Original Articles

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

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A B S T R A C T

Zostera marina flourish along the west coast of Cotentin, in cohabitation with extensive oyster cultivation. In 2016, seasonal sampling was carried out based on five combinations of conditions involving vegetated and unvegetated areas, presence or absence of oyster tables and a control station without either eelgrass or oyster cultivation. The sediments consisted of muddy sandy gravel and no significant difference of sediment composition was observed between stations and seasons. A total of 147 taxa and 8404 individuals were recorded over a period of the one year with a sampling effort of 5 m². The effects of oyster farming are relatively limited, and are not a handicap for the extension of *Zostera* meadows in this part of the English Channel. Nevertheless, low Taxonomic Richness and abundances characterize the tractor pathway. Macrofauna abundances, biomasses and number of eelgrass shoots are similar to those reported at other sites in the English Channel and from the North-eastern Atlantic.

1. Introduction

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

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

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

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

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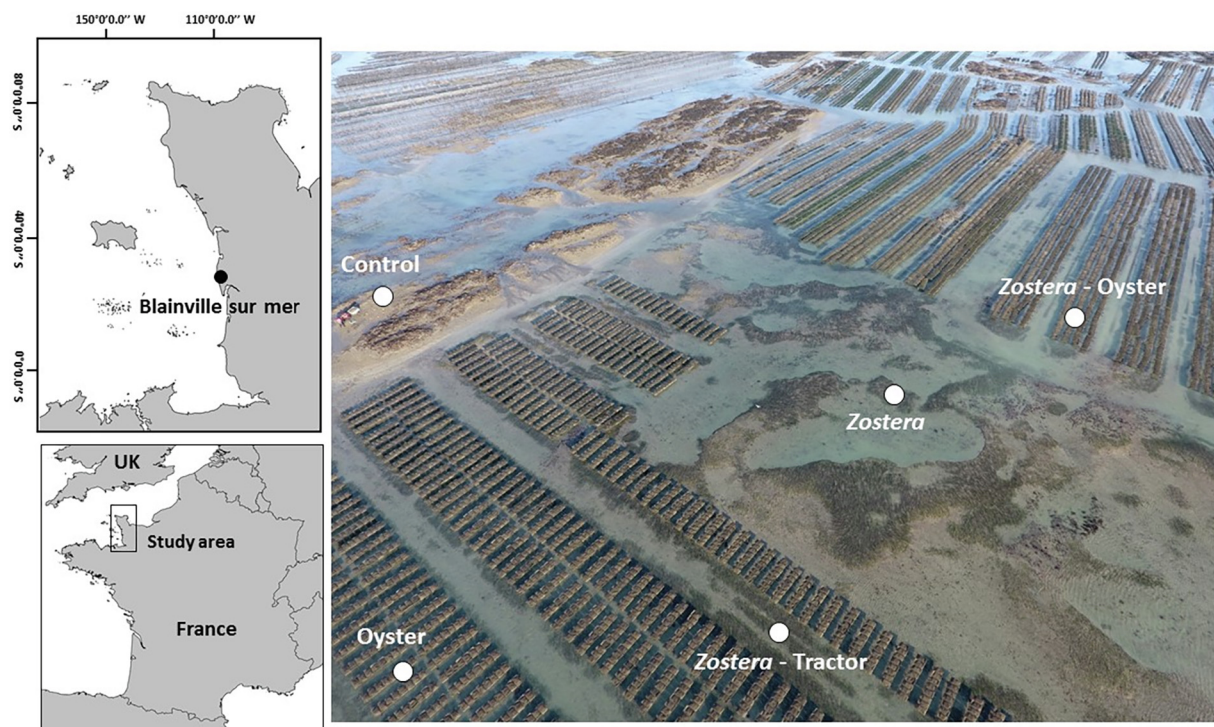 *E-mail address:* jean-philippe.pezy@unicaen.fr (J.-P. Pezy).

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

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

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
Zostera	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
Zostera-Oyster	33.7	58.1	8.1	1.6 ± 0.3	3.0 ± 0.4
Zostera-Tractor	31.0	62.1	6.8	2.5 ± 0.1	2.0 ± 0.4

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

Factor		DF	F	P
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		

Moreover, oyster farming occupies large areas of tidal flats along the Cotentin west coast, raising the issue of environmental impact. Studies have shown that shellfish farming has a highly variable impact on benthic macrofauna (Forrest et al., 2009); a study in the Bay des Veys (East Cotentin) has indicated changes in the macrofaunal assemblages associated with *Lanice conchilega* in relation to oyster farming (Dubois et al., 2007). Likewise, the macrofauna associated with *Zostera marina* is expected to be more impacted by oyster farming as seagrasses themselves are sensitive to eutrophication and mechanical stresses

(trampling by workers and tractor pathway) (Hily, 2006).

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

2. Materials and methods

2.1. Study site, sampling and sample treatments

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

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

At each station, eight circular cores (1/32 m^2; 0.15 m deep; total surface of sampling 0.25 m^2) were sampled and sieved on a circular 1-mm mesh-size screen to collect the macrofauna; one additional sample was collected to determine the grain size distribution and organic matter content, the latter being only measured in summer and autumn. Each replicate sample was then sorted in order to separate fauna from sediment. Individuals were identified to the lowest possible taxonomic level (generally, the species level).

Taxonomic richness and abundance were recorded for each replicate. The biomasses of each species were measured for each season.

Table 3
Main seasonal characteristics of the structural indices for the five stations. TR (Taxonomic Richness), total number of species recorder in 0.25 m²; Mean abundance per 1/32 m²; Mean biomass (g AFDW) per 1/32 m²; H': Shannon-Weaver diversity, J: Pielou's evenness; H', J, AMBI and BO2A calculated with the total number of species and abundance per 0.25 m². The color coding corresponds to the Ecological Status of the Water Framework Directive: blue, high status; green: good status and yellow, moderate status.

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

Samples were dried for three days at 60 °C and calcined at 500 °C for 4 h and Biomasses were expressed as AFDW (Ash Free Dry Weight) per 0.25 m² and 1 m².

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

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

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

2.2. Taxonomic diversity analysis

Data were used to calculate the Taxonomic Richness (TR, number of taxa per 0.25 m²) and abundance (individuals per 1/32 m² or 0.25 ind.m⁻²) and the most widely-used biodiversity indices for each station, i.e. the Shannon-Weaver diversity index (H') in $\log_2$ and Pielou's evenness (J) for the five stations and four dates. Data analysis was performed using the PRIMER® version 6 software package (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley, 2006).

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

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

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

2.2.1. Multivariate analysis

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

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

3. Results

3.1. Main environmental characteristics

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

3.2. General characteristics of the fauna

A total of 147 taxa and a total of 8404 individuals were recorded during the one-year sampling effort of 5 m^2. Among these taxa, the macrofauna is dominated by Polychaetes (64 species and 46.0% of abundance), crustaceans (39 species and 32.8%), molluscs (32 species and 19.3%), sipunculids (6 species and 0.9%), echinoderms (3 species and 0.8%), Cnidaria (2 species and 0.1%) and Chordata (1 species and 0.1%). The five dominant species are the polychaetes *Notomastus latericeus* (386 individuals per m^2), *Cirriformia tentaculata* (243 individuals per m^2), *Euclymene oerstedi* (138 individuals per m^2), *Cirratulus cirratus* (116 individuals per m^2) and the sipunculid *Golfingia (Golfingia) elongata* (171 individuals per m^2).

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

The mean abundance per core sample varies from a minimum of 5.6 for the *Zostera*-Tractor station in spring to 108.6 for the Oyster station in summer. Most of the values are comprised between 40 and 80 individuals per 1/32 m^2 (Table 3). A significant seasonal pattern is observed for three of the five stations: Oyster, *Zostera*-Oyster and *Zostera*-Tractor (Table 4).

The mean biomass per core sample varies from a minimum of 0.04 g AFDW for the *Zostera*-Tractor station in spring to 0.47 g AFDW for the *Zostera* station in winter. Most of the values are comprised between 0.2 and 0.4 g AFDW per 1/32 m^2 (Table 3). A significant pattern is observed for two of the five stations: Oyster and *Zostera*-tractor (Table 4).

3.3. Ecological quality status (EcoQS)

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

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

3.4. Spatio-temporal patterns of the macrofauna

At a similarity value of 60%, the cluster dendrogram allows us to separate the stations into four main groups, with one station isolated from the others at two seasons, i.e. *Zostera*-tractor in spring and winter (Fig. 2). The first group includes both other seasons (summer and autumn) at the *Zostera*-tractor station. The three other groups include the four other stations per season (spring, summer and autumn and winter). At 58% similarity, the last group can be separated into two sub-groups for the autumn and winter seasons. In summary, the analysis reveals two main patterns; the *Zostera*-tractor station is separated from the rest of the stations which can be grouped by season.

SIMPER analysis classifies 18 species among the ten top species of each group (Table 5). The polychaete *Notomastus latericeus* is the top species in the four groups, while the other polychaete *Cirriformia*
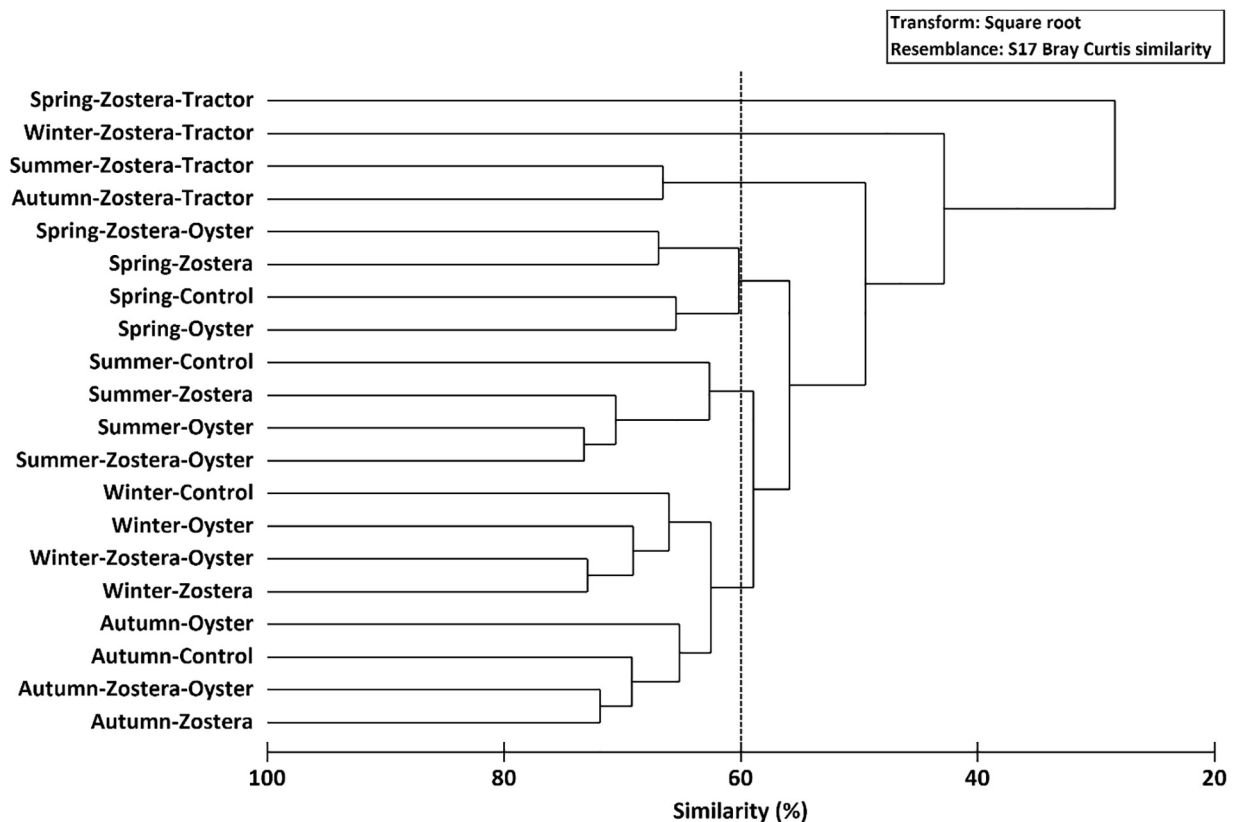
Fig. 2. Cluster dendrogram showing distribution of the five stations (mean abundance for the five stations for each season) according to the Bray-Curtis similarity after square-root transformation of the abundance.

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 $0.25\,m^2$).

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

tentaculata is the second most abundant species except in spring (Table 5). The third and following species differ in terms of abundance in the four groups, showing mainly seasonal changes with time. Molluscs and Crustaceans are classified among the least abundant, while polychaetes and the sipunculid *Golfingia* (*Golfingia*) *elongata* are classified among the most abundant. *G. elongata* is absent among the top ten species at the *Zostera*-Tractor station, while the polychaete *Notomastus latericeus* shows its maximum abundance at this station (Table 5).

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

3.5. Eelgrass shoots

The mean numbers of eelgrass shoots ($1/32\,m^2$) varies from 4 at the *Zostera*-Tractor stations to 12 at the *Zostera* bed station (Fig. 5). The number was intermediate in the *Zostera*-Oyster station (Fig. 5). No difference is observed between the summer and autumn results, while there are significant differences between the three stations associated with *Zostera* (Fig. 4; Table 7).

4. Discussion

4.1. Faunal characteristics and eelgrass shoots

Stations associated with sea grasses correspond to habitat A5.5331 (*Zostera marina/angustifolia* beds on lower shore or infralittoral clean or muddy sand according to the EUNIS habitat classification), whereas
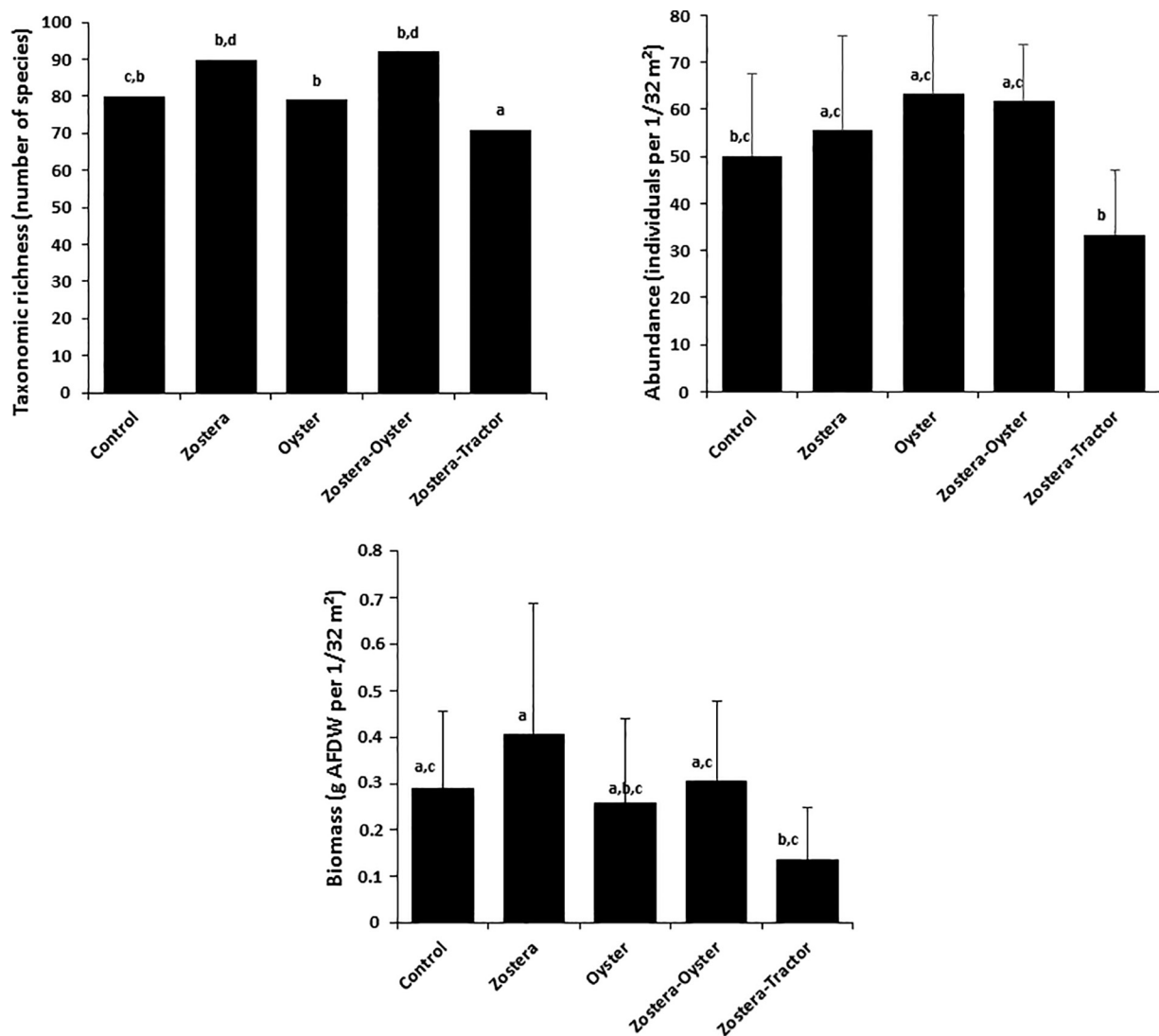
Fig. 3. Taxonomic richness, Abundance, Biomass at the five stations, with results of the Tukey tests.

stations without sea grasses are classified as Cirratulids and *Cerastoderma edule* mixed sediment (A2.421) (http://eunis.eea.europa.eu/habitats-code-browser.jsp).

Diversity assessed for the entire study site is relatively high for intertidal stations (Table 1), with a total of 147 taxa for a sampled area of $5\,m^2$ and a mean TR per station of 38.21 species (for $0.25\,m^2$). These stations show a good ecological status. Species richness at non-vegetated intertidal Water Framework Directive stations ranges from 7.6 species.$0.25\,m^2$ (Bay of Mont-Saint-Michel) to 23.1 at Chausey (Garcia et al., 2014). However, abundances are relatively low (387 individuals.$0.25\,m^2$). Indeed, unvegetated sediment stations in the Bay of Mont-Saint- Michel and Chausey have mean abundances of 179 individuals and 1044 respectively. In this study, communities are largely dominated by Polychaetes and Sipunculids (Table 5), whereas, in other studies, sipunculids show relatively low abundances.

Both unvegetated sediments and *Z. marina* habitats have a relatively low density of molluscs compared to similar habitats (Hily and Bouteille, 1999; Rueda and Salas, 2008; Rueda et al., 2008), which could be explained by trophic competition with farmed oysters. Indeed, all sampling was carried out within the farming area. The exclusion of filter-feeders due to oyster farming is consistent with other studies carried out on non-vegetated sediment (Forrest and Creese, 2006) and on sediment colonized by *Lanice conchilega* (Dubois et al., 2007). According to the study of Dubois et al. (2007), filter-feeders are

completely excluded from oyster parks, whereas carnivorous species are more abundant in these same areas.

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

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

The abundance and biomass of *Zostera marina* shoots have a positive influence on the associated macrofauna of subtidal seagrass beds in Devon (UK) (Attrill et al., 2000). The macrofauna is more abundant in *Zostera* beds than in unvegetated sediments, such as observed in the northern Baltic Sea (Boström and Bonsdorff, 1997).

The abundances of macrofauna in *Zostera marina* beds are of the same order of magnitude ~ 2000 individuals per m^2 (Table 8) as on intertidal sand bars in the western basin of the English Channel and similar to values found at other sites on the English Channel coast (Table 8). Although even higher abundances of organisms can be
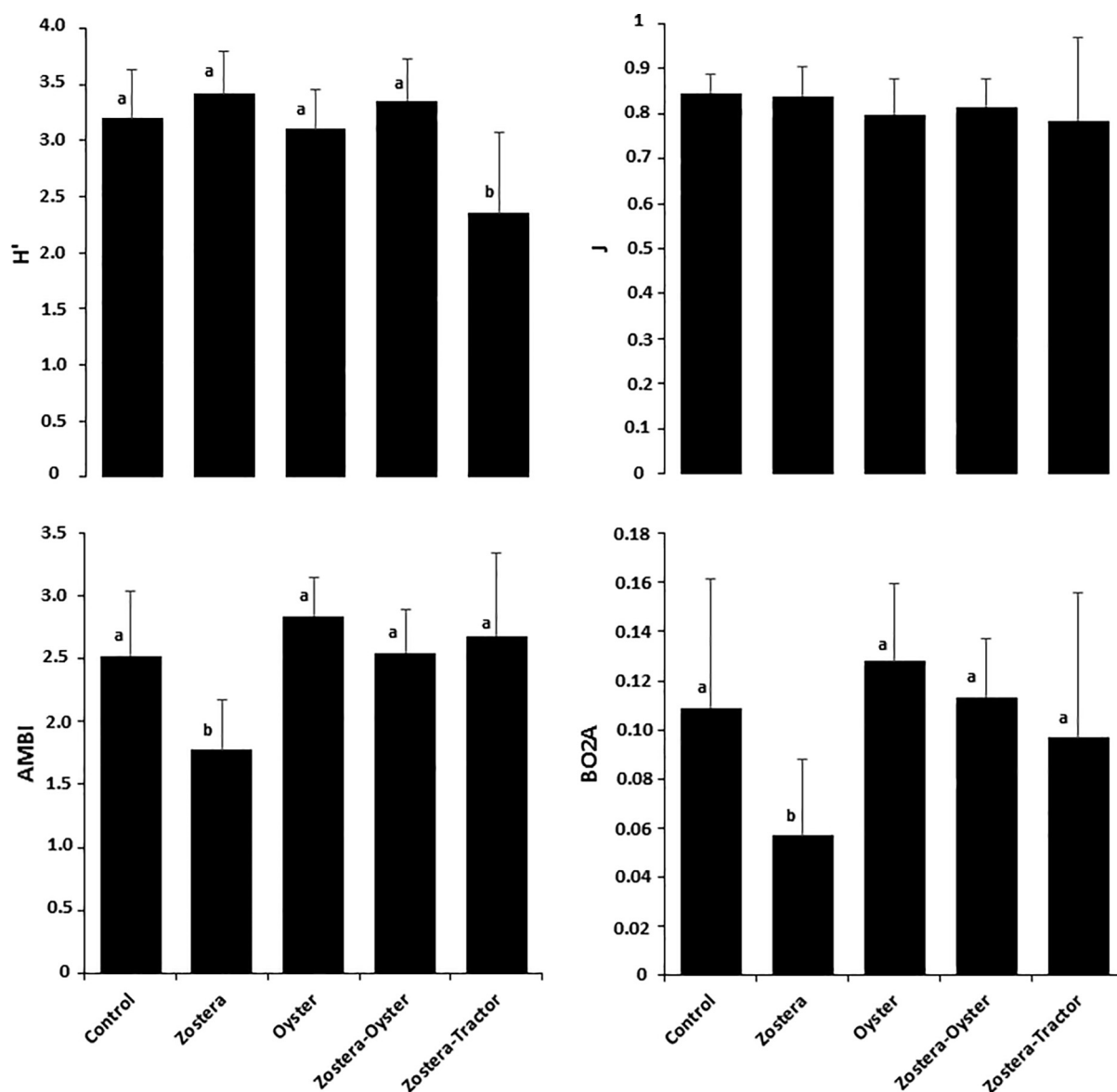
Fig. 4. H′, J, AMBI and BO2A at the five stations, with results of the Tukey tests.

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	p	Tukey
Taxonomic richness	4	21.73	< 0.001	*Zostera*-Tractor ≠ Control; Oyster; *Zostera*; *Zostera*-Oyster
				Control ≠ *Zostera*; *Zostera*-Oyster
Abundance	4	6.80	< 0.001	*Zostera*-Tractor ≠ Oyster; *Zostera*; *Zostera*-Oyster
Biomass	4	8.11	< 0.001	*Zostera*-Tractor ≠ Control; *Zostera*; *Zostera*-Oyster
				Oyster ≠ *Zostera*
H′	4	26.56	< 0.001	*Zostera*-Tractor ≠ Control; Oyster; *Zostera*; *Zostera*-Oyster
J	4	2.19	0.07	
AMBI	4	25.17	< 0.001	*Zostera* ≠ *Zostera*-Tractor; Control; Oyster; *Zostera*-Oyster
BO2A	4	13.40	< 0.001	*Zostera* ≠ *Zostera*-Tractor; Control; Oyster; *Zostera*-Oyster
Σ	155			

attained with the same sieving size (1 mm), a smaller sieving size leads to abundances of up to 50,000 individuals per m² (Table 8). The biomass is also of the same order of magnitude as that found in the Aber Wrac'h on the north Brittany coast (Hily and Bouteille, 1999), but higher than values estimated by Baden (1990) along the Swedish coast in spite of higher abundances (Table 8).

The number of eelgrass shoots varies between 130 and 380 per m². It was in the same order of magnitude than those observed in other part of *Zostera marina* beds of the Northeastern Atlantic (Table 8). However, the areal density of shoots is lower than that found in the Roscoff area where it can reach 800 (Jacobs, 1980).
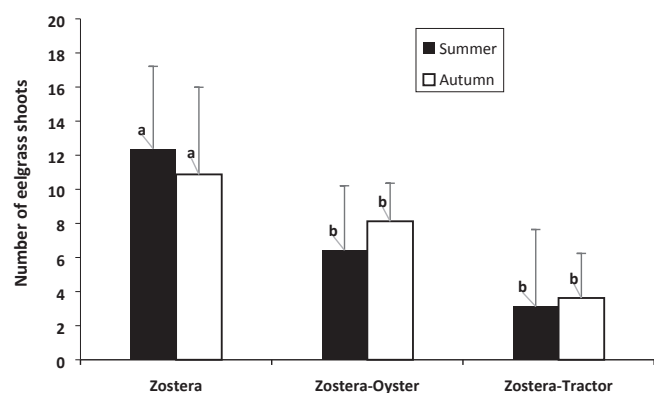
Fig. 5. Number of eelgrass shoots per $1/32\,m^2$ of *Zostera marina* at the *Zostera*, *Zostera*-Oyster and *Zostera*-Tractor stations during summer and autumn.

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	*p*	Tukey
Season	1	0.01	0.91	
Station	2	18.04	< 0.001	*Zostera* ≠ *Zostera*-Oyster; *Zostera*-Tractor
Σ	46			

4.2. Effects of oyster cultivation

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

There is no difference in seagrass macrofauna composition between oyster stations and non-farmed stations, which could be explained by a lack of response in relation to seagrass density. Indeed, seagrass density is one of the most important parameters influencing the assemblage composition (Hily, 2006; Duffy et al., 2015). This absence of any change in shoot density is consistent with the results of Dumbauld and McCoy (2015), who showed that seagrass cover, is similar between oyster farming and non-exploited areas. Therefore, it seems that the *Zostera* habitat is resilient to oyster farming. However, biomasses are much higher at non-farming stations, mostly due to the higher biomass of sipunculids [*Golfingia (Golfingia) elongata*]. Moreover, low Taxonomic Richness and abundances characterize the tractor pathway. Travaille et al. (2015) have shown a negative impact on the number of eelgrass shoots due to the trampling of visitors on intertidal *Zostera marina* seagrass beds in a New Zealand marine reserve.

4.3. Remarks on the sampling protocol and data analysis

The sampling protocol used in this study is adapted to the sampling

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

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

4.4. Conclusions and perspectives

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

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

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 m^2; Biomass: g AFDW per 1 m^2).

Site	Zone	Date	mesh size (mm)	TR	Abundance	Biomass	Eelgrass shoots	Reference
Blainville sur mer, EC	Low intertidal	Annual mean, *Z. marina*	1	147	1900	11.3	130–380	This study
		Annual mean, Bare sand		134	1820	8.7	–	
	Midlittoral	April 2015		50	1620	–	–	Delecrin, unpublished data
				53	1780	–	–	
Roscoff, EC	Intertidal	Annual mean		–	1094–27,350	–	500–800	Jacobs (1980)
Aber Wrach, EC		Winter, three stations on *Z. marina*		65	2232	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	1911–12,229	–	12–144	Webster et al. (1998)
Saint Malo, EC	Intertidal	Annual mean on five years	1	227	3226	–	–	Boyé et al. (2017)
Arcouest, EC				274	4825	–	–	
Sept-Iles, EC				225	6875	–	–	
Callot, EC				342	6664	–	–	
Sainte-Marguerite, EC				245	19,560	–	–	
Molène, Iroise Sea				279	12,665	–	–	
Roscanvel, Brest				302	6668	–	–	
Glénan, Atlantic				289	24,370			
Eo Estuary, Spain		Annual mean		–	13,850–17,835	–	100–253	Curras et al. (1993)
Finsbo, Sweden	0.7 to 2.5 m		0.2	–	28,300	0.51	–	Baden (1990)
Rixö, Sweden				–	12,200	0.37	–	
North Baltic Sea	3–5 m	Mean of 5 stations on *Z. marina*	0.5	30	25,000–50,000	–	50–500	Boström and Bonsdorff (1997)
		Mean of 5 stations on bare sand		18	2500–15,000	–	–	

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