina marginata*, *Chilostomella oolina*, and *Globobulimina* spp.) infaunal taxa. Like at Hole U1390C, the agglutinated taxon *Marsipella* is abundant in these assemblages. The mudline samples at Hole U1389C shows particularly low numbers of stained shells with *M. barleeanum* as the most common taxon. In contrast, Hole U1390C has revealed the most stained shells. In U1390C the assemblage shows a significant number of agglutinating taxa, most prominently *Marsipella cylindrica* and *Saccorhiza ramosa*, and a diverse hyaline fauna with *M. barleeanum*, *Siphonina tubulosa* and *Uvigerina mediterranea* being most abundant. Finally, U1391 is the only site with occurrences of *Bulimina mexicana*, where it is the dominant species alongside *U. mediterranea*.

Epibenthic foraminifera in general and elevated epifaunal species in particular, are absent at most sites. The latter are only represented by *Hanzawaia concentrica* which occurs with single specimens at holes U1390C and U1391B.

#### 4.5. Dead benthic foraminiferal assemblages

Abundances of common (> 3% of the assemblage) unstained benthic foraminifera are summarized in Table 4 and in Fig. 6. While living and dead assemblages share the general abundance patterns of agglutinated, hyaline and miliolid shells as well as occurrences of infaunal taxa, the relative contributions of these taxa sometimes differ between the living and dead assemblages at a given site. Similarly, to the stained assemblages, Hole U1385B stands out from the other sites by having very high amounts (~75%) of agglutinated shells, in particular arborescent astrorhizoid taxa (see also Grunert et al., 2015). The Faro Drift Sites U1386B and U1387A/B share common occurrences of *Amphicoryna scalaris*, *Globocassidulina* spp. (*G. minuta*, *G. subglobosa*) and *M. barleeanum*. Similar to the living assemblages, deep infaunal taxa (most importantly bolivinids, *Bulimina marginata*, *Chilostomella oolina*) are common at both sites, but abundances of individual groups differ.

The unstained foraminiferal assemblage of Hole U1389C differs from the living assemblage as well as from the other sites by high abundances of cibicidids (mostly *Cibicides lobatulus* and *Cibicoides mundulus*) and *Cassidulina laevigata*. Furthermore, Hole U1389C yielded the only dead assemblage that contains shelf-dwelling taxa (5.4%), mainly represented by species of *Elphidium* such as *E. crispum*, *E. excavatum*, *E. gerthi*, and *E. macellum*, and to a lesser degree of *Asterigerinata mamilla*, *Planorbulina mediterraneensis* and *Ammonia beccarii*. Hole U1390C shows common occurrences of astrorhizoid shells, similar to the living fauna at the site, and common abundances of bolivinids (mainly *Brizalina alata*) and *M. barleeanum*. Finally, the dead assemblage of Hole U1391B shows a less balanced composition with remarkably high abundances of *Bulimina mexicana* (25%) and *M. barleeanum* (15%), and common occurrences of *Uvigerina mediterranea*, a pattern that is also reflected in the living assemblage. Elevated epibenthic foraminifera are present at all sites bathed by MOW with the exception of Hole U1390C (Table 4). Abundances vary considerably between 1.3% and 5.6%, with Hole U1391B showing the lowest and Hole U1389C the highest abundances.

## 5. Discussion

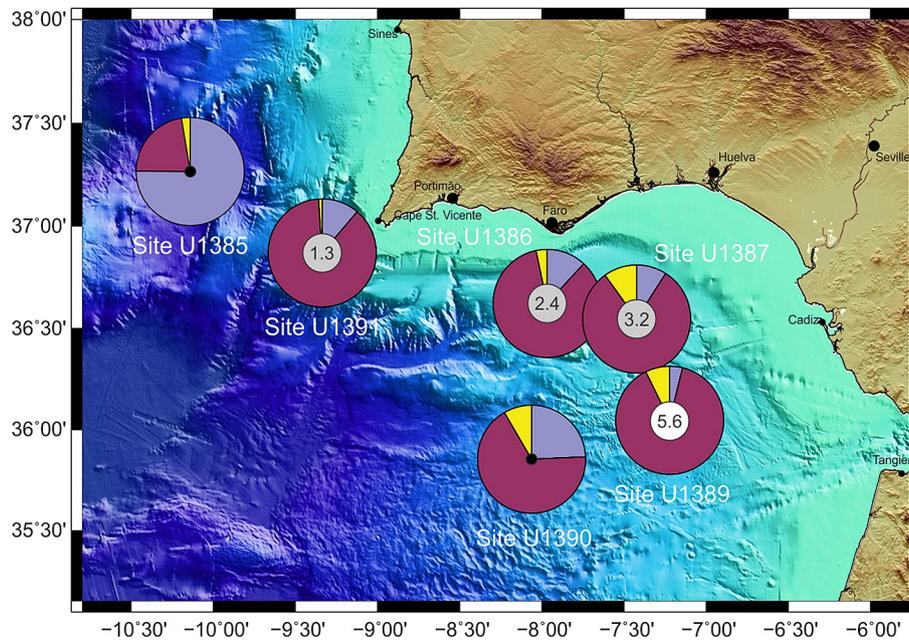
### 5.1. Water samples

#### 5.1.1. Coccolithophore assemblages

Although plankton assemblages from the photic zone only provide snapshot insights into the living communities, they give essential information on the occurrence and distribution of the species and the ecology of different taxa in the sampling area at the time of sampling (Andruleit, 1997). The coccolithophore abundances and species distributions are similar to those reported in previous studies carried out especially along the shoreline of the Western Iberian Margin during the same season (autumn-winter) (Cachão and Moita, 2000; Cachão et al.,

**Table 4**  
Benthic foraminifera of the dead assemblages. Relative abundances of agglutinated, hyaline and miliolid tests; taxa occurring with > 3% in at least one sample; elevated epifaunal taxa (Schönfeld, 2002a); shelf taxa (*Ammonia beccarii*, *Elphidium* spp., *Planorbulina mediterraneensis*).

Site	U1385B	U1386B	U1387A	U1387B	U1389C	U1390C	U1391B
Agglutinated %	75.1	11.8	5.2	12.9	3.8	24.3	11.2
Hyaline %	22.3	84.3	83.2	78.8	87.8	67.3	87.7
Miliolid %	2.6	3.3	11.6	8.3	7.2	8.4	1.1
<i>Ammolagena clavata</i>	1.4	0.1	0.6	–	–	3.0	–
<i>Saccorhiza ramosa</i>	10.1	0.2	0.3	0.1	–	8.9	3.8
Other astrorhizoids	54.3	1.4	1.5	4.9	0.5	9.9	3.0
<i>Amphicoryna scalaris</i>	–	5.3	4.2	8.8	1.2	1.0	0.8
<i>Bolivina/Brizalina</i> spp.	1.7	1.1	4.9	0.8	3.6	5.0	5.0
<i>Brizalina alata</i>	–	0.1	0.4	0.3	1.8	3.5	–
<i>Brizalina dilatata</i>	0.9	0.9	1.9	0.4	1.5	5.0	0.5
<i>Bulimina marginata</i>	0.3	6.9	2.1	3.8	2.5	1.0	0.5
<i>Bulimina mexicana</i>	0.3	2.0	1.5	1.1	1.4	1.0	25.1
<i>Cassidulina laevigata</i>	–	3.3	3.1	3.2	5.1	2.0	1.6
<i>Chilostomella oolina</i>	2.6	2.0	14.0	2.8	1.8	1.5	0.3
<i>Cibicides/Cibicoides</i> spp.	–	2.0	1.8	4.7	5.5	2.0	4.4
<i>Globocassidulina</i> spp.	–	7.0	2.8	5.5	6.4	1.0	–
<i>Hyalinea balthica</i>	–	1.2	0.7	1.9	0.3	1.0	4.1
<i>Melonis barleeanum</i>	–	7.4	5.1	8.8	4.5	7.9	15.6
<i>Uvigerina mediterranea</i>	–	4.1	1.9	6.8	2.6	3.0	8.5
<i>Uvigerina</i> spp.	–	3.6	1.0	3.7	1.5	1.5	1.4
<i>Spirosigmoilina tenuis</i>	0.3	0.1	–	–	0.1	3.5	–
<i>Triloculina tricarinata</i>	–	0.4	8.3	1.4	0.9	–	–
Elevated epifauna							
<i>Cibicides lobatulus</i>	–	1.4	0.9	1.6	2.4	–	–
<i>Cibicides refulgens</i>	–	0.1	0.1	0.3	0.4	–	–
<i>Discanomalina</i> spp.	–	–	0.1	0.2	0.1	–	–
<i>Hanzawaia concentrica</i>	–	0.6	1.3	0.6	1.3	–	0.5
<i>Planulina ariminensis</i>	–	0.3	0.4	0.8	1.4	–	0.8
<i>Spiroplectammina sagittula</i>	–	0.2	–	–	–	–	–
<i>Vulvulina pennatula</i>	–	–	–	–	–	–	0.8
% Elevated epifauna	0.0	2.4	2.8	3.5	5.6	0.0	1.3
<i>Trifarina angulosa</i>	0.3	–	0.1	0.3	0.5	0.5	–
Shelf taxa	–	–	–	–	5.4	–	–



**Fig. 6.** Relative abundances of agglutinated (violet), miliolid (purple), and hyaline (red) benthic foraminiferal shells >125  $\mu\text{m}$  in mudline samples of IODP Expedition 339. Relative abundances of elevated epifaunal foraminifera, considered indicators of increased bottom current velocity, are indicated in the central circle (black: absent; gray: <5%; white: >5%). Note that values for Site U1387 are mean values from the combined assemblages of Holes A and B. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2000; Ferreira and Cachao, 2005; Silva et al., 2008). We did not find significant differences in abundances and species diversity at 5 and 20 m depth likely due to the small difference in water depth. However, we observe spatial differences in the proportions of species/groups of the coccolithophore assemblages recognizing three distinct assemblage groups at Site U1385, Sites U1386–89 and Sites U1390–91, respectively, which are corroborated in the CCA bi-plot diagram (Fig. 3). This indicates unique oceanographic and environmental controls impacting the distribution of the communities at the different sites at the time of the sampling (fall-winter). *E. huxleyi* which is known for its cosmopolitan distribution was abundant at all sites and depths sampled. *C. leptoporus*, *C. pelagicus* and *Helicosphaera* spp. that were rare in the living assemblages at all the sampled sites, were present in the sediment. Their low presence at the time of sampling may indicate that their abundance varies seasonally hence they did not thrive during our sampling period as already postulated in several works in the Mediterranean Sea and Atlantic Ocean (Knappertsbusch et al., 1997; Renaud and Klaas, 2001; Balestra et al., 2004; Bonomo et al., 2012). Other possible factors could have influenced the coccolithophore distributions including nutrients and/or depth zone preference of these species (Baumann et al., 2005 and reference there-in). In our analysis, we were limited because we were only able to gather data at two depths (5 and 20 m). This was due to operational constraints during the IODP cruise, for which drilling occurred at the same time as our water sampling. In the following, we describe specifically the three assemblages that differ in their specie/group proportions.

**5.1.1.1. IODP Site U1385.** Total coccolithophore abundances at this site are the lowest at both depths in comparison to the other sites. Site U1385 is defined by SST of  $\sim 18^\circ\text{C}$  and low nutrient concentrations during the month of December (when we sampled; data from WOA, see Table 1), and it is the deepest ocean site we sampled. The cosmopolitan *E. huxleyi* is the main constituent of the assemblages at this site. The holococcolithophore group is the second most abundant at both depths. High abundances of this group and low nutrient concentrations compared to the other sites corroborate previous studies which have described holococcolithophores as characteristic for oligotrophic surface waters (Dimiza et al., 2008; Cros and Estrada, 2013; Bonomo et al.,

2014; Dimiza et al., 2016) (Table 1, Appendix B). Generally, temperate stratified waters are considered favourable for many coccolithophore taxa resulting in high abundance and diverse community (McIntyre and Bé, 1967; Okada and Honjo, 1973; Baumann et al., 2005). However, at this site the abundance and diversity are both low, suggesting additional factors controlling coccolithophore assemblages, such as surface water circulation, wind conditions, and seasonality (i.e. the time of the year in which the sampling has been done) in addition to water stratification (Friedinger and Winter, 1987; Hagino et al., 2000; Baumann et al., 2005). This interpretation is in line with the results from ordination analysis (Fig. 3) which show samples from Site U1385 far from the environmental vectors and from other stations, highlighting the lack of relationship between the assemblage at this site and the considered environmental variables.

**5.1.1.2. IODP Sites U1386–89.** Sites U1386–89 located on the Iberian Margin in the Gulf of Cadiz. At these sites, *E. huxleyi* is always present and *Gephyrocapsa* spp. occurs in higher concentrations at these four sites than at U1390–91 and U1385. The presence of *Gephyrocapsa* spp. especially in the Gulf of Cadiz has been reported in previous studies carried out in the western part of the Mediterranean Sea where *gephyrocapsids* have been observed in high abundances (Knappertsbusch, 1993). This has been attributed to the lower salinity of the surface water which originates from the Atlantic and is characteristic of the western part of the Mediterranean basin (Knappertsbusch, 1993; Malinverno et al., 2003; Balestra et al., 2008; Ausín et al., 2015). *G. oceanica* has been recognized as a species with a preference for coastal environments (Silva et al., 2008; Guerreiro et al., 2013, 2014) and to respond quickly to nutrient input (Guerreiro et al., 2014). These preferences explain why *G. oceanica* is the most abundant of the *Gephyrocapsa* spp. group at the Gulf of Cadiz (see Appendix B) which receives nutrients from the proximal coastal area. Indeed, CCA locates *Gephyrocapsa* spp. closer to the  $\text{NO}_3$  gradient (Fig. 3). The warm water taxa group shows the highest abundances in this area, corresponding with the high SST data (Table 1). Holococcolithophores are present at these sites but their abundance is lower than abundances reported previously especially from other Mediterranean coastal zones (Dimiza et al., 2008, 2016; Dimiza and Tryantaphyllou, 2010). This group usually prefers warm, stratified and

oligotrophic waters conditions typical of the Mediterranean (Dimiza et al., 2008, 2016; Dimiza and Tryantaphyllou, 2010; Cros and Estrada, 2013), thus low abundances in our samples could be explained by the more eutrophic general conditions at the time of sampling, as suggested by nutrient concentration data (from WOA13) of these stations (Table 1) and scores on the CCA bi-plot diagram close to higher concentrations of  $\text{NO}_3^-$ .

**5.1.1.3. IODP Sites U1390–91.** Sites U1390–91 are characterized by a higher coccolithophore standing stock (total numbers). *E. huxleyi*, *Gephyrocapsa* spp., the small placoliths, and *Syracosphaera* spp. are the major taxa/groups present at these sites. Small placoliths as well as *Syracosphaera* spp. have been associated with turbidity/river discharge and/or iceberg melt (Colmenero-Hidalgo et al., 2004; Marino et al., 2008, 2009; see Appendix B). Indeed, these sites are influenced by the presence of the AC, characterized by high eddy kinetic energy and turbidity (Le Traon and De Mey, 1994). This is also in agreement with the presence of the genus *Gephyrocapsa* that has been associated with turbid coastal environments (Guerreiro et al., 2014). In the CCA analysis these stations appear negatively correlated to SST, thus they are present at slightly colder water consistent with measurements in situ (see Table 1). However, the CCA indicates that the species at these two sites appear to not be influenced by the nutrient content. Thus, the presence of these three taxa/groups has to be related to environmental parameters (such as light or mixed layer depth) other than the measured in situ temperature and climatological nutrient field.

## 5.2. Mudline samples

### 5.2.1. Coccolith distribution

The coccolith distribution observed in the surface sediments shows differences in absolute numbers and assemblage compositions in comparison to the surface waters at the respective sites. The species recovered in the mudline samples may reflect species living at depths >20 m rather than species living at the ocean surface represented by our samples or they could represent species which are present during other seasons of the year. However, this difference may also reflect different sedimentation rates which may dilute or enrich coccolith abundances in mudline sediments. Specifically, the species abundance for the mudline samples is highest at U1385 while coccolithophore abundance in the water column was lowest at this site. The coccolith distribution in the mudline samples can also be influenced by coccolith selective dissolution processes that can happen in the water column prior to arriving at the sediment. In fact, many of the coccoliths of delicate species (such as the holococcoliths), can be dissolved in the water column or in the surface sediment, and as such, are not well preserved as fossils (Hay, 2004 and reference there-in). In our study, we also observe some species that are common in the fossil records at all sites but are rarely found in the water samples including, *C. leptoporus*, *Helicosphaera* spp., and *C. pelagicus*. Similar results have been reported in different North Atlantic studies (Baumann et al., 2000; Balestra et al., 2004) and in the Mediterranean Sea (Malinverno et al., 2003; Balestra et al., 2008; Bonomo et al., 2012). The presence of these species and groups in the sediment but not in the water column has been explained as different bloom timing with respect to the period of water sampling, and possibly due to advective transport from other zones into the study area (Bonomo et al., 2012). However, bias due to the restricted sampling depths cannot be excluded as these species may be dwelling deeper in the water column and hence missed in our depth restricted samples. All these three groups and taxa but in particular, *C. pelagicus* and *C. leptoporus* are considered dissolution-resistant species (Knappertsbusch, 1993; Baumann et al., 2000; Boeckel and Baumann, 2004), and their relative abundance in the sediment may also represent a passive enrichment due to preferred preservation (Findlay, 1998). Similar suggestions have been proposed for the Balearic Sea where higher abundances of *C. leptoporus* are recorded in the sediment sample

when compared to the water column (Cros, 1997). Moreover, increases in absolute and relative abundances of *C. leptoporus* coccoliths close to Sites U1385 and U1391 (Guerreiro et al., 2015) have been related to a stronger and more persistent influence of ENACW in the area (Fiúza et al., 1998). All the mudline samples are also characterized by high abundances of reworked coccoliths which are not related to terrigenous input (Colmenero-Hidalgo et al., 2004), as indicated by low C/N ratio in buried organic matter at the studied sites (Table 1). We thus think that the reworked coccoliths mainly originate from sediments remobilized and eroded by the MOW.

**5.2.1.1. IODP Site U1388.** Clear differences between the living and the fossil assemblages (in particular absolute abundances) are observed also at this site. Only a few specimens of *C. leptoporus* and *C. pelagicus* subsp. *pelagicus* (Figs. 2 and 4), were counted and reworked specimens (of Paleocene and Cretaceous age) were abundant. At this site the overall low abundance of coccoliths and the presence of reworked coccoliths may be related to the MOW which shows the highest current velocity at this location ( $>100 \text{ cm s}^{-1}$ , Hernández-Molina et al., 2011, 2013). The strong influence of the MOW at this site, could thus prevent sedimentation of the coccoliths at the sea floor (through the action of winnowing) but at the same time could remobilize and erode sediments and transport them from afar which would explain the presence of the reworked coccoliths.

**5.2.1.2. IODP Site U1385.** Site U1385 shows high abundances of coccoliths. Significantly greater water depth and lower sedimentation rates (Table 1) may explain the higher abundances at this location in the mudline sample as each sample represents accumulation over a long-time interval. The presence of small placoliths, and *E. huxleyi* can be interpreted as a result of lower velocity of bottom currents that should allow the sedimentation and accumulation of smaller size coccoliths (Ferreira and Cachao, 2005). The presence of *C. pelagicus* subsp. *azorinus* (Fig. 5) in addition to the other two subspecies, is likely associated with the important influence of the northward recirculation of the AC waters and subtropical gyre (Parente et al., 2004; Palumbo et al., 2013).

**5.2.1.3. IODP Sites U1386, U1387 and U1389.** The coccolith record at these locations in the West Iberian Margin is quite diverse although the total abundance is lower in comparison to U1385. In a previous study by Ferreira and Cachao (2005) carried out along the West Iberian Margin with sampling stations much closer to the shoreline, the densities of calcareous nannoplankton were closely related to the granulometry of the surface sediments. This co-variation results from near bottom currents that influence sedimentation of present day coccoliths and the passive transport of reworked forms within the oceanic water masses (Ferreira and Cachao, 2005). It is likely that to some degree similar processes also affect sediments at these sites as well. Another group that is not present in the living assemblage but is found at Sites U1386 and U1387 is the small placolith group. In general, it has been associated with stressed environmental conditions and the increased abundance of this group should indicate less stratification of the water column (Marino et al., 2014; Incarbona et al., 2010). *Gephyrocapsa* is another genus present in these sites at high abundances. The presence of this genus has been considered indicative of temperate waters and water with relatively high nutrient concentration (Giraudeau et al., 1993; Ziveri and Thunell, 2000; Broerse et al., 2000; Ziveri et al., 2004) and it is usually present in high abundance in the Western part of the Mediterranean Sea (Knappertsbusch, 1993). On the other hand, *C. pelagicus* subsp. *azorinus* are found in lower abundances in Site U1386 likely due to the influence of re-suspension and bottom current circulation as the location of this site may be conducive to such currents.

**5.2.1.4. IODP Sites U1390 and U1391.** The amount of coccoliths in the sediment is significantly lower at these two locations compared to the

other sites, likely because of dilution since the sedimentation rates at these sites are quite high (Table 1). In addition, the living coccolithophore assemblage and surface sediment records show some differences as the presence of *C. pelagicus* that is absent in the water samples. Site U1391 is characterized by the presence of the intermediate temperate *C. pelagicus* subsp. *braarudii* (Saez et al., 2003; Ziveri et al., 2004) and the warmer *C. pelagicus* subsp. *azorinus* (Parente et al., 2004; Jordan et al., 2004; Narciso et al., 2006) that may indicate a northward recirculation of the AC waters (Parente et al., 2004; Palumbo et al., 2013) (Fig. 5). However, in Site U1390 the lack of the *C. pelagicus* subsp. *braarudii* may suggest a different pattern in the bottom current circulation. This hypothesis is supported by the presence of *Helicosphaera* spp. just at this site consistent with a different circulation pattern at the sea floor probably because of the different geographic location of the sites. The sites are also characterized by the absence of *E. huxleyi* in the sediments which we attribute to ecological and physical factors rather than dissolution since preservation at these sites is quite good (Stow et al., 2013). Nevertheless, other factors such as different bloom timing and bias due to the restricted sampling depths cannot be ignored to explain the presence/absence of the species mentioned above.

### 5.2.2. Bulk sediment geochemistry

TOC values of the mudline samples are in the range of surface sediment samples of previous studies (Rogerson et al., 2011). Although TOC and TN values show a relatively narrow range the samples fall in two groups that seem to correlate with Holocene sedimentation rates at the different sites, as presented in Table 1 (Stow et al., 2013; Hernández-Molina et al., 2014b; Kaboth et al., 2015; Singh et al., 2015). Sites U1385–U1387 with lower sedimentation rates (15–20 cm/ka) also have lower TOC values while Sites U1389–U1391 have higher sedimentation rates (>30 cm/ka) and TOC. This indicates that both TOC and sedimentation rates reflect higher productivity in the water column at sites U1389–U1391 and that the differences in TOC do not stem only from a dilution effect. Indeed, the C/N ratios <7 are indicative of labile organic matter of marine plankton and exclude a major terrestrial source for our samples (Meyers, 1994). The mudline samples seem to be influenced much by input from major rivers and estuaries on the southern and western Iberian shelf areas (Burdloff et al., 2008; Sánchez-García et al., 2009; Guerra et al., 2015). In these shallow water environments, a considerably higher contribution of terrestrial organic matter is reflected in increased C/N values up to 23. Furthermore, the strong positive correlation between TOC and TN indicates homogeneity of the organic matter sources that supply the sediments (Ruttenberg and Goñi, 1997). The lack of terrestrial sourced organic matter may be attributed to trapping on the shelf and/or the transport into the Mediterranean by surface currents (Freitas and Abrantes, 2002).

Shipboard data from Holocene and upper Pleistocene samples consistently reveal lower TOC (0.76–1.12 wt%) and TN (0.06–0.1 wt%) values and higher C/N ratios (9.3–14.5) at Sites U1385–U1387 and U1389–U1391 and likely indicate the preferential oxidation of nitrogen-rich organic matter during post-depositional diagenesis (Stow et al., 2013). A different process related to the release of inorganic nitrogen seems to occur in the TOC (0.08 wt%) depleted sediments of Site U1388 where lower C/N values than in the mudline sample occur (Müller, 1977; Meyers, 1994).

### 5.2.3. Benthic foraminiferal assemblages in the mudline samples

Mudline samples are prone to disturbances and sediment loss during the advanced piston coring (APC) process as well as during extraction from the core liner. As a result, any interpretation of benthic foraminifera has to consider the possibility of a compromised living and/or fossil fauna. Faunal density and microhabitat preferences of the living assemblages and their comparison to the dead assemblages provide means to address the issue of drilling disturbance in the present study. Previous studies report average standing stock numbers of ~22

specimens/10 cm<sup>3</sup> for foraminifera >250 µm in the Gulf of Cadiz (total range: 2–54; 400–1900 m water depth; Schönfeld, 2002a) and ~14 specimens/10 cm<sup>3</sup> along the Iberian Margin (total range: 7–25; 900–3600 m water depth; Schönfeld, 1997). Numbers for the standing stock of open slope environments at water depths of ~1000 m along the Portuguese Margin (37–40°N) which include also the 150–250 µm size fraction range from 11 to 14 specimens/10 cm<sup>3</sup> and from 80 to 300 specimens/50 cm<sup>2</sup> (Nardelli et al., 2010; Phipps et al., 2012). The standing stock estimates for the living mudline fauna >125 µm (1–8 specimens/10 cm<sup>3</sup>; 14–78 specimens/50 cm<sup>2</sup>) are clearly lower than these values. Low standing stock numbers thus provide a first indication for the possible loss of material in the sampling process. Standing stock numbers on the order of the mudline samples have been described from depths >0.75 cm within the sediment where pore water oxygen as well as food quantity and quality are diminished (Schönfeld, 2001; Nardelli et al., 2010). Microhabitat preferences of the identified stained (living) foraminifera give further indications about biases at each of the individual sites. Five of the six studied sites (U1386–1387, U1389–1391) are located in the high-energy sea-floor environment of the MOW which harbors a significant standing stock of epibenthic foraminifera (Schönfeld, 1997, 2002a, 2002b). While this distribution pattern is clearly reflected in the dead assemblages (see below), the mere absence of epibenthic species from the living assemblages is unexpected. This lack of epibenthic taxa together with the impoverished faunal densities strongly imply that the topmost layer at the sediment/water interface has been compromised or lost entirely during the drilling and sampling process at all sites. In this context, Site U1390 might represent the most complete living assemblage with occurrences of *Saccorhiza ramosa* and *Hanzawaia concentrica* and higher faunal density values.

While the living assemblages are compromised to different degrees, their integration with the dead assemblages allow for a more complete, yet time-averaged (probably ranging from 20 to 300 years based on sedimentation rates in Stow et al., 2013) assessment of foraminiferal assemblage in the study area. Stained shells have been evaluated separately as the varying abundances within the relic fauna still provide important information about organic matter input and the potential relation to the water column conditions.

**5.2.3.1. IODP Site U1389.** Site U1389 is located most proximal to the Gibraltar Strait, on top of the Huelva Drift, flanked by contouritic channels to the north and south where bottom current velocities of ~50–100 cm/s prevail (Madelain, 1970; Kenyon and Belderson, 1973; Zenk, 1975; Nelson et al., 1993; Stow et al., 2013). Our results corroborate previous findings that highest abundances of taxa associated with an elevated epifaunal habitat, in particular *Cibicides lobatulus* and *Planulina ariminensis*, occur in areas of high flow velocities (Schönfeld, 2002a; Rogerson et al., 2011). The fauna also contains species that have been associated with high current speeds and turbulent water such as *Globocassidulina subglobosa*, *Miliolinella subrotunda*, *Rhabdammina abyssorum*, and *Trifarina angulosa*, and warm water currents such as *Cassidulina laevigata* (Mackensen and Hald, 1988; Altenbach et al., 1993; Mackensen et al., 1995; Schönfeld, 2002a). It has been postulated that many of these species are active suspension feeders which exploit the high suspension load transported by the currents. Our data is consistent with previous notions that passive suspension feeders like *Saccorhiza ramosa* which thrive in areas with reduced current velocity and/or at the margins of MOW impingement on the seafloor are replaced by species that prefer an active suspension feeding strategy (Schönfeld, 2002a, 2002b; see Site U1390). It has been demonstrated that the abundance of many agglutinating foraminifera is limited by the grain-size of the sediment available for shell construction (Murray, 2006). It is likely that the higher average grain-size at this location compared to other sites favors species such as *Rhabdammina abyssorum* and *Bigenerina nodosaria* which generally tend to build coarse-grained shells (Jones, 1994).

Site U1389 is the only site in our study, at which substantial amounts of allochthonous shelf-dwelling taxa have been found. Live specimens of these allochthonous foraminifers are restricted to the northern and northeastern shelf in the Gulf of Cadiz (Mendes et al., 2004, 2012). Downslope transport through small gullies crossing the upper slope is thus a likely explanation for their occurrences (Hernández-Molina et al., 2014b). However, along-slope transport of displaced shells from a source area closer to the Gibraltar Strait is an equally plausible explanation as significant amounts of *Ammonia beccarii* and *Elphidium* spp. have been reported from stations along the pathway of MOW further south (Schönfeld, 2002a; Rogerson et al., 2011; Stow et al., 2013). The coincidence of high abundances of elevated epifaunal and shelf taxa has been observed before (Rogerson et al., 2011). The consistency of this pattern raises concerns regarding the autochthonous nature of *C. lobatulus* for which a very broad, inner neritic to bathyal bathymetric range is well documented (e.g., Jones, 1994; Schönfeld, 1997; Mendes et al., 2012; Bolliet et al., 2014; Dorst and Schönfeld, 2013).

Fauna such as in the live and dead assemblages of Site U1389 with equal distributions of deep infaunal (*Bulimina marginata* and *Chilostomella oolina*), intermediate infaunal (*Melonis barleeanum*) and shallow infaunal to epifaunal (cibicidids with *Cibicidoides mundulus* and *Cassidulina laevigata*) taxa are typically observed in mesotrophic environments (Fontanier et al., 2002; Jorissen et al., 2007). Many of these species are thought to process labile organic matter of low quality or refractory organic matter, whereas taxa dependent on a high flux of fresh labile organic matter such as *Uvigerina mediterranea* and *Amphicoryna scalaris* occur rarely at Site 1389 compared to Sites U1386 and U1387 (Altenbach et al., 1999; Fontanier et al., 2002). The increased TOC values, the lowered surface water productivity (see above) and the evidence for downslope transport as well as previous surveys, suggest a heterogenic, largely allochthonous origin of the organic matter deposited at this site. It could originate from downslope transport from the northern shelf, or from reworking and re-suspension of older sediments or from substantial amounts of comparably aged labile organic matter advected from high productivity areas in the Alboran Sea or from organic matter of higher quality produced in the overlying surface waters (Freitas and Abrantes, 2002; Stow et al., 2013). The latter, however, will likely be prevented from settling at this site due to the strong bottom currents. We thus conclude that MOW advection and downslope transport are the primary food sources determining the fauna observed at this site.

**5.2.3.2. IODP Sites U1386 and U1387.** Sites U1386 and U1387 are located on the Faro Drift where current velocities <20 cm/s have been reported (Zenk, 1975; Schönfeld, 2002a, 2002b). The sites share the same elevated epifaunal species including *Cibicides lobatulus*, *Hanzawaia concentrica* and *Planulina ariminensis* as at Site U1389 but at lower abundance. Lower abundances of the elevated epifauna at the Faro Drift is in agreement with previous studies that relate lowered epibenthic values to the deceleration of MOW and increasing loss of suspension load along its pathway (Schönfeld, 2002b).

The assemblages share many similarities with faunas considered typical for the upper MOW core (MU) and in particular to assemblages previously described at the same location (Schönfeld, 2002a). These include frequent occurrences of passive suspension feeders such as *Marsipella elongata* (due to taphonomy only preserved in the live assemblages) and shallow infaunal species dependent on high input of labile organic matter such as *Amphicoryna scalaris* and *Uvigerina mediterranea* (Altenbach et al., 1999; Fontanier et al., 2002, 2008). Taxa known to occupy intermediate (*Melonis barleeanum*) and deep infaunal habitats (bolivinids, *Bulimina marginata*, *Chilostomella oolina*, and *Globobulimina* spp.) are significantly more abundant than at other sites bathed by MOW (Fontanier et al., 2002; Jorissen, 2003). These taxa are particularly well adapted to process low quality, refractory organic matter close to or below the zero-oxygen boundary (Schönfeld, 2001; Fontanier et al., 2002). Deceleration of the MOW not only results in

deposition of considerable amounts of advected biogenic suspension load in this area, but it also allows higher quantities of fresh labile organic matter from the surface water to settle (Freitas and Abrantes, 2002; Rogerson et al., 2011). The latter is even more relevant during summer and fall when an upwelling filament extending eastward from Cape Sines further stimulates primary productivity (Relvas and Barton, 2002). At the same time, it has been suggested that the Faro Drift area is close to a “hotspot” of sediment resuspension, making old, refractory organic matter accessible to the benthic fauna. This combination of food sources may be fostering abundances of taxa able to process this low-quality food source (Freitas and Abrantes, 2002) and freshly deposited organic matter hence resulting in a diverse community.

Faunal difference between Holes U1387A and U1387B which are only a few hundred meters apart may reflect local variability of organic carbon flux, i.e. settling of different amounts and kinds of organic matter from MOW and surface water. Such patchiness in species distribution is well-known from foraminiferal studies (e.g., Fontanier et al., 2003; Gooday, 2003; Schröder-Adams and van Rooyen, 2011). The strong predominance of *Chilostomella oolina* and *Melonis barleeanum* in the time-averaged dead assemblages of Hole U1387A compared to the more even composition at Hole U1387B may point to either the abrupt input of large amounts of organic matter at Hole U1387B, or the sustained input of increased amounts of organic matter of low quality into the sediment at Hole U1387A (Fontanier et al., 2002).

**5.2.3.3. IODP Site U1390.** Site U1390 represents distal settings of the lower MOW core (ML) (Stow et al., 2013). It is located southeast of the Guadalquivir Bank and the Guadalquivir contourite channel, at the margin of the lower MOW core impingement on the sea-floor, where current speeds are as low as 6 cm s<sup>-1</sup> (Schönfeld, 2002a). The mere absence of elevated epifaunal taxa at this site (one *Hanzawaia concentrica* in the living assemblage) is contrasted by the highest abundances of agglutinated foraminifera in the Gulf of Cadiz. The latter are mostly composed of species with arborescent tests such as *Saccorhiza ramosa*, *Marsipella cylindrica*, *Rhabdammina abyssorum* and *Rhizammina algaeformis*. Their tests either extend above the sediment to support suspension feeding (*Marsipella* spp., *S. ramosa*; Altenbach, 1988; Schmiedl et al., 2000) or lie on the surface sediment where they collect detrital particles (*R. abyssorum*; Linke and Lutze, 1993). These species have been frequently reported from current regimes of different strength where organic matter is resuspended (Schmiedl et al., 2000; Koho et al., 2007). *S. ramosa* in particular has been related to well-oxygenated, oligotrophic and mesotrophic environments at bottom current speeds <5 cm/s (Altenbach, 1988; Schmiedl et al., 2000; Koho et al., 2007). In the Gulf of Cadiz, increased abundances of this species have been observed at the margins of MOW impingement where increased settling of its suspension load largely consisting of particles <10 µm occurs (Schönfeld, 1997, 2002a; Freitas and Abrantes, 2002). The predominance of *S. ramosa* in living and dead assemblages of Site U1390 gives further support to these observations. While the suspension load settling from MOW may sufficiently support the arborescent agglutinated foraminifera, abundances of *Uvigerina mediterranea* indicate considerable input of fresh labile organic matter from the surface water which is in agreement with the coccolith assemblages characterized by the *Syracosphaera* spp. and *Helicosphaera* spp. groups (Altenbach et al., 1999; Fontanier et al., 2002). The generally high amount of organic matter in the sediment is reflected in frequent occurrences of infaunal species with intermediate and deep microhabitats such as *Melonis barleeanum*, *Nonionella turgida* and *Chilostomella oolina*. Species occupying these microhabitats show adaptations to thrive on organic matter of low quality (Caralp, 1989; Fontanier et al., 2002). The considerable abundances of bolivinids and in particular *Brizalina dilatata* may be related to the finer-grained sediment in distal areas of MOW, but they may also be opportunistic species blooming at times of maximum organic matter input (see Site U1390; Freitas and Abrantes, 2002; Dorst and Schönfeld, 2013; Enge et al., 2014). *Siphonina tubulosa*, the most

common species alongside *M. barleeanum* in the living assemblage, is most frequently reported in neritic environments but has also been described from recent oligotrophic bathyal settings with particularly warm bottom waters and Pliocene to Miocene hemipelagic sediments in the Gulf of Cadiz (Jones, 1994; Szarek et al., 2007; Stow et al., 2013; Van der Schee et al., 2016). Given the clearly stained shells at this site, its lower, yet consistent abundances at all other sites along MOW, and the absence of any indicators for downslope transport in our samples we consider *S. tubulosa* as autochthonous, probably favored by the warm bottom waters.

**5.2.3.4. IODP Site U1391.** Site U1391 is located at the SW Portuguese Margin in the distal pathway of MOW where flow velocities have decreased to ~5–15 cm/s (Zenk and Armi, 1990; Schönfeld, 1997). In agreement with previous studies, the decrease in bottom current strength is paralleled by low abundances of elevated epifaunal taxa (1.3%) and a poorly diversified epifaunal assemblage (Schönfeld, 1997).

Both live and dead assemblages resemble faunas described previously from the upper slope of the western Iberian Margin (Schönfeld, 1997; Phipps et al., 2012). The predominance of *Bulimina mexicana* and *Uvigerina mediterranea* is characteristic for the lower part of the MOW layer between 1000 and 1400 m water depth where currents are less turbulent and much of MOW's suspension load is deposited and processed by the benthic fauna (Schönfeld, 1997; Schönfeld and Zahn, 2000; Freitas and Abrantes, 2002). At Site U1391 injection of organic carbon of comparably low quality into the sediment may also account for increased abundances of *Melonis barleeanum* which is adapted to process degraded organic matter (Fontanier et al., 2002). However, our new geochemical and faunal data suggest that trophic conditions at this site are predominantly controlled by export productivity from surface waters, hence fresh organic matter. Indeed, the most common faunal elements – *B. mexicana*, *M. barleeanum*, *U. mediterranea* (~50% in dead assemblages, ~67% in live assemblage) – are deposit feeders commonly reported from areas with high input of labile organic matter (Caralp, 1989; Altenbach et al., 1999; Loubere and Fariduddin, 1999, 2003; Nardelli et al., 2010; Phipps et al., 2012). High organic carbon flux is maintained throughout the year off Cape Sines, the largest quantities accumulating during the main upwelling season in summer and fall (Haynes et al., 1993; Voelker and de Abreu, 2011). Seasonal variability of trophic conditions against the background of generally high input of organic matter may explain the strong dominance of a small number of taxa in the assemblages, microhabitat distribution and differences in the presence/absence of certain shallow infaunal taxa between the living and dead assemblages. *B. mexicana*, predominant in both assemblages, exhibits a tolerance against seasonal fluctuations in eutrophic environments (Loubere and Fariduddin, 1999). A slightly more opportunistic behavior has been described for *U. mediterranea*. It shows particularly high abundances during phytoplankton blooms, but occurs frequently in areas of high organic matter flux, explaining its presence in both assemblages (Altenbach et al., 1999; Fontanier et al., 2006). In contrast, the shallow infaunal *Hyalinea balthica*, present only in the dead assemblages, is regarded as a strongly opportunistic species blooming under stressed environmental conditions with increased food and lowered oxygen availability (Fontanier et al., 2002; Hess and Jorissen, 2009). At Site U1391, *H. balthica* may thrive at times of peak organic carbon flux and probably low-oxygen availability during summer. The limitation of *Brizalina alata* and *B. dilatata*, the two most common bolivinids, to the dead assemblages at Site U1391 may suggest a similar strongly opportunistic behavior for these two species. This would be in line with frequent reports of these species from recent and past stressed environments (Drinia et al., 2007; Enge et al., 2014). *M. barleeanum* is known to occupy an intermediate habitat in the sediment and to avoid competition for fresh labile organic matter in the surface layer (Fontanier et al., 2002, 2006). Thriving on less labile and refractory organic matter, this species is considered largely independent of seasonality, explaining its increased abundances in both assemblages.

**5.2.3.5. IODP Site U1385.** Site U1385 is situated at 2587 m water depth, well below the MOW and bathed by NADW, a cold and nutrient poor water mass (Hodell et al., 2015). Its fauna differs remarkably from the other sites by an impoverished calcareous fauna and the strong predominance of agglutinated foraminifera. The change in composition reflects the transition between two major foraminiferal associations commonly observed between 2500 and 3000 m in the North Atlantic (Schönfeld, 1997; Phipps et al., 2012). This transition is most prominently marked by the disappearance of *Uvigerina peregrina* and has been related to a threshold in organic carbon flux (Schönfeld, 1997; Altenbach et al., 1999). Low nutrient concentrations in surface waters and the lowest TOC values of all sites support this interpretation (this is also consistent with the interpretation of the coccolithophores assemblage). Phipps et al. (2012) point out that calcareous foraminifera seem to be more severely affected by deteriorating trophic conditions as they have more elevated trophic requirements. The agglutinated fauna of Site U1385 is dominated by passive suspension feeders with arborescent tests which harvest suspended organic matter in environments of comparably poor food supply (Linke and Lutze, 1993; Koho et al., 2007). Many of the herein found hyaline taxa such as *Bulimina marginata*, *Chilostomella oolina* or *Globobulimina* spp. are most abundant in areas with low oxygen and organic matter of low quality (Bernhard and Sen Gupta, 2003; Jorissen, 2003; Loubere and Fariduddin, 2003). *Uvigerina peregrina* may thus be outcompeted by those foraminifera. The composition of the hyaline fauna with *Bulimina alazanensis*, *Epistominella exigua* and *Pyrulina angusta* in the living assemblage and *Chilostomella oolina*, bolivinids, *Ammolagena clavata* and *Bulimina marginata* in the dead assemblages resembles assemblages recorded throughout the Holocene at this site (Grunert et al., 2015).

## 6. Environmental controls integrating coccolithophore and foraminiferal assemblages

The integration of the spatial distribution of coccolithophores in the surface water and mudline samples with the spatial distribution of the benthic foraminifera, indicates that the assemblages are likely to be affected by the MOW, following a gradient along its pathway. Previous coccolithophore studies conducted mainly on the Portuguese Margin, pointed out the poor correspondences between the sediments and water sample assemblages (Guerreiro et al., 2014, 2015). In general, for coccolithophores, a combination of factors helps to explain the differences in their distribution between the water column and the surface sediment, such as preservation potential, sedimentation rate, bioturbation activity and high terrigenous input (Balestra et al., 2004; Baumann et al., 2005; Balestra et al., 2008; Bonomo et al., 2014). For the benthic foraminiferal assemblages, previous studies carried out in the same locations as this study, have identified food availability, oxygenation and the hydrodynamic regime at the sea-floor as most significant environmental parameters impacting faunal composition (Schönfeld, 1997, 2001, 2002a, 2002b; Nardelli et al., 2010; Rogerson et al., 2011; Phipps et al., 2012), although to which extent these environmental factors determine the distribution pattern is controversial. This data-set, provides an evaluation of these factors through the comparison of trophic conditions in the surface and bottom waters and an estimation of export productivity, although this is a snapshot of one point in time. A relation between surface and bottom water conditions is evident for Sites U1385 (oligotrophic, outside MOW) and U1391 (reduced MOW). Given the positive correlation between TOC and sedimentation rate, burial efficiency seems to play an important role (Epping et al., 2002). For the fossil coccolithophore assemblages this is particularly evident at Site U1385 in which high absolute abundances have been recorded, probably due to the low sedimentation rates at this site (Stow et al., 2013). Our records support notions of Phipps et al. (2012) that organic carbon flux from the surface water rather

than MOW is the dominant limiting factor for benthic assemblages at depths <1000 m along the western Iberian Margin. In contrast, trophic conditions in surface and bottom waters at the Gulf of Cadiz sites seem largely decoupled. Here, coccolithophore assemblages thrive in the water column in high abundances, with the presence of genus such as *Gephyrocapsa* that is more common in the Western part of the Mediterranean Sea (Knappertsbusch, 1993; Malinverno et al., 2003). Sinking labile organic matter, however, is largely transported laterally by the MOW, and in fact, the benthic assemblages are largely dependent on the suspension load carried in the bottom water currents (Freitas and Abrantes, 2002). As highlighted in this and previous studies, the suspension load is exploited by elevated epifaunal foraminifera and, in more distal parts, by arborescent agglutinated foraminifera (Schönfeld, 1997, 2002a). Our data also indicate, in agreement with previous surveys, that the suspension load may have very different sources (surface water, shelf, Mediterranean, re-suspension, and re-working) resulting in different hydrodynamic behavior and organic matter quality (Freitas and Abrantes, 2002). Settlement of different portions of the heterogenic suspended organic matter largely control distribution patterns of benthic assemblages. On the other hand, the influence of the MOW also affects coccolith settlement causing at least partly the differences between mudline and surface samples in all the area.

## 7. Conclusion

Parallel analyses of surface water and mudline samples from the seafloor at the drill sites of IODP Expedition 339 have revealed new insights into the distribution patterns of coccolithophores and benthic foraminifers.

- Coccolithophore assemblages show distinct spatial variability in species composition and diversity between the Gulf of Cadiz and the Western Iberian Margin. The total coccolithophore standing crops are higher in the Gulf of Cadiz, and the abundances of individual taxa are most likely related to environmental factors.
- Differences in composition exist between the extant coccolithophore assemblages in the surface waters and coccolith assemblages in the mudline samples. These differences are attributed to selective dissolution of coccoliths in the water column and to different blooming times related to strength of the AC and upwelling intensity preserved in the time-averaged mudline assemblages. The influence of the MOW also has been considered to partially affect the coccolith settlement. Other factors such as the season of the sampling and the limited depth of the sampling may also play a role which cannot be neglected.
- Distribution patterns in live and dead benthic foraminiferal assemblages seem to be primarily controlled by source, quantity and quality of available food. In the Gulf of Cadiz, MOW carries a considerable amount of advected food particles in its suspension load. Elevated epibenthic foraminifera exploit this niche, and abundances of this group show a clear relationship with current strength as demonstrated in previous studies. At low current speeds and increasing settlement of suspension load, arborescent agglutinated species seem to compete with and sometimes replace the elevated taxa.
- Infaunal taxa primarily thrive on settled organic matter of the suspension load. Their distribution is at least partially related to the quality of the organic matter which is determined by its source (surface water, shelf, Mediterranean, re-suspension, re-working), and increased burial efficiency at increased sedimentation rate. In contrast, benthic assemblages at the western Iberian Margin, situated at the distal end or outside of MOW, are

largely determined by export productivity and mirror trophic conditions in the surface waters.

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