

IMPACT OF THE INVASIVE SEAWEED *SARGASSUM MUTICUM* (PHAEOPHYTA) ON AN INTERTIDAL MACROALGAL ASSEMBLAGE¹

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The impact of the invasive seaweed *Sargassum muticum* (Yendo) Fensholt on a low intertidal macroalgal assemblage was assessed at a semiexposed rocky shore in northern Spain between 2002 and 2004. *Sargassum muticum* plants were removed from the mature macroalgal assemblage and from those occurring along the successional process of the assemblage. Biomass, richness, diversity, and percentage cover of macroalgae in experimental plots were compared with unmanipulated controls. The effect of *S. muticum* removal on the macroalgal assemblage more than 2 years after the beginning of the experiment was negligible. Moreover, no differences between treatments were detected in the general patterns of succession. Only significant differences in *S. muticum* abundance were detected between treatments at the end of the experiment. We suggest that the low abundance of *S. muticum* at this intertidal level and its pseudoperennial life cycle may limit competition with native macroalgae. However, long-term removal experiments may be a more indicator of the impact of *S. muticum* at the upper limit of its vertical distribution.

Key index words: competition; intertidal; invasion; macroalgal assemblages; northern Spain; removal experiment; *Sargassum muticum*; succession

Abbreviations: ANOSIM, analysis of similarity; ANOVA, analysis of variance; H' , species diversity; nMDS, nonmetric multidimensional scaling; S , species richness

Biological invasions in coastal marine habitats have been recognized as one of the main causes of decline of biodiversity and changes in native populations, community dynamics, and major ecosystem processes (Grosholz 2002). The Japanese seaweed *Sargassum muticum* (Yendo) Fensholt was accidentally introduced into European waters in the early 1970s. Since its first record in the English Channel (Farnham et al. 1973), the species rapidly spread north- and southward across the Atlantic coast of western Europe (Critchley et al. 1983, Rueness 1989, Fernández 1999, Karlsson and Loo 1999). Although its occurrence and expansion have been well documented, the ecological conse-

quences on native communities have been poorly studied (Viejo 1997, Stæhr et al. 2000, Wilson 2001, Britton-Simmons 2004) in spite of the potential impact that it may cause due its recognized competitive abilities (Fletcher and Fletcher 1975, Norton 1977).

On the northern coast of Spain, as in other European countries, the species has now become established, mainly in sheltered shores in low intertidal and shallow subtidal habitats (Fernández et al. 1990, Andrew and Viejo 1998). Intertidal rock pools on more exposed localities can also be colonized (Viejo 1997, Andrew and Viejo 1998). *Sargassum muticum* predominantly colonizes highly disturbed habitats (Deysher and Norton 1982, De Wreede 1983, Critchley et al. 1987, Andrew and Viejo 1998), but there is evidence that it is also able to invade saturated macroalgal assemblages (De Wreede 1983, Viejo 1997, Stæhr et al. 2000). The invasion by *S. muticum* at a saturated low intertidal assemblage on the central coast of Asturias (northern Spain) occurred simultaneously with a continuous decrease in the abundance of the native red seaweed *Gelidium spinosum* (S. G. Gmelin) P. C. Silva, which almost three decades ago formed dense stands at this intertidal level, with a small number of accompanying species at low abundance (Anadón and Fernández 1986, Sánchez et al. 2005).

The aims of this work were to study the effects of *S. muticum* on a native intertidal macroalgal assemblage by experimental manipulation of the presence of *S. muticum* and to test how the presence of an invader established in a saturated community can affect the successional process after a strong disturbance. We predicted that in those plots where *S. muticum* plants were removed, the structure of native algal assemblages would recover to the preinvasion state. We asked whether *S. muticum* alters the general model of succession described for this intertidal level (Fernández et al. 1981).

MATERIALS AND METHODS

Study site. The study was carried out from January 2002 to March 2004 at Aramar (43° 36' N, 5° 46' W), a semiexposed locality in northern Spain. The study area was situated on a gently sloping rocky platform moderately exposed to wave action. The upper intertidal is dominated by invertebrates and the mid and low intertidal is dominated by macroalgae (Fernández and Niell 1982). Experiments were performed in the low intertidal (0.4–0.8 m above the lowest astronomical tide) where primary space is dominated by *S. muticum*, *Bifurcaria bifurcata* R. Ross, and *G. spinosum*. At the start of the

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experiments (January 2002), algal density of *S. muticum* (>5 cm) in the study area was 24.64 ± 10.92 plants \cdot m⁻² (mean \pm SE, $n = 6$). The mean length (from holdfast to the tip of the longest branch) was 25.01 ± 3.20 cm (mean \pm SE, $n = 37$). Around May and June, *S. muticum* reaches its maximum size and biomass (103 ± 10.8 cm, mean \pm SE, $n = 10$; F. Arenas, personal communication). However, the largest algae (150–200 cm, personal observation) in the study area are frequently observed at 2–3 m below lowest astronomical tide.

Impact of an invader on a native mature assemblage. During the spring tides of January 2002, 12 permanent 50 \times 50-cm plots were randomly established along 200 m of coastline. The corners of the quadrats were permanently marked using anchor bolts placed in the substratum to allow repeated sampling. Plots were randomly assigned to control or removal treatments with six replicates for each. The removal treatment entailed removing all *S. muticum* plants by carefully detaching their holdfasts with a scraper, both inside the plot and in a 1-m wide buffer zone surrounding the plot. This buffer zone was established to eliminate large algae in the neighborhood of the plots. The removal treatment was maintained over the course of the experiment by periodically removing new *Sargassum* recruits.

Percentage cover of algae was recorded bimonthly with a 50 \times 50-cm PVC quadrat divided by monofilament nylon fishing line into 5 \times 5-cm squares. Two layers of line were used to avoid parallax errors in sighting (Hawkins and Jones 1992). Primary and secondary covers (cover of algae directly on the substratum and overstorey canopy) were recorded at the 81 intersection points (maximum, 162 points), and the data were transformed as specific cover values. For this reason, estimates of cover may add to values greater than 100%.

Species richness (S) and diversity (H') were estimated for each sample. Diversity was calculated using the Shannon-Weaver index (H')

$$H' = -\sum p_i \times \log_2 p_i$$

where p_i is the proportion of total macroalgal cover of the i th species.

Because *G. spinosum* seems to be one of the most affected species since the arrival of *S. muticum* (Sánchez et al. 2005), we also estimated *Gelidium* biomass from percentage cover data and mean length (Dudgeon et al. 1999). The length of 10–15 randomly selected *G. spinosum* in each plot was measured at each sampling date. Mean length was converted into an estimate of dry biomass from linear regression of dry biomass on length ($y = -1.767 + 1.7057x$, $R^2 = 0.54$; $n = 101$). These values were then multiplied by the percentage of cover of *Gelidium* in each plot to estimate total dry biomass of *Gelidium* per plot (2500 cm²).

Effect of an invader on the successional process. Twelve permanent 50 \times 50-cm plots were randomly established in the study site. In January 2002 they were completely cleared of living organisms using a paint scraper and a blowtorch. To minimize edge effects, a cleared buffer zone surrounding each plot was established. The experimental treatments (removal and control plots) were identical to those in the previous experiment. Percentage cover of algae and average length of *G. spinosum* plants were recorded bimonthly at each plot during spring tides as detailed above.

Statistical analysis. The effects of *S. muticum*, both on the successional and mature assemblage, on the percentage cover of dominant species, biomass of *G. spinosum* (only for the mature community experiment), bare rock (only for the successional experiment), species richness (S), and diversity (H') were analyzed using repeated-measures analysis of variance (ANOVA). Treatment (two levels, control and removal) was considered as fixed factor. Thirteen repeated measures

were used in the mature assemblage experiment (January 2002 to March 2004) and a variable number of these measures in the successional experiment, because most of the species were only present during short periods of time. For these species, repeated-measures ANOVA were performed on the period in which they were dominant (March 2002 to November 2002 for *Ulva rigida* C. Agardh, September 2002 to March 2004 for *Stypocaulon scoparium* (Linnaeus) Kützting and *Cladostephus spongiosus* (Hudson) C. Agardh, and November 2002 to March 2004 for *Jania rubens* (Linnaeus) J. V. Lamouroux). Furthermore, the same analysis was conducted between March 2002 and November 2002 for bare rock data. One-way ANOVA was also used to test for differences between treatments (control and removal) in *Sargassum* cover at the end of the successional experiment (March 2004 cover data). Cochran's test was performed to check for homogeneity of variances (Winer 1971), and where appropriate, arcsine and logarithmic transformations were applied. Student's t -tests were used to compare the percentage cover of dominant species at the end of the experiment between control plots from mature and successional experiments. All tests were done with SPSS 11.0 (Chicago, IL, USA) for Windows.

To describe the assemblage responses to treatments, non-metric multidimensional scaling (nMDS) ordinations (Field et al. 1982) were used. These analyses were based on Bray-Curtis similarity matrices derived from cover data after a square root transformation to reduce the influence of dominant species. The relationship between control and *Sargassum* removal plots was compared before manipulation (January 2002), in March 2002, and December 2003 as well as at the end of the experiment (March 2004). To avoid seasonal artifacts, January 2002 with December 2003 and March 2002 with March 2004 were the pair-wise comparisons interpreted in the analyses.

In the first experiment, *S. muticum* was omitted from the data set to check if the possible differences between treatments were caused not by the presence of this species, but by changes in the remaining assemblage. Moreover, the same analysis was also performed omitting the most abundant species (*B. bifurcata*, *G. spinosum*, and *S. muticum*).

Two-way crossed analysis of similarity (ANOSIM) (Clarke 1993) (on square root transformed cover data) was used to test for differences between time and experimental manipulation, removing in each case the effect of the other factor. Time with four levels (January 2002, March 2002, December 2003, and March 2004) and experimental manipulation with two levels (control and removal) were the factors included in the analysis. Pair-wise comparisons were also calculated. Where significant effects of treatment were observed, one-way ANOSIM tests were used to analyze the effect of experimental manipulation on samples from each time separately. When the ANOSIM test indicated significant differences between treatments, the similarity percentage procedure was performed on the data to determine which species contributed most to the dissimilarity between groups. All these calculations were performed using the PC software PRIMER 5.2.9 for Windows (Plymouth Marine Laboratory, Plymouth, UK).

RESULTS

Impact of an invader on a native mature assemblage. Although *S. muticum* remained rare or absent in the removal plots, control plots showed the seasonal pattern of abundance at this latitude (Arenas and Fernández 2000) but with high variability between plots (Fig. 1A). Apart from seasonal changes corresponding to the seasonal pattern of growth, there were no significant changes in the percentage

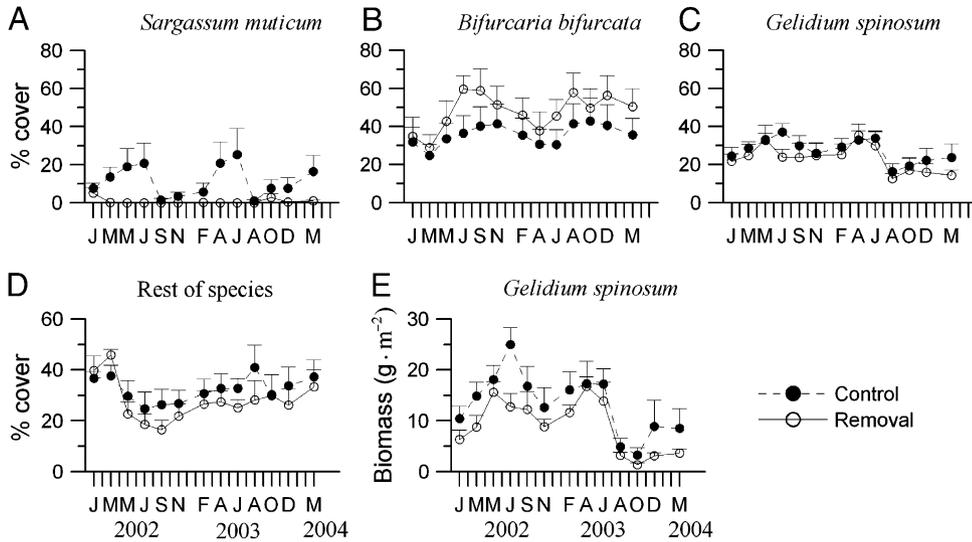


FIG. 1. Percent cover (mean \pm SE) of *Sargassum muticum* (A), *Bifurcaria bifurcata* (B), *Gelidium spinosum* (C), other species present (D), and *G. spinosum* biomass (E) in the mature assemblage removal experiment ($n = 6$). The first data point (January 2002) in each series is a preremoval sample. Control and removal treatments are indicated.

cover of *B. bifurcata*, *G. spinosum* (Fig. 1, B and C, $P > 0.05$; Table 1), and the rest of species (Fig. 1D, $P > 0.05$; Table 1) between control and removal treatments. *Gelidium spinosum* biomass showed the similar temporal dynamics in both treatments (Fig. 1E, $P > 0.05$; Table 1). Temporal variation of species richness (S) and diversity (H') were also similar for both treatments, with the highest values in winter and the lowest in summer (Fig. 2, A and B, $P > 0.05$; Table 1).

TABLE 1. Results of repeated-measures ANOVA testing the effect of *Sargassum muticum* on dominant species, richness (S), and diversity (H') in the mature community experiment.

	Wilks lambda	P
<i>Bifurcaria bifurcata</i>	1.85	0.203
<i>Gelidium spinosum</i>	2.20	0.169
Rest of species	0.51	0.488
<i>Gelidium spinosum</i> biomass	0.18	0.690
Richness (S)	4.47	0.061
Diversity (H')	2.40	0.152

Variances were homogeneous after logarithmic transformation for *G. spinosum* biomass data. Cochran's test for homogeneity of variances, $P > 0.05$.

This trend was consistent during the 2 years of the study.

Bidimensional representations of the nMDS ordination analyses showed no segregation through time between the two treatments considered (Fig. 3A) (differences between treatments: $R = 0.005$, $P > 0.05$, averaged across all time factors). Interannual differences in assemblage structure were detected by two-way crossed ANOSIM (differences between time factors: $R = 0.098$, $P < 0.05$, averaged across both treatment factors). Pair-wise comparisons detected significant differences between January 2002 and December 2003. No significant differences were detected between March 2002 and March 2004. Likewise, the same results were obtained when dominant species were omitted from the analysis (data not shown, Fig. 3B).

Effect of an invader on the successional process. No differences between treatments were detected in the general patterns of succession (Fig. 4, $P > 0.05$ in all cases; Table 2). The first 8 months after the denudation of the plots, ephemeral algae, mainly *U. rigida*, dominated the primary substratum (Fig. 4A). The decline of these species was followed by an increase in abundance of *S. scoparium* (Fig. 4B) and *C. spongiosus* (Fig. 4C), which lasted for approximately the next 12

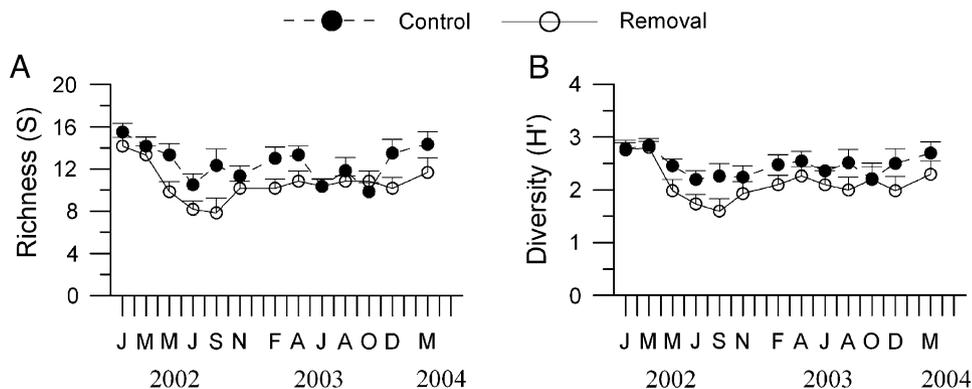


FIG. 2. Species richness (A) and diversity (B) (mean \pm SE) in the mature assemblage removal experiment ($n = 6$). The first data point (January 2002) in each series is a preremoval sample. Control and removal treatments are indicated.

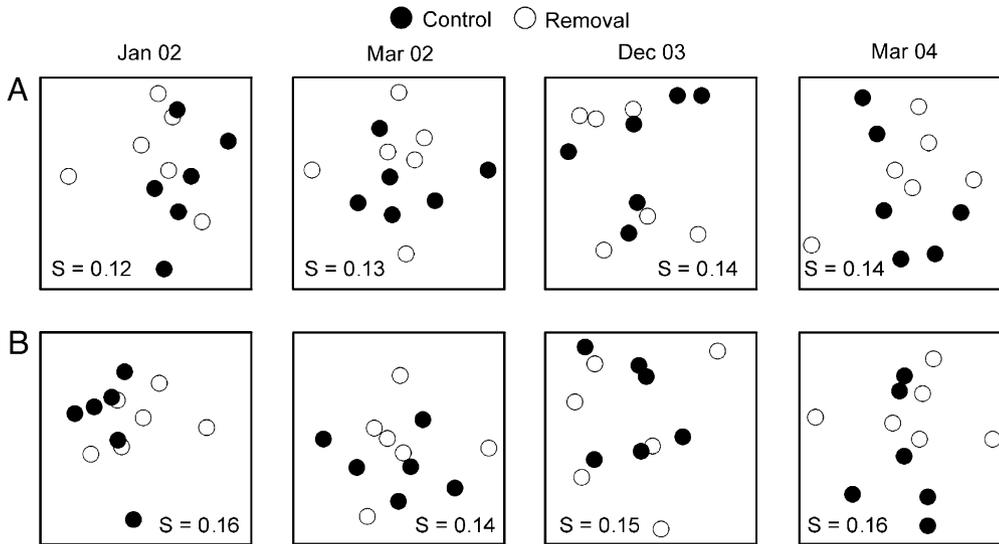


FIG. 3. nMDS ordination showing temporal changes in assemblage structure from January 2002 to March 2004 omitting *Sargassum muticum* (A) and omitting *S. muticum*, *Bifurcaria bifurcata*, and *Gelidium spinosum* (B) from the data set. Control and removal treatments are indicated. S, stress.

months. At the end of this second phase, there was a continuous increase of *J. rubens* (Fig. 4D) as epiphyte on the previous species. Twenty-four months after the start of the experiment, a dense cover of this species dominated the plots. A progressive colonization by *G. spinosum* was observed after the clearance (Fig. 4E). However, at the end of the experiment, *B. bifurcata* cover was very low (<5% cover). During the first spring (2002), *S. muticum* cover was very low, but it increased in abundance each year and by 2004 (Fig. 4F). At the end of the experiment, significant differences in the cover of *S. muticum* between treatments were detected by ANOVA ($F = 11.28$, $df_{1,10}$, $P < 0.01$). The dynamics of percent free space (bare rock), species richness, and diversity reflected the progression of the successional process (Fig. 5). Five months after the initial clearance, all available space at disturbed plots was occupied by a dense cover of seaweeds (Fig.

5A). Species richness and diversity increased from the start of the experiment showing the alternation of successional phases described above, with reduced values during the dominance phase of the species mentioned before (Fig. 5, B and C).

The nMDS analysis is shown in Figure 6. Each of the four dates included in the analysis segregated into an obvious group. This result is consistent with the “successional phase” concept widely cited in the literature and also observed here. Two-way crossed ANOSIM detected significant differences between time and treatment factors: Both time and treatment had effects on assemblage structure after a clearance that completely removed all species (differences between time factors: $R = 0.88$, $P < 0.01$, averaged across both treatments; differences between treatments: $R = 0.106$, $P < 0.05$, averaged across all time factors). Pair-wise comparisons showed differences between

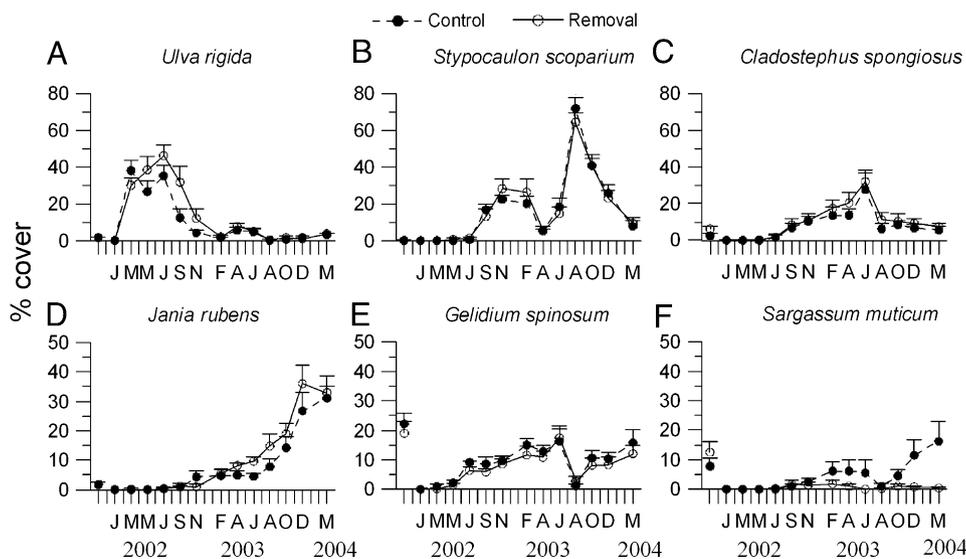


FIG. 4. Percent cover (mean \pm SE) of *Ulva rigida* (A), *Stypocaulon scoparium* (B), *Cladostephus spongiosus* (C), *Jania rubens* (D), *Gelidium spinosum* (E), and *Sargassum muticum* (F) along the successional process ($n = 6$). The first data point in each series belongs to the preclearance sample. Control and removal treatments are indicated.

TABLE 2. Results of repeated-measures ANOVA testing the effect of *Sargassum muticum* on dominant species, richness (S), and diversity (H') in the succession experiment.

	Wilks lambda	P
<i>Ulva rigida</i>	1.56	0.230
<i>Stypocaulon scoparium</i>	0.67	0.430
<i>Cladostephus spongiosus</i>	0.03	0.865
<i>Jania rubens</i>	1.70	0.220
<i>Gelidium spinosum</i>	1.87	0.200
Bare rock	0.73	0.411
Richness (S)	0.63	0.445
Diversity (H')	0.46	0.510

Variances were homogeneous after arcsine transformations for *J. rubens* and *G. spinosum* data. Cochran's test for homogeneity of variances, $P > 0.05$.

January 2002 and December 2003 as well as between March 2002 and March 2004 ($P < 0.01$ in all cases). One-way ANOSIM detected significant differences between control and removal plots in March 2004 ($R = 0.315$, $P < 0.05$), and no differences were found in January 2002, March 2002, and December 2003 ($P > 0.05$ in all cases).

By March 2004 *J. rubens* (22.60%), *G. spinosum* (13.51%), and, only in control plots, *S. muticum* (10.03%) were the species that contributed most of the observed similarity among samples in both control and removal plots (Fig. 7A). The species contributing more to the observed net dissimilarity between treatments in March 2004 are listed in Figure 7B. In March 2004, 2 years after the perturbation, *S. muticum* was the species that explained most to the observed net dissimilarity (12.68%) between groups.

DISCUSSION

Models about community organization predict that the removal of a dominant species from a system generally results in an increase of species richness, diversity, and changes in the relative abundance of understory species (Paine 1966, Dayton 1975, Lubchenco 1978, Clark et al. 2004), although in some cases no significant changes in community structure have been detected (Benedetti-Cecchi and Cinelli 1992, Edgar et al. 2004). In our system, the effect of *S. muticum* removal on the macroalgal assemblage over 2 years was undetectable. In addition, we found no evidence that

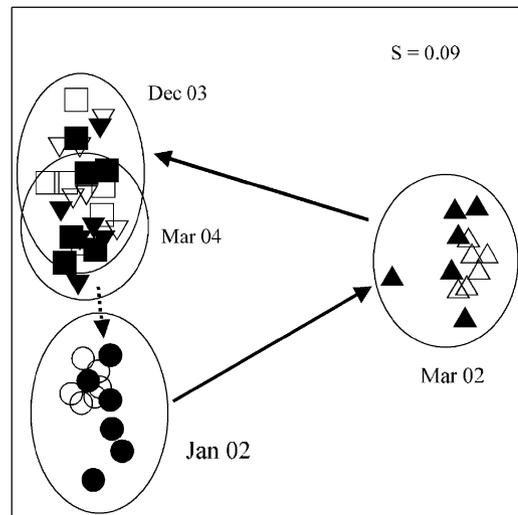


FIG. 6. nMDS ordination showing temporal changes in assemblage structure from initial clearance (January 2002) to the end of the experiment (March 2004) in both control (filled symbols) and removal (open symbols) treatments. S, stress.

S. muticum altered the successional sequence of this macroalgal assemblage. Species richness, diversity, and percentage cover of native macroalgae did not show significant differences between control and removal treatments.

In previous experimental studies testing the impact by *S. muticum* on well-established macroalgal assemblages (Ambrose and Nelson 1982, De Wreede 1983, Viejo 1997, Stæhr et al. 2000, Wilson 2001, Britton-Simmons 2004), its effects varied depending on the habitat studied. However, a general conclusion emerges from these works: The large size of *S. muticum* plants, compared with most native algae in the studied systems, indicates that competition must be mainly for light. Accordingly, this phenomenon should be more evident in densely colonized areas, where it would be more likely to induce changes in resident macroalgal vegetation through competitive interactions (Viejo 1997, Britton-Simmons 2004). Subtidal native communities have shown strong effects by *S. muticum* (Ambrose and Nelson 1982, Stæhr et al. 2000, Britton-Simmons 2004), whereas the intertidal is less affected (De Wreede 1983, Viejo 1997, Wilson 2001). At the start of our experiment, the mean density of *S. muticum* plants in experimental plots was approximately

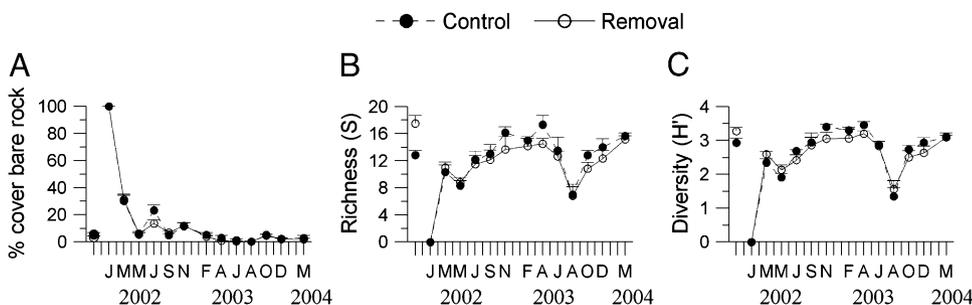


FIG. 5. Bare rock (A) (as percent free space), species richness (B), and diversity (C) (mean \pm SE) along the successional process ($n = 6$). The first data point in each series belongs to the preclearance sample. Control and removal treatments are indicated.

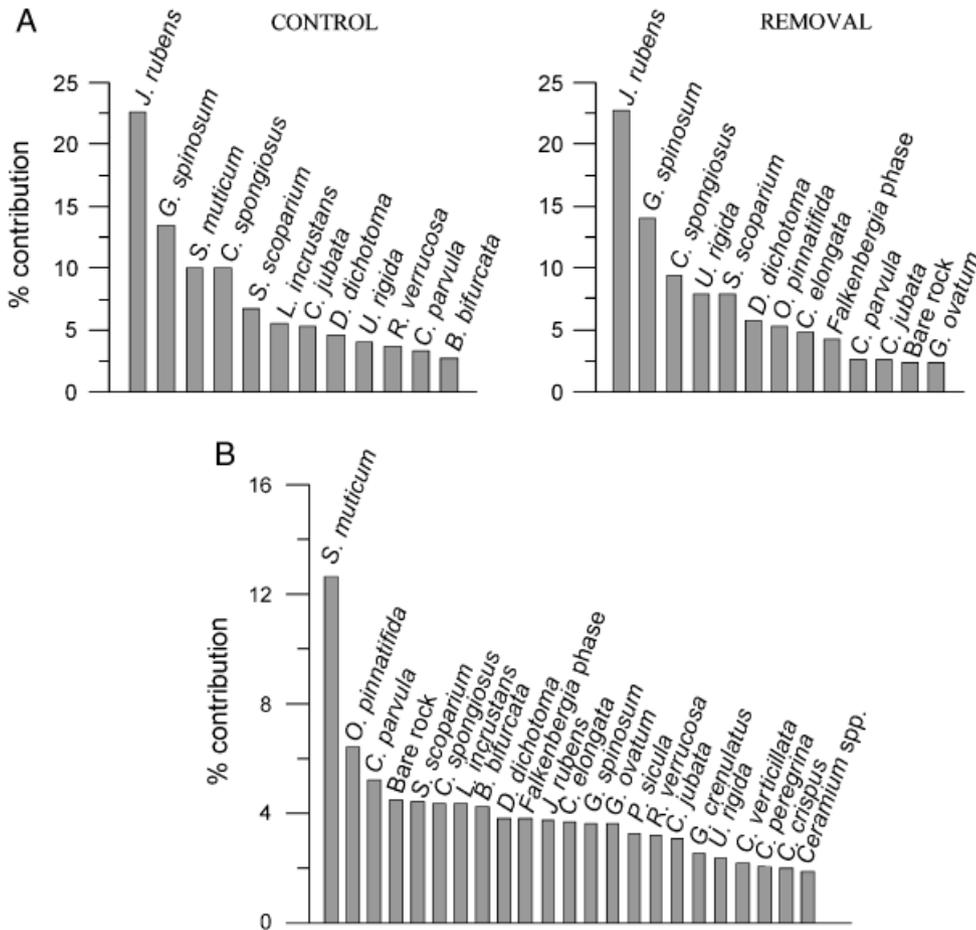


FIG. 7. Relative species contribution (%) to overall similarity (A) and net dissimilarity (B) in assemblage structure between control and removal treatments in March 2004 determined using similarity percentage procedure analysis. A cut-off of 90% was applied.

24 plants · m⁻², much lower than the density reported by Ambrose and Nelson (1982) (56.9 plants · m⁻²) in subtidal areas. The density of *S. muticum* in our experiments was probably insufficient to limit the growth of native species, and this could explain why we did not detect any effect of *S. muticum* on native macroalgal assemblages.

The establishment and spread of *S. muticum* is strongly controlled by the amount of free space (Critchley 1983, Andrew and Viejo 1998, Fernández 1999, Stæhr et al. 2000, Britton-Simmons 2004). It is well known that in addition to disturbance intensity and frequency, the timing of disturbance, particularly the coincidence of free space and propagule availability, is a key determinant of invasion success (Kenelly and Larkum 1983, Kenelly 1987, Benedetti-Cecchi and Cinelli 1994). We performed a disturbance that completely cleared the rock substratum in winter, the period during which the frequency of natural disturbances is the highest at our study site. By spring, when *S. muticum*'s reproduction had started, a dense cover of early colonizers already occupied the experimental plots. Recruitment inhibition by this type of species is a phenomenon widely reported (Connell and Slatyer 1977, Lubchenco 1983, Dethier 1984, Kim and De Wreede 1996, Benedetti-Cecchi 2000), but facilitation has also been found (Turner 1983). Therefore, there is

evidence that invasion resistance by preemption of space may be higher when disturbances occur outside of the reproduction period of the invasive species (Deyscher and Norton 1982, De Wreede 1983, Andrew and Viejo 1998). Our data indicate, nevertheless, that *S. muticum* can recruit during the first successional stages after a perturbation, and therefore it may be a potential competitor for light and space at longer time scales. At the end of the experiments, comparison with control plots from the mature assemblage experiment indicates that cleared plots had not yet reached the final succession stage (Table 3). For this reason, we can-

TABLE 3. Percent cover (mean ± SE) of the most abundant macroalgal species in control plots at the end of the experiments (March 2004).

Species	Control plots	Control scraped plots	Student's <i>t</i> -test
<i>Bifurcaria bifurcata</i>	35.59 ± 8.65	2.67 ± 1.17	<i>P</i> < 0.01
<i>Calliblepharis jubata</i>	5.14 ± 2.76	1.85 ± 0.68	NS
<i>Corallina elongata</i>	2.47 ± 0.70	1.65 ± 0.75	NS
<i>Gelidium spinosum</i>	23.25 ± 5.75	15.63 ± 3.53	NS
<i>Sargassum muticum</i>	16.46 ± 8.31	16.26 ± 6.80	NS
<i>Stypocaulon scoparium</i>	8.23 ± 2.56	5.56 ± 2.17	NS
TOTAL COVER	91.14	43.62	<i>P</i> < 0.01

NS, not significant.

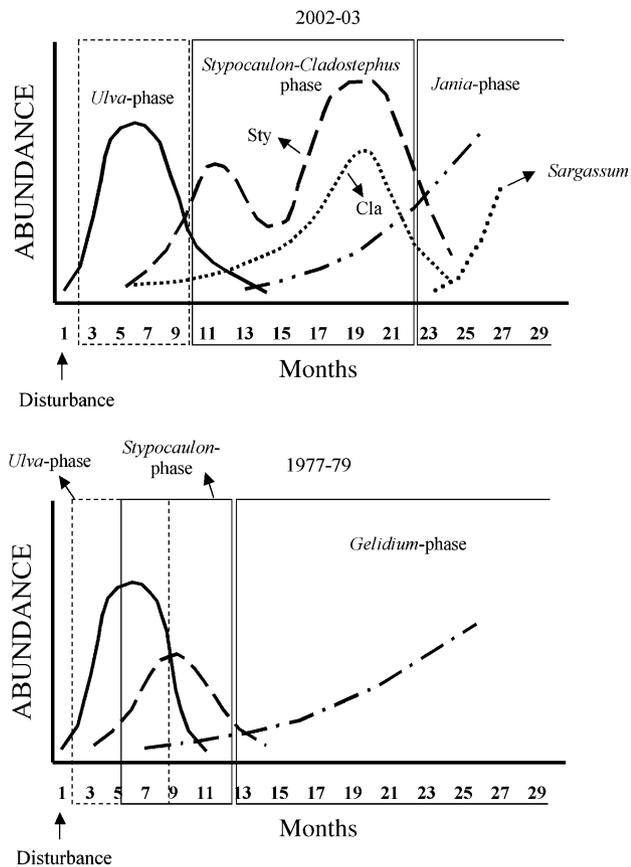


FIG. 8. Conceptual models of the general succession stages that occurred at Aramar over a 2-year period, at two different times: 2002–2003 and 1977–1979. Cla, *Cladostephus spongiosus*; Sty, *Stylocaulon scoparium*.

not determine whether *S. muticum* affects the recolonization of the dominant species such as *B. bifurcata* that needs more than 3 years to recover (Bokenham 1938).

The general pattern of succession that we observed largely differs from that described 25 years ago for the same intertidal assemblage (Fig. 8) (Fernández et al. 1981). Turf species (*S. scoparium*, *C. spongiosus*, and *J. rubens*) in mid-successional phases were more abundant compared with the previous model. This is in accordance with the strong changes observed in the dominance of the macroalgal assemblages growing at the low intertidal since the end of the 1980s, coinciding with the arrival and establishment of *S. muticum* (Sánchez et al. 2005). A monoculture of *G. spinosum* was replaced by a more diverse assemblage dominated by *G. spinosum*, *B. bifurcata*, and *S. muticum*. Moreover, an increase on the relative abundance of turf species (e.g. *S. scoparium*, *C. spongiosus*) has been observed to coincide with the decrease in *G. spinosum* biomass. An increase of sediment entrapment by turf species could inhibit the growth of *G. spinosum*, as suggested by some authors for kelp communities (Kenelly 1987, Kenelly and Underwood 1993, Edwards 1998). Thus, the successional sequence observed here could be a consequence of changes in the relationships among species

affecting competitive hierarchies between them (Menge 1995, Benedetti-Cecchi 2000). However, the ecological interactions underlying the observed field patterns remain unclear.

In conclusion, the results of this study suggest that *S. muticum* did not have a significant impact on the native low intertidal algal assemblage at Aramar. Its low abundance at this intertidal level and its pseudoperennial character (high percentages of covers are only recorded during a few months in the year, Arenas and Fernández 2000) appear to or may limit competitive processes with native species. In addition, the short time scale of this experiment compared with the temporal scale of succession in this system may explain why an impact of *S. muticum* was not detected in this study. Similarly, for all previous studies testing the impact of *S. muticum* on native intertidal communities, a temporal scale of no more than 3 years was always considered (De Wreede 1983, Viejo 1997). Therefore, long-term canopy removal experiments are required to test the impact of *S. muticum* on these habitats, especially when indirect effects could be operating and long-life species are present (i.e. *B. bifurcata*) (Benedetti-Cecchi 2000).

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