IS *SARGASSUM MUTICUM* A BENIGN INVADER OF TIDEPOOLS ON THE PACIFIC COAST OF NORTH AMERICA?

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ABSTRACT

IS *SARGASSUM MUTICUM* A BENIGN INVADER OF TIDEPOOLS ON THE PACIFIC COAST OF NORTH AMERICA

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The Japanese brown alga, *Sargassum muticum*, was first introduced to the Pacific Northwest coast in the early 1940's, and now occupies intertidal and shallow subtidal areas ranging from southern Alaska to southern Baja California. While several studies have shown that *S. muticum* can impact communities on a very local scale, broader-scale changes to the communities it invades are largely unknown. I combined a broad-scale survey of tidepools in rocky intertidal areas that have been invaded by *S. muticum* with a smaller scale experiment that manipulated *S. muticum* abundance to assess the potential effects of the invader on native tidepool communities. Percent cover of sessile species, counts of mobile species, and species richness estimates were compared between areas with high cover of *S. muticum* and those where the invasive alga was absent (either naturally absent or experimentally removed). There was general agreement between the survey and experiment: *S. muticum* had little or no effect on the communities studied. This was surprising since *S. muticum* is a visibly conspicuous alga. The results contrast with findings of previous work and indicate that species invasions may have different consequences for different habitats.

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INTRODUCTION

Introductions of non-indigenous marine organisms are rapidly altering the natural diversity and community structure of coastal marine environments throughout the world (Carlton & Geller 1993). These introductions result largely (and nearly always unintentionally) from human-induced transport mechanisms such as exchange of ballast water in near-shore environments, fouling of ship hulls, or movement of biota associated with species used for aquaculture (Carlton 1987; Ruiz et al. 2000). Because ports and aquaculture are restricted to calm bays and estuaries, nearly all recognized coastal invasions have been confined to these areas (Ruiz et al. 2000). Although several bays and estuaries along the Pacific coast of North America are among the most highly invaded in the world (Ruiz et al. 2000), invasions to the exposed rocky shores of this region have rarely been documented. The brown alga, *Sargassum muticum*, is an exception among marine invaders of this region because it has been successful in moderately wave-exposed rocky intertidal areas as well as in calm bays and estuaries.

Like many invasive species, *S. muticum* has several qualities that enable it to successfully invade new areas and rapidly expand. A single individual is capable of colonizing an area because the alga is monoecious and self-fertile (Deysher & Norton 1982). Plants experience an annual growth cycle, with rapid growth from a small, fibrous basal portion beginning in early spring and persisting (but substantially slowing) through mid-summer (Hales & Fletcher 1989). Maximum growth rates of 4 cm/day have been recorded for plants in early spring (Nicholson et al. 1981). In late spring/early summer, plants become reproductive and begin to release tiny zygotes (Hales & Fletcher 1990). Zygotes have been reported to have minimal dispersal, with most settlement occurring within 2-3 m of the parent plant, although some propagules travel up to 30m (Deysher & Norton 1982). Plants in colder regions typically reproduce for about three months (De Wreede 1983; Hales & Fletcher 1989; Nicholson et al. 1981; Norton & Deysher 1988), while those in warmer waters experience a longer reproductive period. Reproductive plants have been found year-round at Catalina Island, although most reproduction occurs February through August (Hales & Fletcher 1989). A small, first year plant is capable of producing up to three quarters of a million propagules before it dies back or disappears completely in late fall (Norton & Deysher 1988). The reproductive potential for large, older plants is considerably higher. In addition to this high fecundity, *S. muticum* has been shown to alter its morphology depending on the prevalent physical conditions (De Wreede 1980). Plants can be long with relatively few branches in calm, shallow, subtidal water, or "bushy" and dense with many shorter branches in mid-intertidal pools. *S. muticum*'s ability to persist under different physical conditions is combined with a tolerance to an extreme range of temperatures. Lüning and Freshwater (1988) found that *S. muticum* was able to tolerate temperatures ranging from –1.5 to +28° C—a feat rivaled by only 3 out of 47 native Pacific coast algal species tested.

The rate of spread of *S. muticum* has been disjunct and uneven along the Pacific coast of North America (Deysher & Norton 1982). It is thought that the initial introduction through the oyster culture industry occurred in southern British Columbia in the late 1930's, or early 1940's (Nicholson et al. 1981; Norton & Fetter 1981), but that subsequent spread of the alga was due solely to "natural" migration (Deysher & Norton 1982). Vegetative fronds have the ability to break free and float for long distances, eventually becoming reproductive and releasing zygotes (Critchley & Dijkema 1984; Deysher & Norton 1982). If vegetative fronds broke free from plants in northern regions in the early spring, the prevailing winds and currents could carry them far to the south (Deysher & Norton 1982). By the early 1970's, *S. muticum* had reached Baja, California, representing a distance of over 2000 km traveled in approximately 30 years (Farnham 1980). The current range of *S. muticum* is from southern Alaska to Baja California Sur, with large gaps in between (Aguilar-Rosas & Galindo 1990; Espinoza 1990). However, the alga appears to be slowly filling in these gaps where suitable habitat is available.

Non-native species introductions can be ecologically detrimental in a number of ways. An invader may compete for resources such as space, light, or nutrients with native species. Invasive species can also lower native species diversity or abundance through predation or habitat modification (e.g. Bellan-Santini et al. 1996; Ferrer et al. 1997; Race 1982). Some invaders have the potential to affect communities over a large geographic range due to broad physiological tolerances (to salinity, temperature, desiccation, etc.). There are many examples of invasive species severely altering their adopted communities (e.g. Brenchley & Carlton 1983; Grosholz & Ruiz 1995; Grosholz et al. 2000; Race 1982). In contrast, cases where an invasive species appears to have little or no impact on a community other than increasing species richness are less common (but see Roubik & Wolda 2001). Simberloff (1981) first noticed this bias in the literature and it is likely that rather than being less common, invasive species that cause little or no impact continue to be less reported.

Sargassum muticum has been shown to have short-term, localized effects on community structure (e.g. inhibition of recovery of native species Ambrose & Nelson 1982; De Wreede 1983; De Wreede & Vandermeulen 1988; Den Hartog 1997; reducing abundance of native species Staehr et al. 2000; Viejo 1997), but each study done thus far has focused on a unique species or group of species, and has been confined to a small area or single site; thus there is no real evidence that the invader is having any broad-scale impact on its adopted communities. An inherent problem with broad-scale investigations is that they usually require a large sampling effort. One large-scale sampling approach that offers reduced sampling time while maximizing spatial coverage is a survey that documents patterns in community structure. Conclusions from such a survey can be informative in terms of documenting patterns and possible causes for those patterns. However, it may be difficult to rule out alternative mechanisms without doing field manipulations. In this study I combined a broad-scale survey of intertidal communities that have been invaded by *S. muticum* with a smaller scale experiment in which *S. muticum* abundance was manipulated to assess the potential impacts of the invader on native tidepool communities. Using both sampling approaches combines the hypothesis testing of experimental work and the spatial expansiveness of large-scale surveys.

I addressed the following specific questions: (1) Does community structure or species richness vary in relation to *S. muticum* abundance, either within or among sites?

(2) Can such "impacts" be produced in experimental manipulations? (3) What is the likely explanation for the lack of an impact due to *S. muticum*? (4) What implications do these findings have for conservation efforts?

METHODS

Site Descriptions

Descriptions of the sites shown in Figure 1 are given in order from north to south. Cayucos Pt. was a flat, sand-covered rocky reef with some intermixed boulders and larger rock outcrops. Sampling occurred within approximately 100 m of this extensive reef in large, shallow pools and channels that formed at low tide. Alegria was a long, low relief rocky reef with occasional "hogback" rock outcrops. The reef was subject to extreme seasonal fluctuations in sand cover. Sampling was done within approximately 150 m of the reef in long channels that ran parallel to shore. Crystal Cove was a rocky bench, approximately 50 m in length that was surrounded by a sandy beach that experienced seasonal changes in sand level (higher in summer, lower in winter). *Sargassum muticum* occurred in numerous distinct tidepools of variable shapes and depths. Cabrillo National Monument was another low relief, rocky reef that extended for several hundred meters (although sampling was done along approximately 150 m of reef that had restricted public access) and was covered nearly completely by sand in many areas. Sampling was done in large shallow pools and channels. Pta. Clara was a relatively small rocky bench (approximately 30 m in length) with a low-lying area between higher rock outcrops where several large and a few small pools were present. All pools contained large amounts of cobble. Pta. Baja was a large rocky bench (over 100 m in length) with tidepools of variable shapes and depths. This site probably experienced the least amount of sediment scour of all the sites and was also the most exposed. All other sites were subject to moderate wave exposure.

Survey

A comparison of community composition and species richness was made between areas within tidepools that naturally contained *Sargassum muticum* ($SS_{present}$ plots—abbreviation for "Survey, *Sargassum muticum* present") and those that naturally did not contain *S. muticum*, and also had little or no *Phyllospadix scouleri* or *P. torreyi*, (hereafter referred to as *Phyllospadix* spp.) (SS_{absent} plots). I refer to $SS_{present}$ and SS_{absent} samples as 'treatments' in this paper, although they are not treatments in the true, experimental sense. Sampling was restricted to tidepools because *S. muticum* is extremely sensitive to desiccation and is rarely found in areas outside of pools. Plots were 50 x 50 cm and replicates of both 'treatments' were sampled in spring 2000 at each of six sites ranging from Cayucos, CA to Punta Baja, Baja California Norte (Figure 1). The spring sampling corresponded with the maximal size of *S. muticum* plants, which have an annual growth cycle (Aguilar-Rosas & Galindo 1990; Norton & Deysher 1988). Ten replicate plots of each 'treatment' were sampled at four of the six sites, but only eight of each type were sampled at Cabrillo National Monument, and eight $SS_{present}$ and seven SS_{absent} plots were sampled at Cayucos due to time constraints. Mean canopy cover of *S. muticum* ranged from 50% to nearly 100% in $SS_{present}$ plots, reflecting the natural variability in cover among sites (pers. obs.). $SS_{present}$ plots were always sampled in areas of highest *S. muticum* cover within sites. SS_{absent} plots were sampled in areas where

Phyllospadix spp. were absent or rare because surfgrass tended to dominate communities in which it occurred, resulting in a community structure significantly different from that of areas not dominated by surfgrass (Turner 1985; Turner & Lucas 1985). Additionally, the dominant nature of *Phyllospadix* spp. populations suggested that their abundance would not be impacted by the presence of *S. muticum*, a relatively poor competitor (Gunnill 1980; Turner 1985).

$SS_{present}$ plots were interspersed throughout areas ranging from approximately 30-150 m in length, depending on the size of the reef at each site. Random sampling was not used in the interest of minimizing the time spent locating appropriate areas to sample and thus maximizing the number of samples obtained. It is unlikely that this non-random method introduced much bias to the sampling since the dense *S. muticum* canopy obscured my ability to see other species present below. Thus, I could not select plots based on communities, because I could not see them. SS_{absent} plots were selected based on proximately to $SS_{present}$ plots (usually within a few meters), which reduced potential bias since the "choice" for sample location was limited to the nearest appropriate area. When tidepools were large, multiple plots of either the same or different treatments were often sampled within a single pool. This selection method ensured that plot types were not clustered within a site and that samples from each plot type would have similar ranges in tidal height and tidepool structure.

A point quadrat frame similar to that described by Foster et al. (1991) was used to sample percent cover of organisms. At each quadrat location, a narrow rod was lowered through 25 holes spaced evenly in a 50 x 50 cm area located within a slightly larger PVC plate. This quadrat size was chosen because *S. muticum* often occurred in small, upper intertidal pools, and a 50 x 50 cm quadrat was the maximum size appropriate. Sampling 25 points within each quadrat allowed for an acceptable tradeoff between accuracy of sampling within a plot and number of replicate plots sampled. Because variation among replicates was large at many sites, it was essential to obtain many samples in order to have enough power to detect "treatment" effects. When layering occurred under a point, sequential layers were recorded and then moved aside so that the rod could be lowered to the next layer. Taxa occurring in multiple layers were recorded only once. Substrate type was recorded for points where encrusting algae, holdfasts, or sessile invertebrates did not occur on the primary layer. Percent cover for a given taxon was calculated as 4x the number of "hits" recorded for that taxon. Total cover thus exceeded 100% if layering occurred.

Species were identified to the lowest possible taxon and were not lumped into functional groups because 1) species were usually distinguishable and 2) the ecological relevance of the "functional group" approach is questionable (Padilla & Allen 2000; Phillips et al. 1997). Occasionally species were lumped by genus (e.g. *Corallina* spp.), or into small groups (e.g. all "red crusts" excluding non-geniculate corallines) when species could not be identified.

Because mobile invertebrates and fish were not well represented by this percent cover sampling method, these organisms were counted separately within the quadrat. As with percent cover data, species were lumped only if they were difficult to distinguish (e.g. all sculpin were lumped). This method likely resulted in consistent estimates of sculpin, which were cryptic and tended not to move much, but probably underestimated the abundance of other fish species.

Sargassum Removal Experiment

To test the hypothesis that *S. muticum* has caused changes in the structure of the intertidal community, three different treatments were used at Alegria (Santa Barbara County, CA) and Crystal Cove State Park (Orange County, CA, Figure 1). For Treatments 1 and 2, ten 50 x 50 cm areas within tidepools containing high cover of *S. muticum* were selected within a site. These plots were then randomly assigned to either Treatment 1 or Treatment 2. Treatment 1 plots (hereafter referred to as $ES_{removal}$—abbreviation for "Experiment, Sargassum removal") were carefully cleared of all *S. muticum*, both within the 50 x 50 cm plots and the surrounding areas so that no *S. muticum* would impact the plots. *Sargassum muticum* has a very small discoid holdfast (typically ~ 2 cm in diameter) and removal of the alga caused very little disturbance to the plots, thus a disturbance control was not deemed necessary. Treatment 2 ($ES_{present}$) consisted of plots in which *S. muticum* was left alone. Treatment 3 (ES_{absent}) plots were established in locations interspersed among $ES_{removal}$ and $ES_{present}$ plots where *S. muticum* was naturally absent (but that appeared to be suitable habitat for *S. muticum*) from an area large enough that a 50 x 50 cm plot would not be affected by the alga. Five suitable sites for ES_{absent} plots were randomly selected from areas scattered amongst the $ES_{removal}$ and $ES_{present}$ plots. The five replicates of each treatment type were permanently marked to allow for re-sampling of the same areas over time. $ES_{removal}$ treatments were maintained throughout the duration of the sampling but any *S. muticum* that colonized ES_{absent} plots was not removed. Experimental plots were sampled using identical methods to those used for the survey. The experiment was set-up and sampled in Spring 2000 and then sampled at approximately three-month intervals until Spring 2001, for a total of four sampling periods.

ANALYSIS

Non-parametric multivariate analyses for both survey and experimental data were done using the non-metric multi-dimensional scaling (nMDS) routines in the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package (Clarke & Gorley 2001). Unlike parametric multivariate techniques (e.g. MANOVA) the specific PRIMER techniques used in this study do not require multivariate normality or equal sample size, and can incorporate all species sampled, regardless of abundance. All data analyzed with PRIMER techniques were square root transformed to reduce the contribution of very abundant species and increase that of rare species. Triangular similarity matrices were constructed using the Bray-Curtis similarity coefficient. Ordination of samples was performed using nMDS, which maps relative relationships, (based on rank order of dissimilarity distances), between community samples. Those samples that are most similar in community structure plot out closest together, whereas those that are least similar plot out farthest apart. While the location of plots relative to one another is meaningful in nMDS, the orientation of plots is not. This is different from other ordination techniques such as discriminant analysis where the orientation of plots would relate to species composition. The degree to which the display of ranked samples in the nMDS agrees with the original similarity matrix rank order determines the "stress" of the diagram (listed in the upper right hand corner of each nMDS plot). If the display of samples in the nMDS diagram and the matrix rank order are in perfect agreement, stress = 0. A stress value < 0.1 corresponds to an ordination that depicts sample relationships well and a value < 0.2 indicates an ordination that is still meaningful, but should be interpreted with some caution (Clarke 1993). The stress of an nMDS diagram can often be lowered by plotting 3-D representations of the data rather than 2-D, but these more complex representations are often hard to interpret and are thus rarely used. When stress values were high for 2-D nMDS ordinations, they were compared to their respective 3-D ordinations (which had lower stress) to ensure that the patterns depicted were accurate. Significance tests for differences between sample groups were run using appropriate ANOSIM (analysis of similarities) permutation tests. The number of samples present determined the number of possible comparisons and thus influenced the power of these tests and the significance level that could be achieved. The specifics of these tests are discussed individually for each analysis.

Survey: sessile invertebrates, algae, and substrate

Community structure was compared for $SS_{present}$ and SS_{absent} plots using nMDS. All species (excluding *Sargassum muticum*) were included in the analysis. "Species" included 47 species of algae or algal groups, 9 sessile invertebrates or invertebrate groups, and 4 substrate types (see Table 1 for common species). To test for overall differences in community structure among sites and between $SS_{present}$ and SS_{absent} sample groups ('treatment'), a 2-way crossed ANOSIM was run. The 2-way crossed ANOSIM tested the null hypothesis of "no site effect," allowing for the fact that there might be 'treatment' differences, and symmetrically tests a second null hypothesis of "no 'treatment' effect," allowing for possible site differences.

The null hypothesis of "no 'treatment' effect" was rejected in the 2-way crossed ANOSIM discussed above (see Results) indicating that further examination of the individual site trends was needed since a significant result simply indicates that a 'treatment' difference exists somewhere in the data (e.g. at one or more of the sites). Because there is no equivalent in ANOSIM to the interaction term in ANOVA, separate one-way ANOSIMs were done to compare $SS_{present}$ and SS_{absent} plot groups within each site. The results of these analyses were used to determine whether differences due to plot type could be seen at the site level, and if so, whether these differences were constant among sites. The alpha level was adjusted using a Bonferroni correction to account for the increased chance of making a Type 1 error by doing multiple tests.

The results suggest that Alegria could be an 'outlier' and might not represent the general pattern that describes *S. muticum*'s impact (or lack thereof) on tidepool communities. In order to see if an overall result of "no treatment effect" was obtained when Alegria was removed from the data set, a second nMDS and an accompanying 2-way crossed ANOSIM were run without the apparent outlier. Nine 'species' (6 algal species, 2 sessile invertebrates, and 1 substrate type), were removed for this second set of analyses since they were present only at Alegria.

Survey: mobile invertebrates and fish

Analyses similar to those used for percent cover data were run for the mobile invertebrate and fish data. An nMDS was constructed and a corresponding 2-way crossed ANOSIM was run to test the null hypotheses of "no site differences," and "no 'treatment' differences." As with the percent cover data, both 'site' and 'treatment' were significant grouping factors. Separate one-way ANOSIMs were done to test the null hypothesis of "no 'treatment' difference" within each site. Alpha levels were adjusted to correct for multiple tests. Where 'treatment' differences were significant, I did SIMPER ("similarity percentages") analyses, which is a PRIMER technique that determines the relative contributions of individual species to the net dissimilarity in community structure. SIMPER allowed me to determine which species were primarily responsible for the differences between the 'treatments'.

Survey: species richness

A final analysis that was done for both percent cover data and counts of mobile species was a comparison of species richness for samples among sites and between 'treatments'. Percent cover and count data were converted to presence/absence format, which allowed me to calculate the number of species present per plot. I then tested for differences using Model III ANOVAs with 'treatment' fixed and site random. Data were examined for homogeneity of variance and normality using normal distribution probability plots. To meet these assumptions, count data were square root transformed.

Sargassum Removal Experiment

Percent cover and count experimental data were analyzed using nMDS's that depicted both the relative relationships of treatment groups to one another and the change in these relationships over time. The temporal trends that would be expected for each treatment group if *S. muticum* had an impact on tidepool community structure were compared to the empirical patterns (see Results for further explanation). Because ANOSIM cannot test whether the relationship among treatments varied over time (the equivalent of the interaction term in ANOVA), separate 1-way ANOSIMs were used to test for significant differences between $ES_{removal}$ and $ES_{present}$ samples and $ES_{removal}$ and ES_{absent} samples collected during the initial sampling dates and the final sampling dates at both sites. For mobile species, only those that occurred in more than five plots (regardless of treatment) for either the initial or final sampling period were used in the nMDS and ANOSIM analyses. This was because the inclusion of rare species led to spurious grouping patterns in the nMDS ordinations. Rare species were examined for patterns of association with particular treatments (e.g. were most rare species counted only in $ES_{present}$ plots?), and none were found, so their removal did not bias the results in any way. This removal of rare species was only necessary for comparisons between mobile species in experimental treatments because there were so few mobile species present in these plots that the rare species influenced the results more than they did in the analyses of percent cover data for either the experiment or survey, or for analyses of mobile survey data.

Differences in species richness among treatments and between initial and final samples were compared using Model I ANOVAs. Data were examined for homogeneity of variances and normality using normal distribution probability plots. To meet these assumptions, percent cover data for Alegria and count data for Crystal Cove were square root transformed.

RESULTS

Survey: sessile invertebrates, algae, and substrate

An nMDS ordination of the mean values for each plot type (Figure 2a) revealed that 'site' was generally a much stronger factor for plot groupings than 'treatment' (here referring to the natural 'treatments' described in the survey methods), because same site plots clustered together, regardless of 'treatment'. The stress value (0.17) was somewhat high, but the relationships among plot types displayed in the 2-D nMDS were similar to those in the 3-D ordination and are thus valid. The one obvious exception to the 'same site' grouping pattern is Alegria, for which $SS_{present}$ plots group more closely to Cabrillo SS_{absent} plots and SS_{absent} plots group more closely to Crystal Cove $SS_{present}$ plots than they do to one another. A 2-way crossed ANOSIM (Table 2a) revealed that 'site' was indeed a strong grouping factor. 'Treatment' was also a significant grouping factor, but the associated R-statistic indicated that it was not as important in explaining plot type groupings as 'site.' The R-statistic for 'site' was 0.634, indicating a fairly strong tendency for samples from like sites to group together, regardless of 'treatment'. 'Treatment' on the other hand had a small R-statistic (0.061), indicating that relatively few samples grouped by 'treatment'. Because the R-statistic was so low for the 'treatment' factor, it is possible that sample groupings from only one site were driving the pattern. The results of separate 1-way ANOSIMs comparing 'treatment' at each site (Table 2b), revealed that there was indeed only 1 site, Alegria, at which 'treatment' was a significant factor. When Alegria was removed from the analysis, there was almost no change in the spatial relationships of the remaining sample groups (Figure 2b), but the results of a 2-way crossed ANOSIM reveal that 'treatment' was no longer a significant factor (Table 2c). The fact that site was a much stronger factor for sample grouping was also apparent in Figures 3a-c. 'Species' categories are quite broad in these figures, but the general trend of relatively little difference between $SS_{present}$ and SS_{absent} plots within sites as compared to among site differences is quite clear. If *S. muticum* had a major impact on tidepool community structure, one would expect that impact to be clearly expressed across all, or at least a majority of the sites sampled.

Survey: mobile invertebrates and fish

Patterns for plot type groupings displayed in the nMDS constructed for mobile invertebrates and fish (Figure 4) were similar to, although not as apparent as those seen in the nMDS for percent cover data. As with the percent cover data, the corresponding 2-way crossed ANOSIM revealed that the overall R-statistic for the 'site' factor was fairly high (R=0.588, Table 2d) indicating that this was a relatively important factor, and the R-statistic for 'treatment' was low (R=0.144) suggesting that it was not as important, or was important for only a subset of sites. Subsequent 1-way ANOSIMS for individual sites showed that $SS_{present}$ and SS_{absent} samples were significantly different from one another at both Alegria and Pta. Clara although the R-statistic for Pta. Clara was fairly low (R=0.228, Table 2e). SIMPER analysis revealed that the difference between 'treatments' at Alegria could largely be attributed to just one species: the snail, *Tegula funebralis* (Table 3a). This single species was responsible for over 70% of the dissimilarity between

$SS_{present}$ and SS_{absent} samples. At Pta. Clara, 54% of the dissimilarity was due to a higher number of the urchin, *Strongylocentrotus purpuratus,* in SS_{absent} samples (Table 3b). *Tegula funebralis* was also more abundant in SS_{absent} samples, suggesting that *S. muticum* negatively impacted the distribution of the snail. However, the raw data reveal that this difference at Pta. Clara was driven entirely by a large number of *T. funebralis* in a single SS_{absent} sample. The distributions of mobile species groups (Figures 5a & 5b) again indicate that general patterns in the abundance of species were primarily related to site, not presence or absence of *S. muticum*, although these grouping patterns were not as strong as for the percent cover species.

Survey: species richness

Mean numbers of species per sample were plotted for both percent cover data (Figure 6a) and mobile species data (Figure 6b). Two-way ANOVAs testing the null hypotheses of "no 'treatment' differences" and "no site differences" were done for both data sets, and revealed a significant difference in species richness among sites, but not between 'treatments' (Table 4).

Sargassum Removal Experiment: sessile invertebrates, algae, & substrate, and mobile invertebrates & fish

If the invasion of *S. muticum* into tidepool communities caused a change in community structure, the patterns depicted for percent cover and mobile data and the corresponding results would be expected to resemble the pattern depicted in Figure 7, based on the results of the survey. This hypothetical figure visually outlines a possible set of trajectories that the different treatments might be expected to follow if an invasive species altered a community in some manner. On the first sampling date there is no significant difference among treatments. As the treatments are followed through time, the movement of $ES_{present}$ and ES_{absent} plots can be attributed to seasonal changes in community structure, and $ES_{removal}$ plots become significantly different from the other two treatments. These temporal patterns of treatment distributions and groupings were not observed in the nMDS's or in the ANOSIM analyses of the experimental percent cover data (Figures 8a-b, Table 5a), or mobile counts (Figures 9a-b, Table 5b) at either site. Two important points regarding these nMDS figures should be noted. First, the stress for these 2-D ordinations is a bit high, but as with the survey data, these representations were compared to their respective 3-D ordinations, and were found to be very similar. The important features of the data are captured in the simpler 2-D ordinations, namely that there is extensive overlap among the treatments and the removal plots are not behaving differently from the other two treatments. Second, some caution should be used when interpreting the ANOSIM results for mobile counts at Alegria. As mentioned in the Analysis section, rare mobile species were removed from the analyses done for Alegria because inclusion of these species led to spurious patterns in the nMDS ordinations. One result of the removal of these rare species was a reduction in the number of samples available for use in the analyses, since similarity matrices cannot incorporate samples containing no species. Some samples contained only one or two rare species and thus appeared to have no mobile species when these rare species were removed (note that this condition occurred equally across all treatments). This 'reduction' in sample size is reflected in the low number of permutations possible for comparisons between treatments at Alegria (Table 5b). In two cases only 10 permutations are possible and in one case only 35 permutations are possible allowing for minimum p-values of only 0.09 and 0.0278 respectively, which are higher than the adjusted desired α level of 0.025. Thus, the ANOSIM results for mobile species at Alegria should be interpreted cautiously. However, results for all other comparisons are statistically sound, and do not support an effect of *S. muticum* on community structure.

Sargassum Removal Experiment: species richness

Species richness comparisons were made separately for percent cover species and mobile species at each site. Although values for all samples are displayed (Figures 10a-d), only comparisons between initial and final samples were made so that any seasonal differences would not confound the conclusions. Two-way ANOVAs (Tables 6a-6d) revealed that there was no difference in species richness among treatments for percent cover estimates or mobile species counts at Alegria, but there were differences among treatments for both percent cover and count data at Crystal Cove. However, the interaction term was not significant for either of these tests, indicating that the relative relationships among treatments remained the same between initial and final samples.

DISCUSSION

The results of the survey and the experiment were in general agreement: *Sargassum muticm* had little, if any impact on the community structure or species richness in tidepools within the region studied. The combination of the large scale survey, which would have detected major differences between areas with and without *S. muticum*, and the experiment, which was designed to test whether any differences were indeed due to the presence of the alga, made for a strong argument against any major impact. It might be argued that one potential fault of the study is that the experiment was not sampled over a long enough time period to detect potential impacts of *S. muticum*—that a community may take longer than one year to recover from being relieved of the presence of the invader. However, even if full recovery were not reached within a year, a trend towards recovery would be expected. Growth rates for many of the species commonly occurring in the areas studied are not well known, but other work, (e.g. Taylor & Littler 1982) suggests that detectable recovery would be expected within a year long period. This would be especially true for any disturbance-induced effect on other algae, such as abrasion due to a whiplash effect of *S. muticum*, since many algae can persist in a crustose form that is highly disturbance tolerant and can recover rapidly when relieved of the disturbance (Sousa 1980). Thus, it is reasonable to accept the conclusion that *S. muticum* has no major broad-scale impacts on tidepool community structure.

There were a few notable exceptions, however, to this "general" conclusion. A significant difference was found between the survey SS_{absent} and $SS_{present}$ percent cover plots at Alegria. In contrast, lots of overlap existed between the initial experimental ES_{absent} and $ES_{present}$ plots at this site. This result is somewhat perplexing since the ES_{absent} and $ES_{present}$ treatments that were initially sampled for the experiment could essentially be considered a repeat of the survey. Note though, that the R-statistic for the survey data was fairly low, suggesting that the difference between 'treatments' was not strong. The contrasting results between the survey and experimental data at Alegria indicate that if *S. muticum* was indeed affecting the community, the effect was not large. Furthermore, no other site showed a difference in community structure between SS_{absent} and $SS_{present}$ samples so it seems reasonable to suggest that the overall effect is negligible.

Another notable exception to the "no effect" conclusion was the difference between survey 'treatments' in the mobile species data for both Alegria and Pta. Clara. Counts of *Tegula funebralis* were higher in SS_{absent} samples, but this difference appears to be meaningful only at Alegria. At Pta. Clara, the difference is likely due to the patchy nature of this intertidal snail rather than to any effect of *S. muticum*. One SS_{absent} sample contained substantially higher numbers (55) than any other sample (next highest count = 13), and almost certainly caused the difference. Thus, while it is interesting that a pattern of higher *T. funebralis* in SS_{absent} samples was present at two of six sites, it is not convincing evidence for an effect of *S. muticum*. Further argument against any negative impact of *S. muticum* on *T. funebralis* is that the snail was found at two additional sites, and did not show a similar pattern of reduced abundance in $SS_{present}$ samples. Finally, experimental manipulations of *S. muticum* at Alegria did not result in differences in mobile species abundance between treatments (and thus individual species were not examined).

Another species that differed in abundance among experimental treatments was the urchin *Strongylocentrotus purpuratus*. This species was substantially more abundant in SS_{absent} samples than in $SS_{present}$ samples at Pta. Clara (Table 3b). A similar trend was also seen at Pta. Baja (Figure 5a), although community structure was not found to be significantly different at this site (Table 2c). Unfortunately an experimental manipulation of *S. muticum* was not done at either Pta. Clara or Pta. Baja, so this potential effect requires further investigation.

It was quite striking that of all the species examined in this study, *S. purpuratus* was the only one that potentially showed an effect due to the presence of *S. muticum*. Based solely on appearance, one might expect *S. muticum* to be a sort of non-native "foundation" species (sensu Dayton 1984). It can grow to be quite large in pools (up to 1.5 m), is abundant, and has a unique branching structure that would seemingly provide suitable habitat for fish and mobile invertebrates and might also influence understory algae through shading and abrasion. However, it clearly does not have "foundation" species status in the rocky intertidal communities it has invaded along the Pacific Coast. In fact, the results of this study suggest that the complete removal of *S. muticum* would hardly affect the distribution or abundance of co-occurring species. This conclusion is in stark contrast to the "expected" result, given the large number of examples of negative impacts from the invasive species literature (e.g. Carlton & Geller 1993; Grosholz et al. 2000).

How can such a visibly conspicuous alga have so little impact? The answer may be related to the physical attributes of the communities studied. Qualitative observations of the areas along the Pacific Coast where *S. muticum* has successfully invaded reveal that these sites are highly disturbed by sediment scouring. This periodic disturbance has likely facilitated the colonization by *S. muticum*, (Hobbs & Huenneke 1992; Sher et al. 2000), but might also mask any impact of the invasion. Just as Connell's (1975) model predicted that increased environmental harshness would lessen the importance of biological interactions, the factor that likely exerts the most control over the structure of these tidepool communities is disturbance: the impact of all other factors thus becomes negligible. Pools where *S. muticum* tends to be abundant are nearly always subject to some sediment scour. Thus, co-occurring species typically consist of those that can withstand the disturbance and burial that results from sediment movement across the pools. Species such as *Corallina* spp., *Anthopleura* spp., and *Phyllospadix* spp. do well in the harsh conditions associated with sediment scoured environments (Littler et al. 1983; Taylor & Littler 1982). Because these sediment-influenced communities are composed largely of "hardy" or "weedy" species, with life histories that allow them to either withstand burial and scour or take advantage of periods during the year when scour and burial are minimal (Daly & Mathieson 1977; Littler et al. 1983), they are unlikely to be further affected by additional, "lesser" impacts, such as those that would be associated with an invasion by *S. muticum*. The possible shading, "whiplash" effect, or competition that would result from the presence of the invader would likely be negligible in comparison to the disturbance and burial created by sediment movement. Similar results were found by Dethier (1984) for tidepools in Washington, where disturbance intensity and frequency was likely lower than for the tidepools in this study, but was still determined to be the major force in structuring the communities.

Another potential source of support for the hypothesis that these rocky tidepools are structured largely by disturbance is that studies done in the subtidal, an area that generally experiences much lower disturbance levels than these sand influenced intertidal areas, have shown that *S. muticum* does impact community structure (Britton-Simmons pers. comm., Ambrose & Nelson 1982), although this impact may be temporary (Foster & Schiel 1992). However, the potential contrast in disturbance frequency between intertidal and subtidal areas is confounded by the fact that *S. muticum* can grow much larger (up to 10 m, Dawson & Foster 1982) and attain much higher densities (up to 120 plants/m^2; Britton-Simmons pers. comm.) in the subtidal than in tidepools (max length 1.5 m, max density up to 100 small plants/m^2; this study). At these sizes and densities, substantially more shading by *S. muticum* would occur and could thus reduce or prevent growth of native algal species. Recruitment of native species into areas of high *S. muticum* density might also be reduced.

One group of species for which a lack of difference among treatments would not likely be explained by the disturbance hypothesis proposed above is fish. Fish would probably not be affected much by sediment scour, but would seemingly benefit from the additional structure that *S. muticum* adds to tidepools. It is likely however, that only sculpin abundance was recorded in a consistent manner in this study since they tended to be cryptic bottom dwellers that remained in their 'hiding' spots when a quadrat was placed in their pool, as opposed to most other fish species that swam away. Because of their benthic-dwelling nature, sculpin may not benefit from the type of structure that *S. muticum* provides. Their distribution may depend more on the topography of the pool bottoms and the amount of short, turf algae present within the pools more than on canopy-forming species (Love 1996). Non-sculpin fish species might be attracted to larger, three-dimensional algal structure, but these species were not sampled well in this study.

The above conclusions are important for both ecological assessment and management. If concern were to develop regarding the impact of *S. muticum* on native communities, removal efforts would want to focus on the subtidal portion of the population. Of course, if the desire were to eradicate *S. muticum* entirely, removal would need to be done in both areas, and would require substantial resources. These potential management directions stem from three important findings resulting from this work. 1) Conspicuously abundant invasive species do not necessarily have a negative effect on native communities. Careful study, incorporating experimental testing, must be done in order to assess impact. 2) When my results are compared with those of other studies on *S. muticum*, it is apparent that invasion by the alga can have very different consequences depending on the community invaded. 3) It is important to consider how physical factors will interact with the effects of an invasive species. Similar conclusions have been reached for invasive species in other systems (Berman et al. 1992; Fernandes et al. 1999; Herbold & Moyle 1986), and must be considered when assessing impact.

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Table 1

"Common" species found in survey samples. "Common" was defined as a mean of > 5% for a single site/plot type combination (e.g. Cayucos, $SS_{present}$) for percent cover species and a mean of > 1 individual per plot for a single site/plot type for mobile species. Site codes are as follows: CAY = Cayucos, AL = Alegria, CC = Crystal Cove, CAB = Cabrillo National Monument, PC = Pta. Clara, PB = Pta. Baja

Percent cover taxa:	**Sites where taxon was common**
Ulva spp.	CAY, AL, CAB, PC
Dictyota flabellata	CC
Gelidium spp.	CAB
Pterocladia spp.	CAB
Lithothrix aspergillum	CC, CAB
Corallina spp.	AL, CC, CAB, PC, PB
Calliarthron spp.	PB
Non-geniculate coralline	CC, PC, PB
Sarcodiotheca gaudichaudii	CAY
Gracilariopsis lemaneiformis	CAY
Mazzaella leptorhyncos	PC
Red crust	PB
Phyllospadix spp.	CAY, AL
Anthopleura elegantissima/sola	CC
Phragmatopoma californica	CC
Counted taxa:	
Tegula funebralis	AL, PC, PB
Tegula eiseni	CC, CAB
Tegula aureotincta	CC
Acanthina paucilirata	PB
Haminoea vesicula	CAY
Pagurus spp.	CAY, CC, PC, PB
Strongylocentrotus purpuratus	CC, PC, PB
Sculpin	CC, CAB, PC, PB

Table 2

Results of ANOSIM tests for differences in: A) overall percent cover data among sites and between $SS_{present}$ and SS_{absent} sample groups ('treatment'), B) percent cover data between 'treatments' for each site, C) overall percent cover data among sites and between 'treatments', excluding Alegria, D) overall mobile species counts among sites and between 'treatments', E) mobile species counts between 'treatments' for each site. The R-statistic can be interpreted as follows: If R=1, *all* replicates within a factor group are more similar to each other than *any* replicates from another group. If R=0, similarities between and within groups are the same on average. 999 permutations were run for each analysis. Significant p-values are marked with an * and α levels are listed and adjusted using a Bonferroni correction when necessary.

	Type of Test	Factor	Site (for 1-way tests)	R Statistic	p-value	α
A	2-way crossed	site		0.634	0.001*	0.05
		'treatment'		0.061	0.032*	0.05
B	1-way	'treatment'	Cayucos	0.106	0.112	0.008
	"	"	Alegria	0.327	0.001*	0.008
	"	"	Crystal Cove	-0.013	0.514	0.008
	"	"	Cabrillo N. M.	0.046	0.247	0.008
	"	"	Pta. Clara	-0.054	0.759	0.008
	"	"	Pta. Baja	-0.03	0.663	0.008
C	2-way crossed	site		0.673	0.001*	0.05
		'treatment'		-0.003	0.492	0.05
D	2-way crossed	site		0.588	0.001*	0.05
		'treatment'		0.144	0.001*	0.05
E	1-way	'treatment'	Cayucos	0.112	0.152	0.008
	"	"	Alegria	0.454	0.001*	0.008
	"	"	Crystal Cove	0.052	0.178	0.008
	"	"	Cabrillo N. M.	-0.058	0.736	0.008
	"	"	Pta. Clara	0.228	0.004*	0.008
	"	"	Pta. Baja	0.115	0.078	0.008

Table 3

Results of SIMPER analyses. Average abundance (y) of important mobile species in $SS_{present}$ ($y_{present}$) and SS_{absent} (y_{absent}) sample groups at A) Alegria and B) Pta. Clara. Species are listed in order of their contribution (δ_i) to the average dissimilarity (δ=74.86 for Alegria and δ=63.67 for Pta. Clara) between the two groups. Only those species contributing >5% to the average dissimilarity are listed.

	Species	$y_{present}$	y_{absent}	δ_i	δ_I%	$\Sigma\delta_I$%
A	*Tegula funebralis*	8.14	18.86	55.07	71.91	71.91
	sculpin	0.57	0	10.40	13.58	85.49
	Pagurus spp.	0.43	0	6.32	8.26	93.75
B	*Strongylocentrotus purpuratus*	11.40	68.30	34.50	54.19	54.19
	Tegula funebralis	1.80	5.60	8.51	13.37	67.56
	Pagurus spp.	1.90	2.40	7.17	11.26	78.82
	sculpin	0.90	1.20	4.57	7.17	85.99

Table 4
Model III ANOVA comparing species richness estimates for A) percent cover data and B) mobile species counts among sites and between $SS_{present}$ and SS_{absent} ('treatment') samples. The 'treatment' terms were tested as MS 'treatment'/MS interaction. Significant p-values are marked with an *.

	Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
A	'treatment'	2.597	1	2.597	2.072	0.21
	site	107.370	5	21.474	4.976	<0.001*
	'treatment' x site	6.267	5	1.256	0.290	0.917
	error	427.250	99	4.316		
B	'treatment'	0.249	1	0.249	2.234	0.195
	site	17.624	5	3.525	12.007	<0.001*
	'treatment' x site	0.557	5	0.111	0.397	0.862
	error	29.064	99	0.294		

Table 5

Results of one-way ANOSIM tests for differences in A) percent cover data and B) mobile species counts between initial and final treatments. Adjusted $\alpha = 0.025$. Significant p-values are marked with an *.

	Site	Sample	comparison	R Statistic	Number of Permutations	p-value
A	Alegria	initial	$ES_{present}$ vs $ES_{removal}$	0.084	126	0.262
	"	initial	ES_{absent} vs $ES_{removal}$	0.004	126	0.46
	"	final	$ES_{present}$ vs $ES_{removal}$	0.032	126	0.317
	"	final	ES_{absent} vs $ES_{removal}$	0.1	126	0.222
	Crystal Cove	initial	$ES_{present}$ vs $ES_{removal}$	-0.004	126	0.46
	"	initial	ES_{absent} vs $ES_{removal}$	0.088	126	0.278
	"	final	$ES_{present}$ vs $ES_{removal}$	-0.164	126	0.889
	"	final	ES_{absent} vs $ES_{removal}$	0.192	126	0.103
B	Alegria	initial	$ES_{present}$ vs $ES_{removal}$	0.01	56	0.482
	"	initial	ES_{absent} vs $ES_{removal}$	0.204	10	0.30
	"	final	$ES_{present}$ vs $ES_{removal}$	-0.222	10	0.7
	"	final	ES_{absent} vs $ES_{removal}$	0.259	35	0.229
	Crystal Cove	initial	$ES_{present}$ vs $ES_{removal}$	-0.064	126	0.651
	"	initial	ES_{absent} vs $ES_{removal}$	0.068	126	0.302
	"	final	$ES_{present}$ vs $ES_{removal}$	0.02	126	0.389
	"	final	ES_{absent} vs $ES_{removal}$	0.088	126	0.135

Table 6

Model I ANOVA comparing species richness estimates for percent cover data at A) Alegria and B) Crystal Cove and for mobile species counts at C) Alegria and D) Crystal Cove among treatments and between the initial and final samples. Significant p-values are marked with an *

	Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
A	Treatment	0.027	2	0.014	0.082	0.922
	Sample	0.118	1	0.118	0.704	0.410
	Treatment x Sample	0.329	2	0.165	0.983	0.389
	error	4.022	24	0.168		
B	Treatment	44.067	2	22.033	6.265	0.006*
	Sample	53.333	1	53.333	15.166	0.001*
	Treatment x Sample	2.867	2	1.433	0.408	0.670
	error	84.400	24	3.517		
C	Treatment	2.067	2	1.033	0.504	0.610
	Sample	0.533	1	0.533	0.260	0.615
	Treatment x Sample	0.867	2	0.433	0.211	0.811
	error	49.200	24	2.050		
D	Treatment	2.047	2	1.024	4.350	0.024*
	Sample	0.006	1	0.006	0.028	0.869
	Treatment x Sample	0.130	2	0.065	0.276	0.761
	error	5.646	24	0.235		

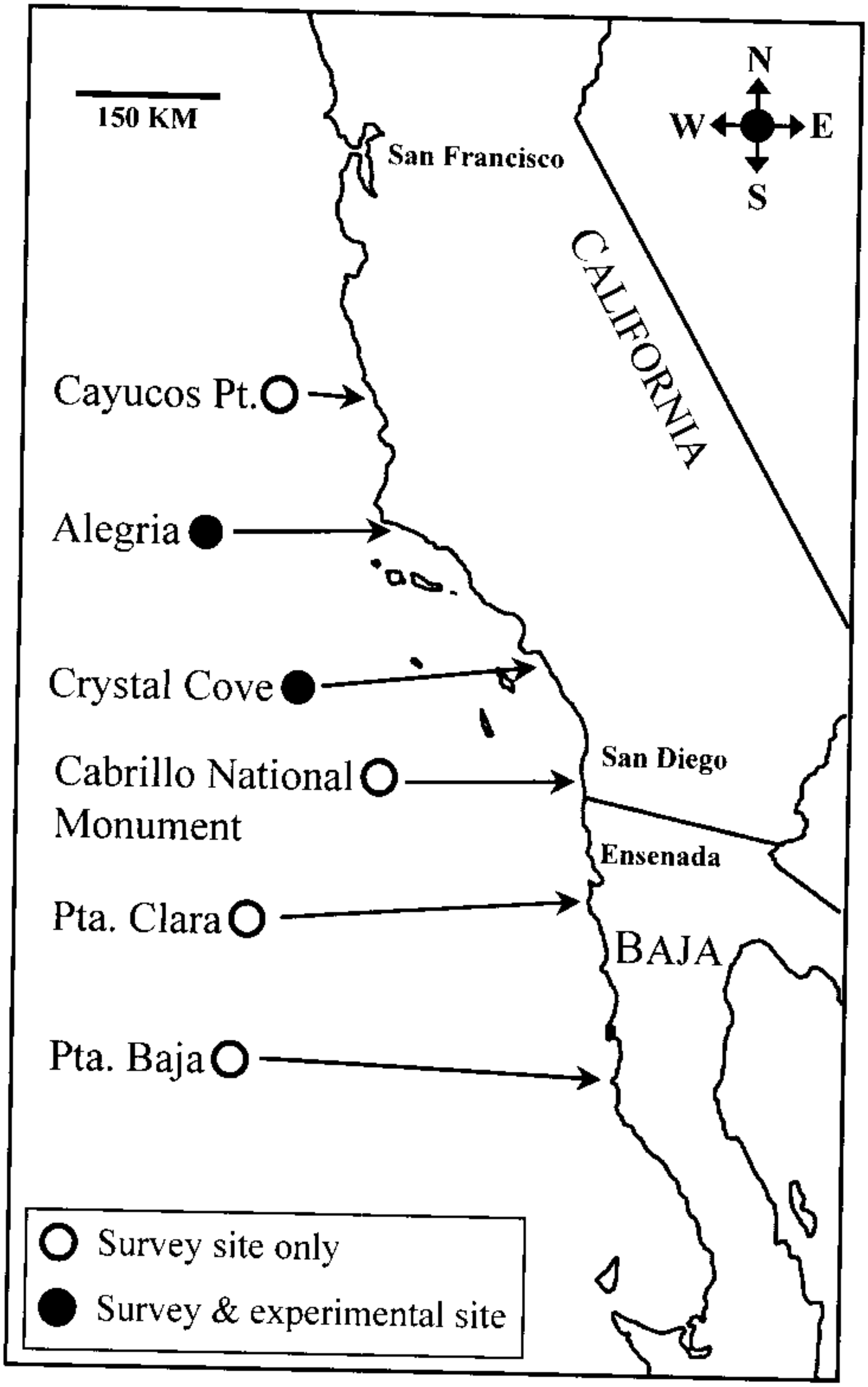


Figure 1. Locations of survey and experimental sites.

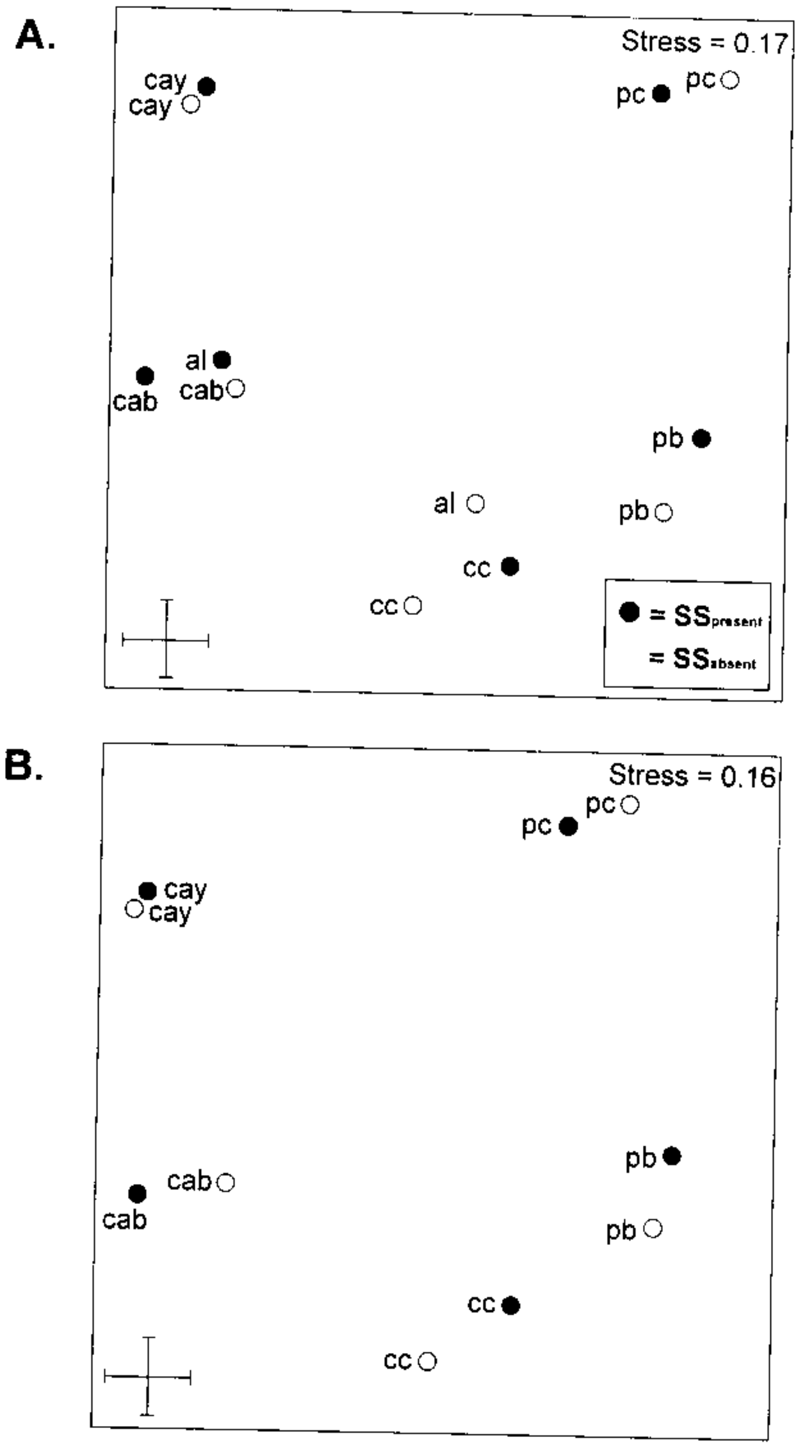


Figure 2. nMDS of survey percent cover data for A) all sites and B) all sites except Alegria. Each point represents the mean of a sample group. "Typical" standard error bars for each point are shown in the lower left corner. Site codes are as follows: cay=Cayucos, al=Alegria, cc=Crystal Cove, cab=Cabrillo Nat'l. Mon., pc=Pta. Clara, pb=Pta. Baja.

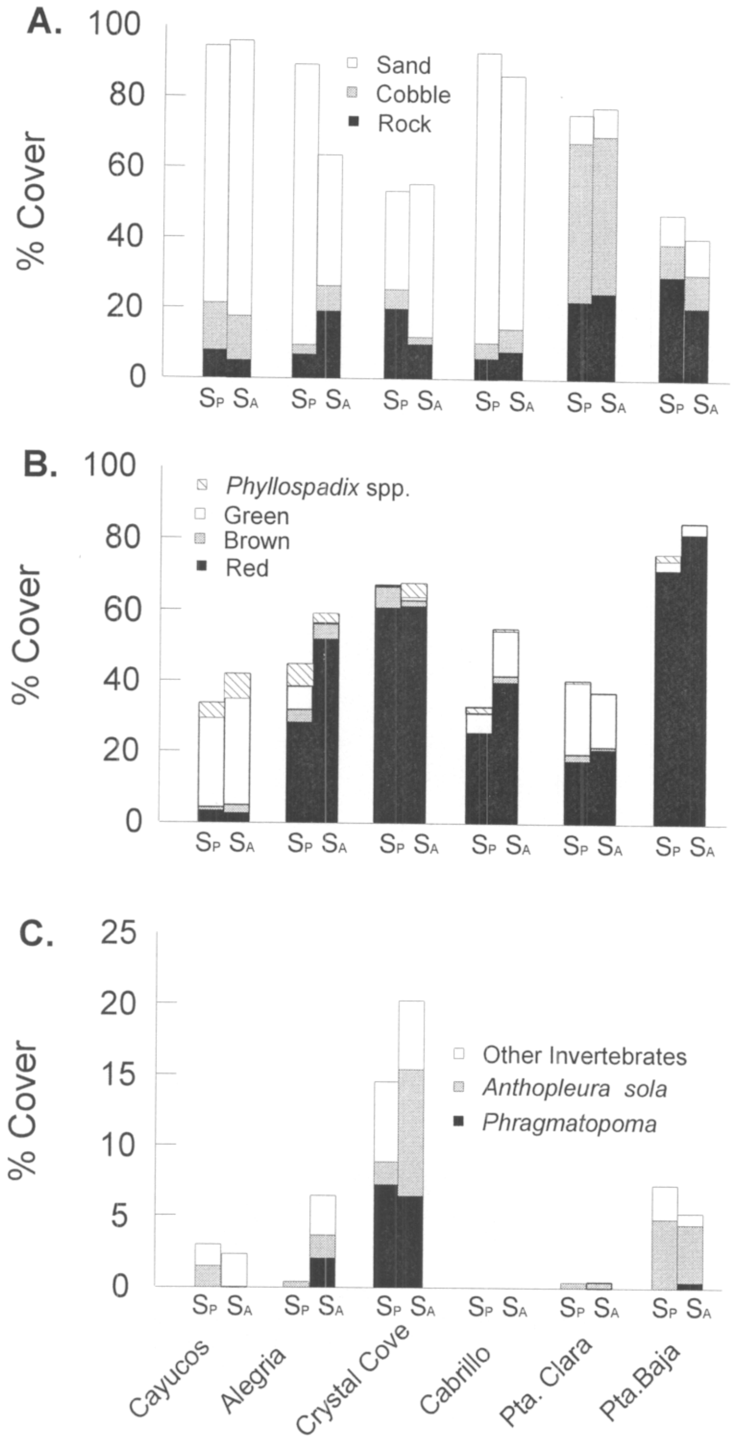


Figure 3. Mean percent cover of A) substrate, B) algae (excluding *S. muticum*) and *Phyllospadix* spp., and c) encrusting invertebrates for survey plots at each of six sites. Substrate and species are grouped according to legends. $S_P = SS_{present}$ plots, $S_A = SS_{absent}$ plots.

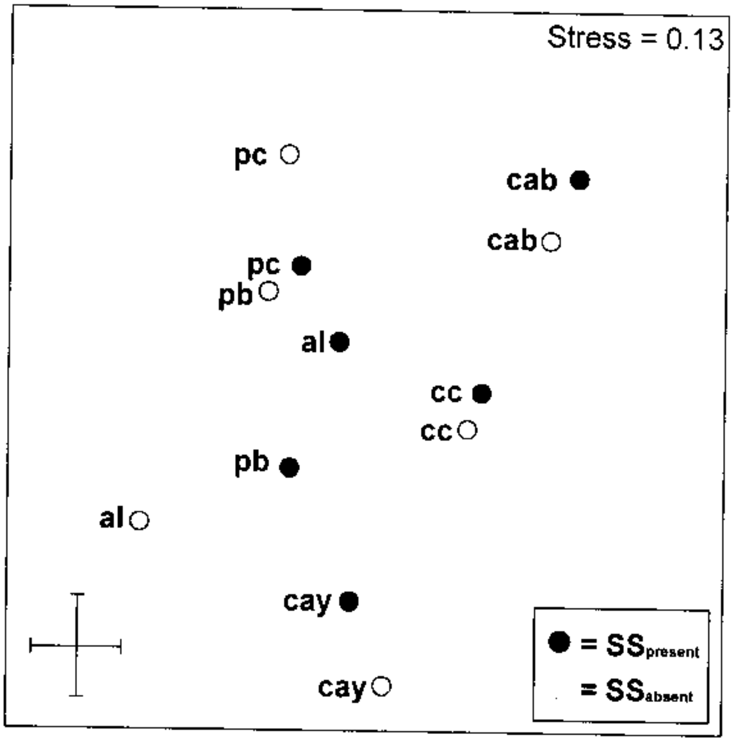


Figure 4. nMDS of survey counts of mobile species. Each point represents the mean of a sample group. "Typical" standard error bars for each point are shown in the lower left corner. Site codes are as follows: cay=Cayucos, al=Alegria, cc=Crystal Cove, cab=Cabrillo Nat'l. Mon., pc=Pta. Clara, pb=Pta. Baja.

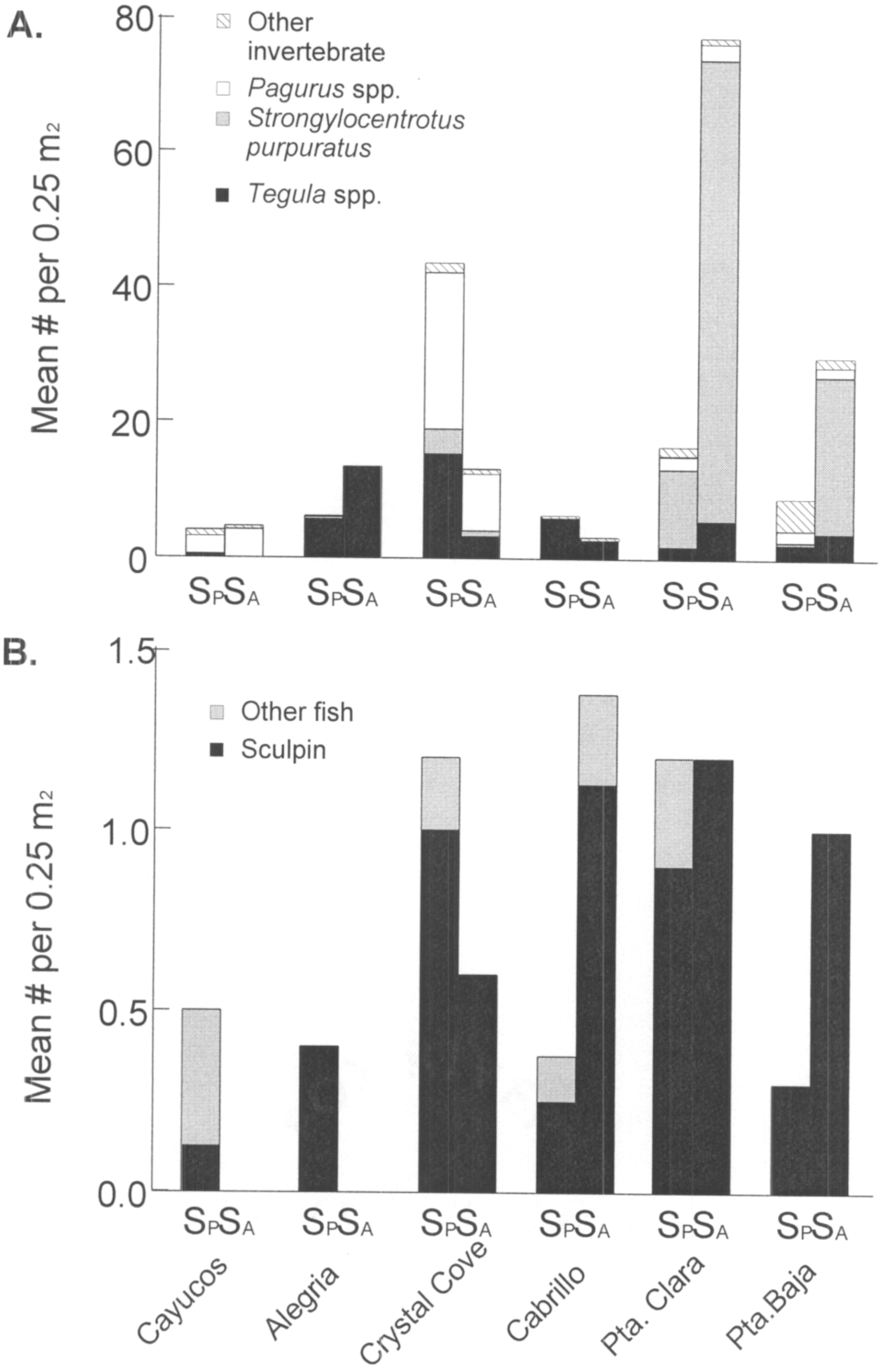


Figure 5. Mean number of A) mobile invertebrates and B) fish counted in survey plots at each of six sites. Species are grouped according to legends. *Tegula* spp. includes *Tegula funebralis, T. eiseni*, and *T. aureotincta*. $S_P = SS_{present}$ plots, $S_A = SS_{absent}$ plots.

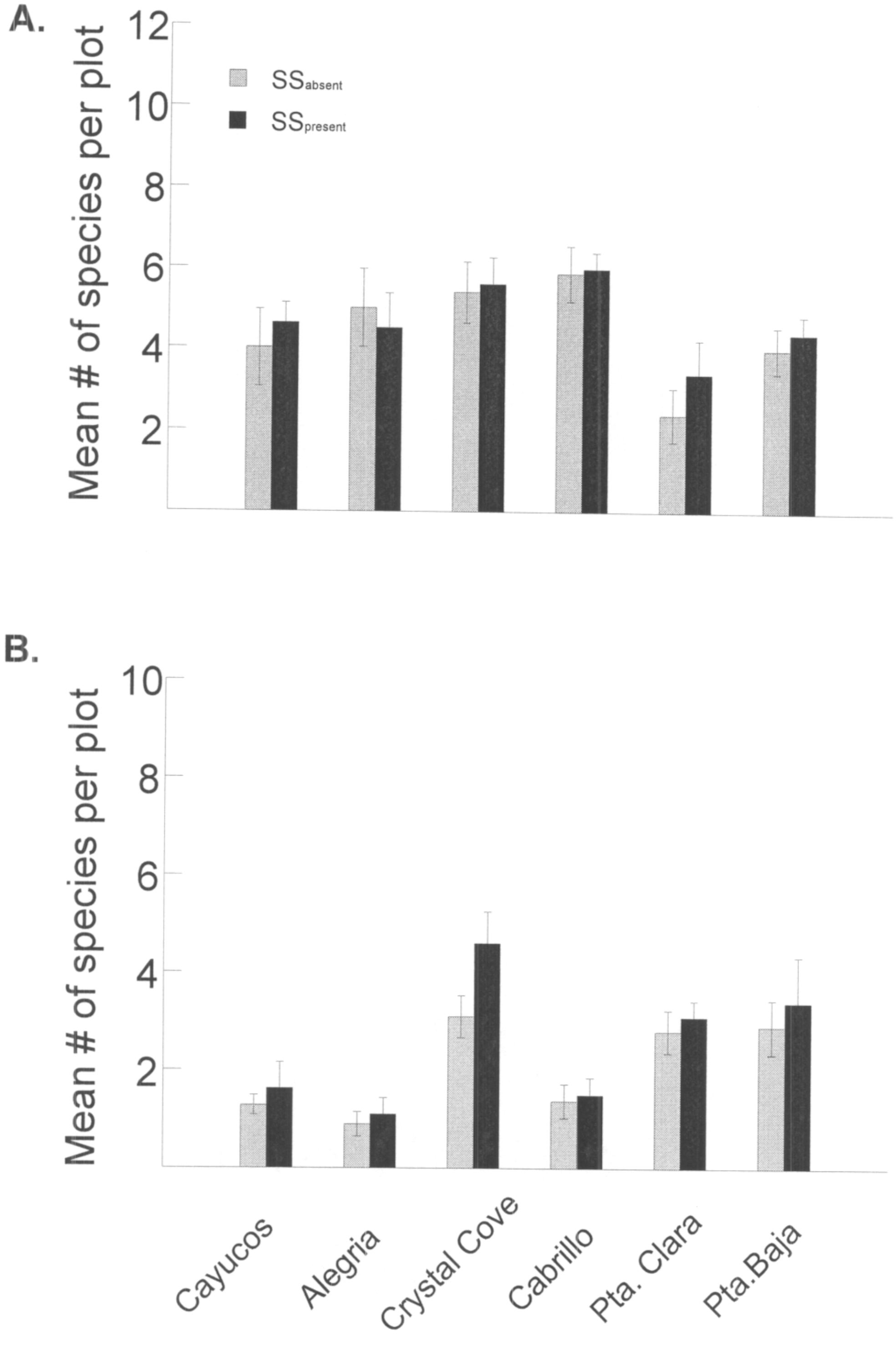


Figure 6. Mean number of species (+/- standard error) for A) percent cover and B) mobile species counts in $SS_{present}$ and SS_{absent} survey plots.

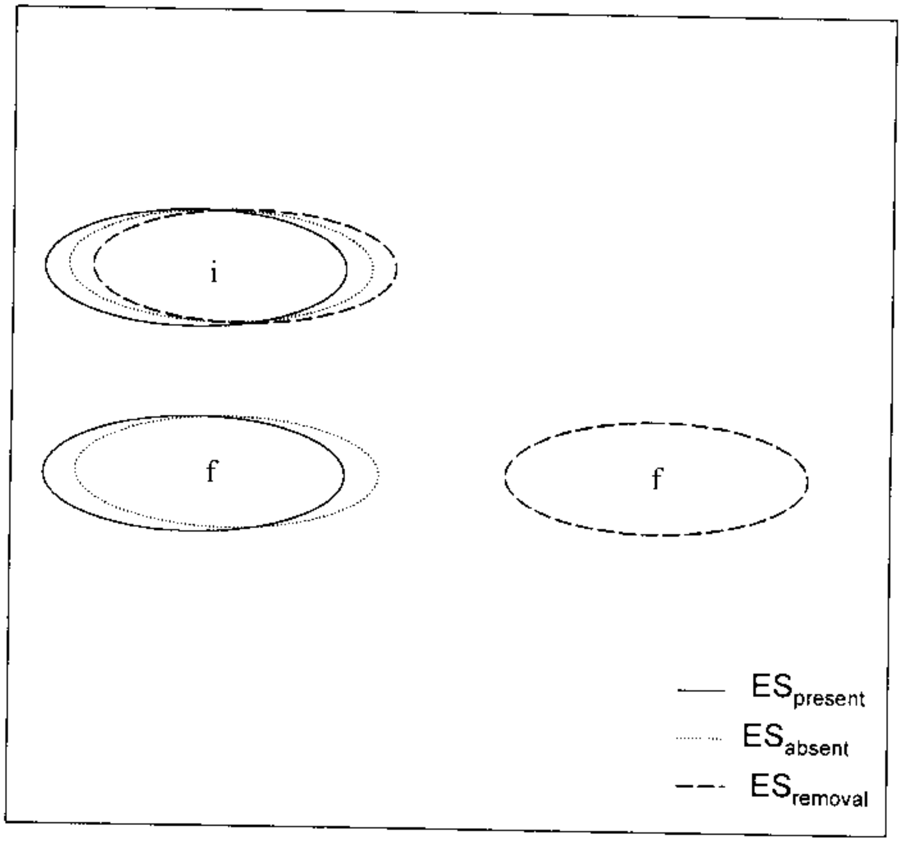


Figure 7. Hypothetical representation of pattern that ES$_{present}$, ES$_{absent}$, and ES$_{removal}$ treatments would be expected to follow over time if *Sargassum muticum* had an impact on community structure. i = initial sample, f = final sample.

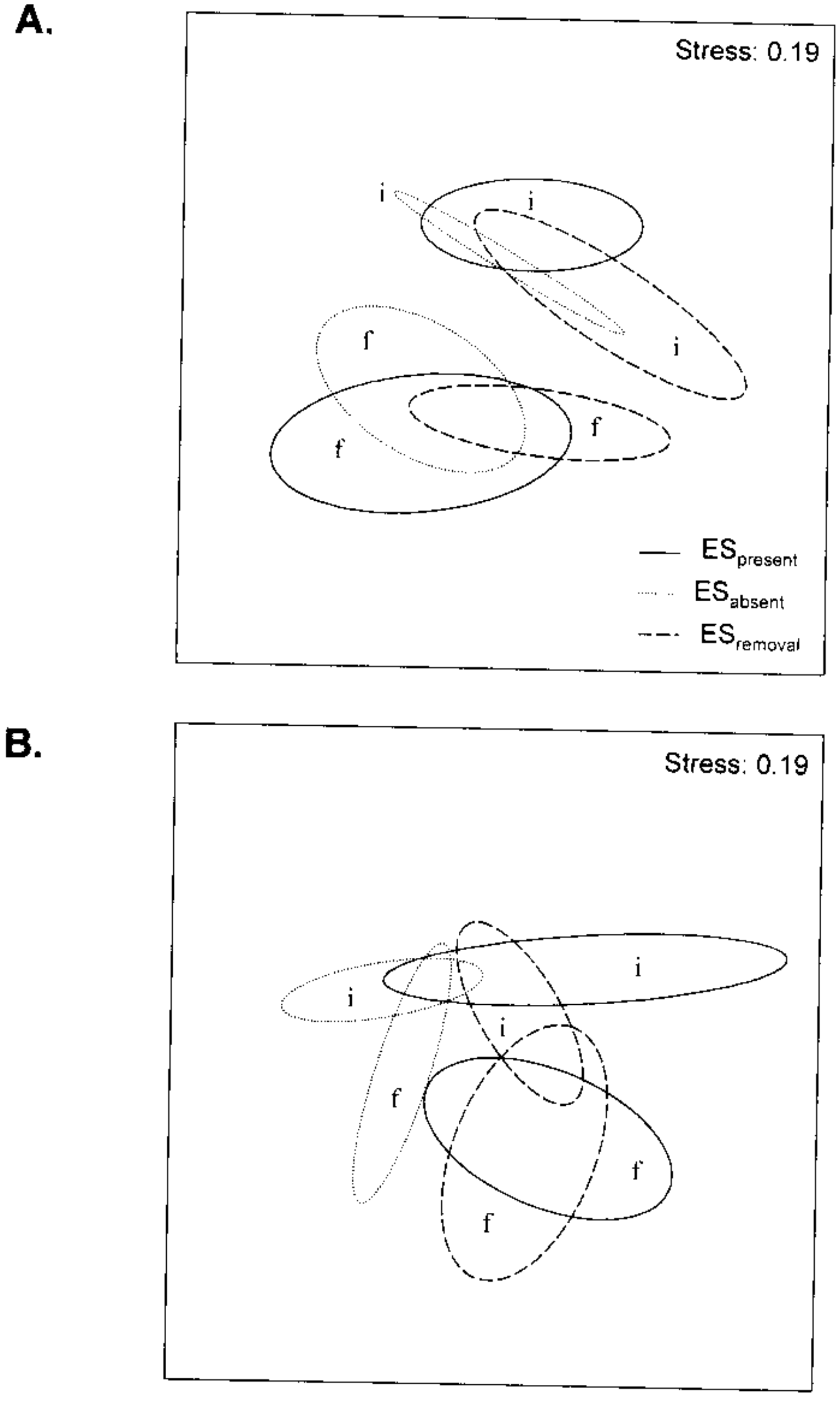
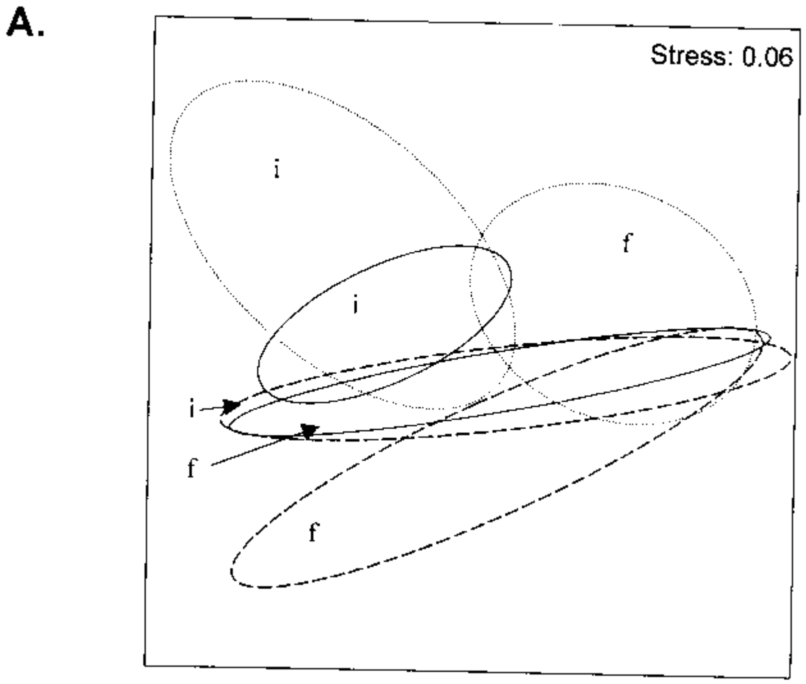


Figure 8. nMDS of percent cover data from experimental treatments over time for initial (i) and final (f) samples at A) Alegria and B) Crystal Cove. Ellipses depict 2-D estimates of standard error for each time/treatment group.



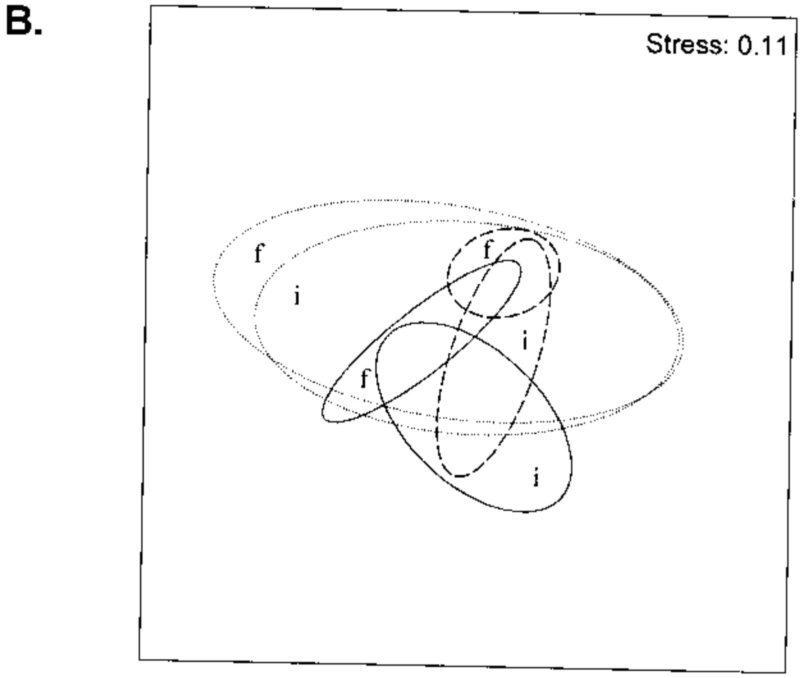


Figure 9. nMDS of mobile species counts from experimental treatments over time for initial (i) and final (f) samples at A) Alegria and B) Crystal Cove. Ellipses depict 2-D estimates of standard error for each time/treatment group. Some plots at Alegria contained no mobile species and thus could not be used in the analysis (see text for explanation). Thus, the standard error was determined using the square root of the mean number of samples.

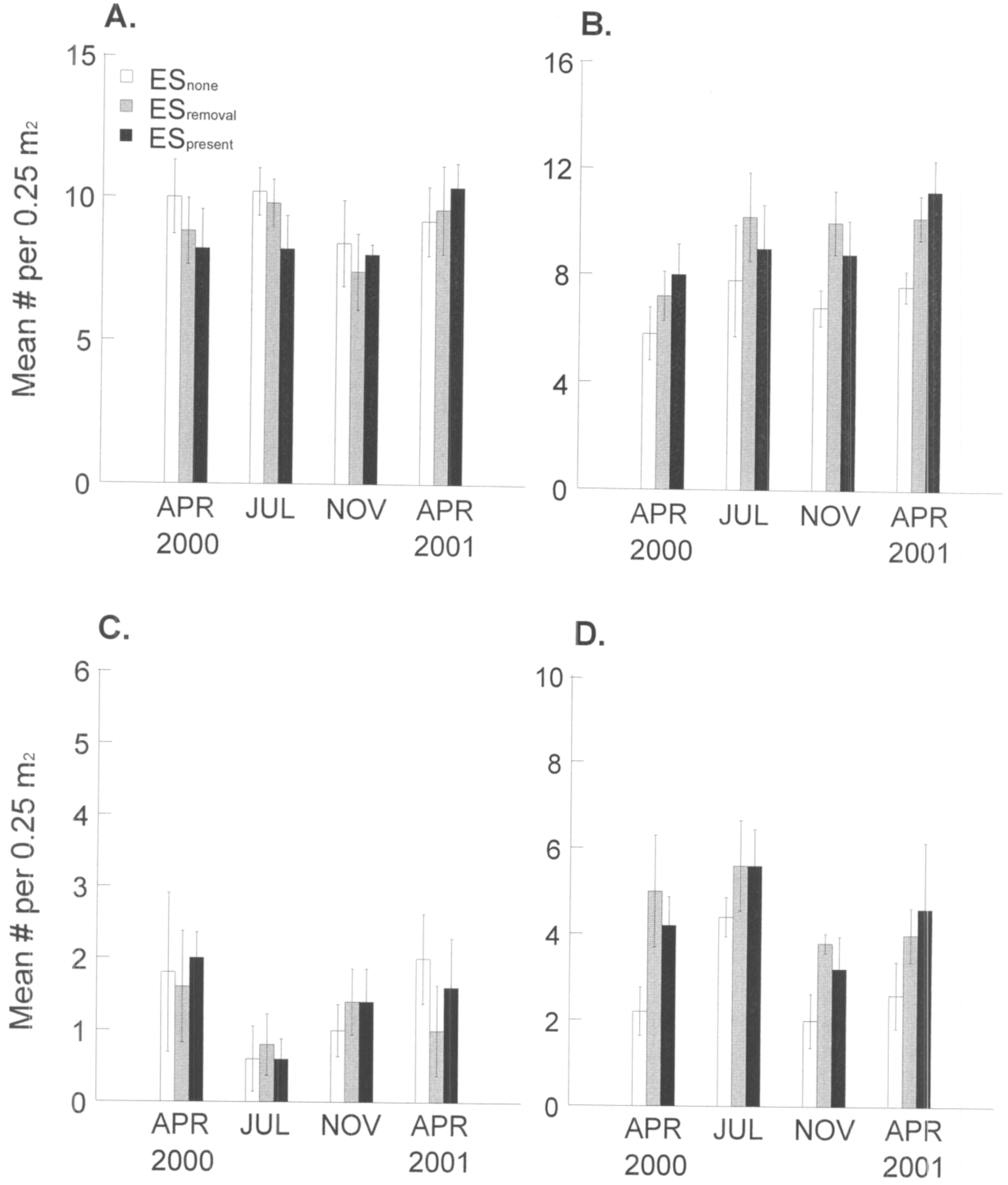


Figure 10. Mean number of species per experimental treatment (+/- standard error) over time for percent cover data at A) Alegria and B) Crystal Cove and for mobile counts at C) Alegria and D) Crystal Cove.