
Palaeoceanographic and palaeoclimatic changes during the last 37,000 years detected in the SE Bay of Biscay based on benthic foraminifera

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Abstract :

Benthic foraminifera assemblages from a sedimentary core (PP10-12; 701 mwd) from the SE Bay of Biscay allow us to trace palaeoceanographic and palaeoclimatic changes occurred in this region during mid MIS 3 (Marine Isotope Stage 3) and MIS 1 interval (37–2.4 ka BP). Results are based on 176 benthic foraminifera species considering their ecology, the difference between autochthonous/allochthonous, preservation and oxygen rates, thus evidencing climatic and oceanographic events. MIS 3 is characterised by waters with a dominance of *Cassidulina laevigata* and *Uvigerina peregrina*. By the end of this interval, waters became colder and less oxygenated indicated by the occurrence of *Melonis affinis*. These conditions persisted at the beginning of MIS 2. The Heinrich Event 1 (H1) is well registered in this core with three intervals (H1a, H1s.s., H1b) where *Hyalinea balthica* dominates. During H1s.s. the coldest waters are registered, and the environment was unstable. These conditions continued during H1b when the occurrence of *Globobulimina affinis* evidences some intervals with anoxia. During Bølling-Allerød (B/A) waters were warmer and low-ventilated indicated by *Bulimina gibba*. *Cassidulina laevigata* dominates the Younger Dryas (YD) and the beginning of Lower Holocene, evidencing the occurrence of cool waters with low-oxygen and high organic matter content. The Lower to Middle Holocene transition is registered as a cold interval: Holocene Cooling Event (HCE-5). From the Middle Holocene onward water temperature were milder based on the dominance of *Uvigerina peregrina*.

Keywords : Palaeoclimatology, Palaeoceanography, Benthic foraminifera, MIS 3-MIS 1, Bay of Biscay

1. Introduction

Earth's climate is conditioned by the interaction between the atmosphere and the ocean by heat and CO₂ mutual exchange. The Atlantic Ocean is the main location of new water masses that travel as a conveyor belt distributing the caloric energy from low to higher latitudes in the planet. In this context it is fundamental to know the dynamic of the AMOC (Atlantic Meridional Overturning Circulation) if we try to characterise millennial climate changes of cold to warm alternating periods of climate of the Quaternary (Rahmstorf et al., 2015).

The AMOC is formed by two interconnected gyres in the North Atlantic: The Subtropical Gyre (STG) and the Subpolar Gyre (SPG). The STG travels to the north transferring heat and salinity to the Nordic seas (Morley et al., 2014) and there is a convection there (Lozier and Stewart, 2008). The SPG flows transporting cold waters to the south. The dynamics between these two gyres caused climatic anomalies in Europe as the Little Ice Age (LIA) and the Warm Medieval Period and other secular anomalies (Thornalley et al., 2009; Morley et al., 2014; Reißig et al., 2019) thus evidencing an atmospheric/oceanic interconnection.

Micropalaeontological data are one of the most used proxies in palaeoceanography and foraminifera are the most popular among them. These faunal analyses are based on the high sensitivity of many foraminifera species to basic environmental parameters of the marine realm (Murray, 2006). The current knowledge of the biology and ecology of living foraminifera species is a useful database to decipher those environmental parameters of the past (Murray, 1991). Thus, the distribution of modern foraminifera species in the Bay of Biscay has been described in the northern margin of the Capbreton Canyon in Aquitaine platform (Caralp et al., 1970; Pujos-Lamy, 1973, Fontanier et al., 2002, 2003; Langezaal et al., 2006; Duchemin et al., 2008; Ernst et al., 2008; Mojtahid et al., 2010) and in the Basque Basin southern canyon region (Pascual et al., 2008; Martínez-García et al., 2013). These works, located from shelf to bathyal profiles, described benthic foraminifera assemblages controlled by parameters as organic carbon flux to the marine benthos, bottom currents and grain size, oxygen content and carbonate saturation of sediments (Mackensen et al., 1995; Jorissen et al., 2007). The distribution of living benthic foraminifera assemblages have been used as proxies of the response of benthic ecosystems to atmospheric changes and rapid climatic changes in the North Atlantic (Baas, 1998; Rasmussen et al., 2002; García et

al., 2013; Grunert et al., 2015) among others. In the Bay of Biscay Martínez-García et al. (2014) described climatic events from the MIS 3 to the Holocene registered in the Basque shelf, however from H1 to Holocene were scarcely recorded due to various sedimentary hiatuses. Rodríguez-Lázaro et al. (2017) studied the palaeoclimatic evolution of the bathypelagic zone of this region during the last 140 ka, that is, MIS 5 to MIS 1 interval, with a low resolution for the MIS 1.

The aim of this work is to provide with new evidence of the response of benthic foraminifera assemblages to rapid climatic changes occurring during modern times of the last glacial cycle in a mesopelagic palaeoceanographic context of the SE Bay of Biscay, with detailed study of H1 to Recent, a poorly known interval.

2. Environmental setting

The study area is located in SE Bay of Biscay (Fig. 1A) north of Cap-Breton Canyon: 701 mwd, Lat (WGS84) 43.836256; Lon (WGS84) -2.123051. Considering the modern water masses in the Bay of Biscay the study area is located in the boundary between the MOW (Mediterranean Outflow Water) with a bathymetry of 1300-700 m and the ENACW (East North Atlantic Central Water) shallower than 700 m (Fig. 1B). In the hydrographic context of the Bay of Biscay the study area belongs to the east border of the NAC (North Atlantic Current) not far from divergence area of STG (subtropical gyre) and SPG (subpolar gyre) (Mary et al., 2017) (Fig. 1A). This particular geographic location favoured the record of climatic changes in the N Atlantic (i.e. García-Soto and Pingree, 2012; Esnaola et al., 2013).

The main surface current in the Bay of Biscay is the European Slope Current (ESC) that flows northwards to the Armorican Shelf (Fig. 1A). This current can revert through the talus and the north Spanish shelf to the southwest during the summer following the talus border (Charria et al., 2013). During fall-winter this current flows northwards converging with the Iberian Poleward Current (IPC) coming from the south along the western Iberian margin (Peliz et al., 2005) (Fig. 1A). The IPC entering the Bay of Biscay is called Navidad current (García-Soto et al., 2002). The winter combination of IPC and ESC forms the European Poleward Current (EPC) (García-Soto and Pingree, 2012) that transports relatively warm and salty water to the Nordic seas. The surface waters from the NAC entering the Bay of Biscay from the northwest (Pingree and García-Soto, 2014) are under the influence of interannual westerlies (Pingree, 2005) associated with the North Atlantic Oscillation (NAO) considered as one of the clues to understand the climatic variability of the N Atlantic.

The palaeoceanographic evolution of the Iberian Margin during the last climatic cycle is considered by Martrat et al. (2007), that evidenced the Antarctic Bottom Water (AABW) input during glacial periods and the colder short-lived intervals of interglacials. During deglacials the early entrance of North Atlantic Deep Water (NADW) from high latitudes is observed, particularly during warmer and free of sea ice interglacials. In the Holocene deep water were more ventilated due to the influence of NADW. During the interval of 20 ka-10 ka, after the deglaciation inception, climatic conditions evolved to low oxygen environments and a decrease of current intensity. This trend is abruptly changed by strong fall of sea-surface T (SST) together with strengthening of bottom currents caused by the entrance of deep waters originated in the south (AABW) (Martrat et al., 2007). After a rapid cooling produced in only several centuries, the absence of ventilation of bottom waters and the lower input of AABW forced the instauration of warmer conditions with SST increase. This trend is repeated during the SST oscillations observed in the last glacial-interglacial climatic cycle.

3. Material and methods

Samples of this study belongs to sedimentary core PP10-12, 18 m long, retrieved south of Landas shelf, 701 mwd, during the oceanographic cruise SARGASS, 2010. The core is composed by homogenous lithology of continuous silt-clay sediment. The bottom core is formed by laminated silty facies indicative of more energetic environment. From level 1561 cm to the top the sediment is homogeneous clay-silt. There is no evidence of reworking. Core was sampled every cm and 121 of these samples were used to micropalaeontologic analyses in this work. As the main aim of work is detailed study of H1 to MIS 1 this interval has been sampled with more detail (1 sample/20 cm) and supplementary intermediate samples were studied to complete the results. As core dating are provided we sampled the bottom half with lower resolution in order to describe the main palaeoenvironments previous to H1. Samples have been washed and sieved and fraction coarser than 63 μm have been picked from micropalaeontology following the standard method (Boltovskoy and Wright, 1976; Murray, 2006). A total of 300 specimens of benthic foraminifera have been picked for every sample and the associated planktonic foraminifera have also been included. Taxonomy for the benthic foraminifera study is based on Loeblich and Tappan (1988) and Holbourn et al. (2013) among others, and updated with WoRMS databases (last reference 30-11-2019).

In order to establish the taphonomic imprint as transport and/or dissolution, the degree of preservation of benthic foraminifera carapaces have been studied. Carapaces are well preserved in general, with few fractures or reworking signals and thus with no evidence of transport nor re-sedimentation. Most important alterations in carapaces are the translucent aspect and red/brown colour only found in few levels of this core. The colour change indicates permineralization occurring in early diagenesis by interstitial fluids affecting the organic matter included in carapaces, in sediment with reducing conditions (Murray, 2006).

The assemblages have been quantified by simple diversity index (S, number of species by sample). Other calculated indices of richness and diversity (as Fisher's α index) do not show significant oscillations in the studied core. The simple Oceanity Index of Murray (1976) (OI; number of planktonic/total foraminifera) that considers the total foraminifera of each sample has been used. For this calculation we have not excluded individuals of infaunal species as suggest Van der Zwaan et al. (1990) nor individuals of stress indicator species as indicate Van Hinsbergen et al. (2005). For that reason, this index is a good indicator of the stress in the bottom waters (Van Hinsbergen et al., 2005). When the bottom waters represent an altered ecosystem, benthic species are virtually absent from the sediment and OI increases drastically as a consequence of the increase of planktonic foraminifera deposited in the bottom. Conversely, when the ecosystem recovers stability, by increasing the oxygen level for example, the lower OI values are reached.

Benthic foraminifera species indicative of oxygen levels have been studied following the classification of Kaiho (1994, 1999) (Appendix 1). In order to evaluate the degree of transportation, to evidence strong supplies from coastal areas to deeper waters in this region, the percentage of benthic allochthonous species transported from the shelf has been calculated (Appendix 2). In this group we found specimens living in estuaries (Cearreta, 1988, 1989, Pascual and Rodríguez-Lázaro, 2006, Pascual et al., 2019), as well as in shelf and coastal sediments of the Bay of Biscay (Pujos-Lamy, 1973; Pascual et al., 2008; Martínez-García et al., 2013).

Chronology of the studied core has been established from 11 AMS¹⁴C dates from planktonic foraminifera (Beta Analytic Inc., Florida, USA) calibrated with 'CalibRev6.0.6' software (Stuiver and Reimer, 1993; Stuiver et al., 2005) using the Marine09.14C calibration (Reimer et al., 2009). These dates have been complemented with the correlation of percentages of planktonic foraminifera *Neogloboquadrina pachyderma* sin ($N_{p_{sin}}$), with $\delta^{18}O$ signature of marine core MD95-2042 (Shackleton,

2001) and Greenland ice core NGRIP GICC05 (Rasmussen et al., 2014; Seierstad et al., 2014), obtaining 40 additional tie-points (Table 1, Fig. 2). The best model correlation has been obtained with a non-linear logistic analysis calculated with PAST software (Hammer et al., 2001).

4. Results

4.1. Chronostratigraphy of core PP10-12

The age model of core PP10-12 allows us grouping samples into stratigraphical units belonging to MIS 3 to MIS 1, with ages into the 36710-2430 years BP interval (Fig. 3). The high sedimentation rate of this core (from 5.1 cm/ka at the beginning of the MIS 2 to 750 cm/ka at the beginning of the MIS 1; mean = 142.25 cm/ka) allows a high-resolution study particularly of MIS 2 and MIS 1. In this way, we found the three sub-stadials of Heinrich event 1 (H1: H1a, H1s.s., H1b) already described in other locations of this region (Martínez-García et al., 2014, 2015).

The high-resolution time obtained in the H1-Lower Holocene interval allow us to identify 29 tie-points between $\delta^{18}\text{O}_{\text{Np}_{\text{sin}}}$ and reference cores, supported by AMS¹⁴C dates obtained for this interval (Table 1; Figs. 2 and 3). In the rest of core 11 further interpretative tie-points have been obtained with lower resolution, so it does not permit such a detailed palaeoenvironmental interpretation.

4.2. Microfaunal analyses

A total of 35630 specimens of benthic foraminifera (BF) grouped in 176 species have been identified in this study (Table 2). Only 12 species count more than 10% in more than two samples (supplementary material). Other 5 species count more than 10% of total in at least one sample, 13 more are <10% to 5% in at least one sample. Remaining species (136) are minority species, 77 of them counting <1% only present in some samples. 31 species are only represented by one individual and 16 more by two specimens. The most abundant (>10% of the total BF, see supplementary material) are: *Cassidulina laevigata* d'Orbigny and *Uvigerina peregrina* Cushman. *Bulimina gibba* Fornasini and *Hyalinea balthica* (Schröter) are secondary species (5-10%). Other less abundant (1-5%) species are: *Bigenerina (Bigenerina) nodosaria* d'Orbigny, *Bolivina spathulata* (Williamson), *Bolivina subaenariensis* Cushman, *Chilostomella oolina* Schwager, *Cibicidoides pachyderma* (Rzehak), *Globobulimina affinis* (d'Orbigny), *Melonis affinis* (Reuss) and *Nonionoides turgidus* (Williamson).

Specimens exhibit in general tests with good preservation except those of *H. balthica* and *B. subaenariensis* found during the Last Glacial Maximum (LGM) and Heinrich H1s.s. intervals.

Benthic foraminifera assemblages present high values of simple S diversity (average: $S = 39$ spp/sample) and diversity is lower during MIS 3 ($S = 21$) (Fig. 4). Diversity is also below average during the beginning of MIS 2, H1a and Middle (Northgrippian) and Upper (Meghalayan) Holocene. Highest values are found during H1b, Bølling/Allerød (B/A), Younger Dryas (YD) and Lower Holocene (Greenlandian). Noteworthy, all of these episodes begin and end with a drastic fall of diversity ($S < 30$) (Fig. 4).

Considering the oxygenic character of the studied benthic foraminifera it is evident the dominance of suboxic (O_2 : 0.3-1.5 ml/l) assemblages with an average of 60% (Fig. 5 and supplementary material). Oxidic ($O_2 > 1.5$ ml/l) species are important in percentage only during H1s.s. and H1b. Species that can live in dysoxic (O_2 : 0.1-0.3 ml/l) waters dominate the record of MIS 2, the B/A (< 45%) and the end of Greenlandian (Lower Holocene, see Fig. 5).

The planktonic/benthic signal of Oceanicity Index (OI) averages 59% throughout the studied core (Fig. 4). This index is lower during MIS 3 (H3: 32%), end of LGM, B/A, YD and beginning of Holocene. OI increases during the rest of Holocene. The OI shows a rapid oscillation (OI: 80%-25%) during H1, and especially during H1s.s. (see Fig. 4). These levels of Heinrich event H1 also evidence the strongest variations of the occurrence of BF coastal species, that increases from the average of 9% to values of 25% reaching the 45% in some levels of H1s.s. (see Fig. 4).

Considering dominant species MIS 3 (levels 1797-1670 cm) is characterized by the assemblage of *C. laevigata* and *U. peregrina*, accompanied by *H. balthica*. Also, in some levels *B. subaenariensis*, *C. pachyderma* and *M. affinis* are present (Fig. 6).

From the beginning of MIS 2 to the end of LGM (27-19 ka cal BP) *C. laevigata* is abundant, accompanied by *B. subaenariensis* and *H. balthica*. These two species contain abundant individuals with brown-colour altered tests that count for more than 40% of the total specimens at the beginning of MIS 2 (Fig. 4). During H1 (a, s.s., b) episodes (19-14.8 ka cal BP) main species *C. laevigata* and *H. balthica* occur anticovariantly. *Cassidulina laevigata* reaches 30% in H1a while *H. balthica* counts for more than 50% in levels of H1s.s. (Fig. 6). *H. balthica* also includes specimens altered with brown colour. Other secondary species are *U. peregrina* (H1a), *B. spathulata* and *M. affinis* (H1ss), *C. oolina*, *G. affinis* and *N. turgidus* (H1b) (Fig. 6).

MIS 1 is represented in this core from sample 921 cm to coretop. In levels of B/A (14.8-12.8 ka cal BP) *B. gibba* is the most abundant species (>25% in some levels) together with *U. peregrina* (17%) both species with oscillating records. Maxima percentages of *U. peregrina* (>40%) are found in earliest and latest levels of B/A. In some levels these species are accompanied by abundant individuals of *M. affinis* and *C. oolina* (see Fig. 6).

During YD (12.8-11.7 ka cal BP) *C. laevigata* is again dominant together with *M. affinis*, though this unit begins and ends with high occurrence of *U. peregrina* (Fig. 6). The Lower Holocene (Greenlandian, 11.7-8.2 ka cal BP) shows comparable assemblages together with *B. gibba*, while *B. spathulata* is important numerically at the beginning of this unit. The Lower to Middle Holocene transition (HCE 5, 8.2 ka cal BP) is marked by the net occurrence of *G. affinis* and *H. balthica* (>20%) (Fig. 6). The Middle Holocene (Northgrippian, 8.2-4.3 ka cal BP) is characterised by the increase of percentage of *U. peregrina* (average: 46%; up to 70% in some levels), together with *G. affinis* at the beginning and *B. (B.) nodosaria* at the end of this unit (Fig. 6). Finally, during the Upper Holocene (Meghalayan, 4.3-2.4 ka cal BP in this core) *U. peregrina* is dominant species and reaches the highest percentage in all core (<72%), being accompanied by *B. (B.) nodosaria* and *C. pachyderma* to the top of this unit (Fig. 6).

5. Discussion

Benthic foraminifera contained in studied core PP10-12 is indicative of benthic particular conditions as oxygenation, organic matter (OM) and productivity of waters (Table 3). The ecology of benthic foraminifera species occurring in this core (Table 1) evidence particular benthic conditions relative to water temperature, oxygenation, organic matter and productivity.

5.1. End of MIS 3 - beginning of MIS 2

During the time of MIS 3 included in this work (36-27 ka cal BP) SE Bay of Biscay bottom waters were cool to temperate as evidenced by the occurrence of shallow-infaunal benthic species *C. laevigata* (Rasmussen et al., 2002). Nevertheless cold and high content organic matter waters arrived seasonally as indicated by the occurrence of *C. laevigata* and *H. balthica*, an intermediate infaunal species that dominated during

MIS 3 in the Mediterranean (Ross, 1984). These waters were less oxygenated as it contained *B. subaenariensis*, indicative of dysoxia (O_2 : 0.1-0.3 ml/l) (Kaiho, 1994).

These organic matter fluxes were intermittent which is supported by the occurrence in some levels of shallow infaunal benthic species as *C. pachyderma* (see Fig. 6), typical of oligotrophic, high-oxygen content and low nutrients waters (Schmiedl et al., 2000; Table 3). At the end of MIS 3 some instability of benthos is detected by the drastic decreasing of diversity (S from 48 to 21 species) and the OI (see Fig. 4). *Melonis affinis* increased as well, a species indicative of very cold waters (from -0.4°C to 9°C) (Murray, 1991); all of this would indicate the arrival of relatively colder waters.

At the beginning of MIS 2 the cold, low oxygen and high OM water conditions persisted. Waters were very cold and became progressively dysoxic as evidenced by the occurrence of abundant specimens of *B. subaenariensis* in the lower levels of MIS 2 (Fig. 6). This species includes many individuals with altered, dark brown or red coloured tests (see Fig. 4), indicative of low oxygen and high OM content waters (reducing conditions). Similar alteration has been observed in tests of *H. balthica* from deep canyons of Mediterranean (Fontanier et al., 2008) and Atlantic (Hess and Jorissen, 2009). This has been interpreted as produced after early colonisation of altered ecosystems, in some cases after the deposition of turbidites. Comparable alteration has been described with the same species in the Aegean Sea after the low oxygen sapropel event S1 (Abu-Zied et al., 2008) as well as in the Ionian Sea (Rosenthal et al., 2011) after the anoxic phase that triggered the deposit of sapropel S5.

5.2. Heinrich Event H1

In the stadial H1 the benthic foraminifera allow recognising three intervals (H1a, H1s.s., H1b) already described in shelf sediments of the Bay of Biscay (Martínez-García et al., 2014, 2015) that are characteristics of the last deglaciation in NW Iberian margin (Naughton et al., 2016). These intervals have been attributed to changes in the direction of jet stream which was produced by mechanisms similar to the modern North Atlantic Oscillation (NAO) (Naughton et al., 2009).

During H1a (19-17.4 ka cal BP) *C. laevigata* dominated, though the increase of *H. balthica* is indicative of progressively colder waters (Fig. 6). This interval was interpreted as a cold and relatively wet interval (Naughton et al., 2016). Penaud et al. (2009) described the most important supply of fluvial terrigenous sediments of the

Celtic-Armorican margin at around 18 ka., considered as a response to the seasonal water supplied by the retreat of European ice sheets (Toucanne et al., 2009).

During H1s.s. (17.4-16.2 ka cal BP) the high occurrence (<50%; Fig. 6) of *H. balthica*, supported by *M. affinis*, indicate cold waters for this interval (see Table 3). Suboxic species were living in these waters though the occurrence of some oxic ($O_2 > 1.5$ ml/l) species as *C. pachyderma* in the sediment (< 67%) would indicate levels with better oxygenation (Table 3) and thus an environmental amelioration. On the other side, altered brown colour tests of *H. balthica* are found (see Fig. 4). In these levels, *C. laevigata* and *H. balthica* exhibit anti-covariant record. All these data are indicative of an unstable period of the benthos, what is supported by the oscillation of the number of species (22-48) as well as the OI (IO: 24-87; see Fig. 4) and also by the entrance of coastal species (<46%) indicative of increasing riverine activity. Episodes with highest values of the Oceanity Index are indicative of an altered ecosystem in a marine bottom depleted of oxygen with scarce life (Van Hinsbergen et al., 2005). In this deteriorated environment we found many benthic coastal foraminifera that have been transported by energetic currents to this bottom. This environmental change is also produced by the episodic arrival of warmer waters evidenced by the high occurrence (highest values of core) of *B. spathulata*, species which prefer temperatures between 17°-25°C (Table 3) (Murray, 2006).

These abrupt climate changes might be related to episodes with thermohaline current reduction (Obbink et al., 2010). Effectively during H1s.s. polar conditions prevailed in NE Europe, with massive iceberg discharges of the ice sheet (Zaragosi et al., 2001), that caused the AMOC shutdown at 17.5 ka cal BP in the N Atlantic (McManus et al., 2004). The ice discharges had triggered drastic conditions in surface waters with seasonal sea ice development around continental borders of the Bay of Biscay (Penaud et al., 2009). Based upon this the benthic foraminifera occurring in some levels of this interval H1s.s. indicate the coldest episodes registered in the whole core.

The instability continues during H1b (16.2-14.8 ka cal BP). Cold waters are evidenced by *H. balthica* and low oxygen indicated by *Globobulimina affinis*, *C. oolina* and *N. turgidus* (Fig. 6). These species are opportunistic, deep infaunal associated with high nutrient and low oxygen content (Table 3) (Bernhard and Sen Gupta, 1999). The oxygen depletion is likely influenced by the AMOC slowdown caused by the massive fresh water discharge from deglaciation by the end of LGM. *Globobulimina affinis* is indicative of dysoxia or even anoxia (Fontanier et al., 2002) and has been previously

associated to massive iceberg discharges during Heinrich events of MIS 4-MIS 2 interval in deeper waters (>2100 m) of the Bay of Biscay (Loncaric et al., 1998; Rodríguez-Lázaro et al., 2017) and also in the Basque shelf during H1 (Martínez-García et al., 2014, 2015). To the top of H1b *G. affinis*, a bathyal species, is replaced by *C. oolina* coincident with high percentage of coastal species (29%; see Fig. 4). *Chilostomella oolina* is typical of dysoxic-anoxic sediments with high OM (Table 3) and replaces *G. affinis* when the quality of OM increases (Fontanier et al., 2002). Thus, shifts of *C. oolina* indicate the amelioration of surface water conditions. This change can be also related to the arrival of surface waters warmer than those from the beginning of H1a and produced by northern displacement of the polar front (Naughton et al., 2009). The same change had been detected in other sites of the Bay of Biscay (Martínez-García et al., 2014, 2015). The end of MIS 2 is marked by an important decrease of the Oceanity Index and diversity (OI = 33; S = 31) (Fig. 4).

From these results we conclude that during MIS 2 benthos in this area was characterised by very cold waters with highly trophic levels and a variable oxygenation. In this interval, H1 is characterised in general by enrichment of organic matter in a low oxygenated benthos. During Heinrich events a big amount of continental ice arrived to the N Atlantic and affected the thermohaline production by reduction of salinity and thus, density of surface waters. The reduction of deep-water formation produced the accumulation of OM in the hypoxic marine bottom (Loncaric et al., 1998). The results based on benthic foraminifera from core PP10-12 support those by Grunert et al. (2015) of the temporal slowdown or even total shutdown of the AMOC during H1 event.

5.3 Bølling-Allerød and Younger Dryas

At the beginning of MIS 1 the Oceanity Index is yet below core average (OI < 60) (Fig. 4) and suboxic specimens dominated (Fig. 5). Nevertheless, during Bølling-Allerød (B/A: 14.8-12.8 ka cal BP), the number of species increased while the occurrence of coastal species drastically decreased (< 12%) (Fig. 4). The increase of disoxic species (> 50%) (Fig. 5) evidences a very low oxygen waters where *B. gibba* dominated. This is a cold to temperate (5°-17°C), extremely eutrophic and anoxic species (Table 3) indicative of low ventilated benthic environments (Fontanier et al., 2002). *B. gibba* is accompanied by *U. peregrina* mostly at the beginning and end of B/A interval (Fig. 6). The relative warming during these two moments could be due to the gradual increase of precipitation and the growing influence of westerlies produced by the reactivation of the AMOC intensity. The warming of B/A had been previously cited in other areas of the Bay of Biscay (Zaragosi et al., 2001; Toucanne et al., 2008; Penaud et al., 2009;

Martínez-García et al., 2014, 2015). In this temperate and extremely dysoxic environment it is registered the entrance of colder waters in particular intervals as Greenland Interstadials GI1d (14.0-13.9 ka cal BP), GI1c2 (13.5 ka cal BP) and GI1b (13.2-13.1 ka cal BP) (Fig. 2). These intervals are identified here by the occurrence of *B. gibba*, *B. subaenariensis*, *C. laevigata* and *C. oolina* (Fig. 6). This cooling might correspond to AMOC oscillations due to freshwater discharges and/or insolation or atmospheric variations related to CO₂ cycle (Liu et al., 2009; Obase and Abe-Ouchi, 2019).

As occurred in the B/A, the Younger Dryas (YD; 12.8-11.7 ka cal BP) started and ended with a strong fall of diversity (YD, $S < 30$; see Fig. 4) as well as with an increase of *U. peregrina* (Fig. 6). The high occurrence of *C. laevigata* during the YD is indicative of the arrival of waters with high OM content (Rasmussen et al., 2002) and *M. affinis* indicates cold waters. These results point to a new cooling, not as strong as H1, probably generated by slowdown of AMOC and southern shift of the polar front (Naughton et al., 2016). The YD cooling has been previously described in the Bay of Biscay by Zaragosi et al. (2001) and Toucanne et al. (2008). These waters progressively warmed during the YD/Lower Holocene-Greenlandian transition since abundant specimens of warm-water foraminifera species, *B. spathulata*, occur at these levels (Fig. 6).

5.4. Holocene

Benthic foraminifera have been used to detect environmental changes in the Holocene, thus Mary et al. (2017), described thermal anomalies in surface waters of the last 10 ka in the Bay of Biscay. Positive (warming) boreal climate would be associated to positive SST during episodes of more intense North Atlantic Current (NAC) in the Subpolar Gyre (SPG). Opposite negative cold anomaly would occur with weaker SPG (Mary et al., 2017).

The beginning of Lower Holocene (Greenlandian; 11.7-8.2 ka cal BP) is characterised by the occurrence of *B. spathulata* indicating warm waters (Table 3). Also appear *U. peregrina*, considered a species typical of the Holocene (Rodríguez-Lázaro et al., 2017) and living in cool to temperate, oxygenated, seasonal flux of high productivity OM waters (Table 3; García et al., 2013). The abundant specimens of *C. laevigata* in some levels indicate the entrance of cool, low oxygen and high OM waters related to upwelling or seasonal flux (Pascual et al., 2008). The OI increases in this stage and reach the maximum value of the core (OI = 94). In this interval of environmental recuperation this elevated OI could be caused by Melt Water Pulse (MWP) 1B

occurred at the YD/Lower Holocene transition (Bard et al., 2010; Carlson and Clark, 2012). The Lower-Middle Holocene (Greenlandian/Nordgrippian) boundary is represented by very cold and dysoxic waters (*H. balthica* and *G. affinis*) (Fig. 6), likely indicative of the Holocene Cooling Event 5 (HCE 5) when climate became colder and dryer due to AMOC slowdown (Alley and Ágústsdóttir, 2005) (8.2 Ka BP; sample 251 cm of core) (see Fig. 2). The occurrence of *B. (B.) nodosaria* (typical T, 15°C; Mathieu, 1986) from the end of Middle Holocene to the end of core points to a warming of the water, with a stable environment (*U. peregrina*) that continued during the Upper Holocene (Megalayan: 4.3-2.4 ka cal BP). To the top of this core (2823-2430 years cal BP) a high concentration of oxygen in waters is detected by abundant individuals of *C. pachyderma*.

6. Conclusions

Benthic foraminifera assemblages allow us to register palaeoceanographic and palaeoclimatic changes in the SE Bay of Biscay during last 37 ka (MIS 3-MIS 1). Quantification of the ecology of main species, diversity, Oceanity Index (OI), percentages of coastal allochthonous and oxygen and organic matter content species permit characterizing environmental parameters as thermal character, oxygenation and productivity and to relate them to climate modifications. On the other side, taxonomic identification of 176 benthic foraminifera species is a contribution to the knowledge of the Quaternary palaeodiversity of the Bay of Biscay.

MIS 3 is characterized by benthic cool waters dominated by the species *C. laevigata* and *U. peregrina*. The entrance of colder waters by the end of MIS 3 is detected by decreasing of diversity (number of species, S) and OI, as well as by the occurrence of *M. affinis*, a typical cold and low-oxygen species. These conditions persisted at the beginning of MIS 2.

In the stadial H1 benthic foraminifera allow us to consider three phases (H1a, H1s.s, H1b). This event is the coldest registered in this work. During H1s.s. waters were extremely cold and the environment was unstable with oscillations of oxygenation of the bottom. During H1b the occurrence of *G. affinis* indicates anoxia in the benthos. To the end of H1b foraminifera indicate the arrival of warmer waters.

The beginning of Bølling-Allerød (B/A) is characterized by the occurrence of suboxic species and the absence of coastal individuals. During the Bølling-Allerød (B/A) *B. gibba* dominated, indicative of warmer and low ventilated waters. Nevertheless, during

B/A punctual influence of colder waters is detected in Greenland Interstadials (GI1d, GIc2 y GI1b).

Cassidulina laevigata is dominant during the Younger Dryas indicating cool, low oxygenated and high organic matter waters.

Lower Holocene waters in the Bay of Biscay tempered as evidenced by species *U. peregrina* and *B. spathulata*. To this milder environment intermittently arrived colder, low-oxygen and high organic matter waters produced by upwelling processes. In the Lower- Middle Holocene boundary waters became colder and dysoxic as evidenced by *H. balthica* and *G. affinis*, characterising the Holocene Cooling Event 5. The Middle and Upper Holocene waters were warmer than previous times (*U. peregrina*, *B. (B.) nodosaria*) and waters were more oxygenated in recent times as indicated by *C. pachyderma*.

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Appendix 1. Benthic foraminifera assemblages indicative of oxygen content (Kahio, 1994, 1999).

Dysoxia indicators ($O_2 = 0.1-0.3$ ml/l): *Bolivina alata*, *Bolivina earlandi*, *Bolivina italica*, *Bolivina pseudoplicata*, *Bolivina pygmaea*, *Bolivina spathulata*, *Bolivina subaenariensis*, *Bulimina gibba*, *Bulimina marginata*, *Bulimina striata*, *Chilostomella oolina*, *Chilostomella ovoidea*, *Eubuliminella exilis*, *Fursenkoina complanata*, *Fursenkoina bradyi*, *Globobulimina affinis*, *Globobulimina auriculata*, *Globobulimina pyrula*, *Globobulimina* sp. cf. *ovula*.

Suboxia indicators ($O_2 = 0.3-1.5$ ml/l): *Bolivinita quadrilatera*, *Cassidulina laevigata*, *Seguenzaella lacunata*, *Evolvocassidulina bradyi*, *Favulina squamosa*, *Fissurina cucullata*, *Fissurina lucida*, *Fissurina marginata*, *Fissurina orbignyana*, *Grigelis guttiferus*, *Gyroidina umbonata*, *Hansenisca soldanii*, *Hoeglundina elegans*, *Homalohedra acuticosta*, *Hyalinonetrion gracillima*, *Laevidentalina advena*,

Laevidentalina elegans, *Laevidentalina filiformis*, *Laevidentalina inornata*,
Laevidentalina subsoluta, *Lagena elongata*, *Lagena hispidula*, *Lagena semistriata*,
Lagena striata, *Lagena substriata*, *Lagena sulcata*, *Lenticulina calcar*, *Lenticulina*
gibba, *Lenticulina iota*, *Lenticulina orbicularis*, *Melonis affinis*, *Melonis pompilioides*,
Neolenticulina peregrina, *Neouvigerina proboscidea*, *Nonion boueanum*, *Nonion*
commune, *Nonionellina labradorica*, *Nonionella* sp. cf. *bradii*, *Nonionoides turgidus*,
Oolina globosa, *Parafissurina malcolmsonii*, *Pseudononion japonicum*, *Pullenia*
bulloides, *Pullenia quinqueloba*, *Reussolina laevis*, *Siphogenerina columellaris*,
Sphaeroidina bulloides, *Stainforthia fusiformis*, *Trifarina angulosa*, *Trifarina bradyi*,
Uvigerina asperula, *Uvigerina auberiana*, *Uvigerina canariensis*, *Uvigerina cushmani*,
Uvigerina peregrina, *Valvulineria bradyana*.

Oxia indicators ($O_2 > 1.5$ ml/l): *Adelosina longirostra*, *Adelosina pulchella*, *Bulimina*
truncana, *Cibicides refulgens*, *Cibicidoides wuellerstorfi*, *Cibicidoides pachyderma*,
Cibicidoides pseudoungeriana, *Globocassidulina crassa*, *Globocassidulina*
subglobosa, *Pyrgo bulloides*, *Pyrgo denticulata*, *Pyrgo elongata*, *Pyrgo ringens*, *Pyrgo*
laevis, *Pyrgo lucernula*, *Pyrgo murrhina*, *Pyrgo williamsoni*, *Quinqueloculina*
lamarckiana, *Quinqueloculina lata*, *Quinqueloculina seminula*, *Sigmopyrgo vespertilio*,
Triloculina tricarinata, *Triloculina trigonula*, *Triloculina oblonga*.

Appendix 2. Benthic foraminifera coastal species present in core PP10-12. The list includes species living in coastal and estuarine settlements of Bay of Biscay (Pujos-Lamy, 1973; Cearreta, 1988, 1989; Pascual and Rodríguez-Lázaro, 2006, Pascual et al., 2008, 2019; Martínez-García et al., 2013).

Ammonia beccarii, *Asterigerinata mamilla*, *Cibicidoides lobatulus*, *Criboelphidium*
excavatum, *Criboelphidium gerthi*, *Elphidium articulatum*, *Elphidium crispum*, *Entzia*
macrescens, *Haynesina depressula*, *Miliolinella circularis*, *Miliolinella elongata*,
Miliolinella subrotunda, *Nonion commune*, *Planorbulina mediterraneensis*, *Porosonion*
granosum, *Quinqueloculina seminula*, *Quinqueloculina lata*, *Rosalina globularis*
Rosalina irregularis, *Rosalina williamsoni*, *Triloculina oblonga*, *Trochammina inflata*

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FIGURE CAPTIONS

Figure 1. A) Location of study area with indication of core PP10-12 (white circle), general oceanic circulation (IPC, Iberian Poleward Current; Navidad Current; NAC, North Atlantic Circulation; ESC, European Slope Current). Yellow discontinuous line indicates the profile of Fig. 1B. B) Main water masses (ENACW_P, subpolar East North Atlantic Central Water; MOW, Mediterranean Outflow Water; NEADW_U, North East Atlantic Deep Water upper component; NEADW_L, North East Atlantic Deep Water lower component; AABW, Antarctic Bottom Water) of the Bay of Biscay. Map modified from Mulder et al. (2012); water masses modified from Castaño-Carrera et al. (2012).

Figure 2. Chronostratigraphy of core PP10-12 based on correlation of percentage of *Neogloboquadrina pachyderma* sin (Npsin) with marine reference core MD95-2042 and ice core NGRIP-GICC05 (2014-12-10 version). Little arrows indicate AMS¹⁴C dates. Tie-points correspond to Heinrich events (H), Greenland stadials (GS), Greenland interstadials (GI), Holocene Cooling Events (HCE) and other warm/cold events registered in Table 1. Grey dashed lines indicate interpretative tie-points. Ages of events from Rasmussen et al. (2014) and Gottschalk et al. (2015). LGM, Last Glacial Maximum; BA, Bølling-Allerød; YD, Younger Dryas; LH, Lower Holocene (Green., Greenlandian); MH, Middle Holocene (North., Northgrippian); UH, Upper Holocene (Megh., Meghalayan).

Figure 3. Age model of core PP10-12 based on 11 dates, 29 tie-points and 11 interpretative tie-points (Table 1). A) Age/core depth correlation (cm) with stratigraphic units (MIS3 to MIS1, with H1, GI1, B/A and Holocene sub-units). Cold Heinrich Events

and Younger Dryas are in grey. Blue stars are AMS ^{14}C ; orange rectangles, tie-points from core NGRIP; green circles, tie-points from core MD95-2042; black rectangles and circles, interpretative tie-points from cores NGRIP and MD95-2042, respectively. B) Age/core depth non-linear logistic analysis of core PP10-12 (rectangles, interpretative tie-points). Correlation $r^2 = 0.98$, calculated with PAST software (Hammer et al., 2001). Acronyms as in Fig. 2.

Figure 4. Occurrence of benthic foraminifera species number (S), and percentages of coastal species, altered specimens and Oceanity Index of core PP10-12. In top of figure main chronostratigraphic units and limits are indicated. H, Heinrich Events. Figure bottom with tie-points (black) and interpretative tie-points (grey) identified in the age model (see Table 1). Green, Holocene Cooling Events; orange, Greenland interstadials; blue, Greenland stadials and Heinrich Events (H). Ages of events from Rasmussen et al. (2014) and Gottschalk et al. (2015). Acronyms as in Fig. 2.

Figure 5. Distribution of benthic foraminifera assemblages characteristic of oxygen level in sediments (Oxic, Suboxic, Dysoxic) in core PP10-12. Details in Table 3. Legend as in Fig. 4.

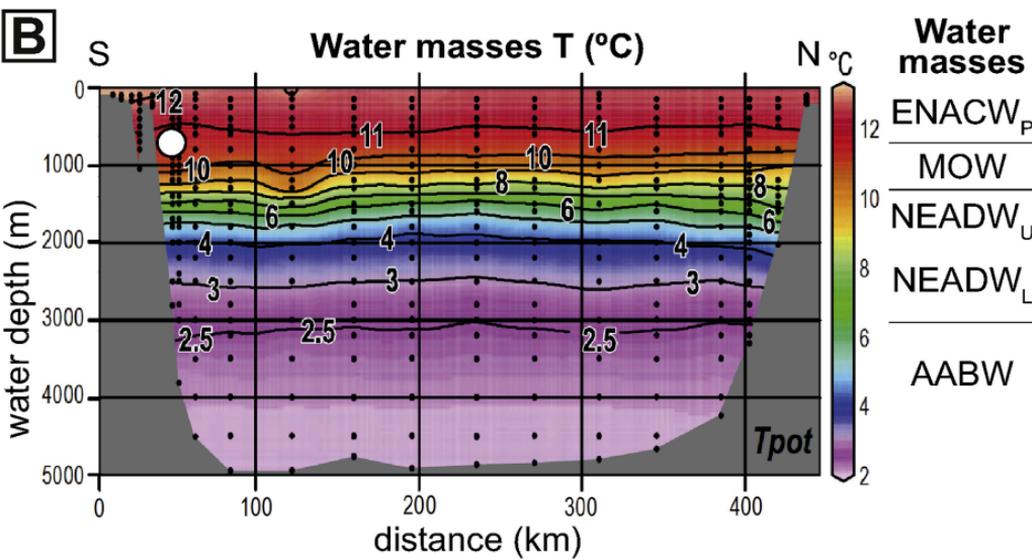
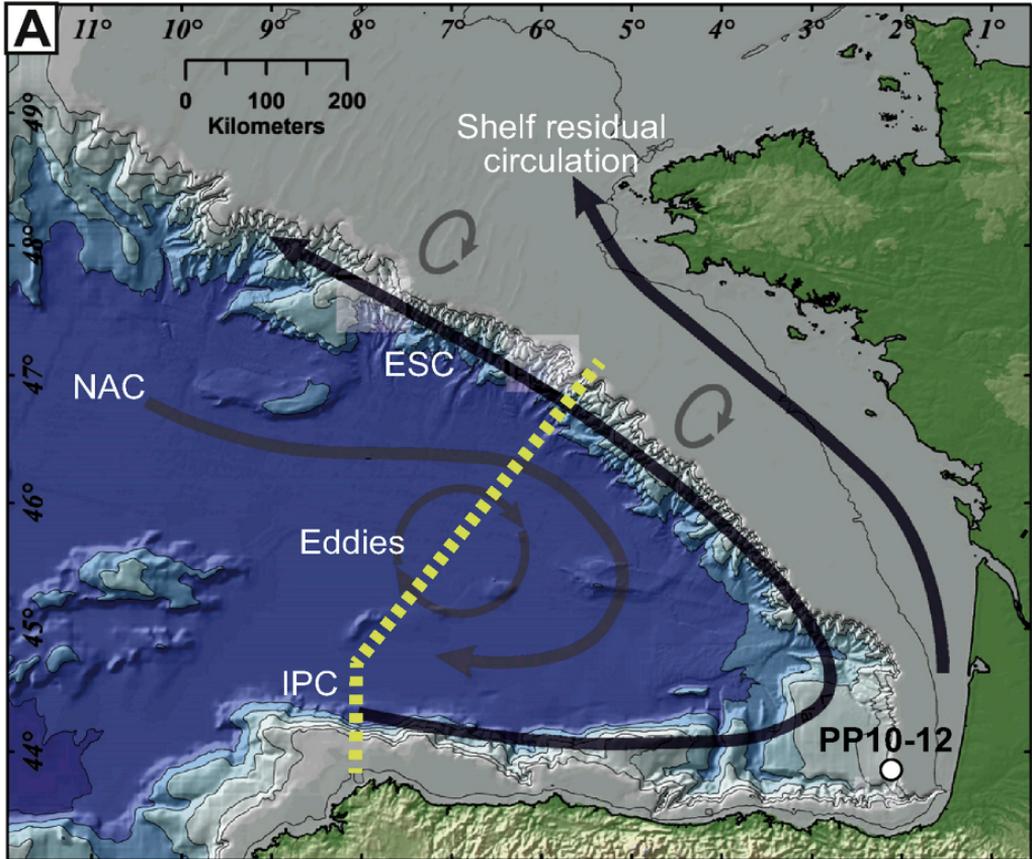
Figure 6. Distribution of percentages of main benthic foraminifera of core PP10-12. Legend as in Fig. 4.

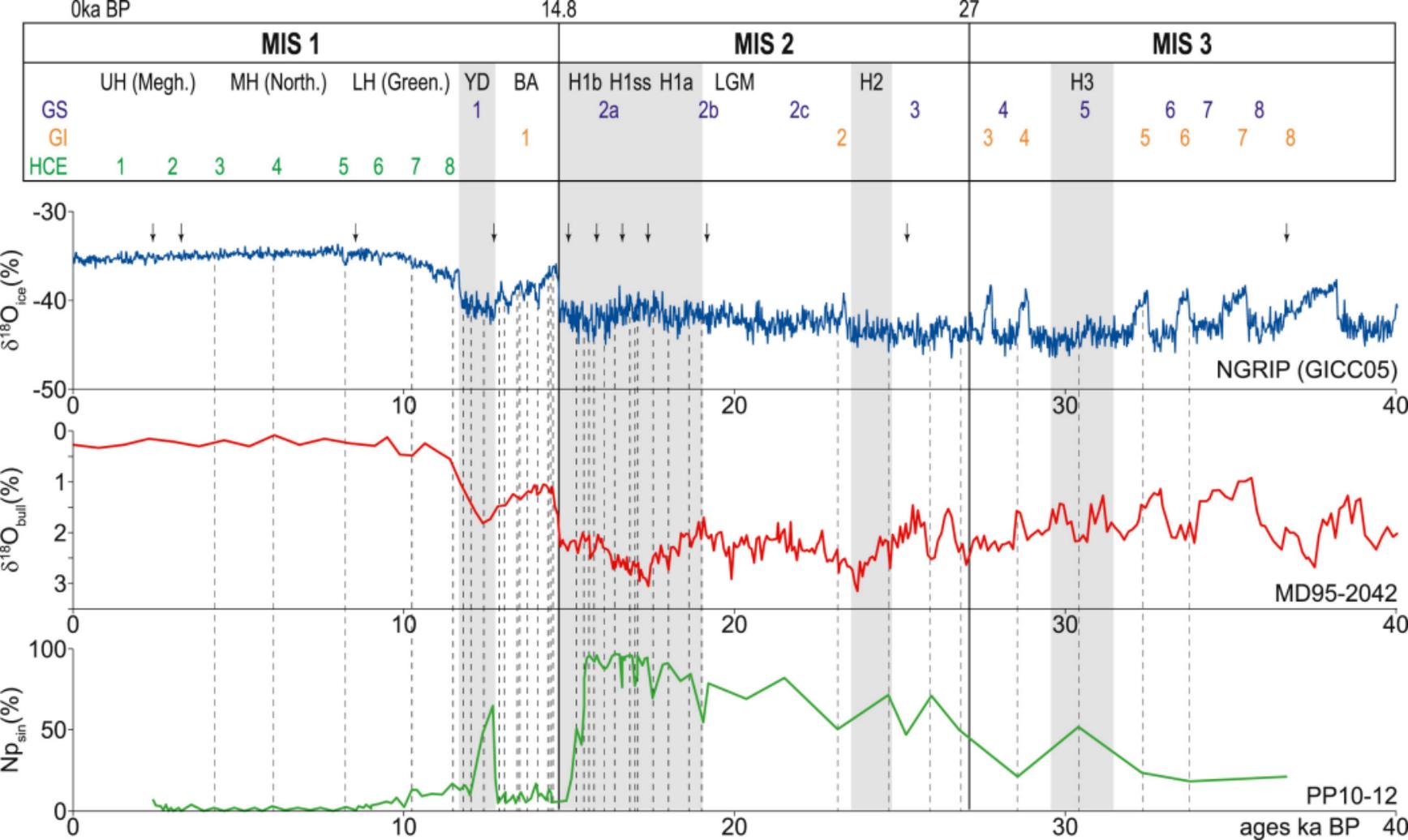
CAPTIONS OF TABLES

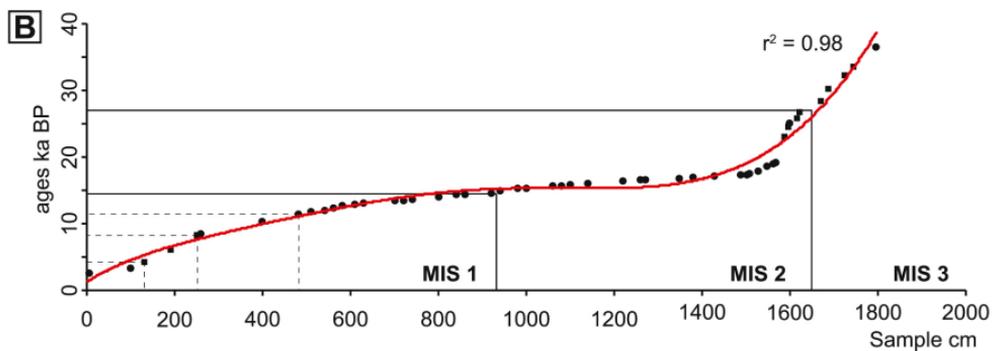
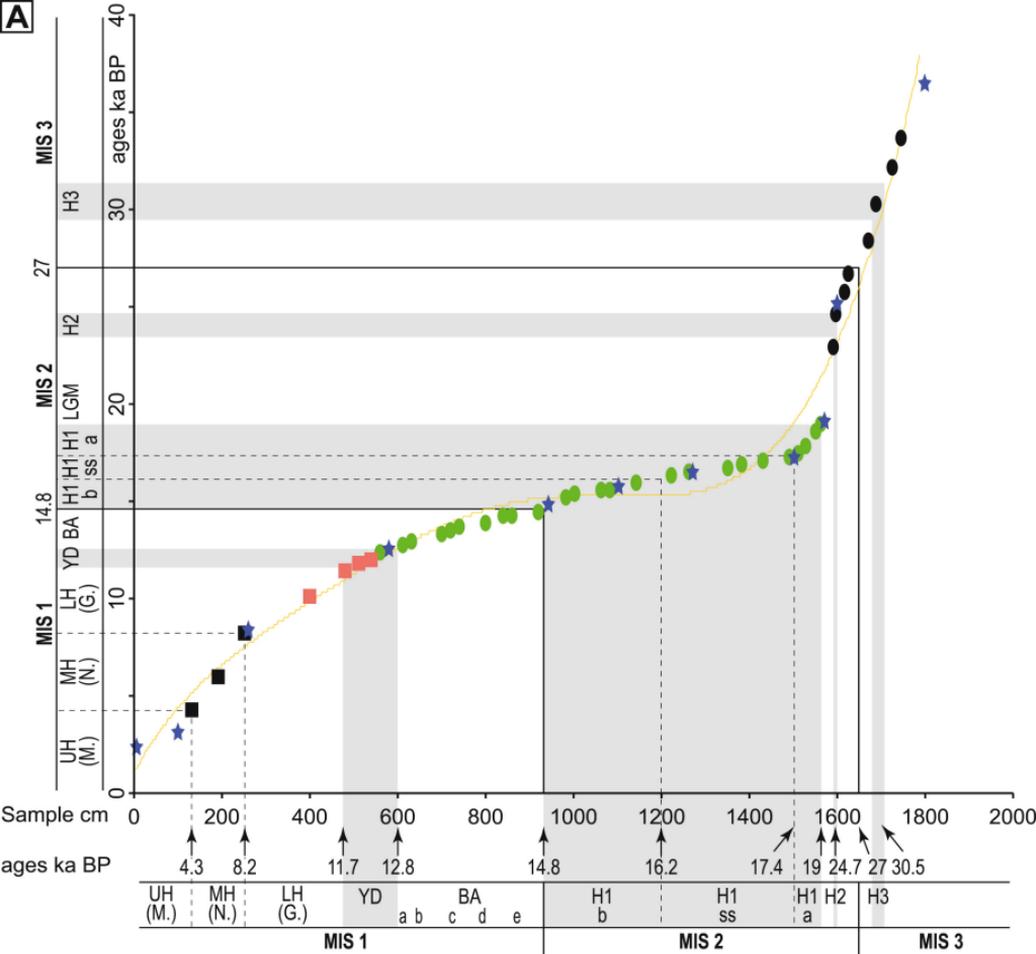
Table 1. Calibrated ages used for the age model of core PP10-12 and tie-points identified as indicated in Fig. 2.

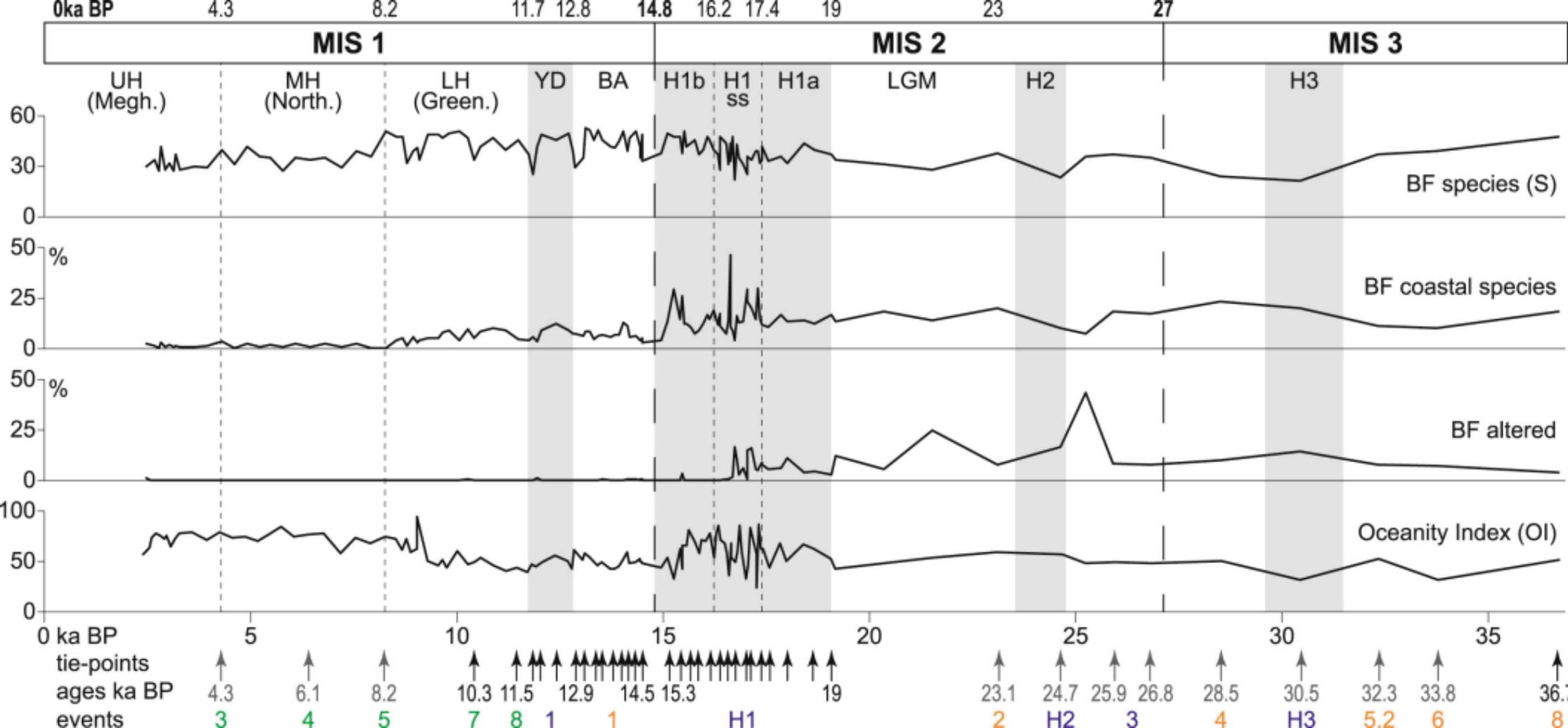
Table 2. Benthic foraminifera species identified from core PP10-12.

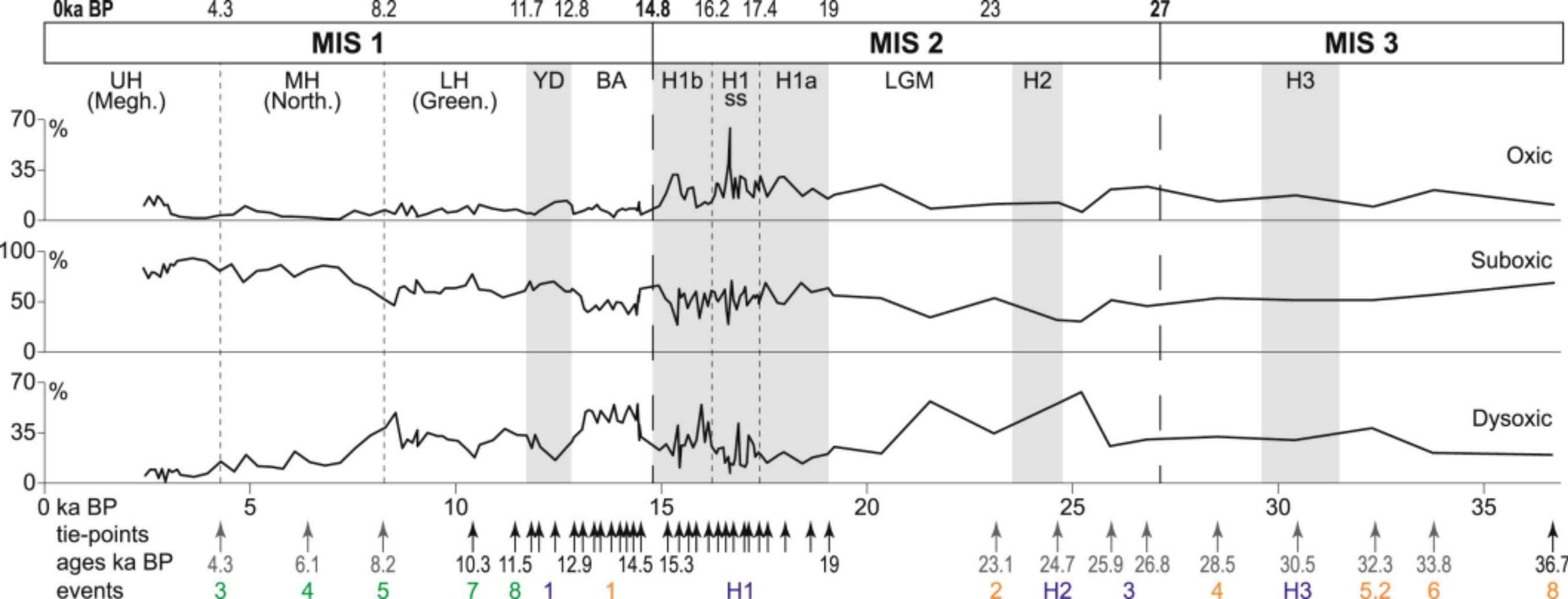
Table 3. Ecological preferences of most characteristic benthic foraminifera species used as proxy for deep-sea changes in core PP10-12.

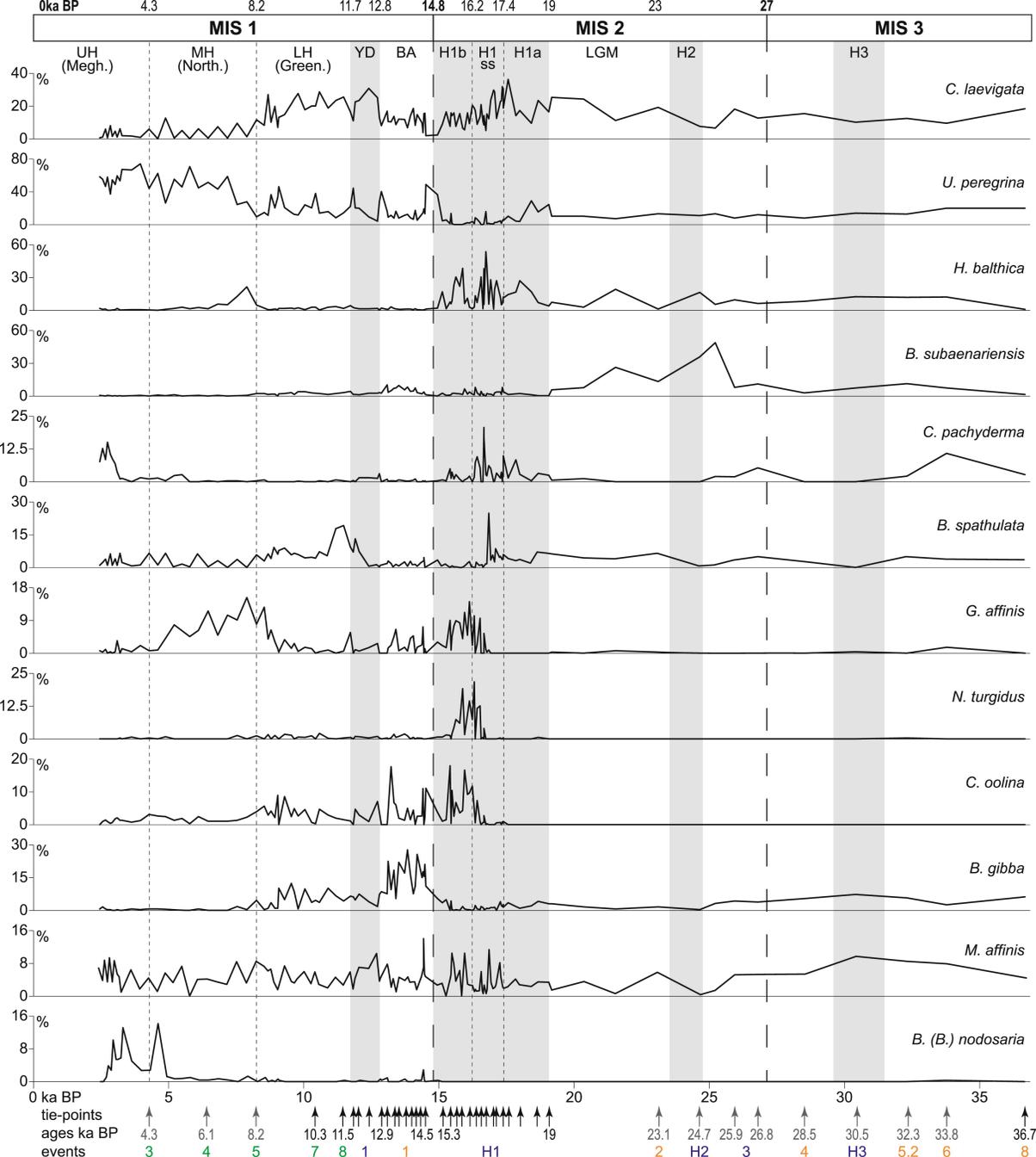












SUPPLEMENTARY MATERIAL

Benthic foraminifera species from core PP10-12 used in this work and counting for more than 10% of individuals in at least 3 samples. Number of specimens and species per sample, Oceanity Index (OI), number of altered tests and thanathocenotic coastal individuals are indicated. The number of specimens indicative of oxygen level (dysoxia, suboxia, oxia) is also depicted.

Journal Pre-proof

core depth (cm)	¹⁴ C age (yrs BP)	Calibrated date 2σ range (cal. yrs BP)	Calibrated date (cal. yrs BP) mean probability
7	2730 +/- 30	2331 - 2574	2430
101	3400 +/- 30	3174 - 3356	3270
261	8080 +/- 30	8437 - 8617	8540
581	11230 +/- 40	12608 - 12823	12710
941	13000 +/- 50	14681 - 15175	14960
1096	13600 +/- 40	15695 - 16037	15860
1276	14180 +/- 50	16405 - 16910	16650
1501	14680 +/- 40	17193 - 17562	17400
1570	16320 +/- 50	18999 - 19401	19190
1600	21300 +/- 80	24973 - 25507	25230
1797	33160 +/- 210	36183 - 37536	36710

core depth (cm)	Date calendar age (yrs BP)	Event	Stratigraphic correlation
131	4280	HCE3	NGRIP
191	6080	HCE4	NGRIP
251	8260	HCE5	NGRIP
401	10280	HCE7	NGRIP
481	11480	HCE8	NGRIP
511	11840	inter-YD cold event	NGRIP
541	12060	inter-YD warm event	NGRIP
561	12400	inter-YD cold event	MD95-2042
611	12860	G11a	MD95-2042
631	13080	G11b	MD95-2042
701	13422	G11c1	MD95-2042
721	13520	G11c2	MD95-2042
741	13740	G11c3	MD95-2042
801	14040	G11d	MD95-2042
841	14360	warm G11e	MD95-2042
861	14420	cold G11e	MD95-2042
921	14500	warm G11e	MD95-2042
981	15260	inter-H1b cold event	MD95-2042
1001	15420	inter-H1b warm event	MD95-2042
1061	15640	inter-H1b cold event	MD95-2042
1081	15760	inter-H1b warm event	MD95-2042
1141	16060	inter-H1b warm event	MD95-2042
1221	16400	inter-H1ss cold event	MD95-2042
1261	16620	inter-H1ss warm event	MD95-2042

1349	16860	inter-H1ss cold event	MD95-2042
1381	17020	inter-H1ss warm event	MD95-2042
1429	17120	inter-H1ss cold event	MD95-2042
1489	17380	inter-H1ss cold event	MD95-2042
1509	17560	inter-H1a warm event	MD95-2042
1527	18000	inter-H1a cold event	MD95-2042
1549	18660	inter-H1a cold event	MD95-2042
1561	19060	inter-H1a warm event	MD95-2042
1589	23100	G12	MD95-2042
1595	24660	H2	MD95-2042
1617	25940	inter-GS3 cold event	MD95-2042
1623	26820	inter-GS3 cold event	MD95-2042
1670	28540	G14	MD95-2042
1688	30440	H3	MD95-2042
1725	32320	G15.2	MD95-2042
1744	33780	G16	MD95-2042

<i>Adelosina longirostra</i> (d'Orbigny, 1846)	<i>Gavelinopsis translucens</i> (Phleger & Parker, 1951)	<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826
<i>Adelosina pulchella</i> (d'Orbigny, 1826)	<i>Glandulina ovula</i> d'Orbigny, 1846	<i>Planulina ornata</i> (d'Orbigny, 1839)
<i>Alveolophragmium orbiculatum</i> Shchedrina, 1936	<i>Globobulimina affinis</i> (d'Orbigny, 1839)	<i>Pleurostomella</i> sp.
<i>Ammonia beccarii</i> (Linnaeus, 1758)	<i>Globobulimina auriculata</i> (Bailey, 1894)	<i>Porosonion granosum</i> (d'Orbigny, 1846)
<i>Amphicoryna bradyi</i> (Silvestri, 1902)	<i>Globobulimina pyrula</i> (d'Orbigny, 1846)	<i>Pseudonodosinella nodulosa</i> (Brady, 1879)
<i>Amphicoryna hirsuta</i> (d'Orbigny, 1826)	<i>Globobulimina</i> sp. <i>ccff. ovula</i> (d'Orbigny, 1839)	<i>Pseudononion japonicum</i> Asano, 1936
<i>Amphicoryna intercellularis</i> (Brady, 1881)	<i>Globocassidulina crassa</i> (d'Orbigny, 1839)	<i>Pullenia bulloides</i> (d'Orbigny, 1846)
<i>Amphicoryna scalaris</i> (Batsch, 1791)	<i>Globocassidulina subglobosa</i> (Brady, 1881)	<i>Pullenia quinqueloba</i> (Reuss, 1851)
<i>Amphicoryna separans</i> (Brady, 1884)	<i>Globulina gibba</i> (d'Orbigny in Deshayes, 1832)	<i>Pyrgo bulloides</i> (d'Orbigny, 1826)
<i>Astacolus crepidulus</i> (Fichtel & Moll, 1798)	<i>Grigelis guttiferus</i> (d'Orbigny, 1846)	<i>Pyrgo elongata</i> (d'Orbigny, 1826)
<i>Asterigerinata mamilla</i> (Williamson, 1858)	<i>Grigelis orectus</i> Loeblich & Tappan, 1994	<i>Pyrgo denticulata</i> (Brady, 1884)
<i>Bigenerina (Bigenerina) nodosaria</i> d'Orbigny, 1826	<i>Gyroidina umbonata</i> (Silvestri, 1898)	<i>Pyrgo laevis</i> Defrance, 1824
<i>Bolivina alata</i> (Seguenza, 1862)	<i>Hansenisca soldanii</i> (d'Orbigny, 1826)	<i>Pyrgo lucernula</i> (Schwager, 1866)
<i>Bolivina earlandi</i> Parr, 1950	<i>Haynesina depressula</i> (Walker & Jacob, 1798)	<i>Pyrgo murrhina</i> (Schwager, 1866)
<i>Bolivina italica</i> Cushman, 1936	<i>Hoeglundina elegans</i> (d'Orbigny, 1826)	<i>Pyrgo ringens</i> (Lamarck, 1804)
<i>Bolivina pseudoplicata</i> Heron-Allen & Earland, 1930	<i>Homalhedra acuticosta</i> (Reuss, 1862)	<i>Pyrgo williamsoni</i> (Silvestri, 1923)
<i>Bolivina pygmaea</i> (Brady, 1881)	<i>Hyalinea balthica</i> (Schröter in Gmelin, 1791)	<i>Pyrgoella irregularis</i> (d'Orbigny, 1839)
<i>Bolivina spathulata</i> (Williamson, 1858)	<i>Hyalinonetron gracillima</i> (Seguenza, 1862)	<i>Pyrgoella sphaera</i> (d'Orbigny, 1839)
<i>Bolivina subaenariensis</i> Cushman, 1922	<i>Karriella bradyi</i> (Cushman, 1911)	<i>Pyrulina angusta</i> (Egger, 1857)
<i>Bolivinita quadrilatera</i> (Schwager, 1866)	<i>Karriella novangliae</i> (Cushman, 1922)	<i>Pyrulina cylindroides</i> (Roemer, 1838)
<i>Buccella frigida</i> (Cushman, 1922)	<i>Laeidentalina advena</i> (Cushman, 1923)	<i>Quinqueloculina lamarkiana</i> d'Orbigny, 1839
<i>Bulimina aculeata</i> d'Orbigny, 1826	<i>Laeidentalina elegans</i> (d'Orbigny, 1846)	<i>Quinqueloculina lata</i> Terquem, 1876
<i>Bulimina gibba</i> Fornasini, 1902	<i>Laeidentalina filiformis</i> (d'Orbigny, 1826)	<i>Quinqueloculina seminula</i> (Linnaeus, 1758)
<i>Bulimina marginata</i> d'Orbigny, 1826	<i>Laeidentalina inornata</i> (d'Orbigny, 1846)	<i>Reophax curtus</i> Cushman, 1920
<i>Bulimina truncana</i> Gumbel, 1868	<i>Laeidentalina subsoluta</i> (Cushman, 1923)	<i>Reophax scorpiurus</i> Montfort, 1808
<i>Bulimina striata</i> d'Orbigny, in Guérin-Méneville, 1832	<i>Lagena elongata</i> Dunikowski, 1879	<i>Reusoolina laevis</i> (Montagu, 1803)
<i>Cancris auricula</i> (Fichtel & Moll, 1798)	<i>Lagena hispidula</i> Cushman, 1913	<i>Rosalina globularis</i> d'Orbigny, 1826
<i>Cassidulina laevigata</i> d'Orbigny, 1826	<i>Lagena semistriata</i> Williamson, 1848	<i>Rosalina irregularis</i> (Rhumbler, 1906)
<i>Chilostomella oolina</i> Schwager, 1878	<i>Lagena striata</i> (d'Orbigny, 1839)	<i>Rosalina williamsoni</i> (Chapman & Parr, 1932)
<i>Chilostomella ovoidea</i> Reuss, 1850	<i>Lagena substriata</i> Williamson, 1848	<i>Sahulia conica</i> (d'Orbigny, 1839)
<i>Cibicides refulgens</i> de Montfort, 1808	<i>Lagena sulcata</i> (Walker & Jacob, 1798)	<i>Seguenzaella lacunata</i> (Burrows & Holland, 1895)
<i>Cibicoides lobatulus</i> (Walker & Jacob, 1798)	<i>Lenticulina calcar</i> (Linnaeus, 1758)	<i>Sigmoilopsis schlumbergeri</i> (Silvestri, 1904)
<i>Cibicoides pachyderma</i> (Rzehak, 1886)	<i>Lenticulina gibba</i> (d'Orbigny, 1826)	<i>Sigmomorphina</i> sp.
<i>Cibicoides pseudoungeriana</i> (Cushman, 1922)	<i>Lenticulina iota</i> (Cushman, 1923)	<i>Sigmopyrgo vespertilio</i> (Schlumberger, 1891)
<i>Cibicoides wuellerstorfi</i> (Schwager, 1866)	<i>Lenticulina orbicularis</i> (d'Orbigny, 1826)	<i>Siphogenerina columellaris</i> (Brady, 1881)
<i>Cornuspira carinata</i> (Costa, 1856)	<i>Lingulina carinata</i> d'Orbigny, 1826	<i>Siphotextularia concava</i> (Karrer, 1868)
<i>Cornuspira foliacea</i> (Philippi, 1844)	<i>Lingulina seminuda</i> Hantken, 1875	<i>Siphouvigerina proboscidea</i> (Schwager, 1866)
<i>Criboelphidium excavatum</i> (Terquem, 1875)	<i>Marginulina obesa</i> Cushman, 1923	<i>Sphaeroidina bulloides</i> d'Orbigny in Deshayes, 1828
<i>Criboelphidium gerthi</i> Van Voorthuysen, 1957	<i>Marginulina similis</i> d'Orbigny, 1846	<i>Spirillina vivipara</i> Ehrenberg, 1843
<i>Cyclammina cancellata</i> Brady, 1879	<i>Marginulinopsis bradyi</i> (Goës, 1894)	<i>Spiroloculina excavata</i> d'Orbigny, 1846
<i>Discorbinella bertheloti</i> (d'Orbigny, 1839)	<i>Marginulinopsis tenuis</i> (Bornemann, 1855)	<i>Spiroloculina henbesti</i> Petri, 1955
<i>Dorothyia pseudoturris</i> (Cushman, 1922)	<i>Melonis affinis</i> (Reuss, 1851)	<i>Spiroloculina nitida</i> d'Orbigny, 1826
<i>Edentostomina cultrata</i> (Brady, 1881)	<i>Melonis pompilioides</i> (Fichtel & Moll, 1798)	<i>Stainforthia fusiformis</i> (Williamson, 1848)
<i>Eggerella bradyi</i> (Cushman, 1911)	<i>Miliolinella elongata</i> Kruit, 1955	<i>Textularia agglutinans</i> d'Orbigny, 1839
<i>Elphidium articulatum</i> (d'Orbigny, 1839)	<i>Miliolinella circularis</i> (Bornemann, 1855)	<i>Textularia pseudogramen</i> Chapman & Parr, 1937
<i>Elphidium crispum</i> (Linnaeus, 1758)	<i>Miliolinella subrotunda</i> (Montagu, 1803)	<i>Textularia sagittula</i> Defrance, 1824
<i>Entzia macrescens</i> (Brady, 1870)	<i>Neononorbina terquemi</i> (Rzehak, 1888)	<i>Trifarina angulosa</i> (Williamson, 1858)
<i>Eponides repandus</i> (Fichtel & Moll, 1798)	<i>Neolenticulina variabilis</i> (Reuss, 1850)	<i>Trifarina bradyi</i> Cushman, 1923
<i>Eubuliminella exilis</i> (Brady, 1884)	<i>Nodosaria simplex</i> Silvestri, 1872	<i>Triloculina oblonga</i> (Montagu, 1803)
<i>Evolvocassidulina bradyi</i> (Norman, 1881)	<i>Nonion boueanum</i> (d'Orbigny, 1846)	<i>Triloculina tricarinata</i> d'Orbigny in Deshayes, 1826
<i>Favulina hexagona</i> (Williamson, 1848)	<i>Nonion commune</i> (d'Orbigny, 1846)	<i>Triloculina trigonula</i> (Lamarck, 1804)
<i>Favulina squamosa</i> (Montagu, 1803)	<i>Nonionella</i> sp. <i>ccff. bradyi</i> (Chapman, 1917)	<i>Trochammina inflata</i> (Montagu, 1808)
<i>Fissurina cucullata</i> Silvestri, 1902	<i>Nonionella labradorica</i> (Dawson, 1860)	<i>Uvigerina asperula</i> Czjzek, 1848
<i>Fissurina marginata</i> (Montagu, 1803)	<i>Nonionoides turgidus</i> (Williamson, 1858)	<i>Uvigerina auferiana</i> d'Orbigny, 1839
<i>Fissurina (Fissurina) orbignyana</i> Seguenza, 1862	<i>Oolina globosa</i> (Montagu, 1803)	<i>Uvigerina canariensis</i> d'Orbigny, 1839
<i>Fissurina lucida</i> (Williamson, 1848)	<i>Orthomorphina perversa</i> (Schwager, 1866)	<i>Uvigerina cushmani</i> Todd, 1948
<i>Fursenkoina bradyi</i> (Cushman, 1922)	<i>Parafissurina malcolmsonii</i> (Wright, 1911)	<i>Uvigerina peregrina</i> Cushman, 1923
<i>Fursenkoina complanata</i> (Egger, 1893)	<i>Patellina corrugata</i> Williamson, 1858	<i>Valvulinera bradyana</i> (Fornasini, 1900)
<i>Gavelinopsis praegeri</i> (Heron-Allen & Earland, 1913)	<i>Pileolina patelliformis</i> (Brady, 1884)	

Species	Microhabitat	Ecological preference
<i>Cassidulina laevigata</i> (d'Orbigny, 1826)	Shallow infaunal (Fontanier et al., 2002)	<i>Cassidulina laevigata</i> is an opportunistic species adapted to high food concentration (Baas et al., 1998), related to high flux of organic carbon (>3 gC/m ² /yr) (Jorissen et al., 2007). It is common in areas with seasonal intermittent organic matter (OM) fluxes (Rasmussen et al., 2002). Suboxic species (Kaiho, 1994), though it can be present in shallow, well oxygenated microhabitats with elevated flux of OM (Stigter et al., 1998). It is related with upwelling currents (Levy et al., 1995). In Portugal it occurs during glacial periods, with maxima coincident with palaeoproductivity (Baas et al., 1998). <i>C. laevigata</i> is also common during MIS 4 and LGM in deep sites from the Bay of Biscay, SW of Landas shelf (Rodriguez-Lazaro et al., 2017).
<i>Uvigerina peregrina</i> Cushman, 1923	Shallow/intermediate infaunal (Fontanier et al., 2002; Singh et al., 2015)	<i>Uvigerina peregrina</i> is a cold-cool water species (2°-15°C) (Murray, 1991). It occurs in sediments rich in OM (Seiglie, 1968; Fontanier et al., 2002; Singh et al., 2015) with high flux of organic carbon (2-3 g/m ² a) (Altenbach, 1988). Typical of mesotrophic and oligotrophic environments (Mojtahid et al., 2010), indicating high productivity (Lutze, 1986; Rai and Singh, 2012; Patarroyo and Martinez, 2016). This species suggests strong seasonality with OM and/or phytodetritus exported from the surface (García et al., 2013). It is suboxic (Kaiho, 1994) and adapted to low-moderate oxygen content (Lutze, 1986; Singh et al., 2015). It can be the main species in upwelling areas (Debenay and Konate, 1987). Its occurrence seems to be influenced by the upper North Atlantic Deep Water (NADW) or the Circumpolar Deep Water (CDW) (Schnitker, 1979). It is also common during MIS 1 from deep areas of the Bay of Biscay (Rodriguez-Lazaro et al., 2017).
<i>Hyalinea balthica</i> (Schröter, 1783)	Shallow/intermediate infaunal (Singh et al., 2015; Fontanier et al., 2002)	<i>Hyalinea balthica</i> is very abundant in N Atlantic cold water masses (Murray, 1973). Dominant species during glacials (Martins and Ruivo Dragao Gomes, 2004), with high percentages during MIS 3, 2, and lower during the Holocene (Ross, 1984). It is considered an opportunistic species that benefits of food availability (Hess and Jorissen, 2009; Rosenthal et al., 2011). Characteristic of low-oxygen sediments with elevated oceanic productivity (Martins and Ruivo Dragao Gomes, 2004), it can be found living in deep sediments with total anoxia (Rosenthal et al., 2011). It is dominant species in the Cap Breton Canyon (N Atlantic), into high OM, mesotrophic to eutrophic, low-oxygen sediments (Hess and Jorissen, 2009), evidencing an early phase of ecosystem recolonisation after turbiditic deposition.
<i>Bolivina subaenariensis</i> Cushman, 1922	Shallow infaunal (Fontanier et al., 2002)	<i>Bolivina subaenariensis</i> is a cold water species (Murray, 2006), characteristic of hypoxic environments it can live in low oxygen sediments with H ₂ S (Pujos-Lamy, 1973). Then it is a proxy species of dysoxic sediments (Kaiho, 1994). It is more abundant when terrigenous decrease and biogenic components increase in sediment (Levy et al., 1995), being dominant in silty, high OM sediments related to upwellings (Sen Gupta et al., 1981). Species associated, together with <i>H. balthica</i> with high OM, low oxygen sediments in meso-eutrophic environments. It is dominant species in the Cap Breton Canyon (N Atlantic) (Hess and Jorissen, 2009) and Saint-Tropez Canyon in the Mediterranean (Fontanier et al., 2008), both species evidencing an early phase of ecosystem recolonisation after turbiditic deposition.
<i>Cibicidoides pachyderma</i> (Rzehak, 1886)	Shallow infaunal (Fontanier et al., 2002)	<i>Cibicidoides pachyderma</i> is present in waters with T higher than 5°C (Healey et al., 2008) and high oxygen content (Schmiedl et al., 2000; Kuhnt et al., 2007). This species lives in oligo-mesotrophic areas (Schmiedl et al., 2000). It is indicator of low to moderate OM availability (Kuhnt et al., 2007) and high energy environments (Kitazato, 1994).
<i>Bolivina spathulata</i> (Williamson, 1858)	Shallow infaunal (Singh et al., 2015)	<i>Bolivina spathulata</i> inhabits waters with T range of 17-25°C (Murray, 2006). It is abundant in poor oxygen, rich OM with elevated productivity environments (Alavi, 1988). It is a species indicator of dysoxia (Kaiho, 1994) (O ₂ : 0.1-0.3 ml/l). Their populations increase rapidly with phytoplankton bloom produced by upwelling (Diz et al., 2006). It stands a wide variety of hydrographic bottom conditions (Singh et al., 2015).
<i>Globobulimina affinis</i> (d'Orbigny, 1839)	Deep infaunal (Fontanier et al., 2002; Geslin et al., 2004)	<i>Globobulimina</i> is a cold water genus. <i>Gl. affinis</i> is bathyal and lives in high OM sediments (Fontanier et al., 2005), in high productivity and low oxygen areas (Hayek and Wilson, 2013; Patarroyo and Martinez, 2016). In the classification of Kaiho, 1994 it is considered as dysoxic species that can stand anoxic conditions (Geslin et al., 2004; Fontanier et al., 2002). Thus it is a useful proxy to detect levels of extremely low oxygen rates (Schonfeld, 2001; Jorissen et al., 2007; Grunert et al., 2015). It occurs during H4 in Portugal (Baas et al., 1998), as well as in H1 and H4 with maxima IRD in Bay of Biscay (Loncaric et al., 1998). Also abundant in deep sites (2882 m) SW of Landas shelf (Bay of Biscay) during MIS 4 to MIS 2 and H6 (Rodriguez-Lazaro et al., 2017).

<i>Nonionoides turgidus</i> (Williamson, 1858)	Deep infaunal (Corliss and Emerson, 1990; Corliss, 1991)	<i>Nonionoides turgidus</i> is an opportunistic species associated with nutrients increasing (Jorissen, 1987; van der Zwaan and Jorissen, 1991; Alve and Bernhard, 1995). It occurs in low hydrodynamic, high low-quality OM, hypoxic sediments (Goineau et al., 2011). It is cited as seasonal species during eutrophization and stratification phases (Jorissen et al., 1992). Living in low oxygen habitats (van der Zwaan and Jorissen, 1991; Bernhard and Sen Gupta, 1999) and it stands permanent oxygen depletion (Moodley et al., 1998). It is considered as suboxic by Kaiho, 1994.
<i>Chilostomella oolina</i> Schwager, 1878	Deep infaunal (Mackensen and Douglas, 1989, Mojtahid et al., 2010). Intermediate infaunal (Fontanier et al., 2002).	<i>Chilostomella oolina</i> is very abundant in S Bay of Biscay, where the OM is included in sediments strongly hypoxic or anoxic (Fontanier et al., 2002). Species indicative of dysoxia (O ₂ : 0.1-0.3 ml/l) (Kahio, 1994), though it can adapt to suboxic conditions (Rathburn and Corliss, 1994). In stressed environments this species has competitive advantage over other living near the surface (Rathburn and Corliss, 1994). In case of low quality degraded OM, this species is replaced by <i>Gl. affinis</i> (Fontanier et al., 2002). Both species prefer living in areas with high OM and low carbonate content (De Rijk et al., 1999).
<i>Bulimina gibba</i> Fornasini, 1902	Deep infaunal (Fontanier et al., 2002; Mendes et al., 2004)	<i>Bulimina gibba</i> is living in cold to temperate waters (5°-17°C) (Murray, 1991) with high productivity (Rai and Singh, 2012), thus it is extremely eutrophic and anoxic (Fontanier et al., 2002). It is a dysoxic species (O ₂ : 0.1-0.3 ml/l) after Kahio, 1994. Abundant during interstadials MIS 5a, c, e, in deep sites (2882 m) of Bay of Biscay (Rodriguez-Lazaro et al., 2017).
<i>Melonis affinis</i> (Reuss, 1851)	Shallow/intermediate infaunal (Fontanier et al., 2002; Grunert et al., 2015; Singh et al., 2015)	<i>Melonis affinis</i> , (previously: <i>Melonis barleeanus</i>) is a cold water species (-0.4° to 9°C) (Murray, 1991) and tolerates high degraded OM content (Fontanier et al., 2002). It is considered as suboxic (Kaiho, 1994), it can occur in oxygen depleted, low nitrates content sediments (Jorissen et al., 1998). It indicates mesotrophic conditions (Grunert et al., 2015; Jorissen, 2003). It is present in deep waters of Landas shelf in Bay of Biscay, during stadial MIS 5d (Rodriguez-Lazaro et al., 2017)
<i>Bigenerina (Bigenerina) nodosaria</i> d'Orbigny, 1826	Epifaunal (Murray, 2006)/Shallow infaunal (Fontanier et al., 2002)	<i>Bigenerina nodosaria</i> inhabits waters with T below 15°C (Mathieu, 1986). It dominates during interglacial periods, as MIS 1 and indicates increasing of surface productivity associated to warm episodes (Angue Minto'o et al., 2016). It is opportunistic in outer shelf of Bay of Biscay after phytoplankton blooms (Duchemin et al., 2008). It has also been associated with marine phytodetritus (Fontanier et al., 2008).

Conflicts of Interest Statement

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or non-financial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

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