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Variability of epifaunal assemblages associated with native and invasive macroalgae

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Abstract. Marine macroalgae harbour abundant and diverse assemblages of epifauna. Patterns of distribution and abundance of epifauna, which are often variable in space and time, differ markedly among macroalgae species. Non-indigenous seaweeds may alter composition and structure of epifaunal assemblages and therefore harbour different assemblages from those associated with native macroalgae. In this study, we analysed the epifaunal assemblages associated with the native algae *Bifurcaria bifurcata* and the invasive alga *Sargassum muticum* on the southern part of the Galician coast (north-west Spain). In particular, we tested the hypothesis that there were differences in the epifaunal assemblages associated with the native and invasive algae. We used a hierarchical spatial sampling design to identify if these differences were consistent over space and time. Results indicated that there were significant differences between epifaunal assemblages associated with both algae. The fact that such differences were, in general, consistent at different spatial scales suggests that biological factors related to the specific habitat might play a more important role than physical factors as determinants of epifaunal distribution. This study also showed that *S. muticum* seems to supply a new and additional habitat for the native epifauna, contributing to increases in the spatial and temporal variability of epifaunal assemblages.

Additional keywords: epifaunal assemblages, epiphytes, Galician coast, invasive and native macroalgae, *Sargassum muticum*, spatio–temporal variability.

Introduction

Marine macroalgae are conspicuous and dominant features of temperate intertidal and subtidal ecosystems, and have important direct and indirect effects on coexisting species (Schmidt and Scheibling 2006). Macroalgae are considered ecosystem engineers because they add spatial complexity to the substratum, modulating availability of resources, and can affect assemblages of associated epibiota, i.e. epifauna and epiphytic algae (Schmidt and Scheibling 2006). In particular, epifaunal assemblages are strongly influenced by marine macroalgae that exist on the coast, because they 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). These epifaunal assemblages often undergo marked spatial and temporal fluctuations owing to a range of physical and biological factors (Caine 1991; Taylor 1998).

Although low host specificity exists between epifaunal invertebrates and their habitat-forming macroalgae (Duffy and Hay 1991; Viejo 1999), many factors such as longevity, cell-wall structure, surface texture, presence of algal epiphytes or presence of allelopathic substances of macroalgae may affect the distribution of free-living epiphytal fauna (Steinberg *et al.* 1998; Dawes *et al.* 2000; Bates 2009). The patterns of distribution and abundance of epifauna are, therefore, very variable among marine macroalgae (see Viejo 1999). For example, phenolic compounds in brown algae are associated with chemical defence against grazers, bacterial, fungal and larval colonisation and epiphytism (Le Lann *et al.* 2008), and they play an important role in shaping patterns of associated assemblages of epifauna (Wikström and Kautsky 2004). Complexity has also been reported as an important factor influencing the composition and structure of epifaunal assemblages associated with different macroalgae (Viejo 1999; Buschbaum *et al.* 2006).

Biological invasions by non-indigenous species can have strong ecological impacts on resident assemblages by changing population dynamics, assemblage structure and ecosystem processes (e.g. Vitousek *et al.* 1997; Piazzi *et al.* 2001; Ross *et al.* 2004; Cummings and Williamson 2008). One of the central questions in invasion research is to what extent an invader might modify biodiversity and ecosystem processes in the native assemblages. Non-indigenous seaweeds may alter composition and structure of epifaunal assemblages and therefore, harbour different assemblages from those associated with native macroalgae (Jones *et al.* 1997; Crooks 2002; Schmidt and Scheibling 2006). The magnitude of this effect depends in part on the ability of epiphytic organisms and free-living epifauna to colonise the non-indigenous species (Wikström and Kautsky 2004). Previous studies on macroalgal invasions have reported conflicting evidence for the ability of epifauna to colonise non-indigenous

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species. Many studies conclude that epiphytal assemblages associated with invasive and native macroalgae are similar, whereas other studies found relevant differences (Wernberg *et al.* 2004; Prado and Thibaut 2008; Vázquez-Luis *et al.* 2008). For example, the invasive alga *Caulerpa taxifolia* harboured different epiphytal assemblages from those on *Zostera capricorni*, but such differences were inconsistent spatially and temporally (Prado and Thibaut 2008). In contrast, epifaunal assemblages associated with the invasive alga *Sargassum muticum* were similar to those associated with native species (Viejo 1999).

Sargassum muticum is an invasive species that since 1986 (see Pérez-Cirera *et al.* 1989) has successfully colonised most of the Galician rias (*sensu* Vilas *et al.* 2005). The rapid spread of *S. muticum* on the Galician coast might have important effects on the composition and structure of native assemblages on rocky shores and sandy beaches (via stranded seaweed). For example, although the impact of *S. muticum* on macroalgal assemblages of rocky shores was limited, the total number of native species and some morpho–functional groups, such as filamentous and foliose algae, were negatively affected by its presence (Olabarria *et al.* 2009). On sandy beaches, this invasive species might alter the food web, as previous results show that it modified temporal food supply when the native brown seaweeds were absent (Rossi *et al.* 2010). So far, there have been no studies dealing with the diversity of epifaunal assemblages associated with invasive and native macroalgae in this area. *S. muticum* can provide a new seaweed habitat for the local epifaunal assemblages, and mobile invertebrates might colonise it if they select it against native seaweed habitats, creating new assemblages with different composition and structure.

Here, we analysed the epifaunal assemblages associated with the native alga *Bifurcaria bifurcata* and the invasive alga *S. muticum*. Both macroalgae, belonging to the family Sargassaceae, are widespread on the Galician coast and dominate the low rocky shore of the intertidal area, forming mixed stands. *B. bifurcata* is a perennial alga, whereas *S. muticum* has a pseudo-perennial cycle comprising one period of growth with two different phases; a winter phase with a moderate growth rate and a faster growth phase during spring (Wernberg *et al.* 2004). The lateral branches of this species detach in summer and early autumn, leaving only a short perennial stipe from which branches regenerate during the following spring. Both species differ slightly in morphology, but they have similar structural complexity.

In particular, we tested the hypothesis that epifaunal assemblages associated with the two macroalgae species differed. In addition, we used a hierarchical spatial sampling design over a variety of spatial scales, ranging from metres to tens of kilometres, to identify whether these differences were consistent over space and time.

Material and methods

Study area and sampling design

Our study 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 18 km apart in the southern region of the Galician coast (Fig. 1). The sampling design included three scales of spatial variability, ranging from metres within a shore to tens of kilometres between rias. Within each ria, we chose three locations 1.5–3 km apart. Locations varied slightly in terms of wave exposure, ranging from semi-exposed to sheltered locations (Alvarez-Salgado *et al.* 1993). Within each location, we selected two sites 10–40 m apart. At each site, we randomly collected five replicates of each macroalga, *Bifurcaria bifurcata* and *Sargassum 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 two seaweeds.

Laboratory analysis

In the laboratory, the seaweeds were vigorously washed in a bucket containing fresh water and then sieved through 0.5-mm mesh to recover mobile macroinvertebrates. We also scrutinised the 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 standardised to numbers per 10 g dry weight of alga (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 ~0.3 to 5.0 cm.

Data analysis

Changes in number of individuals (N), number of species (S) and diversity (H′, Shannon–Wiener index) were analysed using univariate analyses of variance (ANOVA). The ANOVA model included five orthogonal factors: Time = T (3 levels, random, orthogonal); Ria = R (2 levels, random, orthogonal), Location = L (3 levels, random, nested withinn Ria), Site = S (2 levels, random, nested within Location), and Habitat = H (2 levels, fixed, orthogonal). When significant differences among main factors or their interactions were found, Student–Newman–Keuls (SNK) tests were used as *post hoc* comparisons of factors. The homogeneity of variances was examined using Cochran's C-test (Winer *et al.* 1991) and data were square-root transformed when necessary to remove heteroscedasticity (Underwood 1997). In addition, effects of epiphytic algae on the number of individuals, species and diversity were tested using analyses of covariance (ANCOVA), with the same factors used for ANOVA and biomass of epiphytic algae as covariate. These analyses were undertaken only if all assumptions were met (Underwood 1997). For these analyses, we used SPSS software (version 16.0; SPSS Inc., Chicago, IL, USA).

Five-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 among assemblages associated with the two seaweeds (Anderson 2001). The model included the same five factors used for ANOVA (see above). Only

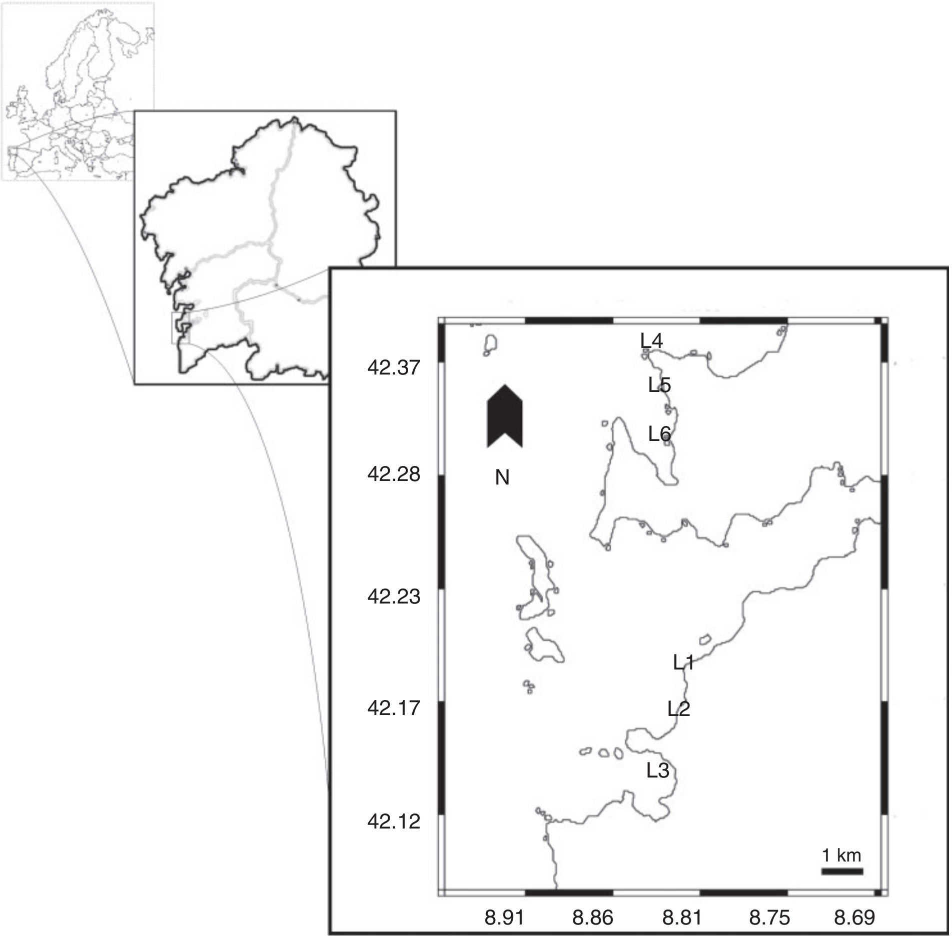

Fig. 1. The study area locations within two rias on the Galician Coast of Spain. L1, Canido; L2, Cabo Estai; L3, Monte Lourido; L4, Cabo Udra; L5, Areas de Bon; L6, Menduiña.

significant effects ($P < 0.05$) were further investigated through a series of pairwise comparisons using the appropriate terms in the model. To visualise multivariate patterns in assemblages, non-metric multidimensional scaling (nMDS) was used to produce two-dimensional ordination plots. Centroids of the five replicates of each habitat were calculated from principal coordinates analysis (McArdle and Anderson 2001) of the full Bray–Curtis matrix similarity matrix among the 360 observations. 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 or dissimilarity between the two 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 δ_i/s.d. (δ_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 greater than or equal to 1 indicated a high degree of consistency. All the multivariate analyses were performed using the PRIMER software package (Clarke and Gorley 2006).

Results

A total of 40 866 individuals belonging to 126 taxa were identified in both habitats (see Accessory publication). Gastropods were consistently the most abundant group associated with both macroalgae across space and time, followed by isopods, amphipods and bivalves. Crustaceans were more abundant in *S. muticum* habitats, whereas bivalves were more abundant in *B. bifurcata* habitat. Ampithoids were the most important family of the amphipods, and they had a peak of abundance in *S. muticum* in July.

Univariate analysis

The number of individuals varied significantly between habitats, but inconsistently over space and time (Table 1). There were more individuals associated with *B. bifurcata* than with *S. muticum* at all locations during March and April (except for location 6 in April; Fig. 3*a*). In July, the opposite occurred, with

Table 1. Univariate analysis of variance (ANOVA) of number of individuals (N), Shannon diversity index (H′), and number of species (S) ($n = 5$)
*Degrees of freedom of the error could not be computed with the Satterthwaite method. T, Time; R, Ria; L, Location; S, Site; H, Habitat

Source	d.f.	N		H′		S	
		F	*P*	*F*	*P*	*F*	*P*
T	2	1.30	0.389	1.04	0.441	1.63	0.323
R	1	0.32	0.606	0.01	0.944	0.00	0.999
H	1	0.14	0.740	1.06	0.449	0.01	0.924
L(R)	4	3.65	0.253	5.49	0.308	7.57	0.218
T × R	2	0.95	0.498	13.19	0.688	3.07	0.259
H × T	2	23.29	**0.041**	8.46	0.106	530.39	**0.002**
H × R*	1			8.76	0.147		
S(L(R))	6	1.25	0.357	0.70	0.655	0.76	0.624
T × L(R)	8	0.84	0.579	0.51	0.827	1.60	0.247
H × L(R)	4	0.21	0.918	1.24	0.369	0.35	0.839
H × T × R	2	0.14	0.865	0.28	0.760	0.02	0.982
T × S(L(R))	12	5.78	**0.002**	2.77	**0.045**	1.71	0.183
H × S(L(R))	6	0.83	0.568	2.34	0.099	3.40	**0.034**
H × T × L(R)	8	3.10	**0.038**	2.25	0.099	2.29	0.094
H × T × S(L(R))	12	0.40	0.964	1.18	0.300	0.91	0.533
Residual	288						
Total	359						

more individuals associated with *S. muticum* at almost all locations (but see location 2 and location 6; Fig. 3*a*). Such spatio–temporal variation was removed by adjusting the values to the influence of the biomass of epiphytes (ANCOVA, $F_{8,12} = 1.42$, $P > 0.05$; Fig. 3*b*). The number of species also varied significantly between habitats, but this variation was not consistent from time to time (Table 1; Fig. 3*c*) or across sites (Table 1; Fig. 3*d*). There were more species in *B. bifurcata* than in *S. muticum* at all times except for July, when the pattern was reversed (Fig. 3*c*); however, the number of species associated with each species varied across sites, and was not always larger in *B. bifurcata* (Fig. 3*d*). This pattern remained the same after adjusting the values to the influence of the biomass of epiphytes, indicating that this variable had no effect on the number of species. In contrast, the diversity did not change significantly between habitats (Table 1).

Table 2. Non-parametric multivariate analysis of variance (PERMANOVA) examining similarities between epifaunal assemblages ($n = 5$)
T, Time; R, Ria; L, Location; S, Site; H, Habitat

Source	d.f.	Pseudo-*F*	*P*(perm)
T	2	3.17	**0.001**
R	1	1.47	0.051
H	1	5.86	**0.001**
L(R)	4	2.44	**0.001**
T × R	2	1.64	**0.033**
T × H	2	2.74	**0.002**
R × H	1	1.10	0.339
S(L(R))	6	1.37	**0.027**
T × L(R)	8	1.32	**0.031**
L(R) × H	4	1.31	**0.027**
T × R × H	2	0.94	0.535
T × S(L(R))	12	1.99	**0.001**
S(L(R)) × H	6	1.19	0.152
T × L(R) × H	8	1.58	**0.002**
T × S(L(R)) × H	12	1.32	**0.006**
Residual	288		
Total	359		

Pairwise tests for pairs of levels of factor Habitat.
Only non-significant results are shown: L6 in March, S2: *P*(perm) = 0.123; L1 in April, S2: *P*(perm) = 0.097; L3 in April, S1: *P*(perm) = 0.066; L5 in March, S1: *P*(perm) = 0.051; L4 in March, S2: *P*(perm) = 0.066.

Multivariate analysis

The epifaunal assemblages varied significantly between habitats, but this variation was not consistent spatially and temporally (Table 2; Fig. 2). *A posteriori* pairwise tests done on these interactions showed that the only epifaunal assemblages that did not differ significantly between habitats were those from one of the sites at location 6 in March and one site at location 1 and one at location 3 in April (Table 2; Fig. 1). In addition, the epifaunal assemblages associated with the two habitats of one site at location 4 and another site at location 5 in March were marginally non-significant. The two-dimensional MDS plots showed a moderate segregation of habitats at all sampling times (Fig. 2).

SIMPER analysis identified nine taxa as important (i.e. contributing to ≥3% of percentage dissimilarity) in discriminating between the habitat *S. muticum* and the habitat *B. bifurcata* (Table 3). *Dynamene bidentata* was more abundant in *S. muticum* than in *B. bifurcata*, and together with *Barleeia unifasciata*, *Cingulopsis fulgida* and *Rissoa parva* were the most important species shaping differences in epifaunal assemblages associated with the two habitats. In contrast, *Bittium reticulatum*, bivalves of the family Mytilidae, and the Nematoda were the most important taxa in *B. bifurcata*. The amphipod *Amphitholina cuniculus* was only found in *B. bifurcata*, and the echinoderm *Amphipholis squamata* was much more abundant in *B. bifurcata* than in *S. muticum* (Accessory publication).

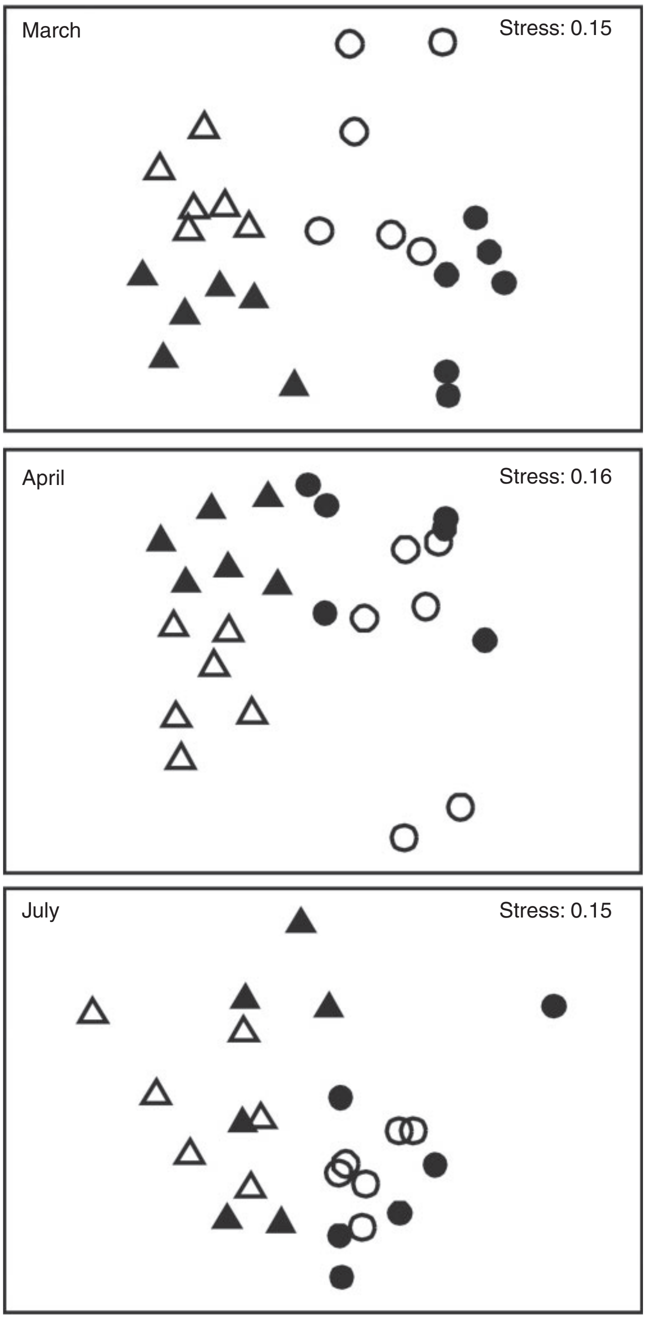

Fig. 2. Non metric multidimensional scaling (nMDS) for epifaunal assemblages associated with the two habitats in each ria at different sampling times (March, April and July) ($n = 5$). ○, *Sargassum muticum* Ria Aldan; ●, *Sargassum muticum* Ria Vigo; △, *Bifurcaria bifurcata* Ria de Aldan; ▲, *Bifurcaria bifurcata* Ria de Vigo.

Discussion

Epifaunal assemblages and habitat specificity

There were significant differences between epifaunal assemblages associated with the native and the invasive seaweed. Nevertheless, this pattern varied across space and time, although in just a few cases. This sporadic spatial and temporal variability in assemblages could be owing in part to some physical and/or biological factors operating at a small spatial scale, i.e. sites. Predation, for example, has been suggested to exert a major influence on epifaunal assemblages in macrophyte beds, and presumably it can vary at a small spatial scale, affecting individual epifaunal species (Edgar and Klumpp 2003). Changes in nutrient availability might also affect the epiphytic load of algae and, indirectly, induce changes in the epifaunal assemblages (see Viejo 1999; Wikström and Kautsky 2004).

In general, the composition of epifaunal assemblages differed between habitats in terms of abundance rather than composition of species. None of the associated epifaunal species was exclusively found in *S. muticum* or *B. bifurcata* habitats, apart from the amphipod *A. cuniculus*, which was only associated with *B. bifurcata*. Moreover, some isopod and amphipod species were much more abundant in *S. muticum* than in *B. bifurcata*. Although the epifaunal assemblages differed between habitats, there were no clear host-plant specialists. However, the differences in the distribution of abundances of epifauna between the two habitats suggest the presence of some mechanisms of host selection. For example, the larger abundance of isopods and amphipods in *S. muticum* might reflect some form 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). This assumption has to be made with caution, however, because further experimental work would be necessary to test hypotheses related to preferences, specificity and choice of habitats (see Olabarria *et al.* 2002). Several studies have reported that low specificity of epifauna to the host plant is quite common in marine systems dominated by macroalgae, presumably because few marine epifaunal organisms live and feed directly on host tissues (Arrontes 1999; Wikström and Kautsky 2004; Prado and Thibaut 2008). In contrast, some studies have reported strong host specificity, likely determined by specific chemical, structural and morphological characteristics of the algal species (Hay *et al.* 1987; Edgar and Klumpp 2003; Schmidt and Scheibling 2006), with the identity of the host species being more important when abiotic conditions were stressful (e.g. Lilley and Schiel 2006; Bates and DeWreede 2007). For example, removal of a dominant canopy-forming algal species on shores exposed to thermal stress had a significant influence on epifaunal assemblages (Lilley and Schiel 2006).

The similar composition of epifaunal species in both habitats could be partly explained by the similar complexity of the two habitats. In fact, one mechanism by which macroalgae might influence their associated epifaunal assemblages is through the provision of complex habitats (Taylor and Cole 1994; Buschbaum *et al.* 2006). Species diversity has been correlated with habitat complexity in a variety of systems, and increased epifaunal densities have often been related to the presence of seaweeds in many marine seagrass meadows (Orth 1992; Parker *et al.* 2001). In our study, diversity did not vary between the two habitats; only the number of individuals and the number of species. Despite both macroalgae having similar complexity, they are functionally different because *S. muticum* has a perennial holdfast that produces an annual vegetative thallus, whereas *B. bifurcata* is a truly perennial macroalga. They also differ slightly in morphology, as *S. muticum* is frondose whereas

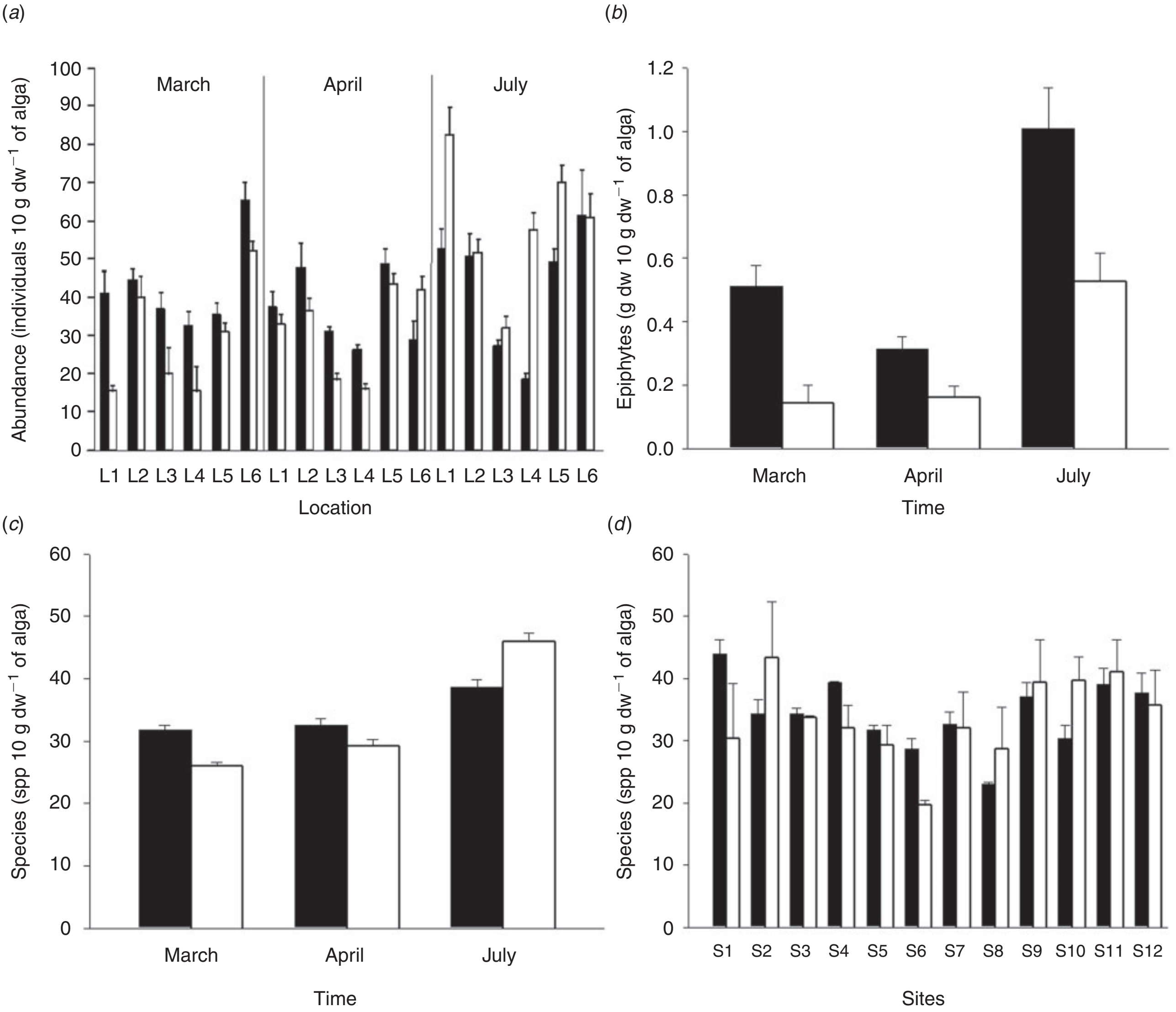

Fig. 3. Mean (per 10 g dry weight of alga +s.e., $n = 5$) of (*a*) abundance of individuals associated with the two habitats at each location (L1–L6) over time; (*b*) biomass of epiphytes (g dry weight) associated with the two habitats over time; (*c*) number of species associated with the two habitats over time; (*d*) number of species associated with the two habitats at each site (S1–S12). ■, *Bifurcaria bifurcata*; □, *Sargassum muticum*.

B. bifurcata is a cylindrical alga. Although temporal stability of habitats has not been considered as an important factor for structure of epifaunal assemblages (Wernberg *et al.* 2004), the different strategies (pseudo-perennial in *S. muticum* and perennial in *B. bifurcata*) and associated habitat provision for epibiota might have an effect on the occurrence and abundance of associated organisms. This hypothesis requires further experimental work in the field.

Epiphytes

The biomass of epiphytes was always greater in *B. bifurcata* than in *S. muticum* (Fig. 3*b*) and influenced the number of individuals associated with these two habitats. Thus, biomass of epiphytes might be an important variable in determining the structure of epifaunal assemblages. Earlier studies have demonstrated a positive correlation between biomass of epiphytes and free-living epifauna, showing that the epiphyte cover might affect the amount of free-living epifauna that can be supported by a seaweed (Worm and Sommer 2000; Parker *et al.* 2001; Wikström and Kautsky 2004). In our study, the effects of the invasive species on composition and structure of epifaunal assemblages was more important in July. In this month, the number of species and the number of individuals increased considerably in *S. muticum* habitat, showing an opposite pattern to those in March and April. This increase matched the peak of biomass of epiphytes in *S. muticum*. As *S. muticum* is less palatable than *B. bifurcata* (i.e. greater phenolic content in *S. muticum*: Le Lann *et al.* 2008), an increasing epiphyte load may favour the colonisation of *S. muticum* by mobile invertebrates, mostly mesograzers (i.e. many amphipods, isopods and gastropods). In fact, many mesograzers and amphipods prefer feeding on epiphytic species (Wikström and Kautsky 2004). Senescence of *S. muticum* plants

Table 3. SIMPER analysis showing the contribution (δ_i) of individual taxa to the average Bray–Curtis dissimilarity between *Bifurcaria bifurcata* and *Sargassum muticum* ($n = 5$)

Taxon	Average abundance		δ_i	δ_i%	δ_i/s.d. (δ_i)
	Bifurcaria bifurcata	*Sargassum muticum*			
Dynamene bidentata	2.15	5.16	5.37	6.99	1.09
Barleeia unifasciata	2.21	3.79	4.50	5.86	1.18
Cingulopsis fulgida	1.49	3.72	4.32	5.63	1.16
Bittium reticulatum	2.77	1.36	3.69	4.81	1.01
Rissoa parva	2.28	2.61	3.51	4.58	1.10
Mytilus galloprovincialis	2.53	0.52	3.42	4.45	0.89
Nematoda	2.14	1.35	2.91	3.79	1.07
Musculus costulatus	2.10	1.02	2.87	3.74	0.92
Amphitoe sp.	0.41	2.09	2.43	3.17	0.98

in July, and consequently a decrease of the phenolic content, might also favour greater colonisation by epiphytic species and grazers than in previous months. This increasing epiphyte load could, as a consequence, increase the structural complexity of the habitat, and therefore might reduce the susceptibility to predation or simply increase the living space (Duffy and Hay 1991; Edgar 1992; Viejo 1999, and references therein). Some authors have, however, argued that temporal fluctuations in patterns of abundance of epifaunal assemblages associated with macroalgae might be more related to the presence of predatory fish (Aoki 1988). In this study, we cannot rule out a potential role of predatory fish in shaping patterns of abundance of epifauna, but this hypothesis requires experimental work in the future.

In summary, the invasive alga *S. muticum* was successfully colonised by epifauna inhabiting native algae and supported different epifaunal assemblages from those in *B. bifurcata*, consistently across space and time (with a few exceptions). The effect of *S. muticum* was more important in July, and coincided with a marked peak of epiphytes in this alga. It is possible that epifauna used epiphytes growing on the macroalga as a food resource and/or living space, rather than the macroalga itself. The fact that differential epifaunal assemblages were found in both habitats at different spatial scales suggests that biological factors related to the specific habitat, e.g. epiphyte load, architecture, and biochemical composition, might play a more important role than physical factors such as wave exposure, water currents, temperature and topography, as determinants of epifaunal distribution. This invasive species, therefore, seems to supply a new and additional habitat for the local epifauna, contributing to increased spatial and temporal variability of epifaunal assemblages. The consequences of these quantitative changes are unknown at the system level, but they could include altered food webs because of these changes in the distribution of food resources in both space and time. These results, in combination with other studies carried out along the Galician coast that have demonstrated differential effects of this species on native assemblages (e.g. Olabarria *et al.* 2009; Rossi *et al.* 2010), highlight the importance of future research into the spread and impact of introduced algae. Because of their worldwide distribution and differential effects in different coastal habitats, introduced algae are potentially important agents of global ecological change.

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