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Does the invasive macro-algae *Sargassum muticum* (Yendo) Fensholt, 1955 offer an appropriate temporary habitat for mobile fauna including non indigenous species?

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A B S T R A C T

The fauna inhabiting the brown seaweed *Sargassum muticum* was studied on a spatial scale along the Normandy coast from the Normand-Breton Gulf to the Bay of Seine (English Channel) in both shallow sandy and rocky tidal pools during the springs 2018 and 2019. In this paper, we test the following hypothesis: do the areas with dense populations of *S. muticum* represent an appropriate habitat for dense motile fauna including other Non-Indigenous Species (NIS)? The ALEX (ALien biotic indEX) is used to ascertain whether or not *S. muticum* favours the establishment of other NIS in this new habitat. Results show that the epifaunal assemblage associated with *S. muticum* differs between the five sampling sites. However, the fauna at all five sites is dominated by arthropoda, especially the amphipods and isopods. In addition, five non indigenous species are observed inhabiting the brown seaweed (four amphipods: *Aoroides longimerus, Aoroides semicurvatus, Monocorophium acherusicum*, *Monocorophium sextonae* and one decapod: *Hemigrapsus sanguineus*). In spite of the presence of Non-Indigenous Species (NIS) associated with the invasive *Sargassum*, the ALEX yields a high Ecological Quality Status for all the sites. Nevertheless, the results suggest that *S. muticum* is a suitable habitat for many invertebrates especially amphipods and isopods, while also representing a potential source of food for several local fish and cephalopod species.

1. Introduction

The macro-algae *Sargassum muticum* (Yendo) Fensholt, 1955 (Ochrophyta, Phaeophyceae), commonly known as Japanese wire weed, is a large brown seaweed originating from the north-western Pacific in Chinese and Japanese waters. It was accidentally introduced along the north-American coasts in the 1940s and more recently in the north-east Atlantic along the European coasts in the 1970s (Farnham et al., 1973). It is known nowadays as a cosmopolitan species (Engelen et al., 2015). For European waters, it was first recorded in 1973 along the coastline of Southern England, then in 1975 at Saint-Vaast La Hougue, a site on the eastern Cotentin peninsula along the French coast of the Channel (Farnham et al., 1973; Cosson et al., 1977). Its introduction into Europe is associated with the voluntary introduction of the Japanese oyster *Crassostrea gigas* (Thunberg, 1793), following a disease that affected populations of the Portuguese oyster *Crassostrea angulata* (Lamarck, 1819) cultivated along the European seabord (Loraine, 1989).

The inherent capacities of this macro-alga (high ecological valence, fragmentation reproduction, high growth rate, etc.) have led to a very rapid expansion of its range, making it one of the most invasive species among macro-algae attracting special concern (Boudouresque and Verlaque, 2002). It is known to occur along most of the western coasts of Europe from the south of Spain to southern Norway (Belsher and Pommellec, 1988).

Along the Normandy coast, on the French side of the English Channel, *Sargassum muticum* is present on all the coasts around the Cotentin peninsula and eastwards along the coastline of the Calvados department, especially in areas of shellfish farming (Baffreau et al., 2018). This seaweed occupies the foreshore zone, particularly in tidal pools where water remains at low tide and is also found along the coastal fringe to depths of 10 m where it can form very dense populations from spring to late summer (June to August). The fronds can attain lengths of up to 10 m. As primary producer of vegetal matter, *S. muticum* is in competition for space, light and nutrients with other seaweeds and the sea grass *Zostera (Zostera) marina* Linnaeus, 1753 (Tracheophyta, Monocots), which are well established in the Mont St Michel Bay as well as in the

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Chausey and Channel Islands (Baffreau et al., 2018). In Normandy, the dense growth of such seaweed has a major negative impact on tourism, navigation and oyster cultivation as well as fishing with traps and pots. This proliferation leads to the accumulation of large quantities of such seaweed on the beach (Givernaud et al. 1991) and corresponds to a large input of detritus as in other areas (Rossi et al., 2010). On the other side, dense populations of *S. muticum* could also afford protection for many motile species, such as certain fish, the shrimp *Palaemon serratus* (Pennant, 1777), amphipods, isopods and cephalopods, in the same way as with the *Laminaria* (Ochrophyta, Phaeophyceae) forests in other areas where the species has been introduced (Norton and Benson, 1983; Takeuchi et al., 1987; Britton-Simmons, 2004).

Several studies have shown that this introduced species had a positive effect on the diversity of motile fauna such as amphipods, isopods and gastropods (Britton-Simmons, 2004; Norton and Benson, 1983; Takeuchi et al., 1987; Viejo, 1997; 1999).

Other *Sargassum* species act also as refuges for invertebrates and fishes, and are known as zones with high diversity in comparison with other intertidal areas covered by other species of macro-algae or without macro-algae (Wakabara et al., 1983; Buschmann, 1990; Duffy, 1990; Metaxas and Scheibling, 1993; Jacobucci et al., 2002; Tanaka and Leite, 2003, 2004; Buschbaum et al., 2006; Leite et al., 2007; Jacobucci et al., 2009; Cacabelos et al., 2010; Guerra-García et al., 2010, 2014; Jacobucci and Leite, 2014; Barreto de Oliveira Machado et al., 2015; Jacobucci et al., 2019).

To evaluate the Ecological Quality Status of areas colonized by the NIS *S. muticum*, various authors have calculated the diversity indices, the Shannon-Wiener and Pielou evenness, as well as the biotic index AMBI (AZTI's Marine Biotic Index) (Borja et al., 2000, 2009; Dauvin, 2018). However, these indices are not suited to assess the impacts of the NIS on benthic communities, while the ALEX (ALien biotic indEX,) was developed to evaluate the impact of NIS on native assemblages (Çinar and Bakir, 2014). This latter index is based on the abundance percentages of different groups defined on the basis of species establishment and invasiveness within samples (Çinar and Bakir, 2014).

To our knowledge, no study has been yet been undertaken to characterize the macrofauna associated with *Sargassum muticum* along the English Channel coast. In the framework of an overview of the Non-Indigenous Species (NIS) of algae and living invertebrates recorded in marine and brackish waters along the Normandy coast in France, we describe the macrofauna associated with the invasive seaweed *Sargassum muticum*. Since this macro-alga is known to be a refuge for motile fauna, we test the hypothesis of whether it could represent an appropriate habitat for other Non-Indigenous Species (NIS) in areas with dense populations of *S. muticum*. For this purpose, ALEX is used to assess the invasive dynamics of *S. muticum* in Normandy and ascertain whether or not it favours the establishment of other NIS in this new habitat.

2. Materials and methods

2.1. Sites and sampling design

The distribution of the macrofauna associated with the invasive algae, *Sargassum muticum* (Yendo) Fensholt, 1955 (Fig. 1) was studied between the 4th and 16th of April 2019 in five sites around the Cotentin Peninsula, where dense populations of this NIS are found along the Normandy coast (Baffreau et al. 2018; Pezy et al., submitted). In addition, the distribution of crustaceans associated with *S. muticum* was also studied between the 5th and 28th of April 2018 in the same five sites around the Cotentin Peninsula. Two sampling sites, Blainville-sur-mer (BSM) and Dielette (DIE), are located on the west coast of the Cotentin peninsula, while two others, at Goury (GOU) and Gatteville-Phare (GAT), are on the north Cotentin coast, and the fifth site at La Hougue (HOU) is on the east coast of the Cotentin (Fig. 1). Two of the sites (BSM and HOU) are located in areas with extensive cultivation of the introduced oyster species *Crassostrea gigas* (Thunberg, 1793). The GOU and GAT samples were collected in rocky tidal pools, while, at the three other sites, the samples were taken in larger shallow pools on sandy gravel (Fig. 1); all the sites are located in the mediolittoral zone.

The fauna was sampled using a suprabenthic sledge equipped with a

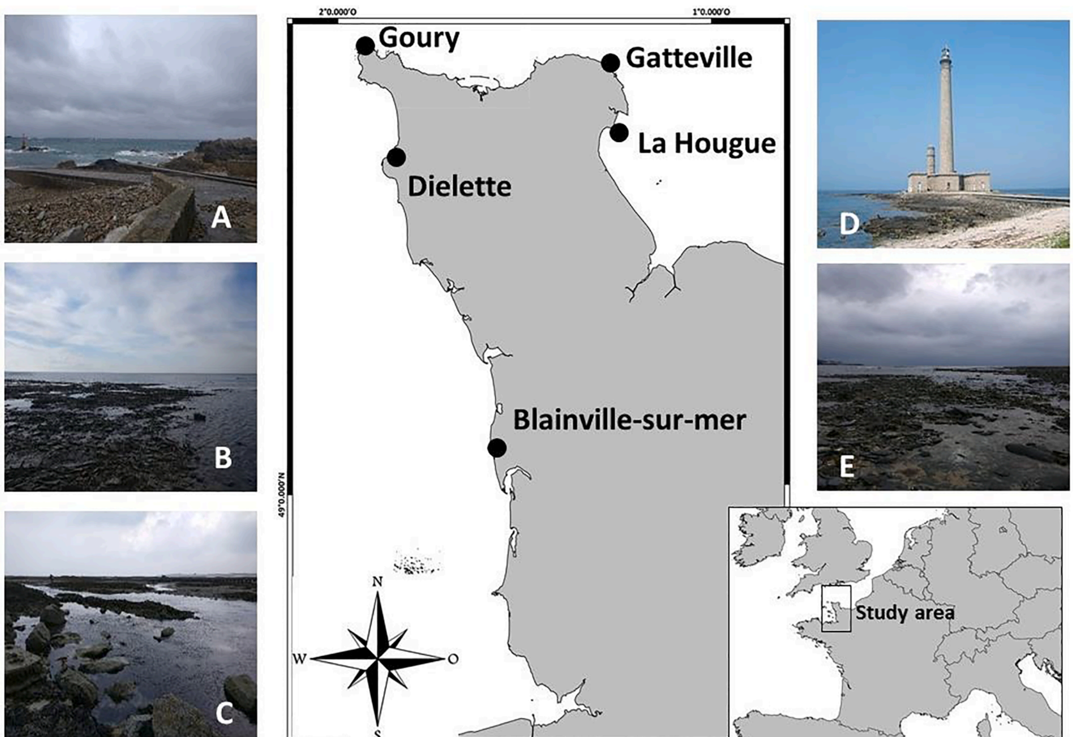

Fig. 1. Map of *Sargassum muticum* sampling sites in Normandy, English Channel (A: Blainville-sur-mer; B: Dielette; C: Goury; D: Gatteville; E: La Hougue).

single box (0.6 × 0.3 m; 0.18 m^2) to filter the water at a height of 0.10–0.40 m above the sea bed. Sampling was carried out in pools at low tide where dense *S. muticum* populations were present. The sampling box was equipped with a WP2 zooplankton net (0.5 mm mesh size). The sledge was operated using three transects of 5 m length, each corresponding to a sampling surface of 3 m^2 and thus a total surface-area of 9 m^2 per site. The organisms collected in the zooplankton net were preserved in 10% formaldehyde solution, and sent to the laboratory for identification. Specimens of the motile macrofauna were sorted, identified, and counted under a dissecting microscope and then stored in alcohol.

2.2. Statistical analyses

Taxon Richness (TR) corresponds to the number of taxa found in the sample of 3 m^2. Data collected in 2019, were used to calculate the abundance A (number of individuals per m^2) and the most commonly used biodiversity indices, i.e. species richness, Shannon-Wiener diversity index (*H'*) in $\log_2$ and Pielou's evenness (*J'*), for each of the five sites. Ecological Status (ES) 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. For *J'*, thresholds are set as follows: <0.2: bad; 0.2–0.4: poor; 0.4–0.6: moderate; 0.6–0.8: good and >0.8: high (Dauvin et al., 2017). Data analysis was performed using the PRIMER® version 6 software package (Plymouth Routines in Multivariate Ecological Research) (Clarke & Gorley, 2006). The biotic index AMBI was also calculated to assess the ecological status of the benthic macrofauna (Borja et al., 2000, 2009; Dauvin, 2018). For AMBI, thresholds are set at <1.2: high; 1.2–3.3: good; 3.3–4.3: moderate; 4.3–6: poor; >5.5: bad.

ALien Biotic IndEX (ALEX) was used to detect the impact of alien species (non-indigenous species) on benthic communities (Çinar and Bakir 2014). This index is based on abundance percentages of different groups defined on the basis of species establishment and invasiveness within each sample (Group I: native species, Group II: casual alien species (NIS), Group III: established alien species (NIS), Group IV: invasive alien species (NIS)). Species were assigned to ALEX groups according to observations of their abundance in the area and the relevant literature (Baffreau et al., 2018). ALEX may vary between 0 and 5, with 0 meaning the complete absence of NIS, and 5 corresponding to an assemblage composed solely of NIS. Therefore, the ecological status of a benthic assemblage can be ranked in one of the following five categories of quality: "high" (0–1), "good" (1–2), "moderate" (2–3), "poor" (3–4) and "bad" (4–5) (Çinar and Bakir, 2014). ALEX was calculated using the formula proposed by Çinar and Bakir (2014):

$$\text{ALien Biotic IndEX (ALEX)} = [(0\times\%GI) + (3\times(\%GII+\%GIII)) + (5\times\%GIV)]/100$$

Finally, the crustaceans taxa collected in 2018 and 2019 at the five sites were classified into four trophic groups: filter feeder, grazers, surface deposit feeders and scavengers (Fersi et al., 2018).

A two-way ANOVA was used to explore spatial structure in terms of Taxon Richness, Abundance, *H'*, *J'*, AMBI and ALEX indices, between sites for 2019. A Shapiro-Wilk normality test and a Bartlett test for homogeneity of variances were performed prior to each ANOVA. The Tukey Honestly Significant Difference test was applied when ANOVA showed significant differences.

Data analysis was performed using non-metric multidimensional scaling ordination (MDS), and a Hierarchical Ascendant Classification (HAC) was created by group average linking using the Bray-Curtis similarity measure (Beals, 1984). In comparison with other similarity measures, the Bray-Curtis is known to be one of the more efficient indexes to highlight similarity between samples (Bloom, 1981).

Sorensen's coefficient for Presence/Absence of taxa, and $\text{Log}_{10}(x + 1)$-transformed abundances (ind. 9 m^2) were used to down-weight the effect of very abundant species.

To identify the species within different groups, the typifying species largely account for the observed assemblage differences, SIMPER (SIMilarity PERcentage) routines were performed using a decomposition of Bray-Curtis similarity on log-transformed abundance data (Clarke and Warwick, 1994). One-way ANOSIM (Analysis Of SIMilarities) permutation test was used to assess if the assemblage differences between sites are statistically significant.

MDS, HAC, SIMPER and ANOSIM were investigated using a multivariate analysis approach with the PRIMER 7 software.

3. Results

3.1. General pattern of 2019 species abundance

Seventy-six taxa and a total of 4,480 individuals were recorded during the 2019 spring survey for a total sampling area of 45 m^2. Among these taxa, the macrofauna associated with *Sargassum muticum* is dominated by the Arthropoda (55 species and 78.3% of abundance), Mollusca (14 species and 15.7%), Chordata (five species and 5.5%) and Echinodermata (two species and 0.5%). The major Phylum, Arthropoda, is mainly composed of crustaceans: Amphipoda (38 species), Decapoda (eight species), Pycnogonida (four species), Isopoda (three species), Cumacea (one species) and Tanaidacea (one species). Amphipods with 2,025 ind. (45.2%) form the dominant group, and then the isopods with 1,735 ind. (38.7%), the gastropods 497 ind. (11.1%), the decapods 129 ind. (2.9%), while the other groups account for only 94 ind. (2.0%).

The dominant species comprise the isopod *Dynamene bidentata* (Adams, 1800) with 1,695 individuals collected from the five stations, then the amphipod *Gammarus locusta* (Linnaeus, 1758), with 697 ind., while the third most abundant species is the gastropod *Rissoa guerinii* Récluz, 1843 (Table 1). Only five other species were recorded, with a total number of individuals >100 and 19 species showing only one individual each.

Out of the 76 taxa, only three were present at the five sites: *Barleeia unifasciata* (Montagu, 1803), *Dynamene bidentata*, and *Rissoa guerinii*. Then, four species were sampled at four sites: *Dexamine spinosa* (Montagu, 1813), *Ischyrocerus anguipes* Kröyer, 1838, *Littorina obtusata* (Linnaeus, 1758), *Palaemon elegans* Rathke, 1837, and 41 (54%) were present at only one site

Among the 76 taxa, five non-indigenous species was recorded during the spring sampling period. Four species of amphipods *Aoroides longimerus* Ren & Zheng, 1996 (HOU), *Aoroides semicurvatus* Ariyama, 2004 (HOU); *Monocorophium acherusicum* (Costa, 1853) (HOU); *Monocorophium sextonae* (Crawford, 1937) (DIE, GAT and HOU) and one species of decapod, *Hemigrapsus sanguineus* (De Haan, 1835) (GOU). Four species were recorded at HOU, while only one non-indigenous species was observed at DIE, GOU and GAT. No NIS was found at BSM.

Table 1
Structural indices for the five stations colonized by *Sargassum muticum*. TR (Taxon~~omic~~ Richness), total number of taxa recorded in 3 m2; Mean abundance per 1 m2; mean H': Shannon-Weaver diversity; J: Pielou's evenness; AMBI; ALEX. The colour coding corresponds to the Ecological Status of the Water Framework Directive: blue, high status; green, good status, yellow, moderate status; orange, low status.

	TR	Abundance	*H'*	*J'*	AMBI	ALEX
Blainville-sur-mer	16	38.78 ± 13.82	2.07 ± 0.24	0.59 ± 0.10	1.05 ± 0.14	0
Dielette	34	28.67 ± 9.39	3.19 ± 0.25	0.75 ± 0.005	1.03 ± 0.36	0.01 ± 0.03
Goury	18	87.89 ± 27.92	2.83 ± 0.15	0.63 ± 0.08	1.31 ± 0.02	0.01 ± 0.01
Gatteville	37	127.33 ± 88.87	1.07 ± 0.13	0.30 ± 0.03	0.98 ± 0.08	0.09 ± 0.08
La Hougue	38	215.22 ± 32.60	3.32 ± 0.13	0.70 ± 0.02	0.78 ± 0.03	0.23 ± 0.07

3.2. Composition of the 2019 fauna

The TR over 3 m^2 varies from a minimum of 16 taxa at BSM to a maximum of 38 taxa at HOU (Table 1). Moreover, TR reaches a minimum at BSM and GOU and a maximum at GAT and HOU (Fig. 2), showing a significant difference (Table 2).

The mean abundance per m^2 varies from a minimum of 28.7 at Dielette to 215.2 at La Hougue (Table 1). The mean abundance shows a gradual increase from the south-west to the north-east (Fig. 3). A significant spatial pattern is observed with minimal values along the West Cotentin coast (BSM, DIE and GOU), an intermediate value at GAT in the North Cotentin (Gatteville) and a maximum value at HOU on the East Cotentin coast (Table 2). Moreover, the numbers of collected individuals are low at both sites of the West Cotentin, moderate in the North and high at the HOU site with 1959 (accounting for 43.32% of the total of sampled individuals) (Table 1).

The Shannon-Wiener diversity index *H'* shows relatively high values (diversified to very diversified), except for GAT (<2) which corresponds to a poorly diversified Ecological Quality Status (EcoQS) (Table 1). GAT and BSM yield the lowest H' diversity (Tables 1 and 2). Pielou's evenness *J'* is minimal at GAT (Table 1), corresponding to a low EcoQS. BSM corresponds to a moderate EcoQS, whereas the other sites show a good EcoQS (Table 1). GAT yields significantly lower values than those measured at the four other sites (Table2).

AMBI shows a high EcoQS at all sites except GOU (good) (Table 1), without significant differences (Table 2).

Using ALEX, all the sites can be classified with high EcoQS, i.e. unaffected by NIS (Table 1), with a significantly higher value at HOU than at the other sites (Table 2).

3.3. Spatial pattern of the 2019 fauna

At a similarity value of 44% for diversity (presence-absence transformation), we can observe a spatial pattern in the species assemblage composition (Fig. 4A). The cluster dendrogram allows to separate the sites into two isolated groups: BSM on the West Cotentin coast with HOU on the East Cotentin coast, and a group made up of the three other sites (Fig. 4A). A dissimilarity exists between the three groups, the Bray-Curtis dissimilarity index = 74.07 between groups A and B, the Bray-Curtis dissimilarity index = 63.29 between groups A and C and the Bray-Curtis dissimilarity index = 61.85 between groups C and B. ANOSIM test reveals that the three groups are significantly different (ANOSIM test, $R = 0.62$; $p < 0.1$).

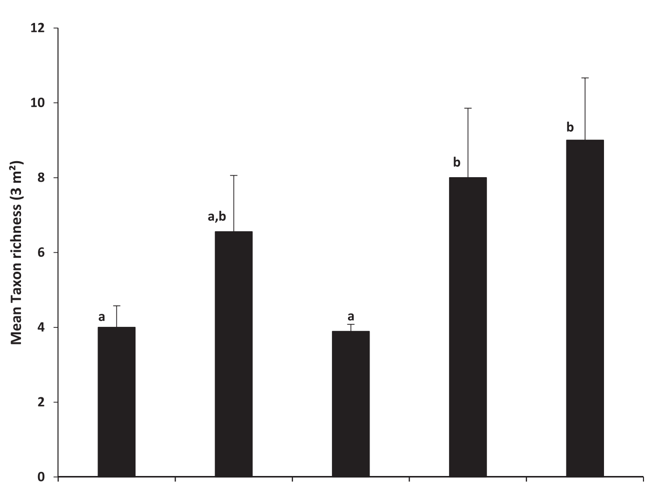

Fig. 2. Mean Taxon richness (number of species on 3 m^2) at the five stations (superscripts: Tukey Honestly Significant Difference test; different letters in the same column indicate significant statistical difference between sites, with upper whiskers indicating maximum standard deviation from mean).

Table 2
One-way ANOVA for five sites on the taxon richness, abundance, *H'*, *J'*, AMBI and ALEX, with results of Tukey tests. dF: degree of freedom; F: variance ratio statistic; p: probability value.

	Factors	dF	F	*p*	Tukey test
TR	Site	4	9.04	< 0.01	Goury; Blainville-sur-mer ≠ Gatteville; La Hougue
Abundance	Site	4	8.61	< 0.01	La Hougue ≠ Dielette; Blainville-sur-mer; Goury
H'	Site	4	74.99	< 0.001	Gatteville ≠ Blainville-sur-mer; Goury; Dielette; La Hougue Blainville-sur-mer ≠ Goury; Dielette; La Hougue
J'	Site	4	25.84	< 0.001	Gatteville ≠ Blainville-sur-mer; Goury; Dielette; La Hougue
AMBI	Site	4	3.42	0.1	
ALEX	Site	4	11.99	< 0.001	La Hougue ≠ Dielette; Blainville-sur-mer; Goury; Gatteville
	∑	10			

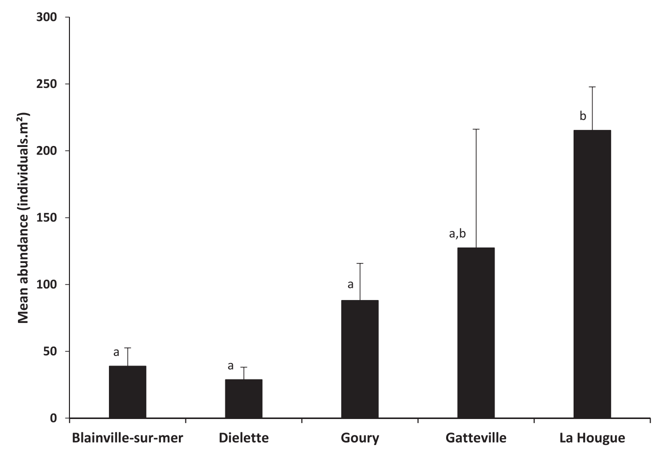

Fig. 3. Mean abundance (individuals per m^2) with upper whisker indicating maximum standard deviation from mean at the five stations (superscript: Tukey test, different letters in the same column indicate significant statistical difference between sites).

At a similarity value of 43% for abundance [Log_{10}(abundance + 1) transformation], the cluster dendrogram allows to separate HOU and DIE from the three other sites which form a single cluster (Fig. 4B). Both analyses show a clear separation of HOU from the other sites, as well as the high similarity between the north Cotentin sites GOU and GAT, and the separation of the other west Cotentin sites BSM and DIE according to the analyses. A dissimilarity exists between the three groups, the Bray-Curtis dissimilarity index = 67.66 between groups A and B, the Bray-Curtis dissimilarity index = 69.02 between groups A and C and the Bray-Curtis dissimilarity index = 61.13 between groups C and B. ANOSIM test reveals that the three groups are significantly different (ANOSIM test, $R = 0.81$; $p < 0.1$).

The TR is highest in the first cluster identified by similarity values on abundance, followed by DIE and HOU, with the mean abundance being highest at HOU and lowest at DIE, while it shows an intermediate value in the third cluster (Table 3). The abundance of NIS is high only at HOU (Table 3).

SIMPER analysis based on the abundance of the fauna leads us to classify 12 species among the six dominant species in each group (Table 3). The isopod *Dynamene bidentata* is the most abundant in two groups, while *Gammarus locusta* is dominant in the third group (Table 3). However, the gastropod *Rissoa guerinii* is the second most abundant species in the three groups (Table 3). The third and following species differ in terms of contribution and abundance in the three groups

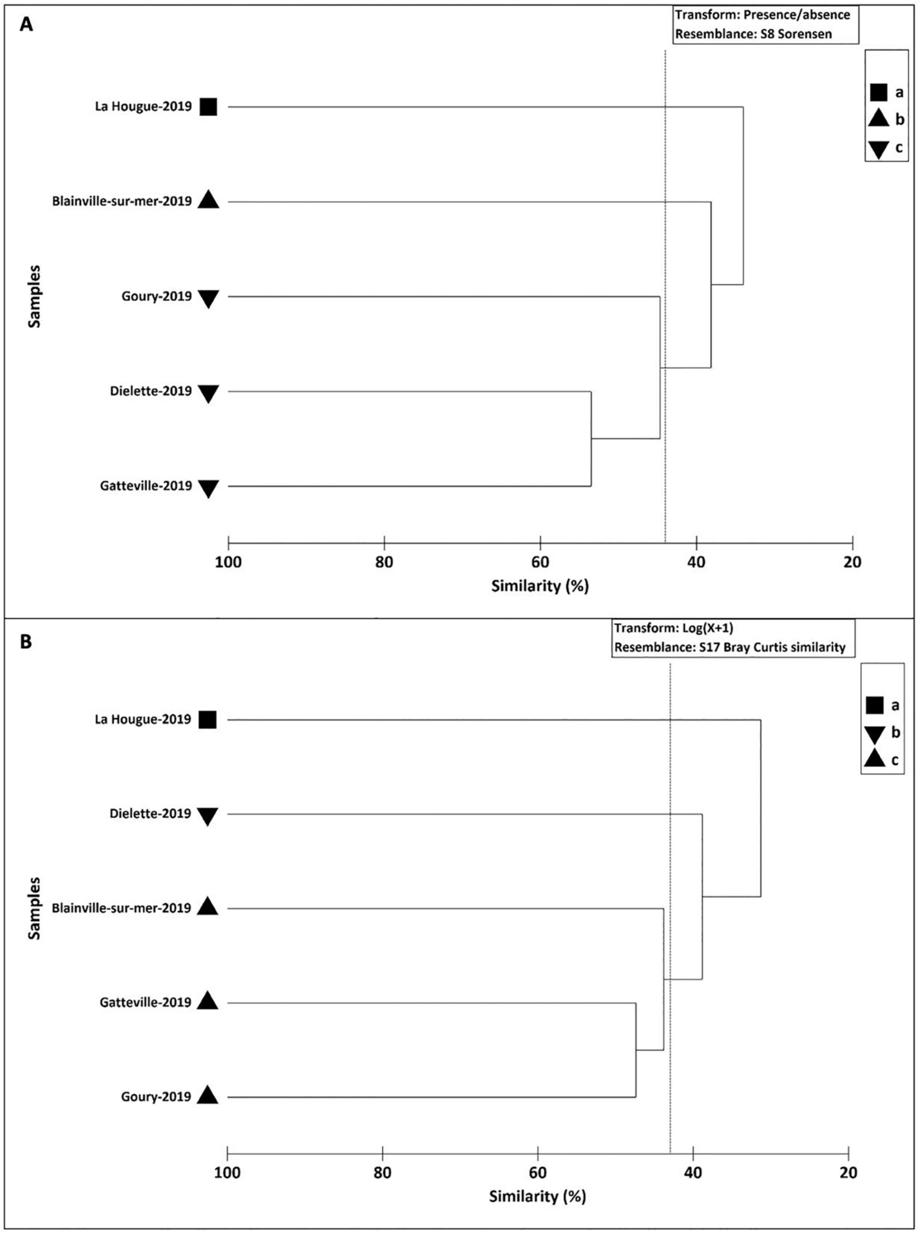

Fig. 4. Cluster dendrogram showing distribution of the five sites according to the Sorensen similarity after Presence-Absence transformation (A) and according to the Bray-Curtis similarity after Log(X + 1) transformation of the abundance.

Table 3
SIMPER analysis for 2019 with cumulative contribution (Cc in %) of the six top species with indication of their abundance (A): number of individuals per 1 m^2. (TR: Taxon Richness; NIS: Non-Indigenous Species).

Blainville-sur-mer; Gatteville; Goury			Dielette			La Hougue		
Species	Cc	A	Species	Cc	A	Species	Cc	A
Dynamene bidentata	35.8	53.7	*Dynamene bidentata*	33.7	9.7	*Gammarus locusta*	29.6	63.7
Rissoa guerinii	50.4	3.1	*Rissoa guerinii*	51.2	5.0	*Rissoa guerinii*	43.6	30.1
Littorina obtusata	58.6	0.8	*Ischyrocerus anguipes*	58.1	2.0	*Aora typica*	53.7	21.8
Idotea granulosa	65.3	0.9	*Idotea granulosa*	62.4	1.2	*Dexamine spinosa*	63.4	20.9
Apherusa cirrus	71.8	4.6	*Elasmopus rapaax*	66.3	1.1	*Caprella acanthifera*	71.8	18.1
Steromphala umbilicalis	77.6	0.6	*Apherusa cirrus*	69.8	1.0	*Dynamene bidentata*	80.0	17.7
TR	45		**TR**	34		**TR**	38	
Mean abundance	84.6		**Mean abundance**	28.7		**Mean abundance**	215.2	
NIS number	2		**NIS number**	1		**NIS number**	4	
NIS mean abundance	0.6		**NIS mean abundance**	0.1		**NIS mean abundance**	8.6	

(Table 3).

3.4. Spatio-temporal pattern of the 2018–2019 crustacean fauna

At a similarity value of 42% for abundance [Log_{10}(abundance + 1) transformation], the cluster dendrogram allows to separate the samples into three groups : A (Gatteville-2018; Gatteville-2019; La Hougue 2018; La Hougue 2019); B (Goury 2019; Blainville 2019; Dielette 2018; Goury 2018) and C (Blainville 2018; Dielette 2019) (Fig. 5).

SIMPER analysis classifies crustacean taxa contribution for each group (Table 4). The isopod *Dynamene bidentata* is the top taxa in two groups (B and C) and second in the group A (Table 4). The other crustacean taxa differ in terms of contributions in the three groups. The group A is mainly composed of amphipods, in particular of Caprellidae (absent in the two others groups). The group B is predominantly at 75% by two isopod taxa (*D. bidentata* and *Idotea* spp.). A mix of amphipod and isopod taxa (Table 4) composes the third group.

A dissimilarity exists between the three groups, the Bray-Curtis dissimilarity index = 62.85 between groups A and B (ANOSIM test, $R = 0.74$; $p < 0.05$), the Bray-Curtis dissimilarity index = 62.25 between groups A and C (ANOSIM test, $R = 0.93$; $p < 0.05$) and the Bray-Curtis dissimilarity index = 60.78 between groups C and B (ANOSIM test, $R = 0.93$; $p < 0.05$).

For the 2018–2019 crustacean community, the predator predominate the trophic groups with 24 taxa, then the deposit feeder (18 taxa), the grazer (12 taxa) and the filter feeder (4 taxa). Grazer are the most important group for 2018–2019, it represent 74.1% of the total abundance, then deposit feeder (17.1%); predator (8.0%) and filter feeder (0.8%). In 2018 at Blainville sur mer, the crustacean abundances were divided into three main trophic groups: grazer (5 taxa), predator (9 taxa) and deposit feeder (4 taxa) (Fig. 6). Whereas in 2019 at Blainville sur mer and in 2018–2019 at the four others sites, grazer was the more abundant trophic group (Fig. 6).

4. Discussion

The distribution and abundance patterns of motile epifauna on the brown seaweed *Sargassum muticum* was studied at low tide in tidal pools on a spatial scale along the Normandy coast from the Normano-Breton Gulf to the Bay of Seine in shallow rocky pools in spring 2018 and 2019.

Table 4
SIMPER analysis for the crustacean fauna of 2018 and 2019 with cumulative contribution (Cc in %) of the three groups.

A		B		C	
Taxa	Cc (%)	Taxa	Cc (%)	Taxa	Cc (%)
Gammarus spp	24.9	*Dynamene bidentata*	61.9	*Dynamene bidentata*	30.5
Dynamene bidentata	42.2	*Idotea* spp.	75.1	*Ischyrocerus anguipes*	51.5
Caprellidae	51.5	*Palaemon elegans*	83.1	*Idotea* spp.	64.6
Monocorophium spp.	60.8	*Gammarus* spp.	88.6	*Apherusa* spp.	75.2
Ischyrocerus anguipes	68.0	*Apohyale prevostii*	92.5	*Hippolyte varians*	82.7
Idotea spp.	74.3			*Apohyale prevostii*	88.2
Palaemon elegans	79.6			*Nymphon gracile*	93.8
Apherusa spp.	83.9				

In agreement with other studies, the motile fauna associated with *S. muticum* is dominated by Arthropoda, especially amphipods and isopods as observed at other Iberian sites (Viejo, 1999; Gestoso et al., 2010, 2012; Engelen et al., 2013). The most abundant species colonizing *S. muticum* is the isopod *Dynamene bidentata,* which is found at all five sampling stations. This result is in line with Viejo (1999) and Gestoso et al. (2012), who found that *D. bidentata* clearly characterizes *Sargassum* tidal pools in northern Spain. This enhanced abundance of amphipods and isopods could be explained by the fact that the Sargassum can acts as a habitat or as refuge from predators for several species. In addition, some grazer's species feed on *Sargassum*. Indeed, *D. bidentata* is known as a grazer that commonly feeds on the macroalgae that it inhabits (Arrontes, 1990; Viejo and Arrontes, 1992). Thus, in the present case, the NIS *S. muticum* acts both as a source of food and represents an additional habitat for several motile species. Nevertheless, Engelen et al. (2011) have shown that mesograzers on the southwest coast of Portugal do not show a specific preference for *S. muticum* and prefer mostly native seaweeds over the invasive brown seaweed. Moreover, the epifauna associated with brown seaweed form essential linkages with higher trophic levels since these taxa are the prey of omnivorous fish and

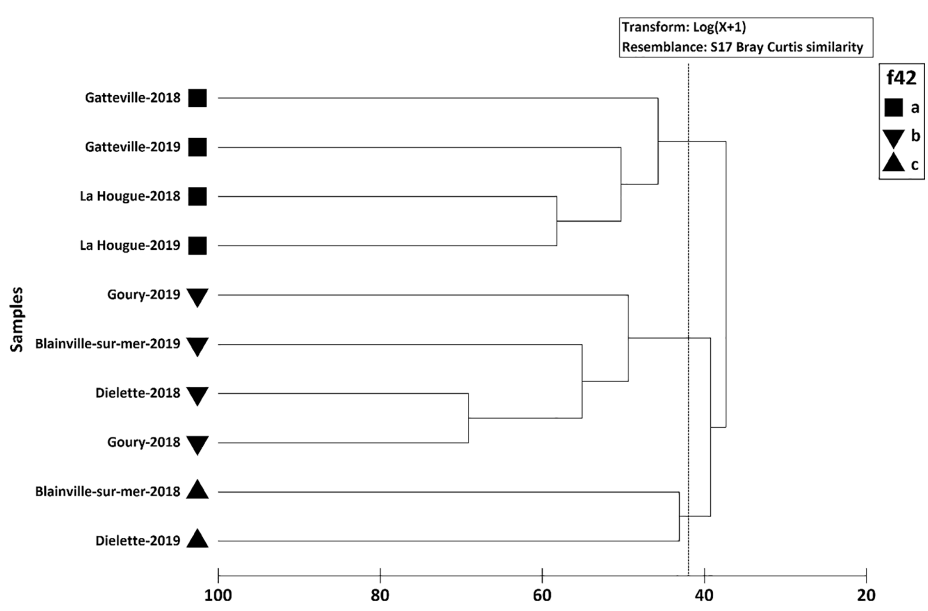

Fig 5. Cluster dendrogram showing distribution of the five sites according to the Bray-Curtis similarity after Log(X + 1) transformation of the crustacean abundance for 2018 and 2019.

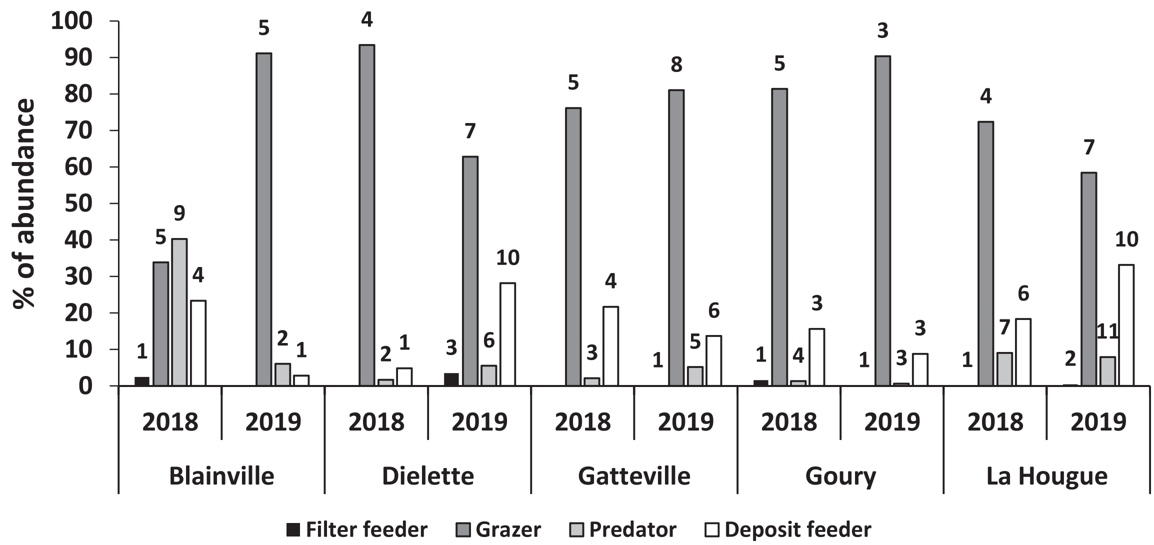

Fig. 6. Distribution of trophic groups according to the mean abundance (% of the number of individuals per 3 m^2) to the crustacean fauna in 2018 and 2019 at the five sites. Superscript above histogram correspond to number taxa in the trophic group.

decapods (Brawley, 1992; Engelen, 2013), which could lead to an increase in secondary production in the local benthic system (Viejo, 1999).

In addition, our study also allowed detecting for the first time in the English Channel, two new Non Indigenous Species: *Aoroides semicurvatus* and *A. longimerus* (Dauvin et al. 2020). These two species originating from Japanese waters suggest that *S. muticum* offers a favourable habitat for NIS. Dauvin et al. (2020) proposed that both these *Aoroides* species were introduced involuntarily from the Atlantic into Normandy due to transfers of the oyster *Crassostrea gigas* (Thunberg, 1793) from French centres of production. La Hougue is an important hot spot in Normandy oyster production, where transfers are permanent between the Bay of Biscay and the English Channel. However, it is surprising that other production centres along the west coast of Cotentin at Blainville-sur-mer have not been not colonized by these amphipod NISs. Supplementary sampling is required to observe these species and confirm oyster transfer as the main transport pathway from Atlantic oyster centres such as Arcachon Bay where these NIS were recorded for the first time in Europe (Gouillieux et al., 2015).

Our results also highlight that the faunal assemblage differs between the five sampling sites (BSM, DIE, GOU, GAT and HOU). In fact, only three species are common to the five sites. This could be explained by the fact that *S. muticum* is associated with a different epifaunal assemblage depending on the tidal exposure of the foreshore zone where it grows (Viejo, 1999). In addition, the differences in epifaunal assemblage could also be linked to variations in salinity or temperature between the intertidal pools (that could imply the size of the pool) (Metaxas and Scheibling, 1993) as well as by the smaller size of *S. muticum* in rocky pools (Schneider and Mann, 1991; Viejo, 1999). However, the La Hougue (HOU) sampling site is stands out from the other sites as it yields the highest taxa richness and the highest number of NIS inhabiting the brown seaweed *S. muticum*. This result could be explained by the fact that La Hougue (HOU) is an important hot spot in Normandy oyster production with permanent transfer between production centres in the Bay of Biscay and the English Channel. In fact, it is known that bivalve aquaculture and transfer activities are important in controlling dispersal and colonization of new zones by NNS species (Brenner et al., 2014). Nevertheless, ALEX shows low values indicating a low percentage of NIS and a High EcoQS for the fauna inhabiting tidal pools colonized by *S. muticum*. But most of the NISs recorded here, including the *Aoroides* spp., were recently introduced into Normandy and are probably in the course of colonizing new habitats including *S. muticum*.

As pointed out by Engelen et al. (2013), previous studies have mainly focused on the effect of *S. muticum* on the ecosystem and specifically its interactions with native algae (Stæhr et al., 2000; Britton-Simmons, 2004; Sanchez et al., 2005; White and Shurin, 2011). In fact, NISs represent a wide range of threats to native ecosystems, and can be responsible for the decline of native species by competition and predation, and thus can lead to a loss of biodiversity (Boudouresque, 2002). In addition, some NISs have the potential to affect communities over a wide geographical range due to broad physiological tolerance.

However, apart from these negative effects, NIS may be integrated harmlessly into ecosystems, and may even contribute to enriching the biodiversity (Goulletquer, 2016). Recent studies have highlighted the potential positive role of NIS in enhancing regional species richness (Sax and Gaines, 2008). In fact, NISs provide both shelter (Wonham et al., 2005; Severns and Warren, 2008) and new sources of food for native species (Carlsson et al., 2009). The effects of the introduction of *S. muticum* on the fauna may be different from site to site, depending on the type of native macroalgae and their abundance. Nevertheless, previous studies have shown little or no difference between *S. muticum* epibiota and that of native macroalgal communities (Viejo, 1999; Engelen et al., 2013), thus suggesting that the effects of *S. muticum* invasion on local fauna abundances and assemblages might be rather limited. However, few studies have investigated the potential influence of *S. muticum* on higher trophic levels. To conclude, our study suggests that *S. muticum* is a suitable habitat for many invertebrates (especially amphipods and isopods) and could represent a potential source of food for several local species which could lead to a potential change in the structure and functioning of the trophic web since invertebrates inhabiting *S. muticum* can be predated by omnivorous decapods and fish (Engelen et al., 2013).

Apart from examining the stomach contents of fish occupying the dense *S. muticum* seaweeds to assess the role of the motile fauna in their regime, it will be interesting in the future to compare the motile fauna living among native seaweeds such as *Laminaria* spp. as well as the sea grass *Zostera marina*. These latter species are known to play an important role as regards the protection of the fauna and the functioning of the trophic web in the littoral zone of the English Channel coasts.

CRediT authorship contribution statement

Aurore Raoux: Investigation, Writing - original draft, Writing - review & editing. **Jean-Philippe Pezy:** Formal analysis, Methodology, Writing - review & editing. **Thomas Sporniak:** Data curation. **Jean-Claude Dauvin:** Writing - original draft, Writing - review & editing, Supervision, Validation, Project administration.

Declaration of Competing Interest

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

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References

Arrontes, J., 1990. Diet, food preference, food preference and digestive efficiency in intertidal isopods inhabiting macroalgae. J. Exp. Mar. Biol. Ecol. 139, 231–249.

Baffreau, A., Pezy, J.P., Rusig, A.M., Mussio, I., Dauvin, J.C., 2018. Les espèces marines et animales et végétales introduites en Normandie. Imprimerie Moderne de Bayeux, France, p. 350.

Beals, E.W., 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Adv. Ecol. 14, 1–55.

Belsher, T., Pommellec, S., 1988. Expansion de l'algue d'origine japonaise Sargassum muticum (Yendo) Fensholt, sur les côtes françaises, de 1983 à 1987. Cah. Biol. Mar. 29, 221–231.

Bloom, S.A., 1981. Similarity Indices in Community Studies: Potential Pitfalls. Mar. Ecol. Prog. Ser. 5, 125–128.

Borja, A., Franco, J., Perez, V., 2000. A marine biotic index to the establish ecology quality of soft-bottom benthos within European estuarine coastal environments. Mar. Poll. Bull. 40, 1100–1114.

Borja, Á., Rodríguez, J.G., Black, K., Bodoy, A., Emblow, C., Fernandes, T.F., Forte, J., Karakassis, I., Muxika, I., Nickell, T.D., Papageorgiou, N., Pranovi, F., Sevastou, K., Tomassetti, P., Angel, D., 2009. Assessing the suitability of a range of benthic indices in the evaluation of environmental impact of fin and shellfish aquaculture located in sites across Europe. Aquaculture 293 (3-4), 231–240.

Boudouresque, C.F., Verlaque, M., 2002. Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. Mar. Pollut. Bull. 44 (1), 32–38.

Brenner, M., Fraser, D., Van Nieuwenhove, K., O'Beirn, F., Buck, B.H., Mazurié, J., Thorarinsdottir, G., Dolmer, P., Sanchez-Mata, A., Strand, O., Flimlin, G., Miossec, L., Kamermans, P., 2014. Bivalve aquaculture transfers in Atlantic Europe. Part B: environmental impacts of transfer activites. Ocean Coast. Manag. 89, 127–138.

Britton-Simmons, K.H., 2004. Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic subtidal communities of Washington State. USA. Mar. Ecol. Prog. Ser. 277, 61–78.

Buschmann, A.H., 1990. Intertidal macroalgae as refuge and food for amphipoda in Central Chile. Aquat. Bot. 36 (3), 237–245.

Buschbaum, Christian, Chapman, Annelise S., Saier, Bettina, 2006. How an introduced seaweed can affect epibiota diversity in different coastal systems. Mar. Biol. 148 (4), 743–754.

Cacabelos, Eva, Olabarria, Celia, Incera, Mónica, Troncoso, Jesús S., 2010. Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. Estuar. Coast. Shelf Sci. 89 (1), 43–52.

Carlsson, Nils OL, Sarnelle, Orlando, Strayer, David L, 2009. Native predators and exotic prey – an acquired taste? Front. Ecol. Environ. 7 (10), 525–532.

Çinar, Melih Ertan, Bakir, Kerem, 2014. ALien Biotic IndEX (ALEX) – A new index for assessing impacts of alien species on benthic communities. Mar. Poll. Bull. 87 (1-2), 171–179.

Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Warwick, R.M., 1994. Changes in Marine Communities: An Approach to Statistical Analyses and Interpretation. Natural Environment Research Council, Plymouth.

Cosson, J., Duglet, A., Billard, C., 1977. Sur la végétation algale de l'étage littoral dans la région de Saint-Vaast-la-Hougue et la présence d'une espèce japonaise nouvelle pour les côtes françaises : *Sargassum muticum* (Yendo) Fensholt (Pheophycea, Fucale). Bull. Soc. Linn. Normandie 105, 109–116.

Dauvin, J.C., Bakalem, A., Baffreau, A., Grimes, S., 2017. Benthic ecological status of Algerian harbours. Mar. Pollut. Bull. 125 (1-2), 378–388.

Dauvin, Jean-Claude, 2018. Twenty years of application of Polychaete/Amphipod ratios to assess diverse human pressures in estuarine and coastal marine environments: a review. Ecol. Indic. 95, 427–435.

Dauvin, J.C., Pezy, J.P., Raoux, A., 2020. First records of *Aoroides longimerus* Ren & Zheng, 1996 and *A. semicurvatus* Ariyama, 2004 (Crustacea, Amphipoda) in the English Channel. BioInv. Rec. 9, 753–762.

Duffy, J. Emmett, 1990. Amphipods on seaweeds: partners or pests? Oecologia 83 (2), 267–276.

Engelen, Aschwin H., Henriques, Nuno, Monteiro, Carla, Santos, Rui, 2011. Mesograzers prefer mostly native seaweeds over the invasive brown seaweed *Sargassum muticum*. Hydrobiologia 669 (1), 157–165.

Engelen, A.H., Primo, A.L., Cruz, T., Santos, R., 2013. Faunal differences between the invasive brown macroalga *Sargassum muticum* and competing native macroalgae. Biol. Inv. 15, 171–183.

Engelen, A.H., Serebryakova, A., Ang, P., Britton-Simmons, K., Mineur, F., Pedersen, M. F., Arenas, F., Fernández, C., Steen, H., Svenson, R., Pavia, H., Toth, G., Viard, F., Santos, R., 2015. Circumglobal invasion by the brown Seaweed *Sargassum muticum*. Oceanogr. Mar. Biol: an Ann. Rev. 53, 81–126.

Farnham, W.F., Fletcher, R.L., Irvine, L.M., 1973. Attached *Sargassum muticum* found in Britain. Nature 243, 231–232.

Fersi, A., Dauvin, J.C., Pezy, J.P., Lassad, N., 2018. Amphipods from tidal channels of the Gulf of Gabès (central Mediterranean Sea). Mediterranean Marine Science 19, 430–453.

Gestoso, Ignacio, Olabarria, Celia, Troncoso, Jesús S., 2010. Variability of epifaunal assemblages associated with native and invasive macroalgae. Mar. Fresh. Res. 61 (6), 724. https://doi.org/10.1071/MF09251.

Gestoso, Ignacio, Olabarria, Celia, Troncoso, Jesús S., 2012. Effects of macroalgal identity on epifaunal assemblages: native species versus the invasive species *Sargassum muticum*. Helgol. Mar. Res. 66 (2), 159–166.

Givernaud, T., Cosson, J., Givernaud-Mouradi, A., 1991. Etude des populations de Sargassum muticum (Yendo) Fensholt sur les côtes de Basse-Normandie (France), in: Elliott, M. et al. (Ed.) Estuaries and Coasts: Spatial and Temporal Intercomparisons. ECSA 19 Symposium, University of Caen, France. pp. 129-132 in: Elliott, M., Ducrotoy, J.P. (Ed.) 1991. Estuaries and coasts: Spatial and temporal intercomparisons. ECSA 19 Symposium, University of Caen, France. International Symposium Series, 3. Olsen & Olsen: Fredensborg. ISBN 87-85215-17-1. VII, 390 pp.

Goulletquer, P., 2016. Guide des organismes exotiques marins. Editions Belin, France.

Gouillieux, B., Lavesque, N., Leclerc, J.C., Le Garrec, V., Viard, F., Bachelet, G., 2015. Three non-indigenous species of *Aoroides* (Crustacea: Amphipoda: Aoroidae) from the French Atlantic coast. J. Mar. Biol. Assoc. U. K. 96, 1651–1659.

Guerra-García, J.M., Rios, M., Gordillo, I., Cabezas, M.P., Baeza-Rojano, E., Izquierdo, D., Corzo, J., Domínguez, J., Varona, S., 2010. Distribution patterns of intertidal and shallow water caprellids associated with macroalgae along the Iberian Peninsula. Zool. Baetica 21, 101–129.

Guerra-García, J.M., Tierno de Figueroa, J.M., Navarro-Barranco, C., Ros, M., Sánchez-Moyano, J.E., Moreira, J., 2014. Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. J. Sea Res. 85, 508–517.

Jacobucci, Giuliano Buza, Leite, Fosca Pedini Pereira, 2014. The role of epiphytic algae and different species of *Sargassum* in the distribution and feeding of herbivorous amphipods. Lat. Am. J. Aquat. Res. 42 (2), 353–363.

Jacobucci, G.B., Moretti, D., Silva, E.M., Leite, F.P.P., 2002. Caprellid amphipods on *Sargassum cymosum* (Phaeophyta): depth distribution and population biology. Nauplius 10, 27–36.

Jacobucci, Giuliano Buzá, Tanaka, Marcel Okamoto, Leite, Fosca Pedini Pereira, 2009. Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore. Aquat. Ecol. 43 (4), 1031–1040.

Jacobucci, G.B., Vieira, E.A., Leite, F.P., 2019. Influence of a narrow depth gradient on the spatial structure of *Sargassum* peracarid assemblages in Southeastern Brazil. Mar. Biodivers. 49, 1001–1011.

Leite, FPP., Tanaka, MO., Gebara, RS., 2007. Structural variation in the brown alga *Sargassum cymosum* and its effects on associated amphipod assemblages. Braz. J. Biol. 67 (2), 215–221.

Loraine, I., 1989. L'algue japonaise Sargassum muticum (Yendo) fensholt. Caractéristiques et répartition, Rapport de fin d'études à l'Ecole Nationale Supérieure Agronomique de Rennes, p. 83.

Metaxas, A., Scheibling, R.E., 1993. Community structure and organization of tide pools. Mar. Ecol. Prog. Ser. 98, 187–198.

Machado, Glauco Barreto de Oliveira, Neufeld, Aline Binato, Dena, Simone Aparecida, Siqueira, Silvana Gomes Leite, Leite, Fosca Pedini Pereira, 2015. Variation of amphipod assemblage along the *Sargassum stenophyllum* (Phaeophyta, Fucales) thallus. Nauplius 23 (1), 73–78.

Norton, T.A., Benson, M.R., 1983. Ecological interactions between the brown seaweed *Sargassum muticum* and its associated epifauna. Mar. Biol. 75, 169–177.

Pezy, J.P., Baffreau, A., Raoux, A., Rusig, A.M., Mussio, I., Dauvin, J.C., submitted. Non-Indigenous species in marine and brackish waters along the Normandy coast. BioInv. Rec.

Rossi, Francesca, Olabarria, Celia, Incera, Mónica, Garrido, Josefina, 2010. The trophic significance of the invasive seaweed *Sargassum muticum* in sandy beaches. J. Sea Res. 63 (1), 52–61.

Sanchez, I., Fernandez, C., Arrontes, J., 2005. Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). J. Phycol. 41, 942–949.

Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction: the future of native biodiversity on islands. Proc. Natl. Acad. Sci. USA 105 (Supplement 1), 11490–11497.

Schneider, Friederike I., Mann, Kenneth H., 1991. Species specific relationships of invertebrates to vegetation in a seagrass bed I. Correlational studies. J. Exp. Mar. Biol. Ecol. 145 (1), 101–117.

Severns, P.M., Warren, A.D., 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. Anim. Conserv. 11, 476-483.

Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T., Krause-Jensen, D., 2000. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Mar. Ecol. Prog. Ser. 207, 79–88.

Takeuchi, I., Kuwabara, R., Hirano, R., Yamakawa, H., 1987. Species composition of the Caprellidea (Crustacea: Amphipoda) of the *Sargassum* zone on the Pacific coast of Japan. Bull. Mar. Sci. 41, 253–267.

Tanaka, Marcel O., Leite, Fosca P.P., 2003. Spatial scaling in the distribution of macrofauna associated with *Sargassum stenophyllum* (Mertens) Martius: analyses of faunal groups, gammarid life habits, and assemblage structure. J. Exp. Mar. Biol. Ecol. 293 (1), 1–22.

Tanaka, Marcel O., Leite, Fosca P.P., 2004. Distance effects on short-term recolonization of *Sargassum stenophyllum* by mobile epifauna, with an analysis of gammarid life habits. J. Mar. Biol. Assoc. U. K. 84 (5), 901–910.

Viejo, Rosa M., 1997. The effects of colonization by *Sargassum muticum* on tidepool macroalgal assemblages. J. Mar. Biol. Assoc. U. K. 77 (2), 325–340.

Viejo, Rosa M, 1999. Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. Aquat. Bot. 64 (2), 131–149.

Viejo, R.M., Arrontes, J., 1992. Interactions between mesograzers inhabiting *Fucus vesiculosus* in northern Spain. J. Exp. Mar. Biol. Ecol. 162, 97–111.

Vincent, C., Heinrich, H., Edwards, A., Nygaard, K., Haythornthwaite, J., 2002. Guidance on typology, classification and reference conditions for transitional and coastal waters. Commission Européenne, CIS WG 2.4 (COAST), 119p.

Wakabara, Y., Tararam, A.S., Takeda, A.M., 1983. Comparative study of the amphipod fauna living on *Sargassum* of two Itanhaém shores. Brazil. J. Crustacean Biol. 3, 602–607.

White, Laura F., Shurin, Jonathan B., 2011. Density dependent effects of an exotic marine macroalga on native community diversity. J. Exp. Mar. Biol. Ecol. 405 (1-2), 111–119.

Wonham, M.J., O'Connor, M., Harley, C.D.G., 2005. Positive effects of a dominant invader on introduced and native mudflat species. Mar. Ecol. Prog. Ser. 289, 109–116.