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1           **Small-scale patches of detritus as habitat for invertebrates within a *Zostera noltei* meadow**

2

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17

18 **Highlights**

- 19 - The paper studies the colonisation of natural vs. artificial eelgrass detritus.
- 20 - Macrofaunal assemblages colonising seagrass shoots are measured.
- 21 - Empty litterbags are used to test for their attractiveness.
- 22 - Macrofaunal assemblages of natural and artificial detritus show no differences.
- 23 - Habitat structural complexity shows no effects on the colonisation of the detritus.

24

25 **Abstract**

26 Seagrass detritus can attract numerous invertebrates as it provides food and substrate within the  
27 meadow or in adjacent environments. Nonetheless, several factors could modify the invertebrate  
28 response to this habitat.

29 In this study, we tested if epifaunal colonisation of *Zostera noltei* detritus was related to substrate  
30 availability rather than food and whether colonising assemblages were similar according to the meadow  
31 structural complexity. Litterbags filled with natural or artificial detritus were deployed within an eelgrass  
32 meadow in a Mediterranean coastal lagoon (Thau lagoon, France). Colonisation appeared to be driven by  
33 the presence of detritus, with similar assemblages in natural and artificial substrate, but with more  
34 individuals than the empty bags, used as controls. There were also no differences according to habitat  
35 complexity. These findings show that detritus, acting as a faunal magnet, plays an important role in  
36 maintaining biodiversity, as epifauna is a critical trophic link between primary producers and consumers.

37

38 **Key-words:** beach-cast; habitat structure; crustaceans; peracarids; polychaetes; leaf litter; macrofauna,  
39 mesograzers; transitional system; wrack.

40

## 41        1. Introduction

42 Seagrasses are a group of marine Magnoliophyta that colonise coastal areas worldwide (Assis et al.,  
43 2020; Short et al., 2007). They form underwater meadows that sustain biodiversity and complex food  
44 webs and contribute to fundamental ecosystem services, including carbon sequestration in marine  
45 sediments (Champenois and Borges, 2012; Costanza et al., 1997; Fourqurean et al., 2012; Unsworth and  
46 Cullen-Unsworth, 2014). Despite their crucial importance, a worldwide decline in seagrass coverage of  
47 7% per year is well-documented (Waycott et al., 2009) as a response to numerous threats (e.g. increased  
48 in the urbanization of coastal zones, eutrophication, extreme climatological events and invasive species)  
49 (Orth et al., 2006). Seagrass meadows are highly productive and a considerable proportion of their  
50 biomass does not enter the green food web pathway (Boudouresque et al., 2016; Valentine and Heck,  
51 1999). Rather, it becomes detritus (or litter) and accumulates within the meadow, or in nearby areas.  
52 Detritus can also be exported to deeper waters or to emerged areas, such as sandy beaches, where it is  
53 often referred to as wrack (especially for seaweeds) or beach-cast (e.g. Beltran et al., 2020).  
54 Seagrass detritus can provide habitat to several benthic invertebrates (Duggins et al., 2016; Kelaher and  
55 Levinton, 2003), which in turn can contribute to regulating seagrass decomposition (Graça, 1993). Small  
56 crustacean peracarids (i.e. amphipods, isopods, tanaidaceans) and gastropod molluscs are often the  
57 most numerous colonizers of the detritus washed to sandy beaches or accumulated within the meadow  
58 (Costa et al., 2019; Gallmetzer et al., 2005; Remy et al., 2018; Wittmann et al., 1981). They represent an  
59 important trophic link between producers and higher consumers and recently they have been proposed  
60 as sentinel species in pollution detection (Lo Brutto et al., 2021).

61 Detritivorous crustaceans can feed on seagrass detritus, as reported for *Gammarus aequicauda*  
62 (Martynov, 1931) and *Gammarella fucicola* (Leach, 1814) (Remy et al., 2018), or on the microbial  
63 community that develops during detritus decomposition (Costa et al., 2019; Remy et al., 2018). Some  
64 animals can also use seagrass and seaweed wrack as occasional or permanent shelter (Duggins et al.,  
65 2016; Remy et al., 2018).

66 During the colonisation of detritus, animals might be attracted from nearby areas, depending on their  
67 feeding, locomotion traits or chemical cues (Baring et al., 2019; Bueno and Leite, 2019). Since seagrass  
68 structural complexity often affects epifaunal distribution (Hovel et al., 2002; Voigt and Hovel, 2019), it can

69 be argued that habitat complexity could mediate epifaunal colonisation of detritus within the meadow, by  
70 affecting the availability of animals in the surroundings.

71 In this study, we investigate the colonisation of *Zostera noltei* Hornemann, 1832 detritus by  
72 macroinvertebrates and explore the relationship between colonisation and habitat complexity. To our  
73 knowledge, the role of habitat complexity in regulating the colonisation of seagrass litter has not been  
74 considered in other studies. We specifically ask whether the detritus can be a food attractiveness or  
75 rather a physical substrate using artificial seagrass detritus to mimic the physical structure and if this  
76 effect varies according to local habitat complexity and availability of animals.

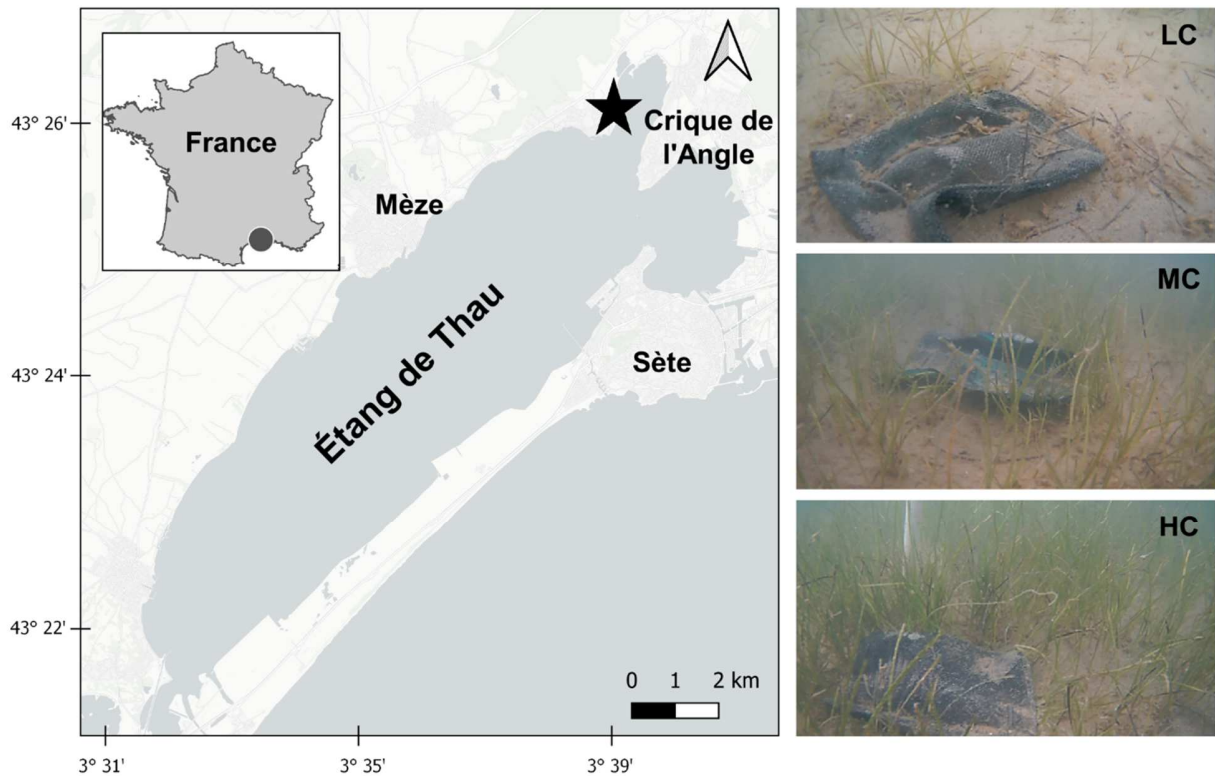
77

## 78 **2. Materials and methods**

### 79 **2.1 Site description**

80 This study was conducted in the lagoon of Thau (Étang de Thau) located on the French Mediterranean  
81 coast (Fig. 1). The lagoon has a surface area of 75 km<sup>2</sup> and an average depth of 3.8-4.5 m. Freshwater  
82 arrives in the lagoon from the Canal du Midi and the Rhone-Sète canal while seawater inputs mostly  
83 occur from the canals of Sète (Millet, 1989). The two eelgrass species, the dwarf eelgrass *Z. noltei* and  
84 the eelgrass *Zostera marina* L., form monospecific or mixed meadows that represent about 22% of the  
85 total macrophyte biomass of the lagoon (Laugier et al., 1999; Plus et al., 2001). Eelgrass detritus  
86 accumulates within the meadows, in adjacent bare sediment and on the shores (pers. obs.).

87



88

89 **Figure 1.** On the left side: map of the study area Thau Lagoon (*Étang de Thau*, France). The study site  
 90 *Crique de l'Angle* is indicated by a black star. On the right side: photo examples of the litterbag in the  
 91 three Habitat Complexity levels (LC as Low Complexity, MC as Medium Complexity and HC as High  
 92 Complexity).

93

## 94 **2.2 Experimental set-up**

95 Two field experiments were done within a *Z. noltei* meadow located in the north-eastern part of the lagoon  
 96 ("Crique de l'Angle", 43° 26' 55.60" N, 3° 39' 58.69" E; Fig. 1) to the depth of 0.5 m in April and May 2018  
 97 for a period of 22 and 19 days, respectively. Each time, we identified 3 areas of different structural  
 98 complexity defined as high, medium and low complexity (hereafter HC, MC and LC, respectively, Fig. 1).  
 99 These areas differed among the two experiments. Within each area, we estimated shoot density by  
 100 counting the individual shoots within 50 x 50 cm metal frame and canopy height by measuring the  
 101 average length of 15 leaves haphazardly sampled within the same plot. In addition, in May we sampled  
 102 for epifauna inhabiting the leaves, using a mesh-bag of 15 cm diameter and 0.2 mm mesh-size. Five  
 103 replicate plots were done per area. The temperature of the sediment surface was also monitored during

104 the whole experimental period in each complexity condition using Hobo Onset data loggers positioned  
105 within the meadow.  
106 We used 15 x10 cm bags, with 1 mm mesh size to add detritus to the different areas (litterbags).  
107 Litterbags were either filled with natural seagrass detritus (NSD) or with an artificial one (ASD). NSD was  
108 collected from the study area as freshly detached green leaves. In the laboratory, epiphytes were  
109 removed by gently scraping the leaf surface with a microscope lame and the leaves cut in 10 cm  
110 fragments. ASD was created by cutting green plastic strips into 0.5 x 10 cm fragments, corresponding to  
111 the size of an NSD fragment. We added 40 NSD or ASD fragments to each litterbag, corresponding to 7 g  
112 Wet weight (WW) of eelgrass detritus. At the beginning of each experiment, 5 NSD and 5 ASD bags were  
113 added to each area and secured with metal pegs to the sediment surface. In May, we also added 9 empty  
114 bags (3 per area). At the end of each experiment, the litterbags were collected by carefully putting them in  
115 plastic bags and transported chilled to the laboratory.  
116 In the laboratory, the litterbags and the mesh-bags were gently rinsed with seawater and the content  
117 sorted for epifauna, leaves and detritus. Individuals were counted and identified to the lowest possible  
118 taxonomic level. Seagrass detritus from the litterbag was rinsed, dried (60°C for 48 h) and weighed to  
119 evaluate the decomposition process.

120

### 121 **2.3 Data analysis**

122 The diversity of the epifaunal assemblages was reported as: Number of individuals (N) per litterbag;  
123 Species richness (S), the total number of species identified in each litterbag; Shannon-Wiener index (H',  
124 using log base 2) (Hill, 1973)

125 A single-component exponential model was used to describe the decomposition process (Petersen and  
126 Cummins, 1974):  $W_t = W_0 e^{-kt}$  where  $W_t$  is the dry weight of seagrass detritus at the time (t),  $W_0$  is the  
127 initial weight and k is the decomposition constant.

128 We used Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) to model the  
129 distribution of colonising fauna, diversity indices and the decomposition rates with *Experimental Period*  
130 (fixed 2 levels: April and May) and *Substrate* (fixed 2 levels: ASD and NSD) as fixed and orthogonal, while  
131 the shoot density was considered as random and continuous (Crawley, 2007).

132 In GLMM models, Gamma distribution and log-link function were used, and a Poisson distribution was  
133 used to model the abundance of dominant species (see below).  
134 The full and reduced models were compared using the Akaike's Information Criterion corrected for small  
135 sample size (AIC<sub>c</sub>). Overdispersion and heteroscedasticity of GLMM model residuals were assessed  
136 visually.  
137 A multivariate approach was used to analyse the whole assemblages associated with the seagrass  
138 meadows and the assemblages colonising the detritus using the permutational analyses of variance  
139 (PERMANOVA, Anderson et al., 2008) and the factors previously described. PERMANOVA analyses were  
140 based on Bray-Curtis dissimilarities matrix, calculated after square-root transformation of raw data to  
141 reduce the importance of the highly abundant species. Each term was tested by 4999 random  
142 permutations (Anderson et al., 2008). The dominant species were selected using the SIMPER (Similarity  
143 Percentage breakdown, Clarke, 1993) procedure with a 60% cut-off. Non-metric multidimensional scaling  
144 ordination plot (nMDS, Clarke, 1993) was used to visualize differences among assemblages, considering  
145 stress values <0.2 (Clarke, 1993). In case of significant effects in the interaction term, comparisons were  
146 calculated using PERMANOVA Pairwise tests and *a posteriori* Tukey's tests for GLMM.  
147 To control for the procedural effect of using litterbags, diversity indices calculated for the (GLM) and the  
148 epifaunal assemblages of empty and filled litterbags were compared (GLM, *Litterbag*, 2 levels: Empty and  
149 Filled with NSD).  
150 Statistical analyses were run using the R environment (version 4.0.0) in RStudio (1.3.959) with the  
151 packages *bbmle* (Bolker and Development Core Team, 2020), *DHARMA* (Hartig, 2021), *glmmTMB*  
152 (Brooks et al., 2017), *multcomp* (Hothorn et al., 2008), *tidyverse* (Wickham, 2017) and *vegan* (Oksanen et  
153 al., 2018).

154

### 155 **3. Results**

#### 156 ***3.1 Eelgrass habitat complexity and associated epifauna***

157 Shoot density was one order of magnitude higher in HC and MC than LC and in May leaf length in HC  
158 was twice the LC. Sediment surface temperature, within the canopy, was slightly lower in HC, both in April  
159 and May (Table 1).



160

161 **Table 1.** Mean and Standard Error ( $\pm$  S.E.) for *Z. noltei* shoots density ( $n\ m^{-2}$ ), canopy height (cm) and  
162 Surface Sediment Temperature ( $^{\circ}C$ ) in April and May corresponding to the date when litterbags were  
163 deployed in the 3 areas (HC, MC and LC).

Experimental Period	Habitat Complexity	Shoots density ( $n\ m^{-2}$ )		Leaves Length (cm)		Surface sediment Temperature ( $^{\circ}C$ )	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
April	HC	2660.0	308.2	12.4	0.4	17.2	0.2
	MC	2000.0	287.4	12.2	0.4	17.6	0.2
	LC	147.2	63.5	11.4	0.7	17.7	0.2
May	HC	2580.0	183.8	20.6	0.8	19.0	0.2
	MC	1132.0	375.7	13.8	0.5	19.1	0.1
	LC	109.6	66.3	10.2	0.6	19.2	0.2

164

165 In May, a total of 16 taxa and 1797 epifaunal individuals was sampled within the eelgrass meadow,  
166 including 12 crustaceans, 1 annelid and 3 molluscs species (Natural Community, Table S1). Less than 10  
167 individuals scattered among few replicates were found in LC areas and therefore this level of the  
168 treatment *Habitat Complexity* was excluded from statistical analyses. PERMANOVA analysis did not  
169 identified significant differences in the epifauna community between the two more complex habitats ( $MS =$   
170  $0.572$ ,  $Pseudo-F_{1,8} = 24.521$ ,  $P(\text{perm}) = 0.999$ ). The number of individuals and species were significantly  
171 higher in HC than in MC (GLM,  $p < 0.001$ ).

172

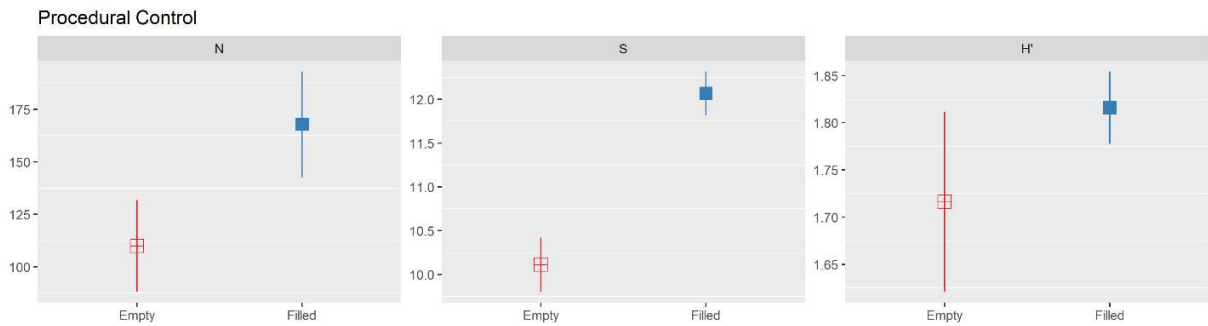
### 173 **3.2 Eelgrass detritus decomposition**

174 The best GLMM models to describe the decomposition rate included the *Experimental Period* (Table  
175 S2a), showing a significant higher decomposition rate in April than in May ( $0.0259 \pm 0.0107$  and  $0.0176 \pm$   
176  $0.0084\ \text{day}^{-1}$ , respectively) (GLMM,  $p < 0.05$ , Fig. S1; Table S3a).

177

### 178 **3.3 Procedural control**

179 There were clear differences between empty and filled litterbags, which had significantly higher numbers  
180 of species and individuals (GLM,  $p < 0.001$ ), despite some taxa reported in the controls (Fig. 2).



181

182 **Figure 2.** Diversity Indices (N, S and H', mean  $\pm$  S.E.) calculated on the Procedural Control dataset.

183

### 184 **3.4 Litterbag colonisation**

185 A total of 11270 individuals of 26 taxa, including 2 polychaetes, 18 crustaceans (13 Amphipoda, 4 Isopoda  
 186 and 1 Tanaidacea), 5 molluscs species (2 Bivalvia and 3 Gastropoda) and chironomidae larvae were  
 187 identified during the two experiments (Table S1).

188 The number of individuals and species were significantly higher in April than in May and a slightly more  
 189 diverse assemblage associated with the ASD (GLMM,  $p < 0.001$ , Fig. 3, Table S2b-S3b).

190 PERMANOVA analysis identified significant differences in the epifauna community for the Experimental  
 191 Period x Habitat Complexity interaction, with significant differences between all the comparisons for both  
 192 experimental periods ( $p < 0.001$ , Table 2, Fig. 4) and no significant differences related to the Substrate.

193 The Anellida polychaete Capitellidae, three species of amphipods [*Ampithoe ramondi*, *Erichthonius*  
 194 *argenteus* and *Gammarus insensibilis* (Stock, 1966)], the isopod *Idotea sp.* and the tanaidacean  
 195 *Chondrochelia savignyi* contributed the most to the observed dissimilarity between the Habitat Complexity  
 196 and Experimental Period interaction of PERMANOVA (SIMPER, Table S4).

197 Colonization of litterbags was explained by the Substrate for *A. ramondi*, *E. argenteus*, *G. insensibilis* and  
 198 Fam. Capitellidae, with significantly more individuals in ASD for *A. ramondi*, *E. argenteus* and Fam.

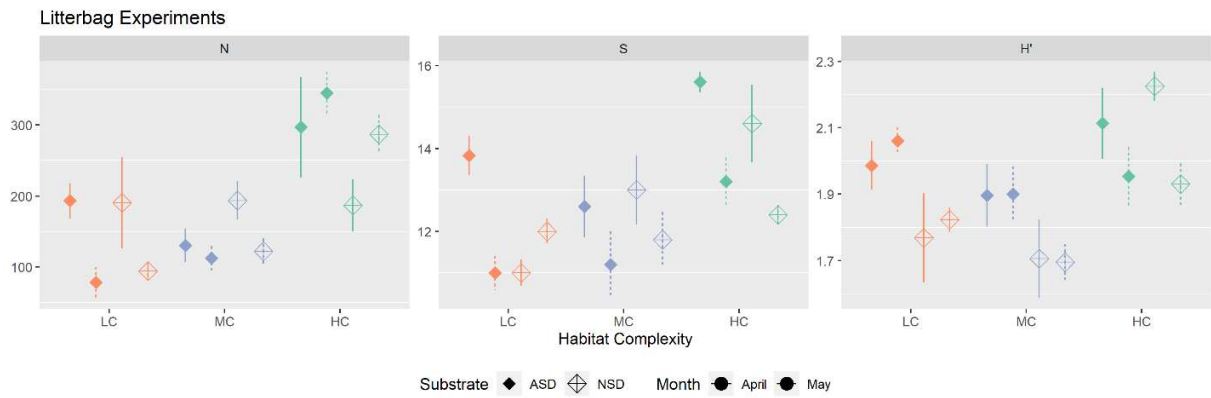
199 Capitellidae (GLMM,  $p < 0.001$ , Fig. 5a, b, d, Table S2b-S3b), while *G. insensibilis* showed higher values in  
 200 NSD (GLMM,  $p < 0.001$ , Fig. 5c, Table S2b-S3b). The interaction Experimental Period x Substrate was

201 included in the GLMM models for *Idotea sp.* and *C. savignyi* with more individuals colonizing both

202 substrates in April for the first one and the ASD during both experimental periods for the latter (GLMM,

203  $p < 0.01$ , Fig. 5e, f, Table S2b-S3b).

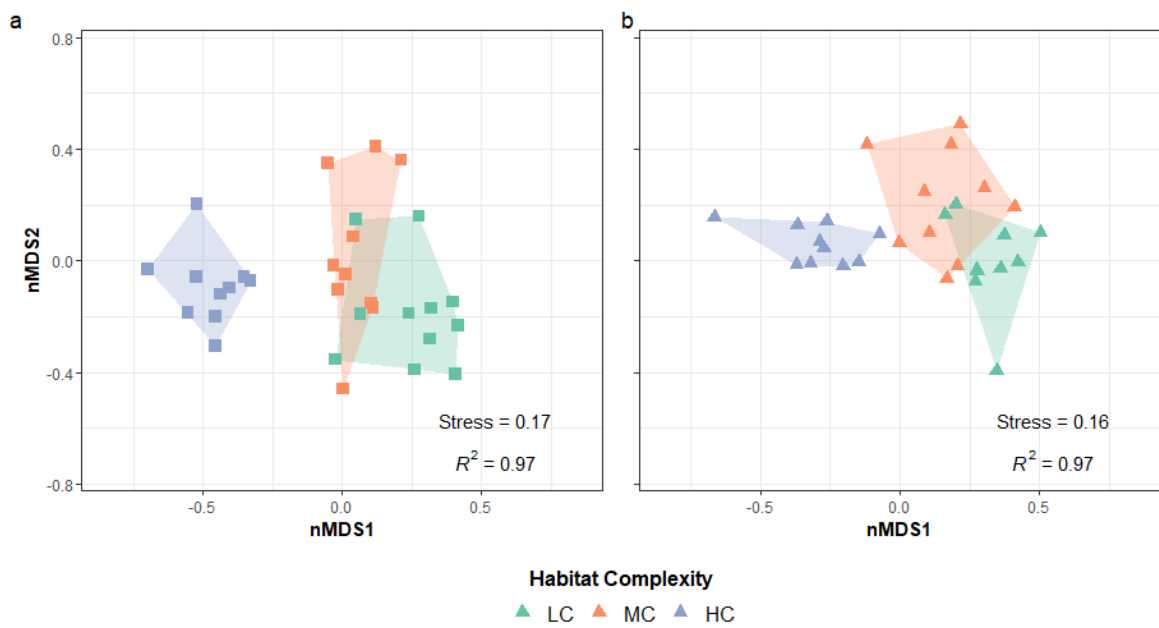
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205

206 **Figure 3.** Diversity Indices (N, S and H', mean  $\pm$  S.E.) calculated on the Litterbag Experiments dataset.

207

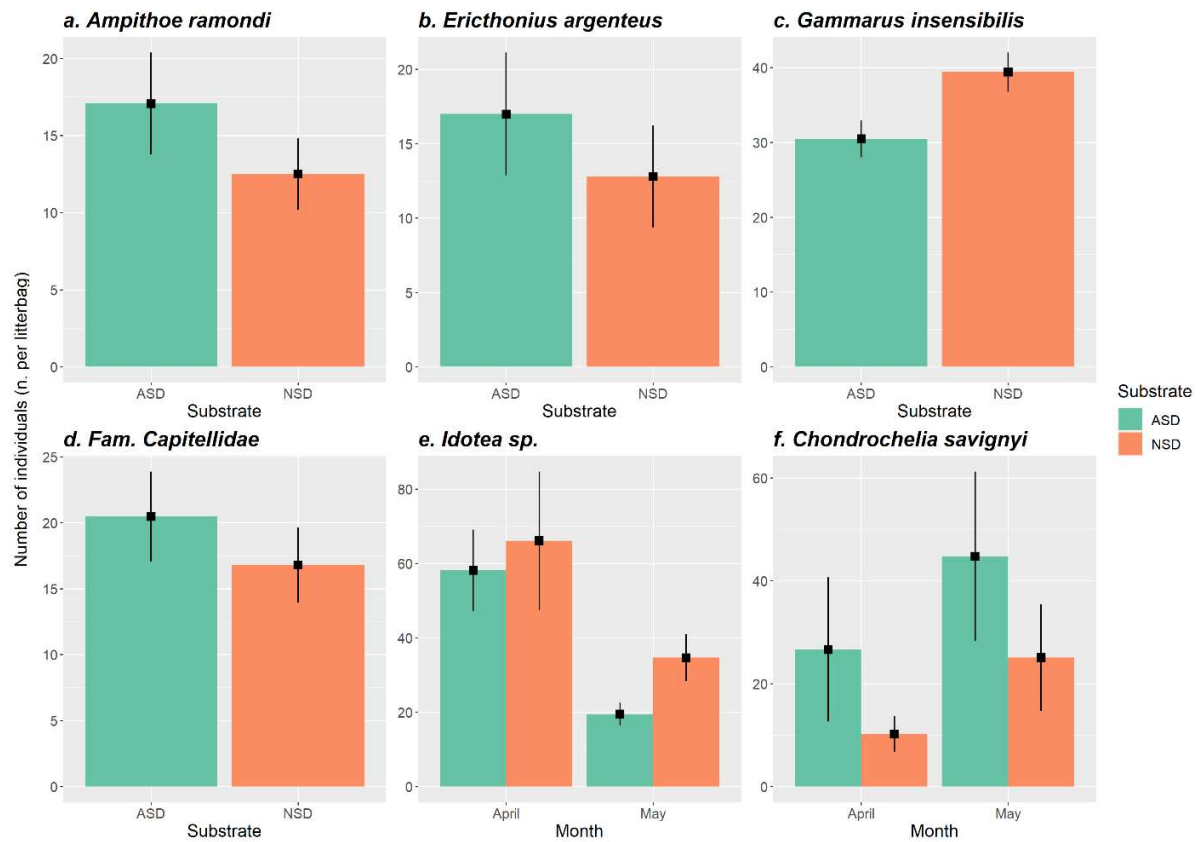


208

209 **Figure 4.** nMDS ordination and convex hulls of the significant groups identified by the PERMANOVA

210 analysis for the Litterbag Experiment dataset during the (a) April and (b) May experiments.

211



212

213 **Figure 5.** Number of individuals per litterbag (n. per litterbag, mean  $\pm$  S.E.) of the taxa indicated by  
 214 SIMPER and for the significant results indicated by the GLMM analysis (Table S3).

215

216 **Table 2.** Summary results of Permutational multivariate analysis of variance (PERMANOVA) and Pairwise  
 217 comparisons on the Litterbag Experiments dataset (details of the designs are explained in the Methods  
 218 section). Significant results are marked in bold ( $p < 0.05$ ). *df*: degree of freedom; *MS*: Mean Square.

	Source	df	MS	Pseudo-F	P(perm)
<b>Litterbag experiments</b>	Experimental period (E)	1	0.155	7.885	<b>0.000</b>
	Habitat Complexity (HabC)	2	0.351	17.817	<b>0.000</b>
	Substrate (S)	1	0.040	2.036	0.083
	E x HabC	2	0.099	5.050	<b>0.000</b>
	E x S	1	0.022	1.104	0.364
	HabC x S	2	0.017	0.871	0.543
	E x HabC x S	2	0.035	1.791	0.083
	Residuals	48	0.020		
	<i>Pairwise comparisons</i>		<i>P(perm)</i>		

April	<i>HC vs LC</i>	<b>0.000</b>
	<i>HC vs MC</i>	<b>0.000</b>
	<i>LC vs MC</i>	<b>0.000</b>
May	<i>HC vs LC</i>	<b>0.000</b>
	<i>HC vs MC</i>	<b>0.000</b>
	<i>LC vs MC</i>	<b>0.005</b>

219

#### 220 **4. Discussion**

221 Before discussing the outcomes of the colonisation experiments, we want to make some considerations  
 222 about our protocol. In order to control for possible biases, we estimated differences in the decomposition  
 223 rate of the eelgrass detritus across the levels of habitat complexity and measured the use of litterbags as  
 224 a possible artefact for colonization. Decomposition rates were comparable to those reported for *Z. noltei*  
 225 and *Z. marina* on the northern Spanish Mediterranean coast with similar results among experiments  
 226 ( $0.015 \pm 0.002$  and  $0.019 \pm 0.001$  d<sup>-1</sup>; respectively, Cebrián et al., 1997). The small differences between  
 227 the two experimental periods, April and May, might be due to temperature increases. High temperature  
 228 can stimulate the activity of heterotrophic bacteria (Lopez et al., 1998; Mateo et al., 1996) until an optimal  
 229 growth, after which increasing temperature can have opposite effects on the microbial community  
 230 (Pedersen et al., 2011).

231 We used empty litterbags to control for the artifact effect due to the structure of the bag used to deploy  
 232 the detritus. Litterbags can be indeed an attraction for macroinvertebrates (Cortes et al., 1997). Our test  
 233 showed that few taxa colonised the empty bags compared to filled bags, showing that it was the detritus  
 234 contained in the litterbags that acted as a faunal magnet (Duggins et al., 2016; Remy et al., 2017).

235 In this study, we investigated the importance of the habitat complexity in shaping the assemblages  
 236 colonizing the detritus and in affecting its role as an attractor of invertebrates (Duggins et al., 2016). The  
 237 litterbags were placed within the eelgrass meadow in contrasting shoot density and canopy height, within  
 238 the range reported for *Z. noltei* in the same area (Laugier et al., 1999; Plus et al., 2003). In general, a  
 239 decrease in structural complexity corresponds to a reduced number of individuals, often due to the  
 240 availability of food and substrate used as shelter (Smith et al., 2014). In our study, we found a decrease in  
 241 diversity from high to medium complexity treatment, where however seven crustacean species were still  
 242 present. This highlights that a medium level of complexity could still host a diverse epifauna community.

243 Instead, the lowest complexity treatment harbored only a few, scattered taxa indicating a fast drop of  
244 species while progressing with habitat loss. Despite litterbags placed within highly complex canopy  
245 always had more individuals and more species, there was not a clear effect of the habitat complexity on  
246 the epifaunal colonisation of detritus, probably indicating a supply of larvae and juveniles from outside the  
247 local species pool.

248 We used artificial seagrass to mimic the structure of the natural detritus while disentangling the effect of  
249 food attractiveness vs. physical habitat availability. Literature reports cases of seagrass mimic applied to  
250 study settlement, recruitment, colonization, and community development in coastal ecosystems (e.g.  
251 Donnarumma et al., 2014; Lee et al., 2001) and artificial wrack buried into the sediment was used to  
252 assess their effect on macrofaunal assemblages (Rossi and Underwood, 2002).

253 Both Natural and Artificial detritus attracted a diverse and variable epifaunal community. Some species  
254 seemed to be more abundant in the artificial detritus, while others in the natural one. However, the  
255 epifauna did not select the natural substrate more often than the artificial substrate. Rather, some species  
256 opportunistically used either one or the other type of detritus, probably feeding also on the microbial  
257 biofilm growing on senescent leaves. Several mesograzers can show a low level of host-specificity and,  
258 rather, adaptability to different substrates, as found in two coexisting seagrass species, *Zostera*  
259 *caulescens* Miki, 1932 and *Z. marina* in northeastern Japan meadows (Nakaoka, 2005; Nakaoka et al.,  
260 2001).

261 In our study, only a few species showed a preference for one substrate or the other. The amphipods *A.*  
262 *ramondi* and *E. argenteus*, the polychaets of Fam. Capitellidae and the tanaid *C. savignyi* were more  
263 abundant in the artificial substrate, whereas the gammarid *G. insensibilis* showed the opposite pattern.  
264 *Ampithoe ramondi* is a cosmopolitan species found in the shallow water of tropical, subtropical and  
265 temperate zones (Griffiths, 1973). Despite many species included in Amphitoidae and Ischyroceridae  
266 families are herbivores or detritivores (Guerra-García et al., 2014), *A. ramondi* is usually described as a  
267 facultative grazer capable to alternate different feeding modes (i.e. grazing, suspension and deposit-  
268 feeding) depending on food availability (Vázquez-Luis et al., 2013), while information on *E. argenteus*  
269 feeding preferences is lacking. The Fam. Capitellidae is described as not selective (Fauchald et al., 1979)  
270 but opportunistic (Linton and Taghon, 2000).

271 The tanaid *C. savignyi* is often associated with seagrass meadows and detritus (Como et al., 2008; Costa  
272 et al., 2019) and despite that, tanaids are usually reported as mesoherbivores (Gambi et al., 2003), with  
273 bacteria and diatoms also represent a large part of their diet (Blazewicz-Paszkowycz and Ligowski,  
274 2002). Instead, *G. insensibilis* has been reported as a herbivore/detritivore that directly feeds on detrital  
275 macroalgae (Costantini and Rossi, 1995), which potentially explains the fact that it was more often found  
276 in natural detritus. These species might also feed on the microbial biofilm associated with the detritus, as  
277 in general reported for detritivorous (Fenchel, 1970), highlighting a generalist/opportunistic behaviour. On  
278 the whole, many taxa are domicolous forms, in some cases tubes-builders (Bertocci et al., 2017; Plicanti  
279 et al., 2017; Scipione, 2013). Their distribution regardless of the substrate type showed that eelgrass  
280 detritus can be used uniquely as physical habitat by some species and also as a food source by others.

281

## 282 **5. Conclusions**

283 Using a seagrass meadow in Thau lagoon (France) as a case study area, this study provides new  
284 information about the role of habitat complexity in shaping the colonisation of seagrass detritus. It also  
285 shows that eelgrass detritus does not always attract invertebrates directly, letting us hypothesize that  
286 microbial biofilm growing on senescent leaves could be more important as a food attractor/resource for  
287 some epifauna species. The fact that a dead substrate such as the eelgrass detritus is colonized by a rich  
288 and diverse community, even in a short period of time, highlights the crucial role of this component within  
289 the seagrass meadow.

290

## 291 **Data accessibility statement**

292 Raw datasets can be accessed and cited through Zenodo (<https://doi.org/10.5281/zenodo.5304675>).

293

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297

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