# Human activities and environmental variables drive infaunal community structure and functioning in West African mangroves

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## ARTICLE INFO

## ABSTRACT

In West African tropical estuaries, such as the Saloum Delta (Senegal), mangroves provide specific socio-economic functions including various natural food resources for local human populations. Mangrove-habitat loss is therefore of great concern, in terms of conservation and management, and highlights the need to study West African mangrove under human-induced pressures. Based on data from 2007 to 2008, this study aimed to establish a conditions report for two of the main Southern West Senegal mangroves areas: the Sine Saloum and the Petite Côte. We assessed the influence of environmental variables and human-induced pressures (i.e. shellfish harvesting and heavy metals (potentially toxic elements, PTEs)) on infaunal community structure and functions through trait-based approaches.

Reflecting for example changing seasons and hypersaline events, the Saloum environmental variables and their temporal dynamics greatly impacted infaunal communities in the subtidal zone. In the intertidal area, closer to anthropogenic disturbances, pressures related to human activities took precedence over environmental variables in explaining infaunal community structure. Shellfish harvesting resulted in a significant decrease ($p < 0.05$) in total macrofaunal abundance ($933.79 \pm 626.34$ ind m$^{-2}$ in unexploited stations compared to $140.92 \pm 71.99$ ind m$^{-2}$ in exploited stations; mean $\pm$ SE) in addition to a decline in biomass and taxonomic richness. Intertidal species composition was affected by both shellfish harvesting and PTEs. PTEs were also associated with a significant decrease in functional diversity and particularly with a change in macrofaunal living habits. The combination of an RLQ and fourth-corner analysis highlighted a significant association between feeding modes and sediment grain size in both tidal areas.

This study provides a needed deeper understanding of the unintended effects of human activities on infaunal communities and their functioning, in a highly valuable system for humans. Pinpointed factors driving infaunal community structure and functions provide important insights for future research, as well as reference points for the implementation of management measures.

## 1. Introduction

Many human socio-economic activities, from dam-building and skyscraper construction to forest clearing and dredging and canalization of water courses, constitute cases where humans effectively act as ecosystem engineers, modulating the flow of resources to other species by causing physical or chemical state changes in biotic and abiotic materials (Berke, 2010; Jones et al., 1994). Following their attempt to enhance their environment, humans are now facing unforeseen and unintended consequences (Gutiérrez et al., 2011; Smith, 2007), such as

increasingly threatened ecosystems, e.g., mangroves (Duke et al., 2007; Walters et al., 2008). Today, in the context of conservation, our efforts are increasingly geared towards reducing and reversing human modification of environments. Interest is consequently growing in understanding the nature and consequences of the environmental impacts of human activities and managing these activities to protect the well-being of human society and other life on Earth. Chu and Karr (2013) describe these issues as "humanity's greatest challenge".

Due to their environmental and economic value, growing interest in coastal wetlands arises, in particular for mangrove ecosystems (Lee et al., 2014). Intertidal assemblages of trees and shrubs localized along coastlines and estuaries in tropical and subtropical regions, i.e., mangroves, are highly productive ecosystems (Alongi, 2002; Bouillon et al., 2008). They are associated with both important ecological functions (e. g. primary and secondary production and nutrient cycling) and highly valuable goods and services for human society (Costanza et al., 1997). Not only are mangrove areas important places for human well-being, they are fundamental ecosystem-service hotspots, e.g. forming nurseries and feeding habitats for fish, providing a nutrient filtering function from land towards the open sea, serving as protection against natural disasters and as coastline stabilization (Brito and Naia, 2020), and acting as important fishing and exploitation grounds (Griffiths et al., 2017; Miller-Way and Twilley, 1996).

Almost one-fifth of the world's mangroves are found in Sub-Saharan Africa, and 70% of these are found in West Africa (Corcoran et al., 2007). Located in West Africa, Senegal harbors approximately 6000 km$^2$ of mangrove habitat, distributed along the Southern coast in three main areas: the Sine Saloum, the Petite Côte, and the Casamance. These mangroves contribute considerably to the social and economic well-being of inhabitants living in these regions. However, there was a loss of a quarter of the mangrove total surface area between 1980 and 2006 (Corcoran et al., 2007). The government of Senegal and the international community have since taken action to protect the biodiversity of these areas, because of the related socio-economic activities mainly dominated by fishing and its associated activities (from harvesting of the primary resource to commercialization of further processed fish and seafood products). The Sine Saloum and the Petite Côte areas are of great concern in terms of conservation and management because of the traditional and well-developed fishing activities of Senegalese women, particularly the harvesting of diverse mangrove invertebrates. These fisheries play a significant role in artisanal and small-scale commercial activities, and are important in providing a source of protein and income to coastal communities (Chapman, 1987; Matthews, 2002). Unfortunately, shellfish harvesting is considered a contributing factor of degradation for mangrove ecosystems. For example, techniques used to separate the West African mangrove oysters (*Crassostrea tulipa*) from the trees they are attached to, often injures or even kills the mangrove (Bousso, 1996). In addition to negative impacts observed due to shellfish harvesting, Bodin et al. (2013) highlighted the exposure of these mangroves and associated commercially important marine species to anthropogenic pollution, particularly to heavy metals. Also called "Potentially Toxic Elements (PTEs)", heavy metals are naturally occurring elements (e.g. cadmium (Cd), chromium (Cr), copper (Cu), lead (Pb), zinc (Zn), mercury (Hg), nickel (Ni)), but when present in elevated concentrations, they are typically associated with contamination and being potentially toxic to plants, animals and humans (Gustin et al., 2021; Zhang et al., 2022). Metallic enrichment of mangrove environments arises from human activities, such as mining operations, industrial effluents, agriculture runoff, aquaculture, boating and recreational use of water-bodies, chemical spills, and sewage discharge, associated with the use of artificial substances and fuels or production of waste and undesirable by-products containing heavy metals (C. Li et al., 2022). Such activities are impacting the biogeochemical cycling of heavy metals, hence causing pollution, in ecosystems such as West African mangroves (Bodin et al., 2013) and even in the most remote ecosystems on our planet (Majer et al., 2014).

Unintended consequences following human activities (such as heavy metal contamination) may be detected using bioindicators. Living within mangrove ecosystems, macrobenthic organisms (>1 mm) have intricate relationships with their environment, making them interesting as bioindicators of environmental status (Perus et al., 2007). Macrobenthic organisms are central to several ecosystem functions, e.g. promoting remineralization of organic matter, enhancing oxygen penetration depth in the sediments (Aller and Aller, 1998; Jovanovic et al., 2014), and playing an essential role in energy acquisition for higher trophic levels while serving as central food resource for epibenthic predators and demersal fish (Nilsen et al., 2006; Nordström et al., 2009). Due to their restricted mobility, macrofauna living in the sediment, called infauna, can have limited ability to avoid environmental and anthropogenic pressures. Many ecosystem functions and services provided by benthic infaunal communities are therefore threatened directly by human and terrestrial-driven impacts. As a result, infauna can be particularly impacted by stressors causing physical disturbances of the substratum such as shellfish harvesting (Skilleter et al., 2006; Spencer et al., 1998) or by stressors disrupting biogeochemical cycling of heavy metals and causing contamination (Dong et al., 2021; Ryu et al., 2011; Sizmur et al., 2019). Human ecosystem engineering and environmental disturbances can impact macrofaunal communities resulting in decreased abundance, biomass and/or diversity (Corte et al., 2021; Dauer, 1993; Pearson and Rosenberg, 1987). Moving beyond measures of basic taxonomic diversity to also consider the ecological characteristics of macrofaunal communities is important for evaluations of potential ecosystem functions. Combining both approaches is key in understanding how ecosystem functions are affected due to human activities and in highlighting potential feedback for humans. Ecological traits of macrobenthos (individual-level features of organisms, describing e.g., lifestyle, morphology, physiology, reproductive strategy, or life span) relate directly to their ecological processes and ecosystem function (Cadotte et al., 2011), and can respond rapidly to multiple stressors (Mouillot et al., 2013; Voß and Schäfer, 2017). In the past 20 years, many investigations have utilized a combination of taxonomic and trait diversity, which has developed our understanding of ecosystem function and supported efforts for better ecosystem management and conservation (Bremner et al., 2006; Henseler et al., 2019; Villnäs et al., 2019).

It is of great importance, in terms of conservation and management, to study the impacts of human activities on West African mangroves. Based on data from 2007 to 2008, our study aims to establish a conditions report for mangrove areas located in Southern West Senegal. We aim to disentangle structuring factors for macrobenthic communities at the time in Southern West Senegal by assessing the influence of environmental variables and human engineering impact (shellfish harvesting and heavy metal contamination) on infaunal community structure and functioning. Pinpointing factors driving infaunal community structure and functions in the past may provide important insights for future research, as well as reference points for the implementation of management measures. From a broader perspective, this study also aims to give insight into the unintended effects of human activities on infaunal communities and infauna-related functions through a trait-based approach.

## 2. Materials and methods

### 2.1. Study areas and sampling strategy

Two of the main mangrove areas in Senegal were investigated: the Sine Saloum and the Petite Côte (Fig. 1, Tab. A.1, Fig. A1), located in Southwest Senegal. As potential focal areas in terms of conservation and management, six stations were sampled between 2007 and 2008. Boubo (B) and Saré Makalé (M), near Falia, Dionewar (W), near the village of the same name, and Saré Acath (A), near Niodor, are located in the Sine Saloum region and more specifically in the Saloum Delta, and Diouham
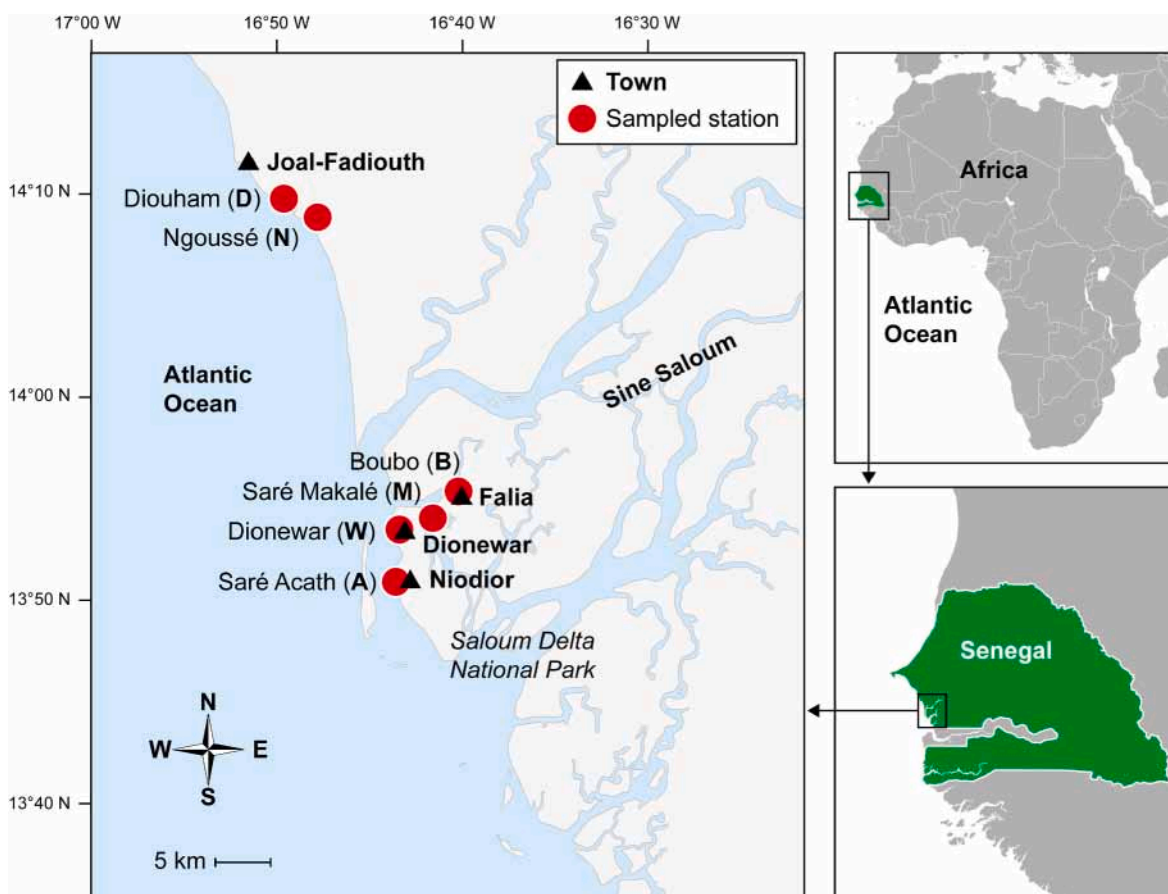
**Fig. 1.** Sampling stations location in Southern West Senegal.

(D) and Ngoussé (N), near Joal-Fadiouth, are located in the Petite Côte. These study areas are subject to a tropical climate with two alternate seasons: (i) a long dry season from November to June, characterized by air and water temperatures of about 17–25 °C and 20–22 °C, respectively, and dominated by hot and dry Harmattan wind, and (ii) a wet season extending from July to October, characterized by seasonal rainfall of about 600 mm, air and water temperatures of about 24–27 °C and 25–27 °C, respectively, and strong South-Eastern winds (Bodin et al., 2011).

The Saloum Delta is characterized by a dense network of small seawater creeks, locally named "bolongs". This "inverse estuary" is distinguished by water salinity that is higher than that of seawater (Barusseau et al., 1985; Descroix et al., 2020). In this particular environment, salinity increases from downstream to upstream due to the combined effects of seawater intrusion linked to weak slope, lack of significant freshwater inputs, and intense evaporation. The upstream area is highly hyperhaline, with salinity reaching 60 to 120 (Simier et al., 2004). Consequently, where salinity is moderate, half the area is occupied by the mangrove forest, mainly *Rhizophora* and *Avicennia* species, but these trees rapidly disappear when salinity increases to more than 60. Upstream, mangrove is thus replaced by extensive intertidal sand and silt flats (Diop et al., 1997; Gning et al., 2010).

The Petite Côte is located 20 km North of the Saloum Delta (Sambou et al., 2008). This lagoon-insular environment is subject to coastal dynamics because of its seaward opening and is composed of extensive mangroves and mudflats. Lying on an island of clamshells, Joal-Fadiouth is the closest city with 3500 inhabitants living on the small area of 500 m in diameter. Both highly open to the sea, poorly supplied with freshwater and subject to hypersaline events during dry seasons, the Saloum inverse estuary and the lagoon in the Petite Côte have previously been described as similar marginal coastal environments (Guiral et al., 1999;

Le Loeuff, 1999; Zabi and Le Loeuff, 1993, 1994).

To assess macrofaunal variability depending on the exposure to human activities, which occur more intensely closer to the coast, sampling was conducted in: (1) the intertidal and (2) the subtidal areas (Fig. 1). In these two tidal zones, stations were randomly selected in areas presenting different exposure to shellfish harvesting and to heavy metals, PTEs (see Fig. A1). In the Saloum delta, shellfish harvesting is based on the rotation of harvesting areas (Descamps, 1991; Sarr, 2005); areas left fallow for several months were considered non-exploited. Levels of PTEs were measured in a different study, conducted by Bodin et al. (2013), where they determined concentrations of 12 trace elements (Li, V, Cr, Mn, Co, Ni, Cu, Zn, Ag, Cd, Pb, and Hg) in surface sediment samples at the same sampling periods and in the same areas as in the present study. Because measurements were not from the exact same geographic coordinates and dates as the present study, we decided not to include the exact concentration values but the ecological conclusions instead (Table 2, Tab. A.1). Bodin et al. (2013) measured anthropogenic contamination with Cd, Hg and Ni in the Petite Côte (corresponding to station D), with Mn and Cr in Dionewar (corresponding to station W) and with Zn, Cu, V, Ag and Pb in both Dionewar (station W) and the Petite Côte (station D). These PTEs have already been shown as presenting a potential ecological risk for macrofaunal communities (Dong et al., 2021; Piló et al., 2016; Ryu et al., 2011).

In the intertidal zone at low tide, for a total of 87 samples, three to five 50 cm × 50 cm replicates were sampled for macrofauna in December 2007 and February, April, June and October 2008 (temporal sampling depended on stations, see Fig. A1). Sediment was scraped within the quadrat to a depth of about 20 cm using a hand shovel. Regarding the subtidal zone, a total of 56 macrofaunal samples were collected with a 0.1 m² Van Veen grab. Three to nine grab samples were taken at each station between 1 and 4 m depth in April, June and

**Table 1**
Traits and functional categories included in this study and their hypothesized relationships with factors responsible for special patterns in infaunal assemblages including traits helping to distinguish between natural and human-induced changes.

| Traits | Categories | Label | Definition | Key mechanisms and functions | Description and relevance | Hypothesized relationships with environment |
|---|---|---|---|---|---|---|
| Feeding mode (Feed) | Suspension/ filter feeder | susp | Feeding on the suspended matter or food particles in the water column. | Food acquisition, productivity, turnover, proxy for energy transfer, strength of benthic-pelagic coupling, prey accessibility | Feeding interactions have long been considered a central factor structuring macrobenthic communities (Pearson and Rosenberg, 1987). Feeding types contribute to production and trophic support, and play a role in nutrient uptake and recycling (Norling et al., 2007). It provides insights into the interactions between different species and their food sources. A diverse set of feeding modes indicates diverse food sources available in an area (Pacheco et al., 2011). The feeding mode is considered to be a proxy for energy fixation/transfer and ecosystem production (Törnroos and Bonsdorff, 2012). Predator–prey relationships and trophic levels are indicators of community structure, and are important for monitoring ecosystem changes enabling quantification of bottom-up linkages with flow webs, top-down linkages with ingestion/production webs and trophic position. | Scrapers and grazers are more abundant in areas with high levels of primary producers, usually found in areas with low depth (Dolbeth et al., 2007) and potentially low hydrodynamics. Predators and scavengers will be associated to areas with high availability of prey (Dolbeth et al., 2007). Scavengers are attracted to areas where physical disturbances occurs and are expected to be more common in areas of high fishing or harvesting intensity. Heavy metals are expected to favor large deposit-feeders (Dong et al., 2021; Piló et al., 2016; Selck et al., 1999). |
| | Scraper/ grazer | graz | Feeding on leaves or other plant parts. | | | |
| | Predator/ scavenger | pred | Feeding on living animals/ carcasses. | | | |
| | Deposit feeder | depo | Feeding on phytoplankton, litters and organic matter in the sediment and water column. | | | |
| Motility (Mov) | Motile Swimmer | swim | Free-swimming organisms. | Mobility, dispersal, susceptibility to cropping/predation and environmental pressures | Despite the generally restricted motility of benthic infauna, the small-scale motility of these organisms is crucial for the ecology of benthic communities. Not only motility provides insights into the ability to avoid physical disturbance (Hinchey et al., 2006) but also into the predatory-prey activities or the creation of biological structures. | Sessile organisms are more subject to changes in the abiotic environment than motile species (Sarà, 1986). Motile species are expected to have a better ability to avoid stressors (e.g. harvesting, heavy metals, drastic change in temperature and salinity …) and to be able to recolonize areas by migration (Gogina et al., 2014; Pacheco et al., 2011). |
| | Motile Crawler | crawl | Move on the sediment surface. | | | |
| | Motile Burrower | burr | Live in burrows within the sediment. | | | |
| | Sessile | sess | Sessile or very limited movement. | | | |
| Living habit (Liv) | Free-living | free | Free-living in the sediment. | Elemental cycling, productivity | Living habits are affecting habitat complexity, with the construction of biological structures for instance, and can influence nutrient recycling and trophic support (Bremner et al., 2006). | Burrow-dwellers and tubicolous are potentially less vulnerable to strong hydrodynamic disturbance, anoxic conditions and water pollution as opposed to free-living species because they can hide in their fixed tubes or burrow (Reise, 2002). |
| | Burrow dweller | dwel | Lives in burrows constructed by other organisms or themselves. | | | |
| | Tubicolous | tubi | Lives in a tube of its own construction. | | | |
| | Attached | atta | Attached on the surface to hard substrate. | | | |
| Maximum adult size (Size) | Very small | VS | 0–0.01 g | Growth rate, productivity, elemental cycling, metabolism, feeding interactions | The organism body size has a crucial relevance in the functioning and dynamics of aquatic systems (Woodward et al., 2005). Body size is correlated with many life-history traits and influences a wide range of biological and ecological functions (Bourassa and Morin, 1995; LaBarbera, 1989; Macdonald et al., 2012; Saiz-Salinas and Ramos, 1999; Warwick and Clarke, 1984). This biometric parameter can be more responsible for the trophic structure than taxonomic identity itself (Jennings et al., 2001). Biomass and biovolume affect the activity and function in the ecosystem (Brown et al., 2004). | Small-bodied species may characterize environments with high instability, the result of environmental/ anthropogenic disturbances imposed on the organisms (Mouillot et al., 2006). We expect small-sized species to be prevalent in high hydrodynamic areas (Donadi et al., 2015) and to have higher P/B ratios (Schwinghamer, 1983) with higher metabolic rates (Gillooly et al., 2001). Harvesting and high levels of heavy metals in the sediment might favor smaller individuals; whereas low levels of heavy metals are expected to be dominated by large-sized individuals (Dong et al., 2021; Piló et al., 2016). |
| | Small | S | 0.01–0.1 g | | | |
| | Medium | M | 0.1–1 g | | | |
| | Large | L | >1 g | | | |

**Table 2**
Covariates with their assumed relevance and expected relationships to structural diversity and to functional diversity and the selected response traits.

| Covariate \| Modalities or unit | | Relevance | Expected relationships with: | |
| --- | --- | --- | --- | --- |
| | | | Structural diversity | Functional diversity and response trait |
| Physical environment variables | **Season** Wet Dry | The Saloum system is subject to a tropical climate with two alternate seasons characterized by drastic changes in temperature, salinity, freshwater discharge, turbidity, sedimentation, currents … Seasonal fluctuations of environmental factors and different land usage patterns may explain macrofaunal community variations by season (Dirisu and Edwin-Wosu, 2022; P. Li et al., 2022). | **Season (Wet):** Abundance (−) Diversity (−) Taxa composition (≠) (Melo et al., 2013) | **Season (Wet):** Functional diversity (stable) Akoumianaki et al. (2013) |
| | **Habitat** Estuary Lagoon | Two of the main Southern West Senegal mangrove areas were investigated: the Sine Saloum and the Petite Côte. These areas are both transition zones between land and sea. They are also insular and present extensive mangroves and mudflats with coastal dynamics. Both poorly supplied with freshwater and subject to hypersaline events during dry seasons, the Saloum inverse estuary and the lagoon in the Petite Côte have previously been described as similar environments (Guiral et al., 1999; Le Loeuff, 1999; Zabi and Le Loeuff, 1993, 1994). Despite their similarities, they still might differ in terms of habitat, the Saloum Delta being an inverse estuary and the Petite Côte a lagoon. Therefore, they might present differences in hydrodynamics and flushing time, making this covariate important to investigate. | **Habitat (Lagoon):** Abundance (stable) Diversity (+) Giménez et al. (2014) | — |
| | **Salinity** (PSU) | Salinity and temperature are major driving variables for macrofaunal communities (P. Li et al., 2022). Salinity has been reported as the main environmental factor affecting benthic macrofauna community composition and structure in estuarine ecosystems (Conde et al., 2013; Little et al., 2017; Verdelhos et al., 2015). Considering climate change (Mahe et al., 2013; Olivry, 1987) and drastic environmental conditions occurring in inverse estuaries (Barusseau et al., 1985; Descroix et al., 2020), salinity and temperature are particularly important factors to consider. Particularly in estuaries and lagoons of West Africa, Zabi and Le Loeuff (1993) showed that macrofaunal species repartition was linked to fluctuations in temperature and salinity. | **Salinity (+):** Abundance (+) Zhong et al. (2020) **Salinity (Hypersaline):** Abundance (−) Lam-Gordillo et al. (2022) | **Salinity (Hypersaline):** Functional diversity (−) Size: VS (+), S (+), M (−), L (−) Feeding mode: depo (+), susp (+) Living habit: dwel (−) Lam-Gordillo et al. (2022) |
| | **Temperature** (°C) | | — | **Temperature (+):** Size: VS (−), S (−), M (+), L (+) (Atkinson and Sibly, 1997; van der Linden et al., 2016) |
| | **Depth** (m) | Benthic invertebrates are restricted to specific depths, which can be related to different hydrostatic pressures and food availability (Warwick, 1984). In our area of interest, Leung Tack (1985) described mollusc species distribution depending on depths. | **Depth (+):** Biomass (−) Zhong et al. (2020) | **Depth (+):** Size: VS (+), S (+), M (−), L (−) LaBarbera (1989) |
| Sediment properties | **Fine particle fraction (% Mud)** (% of particles <63 μm, Silt + Clay) **Median grain size (D50)** (μm) | Sediment characteristics are often a significant explanatory factor in macrofaunal taxonomic and trait composition (Anderson, 2008; Jacquot et al., 2018; Mwakisunga et al., 2020). Used in numerous other benthic studies, median grain size and percentage of fine particles (<63 μm) are complementary in describing sediment properties (Dauwe et al., 1998). | **%Mud (+) and D50 (+):** Abundance (+) (Van Hoey et al., 2004; Zhong et al., 2020) | **%Mud (+):** Feeding mode: susp (−), depo (+) (Shull, 2009; Steele-Petrovic, 1975) |
| Human ecosystem engineering structural factors | **Harvesting** Exploited Unexploited | Human engineering through shellfish harvesting has been identified as one of the factors inducing degradation of mangroves globally and specifically in Southern West Senegal (Gallup et al., 2020). Harvesting activities have community-wide effects in highly diversified tropical ecosystems changing the structure and species composition including targeted and non-targeted species (Jimenez et al., 2015). | **Harvesting (Yes):** Abundance (−) Biomass (−) Aswani et al. (2015) | **Harvesting (Yes):** Size: VS (+), S (+), M (−), L (−) Jimenez et al. (2015) |
| | **Heavy metals (Potentially Toxic Elements, PTEs)** Contaminated with Cd Hg Ni (yes/no) Contaminated with Zn Cu V Ag Pb (yes/no) Contaminated with Mn Cr (yes/no) | Among the major pollutants from anthropogenic inputs that reach mangroves are heavy metals (C. Li et al., 2022; MacFarlane et al., 2007), also called "Potentially Toxic Elements (PTEs)" (Zhang et al., 2022). Bodin et al. (2013) measured anthropogenic contamination with Mn and Cr in Dionewar (station W), with Cd, Hg and Ni in the Petite Côte (station D) and with Zn, Cu, V, Ag and Pb in both Dionewar (station W) and the Petite Côte (station D). PTEs have directly and/or indirectly led to biodiversity and functional diversity loss in macrobenthic communities (Dong et al., 2021; Piló et al., 2016). | **PTEs (+):** Abundance (−) Diversity (−) (Rabaoui et al., 2015; Ryu et al., 2011) | **PTEs (+):** Size: VS (+), S (+), M (−), L (−) Feeding mode: depo (+), pred (−) Living habit: dwel (+), free (−) Motility: crawl (−), swim (−) (Dong et al., 2021; Piló et al., 2016) |

November 2008, as indicated in Fig. A1. Both sampling methods allow collection of infauna as well as sedentary and slow mobile species such as bivalves and gastropods. This sampling approach is less accurate for estimating mobile animals, such as crabs, and using quadrats is restricted to fauna inhabiting the top 20 cm of the sediment. The recorded macrobenthic communities in this study are therefore focused on a component of the sediment community. Crabs that were caught were retained in the dataset. For each site and sampling occasion, three samples of sediment were extracted for grain size analysis. In the subtidal zone, measurements of temperature and salinity were recorded at the bottom of the water column at each station using a YSI Multiparameter probe.

### 2.2. Sample processing

Sediment samples were collected and analyzed for median grain size and fine particle fraction. Sediment grain size was determined by water- (for 63 μm grain size fraction) and dry-sieving, using a series of 14 sieves from 63 μm to 10,000 μm. Sediment grain size characteristics were calculated for median grain size, percentage of gravel, sand and mud. Gravel represents the fraction with particles larger than 2 mm, sand is the fraction ranging from 63 μm to 2 mm, and mud is defined as the sediment exhibiting grain sizes smaller than 63 μm and is described as the fine particle fraction (Blott and Pye, 2001) (Fig. A2).

Regarding macrofaunal analysis, each replicate was treated separately to assess intra-station variability. For both intertidal and subtidal zones, sediments were washed through a 1 mm square-meshed sieve, and retained material was preserved in 7% formalin and stained with 1% Rose Bengal. Macrobenthic organisms were removed from all debris, identified and counted. Taxonomic identification was carried out at family level for polychaetes and at the lowest possible taxonomic level for all other taxa (Gerwing et al., 2020). Mollusca taxa for each sample were dried at 60 °C during 48 h, and dry weight was measured to 0.01 g. The wet weight of non-shellfish taxa for each sample was measured to 0.1 mg after blot-drying on tissue paper. Taxa-specific conversion factors provided by Brey (2001) were used to convert wet weight into dry weight.

Four ecological traits were selected based on their potential ability to reflect key biological and ecological processes with respect to human ecosystem engineering and abiotic stressors. These traits, including feeding mode, motility, living habit and maximum adult size, were subdivided into 16 categories in total (Table 1). Information on these traits was collected for the lowest possible taxonomic level from a variety of published sources: literature (e.g. Jumars et al., 2015), species identification guides (e.g. Kornienko, 2013; Passos et al., 2005), and online databases, such as Polytraits (Faulwetter et al., 2014), BIOTIC —Biology Traits Information Catalogue (MarLIN, 2006), and WoRMS—World Register of Marine Species http://www.marinespecies. org. In cases where trait data for a species were not available, they were inferred from other species in the same genus or the same family (Boyé et al., 2019). Trait categories were then scored using a fuzzy coding approach (Chevene et al., 1994), with a scoring range of 0 (no affinity) to 3 (total affinity towards trait category) (D'Alessandro et al., 2020; Hu et al., 2019; van der Linden et al., 2016).

### 2.3. Statistical analyses

Data collected in the intertidal and the subtidal zones were analyzed separately in all statistical analyses described hereafter.

Macrofauna diversity was assessed employing the following primary community variables and diversity indices (Gray and Elliott, 2009): abundance (Ab), taxonomic richness (S) and Shannon's diversity index (H′) Pielou's evenness (J) and Simpson's diversity index (1-D, hereafter D). In addition to our interest in taxonomic diversity, three multidimensional indices were also considered in this study as components of functional diversity with the following: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Laliberté and Legendre, 2010; Villéger et al., 2008). These indices were built to be complementary (Villéger et al., 2008) and identified as a relevant combination to fill the functional space of a community (Mouchet et al., 2010). FRic describes the amount of trait space occupied by the species within a community and therefore represents the number of trait categories expressed. FEve refers to how evenly species abundances are distributed between the expressed trait categories (low value indicating that some parts of niche space are under-utilized). FDiv defines the distribution of the abundance across the niche space, with a higher value indicating a high degree of niche differentiation (Mason et al., 2005).

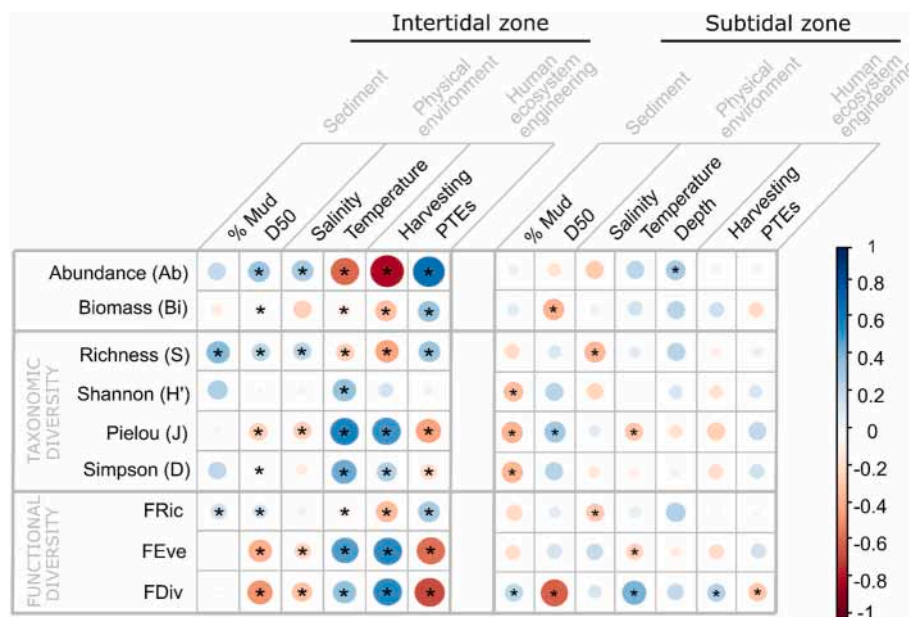To test for significant differences in abundance and biomass (Bi)



**Fig. 2.** Spearman correlation between structural and functional diversity indices and environmental variables (sediment, physical environment and human ecosystem engineering) in the intertidal and subtidal zone. * indicating p < 0.01. % Mud = fine particle fraction of sediment, D50 = sediment median grain size, PTEs = Potentially Toxic Elements, FRic = functional richness, FEve = functional evenness, FDiv = functional divergence. Covariates are further explained in Table 2.

between stations, the Kruskal-Wallis one-way analysis of variance by ranks was used because the data do not meet assumptions for one-way ANOVA. Since the sample sizes are not equal and the assumption of equal variances is not met, we performed this non-parametric test, equivalent to an ANOVA but much more robust to unequal sample sizes and unequal variances across treatment combinations. Provided that significant differences were detected by the test ($p < 0.05$), post-hoc tests for pairwise multiple comparisons (Nemenyi's test) were used to identify differences between pairs of stations.

To test the link between the macrofaunal assemblages based on their beta diversity and the different ecological factors, non-metric multidimensional scaling (nMDS) were performed. First, Bray-Curtis coefficient was used to calculate the dissimilarity matrix for species community structure analysis and then the results were visualized with nMDS. The environmental factors were fitted on the ordination diagrams after a permutation test (999 permutations) allowing to discriminate variables having a significant influence ($p < 0.05$). To ensure the interpretation of the nMDS results, stress values were calculated (Clarke, 1993). This analysis assesses the influence of the following variables on taxa abundances across samples: sampling date, sampling station, habitat, season, salinity, temperature, depth, sediment fine sediment particle fraction (% mud), sediment median grain size (D50), harvesting, and heavy metals (Mn and Cr, Cd, Hg and Ni and/or Zn, Cu, V, Ag and Pb) (Table 2).

To explore the relationship between the ecological traits of macrobenthos and environmental gradients, a combination of RLQ (Dolédec et al., 1996) and fourth-corner analyses (Legendre et al., 1997) according to Dray et al. (2014) was applied. For the RLQ analysis, tables for environmental variables (R), species abundance (L), and traits (Q) were analyzed using Hill-Smith analysis, correspondence analysis (CA), and principal component analysis (PCA), respectively (Dray et al., 2014). The overall significance of this relationship was assessed using a global Monte Carlo test with 49,999 random permutations of models 2 and 4 (Dray et al., 2014; Dray and Legendre, 2008). Model 2 tests whether the distribution of species with fixed traits is influenced by the environmental conditions while model 4 tests whether traits influence the composition of species assemblages found in samples, keeping environmental conditions fixed (Dray et al., 2014). In addition, because RLQ analysis cannot determine which traits are affected by specific environmental variables, fourth-corner analysis, with an adjusted p-value (false discovery rate method, FDR) (Benjamini and Hochberg, 1995) for multiple testing, was applied. Furthermore, by combining both RLQ and fourth-corner analyses, the significance of the association between environmental variables or traits and the RLQ axes was investigated (Dray et al., 2014).

Variance partitioning analysis (VPA) was performed to evaluate the contribution of human ecosystem engineering, sediment properties and environmental factors to the variance in structural and functional diversity. Prior to this analysis, covariates were divided into three groups, one of which was human ecosystem engineering (i.e. shellfish harvesting and heavy metals), another one was variables related to the physical environment (i.e., season, habitat, depth, temperature and salinity) and the last one was sediment variables (i.e., fine particle fraction and median grain size). We computed adjusted $R^2$ following Peres-Neto et al. (2006) recommendations to produce unbiased estimates of the fractions of variation. Separate forward selection on each subset of environmental variables were conducted and only variables explaining a significant variation ($p < 0.05$) were retained in the VPA. To ensure the significance of the VPA, we tested all fractions independently using two-way ANOVA.

All analyses were performed using the R Statistical Software (R Core Team, 2022). The functional diversity indices (FRic, FEve, and FDiv) were calculated using the "FD" package (Laliberté and Legendre, 2010) based on the fuzzy coding matrix of the traits and the abundance of species. Spearman correlation tests between taxonomic and functional indices and environmental variables were performed in the "corrplot" R package (Wei and Simko, 2017). RLQ and fourth-corner analyses were performed in the "ade4" R package (Dray and Dufour, 2007). Both the nMDS and the VPA were performed using the "vegan" package (Oksanen et al., 2011).

## 3. Results

Original data of this study including abundances, biomass, environmental variables and traits are available at Mendeley Data (https://doi.org/10.17632/xtdjv38vst.1). Among the 142 samples in the study, a total of 12,418 macrofauna individuals were identified belonging to 127 different taxa. A total of 71 taxa were found in the intertidal zone and 104 in the subtidal zone with 48 taxa found in both areas. Taxonomic richness was similar in both the Saloum Delta and the Petite Côte with a total of 54 and 51 taxa respectively, and 34 taxa in common.

### 3.1. Infaunal diversity patterns

Regarding diversity, a strong positive correlation was highlighted between temperature and most indicators of taxonomic and functional diversity in the intertidal zone, especially the Pielou index and functional evenness (FEve; Fig. 2). The same was observed for harvesting on diversity in the intertidal zone. On the contrary, temperature and harvesting had a significant negative impact on abundance and biomass in the intertidal zone. In the same zone, PTEs showed a positive relationship with abundance and biomass, while negatively affecting functional evenness and divergence (FDiv; Fig. 2). In the subtidal zone, median grain size (D50) negatively affected functional divergence, while the percentage of mud negatively affected mostly taxonomic diversity indices. Otherwise, temperature had a positive impact on functional divergence (Fig. 2). Overall, functional and taxonomic diversity were mostly affected by human ecosystem engineering variables and temperature in the intertidal zone, while sediment and variables describing the physical environment (salinity, temperature and depth) appeared as the most important factors for the subtidal zone.

### 3.2. Disentangling drivers of infaunal community composition and structure

Overall total abundances did not differ between the intertidal zone ($491.26 \pm 575.56$ ind m$^{-2}$; mean $\pm$ SE) and in the subtidal zone ($369.10 \pm 244.50$ ind m$^{-2}$; mean $\pm$ SE) (Kruskal-Wallis test with $p = 0.20$) (Fig. 3). In most of the stations of both zones, Annelida and Mollusca clearly dominated in terms of abundance and biomass (Fig. 3). However, the tidal zones were different in terms of species composition with an average between-group dissimilarity in species composition of 92.35%, as shown by SIMPER analysis. Indeed, Annelida and Mollusca species dominating the areas were different. In the intertidal zone, Annelida were mainly represented by Capitellidae (132 ind m$^{-2}$; mean), *Golfingia (Golfingia) vulgaris* (96 ind m$^{-2}$; mean) and Nereididae (24 ind m$^{-2}$; mean) and Mollusca by bivalves with *Senilia senilis* (109 ind m$^{-2}$; mean) and *Loripes orbiculatus* (34 ind m$^{-2}$; mean). In the subtidal zone, Annelida were mainly represented by Orbiinidae (52 ind m$^{-2}$; mean), Cirratulidae (21 ind m$^{-2}$; mean) and Goniadidae (19 ind m$^{-2}$; mean) and Mollusca again by bivalves but with *Diplodonta diaphana* (33 ind m$^{-2}$; mean), *Senilia senilis* (33 ind m$^{-2}$; mean) and *Moerella distorata* (30 ind m$^{-2}$; mean). In the intertidal zone, total macrofaunal abundance (Kruskal-Wallis = 64.062, $p < 0.01$; Nemenyi's post-hoc, $p < 0.05$) and biomass (Kruskal-Wallis = 35.643, $p < 0.01$; Nemenyi's post-hoc, $p < 0.05$) were significantly higher at unexploited stations (Ab = $933.79 \pm 626.34$ ind m$^{-2}$, Bi = $5.77 \pm 4.63$ gDW m$^{-2}$; mean $\pm$ SE) compared to exploited stations (Ab = $140.92 \pm 71.99$ ind m$^{-2}$, Bi = $3.33 \pm 2.46$ gDW m$^{-2}$; mean $\pm$ SE) (Fig. 3). No significant difference was found between the different stations in the subtidal area ($p > 0.05$) (Fig. 3).

Variability among stations has been demonstrated in terms of taxonomic characteristics of macrobenthic communities. To identify factors underlying these differences, nMDS analyses were conducted for the
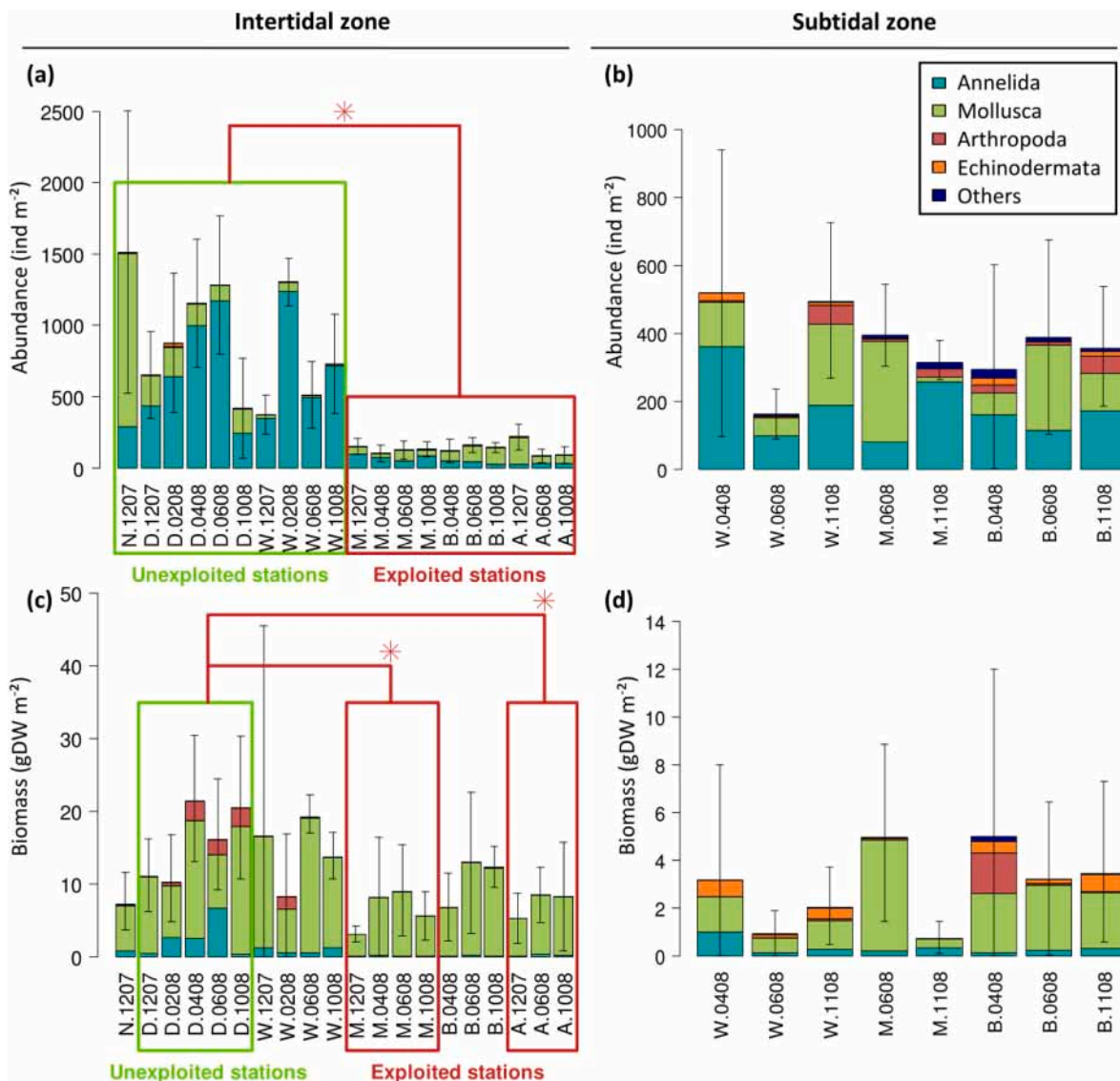
**Fig. 3.** Mean and standard error abundances [ind m$^{-2}$] (a, b) and biomass [gDW m$^{-2}$] (c, d) of macrofaunal taxa in intertidal zone (a, c) and subtidal zone (b, d) for stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N) and Dionewar (W)) and sampled date (December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)). Other taxa (Others) include Porifera, Cnidaria, Platyhelminthes, Nemertea and Chordata. Red stars indicate significant differences (p < 0.05) between stations, based on Kruskal-Wallis tests with Nemenyi's post-hoc tests. Please note the difference in scale between the intertidal and subtidal results. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

intertidal zone (Fig. 4a, c) and for the subtidal zone (Fig. 4b, d). In both tidal zones, nMDS presented stress values of 0.08 corresponding to "good ordinations with no real risk of drawing false inferences", as explained in Clarke (1993). In the intertidal zone, the nMDS explained 63.56% of the total variability in the community structure (Fig. 4a, c). Specifically, factors having a significant influence on the community structure (p < 0.05) were mostly related to human activities with shellfish harvesting (R$^2$ = 0.73) and PTEs (contaminated with Zn, Cu, V, Ag and Pb (R$^2$ = 0.77), with Mn and Cr (R$^2$ = 0.46) and with Cd, Hg and Ni (R$^2$ = 0.46)) (Fig. 4a). Factors related to the physical environment characteristics (temperature (R$^2$ = 0.35), habitat (R$^2$ = 0.31), salinity (R$^2$ = 0.11) and season (R$^2$ = 0.06)) and the sediment properties (D50 (R$^2$ = 0.13), % Mud (R$^2$ = 0.09)) also significantly (p < 0.05) contributed to explain macrofaunal communities patterns (Fig. 4a). Clusters showed the major influence of shellfish harvesting (unexploited vs. exploited stations) in explaining the similarities between stations (Fig. 4c). In the subtidal zone, 36.97% of the total variability in the macrofaunal community structure was explained by the nMDS (Fig. 4b,

d). Factors having a significant influence on the subtidal community structure (p < 0.05) included physical environmental parameters with salinity (R$^2$ = 0.16), depth (R$^2$ = 0.10) and season (R$^2$ = 0.05) in addition to the sediment median grain size (R$^2$ = 0.19) (Fig. 4b). In the subtidal area, the macrobenthic community was more structured by seasons (Fig. 4d) than by shellfish harvesting.

*3.3. Disentangling drivers of infaunal community traits*

Regarding traits, both zones were dominated by deposit feeders, burrowers, sediment dwellers and medium-sized animals, whereas the subtidal zone also presented a high proportion in free-living individuals (Fig. 5b and c). Feeding modes were similar in both zones with a dominance of deposit feeders and suspension/filter feeders and the presence of predators/scavengers (Fig. 5b and c). In terms of motility, both zones were dominated by burrowers and crawlers were more abundant in the subtidal zone than in the intertidal (Fig. 5b and c). Dominance in terms of living habitats was balanced between burrow
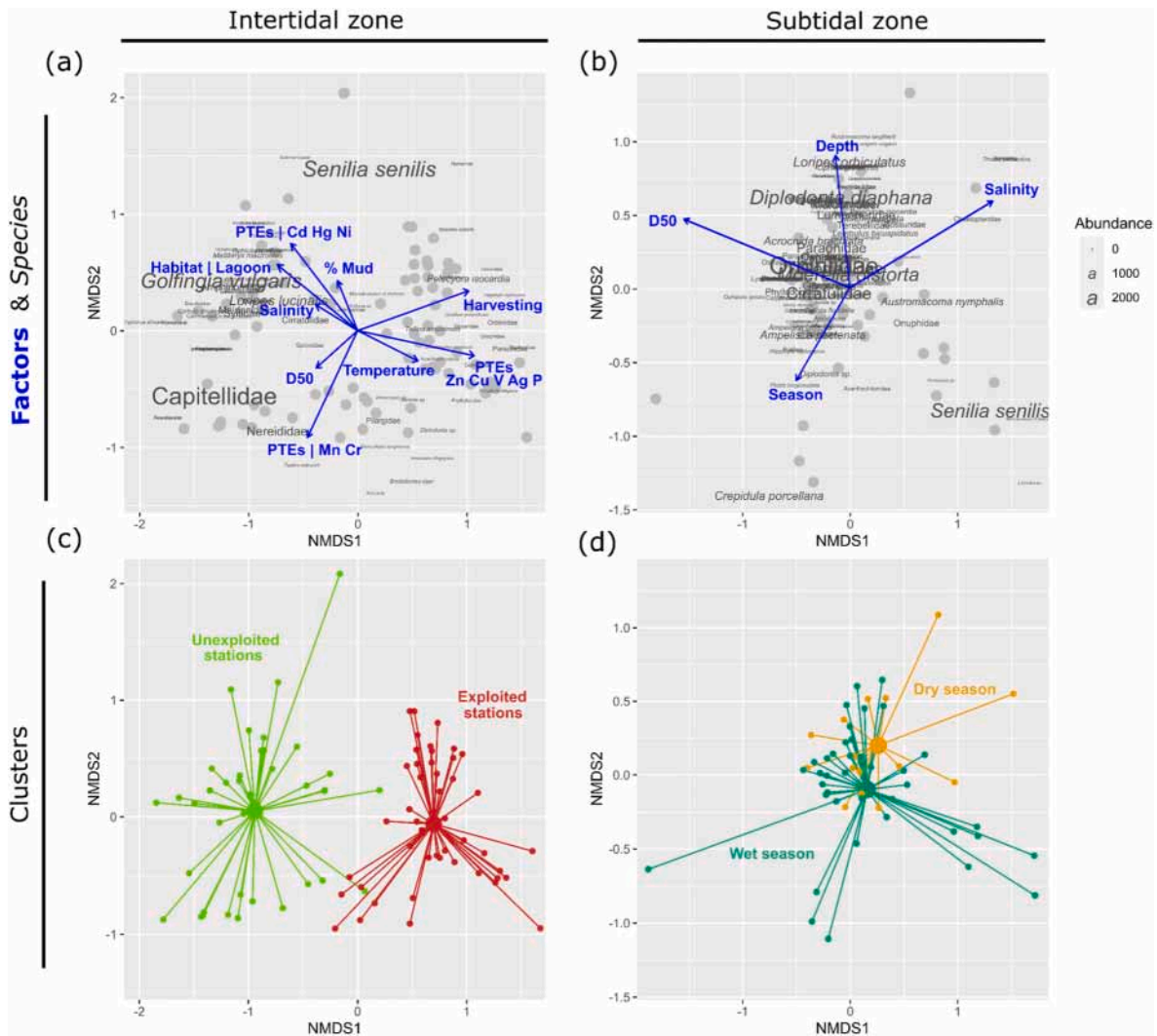
**Fig. 4.** nMDS ordination of untransformed macrofaunal community data (based on Bray- Curtis similarity) in the intertidal zone (a, c) and subtidal zone (b, d). Fitted environmental variables (a, b) with significant influence on the distribution of stations ($p < 0.05$) (blue arrows), macrofaunal taxa present in the different stations and having a significant influence on the distribution of these stations in the analysis (text in dark grey) and stations (grey points) sampled between December 2007 and November 2008. Clusters revealed by hierarchical clustering analysis based on transformed abundances data (Bray-Curtis), grouping unexploited and exploited samples in the intertidal zone (c) and grouping stations depending on season in the subtidal zone (d). Exploited stations are indicated in red and unexploited ones in light green, wet season in dark green and dry season in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

dwellers and free-living individuals in the subtidal zone, whereas the intertidal zone presented higher proportions of burrow dwellers (Fig. 5b and c). Regarding maximum adult sizes, both areas were dominated by medium-sized individuals with a higher proportion of large individuals in the intertidal zone and the presence of small-sized individuals in the subtidal zone (Fig. 5b and c).

In both intertidal and subtidal zones, the RLQ analysis identified that feeding modes were associated with sediment median grain size (D50) (Fig. 6). More specifically, sediment median grain size (D50) presented a negative significant association with suspension/filter feeders (intertidal zone: $R^2 = -0.41$, $p < 0.05$; subtidal zone: $R^2 = -0.27$, $p < 0.05$) and a positive significant association with deposit feeders (intertidal zone: $R^2 = 0.40$, $p < 0.05$; subtidal zone: $R^2 = 0.33$, $p < 0.05$) (Fig. 6ab). In the subtidal zone, suspension/filter feeders were associated with higher temperatures ($R^2 = 0.23$, $p < 0.05$) and deposit feeders were also associated with other variables (Fig. 6b), indeed presenting a negative significant association with temperature ($R^2 = -0.30$, $p < 0.05$) and positive significant associations with the dry season ($R^2 = 0.29$, $p <$

0.05) (Fig. 6b). Also in both tidal areas, living habits were significantly associated with PTEs (Fig. 6). Stations contaminated with Cd, Hg and Ni were negatively associated with burrow dwellers in the intertidal zone ($R^2 = -0.50$, $p < 0.05$) (Fig. 6a) and in the subtidal stations contaminated with Mn and Cr presented a significant positive association with tubicolous ($R^2 = 0.21$, $p < 0.05$) (Fig. 6b). In the intertidal zone, burrow dwellers were also associated with habitat: the lagoon located in the Petite Côte showed fewer burrow dwellers than the Saloum estuary ($R^2 = 0.42$, $p < 0.05$) (Figs. 5a and 6a). In the subtidal zone, tubicolous individuals were also positively associated with the dry season ($R^2 = 0.24$, $p < 0.05$) (Fig. 6b). Motility was associated with both temperature and salinity in the intertidal zone, crawlers were significantly negatively associated with higher salinity ($R^2 = -0.13$, $p < 0.05$) and positively associated with higher temperature ($R^2 = 0.17$, $p < 0.05$) (Fig. 6a). Higher temperatures in the subtidal zone were associated with larger individuals ($R^2 = 0.25$, $p < 0.05$) (Fig. 6b).
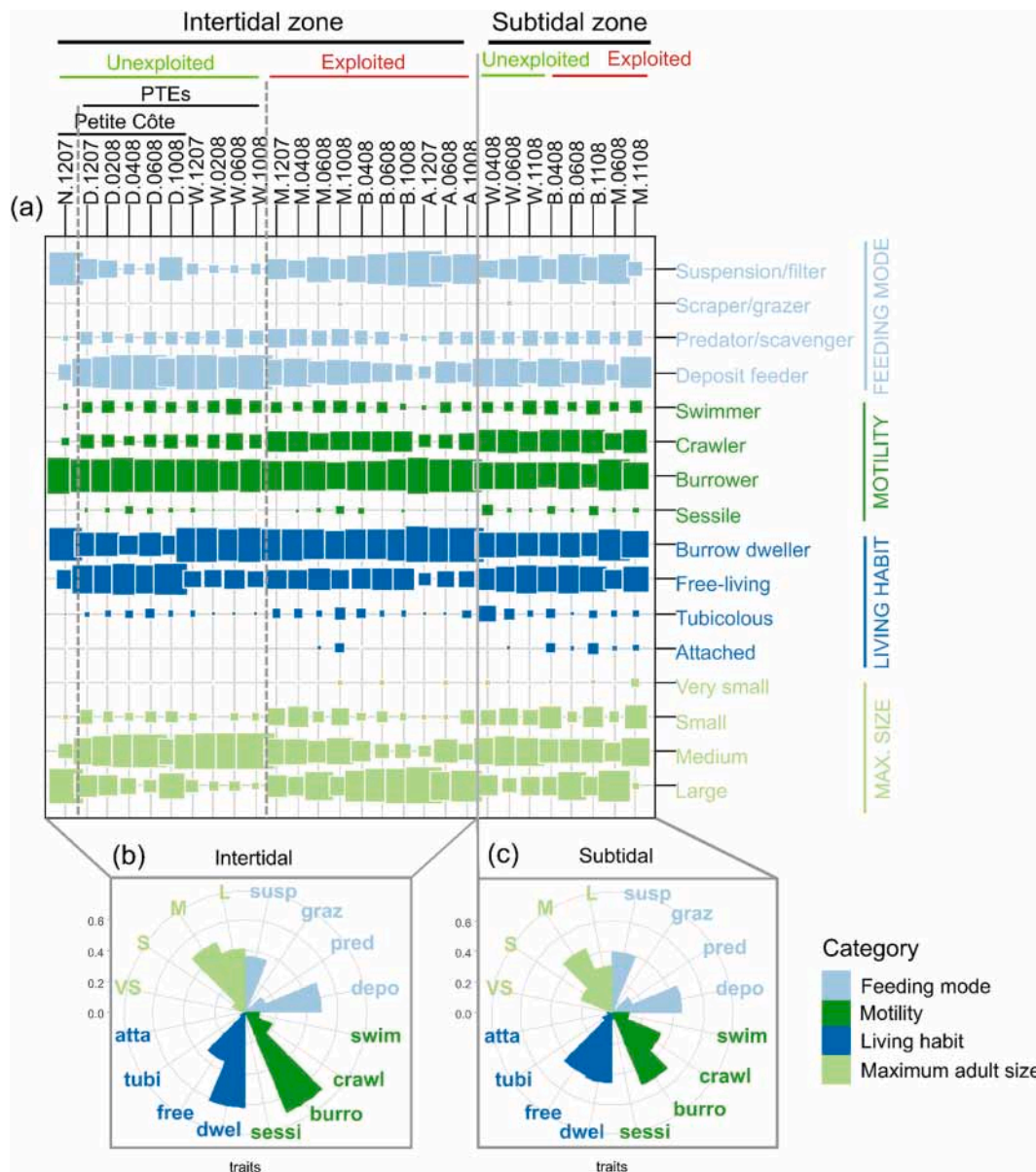
**Fig. 5.** Mean relative abundance [ind m$^{-2}$ reduced in proportions] of the different traits in sampled stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N), Dionewar (W)) at different sampling data (December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)) in intertidal and subtidal zone. Codes for traits are explained in Table 1.

### 3.4. Relative importance of drivers of infaunal structural and functional diversity

In the intertidal zone, results of the variance partitioning analysis showed that human ecosystem engineering (here exemplified through harvesting and PTEs) played a more important role in determining the structural and functional diversity than sediment properties and environmental variables (Fig. 7). The variation in structural diversity explained by human ecosystem engineering, sediment properties and environmental variables alone was 33%, 12% and 22%, respectively, and the variation explained in functional diversity was 35%, 9% and 10%, respectively (Fig. 7). In contrast, results of the VPA showed that sediment and environmental variables were the most important variables in the subtidal zone. The variation in structural diversity in this area explained by human ecosystem engineering, sediment properties and environmental variables alone was 4%, 7% and 14%, respectively. Regarding the functional diversity, the variation explained by human ecosystem engineering, sediment properties and environmental

variables alone was 6%, 18% and 22%, respectively (Fig. 7). Overall, drivers of abundance and traits are more explained with our set of variables in the intertidal than in the subtidal zone (Fig. 7).

## 4. Discussion

To our knowledge, this study is the first in this area to assess the influence of environmental variables and human activities (shellfish harvesting and PTEs) on infaunal community structure and functions through trait-based approaches. So far, studies in Southwest Senegal have mainly focused on fish communities (Diouf, 1996; Ecoutin et al., 2010; Simier et al., 2004), food webs (Faye et al., 2011; Gning et al., 2010), as well as persistent organic pollutants (POPs) and heavy metal contamination in bivalves and gastropods (Bodin et al., 2011, 2013). Only a few studies have focused on the whole invertebrate benthic communities, with the latest studies conducted in 1985 (Ausseil-Badie and Monteillet, 1985; Leung Tack, 1985) and the latest review in 1999 (Le Loeuff, 1999). Infauna data from 2007 to 2008 are thereby valuable
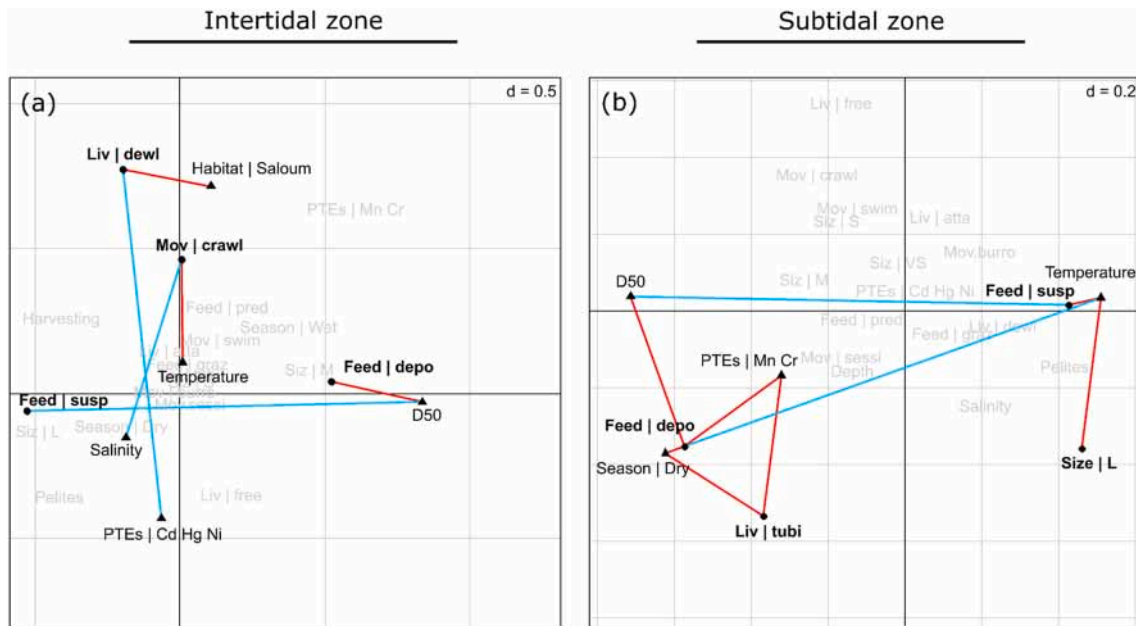
**Fig. 6.** Ordination biplot of significant (p < 0.05) associations identified by the fourth-corner method on the factorial map of RLQ analysis. The values of d give the grid size. Positive significant associations are represented by red lines and negative significant associations by blue lines. Traits are in boldface type and are represented by circles; environmental variables are in lightface type and are represented by triangles. Variables with no significant associations are shown in light grey. P values were adjusted for multiple comparisons using the FDR procedure. Codes for traits and environmental variables are explained in Tables 1 and 2, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
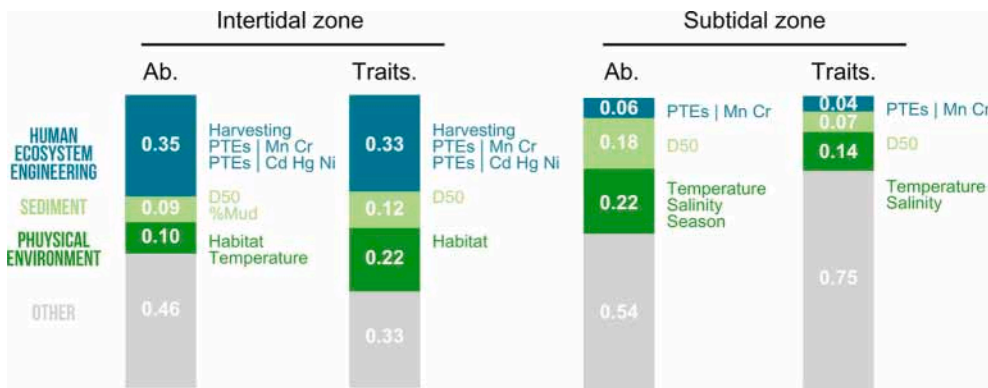


**Fig. 7.** Variance (adjusted $R^2$) of the structural (Ab.) and functional (Traits) diversity uniquely attributed to human ecosystem engineering activities (Human ecosystem engineering) (blue), to sediment variables (Sediment) (light green), and to physical environmental variables (Physical environment) (dark green) in the intertidal and subtidal zones. The residual variance is identified as "Other" (grey). Significant variables (p < 0.05) included in the variance partitioning are listed on the right side of the corresponding histogram. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

in filling a knowledge gap and constitute a valuable conditions report for follow-up research in this region. With environmental data and infaunal samples collected in two of the main Southern West Senegal mangroves areas, the Sine Saloum and the Petite Côte, the present study identified significant relationships between environmental descriptors and the infaunal community structure and functioning.

Six stations at the mouth of the Saloum Delta and a nearby lagoon of the Petite Côte highlighted a dominance of molluscs and polychaetes in terms of taxonomic diversity, abundance and biomass. This qualitative and quantitative dominance is consistent with previous studies on Senegalese macrofauna (Ausseil-Badie and Monteillet, 1985; Bouchet, 1977; Elouard and Rosso, 1977; Leung Tack, 1985; Seck, 1996; Zabi and Le Loeuff, 1993). Highly open to the sea, poorly supplied in freshwater and subject to hypersaline events during dry season, in addition to presenting high proportions of marine species compared to other marginal coastal ecosystems, the Saloum inverse estuary and the lagoon located at Petite Côte are described in the literature as similar ecosystems. Indeed, Zabi and Le Loeuff (1993) described six main marginal coastal habitats in West Africa based on major geomorphological and hydroclimatic parameters and on benthic communities, and one of their

groupings contained both our study areas. This explains our results showing similar taxonomic dominance and richness in both the Saloum Delta and the Petite Côte with a total of 54 and 51 taxa respectively. However, we also observed differences in taxonomic and trait composition, highlighting "habitat" as a driving factor for infaunal communities in the intertidal zone. Smaller proportions of burrow dwellers were found in the Petite Côte, which is mostly explained by the dominance of the free-living Sipuncula *Golfingia (Golfingia) vulgaris* in communities of the Petite Côte, whereas this taxa was found in low abundances in the Saloum Delta. Despite their overall similarities compared to other marginal coastal ecosystems, Guiral et al. (1999) also highlighted small differences in terms of species composition between the two areas, supporting our results.

Seasonal conditions were expected to be of high importance in explaining macrofaunal community structure and functioning; which was confirmed in the subtidal zone. Our results are consistent with previous studies conducted in the same area (Ausseil-Badie and Monteillet, 1985; Le Loeuff, 1999; Zabi and Le Loeuff, 1993) in the subtidal zone but not in the intertidal zone. Rather than focusing only on seasons, Dirisu and Edwin-Wosu (2022) and P. Li et al. (2022) highlighted the

importance of looking at the impact of human activities in the intertidal zone. Indeed, harvesting and PTEs played a major role in determining the structural and functional diversity in the intertidal zone.

Harvesting of intertidal molluscs (e.g. arks (*Senilia senilis*), mangrove oysters (*Crassostrea tulipa*), *Cymbium* spp., *Murex* spp. and *Conus* spp.) appeared as the main structuring factor for infaunal communities in the intertidal zone with a less significant impact in the subtidal zone. This spatial difference in impact may be due to the shellfish collection methods. Practiced at low tide, the collection was still mostly achieved by walking in the intertidal zone, at the time of the sampling. Sometimes, shellfish were also collected using pirogues allowing harvesters to go deeper and to carry heavier loads and to cross deep "bolongs" (Brenier et al., 2009; Descamps, 1991). Shellfish harvesting inevitably leads to a physical disturbance of the substratum and its associated fauna (Skilleter et al., 2006; Spencer et al., 1998). As a consequence, this human engineering activity has the ability to affect the population structure of marine invertebrates and alter nearshore coastal ecosystems (Kaiser et al., 2001; Leitão and Gaspar, 2007; Rick and Erlandson, 2009; Spencer et al., 1998). In our study, shellfish harvesting practices had indeed implications for a subset of community descriptors, namely abundance, biomass, taxonomic richness and composition. The effects of harvesting is usually causing a reduction of infaunal species number and abundance (Aswani et al., 2015; Dirisu and Edwin-Wosu, 2022; Kaiser et al., 2001; Leitão and Gaspar, 2007; Spencer et al., 1998), which is in line with results highlighted in the present study. Higher abundances, biomass and taxonomic richness were detected in stations permanently or temporarily closed to shellfish harvesting. The expected predominance of small-sized species in harvested areas (Jimenez et al., 2015) was only observed with higher levels of small-sized individuals in our exploited stations, but not detected as significant in the RLQ/Fourth-corner combined analyses.

An additional anthropogenic factor was also highlighted as one of the drivers for the macrofaunal community structure in the intertidal zone: the heavy metals studied by Bodin et al. (2013). In particular, areas with Mn and Cr were characterized by high abundances of Maladanid and Capitellid polychaetes. Being among the largest and deepest-dwelling species (Jacquot et al., 2018; Levin et al., 1997), Maldanid polychaetes are potentially less vulnerable to disturbances, such as PTEs, as opposed to free-living species because they can hide in their fixed tubes (Reise, 2002). Regarding Capitellids, they are well-known indicators of disturbance (Pearson and Rosenberg, 1978) and have been shown to dominate areas with extreme enrichment of heavy metals (Ryu et al., 2011). Capitellidae are also known indicators of organic enrichment (Checon et al., 2021). However, Bodin et al. (2011) found relatively low contamination levels of POPs in the sediments of the Petite Côte and the Saloum Delta, at the same period of time, which did not seem to represent an accurate toxicity threat to marine life. In addition to affecting species composition, PTEs also appeared as one of the factors explaining changes in infaunal community traits, in particular affecting living habits in both tidal areas. Sediment is reported to remarkably retain heavy metals, and thus is considered as especially subject to heavy metal pollution (Bodin et al., 2013). Living within these sediments, infauna is shown to be particularly affected as opposed to epifauna (Piló et al., 2016; Wang et al., 2022). These studies are consistent with our findings highlighting a decrease of infaunal burrow dwellers in areas contaminated with Cd, Hg and Ni, in the intertidal area. As previously mentioned, an increase of tubicolous taxa associated with a contamination with Mn and Cr, in the subtidal zone, can be explained by the capacity of these organisms to hide in their fixed tubes to avoid disturbances (Reise, 2002). On top of affecting living habits, PTEs were highlighted as explaining changes in feeding modes in the subtidal area. Feeding mode is a particularly interesting trait used as a proxy for changes in ecosystem functioning (Cardoso et al., 2004; Carvalho et al., 2011; Gaspar et al., 2009; Mistri et al., 2000). The category "deposit feeders" was dominant in contaminated areas. Many previous studies have shown that the presence of contaminants creates a harsh

environment below the sediment surface affecting mainly deposit feeders, and highlighted the association between this feeding mode and metal-contaminated areas (e.g. Carvalho et al., 2011; Dong et al., 2021; Gaston and Young, 1992; Gusmao et al., 2016; Hu et al., 2019; Nunes et al., 2008; Piló et al., 2015, 2016; Selck et al., 1999). It is important to note that grain size is known to influence feeding modes as well as PTE accessibility, bioavailability, bioaccumulation, concentration, and impact upon a system and individual invertebrates. Correlations have been previously reported between heavy metal concentrations and median grain size (Cabrini et al., 2017; El Tokhi et al., 2015), which is also the case in the present study.

As expected, both median grain size and percentage of fine particles (<63 μm) explained a significant part of the infaunal community structure in both intertidal and subtidal areas. Sediment characteristics are indeed often a significant explanatory factor in macrofaunal taxonomic and trait composition (Anderson, 2008; Jacquot et al., 2018; Mwakisunga et al., 2020). In addition, sediment properties were also associated with specific traits in both tidal zones, showing different proportions in deposit and filter feeders depending on sediment median grain size. Both of these feeding strategies were expected to fluctuate with sediment properties because deposit feeding is usually the dominant feeding strategy in muddy sediments and filter feeders tolerance to fine grained and turbid waters depend on their feeding structure (Shull, 2009; Steele-Petrovic, 1975).

In addition to human ecosystem engineering and sediment properties, variations in temperature and salinity were also highlighted as drivers for traits related to motility, in the intertidal zone. These two parameters are already known as major driving variables for macrofaunal communities (Conde et al., 2013; P. Li et al., 2022; Little et al., 2017; Verdelhos et al., 2015). In particular, studies such as Lam-Gordillo et al. (2022) showed that macrofaunal traits can be linked to fluctuations in salinity. Motile species were, for instance, expected to have a better ability to avoid stressors, such as changes in temperature and salinity, and to be able to recolonize areas by migration (Gogina et al., 2017; Pacheco et al., 2011). In the intertidal zone, crawlers with their relatively high mobility were indeed found in different proportions depending on fluctuations in temperature and salinity. As noted by Dong et al. (2021), this trait is beneficial for macrobenthos to expand their range of activities, increase their access to food, and even help them to escape from disturbances quickly. In the subtidal zone, which is further from human activities, physical environment variables take precedence over human activities occurring on the coast. Season, temperature and salinity appeared as significant structuring factors for infaunal communities and their functioning in the subtidal zone. Our study areas being under periodical severe conditions with hypersaline events during the dry season and potential rainfall events with decrease in salinity and temperature during the wet season, these physical environment variables were expected to impact infaunal communities. The dry season was characterized by higher proportions of tubicolous and deposit feeders, mainly represented by Terrebelid and Maldanid polychaetes. With their ability to hide in their fixed tubes, such taxa are potentially less vulnerable to anoxic or hypersaline events occurring during the dry season (Reise, 2002). In addition to living habits, feeding modes again appeared as a particularly interesting trait to detect changes in ecosystem functioning, this time in response to seasonal change and temperature variations in the subtidal zone. Large filter feeders (e.g. *Senilia senilis*, *Loripes orbiculatus*, *Diplodonta diaphana*) were associated with high temperatures. Such a result can be explained by the remarkable adaptive response to the environment of some species like *Senilia senilis* (Zabi and Le Loeuff, 1993). Benthic invertebrates are also known to be restricted to specific depths, which can be related to different hydrostatic pressures and food availability (Warwick, 1984). In our area of interest, depth contributed in explaining the infaunal community structure in the subtidal zone. This is consistent with results by Leung Tack (1985), describing mollusc species distribution depending on depths in the Saloum Delta.

These different results helped to characterize infaunal communities in relation to the environment. Shellfish harvesting played a major role in determining the structural diversity in the intertidal zone. This human ecosystem engineering activity also constitutes an important source of income for Senegalese women (Conchedda et al., 2011; Gallup et al., 2020), as well as an important source of animal protein for local populations in West African mangroves. Conchedda et al. (2011) found that the annual revenues from mangrove resources in Senegal accounted for one-third of the gross national income (GNI) per capita, and that the collection and sale of oysters and clams were the top two principal uses of mangrove resources. At the time of sampling, concerns were raised regarding women's abilities to cope with shellfish decline (Bodin et al., 2011, 2013). Subsequently, women in the region have developed resilience strategies based on new socio-economic practices with a diversification in their activities (e.g. ecotourism, agriculture, aquaculture, market gardening, artisanal mining and sale of salt) (Diouf et al., 2020; Sarr, 2005). Considering management measures taken since the present study in addition to a diversification of human activities (Gallup et al., 2020; Sarr, 2005), it would be valuable to study potential changes in infaunal communities since 2008, both in terms of structure and functioning. Regarding future studies, we would also recommend identifying additional relevant parameters, such as measuring organic content, turbidity and oxygen levels. This would be especially interesting regarding the subtidal zone, where the environmental descriptors included in the present study could explain the structural and functional diversity in a much smaller proportion than in the intertidal zone, as seen in the variance partitioning analysis. Sediment and environmental variables were the most important variables in the subtidal zone and these variables will stay valuable to look at especially considering expected challenges related to climate change (e.g. aridification, sea level rise, and decrease in rainfall). In recent years, several studies have utilized a combination of taxonomic and trait-based diversity approaches, which has developed our understanding of ecosystem function and supported efforts for better ecosystem management and conservation (Henseler et al., 2019; Villnäs et al., 2019). The present study is again an example of the interest in using both taxonomy and traits, which is important to keep in mind for future work. Indeed, the effects of heavy metals would not have been highlighted using only a classic taxonomic approach. Like previous studies (Dong et al., 2021), trait composition of benthic infauna was not randomly distributed across communities and can reflect their strategies to respond to anthropogenic and environmental stressors.

## 5. Conclusion

Based on data collected in 2007–2008, the present study identifies significant relationships between environmental descriptors and the infaunal community structure and functioning in two of the main Southern West Senegal mangroves areas: the Sine Saloum and the Petite Côte. Highly open to the sea and poorly supplied in freshwater, these West African marginal coastal ecosystems are subject to hypersaline events during dry seasons and therefore represent restrictive environments for infaunal communities. As a result, environmental variables characterized by a drastic change in seasons impacted the infaunal communities, especially in the subtidal zone. Closer to anthropogenic disturbances in the intertidal area, pressures related to human ecosystem engineering activities (shellfish harvesting and heavy metals) took precedence over environmental variables in explaining infaunal community structure and trait composition. These results can now serve for future research, providing both important insights and reference points for the implementation of management measures.

## 7. Research data for this article

[dataset] Jacquot, M.P., Nordström, M.C., De Wever, L., Ngom Ka, R., Ka, S., Le Garrec, V., Sadio, O., Diouf, M., Grall, J., Tito de Morais, L., Le Loc'h, F., 2023. Infaunal communities and environmental variables in Senegal, West Africa. Mendeley Data, V1, doi: 10.17632/xtdjv38vst.1.

## CRediT authorship contribution statement

**M.P. Jacquot:** Methodology, Investigation, Formal analysis, Data curation, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **M.C. Nordström:** Methodology, Validation, Writing – review & editing. **L. De Wever:** Formal analysis, Data curation, Writing – review & editing. **R. Ngom Ka:** Methodology, Investigation, Data curation, Conceptualization, Writing – review & editing. **S. Ka:** Data curation, Investigation, Methodology, Writing – review & editing. **V. Le Garrec:** Formal analysis, Writing – review & editing. **J. Raffray:** Data curation, Investigation, Methodology, Writing – review & editing. **O. Sadio:** Methodology, Investigation, Data curation, Writing – review & editing. **M. Diouf:** Data curation, Writing – review & editing. **J. Grall:** Formal analysis, Writing – review & editing. **L. Tito de Morais:** Supervision, Resources, Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **F. Le Loc'h:** Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

## 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

Original data of this study including abundances, biomass, environmental variables and traits are available at Mendeley Data (https://doi.org/10.17632/xtdjv38vst.1).

## APPENDICES.

**Table A.1**
General information and coordinates (latitude, longitude) of the sampling stations.

| Station | ID | Exploitation | Region | Heavy metals | Town | Latitude | Longitude |
|---|---|---|---|---|---|---|---|
| Diouham | D | Unexploited | Petite Côte | Cd Hg Ni Zn Cu V Ag Pb | Fadiouth | 14.15750 | −16.83306 |
| Ngoussé | N | Unexploited | Petite Côte | No | Fadiouth | 14.14167 | −16.80222 |
| Boubo | B | Exploited | Saloum Delta | No | Falia | 13.90806 | −16.70222 |
| Saré Makalé | M | Exploited | Saloum Delta | No | Falia | 13.92667 | −16.68056 |
| Dionewar | W | Unexploited | Saloum Delta | Mn Cr Zn Cu V Ag Pb | Dionewar | 13.88944 | −16.73250 |
| Saré Acath | A | Exploited | Saloum Delta | No | Niodior | 13.84917 | −16.73556 |
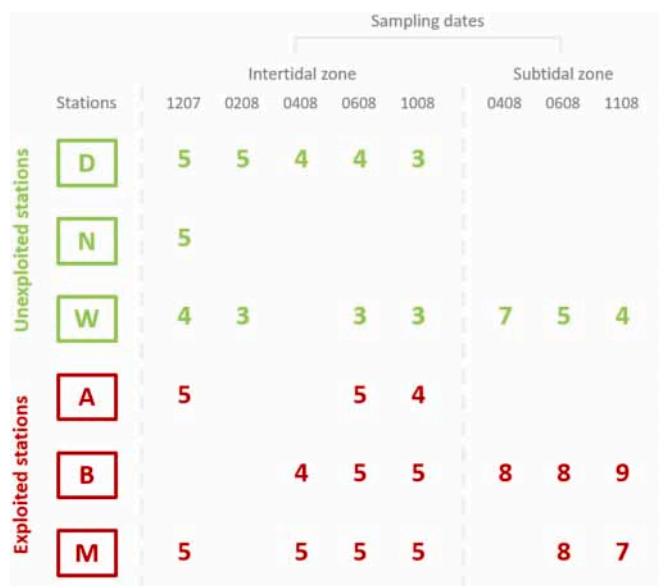


**Fig. A.1.** Number of samples collected for each station at the different sampling dates (December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)), including six sampling stations in the intertidal zone (A, B, D, M, N, W) and three sampling stations in the subtidal zone (B, M, W). Exploited stations are indicated in red and unexploited ones in green.
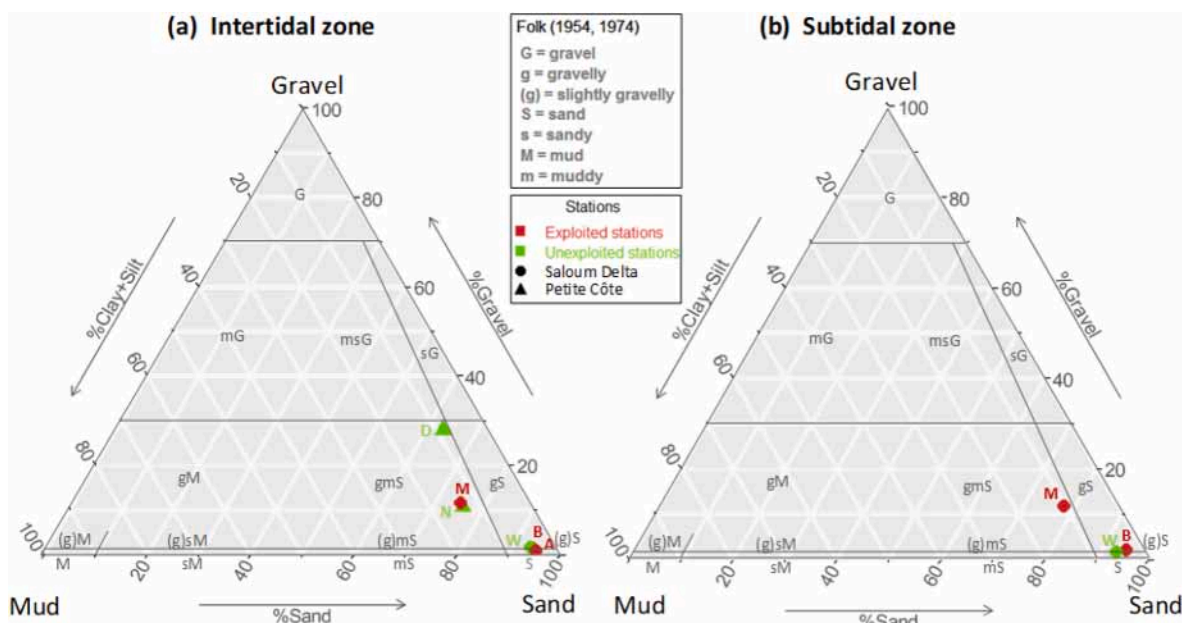


**Fig. A.2.** Ternary diagram of sediment classification scheme from Folk (1974) for (a) the intertidal area and (b) the subtidal area with the different stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N) and Dionewar (W)) depending on their proportion [%] of gravel, sand and mud (clay + silt). Exploited stations are indicated in red and unexploited ones in green with (●) for stations located in the Saloum Delta and (▲) for those located in the Petite Côte.
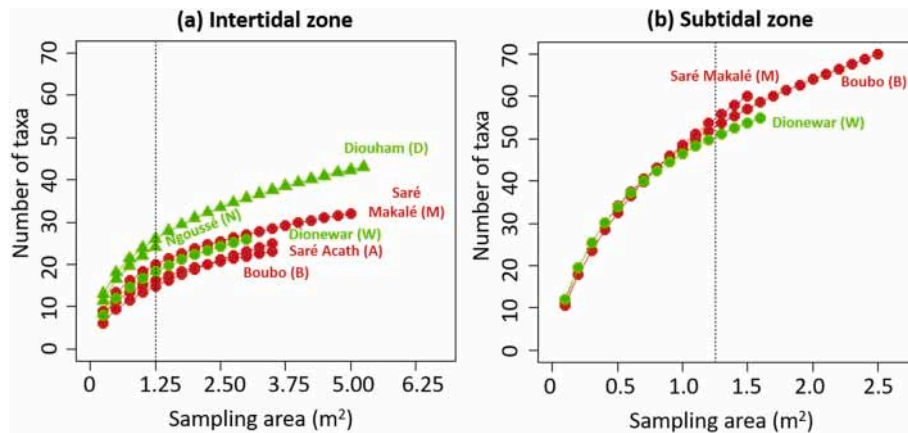
**Fig. A.3.** Rarefaction curves of the number of taxa depending on the number of samples based on intertidal stations (a) and subtidal stations (b). Data are pooled (between December 2007 and November 2008). Exploited stations are indicated in red and unexploited ones in green with (●) for stations located in the Saloum Delta and (▲) for those located in the Petite Côte.



**Fig. A.4.** Dendrogram based on square-root transformation, Bray-Curtis distances, and group-average hierarchical clustering in the intertidal zone (a) and the subtidal zone (b) during December 2007 (1207), February 2008 (0208), April 2008 (0408), June 2008 (0608), October 2008 (1008) and November 2008 (1108)) at different stations (Saré Acath (A), Boubo (B), Diouham (D), Saré Makalé (M), Ngoussé (N) and Dionewar (W)). Exploited stations are indicated in red and unexploited ones in green with (●) for stations located in the Saloum Del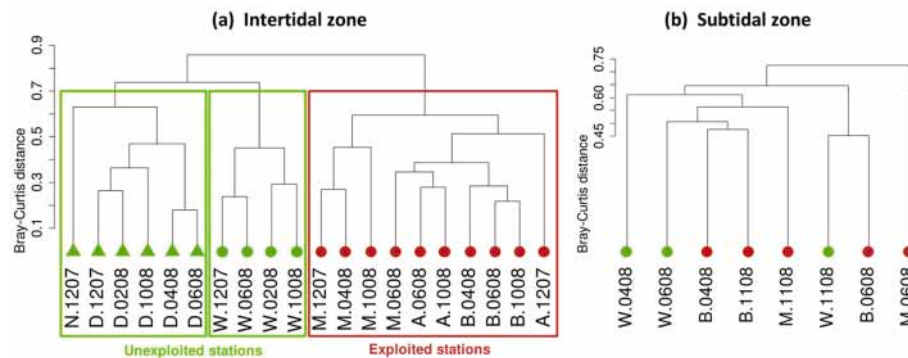ta and (▲) for those located in the Petite Côte. The SIMPROF test identified three significant clusters (p < 0.01) for the intertidal zone (a) and no significant ones for the subtidal zone (b).

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