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**Limited impact of *Sargassum muticum* on native algal assemblages
from rocky intertidal shores**

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ABSTRACT

Invasive species represent a serious threat to natural ecosystems through a range of negative effects on native species in the region invaded. The invasive species *Sargassum muticum* has invaded several temperate regions worldwide including the Galician rocky shoreline (northwestern Spain) in western Europe. The main aim of this study was to assess if colonization by *S. muticum* has any effect on native algal assemblages by experimental removal of *S. muticum*. We predicted that in those plots where *S. muticum* plants were removed, the structure of native algal assemblages would differ from that in plots where *S. muticum* plants were untouched. In addition, we predicted that the effect of *Sargassum* removal would be more important than other causes of variability at the small scale investigated. Results indicated limited impact of *S. muticum* on native assemblages. The impact was only evident on the total number of native taxa and two understory morpho-functional groups, filamentous and foliose algae, rather than on the entire macroalgal assemblages.

Key words: removal experiment, algal assemblages, biological invasions, rocky intertidal, *Sargassum muticum* effects

1. Introduction

The number of species anthropogenically introduced outside their natural ranges is rapidly increasing (Levin et al., 2002). Although only a very small proportion of transported and introduced species becomes invasive, the ability of these species to restructure and, therefore, change the functioning of a recipient habitat is great (Crooks, 2002). After loss of habitat, invasive species are the second leading cause of biodiversity loss, particularly in freshwater ecosystems (Vitousek et al., 1997; Mack et al., 2000; Ross et al., 2004). Besides imposing huge economic costs, invasive species may cause extinction of native species, reduction of genetic diversity, and biotic homogenization through a variety of mechanisms (Rahel, 2000).

Biological invasions are increasing, especially in marine environments where they are linked to the intensification of international shipping, aquaculture and aquarium activity (Verlaque, 1994; Ribera and Bouderesque, 1995). In particular, marine macroalgae are a significant component of marine invasive species with 277 introduced species recorded in a recent review (see Williams and Smith, 2007).

Displacement of existing flora by introduced algal species has been largely reported (Chambers et al., 1993; Piazzzi et al., 2001). Replacement of dominant macroalgae by introduced species may provoke changes of the species composition and their trophic food webs (Piazzzi et al., 2001). Several studies have focused on the effects of exotic algae and impacts on native assemblages (e.g. Viejo, 1997; Stæhr et al., 2000; Piazzzi et al., 2001; Levin et al., 2002; Britton-Simmons, 2004; Sánchez and Fernández, 2005; Strong et al., 2006). Results indicate that impacts of exotic species may vary greatly depending on the invaded assemblages (e.g. Chapman, 1999). For example, the Japanese seaweed *Codium fragile* (Sur.) Harriot ssp. *tomentosoides* (van Goor) Silva has detrimental effects on subtidal kelp communities in the northeast Atlantic Ocean while on the European intertidal shores it occurs in low abundances with no effects on

53 native assemblages (Buschbaum et al., 2006). The green alga *Caulerpa racemosa*
 54 (Forsskål) J. Agardh has strong effects on composition and structure of native
 55 assemblages at different habitats such as rocky bottoms and dead matter of the marine
 56 phanerogam *Posidonia oceanica* (Piazzi et al., 2001). *Sargassum muticum* (Yendo)
 57 Fensholt is native to SE Asia, but its present distribution as an invasive species is
 58 widespread, including Europe, the Mediterranean Sea and the west coast of North
 59 America. This species becomes established in low intertidal and shallow subtidal
 60 habitats where it forms dense stands that may reduce light, dampen flow, increase
 61 sedimentation and reduce ambient nutrient concentrations available for native species
 62 (Britton-Simmons, 2004). In subtidal habitats *S. muticum* has been shown to have
 63 negative effects on native algae (Sánchez and Fernández, 2005), whereas in intertidal
 64 areas some studies suggest that it competes with native algae (e.g. DeWreede, 1983;
 65 Viejo, 1997) while other studies show no effects. These contradicting results suggest
 66 strong site-specific effects of *S. muticum*, making generalizations about the impact of
 67 this species difficult.

68 *S. muticum* was first observed on the Galician coast in 1986 (see Pérez-Cirera
 69 et al., 1989) and has since quickly colonized most of the Galician rias (*sensu* Vilas et
 70 al., 2005) increasing its abundance rapidly. Despite its rapid spread, no studies
 71 assessing consequences of the introduction of this species on native assemblages have
 72 been done in this area so far.

73 The objective of this study was to assess the effect of *S. muticum* on native
 74 algal assemblages using a removal experiment in which the presence of this species
 75 was manipulated. We predicted that if *S. muticum* is removed the remaining
 76 assemblages would be distinct, in terms of composition and structure, from those
 77 found in plots where *S. muticum* was present. In addition, we predicted that the effect

of removal would be more important than other causes of variability at the small spatial scale investigated (sites located 400 m apart).

2. Material and Methods

2.1. Study area

The study was carried out at Monte Lourido (42° 7' 26'' N; 8° 49' 34'' W) in the Galician coast (NW Spain). Two sites 400 m apart were chosen. Site 1 was on a gently sloping rocky platform (~ 2° in slope) running perpendicular to the sea and slightly more exposed than site 2. The upper intertidal was dominated by *Fucus spiralis* and the mid and low intertidal was dominated by red, green or some conspicuous brown macroalgae (i.e. *Sacchoriza polyschides*) depending on the season. Site 2 was a long nearly horizontal platform interrupted at its seaward margin by a series of surge channels that run oblique to the shoreline and are sheltered from the direct wave action. The bottom of these channels was made of cobbles covered with sand. The upper intertidal contained less *F. spiralis* than Site 1 and mid and low intertidal assemblages were poorer in terms of number of species than Site 1. *S. muticum* was very abundant at both sites, although plants from Site 2 were bit longer and reached larger sizes than those at Site 1 (personal observation).

2.2. Experimental design

The experiment was performed in the low intertidal (0.4-0.8 m above the lowest astronomical tide) from April 2006 to March 2008. Ten permanent 50 x 50 cm plots were randomly establish along 80 m at each site. The corners of the plots were permanently marked using epoxy putty (IVEGOR) for identification. At each site, the experimental plots were arranged in a line parallel to shore separated by ~ 5 m and randomly assigned to control (i.e. with *Sargassum*) or removal (i.e. without

Sargassum) treatments with five replicates for each. In plots assigned to the removal treatment, all *S. muticum* was manually eradicated, both from within the plots and from a 50 cm buffer surrounding the plots. Each plant was removed by carefully prying its holdfast off the rock substrate with a scraper. The buffer zone was created in order to reduce shading or other effects of adjacent *S. muticum*. Attention was paid to not damage the understory assemblage or to alter the physical characteristics of the substratum. The removal plots were kept free of *S. muticum* throughout the course of experiment by removing any new *S. muticum* recruits from plots and adjacent buffer zones once a month. The control plots were not altered. The experiment was sampled once prior to the beginning of the experiment and then every month, although time and weather constraints prevented sampling on some dates (site 1 in October 2006 and site 2 in November 2006, January and August 2007).

Percentage cover of macroalgae was estimated using a 50 x 50 cm metallic quadrat divided into 25 sub-quadrats of 10 x 10 cm, and a score from 0 to 4% was given to each taxon in each sub-quadrat after visual inspection. Final cover was obtained by summing over the 25 scores obtained in the sub-quadrats (Dethier et al., 1993). Species were identified in the field but when doubt existed, samples were collected for further identification in the laboratory. Macroalgae were grouped into morpho-functional groups based on similarities in morphology and resource use (foliose, filamentous, corticated, leathery, articulated calcareous and encrusting algae; *sensu* Steneck and Dethier, 1994). In addition, number of native species and diversity (H') were estimated for each plot.

2.3. Statistical analysis

Since experimental plots were repeatedly sampled over time (i.e. 20 sampling dates), a technique that could account for temporal autocorrelation was necessary.

127 Data (percentage cover of main morpho-functional groups, number of native taxa and
128 diversity) were analysed using Population-Averaged Generalized Estimating
129 Equations (PA-GEEs), an extension of GLMs for correlated data (Liang and Zeger,
130 1986). PA-GEEs were run using the “geeglm” procedure in the R program, version
131 R2.2.1 (R Development Core Team 2005), specifying a link function and an error
132 structure for the residuals. We specified a first order autoregressive model AR (1) in
133 all the analyses assuming time dependence for each plot. For data expressed as
134 percentage cover and diversity, a Gaussian distribution of the error terms was
135 assumed and we used an identity link function. For data expressed as number of algal
136 species, a Poisson distribution of the error terms was assumed, and we used a log-link
137 function.

138 Two-way crossed analysis of similarity (ANOSIM) (Clarke, 1993) on fourth
139 root transformed data of percentage cover for each species was used to test for
140 differences in assemblages between treatments and over time at each site separately.
141 Treatment with two levels (control and removal) and time with 10 levels (April, July,
142 September, December 2006 and 2007, and February 2007 and 2008) were the factors
143 in the analysis. Pair-wise comparisons were also calculated. In addition, responses of
144 assemblages to treatments were visualised by non-metric multidimensional scaling
145 (nMDS) on the basis of Bray-Curtis similarity matrices on fourth-root transformed
146 percentage cover data. For all analyses, *S. muticum* was omitted from the data set to
147 check if the possible differences between treatments were caused not by the presence
148 of this species, but by changes in the remaining assemblages. Species that mostly
149 contributed to the dissimilarity/similarity between the two experimental treatments
150 were identified using SIMPER analysis (Clarke, 1993). All the calculations were
151 performed using PRIMER 6 for Windows (Plymouth, UK).

3. Results

The percentage cover of *S. muticum* varied significantly between treatments (PA-GEEs; treatment: estimate: -15.36, standard error: 2.58, $p < 0.001$). Thus in control plots the mean percentage cover of *S. muticum* was 29.3 ± 2.7 and 42.7 ± 3 % at site 1 and site 2, respectively, whereas in removal treatments the mean percentage cover of the alga was 5 ± 1.3 and 7.2 ± 1.7 % at site 1 and site 2, respectively (Fig. 1).

3.1. Effects of *S. muticum* on morpho-functional groups

Removal of *S. muticum* resulted in a significant increase of the mean percentage cover of filamentous and foliose algae ($p < 0.05$; Table 1, Fig. 2 a,b). Mean percentage cover of encrusting algae also increased in those plots where *S. muticum* was removed, but this increase was marginally non-significant ($p = 0.056$; Table 1, Fig. 2c). The removal also affected the mean number of taxa (used as a surrogate measure of native species diversity), with significant lower values occurring in control plots, especially at site 2 ($p < 0.05$; Table 1, Fig. 2 d). The effect of *S. muticum* on these morpho-functional groups was also consistent across sites (i.e. non-significant interaction treatment x site, $p > 0.05$; Table 1). Diversity and percentage cover of corticated, leathery and calcareous algae were not affected significantly by treatments (neither as main effect nor in interaction with site).

3.2. Changes in assemblages

Removal of *S. muticum* did not affect the composition of macroalgal assemblages. Two-way crossed ANOSIM results showed significant differences between sites over time (Table 2, Fig. 3), but not between treatments (differences between treatments: site 1, $R = 0.04$, $p > 0.05$; site 2, $R = 0.08$, $p > 0.05$ averaged across all sampling times). There were only significant differences between treatments in

176 April and September 2007 (Table 2). Time (monthly and interannually) differences in
177 macroalgae assemblage structure (Fig. 3) were also detected by ANOSIM at both sites
178 (differences among time factor: site 1, $R=0.519$, $p<0.01$; site 2, $R=0.465$, $p<0.01$;
179 Table 2; Figure 3). Pair-wise comparisons detected differences in macroalgal
180 assemblages in most cases (Table 2).

181 The foliose alga *Ulva rigida* (7.07%), the encrusting alga *Lithophyllum*
182 *incrustans* (6.62%), the leathery alga *Bifurcaria bifurcata* (6.17%) and the articulated
183 calcareous alga *Corallina officinalis* (4.84%) were the species that mostly contributed
184 to the dissimilarity between assemblages in both control and removal plots over time.
185 In March 2008, 2 years after the start of the experiment, *B. bifurcata* (8.62%), *U.*
186 *rigida* (7.6%), *L. incrustans* (7.28%) and *C. officinalis* (6.06%) still explained the
187 highest contribution to the observed dissimilarity among assemblages.

188 *S. muticum* was very abundant in control plots during the whole experiment,
189 although the percentage cover declined in late summer (illustrated by site 1 in Fig. 4
190 a). The following months after removal, *Ulva rigida* and *Corallina officinalis*
191 dominated the primary substratum (illustrated by site 1 in Fig. 4 b, c; SIMPER). The
192 decrease of the former during autumn and winter was followed by an increase in
193 percentage cover of *L. incrustans* (illustrated by site 1 in Fig. 4 d). In contrast, *B.*
194 *bifurcata* was not abundant in the removal plots (illustrated by site 1 in Fig. 4e). No
195 significant differences between treatments were detected in percentage cover of these
196 native species (PA-GEEs: $p>0.05$) except for *U. rigida* (PA-GEEs: $p<0.01$;
197 Estimate: 2.86, S.E: 1.06; Fig. 4 b).

198 **4. Discussion**

199 Results indicated limited impact of *S. muticum* on native assemblages. The
200 impact was evident on the total number of native taxa and two understory morpho-

functional groups, filamentous and foliose algae, rather than on the entire macroalgal assemblages.. In particular, the total number of taxa as well as the percentage cover of filamentous and foliose algae was smaller in control than removal plots. In addition, these effects were consistent at small spatial scale as predicted.

Studies of *S. muticum* have varied widely in their conclusions about its effect on native assemblages. In general, studies done on intertidal shores have found little (Buschbaum et al., 2006; Harries et al., 2007) or no impact of *S. muticum* (e.g. DeWreede, 1983; Viejo, 1997; Sánchez and Fernández, 2005), but studies in subtidal habitats have indicated relatively strong effects (Ambrose and Nelson, 1982; Stæhr et al., 2000; Britton-Simmons, 2004). Nevertheless, the impact of *S. muticum* on native assemblages not only depends on the type of habitat, but also on the abundance of *S. muticum* (Viejo, 1997; Britton-Simmons, 2004; Stæhr et al., 2000). According to this, effect of *Sargassum* should be more evident in densely colonized areas, where this species should be more likely to provoke changes in native macroalgal assemblages through competitive interactions (Ambrose and Nelson, 1982; Viejo, 1997; Britton-Simmons, 2004). However, at low densities effects of invader on native macroalgal assemblages might be very weak (see Viejo, 1997; Britton-Simmons, 2004). This experiment was conducted at sites where the abundance of *S. muticum* was comparatively low because the low intertidal corresponds to the upper end of its distribution. Therefore, one may expect that the impact of *S. muticum* on native assemblages is weaker because it is less abundant in this tidal zone.

Our results indicated a larger number of native taxa in those plots where *Sargassum* was removed. Results from studies in marine benthic assemblages are scarce and conflicting regarding relationships between diversity and potential for invasion. For example, Dunstan and Johnson (2004) found positive relationships

226 between species richness and abundance of invaders using assemblages of sessile
 227 invertebrates. Conversely, other experimental and observational studies have reported
 228 negative relationships between the numbers of invasive and native taxa (Stachowicz et
 229 al., 1999; 2002; White and Shurin, 2007). In fact, White and Shurin (2007) showed
 230 that *S. muticum* was less abundant in areas with high diversity of native species. In our
 231 study, the observed negative relationship may have different explanations. Firstly,
 232 *Sargassum* may outcompete native species and therefore reduce native diversity, or
 233 secondly, its environmental niche at low intertidal may coincide with areas of low
 234 native diversity. The latter explanation, however, seems very unlikely because the low
 235 intertidal area on the northwestern Iberian rocky shores is not a species-poor zone. In
 236 fact, low intertidal assemblages on this coast are highly diverse and show important
 237 spatial variation in species composition at scale of a few metres (see Araujo et al.,
 238 2005). Nevertheless, this experiment did not allow us to disentangle such possibilities.

239 Previous studies on *S. muticum* have indicated the important role of functional
 240 groups in the invasion process (Viejo, 1997; Britton-Simmons, 2006). Recent findings
 241 of Arenas et al. (2006) have pointed out that identity of functional groups is more
 242 decisive than functional richness in determining the resistance of marine macroalgal
 243 assemblages (Arenas et al., 2006). Functional groups play an important role in the
 244 invasion process due largely to their effect on the primary resource requirements of
 245 space and light (Arenas et al., 2006; Britton-Simmons, 2004; 2006). Alternatively,
 246 different functional groups that present different survival strategies may be affected
 247 differently by invasive species (see Viejo, 1997). In this study we found a negative
 248 effect of *S. muticum* on the percentage cover of foliose and filamentous algae. These
 249 results partially agree with those reported by Viejo (1997) that found an impact of
 250 *Sargassum* on the leathery and foliose algae. Although several mechanisms

underlying the invasion process have been proposed to explain changes in native macroalgal assemblages (Ambrose and Nelson, 1982; Critchley et al., 1990; Vadas et al., 1992; Viejo, 1997; Britton-Simmons 2004) we only can speculate on the causative mechanisms. For example, foliose algae, mainly composed of the opportunistic species *Ulva* sp, might be inhibited by *Sargassum* by pre-emption of space (see Viejo, 1997). Foliose and filamentous algae might be also negatively influenced by *Sargassum* due to competition for light. In fact, Britton-Simmons (2004) has demonstrated experimentally the negative effect of *Sargassum* canopy on growth of understory species and Arenas et al. (2006) have found that filamentous species such as Ceramiales are mainly affected by light.

In summary, results suggest that there was limited effect of *Sargassum* on macroalgal assemblages. It might be possible that the spatial (i.e. 50 x 50 cm plots) and temporal (i.e. 2 years) scales used in this study were not appropriate to detect a stronger impact. In fact, previous studies focused on effects of *Sargassum* on macroalgal assemblages have used larger temporal scales, i.e. ≥ 3 years (e.g. Viejo, 1997; Britton-Simmons, 2004, Sánchez and Fernández, 2005). The fact that two morpho-functional groups were affected by *Sargassum* also highlights the importance of functional groups in the invasion process, and the need to do manipulative experiments in which functional groups are altered (see Arenas et al., 2006; Britton-Simmons, 2006).

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Table 1. Results of Population-Averaged Generalized Estimating Equations examining the effects of *Sargassum muticum* on native algal assemblages

	Number of native taxa		Diversity		Filamentous algae		Foliose algae		Corticated algae		Leathery algae		Calcareous algae		Encrusting algae	
	E	SE	E	SE	E	SE	E	SE	E	SE	E	SE	E	SE	E	SE
Intercept	2.09***	0.04	1.16***	0.03	3.14***	0.38	17.15***	1.22	12.54***	1.31	7.50***	1.45	7.81***	0.99	7.79***	1.54
Treatment (T)	0.07*	0.04	-0.02	0.03	0.81*	0.38	3.06*	1.22	0.04	1.31	-2.17	1.45	0.27	0.99	2.98†	1.54
Site (S)	-0.02	0.04	0.05	0.03	-0.7	0.38	-3.49**	1.22	-2.47	1.31	-3.33*	1.45	0.83	0.99	3.03*	1.54
T x S	0.05	0.04	0.00	0.03	0.04	0.38	-0.10	1.22	2.34	1.31	1.87	1.45	-1.37	0.99	-0.45	1.54
<i>Correlation parameter</i>	0.63	0.04	0.37	0.05	0.18	0.05	0.37	0.04	0.46	0.10	0.89	0.03	0.68	0.06	0.89	0.02
<i>Scale parameter</i>	0.79	0.09	0.08	0.01	47.3	13.68	310	48.8	129.1	22.8	79.8	26.8	58.9	8.97	79	21

E = estimate; SE = standard error. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; †marginally non-significant ($p = 0.056$)

Table 2. Results of the ANOSIM and pair-wise tests for differences on macroalgal assemblages between treatments (control and removal) and sites (1 and 2) over time (dates as in Figure 3)

Years Months	2006		2007		2008	
	Site	Treatment	Site	Treatment	Site	Treatment
April	0.424**	-0.074	0.384**	0.226*	+	+
July	0.414**	0.074	0.48**	0.144	+	+
September	0.521**	0.044	0.232*	0.228*	+	+
December	0.356**	0.02	0.48**	0.134	+	+
February	+	+	0.476**	-0.074	0.214*	-0.022

time (10 levels) and treatment (2 levels) as factors in the analysis. * $p < 0.05$; ** $p < 0.01$; + not sampled

Figure captions

Fig. 1. Percentage cover (mean $\pm$ SE; $n = 100$) of *Sargassum muticum* in control and removal plots over the course of the experiment.

Fig. 2. Percentage cover (mean $\pm$ SE; $n = 5$) of filamentous (a), foliose (b), encrusting algae(c), and number of native taxa (d) at site 1 and site 2.

Fig. 3. Non-metric multidimensional scaling (nMDS) for differences in assemblages showing temporal changes between treatments at site 1 and site 2 ($n = 5$). The first data (April 2006) for each site belongs to the pre-removal samples. Circle: site 1, triangle: site 2.

Fig. 4. Percentage cover (mean $\pm$ SE; $n = 5$) of *Sargassum muticum* (a), *Ulva rigida* (b), *Corallina officinalis* (c), *Lithophyllum incrustans*(d), and *Bifurcaria bifurcata* (e), over time at site 1. The first data point (April 2006) represents the pre-removal samples. *S. muticum* was excluded from the ANOSIM and SIMPER analyses.

Fig. 1 Olabarria et al.

Fig. 2 Olabarria et al.

Fig. 3. Olabarria et al.

Fig. 4 Olabarria et al.