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► To cite this version:

Bastien Lamarque, Bruno Deflandre, Sabine Schmidt, Nicolas Lavesque, Guillaume Bernard, et al.. Assessing spatiotemporal changes in the benthic habitats of the West Gironde Mud Patch through the analyses of surface sediments, benthic macrofauna and sediment profile images. *Continental Shelf Research*, 2026, 298, 105637 (14p.). <10.1016/j.csr.2025.105637>. <hal-05502406>

HAL Id: hal-05502406

<https://hal.science/hal-05502406v1>

Submitted on 24 Apr 2026

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1 **Assessing spatiotemporal changes in the benthic habitats of the West Gironde Mud Patch**
2 **through the analyses of surface sediments, benthic macrofauna and sediment profile images**

3
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18
19 **Abstract**

20 This work aims to refine the current assessment of spatiotemporal changes in the benthic
21 habitats of the West Gironde Mud Patch, which is a high-energy, tidally influenced temperate
22 River-dominated Ocean Margin. This was achieved by: (i) extending the observation period for
23 surface sediment characteristics and benthic macrofauna composition, and (ii) assessing
24 sediment profile image characteristics. Five stations located along a depth gradient were
25 sampled during 8 cruises between summer 2010 and fall 2021. Results confirm the spatial
26 segmentation into proximal and distal parts. Temporal changes were both seasonal and
27 interannual, with different magnitudes depending on descriptors. Temporal changes in
28 surface sediment characteristics were essentially seasonal, occurring mostly in spring.
29 Temporal changes in benthic macrofauna composition were mostly interannual with a
30 significant difference between summer 2010 and all subsequent cruises. This was previously
31 attributed to a major physical disturbance that occurred during the 2013-2014 winter.
32 Extending the observation period therefore suggests that full recovery of benthic macrofauna
33 composition had not yet been achieved 8 years after the postulated disturbance. Temporal

34 changes in sediment profile image characteristics were intermediate, showing: (i) clear
35 seasonal changes at the two deepest stations, mostly associated with a spring increase in tube
36 numbers, and (ii) no significant difference between summer 2010 and the other cruises,
37 except at the deepest station. The overall discrepancy between the benthic macrofauna
38 composition and sediment profile image characteristics may result from the low abundance
39 of bioturbators and differences in the recovery dynamics of benthic macrofauna composition
40 and functionality.

41

42 **Keywords:** West Gironde Mud Patch, Benthic habitats, Surface sediment, Benthic
43 macrofauna, Sediment Profile Imaging, Hydrodynamics

44

45 **Abbreviations:**

46 aRPD: apparent Redox Potential Discontinuity

47 BSS_{95th}: Bottom Shear Stress 95th percentile values

48 Chl-*a*: Chlorophyll *a*

49 nMDS: non-Metric Multidimensional Scaling

50 PCA: Principal Components Analysis

51 PERMANOVA: PERmutational Multivariate ANalyses Of VAriance

52 Phaeo-*a*: Phaeophytin *a*

53 POC: Particulate Organic Carbon

54 RiOMar: River-dominated Ocean Margin

55 SIMPROF: SIMilarity PROFile

56 SPI: Sediment Profile Image

57 WGMP: West Gironde Mud Patch

58

59 **1. Introduction**

60 River-dominated Ocean Margins (RiOMars) are the parts of continental shelves
61 impacted by major rivers freshwater and/or sediment discharges. These areas are the main
62 marine primary depositional areas for riverine particulate continental inputs (Burdige, 2005;
63 McKee et al., 2004). Coastal transition zones and RiOMars provide a large variety of ecosystem
64 functions (Aller et al., 1998; Levin et al., 2001). RiOMars account for 40 to 50% of the burial of
65 continental Particulate Organic Carbon (POC) occurring in continental margins (Blair and Aller,
66 2012; Burdige, 2005; Hedges and Keil, 1995). The assessment of the functioning of their
67 benthic compartments is therefore essential to reach a comprehensive understanding of their
68 contribution to global biogeochemical cycles (Aller, 1998; Blair and Aller, 2012). Two main
69 studies have attempted to classify RiOMars based mainly on geomorphological and
70 biogeochemical features in tropical and subtropical systems (Blair and Aller, 2012; McKee et
71 al., 2004). Their results highlighted the major role of hydrodynamics in controlling RiOMar
72 morphologies and balance between POC mineralization and burial. Blair and Aller (2012)
73 established a clear distinction between: (1) low-energy systems, with both high sedimentation
74 rates and carbon preservation and (2) high-energy tidal and/or wave systems with both high
75 sediment oxygenation and low carbon preservation.

76 The biogeochemical functioning of RiOMar sediments has been extensively studied
77 (Aller, 1998; Aller et al., 2008, 2004, 1996; Aller and Blair, 2006; Bao et al., 2018; Blair et al.,
78 2004; Cathalot et al., 2010; Pastor et al., 2011a). The interactions between this functioning
79 and benthic macrofauna have been first conceptualized by Rhoads et al. (1985), and then
80 directly addressed mostly in tropical and subtropical systems (Aller and Aller, 2004; Aller and
81 Stupakoff, 1996; Aller et al., 1991, 1996; Alongi et al., 1992). Temperate RiOMars have
82 received less attention because large temperate rivers contribute less to the transfer of
83 freshwater from the continent to the ocean (Dagg et al., 2004). Most studies have focussed
84 on low-energy RiOMars, addressing changes in benthic macrofauna composition in relation to
85 river discharges (Hermand et al., 2008; Juan and Cartes, 2011; Martin et al., 2019; Nasi et al.,
86 2020; Salen-Picard et al., 2003; Wijsman et al., 1999). A few have also indirectly assessed the
87 functional consequences of these changes, mostly using the bioturbation index (e.g. Nasi et
88 al., 2019; Vesal et al., 2023). There is still a clear need to address spatiotemporal changes in
89 the composition of benthic macrofauna, and to assess more readily some of their functional
90 consequences in high-energy temperate RiOMars.

91 The West Gironde Mud Patch (WGMP) is a large sedimentary deposit located in the
92 Bay of Biscay (NE Atlantic) off the mouth of the Gironde Estuary. The WGMP is the main
93 depocenter of fine particles originating from this estuary (Jouanneau et al., 1989; Weber et
94 al., 1991). Early sedimentological surveys (Lesueur et al., 2002, 2001; Lesueur and Tastet,
95 1994) attributed a major role to the strong hydrodynamics prevailing in the Bay of Biscay in
96 the spatial structuring of WGMP benthic habitats with a clear separation between a shallower
97 proximal part, where modern sedimentation is only transient, and a deeper distal part where
98 modern sedimentation does take place (Jouanneau et al., 1989). This was later confirmed by
99 the assessments of spatiotemporal changes in surface sediment characteristics and benthic
100 macrofauna composition, which led to the classification of the WGMP as a high-energy
101 temperate tidal RiOMar (Lamarque et al. 2022). These authors also pinpointed major changes
102 in benthic macrofauna composition between 2010 and 2016, and interpreted them as
103 resulting from a recovery process following a major physical disturbance caused by an
104 exceptional series of severe storms in the 2013-2014 winter. However, they emphasised that
105 this interpretation should be considered only as a working hypothesis due to: (i) the limited
106 number of sampling occasions, and (ii) the fact that the initial composition of the benthic
107 macrofauna observed in 2010 had not yet returned by 2016.

108 The present study is first aiming at improving/addressing these two issues by extending
109 the WGMP observation period for surface sediment characteristics and benthic macrofauna
110 composition. Moreover, there is currently no information available regarding potential
111 functional impacts resulting from spatiotemporal changes in benthic macrofauna composition
112 within the WGMP. Sediment Profile Imaging (Rhoads and Young, 1970) provides valuable *in-*
113 *situ* information on early diagenetic processes, including sediment oxygenation and
114 bioturbation (Gerwing et al., 2015; Rhoads and Germano, 1982; Statham et al., 2019; Teal et
115 al., 2013, 2010; Wilson and Vopel, 2012; Wilson et al., 2009; Devereux et al., 2019). This
116 technology has already been successfully deployed in the WGMP through an extensive
117 sampling achieved during a single cruise (Lamarque et al., 2021). Spatial changes in Sediment
118 Profile Image (SPI) characteristics proved largely similar to those derived from the analyses of:
119 (i) surface sediment characteristics, and (ii) benthic macrofauna composition (Lamarque et al.,
120 2022). Conversely, the coherence and complementarity between the assessments of WGMP
121 temporal changes in benthic macrofauna composition, surface sediments and SPI
122 characteristics are yet largely to be tested. The present study is therefore also aiming at

123 assessing spatiotemporal changes in SPI characteristics, and comparing them with those of
124 surface sediment characteristics and benthic macrofauna composition.

125

126 **2. Materials & Methods**

127 **2.1. Sampling**

128 From summer 2010 to fall 2021, 5 stations (1, 2, 3, 8 and 4; **Figure 1**) located along a
129 depth gradient were sampled during 8 cruises (Deflandre, 2016; Deflandre et al., 2021). The
130 sampling aimed to assess: (i) surface sediment characteristics, (ii) benthic macrofauna
131 composition and (iii) Sediment Profile Image (SPI) characteristics. **Table I** details the sampling
132 (i.e., what was sampled and at which site) as it was not always possible to sample all stations.
133 For example, only four stations were sampled in winter 2018 due to poor weather conditions,
134 whereas SPI characteristics were not acquired at station 8 in spring 2021 due to a technical
135 issue. **Table I** also distinguishes between new original results and already published ones.

136

137 **2.2. Data acquisition**

138 **2.2.1 River discharge and Bottom Shear Stress**

139 The mean daily water discharge of the Gironde was obtained by summing the
140 discharges from its two main tributaries: the Garonne and Dordogne rivers. Data were
141 collected at Tonneins (site O900 0010) and Lamonzie Saint-Martin (site P532 0010)
142 (<http://www.hydro.eaufrance.fr>).

143 Bottom shear stress was computed from the outputs of a 3D numerical model (Diaz et
144 al., 2024, 2020) combining the MARS3D hydrodynamic model (Lazure and Dumas, 2008) and
145 the WAVE WATCH III® wave model (Roland and Arduin, 2014). This model has a resolution of
146 ca. 0.5x0.5 km². It integrates realistic hydro-meteorological forcings (i.e., wind, tide, surge and
147 river flow). Hourly outputs of bottom shear stress (BSS) were computed (Soulsby 1997) and
148 daily compiled from 2010 to 2021. The 95th percentiles values (BSS_{95th}) were used to assess
149 the intensity changes of BSS (Lamarque et al., 2022).

150

151 **2.2.2 Surface sediment characteristics**

152 Undisturbed sediment cores (10 cm in internal diameter) were collected using an
153 Uwitec® (Mondsee®) corer in spring (June) 2018, and during all other cruises using a MC6
154 Oktopus GmbH® multicorer. Surface sediment characteristics were assessed in the top half-

155 centimetre of the sediment column. The analytical protocols were strictly identical for all eight
 156 cruises. Sediment grain size distributions were analyzed using a Master Sizer laser
 157 microgranulometer (Malvern®), and the median diameter (D_{50}) was derived since the
 158 distributions were unimodal. POC was measured using a LECO® (St. Joseph®) CS 200 analyser,
 159 after overnight 2M HCl decarbonation of previously freeze-dried sediments. Chlorophyll-*a*
 160 (Chl-*a*) and Phaeophytin-*a* (Phaeo-*a*) were measured on thawed frozen (-20°C) sediment after
 161 overnight acetone extraction (90% final concentration) using a Perkin Elmer® LS-55
 162 spectrofluorometer (Neveux and Lantoiné, 1993). The Chl-*a*/(Chl-*a* + Phaeo-*a*) ratio was used
 163 as an index of the lability of vegetal biomass (Bonifácio et al., 2014; Pastor et al., 2011b).

164

165 **Table I:** Summary of the main categories of parameters assessed at the five studied stations
 166 and during the eight sampling cruises constitutive of the present study. Bold types are
 167 indicative of the parameters only analyzed in the present study. When data have already been
 168 published, the publication is referenced.

Cruises	Category of parameters			References
	Surface Sediment Characteristics	Benthic Macrofauna Composition	Sediment Profile Image Characteristics	
Summer 2010	1, 3, 4	1, 3, 4	1, 3, 4	Massé <i>et al.</i> 2016 & Present study
Fall	1, 2, 3, 8, 4	1, 2, 3, 8, 4	1, 2, 3, 8, 4	
Summer 2017	1, 2, 3, 8, 4	1, 2, 3, 8, 4	1, 2, 3, 8, 4	Lamarque <i>et al.</i> 2022 & Present study
Winter 2018	1, 2, 3, 4	1, 2, 3, 4	1, 2, 3, 4	
Spring (April) 2018	1, 2, 3, 8, 4	1, 2, 3, 8, 4	1, 2, 3, 8, 4	
Spring (June) 2018	1, 2, 3, 8, 4		1, 2, 3, 8, 4	Lamarque <i>et al.</i> 2021
Spring 2021	1, 2, 3, 8, 4	1, 2, 3, 8, 4	1, 2, 3, 4	Present study
Fall 2021	1, 2, 3, 8, 4	1, 2, 3, 8, 4	1, 2, 3, 8, 4	

169

170

171

172 **2.2.3 Benthic macrofauna composition**

173 Benthic macrofauna was sampled using a 0.25 m² Hamon grab (3 replicates), sieved on
174 a 1 mm mesh and fixed with 4% formalin. Individuals were sorted, identified to the lowest
175 tractable taxonomic level (usually species) and counted. Although the protocol was strictly
176 identical for all 8 cruises, taxonomic resolution was degraded to the genus level to avoid any
177 possible operator effect.

178

179 **2.2.4 Sediment Profile Image characteristics**

180 Between 6 (all stations in spring (June) 2018) and 17 (station 2 in spring 2021) SPIs
181 were collected for each combination of stations and cruises using an Ocean Imaging Systems®
182 Sediment Profile Imager fitted with a Nikon® D7100 camera. Individual SPIs were analysed for:
183 (i) mean depths of apparent Redox Potential Discontinuities (aRPDs), (ii) numbers of tubes and
184 fauna (i.e., epifauna plus infauna), (iii) normalized surface areas of subsurface structures (i.e.,
185 surface areas of burrows and oxic voids divided by the total surface area of the sediment
186 column), and (iv) mean depths of oxic voids within the sediment column. All analyses were
187 achieved by the same operator (BL) using the SPIArcBase software (Romero-Ramirez et al.,
188 2013). For each characteristic, means and standard deviations were computed for each
189 combination of stations and cruises.

190

191 **2.3. Data analysis**

192 Euclidean distance based Two-Way (i.e., 3-5 stations and 7-8 cruises, **Table I**) crossed
193 PERmutational Multivariate ANALyses Of Variance (PERMANOVAs; Anderson, 2001) were
194 performed on individual parameters with replication (i.e., benthic macrofauna abundances
195 and individual SPI characteristics) to assess the significance of their spatiotemporal changes.
196 Dissimilarity/distance matrices between combinations of stations and cruises were computed
197 from: (i) all normalized surface sediment characteristics (Euclidean distance), (ii) square root
198 transformed benthic macrofauna composition data (Bray-Curtis dissimilarity), and (iii) all
199 normalized SPI characteristics (Euclidean distance). Hierarchical clustering (average group
200 linking) and either Principal Component Analyses (PCA, surface sediment and SPI
201 characteristics) or non-metric MultiDimensional Scaling (nMDS, benthic macrofauna
202 composition) were then achieved to: (i) define stations*cruises groups, and (ii) describe
203 spatiotemporal changes. SIMilarity PROFile procedures (SIMPROF; Clarke et al., 2008) were

204 used to test for the statistical significance (5% threshold) of differences between groups
205 resulting from hierarchical clustering. One-Way PERMANOVAs (with station as a fixed factor)
206 were achieved on distances/dissimilarities for stations 1, 3 and 4 to assess inter-station
207 differences in the magnitude of temporal changes between summer 2010 and 2016-2021
208 cruises.

209 All analyses were performed using the PRIMER® 6 software package (Clarke and
210 Warwick, 2001) with the PERMANOVA+ add-on (Anderson et al., 2008).

211

212 **3. Results**

213 **3.1. River discharges and Bottom Shear Stress**

214 River discharges presented a clear seasonal pattern with a high levels in winter and
215 spring and a low values in summer and fall (**Figure 2A**). The fall 2016 and 2021, summer 2017,
216 and to a lesser extent, the summer 2010 and spring 2021 cruises took place during low
217 discharge periods. Conversely, the three cruises in 2018 took place during a high discharge
218 period; 5, 87 and 136 days after the January 2018 flood, respectively. Bottom Shear Stress 95th
219 percentile values (BSS_{95th}) decreased with station depth (data not shown) but showed similar
220 temporal changes at all 5 studied stations. At station 3, BSS_{95th} showed a clear seasonal cycle
221 with a succession of peaks induced by winter storms, and conversely low values during
222 summer and fall (**Figure 2B**). The major event was the succession of BSS_{95th} peaks (up to 3.23
223 $N.m^{-2}$) during the 2013-2014 winter. There was no such equivalent between spring 2018 and
224 fall 2021. The summer 2010, fall 2016 and 2021, summer 2017, spring (June) 2018 and 2021
225 cruises were conducted during periods of low BSS_{95th} (i.e., $< 0.5 N.m^{-2}$), whereas the winter
226 2018 and spring (April) 2018 cruises both took place during periods of high BSS_{95th} .

227

228 **3.2. Surface sediment characteristics**

229 Except for the two spring 2018 cruises (16 and 17 μm in April and June, respectively),
230 the median grain size (D_{50}) of surface sediments at station 1 were between 46 (summer 2010)
231 and 92 μm (winter 2018). The D_{50} recorded at the other 4 stations were lower (i.e., around 20
232 μm) and showed only limited spatiotemporal changes (**Figure 3A** and **Supplementary**
233 **materials**). Particulate Organic Carbon (POC) concentrations tended to increase with station
234 depth, reaching a maximum value of 1.66 %DW at station 4 during winter 2018 (**Figure 3B** and
235 **Supplementary materials**). The only exception to this overall pattern was the winter 2018

236 cruise with a maximum value of 1.65 %DW at station 2. POC concentrations also tended to be
237 lower during the spring and fall 2021 than during other cruises. Except during the two spring
238 2018 cruises, chlorophyll-*a* (Chl-*a*) concentrations tended to be low, and did not show marked
239 changes between stations (**Figure 3C** and **Supplementary materials**). Concentrations were
240 high in spring 2018 at stations 2 to 4 with a maximal value of 5.86 $\mu\text{g.gDW}^{-1}$ at station 4 in
241 April 2018. High concentrations were also observed at station 1 in June 2018 (2.73 $\mu\text{g.gDW}^{-1}$).
242 Chl-*a* in Spring 2021 was not as high as in Spring 2018, with a maxim value of 2.04 $\mu\text{g.gDW}^{-1}$
243 at station 4. Otherwise, concentrations ranged from 0.23 $\mu\text{g.gDW}^{-1}$ (station 1 in summer 2017)
244 to 1.39 $\mu\text{g.gDW}^{-1}$ (station 4 in fall 2016), except at station 2 in winter 2018 with 2.09 $\mu\text{g.gDW}^{-1}$.
245 Chlorophyll-*a* / (Chlorophyll-*a* + Phaeophytin-*a*) ratios (Chl-*a*/(Chl-*a*+Phaeo-*a*)), expressed in
246 %, were between 10.0 (station 2 in fall 2016 and station 8 in spring 2021) and 26.6 (station 1
247 in June 2018) (**Figure 3D** and **Supplementary materials**). They did not show a clear
248 spatiotemporal pattern except in June 2018, when there was a clear decrease between station
249 1 (26.6) and 4 (15.1).

250 The first two axes of the Principal Components Analysis (PCA) based on surface
251 sediment characteristics explained 86.2% of the total variance (**Figure 4**). The spatial (depth)
252 gradient was mainly characterized by the opposition between D_{50} and POC concentrations.
253 Temporal variability was mainly driven by changes in Chl-*a* and Phaeo-*a* concentrations and
254 Chl-*a*/(Chl-*a*+Phaeo-*a*). These descriptors contributed to differentiate the two spring (April
255 and June) 2018 cruises at station 2, 3, 8 and 4, as well as the spring (June) 2018 cruise at station
256 1. During these two cruises, station 1 also featured lower D_{50} and higher POC values. At
257 stations 1, 3 and 4, there were no clear differences in surface sediment characteristics during
258 summer 2010 compared to all other cruises except for the spring (April and June) 2018 ones
259 (see above). There were no significant differences among these three stations in the
260 magnitude of changes in surface sediment characteristics between the summer 2010 and all
261 other cruises (1-WAY PERMANOVA, $p=0.356$).

262

263 **3.3. Benthic macrofauna composition**

264 Mean macrobenthic abundances ranged from 89 (station 8 in summer 2017) to 1628
265 ind.m^{-2} (station 1 in summer 2010) (**Supplementary materials**). They differed significantly
266 between stations and cruises, with a significant interaction between these two factors (2-WAY
267 PERMANOVA, $p<0.05$ in all cases). Abundances tended to be higher at station 1, decreasing

268 with station depth, except at stations 8 and 4 during both spring (i.e., April 2018 and spring
269 2021) cruises mostly due to high abundances of *Ampelisca* spp. (e.g. 183 and 593 ind.m⁻² at
270 stations 8 and 4, respectively in spring 2018; and up to 540 ind.m⁻² at station 8 in spring 2021).
271 Abundances also tended to be higher at stations 2 and 3 in spring and fall 2021.

272 Spatial and temporal changes in benthic macrofauna composition were, respectively,
273 associated with the horizontal and vertical dimensions in the first plane of the non-Metric
274 Multidimensional Scaling (**Figure 5**). Temporal changes occurred over two different time
275 scales with: (i) major changes between summer 2010 and fall 2016, and (ii) more restricted
276 ones between fall 2016 and 2021. The SIMilarity PROFile (SIMPROF) procedure identified
277 seven groups of stations*cruises. The six groups from 2016 to 2021 were clearly related to
278 station depth. The seventh group consisted of stations 3 and 4 in summer 2010. Macrobenthos
279 compositions at station 1 also differed between summer 2010 and all 2016-2021 cruises.
280 There were thus significant differences in benthic macrofauna composition between the 2010
281 and 2016-2021 cruises at the three stations sampled in summer 2010. These changes were
282 larger at stations 3 and 4 than at station 1 (1-WAY PERMANOVA and associated pairwise tests;
283 $p < 0.005$ in all cases).

284

285 **3.4. Sediment Profile Image characteristics**

286 A total of 423 Sediment Profiles Images (SPIs) were collected. Representative examples
287 from stations 1, 3 and 4 in summer 2010, fall 2016 and spring (April) 2018 are shown in **Figure**
288 **6**. The mean values and standard deviations of individual SPI characteristics for each
289 combination of stations and cruises are given in **Supplementary Materials**. Almost all mean
290 individual SPI characteristics differed significantly ($p_{\text{PERMANOVA}} < 0.05$) between stations and
291 cruises with a significant interaction ($p < 0.05$) between these two factors. The only exception
292 was the mean depth of oxidic void, which differed significantly ($p < 0.05$) only between stations.
293 Except during spring 2021, the mean depth of the apparent Redox Potential Discontinuity
294 (aRPD) was lower at station 1, ranging from 22.4 to 47.4 mm in summer 2010 and fall 2021,
295 respectively. It increased from stations 2 to 4, where it reached a maximum of 107.4 mm in
296 summer 2017 (**Figure 7A**). Except for station 1, the aRPD mean depths were lower in spring
297 and fall 2021 and the magnitude of their temporal changes tended to be higher at stations 1
298 and 4. The oxidic void mean depth was lower at station 1 (from 12.4 to 51.5 mm in winter 2018
299 and spring 2021, respectively) and tended to increase with station depth except in fall 2016

300 **(Figure 7B)**. The mean number of fauna per SPI was generally higher at stations 1 and 2,
301 especially in summer 2017 (maximum value of 4.3 ind.SPI⁻¹ at station 2), and tended to
302 decrease with depth **(Figure 7C)**. The only exception was summer 2010, where the values were
303 much lower and tended to increase offshore (i.e., from 0.1 to 0.8 ind.SPI⁻¹ at stations 1 and 4,
304 respectively). In summer 2010, the mean number of tubes per SPI was highest at station 1 (2.9
305 tubes.SPI⁻¹) and much lower at stations 3 and 4 (0.2 and 0.1 tubes.SPI⁻¹, respectively) **(Figure**
306 **7D)**. The same spatial pattern was observed in summer 2017. Values were also higher at
307 station 1 in fall 2016 (8.3 tubes.SPI⁻¹). Conversely, both spring (April and June) 2018 and 2021
308 cruises presented an opposite pattern, with lower values at stations 1 and 2 (1.0 and 2.5
309 tubes.SPI⁻¹ in spring (April) 2018, respectively) and maximum ones at stations 8 and 4 (e.g.
310 11.7 and 13.0 tubes.SPI⁻¹ in spring (April) 2018, respectively). The mean normalized surface
311 area of subsurface structures tended to increase with depth during all cruises except fall 2021
312 **(Figure 7E)**. For each cruise, values were minimal at station 1 (between 0.9 and 1.8 % in spring
313 2021 and spring (April) 2018, respectively). Absolute values and spatial changes were
314 especially contrasted between summer 2010 and fall 2021. In summer 2010, there was a
315 strong increasing trend with depth (ending with a value of 12.1 % at station 4).

316 The first two axes of the PCA based on SPI characteristics mean values explained 70.6%
317 of their total variance (i.e., 49.8% and 20.8%, respectively) **(Figure 8)**. The first axis was
318 characterized by an opposition between the number of fauna and subsurface features, such
319 as normalized surface area of subsurface structures, oxic void and aRPD depths. This axis
320 correlated well with station depth. The second axis was mostly driven by the number of tubes
321 and mainly associated with temporal changes in SPI characteristics during spring (April and
322 June) 2018 (stations 8 and 4) and fall 2021 (station 3). The SIMPROF procedure resulted in the
323 identification of three groups of stations*cruises. The first group consisted of all the cruises at
324 station 1, as well as the fall 2016 and 2021, summer 2017 and spring (April) 2018 cruises at
325 station 2. These cruises corresponded to higher abundances of fauna (especially *Amphiura*
326 spp.). The second group was composed of all other combinations of stations and cruises, with
327 the exception of summer 2010 and 2017 at station 4. These two summers formed a third
328 group due to a low number of tubes (summer 2010 and 2017) and either a low number of
329 fauna (summer 2017) or a high normalized surface area of subsurface structures (summer
330 2010). The magnitude of temporal changes in SPI characteristics between summer 2010 and
331 the other cruises was significantly higher at station 4 than at station 1 and 3 (1-WAY

332 PERMANOVA, $p=0.017$ and associated pairwise tests). At station 1, there were no clear
333 differences in SPI characteristics between summer 2010 and all other cruises. The same was
334 also true for station 3, except for fall 2021 (see above). At station 4, SPI characteristics in
335 summer 2010 and summer 2017 differed significantly from those recorded during all other
336 cruises.

337

338 **4. Discussion**

339 **4.1. Extending the observation period of surface sediment characteristics and benthic** 340 **macrofauna composition**

341 In the continuity of previous works (Lamarque et al., 2022, 2021), the present study is:
342 (i) including summer 2010 data for surface sediment characteristics, and (ii) extending the end
343 of the observation period of both surface sediment characteristics and benthic macrofauna
344 composition from spring (April) 2018 to fall 2021. This allowed for both assessing surface
345 sediment characteristics prior the postulated major winter 2013-2014 disturbance and further
346 assessing the recovery of benthic macrofauna composition since there had been no major
347 series of winter storms such as during the 2013-2014 winter between 2018 and 2021 (**Figure**
348 **2**).

349

350 **4.1.1 Surface sediment characteristics**

351 The incorporation of the summer 2010 surface sediment characteristics data from 3 of
352 the 5 sampled stations did not provide evidence of significant differences in surface sediment
353 characteristics between summer 2010 and all other cruises, except for the two in spring 2018
354 (**Figure 4**). This clearly differs from what was observed for benthic macrofauna (**Figure 5**), and
355 suggests a higher stability and/or a faster recovery of surface sediment characteristics after
356 the winter 2013-2014 postulated disturbance. However, it should be pointed out that this
357 discrepancy may also be due to differences in the nature of sediment and benthic macrofauna
358 data. During the present study, the detection of significant changes between stations*cruises
359 was achieved using SIMilarity PROFile (SIMPROF) procedures (Clarke et al., 2008). A major
360 difference between macrofauna versus surface sediment characteristics is the number of
361 variables considered (i.e., 127 genus vs. 5 surface sediment characteristics). The SIMPROF
362 procedure includes performing several SIMPROF tests. The statistical power of each test, and
363 thus of the whole SIMPROF procedure, increases with the number of variables considered

364 (Clarke et al., 2014). Therefore, the relative inability to detect significant differences between
365 the summer 2010 and 2016-2021 cruises based on surface sediment characteristics may partly
366 result from the low number of considered variables. Anyhow, the lack of clear differences in
367 surface sediment characteristics between the summer 2010 and all other cruises does not
368 allow us to fully test the hypothesis of a recovery process following the winter 2013-2014
369 exceptional series of major storms.

370 From fall 2016 to 2021, the main significant temporal changes in surface sediment
371 characteristics occurred at stations 2, 3, 8 and 4 (i.e., within the distal part of the WGMP)
372 during the spring 2018 cruises (**Figure 4**), with higher chloropigment concentrations than
373 during all other cruises (**Figure 3C** and **Supplementary materials**). As suggested by Relexans
374 et al. (1992), these changes are likely seasonal, even though the surface sediment
375 characteristics recorded at stations 2, 3, 8 and 4 during spring 2021 did not differ significantly
376 from those recorded during other seasons and sampling years (**Figure 4**). Year-to-year
377 differences in surface sediment characteristics between spring cruises may be due to: (i) the
378 precise timing of sampling relative to the temporal dynamics of the spring bloom, and (ii)
379 between year differences in the intensity of this bloom. The differences between the April and
380 June 2018 cruises are obviously linked to differences in timing, as both cruises took place in
381 the same year. The differences between the two spring 2018 cruises and the spring 2021
382 cruise probably result at least partly from the lower intensity of the spring bloom in 2021, as
383 suggested by the lower values of surface water chlorophyll-*a* concentrations derived from
384 satellite imagery in spring 2021 (Dubosq et al., 2022).

385 At station 1 (i.e. within the proximal part), the characteristics of the surface sediment
386 also differed between the two spring 2018 cruises and the spring 2021 one. This was not only
387 due to higher chloropigment concentrations, but also to lower median grain size during the
388 spring 2018 cruises (**Figure 3 A, B and C**, respectively). During both spring 2018 cruises, station
389 1 had much finer surface sediments than during any other cruise including the spring 2021
390 one (**Figure 3A**). Particle export from the Gironde Estuary are maximal during spring tides of
391 high discharge periods (Constantin et al., 2018). These conditions were prevailing just prior to
392 the spring (April) 2018 cruise (**Figure 2A**). The sedimentation and persistence of fine surface
393 sediments in the proximal part of the WGMP further require low hydrodynamic conditions,
394 which was the case between the two spring 2018 cruises (average BSS_{95th} of $0.35 \text{ N}\cdot\text{m}^{-2}$, **Figure**
395 **2B**). A major difference between spring 2018 and spring 2021 was the lower fluvial discharge

396 in 2021 (**Figure 2A**), likely resulting in lower export of fine particles from the Gironde. This
397 probably accounts for the presence of coarser surface sediments at station 1 in 2021.

398 Overall, our results support the occurrence of seasonal changes mostly affecting
399 chloropigment concentrations over the whole WGMP and surface sediment grain size in its
400 proximal part. Their magnitude varies within and between years, depending on (i) the timing
401 of sampling relative to the spring bloom, (ii) year-to-year variability in its intensity, (iii) fluvial
402 discharge, and (iv) local hydrodynamics.

403

404 **4.1.2 Benthic macrofauna composition**

405 Before the present study, the current observations and working hypotheses regarding
406 the temporal changes in the composition of the WGMP benthic macrofauna were as follows:
407 (i) the occurrence of major changes throughout the depth gradient between summer 2010
408 and fall 2016, attributed to the exceptional series of severe storms during winter 2013-2014;
409 (ii) the appearance of larger changes between summer 2010 and fall 2016 at deep stations;
410 and (iii) the superposition of seasonal and interannual changes during the recovery period
411 following the postulated winter 2013-2014 disturbance (Lamarque et al., 2022). However,
412 these interpretations were speculative because the significance of the differences in
413 magnitude between 2010 and 2016-2018 changes with respect to station depth had not been
414 statistically tested. Furthermore, it was difficult to discern seasonal and interannual changes
415 as each season had only been sampled once during different years starting in fall 2016.

416 The present study intended at further tackling the hypothesis of a recovery process
417 taking place after the major physical disturbance of winter 2013-2014. The present study
418 strongly suggests that the recovery process was not fully achieved 8 years after this
419 disturbance. Such a duration is consistent with the time observed for the full recovery of
420 macrobenthic communities following different types of anthropogenic disturbances (e.g. at
421 least 10 years in Dauvin, 1998; and at least 15 years in Josefson et al., 2008). Moreover, the
422 kinetics of benthic community recovery depends on the spatial scale of the disturbance (Zajac
423 et al., 1998; Norkko et al., 2010). In the case of large-scale disturbance, such as postulated for
424 the WGMP, the availability of recolonizing individuals imported from neighbouring areas is a
425 key factor controlling the kinetics of secondary succession (Zajac et al., 1998). The WGMP is
426 surrounded by coarser sediments and is well isolated from other potentially undisturbed
427 muddy habitats (Lesueur et al., 2002), which certainly contributes to the slowdown the

428 recovery process. The lack of return to initial benthic fauna composition by the end of the
429 extended observation period (2021) therefore does not constitute a proof of the absence of
430 such an ongoing process in the WGMP. This clearly calls for a further extension of the benthic
431 macrofauna observation period. According to station depth, the return period for exceptional
432 winter storms affecting the sediment column in the distal part of the WGMP is estimated
433 between 30 and 80 years (Lesueur et al., 2002). Since the current observation period ends
434 only 8 years after the postulated disturbance, its extension will likely allow for a further
435 assessment of a possible recovery process before a new series of exceptionally severe storms
436 will take place and induce a new major disturbance.

437 In the present study, we tested the statistical significance of differences in the
438 magnitude of temporal changes in benthic macrofauna composition between summer 2010
439 and the other cruises. The results showed that these changes were significantly larger at
440 stations 3 and 4 than at station 1, supporting and refining the initial qualitative observations
441 reported by Lamarque et al. (2022). The response of benthic communities to major
442 disturbances depends strongly on the state of the macrofauna composition prior to the
443 disturbance, which is reflecting the baseline intensity of disturbances affecting the studied
444 system (Kaiser et al., 2002; Probert, 1984). In the WGMP, sediment instability is mostly
445 induced by the intensity of local hydrodynamics, which decreases with depth (Lesueur et al.,
446 2002; Masselink et al., 2016). The deepest part of the WGMP is not subject to recurrent
447 (frequent) physical disturbances, allowing macrobenthic communities to develop and
448 maintain advanced, mature successional stages. At station 4, this results in the presence of
449 the EUNIS A5.361 habitat (“Seapens and burrowing megafauna in circalittoral fine mud”;
450 Bajjouk et al., 2015). The SPI characteristics recorded at this station indicate a strong
451 bioturbation activity (Lamarque et al., 2021; Massé et al., 2016; **Figure 6**), which is
452 characteristic of mature communities (Pearson and Rosenberg, 1978) where sensitive taxa are
453 dominant (Rosenberg et al., 2004). In contrast, the community at station 1 is the “*Amphiura*
454 *filiformis*-*Kurtiella bidentata*-*Abra nitida* community in cohesive muddy sands off wave
455 exposed coast”, which consists of taxa tolerant of recurrent physical disturbances (Hiscock,
456 1984; Picton et al., 1994). Differences in taxon sensitivity and tolerance levels in the shallower
457 (station 1) and deeper (stations 3 and 4) parts of the WGMP may thus account for differences
458 in the magnitude of impacts of major physical disturbances on benthic macrofauna
459 composition.

460 Until now, the rationale for seasonal changes in benthic macrofauna composition was
461 indirect and consisted of: (i) the trend toward closed temporal trajectories of individual
462 stations based on annual Julian days, and (ii) the fact that water discharges cumulated over
463 the last 100 days before sampling correlated best with temporal changes in benthic
464 macrofauna composition (Lamarque et al., 2022). The present study further suggests the
465 occurrence of a seasonality at deep stations through the close positioning of the spring (April)
466 2018 and spring 2021 cruises at stations 8 and 4 on the first plan of the nMDS plot based on
467 benthic macrofauna composition (**Figure 5**, Bray Bray-Curtis similarity > 0.65 in all cases). An
468 interannual component was also evident at stations 2 and 3, where benthic macrofauna
469 composition during the spring and fall 2021 cruises differed significantly from those of all
470 other cruises. The analysis of the positioning of benthic macrofauna composition at all five
471 studied stations between fall 2016 and fall 2021 therefore confirms the combined influence
472 of seasonal and interannual factors driving temporal changes during this period. Furthermore,
473 it suggests that the seasonal variation is the dominant factor at stations 8 and 4 (with a clear
474 spring differentiation), whereas interannual variation is more pronounced at stations 2 and 3
475 (with a marked differentiation between spring and fall 2021).

476

477 **4.2. Insights from sediment profile Imagery**

478 **4.2.1 Delimitation of the WGMP proximal and distal parts**

479 Jouanneau et al. (1989) stated that evidence of modern sedimentation in the WGMP
480 only appears below 48 m depth, whereas Lesueur et al. (2002) defined the boundary between
481 the proximal and distal parts at 40 m depth. This depth was recently refined to 42.5m based
482 on both surface sediment and SPI characteristics measured at 32 stations during the spring
483 (June) 2018 cruise (Lamarque et al., 2021). During the present study, except for the two spring
484 2018 cruises (see below), all station 1*cruises differed significantly from all other
485 combinations of stations and cruises when classified based on surface sediment
486 characteristics (**Figure 3**). However, when classifying stations*cruises based on SPI
487 characteristics, about half of station 2 (48 m depth) sampling cruises grouped with station 1
488 cruises (**Figure 8**). This is roughly consistent with the previously reported delimitation depths,
489 but also shows that the boundary between the proximal and the distal parts depends on the
490 types of parameters considered and the timeframe of the assessment. Overall, this suggests

491 a gradual transition between the proximal and distal parts of the WGMP, likely occurring
492 between stations 1 and 2 (i.e., between 42 and 48m depth).

493

494 **4.2.2 Temporal changes between summer 2010 and 2016-2021**

495 There was less obvious evidences of significant temporal changes in SPI characteristics
496 between summer 2010 and all other cruises than for benthic macrofauna composition
497 (**Figures 8**). Key bioturbators are mainly responsible for creating the biological activity traces
498 captured in SPIs. These taxa tend to be under-sampled by grabs because they are usually deep-
499 burrowers (Wilson et al., 2009). This clearly complicates cross-referencing compositional and
500 functional data. Nevertheless, as already pinpointed for surface sediment characteristics, a
501 major difference between macrofauna and SPI characteristics is the number of variables
502 considered (i.e., 127 genera vs. 5 SPI characteristics). Moreover, changes in the values of the
503 five SPI characteristics used in the present study operate over different time scales. Together
504 with apparent Redox Potential Discontinuity (aRPD) depth, fauna and tube numbers tend to
505 integrate changes over short time periods. The integration time period for the normalized
506 surface area of subsurface structures is likely much longer due to the presence of large
507 numbers of unoccupied burrows in marine sediments (Rosenberg et al., 2008). The integration
508 time period of oxic void mean depth should probably be considered as intermediary, due to
509 the nature of the considered variable (i.e., depth and not surface). All five SPI characteristics
510 were centered and reduced prior to multivariate analyses. This gave them the same weight in
511 all analyses including SIMPROF, which may have hampered the detection of significant
512 changes occurring over different time scales.

513 At stations 1 and 3, the SPI characteristics did not differ significantly between summer
514 2010 and all other cruises, which is different from what was recorded for benthic macrofauna
515 composition. Several studies have already shown that the kinetics of benthic macrofauna
516 recovery in functionalities and taxonomic composition may differ (Bolam, 2014; Guarinello et
517 al., 2022; Macleod et al., 2008; Shojaei et al., 2021). This may result from a reduced initial
518 impact of the disturbance and/or a faster recovery. The relative importance of these two
519 processes cannot be directly assessed for the WGMP, as the first sampling after the postulated
520 disturbance occurred only in fall 2016 (i.e., approximately 2.5 years later). There is, however,
521 indirect evidence suggesting that the initial impacts may have been smaller for SPI
522 characteristics than for benthic macrofauna composition. Due to their positioning below the

523 disturbed top sediment layer, the key bioturbators tend to be less affected by physical
524 disturbances than the macrobenthic taxa as a whole (Beauchard et al., 2023; Tiano et al.,
525 2020), including storms (Posey et al., 1996). These key bioturbators were thus likely less
526 impacted by the postulated 2013-2014 winter disturbance, which may have resulted in a
527 lower initial impact on SPI characteristics as well.

528 At station 4, there were significant temporal changes in SPI characteristics. However,
529 it remains unclear whether these differences reflect seasonal (summer versus all other
530 seasons) or interannual (2010 versus 2016-2021) changes, as this approach separated
531 summers 2010 and 2017 from all other cruises. The mean normalized surface area of
532 subsurface structures, was almost twice as high in summer 2010 as during all other cruises. As
533 pointed above, this variable reflects biological activity integrated over long time periods.
534 Lesueur et al. (2002) reported a return period of nearly 80 years for major storm events at a
535 depth of 64 m (i.e., between stations 3 and 4), whereas Masselink et al. (2016) identified the
536 2013-2014 winter as the most energetic since at least 1948. The high normalized surface areas
537 of subsurface structures recorded in summer 2010 may thus have resulted from the slow
538 accumulation of subsurface structures over an extended time interval during which the
539 intensity of physical disturbance remained below the threshold generating a major impact on
540 surface sediment. According to this hypothesis, this threshold was exceeded during the 2013-
541 2014 winter, resulting in an abrupt diminution of the surface area of subsurface structures.
542 The apparent lack of recovery likely reflects the mismatch in timescales associated with the
543 slow accumulation of biological traces before summer 2010 (>65 years according to Masselink
544 et al., 2016) and the short duration of our observation period since the postulated disturbance
545 in winter 2013-2014 (ca. 8 years). Here again an extension of the current WGMP observation
546 period would allow to further explore this hypothesis.

547

548 **4.2.3 Temporal changes between fall 2016 and fall 2021**

549 The most important changes in SPI characteristics took place between fall 2016 and
550 spring 2021: (1) at stations 4 and 8 during the spring (April and June) 2018 cruises, and (2) at
551 station 3 during fall 2021 (**Figure 8**). In all three cases, these changes were mostly
552 characterized by a significant increase in the number of tubes (**Figure 7D**), which is in good
553 agreement with the association of this variable with short time scales. Based on benthic
554 macrofauna composition, the peaks in tube number during spring 2018 can be related to the

555 high abundances of the amphipod *Ampelisca* spp. (see above). Most species in this genus are
556 indeed known to construct small tubes that degrade rapidly after being abandoned (Bellan-
557 Santini and Dauvin, 1988; Mills, 1967). It should however be pointed out that high numbers
558 of *Ampelisca* spp. were also recorded in spring 2021 at these two stations (see above), but
559 without a concomitant increase in tube number (**Figure 7D**). Moreover, the high number of
560 tubes recorded at station 3 in fall 2021 was not due to *Ampelisca* spp. (BL, personal
561 observations) and we were not able to establish a clear relationship between the abundance
562 of any macrobenthic genus and this peak. Tube numbers at station 1 also tended to be higher
563 during both fall 2016 and 2021 (**Figure 7D**) and the summer 2010 and 2017 cruises grouped
564 together when considering all five SPI characteristics (**Figure 8**). Main changes in SPI
565 characteristics during the 2016-2021 period should therefore likely be considered seasonal.
566 Conversely, there was no evidence of any clear interannual trend over this period.

567

568 **5. Conclusions**

569 Results confirm the segmentation of the West Gironde Mud Patch (WGMP) in a
570 proximal and a distal part and the existence of depth gradients in the latter. Temporal changes
571 are both seasonal and interannual and the magnitude of these two components differs
572 between descriptors. Temporal changes in surface sediment characteristics are essentially
573 seasonal, occurring mostly in spring in relation to the sedimentation of: (i) the phytoplanktonic
574 bloom in the distal part, and (ii) fine particles from the Gironde Estuary in the proximal part.
575 Interannual changes are limited and mostly associated with differences in the capture of
576 seasonal changes, which may result from: true interannual changes in driving factors, and/or
577 interactions between sampling timing and the temporal dynamics of driving factors.
578 Conversely, temporal changes in benthic macrofauna composition are mostly interannual,
579 showing a marked difference between summer 2010 and all other cruises. Previously, this was
580 attributed to a major storm-induced disturbance during the 2013-2014 winter, based on an
581 observation period ending in spring 2018. However, our extended observation period shows
582 that benthic macrofauna composition still significantly differs between summer 2010 and fall
583 2021, suggesting that a full recovery was not yet achieved 8 years after the postulated
584 disturbance. This is nevertheless compatible with the reported time durations for the full
585 recovery of disturbed benthic habitats and clearly calls for an extension of the observation
586 period of benthic macrofauna composition. Seasonal changes in benthic macrofauna

587 composition mostly occur during spring at the two deepest stations and are mainly due to a
588 burst of *Ampelica* spp. Temporal changes in SPI characteristics are somewhat intermediate
589 with clear seasonal changes at the two deepest stations, mostly associated with a spring
590 increase in tube numbers, and no significant difference between summer 2010 and all other
591 cruises, except at the deepest station. Together with the apparent stability of sediment
592 characteristics over the whole observation period, the overall discrepancy between SPI
593 characteristics and benthic macrofauna composition may be due to the low contribution of
594 the bioturbators to fauna composition and the differences in recovery kinetics of benthic
595 macrofauna composition and functionality. Moreover, the summer 2010 cruise is
596 characterized by a high surface area of subsurface structures, which may result from the slow
597 accumulation of those structures over an extended time interval between two major
598 consecutive physical disturbances affecting the deepest part of the WGMP.

599

600 **Author Contributions**

601 Conceptualization, B.L., B.D., and A.G.; Data curation, B.L.; Formal analysis, B.L. and
602 A.G.; Funding acquisition, B.D. and A.G.; Investigation, B.L., B.D., S.S., G.B., A.R.-R. and A.G.;
603 Methodology, B.L., B.D., S.S., A.R.-R., M.D. (Mélanie Diaz), F.G. (Florent Grasso), A.S. and A.G.;
604 Resources, B.L., B.D., S.S., G.B., N.L., F.G. (Frédéric Garabetian), C.F., S.R., F.G. (Florent Grasso),
605 M.D. (Mélanie Diaz), A.S., D.P., M.D. (Martin Danilo) and A.R.-R.; Validation, B.L., B.D., and
606 A.G.; Visualization, B.L. and A.G.; Writing—original draft, B.L. and A.G.; Writing—review and
607 editing, B.L., S.S., G.B., F.G. (Frédéric Garabetian), B.D., C.F., S.R., A.R.-R. and A.G. All authors
608 have read and agreed to the published version of the manuscript.

609

610 **Acknowledgments**

611 This work was supported by: (1) the JERICO-NEXT project (European Union's Horizon
612 2020 Research and Innovation program under grant agreement no. 654410), (2) the VOG
613 project (LEFE-CYBER and EC2CO-PNEC), and (3) the MAGMA project (COTE cluster of
614 Excellence ANR-10-LABX-45; Conseil Régional Nouvelle-Aquitaine convention no. 2019-
615 1R20107; and the Office Français de la Biodiversité OFB.21.1083). Operations at sea were
616 funded by the French National Oceanographic Fleet. The authors wish to thank the crew of
617 the R/V Côtes de la Manche for their help during field operations, Marie Claire Perello, Pascal
618 Lebleu and Hervé Derriennic for their help during sampling and analyses.

619

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Preprint not peer reviewed