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Similar epiphytic macrofauna inhabiting the introduced *Sargassum muticum* and native fucoids on the Atlantic coast of Morocco

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Abstract – The diversity and structure of epiphytic macrofaunal assemblages on the introduced invasive brown macroalga *Sargassum muticum* and native fucoids (*Bifurcaria bifurcata*, *Cystoseira humilis*, *Cystoseira tamariscifolia* and *Sargassum vulgare*) were compared over a 1-year period in intertidal rockpools on the Atlantic coast of Morocco. In comparison with the epiphytic fauna associated to other macroalgae from European shores, we found that the associated epiphytic macrofauna was moderately diverse (H'<3 bit) and was mainly dominated by gastropods and crustaceans. The most abundant taxa were the isopod *Dynamene bidentata* and the gastropods *Steromphala umbilicalis* and *Steromphala pennanti*. The epiphytic macrofauna community structure differed slightly between the invader and the natives along the year. There was significant temporal variation in the total number of individuals of epiphytic macrofauna per thallus dry weight for the associated epifauna with the highest abundance found on *C. tamariscifolia* in the spring. The composition of the epiphytic macrofauna on each macroalga species was fairly constant over time. Overall, our results demonstrated that the mobile epiphytic macrofauna on this rocky area showed low macroalgal specificity. They also revealed that the invader *S. muticum* supports similar epiphytic macrofaunal communities as the native brown macroalgae and provides an additional appropriate habitat for a generalist associated epiphytic macrofauna.

***Sargassum muticum* / native fucoids / macroalgal epifauna / intertidal community structure / invasive species / rockpools / Morocco**

INTRODUCTION

Macroalgae are important coastal primary producers worldwide, acting as biogenic habitats or habitat-forming organisms and supporting a high density and diversity of associated epibiota such as epiphytic fauna and flora (e.g. Buschbaum *et al.,* 2006; Schmidt & Scheibling, 2006; Christie *et al.,* 2009; Cacabelos *et al.,* 2010; Soler-Hurtado & Guerra-García, 2011; Bedini *et al.,* 2014). Marine macroalgae play a fundamental role in coastal ecosystems by functioning as ecological engineering species (Christie *et al.,* 2009), and also by providing protection and

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shelter from predators (reduce predation risk), and good feeding grounds for many organisms especially juvenile specimens. Furthermore, they increase the space for settlement (Bologna & Heck, 2000; Wikström & Kautsky, 2004; Cacabelos *et al.,* 2010), attenuate current velocity and protect organisms from wave action, heat and desiccation (Moore, 1978; Hicks, 1980). These organisms (mesograzers) are important in transferring primary production to higher trophic levels (Taylor, 1998a). Changes in macroalgae-associated epiphytic macrofauna communities are related to several biological factors including habitat morphological complexity (Russo, 1990; Gee & Warwick, 1993; Guerra-García, 2001; Chemello & Milazzo, 2002; Schreider *et al.,* 2003; Buschbaum *et al.,* 2006; Veiga *et al.,* 2014), life cycles (Gee & Warwick, 1994; Sánchez-Moyano *et al.,* 2001), chemical defenses (e.g. Sieburth & Conover, 1965; Withers *et al.,* 1975; Gorham & Lewey, 1984; Steinberg *et al.,* 1998; Stiger *et al.,* 2004; Wright *et al.*, 2004; Plouguerné *et al.,* 2006; Cacabelos *et al.,* 2010), and also to some physical stressful factors related to the hydrodynamics such as wave exposure and tidal height (Beckley & McLachlan, 1979; Guerra-García, 2001; Schreider *et al.,* 2003).

Marine coastal ecosystems are susceptible to biological introductions due to their open nature and the large dispersive potential/ability to drift of many marine species (Stæhr *et al.*, 2000; Salvaterra *et al.,* 2013). Many introduced macroalgae are able to monopolize space and to quickly spread, thanks to their capability for vegetative growth and their efficient dispersal mechanisms (Valentine *et al.*, 2007). Thus, they are responsible for severe worldwide biological invasions, with important effects and serious ecological impacts on native species, communities and ecosystems (e.g. Piazzi *et al.,* 2001; Grosholz, 2002; Buschbaum *et al.,* 2006; Schaffelke & Hewitt, 2007; McKinnon *et al.,* 2009; Byers *et al.,* 2010; Pacciardi *et al.,* 2011; Gestoso *et al.,* 2012; Mineur *et al.,* 2015; Thomsen *et al.*, 2015). Invading macroalgae, indeed, are becoming one of the most important threats leading to the decline of the marine biodiversity (Stachowicz *et al.,* 2002; Schaffelke *et al.*, 2006; Schaffelke & Hewitt, 2007). These invasions affect resident assemblages by changing population dynamics and assemblage structure, altering ecosystem processes, disrupting trophic dynamics, disturbing and degrading habitats, or directly competing or parasitizing upon native species (Ruiz *et al.,* 1999; Gestoso *et al.,* 2010, 2012). The impacts of invasive species depend not only on intrinsic biological traits of the invader but also on the extrinsic characteristics of the recipient communities (Cacabelos *et al.,* 2010).

The Japanese macroalga *Sargassum muticum* (Yendo) Fensholt is considered to be one of the most aggressive marine invaders (Norton, 1976; Boudouresque & Verlaque, 2002). Currently, this brown alga has a distribution almost covering the entire northern hemisphere and is predicted to increase habitat heterogeneity and substratum availability, providing suitable living conditions for many associated organisms (Buschbaum *et al.,* 2006; Harries *et al.*, 2007). To evaluate the potential effects of this invasive species incurred to native biota, previous studies on European coasts have focused on the epiphytic macrofauna inhabiting this invasive macroalga and native macroalgae (e.g. Viejo, 1999; Wernberg *et al.*, 2004; Buschbaum *et al.,* 2006; Monteiro *et al.,* 2009; Gestoso *et al.,* 2010, 2012; Engelen *et al.,* 2013; Salvaterra *et al.,* 2013; Veiga *et al.,* 2014). Recently this introduced species was reported in the northwestern Atlantic coast of Morocco (Sabour *et al.,* 2013). Unfortunately, no information regarding the interaction between this invader and the local biota is available for these recently colonised coasts. Moreover, in Morocco, studies concerning the epiphytic macrofauna associated with macroalgae – especially the invasives – have never been undertaken. Consequently, there is a complete and general lack of data from this geographical zone. The present work tried to fill this gap by providing a first investigation in the composition and abundance of macroalgae-associated epiphytic macrofauna from the El Jadida coastline, Morocco. It represents a comparative analysis to assess the potential impact of *S. muticum* by investigating possible differences in the epiphytic macrofauna composition and abundance between this invader and native brown macroalgae.

The main objectives of this paper were 1) to characterise and compare the epiphytic macrofauna inhabiting the invasive macroalga *Sargassum muticum* and four autochthonous fucoid species (*Bifurcaria bifurcata, Cystoseira humilis, Cystoseira tamariscifolia* and *Sargassum vulgare*) and 2) to describe temporal variation over a year in the abundance of epiphytic macrofaunal assemblages in these five fucoid species representing the most common algal canopy on the El Jadida coastline.

MATERIAL AND METHODS

Study site, sampling and laboratory analyses

Fieldwork was carried out along the the El Jadida shoreline (33°14'47.5"N 8°32'31.9"W) located on the Atlantic coast of Morocco (Fig. 1) on an intertidal shallow rocky platform. The sampling site (called "Saada") is an open wave-exposed coastal area consisting of an intertidal platform of rocky substratum (bedrocks) with tidal pools of 1–4 m deep (Belattmania *et al.,* 2017), which consist of a diverse macroalgal community (intermixed species) dominated by the invasive brown alga *Sargassum muticum*.

The samples were collected monthly at low tide from January to December 2015. The epiphytic macrofaunal assemblages associated to *Sargassum muticum* and the native Fucales (*Bifurcaria bifurcata, Cystoseira humilis*, *C. tamariscifolia* and *S. vulgare*) (Table 1) were sampled at four sampling points along a horizontal transect in the intertidal zone. In each point and for each macroalgal species, three replicates were haphazardly chosen from rockpools of the same tidal level. Each of these replicates consisted in a set of five individual thalli of that species. However, for *S. vulgare* and *C. tamariscifolia* the number of replicates depends on the macroalgae life cycle and density, as they overwinter just as holdfasts with a very short thallus structure. The design was similar to that in Engelen *et al.* (2013). The collected macroalgal samples were kept in plastic bags filled immediately after collection with 5% buffered formalin-seawater solution and transported to the laboratory for further sorting. In the laboratory, macroalgae were washed in freshwater and shaken several times vigorously to remove the associated epiphytic macrofauna. The water was subsequently sieved through 0.5 mm mesh size to recover released specimens. The entire thalli of macroalgae were also scrutinised to find and individually remove the epibionts still attached to them. Then, all collected organisms were stored in 70% ethanol for identification to the lowest possible taxonomic level and counting. The macroalgae were dried at 60°C for 72 h then weighed to determine macroalgal dry weight (DW).

Environmental variables were measured monthly during the study period to test their correlation with epiphytic macrofaunal patterns: air temperature (Ta), seawater temperature (Tw) and salinity (with a thermosalinometer "WTW LF340"), pH (with a portable pH meter "pHScan WP 1/2"), dissolved oxygen (DO, with a

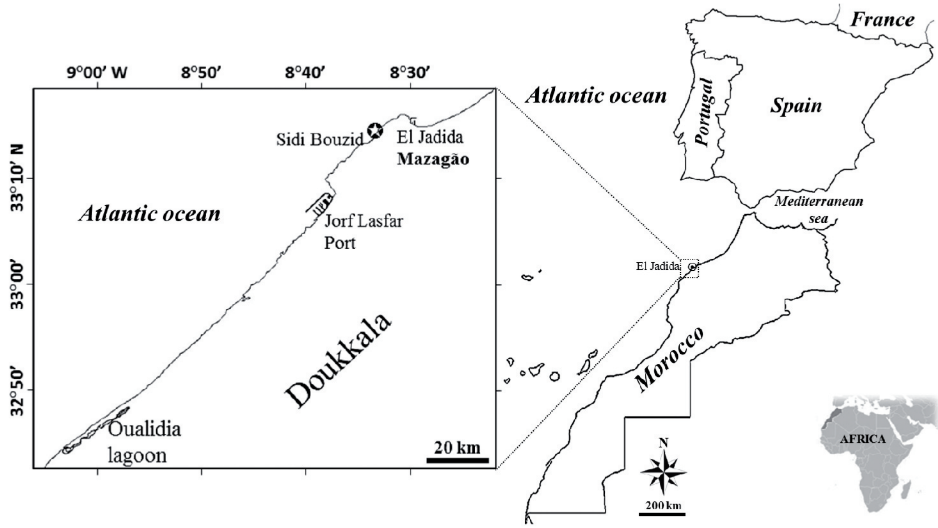


Fig. 1. Geographical location of the sampling site (✪).

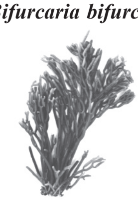
portable dissolved oxygen meter "HANA, HI 9142"), nitrogen (as NO_2^- and NO_3^-), phosphates (as PO_4^{3-}) and suspended matter (SM). Seawater samples were collected using polyethylene bottles, kept in the field in a coolbox at 4°C. In the laboratory, samples were filtered through Whatman® glass microfiber filters (GF/C 47 mm diameter, 1.2 µm pore size) to estimate the SM and to analyse the nutrient content according to Aminot and Chaussepied (1983).

Data analysis

Univariate analyses

The diversity of the epiphytic macrofauna community was characterised using species richness (S), abundance (N), Shannon-Wiener's diversity (H', as $\log_2$) (Shannon & Weaver, 1963) and Pielou's evenness (J') (Pielou, 1966). All biological indices were calculated first per replicate (each replicate corresponding to a set of 5 thalli) and were then rescaled to to 10 g of macroalgae dry weight for each replicate. Two-way ANOVA was applied to test the effects of host macroalgal species and seasons on the epiphytic macrofauna abundance, species richness and diversity considering macroalgal habitats (5 levels) and sampling seasons (4 levels) as fixed factors. One-way ANOVA was used to test for the possible seasonal differences in these indices within each macroalgal habitat separately and also for differences in environmental variables among seasons. When significant effects of the main factors or their interactions were found, the *post hoc* comparison test (Tukey's pairwise comparison test "HSD") was performed. Prior to both ANOVA analyses, data were tested with Kolmogorov-Smirnov's test and Levene's test to meet parametric assumptions of normality and homogeneity of variance, respectively, and data were log or square-root transformed in cases where assumptions for parametric testing

Table 1. Structural characteristics of macroalgal species sampled from the Moroccan Atlantic coast.

Species	*Thalli structural description*		*Wet weight (g)*	*Height (cm)*	*Biovolume (ml)*
Sargassum muticum 	Strongly branched with tiny flat leave-like fronds and round air-bladders.	mean:	58.80	46.37	63.08
		min:	9.00	13.70	10.00
		max:	151.00	125.20	160
Sargassum vulgare 	Bush-like thalli with stem compressed filiform, branch-like leaves lanceolate serrated and spherical air-vesicles	mean:	32.55	25.41	35.50
		min:	12.50	14.10	14.00
		max:	71.80	35.20	73.00
Cystoseira tamariscifolia 	Bushy thalli strongly and irregularly branched	mean:	43.99	24.03	46.00
		min:	16.00	15.10	19.00
		max:	89.00	44.50	75.00
Cystoseira humilis 	Irregularly branched with lower parts bush shaped, flattened into foliar expansions and primary laterals relatively elongated	mean:	36.12	29.24	38.92
		min:	15.60	19.20	18.00
		max:	70.50	48.70	75.00
Bifurcaria bifurcata 	Cylindrical elongated fronds, unbranched near base then forked dichotomously from about halfway up the thallus	mean:	33.34	21.73	35.50
		min:	14.80	15.00	15.00
		max:	50.40	30.90	54.00

could not be met. The Spearman correlation coefficient was used to investigate the relationships between environmental and epiphytic macrofaunal data by pooling their density and species richness for all the macroalgae for each season according to Ba-Akdah *et al.* (2016).

Multivariate analyses

Permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; Anderson *et al.,* 2008) was applied to test for effects of season (fixed factor, 4 levels) and habitat-providing macroalgal species (fixed factor: 5 levels, the invasive species and the natives) on the epiphytic macrofaunal community structure, based on Bray–Curtis similarity matrix calculated on log (x+1) transformed data. Season is used in the sense of time points along the year to assess variability along the studied year. Significant effects ($p \leq 0.05$) were further investigated based on a series of pairwise comparisons. Canonical analysis of principal coordinates (CAP) (Anderson & Willis, 2003) was performed to visualize the multivariate patterns in the fauna assemblages. Similarity percentages (SIMPER) analysis (Clarke, 1993; Clarke & Warwick, 1994) was used to identify the species mostly contributing to similarities in macrofauna communities within macroalgal groups, and those accounting for differences/dissimilarities among the epiphytic macrofauna of macroalgal hosts. The species contribution was restricted to 60% of the average cumulative dissimilarity due to the high number of macrofauna species detected by the SIMPER. In each comparison performed, the most discriminating epiphytic macrofauna species were considered to be the species with the highest contribution (≥10%) to the differences among macroalgal habitats.

RESULTS

Environmental data

The PO_4^{3-} concentration varied from <1 µM in winter to 3.71 µM in summer. The maximum value of nitrogen ($NO_3^- + NO_2^-$) was found during autumn and the lower one at summertime (Table 2). The air and seawater temperatures ranged from 14 to 23°C and from 15°C to 20°C, respectively with maximum values in summer. The highest values of dissolved oxygen were recorded in spring (>10 mM on average) and the lowest ones (<3 mM on average) in autumn. Suspended matter values were generally higher than 10 mg/l but reached 50 mg/l in summer (Table 2). The salinity exceeded 37 PSU during spring and summer and showed lower values in winter (Table 2). Significant seasonal differences were detected only for phosphates, seawater temperature, salinity, and dissolved oxygen (Table 3). Positive significant correlation was obtained between salinity and seawater temperature ($r=0.703$, $p<0.05$). The air temperature was positively correlated with seawater temperature ($r=0.799$, $p<0.01$).

Biological data analysis

A total of 7,853 individuals of epiphytic macrofauna collected corresponding to 57 taxa, were identified in all macroalgae with a maximum of 47 species and a minimum of 23 species found in *S. muticum* and *S. vulgare*, respectively (Table 4). Gastropods and amphipods were the most species-rich groups accounting for 58% of the total number. The isopod *Dynamene bidentata* (Adams, 1800) and the gastropods *Steromphala umbilicalis* (da Costa, 1778) and *Steromphala pennanti*

Table 2. Abiotic variables measured at the sampling site during the study period.

	N (µmol/l)	*PO43- (µmol/l)*	*Ta (°C)*	*Tw (°C)*	*pH*	*DO (mmol/l)*	*SM (mg/l)*	*salinity (PSU)*
Winter	9.53±1.21	0.49±0.02	14.00±1.00	15.50±0.50	7.98±0.02	9.14±1.19	17.60±2.00	33.30±0.13
	10.11±1.49	0.64±0.07	14.50±0.50	16.00±0.90	8.10±0.05	9.50±0.67	18.60±1.00	34.68±0.43
	11.98±0.88	0.49±0.01	15.00±0.70	17.00±0.40	8.13±0.01	13.47±1.30	9.50±1.00	36.07±0.10
Spring	23.78±2.52	0.92±0.02	15.00±0.50	16.50±0.50	8.39±0.02	12.51±1.13	15.00±3.00	38.65±0.09
	24.17±2.09	1.21±0.31	19.00±1.00	18.00±1.00	7.80±0.04	10.17±0.82	11.10±0.50	37.50±0.31
	9.84±0.81	1.50±0.18	20.00±0.50	19.00±0.50	7.95±0.05	11.73±1.18	15.80±3.00	36.63±0.23
Summer	8.52±0.48	1.35±0.03	21.00±0.10	20.00±1.00	7.90±0.02	8.56±0.90	55.10±2.00	38.71±0.12
	7.62±1.27	1.92±0.23	23.25±0.50	19.50±0.50	7.90±0.01	6.22±0.52	30.80±1.00	38.50±0.43
	11.85±1.50	3.71±0.50	20.50±0.50	18.500±1.00	7.90±0.01	3.89±0.68	6.50±0.70	38.84±0.20
Autumn	29.70±2.68	2.42±0.68	19.00±1.00	18.00±0.20	7.90±0.03	2.25±0.20	13.00±2.00	37.55±0.13
	23.61±2.43	2.35±0.88	18.00±0.90	17.00±0.50	8.03±0.01	1.64±0.08	15.00±1.00	37.10±0.22
	9.66±0.62	1.92±0.10	17.00±0.20	16.00±1.00	8.04±0.02	1.79±0.03	18.80±0.50	36.26±0.14

Data are represented as mean values of triplicate samples ± SE, N = nitrite + nitrate, PO_4^{3-} = orthophosphates, Ta = air temperature, Tw = water temperature, DO = dissolved oxygen, SM = suspended matter.

Table 3. One-way ANOVA analysis and post-hoc HSD test for the season effect on the environmental data.

Source of variation	*df*	*MS*	*F*	*P*	*W-Sp*	*W-Su*	*W-A*	*Sp-Su*	*Sp-A*	*Su-A*
N	3	1061624.972	2.375	0.146						
PO43-	3	22052.889	5.302	**0.026**	0.863	**0.038**	**0.049**	0.915	0.719	0.989
Ta	3	153802.083	3.486	0.070						
Tw	3	51857.639	5.562	**0.023**	0.599	**0.019**	0.586	1.000	1.000	1.000
pH	3	171.667	0.645	0.607						
DO	3	590449.444	18.543	**0.001**	0.967	0.348	**0.001**	**0.029**	**0.001**	0.330
SM	3	2.083	1.136	0.391						
Salinity	3	85257.222	9.950	**0.004**	**0.021**	**0.003**	0.139	0.565	0.864	0.235

df = degree of freedom, MS = mean square, W = winter, Sp = spring, Su = summer, A = autumn. The global F-ratios and pairwise p-values are shown. Significant p-values are reported in bold.

(Philippi, 1846) were the most numerically dominant epiphytic macrofaunal taxa and were common to all habitats and seasons (Table 4).

The fauna abundance, species richness and Shannon's diversity and Pielou's evenness significantly differed among macroalgae and seasons (except evenness), but no significant interaction effect (macroalga x season) was detected (2-way ANOVA, Table 5). The natives *S. vulgare* and *C. tamariscifolia* showed the highest mean epiphytic macrofauna abundances (Fig. 2), whereas the invasive depicted values not exceeding 21.3±1.4 ind./10 g DW as maximum during the winter. Only the abundance of the epiphytic macrofauna associated with *C. tamariscifolia* significantly differed among seasons (1-way ANOVA, Table 6). The highest richness was recorded on *S. muticum* and *C. tamariscifolia* over all seasons (Fig. 3). Only the associated epiphytic macrofauna of *S. vulgare* showed significant among-season differences in species richness (Table 6).

The three dominant epiphytic macrofauna species peaked in different seasons and macroalgae. *S. pennanti* showed the highest density on *S. muticum* in spring (20.27 ind./10 g macroalgae DW) and *S. umbilicalis* and *D. bidentata* exclusively showed their maxima on *C. humilis* in summer (62.06 ind./10 g DW) and winter (67.85 ind./10 g DW) respectively.

The diversity H' values in all macroalgae were lower than 3 bit during the four seasons, with the highest values registered in *C. tamariscifolia* and *S. vulgare* (Fig. 4). Significant seasonal variation of H' index was mainly found for *S. muticum* and *B. bifurcata* (Table 6).The evenness J' was exclusively higher in *B. bifurcata* than in the other macroalgal species (Fig. 5). No significant among-season differences were found for J' in all macroalgae, except *S. vulgare*.

Correlation analysis showed no significant relationships between the epiphytic macrofauna pooled density and all environmental data. The density of the most abundant species *S. pennanti* was negatively related to phosphates and air temperature ($r=-0.65$ and $r=-0.58$ respectively, $p<0.05$), and positively related to suspended matter ($r=0.63$, $p>0.05$). The density of *S. umbilicalis* was positively related to the seawater temperature ($r=0.63$, $p<0.05$). No significant correlations were found between the density of *D. bidentata* and environmental measures.

Table 4. Mean mobile epiphytic macrofauna density found on *Sargassum muticum* and native fucoid macroalgae during seasonal samplings (per 10g Dry Weight.

Species	*Sargassum muticum*		*Cytoseira humilis*		*Cytoseira tamariscifolia*		*Sargassum vulgare*		*Bifurcaria bifurcata*	
	D ± SE	*F*	*D ± SE*	*F*	*D ± SE*	*F*	*D ± SE*	*F*	*D ± SE*	*F*
Nemertea	0.02±0.01	50	0.04±0.03	25	0.13±0.13	25			0.01±0.00	25
Polychaeta										
Eupolymnia nesidensis	0.01±0.01	25	0.01±0.01	25					0.01±0.01	50
Eulalia viridis	0.05±0.02	100	0.01±0.01	50			0.14±0.14	25	0.09±0.04	50
Eunice vittata	0.10±0.04	75	0.04±0.02	75	0.03±0.03	25			0.07±0.03	50
Platynereis dumerilii	0.54±0.13	100	0.33±0.13	50	1.60±0.78	50	1.20±0.73	50	0.41±0.07	100
Syllis prolifera			0.01±0.01	25	0.06±0.06	25			0.01±0.01	50
Lepidonotus clava	0.05±0.03	100	0.02±0.01	25	0.11±0.07	25			0.02±0.01	50
Branchiomma sp.	0.01±0.01	50							0.02±0.02	25
Mollusca										
Gastropoda										
Steromphala pennanti	2.21±0.33	100	2.15±0.32	100	1.96±0.62	100	5.34±1.86	75	0.10±0.17	100
Steromphala umbilicalis	3.80±0.43	100	7.72±1.05	100	10.72±2.54	100	10.97±2.46	100	1.65±0.16	100
Chauvetia brunnea	0.16±0.06	75	0.05±0.03	50	1.49±0.51	100	0.22±0.15	25	0.07±0.03	75
Mitrella alvarezi	0.01±0.01	50	0.06±0.05	25						
Rissoa parva	0.39±0.12	100	0.38±.12	75	1.05±0.41	100	1.08±0.73	75	0.09±0.05	50
Omalogyra sp.	0.14±0.13	50								
Nassarius sp.	0.02±0.01	50	0.01±0.01	25					0.01±0.01	25
Littorina tenebrosa	0.08±0.04	50	0.02±0.01	50			0.10±0.10	25	0.01±0.00	25
Littorina neritoides	0.01±0.01	25					0.10±0.10	25		
Tricolia pullus	0.01±0.00	50	0.01±0.01	25	0.16±0.16	25			0.01±0.00	25
Bittium reticulatum	0.15±0.05	25	0.14±0.06	75	2.34±1.89	50	0.67±0.57	25	0.08±0.03	50
Monophorus perversus	0.01±0.01	25								

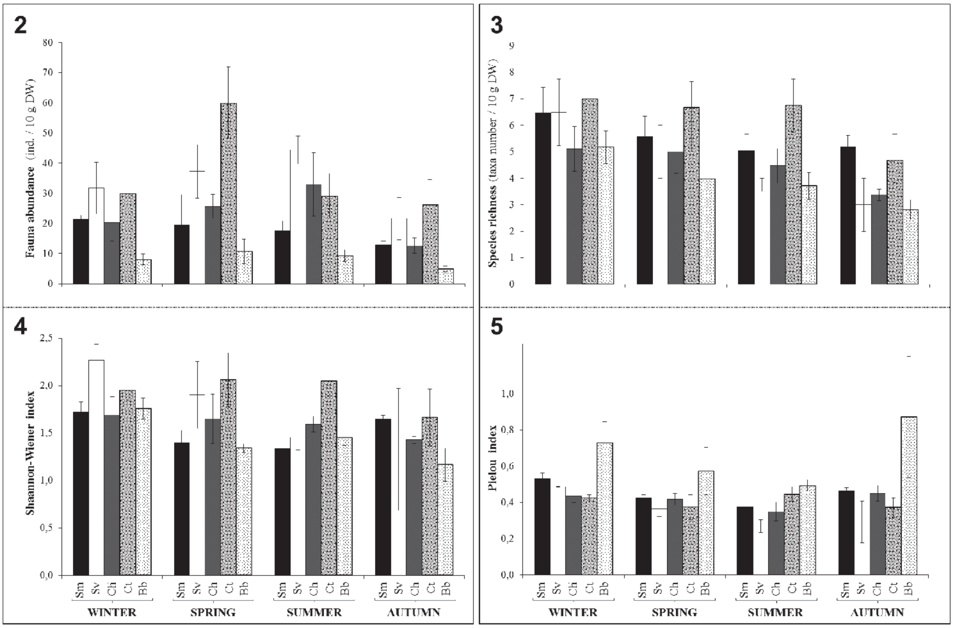
D = mean density as number of individuals per 10 g of macroalga dry weight; SE = standard error; F = frequency of occurrence during sampling seasons (%).

Table 4. Mean mobile epiphytic macrofauna density found on *Sargassum muticum* and native fucoid macroalgae during seasonal samplings (per 10g Dry Weight *(continued)*.

Species	*Sargassum muticum*		*Cytoseira humilis*		*Cytoseira tamariscifolia*		*Sargassum vulgare*		*Bifurcaria bifurcata*	
	D ± SE	*F*	*D ± SE*	*F*	*D ± SE*	*F*	*D ± SE*	*F*	*D ± SE*	*F*
Bittium sp.									0.01±0.00	25
Nodulus contortus			0.03±0.02	25	0.11±0.11	25				
Ocinebrena sp.	0.01±0.01	25	0.00±0.00	25	0.02±0.02	25				
Fusinus sp.	0.02±0.01	25	0.01±0.01	25					0.01±0.00	25
Bivalvia										
Musculus costulatus	0.08±0.03	50	0.10±0.04	75	0.13±0.09	50			0.06±0.02	25
Arthropoda										
Pycnogonida										
Ammotheidae	0.01±0.01	25	0.02±0.02	25	0.01±0.01	25	0.41±0.37	25		
Amphipoda										
Ampithoe sp.	0.15±0.09	50	0.08±0.05	50	1.52±1.51	50	0.20±0.20	25	0.01±0.01	25
Ampelisca lusitanica	0.01±0.00	25							0.02± 0.01	50
Amphitholina cuniculus	0.21±0.09	75	0.39±0.16	75	1.57±0.68	100	0.74±0.51	25	0.19±0.07	100
Apherusa cf. *ovalipes*	0.57±0.15	100	0.34±0.11	100	3.33±1.08	100	1.30±0.57	75	0.06±0.02	75
Aora spinicornis	0.74±0.15	100	0.95±0.21	100	2.40±0.77	100	4.46±1.91	75	0.30±0.11	75
Jassa sp.					0.05±0.05	50				
Ericthonius sp.	0.28±0.19	25	0.20±0.09	25	0.38±0.25	25			0.01±0.01	25
Caprella acanthifera	0.03±0.02	25	0.09±0.05	50	0.19±0.19	25			0.05±0.03	75
Elasmopus vachoni	0.14±0.05	75	0.11±0.05	75	0.37±0.30	50			0.05±0.02	75
Stenothoe sp.					0.01±0.01	25				
Oedicerotidae									0.01±0.00	25
Lysianassidae					0.01±0.01	25			0.01±0.00	25
Calliopiidae	0.33±0.14	75	0.29±0.08	100			0.39±0.39	25	0.03±0.02	25

Ampithoidae	0.44±0.22	50	0.47±0.14	75	0.67±0.49	25	2.22±1.30	50	0.05±0.03	50
Prrierella audouiniana									0.01±0.00	25
Bathyporeia sp.									0.01±0.00	25
Apolochus neapolitanus	0.05±0.04	50			0.01±0.01	25				
Isopoda										
Dynamene bidentata	6.92±1.15	100	6.57±1.00	100	7.32±1.86	100	4.16±1.37	100	4.00±0.60	100
Stenosoma cf. *acuminatum*	0.18±0.05	100	0.39±0.10	75	0.46±0.31	50	1.10±1.10	25	0.05±0.02	50
Stenosoma cf. *capito*	0.12±0.04	75	0.17±0.10	50	0.03±0.03	25			0.03±0.02	50
Limnoriidae			0.01±0.01	25						
Stenosoma cf. *nadejda*	0.04±0.02	50	0.09±0.05	75					0.01±0.00	25
Paranthura nigropunctata	0.02±0.02	25			0.03±0.03	25			0.01±0.00	25
Cleantis sp.	0.01±0.01	25								
Decapoda										
Hyas cf. coarctatus			0.01±0.01	25	0.02±0.02	25	0.37±0.37	25		
Hippolyte varians	0.09±0.04	75	0.09±0.05	75	0.26±0.18	50	0.20±0.20	25	0.01±0.01	25
Tanaidacea										
Chondrochelia savignyi	0.02±0.01	50	0.07±0.04	50			0.37±0.37	25	0.02±0.02	25
Echinodermata										
Astereina gibbosa	0.01±0.01	50	0.02±0.02	25	0.06±0.06	25	0.08±0.08	25	0.01±0.00	25
Amphipholis squamata	0.03±0.01	50	0.04±0.03	25					0.06±0.03	50
Chordata										
Syngnathus acus	0.01±0.00	25								
Opeatogenys cadenati	0.04±0.02	50	0.14±0.08	25			0.10±0.10	25	0.02±0.01	50

D = mean density as number of individuals per 10 g of macroalga dry weight; SE = standard error; F = frequency of occurrence during sampling seasons (%).



Figs 2-5. **2.** Mean fauna abundance, **3.** Species richness, **4.** Fauna diversity, and **5.** Evenness of epiphytic macrofauna communities on *Sargassum muticum* (Sm), *Sargassum vulgare* (Sv), *Cystoseira humilis* (Ch), *Cystoseira tamariscifolia* (Ct), and *Bifurcaria bifurcata* (Bb). Error bars represent standard errors (n=36).

Species richness was negatively correlated with phosphates ($r=-0.93$, $p<0.001$), seawater and air temperatures ($r=-0.66$ and $r=-0.62$ respectively, $p<0.05$) and positively correlated with the dissolved oxygen and salinity ($r=0.65$ and $r=0.66$ respectively, $p<0.05$).

The epiphytic macrofaunal assemblages differed significantly among macroalgae over seasons (PERMANOVA, macroalga x season interaction, $p=0.004$; Table 7). During winter the epiphytic macrofauna composition of *S. muticum* differed from that of the native macroalgae (PERMANOVA, pairwise test; Fig. 6), except *C. humilis* ($p=0.088$) and *S. vulgare* ($p=0.124$). In spring (Fig. 7), the fauna of *S. muticum* mainly differed from that of *C. tamariscifolia* ($p=0.001$) and *B. bifurcata* ($p=0.021$). The latter had a fauna composition different from all native macroalgae with p values ranging from 0.001 to 0.046. During summer, *S. muticum* showed fauna composition differing from that of all native macroalgae (PERMANOVA, pairwise test, $0.001<p<0.032$; Fig. 8). In autumn, the fauna composition of *S. muticum* did not differ from that of *S. vulgare* (PERMANOVA. pairwise test, Fig. 9). SIMPER analysis showed moderate average dissimilarities (from 43.7 to 79.0) among the macroalgae over seasons (Table 8). The isopod *D. bidentata* and the gastropods *S. umbilicalis* and *S. pennanti* were the most important contributive species to the dissimilarity of epiphytic macrofaunal assemblages between *S. muticum* and the natives throughout all seasons. These species were more abundant on *S. muticum* than on *B. bifurcata*. The gastropod *Chauvetia brunnea* (Donovan, 1804) was the most important species shaping differences in epiphytic macrofaunal assemblages

Table 5. Two-way ANOVA results for the season and algal species effects on diversity of the associated epiphytic macrofauna community.

	df	*MS*	*F*	*P*
Abundance				
Macroalgae	4	10356137.290	8.886	**0.000**
Season	3	4268712.015	3.663	**0.018**
Macroalgae x season	12	1704634.146	1.463	0.146
Species richness				
Macroalgae	4	97315.690	3.048	**0.013**
Season	3	168068.748	5.264	**0.003**
Macroalgae x season	12	14074.924	0.441	0.970
Diversity H' index				
Macroalgae	4	3196.551	2.346	**0.045**
Season	3	6544.123	4.000	**0.005**
Macroalgae x season	12	969.635	0.708	0.780
Evenness J' index				
Macroalgae	4	1370.198	6.002	**0.000**
Season	3	373.010	1.634	0.194
Macroalgae x season	12	179.503	0.786	0.699

df = degree of freedom; MS = mean square; F = statistics. Significant P-values are reported in bold.

Table 6. One-way ANOVA analysis for the season effect on biotic data (N, S, H' and J') of the associated epiphytic macrofauna in each macroalgal habitat

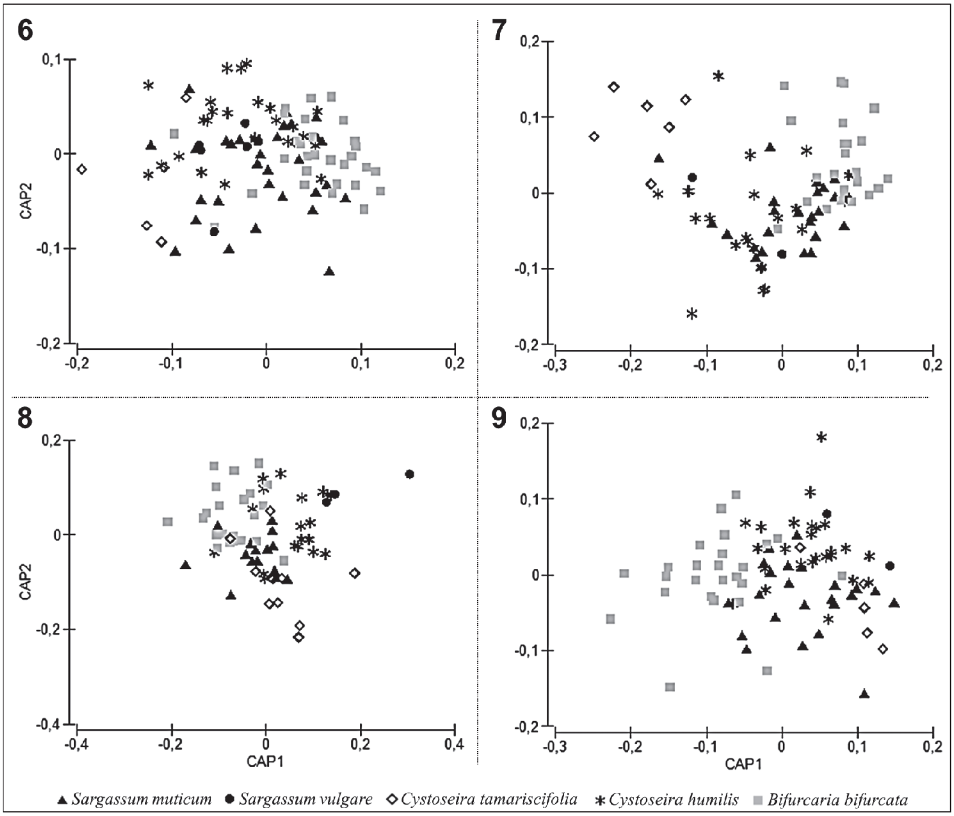
Macroalgae	*N*		*S*		*H'*		*J'*	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Sargassum muticum	0.451	0.723	0.797	0.529	4.656	**0.036**	3.494	0.070
Sargassum vulgare	2.753	0.112	4.058	**0.050**	3.565	0.067	6.386	**0.016**
Cystoseira humilis	1.810	0.223	1.678	0.248	0.826	0.515	1.123	0.396
Cystoseira tamariscifolia	4.235	**0.046**	0.440	0.731	0.668	0.595	0.700	0.578
Bifurcaria bifurcata	1.028	0.430	3.615	0.065	4.694	**0.036**	0.815	0.521

N = abundance, S = species richness, H' = Shannon-Wiener's diversity, J' = Pielou's evenness. Degree of freedom = 3, Significant P-values are reported in bold.

Table 7. Permutational multivariate analysis of variance (PERMANOVA) testing for differentiation among epiphytic macrofaunal assemblages across macroalgal host species and seasons.

Source	*df*	*Pseudo-F*	*P (perm)*
Macroalga	4	8.0248	**0.001**
Season	3	4.3346	**0.001**
Macroalga x season	12	1.5429	**0.004**
Total	330		

df = degree of freedom. Significant P-values are reported in bold.



Figs 6-9. Canonical analysis of principal coordinates (CAP) ordinations of epiphytic macrofauna communities associated with *Sargassum muticum* and native macroalgae *Cytoseira humilis*, *Cystoseira tamariscifolia*, *Sargassum vulgare*, *Bifurcaria bifurcata* during: **6.** Winter, **7.** Spring, **8.** Summer, and **9.** Autumn.

associated with *S. muticum* and *C. tamariscifolia* during spring with higher abundance on *C. tamariscifolia*. The amphipod *Aora spinicornis* Afonso, 1976 was among the important contributors to the differences in the epiphytic macrofauna associated to *S. muticum* and *S. vulgare* during summer and it was much more abundant on *S. vulgare* than on *S. muticum*. The amphipod *Amphitholina cuniculus* (Stebbing, 1874) exclusively contributed to the difference between *C. tamariscifolia* and *S. muticum* during autumn. This amphipod depicted higher abundance on *C. tamariscifolia* compared to *S. muticum.* In general, analysing the species accounting for dissimilarities among these macroalgae revealed that it was largely the same species that were also characteristic for identifying epiphytic macrofauna of the respective macroalgal hosts (Table 8), i.e. epiphytic macrofauna are mainly distinguished by comparison of common species, rather than by rare or missing species. Furthermore, it was obvious that the invader *S. muticum* did not shelter a distinctive group of species compared to the native algal hosts, particularly *C. humilis* and *S. vulgare*.

Table 8. SIMPER analysis of the epiphytic macrofauna associated with *Sargassum muticum* (Sm) and native macroalgae *Bifurcaria bifurcata* (Bb), *Cystoseira tamariscifolia* (Ct), *Sargassum vulgare* (Sv) and *Cystoseira humilis* (Ch) during sampling seasons

WINTER					
	Sm (28.58)	Bb (31.53)	Ct (23.16)	Sm/Bb [71.50]	Sm/Ct [79.04]
	Average abundance			Dissimilarity contribution (%)	
Dynamene bidentata	1.48	0.88	1.25	17.53	12.14
Steromphala pannanti	0.76	0.80	0.60	12.94	6.97
Steromphala umbilicalis	0.86	0.64	1.12	10.81	8.08
Platynereis dumerilii	0.34	0.33	0.47	6.45	3.88
Aora spinicornis	0.45	0.02	0.90	5.44	8.37
Rissoa parva	0.34	0.08	1.12	4.14	8.35
Apherusa cf. *ovalipes*	0.22	0.11	1.22	3.53	9.43
SPRING					
	Sm (42.88)	Bb (41.93)	Ct (49.50)	Sm/Bb [59.58]	Sm/Ct [66.02]
	Average abundance			Dissimilarity contribution (%)	
Dynamene bidentata	1.50	1.50	1.87	24.33	12.25
Steromphala umbilicalis	1.46	0.86	2.81	17.81	12.62
Steromphala pennanti	0.77	0.47	-	13.00	-
chauvetia brunnea	0.09	-	1.63	-	14.39
Apherusa cf. *ovalipes*	0.28	-	1.22	-	11.04
Bittium reticulatum	0.02	-	0.89	-	8.71

Average similarities are shown in parentheses and average dissimilarities for each comparison are shown in brackets.

Table 8. SIMPER analysis of the epiphytic macrofauna associated with *Sargassum muticum* (Sm) and native macroalgae *Bifurcaria bifurcata* (Bb), *Cystoseira tamariscifolia* (Ct), *Sargassum vulgare* (Sv) and *Cystoseira humilis* (Ch) during sampling seasons *(continued)*

SUMMER									
	Sm (58.96)	Bb (63.21)	Ct (49.23)	Ch (58.22)	Sv (62.67)	Sm/Bb [44.10]	Sm/Ct [48.24]	Sm/Ch [43.79]	Sm/Sv [44.63]
	Average abundance					Dissimilarity contribution (%)			
Steromphala pennanti	1.02	0.23	1.24	0.69		20.02	11.52	16.59	
Steromphala umbilicalis	1.60	1.16	2.25	2.42	2.73	19.61	13.31	20.22	16.74
Dynamene bidentata	2.14	1.67	1.58	2.12	1.73	16.22	13.65	14.46	14.09
Platynereis dumerilii	0.31		1.01				12.36		
Amphitholina cuniculus	0.06		0.52				6.64		
Aora spinicornis	0.22				2.29				26.01
Apherusa cf. *ovalipes*	0.20				1.22				14.51
AUTUMN									
	Sm (48.23)	Bb (42.29)	Ct (34.29)	Ch (43.88)		Sm/Bb [60.30]	Sm/Ct [61.15]	Sm/Ch [56.29]	
	Average abundance					Dissimilarity contribution (%)			
Dynamene bidentata	1.47	0.90	1.72	1.16		19.08	10.96	14.92	
Steromphala pennanti	0.80	0.38		0.47		17.04		15.46	
Steromphala umbilicalis	1.00	0.69	0.92	1.48		15.91	9.64	16.52	
Aora spinicornis	0.53	0.03	1.22	0.33		10.35	13.02	10.48	
Amphitholina cuniculus	0.30		1.18	0.28			12.59	7.43	
Apherusa cf. *ovalipes*	0.30		1.19				12.22		

Average similarities are shown in parentheses and average dissimilarities for each comparison are shown in brackets.

DISCUSSION

The present study showed that epiphytic macrofaunal assemblages associated with the invasive *Sargassum muticum* were markedly distinct from those of the natives, *Bifurcaria bifurcata* and *Cystoseira tamariscifolia*, but were only slightly different from those of *C. humilis* and *S. vulgare* depending on the season. The faunal diversity of *S. muticum* was among the lowest compared to the native macroalgae. However, in general, epiphytic macrofaunal assemblages inhabiting local macroalgae successfully colonised the invasive *S. muticum* and they were characterised by moderate abundance and diversity, compared with those described for other macroalgal habitats (e.g. Gestoso *et al.,* 2012; Janiak *et al.,* 2012; Engelen *et al.,* 2013). Most previous studies, like our study, showed there were no or limited differences in the associated epiphytic macrofaunal assemblage structure between native and invasive macroalgae. For instance, the comparison of *S. muticum* to a similar indigenous alga *Halidrys siliquosa* showed that both species had a very similar epiphytic macrofauna community (Wernberg *et al.*, 2004; Buschbaum *et al.,* 2006). On the southern Portuguese coast (Engelen *et al.,* 2013) and the northern Spain (Viejo, 1999), the macrofauna associated with *S. muticum* exhibited negligible differentiation in diversity relative to that in native macroalgae. In contrast, a few studies differed from this general trend and highlighted major differences between the macrofauna colonising *S. muticum* and native macroalgae: on the southern part of the Galician coast, NW Spain, *S. muticum* harbored a macro-invertebrate assemblage markedly different from that of the native alga *Laminaria ochroleuca* where the sampling time, the epiphytic load and the height on the shore were the most important factors shaping epiphytic macrofaunal assemblages (Cacabelos *et al.,* 2010). On the same coast, *S. muticum* supported epiphytic macrofaunal assemblages that were different from those of *B. bifurcata,* and this difference was more consistent across space and time (Gestoso *et al.,* 2010). Significant differences were found in the abundance, species richness and the structure of macrofaunal assemblages associated with *S. muticum* and the native species *Chondrus crispus* and *B. bifurcata* in northern Portugal (Veiga *et al.,* 2014). All these studies show that there is no simple answer to the question of whether this invasive species hosts different faunal communities than the native species, and additional factors might be responsible for the differences among studies.

The shape, and morphological and structural habitat complexity of the host macroalgae have a seasonal variability that might be important in determining patterns of abundance and structure of the associated epiphytic macrofauna (Guerra-García, 2001). Abundance and community composition of associated organisms can be strongly influenced by the architecture of the host algae, and morphological complexity of macroalgae is often positively correlated with the number of species associated (e.g. Hacker & Steneck, 1990; Gee & Warwick, 1993, 1994; Taylor & Cole, 1994; Buschbaum *et al.,* 2006; Munari *et al.,* 2015). Indeed, the most structurally complex algae commonly sustain higher animal diversity and abundance by increasing living/colonisable space for fauna and epiphytic algae (Morse *et al.,* 1985; Gee & Warwick, 1994; Chemello & Milazzo, 2002; Taniguchi *et al.,* 2003; Bedini *et al.,* 2014), and providing more vacant ecological niches to occupy (Matias *et al.,* 2007). They enhance availability and variety of food organisms in terms of periphytic algae and detritus (Higler, 1975; Glowacka *et al.,* 1976; Fretter & Manley, 1977), suitable feeding surfaces, modification of micro-environmental conditions (Gibbons, 1988a) and they also increase protection from predation by reducing the foraging effectiveness of predators (Coull & Wells, 1983; Gibbons, 1988b). This is supported by studies showing that the assemblage on *S. muticum* is more abundant and species-rich compared to the morphologically simple native *s*pecies *Saccharina latissima* and *Dictyota dichotoma* (Giver, 1999; Harries *et al.*, 2007). The thalli of *S. muticum*, like those of other structurally complex algae (Tanaka & Leite, 2003; Wikström & Kautsky, 2004), may create a high number of microhabitats, hosting organisms with different requirements (Russo, 1990; Gee & Warwick, 1994; Taylor, 1998b; Cacabelos *et al.,* 2010). However, this was not the case in the present study where *S. muticum* sheltered similar fauna diversity to that of the native algae with simple morphological complexity (namely *B. bifurcata,* a cylindrical species) (see Table 1). In fact, our results corroborated those of Engelen *et al.* (2013), which stated that habitat complexity did not seems to be the key variable that determined the richness and abundance of macrofaunal species associated with macroalgae, as it commonly would be thought. Consequently, the habitat choice/preference of fauna species involves more than the main hypothesis of morphological complexity. To sum up, although algal habitat architecture seems to play a significant role in shaping abundance and diversity of epiphytic macrofaunal assemblages, in our study the structural complexity of the invasive macroalga differed from that of native species but hosted similar assemblages. Therefore, our findings suggested that the invasive macroalga, despite being structurally different from native species, did not seem to induce changes in the associated epiphytic macrofauna (in contrast with the statement of Veiga *et al.*, 2014).

A major difference in the comparison of the epiphytic macrofauna associated with *S. muticum* on a Moroccan coast (present study) with that from Portugal (Engelen *et al.,* 2013) is that, on the southern Portuguese coast *S. muticum* hosted a total of 68 species, mainly dominated by annelids, which is much higher than what we encountered (46 species) crowned by gastropods. Discriminating species (i.e., those that contributed most to the dissimilarity among groups) in both studies were completely different. This might be due to the strong temperature gradient along the Iberian Atlantic coasts that delineates the southern distribution limit for many organisms (Lima *et al.,* 2007; Engelen *et al.,* 2013). The Moroccan coast here studied is an upwelling zone that is favorable habitat for algal species that are typical of colder zones and are absent from warmer south Portugal (e.g., Neiva *et al.,* 2015; Assis *et al.,* 2016; Lourenço *et al.,* 2016), and it can be hypothesised that this coastal distributional gap, magnified by Atlantic waters separating the two continents, might limit the presence of some faunal species in Morocco due to dispersal barriers.

The seasonal variations of the epiphytic macrofauna abundance and species richness might coincide with the seasonality of host algal species (Guerra-García *et al.,* 2011), and probably relied on the variations of macroalgae life cycle (Sánchez-Moyano *et al.*, 2001). Fauna abundances peaked in spring for the most studied macroalgae (e.g. *C. tamariscifolia*, *S. muticum*, *B. bifurcata*); this season corresponded to the exponential vegetative growth of algae coinciding with maximal algal biomass. Effectively, many studies have found that maximal abundances of epiphytic macrofauna were recorded during periods of maximal algal biomass (e.g. Edgar, 1983; Duffy, 1990). In previous reports, such abundance peaks generally occurred in spring or summer (Viejo, 1999; Wernberg *et al.,* 2004; Pacios *et al.,* 2011) except in some tropical studies (Russo, 1989). Furthermore, the low abundance detected in autumn corresponded to the decline of macroalgae according to the life cycle for the most studied species except for *S. muticum* (pseudo-perennial life cycle) where the thalli senescence happened in mid-august (summer). In fact, fertile individuals of *S. muticum* can only be found from April to July. After the end of the reproductive period, the vegetative growth rate declines rapidly and the lateral branches start to degenerate, leaving only a discoid holdfast from which primary laterals regenerate during the following winter (Sabour, *pers. observ.*). Associated organisms are lost with the shedding of branches triggering the epiphytic macrofauna abundance decrease.

Regarding the fauna specificity, in this study, the macroalgal associated epiphytic macrofauna has opportunistic behavior with low host-plant specificity. Most fauna species are habitat-non-selective (generalist) and have a non-specific relationship with their hosts (similar dominant species, a high number of common species and very few taxa were found in just one algal species). A similar result was previously reported in New Zealand (Taylor & Cole, 1994) where epiphytic macrofaunal species were not highly host specific to various brown algae species. Also, this low host-alga specificity expressed by the fauna associated to *S. muticum* and several native macroalgae was reported on the coasts of southern Portugal (Engelen *et al.,* 2013) and northern Spain (Viejo, 1999). The low degree of specificity of the epiphytic macrofauna to the host detected in marine ecosystems is generally due to the dominance of generalist fauna species (generalist habits of mesograzers consuming the host itself) or the existence of an indirect relationship mediated by the presence of epiphytic algae (Viejo, 1999).

Previous studies investigating the ecological impact of introduced macroalgae, particularly those on the macroalgal-associated fauna pointed out a severe effect reflected by a decrease in the diversity and abundance of epiphytic macrofaunal species (Tippets, 2002; Schmidt & Scheibling, 2006). However, other studies reported that the invasive species did not cause any significant effects on the associated epiphytic macrofauna or were even beneficial as the introduction of *Gracilaria vermiculophylla* in the southeastern USA, for example, which resulted in an increase in epiphytic macrofauna abundances (Byers *et al.,* 2012). In the present research, similarities found between epiphytic macrofauna assemblages of *S. muticum* and some native macroalgae indicated that the introduction of *S. muticum* on intertidal rocky shores of Morocco seems to have a limited impact on the associated animals. This was also the case for rocky shores of Helgoland, German Bight (Buschbaum *et al.,* 2006) and intertidal pools of the western and southern coasts of Portugal (Engelen *et al.,* 2013).

In conclusion, this study demonstrated that the epiphytic macrofauna assemblage associated to macroalgae depended on macroalgal identity and varied along a year. The communities on *S. muticum* were slightly different from those on some native macroalgae. The invasive *S. muticum* seemed to provide a suitable habitat for a variety of the macrofauna taxa and its pseudo-perennial life history appeared to have no effect on the native epiphytic macrofaunal, which showed little host specificity to the habitat-providing algal species. This study also indicated that the temporal variation of the community of epiphytic macrofauna along a year was not only influenced by the macroalgae as substrate/habitat, but also by the environmental conditions.

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