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2 **Sediment grain size and benthic community structure in the eastern English**
3 **Channel: species-dependent responses and environmental influence**

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14 **Abstract**

15 This study addresses the scarcity of evidence on the relationship between benthic communities and
16 coarse-grained sediments in the eastern English Channel. The region's geological history contributes
17 to its predominantly coarse sediment composition. The study employs ternary plots to visualize
18 benthic species' preferences and tolerance for sediment types, revealing their effectiveness.
19 Redundancy Analyses (RDA) and species-level quantile regressions explore the influence of grain size
20 on benthic species distribution. The results indicate a moderate impact of grain size, influenced by
21 hydrodynamics. Estuaries, particularly the Seine Estuary, significantly shape benthic species
22 distribution. Quantile regressions underscore the varied responses of benthic communities along the
23 grain size gradient. The study underscores the importance of considering coarse sediments, offering
24 insights into the complex relationship between benthic communities and sediment characteristics.

25 **Keywords:** coarse sediments, species distribution, sediment type, grain size analysis, marine aggregate
26 extraction, offshore wind farms

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28 1. Introduction

29 The English Channel (EC) is a shallow epicontinental sea located between the United Kingdom to the
30 north and France to the south. It serves as a crucial seaway connecting the North Sea and the Atlantic
31 Ocean. The geological history and hydrodynamic forces that have shaped the EC have resulted in a
32 predominant coarse seabed composition (Dingwall, 1975; Larssonneur et al., 1982; Hamblin et al.,
33 1992). Approximately 80% of the Channel's seabed consist of coarse sediments, ranging from coarse
34 sands to pebbles, which have accumulated in an extensive network of paleo-valleys (Gupta et al.,
35 2007). These sediment deposits, some several meters thick, represent a significant source of accessible
36 aggregates. These unique characteristics of the EC makes it an intriguing and important area for
37 scientific research and resource exploitation (Dauvin and Lozachmeur, 2006; Dauvin, 2019), leading to
38 its recognition as one of the most anthropogenically influenced seas in the world (Halpern et al., 2008).

39 Numerous studies have highlighted the significant role of sediment characteristics, controlled by
40 sources, geological heritage, hydrodynamic forcings and depth, in shaping benthic communities
41 (Petersen, 1913; Ford, 1923; Sanders, 1958; Buchanan, 1963; Cabioch, 1968; Young and Rhoads, 1971;
42 Gray, 1974; Buchanan et al., 1978; Fresi et al., 1983; Clabaut and Davoult, 1989; Seiderer and Newell,
43 1999; Newell et al., 2001; Anderson, 2008; Foveau, 2009; Cooper and Barry, 2017). Early investigations,
44 primarily the oldest and most historical ones, concluded that sediment played a prominent role in
45 benthic community structure (Petersen, 1913; Ford, 1923; Sanders, 1958; Buchanan, 1963; Gray, 1974;
46 Buchanan et al., 1978; Fresi et al., 1983; Anderson, 2008). Several sediment parameters have been
47 identified as potential drivers of benthic community structure, which can be grouped into five
48 categories: 1) grain size, 2) organic matter content, 3) microbial composition, 4) sediment stability or
49 erodibility and 5) amensalistic interactions (see Snelgrove and Butman, 1994, for review). Other studies
50 present more nuanced views and emphasize the moderate importance of sediment (Tyler and Banner,
51 1977; Warwick and Davies, 1977; Seiderer and Newell, 1999; Newell et al., 2001) whilst few studies
52 conclude that sediment only plays a minor role (Larsen, 1979; Flint and Holland, 1980; Snelgrove and
53 Butman, 1994).

54 Despite these differences, it is important to note that the majority of these works have primarily
55 focused on fine-grained sediments, which are less common in the subtidal domain of the EC. The
56 scarcity of quantitative data on coarse sediments in the eastern EC can be attributed primarily to
57 technical limitations. In the past, sediment sampling in these areas was primarily conducted using
58 dredges, such as the anchor-type and Rallier du Baty dredges, during explorative surveys led by
59 Norman Holme and Louis Cabioch in the 1960s and 1970s to assess benthic community distribution
60 (Dauvin, 2015). However, these dredges only allowed for qualitative or semi-quantitative collection of

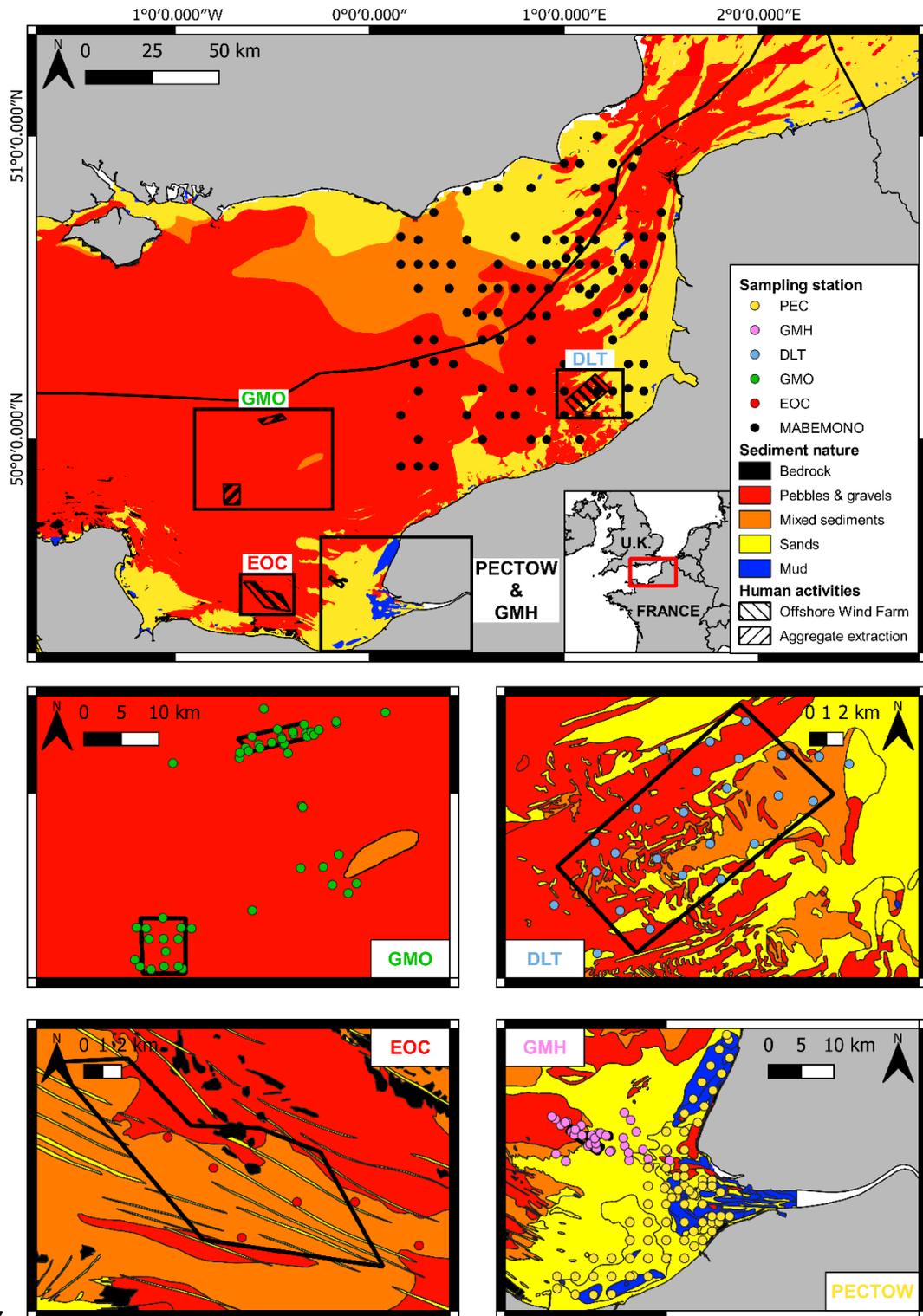
61 benthic organisms at best in coarse sediments. Consequently, there have been limited quantitative
62 studies examining the natural spatial and temporal variability of communities associated with coarse
63 sediments in this region, as on a global scale (Lozach and Dauvin, 2012; Pezy and Dauvin, 2021). The
64 use of the Hamon grab, which became more widespread, facilitated the quantitative sampling of
65 coarse sediments. Nevertheless, the sampling of such sediments remains challenging due to their
66 hardness and because of the overdispersion of large dominant organisms (Dauvin and Ruellet, 2008).
67 Thus, in this sea, most quantitative data regarding coarse seabed have been acquired recently, and
68 only within relatively limited surface areas, as these samplings were mostly conducted as part of
69 environmental monitoring of marine aggregate extraction on the 20 concessions located in the EC
70 (Seiderer and Newell, 1999; Boyd and Rees, 2003; Newell et al., 2004; Cooper et al., 2007; Foden et
71 al., 2009; Foveau, 2009; Desprez et al., 2010). However, it's worth noting that this information is
72 somewhat different for the English side of the Channel, as the OneBenthic initiative has recently
73 facilitated the association of data gathered at these extraction sites to further investigate the benthos-
74 sediment relationship (Cooper and Barry, 2017). Thus, only few studies have investigated the
75 relationship between grain size and benthic organisms in the EC (Seiderer and Newell, 1999; Newell et
76 al., 2001), and only at relatively small spatial scales.

77 This lack of knowledge is all the more prejudicial insofar as many anthropic activities are carried out
78 on coarse substrate in the EC, as well as on a global scale. These activities are represented by aggregate
79 extraction, marine disposal, the establishment of wind farms or by bottom fishing activities (Dauvin,
80 2012, 2019). The determination of the benthos-relationship is of utmost importance, as it has the
81 potential to predict how benthos could be affected by these activities. For instance, marine aggregate
82 extraction not only leads to a fining of grain size in the zone but also disturbs the vertical structure of
83 sediments (Desprez, 2000; Boyd and Rees, 2003; Newell et al., 2004; Cooper et al., 2007; Foden et al.,
84 2009, 2010; Desprez et al., 2010; Le Bot et al., 2010). Similarly, the establishment of wind farms can
85 result in localized organic matter enrichment (Boehlert and Gill, 2010; Lindeboom et al., 2011; Wang
86 et al., 2019; Ivanov et al., 2021; Robert et al., 2021), while fishing activities may cause the upwelling of
87 initially deeper sediment layers, thereby altering the sediment envelope of the environment (Foden et
88 al., 2010; Bradshaw et al., 2021). Moreover, it is crucial to be aware of the autoecology of species that
89 compose benthic communities, especially since this compartment is very regularly used to assess the
90 environmental quality of an area (Zettler et al., 2013).

91 The scopes of this study are therefore to determine the influence of grain size on the distribution of
92 benthic species in the eastern EC and to identify which species are associated with coarse sediments,
93 which are predominant in this marine environment.

94 2. Material and methods

95 2.1. Data collection and sampling strategy



96 z

97 Figure 1: Maps displaying the sampling station locations for the different monitoring programs. The Wentworth scale is used
 98 for sediment nature classification. The top map exclusively shows the locations of stations from the MABEMONO monitoring
 99 program and the spatial extent of the smaller sites. The four smaller maps indicate the locations of GMO (Granulats de la
 100 Manche Orientale) stations in the top-left, DLT (Dieppe Le Tréport) stations in the top-right, EOC (Éoliennes Offshore du

101 *Calvados*) stations in the bottom-left, PEC (PECTOW, yellow) and GMH (*Granulats Marins Havrais*, pink) stations in the bottom-
102 right. Sources: dataSHOM.

103 The data used for this study are derived from various monitoring programs and studies conducted over
104 the past two decades in the eastern EC (Table S1 for more details). All samples were collected using
105 Hamon or Van Veen grabs, allowing for quantitative sampling of benthic organisms. Stations sampled
106 using the Rallier du Baty dredge during some campaigns such as MABEMONO were excluded from the
107 analyses.

108 2.2. Data preparation

109 As some of the data were collected more than ten years ago, all species names were checked and
110 updated using World Register of Marine Species (WoRMS Editorial Board, 2023) on March 24, 2023.
111 Similarly, to avoid excessive abundance resulting from recruitment of various species, only individuals
112 collected on 2 mm mesh sieves were considered in the analyses described below (Lozach and Dauvin,
113 2012). In addition, to avoid influence of rare species, only those present in at least 3% of the samples
114 (676 species on the 852 initial ones) were retained for the analyses. Furthermore, to enable
115 comparison of abundances collected at different sites, the abundances were standardized to a surface
116 of one square meter (1 m²). Finally, while this study primarily focuses on the role of coarse sediments
117 in the distribution of benthic species in the EC (prevalent in this sea and subject to numerous
118 anthropogenic activities), the addition of data from finer sediment facies was necessary to account for
119 all habitats encountered in the eastern EC and avoid bias in the analyses.

120 2.3. Sedimentary analyses

121 2.3.1. Grain size distribution analyses

122 Several granulometric variables were derived from the grain size distribution (GSD) data, obtained
123 through dry sieving. The diversity of the data used implies a range of sieve sizes, with the number of
124 sieves varying between 6 (for the finest sediments) and 32 sieves. However, all employed sieve ranges
125 had at least one sieve size of 63 µm and 2000 µm as finest and coarsest sieves, respectively, allowing
126 for interpretation of the results using the Wentworth scale. The granulometric variables included
127 sediment classification variables (gravel, sand, and mud percentages, following the Wentworth scale),
128 arithmetic variables (mean and median), distribution parameters (sorting, skewness, kurtosis), and
129 modal variables (main mode, number of modes). All grain size parameters were computed using the
130 arithmetic methods of moments, as reviewed in Blott and Pye (2001).

131 2.3.2. End-members analyses

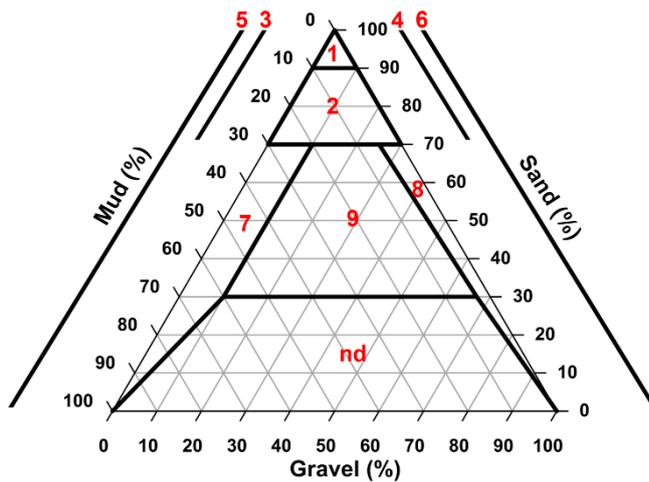
132 The number of modes in the GSD was determined using an End-Member Modeling Analysis (EMMA)
133 approach. EMMA is a valuable and flexible statistical approach in sedimentology that helps to identify

134 and quantify the underlying processes involved in sediment generation and deposition (Weltje, 1997;
135 Dietze et al., 2012, 2022). This method can effectively unmix multimodal GSD, providing insights into
136 sediment provenance, transport mechanisms, and depositional environments (Dietze et al., 2012,
137 2022).

138 EMMA was performed following the procedure outlined by Dietze et al. (2012) and Dietze and Dietze
139 (2019) with the 'EMMAgeo' package in R (Dietze and Dietze, 2019). Prior to the analyses, the data were
140 regularized using linear interpolations, considering the variations in sieve number and sizes used to
141 examine the GSD across the different study sites. To mitigate scale effects, a weighting coefficient ($l =$
142 0.01) was applied to obtain a weighted matrix (Klovan and Imbrie, 1971) with unbiased variables (size
143 classes), which is common for variables with high variability (Weltje, 1997). After computing the EMMA
144 for each station within a site, the percentage of membership to one or more end-members was
145 determined, and the number of end-members with a membership percentage greater than 5% was
146 retained to define the number of modes characterizing the station. Finally, EMMA was employed to
147 determine the membership percentage to a fine sand mode of a station (referred to as “End-Member
148 1” or “EM1” hereafter), by constraining the analysis to only two end-members. The aim of this
149 approach is to distinguish the fine sand fraction (grain size ranging from $82\ \mu\text{m}$ to $820\ \mu\text{m}$) from the
150 coarser fraction of sediment (grain size exceeding $820\ \mu\text{m}$). Thus, for all sites (except for PECTOW,
151 which exhibited a high mud percentage), EM1 represented the finest end-member of the distribution.
152 The distribution curves of the EM1 from the different study sites were then used to model a “global”
153 EM1 distribution after fitting a Gaussian function using the least squares method. This approach has
154 allowed the determination of a Gaussian function that represents the percentage of fine sand for the
155 multivariate analyses (as described in section 2.6.).

156 2.4. Plotting the benthos sedimentary envelope using ternary plots

157 Glémarec (1969) introduced a method for classifying benthic organisms according to their observed
158 distribution in relation to sediment grain size using Shepard's diagram (Shepard, 1954). This
159 classification system, which is based on nine classes following the sediment preference of organisms
160 (Glémarec and Monniot, 1966; Glémarec, 1969), presents numerous advantages, as it enables an
161 objective and visual classification of species within one or multiple granulometric classes (Fig. 2).
162 Additionally, it facilitates the examination of the sedimentary envelope size that can be occupied by
163 these organisms.



164

165 *Figure 2: Ternary plot illustrating the classification proposed by Glémarec. The different classes correspond to: 1) strictly sand-*
 166 *dwelling organisms, 2) tolerant sand-dwelling organisms, 3) muddy-sand-dwelling organisms, 4) clean-sand-dwelling*
 167 *organisms, 5) sandy-muddy-dwelling organisms, 6) sandy-gravelly-dwelling organisms, 7) muddy-dwelling organisms, 8)*
 168 *gravelly-dwelling organisms, and 9) well-mixed-sediment dwelling species (adapted from Glémarec, 1969). The term “nd”*
 169 *denotes “not defined”, as this group was not defined by the original author.*

170 Initially, the data presented in the ternary plot were only based on occurrence data, where each
 171 observation of at least one individual in a gravel/sand/mud condition was represented by a point
 172 within the triangle. In this study, we propose an enhanced version of the plot by incorporating
 173 abundance data through the implementation of an Inverse Weighted Distance (IDW) interpolation
 174 calculation. This approach allows us to estimate abundances for unsampled gravel/sand/mud
 175 conditions and provides a more gradual representation of the data. The graphical representations were
 176 generated using R-4.2.2 software with the 'Ternary' package (Smith, 2017). As interpolations required
 177 a certain number of observations, only taxa with more than 30 observations were selected, totaling
 178 229 species.

179 2.5. Fauna rates of changes along a sedimentary gradient

180 Quantile Regression (QR, Koenker and Bassett, 1978) is a statistical approach increasingly recognized
 181 in ecological research (Dunham et al., 2002; Cade and Noon, 2003; Anderson, 2008; Zettler et al.,
 182 2013). QR explores ecological data by assessing quantiles, providing insights into complex
 183 relationships. This method is valuable for estimating slopes, especially near maximum responses, even
 184 with a limited factor subset.

185 Thus, Quantile Regression Spline Models (QRSM) were fitted using the `bs()` function from the R 'base'
 186 package (Hastie, 1992) in combination with the `rq()` function from the 'quantreg' package (Koenker,
 187 2022). These models were applied to analyze the abundance of the 41 most prevalent species, with
 188 the percentage of gravel (% grain size > 2 mm) treated as a continuous variable (see section 3.4. for
 189 more details). The quantile levels employed ranged from the 85th to the 95th ($\tau = 0.85 - 0.95$) with 5%
 190 increments. To construct the B-splines, the piecewise polynomial degree was set to 2, 3, 4, or 5. The

191 selection of the appropriate degree was based on the small-sample-correction version of Akaike's
192 Information Criterion (AICc), ensuring the use of a parsimonious model (Hurvich and Tsai, 1989;
193 Burnham and Anderson, 2004; Cade et al., 2005). The maximum value derived from the selected model
194 was considered as the optimum for each species.

195 To determine the 95% confidence interval of this optimum value, a Monte-Carlo Marginal
196 Bootstrapping (MCMB) procedure was performed with 10,000 replications. The 95% boundaries of the
197 bootstrapped optimum were then calculated for each species, representing the confidence interval of
198 the optimum value at the 95% level. These analyses help to identify how the coarse sediment fraction
199 (represented here by the gravel percentage) influences the abundance of benthic species and,
200 consequently, their affinity and tolerance to coarse sediments in the eastern EC. This information is
201 highly complementary to the insights gained from the ternary plots (see section 2.4.).

202 2.6. Multivariate analyses

203 2.6.1. Assessing grain size characteristics contribution to species distribution

204 Several studies have investigated species distribution along sediment grain size gradient, each using a
205 different grain size parameter to assess this relationship (*e.g.*, mud percentage, median). However,
206 depending on the sediment composition of the studied sites, some granulometric parameters might
207 be more or less relevant in correlating species distribution with a sedimentary gradient.

208 To determine which grain size parameter is the most relevant for describing the distribution of benthic
209 species in the eastern EC, a Redundancy Analysis (RDA) was conducted on the species-abundance data
210 transformed by Hellinger (Legendre and Gallagher, 2001). These data were compared with the
211 different granulometric parameters presented in section 2.3. Variable selection was performed using
212 the `ordistep()` function from the 'vegan' package (Oksanen et al., 2022). For each test, 999
213 permutations were conducted, with a p-value threshold of 0.06 for exclusion and 0.05 for inclusion.
214 Both forward and backward procedures were applied, resulting in a similar final model. Once selected,
215 the absence of collinearity was assessed by calculating the Variance Inflation Factor (VIF), and variables
216 with VIF exceeding 10 were removed from the analysis due to potential collinearity (Marquandt, 1980).
217 The analyses were conducted on the entire set of taxa (after the species selection detailed in section
218 2.2.), as well as on a subset of "grain size-sensitive" species identified using ternary plots and QRSM
219 (see sections 2.4. and 2.5.) and after calculating the Spearman rank correlation coefficient (ρ) between
220 abundances and various granulometric parameters. Species with an absolute ρ value greater than or
221 equal to 0.5 were considered sensitive.

222 An equivalent procedure with additional environmental variables added to the model was also
223 conducted (Table S2 for more details).

224 2.6.2. Mapping benthos and sediment spatial distribution in the eastern English

225 Channel

226 To complement the information provided by the different RDA analyses, two Hierarchical Ascending
227 Clustering (HAC) were performed to visualize the distribution of biological communities in relation to
228 GSD parameters within the eastern EC. For the DLT site, where data were collected on multiple dates
229 at the same station, the winter sampling data (predominant for the other sites) were prioritized. Thus,
230 the biological data were transformed using $\log(x+1)$ to minimize the effect of highly abundant species,
231 and the granulometric parameters used in subsection 2.6.1. were scaled to standardize the variables.
232 On these transformed data, a Bray-Curtis distance matrix for benthic organism abundance data and a
233 Manhattan distance matrix for granulometric parameters were computed. As these two distance
234 matrices were non-Euclidean, they were square root transformed before being used to perform a
235 Ward's Hierarchical Agglomerative Clustering, using an algorithm implementing the Ward's criterion
236 (Ward, 1963; Murtagh and Legendre, 2014). The formed clusters were then plotted on a map to
237 visualize the spatial correspondence that may exist between the two types of clustered data, and the
238 percentage of correspondence between the two classifications was subsequently determined by
239 calculating the Spearman correlation coefficient (ρ). Finally, heatmaps were plotted and associated
240 with the HAC to determine which granulometric parameters and species contributed the most to the
241 formation of the different clusters, using $\log(x+1)$ and scaled data used for the biological and grain size
242 datasets, respectively.

243 3. Results

244 3.1. Biological data summary

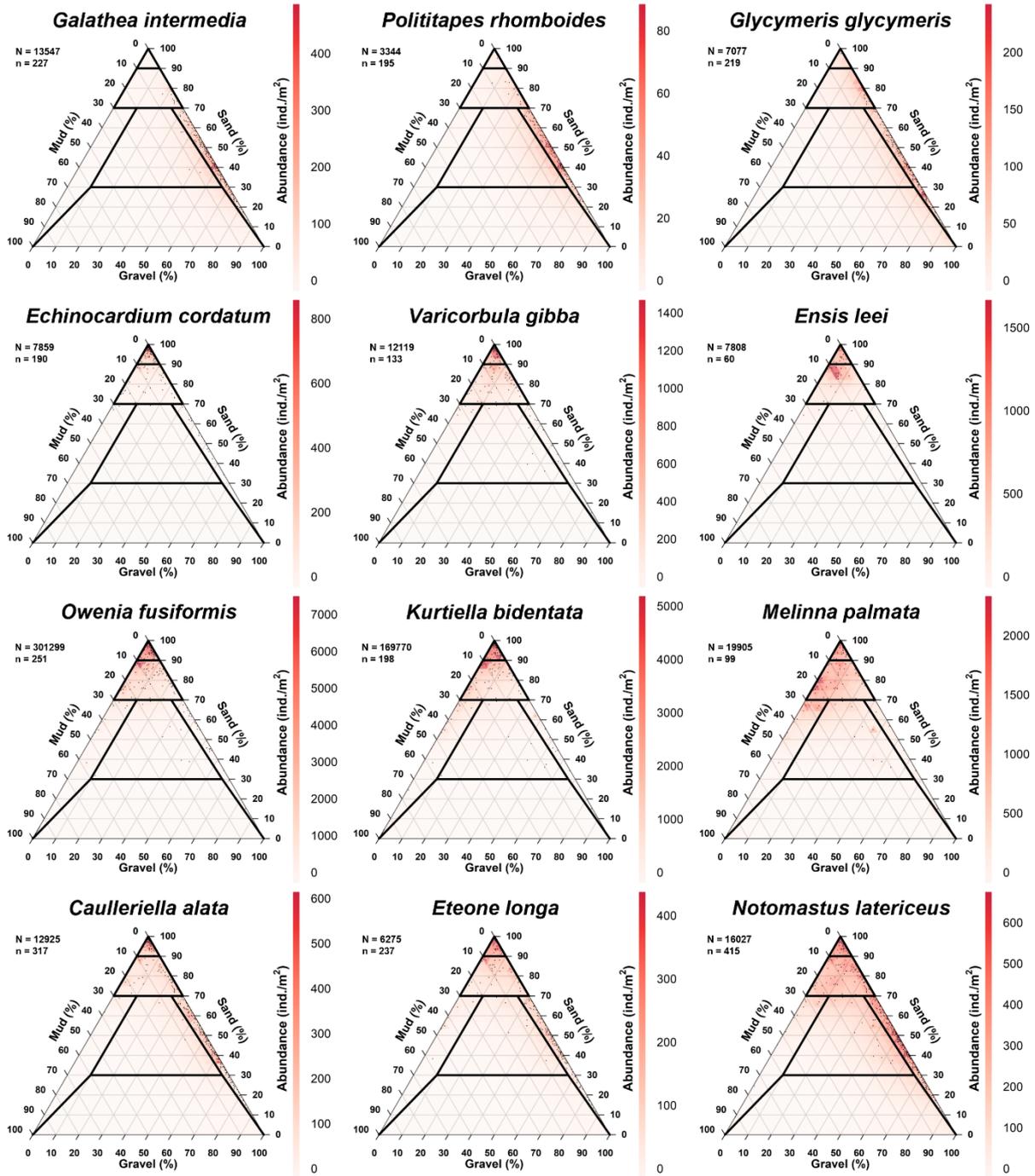
245 The selected species for the analyses (676 in total) were dominated by polychaetes (46%, comprising
246 311 species), malacostracans (24%, 162 species), bivalves (15%, 101 species), and gastropods (4%, 27
247 species). The most common species were the polychaetes *Nephtys hombergii* (54% occurrence),
248 *Notomastus latericeus* (54%), and *Owenia fusiformis* (50%), and the most abundant species were
249 *Owenia fusiformis* (466.6 ind./m², mean abundance), *Kurtiella bidentata* (246.1 ind./m²), and
250 *Acrocnida brachiata* (87.7 ind./m²).

251 3.2. Species envelope identification

252 The ternary plots provide a valuable visualization of the sediment in which the studied species are
253 most commonly found (Fig. 3). One can observe species that are predominantly associated with gravel
254 or sandy gravel habitats, like *Galathea intermedia*, *Polititapes rhomboides* or *Glycymeris glycymeris*,
255 species that show a preference for sandy habitats as *Echinocardium cordatum*, *Varicorbula gibba* or
256 *Ensis leei*, as well as species that are more ubiquitous, occurring across different grain size conditions

257 like *Caulleriella alata*, *Eteone longa* or *Notomastus latericeus* (Fig. 3). Interestingly, none of the species
258 in the dataset appears to be strictly mud-dwelling. While some species can be found in muddy
259 sediments, like *Owenia fusiformis*, *Kurtiella bidentata* or *Melinna palmata* (Fig. 3), it seems that none
260 of them exhibit a true preference for highly muddy habitats (mud content exceeding 20%), but rather
261 prefer less muddy environments. The presence of certain species in muddy habitats appears to reflect
262 a certain tolerance to this grain size fraction rather than a genuine attraction to such environments.

263 These ternary plots are also useful to reveal differences in species sensitivities to changes in grain size.
264 While some species exhibit a distinct peak in abundance within a specific sediment envelope and a
265 decrease as conditions deviate from their preferred range (Fig. 3, *Galathea intermedia*, *Echinocardium*
266 *cordatum* or *Varicorbula gibba*), other species like *Notomastus latericeus* display a broader peak of
267 maximum abundance, resulting in a wider range of grain size where these species are found in high
268 abundance, indicating a higher tolerance to variations in sediment composition.



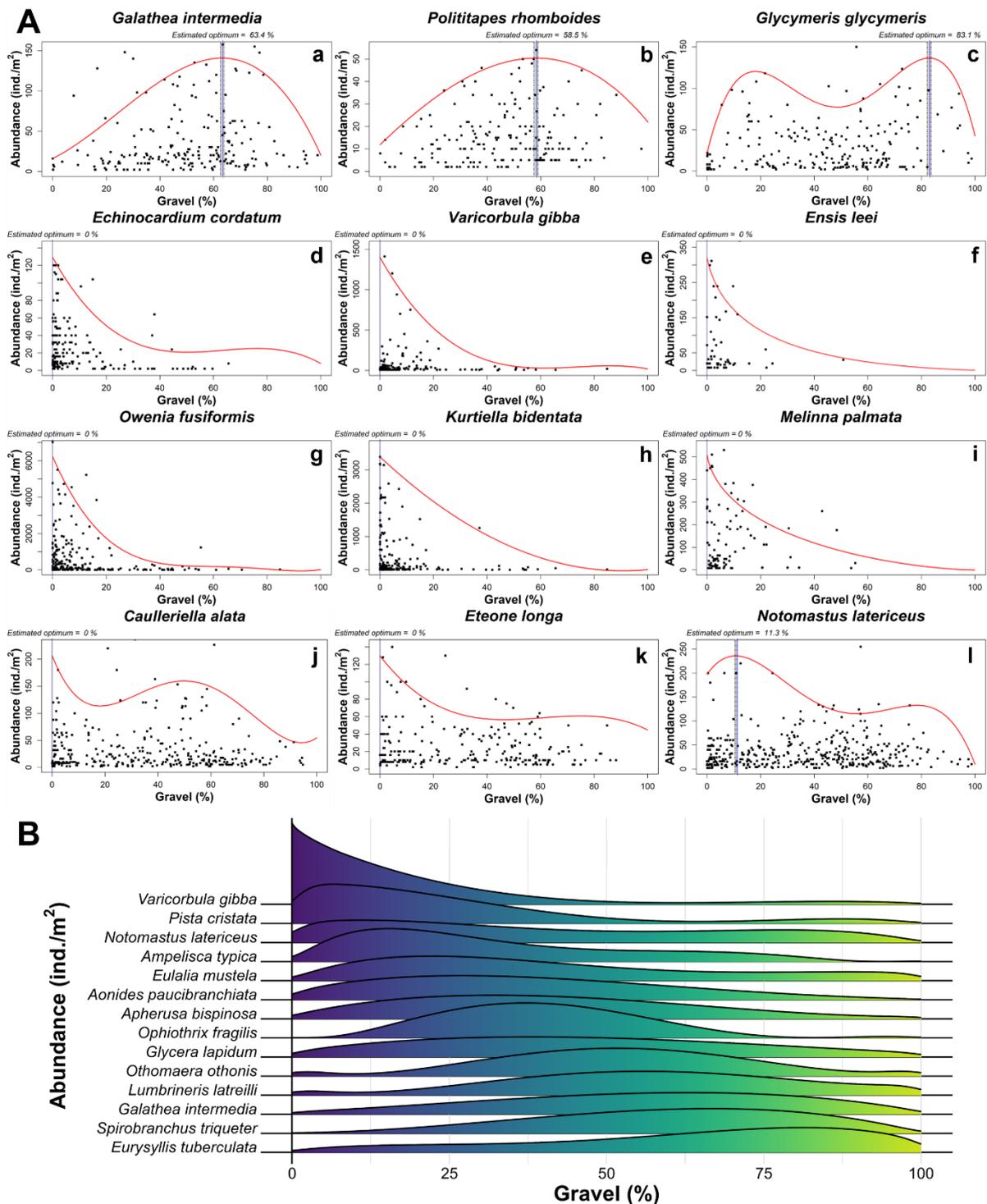
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270
271

Figure 3: Ternary plots of 12 species. Grain size fractions (mud, sand and gravel) are based on the Wentworth scale. N represents the total abundance and n denotes the occurrence of the species across all samples.

272 3.3. Fauna changes along a sedimentary gradient

273 Applying QR to the abundance distributions of multiple species allows for distinguishing several typical
274 responses based on the “edaphotope” (specific sediment or substrate conditions that are favorable to
275 a species) of the species along a grain size gradient, represented here by the percentage of gravel in
276 the sediment (for the reasons discussed later in section 3.4.). Thus, the biological response can take
277 the form of a skewed Gaussian distribution (Fig. 4a-b), a more or less gradual decreasing gradient (Fig.
278 4d-i, k), or a multimodal response (Fig. 4c, j, l). Species identified as predominantly gravel-dwelling in
279 the ternary plots (Fig. 3), except for *Glycymeris glycymeris*, appear to exhibit a Gaussian response, with
280 asymmetry tending towards lower percentages of gravel. Sand-dwelling and mud-dwelling species, on
281 the other hand, all show a decreasing curve along the grain size gradient, indicating a preference for
282 finer environments. Finally, more ubiquitous species (except for *Eteone longa*) and *Glycymeris*
283 *glycymeris* display a multimodal response, suggesting the potential existence of multiple grain size
284 preferences and validating the suitability of using B-splines to model the responses of different species.



285

286 Figure 4: (A) Quantile regression of 12 species encountered in the English Channel. The solid blue line represents the estimated
 287 optimal percentage of gravel for the species. The two dashed lines represent the lower and upper bounds of the 95%
 288 confidence interval around the estimated optimal value. In order to avoid overcrowding the graphical representation, only
 289 abundances below the 95th quantile were depicted in some cases. (B) Expected species successions along gravel gradient. Each
 290 ridge has been drawn using a quantile regression.

291 It is also interesting to note that for the two gravel-dwelling species exhibiting a Gaussian response
 292 (Fig. 4a-b), the percentages of gravel associated to the highest abundances are relatively close, being
 293 63% for *Galathea intermedia* and 58.3% for *Polititapes rhomboides*. Other species that can be
 294 identified as preferring coarse habitats have shown optimal gravel percentages of a similar magnitude.

295 This is notably the case for *Leptochiton scabridus* (63.5%, data not shown) and *Spirobranchus triqueter*
296 (66.9%, Fig. 4B), two species that live anchored to hard substrates. *Glycymeris glycymeris*, showing a
297 different response, has an optimal gravel percentage identified at 82.6%, with a potential second
298 preference observed around 20% of gravel, which is also reflected in the ternary plot of this species
299 (Fig. 3).

300 By sorting these species according to their optimal gravel percentage, it is possible to visualize the
301 gradual turnover of potentially dominant species (Fig. 4B) along a gravel gradient, which corresponds
302 to an inshore-offshore gradient in the eastern EC. This turnover would lead from communities
303 dominated by sandy-dwelling species such as *Varicorbula gibba* and *Pista cristata* in coastal areas
304 (potentially with mud-tolerant species such as *Owenia fusiformis* or *Melinna palmata* when mud is
305 present, especially in estuaries and coastal embayment with muddy sediments) to offshore
306 communities dominated by more gravel-dwelling species such as *Galathea intermedia*, *Spirobranchus*
307 *triqueter*, and *Eurysyllis tuberculata* (Fig. 4B).

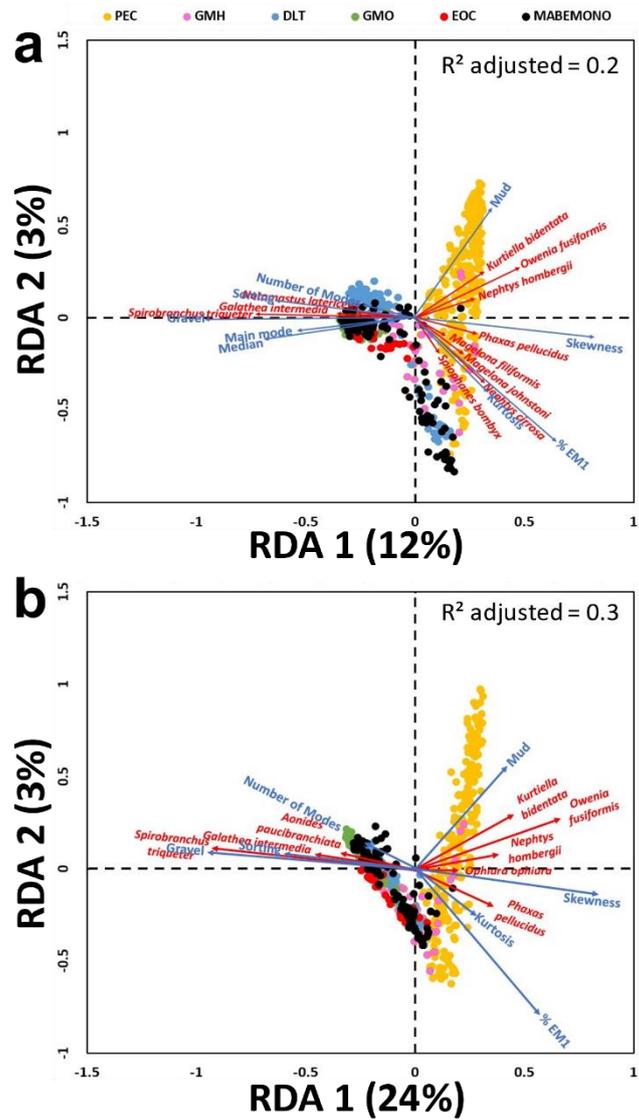
308 3.4. Grain size parameters influence on benthos distribution

309 Redundancy analysis (RDA) was performed on all taxa, examining their abundance in relation to various
310 granulometric parameters (Fig. 5a). Along the first axis of this RDA, which explains 12% of the total
311 inertia, stations characterized by a high percentage of gravel, a high sorting value (*i.e.*, poorly sorted),
312 and a high median (DLT, EOC, and GMO) are opposed to stations with an elevated positive skewness
313 (suggesting a gaussian asymmetry towards coarser sediments), observed for PEC, some GMH and
314 MABEMONO stations. The apparent opposition along axis 1 is therefore highly explained by grain size
315 parameters, separating stations characterized by a coarser sediment (gravelly or even coarser) from
316 those with finer sediment (sandy or finer). The coarser stations are characterized by high abundances
317 of *Galathea intermedia*, *Spirobranchus triqueter*, *Notomastus latericeus* (Fig. 5a), and *Glycymeris*
318 *glycymeris* (not shown). On the other hand, the stations with finer grain size exhibit high abundances
319 of *Owenia fusiformis*, *Kurtiella bidentata*, *Phaxas pellucidus*, *Magelona* spp., and *Spiophanes bombyx*
320 (Fig. 5a). These observations align with the findings of the ternary plots (Fig. 3), where *Galathea*
321 *intermedia* and *Glycymeris glycymeris* were identified as species associated with gravels, while *Owenia*
322 *fusiformis* and *Kurtiella bidentata* were associated with sandy and muddy environments.

323 Axis 2 of the RDA, on the other hand, explains only a very negligible fraction of the variance in benthic
324 distributions, with a constrained eigenvalue lower than the unconstrained eigenvalue. This calls for
325 caution in interpreting this component. Although this variable is poorly represented on axis 2, being
326 more intermediate between components 1 and 2, the percentage of mud appears to be the sediment
327 parameter that most discriminates the stations along axis 2 (Fig. 5a). The eastern EC is a relatively low-

328 mud marine environment (Larsonneur et al., 1982), and only a few sediment stations included in this
329 study, mainly from the PECTOW survey, exhibited a sufficiently significant mud percentage to be
330 detectable. Hence, the only stations differentiated along axis 2 are those from PECTOW (along with a
331 few estuarine stations from MABEMONO and GMH). This may explain the observed Guttman effect
332 (Guttman, 1953), which is commonly observed when representing such variables in a multivariate
333 space (Dauvin, 1988; Davoult, 1990). The adjusted R^2 of this RDA is reaching 0.2, which indicated that
334 grain size parameters can explain 20% of total benthos distribution in the eastern part of the EC.

335 However, as shown by the ternary plots (Fig. 3), it appears that certain benthic species are more
336 affected by the grain size characteristics of the environment than others. Therefore, a second RDA was
337 performed after selecting 30 “grain size-sensitive” taxa. This analysis aimed to evaluate the most
338 discriminant parameters for these species (Fig. 5b). The results of this second RDA are relatively
339 consistent with those of the first RDA (Fig. 5a). By focusing only on these “grain size-sensitive” species,
340 it is observed that the adjusted R^2 of the overall RDA reaches 0.3, suggesting that, for these species,
341 their distribution and abundance can be explained up to 30% by sediment grain size alone. The variable
342 that appears to most constrain species distribution is the percentage of gravel, which is well
343 represented on axis 1 (Fig. 5b). Therefore, this variable was selected to plot QR (see section 3.3.) in
344 order to study the distributional changes in abundances along a grain size gradient. Here, it appears
345 that grain size characteristics have a moderate influence on the distribution of benthic species, but it
346 is important to evaluate the contribution of other environmental variables to this distribution.

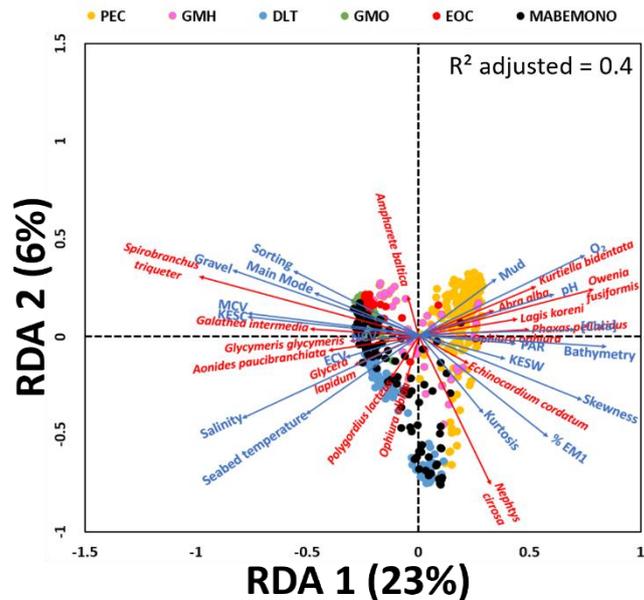


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Figure 5 : Redundancy analysis (RDA) results showing the relationships between granulometric parameters and transformed Hellinger abundance (a) all taxa sampled, present in at least 3% of all samples and (b) "grain size-sensitive" taxa of benthic species (scaling 2). The variable "Main mode" represents the grain size of the dominant mode. The colored points represent the station, as follows: yellow for PECTOW, pink for GMH, blue for DLT, green for GMO, red for EOC and black for MABEMONO.

352 3.5. Grain size and environment influence on benthos distribution

353 Similar to the RDA analyses conducted with granulometric parameters alone (section 3.4.), the RDA
354 incorporating other environmental variables also exhibits a Guttman effect (Fig. 6, Guttman, 1953),
355 albeit with more nuances. This effect and the added variables contribute to a diagonalization of the
356 eigenspace, which is no longer solely interpretable in terms of components 1 and 2, but rather in terms
357 of an intermediate component, situated between components 1 and 2. This has also been emphasized
358 by Dauvin (1988), who recommended interpreting the observations' projections in the principal
359 component plane as a whole, rather than considering axes 1 and 2 separately. One of these
360 components involves the percentage of gravel, sorting value, grain size of the main mode, skewness,
361 as well as variables related to current dynamics (MCV) and wave exposure (KESW). In the upper left of
362 the eigenspace, the stations are characterized by a high percentage of gravel, an elevated negative
363 skewness (indicating a Gaussian asymmetry towards finer sediments), and strong hydrodynamics (*e.g.*,
364 high current velocity), but no or a weak influence of waves. On the contrary, in the lower right of the
365 eigenspace, stations presented a lower gravel fraction, a higher percentage of sand (as indicated by
366 the membership percentage in EM1, Fig. 6), and a more nuanced hydrodynamics condition, with the
367 exception of waves that bring a significant amount of energy to these stations (KESW on Fig. 6). This
368 component represents an inshore-offshore gradient, with coastal stations (lower right) characterized
369 by moderate tidal currents, strong wave exposure, prone to the accumulation of fine sand sediment
370 (high membership percentage in EM1). Conversely, the stations depicted in the upper left would likely
371 correspond to offshore stations, characterized by strong hydrodynamics, no wave influence and a
372 predominantly coarse sediment composition.



373
 374 Figure 6: Redundancy analysis (RDA) results showing the relationships between granulometric parameters, environmental
 375 variables, and transformed Hellinger abundance of benthic species present in at least 3% of all samples (scaling 2). The variable
 376 "Main Mode" represents the grain size of the dominant mode. Bathymetry is in negative values. MCV: Maximum Current
 377 Velocity. KESW: Kinetic Energy at the Seabed due to Waves. The colored points represent the station, as follows: yellow for
 378 PECTOW, pink for GMH, blue for DLT, green for GMO, red for EOC and black for MABEMONO.

379 The second component, which also exhibits a somewhat diagonal orientation, is characterized by
 380 strong correlations with pH, oxygen concentration, salinity, bottom temperature, and percentage of
 381 mud in the sediment. Therefore, stations located in the upper-right quadrant of the eigenspace are
 382 characterized by high mud percentage, high oxygen concentration, higher pH, and lower salinity and
 383 bottom temperature compared to stations in the lower-left quadrant of the eigenspace. This
 384 component can be interpreted as the effects of estuaries, particularly the Seine estuary, on the
 385 environment. Thus, stations in the upper-right quadrant are heavily influenced by inputs from the
 386 Seine River, resulting in significant desalination of the environment, lower bottom temperatures, and
 387 substantial input of suspended matter, which explains the high percentage of mud at these stations.
 388 These stations are characterized by high abundances of species such as *Owenia fusiformis*, *Kurtiella*
 389 *bidentata*, *Abra alba*, and *Lagis koreni*. In contrast, stations in the lower-left quadrant exhibit a weaker
 390 (or no) estuarine influence, with warmer bottom temperatures and no desalination effects. These
 391 stations are notably characterized by high abundances of *Glycymeris lapidum* and *Polygordius lacteus*.

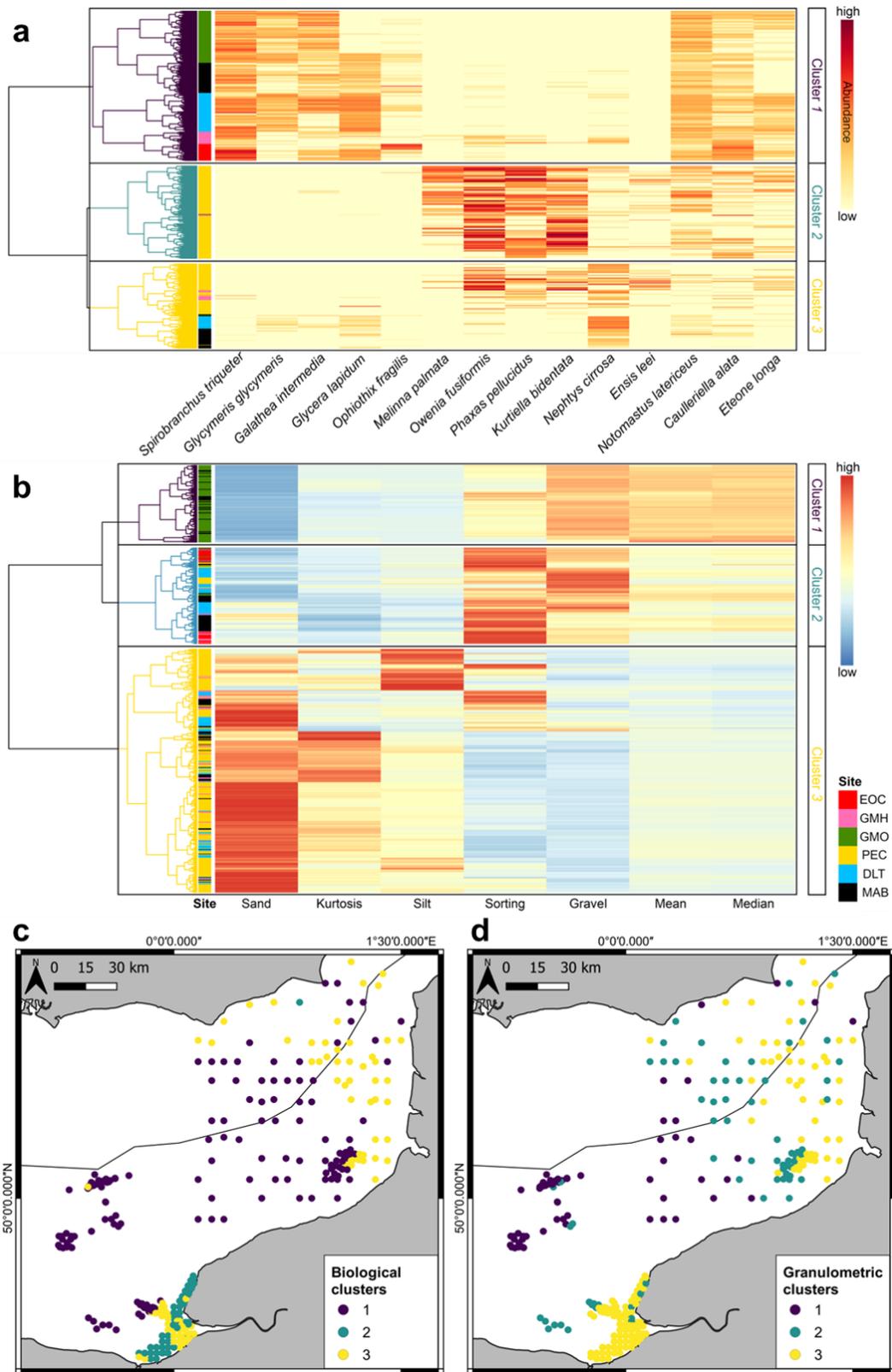
392 3.6. Mapping benthos and granulometric patterns

393 Hierarchical clustering revealed three major biological and granulometric clusters in the eastern EC.
 394 For the biological data (Fig. 7a, c), cluster 1 includes all stations from GMO and EOC sites, most stations
 395 from DLT and GMH sites, and some stations from the MABEMONO survey. This cluster was
 396 characterized by high abundances of species such as *Spirobranchus triqueter*, *Glycymeris glycymeris*,
 397 and *Galathea intermedia*. Cluster 2 consists almost exclusively of stations from the PECTOW survey,

398 except for one station from the MABEMONO survey (located offshore of the Rother River, UK, Fig. 7c)
399 and two stations from the GMH site, situated in the southeast part of this sector. This second cluster
400 was primarily characterized by high abundances of species such as *Melinna palmata*, *Owenia*
401 *fusiformis*, or *Kurtiella bidentata*. Lastly, cluster 3 comprises the remaining stations from PECTOW,
402 GMH, DLT, and MABEMONO, and was notably characterized by high abundances of the species
403 *Nephtys cirrosa*. The species *Notomastus latericeus*, *Caulleriella alata*, and *Eteone longa*, on the other
404 hand, did not appear to show higher abundances in one cluster over the other, in line with the patterns
405 observed in the ternary plots (Fig. 3).

406 Regarding the granulometric parameters (Fig. 7b, d), cluster 1 consists almost exclusively of data from
407 the GMO and the MABEMONO surveys, characterized by a relatively high percentage of gravel, a high
408 mean and median, and a medium sorting value. Cluster 2 includes stations from MABEMONO, DLT,
409 GMH, some stations from GMO, PECTOW, and all stations from EOC. In contrast to cluster 1, this
410 second cluster also exhibited a high percentage of gravel, but with a lower mean and median value, as
411 well as a higher sorting value (indicating a poorer sediment sorting). Lastly, cluster 3 encompasses
412 stations from the PECTOW, DLT, MABEMONO, and GMH surveys. This cluster was generally
413 characterized by a high percentage of sand or mud.

414 There is a strong spatial correlation between benthic communities and granulometric parameters
415 within the formed clusters (Fig. 7c-d). By grouping clusters 1 and 2 from the granulometric clustering,
416 we obtain a cluster that closely resembles cluster 1 from the biological data clustering. Similarly, when
417 we group biological clusters 2 and 3, we get a cluster that closely matches granulometric cluster 3.
418 These groupings lead to a relatively high Spearman coefficient, indicating an 84% spatial match
419 between biological and granulometric clusters (Spearman's $\rho=0.84$, $p<0.001$). Lastly, the clustering of
420 granulometric parameters remarkably corresponds to the distribution of surface sediments in the
421 eastern EC (Fig. 1).



422

423 *Figure 7: Hierarchical clustering and heatmap of (a) benthic abundance data and (b) granulometric parameters, and*
 424 *localization of the corresponding (c) biological and (d) granulometric clusters. Abundance data were log(x+1) transformed and*
 425 *granulometric parameters were scaled. Distance used were squared-root Bray-Curtis for biological data and squared-root*
 426 *Manhattan for granulometric parameters. Both hierarchical clustering were built using Ward's agglomerative algorithm*
 427 *(Ward, 1963; Murtagh and Legendre, 2014).*

428 4. Discussion

429 4.1. Plotting species sedimentary envelope

430 Ternary plots have proven to be powerful representations to distinguish gravel-dwelling, sand-
431 dwelling, and ubiquitous species. Many correspondences in classification between those initially
432 proposed by Glémarec (1969) for the continental shelf of the north of Bay of Biscay and the eastern
433 part of the EC have been noted. Species such as *Glycymeris glycymeris*, *Polititapes rhomboides*, *Ensis*
434 *spp.*, *Abra alba*, or *Owenia fusiformis* were generally classified into the same categories (Glémarec,
435 1969). This highlights the applicability of this classification method for the eastern part of the EC.
436 However, these representations did not succeed to reveal any true mud-dwelling species in the eastern
437 EC, in contrast to what has been observed on the North of Bay of Biscay continental shelf (Glémarec,
438 1969), where few species like *Abra nitida*, *A. segmentum*, *Sternaspis scutata*, or *Thyasira flexuosa* have
439 been classified as strict mud-dwellers. Only *Melinna palmata* appears to come close to this
440 classification, although it seems to prefer slightly muddy sandy grounds (% mud < 20%), classifying it
441 as a mud-tolerant sand-dwelling species rather than a strict mud-dwelling species. Several hypotheses
442 could be proposed to explain the absence of strict mud-dwelling species in the eastern EC. The most
443 likely hypothesis is the absence or under-sampling of such habitats. Indeed, the only data from muddy
444 stations were obtained from certain PECTOW monitoring stations. However, as indicated by RDA, the
445 estuarine influence present at these stations is so significant that the high variability in salinity and
446 temperature occurring there may not allow for the observation of the true abundances that potential
447 mud-dwelling species could exhibit under optimal environmental conditions. This bias could be
448 overcome by sampling a greater number of muddy habitats, which are less affected by the
449 environmental variations induced by the Seine Estuary, by complementing these data with stable
450 muddy habitats found in the eastern part of the EC (which are very scarce locations in this part of the
451 EC, Larsonneur et al., 1982). Including data from the western part of the EC can also be a solution, but
452 it must have to deal with the apparent climatic gradient when considering this part of the EC (Holme,
453 1961, 1966; Rees et al., 1999), even if the biotic homogenization (Olden and Rooney, 2006) would tend
454 to partially mitigate this gradient (Bolam et al., 2008).

455 4.2. Modeling species response along a grain size gradient

456 4.2.1 On the choice of conditional and response variables for investigating benthic species 457 distributions

458 At the scale of the eastern EC, RDA analyses appeared to indicate that gravel percentage was the most
459 relevant variable for discriminating the distribution of different samples and providing a better
460 description of benthic species distributions within this system, especially along the inshore-offshore

461 gradient. Hence, this variable was used to study the biological response along a grain size gradient
462 using QR. This finding is not surprising, considering the extensive coverage of coarse substrates in this
463 area, which account for over 80% of its surface (Larsonneur et al., 1982). Conversely, mud percentage
464 is a less relevant variable for studying the entire eastern EC system, as the only true muddy areas
465 investigated in this study were located at the Seine Estuary mouth (as underlined in section 4.1.).
466 However, similar to the findings underlined by Anderson (2008), the RDA analyses highlighted the
467 importance of using mud percentage to study the estuarine influence on benthic communities along a
468 grain size gradient, which is beyond the scope of this study (but discussed in more detail in subsection
469 4.5.2.). As emphasized by Anderson (2008), percentage of mud can serve as a proxy for various other
470 environmental factors in these estuarine systems, such as relative exposure, wave action,
471 permeability, porosity, or oxygen content (Gray, 1974; Anderson, 2008). On the other hand, Zettler et
472 al. (2013) and Cozzoli et al. (2013) opted to use the median of the GSD (d_{50}) and loss on ignition (LOI, a
473 proxy for sediment organic fraction) to model QR for different species sampled in major European
474 estuaries, in order to reconstruct the response of the species along the substrate gradient for each
475 salinity class. The use of these variables is justified as the compared estuaries in these studies are
476 spatially distant and may exhibit distinct hydrodynamic and sedimentary characteristics between the
477 sites. The differences in hydrological context in this case challenge the definition of mud, as the
478 mobilizing currents of the fine fraction may vary between these different estuaries (Dyer, 1995; Blott
479 and Pye, 2012). The use of d_{50} and LOI, which can be measured worldwide, is therefore particularly
480 justified within the framework of these studies. These observations underscore the necessity, for each
481 studied system, to judiciously select the most representative continuous environmental variable(s) to
482 investigate the distribution of benthic species along an environmental gradient, as well as the variable
483 that best represents the ecological relationship under study.

484 However, it should be noted that the measured variable (in this case, specific abundances per square
485 meter) could be replaced by a more representative biological variable that captures how well the
486 species thrives in the environment. Biomass, for example, would be a much more suitable choice, as it
487 indirectly represents the population size and also takes into account the species' ability to survive in a
488 given habitat (with the fittest and older individuals being more massive). This holds particularly true
489 for less mobile species like bivalves, where *Glycymeris glycymeris*, *Polititapes rhomboides*, *Kurtiella*
490 *bidentata* or *Phaxas pellucidus* serve as good candidates for capturing the effect of a grain size gradient
491 in the eastern EC. Unfortunately, this variable is relatively time-consuming to measure, which explains
492 why it is rarely used, and major protocol differences can make comparisons between different surveys
493 challenging.

494 4.2.2. Using quantile regressions for investigating benthic species distributions

495 This study, along with several previous ones (Cade and Noon, 2003; Thrush et al., 2003; Anderson,
496 2008; Vaz et al., 2008; Zettler et al., 2013), has highlighted the value of using QR, or more generally,
497 non-parametric regression methods. There are several advantages to consider when using these
498 methods. One major advantage is that they help to mitigate the influence of outliers, a common issue
499 in ecology (Benhadi-Marín, 2018), as mean-based regression methods are more sensitive to outliers
500 (Koenker and Bassett, 1978; Anderson, 2008). This characteristic has been particularly evident in
501 species that exhibit high variability in their biological response, such as polychaetes like *Notomastus*
502 *latericeus* or *Melinna palmata*, for example.

503 Furthermore, by modeling only the upper quantiles of distributions, it is assumed that the effects of
504 unmeasured variables will cause abundances to decrease (*i.e.*, become more limiting) rather than
505 being facilitative (Kaiser et al., 1994; Terrell et al., 1996; Cade et al., 1999, 2005). For instance, in the
506 context of the eastern EC, even though the influence of the Seine Estuary on benthic communities has
507 been identified as a structuring force, QR have allowed to separate this effect and investigate the
508 distribution of several benthic species along a grain size gradient. This was achieved even when these
509 species showed sensitivity to the conditions imposed by the Seine Estuary (*e.g.*, strong desalination,
510 decrease in bottom temperature). Thus, one of the major challenges in ecology, which is the unequal
511 variation of ecological data due to complex interactions between unmeasured factors, can be partially
512 overcome, enabling researchers to focus on the effect of the variable of interest and understand how
513 the environment limits the species' distribution.

514 Lastly, it is worth noting that biological responses exhibit unequal variations along a continuous
515 variable, implying that there is more than a single rate of change describing the relationship between
516 a response variable and measured predictor variables (Cade and Noon, 2003). QRSM are well-suited
517 for this purpose, as they estimate multiple rates of change from the minimum to maximum response,
518 providing a more comprehensive understanding of the relationships between variables that may be
519 missed by other regression methods, particularly linear ones. Therefore, QR are a statistically robust
520 tool for modeling species' responses to conditional environmental variables and studying the concept
521 of limiting factors and the modeling of the “outer envelope” of species' distributions (Thrush et al.,
522 2003; Zettler et al., 2013).

523 However, some limitations to using these statistical tools should be noted. One major disadvantage is
524 that these models are dedicated to describing patterns in relation to a conditional variable, rather than
525 attributing cause to this relationship (Ysebaert et al., 2002; Anderson, 2008). They provide valuable
526 information about the type of response, optimum, or tolerance of a species to an environmental

527 variable without explaining the underlying biological causes. Consequently, the resulting models tend
528 to describe potential rather than actual patterns of species distributions (Vaz et al., 2008). To
529 complement these observations, further research is needed to investigate why such relationships are
530 observed and the true involvement of the conditional variable in the observed distributions. As
531 suggested by Snelgrove and Butman (1994), more experimental studies (using eco-hydraulic flumes or
532 mesocosms for instance) should be conducted to better understand the benthos-sediment
533 relationship, including the involvement of related factors such as hydrodynamics or larval settlement
534 in this relationship in order to include this knowledge into future models.

535 Another major limitation of using QR is the sample size. QR require a minimum amount of information
536 to be accurately modelled. In this study, for instance, only the 41 most abundant species were selected
537 for these analyses. Consequently, rare species that are highly specific to certain conditions are
538 disadvantaged. Additionally, samples must be adequately distributed across each order of magnitude
539 of the continuous scale under study (Thrush et al., 2005), to capture the entire variation of the
540 biological response along the conditional variable. In this study, a significant number of stations
541 characterized by high percentages of gravel (up to 98.8%) and stations depleted in gravel (down to
542 0%), characterized by high percentages of sand, mud, or a mixture of both, were included in these
543 analyses, thereby considering all the habitats encountered in the eastern EC, except for the muddy-
544 gravel habitats with high abundances of *Ophiothrix fragilis* found in scarce locations of the central Bay
545 of Seine (Dauvin and Ruellet, 2008; Lozach et al., 2011; Murat et al., 2016).

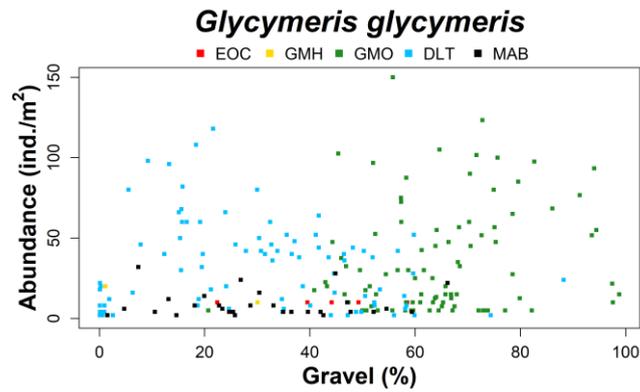
546 Finally, although quite suitable, this method is currently relatively underutilized, particularly in the
547 context of the benthos-sediment relationship, which limits the extent of result comparisons (Cade and
548 Noon, 2003).

549 4.3. Species response along a grain size gradient

550 Using QRSM, Anderson (2008) found comparable biological responses to those reported in this study
551 when examining the correlation between mud percentage and estuarine species abundance. This
552 author identified four main response types: (i) a decline in abundance as mud content increased, (ii) a
553 unimodal relationship with a relatively precise estimated optimum, (iii) a unimodal relationship with a
554 relatively low precision in the estimated optimum, and (iv) an increase in abundance with increasing
555 mud content. Equivalents can be hypothesized with the gravel percentage, with decreasing
556 relationships as the gravel percentage increases (suggesting an increasing relationship with the
557 increase of sand, mud, or a mixture of both), and more or less spread unimodal relationships (skewed
558 Gaussians) with varying precision in the estimated optimum.

559 Additionally, similar to the observations made for *Glycymeris glycymeris* or *Caulleriella alata*, Anderson
560 (2008) also identified taxa exhibiting potentially multimodal responses within the Nereidae family or
561 the genus *Paracalliope* spp. This highlights the importance of using B-splines to model the response of
562 different species. However, it is possible that these multimodal responses could be attributed, at least
563 for some species, to a major methodological bias. Indeed, once the sediment is sampled, the vertical
564 structure is lost, as current sampling methods do not retain this information. It is therefore possible
565 that the actual sediment envelope of the species, the one in which the species is located, potentially
566 burrowed, may have characteristics that differ significantly from the “averaged” information obtained
567 by studying the GSD from sediment samples.

568 Take, for example, *Glycymeris glycymeris*. Although this species has been observed in both gravelly
569 and sandy environments (Ansell and Trueman, 1967), which seems to be confirmed by the results here,
570 it is possible that this species is actually present only within a gravelly envelope, burrowed under the
571 first centimeters of the sandy sediment. In fact, when examining the distribution of this species along
572 the gravel gradient (Fig. 8), we can observe that the density peak neighboring 20% of gravel is observed
573 at Dieppe Le Tréport (DLT on Fig. 8), while the second peak detected by QR, around 80%, corresponds
574 to abundances measured only at GMO. The DLT site is known to exhibit vertical stratification of its
575 sediments, characterized by the presence of sand ripples overlying coarse sediments (visible on Fig. 1,
576 Ferret, 2011). The sand present at this site may therefore potentially “dilute” high percentage of gravel
577 found deeper, where *G. glycymeris* typically burrows. At the GMO site, gravels occupy the upper
578 sediment layers, including the envelope where *G. glycymeris* is present (G-tec pers. comm.), which
579 could explain why *G. glycymeris* is more abundant there. However, this hypothesis is probably not
580 verifiable since the depth to which *G. glycymeris* burrows appears to depend on the substratum (Ansell
581 and Trueman, 1967). In sand, this species is not deeply buried, and the posterior valve and mantle
582 margins are visible just above the surface (Ansell and Trueman, 1967). In gravel, animals bury deeper,
583 reaching depths of 'several cm' (Ansell and Trueman, 1967). Therefore, the two optima detected by
584 QR are likely not solely attributable to the bias described earlier, potentially implying the existence of
585 two ecotypes within this species.



586

587 *Figure 8: Distribution of Glycymeris glycymeris abundances along a gravel percentage gradient. The points have been colored*
 588 *to represent the station where the abundance was measured.*

589 To overcome this challenge, it would be interesting to investigate the vertical structure of sediments
 590 at the different study sites and examine the vertical positioning of benthic species within the sediment.
 591 Currently, there is limited data available on the vertical distribution of benthic species within coarse
 592 sediments (Trueman et al., 1966; Dorgan, 2015), especially when they exhibit grain size stratification
 593 (Navon, 2016). The scarcity of existing data on vertical sediment and biological distributions may be
 594 historically attributed to technical limitations. For muddy sediments, typically characterized by high
 595 levels of silt and clay, the use of Sediment Profile Imaging (SPI) has proven effectiveness in studying
 596 sediment characteristics (vertical structuring, oxidized layer) and biological features (species burial
 597 depth). However, in coarser and highly sandy environments, traditional SPI methods are less suitable
 598 as they do not allow sufficient penetration into the sediment (Germano et al., 2011). To address this
 599 challenge, the application of a DynamicSPI (DySPI) could be highly beneficial (Blanpain et al., 2009), as
 600 the penetration mode of this device enables vertical investigation of coarser sediments.

601 4.4. Correspondence between sediment grain size and benthic community structure in 602 the eastern English Channel

603 In the eastern EC, several authors have found a relatively moderate correspondence between
 604 sediment composition and the distribution of benthic species (Seiderer and Newell, 1999; Newell et
 605 al., 2001). These studies obtained Spearman correlation coefficients (ρ) ranging from 0.37 (Seiderer
 606 and Newell, 1999) to 0.44 (Newell et al., 2001) between biological communities and sediment grain
 607 size at best, albeit primarily focusing only on coarse sediments and at a relatively small spatial scale.
 608 According to these authors, such low values suggest that sediment grain size may play a minor role in
 609 controlling benthic community structure. On a larger scale, encompassing both the eastern and
 610 western EC (but only on the English side and with a limited number of stations), Rees et al. (1999) also
 611 observed a moderate explanation of benthic community variability by sediment grain size ($\rho = 0.40$ for
 612 sediment median diameter alone). Similarly, with a substantial dataset that still only encompassed the
 613 English side of the EC and the surrounding waters of the United Kingdom, Cooper and Barry (2017)

614 found a 30% correlation between sand content and macrofaunal data. It's worth noting that the
615 highest explanatory rate, reaching 42%, was achieved when considering the current velocity along with
616 the sediment sand and mud percentages (Cooper and Barry, 2017). Thus, in line with the results of this
617 study, these authors also emphasize that sediment composition is not the exclusive primary factor
618 shaping benthic communities, as underlined by Bolam et al. (2008). Using side-scan sonar to
619 characterize sediment, similar perspectives have been obtained at various coarse sediment sites in the
620 EC, showing that seabed morphology (and not solely grain size composition) also has a significant
621 influence on benthic assemblages (Brown et al., 2001, 2002, 2004a, 2004b). These findings are
622 consistent with the results of this study, where grain size factors alone constrain the distribution of
623 species abundances in the eastern EC by "only" 20%. Despite this described minor contribution,
624 Seiderer and Newell (1999) still note a relatively strong correspondence between sediment
625 composition and the distribution of several species, such as *Sabellaria spinulosa*, which is mainly found
626 in coarse sand and gravelly substrates (2000-16000 μm). In the case of the eastern EC, this species has
627 also been observed in similar sediment conditions. Out of 48 occurrences, *Sabellaria spinulosa* was
628 associated with high percentages of gravel (ranging from 21% to 98%, with an average percentage of
629 57%) and coarse sand (ranging from 2% to 79%, with an average percentage of 43%), primarily at the
630 EOC and GMO sites, with a mean median grain size of 4230 μm . *Sabellaria spinulosa* is not the only
631 species showing a strong correspondence between its distribution and sediment composition, as
632 indicated by the strong spatial correlation ($\rho=0.84$) between the biological and granulometric clusters.
633 Other species such as *Galathea intermedia*, *Glycymeris glycymeris*, *Polititapes rhomboides*,
634 *Spirobranchus triqueter*, *Owenia fusiformis*, *Abra alba* or *Phaxas pellucidus* have shown high sensitivity
635 to grain size variations, exhibiting a strong correspondence between distribution and sediment
636 composition, as described by Seiderer and Newell (1999). By selecting these taxa, the percentage of
637 species distribution explained by granulometric parameters alone reached 30%, indicating that for
638 these species, grain size is a slightly more significant factor than for other more ubiquitous species.
639 These results, with some previous ones (Longhurst, 1958; Buchanan, 1963; Cassie and Michael, 1968;
640 Hughes and Thomas, 1971), collectively highlight the importance of a species-dependent approach to
641 study the benthos-sediment grain size relationship, which has been relatively understudied, where
642 most analyses focusing on the relationship between sediment composition and benthic assemblages
643 (Petersen, 1913; Ford, 1923; Seiderer and Newell, 1999; Newell et al., 2001).

644 By examining the benthos-grain size relationship after incorporating data from coarse environments
645 allows us to introduce some nuances to the conclusions drawn by Snelgrove and Butman (1994). At
646 the scale of the eastern EC, these parameters account for 20% of the variations in benthic communities
647 (a significant portion of the total variability), allowing for a good overall description of the community

648 distribution on a wide spatial scale, encompassing a great range of grain size. This is notably evident
649 through the 84% spatial match between the biological and grain size clusters (Fig. 7c-d). Furthermore,
650 it's worth noting that these conclusions may vary for species-level approaches (see previous sections
651 for more details), as not all species exhibit the same sensitivity to sediment grain size composition,
652 especially when the study area is primarily composed of coarse sediments. Indeed, coarse sediments
653 seem to support numerous species that require the presence of a coarse sediment fraction (such as
654 gravel or pebbles) for anchorage, for instance. This may also explain why the grain size-benthos
655 relationship appears to be more pronounced for such sediments when compared to sandy or muddy
656 ones.

657 4.5. Benthos shaping in the eastern English Channel

658 4.5.1. Sedimentary contribution to benthos structure

659 Several hypotheses can be formulated regarding how sediment grain size can affect the distribution of
660 benthic communities. The most obvious hypothesis is directly related to the physical substrate
661 provided by the sediment. Among the species identified as “grain size-sensitive”, *Spirobranchus*
662 *triqueter* and *Owenia fusiformis* perfectly fit this notion. In the case of *Spirobranchus triqueter*, it
663 indeed requires a relatively coarse and stable substrate to anchor its calcareous tube (Tillin and Tyler-
664 Walters, 2016). For *Owenia fusiformis*, the presence of sufficiently fine elements in the vicinity is
665 necessary for tube construction, without being too fine (Pinedo et al., 2000; Noffke et al., 2009). For
666 other “grain size-sensitive” species, the relationship may be less obvious, and several hypotheses have
667 been proposed. In these cases, sediment grain size is likely just a correlated variable to the true causes
668 driving their distributions (Snelgrove and Butman, 1994). In their review, Snelgrove and Butman (1994)
669 identified five major aspects of sediment variables to which benthos could respond. These aspects
670 include grain size (as discussed earlier), sediment organic matter content, microbial composition of the
671 sediment (bacteria and microalgae, particularly in finer sediments), sediment stability, and
672 amensalistic relationships occurring within the sediment (see Snelgrove and Butman, 1994, for details).
673 To summarize these last four major aspects, they particularly would influence the trophic ecology of
674 benthic species. For instance, deposit-feeders are more abundant in muddy habitats, while
675 suspension-feeders tend to have higher density in sandier areas (Sanders, 1958; Sanders et al., 1962;
676 Rhoads and Young, 1970; Rhoads, 1974). Based on this observation, Rhoads and Young (1970)
677 proposed the hypothesis of “trophic group amensalism” to explain the exclusion of suspension feeders
678 by deposit feeders in muddy habitats. According to this hypothesis, deposit feeders are less favored in
679 sandy areas due to the higher horizontal sediment fluxes (except for the “turbidity-influenced facies”
680 areas defined by Retière, 1979), which are more favorable for suspension feeders. On the other hand,
681 in muddy sediments, the resuspension of fine matter caused by the sediment reworking by deposit

682 feeders inhibits the filtering activity and larval burying of suspension feeders (Rhoads and Young, 1970;
683 Rhoads, 1974). While this hypothesis has received criticism in several aspects (see Snelgrove and
684 Butman, 1994, for review), it is one of the hypotheses explaining how sediment properties can
685 indirectly influence the distribution of benthic species, categorized into different functional groups.

686 However, it is important to note that the results presented here are based solely on a correlational
687 basis, which does not provide any explanation for the underlying mechanisms driving the observed
688 relationship (a limitation that was also highlighted in the species-based approach using QMRS, as
689 discussed in subsection 4.2.2.). Further experimental studies are needed to clarify these mechanisms
690 and determine the true implications of sedimentary factors in this relationship. Additionally, as
691 highlighted by Snelgrove and Butman (1994), the relationships between benthos and sediment may
692 be (perhaps exclusively) influenced by factors other than sediment properties. This perspective is
693 based on the understanding that sediment properties are reflective of boundary-layer flow and
694 sediment-transport regimes.

695 4.5.2. Other parameters influencing benthos structure

696 Among the non-sedimentary factors influencing the distribution of benthic species, hydrodynamic
697 regime is likely one of the most influential factors shaping benthic community structure (Jumars and
698 Nowell, 1984; Davoult et al., 1988; Snelgrove and Butman, 1994). This suggestion is supported in the
699 eastern EC, where the RDA results demonstrate a strong correlation between hydrodynamic
700 parameters (*e.g.*, maximum current velocity) and granulometric parameters (particularly gravel
701 percentage). Thus, it seems reasonable to consider granulometric characteristics as a reflection of the
702 hydrodynamic conditions, which have a greater impact on benthic communities than granulometric
703 parameters alone (although the influence of these parameters is likely not negligible, at least for
704 certain species, as discussed in subsection 4.5.1). This statement, however, must be nuanced for the
705 particular case of the EC. Indeed, this sea is classically described as being a sediment-starved platform
706 with coarse sediments that are less susceptible to mobilization by the prevailing currents, generating
707 “lag deposits” (Larsonneur et al., 1982; Reynaud et al., 2003). These coarse sediments are, in fact,
708 inherited from fluvial deposits during the last glacial period and subsequently reworked during the
709 Holocene transgression (Dingwall, 1975; Larsonneur et al., 1982). Additionally, the characteristics
710 attributed to the extensive bioclastic sediment cover (Larsonneur et al., 1982) in the EC should not be
711 overlooked. These sediments correspond to *in situ* production and may thus not be in equilibrium with
712 hydrodynamic conditions (Larsonneur et al., 1982). Moreover, their size is likely to decrease over time
713 due to fragmentation (Zuschin et al., 2003; Rieux, 2018). However, hydrodynamic forcing can still
714 influence benthic communities through various processes, including larval dispersal and settlement
715 through passive and active mechanisms (Thorson, 1957; Butman, 1987), as well as on trophic aspects

716 by influencing the vertical and horizontal fluxes of organic matter (Sanders, 1958; Wildish, 1977), which
717 may partially explain the “trophic group amensalism” hypothesis presented in subsection 4.5.1.
718 (Rhoads and Young, 1970; Rhoads, 1974).

719 The RDA analysis also reveals an effect of the Seine River in the eastern EC, particularly in terms of
720 salinity drops and high seasonal temperature variations that can influence benthic communities.
721 Similar influences have been observed by Thiébaud et al. (1997), Ghertsos et al. (2001) and Dauvin et
722 al. (2017), but only at the smaller scale of the river mouth. Here, the observed effect appears to be
723 more gradual and follows the “coastal flow” also called “Region Of Freshwater Influence”, or ROFI,
724 which has already been described as impacting biological communities, both benthic (Cabioch and
725 Glaçon, 1977, leading to the presence of *Conopeum* facies as indicators of salinity decreases) and
726 phytoplanktonic (Brylinski et al., 1984; Quisthoudt, 1987). Based on samplings conducted along the
727 English coast (including the North Sea, the EC, and the Bristol Channel), Rees et al. (1999) also detected
728 the significant contribution of major estuaries discharging into these seas, particularly highlighting the
729 influences of the Elbe/Weser, Tees, the Wash, Thames, Bristol Channel, Morecambe Bay, and Belfast
730 Lough. Therefore, it is not surprising that at the scale of the eastern EC, the contribution of the Seine
731 River plays a major role in shaping the distribution of benthic species.

732 5. Conclusions

733 This study explored the relationship between sediment grain size and benthic community structure in
734 the eastern English Channel (EC). The results indicated that the correspondence between sediment
735 composition and the distribution of benthic species is moderate, but it also depends on scale and
736 species. Some species, termed “grain size-sensitive”, showed a strong correspondence between their
737 distribution and sediment composition, while others exhibited more ubiquitous responses. Sediment
738 grain size alone accounted for approximately 20% of the distribution of species abundances in the
739 eastern EC, indicating that other factors also play significant roles. The results also highlight the
740 importance of considering hydrodynamic influences, where the maximum current velocity was found
741 to be a relevant factor. The Seine River's influence on benthic communities was also evidenced, leading
742 to salinity decrease, turbidity increase and high seasonal temperature variability that influence some
743 species' distributions. Quantile regression revealed non-linear responses along grain size gradient for
744 several species, with some showing multimodal patterns. This approach provided a comprehensive
745 understanding of the relationships between species and sediment characteristics, taking into account
746 species-specific responses and the influence of environmental factors.

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750 CRediT authorship contribution statement

751 **Nathan Chauvel**: Conceptualization, Formal analysis, Investigation, Visualization, Methodology,
752 Writing – original draft. **Aurore Raoux**: Data curation, Writing – review & editing. **Pierre Weill**:
753 Supervision, Methodology, Writing – review & editing. **Laurent Dezilleau**: Supervision, Writing – review
754 & editing. **Yann Méar**: Formal analysis, Writing – review & editing. **Anne Murat**: Formal analysis,
755 Writing – review & editing. **Emmanuel Poizot**: Formal analysis, Writing – review & editing. **Aurélie**
756 **Foveau**: Data curation, Writing – review & editing. **Nicolas Desroy**: Data curation, Writing – review &
757 editing. **Éric Thiébaud**: Data curation, Writing – review & editing. **Jean-Claude Dauvin**: Data curation,
758 Writing – review & editing. **Jean-Philippe Pezy**: Data curation, Supervision, Methodology, Writing –
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770 Appendix A. Supplementary data

771 Table S1: Summary of the methodological characteristics employed to collect the various data used. In the 'No. of stations
 772 (replicates)' column, the number preceding the letters F and S designates the number of replicates for faunistic and
 773 sedimentary analyses, respectively.

Site	MABEMONO	PECTOW (PEC)	Éoliennes Offshores du Calvados (EOC)	Granulats Marins Havrais (GMH)	Granulats de la Manche Orientale (GMO)			Dieppe Le Tréport (DLT)
Surveys	MABEMONO (MacroBenthos de la Manche Orientale et du sud de la mer du Nord)	PECTOW (<i>PECTinaria koreni</i> and <i>OWenia fusiformis</i>)	NA	NA	ROVMACE	GIE GMO monitoring program	BEMACE	NA
Date	-From March 2006 to November 2007	-March 2001, 2006, 2011 & 2016	-March 2020 & 2021	-February 2013 & 2021	-April 2009 -August 2009 -April 2010	-April 2018	-June 2007 -September 2007	-September 2014/2015 -March 2015/2016
Human activity	NA	NA	Future location of an offshore wind farm (2025)	Aggregate extraction (open in 2019)	Aggregate extraction (began in 2012)			Future location of an offshore wind farm (2025)
N° stations (replicates)	101 (3F 1S)	73 (5F 1S)	6 (3F 1S)	18 (5 F 1S) and 20 (3F 1S)	20 (3F 1S)	99 (3F 1S)	25 (3F 1S)	
Sampling	0.25 m ² Hamon grab	Van Veen and Hamon grabs (0.1 and 0.25 m ²)	0.1 m ² Van Veen grab	0.1 m ² Hamon grab	0.1 m ² Van Veen grab	0.25 m ² Hamon grab	Van Veen grab (0.1 m ²)	
GSD analysis	20 sieves from 50 to 50000 µm	-2001, 2006, 2016: 14 sieves from 63 to 10000 µm -2011: 32 sieves from 50 to 63000 µm	27 sieves from 63 to 25000 µm	32 sieves from 50 to 63000 µm	32 sieves from 50 to 63000 µm	20 sieves from 50 to 50000 µm	32 sieves, from 50 to 63000 µm	
Sediment characteristics	Overview of the sediment types encountered in the eastern English Channel	More or less muddy sands	Medium-grained sediment, consisting mostly of relatively clean sands, occasional occurrences of gravels	West-to-east gradient of decreasing sediment grain size	Coarse substrate relatively homogeneous, characterized by a bed of sandy gravel			Three main sediment facies, arranged in a fining gradient from southwest to northeast. Sand dunes.
Data sources	Foveau (2009)	https://doi.org/10.18142/154 Bacouillard et al. (2020)	Raoux et al. (2021)	Pezy et al. (2013); Pezy et al. (2021)	Pezy et al. (2019)	Lozach (2011)	Lozach (2011)	Pezy (2017)

Variable (Acronym in multivariate analyses, if relevant)	Spatial resolution (Approximate values)	Value	Units	Source
Bathymetry	115 x 115 m ²	Measured and modelled values	meters (m)	https://emodnet.ec.europa.eu/en
Photosynthetic Active Radiation at the seabed (PAR)	100 x 100 m ²	Satellite measurements	mol.photon.m ⁻² .d ⁻¹	https://emodnet.ec.europa.eu/en
Average Kinetic Energy at the Seabed due to Waves (KESW)	100 x 100 m ²	90 th percentile annual average obtained from models	N.m ² .s ⁻¹	https://emodnet.ec.europa.eu/en
Maximum Current Velocity (MCV)	-	Ranges of maximum current values obtained from numerical models	m.s ⁻¹	https://data.shom.fr/
Seabed temperature	7 x 7 km ²	Monthly average values derived from models	°C	https://doi.org/10.48670/moi-00059
Salinity	7 x 7 km ²	Monthly average values derived from models	-	https://doi.org/10.48670/moi-00059
Mass concentration of chlorophyll a ([Chla])	7 x 7 km ²	Monthly average values derived from models	mg.m ⁻³	https://doi.org/10.48670/moi-00058
pH	7 x 7 km ²	Monthly average values derived from models	-	https://doi.org/10.48670/moi-00058
O₂ concentration (O₂)	7 x 7 km ²	Monthly average values derived from models	mmol.m ⁻³	https://doi.org/10.48670/moi-00058

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