



**Live (stained) benthic foraminifera from the  
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shelf sedimentary unit.**

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Live (stained) benthic foraminifera from the West-Gironde Mud Patch (Bay of Biscay, NE Atlantic): Assessing the reliability of bio-indicators in a complex shelf sedimentary unit.

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## 0. Abstract

Live (Rose Bengal stained) shelf foraminiferal faunas have been studied at seven stations located along a shore-open ocean transect between 39–69-m depth in the West-Gironde Mud Patch (WGMP) (Bay of Biscay, NE Atlantic) to understand how complex environmental conditions (e.g., organic matter, oxygenation, sedimentary facies) control their ecological patterns (i.e., diversity, faunal composition, standing stock, and microhabitats). To do so, the WGMP was sampled in August 2017, at the end of the succession of phytoplankton blooms

occurring in spring and summer. This morpho-sedimentary unit is bathed by well-oxygenated bottom waters and characterized by clay-silt facies containing variably degraded phytodetritus and traces of terrestrial organic matter. Oxygen penetration depth within the sediment is less than  $7\pm 3$  mm, indicating efficient organic matter in-sediment mineralisation by aerobic respiration. Foraminiferal richness (S) presents relatively moderate values ranging between 15–35 taxa. According to Shannon Index  $H'$ , foraminiferal diversity tends to increase with water depth. Accordingly, the relative contribution of *Eggerelloides scaber*, the dominant foraminiferal species at all stations, decreases with increased depth and decreased proximity to the coast. The shallowest station (Station 1, 39 m), closest to the shore, is characterised by *E. scaber*, *Quinqueloculina laevigata* and *Ammonia beccarii*, species typical of inner-shelf environments constrained by high-energy hydrodynamics and river discharge. Surficial sediments at Station 1 constitute of winnowed sands depleted in organic carbon. Towards the centre of the WGMP, where clay-silt facies contain variably degraded marine phytodetritus and terrestrial organic compounds, foraminiferal faunas are characterized by *Bulimina aculeata*, *Ammonia falsobeccarii*, *Nouria polymorphinoides* and *Nonionoides turgidus*. Yet *E. scaber* remains the most dominant taxon. Deeper stations (>55 m depth) located at the distal part of the mud patch are dominated by *B. aculeata*, *A. falsobeccarii*, *N. polymorphinoides* and *E. scaber*. Accompanying these taxa are *Bulimina marginata*, *Rectuvigerina phlegeri*, *Nonion faba* and *Paracassidulina neocarinata*, which are typical of mid- and outer-shelf ecosystems enriched in sedimentary organic matter.

Keywords: Benthic foraminifera; West-Gironde Mud Patch, Diversity, Organic matter, Sedimentary environment

## 1. Introduction

Continental shelves are areas of high primary production, playing a major role in the sequestration and mineralization of organic carbon (Walsh et al., 1981; Hargrave, 1985; Smith and MacKenzie, 1987; Walsh, 1988; Jahnke et al., 1990; Walsh, 1991; Wollast, 1991; Hedges and Keil, 1995; Bauer and Druffel, 1998). Indeed, biogeochemical cycles are exacerbated within the water column and sediments along the continental shelf where rivers deliver large quantities of dissolved nutrients and organic matter into coastal waters (Hedges et al., 1997). Among these nutrients, nitrate and phosphate stimulate the seasonal or perennial appearance of high primary production plumes along the continental shelf, leading to increased export of phytodetritus to the seafloor (Lohrenz et al., 1990; Lohrenz et al., 1997; Dagg and Breed, 2003). Rivers further release large quantities of particulate organic compounds from terrestrial sources and large quantities of freshwater phytoplankton onto continental shelves (Mopper and Degens, 1977; Eppley, 1984; Romankevich, 1984). When not degraded in the water column or exported laterally along continental slopes, this complex particulate organic matter (terrestrial organic matter and exported phytoplankton production) concentrates in muddy environments on continental shelves (e.g., mud belt, mud patch) where it is buried and then variably degraded by diagenetic processes (Froelich et al., 1979; Canfield et al., 1993). The efficiency of organic carbon burial and its final sequestration thus depends on (1) the deposition flux of organic matter at the sediment-water interface, (2) the rate of mineralization in surface sediments, and (3) the hydrosedimentary processes determining benthic biotope architecture (McKee et al., 2004).

The West-Gironde Mud Patch (WGMP) is a perfect example of a shelf environment where organic compounds from various sources (mainly marine phytodetritus) accumulate within fine sediments (Lamarque et al., 2021; Dubosq et al., in press; Dubosq et al., in prep). Together with the South-Gironde Mud Patch, the WGMP constitutes a particular set of

76 morpho-sedimentary units that spread between 30–70 m water depth, covering the gravels and  
77 sands of the Northern Aquitaine continental shelf (Bay of Biscay, France) (Lesueur et al.,  
78 1996; 2002; Cirac et al., 2000). These muddy patches extend off the two main channels of the  
79 Gironde Estuary, the main source of the fine-grained sediments within the WGMP (Fig. 1)  
80 (Lesueur et al., 1996). The WGMP comprises of Gironde River silt deposited during flood  
81 events, and a smaller portion of inner continental shelf silts and fine sand deposited during  
82 periods of high energy (i.e., storms). Due to the complexity of its spatial structure, temporal  
83 dynamics and environmental characteristics, the WGMP has been the subject of intense  
84 multidisciplinary investigation for more than ten years (e.g., the BIOMIN project between  
85 2009–2013, the VOG project between 2018–2019, the JERICO-NEXT European project with  
86 this study). In combination with geochemical, geophysical, sedimentological and biological  
87 analyses, these projects have aimed to describe the mineralization processes of organic  
88 compounds in the mudflat, taking into account (1) the activity of the benthic organisms  
89 thriving there (e. g. bioturbation, aerobic/anaerobic respiration), by (2) integrating the  
90 hydrosedimentary dynamics structuring this morpho-sedimentary unit in space and time, and  
91 by (3) trying to define in fine, reliable bio-indicators of the mudflat in all its complexity  
92 (Lamarque et al., 2021; Dubosq et al., in press; Dubosq et al., in prep.). Benthic foraminifera  
93 constitute relevant proxies for studying present and past marine environments since their  
94 faunal communities (diversity, standing stock, microhabitat), their spatial distribution and  
95 their temporal dynamics are controlled by numerous physico-chemical parameters including  
96 exported organic matter flux, bottom- and pore-water oxygenation and sedimentary substrate  
97 (e.g., Gooday, 2003; Murray, 2006; Jorissen et al., 2007). The impact of seasonal  
98 phytodetritus input and the role of environmental oxygenation on benthic foraminiferal fauna  
99 has already been studied in “La Grande Vasière”, a mud belt located on the outer continental  
100 shelf (between 80–130 m deep) northwest of the WGMP (Duchemin et al., 2005; 2008) (Fig.

1). These works have shown that living benthic communities respond to episodic inputs of organic matter related to phytoplankton blooms from spring to autumn. Certain opportunistic species (i.e. *Nonionella iridea*, *Cassidulina carinata* according to the taxonomy of Duchemin et al., 2008) dominate the Grande Vasière mud belt fauna. Foraminiferal diversity, standing stock and vertical distribution within sediments shifts with water depth (Duchemin et al., 2005; 2008).

Following the Grande Vasière studies, the aim of our paper is to assess the relevance of using benthic foraminifera as bio-indicators of the various environmental conditions prevailing along the WGMP. To do so, we can draw on geochemical, geophysical and sedimentological data acquired during the 2017 oceanographic JERICOBENT-2 cruise (Deflandre, 2017; Dubosq et al., in prep; complementary sedimentological analysis presented in this paper). These data are compared to the faunal characteristics (diversity, standing stock, microhabitats) of the foraminiferal communities sampled at the seven stations ranging from 36–69 meters water depth (Fig. 1).

## 2. Material and Methods

### 2.1. Water parameters

This investigation is based on data obtained at seven stations sampled during the JERICOBENT-2 cruise in August 2017 (Fig. 1; Table 1) (Deflandre, 2017). Stations are organized according to a bathymetric gradient from the proximal part of the WGMP (Station 1, 39 m) to the distal (Station 4, 69 m) (Fig. 1; Table 1). Bottom water temperature (CTD measurements) decreases gradually from 14.6°C at station 1 (39 m) to 12.7°C at station 4 (69 m), whereas bottom water salinity (Conductivity-Temperature-Depth measurements) is constant (35.2) (Table 1). Bottom water oxygenation stays relatively high at all sites (between 184–197  $\mu\text{M}$ ) (Table 1), oxygen penetration depth (OPD) within the sediments is relatively

limited ( $< 1$  cm) indicating a relatively enhanced oxygen demand to degrade organic compounds compared to open-slope environments (Fontanier et al., 2002; Dubosq et al., in prep).

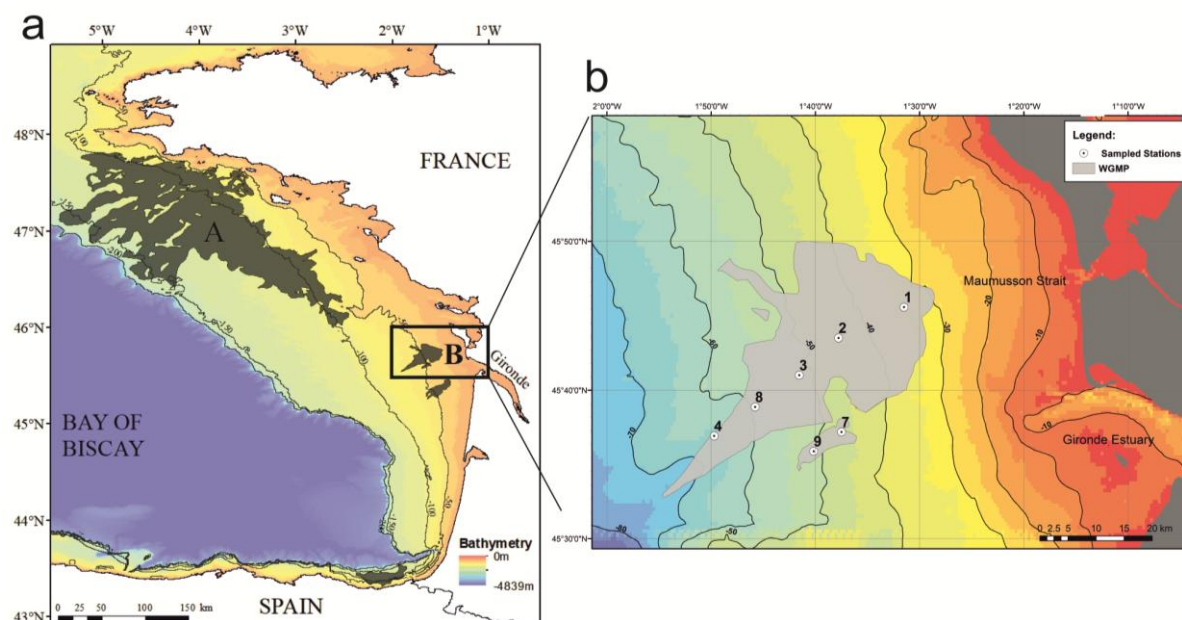


Figure 1. (a) Map of the Bay of Biscay continental shelf with the locations of mud belts and patches: A - La Grande Vasière Mud Patch and B - The Gironde Mud Patch (b) Map of the West Gironde Mud Patch showing the location of 7 sampling stations (white dots). The synoptic map of the WGMP has been determined during the JERICOBENT-5-TH cruise (Gillet and Deflandre, 2018)

Station	Sampling period	Depth (m)	Latitude	Longitude	BWT (°C)	BWS (psu)	BWO <sub>2</sub> (μM)	% Sat.	OPD (cm) (N)
1	August 2017	39	45°45.550'	1°31.335'	14.6	35.2	184.7	71.9	0.36 ± 0.16 (10)
2	August 2017	47	45°43.567'	1°37.657'	13.6	35.2	196.5	83.0	0.61 ± 0.32 (12)
7	August 2017	50	45°37.278'	1°37.544'	13.6	35.2	192.4	73.6	0.34 ± 0.07 (12)
9	August 2017	54	45°35.917'	1°40.062'	13.1	35.2	190.3	71.9	0.42 ± 0.04 (12)
3	August 2017	56	45°40.973'	1°41.762'	13.4	35.2	193.5	73.3	0.66 ± 0.25 (12)
8	August 2017	61	45°38.925'	1°45.825'	12.9	35.2	186.2	69.5	0.46 ± 0.12 (6)
4	August 2017	69	45°43.993'	1°37.427'	12.7	35.2	185.3	69.2	0.37 ± 0.08 (11)

Table 1. Location of the seven stations sampled during the JERICOBENT-2 cruise (August 2017) including station coordinates and depth. Physico-chemical parameters including BWT (bottom-water temperature in °C) and BWS (bottom-water salinity in psu) were extrapolated

from CTD casts at each site.  $BWO_2$  (bottom-water oxygen in  $\mu M$ ) was measured in water overlying the sediment-water interface (SWI) of cores gathered during the JERICOBENT-2 cruise (Dubosq et al., in prep). Oxygen saturation (in %) of bottom water was also calculated (Dubosq et al., in prep). OPD (oxygen penetration depth in cm below the SWI) was determined after  $N$  in-situ measurements with a benthic profiler deployed at each station during the JERICOBENT-2 cruise.

## 2.2 Sediment sampling

Sediment samples were collected with a Barnett-type multiple corer equipped with Plexiglas tubes (9.6 mm internal diameter, surface area of 72 cm<sup>2</sup>) (Barnett et al., 1984). The multi-corer allowed for sampling of the uppermost decimeters of the sediment column, the overlying bottom waters, and a comparatively undisturbed sediment-water interface. At each station, the multi-corer was deployed three to five times to get enough material for geochemical, sedimentological and biological investigations. Descriptors of sedimentary organic matter as well as the mineralization processes of organic compounds at and below the sediment-water interface are described in detail by Dubosq et al. (in press; in prep). We refer to a partial synthesis of their results in the discussion with data summarized in Tables 1 and 2.

## 2.3. Sedimentological analysis

At each station, one entire core was radiographed with a Scopix system, which consists of an X-Ray imaging system combined with image analysis software (Migeon et al., 1999) (Fig. 2). The aim of the X-ray radiography is to detect the presence of discrete sedimentary structures (e.g., erosional surfaces, burrows, coarse sedimentary layers). To visually evaluate changes, core photographs were also taken (Fig. 2). Particle grain sizes were measured with a Malvern Laser Diffraction Particle Sizer (type 2600). This technique was applied to sediment samples



belonging to the previously radiographed and photographed core and allowed for the calculation of grain size frequency  $D_{50}$ . To do so, each core was subsampled every 0.5 cm between 0–1 cm depth, every 1 cm between 1–4 cm depth, then every 2 cm between 4–22 cm depth, and with an adaptative resolution deeper downcore.

Station	OC		TN		C:N ratio		Chl- <i>a</i>	Chl- <i>b</i>	Phaeo- <i>a</i>	Chl- <i>a</i> /(Chl- <i>a</i> + Phaeo- <i>a</i> )	Pigments
	%DW	N	%DW	N		N	µg/g	µg/g	µg/g		N
1	0.30 ± 0.04	6	0.03 ± 0.00	5	12.11 ± 1.59	5	0.23 ± 0.09	<DL	1.46 ± 0.46	0.13 ± 0.02	3
2	0.89 ± 0.06	5	0.10 ± 0.01	5	10.07 ± 1.07	5	1.15 ± 0.20	0.10 ± 0.04	6.65 ± 0.88	0.15 ± 0.03	3
7	1.80 ± 0.13	5	0.20 ± 0.01	5	10.61 ± 0.59	5	1.82 ± 0.42	0.11 ± 0.06	13.55 ± 2.92	0.12 ± 0.00	3
9	1.38 ± 0.12	5	0.14 ± 0.02	5	11.99 ± 2.76	5	1.48 ± 0.71	0.15 ± 0.02	9.67 ± 3.71	0.13 ± 0.01	3
3	1.23 ± 0.12	5	0.13 ± 0.01	5	10.70 ± 0.68	5	0.87 ± 0.05	0.05 ± 0.02	6.07 ± 1.64	0.13 ± 0.03	3
8	1.21 ± 0.10	5	0.13 ± 0.01	5	11.13 ± 0.38	5	0.77 ± 0.29	0.07 ± 0.08	5.25 ± 0.57	0.13 ± 0.04	3
4	1.38 ± 0.05	5	0.14 ± 0.00	5	11.16 ± 0.29	5	0.91 ± 0.18	0.09 ± 0.07	6.90 ± 1.28	0.12 ± 0.04	3

Table 2. Organic descriptors in the surface sediment (i.e. the 0–0.5 cm interval below the sediment-water interface) at the seven stations sampled during the JERICOBENT-2 cruise (August 2017) (Dubosq et al., in prep): Organic content (OC in % DW), Total nitrogen content (TN in % DW), C/N atomic ratio, Chlorophyllic pigment content (i.e. Chl-*a*, Chl-*b* and Phaeo-*a*) and their freshness index Chl-*a*/(Chl-*a*+Phaeo-*a*).

#### 2.4. Foraminiferal faunal analysis

Foraminiferal faunas were studied in a single core per station. Onboard, each core was sliced horizontally every 0.5 cm from the sediment-water interface to a depth of 2 cm, then every centimeter between 2–10 cm depth. Samples (12 slices per core) were transferred into 500 cm<sup>3</sup> bottles, which were filled with 95% ethanol containing 2 g/L Rose Bengal stain, commonly used to identify live foraminifera (Walton, 1952; Murray & Bowser, 2000).

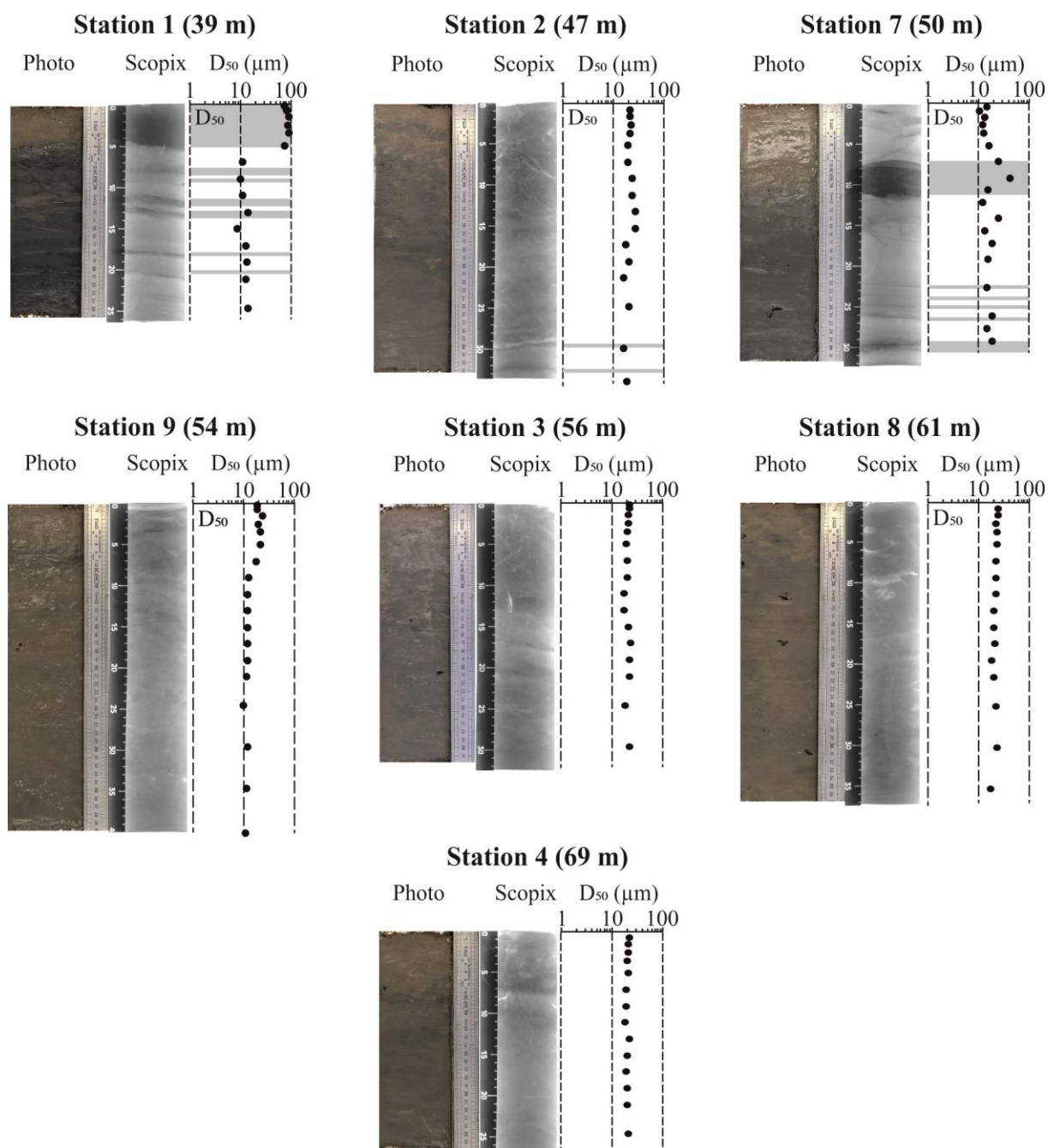


Figure 2. Photograph and X-Ray radiograph (Scopix) of split cores collected at the seven stations from the WGMP with grain size frequency  $D_{50}$ .

All samples were gently shaken for several minutes to obtain a homogeneous mixture. At the laboratory (one month after the cruise), samples were sieved through 150  $\mu\text{m}$  mesh screens, and sieve residues were stored in 95% ethanol. Stained foraminifera belonging to the  $>150$   $\mu\text{m}$  fraction were sorted in wet samples and stored in Plummer slides. One concern with using

Rose Bengal is that it may stain the protoplasm of dead foraminifera that may be relatively well-preserved for long time periods under the generally anoxic conditions prevailing in deep sediments (Corliss & Emerson, 1990; Bernhard, 2000). We therefore applied very strict staining criteria (i.e., all chambers, except the last chamber, stained in bright pink), and compared doubtful individuals to perfectly stained specimens of the same species found in the superficial sediment layers. For miliolids, doubtful specimens were broken to inspect test interior. Most stained foraminifera were identified at species level and checked with the World Foraminifera Database (Hayward et al, 2021) for current taxonomic nomenclature (see Appendix A for taxonomical references and Appendix B for census data). Because samples were preserved and sorted in ethanol, many soft-shelled foraminiferal species may have shrunk and become unrecognizable during picking. Thus, our counts probably underestimate the soft-shelled foraminiferal abundance. We obtained digital photographs of major species using a scanning electron microscope at Angers University (Fig. 3). For each core, we calculated different indices to assess diversity. First, we calculated Species Richness (S) and then Shannon index,  $H'$  (log base  $e$ ) as an information-statistic index as described in Murray (2006). We determined the Berger-Parker index, which represents the highest relative contribution (in %) calculated for the dominant taxon at each station. A Q-mode cluster analysis based on normalized relative abundances  $P_i$  values was applied for the seven stations and the 13 major species ( $\geq 2.5\%$ ), with  $P_i$  defined as:

$$P_i = \text{Arc sin}(\sqrt{p_i})$$

in which “ $p_i$ ” is the relative frequency of the “ $i$ th” species, and “ $P_i$ ” is the normalized value of  $p_i$  (J. Hohenegger, personal communication). We constructed a tree diagram using Ward’s method based on Euclidian distance. To do so, we used the PAST Software (Hammer et al., 2001).

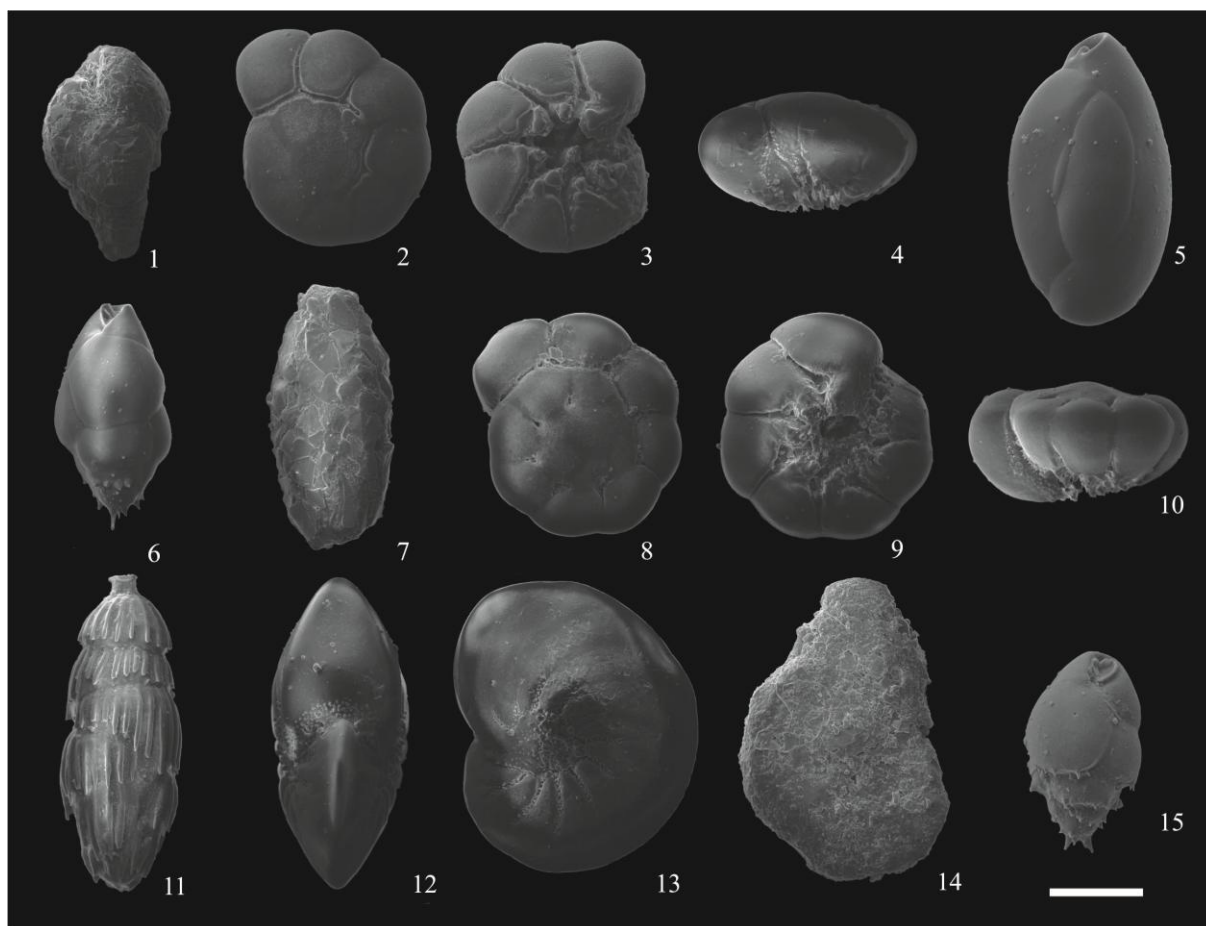


Figure 3. SEM photographs of some major foraminiferal taxa observed in our study area. 1 *Eggerelloides scaber*; 2, 3, 4 *Ammonia beccarii* (dorsal, umbilical and lateral views); 5 *Quinqueloculina laevigata*; 6 *Bulimina aculeata*; 7 *Nouria polymorphinoides*; 8, 9, 10 *Ammonia falsobeccarii* (dorsal, umbilical and lateral views); 11 *Rectuvigerina phlegeri*; 12, 13 *Nonion faba* (frontal and lateral views); 14 *Ammoscalaria pseudospiralis*; 15 *Bulimina marginata*. Scale bar represents 100  $\mu\text{m}$ .

Using Q-mode cluster analysis, we applied the Indicator Value (IV) Method (Dufrêne and Legendre, 1997) with the 13 major species in order to determine indicative species in each cluster of stations. For this purpose, we used the following formula:

$$IV_{(i,\alpha)} = A_{(i,\alpha)} \times B_{(i,\alpha)} \times 100$$

$$A_{(i,\alpha)} = \frac{N_{individuals_{(i,\alpha)}}}{N_{individuals_{(i)}}}$$

$$B_{(i,\alpha)} = \frac{N_{stations_{(i,\alpha)}}}{N_{stations_{(\alpha)}}}$$

$N_{individuals_{(i,\alpha)}}$  is the mean number of individuals belonging to the species  $i$  and present in the cluster  $\alpha$ .  $N_{individuals_{(i)}}$  is the sum of the mean numbers of individuals of species  $i$  occurring in all clusters.  $N_{stations_{(i,\alpha)}}$  is the number of stations in the cluster  $\alpha$  where the species  $i$  is present.  $N_{stations_{(\alpha)}}$  is the total number of sites in the cluster  $\alpha$ . P values were calculated based on 999 permutations using R package "labdsv" (Roberts 2019; R core team 2020).

## 2.5. Additional details

Our study concerns benthic foraminiferal faunas sampled at a specific time of the year and constitute an ecological snapshot and not a temporal survey. Our investigation into the seasonal dynamics of WGMP benthic fauna remains a work in progress and will be the subject of future publications. Therefore, in this paper, we have focused on benthic foraminiferal communities belonging to the >150- $\mu$ m-size fraction as bio-indicators of average environmental conditions at each of our seven stations at the end of a sustained period of increased primary productivity. Seasonal monitoring incorporating smaller benthic foraminifera (e.g., belonging to the 63–150  $\mu$ m-size fraction) will certainly provide valuable additional information on the temporal variability of ecological conditions in this mudflat. But this is not the goal of this study. Furthermore, our study is based on the analysis of a single core per station. Although it is recommended to study several replicates at each site to obtain a more robust, averaged view of foraminiferal faunas (Schönfeld et al., 2012), a lot of studies published for the last decades on the ecology of benthic foraminifera sampled in large study

areas integrating various marine ecosystems does not follow this recommendation (e.g., Fontanier et al., 2002; Duchemin, 2005; 2008; Goineau et al., 2011; Dessandier et al., 2015; 2016). Conversely, environmental interpretations of modern foraminiferal faunas are mostly based on a single sample per site. We therefore consider in this study that even if small-scale (metric) spatial variability exists between benthic faunas living at the same station, this variability does not hide the faunal variability existing at the spatial scale of the WGMP, given that the seven sampled stations are several kilometres apart from each other. Finally, the many recent studies exclusively using >150  $\mu\text{m}$ -sized benthic foraminifera living in the Bay of Biscay (e.g., Fontanier et al., 2002; Ersnt et al., 2005; Langezaal et al., 2006; Duchemin et al., 2005; 2008) sufficiently provide reliable information concerning what we might expect in terms of foraminiferal diversity, standing stock and distribution on the Aquitaine Shelf. Our study adds new and precious data about benthic environments from a river-dominated inner shelf.

### 3. Results

#### 3.1. Sedimentary features

Station 1 (depth 39 m) is characterized by a 5 cm-thick surface layer made of very fine sand ( $D_{50} > 75 \mu\text{m}$ ) (Fig. 2). Beneath this layer, dark grey sediments are made of highly compacted and sticky mud ( $D_{50} \sim 10 \mu\text{m}$ ) within which some dense-material laminae are visible. Station 2 (depth 47 m) is characterized by a clay-silt facies ( $D_{50}$  ranging between 15–25  $\mu\text{m}$ ) throughout the sampled section. Horizontal, vertical and oblique biological structures (i.e. burrows) are abundant all along the core (Fig. 2). Station 7 (depth 50 m) constitutes a 4 cm-thick subsurface layer made of sandy silt ( $D_{50}$  reaching 50  $\mu\text{m}$ ) between 7–11 cm depth. Above and below this layer are sediments composed of fine particles ( $D_{50} < 27 \mu\text{m}$ ). Millimetric laminae are visible between 20 and 30 cm depth (Fig. 2). Station 9 (54 m) is

characterized by a silty layer ( $D_{50} \sim 20 \mu\text{m}$ ) 7 cm thick overlying very fine sediments ( $D_{50} \sim 10 \mu\text{m}$ ). Two gastropod shells of *Turritella communis* were found in the 10 first cm. Stations 3, 8 and 4 (between 56–69 m deep) present homogeneous facies made of clayey silt ( $D_{50}$  ranging between 15–25  $\mu\text{m}$ ). Biological structures (i.e., burrows) are abundant all along these three cores (Fig. 2).

### 3.2. Foraminiferal faunas ( $>150 \mu\text{m}$ )

#### 3.2.1 Diversity Indices

Total foraminiferal standing stocks vary between 1,299 individuals/core at Station 7 (50 m) and 3,737 individuals/core at Station 9 (54 m) (Fig. 4a; Appendix B). There is no trend following water depth. Species richness  $S$  (/core) ranges between 18 at Station 7 and 31 taxa at the deepest Station 4 (69 m depth) (Fig. 4a; Appendix B). Excluding Station 1 (39 m), species richness  $S$  increases gradually with water depth along the WGMP. The  $H'$  (/core) is low (1.6) at Station 1 and increases with water depth to 2.4 at Station 4 (Fig. 4b). Berger-Parker index (/core) decreases with water depth between 0.24–0.55.

#### 3.2.2 Foraminiferal Composition and Microhabitat

As a general trend, the relative abundance of rotaliid species in the total living fauna increases with water depth, from 25% of the total fauna at Station 1 (39 m) to 64% at Station 8 (60 m). Conversely, the relative abundance of textulariid taxa is relatively high at Stations 1, 2 and 7 ( $< 50 \text{ m}$ ) (% of the total fauna ranging between 60–70%) and reaches lower values at stations 3, 8 and 4 ( $< 56 \text{ m}$ ) (% ranging between 35–40%). Miliolids are only abundant at Station 1 (12% of the total fauna). At Station 1 (39 m), *Eggerelloides scaber* (55% of the total fauna; Fig. 3[1]) is the dominant species (Fig. 5a). It presents an erratic down-core vertical distribution with no preferential microhabitat. *Quinqueloculina laevigata* (13% of the total

299 fauna; Fig. 3[5]) and *Ammonia beccarii* (12% of the total fauna; Fig. 3[2–4]) are two other  
 300 major calcareous species. Their abundances are greatest within the uppermost 0.5 cm of the  
 301 sediment column. *Bulimina aculeata* (7% of the total fauna; Fig. 3[6]), a calcareous species,  
 302 presents a plurimodal distribution with a density maximum in the 3–4 cm interval (Fig. 5a).  
 303 The agglutinated *Nouria polymorphinoides* (4% of the total fauna; Fig. 3[7]) preferentially  
 304 occupies the 0–0.5 cm interval (Fig. 5a). At Station 2 (47 m), *E. scaber* (50% of the total  
 305 fauna) has a plurimodal distribution with a density maximum recorded in the 0–0.5 cm  
 306 interval (Fig. 5b). *Bulimina aculeata* (15% of the total fauna) shows a bimodal distribution  
 307 similar to Station 1. *Ammonia falsobeccarii* (9% of the total fauna) (Fig. 3[8–10]) and *A.*  
 308 *beccarii* (10% of the total fauna) are secondary species. *Nouria polymorphinoides* (5% of the  
 309 total fauna) preferentially occupies the 0–0.5-cm interval. At Station 7 (50 m) *E. scaber* (52%  
 310 of the total fauna) shows a peculiar vertical distribution with two maxima recorded in the 0–  
 311 0.5 cm and 9–10 cm intervals respectively (Fig. 5c). *Nouria polymorphinoides* (16% of the  
 312 total fauna) and *A. falsobeccarii* (8% of the total fauna) show the same microhabitat pattern as  
 313 *E. scaber*. *Nonionoides turgidus* (5% of the total fauna) and *B. aculeata* (5% of the total  
 314 fauna) are subsidiary calcareous species. *Nonionoides turgidus* inhabits the subsurface  
 315 sediments, 2–3 cm below the sediment-water interface. At Station 9 (54 m), *E. scaber* (44%  
 316 of the total fauna) constitutes a bimodal distribution with maxima recorded in the 0–0.5 cm  
 317 and 6–7 cm intervals (Fig. 5d). The secondary taxon *B. aculeata* (25% of the total fauna)  
 318 follows an erratic vertical distribution with two peaks at the 0–0.5 cm and 9–10 cm intervals.  
 319 Other major species, *A. falsobeccarii* (8% of the total fauna) and *N. polymorphinoides* (8% of  
 320 the total fauna), are more abundant in the 0–0.5 cm interval. *Nonion faba* (4% of the total  
 321 fauna) (Fig. 3[12–13]) presents a density maximum recorded between 1.5–3 cm. *Nonionoides*  
 322 *turgidus* (2.5% of the total fauna) is characterised by a density maximum recorded at the 3–4  
 323 cm interval. At Station 3 (56 m), *E. scaber* (30% of the total fauna) preferentially occupies the



uppermost two centimeters of the sediment (Fig. 5e). *Bulimina aculeata* (23% of the total fauna), *A. falsobeccarii* (21% of the total fauna) and *Bulimina marginata* (11% of the total fauna) (Fig.3[15]) present erratic vertical distributions with density maxima recorded in the 0–0.5-cm interval. *Nouria polymorphinoides* (7% of the total fauna) preferentially occupies the 0–0.5-cm interval. At Station 8 (61 m), *E. scaber* (25% of the total fauna) comprises an erratic vertical distribution with a density maximum in the 2–3 cm interval (Fig. 5f). *Bulimina aculeata* (21% of the total fauna) has a plurimodal distribution with maxima recorded in the 0–0.5 cm, 4–3 cm and 6–7 cm intervals. *Ammonia falsobeccarii* (20% of the total fauna) has two maxima in the 0–0.5 cm and 1.5–3 cm intervals. *Nonion faba* (11% of the total fauna) is most abundant between 1–3 cm. *Nouria polymorphinoides* (7% of the total fauna) and *B. marginata* (7% of the total fauna) are characterised by density maxima recorded in the uppermost centimeter of sediment. At Station 4 (69 m), *E. scaber* (25% of the total fauna) is still the dominant taxon presenting a plurimodal vertical distribution (Fig. 5g). *Ammonia falsobeccarii* (15% of the total fauna) is most abundant in the uppermost centimeter of sediment. *Nouria polymorphinoides* (13% of the total fauna) occupies the uppermost 2 cm of the sediment. *Nonion faba* (11% of the total fauna) is most abundant between 2–4 cm. It is worthy to note the occurrence of *Rectuvigerina phlegeri* (6% of the total fauna) (Fig.3[11]) and *Paracassidulina neocarinata* (4%) in the uppermost half centimeter of the sediment.

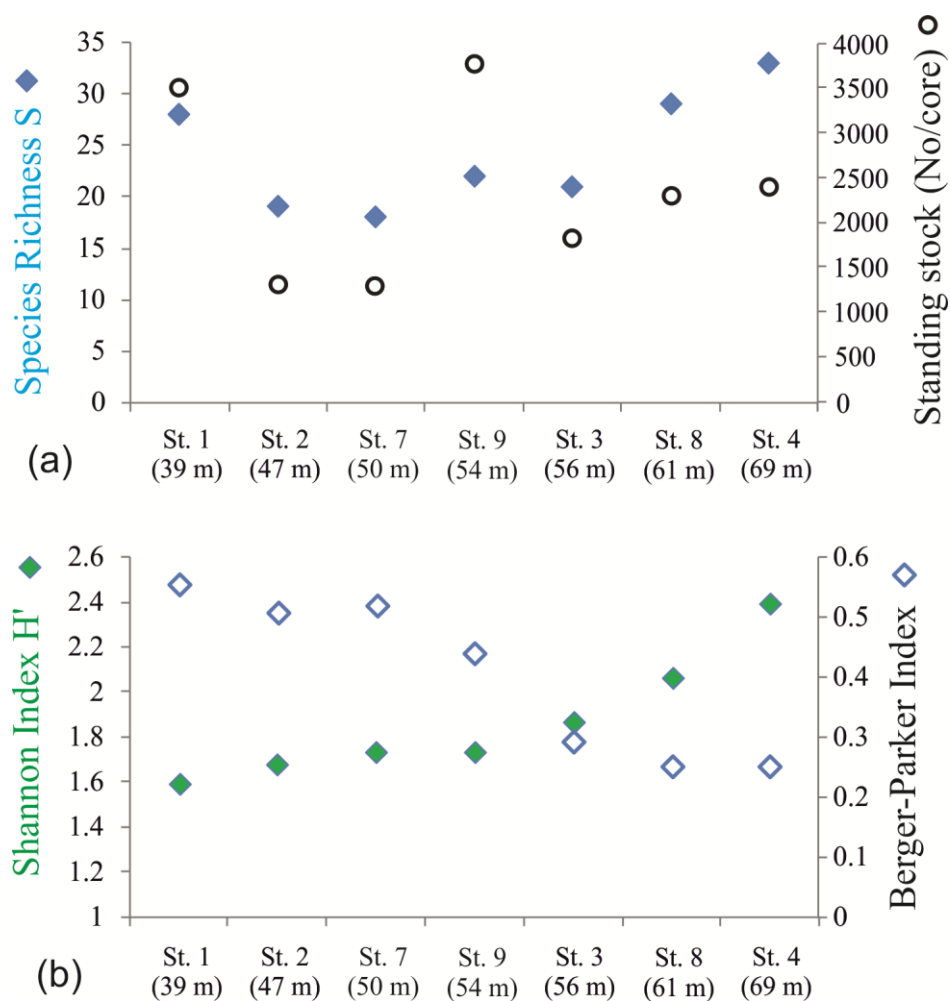
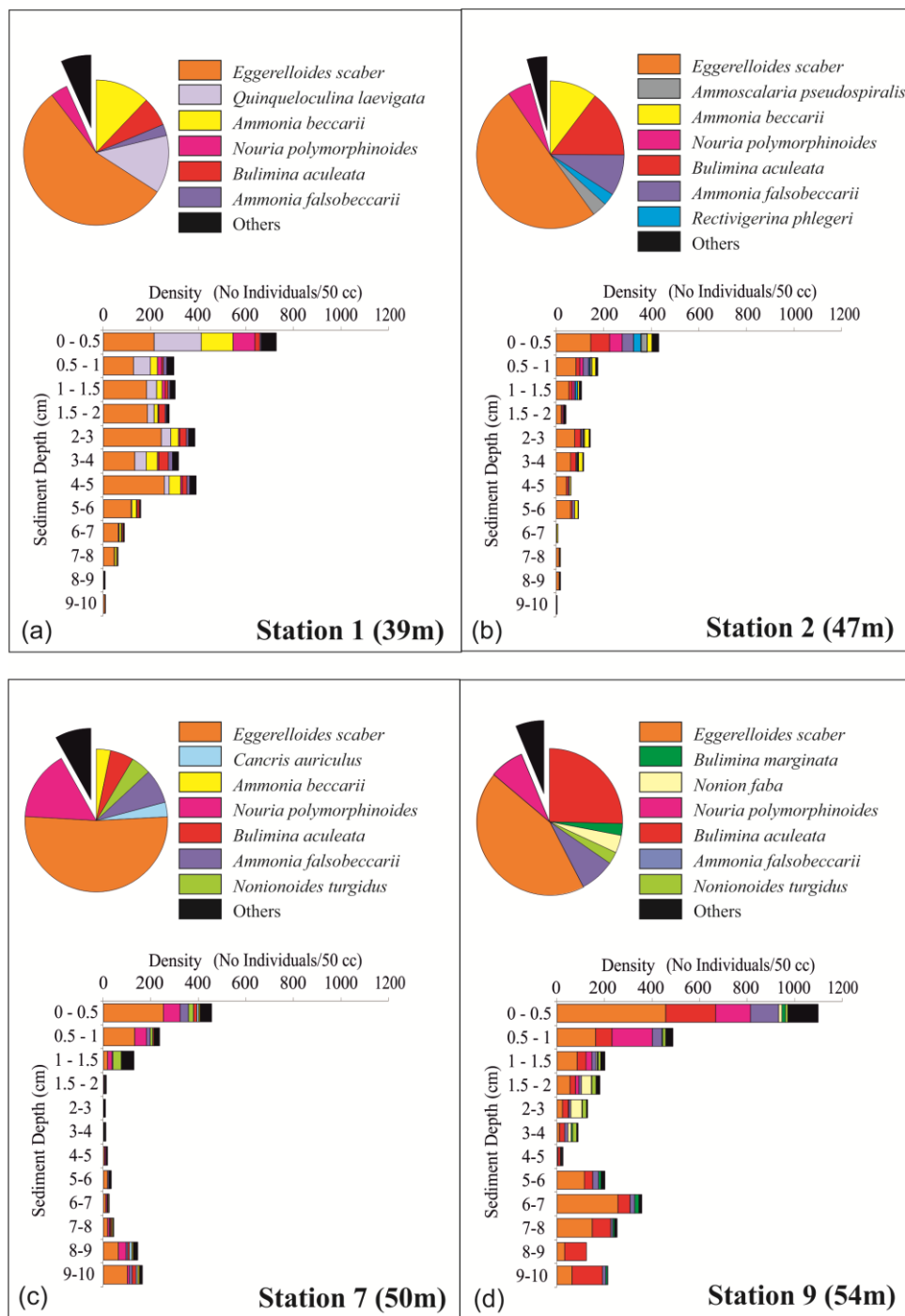
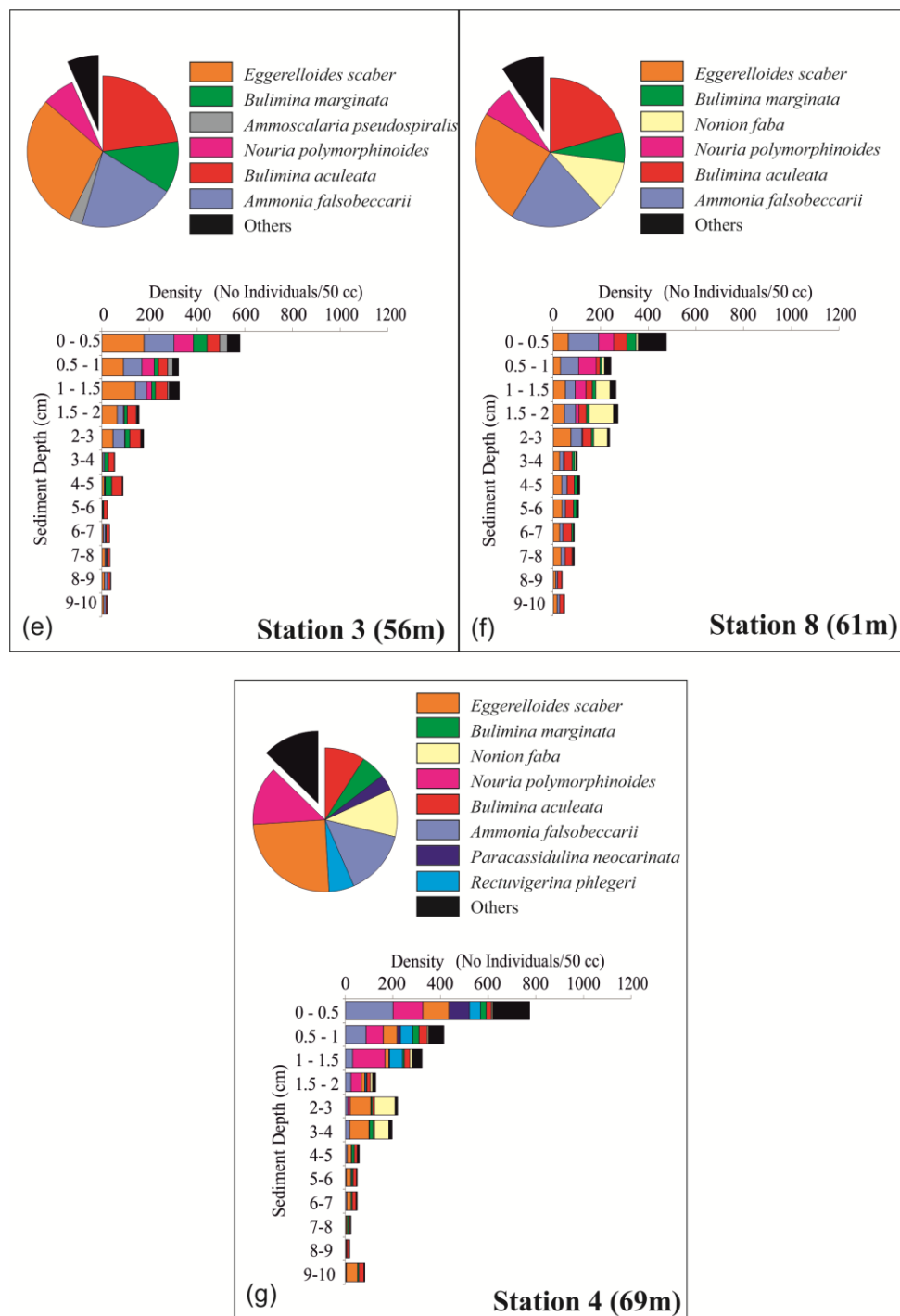


Figure 4. (a-b) Ecological indices describing foraminiferal faunas at the seven stations from the WGMP. (a) Species Richness ( $S$ ) and foraminiferal standing stocks (no. individuals/core); (b) Shannon ( $H'$ ) and Berger-Parker indices.



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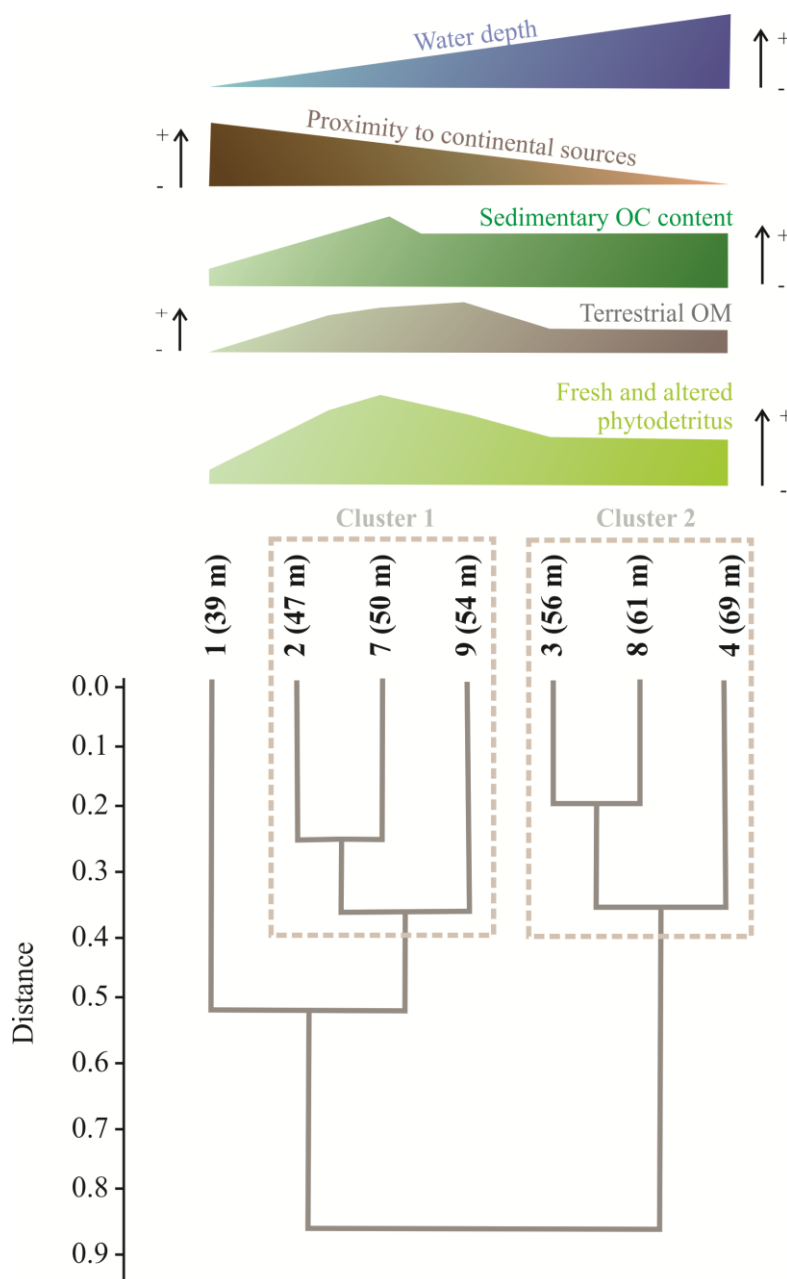
347 Figure 5. (a-g) Foraminiferal composition and down-core distribution of live benthic  
 348 foraminifera in the seven cores gathered in the WGMP. Pie charts represent the composition  
 349 of live benthic foraminiferal faunas (composition in % of total fauna). The number of  
 350 individuals belonging to the  $>150 \mu\text{m}$ -size fraction found in each level is standardized for a  
 351  $50 \text{ cm}^3$  sediment volume. In both pie charts and core distribution, only taxa with relative  
 352 abundances  $>2.5\%$  are pictured.



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 359 abundances  $>2.5\%$  are pictured.

### 3.2.3 Q-mode clustering and Indicative Values (IV)

Based on faunal content, Q-mode cluster analysis of the seven stations reveals two groups of three stations and one isolated site (Fig. 6). The calculation of Indicative Values (IV) for the 13 major species of our study area shows a marked spatial variability for some taxa as well as species common to certain areas (Table 3). Station 1 (39 m), which is isolated by cluster analysis, is characterized by *Q. laevigata* (IV = 84%), *A. beccarii* (IV = 69%), and *E. scaber* (IV = 42%). Cluster 1 consisting of Stations 2, 7 and 9 (water depth comprised between 47–54 m), is characterized by *N. turgidus* (IV = 77%), *Canceris auriculus* (IV = 46%), *N. polymorphinoides* (IV = 43%). Cluster 2 includes Stations 3, 8 and 4 (all deeper than 56 m) and is characterized by *P. neocarinata* (IV = 98%), *N. faba* (IV = 80%), *B. marginata* (IV = 79%), *A. falsobeccarii* (IV = 63%), *Ammoscalaria pseudospiralis* (IV = 48%), *B. aculeata* (IV = 45%) and *R. phlegeri* (IV = 44%). Permutation test based on 999 iterations reveals that *N. turgidus* can be considered as a robust indicator (p-value < 0.05) for Cluster 1 whereas *N. faba*, *B. marginata* and *A. falsobeccarii* are significantly indicative of Cluster 2.



375

376 Figure 6. Q-mode cluster analysis of the seven stations following the Ward's method based on  
 377 transformed percentages  $P_i$  of major foraminiferal species (>2.5%). Environmental trends  
 378 (station water depth, proximity to continental sources, sedimentary organic matter content,  
 379 terrestrial organic matter, fresh and degraded phytodetritus) are pictured. Dotted boxes  
 380 correspond to groups identified by Q-mode cluster analysis (Clusters 1 and 2).

IndVal (IV)	Station 1 (39 m)	Cluster 1	Cluster 2
<i>Ammonia beccarii</i>	<b>69</b>	29	2
<i>Ammonia falsobeccarii</i>	9	28	<b><u>63</u></b>
<i>Bulimina aculeata</i>	17	39	<b>45</b>
<i>Bulimina marginata</i>	5	16	<b><u>79</u></b>
<i>Cancris auriculus</i>	17	<b>46</b>	37
<i>Nonion faba</i>	1	18	<b><u>80</u></b>
<i>Nonionoides turgidus</i>	3	<b><u>77</u></b>	21
<i>Paracassidulina neocarinata</i>	0	6	<b>98</b>
<i>Rectuvigerina phlegeri</i>	23	32	<b>44</b>
<i>Quinqueloculina laevigata</i>	<b>84</b>	5	11
<i>Ammoscalaria pseudospiralis</i>	7	44	<b>48</b>
<i>Eggerelloides scaber</i>	<b>42</b>	37	20
<i>Nouria polymorphinoides</i>	17	<b>43</b>	41

Table 3. Indicator values (IndVal – IV in %) of the major station species of the groups defined by *Q*-mode cluster analysis. Indicator values are calculated according to Dufrêne and Legendre (1997) (see Material and Methods). For each species, IV are indicated by red shading, and the maximum IV by bold numbers. Underlined IV are significant with a *p*-value < 0.05.

#### 4. Discussion

##### 4.1. Environmental features of the West-Gironde Mud Patch in August 2017

Sedimentological studies carried out over the last three decades on the WGMP have shown that this seafloor feature is difficult to isolate, define and categorise (e.g., Lesueur et al., 1991; 1996; 2002; Cirac et al., 2016) (Fig. 1). The boundaries between the muddy WGMP facies (silt-clay) and the sands of the surrounding Aquitaine Shelf are hard to define as episodic inputs of suspended matter from the Gironde River associated with storm-induced bottom currents cause these facies to migrate several hundred metres from their source (Cirac et al., 2000; Lesueur et al., 2002). Figure 2 shows that Stations 1 and 7, located at the edge of the WGMP (presumably within the zone of shifting boundaries), present complex sedimentary facies where sandy layers are intercalated in finer sediments. Such sedimentary patterns were also documented in core samples collected in Autumn 2016 and in June 2018 during the

400 JERICOBENT-1 and JERICOBENT-5 cruises (Deflandre, 2016; Gilet and Deflandre, 2018;  
 401 Lamarque et al., 2021; Dubosq et al., in press). Whereas Station 1 is, due to its coastal  
 402 proximity, impacted by episodic high-energy hydrodynamics causing low sediment  
 403 deposition, massive but sporadic sedimentary deposits characterize Station 7 (Dubosq et al.,  
 404 in press). All other stations from within the WGMP present relatively continuous sediment  
 405 accumulation with rates ranging between 0.3–0.5 cm yr<sup>-1</sup> (Dubosq et al., in press). This lateral  
 406 and vertical heterogeneity in the sedimentary architecture of the WGMP influences the  
 407 geochemical processes at the sediment-water interface (Dubosq et al, in press; in prep.). In  
 408 August 2017, at Station 1 (39 m), the sandy surface, assumedly winnowed, is depleted in  
 409 organic matter (<0.3% DW), fresh ([Chl-*a*] = 0.23 µg/g) and degraded ([Phaeo-*a*] = 1.46  
 410 µg/g) pigment compounds (Table 2). Conversely, at Station 7 (50 m) where the surface  
 411 sediments are the most fine and clayey of the seven stations, the organic carbon (1.8% DW)  
 412 and fresh ([Chl-*a*] = 1.82 µg/g) and degraded ([Phaeo-*a*] = 13.55 µg/g) chlorophyll pigment  
 413 contents are the highest in our study area (Table 2). As a possible consequence of an efficient  
 414 aerobic mineralization of labile organic compounds, oxygen penetration at Station 7 is the  
 415 shallowest of our seven-stations transect (OPD ~ 0.34 cm: Table 1). Stations 9 (54 m) and 4  
 416 (69 m), also located close to the limits of the WGMP, present relatively homogeneous silt-  
 417 clay facies where organic compounds accumulate in relatively high quantities (OC = 1.4%  
 418 DW) (Table 2). There, oxygen penetration enables efficient organic matter degradation via  
 419 aerobic respiration below the sediment-water interface (< 0.42 cm). Finally, Stations 2 (47 m),  
 420 3 (56 m) and 8 (61 m) located along the central axis of the WGMP show muddy facies  
 421 moderately enriched in organic compounds (OC between 0.9–1.2% DW) and moderate OPD  
 422 (0.46 – 0.66 cm) (Table 1). In our study area, late summer corresponds to the end of a long  
 423 sequence of enhanced phytoplankton production initiated in late winter/early spring (Fig. 7).  
 424 Lampert (2001) has studied phytoplankton successions on the inner shelf facing the Gironde



River estuary. Other studies have also briefly described the seasonal evolution of primary production in the Bay of Biscay using satellite images (SeaWiFS/NASA data) to interpret chlorophyll-*a* pigment concentration in surface waters (Lampert et al., 2002; Fontanier et al., 2003; Duchemin et al., 2008). Both offshore and on the shelf, diatoms and coccolithophores bloom during the boreal spring (April–May) (Lampert, 2001; Fontanier et al., 2003; Duchemin et al., 2008) (Fig. 8). Thereafter, autotrophic marine dinoflagellates and cyanobacteria form a Deep Chlorophyll Maximum during the summer stratification of surface waters (Lampert, 2001). Phototrophic productivity in the coastal zone close to the Gironde estuary is particularly intense (Lampert, 2001). Therefore, the export of marine phytodetritus between spring and late summer due to the phytoplankton bloom may explain the relatively high content of both degraded and fresh chlorophyll *a* (i.e., phytodetritus) in the surface sediments of our study area, especially in the central and distal areas of the WGMP (Stations 2, 9, 7, 3, 4 and 8) where hydrodynamic energy remodelling the sea floor is weaker compared to sandy Station 1 (Table 1). The presence of fresh chlorophyll *b* pigment ([Chl-*b*] >0.10 µg/g), which originates from land plants, demonstrates that terrestrial organic compounds have recently accumulated in the mud patch. This continental imprint is relatively well marked in the central WGMP (Stations 2, 9 and 7; [Chl-*b*] >0.10µg/g) (Table 2).

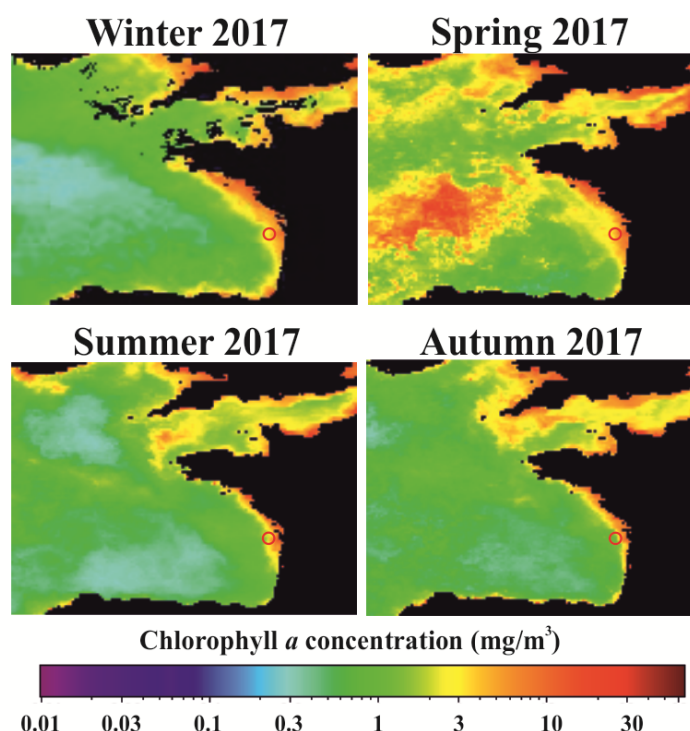


Figure 7. Synthetic seasonal maps of Chlorophyll *a* concentration in surface waters of the Bay of Biscay in 2017. Maps are based on MODIS satellite images (SNPP VIIRS Chlorophyll Concentration, OC3 Algorithm – Seasonal winter, spring, summer and autumn 2017 - <https://oceancolor.gsfc.nasa.gov/>). Red circles indicate our study area.

#### 4.2. Benthic foraminifera biofacies and environmental implications

By the Q-mode clustering of the seven stations and by the IndVal calculation of our 13 most abundant species, benthic foraminifera living in the West-Gironde Mud Patch can be grouped into three main biofacies (Table 3, Fig. 5a–g). These can be further correlated with a clear bathymetric gradient and gradual changes of sedimentary and geochemical parameters (Fig. 6). The shallowest Station 1 (39 m), characterized by sandy sediments and low organic matter content, is dominated by *E. scaber* (55%), *A. beccarii* (12%) and *Q. laevigata* (13%) (Fig. 5a). At the other six stations characterized by clay-silt facies and variably enriched in organic carbon, foraminiferal diversity (i.e. Shannon index and simple diversity) increases and the cumulative contribution of *E. scaber*, *A. beccarii* and *Q. laevigata* decreases strongly

with increasing water depth. Our observations at Station 1 are in agreement with many publications where both *E. scaber*, *A. beccarii* and *Quinqueloculina* spp. are described in inner-shelf, either prodeltaic or estuarine environments, near river mouths (e.g., Barmawidjaja et al., 1992; Debenay and Redois, 1997; Diz et al., 2006; Diz and Francés, 2008; Goineau et al., 2011; Mendes et al., 2012; Dessandier et al., 2015; 2016). For instance, Dessandier et al. (2016) documented a strong contribution of both *E. scaber* and *A. beccarii* at the shallower sites (< 50 m depth) of a bathymetric transect in front of the Tagus River (Portugal, NE Atlantic). Like Station 1, those inner-shelf environments were characterized by sandy sediments ( $Q_{50} > 100 \mu\text{m}$ ) and very low organic carbon content (< 0.05 % DW). Goineau et al. (2011) similarly described a strong contribution of *E. scaber* (*Eggerella scabra* in their study), *A. beccarii* (*Ammonia beccarii* f. *beccarii* in their study) and *Quinqueloculina* spp. at stations sampled in inner-shelf environments from the Gulf of Lions (France, Western Mediterranean Sea). Those stations were located between 15–37 m depth on a relict prodeltaic lobe, adjacent to the Grand Rhône River and were subject to high-energy hydrodynamics. They were characterized by sandy sediments with low organic matter comprised of continental and degraded compounds (OC content < 1.1 % DW, C:N ratio ranging between 11.5–17.7). It seems that *E. scaber*, *A. beccarii* and *Q. laevigata* thrive preferentially in shallow-water environments where hydro-sedimentary constraints (i.e., sedimentary reworking, winnowing and erosion by strong bottom currents) are enhanced. It is noteworthy that the erratic vertical distribution of *E. scaber* within anoxic sediments of all our stations underline its capacity to thrive under low oxygenation without any preference for fresh food (Diz et al., 2006; Langlet et al., 2014). Such patterns have also been documented in laboratory experiments simulating hypoxia and/or organic supply with sediment material sampled in the Bay of Biscay (Ernst et al., 2005).

Q-mode analysis Cluster 1 groups stations located in the central part of the WGMP (between 47–54 m water depth). There, organic compounds (OC content between 0.9–1.8 % DW) with fresh and degraded marine phytodetritus ([Chl-*a*] >1.15 µg/g; [Phaeo-*a*] > 6.65 µg/g) and terrestrial organic matter ([Chl-*b*] > 0.10 µg/g) focus in muddy sediments (Table 2; Fig. 6). Foraminiferal faunas are characterized by a relatively high contribution of *B. aculeata*, *A. falsobeccarii*, *N. polymorphinoides* and, to a lesser degree, *N. turgidus* (Fig. 5b-d). *Cancris auriculus* and *A. pseudospiralis* are both complementary and indicative (IV>44) species (Table 3). *Eggerelloides scaber* is still the dominant species of all stations grouped in this cluster. *Bulimina aculeata* was described in the Gulf of Cadiz (SW Iberian Peninsula) between water depths of 30–100 m by Mendes et al. (2012). This species occurs in muds associated with weak hydrodynamics, in-sediment enhanced hypoxia and high organic matter content. *Nouria polymorphinoides* with *C. auriculus* and *A. pseudospiralis* were documented in shelf environments between depths of 27–75 m in the Gulf of Guinea due to the high primary productivity and fresh organic matter found in the sediments along the Ivory Coast and near the Volta Delta (Altenbach et al., 2003). Debenay and Redois (1997) described live and dead *A. falsobeccarii* (*Eponides falsobeccarii* in their study), *C. auriculus* and *A. pseudospiralis* (*Ammobacculites pseudospirale* in their study) on the shelf off Senegal (NW Africa), at the mouth of the Senegal River. Goineau et al. (2011) have also documented the dominance of both living *E. scaber* (*Eggerella scabra* in their study) and *N. turgidus* (*Nonionella turgida* in their study) at depths ranging between 47–62 m close to the Rhône River mouth. There, both species take advantage of terrestrial and marine organic compounds buried within the sediments (Goineau et al., 2011). *Nonionoides turgidus* is often considered an opportunistic and stress-tolerant taxon thriving in hypoxic and eutrophic conditions (Duchemin et al., 2008; Goineau et al., 2011). Its relatively deep infaunal microhabitat (> 2 cm depth) in our study area confirms both trophic and metabolic strategies.

Cluster 2 groups stations with silt-clay facies located between 56–60 m depth in the distal section of the WGMP. There, sedimentary organic carbon content is moderate with values ranging between 1.2–1.4% DW (Table 2). Fresh and degraded phytodetritus are available in a lesser quantity compared to the central area of the WGMP (Fig. 5e–g). *Paracassidulina neocarinata*, *N. faba*, *B. marginata*, *A. falsobeccarii*, *B. aculeata* and *R. phlegeri* are the most indicative species of this ‘outer-WGMP’ cluster (Table 3). Those taxa are all commonly recorded in mid- to outer-shelf environments (e.g., Debenay and Redois, 1997; Fontanier et al., 2002; Langezaal et al., 2006; Duchemin et al., 2005; 2008; Goineau et al., 2011; Dessandier et al., 2015; 2016). For example, *N. faba*, *B. marginata* and *P. neocarinata* dominate the >150 µm-sized faunas sampled between 80–140 m depth in La Grande Vasière mud belt in the Bay of Biscay (NE Atlantic) (Duchemin et al., 2005; 2008). In Goineau et al. (2011), *P. neocarinata* (*Cassidulina carinata* in their study), *N. faba* (*Nonion fabum* in their study), and *R. phlegeri* statistically clustered together and were indicative of benthic ecosystems located between 44–86 m depth under the influence of the Rhône River plume. These species thrived in very fine sediments ( $D_{50} \sim 10 \mu\text{m}$ ) with moderate organic carbon content (OC between  $\sim 1.1$ – $1.3\%$  DW). These environmental conditions are close to those found at the distal end of the WGMP. In Dessandier et al. (2016), *P. neocarinata* (*Cassidulina carinata* in their study), *R. phlegeri* and *N. faba* (*Nonion scaphum* in their study) were documented between 50–100 m depth in mid- and outer-shelf environments characterized by silt to fine-sand facies supporting moderate quantities of organic compounds. In all studies comparable to our study area, *P. neocarinata* and *R. phlegeri*, present a shallow infaunal microhabitat typical of species feeding preferentially on labile organic compounds available in the most oxygenated sediments. *Paracassidulina neocarinata* behave as an opportunistic species relying on freshly deposited phytodetritus produced during spring to early summer blooms (Fontanier et al., 2003; Duchemin et al., 2008). In our study area, *N. faba* inhabits an

intermediate infaunal distribution traversing the dysoxic and the anoxic sediments (Fig. 5f–g). This pattern agrees with all other publications where this outer-shelf species is documented (e.g., Fontanier et al., 2002, Langezaal et al., 2006; Goineau et al., 2011; Dessandier et al., 2016). Though *N. faba*'s putative abilities such as denitrifying metabolism or endosymbiosis with procaryotes are still debated. In subsurface sediment layers, *N. faba* can rely on fresh or degraded organic compounds actively buried in deeper sediments (Fontanier et al., 2002; Duchemin et al., 2008). Alternatively, this species may migrate toward the sediment surface to gather fresher phytodetritus (Langezaal et al., 2006).

#### 4.3. An ecological continuum through the muddy environments of the Bay of Biscay

Our investigation allows us to appreciate the faunal continuum existing in the Bay of Biscay from the WGMP (40–70 m) (our study area) to the Grande Vasière located between 80–130 m depth on the outer continental shelf (Duchemin et al., 2005; 2008). Although geographically disconnected (Fig. 1), these two muddy environments have dominant foraminiferal species that appear clearly organized along a range of correlated environmental gradients. *Nonion faba*, *B. marginata* and *P. neocarinata*, typical of the deepest part of the WGMP, are all dominant in the Grande Vasière (Duchemin et al., 2008). These species can be considered specialists preferentially living in fine sediments from open-ocean environments and relying on marine phytodetritus derived from median and outer shelf primary production (i.e., diatoms and coccolithophore blooms in spring). In contrast, other species, although dominant in the distal WGMP, are absent from the outer continental shelf. This is notable in regard to *A. falsobeccarii*, *B. aculeata* and *R. phlegeri* which seem restricted to the WGMP potentially due to trophic preferences (i.e., phytodetritus associated with coastal primary production, terrestrial organic compounds) or a higher competitive ability compared to taxa living in deeper ecosystems. Other species which are clearly dominant in the proximal part of

the WGMP (*E. scaber*, *Q. laevigata*, *A. beccarii*) are extremely rare or even absent in the Grande Vasière (Duchemin et al., 2008). As explained previously, these species are considered to be generalists with the ability to proliferate in hydrodynamically-impacted costal ecosystems where hydro-sedimentary pressure and food availability represent major ecological constraints. To summarize, our Bay of Biscay study illustrates the utility of using foraminiferal faunas with muddy environmental preferences to discriminate well-oxygenated biotopes and how they are variably impacted by spatially disparate hydrodynamics and their correlated deposition of organic compounds. Due to their propensity to be readily preserved in the fossil record, the calcareous benthic foraminifera of the WGMP and Grand Vasière could be successfully used in sedimentary records to rebuild precisely how muddy sedimentary units developed in the Bay of Biscay during the Late Holocene.

## 5. Conclusions

Live (Rose-Bengal stained) shelf foraminiferal faunas have been studied at seven stations between 39–69-m depth in the West-Gironde Mud Patch (WGMP) (Bay of Biscay, NE Atlantic) to understand how complex environmental conditions (e.g., organic matter, oxygenation, sedimentary facies) control foraminiferal ecological patterns (i.e., diversity, faunal composition, standing stock, and microhabitats). The main conclusions of this work are:

- (1) In the WGMP, foraminiferal simple diversity (S) presents relatively moderate values ranging between 15–35 taxa. According to Shannon Index  $H'$ , foraminiferal diversity tends to increase with water depth. The relative contribution of *Eggerelloides scaber*, the dominant foraminiferal species at all stations, decreases with decreased proximity to the coast and increased depth in the WGMP.

(2) The shallowest station (Station 1, 39 m) proximal to the WGMP is characterized by the relatively important contribution of *Eggerelloides scaber*, *Quinqueloculina laevigata* and *Ammonia beccarii*, which are all typical of inner-shelf environments constrained by high-energy hydrodynamics and river discharge. There, surface sediments are comprised of winnowed sand strongly depleted in organic matter.

(3) In the central part of the WGMP where variably degraded marine phytodetritus and terrestrial organic compounds are concentrated within clay-silt facies, foraminiferal faunas are characterized by a relatively high contribution of *Bulimina aculeata*, *Ammonia falsobeccarii*, *Nouria polymorphinoides* and *Nonionoides turgidus*. The agglutinated *Eggerelloides scaber* is still the most important taxon.

(4) The deeper stations (>55 m depth) located distally within the mud patch are characterised by the high contribution of *B. aculeata*, *A. falsobeccarii* and *N. polymorphinoides*. But they are accompanied by *Bulimina marginata*, *Rectuvigerina phlegeri*, *Nonion faba* and *Paracassidulina neocarinata*, typical of mid- and outer-shelf ecosystems where fine sediments and organic compounds accumulate.

Finally, our unique study underlines the foraminiferal continuum existing through the muddy environments of the Bay of Biscay, between the WGMP and the Grande Vasière.

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804 **Appendix captions**

805

806 **Appendix A**

807 Major foraminiferal species ( $\geq 5\%$ ) identified in the West-Gironde Mud Patch, with reference  
808 to plates and figures in the literature. Supplementary data associated with this article can be  
809 consulted in the online version at xxxx.

810

811 **Appendix B**

812 Census data for live (stained) benthic foraminifera in the  $>150\ \mu\text{m}$  fraction for the seven  
813 stations sampled in the West-Gironde Mud Patch. N.B. Numbers are not standardized for  
814 sediment volume. Supplementary data associated with this article can be consulted in the  
815 online version at xxxx.