RESEARCH ARTICLE

Spatiotemporal variation of the epifaunal assemblages associated to *Sargassum muticum* on the NW Atlantic coast of Morocco

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Abstract

Epifaunal assemblages inhabiting the non-indigenous macroalga *Sargassum muticum* (Yendo) Fensholt were investigated on two physically distinct intertidal rocky (S1) and sandy (S2) sites along the Atlantic coast of Morocco. The objective of this study was to test whether the habitat-forming marine alga *S. muticum* invasive in these sites supported different epifaunal assemblages under different environmental conditions and through time. The gastropods *Steromphala umbilicalis*, *S. pennanti*, and *Rissoa parva* and the isopod *Dynamene bidentata* were the most contributive species to the dissimilarity of epifaunal assemblage structure between both sites throughout seasons. SIMPER analysis showed a dissimilarity of 58.3–78.5% in the associated species composition of *S. muticum* between study sites with respect to sampling season. Species diversity and total abundance were significantly higher at the rocky site compared to the sandy site. PERMANOVA analyses showed significant differences of associated epifaunal assemblage structure for the season and site interaction. Accordingly, site and season were determinant factors conditioning the role of habitat in structuring epifaunal assemblages.

Introduction

Marine macroalgae can be relevant as biogenic structures. They are known among the true autigenic epibenthic ecosystem engineers and some species are referred to as "foundation species" that have strong effects on local community structure through the mechanisms of environment stabilization, provision of critical food resources, and/or creation of biogenic habitat (Ellison et al. 2005; Jones and Thornber 2010; Ramus et al. 2017; Metzger et al. 2019). Marine macroalgae perform various functions and have a major effect on the structure of marine communities (Stachowicz 2001; Cacabelos et al. 2010). They offer refuge from predation and competition (Ware et al. 2019). They provide shelter and food (generating in situ detritus and nutrients after decomposition) and spawning and nursery grounds for many organisms, especially the earliest life stages (Buschmann 1990; Taylor 1998; Fredriksen et al. 2005). They increase space for settlement and protect the organisms from physical stress including wave action, heat, and desiccation (Hicks 1980; Wikström and Kautsky 2004; Cacabelos et al. 2010). They may modify the hydrodynamism near the sea floor, with potentially significant ecological effects on sedimentation.

Interactions between macroalgae and their associated fauna can be influenced by physical (i.e., wave action, aerial exposure, irradiance, temperature ranges and time available for nutrient exchange, accumulation of sediments, and desiccation) and biological (i.e., grazing) factors (Bertness et al. 1999; Mueller et al. 2015; Umanzor et al. 2017). Macrobenthic fauna distribution patterns are eventually the result of a complex interaction of various processes operating both within the water column as well as the sedimentary environment (Bolam et al. 2008). At large spatial scales for

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example, gradients such as temperature, salinity, and depth generally produce changes in species distributions and in structure, organization, and functioning of the assemblage, while changes in habitat characteristics (e.g., sediment granulometry, and type of substratum) are thought to greatly influence assemblage structure at more local scales (Gray 2001; Giberto et al. 2004; Bremner et al. 2006; Labrune et al. 2007). Spatial variability of epifaunal assemblages among and within habitats may be shaped by temporal variation at different scales ranging from weeks to months (Taylor 1998; Cacabelos et al. 2010; Jones and Thornber 2010). On a similar line, modifications in coastal habitat-forming macroalgae might induce changes in the abundance, richness, or composition of faunal assemblages, and consequently may have great repercussions on the ecosystems (Engelen et al. 2013).

The introduction of non-indigenous macroalgae causes many serious ecological impacts affecting native marine communities, eroding biodiversity and modifying and/or disrupting the normal functioning of ecosystems (Schaffelke and Hewitt 2007; Bedini et al. 2015; Smith 2016). However, in some cases, the effects are not detectable or even positive (Thomsen 2010; Guerra-García et al. 2012; Thomsen et al. 2013). For example, some invasive habitat formers may be considered as sources of valuable ecosystem functions where native foundation species have been lost (Ramus et al. 2017).

Sargassum muticum (Yendo) Fensholt is a habitat-forming brown alga native from south-east Asia and recorded in Morocco since 2011 (Sabour et al. 2013). However, it has received very little attention despite being common in rocky intertidal habitats in the region of El Jadida (Belattmania et al. 2018a, b). *S. muticum* thalli can grow to lengths of up to 5 m (Sabour et al. 2013), and they are composed of two distinct parts: a perennial part, which contains the holdfast and one or more short main axes; and an annual part, consisting of variably sized secondary axes. *S. muticum* has a pseudo-perennial life cycle comprising a winter phase with a moderate growth rate and a faster growth phase during spring (Wernberg et al. 2004).

This algal species has been introduced in Europe in the early 1970s and is currently widespread in numerous regions worldwide (Engelen et al. 2015). *S. muticum* has many characteristics that make it a successful invader, including high growth rates; rapid colonization of space; tolerance to temperatures between -1 °C and 30 °C and survival in salinities below 10‰; high photosynthetic rates; copious reproduction, including asexual and self-fertilization strategies and efficient multiple dispersal mechanisms due to floating and drifting fertile thalli; and high habitat complexity (Norton 1976, 1977a, b; Critchley 1983; Hales and Fletcher 1989; Viejo 1997). The low tolerance of *S. muticum* to desiccation precludes colonization of regularly emerged littoral areas (Norton 1977a). The optimal tidal zone for *S. muticum* establishment is the extreme lower shore and shallow sublittoral fringe (Harries

et al. 2007). *S. muticum* rarely occurs deeper than a few meters and the subtidal range is thought to be linked to water clarity and the availability of sufficient light for growth (Norton 1977a; Thomsen et al. 2006). Strong wave action induces the plant breakage and fragmentation, and populations are unable to establish in wave-exposed locations (Viejo et al. 1995). Thus, *S. muticum* colonizes mainly the sheltered shores where it often forms dense monospecific beds, whereas it is largely restricted to rock pools on exposed shores (Critchley 1983; Critchley et al. 1983; Fernández et al. 1990; Andrew and Viejo 1998a, b; Harries et al. 2007). *S. muticum* can establish on a variety of substrata, including bedrock to pebbles, shell fragments scattered on the sediment surface (Harries et al. 2007), wood, mooring lines, and wharves (Curiel et al. 1998) that provide an attachment point for the holdfast.

The present work aims at (i) identifying the main environmental drivers shaping spatial dynamics of the non-indigenous brown alga *S. muticum* along the El Jadida shoreline (northwestern Atlantic coast of Morocco); (ii) discussing about the observed distribution patterns of macro-epifauna associated with this habitat-forming macroalga; (iii) exploring potential differences of associated epifaunal assemblages between sandy and rocky intertidal sites situated at different elevations and also differing for substrate, hydrodynamics, and exposition; and (iv) raising hypotheses to explain the question whether *S. muticum*-associated epifauna assemblages between two intertidal sites under dissimilar environmental conditions are distinct and their differences would be reflected in differences in diversity, abundance, and taxonomic composition, and whether site and season influence the structure of these communities.

Material and methods

Study areas

The sampling sites (S1 and S2) are located along the El Jadida shoreline on the northwestern Atlantic coast of Morocco (Fig. 1). In this area, the tide is semidiurnal with an average period of around 745 min (12 h and 25 min) and defined by a semidiurnal tidal cycle, consisting of two high and two low tides of different entity. The average tide amplitude is 4 m during spring tides and 2 m for neap tides. The Moroccan Atlantic coast is generally exposed to a strong energy characterized by swells from the north Atlantic mainly of west to northwest origin, but the most dominant swells are those of the north-northwest and north-eastern dial west. The first site S1 (33° 14′ 47.5″ N; 8° 32′ 31.9″ W) oriented north-westward is a fully wave-exposed coastal area. The S1 consists of an intertidal platform of rocky substratum (bedrock) with a marked roughness and sheltered shallow areas protected against the strong wave action by artificial reefs called "Bechkiras"

Fig. 1 Geographical position and location of sampling sites (S1 and S2)

(Fig. 2a). These rockpools host a diverse macroalgal community (intermixed species) dominated by the invasive *S. muticum* showing persistent, dense, and extensive canopy, especially during periods of optimal growth. The second site S2 (33° 15′ 11.5″ N; 8° 29′ 54.1″ W) facing northeast is moderately protected from the wave action. The S2 consists of a sandy beach with shallow intertidal soft bottoms and few patches of outcroppping rocks providing hard substrates. In
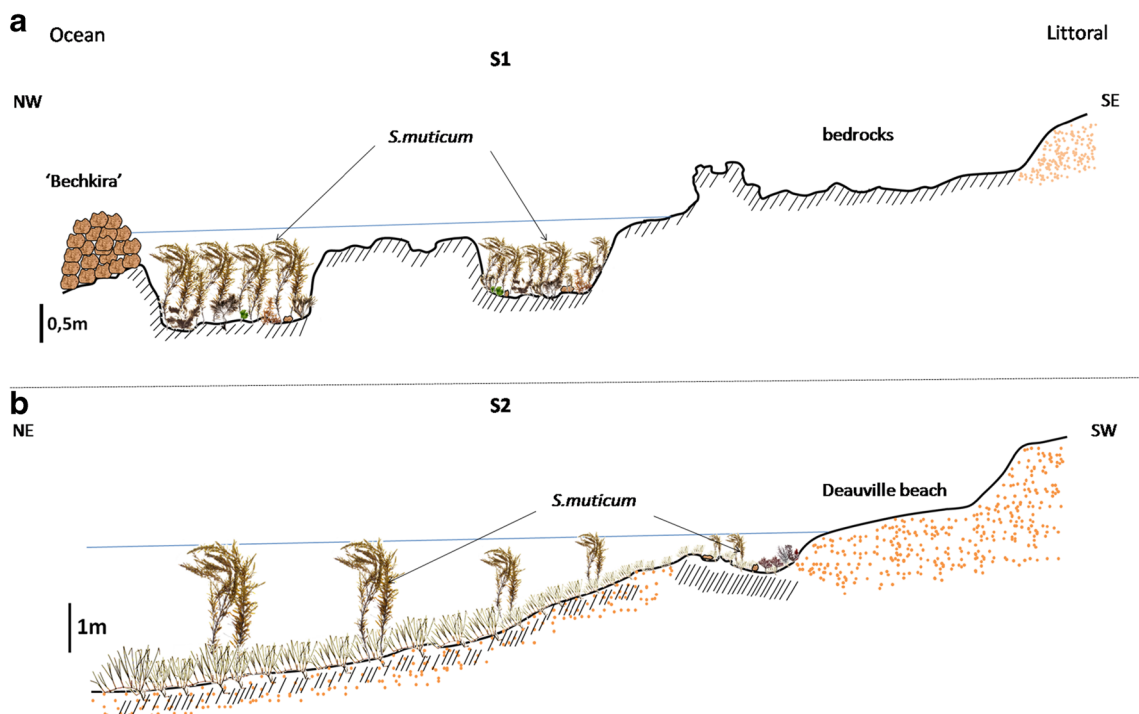

Fig. 2 Intertidal area profile in sites S1 (**a**) and S2 (**b**) with a schematic illustration of *Sargassum muticum* thalli

this area, *S. muticum* thalli are restricted to bedrock covered by sand and they constitute scattered stands with large thalli constantly submerged by a body of water whose depth at low tide always exceeds 1 m (Fig. 2b).

Sampling design and sample processing

To test the hypothesis that the structure of epifaunal assemblages inhabiting *S. muticum* differ between physically distinct intertidal shores, thalli of the macroalga were sampled from two sites (separated by six kilometers) under different environmental conditions on the El Jadida coastline. Sampling was conducted at low tides (0.3–0.5 m) on a monthly basis over a 1-year period from January to December 2015. Three random replicates (separated by 5 m) per site were collected. For each replicate five individual thalli were carefully detached from the substratum, enclosed in a plastic bag,
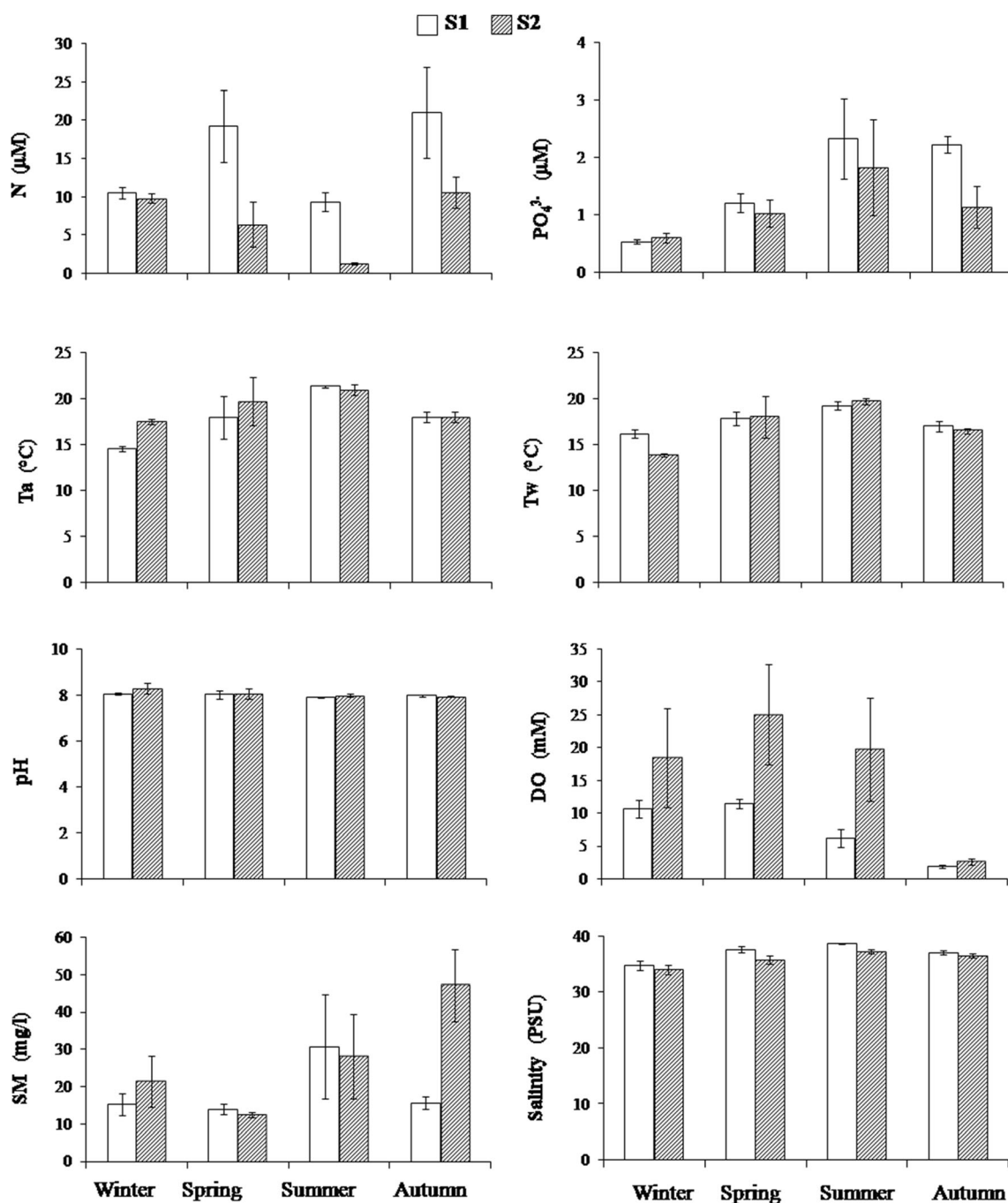

Fig. 3 Physicochemical variables measured in sites S1 and S2. N, nitrite + nitrate; PO_4^{3-}, orthophosphates; Ta, air temperature; Tw, water temperature; DO, dissolved oxygen; SM, suspended matter

Table 1 Two-way ANOVA analysis testing the effect of site and season on physicochemical parameters

Source of variation	df	F	p
Nitrogen (nitrate + nitrite)			
Site	1	14.086	*0.002*
Season	3	4.350	*0.020*
Site × season	3	1.501	0.252
Orthophosphates			
Site	1	1.928	0.184
Season	3	5.588	*0.008*
Site × season	3	0.752	0.537
Air temperature			
Site	1	1.505	0.238
Season	3	6.934	*0.003*
Site × season	3	0.957	0.437
Water temperature			
Site	1	0.810	0.381
Season	3	8.579	*0.001*
Site × season	3	0.887	0.469
pH			
Site	1	0.814	0.373
Season	3	1.413	0.276
Site × season	3	0.415	0.744
Dissolved oxygen			
Site	1	0.810	0.381
Season	3	8.579	*0.001*
Site × season	3	0.887	0.469
Suspended matter			
Site	1	2.393	0.141
Season	3	2.573	0.090
Site × season	3	2.133	0.136
Salinity			
Site	1	6.688	0.179
Season	3	12.995	*0.000*
Site × season	3	0.633	0.605

Significant *p* values are in italics

df, degree of freedom; *F*, statistic, *p*, *p* value

fixed in 5% buffered formalin-seawater solution, and brought to the laboratory for sorting. In the laboratory, each replicate was washed in tap water. The latter was subsequently sieved using a 0.5-mm mesh screen to recover released macro-epifaunal specimens. The macroalga thalli were also examined to pick and individually remove specimens remained entangled in the algal fronds. Hereafter, all collected organisms were preserved in 70% ethanol until sorted, counted, and identified to the lowest possible taxonomic level (usually species) using a binocular stereo microscope. The thalli were dried in a stove at 60 °C for 72 h then weighed to measure macroalgal dry weight (DW).

The environmental variables measured during monthly sampling over the study period (January to December 2015) included air temperature (Ta), seawater temperature (Tw), salinity, pH, dissolved oxygen (DO), nitrogen (as NO_2^- and NO_3^-), phosphates (as PO_4^{3-}), and suspended matter (SM). Ta was recorded with a stick thermometer, salinity and Tw with a WTW LF340 thermosalinometer, pH with a portable pHScan WP ½ pH-meter, DO with a portable HANA, and HI 9142 oxygen meter; nitrogen, phosphates, and SM analyses were made in the laboratory. Seawater samples were collected using polyethylene sampling bottles and enclosed 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 assess the SM and to measure the nutrient contents (NO_2^- + NO_3^- and PO_4^{3-}) according to the methodology described by Aminot and Chaussepied (1983). Values of environmental variables were seasonally averaged.

Data analysis

Data about associated epifauna were analyzed through several univariate measures including species richness, i.e., number of taxa (S), abundance (N), diversity (as Shannon-Wiener's H′) (Shannon and Weaver 1963), and evenness (as Pielou's J') (Pielou 1966). All biological indices were calculated per replicate and were then rescaled to 10 g of macroalga dry weight.

Two-way ANOVA was applied to test for the effects of sampling site and time on the epifauna abundance, species richness and diversity, and on environmental variables considering sampling site (S1 and S2) and season (winter, spring, summer, autumn) as fixed factors. Whenever significant effects of the main factors or their interactions were found, the source of difference was identified using the pairwise comparisons based on a post hoc test (Tukey's honestly significant difference "HSD" test) set at the 5% significance level.

Table 2 Tukey's honestly significant difference (HSD) test coupled with two-way ANOVA applied to significant effects of study site and season on physicochemical parameters

Seasons	N	PO_4^{3-}	Ta	Tw	DO	Salinity
Winter/spring	0.816	0.544	0.116	*0.027*	0.327	*0.006*
Winter/summer	0.403	*0.007*	*0.002*	*0.001*	0.972	*0.000*
Winter/autumn	0.279	0.062	0.356	0.263	0.150	*0.004*
Spring/summer	*0.024*	0.100	0.199	0.343	0.561	0.175
Spring/autumn	0.750	0.520	0.892	0.592	0.005	0.999
Summer/autumn	*0.015*	0.697	0.056	*0.038*	0.069	0.220

Significant *p* values are in italics

Ta, air temperature; *Tw*, water temperature; *DO*, dissolved oxygen; *N*, nitrite + nitrate; PO_4^3, orthophosphates

Table 3 Monthly variations in length, density, and fertility of *Sargassum muticum* populations in study sites

	Thallus length (cm)		Density (thallus/m^2)		Fertility	
	S1	S2	S1	S2	S1	S2
January	45.00 ± 1.15	60.00 ± 2.08	44.33 ± 3.28	21.33 ± 1.20		
February	51.00 ± 2.08	73.33 ± 2.03	44.00 ± 2.08	19.00 ± 1.15		
March	49.00 ± 2.08	131.33 ± 3.53	47.67 ± 4.63	16.33 ± 0.33	*	
April	71.00 ± 2.08	180.67 ± 4.33	44.33 ± 0.67	13.33 ± 0.88	*	*
May	94.00 ± 2.65	210.00 ± 6.08	44.33 ± 0.88	10.00 ± 0.58	*	*
June	113.00 ± 4.73	261.67 ± 3.53	43.00 ± 6.24	5.00 ± 0.58	*	*
July	63.33 ± 6.01	53.67 ± 7.51	35.00 ± 1.73	5.00 ± 0.58	*	*
August	38.67 ± 2.73	29.67 ± 3.28	23.33 ± 0.88	4.33 ± 0.67		
September	15.00 ± 1.73	11.00 ± 2.08	21.00 ± 1.53	3.33 ± 0.33		
October	11.67 ± 0.88		24.67 ± 1.76			
November	25.67 ± 1.76	21.67 ± 2.33	22.00 ± 2.52	6.67 ± 0.33		
December	36.00 ± 2.65	32.33 ± 2.33	25.00 ± 0.58	10.00 ± 0.58		

*Presence of the receptacles

Assumptions for homogeneity of variance (Levene's test) and normality (Kolmogorov-Smirnov test) were checked for prior to ANOVA analyses; and transformations were made when necessary (if the assumption to meet homogeneity failed) to remove heteroscedasticity (Underwood 1997). These statistical analyses were carried out in SPSS v11.5 software.

Differences in the epifaunal assemblage structure between both sampling sites (fixed factor: 2 levels, S1 and S2) and among seasons (fixed factor: 4 levels, winter, spring, summer, autumn) were explored using non-parametric permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; Anderson et al. 2008) on the basis of Bray-Curtis similarity matrix constructed from square root-transformed data. Only significant effects ($p < 0.05$) were further investigated through a series of a posteriori multiple pairwise comparisons used to test for differences between/within groups for pairs of levels of the selected factors (i.e., site and season). Permutational test of multivariate dispersions (PERMDISP, Anderson 2004; Anderson et al. 2008) was undertaken to check for homogeneity of dispersions between sites and among seasons. Non-metric multidimensional scaling (nMDS) analysis (Clarke and Warwick 2001) was performed to visualize on ordination plots differences in the multivariate patterns in epifaunal assemblages. The SIMPER procedure (Clarke 1993) was applied to identify the percentage contribution of each taxon and to detect species contributing mostly to the observed Bray-Curtis dissimilarities and differences revealed by PERMANOVA. In each comparison carried out, taxa were considered among the most discriminating epifauna species if their contribution to percentage dissimilarity was ≥ 5%. Multivariate analyses were performed by means of PRIMER v6.1 software package (Plymouth Marine Laboratory).

Results

Environmental data

The physicochemical parameters measured in sites S1 and S2 during the study period are reported in Fig. 3. The nitrogen ($NO_3^- + NO_2^-$) values showed a significant spatiotemporal heterogeneity ($p < 0.05$; Table 1) between summer and spring and between summer and autumn ($p < 0.05$; Table 2). In S1, nitrogen rate increased from winter to spring and strongly decreased in summer. In S2, nitrogen contents decreased between winter and summer, and rose in autumn (Fig. 3). Generally, waters seemed to be more concentrated in nitrogen in S1 compared to S2. The PO_4^{3-} values were comparable in both sites ($p > 0.05$) but differed significantly at seasonal scale ($p < 0.01$) with a relevant increase in summer (Fig. 3). Temperatures generally exceeded 15 °C on average in both sites, showing a clear and significant seasonal variability ($p < 0.01$) with the highest values recorded in summer (≥ 20 °C) (Fig. 3). The pH values not exceeded 8.32 (Fig. 3) indicating neither inter-season nor inter-site heterogeneity ($p > 0.05$; Table 1) with low standard errors not exceeding 0.1 (Fig. 3). Dissolved oxygen levels varied from 1.89 to 25.05 mM (Fig. 3) with significant variation among seasons, particularly between spring and autumn ($p < 0.01$; Tables 1 and 2) without any significant spatial variability ($p > 0.05$; Table 1). The suspended matter did not show any clear trend within sites and no significant ($p > 0.05$) spatiotemporal heterogeneity was detected. Salinity values ranged from 34.04 to 38.69 PSU (Fig. 3) and exhibited significant ($p < 0.01$; Tables 1 and 2) temporal variability tending to increase during warm seasons in both studied sites.

Table 4 Total list of macro-epifauna species associated to *Sargassum muticum* at the studied sites on the El Jadida shoreline

Taxa	S1	S2
Nemertea	+	
Polychaeta		
Branchiomma sp. 1	+	
Eulalia viridis (Linnaeus, 1767)	+	
Eunice vittata (Delle Chiaje, 1828)	+	+
Eupolymnia nesidensis (Delle Chiaje, 1828)	+	
Lepidonotus clava (Montagu, 1808)	+	
Platynereis cf. *dumerilii (*Audouin & Milne Edwards, 1834)	+	+
Mollusca Gastropda		
Bittium reticulatum (da Costa, 1778)	+	
Chauvetia brunnea (Donovan, 1804)	+	+
Fusinus sp. 1	+	
Littorina saxatilis (Olivi, 1792)	+	+
Melarhaphe neritoides (Linnaeus, 1758)	+	
Mitrella alvarezi Rolán & Luque, 2002	+	
Monophorus perversus (Linnaeus, 1758)	+	
Nassarius sp. 1	+	
Ocinebrina sp. 1	+	
Omalogyra sp. 1	+	
Rissoa parva (da Costa, 1778)	+	+
Steromphala pennanti (Philippi, 1846)	+	+
Steromphala umbilicalis (da Costa, 1778)	+	+
Tricolia pullus (Linnaeus, 1758)	+	+
Mollusca Bivalvia		
Musculus costulatus (Risso, 1826)	+	+
Pycnogonida		
Ammotheidae undetermined	+	
Crustacea Amphipoda		
Ampelisca lusitanica Bellan-Santini & Marques, 1987	+	
Amphitholina cuniculus (Stebbing, 1874)	+	+
Ampithoe sp. 1	+	
Ampithoidae undetermined	+	
Aora spinicornis Afonso, 1976	+	+
Apherusa cf. *ovalipes* Norman & Scott, 1906	+	+
Apolochus neapolitanus (Della Valle, 1893)	+	
Calliopiidae undetermined	+	
Caprella acanthifera Leach, 1814	+	+
Elasmopus vachoni Mateus & Mateus, 1966	+	+
Ericthonius sp. 1	+	
Lysianassidae undetermined		+
Crustacea Isopoda		
Cleantis sp. 1	+	+
Dynamene bidentata (Adams, 1800)	+	+
Paranthura nigropunctata (Lucas, 1846)	+	
Stenosoma cf. *acuminatum* Leach, 1814	+	+
Stenosoma cf. *capito* (Rathke, 1837)	+	+
Stenosoma cf. *nadejda* (Rezig, 1989)	+	
Crustacea Decapoda		
Hippolyte varians Leach, 1814	+	+
Hyas cf. *coarctatus* Leach, 1816		+
Crustacea Tanaidacea		
Chondrochelia savignyi (Kroyer, 1842)	+	
Echinodermata		
Amphipholis squamata (Delle Chiaje, 1828)	+	+
Asterina gibbosa (Pennant, 1777)	+	
Chordata		
Opeatogenys cadenati Briggs, 1957	+	+
Syngnathus acus Linnaeus, 1758	+	

Biological data analysis

The monitoring of some paramertes of phenology and life cycle of the invader *S. muticum* in the two sites is illustrated on the Table 3. *S. muticum* has two distinct growth phases: the first one with a slower growth in winter followed by a second phase characterized by faster growth during spring-early summer. The elongation of the thalli in S2 reached a maximum value of 261.67 cm in June, whereas in S1 the maximum size of the alga not exceeded 115 cm.

S. muticum population in S1 showed densities ranging from 21 to 47 ind.m^{-2}; the greatest densities were recorded during winter to early summer, subsequently, densities not exceed 25 ind.m^{-2} (Table 3). In S2, density values of 13–21 ind.m^{-2} were recorded during winter and early spring before decreasing in June (Table 3). *S. muticum* thalli developed receptacles on the tertiary branches earlier in S1 site (starting from March) than in S2 site (April).

A total of 48 taxa of epifauna associated with *S. muticum* were recovered and recorded over the duration of the sampling period (Table 4) with 21 species common to both studied sites. However, some species (i.e., the Polychaeta *Eulalia viridis*, *Eupolymnia nesidensis*, and *Lepidonotus clava*; the gastropods *Bittium reticulatum* and *Monophorus perversus*; the amphipods *Apolochus neapolitanus* and *Ampelisca lusitanica*; and the isopod *Paranthura nigropunctata*) were exclusively found in S1. The gastropods *Steromphala umbilicalis* (52% of all individuals of all taxonomic groups), *Rissoa parva* (15%), and *Steromphala pennanti* (10%) were the most abundant associated species at the sandy site S2, while the isopod *Dynamene bidentata* (37%) and the gastropods *S. umbilicalis* (20%) and *S. pennanti* (12%) dominated the *S. muticum*-associated epifauna communities in the site S1. *D. bidentata*, *R. parva, S. umbilicalis*, and *S. pennanti* exhibited seasonal changes in abundance as well as spatial discrimination between the two sites. Crustaceans and gastropods had the highest number of individuals and were the most species-rich taxonomic groups accounting for 77 and 82% of the total number of species in S1 and S2, respectively (Fig. 4).

The mean seasonal values of community structure attributes (abundance, number of species, and diversity indices H′ and J′) of the associated epifauna at both sites are reported in the Figs. 5 and 6. The abundance differed significantly between S1 and S2 ($p < 0.05$; Table 5). Generally, *S. muticum* seemed to host on average more individuals in the rocky site compared to S2, particularly, during winter and spring (Fig. 5a). The number of epifaunal species associated to *S. muticum* showed comparable values between sites (Fig. 5b) with no significant differences within site and season (Fig. 5b) and no interaction effect between both factors ($p >$ 0.05; Table 5). Significant spatiotemporal variability was detected for Shannon-Wiener's index ($p < 0.05$; Tables 5 and 6)
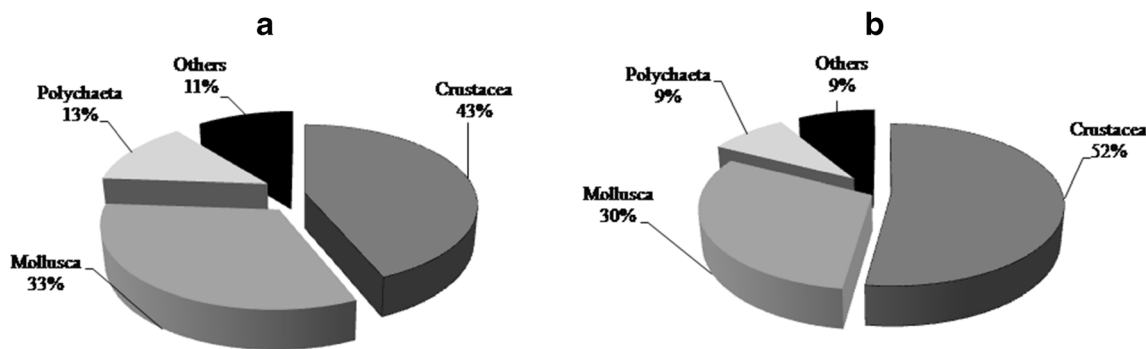
Fig. 4 Mean composition of the epifauna associated with *Sargassum muticum* collected from rocky site (**a**) and sandy site (**b**) along the El Jadida shoreline

with higher values in S1 than S2 (Fig. 6a). Shannon-Wiener's index showed synchronous dynamics between both sites, and exhibited the highest values during cold periods (Fig. 6a). Pielou's J' depicted similar trends on both sites (Fig. 6b) without any significant differences between sites and among seasons ($p > 0.05$; Table 5).

PERMANOVA analysis pointed out significant differences in the structure of epifaunal assemblages between both sites and among seasons (Table 7). PERMDISP tests indicated no significant heterogeneity of dispersions for the factor

'site' suggesting a homogeneous dispersion between sites (PERMDISP, $F = 0.046$; P (perm) = 0.854). However, there was no homogeneity of multivariate dispersion ($F = 7.069$; P (perm) = 0.001) in the season effect. This was essentially due to the noteworthy variation of species structure between the cold season (winter) and warm seasons (spring and summer) (PERMDISP pairwise comparisons; P (perm) from 0.010 to 0.024). The two-dimensional nMDS plot (Fig. 7)
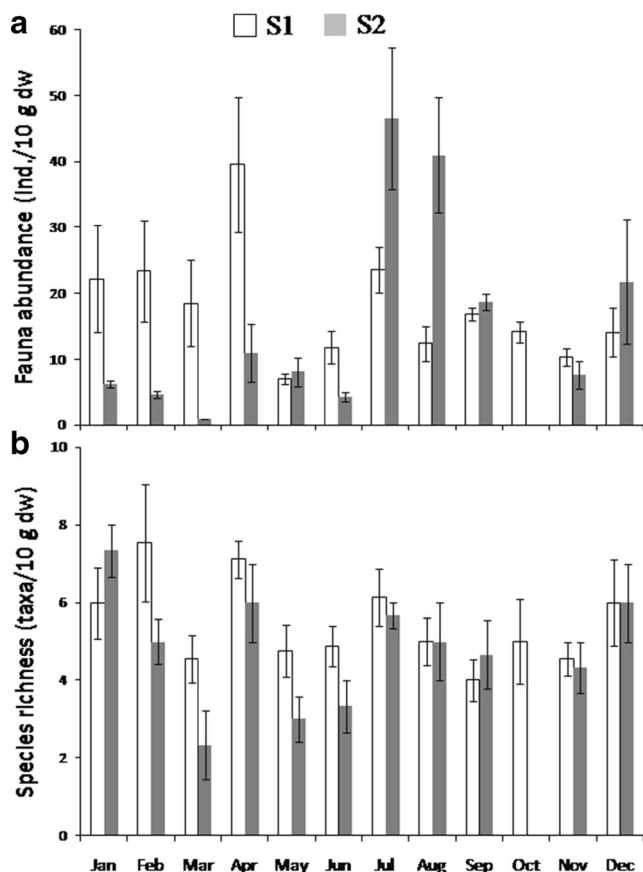

Fig. 5 Monthly variation of **a** fauna abundance and **b** species richness of the macro-epifauna associated to *Sargassum muticum* on site S1 (empty bars) and S2 (gray bars). Error bars represent standard errors
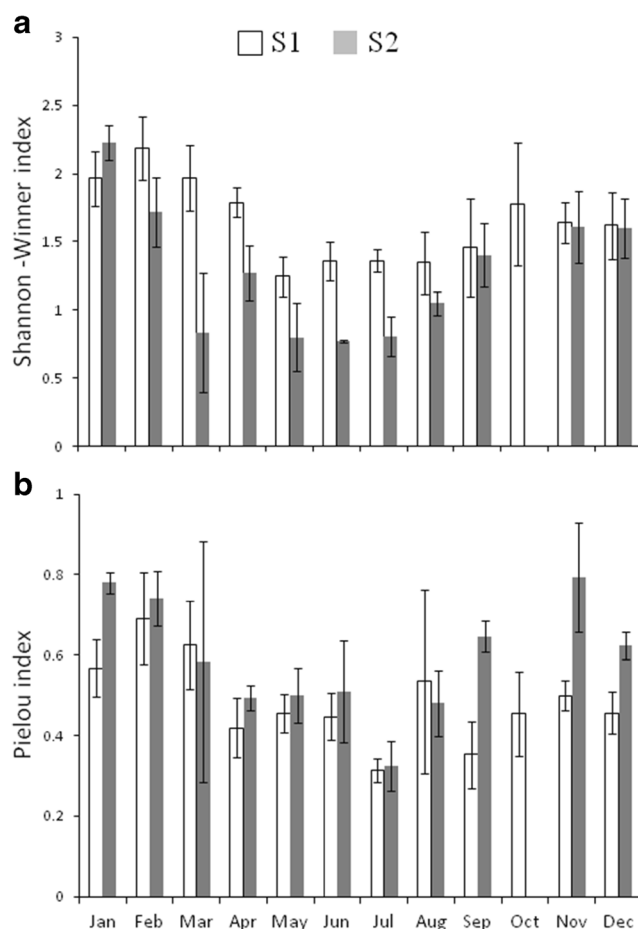

Fig. 6 Monthly variation of **a** Shannon-Wiener's diversity and **b** Pielou's evenness of the macro-epifauna associated to *Sargassum muticum* on site S1 (empty bars) and S2 (gray bars). Error bars represent standard errors

Table 5 Two-way ANOVA analysis testing the effects of site and season on epifauna abundance, species richness, and diversity indices

Source of variation	df	F	P
Abundance			
Site	1	4.437	*0.046*
Season	3	0.028	0.993
Site × season	3	0.229	0.874
Species richness			
Site	1	0.000	0.997
Season	3	0.410	0.748
Site × season	3	0.206	0.891
Diversity H′ index			
Site	1	6.180	*0.026*
Season	3	5.169	*0.012*
Site × season	3	0.483	0.699
Evenness J' index			
Site	1	1.074	0.316
Season	3	2.619	0.089
Site × season	3	0.406	0.751

Significant *p* values are in italics

df, degree of freedom; *F*, statistic

corroborated the results highlighted by the PERMANOVA analysis, showing a certain discrimination between studied sites for each season. SIMPER analysis showed moderate average dissimilarities (from 58.34 to 78.53) between sites and seasons (Table 8). The isopod *D. bidentata* and the gastropods *S. umbilicalis, S. pennanti*, and *R. parva* were the most important contributive species to the observed dissimilarity of macro-epifaunal assemblages between S1 and S2 throughout all seasons. *D. bidentata* was more abundant in the S1 site than in S2 during all sampling seasons. Both species of the genus *Steromphala* showed higher abundance in S1 during spring, whereas they were represented by more individuals in S2 during summer. *R. parva* displayed more individuals in S2 in both summer and autumn. In general, the dissimilar distribution of species between S1 and S2 was mainly due to the variation in abundance of the most common taxa.

Table 6 Tukey's post hoc test comparaison for diversity H′ index

Season	p values
Winter/spring	*0.023*
Winter/summer	*0.032*
Winter/autumn	0.820
Spring/summer	0.998
Spring/autumn	0.151
Summer/autumn	0.195

Significant *p* values are in italics

Discussion

The present paper highlights the ecological role of the introduced alga *S. muticum* by harboring abundant and diverse epifaunal assemblages, as expected for an engineer species. However, differences have been detected between the two analyzed sites with the rocky biotope (S1) hosting more diversified and abundant epibiont associations throughout seasons except for summer when the macroalga seems to support more epifaunal individuals in the sandy biotope (S2). This would be related to a slight time shift of the annual life cycle of this alga between the two sites. This shift is presumably linked to the local morphology, bottom nature, and hydrodynamism characterizing the two sampling sites. On the rocky site, the shallow rockpools limit the length and the apical growth of *S. muticum* thalli that are continually truncated at the growing tips of their primary axes level with the surface of the pool under the wave action. This promotes the production of lateral secondary and tertiary branches and, consequently, the earlier appearance of the receptacles (at the beginning of March). After the reproductive period, lateral branches start to degenerate in summer. On the sandy site, with water depths beyond 1 m at low tide, the alga undergoes its highest vegetative growth from winter to early summer with thallus lengths exceeding 2.60 m. The elongation of thalli seems to take over the branching, causing a delay of the fertility, thus restricting the earlier degeneration of the thalli in summer.

The spatial variation of epifaunal assemblages inhabiting *S. muticum* along the El Jadida coast is probably linked to the degree of cover of *S. muticum* populations in each study site. Larger macrophyte beds are known to host greater species richness than small beds (Källén et al. 2012). It has been reported that the epifaunal diversity declines with reducing patch size of kelps, and epifaunal assemblages occurring on low-density kelp reefs are different from those recorded in high-density kelp reef (Shelamoff et al. 2019, 2020). Reasons for such variations may be related to the species-area relationship, linking the number of species to the surface available for colonization (Anderson 1998; Hirst and Attrill 2008; Källén et al. 2012). Alternatively, small patches can offer a refuge for species that are poorer competitors, and hence loosers in larger areas (Anderson 1998), whereas larger beds provide more microhabitats and niches, promoting colonization of several species (Anderson 1998; Hirst and Attrill 2008; Källén et al. 2012).

The *S. muticum* population is well established at the rocky site, where the alga stands maintain high densities from winter to late spring. In contrast, this alien is not able to develop dense populations on the sandy beach (S2). The low density seems caused by the detachment of the *S. muticum*'s thalli feebly attached to the shallow intertidal bedrock covered with sand. Although the lenght of *S. muticum* thalli is favored by the depth of the water column, the density of this invader

Table 7 PERMANOVA analysis testing for differences in the epifaunal assemblage structure between sites (S1 vs. S2) and seasons

Source		df		Pseudo-*F*		*P* (perm)	
Site		1		8.468		*0.001*	
Season		3		3.6864		*0.001*	
Site × season		3		2.2505		*0.002*	
Pairwise tests							
	Winter		Spring		Summer		Autumn
	T	*P* (perm)	*T*	*P* (perm)	*t*	*P* (perm)	*t*	*P* (perm)
S1/S2	1.863	*0.001*	1.453	*0.034*	1.936	*0.036*	2.341	*0.003*

Significant *p* values are in italics

appears to be mainly affected by the substrate type as a forcing factor acting at local scale. This alien species commonly prefers hard substrates (Norton 1977b; North 1973; Fletcher and Fletcher 1975) but may occasionally grow on mixed substrates containing sand, gravel, and stones (den Hartog 1997). According to Thomsen et al. (2006), stones < 10 cm in diameter are considered as inappropriate substrates for *S. muticum* settlement. This alga could unsuccessfully settle on sandy substrates, where it is also prone to tissue loss produced by sand abrasion (Morrell and Farnham 1982). The

establishment of a sustained vegetation cover of *S. muticum* on the studied rocky biotope could also dependent on the availability of nutrients (high nitrogen content in S1 compared to S2). In coastal ecosystems, the generally high nutrient content facilitates the establishment of invasive macroalgae (Ceccherelli and Cinelli 1997; Steen 2003; Sánchez and Fernández 2006). The spread of *S. muticum* in northern Spain has been modeled by the interaction between nutrient enrichment and the availability of space including the lack of native canopy algae resisting *S. muticum* establishment
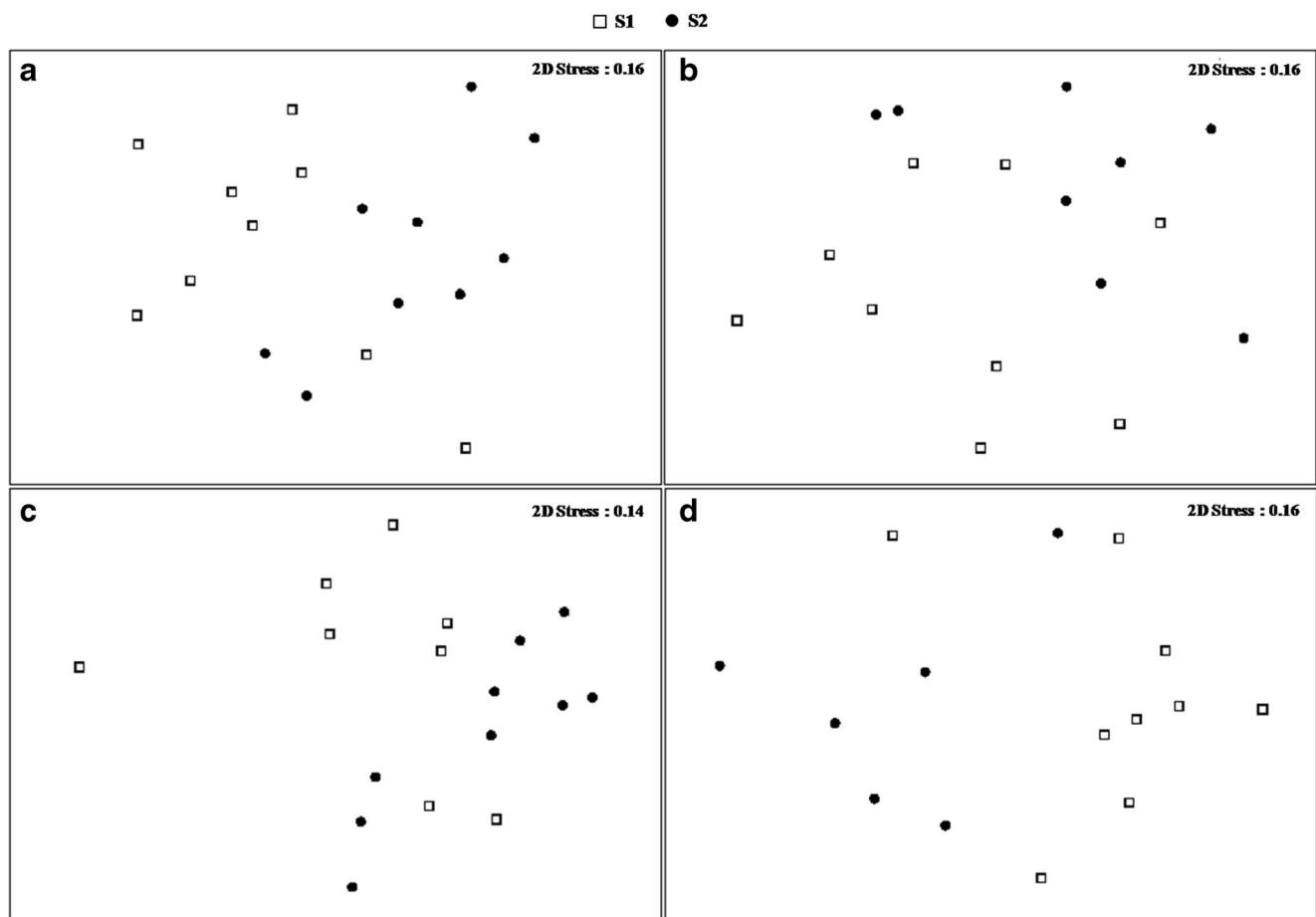

Fig. 7 Non-metric multidimensional scaling (nMDS) ordinations of macro-epifauna assemblages associated to *Sargassum muticum* in site S1 and S2 during winter (**a**), spring (**b**), summer (**c**), and autumn (**d**)

Table 8 SIMPER analysis of the macro-epifauna associated to *Sargassum muticum* in S1 and S2 sites during sampling seasons

Species	S1 Average abundance	S2	Average Dissimilarity	Dissimilarity contribution (%)
Winter (75.22)				
Dynamene bidentata	2.66	0.62	14.56	19.35
Apherusa cf. *ovalipes*	0.77	0.29	5.22	6.94
Steromphala umbilicalis	1.07	0.83	5.09	6.77
Chauvetia brunnea	0.60	0.06	4.74	6.31
Aora spinicornis	0.67	0.00	4.67	6.21
Ericthonius sp.	0.86	0.00	4.53	6.02
Steromphala pennanti	0.66	0.49	4.52	6.01
Rissoa parva	0.37	0.48	3.56	4.93
Spring (58.34)				
Dynamene bidentata	3.23	1.28	16.48	28.24
Steromphala umbilicalis	2.44	1.44	9.86	16.89
Steromphala pennanti	1.14	0.88	8.86	15.19
Summer (59.09)				
Steromphala umbilicalis	2.40	4.36	13.05	22.11
Steromphala pennanti	0.85	1.51	7.78	13.19
Dynamene bidentata	1.11	1.09	7.07	11.98
Rissoa parva	0.71	1.04	5.94	10.06
Tricolia pullus	0.00	0.93	5.19	8.80
Bittium reticulatum	0.70	0.00	4.30	7.29
Autumn (78.53)				
Rissoa parva	0.00	2.47	18.17	23.13
Dynamene bidentata	1.70	0.42	11.29	14.37
Steromphala umbilicalis	1.15	1.00	7.79	9.92
Hippolyte varians	0.16	0.81	6.41	8.16
Steromphala pennanti	0.76	0.39	6.26	7.98
Opeatogenys cadenati	0.09	0.64	4.38	5.58

Average dissimilarities for site comparison during each season are shown in parentheses

(Sánchez and Fernández 2006). In addition, it has been reported that *S. muticum* finds a refugium in wave-protected tide pools and that it cannot develop under severe hydrodynamic conditions (Andrew and Viejo 1998b). In exposed locations, strong wave action causes plant fragmentation and populations are unable to recover to their former ecological stage in such locations (Viejo et al. 1995). Consequently, the hydrodynamic conditions and the absence of a suitable substratum could also be regarded as a limiting factor for *S. muticum* occurrence in the sandy site.

The structure of the macro-epifauna associated with *S. muticum* differed significantly between the two study sites. Similar results have been highlighted by Buschbaum et al. (2006) who reported how the community structure and species composition associated to *S. muticum* varied significantly between a rocky shore of the island of Helgoland and a soft sediment environment near the island of Sylt (North Sea, German Bight). The spatial distribution of epifaunal communities is influenced not only by the algae as habitat but also by the hydrodynamic conditions of the environment (Guerra-García et al. 2011). Several studies have revealed major differences in the epiphytic invertebrate composition on various species of macroalgae across gradients of wave exposure (e.g., Beckley and McLachlan 1979; Tararam and Wakabara 1981; Edgar 1983; Moore 1972, 1985; DeFelice and Parrish 2001). Taxonomic richness, abundance, and diversity of invertebrate assemblages showed significant negative relationships with exposure to wave energy at Hanalei Bay, Kauai, Hawaii (DeFelice and Parrish 2001). In this study, the presence of rocky pools and breakwater structures in S1 provide protection to thalli and their associated organisms from wave action. This could partly explain the relatively high epifauna diversity recorded from this site. The substratum type, otherwise, would not be considered a forcing/key factor for the spatial patterns of the epifauna composition associated to *S. muticum* along the El Jadida coastline. Some species found exclusively within the shallow rocky pools in S1 were previously recorded in sandy and/or muddy biotopes (Watson 1886; Marques and Bellan-Santini 1987; Martínez et al. 2007; Scipione and Zupo 2010).

S. muticum is a pseudo-perennial alga. Thus, associated epifaunal assemblages are lost after the natural detachment of the lateral branches in late summer. An annual recolonisation of the alga is necessary because only a few species remain attached to the basal fixation system, maintaining their presence during winter (Norton and Benson 1983; Jephson and Gray 1977; Buschbaum et al. 2006). Therefore, recolonisation of *S. muticum* by the epifaunal organisms could be potentially ruled by other macroalgal species present at each study sites. Actually, most of algal species colonizing the site S1 (mainly represented by the brown algae belonging to Fucales, Dictyotales, Sphacelariales, Laminariales, and Tilopteridales, and some red algae belonging to Gelidiales, Gigartinales, and Gracilariales) are absent from the site S2 which is characterized by the dominance of red algae (Rhodymeniales, Ceramiales, Gigartinales, Gracilariales, Halymeniales, Plocamiales, and Nemaliales) with only some species of brown algae (mainly Dictyotales) and green algae (Bryopsidales).

The selection of seaweed hosts by marine invertebrate epifauna based on internal (such as cell structure and cell wall components, energetic storage products, and defensive biochemistry) and external features (morphology) of seaweeds; yet, thallus form has been shown to be a stronger regulator of invertebrate epifauna than palatability or defensive chemistry (Dean and Connell 1987; Norderhaug 2004).

The observations of invertebrate richness across algal morphology, generally, tend to follow common perceptions about relationships between algal thallus complexity and invertebrate diversity (Chemello and Milazzo 2002; Bates 2009; Veiga et al. 2014). Specifically, the complexly branching corticated algae in S1 (like *Cystoseira humilis, C. tamariscifolia, Fucus guiryi, Sargassum vulgare, Gelidium pulchelum,* and *Gelidium spinulosum*) could have the most associated invertebrates providing a more diverse source for the annual recolonisation of *S. muticum*, whereas algae with simple morphology in S2 (like *Grateloupia lanceola, Laurencia obtusa, Osmundea pinnatifida, Gymnogongrus patens, Codium decorticatum,* and *C. tomentosum*) could host the fewest associated invertebrates.

In conclusion, the present investigation revealed that the macro-epifauna associated with the invasive *S. muticum* is more diverse and abundant in the rocky site than in the sandy site throughout seasons except for summer. Furthermore, the structure of epifaunal assemblages associated with this alien macroalga differed significantly between the two study sites. The orientation of the shoreline, the topographic and bottom morphology, and the type of substrate of each beach in addition to the hydrodynamic factors (waves, swells, currents) and the local occurrence of anthropogenic artifacts seem to influence the establishment and the development of *S. muticum,* generating a shift in the life cycle (growth, reproduction, and degeneration periods) between the two sites. This determines, albeit indirectly, the spatiotemporal variability in composition and abundance of the associated macro-epifauna.

Compliance with ethical standards

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