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Sediment grain size and benthic community structure in the eastern English Channel: Species-dependent responses and environmental influence

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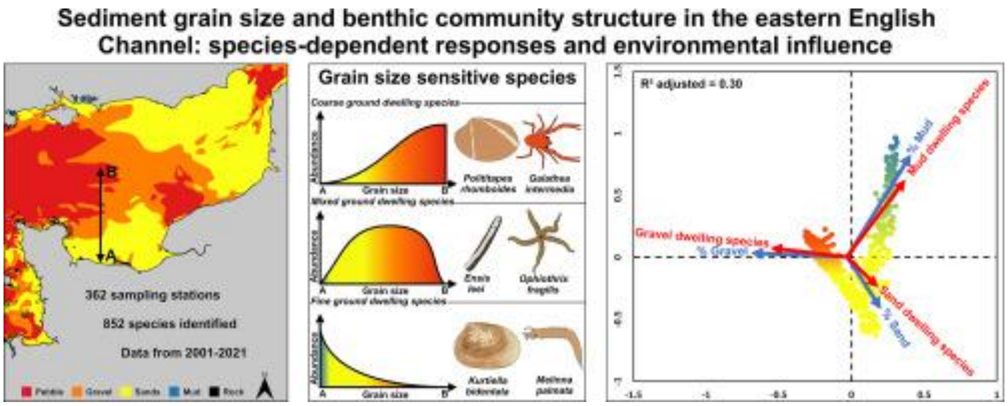
Abstract :

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

Graphical abstract



Highlights

► Sediment grain size moderately influences benthic communities. ► Benthos-sediment relationship is stronger in coarse sediments than in finer ones. ► Species-dependent approach is crucial for studying this complex relationship. ► Quantile regressions and ternary plots are valuable tools for such investigations.

Keywords : Coarse sediments, Species distribution, Sediment type, Grain size analysis, Marine aggregate extraction, Offshore wind farms

1. Introduction

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

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

Despite these differences, it is important to note that the majority of these works have primarily focused on fine-grained sediments, which are less common in the subtidal domain of the EC. The scarcity of quantitative data on coarse sediments in the eastern EC can be attributed primarily to technical limitations. In the past, sediment sampling in these areas was primarily conducted using dredges, such as the anchor-type and Rallier du Baty dredges, during explorative surveys led by Norman Holme and Louis Cabioch in the 1960s and 1970s to assess benthic community distribution (Dauvin, 2015). However, these dredges only allowed for qualitative or semi-quantitative collection of benthic organisms at best in coarse sediments. Consequently, there have been limited quantitative studies examining the natural spatial and temporal variability of communities associated with coarse sediments in this region, as on a global scale (Lozach and Dauvin, 2012; Pezy and Dauvin, 2021). The use of the Hamon grab, which became more widespread, facilitated the quantitative sampling of coarse sediments. Nevertheless, the sampling of such sediments remains challenging due to their hardness and because of the overdispersion of large dominant organisms (Dauvin and Ruellet, 2008). Thus, in this sea, most quantitative data regarding coarse seabed have been acquired recently, and only within relatively limited surface areas, as these samplings were mostly conducted as part of environmental monitoring of marine aggregate extraction on the 20 concessions located in the EC (Seiderer and Newell, 1999; Boyd and Rees, 2003; Newell et al., 2004; Cooper et al., 2007; Foden et al., 2009; Foveau, 2009; Desprez et al., 2010). However, it's worth noting that this information is somewhat different for the English side of the Channel, as the OneBenthic initiative has recently facilitated the association of data gathered at these extraction sites to further investigate the benthos-sediment relationship (Cooper and Barry, 2017). Thus, only few studies have investigated the relationship between grain size and benthic organisms in the EC (Seiderer and Newell, 1999; Newell et al., 2001), and only at relatively small spatial scales.

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

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

2. Material and methods

2.1. Data collection and sampling strategy

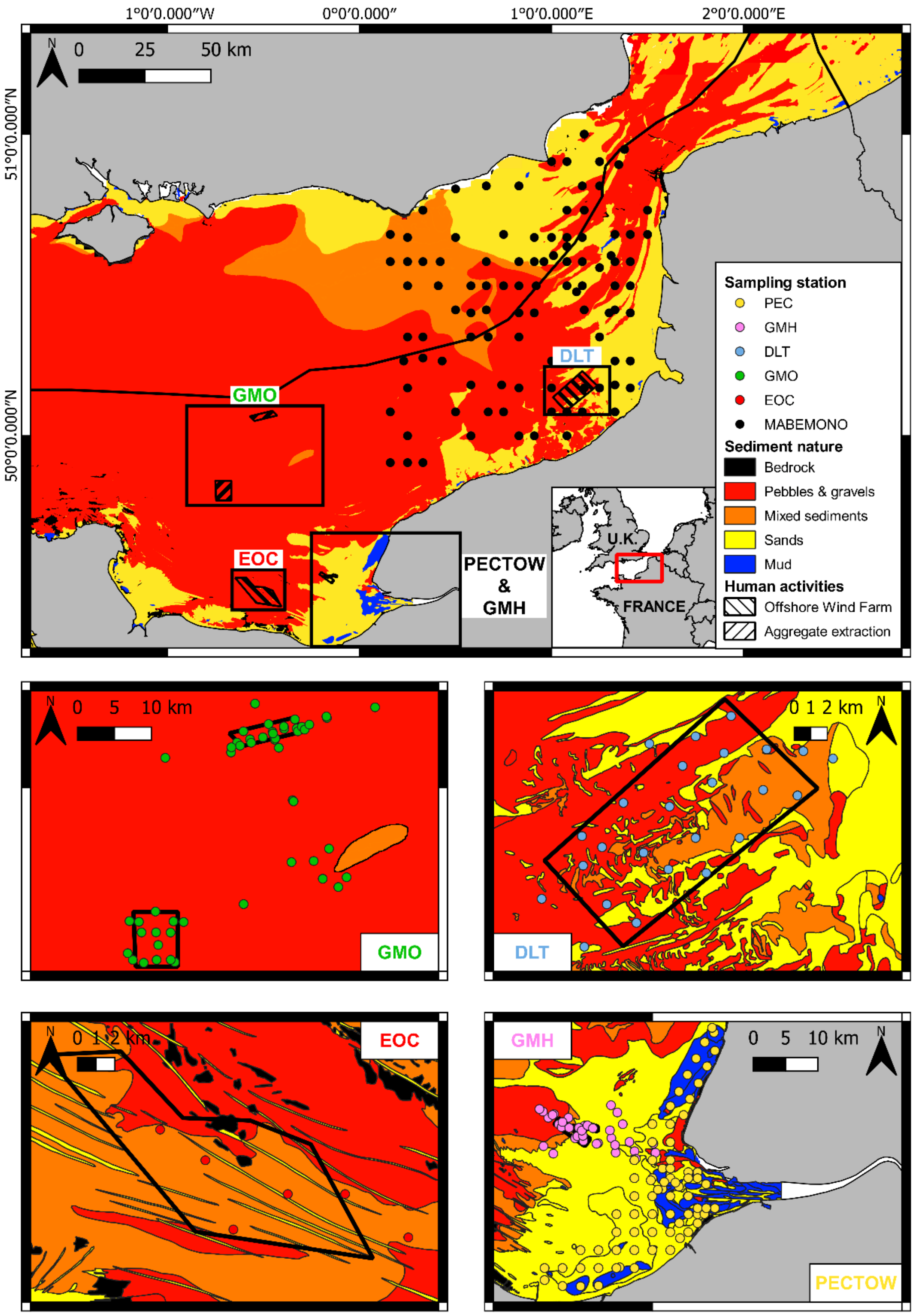


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Figure 1: Maps displaying the sampling station locations for the different monitoring programs. The Wentworth scale is used for sediment nature classification. The top map exclusively shows the locations of stations from the MABEMONO monitoring program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

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

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

2.2. Data preparation

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

2.3. Sedimentary analyses

2.3.1. Grain size distribution analyses

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

2.3.2. End-members analyses

The number of modes in the GSD was determined using an End-Member Modeling Analysis (EMMA) approach. EMMA is a valuable and flexible statistical approach in sedimentology that helps to identify and quantify the underlying processes involved in sediment generation and deposition (Weltje, 1997; Dietze et al., 2012, 2022). This method can effectively unmix multimodal GSD, providing insights into sediment provenance, transport mechanisms, and depositional environments (Dietze et al., 2012, 2022).

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

2.4. Plotting the benthos sedimentary envelope using ternary plots

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

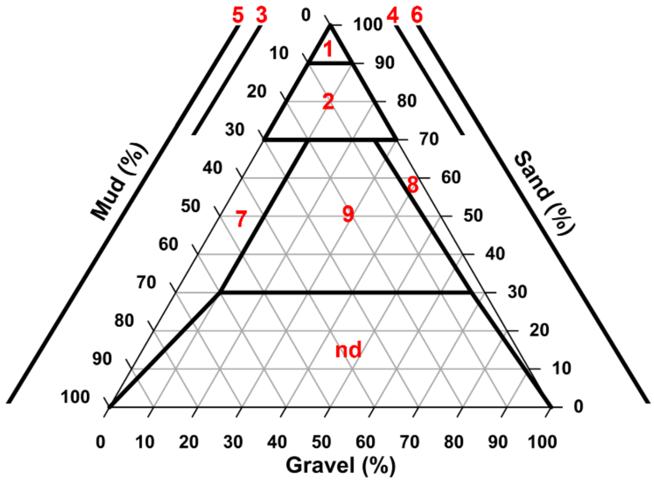

Figure 2: Ternary plot illustrating the classification proposed by Glémarec. The different classes correspond to: 1) strictly sand-dwelling organisms, 2) tolerant sand-dwelling organisms, 3) muddy-sand-dwelling organisms, 4) clean-sand-dwelling organisms, 5) sandy-muddy-dwelling organisms, 6) sandy-gravelly-dwelling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

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

2.5. Fauna rates of changes along a sedimentary gradient

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

Thus, Quantile Regression Spline Models (QRSM) were fitted using the bs() function from the R 'base' package (Hastie, 1992) in combination with the rq() function from the 'quantreg' package (Koenker, 2022). These models were applied to analyze the abundance of the 41 most prevalent species, with the percentage of gravel (% grain size > 2 mm) treated as a continuous variable (see section 3.4. for more details). The quantile levels employed ranged from the 85th to the 95th (τ = 0.85 - 0.95) with 5% increments. To construct the B-splines, the piecewise polynomial degree was set to 2, 3, 4, or 5. The selection of the appropriate degree was based on the small-sample-correction version of Akaike's Information Criterion (AICc), ensuring the use of a parsimonious model (Hurvich and Tsai, 1989; Burnham and Anderson, 2004; Cade et al., 2005). The maximum value derived from the selected model was considered as the optimum for each species.

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

2.6. Multivariate analyses

2.6.1. Assessing grain size characteristics contribution to species distribution

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

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

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

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

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

3. Results

3.1. Biological data summary

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

3.2. Species envelope identification

The ternary plots provide a valuable visualization of the sediment in which the studied species are most commonly found (Fig. 3). One can observe species that are predominantly associated with gravel or sandy gravel habitats, like *Galathea intermedia*, *Polititapes rhomboides* or *Glycymeris glycymeris*, species that show a preference for sandy habitats as *Echinocardium cordatum*, *Varicorbula gibba* or *Ensis leei*, as well as species that are more ubiquitous, occurring across different grain size conditions like *Caulleriella alata*, *Eteone longa* or *Notomastus latericeus* (Fig. 3). Interestingly, none of the species in the dataset appears to be strictly mud-dwelling. While some species can be found in muddy sediments, like *Owenia fusiformis*, *Kurtiella bidentata* or *Melinna palmata* (Fig. 3), it seems that none of them exhibit a true preference for highly muddy habitats (mud content exceeding 20%), but rather prefer less muddy environments. The presence of certain species in muddy habitats appears to reflect a certain tolerance to this grain size fraction rather than a genuine attraction to such environments.

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

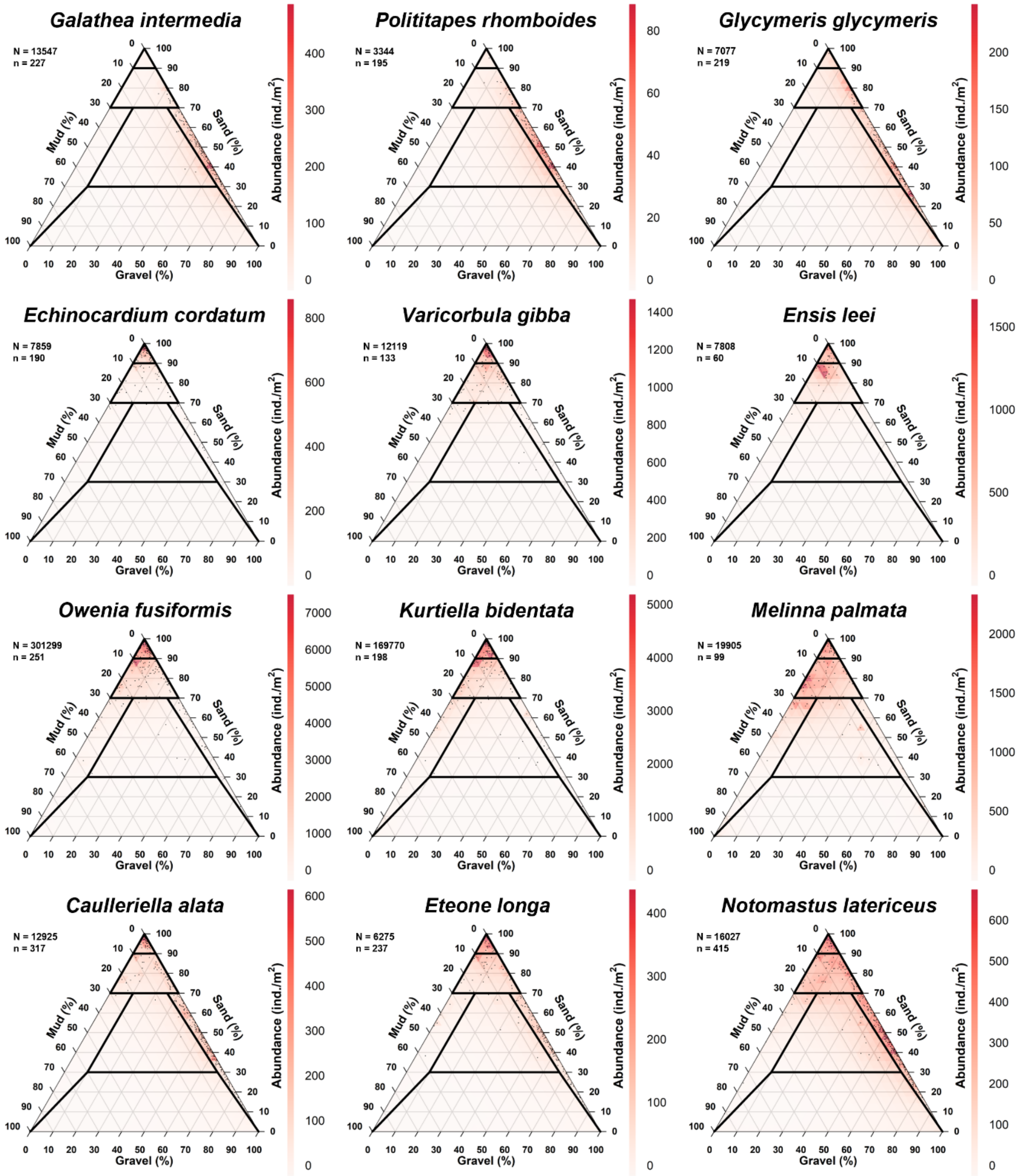

Figure 3: Ternary plots of 12 species. Grain size fractions (mud, sand and gravel) are based on the Wentworth scale. N represents the total abundance and n denotes the occurrence of the species across all samples.

3.3. Fauna changes along a sedimentary gradient

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

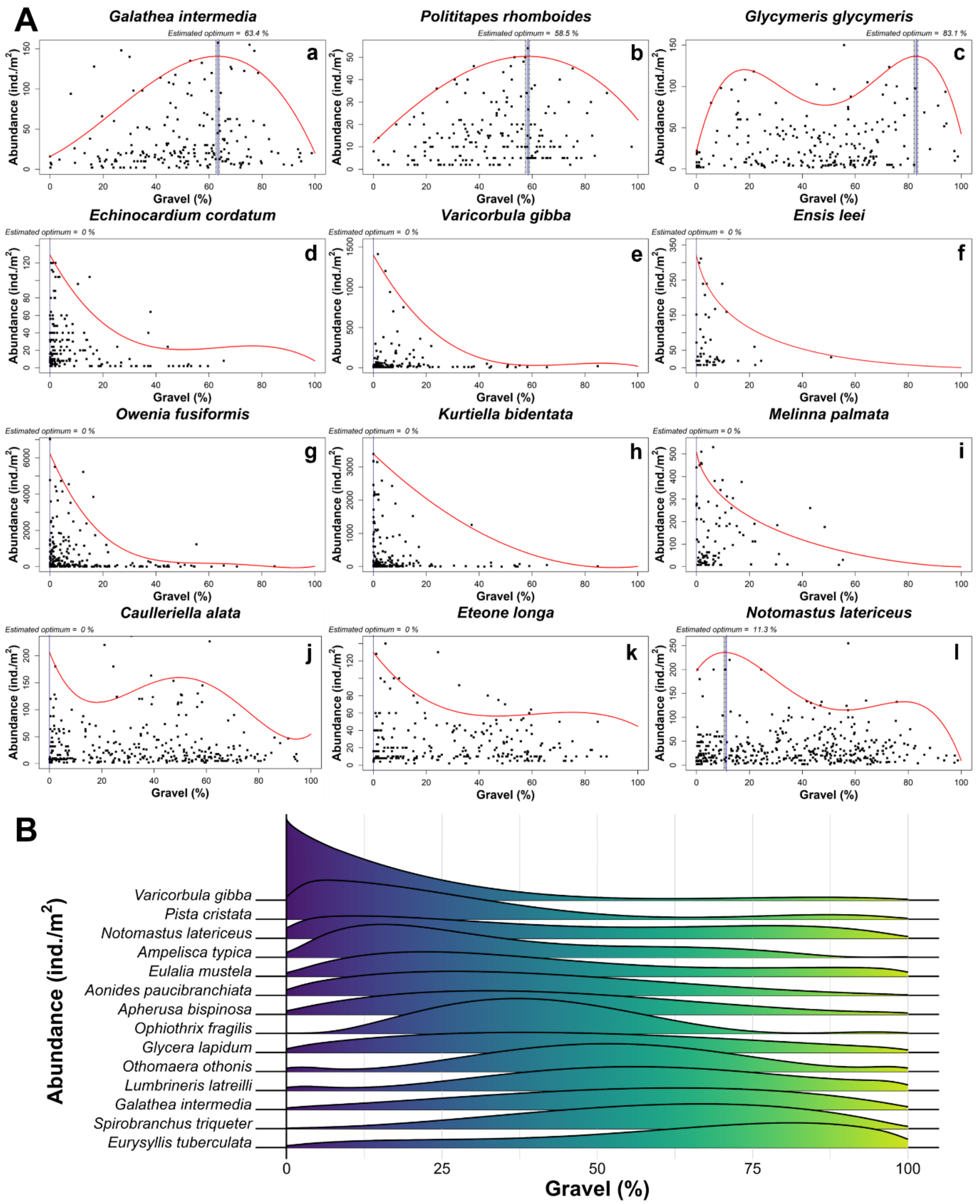

Figure 4: (A) Quantile regression of 12 species encountered in the English Channel. The solid blue line represents the estimated optimal percentage of gravel for the species. The two dashed lines represent the lower and upper bounds of the 95% confidence interval around the estimated optimal value. In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

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

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

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

3.4. Grain size parameters influence on benthos distribution

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

Axis 2 of the RDA, on the other hand, explains only a very negligible fraction of the variance in benthic distributions, with a constrained eigenvalue lower than the unconstrained eigenvalue. This calls for caution in interpreting this component. Although this variable is poorly represented on axis 2, being more intermediate between components 1 and 2, the percentage of mud appears to be the sediment parameter that most discriminates the stations along axis 2 (Fig. 5a). The eastern EC is a relatively low-mud marine environment (Larsonneur et al., 1982), and only a few sediment stations included in this study, mainly from the PECTOW survey, exhibited a sufficiently significant mud percentage to be detectable. Hence, the only stations differentiated along axis 2 are those from PECTOW (along with a few estuarine stations from MABEMONO and GMH). This may explain the observed Guttman effect (Guttman, 1953), which is commonly observed when representing such variables in a multivariate space (Dauvin, 1988; Davoult, 1990). The adjusted R^2 of this RDA is reaching 0.2, which indicated that grain size parameters can explain 20% of total benthos distribution in the eastern part of the EC.

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

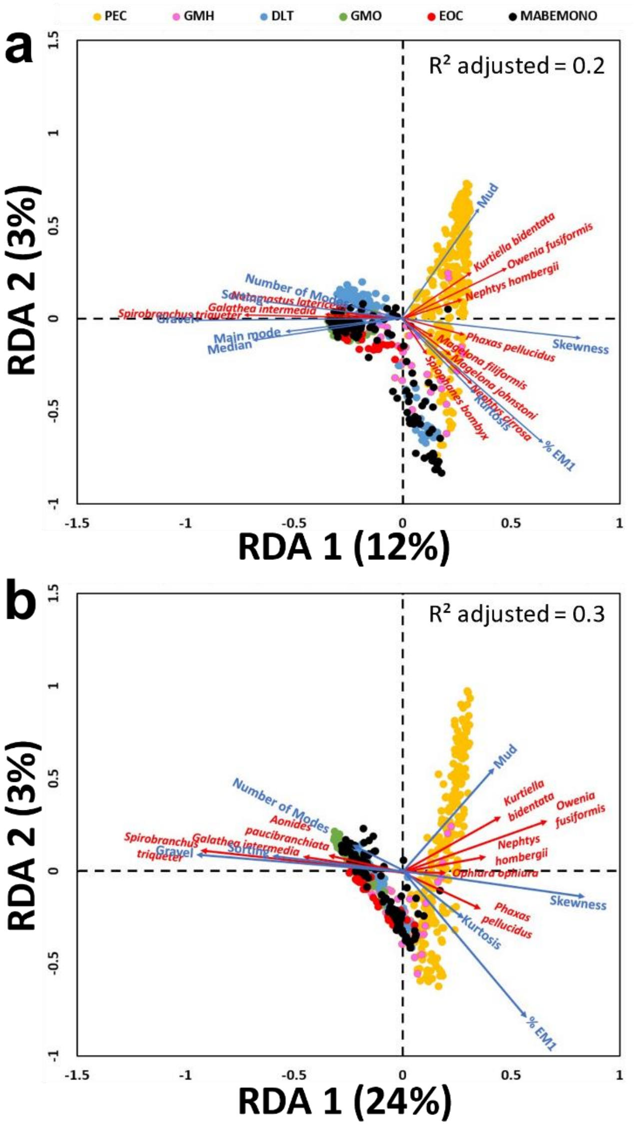

Figure 5 : Redundancy analysis (RDA) results showing the relationships between granulometric parameters and transformed Hellinger abundance (a) all taxa sampled, present in at least 3% of all samples and (b) "grain size-sensitive" taxa of benthic species (scaling 2). The variable "Main mode" represents 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.

3.5. Grain size and environment influence on benthos distribution

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

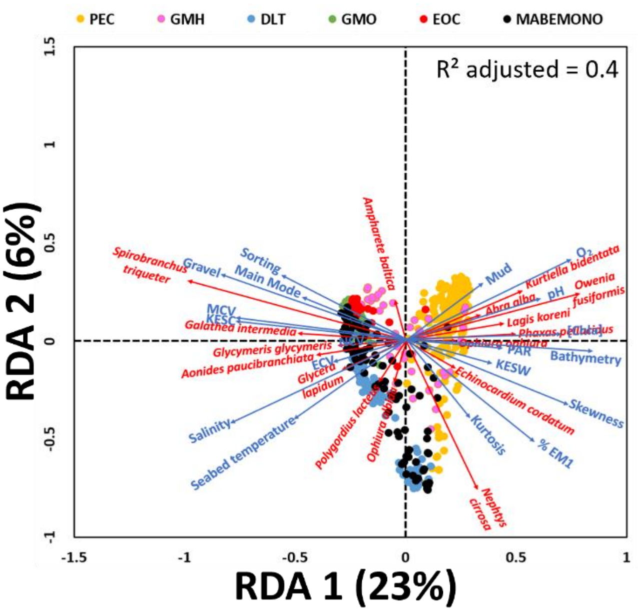

Figure 6: Redundancy analysis (RDA) results showing the relationships between granulometric parameters, environmental variables, and transformed Hellinger abundance of benthic species present in at least 3% of all samples (scaling 2). The variable "Main Mode" represents the grain size of the dominant mode. Bathymetry is in negative values. MCV: Maximum Current Velocity. KESW: Kinetic Energy at the Seabed due to Waves. 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.

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

3.6. Mapping benthos and granulometric patterns

Hierarchical clustering revealed three major biological and granulometric clusters in the eastern EC. For the biological data (Fig. 7a, c), cluster *1* includes all stations from GMO and EOC sites, most stations from DLT and GMH sites, and some stations from the MABEMONO survey. This cluster was characterized by high abundances of species such as *Spirobranchus triqueter*, *Glycymeris glycymeris*, and *Galathea intermedia*. Cluster *2* consists almost exclusively of stations from the PECTOW survey, except for one station from the MABEMONO survey (located offshore of the Rother River, UK, Fig. 7c) and two stations from the GMH site, situated in the southeast part of this sector. This second cluster was primarily characterized by high abundances of species such as *Melinna palmata*, *Owenia fusiformis*, or *Kurtiella bidentata*. Lastly, cluster *3* comprises the remaining stations from PECTOW, GMH, DLT, and MABEMONO, and was notably characterized by high abundances of the species *Nephtys cirrosa*. The species *Notomastus latericeus*, *Caulleriella alata*, and *Eteone longa*, on the other hand, did not appear to show higher abundances in one cluster over the other, in line with the patterns observed in the ternary plots (Fig. 3).

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

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

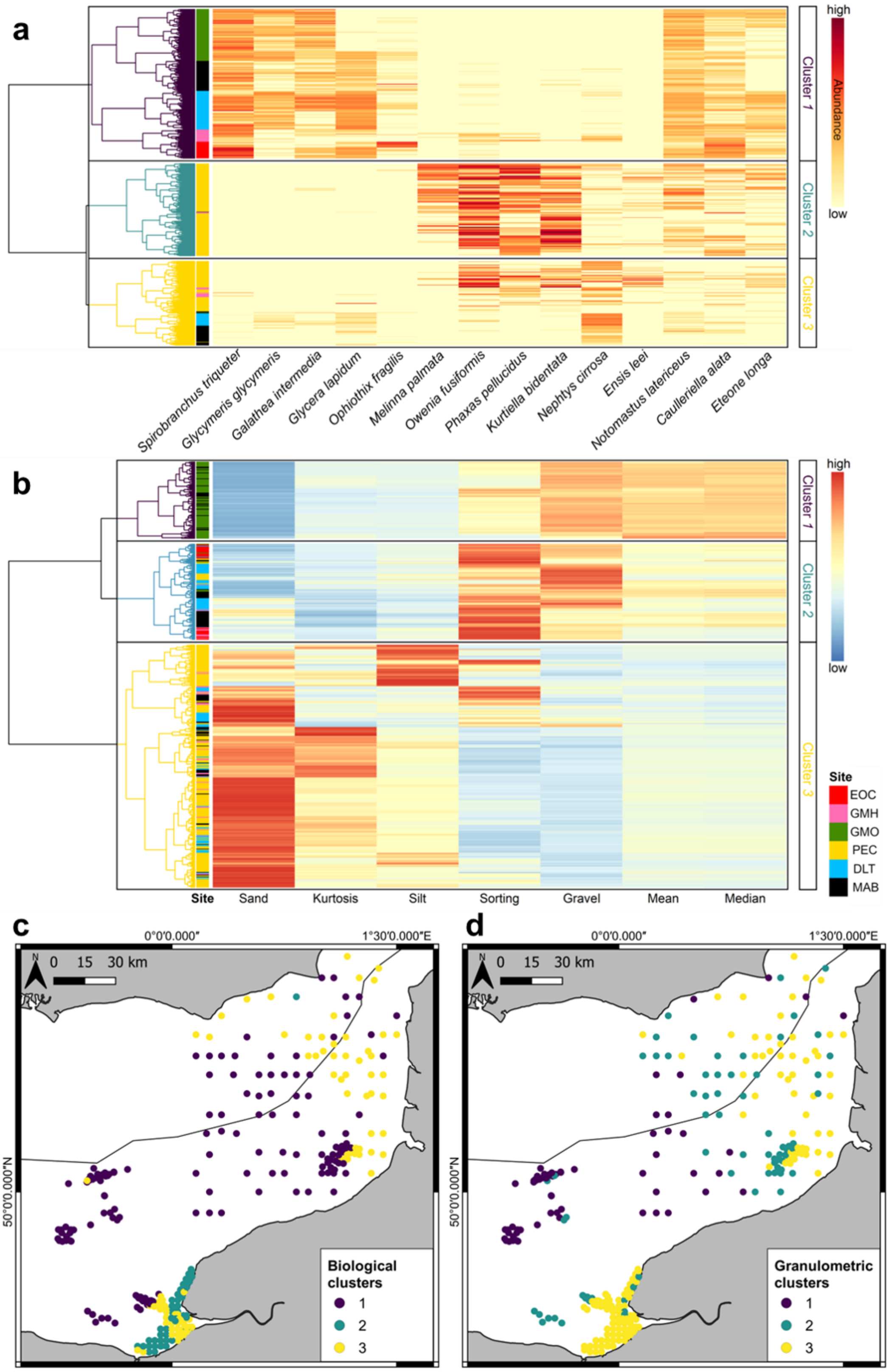

Figure 7: Hierarchical clustering and heatmap of (a) benthic abundance data and (b) granulometric parameters, and localization of the corresponding (c) biological and (d) granulometric clusters. Abundance data were log(x+1) transformed and granulometric parameters were scaled. Distance used were squared-root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

4. Discussion

4.1. Plotting species sedimentary envelope

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

4.2. Modeling species response along a grain size gradient

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

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

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

4.2.2. Using quantile regressions for investigating benthic species distributions

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

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

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

However, some limitations to using these statistical tools should be noted. One major disadvantage is that these models are dedicated to describing patterns in relation to a conditional variable, rather than attributing cause to this relationship (Ysebaert et al., 2002; Anderson, 2008). They provide valuable information about the type of response, optimum, or tolerance of a species to an environmental variable without explaining the underlying biological causes. Consequently, the resulting models tend to describe potential rather than actual patterns of species distributions (Vaz et al., 2008). To complement these observations, further research is needed to investigate why such relationships are observed and the true involvement of the conditional variable in the observed distributions. As suggested by Snelgrove and Butman (1994), more experimental studies (using eco-hydraulic flumes or mesocosms for instance) should be conducted to better understand the benthos-sediment relationship, including the involvement of related factors such as hydrodynamics or larval settlement in this relationship in order to include this knowledge into future models.

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

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

4.3. Species response along a grain size gradient

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

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

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

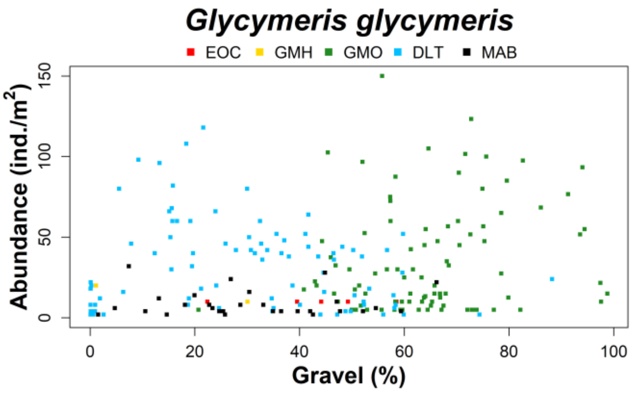

Figure 8: Distribution of Glycymeris glycymeris *abundances along a gravel percentage gradient. The points have been colored to represent the station where the abundance was measured.*

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

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

In the eastern EC, several authors have found a relatively moderate correspondence between sediment composition and the distribution of benthic species (Seiderer and Newell, 1999; Newell et al., 2001). These studies obtained Spearman correlation coefficients (ρ) ranging from 0.37 (Seiderer and Newell, 1999) to 0.44 (Newell et al., 2001) between biological communities and sediment grain size at best, albeit primarily focusing only on coarse sediments and at a relatively small spatial scale. According to these authors, such low values suggest that sediment grain size may play a minor role in controlling benthic community structure. On a larger scale, encompassing both the eastern and western EC (but only on the English side and with a limited number of stations), Rees et al. (1999) also observed a moderate explanation of benthic community variability by sediment grain size (ρ = 0.40 for sediment median diameter alone). Similarly, with a substantial dataset that still only encompassed the English side of the EC and the surrounding waters of the United Kingdom, Cooper and Barry (2017) found a 30% correlation between sand content and macrofaunal data. It's worth noting that the highest explanatory rate, reaching 42%, was achieved when considering the current velocity along with the sediment sand and mud percentages (Cooper and Barry, 2017). Thus, in line with the results of this study, these authors also emphasize that sediment composition is not the exclusive primary factor shaping benthic communities, as underlined by Bolam et al. (2008). Using side-scan sonar to characterize sediment, similar perspectives have been obtained at various coarse sediment sites in the EC, showing that seabed morphology (and not solely grain size composition) also has a significant influence on benthic assemblages (Brown et al., 2001, 2002, 2004a, 2004b). These findings are consistent with the results of this study, where grain size factors alone constrain the distribution of species abundances in the eastern EC by “only” 20%. Despite this described minor contribution, Seiderer and Newell (1999) still note a relatively strong correspondence between sediment composition and the distribution of several species, such as *Sabellaria spinulosa*, which is mainly found in coarse sand and gravelly substrates (2000-16000 µm). In the case of the eastern EC, this species has also been observed in similar sediment conditions. Out of 48 occurrences, *Sabellaria spinulosa* was associated with high percentages of gravel (ranging from 21% to 98%, with an average percentage of 57%) and coarse sand (ranging from 2% to 79%, with an average percentage of 43%), primarily at the EOC and GMO sites, with a mean median grain size of 4230 µm. *Sabellaria spinulosa* is not the only species showing a strong correspondence between its distribution and sediment composition, as indicated by the strong spatial correlation (ρ=0.84) between the biological and granulometric clusters. Other species such as *Galathea intermedia*, *Glycymeris glycymeris*, *Polititapes rhomboides*, *Spirobranchus triqueter, Owenia fusiformis*, *Abra alba* or *Phaxas pellucidus* have shown high sensitivity to grain size variations, exhibiting a strong correspondence between distribution and sediment composition, as described by Seiderer and Newell (1999). By selecting these taxa, the percentage of species distribution explained by granulometric parameters alone reached 30%, indicating that for these species, grain size is a slightly more significant factor than for other more ubiquitous species. These results, with some previous ones (Longhurst, 1958; Buchanan, 1963; Cassie and Michael, 1968; Hughes and Thomas, 1971), collectively highlight the importance of a species-dependent approach to study the benthos-sediment grain size relationship, which has been relatively understudied, where most analyses focusing on the relationship between sediment composition and benthic assemblages (Petersen, 1913; Ford, 1923; Seiderer and Newell, 1999; Newell et al., 2001).

By examining the benthos-grain size relationship after incorporating data from coarse environments allows us to introduce some nuances to the conclusions drawn by Snelgrove and Butman (1994). At the scale of the eastern EC, these parameters account for 20% of the variations in benthic communities (a significant portion of the total variability), allowing for a good overall description of the community distribution on a wide spatial scale, encompassing a great range of grain size. This is notably evident through the 84% spatial match between the biological and grain size clusters (Fig. 7c-d). Furthermore, it's worth noting that these conclusions may vary for species-level approaches (see previous sections for more details), as not all species exhibit the same sensitivity to sediment grain size composition, especially when the study area is primarily composed of coarse sediments. Indeed, coarse sediments seem to support numerous species that require the presence of a coarse sediment fraction (such as gravel or pebbles) for anchorage, for instance. This may also explain why the grain size-benthos relationship appears to be more pronounced for such sediments when compared to sandy or muddy ones.

4.5. Benthos shaping in the eastern English Channel

4.5.1. Sedimentary contribution to benthos structure

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

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

4.5.2. Other parameters influencing benthos structure

Among the non-sedimentary factors influencing the distribution of benthic species, hydrodynamic regime is likely one of the most influential factors shaping benthic community structure (Jumars and Nowell, 1984; Davoult et al., 1988; Snelgrove and Butman, 1994). This suggestion is supported in the eastern EC, where the RDA results demonstrate a strong correlation between hydrodynamic parameters (*e.g.*, maximum current velocity) and granulometric parameters (particularly gravel percentage). Thus, it seems reasonable to consider granulometric characteristics as a reflection of the hydrodynamic conditions, which have a greater impact on benthic communities than granulometric parameters alone (although the influence of these parameters is likely not negligible, at least for certain species, as discussed in subsection 4.5.1). This statement, however, must be nuanced for the particular case of the EC. Indeed, this sea is classically described as being a sediment-starved platform with coarse sediments that are less susceptible to mobilization by the prevailing currents, generating “lag deposits” (Larsonneur et al., 1982; Reynaud et al., 2003). These coarse sediments are, in fact, inherited from fluvial deposits during the last glacial period and subsequently reworked during the Holocene transgression (Dingwall, 1975; Larsonneur et al., 1982). Additionally, the characteristics attributed to the extensive bioclastic sediment cover (Larsonneur et al., 1982) in the EC should not be overlooked. These sediments correspond to *in situ* production and may thus not be in equilibrium with hydrodynamic conditions (Larsonneur et al., 1982). Moreover, their size is likely to decrease over time due to fragmentation (Zuschin et al., 2003; Rieux, 2018). However, hydrodynamic forcing can still influence benthic communities through various processes, including larval dispersal and settlement through passive and active mechanisms (Thorson, 1957; Butman, 1987), as well as on trophic aspects by influencing the vertical and horizontal fluxes of organic matter (Sanders, 1958; Wildish, 1977), which may partially explain the "trophic group amensalism" hypothesis presented in subsection 4.5.1. (Rhoads and Young, 1970; Rhoads, 1974).

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

5. Conclusions

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

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CRediT authorphip contribution statement

Nathan Chauvel: Conceptualization, Formal analysis, Investigation, Visualization, Methodology, Writing – original draft. **Aurore Raoux**: Data curation, Writing – review & editing. **Pierre Weill**: Supervision, Methodology, Writing – review & editing. **Laurent Dezilleau**: Supervision, Writing – review & editing. **Yann Méar**: Formal analysis, Writing – review & editing. **Anne Murat**: Formal analysis, Writing – review & editing. **Emmanuel Poizot**: Formal analysis, Writing – review & editing. **Aurélie Foveau**: Data curation, Writing – review & editing. **Nicolas Desroy**: Data curation, Writing – review & editing. **Éric Thiébaut**: Data curation, Writing – review & editing. **Jean-Claude Dauvin**: Data curation, Writing – review & editing. **Jean-Philippe Pezy**: Data curation, Supervision, Methodology, Writing – review & editing.

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Appendix A. Supplementary data

Table S1: Summary of the methodological characteristics employed to collect the various data used. In the 'No. of stations (replicates)' column, the number preceding the letters F and S designates the number of replicates for faunistic and 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 (*PECTinaria koreni* and *OWenia fusiformis*)	NA	NA	GIE GMO monitoring program	ROVMACE	BEMACE	NA
Date	-From March 2006 to November 2007	-March 2001, 2006, 2011 & 2016	-March 2020 & 2021	-February 2013 & 2021	-April 2018	-April 2009 -August 2009 -April 2010	-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 m² Hamon grab	Van Veen and Hamon grabs (0.1 and 0.25 m²)	0.1 m² Van Veen grab	0.1 m² Hamon grab	0.1 m² Van Veen grab	0.25 m² Hamon grab		Van Veen grab (0.1 m²)
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	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)

Table S2: Supplementary environmental variables added for the multivariate analyses.

Variable (Acronym in multivariate analyses, if relevant)	Spatial resolution (Approximate values)	Value	Units	Source
Bathymetry	115 x 115 m²	Measured and modelled values	meters (m)	https://emodnet.ec.europa.eu/en
Photosynthetic Active Radiation at the seabed (PAR)	100 x 100 m²	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 m²	90th 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 km²	Monthly average values derived from models	°C	https://doi.org/10.48670/moi-00059
Salinity	7 x 7 km²	Monthly average values derived from models	-	https://doi.org/10.48670/moi-00059
Mass concentration of chlorophyll a ([Chla])	7 x 7 km²	Monthly average values derived from models	$mg.m^{-3}$	https://doi.org/10.48670/moi-00058
pH	7 x 7 km²	Monthly average values derived from models	-	https://doi.org/10.48670/moi-00058
O_2 concentration (O_2)	7 x 7 km²	Monthly average values derived from models	$mmol.m^{-3}$	https://doi.org/10.48670/moi-00058

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