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ORIGINAL ARTICLE

Effects of macroalgal identity on epifaunal assemblages: native species *versus* the invasive species *Sargassum muticum*

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Abstract Seaweeds are a refuge from stressful conditions associated with life on rocky intertidal shores, and there is evidence that different macrophytes support different assemblages of mobile epifauna. Introduction of non-indigenous macroalgae may have a great impact on associated epifaunal assemblages and ecosystem processes in coastal areas. Previous studies have reported conflicting evidences for the ability of epifauna to colonize non-indigenous species. Here, we analyzed epifaunal assemblages associated with three species of macroalgae that are very abundant on intertidal shores along the Galician coast: the two native species *Bifurcaria bifurcata* and *Saccorhiza polyschides* and the invasive species *Sargassum muticum*. We collected samples of each species from three different sites at three different times to test whether variability of epifaunal assemblages was consistent over space and time. Epifaunal assemblages differed between the three macroalgae. Results suggested that stability and morphology of habitat played an important role in shaping the structure of epifaunal assemblages. This study also showed that the invasive *S. muticum* offered a suitable habitat for many invertebrates.

Keywords Epifaunal assemblages · Macroalgae · *Sargassum muticum* · Morphology · Epiphytes · Galician coast

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Introduction

Intertidal rocky shores on temperate latitudes are often dominated by macroalgae that harbor epifaunal assemblages of associated epibiota, i.e., epifauna and epiphytic algae (Schmidt and Scheibling 2006). In particular, epifaunal assemblages are very influenced by marine macroalgae that exist on the coast, because many invertebrates use macroalgae as a refuge from physical stress, protection from predators, and many of them are herbivores that consume epiphytic algae or the host plant itself (Duffy 1990; Bell 1991; Viejo 1999). There is evidence that different macrophytes support different assemblages of mobile epifauna (Cacabelos et al. 2010 and references therein), and this may be due to several biological factors such as life cycles, algal structure (sensu McCoy and Bell 1991; Gee and Warwick 1994), presence of algal epiphytes (Dawes et al. 2000), habitat complexity (Buschbaum et al. 2006; Schreider et al. 2003), chemical defences (Steinberg et al. 1998), or physical factors (e.g., wave exposure or tidal height) (Chemello and Milazzo 2002; Schreider et al. 2003). Behavioral choices of animals may also account for patterns of distribution, with larger abundance of species in their preferred host habitats (Chapman 2000).

Currently, most ecosystems are affected by an increasing rate of biological invasions that may have strong ecological impacts on resident assemblages (Vitousek et al. 1997; Piazzi et al. 2001; Ross et al. 2004). Together with climate change, non-indigenous macroalgae are becoming one of the most important threats to marine biodiversity (Stachowicz et al. 2002), and changes associated with these introductions may have a great impact on associated epifaunal assemblages and ecosystem processes in coastal areas (Jones et al. 1997; Crooks 2002; Schmidt and Scheibling 2006). The magnitude of this effect will depend in part on the ability of epiphytic organisms and free-living epifauna to colonize non-indigenous species (Wikström and Kautsky 2004).

Previous studies have reported conflicting evidences for the ability of epifauna to colonize non-indigenous species. Some studies showed no differences between epifaunal assemblages associated with native and invasive macroalgae (e.g. Viejo 1999; Parker et al. 2001; Edgar and Klumpp 2003), whereas other works found relevant differences (Wernberg et al. 2004; Vázquez-Luis et al. 2008; Prado and Thibaut 2008). In general, most marine invertebrates are associated with multiple macroalgal families as habitats (Hay and Fenical 1988) in contrast with, for example, most species of terrestrial herbivorous insects that show habitat specialization (Fox and Morrow 1981). However, selection of host macroalgae by marine invertebrate is largely dependent upon the identity of the host species (Wernberg et al. 2004; Wikström and Kautsky 2004; Bates 2009).

Sargassum muticum is an invasive species that since 1986 (see Pérez-Cirera et al. 1989) has successfully colonized the shallow subtidal and the low intertidal shores of the Galician coast (northwestern Spain). There, it coexists on exposed and semi-exposed shores with native brown seaweeds such as *Bifurcaria bifurcata* and *Saccorhiza polyschides*, forming mixed stands. Due to intrinsic differences between macroalgae (i.e. structural complexity, phenology, morphology, chemical composition, epiphyte load), we could expect differences in epifaunal assemblages associated.

In this study, purely mensurative, the main aim was to compare the epifaunal assemblages associated with three different macroalgae, the invasive species *S. muticum* and the native species *B. bifurcata* and *S. polyschides.* In addition, we wanted to know whether variability of epifaunal assemblages associated with the three macroalgae was consistent over space and time.

Materials and methods

Study area and sampling design

Sites were located in the lower intertidal zone (0.4–0.8 m above the lowest astronomical tide) on the eastern side of two rias, Ria de Aldan (42°20′N; 8°51′W) and Ria de Vigo (42°10′N; 8°51′W), located in the southern region of the Galician coast, NW Spain (see Gestoso et al. 2010 for detailed description of area). We randomly chose three sites from a pool of available sites with slightly different wave exposure, and dominated by the three macroalgae forming mixed stands. In each site, we randomly collected five replicates of each macroalga, *B. bifurcata*, *S. polyschides*, and *S. muticum*. Each replicate was carefully placed into a plastic bag and taken to the laboratory for further sorting. Using this procedure, we were able to sample motile organisms closely associated with the host macroalga, e.g., gastropods and amphipods. All samples were preserved with 70% ethanol. Each site was sampled in March, April, and July 2006, the period of greatest cover of the three seaweeds.

Laboratory analysis

In the laboratory, the seaweeds were vigorously washed in a bucket containing freshwater and then sieved through 0.5-mm mesh to recover mobile macroinvertebrates. We also scrutinized the entire thalli of macroalgae to find the epibionts attached to them. Then, all organisms collected were identified to the lowest possible taxonomic level using dissecting and light microscopes, counted and placed in 70% ethanol. Epiphytic algae were removed from macroalgae, and both macroalgae and epiphytes were dried at 60°C for 72 h and weighed. Animal abundance was quantified and standardized to numbers per 10 g alga dry weight (without algal epiphytes). In the case of fragmented animals (such as polychaetes), only heads were counted. Animals included in this study were within a size range from roughly 0.3 to 5 cm.

Data analysis

Changes in number of species (S), number of individuals (N) and diversity (H′, Shannon–Wiener index) were analyzed using orthogonal three-factor analyses of variance (ANOVA). The ANOVA model included Time (3 levels; March, April, and July) and Site (3 levels) as random factors, and Habitat (3 levels: *B. bifurcata*, *S. polyschides*, and *S. muticum*) as a fixed factor. When significant differences between main factors or their interactions were found, Student–Newman–Keuls (SNK) tests were used as a posteriori comparison. The homogeneity of variances was examined using Cochran's C-test, and data were transformed when necessary to remove heteroscedasticity (Underwood 1997). In order to investigate the relationship between epiphytic biomass and epifaunal assemblages, Kendall′s coefficient of rank correlation (τ) was calculated for each univariate parameter (N, S, H′) in each macroalga.

Three-factor orthogonal non-parametric multivariate analysis of variance (PERMANOVA) on a Bray–Curtis similarity matrix calculated on square root transformed data was used to test the hypothesis about differences between assemblages associated with the three seaweeds (Anderson 2001). Only significant effects ($P < 0.05$) were further investigated through a series of pairwise comparisons using the appropriate terms in the model. To graphically visualize multivariate patterns in assemblages, non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordination plots. This required plots of the centroids that were calculated from principal coordinates analysis obtained from the full Bray–Curtis dissimilarity matrix among the 45 observations in each habitat (McArdle and Anderson 2001). Euclidean distances were then obtained between each pair of centroids and used as the input matrix for the nMDS. SIMPER analysis (Clarke 1993) was performed to identify the species that mostly contributed to similarity/dissimilarity between the 3 habitats. We obtained the percentage contribution ($\delta_i\%$) of each taxon to the Bray–Curtis dissimilarity between habitats. Species (or taxa) were considered important if their percentage dissimilarity was $\geq 3\%$ (Benedetti-Cecchi and Chato Osio 2007). The ratio $\delta_i/\mathrm{SD}(\delta_i)$ was used to indicate the consistency with which a given taxon contributed to the average dissimilarity in all pairwise comparisons of samples between the two habitats. Values ≥ 1 indicated a high degree of consistency. All the multivariate analyses were performed using PRIMER software package (Clarke and Gorley 2006).

Results

Gastropods were the most abundant group in the three habitats accounting for 27 to 45% of the total abundance (Fig. 1a). Bivalves were the second more abundant group in *B. bifurcata* (Fig. 1b), whereas isopods and polychaetes were the following more abundant groups associated with *S. muticum* and *S. polyschides*, respectively (Fig. 1c, d). Isopods were the less abundant group associated with *B. bifurcata* and *S. polyschides*, whereas bivalves were the less abundant group associated with *S. muticum*.

Univariate analyses

Analyses of variance revealed no significant differences between habitats for number of species, whereas number of individuals and diversity changed across habitats, but inconsistently over time and site (i.e. significant interaction Habitat × Time × Site; Table 1). In general, number of individuals was larger in *S. polyschides* than in the other two macroalgae, with a peak of abundance than varied temporally in each site (Fig. 2a). Whereas in *S. muticum*, abundance peaked in July, in all sites (SNK tests, $P < 0.05$), abundance in *B. bifurcata* did not show significant temporal variability (Table 1; Fig. 2a). Diversity showed a significant tendency to increase in July for epifaunal assemblages associated with *S. muticum* and *S. polyschides* (SNK test, $P < 0.05$), but in general *B.*, *bifurcata* was the most diverse habitat (Fig. 2b).

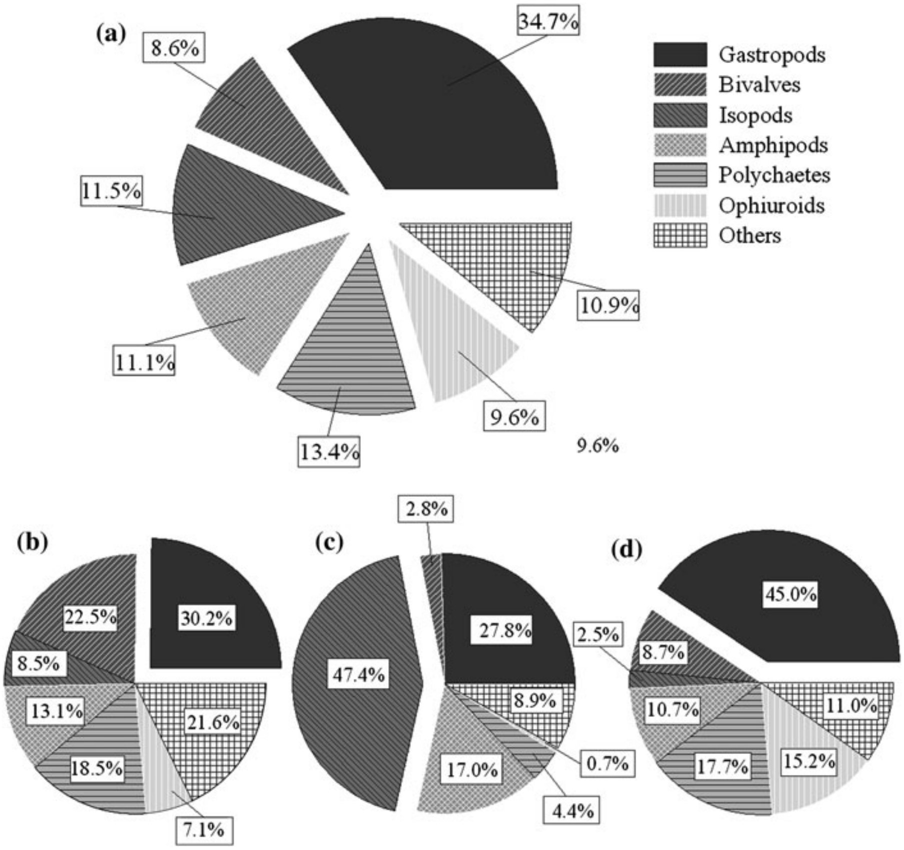

Fig. 1 Percentage of most abundant groups found in epifaunal assemblages. **a** Total percentage of main taxa in the three habitats; **b** percentage of main taxa associated with *Bifurcaria bifurcata*; **c** percentage of main taxa associated with *Sargassum muticum*; and **d** percentage of main taxa associated with *Sacchoriza polyschides*

Table 1 Univariate analyses of variance (ANOVA) of number of species (S), number of individuals (N), and Shannon diversity index (H′) ($n = 5$)

Source	*df*	S		N		H′	
		F	*P*	*F*	*P*	*F*	*P*
T	2	0.364	0.713	6.534	0.358	1.272	0.373
S	2	1.410	0.342	0.099	0.913	1.126	0.435
H	2	0.172	0.849	0.667	0.610	0.102	0.905
T × S	4	3.141	0.079	0.604	0.671	1.358	0.329
T × H	4	1.785	0.225	0.945	0.486	3.269	0.072
S × H	4	1.433	0.307	1.126	0.409	1.415	0.313
T × S × H	8	1.345	0.229	2.777	0.008	1.987	0.055
Res	108						
Total	134						
Cochran's *C* test		$C = 0.7170$ ($P < 0.01$)		$C = 0.1699$ ($P < 0.05$)		$C = 0.1513$ (not significant)	
Transformation		Ln(x)		Sqrt($x + 1$)		None	

Time (3 levels, random, orthogonal), Site (3 levels, fixed orthogonal), and Habitat (3 levels, fixed, orthogonal)

Time = T, Site = S, Habitat = H

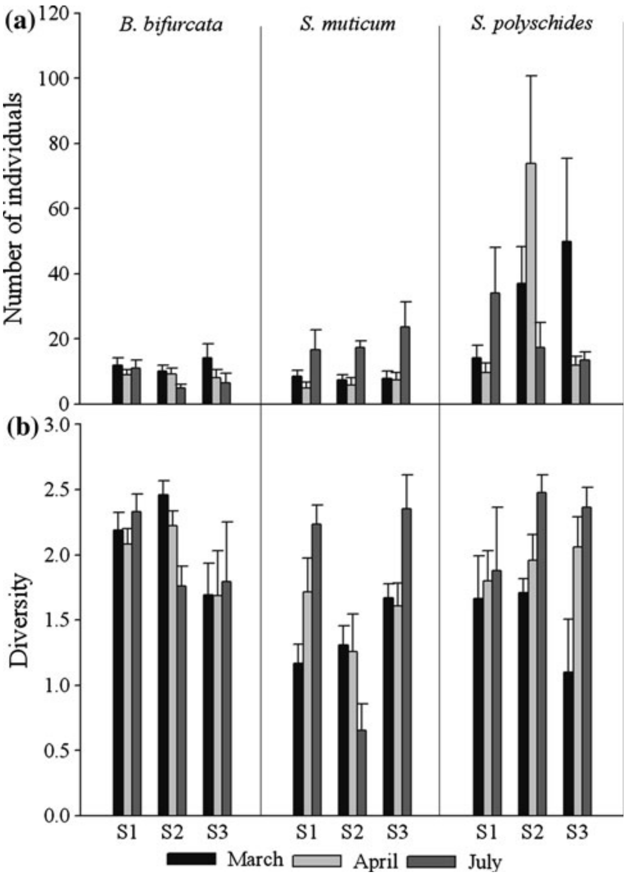

Fig. 2 Mean (+SE, $n = 5$) of **a** number of individuals; and **b** diversity of epifaunal assemblages associated with *Bifurcaria bifurcata*, *Sargassum muticum* and *Saccoriza polyschides* in March, April, and July in each site. Data were standardized per 10 g dry weight of alga

Epiphytic biomass varied among habitats, although the greatest biomass was found in *S. polyschides* (Fig. 3). There was a significant positive correlation between the epiphytic biomass and the number of species, number of individuals and diversity in *S. muticum* and *S. polyschides*, although correlation values were low. Correlations were generally higher in *S. polyschides* (number of species, $\tau = 0.414$; number of individuals, $\tau = 0.333$; diversity, $\tau = 0.455$; $P < 0.01$; $n = 45$) than in *S. muticum* (number of species, $\tau = 0.239$, $P < 0.05$; number of individuals, $\tau = 0.512$, $P < 0.01$; diversity, $\tau = 0.237$, $P < 0.05$; $n = 45$).

Multivariate analyses

There was variation among epifaunal assemblages associated with the three macroalgae, but such variation was not consistent across space and time (i.e., significant interaction Time × Site × Habitat; Table 2). In general, epifaunal assemblages differed between the three macroalgae in all sites over time (Fig. 4), although such differences were not significant in only one site during April (pairwise test, $P > 0.05$; Table 2). SIMPER analysis (Table 3) showed high average dissimilarities between the three habitats (*B. bifurcata* and *S. muticum* = 87.44; *B. bifurcata* and *S. polyschides* = 92.19; *S. muticum* and *S. polyschides* = 95.57). *Dynamene bidentata* was the species that mostly contributed to dissimilarity between *B. bifurcata* and *S. muticum* and *S. muticum* and *S. polyschides*, whereas *Bittium reticulatum* was the most important species contributing to dissimilarity between *B. bifurcata* and *S. polyschides* (Table 3).

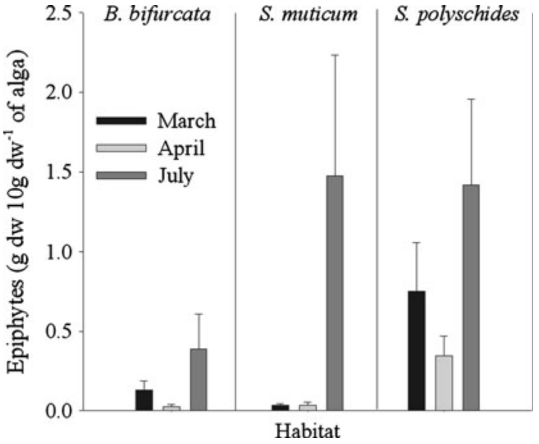

Fig. 3 Mean dry weight of alga (+S.E., $n = 15$) of biomass of epiphytes associated with the three habitats over time. Data were standardized per 10 g dry weight of alga

Table 2 Non-parametric multivariate analysis of variance (PERMANOVA) examining similarities between epifaunal assemblages ($n = 5$)

Source	*df*	Pseudo-F	*P* (perm)
T	2	2.3208	0.003
S	2	2.8155	0.001
H	2	3.6431	0.001
T × S	4	2.3420	0.001
T × H	4	2.2785	0.001
S × H	4	1.7521	0.004
T × S × H	8	1.5173	0.001
Res	108		
Total	134		

Time (3 levels, random, orthogonal), Site (3 levels, random, orthogonal), and Habitat (3 levels, fixed, orthogonal)

Pairwise tests for pairs of levels of factor Habitat. Only non-significant results are shown: L3 in April: *P* (perm) = 0.063

Time = T, Site = S, Habitat = H

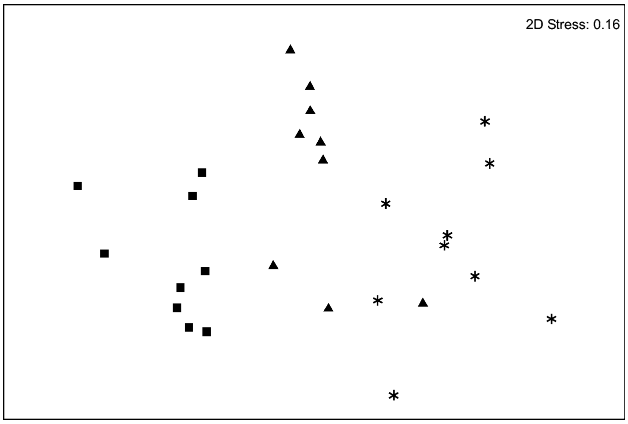

Fig. 4 Non-metric multidimensional scaling (nMDS) for epifaunal assemblages associated with the three macroalgae ($n = 5$). Centroids of *Sargassum muticum* (*asterisk*), *Bifurcaria bifurcata* (*filled triangle*), and *Saccorhiza polyschides* (*filled square*)

Table 3 SIMPER analysis showing the contribution ($\overline{\delta}_i$) of individual taxa to the average Bray–Curtis dissimilarity between *Bifurcaria bifurcata*, *Sargassum muticum*, and *Saccorhiza polyschides* ($n = 45$)

Taxon	Average abundance		$\overline{\delta}_i$	$\overline{\delta}_i$%	$\overline{\delta}_i$/SD(δ_i)
	B.bifurcata	*S. muticum*			
Dynamene bidentata	0.62	4.52	19.85	22.70	1.13
Mytilus galloprovincialis	1.09	0.20	5.67	6.49	0.68
Bittium reticulatum	0.92	0.49	5.36	6.13	0.79
Cingulopsis fulgida	0.19	0.93	4.68	5.36	0.74
Nematoda	0.57	0.20	3.48	3.98	0.71
Rissoa parva	0.34	0.56	3.32	3.80	0.72
Caprella pernantis	0.03	0.56	3.21	3.67	0.46
Capitellidae	0.61	0.03	3.20	3.66	0.44
	B.bifurcata	*S. polyschides*			
Bittium reticulatum	0.92	8.49	9.79	10.62	0.74
Mytilus galloprovincialis	1.09	1.77	6.66	7.23	0.60
Sabellidae	0.10	3.20	6.56	7.11	0.80
Ophiotrix fragilis	0.02	2.83	5.39	5.85	0.68
Rissoa parva	0.34	1.60	5.12	5.55	0.45
Amphiura securigera	0.32	1.84	4.44	4.82	0.74
	S. muticum	*S. polyschides*			
Dynamene bidentata	4.52	0.04	15.48	16.20	1.00
Bittium reticulatum	0.49	8.49	8.83	9.24	0.65
Sabellidae	0.05	3.20	6.43	6.73	0.78
Rissoa parva	0.56	1.60	5.43	5.68	0.47
Ophiotrix fragilis	0.01	2.83	5.31	5.56	0.66
Mytilus galloprovincialis	0.20	1.77	4.87	5.09	0.46
Cingulopsis fulgida	0.93	0.80	3.82	4.00	0.73
Amphiura securigera	0.10	1.84	3.79	3.97	0.71

Discussion

In line with our prediction, epifaunal assemblages differed between the three macroalgae. Differences mainly due to changes in abundance of individuals of each species and composition of the main faunistic groups were generally consistent over space and time. Our results are, therefore, in agreement with previous studies that have found differences in composition and structure of epifaunal assemblages associated with native and invasive macroalgae (Wernberg et al. 2004; Vázquez-Luis et al. 2008; Prado and Thibaut 2008).

The total number of individuals and diversity associated with the three macroalgae differed. In general, *S. polyschides* had the largest number of individuals, whereas *B. bifurcata* had the greatest diversity. Several studies have pointed out that number of individuals and identity of species in epifaunal assemblages are related to morphology and/or structural complexity of macroalgae (Taylor and Cole 1994; Wernberg et al. 2004; McDonald and Bingham 2010). Here, the fact that the number of individuals was larger *in S. polyschides* could be in part due to the complex structure of *S. polyschides* holdfast. The holdfast of this species has a bulbous structure with a complex internal channeling system and so considerable intersticial space for epifauna (McKenzie and Moore 1981). In contrast, *B. bifurcata* and *S. muticum* have more simple holfasts; the holdfast of *B. bifurcata* is composed of intertwined rhizoidal growths, whereas *S. muticum* has a disk-shape holdfast (Hiscock 1979; Critchley et al. 1990). Not only number of individuals but also identity of epifaunal species could be influenced by differences in the structure of holdfasts (see Arroyo et al. 2004).

Differences in biomass of epiphytes could also account for patterns of abundance of epifauna. In fact, previous studies have indicated a positive correlation between biomass of epiphytes and free-living epifauna (Worm and Sommer 2000; Parker et al. 2001; Wikström and Kautsky 2004). An increase of epiphyte load might increase food resources or complexity of macroalgal habitat affecting the composition and abundance of epifauna. The trophic role of epiphytes over the increase in structural complexity could be important in increasing diversity of different taxa such as gastropods, isopods, or amphipods (Viejo 1999). For example, the herbivorous isopod *D. bidentata* that was the most abundant species associated with *S. muticum* showed a peak of abundance in July, matching the peak of epiphytic algae. The importance of epiphytic load as food resource for herbivorous and omnivorous taxa has been previously highlighted (Bologna and Heck 1999). In contrast, the role of epiphytes in habitat structure seems to play only a limited role in determining the density of most mobile epifauna, although it appears to be important in augmenting the settlement of bivalves (Bolongna and Heck 1999).

Multivariate analysis indicated that structure of epifaunal assemblages differed between macroalgae. Previous works obtained similar results when comparing how different species of macroalgae modulated abundance, species richness and diversity of assemblages associated (Taylor and Cole 1994; Chemello and Milazzo 2002). In addition, several studies found differences in composition and structure of epifaunal assemblages associated with native and invasive macroalgal species (Wernberg et al. 2004; Wikström and Kautsky 2004; Schmidt and Scheibling 2006; Harries et al. 2007; Vazquez-Luis et al. 2008). Here, native species supported a similar proportion of the most abundant taxa (see Fig. 3), whereas the invasive species supported basically 3 main taxa (i.e. gastropods, isopods and amphipods). Nevertheless, epifaunal assemblages associated with the two native species were more dissimilar than those associated with the native *B. bifurcata* and the invasive *S. muticum* in terms of species composition and abundance. Thus, other factors rather than the origin of species (i.e. native vs invasive) seemed to play a more important role. For example, the larger abundance of isopods and amphipods in *S. muticum* might respond to certain mechanism of host selection, because many species of these groups remain in constant contact with surfaces and associate preferentially with microhabitats that closely match their body size (Viejo 1999; Parker et al. 2001). Nevertheless, this assumption has to been taken with caution, because in marine habitats small herbivores tend to be generalists and very few species are host plant specialists (Hay and Steinberg 1992; McDonald and Bingham 2010).

Morphology and complexity of macroalgae might also be important factors in shaping the structure of these assemblages and determining habitat choice (see Schreider et al. 2003; Wernberg et al. 2004; Schmidt and Scheibling 2006; Cacabelos et al. 2010). For example, certain crustaceans are more abundant in branched macroalgae than in macroalgae with a foliose morphology (McDonald and Bingham 2010). *B. bifurcata* and *S. muticum* have similar morphology in comparison with *S. polyschides*, and thus, we could expect that epifaunal assemblages associated with these species were more similar. On the other hand, habitat stability (as influenced by habitat longevity) could be also an important factor affecting habitat selection in some crustaceans (Duffy and Hay 1991; Wernberg et al. 2004). In this case, *B. bifurcata* and *S. muticum* with monophasic life cycles (Jensen 1974; Britton-Simmons 2004) offered a more stable habitat than *S. polyschides* with a biphasic life cycle (Bartsch et al. 2008).

In summary, epifaunal assemblages varied among the three macroalgae. Nevertheless, assemblages associated with the native *B. bifurcata* and the invasive *S. muticum* were more similar than those associated with *S. polyschides*. These results suggested that stability and morphology of habitat played an important role in shaping the structure of epifaunal assemblages. Results suggest that the impact of *S. muticum* invasion on the epifaunal assemblages depends on the similarities between the invasive and the local seaweeds, but it is also related to the impact of the invasion on the macroalgal assemblages. Here, the invasive *S. muticum* offered a suitable habitat for many invertebrates especially gastropods and isopods. The consequences of these qualitative and quantitative changes of epifauna are unknown, although they could alter the structure and trophic dynamic of the system since invertebrates inhabiting macroalgae are the prey of omnivorous fishes and decapods (Williams 1992). Nevertheless, the effects of introduction of *S. muticum* on the epifauna may be different among sites, depending on the type of native macroalgae and their abundance.

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