
Seasonal variability of living benthic foraminifera from the West-Gironde mud patch (Bay of Biscay, NE Atlantic): Three contrasted periods under the stereomicroscope

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Abstract :

Living continental shelf foraminifera were studied at three stations along a shore to open ocean transect between 39 and 69 m depth in the West-Gironde Mud Patch (WGMP) (Bay of Biscay, NE Atlantic). The aim of this work was to understand how the complex temporal variability of the environmental conditions (e.g., hydrosedimentary processes, sedimentary organic matter, oxygenation levels) controls foraminiferal ecological patterns (i.e., diversity, faunal composition, standing stock, and microhabitats). The WGMP was sampled during three different seasons (boreal summer – August 2017; winter – February 2018 and spring – April 2018), with very different meteorological patterns and benthic environmental conditions. The sedimentary facies at the shallowest station (Station 1, 39 m) varies significantly due to hydrometeorological constraints (strong storms and swells), which are extremely marked in late autumn and during the winter. The erosion of the sandy substrate by strong bottom currents and the deposition of a silty surface layer leads to the recorded spectacular drop in foraminiferal diversity and density recorded in February and April 2018. All foraminiferal species were affected by this hydrosedimentary instability, likely due to the partial destruction of their microhabitat by intense erosional and depositional processes. At the middle WGMP station (Station 2, 47 m), benthic fauna changed much more gradually. The sedimentary imprint of the spring phytoplankton bloom is clearly recorded in April 2018 with an increase in fresh and altered phytopigment content in surface sediments. *Eggerelloides scaber*, a deposit feeder and hypoxia-tolerant species, dominated the 2017 summer foraminiferal fauna but was gradually replaced by *Ammonia falsobeccarii*, a phytophagous taxon considered quite reactive to spring bloom inputs. At the distal WGMP (Station 4, 69 m), *E. scaber* and *A. falsobeccarii* were outcompeted and gradually replaced by *Nonion faba* and *Nonionoides turgidus*, both highly adaptable species able to settle down in surface and subsurface sediments during the spring bloom periods. Able to endure a range of microhabitats and food availability, there they rely on both fresh and altered phytodetritus. We propose a conceptual scheme summarizing the putative interconnexion between foraminiferal faunas, geochemistry and physics in the WGMP.

Highlights

► Seasonal variability of living benthic foraminifera is studied in the WGMP. ► Hydrosedimentary processes and food availability control foraminiferal changes. ► A conceptual scheme shows the interconnexion between foraminifera and biotopes.

Keywords : Benthic foraminifera, West-Gironde Mud Patch, Temporal variability, Diversity, Organic matter, Hydrosedimentary processes

50 **1. Introduction**

51 In the 21st century, the world's oceans are more than ever, subject to disastrous
52 anthropogenic pressures (e.g., heavy metal and plastic pollution, overfishing) and the
53 relentless strain imposed by uncontrollable climate change (e.g., ocean acidification, lethal
54 marine heat waves, deoxygenation, loss of sea ice) (Halpern et al., 2015; 2019). It is vitally
55 for us to define strategic marine areas (i.e., containing valuable resources) and to ensure their
56 protection and sustainable management using effective environmental (bio-)indicators. It is
57 essential to arm ourselves with the robust observation strategies to ensure rigorous and
58 reliable environmental monitoring (e.g., Halpern et al., 2019). Within the framework of the
59 JERICO-NEXT programme (Joint European Research Infrastructure network for Coastal
60 Observatory-Novel European eXpertise for coastal observaTories; European Union's Horizon
61 2020 Research and Innovation program under grant agreement no. 654410, 2015-2019), a
62 group of marine study areas have been defined along European coasts to exhaustively study as
63 the ecological characteristics of benthic communities with respect to variability of physico-
64 chemical conditions prevailing in their associated ecosystems. The major goals of this project
65 are to assess (1) the natural interconnexion between biology, geochemistry and physics in
66 complex shallow-water environments and (2) ascertain the quality of certain coastal areas that
67 are currently subject or may be soon subject to anthropogenic and climate-related
68 disturbances. Off the Gironde Estuary, the West-Gironde Mud Patch (WGMP) has been the
69 subject of special scientific monitoring since 2009 (e.g., the BIOMIN project between 2009–
70 2013, the VOG project between 2018–2019, the JERICO-NEXT European project with this
71 study) (Massé et al., 2016; Lamarque et al., 2021; 2022; Dubosq et al., 2021; 2022a;
72 Fontanier et al., 2022). This mud patch, located at a depth of 30–70 m and 40 km offshore, is
73 important to local fisheries and a remarkable area where fine sediments accumulate and focus
74 organic matter from an array of different sources (marine phytodetritus and continental

75 organic compounds) generating an area of much higher benthic diversity than would
76 otherwise be found in such a sandy environment (Lamarque et al., 2021; 2022; Dubosq et al.,
77 2021; 2022a; Fontanier et al., 2022). Together with the South-Gironde Mud Patch, the
78 WGMP constitutes a particular set of morpho-sedimentary units covering the gravels and
79 sands of the Northern Aquitaine continental shelf (Bay of Biscay, France) (Lesueur et al.,
80 1996; 2002; Cirac et al., 2000). Both mud patches extend off the two main channels of the
81 Gironde Estuary, the main source of the WGMP's fine-grained sediments (Fig. 1) (Lesueur et
82 al., 1996). The WGMP comprises of Gironde River silt deposited during flood events, and a
83 smaller portion of inner continental shelf silts and fine sand deposited during periods of high
84 energy (i.e., storms). By combining geochemical, geophysical, sedimentological and
85 biological analyses, the complexity of its spatial structure, temporal dynamics and
86 environmental characteristics have been recently enlightened by a series of publications
87 (Lamarque et al., 2021; 2022; Dubosq et al., 2021; 2022a; Fontanier et al., 2022).

88 Based on the extensive investigation and description of the WGMP's organic matter
89 and sedimentary facies, Lamarque et al. (2021) demonstrated that the WGMP can be
90 subdivided into proximal and distal areas. Each area features their own suite of surface
91 organo-sedimentary characteristics, notably with the distal section (deeper than 42.5 m)
92 further notably bioturbated. For this one-shot synoptic survey (i.e., a single sampling cruise
93 performed in June 2018), there was no evidence of bottom trawling spatially impacting the
94 WGMP, as opposed to bottom shear stress related to hydro-meteorological forcing (i.e., wind,
95 tide, surge, and river flow). Dubosq et al. (2021) published a thorough study of the WGMP's
96 organic carbon burial based on sedimentary facies and accumulation rates from samples
97 collected in October 2016. Sedimentary structures indicated episodic sandy inputs overlying
98 older deposits at proximal areas of the WGMP, and relatively continuous sedimentation in the
99 distal area, with a maximum sediment accumulation rate (0.48 cm.yr^{-1}) at 47 m depth (the

100 depocenter of the WGMP). Organic carbon burial rates increased with water depth and
101 reached $44 \text{ g C.m}^{-2}\text{.yr}^{-1}$ at depths greater than 62 m. Fontanier et al. (2022) have investigated
102 the living (stained) benthic foraminifera (Eukaryota, Rhizaria, Retaria) sampled in August
103 2017 at 7 stations located in the WGMP. Benthic foraminifera constitute reliable proxies for
104 studying present and past marine environments since their faunal communities (diversity,
105 standing stock, microhabitat), spatial distribution and temporal dynamics are controlled by
106 numerous physico-chemical parameters including exported organic matter flux, bottom- and
107 pore-water oxygenation and sedimentary substrate (e.g., Gooday, 2003; Murray, 2006;
108 Jorissen et al., 2007). In the WGMP, foraminiferal richness (S) presented relatively moderate
109 values ranging between 15–35 taxa and a Shannon Index H' that distally increased with water
110 depth. Accordingly, the relative contribution of *Eggerelloides scaber*, the dominant
111 agglutinated species at all stations, decreased with increased depth and decreased proximity to
112 the coast. The shallowest station (Station 1, 39 m), closest to the shore, was characterised by
113 *E. scaber*, *Quinqueloculina laevigata* and *Ammonia beccarii*, taxa typical of inner-shelf
114 environments constrained by high-energy hydrodynamics and river discharge. Surficial
115 sediments at Station 1 constituted of winnowed sands depleted in organic carbon. Towards the
116 centre of the WGMP, where clay-silt facies contained variably degraded marine phytodetritus
117 and terrestrial organic compounds, foraminiferal faunas were characterized by *Bulimina*
118 *aculeata*, *Ammonia falsobeccarii*, *Nouria polymorphinoides* and *Nonionoides turgidus*. Yet
119 *E. scaber* remained the most dominant taxon. Deeper stations (>55 m depth) located at the
120 distal end of the mud patch were dominated by *B. aculeata*, *A. falsobeccarii*, *N.*
121 *polymorphinoides* and *E. scaber*. Accompanying these taxa were *Bulimina marginata*,
122 *Rectuvigerina phlegeri*, *N. faba* and *Paracassidulina neocarinata*, which are typical of mid-
123 and outer-shelf ecosystems enriched in sedimentary organic matter. With a temporal survey of
124 the macrofaunal communities (4 seasonal samplings over both short [2016–2018) and long

125 [2010–2018) time scales), Lamarque et al. (2022) highlighted both surface sediment and
126 benthic macrofauna spatial patterns mainly constrained by hydrodynamics. This variability
127 reflected seasonal changes, but benthic macrofauna composition also revealed pluriannual
128 changes corresponding to major disturbances likely caused by a series of severe storms. To
129 summarize, previous work has shown that current hydrosedimentary processes (erosion,
130 transport and deposition of sediments by bottom currents) substantially impact (1) the mudflat
131 facies, (2) the distribution of sedimentary organic matter (continental vs. marine, labile vs.
132 refractory), (3) the spatial distribution of benthic fauna (macrofauna and foraminifera) and (4)
133 the temporal dynamics of macrofaunal communities. Interestingly, Dubosq et al. (2022a) who
134 investigated the water column structure (temperature, salinity, dissolved, oxygen, turbidity,
135 Chl-*a* concentration, pH) over the different seasons between 2016 and 2021, documented that
136 a seasonal bottom water deoxygenation (oxygen saturation minimum down to 45%) occurs in
137 late summer and autumn. This might be related to the combined effect of water column
138 thermal stratification, the settling of organic matter produced in surface waters and the
139 advection of deoxygenated waters from north of the Bay of Biscay.

140 Seasonal benthic foraminiferal variability is yet to be studied in this location and here
141 we present a description of them during three seasons. The effect of seasonally exported
142 phytodetritus input and the role of environmental oxygenation on benthic foraminiferal fauna
143 has already been investigated at “La Grande Vasière”, a muddy belt located on the outer shelf
144 (between 80–130 m deep) northwest of the WGMP (Duchemin et al., 2005; 2008) (Fig. 1).
145 These studies have shown that living benthic fauna responds to seasonal inputs of organic
146 matter related to phytoplankton blooms from spring to autumn. Opportunistic foraminiferal
147 species including *Nonionella iridea* and *Cassidulina carinata* dominate the Grande Vasière
148 mud belt fauna. This is the first reporting of seasonal benthic foraminiferal data from the
149 WGMP, a location closer to the continental coastline than La Grande Vasière. Three stations

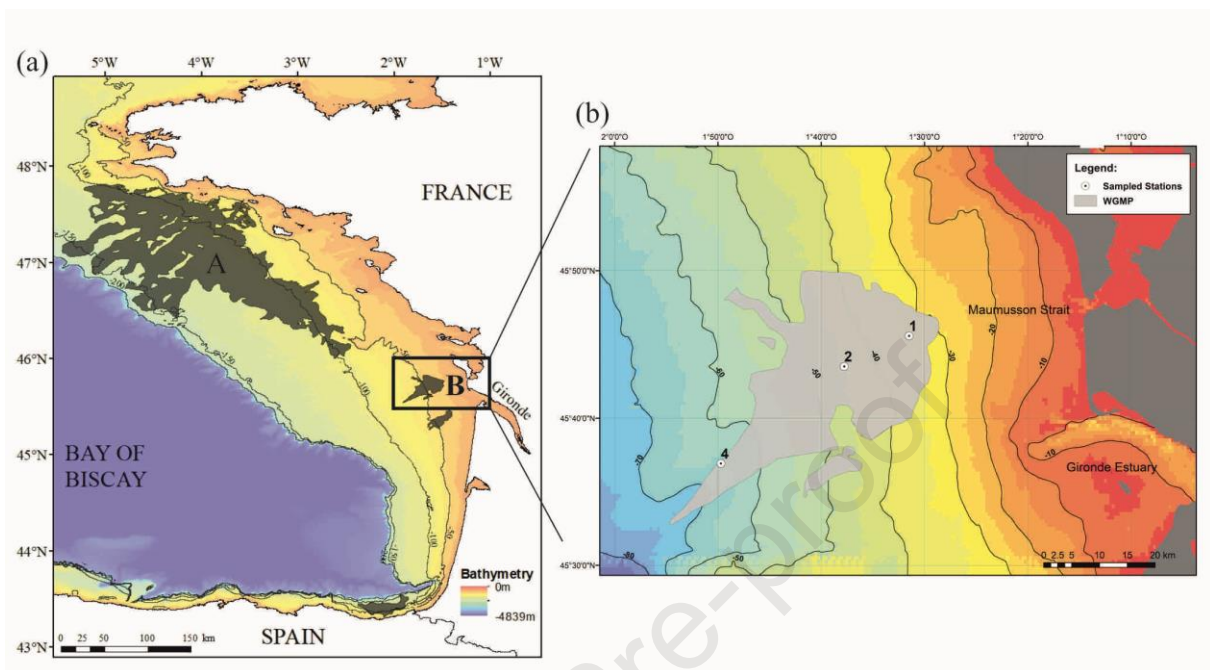
150 at depths between 39–69 m were sampled in August 2017 (data already published by
151 Fontanier et al. 2022), February 2018 and April 2018, covering very different periods of water
152 column structure, hydrosedimentary constraints and organic matter deposition. These three
153 stations were chosen because they have their own established faunal and environmental
154 features (Fontanier et al 2022). These include coastline-proximal modern sandy deposits at
155 one station, fine sediments at another in the depocentre part of the mud patch, and a
156 pronounced marine-influenced mudflat station at the distal part of the WGMP. To investigate
157 the seasonal changes of benthic foraminiferal fauna, we drew on geochemical, geophysical
158 and sedimentological data acquired during the 2017 and 2018 oceanographic cruises
159 JERICOBENT-2, JERICOBENT-3 and JERICOBENT-4 (Deflandre, 2017; 2018a; 2018b).
160 These data, many already published or in press (Lamarque et al., 2022; Dubosc et al., 2021;
161 2022), are compared to the faunal characteristics (diversity, standing stock, microhabitats) of
162 the sampled foraminiferal communities at the three stations to assess how complex the
163 temporal variability of the environmental conditions (e.g., organic matter, oxygenation,
164 hydrosedimentary processes) control ecological patterns. We intend to propose a conceptual
165 model depicting the putative interconnexion between the temporal dynamics of the benthic
166 fauna and the seasonal changes of the investigated ecosystems.

167

168 **2. Study area between August 2017 and April 2018**

169 The WGMP is located between 40–80 km from the Gironde Estuary (Fig. 1). This study is set
170 up on data obtained at three stations (Stations 1, 2 and 4) sampled during the JERICOBENT-
171 2, JERICOBENT-3 and JERICOBENT-4 cruises, in August 2017, February 2018 and April
172 2018, respectively (Fig. 1; Table 1) (Deflandre, 2017; 2018a; 2018b). Sampling stations are
173 organized along a bathymetric gradient from the shallowest site and coastal (proximal) end of

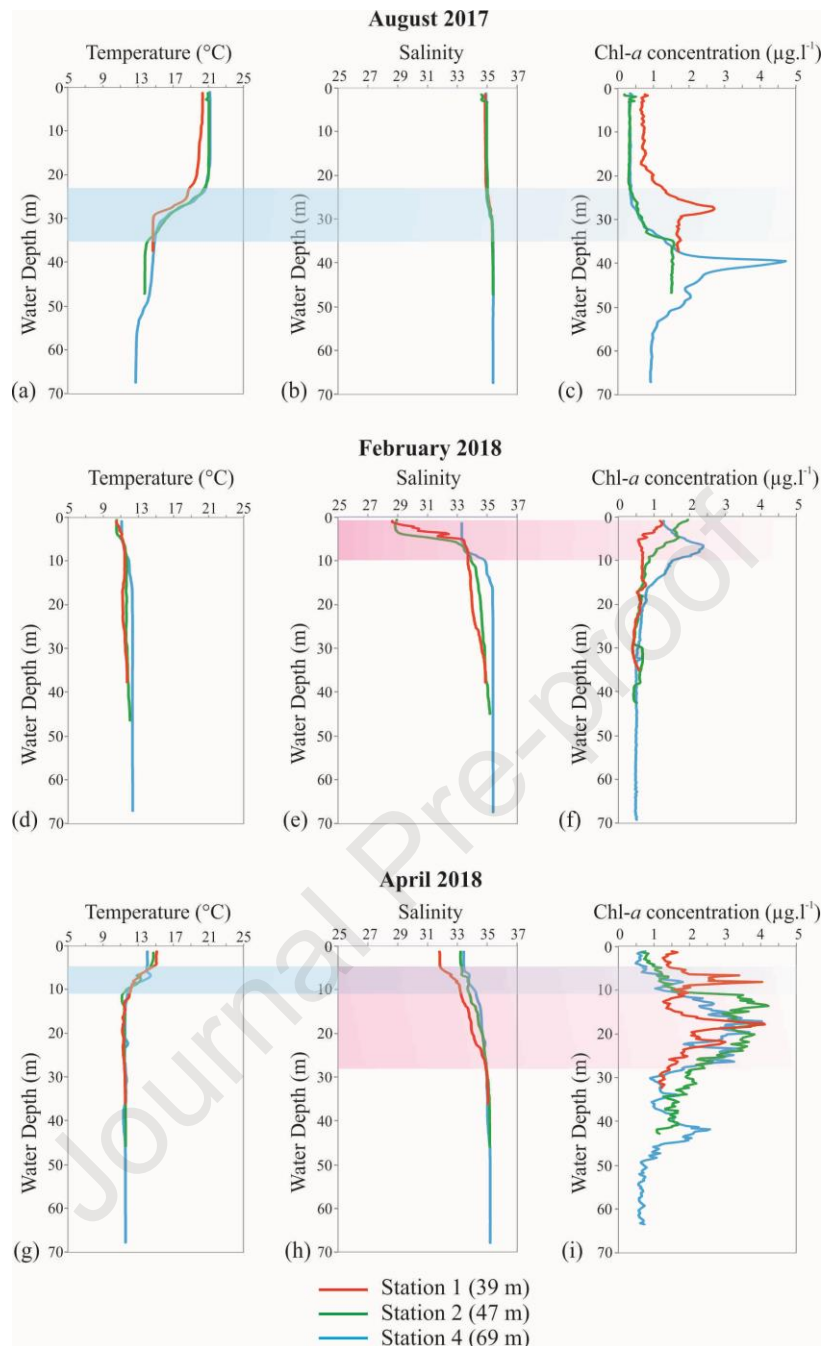
174 the WGMP (Station 1, 39 m) to the deepest and most remote end (distal) of the WGMP
 175 (Station 4, 69 m) (Fig. 1; Table 1).



176

177 *Figure 1. (a) Map of the Bay of Biscay continental shelf with the locations of mud belts and*
 178 *mud patches: A - La Grande Vasière Mud Patch pictured in dark grey and B - The West*
 179 *Gironde Mud Patch pictured in dark grey (b) Map of the West Gironde Mud Patch (pictured*
 180 *in light grey) showing the location of the 3 sampling stations (white dots). The synoptic map*
 181 *of the WGMP has been determined during the JERICOBENT-5-TH cruise (Gillet and*
 182 *Deflandre, 2018)*

183



184

185 *Figure 2 (a-i) CTD measurements of temperature, salinity, Chl-a concentration and turbidity*186 *in the water column at Stations 1, 2 and 4 from the WGMP (Dubosq et al., 2022a). Chl-a*187 *content is measured with CTD. The three sampling periods of August 2017, February 2018*188 *and April 2018 are plotted. Shaded areas in blue represent mean seasonal thermoclines.*189 *Shaded areas in red represent mean seasonal haloclines. CTD Measurement data are*190 *available on SEANOE (<https://www.seanoe.org/data/00783/89508/>) (Dubosq et al., 2022b).*

191

192 Water column temperature shows a notable seasonal change marked by (1) a strong
193 thermocline between 20–35 m depth in August 2017 (boreal summer) (ΔT between 5–7°C
194 depending on the station) (Fig. 2a), (2) a thermal homogenization of the water column during
195 the following boreal winter (February 2018) ($T = \sim 12^\circ\text{C}$) (Fig. 2d), and (3) the establishment
196 of a new thermocline between 5–10 m depth two months later, in boreal spring (April 2018)
197 (ΔT between 2.5–4°C depending on the station) (Fig. 2g) (Dubosq et al., 2022a; 2022b).

198 Salinity in the water column is relatively homogeneous in August 2017 with average values
199 close to 35, although slightly lower in the first 25 meters (Fig. 2b) (Dubosq et al., 2022a;
200 2022b). In February 2018, a marked halocline is recorded in the surface waters (uppermost 10
201 meters) with a salinity decrease toward the sea surface, that varies between stations ($\Delta S = 5$ at
202 Station 1, $\Delta S = 4$ at Station 2 and $\Delta S = 1.5$ at Station 4) (Fig. 2e). This salinity depletion is
203 mainly related to the enhanced Gironde winter outflow and its offshore imprint (Lamarque et
204 al., 2022; Dubosq et al., 2022a). In April 2018, a less pronounced but deeper (between 5–27
205 m) halocline was observable in the water column (Fig. 2h). In August 2018, chl-*a* maxima
206 were observed in and below the summer thermocline (Dubosq et al., in press). In particular,
207 two peaks of 2.6 $\mu\text{g}\cdot\text{l}^{-1}$ and 4.7 $\mu\text{g}\cdot\text{l}^{-1}$ were recorded at 28 m and 40 m depths at Station 1 and
208 Station 4 respectively (Fig. 2c). In February 2018, moderately elevated Chl-*a* contents were
209 mainly recorded at the sea surface at Station 1 (39 m) and to ~8 m at Station 4 (69 m) (Fig.
210 2e). These maxima oscillate between 1.2 $\mu\text{g}\cdot\text{l}^{-1}$ –2.4 $\mu\text{g}\cdot\text{l}^{-1}$. At Stations 1 (depth 39 m) and 2
211 (47 m), near the sea floor, fluorescence tends to rise to moderate values. In April 2018, Chl-*a*
212 values were very high in subsurface waters, especially between 5–30 m depths (at the
213 halocline) (Fig. 2i). Numerous peaks near 4 $\mu\text{g}\cdot\text{l}^{-1}$ were recorded at the three stations. This was
214 the phytoplankton spring bloom already extensively described in literature (Lampert, 2001,
215 Lampert et al., 2002; Fontanier et al., 2003). Although no water column turbidity data was
216 available in August 2017, multi-year turbidity data shows a dramatic increase in background

217 water turbidity values in February 2018 at Stations 1 and 2 (65 and 50 NFU, respectively)
218 (Dubosq et al., 2022a). This may be related to notable winter storms which occurred over the
219 transition between 2017 and 2018 (Lamarque et al., 2022b). In April 2018, turbidity remained
220 relatively high at Station 2 (25 NTU) but lower at Station 1 (< 9 FNU). The bottom waters of
221 Station 4 were less turbid in all seasons (< 8 FNU) (Dubosq et al., 2022a). At each station,
222 bottom water temperature (based on Conductivity-Temperature-Depth measurements)
223 decreased between August 2017 and April 2018, from 14.6°C – 11.6°C at Station 1 (39 m),
224 from 13.6°C – 11.6°C at Station 2 (47 m) and from 12.7°C – 11.6°C at Station 4 (69 m) (Dubosq
225 et al., 2022a) (Table 1). Bottom water salinity (Conductivity-Temperature-Depth
226 measurements) stayed relatively constant through time and space with values ranging between
227 34.8 – 35.4 (Table 1) (Dubosq et al., 2022a). Bottom water oxygenation was high at all sites
228 (between 184 – 256 μM), with the strongest values recorded in February 2018 (winter
229 conditions) and the lowest values recorded in August 2017 (summer conditions) (Table 1)
230 (Dubosq et al., 2022a). Oxygen penetration depth (OPD) within the sediments was relatively
231 limited (< 0.7 cm) indicating a relatively enhanced oxygen demand to degrade organic
232 compounds (unpublished data). Diffusive oxygen uptake (DOU) calculated according to the
233 model by Berg et al. (1998) was at maximum at the deepest Station 4 whenever this site was
234 sampled (Table 1) (unpublished data). Lamarque et al. (2022) have investigated the potential
235 impact of hydro-meteorological forcings on the seafloor over our study period (Fig. 3a–b).
236 Gironde River outflow presents a clear seasonal pattern with winter floods resulting in
237 enhanced river discharge (e.g., $5,600$ $\text{m}^3 \cdot \text{s}^{-1}$ on January the 23rd 2018) and a low-water period
238 in summer and fall 2017 (with Gironde Estuary outflow lower than 800 $\text{m}^3 \cdot \text{s}^{-1}$). This seasonal
239 variability has no significant impact on the spatial structuration of surface sediment
240 characteristics in the WGMP (Lamarque et al., 2022). Bottom Shear Stress (BBS) mainly
241 related to wind-induced swell was also calculated in Lamarque et al. (2022) (Fig. 3b).

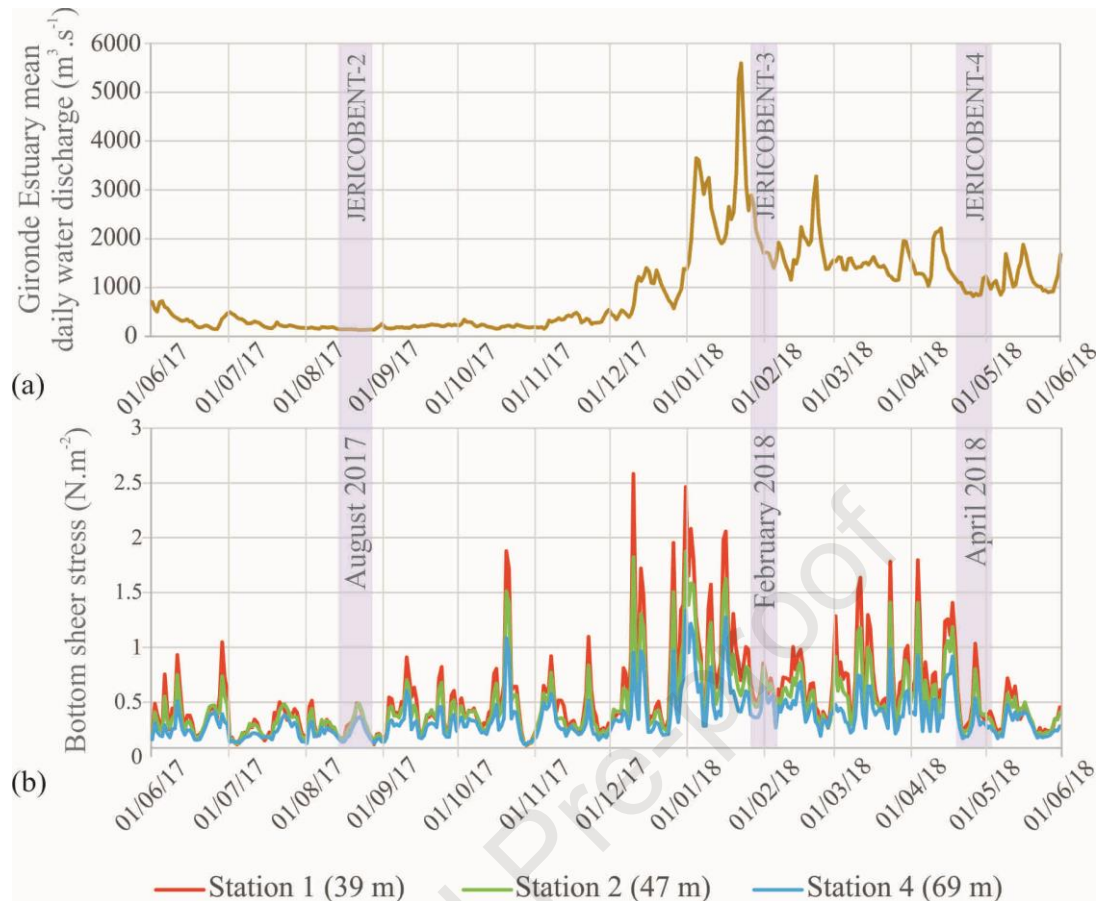
242 Noticeably, the August 2017 cruise was conducted during a low-BSS episode (i.e., $< 0.5 \text{ N.m}^{-2}$)
 243 ²) as opposed to the February 2018 and the April 2018 cruises, which both took place during a
 244 high-BSS periods. Bottom Shear Stress peaks (e.g. $>2.0 \text{ N.m}^{-2}$ at Station 1) in 2018 are
 245 noticeably related to late-fall and winter storms. According to Lamarque et al. (2022), high
 246 BSS values would explain the temporal changes of sediment characteristics recorded at the
 247 shallower Station 1 (39 m).

248

Station	Depth (m)	Latitude	Longitude	Sampling period	BWT ($^{\circ}\text{C}$)	BWS	BWO ₂ (μM)	% Sat.	OPD (cm) (N)	DOU ($\text{mmol m}^{-2} \text{d}^{-1}$) (N)
1	~39	45°45.550'	1°31.335'	August 2017	14.6	35.2	184.7	71.9	0.36 ± 0.16 (10)	2.87 ± 1.17 (10)
				February 2018	11.8	34.8	219.7	79.0	0.41 ± 0.08 (7)	2.82 ± 0.74 (7)
				April 2018	11.6	35.0	180.6	65.8	0.56 ± 0.29 (11)	5.76 ± 2.36 (11)
2	~47	45°43.567'	1°37.657'	August 2017	13.6	35.2	196.5	83.0	0.61 ± 0.32 (12)	3.23 ± 0.50 (12)
				February 2018	12.1	35.2	255.7	94.4	0.53 ± 0.09 (4)	4.57 ± 3.44 (4)
				April 2018	11.6	35.1	218.1	79.5	0.70 ± 0.10 (12)	4.12 ± 1.66 (12)
4	~69	45°43.993'	1°37.427'	August 2017	12.7	35.2	185.3	69.2	0.37 ± 0.08 (11)	5.92 ± 2.89 (11)
				February 2018	12.4	35.4	255.4	94.6	0.65 ± 0.08 (7)	5.53 ± 1.57 (7)
				April 2018	11.6	35.2	236.6	87.7	0.38 ± 0.06 (10)	8.96 ± 2.20 (10)

249

250 *Table 1. Location of the three stations sampled during the JERICOBENT-2, -3 and -4 cruises*
 251 *(August 2017, February 2018 and April 2018) including station coordinates and depth.*
 252 *Physico-chemical parameters including BWT (bottom-water temperature in $^{\circ}\text{C}$) and BWS*
 253 *(bottom-water salinity) were extrapolated from CTD casts at each site (Dubosq et al, 2022a).*
 254 *BWO₂ represents bottom-water oxygen in μM (Dubosq et al., 2022a). Oxygen saturation (in*
 255 *%) of bottom water was also calculated by Dubosq et al. (2022a). OPD (oxygen penetration*
 256 *depth in cm below the SWI) was determined after N in-situ measurements with a benthic*
 257 *profiler deployed at each station. DOU (Diffusive Oxygen Uptake in $\text{mmol m}^{-2} \text{d}^{-1}$) was*
 258 *calculated according to the model by Berg et al. (1998) (unpublished data).*



259

260 *Figure 3 (a-b) Temporal changes in Gironde Estuary mean daily water discharge (a) and in*
 261 *the 95th percentile of Bottom Shear Stress at stations 1, 2 and 4 (b) between June 2017 and*
 262 *June 2018. Sampling periods (JERICOBENT-2, -3 and -4 cruises) are indicated by shaded*
 263 *areas. This figure is modified from Lamarque et al. (2022) (with courtesy of B. Lamarque).*

264

265

3. Material and Methods

266

3.1 Sediment sampling

267 At each station, sediment samples were gathered with a Barnett-type multiple corer equipped
 268 with Plexiglas tubes (9.6 cm internal diameter, surface area of 72 cm^2) (Barnett et al., 1984).

269 The multi-corer allowed for sampling of the uppermost decimeters of the sediment column,
 270 the overlying bottom waters, and a comparatively undisturbed sediment-water interface. At

271 each station, the multi-corer was deployed several times (three to five) to sample enough

272 material for geochemical, sedimentological and biological investigations. Descriptors of

273 sedimentary organic matter as well as the mineralization processes of organic compounds at,
 274 and below the sediment-water interface are described in detail by Dubosq et al. (2021) and
 275 Lamarque et al. (2022). We refer to a partial synthesis of their results in the discussion with
 276 data summarized in Tables 1 and 2a–b.

Station	Sampling period	OC		TN		C:N ratio		Chl- <i>a</i> μg g ⁻¹	Phaeo- <i>a</i> μg g ⁻¹	Chl- <i>a</i> /(Chl- <i>a</i> + Phaeo- <i>a</i>)	
		%DW	N	%DW	N		N				N
1	August 2017	0.31 ± 0.04	5	0.03 ± 0.00	5	12.11 ± 1.59	5	0.23 ± 0.09	1.46 ± 0.46	0.13 ± 0.02	3
	February 2018	0.28 ± 0.15	5	0.03 ± 0.01	5	10.70 ± 1.40	5	0.52 ± 0.37	2.53 ± 1.58	0.16 ± 0.02	3
	April 2018	0.92 ± 0.21	5	0.12 ± 0.03	5	9.17 ± 0.87	5	0.66 ± 0.05	3.67 ± 0.38	0.15 ± 0.01	3
2	August 2017	0.89 ± 0.06	5	0.10 ± 0.01	5	10.07 ± 1.07	5	1.15 ± 0.20	6.65 ± 0.88	0.15 ± 0.03	3
	February 2018	1.02 ± 0.54	5	0.12 ± 0.06	5	10.32 ± 1.00	5	2.09 ± 0.72	9.61 ± 2.47	0.18 ± 0.02	3
	April 2018	1.14 ± 0.39	5	0.13 ± 0.05	5	9.92 ± 0.47	5	4.54 ± 1.96	18.16 ± 8.17	0.20 ± 0.01	3
4	August 2017	1.38 ± 0.05	5	0.14 ± 0.00	5	11.16 ± 0.29	5	0.91 ± 0.18	6.90 ± 1.28	0.12 ± 0.04	3
	February 2018	1.54 ± 0.14	5	0.19 ± 0.02	5	9.48 ± 0.57	5	1.12 ± 0.17	9.51 ± 1.86	0.11 ± 0.01	3
	April 2018	1.42 ± 0.13	5	0.18 ± 0.02	5	9.44 ± 0.48	5	5.86 ± 0.85	29.35 ± 2.83	0.17 ± 0.01	3

277

Station	Sampling period	δ ¹³ C _{OM}	δ ¹⁵ N _{OM}	N	THAA	EHAA	EHAA/THAA	
		‰	‰		mg g ⁻¹ DW	mg g ⁻¹ DW	%	N
1	August 2017	-24.44 ± 0.35	4.71 ± 0.09	2	0.51 ± 0.18	0.16 ± 0.04	32.23 ± 3.79	
	February 2018	-25.12 ± 0.23	4.16 ± 0.27	2	0.72 ± 0.32	0.29 ± 0.12	40.97 ± 2.04	
	April 2018	-24.29 ± 0.00	5.78 ± 0.05	2	0.98 ± 0.51	0.26 ± 0.04	29.61 ± 11.03	
2	August 2017	-24.22 ± 0.55	5.82 ± 0.01	2	3.23 ± 0.29	0.61 ± 0.02	18.91 ± 1.36	
	February 2018	-24.58 ± 0.48	5.80 ± 0.25	2	3.10 ± 0.16	0.59 ± 0.14	19.00 ± 4.24	
	April 2018	-24.05 ± 0.05	5.89 ± 0.00	2	3.94 ± 0.67	0.56 ± 0.07	14.23 ± 1.44	
4	August 2017	-24.03 ± 0.38	5.73 ± 0.12	2	4.10 ± 0.19	0.38 ± 0.02	9.14 ± 0.50	
	February 2018	-23.91 ± 0.10	5.64 ± 0.08	2	4.32 ± 0.43	0.57 ± 0.07	13.30 ± 3.00	
	April 2018	-23.74 ± 0.31	5.80 ± 0.14	2	4.56 ± 0.49	0.72 ± 0.20	15.27 ± 2.81	

278

279 *Table 2 Organic matter descriptors in the surface sediment (i.e. the 0–0.5 cm interval below*
 280 *the sediment-water interface) at the three stations sampled during the JERICOBENT-2, -3*
 281 *and -4 cruises (August 2017, February, 2018 and April 2018) (Lamarque et al., 2022) :*
 282 *Organic content (OC in % DW), Total nitrogen content (TN in % DW), C:N atomic ratio,*
 283 *Chlorophyllic pigment content (i.e. Chl-*a* and Phaeo-*a*) and their freshness index Chl-*a*/(Chl-*
 284 **a*+Phaeo-*a*), Stable carbon and nitrogen isotopic signatures of sedimentary organic matter*
 285 *(i.e. δ¹³C_{OM} and δ¹⁵N_{OM}), Amino acid content (i.e. THAA for Totally Hydrolyzable Amino*
 286 *Acids and EHAA for Enzymatically Hydrolyzable Amino Acids) and their lability index*
 287 *(EHAA/THAA).*

288

289

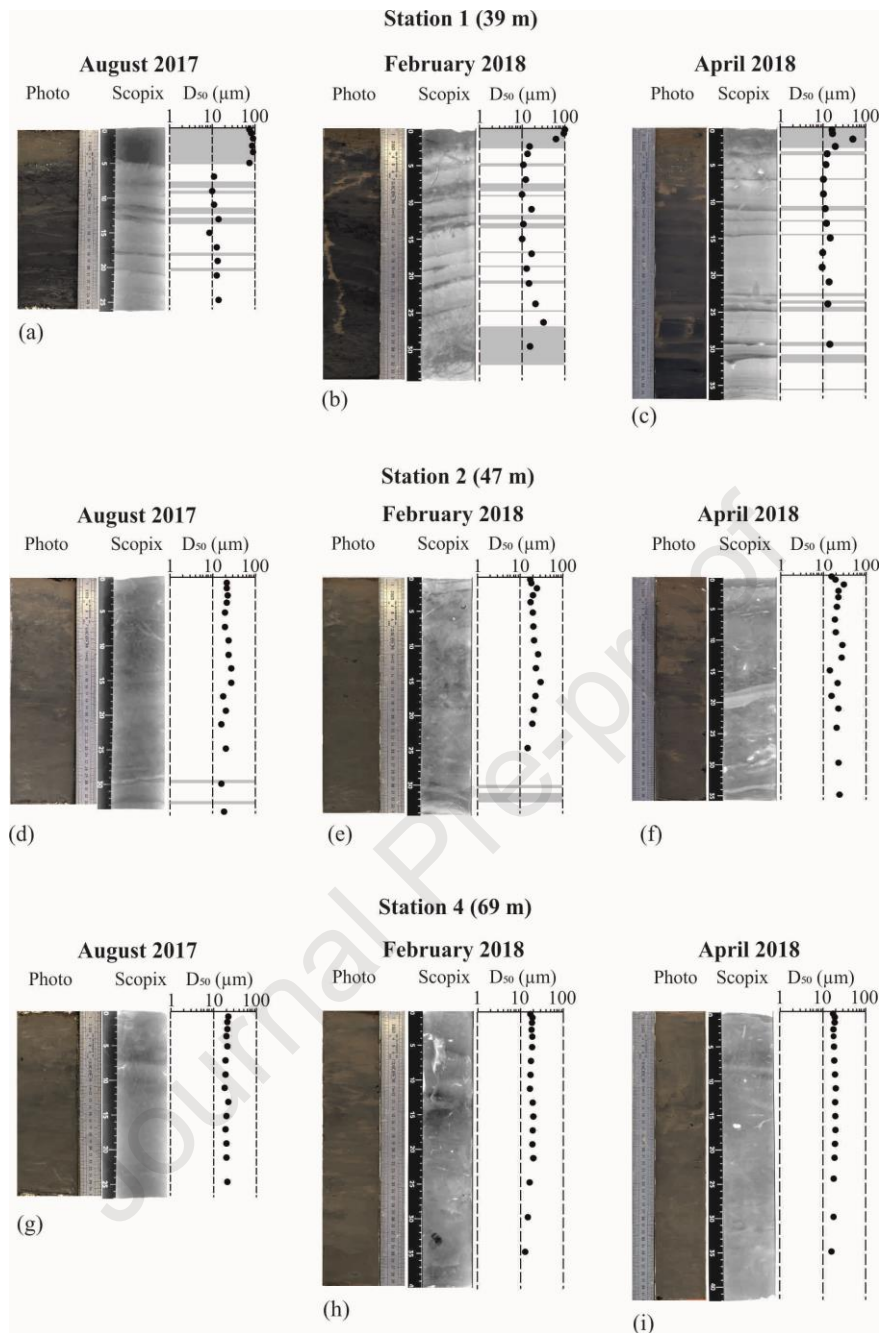
3.2 Sedimentological analysis

290 At each station and at the occasion of the three sampling periods, we radiographed one entire
291 core with a Scopix system, which consists of an X-Ray imaging device combined with image
292 analysis software (Migeon et al., 1999) (Fig. 4). The aim of the X-ray radiography is to detect
293 the presence of discrete sedimentary structures (e.g., coarse sedimentary layers, erosional
294 surfaces, burrows, large shells). To visually evaluate changes, we also photographed the cores
295 (Fig. 4). Particle grain size was measured with a Malvern Laser Diffraction Particle Sizer
296 (type 2600). This technique was applied to sediment samples belonging to the previously
297 radiographed and photographed core and allowed for the calculation of grain size frequency
298 D_{50} . To do so, each core was subsampled every 0.5 cm between 0–1 cm depth, every 1 cm
299 between 1–4 cm depth, then every 2 cm between 4–22 cm depth, and with an adaptative
300 resolution deeper downcore.

301

302 *3.3 Foraminiferal faunal analysis*

303 Foraminiferal fauna was examined in a single core per station. Onboard, each core was sliced
304 horizontally every 0.5 cm from the sediment-water interface to a depth of 2 cm, then every
305 centimeter between 2–10 cm depth. Samples (12 slices per core) were stored into 500 cm³
306 bottles which were then, filled with 95% ethanol containing 2 g/L Rose Bengal stain,
307 commonly used to identify living foraminifera (Walton, 1952; Murray & Bowser, 2000).



308

309 *Figure 4. Photograph and X-Ray radiograph (Scopix) of split cores collected at the three*
 310 *stations from the WGMP with grain size frequency D_{50} . Three sampling periods (August*
 311 *2017, February 2018, April 2018) are documented.*

312

313 All samples were gently shaken for several minutes to obtain a homogeneous mixture. At the
 314 laboratory, samples were sieved through 150 μm mesh screens, and sieve residues were stored
 315 in 95% ethanol. Stained foraminifera belonging to the >150 μm fraction were sorted in wet

316 samples using a stereomicroscope. They were stored in Plummer slides. One concern with
317 using Rose Bengal is that it may stain the protoplasm of dead foraminifera that may be
318 relatively well-preserved for long time periods under anoxic conditions prevailing in deep
319 sediments (Corliss & Emerson, 1990; Bernhard, 2000). We therefore applied very strict
320 staining criteria (i.e., all chambers, except the last chamber, stained in bright pink), and
321 compared doubtful individuals to perfectly stained specimens of the same species found in the
322 superficial sediment layers. For miliolids, doubtful specimens were broken to inspect test
323 interior. Most stained foraminifera were identified to the species level and checked with the
324 World Foraminifera Database (Hayward et al, 2021) for current taxonomic nomenclature (see
325 Appendix A for taxonomical references and Appendix B for census data). Because samples
326 were preserved and sorted in ethanol, many soft-shelled foraminiferal species may have
327 shrunk and become unrecognizable during picking. Thus, our counts probably underestimate
328 the soft-shelled foraminiferal abundance. For each core, we calculated different indices to
329 assess diversity. First, we calculated Species Richness (S) and then Shannon index, H' (log
330 base e) as an information-statistic index as described in Murray (2006). We determined the
331 Berger-Parker index, which represents the highest relative contribution (%) calculated for the
332 dominant taxon at each station. Each diversity index was calculated for the entirety of each
333 core studied. Digital photographs of major species (performed with a scanning electron
334 microscope) are available in Fontanier et al. (2022).

335

336 **4. Results**

337 *4.1 Sedimentary features at the seafloor*

338 In August 2017, Station 1 was characterized by a 5 cm-thick surface layer made of very fine
339 sand ($D_{50} > 75 \mu\text{m}$) (Fig. 4a). In February 2018, a sandy surface layer was still observed (D_{50}
340 $> 85 \mu\text{m}$) but its thickness was limited to the uppermost two centimeters (Fig. 4b). In April

341 2018, the uppermost centimeter was characterized by clay-silt facies ($D_{50} \sim 17 \mu\text{m}$) covering a
342 thin silty basal layer ($D_{50} \sim 50 \mu\text{m}$) (Fig. 4c). Beneath these surficial layers were dark grey
343 sediments comprising of highly compacted and sticky mud (D_{50} ranging between $10\text{--}30 \mu\text{m}$)
344 within which some dense (more silty) laminae were visible (Fig. 4a-c). Regardless of
345 sampling season, Station 2 was characterized by clay-silt facies (D_{50} ranging between $15\text{--}30$
346 μm) throughout the sampled section (Fig. 4d-f). Horizontal, vertical and oblique biological
347 structures (i.e., burrows) were abundant all along the cores, especially in April 2018. Station 4
348 presented homogeneous facies made of clayey silt (D_{50} ranging between $11\text{--}22 \mu\text{m}$) without
349 significant seasonal change (Fig. 4g-i).

350

351 *4.2 Foraminiferal faunas (>150 μm)*

352 *4.2.1 Additional details*

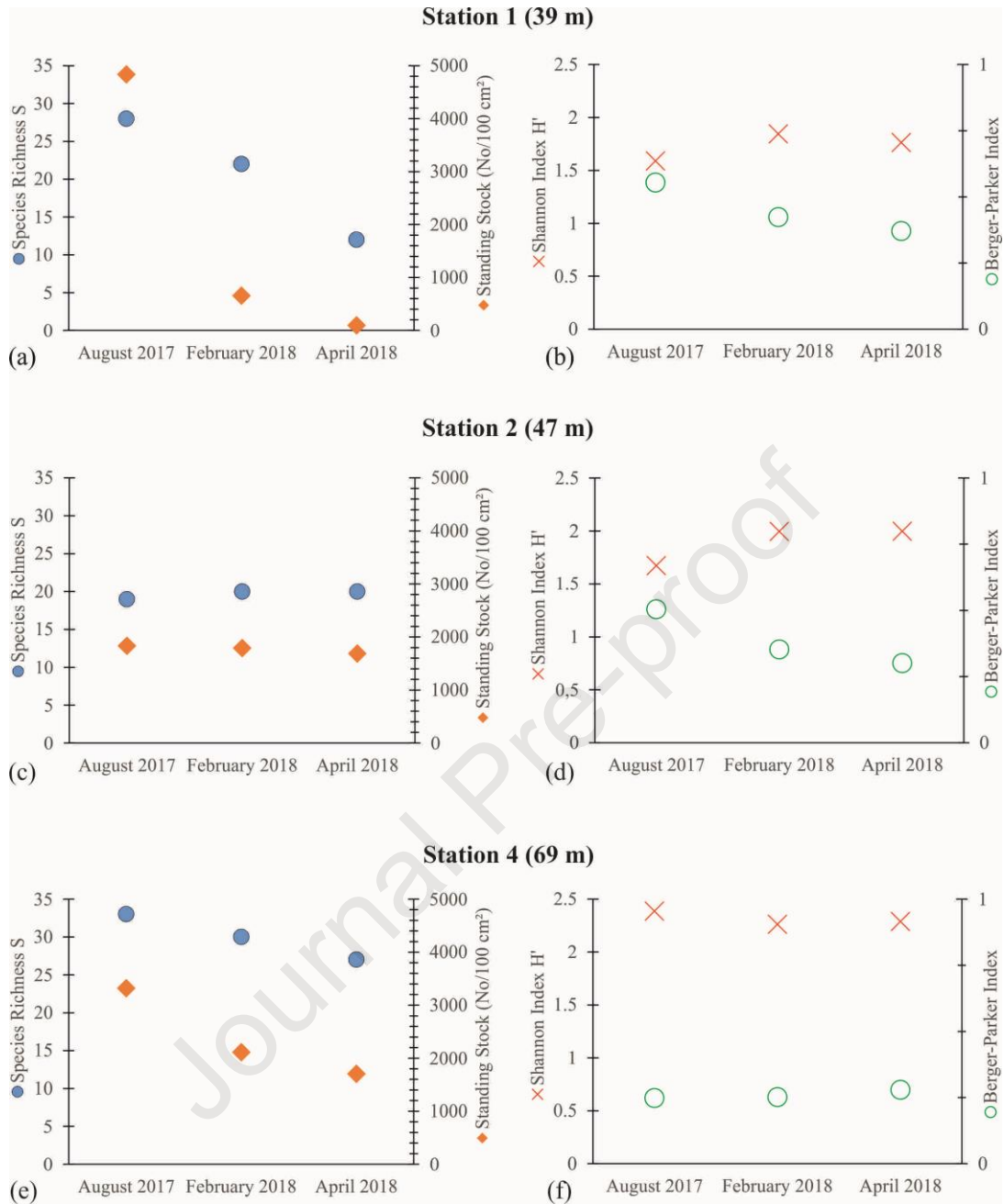
353 In this paper, we have focused on benthic foraminiferal communities above the $150 \mu\text{m}$ -size
354 fraction as bio-indicators of environmental conditions at three different stations for three
355 seasons (summer 2017, winter 2018 and spring 2018). Although it is recommended to study
356 several replicates at each site to obtain a more robust, averaged view of foraminiferal faunas
357 (Schönfeld et al., 2012), many publications on benthic foraminiferal ecology sampled in large
358 study areas integrating various marine ecosystems do not follow this recommendation (e.g.,
359 Fontanier et al., 2002; 2022; Duchemin, 2005; 2008; Goineau et al., 2011; Dessandier et al.,
360 2015; 2016). Environmental interpretations of modern foraminiferal faunas are frequently
361 based on a single sample per site (eg., Fontanier et al., 2022; de Oliveira et al., 2022; Natsir,
362 2022; Mamo et al., 2023). We therefore consider in this study that even if small-scale (metric)
363 spatial variability exists between benthic faunas living at the same station, this variability does
364 not hide the faunal variability existing at the spatial scale of the WGMP, given that the three
365 sampled stations are several kilometres apart from each other and belong to different

366 statistically derived faunal clusters (Fontanier et al. 2022). Finally, many recent studies
367 exclusively using $>150\ \mu\text{m}$ -sized benthic foraminifera living in the Bay of Biscay (e.g.,
368 Fontanier et al., 2002; Ersnt et al., 2005; Langezaal et al., 2006; Duchemin et al., 2005; 2008)
369 sufficiently elucidate foraminiferal diversity, standing stock and distribution on the Aquitaine
370 Shelf. Our study adds new and precious data about the temporal variability of benthic
371 environments from an inner-shelf mud patch.

372

373 *4.2.2 Standing Stocks and Diversity Indices*

374 At Station 1, total foraminiferal standing stocks decreased during the three sampling periods
375 from 4,839 individuals/100 cm^2 to 97 individuals/100 cm^2 (Fig. 5a). Accordingly, species
376 richness decreases also from 28 to 12 taxa throughout this time (Fig. 5a). The H' (/core)
377 values were low ranging between 1.59 in August 2017 and 1.84 in February 2018 (Fig. 5b).
378 Berger-Parker index (/core) decreased during the three sampling periods between 0.37–0.55.
379 At Station 2, total foraminiferal standing stocks decreased very slightly during the three
380 sampling periods between 1,835–1,690 individuals/100 cm^2 (Fig. 5c). Species richness is
381 almost invariable (values ranging between 19 and 20 taxa). The H' (/core) increased between
382 August 2017 (1.67) and April 2018 (1.99) (Fig. 5d). Berger-Parker index (/core) decreased
383 during the three sampling periods between 0.30–0.50. At Station 3, total foraminiferal
384 standing stocks decreased during the three sampling periods between 3,319–1,706
385 individuals/100 cm^2 (Fig. 5e). Species richness, which was higher compared to the other
386 stations, diminished between sampling seasons (values ranging between 27 and 3 taxa). The
387 H' (/core) varied between 2.26 in February 2018 and 2.38 in August 2017 (Fig. 5f). Berger-
388 Parker index (/core) increased very slightly during the three sampling periods between 0.25–
389 0.28.



390

391 *Figure 5. (a-b) Standing stocks and ecological indices describing foraminiferal faunas at the*
 392 *three stations 1, 2 and 4 from the WGMP during the three sampling periods. (a, c, e) Species*
 393 *Richness (S) and foraminiferal standing stocks (no. individuals/100 cm²); (b, d, f) Shannon*
 394 *(H') and Berger-Parker indices.*

395

396 *4.2.3 Foraminiferal Composition and Microhabitat*

397 At Station 1, *E. scaber*, the dominant species in August 2017 (55% of the total fauna; Fig. 6a),
398 progressively decreased in relative abundance in February and in April 2018 (42% and 27%
399 of the total fauna, respectively; Fig. 6b–c). Its absolute density diminished noticeably from
400 1,931 individuals/core in August 2017 to 19 individuals/core in Spring 2018 (Appendix B).
401 *Eggerelloides scaber* showed an erratic down-core vertical distribution with no preferential
402 microhabitat in August 2017. Then, in February and April 2018, it thrived preferentially in the
403 uppermost sediments with density maxima recorded in the top 3 cm (Fig. 6a). In terms of both
404 absolute and relative abundance, *Q. laevigata* followed the same trend as *E. scaber* with
405 values decreasing drastically between summer 2017 and spring 2018 (Fig. 6b–c and Appendix
406 B). Its microhabitat was erratic in August 2017 and changed to a shallow infaunal preference
407 in February and April 2018 (Fig. 6a). The relative proportion of *A. beccarii* increased from
408 12%–37% during the three sampling periods even if its absolute abundance decreased
409 gradually from 423 individuals/core in August 2017 to 26 individuals/core in April 2018. Its
410 vertical distribution also shows a preference for surficial sediments. *Bulimina aculeata*
411 showed an increase in its relative proportion throughout the sampling period (from 6%–14%)
412 whereas its absolute abundance decreased gradually from August 2017 to April 2018 (from
413 228–10 individuals/core) (Fig. 6a–c and Appendix B). It illustrated a plurimodal distribution
414 in August 2017 and in February 2018 (Appendix B).

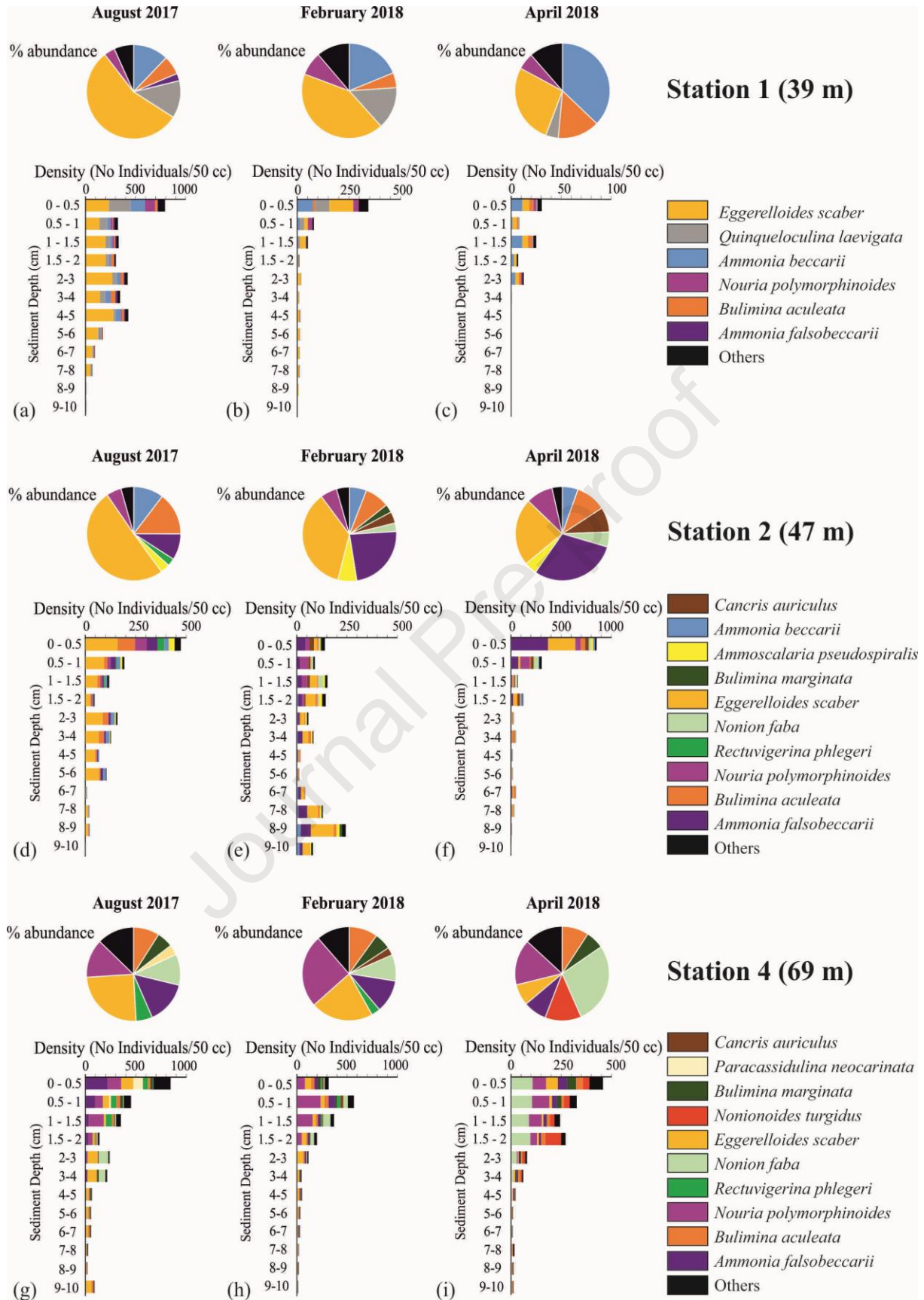
415

416 At Station 2, *E. scaber* (50% of the total fauna) was a dominant species during the three
417 sampling periods but its relative contribution decreased from 50% in August 2017 to 23% in
418 April 2018 (Fig. 6d–f). Its absolute abundance diminished from 667 individuals/core to 282
419 individuals/core (Appendix B). Showing an erratic down-core vertical distribution in August
420 2017 and in February 2018, it lived preferentially in the 0–0.5-cm interval in April 2018 (Fig.
421 6d–e). *Ammonia beccarii* constituted a major contributing taxon which decreased from 10%

422 to 5% between August 2017 and April 2018. Its absolute abundance diminished from 137
423 individuals/core to 68 individuals/core over the same period (Appendix B). *Ammonia beccarii*
424 exhibited a strongly erratic down-core vertical distribution. *Bulimina aculeata* showed
425 relative abundances ranging between 8% in February 2018 and 14% in August 2017. Its
426 absolute abundance decreased between August 2017 and April 2018 with values ranging
427 between 194 individuals/core and 127 individuals/core, respectively and showed a plurimodal
428 vertical distribution. *Ammonia falsobeccarii*'s relative contribution increased over the three
429 sampling periods (from 9% to 30% of the total fauna) (Fig. 6d–f). Its absolute abundance
430 tripled between August 2017 and April 2018 with values ranging between 119
431 individuals/core and 366 individuals/core (Appendix B). *Nouria polymorphinoides* (5% of the
432 total fauna in August 2017 increasing to 9% in April 2018) preferentially occupied the 0–0.5
433 cm interval in summer, then the 0.5–1 cm interval in winter and in spring 2018 (Fig. 6d–f). Its
434 absolute abundance increased slightly between August 2017 and April 2018 with values
435 ranging between 72 individuals/core and 111 individuals/core (Appendix B).

436
437 At Station 4, *E. scaber* was the dominant taxon in August 2017 and February 2018 (25% and
438 21% of the total fauna) presenting a plurimodal vertical distribution (Fig. 6g–h). Its relative
439 abundance decreased to 7% in April 2018 (Fig. 6i) and absolute abundance diminished
440 drastically from 594 individuals/core to 90 individuals/core between August 2017 to April
441 2018 (Appendix B). *Ammonia falsobeccarii* relative abundance decreased gradually from
442 15% to 8% over the three sampling periods whereas its absolute abundance decreased from
443 351 individuals/core to 98 individuals/core (Fig. 6g–I, Appendix B). This species
444 preferentially occupied the uppermost centimeter of sediment. *Nonion faba* increased from
445 11% to 28% of the total fauna over the three sampling periods (Fig. 6g–i). Its absolute
446 abundance increased from 256 individuals/core to 344 individuals/core between August 2017

447 and April 2018 (Appendix B). It was the most abundant between 2–4 cm in August 2017,
448 between 0.5–1.5 cm in February 2018 and between 0–1 cm in April 2018 (Appendix B).
449 *Nouria polymorphinoides*, a dominant taxon over the three sampling periods (values ranging
450 between 13% and 25% of the total fauna), preferentially occupied the uppermost 2 cm of
451 sediment. Its absolute abundance ranged between 193 individuals/core (April 2018) to 383
452 individuals/core (February 2018). *Nonionoides turgidus* was an abundant species (12%) in
453 April 2018, with 153 individuals/core (Fig. 6i, Appendix B).



454

455 Figure 6. (a-c) Foraminiferal composition and down-core distribution of live benthic
 456 foraminifera at the three stations 1 (a), 2(b) and 4 (c) sampled in August 2017, February

457 2018 and April 2018. Pie charts represent the composition of live benthic foraminiferal
458 faunas (composition in % of total fauna). The number of individuals belonging to the >150
459 μm -size fraction found in each level is standardized for a 50 cm^3 sediment volume. In both pie
460 charts and core distribution, only taxa with relative abundances >2.5% are pictured.

461

462 **5. Discussion**

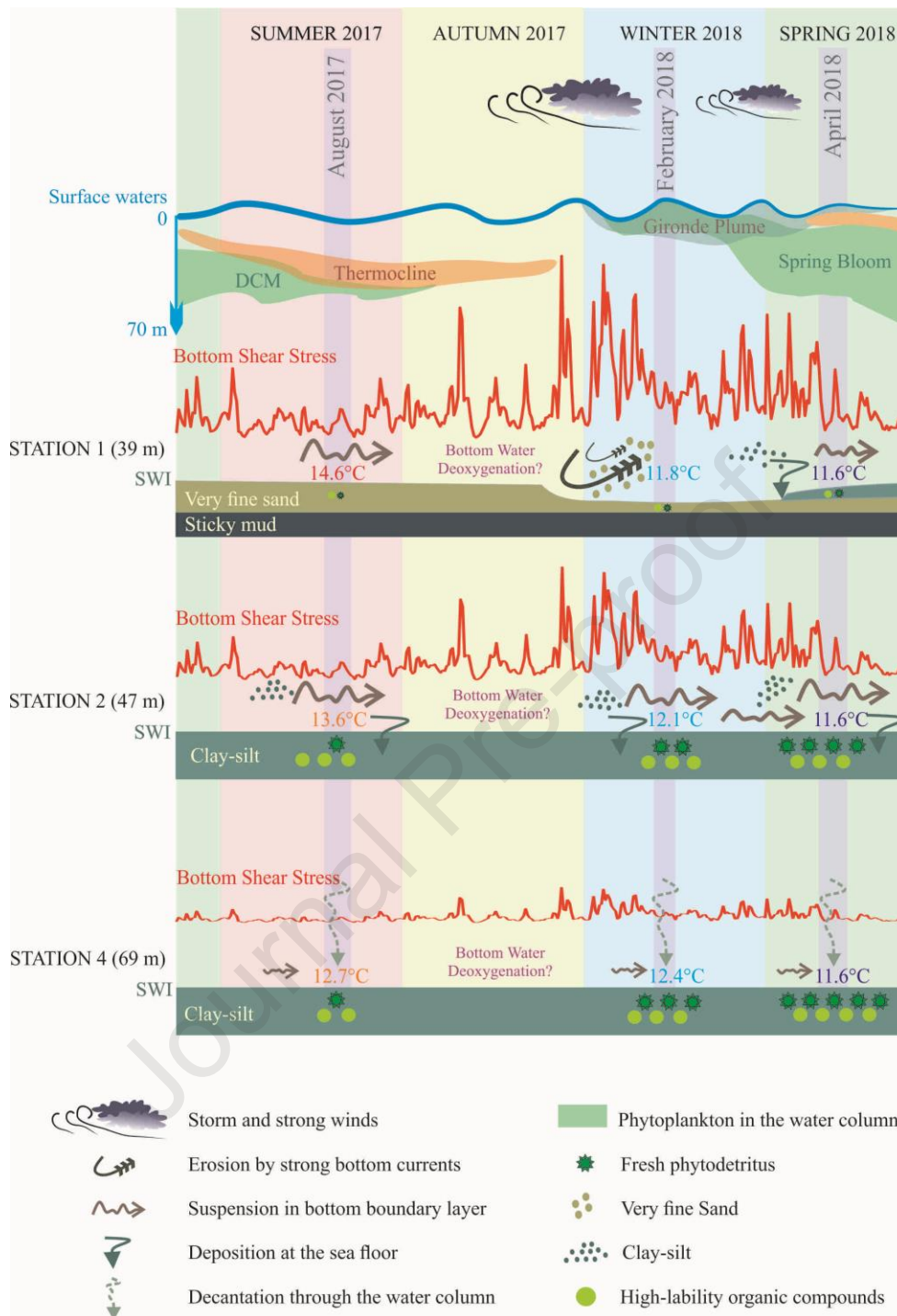
463 *5.1. Spatial and temporal variability of the WGMP (August 2017–April 2018)*

464 As already suggested by Lamarque et al. (2022), the comparison of our sedimentary
465 observations with Bottom Shear Stress (BSS) data indicates that the WGMP's
466 morphosedimentary characteristics have a seasonal variability largely dictated by
467 hydrometeorological constraints (Fig. 3b, Fig. 4). At Station 1 (39 m), the shallowest in our
468 transect, the sedimentary facies are the most variable. The sandy deposit observed in August
469 2017 was partially eroded by bottom currents likely linked to repeated storms in late autumn
470 and the following winter, and then covered by silty surface sediments before the April 2018
471 sampling (Fig. 3b, Fig. 4). Water column turbidity data show the existence of a basal
472 boundary layer a few metres thick, which was present during both February and April 2018
473 sampling cruises (Dubosq et al., 2022a), and which could be the product of bottom current
474 suspension of sedimentary material at Station 1. That being said, it is always possible that this
475 temporal variability is merely an echo of the small-scale spatial variability of the sedimentary
476 facies at Station 1, known to be located at the boundary between the mud patch and the
477 surrounding sandy environment (Dubosq et al., 2021). At Stations 2 (47 m) and 4 (69 m),
478 located deeper in the mud patch, the sedimentary facies were remarkably constant over the
479 three sampling periods. However, turbidity data also suggests the existence of a basal
480 boundary layer at Station 2 of suspended material (Dubosq et al., 2022a). This benthic

481 boundary layer is present in the median zone of the WGMP and could play a fundamental role
482 in the distribution of the finest particles and their organic load within the mud patch.

483 All stations show a temporal change in organic compounds accumulated below the sediment-
484 water interface. There is a marked enrichment of fresh and altered phytodetritus (chl-*a* and
485 phaeo-*a* content increasing over time) of a more marine origin (C:N ratio decreasing from 12
486 to 9) over the three seasons (Table 2). The temporal change in chlorophyll pigment content is
487 remarkable particularly at Station 4 (from 0.9 $\mu\text{g}\cdot\text{g}^{-1}$ to 5.9 $\mu\text{g}\cdot\text{g}^{-1}$ for chl-*a*, from 6.9 $\mu\text{g}\cdot\text{g}^{-1}$ to
488 29.3 $\mu\text{g}\cdot\text{g}^{-1}$ for phaeo-*a*) which is also accompanied by an increase of high-lability organic
489 matter (EHAA content increasing from 0.38 $\mu\text{g}\cdot\text{g}^{-1}$ to 0.72 $\mu\text{g}\cdot\text{g}^{-1}$ DW). Logically, diffusive
490 oxygen uptake (DOU), which echoes the aerobic mineralization of organic compounds, is
491 enhanced in April 2018 (Table 1). These important inputs of fresh and altered phytodetritus in
492 the spring period are not surprising in the Bay of Biscay. They are the sedimentary expression
493 of phytoplankton blooms occurring from the end of March until summer (e.g., Labry et al.,
494 2001; Lampert, 2001; Lampert et al., 2002; Fontanier et al., 2003; Dubosq et al., 2022a). The
495 warming of surface waters from the beginning of spring as well as the availability of nutrients
496 (e.g., nitrate, phosphate) stimulates the reproduction of diatoms and coccolithophores
497 (Lampert, 2001; González-Gil et al., 2017), resulting in high Chl-*a* concentration in the water
498 column in April 2018 (Fig. 2i). But this must be considered with the contribution of the
499 Gironde River plume and its nutrient supply to the region's surface waters as it could enhance
500 the phytoplankton bloom in late winter and early spring (Labry et al., 2001). The sedimentary
501 contribution of the Gironde River to the spatio-temporal dynamics of the mudflat is much
502 more difficult to establish. The high floods recorded during the winter period, especially in
503 January (Fig. 3a), have no effect on the C:N ratio of the organic matter of the WGMP (i.e., no
504 increase in C:N ratio values). On the contrary, between August 2017 and February 2018 the
505 C:N ratio of the organic compounds decreases suggesting the preferential deposition of

506 marine phytodetritus. Moreover, the increased remineralisation of organic compounds in
507 spring 2018 does not seem to have a major impact on the oxygenation of the bottom water,
508 which remains in oxic conditions ($BWO_2 > 180 \mu\text{mol.L}^{-1}$) (Dubosq et al., 2022a). This is
509 ecologically very important considering that bottom water dysoxia (even episodic) ($BWO_2 <$
510 $45 \mu\text{mol.L}^{-1}$) can induce substantial imbalance in benthic foraminiferal communities,
511 seasonally creating high mortality and drops in diversity (e.g., Bernhard and Sen Gupta, 1999;
512 Murray, 2006). This does not mean that deoxygenation of the bottom waters did not occur
513 during the autumn 2017 period (which we unfortunately did not sample). Oxygen depletion of
514 bottom waters (between 50 and 60% of oxygen saturation) has been documented by Dubosq
515 et al. (2022a) for the 2016 and 2021 autumnal periods. It should be noted that oxygenation is
516 maximal at all three sites in February 2018, when winter convection allows vertical
517 homogenisation of the water column offshore and lateral advection of well-oxygenated water
518 along the shelf floor (González-Gil et al., 2017). In figure 7, we propose a conceptual scheme
519 showing the summarised impact of hydrometeorological conditions (storms and associated
520 high swells) as well as the importance of the phytoplankton bloom on the sediment structuring
521 of the WGMP (inorganic sediments and organic matter) between August 2017 and April
522 2018.



523

524 *Figure 7. Conceptual diagram representing the spatial and temporal variability of the West-*
 525 *Gironde Mud Patch between summer 2017 and spring 2018. The hydrosedimentary processes*
 526 *(e.g., erosion, suspension) presumed to impact the sediment-water interface (SWI) of the three*
 527 *stations (Station 1, 2 and 4) are pictured by signs explained in the legend. The major*
 528 *hydrometeorological conditions retained in this figure vary depending on the depth of the*

529 sample site and are expressed via BSS values (Lamarque et al., 2021). Both the Gironde River
530 plume, which is clearly documented in winter, and spring phytoplankton bloom are pictured.
531 Bottom Water Temperatures (BWT) and the approximate position of the thermocline in the
532 water column are exhibited along with sedimentary features and concentration of
533 sedimentary organic compounds (fresh phytodetritus, labile compounds). A Deep Chlorophyll
534 Maximum (DCM) is illustrated during the summer stratification of surface waters.

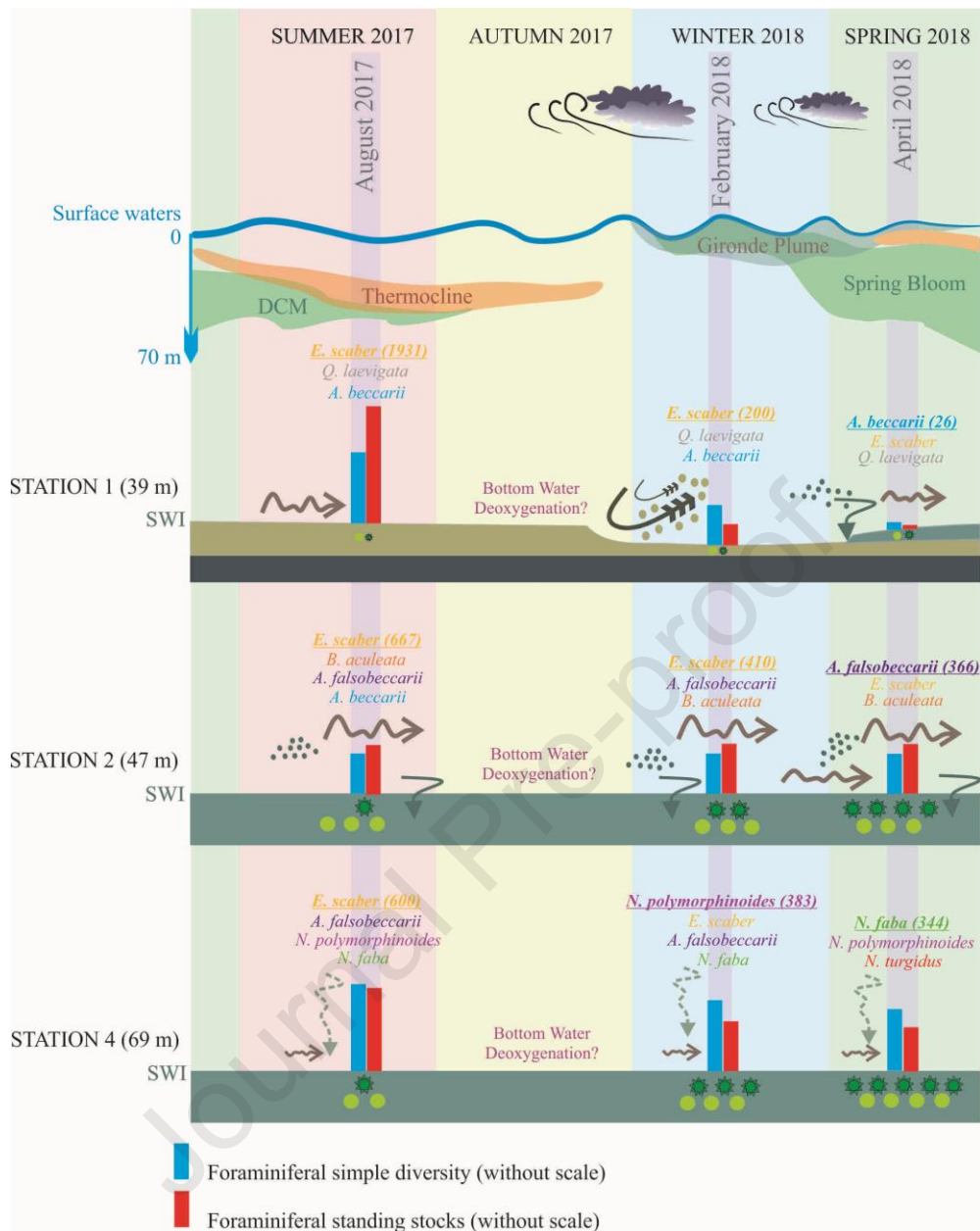
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536 5.2 Benthic foraminiferal variability

537 5.2.1 The proximal mud patch – Station 1

538 The most remarkable feature of our living benthic foraminiferal dataset is the impressive drop
539 in faunal diversity and standing stocks at Station 1 between August 2017 and April 2018 (S
540 decreasing from 28 to 12 taxa and standing stocks decreasing from 4,839 individuals/100 cm²
541 to 97 individuals/100 cm²) (Fig. 5a, Fig. 6a–c, Fig. 8). Such an alteration of the unicellular
542 meiofauna cannot be the result of any autumnal bottom-water deoxygenation. Foraminiferal
543 fauna can undergo compositional change, a drop in abundance and decreased diversity when
544 bottom water oxygenation reaches critical values (i.e., dysoxia, <45 µmol.L⁻¹) (Bernard and
545 Sen Gupta, 1999), but this is not the case in our study area, where bottom water stays oxic
546 even during so-called deoxygenation events (Dubosq et al., 2022a). It seems simplistic, to
547 hold a drop in bottom water temperature (by 3°C) as solely responsible for this faunal decline
548 (Gross, 2000). *Eggerelloides scaber*, the dominant species of Station 1, can live and dominate
549 benthic faunas in the colder waters of the North Sea Shelf (see literature review by Murray,
550 2006). The cause of this faunal regression must be sought in the impact of hydrosedimentary
551 conditions on the microhabitats occupied by foraminifera. The erosive and depositional
552 processes hypothesised to have impacted Station 1 during the winter (Fig. 7) may constitute
553 extremely restrictive ecological parameters for benthic fauna. In submarine canyons subject to

554 turbidity flows or on continental shelves subject to the colossal energy of a tsunami, benthic
555 faunas with low diversity are documented (Hess et al. 2005; Tsujimoto et al, 2020). Faunal
556 communities reflect the remnants of moribund adult assemblage or the first stages of a
557 recolonising substrate following the physical disturbance that destroyed the original benthic
558 habitat (e.g., Anchutz et al., 2002; Hess et al., 2005; Koho et al., 2007; Hess and Jorissen,
559 2009; Toyofuku et al., 2014). Opportunistic pioneer species can then be observed in low-
560 diversity faunas (such as *Psammospaera fusca* in Toyofuku et al., 2014). The same applies
561 to ecosystems in prodeltaic zones subject to sedimentary instability often linked to the inflow
562 of coastal rivers (Goineau et al., 2012). In these situations, benthic fauna can be reduced to a
563 single species, as illustrated by the over-dominance of *Leptohalysis scottii* in a 24 m-depth
564 station located 2 km from the mouth of the Rhône prodelta (Goineau et al., 2012). The
565 appearance of this opportunistic pioneer taxon followed an exceptional flood of the Rhône
566 and the sudden deposition of massive muddy sediments. In our case, the faunal composition
567 of Station 1 changed very little between August 2017 and April 2018 (Fig. 8). *Eggerelloides*
568 *scaber*, *A. beccarii* and *Quinqueloculina* spp. which are dominant at all 3 sampling periods,
569 are usually considered as neritic species living in shallow benthic environments with high
570 hydrodynamic energy and often connected to river mouths (e.g., Barmawidjaja et al, 1992;
571 Debenay and Redois, 1997; Diz et al, 2006; Diz and Francés, 2008; Goineau et al, 2011;
572 2012; Mendes et al, 2012; Dessandier et al, 2015; 2016; Fontanier et al, 2022). These taxa
573 seem to struggle within the proximal mud patch due to the probable partial destruction of their
574 microhabitat by intense erosional and depositional processes.



575

576 Figure 8. Conceptual diagram representing the spatial and temporal variability of
 577 foraminiferal faunas (>150 μm size fraction) in the West-Gironde Mud Patch between
 578 summer 2017 and spring 2018. The hydrosedimentary processes (e.g., erosion, suspension,
 579 deposition) assumedly affecting the water-sediment interface (SWI) of the three stations
 580 (Station 1, 2 and 4) are represented by figures explained in Figure 8. The nature of the
 581 sediments and the concentration of different sedimentary organic compounds are also shown
 582 (see caption of Figure 8 for further information). Underlined species are dominant in terms of
 583 relative abundance. The values between parentheses indicate the number of individuals per

584 core. The blue bars represent the simple diversity S . The red bars indicate the total
585 foraminiferal standing stocks. The height of the bars is used for comparison.

586

587 5.2.2 The median mud patch – Station 2

588 Although *E. scaber* is the dominant species at Station 2 in August 2017 and February 2018,
589 its absolute and relative abundances decrease over the three sampling periods. Absolute
590 abundance was diminished from 667 individuals/core to 282 individuals/core, and relative
591 abundance was decreased from 50% in August 2017 to 23% in April 2018 (Fig. 6d–f, Fig. 8).
592 In contrast, *A. falsobeccarii*, which is also a major species within the mud patch, shows a
593 gradual increase of absolute and relative abundances between summer 2017 and spring 2018
594 (threefold increase in standing stocks) (Fig. 6d–f, Fig. 8). This pattern follows the progressive
595 enrichment of surface sediments in fresh and degraded phytopigments as well as the relative
596 increase in OC content (Table 2, Fig. 7). This faunal trend suggests that phytodetritus plays a
597 significant ecological role in the seasonal dynamics of *A. falsobeccarii*, making a
598 phytophagous taxon quite reactive to the spring bloom inputs. This is unlike *E. scaber*, which
599 is more adapted to rely on altered and deeply buried organic compounds (Fontanier et al.,
600 2022). The erratic vertical distribution of *E. scaber* within anoxic sediments at our three
601 stations (Fig. 6a–i) underlines its capacity to thrive under low oxygenation without any
602 preference for fresh food (Diz et al., 2006; Langlet et al., 2014). Such behavior has also been
603 documented in laboratory experiments simulating hypoxia and/or organic supply with
604 sediment material sampled in the Bay of Biscay (Ernst et al., 2005). The microhabitat of *A.*
605 *falsobecarrii*, restricted to the first half centimetre below the sediment-water interface in April
606 2018 (Fig. 6f) seems to argue for its trophic preference for freshly deposited phytodetritus.
607 However, it is of note that this assumed seasonal response of *A. falsobeccarii* does not result
608 in a general increase in the standing stock of benthic foraminiferal fauna, as might be

609 expected when opportunistic species react strongly to changes in preferred food supply. Only
610 some other secondary species (*Nouria polymorphinoides*, *Cancris auriculus*, *N. faba*) show a
611 notable but moderate burst of their absolute abundance in spring 2018. This could be linked to
612 the fraction studied in this paper (>150 µm size fraction) which does not necessarily include
613 the most opportunistic taxa, those of small size such as *Epistominella* spp., *Bolivina* spp. and
614 *Cassidulina* spp. which can develop significant numbers in a few weeks after a sudden influx
615 of phytodetritus (e.g., Fontanier et al., 2003; Duijnsteet al., 2004; Langezaal et al., 2006;
616 Duchemin et al., 2008; Goineau et al., 2012).

617

618 4.2.3 The distal mud patch – Station 4

619 At Station 4, the empirical relationship linking *A. falsobeccarii* to the seasonal enrichment of
620 surface sediments in chlorophyll pigment is not reflected. On the contrary, its relative and
621 absolute abundances decrease over the three sampling periods while the sediment is gradually
622 enriched in fresh and degraded chlorophyll-a (relative abundance decreasing gradually from
623 15% to 8% over the three sampling periods, absolute abundance decreasing from 351
624 individuals/core to 98 individuals/core) (Fig. 6g–i, Fig. 8). The apparent interpretive
625 contradiction between the observations made at Stations 2 and 4 could be explained by the
626 role of biotic factors on the development of the different foraminiferal populations. The
627 regression of *A. falsobeccarii* (and also *E. scaber*) could be linked to the competition between
628 species for access to different food sources. This interspecific constraint is often neglected in
629 the understanding of the ecology of benthic foraminifera. At Station 4, the most
630 taxonomically diverse of the stations studied, *N. faba* and *N. turgidus* are better adapted than
631 *A. falsobeccarii* to take advantage of seasonal inputs of fresh and degraded phytodetritus.
632 Their respective ability to occupy deeper microhabitats in the sediment allows them to access
633 more degraded organic matter buried deep in the sediment, especially in spring 2018 (Fig. 6i).

634 In fact, *N. faba* is commonly described in mid- and outer-shelf environments including from
635 subsurface sediments (e.g., Debenay and Redois, 1997; Fontanier et al., 2002; Langezaal et
636 al., 2006; Duchemin et al., 2005; 2008; Goineau et al., 2011; Dessandier et al., 2015; 2016).
637 This species dominates the >150 μm -sized faunas sampled between 80–140 m depth in La
638 Grande Vasière mud belt in the Bay of Biscay (NE Atlantic), especially in spring during the
639 bloom period (Duchemin et al., 2005; 2008). Documented as a deep infaunal dweller at a 150
640 m-depth station in the Southern Bay of Biscay (Langezaal et al., 2006), this taxon is capable
641 of migration upward to surface sediments to access fresher phytodetritus . This microhabitat
642 and trophic plasticity makes *N. faba* an excellent competitor for space and food during spring
643 bloom episodes in the WGMP. *Nonionoides turgidus* is a very reactive species within the
644 distal part of the mud patch (its standing stocks increasing from 11 individuals/core in
645 February to 153 individuals/core in April). Goineau et al. (2011) also documented the
646 dominance of *N. turgidus* (*Nonionella turgida* in their study) at depths ranging between 47–62
647 m close to the Rhône River mouth. There, this species takes advantage of terrestrial and
648 marine organic compounds buried within the sediments (Goineau et al., 2011; 2012). *N.*
649 *turgidus* has been documented in the La Grande Vasière mud belt where it dominates
650 autumnal faunas to benefits from the combination of continental organic matter and altered
651 marine phytodetritus (Duchemin et al., 2008).

652

653 **6. Conclusions**

654 Living shelf foraminiferal faunas have been studied at three stations located along a shore to
655 open ocean transect between 39–69 m depth in the West-Gironde Mud Patch (WGMP) (Bay
656 of Biscay, NE Atlantic) to understand how complex the temporal variability of the
657 environmental conditions (e.g., hydrosedimentary process, sedimentary organic matter,
658 oxygenation level) control their ecological patterns (i.e., diversity, faunal composition,

659 standing stock, and microhabitats). To do so, the WGMP was sampled in August 2017 (boreal
660 summer), February 2018 (winter) and April 2018 (spring), which are very different in terms
661 of meteorological patterns and benthic environmental conditions. The main findings of this
662 study are:

663

664 (1) The shallowest station (Station 1, 39 m) closest to shore is subject to significant
665 variability in sedimentary facies in relation to hydrometeorological constraints (strong
666 storms and swells), which are extremely marked in late autumn and throughout winter.
667 The erosion of the sandy substrate by strong bottom currents and the deposition of
668 silty surface layer leads to a marked drop in the diversity and density of adult
669 foraminifera in February and April 2018. All species are affected by this
670 hydrosedimentary instability, due to the partial destruction of their microhabitat by
671 intense erosional and depositional processes.

672 (2) At the station located in the central area of the WGMP (Station 2, 47 m), benthic fauna
673 changes in a more gradual manner. The sedimentary imprint of the spring
674 phytoplankton bloom is clearly recorded in April 2018 with an increase in fresh an
675 altered phytopigment content in the surface sediment. *Eggerelloides scaber*, a deposit
676 feeder and hypoxia-tolerant species, dominated the 2017 summer foraminiferal fauna
677 and was gradually replaced by *A. falsobeccarii* which may be considered a
678 phytophagous taxon that is reactive to spring bloom inputs.

679 (3) At the most ocean-ward station of the WGMP (Station 4, 69 m), *E. scaber* and *A.*
680 *falsobeccarii* are outcompeted and gradually replaced by *N. faba* and *N. turgidus*.
681 Both species present microhabitat and dietary plasticity that helps them to settle in
682 surface and subsurface sediments during the spring bloom period. There, they rely on
683 both fresh and altered phytodetritus.

684

685 **Acknowledgement**

686 We would like to thank the crews and the captain of the Côte de la Manche (CNRS-INSU)
687 during the JERICOBENT-2, JERICOBENT-3 and JERICOBENT-4 cruises. We have special
688 thoughts for all scientific members who participated to this scientific mission. This work was
689 supported by: (1) the JERICO-NEXT project (European Union's Horizon 2020 Research and
690 Innovation program under grant agreement no. 654410), (2) the VOG project (LEFE-CYBER
691 and EC2CO-PNEC), and (3) the MAGMA project (COTE cluster of Excellence ANR-10-
692 LABX-45). Finally, we thank all reviewers who have provided very useful comments to
693 improve the overall quality of this paper.

694

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940 **Appendix captions**

941

942 **Appendix A**

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

946

947 **Appendix B**

948 Census data for live (stained) benthic foraminifera in the $>150\ \mu\text{m}$ fraction for the three
949 stations sampled in the West-Gironde Mud Patch and for the three sampling periods. N.B.
950 Numbers are not standardized for sediment volume. Supplementary data associated with this
951 article can be consulted in the online version at xxxx.

Station	Depth (m)	Latitude	Longitude	Sampling period	BWT (°C)	BWS	BWO ₂ (μM)	% Sat.	OPD (cm) (N)	DOU (mmol m ⁻² d ⁻¹) (N)
1	~39	45°45.550'	1°31.335'	August 2017	14.6	35.2	184.7	71.9	0.36 ± 0.16 (10)	2.87 ± 1.17 (10)
				February 2018	11.8	34.8	219.7	79.0	0.41 ± 0.08 (7)	2.82 ± 0.74 (7)
				April 2018	11.6	35.0	180.6	65.8	0.56 ± 0.29 (11)	5.76 ± 2.36 (11)
2	~47	45°43.567'	1°37.657'	August 2017	13.6	35.2	196.5	83.0	0.61 ± 0.32 (12)	3.23 ± 0.50 (12)
				February 2018	12.1	35.2	255.7	94.4	0.53 ± 0.09 (4)	4.57 ± 3.44 (4)
				April 2018	11.6	35.1	218.1	79.5	0.70 ± 0.10 (12)	4.12 ± 1.66 (12)
4	~69	45°43.993'	1°37.427'	August 2017	12.7	35.2	185.3	69.2	0.37 ± 0.08 (11)	5.92 ± 2.89 (11)
				February 2018	12.4	35.4	255.4	94.6	0.65 ± 0.08 (7)	5.53 ± 1.57 (7)
				April 2018	11.6	35.2	236.6	87.7	0.38 ± 0.06 (10)	8.96 ± 2.20 (10)

Station	Sampling period	OC		TN		C:N ratio		Chl- <i>a</i> μg g ⁻¹	Phaeo- <i>a</i> μg g ⁻¹	Chl- <i>a</i> /(Chl- <i>a</i> + Phaeo- <i>a</i>)	N	Station	Sampling period	δ ¹³ C _{OM} ‰	δ ¹⁵ N _{OM} ‰	N	THAA mg g ⁻¹ DW	EHAA mg g ⁻¹ DW	EHAA/THAA	
		%DW	N	%DW	N	N	N												%	N
1	August 2017	0.31 ± 0.04	5	0.03 ± 0.00	5	12.11 ± 1.59	5	0.23 ± 0.09	1.46 ± 0.46	0.13 ± 0.02	3	1	August 2017	-24.44 ± 0.35	4.71 ± 0.09	2	0.51 ± 0.18	0.16 ± 0.04	32.23 ± 3.79	3
	February 2018	0.28 ± 0.15	5	0.03 ± 0.01	5	10.70 ± 1.40	5	0.52 ± 0.37	2.53 ± 1.58	0.16 ± 0.02	3		February 2018	-25.12 ± 0.23	4.16 ± 0.27	2	0.72 ± 0.32	0.29 ± 0.12	40.97 ± 2.04	3
	April 2018	0.92 ± 0.21	5	0.12 ± 0.03	5	9.17 ± 0.87	5	0.66 ± 0.05	3.67 ± 0.38	0.15 ± 0.01	3		April 2018	-24.29 ± 0.00	5.78 ± 0.05	2	0.98 ± 0.51	0.26 ± 0.04	29.61 ± 11.03	3
2	August 2017	0.89 ± 0.06	5	0.10 ± 0.01	5	10.07 ± 1.07	5	1.15 ± 0.20	6.65 ± 0.88	0.15 ± 0.03	3	2	August 2017	-24.22 ± 0.55	5.82 ± 0.01	2	3.23 ± 0.29	0.61 ± 0.02	18.91 ± 1.36	3
	February 2018	1.02 ± 0.54	5	0.12 ± 0.06	5	10.32 ± 1.00	5	2.09 ± 0.72	9.61 ± 2.47	0.18 ± 0.02	3		February 2018	-24.58 ± 0.48	5.80 ± 0.25	2	3.10 ± 0.16	0.59 ± 0.14	19.00 ± 4.24	3
	April 2018	1.14 ± 0.39	5	0.13 ± 0.05	5	9.92 ± 0.47	5	4.54 ± 1.96	18.16 ± 8.17	0.20 ± 0.01	3		April 2018	-24.05 ± 0.05	5.89 ± 0.00	2	3.94 ± 0.67	0.56 ± 0.07	14.23 ± 1.44	3
4	August 2017	1.38 ± 0.05	5	0.14 ± 0.00	5	11.16 ± 0.29	5	0.91 ± 0.18	6.90 ± 1.28	0.12 ± 0.04	3	4	August 2017	-24.03 ± 0.38	5.73 ± 0.12	2	4.10 ± 0.19	0.38 ± 0.02	9.14 ± 0.50	3
	February 2018	1.54 ± 0.14	5	0.19 ± 0.02	5	9.48 ± 0.57	5	1.12 ± 0.17	9.51 ± 1.86	0.11 ± 0.01	3		February 2018	-23.91 ± 0.10	5.64 ± 0.08	2	4.32 ± 0.43	0.57 ± 0.07	13.30 ± 3.00	2
	April 2018	1.42 ± 0.13	5	0.18 ± 0.02	5	9.44 ± 0.48	5	5.86 ± 0.85	29.35 ± 2.83	0.17 ± 0.01	3		April 2018	-23.74 ± 0.31	5.80 ± 0.14	2	4.56 ± 0.49	0.72 ± 0.20	15.27 ± 2.81	3

- Seasonal variability of living benthic foraminifera is studied in the WGMP.
- Hydrosedimentary processes and food availability control foraminiferal changes.
- A conceptual scheme shows the interconnexion between foraminifera and biotopes.

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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:

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