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Quantifying bioturbation across coastal seascapes: habitat characteristics modify effects of macrofaunal communities

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Key words

Bioturbation, Benthic fauna, Context-dependence, Sediment, Habitat characteristics, Community functional composition

Abstract

Bioturbation by benthic macrofauna communities plays a significant role in the setting and maintenance of important ecosystem functions and the delivery of associated ecosystem services. We investigated the context-dependence of bioturbation performed by natural benthic communities in the coastal northern Baltic Sea by quantifying three bioturbation metrics (particle mixing intensity, surface sediment reworking and bioturbation depth) across 18 sites ranging from cohesive muddy sediments to non-cohesive coarse sands, while accounting for the complexity of natural communities and habitat characteristics. We identified two distinct patterns of bioturbation; in fine sediments bioturbation rates were highly variable and in coarse sediments bioturbation rates were less variable and characterized by lower maximal values. Using distance-based linear multiple regressions, we found that 75.5% of the variance in bioturbation rates in fine sediment could be explained by key functional groups/species abundance and/or biomass (i.e. biomass of the gallery-diffusors and abundances of biodiffusors, surface modifiers, conveyors and gallery diffusors, respectively). In coarse sediment, 47.8% of the variance in bioturbation rates could be explained by a combination of environmental factors (grain size, organic matter content, buried plant material) and faunal functional groups, although fauna alone explained only 13% of this variance. Bioturbation in fine sediments was therefore more predictable based on the composition of benthic fauna. In coarse sediment, the bioturbation activities of benthic fauna were strongly modified by habitat characteristics (including the presence of buried plant material, sediment organic content and grain size) whereas in fine sediments this was not the case. Our results therefore highlight that variability in spatial patterns of bioturbation is a result of complex relationships between macrofauna community structure, sediment type and other habitat characteristics, likely modifying bioturbation performance of individual fauna.

Introduction

Since Darwin's first quantitative estimation of bioturbation by earthworms in the 19th century, the recognition of the major importance of this process for the formation and the functioning of soils and sediments has been well established (Lavelle et al. 2006, Kristensen et al. 2012). However, the factors modifying bioturbation activities by natural invertebrate communities of soils and sediments are still poorly known (Meysman et al. 2006). Changes in the extent and timing of particle movement associated with macrofauna profoundly influence how sedimentary habitats are structured and how organic matter is stored or processed in marine and freshwater sediments (Josefson et al. 2002, Mermillod-Blondin and Rosenberg 2006, Snelgrove et al. 2018) or terrestrial soils (Wall et al. 2012). Understanding the drivers of bioturbation and variations in its intensity is key for assessing how coastal systems act as critical biogeochemical transition zones. However, quantitative data on bioturbation across natural environmental gradients are rare (Wheatcroft and Martin 1996, Sturdivant et al. 2012, Aschenbroich et al. 2017), impeding our mechanistic understanding of this important process. Moreover, many bioturbation studies focus on the role of individual species in highly controlled experiments but it is difficult to predict the cumulative effects of the whole bioturbating benthic community based on a species-by-species analysis because of the potential for species interactions and niche partitioning to affect net particle flux (Mermillod-Blondin et al. 2004, de Backer et al. 2011).

Bioturbation, is defined as all transport processes carried out by animals that directly or indirectly affect sediment matrices. These processes include both particle mixing (reworking) and burrow ventilation (Kristensen et al. 2012) and collectively influence the transformation and retention of organic matter inputs settling on the seafloor (Solan et al.

2004, Josefson et al. 2002, 2012), affecting nutrient fluxes between the sediment and the water column. The ability of benthic fauna to mix sediment particles depends on their specific life-strategy such as the depth strata of sediment they occupy, their mobility and locomotion characteristics, and their feeding behavior. Benthic macrofaunal species have thus been classified into several bioturbation functional groups (François et al. 1997, Gérino et al. 2007). This classification defines particle mixing modes differing in terms of mixing depth, volume of sediment handled, main direction and kinetics of particle transfer between the sediment-water interface and deeper strata (and *vice versa*), thereby affecting oxygen penetration depth into the sediment and the associated redox front as well as the burial of (fresh) organic matter or its release when previously buried. Different functional groups then have different effects on ecosystem functions such as sediment uptake of oxygen, carbon and nutrients (Michaud et al. 2005, 2006).

Changes in benthic community composition (species or functional) along natural environmental gradients, interacting with habitat characteristics such as sediment grain size (Dorgan et al. 2006), organic matter quantity and quality (Bernard et al. 2016, Morys et al. 2016), or the presence of elements stabilizing sediments (such as rhizomes and roots) (Bernard et al. 2014) are all predicted to affect bioturbation. Changes in sediment type (grain-size and/or organic matter content) can radically change the mode of bioturbation exhibited by a given species, as for example shown through changes in burrowing strategy in the crab *Austrohelice crassa* (Needham et al. 2010). Sediment type is also known to modify behaviour associated with particle mixing and bioirrigation (e.g. burrowing) in polychaetes of the genus *Marenzelleria* (Quintana et al. 2018) and of the nereididae family (Dorgan et al. 2006), and in bivalves such as *Macoma balthica* (Olafsson 1989) and *Mya arenaria* (Alexander et al. 1993). These 4 last taxa occupy a wide range of sediment types in the coastal Baltic Sea where they are indeed dominating infauna communities (Bonsdorff et al. 1996, Gammal et al. 2019). This clearly complicates the assessment of species and biodiversity effects on the net bioturbation rates of benthic communities and on ecosystem functioning along such gradients.

In this paper, we focused on the context-dependence of community-wide bioturbation and the identification of key drivers of change across different habitat types in the coastal zone. This is of particular importance since the complex mosaic of habitats of the coastal zones are recognized for their nutrient filtering role (Almroth-Rossel et al. 2016) and intense benthic-pelagic coupling (Grall and Chauvaud 2002, Griffiths et al. 2017, Joensuu et al. 2018). We quantified particle mixing across 18 different sites ranging from cohesive muddy sediments to non-cohesive coarse sands while accounting for the complexity of natural communities. We hypothesized that from fine mud to coarse sand habitats, the rates of particle mixing are controlled by (1) the functional characteristics in terms of bioturbation group composition of resident benthic macrofauna communities, but are also modified by (2) the different physical characteristics (cohesiveness) of the sediment, and (3) structural elements in the sediment such as plant roots and rhizomes.

Material and Methods

Study area. Field sampling took place in the Northern Baltic Sea near Tvärminne Zoological Station (TZS, SW Finland, **Figure 1**). This complex archipelago system is characterized by a mosaic of diverse shallow benthic habitats. Soft sediments range from very fine mud to coarse sand, mostly depending on exposure to waves and dominant winds (Valanko et al. 2010). These habitats are characterized by classical brackish-water benthic macrofauna communities with low species and functional biodiversity and low species turnover. The same restricted pool of species is distributed across a wide variety of shallow soft-sediment habitats in the Baltic Sea (Gogina and Zettler 2010). Dominant taxa include hydrobid gastropods, the bivalves *Macoma balthica*, *Cerastoderma glaucum* and *Mya*

Site n°	Site name	Depth (m)	Salinity	Sediment D_{50} (µm, mean ± sd)	Sediment organic content (%, mean ± sd)	Plant material (ml, mean ± sd)	Shells (ml, mean ± sd)	Pebbles (ml, mean ± sd)

arenaria, Oligochaetes as well as the polychaetes *Marenzelleria* spp. and *Hediste diversicolor* (Gammal et al. 2019).

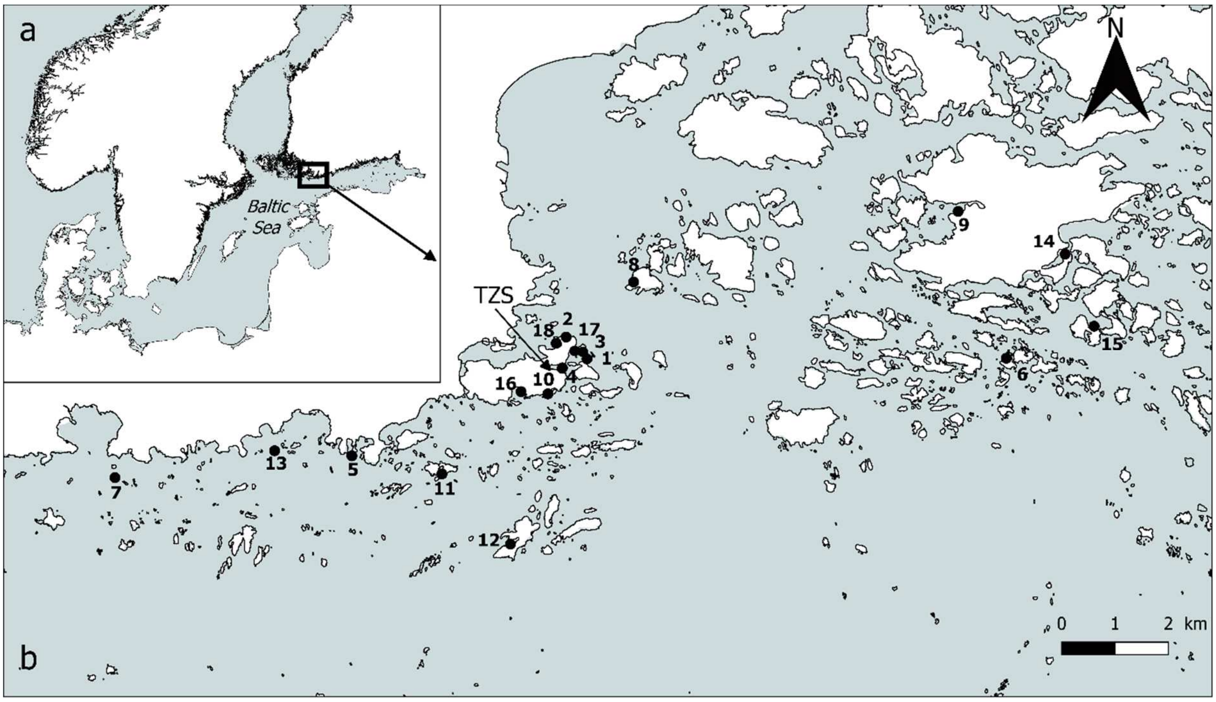


Figure 1: Location of the study area in the Baltic Sea (a) and of the 18 study sites within the archipelago in the vicinity of Tvärminne Zoological Station (TZS; b).

We sampled 18 sites between the 6th of August and the 8th of September 2014 (**Figure 1, Table 1**). All sites were in the shallow subtidal (between 2 and 4 m) and were chosen in order to encapsulate the large variability in habitat diversity (in terms of sediment types) encountered in the area within this depth-range. *In situ* temperature ranged from 14 to 23 °C and great attention was paid to the order the sites were sampled to make this range similar for all major habitat types (Gammal et al. 2019).

Table 1: The 18 study sites and their main environmental characteristics. Plant material, shells and pebbles refer to the volume of these elements found in the sediment cores used for incubations.

1	*Kvarngrunden S*	3.9	5.2	160.9 ± 4.6	0.57 ± 0.02	0.33 ± 0.29	0.17 ± 0.29	4.17 ± 3.33
2	*Långholmen N*	3.2	5.2	274.0 ± 37.7	0.61 ± 0.13	1.33 ± 1.16	1.00 ± 1.73	13.50 ± 5.77
3	*Kvarnskär S*	3.0	5.1	154.7 ± 24.4	0.64 ± 0.21	0.67 ± 0.29	0.50 ± 0.00	1.83 ± 1.04
4	*Krogarviken*	2.3	5.2	34.21 ± 10.2	4.54 ± 0.29	0.33 ± 0.29	0.00	0.33 ± 0.58
5	*Klobbarn*	3.0	5.1	498.9 ± 43.7	0.57 ± 0.05	0.67 ± 1.15	1.00 ± 1.32	3.50 ± 1.32
6	*Fladalandet W*	2.6	5.1	538.6 ± 270.7	0.96 ± 0.31	7.83 ± 5.25	2.00 ± 0.87	31.00 ± 38.43
7	*Täktbukten utanför*	3.0	5.4	223.0 ± 11.4	0.26 ± 0.04	0.00	0.33 ± 0.58	3.50 ± 3.50
8	*Kalvön W*	3.0	5.4	464.7 ± 131.0	0.72 ± 0.03	0.33 ± 0.29	0.17 ± 0.29	39.00 ± 26.96
9	*Älgö inner*	2.9	5.1	48.9 ± 18.1	4.49 ± 0.44	0.00	0.00	1.00 ± 0.5
10	*Klobben*	3.0	5.4	216.9 ± 11.2	1.81 ± 0.47	1.67 ± 1.04	0.33 ± 0.58	4.83 ± 4.93
11	*Vindskären (Kyan)*	3.0	5.6	550.7 ± 121.8	0.51 ± 0.07	0.00	0.50 ± 0.87	3.00 ± 2.18
12	*Storlandet W*	3.8	5.5	325.8 ± 43.6	0.61 ± 0.04	0.00	0.50 ± 0.87	28.33 ± 10.51
13	*Henriksberg*	3.2	5.7	376.0 ± 105.0	0.40 ± 0.21	1.67 ± 2.89	0.67 ± 0.29	23.33 ± 9.07
14	*Verkholmsfladan*	1.7	5.4	421.3 ± 92.2	0.58 ± 0.20	1.17 ± 0.76	0.33 ± 0.29	5.00 ± 2.00
15	*Modermagan N*	2.4	5.6	25.9 ± 1.7	15.78 ± 0.42	0.50 ± 0.5	0.00	0.33 ± 0.29
16	*Ångbåtsbryggan*	3.4	5.6	272.6 ± 23.3	0.71 ± 0.20	0.83 ± 0.58	0.33 ± 0.58	3.67 ± 2.57
17	*Långholmen S (sundet)*	3.7	5.6	138.6 ± 34.7	0.71 ± 0.20	1.00 ± 0.00	0.17 ± 0.29	3.83 ± 0.76
18	*Äskskär*	2.5	5.5	78.2 ± 34.0	3.20 ± 0.34	0.67 ± 0.76	0	2.00 ± 3.04

Sampling design. At each site, three intact sediment cores (internal diam. 8.4 cm, approximately 15 cm of sediment + 15 cm of bottom water) were collected along a 20 m transect using SCUBA-diving. Cores were capped and kept upright in a tank filled with sea water while transported to the lab. The sediment cores were collected from different types of habitat patches (*i.e.* in the direct vicinity of vegetation or within bare sediment patches) in order to include the maximum within-site variation of vegetation cover at the site scale. Habitat characteristics were assessed around each core (within a 50 x 50 cm frame) by sampling the sediment surface using three cut-off syringes (diameter 3.5 cm) for the measurements of sediment grain size and porosity (0-3 cm depth layer), organic content and chlorophyll *a* concentration (0-0.5 cm depth layer). Sediment samples were kept frozen in the dark until analysis.

The three cores collected were consecutively used to measure: (1) particle mixing rates, (2) macrofauna species diversity, density and biomass, and (3) the volume occupied by elements structuring the sediment matrix (plant material, pebbles, shell hash).

Sediment characteristics. For grain size determination, hydrogen peroxide (6%) was used to dissolve organic material. Grain sizes were separated into <63, 63–125, 125-250, 250–500, 500-1000, 1000-2000 and >2000 µm fractions by wet sieving and the dry weight was obtained for each fraction (48 h at 60°C) and the median sediment grain size (D50) calculated. Organic content was calculated as percentage of dry sediment weight lost after ignition (3h at 500°C). Sediment porosity was determined from the water content calculated after drying the samples (48 h at 60°C), using a weighted average sediment particle density taking into account a particle density varying from 1.25 g cm^{-3} for a fully organic sediment to 2.65 g cm^{-3} for a mineral sediment (Boyd 1995, Avnimelech et al. 2001). Chlorophyll *a* content (µg. g^{-1} dry sediment) was determined after extraction from freeze-dried sediment in 90% acetone for 24 h and measured spectrophotometrically. An acidification step was included to separate degradation products from chl *a* (Sartory, 1982).

Particle mixing. Site-specific sediment particle mixing was assessed through incubation of intact sediment cores using luminophores as sediment particle tracers (Mahaut and Graf 1987). First, sediment cores were immersed in a water tank and supplied with natural running sea water in a temperature-controlled room (temperature adjusted to follow the *in situ* temperature) for acclimatization 24h prior to the start of experiments. An average 15h/9h light/dark regime was reproduced for the entire acclimatization and incubation time. At the beginning of the experiments, the flow through each core was stopped and 2 g DW (Dry Weight) of luminophores (eco-trace®, https://environmentaltracing.com/about, density = 2.5 g cm^{-3}) were suspended, homogenized in seawater and spread at the sediment surface carefully avoiding resuspension of sediment using a Pasteur pipette. Two size fractions of luminophores were used (“mud” with particle diameter between 10 and 70 µm and “sand” between 125 and 250 µm) and mixed in proportions reflecting site-specific surface sediment grain sizes. Luminophores were allowed to settle for 1h before flow-through was restarted. The incubation lasted 8 days (Gilbert et al 2003, Hedman et al. 2011, Kauppi et al. 2018b).

At the end of incubation, a photograph of the sediment surface from above was taken. From this, the percentage of surface reworked (SR) was obtained by subtracting the surface still occupied by luminophores from the core surface using image analysis (see below). Cores were subsequently sliced (0.5 cm thick slices on the first 2 cm, 1 cm thick down to 9 cm and 2 cm thick down to 15 cm). Slices were homogenized and an approx. 30 g aliquot of sediment was sampled for luminophore counting after ensuring that no macrofauna were trapped. The remaining sediment was sieved on a 0.5 mm sieve to retain macrofauna. Sediment aliquots were freeze-dried and 1 g of dry sediment photographed under UV light using a digital camera. Luminophore pixels were counted after a binarization step (based on the RGB level) for each image corresponding to a single slice using image analysis software (Maire et al. 2006). The relative concentrations of luminophores in each slice were then used to compute corresponding vertical depth profiles. These profiles were used for: (1) the determination of the Maximum Penetration Depth (MPD) of the tracers during the course of the experiment, and (2) the mathematical fitting of a Continuous Time Random Walk (CTRW) model (Meysman et al. 2008) used to derive a single normal biodiffusion coefficient (D_b^N in $cm^2.yr^{-1}$) value reflecting particle mixing intensity by the resident macrofauna (Meysman et al. 2008; Bernard et al. 2014). Data profiles for all sites together with corresponding model fits are provided in appendix A.

Macrofauna were collected from each core on a 0.5 mm sieve. They were identified to the lowest possible taxonomic level, counted and their biomasses assessed (wet weight: wwt). Adult bivalves were separated from juveniles using a cut set at 5 mm (total shell length). The 14 benthic macrofauna taxa found were separated in the dataset into 6 bioturbation functional groups related to their specific influence on the mixing of sediment particles based on literature (Table 2). We distinguished six different functional groupings: (1) Surface sediment modifiers (Surf), moving sediment particles through living and feeding at the sediment surface, (2) Tube dwellers (Tub), feeding at the sediment surface and building tubes while agglomerating sediment particles with mucus, therefore stabilizing the sediment structure (through the presence of dense tube mats), (3) Filtering biodiffusors (Biodif fil), positioned within the sediment and suspension-feeding using their immobile inhalant siphon, therefore randomly moving particles in a very restricted volume of the sediment, (4) Biodiffusors (Biodif), living within the sediment and actively mixing particles mostly through foraging at the sediment surface or in the sub-surface layer. Particle mixing is created by the feeding and maintenance of semi-permanent small galleries in the cases of polychaetes or amphipods, or by deposit-feeding using mobile siphons for adult deposit-feeding bivalves, (5) Gallery diffusors (Gal), feeding both at the sediment surface and in the subsurface layer, actively creating galleries within the sediment lined with mucus, therefore mixing particles randomly inside galleries, and (6) Conveyor-belt (Conv), moving particles directly between sediment surface and deeper layers through feeding.

Note that these bioturbation functional groups are not exclusive, *i.e.* a species can exhibit several particle-mixing modes at the same time. They, however, correspond to an assumed species-specific principal particle-mixing mode.

Table 2: The 14 benthic macrofauna taxa found during the study, together with their bioturbation functional group and corresponding literature references. Surf: Sediment surface modifiers; Biodif fil: Filtering biodiffusors; Conv: Conveyor-belt; Biodif: Biodiffusors; Tub: Tube dwellers; Gal: Gallery diffusors (see text for details).

Taxon	Functional group	Reference
Bathyporeia pilosa	Surf	Queirós et al. 2013
Cerastoderma glaucum (>5mm)	Biodif fil	Urban-Malinga et al. 2014
Cerastoderma glaucum (<5mm)	Surf	Zwarts and Wanink 1989
Chironomidae	Conv	Matisoff and Wong 2000
Corophium volutator	Biodif	Mermillod-Blondin et al. 2004
Hydrobiidae	Surf	Norkko et al. 2010
Macoma (Limecola) balthica (>5mm)	Biodif	Michaud et al.2005, 2006 Hedman et al. 2008
Macoma (Limecola) balthica (<5mm)	Surf	Zwarts and Wanink 1989 Norkko et al. 2013
Manayunkia aestuarina	Tub	Lewis 1968
Marenzelleria spp.	Biodif	Hedman et al. 2008
Monoporeia affinis	Biodif	Hedman et al. 2008
Mya arenaria	Biodif fil	Michaud et al. 2005, 2006 Urban-Malinga et al. 2014
Hediste diversicolor	Gal	Mermillod-Blondin et al. 2004 Urban-Malinga et al. 2014
Oligochaeta	Conv	Gérino et al. 2007 Norkko et al. 2010
Cyanophthalma obscura	Conv	GB Pers. obs.
Pygospio elegans	Tub	Brey 1991

Sediment structural elements. After macrofauna sorting, remaining material on the 0.5 mm sieve was passed through an 8 mm sieve and plant material (dead or alive roots and rhizomes from aquatic phanerogams) separated from pebbles and shells hash. The volumes occupied by these 3 “structural” types were measured separately by ethanol displacement in graduated cylinders.

Data analyses. The aim was to identify the different biotic or abiotic factors, and their interactive effects in explaining the variability in particle mixing rates measured across a range of soft-sediment habitats. All measurements of (1) habitat characteristics, (2) macrofauna assemblages and (3) bioturbation (particle mixing) metrics (% of SR, MPD, D_b^N) were scaled to the plot-scale (0.25 m²).

Individual plot-scale sediment types were first compared using the relative contributions of the different grain size fractions (in %) in the 54 samples. Data were first square-root transformed, normalized and then a cluster analysis based on the Euclidean distance followed by Principal component analysis (PCA) was performed in order to delineate distinctive groups in term of sediment type.

Based on this delineation, the dataset was subdivided into “fine” and “coarse” sediments, although a third transitional sub-group could be identified within the fine sediment group. The subsequent analyses concentrated on the two groups, fine and coarse, since the use of three groups did not add any explanatory power (Appendix C). Differences in the three particle mixing metrics as well as macrofaunal abundance, biomass and diversity between fine and coarse sediments were assessed using one-way univariate Permutation Analysis of Variances (PERMANOVAs) based on Euclidean distance and associated dispersion analyses (PERMDISP). Because of the uneven sample size (n=21 for fine and n=33 for coarse sediments), the design was unbalanced. For unbalanced designs in PERMANOVA and PERMDISP analyses, it has been demonstrated that large dispersions associated with small sample numbers increases rejection rates while conversely, large dispersions associated with large number of samples results in a conservative test (Anderson & Walsh, 2013). Hence, in order to ensure that our statistical results were not driven by such effects, we conducted, where necessary, 10 times per tested variable: (1) a random selection of 21 values within the coarse samples to make the design balanced and (2) performed both one-way PERMANOVA and PERMDISP analyses. In all cases, we detected the same effects (in terms of both PERMANOVA and PERMDISP tests) as when using the original unbalanced design. The unbalanced design was then kept throughout, involving the 54 samples.

The distribution of mud content (<63 μm), median grain size (D50), porosity, organic content, and total chlorophyll *a* content within the two “sediment type” groups was examined using a PCA analysis performed on these 5 variables. The coordinates of all plots onto the two first PCA axes were then used to reduce these parameters to two latent variables (PC1 and PC2) for subsequent analyses.

The contribution of faunal (functional group abundances and biomasses) and environmental factors explaining the variability in the measured bioturbation metrics was investigated using a distance-based redundancy analysis (dbRDA) performed with the DistLM option in the PERMANOVA + add-on for PRIMER (Anderson et al. 2008). Forward selection was used to build models using AIC selection criterion. These relationships were investigated across the whole gradient involving all cores, for fine and coarse sediments separately, and also for the three groups separately (i.e. including the both sub-groups of the fine sediments), using first only faunal data and subsequently both faunal and environmental data. Bioturbation metrics (% of SR, MPD, D_b^N) were used as the response multivariate data cloud. D_b^N was Log-transformed in the whole dataset and the fine sediments dataset because its distribution was heavily right-skewed. No transformation was needed for any of the other bioturbation metrics in either dataset. The distribution of explanatory variables was also checked and these were transformed in case of heavy right-skewed distribution. Faunal data included both abundances and biomasses when, for a given functional group, the correlation between the two (assessed using Pearson correlation r) was below 0.8 in order to avoid issues related with multi-collinearity (Anderson et al. 2008). Environmental explanatory variables included the three "structural" variables (Plant, Pebbles, and Shells) as well as PC1 and PC2. For the analysis of the whole dataset involving all the cores, the variable "Cohesiveness" was also included as an explanatory variable; it consisted in a binary variable representing the above mentioned division between fine and coarse sediments based on grain size sediment fractions.

Results

Sediment types. The visualisation of the sampling plots on the dendrogram plot shown in **figure 2a** as well as on **figure 2b** showing the plane defined by the two principal component axes based on the percentages of the different sediment grain size fractions clearly discriminated two groups hereafter referred to as “fine” and “coarse” sediments (**Figure 2**). A third transitional sub-group could be identified within the fine group, but including three groups in the subsequent analyses did not improve the explanatory power and the results presented here focus on the two groups. Indeed, the two groups are well separated along the first principal coordinate axis defined by very fine sand and mud fractions on the one hand and coarse sediment fractions on the other hand, and representing 59% of the total variance. The use of this approach was justified by the fact that: “the transition between cohesive and non-cohesive sediment behavior can be parameterized [in erosion models] through a critical mud fraction that depends on the sand grain size: the coarser the sand, the higher the mud content before the sediment becomes cohesive” (Le Hir et al. 2011). The “fine” group consisted of 21 plots where fine particles (<250 µm) represented between 93 and 99.9% of the total sediment. The same sediment fraction represented from 53 to less than 1% in the “coarse” group, consisting of 33 plots.

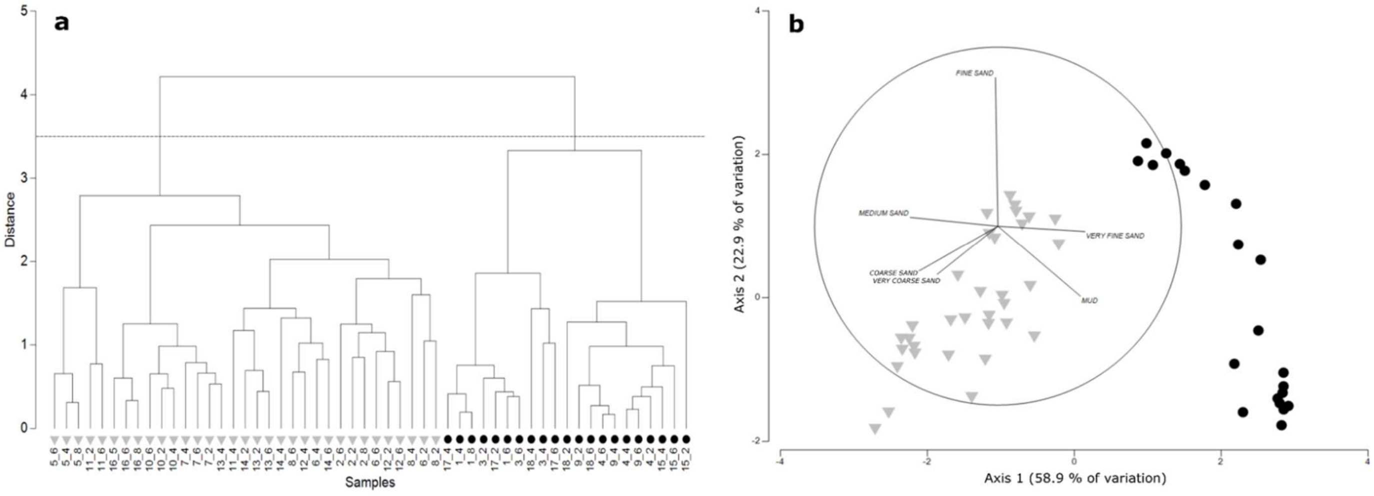


Figure 2: Dendrogram resulting from the Euclidean distance-based clustering of sediment samples using the relative square rooted contribution of the different grain size classes (a) and projection of the sediment samples on the plane defined by the principal components 1 (Axis 1) and 2 (Axis 2) following a PCA analysis based on the same data (b). Solid line in (a) indicates the distance level at which samples were separated into fine (black circles) and coarse (grey triangles) sediments. Vectors in (b) illustrate the correlation levels of the grain size classes with Axes 1 and 2.

Mud content, porosity, organic content, total chlorophyll *a* content and median grain size within the two groups differentiated along the two first principal component axes (**Figure 3).** PC1 and PC2 accounted for 80.8 and 12.1%, respectively, of the total variance.

PC1 correlated positively with sediment organic content (log transformed, R= 0.486), porosity (log transformed, R=0.485), mud content (R= 0.474) and total chlorophyll *a* content (R=0.413), and negatively with median grain size (R= -0.366). Fine sediments were well spread all along this first axis whereas coarse ones were less dispersed and particularly corresponded to low scores on the PC1.

PC2 correlated substantially only with sediment D50 (R= -0.817) and total chlorophyll *a* content (R= -0.539), the three other descriptors being poorly described by this component. It provided a good discrimination of fine sediments at the higher end of the PC2 axis from coarse sediments spread toward more negative scores.

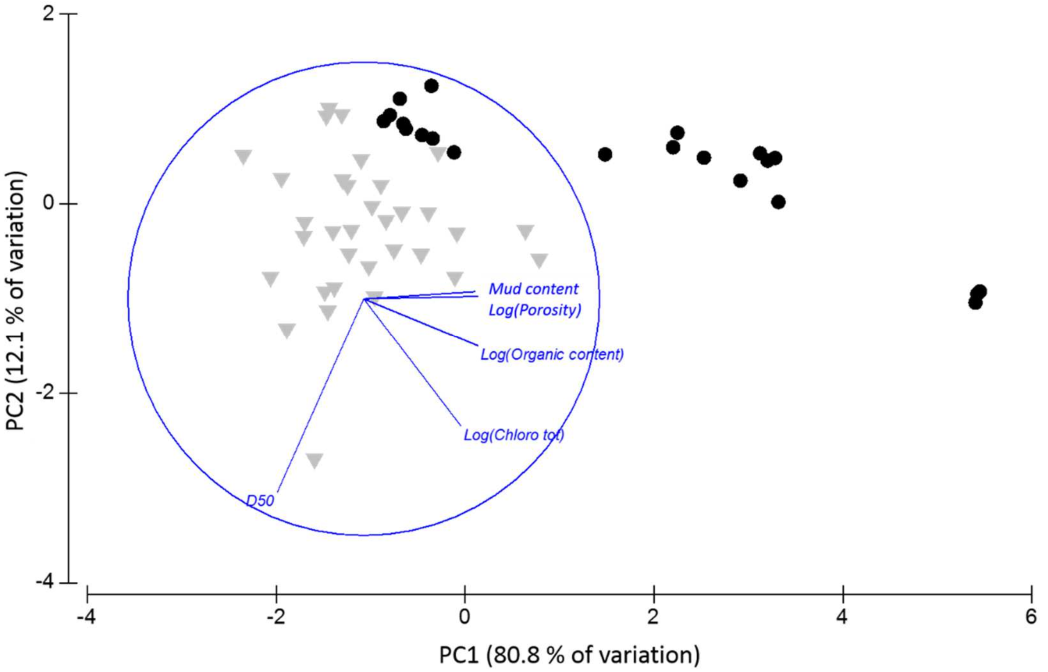


Figure 3: Projection of the sediment samples in fine (black circles) and coarse sediments (grey triangles) on the plane defined by the principal components 1 (PC1) and 2 (PC2) following a

PCA analysis based on their main sediment characteristics (Mud content, log transformed porosity log (Porosity), log transformed sediment organic content log(Organic content), log transformed total chlorophyll content log(Chloro tot) and median grain size D50). Vectors illustrate the correlation levels of the sediment descriptors with PC1 and PC2.

The volume occupied by plant material (roots and rhizomes) in the cores was 0.5 ± 0.09 ml in fine sediments ($\bar{x}$ ± SE; min-max: 0 – 1.5 ml) whereas it was 1.2 ± 0.42 ml in coarse ($\bar{x}$ ± SE; min-max: 0 – 13 ml).

Macrofauna. Univariate one-way PERMANOVAs revealed that macrofauna abundance (Pseudo-F= 29.07, $p< 0.01$), species richness (Pseudo-F= 46.86, $p< 0.01$) and functional richness (Pseudo-F= 45.72, $p< 0.01$) were significantly higher in coarse sediments than in fines ones (**Figure 4**). In contrast, biomass did not exhibit any significant differences between the two sediment types (Pseudo-F= 1.43, $p=0.26$). No significant differences in the variability of abundance, species and functional richness and biomass were detected between the two sediment groups (PERMDISP, $p >0.05$).

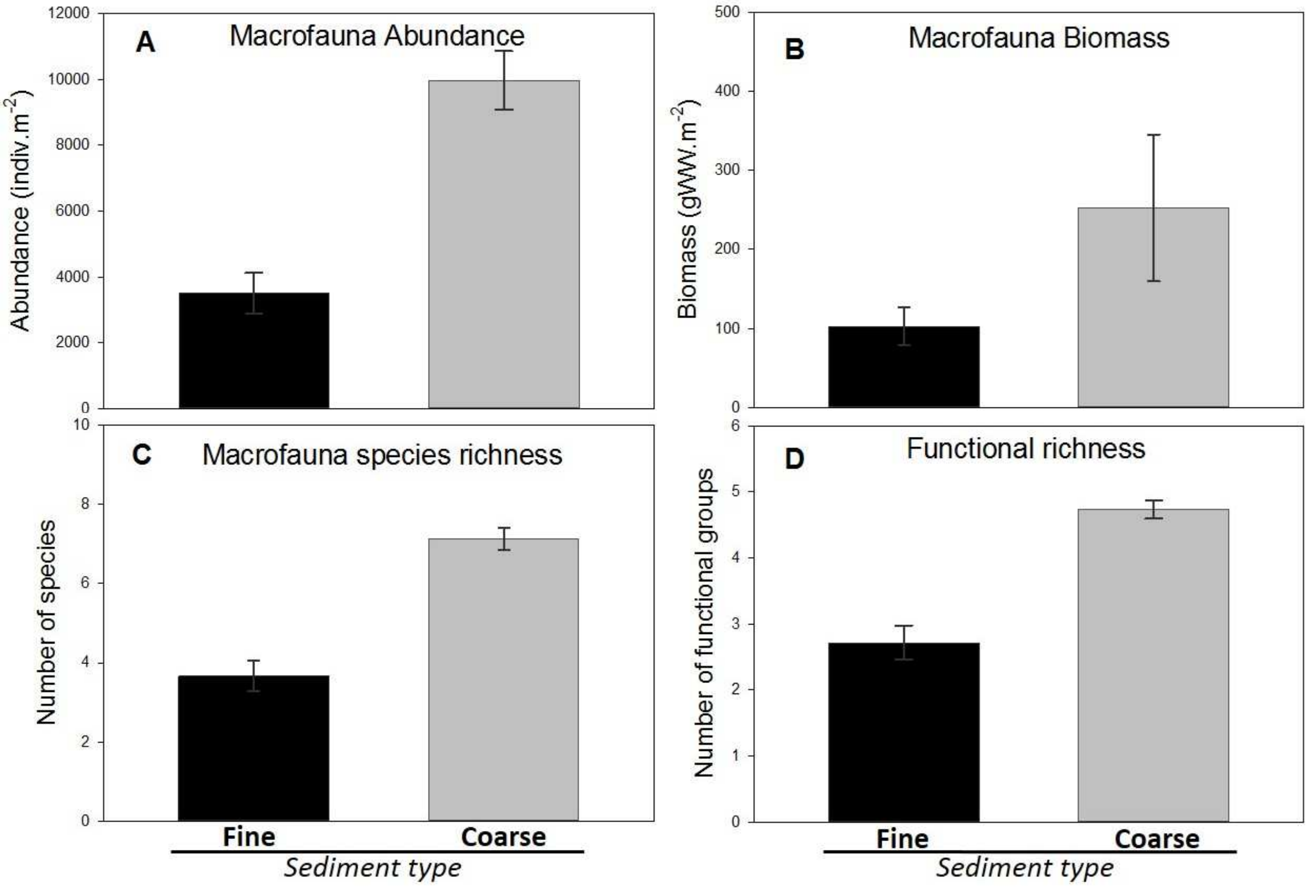


Figure 4: Means (+/- SE) of benthic macrofauna characteristics in fine (black bars) and coarse (grey bars) sediments.

Mean abundance was 3506 ± 615 individuals.m^{-2} ($\bar{x}$ ± SE; min-max: 722 - 9386 ind.m^{-2}) in fine sediments, and 9975 ± 885 ($\bar{x}$ ± SE; min-max: 2527 - 24909 ind.m^{-2}) in coarse sediments. An average of 3.7 ± 0.4 ($\bar{x}$ ± SE; min-max: 1 - 8) taxa per core were found in fine sediments versus 7.1 ± 0.3 ($\bar{x}$ ± SE; min-max 5 - 10) in coarse. This corresponded to 2.71 ± 0.3 ($\bar{x}$ ± SE; min-max: 1 - 5) and 4.7 ± 0.3 ($\bar{x}$ ± SE; min-max: 3 - 6) bioturbation functional groups in fine and coarse sediments, respectively. Thus the coarse sediments had higher functional richness. Only Surface modifiers were present in all of the cores sampled in both sediment types. The frequency of occurrence in fine *versus* coarse sediment cores was 62%

and 100% for Biodiffusors, 48% and 92% for Conveyors, 43% and 79% for Gallery-diffusors, 10% and 70% for Tube dwellers and 10% and 21% for Filtering biodiffusors, respectively.

A closer examination of the differences in community structure based on the abundances of the different bioturbation functional groups between fine and coarse was carried out through an nMDS analysis **(Figure 5)** and associated PERMANOVA and PERMDISP tests. The macrobenthic communities differed significantly between fine and coarse sediments (PERMANOVA, Pseudo-F=12.87, $p<0.01$). It should here be underlined that they did not differ between the two sub-groups distinguished within fine sediments (pairwise PERMANOVA, t=0.88, p=0.54), although communities in coarse sediments significantly differed from both (pairwise PERMANOVA, t=3.0, $p<0.01$ and t=3.1, $p<0.01$). For all bioturbation functional groups, we found higher abundances in the coarse sediment. Variability in the assemblages across sites within sediment type groups, was significantly higher in fine sediments (PERMDISP, $p<0.05$), which can also be observed in the spread of data points in the MDS plot for fine and coarse sediments, respectively. Similar pattern could be observed when focusing on biomasses of the different functional groups (Appendix B).

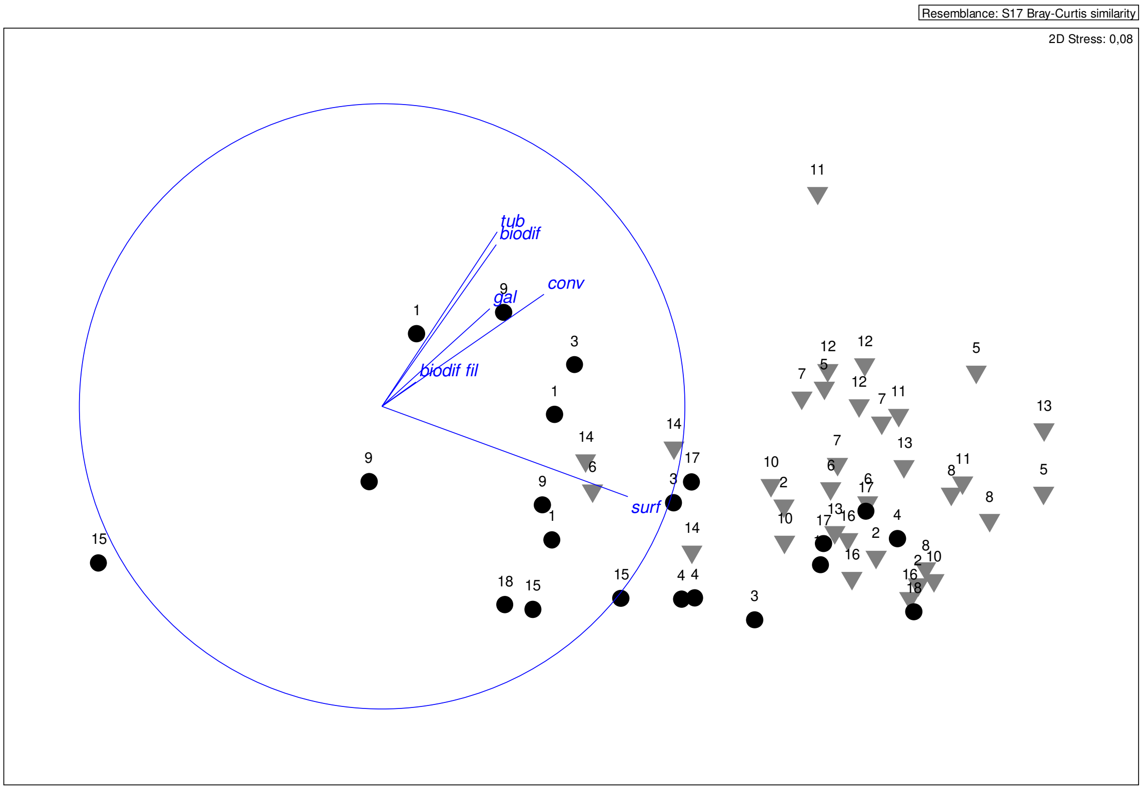


Figure 5: Non-metric multidimensional scaling ordination of macrofauna community functional composition in “fine” (black dots) and “coarse” (grey triangles) sediment. Data are based on abundances of bioturbation functional groups and ordinated using Bray-Curtis similarity resemblance index. Vectors indicate Pearson correlation levels of the different functional groups (Biodif fil: Filtering biodiffusors; Conv: Conveyor-belt; Biodif: Biodiffusors; Tub: Tube dwellers; Gal: Gallery diffusors).

Macrobenthic assemblages in fine sediments can therefore be considered as less abundant and less diverse in terms of both species and functional composition, and particularly more spatially variable regarding their bioturbation functional composition.

Bioturbation (Particle mixing). Generally, we found distinct differences in bioturbation metrics between fine and coarse sediments. The variability in particle mixing intensity (D_b^N), as revealed using PERMDISP test ($p<0.05$), was significantly higher in fine sediments than in coarse sediments, although no global differences in mean values were detected (PERMANOVA, pseudo-F= 1.19, p=0.69). Particle mixing intensities in fine sediment varied between 0 and 167.17 cm^2.yr^{-1} to be compared with a range between 0 and

16.42 $cm^2.yr^{-1}$ in coarse sediments. Corresponding sediment type averages were 12.05 ± 7.9 ($\bar{x}$ ± SE) and 5.29 ± 0.92 ($\bar{x}$ ± SE) $cm^2.yr^{-1}$, respectively **(figure 6 a)**.

Maximum penetration depth (MPD) did not significantly differ between the two sediment types (PERMANOVA, pseudo-F= 0.28, p=0.23 and PERMDISP >0.05) with maximum penetration depth of 4.7 ± 0.7 ($\bar{x}$ ± SE) cm in fine sediments versus 5.1 ± 0.5 ($\bar{x}$ ± SE) cm in coarse sediments **(figure 6 b)**.

The surface sediment was significantly more intensively reworked (SR) in coarse than in fine sediments (PERMANOVA, pseudo-F= 48.79, p<0.05). However, the variability in SR was higher in fine sediments (PERMDISP test <0.05). SR was 46.7 ± 5.9% in fine sediments ($\bar{x}$ ± SE; min-max: 9.6 - 89.9%) whereas it was 84.4 ± 2.2% in coarse ($\bar{x}$ ± SE; min-max: 69.0 - 97.8%) **(figure 6 c)**.

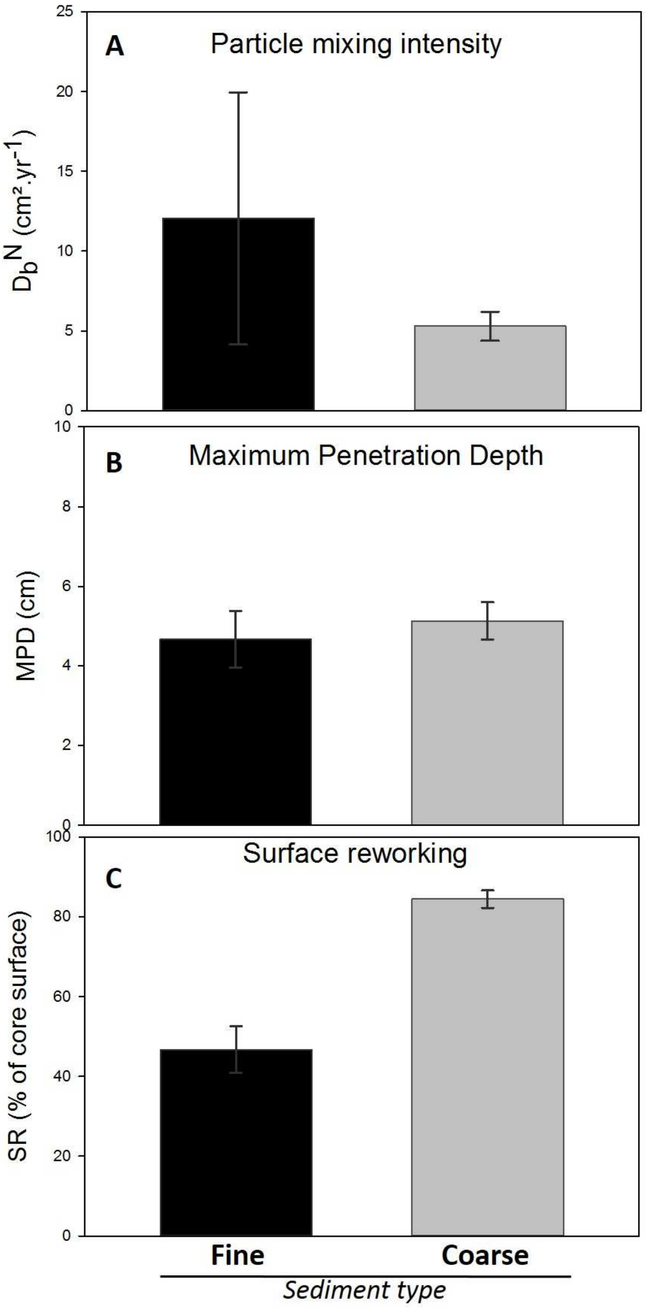


Figure 6: Means (+/- SE) of the 3 bioturbation metrics in fine (black bars) and coarse (grey bars) sediments.

Biotic and abiotic variables driving particle mixing. By accounting for biotic and abiotic variables we could explain a high proportion of the variance in particle mixing, i.e. 75.5% in fine sediments, 47.8% in coarse sediments and 33.5 % across the whole gradient (All cores), respectively. The variance explained was also tested for the third transitional sub-group identified within the fine sediment group (results presented in Appendix C), but this sub-division into three groups did not change the conclusions gained from two groups (but resulted in less statistical power) and thus this grouping is not further discussed here.

Across the whole gradient, 33.5% of the variability in the multivariate data cloud consisting of the 3 bioturbation metrics was significantly explained by a model that included the abundances of Biodiffusors (Biodif), the biomass of Gallery diffusors (Gal) and cohesiveness (**Table 3b**). These 3 descriptors individually explained (assessed through marginal tests, **Table 3a**) a significant proportion of the bioturbation pattern and also discriminated fine from coarse sediment **(Figure 7)**. When considering only fauna as explanatory variables, we could explain a smaller proportion of the total variance (31.5 %, AIC=45.9, p= 0.03) with a model including the abundances of Biodiffusors (Biodif), the biomass of Gallery diffusors (Gal) and the abundance of surface modifiers. Although PC1 was found to significantly explain 14.9 % of the total variability in the multivariate data cloud consisting of the 3 bioturbation metrics when fitted alone **(Table 3a)**, it did not improve the model including biological variables when fitted sequentially, in contrast to the binary variable “cohesiveness” **(Table 3b)**.

In fine sediments, 75.5% of the variability in the multivariate data cloud consisting of the 3 bioturbation metrics was significantly explained by a model that included the biomass of Gallery diffusors (Gal) followed by the abundances of Biodiffusors (Biodif), Surface modifiers (Surf), Conveyors (Conv) and Gallery diffusors (Gal) (**Table 3b**). These 5 descriptors individually explained (assessed through marginal tests, **Table 3a**) a significant proportion of the bioturbation pattern, with particularly the biomass of Gallery diffusors accounting for 30.3% of the total variability. Graphical representations by dbRDA of the relationship with these explanatory variables highlight the distribution of D_b^N (log-transformed, **Figure 8a**) and MPD (**Figure 8b**). Increasing D_b^N were associated with increasing biomasses of Gallery diffusors and abundances of Conveyors and Gallery diffusors, whereas increasing MPD (as well as SR, not shown here) were associated with increasing in the values of all the 5 explanatory variables identified by the model. No improvement of the model was found when including environmental explanatory variables although PC2 could solely explain (marginal test) 13% of the total variability (p=0.05), mostly corresponding to a decrease in D_b^N with PC2.

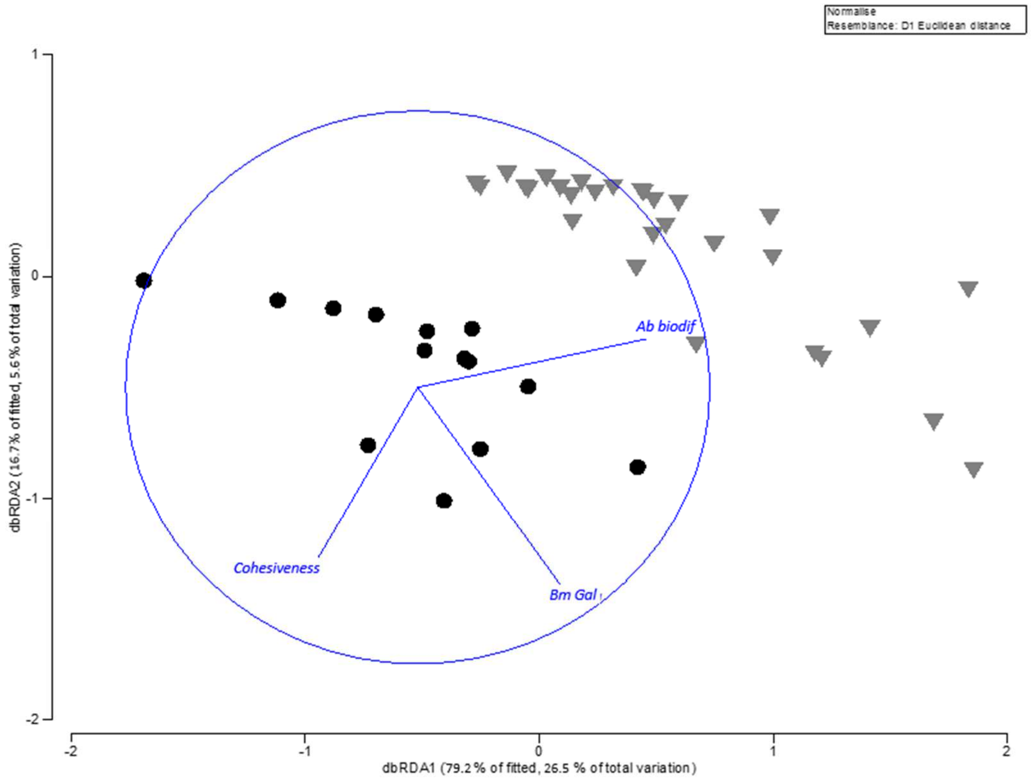
In coarse sediments, only the abundance of Gallery diffusors was found to be significant, and explained 9% of the variability in bioturbation patterns **(Table 3a)** when taking into account only the fauna data as explanatory variables. Conversely, when running the analysis using both fauna and environmental explanatory variables, 47.8% of the variability in the bioturbation metrics pattern was explained, although slightly non-significantly (p=0.1), by a model (identified on the basis of the AIC criterion) that included first the below-ground volume occupied by plant material (Plant), significantly explaining 9.7% of the variability, followed by abundance of Gallery diffusors, coordinates on PC1, abundances of Tube builders, Conveyors, biomasses of Surface modifiers, PC2 and the biomass of filtering biodiffusors. It should be emphasised that taking environmental explanatory variables into account resulted in the inclusion of more fauna variables into the model (with more explanatory power) than when using only fauna data as explanatory variables. This model highlights the distribution of D_b^N (log-transformed, **Figure 8c**) and MPD (**Figure 8d**) and revealed that increasing DbN were more correlated with (1) increasing biomasses of Surface modifiers and filtering biodiffusors and abundances of Gallery diffusors and conversely with (2) decreasing Plant, PC1 and abundances of Tube builders **(Figure 8c)**. Interestingly, variability in MPD seemed to be only affected by PC2 and abundances of Conv with a trend toward lower MPD for the highest values of these two last variables **(Figure 8d)**. No specific trends were observed in the variability of SR (not shown).

Table 3: Distance-Based Linear Model results between predictors (faunal and environmental) and bioturbation metrics (SR, D_b^N, MPD) in fine and coarse sediments. A: Marginal tests (predictor variables fitted individually). B: sequential tests (using Forward selection and AIC selection criteria). Ab and Bm indicate abundance and biomass of the functional groups: surface modifiers (Surf); filtering biodiffusors (Biodif fil); conveyors-belt (Conv), biodiffusors (Biodif); tube dwellers (Tub) and gallery-diffusors (Gal). Plant: below-ground volume of plant material; Pebbles: below-ground volume of pebbles; Shells: below-ground volume of shell hash. PC1: coordinates along the first principal component of the PCA analysis (figure 3); PC2: coordinates along the second principal component of the PCA analysis (figure 3). Bold font indicates significant results ($p<0.05$).

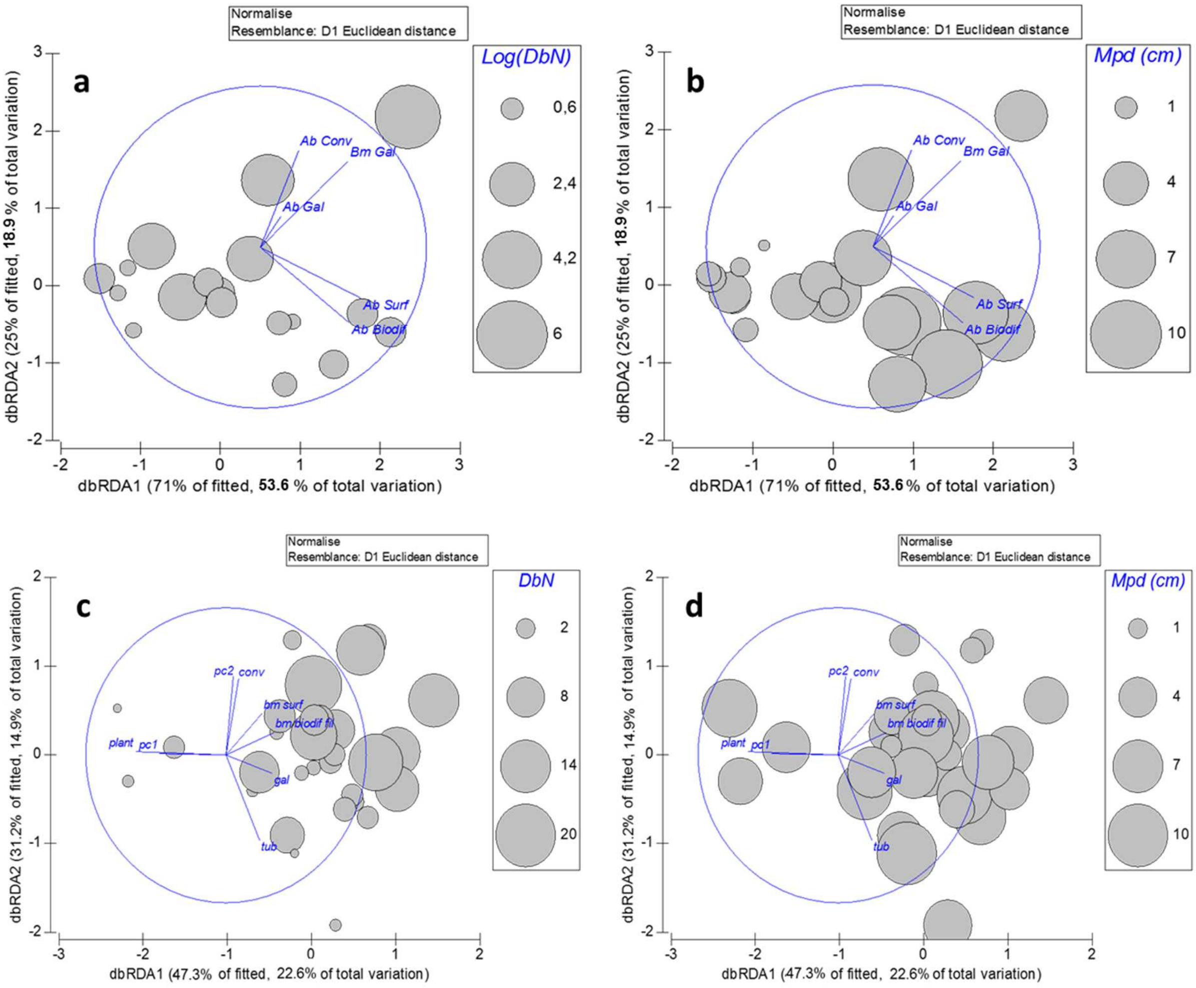
a	Variable	Pseudo-F	p	Variance explained (%)
All cores	**Ab Surf**	**6.18**	**<0.01**	**10.6**
	Ab Biodif fil	0.38	0.78	0.7
	Ab Conv	**7.41**	**<0.01**	**12.5**
	Ab Biodif	**10.85**	**<0.01**	**17.3**
	Ab Tub	**4.05**	**<0.01**	**7.2**
	Ab Gal	**8.11**	**<0.01**	**13.5**
	Plant	0.36	0.769	0.7
	Pebbles	**4.63**	**<0.01**	**8.1**
	Shells	0.94	0.457	1.7
	Bm Surf	**4.46**	**<0.01**	**7.9**
	Bm Conv	**4.81**	**<0.01**	**8.5**
	Bm Biodif	4.69	0.226	2.9
	Bm Gal	**5.83**	**<0.01**	**10.1**
	PC1	**9.13**	**<0.01**	**14.9**
	PC2	0.44	0.729	0.8
	Cohesiveness	**10.28**	**<0.01**	**16.5**
Fine sediment	**Ab Surf**	**5.46**	**<0.01**	**22.3**
	Ab Biodif fil	0.47	0.64	2.4
	Ab Conv	**3.98**	**0.02**	**17.3**
	Ab Biodif	**4.60**	**0.02**	**19.5**
	Ab Tub	0.88	0.46	4.4
	Ab Gal	**4.26**	**0.02**	**18.3**
	Plant	3.19	0.36	5.3
	Pebbles	2.38	0.09	11.1
	Shells	0.12	0.94	0.6
	Bm Gal	**8.27**	**<0.01**	**30.3**
	PC1	1.19	0.30	5.9
	PC2	2.88	0.05	13.0
Coarse sediment	Ab Surf	0.56	0.66	1.8
	Ab Biodif fil	0.07	0.98	2.2
	Ab Conv	1.51	0.22	4.6
	Ab Biodif	1.22	0.30	3.8
	Ab Tub	2.42	0.06	7.2
	Ab Gal	**3.08**	**0.02**	**9.0**
	Plant	**3.35**	**0.02**	**9.7**
	Pebbles	1.25	0.29	3.9
	Shells	0.27	0.85	8.5
	Bm Surf	0.70	0.56	2.2
	Bm Biodif fil	1.42	0.21	4.4
	Bm Conv	2.13	0.09	6.4
	Bm Biodif	0.75	0.53	2.4
	Bm Tub	0.43	0.73	1.4
	Bm Gal	1.01	0.39	3.2
	PC1	**2.85**	**0.03**	**8.4**
	PC2	0.49	0.70	1.6

b	Variable	AIC	Pseudo-F	p	Part of variance explained (%)	Cumul. part of variance explained (%)
All cores	**+Ab Biodif**	**52.08**	**10.85**	**<0.01**	**17.3**	**17.3**
	+Bm Gal	**47.08**	**7.06**	**<0.01**	**10.1**	**27.4**
	+Cohesiveness	**44.35**	**4.58**	**<0.01**	**6.1**	**33.5**
Fine sediment	**+Bm Gal**	**18.19**	**8.27**	**<0.01**	**30.3**	**30.3**
	+Ab Biodif	**13.10**	**8.21**	**<0.01**	**21.8**	**53.1**
	+Ab Surf	**6.82**	**5.29**	**<0.01**	**11.4**	**63.5**
	+Ab Conv	**4.07**	**3.66**	**0.02**	**6.8**	**70.3**
	+Ab Gal	**3.10**	**3.16**	**0.03**	**5.2**	**75.5**
Coarse sediment	**+Plant**	**33.85**	**3.35**	**0.02**	**9.7**	**9.7**
	+Ab Gal	**34.54**	**3.16**	**0.03**	**8.6**	**18.4**
	+PC1	34.23	5.30	0.12	5.5	23.9

	+Ab Tub	33.96	4.87	0.11	5.1	28.9
	+Ab Conv	33.46	4.97	0.10	5.2	34.1
	+Bm Surf	33.11	4.36	0.14	4.5	38.7
	+PC2	32.60	4.31	0.15	4.5	43.1
	+Bm Biodif fil	31.81	4.43	0.10	4.6	47.8



<u>Figure 7</u>: Graphical dbRDA representations of the relationship between the set of predictors identified by the model and Euclidean distances of the bioturbation metrics (SR, D_b^N, MPD) within the entire data set. Black circles represent fine sediment whereas grey triangles represent coarse sediment.



<u>Figure 8</u>: Graphical dbRDA representations of the relationships between the set of predictors identified by the model and Euclidean distances of the bioturbation metrics (D_b^N, MPD, SR) in Fine sediment (a, b) and Coarse sediment (c, d). Bubbles illustrate the distribution of the bioturbation metric within the constrained plane.

Discussion

Bioturbation is a key process that links seafloor biodiversity to ecosystem functioning. Our aim was to assess how bioturbation performed by resident macrofauna communities is influenced by local environmental conditions across different types of sedimentary habitats. In order to quantify this context dependence, we encompassed a range and variability of habitats, in terms of sediment types and macrofauna community characteristics, which are typical for the soft-sediment environments encountered in the northern Baltic Sea coastal archipelagos (Norkko et al. 2013; Villnäs et al. 2017). While accounting for the functional characteristics of the faunal communities and the strong variations in environmental characteristics across sites, we could explain a high proportion of the variance in the quantified bioturbation metrics, from 33.5 % across the whole gradient to 47.8% and 75.5% in coarse sediments and fine sediments, respectively.

Overall, our results highlight that across such sedimentary habitats, one can identify two different patterns of bioturbation displayed by resident benthic fauna, i.e. higher variability and maximum particle mixing intensities associated with fine sediments *versus* lower variability and amplitude associated with coarse sediments. The fine sediments are characterized by benthic macrofaunal communities which are low in abundance, species and functional richness and with high patchiness (at the scale of our measurements). Therefore, the high variability in bioturbation metrics, almost exclusively explained by key functional groups (without any additional variance explained by environmental variables) suggests that the activity of fauna (individual performance) is not restricted, *i.e.* negatively affected by habitat characteristics. The coarse sediments, on the other hand, are characterized by more abundant, species rich and functionally diverse macrofaunal communities that are less variable in terms of their composition. In these coarse sediments, however, bioturbation seems to be strongly restricted by environmental constraints associated with (1) coarser sediment structure, and (2) plant roots-rhizomes network and other sub-surface structures such as polychaete tube mats limiting bioturbation rates. Although the transition zone between strictly cohesive (mud) to strictly non-cohesive sediments (sand) is diffuse (Dorgan et al. 2006), taking into account the differences between the two sediment types clearly improves our understanding of the context-dependence of bioturbation patterns. This is, for instance, exemplified by the lower percentage of variance in the quantified bioturbation metrics that could be explained across the whole gradient, i.e. when taking all cores into account (33.5%). Moreover, only the binary variable “cohesiveness”, in contrast to the other continuous variables describing sediment characteristics, increased the percentage of variance that could be explained in addition to biological variables across the whole gradient. This is likely confirming the coexistence of two distinct bioturbation patterns encompassing different drivers across the gradient.

There is a growing interest in understanding and describing spatial variability of bioturbation and its effect on ecosystem functioning in soils and sediments. Studies reporting quantitative measurements of bioturbation along sedimentary gradients have mostly focused on the sole effect of benthic community composition as drivers of site-specific differences in particle mixing intensity (Gérino et al. 2007; Morys et al. 2017). Additionally, and in contrast to our site-specific measurements, most previous studies have used "passive" proxies such as the Bioturbation potential index BPc, which is calculated from benthic community trait composition, to infer bioturbation metrics (Solan et al. 2006; Queirós et al. 2013; Braeckman et al. 2014). However, the calculation method of this index is built on the assumption that the bioturbation potential of a given species is independent of changes in the biotic and/or abiotic habitat characteristics or species interactions. Therefore, the bioturbation potential of a whole community is calculated by a simple summation of all these individual potentials. Our results, however, demonstrate complex interactions between biotic and abiotic habitat characteristics that strongly modifies bioturbation across sedimentary habitats, and suggest that the utility of the BPc method for unravelling the role of fauna across different sedimentary habitats is limited. Nevertheless, the principles of such a method seems clearly appropriate for habitats where the functional composition of the fauna could explain a high proportion of the variation in bioturbation and where no interactions with the habitat characteristics could be detected, *i.e.* in fine sediments.

Control of bioturbation in fine and coarse sediments: space for individual performance vs environmental constraints

The combination of the abundances and/or biomasses of the 5 bioturbation functional groups, explained 75.5% of the variance in bioturbation patterns (defined by the three measured bioturbation metrics) with no further improvement of the model when adding environmental explanatory variables in fine sediments. Conversely, in coarse sediments, the fauna alone accounted for only a marginal part of the variance of bioturbation patterns whereas the inclusion of environmental variables greatly improved the model and the variance explained (47.7%) and further allowed for the inclusion of more fauna variables into the model. This suggests that macrofauna activities in fine sediments were not affected by changes in sediment properties or habitat structural elements (roots and rhizomes etc.). Conversely, these individual performances are likely affected by environmental variables in coarse sediments. Visual observations of our experimental cores confirmed such differences since only in fine sediment cores, could one observe well-developed bioturbation features showing the intense mixing of tracers such as (1) dense and extensive networks of burrows filled with luminophores, typical of a high influence of single individuals of gallery diffusors (*Hediste diversicolor*), and (2) clear conical shape networks of siphonal galleries also filled with luminophores, typically indicative of the bioturbation performed by large individuals of *Macoma balthica* while deposit feeding at the sediment surface (in this sediment type corresponded to the Biodiffusor group). These two functional groups were identified as the most relevant ones to explain the variance in particle mixing intensity (**Figure 8a, 8b**) in fine sediments (**Table 3**). Bioturbation in fine sediments (encompassing sediments ranging from mud to fine sand) was therefore considerably more predictable on the basis of the composition of benthic fauna than in coarse sediments.

In coarse sediments, the inclusion of three environmental explanatory variables (Plant, PC1, PC2) explained a substantial part of the variability in bioturbation (**Table 3b**). The effect of the volume of plant material was highly correlated with that of sediment organic content

(PC1) (**Figure 8c, 8d**), probably because of: (1) enhanced sedimentation of organic-rich fine particles due to the presence of a plant canopy reducing bottom current velocity (Fonseca and Fisher 1986), and (2) the presence of organic-rich detritus due to sub-surface plant and animal structures. This is coherent with the observed restriction of bioturbation intensity but not of bioturbation depth (**Figure 8b,8c**), indicative of a limitation of individual bioturbation performance. This could be caused by sediment compaction induced by the roots-rhizome network (Brenchley 1982) or any structure within the sediment column limiting the movement of macrofauna and thus reduced particle mixing intensity (Bernard et al. 2014, Aschenbroich et al. 2017). Similar physical effects were observed with high abundances of tube builders (*Pygospio elegans*; **Figure 8**) that are also known to stabilize and compact the sediment while constructing dense mats (Brenchley 1982) limiting bioturbation intensity (Wheatcroft and Martin 1996, Bernard et al. 2014) but not MPD, since these structures can reach significant depth and therefore promote some particles falling down to the end of the tubes.

Apart from large spatial variations in habitat characteristics, archipelago ecosystems from the northern Baltic Sea are particularly influenced by a well-marked seasonality resulting in large amplitudes of water temperature (Kauppi et al. 2018a), nutrient concentration, and light intensity reaching the seafloor (Attard et al. 2019). This also affects primary production influencing the quantity and quality of organic matter input to the seafloor. Our experiments took place in late summer, characterized by the highest temperatures and the peak productivity of the system. Temperature and organic matter quantity and quality are known as the main drivers of bioturbation activities by benthic organisms. Although low temperatures generally strongly restrict particle mixing (Bernard et al. 2016), the effect of the changes in organic content (in the sediment or the water column) on bioturbation activities is more difficult to predict (Wheatcroft and Martin 1996) because species, even when closely related, can exhibit different adaptive strategies leading to either an enhancement or a restriction of particle mixing (Maire et al. 2006).

Direct and indirect modification of bioturbation performance by changes in sediment physical structure

In coarse sediments, coarser grains, indicated by the lower values of the PC2 variable, were correlated with lower bioturbation intensities (**Figure 7c, 7d**). The effect of grain size could be related to both direct and indirect changes in individual bioturbation performance through an increase in the physical constraints induced by coarser sediment grains (Dorgan et al. 2006). This first directly shows that the mechanics of particle movement induced by the fauna while digging or actively deposit feeding are likely different in sand and mud (Eldon & Kristofferson 1978; Tallqvist, 2000), therefore affecting measured bioturbation rates. Differences in mechanical properties (such as granularity and/or cohesiveness) of marine soft sediments are also known to influence burrowing behavior of nereid polychaetes (Dorgan et al. 2006), and maintenance of decapod burrows and subsequent species-specific bioturbation activity (Needham et al. 2010). This is in agreement with the lower explanatory power detected for abundances of Gallery diffusors (*H. diversicolor*) across the whole gradient and even more in coarse sediment associated with lower bioturbation intensity, compared to the one found in fine sediments. It thereby suggests a restriction of the individual bioturbation performance of Gallery diffusors induced by a coarser and less cohesive sediment matrix. This suggests that only significant increases in abundance in sandy sediments will compensate for the physical constraints affecting individual performances.

The fact that biomasses of the filtering biodiffusor group (Biodif fil), corresponding to the two bivalve species, *Mya arenaria* and *Cerastoderma glaucum*, was found as key to explain the variance of bioturbation pattern in coarse sediments highlights a good adaptation of these thick-shell bivalve species to physically constraining environments. In coarse non-cohesive granular sediments, siphon retraction creates depressions in which particles are buried due to gravity. The lack of sediment cohesion also explains for example our visual observation of the cores with *M. arenaria*, where tubular structures evenly filled with well-mixed sand and luminophores were observed from the sediment surface to the shell position (ca 10 cm below the sediment surface).

Across grain size gradients, benthic species may switch from deposit- to suspension feeding (Olafsson 1986, Riisgård and Kamerans 2001), resulting in lower particle mixing intensities (Josefson et al. 2002, Bernard et al. 2016). Interestingly, most of the species in the present study are known to be able to perform such a switch. This is particularly the case of the gallery-diffusor *H. diversicolor* (Riisgård 1991, Evrard et al. 2012), the tube-building polychaete *P. elegans* (Riisgård and Kamerans 2001) and the Biodiffusors *M. balthica* (Olafsson 1986; Riisgård and Kamerans 2001), *Corophium volutator* (Riisgård and Schotge 2007) and *Marenzelleria* spp. (Karlson et al. 2015). However, there can be multiple mechanisms underlying changes in feeding strategy and these can be species- or population-specific (Riisgård and Kamerans 2001). Hence they are difficult to reproduce in experimental set-ups. A potential switch between deposit- and suspension feeding in the Biodiffusor species with increasing grain size in the coarse sediments could nevertheless explain why (1) we did not detect any effect of this functional group on bioturbation patterns, and (2) the relatively low level of variance in bioturbation metrics found in this sediment type (**Table 3**). This suggests the need for differential sediment type-explicit bioturbation group coding for (some of) these species in future studies.

In conclusion, by investigating and actually quantifying natural bioturbation patterns in a range of sediment types, we show that the variability in spatial patterns of community bioturbation is a result of complex relationships between benthic macrofauna community structure, sediment type and other habitat characteristics, likely modifying the individual bioturbation performances of the fauna. The same dominant species may have contrasting effects on bioturbation metrics depending on sediment type. This suggests that spatial patterns of ecosystem services underpinned by bioturbation, such as organic matter remineralization and carbon sequestration, may be affected by these complex biodiversity-ecosystem process relationships (Snelgrove et al. 2014). It therefore highlights the need for carefully integrating habitat heterogeneity when mapping ecosystem functions and services provided by benthic communities across spatial scales useful for management.

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