LONG-TERM CHANGES IN THE STRUCTURE OF INTERTIDAL ASSEMBLAGES AFTER INVASION BY *SARGASSUM MUTICUM* (PHAEOPHYTA)[1]

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The macroalgal assemblages at the low intertidal zone were studied at three localities on the north coast of Spain between 1977 and 2002. Two of these localities were invaded at the end of the 1980s by the brown seaweed *Sargassum muticum* (Yendo) Fensholt (Phaeophyta, Sargassaceae), whereas the third locality remained free of the invader. In 2002, distinct algal assemblages were noticed in invaded and noninvaded localities. No major changes were detected in the noninvaded locality. Apart from the obvious presence of *S. muticum*, the changes observed in the invaded localities included a significant reduction in abundance of the previous dominant species (the red alga *Gelidium spinosum* (S. G. Gmelin) P. C. Silva) as well as an increased number of species and diversity, increased primary productivity, and variations in the seasonal abundance patterns of some species. We speculate that the arrival of *S. muticum* had a negative effect on the dominant native *G. spinosum*, probably related to competition for light. This resulted in indirect positive effects on other species of the assemblage (such as *Bifurcaria bifurcata* R. Ross). Other small epiphytic opportunistic species might also have been benefited from the presence of *S. muticum*, because the invader has a rich associated epiphytic assemblage.

Key index words: biomass; competition; growth cycle; invasion; long-term change; macroalgal assemblages; northern Spain; *Sargassum muticum*

Abbreviation: DW, dry weight

The arrival of exotic seaweeds to new areas has become an increasing phenomenon during the last decades (Verlaque 1994, 2001, Boudouresque and Verlaque 2002), mainly due to dispersal via human-mediated transport (Bax et al. 2001). However, the impact of nonindigenous species on native communities is highly variable. Many invasions have unnoticeable effects, and only a small proportion of successful establishments (the tens rule, Williamson 1996) causes severe modifications on native assemblages (Vitousek 1990, Ceccherelli et al. 2002, Grosholz 2002). However, this observation may be biased. Although some impacts are easily and quickly detected (e.g. *Caulerpa* spp. in the Mediterranean, Ceccherelli and Campo 2002), sometimes more time is needed before impacts are evident (Viejo 1997).

One of the best known alien species in Europe is the brown seaweed *Sargassum muticum* Yendo (Fensholt). Its expansion along the European coasts is a case of well-documented invasion. The species is native from Japan and was reported for the first time in England in 1973 (Farnham et al. 1973). However, the first observation of drift material in Europe was at Cap Gris-Nez (Pas de Calais, France) in 1972 (Coppejans et al. 1980). It has subsequently spread north and southward along the coasts of Europe, from Portugal in the south (R. Santos, personal communication) to Scandinavia in the north (Rueness 1989, Karlsson and Loo 1999, Steen 2004). *Sargassum muticum* was first recorded in Spain in 1985 (Casares et al. 1987). Since then, it has successfully colonized shallow subtidal habitats in sheltered shores and intertidal rock pools and the low intertidal levels on more exposed zones (Gorostiaga et al. 1988, Andrew and Viejo 1998, Fernández 1999). The invasive success of *S. muticum* has been related to the combination of opportunistic features and perennial persistence (Norton 1976). High growth rates and effective mechanisms of short and long range dispersion have been considered, among others, as responsible of its successful spread (Norton 1977). However, its possible impact on native communities is poorly studied. The few examples in the literature show that the impact of *S. muticum* on native communities is highly variable depending on the habitat or species assemblages. Generally, studies of intertidal communities have found little or no effects (De Wreede 1983, Viejo 1997), whereas those performed in subtidal habitats revealed significant impacts (Ambrose and Nelson 1982, Stæhr et al. 2000, Britton-Simmons 2004).

In this article, we report changes in a low intertidal assemblage in a semiexposed rocky shore on northern Spain over a temporal scale of 25 years. To detect changes induced by *S. muticum*, we compare species assemblages of three localities, before and after the arrival and establishment of the species.

MATERIALS AND METHODS

Study sites. The study is based on data of macroalgal abundances at the low intertidal zone (0.4–0.8 m above the lowest astronomical tide) on the north shore of Spain. Three localities, within a shore stretch of 25 km, were considered: Ara-

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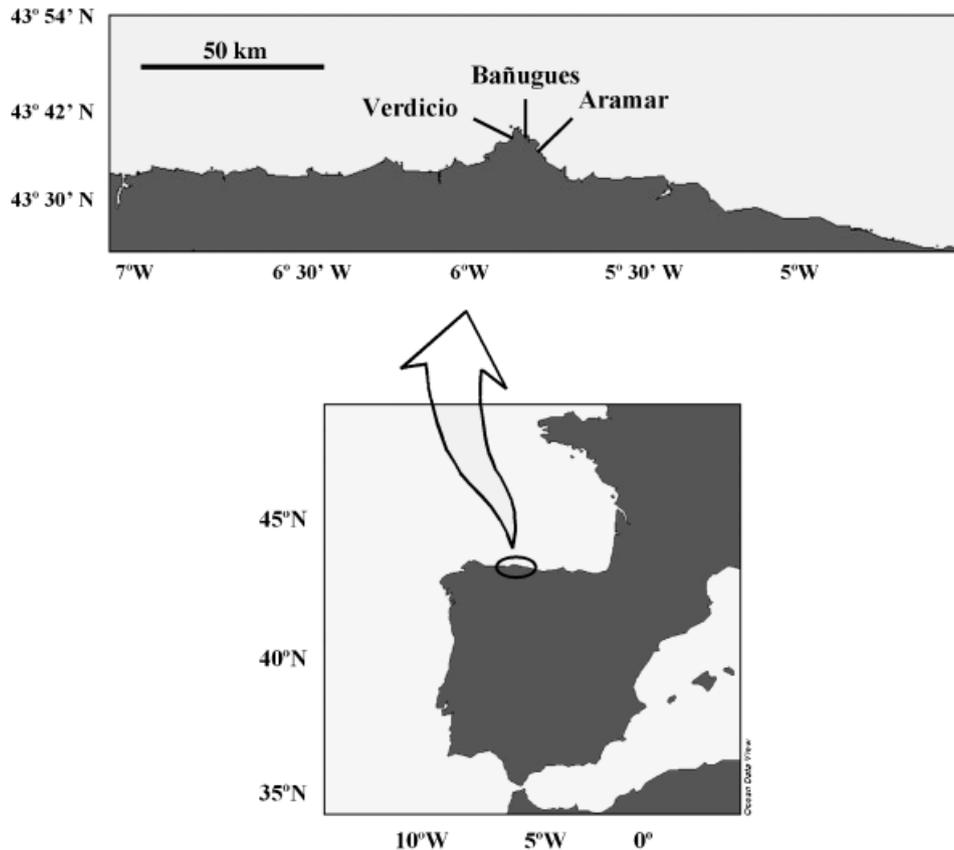
Fig. 1. Map of northern Spain showing the study sites.

mar (43° 36′ N, 5° 46′ W), Bañugues (43° 38′ N, 5° 48′ W), and Verdicio (43° 39′ N, 5° 50′ W) (Fig. 1).

Aramar is a small sheltered bay. A few years after the first occurrence of *S. muticum* at this locality (Fernández et al. 1990), a dense population of this species was established within the *Gelidium spinosum* (S. G. Gmelin) P. C. Silva-dominated assemblage. The collecting site was located on a gently sloping rock platform semiexposed to wave action and parallel to the shoreline.

Bañugues is a heterogeneous wave-cut rock platform with many large blocks and boulders (Arrontes 1990) and semiexposed to wave action. The zonation pattern of this zone is similar to Aramar (Fernández and Niell 1982). This locality was also invaded by *S. muticum* around 1988–1990 (Fernández 1999).

Verdicio is a small rocky platform facing north and exposed to severe wave action. Macroalgal communities in this area

have been described by several authors (Anadón and Niell 1981, Anadón 1983). The low intertidal level is dominated almost exclusively by *G. spinosum*. Wave exposure is high enough to prevent the establishment of *Sargassum* plants at this locality (Andrew and Viejo 1998). At present, this locality has not been invaded by *S. muticum*.

Collection of data. Data were compiled from the literature and from unpublished academic reports. Additional data were collected in January and July 1996 and monthly in 2002. Available data for the study and analyses and the number of replicates for each sampling date are summarized in Table 1. Samples are from three localities, two invaded by *S. muticum* (Aramar and Bañugues) and one not invaded (Verdicio). However, the number of available years per period (before and after the arrival of *S. muticum*) and the number of months sampled in each year are variable between localities (see Table 1).

TABLE 1. Macroalgal abundance data available for the study and analyses.

Locality	Invasion period	Year	Samples per month (50 × 50 cm)	Sampled months	Data source
Aramar	Before	1977	2–5	January to December	Anadón and Fernández 1986
		1985	2	January to December	J. Arrontes, unpublished PhD thesis
	After	1996	3	January and July	This work
		2002	3	January and July	This work
Bañugues	Before	1977	2–3	January and July	Anadón and Fernández 1986
		1985	2	January to December	J. Arrontes, unpublished PhD thesis
	After	1996	3	January and July	This work
Verdicio	Before	1977	2	January and July	R. Anadón, unpublished report
	After	1996	3	January and July	This work

TABLE 2. Dominant species used in the nonparametric analysis.

	Aramar				Bañugues			Verdicio	
Species	1977	1985	1996	2002	1977	1985	1996	1977	1996
Bifurcaria bifurcata	+	+	+	+	+	+	+	+	+
Calliblepharis jubata	+	+	+	+	+	+	+	−	+
Chondrus crispus	+	+	+	+	+	+	+	+	+
Corallina spp.	+	+	+	+	+	+	+	+	+
Cystoseira baccata	+	+	+	+	+	−	+	−	−
Gelidium corneum	+	+	+	+	+	+	+	+	+
Gelidium spinosum	+	+	+	+	+	+	+	+	+
Jania spp.	+	+	+	+	−	+	+	−	+
Laminaria ochroleuca	−	−	−	−	−	−	−	+	−
Mesophyllum lichenoides	+	+	+	+	+	+	+	+	+
Peyssonnelia atropurpurea	+	−	+	+	+	−	+	−	+
Phyllophora sicula	+	−	+	+	−	−	+	−	−
Pterocladiella capillacea	−	−	−	+	+	−	−	+	−
Pterosiphonia complanata	+	+	+	+	+	+	+	−	+
Sargassum muticum	−	−	+	+	−	−	+	−	−
Stypocaulon scoparium	+	+	+	+	+	+	+	−	+

+, presence; −, absence.

In all cases, sampling consisted of complete removal of all algae present in randomly chosen 50 × 50-cm plots. In the laboratory, algae were identified to species, dried to constant weight (60° C, 48 h), and weighed to the nearest 0.01 g. Any species present but with biomass below 0.01 g dry weight (DW) was arbitrary assigned to an abundance of 0.01 g *Lithophyllum incrustans* Philippi and other encrusting species were not considered in the quantitative analysis because of the difficulty of the collection. The taxonomy of species from records before 1996 was corrected by following Guiry and Nic Dhonncha (2004).

Data were obtained by different researchers. To protect our results from possible errors derived from differences in taxonomic skills for some groups of algae (e.g. Ceramiales), in some analyses we used a subset of easily identifiable species (Table 2). Criteria for selection were as follows: 1) conspicuous and erect algae larger than 5 cm; 2) if smaller than 5 cm, those that usually form dense turfs; and 3) those easy to identify in the field. The biomass of the selected subset of species was always above 95% of the total macroalgal biomass in each sample.

Data analyses. To detect changes in the structure of macroalgal assemblages and unequivocally associate them to the invasion by *S. muticum*, a beyond BACI statistical analysis is required (Underwood 1992). However, the structure of our data (absence of proper temporal and spatial replication) prevented the application of this type of analysis (Table 1). Consequently, changes in the structure of macroalgal assemblages were assessed by two different analytical approaches: 1) by using multivariate ordination methods on the selected subset of species and the complete set of dates and localities and 2) by the analysis of the temporal patterns in Aramar, the most intensely sampled locality. In the latter, we focused on the changes in the number of species, dominance, primary production, and patterns of abundance of dominant species. With these analyses, it is not possible to infer causality between the arrival of *S. muticum* and changes in the macroalgal assemblage. Nevertheless, results can reveal the existence of changes in the structure of macroalgal assemblages and whether or not they are associated to the arrival of *S. muticum*.

The similarity of macroalgal assemblages before and after the arrival of *S. muticum* was analyzed using nonparametric multidimensional scaling ordination and the Bray-Curtis coefficient as similarity index (Clarke and Green 1988, Clarke 1993). The multivariate analyses were performed using PRIMER 5.2.9 (Plymouth Marine Laboratory, Plymouth, UK) on standardized square-root transformed data of biomass. The major objective was the assessment of the changes in the native community after the invasion by *S. muticum*. However, the mere presence of *S. muticum* in a fraction of the samples might influence the ordination of the samples, even though the native macroalgal assemblage remained unaltered. Thus, separate analyses were done including and omitting *S. muticum* from the data sets. Replicated samples from the same sampling date and locality were pooled to reduce variability in the data set. One-way analysis of similarity (ANOSIM) was used to test for differences between the two groups of samples, before and after the invasion by *S. muticum*. The contribution of each species to the observed dissimilarity between groups was estimated using the similarity percentages procedure.

A crude estimation of the variation in the number of species was obtained from the cumulative number of species identified in samples collected in January and July in all four years (1977, 1985, 1996, and 2002). Dominance curves were constructed for the same data.

Net primary production was estimated following the method of the increase in biomass (ΔB) at monthly intervals (Anadón and Fernández 1984). The method consists of the calculation of the production of the main species that configure the assemblage and the production of the rest of species, separately. The equation used was $P_i = \Sigma \Delta B_i + \Sigma \Delta B_r$ where B_i is the biomass of the main species and B_r the biomass of the rest of species as a whole.

An additional analysis investigated changes in the seasonal patterns in the two most abundant species (*G. spinosum* and *Bifurcaria bifurcata* R. Ross) and total biomass. A factorial analysis of variance considered three factors: year (Y, fixed) with three levels (1977, 1985, and 2002), season (S, fixed) with four levels (winter, spring, summer, and autumn), and date (D, random) nested in the interaction Y × S and with two sampling dates per year and season. There were two replicates in each sampling date. Year was considered fixed because we were interested in the differences in those specific years (2 years before the arrival of *S. muticum* with data obtained by two different researchers and 1 year after the arrival). Season was considered fixed and orthogonal with year because we compared abundances among periods with distinct environmental conditions (seasons). We did not consider seasons as mere different intervals of time within each year. Season as a main effect was not relevant in this study. Instead, we investigated whether or not seasonal patterns of abundance were consistent across years

(interaction Y × S). Selected sampling dates were coincident with two spring tides in the central part of each season, and thus date is random and nested in the interaction. We were not specifically interested in the effect of date. It was included in the analysis because replication in time is needed to detect significant Y × S effects. Cochran's C test was used to test for homogeneity of variances. A posteriori Student-Newman-Keuls multiple comparisons tests were done for relevant significant effects.

RESULTS

Multivariate analyses revealed clear changes in the macroalgal assemblage structure in localities invaded by *S. muticum*. The ordination of samples from the complete data set of dates and localities showed two well-defined groups (Fig. 2). One group was formed by all the samples of Aramar 2002, Aramar 1996, and Bañugues 1996 (samples collected after the arrival of *S. muticum*, hereafter named invaded samples), and the other group was formed by the samples of 1977 and 1985, Bañugues 1977 and 1985, and Verdicio 1977 and 1996 (samples collected before the arrival of *S. muticum*, hereafter named noninvaded samples). The separation of these groups was confirmed by the ANOSIM test (overall $P < 0.01$, using random samples of 999 permutations). The same groups were still evident when *S. muticum* was removed from the data set. The ordination pattern of samples was almost identical, and therefore data are not shown. Differences among the two groups were again significant (ANOSIM test, overall $P < 0.01$).

The contribution of species to the observed net dissimilarity between the two groups of samples (invaded and noninvaded) when *S. muticum* was included in the analysis were identified by the similarity percentages procedure (Fig. 3). *Sargassum muticum* contributed most (17.31%) to the observed dissimilarity due to its great abundance in invaded localities. Other species,

FIG. 3. Average contribution ($\pm$ SE) to net dissimilarity between the group of invaded samples and the group of noninvaded samples.

such as *B. bifurcata* (15.22%) and *G. spinosum* (12.61%), also contributed to the observed group separation, in these cases due to their increase or decrease in biomass respectively.

Changes in temporal patterns at Aramar. Annual patterns (1977, 1985, and 2002) of total seaweed biomass and that of the dominant species are shown in Figure 4. In 1977 and 1985 the Rhodophyta *G. spinosum* dominated the macroalgal assemblage with more than 90% of the total biomass. By 2002 great changes had occurred as *B. bifurcata*, *G. spinosum*, and *S. muticum* now codominate with 34%, 19%, and 16% of the total biomass respectively (percentages are referred to yearly average). Apart from the obvious presence of *S. muticum*, the most striking change in the period between 1985 and 2002 was a dramatic decline in the biomass of *G. spinosum*. The yearly average biomass of *G. spinosum* dropped from approximately 190 g DW $\cdot$ 0.25 m^{-2} in 1977 and 1985 to 70 g DW $\cdot$ 0.25 m^{-2} in 2002. *Bifurcaria bifurcata* exhibited a 10-fold increase in biomass. As a consequence of these changes, the annual pattern of biomass of the macroalgal assemblage has drastically changed. Only one distinct biomass peak existed in summer 1977 and 1985. This peak was generated by the abundance maximum *G. spinosum*. In 2002, a longer period of high biomass, generated by sequential maxima of *S. muticum* and *B. bifurcata*, was recognized. From the remaining species, only *Calliblepharis jubata* (Goodenough and Woodward) Kützing showed conspicuous changes (Fig. 4). Its increase in abundance is probably associated with the presence of *S. muticum* because it is one of its most common epiphytes.

Despite the fact that the samples were collected and identified by different researchers, an evident trend in the species richness was observed from 1977 to 2002 (Fig. 5A). Dominance plots constructed for 1977, 1986,

FIG. 2. Nonparametric multidimensional scaling plot of standardized root square transformed macroalgal abundance data for all localities including *Sargassum muticum*. Each point represents the monthly mean of two samples. Triangles, Aramar; quadrats, Verdicio; diamonds, Bañugues. Filled symbols, before the arrival of *S. muticum*; open symbols, after the arrival of *S. muticum*. Circled symbols, with *S. muticum*.

FIG. 4. Seasonal changes in species abundance in Aramar in 1977, 1985, and 2002. Data are means ± SE (n = 2–5).

1996, and 2002 (Fig. 5B) showed that before the arrival of *S. muticum* (1977 and 1985) the assemblage was dominated by a few species, leading to an elevated biomass curve. In contrast, a more diverse distribution has developed after the establishment of *S. muticum* (1996 and 2002).

Net primary production increased from 1985 (1095 g DW · m^{-2} · year^{-1}) to 2002 (2679 g DW · m^{-2} · year^{-1}) (Table 3). *Sargassum muticum* and *B. bifurcata* were the species that contributed more to this increase. *Gelidium spinosum* production decreased from 1977–1985 (510–673 g DW · m^{-2} · year^{-1}) to 2002 (221.1 g DW · m^{-2} · year^{-1}).

Table 4 shows the results of the nested analysis of variance for mean differences in abundance of *G. spinosum*, *B. bifurcata*, and total biomass. Variations in the seasonal patterns in the abundance (significant interaction Y × S term) were observed only for *B. bifurcata*. No significant differences in biomass were observed among seasons in 1977 and 1985. But in 2002 the biomass of *B. bifurcata* was significantly higher in summer and autumn than in winter and spring. Year as main effect was significant in all three cases. Biomass of *G. spinosum* was significantly smaller in 2002, whereas that of *B. bifurcata* and total biomass were larger in 2002

(Table 5). Because of the significant Y × S effect for *B. bifurcata*, the main effect of year is not interpretable for this species. However, a highly significant year effect reinforces the conclusion that the abundance of *B. bifurcata* was greatly increased after the arrival of *S. muticum*.

DISCUSSION

Changes in the identity and abundance of dominant species and increased species richness and diversity were recorded in algal assemblages at two localities on the northern coast of Spain during the late 1980s. Algal assemblages at the low intertidal level before 1985 were dominated by the red alga *G. spinosum*, with a small number of accompanying species at low abundance. The low tidal levels in the same localities are today dominated by a mixed assemblage of species. These changes coincided with the invasion and spread of the brown alga *S. muticum* in the same localities. We suggest that changes were caused by the invasion of *S. muticum* because of the temporal coincidence between the arrival of *S. muticum* and the modification of the assemblages and also because assemblages in one close locality not invaded by *S. muticum* (Verdicio) remained almost unaltered. However, it is obvious that unam-
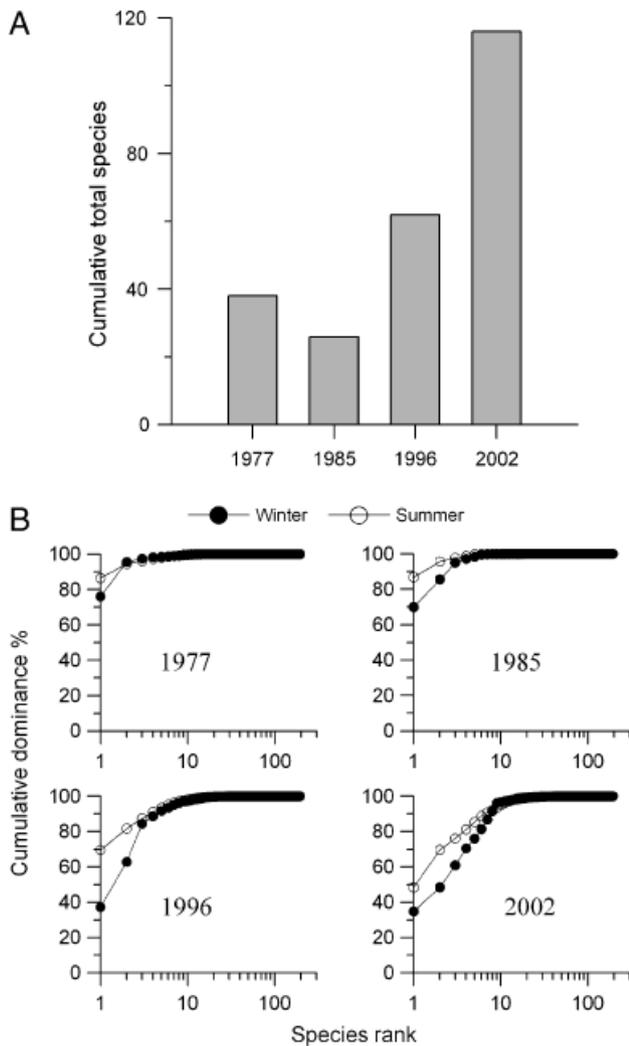
FIG. 5. Cumulative number of species (A) and dominance plots (B) in Aramar in 1977, 1985, 1996, and 2002 both in winter (January) and summer (July).

biguous identification of the causes of variation requires manipulative experiments with adequate temporal and spatial replication and proper controls (e.g. BACI sampling designs, Underwood 1992).

Several alternative processes, however, might also be responsible for the changes observed. The most

TABLE 3. Net production values at the *Gelidium spinosum*–dominated assemblage in Aramar in 1977, 1985, and 2002.

Species	Production (g DW·m^{-2}·year^{-1})		
	1977	1985	2002
Bifurcaria bifurcata	255	172	1019
Calliblepharis jubata	20.5	5.6	82.9
Chondrus crispus	8.2	166	151
Gelidium spinosum	510	673	221
Sargassum muticum	–	–	658
Stypocaulon scoparium	12.1	29.4	133
Remaining species	163	49.9	414
Annual production	969	1096	2679

likely process could be the well-known change in the composition of marine flora along the coast of northern Spain and the displacement of distributional boundaries (Miranda 1931, Fischer-Piette 1957, Anadón and Niell 1981, Fernández and Niell 1982, Anadón 1983, Lüning 1990). Algal assemblages in the northwest coast of Spain have evident affinities with assemblages of more northern European localities, whereas localities on the east part of the coast have a clear southern character (Van den Hoek 1975). Variations in summer upwelling conditions along the coast appear to be responsible for the change in abundance and distribution of two *Fucus* species (Arrontes 1993, 2002). The causes for the displacement of distributional boundaries for other species remain unknown, but they might also be related to yearly variations in upwelling intensity. If this is the case, the change in algal assemblages would be at a regional scale and not limited to some localities, as observed in the present study. Local environmental changes could be invoked, such as increased load of nutrients. However, an increase in the load of nutrients commonly favors low levels of species diversity and dominance of opportunistic species (Nielsen and Sand-Jensen 1990, Hardy et al. 1993, Pedersen and Borum 1996, Middelboe and Sand-Jensen 2000), which was not the case in this study.

Although we are reasonably confident that changes are due to *S. muticum*, we can only speculate on the causative mechanisms. Large canopy species can influence the abundance and composition of understorey species in different ways (Kennelly 1989), for example, by shading (Ambrose and Nelson 1982, Reed and Foster 1984, Critchley et al. 1990), by scouring (Black 1974), or by releasing of chemicals (Dayton et al. 1984). We suggest that the process operating since the arrival of *S. muticum* is related to competition for light, mainly with *G. spinosum*. Britton-Simmons (2004) demonstrated experimentally the negative influence of *S. muticum* canopy on the growth of other understorey species and did not find evidence that *S. muticum* altered the amount of inorganic nutrients in seawater. On the northern coast of Spain, *S. muticum* exhibits a well-marked seasonal cycle of growth with a slow-growth phase starting in October–November and a fast-growth phase during spring and early summer (Arenas and Fernández 2000). High growth rates and high covers (2.08 cm·d^{-1} and >90% cover; Arenas et al. 1995, Fernández 1999) are recorded during this phase. From mid-summer (July), senescence provokes the lost of branches and the species persists via perennial bases until the new slow-growth period. The abundance and growth cycle of *S. muticum* is critical because its abundance peak is coincident with the peak of abundance of *G. spinosum*. Because *G. spinosum* is a perennial species and almost monopolized the space at low tidal levels in the localities studied, a decrease in its abundance might favor increases in abundance of other species already present or colonization from adjacent areas. The species favored by the reduced abundance of *G. spinosum* may include species whose

TABLE 4. Analysis of variance for interannual, seasonal, and monthly differences in abundance (biomass) of *Gelidium spinosum*, *Bifurcaria bifurcata*, and total biomass in Aramar.

Source	df	G. spinosum			B. bifurcata			Total biomass		
		MS	F	P	MS	F	P	MS	F	P
Year	2	17330.84	17.55	0.0003	23368.42	32.07	0.0000	62961.69	13.72	0.0008
Season	3	14436.97	14.62	0.0003	6122.61	8.40	0.0028	25740.07	5.61	0.0122
Year × season	6	2184.07	2.21	0.1140	3309.41	4.54	0.0125	3945.82	0.86	0.5502
Time (year × season)	12	987.35	5.42	0.0002	728.65	1.36	0.2502	4589.74	8.59	0.0000
Residual	24	182.18			535.09			534.54		

Variances were homogeneous and data were not transformed (Cochran's C test, $P > 0.05$ in all cases). MS, mean square.

abundance maxima occur after the decay of *S. muticum* (e.g. *B. bifurcata*) and epiphytes, including those on *S. muticum* (e.g. *C. jubata*).

The impact of *S. muticum* on native communities apparently not only depends on the type of habitat colonized, but also on the abundance of *S. muticum*. Ambrose and Nelson (1982), Stæhr et al. (2000), and Britton-Simmons (2004) showed that in subtidal areas where *S. muticum* has profusely colonized, it induced negative changes on canopy species. Nevertheless, experiments performed on intertidal habitats have found little or no effect (De Wreede 1983, De Wreede and Vandermeulen 1988, Viejo 1997). However, De Wreede (1983) and Viejo (1997) found that only in those zones where *S. muticum* profusely colonized, the invader inhibited the recruitment of *Neorhodomela larix* (Turner) Masuda and reduced the abundance of *B. bifurcata* respectively.

In conclusion, we believe that the long-term changes observed at these low intertidal assemblages are caused by *S. muticum*. Competitive reduction of abundance of the previous dominant species, *G. spinosum* appears to be a likely explanation. Shading by *S. muticum* could also explain the changes in the case of some epiphytes and understorey species. Also, provision of new space (*S. muticum* itself) might favor an increased number of new epiphytic species. We suggest that indirect beneficial effects on many species (such as *B. bifurcata* and other small epiphytic opportunistic species) have been operating after the establishment of *S. muticum*. However, adequate experimentation at large temporal scales is needed to unambiguously identify these changes.

TABLE 5. Results of Student-Newman-Keuls multiple comparisons test.

	Year of sampling		
	Gelidium spinosum	Bifurcaria bifurcata	Total biomass
Year	1977 = 1985 > 2002	1977 = 1985 < 2002	1977 = 1985 < 2002

	Year × Season	
	Year	B. bifurcata
Season	1977	Wi = Sp = Su = Au
	1985	Wi = Sp = Su = Au
	2002	Wi = Sp < Su = Au

Wi, Winter; Sp, Spring; Su, Summer; Au, Autumn.

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