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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.**

C. Fontanier, B. Deflandre, S. Rigaud, B. Mamo, N. Dubosq, B. Lamarque, D.
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► **To cite this version:**

C. Fontanier, B. Deflandre, S. Rigaud, B. Mamo, N. Dubosq, et al.. 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.. Continental Shelf Research, 2021, 232, pp.104616. 10.1016/j.csr.2021.104616 . hal-04294644

HAL Id: hal-04294644

<https://hal.science/hal-04294644>

Submitted on 23 Jan 2024

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2 Atlantic): Assessing the reliability of bio-indicators in a complex shelf sedimentary unit.

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 ± 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).

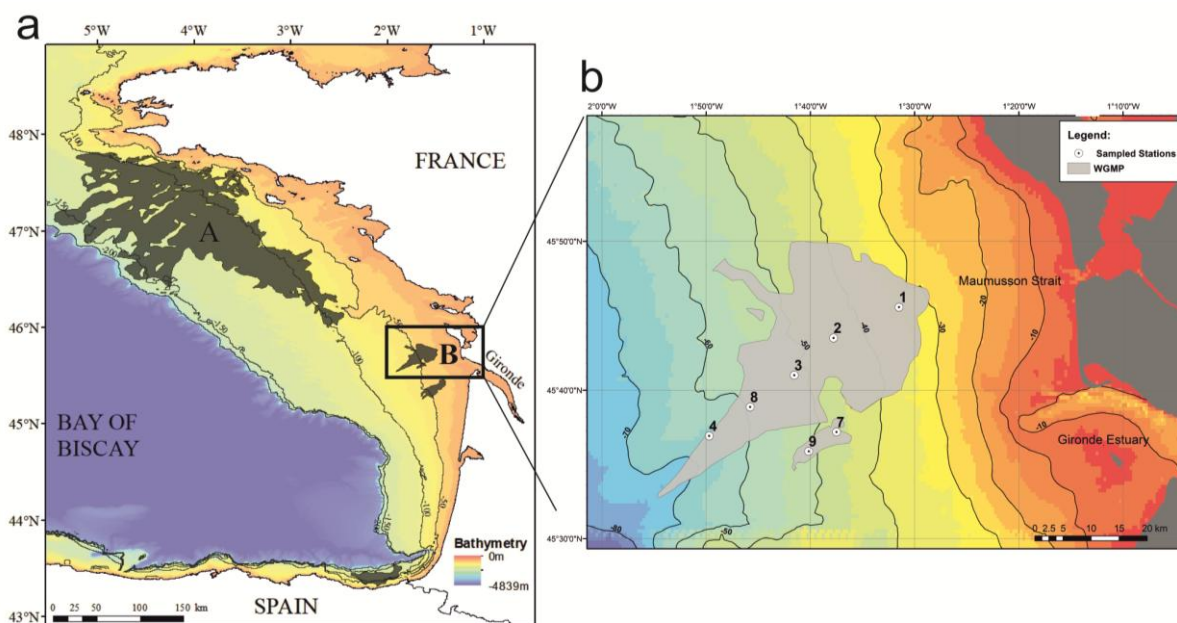
115

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 ₂ (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 μM) 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 cm²) (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 adaptative 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

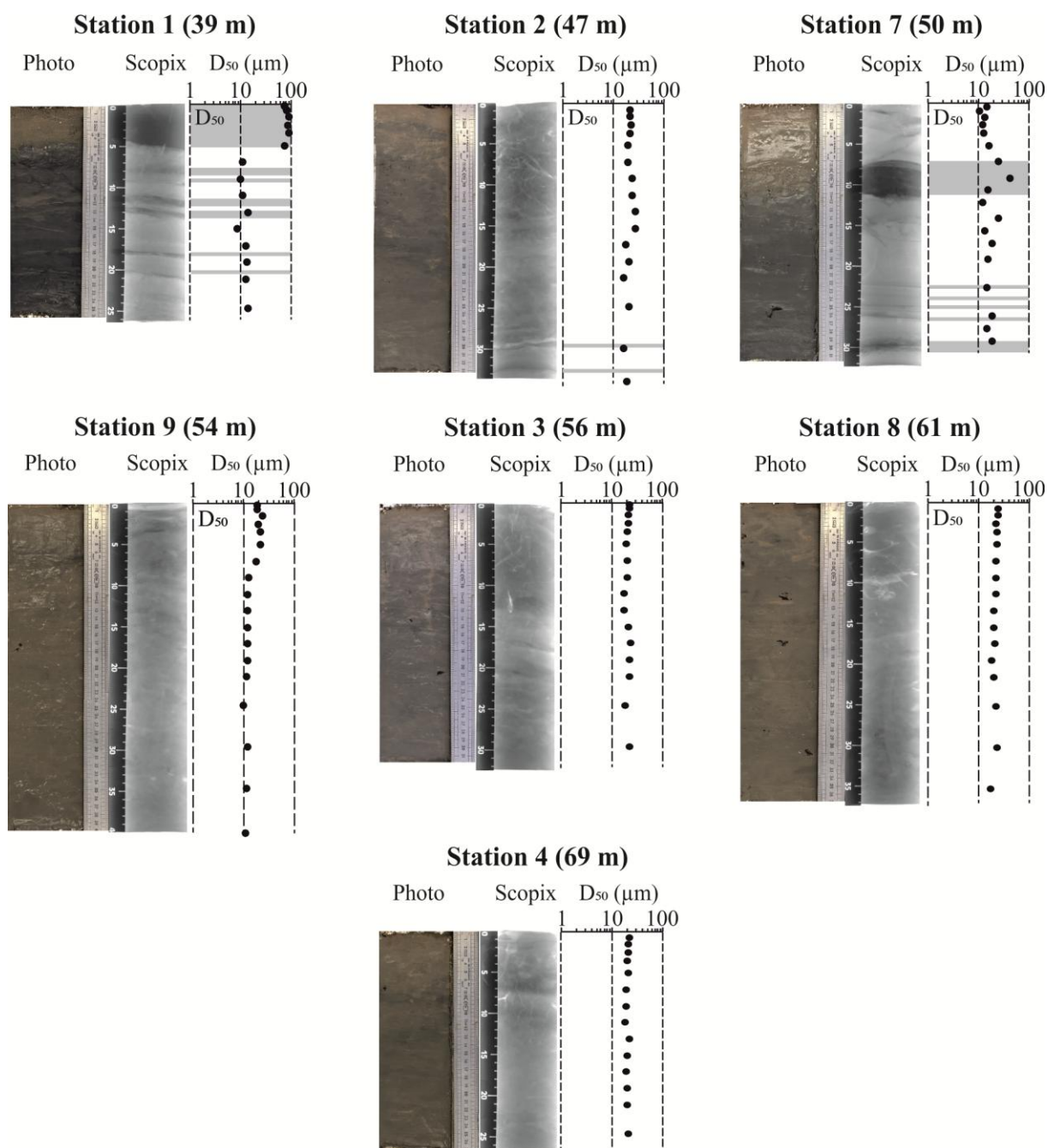
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171 *Table 2. Organic descriptors in the surface sediment (i.e. the 0–0.5 cm interval below the*
 172 *sediment-water interface) at the seven stations sampled during the JERICOBENT-2 cruise*
 173 *(August 2017) (Dubosq et al., in prep): Organic content (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 cm³ 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

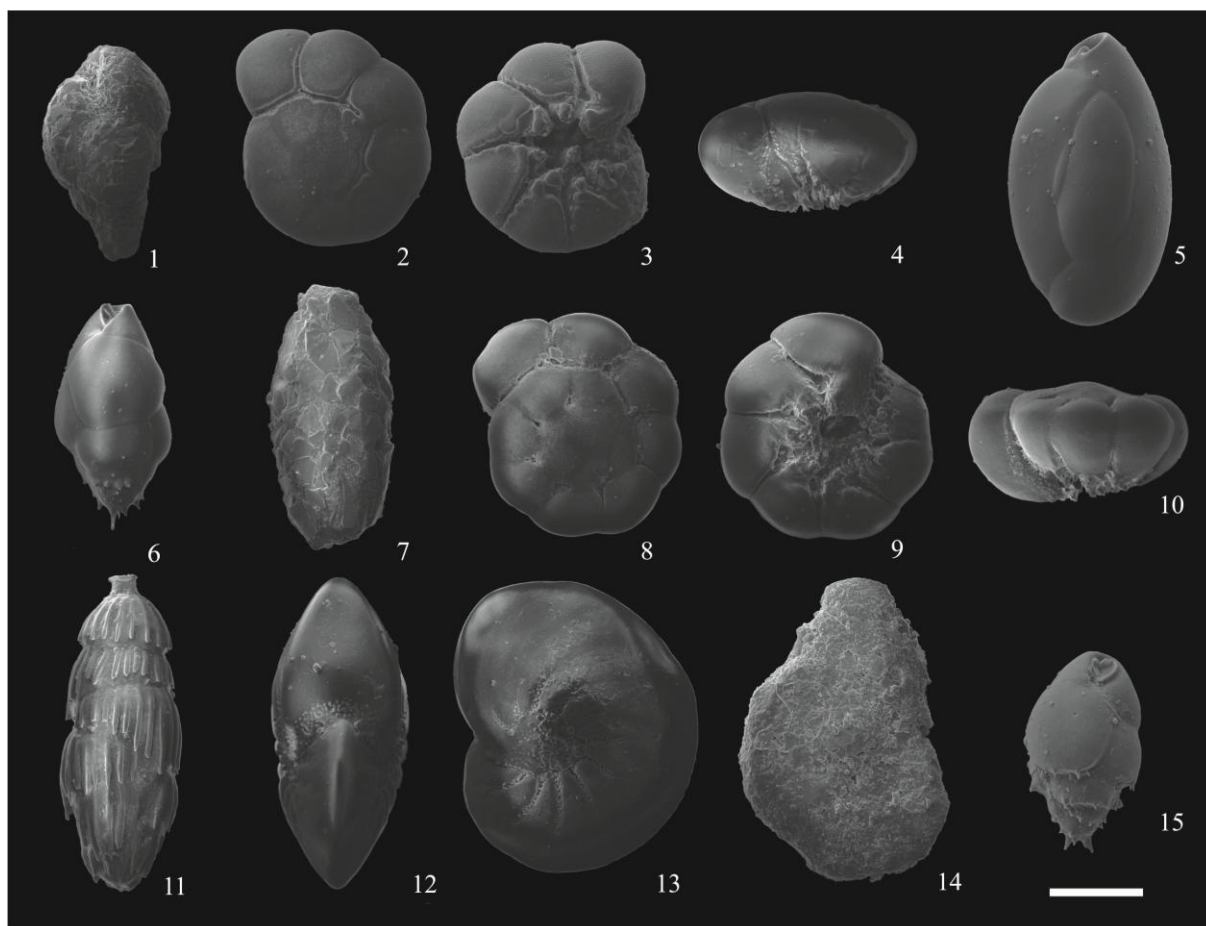
187 All samples were gently shaken for several minutes to obtain a homogeneous mixture. At the
 188 laboratory (one month after the cruise), samples were sieved through 150 μm mesh screens,
 189 and sieve residues were stored in 95% ethanol. Stained foraminifera belonging to the >150
 190 μm fraction 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
$$P_i = \text{Arc sin}(\sqrt{p_i})$$

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 μ 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 α . $N_{individuals_{(i)}}$ 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 α where the
 231 species i is present. $N_{stations_{(\alpha)}}$ is the total number of sites in the cluster α . 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- μ 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 μ 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 μm)
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 μm) 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 μm). 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 μm). 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.

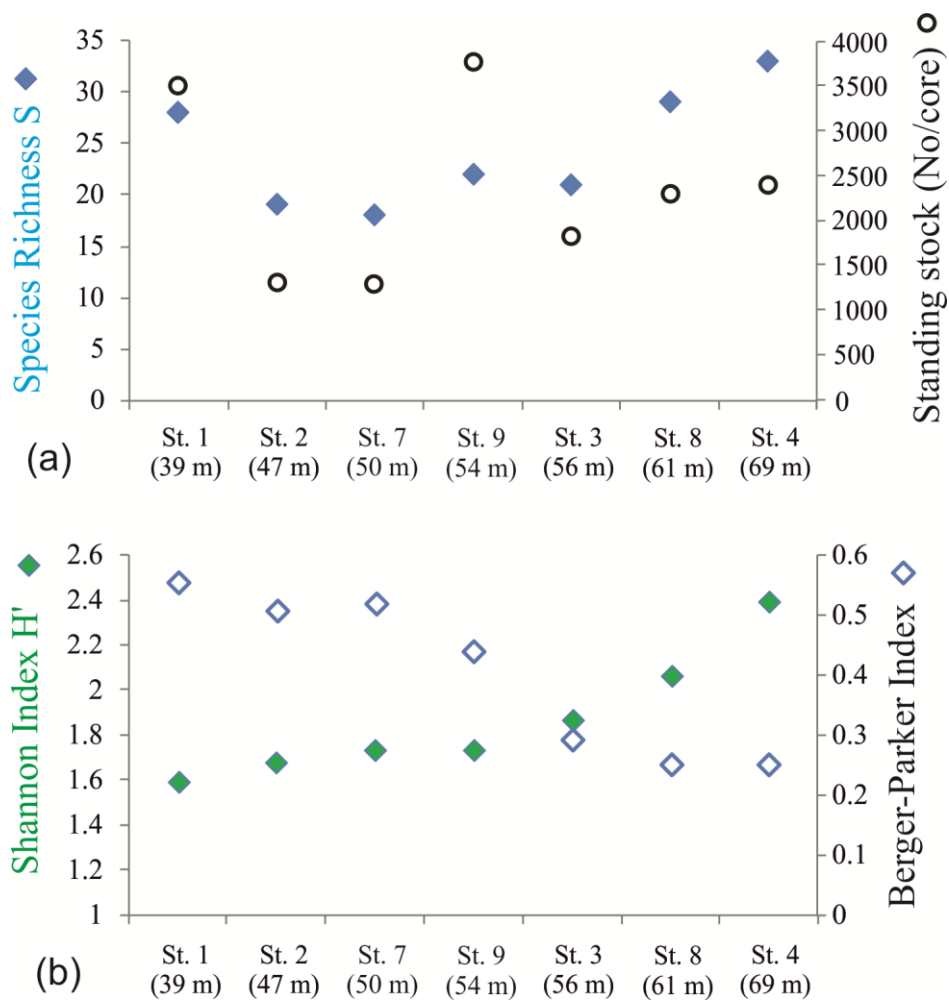
289

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

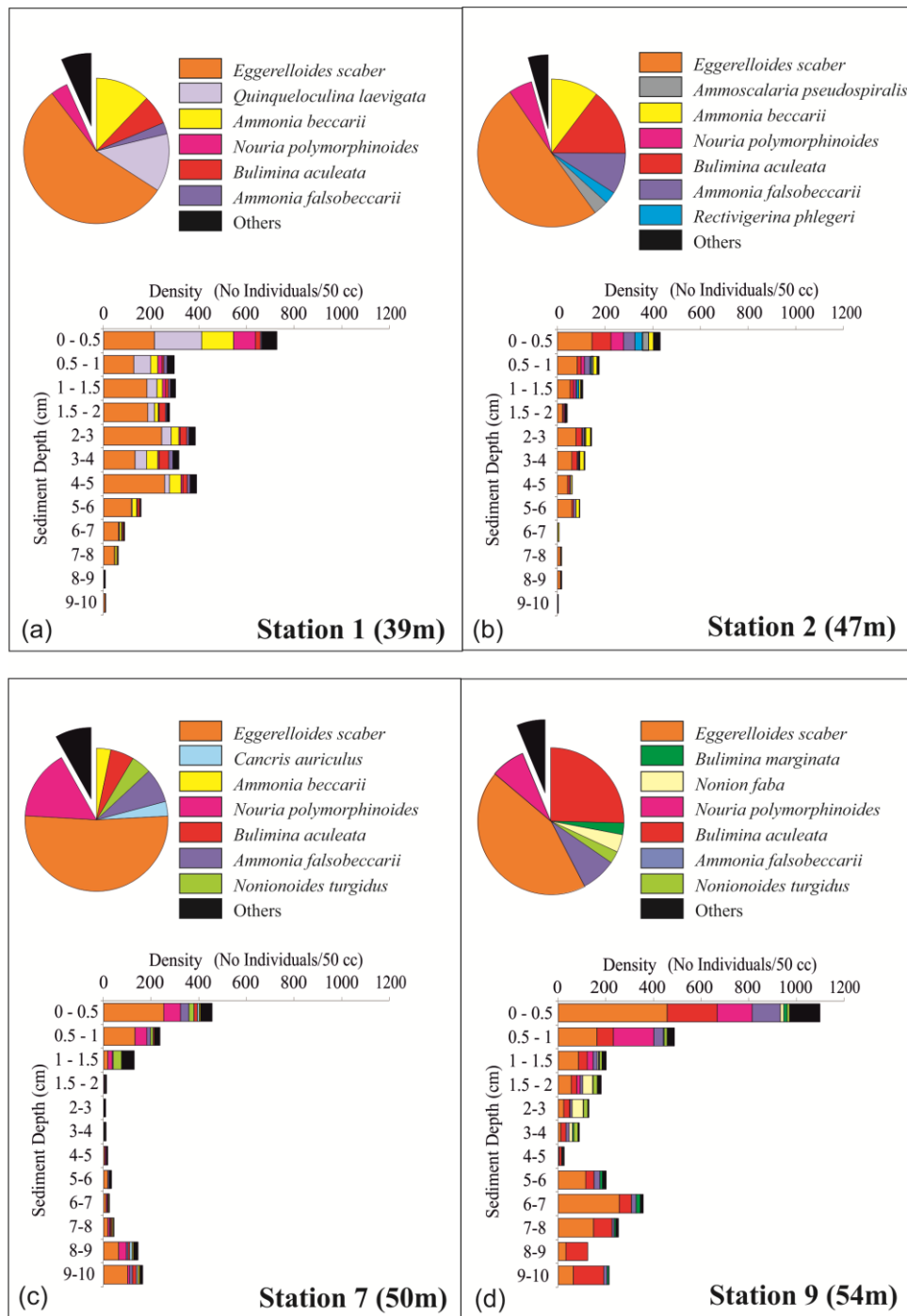
299 fauna; Fig. 3[5]) and *Ammonia beccarii* (12% of the total fauna; Fig. 3[2–4]) are two other
300 major calcareous species. Their abundances are greatest within the uppermost 0.5 cm of the
301 sediment column. *Bulimina aculeata* (7% of the total fauna; Fig. 3[6]), a calcareous species,
302 presents 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.



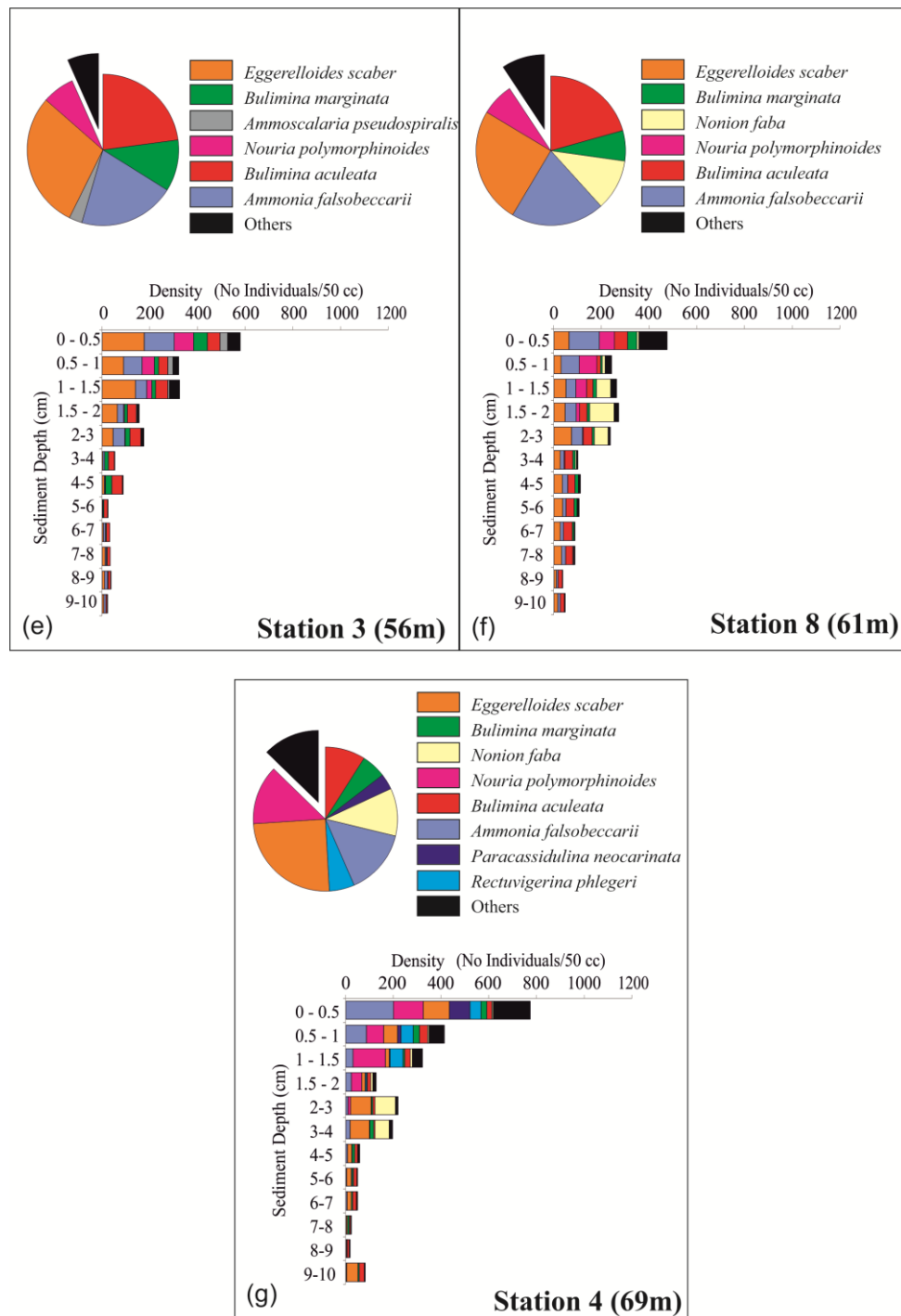
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343 *Figure 4. (a-b) Ecological indices describing foraminiferal faunas at the seven stations from*344 *the WGMP. (a) Species Richness (S) and foraminiferal standing stocks (no. individuals/core);*345 *(b) Shannon (H') and Berger-Parker indices.*



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 μm -size fraction found in each level is standardized for a*
 351 *50 cm³ sediment volume. In both pie charts and core distribution, only taxa with relative*
 352 *abundances >2.5% are pictured.*



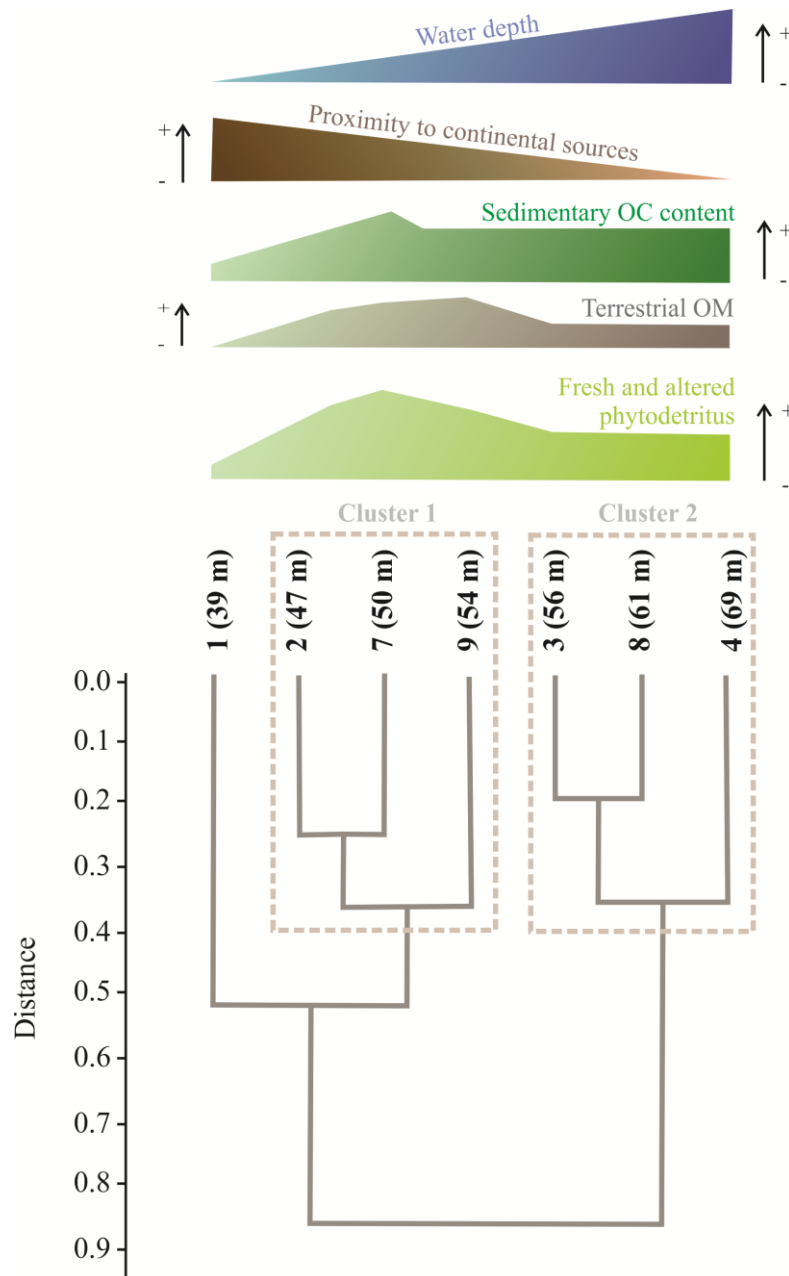
353

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 356 *of live benthic foraminiferal faunas (composition in % of total fauna). The number of*
 357 *individuals belonging to the >150 μ m-size fraction found in each level is standardized for a*
 358 *50 cm³ 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>	69	29	2
<i>Ammonia falsobeccarii</i>	9	28	<u>63</u>
<i>Bulimina aculeata</i>	17	39	45
<i>Bulimina marginata</i>	5	16	<u>79</u>
<i>Cancris auriculus</i>	17	46	37
<i>Nonion faba</i>	1	18	<u>80</u>
<i>Nonionoides turgidus</i>	3	<u>77</u>	21
<i>Paracassidulina neocarinata</i>	0	6	98
<i>Rectuvigerina phlegeri</i>	23	32	44
<i>Quinqueloculina laevigata</i>	84	5	11
<i>Ammoscalaria pseudospiralis</i>	7	44	48
<i>Eggerelloides scaber</i>	42	37	20
<i>Nouria polymorphinoides</i>	17	43	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

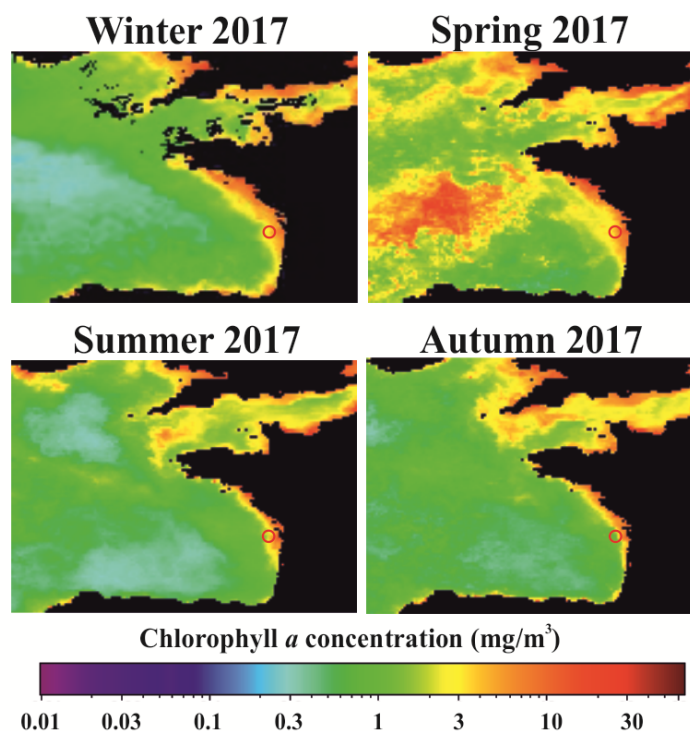
388 **4. Discussion**

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⁻¹ (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

601 **Acknowledgement**

602 We would like to thank the crews and the captain of the Côte de la Manche (CNRS-INSU)
603 during the JERICOBENT-2 cruise. We have special thoughts for all scientific members who
604 participated to this scientific mission. This work was supported by: (1) the JERICO-NEXT
605 project (European Union's Horizon 2020 Research and Innovation program under grant
606 agreement no. 654410), (2) the VOG project (LEFE-CYBER and EC2CO-PNEC), and (3) the

607 MAGMA project (COTE cluster of Excellence ANR-10-LABX-45). NASA is acknowledged
608 as a source of MODIS Satellite images (<https://modis.gsfc.nasa.gov/>). Finally, we thank both
609 reviewers who have provided very useful comments to improve the overall quality of this
610 paper.

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.