Comparison of living and dead benthic foraminifera on the Portuguese margin: Understanding the taphonomical processes

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ABSTRACT

Dead benthic foraminifera (> 150 μm) were studied in 23 sediment cores from the Portuguese Margin at water depths between 20 and 2000 m and located on 4 transects off the Douro, Mondego, Tagus and Sado river mouths and 1 transect in the Estremadura. For 10 stations, the dead faunal vertical distribution (0–8 cm) was first investigated in 4 different sediment horizons per core to evaluate the sampling effort necessary to have a representation of the dead fauna deposited under different environmental areas. As a result, it appears that the faunal vertical distribution is constant, except for the deepest environments where fragile taxa were identified in the top layers only. Dead foraminiferal assemblages in the 4–5 cm layer for all stations were then compared to previously published living foraminiferal assemblages (of March 2011) from the same cores to evaluate the taphonomical processes affecting major species. This improves the knowledge of the faunal distribution for a better benthic foraminiferal proxy for paleostudies. There was a considerable loss of some species in the dead fauna. Firstly, this concerns the fragile organic-cemented agglutinated taxa such as *Reophax* spp., *Glomospira charoides*, or *Bathysiphon* spp. Secondly, some calcitic species such as *Nonion scaphum*, *Cancris auriculus*, *Ammonia beccarii* or *Bulimina aculeata* that were particularly abundant in the living fauna on the inner shelf under the late winter high river discharge conditions, were also far less dominant in the dead fauna. Lastly, other species like *Cassidulina carinata*, *Valvulineria bradyana*, and *Bulimina marginata* systematically showed higher abundance in the dead fauna at the mid shelf. These species, related to eutrophic conditions occurring in summer during the upwelling activity, were therefore not well represented in the living fauna, collected in March. Transport of allochthonous specimens may also account for higher contribution in the dead community of some species like *Cibicides lobatulus*, *Asterigerinata mamilla* or *Haynesina depressula*, especially in coastal environments where hydrodynamic processes (river flood, winter storm, coastal drift) are more vigorous. Several species (*U. mediterranea*, *U. bifurcata*, *T. agglutinans*, *H. balthica* or *B. costata*), however, show little or no difference in both abundance and spatial occurrence between the living and dead faunas and provide a stable signal for paleoclimatic investigations.

1. Introduction

Benthic foraminifera are known to be sensitive to environmental conditions (Murray, 2006) such as sediment type (Mackensen et al., 1985), oxygen concentration (Gupta and Machain-Castillo, 1993; Jorissen et al., 1995), organic matter flux and quality (Altenbach and Sarnthein, 1989; Goineau et al., 2011; Dessandier et al., 2015, 2016) or pollution (Alve, 1995; Martins et al., 2015a). Because of their ability to reflect environmental changes and to have an overall good preservation potential, fossil benthic foraminifera assemblages have been widely used as a proxy for paleoenvironmental reconstructions (Jorissen et al., 2007 and references therein). In order to make these interpretations valid, it is necessary to know whether the fossil record is representative of the living fauna and to understand the taphonomic processes, affecting the composition and preservation from dead to fossil assemblages, such as transport, test destruction, bioturbation, and life processes (see review in Murray, 2006).

The fossil benthic foraminiferal record is affected by the taphonomic loss which decreases with sediment depth and bioturbation (Loubere et al., 1993; Berkeley et al., 2007). Taphonomic processes can be responsible for the decrease of absolute number of tests and of the species diversity (Smith et al., 1987). Agglutinated species are particularly affected by early diagenesis, especially organically-cemented species (Schnitker et al., 1980; Goldstein and Barker, 1988; Murray and Alve, 1999). The iron-rich organic cements are particularly altered by organic matter remineralization (Douglas et al., 1980). Calcareous species can also be affected by test breakage due to physical re-sedimentation,

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transport, dissolution, bio-erosion, macrofaunal predation and reproduction (Cottey and Hallock, 1988). Dissolution processes of calcareous species are important in low pH sediments under early diagenesis influence (Alve and Murray, 1994; Murray and Alve, 1999; Murray and Pudsey, 2004). Because of these processes, it appears essential to study the dead fauna under the taphonomically active zone (Davies et al., 1989). Transport of small size taxa could be responsible for high abundances of allochthonous species which can alter paleoreconstructions. This was shown to be especially obvious in submarine canyons where sediment focusing can be strong (Duros et al., 2012, 2013). Test production rates could also vary the proportions of taxa in biocenose and thanatocenose (Loubere, 1989; de Stigter et al., 1999). In addition, the dead faunal community of a discrete layer represents averaged periods which reflect faunal distribution of different seasons and associated water settings (Murray, 2006).

Studies comparing dead and living foraminifera are scarce in dynamic shelf environments (e.g., Alve and Murray, 1997; Mendes et al., 2013; Goineau et al., 2015). To the best of our knowledge, a very low number of such studies were conducted on the Iberian Margin (Diz and Frances, 2009; Mendes et al., 2013), despite several paleostudies based on fossil benthic foraminiferal assemblages in this area (e.g., Schönfeld and Zahn, 2000; Diz et al., 2002; Bartels-Jónsdóttir et al., 2006a, 2006b; Martins et al., 2006; Rosa et al., 2007; Mendes et al., 2010). In addition, previous studies which aimed at understanding the dead benthic foraminiferal preservation in sediment have not investigated the variation of dead foraminifera with sediment depth (Diz and Frances, 2009; Duros et al., 2012, 2013; Mendes et al., 2013; Goineau et al., 2015).

Hence, the main objective of this study is a comparison between dead and living faunas to understand the taphonomical processes, showing which species do not fossilize and why, and what this may imply for paleostudies. For this purpose, we investigated the vertical and spatial distributions of dead benthic foraminifera in a large number of stations along the Portuguese margin 1) to describe the faunal distribution and diversity of recently dead fauna in different marine environments, 2) to compare those with living fauna from the same stations, and 3) to evaluate the potential preservation of living fauna under the influence of taphonomic processes.

2. Study area

Our study concerns a large zone of the Portuguese Margin spanning from the Douro River mouth in the north to the Sado River mouth in the south (Fig. 1). The Douro and Tagus rivers are the major sources of terrestrial particles to the shelf and the adjacent slope (Dias et al., 2002). The Douro River has a drainage basin of 95,700 km^2 and an annual mean water discharge of 505 m^3 s^{-1} (Azevedo et al., 2010). The Tagus River is located in the central part of the Peninsula with a watershed of about 80,600 km^2 and has an annual mean water discharge of 360 m^3 s^{-1} (Jouanneau et al., 1998). The Tagus River has a large mesotidal estuary with an area of 340 km^2 (Vale and Sundby, 1987). Both rivers are characterized by strong seasonal variations of their discharge, controlled by maximal rainfall in winter (Aguiar and Ferreira, 2005; Azevedo et al., 2008). River discharges also control the water stratification and the transport of chlorophyll in the water column (Relvas et al., 2007). Smaller rivers are also present along the Portuguese coast. Two of them, relevant for this study, are the Sado River and the Mondego River, which have mean annual discharges of < 10 m^3 s^{-1} (Richter et al., 2009) and 72 m^3 s^{-1} (Pardal et al., 2002), respectively.

The western Iberian Margin is a narrow (20 to 34 km) shelf (Dias et al., 2002). The shelf break is located between 130 and 150 m water depth. The hydrodynamic is driven by the seaward decrease in influence of wave action, tidal and rip currents, and storm surges, determining the particle size distribution on shelf sediments (Oliveira et al., 2007). Although the Portugal Coastal Counter Current hinders material export from the shelf to the ocean in general, a transport of fine material occurs during storm events from the mid-shelf area that is subsequently eroded due to the northward slope

current on the outer shelf (Vitorino et al., 2002a). Around 100 m water depth, where seasonal thermal stratification of surface waters occurs, the finest particles are deposited in accumulation areas, especially off the Douro and Tagus rivers, hence forming a mudbelt (Jouanneau et al., 1998; Dias et al., 2002). These accumulation zones are composed of mixed sources of marine, estuarine and terrestrial organic matter (Schmidt et al., 2010).

The dominant regional surface current (Portugal Current) flows southward and transports material from the shelf to the deep ocean during winter storms (Vitorino et al., 2002b). The Eastern North Atlantic Central Water (ENACW) is characterized by a decrease of salinity under the surface currents, with a minimum of 35.6 at 450–500 m water depth (Oliveira et al., 2007). The Mediterranean Outflow Water (MOW) flows northward between 600 and 1600 m water depth. The transition zone between the ENACW and the MOW is responsible for a mixing of different dense water masses (van Aken, 2000a, b), producing a sediment reworking of the finest particles at around 500 m water depth on the northern Portuguese Margin (McCave and Hall, 2002). However, the narrow shelf and steeper slope probably restrains this phenomenon in the south. The North Atlantic Deep Water (NADW) flows southward under 1600 m water depth. Between May and September, the Azores high pressure system is driven closer to the coast, which together with the associated northerly winds makes the colder, less salty and nutrient enriched subsurface water (from 60 to 120 m water depth) rise to the surface along the Iberian Margin (Fiúza, 1983). This upwelling leads to an increased productivity in summer along a 50 km wide zone. The main upwelling front is oriented along the bathymetry off the 100 m isobath in the northern part of the Iberian Peninsula and turning slightly offshore southward (Peliz et al., 2002). Most of the primary production increases during upwelling events, especially cyanobacteria and diatoms which are dominant on the Iberian Margin and well described by the chlorophyll *a* content (Tilstone et al., 2003). Major phytoplankton blooms occur in spring, between April and May, and in autumn, in November (Ferreira and Duarte, 1994). In winter, the Azores high moves south which results in southerly winds and downwelling conditions. The downwelling conditions lead to the deposition of sediments on the shelf (Frouin et al., 1990). Winter storms can remobilize the sediment and transport it northward by bottom currents (Dias et al., 2002; Vitorino et al., 2002a) and eventually deposit it in the mid-shelf mudbelt between 50 and 130 m water depth (Vitorino et al., 2002b).

3. Material and methods

3.1. Sample collection

Sediment cores were obtained along five E-W transects using an Oktopus GmbH multicorer during the PACEMAKER 64PE332 cruise on board R/V Pelagia between 14 and 29 March 2011 (Table 1, Fig. 1). 4 transect samplings were conducted off the mouths of the Douro, Mondego, Tagus and Sado rivers, and 1 transect in the Estremadura region where fluvial influence is expected to be lower. The sampling campaign took place shortly after the period of maximal river runoff (Azevedo et al., 2008) and before the phytoplankton spring bloom and seasonal upwelling prevailing in this area (Fiúza, 1983; Ferreira and Duarte, 1994).

3.2. Benthic foraminiferal sampling and analyses

For faunal analysis, one sediment core was sliced on board at each station; every 0.5 cm from the sediment–water interface down to 2 cm depth, and every 1 cm from 2 to 10 cm depth. Each sample was preserved in 96% ethanol containing 1 g l^{-1} of Rose Bengal, a commonly used stain for live foraminiferal identification (Walton, 1952; Murray and Bowser, 2000). To save time, only the > 150 μm size fraction was investigated although we were aware that not considering the fine fraction could bias the benthic foraminiferal assemblages. All the living foraminifera were picked on all wet samples slices and no replicate samples were investigated for this study. These data are presented in
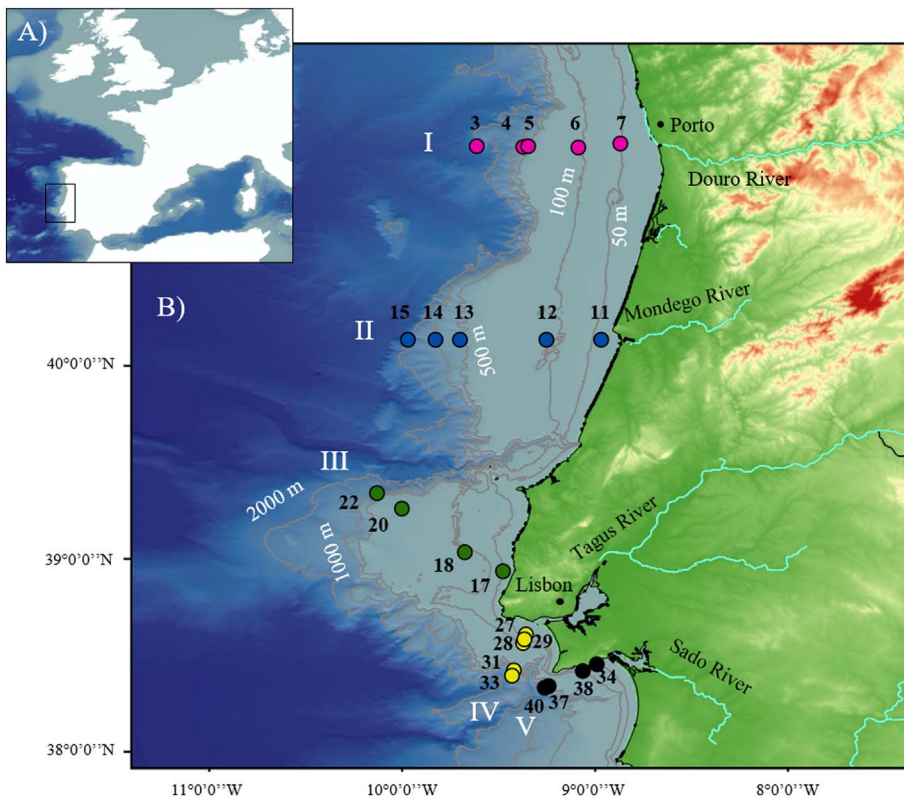
Fig. 1. A) Geographical localization of the study area and B) sampling sites of five transects: I) Douro, II) Mondego, III) Estremadura, IV) Tagus, and V) Sado.

Dessandier et al. (2016). After sediment drying, dead foraminifera were picked on the same samples used for the living foraminiferal study. For 3 stations on the shelf (St. 6, 12 and 28) all sediment intervals (0 to 10 cm) were studied, but for the other 7 stations (St. 3, 7, 20, 27, 29, 31 and 33) only 4 sediment depth intervals (0–0.5, 0.5–1, 4–5 and 7–8 cm) were investigated. Since the data from the 3 shelf stations showed similar distribution in all intervals we decided to show in the present study only the same 4 common intervals for better homogeneity of the

results. In addition, the 4–5 cm interval of all stations was also analyzed (Table 1). For all samples, a minimum of 250 specimens of dead benthic foraminifera were picked to guarantee a valuable representation of faunas (Murray, 2006). For tubular agglutinated species, we used a minimum number of 3 fragments to count 1 tubular specimen, as was previously described in Koho et al. (2007 and 2008) on the Portuguese Margin. When required, samples were divided using an Otto microsplitter. Dead foraminiferal densities are presented as benthic

Table 1
Information on sampling stations. At all stations, each 4–5 cm sediment layer was analyzed. The stations where four sediment horizons (i.e., 0–0.5, 0.5–1, 4–5, and 7–8 cm) were analyzed are indicated in bold.

Cruise	Transect	Sample station	Longitude	Latitude	Water depth	Sampling date
			°W	°N	(m)	(dd/mm/yyyy)
64PE332	**Douro**	**3**	**9.61**	**41.14**	**1989**	**17/03/2011**
64PE332	Douro	4	9.37	41.13	1007	17/03/2011
64PE332	Douro	5	9.34	41.14	506	17/03/2011
64PE332	**Douro**	**6**	**9.08**	**41.13**	**110**	**16/03/2011**
64PE332	**Douro**	**7**	**8.87**	**41.15**	**51**	**16/03/2011**
64PE332	Mondego	11	8.97	40.13	28	19/03/2011
64PE332	**Mondego**	**12**	**9.25**	**40.13**	**108**	**19/03/2011**
64PE332	Mondego	13	9.70	40.13	505	19/03/2011
64PE332	Mondego	14	9.83	40.13	981	19/03/2011
64PE332	Mondego	15	9.97	40.13	1808	20/03/2011
64PE332	Estremadura	17	9.48	38.93	48	21/03/2011
64PE332	Estremadura	18	9.67	39.03	116	21/03/2011
64PE332	**Estremadura**	**20**	**10.00**	**39.26**	**308**	**21/03/2011**
64PE332	Estremadura	22	10.13	39.34	1100	22/03/2011
64PE332	**Tagus**	**27**	**9.36**	**38.61**	**20**	**24/03/2011**
64PE332	**Tagus**	**28**	**9.37**	**38.56**	**94**	**24/03/2011**
64PE332	**Tagus**	**29**	**9.36**	**38.58**	**48**	**25/03/2011**
64PE332	**Tagus**	**31**	**9.42**	**38.42**	**479**	**25/03/2011**
64PE332	**Tagus**	**33**	**9.43**	**38.39**	**1000**	**26/03/2011**
64PE332	Sado	34	8.99	38.45	48	26/03/2011
64PE332	Sado	37	9.24	38.34	516	28/03/2011
64PE332	Sado	38	9.06	38.42	98	28/03/2011
64PE332	Sado	40	9.26	38.33	979	29/03/2011

foraminifera number (BFN) per mg of dry sediment. In order to evaluate the potential use of the 4–5 cm sediment layer as a good representative thanatocenose in different environments, the Renkonen similarity was calculated between the relative abundance of dead faunas in the 4–5 cm sediment layer and percentages of integrated 0–8 cm layers, meaning percentages of the sum of sediment samples between 0 and 8 cm.

Faunal diversity indices were calculated for living and dead communities on raw data. Species diversity was determined with the Shannon index H (Eq. (1), Shannon and Weaver, 1949). In order to compare the distribution of species among samples, the evenness E index (Eq. (2) after Buzas and Gibson, 1969) was also calculated as follows:

$$H' = -\sum_{i:S}^{i:1} \left(\frac{ni}{N}\right) \times \ln\left(\frac{ni}{N}\right)$$

(1)

$$E = eH/S$$

(2)

where n_i is the number of individuals in the sample for the species "i", N the total number of individuals for the same sample and S the species richness given as the number of species. Shannon and Evenness indices were calculated using the PAST software (Hammer et al., 2001). Faunal statistics on living species, calculated using similar equations, were already presented by Dessandier et al. (2016).

Dead-living ratios allow the comparison of living and dead proportions of species, calculated using the formula %Living/(%Living + %Dead), i.e., L/(L + D), on species which account for at least 5% of one of the two communities, dead or living (Jorissen and Wittling, 1999; Duros et al., 2012). In order to estimate similarity between dead and living communities, and also between different sediment layers of the dead fauna, we applied the Renkonen similarity (Eq. (3)) as follows:

$$P = \sum_i min(P1i, P2i)$$

(3)

where *P1i* is the percentage of species "i" in the living community and *P2i* is the percentage of species "i" in the dead community (Renkonen, 1938; Wolda, 1981). This similarity index ranges from 0 (no similarity) to 100% (perfect similarity), so we assume that 40% represents high similarity (meaning that species distributions have 40% in common between the two communities) as it was observed as maximal similarity in another study (Duros et al., 2013). Living percentages were calculated using the total number of species in all samples (0–8 cm) and compared with percentages of dead species of the 4–5 cm layer for all stations. This calculation was also performed between the 4–5 cm sediment layer of the dead fauna and percentages of integrated dead faunal sediment layers (0–0.5, 0.5–1, 4–5, and 7–8 cm sediment depth) to evaluate the use of the 4–5 cm sediment layer as representative of all recent dead faunas.

Two-way Cluster analyses (Q-mode and R-mode) were performed using the Bray-Curtis similarity on the raw data of major species (> 5% in at least two stations) of the dead fauna (4–5 cm sediment layer) under PRIMER v.6.0 software. All maps of dead faunal diversity and species relative abundances are based on the 4–5 cm sediment layer. Classes of interpolation of diversity indices were determined by Jenks natural step and maps were performed using Arc Gis® software. The used metric coordinates are based on the GCS_WGS_1984.

4. Results

4.1. Distribution of dead benthic foraminiferal faunas

4.1.1. Vertical distribution of faunas in the top 8 cm of sediment cores

In order to assess the distribution variability of dead benthic foraminifera in sediments, abundances of major species were compared for 10 stations from different transects and water depths (Fig. 2). The dead faunal distribution with sediment depth is generally equal within the
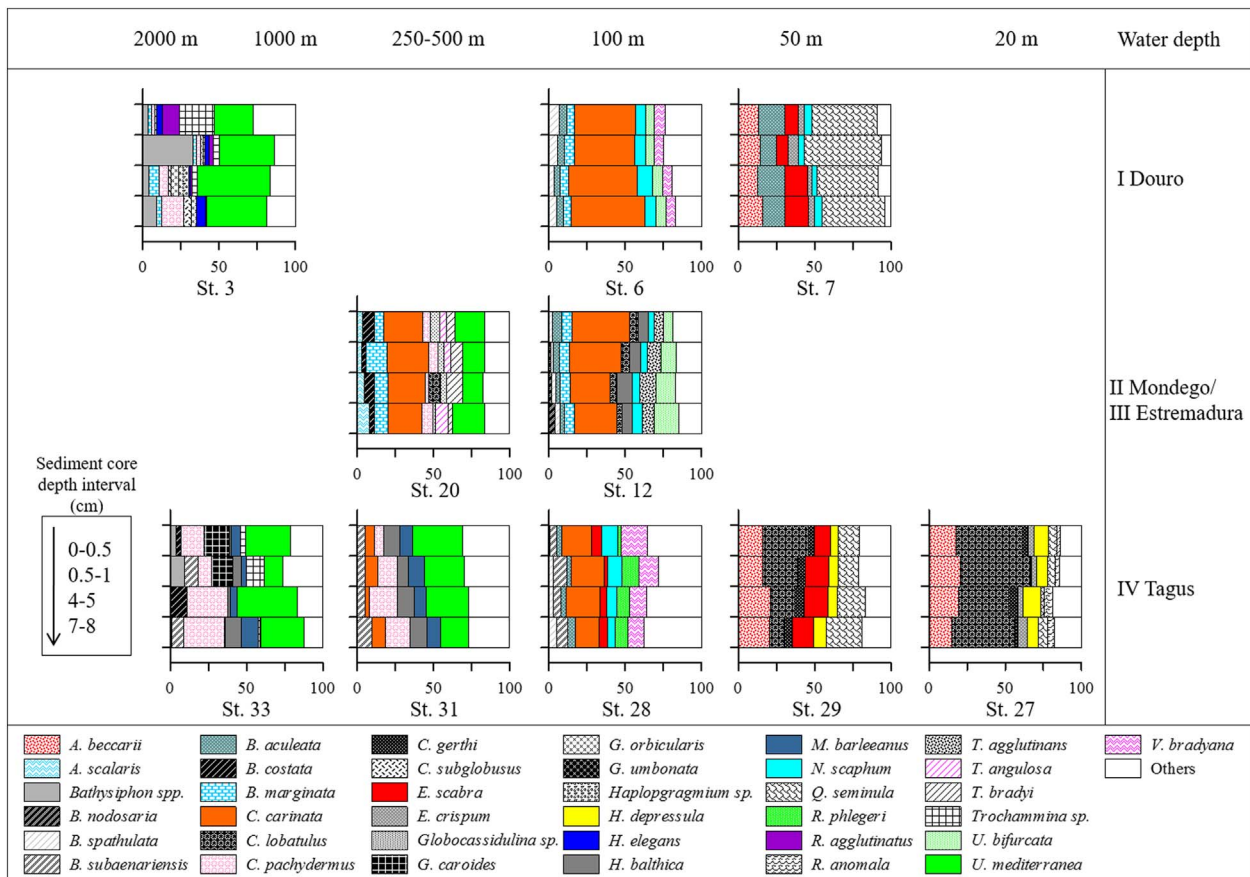

Fig. 2. Vertical distribution (%) of major dead species (> 5%) in the sediment intervals of 0–0.5, 0.5–1, 4–5, and 7–8 cm.

investigated intervals. This was true for stations between 20 and 500 m water depth (St. 27, 28, 29, 6, 7, 12, 20 and 31). Species observed in the upper layer were found in similar amount in all other layers. *Cibicides lobatulus*, present at shallow stations off the Tagus River only, showed an abundance decrease with increasing sediment depth at St. 29. At 1000 and 2000 m water depth (St. 33 and 3, respectively), and faunal distributions showed larger variations down the sediment cores. At those stations, agglutinated taxa such as *Trochammina* sp., *Glomospira charoides*, *Bathysiphon* spp., *Haplophragmium bradyi* and *Reophax agglutinatus* were not present in all samples. Calcareous taxa such as *Cibicides pachydermus*, *Uvigerina mediterranea* and *Rosalina anomala* also showed variations.

The Renkonen values varied between 47% at St. 3 and 92% at St. 6 (Fig. 3). The similarity was most of the time extremely good (> 80%), except for two deep stations where the Renkonen similarity was lower: 66% at 1000 m (St. 33) and 47% at 2000 m water depth (St. 3). The overall very good similarity gave us confidence to extend the study to all the sampling stations but for only one interval between 4 and 5 cm.

4.1.2. Densities and diversities of dead faunas from the 4–5 cm sediment layer

A total of 110 dead species were found in the whole study area (82 perforates, 22 agglutinates, and 6 miliolids). 27 species represented > 5% of the total faunas in at least one core and were considered as major species of the study area. Among those, 24 species were perforates, 2 species were agglutinated and 1 species belonged to miliolids. The specific richness (S) and the Shannon index (H) showed a similar trend together (Fig. 4A and B) with highest values on the Estremadura transect at 100 and 1000 m depth (H > 2.8 and S = 42) and minimum values at coastal stations off the Douro River, the Mondego River, and in the Estremadura (H < 1.8 and S < 20). The Evenness index (E, Fig. 4C) was quite different with E > 0.50 sometimes in the deep environment (1000 m depth in the Estremadura), in the slope (500 m depth off the Mondego River), in the shelf (100 m depth off the Tagus River), and in the coastal environment (50 m depth off the Sado River). Lowest values (E < 0.30) were found at 100 and 2000 m depth off the Douro River, at 50 and 2000 m depth off the Mondego River, at 50 m depth in the Estremadura, and at 1000 m depth off the Sado River.

Relative abundances of major dead species are plotted for each station across the 5 transects (Fig. 5). At the coastal stations of < 50 m depth (St. 7, 11, 17, 24, 27, 29 and 34), *Ammonia beccarii* that ranged between 6 and 24% and *Quinqueloculina seminula* (2–61%) were the most abundant. *Eggerelloides scaber* reached high abundances off the Douro and Tagus rivers only (St. 7 and 29). *Cibicides lobatulus* (33–50%) was relatively abundant off the Mondego and Tagus rivers (St. 11, 27 and 29). *Asterigerinata mamilla* and *Planorbulina mediterranensis* were only abundant off the Sado River (St. 34) with values of 21 and 11%, respectively. In the Estremadura, only *A. beccarii*, *Q. seminula* and *Elphidium crispum* were abundant with values above 5%.
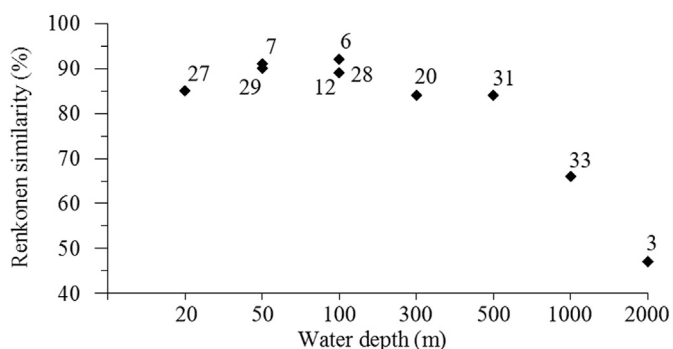

Fig. 3. Renkonen similarities between the dead fauna of the sediment layer 4–5 cm and the integrated 0–8 cm sediment layer (i.e., % based on the 4 sediment horizons) plotted against water depth. The numbers represent the stations.

At 100 m depth (St. 6, 12, 18, 28 and 38), *Cassidulina carinata* (17–45%), *Nonion scaphum* (7–15%) and *Uvigerina bifurcata* (2–14%) were dominant on all transects except for *U. bifurcata* which was not present off the Tagus River. *Valvulineria bradyana* was found off the Douro, Tagus and Sado rivers. *Textularia agglutinans* was encountered off the Mondego and Sado rivers and in the Estremadura.

Between 300 and 500 m water depth (St. 5, 13, 20, 31 and 37), *C. carinata* (16–24%) was again dominant off the Douro, Mondego rivers and in the Estremadura. The *Cibicides* genus was abundant on the Douro, Mondego, Estremadura, and Sado transects. We specifically found there *C. ungerinanus*, *C. lobatulus*, and *C. pachydermus*. *Uvigerina mediterranea* (16–42%) was only present off the Tagus and Sado rivers at this depth.

Finally, between 1000 and 2000 m depth (St. 3, 4, 15, 22, 33 and 40), *U. mediterranea* (24–72%) was always dominant off the Douro, Mondego, Tagus, and Sado rivers. *Cibicides pachydermus* was also present in all transects reaching up to 27% at St. 33. *Melonis barleeanus* (5–11%) was well represented off the Douro River and in the Estremadura.

4.2. Clusters analyses on dead fauna

The two-way cluster analysis based on the 27 major species and 23 stations allowed the identification of 5 thanatofacies (Q-mode) and 7 groups of species (R-mode) as well as 3 isolated species (Fig. 6). Thanatofacies A was composed of the coastal stations (50 m depth) off the Douro River (St. 7) and in the Estremadura (St. 17). Thanatofacies B included all the other coastal stations between 20 and 50 m depth off the Mondego (St. 11), Tagus (St. 27 and 29) and Sado rivers (St. 34). Thanatofacies C corresponded to the deepest stations off the Douro (St. 3, 2000 m depth), Mondego (St. 14 and 15 at 1000 and 2000 m depth, respectively), Tagus (St. 31 and 33 at 500 and 1000 m depth, respectively), and Sado (St. 37 and 40 at 500 and 1000 m depth, respectively) rivers. Thanatofacies D grouped all the stations at 100 m depth while thanatofacies E was composed of the stations at 500–1000 m water depth off the Douro River (St. 4 and 5), the Mondego River (St. 13), and in the Estremadura (St. 20 and 22).

Group 1 was made of *A. mamilla*, *P. mediterranensis*, *R. anomala* and *C. gerthi*. Group 2 corresponded to *Bulimina aculeata*, *E. scaber*, *A. beccarii* and *Q. seminula*. Group 3 included *C. pachydermus* and *U. mediterranea*. Group 4 was formed by *N. scaphum* and *V. bradyana*. Group 5 was composed of *T. agglutinans*, *Bulimina marginata*, *U. bifurcata*, *Bolivina spathulata* and *Hyalinea balthica*. Group 6 included *C. ungerianus* and *P. ariminensis*. Group 7 was formed by *T. bradyi*, *M. barleeanus*, *B. costata* and *Globocassidulina subglobosa*. Finally, 3 species were isolated by the cluster analysis: *C. lobatulus*, *E. crispum* and *C. carinata*.

Thanatofacies A was characterized by species of Group 2: *Q. seminula*, *A. beccarii*, *B. aculeata* and *E. scaber* to a lesser extent. The thanatofacies B also showed high relative abundance of *A. beccarii* and *Q. seminula*, and species of Group 1 with *A. mamilla*, *Haynesina depressula* and secondary species such as *P. mediterranensis*. The isolated species *Cibicides lobatulus* and *Elphidium crispum* reached their highest relative abundance in the thanatofacies B. Thanatofacies C was associated with *U. mediterranea* and *C. pachydermus*, corresponding to Group 3. Thanatofacies D was dominated by *C. carinata* and by species of Group 4: *N. scaphum* and *V. bradyana*. Group 5 with *T. agglutinans*, *B. marginata*, *U. bifurcate* was abundant in stations of thanatofacies D and E with the isolated species *C. carinata*. *Cibicides ungerianus* and *P. ariminensis* (Group 6) were found in thanatofacies E but this thanatofacies was also characterized by species of Group 7: *T. bradyi*, *M. barleeanus*.

4.3. Comparison between dead and living faunas

The Renkonen similarity (Table 2) revealed higher differences between the two communities in deep environments (500–2000 m depth) than in shallow environments in the northern part (from Douro to

Specific richness
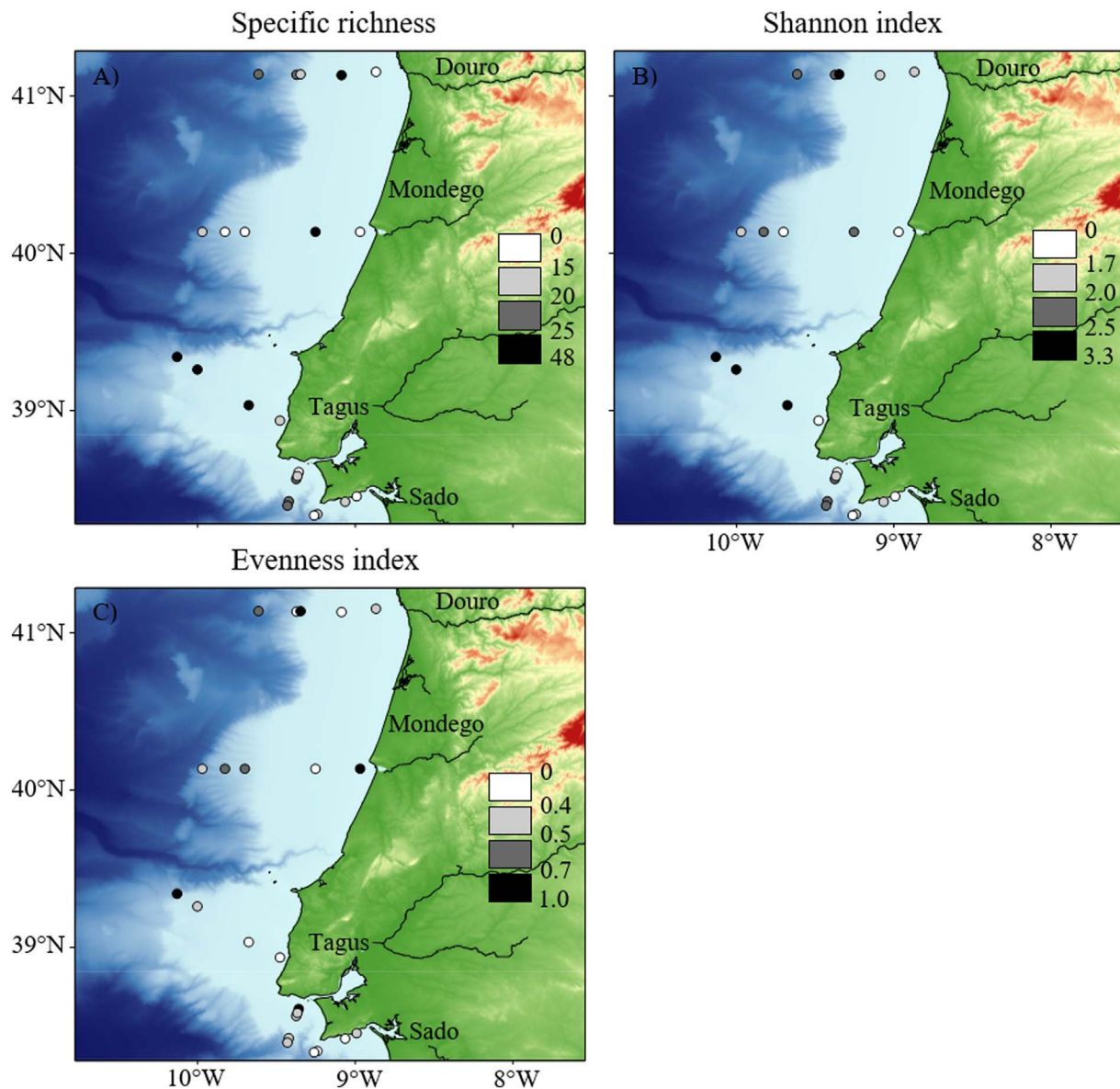

Shannon index

Evenness index

Fig. 4. Diversity indices of the dead fauna at the 4–5 cm sediment layer: A) specific richness, B) Shannon index, and C) Evenness index.

Estremadura transects) while this was the contrary in the southern part (Tagus and Sado transects) of the margin. This suggested that there was a north-south change in species distribution mainly responsible for the high similarity in deep environments off the Tagus and Sado river mouths.

Living and dead faunas were plotted together to make a comparison (Fig. 7) following the same species groups defined in the dead faunal cluster analysis (Fig. 6). L/(L + D) values based on the major dead species (> 5%) in Table 2 allowed this comparison at species level. Group 1 was characterized by high relative contribution in the dead fauna (20–52%) in the southern part of the study area (off the Tagus and Sado river mouths), especially at coastal sites of thanatofacies B, St. 34 and 27 (Fig. 7, cluster 1) with all L/(L + D) values inferior to 0.15 for species of this group except for *C. gerthi* (Table 2).

Group 2 showed its highest relative abundance at the coastal stations in both living and dead faunas (Fig. 7, cluster 2). A real difference was however observed at 100 m depth (thanatofacies D) where this group reached > 20% of the living community at St. 12, 28 and 38 against < 15% in the dead fauna. This group also contributed more to the living assemblages at 500 m depth off the Mondego River (St. 13). This trend was, however, opposed between most of the species in this

group and *Q. seminula* which shows very low L/(L + D) values (Table 2), explaining the low difference between living and dead assemblages of this group in Fig. 7.

Group 3 was present in both living and dead communities at the deep stations (thanatofacies C) without clear trend, showing higher relative contribution in dead or living assemblages depending on the stations (Fig. 7, cluster 3). Group 4 contributed more to the living fauna in all stations where it was present (Fig. 7, cluster 4) and showed a living relative abundance higher than 25% between 50 and 100 m depth off the Douro, Tagus and Sado river mouths (St. 6, 7, 28, 29, 34 and 38, thanatofacies A, B and D). However, this was essentially due to *N. scaphum* (L/(L + D) of 0.56–0.99), while *V. bradyana* contributed more to the dead fauna with L/(L + D) ranged between 0.16 and 0.43 (Table 2).

Group 5 presented the relative contribution of the same order in living and dead assemblages (Fig. 7, cluster 5) even though it was a little higher in the dead than in the living fauna in the northern part of the margin (St. 3, 4, 5, 6, 12 and 13). In this group, only *H. balthica* clearly showed higher relative abundance in the dead than in the living fauna (L/(L + D) > 0.44, Table 2). Group 6, as well as the two isolated species *C. lobatulus* and *E. crispum*, were only present as major
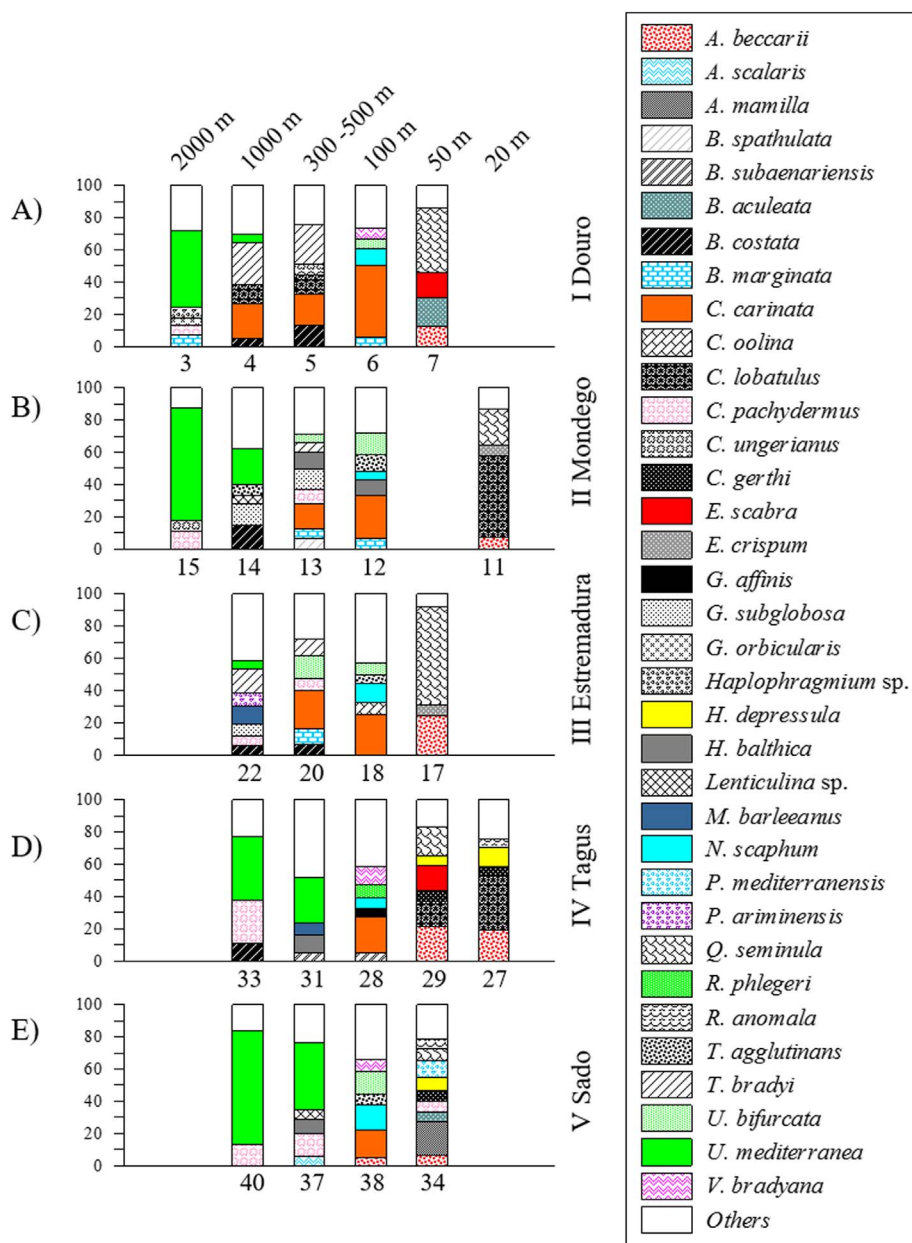
species (> 5%) in the dead fauna (Fig. 7). Group 7 showed higher relative abundances in the dead fauna at all the stations where it was present except at station 40 (Fig. 7, cluster 7). Finally, the isolated species *C. carinata* was almost totally absent in the living fauna, while it was very abundant in the dead assemblage (20–25%) in most of the shelf stations with L/(L + D) values all inferior to 0.25 (Table 2).

5. Discussion

The present study aimed at comparing the faunal distribution of living fauna of the late winter of 2011 with the dead fauna from the same samples, which represent modern fauna of the last century at most. Consequently, comparison of dead and living assemblages could provide information on several processes, such as the influence of sedimentation rates, test destructions, transport processes, growth rates and opportunistic behaviors, well known to affect the faunal records and bias the paleoreconstructions (Murray, 2006). It could also help to prevent biases linked to the lack of individuals (using living specimens only), showing which species are really representative of the different

environments on a longer period.

5.1. Influence of sedimentation rates

The analysis of the vertical distribution of dead benthic foraminifera was performed at different water depths, from 20 to 2000 m, and various locations relative to rivers were investigated in order to evaluate the bathymetrical influence on the faunal preservation, as well as the river influence. Both the water depth and river influence affected the rates of sediment accumulation, which were substantially different in the shallow and deep sites. At 100 m depth, the sedimentation rate was about 0.2/0.3 cm yr^{-1} off the Tagus and Douro rivers and in the Galicia shelf (Dias et al., 2002; Jouanneau et al., 2002; Alt-Epping et al., 2009). At 50 m water depth, the sedimentation rate could be 2 times higher than at 100 m depth, as observed off the Douro River (Dessandier et al., 2015), and so massive deposition events in the prodelta of the Douro or Tagus rivers during flood events cannot be excluded. In deeper environments (1000–2000 m depth), except for canyons, the sedimentation rate was classically low as observed on Albuquerque and
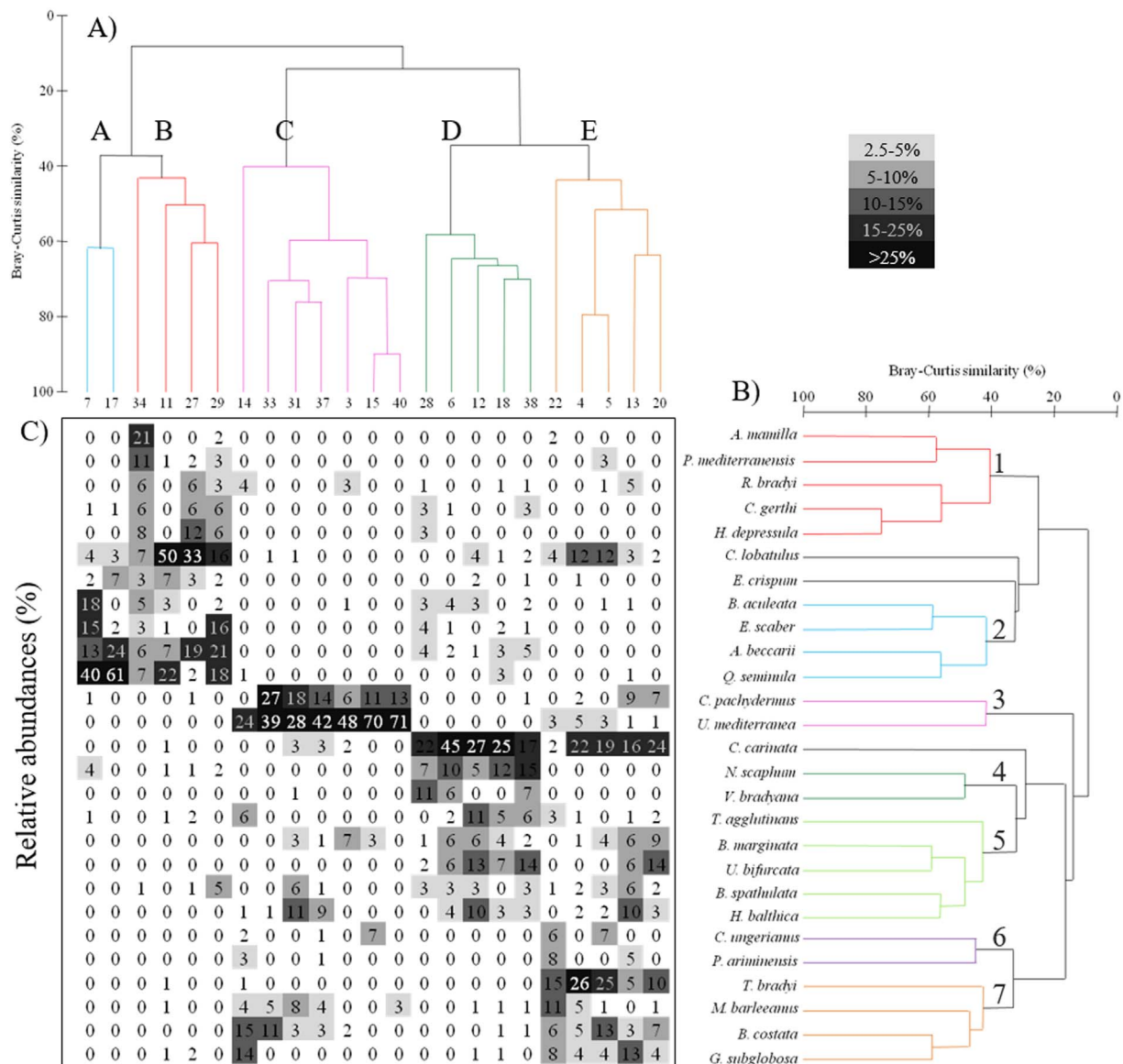
Fig. 6. Two-way cluster analyses based on Bray-Curtis similarities calculated with the raw data of the major dead species at the 4–5 cm sediment layer: A) Q-mode cluster, B) R-mode cluster. C) Relative abundances (%) of major dead species at each station.

Estremadura slopes and on the open shelf and slope close to the Nazaré canyon (de Stigter et al., 2007, 2011), and off the Douro River where it was 5 times less than at 50 m water depth (Dessandier et al., 2015). Consequently, the 1-cm sediment layer represents about 1–2 years at 50 m water depth and approximately 10 years at 2000 m water depth. This implied that short-term variations could be observed in coastal environments, but probably less at deep sites where the signal was averaged over longer periods. Considering the different sedimentation rates of the studied stations, the analysis of vertical dead faunal distributions has to be considered with caution. Also, as proposed by Alve (1996), high sedimentation rates > 1 mm yr^{-1} may prevent test destructions and therefore could influence the preservation of agglutinated taxa. Our results, showing a fairly homogenous vertical distribution of dead benthic foraminifera, suggested that a single sediment layer in our study area, where the sedimentation rate was fairly high, is well representative of dead benthic foraminiferal assemblages down to 8 cm. However, the even vertical distribution might also be the consequence of sediment mixing by bioturbation. Although we could not exclude its influence within the sediment mixed layer, ^{210}Pb profiles published in the same study area by de Stigter et al. (2007, 2011), as

well as the previous living benthic foraminiferal results published by Dessandier et al. (2016) showing classical living distribution of benthic foraminifera and oxygen profiles, did not indicate a strong bioturbation for the considered stations. The good similarity of the dead fauna data between the 4–5 cm sediment layer and the integrated 0–8 cm sediment interval (Fig. 3) indicated that the 4–5 cm interval is very representative of dead fauna, at least for the shelf and upper slope stations. The 4–5 cm depth interval was also considered instead of the top layer as it restrains the underestimation of deep infauna (Goldstein, 1988; Loubere, 1989). This depth was clearly within the sediment mixed layer, active until 5 to 10 cm in most of the shelf and open sea sediments in the Iberian Margin (de Stigter et al., 2007, 2011), and so representative of the thanatocenose, in "sub-fossil" transition (Goineau et al., 2015). Therefore, the following interpretations of the dead assemblages and thanatofacies were done for this 4–5 cm interval.

5.2. Test destruction

Numerous studies concerning the dead benthic foraminiferal distribution have identified two types of faunas, the non-fossilizing and

Table 2

Renkonen similarity between 4 and 5 cm sediment layer of the dead fauna and integrated 0–10 cm sediment layer of the living fauna and the L/(L + D) ratios of the major species (> 5% in at least one sample). 0.4 < Values of < 0.6 are in gray, > 0.5 values are in black (i.e., higher relative abundance in the living fauna).

| Transect	Douro					Mondego					Estremadura				Tagus					Sado			
Station	3	4	5	6	7	11	12	13	14	15	17	18	20	22	27	28	29	31	33	34	37	38	40
Water depth (m)	1989	1007	506	110	51	28	108	505	981	1808	48	116	308	1100	20	94	48	479	1000	48	516	98	979
Renkonen similarity (%)	30	13	12	31	52	34	32	16	7	24	43	48	35	27	20	31	40	30	62	13	35	31	80
A. beccarii	–	–	–	–	0.57	0.82	–	1.00	–	–	0.65	–	–	–	0.70	–	0.18	–	–	0.31	–	–	–
A. mamilla	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.15	–	–	–	–
B. spathulata	–	–	–	–	–	–	–	0.00	–	–	–	–	–	–	0.99	–	–	–	–	–	–	–	–
B. aculeata	–	–	–	–	0.51	0.88	0.88	–	–	–	–	–	–	–	–	–	–	–	–	0.83	–	0.92	–
B. costata	–	–	0.19	–	–	–	–	–	0.23	–	–	–	0.00	0.45	–	–	–	–	0.52	–	–	–	–
B. marginata	0.12	–	–	0.05	–	–	0.14	0.41	–	–	–	0.06	–	–	–	–	–	0.90	–	–	–	–	–
C. carinata	–	0.00	0.00	0.00	–	–	0.00	0.22	–	–	–	0.25	0.05	–	–	0.06	–	–	–	–	–	0.05	–
C. lobatulus	–	0.00	0.00	–	–	0.00	–	–	–	–	–	–	–	–	0.00	–	0.00	–	–	0.00	–	–	–
C. pachydermus	0.00	–	–	–	–	–	–	0.00	–	0.54	–	–	–	–	–	–	–	–	–	–	0.00	–	0.00
C. ungerianus	–	–	0.00	–	–	–	–	–	–	0.57	–	–	–	–	–	–	–	–	–	–	–	–	–
C. gerthi	–	–	–	–	–	0.84	0.97	–	–	–	–	–	–	–	–	–	–	–	–	0.00	–	–	–
E. scaber	–	–	–	–	0.49	–	–	–	–	–	–	–	–	–	0.96	–	0.75	–	–	–	–	–	–
E. crispum	–	–	–	–	–	–	0.00	–	–	–	0.06	–	–	–	0.00	–	–	–	–	–	–	–	–
G. subglobosa	–	–	–	–	–	–	–	0.00	0.00	–	–	–	0.59	0.07	–	–	–	–	–	–	–	–	–
H. depressula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.00	–	0.00	–	–	0.01	–	–	–
H. balthica	–	–	–	–	–	–	0.14	0.00	–	–	–	–	–	–	–	–	–	0.44	0.40	–	0.00	–	–
M. barleeanus	–	0.76	–	–	–	–	–	–	–	–	–	–	–	0.17	–	–	0.72	0.58	–	–	0.00	–	0.68
N. scaphum	–	–	–	0.89	0.87	–	–	0.78	–	–	0.56	–	–	–	–	0.80	0.91	–	–	0.99	0.61	–	–
P. mediterranensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08	–	–	–
P. ariminensis	–	–	–	–	–	–	–	–	–	–	–	–	–	0.32	–	–	–	–	–	–	–	–	–
Q. seminula	–	–	–	–	0.18	0.53	–	–	–	–	0.21	–	–	–	0.00	–	0.42	–	–	0.00	–	–	–
R. anomala	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.00	–	–	–
T. agglutinans	–	–	–	–	–	–	0.30	–	–	–	0.58	0.88	–	–	–	–	–	–	–	–	–	0.00	–
T. bradyi	–	0.04	0.33	–	–	–	–	0.00	–	1.00	–	0.67	0.00	–	–	–	–	–	–	–	–	–	–
U. bifurcata	–	–	–	0.61	–	–	0.37	0.43	–	–	–	0.39	0.57	1.00	–	–	–	1.00	–	–	–	0.19	–
U. mediterranea	0.21	0.85	–	–	–	–	–	0.60	0.00	–	–	–	0.72	–	–	–	0.39	0.56	–	0.4	–	0.51	
V. bradyana	–	–	–	0.43	–	–	–	–	–	–	–	–	–	–	–	0.17	–	–	–	–	–	0.16	–

fossilizing faunas (Mackensen et al., 1990; Goineau et al., 2015). The non-fossilizing fauna were mostly agglutinated species where there was no carbonate dissolution, with organic-cement and particularly those with iron-rich test that could be destroyed because of organic matter mineralization (Douglas et al., 1980; Murray and Alve, 1999). Macrofaunal predation could also be responsible for organic cement destruction (Kuhnt et al., 2000). *Reophax* spp., *Trochammina* spp., *Haplophragmoides bradyi* or *Glomospira charoides* showed significant loss between the living and dead communities. *Cribrostomoides subglobusus* slightly decreased, while the more resistant *E. scaber* (Mackensen and Douglas, 1989), showed similar relative contribution in both dead and living faunas. Because of the numerous agglutinated species in the living community in deep environments in this study area (Koho et al., 2007, 2008; Phipps et al., 2012; Dessandier et al., 2016), all the agglutinated species were considered for the vertical distribution in order to determine which were the fossilizing and non-fossilizing species on the Portuguese Margin.

Our results suggested that in deep environments, *Rhabdammina* spp., *Trochammina* spp., *Reophax* spp. and *G. charoides* were only resistant in the first cm of the sediment, while *C. subglobusus*, *Haplophragmoides bradyi* appeared more resistant, with dead individuals present in deeper layers (Fig. 2). This surface preservation could be linked to the very low sedimentation rates in deep environments. *Bathysiphon* spp. showed high relative abundances down to 8 cm in the dead fauna suggesting a good preservation in surface sediment, even though these species were more abundant in the living assemblages (Fig. 5 in Dessandier et al., 2016). de Rijk and Troelstra (1999) suggested that fine-grain agglutinated species which includes *Bathysiphon* spp., *Textularia* spp. or *Eggerelloides* spp. were more resistant to test degradation. At mid-shelf stations, *E. scaber* and *T. agglutinans* did not present any evidence for destruction, while *Clavulina cylindrica* totally disappears. At 500 and 100 m depth in the Estremadura, *B. nodosaria* was well preserved because of high sedimentation rates.

The calcareous fauna could also be affected by dissolution in acidic environments, especially in organic-rich sediments (Alve and Murray, 1994; Murray and Alve, 1999; Murray and Pudsey, 2004). No clear evidences of calcareous dissolution were found on benthic foraminiferal tests from this study. However, some species (such as *Hoeglundina elegans* or *G. orbicularis*) were previously interpreted as fragile taxa because of aragonitic tests (Duros et al., 2012, 2013). These species also showed clearly higher relative abundance in the living fauna of the present study. This possible test destruction did not seem to increase with sediment depth suggesting a quick destruction in surface sediments. Other fragile species such as *Cancris auriculus* which was among the most abundant in the living fauna between 50 and 100 m depth, was not, or very poorly, preserved in the dead community. This may also be the consequence of mechanical breakdown of the tests, although we cannot exclude that the higher contribution of certain fragile species in the living faunas could also be the consequence of the seasonal conditions that may have been more favorable just before the period of sampling.

5.3. Transport processes

Transport processes are easily detected by the presence of exotic species which are imported to the study area with sometimes chamber breakage or worn tests (Alve and Murray, 1997). Such transport on the Portuguese Margin might result from the local hydrodynamics driven by coastal currents, wave actions and winter storms, particularly active close to the coast. Species of Group 1 and isolated species from the cluster analysis *E. crispum* and *C. lobatulus* were classically observed in estuarine or lagoon environments (Hayward, 1993; Debenay and Guillou, 2002; Martins et al., 2015a) in continental areas where the salinity and the temperature were more variable than in our study area. In the Portuguese margin specifically, these species were found in surface sediments of very shallow waters in Portuguese rivers or
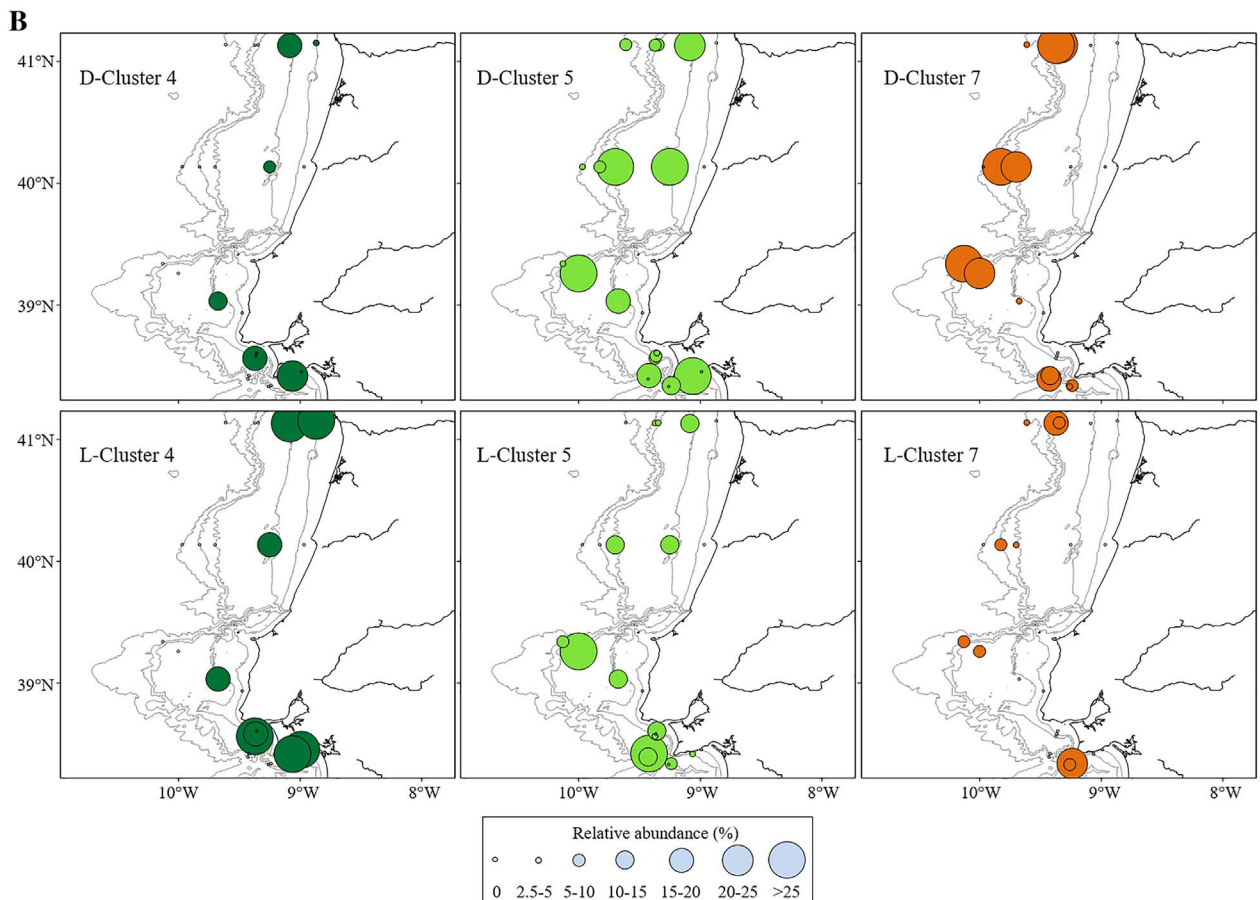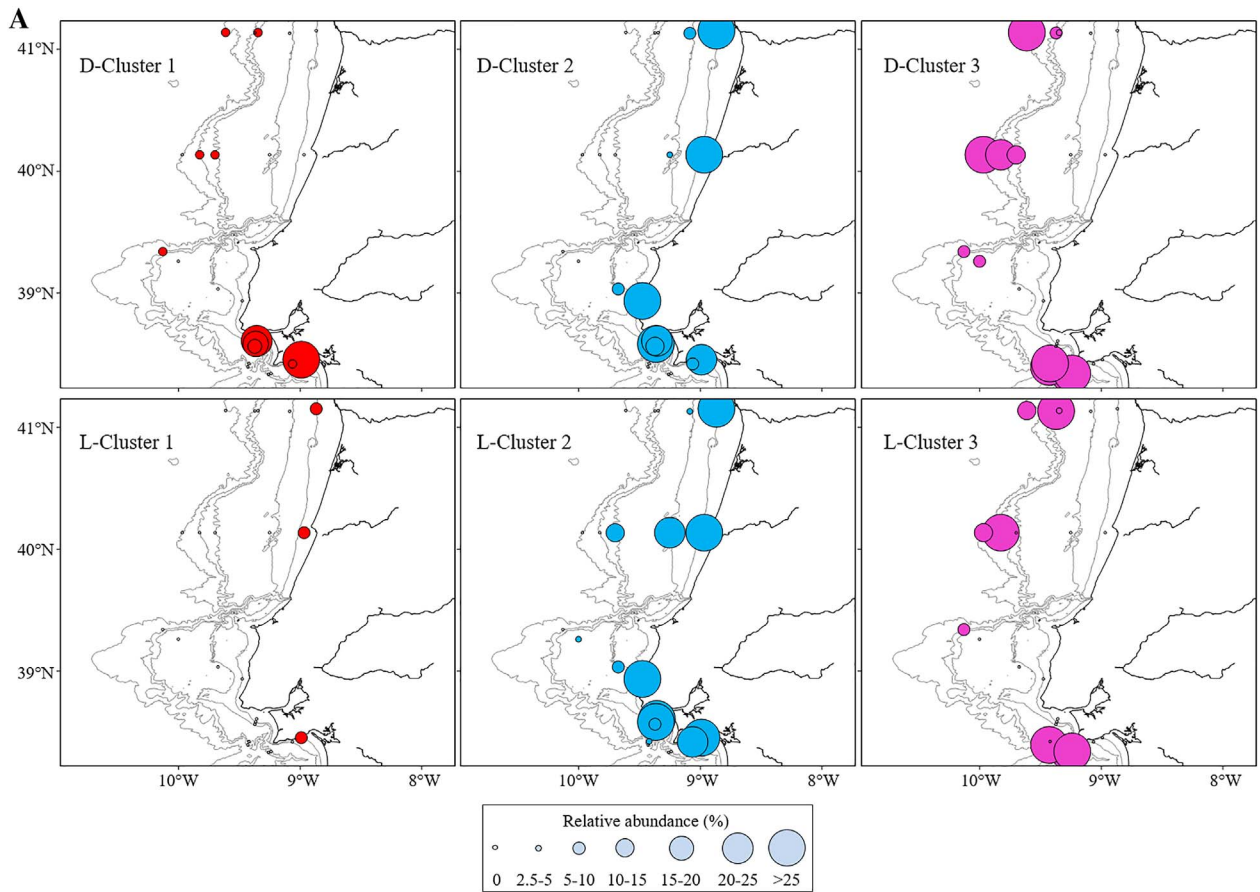
(caption on next page)

Fig. 7. Relative abundances of faunal groups and isolated species defined by R-mode cluster analysis for the dead (D) fauna and the living (L) fauna. Note that the relative abundances of Cluster 6 and isolated species are plotted only for the dead fauna, because of their extremely low faunal abundances in the living fauna, except for *Cibicides carinata*.
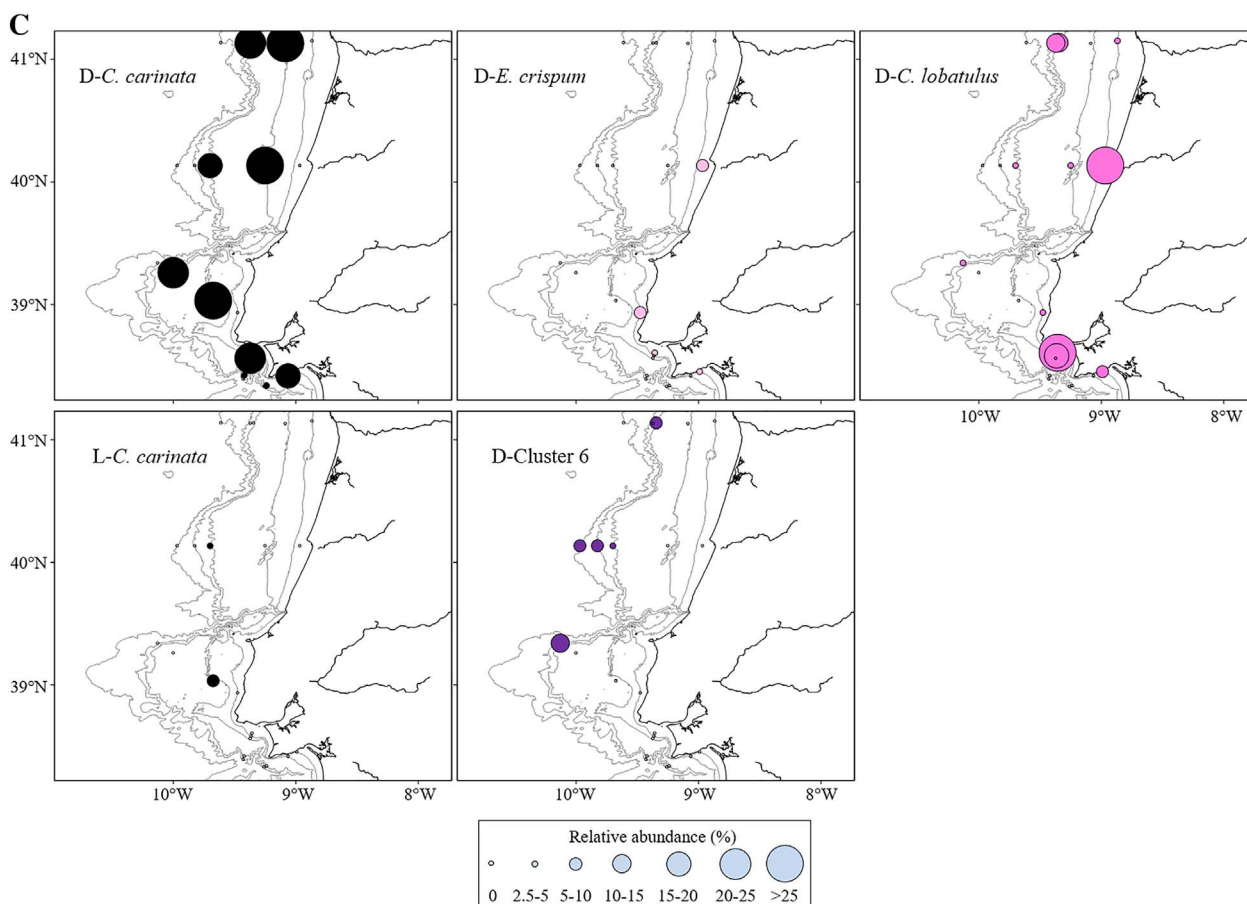
Fig. 7. (continued)

lagoons (Diz et al., 2004; Martins et al., 2015a). In the northern part, there was a bathymetrical shift of this group of species from coastal stations in the living fauna to deeper stations in the dead fauna. These taxa were mostly found in the dead fauna (Fig. 7, Table 2) and represented a very few number of individuals in the living community (Dessandier et al., 2016). A transport from coastal waters and estuarine environments might be responsible for their occurrence on the shelf. *Elphidium crispum* and *C. lobatulus* were also abundant in the dead fauna in offshore environments (50–100 m depth) along the Portuguese Margin (Martins et al., 2015b), whereas they represented non-major species in living assemblages off the Tagus River (Bartels-Jónsdóttir et al., 2006b) or in the Ria de Vigo (Diz and Francés, 2008). This appeared to be also the case for *C. lobatulus*, well known to colonize estuarine environments, often attached on vegetated seabed (e.g., Freiwald, 1995). Winter storms could be responsible for the transport of a part of all coastal species to 100 m depth as it is the case for terrestrial sediments (Jouanneau et al., 1998; Dias et al., 2002). *Elphidium* spp. were classically observed in very shallow waters in the vicinity of river mouths (Mendes et al., 2004, 2012; Mojtahid et al., 2009), where this species could be transported after surface sediment mobilization.

Species of Group 1 showed high abundances essentially off the Tagus and Sado rivers, hence only in the southern part of the study area, suggesting that the transport effect was higher in this part of the margin than in the north. The steeper shelf in the south could be one explanation. Thus, we can hypothesize that the swell was stronger in this part of the margin and the transported benthic foraminifera from

the coast could reach deeper environments. Those epiphytic species might also be living on the seagrasses that massively cover the lower estuary of the Tagus and are transported seaward following storms (Bock and Moore, 1968; Boltovskoy and Lena, 1969; Spindler, 1980). This transport of allochthonous species was responsible for higher benthic foraminiferal diversity in southern coastal stations as shown by the Shannon index (Fig. 4C).

Because of its morphology, *C. carinata* is often suspected to be transported by currents (e.g., Duros et al., 2013). In late winter, *C. carinata* was observed, albeit in very low abundances in the living assemblages, at 100, 500 and 1000 m depth on the Douro, Tagus and Estremadura transects (Dessandier et al., 2016). In the dead fauna, *C. carinata* was the most abundant at all 100 m stations and found as deep as 1000 m water depth off the Douro River (albeit with lower abundance), which corresponded to the area of influence of the summer upwelling. Consequently, the high abundances of this species in dead fauna are less likely to be linked to transport processes at the mid-shelf. Its occurrence at deeper stations (1000–2000 m depth) may result from the transport by offshore currents, even though the number of individuals of this species in deep environments is relatively low. However, the mixing zone between the ENACW and the MOW at 500 m depth produced a sediment reworking, because of the different water mass densities (McCave and Hall, 2002), and may have been responsible for sandy sediments in this zone (Dessandier et al., 2016). This sediment reworking could be the source of the upwelling driven species on the slope (i.e., *C. carinata*), where the specific richness and

the Shannon index were probably increased by these allochthonous species inputs (Fig. 4B and C) and where the Renkonen similarity was the lowest of the study area (Table 2).

5.4. Biological processes

5.4.1. Impact of the river discharges

In the areas under the river influence (50–100 m depth), the sampling period of living fauna at the end of winter (following the strongest river discharge period) seemed to directly impact the dead/living proportions. The species with tolerance to river borne organic matter (such as *N. scaphum*, *C. auriculus* or *B. aculeata*), associated with nutrients exports from land and blooms of coccolithophorids (Dessandier et al., 2015), showed higher abundances in the living fauna during winter. However, the period from spring to fall is usually characterized by several phytoplanktonic blooms that might favor the presence of large amounts of opportunistic species. At 50 m depth, the species of Group 2 (*A. beccarii*, *B. aculeata* and *E. scaber*) were typically observed living at coastal stations on the Portuguese margin in the vicinity of rivers (Dessandier et al., 2016) and showed higher relative abundance in the living fauna (Table 2). They have shown preferences for sandy sediments in river influenced areas such as the Guadiana and Rhône rivers where coastal currents are highly energetic (Mendes et al., 2004; Diz and Francés, 2008; Mojtahid et al., 2009; Goineau et al., 2011). They also showed an affinity for labile organic matter in areas where terrestrial nutrient export is important and is associated with phytoplanktonic blooms (Dessandier et al., 2016). At 100 m depth, *N. scaphum* is more present in the living community (Table 2), was also described as controlled by terrestrial inputs off the Portuguese rivers (Dessandier et al., 2015, 2016). The similarity between dead and living communities is higher for the Estremadura stations where the river influence is negligible, while off the Tagus, Douro and Sado river mouths the low similarity (Table 2) might results from the seasonal presence of river tolerant species.

Comparing the present faunal results with several studies on the Portuguese Margin (e.g., Levy et al., 1995; Bartels-Jónsdóttir et al., 2006b; Rosa et al., 2007; Diz and Francés, 2008); the 100–500 m water depth environment showed a significant difference in the faunal distribution. This environment has high relative abundances of living or dead *Bolivina* spp. that were not observed either in the dead or in the living faunas at other stations. In this study we only investigated the > 150 μm size fraction and many species of *Bolivina* are often smaller and classically found in the 63–150 μm fraction (e.g., Fontanier et al., 2003; Mendes et al., 2004), which might explain their very low occurrence in our samples.

5.4.2. Upwelling and spring bloom influence

The summer upwelling and spring bloom periods, seemed to result in higher contribution of more opportunistic species, which showed higher relative abundance in the dead fauna explaining the lower similarity between dead and living communities at mid-shelf environments. The preference for fresh marine organic matter characterized *C. carinata*, *B. marginata* and *H. balthica*, well known to have opportunistic behaviors under eutrophic conditions (e.g., Jorissen et al., 1992; de Rijk et al., 2000; Fontanier et al., 2003; Goineau et al., 2015). This is highlighted by a decrease in the diversity (e.g., low Evenness values)in samples where *C. carinata* is dominant. Several authors found *C. carinata* as dominant in the Iberian shelf in fossil or dead faunas (Levy et al., 1995; Mendes et al., 2004; Bartels-Jónsdóttir et al., 2006a; Martins et al., 2006, 2015a). Nevertheless, no study conducted in various periods of the year, in February (Mendes et al., 2012), in May and October (Koho et al., 2007, 2008) or in September (Phipps et al., 2012), has shown this taxon to be that abundant (i.e., > 10%) in the living fauna. This might suggest that the period of production of *C. carinata* was restrained to the very upwelling season only, which reached a maximum between June and August (Fiúza, 1983).

Valvulineria bradyana (Group 4) was also considered as controlled by upwelling events in the Portuguese Margin or observed following major phytoplankton blooms (Bartels-Jónsdóttir et al., 2006a; Martins et al., 2006). *Textularia agglutinans* and *U. bifurcata* belonging also to Group 5, were less opportunistic, explaining lower relative abundance than the three previous described taxa. This relative lower abundance of these species was also described by Goineau et al. (2015) because of the opportunistic behavior of other dominant species. This highlights the importance of the opportunistic species identification for evaluating the signal of fossil species densities. The clear trends of the L/(L + D) ratio showing higher abundance in the dead than in the living fauna (Table 2) suggested that these species developed during the spring bloom or the summer upwelling, while they were minor component during the winter season in the living fauna. These species were previously interpreted as a high competitor in the Iberian upwelling area, adapted to cold and nutrient-enriched waters (Levy et al., 1995; Bartels-Jónsdóttir et al., 2006a; Martins et al., 2006, 2015b). Their ability to generate numerous offspring had an influence on the living/dead proportions of other species, decreasing the relative abundance in the dead fauna of species with more constant production rate, as suggested by Goineau et al. (2015).

In deeper environments, species of Group 7, i.e., *T. bradyi*, *G. subglobosa* and *B. costata* showed higher abundance in the dead fauna. These species were probably responding to fresh marine organic matter inputs (Murray, 2006), but our sampling period did not record the upwelling or spring bloom conditions resulting in the major fresh marine inputs of organic matter. This group presented a geographical distribution with the highest relative abundance in the northern part of the study area. The influence of a phytoplankton bloom during upwelling conditions extended seaward in a large zone in the northern part of the Portuguese Margin but was more restricted along the coast in the south (Peliz et al., 2002), which could explain the occurrence of these species on the northern slope only.

5.4.3. Production rates related to microhabitats

The production rates of individuals could drastically vary depending on the microhabitats, because of the different needs of energy for production of species living at different oxygen depletion levels (Loubere, 1989; de Stigter et al., 1999). Deep infaunal species (e.g., *Globobulimina affinis*, *Chilostomella oolina*), found in this study in living assemblages only, are known to have typically low production rates (Loubere, 1989; de Stigter et al., 1999) and were previously found in higher proportions in the living community (Jorissen and Wittling, 1999; de Stigter et al., 1999; Duros et al., 2012), with tolerance for degraded or refractory organic matter (Dessandier et al., 2016) which is resistant to remineralization.

On the contrary, surface sediment species such as *Q. seminula* or *C. pachydermus* had a much higher proportion in the dead fauna than in the living one (Table 2) which might be the result of high production rates, as it was described for epiphytic species and surface infaunas (Loubere, 1989; de Stigter et al., 1999). Higher relative abundance of these species could also be a consequence of the decrease of *N. scaphum* and *A. beccarii*, which were most dominant in winter under the riverine influence.

5.5. Paleoenvironmental reconstructions

The results of the present study highlighted the importance of the knowledge about benthic foraminiferal ecology and taphonomical processes before the use of benthic foraminifera as a paleoenvironmental proxy. The deep environments of the Portuguese Margin were affected by higher test destruction, which suggests that the fragile taxa such as *Bathysiphon* spp., *Reophax* spp. or *Trochammina* spp. have to be carefully considered. However those species are not specifically dominant in shelf environments and their loss may not alter significantly the fossil assemblages. In coastal environments, the transport processes

could bias the interpretations; in this case, *C. lobatulus, Elphidium crispum* or species of Group 1 (Fig. 6) were allochtonous and these species should be considered carefully in paleoenvironmental studies, because they are often transported in in this region.

This study also showed the potential of some species as bio-indicators of environmental changes, thanks to the ecology of species defined in previous studies on living fauna and to the difference between dead and living faunas. *Nonion scaphum* and species of Group 2 (Fig. 6) indicated river discharges influence on the Portuguese Margin. Some other species such as *U. bifurcata, U. mediterranea* or *T. agglutinans* (in gray in Table 2) showed good preservation as they were found with similar relative contribution in the dead and living communities. These species appeared to be good candidates for long term paleorecords as they were typical of stable and rich trophic conditions on the Iberian Margin, suggesting that their disappearance in fossil records might suggest a strong climatic change.

6. Conclusion

This study on the Portuguese Margin aimed at comparing the dead and living faunas from the same cores sampled in March 2011, in the top few centimeters of the sediment. The results of our study highlighted that in a selection of stations in the Portuguese Margin environment, the vertical distribution of dead faunas was constant, except in the deepest environments, giving us the confidence to extend the comparison with the living fauna using one single interval only. This comparison allowed us to identify various processes (e.g., test destruction, transport, and production rate) which have to be taken into consideration before using fossils of benthic foraminifera as paleoenvironmental indicators:

1) A large number of paleoenvironmental studies were conducted in deep environments due to older sediment records. However, paleointerpretations based on fossil benthic foraminifera have to be done with much care in these environments. Our results indicated that fossil faunas were more affected by destruction in these environments, as shown by many loss of agglutinated species (e.g., *Bathysiphon* sp., *Reophax* spp.). This confirms that organically-cemented tests or coarse grain size agglutinated species are more fragile, and that test destruction increase with decreasing sedimentation rate. Shallow areas may experience sediment reworking and bioturbation, but it is shown in this study that they may represent a good location for reconstructing river discharge and upwelling activities on the Portuguese Margin and their relation to regional climate for recent climatic periods.

2) Southern coastal species *C. lobatulus, A. mamilla* and *H. depressula* showed stronger seaward transport off the Tagus and Sado rivers than in the northern part of the Portuguese margin. The mixing zone between the MOW and the ENACW responsible for the sediment mobilization at 500 m depth was also probably responsible for species transport to deeper environments.

3) Paleoreconstructions of river discharges have to focus on the winter species, which accurately represent the conditions triggered by the river inputs. Indeed, river-influenced species (*N. scaphum, A. beccarii, B. aculeata, E. scaber*) showed higher contribution in the living fauna because of the favorable conditions during the period of sampling. Nevertheless, opportunistic species such as *C. carinata, V. bradyana* or *B. marginata*, most likely more present in spring-summer, showed higher relative contribution in the dead fauna than the winter species. The signal of winter species was consequently diluted by the species that respond to a phytoplankton bloom and reproduce in high quantities. This has to be considered in paleoreconstruction of river discharges, since the contribution of winter species could represent a small part of the signal even after strong river discharges. On the contrary, *U. mediterranea* and *M. barleeanus* did not show any seasonal preference, probably because of their

tolerance to low organic matter quality, and thus represent stable species for paleoreconstructions of long term climate changes.

4) Unlike deep infaunal species, which showed higher abundance in the living fauna, surface sediment species (such as *Q. seminula* and *C. pachydermus*) produced numerous individuals, resulting in a higher abundance in the dead fauna, hence potentially creating a bias in the paleoenvironmental interpretation.

Appendix A. Taxonomic references and plates list

Ammonia beccarii var. *tepida* (Linné, 1758) (Mendes et al., 2004, plate 1: 1a, b).

Amphycorina scalaris (Batsch, 1791) (thesis C. Fontanier, plate 5, p.403: fig. A).

Anomalinoides minimus (Forster, 1892) (Cetean et al., 2011, plate 3: 2a, b).

Asterigerinata mammalia (Williamson, 1858) (thesis R. H. Abu Zied, plate 9: 12,13).

Bathysiphon sp.2 (Koho et al., 2007, plate 42: 2).

Bigenerina nodosaria (d'Orbigny, 1926) (thesis C. Fontanier, plate 1, p.395: fig. J).

Biloculina sphaera (d'Orbigny, 1839).

Bolivina italica (Cushman, 1936) (Mendes et al., 2012, Fig. 2: 7a, b).

Bolivina spathulata/dilatata (Williamson, 1858) (Mendes et al., 2004, plate 2: 1).

Bolivina subaenariensis (Cushman, 1922) (Mendes et al., 2004, plate 2: 10).

Bulimina aculeata (d'Orbigny, 1826) (Mendes et al., 2004, plate 2: 3).

Bulimina affinis (d'Orbigny, 1826) (Majewski and Anderson, 2009, plate 4: 3–4).

Bulimina costata (d'Orbigny, 1852) (Kirci-Elmas et al., 2008, plate 2, p.165: 19–20).

Bulimina inflata (Seguenza, 1862) (thesis C. Fontanier, plate 5, p. 403: fig. M).

Bulimina marginata (d'Orbigny, 1826) (Koho et al., 2007, plate 43: 9).

Cancris auriculus (Fichtel and Moll, 1798) (Larkin and Gooday, 2009, plate 4: 1–2).

Cassidulina carinata (Silvestri, 1896) (thesis A. Goineau, plate 1, p. 294: photo 5).

Cassidulina crassa (d'Orbigny, 1839) (thesis C. Fontanier, plate 6, p. 405: fig. A).

Chilostomella oolina (Schager, 1878) (Wiedicke and Weiss, 2006, fig. 8–1).

Cibicides kullenbergi (Parker, 1953) (Koho et al., 2008, plate 64: 1a, b, c).

Cibicides lobatulus (Walker and Jacob, 1798) (Milker et al., 2009, plate 1: 6, 7 and 8).

Cibicides pachydermus Rzehak, 1886) (Abu Zied et al., 2008, plate III: 3–5).

Cibicides ungerianus (d'Orbigny, 1846) (Schweizer et al., 2015).

Clavulina cylindrica (d'Orbigny, 1826) (thesis C. Fontanier, plate 1, p. 395: fig. F).

Coryphostoma sp. (thesis C. Fontanier, plate 405: fig. L and M).

Cribroelphidium gerthi (Van Voorthhuysen, 1957) (Mendes et al., 2004, plate 1: 9).

Cristellaria crepidula (Fichtel and Moll, 1798).

Cribrostomoides suglobusus (Cushman, 1910) (thesis C. Fontanier, plate 1, p.395: fig. G).

Eggerelloides scaber (Williamson, 1858) (Mendes et al., 2004, plate 1: 3a, b).

Elphidium crispum (Linné, 1758) (Mendes et al., 2004, plate 1: 6).

Epistominella vitrea (Parker, 1953) (Mendes et al., 2004, plate 2: 2a, b).

Glandulina ovula (d'Orbigny, 1846) (Figueroa et al., 2006, plate 24: 11a, b).

Globobulimina affinis (d'Orbigny, 1839) (Licari and Mackensen, 2005, plate 2: 6).

Globocassidulina crassa (d'Orbigny, 1839) (Milker et al., 2009, plate 2: 16).

Globocassidulina subglobosa (Brady, 1881) (thesis R. H. Abu Zied, plate 6: 8).

Gyroidina orbicularis (d'Orbigny, 1826) (thesis C. Fontanier, plate 7, p.407: fig. L and M).

Gyroidina umbonata (Silvestri, 1898) (thesis C. Fontanier, plate 7, p. 407: fig. N and O).

Hanzawaia boueana (d'Orbigny, 1846) (Mohjtaid et al., 2009, plate 3: 35).

Haplopgragmoides sp. (Robertson, 1891) (Holbourn and Henderson, Figure 1.1-19: 14–16).

Haynesina depressula (Walter and Jacob, 1798) (thesis R. H. Abu Zied, plate 9: 15–16).

Hoeglundina elegans (d'Orbigny, 1878) (Koho et al., 2008, plate 64: 2a, b).

Hyalinea balthica (Schröter, 1783) (thesis C. Fontanier, plate 8, p. 409: fig. F).

Jadammina macrescens (Brady, 1870) (Vance et al., 2006, plate 1: Figure 4).

Labrospira jeffreysi (Williamson, 1858) (Majewski and Anderson, 2009, plate 3: 6).

Lagena gracilis (Williamson, 1848) (Majewski and Anderson, 2009, plate 4: 1).

Lagena laevis (Montagu, 1803) (Laprida and Bertels-Psotka, plate 4: 4).

Lagena striata (d'Orbigny, 1839) (Kaminski et al., 2002, plate 2: 4).

Lenticulina sp. (Lamarck, 1804) (Okosun and Alkali, 2012, plate 3: 13).

Melonis barleeanus (Williamson, 1858) (Koho et al., 2007, plate 64: 7a,b).

Neolenticulina variabilis (Reuss, 1850) (Larkin and Gooday, 2009, plate 3: 6).

Nonionella iridea (Heron-Allen and Earland, 1932) (Mendes et al., 2004, plate 2: 6a, b).

Nonionella turgida (Williamson, 1858) (Diz and Francés, 2008, plate 183: 9).

Nonion scaphum (Fichtel and Moll, 1798) (Mendes et al., 2004, plate 1: 10).

Planulina ariminensis (d'Orbigny, 1826) (thesis R. H. Abu Zied, plate 8: 16–17).

Planulina wuellerstorfi (Schwager, 1866) (thesis C. Fontanier, plate 6, p. 405: fig. G).

Planorbulina mediterranensis (d'Orbigny, 1826) (Ribes et al., 2000, plate 1: 5).

Procerolagena gracilis (Seguenza, 1862) (Majewski and Anderson, 2009, plate 4: 1).

Pullenia bulloides (d'Orbigny, 1846) (thesis C. Fontanier, plate 9, p.411: fig. L and M).

Pullenia quinqueloba (Reuss, 1851) (thesis C. Fontanier, plate 9, p.411: fig. N and O).

Quinqueloculina seminula (Linné, 1758) (thesis C. Fontanier, plate 11, p.415: fig. J).

Rectuvigerina phlegeri (Mathews, 1945) (thesis C. Fontanier, plate 10, p.413: fig. A).

Reophax agglutinatus (Cushman, 1913) (Larkin and Gooday, 2009, plate 2: 1).

Reophax scorpiurus (Brady, 1881) (Milker et al., 2009, plate 1: 1).

Reophax sp.2 (Koho et al., 2007, plate 42: 8).

Reophax sp.3 (Koho et al., 2007, plate 42: 9).

Reophax spiculifer (Brady, 1879).

Rosalina anomala (Terquem, 1875) (thesis R. H. Abu Zied, plate 8: 8).

Sigmoilinita tenuis (Czjek, 1848) (Kirci-Elmas et al., 2008, plate 2, p.165: 8).

Siphonina reticulata (Czjzek, 1884) (Hinsbergen et al., 2005, plate 1: 16).

Siphotextularia flintii (Cushman, 1911) (Kirci-Elmas et al., 2008, plate 2, p.165: 3).

Spiroplectinella sagittula (d'Orbigny, 1839) (Milker et al., 2009, plate 1: 7, 8 and 9).

Spiroplectinella earlandi (Parker, 1952) (Bellier, Mathieu and Granier, 2010, plate 1: a).

Textularia agglutinans (d'Orbigny, 1839) (thesis A. Goineau, plate 1, p.294: photo 12).

Textularia sagittula (Defrance, 1824) (thesis R. H. Abu Zied, plate 1: 16–17).

Trifarina angulosa (Williamson, 1858) (Milker et al., 2009, plate 3: 2).

Trifarina bradyi (Cushman, 1923) (thesis C. Fontanier, plate 10, p.413: figs. F and G).

Uvigerina bifurcata (d'Orbigny, 1826) (Lutze, 1986, plate 4: Figures 5-8).

Uvigerina elongasrtiata (Lutze, 1986) (Koho et al., 2008, plate 64: 5a, b).

Uvigerina mediterranea (Lutze, 1986) (Koho et al., 2008, plate 64: 6a, b).

Valvulineria bradyana (Fornasini, 1900) (Koho et al., 2007, plate 43: 10a, b).

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marmicro.2018.01.001.

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