



HAL
open science

Limited impact of on native algal assemblages from rocky intertidal shores

Celia Olabarria, Iván F. Rodil, Mónica Incera, Jesús S. Troncoso

► **To cite this version:**

Celia Olabarria, Iván F. Rodil, Mónica Incera, Jesús S. Troncoso. Limited impact of on native algal assemblages from rocky intertidal shores. *Marine Environmental Research*, 2009, 67 (3), pp.153. 10.1016/j.marenvres.2008.12.007 . hal-00501991

HAL Id: hal-00501991

<https://hal.science/hal-00501991>

Submitted on 13 Jul 2010

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

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

Celia Olabarria, Iván F. Rodil, Mónica Incera, Jesús S. Troncoso

PII: S0141-1136(08)00262-6
DOI: [10.1016/j.marenvres.2008.12.007](https://doi.org/10.1016/j.marenvres.2008.12.007)
Reference: MERE 3311

To appear in: *Marine Environmental Research*

Received Date: 3 October 2008
Revised Date: 18 December 2008
Accepted Date: 22 December 2008

Please cite this article as: Olabarria, C., Rodil, I.F., Incera, M., Troncoso, J.S., Limited impact of *Sargassum muticum* on native algal assemblages from rocky intertidal shores, *Marine Environmental Research* (2008), doi: [10.1016/j.marenvres.2008.12.007](https://doi.org/10.1016/j.marenvres.2008.12.007)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.



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

Celia Olabarria^{1*}, Iván F. Rodil¹, Mónica Incera², Jesús S. Troncoso¹

¹Departamento de Ecología e Biología Animal, Facultade de Ciencias del Mar,

Universidade de Vigo, 36200Vigo, Spain.

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

Vigo, Spain

*Corresponding author: colabarria@uvigo.es

ACCEPTED MANUSCRIPT

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

18

19

20

21

22

23

24

25

26

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 ± 2.7 and 42.7 ± 3 % at
156 site 1 and site 2, respectively, whereas in removal treatments the mean percentage
157 cover of the alga was 5 ± 1.3 and 7.2 ± 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 x 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. ≥ 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

272 **Acknowledgments**

273 This research has been supported by the Spanish Government through the
274 Ministry of Education and Science (PROJECT CGL2005-02269). Funds to I.F. Rodil
275 were provided in the course of a Maria Barbeito grant (Xunta de Galicia).

276 **References**

- 277 Ambrose, R.F., Nelson, B.V., 1982. Inhibition of giant kelp recruitment by an
278 introduced brown alga. *Botanica Marina* 25, 265-267.
- 279 Araujo, R., Bárbara, I., Sousa-Pinto, I., Quintino, V., 2005. Spatial variability of
280 intertidal rocky shore assemblages in the northwest coast of Portugal.
281 *Estuarine, Coastal and Shelf Science* 64, 658-670.
- 282 Arenas, F., Sánchez, I., Hawkins, S.J., Jenkins, S.R., 2006. The invasibility of marine
283 algal assemblages: role of functional diversity and identity. *Ecology* 87 (11),
284 2851-2861
- 285 Britton-Simmons, K.H., 2004. Direct and indirect effects of the introduced alga
286 *Sargassum muticum* on benthic, subtidal communities of Washington State,
287 USA. *Marine Ecology Progress Series* 277, 61-78.
- 288 Britton-Simmons, K.H., 2006. Functional group diversity, resource preemption and
289 the genesis of invasion resistance in a community of marine algae. *Oikos* 113,
290 395-401.
- 291 Buschbaum, C., Chapman, A.S., Saier, B., 2006. How an introduced seaweed can
292 affect epibiota diversity in different coastal systems. *Marine Biology* 148, 743-
293 754.
- 294 Chambers, P.A., Barko, J.W., Smith, C.S., 1993. Evaluation of invasions and declines
295 of submersed aquatic macrophytes. *Journal of Aquatic Plant Management* 31,
296 218-220.
- 297 Chapman, A.S., 1999. From introduced species to invader: what determines variation
298 in the success of *Codium fragile* ssp. *tomentosoides* (Chlorophyta) in the
299 North Atlantic Ocean?. *Helgolander Meeresunters* 52, 277-289.
- 300 Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community
301 structure. *Australian Journal of Ecology* 18, 117-143.
- 302 Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological
303 invasions: The role of ecosystem engineers. *Oikos* 97, 153-166.
- 304 Critchley, A.T., De Visscher, P.R.M., Nienhuis, P.H., 1990. Canopy characteristics of
305 the brown alga *Sargassum muticum* (Fucales, Phaeophyta) in Lake
306 Grevelingen, southwest Netherlands. *Hydrobiologia* 204/205, 211-217.

- 307 Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual *versus* random-
308 point percent cover estimations: 'objective' is not always better. *Marine Ecology*
309 *Progress Series* 110, 9–18.
- 310 DeWreede, R.E., 1983. *Sargassum muticum* (Fucales, Phaeophyta): regrowth and
311 interaction with *Rhodomela larix* (Ceramiales, Rhodophyta). *Phycologia* 22,
312 153-160.
- 313 Dunstan, P.K., Johnson, C.R., 2004. Invasion rates increase with species richness in a
314 marine epibenthic community by two mechanisms. *Oecologia* 138, 285-292.
- 315 Harries, D.B., Harrow, S., Wilson, J.R., Mair, J.M., Donnan, D.W., 2007. The
316 establishment of the invasive alga *Sargassum muticum* on the west coast of
317 Scotland: a preliminary assessment of community effects. *Journal of Marine*
318 *Biological Association of United Kingdom* 87, 1057-1067.
- 319 Levin, P.S., Coyer, J.A., Petrik, R., Good, T.P., 2002. Community-wide effects of
320 nonindigenous species on temperate rocky reefs. *Ecology* 83 (11), 3182-3193.
- 321 Liang, K.Y., Zeger, S.L., 1986. Longitudinal data analysis using generalized linear
322 models. *Biometrika* 73 (19), 13-22.
- 323 Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A.,
324 2000. Biotic invasions: causes, epidemiology, global consequences, and
325 control. *Ecological Applications* 10, 689-710.
- 326 Pérez-Cirera, J.L., Cremades, J., Bárbara, I., 1989. Precisiones sistemáticas y
327 sinecológicas sobre algunas algas nuevas para Galicia o para las costas
328 atlánticas de la Península Ibérica. *Anales del Jardín Botánico de Madrid* 46,
329 35-45.
- 330 Piazzzi, L., Ceccherelli, G., Cinelli, F., 2001. Threat to macroalgal diversity: effects of
331 the introduced green alga *Caulerpa racemosa* in the Mediterranean. *Marine*
332 *Ecology Progress Series* 210, 140-159.
- 333 Rahel, F.J., 2000. Homogenization of fish faunas across the United States. *Science*
334 288, 854-856.
- 335 R Development Core Team, 2005. R: A language and environment for statistical
336 computing, reference index version 2.1.1. R Foundation for Statistical
337 Computing, Vienna, Austria. Available from: <http://www.R-project.org>
- 338 Ribera, M.A., Bouderesque, C.F., 1995. Introduced marine plants, with special
339 referente to macroalgae: mechanisms and impact, in: Round, F.E., Chapman,
340 D.J., *Progress in Phycological Research*, Biopress LTD Publ., pp. 187-268.

- 341 Ross, D.J., Johnson, C.R., Hewitt, C.L., Ruiz G.M., 2004. Interaction and impacts of
342 two introduced species on a soft-sediment marine assemblage in SE Tasmania.
343 Marine Biology 144, 747-756.
- 344 Sánchez, I., Fernández, C., 2005. Impact of the invasive seaweed *Sargassum muticum*
345 (Phaeophyta) on an intertidal macroalgal assemblage. Journal of Phycology
346 41, 923-930.
- 347 Stachowicz, J.J., Whitlatch, R.B., Osman, R.W., 1999. Species diversity and invasion
348 resistance in a marine ecosystem. Science 286, 1577-1579.
- 349 Stachowicz, J.J., Fried, H., Osman, R.W., Whitlatch, R.B., 2002. Biodiversity,
350 invasion resistance, and marine ecosystem function: reconciling pattern and
351 process. Ecology 83, 2575-2590.
- 352 Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of
353 algal-dominated communities. Oikos 69 (3), 476-497.
- 354 Strong, J.A., Dring, M.J., Maggs, C.A., 2006. Colonisation and modification of soft
355 substratum habitats by the invasive macroalga *Sargassum muticum*. Marine
356 Ecology Progress Series 321, 87-97.
- 357 Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T., Krause-Jensen, D., 2000.
358 The invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible
359 impact on the indigenous macroalgal community. Marine Ecology Progress
360 Series 207, 79-88.
- 361 Vadas R.L. Sr., Johnson, S., Norton, T.A., 1992. Recruitment and mortality of early
362 post-settlement stages of benthic algae. British Phycological Journal 27, 331-
363 351.
- 364 Verlaque, M., 1994. Checklist of introduced plants in the Mediterranean: origins and
365 impact on the environment and human activities. Oceanologica Acta 17, 1-23.
- 366 Viejo, R.M., 1997. The effects of colonization by *Sargassum muticum* on tidepool
367 macroalgal assemblages. Journal of Marine Biological Association of the
368 United Kingdom 77, 325-340.
- 369 Vilas, F., Bernabeu A., Méndez G., 2005. Sediment distribution pattern in the Rias
370 Baixas (NW Spain): main facies and hydrodynamic dependence. Journal of
371 Marine Systems. 54, 261-276.
- 372 Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human
373 domination of Earth's Ecosystems. Science 277, 494-499.

- 374 White, L.F., Shurin, J.B., 2007. Diversity effects on invasion vary with life history
375 stage in marine macroalgae. *Oikos* 116 (7), 1193-1203.
- 376 Williams, S.L., Smith, J.E., 2007. A global review of the distribution, taxonomy and
377 ecological impacts of introduced seaweeds. *Annual Review of Ecology*
378 *Evolution and Systematics* 38, 327-359.
- 379
- 380

ACCEPTED MANUSCRIPT

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

ACCEPTED MANUSCRIPT

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.

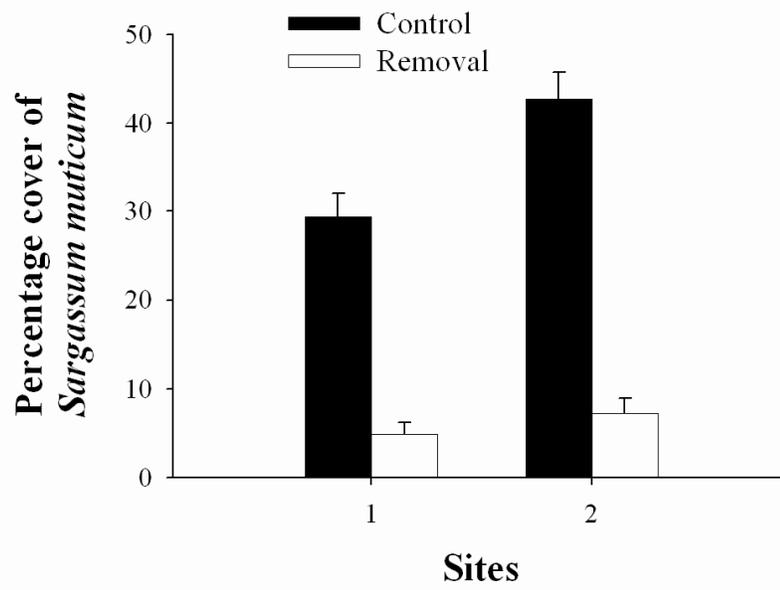


Fig. 1 Olabarria et al.

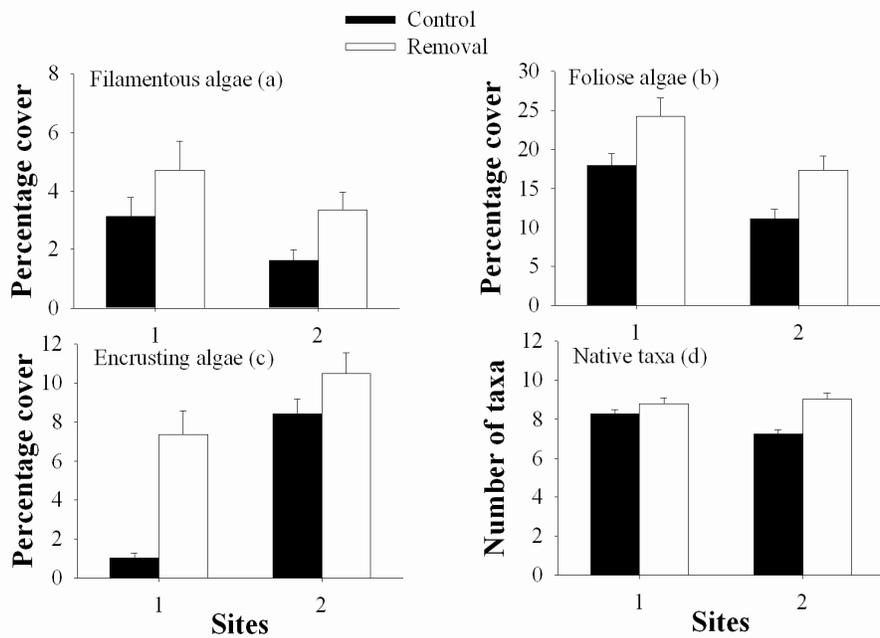


Fig. 2 Olabarria et al.

ACCEPTED MANUSCRIPT

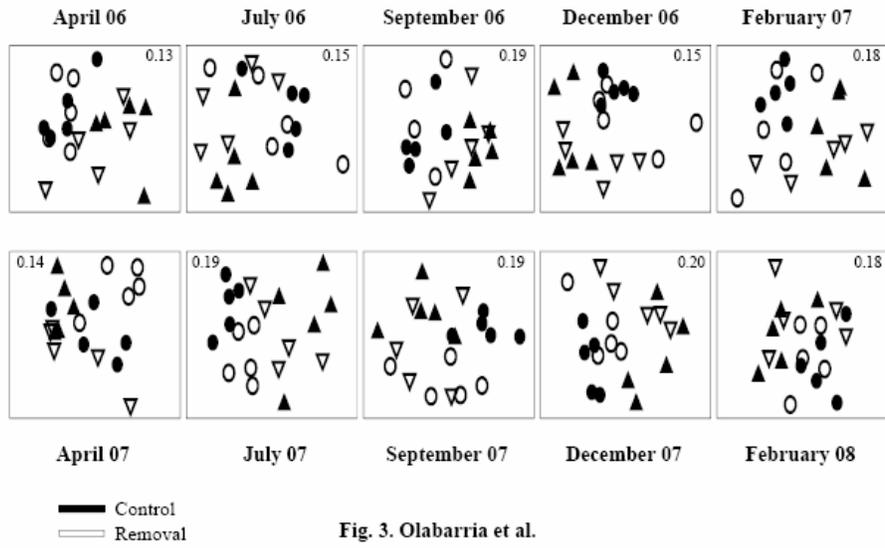


Fig. 3. Olabarria et al.

ACCEPTED MANUSCRIPT

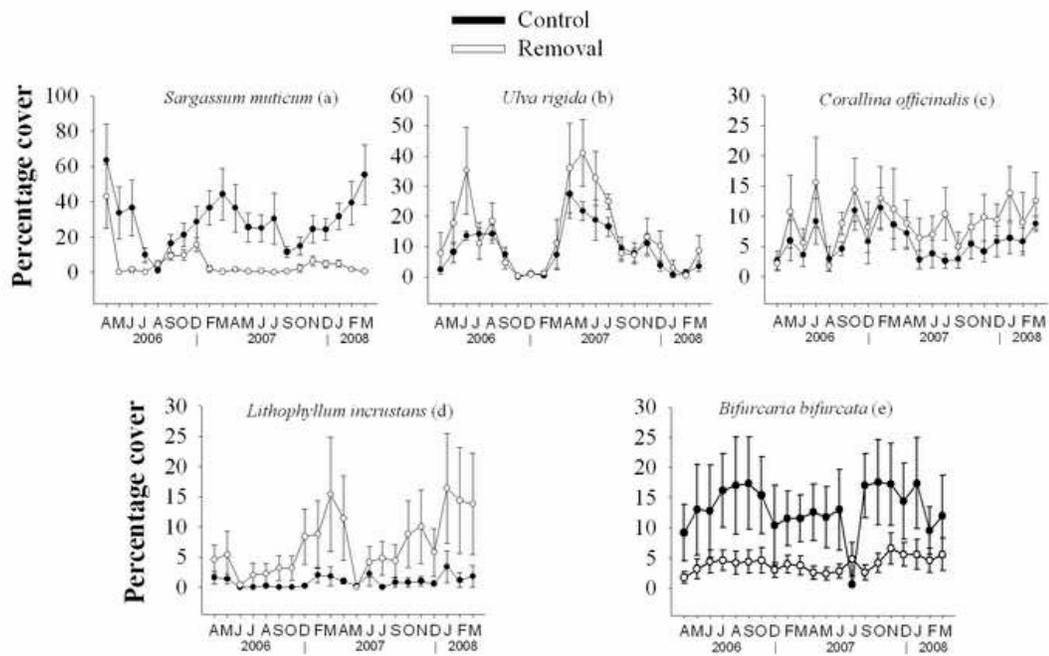


Fig. 4 Olabarria et al.