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To cite this version:

Pierre-Antoine Dessandier, Jérôme Bonnin, Jung-Hyun Kim, Sabrina Bichon, Bruno Deflandre, et al.. Impact of organic matter source and quality on living benthic foraminiferal distribution on a river-dominated continental margin: A study of the Portuguese margin. Journal of Geophysical Research: Biogeosciences, 2016, 121, pp.1689-1714. 10.1002/2015JG003231 . insu-03618909

HAL Id: insu-03618909

https://insu.hal.science/insu-03618909v1

Submitted on 24 Mar 2022

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JGR

Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE

10.1002/2015JG003231

Key Point:
- Benthic foraminifera are controlled by quantity, quality and source of organic matter

Supporting Information:
- Supporting Information S1
- Data Set S1

Correspondence to:
P.-A. Dessandier,
p.dessandier@epoc.u-bordeaux1.fr

Citation:
Dessandier, P.-A., J. Bonnin, J.-H. Kim, S. Bichon, B. Deflandre, A. Grémare, and J. S. Sinninghe Damsté (2016), Impact of organic matter source and quality on living benthic foraminiferal distribution on a river-dominated continental margin: A study of the Portuguese margin, *J. Geophys. Res. Biogeosci.*, *121*, 1689–1714, doi:10.1002/2015JG003231.

Received 2 OCT 2015
Accepted 7 JUN 2016
Accepted article online 11 JUN 2016
Published online 30 JUN 2016

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Impact of organic matter source and quality on living benthic foraminiferal distribution on a river-dominated continental margin: A study of the Portuguese margin

Pierre-Antoine Dessandier[1], Jérôme Bonnin[1], Jung-Hyun Kim[2,3], Sabrina Bichon[1], Bruno Deflandre[1], Antoine Grémare[1], and Jaap S. Sinninghe Damsté[2]

[1]UMR-EPOC 5805 CNRS, University of Bordeaux, Pessac, France, [2]NIOZ Royal Netherlands Institute for Sea Research, Den Burg, Netherlands, [3]Department of Marine Science and Convergence Technology, Hanyang University ERICA Campus, Ansan, South Korea

Abstract Living (rose Bengal stained) benthic foraminifera were investigated on surface sediments from 23 stations from the river-dominated northwestern Portuguese margin. Samples were collected in March 2011, following the period of the maximum rainfall over the Iberian Peninsula, between 20 and 2000 m water depth along five cross-margin transects. Four of them are located off the Douro, Mondego, Tagus, and Sado Rivers and one off the Estremadura coast. The major objectives of this study are (1) to assess the impact of organic matter of various origin and quality on the benthic foraminifera and (2) to investigate the spatial differences of faunal distribution from coastal waters to the deep sea under river influences. To do this, sedimentological and biogeochemical characteristics of the sediments were identified by measuring grain size, oxygen penetration depth, total organic carbon (TOC) content, stable carbon isotopic composition of TOC ($\delta^{13}C_{TOC}$) and concentration of pigments and amino acids. Based on the principal component and cluster analyses of the environmental data, three major geographical groups are identified: (1) deep stations, (2) coastal and middle slope stations, and (3) shelf stations under river influence. At the deepest stations, species are associated with high organic matter (OM) quantity but low OM quality, where *Uvigerina mediterranea*, *Hoeglundina elegans*, and agglutinated species such as *Reophax scorpiurus* or *Bigenerina nodosaria* are dominant. All stations off the Sado River, which is the most affected area by the anthropogenic influence, are also characterized by high quantity but low quality of OM with the minimum faunal density and diversity within the study area. Middle slope stations are associated with low OM content and coarse sediments (Q_{50}) with the predominance of *N. scaphum*. Shallow shelf stations close to the Douro and Tagus River mouths show a dominance of taxa (e.g., *Ammonia beccarii*, *Bulimina aculeata*, *Eggerelloides scaber*, *Nonion scaphum*, *Cancris auriculus*, and *Quinqueloculina seminula*) adapted to environments characterized by high OM quality (high fresh chlorophyll (Chl *a*/Phaeo)) and available amino acids (enzymatically hydrolyzable amino acid (EHAA)/total enzymatically hydrolyzable amino acid (THAA)). The Biotic and Environmental linking analysis suggests that the benthic foraminiferal distribution is mostly controlled by three environmental parameters, i.e., TOC (quantity), EHAA/THAA (quality), and $\delta^{13}C_{TOC}$ (source). Hence, this study clearly highlights that the quantitative and qualitative inputs of OM and its source are the most important factors controlling the living benthic foraminiferal distribution with clear influences between the different rivers. This study also suggests a good tolerance of several species for river discharges where the OM quality is high.

1. Introduction

Living benthic foraminifera are well known to be sensitive to environmental conditions such as temperature, salinity, pH, water depth, grain size, oxygen, and organic matter (OM), making these organisms very useful for environmental investigations (see reviews by *Gooday* [2003], *Murray* [2006], and *Jorissen et al.* [2007]). Even though benthic foraminifera have been studied for decades, their ecological preferences are not yet fully understood. Oxygen concentrations in the sediment and OM fluxes toward the sea floor [*Jorissen et al.*, 1995] as well as OM quality [*Schönfeld*, 2001; *Fontanier et al.*, 2002] were shown to be the major parameters controlling faunal abundances and distributions in deep sea environments. In coastal environments other variables such as active bioturbation, current and wave regime, biotic interactions, and sewage in polluted environments maybe very significant for benthic foraminiferal distribution [*Loubere and Fariduddin*, 1999; *Murray*, 2006, and references therein]. The impact of nutritional value of OM on the living benthic foraminifera has been recently studied based on analyses of lipids, sugars, and amino acids [*Fontanier et al.*, 2008; *Goineau et al.*, 2011; *Martins*

et al., 2015]. However, further investigations on the relation between the organic matter quality and the benthic foraminiferal distribution are required to better calibrate this bioindicator for past and modern environmental reconstructions.

Coastal marine ecosystems influenced by rivers are generally characterized by organic-rich sediments resulting from large supplies of terrestrial OM and enhanced marine primary productivity sustained by the high river nutrient input [*McKee et al*., 2004]. These highly productive areas are responsible for 25% of the primary production [*Hedges and Keil*, 1995] and even contain 80% of the total marine OM [*Wollast*, 1991]. In such shallow ecosystems, high OM inputs from rivers enhance benthic meiofaunal biomass [*Danovaro et al*., 2000] and also trigger eutrophication resulting in drastic oxygen depletion [*Jorissen et al*., 1992]. Although continental OM input is considered as predominantly refractory in nature it is still sufficiently labile to impact biological communities and biogeochemical cycles [*Mayer et al*., 2008]. OM lability requirement for benthic foraminifera is complex and appears dependant on distance from the continent, microhabitats, and species. Previous studies on benthic foraminiferal communities along continental shelves argue that specialized species are well developed in environment strongly affected by river discharges [*Mendes et al*., 2004, 2012; *Mojtahid et al*., 2009; *Goineau et al*., 2011, 2012]. Therefore, benthic foraminiferal ecology has to be further studied in such environments to better evaluate the impact of their discharges and associated OM supply on the benthic foraminiferal abundances and distributions.

For this, the living benthic foraminifera and environmental parameters from the western Iberian margin, a well-studied area in terms of sedimentology and OM sources [*Jouanneau et al*., 1998; *Dias et al*., 2002; *García et al*., 2010; *Martins et al*., 2012; *Zell et al*., 2015] has been investigated. This study area is also well characterized in terms of anthropogenic contamination of trace metals and $\delta^{15}N$ variations due to agriculture and industrialization of the Iberian Peninsula [*Alt-Epping et al*., 2007; *Martins et al*., 2012], in the Douro estuary [*Mucha et al*., 2003, 2004, 2005] or the Tagus and Sado estuaries [*Caçador et al*., 1996; *Jouanneau et al*., 1998]. Most of these studies focusing on As, Zn, Cr, Cu, and Pb have shown high trace metal concentrations linked to the anthropogenic contamination in Portuguese estuaries. Benthic foraminiferal distribution was also investigated all along the Portuguese margin. These studies were mostly focused on particular setting such as the coastal waters [*Levy et al*., 1995; *Martins et al*., 2015], the gulf of Cadiz [*Schönfeld*, 1997, 2001, 2002a, 2002b; *Mendes et al*., 2012],the Guadiana and Guadalquivir shelf [*Mendes et al*., 2004, 2012], the Nazaré and Lisbon-Setùbal canyons [*Koho et al*., 2007, 2008], the Cape Sines [*Phipps et al*., 2012], the Tagus prodelta [*Bartels-Jónsdóttir et al*., 2006], and the Ría de Vigo [*Diz et al*., 2004, 2006; *Diz and Francés*, 2008]. In this paper we propose a broader study on open marine setting ranging from the inner shelf to the outer slope and covering a wide spatial area extending from the Douro River to the Sado River in order to evaluate a large set of environmental settings under variable river influences.

We therefore aim to investigate the response of benthic foraminiferal assemblages in terms of density, diversity, and distribution to variable OM amount, source, and quality of four Iberian Rivers in order to identify the main factors controlling the living benthic foraminiferal abundances and distributions. We present results of living (Rose Bengal stained) benthic foraminiferal assemblages from 23 stations located on five bathymetrical transects along the northwest Portuguese margin. Relationships between the foraminiferal distributions and a range of environmental parameters, including qualitative descriptors of OM (i.e., $\delta^{13}C_{TOC}$, amino acids, and pigment ratios), are discussed to better understand the benthic foraminiferal ecology in such river-dominated coastal ocean margin.

2. Material and Methods

2.1. Study Area

The study area is the open continental margin of the western Iberian Peninsula in the North Atlantic Ocean. The Portuguese continental shelf ranges from 20 to 34 km in width, and the shelf break varies between 130 and 150 m water depth. The marine sediments along the shelf are mainly supplied by the Douro and Tagus Rivers [*Araújo et al*., 1994; *Jouanneau et al*., 1998; *Dias et al*., 2002] and by smaller rivers like the Sado and Mondego Rivers. The hydrodynamics of the inner shelf in winter, period of our study, is essentially driven by the waves regime, particularly during recurrent storms and internal (both tidal and near-inertial) currents that may create local regular downwelling and rare upwelling conditions [e.g., *Vitorino et al*., 2002a, 2002b] that promote sediment dispersal on and off the shelf. Relatively fine sediments are deposited at middepth

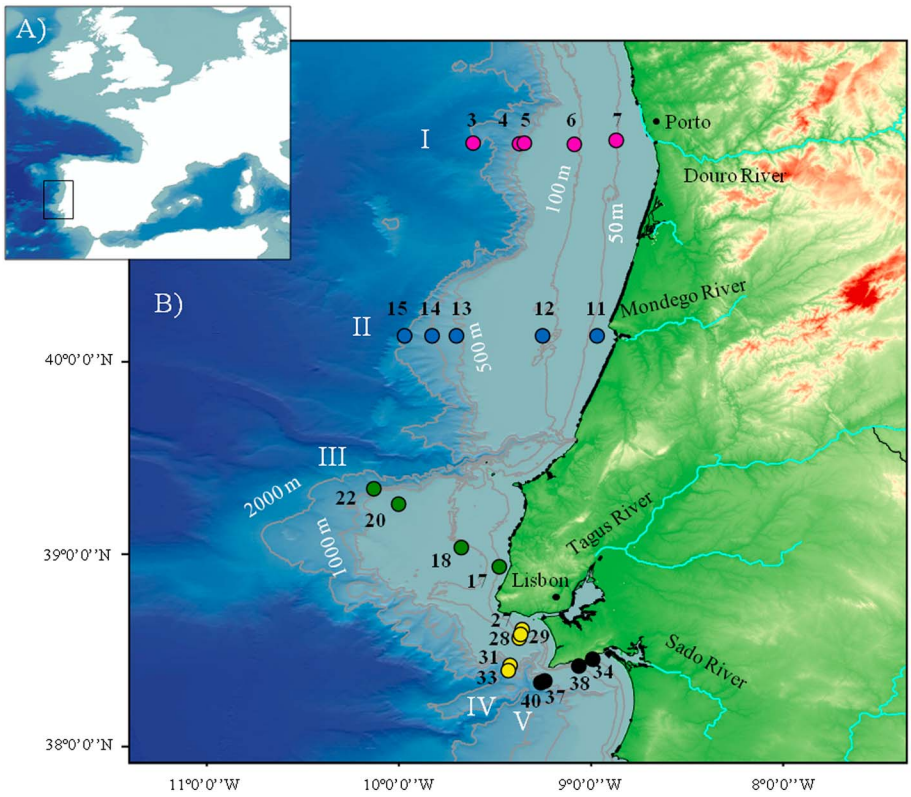

Figure 1. (a) General location map of the study area and (b) detailed sampling locations along the five transects: (I) Douro, (II) Mondego, (III) Estremadura, (IV) Tagus, and (V) Sado.

on the shelf where rocky outcrops, situated around 120 m water depth [*Mougenot*, 1985; *Dias et al.*, 2002], do retain most of the sediment in mud accumulation areas, off the Douro and Tagus Rivers [*Jouanneau et al.*, 1998, 2002; *Dias et al.*, 2002]. These mud patches are characterized by mixed sources of OM: marine, estuarine, and terrestrial [*Schmidt et al.*, 2010].

The regional hydrology is composed of the Eastern North Atlantic Central Water (ENACW) found from below the surface mixed layer down to about 500 m water depth [*van Aken*, 2000a, 2000b]. Below 500 m the salinity increases as result of the Mediterranean Outflow Water (MOW) flows northward between 600 and 1600 m water depth. The North Atlantic Deep Water flows southward beneath 1600 m water depth. Between May and September, the Azores high-pressure system is driven closer to the coast, which, associated with the northern 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], with maximal intensity in July [*Álvarez-Salgado et al.*, 2003]. This upwelling leads to increased productivity in summer along a 50 km wide zone. In winter, the Azores high moves south, which results in southerly winds and downwelling conditions [*Frouin et al.*, 1990]. The downwelling season extends from the beginning of October to the end of March [*Álvarez-Salgado et al.*, 2003]. This study concerns the central northern part of Portuguese margin, between 41°N off the Douro River and 38°N off the Sado River (Figure 1). Located in the north of the Iberian Peninsula, the Douro River has a drainage basin of 95,700 km^2 and an annual mean water discharge of 500 $m^3 s^{-1}$ [*Azevedo et al.*, 2010]. The mean phytoplankton quantity exported by the Douro estuary is estimated of 2600 t C yr^{-1} [*Saraiva et al.*, 2007]. In the central part of the Peninsula, the Tagus River watershed is about 80,600 km^2 with 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 have strong seasonal changes in discharge. There are also smaller rivers that enter the ocean along the Portuguese coast, i.e., the Sado River with a mean annual discharge value <10 $m^3 s^{-1}$ [*Richter et al.*, 2009], and the Mondego River, with a mean annual discharge of 82 $m^3 s^{-1}$ [*Pardal et al.*, 2002].

Table 1. Information on Sampling Stations and Total Faunal Densities

Sample Name	Sample Stations	Longitude (°W)	Latitude (°N)	Water Depth (m)	Sampling Date (dd/mm/yyyy)	Densities (ind. 100 cm^{-2})
			I. Douro Transect			
64PE332-3-7	3	9.61	41.14	1989	17/03/2011	172
64PE332-4-1	4	9.37	41.13	1007	17/03/2011	178
64PE332-5-2	5	9.34	41.14	506	17/03/2011	30
64PE332-6-1	6	9.08	41.13	110	16/03/2011	2169
64PE332-7-2	7	8.87	41.15	51	16/03/2011	1012
			II. Mondego Transect			
64PE332-11-2	11	8.97	40.13	28	19/03/2011	10
64PE332-12-1	12	9.25	40.13	108	19/03/2011	518
64PE332-13-3	13	9.70	40.13	505	19/03/2011	22
64PE332-14-4	14	9.83	40.13	981	19/03/2011	32
64PE332-15-1	15	9.97	40.13	1808	20/03/2011	117
			III. Estremadura Transect			
64PE332-17-2	17	9.48	38.93	48	21/03/2011	176
64PE332-18-5	18	9.67	39.03	116	21/03/2011	1237
64PE332-20-2	20	10.00	39.26	308	21/03/2011	311
64PE332-22-6	22	10.13	39.34	1100	22/03/2011	170
			IV. Tagus Transect			
64PE332-27-3	27	9.36	38.61	20	24/03/2011	5
64PE332-28-1	28	9.37	38.56	94	24/03/2011	800
64PE332-29-2	29	9.36	38.58	48	25/03/2011	98
64PE332-31-2	31	9.42	38.42	479	25/03/2011	131
64PE332-33-1	33	9.43	38.39	1000	26/03/2011	166
			V. Sado Transect			
64PE332-34-2	34	8.99	38.45	48	26/03/2011	107
64PE332-37-2	37	9.24	38.34	516	28/03/2011	191
64PE332-38-2	38	9.06	38.42	98	28/03/2011	227
64PE332-40-1	40	9.26	38.33	979	29/03/2011	210

2.2. Collection and Processing of Samples

The material used in this study was collected during the PACEMAKER 64PE332 cruise on the R/V *Pelagia* between 14 and 29 March 2011. Twenty-three sediment cores were retrieved along five cross-shore transects from 20 to 2000 m water depth; four transects off the Douro, Mondego, Tagus, and Sado Rivers and 1 intermediate transect, disconnected from rivers inputs in Estremadura region (Table 1 and Figure 1). The sampling was set up to take place after the period of maximal winter river runoff in the January–March period [*Aguiar and Ferreira*, 2005; *Azevedo et al*., 2008; *Garel et al*., 2009] and before the phytoplankton spring bloom and seasonal upwelling prevailing commonly in this area between June and August.

Sediment cores were retrieved using an Oktopus GmbH multicorer equipped with eight tubes of 6 cm diameter and four tubes of 10 cm diameter. Benthic foraminiferal samples as well as depth profiles of oxygen were obtained using 10 cm tubes except at stations 5 and 20 where they have been performed using 8 cm tubes. Sediment cores were sliced on board every 0.5 cm from the surface to 2 cm and every centimeter down to 10 cm when possible. Geochemical analyses were performed on a specific core from the same multicorer deployment. The samples were stored in 4°C refrigerator to be preserved for geochemical analyses. For some cores, only the first 5 cm of sediments were sampled due to technical failure on board. To keep certain homogeneity of our faunal data set, we based our faunal results on the first 5 cm of all stations.

2.3. Sedimentological and Geochemical Analyses

Sediment grains size was measured for the surface sediments of each station (i.e., 0–2 cm) using Malvern™ Mastersizer S laser diffractometer (maximal size detection of 880 μm) on wet bulk sediment without treatment. The presence of unimodal distribution in all grain size spectrums allows the use of medium grain size mode (Q_{50}).

Profiles of oxygen concentration down the sediment and oxygen penetration depth (OPD) were measured directly on board for each station using Clark's type microelectrodes [*Revsbech*, 1989] of 100 μm diameter

(OX100, Unisense A/S) immediately after recovery of the sediment in a temperature controlled container corresponding to the in situ bottom water temperature. Linear calibration was achieved using the O_2 concentration of the oxygenated subsurface seawater and the zero oxygen in a solution of sodium ascorbate and NaOH (both at 0.1 *M*). Oxygen profiles were processed using PRO_2FLUX software [*Deflandre and Duchêne*, 2010]. Due to technical failure the oxygen could not be measured for stations 3, 5, 13, and 33.

The OM descriptors were characterized by the analyses of total organic carbon (TOC), $\delta^{13}C_{TOC}$, chlorophyll *a* (Chl *a*), chlorophyll *a*/phaeopigments (Chl *a*/Phaeo), amino acids such as total and enzymatically hydrolyzable amino acids (THAA and EHAA), and the EHAA/THAA ratio. TOC and Chl *a* indicate total OM and phytodetritus amount, while OM quality is evaluated using Chl *a*/Phaeo ratio which indicates the freshness of the phytodetritic matter and amino acids, which are good descriptors of the nutritional value of OM [*Grémare et al*., 2005; *Dessandier et al*., 2015]. The OM source is estimated by the measure of $\delta^{13}C_{TOC}$ [*Gordon and Goñi*, 2003]. Based on the results of *Dessandier et al*. [2015], all parameters except amino acids were measured on the surface samples (0–0.5 cm) only, considering that the organic content of surface sediments provide a well representation of environmental conditions. Because too little material from the core tops was remaining, amino acids were determined on the 0.5–1 cm layer, considering its very low vertical variation in the first 2 cm [*Dessandier et al*., 2015].

TOC content and $\delta^{13}C_{TOC}$ were measured on freeze-dried and grounded sediments decarbonated with 2 mol L^{-1} HCl overnight at 50°C, using a Thermo Flash EA 1112 Elemental Analyzer interfaced with a Thermo Finnigan Delta^{Plus} mass spectrometer.

Chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo) were extracted (overnight, 4°C) with 98% acetone (final concentration taking into account sediment water content) and centrifuged. Their supernatant was used to assess chlorophyll *a* and phaeopigments according to *Neveux and Lantoine* [1993]. The Chl *a*/Phaeo ratios were computed for each station.

Amino acids were measured in triplicate as described in *Dessandier et al*. [2015]. The EHAA/THAA ratios were used as an indicator of OM quality [*Grémare et al*., 2005].

2.4. Living (Stained) Benthic Foraminiferal Analysis

Benthic foraminiferal samples were preserved in 96% ethanol containing1 g L^{-1} of Rose Bengal to stain endoplasm of living benthic foraminifera [*Walton*, 1952]. Samples were wet sieved over 63 and 150 μm mesh sieves. Because analyzing the fine fraction (>63 μm) is time consuming and because more than 200 samples were considered for this study, we decided to analyze only the >150 μm size fraction *w* for this study and keep the 63–150 μm for future studies. However, we are aware that the >150 μm fraction may give a biased signal of the total fauna and that our interpretations could be different if the 63–150 μm fraction would be considered. This is mainly true in the deepest environments where the proportion of small size calcareous benthic foraminifera is increasing in the study area [*Phipps et al*., 2012]. On the shelf, we may, for instance, expect an underestimation of species *Bolivina* spp., *Epistominella vitrea*, or *Nonionella iridea*, which are typically observed in the >63 μm size fraction [*Mendes et al*., 2004; *Mojtahid et al*., 2009]. The live specimens were sorted from the complete samples, from the surface down to 5 cm. Stained specimens were picked under wet conditions (~50% ethanol) with a stereomicroscope and stored in micropaleontological slides. Rose Bengal may also stain protoplasm of well-preserved dead foraminifera. This is particularly true for deep sediment samples but less problematic for well-oxygenated surface coastal sediments. In order to limit this issue, a strict staining criterion was observed: all chambers except the last one have to be stained [*Fontanier et al*., 2002; *Phipps et al*., 2012]. Some nontransparent tests (miliolids or agglutinated taxa) were broken to ensure that protoplasms were stained. All the livings specimens were considered; according to *Fatela and Taborda* [2002], 100 individuals constitute a statistically representative sample when each species represents >5% of the assemblage. In some cases, less than 100 living specimens were found, but we consider the very low faunal density as a signal of its own. The diversity indices and relatives abundances for those stations were then considered with caution in these cases. The living specimens were summed by core and expressed as total standing stock (TSS) for a 100 cm^2 surface. Percentages of major species (>7%) were expressed, while minor species were grouped in a category named "Others." The limit of 5% is normally used in the literature. However, in our study, with the large number of stations covering large spatial range this 5% threshold was not sufficient to highlight the major species only and to keep figures easy to read. We therefore used the limit

Table 2. Environmental Parameters Measured on Surface Samples (0–0.5 cm)

Sample Name	St.	Water Depth (m)	TOC (wt %)	$\delta^{13}C_{TOC}$ (‰ VPDB)	THAA (nmol mg^{-1})	EHAA (nmol mg^{-1})	EHAA/THAA (%)	Q_{50} (μm)	OPD (cm)	Chl *a* (μg g^{-1})	Phaeo (μg g^{-1})	Chl *a*/Phaeo
					I. Douro Transect							
64PE332-3-7	3	1989	0.93	−22.09	31.0	3.7	12	7	-	0.17	18.52	0.01
64PE332-4-1	4	1007	0.75	−22.01	6.8	1.2	18	17	1.76	0.08	8.48	0.01
64PE332-5-2	5	506	0.12	−21.06	23.6	3.0	13	190	-	0.04	4.85	0.01
64PE332-6-1	6	110	0.30	−24.09	38.9	7.6	19	32	0.64	0.51	26.09	0.02
64PE332-7-2	7	51	0.01	−22.09	5.7	2.1	37	104	1.2	0.16	5.11	0.03
					II. Mondego Transect							
64PE332-11-2	11	28	0.00	−22.08	2.2	0.4	16	162	0.8	0.03	1.79	0.02
64PE332-12-1	12	108	0.11	−22.22	7.7	1.2	15	137	0.89	0.36	9.51	0.04
64PE332-13-3	13	505	0.04	−22.09	4.4	0.5	11	91	-	0.09	3.16	0.03
64PE332-14-4	14	981	0.30	−22.58	10.6	1.5	15	56	2.91	0.20	4.97	0.04
64PE332-15-1	15	1808	0.82	−22.39	25.2	3.4	14	7	2.97	0.32	10.02	0.03
					III. Estremadura Transect							
64PE332-17-2	17	48	0.01	−21.43	3.0	0.5	17	197	3.23	0.11	2.20	0.05
64PE332-18-5	18	116	0.83	−22.18	34.1	4.5	13	17	0.7	0.87	22.72	0.04
64PE332-20-2	20	308	0.21	−22.21	6.2	0.6	10	169	0.8	0.15	5.54	0.03
64PE332-22-6	22	1100	1.07	−22.28	15.8	2.1	14	22	2.47	0.14	3.89	0.04
					IV. Tagus Transect							
64PE332-27-3	27	20	0.05	−23.99	7.3	1.4	19	145	0.92	0.46	5.90	0.08
64PE332-28-1	28	94	0.38	−24.93	35.6	4.7	13	15	0.72	1.99	33.02	0.06
64PE332-29-2	29	48	0.01	−22.70	6.1	0.8	12	115	0.89	0.13	4.57	0.03
64PE332-31-2	31	479	0.66	−21.86	42.8	3.6	8	10	1.51	0.13	53.31	0.00
64PE332-33-1	33	1000	0.70	−22.19	38.4	3.9	10	8	-	0.08	22.98	0.00
					V. Sado Transect							
64PE332-34-2	34	48	0.84	−24.40	57.0	5.4	9	17	0.3	2.74	31.67	0.09
64PE332-37-2	37	516	0.70	−23.10	33.4	3.6	11	11	1.44	0.33	22.61	0.01
64PE332-38-2	38	98	0.37	−21.73	28.5	3.0	10	38	0.6	1.09	12.16	0.09
64PE332-40-1	40	979	0.84	−22.37	37.1	4.2	11	7	1.6	0.25	7.78	0.03

of 7% considering that species between 5 and 7% in this study did not provide any essential information. Complete data are available in the supporting information.

Diversity indices were calculated on faunal data using the PAST software [*Hammer et al.*, 2001] based on the raw data of living individuals observed on 0–5 cm sediment interval. Specific richness (*S*) corresponds to the observed number of species for a given station, Shannon (*H'*) [*Shannon and Weaver*, 1949] and Evenness (*E*) [*Buzas and Gibson*, 1969] indices were calculated to evaluate the faunal diversity of each station.

2.5. Statistical Analyses

Multivariate statistics were applied on both faunal and environmental data. Principal component analysis (PCA) based on sedimentological and geochemical normalized data (subtracted from the mean value and divided by the standard deviation) was used to characterize the environmental conditions within each transect and stations. Only surface data of the environmental parameters were used considering TOC, $\delta^{13}C_{TOC}$, Chl *a*, Chl *a*/Phaeo, THAA, EHAA, EHAA/THAA, and grain size (Q_{50}). PCA was coupled with a Q mode cluster analysis (group average mode), based on Euclidean distances. R mode cluster analysis (group average mode) based on Bray-Curtis similarity was applied to the raw data of major taxa observed in the study to distinguish faunal groups. Major taxa were then computed on the environmental PCA as supplementary variables based on the correlation coefficient (*r*) of species abundances with PC1 and PC2 to highlight the influence of environmental parameters on benthic foraminifera. Although the investigated stations show variable TSS, we decided to keep all of them to highlight their variable environmental settings.

The faunal-environmental correlation was applied to investigate the environmental control on faunal distribution using the BIOENV analysis (Biotic and Environmental linking). This test was performed to determine the major parameters responsible for the total faunal variance for all stations. Prior to this, environmental variables were chosen after the calculation of Spearman correlation on normalized data. The environmental

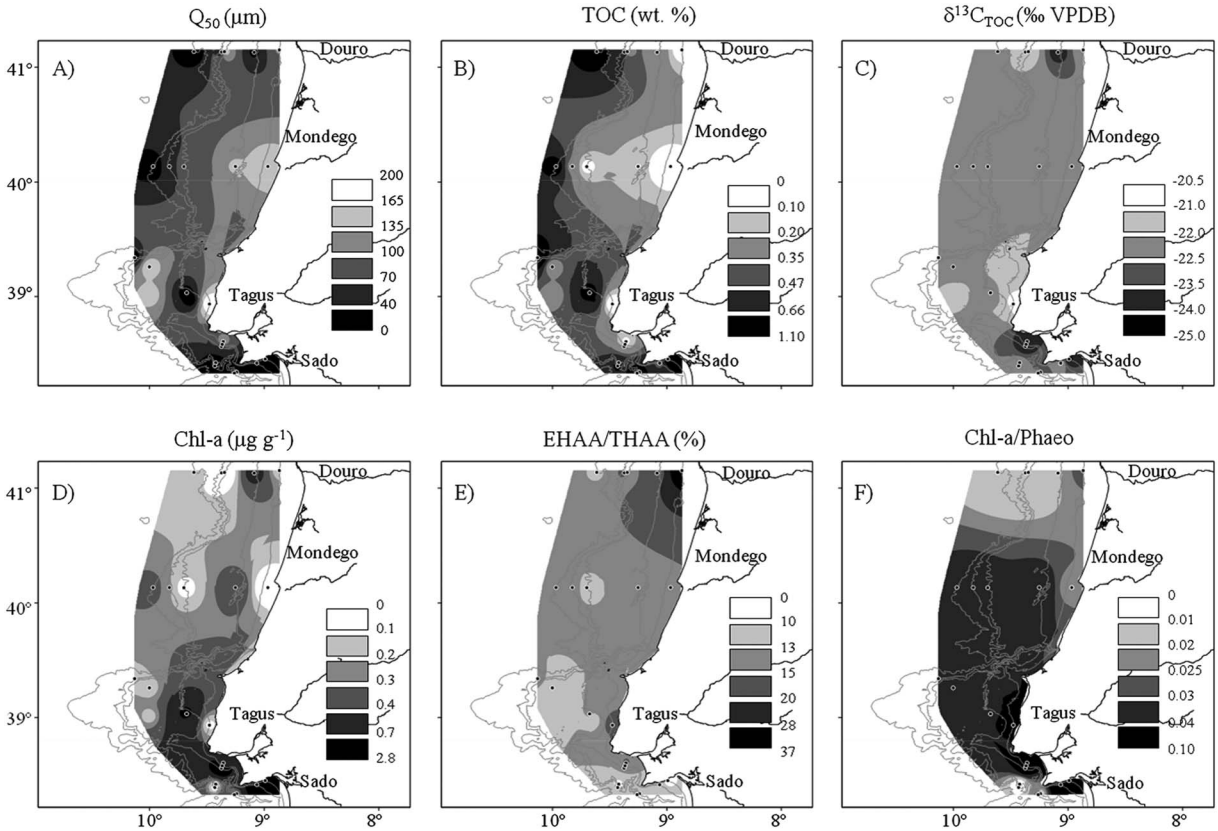

Figure 2. Spatial distribution patterns of major environmental parameters determined for BIOENV analysis: (a) Grain size (Q_{50}), (b) total organic carbon (TOC), (c) $\delta^{13}C_{TOC}$, (d) chlorophyll *a* (Chl *a*), (e) enzymatically/total amino acids ratio (EHAA/THAA), and (f) chlorophyll *a*/phaeopigments ratio (Chl *a*/Phaeo). The filled black circles indicate the sample locations investigated. The data were interpolated using the Arc GIS® software on theGCS_WGS_1984 coordinate system with Inverse Distance Weighted (IDW) and standard deviation classes.

matrix was calculated with Euclidean distances as for the PCA. The faunal matrix was calculated with the Bray-Curtis similarity formula on nontransformed data. All these analyses were performed using the PRIMER version 6.0 software [*Clarke and Warwick*, 1994].

3. Results

3.1. Sediment Grain Size Distribution and Geochemical Parameters

The sediments from the coast to the deep sea show a succession of various grain sizes. The coarsest sediments were found at coastal stations from the Estremadura region (Table 2 and Figure 2a). Coastal stations (20–50 m depths) were characterized by sandy sediments (>100 µm) except off the Sado River. At 100 m depth, silty sediments (>40 µm) were found along the coast except off the Mondego River where the mean grain size was 137 µm. Between 300 and 500 m depth, a north-south gradient was observed with coarser sediments off the Douro, Mondego, and Estremadura transects, while the grain size was <15 µm off the Tagus and Sado Rivers. The finest sediments of all transects were typically observed at deep stations.

The OPD varied from 0.3 cm at St. 34 to 3.23 cm at St. 17; in these shallowest sites (i.e., 50 m depth) the OPD is the most variable (Table 2). The OPD was <1 cm in midshelf stations (100 m depth) in four of the five transects. At the deep stations, the OPD was generally deeper than 1 cm (from 1.6 to 2.97 cm).

TOC content is lowest at the coastal stations with values <0.10 wt % except off the Sado River where it reaches 0.84 wt % (Figure 2b). Intermediate values were measured at 100 m depth (~0.3 wt %), except in Estremadura region where a TOC content of 0.83 wt % is measured. As previously indicated for the grain size, between 300 and 500 m water depth, TOC content was different between the northern part (of the Douro, Mondego, and Estremadura transects) and the southern part (off the Tagus and Sado Rivers) with TOC <0.21 wt % and TOC >0.6 wt %, respectively. The deepest stations in the northern part reached up to

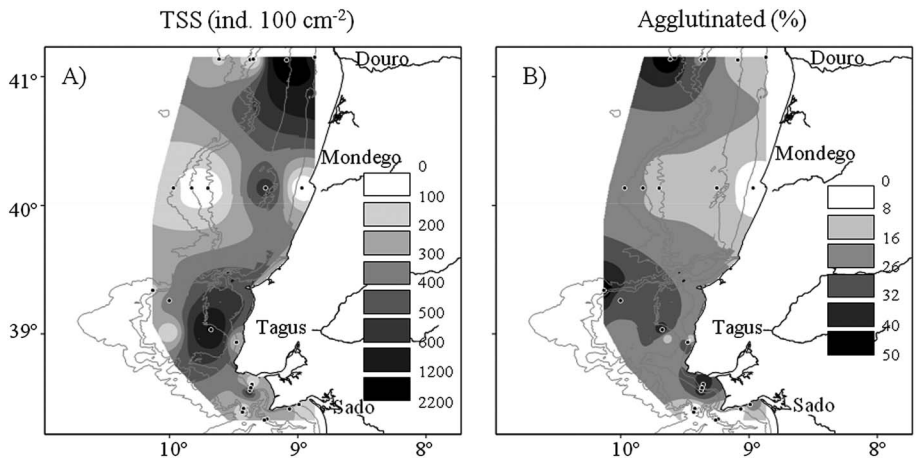

Figure 3. (a) Total standing stock (TSS) of living benthic foraminifera (ind. 100 cm^{-2}) and (b) relative contributions of agglutinated species to the total living foraminiferal faunas in the top 5 cm of the sediment.

~1 wt %, and a little less in the southern part. Stations of the Mondego transect appeared to be the least OM riched, while all stations off the Sado River showed high TOC content. $\delta^{13}C_{TOC}$ was more homogenous in the study area, but extreme values, between −21.0 and −24.9‰ (Figure 2c), were locally measured. The coastal station in the Estremadura region had a more positive $\delta^{13}C_{TOC}$ value than those of stations off the Iberian Rivers. Lowest values (<−24‰) were observed at 100 m depth off the Douro and Tagus Rivers and at 50 m depth off the Sado River. Relatively negative values for$\delta^{13}C_{TOC}$ were also measured at 20 m depth off the Tagus River and at 500 m water depth off the Sado River.

The spatial distribution of THAA was similar to that of TOC, with the highest value of 57 nmol mg^{-1} at 50 m depth off the Sado River and high concentrations at deep stations from 15.8 to 37.1 nmol mg^{-1} (Table 2). Stations at 100 m depth also showed elevated values with a THAA concentration around 30 nmol mg^{-1}, except off the Mondego River (8 nmol mg^{-1}). The distribution of EHAA concentrations followed the same trend as observed for the THAA concentrations, with minimal value of 0.4 nmol mg^{-1} (30 m depth) off the Mondego River and relatively high values off the Sado River from 3.0 to 5.4 nmol mg^{-1}. However, the highest value was not observed at the same station but at 100 m depth off the Douro River where the concentration is significantly higher than in other stations (7.6 nmol mg^{-1}) (Table 2). The EHAA/THAA ratio was quite high along the coastal station of the Douro transect (Figure 2e) with a maximum value of 37% at St. 7 (50 m depth). High EHAA/THAA values were generally measured at coastal stations except for the coastal station off the Sado River where the value merely reaches 9% (Table 2).

The Chl *a* concentration ranges from 0.03 μg g^{-1} (30 m depth) off the Mondego River to ~3.0 μg g^{-1} (50 m depth) off the Sado River. The highest concentrations were in any case observed at 100 m depth (Figure 2 d). The Chl *a* concentration is higher along the Sado transect at all depths. Phaeopigments follow a similar trend except at 500 m water depth off the Tagus River where the phaeopigments concentrations reached locally up to 53 μg g^{-1} (Table 2). Pigment concentration was substantially higher close to the coast in the south of the study area. The Chl *a*/Phaeo ratio showed a somehow clearer trend with lowest values off the Douro and Mondego Rivers (Figure 2f). Ratios were generally higher off Tagus and Sado but <0.03 in most stations off the Douro and Mondego Rivers and in the Estremadura region, with a trend of decrease with from the coast to the deep sea except off the Mondego River.

3.2. Living Benthic Foraminifera

3.2.1. Spatial Density and Diversity

The data for TSS for the upper 5 cm of the sediments for all the stations are presented in Figure 3 and Table 1. For each transect, highest TSS were found at 100 m depth. The highest TSS values were found off the Douro River (2169 ind. 100 cm^{-2}) and the lowest TSS off the Sado River (227 ind. 100 cm^{-2}). Coastal stations (20 to 50 m water depth) presented very low (5 ind. 100 cm^{-2} at 20 m depth off the Tagus River) to low (176 ind. 100 cm^{-2} at 50 m depth on the Estremadura transect) TSS ranging from to and for those stations relatives

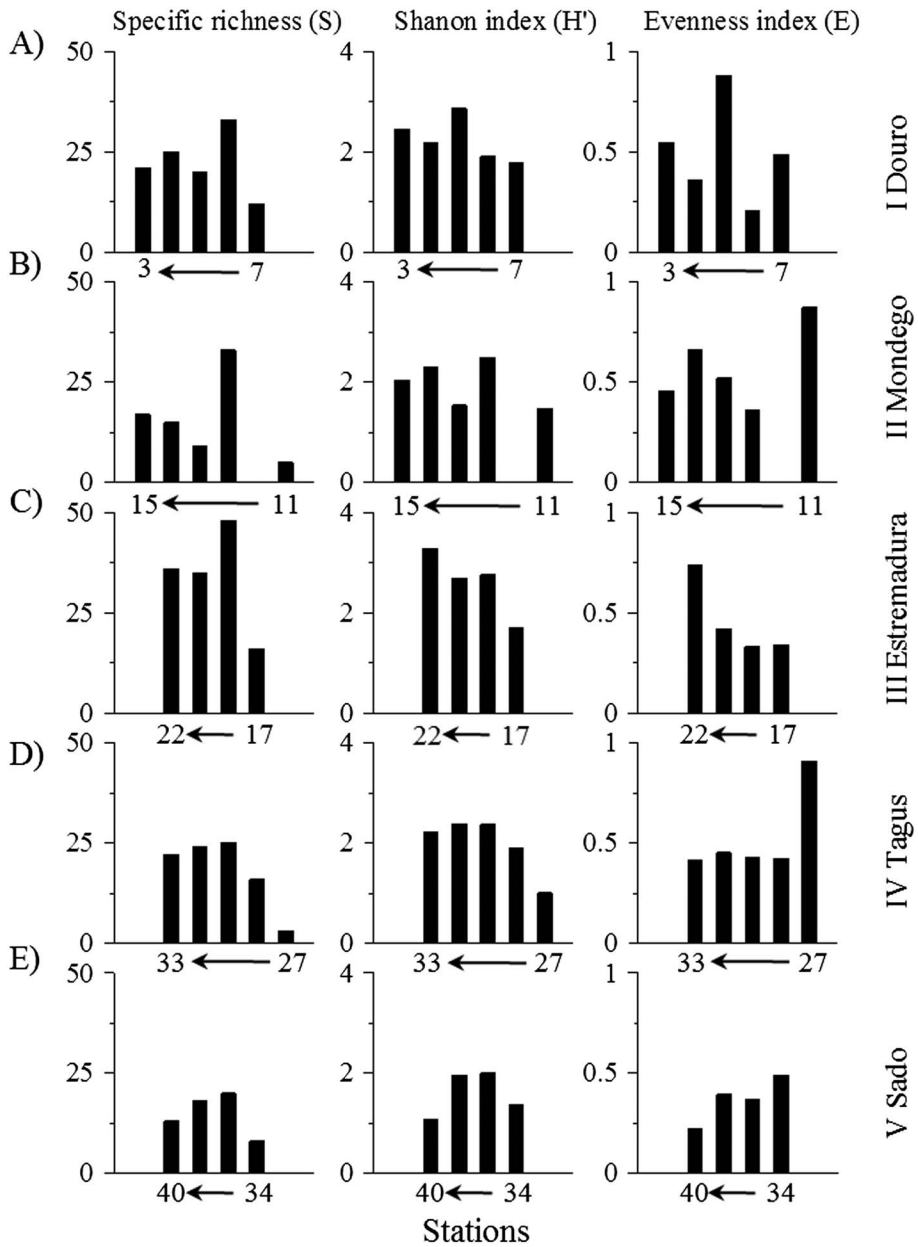

Figure 4. Diversity indices of each station: (a) (I) Douro, (b) (II) Mondego, (c) (III) Estremadura, (d) (IV) Tagus, and (e) (V) Sado transects. Stations are arranged according to water depth from the right to the left: 20 m, 50 m, 100 m, 300–500 m, 1000 m, and 2000 m.

abundances have to be considered very carefully. Conversely, the coastal station off the Douro River exceeded 1000 ind. cm^{-2} at 50 m depth. At equivalent depths, the values for TSS for the Mondego and Sado stations were lower than those for the other transects. The highest percentages of agglutinated taxa (>40%) were found in the Estremadura region with maxima at 100 and 1000 m depth. The percentages of agglutinated species increased seaward along the Douro, Mondego, and Estremadura transects (Figure 3b), while most of agglutinated species off the Tagus and Sado Rivers were found at 20 and 50 m depths.

As previously indicated for the TSS, the specific richness (*S*) was systematically higher at 100 m stations with 48 species found in the Estremadura region and 20 species off the Sado River. At the shallowest stations, lowest diversity were found with only 3 species at 20 m depth off the Tagus River and 16 species at 50 m depth in the Estremadura and Tagus transects (Figure 4a). The *H′* and *E* indices did not show any clear trend with water depth (Figures 4b and 4c). *H′* was highest in the Estremadura transect and lowest off the Sado

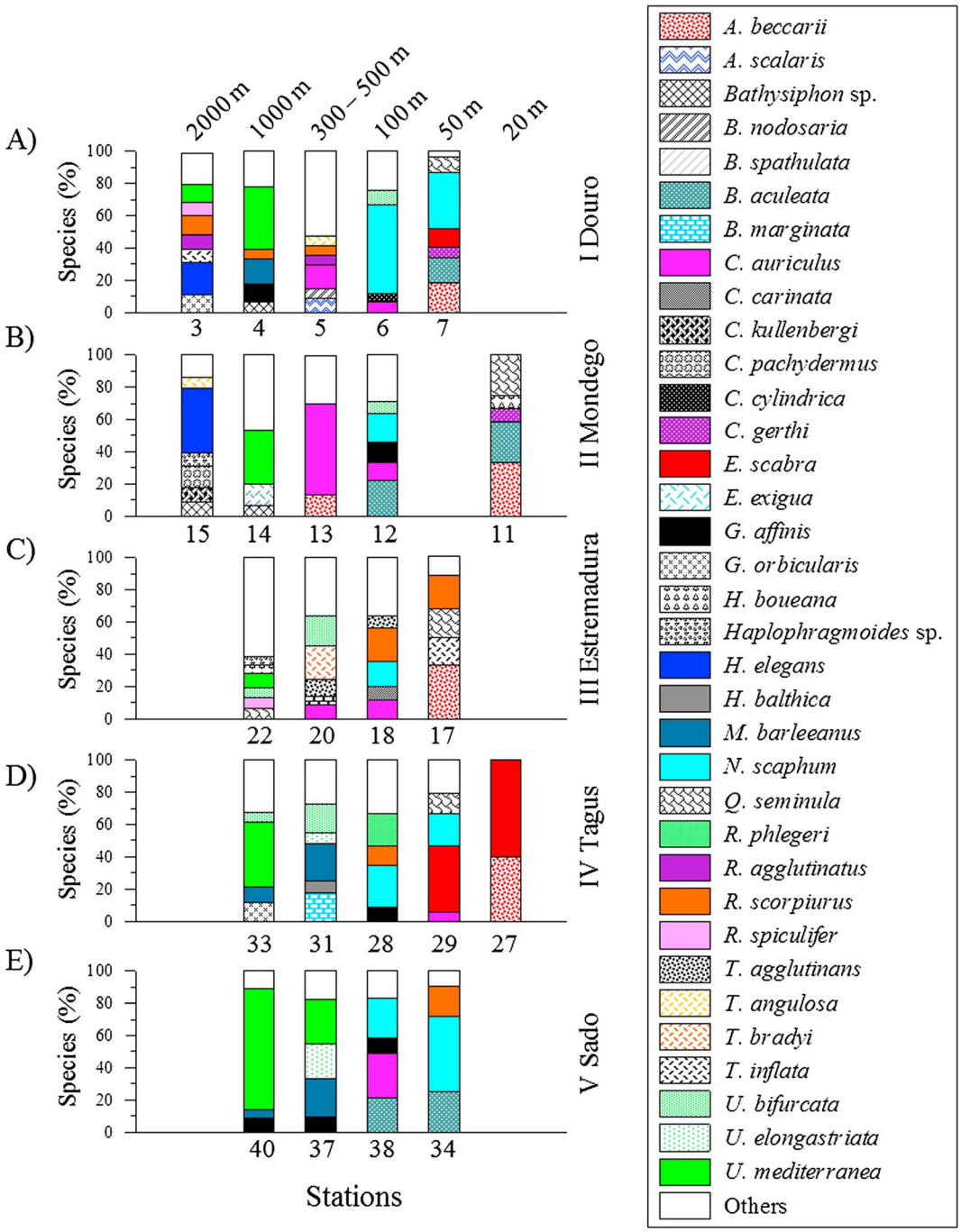

Figure 5. Relative contributions (%) of the major species (>7%) to the living benthic foraminiferal faunas from the top 5 cm of (a) (I) Douro, (b) (II) Mondego, (c) (III) Estremadura, (d) (IV) Tagus, and (e) (V) Sado transects. Stations are arranged in function of water depth.

River. The *E* appeared to decrease with TSS increase showing high coastal values and low values at 100 m depth, even if some coastal values have to be considered with caution considering the very low TSS.

3.2.2. Composition of Foraminiferal Faunas

In the whole study area, 85 major species were found with 65 calcareous, 15 agglutinates, and 5 miliolids. The species distribution for all transects is presented as a function of water depth (Figure 5). The most abundant taxa found at coastal stations, at 20 (St. 11 and 27) and 50 m (St.7, 29, and 34) water depth were *Ammonia beccarii*, *Bulimina aculeata*, *Eggerelloides scaber*, *Nonion scaphum*, and *Quinqueloculina seminula*. *N. scaphum*

was called *Nonion fabum* in *Goineau et al*. [2011] and *Mendes et al*. [2004], *Nonion boueanum* in *Diz et al*. [2002], or *Nonion asterizans* in *Bartels-Jónsdóttir et al*. [2006]; the taxonomic reference used in this study was found in *Mojtahid et al*. [2009] in plate I, 1. *Ammonia beccarii* was observed at coastal sites only. It ranged from 19 to 33% at 50 m, and although it is present at St.27 and St.11 as well, very low faunal density there makes the relatives abundances difficult to interpret. *B. aculeata* was present off the Douro (16%), Mondego (25%), and Sado (25%) Rivers while *E. scaber* was found off the Douro (11%) and Tagus Rivers only (41% at 50 m and 60% at 20 m). *N. scaphum* was the most abundant species off Douro (35%) and Sado (47%) Rivers. *Quinqueloculina seminula* was found between 10 and 25% at coastal stations except off the Sado River where *Reophax scorpiurus* was abundant (18%). At 100 m depth, the TSS was generally high with few species with relative abundances >7%. Among them, *N. scaphum* and *Cancris auriculus* were present at all stations. *N. scaphum* was dominant off the Douro River (55%), while *C. auriculus* was abundant off the Sado River (28%). On the upper slope at 500 m depth, the faunal distribution was more contrasted. *C. auriculus* was abundant off the Douro (15%) and Mondego (57%) Rivers, whereas *Uvigerina bifurcata* was the most abundant (19%) in the Estremadura region and off the Tagus River (18%). *Uvigerina mediterranea* was present off the Sado River (27%). At 1000 m depth, *U. mediterranea* was highly abundant off the Douro (39%), Mondego (33%), Tagus (40%), and Sado (75%) transects, but *Melonis barleeanus* was also abundant off the Douro (16%), Tagus (23%), and Sado (24%). At 2000 m depth, the faunas along the Douro and Mondego transects were dominated by *H. elegans* with 20 and 40%, respectively. Agglutinated species were abundant off the Douro River such as *Reophax scorpiurus* (11%), *Reophax spiculifer* (9%), and *Reophax agglutinatus* (8%). At the Mondego deepest stations, other abundant species were *Cibicides pachydermus* (13%), *Haplophragmoides* sp. (9%), and *Cibicides kullenbergi* (9%).

3.2.3. Vertical Distribution Within the Sediment

Vertical distribution of the living foraminifera and the associated OPD are shown in Figure 6. For all stations, the maximum TSS was observed in the upper 2 cm. Most stations showed a decrease in foraminiferal density with increasing sediment depth. Stations enriched in OM had different distributions with maximal densities observed between 1 and 2 cm below the OPD. Exceptions were stations 18 and 20 of the Estremadura region with the display of a clear surface maximum (0–0.5 cm). Living individuals were often found below the OPD in coastal stations and less frequently in deep stations. In anoxic microhabitats in the shelf *N. scaphum* was dominant together with *A. beccarii*, *B. aculeata*, *C. auriculus*, and *G. affinis*. At deeper stations, *M. barleeanus*, *U. bifurcata*, *U. elongastriata*, and *U. mediterranea* were dominant below the OPD. A general higher number of species were present in well-oxygenated sediments than in anoxic zones. Most of agglutinated species showed high abundances in only well-oxygenated environments.

3.3. Statistical Analyses

Principal component analysis (PCA) was performed on environmental data (TOC, $\delta^{13}C_{TOC}$, Chl *a*, Chl *a*/Phaeo, THAA, EHAA, EHAA/THAA, and Q_{50}) to identify different environmental niches in the study area. The first two principal components explained 72% of the total variance (Figure 7a). On the first principal component (PC1, explaining 50% of the variance) the negative loading of Q_{50}, $\delta^{13}C_{TOC}$, and EHAA/THAA was opposed to the positive loading of all other parameters. On the second principal component (PC2, explaining 22% of the variance), $\delta^{13}C_{TOC}$ and TOC were negatively loaded while EHAA/THAA, Chl *a*, and Chl *a*/Phaeo were positively loaded. Three groups of stations emerged from the cluster analysis (Figure 7b). Most of the coastal stations (7, 11, 17, 27, and 29) with stations off the Mondego (12, 13, and 14) and two slope stations (5 and 20) represent a group (cluster 1) in the left-hand part of the PC1 versus PC2 plot and are characterized by coarse grain size (high Q_{50}) and high OM quality, highlighted by EHAA/THAA. A second group (cluster 2) composed of the deepest stations (3, 4, 15, 22, 37, and 40) with the 100 m station of the Estremadura transect (18) lies on the bottom part of the PC2 and is associated with fine sediments (i.e., high Q_{50}) and high OM content (TOC). The stations at 100 m off the Douro, the Tagus and the Sado Rivers (St. 6, 28, and 38), are grouped with the coastal station off the Sado River (34) in the cluster 3, showing positive loading of phytoplanktonic abundance and freshness (Chl *a* and Chl *a*/Phaeo ratio) and negative loading of marine OM ($\delta^{13}C_{TOC}$) and TOC content. Accordingly, our PCA results reveal that three groups have distinctive environmental conditions, showing sandy sediments (cluster 1), high organic content (cluster 2), and high phytopigments content (cluster 3).

The 12 dominant species of the whole study area were plotted as supplementary variables in the PCA (Figure 7c) to correlate their abundances with environmental parameters. R mode cluster based on the

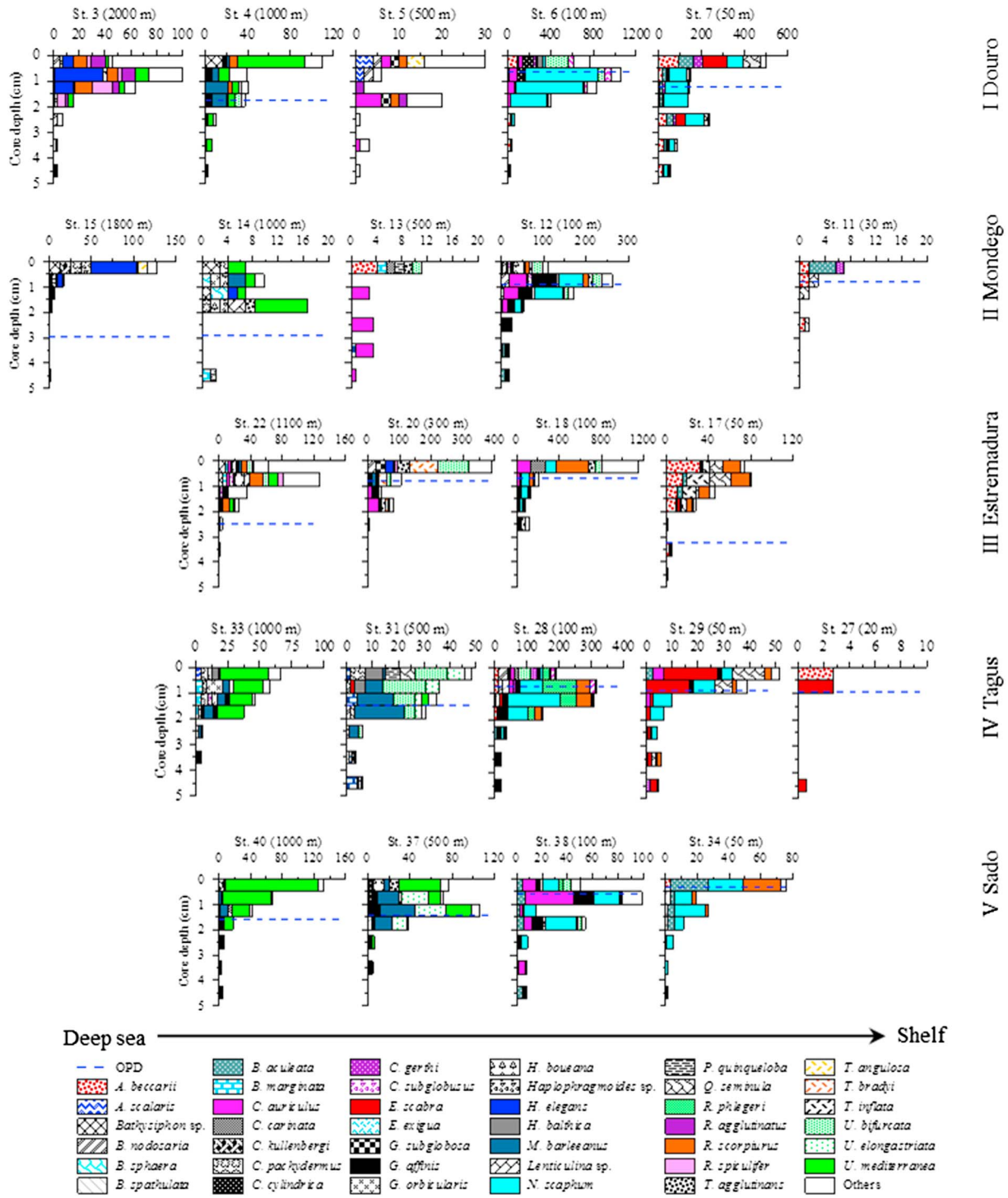

Figure 6. Species densities (ind. 50 cm^{-3}) and oxygen penetration depth on 0–5 cm profiles in the sediment for the 23 stations: I (Douro), II (Mondego), III (Estremadura), IV (Tagus), and V (Sado) transects.

Bray-Curtis similarity was applied on the 12 dominant taxa of the whole study to determine faunal groups (Figure 7d). Four groups were then determined: coastal species (group 1), composed of *A. beccarii*, *B. aculeata*, *E. scaber*, and *Q. seminula*. These species are loaded negatively with the PC1 and positively with the PC2 like the grain size (Q_{50}) and the EHAA/THAA ratio. Group 2 is composed of *N. scaphum*, *U. bifurcata*, and *C. auriculus*, loaded positively with PC1 and PC2, associated with Chl *a* and Chl *a*/Phaeo. Group 3 is composed

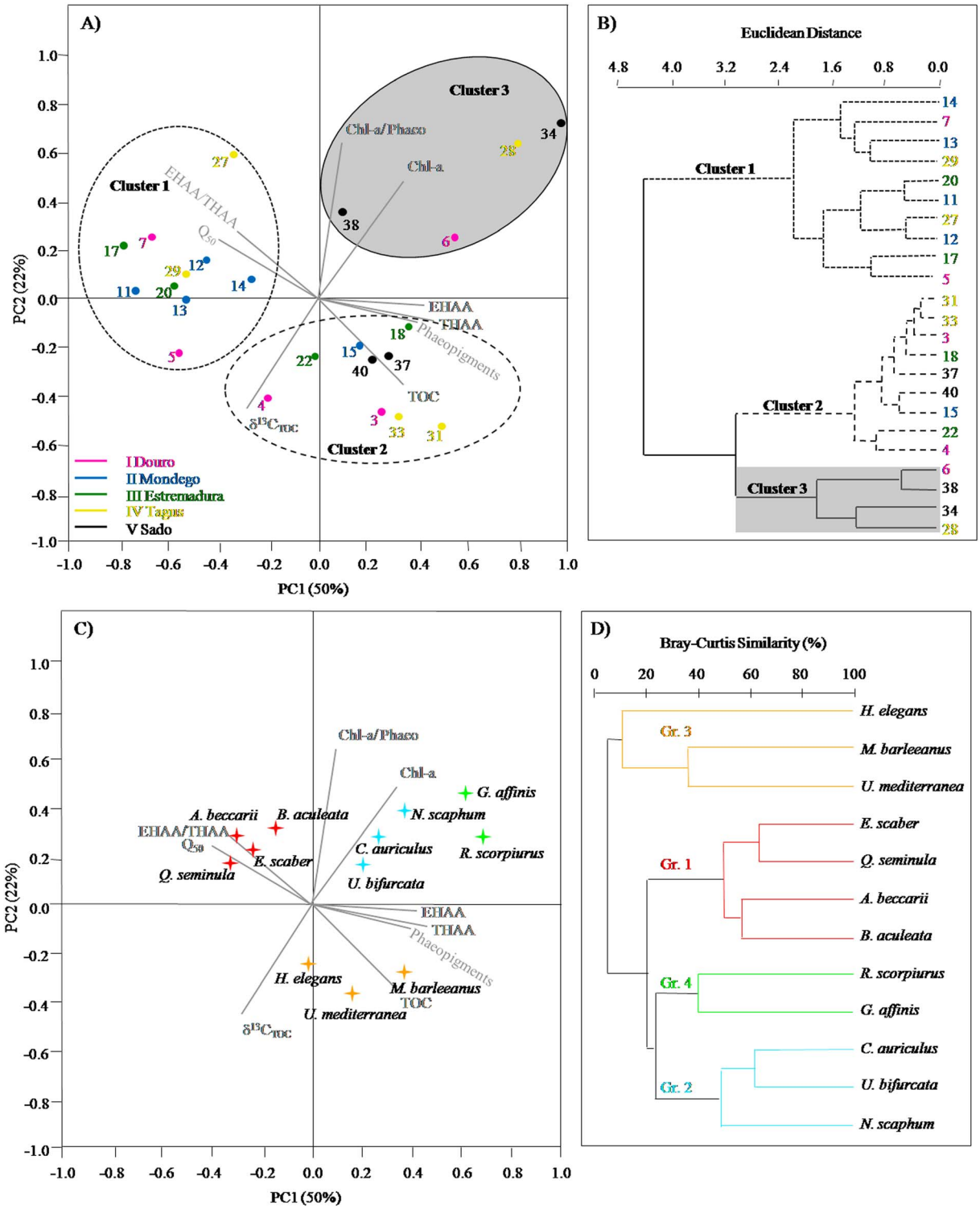

Figure 7. (a) Principal component analysis (PCA). (b) Q mode cluster analysis based on the surface data of environmental parameters: TOC, $\delta^{13}C_{TOC}$, Chl *a* (chlorophyll *a*), Chl *a*/Phaeo (chlorophyll *a*/phaeopigments), phaeopigments, THAA (total hydrolyzable amino acids), EHAA (enzymatically hydrolyzable amino acids), EHAA/THAA, and grain size mode (Q_{50}). Station points are I (Douro): in pink, II (Mondego): in blue, III (Estremadura): in green, IV (Tagus): in yellow, and V (Sado): in black. (c) PCA of environmental parameters with the 12 most abundant species as secondary variables. (d) R mode cluster analysis based on the Bray-Curtis similarity calculated on the raw data of the 12 dominant species.

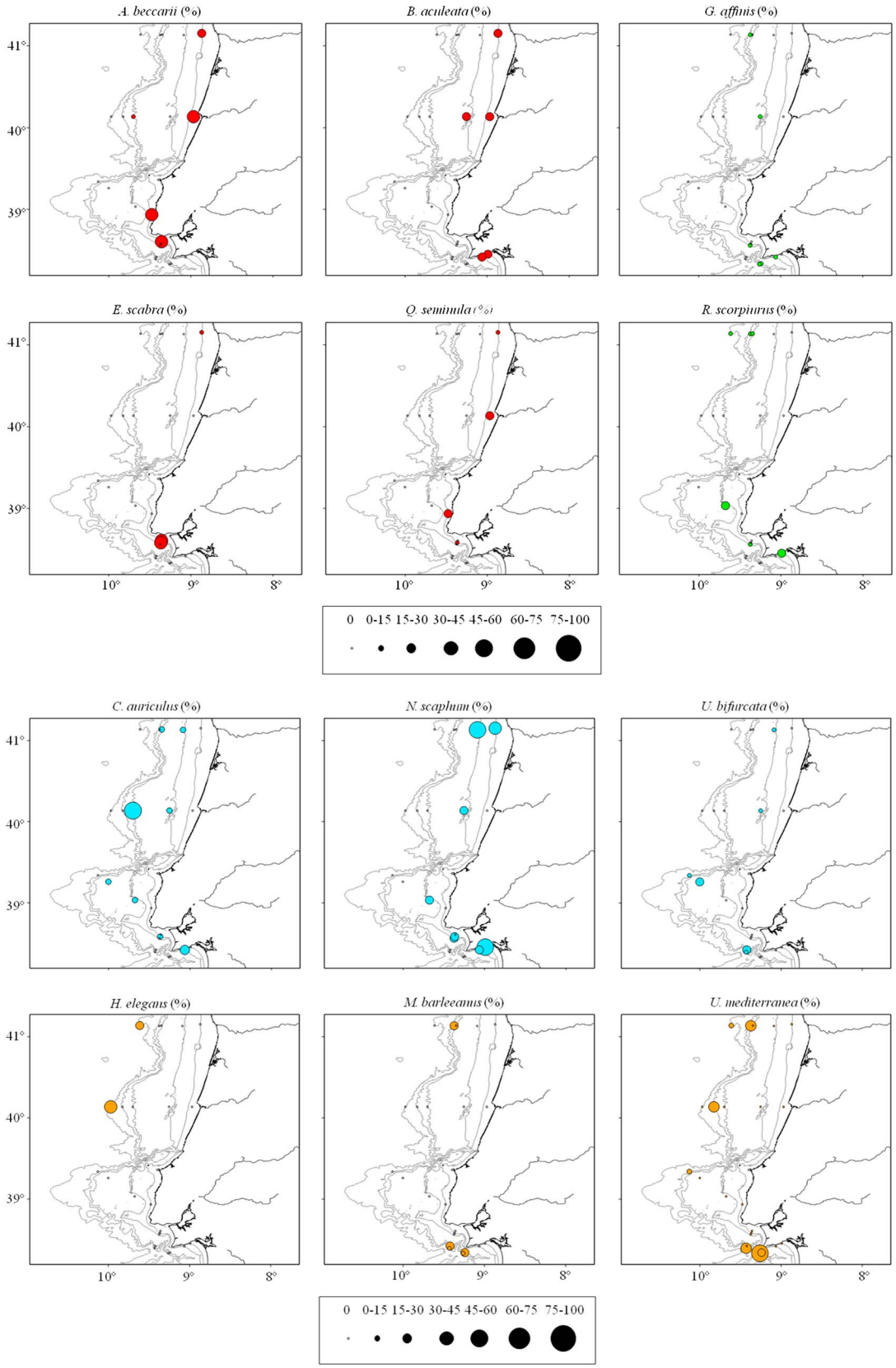

Figure 8. Bubble points representing percentages of dominant species to the TSS of living benthic foraminifera. Coastal species are in red, midshelf species in blue, deep species in orange, and high trophic species in green. The four groups were defined as the faunal R mode cluster analysis (see also Figure 7d).

Table 3. BIOENV Analysis Results[a]

Correlation Coefficient	Environmental Parameter Matrices
0.329 *(0.02)*	TOC, $\delta^{13}C_{TOC}$, EHAA/THAA
0.320 *(0.05)*	TOC, $\delta^{13}C_{TOC}$, EHAA/THAA, THAA
0.319 *(0.04)*	TOC, $\delta^{13}C_{TOC}$, EHAA/THAA, Chl *a*
0.246 *(0.04)*	TOC, $\delta^{13}C_{TOC}$, EHAA, THAA, EHAA/THAA, Chl *a*, Chl *a*/Phaeo, Q_{50}

[a]*P* values are in italics.

by *H. elegans*, *U. mediterranea*, and *M. Barleeanus*. These species are negatively loaded with the PC2, correlated with $\delta^{13}C_{TOC}$ and TOC. Finally, *G. affinis* and *R. scorpiurus* compose the group 4, positively loaded with PC1, without clear correlation with any environmental parameter. The abundance of each of the dominant species represented in the R mode cluster is shown for the whole study area in Figure 8. Species of group 1 are abudant at coastal stations. *Ammonia beccarii* and *Q. seminula* are abundant at all coastal stations except off the Sado River. High percentages of these species were also found of the Estremadura region. Conversely, *E. scaber* was only found between 20 and 50 m depth off the Douro and Tagus Rivers, while *B. aculeata* was observed at 50 and 100 m off the Douro, Mondego, and Sado Rivers. Species of group 2 are abundant at midshelf stations. These species are abundant at all stations at 100 m water depth and *N. scaphum* is also abundant at 50 m water depth off the Douro, Tagus, and Sado Rivers dominant for most of them. Species of group were essentially found at lower slope between 500, 1000, and 2000 m depth off the Douro, Mondego, Tagus, and Sado Rivers. *Hoeglundina elegans* appears a little less similar to the other two species mainly because it occurs in the two 2000 m depth stations only. However, due to its abundance in deep sites like *U. mediterranea* and *M. barleeanus*, we decided keep these species in the same group. Higher abundances were observed off the Sado River. Finally, some dominant species such as *G. affinis* and *R. scorpiurus* (group 4) are not related to any particular bathymetrical environment. *Reophax scorpiurus* is abundant at deep stations in the northern part of our study, while it was found at 100 m water depth in the Estremadura and Tagus transects and close to the Sado River mouth. *Globobulimina affinis* was found in all transect between 100 and 1000 m depth. This taxon is particularly abundant off the Sado River at 100, 500, and 1000 m water depth.

The BIOENV (Biotic and Environmental linking) analysis was performed on the living benthic foraminifera data and on the sedimentary and geochemical data (TOC, $\delta^{13}C_{TOC}$, phaeopigments, Chl *a*, Chl *a*/Phaeo, THAA, EHAA, EHAA/THAA, and Q_{50}) to determine the main environmental parameters controlling the spatial distribution of benthic foraminifera. The BIOENV analysis indicates that the best correlation (Rho = 0.329) between the benthic foraminiferal distribution and the environmental conditions is mainly driven by the TOC, $\delta^{13}C_{TOC}$, and the EHAA/THAA ratio (Table 3).

4. Discussion

This study is based on the data from the 23 stations located at different depth on a large north-south geographical area along the Portuguese margin. Hence, the data set is fairly representative of the different environmental conditions encountered off the Iberian margin. Among the stations investigated in this work, 12 stations were located on the shelf under the potential influence of nutrients and terrestrial OM inputs from rivers. Deeper stations from the upper to lower continental slope allowed a comparison with different physiographic, sedimentological, and trophic conditions. The sampling was done in late winter, a period of maximum river runoff that limits this study to particular conditions, and we consequently cannot extrapolate these results as representative for the other season conditions.

4.1. Sediment Characteristics and Organic Matter Distribution

Based on the PCA (Figure 7a), three major clusters were determined corresponding to different environmental conditions. Cluster 1 represents coastal and upper slope stations of the northern part of the study area which are characterized by sandy sediments (Figure 2a), low OM content (Figure 2b) due to low adsorption of organic particles on coarse sediments, and therefore deep OPD (Figure 6) due to low diagenetic processes. Concerning the coastal stations, the distribution of sediments on the Iberian margin (Figure 2a) is mainly controlled by the coastal currents, influence of wave action and storm surges, and fluvial inputs

[*Peliz et al*., 2005; *Oliveira et al*., 2007], as well as by downwelling activity and wind forcing [*Álvarez-Salgado et al*., 2003; *Otero et al*., 2008], resulting in coarse low TOC sediments between 20 and 50 m depths (Figure 2b). This was, however, not observed off the Sado where fine sediments were found at coastal stations. This might result from the weak flow of the Sado Rivers as compared to Douro and Tagus [*Loureiro et al*., 1986]. For the upper slope stations (around 500 m water depth), the ENACW at the shelf break and the upper slope, and the MOW below 500 m water depth may produce sediments reworking at this depth [*McCave and Hall*, 2002] and hence explain the presence of mainly coarse sediment at 500 m off the Douro and Mondego Rivers and the Estremadura region (Figure 2a). Again, no coarse sediment was observed on the upper slope off the Sado as a probable consequence of finer materiel delivered by the river, a narrow shelf, and a steeper slope at this location that may restrain the influence of the ENACW and MOW on sediment reworking there. In coastal environment, the $\delta^{13}C_{TOC}$ values between −22 and 23‰ indicated mixed OM with a probably large contribution of marine organisms (Figure 2c). Indeed, the typical marine $\delta^{13}C_{TOC}$ is between −23 and −18‰, while terrestrial soils between −29 and −27‰ [*Gordon and Goñi*, 2003]. However, the $\delta^{13}C_{TOC}$ has to be considered with caution at these sites because of the low TOC content in coarse sediments close to the river mouths (Figure 2b) and could be influenced by freshwater phytoplankton which $\delta^{13}C_{TOC}$ signature is typically between −29 and −22‰ [*Gordon and Goñi*, 2003]. Indeed, some studies indicated that fluvial phytodetritus may be exported on the shelf off the Douro and Tagus Rivers [*Magalhães et al*., 2002; *Saraiva et al*., 2007; *Azevedo et al*., 2008]. Most of the particles delivered by the rivers are deposited farther seaward inducing that coastal sediments might consequently have a marine $\delta^{13}C_{TOC}$ signal in the area [*Schmidt et al*., 2010]. The nutritional value of the OM as indicated by the EHAA/THAA [*Grémare et al*., 2005] is highest close to the coast under river influence (Figure 2e) hence indicating fresh OM supply contrary to what is often expected [*Martins et al*., 2015]. This is, however, in good agreement with the predominant contribution of marine organic matter as revealed by $\delta^{13}C_{TOC}$ results in this study (Figure 2c). Nutrients export from rivers might enhance coastal marine primary production and results in an increase of the OM quality there [*Alt-Epping et al*., 2007]. This is particularly true in winter when nutrient input from Iberian Rivers is high [*Varela et al*., 2005; *Prieto et al*., 2009]. This land-influenced primary production in winter is commonly characterized in the study area by coccolithophores blooms during water stratification conditions [*Abrantes and Moita*, 1999].

Cluster 2 represents the deep water stations (i.e., 1000 to 2000 m depth) and the 100 m station of Estremadura transect. These stations are composed of very fine sediments with relatively high TOC contents with predominant marine origin as revealed by $\delta^{13}C_{TOC}$, but of low quality as shown by the low amino acids values (Figure 2). The range of TOC values measured in deep environments in our study (Table 2) is in good agreement with values measured on the edge of the Nazaré Canyon (0.6–1.1% [*Koho et al*., 2008]), in the NW Iberian margin (0.1 to 1.4% [*Schmidt et al*., 2010]) or in the Gulf of Cadix (0.2 to 0.8% [*Schönfeld*, 2001]). Most of the OM in the Portuguese margin is supplied by marine primary production during the seasonal upwelling [*Alt-Epping et al*., 2007] that is active between June and September [*Fiúza*, 1983]. The main upwelling front is aligned with the bathymetry near the 100 m isobaths along a 50 km wide zone in the northern part of Iberian Peninsula and turning slightly offshore in the southern part [*Peliz et al*., 2002]. Upwelling-derived OM reaches the seabed and may be deposited predominantly in mud patches and deep environments. During the winter period, the marine primary production is most probably limited [*Ferreira and Duarte*, 1994], but relatively large amounts of predegraded OM could be stored for a long time in the fine sediments at those depths. The diagenetic state of the Chl *a* (Chl *a*/Phaeo) and OM quality (EHAA/THAA) show clearly the highest degradation of OM in these stations in the water column before they reach the seabed. This reduces oxygen consumption in surface sediments and results to a consequently deep OPD.

Finally, cluster 3 represents midshelf (~100 m water depth) off the Douro, Tagus, and Sado Rivers. Fine sediments at those stations are characterized by more negative $\delta^{13}C_{TOC}$ values, suggesting a terrestrial origin of OM (Figure 2c). Terrestrial particles are mainly clays and silts, with relatively high organic adsorption ability, partly because of the presence of dams in the rivers that restrain coarser sediments [*Dias et al*., 2002; *Martins et al*., 2012]. This fine grain size distribution is responsible of high OM content in sediments off the major terrestrial OM supply. High TOC values were already measured in mudbelt sediments around 100 m depth in the northern part of the Portuguese coast [*Schmidt et al*., 2010]. This OM is mainly composed of fresh phytodetritus as underlined by Chl *a* and Chl *a*/Phaeo ratio which is higher within the Tagus prodelta and off the Sado River (Figure 2f).

4.2. Faunal Response to Environmental Conditions

4.2.1. Faunal Density, Diversity, and Microhabitats

Large differences in TSS were observed in the study area, which we primarily attribute to grain size and TOC content variation with coarse sediments extremely poor in TOC at coastal and upper slope stations and finer sediments at midshelf and outer slope. This probably explains the very low TSS at coastal stations off the Mondego and Tagus Rivers (St. 11 and 27, respectively). However, due to the very limited number of specimens observed at those stations benthic foraminiferal data from those depths have to be considered with caution in terms of relative contribution and diversity indices. Nevertheless, such low TSS at coastal stations, where coarse sediments are found and located directly in front of a river indicates that such setting is not favorable for benthic foraminifera, at least during winter condition. Maximum TSS were found at 100 m depth on the Douro, Estremadura, and Tagus transects where the sediments are enriched in Chl *a*. On the Douro mud patch, TSS is more than twice larger compared to other mud patch stations although TOC, Chl *a*, EHAA, and THAA values are not higher. A local bloom of the coccolithophores *Emiliania huxleyi*, occurring in high concentration (3360 cells mL^{-1}, J. Giraudeau, personal communication, 2015) in surface water (upper 10 m of the water column) near the Douro mud patch during the sampling period, might explain higher benthic foraminiferal TSS at this station. In addition, St. 7 (50 m depth) station off the Douro River, where the TOC is low (0.01 wt %) but where the EHAA/THAA ratio is the highest (37%), also shows one of the highest TSS values. This suggests an episodic export of terrestrial nutrients that might have triggered the observed coccolithophores bloom resulting in a rapid response of opportunistic benthic foraminiferal species such as *N. scaphum*, *A. beccarii*, *B. aculeata*, and *E. scaber*. This episodic export is probably linked with flood conditions and opportunistic behavior of these species that could quickly recolonize the environment after sediment perturbation as suggested in *Dessandier et al*. [2015] and also observed off the Rhône River by *Goineau et al*. [2012].

All coastal stations located in front of rivers reveal low diversity and high Evenness index, suggesting a tolerance of a low number of species to this particular environment. The maximum values of the Shannon index were found in the Estremadura transect, where higher abundances of agglutinated taxa were also observed. There, sediment with high TOC in an area less impacted by the river could favor these taxa and explain their higher diversity without OM quality impact on these tolerant species. Specific richness is highest at 100 m depth, where the quantitative and qualitative descriptors of OM are high. Evenness is, however, relatively low in all the stations at 100 m depth where *N. scaphum* is dominant, i.e., $>$15% of the assemblage. This is comparable to what was observed on the Rhone prodelta where *N. scaphum* was dominant and Evenness low, especially in poorly oxygenated sediments under relatively high OM supply from the Rhône River [*Goineau et al*., 2011]. A low *E* was also observed at deep stations on the Tagus and Sado transects as the result of the dominance of the assemblages by *U. mediterranea* that might respond preferentially to sediments enriched in low-quality OM.

Oxygen concentration and OM content in the sediment [e.g., *Jorissen et al*., 1995] as well as OM quality [e.g., *Schönfeld*, 2001; *Fontanier et al*., 2002] are major environmental parameters typically considered to control benthic foraminiferal density and distribution. In most of our stations, the vertical distribution of benthic foraminifera shows maximum density above the OPD (Figure 6). At 100 m stations, however, (except St. 18 of the Estremadura transect, not directly connected to river inputs), the maximum density is observed below the surface sample, and in three cases below the OPD, i.e., in anoxic sediments (St. 6, 28, and 38). Benthic foraminiferal microhabitats at those stations are deeper than at other sites. For the Douro, *Dessandier et al*. [2015] have recently suggested that benthic foraminiferal microhabitats are controlled by phytodetritus quantity and quality as indicated by high Chl *a* content and Chl *a*/Phaeo ratio below 2 cm sediment depth. There, four taxa are abundant: *N. scaphum*, *B. aculeata*, *C. auriculus*, and *G. affinis*. These species were already observed in anoxic environments elsewhere, where high amount of OM was present [*Fontanier et al*., 2002; *Mojtahid et al*., 2010; *Dessandier et al*., 2015]. In the whole study area, *N. scaphum* and *M. barleeanus* occupy intermediate microhabitats tolerating anoxic conditions and *G. affinis* only occupies deep microhabitat especially at 100 m stations and off the Sado River.

The main environmental parameters impacting benthic foraminifera distribution can be highlighted using the BIOENV analysis [*Mucha et al*., 2003; *Urra et al*., 2011]. Our results indicate that three parameters (TOC, $\delta^{13}C_{TOC}$, and EHAA/THAA), among all the parameters measured in our study, appear to be best correlated with the faunal variance. This suggests the importance of OM quantity (TOC), quality (EHAA/THAA ratio),

and source ($\delta^{13}C_{TOC}$) for living benthic foraminifera. TOC control on benthic fauna is in good agreement with recent results from the south Iberian margin where *Martins et al*. [2015] found a good correlation between benthic faunas and TOC during the spring bloom of April/May. The OM characterization in the Portuguese Margin is driven by upwelling conditions in summer and spring phytoplanktonic blooms [*Ferreira and Duarte*, 1994]. Our data further suggest that the OM quality and source (terrestrial versus marine) are also determining the faunal distribution in late winter, probably related to less marine/more terrestrial export and river discharge. The OM quantity may then explain the particularly low faunal density and diversity off the Sado River, where the quantitative descriptors were high (e.g., TOC and Chl *a*) while its qualitative descriptors were the lowest (as is evident from low Chl *a*/Phaeo and EHAA/THAA ratios).

4.2.2. Distribution Patterns of Foraminiferal Faunas

Taxa of group 1 are mainly associated with the sandy stations of Q mode cluster 1 (*A. beccarii* and *Q. seminula*) and a little less with shallow shelf stations of cluster 3 (*E. scaber* and *B. aculeata*), suggesting a significant influence of OM quality (Figures 7a and 7c) and fluvial input on these species. *A. beccarii* is well known to colonize environment under river influence and estuarine ecosystem close to the study area [*Diz and Francés*, 2008; *Mendes et al*., 2012] with a preference for sandy sediment [*Jorissen*, 1988; *Celia Magno et al*., 2012]. *Quinqueloculina seminula* is a typical shallow infaunal sometimes found in oligotrophic conditions [*Fontanier et al*., 2002] but often observed with *E. scaber* in conditions under strong riverine influence [*Goineau et al*., 2011; *Mendes et al*., 2012]. In our study, *A. beccarii* and *Q. seminula* are abundant under fluvial influence and also outside direct river outflow (St.17) and could be influenced by highly energetic coastal currents, responsible for coarse sediments and low organic content. At this station, Chl *a* concentration is also low and amino acid data reveal high-quality OM. The plume of the Tagus River flows northward [*Jouanneau et al*., 1998] and thus also influences this environment. *Eggerelloides scaber* was only observed where OM has a dominant terrestrial origin and where pigment concentrations are high hence indicating high-quality OM. *Eggerelloides scaber* is typically found in very shallow water and prodeltaic environments [*Goineau et al*., 2011; *Mendes et al*., 2012]. Furthermore, this species is frequently observed in sandy sediment supplied with terrestrial OM [*Debenay and Redois*, 1997; *Mendes et al*., 2004; *Diz and Francés*, 2008; *Duchemin et al*., 2008; *Goineau et al*., 2011]. This species has been previously described as tolerant to organic contamination in areas under anthropic influence [*Alve*, 1995; *Bartels-Jónsdóttir et al*., 2006]. It has shown particular tolerance to most kinds of contaminants [*Frontalini and Coccioni*, 2008, 2011] as heavy metals which were measured in excess in both estuaries of Tagus and Sado [*Caçador et al*., 1996; *Caeiro et al*., 2009]. *Bulimina aculeata* is abundant in the same context but at deep microhabitats (Figure 6) and is typical of high OM input and/or oxygen depleted environments [*Mojtahid et al*., 2009]. It was shown to be associated with mix of marine and continental OM in the Gulf of Lions [*Goineau et al*., 2011]. It is also well known to respond quickly to fresh organic matter inputs [*Kitazato et al*., 2003; *Nomaki et al*., 2005; *Eberwein and Mackensen*, 2006]. Species of group 1 were observed in various prodeltaic sediments [*Jorissen*, 1987; *Mendes et al*., 2004; *Rossi and Vaiani*, 2008] and showed tolerance for coarse sediments under the influence of river discharges [*Diz and Francés*, 2008]. The presence of these taxa confirms their preference for the very coastal environment impacted by rivers, intermittent exports of terrestrial and labile OM. All these species were found in coastal environments along the Portuguese coast by *Martins et al*. [2015], but with lower relative contribution since only the dead faunas were considered and since the authors found more epiphytic species in those inshore environments. Those epiphytic species were nearly absent from the late winter living assemblages in the present study.

Taxa of the group 2 are mainly dominated by *Nonion scaphum*. This species was reported in previous studies associated with continental OM close to river mouths [*Debenay and Redois*, 1997; *Duchemin et al*., 2008; *Mojtahid et al*., 2009] and also in anoxic sediments where fresh OM is available [*Fontanier et al*., 2002]. In this study, *N. scaphum* indicates affinity for OM-rich sediments, especially where Chl *a* content is high (Figure 7c). It systematically occurs directly below the OPD, under the fluvial influence where a predominant riverine influence was evident. *Nonion scaphum* was sometimes described as controlled by the upwelling activity in the Iberian margin [*Levy et al*., 1995; *Diz et al*., 2002]. However, considering that the sampling period (i.e., in March) corresponds to the period of the year while the lowest upwelling activity is generally observed [*Fiúza*, 1983], the living specimens of this species are probably rather controlled by fluvial discharges. This species seems to respond to coccolithophores blooms, mainly observed off the Douro River, which is linked to winter conditions in this study area [*Abrantes and Moita*, 1999]. This probably explains the lower proportion of this species in the dead community (P.-A. Dessandier et al., unpublished data) and the higher dominance

of *Bolivinidae*, *Buliminidae*, and *C. laevigata* during spring period [*Martins et al*., 2015] and in the fossil record along the Portuguese margin [*Bartels-Jónsdóttir et al*., 2006; *Rosa et al*., 2007], even though these species are probably more opportunistic [*Goineau et al*., 2015]. *Cancris auriculus* and *U. bifurcata* are more abundant on upper slope sediments occupying slightly different microhabitats. *Uvigerina bifurcata* is observed in clear oxic sediments, while *C. auriculus* occurs regularly below the OPD. *Uvigerina bifurcata* was found at deeper environments on the southern Estremadura and Tagus transects reflecting the environmental difference between the northern and the southern parts of the margin at this depth. *Clavulina cylindrica* and *R. phlegeri* were also observed off the Douro and Tagus rivers, respectively. These two species confirm their preference for high-quality OM under fluvial influence. *R. phlegeri* was already observed in sediments with OM content from continental origin off the Rhône River [*Mojtahid et al*., 2009; *Goineau et al*., 2011]. *Clavulina cylindrica* has shown a preference for high-quality OM resources in the Bay of Biscay [*Fontanier et al*., 2002].

Group 3 is characterized by species in association with relatively high amounts of OM (high TOC of marine origin as show by the $\delta^{13}C_{TOC}$, Figure 7c), but of lower quality than on the shelf showing anticorrelation with EHAA/THAA (Figure 7c). Stable conditions could be expected at this depth, without coastal currents and direct fluvial influence, where sediments are the finest of the study area. In a recent study based on stations ranging from ~300 to 5000 m depth on the southern Portuguese margin, *Phipps et al*. [2012] did not report *H. elegans* in their stations; consequently, this species may rather be concentrated in the northern Portuguese slope. *Hoeglundina elegans* was only found at 2000 m depth off the Douro and Mondego Rivers, but since no station was retrieved at this depth on the other transects, we cannot exclude based on our results that this species was restricted only to the northern part of our study area. *Melonis barleeanus* was correlated with water depth in the Gulf of Lion under unstressed conditions and marine-derived OM [*Goineau et al*., 2011]. *Melonis barleeanus* and *Uvigerina* spp. are often dominant in the open slope area under eutrophic or mesoeutrophic environments with low-quality OM, because of the predegradation of organic compounds, associated with bacterial consortia [*Fontanier et al*., 2002; *Contreras-Rosales et al*., 2012].

Most of agglutinated species were also found at deep water stations (Figure 3). Agglutinated species are able to colonize eutrophic, mesoeutrophic, and oligotrophic environments [*Altenbach et al*., 1999; *Phipps et al*., 2012]. Species such as *Bigenerina nodosaria*, *Bathysiphon* sp., *Haplophragmoides* sp., *Textularia agglutinans*, *Reophax agglutinatus*, and *Reophax spiculifer* were essentially found in deep water environments where refractory OM was present. *Bathysiphon* spp. and *Reophax* spp. were described in settings close to the study area, i.e., in deep water environments with sediments enriched in OM but of low freshness [*Koho et al*., 2007, 2008; *Phipps et al*., 2012]. *Bigenerina nodosaria* and *T. agglutinans* are eutrophic species well developed in environments under high marine productivity [*Fontanier et al*., 2002]. *Koho et al*. [2007] indicated the occurrence of *Bathysiphon* spp. in sediments with high OM content and *Reophax* spp. associated with refractory OM in the Nazaré canyon. *Reophax agglutinatus* and *R. spiculifer* were abundant off the Douro in sediment with both high and low OM contents (St. 3, 4, and 5), suggesting that this species is adapted to variable trophic conditions. We hypothesize that the agglutinated test construction of those species may represent an energetic economy in comparison with calcification used by calcareous benthic foraminifera. This could at least partly explain why agglutinated species are less sensible to variations of OM quantity and lability [*Koho et al*., 2008; *Phipps et al*., 2012].

Finally, the group 4, composed of *G. affinis* and *R. scorpiurus*, does not show a clear spatial distribution and seem to be linked with high OM quantity only (EHAA, THAA, and Chl *a*; Figure 7c). *Reophax* genus has been observed in highly variable trophic conditions and seems to tolerate variable OM quality [e.g., *Altenbach et al*., 1999; *Phipps et al*., 2012], albeit refractory OM in most cases [*Gooday et al*., 1996; *Koho et al*., 2007]. *R scorpiurus* is one of the major agglutinated species of the whole study area and the most ubiquitous. Contrary to *E. scaber*, restrained to coastal environments or *C. cylindrica* in the Douro mud patch, *R. scorpiurus* was found at all water depths and in four of the five examined transects. Its distribution closely matches the stations of cluster 1 where the TOC content is high but its nature is more refractory and of marine origin. *G. affinis* is a typical deep infauna, tolerating anoxic conditions [*Jorissen et al*., 1995], which is dependent on aerobic and anaerobic bacterial consortium degrading more or less refractory OM [*Fontanier et al*., 2002]. On the Iberian margin, this species has shown preference for high quantity of phytopigments and no clear evidence for preference for a high TOC content [*Schönfeld*, 2001]. *G. affinis* is particularly abundant below the OPD in anoxic sediments within sediments of low OM quality.

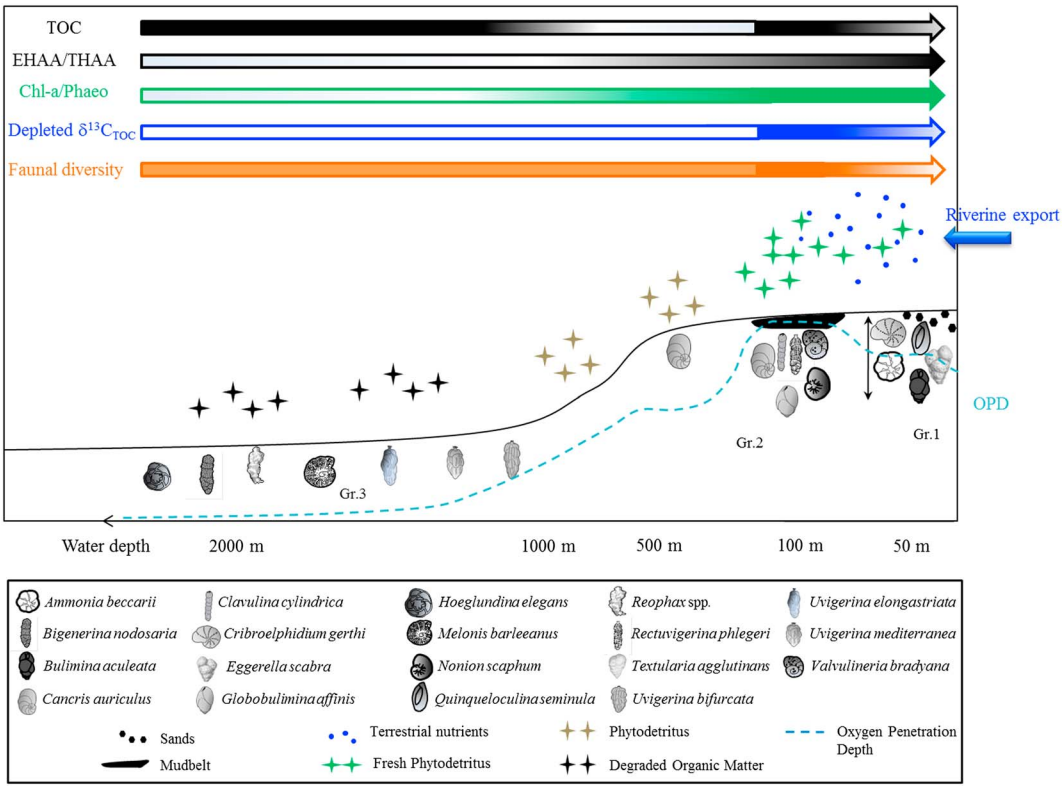

Figure 9. Synthetic scheme of major species distribution in function of environmental conditions. Note that depleted $\delta^{13}C_{TOC}$ values indicate a higher proportion of terrestrial-derived OM.

G. affinis is dominant off the Sado River at stations characterized by low faunal diversity. The contamination of trace metals of the Tagus estuary was observed to be exported by a benthic nepheloid layer toward the south [*Jouanneau et al.*, 1998]. Our sampling area from the Sado transect are directly under the influence of the Tagus River plume and may be impacted by trace metals exported. Contaminants were also measured in excess in the Sado estuary [*Caeiro et al.*, 2009]. *Alve* [1995], *Armynot du Châtelet and Debenay* [2010], and *Frontalini and Coccioni* [2011] argued that environmental pollution was responsible for a decrease in density and diversity of benthic foraminifera. The poorly diverse faunas in this transect were essentially represented by *N. scaphum*, *C. auriculus*, and *B. aculeata* which were identified as tolerant of anthropogenic contamination along the French Mediterranean coast [*Barras et al.*, 2014]. This could be investigated in the study area to explain the results off Sado River and evaluate influence of anthropogenic activities on benthic ecosystems.

5. Synthesis and Conclusion

The distribution of living benthic foraminifera on the Portuguese margin in late winter shows a clear disparity between the shelf and deep environments. Our data set, including data on grain size distribution, oxygen penetration depth, and quantitative and qualitative descriptors of OM allowed a better understanding of benthic foraminiferal ecology in this well-studied Portuguese margin. A synthesis of living faunal distributions and main environmental controls on this river-dominated continental margin is shown in Figure 9.

Our results show three different environments: (1) coarse sediments with low quantity but high OM quality found at coastal and upper slope stations of the northern part of the study area; (2) silty sediments at around 100 m depth enriched in relatively fresh phytodetritus and mixed terrestrial and marine OM off the Douro, the Tagus, and the Sado rivers; and (3) muddy sediments rich in low OM quality found at deep environments.

Species of group 1 (Gr. 1) are limited to coastal stations, located at 20 and 50 m depth. They show a good development above and below the OPD. Most of these species might tolerate low OM content that probably limits the faunal diversity. The midshelf group (Gr. 2) corresponds to species living at 100 m depth where

mixed marine and estuarine primary production is triggered by nutrients export from the nearby rivers. *N. scaphum* is by far the dominant species of our study area, especially in suboxic to anoxic sediments. Group 3 (Gr. 3) is composed of species present in stations spanning between 500 and 2000 m water depth where OM quality is low probably resulting from increased degradation of before reaching sediments. The dominant taxa of this group are calcareous (*M. barleeanus*, *H. elegans*, and *U. mediterranea*) but could be associated with agglutinated species (*Reophax* spp., *B. nodosaria*, and *Haplophragmoides* sp.). The species of group 4 (Gr. 4), *G. affinis* and *R. scorpiurus*, are distributed without clear geographical trend and are associated with maximum OM quantity but highly variable OM quality.

The stations off the Sado River showed surprisingly low faunal diversity and density even though the TOC contents were the highest among all five transects, but where poor OM quality was found. Such poor faunas might be related to the anthropogenic influence that has been observed in the vicinity of the Sado River [*Mil-Homens et al*., 2006; *Caeiro et al*., 2009]. It appears therefore particularly interesting to investigate the effect of pollution on faunas in this area by looking at, e.g., heavy metals impact. Based on the PCA and BIOENV results, three major geographical groups are identified: (cluster 1) sandy stations, (cluster 2) deep stations, and (cluster 3) river-dominated stations. Accordingly, our study highlights that not only the quantity but also the source and quality of OM are the important factors controlling the living benthic foraminiferal distribution in a river-dominated marine setting. The use of benthic foraminifera can be valuable as a biomonitoring tool for the river-dominated marine ecosystems.

Appendix A: Taxonomic List

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

Amphycorina scalaris (Batsch, 1791) [*Fontanier*, 2003, plate 5, p.403: Figure A]

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

Asterigerinata mamilla (Williamson, 1858) [*Abu-Zied*, 2001, plate 9: 12,13]

Bathysiphon sp.2 [*Koho et al*., 2007, plate 42: 2]

Bigenerina nodosaria (d'Orbigny, 1926) [*Fontanier*, 2003, plate 1, p.395: Figure J]

Biloculina sphaera (d'Orbigny, 1839)

Bolivinaitalica (Cushman, 1936) [*Mendes et al*., 2012, Figure 2: 7a, b]

Bolivinaspathulata/dilatata (Willimason, 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) [*Elmas et al*., 2008, plate 2, p.165: 19–20]

Bulimina inflata (Seguenza, 1862) [*Fontanier*, 2003, plate 5, p. 403: Figure M]

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

Cancrisauriculus (Fichtel and Moll, 1798) [*Larkin and Gooday*, 2009, plate 4: 1–2]

Cassidulina carinata (Silvestri, 1896) [*Goineau*, 2011, plate 1, p. 294: photo 5]

Cassidulina crassa (d'Orbigny, 1839) [*Fontanier*, 2003, plate 6, p. 405: Figure A]

Chilostomella oolina (Schager, 1878) [*Wiedicke and Weiss*, 2006, Figure 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)

Clavulina cylindrica (d'Orbigny, 1826) [*Fontanier*, 2003, plate 1, p. 395: Figure F]

Coryphostoma sp. [*Fontanier*, 2003, plate 405: Figures 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) [*Fontanier*, 2003, plate 1, p.395: Figure G]

Eggerella scabra (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) [*Abu-Zied*, 2001, plate 6: 8]

Gyroidina orbicularis (d'Orbigny, 1826) [*Fontanier*, 2003, plate 7, p.407: Figures L and M]

Gyroidina umbonata (Silvestri, 1898) [*Fontanier*, 2003, plate 7, p. 407: Figures N and O]

Hanzawaia boueana (d'Orbigny, 1846) [*Mojtahid et al*., 2009, plate 3: 35]

Haplopgragmoides sp. (Robertson, 1891) [*Holbourn and Henderson*, 2002: 1.1–19: 14–16]

Haynesina depressula (Walter and Jacob, 1798) [*Abu-Zied*, 2001, plate 9: 15–16]

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

Hyalinea balthica (Schröter, 1783) [*Fontanier*, 2003, plate 8, p. 409: Figure F]

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*, 2003, plate 4: 4]

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

Lenticulina sp. (Lamarck, 1804) [*Chukwu et al*., 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) [*Mojtahid et al*., 2009, plate 1: 1]

Planulina ariminensis (d'Orbigny, 1826) [*Abu-Zied*, 2001, plate 8: 16–17]

Planulina wuellerstorfi (Schwager, 1866) [*Fontanier*, 2003, plate 6, p. 405: Figure 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) [*Fontanier*, 2003, plate 9, p.411: Figures L and M]

Pullenia quinqueloba (Reuss, 1851) [*Fontanier*, 2003, plate 9, p.411: Figures N and O]

Quinqueloculina seminula (Linné, 1758) [*Fontanier*, 2003, plate 11, p.415: Figure J]

Rectuvigerina phlegeri (Mathews, 1945) [*Fontanier*, 2003, plate 10, p.413: Figure 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) [*Abu-Zied*, 2001, plate 8: 8]

Sigmoilinita tenuis (Czjek, 1848) [*Elmas et al*., 2008, plate 2, p.165: 8]

Siphoninareticulata (Czjzek, 1884) [*Van Hinsbergen et al*., 2005, plate 1: 16]

Siphotextularia flintii (Cushman, 1911) [*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 et al*., 2010, plate 1: a]

Textularia agglutinans (d'Orbigny, 1839) [*Goineau*, 2011, plate 1, p.294: photo 12]

Textularia sagittula (Defrance, 1824) [*Abu-Zied*, 2001, plate 1: 16–17]

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

Trifarina bradyi (Cushman, 1923) [*Fontanier*, 2003, plate 10, p.413: Figures F and G]

Trochammina inflata (Montagu, 1808) [*Fatela et al*., 2009, plate 2: 5]

Uvigerina bifurcata (d'Orbigny, 1826) [*Wang and Lutze*, 1986, plate 4: Figures 5–8]

Uvigerina elongastriata (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]

Acknowledgments
The research leading to these results has received funding from the European Research Council (ERC) under the European Union's Seventh Framework Program (FP7/2007-2013) ERC grant [226600]. We thank the crew of the R/V *Pelagia* and Silvia Nave at LNEG for the help of the PACEMAKER cruise preparation. We also thank Laurence Costes for amino acids analysis at EPOC and the BIOMIN project (PNEC-EC2CO and LEFE programs from INSU) for the financial support of analyses. This paper greatly benefited from the very constructive comments of F. Frontalini and two anonymous reviewers. To access the data used in this paper, contact p.dessandier@epoc.u-bordeaux.fr.

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