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

**Celia Olabarria<sup>1\*</sup>, Iván F. Rodil<sup>1</sup>, Mónica Incera<sup>2</sup>, Jesús S. Troncoso<sup>1</sup>**

*<sup>1</sup>Departamento de Ecología e Biología Animal, Facultade de Ciencias del Mar,*

*Universidade de Vigo, 36200Vigo, Spain.*

*<sup>2</sup>Centro Tecnológico del Mar-Fundación CETMAR, C/Eduardo Cabello s/n, 36208*

*Vigo, Spain*

\*Corresponding author: colabarria@uvigo.es

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## 1 ABSTRACT

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

15  
16 *Key words:* removal experiment, algal assemblages, biological invasions, rocky  
17 intertidal, *Sargassum muticum* effects

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## 27 1. Introduction

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

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

42           Displacement of existing flora by introduced algal species has been largely  
43 reported (Chambers et al., 1993; Piazzini et al., 2001). Replacement of dominant  
44 macroalgae by introduced species may provoke changes of the species composition  
45 and their trophic food webs (Piazzini et al., 2001). Several studies have focused on the  
46 effects of exotic algae and impacts on native assemblages (e.g. Viejo, 1997; Stæhr et  
47 al., 2000; Piazzini et al., 2001; Levin et al., 2002; Britton-Simmons, 2004; Sánchez and  
48 Fernández, 2005; Strong et al., 2006). Results indicate that impacts of exotic species  
49 may vary greatly depending on the invaded assemblages (e.g. Chapman, 1999). For  
50 example, the Japanese seaweed *Codium fragile* (Sur.) Harriot ssp. *tomentosoides* (van  
51 Goor) Silva has detrimental effects on subtidal kelp communities in the northeast Atlantic  
52 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

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

## 80 **2. Material and Methods**

### 81 *2.1. Study area*

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

### 95 *2.2. Experimental design*

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

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

114 Percentage cover of macroalgae was estimated using a 50 x 50 cm metallic  
115 quadrat divided into 25 sub-quadrats of 10 x 10 cm, and a score from 0 to 4% was  
116 given to each taxon in each sub-quadrat after visual inspection. Final cover was  
117 obtained by summing over the 25 scores obtained in the sub-quadrats (Dethier et al.,  
118 1993). Species were identified in the field but when doubt existed, samples were  
119 collected for further identification in the laboratory. Macroalgae were grouped into  
120 morpho-functional groups based on similarities in morphology and resource use  
121 (foliose, filamentous, corticated, leathery, articulated calcareous and encrusting algae;  
122 *sensu* Steneck and Dethier, 1994). In addition, number of native species and diversity  
123 ( $H'$ ) were estimated for each plot.

### 124 2.3. Statistical analysis

125 Since experimental plots were repeatedly sampled over time (i.e. 20 sampling  
126 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).

### 152 3. Results

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

#### 158 3.1. Effects of *S. muticum* on morpho-functional groups

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

#### 170 3.2. Changes in assemblages

171 Removal of *S. muticum* did not affect the composition of macroalgal  
172 assemblages. Two-way crossed ANOSIM results showed significant differences  
173 between sites over time (Table 2, Fig. 3), but not between treatments (differences  
174 between treatments: site 1,  $R = 0.04$ ,  $p > 0.05$ ; site 2,  $R = 0.08$ ,  $p > 0.05$  averaged across  
175 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-

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

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

222         Our results indicated a larger number of native taxa in those plots where  
223 *Sargassum* was removed. Results from studies in marine benthic assemblages are  
224 scarce and conflicting regarding relationships between diversity and potential for  
225 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

251 underlying the invasion process have been proposed to explain changes in native  
252 macroalgal assemblages (Ambrose and Nelson, 1982; Critchley et al., 1990; Vadas et  
253 al., 1992; Viejo, 1997; Britton-Simmons 2004) we only can speculate on the causative  
254 mechanisms. For example, foliose algae, mainly composed of the opportunistic  
255 species *Ulva* sp, might be inhibited by *Sargassum* by pre-emption of space (see Viejo,  
256 1997). Foliose and filamentous algae might be also negatively influenced by  
257 *Sargassum* due to competition for light. In fact, Britton-Simmons (2004) has  
258 demonstrated experimentally the negative effect of *Sargassum* canopy on growth of  
259 understory species and Arenas et al. (2006) have found that filamentous species such  
260 as Ceramiales are mainly affected by light.

261 In summary, results suggest that there was limited effect of *Sargassum* on  
262 macroalgal assemblages. It might be possible that the spatial (i.e. 50 x 50 cm plots)  
263 and temporal (i.e. 2 years) scales used in this study were not appropriate to detect a  
264 stronger impact. In fact, previous studies focused on effects of *Sargassum* on  
265 macroalgal assemblages have used larger temporal scales, i.e.  $\geq 3$  years (e.g. Viejo,  
266 1997; Britton-Simmons, 2004, Sánchez and Fernández, 2005). The fact that two  
267 morpho-functional groups were affected by *Sargassum* also highlights the importance  
268 of functional groups in the invasion process, and the need to do manipulative  
269 experiments in which functional groups are altered (see Arenas et al., 2006; Britton-  
270 Simmons, 2006).

271

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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

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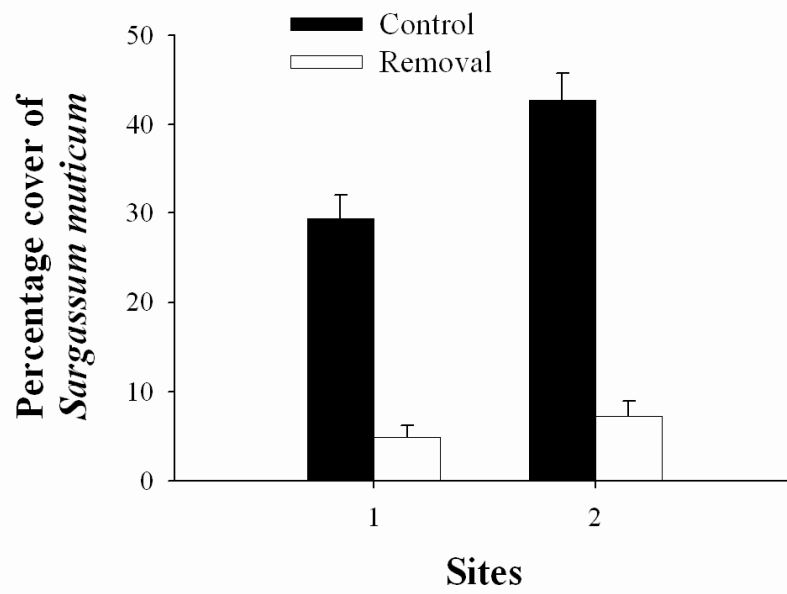
**Figure captions**

**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.

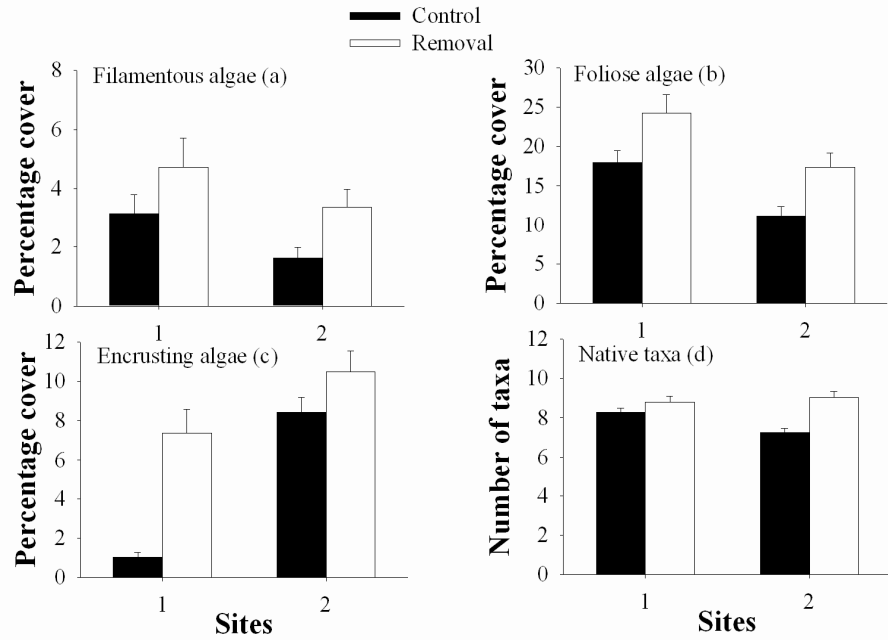


Fig. 2 Olabarria et al.

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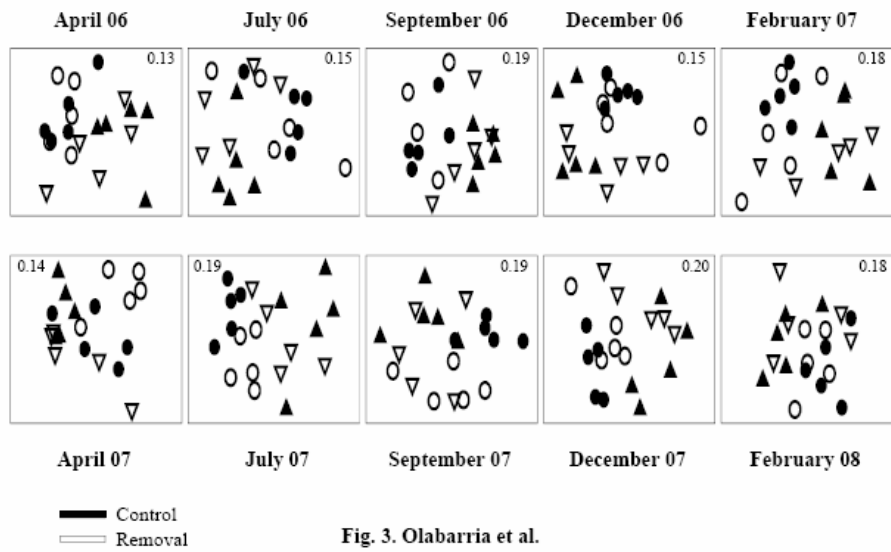


Fig. 3. Olabarria et al.

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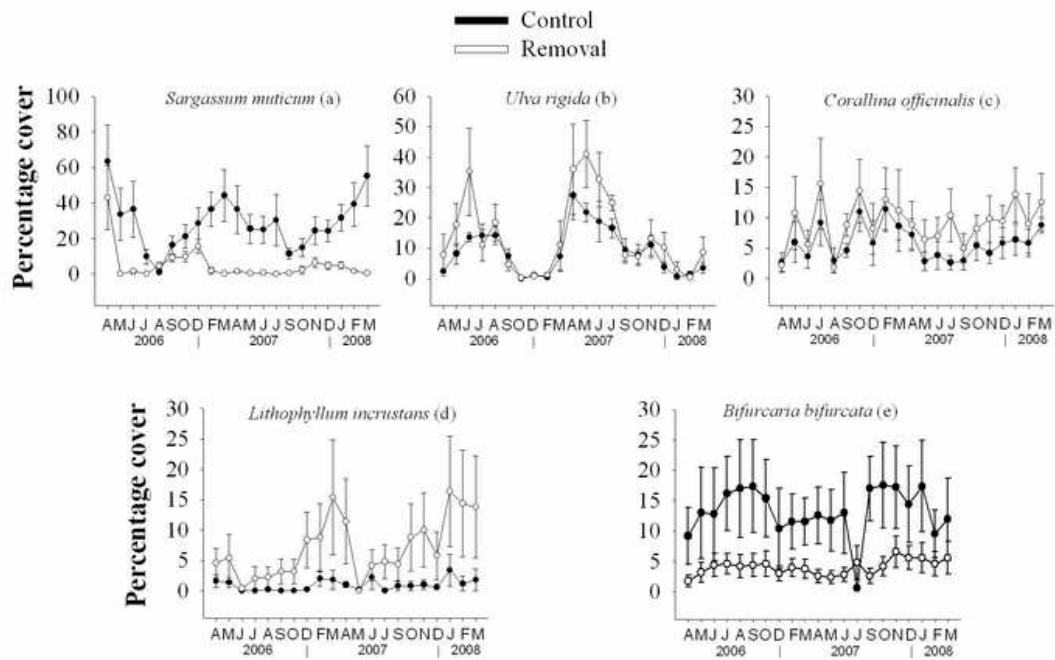


Fig. 4 Olabarria et al.

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