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

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► **To cite this version:**

Auriane Jones, Stanislas Dubois, Nicolas Desroy, Jérôme Fournier. Interplay between abiotic factors and species assemblages mediated by the ecosystem engineer *Sabellaria alveolata* (Annelida: Polychaeta). *Estuarine, Coastal and Shelf Science*, 2018, 200, pp.1-18. 10.1016/j.ecss.2017.10.001 . hal-02323051

HAL Id: hal-02323051

<https://hal.science/hal-02323051v1>

Submitted on 10 Jun 2021

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3 **1 Title**

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5 2 Interplay between abiotic factors and species assemblages mediated by the ecosystem engineer *Sabellaria*
6
7 3 *alveolata* (Annelida: Polychaeta)

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28 **15 Abstract**

29 16 *Sabellaria alveolata* is a gregarious polychaete that uses sand particles to build three-dimensional structures known
30 17 as reefs, fixed atop rocks or built on soft sediments. These structures are known to modify the local grain-size
31 18 distribution and to host a highly diversified macrofauna, altered when the reef undergoes disturbances. The goal
32 19 of this study was to investigate the different sedimentary and biological changes associated with the presence of a
33 20 *S. alveolata* reef over two contrasting seasons (late winter and late summer), and how these changes were linked.
34 21 Three different sediments were considered: the engineered sediment (the actual reef), the associated sediment (the
35 22 soft sediment surrounding the reef structures) and a control soft sediment (*i.e.* no reef structures in close proximity).
36 23 Univariate and multivariate comparisons of grain-size distribution, soft sediment characteristics (organic matter
37 24 content, chlorophyll *a*, pheopigments and carbohydrate concentrations) and macrofauna were conducted between
38 25 the different sediment types at both seasons and between the two seasons for each sediment type. A distance-based
39 26 redundancy analyses (dbRDA) was used to investigate the link between the different environmental parameters
40 27 and the macrofauna assemblages. Finally, we focused on a disturbance continuum of the engineered sediments
41 28 proxied by an increase in the mud present in these sediments. The effects of a continuous and increasing
42 29 disturbance on the associated fauna were investigated using pairwise beta diversity indices (Sørensen and Bray-
43 30 Curtis dissimilarities and their decomposition into turnover and nestedness). Results showed a significant effect

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62 31 of the reef on the local sediment distribution (coarser sediments compared to the control) and on the benthic
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64 32 primary production (higher in the associated sediments). At both seasons, *S. alveolata* biomass and sediment
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66 33 principal mode were the environmental parameters which best differentiated the engineered, associated and control
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68 34 sediment assemblages. These two parameters are under the ecosystem engineer's influence stressing its importance
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70 35 in structuring benthic macrofauna. Furthermore, in late summer but not in late winter, presence/absence and
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72 36 abundance based beta diversity were positively correlated to our disturbance proxy (mud content) a tendency
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74 37 driven by a species replacement and a rise in the associated fauna density. Our first set of results highlight the
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76 38 importance of *S. alveolata* reefs as benthic primary production enhancers via their physical structure and their
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78 39 biological activity. The results obtained using beta diversity indices emphasize the importance of recruitment in
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80 40 structuring the reef's macrofauna and – paradoxically – the ecological value of *S. alveolata* degraded forms as
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82 41 biodiversity and recruitment promoters.

82 42 **Keywords**

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84 43 Honeycomb worm, macrobenthos, benthic primary production, habitat disturbance, silt, beta diversity, France,
85
86 44 Brittany, Mont Saint-Michel Bay

88 45 **Abbreviations**

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90 46 MSMB, Mont Saint-Michel Bay; MPB, Microphytobenthos; TOM, Total organic matter; Chl *a*, Chlorophyll *a*;
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92 47 Pheo, Pheopigments; Ins, Insoluble carbohydrates; Sol, Soluble carbohydrates; dbRDA, Distance-based
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94 48 redundancy analysis; CPUE, Catch-per-unit-effort

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121 **61 1. Introduction**
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123 62 Ecosystem engineers are organisms capable of modifying their local environment through their physical
124 63 presence (*i.e.* autogenic engineers) and/or their biological activity (*i.e.* allogenic engineers), “directly or indirectly
125 63 modulating the availability of resources to other species” (Jones et al., 1994). Ultimately, these species maintain,
126 64 modulating the availability of resources to other species” (Jones et al., 1994). Ultimately, these species maintain,
127 64 modify, create or even destroy habitats (Bouma et al., 2009; Jones et al., 1994). The abiotic modifications caused
128 65 by ecosystem engineers can lead to facilitation for some organisms (Hacker and Gaines, 1997) and inhibition
129 66 by ecosystem engineers can lead to facilitation for some organisms (Hacker and Gaines, 1997) and inhibition
130 66 through negative species interaction for others (Bouma et al., 2009; Jones et al., 1997). Nonetheless, bioengineered
131 67 habitats are often reported to host a more diverse species assemblage than the adjoining non-engineered habitats
132 67 (Ataide et al., 2014; De Smet et al., 2015; Jones et al., 1997; Stachowicz, 2001). Physical ecosystem engineering
133 68 appears to be particularly important where the environment is extreme (*e.g.* thermic, hydrodynamic and/or hydric
134 68 stress), like in temperate intertidal areas (Bouma et al., 2009; Jones et al., 1997). Indeed, according to Jones et al.
135 69 (1997, 1994), these extreme conditions might have favored the selection of “extended phenotype engineers”
136 69 through enhanced survival of the engineer and the cohabiting fauna (Dawkins, 1982). These engineer species
137 70 create complex habitats that reduce local pressures such as predation or thermal stress, whilst increasing
138 70 biodiversity (Bouma et al., 2009). Ultimately, such favorable environmental changes can lead to an interesting
139 71 paradox where “the spatial extent of the realized niche of a species can be larger than the spatial range predicted
140 71 by the fundamental niche” as described by Bruno et al. (2003) and reported for mussels and barnacles in
141 71 *Ascophyllum nodosum* canopies by Bertness et al. (1999).
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153 73 Temperate coasts host a striking number of ecosystem engineering species, spanning from mollusks (for
154 73 a review see Gutiérrez et al. (2003)) and polychaetes (*e.g.* *Lanice conchilega* (De Smet et al., 2015)) to canopy-
155 73 forming algae (*e.g.* *Ascophyllum nodosum* (Bertness et al., 1999)). Along the European coastline, a particular
156 73 ecosystem engineer has the ability to build three-dimensional structures on top of sediments qualified as reefs
157 73 (Holt et al., 1998). This species is a common gregarious tubicolous polychaete called *Sabellaria alveolata*
158 73 (Linnaeus, 1767), a.k.a. the honeycomb worm. It generally lives in the intertidal zone from mid to low tide levels
159 73 and can be found from Scotland and Ireland to Morocco (Muir et al., 2016). *Sabellaria alveolata* uses sand particles
160 73 remobilized by waves and tidal action to build the tube in which it lives (Le Cam et al., 2011). Since the pelagic
161 73 larvae are attracted by the L-dopa present in the organic cement produced by the adult worms for their tube-
162 73 building activity, they will tend to settle on existing reefs (Pawlik, 1988; Wilson, 1968). This phenomenon coupled
163 73 with favorable environmental conditions (*i.e.* grain-size structure, hydrodynamic processes, food availability and
164 73 water temperature) can lead to the development of large biogenic reefs (Holt et al., 1998). These structures are
165 73 commonly found on rocky substrata as veneers or hummocks where they rarely exceed 50 cm in height for a few
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180 92 tens of square meters but in some rare instances, they can be found in soft bottom areas where they can grow up
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182 93 to two meters in height and several hectares in size (Holt et al., 1998; Noernberg et al., 2010). The largest of these
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184 94 formations, which is also the largest biogenic habitat in Europe, is located in the Mont Saint-Michel Bay (MSMB)
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186 95 in France (Desroy et al., 2011; Dubois et al., 2002).

187 96 The research around this species has mainly focused on its physiology (*i.e.* reproduction, fecundity,
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189 97 feeding mode) (Dubois et al., 2003, 2005, 2006a, 2009) and its tube building activity (Fournier et al., 2010; Le
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191 98 Cam et al., 2011). Other studies have looked into the ecology of reefs with a particular interest on the associated
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193 99 fauna (Dias and Paula, 2001; Porta and Nicoletti, 2009; Schlund et al., 2016) and factors influencing it such as the
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195 100 reef's different growth stages (Dubois et al., 2002), epibionts (Dubois et al., 2006b), human trampling (Plicanti et
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197 101 al., 2016) and ecological status (Desroy et al., 2011). A large part of these studies has focused on *Sabellaria*
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199 102 *alveolata* reefs on rocky substrata and not on soft sediment. Reefs developing on soft sediment are far less frequent
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201 103 along the European coast (*i.e.* MSMB and Bourgneuf Bay in France) (Holt et al., 1998). Nonetheless, they
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203 104 constitute exceptional locations composed of two distinct entities: the actual three-dimensional reef structures
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205 105 (engineered sediment), which is spatially discontinuous and the soft sediment present between the reef structures
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207 106 (associated sediment) (Desroy et al., 2011). Several kilometers separate them from the nearest rocky shore which
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209 107 signifies, in contrast to the veneer form of *S. alveolata* structures, complete isolation from most of the juvenile and
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211 108 adult fauna inhabiting these rocky shores. Furthermore, their physical borders are easy to visualize against the
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213 109 surrounding soft sediment. These sites give us the chance to study different components of *S. alveolata*'s
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215 110 engineering effect (Passarelli et al., 2014; Wright et al., 2006). This engineering effect can be seen from both an
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217 111 environmental and a biological perspective by looking at how the ecosystem engineer modifies the local
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219 112 sedimentary characteristics and how the biodiversity changes between a control sediment, the associated and the
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221 113 engineered sediments. The control soft sediment represents the baseline or the unmodified state before the
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223 114 honeycomb worms start building reefs, hence representing a new structural state (Jones et al., 2010).

224 115 This biogenic habitat is not structurally homogenous, mainly due to multiple disturbances; direct natural
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226 116 disturbances such as storms and cold winters, direct anthropogenic disturbances such as trampling and indirect
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228 117 anthropogenic disturbances through shellfish farming and coastal engineering. These disturbances lead to a gradual
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230 118 modification of the reef visible through disaggregation, increasing fine sediments, decreasing ecosystem engineer
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232 119 density and increasing epibiont cover, causing a number of changes in the associated fauna (Dubois et al., 2006b,
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234 120 2002; Plicanti et al., 2016). Modifications of the associated fauna have been investigated in several categorical
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236 121 ways but never along a disturbance continuum (Dubois et al., 2006b, 2002; Plicanti et al., 2016). To understand

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239 122 the changes in the associated fauna along this continuum, we chose to focus on the beta diversity seen as “the
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241 123 extent of change in community composition” as defined by Whittaker (1960) and on an abundance-based
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243 124 dissimilarity measurement using the Bray-Curtis dissimilarity. Analyzing beta diversity in a *S. alveolata* reef can
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245 125 help us understand the functioning of this biogenic habitat and give more relevant information to decision makers
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247 126 regarding conservation issues. First, taking into account the three previously defined sediment types (control,
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249 127 associated and engineered sediments), we tested in a categorical way, the following hypotheses: (1) the engineered
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251 128 sediment affects the different sedimentary characteristics of the associated sediment, especially grain-size, organic
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253 129 matter content and microphytobenthos and (2) the diversity and species composition of both the engineered and
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255 130 the associated sediments are different from the control sediment. We also looked into potential changes between
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257 131 late winter and late summer, regarding sediment composition and macrofauna assemblages for each sediment type.
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259 132 Then, using beta diversity and dissimilarity measurements, we tested the following hypothesis: an increasing
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261 133 disturbance of the engineered sediment promotes (1) beta diversity and more specifically species turnover and (2)
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263 134 abundance-based dissimilarity and more specifically abundance gradients.

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264 136 **2. Materials and methods**

265 137 **2.1. Study area**

267 138 This study took place in the central part of the MSMB where the largest bioconstruction in Europe is
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269 139 located; the Sainte-Anne reef (48°38'700N and 1°40'100W), built by the honeycomb worm *Sabellaria alveolata*
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271 140 (Desroy et al., 2011). This reef is situated in the lower intertidal zone (*i.e.* between the - 2 and the - 4 m isobaths
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273 141 (Noernberg et al., 2010)), parallel to the coast and to the dominant tidal currents and also near important blue
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275 142 mussel (*Mytilus edulis*) cultures. In 2014, the maximal dimensions of the Sainte-Anne reef were 2.5 km in length
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277 143 for 1 km in width and the engineered sediment represented about 32 ha for about 128 ha of associated sediment
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279 144 (unpublished results). The area located in the central part of the bay and along the same isobath as the reef is
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281 145 characterized by medium to muddy sands (Bonnot-Courtois et al., 2009) and by a species poor “*Macoma balthica*
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283 146 community” (Dubois et al., 2002).

284 147 **2.2. Sampling design and laboratory analyses**

286 148 Two sampling areas were defined; the Sainte-Anne reef area and a control area. The reef area was
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288 149 composed of two sediment types, the engineered and the associated sediments (Fig. 1). The control area was a soft
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290 150 sediment zone located 1.5 km North-East of the reef area and on the same bathymetric level. It was characteristic
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292 151 of the medium to muddy sands found in this part of the bay (Bonnot-Courtois et al., 2009). Sampling took place

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298 152 over a two-day period in late winter (late February) and late summer (late September). These two seasons were
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300 153 chosen because they are highly contrasted environmentally (*e.g.* hydro-sedimentary features) and biologically (*e.g.*
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302 154 recruitment patterns, species turnover, growth rates). Indeed, winter is a period of low biological activity and high
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304 155 environmental pressures (cold temperatures, wind and storms) while late summer is a post-recruitment period with
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306 156 a higher biological activity (Arbach Leloup et al., 2008; Cugier et al., 2010). Hence, sampling at these two seasons
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308 157 helps us to have a more complete picture of the dynamics happening in our different study zones.

309 158 To investigate the effects of *S. alveolata* on diversity and species composition, we compared the
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311 159 macrofauna associated with the three different sediment types: the *S. alveolata* reefs, the sediments present around
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313 160 these structures and the control soft sediments. For each sediment type (*i.e.* engineered, associated and control
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315 161 sediment, Fig. 1), ten stations were sampled. Every engineered sediment station was paired with an associated
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317 162 sediment station, in order to investigate how the reef structures modify the adjoining soft sediment. The stations
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319 163 were at least 75 m apart and at each station, six samples separated by at least 5 m were randomly taken at low tide.
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321 164 The first three samples were done using a 18.5 cm side corer (269 cm²) to a depth of 15 cm (core samples). For
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323 165 engineered sediments, this depth corresponds to the layer where *Sabellaria alveolata* and more than 90% of all
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325 166 species live (Dubois et al., 2002). The other three samples were done using a 1 m² quadrat in order to estimate the
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327 167 over dispersed macrofauna, mainly composed of bivalves and gastropods (quadrat samples). All engineered
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329 168 sediment samples (core and quadrat samples) were taken at least 1 m from the reef edge to avoid a known border
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331 169 effect on the macrofauna diversity (Gruet, 1972), while the associated sediment samples (core and quadrat
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333 170 samples) were taken at least 1 m away from the reef structures. The soft sediment core samples were sieved through
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335 171 a 1-mm square mesh on site while the engineered sediment core samples were taken back to the laboratory where
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337 172 they were broken apart under water and the fauna retained on a 1-mm square mesh was collected. Associated and
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339 173 control quadrat samples were done by sieving on site the first 5 cm of sediment through a 5-mm square mesh. For
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341 174 the engineered quadrat samples, we sampled by hand all the visible macrofauna located on the reef and inside the
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343 175 reef interstices. All core and quadrat samples were fixed in a 5% formaldehyde solution, after which all the
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345 176 macrofauna was sorted, counted and identified to the species or genus level (except for nemerteans, oligochaetes
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347 177 and nematodes) and finally preserved in a 70% ethanol solution. For each engineered sediment core sample, all
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349 178 the *Sabellaria alveolata* were weighted (total wet weight).

346 179 To look at how the ecosystem engineer modifies its environment, we randomly collected three sediment
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348 180 samples for grain-size distribution, total amount of organic matter (TOM), pigment concentration (*i.e.* chlorophyll
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350 181 *a* and pheopigments) and total carbohydrate concentration (*i.e.* soluble and insoluble carbohydrates), at each
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357 182 associated and control sediment station. For the grain-size distribution, the first 5 cm of sediments were sampled
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359 183 using a small plastic core (19 cm²). For all the other sedimentary characteristics, only the first centimeter of
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361 184 sediment was sampled using a plastic petri dish (57 cm²). Additional samples were collected in order to
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363 185 characterize the sediments constituting the *Sabellaria alveolata* tubes as well as the sediments potentially trapped
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365 186 within the biogenic structure. These consisted in randomly collecting three small reef parts (about 8 x 3 cm) in
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367 187 each engineered sediment station. Sediment grain-size distribution was obtained by mechanical sieving using
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369 188 AFNOR calibrated sieves (from 25 mm to 63 µm) and granulometric parameters were estimated using the 'G2Sd'
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371 189 package in R v. 3.3.0 (Fournier et al., 2014). Prior to mechanical sieving, the engineered sediments were cautiously
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373 190 broken into their original elements, *i.e.* mostly bioclasts as evidenced in Le Cam et al. (2011). For all the other
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375 191 analyses, the sediments were first freeze-dried in order to work on dry matter. TOM was determined as the
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377 192 difference between the weight of freeze-dried sediment and the weight after 4 hours at 450° (Aminot and Kerouel,
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379 193 2004). Pigment concentrations (µg.g⁻¹ dry sediment) were estimated using the monochromatic technique
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381 194 (Lorenzen, 1967) described in Aminot and Kerouel (2004). The chlorophyll *a* (Chl *a*) concentration was used as a
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383 195 proxy for microphytobenthos (MPB) biomass (Jeffrey et al., 1997) while pheopigments (Pheo) concentration gave
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385 196 us information about the amount of degraded photoautotrophs. Soluble carbohydrates (Sol) present in the sediment
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387 197 were extracted by hydrolysis (100°C for 45 min), after which the pellets were treated with sulfuric acid (H₂SO₄)
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389 198 and placed 4 hours at 100°C in order to obtain the insoluble carbohydrates (Ins). Sol and Ins concentrations (µg.g⁻¹
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391 199 dry sediment) were then estimated by colorimetric phenol sulfuric dosage (Dubois et al., 1956). Sol were
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393 200 considered as being an important labile source of carbon for consumers living in the sediment such as bacteria and
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395 201 deposit-feeding invertebrates (Bellinger et al., 2009) while the insoluble carbohydrates to soluble carbohydrates
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397 202 ratio (Ins/Sol) was used as a proxy for the C/N ratio and as a TOM degradation index (Delmas, 1983).

395 203 **2.3. Data analysis**

396 204 **2.3.1. Biological and environmental engineering effects**

398 205 Since macrofauna was sampled using two different techniques (cores and quadrats), densities of species
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400 206 were estimated using the catch-per-unit-effort (CPUE) method, *i.e.* the ratio between the total catch and the total
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402 207 amount of effort used to harvest the catch (Skalski et al., 2005). At one sampling location, when a species was
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404 208 only collected by core or quadrat, its density was estimated using the corresponding sampling surface. However,
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406 209 when a species was sampled by both methods, cumulated abundances were divided by the sum of each gear's
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408 210 CPUE. This estimation method was used for 17 species in late winter and 15 in late summer, taking into account
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410 211 all three sediment types. Species' densities were calculated using the formula:

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

where $density_A$ is species' A abundance per m^2 , $abundance_{Aq}$ 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 ($1 m^2$) and $CPUE_c$ is the core's catch-per-unit-effort ($0.0269 m^2$).

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 $1 m^2$ 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

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474
475 242 sediments, also using permanovas. Prior to performing permanovas, we tested for homogeneity of dispersions
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477 243 using the PERMDISP PRIMER routine (Anderson et al., 2008). When raw data presented significantly different
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479 244 dispersions between the three sediment types ($p < 0.05$), it was log transformed (in late winter: principal mode,
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481 245 TOM, Chl *a*, Pheo, macrofauna density with and without *S. alveolata*, N0 with and without *S. alveolata* and N2
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483 246 with *S. alveolata*, in late summer: macrofauna density with and without *S. alveolata*, N0 with and without *S.*
484
485 247 *alveolata* and N1 without *S. alveolata*). When log transformation did not lead to homogenous dispersions (in late
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487 248 winter: % mud, % sand and Sol, in late summer: TOM, Chl *a*, Sol, N1 and N2 calculated with *S. alveolata*), non-
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489 249 parametric statistical tests were performed (Kruskal-Wallis test for the granulometric and macrofauna parameters
490
491 250 and Wilcoxon-Mann-Whitney for the other environmental parameters).

491 251 In order to evaluate if the different environmental and macrofauna parameters were significantly different
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493 252 between late winter and late summer for each sediment type, one-factor permanovas were performed, with season
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495 253 considered as a fixed factor. We chose to perform one-factor rather than two-factor univariate analysis of variance
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497 254 (in this case with sediment type and season as fixed factors), because we lacked replication inside each season for
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499 255 our different sediment types (Underwood, 1997). As previously mentioned, permanovas (9999 permutations) were
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501 256 used rather than t-tests because none of the investigated variables were normally distributed. Homogeneity of
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503 257 dispersions was also tested (PERMDISP) and data was transformed when necessary (square-root transformation
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505 258 for TOM in the associated sediments, log transformation for macrofauna density with *S. alveolata* in the control
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507 259 sediments and for macrofauna density without *S. alveolata* in the engineered sediments). The Permanovas,
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509 260 PERMDISP routines and PCOs were performed using the PRIMER v6 software with the PERMANOVA+ add-
510
511 261 on (Anderson et al., 2008). *Post-hoc* Kruskal-Wallis tests were performed with the ‘kruskalme’ function from the
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513 262 ‘pgirmess’ package (Giraudoux, 2016) using R version 3.3.0 (R Core Team, 2016).

513 263 **2.3.2. Linking environmental and biological engineering effects**

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515 264 The relationship between the environmental characteristics and the macrofauna present in the three
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517 265 sediment types was investigated using distance-based linear models (DistLM). In line with Legendre and Anderson
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519 266 (1999) and McArdle and Anderson (2001), DistLM models were coupled to a distance-based redundancy analysis
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521 267 (dbRDA) to define the best fitted model in a multi-dimensional space in a way similar to a constrained PCO.
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523 268 DistLM models were built using the Bayesian Information Criterion (BIC) to identify “good” models and the ‘best’
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525 269 procedure to select the variables according to the BIC. Prior to the DistLM and dbRDA analysis, the environmental
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527 270 parameters were displayed using Draftsman plots and the ones presenting an important skewness were transformed
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529 271 to approach normality (Anderson et al., 2008). If two predictor variables were strongly correlated ($r^2 > 0.80$), one

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534 272 of them was removed from the analysis in order to avoid multi-collinearity (Dormann et al., 2013). Except for the
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536 273 grain-size data, environmental parameters used to characterize an engineered sediment sample were the same as
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538 274 for its corresponding associated sediment sample. For late winter, the final predictor data set contained the % sand,
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540 275 Pheo (both square-root transformed), % mud, TOM, *S. alveolata* biomass (all three fourth-root transformed),
541
542 276 principal mode and Ins/Sol (both log transformed). For late summer, the final predictor data set was the same as
543
544 277 for late winter, except the % sand which was removed (absolute correlation with % mud > 0.8). *S. alveolata*
545
546 278 biomass was used rather than abundance because this parameter provides more information about ecosystem
547
548 279 functioning (Cardinale et al., 2013). *S. alveolata* biomass was considered as a predictor variable since it physically
549
550 280 modifies its environment and it was consequently removed from the macrofauna data set. The DistLM models and
551
552 281 dbRDA analysis were performed using the PRIMER v6 software with the PERMANOVA+ add-on (Anderson et
553
554 282 al., 2008).

554 283 **2.3.3. Disturbances and biological engineering effect**

556 284 At its climax, a *S. alveolata* reef is formed by 100% honeycomb worm tubes, leaving virtually no space
557
558 285 for infaunal organisms. When natural or anthropogenic disturbances (e.g. storms, trampling) physically damage
559
560 286 the reef, tubes are destroyed, freeing up space. This new available space can be filled either with other organisms
561
562 287 such as the oyster *Magallana gigas* (formerly known as *Crassostrea gigas*) or by fine particles. Fine particles
563
564 288 accumulate from suspended sediments, or from the feces and pseudofeces of *S. alveolata* and other bivalves
565
566 289 (biodeposition) (Dubois et al., 2006b). In either case, this fine sediment can end up trapped inside the *S. alveolata*
567
568 290 reefs. Consequently, the increased deposition of mud inside the engineered sediments is the result of several
569
570 291 different and often concomitant disturbances. Fine sediment deposition has previously been recognized as a
571
572 292 significant disturbance to stream macroinvertebrates (Mathers et al., 2017) and benthic habitats (Balata et al., 2007;
573
574 293 Mateos-Molina et al., 2015; Miller et al., 2002). Similarly, we chose to consider mud content as a proxy for
575
576 294 disturbance. This proxy was also chosen because it is independent from *Sabellaria alveolata* population dynamics
577
578 295 and physiological state. Finally, using the mud content makes the two seasons readily comparable.

579 296 Beta diversity was calculated using pairwise multivariate distances since they are independent of sample
580
581 297 size and regional diversity (gamma diversity) allowing accurate potential comparisons among regions (Bennett
582
583 298 and Gilbert, 2016). We chose to use the presence/absence based indices presented by Baselga (2010) in order to
584
585 299 partition total beta diversity, expressed by Sørensen dissimilarity (β_{sor}), into the turnover (β_{sim}) and nestedness
586
587 300 (β_{nes}) components. In this case, $\beta_{\text{sor}} = \beta_{\text{sim}} + \beta_{\text{nes}}$. Under conditions of equal species richness, $\beta_{\text{sor}} = \beta_{\text{sim}}$ and $\beta_{\text{nes}} =$
588
589 301 0, while under conditions of unequal species richness, β_{sim} and β_{nes} vary between 0 and β_{sor} . Sørensen dissimilarity

591
592
593 302 varies between 0 and 1, with 0 indicating that two samples have identical species list and 1 indicating no common
594
595 303 species (Baselga, 2010). For β_{sim} , 0 indicates complete nestedness, and a maximal value of 1 can be found if in one
596
597 304 of the two considered samples, there are no species recorded and in the other, the number of species is maximal
598
599 305 (Koleff et al., 2003). To have a complementary vision of how disturbance affected the associated fauna abundance,
600
601 306 the abundance-based dissimilarity (Bray-Curtis dissimilarity, d_{BC}) was also partitioned into balanced changes in
602
603 307 abundance (d_{BC-bal}) and abundance gradients (d_{BC-gra}), which are closely related to turnover and nestedness
604
605 308 components respectively (Baselga, 2013). These indices were computed after removing *S. alveolata* from the
606
607 309 presence/absence and density matrices. They were calculated using the pairwise measures in order to have the beta
608
609 310 diversity and the dissimilarities for each pair of samples (*i.e.* 435 pairs). Then, using Euclidian distance, all the
610
611 311 mud content pairwise differences were calculated. Finally, using the different pairwise measures, we performed
612
613 312 Mantel tests (9999 permutations) for late winter and late summer data, to test the null hypothesis of no relationship
614
615 313 between the mud content distance matrix and each beta diversity matrix. A p-value below 0.05 indicates a
616
617 314 significant correlation between the two investigated distance matrices, with the sign of the r-value indicating if the
618
619 315 two matrices are positively or negatively associated. The beta diversity indices were computed using the ‘beta.pair’
620
621 316 function, and the Bray-Curtis dissimilarity indices using the ‘bray.part’ function, both from the ‘betapart’ R
622
623 317 package (Baselga, 2013). The Mantel tests were performed using the ‘mantel.rtest’ function from the ‘ade4’ R
624
625 318 package (Dray and Dufour, 2007).

623 319 To test the link between the macrofaunal assemblages based on their respective beta diversity and
624
625 320 dissimilarity indices and the disturbance parameter (*i.e.* mud content), non-metric multidimensional scaling
626
627 321 ordinations (nMDS) were successively performed for each index (β_{sor} , β_{sim} , β_{nes} , d_{BC} , d_{BC-bal} and d_{BC-gra}) and at each
628
629 322 sampling period (late winter and late summer) using the ‘metaMDS’ function of the ‘MASS’ R package (Venables
630
631 323 and Ripley, 2002). Then, the ‘envfit’ function (‘vegan’ R package) was used to test if the mud content was
632
633 324 significantly correlated with each ordination (Oksanen et al., 2016). When a correlation was significant, the mud
634
635 325 contents were fitted and plotted on the given nMDS using the ‘ordisurf’ function of the ‘vegan’ R package
636
637 326 (Oksanen et al., 2016). All these analyses were performed using R version 3.3.0 (R Core Team, 2016).

637 327

638 328 **3. Results**

640 329 **3.1. Environmental engineering effect**

641 330 Mean values of grain-size distribution parameters measured within each sediment type are reported in
642
643 331 Table 1a. Analyses revealed significant differences between the sediment types for all tested metrics in late winter
644
645
646
647
648
649

650
651
652 332 ($p < 0.001$) and for all but one in late summer (mud content). At both periods, there was a strong engineering effect
653
654 333 on the principal mode marked by a significantly coarser sediment in the engineered and associated sediments than
655
656 334 in the control sediments (Table 1a). In late winter, the sorting index S_0 was significantly lower in the engineered
657
658 335 and associated sediments than in the control and mud content was significantly lower in the associated sediments
659
660 336 than in the other two sediment types. Finally, the sand content was significantly higher in the engineered sediment
661
662 337 relative to the other sediment types. In late summer, associated sediments had a higher sorting index than the
663
664 338 engineered sediments and one comparable to the control sediments. Although associated sediments were also
665
666 339 characterized by a higher mud content in late summer compared to late winter (permanova: $p = 0.0051$), no
667
668 340 significant difference was observed between the three sediment types. For all grain-size parameters, the control
669
670 341 sediments showed no significant changes between late winter and late summer (permanova: $p(\text{principal mode}) =$
671
672 342 0.23 , $p(S_0) = 0.60$, $p(\text{mud}) = 0.37$ and $p(\text{sand}) = 0.42$). The pattern was similar for the engineered sediments
673
674 343 (permanova: $p(\text{principal mode}) = 0.059$, $p(S_0) = 0.78$, $p(\text{mud}) = 0.78$ and $p(\text{sand}) = 0.39$). The associated sediments
675
676 344 showed significant changes in their grain-size distribution between late winter and late summer. In late winter,
677
678 345 they were much more homogenous than in late summer (Table 1) and they became significantly muddier between
679
680 346 the two sampling campaigns (permanova: $p = 0.0051$) leading to a significant decrease in the principal mode
681
682 347 (permanova = 0.025).

680 348 The comparison of sedimentary parameters revealed a strong engineering effect at both periods regarding
681
682 349 TOM, Chl *a* and Sol (Table 1b, $p < 0.005$). In both seasons, TOM was consistently twice as high in the engineered
683
684 350 environment than in the control zone. Organic matter content also showed a significant decrease between late
685
686 351 winter and late summer in the reef zone (permanova: $p = 0.029$) and no significant temporal change in the control
687
688 352 sediments (permanova: $p = 0.29$). Similarly, Chl *a* concentration was ten times higher in the soft sediments adjacent
689
690 353 to the engineered structures than in the control and did not display any significant temporal changes in either the
691
692 354 control (permanova: $p = 0.29$) or the associated sediments (permanova: $p = 0.72$). Sol concentration was also
693
694 355 consistently four times higher in the reef environment than in the control and displayed a temporal stability similar
695
696 356 to the Chl *a* (permanova: $p(\text{control}) = 0.87$ and $p(\text{associated}) = 0.82$). In late winter, the Pheo concentration was
697
698 357 significantly higher in the control than in the associated sediments while in late summer, there was no significant
699
700 358 difference. In both sediment types, Pheo concentrations did not show significant changes between the two sampling
701
702 359 campaigns (permanova: $p(\text{control}) = 0.10$ and $p(\text{associated}) = 0.11$). Finally, Ins/Sol was not significantly different
703
704 360 between associated and control sediments in late winter and late summer, and was significantly higher in late
705
706 361 winter compared to late summer for the control sediments (permanova: $p = 0.0001$). This temporal pattern was not

709
710
711 362 detected in the associated sediments (permanova: $p = 0.28$) probably because of the important variability in late
712
713 363 winter (Table 1).

715 364 **3.2. Biological engineering effect**

717 365 In late winter, 9244 organisms belonging to 121 different taxa were sampled in the cores and 8478
718
719 366 organisms belonging to 26 different taxa were sampled with the quadrats (see the Appendix for a complete list of
720
721 367 species). Comparatively, in late summer more organisms and taxa were sampled with the cores (23463
722
723 368 organisms/125 taxa) while fewer organisms and more taxa were sampled with the quadrats (4677 organisms/30
724
725 369 taxa). For all sediment types, total species richness was consistently higher in late summer than in late winter but
726
727 370 this difference was significant only for the control and engineered sediments (permanova: $p(\text{control}) = 0.039$,
728
729 371 $p(\text{associated}) = 0.071$ and $p(\text{engineered}) = 0.0001$).

730 372 PCOs and one-way permanovas performed on density matrices indicated that the three sediment types
731
732 373 significantly differed ($p < 0.05$) in their associated fauna at both sampling periods, confirming our *a priori* sediment
733
734 374 type grouping (Fig. 2 and Fig. 3). PCO axis 1 explained in late winter and late summer, respectively 26.1 and
735
736 375 30.3% of the total variation present in the resemblance matrix and clearly separated the engineered samples from
737
738 376 the control samples. PCO axis 2 explained in late winter and late summer, respectively 14.6 and 14.8% of the total
739
740 377 variation and discriminated the engineered and control samples from the associated samples. In both seasons,
741
742 378 engineered samples were highly clustered compared to the more scattered associated and control sediments
743
744 379 samples. In late winter, the control and associated sediments were well separated while there was a small overlap
745
746 380 between the associated and engineered sediments (Fig. 2). In late summer, there was an overlap between the
747
748 381 associated and control sediments (Fig. 3). This overlap was mostly due to bivalves like *Limecola balthica* or
749
750 382 *Cerastoderma edule* and to the polychaete *Nephtys hombergii* (Fig. 3 and Appendix). Finally, engineered
751
752 383 sediments were characterized by a much greater number of species correlated at more than 60% with each PCO
753
754 384 axis (11 in late winter and 17 in late summer) than the associated (3 in late winter and 1 in late summer) and the
755
756 385 control sediments (3 in late winter and 6 in late summer).

757 386 Mean macrofauna diversity indices and densities were calculated within each sediment type and for each
758
759 387 sampling campaign (Table 2a and b). At the sediment type scale, one-way permanovas showed significant
760
761 388 differences between engineered sediments on the one hand and associated and control sediments on the other, for
762
763 389 all the diversity measurements and densities at both periods. There were two exceptions regarding N1 and N2
764
765 390 calculated in late summer with *S. alveolata* taken into account. In these cases, there were no significant differences
766
767 391 between the three sediment types. When *S. alveolata* was taken into account, total macrofauna density was 20

768
769
770 392 times higher in the engineered sediments at both periods. This difference was maintained even after *S. alveolata*
771
772 393 was removed from the data set but it was reduced to an average 5-fold difference. The engineered sediment was
773
774 394 also home to significantly more species (mean species richness N0) than the associated and control sediments and
775
776 395 this, whatever the situation.

777 396 Regarding macrofauna density, N1 and N2, associated and control sediments presented similar temporal
778
779 397 patterns when comparing late winter and late summer. Their respective macrofauna density increased significantly
780
781 398 between the two campaigns (permanova: $p(\text{control}) = 0.023$ and $p(\text{associated}) = 0.018$) while N1 and N2 showed
782
783 399 non-significant differences (permanova: $p(\text{control-N1}) = 0.15$, $p(\text{control-N2}) = 0.25$, $p(\text{associated-N1}) = 0.83$ and
784
785 400 $p(\text{associated-N2}) = 0.53$). Between late winter and late summer, the engineered sediments presented a significant
786
787 401 increase in the total macrofauna density (permanova: $p(\text{density with } S. \text{ alveolata}) = 0.0001$) only driven by a
788
789 402 significant increase in the associated fauna density (permanova: $p(\text{density without } S. \text{ alveolata}) = 0.0001$ and $p(S.$
790
791 403 *alveolata* density) = 0.54). They also showed a significant increase in the case of N1 and N2 calculated with *S.*
792
793 404 *alveolata* (permanova: $p(N1) = 0.0007$ and $p(N2) = 0.0001$), a change which was not significant once the engineer
794
795 405 species was removed (permanova: $p(N1) = 0.089$ and $p(N2) = 0.73$).

796 406 **3.3. Linking environmental and biological engineering effects**

797 407 DistLM and dbRDA analysis were performed in late winter (Fig. 4a) and late summer (Fig. 4b) with *S.*
798
799 408 *alveolata* biomass considered as an environmental parameter. In both seasons, *S. alveolata* biomass was the
800
801 409 parameter which best explained the relationship between environmental parameters and macrofauna assemblages
802
803 410 (18.0% in late winter and 24.8% in late summer). In late winter, the most parsimonious model, explaining 33.6%
804
805 411 of the total variation in species assemblages, was defined by (1) *Sabellaria* biomass (square-root transformed,
806
807 412 18.0%), (2) principal mode (log transformed, 13.2%) and (3) total organic matter content (fourth-root transformed,
808
809 413 10.7%, Fig. 4). The first two axes explained 91.6% of the fitted variation and 30.7% of the total variation. Species
810
811 414 assemblage were structured according to two gradients. The first was driven by *S. alveolata*, and separated
812
813 415 engineered sediments from the two other types. The second was driven by the sediment principal mode and the
814
815 416 total organic matter content and separated the associated from the control sediments (Fig. 4a). In late summer, the
816
817 417 most parsimonious model explained 40.7% of the total variation in species assemblages. It was defined by the
818
819 418 same first two variables as for late winter: *Sabellaria* biomass (square-root transformed, 24.8%) and principal
820
821 419 mode (log transformed, 16.9%). The third selected variable differed from late winter since it was the mud content
822
823 420 (fourth-root transformed) and it explained only a very small part of the total variation (0.079%). The first two axes
824
825 421 explained 87.5% of the fitted variation and 35.6% of the total variation. Again, species assemblages were

827
828
829 422 structured according to two gradients but they did not separate the different sediment types as clearly as in late
830
831 423 winter. *S. alveolata* still defined the first gradient and clearly separated the engineered sediments from the two soft
832
833 424 sediments. The opposition between the principal mode and the mud content defined the second gradient. Along
834
835 425 this gradient, the distinction associated/control sediments was not well defined. Indeed, there were three associated
836
837 426 sediment samples characterized by high mud contents and isolated from the rest of the associated sediment samples
838
839 427 (Fig. 4b).

840 428 **3.4. Disturbances and biological engineering effect**

842 429 Consistent mean values in late winter (10%) and late summer (9.59%), confirm the choice of the mud
843
844 430 content as a suitable 'disturbance parameter' (Table 1a). Indeed, these values did not significantly vary between
845
846 431 the two contrasted seasons we sampled (permanova: $p = 0.78$). In contrast, the mean *S. alveolata* density almost
847
848 432 doubled between late winter ($7682 \pm 3312 \text{ ind.m}^{-2}$) and late summer ($12844 \pm 14262 \text{ ind. m}^{-2}$), with a very high
849
850 433 summer variability, leading to no significant change (permanova: $p = 0.54$). Oppositely, the mean *S. alveolata*
851
852 434 biomass by surface unit significantly decreased between late winter ($646 \pm 317 \text{ g. m}^{-2}$) and late summer ($318 \pm$
853
854 435 211 g. m^{-2}) (permanova: $p = 0.0001$).

855 436 Mantel tests performed between the mud content distance matrix and the different beta diversity matrices
856
857 437 showed a clear temporal difference between late winter and late summer. The tests were not significant when
858
859 438 performed using the late winter data sets ($p > 0.05$, Table 3), while they revealed a significant and positive
860
861 439 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}
862
863 440 ($p < 0.001$, $r = 0.38$) and $d_{\text{BC-gra}}$ ($p < 0.001$, $r = 0.29$) (Table 3) using the late summer data sets. These results
864
865 441 indicate that in late winter, an increase in mud content, used as a proxy for disturbance, does not lead to beta
866
867 442 diversity changes but in late summer, it leads to (1) an increase in beta diversity driven by a species replacement
868
869 443 and (2) an increase in abundance based dissimilarity driven by an abundance gradient. Ordination plots of
870
871 444 similarities (nMDS) of macrofaunal assemblages based on β_{sor} , β_{sim} , β_{nes} , d_{BC} , $d_{\text{BC-bal}}$ and $d_{\text{BC-gra}}$ indices were
872
873 445 performed in late winter and late summer (Fig. 5 and 6). In late winter, the correlation between the mud content
874
875 446 and the different nMDS plots was significant for β_{sor} ($p = 0.008$), β_{nes} ($p = 0.023$), d_{BC} ($p = 0.019$) and $d_{\text{BC-gra}}$ ($p =$
876
877 447 0.027). The mud content explained 30.67% of the ordination based on β_{sor} and 24.54% of the ordination based on
878
879 448 β_{nes} . Similarly, 26.93% and 24.51% of the ordination based on d_{BC} and $d_{\text{BC-gra}}$ respectively were explained by the
880
881 449 mud content. In late summer, the correlation between the mud content and the different nMDS plots was significant
882
883 450 and much higher for all the indices; β_{sor} ($p = 0.001$), β_{nes} ($p = 0.036$), β_{sim} ($p = 0.001$), d_{BC} ($p = 0.001$), $d_{\text{BC-gra}}$ ($p =$
884
885 451 0.002) and $d_{\text{BC-bal}}$ ($p = 0.006$). Indeed, the mud content explained over 50% of the ordination based on β_{sor} ($r^2 =$

886
887
888 452 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-gra} ($r^2 = 41.33\%$),
889
890 453 and between 20 and 30% of β_{nes} ($r^2 = 21.25\%$) and d_{BC-bal} ($r^2 = 29.56\%$). When the correlation was significant, the
891
892 454 fitted mud contents were plotted on the corresponding nMDS plots (Fig. 5 and 6). The correlation between the
893
894 455 disturbance proxy and the different nMDS plots showed a pattern similar to the one revealed by the late summer
895
896 456 Mantel test, with beta diversity changes mainly driven by a species turnover and an abundance gradient.

897 457 898 458 **4. Discussion**

899 459 **4.1. Engineered structures cause grain-size distribution changes**

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901
902 460 Environmental engineering effects are composed of two types of changes, structural and abiotic changes,
903
904 461 structural changes being caused by ecosystem engineers and inducing abiotic changes (Jones et al., 2010). *S.*
905
906 462 *alveolata* is capable of biologically modifying soft sediments by selectively gluing together bioclastic sand
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908 463 particles, in order to build its tube (Fournier et al., 2010). This leads to the transformation of an initial soft sediment
909
910 464 into a three-dimensional hard substratum with a long lasting resistance to physical loading via the secreted organic
911
912 465 cement (Le Cam et al., 2011). *Sabellaria alveolata* can therefore be considered as a “structural engineer” according
913
914 466 to Berke (2010). Structural changes caused by physical ecosystem engineers result in a variation in the distribution
915
916 467 of fluid and solid material termed abiotic changes (Jones et al., 2010). In the case of *S. alveolata*, a direct abiotic
917
918 468 engineering effect observable through the engineered sediments and an indirect one, observable through the
919
920 469 associated sediments, were detected. Engineered and associated sediments presented, at both sampling periods, a
921
922 470 coarser texture than the control sediments, confirming the impact Sabellariidae polychaetes have on the local
923
924 471 sediment’s texture by selecting sand particles of a specific size to build their tubes (*Phragmatopoma caudata* (=
925
926 472 *P. lapidosa*) (Gram, 1968; Kirtley and Tanner, 1968; Main and Nelson, 1988), *Sabellaria vulgaris* (Wells, 1970),
927
928 473 *Sabellaria nanella* (Bremec et al., 2013)). Ultimately, these bioconstructing Sabellariidae species create reefs
929
930 474 characterized by a grain-size distribution different from the local soft sediments. The case of the associated
931
932 475 sediments raises the question of the definition of a reef habitat. In Europe, “reefs” are recognized as a marine
933
934 476 habitat to be protected and are listed under Annex I of the EC Habitats Directive (Council Directive EEC/92/43
935
936 477 on the Conservation of Natural Habitats and of Wild Fauna and Flora) under the designation of Special Areas of
937
938 478 Conservation (SACs). They are defined as “submarine or exposed at low tide, rocky substrates and biogenic
939
940 479 concretions”. In the light of our findings, we can very well consider the engineered and the associated sediments
941
942 480 as the same sediment but under two different forms, a consolidated (engineered sediments) and an unconsolidated

945
946
947 481 form (associated sediments). Hence, we propose to widen the definition of a “reef” to include the non-engineered
948
949 482 sediments under its direct influence.

950
951 483 The main difference between the engineered and associated sediments concerns their mud content. At
952
953 484 both seasons, the engineered sediments have a mean mud content around 10 %, as previously observed by Le Cam
954
955 485 et al. (2011). *Sabellaria wilsoni* veneers have also been reported to present consistent silt and clay contents across
956
957 486 two contrasting seasons (rainy and dry seasons in Ataide et al., 2014) indicating that Sabellariidae polychaetes
958
959 487 build new habitats presenting stable sedimentary conditions. The mud present in the engineered sediments is
960
961 488 located in small cracks and crevices protected from the main hydrodynamic processes (*i.e.* winter storms, tidal
962
963 489 currents and swell). Conversely, the associated sediments are characterized by a steep and significant increase in
964
965 490 mud content between winter (2 %) and summer (21 %). As shown by Caline et al. (1988) for the Sainte-Anne reef
966
967 491 (MSMB), localized mud depositions are linked to hydrodynamic and associated hydro-sedimentary processes
968
969 492 induced by the presence of the reef itself and of the mussel farms (bouchots) in front of the reef (McKindsey et al.,
970
971 493 2011). These mud depositions are observed behind reef structures important enough to act as physical barriers
972
973 494 (Caline et al., 1988), where they are generally superficial and consequently easily eroded by strong wave action,
974
975 495 limiting their presence in winter.

974 496 **4.2. Engineered structures enhance benthic primary production and potentially microbial activity**

976 497 As reported by Jones et al. (2010), abiotic changes induced by physical engineering activity can
977
978 498 themselves cause biotic changes. Our results clearly show that at both seasons, associated sediments have a higher
979
980 499 organic matter content compared with the control sediments. At both seasons, high levels of organic matter were
981
982 500 associated with high chlorophyll *a* concentrations, indicating that part of the organic matter present in the
983
984 501 associated sediments is the consequence of MPB development. The high benthic primary production promoted by
985
986 502 the Sainte-Anne reef, compared to a generally lower benthic production in the MSMB as measured by Davoult et
987
988 503 al. (2008) and Migné et al. (2009), confirms its important biotic engineering effect. Similar results were found for
989
990 504 the invading intertidal reef-forming polychaete *Ficopomatus enigmaticus* (Bruschetti et al., 2011), for shallow
991
992 505 oyster reefs (*Crassostrea virginica*, Newell et al., 2002) and for intertidal mussel beds (Engel et al., 2017). According
993
994 506 to Berke (2010), “structural engineers operate through similar processes and have similar types of effects”.
995
996 507 Consequently, the creation of benthic primary production hotspots by reef-building structural engineers could be
997
998 508 a general property of these marine species. Nonetheless, this phenomenon was observed at the scale of the largest
999
1000 509 and probably oldest *S. alveolata* reef in Europe (Audouin and Milne-Edwards, 1832) and the study by Engel et al.
1001
1002 510 (2017) highlighted the importance of the size and age of the bioconstruction in promoting local benthic microalgae.
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1004
1005
1006 511 Hence, further studies are needed to confirm the general role of *S. alveolata* reefs as “biological power stations”
1007
1008 512 (Engel et al., 2017).

1009
1010 513 Furthermore, the high chlorophyll *a* concentrations measured in late winter and late summer indicate that
1011
1012 514 *S. alveolata* reefs promote an important benthic primary production all year round, that could be a relevant food
1013
1014 515 source for deposit- (Kanaya et al., 2008) and suspension-feeders (Lefebvre et al., 2009) through resuspension
1015
1016 516 processes (Hylleberg, 1975; Ubertini et al., 2015). In the associated sediments, MPB often grows on small
1017
1018 517 accumulations of pure mud and is consequently easily eroded and available to consumers. Such benthic primary
1019
1020 518 production may have a trophic importance during the winter months (Lefebvre et al., 2009), when the
1021
1022 519 phytoplankton production is typically low (Arbach Leloup et al., 2008; Cugier et al., 2010). Filter feeding mollusks
1023
1024 520 are known to stimulate MPB growth (Engel et al., 2017; Newell et al., 2002) via inorganic nutrient release (*i.e.*
1025
1026 521 carbon, nitrogen and phosphorus (van Broekhoven et al., 2014)) and bacterial remineralization of their biodeposits
1027
1028 522 (van Broekhoven et al., 2015). Similarly, *S. alveolata* produces large amounts of feces and pseudofeces visible on
1029
1030 523 the sediment (Dubois et al., 2005), that could favor MPB growth. Primary production could also be enhanced by
1031
1032 524 the presence of other suspension-feeders living in the engineered sediments, such as *Magallana gigas*, which can
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1034 525 reach densities of 100 ind.m⁻² as measured in the disturbed engineered sediments using the quadrats. As already
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1036 526 observed in *Ficopomatus enigmaticus* reefs (Bruschetti et al., 2011), *S. alveolata* reefs probably increase the
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1038 527 benthic-pelagic coupling by linking pelagic organic matter to the benthic compartment via their suspension-feeding
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1040 528 activity and biodeposition.

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1042 529 In late winter and late summer, associated sediments had consistently higher soluble carbohydrate
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1044 530 concentrations than the control sediments. Carbohydrates are the components of the mucus coating the pseudofeces
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1046 531 produced by *S. alveolata* and other suspension-feeders (van Broekhoven et al., 2015). Hence, when these
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1048 532 pseudofeces are deposited on the associated sediments, it could increase their concentration in soluble
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1050 533 carbohydrates. Soluble carbohydrates also compose the extracellular polymeric substances produced by benthic
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1052 534 diatoms (Bellinger et al., 2009) and are an important source of organic carbon, rapidly consumed by heterotrophic
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1054 535 microorganisms present in the sediment (Bhaskar and Bhosle, 2005; Goto et al., 2001). Consequently, *S. alveolata*
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1056 536 presence could support all year round an important bacterial activity through the soluble carbohydrates excreted
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1058 537 by the diatoms and present in the mucus coating the biodeposits. This organic carbon can either be used by the
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1060 538 bacteria for their growth (bacterial biomass production) or be remineralized (bacterial respiration) as showed by
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1062 539 Hubas et al. (2006). In the first case, the bacteria can be a source of food for infaunal organisms such as nematodes
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1064 540 and become an important trophic link in structuring energy fluxes in the community (Pascal et al., 2009, 2008). In

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1065 541 the second case, the bacteria release inorganic nutrients such as carbon (Jiao et al., 2010), which can then be used
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1067 542 by photoautotrophs present in the sediment (e.g. diatoms) or in the water column (e.g. phytoplankton) further
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1069 543 maintaining the local primary production.

1070 544 Furthermore, according to Delmas (1983), an insoluble/soluble carbohydrate ratio (Ins/Sol) ranging
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1072 545 between 6 and 8 indicates a low degradation rate of the organic matter, while a ratio varying between 10 and 30
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1074 546 reflects a high degradation rate. Delmas (1983) also suggests using the Ins/Sol ratio as a proxy for the C/N ratio.
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1076 547 Mean Ins/Sol ratios were not significantly different between the associated and control sediments with values
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1078 548 around 8.6 in late winter, and 6.0 in late summer, indicating that *S. alveolata* does not affect the organic matter
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1080 549 degradation rate in soft sediments; it is consistently of good quality and weakly degraded. Nonetheless, in late
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1082 550 summer, the organic matter present in the control and associated sediments appears less degraded and more easily
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1084 551 incorporable in the food web than in late winter, probably in response to a higher biological activity of
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1086 552 photoautotrophs and bacterial communities (Hubas et al., 2006).

1087 553 **4.3. Engineered structures create an original macrofauna assemblage linked to the sedimentary changes**

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1089 554 In addition to promoting the local benthic production, *S. alveolata* strongly modifies the macrofauna
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1091 555 assemblages present in the engineered and associated sediments compared to the control sediments and this
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1093 556 difference is present at both sampling seasons. Consequently, *S. alveolata* engineers two original species
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1095 557 assemblages, one associated with the actual bioconstructions and the other associated with the sediments
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1097 558 surrounding these structures. In late winter and late summer, the environmental parameter primarily responsible
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1099 559 for macrofauna differences between the three sediment types is the ecosystem engineer via its biomass. Studies on
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1101 560 other ecosystem engineers have demonstrated a similar structuring effect of the engineer on the macrofauna, for
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1103 561 example via *Haploops nirae* density in subtidal mats (Rigolet et al., 2014) and *Lanice conchilega* density in
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1105 562 intertidal beds (De Smet et al., 2014). The benthic macrofauna is secondarily structured by the principal mode and
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1107 563 the organic matter content of the sediments, two environmental parameters reported to structure soft sediment
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1109 564 macrofauna communities in a large diversity of sites such as the intertidal flats of the Schelde estuary (Ysebaert
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1111 565 and Herman, 2002) and over multiple spatial scales in Portuguese transitional water systems (Veiga et al., 2016).
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1113 566 In our case, these two parameters are influenced by *S. alveolata*, indicating the importance of this engineer species
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1115 567 in structuring the local benthic macrofauna.

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1117 568 Structural diversity analyses indicate that assemblages present in the associated and control sediments are
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1119 569 similarly structured in late winter and late summer. Dominant species are mainly polychaetes (e.g. *Goniadella*
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1121 570 *bobrezkii*) and mollusks species (e.g. *Crepidula fornicata*) in the associated sediments and the mollusks *Limecola*

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1124 571 *balthica* and *Cerastoderma edule* in the control sediments, with a consortium of less abundant species.
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1126 572 Furthermore, the benthic fauna present in the associated sediments appears as a combination of species living in
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1128 573 the two other sediment types, enriched by polychaete species such as *Glycera tridactyla*, *Protodorvillea kefersteini*
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1130 574 and *Saccocirrus papillocercus*. These three polychaete species are either carnivore-scavengers or surface deposit-
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1132 575 feeders, with important movement capacities, key biological traits in organic matter rich and variable environments
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1134 576 (Rigolet et al., 2014) like the associated sediments. The overlapping observed between the control and associated
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1136 577 sediments is much more pronounced in late summer, after the recruitment period (Thorin et al., 2001) and is caused
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1138 578 by a few species (e.g. *Cerastoderma edule*, *Limecola balthica* or *Nephtys hombergii*). *Cerastoderma edule*
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1140 579 recruitment and settlement of macrozoobenthos larvae is known to be enhanced coastward of mussel beds due to
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1142 580 a decrease in hydrodynamic forces caused by these bioengineered habitats (Commito et al., 2005; Donadi et al.,
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1144 581 2014, 2013). Similarly, *S. alveolata* reefs act as natural breakwaters limiting hydrodynamic energy, which could
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1146 582 lead to an enhanced recruitment of macrobenthic species like *Cerastoderma edule* and *Limecola balthica*. This
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1148 583 phenomenon is a lot less visible in winter maybe indicating that these species do not survive the variable
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1150 584 environmental conditions characterizing the associated sediments or the winter temperatures. Indeed, locals
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1152 585 repeatedly come to the Sainte-Anne reef to dig up bivalves like cockles (*Cerastoderma edule*) and Japanese carpet
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1154 586 shells (*Ruditapes philippinarum*) enhancing small-scale spatial heterogeneity and potentially leading to changes
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1156 587 in the macrofauna of the associated sediments (Watson et al., 2017). We also recorded inside the associated
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1158 588 sediments some species generally present in the engineered sediments, like *P. cultrifera* or *G. vulgaris*. This can
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1160 589 be caused by the presence of broken reef parts in the associated sediments, because of the variable sedimentary
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1162 590 preferences of some species (e.g. *G. vulgaris*) or because of the use of the associated sediments by some species
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1164 591 to move between reef patches (e.g. *Perinereis cultrifera*).

1161 592 Species richness and associated macrofauna density were always highest in the engineered sediments than
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1163 593 in the two soft sediments, stressing *S. alveolata*'s role in enhancing local biodiversity and abundance. Our results
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1165 594 confirm previous studies on *S. alveolata* reefs (Dias and Paula, 2001; Dubois et al., 2002; Holt et al., 1998) and
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1167 595 agree with a large body of literature reporting positive effects of tubicolous polychaete species (De Smet et al.,
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1169 596 2015), reef-building polychaetes (McQuaid and Griffiths, 2014) and bivalves (Gutiérrez et al., 2003; Lejart and
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1171 597 Hily, 2011; Norling and Kautsky, 2007) on species richness and associated fauna abundances. Intertidal engineers
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1173 598 like *S. alveolata* create new complex habitats that reduce pressures such as thermal and hydric stress and increase
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1175 599 the number of primary producers (i.e. MPB and ulva), potentially extending trophic niches and overall leading to
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1177 600 a biodiversity increase (Bouma et al., 2009; Jones et al., 1997; Stachowicz, 2001). New environmental conditions

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601 created by *S. alveolata* also lead to the paradox mentioned by Bertness et al. (1999), and facilitate the colonization
602 of intertidal zones by subtidal species, like the polychaete *Spirobranchus lamarcki* or the gastropod *Crepidula*
603 *fornicata*.

604 Structural diversity indices calculated for the engineered sediments (considering *S. alveolata*) and the beta
605 diversity analysis both reveal a change between late winter and late summer in how the macrofauna is structured.
606 In late winter, N1 and N2 are both significantly lower than in the two other sediment types while in late summer,
607 macrofauna density in the engineered sediments is distributed similarly than in the associated and control
608 sediments. Consequently, during winter *S. alveolata* dominates more strongly the engineered sediments than the
609 dominant species present in the associated and control sediments, a result similar to the *Haploops nirae* habitats
610 in summer (Rigolet et al., 2014). Differently, in late summer *S. alveolata* does not affect the community structure
611 in a different way than other abundant species do in the associated (*Crepidula fornicata*, *Cirriformia tentaculata*,
612 *Mediomastus fragilis*, *Goniadella bobrezkii*) and control sediments (*Cerastoderma edule*, *Limecola balthica*,
613 *Lanice conchilega*, *Malmegrenia arenicolae* and *Nephtys* spp.). Regarding beta diversity, it significantly increases
614 along the disturbance gradient in late summer but not in late winter. These observed contrasts between the two
615 seasons can have two causes, probably acting in synergy: a low *S. alveolata* recruitment and an important
616 recruitment of associated species. This last argument was also suggested by Mateo-Ramirez et al. (2015) to explain
617 the increase in decapod abundance associated with *Posidonia oceanica* meadows, between winter-spring and
618 summer-autumn. In the MSMB, the recruitment success of *S. alveolata* is known to be strongly year-to-year
619 variable depending on the synchrony between favorable environmental conditions (tidal and meteorological
620 conditions) and main reproductive periods (Ayata et al., 2009), and 2015 seemed to be a year characterized by low
621 settlement rates (pers. obs.). A weak *S. alveolata* recruitment leads to a decrease in spatial competition between
622 the engineer and other macrofauna species favoring recruitment of associated species. Indeed, between winter and
623 summer, many other benthic species recruit in the MSMB (Thorin et al., 2001) and biogenic habitats like *Mytilus*
624 *edulis* and *Crepidula* spp. beds, are known to favor recruitment of pelagic larvae (Berke, 2010) by affecting
625 boundary-layer flow (Eckman, 1983). Consequently, a low *S. alveolata* recruitment associated with the upraised
626 position of the reef in a soft bottom environment and the absence of neighboring hard substratum, one exception
627 being the off-bottom mussel farms, lead to an important recruitment of benthic larvae to the Sainte-Anne reef. The
628 hard nature of the engineered sediments can also act as either a support for egg capsules (e.g. *Nucella lapillus*) or
629 an attractant for pelagic larvae of rocky shore species like *Gibbula umbilicalis* or *Eulalia viridis* (Kingsford et al.,
630 2002). When *S. alveolata* is excluded, N1 and N2 values are systematically higher in the engineered sediments, a

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631 pattern unaffected by season. *Sabellaria alveolata* associated macrofauna shows a structuration similar to *Lanice*
632 *conchilega* intertidal beds (De Smet et al., 2015) when compared to non-engineered sediments. De Smet et al.
633 (2015) also recorded the lack of a temporal effect on N1 and N2. Consequently, despite its strong dominance, *S.*
634 *alveolata* creates a species-rich habitat where individuals are overall equitably distributed between taxa.

635 4.4. Engineered sediment disturbance and mechanisms linked to beta diversity changes

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

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

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1301 661 Between late winter and late summer, many benthic species recruit. The recruitment of benthic species to
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1303 662 soft bottom sediments is known to be under the influence of biotic factors like organic content and food supply
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1305 663 (Snelgrove and Butman, 1994). In spring-summer, the mud present in the disturbed engineered sediments is
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1307 664 probably richer in organic matter, presenting a better quality compared to winter, as suggested by the associated
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1309 665 sediment results. Multiple facts go in this direction. First, part of the spring phytoplankton bloom is known to
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1311 666 sediment, potentially enriching the mud in fresh organic matter (Cugier et al., 2010). Second, during spring and
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1313 667 summer green algae develop on the reef (Dubois et al., 2006b) enriching the mud in fresh detritus. Finally, in
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1315 668 spring and summer *S. alveolata* and other suspension-feeders (*Magallana gigas* and *Mytilus cf. galloprovincialis*)
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1317 669 increase their metabolic rates (Gillooly et al., 2001) and consequently produce more feces and pseudofeces, which
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1319 670 could further enrich the mud in organic matter. In the end, changes in abiotic factors (topographic complexity,
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1321 671 spatial competition and presence of microdepositional environments (small gapes in the reef filled with fine
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1323 672 sediments, Snelgrove et al., 1993)) associated with changes in trophic factors (trophic competition, trophic cues
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1325 673 (green algae and MPB present on and around the tubes – pers. obs.)) probably act in synergy and cause the
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1327 674 recruitment of a richer and different assemblage of species in the disturbed reef parts compared to the undisturbed
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1329 675 ones. Indeed, our results show an increase settlement of opportunistic and deposit-feeding species, like *Capitella*
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1331 676 *capitata*, *Cirriformia tentaculata*, *Parathelepus collaris* and *Tharyx killariensis*, and of species presenting a high
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1333 677 affinity for mud (*Corophium volutator*) in the more disturbed reefs. In the same time, the release in spatial and
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1335 678 trophic competition linked to a decrease in the engineer density, favors the settlement of suspension-feeding
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1337 679 species like *Magallana gigas* and *Porcellana platycheles*. In late summer, some of these species are present in
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1339 680 very high densities like *P. platycheles* (up to 9000 ind.m⁻²), *Achelia* spp. (up to 7000 ind.m⁻²) or *Corophium*
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1341 681 *volutator* (up to 5000 ind.m⁻²), while the others are less abundant. In the end, the interplay between recruitment
1342
1343 682 and the engineered sediments dynamics seem responsible for the observed species turnover and abundance
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1345 683 increase along the disturbance gradient. In addition, other factors linked to an increasing disturbance, like a higher
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1347 684 oyster cover (*Magallana gigas*) probably also structure the associated fauna as shown by Dubois et al. (2006).
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1349 685 Indeed, oyster shells provide a suitable substratum for many sessile species and are known to enhance species
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1351 686 richness and abundance (Lejart and Hily, 2011).

1347 687 Finally, the late winter and late summer multidimensional ordinations also show that at both seasons, mud
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1349 688 rates above 10-12% induce a homogenization of the species composition, congruently with results of Balata et al.
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1351 689 (2007). They reported that in subtidal rocky reefs structured by the coralline algae *Lithophyllum* spp., the
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1353 690 sedimentation “reduced the dissimilarity between assemblages overriding the influence of inclination of the
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691 substratum on beta diversity”. The packing of samples ordinated by d_{BC} is also greater for mud contents above
692 12% indicating that high mud contents not only streamline the species composition but also their absolute
693 abundances.

694
695 **Conclusion**
696 Our results illustrate the need to protect a system in its integrity and not just parts of it. In our case, future
697 conservation plans should consider *S. alveolata* reefs and associated sediments as an ecological entity. These
698 habitats are in theory targeted by the European Union’s Habitats Directive 92/43/EEC (habitat type 1170 ‘Reef’)
699 but in practice, very few reefs are protected. In the Sainte-Anne reef, a local legislation prohibits the harvesting of
700 bivalves in the associated soft sediments (e.g. *Ruditapes philippinarum*) but not on the engineered sediments (e.g.
701 *Magallana gigas*) increasing anthropogenic disturbances to the reef. In this context, prohibiting such practices
702 until interactions between *S. alveolata* and *M. gigas*, particularly regarding benthic primary production and trophic
703 competition, are clearly elucidated, should be considered.

704 Furthermore, the biogenic habitat created by *S. alveolata* is home to an original species assemblage
705 presenting a high richness and density all year round, a case similar to many other structural engineers (Berke,
706 2010; Jones et al., 1994). These habitats are subject to numerous environmental and anthropogenic disturbances
707 leading to changes in their physical structuration and complexity. In the MSMB, these changes are associated with
708 the establishment of mud inside the engineered sediments, the increase in microhabitat availability and more
709 diversified food sources. All year round, these differences act as environmental filters for post-recruits and
710 juveniles. During the summer recruitment period, these differences act as cues for settling larva, leading to an
711 enhanced recruitment inside the more disturbed reefs. In the end, during the spring-summer period, an increasing
712 disturbance leads to an increase in species richness, a change in the species present in the engineered sediments
713 (turnover) and to higher abundances (abundance gradient). This species turnover pleads for a recognition of the
714 ecological value the “degraded” *S. alveolata* reefs have, as biodiversity and recruitment promoters.

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

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721 **Acknowledgments**

722 This project was funded by an EC2CO DRIL (CNRS) grant. A. G. J. was supported by the "Laboratoire
723 d'Excellence" LabexMER (ANR-10-LABX-19) and co-funded by a grant from the French government under the
724 program "Investissements d'Avenir" and by a Région Bretagne/Ifremer PhD grant. Our funding source had no
725 involvement in the different phases of this study. We wish to thank all the people that helped us on the field
726 (François Gaudin, Patrick Le Mao, Anthony Sturbois, Daniel Gerla, Julien Chevé, Françoise Dagault, Claire
727 Rollet, René Taraud and of course Pompon) and in the lab (Ségolène Jambut, Anne Verdurmen, Célia Bellengier,
728 Julia Penot and Angelica Navarro). Daniel Delmas provided technical help for sediment analyses. We also thank
729 Thibault Androuin, Martin Marzloff and Rémi Prudhomme for their comments on an earlier draft of the manuscript
730 and Amelia Curd for the English editing.

731

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Figure captions

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1773 1054 **Fig. 1.** Schematic overview presenting the habitat modifications caused by (1) the establishment of an ecosystem
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1775 1055 engineer and (2) disturbances of the engineered sediment. Recruitment of *S. alveolata* leads to the formation of a
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1777 1056 biologically modified sediment (engineered sediment) and to a soft sediment under the influence of the engineered
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1779 1057 sediment (associated sediment). Engineered sediment then face direct (e.g. trampling, storms) and/or indirect
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1781 1058 disturbances (e.g. shellfish farming) which can lead to a gradual alteration.
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1784 1060 **Fig. 2.** PCO analysis of macrobenthos associated with the three sediment types in late winter. The analysis is based
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1786 1061 on Bray-Curtis similarities of log transformed density data. The black diamonds, the grey squares and the light
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1788 1062 grey circles represent the engineered, the associated and the control sediment samples respectively. Vectors
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1790 1063 represent species correlating more than 60% with one of the first two PCO axes. The correlations are based on
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1792 1064 Spearman coefficients. ASIM: *Achelia simplex*, CEDU: *Cerastoderma edule*, CFOR: *Crepidula fornicata*, CMAE:
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1794 1065 *Carcinus maenas*, CVOL: *Corophium volutator*, GBOB: *Goniadella bobrezkii*, GUMB: *Gibbula umbilicalis*,
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1796 1066 GVUL: *Golfingia vulgaris*, LBAL: *Limecola balthica*, LLEV: *Lekanesphaera levii*, LRUG: *Lekanesphaera*
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1798 1067 *rugicauda*, McfGAL: *Mytilus cf. galloprovincialis*, MFRA: *Mediomastus fragilis*, MGIG: *Magallana gigas*,
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1800 1068 MPAL: *Melita palmata*, NCIR: *Nephtys cirrosa*, NLAP: *Nucella lapillus*, PCUL: *Perinereis cultrifera*, PPLA:
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1802 1069 *Porcellana platycheles*.
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1804 1070
1805 1071 **Fig. 3.** PCO analysis of macrobenthos associated with the three sediment types in late summer. The analysis is
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1807 1072 based on Bray-Curtis similarities of log transformed density data. The black diamonds, the grey squares and the
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1809 1073 light grey circles represent the engineered, the associated and the control sediment samples respectively. Vectors
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1811 1074 represent species correlating more than 60% with one of the first two PCO axes. The correlations are based on
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1813 1075 Spearman coefficients. AECH: *Achelia echinata*, ALAE: *Achelia laevis*, ASIM: *Achelia simplex*, CEDU:
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1815 1076 *Cerastoderma edule*, CMAE: *Carcinus maenas*, CVOL: *Corophium volutator*, EORN: *Eulalia ornata*, GBOB:
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1817 1077 *Goniadella bobrezkii*, GMAX: *Gnathia maxillaris*, GUMB: *Gibbula umbilicalis*, GVUL: *Golfingia vulgaris*,
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1819 1078 LBAL: *Limecola balthica*, LCON: *Lanice conchilega*, LLEV: *Lekanesphaera levii*, LRUG: *Lekanesphaera*
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1821 1079 *rugicauda*, MARE: *Malmgrenia arenicolae*, McfGAL: *Mytilus cf. galloprovincialis*, MFRA: *Mediomastus*
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1823 1080 *fragilis*, MGIG: *Magallana gigas*, MPAL: *Melita palmata*, NCIR: *Nephtys cirrosa*, NEMA: *Nematoda* spp.,
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1825 1081 NEME: *Nemerte* sp., NHOM: *Nephtys hombergii*, NLAP: *Nucella lapillus*, NMIN: *Nephasoma minutum*, OCTE:
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1827 1082 *Odontosyllis ctenostoma*, PCUL: *Perinereis cultrifera*, PPLA: *Porcellana platycheles*.
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1832 1084 **Fig. 4.** dbRDA plots based on a) the late winter data set and b) the late summer data set and representing the three
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1834 1085 sediment type macrofauna composition as explained by the set of environmental parameters composing the most
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1836 1086 parsimonious explanatory model. Vectors represent the environmental parameters selected by the DistLM routine.
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1838 1087 The black diamonds, the grey squares and the light grey circles represent the engineered, the associated and the
1839 1088 control sediment samples respectively.
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1843 1090 **Fig. 5.** Late winter nMDS ordination plots of the benthic macrofauna assemblages based on a) the Sørensen total
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1845 1091 beta diversity, b) the nestedness component of the total beta diversity, c) the Bray-Curtis index of dissimilarity and
1846 1092 d) the abundance gradient component of the Bray-Curtis dissimilarity. The stress value of the nMDS is indicated
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1848 1093 on each plot. The lines indicate the different fitted mud contents obtained using the ‘ordisurf’ function.
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1852 1095 **Fig. 6.** Late summer nMDS ordination plots of the macrofauna benthic assemblages based on a) the Sørensen total
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1854 1096 beta diversity, b) the turnover component of the total beta diversity, c) the nestedness component of the total beta
1855 1097 diversity, d) the Bray-Curtis index of dissimilarity, e) the abundance gradient component of the Bray-Curtis
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1857 1098 dissimilarity and f) the balanced variation in abundances component of the Bray-Curtis dissimilarity. The stress
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1859 1099 value of the nMDS is indicated on each plot. The lines indicate the different fitted mud contents obtained using
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1861 1100 the ‘ordisurf’ function.

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1884 1112 **Figures 1, 2, 3, 4a and 4b, 5 and 6**
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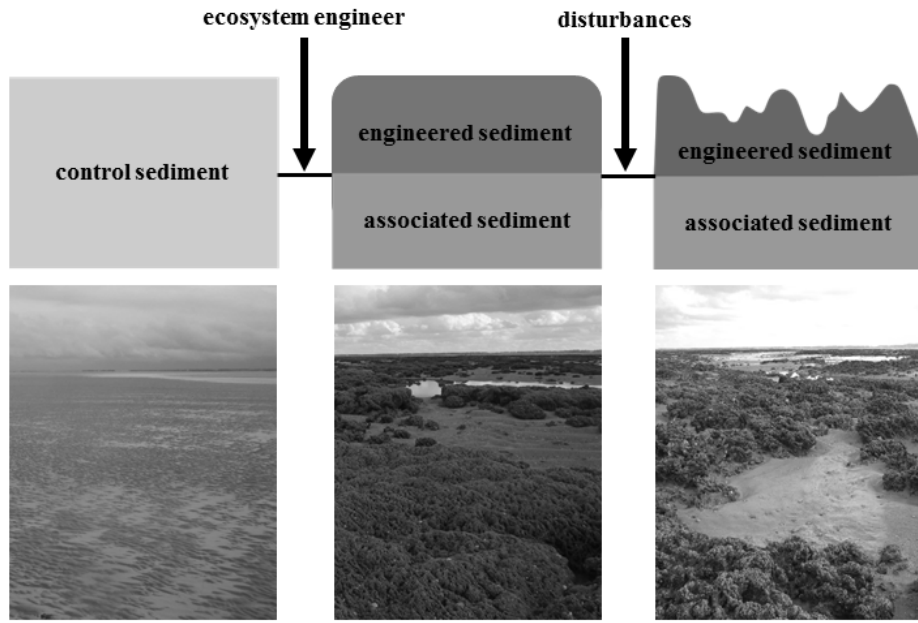
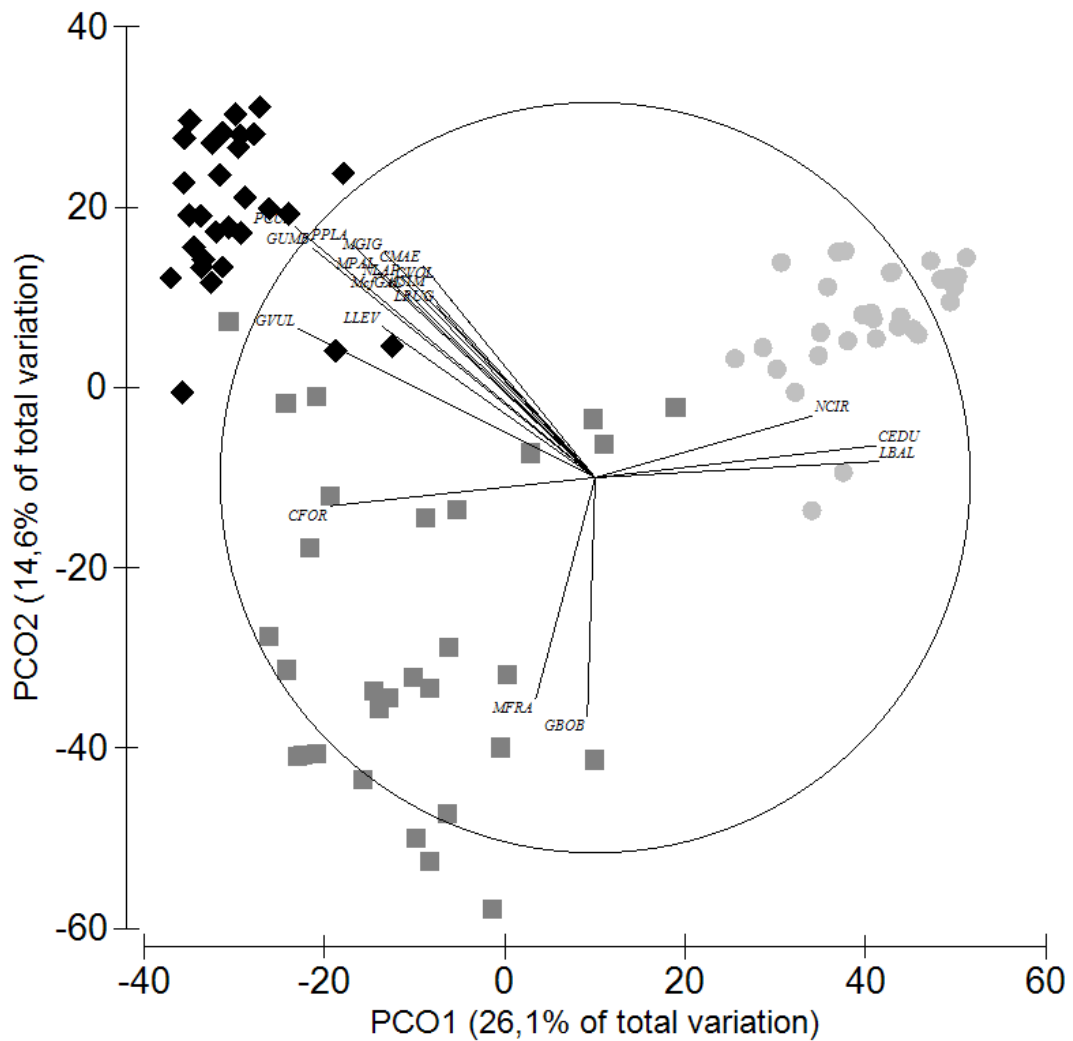


Fig. 1.



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Fig. 2.

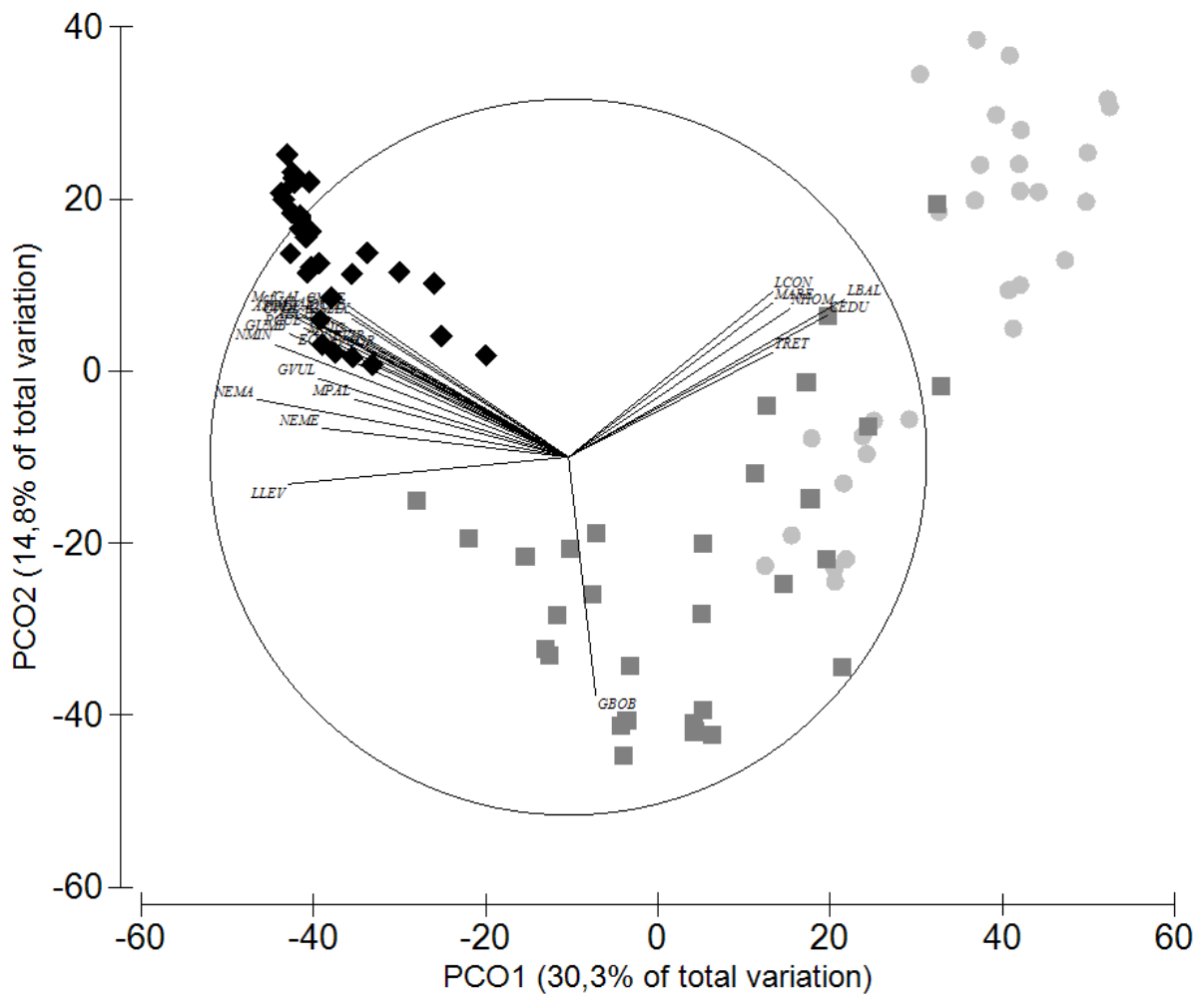
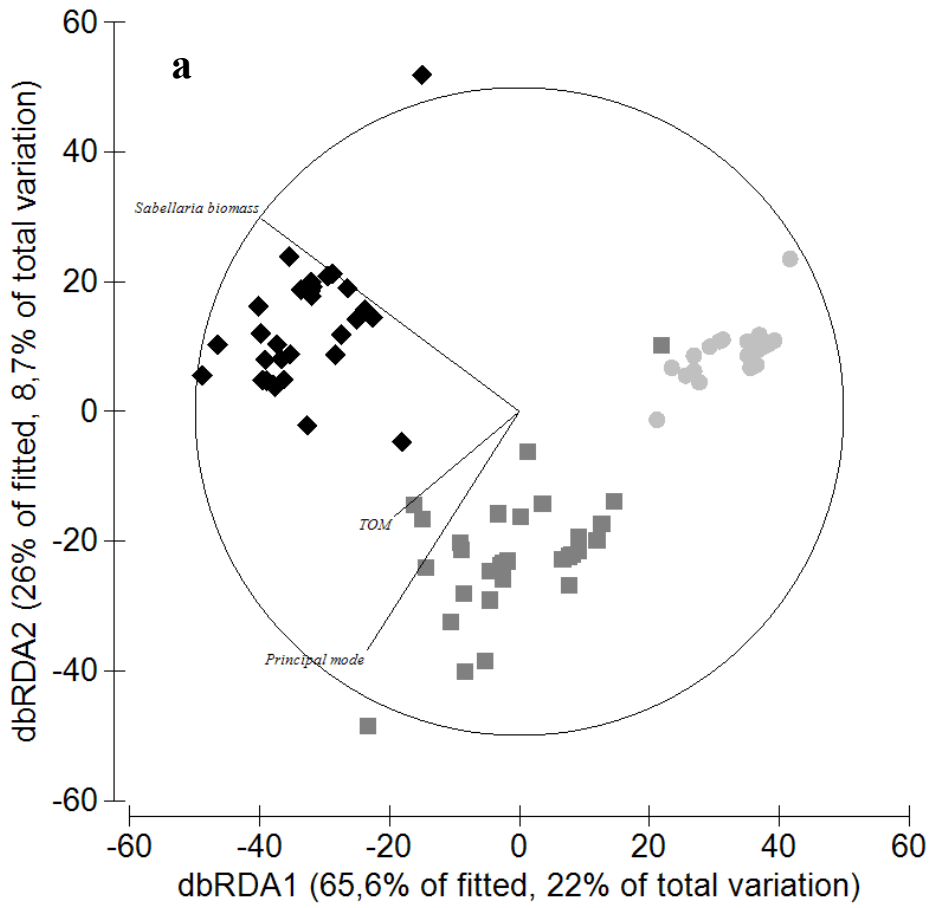
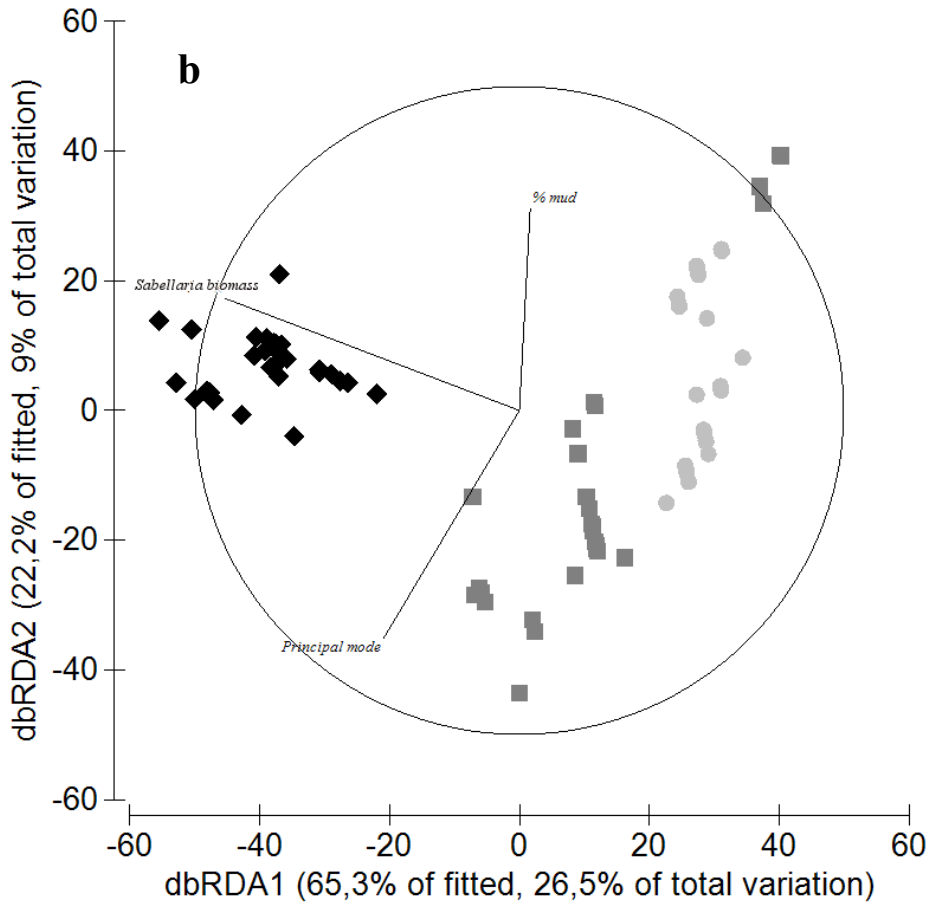


Fig. 3.

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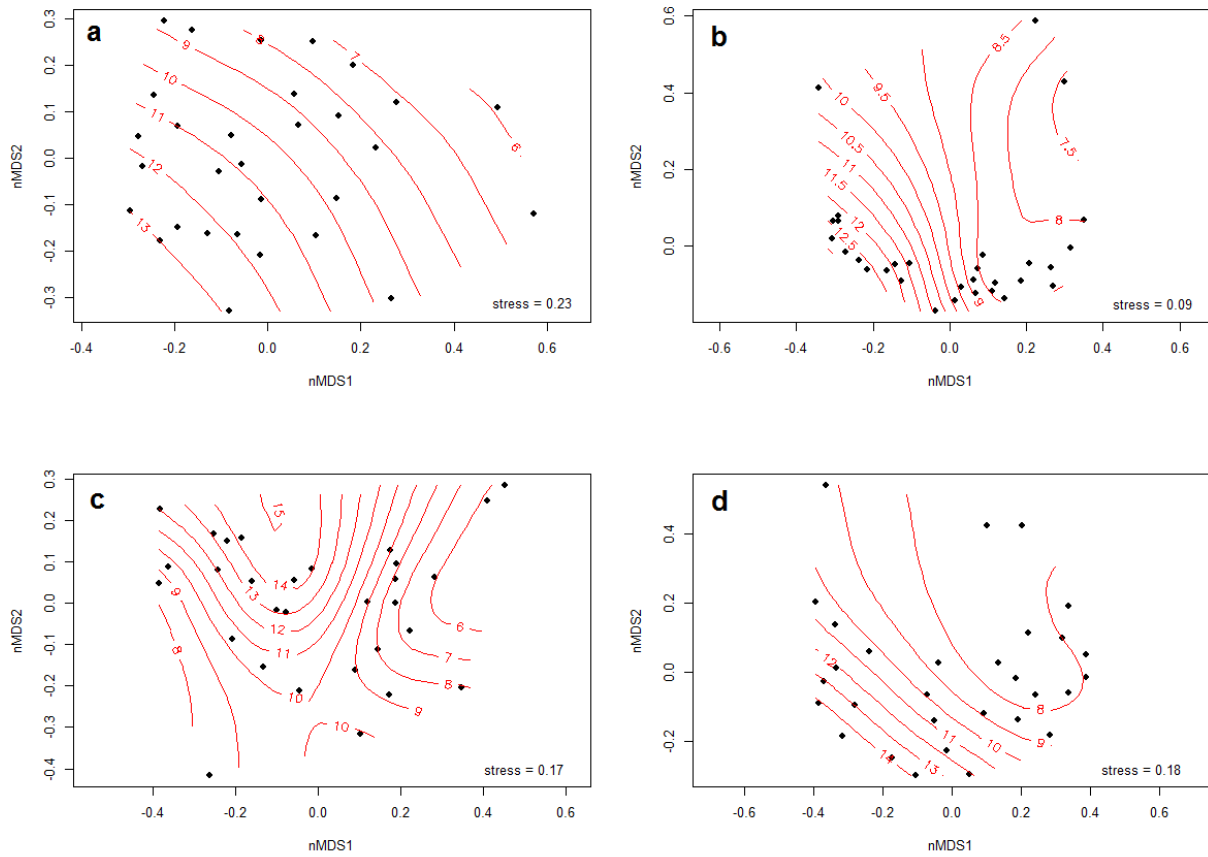
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1125 **Fig. 4a and b.**



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1127 **Fig. 5.**

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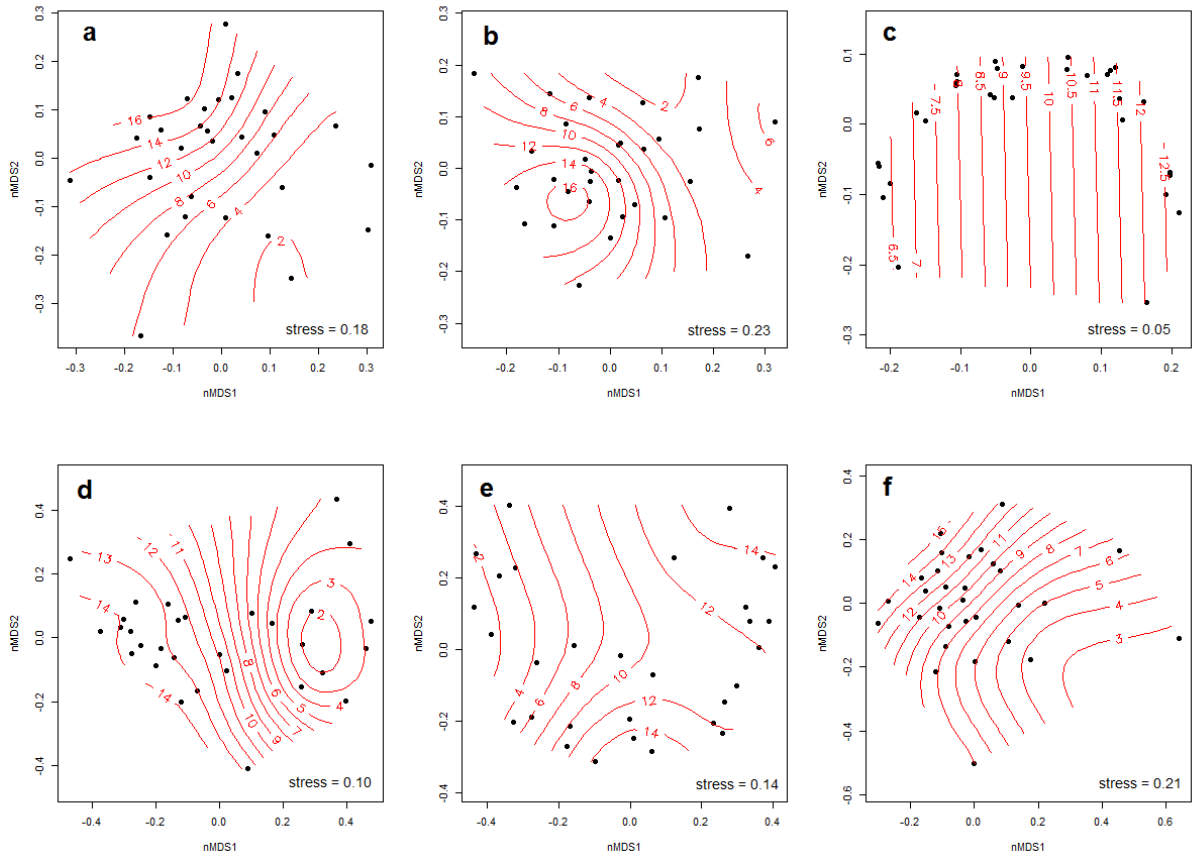


Fig. 6.

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1143 **Tables 1, 2 and 3**

1144 **Table 1** Mean values (\pm standard errors) for (a) the grain-size parameters of the three sediment types (engineered,
1145 associated and control) and (b) the environmental parameters for the associated and the control sediments.
1146 Significant differences ($p < 0.05$) of the one-way ANOVAs are in bold and for (a), *post-hoc* results are designated
1147 by superscript letters indicating homogenous groups of samples. TOM: total organic matter content, Chl *a*:
1148 chlorophyll *a* concentration, Pheo: pheopigments concentration, Sol: soluble carbohydrates concentration, Ins/Sol:
1149 ratio of the concentration of insoluble carbohydrates on soluble carbohydrates.

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

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

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1163 Table 2 Mean values (\pm standard errors) for the total macrofauna density (number of individuals.m⁻²), N0, N1 and
1164 N2 with (a) *Sabellaria* taken into account and (b) *Sabellaria* excluded, for the three sediment types (engineered,
1165 associated and control) and at both sampling periods (late winter and late summer). N0 represents the species
1166 richness, N1 the exponential of the Shannon-Winner diversity and N2 the inverse of the Simpson dominance index.
1167 Significant differences ($p < 0.05$) of the one-way ANOVAs are in bold and *post-hoc* results are designated by
1168 superscript letters indicating homogenous groups of samples.

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

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1183 Table 3 Results of the Mantel tests between (a) the different beta diversity matrices and the mud content distance
1184 matrix and (b) the different abundance-based dissimilarity matrices and the mud content distance matrix at both
1185 sampling periods (late winter and late summer). β_{sor} is the Sørensen pairwise dissimilarity and accounts for the
1186 total beta diversity, β_{sim} is the Simpson pairwise dissimilarity and accounts for the turnover component of the total
1187 beta diversity, β_{nes} is the nestedness-resultant dissimilarity and accounts for the nestedness component of the total
1188 beta diversity; $\beta_{\text{sor}} = \beta_{\text{sim}} + \beta_{\text{nes}}$. d_{BC} is the Bray-Curtis index of dissimilarity and accounts for the total abundance-
1189 based dissimilarity, $d_{\text{BC-bal}}$ is the balanced variation in abundances component of the Bray-Curtis dissimilarity and
1190 is equivalent to an abundance-based turnover, $d_{\text{BC-gra}}$ is the abundance gradient component of Bray-Curtis
1191 dissimilarity and is equivalent to an abundance-based nestedness; $d_{\text{BC}} = d_{\text{BC-bal}} + d_{\text{BC-gra}}$. Significant simulated p-
1192 values ($p < 0.05$) and associated observed correlation are in bold.

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

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1201 **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
1202 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 <i>Acromegalomma vesiculosum</i>	0.00	0.00	0.00	0.00	0.00	2.48
<i>Ampharete baltica</i>	0.00	0.00	0.00	0.00	1.24	0.00
<i>Aonides oxycephala</i>	0.00	1.24	0.00	0.00	0.00	0.00
<i>Aonides paucibranchiata</i>	0.00	0.00	0.00	0.00	6.20	0.00
<i>Armandia polyophtalma</i>	1.24	0.00	0.00	0.00	0.00	0.00
<i>Capitella capitata</i>	6.20	0.00	0.00	1.24	0.00	1.24
<i>Caulleriella alata</i>	0.00	0.00	0.00	1.24	0.00	0.00
<i>Cirriformia tentaculata</i>	0.00	35.96	0.00	0.00	42.16	4.96
<i>Dipolydora flava</i>	0.00	0.00	0.00	0.00	0.00	4.96
<i>Eteone flava</i>	0.00	0.00	0.00	1.24	0.00	0.00
<i>Eteone longa</i>	0.00	0.00	0.00	3.72	3.72	0.00
<i>Eulalia aurea</i>	0.00	0.00	3.72	0.00	0.00	0.00
<i>Eulalia clavigera</i>	0.00	0.00	9.92	0.00	0.00	1.24
<i>Eulalia ornata</i>	0.00	0.00	1.24	0.00	0.00	93.01
<i>Eulalia viridis</i>	0.00	0.00	22.32	0.00	0.00	27.28
<i>Eumida arctica</i>	0.00	0.00	0.00	0.00	0.00	1.24
<i>Eumida sanguinea</i>	12.40	1.24	16.12	14.88	0.00	47.12
<i>Eunereis longissima</i>	0.00	0.00	0.00	3.72	0.00	0.00
<i>Glycera alba</i>	3.72	4.96	2.48	13.64	13.64	1.24
<i>Glycera tridactyla</i>	0.00	1.24	0.00	0.00	1.24	0.00
<i>Goniadella bobrezkii</i>	1.24	228.17	0.00	14.88	189.73	11.16
<i>Lanice conchilega</i>	62.00	0.00	0.00	602.67	8.68	0.00
<i>Lepidonotus squamatus</i>	0.00	0.00	2.48	0.00	0.00	0.00
<i>Magelona johnstoni</i>	1.24	0.00	0.00	1.24	0.00	0.00
<i>Malacoceros fuliginosus</i>	1.24	0.00	0.00	3.72	0.00	0.00
<i>Malmgrenia arenicolae</i>	6.20	3.72	0.00	142.61	2.48	0.00

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2403							
2404	<i>Mediomastus fragilis</i>	6.20	65.72	6.20	13.64	280.26	44.64
2405	<i>Myrianida</i> sp.	0.00	2.48	0.00	0.00	0.00	0.00
2406	<i>Mysta picta</i>	1.24	0.00	0.00	0.00	0.00	0.00
2407	<i>Nephtys cirrosa</i>	59.52	0.00	0.00	54.56	8.68	0.00
2408	<i>Nephtys hombergii</i>	17.36	0.00	0.00	55.80	38.44	0.00
2409	<i>Nephtys</i> sp.	1.24	0.00	0.00	0.00	0.00	0.00
2410	<i>Notomastus latericeus</i>	16.12	2.48	1.24	48.36	2.48	48.36
2411	<i>Odontosyllis ctenostoma</i>	0.00	1.24	12.40	0.00	0.00	271.57
2412	<i>Odontosyllis gibba</i>	0.00	1.24	29.76	0.00	0.00	0.00
2413	<i>Parathelepus collaris</i>	0.00	0.00	0.00	0.00	1.24	49.60
2414	<i>Perinereis cultrifera</i>	0.00	7.44	164.93	0.00	1.24	146.33
2415	<i>Pholoe inornata</i>	0.00	0.00	1.24	1.24	0.00	7.44
2416	<i>Phyllodoce laminosa</i>	0.00	0.00	2.48	0.00	0.00	11.16
2417	<i>Phyllodoce mucosa</i>	0.00	0.00	0.00	11.16	0.00	0.00
2418	<i>Polycirrus aurantiacus</i>	0.00	3.72	0.00	0.00	0.00	0.00
2419	<i>Polycirrus</i> sp.	0.00	0.00	7.44	0.00	0.00	0.00
2420	<i>Protodorvillea kefersteini</i>	0.00	1.24	0.00	0.00	6.20	0.00
2421	<i>Pseudopolydora pulchra</i>	0.00	1.24	0.00	0.00	0.00	0.00
2422	<i>Pseudopotamilla reniformis</i>	0.00	0.00	0.00	0.00	0.00	3.72
2423	<i>Pygospio elegans</i>	4.96	0.00	0.00	0.00	0.00	6.20
2424	<i>Sabellaria alveolata</i>	0.00	47.12	7682.22	0.00	48.36	12844.62
2425	<i>Saccocirrus papillocercus</i>	0.00	1.24	0.00	0.00	13.64	0.00
2426	<i>Scalibregma celticum</i>	0.00	1.24	0.00	0.00	0.00	0.00
2427	<i>Scoelepis (Parascoelepis) tridentata</i>	1.24	0.00	0.00	0.00	0.00	0.00
2428	<i>Scoelepis (Scoelepis) cantabra</i>	0.00	0.00	0.00	0.00	2.48	0.00
2429	<i>Scoloplos (Scoloplos) armiger</i>	14.88	0.00	0.00	4.96	0.00	0.00
2430	<i>Sphaerosyllis bulbosa</i>	0.00	0.00	0.00	0.00	14.88	7.44
2431	<i>Sphaerosyllis</i> sp.	0.00	1.24	0.00	0.00	0.00	0.00
2432	<i>Spio martinensis</i>	6.20	0.00	0.00	0.00	0.00	0.00
2433	<i>Spio symphyta</i>	0.00	0.00	0.00	2.48	0.00	0.00
2434	<i>Spirobranchus lamarcki</i>	0.00	22.32	24.80	0.00	14.88	68.20
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2445	<i>Spirobranchus triqueter</i>	0.00	0.00	1.24	0.00	0.00	0.00
2446	<i>Sthenelais boa</i>	0.00	0.00	1.24	0.00	0.00	0.00
2447	<i>Syllis garciai</i>	0.00	1.24	0.00	0.00	2.48	3.72
2448	<i>Syllis gracilis</i>	0.00	0.00	2.48	0.00	1.24	11.16
2449	<i>Tharyx killariensis</i>	126.49	2.48	0.00	1.24	2.48	1.24
2450	<i>Thelepus setosus</i>	0.00	0.00	0.00	0.00	1.24	28.52
2451	<i>Websterinereis glauca</i>	0.00	0.00	0.00	1.24	1.24	0.00
2452							
2453	Crustacea <i>Anapagurus</i> sp.	0.04	0.00	0.00	0.00	0.00	0.00
2454	<i>Athanas nitescens</i>	0.00	1.24	1.24	0.00	0.00	1.24
2455	<i>Bathyporeia elegans</i>	0.00	0.00	0.00	7.44	0.00	0.00
2456	<i>Bathyporeia guilliamsoniana</i>	34.72	0.00	0.00	0.00	0.00	0.00
2457	<i>Bathyporeia nana</i>	0.00	0.00	0.00	1.24	0.00	0.00
2458	<i>Bathyporeia pelagica</i>	1.24	0.00	0.00	4.96	0.00	0.00
2459	<i>Bathyporeia pilosa</i>	0.00	0.00	0.00	2.48	0.00	0.00
2460	<i>Bodotria pulchella</i>	0.00	0.00	0.00	0.00	1.24	0.00
2461	<i>Bodotria scorpioides</i>	1.24	0.00	0.00	0.00	1.24	0.00
2462	<i>Cancer pagurus</i>	0.00	0.00	2.48	0.00	0.00	1.24
2463	<i>Carcinus maenas</i>	2.48	0.00	29.76	7.44	1.24	89.28
2464	<i>Cleantis prismatica</i>	0.00	1.24	0.00	4.96	0.00	0.00
2465	<i>Corophium arenarium</i>	3.72	0.00	18.60	0.00	0.00	29.76
2466	<i>Corophium volutator</i>	0.00	0.00	64.48	0.00	0.00	403.02
2467	<i>Crangon crangon</i>	0.08	0.00	0.00	0.00	0.00	0.00
2468	<i>Cumopsis goodsir</i>	1.24	0.00	0.00	62.00	1.24	0.00
2469	<i>Diogenes pugilator</i>	0.11	0.00	0.00	0.11	0.00	0.04
2470	<i>Eocuma dollfusi</i>	6.20	0.00	0.00	6.20	0.00	1.24
2471	<i>Erichthonius punctatus</i>	0.00	0.00	0.00	0.00	0.00	2.48
2472	<i>Eurydice pulchra</i>	0.00	0.00	0.00	2.48	0.00	0.00
2473	<i>Gammaropsis nitida</i>	0.00	0.00	4.96	0.00	0.00	2.48
2474	<i>Gnathia maxillaris</i>	0.00	0.00	9.92	0.00	0.00	90.52
2475	<i>Hemigrapsus</i> sp.	0.00	1.24	1.24	0.00	0.00	0.00
2476	<i>Jaera (Jaera) albifrons</i>	1.24	0.00	0.00	1.24	0.00	0.00
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2486		<i>Jassa ocia</i>	0.00	0.00	26.04	0.00	1.24	60.76
2487		<i>Lekanesphaera levii</i>	8.68	13.64	171.13	12.40	47.12	358.38
2488		<i>Lekanesphaera rugicauda</i>	3.72	3.72	79.36	9.92	9.92	49.60
2489		<i>Leptocheirus</i> sp.	0.00	0.00	1.24	0.00	0.00	0.00
2490		<i>Liocarcinus holsatus</i>	0.00	0.00	0.00	0.12	0.00	0.00
2492		<i>Melita palmata</i>	0.00	9.92	161.21	1.24	6.20	117.81
2493		<i>Microdeutopus</i> sp.	0.00	0.00	1.24	0.00	0.00	0.00
2494		<i>Nymphon brevirostre</i>	0.00	0.00	0.00	0.00	0.00	2.48
2495		<i>Orchomene humilis</i>	0.00	0.00	0.00	1.24	0.00	0.00
2496		<i>Phtisica marina</i>	0.00	0.00	0.00	1.24	0.00	0.00
2497		<i>Porcellana platycheles</i>	0.00	2.48	711.80	0.00	1.24	2679.79
2498		<i>Portumnus latipes</i>	1.24	0.00	0.00	0.31	0.00	0.00
2499		<i>Pseudocuma (Pseudocuma) longicorne</i>	3.72	0.00	0.00	0.00	0.00	0.00
2500		<i>Pseudomystides limbata</i>	0.00	0.00	4.96	0.00	0.00	0.00
2501		<i>Siphonoecetes (Centraloecetes) kroyeranus</i>	1.24	0.00	0.00	11.16	0.00	0.00
2502		<i>Thia scutellata</i>	0.12	0.00	0.00	0.00	0.00	0.00
2503		<i>Tryphosites longipes</i>	0.00	0.00	0.00	1.24	0.00	0.00
2504		<i>Urothoe brevicornis</i>	2.48	0.00	0.00	2.48	0.00	0.00
2505		<i>Urothoe elegans</i>	0.00	0.00	0.00	1.24	0.00	0.00
2506		<i>Urothoe poseidonis</i>	3.72	0.00	0.00	12.40	0.00	1.24
2507		<i>Urothoe pulchella</i>	23.56	0.00	0.00	24.80	0.00	0.00
2508		<i>Urothoe</i> sp.	2.48	0.00	0.00	0.00	0.00	0.00
2509								
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2511	Mollusca	<i>Abra alba</i>	0.19	0.06	0.00	1.26	0.07	0.00
2512		<i>Acanthochitona crinita</i>	0.00	0.00	4.96	0.00	0.00	0.00
2513		<i>Aeolidia papillosa</i>	0.00	0.00	1.24	0.00	0.00	0.00
2514		<i>Buccinum undatum</i>	0.00	0.00	1.24	0.00	0.00	0.00
2515		<i>Cerastoderma edule</i>	70.95	0.12	0.11	18.39	0.20	0.06
2516		<i>Crepidula fornicata</i>	0.64	25.11	26.76	0.00	15.54	7.11
2517		<i>Gibbula cineraria</i>	0.00	0.00	0.23	0.00	0.00	0.12
2518		<i>Gibbula umbilicalis</i>	0.00	0.15	26.02	0.00	0.00	39.53
2519		<i>Lacuna pallidula</i>	0.00	0.00	0.00	0.00	0.00	1.24
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2527	<i>Limecola balthica</i>	89.00	0.12	0.03	187.04	3.97	0.00
2528	<i>Littorina littorea</i>	0.00	0.00	3.16	0.00	0.00	1.40
2529	<i>Littorina saxatilis</i>	0.00	0.00	0.04	0.00	0.00	0.00
2530	<i>Macomangulus tenuis</i>	0.27	0.00	0.00	0.52	0.03	0.00
2531	<i>Magallana gigas</i>	0.00	0.00	17.60	0.00	0.12	23.31
2532	<i>Modiolula phaseolina</i>	0.00	0.00	0.00	0.00	0.00	21.08
2533	<i>Modiolus</i> sp.	0.00	0.00	0.00	0.00	0.00	14.88
2534	<i>Mytilus</i> cf. <i>galloprovincialis</i>	1.24	0.31	5.13	0.76	0.20	10.91
2535	<i>Nucella lapillus</i>	0.00	0.04	6.21	0.00	0.00	8.10
2536	<i>Ocenebra erinaceus</i>	0.00	0.03	0.52	0.00	0.08	0.25
2537	<i>Ostrea edulis</i>	0.00	0.00	0.04	0.00	0.00	0.04
2538	<i>Phorcus lineatus</i>	0.00	0.00	0.00	0.00	0.00	0.04
2539	<i>Polititapes aureus</i>	0.00	0.00	2.48	0.00	0.00	0.00
2540	<i>Polititapes rhomboides</i>	0.00	0.04	0.07	0.00	0.00	0.00
2541	<i>Ruditapes decussatus</i>	0.00	0.04	0.03	0.00	0.11	0.03
2542	<i>Ruditapes philippinarum</i>	0.24	0.39	0.25	0.28	0.99	0.10
2543	<i>Scrobicularia plana</i>	0.00	0.00	0.00	1.24	0.00	0.00
2544	<i>Spisula elliptica</i>	0.00	0.00	0.00	0.00	2.48	0.00
2545	<i>Spisula solida</i>	0.04	0.41	0.00	0.91	0.16	0.00
2546	<i>Tritia reticulata</i>	6.73	0.08	0.24	3.61	0.35	0.10
2547	<i>Venerupis corrugata</i>	0.12	0.54	0.81	0.16	0.23	1.62
2548	<i>Venus verrucosa</i>	0.00	0.00	0.00	0.00	0.04	0.00
2549							
2550	Ascidacea						
2551	<i>Microcosmus claudicans</i>	0.00	0.00	0.00	0.00	0.00	9.92
2552	<i>Molgula</i> sp.	0.00	0.00	0.00	0.00	1.24	7.44
2553	<i>Phallusia mammillata</i>	0.00	0.00	0.00	0.00	0.00	1.24
2554	<i>Polycarpa fibrosa</i>	0.00	0.00	0.00	0.00	0.00	14.88
2555	<i>Polyclinum aurantium</i>	0.00	0.00	11.16	0.00	0.00	0.00
2556	<i>Pyura microcosmus</i>	0.00	0.00	7.44	0.00	0.00	0.00
2557	<i>Styela clava</i>	0.00	0.00	7.44	0.00	0.00	16.12
2558							
2559	Anthozoa						
2560	<i>Actinia equina</i>	0.00	0.00	0.00	0.00	0.03	0.04
2561	<i>Anemona</i> sp.	0.00	0.00	0.00	0.00	0.00	1.24
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	<i>Cereus pedunculatus</i>	2.48	9.92	64.48	0.00	2.48	58.28
	<i>Urticina felina</i>	0.00	0.00	0.00	0.00	0.00	0.04
Pycnogonida	<i>Achelia echinata</i>	0.00	1.24	54.56	0.00	4.96	1311.99
	<i>Achelia laevis</i>	0.00	0.00	8.68	0.00	1.24	261.65
	<i>Achelia simplex</i>	0.00	1.24	95.49	0.00	2.48	962.29
	<i>Anoplodactylus virescens</i>	0.00	0.00	0.00	0.00	0.00	17.36
Sipuncula	<i>Golfingia (Golfingia) elongata</i>	0.00	3.72	6.20	0.00	0.00	57.04
	<i>Golfingia (Golfingia) vulgaris vulgaris</i>	0.00	24.80	192.21	0.00	8.68	130.21
	<i>Nephasoma (Nephasoma) minutum</i>	0.00	22.32	62.00	0.00	16.12	626.23
	<i>Phascolion (Phascolion) strombus strombus</i>	0.00	1.24	0.00	0.00	0.00	0.00
Echinodermata	<i>Acrocnida spatulispina</i>	1.24	0.00	0.00	1.24	0.00	0.00
	<i>Amphipholis squamata</i>	0.00	2.48	0.00	0.00	2.48	49.60
Other	<i>Nematoda</i>	1.24	6.20	9.92	1.24	102.93	2368.53
	<i>Nemertea</i>	0.00	11.16	69.44	6.20	47.12	184.77
	<i>Oligochaeta</i>	0.00	0.00	1.24	0.00	33.48	38.44
Insecta	<i>Axelsonia littoralis</i>	0.00	0.00	79.36	0.00	0.00	13.64
	<i>Hydrogamasus sp.</i>	0.00	0.00	14.88	0.00	0.00	8.68
Vertebrata	<i>Lipophrys pholis</i>	0.00	0.00	0.04	0.00	0.00	0.12

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