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Inducing mussel beds, based on an aquaculture long-line system, as nature-based solutions: Effects on seabed dynamics and benthic communities

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ABSTRACT

Nature-based solutions (NbS) offer a promising path to enhance climate-resilient shorelines. For instance, the creation of mussel beds in subtidal sandy shore systems provides a versatile strategy for coastal management, reinforcing coastal defense and fostering biodiversity, ultimately strengthening the resilience and well-being of coastal communities. This study analysed the changes in seabed dynamics and surrounding benthic communities as a result of the formation of mussel beds (*Mytilus edulis*) using an aquaculture longline system. Therefore, a comprehensive monitoring approach at two sites characterized by distinct hydrodynamic conditions was applied over a three-year period. To assess the effects, a before/after control/impact design (BACI) was employed. Seabed dynamics were evaluated by observing mussel bed persistence, erosion/deposition, and sediment composition. The influence on the benthic community included assessments of community structure and biodiversity. Finally, the impact of mussels, hydrodynamic conditions, and their interactions on seabed dynamics and benthic communities was examined using linear mixed models (LMMs). Factors such as mussel presence, *Lanice conchilega* abundance, shell cover, and sediment composition played a role in shaping the distinct characteristics observed between two different sites: a site that lies at a location that is more sheltered from hydrodynamic conditions, and a second site that is exposed to higher current and wave conditions. The sheltered site exhibited higher species density, richness, biomass, and diversity compared to the exposed site. In relation to the mussel bed development, mussel patches were found at both sites (with higher occurrence at the sheltered site) in the 2nd and 3rd years (mainly in summer towards early winter). The influence of mussels on sediment deposition was noticeable at the sheltered site, albeit lacking statistical significance, suggesting their potential role in erosion/deposition mechanisms. Also, a higher proportion of very fine sand was observed in the mussel bed compared to the bare sand. However, due to the absence of higher-density permanent mussel beds and irregular sedimentation/erosion patterns throughout the study period, no significant effect of the mussel beds on the community structure or diversity was found. In order to achieve a sustained and dense mussel bed and maximize the potential impact of mussels in combating climate change (e.g., shore protection and biodiversity enrichment), additional measures to increase coastal resilience against harsh hydrodynamic conditions may be necessary.

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1. Introduction

Coastal low-lying regions are home to over 700 million people, making them one of the most densely populated regions on the planet [1]. These areas have always been desirable for human settlement due to their vast array of economic and social benefits, including fishing, tourism, and trade. However, climate events such as rising sea levels, storm surges, flooding, and erosion pose threats to coastal communities by impacting coastal land, habitation, agricultural production, and coastal ecosystems [2,3]. Traditional engineering techniques (e.g., dyke, seawall, dam), although widely used, may provide challenges, such as disrupting natural sediment transport and altering beach habitat, and become unsustainable in most locations around the world [4]. Therefore, the implementation of more sustainable, cost effective, dynamic, nature-based solutions (NbS) are needed to withstand storms and climate change by making proper use of nature. Biogenic reefs (e.g., mussels, oysters), sand dunes, saltmarshes, mangroves, seagrasses, and tidal wetlands, for example, have the potential to protect coastlines from erosion, strong waves, and flooding by attenuating waves and stabilizing sediment [5-8].

Mussels are a good example of an ecosystem engineer, with growing recognition of their ecological significance as candidates for NbS [9-13]. They form a dense bed by attaching themselves to one another with strong threads, the byssus to the substratum, to improve the stability of mussel beds [14]. Their three-dimensional reef structure increases the complexity and heterogeneity of the surrounding sediment environment- i.e., autogenic engineering [10,15-17]; also removes large quantities of suspended material from the water column- i.e., allogenic engineering [18-21]. Mussel beds modify water flow and wave action, thereby influencing sediment consolidation, deposition, and stabilization [22] and encouraging carbon storage [23]. Moreover, a diverse range of plant and animal species, including algae, worms, snails, shrimps, sea stars, fish, and crabs, thrive in their complex structure [24-26]. Several studies have demonstrated the influence of mussel beds on the structure of neighboring communities, affecting variables such as diversity, biomass, and abundance [12,27-29].

Despite their significance as NbS, mussel beds have suffered considerable damage or loss due to both natural processes and anthropogenic activities [30]. As awareness grows and understanding deepens about the vital role these habitats play, there is a concerted push to restore bivalve beds to establish stable populations. Consequently, the creation of mussel beds using traditional longline aquaculture techniques [31,32] has gained widespread popularity among restoration initiatives. Coastbusters 1.0 (CB 1.0), the first pilot-project to test the feasibility of mussel beds as NbS, was set-up in the period 2017–2020 in the Belgian part of the North Sea near De Panne [33]. Utilizing a modified mussel aquaculture longline system with dropper lines, Coastbuster was able to efficiently attract mussel larvae [34]. These mussels detach in clusters and fall to the seafloor under the lines when they reach a certain size and density [33]. Together, these mussel clusters cover the seafloor directly to form a mussel bed and are expected to influence its surrounding environment. Preliminary findings of CB 1.0 indicate that mussel densities and sizes varied between different types of dropper lines (e.g., with or without filaments), potentially resulting in differences in underneath mussel bed development. However, the developed mussel beds were observed temporarily, exhibiting a limited effect on sediment and macrofaunal communities [33]. Although the first finished project has provided valuable insights into mussel bed development and their ecosystem impacts in a sandy foreshore, limitations in the sampling design, monitoring techniques and the absence of long-term data have hindered the establishment of conclusive evidence regarding the influence of mussel beds on the seabed.

To address this knowledge gap, this study, as part of Coastbusters 2.0 (CB 2.0), aims to investigate how mussel beds are formed by an aquaculture longline system and influence the seabed dynamics and the surrounding benthic community characteristics (e.g., biodiversity, community structure). Building upon insights from CB 1.0, the study adopts a new setup by extending the existing sheltered site with an exposed site to evaluate the approach under two slightly different hydrodynamic conditions. A combination of multiple monitoring techniques, such as multibeam surveys, van Veen grab, and diving, along with long-term data collection, were combined and employed during 2020–2022 at two experimental sites: the exposed and sheltered sites near De Panne. A before/after control/impact-design (BACI) was followed to assess the effects of the mussels under different hydrodynamic conditions [35]. Therefore, the hypothesis of this study is that the aquaculture longline system will generate mussel beds/patches and affect seabed morphology, sediment characteristics, and benthic community characteristics in both sheltered and exposed hydrodynamic conditions. Overall, the study aims to contribute to the understanding of the role of *Mytilus edulis* as a NbS for coastal management subjected to different hydrodynamic conditions in a sandy foreshore environment through the implementation of multiple monitoring measurements.

2. Materials and methods

2.1. Site description

The Belgian part of the North Sea is a shallow sea with an area of approx. 3600 km^2. This area is distinguished by complex subtidal sandbanks and a highly variable benthic sedimentary environment [36]. The governing hydrodynamic conditions are primarily influenced by the tidal regime and the prevailing wind and wave patterns [37].

Two experimental setups were installed on June 26, 2020, in the western coastal area of the Belgian part of the North Sea (in front of the coastal municipality of De Panne) at two sites characterized by different hydrodynamic conditions (Fig. 1: A). The sheltered site (51°07′19.2″ N, 2°35′16.8″ E) and exposed site (51°07′22.2″ N, 2°33′28.5″ E) are situated at distances of 2 km and 5 km from the shoreline, respectively. The sheltered site is set up in the southwestern region of the Broers bank, on the leeward side of the Trapegeer bank, affording greater protection from the effects of waves and currents. Conversely, the exposed setup is located on the Trapegeer bank, facing more powerful waves and current activity in the open sea. This difference is demonstrated by stronger bottom currents compared to the sheltered site (Appendix 1), a distinction likely attributed to the exposed site's bathymetric characteristics, including its location in the southern part of Westdiep, a deep trough channeling a significant water volume. Both locations exhibit an average water depth of 5 m (TAW, horizontal water level reference in Belgium) and are distinguished by sediment grain sizes ranging from fine to medium sand.

2.2. Installation and monitoring design

The installation of the mussel bed is based on the use of a modified longline aquaculture technique that enables the kickstart of the biogenic reef formation. The dropper lines, each extending 3 m in length, were

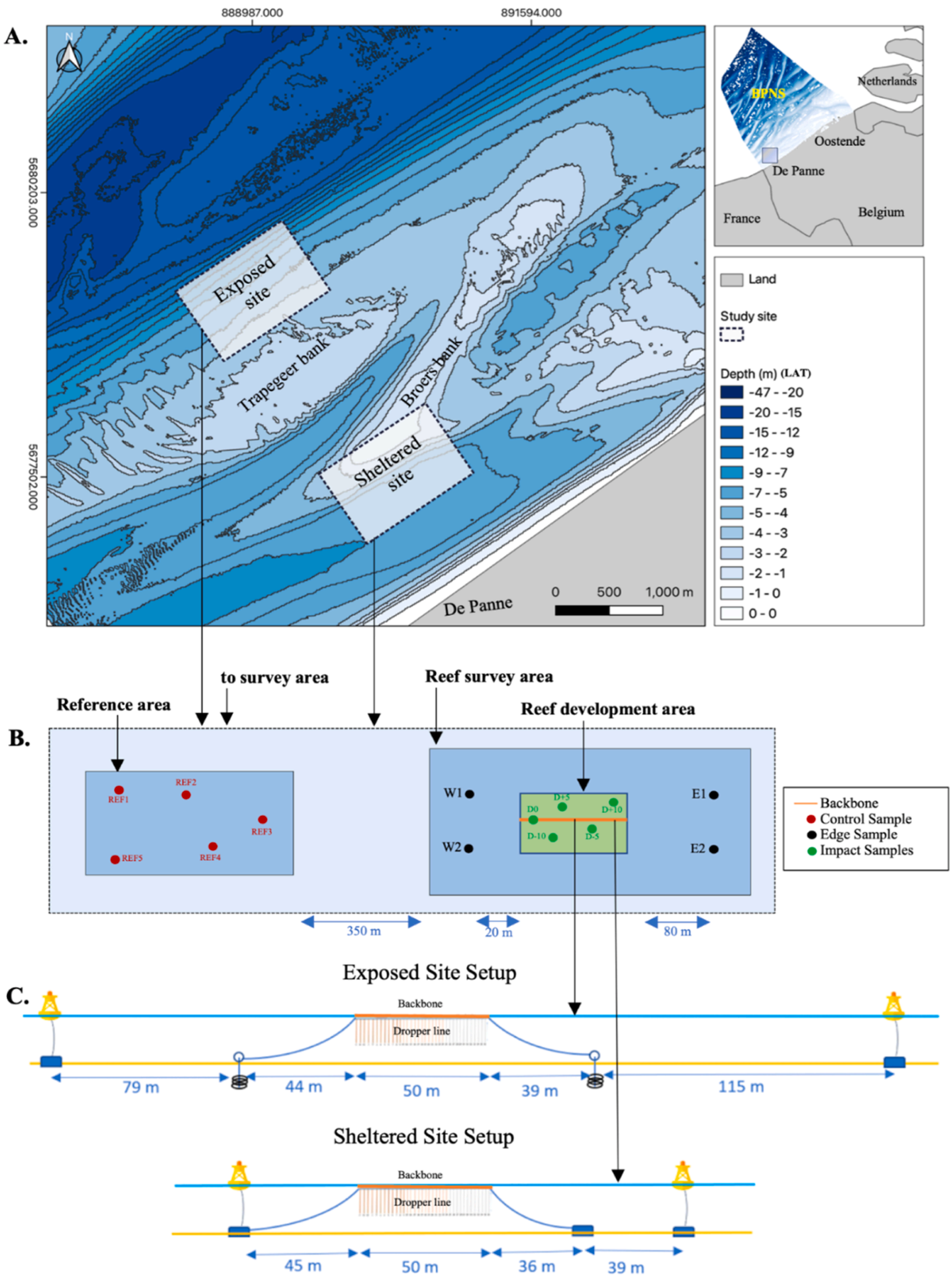

Fig. 1. A: Bathymetry map and location of experimental site **B:** Diagrammatic layout of sampling design (not scaled). Different areas containing control samples (REF1, REF2, REF3, REF4, REF5), edge samples (W1, W2, E1, E2), and impact samples (D0, $D \pm 5$, $D \pm 10$); **C:** Diagrammatic layout of aquaculture installation.

Table 1
Sampling campaigns (T0-T3) conducted before and after the installation of the setup for the collection of macrobenthos, sediment characteristics, bathymetric and visual data.

Sampling campaigns corresponding to different site situations	Timing of macrobenthos and sediment sampling campaigns	Timing of video and bathymetry sampling campaigns
T0	15/06/20 (Summer)	May 2020 (Spring)
Installation: 26/06/20 (Summer)		
T1	07/09/20 (Fall)	2020 (Summer, Fall, and Winter)
T2	28/09/21 (Fall)	2021 (Spring, Summer, Fall, and Winter)
T3	05/09/22 (Fall)	2022 (Spring, Summer, Fall, and Winter)

systematically positioned over a length of 50 m at one-meter intervals, fastened to the ocean's surface by a nylon line 'backbone' supported by buoys. At each site (exposed and sheltered), three backbone longlines with 36 dropper lines were installed. Three types of materials were utilized for the dropper lines: 12 biobased 22 mm diameter, 12 biobased 12 mm diameter, and 12 constructed from Deltaflex with a diameter of 20 mm. Additional weights of approximately 10 kg (made of sandbag, rock, and concrete (CEM III/C)) were attached to the bottom of each dropper line to maintain verticality in the water (Fig. 1: B-C). After the installation of the aquaculture setup, spat (mussel larvae) are expected to attach to the dropper lines and grow to a sufficient size and amount to cover the line. When they grow too heavy to be held, they break off and fall in clumps to the seafloor, thus forming a mussel bed underneath. To comprehensively capture the formation of the mussel bed and its surrounding environmental conditions, a multi-faceted monitoring approach was employed using Van Veen grabs, diving surveys, and multibeam measurements.

2.3. Experimental design

The sampling of the seafloor is based on a BACI sampling design and a temporal window of three years (June 2020 to September 2022). Macrobenthos and sediment samples were collected during four sampling campaigns. Video material containing seabed and bathymetry data was collected seasonally (spring, summer, fall, and winter) four times each year. Samples were collected before (called 'T0') and after (called 'T1', 'T2', and 'T3') installing the reef setup to observe how the site changed over time (Table 1).

The sheltered and exposed sites were divided into three surveying areas: (1) Reef development area: which is the area directly underneath the experimental setup; (2) Reef survey area: a large area surrounding the reef development area (3) Reference area: small area towards the western site of the reef development area where no impact of the experimental setup and the formed reef is expected. In total, fourteen sampling stations in three different areas at both the sheltered and exposed sites were constructed. Five sampling points were selected at the start of the monitoring activities at each reef development and reference area to ensure sampling at the same points afterwards. At the reference area, these sampling points are control samples (REF1, REF2, REF3, REF4, and REF5), while another five sampling points are used at the reef development area, known as impact samples, are separated by 5 m at 0 m, ±5 m, and ±10 m distance from the central backbone, respectively. Moreover, 4 edge sampling points (E1, E2, W1, and W2) located in the reef survey area, two from 80 m from the eastern side and two from 20 m from the western side of the reef development area were designed (Fig. 1: B). These edge samples are employed to monitor the possible effects of the experimental setup in the wider surrounding environment. Therefore, the establishment of the above sampling points and areas allows us to investigate three different factors. The 'Area' factor is fixed, and it compares the impact area (reef development area) against the control area (reference area) by adding an extra edge area (reef survey area). The 'Site' fixed factor compares two different hydrodynamic conditions, sheltered and exposed site, while the 'Campaign' is random and indicates the different sampling times (T0, T1, T2, and T3).

2.4. Sampling protocol and laboratory analysis

2.4.1. Macrobenthos and sediment

Samples of macrobenthos and sediment were taken during the day using a Van Veen grab that featured a sampling area of 0.1 m^2. Before rinsing the Van Veen sample, sediment samples were collected from the sample using a PVC tube (5 cm in diameter). Samples were rinsed onboard using a 1 mm mesh and placed on a 6 % formaldehyde in seawater mixture for long-term storage. After being labeled, samples were transported back to the laboratory (ILVO laboratory at the InnovOcean Campus) for further analysis. Macrobenthic samples were stained with eosine to make them easier to see and cleaned in the lab before analyzing the fauna. The organisms were classified at the lowest possible taxonomic level. Following this, the organisms were counted, and wet weight was recorded to the nearest 0.0001 g. Finally, the identified species were placed in labeled vials and preserved in 70 % ethanol. For the purposes of analysis, the measurements of density and biomass were normalised per square meter (m^{-2}). Sediment composition (percentages of mud, silt, sand, and gravel), and median grain size were determined for each sample by means of laser diffraction using the Malvern Mastersizer. Before laser diffraction, the fraction of sand larger than 1000 m was removed using a sieve. The determination of the percentage of total organic carbon (TOC) in the sediment samples was carried out using a modified Walkley-Black titration method [38].

2.4.2. Seabed morphology

To characterize the seabed morphology (e.g., epifauna) and possible mussel bed presence, two video transects per area were recorded by a scientific dive team in spring, summer, fall, and winter from 2020 to 2022. The video transect was conducted only for the impact area underneath the experimental setup and for the control area, using a marked rope for guidance. Samples for both the control and impact areas corresponding to the exposed and sheltered sites during fall 2021 and fall 2022, as well as the control area of both sheltered and exposed sites during winter 2020 and the control area of the exposed site during spring 2021, were not collected due to unfavorable weather conditions (kept blank in Fig. 2). Additionally, a NORBIT Wideband Multibeam System (WBMS) was installed on RIB Zeekat, and four surveys were conducted each year during the spring, summer, fall, and winter seasons to collect bathymetry data across the site. Wave data were collected from a Trapegeer buoy to explain any significant changes in bathymetry resulting from seasonal storm events. These wave data represent a common dataset for both the sheltered and exposed sites. The diving activities and the multibeam sampling were performed by Flanders Marine Institute (VLIZ).

2.5. Data analysis

2.5.1. Macrobenthic data

The macrobenthic dataset underwent a thorough screening process prior to analysis. Datasets were checked, and species not typical of the macrobenthic fauna (Van Veen grab based) were removed, such as copepods as well as planktonic species. Taxa (e.g., Corophium, *Eteone, Jassa*, Oligochaeta, *Owenia* etc.) that are difficult to identify at the species level were lumped together at the lowest possible taxonomic level. Additionally, station T0_SHL_D5 from the T0 sampling campaign in the sheltered impact area was excluded from the analysis due to its inadequate preservation during sampling.

Macrobenthic community structure is characterized by analyzing species richness (spp.sample^{-1}), density (indv.m^{-2}), biomass (gm.m^{-2}), Simpson index (1-λ'), and Shannon index (H'(loge)). The concept of species richness refers to the overall count of species or taxa present within a given area without taking into account their relative abundance distribution. In contrast, the Shannon index exhibits a heightened degree of sensitivity to species richness, whereas the Simpson index is less sensitive to rare species and places greater emphasis on those that are more abundant. A non-metric multidimensional scaling (n-MDS) was carried out using macrobenthos abundance data with 'area' (control, edge, and impact area), 'campaign' (T0, T1, T2, and T3), 'site' (exposed and sheltered), and sample clusters as factors to visualize changes in species composition. A PERMANOVA test was followed by a PERMDISP using the function 'pairwise.adonis' to check for homogeneity of multivariate dispersions for the different factors. Finally, a SIMPER analysis was carried out to determine which taxa most contributed to the differences between the relevant factors.

2.5.2. Seabed morphology

Video snapshot analysis technique was used to characterize the seabed. The process includes the analysis of the snapshot using ImBatch software version 7.3.0. Given the low visibility and snapshots' low quality, color, contrast, and brightness were modified by "Auto enhancement 1**"**. Once the snapshots' quality was improved, they were divided into 8 quadrats to monitor mussel bed formation and characterize the seafloor. Four seabed types were observed: shell cover, sand cover, mussel cover, and *L. conchilega* cover, based on a decision table for the sediment and class variables (Appendix 2). The snapshot was finally georeferenced by interpolating coordinates along the transect line and applying a 0.5 m perpendicular offset. The resulting data were imported into QGIS software as point data, and seabed types were represented using pie charts; bar plots were created using R to visualize the percentage coverage of each habitat across the seasons, enabling observation of the persistence of the 4 seabed types over time.

The morphology of the seafloor and changes in bathymetry were analysed based on the multibeam surveys. Changes in elevation between two sampling campaigns were used to determine sediment erosion and deposition in different areas, and the resulting differences were visualized using QGIS software. 'Zonal Statistics' tool available in QGIS was used to calculate mean elevation for a specific area (control area, impact area, edge area) and sampling point (D0, $D \pm 5$, $D \pm 10$, REF1, REF2, REF3, REF4, REF5, E1, E2, W1, W1). To mitigate potential errors caused by the slight offset between sampling points and bathymetry data, individual point-specific values within the site were obtained by calculating the mean value of a 10-meter polygon around each sampling point instead of relying on the exact sampling point location. This approach aimed to minimize inaccuracies by incorporating a broader spatial area around each sampling point.

2.5.3. Ecology and environmental drivers

A Principal Components Analysis (PCA) was conducted on various factors, including sediment composition, seabed characteristics, depth, and erosion/accretion, to examine the differences in environmental parameters across the macrobenthic community. In the case of missing values for the environmental variables (mussel, *Lanice*, shell cover, crab, and starfish densities), an interpolation method was employed based on nearby samples instead of excluding the samples from the analysis. This approach allowed for the utilization of the available data and provided a more comprehensive representation of the environmental conditions across the study area. In order to mitigate the impact of data dimensions, a logarithmic transformation of the environmental variables was executed using the formula log $(x + 1)$ [39].

2.5.4. Statistical analysis

Data visualization and statistical analysis were conducted using QGIS version 3.24.2 and R version 4.3.0 (2023–04–21), with different packages like 'ade4', 'vegan', and 'lme4'. The impact of mussels, hydrodynamic conditions, and their interactions on seabed dynamics and benthic communities was examined using linear mixed models (LMMs). The categorical fixed effects in this study were 'Area' (control, edge, and impact) and 'Site' (sheltered and exposed), while 'Campaign' (T0, T1, T2, and T3) was considered a categorical random effect. When the area or the interaction between area and site was found to be significant, a post-hoc analysis was performed using the Bonferroni method to detect any significant differences between group means. All the reported mean values are presented as the mean ± standard deviation (SD), except for sediment composition, which is reported as the mean ± standard error (SE). A significance level of $p < 0.05$ was considered to be significant in all tests. To test for normality and linearity of residuals, a QQ-plot was used for visual inspection, and a Shapiro-Wilks test was conducted. To verify the homogeneity of variances, Levene's test was carried out. In cases where data heterogeneity needed to be reduced, a log $(x + 1)$ or root transformation was applied. However, for some data sets, log or square root transformation failed to produce normally distributed data; in such cases, a Box-Cox procedure was used to obtain the lambda value, which was then employed for power transformation. A Non-Parametric Scheirer-Ray-Hare test was used when the data could not meet the normality assumptions (Appendix 3).

3. Results

3.1. Effect on seabed morphology

3.1.1. Seabed characteristics: mussel patches/beds persistence

The formation and persistence of mussel patches/beds, as well as other dominant habitats such as *L. conchilega* and shell, were observed throughout the sampling period around the mussel line (Fig. 2: A). Overall, the control area of the exposed site is dominated by bare sand with a small amount of shell-dominated sand and infrequently observed *L. conchilega* aggregates, whereas small mussel patches were observed between summer and winter at the impact area. On the other hand, the sheltered site consists mainly of shell mixed sand, *L. conchilega* reef, and mussel patches, with a comparatively higher amount of mussel patches at the impact area. A distinct seasonal pattern is observed, with mussel patches increasing from summer to winter and decreasing to a negligible amount by spring. The highest occurrence of mussel patches, accounting for 14.4 % in the sheltered site and 2.8 % in the exposed site, was reported during the last winter sampling in 2022. Additionally, as the presence of mussels increased, a decline in *L. conchilega* reefs was observed over time. In 2020, a substantial portion of the seabed was covered by sand or a mixture of sand and shells. However, within two

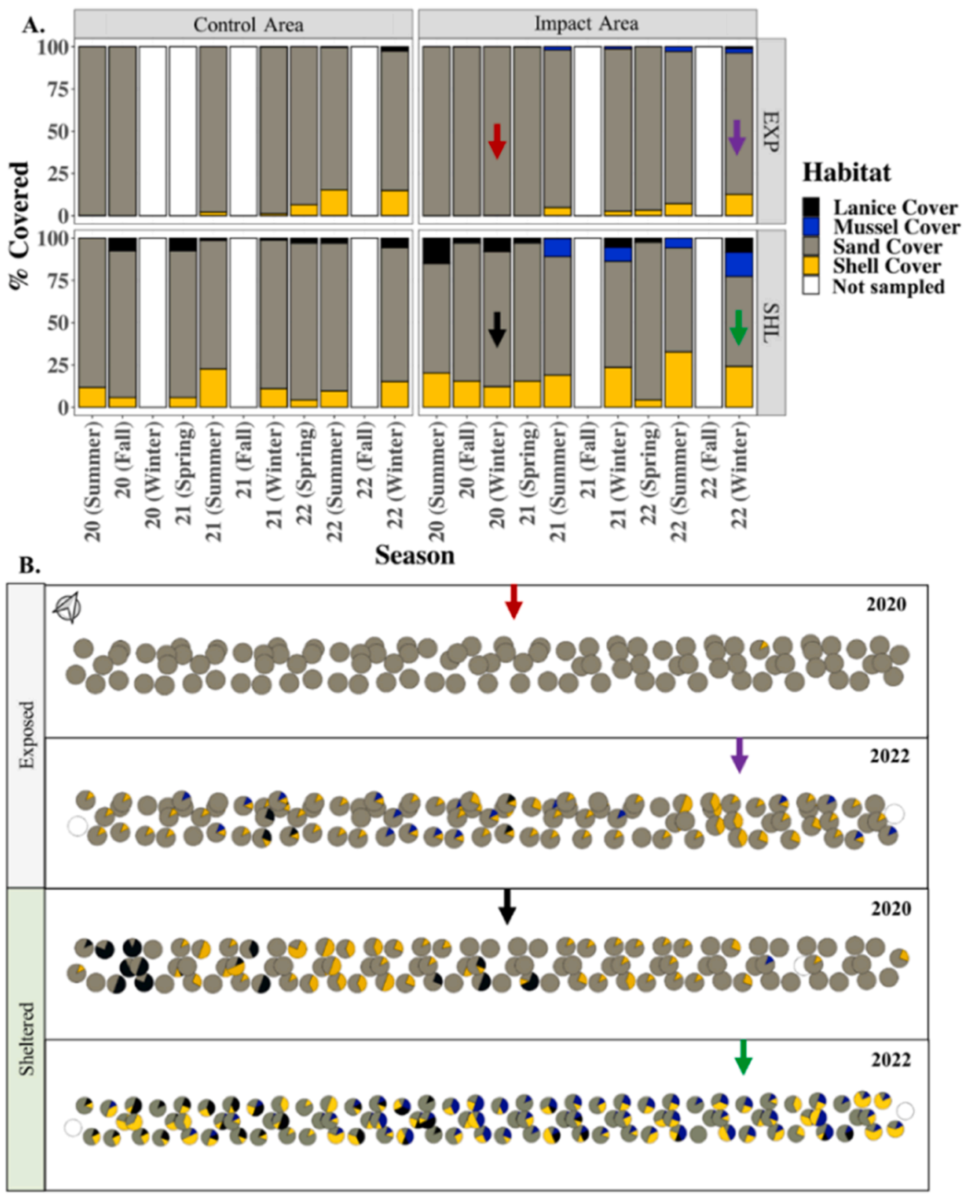

Fig. 2. Temporal variability in the mussel bed persistent for the control (CA) and impact (IA) areas under sheltered (SHL) and exposed (EXP) hydrodynamic conditions. A: Showing percentage of the seabed covered by different habitats (mussel, *Lanice*, shell, and sand). B: A visual representation of the seafloor along the mussel line transect (impact area) at the start (2020) and end (2022) of the project, derived from the analysis of video snapshots using the QGIS software. Here, the red and black arrows show the winter 2020 campaign for respectively the exposed and sheltered sites, while purple and green denote the 2022 winter campaign for respectively the exposed and sheltered sites.

years of the mussel line installation, it was observed that 22.7 % of the impact area in the sheltered site and 3.6 % in the exposed site had been colonized by either *L. conchilega* or mussel patches (Fig. 2: B).

3.1.2. Changes in seabed: erosion and accretion

Based on sediment dynamics, the difference map between 'before' (T0) and 'after' (T3) the installation of the experimental setups (Fig. 3) describes the effect of the interaction between mussel lines/mussel patches and hydrodynamic conditions on the erosion and accretion patterns of the study sites. Overall, the erosion and deposition of sediment were notably influenced by the hydrodynamic conditions (p = 0.04). The exposed site experienced the highest level of erosion as observed in the control, edge, and impact areas, while less erosion was observed at the control and edge areas of the sheltered site, with some accretion at the impact area in the immediate vicinity of the mussel line (Fig. 3). Map shows that area locally had an impact on the morphology of the seabed. An overall increase in sediment deposition of 2.3 ± 19.3 cm was observed in the sheltered site at the impact area (Table 2). However, these observed changes in erosion and deposition did not exhibit statistical significance across the control, edge, and impact areas ($p = 0.69$). Occurrence of accretion was also observed in the impact area of the exposed site, with a mean value of 5.8 ± 14.9 cm. Although this only occurred during the period between fall 2020 and 2021. Conversely, a significant erosion of 22.1 ± 11.7 cm was observed in the subsequent year, between 2021 and 2022 (Table 2). The erosion and accretion patterns of both the sheltered and exposed sites show more or less similar trends, with minimal erosion in the year 2020, relatively lower erosion or some deposition in 2021, and the highest erosion in 2022. This pattern can be linked to the common storm events in this area, as recorded by the Trapegeer buoy. The buoy data indicates a series of storm events (wave heights > 250 cm) in 2020 and the beginning of 2022 (Fig. 7).

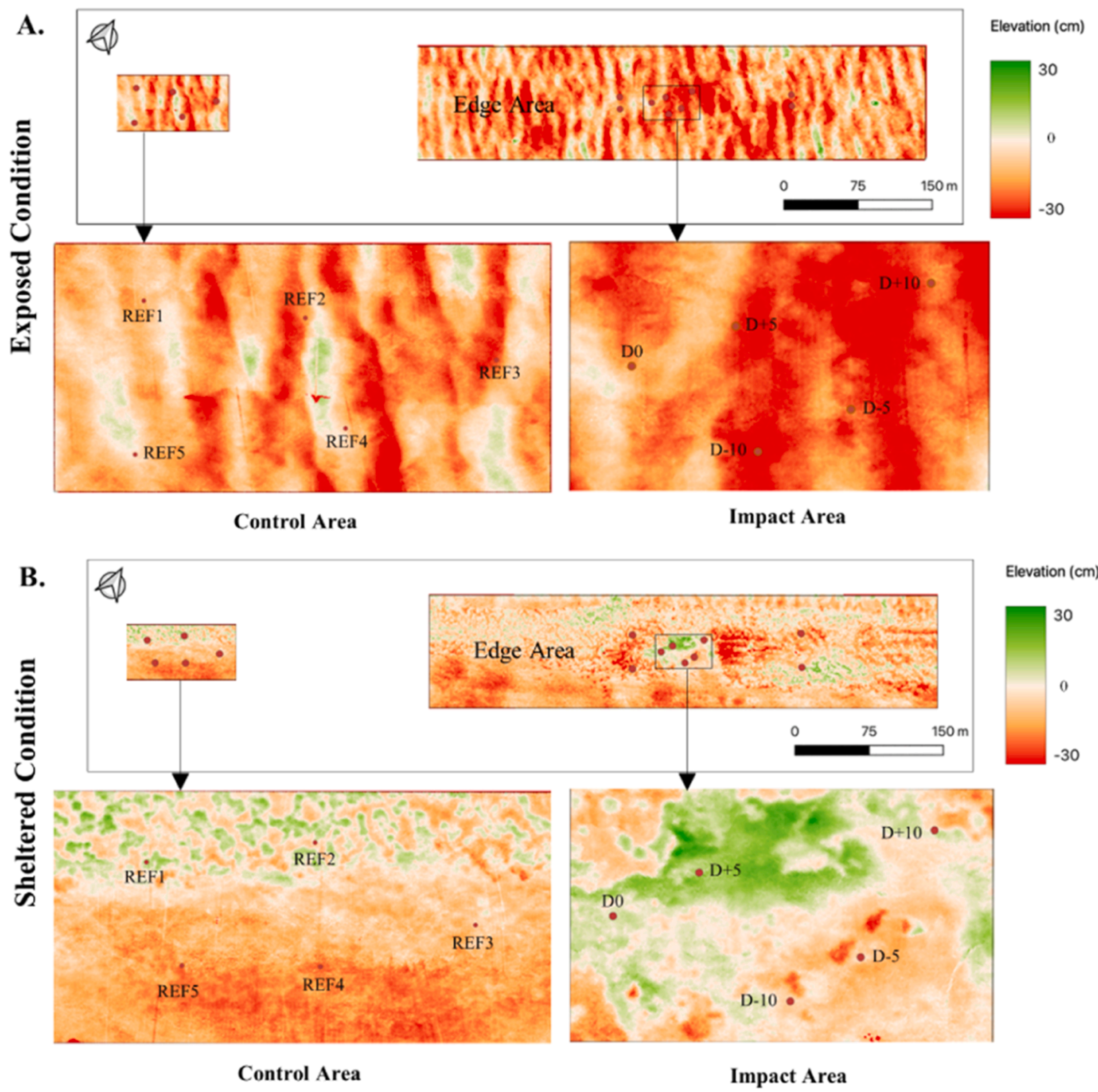

Fig. 3. Changes in elevation between T0 (2020_Summer) and T3 (2022_Fall). **A:** Exposed site; **B:** Sheltered site. Red and green colors indicate erosion and accretion, respectively. D0, D + 5, D - 5, D + 10, and D - 10 are the benthic sampling points for the impact area; REF1, REF2, REF3, REF4, and REF5 are the benthic sampling points for the control area.

Table 2
Temporal variability in the sediment erosion/accretion (cm) for the control (CA), edge (EA) and impact (IA) areas under sheltered (SHL) and exposed (EXP) hydrodynamic conditions (Mean ± SD).

Site	Year	CA	EA	IA	Duration
EXP	2020	1.5 ± 12.5	−0.8 ± 6.6	−4.6 ± 14.3	Summer '20 to Fall '20
	2021	−2.1 ± 13.6	−0.5.0 ± 13.0	5.8 ± 14.9	Fall '20 to Fall '21
	2022	−13.0 ± 13.9	−13.4 ± 13.0	−22.1 ± 11.7	Fall '21 to Fall '22
	Overall	**−13.6 ± 12.7**	**−19.2 ± 6.5**	**−20.9 ± 10.9**	Summer '20 to Fall '22
SHL	2020	−3.2 ± 17.2	0.04 ± 9.1	−0.6 ± 19.0	Summer '20 to Fall '20
	2021	2.4 ± 18.8	1.3 ± 8.5	7.9 ± 19.6	Fall '20 to Fall '21
	2022	−9.0 ± 22.5	−12.0 ± 7.1	−5 ± 19.9	Fall '21 to Fall '22
	Overall	**−9.9 ± 21.2**	**−10.8 ± 7.9**	**2.3 ± 19.3**	Summer '20 to Fall '22

Here, Overall shows the changes in sediment erosion/accretion between the start and end of the setup.

3.1.3. Sediment characteristics

The sediment composition in the study area predominantly consists of fine sand, medium sand, mud, and very fine sand, with a small amount of coarse, very coarse, and gravel pebbles (Appendix 4). Hydrodynamic condition (site) had significant effects on fine sand ($p = 0.0033$), very fine sand ($p < 0.001$), medium sand ($p < 0.001$), and mud ($p < 0.001$). A notable distinction is evident in the percentages of mud content, as the sheltered site exhibits a considerably higher mud content in comparison to the exposed site (Appendix 4). However, no major changes in sediment composition were observed between the control, edge, and impact areas within the combined site, except for very fine sand. A significant effect of area has been observed only on the percentage of very fine sand ($p = 0.033$), particularly between the control and impact areas ($p = 0.036$). Furthermore, when considering sheltered and exposed sites separately, no significant differences were found between the control, edge, and impact areas for any of the sediment properties, except for certain temporal variations. Highest percentage of very fine sand was observed under the sheltered edge area at T0 (11.26 ± 0.96) and lowest percentage under the exposed control area at T0 (0.802 ± 0.124) campaign. Over time, a temporal pattern emerged with a decrease in mud content from T0 to T3 in the sheltered site. The mud

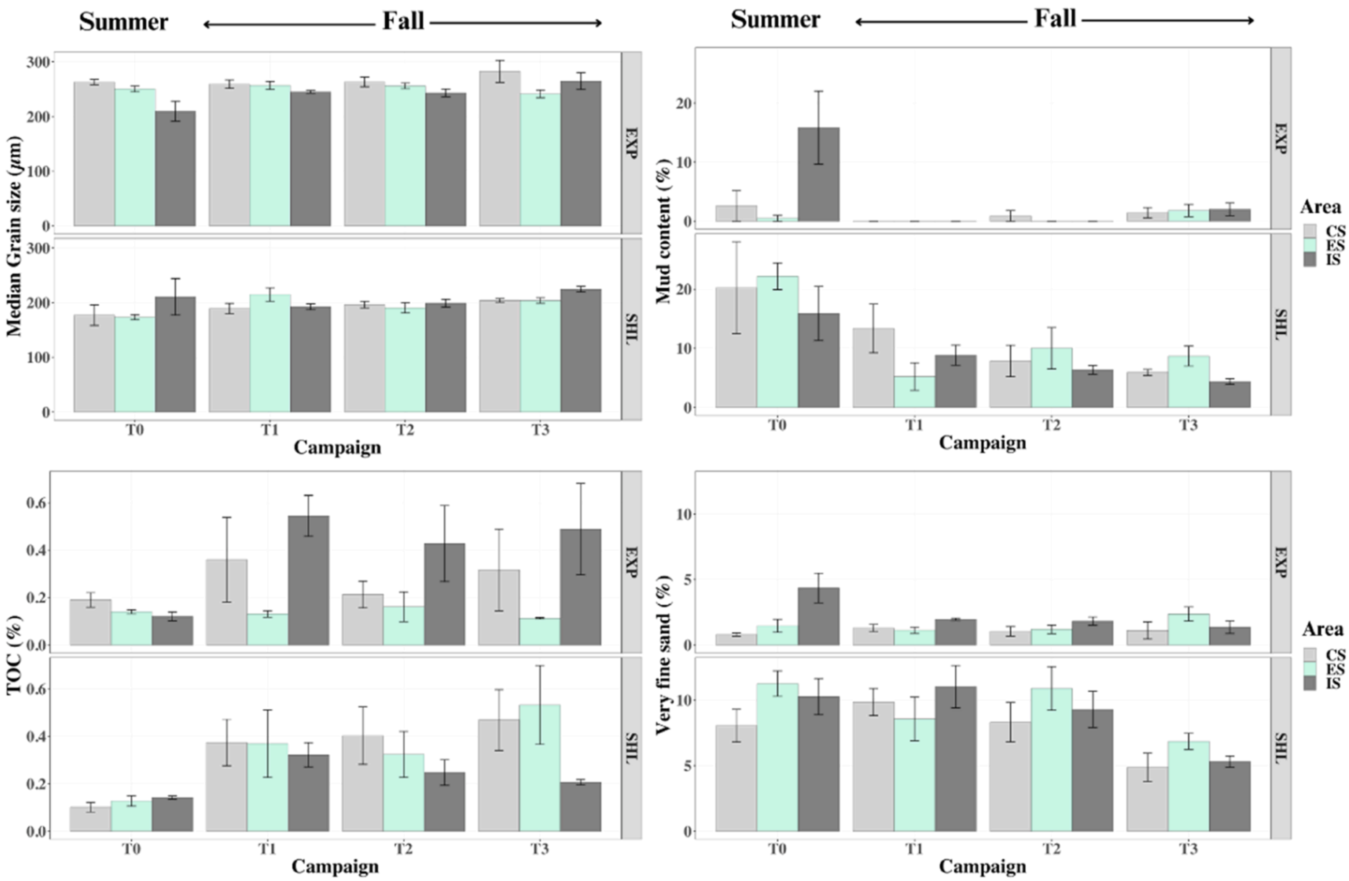

Fig. 4. Temporal variability in the sediment composition (median grain size, mud content, very fine sand) and total organic carbon (TOC) for the control (CS), edge (ES), and impact (IS) samples under sheltered (SHL) and exposed (EXP) hydrodynamic conditions.

content decreases from 20.251 ± 7.777 % to 5.920 ± 0.516 % in the control area, 22.192 ± 2.255 % to 8.684 ± 1.693 % in the edge area, and from 15.891 ± 4.562 % to 4.382 ± 0.487 % in the impact area. In contrast, the exposed site consistently had a low percentage of mud, and no mud was found during the T1 sampling campaign. The median grain size was significantly higher ($p < 0.001$) in the exposed site than in the sheltered site (Fig. 4). However, a minimal effect (0.109) was observed between the areas for the combined site, with a significant difference ($p = 0.003$) only noted between the control and impact areas of the exposed site, showing a comparatively higher value in the control area. The maximum value of the median grain size was observed in the control area of the exposed condition during T3 (282.64 ± 20.17 µm), while the minimum was found in the edge area of the sheltered condition during T0 (173.5 ± 4.49 µm). Additionally, the study examined the variation in total organic carbon (TOC) and found that the sheltered site had a higher amount of TOC compared to the exposed site ($p = 0.015$). Meanwhile, the area had minimal influence on the percentage of organic carbon ($p = 0.051$), with only significant differences ($p = 0.046$) between edge and control area. In the sheltered site, the difference in TOC between the control/edge areas and the impact area increased as time progressed, although there were no significant differences among the control, edge, and impact areas. However, in the exposed site, the impact area exhibited significantly higher TOC levels compared to the edge area ($p < 0.001$). The highest percentage of TOC was observed in the impact area during the T1 campaign (0.544 ± 0.086), while the lowest percentage was recorded in the edge area during the T3 campaign (0.112 ± 0.003).

3.2. Effect on macrobenthic communities

3.2.1. Density, biomass, and diversity

A total of 156 macrobenthic taxa were recorded throughout the four sampling campaigns. The three most dominant groups were Polychaeta (40.9 %), Oligochaeta (28.9 %), and Bivalvia (26.7 %); with a small amount of Amphipoda (1.8 %), Echinodermata (1 %), Decapoda, and Cumacea. Oligochaetes were found in the greatest abundance in the sheltered site and were almost absent in the exposed site (Fig. 5). Relative abundance of different taxonomic groups varied between the control, edge, and impact areas, with slightly more polychaeta in the edge and impact areas than in the control. Over time, there was a decrease in the abundance of Polychaeta concurrent with an increase in Bivalvia both in the exposed and sheltered sites.

Differences in the density, biomass, species richness, Simpson and Shannon index were observed across the two sites (respectively, $p < 0.001$, $p < 0.001$, $p < 0.001$, $p = 0.001$, and $p < 0.001$). All the indices were found to be higher in the sheltered site compared to the exposed site. Both Shannon (Appendix 5) and Simpson showed almost similar diversity pattern. Conversely, the 'area' had no significant effect ($p > 0.05$) on any of the indices, including density, biomass, and diversity. However, the interaction between 'area' and 'site' did affect the Shannon index ($p = 0.015$), although no significant differences were observed between control, edge, and impact areas within sheltered and exposed sites. In general, both sheltered and exposed sites did not exhibit significant differences between the control, edge, and impact areas for any of the indices, except for certain temporal variations. The highest density was reported in the sheltered edge area at T0 (26,032.5 ± 9179.66 indv.m-2), while lowest was reported in the exposed control area at T1 (774.0 ± 433.51 indv.m-2). The biomass had its lowest and

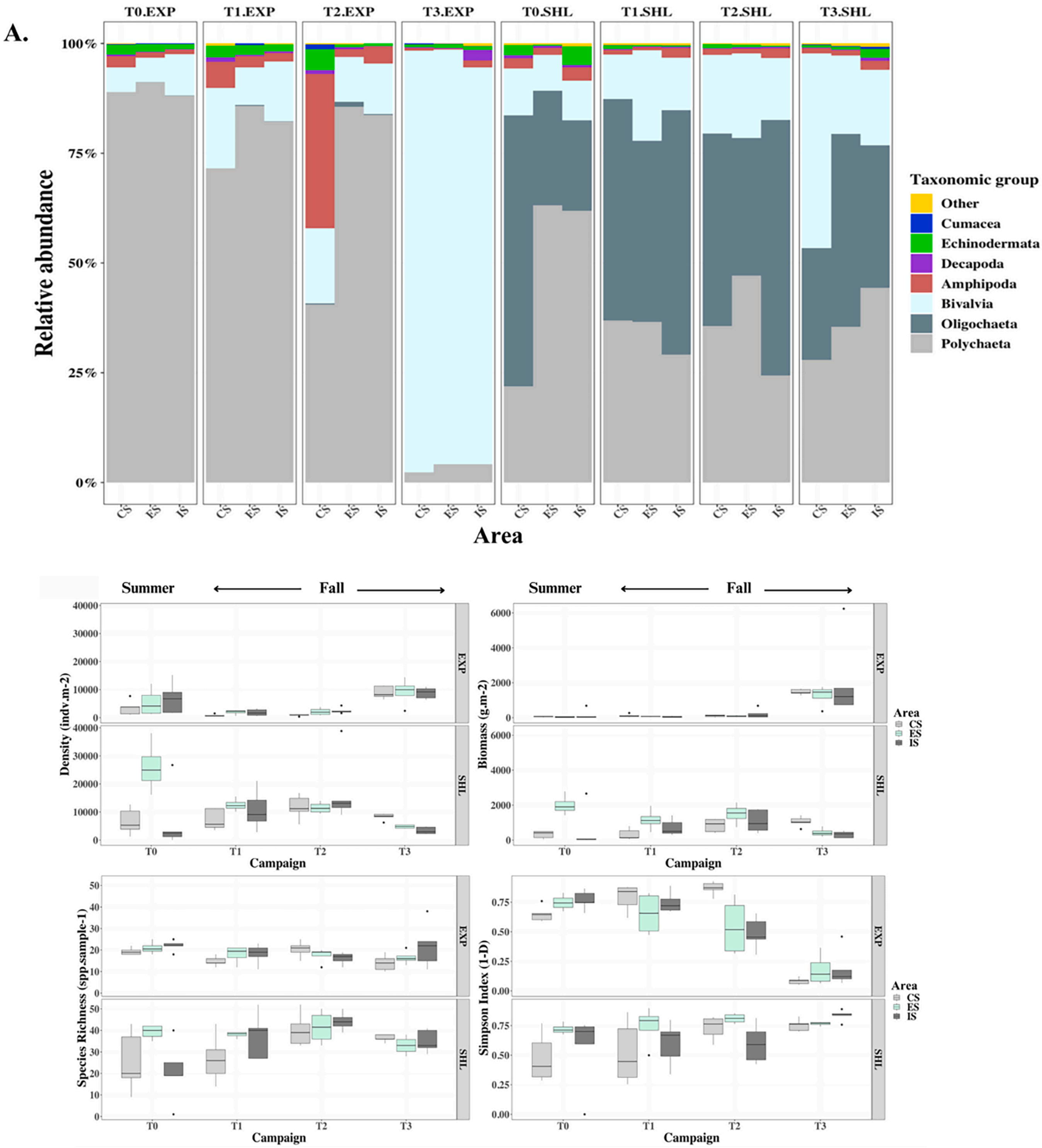

Fig. 5. A: Relative abundance of different taxa. B: Temporal variability in the macrobenthos Species Richness (spp.sample^{-1}), Density (inv.m^{-2}), Biomass (g.m^{-2}), and Simpson Index (1-D) for the control (CS), edge (ES) and impact (IS) samples under sheltered (SHL) and exposed (EXP) hydrodynamic conditions.

highest values in the exposed site during the T0 at the edge area (41.75 ± 28.36) and during the T3 at the impact area (2120.91 ± 2336.44 gm. m-2), respectively. Species richness was slightly higher in the impact and edge areas than in the control area, with its highest values found during T2 in the sheltered impact area (44.20 ± 4.15 spp.sample-1) and lowest value found during T1 in the exposed control area (14 ± 3.68 spp.sample-1). The sheltered site exhibited temporal variability, as indicated by an increase in species richness from T0 to T2, followed by a slight decrease at T3 (Fig. 5). Simpson index had its lowest and highest values in the exposed control area, respectively, at T3 (0.083 ± 0.028) and T2 (0.869 ± 0.057), and a temporal pattern can be observed, with an increasing trend in the sheltered site and a decreasing trend in the exposed site.

3.2.2. Community composition

nMDS showed clear differences between exposed and sheltered conditions as well as T0, T1, T2, and T3 campaigns (Fig. 6). However, no clear differences between control, edge, and impact areas were

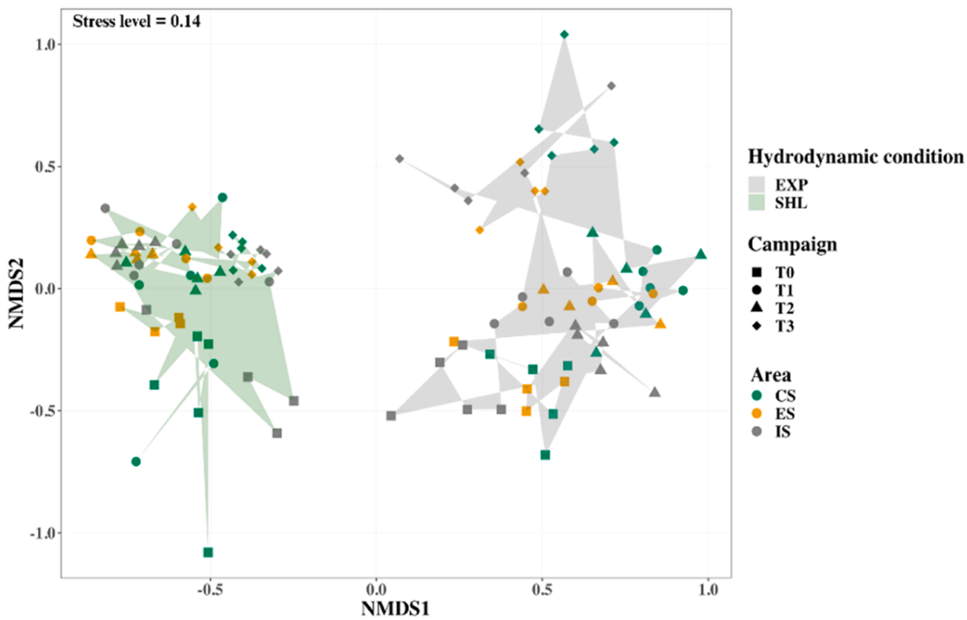

Fig. 6. Non-metric multidimensional scaling (NMDS) of the macrobenthos community shows the differences between control (CS), edge (ES), and impact (IS) samples across T0, T1, T2, and T3 campaigns under sheltered (SHL) and exposed (EXP) hydrodynamic conditions. The analyses were performed using abundance data of species and based on Bray-Curtis dissimilarity.

Table 3
The pairwise differences between control (CA), edge (EA), and impact (IA) areas (PERMANOVA).

Site	Pairs	F.Model	R^2	*p* value
Combined (SHL and EXP)	CA vs EA	1. 212,991	0.01703328	0.2611
	CA vs IA	1. 146,014	0.01466504	0.2935
	EA vs IA	0. 533,415	0.00767135	0.8078
EXP	CA vs EA	1.929360	0.05369870	0.0841
	CA vs IA	2.586085	0.06371851	0.0323
	EA vs IA	0.268388	0.00783195	0.9517
SHL	CA vs EA	2.074001	0.05749296	0.0487
	CA vs IA	1.918192	0.04928779	0.0712
	EA vs IA	1.793534	0.05154790	0.1022

Table 4
Top five contributing taxa that best differentiate between exposed (EXP) and sheltered (SHL) hydrodynamic conditions, as determined by SIMPER analysis.

Top 5 contributing taxa	Av. abundances		Contribution (%)
	Sheltered	Exposed	
Oligochaeta	61.21	0.76	14.5
Ensis leei	16.21	22.42	7.4
Cirratulidae	24.57	0.36	5.5
Magelona johnstoni	5.02	19.41	4.1
Lanice conchilega	20.68	1.14	3.9

observed. The results from the PERMANOVA test indicated that the community composition was significantly influenced by site (R^2 = 0.288, $p = 0.001$), area ($R^2 = 0.02$, $p = 0.001$), and sampling campaign ($R^2 = 0.2$, $p = 0.001$). Additionally, two of the interaction terms, site: sampling campaign ($R^2 = 0.133$, $p = 0.001$) and site: area ($R^2 = 0.024$, $p = 0.001$), were also found to have a significant effect on the macrobenthos community. The hydrodynamic conditions (site) contributed 28 % of the variance according to the R^2 values, followed by the sampling campaign at 20 %. There were no statistically significant differences in community composition between the control and edge ($p = 0.261$), the control and impact ($p = 0.294$), or the edge and impact areas ($p = 0.808$) (Table 3) within the combined site. However, differences between control and edge areas ($p = 0.049$) of sheltered site and the control and impact areas ($p = 0.032$) of exposed site were statistically significant.

The SIMPER analysis revealed that Oligochaeta (14.5 %), *Ensis leei* (7.4 %), Cirratulidae (5.5 %), *Magelona johnstoni* (4.1 %), and *Lanice conchilega* (3.9 %) were the top characteristic taxa explaining the difference in benthic communities between the sites (Table 4). Moreover, the abundance of the Oligochaeta, Cirratulidae, and *L. conchilega* was higher in the sheltered condition; on the other hand, *E. leei* and *M. johnstoni* were most abundant in the exposed condition.

3.3. Ecology and environmental drivers

The mean values of the environmental variables for control, edge, and impact areas between two sites are displayed in a table (Appendix 6). To explore which environmental drivers are linked to differences in benthic community characteristics, a principal component analysis (PCA) was performed (Appendix 7). The first two principal component axes described 49.15 % of the variation in the data and thus provided insights into the dominant correlations. The first axis, which accounted for 33.43 % of the total variability, was primarily linked to variations in sediment particle size (mud, very fine sand, medium sand, grain size, fine sand, and coarse), erosion/deposition, crab density, shell cover, *L. conchilega* cover, and elevation. These environmental parameters exhibited distinct differences between the exposed site (EXP_CS, EXP_ES, and EXP_IS) and the sheltered site (SHL_CS, SHL_ES, and SHL_IS). The second axis, explaining 15.72 % of the total variability, was found to be linked to changes in TOC, starfish density, mussel cover, very coarse sand, and gravel pebbles. The presence of mussel, *L. conchilega*, shell cover, gravel/pebbles, and very coarse sand distinguished SHL_CS from SHL_ES and SHL_IS, particularly during the T3 campaigns.

4. Discussion

4.1. Effect of hydrodynamic conditions on seabed dynamics and benthic communities

Central to CB 2.0 project is the implementation of a comprehensive monitoring program to assess the ecological and morphological evolution of biogenic reefs and seafloor benthic communities at two distinct sites under the action of different hydrodynamic conditions. These sites

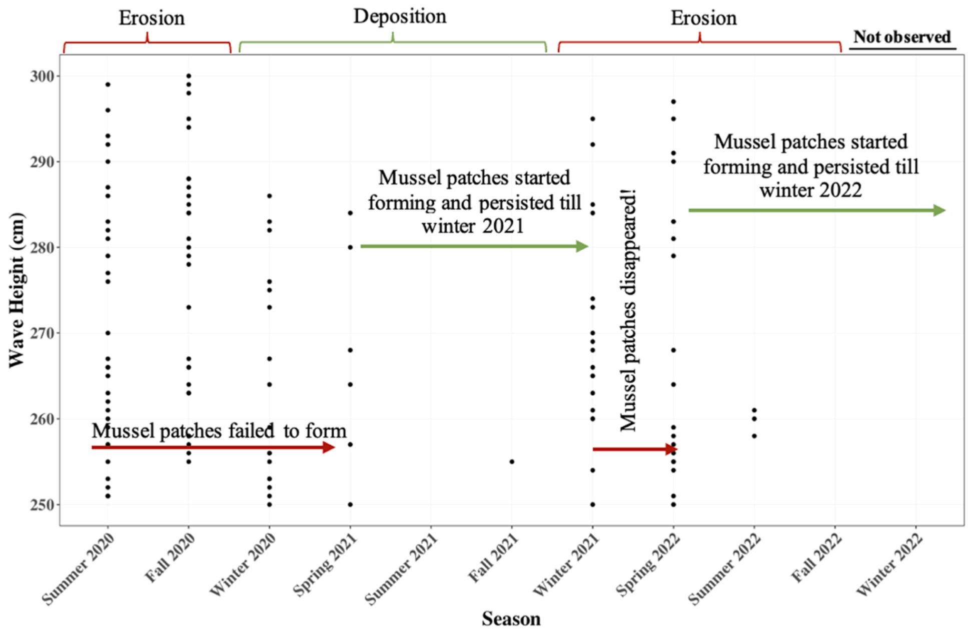

Fig. 7. Relationship between significant wave height (from Trapegeer buoy) and its connection to the formation of mussel patches and seabed erosion for sheltered and exposed sites. Each dot on the graph represents a single wave that occurred during a specific season, displaying its corresponding height. A season with a higher number of dots indicates a greater occurrence of storm events. Here, significant wave height exceeding 250 cm occurs rarely at the location of the Trapegeer buoy (Meetnet Vlaamse Banken) and represents the 99.6th percentile. An overview of erosion/deposition patterns is available in Table 2, and mussel formation is shown in Figure 2.

in front of the coastal community of De Panne (Belgium) include a sheltered site on the leeward side of the Trapegeer sand bank and an exposed site facing more intense waves and current activity from the open sea. The variance in location and subjection to slightly different hydrodynamic conditions is expected to result in differences in seabed morphology, sediment characteristics, and macrobenthic communities.

In our study, seabed morphology showed complex sediment dynamics mostly influenced by strong seasonal waves and currents. In general, sediment erosion was significantly higher at the exposed site compared to the sheltered site, conforming to the more energetic hydrodynamic conditions of the exposed site. Average sediment erosion at the sheltered site was about -10 cm, with some deposition occurring in the mussel impact area. On the other hand, the exposed site encountered erosion of up to -20.9 cm between 2020 and 2022. This pattern is commonly observed, as the exposed site is regularly subjected to intense hydrodynamic conditions, resulting in substantial seabed erosion during storm events. A temporal pattern of erosion/accretion emerges, which can also be attributed to the local hydrodynamic conditions, as evidenced by the increased erosion observed during the years 2020 (Summer 20 to Fall 20) and 2022 (Fall 21 to Fall 22), coinciding with a series of storm events (Fig. 7). This is supported by Kriebel and Dean (1993) [40], who stated that the key forces influencing morphological changes, including erosion and accretion, can be described by various factors such as storm surge, storm duration, and wave (height, energy, and direction). The higher erosion rate, as observed at the exposed site, shall alter substrate sediment characteristics, which in turn can shape the composition of benthic communities.

Sediment properties differ between the two sites, with higher amounts of organic carbon, mud, and very fine sand in the sheltered site compared to the exposed site. This finding was consistent with expectations, as higher energetic hydrodynamic conditions hinder the settling of fine sand particles, resulting in an increased abundance of coarse sediment and a larger median grain size [41,42]. Also, a clear temporal pattern can be observed in the mud content of the sheltered site, indicating a decrease of approximately 10 % between 2020 and 2022. The higher mud content observed initially, particularly in the T0 sample collected during summer, can be linked to two possible events: (1) the influx of organic matter into the sediment resulting from the spring phytoplankton bloom [43,44] and/or (2) the fact that the sheltered site was slightly disturbed shortly before sampling by removing the blocks and bags on the seafloor from the pilot project. Apart from T0, the overall mud content aligns with the findings of previous studies [33,36] conducted in the same region.

As sediment composition differs between sites, this should be reflected in the benthic community structure as well, due to their interdependence [36]. The sheltered site exhibits higher density, biomass, richness, and diversity compared to the exposed site. This finding aligns with previous studies indicating that lower-flow environments or finer sand habitats exhibit higher levels of density, biomass, species richness, and diversity [12,36,45-47]. Community composition based on PERMANOVA also showed that the factor site (differing in hydrodynamic condition) was contributing the most to the variance (28 %) between stations in the sheltered and exposed sites. The taxa Oligochaete, *E. leei*, Cirratulidae, *M. johnstoni*, and *L. conchilega* predominantly explained the compositional differences. Among these, Oligochaete, Cirratulidae, and *L. conchilega* were primarily found in sheltered sites, as they exhibit a preference for living in shallow, muddy, fine sand bottoms [36,48,49].

4.2. Mussel occurrence on the seabed

Mussel, as a reef-building organism, has the ability to impact local hydrodynamics and seabed dynamics through its complex three-dimensional formations on the sediment surface by enhancing near-bed turbulence and decreasing the velocity of water currents [10,15,16,50]. However, their effectiveness is subject to various factors, including recruitment pattern, reef size, persistence, predation, and the specific hydrodynamic conditions in which they are established [30,51-53].

The seabed in the experimental area was predominantly composed of sand, with varying amounts of shells, *L. conchilega* presence, and mussel patches that exhibited fluctuations over time. Using a customized dropper line and longline system, it was possible to attract mussel larvae and establish their presence on the seafloor in a shallow environment of bare sandy sediment. The size of the mussel bed underneath the installation depends on the dropper line material, submersion time of dropper lines, and hydrodynamics, as those factors determine the number of mussels available on the installation itself [33]. However, challenges in sustaining the mussel bed year-round were encountered. Meanwhile, findings from a study conducted in the offshore waters of the UK revealed a gradual expansion of mussel coverage over time, suggesting potential for the formation of mussel beds using long line mussel aquaculture on the offshore seabed [54]. Observations from CB 2.0 revealed that mussel patches were primarily present during late summer and early fall but disappeared in subsequent seasons, consistent with the findings of CB 1.0 [33]. In CB 1.0, dedicated seasonal monitoring was lacking, so the complex spatiotemporal and seasonal patterns were more evident in this study (CB 2.0), with the absence of mussels at the beginning of the project in 2020. This absence could potentially be attributed to a delayed experimental setup due to COVID-19 pandemic-related restrictions, resulting in missing the major recruitment of mussel spat. Additional concurrent storm events were observed in summer 2020, which is not typical (Fig. 7). However, starting in the summer of 2021, mussel colonization began on the seabed and persisted throughout the winter in the sheltered area before disappearing in the following spring of 2022. Mussel colonization resumed again during the summer of 2022 and reached its peak during the winter of the same year. In the exposed region, a similar seasonal and temporal pattern was observed, with a considerably lower number of mussel patches than in the sheltered site. This observation led to the hypothesis that it is possible to establish temporary mussel patches in both environments, but possibly longer time is needed to achieve the biogenic reef goals in the case of more energetic hydrodynamic conditions. Notably, energetic hydrodynamic conditions, including extreme current and wave loading, have been considered one of the main limiting factors in the formation and persistence of mussel beds [26,55-57]. The seasonal reduction or disappearance of mussel beds can be attributed to the occurrence of multiple storm events (defined as moments with waves > 250 cm) reported between winter 2021 and spring 2022 (Fig. 7), consistent with the observations in intertidal mussel beds of the Wadden Sea following cold and stormy winters [56]. Another well-known factor that prevents mussel beds from expanding is predation. It is well documented that the presence of common starfish, crabs, and sea urchins in mussel beds has been shown to be detrimental to the survival of mussels [30,33,58,59]. Throughout the study period, common starfish (*Asterias* spp.) and crabs (*Liocarcinus* spp. and *Necora* spp.) were consistently observed on the seabed, with starfish being the dominant predator. The sheltered site exhibited a higher population of starfish, while the exposed site showed limited numbers of both crabs and starfish. Within the sheltered site, a temporal pattern of increasing starfish density, peaking at 25 individuals/m^2 in winter 2021, coinciding with mussel reef formation on the seabed, was consistent with the findings of the pilot project conducted by Goedefroo et al. (2022) [33]. However, this trend did not align with the increased mussel occurrence observed in the following year (Winter 2022), when the seabed hosted the highest abundance of mussel patches. Research indicates that starfish typically consume one mussel per day (depending on the size of the mussel and starfish), while shore crabs are known to consume 23 mussel seeds daily [60]. These findings highlight the challenges and complexities associated with establishing and maintaining mussel beds in high-energy environments. Further research and management strategies are warranted to better understand and address these factors in order to support the growth and persistence of mussel populations.

However, *L. conchilega*, another biogenic aggregation-forming species, was observed in both the control and impact areas, with a comparatively higher amount in the sheltered site than the exposed. The tube structures may serve as suitable substrates for mussel settlement by creating complex burrow structures in the sediment, making them a valuable steppingstone in the process of mussel bed formation [26,61]. In this study, no data is available to prove this, but their occurrence has probably played a role in the differences observed over time and between sites in the benthic community characteristics. This widely distributed polychaeta is recognized as a biodiversity hotspot within the inter and subtidal soft sediments of the North Sea and also has the potential to stabilize the sediment [62].

4.3. Effect of mussel patches on seabed dynamics and benthic communities

Biogenic reefs have the potential to safeguard coastlines against erosion, waves, and flooding by attenuating wave energy and stabilizing sediment [5-8]. Mussels, in particular, form a dense bed by attaching themselves to one another using robust threads and anchoring to the substratum, which effectively traps sediment and enhances the overall stability of the seabed [14,16]. Changes in erosion and deposition at the exposed site exhibited no considerable difference between the impact, control, and edge areas. However, in the sheltered site, a more pronounced sediment accretion (up to +2.3 cm) in the impact area compared to the control (up to −9.9 cm) and edge (up to −10.8 cm) areas was observed, but it was not statistically significant. Except when the highest presence of mussel beds/patches and *L. conchilega* was observed on the seabed within the sheltered site, a relatively lower amount of sediment erosion was recorded. Linking this to the morphological effect of the mussel patches is still uncertain due to the low abundance of mussel patches. It can also not be distinguished from the potential effect of the presence of *L. conchilega* on the seabed dynamics, as it is known to facilitate sedimentation when present in high densities [49]. Nevertheless, as the mussel patches were small and temporary, more long-lasting monitoring is needed to confirm.

Changes in sediment (erosion/deposition) and the presence of mussel beds or suspended mussel cultures can result in alterations to organic matter and fine sediment at a local scale [12,52,63]. Although sediment erosion/deposition were irregular and the presence of mussel patches was not persistent throughout the study period, a notable impact of the mussel was observed on the concentration of very fine sand. The amount of very fine sand was significantly higher in the mussel impact area, both at the sheltered and exposed sites. However, no significant influence of the area was detected on the mud content and total organic carbon. Total organic carbon varied inconsistently across areas and sites, with higher concentrations in the exposed site's impact area and lower concentrations in the sheltered impact area with more mussel presence. This finding contradicts the expectation that seabed in or around mussel beds and mussel cultivation installations would have higher rates of carbon fixation and facilitate increased carbon burial compared to the surrounding sediments [23,64]. Also, *L. conchilega,* as a biogenic species, has the potential to influence sedimentary processes, thereby exerting an impact on the decomposition of organic matter and the production of nutrients in the surrounding environment [65]. However, in the experiment area, the presence of *L. conchilega* was consistent across different areas and higher in the sheltered site. Therefore, the role of *L. conchilega* and mussels alone may not explain the absence of organic matter effects. This lack of effect could potentially be attributed to the fact that the study sites are located in a shallow, dynamic coastal system, as currents might play an important role by moving away biodeposits [65] from the impact area, therefore masking a possible influence of the mussel presence. On the other side, an abundance of benthic life was found at the study sites, so how this contributes to the consumption of organic matter should be investigated as well.

Understanding the influence of biogenic habitats on surrounding benthic fauna is essential for effectively conserving marine ecosystems [66]. While mussels are recognized for forming dense aggregations and providing habitat for a wide range of macroinvertebrate communities [67], the impact of mussels on the community varies depending on environmental settings, traits, and the structure of the habitat itself [10, 68-70]. The findings of this study indicate that the mussel beds and suspended mussel aquaculture system didn't exhibit any effects on benthic community structure at the study sites. No significant difference can be observed between control and impact for any of the indices, including density, biomass, richness, and diversity. A study on global habitat engineers in coastal sediment found that mussel beds were not always associated with higher species richness and diversity compared to ambient sediments without mussels, and their effects on associated species were site-specific [10]. A similar observation was made in the pilot project of this study, where no significant impact of the mussel installation area on the community structure was found, except for lower diversity indices in the impact area [33]. This lack of effect can probably be mainly attributed to the insufficient density and persistence [67] of mussel patches, which limited their ability to exert a substantial influence on the sediment characteristics and seabed morphology, thus resulting in the observed changes in the community. Moreover, the substantial occurrence of *L. conchilega* in our study area may contribute to reducing the variation in community structure between the impact and control areas, potentially overshadowing some potential influence of mussel patches on the macrobenthic community.

4.4. Temporal pattern in macrobenthic community characteristics

Although the temporal variability was not statistically analyzed, noticeable changes in community structures were observed between the T0 and T3 campaigns. Specifically, an increase in species diversity was observed in the sheltered site, while a decrease was observed in the exposed site. Additionally, the relative abundance of different taxa exhibited some temporal patterns, with a decrease in the abundance of Polychaeta concurrent with an increase in Bivalvia. During the last (T3) campaign, non-indigenous species *E. leii* emerged as the dominant Bivalvia in the exposed site (Appendix 8) in an area characterized by low mud and higher hydrodynamic conditions. Despite a notable increase in the percentage of seabed covered by mussels and *L. conchilega* observed at that time in the exposed site, the recruitment of the more abundant *E. leii* couldn't be explained solely by this, as no significant difference in abundance was observed between the control and impact areas. Consequently, the rapid burrowing ability of this organism may account for its success in thriving within the dynamic and exposed environment of the North Sea [71,72]. Furthermore, the lack of persistence in the development of mussel patches suggests that the temporal changes observed are more likely associated with broader environmental shifts than being directly linked to the impact of the biogenic reef species.

4.5. Limitations and recommendations

NbS, a globally employed strategy to address the impacts of climate change, necessitates a dedicated monitoring program for tracking the implementation of NbS tools, especially for adaptation and mitigation of coastal pressures like erosion and biodiversity loss. This study's strength lies in its demonstration of an approach to monitoring seabed morphology and benthic communities, despite the absence of a successful NbS solution using mussels in the studied sites.

For an effective implementation of this engineering approach in a highly dynamic environment, various factors need to be taken into account. External pressures, including hydrodynamic conditions (e.g., waves and currents) and predation by crabs and starfish, can present obstacles to the establishment of mussel patches. To mitigate the factors leading to mussel population depletion on the seafloor, it is essential to cultivate a sufficient abundance of mussels using the employed aquaculture setup until a self-sustaining mussel seabed ecosystem is established. In our study, the mussel abundance on the installation varied over the season-years (highest values in autumn/winter 2021 and 2022) and depended on the type of rope material used at the aquaculture setup [73]. Therefore, future research should prioritize addressing these pressures and implementing mitigation measures to ensure the establishment of dense and longer-lasting mussel beds. This study affirms the potential of developing mussel beds in subtidal areas to potentially reduce erosion and provide ecosystem benefits. However, to achieve successful and effective mussel-based eco-engineering in challenging hydrodynamic conditions, it is crucial to integrate it within a broader ecological framework. Strategically placing mussel beds in proximity to other ecosystems (e.g., marshes, seagrasses, *L. conchilega* reefs, oyster reefs) can be used to enhance overall ecological and morphological resilience [5,12,20,74].

Finally, a well-structured monitoring program incorporating various techniques is essential for a comprehensive understanding of possible changes due to adaptive solutions. Each technique offers a unique perspective, enabling us to capture diverse aspects of ecological dynamics, stretching from species diversity to environmental parameters. Employing a multidimensional approach not only enhances the accuracy and reliability of data but also allows for cross-validation, ensuring that recorded biodiversity closely reflects the reef's actual diversity, e.g., epifauna counts combined with macrobenthic community data. By combining classic techniques such as Van Veen grabs with other monitoring techniques, we gain a more detailed understanding of the reef's habitat and the interactions between the benthic organisms and the surrounding environment. Moreover, it provides a nuanced understanding of complex ecological interactions by capturing different facets of the ecosystem, e.g., exhibited predation, through video surveys. Relying on a single technique may lead to missing critical information, while a multifaceted approach through the integration of various monitoring methods reduces the risk of overlooking critical factors, e.g., the influences of hydrodynamic and sedimentological changes. In regard to the video survey techniques for seabed characterization by diving, it gives a very detailed look, but the aerial coverage is very low (only under the dropper line, 2 m on a 50 m stretch; installation area covering Xm^2). One major lesson learned is that such detailed information can only be reached with the expansion of the sample size and the implementation of consistent sampling campaigns based on various monitoring tools within a specific season or at regular intervals throughout the year. This should provide a better understanding of the interactions within the coastal ecosystem, facilitating informed decision-making for management, and the successful implementation of NbS. In essence, a comprehensive monitoring program ensures that interventions are evidence-based, adaptive, and ultimately effective in safeguarding our coastal habitat.

5. Conclusions

This research provides novel insights into the role of *Mytilus edulis* as NbS in different hydrodynamic conditions, employing a wide array of monitoring techniques. The study successfully demonstrated the establishment of mussel patches on the seabed using traditional aquaculture techniques in both sheltered and exposed sites with varying hydrodynamic conditions. However, maintaining their sustainability year-round and establishing a self-sustaining mussel bed proved challenging due to challenging environmental conditions (e.g., storm events) and predation. While mussel beds showed limited effects, hydrodynamic conditions strongly influenced both the seabed dynamics and macrobenthic communities. Achieving a self-sustaining mussel bed necessitates further research and the implementation of effective reef management strategies. These efforts should emphasize a comprehensive understanding of and solutions for the limiting factors, highlighting the critical need for advanced monitoring techniques.

Data availability

Data will be made available on request.

NBS impacts and implications

The Coastbusters project initiative leads the way in establishing mussel beds using an aquaculture long line system, representing Nature-based Solutions (NbS) designed to tackle environmental, economic, and social challenges. From an environmental perspective, the initiative enhances biodiversity and stabilizes seabeds, serving as a natural defense against coastal erosion. On a social level, it ignites scientific interest and community involvement, nurturing awareness and a profound connection with coastal surroundings. In economic terms, it opens avenues in aquaculture, tourism, and research, all while diminishing the need for expensive artificial defenses. In summary, Coastbusters stands out as a comprehensive and sustainable NbS solution, reinforcing coastlines and enriching marine ecosystems.

CRediT authorship contribution statement

Mazharul Islam: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing, Visualization. **Alexia Semeraro:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing, Supervision. **Kobus Langedock:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Ine Moulaert:** Conceptualization, Writing – review & editing. **Vicky Stratigaki:** Funding acquisition, Writing – review & editing. **Tomas Sterckx:** Funding acquisition. **Gert Van Hoey:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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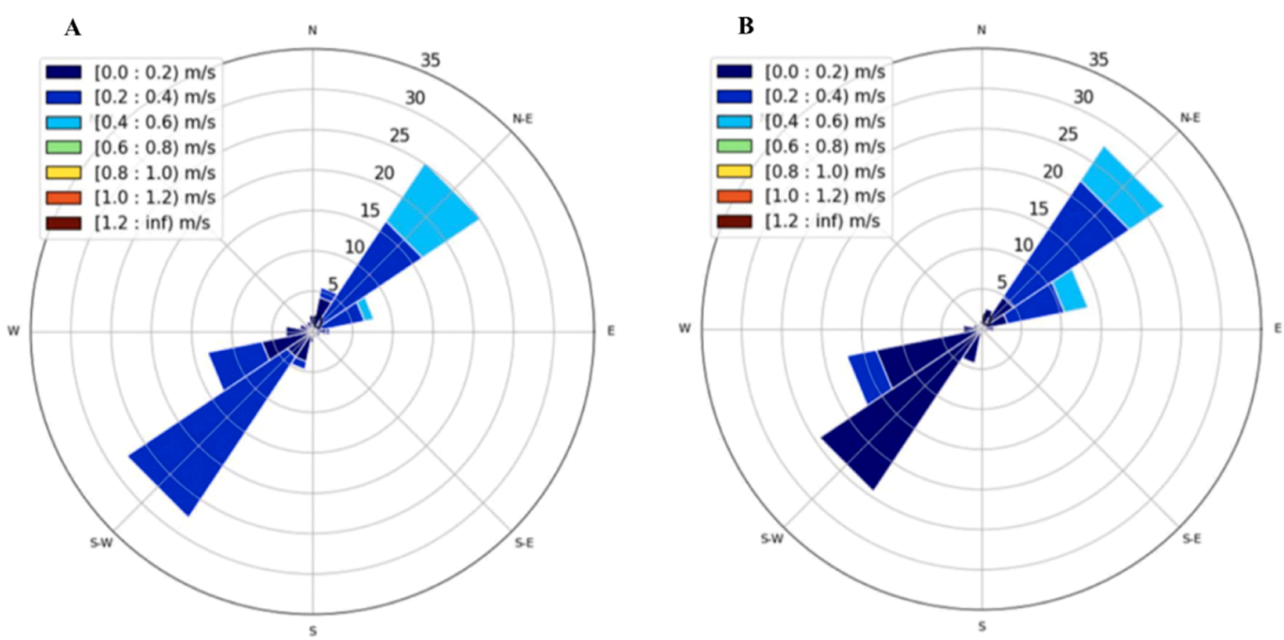
Appendix



Appendix 1. Bottom currents in exposed (A) and sheltered (B) sites of the study area. Here, concentric circles depict the percentage of time currents flow in a particular direction, with vector colors indicating magnitude. Both sites exhibit the typical current pattern of the Belgian coast: north-eastward currents prevail for approximately half the time during rising tides, shifting to south-westward flow for the remainder as water levels decrease. Tidal current information was collected and shown using three years of data (01/06/2017 - 01/06/2020) from the Royal Belgian Institute of Natural Science's operational model [75].

Appendix 2

Decision table for the sediment and class variables. Conditions are shown in bold as a percentage of quadrats. That class was chosen when those conditions (in bold) were met. Visibility accepted = less than 4/8 quadrats of invisible elements. Unknown denotes the impossibility of identifying that feature on the seafloor [76].

Class	Sand	Shells	*L. conchilega*	Mussels	Invisibility
Unknown (UN)	Unknown-50 %	Unknown	Unknown	Unknown	**>/=4/8**
Bare sand (BS)	**>=6/8**	Doesn't matter	None	None	Acceptable
Bare sand with shells (BSS)	**<6/8**	**<6/8**	None	None	Acceptable
Shell dominated sand (SDS)	Doesn't matter	**>=6/8**	None	None	Acceptable
Lanice sparse (LS)	Doesn't matter	Doesn't matter	**<=2/8**	None	Acceptable
Lanice patchy (LP)	Doesn't matter	Doesn't matter	**2/8->6/8**	None	Acceptable
Lanice dominated (LD)	Doesn't matter	Doesn't matter	**>=6/8**	None	Acceptable
Mussel sparse (MS)	Doesn't matter	Doesn't matter	Doesn't matter	**<=2/8**	Acceptable
Mussel patchy (MP)	Doesn't matter	Doesn't matter	Doesn't matter	**2/8->6/8**	Acceptable
Mussel dense bed (MD)	Doesn't matter	Doesn't matter	Doesn't matter	**>=6/8**	Acceptable

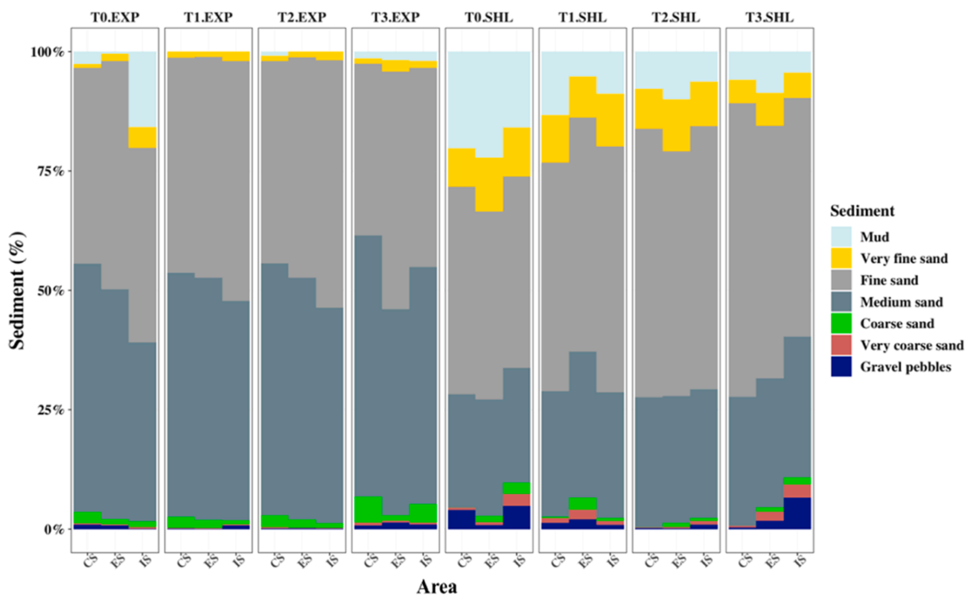
Appendix 3

Output of statistical analysis for the control (CA), edge (EA), and impact (IA) areas under sheltered (SHL) and exposed (EXP) hydrodynamic conditions.

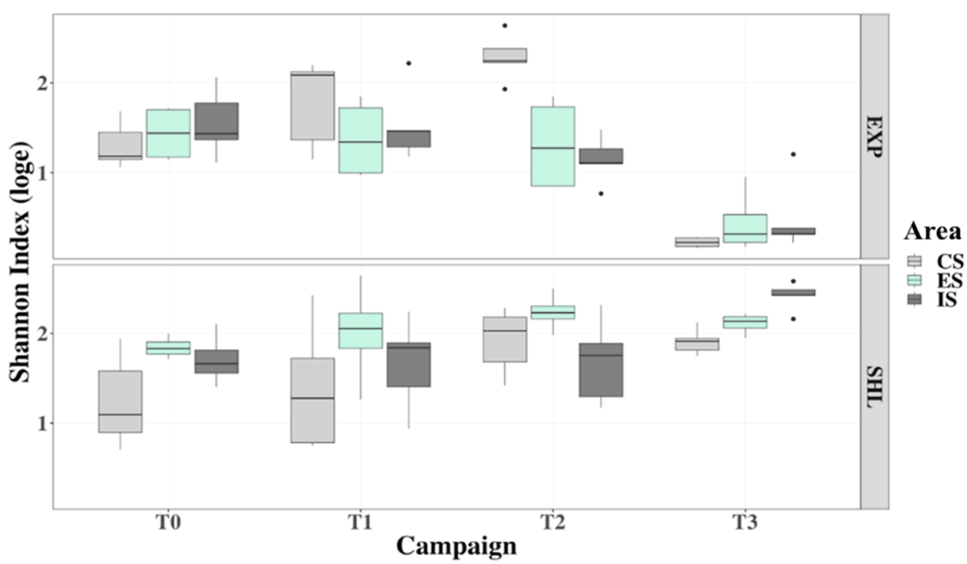
Group	Site	Area	Area: Site	Transformation
Sediment				
Erosion/ deposition	F (1,76) = 12.342 **P < 0.001**	F (2,76) = 0.912 p = 0.406	F (2, 76) = 3.590 p = 0.0323	no
TOC	F (1107.02) = 6.099 **p = 0.015**	F (2107.06) =3.0511 p = 0.051	F (2, 107.02) = 7.146 **p = 0.001**	Box-Cox
Mud	Test statistic D = 0.953, df = 1 **p < 0.001**	Test statistic D = 0.953, df = 2 p = 0.82	Test statistic D = 0.953, df = 2 p = 0.251	Box-Cox
Very fine sand	F (1107) = 248.84 **p < 0.001**	F (2107.08) = 3.528 **p = 0.033**	F (2, 107) = 0.795 p = 0.454	no
Median grain size	F (1106.03) = 161.655 **p < 0.001**	F (2106.07) = 2.261 p = 0.109	F (2, 106.03) = 5.592 **p = 0.005**	Box-Cox
Medium Sand	Test statistic D = 1, df = 1 **p < 0.001**	Test statistic D = 1, df = 2 p = 0.357	Test statistic D = 1, df = 2 p = 0.266	Box-Cox
Fine sand	Test statistic D = 1, df = 1 **p = 0.003**	Test statistic D = 1, df = 2 p = 0.974	Test statistic D = 1, df = 2 **p = 0.026**	Box-Cox
Abundance, biomass, and diversity				
Density	F (1102.03) = 42.98 **p < 0.001**	F (2102.03) = 2.27 p = 0.108	F (2102.08) = 2.0320 p = 0.136	log
Biomass	F (1102) = 37.82 **p < 0.001**	F (2102) = 0.997 p = 0.373	F (2102) = 2.8640 p = 0.062	log
Shannon	F (1102.03) = 32.543 **p < 0.001**	F (2102.03) = 0.231 p = 0.794	F (2102) = 4.369 **p = 0.015**	Box-cox
Simpson	F (1102.03) = 6.9370 **p = 0.001**	F (2102.02) = 0.259 p = 0.773	F (2102) = 2.753 p = 0.068	Box-cox
Richness	F (1102.03) = 155.747 **p < 0.001**	F (2102.03) = 2.682 p = 0.073	F (2102.03) = 0.956 p = 0.388	no
Pairwise PERMANOVA				
Area	**Site**	**Campaign**	**Site: Campaign**	**Area: Site**
F = 3.012 R^2 = 0.02 **p = 0.001**	F = 85.647 R^2 = 0.288 **p = 0.001**	F = 19.804 R^2 = 0.2 **p = 0.001**	F = 13.204 R^2= 0.133 **p = 0.001**	F = 3.608 R^2 = 0.024 **p = 0.001**

Here, bold formatting is used for statistically significant values.

Area refers to control, edge, and impact area; **Site** refer to sheltered and exposed site; **Campaign** includes T0, T1, T2, and T3.



Appendix 4. Temporal variability in the sediment composition for the control (CS), edge (ES), and impact (IS) samples under sheltered (SHL) and exposed (EXP) hydrodynamic conditions.



Appendix 5. Temporal variability in the Shannon Diversity for the control (CS), edge (ES) and impact (IS) samples under sheltered (SHL) and exposed (EXP) hydrodynamic conditions.

Appendix 6

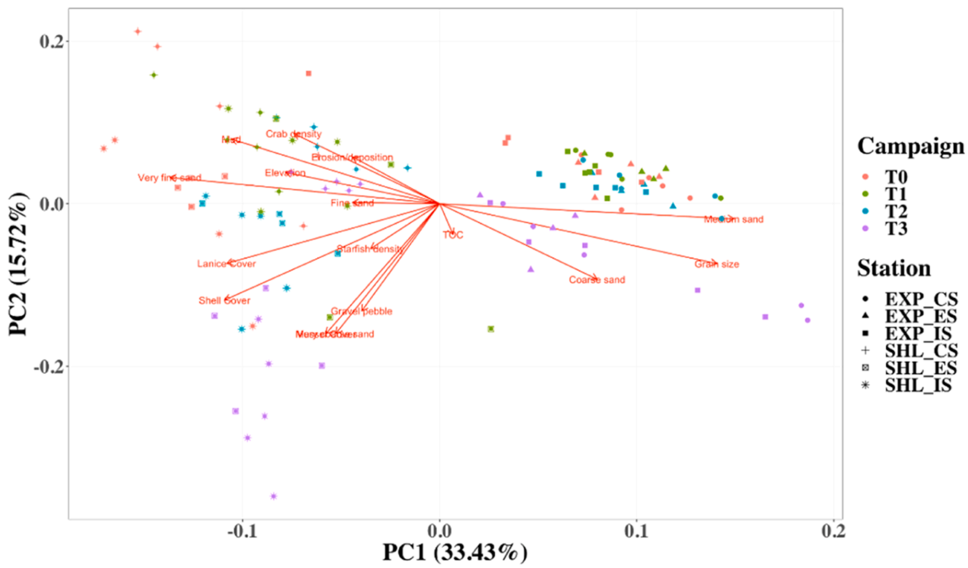
Mean value (± SD) of all the variables used in PCA. Here, EXP_CS represents the control samples of the exposed site, EXP_ES represents the edge samples of the exposed site, EXP_IS represents the impact samples of the exposed site, while SHL_CS represents the control samples of the sheltered site, SHL_ES represents the edge samples of the sheltered site, and SHL_IS represents the impact samples of the sheltered site.

Station group	Mud (%)	Very fine sand (%)	Fine sand (%)	Medium sand (%)	Coarse sand (%)	Very coarse sand (%)	Gravel pebbles (%)	Starfish (indv. m^{-2})
EXP_CS	1.23 ± 3.09	1.07 ± 0.84	41.14 ± 8.35	52.62 ± 6.68	3.15 ± 3.08	0.33 ± 0.26	0.47 ± 0.89	0.03 ± 0.05
EXP_ES	0.58 ± 1.29	1.54 ± 0.9	47.49 ± 4.76	48.17 ± 5.49	1.4 ± 0.9	0.22 ± 0.16	0.59 ± 1.22	0.04 ± 0.05
EXP_IS	4 ± 9.72	2.31 ± 1.82	46.41 ± 8.55	44.78 ± 8.51	1.74 ± 2.24	0.28 ± 0.19	0.47 ± 0.84	0.05 ± 0.05
SHL_CS	11.84 ± 11.04	7.77 ± 3.13	52.28 ± 10.3	26.1 ± 3.21	0.06 ± 0.15	0.51 ± 0.51	1.43 ± 2.66	1.12 ± 1.94
SHL_ES	11.53 ± 8.02	9.39 ± 2.98	48.16 ± 8.23	27.13 ± 4.02	1.39 ± 1.86	1.21 ± 1.39	1.19 ± 1.68	0.73 ± 0.82
SHL_IS	8.16 ± 7.12	8.85 ± 3.71	49.4 ± 8.3	26.58 ± 4	1.39 ± 2.22	1.87 ± 2.34	3.76 ± 6.05	1.95 ± 5.4
Station group	**TOC (%)**	**Grain size (µm)**	**Elevation (cm)**	**Mussel Cover (%)**	**Lanice Cover (%)**	**Shell Cover (%)**	**Erosion/ deposition (cm)**	**Crab (indv. m^{-2})**
EXP_CS	0.27 ± 0.27	267.1 ± 26.14	5.18 ± 0.09	0.06 ± 0.11	0.66 ± 1.17	4.09 ± 6.48	−13.6 ± 12.7	0.03 ± 0.04
EXP_ES	0.14 ± 0.06	251.2 ± 12.83	5.04 ± 0.14	0.94 ± 1.07	0.31 ± 0.49	3.86 ± 5.42	−19.2 ± 6.5	0.03 ± 0.04
EXP_IS	0.39 ± 0.32	241.77 ± 33.74	5.1 ± 0.12	0.94 ± 1.06	0.31 ± 0.48	3.86 ± 5.39	−20.9 ± 10.9	0.03 ± 0.04

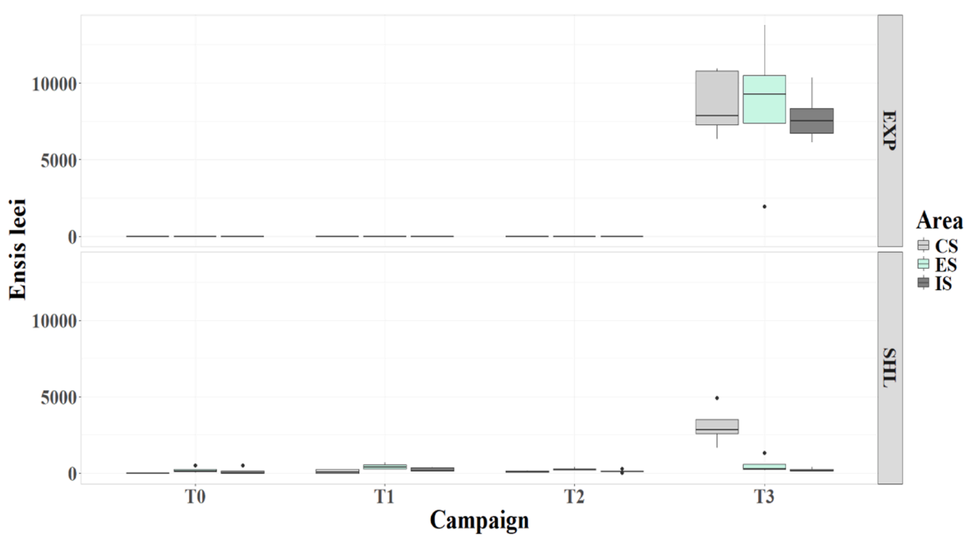
(continued on next page)

Appendix 6 (*continued*)

Station group	Mud (%)	Very fine sand (%)	Fine sand (%)	Medium sand (%)	Coarse sand (%)	Very coarse sand (%)	Gravel pebbles (%)	Starfish (indv. m^{-2})
SHL_CS	0.34 ± 0.25	191.75 ± 24.85	5.84 ± 0.12	0.09 ± 0.17	3.47 ± 3.25	10.94 ± 3.49	−9.9 ± 21.2	0.18 ± 0.18
SHL_ES	0.34 ± 0.26	195.66 ± 21.84	5.11 ± 0.23	5.89 ± 6.05	7.66 ± 4.51	20.89 ± 3.55	−10.8 ± 7.9	0.09 ± 0.09
SHL_IS	0.23 ± 0.1	210.65 ± 50.93	5.38 ± 0.11	5.89 ± 6.01	7.66 ± 4.48	20.89 ± 3.52	+2.3 ± 19.3	0.09 ± 0.08



Appendix 7. Principal component analysis (PCA) of the environmental variables (Log [x+1] transformed) to explain the structure of macrobenthos for the combined station group in different campaigns. Here, EXP_CS represents the control samples of the exposed site, EXP_ES represents the edge samples of the exposed site, EXP_IS represents the impact samples of the exposed site, while SHL_CS represents the control samples of the sheltered site, SHL_ES represents the edge samples of the sheltered site, and SHL_IS represents the impact samples of the sheltered site.



Appendix 8. Temporal variability in the *Ensis leii* density (indv.m^{-2}) for the control (CS), edge (ES), and impact (IS) samples under sheltered (SHL) and exposed (EXP) hydrodynamic conditions.

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