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3

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18

## 19 **0. Abstract**

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

26 occurring in spring and summer. This morpho-sedimentary unit is bathed by well-oxygenated  
27 bottom waters and characterized by clay-silt facies containing variably degraded phytodetritus  
28 and traces of terrestrial organic matter. Oxygen penetration depth within the sediment is less  
29 than  $7\pm 3$  mm, indicating efficient organic matter in-sediment mineralisation by aerobic  
30 respiration. Foraminiferal richness (S) presents relatively moderate values ranging between  
31 15–35 taxa. According to Shannon Index  $H'$ , foraminiferal diversity tends to increase with  
32 water depth. Accordingly, the relative contribution of *Eggerelloides scaber*, the dominant  
33 foraminiferal species at all stations, decreases with increased depth and decreased proximity  
34 to the coast. The shallowest station (Station 1, 39 m), closest to the shore, is characterised by  
35 *E. scaber*, *Quinqueloculina laevigata* and *Ammonia beccarii*, species typical of inner-shelf  
36 environments constrained by high-energy hydrodynamics and river discharge. Surficial  
37 sediments at Station 1 constitute of winnowed sands depleted in organic carbon. Towards the  
38 centre of the WGMP, where clay-silt facies contain variably degraded marine phytodetritus  
39 and terrestrial organic compounds, foraminiferal faunas are characterized by *Bulimina*  
40 *aculeata*, *Ammonia falsobeccarii*, *Nouria polymorphinoides* and *Nonionoides turgidus*. Yet  
41 *E. scaber* remains the most dominant taxon. Deeper stations (>55 m depth) located at the  
42 distal part of the mud patch are dominated by *B. aculeata*, *A. falsobeccarii*, *N.*  
43 *polymorphinoides* and *E. scaber*. Accompanying these taxa are *Bulimina marginata*,  
44 *Rectuvigerina phlegeri*, *Nonion faba* and *Paracassidulina neocarinata*, which are typical of  
45 mid- and outer-shelf ecosystems enriched in sedimentary organic matter.

46

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

49

50

## 51           **1. Introduction**

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

72           The West-Gironde Mud Patch (WGMP) is a perfect example of a shelf environment  
73 where organic compounds from various sources (mainly marine phytodetritus) accumulate  
74 within fine sediments (Lamarque et al., 2021; Dubosq et al., in press; Dubosq et al., in prep).  
75 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.

101 1). These works have shown that living benthic communities respond to episodic inputs of  
102 organic matter related to phytoplankton blooms from spring to autumn. Certain opportunistic  
103 species (i.e. *Nonionella iridea*, *Cassidulina carinata* according to the taxonomy of Duchemin  
104 et al., 2008) dominate the Grande Vasière mud belt fauna. Foraminiferal diversity, standing  
105 stock and vertical distribution within sediments shifts with water depth (Duchemin et al.,  
106 2005; 2008).

107 Following the Grande Vasière studies, the aim of our paper is to assess the relevance  
108 of using benthic foraminifera as bio-indicators of the various environmental conditions  
109 prevailing along the WGMP. To do so, we can draw on geochemical, geophysical and  
110 sedimentological data acquired during the 2017 oceanographic JERICOBENT-2 cruise  
111 (Deflandre, 2017; Dubosq et al., in prep; complementary sedimentological analysis presented  
112 in this paper). These data are compared to the faunal characteristics (diversity, standing stock,  
113 microhabitats) of the foraminiferal communities sampled at the seven stations ranging from  
114 36–69 meters water depth (Fig. 1).

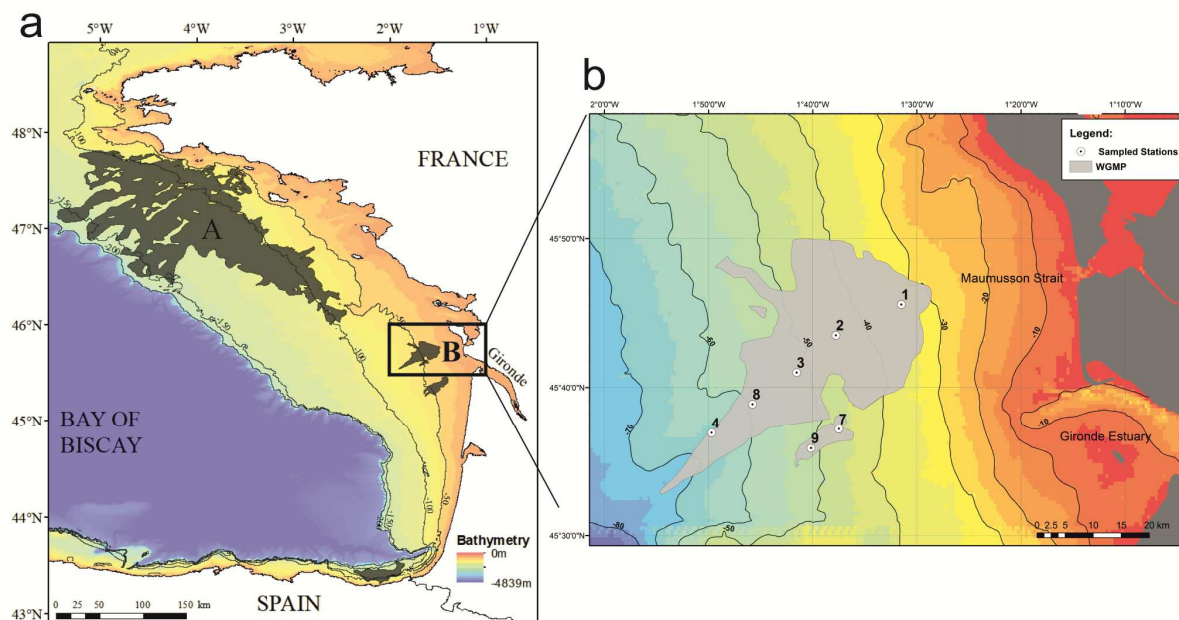
115

## 116 **2. Material and Methods**

### 117 *2.1. Water parameters*

118 This investigation is based on data obtained at seven stations sampled during the  
119 JERICOBENT-2 cruise in August 2017 (Fig. 1; Table 1) (Deflandre, 2017). Stations are  
120 organized according to a bathymetric gradient from the proximal part of the WGMP (Station  
121 1, 39 m) to the distal (Station 4, 69 m) (Fig. 1; Table 1). Bottom water temperature (CTD  
122 measurements) decreases gradually from 14.6°C at station 1 (39 m) to 12.7°C at station 4 (69  
123 m), whereas bottom water salinity (Conductivity-Temperature-Depth measurements) is  
124 constant (35.2) (Table 1). Bottom water oxygenation stays relatively high at all sites (between  
125 184–197 µM) (Table 1), oxygen penetration depth (OPD) within the sediments is relatively

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



129  
 130 *Figure 1. (a) Map of the Bay of Biscay continental shelf with the locations of mud belts and*  
 131 *patches: A - La Grande Vasière Mud Patch and B - The Gironde Mud Patch (b) Map of the*  
 132 *West Gironde Mud Patch showing the location of 7 sampling stations (white dots). The*  
 133 *synoptic map of the WGMP has been determined during the JERICOBENT-5-TH cruise*  
 134 *(Gillet and Deflandre, 2018)*

135

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)

136  
 137 *Table 1. Location of the seven stations sampled during the JERICOBENT-2 cruise (August*  
 138 *2017) including station coordinates and depth. Physico-chemical parameters including BWT*  
 139 *(bottom-water temperature in °C) and BWS (bottom-water salinity in psu) were extrapolated*

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

146

## 147 2.2 Sediment sampling

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

157

## 158 2.3. Sedimentological analysis

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



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

169

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

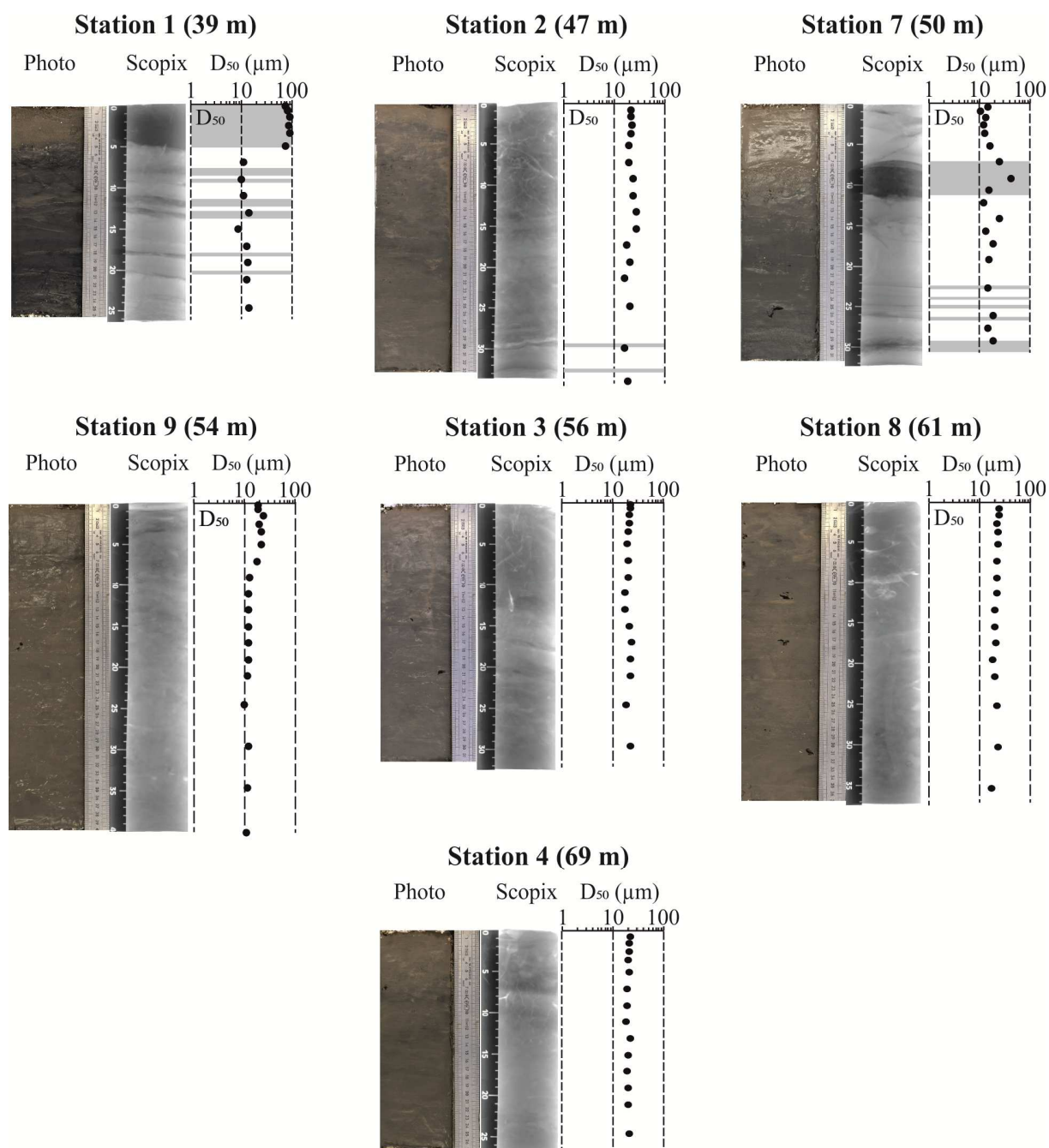
170

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

176

#### 177 2.4. Foraminiferal faunal analysis

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



183

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

186

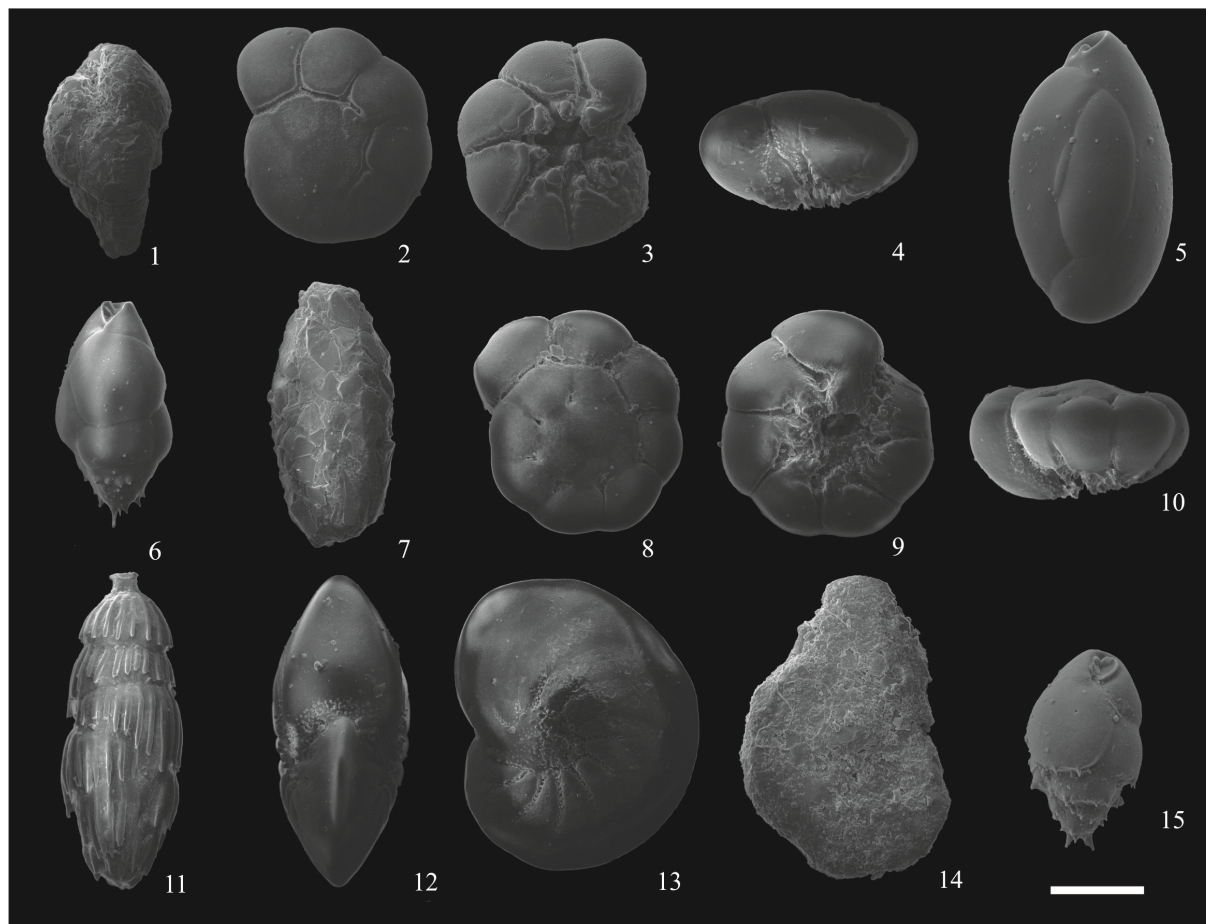
187 All samples were gently shaken for several minutes to obtain a homogeneous mixture. At the  
 188 laboratory (one month after the cruise), samples were sieved through 150  $\mu\text{m}$  mesh screens,  
 189 and sieve residues were stored in 95% ethanol. Stained foraminifera belonging to the >150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

191 Rose Bengal is that it may stain the protoplasm of dead foraminifera that may be relatively  
192 well-preserved for long time periods under the generally anoxic conditions prevailing in deep  
193 sediments (Corliss & Emerson, 1990; Bernhard, 2000). We therefore applied very strict  
194 staining criteria (i.e., all chambers, except the last chamber, stained in bright pink), and  
195 compared doubtful individuals to perfectly stained specimens of the same species found in the  
196 superficial sediment layers. For miliolids, doubtful specimens were broken to inspect test  
197 interior. Most stained foraminifera were identified at species level and checked with the  
198 World Foraminifera Database (Hayward et al, 2021) for current taxonomic nomenclature (see  
199 Appendix A for taxonomical references and Appendix B for census data). Because samples  
200 were preserved and sorted in ethanol, many soft-shelled foraminiferal species may have  
201 shrunk and become unrecognizable during picking. Thus, our counts probably underestimate  
202 the soft-shelled foraminiferal abundance. We obtained digital photographs of major species  
203 using a scanning electron microscope at Angers University (Fig. 3). For each core, we  
204 calculated different indices to assess diversity. First, we calculated Species Richness ( $S$ ) and  
205 then Shannon index,  $H'$  (log base  $e$ ) as an information-statistic index as described in Murray  
206 (2006). We determined the Berger-Parker index, which represents the highest relative  
207 contribution (in %) calculated for the dominant taxon at each station. A Q-mode cluster  
208 analysis based on normalized relative abundances  $P_i$  values was applied for the seven stations  
209 and the 13 major species ( $\geq 2.5\%$ ), with  $P_i$  defined as:

$$210 \quad P_i = \text{Arc sin}(\sqrt{p_i})$$

211 in which “ $p_i$ ” is the relative frequency of the “ $i$ th” species, and “ $P_i$ ” is the normalized value of  
212  $p_i$  (J. Hohenegger, personal communication). We constructed a tree diagram using Ward’s  
213 method based on Euclidian distance. To do so, we used the PAST Software (Hammer et al.,  
214 2001).

215



216  
 217 *Figure 3. SEM photographs of some major foraminiferal taxa observed in our study area. 1*  
 218 *Eggerelloides scaber; 2, 3, 4 Ammonia beccarii (dorsal, umbilical and lateral views); 5*  
 219 *Quinqueloculina laevigata; 6 Bulimina aculeata; 7 Nouria polymorphinoides; 8, 9, 10*  
 220 *Ammonia falsobeccarii (dorsal, umbilical and lateral views); 11 Rectuvigerina phlegeri; 12,*  
 221 *13 Nonion faba (frontal and lateral views); 14 Ammoscalaria pseudospiralis; 15 Bulimina*  
 222 *marginata. Scale bar represents 100  $\mu$ m.*

223  
 224 Using Q-mode cluster analysis, we applied the Indicator Value (IV) Method (Dufrêne and  
 225 Legendre, 1997) with the 13 major species in order to determine indicative species in each  
 226 cluster of stations. For this purpose, we used the following formula:

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

227

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

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

228  $N_{individuals_{(i,\alpha)}}$  is the mean number of individuals belonging to the species  $i$  and present in  
 229 the cluster  $\alpha$ .  $N_{individuals_{(i)}}$  is the sum of the mean numbers of individuals of species  $i$   
 230 occurring in all clusters.  $N_{stations_{(i,\alpha)}}$  is the number of stations in the cluster  $\alpha$  where the  
 231 species  $i$  is present.  $N_{stations_{(\alpha)}}$  is the total number of sites in the cluster  $\alpha$ . P values were  
 232 calculated based on 999 permutations using R package "labdsv" (Roberts 2019; R core team  
 233 2020).

234

### 235 2.5. Additional details

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

249 areas integrating various marine ecosystems does not follow this recommendation (e.g.,  
250 Fontanier et al., 2002; Duchemin, 2005; 2008; Goineau et al., 2011; Dessandier et al., 2015;  
251 2016). Conversely, environmental interpretations of modern foraminiferal faunas are mostly  
252 based on a single sample per site. We therefore consider in this study that even if small-scale  
253 (metric) spatial variability exists between benthic faunas living at the same station, this  
254 variability does not hide the faunal variability existing at the spatial scale of the WGMP,  
255 given that the seven sampled stations are several kilometres apart from each other. Finally, the  
256 many recent studies exclusively using  $>150\ \mu\text{m}$ -sized benthic foraminifera living in the Bay  
257 of Biscay (e.g., Fontanier et al., 2002; Ersnt et al., 2005; Langezaal et al., 2006; Duchemin et  
258 al., 2005; 2008) sufficiently provide reliable information concerning what we might expect in  
259 terms of foraminiferal diversity, standing stock and distribution on the Aquitaine Shelf. Our  
260 study adds new and precious data about benthic environments from a river-dominated inner  
261 shelf.

262

### 263 **3. Results**

#### 264 *3.1. Sedimentary features*

265 Station 1 (depth 39 m) is characterized by a 5 cm-thick surface layer made of very fine sand  
266 ( $D_{50} > 75\ \mu\text{m}$ ) (Fig. 2). Beneath this layer, dark grey sediments are made of highly compacted  
267 and sticky mud ( $D_{50} \sim 10\ \mu\text{m}$ ) within which some dense-material laminae are visible. Station  
268 2 (depth 47 m) is characterized by a clay-silt facies ( $D_{50}$  ranging between 15–25  $\mu\text{m}$ )  
269 throughout the sampled section. Horizontal, vertical and oblique biological structures (i.e.  
270 burrows) are abundant all along the core (Fig. 2). Station 7 (depth 50 m) constitutes a 4 cm-  
271 thick subsurface layer made of sandy silt ( $D_{50}$  reaching 50  $\mu\text{m}$ ) between 7–11 cm depth.  
272 Above and below this layer are sediments composed of fine particles ( $D_{50} < 27\ \mu\text{m}$ ).  
273 Millimetric laminae are visible between 20 and 30 cm depth (Fig. 2). Station 9 (54 m) is

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

279

### 280 3.2. Foraminiferal faunas ( $>150 \mu\text{m}$ )

#### 281 3.2.1 Diversity Indices

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

289

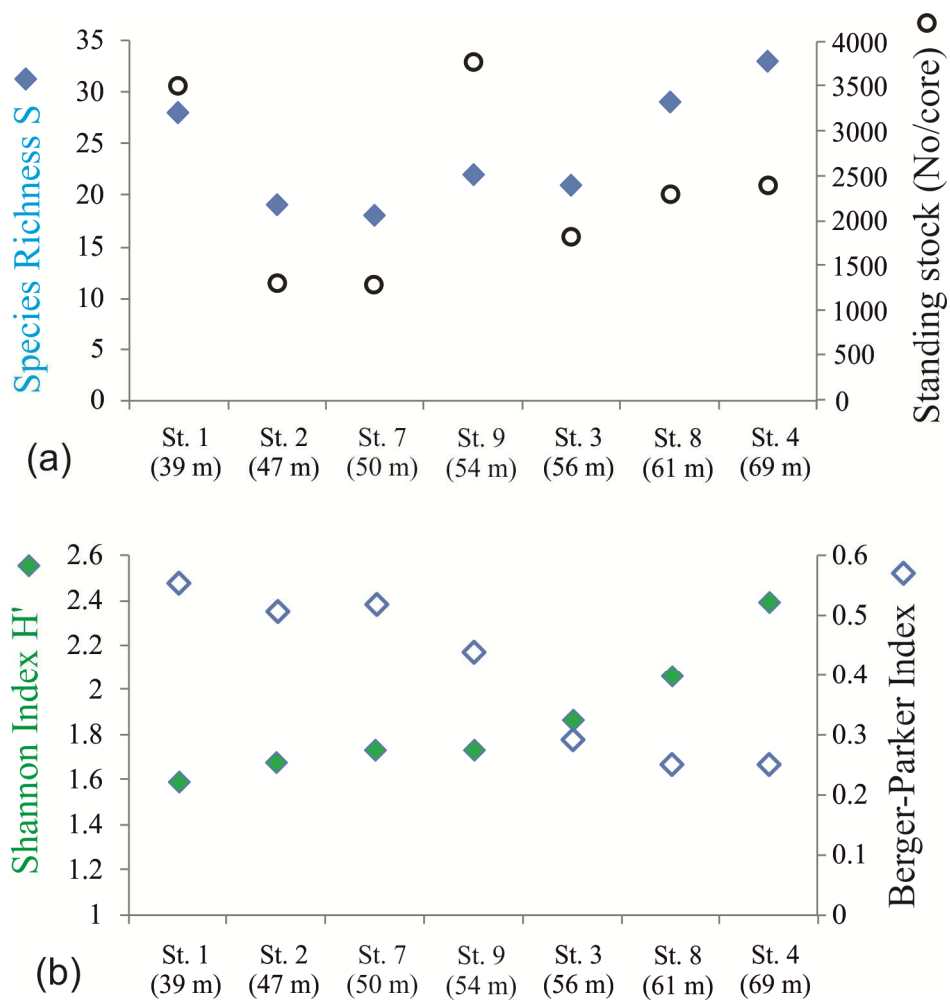
#### 290 3.2.2 Foraminiferal Composition and Microhabitat

291 As a general trend, the relative abundance of rotaliid species in the total living fauna increases  
292 with water depth, from 25% of the total fauna at Station 1 (39 m) to 64% at Station 8 (60 m).  
293 Conversely, the relative abundance of textulariid taxa is relatively high at Stations 1, 2 and 7  
294 ( $< 50$  m) (% of the total fauna ranging between 60–70%) and reaches lower values at stations  
295 3, 8 and 4 ( $< 56$  m) (% ranging between 35–40%). Miliolids are only abundant at Station 1  
296 (12% of the total fauna). At Station 1 (39 m), *Eggerelloides scaber* (55% of the total fauna;  
297 Fig. 3[1]) is the dominant species (Fig. 5a). It presents an erratic down-core vertical  
298 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

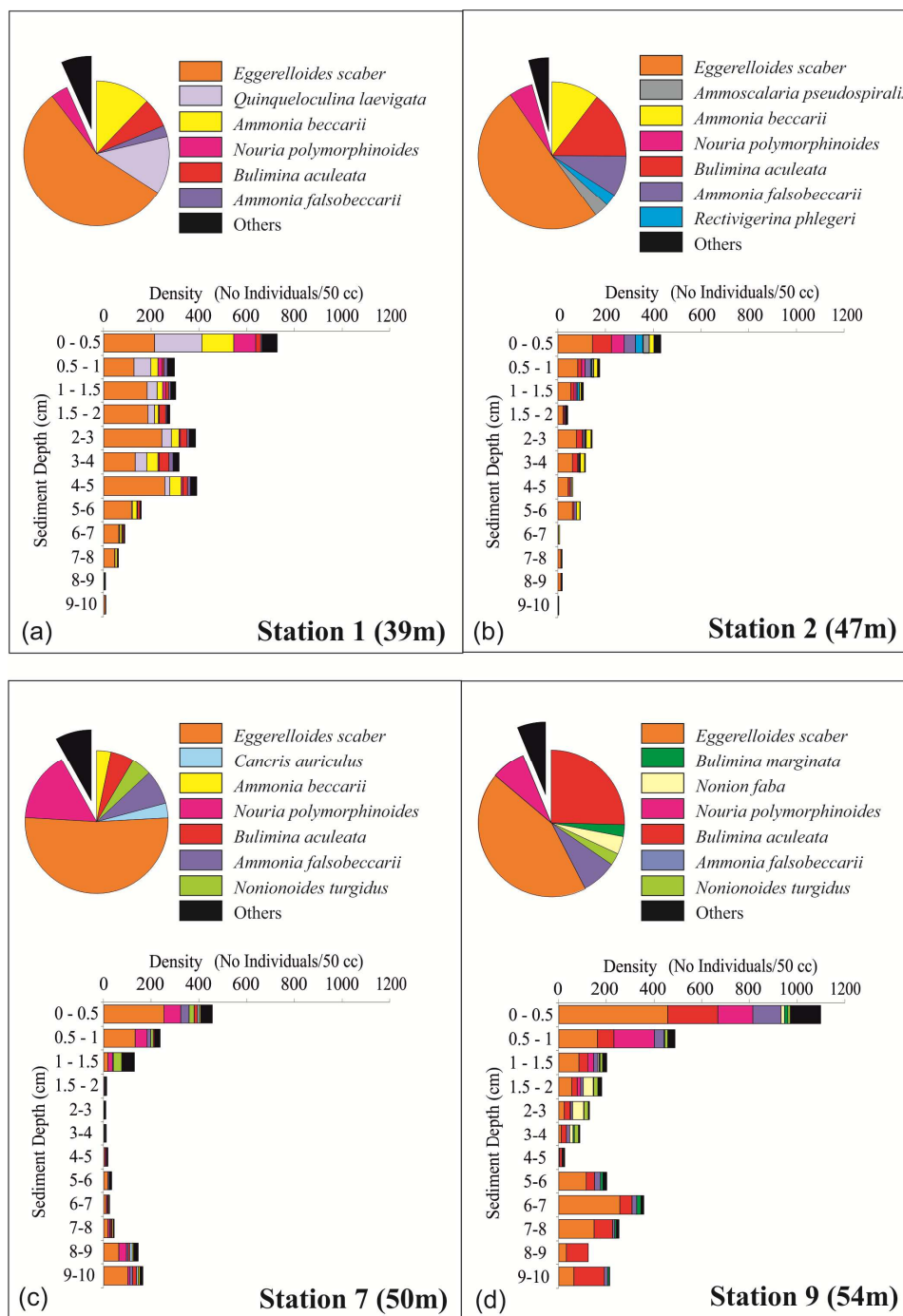


324 uppermost two centimeters of the sediment (Fig. 5e). *Bulimina aculeata* (23% of the total  
325 fauna), *A. falsobeccarii* (21% of the total fauna) and *Bulimina marginata* (11% of the total  
326 fauna) (Fig.3[15]) present erratic vertical distributions with density maxima recorded in the  
327 0–0.5-cm interval. *Nouria polymorphinoides* (7% of the total fauna) preferentially occupies  
328 the 0–0.5-cm interval. At Station 8 (61 m), *E. scaber* (25% of the total fauna) comprises an  
329 erratic vertical distribution with a density maximum in the 2–3 cm interval (Fig. 5f). *Bulimina*  
330 *aculeata* (21% of the total fauna) has a plurimodal distribution with maxima recorded in the  
331 0–0.5 cm, 4–3 cm and 6–7 cm intervals. *Ammonia falsobeccarii* (20% of the total fauna) has  
332 two maxima in the 0–0.5 cm and 1.5–3 cm intervals. *Nonion faba* (11% of the total fauna) is  
333 most abundant between 1–3 cm. *Nouria polymorphinoides* (7% of the total fauna) and *B.*  
334 *marginata* (7% of the total fauna) are characterised by density maxima recorded in the  
335 uppermost centimeter of sediment. At Station 4 (69 m), *E. scaber* (25% of the total fauna) is  
336 still the dominant taxon presenting a plurimodal vertical distribution (Fig. 5g). *Ammonia*  
337 *falsobeccarii* (15% of the total fauna) is most abundant in the uppermost centimeter of  
338 sediment. *Nouria polymorphinoides* (13% of the total fauna) occupies the uppermost 2 cm of  
339 the sediment. *Nonion faba* (11% of the total fauna) is most abundant between 2–4 cm. It is  
340 worthy to note the occurrence of *Rectuvigerina phlegeri* (6% of the total fauna) (Fig.3[11])  
341 and *Paracassidulina neocarinata* (4%) in the uppermost half centimeter of the sediment.



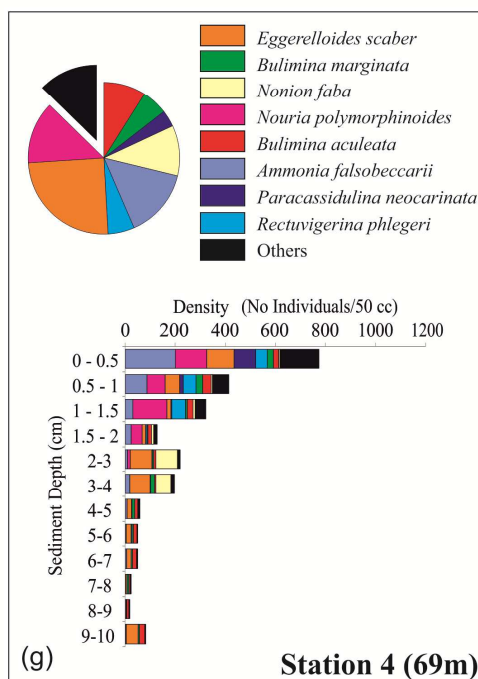
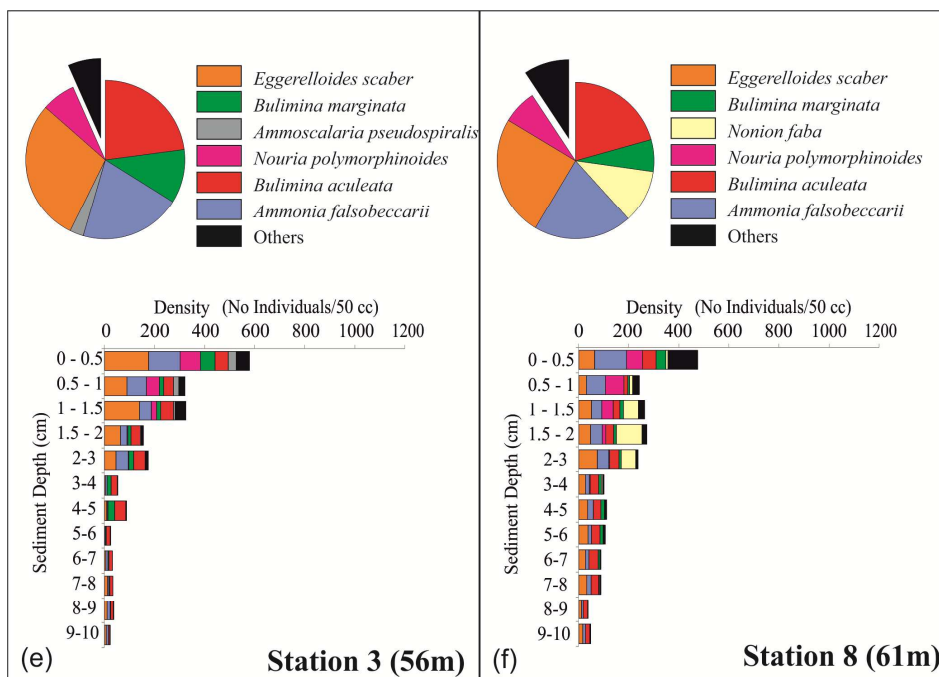
342

343 *Figure 4. (a-b) Ecological indices describing foraminiferal faunas at the seven stations from*344 *the WGMP. (a) Species Richness ( $S$ ) and foraminiferal standing stocks (no. individuals/core);*345 *(b) Shannon ( $H'$ ) and Berger-Parker indices.*



346

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.*



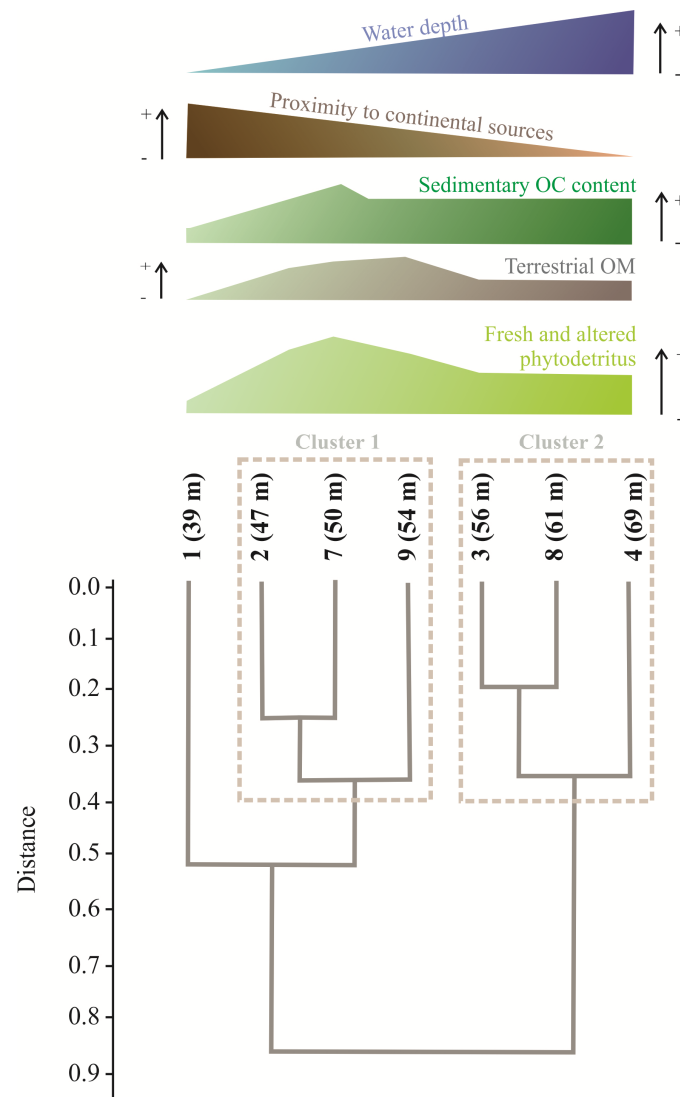
353

354 *Figure 5. (a-g) Foraminiferal composition and down-core distribution of live benthic*355 *foraminifera in the seven cores gathered in the WGMP. Pie charts represent the composition*356 *of live benthic foraminiferal faunas (composition in % of total fauna). The number of*357 *individuals belonging to the >150  $\mu\text{m}$ -size fraction found in each level is standardized for a*358 *50  $\text{cm}^3$  sediment volume. In both pie charts and core distribution, only taxa with relative*359 *abundances >2.5% are pictured.*

## 360 3.2.3 Q-mode clustering and Indicative Values (IV)

361 Based on faunal content, Q-mode cluster analysis of the seven stations reveals two groups of  
362 three stations and one isolated site (Fig. 6). The calculation of Indicative Values (IV) for the  
363 13 major species of our study area shows a marked spatial variability for some taxa as well as  
364 species common to certain areas (Table 3). Station 1 (39 m), which is isolated by cluster  
365 analysis, is characterized by *Q. laevigata* (IV = 84%), *A. beccarii* (IV = 69%), and *E. scaber*  
366 (IV = 42%). Cluster 1 consisting of Stations 2, 7 and 9 (water depth comprised between 47–  
367 54 m), is characterized by *N. turgidus* (IV = 77%), *Canceris auriculus* (IV = 46%), *N.*  
368 *polymorphinoides* (IV = 43%). Cluster 2 includes Stations 3, 8 and 4 (all deeper than 56 m)  
369 and is characterized by *P. neocarinata* (IV = 98%), *N. faba* (IV = 80%), *B. marginata* (IV =  
370 79%), *A. falsobeccarii* (IV = 63%), *Ammoscalaria pseudospiralis* (IV = 48%), *B. aculeata*  
371 (IV = 45%) and *R. phlegeri* (IV = 44%). Permutation test based on 999 iterations reveals that  
372 *N. turgidus* can be considered as a robust indicator (p-value < 0.05) for Cluster 1 whereas *N.*  
373 *faba*, *B. marginata* and *A. falsobeccarii* are significantly indicative of Cluster 2.

374



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

381

382 *Table 3. Indicator values (IndVal – IV in %) of the major station species of the groups defined*  
383 *by Q-mode cluster analysis. Indicator values are calculated according to Dufrêne and*  
384 *Legendre (1997) (see Material and Methods). For each species, IV are indicated by red*  
385 *shading, and the maximum IV by bold numbers. Underlined IV are significant with a p-value*  
386 *< 0.05.*

387

#### 388 **4. Discussion**

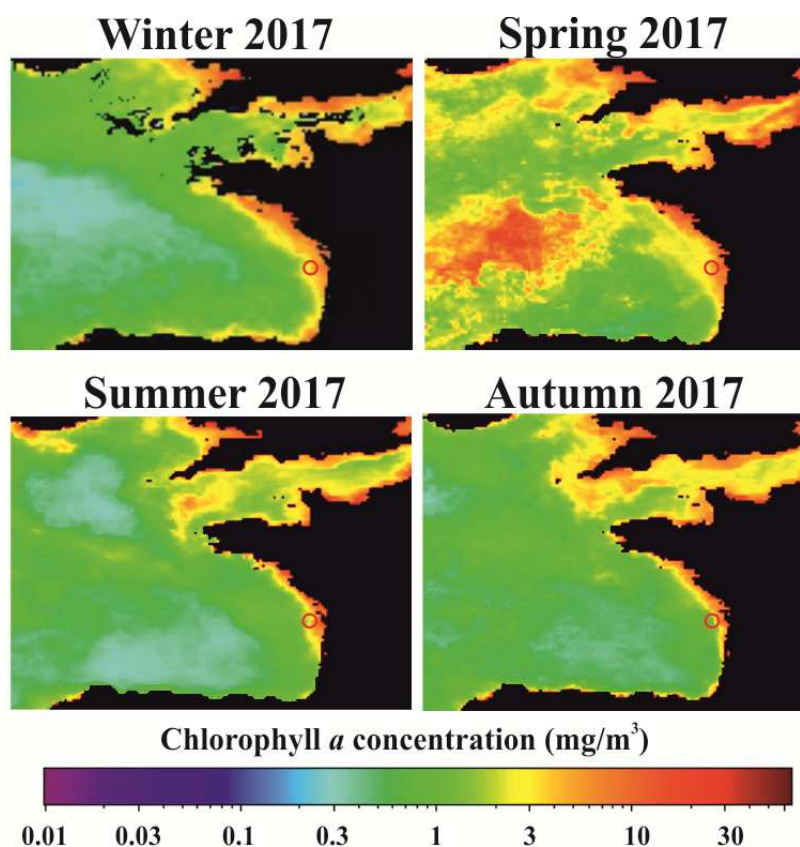
##### 389 *4.1. Environmental features of the West-Gironde Mud Patch in August 2017*

390 Sedimentological studies carried out over the last three decades on the WGMP have shown  
391 that this seafloor feature is difficult to isolate, define and categorise (e.g., Lesueur et al., 1991;  
392 1996; 2002; Cirac et al., 2016) (Fig. 1). The boundaries between the muddy WGMP facies  
393 (silt-clay) and the sands of the surrounding Aquitaine Shelf are hard to define as episodic  
394 inputs of suspended matter from the Gironde River associated with storm-induced bottom  
395 currents cause these facies to migrate several hundred metres from their source (Cirac et al.,  
396 2000; Lesueur et al., 2002). Figure 2 shows that Stations 1 and 7, located at the edge of the  
397 WGMP (presumably within the zone of shifting boundaries), present complex sedimentary  
398 facies where sandy layers are intercalated in finer sediments. Such sedimentary patterns were  
399 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



425 River estuary. Other studies have also briefly described the seasonal evolution of primary  
426 production in the Bay of Biscay using satellite images (SeaWiFS/NASA data) to interpret  
427 chlorophyll-*a* pigment concentration in surface waters (Lampert et al., 2002; Fontanier et al.,  
428 2003; Duchemin et al., 2008). Both offshore and on the shelf, diatoms and coccolithophores  
429 bloom during the boreal spring (April–May) (Lampert, 2001; Fontanier et al., 2003;  
430 Duchemin et al., 2008) (Fig. 8). Thereafter, autotrophic marine dinoflagellates and  
431 cyanobacteria form a Deep Chlorophyll Maximum during the summer stratification of surface  
432 waters (Lampert, 2001). Phototrophic productivity in the coastal zone close to the Gironde  
433 estuary is particularly intense (Lampert, 2001). Therefore, the export of marine phytodetritus  
434 between spring and late summer due to the phytoplankton bloom may explain the relatively  
435 high content of both degraded and fresh chlorophyll *a* (i.e., phytodetritus) in the surface  
436 sediments of our study area, especially in the central and distal areas of the WGMP (Stations  
437 2, 9, 7, 3, 4 and 8) where hydrodynamic energy remodelling the sea floor is weaker compared  
438 to sandy Station 1 (Table 1). The presence of fresh chlorophyll *b* pigment ([Chl-*b*] >0.10  
439  $\mu\text{g/g}$ ), which originates from land plants, demonstrates that terrestrial organic compounds  
440 have recently accumulated in the mud patch. This continental imprint is relatively well  
441 marked in the central WGMP (Stations 2, 9 and 7; [Chl-*b*] >0.10 $\mu\text{g/g}$ ) (Table 2).



442

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

447

#### 448 4.2. Benthic foraminifera biofacies and environmental implications

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

456 organic carbon, foraminiferal diversity (i.e. Shannon index and simple diversity) increases  
457 and the cumulative contribution of *E. scaber*, *A. beccarii* and *Q. laevigata* decreases strongly  
458 with increasing water depth. Our observations at Station 1 are in agreement with many  
459 publications where both *E. scaber*, *A. beccarii* and *Quinqueloculina* spp. are described in  
460 inner-shelf, either prodeltaic or estuarine environments, near river mouths (e.g., Barmawidjaja  
461 et al., 1992; Debenay and Redois, 1997; Diz et al., 2006; Diz and Francés, 2008; Goineau et  
462 al, 2011; Mendes et al., 2012; Dessandier et al., 2015; 2016). For instance, Dessandier et al.  
463 (2016) documented a strong contribution of both *E. scaber* and *A. beccarii* at the shallower  
464 sites (< 50 m depth) of a bathymetric transect in front of the Tagus River (Portugal, NE  
465 Atlantic). Like Station 1, those inner-shelf environments were characterized by sandy  
466 sediments ( $Q_{50} > 100 \mu\text{m}$ ) and very low organic carbon content (< 0.05 % DW). Goineau et  
467 al. (2011) similarly described a strong contribution of *E. scaber* (*Eggerella scabra* in their  
468 study), *A. beccarii* (*Ammonia beccarii* f. *beccarii* in their study) and *Quinqueloculina* spp. at  
469 stations sampled in inner-shelf environments from the Gulf of Lions (France, Western  
470 Mediterranean Sea). Those stations were located between 15–37 m depth on a relict prodeltaic  
471 lobe, adjacent to the Grand Rhône River and were subject to high-energy hydrodynamics.  
472 They were characterized by sandy sediments with low organic matter comprised of  
473 continental and degraded compounds (OC content < 1.1 % DW, C:N ratio ranging between  
474 11.5–17.7). It seems that *E. scaber*, *A. beccarii* and *Q. laevigata* thrive preferentially in  
475 shallow-water environments where hydro-sedimentary constraints (i.e., sedimentary  
476 reworking, winnowing and erosion by strong bottom currents) are enhanced. It is noteworthy  
477 that the erratic vertical distribution of *E. scaber* within anoxic sediments of all our stations  
478 underline its capacity to thrive under low oxygenation without any preference for fresh food  
479 (Diz et al., 2006; Langlet et al., 2014). Such patterns have also been documented in laboratory

480 experiments simulating hypoxia and/or organic supply with sediment material sampled in the  
481 Bay of Biscay (Ernst et al., 2005).

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

505 (Duchemin et al., 2008; Goineau et al., 2011). Its relatively deep infaunal microhabitat (> 2  
506 cm depth) in our study area confirms both trophic and metabolic strategies.

507 Cluster 2 groups stations with silt-clay facies located between 56–60 m depth in the distal  
508 section of the WGMP. There, sedimentary organic carbon content is moderate with values  
509 ranging between 1.2–1.4% DW (Table 2). Fresh and degraded phytodetritus are available in a  
510 lesser quantity compared to the central area of the WGMP (Fig. 5e–g). *Paracassidulina*  
511 *neocarinata*, *N. faba*, *B. marginata*, *A. falsobeccarii*, *B. aculeata* and *R. phlegeri* are the  
512 most indicative species of this ‘outer-WGMP’ cluster (Table 3). Those taxa are all commonly  
513 recorded in mid- to outer-shelf environments (e.g., Debenay and Redois, 1997; Fontanier et  
514 al., 2002; Langezaal et al., 2006; Duchemin et al., 2005; 2008; Goineau et al., 2011;  
515 Dessandier et al., 2015; 2016). For example, *N. faba*, *B. marginata* and *P. neocarinata*  
516 dominate the >150 µm-sized faunas sampled between 80–140 m depth in La Grande Vasière  
517 mud belt in the Bay of Biscay (NE Atlantic) (Duchemin et al., 2005; 2008). In Goineau et al.  
518 (2011), *P. neocarinata* (*Cassidulina carinata* in their study), *N. faba* (*Nonion fabum* in their  
519 study), and *R. phlegeri* statistically clustered together and were indicative of benthic  
520 ecosystems located between 44–86 m depth under the influence of the Rhône River plume.  
521 These species thrived in very fine sediments ( $D_{50} \sim 10 \mu\text{m}$ ) with moderate organic carbon  
522 content (OC between ~1.1–1.3% DW). These environmental conditions are close to those  
523 found at the distal end of the WGMP. In Dessandier et al. (2016), *P. neocarinata* (*Cassidulina*  
524 *carinata* in their study), *R. phlegeri* and *N. faba* (*Nonion scaphum* in their study) were  
525 documented between 50–100 m depth in mid- and outer-shelf environments characterized by  
526 silt to fine-sand facies supporting moderate quantities of organic compounds. In all studies  
527 comparable to our study area, *P. neocarinata* and *R. phlegeri*, present a shallow infaunal  
528 microhabitat typical of species feeding preferentially on labile organic compounds available  
529 in the most oxygenated sediments. *Paracassidulina neocarinata* behave as an opportunistic

530 species relying on freshly deposited phytodetritus produced during spring to early summer  
531 blooms (Fontanier et al., 2003; Duchemin et al., 2008). In our study area, *N. faba* inhabits an  
532 intermediate infaunal distribution traversing the dysoxic and the anoxic sediments (Fig. 5f–g).  
533 This pattern agrees with all other publications where this outer-shelf species is documented  
534 (e.g., Fontanier et al., 2002, Langezaal et al., 2006; Goineau et al., 2011; Dessandier et al.,  
535 2016). Though *N. faba*'s putative abilities such as denitrifying metabolism or endosymbiosis  
536 with procaryotes are still debated. In subsurface sediment layers, *N. faba* can rely on fresh or  
537 degraded organic compounds actively buried in deeper sediments (Fontanier et al., 2002;  
538 Duchemin et al., 2008). Alternatively, this species may migrate toward the sediment surface  
539 to gather fresher phytodetritus (Langezaal et al., 2006).

540

#### 541 *4.3. An ecological continuum through the muddy environments of the Bay of Biscay*

542 Our investigation allows us to appreciate the faunal continuum existing in the Bay of  
543 Biscay from the WGMP (40–70 m) (our study area) to the Grande Vasière located between  
544 80–130 m depth on the outer continental shelf (Duchemin et al., 2005; 2008). Although  
545 geographically disconnected (Fig. 1), these two muddy environments have dominant  
546 foraminiferal species that appear clearly organized along a range of correlated environmental  
547 gradients. *Nonion faba*, *B. marginata* and *P. neocarinata*, typical of the deepest part of the  
548 WGMP, are all dominant in the Grande Vasière (Duchemin et al., 2008). These species can be  
549 considered specialists preferentially living in fine sediments from open-ocean environments  
550 and relying on marine phytodetritus derived from median and outer shelf primary production  
551 (i.e., diatoms and coccolithophore blooms in spring). In contrast, other species, although  
552 dominant in the distal WGMP, are absent from the outer continental shelf. This is notable in  
553 regard to *A. falsobeccarii*, *B. aculeata* and *R. phlegeri* which seem restricted to the WGMP  
554 potentially due to trophic preferences (i.e., phytodetritus associated with coastal primary

555 production, terrestrial organic compounds) or a higher competitive ability compared to taxa  
556 living in deeper ecosystems. Other species which are clearly dominant in the proximal part of  
557 the WGMP (*E. scaber*, *Q. laevigata*, *A. beccarii*) are extremely rare or even absent in the  
558 Grande Vasière (Duchemin et al., 2008). As explained previously, these species are  
559 considered to be generalists with the ability to proliferate in hydrodynamically-impacted  
560 costal ecosystems where hydro-sedimentary pressure and food availability represent major  
561 ecological constraints. To summarize, our Bay of Biscay study illustrates the utility of using  
562 foraminiferal faunas with muddy environmental preferences to discriminate well-oxygenated  
563 biotopes and how they are variably impacted by spatially disparate hydrodynamics and their  
564 correlated deposition of organic compounds. Due to their propensity to be readily preserved in  
565 the fossil record, the calcareous benthic foraminifera of the WGMP and Grand Vasière could  
566 be successfully used in sedimentary records to rebuild precisely how muddy sedimentary  
567 units developed in the Bay of Biscay during the Late Holocene.

568

## 569 **5. Conclusions**

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

576

577 (1) In the WGMP, foraminiferal simple diversity (S) presents relatively moderate values  
578 ranging between 15–35 taxa. According to Shannon Index  $H'$ , foraminiferal diversity  
579 tends to increase with water depth. The relative contribution of *Eggerelloides scaber*,

580 the dominant foraminiferal species at all stations, decreases with decreased proximity  
581 to the coast and increased depth in the WGMP.

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

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

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

597  
598 Finally, our unique study underlines the foraminiferal continuum existing through the muddy  
599 environments of the Bay of Biscay, between the WGMP and the Grande Vasière.

600

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611

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- 803

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.