



Response of macrobenthic and foraminifer communities to changes in deep-sea environmental conditions from Marine Isotope Stage (MIS) 12 to 11 at the “Shackleton Site”



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ABSTRACT

Integrative research including facies characterization, ichnological composition and foraminifer analysis has been conducted on cores from Site U1385 of the IODP Expedition 339 to evaluate the incidence of Marine Isotope Stage (MIS) 12 and MIS 11 on deep-sea environmental changes. Four color facies groups have been differentiated, showing variable transitions between them (bioturbated, gradual and sharp contacts). Trace fossil assemblage, assigned to the *Zoophycos* ichnofacies, consists of light and dark filled structures, with *Alcyonidiopsis*, *Chondrites*, *Nereites*, *Planolites*, *Spirophyton*, *Thalassinoides*, *Thalassinoides*-like structures, and *Zoophycos*. A deep-sea multi-tiered trace fossil community is interpreted, revealing predominance of well-oxygenated bottom and pore-waters, as well as abundance of food in the sediment for macrobenthic tracemaker community. Changes in environmental parameters are interpreted to be associated with significant variations in trace fossil distribution according to the differentiated intervals (A to M). Benthic foraminifer concentration in the sediments and variations of the planktonic foraminifer assemblages suggest significant changes in surface productivity and food supply to the sea floor since the ending of MIS 13 to the end of MIS 11 that could be correlated with the registered changes in facies and trace fossil assemblages. At the end of MIS 13 values of annual export productivity were very low, that together with the presence of light-color sediments and the continuous presence of light *Planolites* and *Thalassinoides*, reveal lower organic carbon flux to the bottom and high oxygen conditions (interval A). Afterwards the organic matter supply increased rapidly and remained very high until Termination V, determining an eutrophic environment, expressed by high benthic foraminifer accumulation rates, and reduced availability of oxygen, that correlate with the record of *Spirophyton* and *Zoophycos*, and the presence of *Chondrites*, observed in intervals B and D. Lower benthic foraminifer accumulation rates during MIS 11 suggest an oligotrophic environment at the bottom consistent with lower inputs of organic carbon, associated with high oxygen content of bottom waters that agrees with the lighter color of the sediments as well as by the continuous presence of light *Planolites* and *Thalassinoides* in the differentiated interval M. The evolution of the macrobenthic tracemaker community during MIS 12 and MIS 11 responds to major changes in bottom water ventilation probably linked to variations in deep water (North Atlantic) thermohaline circulation, determining variations in oxygen and food availability.

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1. Introduction

Glacial/interglacial climatic cycles occurring during the Quaternary have been extensively studied due to their incidence on variations in the atmosphere/ocean dynamics and on the involved biota, including

hominids. From several glacial/interglacial episodes, some of them are of special interest, as occurs with those corresponding with the Marine Isotope Stage (MIS) 12 and 11 (MIS 12 and MIS 11). The time interval involving MIS 12 and MIS 11 is considered one of the most extreme glacial and interglacial periods of the middle Pleistocene. The glacial MIS 12 is characterized by strong cold conditions, and the interglacial MIS 11 is one exceptionally long interglacial warm period. The Mid-Brunhes Event (MBE), close to the MIS 12/MIS 11 transition, at around 450 ka BP, a climatic transition between MIS 13 and MIS 11, separates 2 significantly different climatic modes, with interglacials characterized

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by only moderate warmth previous to this event (early Middle Pleistocene interglacials; 780–450 ka), and interglacial characterized by greater warmth after this event (Middle and Late Pleistocene interglacials; after 450 ka) (i.e., Candy et al., 2010). The transition MIS 12/11, corresponding with Termination V, is the longest glacial Termination of the past 450 ka, having major incidence for the biogeography and human occupation (Candy et al., 2014).

MIS 11 is considered as one of the appropriate climate analogs for the Holocene, being of special interest even for the analysis of future climate variations, which is reflected by the amount of information obtained on this episode (see two consecutive reviews by Droxler et al., 2003; Candy et al., 2014). All this information allows a detailed characterization of MIS 11, the warm climatic features, and the induced changes in the atmosphere/ocean dynamics. Thus, according to the last revision by Candy et al. (2014), and references therein, several features of MIS 11 are the following: a) the warm episode MIS 11 consists of an interglacial (MIS 11c) and several interstadial and stadial events (i.e., MIS 11a and MIS 11b), with differences in the number and magnitude according to the studied records, b) MIS 11c is a long warm climate period that lasted for about 25–30 ka, c) temperature data reveals that MIS 11 was an interglacial of relatively moderate warmth, similar to, or slightly cooler than the Holocene, and d) most of the evidences suggest that MIS 11c is characterized by sea levels significantly above those from the Holocene, even turnovers in fauna are consistent with prolonged period of lower sea levels at the beginning and middle part of MIS 11c.

Detailed analyses of MIS 11 and MIS 12 have been conducted in a number of studies on marine, ice core, lacustrine and terrestrial sequences, involving numerous biotic (i.e., pollen and foraminiferal assemblages) and abiotic (i.e., stable isotope and elemental chemistry) proxies, allowing interpretation of environmental parameters such as the global ice volume or sea surface temperatures. In this sense, as pointed out by Candy et al. (2014) for the identification of MIS 11 in British terrestrial record, terrestrial deposits contain numerous proxies

allowing interpretation of different environmental parameters, whereas ice and marine core records contain, frequently, a single proxy. In marine cores the usually applied biotic proxies are foraminiferal (benthic and planktonic) assemblages. In this sense, little attention has been focused on the ichnological record; being very scarce, near absent, the approaches are based on the study of the trace fossil assemblage (see Löwemark et al., 2006, 2012, on trace fossil assemblage studies including MIS 11 in the eastern Mediterranean Sea and Arctic Ocean, respectively). Here we present a detailed ichnological analysis of MIS 11 and MIS 12 on cores from IODP Expedition 339 Site U1385, in order to interpret changes in deep-sea environmental conditions, affecting the macrobenthic environment. Integration with information from benthic and planktonic foraminifers, allows integrative interpretations. Moreover, paleoceanographic implications will be assessed.

2. Site U1385 at IODP Expedition 339

IODP Site U1385 is located off the west Iberian Margin (37°34.285'N, 10°7.562'W; Fig. 1), on a spur, the Promontorio dos Principes de Avis, along the continental slope of the southwestern Iberian margin, at a water depth of 2578 m b.s.l. (Hodell et al., 2013a). This Site U1385, was drilled near the position of core MD01-2444 (Vautravers and Shackleton, 2006; Martrat et al., 2007; Skinner and Elderfield, 2007; Margari et al., 2010; Expedition 339 Scientists, 2013a; Hodell et al., 2013b), one of the cores retrieved from the SW Iberian Margin by the R/V Marion Dufresne in 1995, 1999 and 2011, including Core MD95-2042 (the “Shackleton Site”) used as a key archive to approach millennial-scale climate variability over the last glacial cycle (Shackleton et al., 2000, 2004). Site U1385 was drilled to create a marine reference section of sub-Milankovitch (millennial-scale) climate variability and changes in surface and deep-water circulation occurring during the Pleistocene (Expedition 339 Scientists, 2013a,b).

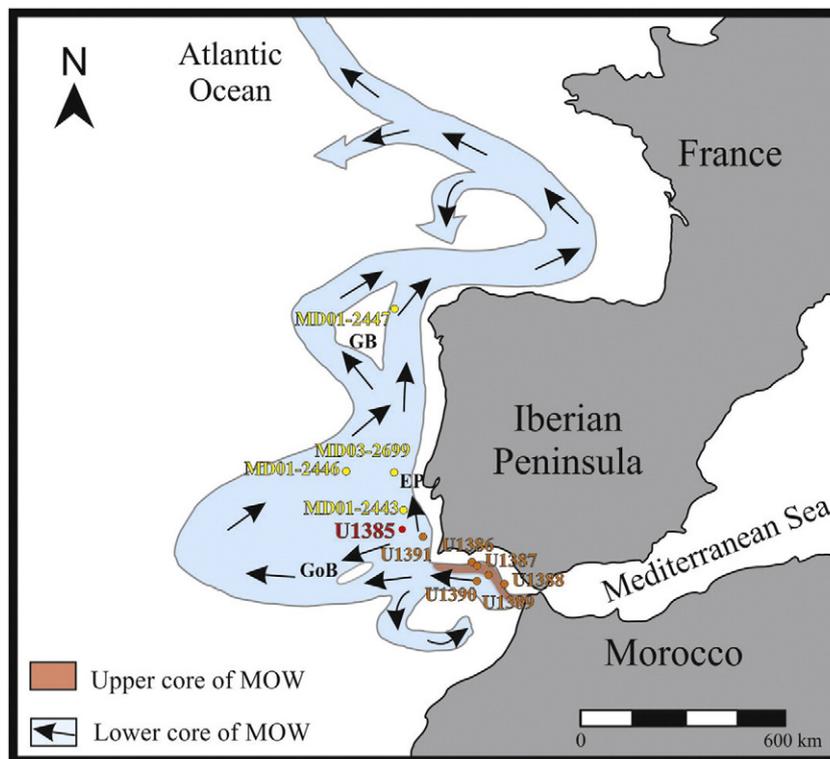


Fig. 1. General circulation pattern of the Mediterranean Outflow Water (MOW) (Expedition 339 Scientists, 2013b), with location of IODP Expedition 339 drill sites (red point for Site U1385 and orange points for the rest of sites), together with sites MD01-2447 (Desprat et al., 2005) in the North, MD01-2446 and MD03-2699 (Voelker et al., 2010) in the central, and MD01-2443 (de Abreu et al., 2005) in the South of the West Iberian Margin (blue points). Note: GB, Galicia Bank; EP, Extremadura Promontory; GoB, Goringe Bank.

At Site U1385 five Holes were cored, recovering a total of around 622 m of a uniform lithologic unit dominated by bioturbated calcareous muds and calcareous clays (Expedition 339 Scientists, 2013a,b), with no notable gaps or disturbed intervals to 166.5 mcd (Expedition 339 Scientists, 2013a; Hodell et al., 2013a). Recently a very low sedimentation rate, a condensed section in which the complete interval from 415 to 431 ka is compressed into 4 cm, has been recognized at the early MIS 11 (Hodell et al., 2015-in this issue; Sánchez-Goñi et al., submitted for publication). The site contains a complete record from the Holocene to 1.43 Ma (MIS 46), allowing a fine-tuning by correlation of millennial events to ice core and speleothem records for the last 800 ka (Hodell et al., 2013a, 2015-in this issue). High-resolution sampling at 1 cm intervals enables resolving millennial climate events, as well as glacial–interglacial cycles, including their corresponding Terminations.

Site U1385 is close to site MD01-2443 (Fig. 1; de Abreu et al., 2005) in the South of the West Iberian Margin, that yielded significant records of MIS 11 for the interpretation of the involved climatic changes. On this base, Site U1385 is of major interest to study MIS 11 and MIS 12.

3. Material and methods

The research has been conducted on Cores 7H-4 to 7H-1 from Hole U1385D (“Shackleton Site”). Facies characterization has been integrated with the analysis of trace fossils, and benthic/planktonic foraminifers.

Facies analysis is based on the study of lithological composition, type of contacts, and primary sedimentary structures, with special attention to stratigraphic variations. Digital image treatment allows recognition of variations in color, difficult to recognize based, exclusively, on visual observations (Dorador and Rodríguez-Tovar, submitted for publication). Ichnological analysis focused on trace fossil assemblages, including trace fossil composition, infilling material, cross-cutting relationships, tiering structure, and relative abundances. Ichnotaxonomical classification was conducted as the ichnogenus level, as usual for core analysis. Ichnological analysis consists of detailed observations of half-cut sections of the core in the IODP core repository at Bremen (Germany), together with the study of high-resolution images. Several techniques of digital image treatment to improve the trace fossil visibility were applied for ichnological characterization (Dorador and Rodríguez-Tovar, 2014; Dorador et al., 2014a,b; Rodríguez-Tovar and Dorador, 2014, in press).

Sampling for export productivity (Pexp) reconstruction and isotope studies was performed every 20 cm providing an estimated average 2 ka resolution record, and for counts on both benthic and planktonic foraminifers sampling was performed at an average 4.6 cm separation, providing an estimated average 0.79 ka resolution. Samples (1 cm-thick) were freeze-dried, weighed and washed over a 63 µm mesh sieve. The >63 µm residue was dried, weighed and sieved again to separate and weigh the >150 µm fraction. Counts on planktonic and benthic foraminifer taxa were conducted on this sediment fraction, which was successively split until a minimum of 300 specimens were obtained. Planktonic species were used to reconstruct Pexp with the modern analog technique (MAT) (Hutson, 1980) and the modern analog database compiled by Salgueiro et al. (2010). Stable isotopes were measured on the planktonic foraminifer *Globigerina bulloides* picked from the 250 to 355 µm size fraction and the benthic foraminifer *Cibicides wuellerstorfi* from the >212 µm fraction (see Hodell et al., 2015-in this issue). Isotopic measurements were performed at the Godwin Laboratory (University of Cambridge, Cambridge, United Kingdom) on a VG SIRA mass spectrometer with automatic carbonate preparation system and calibrated to the Vienna Peedee Belemnite (VPB) standard, allowing an analytical precision better than 0.08‰.

The age model of the studied section is based on the correlation of the benthic oxygen isotope record to the global benthic LR04 isotope stack (Lisiecki and Raymo, 2005; see Hodell et al., 2015-in this issue).

4. Results

4.1. Facies characterization

As in general for the entire Site U1385, the studied interval consists of bioturbated calcareous muds and calcareous clays (Expedition 339 Scientists, 2013a,b). Primary sedimentary structures (i.e., lamination) are near absent; occasionally horizontal lamination into the darker/black intervals is observed (Expedition 339 Scientists, 2013a,b). Moreover, no significant changes in grain size are observed. In this general, homogenized, pattern, clear differentiations can be recognized, mainly related to variations in color, probably associated with the organic matter content, usually linked to changes in the trace fossil assemblage (see below). These variations in color can be observed directly on cores, but are even more evident when digital image treatment is applied (Dorador and Rodríguez-Tovar, submitted for publication). Thus, mainly according to variations in color, upper and lower contacts, and ichnological composition, several intervals have been differentiated (A to M); see Table 1 and Fig. 2 for a detailed characterization of the intervals. These intervals can be grouped into four color groups, from light tone gray/greenish, middle dark tone gray/greenish, very dark tone gray/greenish and dark/black, showing variable transitions between them (bioturbated, gradual and sharp contacts). From here we will refer to gray tone in substitution for gray/greenish.

As a general picture, light tone gray sediments are dominant, mainly registered and thicker in the lower/middle part of Core U1385D-7H-4 (interval A), and in the upper part of U1385D-7H-2 and the entire U1385D-7H-1 (interval M). Another thinner light interval is registered at the base of Core U1385D-7H-3 (interval E). In general these intervals show a relatively scarce trace fossils filled with light material.

At the opposite, dark/black intervals are scarce and thin, being located exclusively in the middle and upper parts of Core U1385D-7H-4 (intervals B and D). These intervals are characterized by dark trace fossils, which occasionally are also observed downward into the upper parts of the lighter intervals below (intervals A and C).

Middle and dark gray tone intervals are dominant in Cores U1385D-7H-2 and 3 (intervals F, G, H, I, J, K, and L), and are also registered in the upper part of Core U1385D-7H-4 (interval C). Middle gray tone intervals (intervals C, G, I, and lower K) mainly consist of a well developed light trace fossil assemblage on a mottled background. In the very dark tone gray intervals (intervals F, H, J and upper K) light and dark trace fossils are observed on a light/dark mottled background. Two intervals (intervals J and L) into the dark gray intervals show slight differences in color, with the presence of grayish/blue/pink sediments.

4.2. Ichnological analysis

Digital image treatment allows a clear differentiation between biodeformational structures and trace fossils (Dorador and Rodríguez-Tovar, 2014; Dorador et al., 2014a,b; Rodríguez-Tovar and Dorador, 2014, in press). Biodeformational structures, showing undifferentiated outlines and the absence of a defined geometry, which impede an ichnotaxonomical classification (see Uchman and Wetzel, 2011; Wetzel and Uchman, 2012), are registered as a mottled background, with color mixture and predominance of lighter or darker sediments related to the recognized intervals. Trace fossils show a variable degree of diffusiveness, from diffuse to discrete structures, as well as variable infilling material, from light to dark, being clearly distinguished from the host sediment based on their characteristic shape, although, sometimes, this differentiation is difficult.

4.2.1. Trace fossil assemblage

In general, a relatively diverse trace fossil assemblage was recognized, including structures filled with light and dark sediments (light and dark filled structures), consisting of *Alcyonidiopsis*, *Chondrites*, *Nereites*, *Planolites*, *Spirophyton*, *Thalassinoides*, *Thalassinoides*-like structures, and

Table 1
Differentiated intervals with lithological and ichnological features.

Interval (thickness/location)	Facies color	Contacts	Background	Light traces	Dark traces	Cross-cutting relationships
A (75 cm): from 150 to around 75 cm of U1385 7H4	Light tone gray	Bioturbated upper contact	Mottled background	Diffuse <i>Thalassinoides</i> (ITh) & <i>Planolites</i> (IPI)	<i>Chondrites</i> (dCh) from 89 to 75 cm	dCh crosscutting ITh & IPI
B (14 cm): from 75 to 61 cm of U1385 7H4	Dark/black	Gradual upper contacts	Mottled background	<i>Thalassinoides</i> from 67 to 61 cm	Dominant <i>Chondrites</i> (dCh), <i>Planolites</i> (dPI) & <i>Thalassinoides</i> (dTh) at the base	dCh crosscutting dTh & dPI
C (43 cm): from 61 to 18 cm of U1385 7H4	Middle dark tone gray	Bioturbated upper contact	Mottled background	Diffuse <i>Thalassinoides</i> (ITh) and <i>Planolites</i> (IPI)	Dominant <i>Chondrites</i> (dCh), <i>Planolites</i> (dPI), <i>Thalassinoides</i> (dTh), <i>Spirophyton</i> (dSp) & <i>Zoophycos</i> (dZo)	Dark traces crosscutting light traces & dCh crosscutting dPI, dTha & dSp
D (13 cm): from 18 to 5 cm of U1385 7H4	Dark/black	More or less shap upper contact			Dominant <i>Chondrites</i> (dCh) & <i>Zoophycos</i> (dZo). <i>Thalassinoides</i> (dTh) at the base	dCh crosscutting dTh
E (35 cm): from 5 cm of U1385D 7H4 to 119 cm of U1385 7H3	Light tone gray	Sharp upper contact, channel morphology	Mottled background, especially on top	Discrete, dominant <i>Thalassinoides</i> (ITh), and few <i>Planolites</i> (IPI)		
F (58 cm): from 119 to 61 cm of U1385 7H3	Very dark tone gray, with increasing darker upward	Sharp upper contact	Mottled background	<i>Planolites</i> (IPI), on top	<i>Planolites</i> (dPI) & <i>Thalassinoides</i> (dTh), then <i>Zoophycos</i> (dZo). Probable <i>Thalassinoides</i> -like (dTh-1)	dZo cross-cutting dTh on top
G (74 cm): from 61 of U1385 7H3 to 137 cm of U1385 7H2	Middle dark tone gray, with a thick (56 cm) darker horizon at the middle part	Bioturbated upper contact	Mottled background at the lighter parts	<i>Thalassinoides</i> (ITh) and <i>Planolites</i> (IPI) as exclusive in the lighter part, and also in the upper part of the darker horizon	Diffuse, abundant <i>Zoophycos</i> (dZo), but also <i>Thalassinoides</i> (dTh-1), and probable <i>Planolites</i> (dPI) in the darker horizon	dZo cross-cutting dTh dCh cross-cutting the rest of traces
H (33 cm): from 137 to 104 cm of U1385 7H2	Very dark tone gray	Bioturbated upper contact	Mottled background	Probable <i>Thalassinoides</i> (ITh) on top	Dominant, near exclusive, <i>Zoophycos</i> (dZo)	
I (12 cm): from 104 to 92 cm of U1385 7H2	Middle dark tone gray	Sharp/bioturbated upper contact? Minor erosion?	Mottled background	<i>Planolites</i> (IPI) & probable <i>Thalassinoides</i> (ITh)	<i>Planolites</i> (dPI), <i>Thalassinoides</i> (dTh) & dominant, diffuse, <i>Zoophycos</i> (dZo)	dZo cross-cutting dPI and dTh
J (18 cm): from 92 to 74 cm of U1385 7H2	Very dark grayish/blue/pink	Mixture of sediments Sharp/bioturbated upper contact?	Mottled background	<i>Thalassinoides</i> (ITh) & <i>Planolites</i> (IPI)	Diffuse <i>Planolites</i> (dPI) <i>Thalassinoides</i> , (dTh) and <i>Zoophycos</i> (dZo)	dZo cross-cutting dTh
K (47 cm): from 74 to 27 cm of U1385 7H2	Middle to very dark tone gray/pink	Darker color upward. Sharp upper contact?	Mottled background	Diffuse <i>Planolites</i> (IPI) & <i>Thalassinoides</i> (ITh)	Diffuse <i>Zoophycos</i> (dZo)	
L (12 cm): from 27 to 15 cm of U1385 7H2	Very dark grayish/blue/pink	Gradual contact to lighter color & decreasing bioturbation	Mottled background	<i>Thalassinoides</i> (ITh) & <i>Planolites</i> (IPI), sinuous traces	<i>Planolites</i> (dPI), sinuous, bifurcate traces	
M (165 cm): from 15 cm of U1385D 7H2 to 0 of U1385D 7H1	Light tone gray with darker intercalation	Gradual alternations in color	Mottled background	Diffuse <i>Planolites</i> (IPI), <i>Thalassinoides</i> (ITh) & local <i>Nereites</i> (INe)	Diffuse <i>Planolites</i> (dPI) and <i>Thalassinoides</i> (dTh), probably <i>Zoophycos</i> (dZo),	

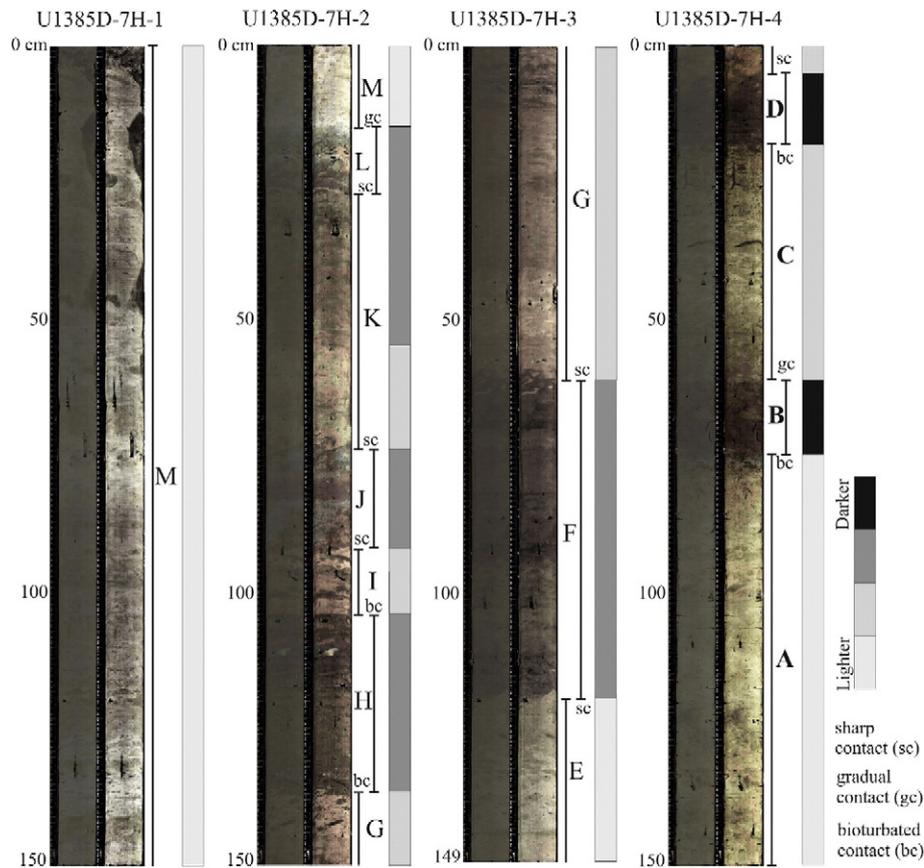


Fig. 2. Studied cores from Hole U1385D-7H-1 to U1385D-7H-4, showing the recognized intervals A to M, contacts, and color differentiation. Left and right parts of the cores before and after digital image treatment.

Zoophycos (Figs. 3, 4). Moreover, undifferentiated sinuous traces have been observed in interval L. Light infilling traces refer to those light traces slightly darker than the light host sediment. Light infilling *Planolites* and *Thalassinoides* are the dominant, near exclusive, ichnotaxa, whereas light *Nereites* are locally observed (Fig. 3). Dark infilling traces can be produced into the middle and very dark tone gray intervals or into the dark/black sediments. In the dark trace fossil assemblage *Zoophycos* is dominant, *Planolites* and *Thalassinoides* are frequent, while *Alcyonidiopsis*, *Chondrites*, *Spirophyton*, and *Thalassinoides*-like structures are rare (Fig. 4).

The trace fossil assemblage can be assigned to the *Zoophycos* ichnofacies, typical for deep-sea environments, as was previously proposed for Site U1385 (Rodríguez-Tovar and Dorador, 2014). As a general rule, dark trace fossils are registered as cross-cutting light ones. Into the dark trace fossil assemblage, usually *Chondrites* and *Zoophycos* are observed cross-cutting the rest of traces, such as *Planolites*, *Spirophyton* and *Thalassinoides*. A brief description of the differentiated ichnotaxa is as follows:

Alcyonidiopsis corresponds to a single elongate cylinder, slightly oblique, dark filled, 30 mm long and 6 mm wide, showing a pelloidal-like outline (see Uchman, 1999; Rodríguez-Tovar and Uchman, 2010 for interpretation).

Chondrites is generally observed as dense clusters of circular to elliptical spots, and short tubes, filled with dark sediment; occasionally branching. Mainly small forms (<1.5 mm wide) are observed that could correspond to *Chondrites intricatus* (Brongniart, 1823).

Nereites consists of small-medium size (2–5 mm diameter) circular to elliptical forms, with a dark-filled internal zone surrounded by a light filled envelope, observed as closed (paired) structures in horizontal planes.

Planolites occurs as unlined, unbranched, and mainly as circular to subcircular cylindrical tubular forms (4–7 mm in diameter, 5–2.5 mm

in length). It is largely registered as horizontal or slightly oblique, filled with light or dark sediment, with a variable grade of diffusiveness. Fill is structureless, with different lithologies from the host rock.

Spirophyton is registered as a single trace consisting of a central, axial, J-shaped shaft (around 8 cm high), with alternating horizontal structures (around 2–3 mm wide and 20 mm long) extending from the axial shaft. Spreite has not been observed. Similar to *Zoophycos*, it differs by the small size and shape of horizontal structures.

Thalassinoides is observed as large, oval spots, circular to subcircular (6–12 mm wide), together with straight or slightly winding, horizontal to oblique smooth cylinders (20–43 mm long), showing a variable grade of diffusiveness. Structures are filled with light or dark sediment. Occasionally, mainly light filled *Thalassinoides*, are observed in clusters of circular to elliptical spots, corresponding to variable cross-sections of branching burrow systems.

Thalassinoides-like structures occur locally as circular to subcircular sections, 6–12 mm wide, filled with dark sediment. The shape is similar to *Thalassinoides*, but showing a variably developed irregular wall, resembling *Ophiomorpha*.

Zoophycos, is registered as repeated, more or less horizontal, spreiten structures (2–8 mm wide), consisting of alternating dark and light material. A variable degree of diffusiveness is observed, determining a more or less clear differentiation of the lamellae into the lamina. Frequently several horizontal traces (up to 6), probably belonging to a unique structure, are observed, evidencing a depth of penetration at least of 16 cm.

4.2.2. Distribution

The trace fossil assemblage shows clear variations along the differentiated intervals that can be related to the features (color) of the host sediment (Fig. 5). Light trace fossil assemblage, consisting of *Planolites*

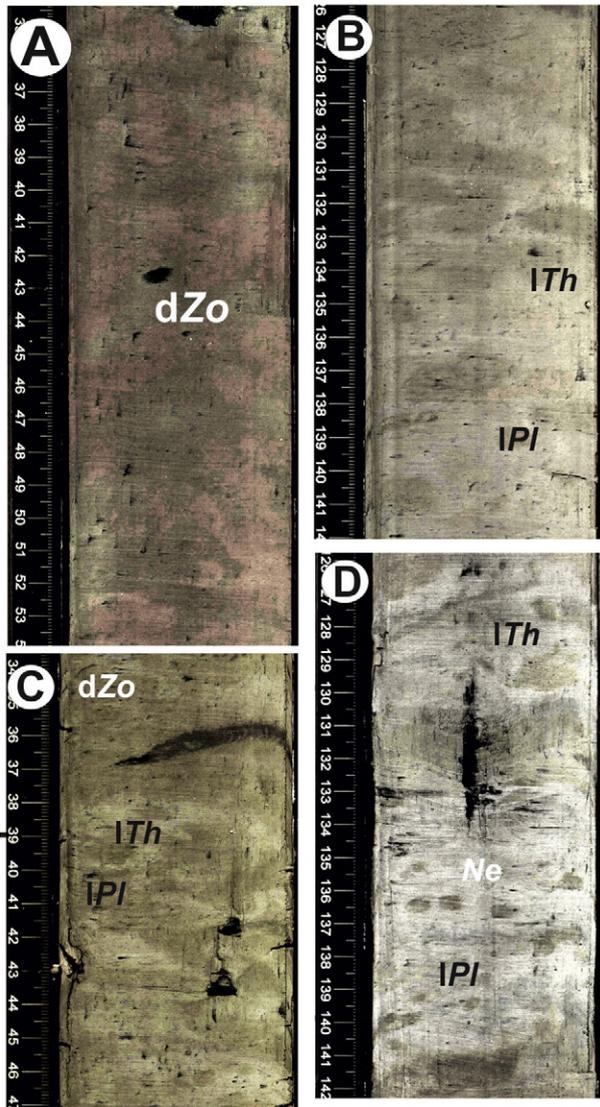


Fig. 3. Light trace fossils and local dark *Zoophycos* from gray (light, middle and dark tones) intervals. (A) Diffuse dark *Zoophycos* (dZo) from dark tone gray interval K (U1385D-7H-2) on a well-developed mottled background. (B) Light *Thalassinoides* (lTh) and *Planolites* (lPl) from light tone gray interval E (U1385D-7H-3). (C) Light *Thalassinoides* (lTh) and *Planolites* (lPl), and dark *Zoophycos* (dZo) from middle tone gray interval C (U1385D-7H-4). (D) Light *Thalassinoides* (lTh) and *Planolites* (lPl), and *Nereites* (Ne) from light tone gray interval E (U1385D-7H-1).

and dominant *Thalassinoides*, is registered in most of the intervals, except, in the dark/black interval D, being dominated by light and middle gray tone intervals (A, C, E, G, I and M). However, in the light tone intervals (A and M), this light trace fossil assemblage is comparatively scarce, and the mottled background is less developed. The light trace fossil assemblage represents the bioturbation of tracemakers during deposition of the lighter host sediment. The dark trace fossil assemblage consists of frequent *Planolites* and *Thalassinoides*, associated with middle and very dark gray tone intervals, reflecting the mixture of phases of sedimentation corresponding to different colors; bioturbation by shallowest and shallow tier organisms produces the observed mixture of colored sediment. These trace dark *Planolites* and *Thalassinoides* are also observed in intervals showing a more or less developed alternation, not mixture, of colored sediments, such as in interval M. Occasionally, this assemblage is also registered at the base of black/dark color sediment (intervals B and D), probably reflecting a progressive, gradual, change. *Zoophycos* is the dominant dark trace fossil, observed in middle and very dark gray intervals, as well as in the black/dark ones. This trace

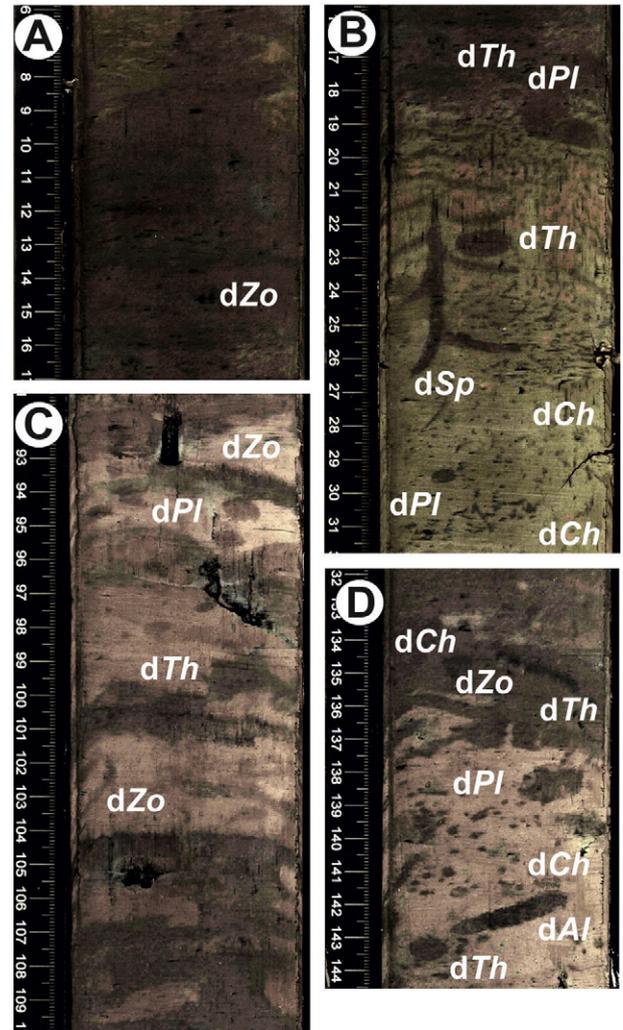


Fig. 4. Dark trace fossils from gray (middle and dark tone) and dark/black intervals. (A) Dark *Zoophycos* (dZo) from the dark/black interval D (U1385-7H-4). (B) Dark *Chondrites* (dCh), *Planolites* (dPl), *Spirophyton* (dSp) and *Thalassinoides* (dTh) from the upper part of the middle gray tone interval C transition to dark/black interval D (U1385-7H-4). (C) Dark *Thalassinoides* (dTh) and dark *Zoophycos* (dZo) from the upper part of dark gray tone interval H to middle gray tone interval I (U1385-7H-2). (D) Dark *Alcyonidiopsis* (dAl), *Chondrites* (dCh), *Planolites* (dPl), *Thalassinoides* (dTh) and *Zoophycos* (dZo) from the upper part of the middle gray tone interval G transition to dark gray tone interval H (U1385-7H-2).

originated during deposition of darker sediments, probably revealing latter phases of bioturbation by the dark trace fossil community, after *Planolites* and *Thalassinoides* producer. *Chondrites* and *Spirophyton* are mainly related to the dark/black intervals (B and D), are even located downward in the lighter intervals below, and associated with the particular environmental conditions of these dark (black) sediments.

4.3. Micropaleontological analysis

Benthic oxygen-isotope values have been used to identify MIS 13 to MIS 11 in the sediment cores. Based on the benthic oxygen isotope record glacial Termination V was recorded in IODP Site U1385 at around 55.70 crmcd. The previously described intervals A to M correspond to the final stages of MIS 13 (intervals A, B and half of the C), MIS 12 (half of interval C, intervals D–L and the first 20 cm of interval M), and early MIS 11 (the rest of interval M) (Fig. 6).

Analysis of the planktonic/benthic foraminifer ratio (Fig. 6d) reveals that planktonic microfauna is more abundant, in general, during interglacial conditions. However, during early glacial substage MIS 12b (and coinciding with interval G) elevated percentages of planktonic

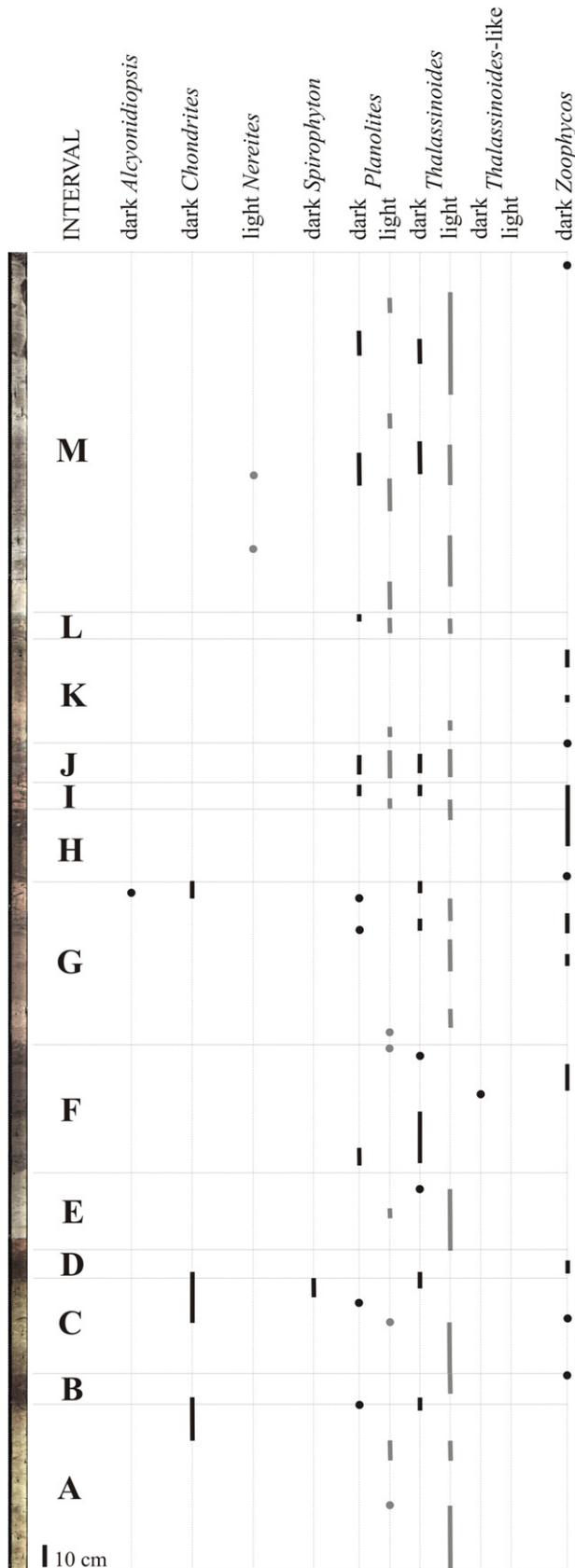


Fig. 5. Distribution of light and dark trace fossils in the studied cores from Hole 1385D-7H-4 (bottom) to U1385D-7H-1 (top), according to the differentiated intervals A to M.

foraminifers were also recorded. These high planktonic/benthic values are mainly due to low benthic production, expressed both by concentration (Fig. 6e) and accumulation rate (Fig. 6f). Benthic accumulation rate (measured in number of tests per cm^2 and ka) is higher during the glacial stage, especially at the beginning and end of the stage. The extraordinarily high number of benthic foraminifers per mass of sediment (Fig. 6e) during the glacial maximum MIS 12a, is probably due to low accumulation of other sedimentary components at this time (Fig. 6). Export productivity (P_{exp}) is low during MIS 11 and much higher in MIS 12, especially in the early part of this stage, as well as during the last part of MIS 13. In consequence, during the interglacial periods MIS 11 and MIS 13 low P_{exp} at the surface corresponds to low concentration of benthic foraminifers at the sea floor (Fig. 6e, h). By contrast, high P_{exp} in MIS 12 is linked, in general, to higher benthic foraminifer production.

5. Interpretation and discussion

5.1. Facies distribution and trace fossil composition

Major factors determining ichnological features (i.e., abundance, composition and diversity of trace fossil assemblages) in a deep-sea setting are food availability, bottom and pore-water oxygenation, substrate consistency, and rate of sedimentation (Wetzel, 1991; Uchman et al., 2008, 2013a,b; Rodríguez-Tovar et al., 2009a,b; Rodríguez-Tovar and Uchman, 2010; Uchman and Wetzel, 2011; Wetzel and Uchman, 2012; Rodríguez-Tovar and Reolid, 2013; Rodríguez-Tovar and Dorador, 2014). In the case study, the generalized mottled background, together with the observed trace fossil assemblage, reveals a deep-sea multi-tiered trace fossil community, interpreted as revealing predominance of well-oxygenated bottom and pore-waters, as well as abundance of food in the sediment for macrobenthic tracemaker community, as previously interpreted for Site U1385 (Rodríguez-Tovar and Dorador, 2014). In the generalized context of relatively good environmental conditions for the macrobenthic habitat, several changes can be interpreted, determining variations in facies and ichnological features.

Lighter sediments, as those represented by intervals A, E and M, are characterized by a relatively poorly developed mottled background together with light *Thalassinoides* and *Planolites*. *Thalassinoides* and *Planolites*, as facies-crossing forms, are found in a great variety of marine environments, usually associated with oxygenated sediments. *Thalassinoides* is related to soft but cohesive sediments (see Fürsich, 1973; Ekdale et al., 1984; Ekdale, 1992; Schlirf, 2000), and *Planolites*, an actively filled burrow, is interpreted as a pascichnion in shallow tiers (see Pemberton and Frey, 1982; Keighley and Pickerill, 1995 for discussion). Thus, good environmental conditions (mainly bottom and pore-water oxygenation, and food availability) can be interpreted, at least in the upper centimeters of the substrate, where shallowest and shallow tier communities are developed. Variations in the relative abundance of light *Planolites* and *Thalassinoides*, as well as in the diffusiveness can correspond with the rate of deposition and the firmness. The presence of dark *Planolites* and *Thalassinoides*, together with the local record of *Nereites* at interval M could reveal fluctuations in the organic matter content probably associated with variations in the detrital input and in the surface export productivity as revealed by planktonic foraminifer-reconstructed P_{exp} (Fig. 6h); the latter is interpreted as a shallow tier, pascichnia structure, in deep-marine, low energetic, oxygenated, environments (Uchman, 1995; Mángano et al., 2002; Wetzel, 2002; Löwemark et al., 2012), associated with increase food flux, feeding on microbes that occur in high concentrations (Wetzel, 2002; Löwemark et al., 2012).

Dark/black sediments, as represented by intervals B and D, reveal significant changes in the environmental conditions. The presence of dark *Planolites* and *Thalassinoides* at the base of the intervals, and then *Zoophycos* and dominant *Chondrites* could be interpreted as a gradual deterioration of the environmental conditions, probably related to increase in the organic matter content and decreasing oxygenation

more favorable for *Zoophycos* and *Chondrites* tracemakers. Both, *Zoophycos* and *Chondrites* are deep tier feeding structures. In general, *Zoophycos* producer has been related to variations in energy, sedimentation rate, food content, or bottom-water oxygenation; its relative independence of substrate features would allow for colonization of sediments with comparative low oxygenation, or even to collect food particles from the sea floor (e.g., Löwemark and Schäfer, 2003; Rodríguez-Tovar and Uchman, 2006, 2008). Several ethological models have been proposed of *Zoophycos* tracemaker (see Löwemark and Werner, 2001; Bromley and Hanken, 2003; Löwemark and Schäfer, 2003; Löwemark et al., 2004; Löwemark, 2015). *Chondrites* tracemaker is associated with poorly oxygenated bottom or pore waters, able to

live in dysaerobic conditions, at the aerobic–anoxic interface, as a chemosymbiotic organism (Seilacher, 1990; Fu, 1991). Upwards in the dark/black intervals, a progressive return improvement can be envisaged by the presence of light structures (i.e., light *Thalassinoides*) in the upper part. The presence in the interval D of a well-developed dark trace fossil assemblage consisting of discrete structures, could be associated with a decrease in the sedimentation rate, increase in firmness and higher time of bioturbation, together with local concentration of food. This agrees with the record of delicate, complex, structures of *Spirophyton* and *Zoophycos*. *Spirophyton* has been interpreted, mainly for marine-margin deposits, as revealing an opportunistic strategy; formed rapidly after sudden influxes of organic material (Miller and Johnson, 1981; Miller, 1991, 2003; Bromley, 1996; Gaillard et al., 1999). The *Zoophycos* tracemaker is interpreted as bioturbating firmer, organic rich substrates with oxygen depleted pore waters (e.g., Rodríguez-Tovar and Uchman, 2004a,b; Rodríguez-Tovar and Dorador, 2014, and references therein). Distribution of *Zoophycos* has been related to Milankovitch orbital scale climatic changes, determining variations in the organic matter content and flux (Rodríguez-Tovar et al., 2011).

Middle and dark gray tone sediments, corresponding to intervals C, F, G, H, I, J, K, and L, reveal, in general, variable intermediate cases between dark/black sediments and the lighter ones. Both types of sediments consist of a well-developed mottled background in the first case with dominance of light color sediments while in the second a mixture between light and dark sediments is observed. In both cases *Planolites* and *Thalassinoides* are the most abundant traces, being light structures dominant in the first case while in dark gray tone sediments dark *Planolites* and *Thalassinoides* are also observed. Dark *Zoophycos* are also registered, especially in the dark gray tone intervals, but dark *Chondrites* are not observed. Middle and dark gray tone sediments could reflect a generalized good bottom and pore-water oxygen conditions and higher abundance in the organic matter content at the surface but also in the first centimeters of the sediment, allowing bioturbation by shallowest, shallow and middle tiers tracemakers. When input of organic matter content (as indicated by Pexp) is maintained during a comparatively long time (Intervals F, or H to K), deep tier traces, i.e., *Zoophycos*, can be developed, probably reflecting a comparatively higher organic matter content and a slight decrease in oxygenation probably related to the presence of the poorly ventilated and benthic $\delta^{13}\text{C}$ -depleted Antarctic bottom water AABW (Adkins et al., 2005; Hoogakker et al., 2006) (Fig. 6b).

5.2. Environmental conditions during MIS 13–MIS 11 and the macrobenthic and foraminifer record

The benthic foraminifer concentration in the sediments and variations of the planktonic foraminifer assemblages suggest significant changes in surface water productivity and food supply to the sea floor occurring in the Portuguese margin during MIS 12 and MIS 11 that could be correlated with the registered changes in facies and trace fossil

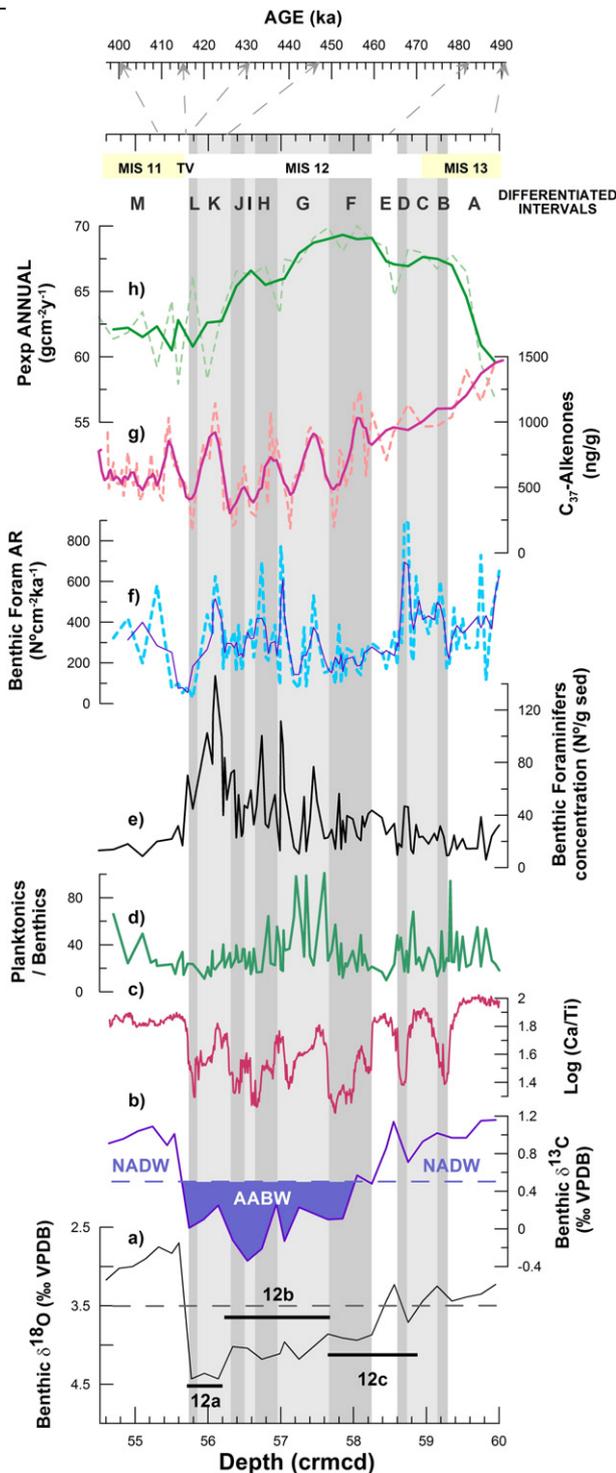


Fig. 6. Stratigraphic and temporal distribution of intervals A to M, differentiated according to color and trace fossil assemblage, and comparison with foraminifer records and other data from IODP-U1385. a) Benthic $\delta^{18}\text{O}$ (‰ VPDB) (Hodell et al., 2015-in this issue); sub-stages are named according to Railsback et al. (2015); horizontal dashed line shows the ice volume threshold separating stable and unstable climatic conditions (McManus et al., 1999). b) Benthic $\delta^{13}\text{C}$ record (‰ VPDB); filling indicates typical values for Antarctic Bottom Water (AABW) according to Adkins et al. (2005). c) Log Ca/Ti record (Hodell et al., 2015-in this issue). d) Planktonic/benthic foraminifer ratio. e) Benthic foraminifer concentration in number of tests per gram of dry sediment. f) Benthic foraminifer accumulation rate in number of tests per cm^2 and ka (dashed line) and 3-point running mean (solid). g) Total alkenone concentration (ng/g) of 37 carbon atoms (Maiorano et al., 2015-in this issue; courtesy of T. Rodrigues) reflects the coccolithophore productivity (dashed line) and 5-point running mean (solid). h) Export productivity (dashed line) and 3-point running mean (solid). Glacial and interglacial stages are highlighted by horizontal bands. Vertical bands correspond to the differentiated intervals with lithological and ichnological features, with its facies color highlighted: light gray (in white)–middle dark gray–very dark/black. Control points linking depth (cmrcmd) to LR04-reconstructed age (Hodell et al., 2015-in this issue) are represented by arrows.

assemblages (Fig. 6). Similar changes occurred across the more recent Terminations IV, II and I (Grunert et al., 2015-in this issue; Rodríguez-Tovar et al., 2015-in this issue).

Benthic communities living at the sea floor are limited by the flux of organic carbon reaching the sea floor that, in turn, are a function of Pexp and oxygen content along the water column and interstitial waters within the sediments. Higher densities of benthic foraminifers in bottom sediments have been related to higher rates of organic carbon supply to the sea floor, both in the same Site U1385 (Grunert et al., 2015-in this issue; Rodríguez-Tovar et al., 2015-in this issue) and in other locations (Schmiedl et al., 1997; Wollenburg et al., 2004; Mojtahid et al., 2009).

A trend of increased productivity both primary, according to coccolithophores (NAR) and alkenone data (Maiorano et al., 2015-in this issue), and secondary, according to planktonic foraminifer-reconstructed Pexp (Fig. 6g–h), occurred during the final stage of MIS 13 coinciding with warm SST inferred from the Ca/Ti record in our site (Hodell et al., 2015-in this issue). Low abundance of the coccolithophore *Florisphaera profunda* (Maiorano et al., 2015-in this issue), suggests a less stratified upper water column. During MIS 11 Pexp was very low and both intervals coincided with the presence of light-color sediments as well as with the continuous presence of light *Planolites* and *Thalassinoides* in the differentiated intervals A and M (Fig. 6). By contrast, during MIS 12 Pexp is higher, especially in the early part, but decreases towards the end of the stage. Benthic foraminifer accumulation rates do not follow this trend. This decoupling between Pexp, and benthic accumulation rates can be the result of the changing conditions of water column oxidation that are mainly reflected by the benthic $\delta^{13}\text{C}$ record. The high benthic $\delta^{13}\text{C}$ during MIS 11 and MIS 13 reflects the high bottom water oxygenation during these interglacial periods. Higher bottom water ventilation tends to decrease the accumulation of organic matter in the sediments and therefore reduce food availability for the macrobenthic and microbenthic communities.

Microbenthic fauna proliferated during the glacial stage as reflected by the higher benthic foraminifer accumulation rates, which can reach values over 800 individuals/cm²ka. Similar enhanced fluxes of organic matter occurred also in the South Atlantic upwelling region during this glacial period (Schmiedl and Mackensen, 1997). This high organic carbon flux to the bottom, due to high Pexp and/or poor bottom water ventilation, allowed an eutrophic environment expressed by high benthic foraminifer accumulation rates. Nevertheless, high amounts of organic matter reaching the bottom could reduce the availability of oxygen and produce a subsequent impoverishment of the benthic habitat when bottom water ventilation is low (Grunert et al., 2015-in this issue; Rodríguez-Tovar et al., 2015-in this issue). These conditions happened during short intervals along MIS 12 and in Termination V when the Site was under the influence of less oxygenated bottom water (AABW), and are registered by the micro-benthos, as a decrease in benthic foraminifer accumulation rate coupled with increase in both Pexp and total alkenone production (Fig. 6). Macrobenthos also reveals the punctual pulse (increasing) in organic matter reaching the bottom, by the record of *Spirophyton* and *Zoophycos*, and the associated decrease in oxygen availability mainly revealed by the presence of *Chondrites*, observed in intervals B and D (Fig. 6). Differentiation of several intervals (A to L) during the ending of MIS 13 and the whole MIS 12, based on the trace fossil record agrees with the idea that tracemakers are more sensitive than foraminifers to depth variations in the redox boundary in near-surface sediments leading to the movement of trace-fossil tiers, as indicated by Baas et al. (1998) and also recently demonstrated by Rodríguez-Tovar et al. (2015-in this issue). Termination V, similarly to more recent Terminations II and IV and in opposition to Termination I (Rodríguez-Tovar et al., 2015-in this issue), was characterized by increasing Pexp and accumulation of organic matter without depletion of oxygenation, as increasing $\delta^{13}\text{C}$ coinciding with the lighter color interval M suggests (Fig. 6).

By contrast with MIS 12, lower benthic foraminifer accumulation rates during MIS 11 indicate an oligotrophic environment at the bottom and

are consistent with lower inputs of organic carbon inferred from total alkenone accumulation (Maiorano et al., 2015-in this issue) and planktonic foraminifer Pexp, as well as with low NAR (Maiorano et al., 2015-in this issue). This oligotrophic environment is characteristic of peak interglacial periods in this region, as studies on sediments ranging from MIS 6 to the Holocene show (Pailler and Bard, 2002). Oxygen consumption in deep sea waters during MIS 11 due to the weak organic carbon supply was low which, together with the presence of the more ventilated North Atlantic Deep Water (NADW) as can be inferred from the high values of benthic $\delta^{13}\text{C}$ (Fig. 6b), resulted in higher oxygen content of bottom waters. This agrees with the lighter color of the sediments in the differentiated interval M, as well as by the continuous presence of light *Planolites* and *Thalassinoides*. This higher bottom-water oxygen concentration during the interglacial compared to the previous glacial maximum occurred on the Portuguese margin also during the last two climatic cycles (Hoogakker et al., 2015), and can be related to increased ventilation linked to a reorganization of ocean circulation after deglaciations (McManus et al., 2004). Oscillations in Pexp during these interglacial produced fluctuations of the organic matter content in the bottom, which is registered in the macrobenthos by the presence of dark *Planolites* and *Thalassinoides*, and the local record of *Nereites*. North Atlantic coccolithophore analyses allow for envisaging a relationship between lighter color sediments and high coccolith content in MIS 11 (Amore et al., 2012; Marino et al., 2014; Maiorano et al., 2015-in this issue).

The low availability of organic matter for benthic macro- and microfauna along MIS 11 could evidence a possible stratification of the superficial water masses in the area, as indicated by higher percentage of the coccolithophore *F. profunda* compared with the previous interglacial (Maiorano et al., 2015-in this issue), or be related to a reduced input of land-derived nutrients during the sea level highstand (Rodrigues et al., 2011). Such possibility should be explored with the study of planktonic fauna and the evolution of the sea surface conditions for the same period in the same site.

In a few cases, trace fossil assemblage in sediments corresponding to MIS 12 and MIS 11 has been characterized. At the eastern Mediterranean Sea, and in relation with the ichnological response to late Quaternary sapropel formation, a detailed trace fossil analysis was conducted on two cores from the last 400 ka, involving the base part of MIS 11 (Löwemark et al., 2006). As a general pattern, the sediment in the two cores is characterized by mottled burrows, with few trace fossils of *Scolicia*, *Thalassinoides*, *Chondrites*, and *Trichichnus*, attributed to well-oxygenated and warm bottom waters in an oligotrophic environment typical for non-sapropel times (Löwemark et al., 2006). Recently, variability in trace fossil abundance and diversity associated with glacial–interglacial cycles, including MIS 11, was recognized in Late Quaternary sediment cores from the Arctic Ocean; during interglacial periods the increase food flux, rather than changes in deep water circulation, is responsible for higher abundance and diversity (i.e., *Scolicia*, *Planolites* or *Nereites*), while in glacial interval characterized by extremely low food flux consist of impoverished ichnofauna dominated by *Trichichnus* and *Chondrites* (Löwemark et al., 2012).

Obtained results allow addressing interpretations on local (?) paleoceanographic dynamics. Although higher resolution climatic records need to be carried out in this time period, benthic $\delta^{13}\text{C}$ data prove that the evolution of macrobenthic tracemaker community during MIS 12 and MIS 11 responded to major changes in bottom water ventilation probably linked to variations in deep water thermohaline circulation, determining variations in oxygen and food availability.

During glacial MIS 12 a higher planktonic foraminifer-reconstructed Pexp from surface waters, together with reduced deep water formation in the North Atlantic probably resulted in higher accumulation rates of organic matter in the sea floor, favoring the development of macrobenthic communities typically living in these environments, characterized by comparatively high food, and low oxygen availability. This was probably more intense at some particular time periods such as intervals B and D that may be linked to times of extremely poor

bottom-water ventilation associated with cooling events at the surface. In particular, dark intervals during MIS 12 show low Ca/Ti ratios (Fig. 6c) that are usually associated with cool stadials in the Portuguese margin (Hodell et al., 2013b, 2015-in this issue). The low benthic $\delta^{13}\text{C}$ values during MIS 12, especially in the dark intervals, indicate low bottom water ventilation probably due to a higher influence of AABW during this time period. Low bottom water oxygenation favored the preservation of organic matter, increasing food availability for the benthic macrofauna, even though the flux of organic matter from the surface was low.

By contrast, intense North Atlantic deep water formation during MIS 11 (interval M) (Poirier and Billups, 2014), and probably late MIS 13 (interval A), together with lower export production at the surface led to more oxygenated bottom waters in the Portuguese margin, determining a well-developed deep-sea tiered assemblage.

Near Termination V an extremely low sedimentation rate has been recognized based on the chronology elaborated for this site (Hodell et al., 2015-in this issue). The lowermost 40 cm at the base of MIS 11 (bottom of interval M) represent a condensed interval of 30 ka, with a more extreme condensation recorded in the first 5 cm at the base of this interval.

6. Conclusions

The present study including facies characterization, ichnological composition and foraminifer analysis, allowed interpretation of deep-sea paleoenvironmental conditions during the transition MIS 13/MIS 12, MIS 12 and MIS 11.

A generalized context of well-oxygenated bottom and pore-waters, as well as abundance of food in the sediment for macrobenthic tracemaker community can be interpreted, with marked changes in these paleoenvironmental factors as revealed by variations in composition and distribution of trace fossils according to the differentiated intervals A to M.

Benthic foraminifer concentration in the sediments and variations of the planktonic foraminifer assemblages suggest significant changes in surface productivity and food supply to the sea floor during MIS 12 and MIS 11 that could be correlated with the registered changes in facies and ichnology.

The end of MIS 13 is characterized by low values of annual export productivity, that together with the presence of light-color sediments and the continuous presence of light *Planolites* and *Thalassinoides* at interval A, reveals relatively low organic carbon flux to the bottom and high oxygen conditions. These initial conditions were changed during development of MIS 12, showing the rapid increase in the organic matter supply and then remaining very high until Termination V, determining a eutrophic environment, as is revealed by high benthic foraminifer accumulation rates. This change and the associated reduced availability of oxygen, correlate with the record of *Spirophyton* and *Zoophycos*, and the presence of *Chondrites*, observed in intervals B and D. During MIS 11 lower benthic foraminifer accumulation rates are registered suggesting an oligotrophic environment at the bottom, associated with lower inputs of organic carbon, and high oxygen content of bottom waters, in agreement with the lighter color of the sediments as well as the continuous presence of light *Planolites* and *Thalassinoides* at interval M.

In conclusion, the evolution of macrobenthic tracemaker community during MIS 12 and MIS 11 responded to major changes in bottom water ventilation probably linked to variations in deep water (North Atlantic) thermohaline circulation.

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Appendix A. Planktic foraminifer species and morphotypes used to reconstruct export productivity

Beella digitata

Globigerina bulloides

Globigerina falconensis

Globigerinella calida

Globigerinella siphonifera (aequilateralis)

Globigerinita glutinata

Globigerinoides ruber (pink)

Globigerinoides ruber (white)

Globigerinoides sacculifer

Globigerinoides trilobus

Globorotalia hirsuta

Globorotalia inflata

Globorotalia scitula

Globorotalia truncatulinoides

Globoturborotalita rubescens

Globoturborotalita tenella

Neogloboquadrina dutertrei

Neogloboq. pachyderma (dextral)

Neogloboq. pachyderma (sinistral)

Orbulina

Pulleniatina obliquiloculata

Turborotalita humilis

Turborotalia quinqueloba

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