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3 Anthropogenic impact of oyster farming on macrofauna biodiversity in an eelgrass
4 (*Zostera marina*) ecosystem of the English Channel

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15

16 **ABSTRACT**

17

18 *Zostera marina* flourish along the west coast of Cotentin, in cohabitation with extensive
19 oyster cultivation. In 2016, seasonal sampling was carried out based on five combinations of con-
20 ditions involving vegetated and unvegetated areas, presence or absence of oyster tables and a
21 control station without either eelgrass or oyster cultivation. The sediments consisted of muddy
22 sandy gravel and no significant difference of sediment composition was observed between sta-
23 tions and seasons. A total of 147 taxa and 8,404 individuals were recorded over a period of the
24 one year with a sampling effort of 5 m². The effects of oyster farming are relatively limited, and
25 are not a handicap for the extension of *Zostera* meadows in this part of the English Channel.
26 Nevertheless, low Taxonomic Richness and abundances characterize the tractor pathway.
27 Macrofauna abundances, biomasses and number of eelgrass shoots are similar to those reported
28 at other sites in the English Channel and from the North-eastern Atlantic.

29

30 Keyword: • human activity • seasonal changes • diversity • ecological status • tractor pathway

31

32 **1. Introduction**

33

34 *Zostera marina* is the main eelgrass species inhabiting the intertidal zone of the western
35 basin of the English Channel, the second existing species *Z. noltei* is rare and occupies only small

36 muddy areas mainly in estuaries (Hily and Bouteille, 1999; Jackson et al., 2006). *Z. marina*
37 colonizes large areas of lower medio- and infralittoral soft sediments along the North Brittany
38 coast (Hily and Bouteille, 1999) and in the Normand-Breton Gulf along the west coast of the
39 Cotentin, as well as vast areas in the Chausey Islands (Guillaumont et al., 1987; Godet et al.,
40 2008) and the Channel Islands such as Jersey (Jackson et al., 2006), and also along the English
41 coast mainly in Cornwall around Plymouth (Saunders et al., 2003) and the Isles of Scilly
42 (Bowden et al., 2001). Moreover, the habitat is heterogeneous since the eelgrass tends to colonize
43 the substratum in patches (Hily and Bouteille, 1999; Duffy, 2006; Duffy et al., 2015), resulting
44 in a mosaic of bare sand and vegetated habitats that facilitate different macrofaunal, epifaunal
45 and infaunal assemblages. Indeed, *Z. marina* stabilizes the sediment and is therefore antagonistic
46 to bioturbator species, which are dominant in unvegetated soft sediment (Duffy et al., 2015).

47 Previous studies have shown higher diversity and abundance in vegetated compared with
48 unvegetated sediments, with a higher proportion of epifaunal species in vegetated habitats
49 (Saunders et al., 2003; Duffy et al., 2015; Boyé et al., 2017; Wong, 2017). Eelgrasses have also
50 been shown to have an effect on food webs, increasing the proportion of grazing and scavenging
51 species (Blanchet et al., 2005). In addition, the trophic web of eelgrasses contains more trophic
52 levels than surrounding habitats without seagrass (Hily and Bouteille, 1999).

53 Seagrass beds has a high natural heritage value and is developed under favourable
54 conditions in a wide intertidal zone (which extends over 5 km during equinoctial spring tides,
55 when the tidal range reaches 12 m) on the western coast of the Cotentin Peninsula (Fig. 1). This
56 intertidal zone is mainly composed of a mixture of sandy, gravelly, sandy-rocky and rocky areas
57 where *Zostera marina* beds have now flourished for several years after major diseases during the
58 mid-20th century (Den Hartog, 1987; Guillaumont et al., 1987; Hily et al., 2002; Godet et al.,
59 2008). In the Normand-Breton Gulf, *Zostera marina* meadows is also present in shallow waters
60 down to 10 m below the chart datum level in clear waters such as found around Chausey and
61 Jersey (Jackson et al., 2006; Godet et al., 2008).

62 In spite on their importance as a natural heritage habitat, the macrofauna of eelgrass beds
63 along the Cotentin coast are yet to be studied to understand their structure and functioning in
64 comparison with other areas in the Western Channel and the Northeast Atlantic.

65 Moreover, oyster farming occupies large areas of tidal flats along the Cotentin west coast,
66 raising the issue of environmental impact. Studies have shown that shellfish farming has a highly
67 variable impact on benthic macrofauna (Forrest et al., 2009); a study in the Bay des Veys (East
68 Cotentin) has indicated changes in the macrofaunal assemblages associated with *Lanice*

69 *conchilega* in relation to oyster farming (Dubois et al., 2007). Likewise, the macrofauna
70 associated with *Zostera marina* is expected to be more impacted by oyster farming as seagrasses
71 themselves are sensitive to eutrophication and mechanical stresses (trampling by workers and
72 tractor pathway) (Hily, 2006).

73 In this study, we use a seasonal approach to evaluate the small-scale effect of oyster
74 farming on macrofaunal assemblages developed on bare sediment habitats and *Z. marina*
75 meadows of the Normandy west coast by comparing the macrofauna under oyster tables to other
76 assemblages located away from the tables. We apply a structural analysis, including the use of
77 Biotic Indices, to investigate the impact of oyster farming and tractor traffic on the macrofauna
78 of this habitat of high natural heritage value.

79

80 **2. Materials and methods**

81

82 *2.1. Study site, sampling and sample treatments*

83

84 Sampling campaigns were performed in 2016 on an oyster farming area at Blainville-sur-
85 Mer in February (winter), May (spring), September (summer) and November (autumn) during
86 low spring tides (tidal coefficient > 100) (Fig. 1). Five stations were sampled (Fig. 1):

- 87 • one station with both eelgrass and oyster farming (Oyster-*Zostera*);
- 88 • one unvegetated station with farming (Oyster);
- 89 • one station with eelgrass but without farming (*Zostera*);
- 90 • one station with eelgrass development inside the tractor pathway (*Zostera*-Tractor);
- 91 • one station without either eelgrass or oyster farming (Control).

92 At each station, eight circular cores (1/32 m²; 0.15 m deep; total surface of sampling 0.25
93 m²) were sampled and sieved on a circular 1-mm mesh-size screen to collect the macrofauna; one
94 additional sample was collected to determine the grain size distribution and organic matter content,
95 the latter being only measured in summer and autumn. Each replicate sample was then sorted in
96 order to separate fauna from sediment. Individuals were identified to the lowest possible
97 taxonomic level (generally, the species level).

98 Taxonomic richness and abundance were recorded for each replicate. The biomasses of
99 each species were measured for each season. Samples were dried for three days at 60°C and
100 calcined at 500°C for 4 h and Biomasses were expressed as AFDW (Ash Free Dry Weight) per
101 0.25 m² and 1 m².

102 The numbers of eelgrass shoots were also estimated in each core.

103 The sediment samples were dried at 60°C for three days, and the particles were then passed
104 through an eight-sieve column (8, 4, 2, 1, 0.5, 0.250, 0.125 and 0.050 mm) fitted into a.
105 mechanical sieve shaker. Each fraction was then weighed to calculate the contribution of each
106 fraction to the total weight. The sediment samples are classified according to Wentworth's grain-
107 size scale (Wentworth, 1922): <50 µm, silt clay; [50–125 µm], very fine sand; [125–250 µm], fine
108 sand; [250–500 µm], medium; [500–1000 µm], coarse sand; [1000–2000 µm], very coarse sand;
109 [2000–4000 µm], gravel, [4000–8000 µm], granules; and >8000 µm, pebbles. Finally, four grain-
110 size classes are considered for the definition of sediment types: fine fraction (< 50 µm); sand (50-
111 2000 µm), very coarse sand and gravel (2000–4000 µm) and granules and gravels (> 4000 µm).

112 Samples for organic matter analysis were dried for three days at 60°C and then calcined at
113 500°C for 4 h.

114

115 2.2. Taxonomic diversity analysis

116

117 Data were used to calculate the Taxonomic Richness (TR, number of taxa per 0.25 m²)
118 and abundance (individuals per 1/32 m² or 0.25 ind.m⁻²) and the most widely-used biodiversity
119 indices for each station, i.e. the Shannon-Weaver diversity index (H') in log₂ and Pielou's
120 evenness (J) for the five stations and four dates. Data analysis was performed using the PRIMER®
121 version 6 software package (Plymouth Routines in Multivariate Ecological Research) (Clarke and
122 Gorley, 2006).

123 The Ecological Status indicating the quality of the station was estimated from H' values
124 according to the thresholds defined previously by Vincent et al. (2002): 0-1, bad; 1-2: poor; 2-3:
125 moderate; 3-4 good and > 4: high. Dauvin et al. (2017) had proposed thresholds for J', respectively
126 <0.20 bad; 0.20-0.40: poor; 0.40-0.60: moderate; 0.60-0.80 good and > 0.80: high.

127 The biotic indices AMBI and BO2A were also calculated to assess the ecological status of
128 the macrofauna (Borja et al., 2000, 2009; Dauvin et al., 2012, 2016).

129 A two-way ANOVA was used to test spatio-temporal changes (stations and seasons factors)
130 for TR, A, H', J, AMBI, and BO2A. Prior to each ANOVA, a Shapiro-Wilk normality test and a
131 Bartlett test for homogeneity of variances were performed. The Tukey Honestly Significant
132 Difference test was applied when ANOVA showed significant differences.

133

134 2.3.2. Multivariate analysis

135

136 Data analysis was performed by non-metric multidimensional scaling ordination (MDS),
137 and Hierarchical Ascendant Classification (HAC) created using group average linking with the
138 Bray-Curtis similarity measure. Sorensen's coefficient for Presence/Absence of taxa, and
139 $\text{Log}_{10}+1$ -transformed abundances (0.25 ind.m²) were used to down-weight the importance of the
140 very abundant species. To identify within different groups which species primarily accounted for
141 the observed assemblage difference, SIMPER (SIMilarity PERcentage) routines were performed
142 using a decomposition of Bray-Curtis similarity on log-transformed abundance data (Clarke and
143 Gorley, 2006).

144

145 **3. Results**

146

147 *3.1. Main environmental characteristics*

148

149 The sediments are a mixture of gravel (33-61 %) and sand (36-62 %), with the percentage
150 of fine particles varying between 3 and 9 % (Table 1). There are no significant differences of
151 sediment composition between stations and seasons (Table 2). Hence, the sediments are
152 heterometric and correspond to muddy sandy gravel. The OM content is comprised between 1.6
153 and 3 %, showing significant differences between the two seasons (summer/autumn) (ANOVA_{1,28}
154 $F=7.87$; $p<0.01$), with higher values in autumn than in summer, but no differences between the
155 stations (ANOVA_{4,25} $F=0.28$; $p=0.89$) (Table 1).

156

157 *3.2. General characteristics of the fauna*

158

159 A total of 147 taxa and a total of 8,404 individuals were recorded during the one-year
160 sampling effort of 5 m². Among these taxa, the macrofauna is dominated by Polychaetes (64 spe-
161 cies and 46.0 % of abundance), crustaceans (39 species and 32.8 %), molluscs (32 species and
162 19.3 %), sipunculids (6 species and 0.9 %), echinoderms (3 species and 0.8 %), Cnidaria (2 species
163 and 0.1 %) and Chordata (1 species and 0.1 %). The five dominant species are the polychaetes
164 *Notomastus latericeus* (386 individuals per m²), *Cirriformia tentaculata* (243 individuals per m²),
165 *Euclymene oerstedii* (138 individuals per m²), *Cirratulus cirratus* (116 individuals per m²) and the
166 sipunculid *Golfingia (Golfingia) elongata* (171 individuals per m²).

167 Table 3 summarizes the main seasonal characteristics of the macrofauna. TR varies from
168 a minimum of 20 for the *Zostera*-Tractor station in spring to a maximum of 53 for the *Zostera*-
169 Oyster station in autumn. Most of the values are comprised between 34 and 49. A significant
170 seasonal pattern is observed for the Oyster and *Zostera*-Tractor stations (Table 2).

171 The mean abundance per core sample varies from a minimum of 5.6 for the *Zostera*-Trac-
172 tor station in spring to 108.6 for the Oyster station in summer. Most of the values are comprised
173 between 40 and 80 individuals per 1/32 m² (Table 3). A significant seasonal pattern is observed
174 for three of the five stations: Oyster, *Zostera*-Oyster and *Zostera*-Tractor (Table 4).

175 The mean biomass per core sample varies from a minimum of 0.04 g AFDW for the *Zos*-
176 *tera*-Tractor station in spring to 0.47 g AFDW for the *Zostera* station in winter. Most of the values
177 are comprised between 0.2 and 0.4 g AFDW per 1/32 m² (Table 3). A significant pattern is ob-
178 served for two of the five stations: Oyster and *Zostera*-tractor (Table 4).

179

180 3.3. Ecological Quality Status (EcoQS)

181

182 The Shannon-Weaver diversity index H' shows high values, except in summer and autumn
183 at the *Zostera*-tractor station (< 3.0) corresponding to a moderate EcoQS (Table 3). Among the
184 other values obtained, nine correspond to good EcoQS and nine to excellent EcoQS (Table 3).
185 Pielou's evenness J is at a maximum at the *Zostera*-tractor station, corresponding to an excellent
186 EcoQS in spring and winter when the TR and abundance are the lowest (Table 3). For both of the
187 other stations, the J values yield a moderate EcoQS, being also moderate at the oyster station in
188 summer, and good for all stations and seasons (Table 3). AMBI shows a good EcoQS at all sta-
189 tions and seasons, while BO2A gives a moderate EcoQS in three cases (Control in winter, and
190 Oyster in spring and summer) and a good EcoQS for all the other cases.

191 Nevertheless, H' shows a significant seasonal pattern for both *Zostera* and Oyster stations,
192 while J values show significant seasonal differences for all stations (Table 4). AMBI shows a
193 significant seasonal difference for the Oyster station, and BO2A gives a significant seasonal dif-
194 ference between summer and winter at the Control station (Table 4).

195

196 3.4. Spatio-temporal patterns of the macrofauna

197

198 At a similarity value of 60 %, the cluster dendrogram allows us to separate the stations
199 into four main groups, with one station isolated from the others at two seasons, i.e. *Zostera*-tractor

200 in spring and winter (Fig. 2). The first group includes both other seasons (summer and autumn) at
201 the *Zostera*-tractor station. The three other groups include the four other stations per season
202 (spring, summer and autumn and winter). At 58 % similarity, the last group can be separated into
203 two sub-groups for the autumn and winter seasons. In summary, the analysis reveals two main
204 patterns; the *Zostera*-tractor station is separated from the rest of the stations which can be grouped
205 by season.

206 SIMPER analysis classifies 18 species among the ten top species of each group (Table 5).
207 The polychaete *Notomastus latericeus* is the top species in the four groups, while the other
208 polychaete *Cirriformia tentaculata* is the second most abundant species except in spring (Table
209 5). The third and following species differ in terms of abundance in the four groups, showing
210 mainly seasonal changes with time. Molluscs and Crustaceans are classified among the least
211 abundant, while polychaetes and the sipunculid *Golfingia (Golfingia) elongata* are classified
212 among the most abundant. *G. elongata* is absent among the top ten species at the *Zostera*-Tractor
213 station, while the polychaete *Notomastus latericeus* shows its maximum abundance at this station
214 (Table 5).

215 TR at the *Zostera*-tractor station is significantly lower than at the four other stations, but
216 is higher at both other stations with *Zostera* than at the Control and Oyster stations (Figs. 3 and 4;
217 Table 6). The abundances, biomasses and H' are significantly lower at the *Zostera*-Tractor station
218 than the other stations; similarly AMBI and BO2A give lower EcoQS for this station than the
219 other stations (Figs. 3 and 4; Table 6).

220

221 3.5. Eelgrass shoots

222

223 The mean numbers of eelgrass shoots (1/32 m²) varies from 4 at the *Zostera*-Tractor
224 stations to 12 at the *Zostera* bed station (Fig. 5). The number was intermediate in the *Zostera*-
225 Oyster station (Fig. 5). No difference is observed between the summer and autumn results, while
226 there are significant differences between the three stations associated with *Zostera* (Fig 4; Table
227 7).

228

229 4. Discussion

230

231 4.1. Faunal characteristics and eelgrass shoots

232

233 Stations associated with sea grasses correspond to habitat A5.5331 (*Zostera marina/an-*
234 *gustifolia* beds on lower shore or infralittoral clean or muddy sand according to the EUNIS
235 habitat classification), whereas stations without sea grasses are classified as Cirratulids and *Ce-*
236 *rastoderma edule* mixed sediment (A2.421) ([http://eunis.eea.europa.eu/habitats-code-](http://eunis.eea.europa.eu/habitats-code-browser.jsp)
237 [browser.jsp](http://eunis.eea.europa.eu/habitats-code-browser.jsp)).

238 Diversity assessed for the entire study site is relatively high for intertidal stations (Table
239 1), with a total of 147 taxa for a sampled area of 5 m² and a mean TR per station of 38.21
240 species (for 0.25 m²). These stations show a good ecological status. Species richness at non-
241 vegetated intertidal Water Framework Directive stations ranges from 7.6 species.0.25 m² (Bay
242 of Mont-Saint-Michel) to 23.1 at Chausey (Garcia et al., 2014). However, abundances are rel-
243 atively low (387 individuals.0.25 m²). Indeed, unvegetated sediment stations in the Bay of
244 Mont-Saint- Michel and Chausey have mean abundances of 179 individuals and 1,044 respec-
245 tively. In this study, communities are largely dominated by Polychaetes and Sipunculids (Table
246 5), whereas, in other studies, sipunculids show relatively low abundances.

247 Both unvegetated sediments and *Z. marina* habitats have a relatively low density of mol-
248 luscs compared to similar habitats (Hily and Bouteille, 1999; Rueda and Salas, 2008; Rueda et
249 al., 2008), which could be explained by trophic competition with farmed oysters. Indeed, all
250 sampling was carried out within the farming area. The exclusion of filter-feeders due to oyster
251 farming is consistent with other studies carried out on non-vegetated sediment (Forrest and
252 Creese, 2006) and on sediment colonized by *Lanice conchilega* (Dubois et al., 2007). According
253 to the study of Dubois et al. (2007), filter-feeders are completely excluded from oyster parks,
254 whereas carnivorous species are more abundant in these same areas.

255 Relatively few inventories of macrobenthic species in *Z. marina* habitats are available on
256 healthy large seagrass beds in the western basin of the English Channel (Hily and Bouteille,
257 1999 for Roscoff; Hamon, 1983 for Chausey, and Ollivier, 1968 for Dinard). Contrary to our
258 results, these former studies list amphipods as the dominant taxa in seagrass beds, while sipun-
259 culids, which are abundant in our study, were almost absent from these sites.

260 Sipunculids are deposit feeders and would therefore be favored by a small increase in
261 organic matter content, which might explain their presence in our study. They show low abun-
262 dances or are absent at the *Zostera*-Tractor station, and seem to be sensitive to compaction by
263 the traffic of tractors between oyster tables.

264 The abundance and biomass of *Zostera marina* shoots have a positive influence on the
265 associated macrofauna of subtidal seagrass beds in Devon (UK) (Attrill et al., 2000). The

266 macrofauna is more abundant in *Zostera* beds than in unvegetated sediments, such as observed
267 in the northern Baltic Sea (Boström and Bonsdorff, 1997).

268 The abundances of macrofauna in *Zostera marina* beds are of the same order of magni-
269 tude ~ 2,000 individuals per m² (Table 8) as on intertidal sand bars in the western basin of the
270 English Channel and similar to values found at other sites on the English Channel coast (Table
271 8). Although even higher abundances of organisms can be attained with the same sieving size
272 (1 mm), a smaller sieving size leads to abundances of up to 50,000 individuals per m² (Table
273 8). The biomass is also of the same order of magnitude as that found in the Aber Wrac'h on the
274 north Brittany coast (Hily and Bouteille, 1999), but higher than values estimated by Baden
275 (1990) along the Swedish coast in spite of higher abundances (Table 8).

276 The number of eelgrass shoots varies between 130 and 380 per m². It was in the same
277 order of magnitude than those observed in other part of *Zostera marina* beds of the Northeastern
278 Atlantic (Table 8). However, the areal density of shoots is lower than that found in the Roscoff
279 area where it can reach 800 (Jacobs, 1980).

280

281 4.2. Effects of oyster cultivation

282

283 The effects of oyster farming at a small scale are rather limited, with no changes in com-
284 munity dominance or diversity and relatively minor changes in abundance. Indeed, oyster farm-
285 ing has been known to have a relatively small impact on macrobenthic fauna compared to fish
286 farming (Forrest et al., 2009). In addition, impacts are highly dependent on environmental pa-
287 rameters (Forrest et al, 2009; Pearson and Black, 2001). Indeed, the effects of oyster farming
288 depend on the amount of biogenic deposit produced, which itself is correlated with phytoplank-
289 ton production and farming density, as well as the potential of the environment to preserve the
290 deposit. Our study area is located in a megatidal region, which could facilitate the dispersal of
291 biogenic material and therefore decrease the impact of oyster farming at the local scale (Pearson
292 and Black, 2001). However, non-vegetated sediment stations show particularly high values of
293 abundance, TR and biomass, suggesting a small enrichment effect. Similarly, Walls et al. (2017)
294 has shown that kelp cultivation has no effect on the biomass of *Zostera marina* in Dingle Bay
295 (southwestern Ireland).

296 There is no difference in seagrass macrofauna composition between oyster stations and
297 non-farmed stations, which could be explained by a lack of response in relation to seagrass

298 density. Indeed, seagrass density is one of the most important parameters influencing the as-
299 semblage composition (Hily, 2006; Duffy et al., 2015). This absence of any change in shoot
300 density is consistent with the results of Dumbauld and McCoy (2015), who showed that seagrass
301 cover, is similar between oyster farming and non-exploited areas. Therefore, it seems that the
302 *Zostera* habitat is resilient to oyster farming. However, biomasses are much higher at non-farm-
303 ing stations, mostly due to the higher biomass of sipunculids [*Golfingia (Golfingia) elongata*].
304 Moreover, low Taxonomic Richness and abundances characterize the tractor pathway. Travaille
305 et al. (2015) have shown a negative impact on the number of eelgrass shoots due to the tram-
306 pling of visitors on intertidal *Zostera marina* seagrass beds in a New Zealand marine reserve.

307

308 4.3. Remarks on the sampling protocol and data analysis

309

310 The sampling protocol used in this study is adapted to the sampling of low-mobility
311 species (infauna). However, it underestimates the presence of swimming and walking species.
312 Mobile epibenthic fauna are known to be diverse in *Zostera marina* beds (Ledoyer, 1964; Baden
313 and Pihl, 1984; Esquete et al., 2011). Baden and Pihl (1984) recorded 10 crustaceans (mostly
314 shrimps) and 10 fishes in *Z. marina* meadows on the west coast of Sweden (1980-1982), with
315 crustaceans predominating in abundance and biomass throughout the year. Indeed, non-quantitative
316 trawling in our study area has revealed the presence, sometimes quite abundant, of over
317 20 species of shrimp, crabs and amphipods that were not sampled in the benthic corer (un-
318 published data in C. Delecrin, Masters 2 dissertation). Esquete et al. (2011) has reported 113
319 species of peracarid, with a dominance of the tanaid *Apseudopsis latreillii*, in the O Grove Inlet,
320 NW Iberian Peninsula). Rueda et al. (2008) and Rueda and Salas (2008) have shown that the
321 abundance of mollusc scavengers and carnivores is higher in nocturnal than in diurnal samples
322 from *Zostera marina* beds (12-14 m) in the Alboran Sea (southern Spain).

323 In our study, biomass-weighted analyses prove to be less sensitive to changes between
324 the different habitats, although biomass highlights stronger differences between seagrasses sta-
325 tions and unvegetated stations. Nevertheless, biomasses are low at the tractor-pathway station.

326

327 4.2. Conclusions and perspectives

328

329 In spite that *Zostera marina* meadow was flourished along the west coast of Cotentin, in
330 cohabitation with extensive oyster cultivation; there was no information on the macrofauna asso-
331 ciated with this protected species in Normandy. In 2016, a seasonal sampling was carried out
332 based on five combinations of conditions involving vegetated and unvegetated areas, presence or
333 absence of oyster tables and a control station without either eelgrass or oyster cultivation, to in-
334 vestigate the structure of the infauna at Blainville-sur-mer. The sediments consisted of heteroge-
335 neous muddy sandy gravel which is largely present in the intertidal zone of the west coast of
336 Cotentin (western part of the English Channel). Macrofauna abundances, biomasses and number
337 of eelgrass shoots are similar to those reported at other sites in the English Channel and of the
338 north-eastern Atlantic. The effects of oyster farming are relatively limited, and are not a handicap
339 for the extension of *Zostera* meadows in this part of the English Channel; but low Taxonomic
340 Richness and abundances characterize the tractor pathway.

341 Oyster farming appears to affect macrobenthic communities by organic enrichment (Cas-
342 tel et al., 1989; Forrest et al., 2009). It could be interesting to investigate whether this lack of
343 response is due to the low degree of organic enrichment at our study site. In addition, our results
344 suggest that there is a larger scale effect of oyster farming mediated by competition for food.
345 Indeed, in this study, mollusc abundances are relatively low at all stations. Therefore, it
346 would be interesting to test this effect by sampling similar habitats outside the farming area.
347 Sampling could be performed at increasing distances away from the oyster tables (e.g. 100, 200,
348 500 and 1000 m) so as to identify the distance at which there is nil effect of oyster farming. In
349 addition, sampling could be carried out at high tide to collect free-living epifaunal species. Fi-
350 nally, sampling shows that the season has an effect on the community. Duffy et al. (2015) has
351 also shown that differences between non-vegetated sediment and seagrass beds are greater in
352 summer, and also that the environmental impact on macrobenthic communities changes
353 throughout the annual cycle. Hence, the importance of estimating the macrobenthic communi-
354 ties by seasonal samplings and not merely over a single annual sampling period must be pro-
355 longed.

356

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358

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366

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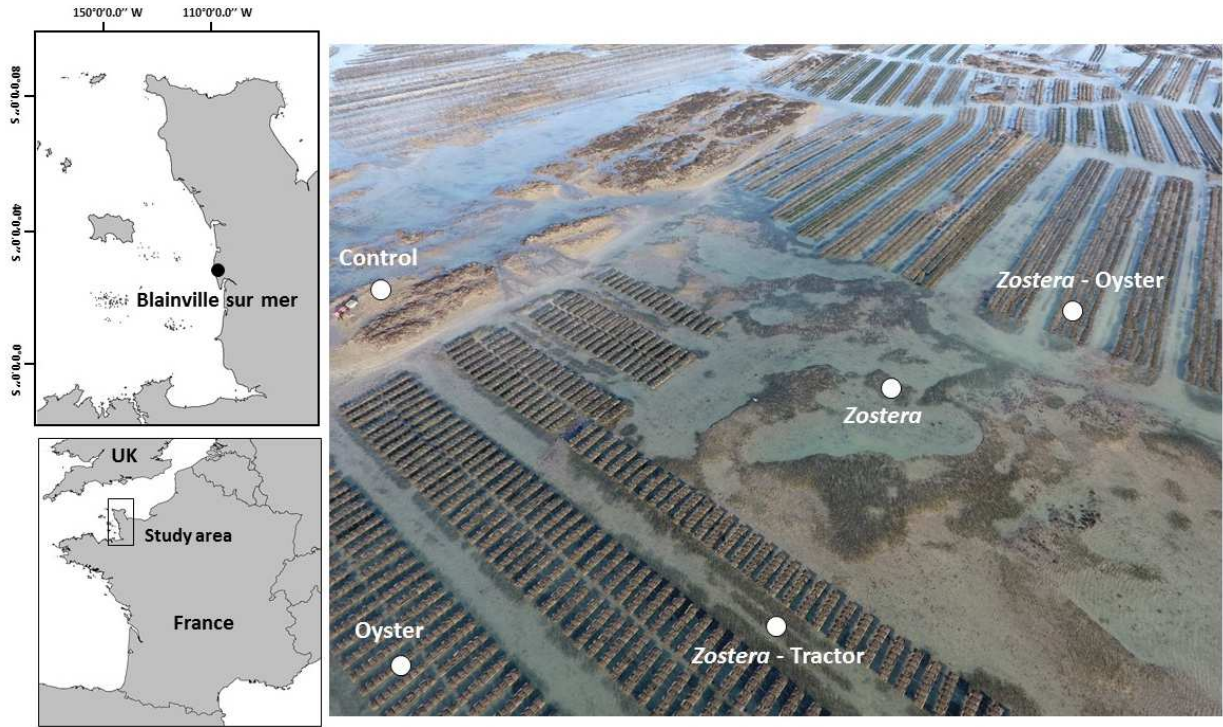
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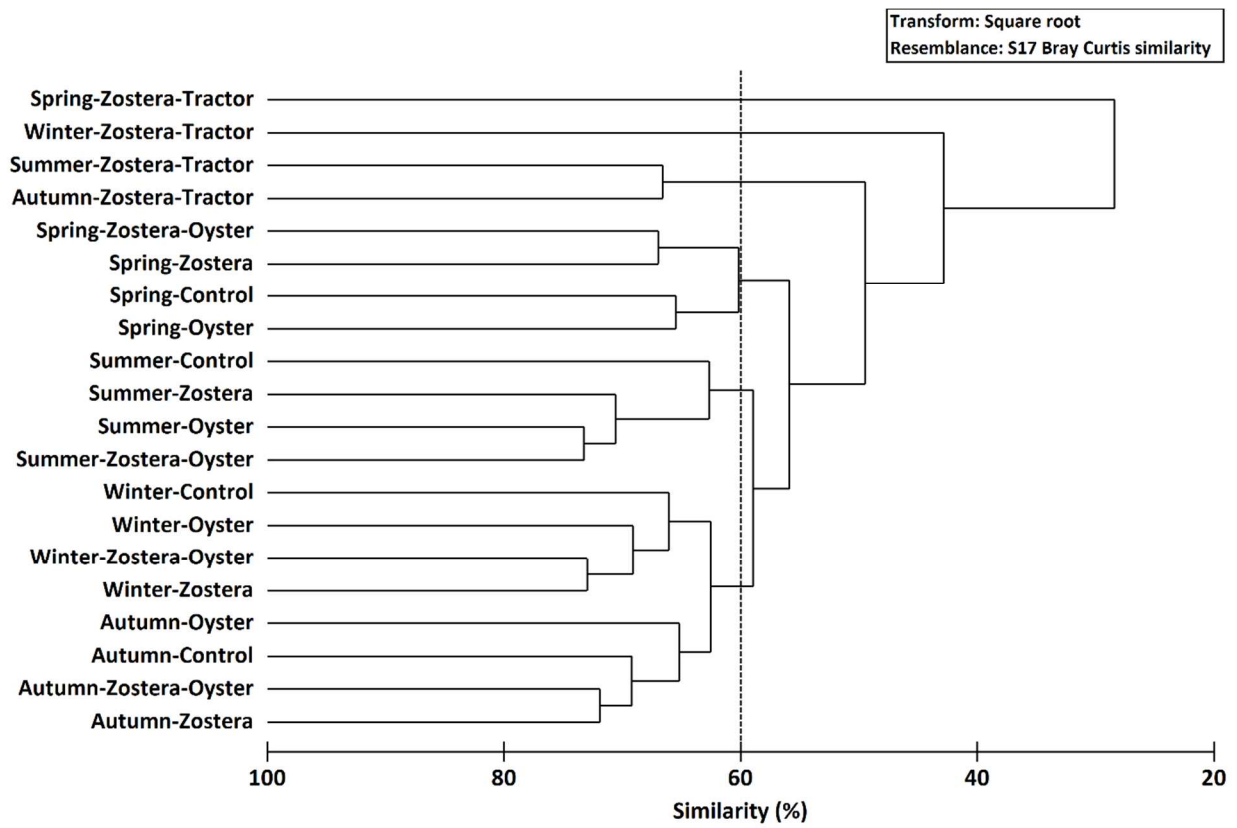
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496

497 Fig. 1. Localization of the Control, Oyster, *Zostera*, *Zostera*-Tractor and *Zostera*-Oyster stations
498 at the Blainville sur Mer site, in the Normand-Breton Gulf in the western basin of the
499 English Channel.
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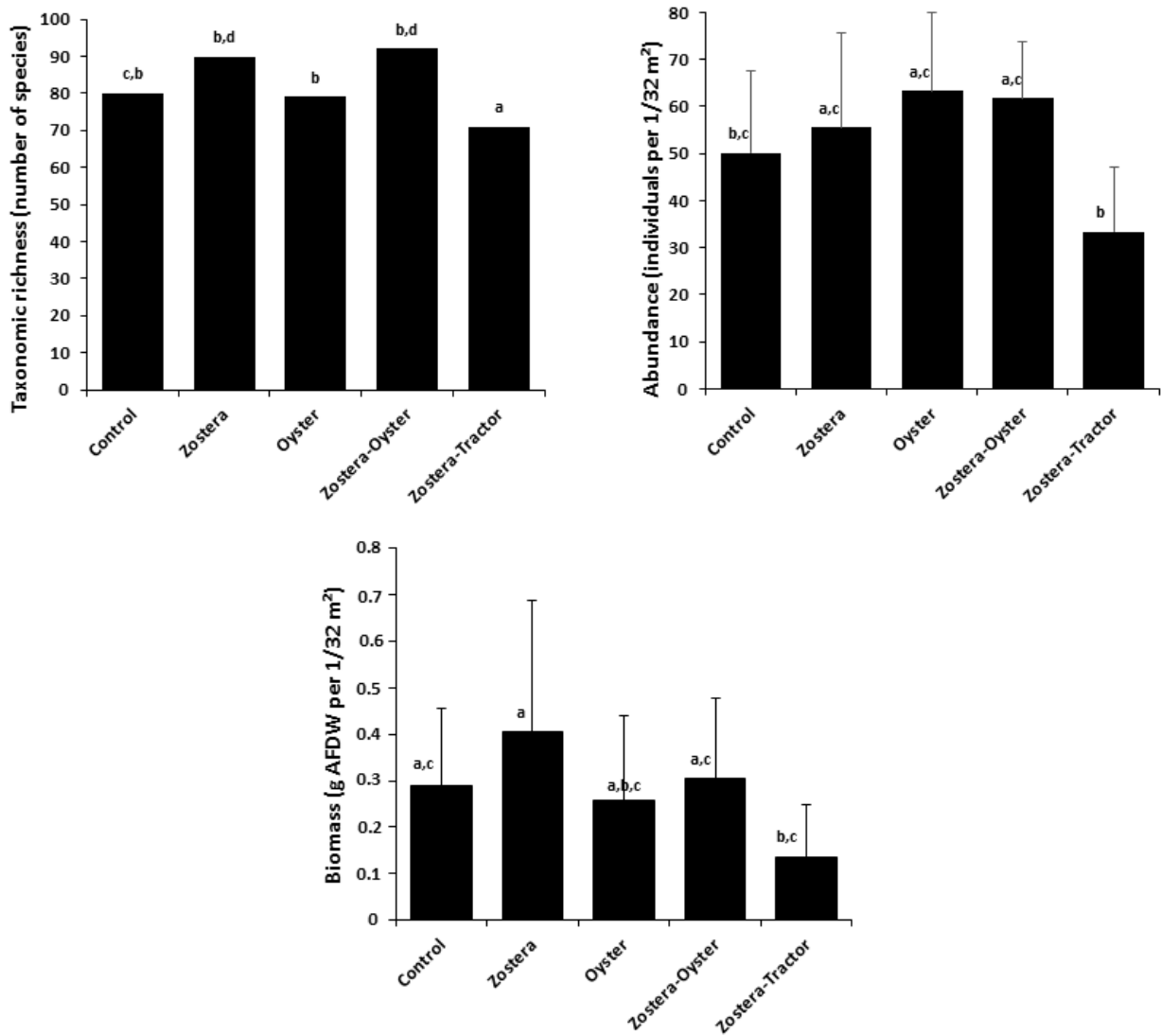


507 Fig. 2. Cluster dendrogram showing distribution of the five stations (mean abundance for the five
 508 stations for each season) according to the Bray-Curtis similarity after square-root
 509 transformation of the abundance.



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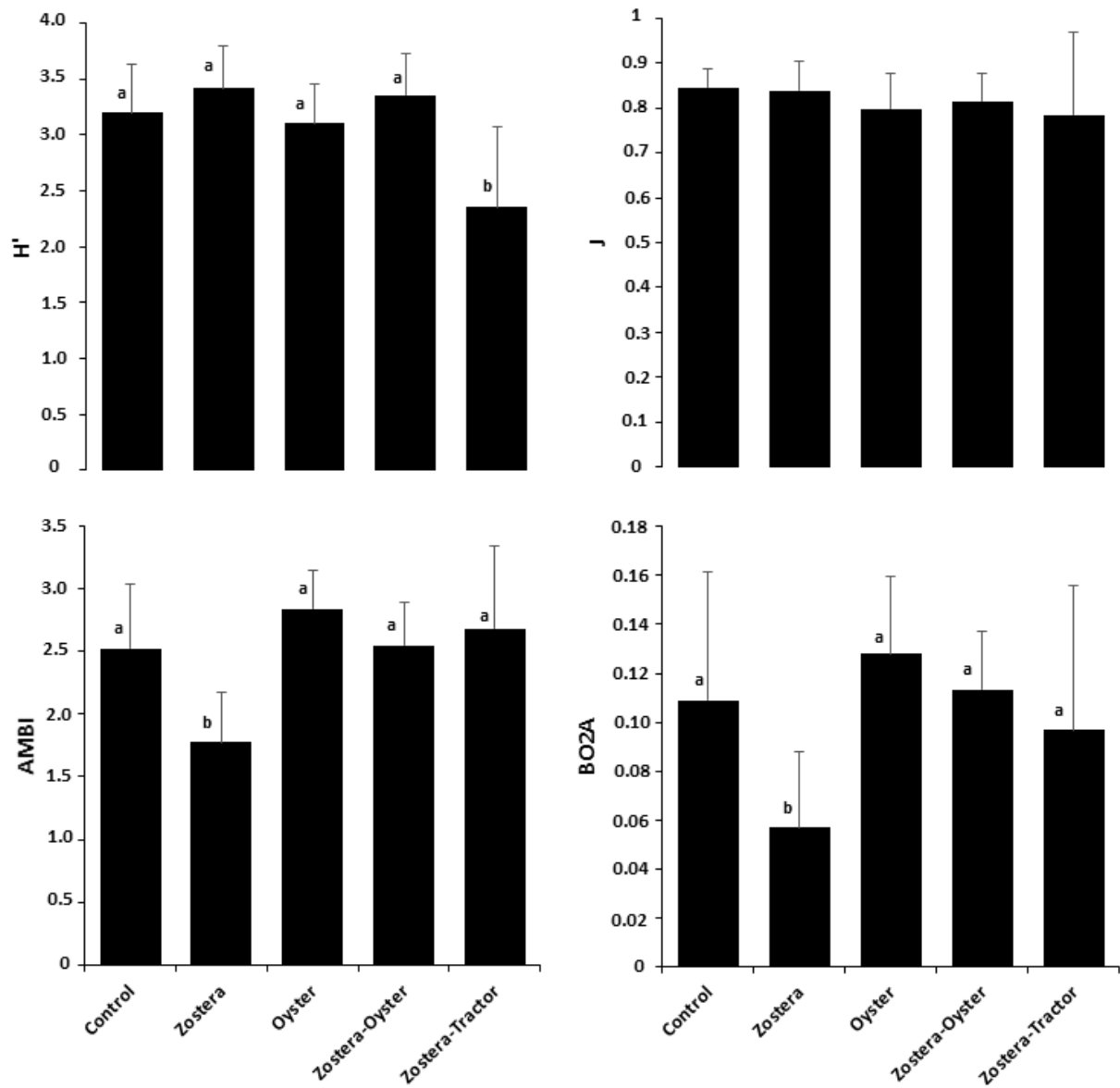
517 Fig. 3. Taxonomic richness, Abundance, Biomass at the five stations, with results of the Tukey
518 tests.



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531 Fig. 4. H', J, AMBI and BO2A at the five stations, with results of the Tukey tests.

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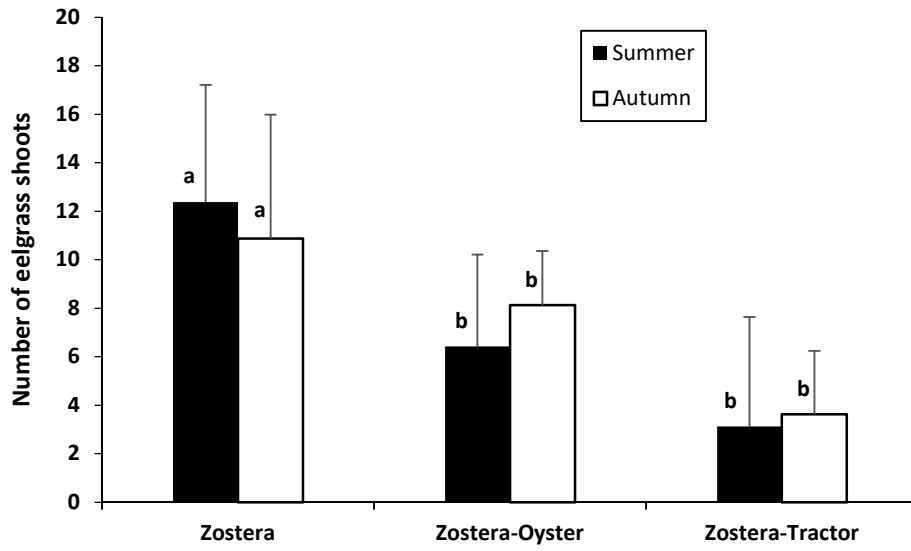
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Fig. 5. Number of eelgrass shoots per 1/32 m² of *Zostera marina* at the *Zostera*, *Zostera*-Oyster and *Zostera*-Tractor stations during summer and autumn.



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550 Table 1. Mean sediment composition with percentage (%) gravel, sand and silts-clays at the five
551 stations and mean Organic Matter content (%) with standard deviation in summer and autumn for
552 five stations.

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Station	Sediment composition			Organic Matter	
	Gravel	Sand	Silts-Clays	Summer	Autumn
Control	60.6	36.4	3.0	1.9 ± 0.5	2.6 ± 0.8
<i>Zostera</i>	45.9	44.8	9.3	2.0 ± 0.8	2.7 ± 0.8
Oyster	48.2	45.4	6.4	2.3 ± 0.4	2.9 ± 0.3
<i>Zostera</i> -Oyster	33.7	58.1	8.1	1.6 ± 0.3	3.0 ± 0.4
<i>Zostera</i> -Tractor	31.0	62.1	6.8	2.5 ± 0.1	2.0 ± 0.4

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556 Table 2. One way ANOVA results for the sediment composition between the two seasons and the
 557 stations. DF = degrees of freedom; F = F-statistic; *P* = *P-value*.

	Factor	DF	F	<i>P</i>
Season	Gravel	1	0.13	0.73
	Sand	1	0.11	0.75
	Silts-Clays	1	0.04	0.84
	Σ	8		
Station	Gravel	4	4.35	0.07
	Sand	4	3.59	0.10
	Silts-Clays	4	0.74	0.60
	Σ	5		

558

559 Table 3. Main seasonal characteristics of the structural indices for the five stations. TR
 560 (Taxonomic Richness), total number of species recorder in 0.25 m²; Mean abundance per 1/32 m²;
 561 Mean biomass (g AFDW) per 1/32 m²; H': Shannon-Weaver diversity, J: Pielou's evenness; H',
 562 J, AMBI and BO2A calculated with the total number of species and abundance per 0.25 m². The
 563 color coding corresponds to the Ecological Status of the Water Framework Directive: blue, high
 564 status; green: good status and yellow, moderate status.
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Station	Season	TR	Mean Abundance	Mean Biomass	H'	J'	AMBI	BO2A
Control	Spring	39	50.9 ± 6.1	0.33 ± 0.14	3.65	0.69	2.61	0.12
	Summer	49	65.7 ± 38.0	0.25 ± 0.17	4.14	0.74	2.25	0.06
	Autumn	42	46.9 ± 13.4	0.35 ± 0.16	4.10	0.76	2.46	0.11
	Winter	35	37.0 ± 12.5	0.22 ± 0.18	3.81	0.74	2.78	0.14
Zostera	Spring	45	53.0 ± 14.5	0.41 ± 0.21	3.74	0.62	1.56	0.04
	Summer	48	65.1 ± 40.8	0.39 ± 0.37	4.17	0.75	2.17	0.06
	Autumn	48	55.1 ± 10.4	0.35 ± 0.11	4.17	0.75	1.82	0.06
	Winter	42	49.0 ± 14.3	0.47 ± 0.39	4.27	0.79	1.88	0.07
Oyster	Spring	32	39.7 ± 9.0	0.17 ± 0.16	3.64	0.73	2.82	0.14
	Summer	47	108.6 ± 36.5	0.16 ± 0.10	3.30	0.59	3.10	0.14
	Autumn	48	62.7 ± 12.8	0.37 ± 0.22	3.56	0.64	2.75	0.11
	Winter	40	42.1 ± 8.1	0.32 ± 0.15	4.12	0.77	2.68	0.12
Zostera-Oyster	Spring	44	46.4 ± 2.4	0.29 ± 0.21	3.82	0.70	2.49	0.11
	Summer	49	75.5 ± 15.2	0.30 ± 0.17	3.66	0.65	2.64	0.11
	Autumn	53	80.4 ± 24.7	0.27 ± 0.10	3.96	0.69	2.46	0.11
	Winter	41	44.7 ± 5.7	0.36 ± 0.21	4.16	0.78	2.64	0.12
Zostera-Tractor	Spring	20	5.6 ± 2.6	0.04 ± 0.02	3.89	0.90	2.33	0.10
	Summer	39	61.4 ± 27.6	0.11 ± 0.11	2.67	0.51	2.93	0.08
	Autumn	38	48.0 ± 14.9	0.24 ± 0.10	2.63	0.50	2.96	0.08
	Winter	30	18.6 ± 9.6	0.15 ± 0.10	4.16	0.85	2.54	0.12

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568 Table 4. One-way ANOVA for the seasons (Spr: Spring; Sum: Summer; Aut: Autumn; Win:
 569 Winter) on the taxonomic richness, abundance, biomass, H', J, AMBI and BO2A with Tukey tests
 570 on the five stations.

		DF	F	p	Tukey
Taxonomic richness	Control	3	0.72	0.55	
	Zostera	3	0.51	0.68	
	Oyster	3	4.37	< 0.05	Spr ≠ Aut; Sum
	Zostera-Oyster	3	1.40	0.26	
	Zostera-Tractor	3	9.39	< 0.001	Spr ≠ Aut; Sum; Win
Abundance	Control	3	2.51	0.08	
	Zostera	3	0.60	0.62	
	Oyster	3	19.86	< 0.001	Sum ≠ Spr; Aut; Win
	Zostera-Oyster	3	12.13	< 0.001	Win ≠ Sum; Aut & Spr ≠ Sum; Aut
	Zostera-Tractor	3	19.54	< 0.001	Spr ≠ Aut; Sum & Win ≠ Aut; Spr
Biomass	Control	3	1.20	0.33	
	Zostera	3	0.24	0.87	
	Oyster	3	3.50	< 0.05	Sum ≠ Aut
	Zostera-Oyster	3	0.43	0.73	
	Zostera-Tractor	3	6.15	< 0.01	Aut ≠ Spr; Sum
H'	Control	3	1.41	0.26	
	Zostera	3	4.35	< 0.05	Win ≠ Spr
	Oyster	3	4.82	< 0.01	Win ≠ Sum; Aut; Spr
	Zostera-Oyster	3	2.31	0.10	
	Zostera-Tractor	3	2.44	0.08	
J	Control	3	5.39	< 0.01	Spr ≠ Aut; Win
	Zostera	3	6.86	< 0.01	Spr ≠ Sum; Win
	Oyster	3	16.26	< 0.001	Sum; Aut ≠ Spr; Win
	Zostera-Oyster	3	11.86	< 0.001	Sum ≠ Spr; Win & Win ≠ Aut; Spr
	Zostera-Tractor	3	17.99	< 0.001	Sum; Aut ≠ Spr; Win
AMBI	Control	3	2.80	0.06	
	Zostera	3	1.35	0.28	
	Oyster	3	3.93	< 0.05	Sum ≠ Aut; Win
	Zostera-Oyster	3	1.20	0.33	
	Zostera-Tractor	3	1.75	0.18	
BO2A	Control	3	4.57	< 0.01	Win ≠ Sum
	Zostera	3	1.50	0.24	
	Oyster	3	2.12	0.12	
	Zostera-Oyster	3	0.66	0.58	
	Zostera-Tractor	3	0.85	0.48	
	Σ	28			

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Table 5. SIMPER analyses with cumulative contribution (Cc in %) of the ten top species with indication of their mean abundance (A): number of individuals per 0.25 m²).

Summer & Autumn (Zostera-Tractor)			Spring (Oyster; Control; Zostera; Oyster- Zostera)			Summer (Oyster; Control; Zostera; Oyster- Zostera)			Winter & Autumn (Oyster; Control; Zostera; Oyster- Zostera)		
Species	Cc	A	Species	Cc	A	Species	Cc	A	Species	Cc	A
<i>Notomastus latericeus</i>	26.9	31.3	<i>Notomastus latericeus</i>	11.9	6.7	<i>Notomastus latericeus</i>	10.9	18.9	<i>Notomastus latericeus</i>	11.0	9.4
<i>Cirriiformia tentaculata</i>	38.9	7.5	<i>Golfingia (Golfingia) elongata</i>	23.0	8.5	<i>Cirriiformia tentaculata</i>	21.8	14.8	<i>Cirriiformia tentaculata</i>	21.4	8.7
<i>Caulleriella alata</i>	47.2	3	<i>Cirratulus cirratus</i>	33.5	8.9	<i>Euclymene oerstedii</i>	29.1	5.9	<i>Golfingia (Golfingia) elongata</i>	30.9	6.6
<i>Glyceras tridactyla</i>	51.6	1	<i>Euclymene oerstedii</i>	43.2	5.7	<i>Caulleriella alata</i>	35.7	6.9	<i>Euclymene oerstedii</i>	37.9	4.8
<i>Nucula hanleyi</i>	56.0	0.9	<i>Aonides oxycephala</i>	48.8	2.1	<i>Golfingia (Golfingia) elongata</i>	42.0	0.5	<i>Cirratulus cirratus</i>	44.7	3.5
<i>Cirratulus cirratus</i>	60.0	0.9	<i>Hilbigneris gracilis</i>	53.6	1.4	<i>Aonides oxycephala</i>	47.0	4.0	<i>Aonides oxycephala</i>	49.7	2.0
<i>Processa edulis edulis</i>	64.1	0.7	<i>Caulleriella alata</i>	58.1	1.2	<i>Lumbrineras latreilli</i>	51.5	2.5	<i>Caulleriella alata</i>	53.7	1.6
<i>Abra alba</i>	67.2	0.5	<i>Cirriiformia tentaculata</i>	62.5	1.7	<i>Bittium reticulatum</i>	55.6	2.1	<i>Lumbrineris latreilli</i>	57.7	1.4
<i>Aonides oxycephala</i>	70.3	0.5	<i>Glyceras tridactyla</i>	66.0	0.7	<i>Dexamine spinosa</i>	59.1	2.3	<i>Calyptrea chinensis</i>	60.5	1.1
<i>Bittium reticulatum</i>	73.5	0.9	<i>Tritia reticulata</i>	69.1	0.6	<i>Processa edulisedulis</i>	62.0	1.2	<i>Abra alba</i>	63.2	0.8

Table 6. One-way ANOVA for the five stations (Control, *Zostera*, Oyster, *Zostera*-Oyster, *Zostera*-Tractor) on the taxonomic richness, abundance, H', J, AMBI and BO2A, with Tukey tests on the five stations.

	Df	F	<i>p</i>	Tukey
Taxonomic richness	4	21.73	<0.001	<i>Zostera</i> -Tractor ≠ Control; Oyster; <i>Zostera</i> ; <i>Zostera</i> -Oyster Control ≠ <i>Zostera</i> ; <i>Zostera</i> -Oyster
Abundance	4	6.80	<0.001	<i>Zostera</i> -Tractor ≠ Oyster; <i>Zostera</i> ; <i>Zostera</i> -Oyster
Biomass	4	8.11	<0.001	<i>Zostera</i> -Tractor ≠ Control; <i>Zostera</i> ; <i>Zostera</i> -Oyster Oyster ≠ <i>Zostera</i>
H'	4	26.56	<0.001	<i>Zostera</i> -Tractor ≠ Control; Oyster; <i>Zostera</i> ; <i>Zostera</i> -Oyster
J	4	2.19	0.07	
AMBI	4	25.17	<0.001	<i>Zostera</i> ≠ <i>Zostera</i> -Tractor; Control; Oyster; <i>Zostera</i> -Oyster
BO2A	4	13.40	<0.001	<i>Zostera</i> ≠ <i>Zostera</i> -Tractor; Control; Oyster; <i>Zostera</i> -Oyster
Σ	155			

Table 7. Two-way ANOVA for the three stations (*Zostera*, *Zostera*-Oyster and *Zostera*-Tractor) on the number of eelgrass shoots of *Zostera marina*, with Tukey tests on the five stations.

	Df	F	<i>p</i>	Tukey
Season	1	0.01	0.91	
Station	2	18.04	<0.001	<i>Zostera</i> ≠ <i>Zostera</i> -Oyster; <i>Zostera</i> -Tractor
Σ	46			

Table 8. Main structural characteristics of macrofauna and eelgrass shoots of *Zostera marina* from the Northeastern Atlantic. EC: English Channel. (TR: Taxonomic Richness; Abundance: individuals number per 1 m²; Biomass: g AFDW per 1 m²).

Site	Zone	Date	mesh size (mm)	TR	Abundance	Biomass	Eelgrass shoots	Reference
Blainville sur mer, EC	Low intertidal	Annual mean, <i>Z. marina</i>	1	147	1,900	11.3	130-380	This study
		Annual mean, Bare sand		134	1,820	8.7	-	
	Midlittoral	April 2015		50	1,620	-	-	Delecrin, unpublished data
				53	1,780	-	-	
Roscoff, EC	Intertidal	Annual mean	-	1,094-27,350	-	500-800	Jacobs, 1980	
Aber Wrach, EC		Winter, three stations on <i>Z. marina</i>	65	2,232	17.03	360	Hily and Bouteille, 1999	
		Winter, three stations on bare sand	16	197	1.24	-		
Cornwall, EC	1-6 m	July 1996	0.5	83	1,911-12,229	-	12-144	Webster et al., 1998
Saint Malo, EC	Intertidal	Annual mean on five years	1	227	3,226	-	-	Boyé et al., 2017
Arcouest, EC				274	4,825	-	-	
Sept-Iles, EC				225	6,875	-	-	
Callot, EC				342	6,664	-	-	
Sainte-Marguerite, EC				245	19,560	-	-	
Molène, Iroise Sea				279	12,665	-	-	
Roscanvel, Brest				302	6,668	-	-	
Glénan, Atlantic				289	24,370	-	-	
Eo Estuary, Spain				-	13,850-17,835	-	100-253	Curras et al. 1993
Finsbo, Sweden				0.7 to 2.5 m	Annual mean	0.2	-	28,300
Rixö, Sweden	-	12,200	0.37				-	
North Baltic Sea	3-5 m	Mean of 5 stations on <i>Z. marina</i>	0.5	30	25,000-50,000	-	50-500	Boström and Bonsdorff, 1997
		Mean of 5 stations on bare sand		18	2,500-15,000	-	-	