
Linking multiple facets of biodiversity and ecosystem functions in a coastal reef habitat

Jones Auriane ^{1,2,3,*}, Denis Lionel ⁴, Fournier Jonathan ^{5,6}, Desroy Nicolas ², Duong Gwendoline ⁴, Dubois Stanislas ¹

¹ IFREMER, Laboratoire Centre de Bretagne, DYNECO, Laboratoire d'Ecologie Benthique Côtière (LEBCO), 29280, Plouzané, France

² IFREMER, Laboratoire Environnement et Ressources Bretagne nord, BP 80108, 35801, Dinard cedex, France

³ ESE, Ecology and Ecosystem Health, AGROCAMPUS OUEST, INRA, 65 rue de Saint-Brieuc, 35042, Rennes, France

⁴ Univ. Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 62930, Wimereux, France

⁵ CNRS, UMR 7204 CESCO, 75005, Paris, France

⁶ MNHN, Station de Biologie Marine, BP 225, 29182, Concarneau cedex, France

* Corresponding author : Auriane Jones, email address : jones.ecology@gmail.com

Highlights

► We studied the functioning of a reef habitat, linking it to macrofauna diversity ► We measured oxygen and nutrient fluxes using core incubations ► The reef structures had higher fluxes than the neighboring soft sediments ► The reef-builder's biomass and temperature were the main drivers of reef fluxes ► An intermediate level of macrofauna trait diversity maximized these fluxes

Keywords : Functional diversity, Biogeochemical fluxes, Respiration, Bioturbation, Community composition, Benthos, Ecosystem engineer, *Sabellaria alveolata*, English channel

51 1. INTRODUCTION

52 Ecosystems worldwide are experiencing increasing rates of biodiversity loss mainly
53 caused by land and sea use changes, direct resource exploitation and climate change (IPBES
54 2019). This biodiversity crisis triggered in the 1990s a new line of work investigating the
55 links between biodiversity and ecosystem functioning and the mechanisms underpinning these
56 relationships, known today as BEF research (Hooper and Vitousek, 1997; Tilman, 1997).
57 Focusing first on terrestrial autotrophic ecosystems, many experimental studies found that an
58 increase in plant species richness led to an increase in ecosystem functions, such as primary
59 production and nutrient cycling (Cardinale et al., 2011; Hector et al., 1999; Naeem et al.,
60 1996). Nonetheless, species richness is not the unique driver of ecosystem functioning and
61 considering the diversity of functions performed by species (*i.e.* functional diversity) is also
62 key when studying BEF relationships (Hooper et al., 2005). For example, functional identity
63 of species and functional diversity among grassland species, rather than species diversity per
64 se, together promote primary production and decomposition (Mouillot et al., 2011). More
65 generally, ecosystem functioning can be promoted by a higher diversity of species and their
66 functional traits through mechanisms like resource partitioning and niche complementarity, as
67 stated by the diversity hypothesis (Tilman, 1997). Among species assemblages, dominant
68 species and their traits can also promote an ecosystem's functioning through a selection effect
69 linked to competitive differences (Cadotte, 2017), as stated by the mass ratio hypothesis
70 (Grime, 1998).

71 In aquatic ecosystems, sediments and microorganisms are key in regulating
72 biogeochemical functions like organic matter remineralization and nutrient cycling (Jones et
73 al., 1985). Larger benthic fauna able to rework sediments (bioturbation) and/or to transfer
74 solutes (bioirrigation) also influence strongly these functions (Kristensen, 1988; Stief, 2013).
75 High densities of sediment-reworking species (*e.g.* fiddler crabs *Uca* spp. in Kristensen

76 (2008)) modify the sediment resource through various biological activities like feeding,
77 burrowing or ventilation and can be considered as allogenic ecosystem engineers (Jones et al.,
78 1994). Conversely, autogenic ecosystem engineers like mangrove trees or salt marsh plants
79 “change the environment via their own physical structures”, often creating new habitats
80 (Jones et al., 1997, 1994). Many different organisms engineer marine habitats, from mollusks
81 (*e.g. Crassostrea virginica*) and polychaetes (*e.g. Phragmatopoma caudata*) to cnidarians
82 (*e.g. scleractinian corals*) and plants (*e.g. Zostera marina*) (Goldberg, 2013). These engineers
83 often have a positive effect on local species richness through the reduction of abiotic and
84 biotic pressures like thermal stress and predation (Romero et al., 2015; Stachowicz, 2001) and
85 could also promote, through their density, the functioning of the engineered ecosystem, a
86 potential role called the engineer effect.

87 Classically, BEF studies in aquatic ecosystems focused on soft sediments, considering
88 biogeochemical fluxes as the response variable while controlling for macrofauna species
89 richness and/or functional group richness. Such studies generally reported positive BEF
90 relationships, while stressing the role of the species’ functional identity and density (Covich et
91 al., 2004; Gamfeldt et al., 2015). In such controlled experiments, interspecific interactions like
92 resource use complementarity are limited by the manipulation of low diversity levels that
93 represent only a fraction of the local species pool (Brose and Hillebrand, 2016; Thrush and
94 Lohrer, 2012). Conversely, observational *in situ* studies can consider natural multi-trophic
95 communities along environmental gradients (Godbold and Solan, 2009) helping for example,
96 to tease apart the effects of abiotic and biotic factors on ecosystem processes (Brose and
97 Hillebrand, 2016). More generally, new hypothesis and “a more integrated empirical approach
98 to BEF research” can stem from observational studies (Thrush and Lohrer, 2012).

99 We aimed at bringing new insights on BEF relationships drawn from observations of a
100 temperate reef ecosystem built by a primary consumer, the honeycomb-worm *Sabellaria*

101 *alveolata*. Despite their ubiquity and the many ecosystem services they provide (IPBES,
102 2019; Romero et al., 2015), bivalve and polychaete reefs are rarely investigated in the context
103 of BEF research. Studies measuring functions like respiration or calcification, mainly focus
104 on the engineer species, overlooking the role the associated organisms could have in
105 regulating these functions (Kellogg et al., 2013; Lejart et al., 2012; Newell et al., 2002; Smyth
106 et al., 2016). Natural diversity gradients often occur in ecosystems dominated by an engineer
107 species (*e.g.* mussels, oysters, tubicolous worms), giving us the opportunity to investigate
108 how this particular species and the associated fauna influence functions like biogeochemical
109 fluxes (Bouma et al., 2009; Jones et al., 2018; Norling and Kautsky, 2007).

110 *Sabellaria alveolata* is an intertidal ecosystem engineer distributed along the European
111 Atlantic coast from Scotland to Morocco (Muir et al., 2016). Once settled on the seabed, this
112 polychaete builds a tube using mostly bioclastic particles (Le Cam et al., 2011). When
113 environmental conditions are favorable, *S. alveolata* can form bioconstructions on rocky
114 shores or on soft sediments (Dubois et al., 2002; Gruet, 1972; Holt et al., 1998), where a
115 diverse and abundant fauna establishes (Dias and Paula, 2001; Jones et al., 2018; Porta and
116 Nicoletti, 2009). These habitats undergo natural cycles of growth (progradation) and decline
117 (retrogradation) (Curd et al. 2019) forced by abiotic factors like particle availability (Le Cam
118 et al., 2011) and hydrodynamic forces (Gruet, 1986) and by biotic factors like recruitment
119 strength (Ayata et al., 2009; Dubois et al., 2007a) and interspecific competition (Dubois et al.,
120 2007b). These cycles are mostly characterized by modifications of the reef's physical
121 structure (Curd et al., 2019) and by changes in the associated fauna in terms of richness,
122 abundance and composition (Dubois et al., 2002). Anthropogenic disturbances like trampling
123 and coastal modifications can also modify the reef's structure and the associated fauna
124 (Desroy et al., 2011; Dubois et al., 2006; Jones et al., 2018; Plicanti et al., 2016).

125 In this study, we investigated the biogeochemical functioning of a reef habitat engineered
126 by *S. alveolata* and evaluated the relative support of the engineer effect hypothesis, the
127 diversity hypothesis, and the mass-ratio hypothesis on driving key benthic processes taking
128 place in the sediments glued into bioconstructions by the tube-building activity of *S. alveolata*
129 (*i.e.* engineered sediments). First, we measured and compared the sediment-water fluxes (*i.e.*
130 oxygen, ammonium, nitrate, and nitrite) in the engineered sediments and in the surrounding
131 soft sediments. Then, using a multiple linear regression approach (model selection and effect
132 size calculation), we investigated the relative importance of the engineer itself (engineer effect
133 hypothesis) and of the macrofauna associated to the engineered sediments, in terms of
134 taxonomic or functional diversity (diversity hypothesis) and in terms of biological trait
135 dominance (mass-ratio hypothesis) on the different biogeochemical fluxes.

136

137 2. MATERIAL AND METHODS

138 2.1. Study area

139 The bay of Mont-Saint-Michel is a macrotidal bay located in the English Channel between
140 Brittany and Normandy, characterized by an intertidal zone covering over 250 km² and a
141 mean spring tide range of 14.5 m (Bonnot-Courtois et al., 2004). In its central part, the Sainte-
142 Anne reef (48°38'700N and 1°40'100W) is the largest bioconstruction in Europe, built by the
143 gregarious and tubicolous polychaete *S. alveolata* (Gruet, 1972; Holt et al., 1998). This part of
144 the bay is characterized by a high proportion of bioclastic sediments with increasing medium
145 grain size from the intertidal to the subtidal zone (Bonnot-Courtois et al., 2004). The Sainte-
146 Anne reef is located in the lower intertidal zone (between the -2 and -4 m isobaths), parallel
147 to the coastline, perpendicular to the dominant tidal currents and *ca.* 3 km from the shoreline
148 (Dubois et al., 2006; Noernberg et al., 2010). Because *S. alveolata* bioconstructions occur in
149 systems where this species finds soft sediment material to build its tube and hard substrata to

150 settle on (Curd et al. 2019), the Sainte-Anne reef is composed of a mosaic of structures built
151 by the engineer species (hereafter called engineered sediment, 32 ha in 2014, pers. obs.)
152 surrounded by soft sedimentary features (Jones et al., 2018).

153

154 *2.2. Field sampling and experimental set-up*

155 We sampled four dominant sediment typologies according to Curd et al. (2019): (1)
156 engineered sediment in prograding phase, identified by growing and expanding tubes, without
157 epibiontes (hereafter called Undisturbed Engineered Sediment or UES), (2) engineered
158 sediment in retrograding phase, identified by tubes lacking apertures, often covered by
159 biofilm and epibiontes (hereafter called Disturbed Engineered Sediment or DES), (3) soft
160 sediment composed of coarse sand (CS) with bioclastic elements and (4) soft sediment
161 composed of fine and muddy sand (MS). We sampled these four typologies 3 times over a
162 year, according to a temperature gradient: in winter (February, water temperature = 8°C), in
163 spring (April, water temperature = 12°C) and in summer (September, water temperature =
164 17°C). During each sampling period, we randomly extracted four cores – at low tide – across
165 a surface of *ca.* 100 m² of each sediment typology using either a toothed metal corer (15 cm
166 diameter) for the engineered sediment cores or 35-cm long Perspex tubes (15 cm diameter)
167 for the soft sediment cores. We immediately transferred the engineered sediment cores into
168 35-cm long Perspex tubes (15 cm diameter), sealed all the tubes and transported them to the
169 laboratory where we placed them inside a dark refrigerated room. Prior to the coring, we
170 collected 40 liters of seawater next to the reef - during high tide - using inflatable bags to
171 avoid bubbles that we stored in a dark room at the *in situ* water temperature.

172 In the laboratory, we filled the Perspex tubes with the collected water, sealed them with
173 caps equipped with small magnetic stirrers, connected them *via* a tube to the inflatable water
174 reserve tank and incubated them respecting the *in situ* water temperature. We started the

175 incubations *ca.* 2 hours after the sampling and incubated the 16 cores sampled during each
176 campaign between 3 and 15 hours, until a loss of 30% of the initial dissolved oxygen
177 concentration measured in each core. During the incubations, we sampled 6 to 8 times both
178 the water overlying the sediment and the water from the reserve tank (control water) using a
179 60 ml plastic syringe (see Denis et al. (2001) for further details on the incubation set up).
180 Finally, we measured the oxygen, ammonium, nitrate, and nitrite concentrations in all the
181 water samples, and we used the difference between concentration changes in the overlying
182 water of each core and control water to calculate the sediment-water fluxes.

183

184 *2.3. Flux measurements and calculations*

185 To determine oxygen concentration, we gently transferred the required volume from the
186 60 ml plastic syringe into a 10 ml glass flask using a tubing and allowing overflow from the
187 flask to avoid air bubbles. We then measured oxygen concentration using an oxygen Clark-
188 type microsensor (Revsbech, 1989) characterized by a 90 % response time of <8s, a stirring
189 sensitivity of <1.5 % and a current drift of <1 % h⁻¹ (Unisense A/S, Aarhus, Denmark, 100µm
190 tip diameter). Linear two-point calibration of each microelectrode was systematically
191 performed before and after each series of measurements. Zero oxygen current was measured
192 in the anoxic zone of an additional sediment core with muddy sediments while a 100%
193 oxygen level was calibrated using air-bubbled water. To determine the other concentrations,
194 we filtered the volume remaining in the syringe through GF/F Whatman glass fiber filters
195 before transferring them into a 20 ml polyethylene flask for ammonium analysis and a 10ml
196 polyethylene tube for nitrate and nitrite analysis. We immediately carried out the ammonium
197 analysis following the indophenol-blue method (Solórzano, 1969). We froze the remaining
198 samples and measured later on the nitrate and nitrite concentrations using a Seal autoanalyzer,
199 following the protocol of Tréguer & Le Corre (1975). We determined the fluxes by regressing

200 the change in overlying water concentration versus time and considered fluxes as null when
201 non-significant regressions (Pearson correlation, $p > 0.05$) based on changes over time were
202 less than the analytical variability. For all fluxes, we systematically applied a correction for
203 water replacement. We measured a significant oxygen consumption during all the incubations
204 ($p < 0.05$). We considered the ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-) fluxes
205 (from the sediment to the overlying water) from the following cores as null; two spring CS
206 cores for the NH_4^+ fluxes, all the summer MS cores for the NO_3^- fluxes and two spring MS
207 cores, one summer MS core and one summer CS core for the NO_2^- fluxes. Finally, we
208 expressed the nitrate and nitrite fluxes of each core as a sum we called nitrate + nitrite flux
209 (NO_{2+3}) and considered the oxygen flux as going from the overlying water to the sediment,
210 hereafter called the sediment oxygen demand (SOD).

211

212 *2.4. Macrofauna taxonomic and functional diversity*

213 At the end of each incubation, we fixed the sediment cores using a 5 % formaldehyde
214 solution, before sieving them through a 1-mm square mesh. We sorted the macrofauna (>1
215 mm) and identified it to the lowest taxonomic level, often species level (except for
216 Nemertean, Nematodes and Tubificoides, see Table S1). For each core, we measured the
217 abundance and the ash-free dry weight (AFDW – 4 hours at 550°C) of each taxonomic group
218 including the engineer species *S. alveolata* and then standardized the different measurements
219 taken for each core (fluxes, macrofauna abundance and biomass) to unit surface. First, we
220 characterized the macrofauna according to each species taxonomic identity, before calculating
221 Hill's indices (*i.e.* the number equivalents of three diversity indices), always including *S.*
222 *alveolata* (Hill, 1973): the species richness (SR), the exponential of Shannon-Wiener (\log_e)
223 calculated using either the abundance ($N1_{ab}$) or the biomass ($N1_{biom}$) and the inverse of
224 Simpson's dominance calculated using either the abundance ($N2_{ab}$) or the biomass ($N2_{biom}$).

225 Hill's indices are recommended for the study of benthic communities (Gray, 2000) and have
 226 the "doubling" property, making their interpretation more straightforward than the raw
 227 Shannon-Wiener and Simpson dominance

228

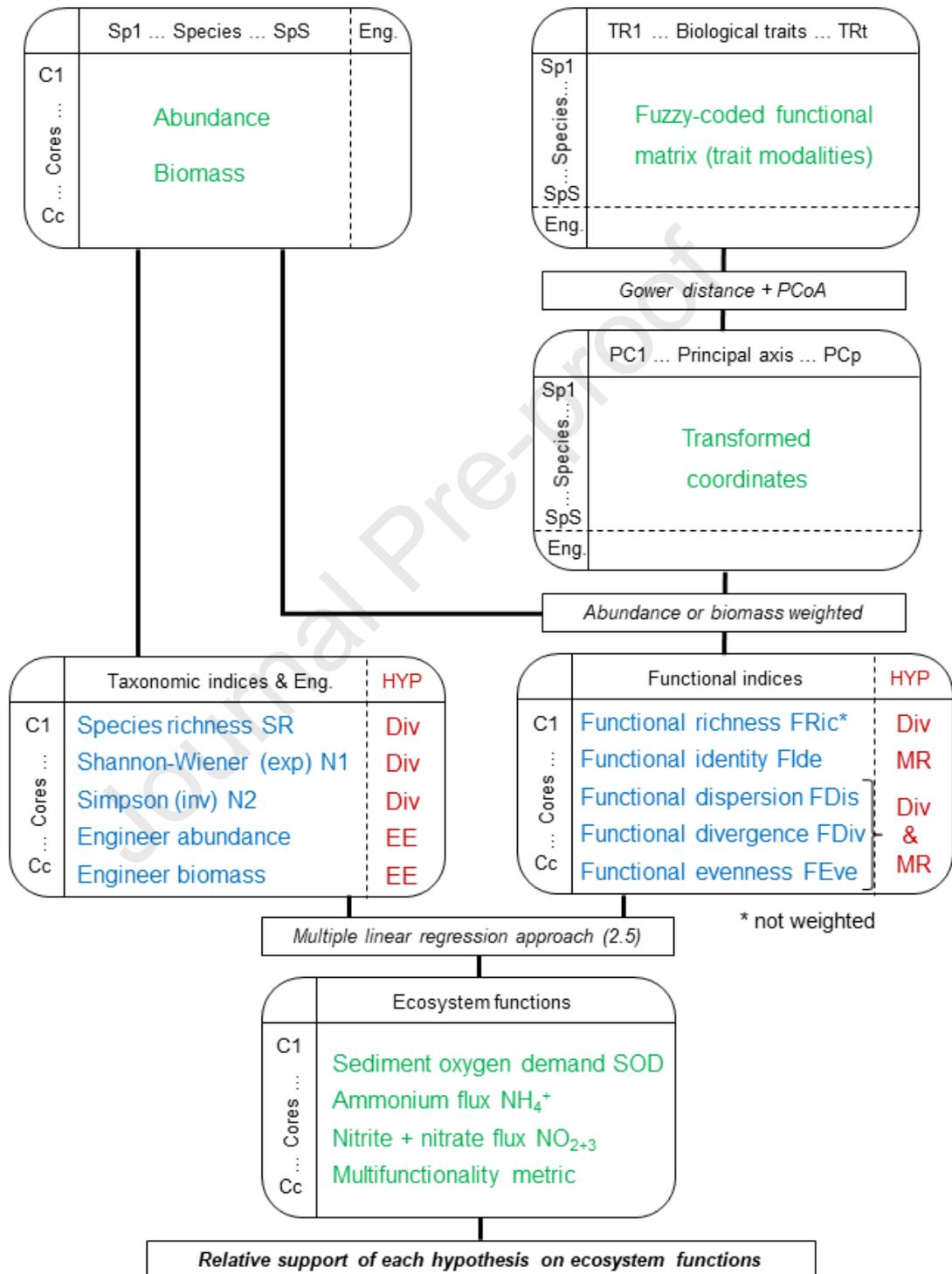
229 **Table 1.** Macrofauna biological traits and associated modalities used to calculate the
 230 functional diversity indices. For each trait, we indicated the macrofauna processes linked to
 231 organic matter remineralization and nutrient cycling, along with the macrofauna processes
 232 linked to the ecosystem functions via microorganism processes.

Trait and associated modalities	Direct macrofauna processes	Via microorganism processes	References
Maximum size (literature, mm): <10 [10-50[[50-100[[100-200[>200	respiration, excretion of DIN	egestion of POM via remineralization, transport of solutes and O ₂ via nitrification, denitrification	Hildrew et al. (2007); Kristensen (1988); Shumway (1979); Vanni (2002)
Daily movement capacity: No movement Low (<1 m) Medium (1-10 m) High (>10 m)	respiration, excretion of DIN	transport of solutes and O ₂ via nitrification, denitrification, remineralization	Kristensen (1988); Queirós et al. (2013); Shumway (1979)
Sediment reworking: Epifauna Surficial modifiers Upward and downward conveyors Biodiffusors Regenerators		transport of solutes and O ₂ via nitrification, denitrification, remineralization	Janson et al. (2012); Queirós et al. (2013); Solan et al. (2004); Thrush et al. (2006)
Feeding mode: Suspension feeder Surface deposit feeder Sub-surface deposit feeder Predator-scavenger Grazer	respiration, excretion of DIN, ingestion of POM	egestion of POM via remineralization	Janson et al. (2012); Kristensen (1988); Thrush et al. (2006)
Bathymetric preference: Intertidal Subtidal		informs indirectly on the engineered sediment's thermal properties which can mediate microorganism processes	Gutiérrez and Jones (2006)

233 DIN: dissolved inorganic nitrogen, POM: particulate organic matter
234 indices (Hill, 1973). The indices N1 and N2 both increase when the sample diversity increases
235 but N1 is sensitive to the abundance or biomass variations of rare or uncommon species while
236 N2 is sensitive to the variations of the most common species. Then, we characterized the
237 macrofauna according to a set of biological traits (five categorical traits each divided into
238 modalities) known to directly or indirectly affect individual processes (“effect traits” *sensus*
239 Lavorel & Garnier (2002)), such as aerobic respiration, which themselves affect benthic
240 ecosystem functions such as nitrogen cycling and organic matter remineralization (Table 1).
241 These ecosystem functions are estimated by measuring oxygen and solute fluxes (*i.e.* NH_4^+ ,
242 NO_3^- , NO_2^-) between the sediment and the overlying water. We used the two main
243 components of the bioturbation potential (Queirós et al., 2013), mobility and sediment
244 reworking, rather than the bioturbation potential per se because both components are
245 influenced by habitat structure (Godbold et al., 2011), a characteristic differing between UES
246 and DES zones of the reef (Curd et al., 2019; Jones et al., 2018). Furthermore, transferring
247 bioturbation potential across space and time is only possible if the species body size is
248 constant (Queirós et al., 2013), which was not the case since we sampled across three
249 different periods.

250 Some species present different modalities for certain traits like *Carcinus maenas*, which
251 can behave as a grazer and as a predator-scavenger (2 modalities in the feeding mode trait).
252 To take into account this intraspecific variability, we fuzzy coded the categorical traits by
253 assigning a value between 0 (no affinity) and 3 (strict affinity) to each modality of a given
254 trait depending on the species affinity for the modality, with 1 and 2 indicating intermediate
255 affinities (Chevenet et al., 1994). The sum of the values attributed to all the modalities of a
256 given trait was always equal to three except for the tidal position, which could be equal to
257 four if the species had an equal affinity for the intertidal and subtidal modalities. We

258 recovered most of the information on polychaete feeding mode and daily movement capacity
 259 from Fauchald & Jumars (1979) and Jumars et al. (2015). The rest was recovered from peer-
 260 reviewed journals



261

262 **Figure 1.** Framework used to study the relative support of the diversity hypothesis (Div), the
 263 mass ratio hypothesis (MR) and the engineer effect hypothesis (EE) on ecosystem functions

264 (here biogeochemical fluxes) in the context of a community structured by an ecosystem
265 engineer (Eng.). Each index in blue is used to test a specific hypothesis (HYP) in red and all
266 the indices along with the water temperature, were first considered as explanatory variables in
267 the multiple linear regression approach detailed in part 2.5. Adapted from Villéger et al.
268 (2008).
269 (Guerra-García et al., 2014; Navarro-Barranco et al., 2013) and biological trait databases
270 (Marine species identification portal, BIOTIC).

271 Using the biological traits matrix defined for the 43 species identified in the UES and
272 DES cores ($n = 24$), we calculated several functional indices following the framework
273 detailed in Figure 1 and using the R packages presented in Table 2. We used the Gower
274 distance to calculate the functional distance between each pair of species and then performed
275 a principal coordinate analysis (PCoA) on the distance matrix (Laliberté and Legendre, 2010;
276 Villéger et al., 2008) to represent each species in a multidimensional functional space, each
277 dimension (PCoA axis, 42 axes in total) being a combination of traits. Finally, we calculated
278 for each core, several functional diversity and identity indices using different data types
279 (Table 2) and weighted each index (except functional richness) by species relative abundance
280 (ab in subscript) or relative biomass (biom in subscript) (Fig. 1). *Sabellaria alveolata* was
281 always included in the data sets used to calculate the indices. Functional richness was
282 standardized by the 'global' functional richness (including all species recorded in the UES
283 and DES cores) to constrain it between 0 and 1 (Laliberté and Legendre, 2010).

284

285 *2.5. Statistical analyses*

286 First, we tested the effect of sediment typology (four levels: CS, MS, UES and DES),
287 sampling period (three levels: spring, summer and winter) and their interaction on the
288 different fluxes (SOD, NH_4^+ and NO_{2+3}) using an analysis of variance (ANOVA) with a two-
289 way crossed balanced design. If the interaction term was significant for a flux, we performed
290 Tukey HSD post-hoc tests to disentangle which sediment typology x sampling period cores

291 presented significantly higher or lower fluxes than others. After running the ANOVAs, we
292 checked each model's residuals for normality using a histogram and for homoscedasticity by
293 plotting them against the predicted values (Zuur et al., 2010).

Journal Pre-proof

294 **Table 2.** Definition and associated information (data type, key references, R functions and weighting procedure) on the five functional indices
 295 (diversity and identity). The first four PCoA axes represent 60% of the total inertia. See Figure 4 for a graphical illustration of each index.

Functional indices	Name	Definition	Data type	Unweighted or weighted	Key references	R function
Functional identity	FIde	Weighted average position on the selected functional space axis (PCoA axis)	PCoA axis 1, 2 or 3	Weighted by abundance or biomass	Mouillot et al. (2013)	multidimFD
Functional richness	FRic	Multidimensional functional space filled by all species in a community	PCoA axes 1 to 4	Unweighted	Villéger et al. (2008); Laliberté and Legendre (2010)	dbFD
Functional dispersion	FDis	Weighted average distance to the weighted average mean trait values of the community	Uncorrected functional distance matrix	Weighted by abundance or biomass	Laliberté and Legendre (2010)	dbFD
Functional divergence	FDiv	Weighted average deviation of the Euclidian distance between the position of all the species in the functional space and the unweighted center of gravity of the vertices of the convex hull	PCoA axes 1 to 4	Weighted by abundance or biomass	Villéger et al. (2008)	dbFD
Functional evenness	FEve	Regularity of abundance or biomass distributions in the functional space along the shortest minimum spanning tree linking all the species	PCoA axes 1 to 42	Weighted by abundance or biomass	Villéger et al. (2008); Laliberté and Legendre (2010)	dbFD

296 sediment core a multifunctionality metric using the mean of the four standardized fluxes
297 (mean = 0 and SD = 1), to give them the same weight (Mouillot et al., 2011).

298 Then, to estimate the importance of macrofauna vs meiofauna + microorganisms in
299 organic matter processing, we calculated the macrofauna-normalized SOD ($\text{mmol O}_2 \cdot \text{day}^{-1} \cdot \text{g}$
300 AFDW^{-1}) for each core by dividing the daily oxygen consumption ($\text{mmol O}_2 \cdot \text{day}^{-1}$) by the
301 total macrofauna biomass (g AFDW). Values inferior to 1 indicate processes are
302 predominantly driven by macrofauna whereas values superior to 1 indicate processes are
303 predominantly driven by meiofauna and microorganisms (Stenton-Dozey et al., 2001 in
304 Clough et al., 2005). A multifunctionality metric was also calculated for each engineered
305 sediment core as the mean of the four fluxes after standardizing each of them (mean of 0 and
306 standard deviation of 1) to give them the same weight (Mouillot et al., 2011).

307 Finally, we implemented a multiple linear regression approach (ordinary least-square
308 regressions) to determine the relative importance of (1) water temperature, (2) the engineer *S.*
309 *alveolata* (engineer effect hypothesis), (3) macrofauna diversity in terms of species or
310 biological traits (diversity hypothesis) and (4) the functional traits of the dominant species
311 (mass-ratio hypothesis) on the four ecosystem functions measured in the engineered
312 sediments. Each index presented in Figure 1 is used to test one hypothesis, except FDis, FDiv
313 and FEve, which are used to test the diversity and mass-ratio hypotheses (Mokany et al.,
314 2008), as their values are driven by macrofauna traits and macrofauna abundance or biomass.
315 We considered the 24 incubated engineered sediment cores as statistically independent
316 replicates because the cores were physically isolated from each other during the flux
317 measurements (independent incubations) and the processes we measured take place at spatial
318 scales inferior to the *in situ* distance separating two cores (Hewitt et al., 2005). Indeed, the
319 cores sampled in the UES and DES sediment typologies were extracted from different
320 engineered sediment patches across a surface of *ca.* 100 m² and most of the engineered

321 sediment benthic macrofauna being sessile or presenting a low mobility, their movements are
322 constrained to a given engineered sediment patch (Table 1, Fig. 4 and 5).

323 First, we reduced the number of explanatory variables, previously standardized
324 (Schielzeth, 2010), to consider in the multiple linear regressions by removing variables that
325 were highly correlated ($|r| > 0.8$, Spearman correlations) (Godbold and Solan, 2009). We
326 removed $N2_{ab}$ and $N2_{biom}$ as they were highly correlated with $N1_{ab}$ ($r = 0.98$) and $N1_{biom}$ ($r =$
327 0.98), respectively, $FIde2_{ab}$ and $FIde2_{biom}$ as they were highly correlated with $FIde1_{ab}$ ($r = -$
328 0.97) and $FIde1_{biom}$ ($r = -0.87$), respectively and $FDiv_{ab}$ and $FDiv_{biom}$ as they were highly
329 correlated with $FDis_{ab}$ ($r = -0.85$) and $FDis_{biom}$ ($r = -0.90$), respectively. After this step, we had
330 one environmental variable (temperature), two variables associated to the engineer effect
331 hypothesis (*S. alveolata* abundance and biomass), four variables associated to the diversity
332 hypothesis (SR, $N1_{ab}$, $N1_{biom}$ and FRic), four variables associated to the mass-ratio hypothesis
333 ($FIde1_{ab}$, $FIde1_{biom}$, $FIde3_{ab}$ and $FIde3_{biom}$) and four variables associated to the diversity and
334 mass ratio hypotheses ($FDis_{ab}$, $FDis_{biom}$, $FEve_{ab}$ and $FEve_{biom}$).

335 Secondly, we built first and second-degree polynomial regressions between each
336 explanatory variable and each ecosystem function, as preliminary inspections of the biplots
337 indicated the presence of quadratic relations (Thrush et al., 2017). Prior to this second step,
338 we squared the 15 remaining explanatory variables to build raw second-degree polynomial
339 regressions and the second-degree terms were standardized to improve the interpretability of
340 the multiple linear regression coefficients (Schielzeth, 2010). Regarding temperature, we only
341 considered first-degree linear regressions, as water temperature inside small ranges (here 9°C)
342 will have positive effects on biogeochemical fluxes such as SOD, according to the Q10 of 2
343 general relation (Herbert, 1999; Hildrew et al., 2007; Thamdrup et al., 1998).

344 Thirdly, the variable associated to each hypothesis that had a significant effect on a given
345 ecosystem function ($p < 0.05$) and explained the highest amount of ecosystem function

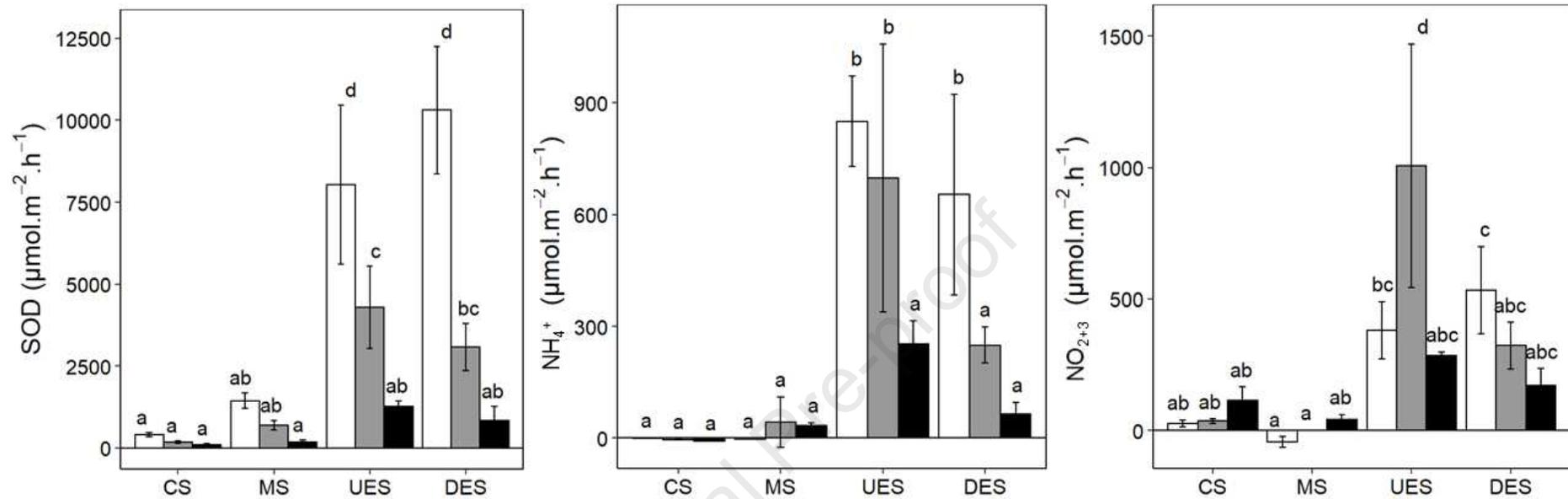
346 variability (adjusted R^2) was included in the four initial multiple linear models. The following
347 explanatory variables were considered in each initial multiple linear model: for SOD,
348 temperature, *S. alveolata* biomass (first-degree), FId_{1ab} (second-degree) and $FDis_{ab}$ (second-
349 degree); for NH_4^+ , temperature, *S. alveolata* biomass (first-degree), SR (first-degree), FId_{1ab}
350 (first-degree) and $FDis_{ab}$ (second-degree); for NO_{2+3} , temperature, *S. alveolata* abundance
351 (first-degree), N_{1ab} (first-degree) and $FE_{ve_{ab}}$ (second-degree); for the multifunctionality
352 metric, temperature, *S. alveolata* biomass (first-degree), SR (first-degree), FId_{1biom} (first-
353 degree) and $FDis_{ab}$ (second-degree).

354 Finally, to determine the minimal adequate models (final multiple linear models), we
355 selected the subset of predictors that minimized the Akaike information criterion (AIC) using
356 the 'ols_step_best_subset' function from the 'olsrr' package. If two models had AIC
357 differences of less than 2, we chose the one with the lowest Mallows' C_p to select the most
358 parsimonious model (Godbold and Solan, 2009). Before running the model selection
359 procedure, we removed the explanatory variables that presented high levels of collinearity
360 based on a threshold of the variance inflation factor of 10. For SOD and NH_4^+ , we removed
361 FId_{1ab} , which was highly correlated with $FDis_{ab}$ ($r = 0.99$) and defined reduced multiple
362 linear models. After running each model (initial, reduced, and final multiple linear
363 regressions), we checked the residuals for normality using a histogram and for
364 homoscedasticity by plotting them against the predicted values (Zuur et al., 2010). To
365 estimate the independent effect of each selected predictor on a given ecosystem function, we
366 calculated the standardized partial regression coefficients and represented this independent
367 effect using partial linear regression plots (Schielzeth, 2010). We considered a significance
368 level of 0.05 for all the tests.

369

370 3. RESULTS

Journal Pre-proof



372

373 **Figure 2.** Sediment oxygen demand (SOD), ammonium flux (NH_4^+) and the sum of nitrate and nitrite fluxes (NO_{2+3}) measured for the four
 374 sediment typologies (mean \pm SD, n = 4), coarse sand (CS), muddy sand (MS), undisturbed engineered sediments (UES) and disturbed engineered
 375 sediments (DES) in spring (white), summer (grey) and winter (black). The results of the post-hoc tests performed after the two-way crossed
 376 ANOVA (sediment typology x sampling period) are presented as letters above each barplot, considering a p-value of 0.05.

377 Visually, the SOD, NH_4^+ and NO_{2+3} fluxes appeared higher in the undisturbed (UES) and
378 disturbed (DES) engineered sediments compared to the coarse (CS) and muddy (MS)
379 sediments across the three sampling periods. The engineered sediment fluxes appeared
380 maximal in spring (Fig. 2 and Table S2). The mean SOD ranged from a minimum of 105
381 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in winter for the CS cores to a maximum of 10 309 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ in spring for the
382 DES cores. Sediment typology ($F(3,36) = 68.83, p < 0.001$), sampling period ($F(2,36) =$
383 $81.95, p < 0.001$) and their interaction ($F(6,36) = 20.96, p < 0.001$) had statistically significant
384 effects on the SOD. The CS cores and the winter MS cores had the lowest SOD while the
385 spring UES and DES cores and the summer UES cores had, respectively the first and second
386 highest SOD. The spring and summer MS cores, the winter UES and DES cores and the
387 summer DES cores had intermediate SOD (spring and summer MS and winter UES and DES
388 \leq summer DES \leq summer UES, Fig. 2).

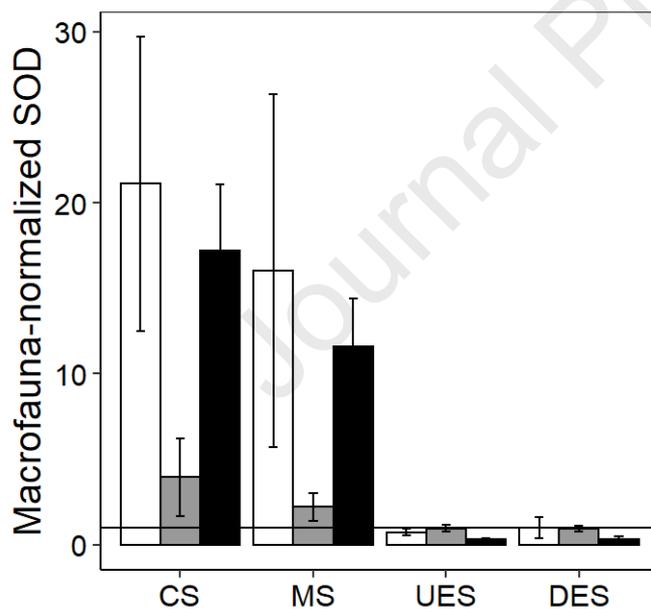
389 The mean NH_4^+ fluxes ranged from slightly negative (between -7.9 and -0.8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$)
390 for all the CS cores and for the MS cores in spring to above 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ for all the UES
391 cores and for the spring and summer DES cores with the maximum values measured in the
392 spring UES cores ($850.40 \pm 121.79 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$). Sediment typology ($F(3,36) = 51.14, p <$
393 0.001), sampling period ($F(2,36) = 17.72, p < 0.001$) and their interaction ($F(6,36) = 7.26, p <$
394 0.001) had statistically significant effects on the NH_4^+ fluxes. All the CS, MS, the winter UES
395 and the spring and winter DES cores had significantly lower NH_4^+ fluxes than the spring and
396 summer UES cores and the spring DES cores (Fig. 2).

397 All the NO_{2+3} fluxes were on average positive except in the spring MS cores (-43.7
398 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$). The summer MS cores had mean NO_{2+3} fluxes near zero ($0.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$)
399 while the rest of the soft sediment cores had mean fluxes between 26.0 and 114.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$
400 ¹. All the engineered sediment cores had mean fluxes above 170.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ with the
401 maximum values measured in the summer UES cores ($1\ 006.9 \pm 463.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$).

402 Sediment typology ($F(3,36) = 35.89, p < 0.001$), sampling period ($F(2,36) = 6.41, p = 0.004$)
 403 and their interaction ($F(6,36) = 9.17, p < 0.001$) had statistically significant effects on the
 404 NO_{2+3} fluxes. The spring and summer MS cores presented the lowest NO_{2+3} fluxes while the
 405 summer UES and the spring DES cores presented, respectively the first and second highest
 406 NO_{2+3} fluxes. The rest of the cores presented intermediate NO_{2+3} fluxes (winter CS and MS \leq
 407 winter UES and DES and spring DES \leq spring UES, Fig. 2).

408 Calculation of the macrofauna-normalized SOD for each core indicated that meiofauna
 409 and microorganisms predominantly drove organic matter processing in the CS and MS
 410 (macrofauna-normalized SOD $\gg 1$). Differently, macrofauna was the principal driver of
 411 organic matter processing in the UES and DES (Fig. 3).

412



413

414 **Figure 3.** Macrofauna-normalized sediment oxygen demand (SOD) in $\text{mmol O}_2 \cdot \text{day}^{-1} \cdot \text{g}$
 415 AFDW^{-1} (mean \pm SD, $n = 4$) calculated for the four sediment typologies, coarse sand (CS),
 416 muddy sand (MS), undisturbed engineered sediments (UES) and disturbed engineered
 417 sediments (DES) in spring (white), summer (grey) and winter (black). The horizontal line
 418 represents a macrofauna-normalized SOD value of one. To improve readability, we removed
 419 one winter CS core with a macrofauna-normalized SOD above 30 ($140.5 \text{ mmol O}_2 \cdot \text{day}^{-1} \cdot \text{g}$
 420 AFDW^{-1}).

421 3.2. Functional diversity and identity indices

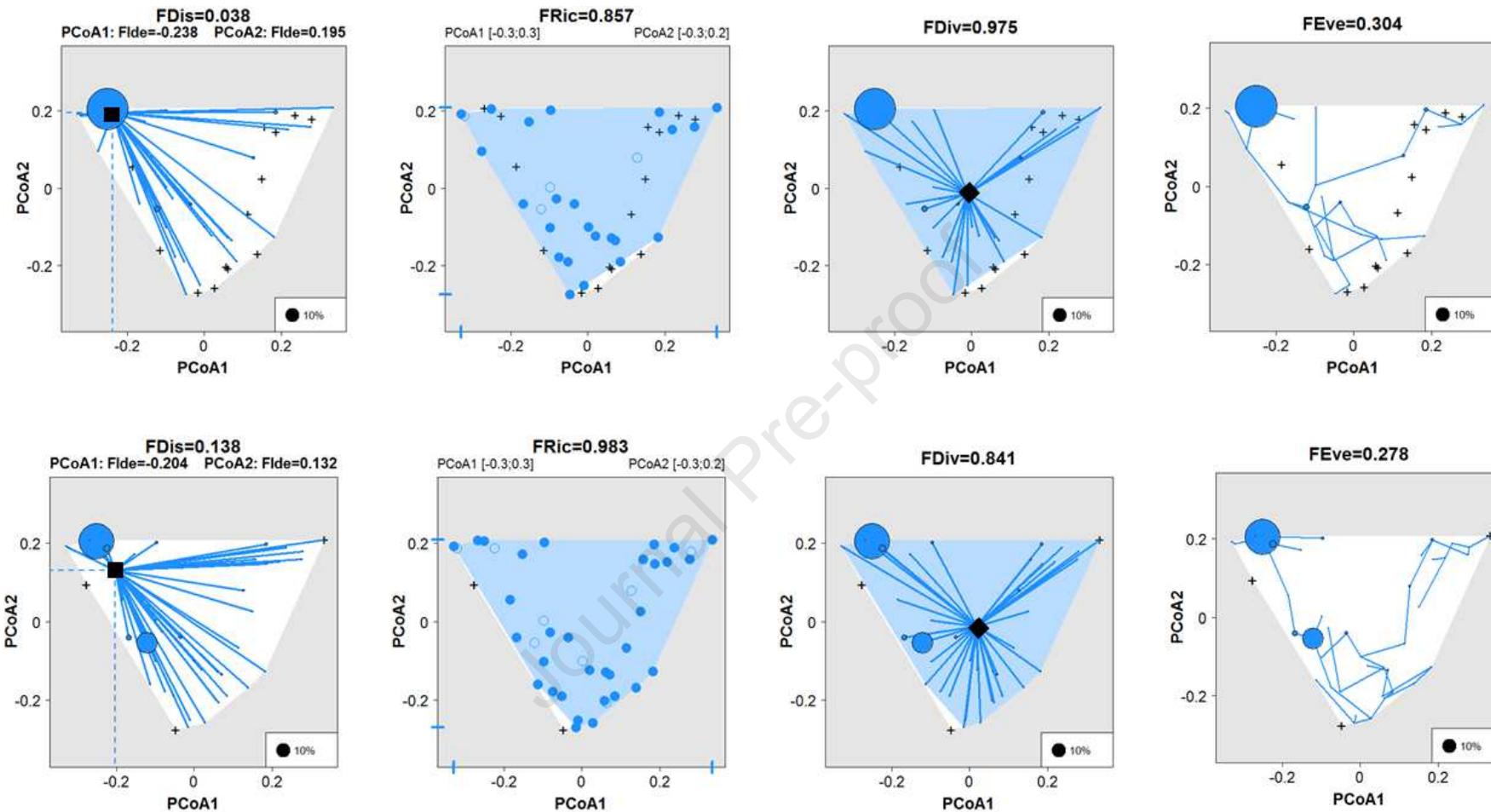
422 Each functional index weighted by biomass was significantly and positively correlated
423 with its abundance-weighted version, except FEve. Functional richness, FDis, FDiv, FIde1
424 and FIde2 weighted by biomass and abundance presented values intricately linked to the
425 engineered sediment types (UES vs DES). The other functional indices appeared to be
426 completely independent from the engineered sediment type (FEve) or weakly linked to it
427 (FIde3).

428 As an illustration (Fig. 4), we calculated the different functional indices using the mean
429 macrofauna biomass across all the DES (n = 12) and all the UES cores (n = 12). The mean
430 DES core had a higher FRic (0.98) than the mean UES core (0.86) indicating there were more
431 functionally dissimilar species in DES than in UES. Functional dispersion followed the same
432 pattern with a higher value in the mean DES core (0.14) than in the mean UES core (0.04). If
433 a species dominates an assemblage (e.g. *S. alveolata* in UES, Table S1), it will attract the
434 weighted-mean position of the assemblage and the FDis will be small. Differently, if two
435 species have high abundances or biomasses and are distant in the functional space (i.e.
436 functionally dissimilar), like *S. alveolata* and the crustacean *Porcellana platycheles* in the
437 DES cores (Fig. 5 and Table S1), both will attract the weighted-mean position of the
438 assemblage and the FDis will be higher. Functional divergence was higher in the mean UES
439 (0.98) than in the mean DES core (0.84) because *S. alveolata*, which presents trait modalities
440 very different from the “average species” represented by the unweighted center of gravity of
441 the convex hull vertices (Fig. 5), dominates the UES cores while it dominates less the DES
442 cores (Table S1).

443 The mean UES core was characterized by negative FIde1 (-0.24) and positive FIde2 (0.19)
444 while the mean DES core was characterized by higher and negative FIde1 (-0.20) and by
445 lower and positive FIde2 (0.13). The first PCoA axis is mainly associated to a daily

446 movement capacity gradient with negative values corresponding to species presenting none to
447 low movement capacities (e.g. *Sabellaria alveolata*) and higher values corresponding to

Journal Pre-proof

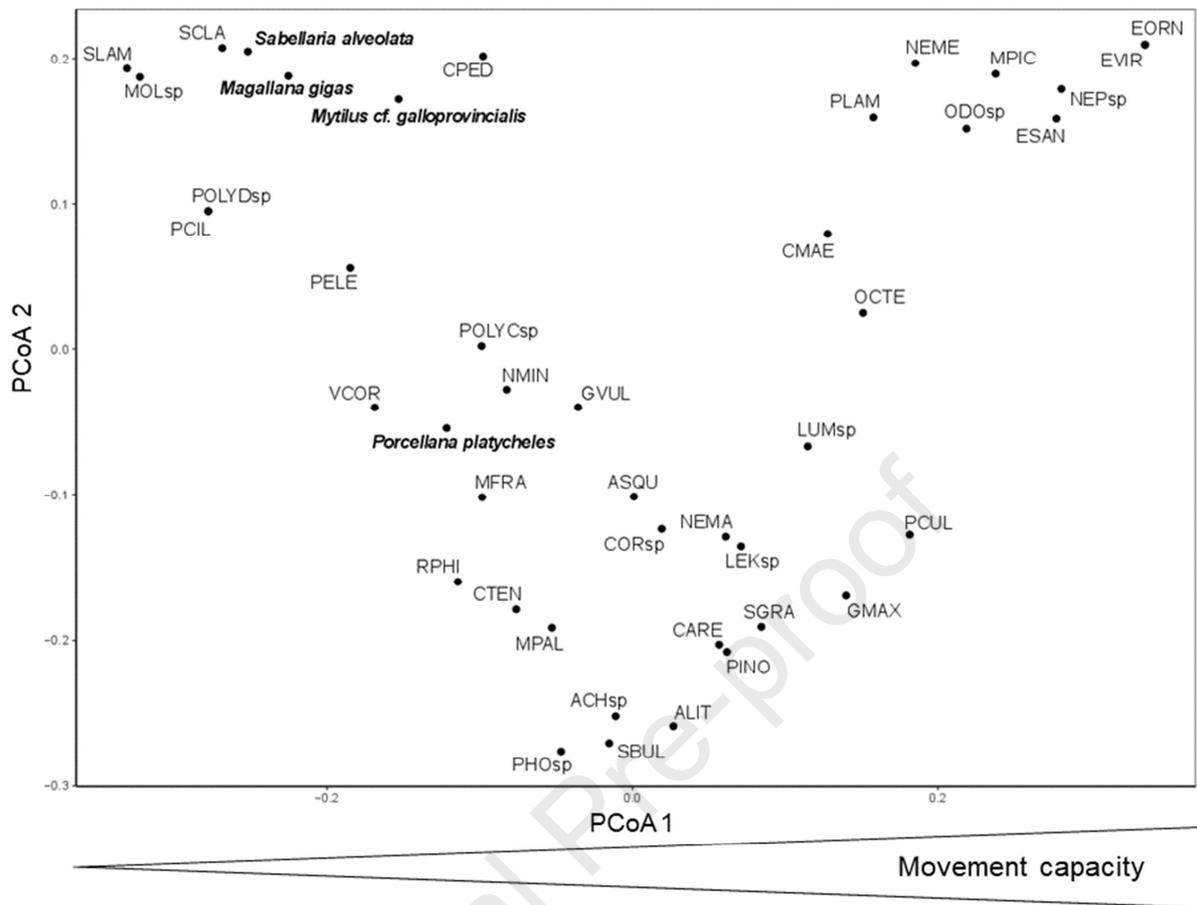


448

449 **Figure 4.** Two-dimensional illustration of the five functional indices (functional dispersion = FDis, functional identity = FIde, functional richness
 450 = FRic, functional divergence = FDiv, functional evenness = FEve) based on the species identified in the 12 undisturbed (top line) and 12
 451 disturbed (bottom line) engineered sediment cores. The black crosses indicate species absent from an engineered sediment type but present in the
 452 global pool of species. Except for FRic, the dots are proportional to each species' mean biomass. In the FDis panels, the black squares and

453 dashed lines represent the weighted-mean position of the species in the multidimensional space and the weighted-mean positions of the species
454 on the first and second axis (FIde1 and FIde2), respectively. In the FRic panels, the colored convex polygons represent the projection of the
455 multidimensional convex hull in 2D, the filled symbols represent the species used as vertices in the multidimensional space and the bold bars on
456 the axes represent the minimum and maximum values on each axis. In the FDiv panels, the black diamonds represent the center of gravity of the
457 vertices. In the FEve panels, the blue lines represent the minimum spanning tree linking all species in the multidimensional space.

Journal Pre-proof



458
 459 **Figure 5.** Position, on the first two axes of the functional space, of all the species present at
 460 the global engineered sediment level and identified by their full or abbreviated names (see
 461 Table S1). *Sabellaria alveolata* is the engineer species while *Porcellana platycheles* is the
 462 second dominant species in the disturbed engineered sediment cores. *Magallana gigas* and
 463 *Mytilus cf. galloprovincialis* are two other engineer species present as epibionts on the
 464 engineered sediments.

465

466 increasingly mobile species (e.g. errant polychaetes such as *Eulalia viridis*, EVIR) (Fig. 5).

467 The second PCoA axis is mainly associated to the sediment reworking trait with positive

468 values generally corresponding to epifauna (e.g. *Magallana gigas*) and biodiffusors (e.g.

469 Nemerteans, NEME), values close to 0 corresponding to upward and downward conveyors

470 (e.g. *Mediomastus fragilis*, MFRA and *Pygospio elegans*, PELE) and negative values

471 corresponding to surficial modifiers (e.g. *Lekanesphaera* sp., LEKsp) (Fig. 5). Consequently,

472 functional identity values on the first two PCoA axes can bring direct indications on which

473 modalities are key in driving the different ecosystem functions. The other biological traits
474 (size, feeding mode and bathymetric preference) were not associated with a specific PCoA
475 axis.

476

477 *3.3. Relative importance of macrofauna and temperature on the engineered sediment* 478 *biogeochemical functioning*

479 The minimal adequate models contained three or four predictors and explained *ca.* 70% of
480 the ecosystem function variability (Table 3). All the models contained water temperature, a
481 predictor associated to the engineer effect hypothesis (*S. alveolata* biomass or abundance) and
482 a predictor associated to both the diversity and mass-ratio hypotheses (FDis_{ab} or FEve_{ab}).
483 Furthermore, FDis_{ab} and FIde1_{ab} appeared correlated at 0.99 (Spearman correlation) indicating
484 that when FDis_{ab} increases, the abundance of species with medium to high movement
485 capacities also increases (Figure S3). One UES core sampled in summer was closer to the
486 summer DES cores than to the other summer UES cores because of a higher FDis_{ab} and a
487 lower engineer abundance. Nonetheless, the fluxes of this unexpectedly different core in
488 terms of macrofauna characteristics were in line with the partial linear regressions (Fig. 6),
489 which seems to indicate our minimal adequate models are not the result of an UES/DES
490 dichotomy.

491 a. Engineer effect hypothesis

492 Based on the standardized slopes also called standardized partial regression coefficients or
493 effect sizes (β), the engineer had a positive effect on the four functions (Fig. 6). Engineer
494 biomass (mean = 125, SD = 94) was the predictor with the strongest effect on the SOD (mean
495 = 4640, SD = 3750) and NH₄⁺ (mean = 462, SD = 330) fluxes, holding all the other predictors
496 of each model statistically constant. An increase by one population SD of *S. alveolata*
497 biomass increases the SOD and NH₄⁺ fluxes by 0.63 and 0.59 population SD, respectively

498 (Table 3). Considering the multifunctionality metric model, engineer biomass had an effect of
 499 comparable magnitude to FDis_{ab} (Table 3). Finally, engineer abundance (mean = 4765, SD =
 500 13 936) was

501 **Table 3.** Minimal adequate models (ordinary least-square regressions) explaining the
 502 standardized ecosystem functions (sediment oxygen demand (SOD), ammonium flux (NH₄⁺),
 503 sum of nitrate and nitrite fluxes (NO₂₊₃) and the multifunctionality metric). We expressed the
 504 slope estimates as effect sizes (β) to compare their relative effects on each function.

	df	RSE	F statistic	β	P
SOD adjusted R² = 0.73					
Model	3		21.3		< 0.001
Error	20	0.52			
Biomass				0.63	< 0.001
FDis _{ab} ²				-0.31	0.025
Temperature				0.23	0.048
NH₄⁺ adjusted R² = 0.69					
Model	3		18.4		< 0.001
Error	20	0.55			
Biomass				0.59	< 0.001
Temperature				0.45	0.001
FDis _{ab}				-0.35	0.011
NO₂₊₃ adjusted R² = 0.70					
Model	3		19.0		< 0.001
Error	20	0.55			
Abundance				0.62	< 0.001
Temperature				0.30	0.031
FEve _{ab}				-0.25	0.076
Multifunctionality metric adjusted R² = 0.73					
Model	4		17.0		< 0.001
Error	19	0.51			
Temperature				0.52	< 0.001
Biomass				0.37	0.021
FDis _{ab}				-0.38	0.008
FDis _{ab} ²				-0.32	0.035

505 df: degree of freedom, RSE: Residual standard error, Abundance: *S. alveolata* abundance,
 506 Biomass: *S. alveolata* biomass, FEve: functional evenness, FDis: functional dispersion. The
 507 subscripts ab indicates that the index was weighted using species abundance.

508

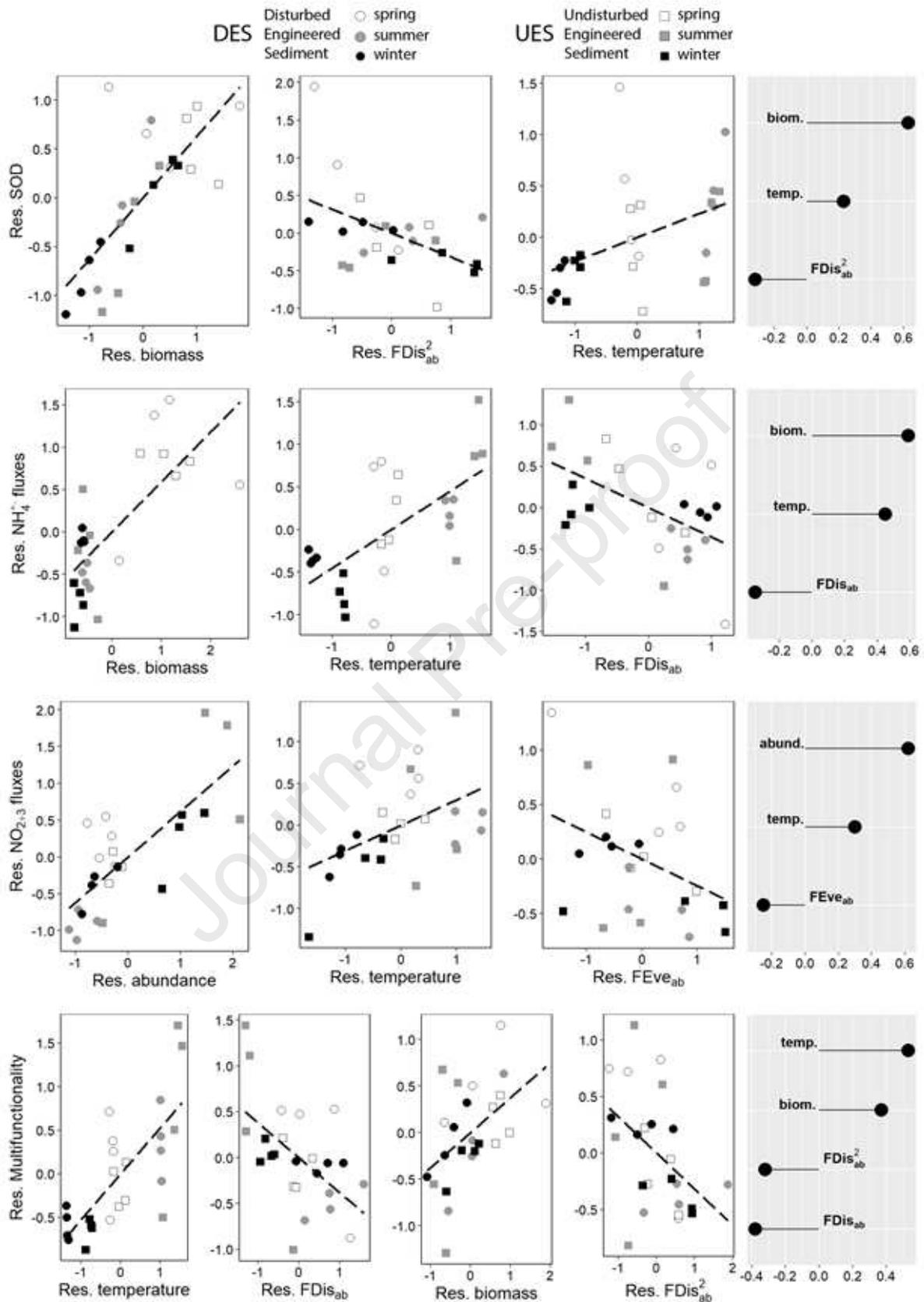
509 the predictor with the strongest effect on the NO_{2+3} fluxes (mean = 450, SD = 334), holding
510 all the other predictors of the model statistically constant (Table 3).

511 b. Diversity and mass-ratio hypotheses

512 Two functional indices weighted by abundance were retained in the minimal adequate
513 models, FDis (mean = 0.18, SD = 0.11) and FEve (mean = 0.61, SD = 0.11), and both
514 predictors always presented negative standardized slopes (Fig. 6). The functional dispersion
515 displayed a simple linear effect on the NH_4^+ fluxes, a simple quadratic effect (concave form)
516 on the SOD and a more complex quadratic effect on the multifunctionality metric (*i.e.*
517 concave form with low values of FDis_{ab} eliciting higher values of the multifunctionality
518 metric than high values of FDis_{ab}). It was the predictor with the weakest effect on the NH_4^+
519 fluxes and with the second strongest effect on the SOD. The functional evenness displayed a
520 simple linear effect on the NO_{2+3} fluxes and was the predictor with the weakest effect, holding
521 all the other predictors of the model statistically constant (Table 3).

522 c. Water temperature

523 Based on the standardized partial regression coefficients, the water temperature (mean =
524 12.33, SD = 3.76) had a positive effect on the four ecosystem functions, all other predictors of
525 each model being held statistically constant (Table 3). It was the predictor with the strongest
526 effect on the multifunctionality metric, with the second strongest effect on the NH_4^+ and
527 NO_{2+3} fluxes and with the smallest effect on the SOD (Fig. 6). Increasing the water
528 temperature by one population SD increases the different functions by 0.23 (SOD) to 0.52
529 (multifunctionality, SD = 0.83) population SD (Table 3).



530
531
532
533

Figure 6. Partial linear regression plots (left) and standardized partial regression coefficients (effect sizes, right) of the predictors retained in the minimal adequate models explaining the

534 standardized ecosystem functions (sediment oxygen demand (SOD), ammonium flux (NH_4^+),
535 sum of nitrate and nitrite fluxes (NO_{2+3}) and the multifunctionality metric). Abundance
536 (abund.) and biomass (biom.) refer to the engineer *S. alveolata* abundance and biomass,
537 respectively. FDis_{ab} and FEve_{ab} refer to the functional dispersion and functional evenness,
538 respectively, both weighted by species abundance.

539

540 4. DISCUSSION

541 The study of the link between taxonomic diversity, functional diversity and ecosystem
542 functions is complex but crucial if we are to understand in a more holistic way ecosystem
543 functioning and the impact of disturbances on this functioning (Brose and Hillebrand, 2016;
544 Gamfeldt et al., 2015). Using *Sabellaria alveolata* reefs as a study case, we started to fill the
545 gap relative to the role played by biodiversity in the functions performed by tubicolous
546 structural engineers (Berke, 2010), building upon studies on the biogeochemical functioning
547 of bivalve reefs (see Stief (2013) and references therein). This study is a necessary first step
548 towards conceiving more controlled *in situ* experiments by removing potentially key species
549 such as highly mobile biodiffusers (e.g. *Eulalia viridis*) or manipulating the physical
550 disturbance of the reef by clearing out small *S. alveolata* tube patches.

551

552 4.1. Biogenic structures promote biogeochemical fluxes in coastal waters

553 Microorganisms and meiofauna were probably the main drivers of the oxygen and solute
554 fluxes measured in the soft sediments surrounding the engineered sediments along with
555 physico-chemical mechanisms such as diffusion and advection. Indeed, solutes transfer
556 mechanisms inside the first 10 cm of these soft sediments are probably dominated by
557 advection in the highly permeable CS sediments and by diffusion in the less permeable MS
558 sediments (Huettel et al., 2003). Macroinvertebrates were also relatively scarce with average
559 abundances between 226 ind.m^{-2} (winter) and 4145 ind.m^{-2} (spring) in the MS, 636 ind.m^{-2}

560 (winter) and 1556 ind.m⁻² (spring) in the CS. Consequently, macrofauna was probably not a
561 driving force in these sediments, either in terms of solute transfer via bioturbation or in terms
562 of oxygen uptake as indicated by a macrofauna-normalized SOD above 1 (Clough et al.,
563 2005). Conversely, macrofauna was across the three periods the main driver of the engineered
564 sediment oxygen uptake, as indicated by a macrofauna-normalized SOD close or below 1
565 (Clough et al., 2005). Since, we did not measure microbial respiration or biomass during our
566 study, we focused on the engineered sediments for which we had information on what
567 appeared to be the driving force of its biogeochemical functioning, the macrofauna.

568 Across the three periods, we measured higher SOD, NH₄⁺ and NO₂₊₃ fluxes in the
569 engineered sediments compared to the CS and MS, a difference we attribute at least partly to
570 the 8 (summer) to 1000 (winter) times higher macrofauna biomass in the UES and DES
571 compared to the CS and MS. Indeed, community biomass and oxygen consumption are often
572 strongly correlated (Braeckman et al., 2010; Clough et al., 2005; Norkko et al., 2013) through
573 the positive link between individual body mass and respiration rate (Gillooly et al., 2001;
574 Hildrew et al., 2007). Macrofauna can also account for 10 to 70% of community NH₄⁺ fluxes
575 from the sediment through ammonium excretion (Kristensen, 1988; Vanni, 2002). Despite
576 representing between 45 and 97% of the macrofauna abundance in the engineered sediments,
577 *Sabellaria alveolata* creates, through the structures it builds and its biological activity, an
578 environment favorable to other macroinvertebrates (Dubois et al., 2002; Jones et al., 2018)
579 and probably also to a community of meiofauna and microorganisms (Ataide et al., 2014;
580 Kristensen and Kostka, 2005; Passarelli et al., 2014). Indeed, meiofauna and especially
581 nematodes are often more diverse and abundant inside biogenic structures such as *Sabellaria*
582 *wilsoni* reefs compared to neighboring bare sediments (Ataide et al., 2014). Furthermore, the
583 colonization of macrofauna tubes by prokaryotic communities is known to be stimulated by
584 the host's organic secretions that represent a food source for these organisms, probably

585 affecting global biogeochemical processes (Kristensen and Kostka, 2005; Passarelli et al.,
586 2014). For example, burrows built by polychaetes like *Hediste diversicolor*, that penetrate the
587 anaerobic subsurface sediment, promote microbial abundance and activity, increasing O₂
588 consumption and nutrient release from the sediment (Mermillod-Blondin et al., 2004; Reise,
589 1981). Consequently, meiofauna and even more so microorganisms surely play an important
590 part in the engineered sediments biogeochemical fluxes, mainly through aerobic respiration,
591 dissolved inorganic nitrogen excretion, particulate organic nitrogen remineralization,
592 ammonium assimilation, nitrification and denitrification (Herbert, 1999; Kristensen, 1988;
593 Vanni, 2002).

594 Overall, oxygen consumption, ammonium and oxidized nitrogen release were enhanced in
595 the sediments engineered by *S. alveolata* compared to bare substratum, as reported for bivalve
596 reefs (Kellogg et al., 2013; Norling and Kautsky, 2007). The mechanisms promoting
597 biogeochemical fluxes in *S. alveolata* reefs and other polychaete reefs are probably the same
598 as in bivalve reefs and involve the dense macrofauna and the associated microorganisms
599 (Passarelli et al., 2014; Stief, 2013). First, the engineered structures (bivalve shells or
600 polychaete tubes) extend the surface available for colonization by nitrifying and denitrifying
601 microorganisms, which benefit from the metabolic waste products excreted by the engineer
602 species (ammonium and carbon dioxide). Second, microorganisms can use the large amounts
603 of biodeposits, including large quantities of extracellular polymeric substances such as mucus,
604 produced by bivalves and polychaetes (*i.e.* egestion of particulate organic matter), as a source
605 of labile organic matter (Gutiérrez et al., 2003; Heisterkamp et al., 2013).

606

607 4.2. Biogeochemical fluxes in engineered habitats: a comparison

608 We compared our results with fluxes measured in a polychaete reef built by the invasive
609 serpulid polychaete *Ficopomatus enigmaticus* (Keene, 1980), in a restored subtidal

610 *Crassostrea virginica* reef (Kellogg et al., 2013) and in a mudflat structured by *Upogedia*
611 *pugettensis*, a bioirrigating shrimp (D'Andrea and DeWitt, 2009) (Table 4). The two
612 polychaete reefs had close community respiration rates (between the spring DES values and
613 the early March values) and maximal NO_{2+3} fluxes (between the summer UES values and the
614 November values) while maximal NH_4^+ fluxes were two folds higher in our study (spring
615 DES) compared with the November values. For close water temperatures (12°C in this study
616 and 14.5°C in Kellogg et al. (2013)), the respiration rates measured in the *S. alveolata* and *C.*
617 *virginica* reefs were close. The maximal NH_4^+ and NO_{2+3} fluxes measured for the *S. alveolata*
618 reef were comparable to the ones measured respectively in April and June at the restored
619 oyster reef. Finally, maximal daily community respiration rates and NH_4^+ fluxes in this study
620 were like the ones reported for the high *U. pugettensis* density plots (Table 4). Differently,
621 maximal NO_{2+3} fluxes measured in the engineered sediments were two folds greater than the
622 ones recorded in high *U. pugettensis* density plots.

623 This comparison highlights a few interesting points on biogeochemical fluxes and
624 ecosystem engineers. First, the extend and the shape of the polychaete reefs seems to affect
625 NH_4^+ fluxes probably via the amount of organic matter trapped inside and between the
626 engineered structures. Indeed, *S. alveolata* reefs are composed of coalescent hummock
627 structures that completely recover the initial substrate (Jones et al., 2018) whereas *F.*
628 *enigmaticus* reefs are discontinuous structures between which water can pass and flush out the
629 accumulated organic matter (Bruschetti et al., 2011). Second, structural engineers like *S.*
630 *alveolata* and oysters that build coalescent structures, enhance in similar amounts sediment
631 oxygen demand, ammonium, and nitrates + nitrites fluxes. Finally, habitats built by reef-
632 forming species such as bivalve and tubicolous structural engineers could have a higher
633 potential as organic nitrogen recyclers than burrowing and bioturbating infauna like *U.*
634 *pugettensis* in engineered soft sediments (Berke, 2010).

635 **Table 4.** Sediment oxygen demand (SOD), ammonium (NH_4^+) and nitrate + nitrite fluxes (NO_{2+3}) measured in engineered habitats built by
 636 polychaetes, bivalves and crustaceans and reported in this study and three others. D'Andrea & DeWitt (2009) measured fluxes in a mudflat
 637 colonized by low, medium, and high densities of *Upogedia pugettensis*.

Engineered habitat	Study location and reference	Type of flux reported	SOD	NH_4^+	NO_{2+3}
<i>Sabellaria alveolata</i> (polychaete) reef	English Channel coast (bay of Mont-Saint-Michel, France), this study	Min – max across spring (12°C), summer (17°C) and winter (8°C)	0.03 (winter DES) – 0.33 (spring DES) $\text{g O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	0.06 (winter DES) – 0.85 (spring UES) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	0.17 (winter DES) – 1.01 (summer UES) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$
		Min – max in spring and summer (daily values)	Spring: 8.03 (193) – 10.31 (247) $\text{mmol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ Summer: 3.08 (74) – 4.24 (102) $\text{mmol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	Spring: 0.65 (15.6) – 0.85 (20.4) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ Summer: 0.25 (6) – 0.70 (16.8) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	Spring: 0.38 (9.12) – 0.53 (12.72) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ Summer: 0.32 (7.68) – 1.01 (24.24) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$
<i>Ficopomatus enigmaticus</i> (polychaete) reef	Mediterranean Sea (Tunisia), Keene 1980	exact temperature unknown	0.24 (early March) – 1.17 (late March) $\text{g O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	0.40 (November) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$	1.05 (November) $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$
Restored <i>Crassostrea virginica</i> (bivalve) reef	Maryland coast (USA), Kellogg et al. 2013	Comparable values	12.87 $\text{mmol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (November, 14.5°C)	0.8 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (April, 15.1°C)	0.46 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ 1.3 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ (June, 25.7°C)
Mudflat colonized by bioirrigating shrimp <i>Upogedia pugettensis</i> (crustacean)	Oregon coast (USA), D'Andrea & DeWitt 2009	Summer (17.1°C)	97.4 (low density) – 225.7 (high density) $\text{mmol m}^{-2}\cdot\text{d}^{-1}$	7.11 (low density) – 16.37 (high density) $\text{mmol m}^{-2}\cdot\text{d}^{-1}$	1.16 (medium density) – 11.38 (high density) $\text{mmol m}^{-2}\cdot\text{d}^{-1}$

638 4.3. *Sabellaria alveolata* and water temperature are the main drivers of the engineered
639 sediment biogeochemical functioning

640 What we termed the engineer effect (*i.e.* the engineer *S. alveolata* promotes, through its
641 density, the biogeochemical functioning of the engineered sediments) mainly results from the
642 combined biological activity of the engineer species *S. alveolata per se*, as well as the
643 meiofauna and microorganisms associated to each individual and its tube, a community likely
644 specific to complex structures like polychaete tubes (Mermillod-Blondin et al., 2004; Reise,
645 1981; Tout et al., 2014) with a temperature-dependent activity (Herbert, 1999; Thamdrup et
646 al., 1998). This study based on observational data helped us to determine some of the main
647 drivers of the biogeochemical functioning of a *S. alveolata* reef; the engineer, the water
648 temperature and the associated macrofauna through their biological traits, strongly supporting
649 the engineer effect hypothesis and giving some support to the diversity hypothesis but only at
650 relatively low levels of functional diversity. The use of terms like “effect” or “driver” are
651 somehow abusive since real causality between predictors and response variables can only be
652 determined through controlled experiments. Nonetheless, we believe this study is a first step
653 towards better understanding the functioning of these complex habitats, helping us to better
654 conserve and manage them.

655 In sediments engineered by *S. alveolata*, the number one driver of community respiration,
656 was *S. alveolata* biomass. Water temperature was not the main driver of SOD like we
657 expected according to the Q10 of 2 relation (Hildrew et al., 2007) and subtidal studies on soft
658 sediments and oyster reefs (Janson et al., 2012; Kellogg et al., 2013). Nonetheless,
659 temperature still had a small positive effect on the SOD. We measured the highest SOD
660 values in spring (12°C) and not in summer (17°C), a difference we mainly attribute to the 2-3
661 times higher engineer biomass in spring compared to summer, but also to the ripe and heavy
662 individuals ready to spawn in spring (Dubois et al., 2007a). Biomass can have a strong

663 influence on respiration rates at the individual and community level, a biomass effect we
664 observed here which clearly surpassed the effect of temperature on the SOD (Braeckman et
665 al., 2010; Clough et al., 2005; Hildrew et al., 2007; Norkko et al., 2013). Structural ecosystem
666 engineers such as *S. alveolata* can also act as agents of biogeochemical heterogeneity through
667 the structural changes they cause, affecting heat transfer processes and temperature dependent
668 microbial activity (Gutiérrez et al., 2003). Temperature loggers placed inside the reefs
669 revealed that the engineered sediments present lower heat transfers than the surrounding
670 coarse sediments (Jones, pers. obs.), indicating water temperature variations could be buffered
671 inside these sediments, probably reducing temperature-dependent aerobic respiration
672 (Thamdrup et al., 1998; Woodin et al., 2010).

673 *Sabellaria alveolata* biomass was also the number one driver of the NH_4^+ fluxes, a result
674 probably caused by two processes positively correlated to the engineer biomass and stronger
675 in spring than in summer: excretion and egestion. First, the engineer biomass has a positive
676 effect on the NH_4^+ fluxes probably because of higher excretion rates of *S. alveolata* in spring
677 when its mean biomass is the highest, a seasonality also recorded for the gastropod *Crepidula*
678 *fornicata* (Martin et al., 2006). *Sabellaria alveolata* probably also egests more feces and
679 pseudofeces (Dubois et al., 2006) in spring during the phytoplankton bloom and the main
680 reproductive season, as recorded for *Modiolus modiolus* (Navarro and Thompson, 1997).
681 These biodeposits are rapidly remineralized by associated bacteria, producing NH_4^+ (Stief,
682 2013) and linking the engineer biomass and NH_4^+ fluxes. Temperature was the second most
683 important driver of the NH_4^+ fluxes, an effect probably linked to the temperature-dependent
684 metabolic rates of the meio and macrofauna (excretion and egestion) and associated bacteria
685 (nitrogen remineralization) (Gillooly et al., 2001; Magni et al., 2000).

686 The first and second most important drivers of NO_{2+3} fluxes were *S. alveolata* abundance
687 and water temperature, respectively, probably through the promotion of nitrification by the

688 engineer and its tube and the temperature-dependent activity of nitrifying bacteria. The
689 transformation of NH_4^+ into NO_2^- and then NO_3^- requires ammonium, oxygen, and the
690 presence of aerobic nitrifying microorganisms, more active at higher water temperatures
691 (Herbert, 1999). First, a diverse community of microorganisms including nitrifying bacteria
692 are probably directly associated to the surface of *S. alveolata* as shown for other polychaetes,
693 amphipods and bivalve soft tissues (Welsh and Castadelli, 2004). Secondly, *S. alveolata*
694 density is also an indirect measure of tube density, tubes that are home to nitrifying bacteria
695 (D'Andrea and DeWitt, 2009) and act as vectors allowing oxygen to penetrate deeper into the
696 engineered sediment, ultimately promoting nitrification. Finally, the vertical movements of *S.*
697 *alveolata* in its tube increases the oxygen fluxes from the overlying water to the deeper
698 engineered sediment layers further promoting nitrification, as reported in the burrows of many
699 soft sediment organisms (Woodin et al., 2010).

700

701 *4.4. Biological traits of associated macrofauna is a secondary driver of the engineered*
702 *sediments biogeochemical functioning*

703 Using a multiple linear regression approach, we never detected a significant effect of
704 indices only used to test the diversity hypothesis (SR, N1 and FRic) or the mass-ratio
705 hypothesis (FIdel and FIdel3), on a flux. If there is an effect of a higher associated
706 macrofauna diversity or biological trait dominance on the fluxes, it is mostly accounted for by
707 *S. alveolata* abundance or biomass (engineer effect hypothesis) and by functional dispersion
708 (FDis) or functional evenness (FEve) (diversity and mass ratio hypotheses). Indeed, a
709 decrease in the abundance of *S. alveolata* is linked to an opposite increase in the abundance
710 and richness of associated macrofauna (Dubois et al., 2002; Jones et al., 2018). Furthermore,
711 75% of the species richness variability can be explained by *S. alveolata* biomass (negative
712 effect) and FDis_{ab} (positive effect). Finally, FDis_{ab} and FIdel_{ab} have a 0.99 correlation

713 indicating $FDi_{s_{ab}}$ increases with an abundance increase of higher mobility species (movement
714 capacity trait) and this index can also be used to test the mass-ratio hypothesis.

715 Functional dispersion, only weighted by abundance, was the second most important driver
716 of the SOD and multifunctionality metric, displaying in both cases a concave form (second
717 degree polynomial form with a negative effect size), a form also detected in sandy sediments
718 when relating benthic species richness and ammonium fluxes (Thrush et al., 2017). Maximal
719 values of the two functions were detected for $FDi_{s_{ab}}$ values of *ca.* 0.19 for SOD and *ca.* 0.16
720 for the multifunctionality metric, corresponding to the middle of the disturbance continuum
721 present in the engineered sediments (slightly disturbed reefs). Bumped-shaped relationships
722 seem to be relatively common in cross community studies possibly because the explanatory
723 variables are more variable and have a wider range of values in these studies than in a single
724 community type helping to detect these functional forms (Mittelbach et al., 2001; Thrush and
725 Lohrer, 2012). We deliberately sampled two different engineered sediment typologies
726 characterized by different communities dominated by the engineer species but with a large
727 diversity gradient, favoring the detection of this concave functional form.

728 Mechanisms linked to the diversity hypothesis such as resource partitioning and niche
729 complementarity (Tilman, 1997) or non-additive interactions among species through trait
730 redundancy (insurance hypothesis, Yachi and Loreau (1999)) probably explain the positive
731 effect low functional diversity has on the SOD and the global biogeochemical functioning
732 (Brose and Hillebrand, 2016). The presence of species with modalities like *S. alveolata*,
733 especially regarding their mobility (*e.g.* *Magallana gigas*, *Mytilus cf. galloprovincialis*), limit
734 the functional loss due to the increasing disturbance and the resulting decrease of the engineer
735 species abundance (Dubois et al., 2006, 2002). Other species with no to low movement
736 capacities and with modalities complementary to *S. alveolata* (*e.g.* *Venerupis corrugata*)

737 regarding other traits (e.g. sediment reworking) enhance the global biogeochemical
738 functioning of the engineered sediments (Bruno et al., 2003; Stachowicz, 2001).

739 In a second phase, interferences between species' modalities (i.e. interference
740 competition) seem to limit biogeochemical processes like organic matter remineralization,
741 leading to the negative effect of high functional diversity on biogeochemical fluxes (Brose
742 and Hillebrand, 2016). Indeed, structural engineers such as *S. alveolata* likely build habitats
743 where the local environmental conditions are optimal for them and where they are likely the
744 best performing species of the assemblage for most ecosystem functions, including
745 biogeochemical fluxes (Gamfeldt et al., 2015). Consequently, a functional dispersion above
746 0.16-0.19 could translate into a stronger spatial and/or trophic competition between the
747 associated macrofauna and *S. alveolata* (Dubois et al., 2006; Jones et al., 2018), potentially
748 leading to lower metabolic rates of the engineer species (e.g. respiration) and to lower global
749 fluxes. Functionally dissimilar species could also disrupt the local conditions created by the
750 engineer, for example through the destruction of *S. alveolata* tubes (e.g. *Carcinus maenas*
751 excavate *S. alveolata* tubes), decreasing nutrient cycling.

752 Furthermore, functional dispersion weighted by abundance had a strictly negative effect
753 on the NH_4^+ fluxes. Considering the strong correlation between FDis_{ab} and FIde_{ab} , this result
754 supports the mass-ratio hypothesis and is probably linked to the same mechanisms as the ones
755 explaining the negative effect of higher functional diversity levels on the SOD and
756 multifunctionality. Even at low functional diversity levels, we did not detect a positive effect
757 of increasing diversity on the NH_4^+ fluxes. The loss of *S. alveolata* type species in terms of
758 mobility and the addition of species with different modality combinations seems to rapidly
759 impair NH_4^+ fluxes, probably through the loss of sessile bivalves and polychaetes, organisms
760 that strongly influence these fluxes through excretion and biodeposit production (Stief, 2013).

761 Finally, functional evenness (abundance weighted only), an index informing on the
762 regularity of the abundance distribution in the functional space, had a weak negative effect on
763 the NO_{2+3} fluxes. A high value of FEve indicates a homogenous distribution of the species
764 and of their abundance in the functional space with similar distance between species (Villéger
765 et al., 2008). Consequently, NO_{2+3} fluxes seem to be promoted by the presence of several
766 clumps of species with similar trait combinations, indicating that a certain level of biological
767 trait redundancy associated to a certain level of species richness (*ca.* 10 species), is necessary
768 for an optimal nitrogen cycling in the reef.

769

770 4.5. Global biogeochemical functioning of the engineered sediments

771 Overall, the biogeochemical functioning of the sediments engineered by *S. alveolata* was
772 much more intense than that of the soft sediments surrounding the engineered sediments, a
773 difference likely linked to the abundant and diversified macrofauna, meiofauna and
774 microorganisms promoted by the reef structures and the engineer itself. Focusing on the
775 engineered sediments, we found that water temperature is the main driver of their global
776 biogeochemical functioning, followed by *S. alveolata* biomass and the macrofauna functional
777 dispersion weighted by abundance. Consequently, tubicolous structural engineers such as *S.*
778 *alveolata* have biomass-dependent effects on biogeochemical fluxes as do burrowing and
779 bioturbating infauna (Braeckman et al., 2010; D'Andrea and DeWitt, 2009; Norkko et al.,
780 2013; Thrush et al., 2017), suggesting this could be a general property of many marine
781 ecosystem engineers. Furthermore, the concave effect FDis_{ab} has on the multifunctionality
782 metric brings support to the diversity hypothesis at low levels of functional dispersion (0.01-
783 0.16), when sessile species with complementarity modalities for other traits dominate the
784 engineered sediments. When functional dispersion is higher (0.16-0.36), the biogeochemical
785 functioning of the engineered sediments is promoted by higher abundances of species with no

786 to low movement capacities (higher $F_{Ide1_{ab}}$), bringing support to the mass-ratio hypothesis, as
787 found in autotrophic terrestrial systems (Díaz et al., 2007; Garnier et al., 2004; Mokany et al.,
788 2008) and across field studies on soil fauna (Gagic et al., 2015). The concave effect of $F_{Dis_{ab}}$
789 on the multifunctionality metric also indicates an intermediate macrofauna trait diversity
790 could maximize the global biogeochemical functioning of a *S. alveolata* reef through trait
791 redundancy and niche complementarity.

792 Maintaining a high abundance and biomass of the engineer species appears paramount if
793 we wish to further maintain ecosystem processes performed by this habitat such as organic
794 matter remineralization and nitrogen cycling; indeed, our results evidence that a good physical
795 status of the reef structure (prograding areas with high tube density) leads to a good ecological
796 functioning of the reef. Local disturbances (reef degradation) can increase species number
797 (Dubois et al., 2020) and possibly enhance functional diversity, which does not appear, at
798 first, as detrimental in terms of biogeochemical fluxes. However, anthropogenic disturbances
799 such as trampling should be limited as much as possible, as they could alter *S. alveolata*
800 biomass in the long term (Desroy et al., 2011; Plicanti et al., 2016). Complementary studies
801 should aim at manipulating disturbance levels and/or species composition, measuring other
802 functions such as primary and secondary production or consumption and studying other *S.*
803 *alveolata* reefs to test if engineer biomass and functional dispersion weighted by abundance
804 could be used as indicators of *S. alveolata* reef functioning.

805

806 CONCLUSION

807 In a conservation goal, identifying indices that inform us on the global functioning of
808 ecosystems and its evolution is paramount. In the case of *S. alveolata* reefs, our study
809 indicates the two most important parameters to measure are the biomass and abundance of the
810 engineer species. In a second step, estimating the abundance of the associated species (and not

811 their biomass) and focusing on their respective movement capacities, a trait associated to a
812 species' sediment reworking abilities (Queirós et al., 2013) and known to affect many
813 biogeochemical fluxes (Braeckman et al., 2010; Ieno et al., 2006; Mermillod-Blondin et al.,
814 2005; Michaud et al., 2005), can help to evaluate more precisely the reef's biogeochemical
815 functioning. Biomass is often considered as more functionally relevant than abundance
816 especially when the process is size-based (Gagic et al., 2015; Mouillot et al., 2011) and large
817 macrofauna have been shown to play a prominent role in soft sediment biogeochemical fluxes
818 (Norkko et al., 2013; Thrush et al., 2006). Nonetheless, soft sediments engineered into hard
819 substrata by *S. alveolata* act as an environmental filter and only relatively small organisms
820 can establish between the engineer tubes and affect biogeochemical fluxes (Jones et al.,
821 2018). Consequently, in this highly size-constrained habitat, abundance appears to be more
822 important than biomass in explaining biogeochemical fluxes.

823

824 **Acknowledgements**

825 This project was funded by an EC2CO DRIL (CNRS) grant. A. G. J. was supported by the
826 "Laboratoire d' Excellence" LabexMER (ANR-10-LABX-19) and co-funded by a grant from
827 the French government under the program "Investissements d'Avenir" and by a Région
828 Bretagne/Ifremer PhD grant. Our funding source was not involved in the different phases of
829 this study. We thank all the people that helped us on the field (Flavie Delanzy, Ludovic
830 Goyot, Bernard Delaunay) and in the lab (Angelica Navarro, Célia Bellengier, Louise
831 Lanrivain). Finally, we wish to thank the two anonymous reviewers who helped improve this
832 manuscript.

833

834 **References**

835

836 Ataide, M.B., Venekey, V., Filho, J.S.R., Santos, P.J.P. dos, 2014. Sandy reefs of *Sabellaria*
837 *wilsoni* (Polychaeta: Sabellariidae) as ecosystem engineers for meiofauna in the

- 838 Amazon coastal region, Brazil. *Marine Biodiversity* 44, 403–413.
839 <https://doi.org/10.1007/s12526-014-0248-x>
- 840 Ayata, S.-D., Ellien, C., Dumas, F., Dubois, S., Thiebaut, E., 2009. Modelling larval dispersal
841 and settlement of the reef-building polychaete *Sabellaria alveolata*: Role of
842 hydroclimatic processes on the sustainability of biogenic reefs. *Continental Shelf*
843 *Research* 29, 1605–1623. <https://doi.org/10.1016/j.csr.2009.05.002>
- 844 Berke, S.K., 2010. Functional groups of ecosystem engineers: a proposed classification with
845 comments on current issues. *Integr. Comp. Biol.* 50, 147–157.
846 <https://doi.org/10.1093/icb/icq077>
- 847 Bonnot-Courtois, C., Fournier, J., Dréau, A., 2004. Recent morphodynamics of shell banks in
848 the western part of the Bay of Mont-Saint-Michel (France) / Morphodynamique
849 actuelle des bancs coquilliers dans la partie occidentale de la baie du Mont-Saint-
850 Michel (France). *Géomorphologie: relief, processus, environnement* 10, 65–79.
851 <https://doi.org/10.3406/morfo.2004.1200>
- 852 Bouma, T.J., Olenin, S., Reise, K., Ysebaert, T., 2009. Ecosystem engineering and
853 biodiversity in coastal sediments: posing hypotheses. *Helgoland Marine Research* 63,
854 95–106. <https://doi.org/10.1007/s10152-009-0146-y>
- 855 Braeckman, U., Provoost, P., Gribsholt, B., Van Gansbeke, D., Middelburg, J.J., Soetaert, K.,
856 Vincx, M., Vanaverbeke, J., 2010. Role of macrofauna functional traits and density in
857 biogeochemical fluxes and bioturbation. *Marine Ecology Progress Series* 399, 173–
858 186. <https://doi.org/10.3354/meps08336>
- 859 Brose, U., Hillebrand, H., 2016. Biodiversity and ecosystem functioning in dynamic
860 landscapes. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 371.
861 <https://doi.org/10.1098/rstb.2015.0267>
- 862 Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Incorporating facilitation into ecological
863 theory. *Trends in Ecology and Evolution* 18, 119–125. [https://doi.org/10.1016/S0169-5347\(02\)00045-9](https://doi.org/10.1016/S0169-5347(02)00045-9)
- 864 Bruschetti, M., Bazterrica, C., Fanjul, E., Luppi, T., Iribarne, O., 2011. Effect of biodeposition
865 of an invasive polychaete on organic matter content and productivity of the sediment
866 in a coastal lagoon. *Journal of Sea Research* 66, 20–28.
867 <https://doi.org/10.1016/j.seares.2011.04.007>
- 868 Cadotte, M.W., 2017. Functional traits explain ecosystem function through opposing
869 mechanisms. *Ecol Lett* 20, 989–996. <https://doi.org/10.1111/ele.12796>
- 870 Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L.,
871 Balvanera, P., O'Connor, M.I., Gonzalez, A., 2011. The functional role of producer
872 diversity in ecosystems. *American journal of botany* 98, 572–592.
873 <https://doi.org/10.1111/j.1461-0248.2007.01037.x>
- 874 Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of
875 long-term ecological data. *Freshwater Biology* 31, 295–309.
876 <https://doi.org/10.1111/j.1365-2427.1994.tb01742.x>
- 877 Clough, L.M., Renaud, P.E., Ambrose Jr., W.G., 2005. Impacts of water depth, sediment
878 pigment concentration, and benthic macrofaunal biomass on sediment oxygen demand
879 in the western Arctic Ocean. *Can. J. Fish. Aquat. Sci.* 62, 1756–1765.
880 <https://doi.org/10.1139/f05-102>
- 881 Covich, A.P., Austen, M.C., Bärlocher, F., Chauvet, E., Cardinale, B.J., Biles, C.L., Inchausti,
882 P., Dangles, O., Solan, M., Gessner, M.O., 2004. The role of biodiversity in the
883 functioning of freshwater and marine benthic ecosystems. *BioScience* 54, 767–775.
- 884 Curd, A., Pernet, F., Corporeau, C., Delisle, L., Firth, L.B., Nunes, F.L.D., Dubois, S.F.,
885 2019. Connecting organic to mineral: How the physiological state of an ecosystem-

- 887 engineer is linked to its habitat structure. *Ecological Indicators* 98, 49–60.
888 <https://doi.org/10.1016/j.ecolind.2018.10.044>
- 889 D'Andrea, A.F., DeWitt, T.H., 2009. Geochemical ecosystem engineering by the mud shrimp
890 *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: Density-
891 dependent effects on organic matter remineralization and nutrient cycling. *Limnol.*
892 *Oceanogr.* 54, 1911–1932. <https://doi.org/10.4319/lo.2009.54.6.1911>
- 893 Desroy, N., Dubois, S.F., Fournier, J., Ricquiers, L., Le Mao, P., Guerin, L., Gerla, D.,
894 Rougerie, M., Legendre, A., 2011. The conservation status of *Sabellaria alveolata* (L.)
895 (Polychaeta: Sabellariidae) reefs in the Bay of Mont-Saint-Michel. *Aquatic*
896 *Conservation: Marine and Freshwater Ecosystems* 21, 462–471.
897 <https://doi.org/10.1002/aqc.1206>
- 898 Dias, A.S., Paula, J., 2001. Associated fauna of *Sabellaria alveolata* colonies on the central
899 coast of Portugal. *Journal of the Marine Biological Association of the United*
900 *Kingdom* 81, 169–170. <https://doi.org/10.1017/S0025315401003538>
- 901 Díaz, S., Lavorel, S., Bello, F. de, Quéfier, F., Grigulis, K., Robson, T.M., 2007.
902 Incorporating plant functional diversity effects in ecosystem service assessments.
903 *PNAS* 104, 20684–20689. <https://doi.org/10.1073/pnas.0704716104>
- 904 Dubois, S., Commito, J.A., Olivier, F., Retière, C., 2006. Effects of epibionts on *Sabellaria*
905 *alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-
906 Michel. *Estuarine, Coastal and Shelf Science* 68, 635–646.
907 <https://doi.org/10.1016/j.ecss.2006.03.010>
- 908 Dubois, S., Comtet, T., Retière, C., Thiébaud, E., 2007a. Distribution and retention of
909 *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-
910 Michel, France. *Marine Ecology Progress Series* 346, 243–254.
911 <https://doi.org/10.3354/meps07011>
- 912 Dubois, S., Orvain, F., MarinLal, J.C., Ropert, M., Lefebvre, S., 2007b. Small-scale spatial
913 variability of food partitioning between cultivated oysters and associated suspension-
914 feeding species, as revealed by stable isotopes. *Marine Ecology Progress Series* 336,
915 151–160. <https://doi.org/10.3354/meps336151>
- 916 Dubois, S., Retière, C., Olivier, F., 2002. Biodiversity associated with *Sabellaria alveolata*
917 (Polychaeta: Sabellariidae) reefs: effects of human disturbances. *Journal of the Marine*
918 *Biological Association of the United Kingdom* 82, 817–826.
919 <https://doi.org/10.1017/S0025315402006185>
- 920 ETI BioInformatics, n.d. Marine species identification portal [WWW Document]. *Marine*
921 *Species Identification Portal*. URL <http://species-identification.org/index.php>
- 922 Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds.
923 Aberdeen University Press.
- 924 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M.,
925 Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharrntke, T., Weisser, W.,
926 Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem
927 functioning better than species-based indices. *Proceedings of the Royal Society B:*
928 *Biological Sciences* 282, 20142620. <https://doi.org/10.1098/rspb.2014.2620>
- 929 Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2015.
930 Marine biodiversity and ecosystem functioning: what's known and what's next? *Oikos*
931 124, 252–265. <https://doi.org/10.1111/oik.01549>
- 932 Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G.,
933 Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant
934 functional markers capture ecosystem properties during secondary succession.
935 *Ecology* 85, 2630–2637. <https://doi.org/10.1890/03-0799>

- 936 Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size
937 and temperature on metabolic rate. *Science* 293, 2248–2251.
938 <https://doi.org/10.1126/science.1061967>
- 939 Godbold, J.A., Bulling, M.T., Solan, M., 2011. Habitat structure mediates biodiversity effects
940 on ecosystem properties. *Proceedings of the Royal Society of London B: Biological*
941 *Sciences* 278, 2510–2518. <https://doi.org/10.1098/rspb.2010.2414>
- 942 Godbold, J.A., Solan, M., 2009. Relative importance of biodiversity and the abiotic
943 environment in mediating an ecosystem process. *Marine Ecology Progress Series* 396,
944 273–282. <https://doi.org/10.3354/meps08401>
- 945 Goldberg, W.M., 2013. *The biology of reefs and reef organisms*. The University of Chicago
946 Press, Chicago and London.
- 947 Gray, J.S., 2000. The measurement of marine species diversity, with an application to the
948 benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine*
949 *Biology and Ecology* 250, 23–49. [https://doi.org/10.1016/S0022-0981\(00\)00178-7](https://doi.org/10.1016/S0022-0981(00)00178-7)
- 950 Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder
951 effects. *Journal of Ecology* 86, 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- 952
- 953 Gruet, Y., 1986. Spatio-temporal changes of sabellarian reefs built by the sedentary
954 polychaete *Sabellaria alveolata* (Linne). *Marine Ecology* 7, 303–319.
955 <https://doi.org/10.1111/j.1439-0485.1986.tb00166.x>
- 956 Gruet, Y., 1972. Aspects morphologiques et dynamiques de constructions de l'Annelide
957 polychete *Sabellaria alveolata* (Linne). *Revue des Travaux de l'Institut des Pêches*
958 *Maritimes* 36, 131–161.
- 959 Guerra-García, J.M., Tierno de Figueroa, J.M., Navarro-Barranco, C., Ros, M., Sánchez-
960 Moyano, J.E., Moreira, J., 2014. Dietary analysis of the marine Amphipoda
961 (Crustacea: Peracarida) from the Iberian Peninsula. *Journal of Sea Research* 85, 508–
962 517. <https://doi.org/10.1016/j.seares.2013.08.006>
- 963 Gutiérrez, J.L., Jones, C.G., 2006. Physical ecosystem engineers as agents of biogeochemical
964 heterogeneity. *BioScience* 56, 227–236. [https://doi.org/10.1641/0006-3568\(2006\)056\[0227:PEEAAO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)056[0227:PEEAAO]2.0.CO;2)
- 965
- 966 Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem
967 engineers: the role of shell production in aquatic habitats. *Oikos* 101, 79–90.
968 <https://doi.org/10.1034/j.1600-0706.2003.12322.x>
- 969 Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos,
970 P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-
971 Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns,
972 A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J.,
973 Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry,
974 A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity
975 and productivity experiments in european grasslands. *Science* 286, 1123–1127.
976 <https://doi.org/10.1126/science.286.5442.1123>
- 977 Heisterkamp, I.M., Schramm, A., Larsen, L.H., Svenningsen, N.B., Lavik, G., de Beer, D.,
978 Stief, P., 2013. Shell biofilm-associated nitrous oxide production in marine molluscs:
979 processes, precursors and relative importance. *Environmental Microbiology* 15, 1943–
980 1955. <https://doi.org/10.1111/j.1462-2920.2012.02823.x>
- 981 Herbert, R.A., 1999. Nitrogen cycling in coastal marine ecosystems. *FEMS Microbiol Rev* 23,
982 563–590. <https://doi.org/10.1111/j.1574-6976.1999.tb00414.x>
- 983 Hewitt, J.E., Thrush, S.F., Halliday, J., Duffy, C., 2005. The importance of small-scale habitat
984 structure for maintaining beta diversity. *Ecology* 86, 1619–1626.
985 <https://doi.org/10.1890/04-1099>

- 986 Hildrew, A.G., Raffaelli, D.G., Edmonds-Brown, R., 2007. Body size: the structure and
987 function of aquatic ecosystems. Cambridge University Press.
988 <https://doi.org/10.1017/CBO9780511611223>
- 989 Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*
990 54, 427–432. <https://doi.org/10.2307/1934352>
- 991 Holt, T.J., Rees, E.I., Hawkins, S.J., Seed, R., 1998. Biogenic reefs. An overview of dynamic
992 and sensitivity characteristics for conservation management of marine SACs. Scottish
993 Association for Marine Science, UK Marine SACs Project.
- 994 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H.,
995 Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J.,
996 Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning:
997 a consensus of current knowledge. *Ecological Monographs* 75, 3–35.
998 <https://doi.org/10.1890/04-0922>
- 999 Hooper, D.U., Vitousek, P.M., 1997. The effects of plant composition and diversity on
1000 ecosystem processes. *Science* 277, 1302–1305.
1001 <https://doi.org/10.1126/science.277.5330.1302>
- 1002 Huettel, M., Røy, H., Precht, E., Ehrenhauss, S., 2003. Hydrodynamical impact on
1003 biogeochemical processes in aquatic sediments. *Hydrobiologia* 494, 231–236.
1004 <https://doi.org/10.1023/A:1025426601773>
- 1005 Ieno, E.N., Solan, M., Batty, P., Pierce, G.J., 2006. How biodiversity affects ecosystem
1006 functioning: roles of infaunal species richness, identity and density in the marine
1007 benthos. *Mar Ecol Prog Ser* 311, 263–271. <https://doi.org/10.3354/meps311263>
- 1008 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, I., 2019.
1009 Summary for policymakers of the global assessment report on biodiversity and
1010 ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity
1011 and Ecosystem Services. Zenodo. <https://doi.org/10.5281/zenodo.3553579>
- 1012 Janson, A.L., Denis, L., Rauch, M., Desroy, N., 2012. Macrobenthic biodiversity and oxygen
1013 uptake in estuarine systems: The example of the Seine estuary. *Journal of Soils and*
1014 *Sediments* 12, 1568–1580. <https://doi.org/10.1007/s11368-012-0557-2>
- 1015 Jones, A.G., Dubois, S.F., Desroy, N., Fournier, J., 2018. Interplay between abiotic factors
1016 and species assemblages mediated by the ecosystem engineer *Sabellaria alveolata*
1017 (Annelida: Polychaeta). *Estuarine, Coastal and Shelf Science*.
1018 <https://doi.org/10.1016/j.ecss.2017.10.001>
- 1019 Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as
1020 physical ecosystem engineers. *Ecology* 78, 1946–1957. [https://doi.org/10.1890/0012-9658\(1997\)078\[1946:PANEOO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2)
- 1021 Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69,
1022 373–386. <https://doi.org/10.2307/3545850>
- 1023 Jones, J.G., Berner, R.A., Meadows, P.S., Durand, B., Eglinton, G., Eglinton, G., Curtis, C.D.,
1024 McKenzie, D.P., Murchison, D.G., 1985. Microbes and microbial processes in
1025 sediments. *Philosophical Transactions of the Royal Society of London. Series A,*
1026 *Mathematical and Physical Sciences* 315, 3–17. <https://doi.org/10.1098/rsta.1985.0025>
- 1027 Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of
1028 polychaete feeding guilds. *Annual Review of Marine Science* 7, 497–520.
1029 <https://doi.org/10.1146/annurev-marine-010814-020007>
- 1030 Keene, W.C., 1980. The importance of a reef-forming polychaete, *Mercierella enigmatica*
1031 *fauvel*, in the oxygen and nutrient dynamics of a hypereutrophic subtropical lagoon.
1032 *Estuarine and Coastal Marine Science* 11, 167–178. [https://doi.org/10.1016/S0302-3524\(80\)80039-9](https://doi.org/10.1016/S0302-3524(80)80039-9)
- 1033
1034

- 1035 Kellogg, M.L., Cornwell, J.C., Owens, M.S., Paynter, K.T., 2013. Denitrification and nutrient
1036 assimilation on a restored oyster reef. *Marine Ecology Progress Series* 480, 1–19.
1037 <https://doi.org/10.3354/meps10331>
- 1038 Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment
1039 processes. *Journal of sea Research* 59, 30–43.
1040 <https://doi.org/10.1016/j.seares.2007.05.004>
- 1041 Kristensen, E., 1988. Benthic fauna and biogeochemical processes in marine sediments:
1042 microbial activities and fluxes, in: *Nitrogen Cycling in Coastal Marine Environments*.
1043 Blackburn, T.H., Sørensen, J., Chichester, pp. 275–299.
- 1044 Kristensen, E., Kostka, J.E., 2005. Macrofaunal burrows and irrigation in marine sediment:
1045 microbiological and biogeochemical interactions, in: *Interactions between Macro- and*
1046 *Microorganisms in Marine Sediments, Coastal and Estuarine Studies*. American
1047 Geophysical Union (AGU), pp. 125–157. <https://doi.org/10.1029/CE060p0125>
- 1048 Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional
1049 diversity from multiple traits. *Ecology* 91, 299–305. <https://doi.org/10.1890/08-2244.1>
- 1050 Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem
1051 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545–
1052 556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- 1053 Le Cam, J.-B., Fournier, J., Etienne, S., Couden, J., 2011. The strength of biogenic sand reefs:
1054 Visco-elastic behaviour of cement secreted by the tube building polychaete *Sabellaria*
1055 *alveolata*, Linnaeus, 1767. *Estuarine, Coastal and Shelf Science* 91, 333–339.
1056 <https://doi.org/10.1016/j.ecss.2010.10.036>
- 1057 Lejart, M., Clavier, J., Chauvaud, L., Hily, C., 2012. Respiration and calcification of
1058 *Crassostrea gigas*: contribution of an intertidal invasive species to coastal ecosystem
1059 co2 fluxes. *Estuaries and Coasts* 35, 622–632. [https://doi.org/10.1007/s12237-011-](https://doi.org/10.1007/s12237-011-9462-y)
1060 9462-y
- 1061 Magni, P., Montani, S., Takada, C., Tsutsumi, H., 2000. Temporal scaling and relevance of
1062 bivalve nutrient excretion on a tidal flat of the Seto Inland Sea, Japan. *Marine Ecology*
1063 *Progress Series* 198, 139–155. <https://doi.org/10.3354/meps198139>
- 1064 MarLIN, 2006. BIOTIC [WWW Document]. BIOTIC - Biological Traits Information
1065 Catalogue. URL www.marlin.ac.uk/biotic
- 1066 Martin, S., Thouzeau, G., Chauvaud, L., Jean, F., Guérin, L., Clavier, J., 2006. Respiration,
1067 calcification, and excretion of the invasive slipper limpet, *Crepidula fornicata* L.:
1068 Implications for carbon, carbonate, and nitrogen fluxes in affected areas. *Limnol.*
1069 *Oceanogr.* 51, 1996–2007. <https://doi.org/10.4319/lo.2006.51.5.1996>
- 1070 Mermillod-Blondin, F., François-Carcaillet, F., Rosenberg, R., 2005. Biodiversity of benthic
1071 invertebrates and organic matter processing in shallow marine sediments: an
1072 experimental study. *Journal of Experimental Marine Biology and Ecology* 315, 187–
1073 209. <https://doi.org/10.1016/j.jembe.2004.09.013>
- 1074 Mermillod-Blondin, F., Rosenberg, R., François-Carcaillet, F., Norling, K., Mauclaire, L.,
1075 2004. Influence of bioturbation by three benthic infaunal species on microbial
1076 communities and biogeochemical processes in marine sediment. *Aquatic Microbial*
1077 *Ecology* 36, 271–284. <https://doi.org/10.3354/ame036271>
- 1078 Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B., Stora, G., 2005. The
1079 functional group approach to bioturbation: The effects of biodiffusers and gallery-
1080 diffusers of the *Macoma balthica* community on sediment oxygen uptake. *Journal of*
1081 *Experimental Marine Biology and Ecology* 326, 77–88.
1082 <https://doi.org/10.1016/j.jembe.2005.05.016>
- 1083 Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B.,
1084 Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship

- 1085 between species richness and productivity? *Ecology* 82, 2381–2396.
 1086 [https://doi.org/10.1890/0012-9658\(2001\)082\[2381:WITORB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2381:WITORB]2.0.CO;2)
- 1087 Mokany, K., Ash, J., Roxburgh, S., 2008. Functional identity is more important than diversity
 1088 in influencing ecosystem processes in a temperate native grassland. *Journal of*
 1089 *Ecology* 96, 884–893. <https://doi.org/10.1111/j.1365-2745.2008.01395.x>
- 1090 Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A
 1091 functional approach reveals community responses to disturbances. *Trends in Ecology*
 1092 *& Evolution* 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- 1093 Mouillot, D., Villéger, S., Scherer-Lorenzen, M., Mason, N.W., 2011. Functional structure of
 1094 biological communities predicts ecosystem multifunctionality. *PloS one* 6, e17476.
 1095 <https://doi.org/10.1371/journal.pone.0017476>
- 1096 Muir, A.P., Nunes, F.L.D., Dubois, S.F., Pernet, F., 2016. Lipid remodelling in the reef-
 1097 building honeycomb worm, *Sabellaria alveolata*, reflects acclimation and local
 1098 adaptation to temperature. *Scientific Reports* 6. <https://doi.org/10.1038/srep35669>
- 1099 Naeem, S., Håkansson, K., Lawton, J.H., Crawley, M.J., Thompson, L.J., 1996. Biodiversity
 1100 and plant productivity in a model assemblage of plant species. *Oikos* 76, 259–264.
 1101 <https://doi.org/10.2307/3546198>
- 1102 Navarro, J.M., Thompson, R.J., 1997. Biodeposition by the horse mussel *Modiolus modiolus*
 1103 (*Dillwyn*) during the spring diatom bloom. *Journal of Experimental Marine Biology*
 1104 *and Ecology* 209, 1–13. [https://doi.org/10.1016/0022-0981\(96\)02681-0](https://doi.org/10.1016/0022-0981(96)02681-0)
- 1105 Navarro-Barranco, C., Tierno-de-Figueroa, J.M., Guerra-García, J.M., Sánchez-Tocino, L.,
 1106 García-Gómez, J.C., 2013. Feeding habits of amphipods (Crustacea: Malacostraca)
 1107 from shallow soft bottom communities: comparison between marine caves and open
 1108 habitats. *Journal of Sea Research* 78, 1–7. <https://doi.org/10.1016/j.seares.2012.12.011>
- 1109 Newell, R.I.E., Cornwell, J.C., Owens, M.S., 2002. Influence of simulated bivalve
 1110 biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory
 1111 study. *Limnol. Oceanogr.* 47, 1367–1379. <https://doi.org/10.4319/lo.2002.47.5.1367>
- 1112 Noernberg, M.A., Fournier, J., Dubois, S., Populus, J., 2010. Using airborne laser altimetry to
 1113 estimate *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs volume in tidal flat
 1114 environments. *Estuarine, Coastal and Shelf Science* 90, 93–102.
 1115 <https://doi.org/10.1016/j.ecss.2010.07.014>
- 1116 Norkko, A., Villnäs, A., Norkko, J., Valanko, S., Pilditch, C., 2013. Size matters: implications
 1117 of the loss of large individuals for ecosystem function. *Sci Rep* 3, 1–7.
 1118 <https://doi.org/10.1038/srep02646>
- 1119 Norling, P., Kautsky, N., 2007. Structural and functional effects of *Mytilus edulis* on diversity
 1120 of associated species and ecosystem functioning. *Marine Ecology Progress Series* 351,
 1121 163–175. <https://doi.org/10.3354/meps07033>
- 1122 Passarelli, C., Olivier, F., Paterson, D.M., Meziante, T., Hubas, C., 2014. Organisms as
 1123 cooperative ecosystem engineers in intertidal flats. *Journal of Sea Research* 92, 92–
 1124 101. <https://doi.org/10.1016/j.seares.2013.07.010>
- 1125 Plicanti, A., Domínguez, R., Dubois, S.F., Bertocci, I., 2016. Human impacts on biogenic
 1126 habitats: Effects of experimental trampling on *Sabellaria alveolata* (Linnaeus, 1767)
 1127 reefs. *Journal of Experimental Marine Biology and Ecology* 478, 34–44.
 1128 <https://doi.org/10.1016/j.jembe.2016.02.001>
- 1129 Porta, B.L., Nicoletti, L., 2009. *Sabellaria alveolata* (Linnaeus) reefs in the central
 1130 Tyrrhenian Sea (Italy) and associated polychaete fauna. *Zoosymposia* 2, 527–536.
 1131 <https://doi.org/10.11646/zoosymposia.2.1.36>
- 1132 Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-
 1133 Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G.,

- 1134 Widdicombe, S., 2013. A bioturbation classification of European marine infaunal
1135 invertebrates. *Ecol Evol* 3, 3958–3985. <https://doi.org/10.1002/ece3.769>
- 1136 Reise, K., 1981. High abundance of small zoobenthos around biogenic structures in tidal
1137 sediments of the Wadden Sea. *Helgolander Meeresunters* 34, 413–425.
1138 <https://doi.org/10.1007/BF01995914>
- 1139 Revsbech, N.P., 1989. An oxygen microsensor with a guard cathode. *Limnol. Oceanogr.* 34,
1140 474–478. <https://doi.org/10.4319/lo.1989.34.2.0474>
- 1141 Romero, G.Q., Gonçalves□Souza, T., Vieira, C., Koricheva, J., 2015. Ecosystem engineering
1142 effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*
1143 90, 877–890. <https://doi.org/10.1111/brv.12138>
- 1144 Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients.
1145 *Methods in Ecology and Evolution* 1, 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- 1147 Shumway, S.E., 1979. The effects of body size, oxygen tension and mode of life on the
1148 oxygen uptake rates of polychaetes. *Comparative Biochemistry and Physiology Part*
1149 *A: Physiology* 64, 273–278. [https://doi.org/10.1016/0300-9629\(79\)90660-1](https://doi.org/10.1016/0300-9629(79)90660-1)
- 1150 Smyth, A.R., Geraldi, N.R., Thompson, S.P., Piehler, M.F., 2016. Biological activity exceeds
1151 biogenic structure in influencing sediment nitrogen cycling in experimental oyster
1152 reefs. *Marine Ecology Progress Series* 560, 173–183.
1153 <https://doi.org/10.3354/meps11922>
- 1154 Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava,
1155 D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306,
1156 1177–1180. <https://doi.org/10.1126/science.1103960>
- 1157 Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities
1158 positive interactions play a critical, but underappreciated, role in ecological
1159 communities by reducing physical or biotic stresses in existing habitats and by
1160 creating new habitats on which many species depend. *BioScience* 51, 235–246.
1161 [https://doi.org/10.1641/0006-3568\(2001\)051\[0235:MFATSO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2)
- 1162 Stief, P., 2013. Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic
1163 macrofauna: mechanisms and environmental implications. *Biogeosciences* 10, 7829–
1164 7846. <https://doi.org/10.5194/bg-10-7829-2013>
- 1165 Thamdrup, B., Hansen, J.W., Jørgensen, B.B., 1998. Temperature dependence of aerobic
1166 respiration in a coastal sediment. *FEMS Microbiol Ecol* 25, 189–200.
1167 <https://doi.org/10.1111/j.1574-6941.1998.tb00472.x>
- 1168 Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., 2006. Functional role of
1169 large organisms in intertidal communities: community effects and ecosystem function.
1170 *Ecosystems* 9, 1029–1040. <https://doi.org/10.1007/s10021-005-0068-8>
- 1171 Thrush, S.F., Hewitt, J.E., Kraan, C., Lohrer, A.M., Pilditch, C.A., Douglas, E., 2017.
1172 Changes in the location of biodiversity–ecosystem function hot spots across the
1173 seafloor landscape with increasing sediment nutrient loading. *Proc. R. Soc. B* 284,
1174 20162861. <https://doi.org/10.1098/rspb.2016.2861>
- 1175 Thrush, S.F., Lohrer, A.M., 2012. Why bother going outside: the role of observational studies
1176 in understanding biodiversity-ecosystem function relationships, in: *Marine*
1177 *Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and*
1178 *Integration*. Oxford University Press.
- 1179 Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity.
1180 *Ecology* 78, 81–92. [https://doi.org/10.1890/0012-9658\(1997\)078\[0081:CIRLAG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2)
- 1182 Tout, J., Jeffries, T.C., Webster, N.S., Stocker, R., Ralph, P.J., Seymour, J.R., 2014.
1183 Variability in microbial community composition and function between different niches

- 1184 within a coral reef. *Microb Ecol* 67, 540–552. <https://doi.org/10.1007/s00248-013->
1185 0362-5
- 1186 Tréguer, P., Le Corre, P., 1975. Manuel d'analyse des sels nutritifs dans l'eau de mer,
1187 Laboratoire d'Océanographie Chimique. Université de Bretagne Occidentale, Brest,
1188 France.
- 1189 Vanni, M.J., 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of*
1190 *Ecology and Systematics* 33, 341–370.
1191 <https://doi.org/10.1146/annurev.ecolsys.33.010802.150519>
- 1192 Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity
1193 indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
1194 <https://doi.org/10.1890/07-1206.1>
- 1195 Welsh, D.T., Castadelli, G., 2004. Bacterial nitrification activity directly associated with
1196 isolated benthic marine animals. *Marine Biology* 144, 1029–1037.
1197 <https://doi.org/10.1007/s00227-003-1252-z>
- 1198 Woodin, S.A., Wethey, D.S., Volkenborn, N., 2010. Infaunal hydraulic ecosystem engineers:
1199 cast of characters and impacts. *Integrative and Comparative Biology* 50, 176–187.
- 1200 Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating
1201 environment: The insurance hypothesis. *Proc Natl Acad Sci U S A* 96, 1463–1468.
- 1202 Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common
1203 statistical problems. *Methods in Ecology and Evolution* 1, 3–14.
1204 <https://doi.org/10.1111/j.2041-210X.2009.00001.x>
1205

Highlights

- We studied the functioning of a reef habitat, linking it to macrofauna diversity
- We measured oxygen and nutrient fluxes using core incubations
- The reef structures had higher fluxes than the neighboring soft sediments
- The reef-builder's biomass and temperature were the main drivers of reef fluxes
- An intermediate level of macrofauna trait diversity maximized these fluxes

Journal Pre-proof

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof