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

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Abstract :

Live (Rose Bengal stained) shelf foraminiferal faunas have been studied at seven stations located along a shore-open ocean transect between 39 and 69-m depth in the West-Gironde Mud Patch (WGMP) (Bay of Biscay, NE Atlantic) to understand how complex environmental conditions (e.g., organic matter, oxygenation, sedimentary facies) control their ecological patterns (i.e., diversity, faunal composition, standing stock, and microhabitats). To do so, the WGMP was sampled in August 2017, at the end of the succession of phytoplankton blooms occurring in spring and summer. This morpho-sedimentary unit is bathed by well-oxygenated bottom waters and characterized by clay-silt facies containing variably degraded phytodetritus and traces of terrestrial organic matter. Oxygen penetration depth within the sediment is less than 7 ± 3 mm, indicating efficient organic matter in-sediment mineralization by aerobic respiration. Foraminiferal richness (S) presents relatively moderate values ranging between 15 and 35 taxa. According to Shannon Index H', foraminiferal diversity tends to increase with water depth. Accordingly, the relative contribution of Eggerelloides scaber, the dominant foraminiferal species at all stations, decreases with increased depth and decreased proximity to the coast. The shallowest station (Station 1, 39 m), closest to the shore, is characterised by E. scaber, Quinqueloculina laevigata and Ammonia beccarii, species typical of inner-shelf environments constrained by high-energy hydrodynamics and river discharge. Surficial sediments at Station 1 constitute of winnowed sands depleted in organic carbon. Towards the centre of the WGMP, where clay-silt facies contain variably degraded marine phytodetritus and terrestrial organic compounds, foraminiferal faunas are characterized by Bulimina aculeata, Ammonia falsobeccarrii, Nouria polymorphinoides and Nonionoides turgidus. Yet E. scaber remains the most dominant taxon. Deeper stations (>55 m depth) located at the distal part of the mud patch are dominated by B. aculeata, A. falsobeccarrii, N. polymorphinoides and E. scaber. Accompanying

these taxa are Bulimina marginata, Rectuvigerina phlegeri, Nonion faba and Paracassidulina neocarinata, which are typical of mid- and outer-shelf ecosystems enriched in sedimentary organic matter.

Highlights

► For the first time, living benthic foraminifera are studied in the WGMP. ► Foraminiferal diversity tends to increase with water depth along the mud patch. ► Hydro-sedimentary processes and food availability control foraminiferal faunas. ► A foraminiferal continuum exists through the WGMP and the Grande Vasière.

1. Introduction

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

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

76 morpho-sedimentary units that spread between 30–70 m water depth, covering the gravels and

77 sands of the Northern Aquitaine continental shelf (Bay of Biscay, France) (Lesueur et al.,

78 1996; 2002; Cirac et al., 2000). These muddy patches extend off the two main channels of the

79 Gironde Estuary, the main source of the fine-grained sediments within the WGMP (Fig. 1)

80 (Lesueur et al., 1996). The WGMP comprises of Gironde River silt deposited during flood

81 events, and a smaller portion of inner continental shelf silts and fine sand deposited during

82 periods of high energy (i.e., storms). Due to the complexity of its spatial structure, temporal

83 dynamics and environmental characteristics, the WGMP has been the subject of intense

84 multidisciplinary investigation for more than ten years (e.g., the BIOMIN project between

85 2009–2013, the VOG project between 2018–2019, the JERICO-NEXT European project with

86 this study). In combination with geochemical, geophysical, sedimentological and biological

87 analyses, these projects have aimed to describe the mineralization processes of organic

88 compounds in the mudflat, taking into account (1) the activity of the benthic organisms

89 thriving there (e. g. bioturbation, aerobic/anaerobic respiration), by (2) integrating the

90 hydrosedimentary dynamics structuring this morpho-sedimentary unit in space and time, and

91 by (3) trying to define in fine, reliable bio-indicators of the mudflat in all its complexity

92 (Lamarque et al., 2021; Dubosq et al., in press; Dubosq et al., in prep.). Benthic foraminifera

93 constitute relevant proxies for studying present and past marine environments since their

94 faunal communities (diversity, standing stock, microhabitat), their spatial distribution and

95 their temporal dynamics are controlled by numerous physico-chemical parameters including

96 exported organic matter flux, bottom- and pore-water oxygenation and sedimentary substrate

97 (e.g., Gooday, 2003; Murray, 2006; Jorissen et al., 2007). The impact of seasonal

98 phytodetritus input and the role of environmental oxygenation on benthic foraminiferal fauna

99 has already been studied in "La Grande Vasière", a mud belt located on the outer continental

100 shelf (between 80–130 m deep) northwest of the WGMP (Duchemin et al., 2005; 2008) (Fig.

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).

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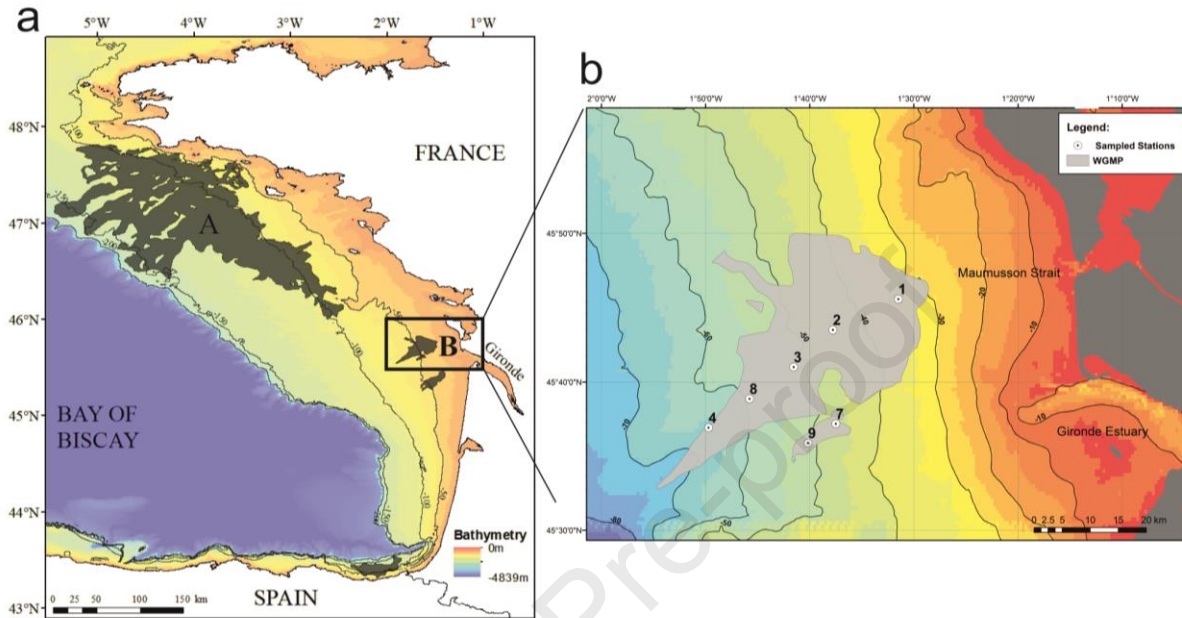
Figure 1. (a) Map of the Bay of Biscay continental shelf with the locations of mud belts and

patches: A - La Grande Vasière Mud Patch and B - The Gironde Mud Patch (b) Map of the

West Gironde Mud Patch showing the location of 7 sampling stations (white dots). The

synoptic map of the WGMP has been determined during the JERICOBENT-5-TH cruise

(Gillet and Deflandre, 2018)

135

Station	Sampling period	Depth (m)	Latitude	Longitude	BWT (°C)	BWS (psu)	BWO₂ (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)

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-*a*	Chl-*b*	Phaeo-*a*	Chl-*a*/(Chl-*a* + Phaeo-*a*)	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

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^3 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).
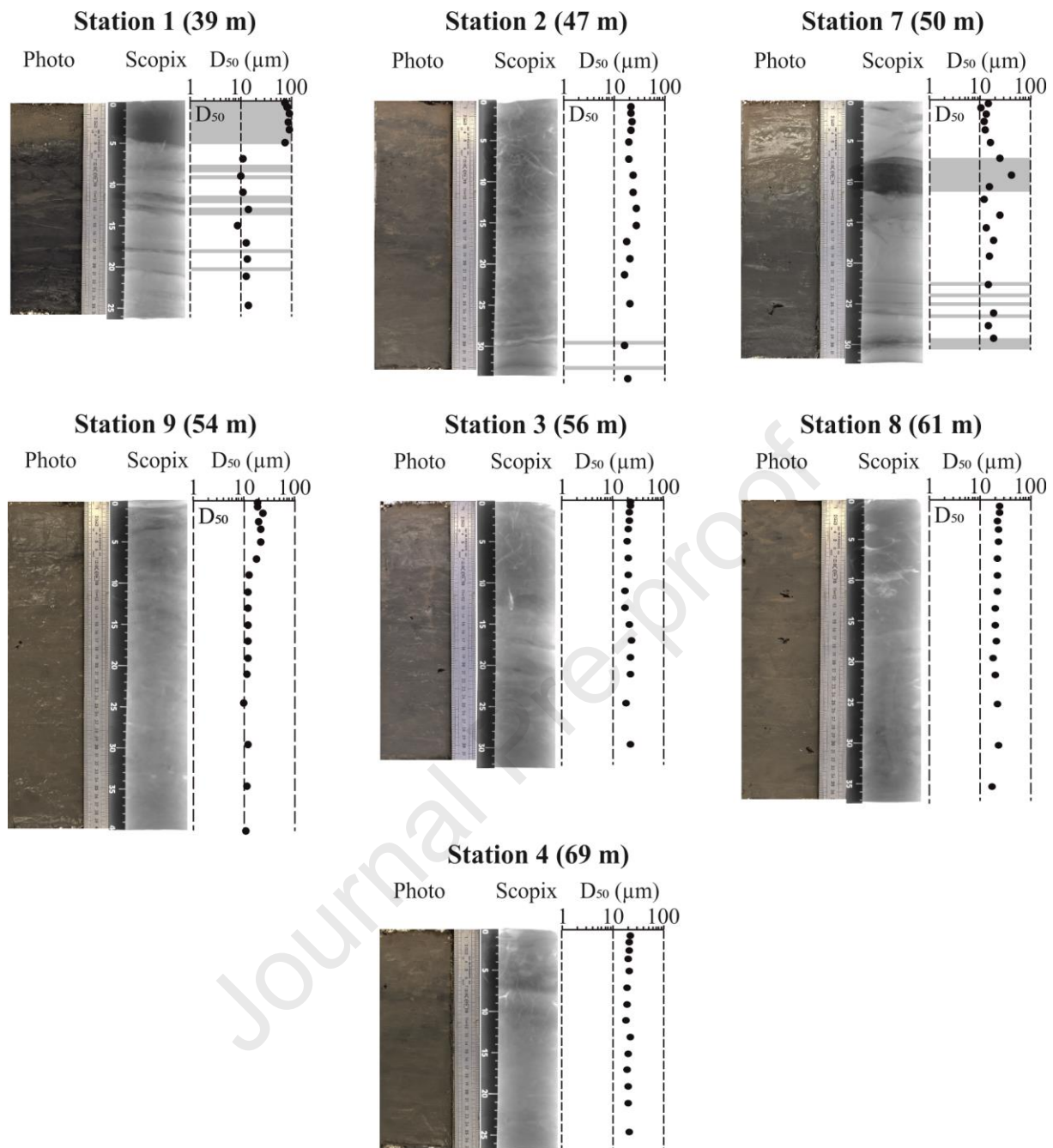
Figure 2. Photograph and X-Ray radiograph (Scopix) of split cores collected at the seven stations from the WGMP with grain size frequency D_{50}.

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

211   in which "p_i" is the relative frequency of the "ith" 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).

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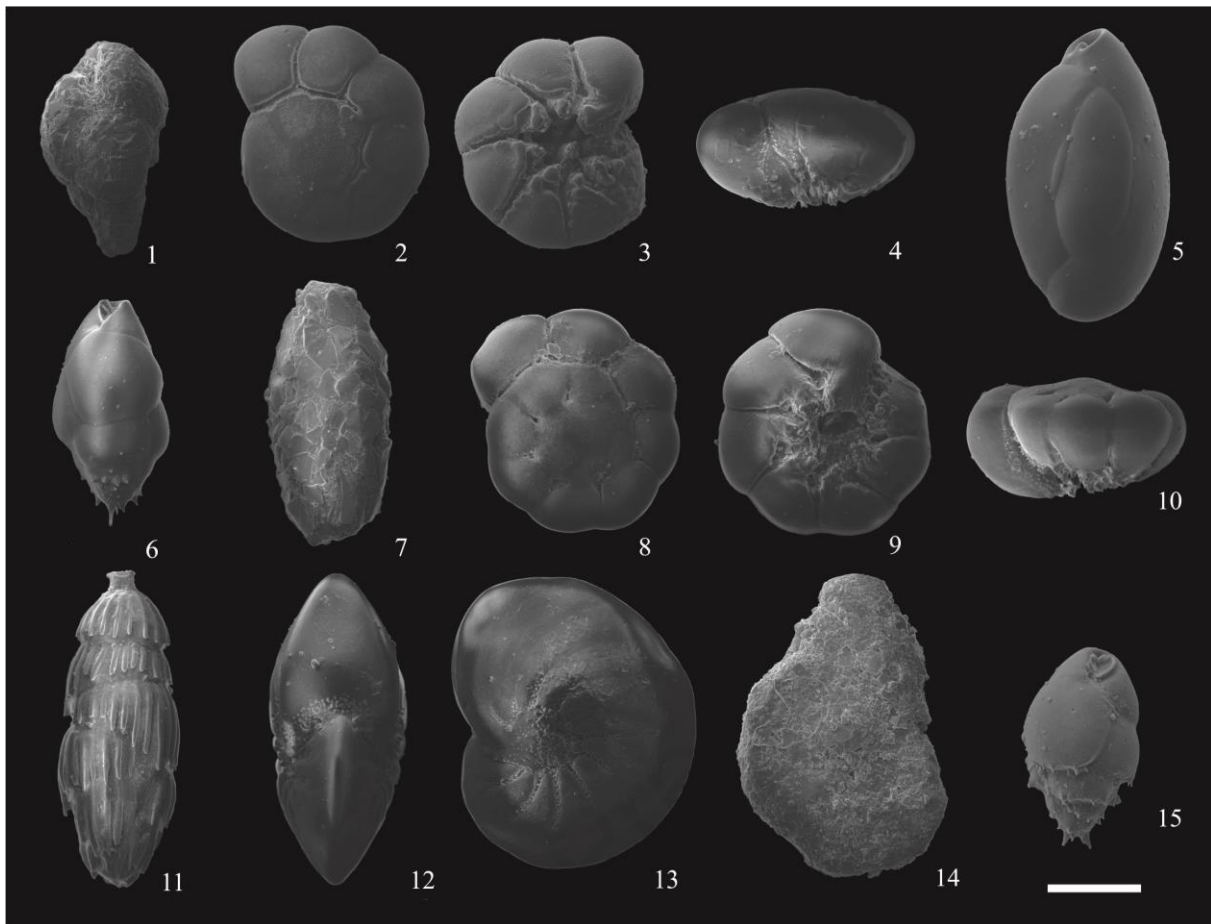
Figure 3. SEM photographs of some major foraminiferal taxa observed in our study area. 1 Eggerelloides scaber; 2, 3, 4 Ammonia beccarii (dorsal, umbilical and lateral views); 5 Quinqueloculina laevigata; 6 Bulimina aculeata; 7 Nouria polymorphinoides; 8, 9, 10 Ammonia falsobeccarii (dorsal, umbilical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

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

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

227

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

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

228 $Nindividuals_{(i,\alpha)}$ is the mean number of individuals belonging to the species i and present in

229 the cluster α. $Nindividuals_{(i)}$ is the sum of the mean numbers of individuals of species i

230 occurring in all clusters. $Nstations_{(i,\alpha)}$ is the number of stations in the cluster α where the

231 species i is present. $Nstations_{(\alpha)}$ 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-µm-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 µm-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 µm-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   ($D_{50} > 75$ µm) (Fig. 2). Beneath this layer, dark grey sediments are made of highly compacted

267   and sticky mud ($D_{50} \sim 10$ µm) 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 ($D_{50} < 27$ µm).

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} ~20 µm) 7 cm thick overlying very fine sediments (D_{50} ~ 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 µm)*

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])

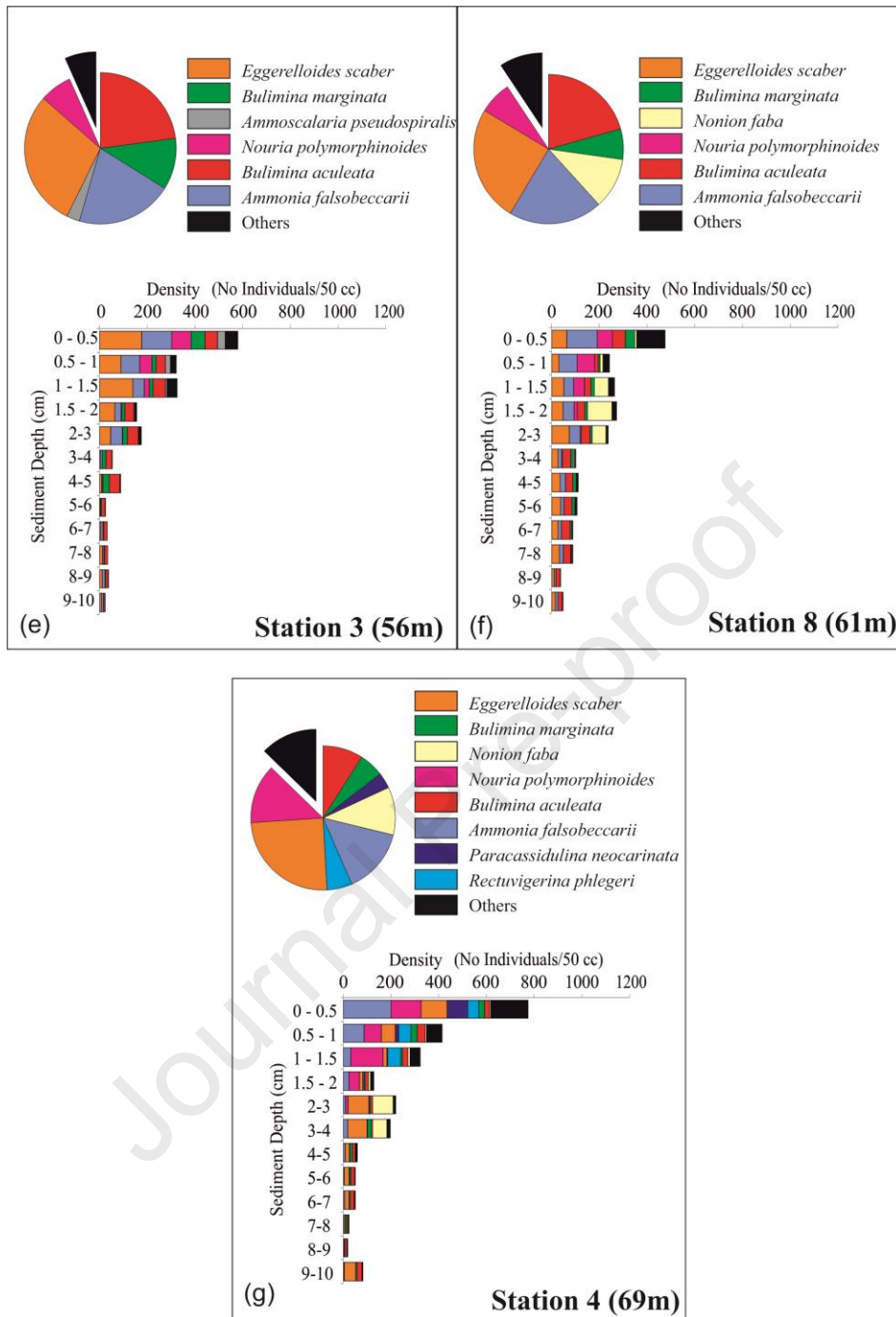341 and *Paracassidulina neocarinata* (4%) in the uppermost half centimeter of the sediment.

342
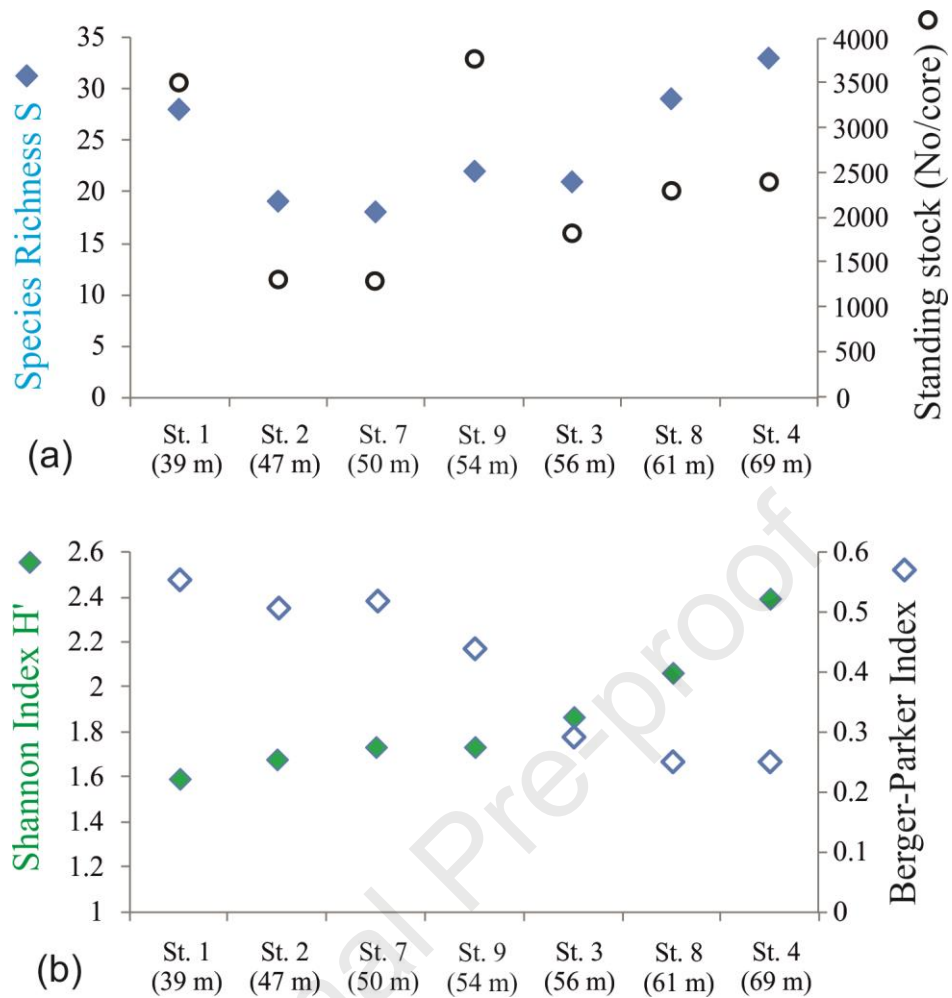
Figure 4. (a-b) Ecological indices describing foraminiferal faunas at the seven stations from

343

the WGMP. (a) Species Richness (S) and foraminiferal standing stocks (no. individuals/core);

344

(b) Shannon (H') and Berger-Parker indices.

345
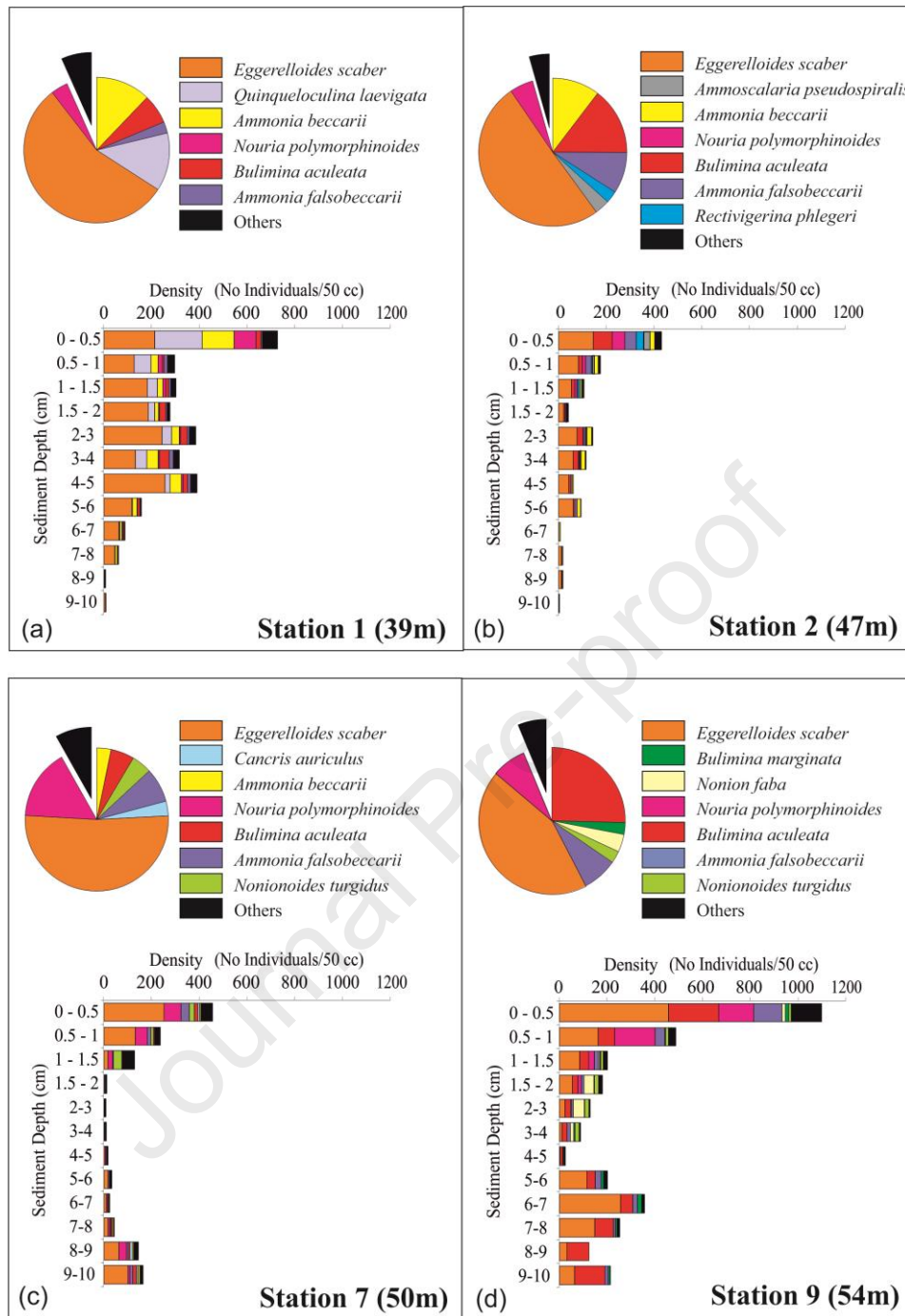
346

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 cm^3 sediment volume. In both pie charts and core distribution, only taxa with relative*

352 *abundances >2.5% are pictured.*

353

Figure 5. (a-g) Foraminiferal composition and down-core distribution of live benthic foraminifera in the seven cores gathered in the WGMP. Pie charts represent the composition of live benthic foraminiferal faunas (composition in % of total fauna). The number of individuals belonging to the >150 µm-size fraction found in each level is standardized for a 50 cm³ sediment volume. In both pie charts and core distribution, only taxa with relative 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%), *Cancris 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
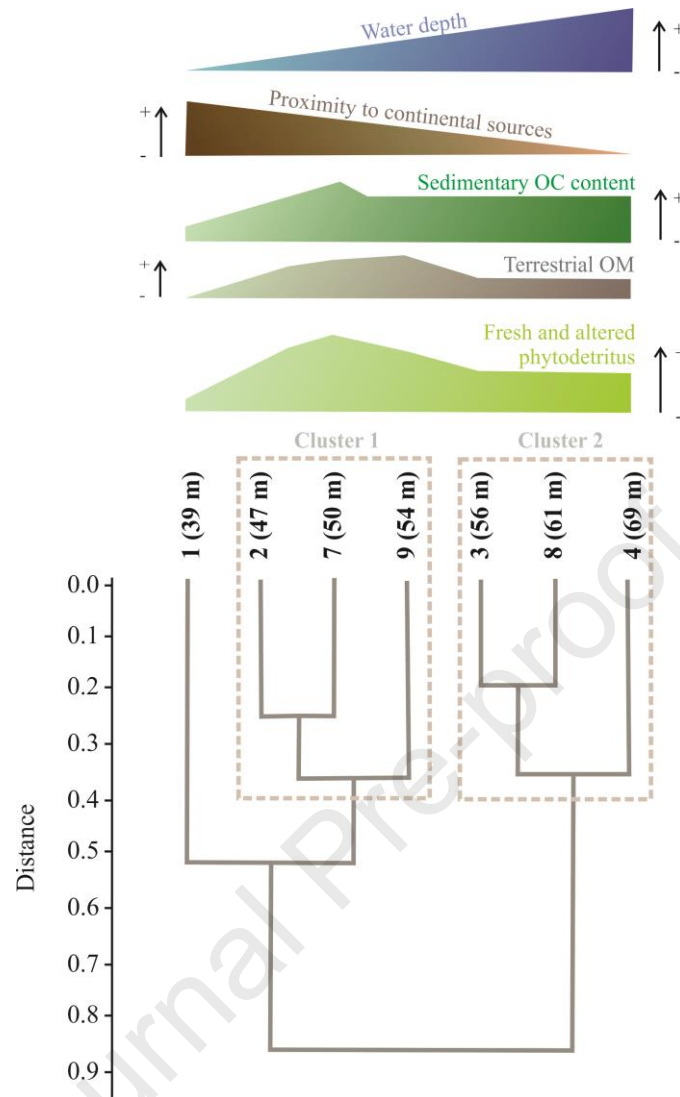
Figure 6. Q-mode cluster analysis of the seven stations following the Ward's method based on transformed percentages Pi of major foraminiferal species (>2.5%). Environmental trends (station water depth, proximity to continental sources, sedimentary organic matter content, terrestrial organic matter, fresh and degraded phytodetritus) are pictured. Dotted boxes correspond to groups identified by Q-mode cluster analysis (Clusters 1 and 2).

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

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

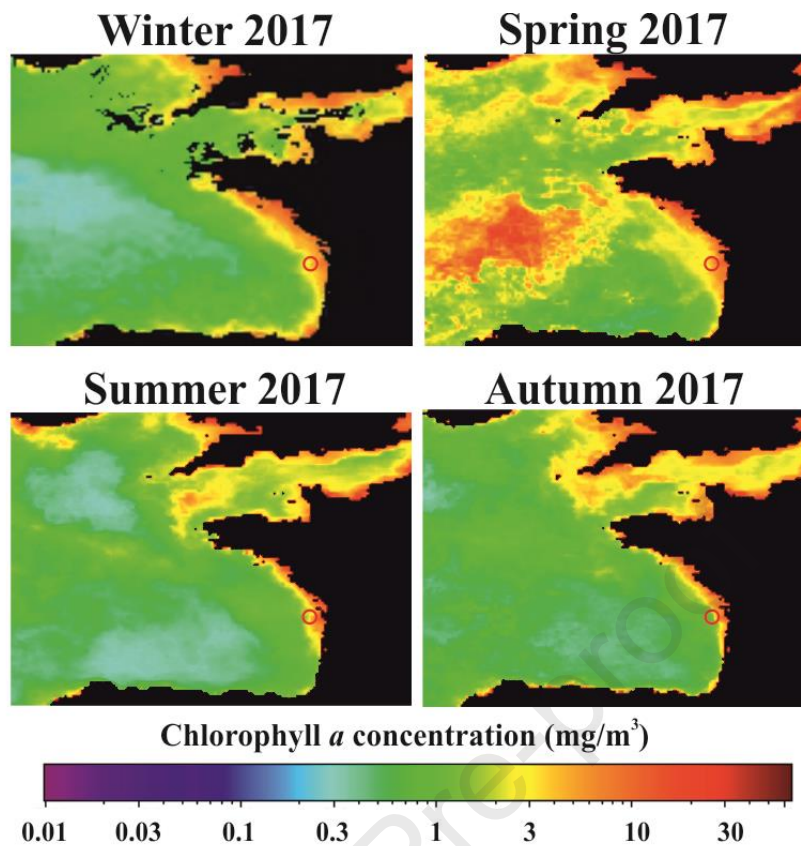## 4. Discussion

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

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

400   JERICOBENT-1 and JERICOBENT-5 cruises (Deflandre, 2016; Gilet and Deflandre, 2018;

401   Lamarque et al., 2021; Dubosq et al., in press). Whereas Station 1 is, due to its coastal

402   proximity, impacted by episodic high-energy hydrodynamics causing low sediment

403   deposition, massive but sporadic sedimentary deposits characterize Station 7 (Dubosq et al.,

404   in press). All other stations from within the WGMP present relatively continuous sediment

405   accumulation with rates ranging between 0.3–0.5 cm yr^{-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   µg/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*] >0.10µg/g) (Table 2).

Winter 2017 · Spring 2017 · Summer 2017 · Autumn 2017

Chlorophyll *a* concentration (mg/m³)

0.01 0.03 0.1 0.3 1 3 10 30

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 µm) 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. falsobeccarrii, 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. falsobeccarrii, 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} ~10 µm) 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. falsobeccarrii, 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 falsobeccarrii, 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. falsobeccarrii* 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

612 **References**

613 Barmawidjaja, D.M., Jorissen, F.J., Puskaric, S. and Van Der Zwaan, G.J., 1992. Microhabitat

614   selection by benthic foraminifera in the northern Adriatic Sea. Journal of

615   Foraminiferal Research. 22(4), 297-317.

616 Barnett, P.R.O., Watson, J. and Connely, D., 1984. A multiple corer for taking virtually

617   undisturbed sample from shelf, bathyal and abyssal sediments. Oceanologica Acta. 7,

618   399-408.

619 Bauer, J.E. and Druffel, E.R.M., 1998. Ocean margins as a significant source of organic

620   matter to the deep open ocean. Nature 392, 482-485.

621 Bernhard, J.M., 2000. Distinguishing live from dead foraminifera: Methods review and proper

622   applications. Micropaleontology 46(1), 38-46.

623 Berthois, L. and Le Calvez, Y., 1959. Deuxième contribution à l'étude de la sédimentation

624   dans le golfe de Gascogne. Revue des Travaux de l'Institut des Pêches Maritimes. vol.

625   23 n° 3: 323-375.

626 Canfield, D.E., Jørgensen, B.B., Fossing, H., Glud, R., Gundersen, J., Ramsing, N.B.,

627   Thamdrup, B., Hansen, J.W., Nielsen, L.P. and Hall P.O.J., 1993. Pathways of organic

628   carbon oxidation in three continental margin sediments. Marine Geology. 113, 27-40.

629   Cirac, P., Berné, S., Castaing, P. and Weber, O., 2000. Processus de mise en place et
630   d'évolution de la couverture sédimentaire superficielle de la plate-forme nord-
631   aquitaine. Oceanologica Acta. 23/6, 663-686.

632   Cirac, P., Hervé, G., Mazières, A. and Simplet, L., 2016. Carte des formations superficielles
633   du   plateau   aquitain   (2016).   EPOC-Université   de   Bordeaux.
634   https://doi.org/10.12770/602a30c5-c338-4e75-a591-baccb8ba1f79.

635   Corliss, B.H. and Emerson, S., 1990. Distribution of Rose Bengal stained deep-sea benthic
636   foraminifera from the Nova Scotia continental margin and Gulf of Maine. Deep-sea
637   Research. 37, 381-400.

638   Cushman, J.A., 1931. The Foraminifera of the Atlantic Ocean. Part 8. Rotaliidae,
639   Amphisteginidae, Calcarinidae, Cymbaloporettidae, Globorotaliidae, Anomalinidae,
640   Planorbulinidae, Rupertiidae and Homotremidae. Bull. U.S. Natl. Mus. 104.

641   Dagg, M.J. and Breed, G.A., 2003. Biological effects of Mississippi River nitrogen on the
642   northern gulf of Mexico--a review and synthesis. Journal of Marine Systems. 43(3-4),
643   133-152.

644   Debenay, J.P. and Redois, F., 1997. Distribution of the twenty seven dominant species of
645   shelf benthic foraminifers on the continental shelf, north of Dakar (Senegal). Marine
646   Micropaleontology. 29(3-4), 237-255.

647   Deflandre, B., 2016. JERICOBENT-1 cruise, Côtes De La Manche R/V.
648   https://doi.org/10.17600/16010400

649   Deflandre, B., 2017. JERICOBENT-2 cruise, Côtes De La Manche R/V.
650   https://doi.org/10.17600/17011000

651   Dessandier, P.-A., Bonnin, J., Kim J.-H., Bichon, S., Grémare, A., Deflandre, B., de Stigter,
652   H. and Malaizé, B., 2015. Lateral and vertical distributions of living benthic

653 foraminifera off the Douro River (western Iberian margin): Impact of the organic

654 matter quality. Marine Micropaleontology, 120, 31–45.

655 Dessandier, P.-A., Bonnin, J., Kim J.-H., Bichon, S., Deflandre, B., Grémare, A. and

656 Sinninghe Damsté, J. S., 2016. Impact of organic matter source and quality on living

657 benthic foraminiferal distribution on a river-dominated continental margin: A study of

658 the Portuguese margin. Journal of Geophysical Research: Biogeosciences, 121, 1689–

659 1714, doi:10.1002/2015JG003231

660 Diz, P., Francés, G. and Roson, G., 2006. Effects of contrasting upwelling-downwelling on

661 benthic foraminiferal distribution in the Ria de Vigo (NW Spain). Journal of Marine

662 Systems. 60, 1-18.

663 Diz, P. and Francés, G., 2008. Distribution of live benthic foraminifera in the Ría de Vigo

664 (NW Spain). Marine Micropaleontology. 66(3-4), 165-191.

665 Dubosq, N, Schmidt, S, Walsh, J. P., Grémare, A., Gilet, H., Lebleu, P., Poirier, D, Perello,

666 M.-C., Lamarque, B. and Deflandre, B. (in press). A first assessment of organic

667 carbon burial in the West Gironde Mud Patch (Bay of Biscay). Submitted in

668 Continental Shelf Research.

669 Duchemin, G., Jorissen, F.J., Le Loc'h, F., Andrieux-Loyer, F., Hily, C. and Thouzeau, G.,

670 2008. Seasonal variability of living benthic foraminifera from the outer continental

671 shelf of the Bay of Biscay. Journal of Sea Research. 59(4), 297-319.

672 Duchemin, G., Jorissen, F.J., Andrieux-Loyer, F., Le Loc'h, F., Hily, C. and Philippon, X.,

673 2005. Living benthic foraminifera from "La Grande Vasière", French Atlantic

674 continental shelf: faunal composition and microhabitats. Journal of Foraminiferal

675 Research. 35, 198-218.

676 Dufrêne, M. and Legendre, P., 1997. Species assemblages and indicator species: The need for

677 a flexible asymmetrical approach. Ecological Monographs. 67(3), 345-366.

678   Eppley, R.W., 1984. Relations between primary production and ocean chlorophyll determined

679   by satellite. In: Global Ocean Flux Study. Natl. Acad. Press, Washington, DC, pp 85-

680   102.

681   Ernst, S., Duijnstee, I., Fontanier, C., Jorissen, F.J. and Van der Zwaan, B., 2005. A

682   comparison of foraminiferal infaunal distributions in field and experimental samples

683   from 550-m depth in the Bay of Biscay. Deep Sea Research Part I: Oceanographic

684   Research Papers. 55 (4), 498-518

685   Fontanier, C., Jorissen, F.J., Chaillou, G., David, C., Anschutz, P. and Lafon, V., 2003.

686   Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in

687   the Bay of Biscay. Deep Sea Research Part I: Oceanographic Research Papers. 50(4),

688   457-494.

689   Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, A., Anschutz, P. and Carbonal, P., 2002.

690   Live benthic foraminiferal faunas from the Bay of Biscay: faunal density,

691   composition, and microhabitats. Deep Sea Research Part I: Oceanographic Research

692   Papers. 49(4), 751-785.

693   Froelich, P.N. et al., 1979. Early oxidation of organic matter in pelagic sediments of the

694   eastern equatorial Atlantic: suboxic diagenesis. Geochimica, Cosmochimica Acta. 43,

695   1075-1090.

696   Gillet, H., Deflandre, B., 2018. JERICOBENT-5-TH cruise, Thalia R/V.

697   https://doi.org/10.17600/18000425

698   Glud, R.N., Gundersen, J.K., Jorgensen, B.B., Revsbech, N.P. and Schulz, H.D., 1994.

699   Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic

700   Ocean: In situ and laboratory measurements. Deep-Sea Research Part I:

701   Oceanographic Research Papers. 41(11 /12), 1767-1788.

702   Goineau, A., Fontanier, C., Jorissen, F.J., Lansard, B., Buscail, R., Mouret, A., Kerhervé, P.,

703   Zaragosi, S., Ernoult, E. and Artéro, C., 2011. Live (stained) benthic foraminifera

704   from the Rhône prodelta (Gulf of Lion, NW Mediterranean): Environmental controls

705   on a river-dominated shelf. Journal of Sea Research. 65, 58–75.

706   Gooday, A.J., 2003. Benthic Foraminifera (Protista) as tools in Deep-water

707   Palaeoceanography: Environmental Influences on Faunal Characteristics. Advances in

708   Marine Biology. 46, 1-90.

709   Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Past: Paleontological Statistics Software

710   Package for Education and Data Analysis. Palaeontologia Electronica, vol. 4, issue 1,

711   art. 4: 9pp., 178kb.

712   Hargrave, B.T., 1985. Particle sedimentation in the ocean. Ecological Modelling. 30, 229-246.

713   Hayward, B.W.; Le Coze, F.; Vachard, D.; Gross, O. 2021. World Foraminifera Database.

714   Accessed at http://www.marinespecies.org/foraminifera on 2021-03-12.

715   doi:10.14284/305

716   Hedges, J.I. and Keil, R.G., 1995. Sedimentary organic matter preservation: an assessment

717   and speculative synthesis. Marine Chemistry. 49(2-3), 81-115.

718   Hedges, J.I., Keil, R.G. and Benner, R., 1997. What happens to terrestrial organic matter in

719   the ocean? Organic Geochemistry. 27(5-6), 195-212.

720   Heron-Allen, E. and Earland, A., 1914. The Foraminifera of the Kerimba Archipelago

721   (Portuguese East Africa) -Part I. Transactions of the Zoological Society of London.

722   20(12): 363-390.

723   Jones, R.W., 1994. The Challenger Foraminifera. Oxford Science Publications - The Natural

724   History Museum, 149 pp.

725   Jorissen, F.J., Fontanier, C., Thomas, E. and Claude Hillaire-Marcel and de Vernal, A., 2007.

726   Chapter Seven Paleoceanographical Proxies Based on Deep-Sea Benthic

727   Foraminiferal Assemblage Characteristics, Developments in Marine Geology.

728   Elsevier, pp. 263-325.

729   Lamarque, B., Deflandre, B., Galindo Dalto, A., Schmidt, S., Romero-Ramirez, A.,

730   Garabetian, F., Dubosq, N., Diaz, M., Grasso, F., Sottolichio, A., Bernard, G., Gillet,

731   H., Cordier, M.-A., Poirier, D., Lebleu, P., Deriennic, H., Danilo, M., Murilo Barboza

732   Tenório, M. and Grémare, A., submitted. Spatial distributions of surface sediment and

733   Sediment Profile Image characteristics in a high energy temperate marine RiOMar: the

734   West Gironde Mud Patch. Submitted in Journal of Marine Science and Engeneering.

735   Lampert, L., Queguiner, B., Labasque, T., Pichon, A. and Lebreton, N., 2002. Spatial

736   variability of phytoplankton composition and biomass on the eastern continental shelf

737   of the Bay of Biscay (north-east Atlantic Ocean). Evidence for a bloom of *Emiliania*

738   *huxleyi* (Prymnesiophyceae) in spring 1998. Continental Shelf Research. 22, 1225–

739   1247.

740   Lampert, L., 2001. Dynamique saisonnière et variabilité pigmentaire des populations

741   phytoplanctoniques dans l'atlantique nord (Golfe de Gascogne). Thèse d'Etat,

742   Université de Bretagne Occidentale, 340 p.

743   Langezaal, A.M., Jorissen, F.J., Brauna, B., Chailloud, G., Fontanier, C., Anschutz, P. and

744   van der Zwaan G.J. 2006. The influence of seasonal processes on geochemical profiles

745   and foraminiferal assemblages on the outer shelf of the Bay of Biscay. Continental

746   Shelf Research. 26(15), 1730-1755.

747   Langlet, D., Baal, C., Geslin, E., Metzger, E., Zuschin, M., Riedel, B., Risgaard-Petersen, N.,

748   Stachowitsch, M., and Jorissen, F. J., 2014. Foraminiferal species responses to in situ,

749   experimentally induced anoxia in the Adriatic Sea, Biogeosciences, 11, 1775–1797,

750   https://doi.org/10.5194/bg-11-1775-2014, 2014.

751 Lesueur, P., Tastet, J.P. and Marambat, L., 1996. Shelf mud fields formation within historical
752   times: examples from offshore the Gironde estuary, France. Continental Shelf
753   Research. 16, 1849–1870.

754 Lesueur, P., Tastet, J.P. and Weber, O., 2002. Origin and morphosedimentary evolution of
755   fine grained modern continental shelf deposits: the Gironde mud fields (Bay of
756   Biscay, France). Sedimentology 49, 1299–1320.

757 Lohrenz, S.E., Dagg, M.J. and Whitledge, T.E., 1990. Enhanced primary production at the
758   plume/oceanic interface of the Mississippi River. Continental Shelf Research. 10(7),
759   639-664.

760 Lohrenz, S.E. Fahnenstiel, G. L., Redalje, D. G., Lang, G. A., Chen, X., and Dagg, M. J.,
761   1997. Variations in primary production of northern Gulf of Mexico continental shelf
762   waters linked to nutrient inputs from the Mississippi River. Marine Ecology Progress
763   Series. 155, 45-54.

764 McKee, B.A., Aller, R.C., Allison, M.A., Bianchi, T.S. and Kineke, G.C., 2004. Transport
765   and transformation of dissolved and particulate materials on continental margins
766   influenced by major rivers: benthic boundary layer and seabed processes. Continental
767   Shelf Research. 24(7-8), 899-926.

768 Mendes, I., Dias, J. A., Schönfeld, J. and Ferreira, Ó., 2012. Distribution of living benthic
769   foraminifera on the northern Gulf of Cadiz continental shelf. Journal of Foraminiferal
770   Research. 42, 18–38

771 Mopper, K. and Degens, E.T., 1977. Organic carbon in the ocean: nature and cycling. In: The
772   Global Carbon Cycle. Wiley, Chichester, pp 293-316.

773 Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge
774   University Press, pp 426.

775 Murray, J.W. and Bowser, S.S., 2000. Mortality, protoplasm decay rate, and reliability of
776   staining techniques to recognize 'living' foraminifera: a review. Journal of
777   Foraminiferal Research. 30, 66-70.

778 Orbigny, A. D. d'., 1826. Tableau méthodique de la classe des Céphalopodes. Annales des
779   Sciences Naturelles. vol. 7: 96-169, 245-314.

780 Orbigny, A. D. d'., 1839. Foraminifères des îles Canaries. Histoire naturelle des Iles Canaries.
781   2(2): 120-146.

782 R Core Team, 2020. R: A language and environment for statistical computing. R Foundation
783   for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

784 Roberts, D. W., 2019. Labdsv: Ordination and Multivariate Analysis for Ecology. R package
785   version 2.0-1.

786 Romankevich, E.A., 1984. Geochemistry of Organic Matter in the Ocean. Springer, Berlin,
787   334 pp.

788 Smith, S. and MacKenzie, F., 1987. The ocean as a net heterotrophic system: implications for
789   the carbon biogeochemical cycle. Global Biogeochemical Cycles. 1, 187-198.

790 Stevenson, F.J. and Cheng, C.N., 1970. Amino acids in sediments: Recovery by acid
791   hydrolysis and quantitative estimation by a colorimetric procedure. Geochimica et
792   Cosmochimica Acta. 34, 77-88.

793 Walsh, J.J., 1988. On the nature of continental shelves. Academic Press Inc., New York, 520
794   pp.

795 Walsh, J.J., 1991. Importance of continental margins in the marine biogeochemical cycling of
796   carbon and nitrogen. Nature 350, 53-55.

797 Walsh, J.J., Rowe, G., Iverson, R. and McRoy, C., 1981. Biological export of shelf carbon is a
798   sink of the global CO_2 cycle. Nature. 292, 196-201.

799   Walton, W.R., 1952. Techniques for recognition of living Foraminifera. Contributions from

800   the Cushman Foundation for Foraminiferal Research. 3, 56-60.

801   Wollast, R., 1991. The coastal organic carbon cycle: fluxes, sources and sinks. In: Ocean

802   Margin Processes in Global Change. Wiley, New York, pp 365-381.

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 µm 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.

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)

Table 1

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

Table 2

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

Table 3

- For the first time, living benthic foraminifera are studied in the WGMP.
- Foraminiferal diversity tends to increase with water depth along the mud patch.
- Hydro-sedimentary processes and food availability control foraminiferal faunas.
- A foraminiferal continuum exists through the WGMP and the Grande Vasière.

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: