



Different paths, same destination: similar functional outcomes in nitrogen cycling within artificialized coastal habitat

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Abstract. Human activities are increasingly affecting coastal ecosystems, with shoreline stabilization structures becoming a prevalent response to sea-level rise and extreme climatic events. While these structures aim to protect coastal communities and infrastructures, their effects on ecosystem functioning, and particularly nitrogen cycling and fixed-nitrogen loss processes such as denitrification, remain poorly understood. To assess the ecological impacts of breakwater construction, we employed a space-for-time substitution approach to examine changes in sediment biogeochemistry, macrobenthic community structure, and nitrogen cycling in an intertidal salt marsh in the St. Lawrence Estuary, Canada. We measured benthic fluxes, denitrification rates, and macrofaunal assemblages at five locations: two landward of the breakwater (impacted sites), one situated immediately seaward of the breakwater (intermediate site) and two reference sites (one vegetated and one unvegetated). Landward sites exhibited finer sediment with higher organic carbon content and supported distinct macrobenthic communities dominated by opportunistic Oligochaetes while reference sites were dominated by Molluscs and Crustaceans. The intermediate seaward site closely resembled the unvegetated reference site in both sediment characteristics and oxygen dynamics. Surprisingly, despite these substantial physical and biological changes, dark total benthic oxygen uptake, NO_3^- , NH_4^+ benthic fluxes and benthic denitrification rates showed no significant differences between impacted and reference sites. This functional similarity suggests a degree of ecosystem plasticity, where different combinations of abiotic and biotic factors can maintain similar ecosystem function. However, such functional plasticity might not apply to all ecosystem services offered by natural salt marshes, emphasizing the importance of careful consideration in coastal management decisions.

1 Introduction

Coastal areas provide essential ecological, economic, and social benefits. They host various ecosystems and support fisheries, aquaculture, recreational and cultural activities. Around 10% of the global population lives in coastal areas less than 10 meters above sea-level, with coastal development rising in recent decades, a trend expected to continue (Neumann et al., 2015).



However, these areas face significant threats from sea-level rise and shoreline erosion (Mentaschi et al., 2018). For instance, a global temperature rise of 2°C above pre-industrial temperatures could lead to a global sea-level rise exceeding 0.2 m by 2040 (Jevrejeva et al., 2016). The most common approach to these threats is shoreline hardening (Gittman et al., 2015) which involves the construction of rigid, engineered structures to stabilize shorelines and protect infrastructures. The main types of shorelines hardening structure include bulkheads, seawalls and breakwaters. Bulkheads are vertical walls built directly on the shoreline to retain soil and prevent land loss due to wave action. Seawalls are robust, vertical or sloped structures designed to protect the shoreline by reflecting wave energy and preventing coastal flooding and erosion. Breakwaters are offshore, barrier-like structures built nearly parallel to the coast to dissipate wave energy and reduce current velocity before they reach the shore. While effective at protecting human settlements, these structures artificialize coastal ecosystems by fundamentally modifying natural habitats, leading to significant socio-ecological changes such as loss of biodiversity and reduction of the intertidal habitat (Bernatchez and Fraser, 2012; Gittman et al., 2016).

Salt marshes are important coastal ecosystems developing in low-energy shorelines, in temperate and cooler regions. They provide some of the most valuable ecosystem services (Barbier et al., 2011). These intertidal habitats play a crucial role in coastal protection by stabilizing sediments, attenuating wave energy, and enhancing sediment deposition, thereby helping to mitigate coastal erosion (Duarte et al., 2013; Gedan et al., 2009). Due to their high productivity and the capacity to enhance sediment deposition, salt marshes contribute to long-term carbon sequestration (Duarte et al., 2013), provide habitat for numerous organisms (Barbier et al., 2011), and play a significant role in nutrient cycling, particularly by acting as nitrogen sinks (Sousa et al., 2008; Valiela and Cole, 2002). This function has gained increasing importance in recent decades with the rise of coastal eutrophication (Pascal et al., 2022; Rabalais et al., 2009). Eutrophication, the excessive supply of water bodies with organic matter (Nixon, 1998), largely driven by nitrogen and phosphorus enrichment, can lead to significant ecosystem degradation (Rabalais et al., 2009).

In this context, understanding nitrogen removal processes in salt marshes is crucial when assessing the impacts of shoreline hardening on coastal ecosystem functioning (Sousa et al., 2008; Valiela and Cole, 2002). Shoreline hardening can alter sediment characteristics, hydrodynamic conditions, and benthic communities (Gittman et al., 2016), all of which influencing nitrogen cycling processes (Albert et al., 2021; Stief, 2013). Two key microbial processes drive nitrogen removal from coastal systems. (i) Denitrification which involves a microbially-mediated oxidation of organic matter (OM) using nitrate (NO_3^-) as an electron acceptor under anaerobic conditions, resulting mainly in the production of dinitrogen gas (N_2), and to a lower extent, potent greenhouse gases as nitrous oxide (N_2O) and carbon dioxide (CO_2). (ii) Anammox (anaerobic ammonium oxidation), produces N_2 through the oxidation of ammonium (NH_4^+) coupled to the reduction of nitrite (NO_2^-) (Devol, 2015). These processes are further influenced by benthic macrofauna, which play key roles in OM mineralization and nitrogen cycling through bioturbation (*sensu* Kristensen et al., 2012), enhancing solute exchanges and nutrient regeneration at the sediment-water interface (Pascal et al., 2016; Snelgrove et al., 2018). Therefore, alterations to coastal environments through shoreline hardening could significantly impact these nitrogen removal pathways, with potential consequences for coastal water quality and eutrophication mitigation. Given the vulnerability of salt marshes to such modification, understanding how nitrogen



cycling is impacted is critical. Salt marshes face increasing threats worldwide (Mcowen et al., 2017) including shoreline hardening (Gedan et al., 2009) that can exceed 50% of the total shoreline length in some regions (Bulleri and Chapman, 2010; Gittman et al., 2015). This extensive shoreline hardening contributes to a phenomenon known as coastal squeezing (Doody, 2013) where natural habitat are trapped between rising seas and hardened shoreline, resulting in habitat loss and degradation (Bernatchez and Quintin, 2016; Bozek and Burdick, 2005). Previous research on bulkhead implementation found no direct effects on nitrogen removal processes but showed these structures can indirectly reduce their overall rates by decreasing the width of salt marshes through coastal squeezing (O'Meara et al., 2015). However, breakwaters differ from bulkheads as they are built offshore. When emergent and built with sufficient crest freeboard (*i.e.*, the vertical distance between the crest of the breakwater and the high-tide level), breakwater create low-energy environments on their landward side (Wang et al., 2021). These conditions promote the sedimentation of fine, organic-rich particles (Gittman et al., 2016), which can substantially alter macrobenthic communities, and biogeochemical processes. Such changes may enhance favourable conditions for denitrification and anammox in the sediment, thereby increasing nitrogen removal rates (Albert et al., 2021; Stief, 2013). Yet, the extent and underlying mechanisms of these impacts remain poorly understood, limiting our ability to predict how different shoreline hardening strategies will affect nitrogen removal processes and associated ecosystem services. This study aims to compare sedimentary biogeochemistry and nitrogen cycling across contrasting areas within an intertidal salt marsh seascape, including areas dominated by salt marsh vegetation, unvegetated sediments, and areas located directly seaward and landward of a breakwater. We hypothesize that the presence of the breakwater causes organic-rich sediment accumulation on its landward side, which alters macrobenthic community structure, increases the sediment oxygen demand and the rates of nitrogen removal processes compared to areas farther from the breakwater.

2 Methods

2.1 Study site

The St. Lawrence Estuary area (Québec, Canada) has already seen an accelerated sea-level rise since the early 1990s (Gibeault et al., 2016), with anticipated relative sea-level rise to 0.67 m by 2100 (Savoie-Ferron et al., 2021), threatening infrastructure and human populations with erosion and flooding. As in many regions worldwide, coastal hardening has been implemented in response to these threats; recent estimates indicate that 10% of the Estuary and Gulf of St. Lawrence coastline is now artificialized by rigid structure (Sauvé et al., 2020). Among these, the Rivière-du-Loup embayment (47°50'29.30" N; 69°33'11.84" W; WSG 84), located on the South shore of the Upper St. Lawrence Estuary (Fig. 1), provides a representative example of such adaptation. It illustrates how coastal protection infrastructure can alter environmental conditions and affect benthic ecosystem functioning.

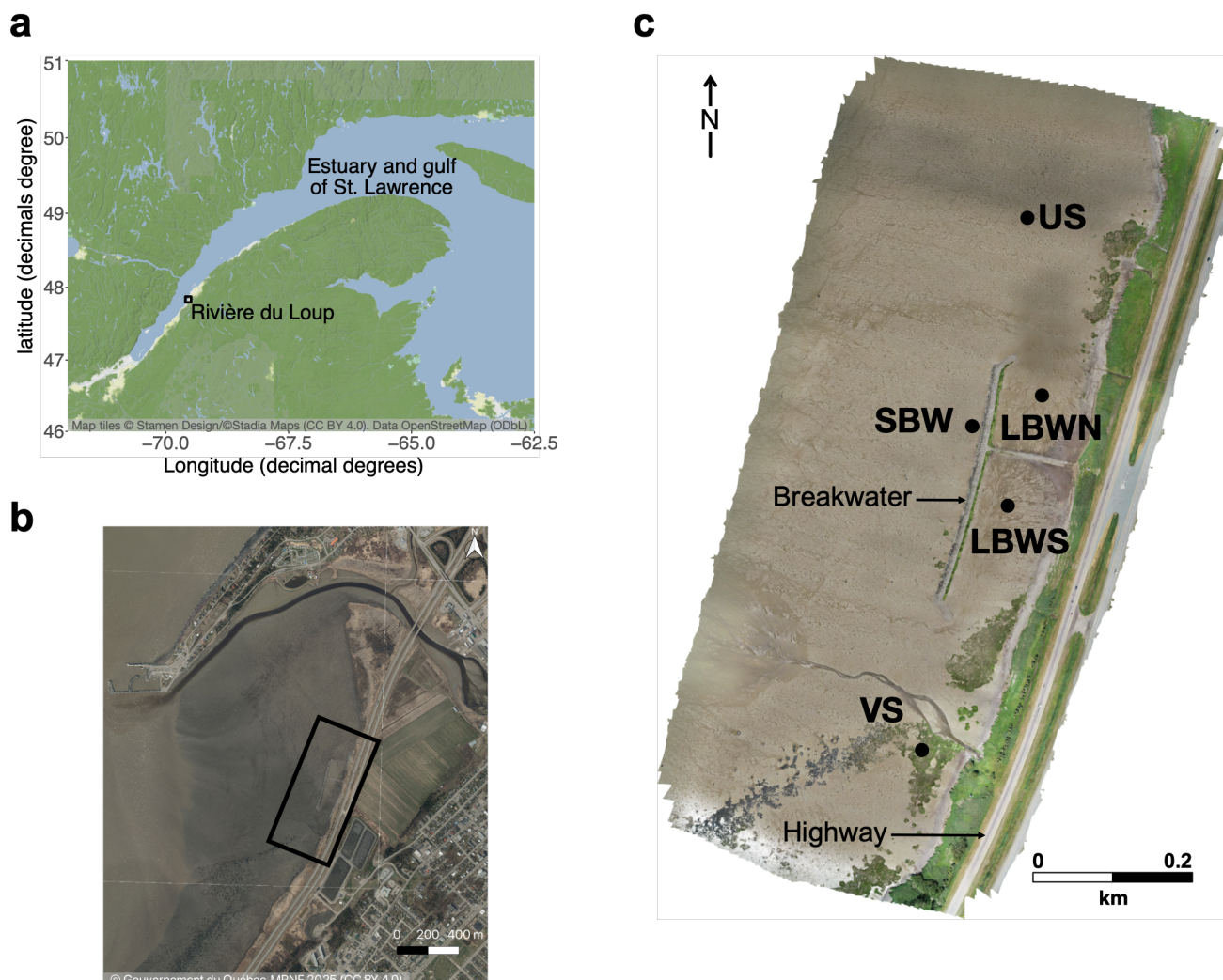


Figure 1: Study site. (a) Location of the study area (open square) in the St. Lawrence system, (b) location of the study site (black rectangle) in the bay of Rivière-du-Loup and (c) aerial view of the sampling location around the breakwater (from Zouaghi et al., 2024). Reference sites: Vegetated Sediment (VS), and Unvegetated Sediment (US); Impacted sites: Southern area landward of the breakwater (LBWS), Northern area landward of the breakwater (LBWN); and Intermediate site: Seaward of the breakwater (SBW). (a) © Stamen Design (CC BY 4.0) / © Stadia Maps; © OpenStreetMap contributors (ODbL), (b) © Gouvernement du Québec (CC BY 4.0; MNRF 2025).

The Rivière-du-Loup embayment receives freshwater inputs from a river located in its northern part, with a mean annual discharge of $14.7 \text{ m}^3 \text{ s}^{-1}$ (from 3.4 to $141.1 \text{ m}^3 \text{ s}^{-1}$). This bay is characterized by a semi-diurnal tide with an amplitude between 0.5 and 3.2 m , and a salt marsh partially covers its intertidal area with cordgrass (*Sporobolus alterniflorus*, formerly known as *Spartina alterniflora*) in the high foreshore. The shoreline has experienced erosion rates ranging from 2.3 to 6.4 m y^{-1} since 1984 (Dionne, 2007), endangering a major highway in addition to reducing the salt marsh area by approximately $62,750 \text{ m}^2$



(Zouaghi et al., 2024). In 2009, the Quebec Government implemented a 300 m-wide breakwater made of boulders to mitigate erosion. It was estimated that the construction of the breakwater *per se* induced a loss of 6,318 m² of salt marsh cover between 2009 and 2011, which has not been compensated for since (Zouaghi et al., 2024). A distinctive feature of this breakwater is that the access path for its construction (perpendicular and towards the center of the breakwater; Fig. 1C) was never removed and now acts as a jetty that is only submerged during high tide events (Zouaghi et al., 2024). In 2010, following the implementation of the breakwater, a storm event coupled with high tides transported and deposited a substantial amount of sediment, which became trapped landward of the breakwater.

2.2 Experimental design

To assess the impacts of the breakwater structure on ecosystem functioning and nitrogen cycling, we adopted a space-for-time approach comparing sites with and without breakwater influence within the same coastal system. This approach assumes that spatial differences in biogeochemical processes and ecosystem functioning reflect the long-term impacts of the breakwater. Five intertidal sites were selected to assess how the breakwater affects sediment characteristics and biogeochemical processes within the intertidal zone. (Fig. 1). Two unvegetated sites located landward of the breakwater, the southern (LBWS) and northern (LBWN) areas, were classified as “impacted”. Two other sites, a vegetated (VS) and an unvegetated (US) sediment areas served as “reference” conditions. A site located seaward of the breakwater (SBW) was designated as “intermediate” to help to distinguish the breakwater’s effects from natural environmental gradients between reference and impacted sites. We acknowledge however that the SBW site could also capture potential offshore effects of the breakwater.

2.3 Seawater, sediment and macrobenthic community sampling procedure

Sampling was performed in June 2021 and 2022, targeting the beginning of the salt marsh growing season following winter ice cover. In this region, winter ice cover and associated ice scouring can drastically reduce plant cover and height as already reported for *Zostera marina* (Pascal et al., 2020). A 20 L volume of seawater was collected at high tide on the sampling day in the bay. This seawater was filtered on-site using a GF/F filter and aerated in an opaque container for later use. At each of the five sites, eight large sediment cores (10 cm diameter, 15 cm long) were manually collected at low tide using transparent acrylic tubing (30 cm long), with few if any core compaction below 1 cm. Additionally, five small sediment cores (2.5 cm diameter, 1 cm long) was collected at each site for analysis surficial sediment characteristics, and stored at – 20 °C until analyses. Six of the eight large sediment cores were kept intact, capped with Styrofoam®, and immediately transported to the laboratory to assess total benthic fluxes. Of the two remaining cores, one was used to measure the vertical distribution of the dissolved O₂ concentrations at the sediment-water interface, and the other for porewater extraction. To assess macrobenthic community structure, sediment from three box corers (40 × 40 × 15 cm depth) was collected at each site. This sediment was sieved through a 0.5 mm mesh and preserved in a 4% buffered formaldehyde solution for further analysis. Due to sampling failure at SBW, total benthic fluxes were assessed on only four sediment cores, and no isotope pairing incubation, porewater extraction, or macrofauna sampling were performed at this site.



2.4 Characterization of the sediment

140 Sediment characteristics were analyzed using samples from the top layer (0 - 0.5 cm) of the small sediment cores collected at each location. The sediment grain size (D_{50}) was assessed by laser diffraction (Malvern Instruments[®], 2 μm detection limit) after OM digestion with hydrogen peroxide on one sediment core. Sediment porosity (ϕ) was determined by measuring water loss after freeze-drying, corrected for sea salt content, using a dry sediment density of 2.65 g cm⁻³. The OM content of the sediment was determined as a loss on ignition (LOI) on the five sediment cores. Due to storage failure, LOI was not assessed at US. Elemental characteristics of the OM, *i.e.*, organic carbon (C_{org}) and total nitrogen (N_{tot}) contents of the sediment were determined on one sediment core using an elemental analyzer (Carlo Erba[®] NC2500). Prior to the C_{org} analysis, inorganic carbon was removed by fuming of sediments in a closed container in the presence of an open beaker of concentrated HCl. The C_{org} stable isotope composition was then measured using a Micromass Isoprime 100 isotope ratio mass spectrometer coupled to an Elementar Vario MicroCube elemental analyzer. Carbon isotope ratios are reported using the delta notation, $\delta^{13}\text{C}_{\text{org}}$, relative to the Vienna Pee Dee Belemnite standard.

2.5 Oxygen and nutrient porewater concentrations

The vertical oxygen distribution within the sediment was measured within an hour from sampling using Clark-type microelectrodes. A 500 mL volume of aerated seawater was gently added at the top of the core and the overlying water was then aerated before starting the O_2 micro-profiling. The core was maintained at in situ temperature (*i.e.*, 9 °C) using ice pack and the overlying water was stirred and kept at 100% of air saturation by gently bubbling it during all the following operations. For each location, we conducted five depth profiles of O_2 concentration, randomly distributed within a single large sediment core. Microelectrodes (OX100, Unisense[®]) were inserted into the sediment at 100 μm intervals using a motor-driven micromanipulator (MU1, Pyroscience[®]). A two-point linear calibration of the electrodes was achieved from measurements of the O_2 concentration of air bubbled overlying water (100% saturation) and the anoxic zone of the sediment (0%). Oxygen diffusive fluxes (DOU in $\text{mmol m}^{-2} \text{h}^{-1}$) were computed from the O_2 gradient between 0 and 500 μm depth below the sediment-water interface using Fick's first law of diffusion, as denoted in the following equation:

$$\text{DOU} = \phi \times \frac{D_0}{(1 - \ln(\phi))^2} \times \frac{\delta C}{\delta z} \quad (1)$$

165 Oxygen penetration depth (OPD) was determined from the micro-profiles as the depth at which O_2 concentration was < 1% of the concentration at the sediment-water interface. Porewater extraction was performed on another large core (< 2 h after the core recovery) using CSS rhizons (Rhizosphere Research Products[®]). Rhizons were horizontally inserted in the sediment core at 0.5, 1, 1.5, 2, 3, 4, 5, 7, and 10 cm depth. To avoid significant overlap between successive samples, porewater extraction was limited to 8 mL. After extraction, porewater samples were stored at - 20 °C until nutrient analyses.



2.6 Intact sediment core incubations and isotope pairing experiments

For vegetated sediment cores containing *S. alterniflorus*, the relatively short leaf length at the beginning of the growing season allowed the vegetation to fit entirely within the core dimensions without modification. Six sediment cores were fitted with PVC lids equipped with a magnetic stirrer. The dissolved O₂ concentration was measured in real time using an optode (O₂ sensor SP; PreSens[®]) connected to a multichannel O₂ meter (OXY-10 SMA; PreSens[®]) through optical fibre cables.

Incubations were performed in the dark at the in situ water temperature (i.e., 9 °C). The incubation duration was adjusted so that O₂ saturation in the overlying water never dropped below 80% of its initial value (typically between 1.5 and 4 h). During the incubations, discrete water samples were collected each hour, filtered (0.2 µm) and stored at – 20 °C for subsequent nutrient analyses. Water removed by sampling was automatically replaced with previously collected and bubbled seawater. After the initial incubation period, two thirds of the overlying water volume in each sediment core was replaced with previously collected and bubbled seawater. The sediment cores were then left open, and the overlying water was gently bubbled with air for two hours. Then, an initial water sample was extracted from the overlying water of all six sediment cores to determine the ambient NO₃[–] concentration before the addition of ¹⁵N – NO₃[–] stable isotope. A calculated volume of a 20 mM ¹⁵N – NO₃[–] solution (99 % atom ¹⁵N, Sigma-Aldrich[®]) was then introduced into the overlying water of each core. The added volume was designed to achieve a nominal concentration equivalent to either 50% or 100% of the ambient concentration, with two sets of three cores. A pre-incubation period of 3 hour was implemented to ensure sufficient diffusion of ¹⁵N – NO₃[–] to the sediment nitrate reduction zone (Nielsen, 1992). During this period, an air bubbling system was used to keep the overlying bottom-water homogeneously saturated with air, maintaining the in situ conditions. Following the pre-incubation, water samples were collected to determine the exact concentration of ¹⁵N – NO₃[–] and the initial ²⁹N₂ and ³⁰N₂ concentrations. Then, the incubations were performed as described above. Discrete water samples were collected using 12 mL Exetainers and directly analysed for ²⁹N and ³⁰N measurements. At the end of the incubations, the remaining water was mixed with the top 5 cm of the sediment column. From the slurry, 12 mL of sample was transferred to an Exetainer to which 200 µL of 7 M ZnCl₂ were added for further ¹⁵N – NH₄⁺ analysis.

The slope (in mmol m^{–3} h^{–1}) from the linear regression of the changes in O₂, nutrients and ^{29,30}N₂ concentrations over incubation duration was used to compute benthic fluxes as follows:

$$J_{\text{benthic}} = \text{slope} \times \frac{V}{A} \quad (2)$$

where J_{benthic} is the flux across the sediment-water interface (mmol m^{–2} h^{–1}), V is the volume of overlying water (m³), and A is the surface of the sediment-water interface (m²).

The validity of the original isotope pairing technique (Nielsen, 1992) was tested by checking the independence of the estimated ²⁸N₂ production and the amount of added ¹⁵N – NO₃[–] (Risgaard-Petersen et al., 2003). No production of ¹⁵N – NH₄⁺ was



detected over the incubation periods, DNRA was thus considered to be negligible. Since no deviation from the original isotope pairing technique was detected, denitrification rates were computed on the six sediment cores following Nielsen 1992:

$$D_{15} = p_{29} + 2 \times p_{30} \quad (3)$$

where D_{15} is the denitrification rate of the $^{15}\text{N} - \text{NO}_3^-$ and p_{29} and p_{30} the production of $^{29}\text{N}_2$ and $^{30}\text{N}_2$, respectively.

$$D_{14} = D_{15} \times (p_{29}/2p_{30}) \quad (4)$$

where D_{14} is the denitrification rate of $^{14}\text{N} - \text{NO}_3^-$. From D_{14} and D_{15} , the denitrification of nitrate diffusing from the overlying water to the nitrate reduction zone (D_w) and the denitrification of nitrate produced within the sediment through nitrification (*i.e.*, coupled nitrification-denitrification; D_n) were calculated as followed:

$$D_w = (^{14}\text{NO}_3^- / ^{15}\text{NO}_3^-) \times D_{15} \quad (5)$$

$$D_n = D_{14} - D_w \quad (6)$$

where $^{14}\text{NO}_3^-$ is the ambient nitrate concentration and $^{15}\text{NO}_3^-$ is the concentration of labelled nitrate added to the overlying water.

2.7 Macrofauna identification

Macrofauna (epi- and infauna) was sorted and identified to the lowest possible taxonomic level (typically species level). Biomass (blotted wet mass; ± 0.0001 g) was determined as well. Using this macrofauna dataset, total density, total biomass and species richness were calculated. In this study, we identified six biological traits characterized by multiple categories to describe the organisms' functional behaviors (Table 1). Taxa were assigned trait modalities using a standard fuzzy coding approach which allowed each taxon to represent multiple trait modalities and thus account for intraspecific variation. Scoring ranges from 0 to 3 were adopted with 0 corresponding to no affinity for a given trait modality, 1 and 2 reflecting a low and high affinity, respectively, and 3 an exclusive affinity. Information on trait expression for all taxa were extracted from Queiros et al. (2013) and Degen and Faulwetter (2019). When information was not available for a given taxon, information was obtained from that of closely related species at the nearest taxonomic level. The community trait expression in each sample was computed from the multiplication of the species density matrix by trait categories matrix.



Table 1: *Biological traits.* List of traits, trait categories and associated abbreviations.

Trait	Categories	Abbreviation
Size	Small (< 1cm)	S_SMA
	Small-medium (1-5 cm)	S_SMM
	Medium (5-10 cm)	S_MED
	Medium-large (10-30 cm)	S_MDL
Mobility	Low	M_LOW
	Medium	M_MD
	High	M_HI
Bioturbation	None	B_NO
	Surface mixing	B_SRM
	Diffusive mixing	B_DIF
Environmental position	Epifauna	P_EPI
	Infauna	P_IN
Feeding Habit	Filter feeder	F_FIL
	Surface deposit feeder	F_SRD
	Subsurface deposit feeder	F_SBD
	Predator	F_PRE
	Scavenger	F_SCA

2.8 Sample analyses

235 NO_3^- (quantification limit 0.6 μM), NO_2^- (quantification limit 0.05 μM), NH_4^+ (quantification limit 0.1 μM) and PO_4^{3-} (quantification limit 0.1 μM) samples were analyzed using an autoanalyzer AA500 (Seal analytical[®]), following Aminot et al. (2009).

240 The isotope $^{28}\text{N}_2$, $^{29}\text{N}_2$ and $^{30}\text{N}_2$ measurements were completed within one week of collection using a membrane inlet mass spectrometer (MIMS, Bay Instruments[®]) (Kana et al., 1994). The protocol followed Kana et al. (2006). Calibration factors for standard sample were computed based on solubility equations (Hamme and Emerson, 2004). To quantify the production of $^{15}\text{N} - \text{NH}_4^+$, the water samples were first gently bubbled with He during 5 min to remove all $^{15}\text{N} - \text{N}_2$ produced during the



incubation. The water samples were then treated with alkaline hypobromite to oxidize NH_4^+ to N_2 prior to analysis using MIMS as described in Yin et al. (2014).

2.9 Data analyses

Data analyses were performed using R software (R Core Team, 2024). Data values are given as means $\pm$ SD. First, linear models (lm function from *stats* package; R Core Team 2024) were fitted to test the effects of *Site* (fixed factor; five levels) on the total macrofauna density, biomass and species number, DOU, OPD, as well as O_2 , nutrients and N_2 total benthic fluxes. Test assumptions were assessed for each model (plotQUnif function from *DHARMA* package; Hartig 2022). Effect sizes were calculated as generalized eta squared (η^2) to quantify the magnitude of *Site* effects, with η^2 values of 0.01, 0.06, and 0.14 representing small, medium, and large effects, respectively. Both p-values and effect sizes are reported (Table S2) given the limited replication ($n = 3$ per site), which may affect statistical power. If a significant effect of the *Site* factor was observed ($p < 0.05$), pairwise tests (Tukey contrast) were performed to characterize the differences between its levels. Second, macrofauna density data were transformed using Hellinger transformation. Sites were grouped using a hierarchical clustering analysis with a ward agglomeration method (hclust function from *stat* package; the number of clusters was determined using the HCPC function from *FactoMineR* package; Lê et al. 2008). Patterns of macrobenthic community assemblage were visualized using principal component analysis (PCA, RDA function from *vegan* package; Oksanen et al. 2022). In addition, the difference in macrobenthic community between clusters was tested using a multivariate analysis of variance (anova.cca function from *vegan* package). Finally, functional diversity was assessed using the dbFD function from the *FD* package (Laliberté and Legendre, 2010), computing functional richness (FRic) and functional evenness (FEve). Community-weighted mean trait values (CWM) were calculated and visualized using PCA as described above. Site effects on functional indices were tested using linear models as described above.

2.10 Methodological considerations

Sediment characteristics were measured with variable replication levels ($n = 1$ to 5) due to analytical constraints. LOI was replicated five times, some parameters were duplicated, while others were measured once per station. The representativeness of these measurements is supported by two observations: (1) low variability among replicated measurements where available, and (2) strong consistency between highly replicated LOI values and corresponding Corg and TN measurements (duplicate or single measurements).

Oxygen microprofiles and porewater nutrients were each measured on separate single sediment core per location. This approach was chosen because biogeochemical heterogeneity of the sediment is often associated with microenvironments (Stockdale et al., 2009). Such approach is considered qualitatively robust (Bull and Taillefert, 2001). Nevertheless, since this sampling design may involve pseudo-replication, statistical results on these measurements should be interpreted cautiously. Measurement representativeness is supported by: (1) consistency among sediment characteristics, oxygen microprofiling, and



porewater nutrient profiles measured in three independent cores per location, and (2) absence of large infauna in cores, limiting potential bias from bioturbation.

Our benthic flux incubations were conducted in the dark to standardize experimental conditions and ensure robust comparisons among sampling sites. This approach inherently excludes potential in situ effects of microphytobenthos or *S. alterniflorus* photosynthesis, both of which can significantly influence sediment oxygenation and nutrient uptake during daylight. However, in intertidal zones near breakwaters, high turbidity and suspended sediment loads, often limit light penetration and thereby reduce photosynthetic activity (Pratt et al., 2014). Moreover, belowground oxygen release by marsh roots correlates with photosynthesis but can persist in darkness (Koop-Jakobsen et al., 2018). As such, our dark incubations represent potential, near-maximum benthic fluxes, under low-light conditions typical of these habitats. While this standardized approach supports reliable site comparisons, we acknowledge that it does not capture the full spectrum of benthic fluxes. We therefore recommend future studies include incubations under natural light to better capture daytime flux dynamics, especially where benthic primary producers are exposed to substantial light during immersion.

3 Results

3.1 Sediment characteristics and biogeochemical properties

Among all sampling locations, surficial sediments consisted of silty clay (Table 2). Overall, impacted sites (LBWN and LBWS) showed finer median grain size compared to reference sites (VS and UV). Correspondingly, sediment organic carbon (OC) and total nitrogen (TN) contents tended to be higher in impacted sites, while VS exhibited the lowest OC and TS contents among sites. The $\delta^{13}\text{C}_{\text{org}}$ signatures remained relatively uniform among all sites, suggesting a common mixture of terrestrial and marine carbon sources through the system. The intermediate sites (SBW) showed similar sediment characteristics to the two reference sites.

Table 2: *Surficial Sediment characteristics.* Median sediment grain size (D_{50} , in μm), porosity (ϕ , volume ratio), loss on ignition (LOI in %), organic carbon content (C_{org} , in %), total nitrogen content (TN, in %), $\delta^{13}\text{C}_{\text{org}}$ signature (in ‰ vs. VPDB). Values are means $\pm$ SD with replication indicated by superscripts (^a $n = 2$, ^b $n = 5$, none : $n = 1$).

Site	D_{50}	ϕ	LOI	C_{org}	TN	$\delta^{13}\text{C}_{\text{org}}$
LBWN	12.9 ± 0.9^a	0.83 ± 0.03^a	11.94 ± 2.11^b	4.08 ± 0.14^a	0.38 ± 0.02^a	-24.3 ± 0.0^a
LBWS	15.3 ± 0.6^a	0.78	11.14 ± 2.13^b	3.52	0.28	-24.7
SBW	20.0	0.75	6.51 ± 0.40^b	2.52	0.23	-24.7
VS	20.5 ± 2.6^a	0.65	6.13 ± 0.89^b	1.09	0.10	-24.6
US	26.8 ± 2.5^a	0.81	--	2.72	0.30	-24.5

Oxygen in the sediment column showed contrasting dynamics among sites (Table S1). Diffusive oxygen uptake (DOU) rates tended to be higher at impacted sites compared to intermediate and reference sites (Fig. 2a). Correspondingly, oxygen penetration depths (OPD) were systematically shallower (Fig. 2b). Similarly, porewater nutrient distributions varied among sites (Fig. 2c). While NO_2^- concentration was near zero throughout the sediment column at all sites, NO_3^- concentration consistently reached its peak at 0.5 cm depth, and then sharply decreased below the detection limit around 4 cm deep in impacted sites and around 6 cm deep in reference sites (Fig. 2c). The peak concentration was notably high at VS. NH_4^+ and PO_4^{3-} concentration increased noticeably with depth with a larger increase at impacted sites compared to reference ones (Fig. 2c). Notably, the increase in PO_4^{3-} concentration started from the sediment surface at impacted sites. In comparison, it started deeper (5 cm deep) at US and PO_4^{3-} concentration was near zero along the sampled sediment column at VS (Fig. 2c).

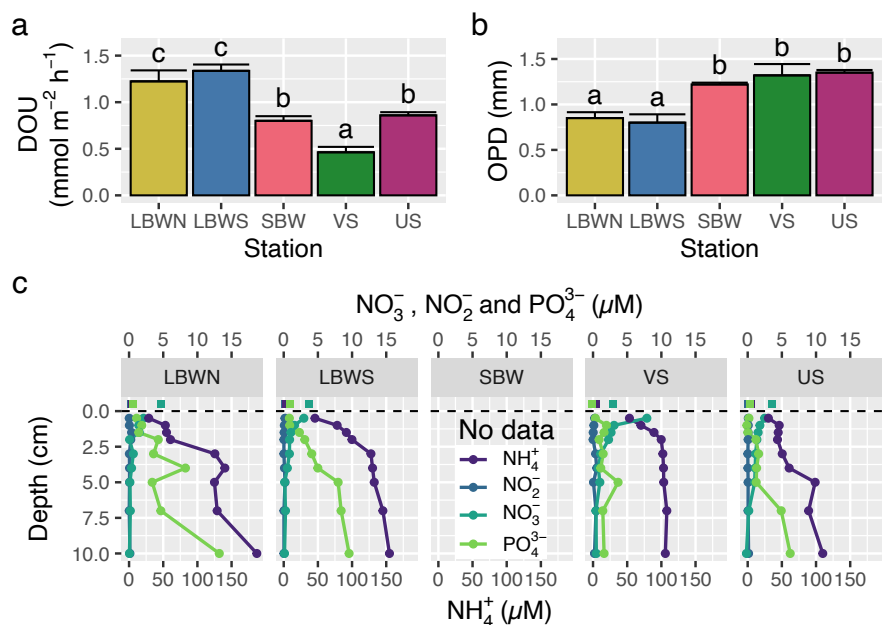


Figure 2: Porewater solute concentrations. (a) Diffusive O_2 uptake (DOU) by the sediment and (b) O_2 penetration depth (OPD). (c) porewater NO_2^- , NO_3^- , NH_4^+ and PO_4^{3-} concentrations at each site ($n = 1$ with 5 pseudo replicates for DOU and OPD). Different letters indicate significant ($p < 0.05$, Tuckey contrast) differences among the different levels of *Site* (a and b)

3.2 Macrobenthic community structure

A total of 2,657 individuals from 12 samples (4 sites $\times$ 3 replicates) were sorted, and 14 taxa were identified (Table S2). Total density, biomass and species richness significantly differed among sites (Table S1). However, these univariate metrics do not allow a clear separation between impacted and reference sites; comparisons must instead be made at the site level. Total



densities tended to be higher at the sites LBWS and LBWN than at VS and US (Fig. 3). Total biomass was significantly lower at LBWN, LBWS and VS than at US. Finally, species richness was lower at LBWN than at LBWS, VS and US.

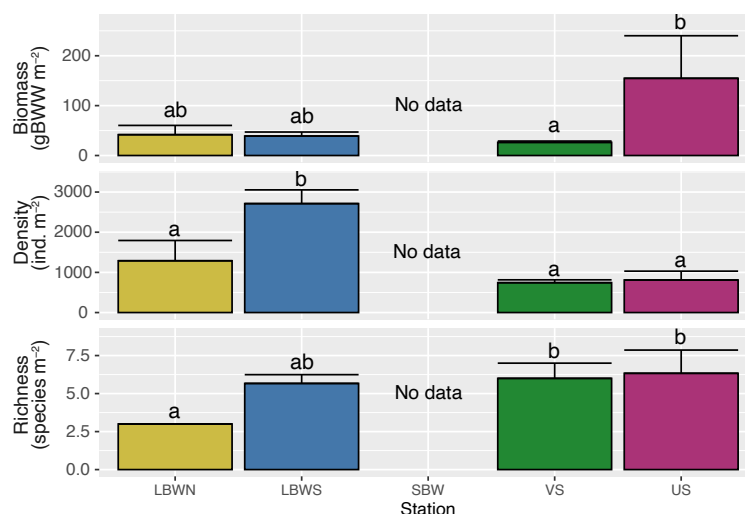


Figure 3: *Univariate descriptors of macrofauna communities.* Total biomass, density and species richness at the sampled sites (n = 3 per site). Different letters indicate significant ($p < 0.05$, Tuckey contrast) differences among the different levels of *Site*.

Based on hierarchical clustering on species density, the sites could be discriminated into three groups (Fig. 4a). Cluster 1 included the impacted sites, cluster 2 corresponded to VS, and cluster 3 corresponded to the US. The statistical significance of these clusters was confirmed by MANOVA (Table S3). The three clusters exhibited distinct macrofaunal assemblages (Figure 4b and c). The impacted sites (cluster 1) were characterized by a high density of Oligochaetes and Polychaete *Hediste diversicolor*, while VS (cluster 2) were characterized by relatively high density of small body grazers (*Gammarus* spp. And Gastropods). US (cluster 3) were distinguished by a relatively high density of the bivalve *Mya* sp. Both clusters 2 and 3 showed notable densities of the bivalve *Macoma balthica* as compared to cluster 1. It is worth noting that while gathered in the same cluster, LBWS showed greater densities of *H. diversicolor* and Oligochaete than LBWN.

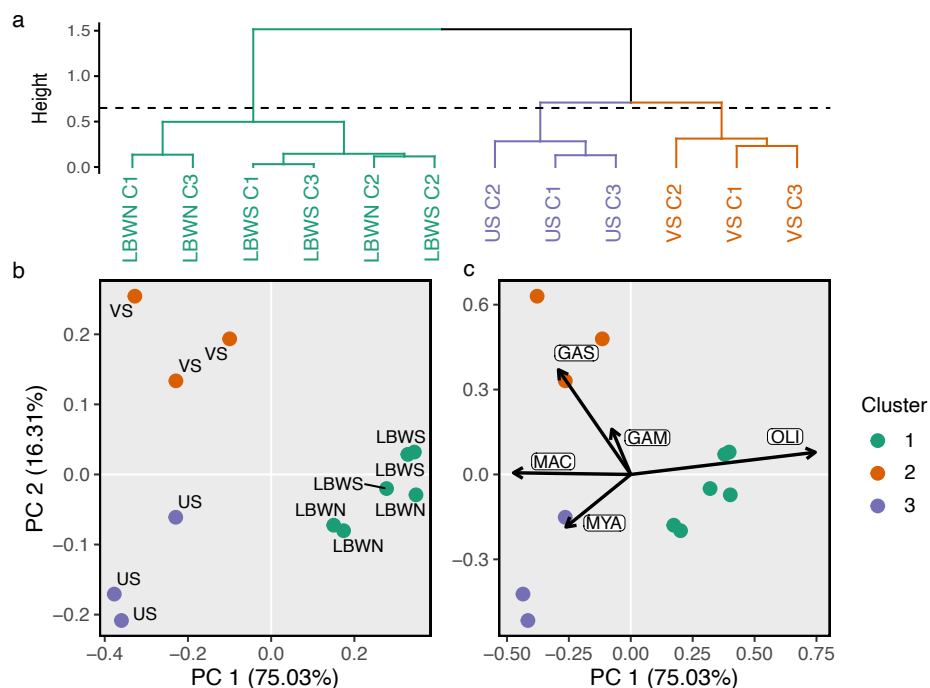


Figure 4: Macrofauna community assemblages. (a) Hierarchical clustering and (b–c) principal component analyses (PCA) of Hellinger-transformed species densities. Panels show (b) scaling 1, and (c) scaling 2. Only variables representing at least 20 % of the total variation are shown. Abbreviations: MYA = *Mya* sp.; MAC = *Macoma balthica*; GAM = *Gammarus* spp.; OLI = Oligochaeta; GAS = Gastropoda.

Functional richness (FRic) differed significantly among sites (Table S1) and was higher at VS and US, intermediate at LBWS and lower at LBWN (Fig. 5a). Functional evenness (FEve) did not differ significantly among sites, although a large effect size (Table S1) suggests the functional evenness differences may exist but require greater sampling effort to confirm. Overall, FEve tended to be higher at LBWN, VS and US than at LBWS (Fig. 5b).

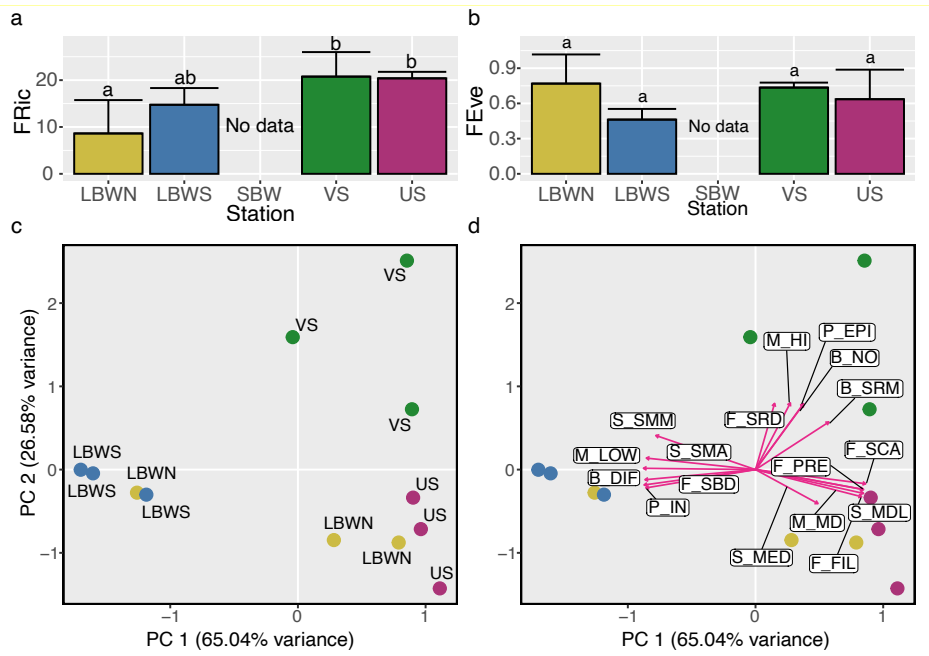


Figure 5: *Macrofauna community trait expression.* (a) Functional richness (FRic) and (b) functional evenness (FEve); (c–d) PCA of community-weighted mean (CWM). Panels show (b) scaling 1, and (c) scaling 2. Only variables representing at least 20 % of the total variation are shown. See Table 1 for trait abbreviations.

Beyond diversity metrics, the community-weighted mean trait composition revealed contrasting spatial patterns (Fig. 5c). Although LBWN and US differed markedly in species composition, they exhibited partial convergence in trait expression (Fig. 5d). US was characterized by larger, more mobile organisms dominated by filter-feeding, predatory and scavenger trait expressions, while LBWN showed a tendency toward this trait profile. In contrast, LBWS and VS maintained clear segregation in trait expression. VS was characterized by epifauna with minimal or surface-restricted bioturbation, while LBWS trait expression was dominated by small-bodied infaunal organisms characterized by subsurface deposit feeding and biodiffusive bioturbation.

3.3 Benthic fluxes

Total O_2 , NO_3^- , and NH_4^+ fluxes differed significantly among sites (Table S1). Total O_2 and NO_3^- fluxes were always negative, indicating an uptake by the sediment while positive total NH_4^+ flux indicated a release by the sediment (Fig. 6a). Similarly to the macrobenthic community structure results, comparison should be made at the site level. Overall, all benthic fluxes followed the same pattern with higher fluxes at LBWS and VS than at LBWN, SBW and US (Fig. 5a). Total denitrification (D_{tot}) also differed significantly among sites (Table S1). Similarly to benthic fluxes, D_{tot} was highest at sites VS and LBWS and lowest at sites LBWN and US (Fig. 6b). The contribution of sedimentary nitrification to total denitrification (coupled nitrification-denitrification; D_n) was higher than 50% at sites LBWN, LBWS and VS and lower than 10% at site US.

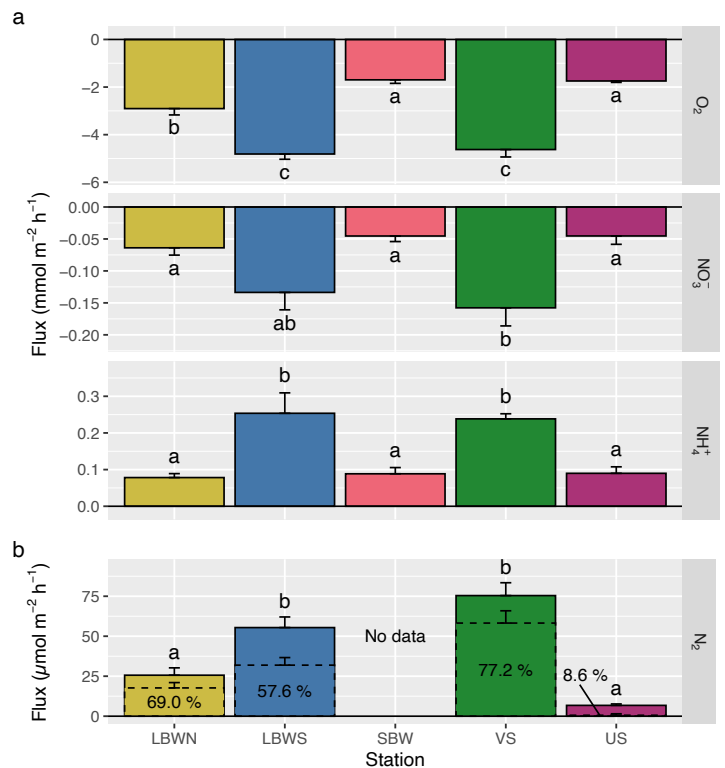


Figure 6: Benthic fluxes (a) O_2 , NH_4^+ and NO_3^- fluxes (in $mmol\ m^{-2}\ h^{-1}$) and (b) N_2 flux (D_{tot} in $\mu mol\ m^{-2}\ h^{-1}$) across the sediment-water interface. The dashed bar plots depict the denitrification of nitrate produced within the sediment through nitrification (D_n) and the percentage represents the proportion of D_{tot} explained by D_n (B). Different letters indicate significant ($p < 0.05$, Tuckey contrast) differences among the different levels of Site. Note that positive values correspond to an uptake by the sediment, and negative values correspond to a release by the sediment. $n = 6$ per site except at SBW where $n = 4$.

4 Discussion

Shoreline stabilization structures have become increasingly prevalent features of coastal ecosystems worldwide (Gittman et al., 2016). This proliferation is driven by the urgent need to protect coastal communities from the impacts of sea-level rise and intensifying extreme climatic events. While previous studies have documented changes in sediment characteristics and macrobenthic communities associated with coastal hardening (see review by Gittman et al., 2016 and references therein), the influence on biogeochemical processes and nitrogen cycling remains limited (but see O'Meara et al., 2015). Our study addresses this knowledge gap by comparing ecosystem functioning among contrasting habitats created by a breakwater construction within a salt marsh system.



4.1 Impact of breakwater construction on benthic habitats

Our study highlights marked alterations in surficial sediment characteristics, with impacted sites (i.e., LBWS and LBWN) accumulating finer and more organic-rich sediment compared to reference and intermediate sites. These observations are consistent with expectations for low-energy depositional environments landward of high-crested breakwaters (Da Silva et al., 2022; van Rijn, 2011; Wang et al., 2021). In contrast, sediments of the intermediate site (SBW) resembled reference sites (i.e., US and VS), suggesting minimal breakwater influence in this area. The consistent sedimentary $\delta^{13}\text{C}_{\text{org}}$ signature among sites suggested a shared origin of organic carbon, likely a mix of terrestrial and marine inputs typical of intertidal zones. This homogeneity suggests that low-energy hydrodynamic conditions landward of the breakwater enhance deposition of fine, organic-rich particles without selective retention of organic matter from specific sources. Therefore, differences among sampled areas are driven by organic carbon quantity, not origin.

Geochemical measurements further support this pattern. Sediment cores from impacted sites showed up to 2.3 times higher diffusive O_2 uptake (DOU) and shallower O_2 penetration depth (OPD) than reference sites (Fig. 2a and b), consistent with enhanced organic carbon mineralization driven by higher organic carbon content (Glud, 2008). These results align well with our porewater nutrient profiles extracted from another sediment core. The decrease in porewater NO_3^- concentration with depth in all sites indicates a consumption by the sediment (Fig. 2c), consistent with our measured NO_3^- benthic fluxes (Fig. 6). This consumption results from the denitrification process, which has been detected among all sites (Fig. 6). VS exhibited a subsurface NO_3^- peak, suggesting coupled nitrification-denitrification, probably enhanced by sedimentary nitrification resulting from rhizosphere oxygenation (Koop-Jakobsen et al., 2018). The quicker NO_3^- consumption in the porewater of impacted sites in the upper four centimeters compared to six centimeters in reference sites suggests a more reduced condition in impacted sites. Similarly, deeper sediment layers in impacted sites exhibit greater increases in NH_4^+ and PO_4^{3-} compared to reference sites, indicating larger ammonification and PO_4^{3-} release, typically associated with the reductive dissolution of iron-oxyhydroxides in anoxic sediment layers (Slomp, 2011). Overall, these O_2 and nutrient profiles suggest more reduced conditions and greater nutrient accumulations in the sediment column in impacted sites compared to reference sites. These changes in sedimentary conditions may have important implications for the capacity of impacted sites to further retain or remove excess nitrogen and thus mitigate coastal eutrophication (Pascal et al., 2022).

4.2 Impact of breakwater construction on macrobenthic community structure

Consistent with previous studies on the ecological impact of shoreline stabilization structure (Bulleri and Chapman, 2010; Dugan et al., 2018; Gittman et al., 2016), impacted sites exhibited distinct assemblages compared to reference sites. Impacted sites were notably dominated by high densities of small-bodied *H. diversicolor* and *Oligochaetes*, the former being tolerant to organic enrichment, and the latter considered opportunistic under such conditions and often associated with fine-grained, organic-rich sediments (Borja et al., 2000). Both *H. diversicolor* and *Oligochaetes* are significant bioturbators (Queirós et al., 2013) that influence sediment structure, biogeochemistry and microbial activity at the sediment-water interface (Kristensen et



400 al., 2012). In contrast, reference sites supported less dense but more diverse communities in terms of species and function. Notably, US appeared to be colonized by larger organisms than VS, as suggested by species traits analysis (Fig. 5d) and the relatively low total density and high total biomass in US (Fig. 3). This difference may reflect the dense root and rhizome network of *S. alterniflorus* in VS, which could hamper the movement and burrowing of larger infauna (Pascal et al., 2020; van Wesenbeeck et al., 2007). The higher density of bioturbative bioturbation at impacted sites, and particularly LBWS (Fig. 5c),
405 suggests that some ecosystem processes, such as sediment oxygenation and nutrient regeneration, may persist despite habitat alteration. However, the lower biodiversity and functional richness and evenness, at these sites may limit functional redundancy thereby reducing the resilience of ecosystem functions to additional stressors.

4.3 Potential convergence in ecosystem functioning

Despite marked differences in sediment characteristics, macrobenthic community structure and trait expression between
410 impacted and reference sites (i.e., LBWN vs. US and particularly LBWS vs. VS), total benthic fluxes and denitrification rates remained similar. These findings, derived from dark incubations (see section 2.10), suggest that distinct benthic environments can yield similar functional outcomes regarding oxygen uptake, nutrient cycling and notably denitrification rate. The high density of subsurface bioturbators at LBWS (Fig. 5c) likely enhances oxygen and nutrient exchange at the sediment-water interface. The sediment irrigation enhances aerobic mineralisation of the OM, stimulates nitrification fuelling coupled
415 nitrification-denitrification, a pattern supported by our isotope pairing results (Fig. 6). In VS, although present, bioturbation is absent or constrained to the sediment surface (Fig. 5c) and thus, similar benthic fluxes probably arise through another pathway. Radial O₂ loss from *S. alterniflorus* roots, may create oxidized zones that can directly or indirectly (i.e., through the oxidation of reduced solutes) favor near sediment surface nitrification, fuelling, here again, coupled nitrification-denitrification. By contrast, LBWN showed a trait expression tendency toward US that could yield similar benthic fluxes. It is worth noting that
420 US is dominated by a few large burrowers (e.g., *Mya* sp.) whose local influence may not be captured at the core scale, leading to low benthic fluxes. Interestingly, despite being both impacted sites and having similar sediment characteristics, LBWN and LBWS exhibited different ecosystem functions based on total benthic fluxes and denitrification rates. This most likely results from the higher density of macrobenthic organisms at LBWS than at LBWN, highlighting the critical role of macrobenthic community activity in shaping biogeochemical processes (Snelgrove et al., 2018). However, the factors driving the variation
425 in macrobenthic community structure between these two areas remain elusive.

From a coastal-management perspective, one of the main issues is whether areal flux rates measured in LBWS can offset, at the seascape level, the functional loss caused by salt marsh vegetation removal. LBWS area (~18,800 m²) is about three times larger than the vegetated area directly lost due to the breakwater implementation (~6,300 m²). Assuming that the measured fluxes capture the whole area heterogeneity, LBWS could compensate for these specific functional capacity losses of that part
430 of the salt marsh. However, it is worth noting that this area is still more than three times smaller than the total vegetated area lost due to combined erosion and breakwater implementation (~62,700 m²) so any functional compensation remains only partial at the scale of the whole seascape.



5 Conclusion

Our study highlights the complex relationships between sediment characteristics, macrobenthic communities, and ecosystem functioning in coastal environments impacted by shoreline hardening structures. We observed that some ecosystem functions (i.e., benthic respiration, nutrient cycling, and denitrification rate) can be maintained through several combinations of abiotic and biotic factors. This finding suggests a degree of functional plasticity within coastal ecosystems. However, it is important to interpret these results carefully. While we observed functional similarities in specific ecosystem functions, natural coastal habitats provide an extensive collection of ecosystem functions and services (Friess et al., 2020; Gedan et al., 2009) that are far from being fully captured by our measurements. The observed functional plasticity may contribute to the resilience of some ecosystem functions at the seascape level. However, it does not imply that artificialized environments can sustain all ecosystem functions and services provided by natural habitats. These findings highlight the challenges in predicting and managing ecosystem responses to shoreline hardening, coastal squeeze and probably other coastal disturbances. It also emphasizes that physical, geochemical, and biological factors should be considered when assessing the functional impact of coastal development projects. Given the increasing pressures on coastal ecosystems (Halpern et al., 2019), future research should assess the ability of artificialized ecosystems to maintain their functions under multiple stressors and investigate their long-term stability under various climate change scenarios. Finally, broader ecological implications of apparent functional plasticity in coastal ecosystems including potential cascading effects on higher trophic levels should be explored. This understanding will be crucial for developing more accurate predictive models and effective management strategies in the face of ongoing coastal development and climate change.

Code and data availability

The data and code supporting this study are archived at the Observatoire global du Saint-Laurent (OGSL) and have been assigned a DOI (<https://doi.org/10.26071/a974587e-583e-4a2c>), which is not yet publicly active. During the review process, access to the data and code is provided to the editor and reviewers via a private link.

Supplement link

The link to the supplement will be included by Copernicus, if applicable.

Author contributions

LP: Conceptualization (lead), Methodology (lead), Investigation (lead), Formal analysis (lead), Visualization (lead), Writing - Original Draft Preparation (lead), Writing – Review and Editing (lead); **EDM:** Investigation (supporting), Writing – Review and Editing (supporting); **DD:** Funding acquisition (lead), Writing – Review and Editing (supporting); **CN:** Investigation



(supporting), Funding acquisition (supporting), Supervision (equal), Writing – Review and Editing (supporting); **LS**: Investigation (supporting), Funding acquisition (supporting), Writing – Review and Editing (supporting); **FZ**: Investigation (supporting); **GC**: Conceptualization (supporting), Investigation (supporting), Funding acquisition (supporting), Supervision (equal), Writing – Review and Editing (supporting).

465 **Competing interests**

The authors declare that they have no conflict of interest.

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Review statement

The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified.

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