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Sediment grain size and bedform morphology and dynamics shape benthic community heterogeneity in submarine dune fields

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The distribution of benthic communities is governed by a multitude of interacting ecological processes. Among these factors, sediment grain size is generally considered as a key structuring factor for benthic communities in the eastern English Channel. However, grain size often oversimplifies the true complexity of the substrate, as the presence of bedforms such as submarine dunes adds another layer of complexity to this relationship. This study utilizes bathymetric, grain size, and macrofauna benthic data collected during four surveys conducted between 2014 and 2016 at the planned site of the Dieppe-Le Tréport offshore wind farm. The significance of these sedimentary characteristics for benthic community structure was examined through multivariate analyses and trophic group studies. The results revealed significant heterogeneity in the benthic communities within dune fields. The troughs and adjacent nondune areas, which are primarily composed of coarse sediments (gravels), support a diverse community dominated by deposit feeders and filter feeders. In contrast, the stoss and lee sides of the dunes present a much less diverse community dominated by predators and scavengers. The mechanisms driving this structuring are discussed, with an emphasis on sediment dynamics and trophic processes.

Keywords Bedforms, Morphological, Dune morphodynamics, Trophic interactions, Offshore wind farm, Marine renewable energy

Historically, the benthic communities of the English Channel have been described sporadically, with major surveys beginning in the 1960s through the work of N. Holme and L. Cabioch¹. These efforts, which continued until the early 2000s, identified the main benthic communities shaped by coarse sediments covering more than 80% of the seabed^{2,3}. Descriptive surveys highlighted bathymetry and sediment type—two interrelated features, particularly in the paleovalley-dominated eastern Channel⁴—as key factors structuring these communities^{5–7}. However, owing to qualitative or semiquantitative sampling and a focus on larger organisms, historical studies have lacked the resolution to assess the role of sediment grain size in benthic distribution^{1,3}. Recent quantitative studies over the past two decades have shown that sediment grain size moderately yet significantly influences benthic communities, closely linked to hydrodynamic conditions^{8,9}. Nevertheless, these studies often oversimplify sediment properties, overlooking the influence of bedforms, which adds considerable complexity to the seabed and its ecological structuring^{10–12}.

These “bedforms” refer to sedimentary features evolving over variable spatial and temporal scales, resulting from sediment transport driven by the interaction between fluid flow and unconsolidated sediment. At small scales, sand ripples (< 0.06 m in height and 0.6 m in wavelength¹³) form transverse to dominant currents and can be reshaped within tidal cycles. Submarine dunes (> 0.06 m in height and 0.6 m in wavelength¹³) exhibit more complex morphologies, such as crescent-shaped barchans, depending on the sediment supply and tidal patterns. Dune migration rates range from a few meters per year (or inactivity^{14,15}) to hundreds of meters annually¹⁶. At the largest scale, stable sandbanks stretch over kilometers, with heights typically exceeding ten meters¹⁷, migrating under residual tidal currents influenced by hydrodynamic conditions, depth, and sediment grain size¹⁸.

In the English Channel, bedforms are mainly coastal, with the exception of those in the eastern region. Here, dunes and sandbanks dominate the seabed, particularly offshore from the Albâtre, Picardy, Opal, and Flanders coasts, as well as within the Dover Strait and the Bay of Somme. These features shape the wide Normandy–Picardy

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sedimentary prism^{4,19}, with dunes exhibiting morphologies ranging from barchans to linear forms, driven by a west-east gradient of sediment fining and reduced current intensity. Dune migration rates range from 17 to 27 m.yr⁻¹ (annual observations) to 1–7 m.yr⁻¹ (decadal observations)^{19,20}.

Few studies have explored how bedforms affect benthic communities, partly due to the nested spatial scales of these features, complicating the understanding of ecological processes^{10,21}. Nonetheless, troughs between bedforms often support greater species diversity than surrounding slopes do^{10–12,20–30}, likely due to current attenuation, which facilitates larval deposition and organic matter accumulation. Conversely, some studies report homogeneous communities across these sediment bodies¹², highlighting the variability in structuring mechanisms.

In response to France's energy diversification strategy, offshore wind farms, including those off the cities of Dieppe and Le Tréport, on the Normandy-Picardy prism, have been planned in the English Channel. Scheduled for operation in 2026, this project will feature 62 turbines with a total capacity of 496 MW. The site presents two key sedimentary features: a west-east gradient of decreasing grain size and morphological changes in subaqueous dunes along this gradient²⁰.

Baseline surveys for wind farms have provided grain size, bathymetric, and benthic data, enabling the integration of seabed characteristics to study their influence on benthic communities. This study examines how seabed grain size, along with dune morphology and dynamics, shapes benthic community structure.

Materials & methods

Site description

The data used in this study originate from the designated area for the Dieppe-Le Tréport (DLT) offshore wind farm, which spans 110 km² and is located 15 km offshore, with water depths ranging from 10 to 30 m and decreasing toward the east. Salinity levels in this area vary between 33.9 (winter) and 34.2 (summer), while temperatures range from 7.6 °C (winter) to 16.5 °C (summer), and turbidity fluctuates between 3.1 NTU (winter) and 0.6 NTU²².

From a sedimentological perspective, two notable characteristics must be highlighted. The first concerns the grain size of the seabed, which decreases from west to east (Fig. 1), as observed at the scale of the Normandy-Picardy sedimentary prism. In the western region, the sediment is primarily composed of sandy gravels, with a median grain size exceeding 1,500 µm. In the central area of the study site, the substrate consists of gravelly sands (median grain size of *ca.* 1,000 µm). To the east, the sediment is primarily composed of medium sand, with a median grain size of less than 500 µm. The second distinct feature of this site is the omnipresence of subaqueous dunes, with the exception of the northern region, where they are absent. Four dune sectors can be identified: a western sector characterized by isolated barchan (crescent shaped) dunes; a southern sector featuring a low-depth field of sinuous dunes; a central sector composed of a field of small dunes displaying superimposed megaripples; and an eastern sector characterized by large pseudolinear dunes (Fig. 1).

Data collection

The benthic macrofauna data were collected during field campaigns conducted as part of the J.P. Pezy PhD thesis²². These sampling efforts consisted of four campaigns held in September 2014, March and September 2015, and March 2016. Each campaign involves the collection of samples from 25 stations using a 0.1 m² van Veen grab (Fig. 1), with five replicates per station. Following collection, the organisms were sieved through a 1 mm mesh circular sieve. Additionally, sediment samples were collected at these stations during the same campaigns to assess their grain size characteristics. These sediment samples were subsequently dry-sieved using a vibrating column with 32 sieves ranging from 50 to 63,000 µm, thereby enabling the determination of the grain size distributions at each station. Finally, bathymetric data were acquired using multibeam echosounders during various campaigns conducted in 2011, 2014, 2015, 2016, and 2018 by G-Tec and GEOxyz for the Eoliennes en Mer Dieppe-Le Tréport group, achieving a maximum resolution of 0.85 m. As the biogeosedimentary and bathymetric surveys were conducted several months apart, temporal variability was not considered in this study. Instead, the focus will be exclusively on spatial variability.

Data Preparation

Macrofauna data

The macrofauna data were used to calculate total abundance (N), taxonomic richness (TR), and the Shannon (H') and Pielou (J') indices for each station. A classification of organisms into six trophic groups was also conducted to investigate the potential trophic influence of bedforms on benthic communities. These trophic groups are analogous to those described by various studies^{3,23–26}: predators (P), scavengers (Scv), filter feeders (F), surface deposit feeders (sDF), subsurface deposit feeders (ssDF), and grazers (G). Given the spatiotemporal differences among these groups, which preclude direct comparisons of raw abundances, the data were subsequently converted to percentages for each station.

Grain size data

Several grain size parameters were derived from the grain size distributions. These included the mean, median, sorting coefficient, and skewness, all of which were calculated using the arithmetic method of moments. The percentages of gravel, sand, and mud were subsequently employed to characterize the substrate composition at each station, using the Folk classification²⁷ (Fig. 1).

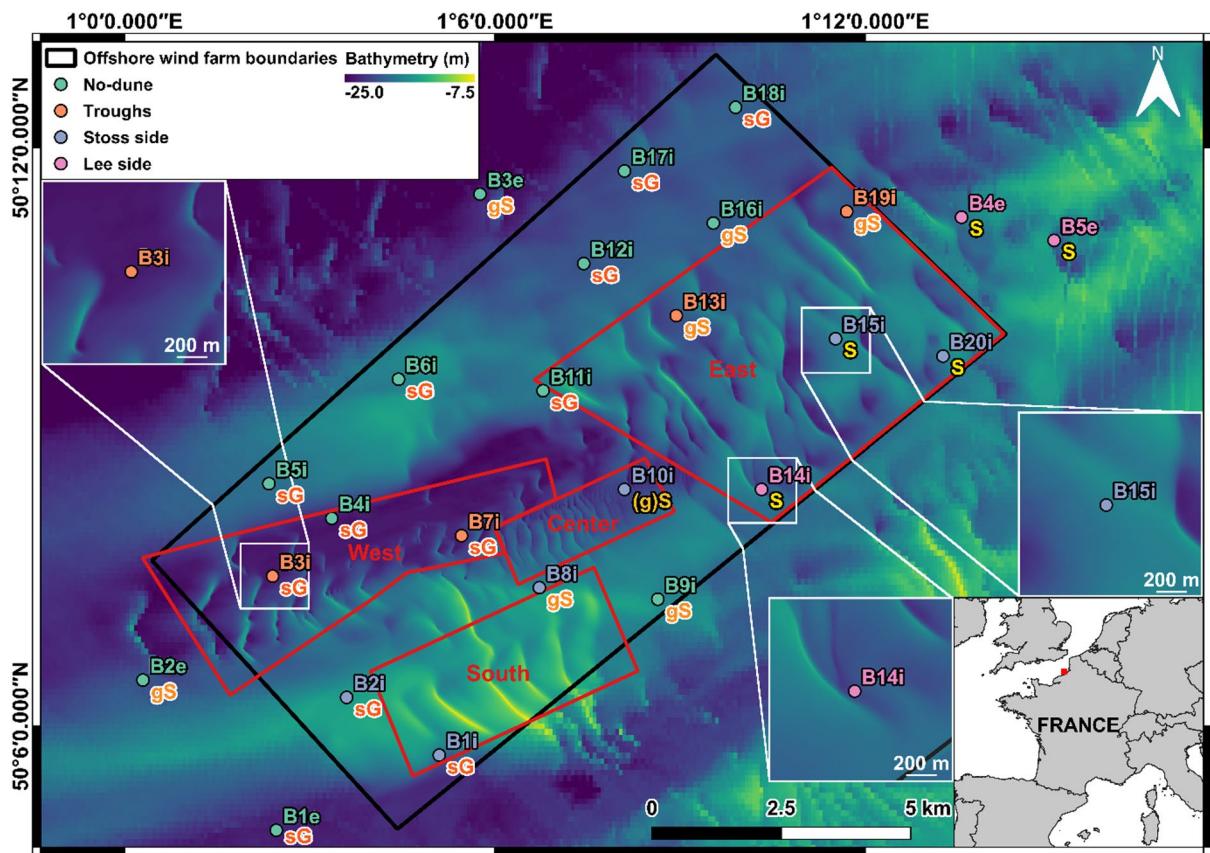


Fig. 1. Bathymetric map (tidal datum; multibeam echosounder) of the planned offshore wind farm at the Dieppe-Le Tréport site. Each point is labeled with a station name (upper labels) and a sedimentary facies classified according to Folk²⁷ (lower label). sG, sandy gravel; gS, gravelly sand; (g)S, slightly gravelly sand and S, sand. The position of each station on the nearest dune (trough, stoss or lee side) is indicated by the color of the point and the station label. Red polygons delineate dune sectors. Bathymetric data sources: inside the wind farm, GEOxyz and G-Tec; outside, HOMONYM project (https://doi.org/10.17183/MNT_ATL100m_HOMONIM_WGS84). This map was generated using QGIS version 3.34.

Bathymetric data

The bathymetric data were used to study the morphology of the various dunes observable at the DLT site. The dunes considered for this study were those with amplitudes greater than 1 m, resulting in the inclusion of 47 dunes within the DLT site. Several morphological characteristics, including height (H), length (L), lengths of the stoss (L_s) and lee (L_l) sides, and wavelength (λ , the distance between two successive crest lines), were measured. The surface area (S), defined as the product of H and L divided by two, and the form factor (f), calculated as S divided by the product of H and λ , were also computed.

Additionally, as bathymetric data were collected during multiple campaigns (in 2011, 2014, 2015, 2016 and 2018), an estimation of the migration rates of the different dunes (c) was calculated. This estimation was subsequently used, jointly with the morphological parameters, to evaluate mass bedload transport (Q_{bm}) using the dune tracking method^{28–30}.

Two classifications of the benthic stations were employed to assess the influence of the dunes on the benthos. The first classification aimed to determine whether a station was located on a dune (lee or stoss side), in a trough between two dunes, or outside a dune field. This classification was based on the distance to the nearest dune crest line, measured along the cross-dune direction (*i.e.*, 60° azimuthal direction). For each station, the following flowchart was applied: if the station was located 45 m downstream of the crest, it was classified as being on a lee side (the smallest lee side measuring 45 m). If the station was situated within 210 m upstream of a crest line, it was classified as being on a stoss side (the shortest stoss side measuring 210 m). If the station was located between two dunes but more than 45 m downstream and more than 210 m upstream of nearby crest lines, it was classified as being in an interdune trough. Finally, if none of these conditions were met, the station was classified as being outside a dune field (Fig. 1).

The second classification focused on the morphometric and dynamic characteristics of the surrounding dunes, averaging their features by sectors that exhibited relatively homogeneous characteristics (as shown in Fig. 1, the “dune sector” approach).

Statistical analyses

Influence of grain size and morphology on benthic abundance, diversity and trophic composition

Three one-way analysis of variance (ANOVA) were employed to assess the influence of grain size and morphological factors on the biological indices and on the percentages of trophic groups. Three fixed factors were considered for these analyses: sedimentary habitat (represented by Folk classification), position on the dune (trough, stoss or lee side), and influence of the dune sector (morphology, dune migration rate, sediment dynamics). The assumptions of ANOVA, *i.e.*, homoscedasticity and normality of residuals, were checked using appropriate statistical tests (Bartlett's test and the Shapiro-Wilk test, respectively). Significant ANOVA results were further analyzed using Tukey's HSD test to identify factor levels exhibiting significant differences in biological indices and trophic group percentages. Pearson correlations between the biological variables and the grain size and morphological characteristics were also calculated to investigate the potential interactions between these factors.

Effects of grain size and morphological factors on benthic structure

To determine whether benthic communities differed significantly across the considered factors (*i.e.*, sedimentary facies, position on the dune and dune sector), permutational multivariate ANOVA (PERMANOVA, 999 permutations³¹) were conducted following the computation of Hellinger dissimilarity matrices for each sample. Indicator values (IndVal³² for statistically comparable modalities were calculated to identify characteristic species affected by each factor.

Additionally, redundancy analyses (RDA) were performed, focusing solely on stations located on or near dunes. The morphometric characteristics of the nearest dune were assigned to each station. To examine the impact of the station position on the dune, the qualitative variable "trough" was converted to a binary variable through dummy coding. The influence of grain size was also incorporated by adding the grain size parameters (presented in the "Grain size data" section) as explanatory variables. All explanatory variables were scaled for the analysis.

Abundance data were transformed using Hellinger transformation to mitigate the effects of extreme abundance values. Backward and forward selection processes (999 permutations) were applied, resulting in a similar model that retained the most relevant explanatory variables while ensuring model parsimony. The absence of multicollinearity was confirmed by calculating the variance inflation factor (VIF), with variables exhibiting VIF values exceeding 10 being excluded from the analyses due to potential multicollinearity.

In conjunction with the RDA, a variance partitioning analysis was conducted to evaluate the contributions of grain size, morphology, and dune position factors (*i.e.*, stations in a trough or not) to the explained variance. The significance of the three explanatory matrices was confirmed through PERMANOVA (999 replications).

Clustering analysis was performed to identify benthic stations with similar compositional characteristics. Abundance data were averaged across all the campaigns, as temporal variability was not addressed in this study. A Hellinger distance matrix was calculated and subsequently applied in a hierarchical clustering algorithm using Ward's criterion^{33,34} to construct a dendrogram. Characteristic species for each cluster were identified through the calculation of IndVal and their significance (999 permutations), enabling the construction of a heatmap associating the most characteristic species of each cluster with the dendrogram. All statistical analyses were performed in R version 4.3.2.

Results

Dune morphology and dynamics

Dunes present mean heights between 2.65 and 5.52 m and mean wavelengths between 268 and 1652 m (Fig. 2). Dunes migrate east–north east in the direction of the residual tidal current, although during periods of less than 2–3 years, dune migration inversions can be observed in the case of sustained wave regimes. Their mean migration rates vary between 1.2 (s.d. 1.27) and 8.05 (s.d. 12.12) m.yr⁻¹ when calculating on annual periods, with rates decreasing from west to east and when longer observation periods are considered. In this area, Ferret²⁰ measured 17.1 to 27.7 m.yr⁻¹ for the period of 2007–2008, which was characterized by a high wind and wave regime and migration distances of up to 20 m at the scale of a few semidiurnal tidal cycles.

Dune dynamics are controlled by the sediment dynamics, and essentially the bedload transport, under the influence of tidal currents interacting with winds and waves. Bedload flux estimations are oriented east–north east in the range of 7.8–9.8 t.m⁻¹.yr⁻¹ during the 2011–2018 period (Fig. 2) and can reach 17.6–374.2 t.m⁻¹.yr⁻¹ during annual to pluriannual periods³⁵. During shorter periods (*e.g.*, the scale of a storm), residual bedload fluxes display greater variability and can reverse toward the west–southwest.

Grain size and morphological influences on biological indices

For all the biological indices examined (N, TR, H', and J'), an increasing gradient was observed in relation to sediment grain size. The coarser facies, particularly those composed of gravel (sandy gravel, sG, and gravelly sands, gS), present higher values than the finer-grained facies, with a more dominant sand fraction (slightly gravelly sands, (g)S, and sands, S). For example, the average number of taxa recorded at stations characterized by sG and gS is 76 and 62, respectively, whereas stations with (g)S and S show averages of 48 and 31 taxa, respectively (Fig. 3).

Significant differences in the biological variables were also observed depending on the position of the benthic stations on the dunes. Stations located in areas without dunes or in interdune troughs presented significantly higher values than those located on the stoss or lee side of the dunes. For example, the average taxonomic richness is 73 and 75 at stations in nondune areas and troughs, respectively, whereas stations on the stoss and lee sides have averages of 45 and 32 taxa, respectively (Fig. 3). Furthermore, no significant differences were found

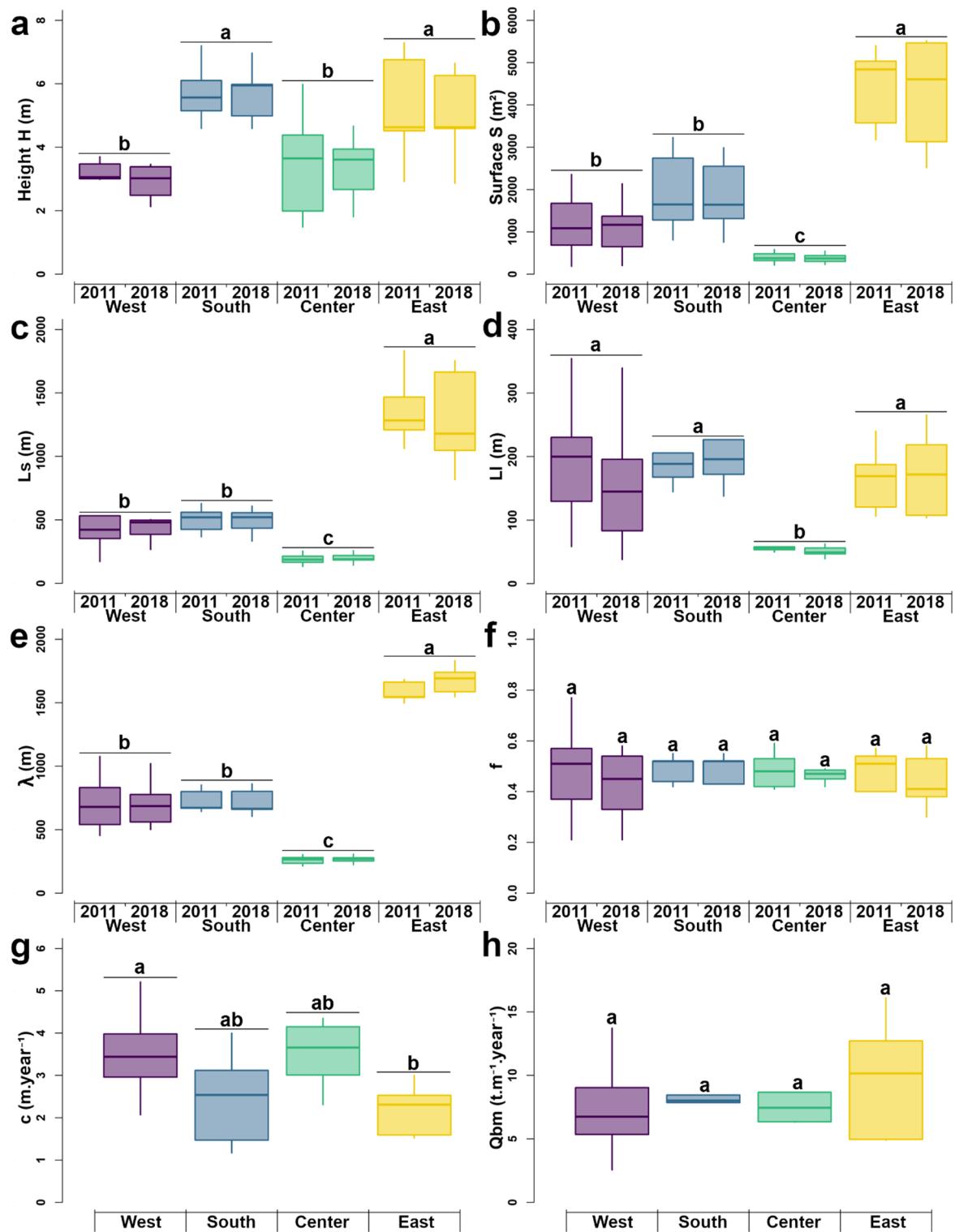


Fig. 2. Key morphodynamic characteristics of the dunes, categorized by dune sector. Ls: stoss side length, LL: lee side length, λ : spacing between dunes, f: shape factor, c: migration rate, and Qbm: mass bedload transport. The letters above the boxplots represent statistically comparable groups (Tukey HSD, $p < 0.05$).

between stations located in nondune areas and those in troughs. Similarly, stations on the stoss and lee sides of the dunes presented statistically comparable values.

When benthic stations are grouped on the basis of their location within different dune sectors, stations in the western sector generally exhibit higher values across all parameters (except for J') than those in other sectors do (Fig. 3). The western sector is characterized by small, sparse, and low surface dunes (Fig. 2). In contrast, the

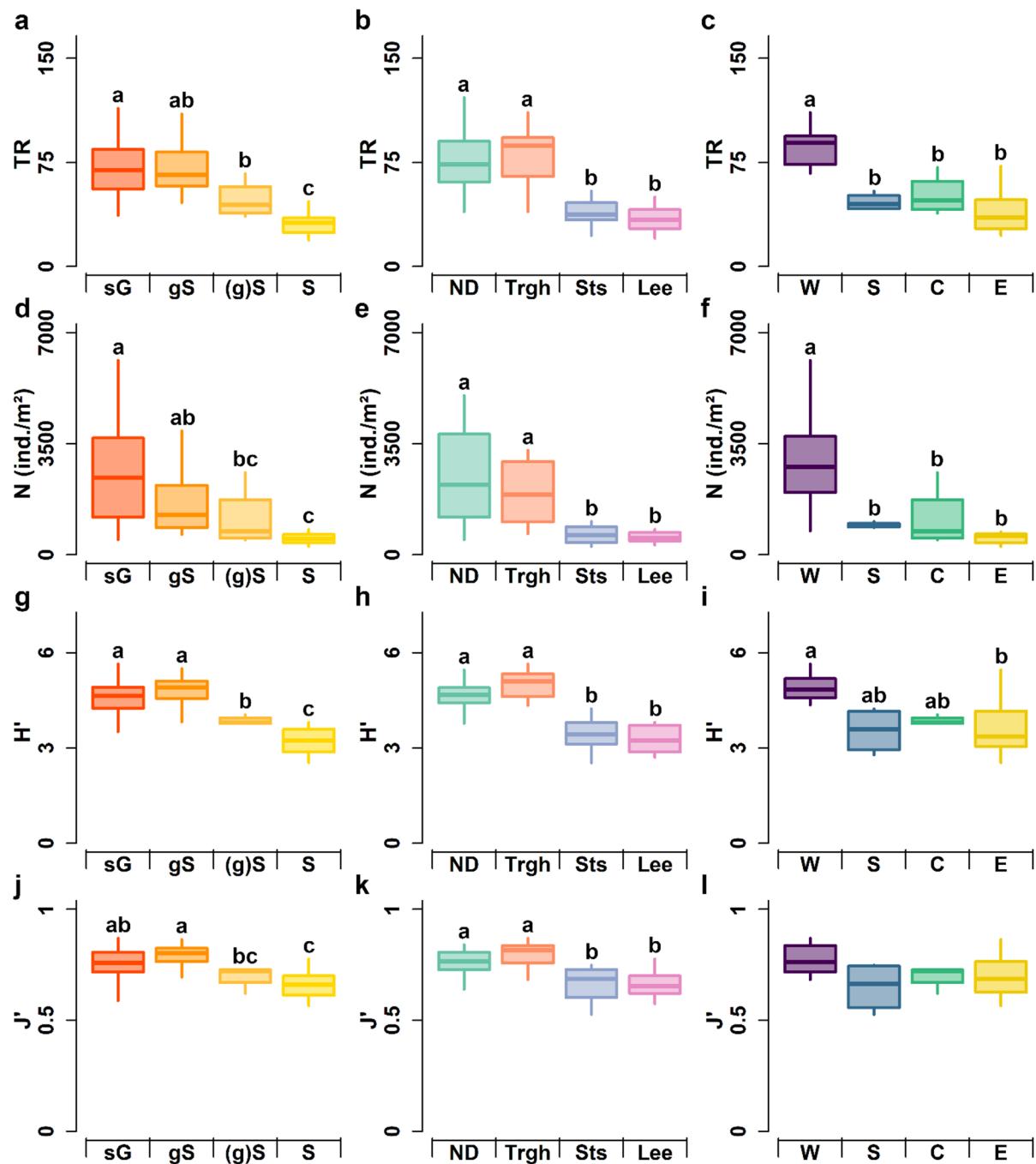


Fig. 3. Biotic variables categorized by sedimentary facies (left column), dune position (central column), and dune sector (right column). TR: Taxonomic richness, N: Abundance, H': Shannon index, J': Pielou's evenness index. Sedimentary facies: sG (sandy gravel), gS (gravelly sand), (g)S (slightly gravelly sand), and S (sand). Dune positions: ND (nondune area), Trgh (trough), Sts (stoss side), Lee (lee side). Dune sectors: W (west), S (south), C (center), and E (east). The letters above the boxplots represent statistically comparable groups (Tukey HSD, $p < 0.05$).

eastern sector, with its high, closely spaced and extensive dunes (Fig. 2), tends to have lower biological index values than the other sectors do (Fig. 3); however, these differences are less pronounced than those observed between the western sector and the other areas.

These findings are consistent with the results of the Pearson correlation analysis, which revealed that grain size (d_{50}) is generally positively correlated with the biological variables, whereas the morphodynamic characteristics of the dunes are negatively correlated with these variables (Fig. 4).

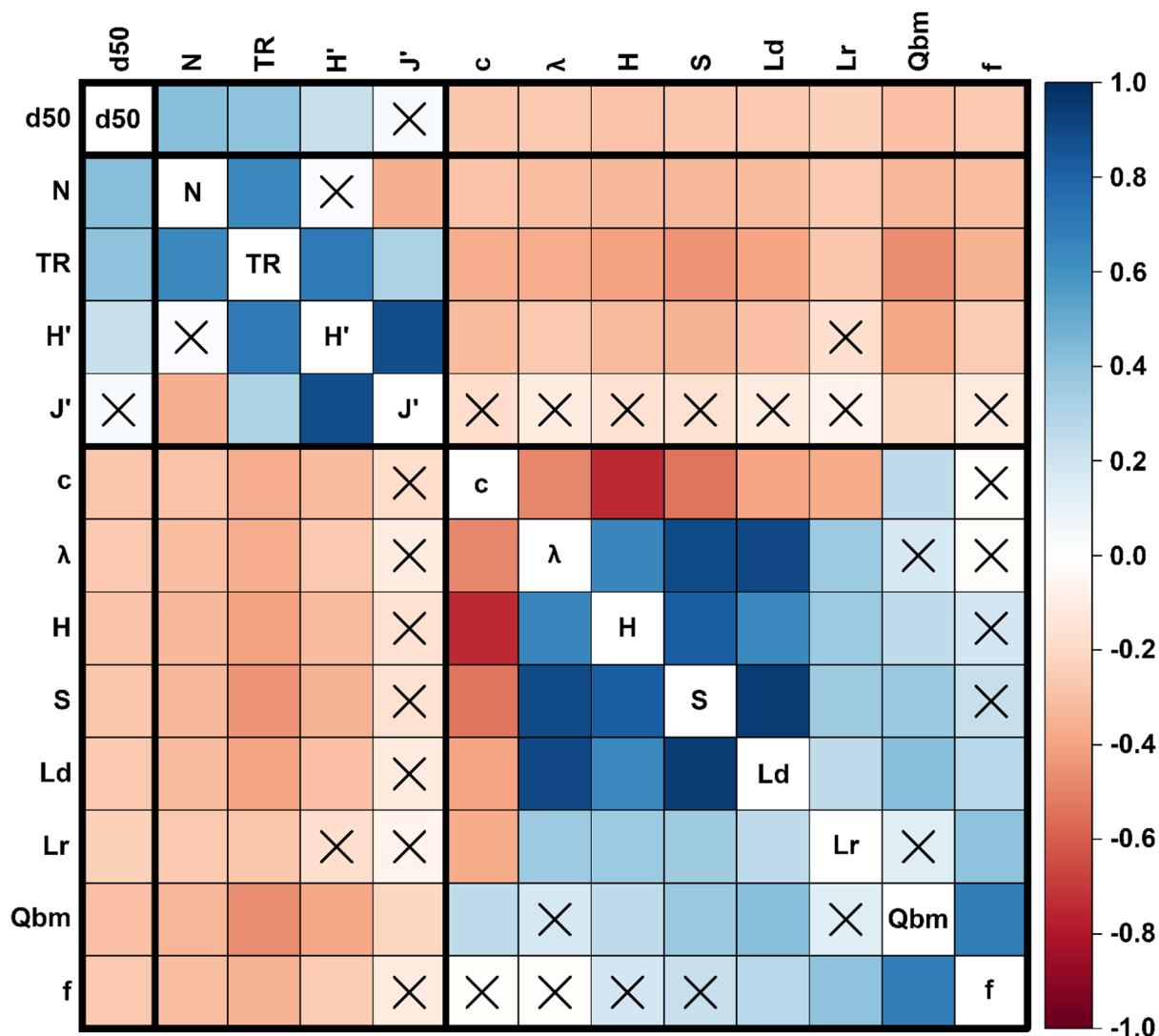


Fig. 4. Pearson correlation coefficients (color scale) between the grain size, biological, and morphodynamic variables of the dunes. d50: Median grain size. TR: Taxonomic richness, N: Abundance, H': Shannon index, J': Pielou's evenness index. c: Migration rate, λ : spacing between dunes, H: dune height, S: dune surface area, Ls: Stoss side length, Ll: Lee side length, and Qbm: mass bedload transport.

Grain size and morphological influences on trophic group composition

Deposit feeders and predators each account for approximately one-third of the benthic community at the DLT site, representing 36.7% and 34.7% of the total abundance, respectively. They are followed by filter feeders, which constitute 15.5% of the community. Scavengers and subsurface deposit feeders contribute in similar proportions, corresponding to 6.4% and 6.1% of the total abundance, respectively. Grazers are the least represented group, making up only 0.6% of the total abundance on average.

The proportions of the six trophic groups vary significantly across the different sediment facies at the DLT site, with the exception of grazers. Predators and scavengers tend to be more abundant in sandy sediments, whereas deposit feeders (both surface and subsurface) and filter feeders dominate in more gravelly substrates (Fig. 5). The transition in trophic group dominance appears to follow a relatively gradual pattern, which is consistent with the grain size gradient of the substrate (Fig. 5).

With respect to station positions on dunes, predators and scavengers are more prevalent on both the stoss and lee sides of dunes. In contrast, filter feeders and subsurface deposit feeders are more common in troughs and in areas without dunes. Surface deposit feeders are less common on the lee sides. Similar to the pattern observed across sediment facies, there were no significant differences in grazer abundance across the different dune positions (Fig. 5).

In terms of the dune sector, predators and scavengers are less abundant in the western and southern sectors and tend to be more prevalent in the eastern and central sectors. The opposite pattern is observed for subsurface deposit feeders, filter feeders, and grazers. Surface deposit feeders are more numerous in the southern sector,

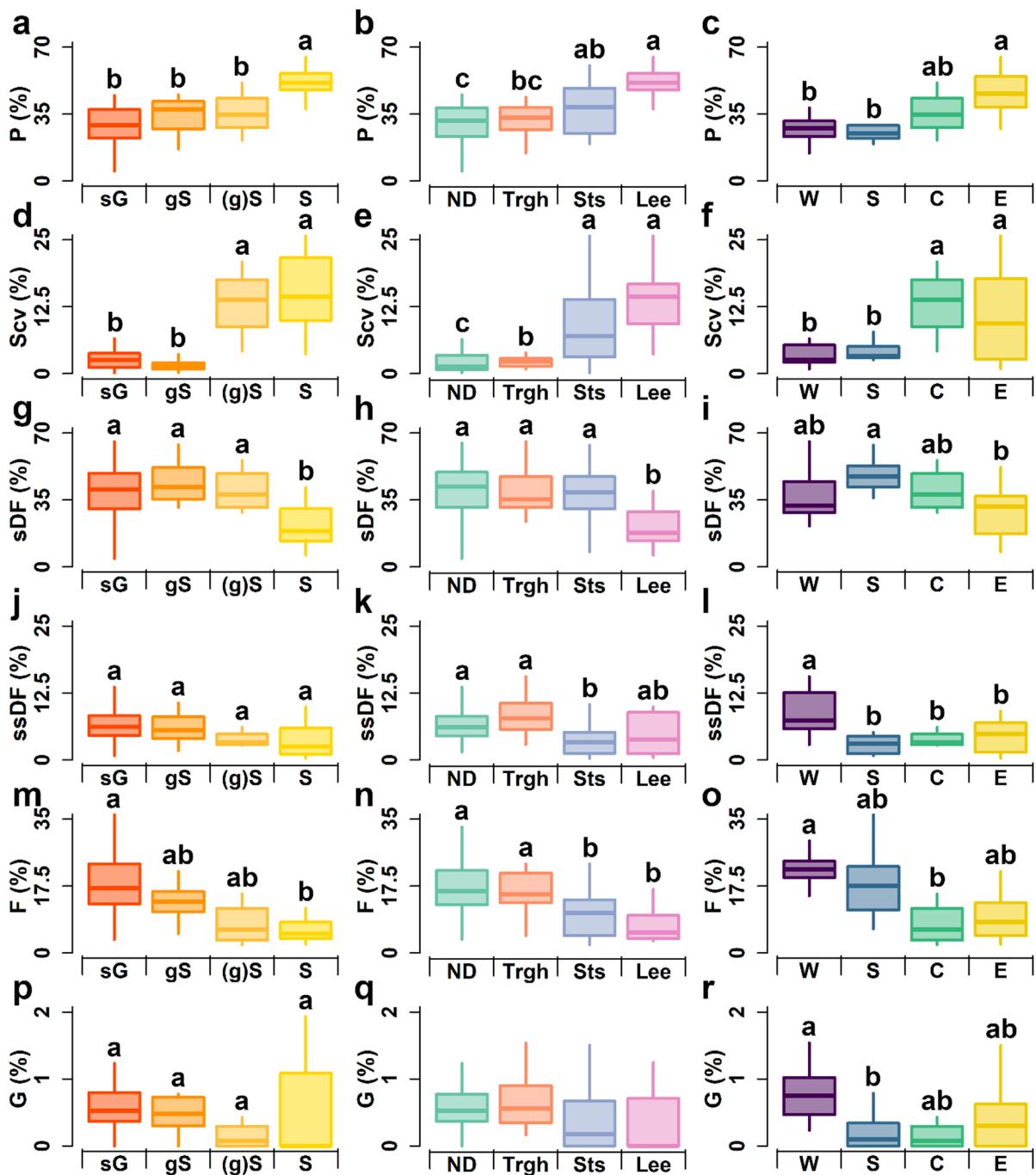


Fig. 5. Trophic group proportions categorized by sedimentary facies (left column), dune position (central column), and dune sector (right column). Sedimentary facies: sG (sandy gravel), gS (gravelly sand), (g)S (slightly gravelly sand), and S (sand). Dune positions: ND (nondune area), Trgh (trough), Sts (stoss side), Lee (lee side). Dune sectors: W (west), S (south), C (center), and E (east). The letters above the boxplots represent statistically comparable groups (Tukey HSD, $p < 0.05$).

present in intermediate proportions in the western and central sectors, and are least abundant in the eastern sector (Fig. 5).

Grain size and morphological influences on species composition

From a grain size perspective, the PERMANOVA indicates a gradient in species composition associated with sediment facies. Facies with a significant gravel component (sG and gS) do not show statistically distinct communities, nor do the sediments dominated by sand ((g)S and S). Likewise, intermediate sediment facies (gS and (g)S) are not significantly different from each other, highlighting a gradual transition in benthic community composition between sG and S, the only facies that were significantly different from each other. The IndVal values

for several species, which are calculated on the basis of the classification by sedimentary facies, are presented in Supplementary Table S1.

In terms of dune position, the species compositions at stations located outside the dune areas and in troughs are significantly different from those on the stoss and lee sides of the dunes (PERMANOVA, $p < 0.05$). No significant differences were found between the stations in the nondune areas and troughs or between the stoss and lee sides of the dunes (PERMANOVA, $p > 0.05$). The IndVal values for several species, which were calculated on the basis of the position of the station on dunes, are presented in Supplementary Table S2.

With respect to the dune sectors, the communities in the nondune areas were significantly different from those in the southern (PERMANOVA, $F = 3.5$, $p < 0.05$), central (PERMANOVA, $F = 6.0$, $p < 0.05$), and eastern sectors (PERMANOVA, $F = 8.6$, $p < 0.01$). The western sector is significantly different from only the eastern sector (PERMANOVA, $F = 4.12$, $p < 0.05$). The IndVal values for several species, which were calculated on the basis of dune sector classification, are presented in Supplementary Table S3.

Benthos structure on the DLT site

Regarding the structure of the benthic community, the arch (or horseshoe) arrangement of the stations on the RDA plot closely reflects their west-east distribution across the DLT site (Fig. 6a). The interactions among the explanatory variables result in a Guttman effect^{36,37}, leading to an organization of these variables along the two main components (RDA1 and RDA2). This diagonal structuring of the multivariate space is a common outcome in such analyses, which typically involve gradual variation in the taxonomic composition of the communities under study^{9,38–40}. Consequently, the interpretation of variables follows the diagonals that intersect the multivariate space (Fig. 6a).

The first diagonal, running from the upper left to the lower right of the plot, is associated with the grain size (d50) and sediment dynamics (reported through the dune migration rate, namely c) gradient of the DLT site. Stations characterized by coarse, less dynamic substrates (primarily sG and gS) tend to be located on the left, whereas those with finer, more dynamic sediments ((g)S and S) are positioned more toward the right. Note that stations with the highest mud content also plot on the left side, although this fraction remains negligible (< 3%). The second diagonal, extending from the upper right to the lower left, corresponds more closely to the gradient in dune morphometric characteristics. The stations located on the right side of the plot are associated with high and large dunes, whereas those on the left side correspond to smaller and spaced dunes (Fig. 6).

Several species appear to be distributed along these gradients. For example, *Spirobranchus triquetus* is more abundant in coarse sediments and areas with a weaker dune influence (troughs and smaller dunes). In contrast, the suprabenthic species *Megaloporus agilis*, the bivalve *Asbjornsenia pygmaea*, and the polychaete *Nephtys cirrosa* are more common in sandy sediments with high and broad dunes, particularly in the eastern sector (Fig. 6a).

Finally, the adjusted R^2 value of the RDA (0.4) indicates that approximately 40% of the variation in benthic abundance can be explained by the selected variables.

The variance partitioning analysis indicated that, among the 40% of explained variance, 7% was attributable solely to sediment grain size variations, 5% to the position of the benthic station on the dune, and 9% to the morphometric characteristics of the surrounding dunes, accounting for approximately 21% of the total variance (Fig. 6b). The remaining 19% is explained by interactions among the explanatory variables, with 13% attributed to the combined interaction of all three categories. This partitioning suggests that, at the scale of the DLT site, the distribution of benthic taxa is driven primarily by complex interactions involving both grain size and seabed morphology and dynamics, which aligns with the conclusions drawn from the RDA.

Benthic community distribution on the DLT site

To identify the species most affected by the grain size and morphological gradients at the DLT site, hierarchical clustering analysis (HCA) of the abundance data was conducted (Fig. 7a), followed by the calculation of IndVal indices for each species within each cluster (Table 1). The HCA revealed two main clusters (clusters 1 and 2 grouped together, and clusters 3 and 4, Fig. 7a). Clusters 1 and 2 are characterized by relatively coarse sediment, with two main differences distinguishing them. The first difference is grain size, where stations in cluster 1 have smaller sediment (average median grain size of 581 μm) than the coarser sediment in cluster 2 (average median grain size of 1,409 μm). The second difference pertains to the spatial location of the stations, with cluster 1 stations situated east of those of cluster 2. This west-east organization reflects the primary gradients in the area (grain size and morphological gradients), as well as the direction of residual tidal currents, which flow in the northeast direction and, in fact, mean residual sediment transport and dune migration²⁰. Despite these differences, some species from cluster 1 are also found at certain stations in cluster 2, albeit with lower abundances (Fig. 7a).

Clusters 3 and 4 are characterized by stations with small-grained sediments, most of which exhibit a sandy facies (Fig. 7). These stations are located primarily in the eastern and central parts of the study area. The main difference between Clusters 3 and 4 lies in the characteristics of the surrounding dunes. All cluster 3 stations are situated in the eastern sector, which is marked by the highest and widest dunes in the study area, with predominantly sandy substrates. In contrast, the two stations in cluster 4 are located in areas where the dunes are smaller, and the substrate is slightly coarser, containing, on average, 10.4% gravel compared with only 0.56% in cluster 3.

Importantly, most species characteristic of cluster 3 were rarely found in clusters 1 and 2, which was further confirmed by the high-fidelity indices of the species associated with cluster 3 (Table 1). Conversely, some species characteristic of cluster 1 are also found, sometimes in high abundance, at the stations in cluster 4, indicating a degree of ecological continuity between these clusters, which is reinforced by their spatial proximity (Fig. 7).

The benthic communities identified by this HCA suggest a gradual distribution of organisms along a west-east axis, with cluster 2-type communities in the west transitioning progressively to cluster 1- or 4-type communities

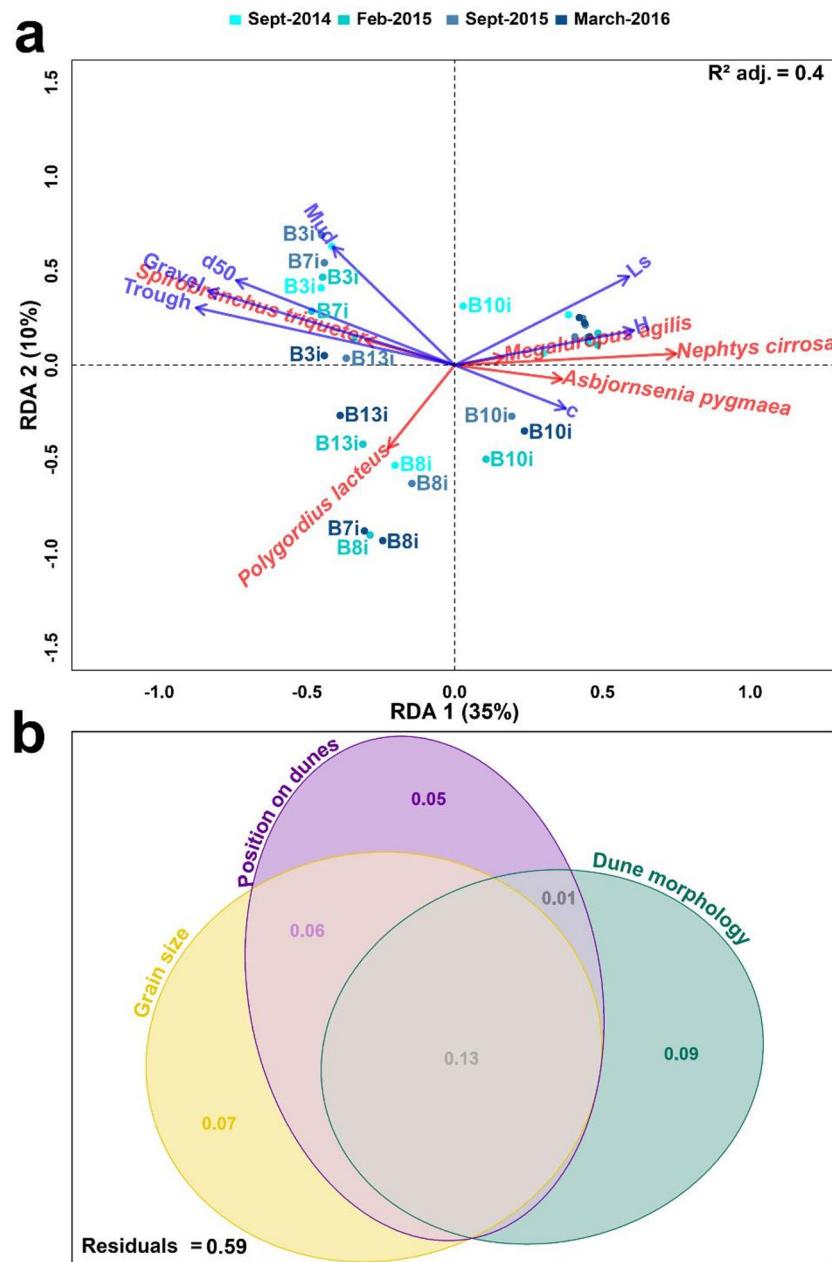


Fig. 6. RDA biplot (a) and variance partitioning (b) of Hellinger-transformed benthic abundances. Ls: Dune stoss side, H: Dune height, c: Dune migration. The overlapping points in the upper right section of the biplot correspond to stations B14i, B15i, and B20i.

and ultimately to cluster 3-type communities in the eastern part of the study area. This spatial organization is particularly evident in Fig. 7b and appears to be associated with the grain size, morphology and dune dynamic gradients that characterize the site (Figs. 1 and 2).

Discussion

Influence of sediment grain size and Dune morphology and dynamics on benthic diversity gradients

The grain size gradient at the DLT site, which decreased from west to east, was positively correlated with the biological diversity gradient. Coarser sediments, such as sandy gravel in the western sector, are associated with higher biodiversity than the sandier substrate in the eastern sector. This relationship is well established in the English Channel^{3,8,41,42}, as coarse, heterogeneous sediments offer greater structural complexity^{43–46}, providing more niches and fostering diverse biological interactions such as predation^{47–54}. Thus, the west–east grain size gradient likely underpins the observed diversity pattern at the DLT site.

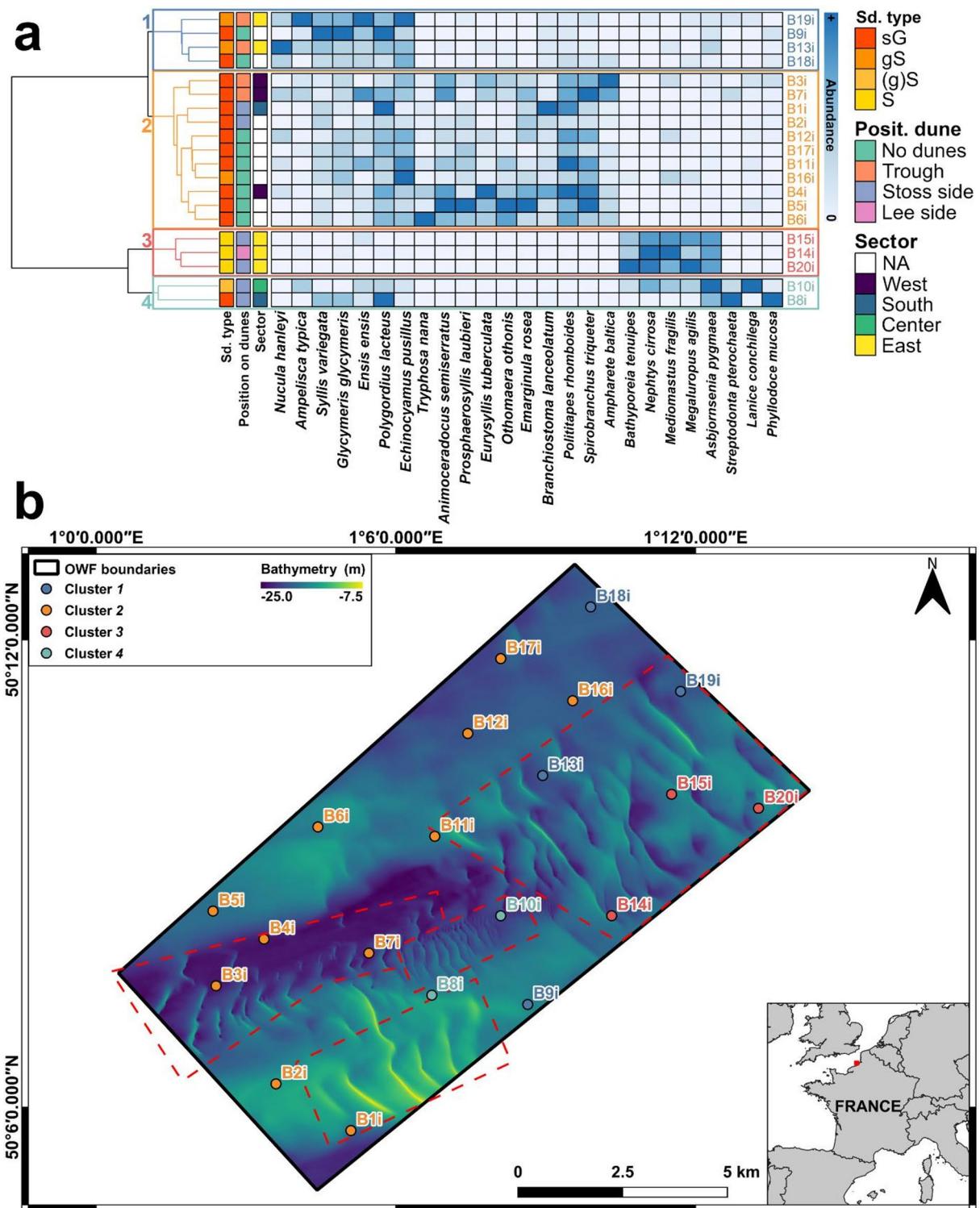


Fig. 7. Hierarchical clustering dendrogram and heatmap (a) and spatial distribution of the different clusters on the Dieppe-Le Tréport site (b). Sd. Type : Sedimentary type. sG (sandy gravel), gS (gravelly sand), (g)S (slightly gravelly sand), and S (sand). Posit. Dune : Position on dune. Bathymetric data sources: GEOxyz and G-Tec. The map was generated using QGIS version 3.34.

However, sediment grain size alone does not fully explain this pattern, as the presence of dunes also shapes benthic diversity. Dunes negatively affect biodiversity, with larger and more extensive dunes causing greater decreases, a pattern that has also been observed for smaller transverse features such as sand ripples⁵⁵. At DLT, near-dune stations show a 52% decrease in taxonomic richness and a 70% decrease in abundance compared with

Species	F _{k=1}	F _{k=2}	F _{k=3}	F _{k=4}	S _{k=1}	S _{k=2}	S _{k=3}	S _{k=4}	IndVal	Cluster
<i>Ampelisca typica</i>	1.00	1.00	1.00	0.50	0.61	0.10	0.02	0.28	0.61	1
<i>Aonides paucibranchiata</i>	1.00	1.00	1.00	1.00	0.51	0.45	0.01	0.02	0.51	
<i>Echinocyamus pusillus</i>	1.00	1.00	0.33	1.00	0.51	0.39	0.00	0.09	0.51	
<i>Ensis ensis</i>	1.00	0.73	0.33	1.00	0.53	0.22	0.05	0.21	0.53	
<i>Glycymeris glycymeris</i>	1.00	1.00	1.00	1.00	0.54	0.21	0.02	0.23	0.54	
<i>Nototropis vedloemensis</i>	1.00	1.00	1.00	1.00	0.50	0.37	0.03	0.09	0.50	
<i>Nucula hanleyi</i>	0.75	0.36	0.00	0.00	0.83	0.17	0.00	0.00	0.63	
<i>Periocoludes longimanus</i>	1.00	1.00	0.67	0.50	0.58	0.28	0.06	0.08	0.58	
<i>Polygordius lacteus</i>	1.00	1.00	1.00	1.00	0.51	0.27	0.02	0.40	0.51	
<i>Syllis variegata</i>	1.00	1.00	0.00	1.00	0.58	0.18	0.00	0.24	0.58	
<i>Acrocnida brachiata</i>	0.75	0.91	0.00	0.00	0.09	0.91	0.00	0.00	0.83	2
<i>Ampharete baltica</i>	0.25	0.91	0.00	0.00	0.14	0.86	0.00	0.00	0.78	
<i>Animoceradocus semiserratus</i>	0.50	1.00	0.00	0.00	0.04	0.96	0.00	0.00	0.96	
<i>Branchiostoma lanceolatum</i>	1.00	1.00	0.67	1.00	0.23	0.72	0.01	0.05	0.72	
<i>Emarginula rosea</i>	0.00	0.91	0.00	0.00	0.00	1.00	0.00	0.00	0.91	
<i>Eurysyllis tuberculata</i>	0.25	1.00	0.00	0.00	0.06	0.94	0.00	0.00	0.94	
<i>Galathea intermedia</i>	1.00	1.00	0.67	1.00	0.22	0.75	0.02	0.01	0.75	
<i>Leptochiton cancellatus</i>	1.00	1.00	0.00	0.00	0.22	0.78	0.00	0.00	0.78	
<i>Othomaera othonis</i>	0.50	1.00	0.00	0.00	0.07	0.93	0.00	0.00	0.93	
<i>Pisidium longicornis</i>	1.00	1.00	1.00	1.00	0.14	0.76	0.07	0.03	0.76	
<i>Polititapes rhomboides</i>	1.00	1.00	0.00	0.50	0.15	0.84	0.00	0.01	0.84	3
<i>Prosphaerosyllis laubieri</i>	0.50	1.00	0.00	0.00	0.06	0.94	0.00	0.00	0.94	
<i>Spirobranchus triquetus</i>	1.00	1.00	0.00	1.00	0.13	0.87	0.00	0.00	0.87	
<i>Tryphosa nana</i>	0.75	1.00	0.33	1.00	0.02	0.97	0.00	0.00	0.97	
<i>Bathyporeia tenuipes</i>	0.00	0.09	1.00	0.50	0.00	0.01	0.85	0.14	0.85	
<i>Magelona johnstoni</i>	0.00	0.00	0.67	0.50	0.00	0.00	0.77	0.23	0.51	
<i>Mediomastus fragilis</i>	0.25	0.27	1.00	0.50	0.02	0.06	0.74	0.18	0.74	
<i>Megaloporus agilis</i>	0.75	0.36	1.00	1.00	0.05	0.02	0.74	0.18	0.74	
<i>Nephtys cirrosa</i>	0.50	0.18	1.00	1.00	0.01	0.00	0.75	0.24	0.75	4
<i>Spiophanes bombyx</i>	0.25	0.00	1.00	0.50	0.04	0.00	0.68	0.28	0.68	
<i>Asbjornsenia pygmaea</i>	1.00	0.91	1.00	1.00	0.09	0.01	0.42	0.51	0.51	
<i>Cirolana cranchii</i>	0.25	0.55	0.00	1.00	0.11	0.24	0.00	0.65	0.65	
<i>Lanice conchilega</i>	0.75	0.73	0.00	1.00	0.05	0.07	0.00	0.88	0.88	
<i>Phyllodoce mucosa</i>	0.75	0.55	0.00	1.00	0.09	0.05	0.00	0.86	0.86	
<i>Streptodonta pterochaeta</i>	0.25	0.09	0.00	1.00	0.04	0.03	0.00	0.93	0.93	

Table 1. Fidelity (F_k) and specificity (S_k) values of various species for the four main clusters (k) identified through hierarchical cluster analysis (HCA). The cluster where each species achieves its highest IndVal value is indicated in the “Cluster” column. Only species with a p-value ≤ 0.01 and an IndVal ≥ 0.5 are included in the table.

areas without dunes, a trend mirrored in other regions, such as the French Flander Bank, where similar biotic reductions have been observed¹².

Notably, at the DLT site, no significant differences in diversity or species composition were found between communities located in troughs and those in areas without bedforms. This lack of distinction suggests a degree of temporal stability and connectivity between these environments, likely maintained by larval dispersion when direct connectivity is not possible. As such, interdune troughs, particularly those with relatively large surface areas, can be considered as hotspots of benthic diversity. Thus, dunes primarily affect the communities located on their slopes, with a stark contrast between the more diverse trough communities and the less diverse slope communities. Such distribution patterns have been documented multiple times at various sites and for different types of bedforms^{10–12,20–64}.

Grain size, dune morphology and dynamics, and benthic diversity are intricately interconnected at the DLT site⁶⁵. In the west, stronger tidal currents are responsible for more intense sediment transport, resulting in sandy sediment depletion and a mostly gravelly substrate. This favors the formation of small, isolated dunes, indicative of sandy sediment depletion^{16,66}, thereby creating extensive coarse-grained interdune trough areas that support diverse communities. Conversely, in the eastern part of the study site, the decrease in current intensity tends to favor sandy sediment accumulation, leading to the development of large, extensive dunes organized into continuous dune fields. This accumulation leaves little to no coarse-grained surface area, explaining the lowest

diversity observed in this sector. Furthermore, the sandy sediments in the east are more easily mobilized by currents, resulting in a more dynamic seabed in the east than in the west.

On the structure of benthic communities in Dune fields

Impact of sediment dynamics and Dune migration on benthic community structure

Sediment transport processes on dunes are frequently cited as the primary factor explaining the impoverishment of benthic communities associated with sedimentary structures^{12,67}. This could account for the observed negative correlation between various biotic parameters and dune migration speed (c), which serves as a proxy for sediment dynamics at the scale of an individual dune (Fig. 4). These movements can lead to the burial of organisms^{68,69} and have an abrasive effect caused by bedload as well as suspended load^{70,71}. Offshore Dunkirk, in the southern North Sea, submarine dunes develop on top of a sandbank and migrate at rates of 40–130 m per year (from a 10-month observation period) and 20.6–37.2 m per year (from a 20-month observation period)¹². High sediment fluxes tend to homogenize benthic communities between the troughs and crests of dunes¹². Furthermore, differential migration speeds among various bedforms contribute to differences in the structural and functional diversity of benthic communities^{12,20,58,61}. At the DLT site, where significant heterogeneity was observed between the troughs and slopes of dunes, dune migration rates derived from annual observation periods are between 1.2 and 8.05 m per year, which is approximately an order of magnitude lower than those of the dunes located off Dunkirk¹². Sedimentary and dune dynamics can be key factors for benthic structuring: homogenization of the benthic community structure is observed in the case of high sediment and dune dynamics, whereas heterogeneity is observed in the case of low sediment and dune dynamics. The question of a dune migration rate threshold value of approximately 10–15 m per year (derived from annual observation periods) to distinguish homogeneous/heterogeneous benthic structures should be considered, but could be further refined through additional studies.

Sediment movements can also impact the metabolism of benthic organisms, potentially causing damage to gills^{72–74}, with some trophic groups being more affected by these mechanisms than others¹². For example, filter feeders are often less abundant in dune-dominated areas^{12,75}, except in large interdune troughs where they can thrive¹¹. The results from the DLT site support this observation, showing that filter feeders are significantly less abundant on both the stoss and lee sides of the dunes than in interdune troughs and areas without dunes. They are also proportionally less common in the central and eastern sectors of the study area, which are characterized by tall and extensive dunes.

Trophic influences on benthic community structure in Dune environments

The influence of trophic mechanisms might also play a significant role in the aggregation of filter feeders, subsurface and surface deposit feeders within interdune troughs. These troughs can serve as zones of organic matter accumulation^{10,21,60,76–78}, providing a beneficial environment for organisms that rely on sedimentary organic matter^{11,58,63,79–83}. This trend is partly evident at the DLT site, where filter feeders, surface and subsurface deposit feeders tend to be more abundant in interdune troughs and dune-free areas, as well as in the western dune sector characterized by smaller, less extensive dunes. This could explain why species such as *Spirobranchus triquetus*, *Galathea intermedia* and *Caullerella alata*, which are filter feeders, surface and subsurface deposit feeders, are more frequently associated with interdune troughs and the western sector.

Similar observations can be made with respect to grain size, where coarser sediments, particularly the voids between gravel particles, can act as traps for organic matter that benthic organisms can utilize^{11,57,84}. Coarse sediments are mainly found in the western dune sector, where less extensive dunes result in a greater interdune surface area. At the DLT site, such differences were previously noted²², where sandy gravel contained significantly more organic matter (2.34%) than did gravelly sands (1.8%), which in turn had higher levels than did clean sands (0.85%).

Conversely, predators and scavengers were more prevalent on dune slopes, a pattern previously reported a few kilometers south²⁰. Several studies have highlighted the dominance of predators and scavengers on dune flanks and crests^{61,85,86}, which can attract relatively high trophic levels, particularly fish^{61,85,86}. For predators, such dynamic environments are often described as ideal for ambush predation, facilitating hunting strategies^{12,61}. Additionally, the local topography may promote the concentration of planktonic larvae, thus benefiting primary consumers^{87,88}. This likely explains the relatively high abundances of certain species, such as *Nephrys cirrosa*, which are known to be particularly prevalent on dune slopes and crests^{10,12,20,57,58,89}.

Scavengers are likely to exploit the high mortality rates observed on dunes¹², where many shell-bearing organisms, such as *Echinocardium cordatum*, have been reported to be fragmented⁵⁷. These findings suggest that trophic interactions play a significant role in shaping the benthic community composition in dune environments.

Influence of species traits and morphosedimentary interactions on benthic community structure

Nevertheless, other functional traits, particularly behavioral and morphological characteristics, likely play a significant role in shaping benthic community composition. Mobility is one of the key factors influencing species distributions, with communities on slopes and crests of bedforms typically dominated by mobile species^{12,21,90}. Although no specific trait-based analysis has been conducted at the DLT site, a similar pattern is expected. Many mobile suprabenthic species, such as *Gastrosaccus spinifer*, *Megaloporus agilis*, and *Bathyporeia tenuipes*, were observed colonizing dune slopes in high abundances. This observation is consistent across other sandbanks and dunes^{10,20,56,90}, including in the eastern English Channel, where large aggregations (“clouds”) of these species have been reported (*Bathyporeia* spp., *G. spinifer*)⁵⁷.

Some exceptions do exist, with a few sessile species, such as *Spisula solida*, *S. elliptica*, *S. subtruncata*, and *Asbjornsenia pygmaea*, also found on the dune slopes at the DLT site. Similar findings were noted a few kilometers south²⁰, where these species presented the highest abundances on the lower part of the gentle slope.

The likely explanation for their presence is the suitability of the dune-provided substrate (primarily sandy)^{61,91}, which matches their preferred habitat^{3,92}. Additionally, their ability to burrow may help them withstand the abrasive nature of these dynamic environments^{93,94}.

Moreover, bedforms are frequently described as potential larval traps^{79,88}, where community structure may be influenced by larval or postlarval migration processes, particularly for species such as *Spisula* spp. which tend to migrate toward sediment types that are favorable for their development^{60,91,95}. This highlights the synergistic effects that occur at the DLT site, where species distribution is strongly linked to both sediment grain size and dune morphology. Similarly, a few kilometers to the south, interdune variability (reflecting differences in grain size and morphometry) and intradune variability (position on the dune) account for approximately 44% of the variation in benthic community composition²⁰. This result is comparable to the 40% of variance explained with the data used in this study. These findings emphasize the complex and multifactorial nature of morphosedimentary gradients and their associated benthic communities at the DLT site. The organization of these gradients cannot be reduced to simple sedimentary characteristics; instead, it involves multiple interacting factors, such as hydrodynamics itself influencing sediment dynamics and, thus, seabed morphology and bedform dynamics, which contribute to the intricate structuring of the local ecosystem.

Conclusion

Using bathymetric, grain size, and benthic data, this study highlights how sediment grain size, dune morphology and dynamics shape benthic communities at the future DLT offshore wind farm site. These factors are interlinked and influenced by local hydrodynamics, creating nested biodiversity gradients with distinct spatial patterns. At the site level, biodiversity is greater in the western sector, where coarse sediments dominate due to limited dune coverage. Conversely, the eastern sector, characterized by sandy substrates and large, continuous dune fields formed by sand accumulation, exhibited lower benthic diversity.

A secondary biodiversity gradient occurs at the dune scale: interdune troughs host more diverse communities than dune flanks do. Sediment and dune dynamics play crucial roles in structuring these communities. High dynamics tend to homogenize the benthos, whereas lower dynamics promote heterogeneity between troughs and flanks. A potential migration threshold of 10–15 m·yr⁻¹ (based on annual observations) appears to influence this heterogeneity, although further research is needed to refine this estimate.

The planned installation of offshore wind turbines at the DLT site could alter dune morphology and hydrodynamic conditions, potentially affecting benthic communities. Particular attention should focus on interdune troughs, which serve as biodiversity hotspots. The relatively slow dune migration rates at the site may mitigate some impacts, but understanding how anthropogenic changes influence these unique habitats remains critical for conservation and management efforts. In particular, impacts during construction (e.g., dune destruction, sediment resuspension, noise pollution) and post-construction effects (e.g., introduction of hard substrates favoring sessile epifauna, noise pollution) warrant careful evaluation. Continued long-term environmental monitoring at such sites is therefore strongly encouraged.

Data availability

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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Author contributions

S.L.B., P.W. and J.P.P. conceived and designed the research. J.P.P. and A.R. conducted the field work. J.P.P. analyzed the samples. S.L.B., J.P.P., T.D. and N.C. analyzed the data. N.C. wrote the manuscript and produced all the figures and tables. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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