



Deep-sea trace fossil and benthic foraminiferal assemblages across glacial Terminations 1, 2 and 4 at the “Shackleton Site” (IODP Expedition 339, Site U1385)



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ABSTRACT

Numerous studies focused on the transitions between glacial and interglacial periods, the so-called terminations, due to the associated significant reorganizations of the ocean–atmosphere system. However, analyses combining macro- and micropaleontological information are near absent. In this research, an integrative study of trace fossils and benthic foraminiferal assemblages is conducted in order to improve the characterization of Terminations 1, 2 and 4, as revealing the response of the macro- and microbenthic habitats to the involved paleoenvironmental changes. For this purpose, selected cores from Site U1385 (IODP Expedition 339) located off the western Iberian Margin, have been studied. Changes in trace fossils and benthic foraminifera related to both long-term variations at the glacial/interglacial scale, and short-term millennial-scale climatic events. Food and oxygen availability have been identified as the main factors determining variations in the macro- and microbenthic community structure across glacial terminations in the context of changes in water mass distribution and productivity in the NE Atlantic. A deep-sea multi-tiered tracemaker community, consisting of biodeformational structures, *Chondrites*, *?Nereites*, *Palaeophycus*, *Planolites*, *Thalassinoides*, and *Zoophycos*, suggest generally well-oxygenated bottom and pore-water conditions during interglacial as well as glacial intervals, with punctual decreases in oxygenation. Short-climatic events registered during Terminations 1, 2, and 4 induce a similar response of trace fossil and benthic foraminifera communities to the variable incidence of food and oxygen availability. Termination 1 shows a severe deterioration of oxic conditions and increasing food availability during the YD and HS 1, favoring appearance/dominance of *Zoophycos*, together with the lowest miliolid and the highest deep infaunal taxa abundances. Short-term climatic events (HS 11, IRE 10.1) associated with Terminations 2 and 4 are characterized by a major incidence of export productivity and accumulation of organic matter respect to depletion oxygenation, especially affecting the microbenthic habitat. Dark sediment intervals of HS 11 and IRE 10.1 are characterized by higher abundances of *Zoophycos*, together with strong peaks in hBFAR values, significant lows in miliolids and lower abundance of deep infaunal taxa. The presence of *Chondrites* during IRE 10.1 also indicates the impoverishment in pore-water conditions deep within the sediment.

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1. Introduction

Climate during the Late Pleistocene is characterized by alternations between cold glacial and warm interglacial periods, with abrupt transitions in between called terminations (e.g., Broecker, 1984; Schulz and Zeebe, 2006). These transitions, occurring in about 10 kyr or less, are associated with major reorganizations of the ocean–atmosphere system (Broecker and Denton, 1989; Paillard, 2009).

Glacial/interglacial transitions show considerable differences in the magnitude of temperature change as well as their duration (Röthlisberger et al., 2008; Lang and Wolff, 2011). In general, termination amplitude is typically greater for the last five terminations (T1 to T5) than the previous six (T6 to T11) (e.g., Lang and Wolff, 2011). Millennial-scale climatic events associated with terminations, such as the Younger Dryas (YD) and Heinrich Stadial (HS) 1 during T1, HS 11 at T2, and Heinrich-type ice-rafting events (IREs) 10.1, 10.3, and 10.4 associated with T4, are of special interest as they determine significant changes in ocean/atmosphere dynamics, affecting water column, water/sediment interface, and sediment

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properties (e.g., Hemming, 2004; Hodell et al., 2008; Stein et al., 2009; Voelker and Abreu, 2011; Channell et al., 2012; Naafs et al., 2013).

Numerous abiotic and biotic proxies have been used to approach environmental changes associated with terminations. At the water/sediment interface and in the sediment, deep-sea benthic assemblages provide a highly useful tool to approach environmental changes, mainly associated with paleoproductivity and bottom/pore water oxygenation. Variations in oxygenation and food availability have been successfully interpreted based on the paleoichnological record (i.e., Rodríguez-Tovar and Uchman, 2004a, b, 2006, 2010, 2011; Rodríguez-Tovar et al., 2004, 2006, 2009a,b; Rodríguez-Tovar, 2005; Uchman et al., 2008, 2013a, b; Monaco et al., 2012, 2015). However, studies on the relationship between glacial/interglacial cycles, the involved environmental changes, and ichnological data are scarce, and mainly focusing on the differentiation between bioturbated and unbioturbated, laminated intervals (e.g., Villa et al., 2003) or variations in the Bioturbation Index (Chondrogianni et al., 2004). Only occasionally the ichnotaxonomical composition of trace fossil assemblages has been presented (e.g., Phillips and Grantz, 1997; Löwemark et al., 2006, 2008, 2012; Rodríguez-Tovar et al., 2011). Benthic foraminifera are classic micropaleontological proxies for past changes in deep water hydrography (see Jorissen et al., 2007 for a review), and they have been used for the reconstruction of bottom water conditions along the western Iberian Margin since the last glacial maximum (Caralp, 1987; Baas et al., 1998; Schönfeld and Zahn, 2000; Schönfeld et al., 2003).

Here, we present an integrative analysis of deep-sea trace fossils and benthic foraminiferal proxies, focusing on changes in composition and distribution, in order to understand paleoenvironmental changes occurring through Terminations 1, 2, and 4 and affecting the macro- and microbenthic habitats. Moreover, the in situ paleoenvironmental information of the trace fossils helps to validate the interpretation of benthic foraminiferal assemblages affected by taphonomic processes (see Grunert et al., submitted for publication this volume, for details).

2. The “Shackleton Site” (IODP Site U1385)

The “Shackleton Sites” refer to a series of cores retrieved from the southwestern Iberian margin, considered of special interest in paleoclimate research. These cores are of particular significance for the study of atmosphere/ocean dynamics in this region, providing detailed and high-fidelity records of changes in environmental parameters associated to climate variability on different time scales (Shackleton et al., 2000, 2004; Fig. 1).

During IODP Expedition 339, Site U1385, located off the western Iberian Margin ($37^{\circ}34.285'N$, $10^{\circ}7.562'W$; Fig. 1), was drilled in November 2011 at 2585 mbsl (Expedition 339 Scientists, 2013b; Fig. 1). It is located close to core MD01-2444, one of the “Shackleton Sites”, which provided an important record of millennial-scale climate variability of the last 190 ka (Vautravers and Shackleton, 2006; Martrat et al., 2007; Skinner et al., 2007; Margari et al., 2010; Voelker and de Abreu, 2011; Channell et al., 2012; Hodell et al., 2013a, b). Five holes were cored at Site U1385

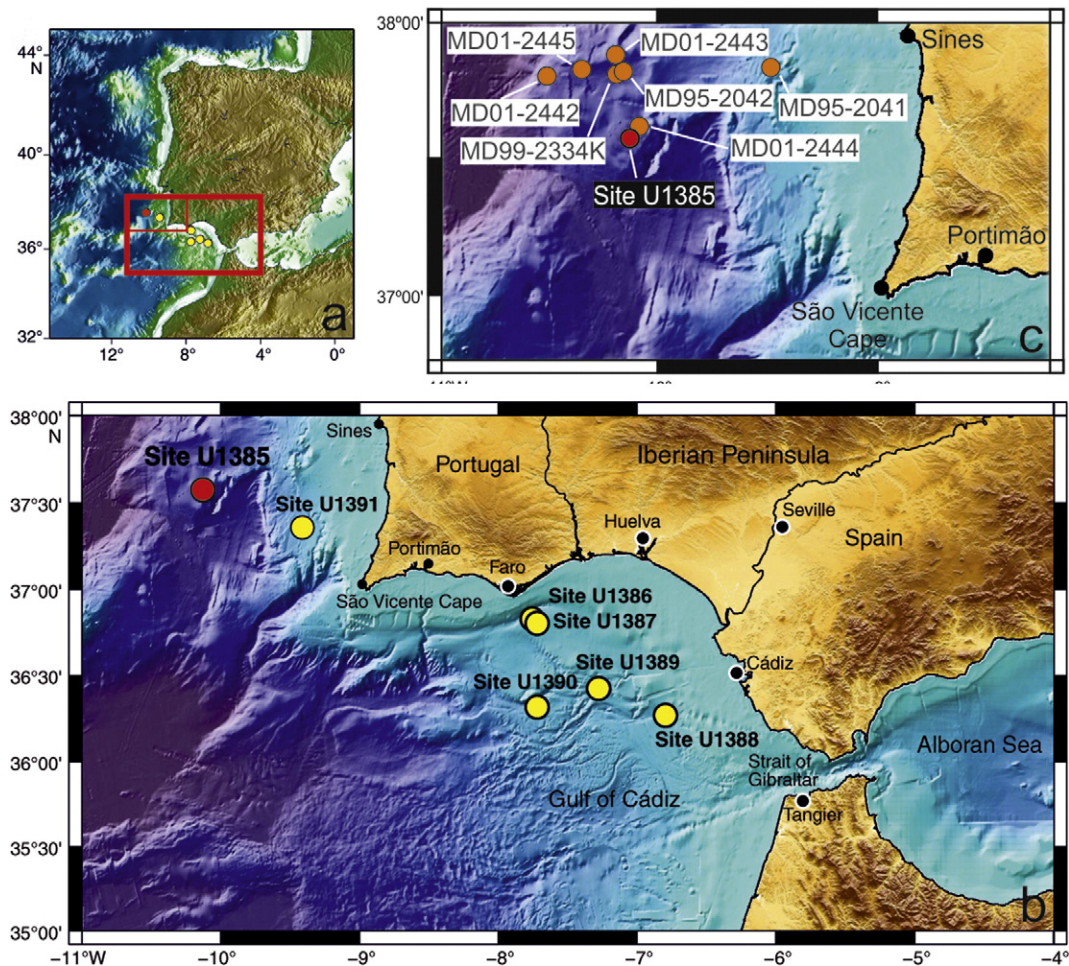


Fig. 1. a, b) Location of the sites of IODP Expedition 339 (Site U1385 marked in red, other sites in yellow). c) Location of Site U1385 (red) together with sites belonging to the “Shackleton Sites” (orange).

with a total recovery of ~622 m and consisting of a uniform lithology dominated by bioturbated calcareous muds and calcareous clays (Expedition 339 Scientists, 2013a, b). Site U1385 contains a complete sedimentary record from the Holocene to 1.43 Ma (Marine Isotope Stage, MIS, 46) that can be correlated to ice core and speleothem records (Hodell et al., 2013a, b).

3. Material and methods

To evaluate the response of the benthic habitat to the environmental changes associated with glacial Terminations 1, 2 and 4, several cores from Site U1385 have been selected for trace fossil and benthic foraminiferal analyses. The selected intervals comprise sections U1385D-1H-1A-0 to U1385D-1H-3A-61 (~360 cm thick), U1385E-3H-5A-20 to U1385E-3H-6A-81 (~210 cm-thick), and U1385E-6H-1A-40 to U1385E-6H-3A-1 (~260 cm-thick) (Fig. 2). The identification of millennial scale events is based on XRF-data (Ca/Ti; Hodell et al., 2013a).

Trace fossil analysis is based on detailed observations of half-cut sections of the cores at the IODP core repository in Bremen (Germany), together with the digital treatment of high-resolution images conducted at the Department of Stratigraphy and Paleontology at the University of Granada (Spain). Ichnological analysis focused on the identification of the trace fossil assemblages, and the ichnofacies and ichnofabric approaches (i.e., Rodríguez-Tovar and Dorador, 2014). Several techniques of digital image analysis have been applied to improve the visibility of bioturbational sedimentary structures (biodeformational structures

and trace fossils; Uchman and Wetzel, 2011; Wetzel and Uchman, 2012), allowing the characterization of ichnological features such as trace fossil composition, cross-cutting relationships, and percentage of bioturbation (as the Bioturbation Index of Reineck, 1963, 1967), among others (Dorador and Rodríguez-Tovar, 2014a, 2014b, 2014c; Rodríguez-Tovar and Dorador, 2014, in press; Dorador and Rodríguez-Tovar, submitted for publication). As what usually occurs with core analysis, ichnotaxonomic identification was limited, in most cases, to the ichnogenus level. Together with the improvement of the ichnological analysis, digital image treatment allows color differentiation in the studied cores (Dorador and Rodríguez-Tovar, submitted for publication this volume).

Benthic foraminiferal analysis is based on quantitative records >125 µm in the studied intervals. A total of 38 samples (14 from Termination 1; 11 from Termination 2; 13 from Termination 4) at a resolution of 20–60 cm have been included in the study (Table 1). A comparison of fossil and mudline assemblages indicates the loss of most agglutinated foraminiferal shells in the uppermost sediment layer and a considerable taphonomic overprint on the fossil assemblages, and the proxy methods applied in the present study have been selected in consideration of this problem (see Grunert et al., submitted for publication this volume, for a detailed discussion). These proxies include the relative abundance of the deep-infaunal taxa *Chilostomella* spp. and *Globobulimina* spp. as indicators of oxygen depletion and eutrophic conditions (Jorissen, 2003; Jorissen et al., 2007); the relative abundance of *Melonis barleeanus* and deep-infaunal taxa as indicators of well-tiered, mesotrophic environments (Fontanier et al., 2002; Jorissen, 2003); the relative abundance of miliolid foraminifera as indicators of comparably well-ventilated, oligotrophic conditions (Kaiho, 1999); and the hyaline benthic foraminifera accumulation rate (hBFAR) as indicator of export productivity. The hBFAR proxy is an adaptation of the BFAR concept of Herguera and Berger (1991), introduced by Grunert et al. (submitted for publication this volume) who argue that the number of benthic foraminifera with hyaline (perforate) shells per gram can be used for an assessment of qualitative changes in export productivity at U1385 (its application outside the study area remains to be tested). The agglutinated/carbonate shell ratio in the study area is largely determined by export productivity (Phipps et al., 2012), and higher trophic demands of hyaline foraminifera result in an increase of their standing stock with increasing food availability. The number of hyaline foraminifera per gram sediment in the residual assemblages of U1385 thus indirectly reflects relative changes in trophic conditions (sedimentation rates are fairly constant at the studied site; Hodell et al., 2013b).

4. Results

4.1. Sediment-color analysis

The three studied intervals show a similar lithological composition of bioturbated calcareous muds and calcareous clays, typical for U1385. In this generalized context, the digital image treatment reveals a distinct differentiation in color between and within the studied sections (Fig. 2). Sections U1385D-1H-1A-0 to U1385D-1H-3A-61 consist of gray/greenish sediments, with two darker intervals, the first in the lower part of the section (U1385D-1H-2A-150 to 100, around 50 cm thick) and the second, shorter, in its middle part (U1385D-1H-2A-45 to 30; around 15 cm thick). There are gradual transitions with the lighter sediments at the bottom and top of each of the dark intervals. Sections U1385E-3H-5A-20 to U1385E-3H-6A-81 consist of light gray/greenish sediments in the middle lower half, and a single darker, near black, interval, around 22 cm thick (U1385E-3H-5A-135 to 113) at the middle part, with gradual transitions at the bottom and top. Above this dark interval, sediments are light gray/greenish, but comparatively darker than those from the middle lower half. Section U1385E-6H-1A-40 to U1385E-6H-3A-1, shows a dominance of light gray/greenish sediments, and a single dark, near black, interval (U1385E-6H-1A-143 to 93; around 50 cm

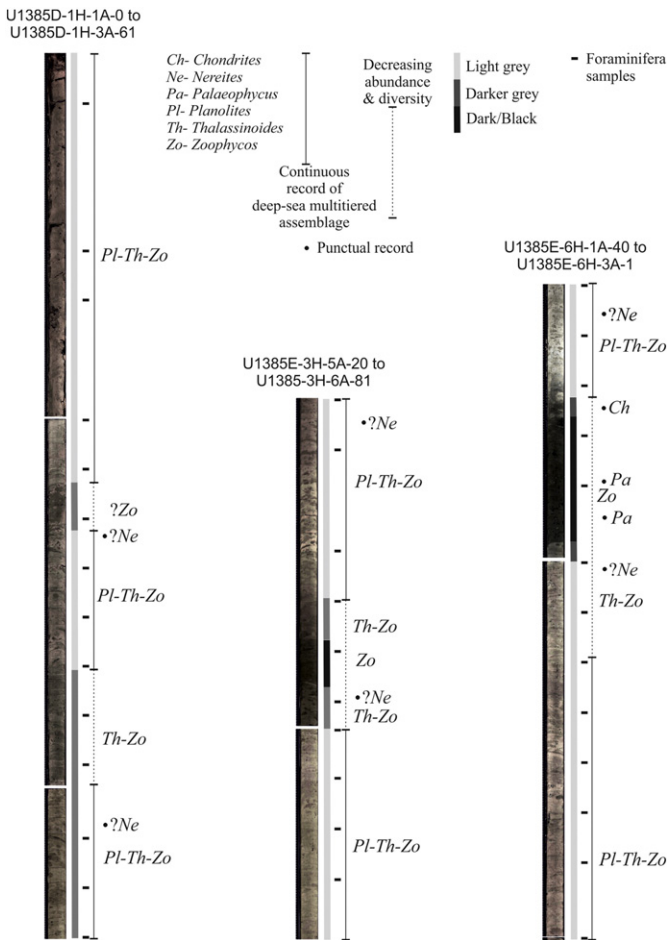


Fig. 2. Correlation of sediment color and deep-sea trace fossil assemblages in the studied sections U1385D-1H-1A-0 to U1385D-1H-3A-21 (Termination 1), U1385E-3H-5A-80 to U1385E-3H-6A-81 (Termination 2), and U1385E-6H-1A-40 to U1385E-6H-3A-1 (Termination 4). Note: Position of the foraminifera samples is indicated.

Table 1
Benthic foraminifera in the studied sections. Asterisks indicate samples that have been split before counting due to the high amount of shell material; the number of asterisks indicates the number of splits. Total number of foraminifera is corrected for the number of splits.

Sample	Depth (m mcd)	Foraminifera		Hyaline		Miliolid		Agglutinated		Intermediate + deep infaunal		Deep infaunal
		(Total)	(Per g)	(Per g)	(%)	(Per g)	(%)	(Per g)	(%)	(%)	(%)	
1.1	0.20	274	22	19	85	1	7	2	8	0	0	
1.2	0.80	419	29	22	75	3	9	5	16	0	0	
1.3	1.00	227	20	16	82	3	14	1	4	0	0	
1.4	1.51	226	38	27	70	11	29	0	0	5	5	
1.5	1.71	395	28	17	61	10	37	0	2	10	10	
1.6	1.91	483	42	30	71	10	24	2	4	8	8	
1.7	2.11	223	28	20	70	8	27	1	3	12	12	
1.8	2.31	448	29	19	66	9	31	1	3	20	20	
1.9	2.51	544	36	27	76	6	18	2	7	24	24	
1.10	2.71	267	18	17	92	1	4	1	4	27	27	
1.11	2.91	684	39	36	93	2	4	1	2	31	30	
1.12*	3.22	773	50	43	85	7	14	1	1	12	11	
1.13	3.42	612	41	36	88	4	9	1	3	11	10	
1.14	3.62	524	45	41	90	1	2	4	8	23	22	
Mean		436	33	26	79	5	16	1	5	13	13	
Stdv		179	10	9	10	4	11	1	4	10	10	
2.1	21.02	331	17	12	71	4	26	0	3	2	2	
2.2	21.22	330	17	12	74	3	21	1	5	0	0	
2.3*	21.62	913	53	30	57	21	40	2	4	0	0	
2.4	21.82	778	43	27	61	16	36	1	3	8	5	
2.5*	22.02	1352	77	74	96	2	2	1	2	16	5	
2.6*	22.22	1370	78	75	96	2	2	1	1	20	5	
2.7	22.33	340	45	38	84	7	15	0	1	8	5	
2.8*	22.53	1103	61	59	97	2	3	0	0	17	16	
2.9*	22.73	1716	113	108	95	5	4	0	0	12	10	
2.10*	22.93	1232	71	68	96	2	3	0	1	15	10	
2.11**	23.13	2700	126	122	96	4	3	0	0	8	7	
Mean		1106	64	57	84	6	14	1	2	10	6	
Stdv		707	35	37	16	6	14	1	1	7	5	
4.1	46.23	294	18	12	67	5	25	1	8	1	0	
4.2	46.43	519	35	20	59	11	32	3	10	1	0	
4.3	46.63	671	36	21	59	11	31	4	10	2	1	
4.4	46.83	595	35	29	82	2	6	4	12	7	4	
4.5	47.03	1109	60	55	93	1	2	4	6	2	2	
4.6	47.33	798	50	47	93	3	5	1	2	2	2	
4.7	47.53	803	39	35	89	4	9	1	1	4	4	
4.8	47.73	896	44	39	89	4	10	1	2	4	4	
4.9	47.93	559	24	21	86	3	12	0	2	3	3	
4.10	48.13	552	30	27	89	3	9	1	30	2	9	
4.11	48.33	688	29	25	89	3	10	0	1	1	1	
4.12	48.53	372	15	13	83	2	11	1	6	7	7	
4.13	48.83	285	24	23	93	0	1	1	6	15	15	
Mean		626	34	28	82	4	13	2	5	4	4	
Stdv		230	12	12	12	3	10	1	4	4	4	

thick), with a sharp contact at the base and a gradual darker upper transition to the lighter sediments.

4.2. Ichnological analysis

Trace fossils (i.e., bioturbational sedimentary structures with sharp outlines and a characteristic recurrent geometry) have been differentiated from a generally mottled background associated to biodeformational structures (i.e., with no distinct outlines and not a recurrent geometry). The trace fossil assemblage shows moderate diversity with the six ichnogenera *Chondrites*, *?Nereites*, *Palaeophycus*, *Planolites*, *Thalassinoides*, and *Zoophycos* (Table 2, Figs. 2–5). The ichnotaxa show variable occurrences between and within the studied intervals. *Planolites* and *Thalassinoides* are the dominant ichnotaxa (>30 specimens), *Zoophycos* is also relatively abundant (15–20 specimens) but not uniformly distributed, while *Palaeophycus* and *?Nereites* are scarce (<10 specimens). *Chondrites* is only locally registered. In general, pascichnia and fodinichnia behaviors are dominant. When visible, the cross-cutting relationship shows a general pattern of *Zoophycos* cross-cutting the rest of the ichnotaxa such as *Planolites*, *Thalassinoides* and *?Nereites*. Locally, *Chondrites* is observed cross-cutting *Thalassinoides*. The registered trace fossil assemblage with abundant *Zoophycos* allows the differentiation of the

Zoophycos ichnofacies, typical for deep-sea environments (e.g., Uchman and Wetzel, 2011; Wetzel and Uchman, 2012; Rodríguez-Tovar and Dorador, 2014). The scarce record of *?Nereites*, an ichnotaxon typical for the *Nereites* ichnofacies but also registered in the *Zoophycos* ichnofacies (e.g., MacEachern et al., 2012), discards the differentiation of the *Nereites* ichnofacies.

In general, lighter gray/greenish intervals are characterized by a higher abundance and diversity of trace fossils, with dominant *Planolites* and *Thalassinoides*, and rare/common *Zoophycos*, while the darker intervals show a decrease in trace fossil abundance, but not a complete disappearance, accompanied by the dominance of *Zoophycos*, and locally *Chondrites*. In almost all cases *?Nereites* is located very close to the onset of darker intervals, except for sections U1385E-6H-1A-40 to U1385E-6H-3A-1 where it occurs below and above (Fig. 2).

Comparative analysis of the three studied intervals reveals a similar trace fossil assemblage, but differences in the relative abundances of ichnotaxa are recognized between sections (Fig. 2). Sections U1385D-1H-1A-0 to U1385D-1H-3A-61 are characterized by a comparatively higher abundance (e.g., more extended distribution) of *Planolites* and *Thalassinoides*, the sparse record of *Zoophycos* and punctual presence of *?Nereites*. Sections U1385E-3H-5W-20 to U1385E-3H-6W-81 show a lower trace fossil abundance, except in the upper part, and the

Table 2

Trace fossil assemblage in the studied sections.

Ichnotaxa	Description	Interpretation	References
<i>Chondrites</i>	Small (~1 mm wide) circular to elliptical spots. No branching observed. Light filling.	Deep tier, feeding structure. Surface ingestor, living chemosymbiotically in dysaerobic conditions at the aerobic–anoxic interface.	Seilacher (1990), Fu (1991), Kotake (1991a), Uchman (1998)
? <i>Nereites</i>	Small-medium size (2–3 mm diameter) circular to elliptical forms, with a dark-filled internal zone surrounded by a light filled envelope. Closed structures in horizontal planes.	Pascichnion by unknown organism in deep-marine, low energetic, oxygenated environments. Modern forms in soft to soupy substrates, related to position of the redox boundary according to sedimentation rate and accumulation of organic matter.	Rindsberg (1994), Uchman (1995), Mángano et al. (2002), Wetzel (2002)
<i>Palaeophycus</i>	Medium size (7–9 mm diameter), circular to subcircular horizontal traces, with a wall. Same filling lithology that the host sediment.	Pascichnia or domichina, facies crossing form. Open tube produced by carnivorous or omnivorous invertebrates, mainly polychaetes or arthropods.	Pemberton and Frey (1982), Keighley and Pickerill (1995), Morrissey et al. (2012)
<i>Planolites</i>	Medium size (5–7 mm in diameter), circular to subcircular form, unlined. Filling different from host sediment.	Pascichnia crossing form. Mainly produced by soft bodied organisms at the shallow tier.	Pemberton and Frey (1982), Keighley and Pickerill (1995)
<i>Thalassinoides</i>	Large (>1 cm in diameter), oval, circular to subcircular, spots and bars.	Domichnial/fodinichnial structure by crustaceans, mostly decapods, in variable environments. Oxygenated, soft but cohesive sediments.	Fürsich (1973), Frey et al. (1984), Ekdale et al. (1984), Ekdale (1992), Schlirf (2000),
<i>Zoophycos</i>	Repeated, more or less, horizontal, spreiten structures (5–7 mm) with alternating dark and light material.	Undiscovered deposit feeder (i.e., sipunculids, polychaete annalids, arthropods, and echiuran worms). Variable behavior and ethological models as fodinichnia, surface ingestors of organic detritus, or chemosymbiotic. Quaternary forms as combination of surface detritus-feeding and cache behavior.	Wetzel and Werner (1981), Ekdale and Lewis (1991), Kotake (1991b), Bromley and Hanken (2003), Löwemark and Schäfer (2003), Löwemark et al. (2004a, b)

dominance of *Thalassinoides* and *Zoophycos*. This pattern of dominance of *Thalassinoides* and *Zoophycos* is also recognized in sections U1385E-6H-1A-40 to U1385E-6H-3A-1, but showing a higher abundance of ?*Nereites*, and the exclusive presence of *Palaeophycus* and *Chondrites*.

Sections U1385D-1H-1A-0 to U1385D-1H-3A-61 show a dominance of *Planolites* and *Thalassinoides* throughout the cores, as well as *Zoophycos* in the light host sediment. *Zoophycos* is present in the darker intervals, as well as *Planolites* and *Thalassinoides* (Fig. 2).

Sections U1385E-3H-5A-20 to U1385E-3H-6A-81 show the dominance of *Thalassinoides* and the presence of *Planolites* and *Zoophycos* in the lighter sediments, above and below the darker interval. The darker interval, with *Zoophycos* in its central part, shows the presence of *Thalassinoides* in the gradual darker gray/greenish transitions at the bottom and top (Fig. 2).

Sections U1385E-6H-1A-40 to U1385E-6H-3A-1 show a similar pattern to sections U1385E-3H-5A-20 to U1385E-3H-6A-81, but with important differences. *Thalassinoides* is dominant, sometimes almost exclusive, in the lighter intervals, above and below the darker interval, with scarce *Planolites*. *Zoophycos* is also frequent in the lower light interval. In the darker/black interval an impoverishment in trace fossils is registered, with *Zoophycos* and *Chondrites* remaining the only relevant taxa, being *Palaeophycus* rare (Fig. 2).

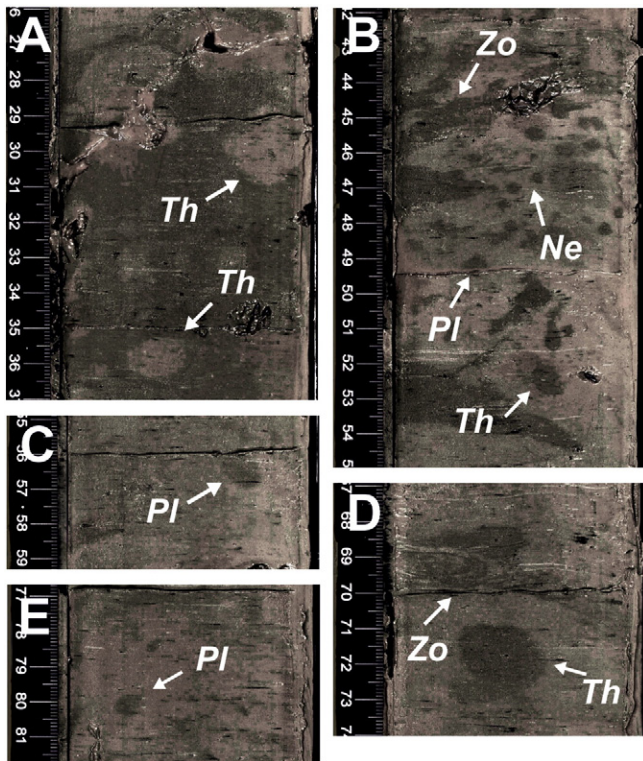


Fig. 3. Trace fossils from sections U1385D-1H-1A-0 to U1385D-1H-3A-21. (A) *Thalassinoides* (*Th*) from the gray darker interval at U1385D-1H-2A (26–36 cm). (B) *Nereites* (*Ne*), *Planolites* (*Pl*), *Thalassinoides* (*Th*), and *Zoophycos* (*Zo*), from the light interval at U1385D-1H-2A (42–55 cm) just below the darker one. (C) *Planolites* (*Pl*) from the light interval at U1385D-1H-2A (55–59 cm). (D) *Zoophycos* (*Zo*) cross-cutting *Thalassinoides* (*Th*) from the light interval at U1385D-1H-2A (67–74 cm). (E) *Planolites* (*Pl*) from the light interval at U1385D-1H-2A (77–81 cm).

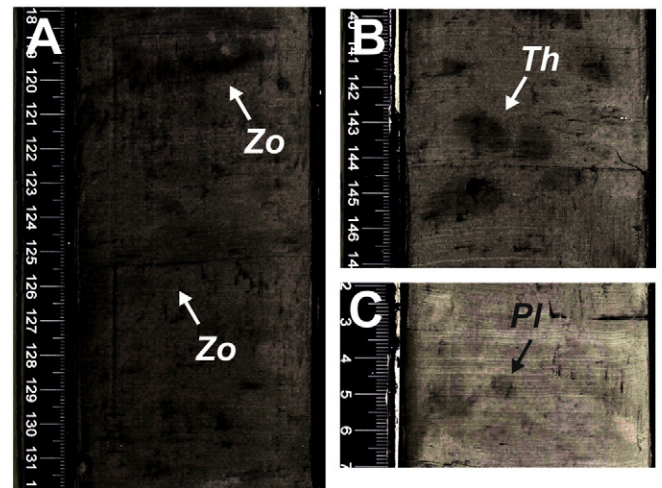


Fig. 4. Trace fossils from sections U1385E-3H-5A-80 to U1385E-3H-6A-81. (A) *Zoophycos* (*Zo*) from the dark interval U1385E-3H-5A (118–132 cm). (B) *Thalassinoides* (*Th*) from the gray darker interval U1385E-3H-5A (140–147 cm) just below the dark one. (C) *Planolites* (*Pl*) from the light interval U1385E-3H-6A (2–7 cm).

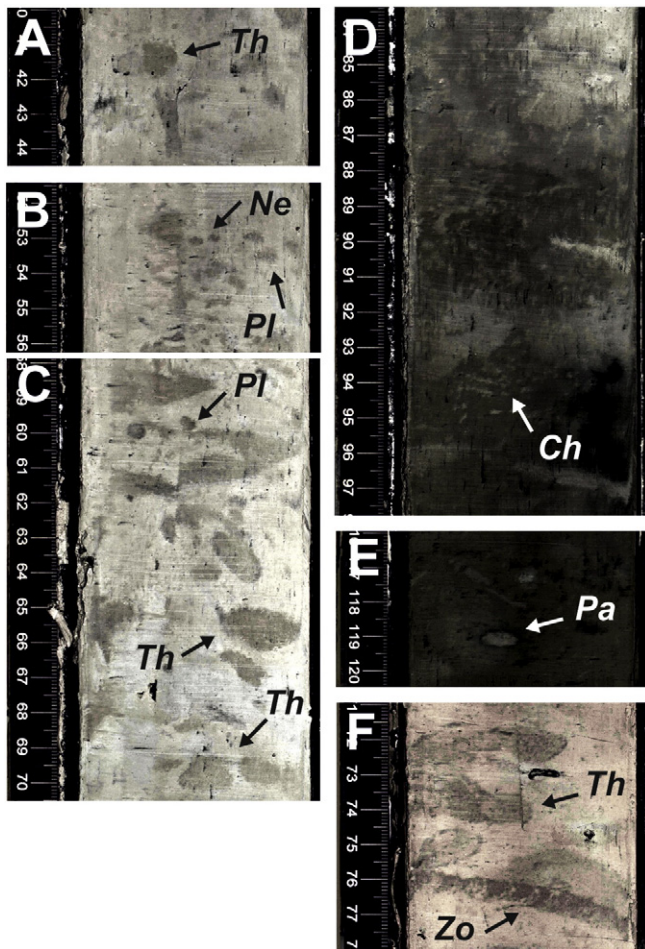


Fig. 5. Trace fossils from sections U1385E-6H-1A-40 to U1385E-6H-3A-1. (A) *Thalassinoides* (*Th*) from the light interval U1385E-6H-1A (40–44 cm). (B) *Nereites* (*Ne*) and *Planolites* (*Pl*) from the light interval U1385E-6H-1A (52–56 cm). (C) *Planolites* (*Pl*) and *Thalassinoides* (*Th*) from the light interval U1385E-6H-1A (58–70 cm). (D) *Chondrites* (*Ch*) from the black interval U1385E-6H-2A (64–98 cm). (E) *Palaeophycus* (*Pa*) from the black interval U1385E-6H-2A (116–120 cm). *Zoophycos* (*Zo*) cross-cutting *Thalassinoides* (*Th*) from the light interval U1385E-6H-2A (71–78 cm).

4.3. Benthic foraminiferal proxies

The results for benthic foraminiferal analysis are shown in Table 1 and Fig. 6. In the data-set of Termination 1, the highest hBFAR values occur prior to HS 1. Numbers subsequently decline and stay at low values with only minor variations. Generally low numbers of miliolid shells, in particular during HS 1, are interrupted by high abundances up to 37% between 2.31 and 1.51 m mcd. *M. barleeanus* occurs very rarely in this data-set, thus the combined records of intermediate and deep infaunal taxa are determined by the latter. Elevated abundances of deep infaunal taxa prior to Termination 1 culminate during HS 1. Thereafter, abundances decline rapidly (contrasting the maximum in miliolid shells), and virtually disappear after the YD.

The data-set of Termination 2 shows significantly higher values of hBFAR for most of the samples compared to Termination 1, particularly prior to HS 11 and during the black interval. Subsequently, values quickly deteriorate. Miliolid shells remain <5% for most samples with a distinct low during the black interval, until abundances suddenly increase at 21.82 m mcd and remain at >20%. Miliolid abundances are inversely correlated to trends in intermediate and deep infaunal taxa that show the highest abundances during the black interval, and low abundances during the miliolid maximum. In contrast to the data-set of Termination 1, *M. barleeanus* is abundant in some samples prior to the end of HS 11,

with a distinct peak during the black interval. Deep infaunal taxa are less abundant than in the data-set of Termination 1, showing increased values only during MIS 6 and at the onset of HS 11.

The data-set of Termination 4 shows an inverse pattern of hBFAR compared to the previous data-sets as values increase towards IRE 10.1 before they rapidly decrease. Miliolid shells are generally rare with the lowest values in the black interval, until they suddenly increase to $\geq 25\%$ at 46.63 m mcd. Intermediate and deep infaunal taxa are significantly less abundant compared to the other data-sets, and increased values do not consistently coincide with darker intervals.

5. Interpretations and discussion

5.1. Trace fossil assemblage

Tcd by Rodríguez-Tovar and Dorador (2014) for the entire U1385 sequence. As interpreted for the entire Site U1385 (Rodríguez-Tovar and Dorador, 2014), trace fossil composition, abundance and cross-cutting relationships reveal a multi-tiered community similar to other deep-sea trace fossil communities (e.g., Ekdale and Bromley, 1984, 1991; Ekdale et al., 1984; Frey and Bromley, 1985; Bromley and Ekdale, 1986; Ekdale, 1988; Bromley, 1996; Rodríguez-Tovar and Uchman, 2004a, b). The uppermost tier is characterized by a mottled background produced by the shallowest activity of benthic tracemakers; the upper tier mainly consists of *Planolites*, occasionally of ?*Nereites* and punctually of *Palaeophycus*, revealing a pascichnia behavior; the intermediate tier is dominated by the domichnia/fodinichnia *Thalassinoides*, while the deep tier is represented by *Zoophycos*, and occasional *Chondrites*, associated with a more complex behavior.

Food availability, bottom water oxygenation, substrate consistency, and rate of sedimentation are of major importance for the abundance and diversity of bioturbation in deep-sea settings, while other factors such as salinity and temperature are of minor significance (Wetzel, 1991; Uchman and Wetzel, 2011; Wetzel and Uchman, 2012; Rodríguez-Tovar and Dorador, 2014). The presence of a deep-sea multi-tiered community in the studied sections with variations in abundance and diversity but not disappearance, suggests generally well-oxygenated bottom and pore-water conditions during interglacial as well as glacial intervals, with punctual decrease in oxygenation (see below). Moreover, the dominance of pascichnia and fodinichnia suggests abundance of food in the sediment.

5.1.1. Long-term patterns across glacial/interglacial cycles

The analysis of the ichnological assemblages (composition, diversity and abundance) in the three sections shows a similar general pattern but with different expression, that reflects the evolution of paleoenvironmental conditions during glacial, early termination, late termination, and interglacial times (Fig. 7): a) Light sediments prior to darker intervals, show a well-developed, comparatively diverse and abundant, deep-sea multitiered community, with dominant *Thalassinoides* and *Planolites*, that could reflect available food associated with moderate export productivity (mesotrophic conditions) and well oxygenated conditions (aerobic to slightly dysaerobic), probably associated with normal glacial conditions; then b) darker sediments, especially black ones, with diminished, almost absent, *Planolites*, presence of *Thalassinoides* and dominance of *Zoophycos*, could indicate impoverishment of environmental conditions, probably increasing organic matter content, associated with high export productivity (eutrophic conditions) and decreasing oxygenation (dysaerobic conditions), during millennial-scale events across terminations; and c) light intervals following darker sediments, showing a rapid recovery of the deep-sea multi-tiered trace fossil assemblage with the dominance of *Planolites* and *Thalassinoides*, could reflect a fast recovery of oxygenated, aerobic, conditions and reduction in export productivity (oligotrophic), probably associated with the end of terminations and the onset of interglacial conditions. Continuity of light sediments in the uppermost part of the

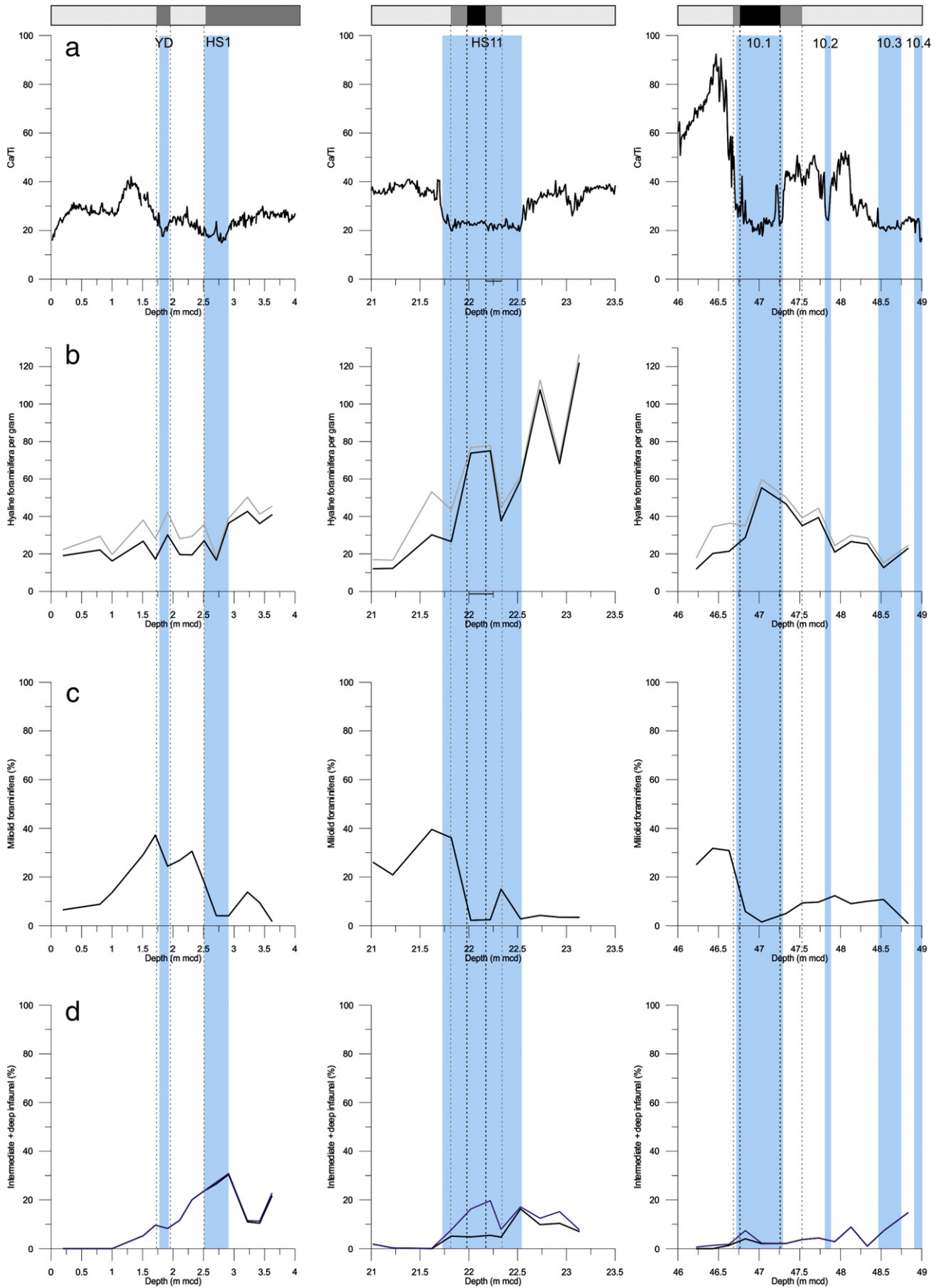


Fig. 6. Trends in benthic foraminiferal proxy data. (a) Sediment color (light gray, dark gray, black) as identified from digital image treatment (Fig. 2), and identification of millennial-scale climatic events based on Ca/Ti records. (b) Trends in the total number of benthic foraminifera per gram (gray) and the total number of hyaline benthic foraminifera per gram (hBFAR; black). (c) Abundance of miliolid shells. (d) Abundance of intermediate and deep infaunal taxa (blue) and deep infaunal taxa (black).

sections, together with maintenance and even increase in the abundance of the trace fossil assemblage reflects stable, even better environmental parameters associated with oligo-mesotrophic environments and similar aerobic conditions during interglacial times. These interpretations accord with previous proposals on the relationships between spatial and temporal variability of bioturbation during glacial–interglacial intervals associated to primary and export productivity, and bottom-water oxygenation (Löwemark et al., 2008, 2012). A strong increase in bioturbation is registered during interglacial intervals as a result of decreasing sea-ice, more open-water conditions, and enhanced primary and export productivity, while glacial periods are characterized by large ice sheets, lowered sea level, limited primary and export productivity, and sparse benthic fauna; cold stages are dominated by small, deeply penetrating trace fossils. Ichological data suggest well-oxygenated bottom waters during interglacial intervals, but bottom water oxygenation remained also fairly oxic during glacial intervals (Löwemark et al., 2012).

5.1.2. Millennial-scale climatic events

Ichological assemblages from Late Quaternary sediments of the Iberian Margin, located close to the studied Site U1385 (cores PO200-10-(8-2, 6-2, 4-2) in Baas et al., 1997, 1998, and M39036 in Löwemark, 2003; Löwemark et al., 2004a), have been previously related to paleoceanographic conditions and short-term climatic changes (Baas et al., 1997, 1998; Löwemark et al., 2004a). Trace fossil assemblages with *Chondrites*, *Planolites*, *Thalassinoides* and *Zoophycos*, and benthic foraminiferal community structure, were mainly related to the degree of bottom-water oxygenation during the last 40 kyr including HS 1 to HS 4 (Baas et al., 1998). Trace fossil tiering denotes suboxic and dysoxic conditions during HS 2 and HS 4, low-oxic bottom water existed during HS 1, and low-oxic to dysoxic bottom-water conditions were present during HS 3 (Baas et al., 1998). The Younger Dryas showed slightly reduced O₂ levels (low oxenic bottom waters). According to Baas et al. (1998), trace-fossil tiering always suggests lower O₂ levels than the benthic

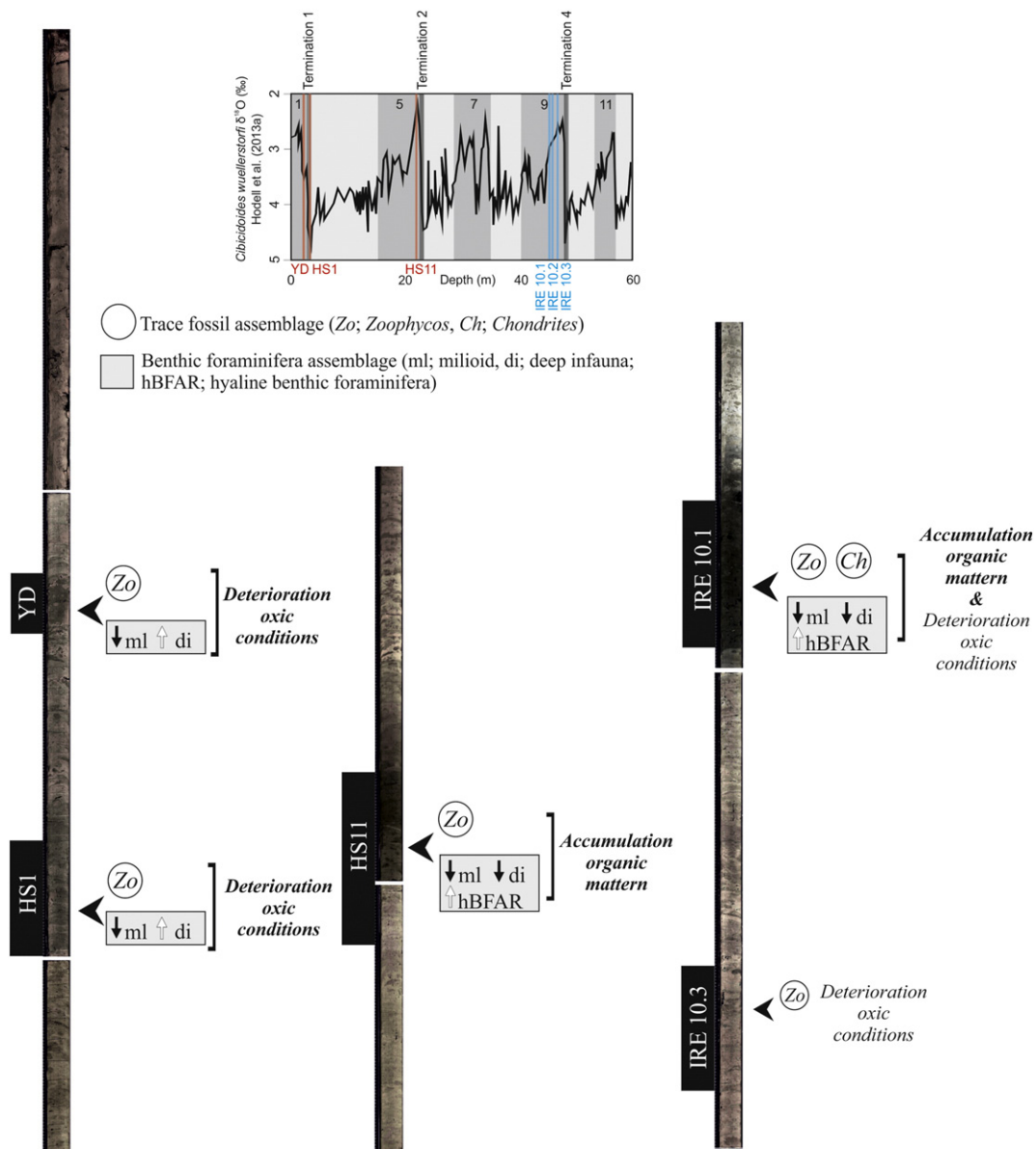


Fig. 7. Major changes in trace fossil and benthic foraminifera proxies in the studied sections, and interpreted variations in paleoenvironmental conditions. Positions of millennial-scale climatic events in the studied cores inferred from Ca/Ti records (Fig. 6). Upper graphic showing benthic oxygen isotope record of *Cibicides wuellerstorfi* (Hodell et al., 2013a) with tentative position of Terminations 1, 2, and 4, and short-term climatic events (YD; Younger Dryas, HS-1 and HS-11; Heinrich Stadials 1 and 11, and IRE; Heinrich-type ice-rafting events 10.1, 10.3, and 10.4).

foraminiferal oxygenation index; apparently, tracemakers are more sensitive than foraminifera to depth variations in the redox boundary in near-surface sediments leading to the movement of trace-fossil tiers. Other environmental conditions such as sedimentation rate, substrate features, ecosystem stability, competition, and especially food availability were also considered as controlling the depth distribution of benthic organisms (Baas et al., 1998). Ichological analysis of Late Quaternary sediments from the southwestern Iberian margin allows the recognition of several ichnocoenoses characterized by a variable record of indistinct bioturbation. *Planolites*, *Thalassinoides*, *Chondrites*, *Trichichnus*, and *Zoophycos* were related to bottom-water environmental conditions (bottom-water oxygenation and particulate organic matter content) linked to Mediterranean Outflow Water strength for the past ~34 kyr, involving climatic events such as the Younger Dryas, Termination 1, and Heinrich Stadials 1, 2, and 3 (Löwemark et al., 2004a).

In the studied sections, millennial-scale climatic events have different effects on the macrobenthic tracemaker community, as revealed by changes in the abundance and diversity (appearances and disappearances) of the trace fossil assemblage (Fig. 7). In the context of generally good environmental conditions during Termination 1, interpreted by dominance of *Thalassinoides* and *Planolites*, slightly darker sediments with gradual contacts could be associated with slight changes during the Younger Dryas and HS 1. However, these events have only minor incidence on the macrobenthic tracemaker community with the appearance of *Zoophycos* (observed in the darker sediments and/or in the lighter sediments below), probably reflecting decreasing oxygenation and increasing food availability associated with comparatively higher export productivity. Short climatic events related to Terminations 2 and 4 have comparatively higher incidence on the macrobenthic tracemaker community. Heinrich Stadial 11 and IRE 10.1 reveal an impoverishment of the macrobenthic tracemaker assemblage, but a higher abundance of *Zoophycos*. Both short climatic events could reflect important diminution in oxygenation (dysaerobic environment) and eutrophic conditions associated with high export productivity. These unfavorable conditions were especially abrupt and marked during development of IRE 10.1, as reflected by the sharp contact and the appearance of *Chondrites*.

The presence of *Nereites*, mainly located just prior to darker sediments, is of particular importance. *Nereites* has been interpreted as restricted to soft to soupy, oxygenated sedimentary environments, above the redox boundary, near the sediment surface, and feeding on microbes that occur in high concentrations (Wetzel, 2002). Their appearance could indicate the first inputs of organic matter at the surface of an oxygenated substrate, during the initial phases of short climatic events such as the YD, HS 1 and HS 11. In the course of these short climatic events an increase in detrital input occurs, associated with higher organic matter content and lower oxygen conditions, resulting in the disappearance of *Nereites* producers and favoring the presence of *Zoophycos* and *Chondrites* tracemakers. Löwemark et al. (2012) recognized the disappearance of *Nereites* during glacial intervals, suggesting either decreased food flux or decreased water oxygenation or a combination of both.

5.2. Benthic foraminifera

The choice and interpretation of the herein applied proxies are determined by a significant taphonomic overprint on the foraminiferal assemblages. The comparison of fossil and recent assemblages from U1385 indicates the loss of almost all epifaunal agglutinated foraminifera due to taphonomic processes shortly after deposition, thus compromising quantitative proxy methods (see Grunert et al., submitted for publication this volume, for information on the mudline samples and a detailed discussion). However, the comparison also suggests that certain selected proxies still reflect qualitative changes in trophic conditions (hBFAR, intermediate and deep infaunal taxa) and oxygenation (miliolids, deep-infaunal taxa) despite the taphonomic bias.

Nonetheless, an underrepresentation of oligotrophic and/or oxic conditions in the records should be considered due to the loss of epifaunal taxa (Jorissen et al., 2007).

Proxy records of interglacial intervals show the greatest similarities between the data-sets. Low hBFAR values, deteriorating miliolid abundances following the inception of interglacial conditions, and the mere absence of intermediate and deep infaunal taxa suggest oligotrophic to mesotrophic conditions at the sea-floor and generally improved ventilation. In particular during MIS 1, conditions seem to resemble present-day conditions (Phipps et al., 2012). In contrast, proxy records of glacial intervals show significant differences between the data-sets regarding hBFAR values and the abundances of intermediate and deep infaunal taxa. While mesotrophic conditions are inferred for glacial stages MIS 2 and MIS 10, strongly elevated hBFAR values suggest eutrophic conditions for MIS 6. Oxygenation depletion towards suboxic conditions seems to be more severe during MIS 2 and MIS 6 than MIS 10.

Considerable differences characterize the short-term stadial events associated with the glacial terminations (Fig. 7). The lowest miliolid abundances are paralleled by the highest abundances of deep infaunal taxa of all samples and indicate strongly reduced ventilation during HS 1. Low hBFAR values and the dominance of hyaline assemblages by deep infaunal taxa potentially indicate increased input of refractory organic matter through ice-rafting over fresh organic matter. Comparably improved conditions are suggested for the early stage of the YD. However, the YD is represented by only one sample and a more significant reduction in ventilation has been suggested in previous studies (Baas et al., 1998).

The more extended HS 11 interval is characterized by different phases that correlate with sediment color. In its early stage, the significant decrease in hBFAR and a minor peak in miliolid foraminifera indicate oligotrophic to mesotrophic conditions, with improved oxygenation compared to HS 1. The middle part of the stadial, corresponding to the black interval, is characterized by a strong increase in hBFAR paralleled by an increase in intermediate infaunal taxa, indicating elevated export productivity. Finally, in its late phase, the contrasting strong increase in miliolids and decrease in hBFAR indicates the re-establishment of better ventilated conditions.

IRE 10.1 is different as it shows an increase in hBFAR over the course of the stadial culminating in the black interval, indicating a significant increase in export productivity. At the same time, miliolid, intermediate and deep infaunal taxa are rare and equally abundant, potentially reflecting intermediate oxic conditions. IREs 10.2 and 10.3, not apparent from sediment color and solely inferred from Ca/Ti data, show low hBFAR values, increased miliolid abundances and rare abundances of deep infaunal taxa, suggesting oligotrophic to mesotrophic conditions and improved ventilation. However, these events are only represented by one sample each, making an interpretation difficult.

All three data-sets share the occurrence of a significant temporary increase in the abundance of miliolid foraminifera following the stadial events that indicate a significant improvement of ventilation in their aftermath.

5.3. Integrative analysis; the macro- and microbenthic response

Food and oxygen availability has been identified as the main factors determining the macro- and microbenthic community structures of deep-sea environments (Jorissen et al., 2007; Uchman and Wetzel, 2011; Wetzel and Uchman, 2012). This is clearly reflected by the co-variance of major changes in Ca/Ti-data, sediment color, trace fossil assemblages and benthic foraminiferal proxies. The independent, yet complementary records also validate the identification of the foraminiferal proxies as useful indicators of qualitative changes in oxygen and food availability despite a taphonomic bias (Grunert et al., submitted for publication this volume).

The integration of the complementary records and their comparison with previous studies on the western Iberian Margin show that major

changes in the local deep-sea environment across glacial terminations might be best understood in the context of paleoceanographic changes in the NE Atlantic as a whole. Macro- and microbenthic data reveal similarities and differences in the response to paleoenvironmental changes across Terminations 1, 2, and 4, and the involved short-term climatic events.

The results for Termination 1 are in agreement with previous studies that relate the deterioration of oxic conditions at the sea-floor during HS 1 to a significantly weakened AMOC and the increased influence of southern sourced water (e.g., Skinner et al., 2003; McManus et al., 2004; Skinner and Shackleton, 2004; Voelker and De Abreu, 2011). Thus, darker sediments are characterized by benthic foraminifera assemblages consisting of the lowest miliolid and the highest deep infaunal taxa abundances, while appearance/dominance of *Zoophycos* is the main ichnological feature. Similarly, with decreasing oxygenation and increasing food availability during the YD favor appearance of *Zoophycos* observed in the darker sediments and/or in the lighter sediments below. Sampling limitations inhibit a conclusive interpretation of the benthic foraminifera record.

Less information is available for Terminations 2 and 4, for which the new data suggest some significant differences to Termination 1, as well as a variable response of macro- and microbenthic communities. Most importantly, benthic foraminifera and sediment color suggest that oxygen depletion seems to be less significant in these periods while changes in export productivity leave a major imprint on the records. Increased productivity for Terminations 2 and 4 compared to Termination 1 has been previously suggested for the Iberian Margin by Thomson et al. (2000). In this context, the higher abundances of *Zoophycos* in the dark intervals of HS 11 and IRE 10.1 coincide with strong peaks in hBFAR values, significant lows in miliolids and lower abundance of deep infaunal taxa compared to HS 1. This indicates that significantly increased accumulation of organic matter as the main driving force. This supports the proposed relationship between *Zoophycos*-rich intervals and increasing organic material reaching the sea floor at the scale of glacial/interglacial periods (Löwemark et al., 2006; Rodríguez-Tovar et al., 2011). The presence of *Chondrites*, sometimes related to organic-rich sediments (Vossler and Pemberton, 1988), associated to IRE 10.1 could confirm this interpretation, but we can't discard the impoverishment of pore-water conditions deep within the sediment considering that the *Chondrites* tracemaker is commonly considered as tolerant to very low oxygen environments (i.e., Ekdale and Bromley, 1984).

In short, as a general rule macro- and microbenthic communities show a similar response to the variable incidence of food and oxygen availability associated to short-term climatic events registered during Terminations 1, 2, and 4. Differences between both communities could be determined by a variable sensitivity to the involved paleoenvironmental parameters.

6. Conclusions

The presented research reveals the usefulness of an integrative analysis of trace fossils and benthic foraminifera data to improve characterization of Terminations 1, 2 and 4, as revealing the response of the macro- and microbenthic habitats to the involved paleoenvironmental changes.

Food and oxygen availability has been identified as the main factor determining variations in the macro- and microbenthic community structures across glacial terminations. Variations in these paleoenvironmental parameters are determined to varying degrees by changes of AMOC intensity and the influence of southern sourced waters as well as variations in productivity along the western Iberian Margin.

The presence of a deep-sea multi-tiered tracemaker community, consisting of biodeformational structures, *Chondrites*, *?Nereites*, *Palaeophycos*, *Planolites*, *Thalassinoides*, and *Zoophycos*, with variations in abundance and diversity but not disappearance, suggests generally well-oxygenated bottom and pore-water conditions during

interglacial as well as glacial intervals, with punctual decrease in oxygenation. At the glacial/interglacial scale, variations in color and in the trace fossil composition are related to available food, associated to export productivity, and oxygenation.

Trace fossil and benthic foraminiferal communities show a similar response to the variable incidence of food and oxygen availability associated with short-term climatic events registered during Terminations 1, 2, and 4. Termination 1 shows a deterioration of oxic conditions and increasing food availability during the YD and HS 1, as revealed by appearance/dominance of *Zoophycos*, together with the lowest miliolid and the highest deep infaunal taxa abundances. Short-climatic events (HS 11, IRE 10.1) of Terminations 2 and 4 are characterized by a major incidence of export productivity and accumulation of organic matter with respect to depleted oxygenation, especially affecting microbenthic habitat. This is revealed by higher abundances of *Zoophycos* in the dark intervals of HS 11 and IRE 10.1 in coincidence with strong peaks in hBFAR values, significant lows in miliolids and lower abundance of deep infaunal taxa. At the macrobenthic habitat, the presence of *Chondrites* associated to IRE 10.1 could also indicate the impoverishment in water-pore conditions deep into the sediment.

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