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Interplay between abiotic factors and species assemblages mediated by the ecosystem engineer *Sabellaria alveolata* (Annelida: Polychaeta)

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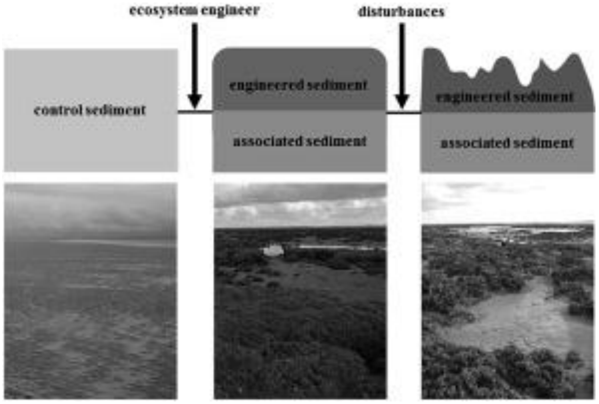
Abstract :

Sabellaria alveolata is a gregarious polychaete that uses sand particles to build three-dimensional structures known as reefs, fixed atop rocks or built on soft sediments. These structures are known to modify the local grain-size distribution and to host a highly diversified macrofauna, altered when the reef undergoes disturbances. The goal of this study was to investigate the different sedimentary and biological changes associated with the presence of a *S. alveolata* reef over two contrasting seasons (late winter and late summer), and how these changes were linked. Three different sediments were considered: the engineered sediment (the actual reef), the associated sediment (the soft sediment surrounding the reef structures) and a control soft sediment (*i.e.* no reef structures in close proximity). Univariate and multivariate comparisons of grain-size distribution, soft sediment characteristics (organic matter content, chlorophyll *a*, pheopigments and carbohydrate concentrations) and macrofauna were conducted between the different sediment types at both seasons and between the two seasons for each sediment type. A distance-based redundancy analyses (dbRDA) was used to investigate the link between the different environmental parameters and the macrofauna assemblages. Finally, we focused on a disturbance continuum of the engineered sediments proxied by an increase in the mud present in these sediments. The effects of a continuous and increasing disturbance on the associated fauna were investigated using pairwise beta diversity indices (Sørensen and Bray-Curtis dissimilarities and their decomposition into turnover and nestedness). Results showed a significant effect of the reef on the local sediment distribution (coarser sediments compared to the control) and on the benthic primary production (higher in the associated sediments). At both seasons, *S. alveolata* biomass and sediment principal mode were the environmental parameters which best differentiated the engineered, associated and control sediment assemblages. These two parameters are under the ecosystem engineer's influence stressing its importance in structuring benthic macrofauna. Furthermore, in late summer but not in late winter, presence/absence and abundance based beta diversity were positively correlated to our disturbance proxy (mud content) a tendency driven by a species replacement and a rise in the associated fauna density. Our first set of results highlight the importance of *S. alveolata* reefs as benthic primary production enhancers via their physical structure and their biological activity. The results obtained using beta diversity indices emphasize the importance of recruitment in structuring the reef's macrofauna and – paradoxically – the ecological value of *S. alveolata* degraded forms as biodiversity and recruitment promoters.

Graphical abstract



Highlights

► *Sabellaria alveolata* is a highly structuring ecosystem engineer via the reefs it creates and the abiotic and biotic modifications it induces. ► Benthic primary production is higher in the immediate vicinity of a *Sabellaria alveolata* reef. ► *Sabellaria alveolata* leads to the establishment of two distinct assemblages: one in the reefs and another in the soft sediment around them. ► An increasing disturbance of the reefs leads to a species turnover and a total abundance increase.

Keywords : Honeycomb worm, Macrobenthos, Benthic primary production, Habitat disturbance, Silt, Beta diversity, France Brittany, Mont Saint-Michel Bay

Abbreviations

MSMB	Mont Saint-Michel Bay
MPB	Microphytobenthos
TOM	Total organic matter
Chl *a*	Chlorophyll *a*
Pheo	Pheopigments
Ins	Insoluble carbohydrates
Sol	Soluble carbohydrates
dbRDA	Distance-based redundancy analysis
CPUE	Catch-per-unit-effort

1. Introduction

Ecosystem engineers are organisms capable of modifying their local environment through their physical presence (*i.e.* autogenic engineers) and/or their biological activity (*i.e.* allogenic engineers), “directly or indirectly modulating the availability of resources to other species” (Jones et al., 1994). Ultimately, these species maintain, modify, create or even destroy habitats (Bouma et al., 2009; Jones et al., 1994). The abiotic modifications caused by ecosystem engineers can lead to facilitation for some organisms (Hacker and Gaines, 1997) and inhibition through negative species interaction for others (Bouma et al., 2009; Jones et al., 1997). Nonetheless, bioengineered habitats are often reported to host a more diverse species assemblage than the adjoining non-engineered habitats (Ataide et al., 2014; De Smet et al., 2015; Jones et al., 1997; Stachowicz, 2001). Physical ecosystem engineering appears to be particularly important where the environment is extreme (*e.g.* thermic, hydrodynamic and/or hydric stress), like in temperate intertidal areas (Bouma et al., 2009; Jones et al., 1997). Indeed, according to Jones et al. (1997, 1994), these extreme conditions might have favored the selection of “extended phenotype engineers” through enhanced survival of the engineer and the cohabiting fauna (Dawkins, 1982). These engineer species create complex habitats that reduce local pressures such as predation or thermal stress, whilst increasing biodiversity (Bouma et al., 2009). Ultimately, such favorable environmental changes can lead to an interesting paradox where “the spatial extent of the realized niche of a species can be larger than the spatial range predicted by the fundamental niche” as described by Bruno et al. (2003) and reported for mussels and barnacles in *Ascophyllum nodosum* canopies by Bertness et al. (1999).

Temperate coasts host a striking number of ecosystem engineering species, spanning from mollusks (for a review see Gutiérrez et al. (2003)) and polychaetes (*e.g. Lanice conchilega* (De Smet et al., 2015)) to canopy-forming algae (*e.g. Ascophyllum nodosum* (Bertness et al., 1999)). Along the European coastline, a particular ecosystem engineer has the ability to build three-dimensional structures on top of sediments qualified as reefs (Holt et al., 1998). This species is a common gregarious tubiculous polychaete called *Sabellaria alveolata* (Linnaeus, 1767), a.k.a. the honeycomb worm. It generally lives in the intertidal zone from mid to low tide levels and can be found from Scotland and Ireland to Morocco (Muir et al., 2016). *Sabellaria alveolata* uses sand particles remobilized by waves and tidal action to build the tube in which it lives (Le Cam et al., 2011). Since the pelagic larvae are attracted by the L-dopa present in the organic cement produced by the adult worms for their tube-building activity, they will tend to settle on existing reefs (Pawlik, 1988; Wilson, 1968). This phenomenon coupled with favorable environmental conditions (*i.e.* grain-size structure, hydrodynamic processes, food availability and water temperature) can lead to the development of large biogenic reefs (Holt et al., 1998). These structures are commonly found on rocky substrata as veneers or hummocks where they rarely exceed 50 cm in height for a few tens of square meters but in some rare instances, they can be found in soft bottom areas where they can grow up to two meters in height and several hectares in size (Holt et al., 1998; Noernberg et al., 2010). The largest of these formations, which is also the largest biogenic habitat in Europe, is located in the Mont Saint-Michel Bay (MSMB) in France (Desroy et al., 2011; Dubois et al., 2002).

The research around this species has mainly focused on its physiology (*i.e.* reproduction, fecundity, feeding mode) (Dubois et al., 2003, 2005, 2006a, 2009) and its tube building activity (Fournier et al., 2010; Le Cam et al., 2011). Other studies have looked into the ecology of reefs with a particular interest on the associated fauna (Dias and Paula, 2001; Porta and Nicoletti, 2009; Schlund et al., 2016) and factors influencing it such as the reef's different growth stages (Dubois et al., 2002), epibionts (Dubois et al., 2006b), human trampling (Plicanti et al., 2016) and ecological status (Desroy et al., 2011). A large part of these studies has focused on *Sabellaria alveolata* reefs on rocky substrata and not on soft sediment. Reefs developing on soft sediment are far less frequent along the European coast (*i.e.* MSMB and Bourgneuf Bay in France) (Holt et al., 1998). Nonetheless, they constitute exceptional locations composed of two distinct entities: the actual three-dimensional reef structures (engineered sediment), which is spatially discontinuous and the soft sediment present between the reef structures (associated sediment) (Desroy et al., 2011). Several kilometers separate them from the nearest rocky shore which signifies, in contrast to the veneer form of *S. alveolata* structures, complete isolation from most of the juvenile and adult fauna inhabiting these rocky shores. Furthermore, their physical borders are easy to visualize against the surrounding soft sediment. These sites give us the chance to study different components of *S. alveolata*'s engineering effect (Passarelli et al., 2014; Wright et al., 2006). This engineering effect can be seen from both an environmental and a biological perspective by looking at how the ecosystem engineer modifies the local sedimentary characteristics and how the biodiversity changes between a control sediment, the associated and the engineered sediments. The control soft sediment represents the baseline or the unmodified state before the honeycomb worms start building reefs, hence representing a new structural state (Jones et al., 2010).

This biogenic habitat is not structurally homogenous, mainly due to multiple disturbances; direct natural disturbances such as storms and cold winters, direct anthropogenic disturbances such as trampling and indirect anthropogenic disturbances through shellfish farming and coastal engineering. These disturbances lead to a gradual modification of the reef visible through disaggregation, increasing fine sediments, decreasing ecosystem engineer density and increasing epibiont cover, causing a number of changes in the associated fauna (Dubois et al., 2006b, 2002; Plicanti et al., 2016). Modifications of the associated fauna have been investigated in several categorical ways but never along a disturbance continuum (Dubois et al., 2006b, 2002; Plicanti et al., 2016). To understand the changes in the associated fauna along this continuum, we chose to focus on the beta diversity seen as “the extent of change in community composition” as defined by Whittaker (1960) and on an abundance-based dissimilarity measurement using the Bray-Curtis dissimilarity. Analyzing beta diversity in a *S. alveolata* reef can help us understand the functioning of this biogenic habitat and give more relevant information to decision makers regarding conservation issues. First, taking into account the three previously defined sediment types (control, associated and engineered sediments), we tested in a categorical way, the following hypotheses: (1) the engineered sediment affects the different sedimentary characteristics of the associated sediment, especially grain-size, organic matter content and microphytobenthos and (2) the diversity and species composition of both the engineered and the associated sediments are different from the control sediment. We also looked into potential changes between late winter and late summer, regarding sediment composition and macrofauna assemblages for each sediment type. Then, using beta diversity and dissimilarity measurements, we tested the following hypothesis: an increasing disturbance of the engineered sediment promotes (1) beta diversity and more specifically species turnover and (2) abundance-based dissimilarity and more specifically abundance gradients.

2. Materials and methods

2.1. Study area

This study took place in the central part of the MSMB where the largest bioconstruction in Europe is located; the Sainte-Anne reef (48°38’700N and 1°40’100W), built by the honeycomb worm *Sabellaria alveolata* (Desroy et al., 2011). This reef is situated in the lower intertidal zone (*i.e.* between the - 2 and the - 4 m isobaths (Noernberg et al., 2010)), parallel to the coast and to the dominant tidal currents and also near important blue mussel (*Mytilus edulis*) cultures. In 2014, the maximal dimensions of the Sainte-Anne reef were 2.5 km in length for 1 km in width and the engineered sediment represented about 32 ha for about 128 ha of associated sediment (unpublished results). The area located in the central part of the bay and along the same isobath as the reef is characterized by medium to muddy sands (Bonnot-Courtois et al., 2009) and by a species poor “*Macoma balthica* community” (Dubois et al., 2002).

2.2. Sampling design and laboratory analyses

Two sampling areas were defined; the Sainte-Anne reef area and a control area. The reef area was composed of two sediment types, the engineered and the associated sediments (Fig. 1). The control area was a soft sediment zone located 1.5 km North-East of the reef area and on the same bathymetric level. It was characteristic of the medium to muddy sands found in this part of the bay (Bonnot-Courtois et al., 2009). Sampling took place over a two-day period in late winter (late February) and late summer (late September). These two seasons were chosen because they are highly contrasted environmentally (*e.g.* hydro-sedimentary features) and biologically (*e.g.* recruitment patterns, species turnover, growth rates). Indeed, winter is a period of low biological activity and high environmental pressures (cold temperatures, wind and storms) while late summer is a post-recruitment period with a higher biological activity (Arbach Leloup et al., 2008; Cugier et al., 2010). Hence, sampling at these two seasons helps us to have a more complete picture of the dynamics happening in our different study zones.

To investigate the effects of *S. alveolata* on diversity and species composition, we compared the macrofauna associated with the three different sediment types: the *S. alveolata* reefs, the sediments present around these structures and the control soft sediments. For each sediment type (*i.e.* engineered, associated and control sediment, Fig. 1), ten stations were sampled. Every engineered sediment station was paired with an associated sediment station, in order to investigate how the reef structures modify the adjoining soft sediment. The stations were at least 75 m apart and at each station, six samples separated by at least 5 m were randomly taken at low tide. The first three samples were done using a 18.5 cm side corer (269 cm²) to a depth of 15 cm (core samples). For engineered sediments, this depth corresponds to the layer where *Sabellaria alveolata* and more than 90% of all species live (Dubois et al., 2002). The other three samples were done using a 1 m² quadrat in order to estimate the over dispersed macrofauna, mainly composed of bivalves and gastropods (quadrat samples). All engineered sediment samples (core and quadrat samples) were taken at least 1 m from the reef edge to avoid a known border effect on the macrofauna diversity (Gruet, 1972), while the associated sediment samples (core and quadrat samples) were taken at least 1 m away from the reef structures. The soft sediment core samples were sieved through a 1-mm square mesh on site while the engineered sediment core samples were taken back to the laboratory where they were broken apart under water and the fauna retained on a 1-mm square mesh was collected. Associated and control quadrat samples were done by sieving on site the first 5 cm of sediment through a 5-mm square mesh. For the engineered quadrat samples, we sampled by hand all the visible macrofauna located on the reef and inside the reef interstices. All core and quadrat samples were fixed in a 5% formaldehyde solution, after which all the macrofauna was sorted, counted and identified to the species or genus level (except for nemerteans, oligochaetes and nematodes) and finally preserved in a 70% ethanol solution. For each engineered sediment core sample, all the *Sabellaria alveolata* were weighted (total wet weight).

To look at how the ecosystem engineer modifies its environment, we randomly collected three sediment samples for grain-size distribution, total amount of organic matter (TOM), pigment concentration (*i.e.* chlorophyll *a* and pheopigments) and total carbohydrate concentration (*i.e.* soluble and insoluble carbohydrates), at each associated and control sediment station. For the grain-size distribution, the first 5 cm of sediments were sampled using a small plastic core (19 cm²). For all the other sedimentary characteristics, only the first centimeter of sediment was sampled using a plastic petri dish (57 cm²). Additional samples were collected in order to characterize the sediments constituting the *Sabellaria alveolata* tubes as well as the sediments potentially trapped within the biogenic structure. These consisted in randomly collecting three small reef parts (about 8 x 3 cm) in each engineered sediment station. Sediment grain-size distribution was obtained by mechanical sieving using AFNOR calibrated sieves (from 25 mm to 63 µm) and granulometric parameters were estimated using the 'G2Sd' package in R v. 3.3.0 (Fournier et al., 2014). Prior to mechanical sieving, the engineered sediments were cautiously broken into their original elements, *i.e.* mostly bioclasts as evidenced in Le Cam et al. (2011). For all the other analyses, the sediments were first freeze-dried in order to work on dry matter. TOM was determined as the difference between the weight of freeze-dried sediment and the weight after 4 hours at 450° (Aminot and Kerouel, 2004). Pigment concentrations ($\mu g.g^{-1}$ dry sediment) were estimated using the monochromatic technique (Lorenzen, 1967) described in Aminot and Kerouel (2004). The chlorophyll *a* (Chl *a*) concentration was used as a proxy for microphytobenthos (MPB) biomass (Jeffrey et al., 1997) while pheopigments (Pheo) concentration gave us information about the amount of degraded photoautotrophs. Soluble carbohydrates (Sol) present in the sediment were extracted by hydrolysis (100°C for 45 min), after which the pellets were treated with sulfuric acid (H_2SO_4) and placed 4 hours at 100°C in order to obtain the insoluble carbohydrates (Ins). Sol and Ins concentrations ($\mu g.g^{-1}$ dry sediment) were then estimated by colorimetric phenol sulfuric dosage (Dubois et al., 1956). Sol were considered as being an important labile source of carbon for consumers living in the sediment such as bacteria and deposit-feeding invertebrates (Bellinger et al., 2009) while the insoluble carbohydrates to soluble carbohydrates ratio (Ins/Sol) was used as a proxy for the C/N ratio and as a TOM degradation index (Delmas, 1983).

2.3. Data analysis

2.3.1. Biological and environmental engineering effects

Since macrofauna was sampled using two different techniques (cores and quadrats), densities of species were estimated using the catch-per-unit-effort (CPUE) method, *i.e.* the ratio between the total catch and the total amount of effort used to harvest the catch (Skalski et al., 2005). At one sampling location, when a species was only collected by core or quadrat, its density was estimated using the corresponding sampling surface. However, when a species was sampled by both methods, cumulated abundances were divided by the sum of each gear's CPUE. This estimation method was used for 17 species in late winter and 15 in late summer, taking into account all three sediment types. Species' densities were calculated using the formula:

$$density_A\,(\text{ind.}\,\text{m}^2) = \frac{(abundance_{Aq} + abundance_{Ac})}{(CPUE_q + CPUE_c)}$$

where $density_A$ is species' A abundance per m², $abundance_{Aq}$ is species' A abundance using the quadrat, $abundance_{Ac}$ is species' A abundance using the core, $CPUE_q$ is the quadrat's catch-per-unit-effort (1 m²) and $CPUE_c$ is the core's catch-per-unit-effort (0.0269 m²).

To assess the effect of *Sabellaria alveolata* on the associated macrofauna and validate our *a priori* grouping into engineered, associated and control sediments, Principal Coordinates Analysis (PCO) were performed for the late winter and late summer data sets. Analyses were performed on a Bray-Curtis similarity matrix calculated from log-transformed densities after *S. alveolata* was removed from the matrix, in order to take into account only the species associated with this sediment type. Indeed, because of its high abundance (*i.e.* on average, 63% of the total abundance), the single presence of *S. alveolata* would automatically cause a strong grouping of engineered sediment samples. Species present in only one sample (*i.e.* in less than 2% of all samples) were excluded from the initial matrix. To identify species typifying each sediment, species that correlated more than 60% with one of the first two axes (*i.e.* Spearman correlations) were plotted on each PCO. In parallel, a one-way univariate permutational ANOVA (permanova) was performed on the same species density matrices as for the PCOs, in order to evaluate if there was a significant difference in the species composition of each sediment type.

Finally, the macrofauna diversity of each replicate (core and associated quadrat) sampled in late winter and late summer, was assessed using Hill's indices; N0 (number of species), N1 (exp (H') where H' is the Shannon-Winner diversity ($\log_e$)) and N2 (1/D where D is the Simpson's dominance index (Hill, 1973)) as recommended by Gray (2000) and the total macrofauna density. These indices inform how the total abundance is partitioned between the different species (Gray, 2000; Whittaker, 1972 for details). Densities calculated using the CPUE method and for 1 m² as previously detailed, were used to calculate N1 and N2. For each replicate, N0 was calculated as the sum of the species richness recorded in the core and the species richness recorded in the associated quadrat. For N0, N1 and N2, *S. alveolata* was either kept or removed from the initial data in order to investigate how this species influences the partitioning of the associated fauna abundance.

To test for significant differences between the three sediment types for the different grain size and macrofauna descriptors and because none of the descriptors fulfilled normality of distribution and homogeneity of variance, permanovas were performed, with sediment type considered as a fixed factor. We used Euclidian distance as a distance measure and ran 9999 permutations for each test. If the main test was significant, pairwise tests were performed. Effect of the presence of the engineered sediment on soft sediment environmental parameters (TOM, Chl *a*, Pheo and Ins/Sol) was investigated by comparing these parameters between associated and control sediments, also using permanovas. Prior to performing permanovas, we tested for homogeneity of dispersions using the PERMDISP PRIMER routine (Anderson et al., 2008). When raw data presented significantly different dispersions between the three sediment types ($p < 0.05$), it was log transformed (in late winter: principal mode, TOM, Chl *a*, Pheo, macrofauna density with and without *S. alveolata*, N0 with and without *S. alveolata* and N2 with *S. alveolata*, in late summer: macrofauna density with and without *S. alveolata*, N0 with and without *S. alveolata* and N1 without *S. alveolata*). When log transformation did not lead to homogenous dispersions (in late winter: % mud, % sand and Sol, in late summer: TOM, Chl *a*, Sol, N1 and N2 calculated with *S. alveolata*), non-parametric statistical tests were performed (Kruskal-Wallis test for the granulometric and macrofauna parameters and Wilcoxon-Mann-Whitney for the other environmental parameters).

In order to evaluate if the different environmental and macrofauna parameters were significantly different between late winter and late summer for each sediment type, one-factor permanovas were performed, with season considered as a fixed factor. We chose to perform one-factor rather than two-factor univariate analysis of variance (in this case with sediment type and season as fixed factors), because we lacked replication inside each season for our different sediment types (Underwood, 1997). As previously mentioned, permanovas (9999 permutations) were used rather than t-tests because none of the investigated variables were normally distributed. Homogeneity of dispersions was also tested (PERMDISP) and data was transformed when necessary (square-root transformation for TOM in the associated sediments, log transformation for macrofauna density with *S. alveolata* in the control sediments and for macrofauna density without *S. alveolata* in the engineered sediments). The Permanovas, PERMDISP routines and PCOs were performed using the PRIMER v6 software with the PERMANOVA+ add-on (Anderson et al., 2008). *Post-hoc* Kruskal-Wallis tests were performed with the 'kruskalmc' function from the 'pgirmess' package (Giraudoux, 2016) using R version 3.3.0 (R Core Team, 2016).

2.3.2. Linking environmental and biological engineering effects

The relationship between the environmental characteristics and the macrofauna present in the three sediment types was investigated using distance-based linear models (DistLM). In line with Legendre and Anderson (1999) and McArdle and Anderson (2001), DistLM models were coupled to a distance-based redundancy analysis (dbRDA) to define the best fitted model in a multi-dimensional space in a way similar to a constrained PCO. DistLM models were built using the Bayesian Information Criterion (BIC) to identify “good” models and the ‘best’ procedure to select the variables according to the BIC. Prior to the DistLM and dbRDA analysis, the environmental parameters were displayed using Draftsman plots and the ones presenting an important skewness were transformed to approach normality (Anderson et al., 2008). If two predictor variables were strongly correlated ($r^2 > 0.80$), one of them was removed from the analysis in order to avoid multi-collinearity (Dormann et al., 2013). Except for the grain-size data, environmental parameters used to characterize an engineered sediment sample were the same as for its corresponding associated sediment sample. For late winter, the final predictor data set contained the % sand, Pheo (both square-root transformed), % mud, TOM, *S. alveolata* biomass (all three fourth-root transformed), principal mode and Ins/Sol (both log transformed). For late summer, the final predictor data set was the same as for late winter, except the % sand which was removed (absolute correlation with % mud > 0.8). *S. alveolata* biomass was used rather than abundance because this parameter provides more information about ecosystem functioning (Cardinale et al., 2013). *S. alveolata* biomass was considered as a predictor variable since it physically modifies its environment and it was consequently removed from the macrofauna data set. The DistLM models and dbRDA analysis were performed using the PRIMER v6 software with the PERMANOVA+ add-on (Anderson et al., 2008).

2.3.3. Disturbances and biological engineering effect

At its climax, a *S. alveolata* reef is formed by 100% honeycomb worm tubes, leaving virtually no space for infaunal organisms. When natural or anthropogenic disturbances (*e.g.* storms, trampling) physically damage the reef, tubes are destroyed, freeing up space. This new available space can be filled either with other organisms such as the oyster *Magallana gigas* (formerly known as *Crassostrea gigas*) or by fine particles. Fine particles accumulate from suspended sediments, or from the feces and pseudofeces of *S. alveolata* and other bivalves (biodeposition) (Dubois et al., 2006b). In either case, this fine sediment can end up trapped inside the *S. alveolata* reefs. Consequently, the increased deposition of mud inside the engineered sediments is the result of several different and often concomitant disturbances. Fine sediment deposition has previously been recognized as a significant disturbance to stream macroinvertebrates (Mathers et al., 2017) and benthic habitats (Balata et al., 2007; Mateos-Molina et al., 2015; Miller et al., 2002). Similarly, we chose to consider mud content as a proxy for disturbance. This proxy was also chosen because it is independent from *Sabellaria alveolata* population dynamics and physiological state. Finally, using the mud content makes the two seasons readily comparable.

Beta diversity was calculated using pairwise multivariate distances since they are independent of sample size and regional diversity (gamma diversity) allowing accurate potential comparisons among regions (Bennett and Gilbert, 2016). We chose to use the presence/absence based indices presented by Baselga (2010) in order to partition total beta diversity, expressed by Sørensen dissimilarity (β_{sor}), into the turnover (β_{sim}) and nestedness (β_{nes}) components. In this case, $\beta_{sor} = \beta_{sim} + \beta_{nes}$. Under conditions of equal species richness, $\beta_{sor} = \beta_{sim}$ and $\beta_{nes} = 0$, while under conditions of unequal species richness, β_{sim} and β_{nes} vary between 0 and β_{sor}. Sørensen dissimilarity varies between 0 and 1, with 0 indicating that two samples have identical species list and 1 indicating no common species (Baselga, 2010). For β_{sim}, 0 indicates complete nestedness, and a maximal value of 1 can be found if in one of the two considered samples, there are no species recorded and in the other, the number of species is maximal (Koleff et al., 2003). To have a complementary vision of how disturbance affected the associated fauna abundance, the abundance-based dissimilarity (Bray-Curtis dissimilarity, d_{BC}) was also partitioned into balanced changes in abundance ($d_{BC\text{-}bal}$) and abundance gradients ($d_{BC\text{-}gra}$), which are closely related to turnover and nestedness components respectively (Baselga, 2013). These indices were computed after removing *S. alveolata* from the presence/absence and density matrices. They were calculated using the pairwise measures in order to have the beta diversity and the dissimilarities for each pair of samples (*i.e.* 435 pairs). Then, using Euclidian distance, all the mud content pairwise differences were calculated. Finally, using the different pairwise measures, we performed Mantel tests (9999 permutations) for late winter and late summer data, to test the null hypothesis of no relationship between the mud content distance matrix and each beta diversity matrix. A p-value below 0.05 indicates a significant correlation between the two investigated distance matrices, with the sign of the r-value indicating if the two matrices are positively or negatively associated. The beta diversity indices were computed using the ‘beta.pair’ function, and the Bray-Curtis dissimilarity indices using the ‘bray.part’ function, both from the ‘betapart’ R package (Baselga, 2013). The Mantel tests were performed using the ‘mantel.rtest’ function from the ‘ade4’ R package (Dray and Dufour, 2007).

To test the link between the macrofaunal assemblages based on their respective beta diversity and dissimilarity indices and the disturbance parameter (*i.e.* mud content), non-metric multidimensional scaling ordinations (nMDS) were successively performed for each index (β_{sor}, β_{sim}, β_{nes}, d_{BC}, $d_{BC\text{-}bal}$ and $d_{BC\text{-}gra}$) and at each sampling period (late winter and late summer) using the ‘metaMDS’ function of the ‘MASS’ R package

(Venables and Ripley, 2002). Then, the ‘envfit’ function (‘vegan’ R package) was used to test if the mud content was significantly correlated with each ordination (Oksanen et al., 2016). When a correlation was significant, the mud contents were fitted and plotted on the given nMDS using the ‘ordisurf’ function of the ‘vegan’ R package (Oksanen et al., 2016). All these analyses were performed using R version 3.3.0 (R Core Team, 2016).

3. Results

3.1. Environmental engineering effect

Mean values of grain-size distribution parameters measured within each sediment type are reported in Table 1a. Analyses revealed significant differences between the sediment types for all tested metrics in late winter ($p < 0.001$) and for all but one in late summer (mud content). At both periods, there was a strong engineering effect on the principal mode marked by a significantly coarser sediment in the engineered and associated sediments than in the control sediments (Table 1a). In late winter, the sorting index S_0 was significantly lower in the engineered and associated sediments than in the control and mud content was significantly lower in the associated sediments than in the other two sediment types. Finally, the sand content was significantly higher in the engineered sediment relative to the other sediment types. In late summer, associated sediments had a higher sorting index than the engineered sediments and one comparable to the control sediments. Although associated sediments were also characterized by a higher mud content in late summer compared to late winter (permanova: $p = 0.0051$), no significant difference was observed between the three sediment types. For all grain-size parameters, the control sediments showed no significant changes between late winter and late summer (permanova: p(principal mode) = 0.23 , p(S_0) = 0.60, p(mud) = 0.37 and p(sand) = 0.42). The pattern was similar for the engineered sediments (permanova: p(principal mode) = 0.059 , p(S_0) = 0.78, p(mud) = 0.78 and p(sand) = 0.39). The associated sediments showed significant changes in their grain-size distribution between late winter and late summer. In late winter, they were much more homogenous than in late summer (Table 1) and they became significantly muddier between the two sampling campaigns (permanova: $p = 0.0051$) leading to a significant decrease in the principal mode (permanova = 0.025).

The comparison of sedimentary parameters revealed a strong engineering effect at both periods regarding TOM, Chl *a* and Sol (Table 1b, $p < 0.005$). In both seasons, TOM was consistently twice as high in the engineered environment than in the control zone. Organic matter content also showed a significant decrease between late winter and late summer in the reef zone (permanova: $p = 0.029$) and no significant temporal change in the control sediments (permanova: $p = 0.29$). Similarly, Chl *a* concentration was ten times higher in the soft sediments adjacent to the engineered structures than in the control and did not display any significant temporal changes in either the control (permanova: $p = 0.29$) or the associated sediments (permanova: $p = 0.72$). Sol concentration was also consistently four times higher in the reef environment than in the control and displayed a temporal stability similar to the Chl *a* (permanova: p(control) = 0.87 and p(associated) = 0.82). In late winter, the Pheo concentration was significantly higher in the control than in the associated sediments while in late summer, there was no significant difference. In both sediment types, Pheo concentrations did not show significant changes between the two sampling campaigns (permanova: p(control) = 0.10 and p(associated) = 0.11). Finally, Ins/Sol was not significantly different between associated and control sediments in late winter and late summer, and was significantly higher in late winter compared to late summer for the control sediments (permanova: $p = 0.0001$). This temporal pattern was not detected in the associated sediments (permanova: $p = 0.28$) probably because of the important variability in late winter (Table 1).

3.2. Biological engineering effect

In late winter, 9244 organisms belonging to 121 different taxa were sampled in the cores and 8478 organisms belonging to 26 different taxa were sampled with the quadrats (see the Appendix for a complete list of species). Comparatively, in late summer more organisms and taxa were sampled with the cores (23463 organisms/125 taxa) while fewer organisms and more taxa were sampled with the quadrats (4677 organisms/30 taxa). For all sediment types, total species richness was consistently higher in late summer than in late winter but this difference was significant only for the control and engineered sediments (permanova: p(control) = 0.039, p(associated) = 0.071 and p(engineered) = 0.0001).

PCOs and one-way permanovas performed on density matrices indicated that the three sediment types significantly differed ($p < 0.05$) in their associated fauna at both sampling periods, confirming our *a priori* sediment type grouping (Fig. 2 and Fig. 3). PCO axis 1 explained in late winter and late summer, respectively 26.1 and 30.3% of the total variation present in the resemblance matrix and clearly separated the engineered samples from the control samples. PCO axis 2 explained in late winter and late summer, respectively 14.6 and 14.8% of the total variation and discriminated the engineered and control samples from the associated samples. In both seasons, engineered samples were highly clustered compared to the more scattered associated and control sediments samples. In late winter, the control and associated sediments were well separated while there was a small overlap between the associated and engineered sediments (Fig. 2). In late summer, there was an overlap between the associated and control sediments (Fig. 3). This overlap was mostly due to bivalves like *Limecola balthica* or *Cerastoderma edule* and to the polychaete *Nephtys hombergii* (Fig. 3 and Appendix). Finally, engineered sediments were characterized by a much greater number of species correlated at more than 60% with each PCO axis (11 in late winter and 17 in late summer) than the associated (3 in late winter and 1 in late summer) and the control sediments (3 in late winter and 6 in late summer).

Mean macrofauna diversity indices and densities were calculated within each sediment type and for each sampling campaign (Table 2a and b). At the sediment type scale, one-way permanovas showed significant differences between engineered sediments on the one hand and associated and control sediments on the other, for all the diversity measurements and densities at both periods. There were two exceptions regarding N1 and N2 calculated in late summer with *S. alveolata* taken into account. In these cases, there were no significant differences between the three sediment types. When *S. alveolata* was taken into account, total macrofauna density was 20 times higher in the engineered sediments at both periods. This difference was maintained even after *S. alveolata* was removed from the data set but it was reduced to an average 5-fold difference. The engineered sediment was also home to significantly more species (mean species richness N0) than the associated and control sediments and this, whatever the situation.

Regarding macrofauna density, N1 and N2, associated and control sediments presented similar temporal patterns when comparing late winter and late summer. Their respective macrofauna density increased significantly between the two campaigns (permanova: p(control) = 0.023 and p(associated) = 0.018) while N1 and N2 showed non-significant differences (permanova: p(control-N1) = 0.15, p(control-N2) = 0.25, p(associated-N1) = 0.83 and p(associated-N2) = 0.53). Between late winter and late summer, the engineered sediments presented a significant increase in the total macrofauna density (permanova: p(density with *S. alveolata*) = 0.0001) only driven by a significant increase in the associated fauna density (permanova: p(density without *S. alveolata*) = 0.0001 and p(*S. alveolata* density) = 0.54). They also showed a significant increase in the case of N1 and N2 calculated with *S. alveolata* (permanova: p(N1) = 0.0007 and p(N2) = 0.0001), a change which was not significant once the engineer species was removed (permanova: p(N1) = 0.089 and p(N2) = 0.73).

3.3. Linking environmental and biological engineering effects

DistLM and dbRDA analysis were performed in late winter (Fig. 4a) and late summer (Fig. 4b) with *S. alveolata* biomass considered as an environmental parameter. In both seasons, *S. alveolata* biomass was the parameter which best explained the relationship between environmental parameters and macrofauna assemblages (18.0% in late winter and 24.8% in late summer). In late winter, the most parsimonious model, explaining 33.6% of the total variation in species assemblages, was defined by (1) *Sabellaria* biomass (square-root transformed, 18.0%), (2) principal mode (log transformed, 13.2%) and (3) total organic matter content (fourth-root transformed, 10.7%, Fig. 4). The first two axes explained 91.6% of the fitted variation and 30.7% of the total variation. Species assemblage were structured according to two gradients. The first was driven by *S. alveolata*, and separated engineered sediments from the two other types. The second was driven by the sediment principal mode and the total organic matter content and separated the associated from the control sediments (Fig. 4a). In late summer, the most parsimonious model explained 40.7% of the total variation in species assemblages. It was defined by the same first two variables as for late winter: *Sabellaria* biomass (square-root transformed, 24.8%) and principal mode (log transformed, 16.9%). The third selected variable differed from late winter since it was the mud content (fourth-root transformed) and it explained only a very small part of the total variation (0.079%). The first two axes explained 87.5% of the fitted variation and 35.6% of the total variation. Again, species assemblages were structured according to two gradients but they did not separate the different sediment types as clearly as in late winter. *S. alveolata* still defined the first gradient and clearly separated the engineered sediments from the two soft sediments. The opposition between the principal mode and the mud content defined the second gradient. Along this gradient, the distinction associated/control sediments was not well defined. Indeed, there were three associated sediment samples characterized by high mud contents and isolated from the rest of the associated sediment samples (Fig. 4b).

3.4. Disturbances and biological engineering effect

Consistent mean values in late winter (10%) and late summer (9.59%), confirm the choice of the mud content as a suitable ‘disturbance parameter’ (Table 1a). Indeed, these values did not significantly vary between the two contrasted seasons we sampled (permanova: p = 0.78). In contrast, the mean *S. alveolata* density almost doubled between late winter (7682 ± 3312 ind.m^{-2}) and late summer (12844 ± 14262 ind. m^{-2}), with a very high summer variability, leading to no significant change (permanova: p = 0.54). Oppositely, the mean *S. alveolata* biomass by surface unit significantly decreased between late winter (646 ± 317 g. m^{-2}) and late summer (318 ± 211 g. m^{-2}) (permanova: p = 0.0001).

Mantel tests performed between the mud content distance matrix and the different beta diversity matrices showed a clear temporal difference between late winter and late summer. The tests were not significant when performed using the late winter data sets (p > 0.05, Table 3), while they revealed a significant and positive correlation between the mud content distance matrix and β_{sor} (p < 0.001, r = 0.24), β_{sim} (p = 0.0066, r = 0.15), d_{BC} (p < 0.001, r = 0.38) and $d_{BC\text{-}gra}$ (p < 0.001, r = 0.29) (Table 3) using the late summer data sets. These results indicate that in late winter, an increase in mud content, used as a proxy for disturbance, does not lead to beta diversity changes but in late summer, it leads to (1) an increase in beta diversity driven by a species replacement and (2) an increase in abundance based dissimilarity driven by an abundance gradient. Ordination plots of similarities (nMDS) of macrofaunal assemblages based on β_{sor}, β_{sim}, β_{nes}, d_{BC}, $d_{BC\text{-}bal}$ and $d_{BC\text{-}gra}$ indices were performed in late winter and late summer (Fig. 5 and 6). In late winter, the correlation between the mud content and the different nMDS plots was significant for β_{sor} ($p = 0.008$), β_{nes} ($p = 0.023$), d_{BC} ($p = 0.019$) and $d_{BC\text{-}gra}$ ($p = 0.027$). The mud content explained 30.67% of the ordination based on β_{sor} and 24.54% of the ordination based on β_{nes}. Similarly, 26.93% and 24.51% of the ordination based on d_{BC} and $d_{BC\text{-}gra}$ respectively where explained by the mud content. In late summer, the correlation between the mud content and the different nMDS plots was significant and much higher for all the indices; β_{sor} ($p = 0.001$), β_{nes} ($p = 0.036$), β_{sim} ($p = 0.001$), d_{BC} ($p = 0.001$), $d_{BC\text{-}gra}$ ($p = 0.002$) and $d_{BC\text{-}bal}$ ($p = 0.006$). Indeed, the mud content explained over 50% of the ordination based on β_{sor} ($r^2 = 53.07\%$) and d_{BC} ($r^2 = 52.76\%$), around 40% of the ordination based on β_{sim} ($r^2 = 39.23\%$) and $d_{BC\text{-}gra}$ ($r^2 = 41.33\%$), and between 20 and 30% of β_{nes} ($r^2 = 21.25\%$) and $d_{BC\text{-}bal}$ ($r^2 = 29.56\%$). When the correlation was significant, the fitted mud contents were plotted on the corresponding nMDS plots (Fig. 5 and 6). The correlation between the disturbance proxy and the different nMDS plots showed a pattern similar to the one revealed by the late summer Mantel test, with beta diversity changes mainly driven by a species turnover and an abundance gradient.

4. Discussion

4.1. Engineered structures cause grain-size distribution changes

Environmental engineering effects are composed of two types of changes, structural and abiotic changes, structural changes being caused by ecosystem engineers and inducing abiotic changes (Jones et al., 2010). *S. alveolata* is capable of biologically modifying soft sediments by selectively gluing together bioclastic sand particles, in order to build its tube (Fournier et al., 2010). This leads to the transformation of an initial soft sediment into a three-dimensional hard substratum with a long lasting resistance to physical loading via the secreted organic cement (Le Cam et al., 2011). *Sabellaria alveolata* can therefore be considered as a “structural engineer” according to Berke (2010). Structural changes caused by physical ecosystem engineers result in a variation in the distribution of fluid and solid material termed abiotic changes (Jones et al., 2010). In the case of *S. alveolata*, a direct abiotic engineering effect observable through the engineered sediments and an indirect one, observable through the associated sediments, were detected. Engineered and associated sediments presented, at both sampling periods, a coarser texture than the control sediments, confirming the impact Sabellariidae polychaetes have on the local sediment’s texture by selecting sand particles of a specific size to build their tubes

(*Phragmatopoma caudata* (= *P. lapidosa*) (Gram, 1968; Kirtley and Tanner, 1968; Main and Nelson, 1988), *Sabellaria vulgaris* (Wells, 1970), *Sabellaria nanella* (Bremec et al., 2013)). Ultimately, these bioconstructing Sabellariidae species create reefs characterized by a grain-size distribution different from the local soft sediments. The case of the associated sediments raises the question of the definition of a reef habitat. In Europe, “reefs” are recognized as a marine habitat to be protected and are listed under Annex I of the EC Habitats Directive (Council Directive EEC/92/43 on the Conservation of Natural Habitats and of Wild Fauna and Flora) under the designation of Special Areas of Conservation (SACs). They are defined as “submarine or exposed at low tide, rocky substrates and biogenic concretions”. In the light of our findings, we can very well consider the engineered and the associated sediments as the same sediment but under two different forms, a consolidated (engineered sediments) and an unconsolidated form (associated sediments). Hence, we propose to widen the definition of a “reef” to include the non-engineered sediments under its direct influence.

The main difference between the engineered and associated sediments concerns their mud content. At both seasons, the engineered sediments have a mean mud content around 10 %, as previously observed by Le Cam et al. (2011). *Sabellaria wilsoni* veneers have also been reported to present consistent silt and clay contents across two contrasting seasons (rainy and dry seasons in Ataide et al., 2014) indicating that Sabellariidae polychaetes build new habitats presenting stable sedimentary conditions. The mud present in the engineered sediments is located in small cracks and crevices protected from the main hydrodynamic processes (*i.e.* winter storms, tidal currents and swell). Conversely, the associated sediments are characterized by a steep and significant increase in mud content between winter (2 %) and summer (21 %). As shown by Caline et al. (1988) for the Sainte-Anne reef (MSMB), localized mud depositions are linked to hydrodynamic and associated hydro-sedimentary processes induced by the presence of the reef itself and of the mussel farms (bouchots) in front of the reef (McKindsey et al., 2011). These mud depositions are observed behind reef structures important enough to act as physical barriers (Caline et al., 1988), where they are generally superficial and consequently easily eroded by strong wave action, limiting their presence in winter.

4.2. Engineered structures enhance benthic primary production and potentially microbial activity

As reported by Jones et al. (2010), abiotic changes induced by physical engineering activity can themselves cause biotic changes. Our results clearly show that at both seasons, associated sediments have a higher organic matter content compared with the control sediments. At both seasons, high levels of organic matter were associated with high chlorophyll *a* concentrations, indicating that part of the organic matter present in the associated sediments is the consequence of MPB development. The high benthic primary production promoted by the Sainte-Anne reef, compared to a generally lower benthic production in the MSMB as measured by Davoult et al. (2008) and Migné et al. (2009), confirms its important biotic engineering effect. Similar results were found for the invading intertidal reef-forming polychaete *Ficopomatus enigmaticus* (Bruschetti et al., 2011), for shallow oyster reefs (*Crassostrea virgina*, Newell et al., 2002) and for intertidal mussel beds (Engel et al., 2017). According to Berke (2010), "structural engineers operate through similar processes and have similar types of effects". Consequently, the creation of benthic primary production hotspots by reef-building structural engineers could be a general property of these marine species. Nonetheless, this phenomenon was observed at the scale of the largest and probably oldest *S. alveolata* reef in Europe (Audouin and Milne-Edwards, 1832) and the study by Engel et al. (2017) highlighted the importance of the size and age of the bioconstruction in promoting local benthic microalgae. Hence, further studies are needed to confirm the general role of *S. alveolata* reefs as "biological power stations" (Engel et al., 2017).

Furthermore, the high chlorophyll *a* concentrations measured in late winter and late summer indicate that *S. alveolata* reefs promote an important benthic primary production all year round, that could be a relevant food source for deposit- (Kanaya et al., 2008) and suspension-feeders (Lefebvre et al., 2009) through resuspension processes (Hylleberg, 1975; Ubertini et al., 2015). In the associated sediments, MPB often grows on small accumulations of pure mud and is consequently easily eroded and available to consumers. Such benthic primary production may have a trophic importance during the winter months (Lefebvre et al., 2009), when the phytoplankton production is typically low (Arbach Leloup et al., 2008; Cugier et al., 2010). Filter feeding mollusks are known to stimulate MPB growth (Engel et al., 2017; Newell et al., 2002) via inorganic nutrient release (*i.e.* carbon, nitrogen and phosphorus (van Broekhoven et al., 2014)) and bacterial remineralization of their biodeposits (van Broekhoven et al., 2015). Similarly, *S. alveolata* produces large amounts of feces and pseudofeces visible on the sediment (Dubois et al., 2005), that could favor MPB growth. Primary production could also be enhanced by the presence of other suspension-feeders living in the engineered sediments, such as *Magallana gigas*, which can reach densities of 100 ind.m^{-2} as measured in the disturbed engineered sediments using the quadrats. As already observed in *Ficopomatus enigmaticus* reefs (Bruschetti et al., 2011), *S. alveolata* reefs probably increase the bentho-pelagic coupling by linking pelagic organic matter to the benthic compartment via their suspension-feeding activity and biodeposition.

In late winter and late summer, associated sediments had consistently higher soluble carbohydrate concentrations than the control sediments. Carbohydrates are the components of the mucus coating the pseudofeces produced by *S. alveolata* and other suspension-feeders (van Broekhoven et al., 2015). Hence, when these pseudofeces are deposited on the associated sediments, it could increase their concentration in soluble carbohydrates. Soluble carbohydrates also compose the extracellular polymeric substances produced by benthic diatoms (Bellinger et al., 2009) and are an important source of organic carbon, rapidly consumed by heterotrophic microorganisms present in the sediment (Bhaskar and Bhosle, 2005; Goto et al., 2001). Consequently, *S. alveolata* presence could support all year round an important bacterial activity through the soluble carbohydrates excreted by the diatoms and present in the mucus coating the biodeposits. This organic carbon can either be used by the bacteria for their growth (bacterial biomass production) or be remineralized (bacterial respiration) as showed by Hubas et al. (2006). In the first case, the bacteria can be a source of food for infaunal organisms such as nematodes and become an important trophic link in structuring energy fluxes in the community (Pascal et al., 2009, 2008). In the second case, the bacteria release inorganic nutrients such as carbon (Jiao et al., 2010), which can then be used by photoautotrophs present in the sediment (*e.g.* diatoms) or in the water column (*e.g.* phytoplankton) further maintaining the local primary production.

Furthermore, according to Delmas (1983), an insoluble/soluble carbohydrate ratio (Ins/Sol) ranging between 6 and 8 indicates a low degradation rate of the organic matter, while a ratio varying between 10 and 30 reflects a high degradation rate. Delmas (1983) also suggests using the Ins/Sol ratio as a proxy for the C/N ratio. Mean Ins/Sol ratios were not significantly different between the associated and control sediments with values around 8.6 in late winter, and 6.0 in late summer, indicating that *S. alveolata* does not affect the organic matter degradation rate in soft sediments; it is consistently of good quality and weakly degraded. Nonetheless, in late summer, the organic matter present in the control and associated sediments appears less degraded and more easily incorporable in the food web than in late winter, probably in response to a higher biological activity of photoautotrophs and bacterial communities (Hubas et al., 2006).

4.3. Engineered structures create an original macrofauna assemblage linked to the sedimentary changes

In addition to promoting the local benthic production, *S. alveolata* strongly modifies the macrofauna assemblages present in the engineered and associated sediments compared to the control sediments and this difference is present at both sampling seasons. Consequently, *S. alveolata* engineers two original species assemblages, one associated with the actual bioconstructions and the other associated with the sediments surrounding these structures. In late winter and late summer, the environmental parameter primarily responsible for macrofauna differences between the three sediment types is the ecosystem engineer via its biomass. Studies on other ecosystem engineers have demonstrated a similar structuring effect of the engineer on the macrofauna, for example *via Haploops nirae* density in subtidal mats (Rigolet et al., 2014) and *Lanice conchilega* density in intertidal beds (De Smet et al., 2014). The benthic macrofauna is secondarily structured by the principal mode and the organic matter content of the sediments, two environmental parameters reported to structure soft sediment macrofauna communities in a large diversity of sites such as the intertidal flats of the Schelde estuary (Ysebaert and Herman, 2002) and over multiple spatial scales in Portuguese transitional water systems (Veiga et al., 2016). In our case, these two parameters are influenced by *S. alveolata*, indicating the importance of this engineer species in structuring the local benthic macrofauna.

Structural diversity analyses indicate that assemblages present in the associated and control sediments are similarly structured in late winter and late summer. Dominant species are mainly polychaetes (*e.g. Goniadella bobrezkii*) and mollusks species (*e.g. Crepidula fornicata*) in the associated sediments and the mollusks *Limecola balthica* and *Cerastoderma edule* in the control sediments, with a consortium of less abundant species. Furthermore, the benthic fauna present in the associated sediments appears as a combination of species living in the two other sediment types, enriched by polychaete species such as *Glycera tridactyla*, *Protodorvillea kefersteini* and *Saccocirrus papillocercus*. These three polychaete species are either carnivore-scavengers or surface deposit-feeders, with important movement capacities, key biological traits in organic matter rich and variable environments (Rigolet et al., 2014) like the associated sediments. The overlapping observed between the control and associated sediments is much more pronounced in late summer, after the recruitment period (Thorin et al., 2001) and is caused by a few species (*e.g. Cerastoderma edule, Limecola balthica* or *Nephtys hombergii*). *Cerastoderma edule* recruitment and settlement of macrozoobenthos larvae is known to be enhanced coastward of mussel beds due to a decrease in hydrodynamic forces caused by these bioengineered habitats (Commito et al., 2005; Donadi et al., 2014, 2013). Similarly, *S. alveolata* reefs act as natural breakwaters limiting hydrodynamic energy, which could lead to an enhanced recruitment of macrobenthic species like *Cerastoderma edule* and *Limecola balthica*. This phenomenon is a lot less visible in winter maybe indicating that these species do not survive the variable environmental conditions characterizing the associated sediments or the winter temperatures. Indeed, locals repeatedly come to the Sainte-Anne reef to dig up bivalves like cockles (*Cerastoderma edule*) and Japanese carpet shells (*Ruditapes philippinarum*) enhancing small-scale spatial heterogeneity and potentially leading to changes in the macrofauna of the associated sediments (Watson et al., 2017). We also recorded inside the associated sediments some species generally present in the engineered sediments, like *P. cultrifera* or *G. vulgaris*. This can be caused by the presence of broken reef parts in the associated sediments, because of the variable sedimentary preferences of some species (*e.g. G. vulgaris*) or because of the use of the associated sediments by some species to move between reef patches (*e.g. Perinereis cultrifera*).

Species richness and associated macrofauna density were always highest in the engineered sediments than in the two soft sediments, stressing *S. alveolata*'s role in enhancing local biodiversity and abundance. Our results confirm previous studies on *S. alveolata* reefs (Dias and Paula, 2001; Dubois et al., 2002; Holt et al., 1998) and agree with a large body of literature reporting positive effects of tubiculous polychaete species (De Smet et al., 2015), reef-building polychaetes (McQuaid and Griffiths, 2014) and bivalves (Gutiérrez et al., 2003; Lejart and Hily, 2011; Norling and Kautsky, 2007) on species richness and associated fauna abundances. Intertidal engineers like *S. alveolata* create new complex habitats that reduce pressures such as thermal and hydric stress and increase the number of primary producers (*i.e.* MPB and ulva), potentially extending trophic niches and overall leading to a biodiversity increase (Bouma et al., 2009; Jones et al., 1997; Stachowicz, 2001). New environmental conditions created by *S. alveolata* also lead to the paradox mentioned by Bertness et al. (1999), and facilitate the colonization of intertidal zones by subtidal species, like the polychaete *Spirobranchus lamarcki* or the gastropod *Crepidula fornicata*.

Structural diversity indices calculated for the engineered sediments (considering *S. alveolata*) and the beta diversity analysis both reveal a change between late winter and late summer in how the macrofauna is structured. In late winter, N1 and N2 are both significantly lower than in the two other sediment types while in late summer, macrofauna density in the engineered sediments is distributed similarly than in the associated and control sediments. Consequently, during winter *S. alveolata* dominates more strongly the engineered sediments than the dominant species present in the associated and control sediments, a result similar to the *Haploops nirae* habitats in summer (Rigolet et al., 2014). Differently, in late summer *S. alveolata* does not affect the community structure in a different way than other abundant species do in the associated (*Crepidula fornicata*, *Cirriformia tentaculata*, *Mediomastus fragilis*, *Goniadella bobrezkii*) and control sediments (*Cerastoderma edule*, *Limecola balthica*, *Lanice conchilega*, *Malmegrenia arenicolae* and *Nepthys spp.*). Regarding beta diversity, it significantly increases along the disturbance gradient in late summer but not in late winter. These observed contrasts between the two seasons can have two causes, probably acting in synergy: a low *S. alveolata* recruitment and an important recruitment of associated species. This last argument was also suggested by Mateo-Ramirez et al. (2015) to explain the increase in decapod abundance associated with *Posidonia oceanica* meadows, between winter-spring and summer-autumn. In the MSMB, the recruitment success of *S. alveolata* is known to be strongly year-to-year variable depending on the synchrony between favorable environmental conditions (tidal and meteorological conditions) and main reproductive periods (Ayata et al., 2009), and 2015 seemed to be a year characterized by low settlement rates (pers. obs.). A weak *S. alveolata* recruitment leads to a decrease in spatial competition between the engineer and other macrofauna species favoring recruitment of associated species. Indeed, between winter and summer, many other benthic species recruit in the MSMB (Thorin et al., 2001) and biogenic habitats like *Mytilus edulis* and *Crepidula* spp. beds, are known to favor recruitment of pelagic larvae (Berke, 2010) by affecting boundary-layer flow (Eckman, 1983). Consequently, a low *S. alveolata* recruitment associated with the upraised position of the reef in a soft bottom environment and the absence of neighboring hard substratum, one exception being the off-bottom mussel farms, lead to an important recruitment of benthic larvae to the Sainte-Anne reef. The hard nature of the engineered sediments can also act as either a support for egg capsules (*e.g. Nucella lapillus*) or an attractant for pelagic larvae of rocky shore species like *Gibbula umbilicalis* or *Eulalia viridis* (Kingsford et al., 2002). When *S. alveolata* is excluded, N1 and N2 values are systematically higher in the engineered sediments, a pattern unaffected by season. *Sabellaria alveolata* associated macrofauna shows a structuration similar to *Lanice conchilega* intertidal beds (De Smet et al., 2015) when compared to non-engineered sediments. De Smet et al. (2015) also recorded the lack of a temporal effect on N1 and N2. Consequently, despite its strong dominance, *S. alveolata* creates a species-rich habitat where individuals are overall equitably distributed between taxa.

4.4. Engineered sediment disturbance and mechanisms linked to beta diversity changes

S. alveolata reefs are subject to various disturbances causing changes in species richness and composition (Dubois et al., 2006b, 2002; Plicanti et al., 2016) but not in diversity indices (Dubois et al., 2002). According to Clarke and Gorley (2006), diversity indices are unable to detect subtle changes in complex communities like *S. alveolata* reefs. Hence, using beta diversity and abundance-based dissimilarity along a continuum can help us detect these changes and better understand how disturbances affect the macrofauna associated with the reef. The Mantel tests indicate that in summer the beta diversity increases along the disturbance gradient, driven by a species turnover and an increase in species abundances. Differently, the multidimensional ordinations based on Sørensen and Bray-Curtis dissimilarities, are at both seasons significantly correlated with the mud content. Consequently, mud appears as a driver of beta diversity changes all year round but its importance increases between late winter and late summer.

All year round, mud can act directly as an environmental filter for some benthic species present inside the reef and lead to a beta diversity increase (Baselga, 2010). Indeed, mud could play the same environmental filter role in the engineered sediments as it does in soft sediments (Anderson, 2008; Ysebaert and Herman, 2002). Disturbances to the reef also increase its structural complexity and frees space creating new microhabitats. The increase in the engineered sediment's complexity and heterogeneity, linked to our disturbance proxy, lead to an increase in species richness and beta diversity (Ellingsen and Gray, 2002) by mechanisms like the provision of refuges from predation and physical stressors (Margiotta et al., 2016). Finally, disturbed engineered sediments are more fragmented than their undisturbed counterparts. The important spatial continuity characterizing platform reefs (Dubois et al., 2002) and engineered sediments in "good ecological status" (Desroy et al., 2011) lead to an increase in the dispersal potential of mobile predators like decapods (*e.g. Carcinus maenas*), gastropods (*e.g. Ocenebra erinaceus*) and errant polychaetes (*e.g. Eulalia viridis*). In an experimental microbial landscape, dispersal had a negative effect on local community, metacommunity and landscape beta diversity (Sørensen dissimilarity) mainly because of predation by generalist predators (Cadotte and Fukami, 2005). Consequently, all year round, negative biotic interactions are probably acting in synergy with environmental sorting and habitat complexity to shape the observed beta diversity changes.

Between late winter and late summer, many benthic species recruit. The recruitment of benthic species to soft bottom sediments is known to be under the influence of biotic factors like organic content and food supply (Snelgrove and Butman, 1994). In spring-summer, the mud present in the disturbed engineered sediments is probably richer in organic matter, presenting a better quality compared to winter, as suggested by the associated sediment results. Multiple facts go in this direction. First, part of the spring phytoplankton bloom is known to sediment, potentially enriching the mud in fresh organic matter (Cugier et al., 2010). Second, during spring and summer green algae develop on the reef (Dubois et al., 2006b) enriching the mud in fresh detritus. Finally, in spring and summer *S. alveolata* and other suspension-feeders (*Magallana gigas* and *Mytilus cf. galloprovincialis*) increase their metabolic rates (Gillooly et al., 2001) and consequently produce more feces and pseudofeces, which could further enrich the mud in organic matter. In the end, changes in abiotic factors (topographic complexity, spatial competition and presence of microdepositional environments (small gapes in the reef filled with fine sediments, Snelgrove et al., 1993)) associated with changes in trophic factors (trophic competition, trophic cues (green algae and MPB present on and around the tubes – pers. obs.)) probably act in synergy and cause the recruitment of a richer and different assemblage of species in the disturbed reef parts compared to the undisturbed ones. Indeed, our results show an increase settlement of opportunistic and deposit-feeding species, like *Capitella capitata*, *Cirriformia tentaculata*, *Parathelepus collaris* and *Tharyx killariensis*, and of species presenting a high affinity for mud (*Corophium volutator*) in the more disturbed reefs. In the same time, the release in spatial and trophic competition linked to a decrease in the engineer density, favors the settlement of suspension-feeding species like *Magallana gigas* and *Porcellana platycheles*. In late summer, some of these species are present in very high densities like *P. platycheles* (up to 9000 ind.m^{-2}), *Achelia* spp. (up to 7000 ind.m^{-2}) or *Corophium volutator* (up to 5000 ind.m^{-2}), while the others are less abundant. In the end, the interplay between recruitment and the engineered sediments dynamics seem responsible for the observed species turnover and abundance increase along the disturbance gradient. In addition, other factors linked to an increasing disturbance, like a higher oyster cover (*Magallana gigas*) probably also structure the associated fauna as shown by Dubois et al. (2006). Indeed, oyster shells provide a suitable substratum for many sessile species and are known to enhance species richness and abundance (Lejart and Hily, 2011).

Finally, the late winter and late summer multidimensional ordinations also show that at both seasons, mud rates above 10-12% induce a homogenization of the species composition, congruently with results of Balata et al. (2007). They reported that in subtidal rocky reefs structured by the coralline algae *Lithophyllum* spp., the sedimentation “reduced the dissimilarity between assemblages overriding the influence of inclination of the substratum on beta diversity”. The packing of samples ordinated by d_{BC} is also greater for mud contents above 12% indicating that high mud contents not only streamline the species composition but also their absolute abundances.

Conclusion

Our results illustrate the need to protect a system in its integrity and not just parts of it. In our case, future conservation plans should consider *S. alveolata* reefs and associated sediments as an ecological entity. These habitats are in theory targeted by the European Union’s Habitats Directive 92/43/EEC (habitat type 1170 ‘Reef’) but in practice, very few reefs are protected. In the Sainte-Anne reef, a local legislation prohibits the harvesting of bivalves in the associated soft sediments (*e.g. Ruditapes philippinarum*) but not on the engineered sediments (*e.g. Magallana gigas*) increasing anthropogenic disturbances to the reef. In this context, prohibiting such practices until interactions between *S. alveolata* and *M. gigas*, particularly regarding benthic primary production and trophic competition, are clearly elucidated, should be considered.

Furthermore, the biogenic habitat created by *S. alveolata* is home to an original species assemblage presenting a high richness and density all year round, a case similar to many other structural engineers (Berke, 2010; Jones et al., 1994). These habitats are subject to numerous environmental and anthropogenic disturbances leading to changes in their physical structuration and complexity. In the MSMB, these changes are associated with the establishment of mud inside the engineered sediments, the increase in microhabitat availability and more diversified food sources. All year round, these differences act as environmental filters for post-recruits and juveniles. During the summer recruitment period, these differences act as cues for settling larva, leading to an enhanced recruitment inside the more disturbed reefs. In the end, during the spring-summer period, an increasing disturbance leads to an increase in species richness, a change in the species present in the engineered sediments (turnover) and to higher abundances (abundance gradient). This species turnover pleads for a recognition of the ecological value the “degraded” *S. alveolata* reefs have, as biodiversity and recruitment promoters.

Finally, our results are in contradiction with a study reporting that increasing disturbances to mussel beds increased patchiness and in the end reduced the diversity of the associated macrofauna (Díaz et al., 2015), highlighting the variable response fauna associated to structural engineers can have to disturbances. These different results also stress the importance of spatial and temporal scale on evaluating the impact disturbances have on biodiversity, as reported by Lepori and Hjerdt (2006) for aquatic systems.

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Figure captions

Fig. 1. Schematic overview presenting the habitat modifications caused by (1) the establishment of an ecosystem engineer and (2) disturbances of the engineered sediment. Recruitment of *S. alveolata* leads to the formation of a biologically modified sediment (engineered sediment) and to a soft sediment under the influence of the engineered sediment (associated sediment). Engineered sediment then face direct (*e.g.* trampling, storms) and/or indirect disturbances (*e.g.* shellfish farming) which can lead to a gradual alteration.

Fig. 2. PCO analysis of macrobenthos associated with the three sediment types in late winter. The analysis is based on Bray-Curtis similarities of log transformed density data. The black diamonds, the grey squares and the light grey circles represent the engineered, the associated and the control sediment samples respectively. Vectors represent species correlating more than 60% with one of the first two PCO axes. The correlations are based on Spearman coefficients. ASIM: *Achelia simplex*, CEDU: *Cerastoderma edule*, CFOR: *Crepidula fornicata*, CMAE: *Carcinus maenas*, CVOL: *Corophium volutator*, GBOB: *Goniadella bobrezkii*, GUMB: *Gibbula umbilicalis*, GVUL: *Golfingia vulgaris*, LBAL: *Limecola balthica*, LLEV: *Lekanesphaera levii*, LRUG: *Lekanesphaera rugicauda*, McfGAL: *Mytilus cf. galloprovincialis*, MFRA: *Mediomastus fragilis*, MGIG:

Magallana gigas, MPAL: *Melita palmata*, NCIR: *Nephtys cirrosa*, NLAP: *Nucella lapillus*, PCUL: *Perinereis cultrifera*, PPLA: *Porcellana platycheles*.

Fig. 3. PCO analysis of macrobenthos associated with the three sediment types in late summer. The analysis is based on Bray-Curtis similarities of log transformed density data. The black diamonds, the grey squares and the light grey circles represent the engineered, the associated and the control sediment samples respectively. Vectors represent species correlating more than 60% with one of the first two PCO axes. The correlations are based on Spearman coefficients. AECH: *Achelia echinata*, ALAE: *Achelia laevis*, ASIM: *Achelia simplex*, CEDU: *Cerastoderma edule*, CMAE: *Carcinus maenas*, CVOL: *Corophium volutator*, EORN: Eulalia ornata, GBOB: *Goniadella bobrezkii*, GMAX: *Gnathia maxillaris*, GUMB: *Gibbula umbilicalis*, GVUL: *Golfingia vulgaris*, LBAL: *Limecola balthica*, LCON: *Lanice conchilega*, LLEV: *Lekanesphaera levii*, LRUG: *Lekanesphaera rugicauda*, MARE: *Malmgrenia arenicolae*, McfGAL: *Mytilus cf. galloprovincialis*, MFRA: *Mediomastus fragilis*, MGIG: *Magallana gigas*, MPAL: *Melita palmata*, NCIR: *Nephtys cirrosa*, NEMA: *Nematoda* spp., NEME: *Nemerte* sp., NHOM: *Nephtys hombergii*, NLAP: *Nucella lapillus*, NMIN: *Nephasoma minutum*, OCTE: *Odontosyllis ctenostoma*, PCUL: *Perinereis cultrifera*, PPLA: *Porcellana platycheles*.

Fig. 4. dbRDA plots based on a) the late winter data set and b) the late summer data set and representing the three sediment type macrofauna composition as explained by the set of environmental parameters composing the most parsimonious explanatory model. Vectors represent the environmental parameters selected by the DistLM routine. The black diamonds, the grey squares and the light grey circles represent the engineered, the associated and the control sediment samples respectively.

Fig. 5. Late winter nMDS ordination plots of the benthic macrofauna assemblages based on a) the Sørensen total beta diversity, b) the nestedness component of the total beta diversity, c) the Bray-Curtis index of dissimilarity and d) the abundance gradient component of the Bray-Curtis dissimilarity. The stress value of the nMDS is indicated on each plot. The lines indicate the different fitted mud contents obtained using the ‘ordisurf’ function.

Fig. 6. Late summer nMDS ordination plots of the macrofauna benthic assemblages based on a) the Sørensen total beta diversity, b) the turnover component of the total beta diversity, c) the nestedness component of the total beta diversity, d) the Bray-Curtis index of dissimilarity, e) the abundance gradient component of the Bray-

Curtis dissimilarity and f) the balanced variation in abundances component of the Bray-Curtis dissimilarity. The stress value of the nMDS is indicated on each plot. The lines indicate the different fitted mud contents obtained using the 'ordisurf' function.

Figures 1, 2, 3, 4a and 4b, 5 and 6

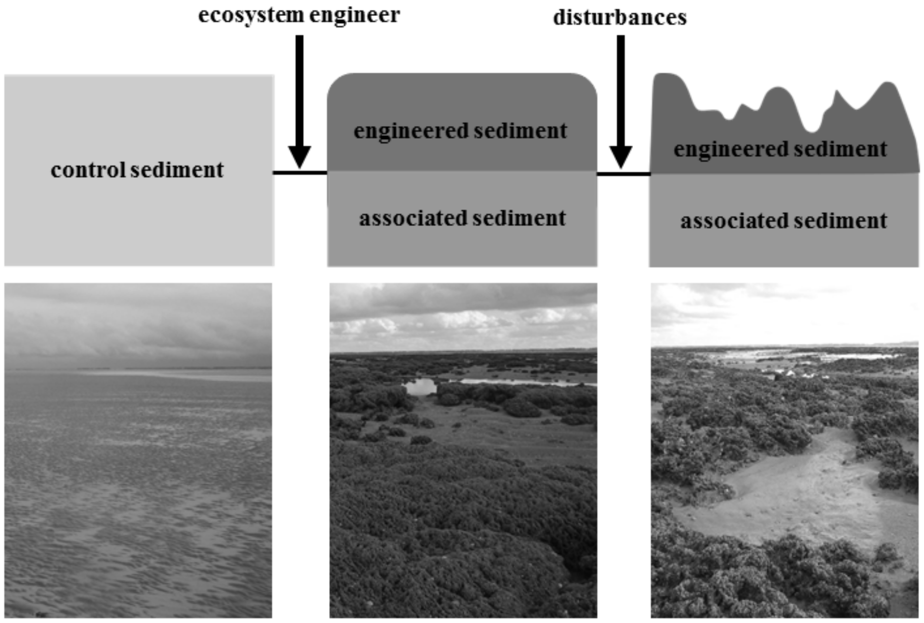


Fig. 1.

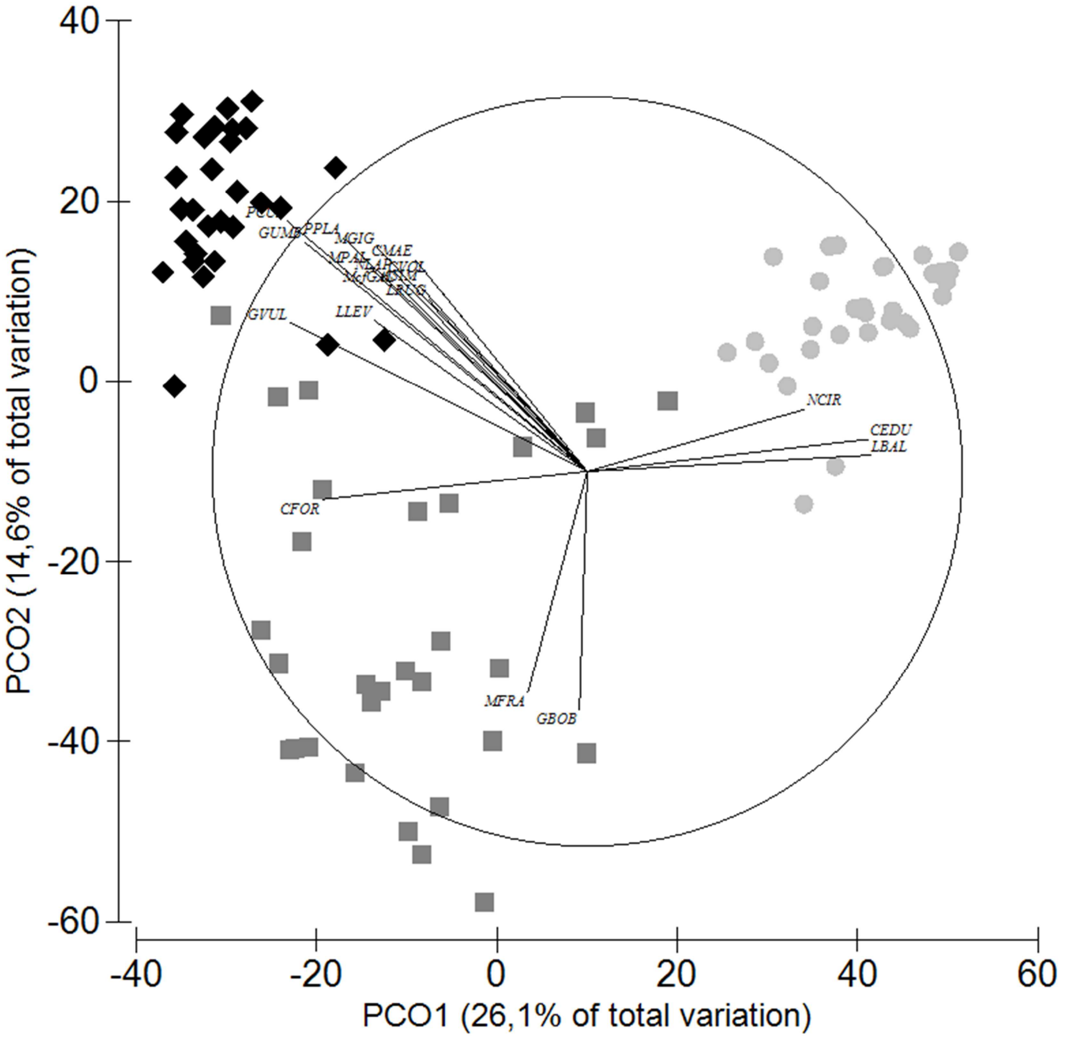

40
20
0
-20
-40
-60
PCO2 (14,6% of total variation)
-40
-20
0
20
40
60
PCO1 (26,1% of total variation)
GUMB
PPLA
MGIG
CMAE
MPAL
NLAR
LRUG
GVUL
LLEV
NCIR
CEDU
LBAL
CFOR
MFRA
GBOB

Fig. 2.

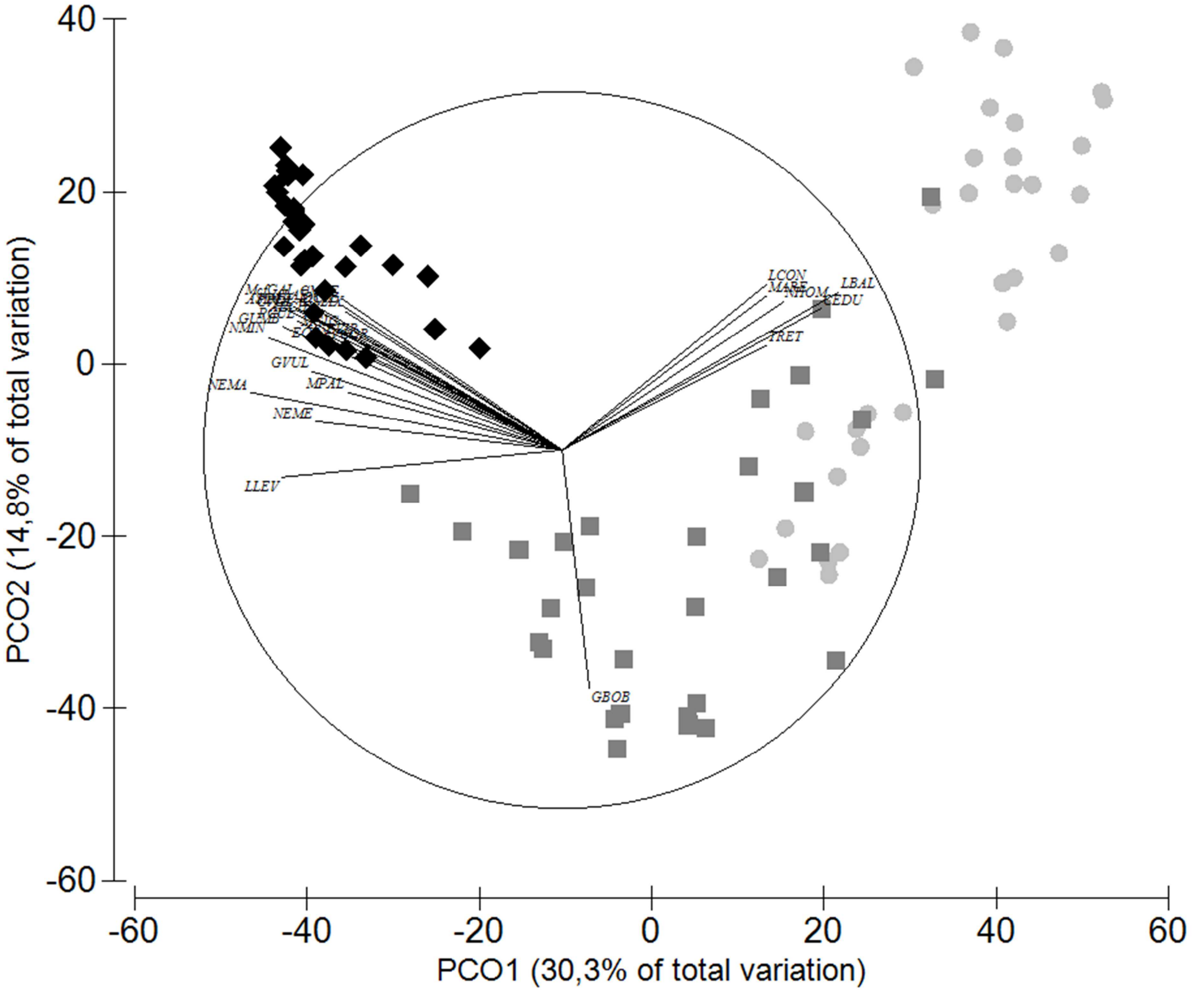
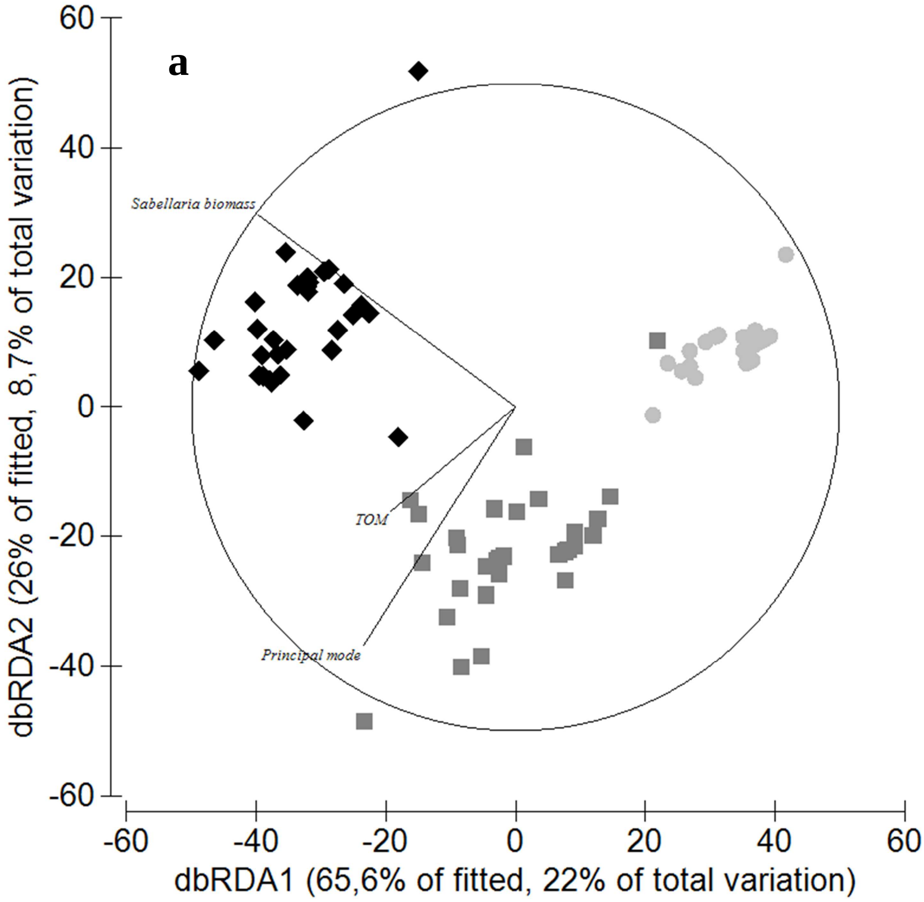

40
20
0
-20
-40
-60
-60
-40
-20
0
20
40
60
PCO1 (30,3% of total variation)
PCO2 (14,8% of total variation)
LCON
MARE
NHOM
LBAL
CEDU
TRET
GBOB
LLEV
NEME
NEMA
MPAL
GVUL
NMIN
McfGAL

Fig. 3.


a
Sabellaria biomass
TOM
Principal mode
dbRDA2 (26% of fitted, 8,7% of total variation)
dbRDA1 (65,6% of fitted, 22% of total variation)
60
40
20
0
-20
-40
-60
-60
-40
-20
0
20
40
60

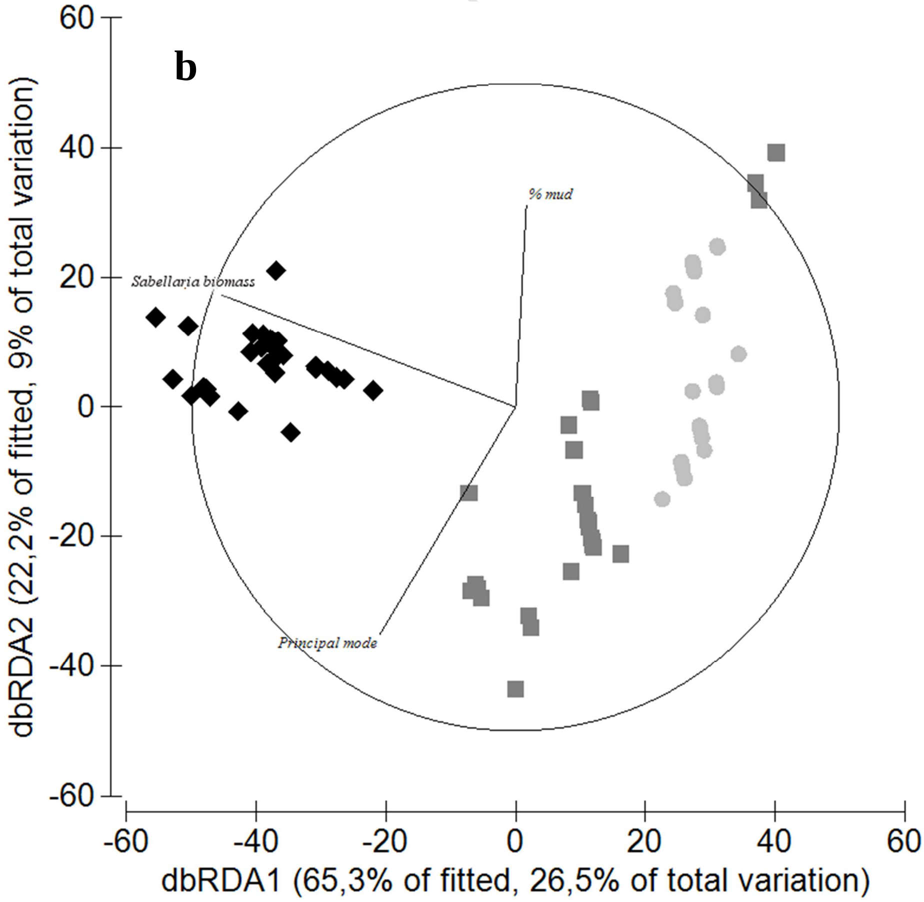

b
% mud
Sabellaria biomass
Principal mode
dbRDA2 (22,2% of fitted, 9% of total variation)
dbRDA1 (65,3% of fitted, 26,5% of total variation)
60
40
20
0
-20
-40
-60
-60
-40
-20
0
20
40
60

Fig. 4a and b.

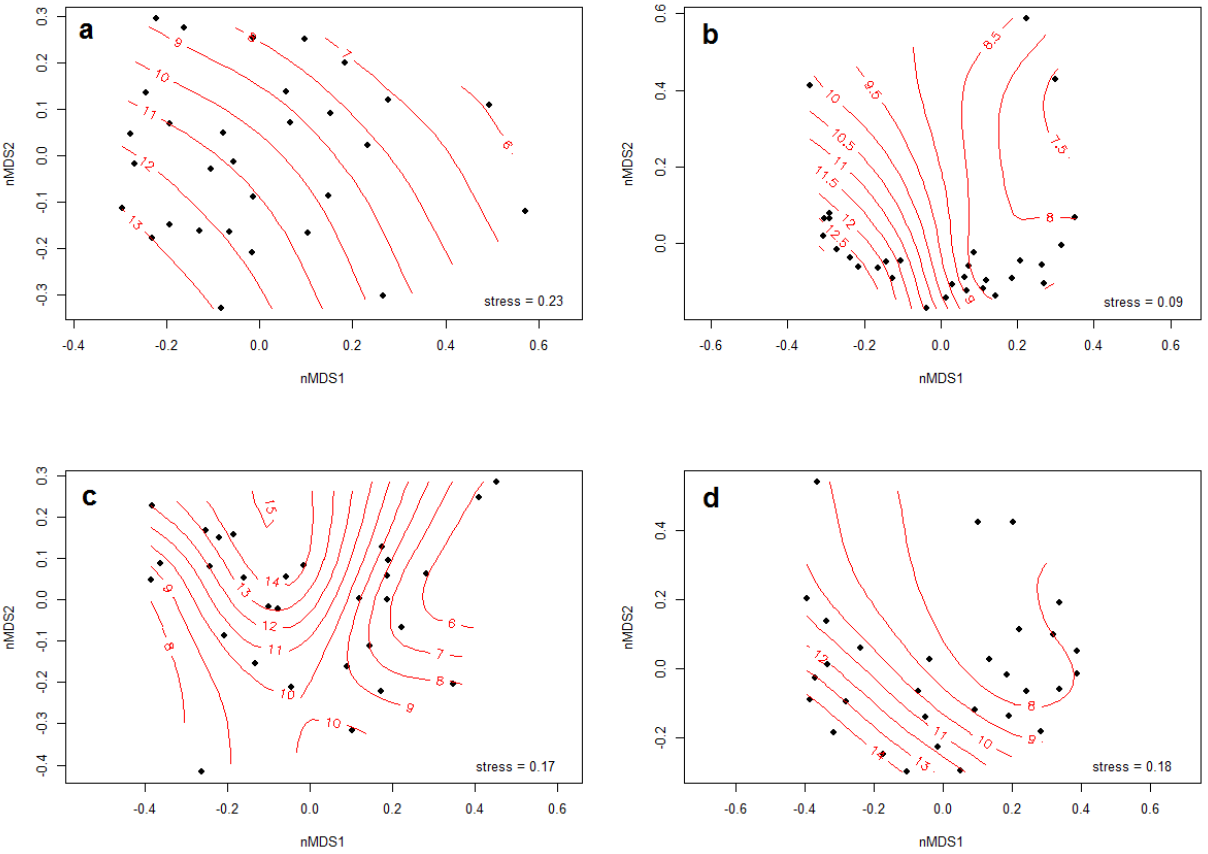


Fig. 5.

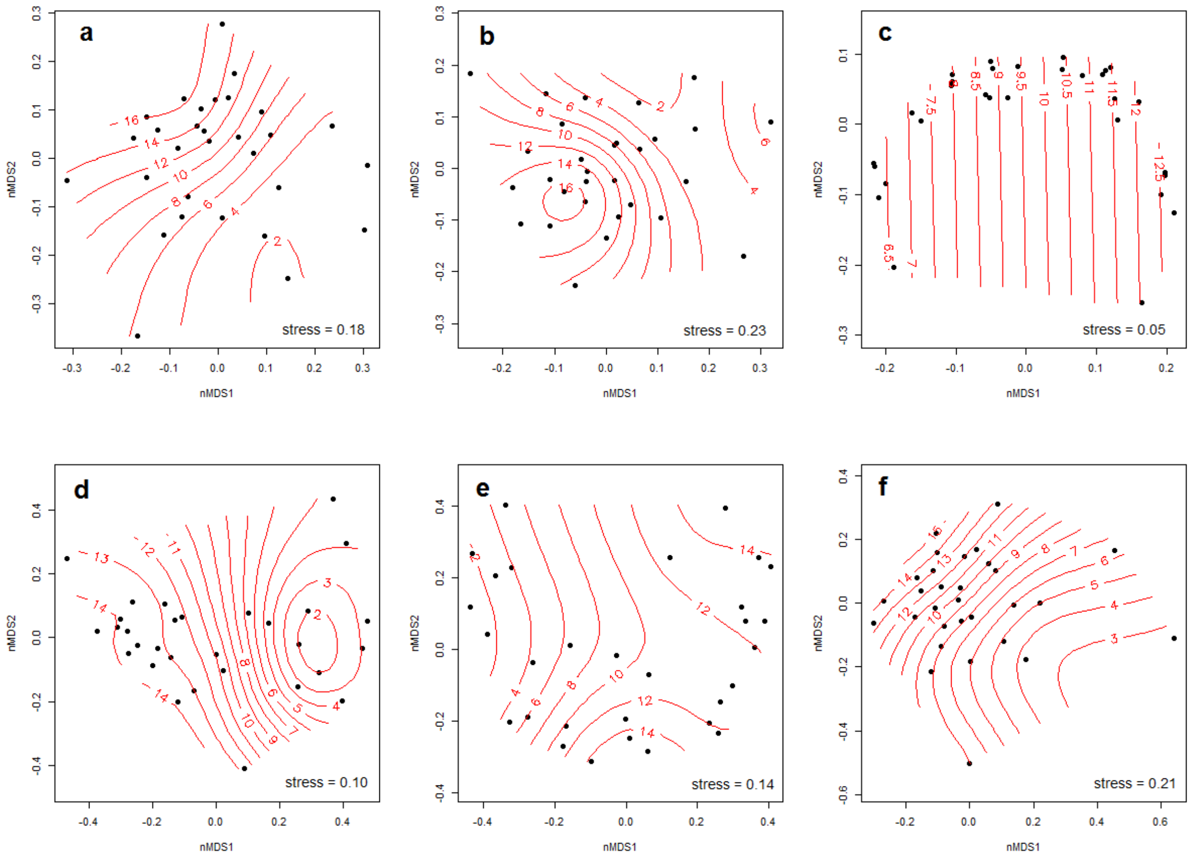

a
stress = 0.18
16
14
12
10
8
6
4
2
b
stress = 0.23
16
14
12
10
8
6
4
2
6
4
c
stress = 0.05
6.5
7
7.5
8
8.5
9
9.5
10
10.5
11
11.5
12
12.5
d
stress = 0.10
14
13
12
11
10
9
8
7
6
5
4
3
2
e
stress = 0.14
2
4
6
8
10
12
14
f
stress = 0.21
15
14
13
12
11
10
9
8
7
6
5
4
3
nMDS1
nMDS2

Fig. 6.

Tables 1, 2 and 3

Table 1 Mean values (± standard errors) for (a) the grain-size parameters of the three sediment types (engineered, associated and control) and (b) the environmental parameters for the associated and the control sediments. Significant differences ($p < 0.05$) of the one-way ANOVAs are in bold and for (a), *post-hoc* results are designated by superscript letters indicating homogenous groups of samples. TOM: total organic matter content, Chl *a*: chlorophyll *a* concentration, Pheo: pheopigments concentration, Sol: soluble carbohydrates concentration, Ins/Sol: ratio of the concentration of insoluble carbohydrates on soluble carbohydrates.

(a)	**Late winter**				**Late summer**			
	Engineered	*Associated*	*Control*	*p-value*	*Engineered*	*Associated*	*Control*	*p-value*
Principal mode (µm)	688 ± 35^{a}	1010 ± 118^{a}	186 ± 8^{b}	**< 0.001**	618 ± 8^{a}	692 ± 74^{a}	201 ± 9^{b}	**< 0.001**
Sorting index (S$_0$)	1.71 ± 0.05^{a}	1.72 ± 0.05^{a}	2.97 ± 0.34^{b}	**< 0.001**	1.69 ± 0.05^{a}	2.98 ± 0.45^{b}	2.70 ± 0.37^{b}	**0.018**
Mud (%) (< 63 µm)	10.00 ± 0.83^{a}	1.84 ± 0.44^{b}	27.38 ± 3.62^{a}	**< 0.001**	9.59 ± 1.22^{a}	20.47 ± 5.37^{a}	21.61 ± 5.23^{a}	0.106
Sand (%) (63-200 µm)	87.19 ± 0.83^{a}	76.74 ± 1.40^{b}	71.69 ± 3.53^{b}	**< 0.001**	85.77 ± 1.40^{a}	65.11 ± 4.09^{b}	76.79 ± 5.17^{ab}	**0.001**

(b)	**Late winter**			**Late summer**		
	Associated	*Control*	*p-value*	*Associated*	*Control*	*p-value*
TOM (%)	6.96 ± 0.72	2.70 ± 0.30	**<0.001**	4.91 ± 0.59	2.26 ± 0.28	**<0.001**
Chl *a* (µg.g^{-1} sediment)	12.21 ± 2.49	2.83 ± 0.58	**0.0022**	13.39 ± 2.24	3.92 ± 0.88	**0.002**
Pheo (µg.g^{-1} sediment)	14.54 ± 0.36	16.18 ± 0.36	**0.0014**	15.56 ± 0.53	15.41 ± 0.29	0.826
Sol (µg.g^{-1} sediment)	442 ± 72	113 ± 25	**0.0027**	467 ± 78	120 ± 25	**<0.001**
Ins/Sol	8.59 ± 2.29	8.63 ± 0.37	0.9998	5.96 ± 0.43	6.32 ± 0.33	0.5175

Table 2 Mean values (± standard errors) for the total macrofauna density (number of individuals.m^{-2}), N0, N1 and N2 with (a) *Sabellaria* taken into account and (b) *Sabellaria* excluded, for the three sediment types (engineered, associated and control) and at both sampling periods (late winter and late summer). N0 represents the species richness, N1 the exponential of the Shannon-Winner diversity and N2 the inverse of the Simpson dominance index. Significant differences ($p < 0.05$) of the one-way ANOVAs are in bold and *post-hoc* results are designated by superscript letters indicating homogenous groups of samples.

	Late winter				**Late summer**			
(a) Macrofauna (*Sabellaria* included in the analyses)								
	Engineered	*Associated*	*Control*	*p-value*	*Engineered*	*Associated*	*Control*	*p-value*
Density	10067 ± 841^{a}	585 ± 102^{b}	629 ± 109^{b}	**<0.001**	23911 ± 2530^{a}	1029 ± 156^{b}	1403 ± 351^{b}	**<0.001**
N0	17 ± 1^{a}	7 ± 1^{b}	8 ± 1^{b}	**<0.001**	26 ± 1^{a}	9 ± 1^{b}	10 ± 1^{b}	**<0.001**
N1	2.92 ± 0.37^{a}	4.46 ± 0.50^{b}	4.54 ± 0.37^{b}	**0.013**	6.01 ± 0.65^{a}	4.61 ± 0.38^{a}	5.22 ± 0.28^{a}	0.229
N2	1.87 ± 0.23^{a}	3.75 ± 0.40^{b}	3.60 ± 0.28^{b}	**<0.001**	3.93 ± 0.44^{a}	3.44 ± 0.30^{a}	4.04 ± 0.25^{a}	0.315
(b) Macrofauna (*Sabellaria* excluded from the analyses)								
	Engineered	*Associated*	*Control*	*p-value*	*Engineered*	*Associated*	*Control*	*p-value*
Density	2385 ± 518^{a}	538 ± 91^{b}	629 ± 109^{b}	**<0.001**	11066 ± 1814^{a}	981 ± 137^{b}	1403 ± 351^{b}	**<0.001**
N0	16 ± 1^{a}	7 ± 1^{b}	8 ± 1^{b}	**<0.001**	25 ± 1^{a}	9 ± 1^{b}	10 ± 1^{b}	**<0.001**
N1	7.73 ± 0.51^{a}	4.30 ± 0.49^{b}	4.54 ± 0.37^{b}	**<0.001**	9.00 ± 0.52^{a}	4.51 ± 0.37^{b}	5.22 ± 0.28^{b}	**<0.001**
N2	5.63 ± 0.42^{a}	3.64 ± 0.39^{b}	3.60 ± 0.28^{b}	**<0.001**	5.82 ± 0.38^{a}	3.36 ± 0.30^{b}	4.04 ± 0.25^{b}	**<0.001**

Table 3 Results of the Mantel tests between (a) the different beta diversity matrices and the mud content distance matrix and (b) the different abundance-based dissimilarity matrices and the mud content distance matrix at both sampling periods (late winter and late summer). β_{sor} is the Sørensen pairwise dissimilarity and accounts for the total beta diversity, β_{sim} is the Simpson pairwise dissimilarity and accounts for the turnover component of the total beta diversity, β_{nes} is the nestedness-resultant dissimilarity and accounts for the nestedness component of the total beta diversity; $\beta_{sor} = \beta_{sim} + \beta_{nes}$. d_{BC} is the Bray-Curtis index of dissimilarity and accounts for the total abundance-based dissimilarity, $d_{BC\text{-}bal}$ is the balanced variation in abundances component of the Bray-Curtis dissimilarity and is equivalent to an abundance-based turnover, $d_{BC\text{-}gra}$ is the abundance gradient component of Bray-Curtis dissimilarity and is equivalent to an abundance-based nestedness; $d_{BC} = d_{BC\text{-}bal} + d_{BC\text{-}gra}$. Significant simulated p-values ($p < 0.05$) and associated observed correlation are in bold.

	Late winter		**Late summer**	
	Observed correlation r	*Simulated p-value*	*Observed correlation r*	*Simulated p-value*
(a) Beta diversity indices				
$\boldsymbol{\beta_{sor}}$	0.13	0.070	**0.24**	**<0.001**
$\boldsymbol{\beta_{sim}}$	0.066	0.23	**0.15**	**0.0066**
$\boldsymbol{\beta_{nes}}$	0.032	0.33	0.077	0.094
(b) Abundance based dissimilarity indices				
$\mathbf{d_{BC}}$	0.14	0.052	**0.38**	**<0.001**
$\mathbf{d_{BC\text{-}bal}}$	0.050	0.28	0.058	0.18
$\mathbf{d_{BC\text{-}gra}}$	0.046	0.28	**0.29**	**<0.001**

Appendix Mean densities (number of individuals.m^{-2}) of species present in each sediment type (control, associated and engineered) at the two sampling seasons (late winter and late summer). The mean densities were calculated using the ten stations sampled in each sediment type and at each season.

	Species	**Late winter**			**Late summer**		
		Control	Associated	Engineered	Control	Associated	Engineered
Polychaete	*Acromegalomma vesiculosum*	0.00	0.00	0.00	0.00	0.00	2.48
	Ampharete baltica	0.00	0.00	0.00	0.00	1.24	0.00
	Aonides oxycephala	0.00	1.24	0.00	0.00	0.00	0.00
	Aonides paucibranchiata	0.00	0.00	0.00	0.00	6.20	0.00
	Armandia polyophthalma	1.24	0.00	0.00	0.00	0.00	0.00
	Capitella capitata	6.20	0.00	0.00	1.24	0.00	1.24
	Caulleriella alata	0.00	0.00	0.00	1.24	0.00	0.00
	Cirriformia tentaculata	0.00	35.96	0.00	0.00	42.16	4.96
	Dipolydora flava	0.00	0.00	0.00	0.00	0.00	4.96
	Eteone flava	0.00	0.00	0.00	1.24	0.00	0.00
	Eteone longa	0.00	0.00	0.00	3.72	3.72	0.00
	Eulalia aurea	0.00	0.00	3.72	0.00	0.00	0.00
	Eulalia clavigera	0.00	0.00	9.92	0.00	0.00	1.24
	Eulalia ornata	0.00	0.00	1.24	0.00	0.00	93.01
	Eulalia viridis	0.00	0.00	22.32	0.00	0.00	27.28
	Eumida arctica	0.00	0.00	0.00	0.00	0.00	1.24
	Eumida sanguinea	12.40	1.24	16.12	14.88	0.00	47.12
	Eunereis longissima	0.00	0.00	0.00	3.72	0.00	0.00
	Glycera alba	3.72	4.96	2.48	13.64	13.64	1.24
	Glycera tridactyla	0.00	1.24	0.00	0.00	1.24	0.00
	Goniadella bobrezkii	1.24	228.17	0.00	14.88	189.73	11.16
	Lanice conchilega	62.00	0.00	0.00	602.67	8.68	0.00
	Lepidonotus squamatus	0.00	0.00	2.48	0.00	0.00	0.00
	Magelona johnstoni	1.24	0.00	0.00	1.24	0.00	0.00
	Malacoceros fuliginosus	1.24	0.00	0.00	3.72	0.00	0.00
	Malmgrenia arenicolae	6.20	3.72	0.00	142.61	2.48	0.00

Mediomastus fragilis	6.20	65.72	6.20	13.64	280.26	44.64
Myrianida sp.	0.00	2.48	0.00	0.00	0.00	0.00
Mysta picta	1.24	0.00	0.00	0.00	0.00	0.00
Nephtys cirrosa	59.52	0.00	0.00	54.56	8.68	0.00
Nephtys hombergii	17.36	0.00	0.00	55.80	38.44	0.00
Nephtys sp.	1.24	0.00	0.00	0.00	0.00	0.00
Notomastus latericeus	16.12	2.48	1.24	48.36	2.48	48.36
Odontosyllis ctenostoma	0.00	1.24	12.40	0.00	0.00	271.57
Odontosyllis gibba	0.00	1.24	29.76	0.00	0.00	0.00
Parathelepus collaris	0.00	0.00	0.00	0.00	1.24	49.60
Perinereis cultrifera	0.00	7.44	164.93	0.00	1.24	146.33
Pholoe inornata	0.00	0.00	1.24	1.24	0.00	7.44
Phyllodoce laminosa	0.00	0.00	2.48	0.00	0.00	11.16
Phyllodoce mucosa	0.00	0.00	0.00	11.16	0.00	0.00
Polycirrus aurantiacus	0.00	3.72	0.00	0.00	0.00	0.00
Polycirrus sp.	0.00	0.00	7.44	0.00	0.00	0.00
Protodorvillea kefersteini	0.00	1.24	0.00	0.00	6.20	0.00
Pseudopolydora pulchra	0.00	1.24	0.00	0.00	0.00	0.00
Pseudopotamilla reniformis	0.00	0.00	0.00	0.00	0.00	3.72
Pygospio elegans	4.96	0.00	0.00	0.00	0.00	6.20
Sabellaria alveolata	0.00	47.12	7682.22	0.00	48.36	12844.62
Saccocirrus papillocercus	0.00	1.24	0.00	0.00	13.64	0.00
Scalibregma celticum	0.00	1.24	0.00	0.00	0.00	0.00
Scolelepis (Parascolelepis) tridentata	1.24	0.00	0.00	0.00	0.00	0.00
Scolelepis (Scolelepis) cantabra	0.00	0.00	0.00	0.00	2.48	0.00
Scoloplos (Scoloplos) armiger	14.88	0.00	0.00	4.96	0.00	0.00
Sphaerosyllis bulbosa	0.00	0.00	0.00	0.00	14.88	7.44
Sphaerosyllis sp.	0.00	1.24	0.00	0.00	0.00	0.00
Spio martinensis	6.20	0.00	0.00	0.00	0.00	0.00
Spio symphyta	0.00	0.00	0.00	2.48	0.00	0.00
Spirobranchus lamarcki	0.00	22.32	24.80	0.00	14.88	68.20

	Spirobranchus triqueter	0.00	0.00	1.24	0.00	0.00	0.00
	Sthenelais boa	0.00	0.00	1.24	0.00	0.00	0.00
	Syllis garciai	0.00	1.24	0.00	0.00	2.48	3.72
	Syllis gracilis	0.00	0.00	2.48	0.00	1.24	11.16
	Tharyx killariensis	126.49	2.48	0.00	1.24	2.48	1.24
	Thelepus setosus	0.00	0.00	0.00	0.00	1.24	28.52
	Websterinereis glauca	0.00	0.00	0.00	1.24	1.24	0.00
Crustacea	*Anapagurus* sp.	0.04	0.00	0.00	0.00	0.00	0.00
	Athanas nitescens	0.00	1.24	1.24	0.00	0.00	1.24
	Bathyporeia elegans	0.00	0.00	0.00	7.44	0.00	0.00
	Bathyporeia guilliamsoniana	34.72	0.00	0.00	0.00	0.00	0.00
	Bathyporeia nana	0.00	0.00	0.00	1.24	0.00	0.00
	Bathyporeia pelagica	1.24	0.00	0.00	4.96	0.00	0.00
	Bathyporeia pilosa	0.00	0.00	0.00	2.48	0.00	0.00
	Bodotria pulchella	0.00	0.00	0.00	0.00	1.24	0.00
	Bodotria scorpioides	1.24	0.00	0.00	0.00	1.24	0.00
	Cancer pagurus	0.00	0.00	2.48	0.00	0.00	1.24
	Carcinus maenas	2.48	0.00	29.76	7.44	1.24	89.28
	Cleantis prismatica	0.00	1.24	0.00	4.96	0.00	0.00
	Corophium arenarium	3.72	0.00	18.60	0.00	0.00	29.76
	Corophium volutator	0.00	0.00	64.48	0.00	0.00	403.02
	Crangon crangon	0.08	0.00	0.00	0.00	0.00	0.00
	Cumopsis goodsir	1.24	0.00	0.00	62.00	1.24	0.00
	Diogenes pugilator	0.11	0.00	0.00	0.11	0.00	0.04
	Eocuma dollfusi	6.20	0.00	0.00	6.20	0.00	1.24
	Ericthonius punctatus	0.00	0.00	0.00	0.00	0.00	2.48
	Eurydice pulchra	0.00	0.00	0.00	2.48	0.00	0.00
	Gammaropsis nitida	0.00	0.00	4.96	0.00	0.00	2.48
	Gnathia maxillaris	0.00	0.00	9.92	0.00	0.00	90.52
	Hemigrapsus sp.	0.00	1.24	1.24	0.00	0.00	0.00
	Jaera (Jaera) albifrons	1.24	0.00	0.00	1.24	0.00	0.00

	Jassa ocia	0.00	0.00	26.04	0.00	1.24	60.76
	Lekanesphaera levii	8.68	13.64	171.13	12.40	47.12	358.38
	Lekanesphaera rugicauda	3.72	3.72	79.36	9.92	9.92	49.60
	Leptocheirus sp.	0.00	0.00	1.24	0.00	0.00	0.00
	Liocarcinus holsatus	0.00	0.00	0.00	0.12	0.00	0.00
	Melita palmata	0.00	9.92	161.21	1.24	6.20	117.81
	Microdeutopus sp.	0.00	0.00	1.24	0.00	0.00	0.00
	Nymphon brevirostre	0.00	0.00	0.00	0.00	0.00	2.48
	Orchomene humilis	0.00	0.00	0.00	1.24	0.00	0.00
	Phtisica marina	0.00	0.00	0.00	1.24	0.00	0.00
	Porcellana platycheles	0.00	2.48	711.80	0.00	1.24	2679.79
	Portumnus latipes	1.24	0.00	0.00	0.31	0.00	0.00
	Pseudocuma (Pseudocuma) longicorne	3.72	0.00	0.00	0.00	0.00	0.00
	Pseudomystides limbata	0.00	0.00	4.96	0.00	0.00	0.00
	Siphonoecetes (Centraloecetes) kroyeranus	1.24	0.00	0.00	11.16	0.00	0.00
	Thia scutellata	0.12	0.00	0.00	0.00	0.00	0.00
	Tryphosites longipes	0.00	0.00	0.00	1.24	0.00	0.00
	Urothoe brevicornis	2.48	0.00	0.00	2.48	0.00	0.00
	Urothoe elegans	0.00	0.00	0.00	1.24	0.00	0.00
	Urothoe poseidonis	3.72	0.00	0.00	12.40	0.00	1.24
	Urothoe pulchella	23.56	0.00	0.00	24.80	0.00	0.00
	Urothoe sp.	2.48	0.00	0.00	0.00	0.00	0.00
Mollusca	*Abra alba*	0.19	0.06	0.00	1.26	0.07	0.00
	Acanthochitona crinita	0.00	0.00	4.96	0.00	0.00	0.00
	Aeolidia papillosa	0.00	0.00	1.24	0.00	0.00	0.00
	Buccinum undatum	0.00	0.00	1.24	0.00	0.00	0.00
	Cerastoderma edule	70.95	0.12	0.11	18.39	0.20	0.06
	Crepidula fornicata	0.64	25.11	26.76	0.00	15.54	7.11
	Gibbula cineraria	0.00	0.00	0.23	0.00	0.00	0.12
	Gibbula umbilicalis	0.00	0.15	26.02	0.00	0.00	39.53
	Lacuna pallidula	0.00	0.00	0.00	0.00	0.00	1.24

	Limecola balthica	89.00	0.12	0.03	187.04	3.97	0.00
	Littorina littorea	0.00	0.00	3.16	0.00	0.00	1.40
	Littorina saxatilis	0.00	0.00	0.04	0.00	0.00	0.00
	Macomangulus tenuis	0.27	0.00	0.00	0.52	0.03	0.00
	Magallana gigas	0.00	0.00	17.60	0.00	0.12	23.31
	Modiolula phaseolina	0.00	0.00	0.00	0.00	0.00	21.08
	Modiolus sp.	0.00	0.00	0.00	0.00	0.00	14.88
	Mytilus cf. *galloprovincialis*	1.24	0.31	5.13	0.76	0.20	10.91
	Nucella lapillus	0.00	0.04	6.21	0.00	0.00	8.10
	Ocenebra erinaceus	0.00	0.03	0.52	0.00	0.08	0.25
	Ostrea edulis	0.00	0.00	0.04	0.00	0.00	0.04
	Phorcus lineatus	0.00	0.00	0.00	0.00	0.00	0.04
	Polititapes aureus	0.00	0.00	2.48	0.00	0.00	0.00
	Polititapes rhomboides	0.00	0.04	0.07	0.00	0.00	0.00
	Ruditapes decussatus	0.00	0.04	0.03	0.00	0.11	0.03
	Ruditapes philippinarum	0.24	0.39	0.25	0.28	0.99	0.10
	Scrobicularia plana	0.00	0.00	0.00	1.24	0.00	0.00
	Spisula elliptica	0.00	0.00	0.00	0.00	2.48	0.00
	Spisula solida	0.04	0.41	0.00	0.91	0.16	0.00
	Tritia reticulata	6.73	0.08	0.24	3.61	0.35	0.10
	Venerupis corrugata	0.12	0.54	0.81	0.16	0.23	1.62
	Venus verrucosa	0.00	0.00	0.00	0.00	0.04	0.00
Ascidiacea	*Microcosmus claudicans*	0.00	0.00	0.00	0.00	0.00	9.92
	Molgula sp.	0.00	0.00	0.00	0.00	1.24	7.44
	Phallusia mammillata	0.00	0.00	0.00	0.00	0.00	1.24
	Polycarpa fibrosa	0.00	0.00	0.00	0.00	0.00	14.88
	Polyclinum aurantium	0.00	0.00	11.16	0.00	0.00	0.00
	Pyura microcosmus	0.00	0.00	7.44	0.00	0.00	0.00
	Styela clava	0.00	0.00	7.44	0.00	0.00	16.12
Anthozoa	*Actinia equina*	0.00	0.00	0.00	0.00	0.03	0.04
	Anemona sp.	0.00	0.00	0.00	0.00	0.00	1.24

	Cereus pedunculatus	2.48	9.92	64.48	0.00	2.48	58.28
	Urticina felina	0.00	0.00	0.00	0.00	0.00	0.04
Pycnogonida	*Achelia echinata*	0.00	1.24	54.56	0.00	4.96	1311.99
	Achelia laevis	0.00	0.00	8.68	0.00	1.24	261.65
	Achelia simplex	0.00	1.24	95.49	0.00	2.48	962.29
	Anoplodactylus virescens	0.00	0.00	0.00	0.00	0.00	17.36
Sipuncula	*Golfingia (Golfingia) elongata*	0.00	3.72	6.20	0.00	0.00	57.04
	Golfingia (Golfingia) vulgaris vulgaris	0.00	24.80	192.21	0.00	8.68	130.21
	Nephasoma (Nephasoma) minutum	0.00	22.32	62.00	0.00	16.12	626.23
	Phascolion (Phascolion) strombus strombus	0.00	1.24	0.00	0.00	0.00	0.00
Echinodermata	*Acrocnida spatulispina*	1.24	0.00	0.00	1.24	0.00	0.00
	Amphipholis squamata	0.00	2.48	0.00	0.00	2.48	49.60
Other	*Nematoda*	1.24	6.20	9.92	1.24	102.93	2368.53
	Nemertea	0.00	11.16	69.44	6.20	47.12	184.77
	Oligochaeta	0.00	0.00	1.24	0.00	33.48	38.44
Insecta	*Axelsonia littoralis*	0.00	0.00	79.36	0.00	0.00	13.64
	Hydrogamasus sp.	0.00	0.00	14.88	0.00	0.00	8.68
Vertebrata	*Lipophrys pholis*	0.00	0.00	0.04	0.00	0.00	0.12