The persistence of open space in the rocky intertidal *Endocladia muricata* assemblage

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Abstract

Open space can be a limited resource in rocky intertidal assemblages, but disturbances continually provide new open space which often recovers to a pre-disturbed condition. However, in a central California intertidal red algal assemblage, open space and aggregations of the dominant red alga, *Endocladia muricata,* tend to persist for long periods.* Laboratory and field studies were designed to determine the causes of this pattern. Results of a 6 year photo sampling of fixed plots in this assemblage at Pescadero Rocks, Stillwater Cove, California suggest that total cover and size distribution of open spaces persist but not necessarily in the same location. This changing pattern was due primarily to loss of open space via algal colonization. Field experiments at Point Pinos, Pacific Grove, California revealed that open space also persisted for at least 2 years in the same location. Thin biofilms affected the cover of *Endocladia* in one experiment. Open space, *E. muricata* and other algal cover, abundance of recruits of other algae as well as the persistence and size of open space, were significantly affected by herbivorous gastropods in all experiments. In turn, these grazers indirectly enabled *E. muricata* to persist but not expand. In absence of grazers, *E. muricata* declined when open space was heavily colonized by *Mastocarpus papillatus.* Light colonization of grazer free treatments by *M. papillatus* resulted in the expansion of *E. muricata* into open spaces via vegetative spreading and recruitment from spores. Colonization by *Porphyra perforata* in grazer free treatments appeared to have no effect on patch dynamics. Differences in heavy versus light recruitment of *M. papillatus* were likely caused by spatial and temporal variability in propagule output, settlement and recruitment. Recruitment magnitude on newly exposed versus "weathered" substrata differed for some algal species. These results suggest that while grazers have the greatest influence on patch dynamics, biofilms and substratum condition can also influence the structure of this assemblage.

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Introduction

Formation of open space in rocky intertidal assemblages is often dependent on a disturbance such as log or wave damage (Dayton 1971; Sousa 1984, 1985). The space created by the disturbance can be colonized by diatoms and ephemeral algae that are commonly replaced by later successional species until the space is occupied once again by the dominant. While biotic and abiotic disturbances continually provide new open space, Dayton (1971) considered open space to be a limited resource and competition for open space increased with higher species recruitment. While other studies have found similar competitive interactions (Sousa 1984), centimeter to meter sized open spaces, uncolonized by macro-organisms, tend to persist adjacent to aggregations of the dominant red alga, *Endocladia muricata* on many central California mid/high intertidal rocky shores.

When algae colonize open space, algal composition can differ depending on the alga's susceptibility to herbivory and competitive ability. Grazers, through consumption of grazer-susceptible species, can indirectly enable grazer-resistant species to succeed (Lubchenco and Gaines 1981). However, some grazer-resistant species, in the absence of grazers, may be out-competed by faster growing species. Lubchenco (1978) noted that high densities of the periwinkle, *Littorina littorea*, influenced algal composition within tidepools by consuming the grazer-susceptible, competitive dominant *Enteromorpha* spp., providing space for the grazer-resistant alga *Chondrus crispus* to establish. De Vogelaere (1991) noted that as a result of the grazing activity of the chiton, *Nutallina californica*, in artificial clearings in central California, the centers of clearings had abundant grazer-susceptible species while grazer-resistant species were more abundant in the borders. Sousa (1984) noted that algal species composition differed within small and large patches as a result of differences in grazer densities, and that grazer-resistant species were more common in small open spaces than in large spaces. Tarpley (1992), found herbivorous gastropods reduced algal abundance and species composition in clearings during succession by consuming small (<1 cm) ephemeral and some juvenile perennial algae, and that these algae had a size refuge. The above studies, however, address early successional colonization dynamics. Few studies have investigated algal dominance and the persistence of open space in late succession. Studies on late succession grazing effects in naturally occurring open spaces may provide insight into causes of open space recovery or lack thereof.

In this study, I tested the importance of grazers, in structuring this assemblage. Grazers may prevent colonization of open space and indirectly enable *Endocladia* to persist virtually free of competition. In the absence of grazers, competitive interactions, biofilms and substratum condition may influence the structure of this assemblage.

Thin biofilms, dominate nearly all areas devoid of macrophytes and sometimes cover the rock surface with a barely detectable slimy film. These films may prevent recruitment of propagules by inhibiting settlement, depleting available nutrients or overgrowing settled propagules. An alga's dominance may be associated with its ability to uptake available nutrients at a higher rate, preempt space, prevent spore settlement or overgrow settled spores or juveniles (Carpenter 1990, Olsen and Lubchenco 1990). In addition, rapid lateral growth and production of allelopathic toxins may play a role. These possibilities have not been investigated. Furthermore, substratum condition appears to influence algal colonization. I have noted that newly exposed rocks, devoid of thin biofilms, were colonized by different algal species than those colonizing substrata that were "weathered." Newly exposed rock surfaces usually result from natural fragmentation or a severe disturbance such as log bashing or boat groundings. I considered all other rock surfaces "weathered."

Field and laboratory experiments were designed to investigate the causes of the aggregated distribution of *Endocladia muricata* and persistence of adjacent open space. I explored possible links between competition, herbivory and recruitment dynamics in the *E. muricata* assemblage by examining the development of *E. muricata* in the presence and absence of herbivorous gastropods and thin bio films as well as the effect of substratum condition on *E. muricata* and other algae cover.

Methods

Long term variation in the *Endocladia muricata* assemblage.

Temporal changes in the square area of open spaces were determined from photographs taken twice/year of four permanent, 1 x 2 m plots as part of a 6 year study (Kinnetic Labs 1992) at Pescadero Rocks (Fig. 1). Since plots were large, six areas in each permanent plot were photographed (24 areas total) on each survey date. Six of these 24 areas were selected and photos examined from 1985 to 1991 to determine if total cover of open space and the size distribution of open spaces persist. In addition, three individual open spaces were tracked in each of the six areas (18 individual spaces total) throughout the 6 years. Species adjacent to tracked open spaces as well as species that colonized them were qualitatively described. Open space cover and size was determined by projecting slides onto a board with a 1 cm^2 grid and measuring the size of all open spaces. Prior to analysis each slide was adjusted to the same scale with the zoom control on the projector. Total cover was the sum of all these sizes. Mean total cover of open space for all bare areas was plotted for each date and a t-test used to compare mean total cover between the first date (March 1985) and the last date (March 1991). Size frequency data were classified into groups for the first and last date for each plot, tested for normality and homoscedasticity and a Kolmogorov-Smirnoff goodness of fit test (Zar 1996) used to compare the mean size frequency distributions. Individually tracked open spaces were summarized in a survivorship table and qualitatively described.

Effect of grazers, thin bio films and substratum condition: Experiment 1

A rocky intertidal site near Point Piños, Pacific Grove, California (Fig. 1), was chosen to test the effects of grazers, films and substratum condition on long term persistence of open space. The study area within the site extended along 300m of shoreline consisting of granite outcrops interspersed with flat, horizontal benches.

A field experiment using a randomized block design was used to reduce error from natural variation among locations within the site while testing grazer, film and substratum effects on open space and algal cover, and on open space size, and abundance of algal recruits. This experiment ran from August 1996 to September 1998. Each block contained six 25 x 25 cm plots. Four blocks, each with one replicate of each treatment, were established on flat surfaces with *E. muricata* aggregations and adjacent open space. The treatments in each block were: +grazers/+films, +grazers/-films, -grazers/+films, -grazers/-films, +grazers/+film with a three-sided fence (fence control) and -grazers/-films with top rock layer chipped (Fig. 2). For all treatments, only the open spaces were manipulated leaving *E. muricata* and other species untouched. The +/- grazer and film treatments were established to directly test the effects of grazers and films.

Limpets, littorines, turban snails and chitons were removed from "-grazer" treatments and plastic mesh fences were constructed around the "-grazer" treatments to prevent grazer access. The randomized block design enabled me to construct one large fence, instead of several small fences, around the "-grazers" treatments minimizing fence artifacts. Grazer free treatments were randomly allocated within the large fence, and the large fence was randomly placed among the "+grazers" treatments of blocks. Two randomly allocated fences had to be constructed around grazer free treatments in one of the blocks since grazer free treatments were not adjacent to one another. Fences were installed using plastic wall anchors and stainless steel bolts inserted into holes drilled into the granite rock. Splash Zone™ was applied at the base of the fence to prevent grazers from crawling under the mesh. Grazers found within fences were removed weekly. A fifth treatment, +grazers/+film treatment surrounded by a three-sided fence, was established to control for possible fence effects. Since seasonal variability in grazer abundance may affect aggregations and open spaces, grazers found within "+grazer" plots were counted monthly.

Brown, red and green films as well as "Petrocoelis" and "Ralfsia" crusts were removed from "-film" treatments. Films were scraped from open spaces using a wire hand brush and a wire brush on a cordless drill. Rocks were scrubbed until they were white in color and the slimy feel, caused by film growth, was no longer present. For the +grazers/-films treatment, grazers were removed from the rock, held in a container of sea water while the films were removed, and then replaced. Grazers were also removed and replaced in an unscraped area as a control. No effects of removal and replacement were noted.

Observations in the study area indicated that newly exposed rock surfaces were colonized by species other than would be seen colonizing "weathered" rock surfaces, so a sixth treatment was established to determine how this difference in substratum condition affected algal cover. The top three mm of granite rock was chipped from the open spaces within –grazer/-film chip treatments. Rock was carefully chipped with a chisel and hammer leaving aggregations of *E. muricata* undisturbed. I compared this treatment to the -grazers/-films treatment. I considered the open spaces of this treatment to be the "weathered" rock surface, since the surface layer of the open space was not newly exposed.

Total percent cover of *E. muricata*, other algae, and open space was measured in grazer, film and substratum condition treatments using a point quadrat method (Foster et al. 1991). Cover data were collected every 2 – 3 months in the field from May 1997 (10 months after the start of the experiment) to September 1998. Analyses and figures for species that never attained greater 10% cover are only considered in the appendices.

Open space sizes were measured from photos imported into the image analysis program, TNTMips®. Size frequency distributions of open spaces were generated from these data. Photos were taken of plots every 2 – 3 months from the start of the experiment in August 1996 through the end of the experiment in September 1998. Photos were taken at a fixed distance and directly in front of each plot to minimize distortion. Size frequencies of open space were measured and statistically compared for photos from August 1996 and September 1998.

The number of recruits were counted in open spaces in the field. Recruits were considered to be any solitary individual alga that was less than 10 mm tall. Counts were done sporadically over the sample period and data from June 1998 and September 1998 were used for statistical analyses. These dates were chosen since they corresponded to the peak reproductive output of the dominant algae *E. muricata* and *M. papillatus*, respectively.

A three-way blocked ANOVA (Zar 1996) [grazers, films and location (as the blocked factor)] was used to test for differences in algal and open space cover among the treatments +grazers/+films, +grazers/-films, -grazers/+films and -grazers/-films. Cover for ephemeral species such as *Porphyra perforata* and the blades of *Iridaea cordata and Mazzaella flaccida* were compared after 1 year since their cover was lower when they reappeared in the second year. The blades of *I. cordata* and *M. flaccida* are generally considered ephemeral and holdfasts perennial (Foster 1982). I considered these two species ephemeral. I also grouped their cover values since they were indistinguishable when small. The perennial species were analyzed after 2 years since their cover was relatively constant throughout the study. Statistical results are presented for grazer, film and block effects for open space and each species. Appendix A provides an example of the full ANOVA analysis including all effects.

Recruit abundance was also compared among treatments with a three-way blocked ANOVA [grazers, films and location (as the blocked factor)]. Two separate tests were run for these data from June 1998 and September 1998 since these dates correspond to the peak reproductive output of *E. muricata* and *M. papillatus*, the two most dominant species in this assemblage.

To determine if open space size was affected by grazers and films, open space size frequency data from photos for the start (August 1996) and end (September 1998) of the experiment were compiled into 100 cm^2 size classes for each treatment. Each size class was treated as a dependent variable and compared to the independent variables of grazers, films and block with a MANOVA (Multivariate Analysis of Variance, Zar 1996).

To test how substratum condition (weathered vs. newly exposed) affected cover of algae and open space, a 2-way ANOVA [substratum type and location (as the blocked factor)] was done comparing the treatments, -grazers/-films (weathered open spaces) versus -grazers/-films with the top rock layer chipped (newly exposed open spaces). As in the ANOVA for grazer and film effects, ephemeral species were analyzed after 1 year and perennial species were analyzed after 2 years. All data met assumptions of normality and homoscedasticity after arcsine transformation.

Effect of grazers and thin bio films: Experiment 2 (June 1997 - September 1998)

The previous experiment was started just after the peak of the *E. muricata* reproductive season and films were scraped from open spaces only once in August 1996. Since marine algal propagule output, settlement (Reed et al. 1988) and recruitment (Dayton 1971, Vadas et al. 1992) may be intermittent in time and space, propagules of *E. muricata* and other algae may not have settled into open spaces before films potentially grew back. Therefore, a second experiment was done from June 1997 to September 1998 to more clearly determine if films may affect recruitment of spores that would potentially settle within open spaces. The effect of grazers was also examined. Data on cover, open space size and number of recruits were examined as in the first experiment.

A randomized block design was also used for this experiment, but treatments were blocked in time. This design was chosen to increase the chances of propagules settling within open spaces by randomly distributing the manipulation of each replicate block over two months. This two month "window" was June 1 to August 1, 1997, a period when abundance of *E. muricata* cystocarpic branches is maximum (Nigg, 1988), and thus propagule release is potentially high. Four blocks in time, each with one replicate of each treatment, were established by randomly selecting from dates within the two month window of high propagule output. Treatment plots (25 x 25 cm) of +grazers/+films, +grazers/- films, -grazers/+films and -grazers/-films were randomly allocated in space on flat surfaces where *E. muricata* aggregations and adjacent open space persisted (Fig. 2, top four boxes). Grazers were counted monthly for comparison with recruitment patterns.

Films were removed as described in the previous experiment. Grazer free treatments were maintained by removing grazers weekly from inside plots and an additional 40 cm buffer instead of fencing. Based on observations at the study site, I could, with hand removal, keep grazer numbers as low in unfenced plots as those in fenced plots in the first experiment.

Cover of algae and open space, recruit abundance and open space size were measured and analyzed as in experiment 1. However, the blocked factor for the ANOVA was date instead of location. Since this experiment ran for 1 year, ephemeral and perennial algae were analyzed concurrently at the end of the experiment.

Results

Long term variation in the *Endocladia muricata* assemblage on Pescadero Rocks.

While total area cover of open space appeared to increase between the March 1985 and March 1991, there was no significant difference in mean total cover ($t=1.91$, $df=7$, $p=0.091$; Fig. 3) or size frequency distributions of open spaces in the six fixed plots (Kolmogorov-Smirnoff goodness of fit test $D_{max}=0.60$, $df=7$, $D_{crit.}=0.48$; Fig. 3). Observation of cover from photos taken during this interval indicate the amount of open space cover fluctuated but never disappeared in this assemblage.

The dynamics of the 18 individual open spaces over the six years indicated no clear pattern of persistence of small versus large open spaces (Table 1). Four of the 18 open spaces remained open over the 6 years. Three of the four were initially between 8 and 16 cm^2 and the fourth was initially 380 cm^2 (Table 1). The remaining 14 disappeared at least once over the 6 years but reappeared in the same location, sometimes disappearing again (Table 1). Disappearance of open space was associated with recruitment by *E. muricata* and *M. papillatus* 29 and 36 % of the time respectively. Other species such as *I. cordata/M. flaccida, Cladophora columbiana*, and *Pelvetia fastigiata* were noted within open spaces that disappeared 3, 14 and 18 % of the time respectively. *I. cordata/M. flaccida* were combined since they could not be distinguished in the photos.

Effect of grazers and thin bio films: Experiments 1 & 2.

Grazer and Film Effects on Open Space and Algal Cover

After 25 months, *Endocladia muricata, Mastocarpus papillatus, Porphyra perforata,* "Petrocelis," *Iridaea cordata, Mazzaella flaccida, Corallina vancouveriensis*, non-geniculate corallines and *Cladophora columbiana*, had colonized the grazer and film treatment plots in experiment 1. Only four of these, *E. muricata, M. papillatus, P. perforata* and non-geniculate corallines, displayed percent cover values greater than 10% (Fig. 4 and Table 2). The other species are listed in Appendix B. Films had no significant effect on any species or open space.

Mean cover of open space declined significantly (p = 0.017) when grazers were absent as compared to when they were present (Fig. 4). Mean cover of *P. perforata* increased significantly (p=0.009) in the open spaces of the grazer free treatments by September 1997 (Fig. 4). *M. papillatus*, recruitment was high in the open spaces of two of the four blocks of –grazer/+film and –grazer/-film treatments but low in open spaces of the grazer free treatments in the other two blocks. *E. muricata* cover appeared lower, in the grazer free treatments of the two blocks where *M. papillatus* had heavily colonized and a trend towards higher cover in the two blocks where *M. papillatus* had lightly colonized (Fig. 5). Regardless of this difference in colonization magnitude among grazer free treatments, *M. papillatus* was significantly greater ($p<0.001$) in the grazer free treatments by September 1998. However, no significant difference in *E. muricata* cover was detected.

In Experiment 2, overall, high algal recruitment also resulted in a significant decline of open space in grazer free treatments in this experiment (Table 3, Fig. 6). *Endocladia muricata*, *Mastocarpus papillatus*, "Petrocelis," *Porphyra perforata*, *Corallina vancouveriensis*, non-geniculate corallines, and *Cladophora columbiana* recruited into the open spaces of treatments in experiment 2 but only *E. muricata* and *M. papillatus* cover was greater than 10 % (other species are presented in appendix C).

Mean cover of *Mastocarpus papillatus* increased significantly ($p=0.040$) in grazer free open spaces but its overall cover was much lower relative to Experiment 1. Grazer free treatments in all four blocks were lightly colonized by *M. papillatus*, as in two of the blocks of the first experiment (Fig. 5). In turn, *E. muricata* cover increased in grazer free treatments from all four blocks and was significantly greater ($p=0.001$) by September 1998 (Fig. 6, Table 3). Data from both experiments demonstrate that a high trend of *M. papillatus* recruitment in open spaces was associated with a trend of low *E. muricata* cover, while low *Mastocarpus* recruitment coincided with significantly higher *Endocladia* cover (Fig. 5). *E. muricata* was also significantly greater ($p=0.035$) in film free treatments. A block effect and block*grazer interaction were noted for *E. muricata* by September 1998 (Table 3).

Open spaces in plots with grazers in both Experiments 1 and 2 did not dramatically disappear and reappear in "+ grazers" treatments as they did in plots at Pescadero Rocks. The size of open spaces appeared to become smaller in the grazer free treatments of Experiment 1 (Fig. 7), but this trend was not statistically significant (Table 4). Significant grazer and block effects were detected for open space size in Experiment 2 (Fig. 7, Table 4).

The effect of films on the number of *E. muricata* and *M. papillatus* recruits in the open spaces of Experiment 1 plots was not statistically significant (Fig. 8). However, recruit abundance was significantly higher in the absence of grazers (Table 5, Fig. 8); grazer free treatments had significantly more recruits of both *E. muricata* and *M. papillatus* in June 1998. By September 1998, only *M. papillatus* recruits were more abundant in grazer free plots. The number of recruits in open spaces did not differ significantly among any treatments in Experiment 2 (Table 5, Fig. 8B). Note that the overall abundance of *E. muricata* recruits trended lower in September 1998.

Effect of substratum condition.

Endocladia. muricata, Mastocarpus papillatus, Porphyra perforata, Iridaea cordata, Mazzaella flaccida, Corallina vancouveriensis, "Petrocelis" and *Cladophora columbiana* recruited into weathered and newly exposed open spaces between August 1996 and September 1998. The cover of the latter two species was less than 10% (Appendix D).

No statistically significant differences were noted for any of the species due to grazers and films (Fig. 9, Table 6). Nevertheless, field observations and trends suggest that differences in recruitment of some species were evident on the newly exposed versus weathered substrata. *I. cordata/M. flaccida* cover on newly exposed surfaces increased from 0 to 25% by September 1997, but was barely detectable on weathered surfaces (Fig. 9). *C. vancouveriensis* cover increased through time on newly exposed surfaces, peaking in cover at 12% versus 3% in weathered open spaces in March 1998 (Fig. 9). Block effects were detected for *E. muricata* and *M. papillatus* by the end of the experiment (Table 6).

Discussion

Long term variation in the *Endocladia muricata* assemblage.

While mean total cover and size frequency of open spaces did not significantly differ at Pescadero Rocks between the first and last date, figure 3 suggests that total cover and open space size increased through time. However, personal observation of open space dynamics over the six years of slides indicated that open space persisted but fluctuated throughout this period. While still persisting in this assemblage, open space does not appear to remain in the same location; 14 of 18 tracked open spaces disappeared, sometimes reappearing over the 6 year period (Table 1). The other four spaces remained open throughout the study. Grazer abundances in this 6 year study were relatively high (Fig. I-9 Kinnetic Labs 1992) and data from my field experiments described below suggest that the persistence of these open spaces may be related to grazers.

The shifting of open space in this habitat may be related to the creation of new open space by periodic biotic (De Vogelaere 1991, Tarpley 1992) and abiotic (Dayton 1971, Sousa 1984, 1985) disturbances, while its disappearance may be due to algal colonization. In turn, the reappearance of a pre-existing open space may be related to the species that initially colonizes the open space. In other words, some open spaces may be temporarily occupied by algae that subsequently disappear. These colonizing algae may be considered fugitive species, appearing in newly formed open spaces free of competitive dominants or predators then disappearing due to competition from other algae or consumption by grazers (De Vogelaere 1991). Interestingly, De Vogelaere (1991) noted that *C. columbiana* and *I. cordata,* which were noted in plots of the present study, were fugitive species within a mussel assemblage at a site in northern California. Therefore, the brief colonization of an open space by a fugitive species may explain the disappearance and reappearance of open spaces. Further research is needed to determine these dynamics and the processes (i.e., seasonal die off, herbivory, competition, physical stress) that cause species to disappear as related to open space dynamics.

Effect of grazers and thin bio films: Experiments 1 & 2.

Films did not have a significant effect on open space persistence or algae cover in Experiment 1, perhaps because films reappeared on film free rocks within 3 weeks. Therefore, only a small window of time with film free substrata may have existed. In fact, bacterial film growth can occur on a substratum within a few hours (Borgeas personal communication). The second experiment attempted to account for spatial and temporal variability of propagule output, settlement and eventual recruitment related to films. The significant increase in *E. muricata* cover in film free treatments suggests that this design was effective. Therefore, film free substrata may have been available during a time when *E. muricata* propagules were settling on substrata.

Studies have demonstrated that biofilm growth in open spaces can influence settlement of algae and invertebrates (Keough and Raimondi 1995, Mihm et al. 1981, Vadas et al. 1992, Wieczorek and Todd 1997). McCook and Chapman (1993) observed that cyanobacterial films slightly enhanced recruitment of fucoids. Borgeas (personal communication) noted a similar facilitation of *Enteromorpha flexuosa* spore settlement. Studies on invertebrates have shown that larvae actively settle on substrata with films and others become non-specifically trapped in the polysacharides of films (Szewzyk et al. 1991). In addition, algal spores and films may compete for limited nutrients on the substratum due to reduced water flow in the boundary layer (Carpenter 1990). Different nutrient uptake rates for spores and films may enable one species to prevail (Carpenter 1990). Most of these studies addressed the effect of films on settlement plates. The present study attempted to test these variables on natural open space in the field and results suggest that films affected algal cover of some species. However, further studies that can account for rapid film development may provide further insight into the effect of films on the persistence of open space.

Results from grazer treatments clearly demonstrate that the persistence of open space and the dominance but not expansion of *E. muricata* is related to grazer activity. Through their activity, grazers may directly consume or indirectly remove attached spores, sporelings and recruits. In all cases, the direct and indirect activity of grazers maintains open space, preventing algal colonization. The importance of open space to the survival of grazers was demonstrated by Underwood and Jernakoff (1981) who noted that grazers placed on algal turfs with nearly 100% cover did not survive. At low densities, grazers are often not able to maintain an existing space open. Tarpley (1992) noted that cleared plots with low densities (relative to average and high densities) of "*Collisella,*" *Lottia* and *Littorina* were overgrown by algae in the high intertidal zone such that grazers could only maintain a small area. In such cases, grazers may lose their attachment space since they may not be able to prevent algal recruitment.

Competitive interactions between algae can also be mediated by the activity of grazers. While this study did not directly investigate algal competition, without grazers, algae compete for space unless some other factor is limiting. Differences in the initial magnitude of colonization can influence which algal species dominate. In my study, variability in recruitment of *M. papillatus* seems to influence the competitive interaction with *Endocladia muricata.* For example, open space in grazer free treatments of Experiment 1 was significantly colonized by several species, but persistence of *E. muricata* adjacent to open spaces depended on the colonizing species and their cover. Variation in these factors may have contributed to the intensity of competitive interactions and eventual composition of the assemblage. While heavy colonization by *M. papillatus* in some blocks resulted in low *E. muricata* cover, *Endocladia* was able to expand vegetatively and via spores into open spaces when *Mastocarpus* colonization was low or non-existent (Fig. 5). Figure 10 summarizes these interactions in a model for the dynamics of this assemblage. *Porphyra* recruitment appeared to have no effect on the persistence of *Endocladia* (personal observation), perhaps because *Porphyra* did not colonize open spaces as heavily and disappeared for months relative to *Mastocarpus.*

Competitive interactions in settlement and post-settlement phases have been linked to the composition of species recruiting into an open space (Connell 1989, Reed 1990, Connolly and Roughgarden 1998). Differences in attachment ability among species can also influence succession (Vadas et al. 1992). Furthermore, it is possible that the success of a competitive colonizer may be related to its ability to reach sexual maturity faster than another (Reed 1990). While intensity of settlement may influence the abundance of open space (Connolly and Roughgarden 1998), my study suggests post-settlement competitive interactions also influence such space as well as the persistence of *E. muricata*. Experiments that specifically investigate these competitive interactions will be insightful.

The difference in colonization magnitude, particularly for *M. papillatus*, among blocks of grazer free treatments in Experiment 1 likely contributed to the non-significant change in cover of *E. muricata*. This disparity in *M. papillatus* colonization among blocks may have been due to spatial variability in propagule dispersal (Sousa 1984), release, settlement (Reed et al. 1988) and recruitment. Settlement and recruitment can vary due to suitability of substrata (Reed et al. 1988), differences in water motion (Ricketts et al. 1985, Johnson and Brawley 1998) and canopy cover (Johnson and Brawley 1998). This variation can occur on scales from millimeters to meters. *E. muricata* cover significantly increased in all grazer free treatments in Experiment 2 (Fig. 6, Table 3), most likely due to a lack of heavy colonization by *M. papillatus* and other algae, releasing *E. muricata* from competition. This was demonstrated by the increase in *Endocladia* cover for the –grazer/-film treatments (Fig. 5). The –grazer/+film treatments yielded the same pattern as well.

General differences in recruitment magnitude, particularly for *Mastocarpus papillatus* and to a lesser extent other algae, between Experiments 1 and 2 were likely due to temporal variability in algal propagule release, settlement (Reed et al. 1988) and recruitment. Once settled, sporelings may be susceptible to post settlement mortality from extreme and variable physical conditions or herbivory (Reed et al. 1988, review in Vadas et al. 1992) which temporally vary. Recruitment has been demonstrated to be influenced by individual or combined temporal variation in abiotic conditions such as desiccation (Review in Vadas et al. 1992), tidal cycles (Johnson and Brawley 1998) and biotic factors such as seasonality of reproduction (Foster et al. 1988). The relative importance of these factors can vary depending on the species (Reed et al. 1988). Cubit (1984) noted that seasonal disappearance of high intertidal algae in the summer was primarily related to slower growth rates related to physiological stress while grazer activity remained relatively consistent throughout the year. In addition, asynchrony between algal recruitment and grazer abundance (Vadas et al. 1992) can lead to increases in algal cover. Furthermore, the adhesive strength of spores can vary with time (Vadas et al 1992) and season (Christie et al. 1970), and the rapidity of spore attachment is crucial particularly for species on an exposed coast (review in Vadas et al. 1992). While spatial variability can also account for this difference in my study, it is likely that seasonal shifts in spore output and settlement may have influenced the differences in cover between Experiment 1 and Experiment 2. The first experiment began in the late summer (August 1996) when heavy *M. papillatus* recruitment coincided with peak cystocarpic condition and the end of *E. muricata*'s reproductive output (Nigg 1988). Light recruitment by *M. papillatus* in Experiment 2 treatments was possibly due to fewer *M. papillatus* propagules (versus *E. muricata* propagules) present at this time of year (Nigg 1988). Similar results were observed in a study of intertidal recovery (Kinnetic Labs 1992). In spring and fall cleared plots in the *Endocladia/Mastocarpus* assemblage over 6 years, cover of the dominant perennial species differed in relation to the season of clearing: *E. muricata* cover was higher in spring-cleared treatments, while *M. papillatus* cover was more abundant in fall clearings (Kinnetic Labs 1992).

The block*grazer interaction suggests that the effect of grazers for Experiment 2 varied by block and this may be related to the slightly different densities of grazers noted in treatments with grazers present. The block effect noted for this experiment indicated that there were overall differences among the blocks related to the date that they were established. Since the blocks were established on different dates this may suggest that *E. muricata* may have been particularly heavy or even light on one or more of the dates. This difference in recruitment magnitude may be related to the intermittent release, settlement and recruitment of algae in time.

While most open spaces followed for 6 years on Pescadero Rocks tended to disappear and reappear, field studies at Point Pinos indicate that open space persists in the same location for at least 2 years, mostly due to inhibition of algal colonization by grazers. Grazer abundances at Pescadero Rocks (Kinnetic Labs 1992) appear similar to those observed at Point Pinos but, it appears that colonization and turnover rates of algae were higher at Pescadero Rocks relative to Point Pinos (personal observation). This difference in combination with a high abundance of grazers may explain why open space persisted for long periods but shifted in location at Pescadero Rocks. The lower abundance of species colonizing open space at Point Pinos in combination with high grazer abundance may explain why open space similarly persisted while in the same location. Further observation at both locations will be insightful

Size frequency data from Point Pinos indicate some open spaces were large (> 400 cm^2). However, these large areas were a maze of small interconnected channels. Only ≈ 25% of large open spaces had maximum gap diameters between borders that were greater than 10 cm. In addition, the maze-like extensions of some large open spaces went beyond the borders of the plot. Therefore, when comparing these data to results from patch recovery experiments, it is important to consider the shape of the open spaces.

Similar gap diameters for open spaces of both small and large areas is likely due to the intrinsic activity of grazers. As colonizers reoccupy large open spaces, grazers may retreat into smaller spaces that they can more easily keep free of colonizers (Foster 1992). Smaller spaces can also provide grazers more protection from predators in both terrestrial (Rice 1987) and marine (Sousa 1985) habitats. Castenholz (1961) suggested that open spaces may be maintained by grazers such as limpets and littorines which consume microalgae, and grazer activity may result in a stable size range for open spaces. Sousa (1984) and Farrell (1989) investigated early succesional dynamics in small and large artificially cleared open spaces and found a difference in the rate of colonization. In the presence of grazers, small spaces were colonized slowly. Sousa (1984) further discovered that in the absence of grazers, there was little difference in recruitment between small and large clearings. Dye (1993) found that the rate of colonization of open spaces of three sizes on South Africa shores was related to size. Small open spaces contained the higher densities of grazers and lower rates of colonization than large open spaces. In addition, he found a positive relationship between the number of grazers and ratio of bare rock to algae. Vadas (1992) observed open spaces to persist for 17 years due to a seasonal cycle of algal recruitment and removal by herbivores.

Even though open space size frequencies in Experiment 1 did not significantly change between August 1996 and September 1998 (Fig. 7A, Table 4), field observations indicated that open spaces became smaller in grazer free treatments in all four blocks. Non-significance was likely from formation of new open space by September 1998 in the 2 blocks where heavy *M. papillatus* recruitment appeared to cause *E. muricata* to disappear. This may be from shading (Reed and Foster 1984) or whiplash (Grant 1977; Foster et al. 1988, Vadas et al 1992) from *M. papillatus* (pers obs.). Studies have demonstrated how foliose, canopy forming species can limit the amount of light reaching understory species (Reed and Foster 1984, Johnson and Brawley 1998). In contrast to the Experiment 1, minimal shading occurred in all grazer free treatments in Experiment 2, associated with light *M. papillatus* recruitment and heavy *E. muricata* recruitment.

Recruit abundance in the first experiment further demonstrated how grazers inhibit recruitment particularly for *Endocladia. muricata* and *Mastocarpus papillatus* (Fig. 8A, Table 5). Algal turfs may inhibit settlement and recruitment by accumulating sediments causing burial and scour (Hruby and Norton 1979, Vadas et al. 1992). Turfs can also positively affect algal recruitment (Benedetti-Cecchi and Cinelli 1992, Vadas et al. 1992). In some cases facilitation of settlement by algal turfs may lead to their demise by enhancing the cover of competitors. Johnson and Brawley (1998) noted that turfs dominated by *E.*

muricata selectively facilitated the establishment of some algae to juvenile stages. My data suggest that *E. muricata* may facilitate settlement of algae into open space at Point Pinos. However, *E. muricata* turfs contain numerous grazers (Glynn 1965, personal observation) which can consume recruits, further demonstrating how grazers can contribute to mediating potiential competition among algae.

Effect of substratum condition.

Substratum condition can play an important role in the composition and cover of species colonizing open spaces. Foster (1982) noted that the crustose holdfasts of various red algae inhibited recruitment of *Mazzaella flaccida* relative to cleared bare rock. Data from my study suggest, though not significantly, a trend of higher colonization of *I. cordata* and *M. flaccida* on newly exposed surfaces. In contrast *Porphyra perforata* recruited onto both substrata equally (Fig. 9). High cover on newly exposed substrata may be related to settlement, attachment and recruitment dynamics of propagules. Regardless of the mechanism, these data suggest severe disturbance to the substratum may result in different algal composition and cover relative to "weathered" substrata at Point Pinos.

Summary

Species potentially compete for the open space provided by disturbances on rocky shores. I demonstrated that grazers influence the structure of the *Endocladia* assemblage by preventing total colonization of open space and contribute to dynamics of indirectly mediating competition among algae. In habitats such as Pescadero Rocks, open space can persist for long periods (>6 years) but shifts in location within the assemblage. In contrast, open spaces persisted but did not change in location within the natural red algal assemblage at Point Pinos. This difference between locations may be linked to a more diverse suite of species which quickly appeared and disappeared from substrata at Pescadero Rocks relative to Point Pinos. Further study of algal recruitment and turnover dynamics at these sites will provide insight into the persistence of open space.

Clearly, herbivorous gastropods played a significant role in the persistence of open space. In their absence, spatial and temporal variability likely contributed to competitive interactions among algae but this was not tested. While grazers play an integral role in the structure of this assemblage, trends suggested that biofilms and substratum condition may also influence the species that colonize an open space for shorter periods of time. These results suggest that grazers may prevent total colonization of open space in this assemblage and enable a species like *Endocladia muricata* to dominate, since it is consumed less than other species. However, no species, including *E. muricata,* will expand into open spaces, since high grazers densities will prevent species from colonizing their vital habitat.

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Table 1. Area of 18 open spaces between March 1985 and March 1991. Numbers are area in cm^2

Number	3/19/85	6/21/85	1/18/86	3/26/86	3/25/87	10/25/87	3/18/88	10/25/88	3/20/89	11/13/89	3/28/91	Open Over Entire 6 Years?
1	5	5	X	X	2	2	5	X	X	X	na	n
2	5	3	11	10	X	2	6	X	X	X	12	n
3	5	X	X	X	X	11	8	X	4	6	11	n
4	8	15	5	48	3	2	18	2	16	5	2	y
5	9	11	16	10	4	2	17	5	76	80	64	y
6	10	1	3	6	X	X	X	X	4	X	X	n
7	10	8	X	X	X	X	48	X	X	X	15	n
8	11	9	46	X	X	55	16	X	16	96	72	n
9	14	10	3	16	60	3	X	X	X	X	64	n
10	16	24	8	66	29	2	26	23	na	na	na	y
11	16	1	1	7	1	2	X	8	3	200	4	n
12	20	8	26	104	7	2	6	X	6	X	5	n
13	20	7	3	9	2	X	2	X	X	32	236	n
14	24	10	13	6	104	7	X	3	X	15	na	n
15	44	11	11	6	13	5	73	22	4	384	X	n
16	180	X	X	28	19	26	14	576	704	800	1128	n
17	200	36	15	X	1	10	10	10	24	464	368	n
18	380	84	68	22	296	56	35	44	152	384	820	y

na = blended with another open space
X = disappeared

Table 2. Experiment 1: Three-way ANOVA's for difference in the cover of open space and algae among grazer and film treatments. Ephemeral species were analyzed in September 1997 while open space and perennial species were analyzed in September 1998. Species listed have >10% cover. Bold type indicates statistically significant values.

Ephemeral Algae

Species	**Parameter**	**df**	**SS**	**F-statistic**	**P-value**
Porphyra perforata	Grazers	1	0.003538	37.071470	**0.009**
	Films	1	0.000010	0.107093	0.764
	Block	3	0.000837	2.923258	0.201

Open Space and Perennial Algae

	Parameter	**df**	**SS**	**F-statistic**	**P-value**
Open Space	Grazers	1	0.000809	23.040827	**0.017**
	Films	1	0.000070	1.162064	0.360
	Block	3	0.000111	1.997128	0.292
Endocladia muricata	Grazers	1	0.000228	0.927061	0.406
	Films	1	0.000027	0.111313	0.761
	Block	3	0.000547	0.740163	0.595
Mastocarpus papillatus	Grazers	1	0.012711	180.192089	**<0.001**
	Films	1	0.000028	0.399516	0.572
	Block	3	0.001025	4.845005	0.114
non-Geniculate Coralline	Grazers	1	0.000101	0.808994	0.435
	Films	1	0.000001	0.011960	0.920
	Block	3	0.001405	3.741641	0.154

Table 3. Experiment 1: Three-way ANOVA's for difference in the cover of open space and algae among grazer and film treatments. Cover data for open space and algae were analyzed in September 1998. Species listed have >10% cover. Bold type indicates statistically significant values.

Open Space and Perennial Algae

	Parameter	df	SS	F-statistic	P-value
Open Space	Grazers	1	0.000948	19.193065	**0.022**
	Films	1	0.000015	0.303294	0.620
	Block	3	0.000095	0.659698	0.630
Endocladia muricata	Grazers	1	0.001261	139.802974	**0.001**
	Films	1	0.000122	13.490070	**0.035**
	Block	3	0.000638	23.581522	**0.014**
Mastocarpus papillatus	Grazers	1	0.000333	11.996997	**0.040**
	Films	1	0.000083	3.000000	0.181
	Block	3	0.000167	1.998999	0.292

Table 4. MANOVA to determine change in size frequency distribution of open spaces for Experiments 1 and 2. Bold type indicates statistically significance values. The size classes 101-200 cm^2 and 301-400 cm^2 were excluded in the Experiment 1 analysis due to correlation with other size classes. The size classes 0-101 cm^2 and 401-500 cm^2 were excluded in the Experiment 2 analysis due to correlation with other size classes. Analyses compared size frequency data for Experiment 1 between August 1996 and September 1998. Size frequency data was analyzed between July 1997 and August 1998 for Experiment 2.

Experiment 1

Source	**Size Class***	**df**	**SS**	**F-statistic**	**P-value**
Grazers	0-100 cm^2	1	8883.0625	0.976011	0.396
	201-300 cm^2	1	16384.0000	0.452938	0.549
	401-500 cm^2	1	10660.2000	7.936685	0.069
	Wilk's Lambda	3		7.531853	0.260
Films	0-100 cm^2	1	4590.0625	0.504325	0.529
	201-300 cm^2	1	16770.2000	0.463616	0.545
	401-500 cm^2	1	106602.000	7.936685	0.067
	Wilk's Lambda	3		58.271475	0.096
Block	0-100 cm^2	1	9515.6875	0.348507	0.795
	201-300 cm^2	1	40090.1000	0.369346	0.782
	401-500 cm^2	1	40294.7000	1.000000	0.500
	Wilk's Lambda	3		1.193978	0.509

Experiment 2

Source	**Size Class***	**df**	**SS**	**F-statistic**	**P-value**
Grazers	100-201 cm^2	1	14400.0000	17.004527	**0.026**
	201-300 cm^2	1	119.1372	0.010884	0.924
	301-400 cm^2	1	2.7897	2524.604729	< **0.001**
	Wilk's Lambda	3		4382.073578	**0.011**
Films	100-201 cm^2	1	4032.2500	4.761563	0.117
	201-300 cm^2	1	63295.0000	5.782593	0.095
	301-400 cm^2	1	544.1723	4.924682	0.113
	Wilk's Lambda	3		50.786916	0.103
Block	100-201 cm^2	1	52602.2000	20.705471	**0.017**
	201-300 cm^2	1	25511.7000	0.776912	0.580
	301-400 cm^2	1	81628.4000	246.241796	< **0.000**
	Wilk's Lambda	3		36.012327	**0.012**

Table 5. Three-way ANOVA's for number of recruits in Experiments 1 and 2 for grazer and film treatments in June and September 1998. Bold values are significant.

Experiment 1

Species	**Date**	**Parameter**	**df**	**SS**	**F-statistic**	**P-value**
Endocladia muricata	June 98	Grazers	1	39.0625	31.779661	**0.011**
		Films	1	1.5625	1.271186	0.341
		Block	3	23.1875	6.288136	0.083
	September 98	Grazers	1	9.0000	8.307692	0.063
		Films	1	0.0000	0.000000	1.000
		Block	3	6.2500	1.923077	0.302
Mastocarpus papillatus	June 98	Grazers	1	36.0000	14.896552	**0.031**
		Films	1	0.2500	0.103448	0.769
		Block	3	6.5000	0.896552	0.535
	September 98	Grazers	1	9.0000	10.800000	**0.046**
		Films	1	1.0000	1.200000	0.353
		Block	3	5.5000	2.200000	0.267

Experiment 2

Species	**Date**	**Parameter**	**df**	**SS**	**F-statistic**	**P-value**
Endocladia muricata	June 98	Grazers	1	9.0000	1.770492	0.275
		Films	1	4.0000	0.786885	0.440
		Block	3	28.2500	1.852459	0.313
	September 98	Grazers	1	0.5625	0.150838	0.724
		Films	1	0.0625	0.016760	0.905
		Block	3	2.6875	0.240223	0.864
Mastocarpus papillatus	June 98	Grazers	1	0.5625	0.457627	0.547
		Films	1	0.5625	0.457627	0.547
		Block	3	2.1875	0.593220	0.661
	September 98	Grazers	1	3.0625	1.195122	0.354
		Films	1	1.5625	0.609756	0.492
		Block	3	6.1875	0.804878	0.569

Table 6. Two-way ANOVA's for change in cover of algae and open space cover on newly exposed and weathered substrata. Species listed had >10% cover. Bold type indicates statistically significant values.

Ephemeral Algae

	Parameter	df	SS	F-statistic	P-value
Iridaea cordata/ Mazzaella flaccida	Substratum	1	0.003415	6.418881	0.085
	Block	3	0.001596	1.000000	0.500
Porphyra perforata	Substratum	1	0.000066	0.297304	0.624
	Block	3	0.003512	5.265057	0.103

Perennial Algae and Open Space

	Parameter	df	SS	F-statistic	P-value
Open Space	Substratum	1	0.000630	4.188037	0.133
	Block	3	0.001049	2.324841	0.253
Endocladia muricata	Substratum	1	0.000066	1.157549	0.361
	Block	3	0.003263	19.042305	**0.019**
Mastocarpus papillatus	Substratum	1	0.000010	0.261010	0.645
	Block	3	0.001487	12.780881	**0.032**
Corallina vancouveriensis	Substratum	1	0.000144	1.000000	0.391
	Block	3	0.001837	4.238754	0.133

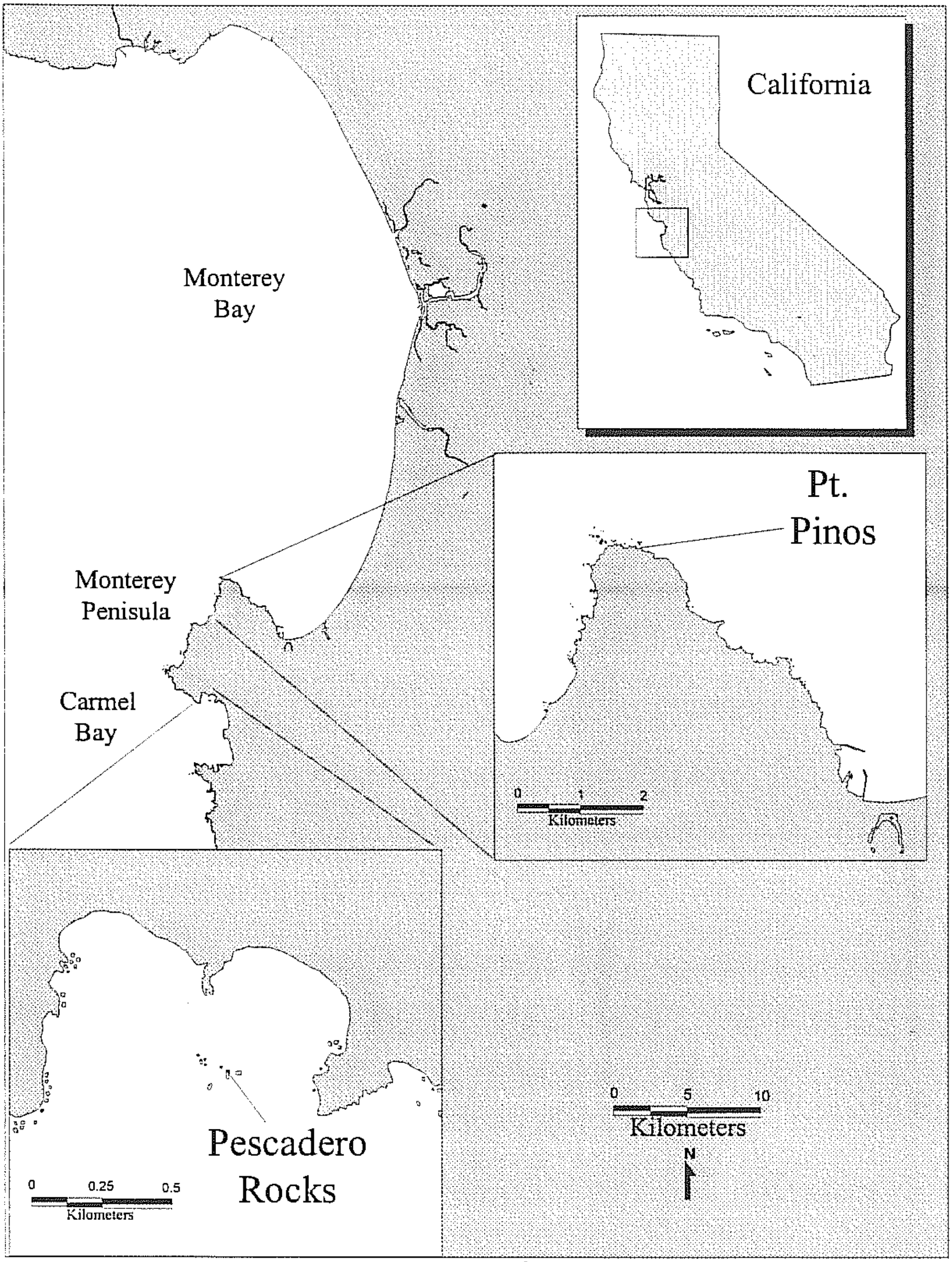


Figure 1. Research Sites Pescadero Rocks (36°34'N; 121°56'W) and Pt. Pinos (36°38'N; 121°55'W).

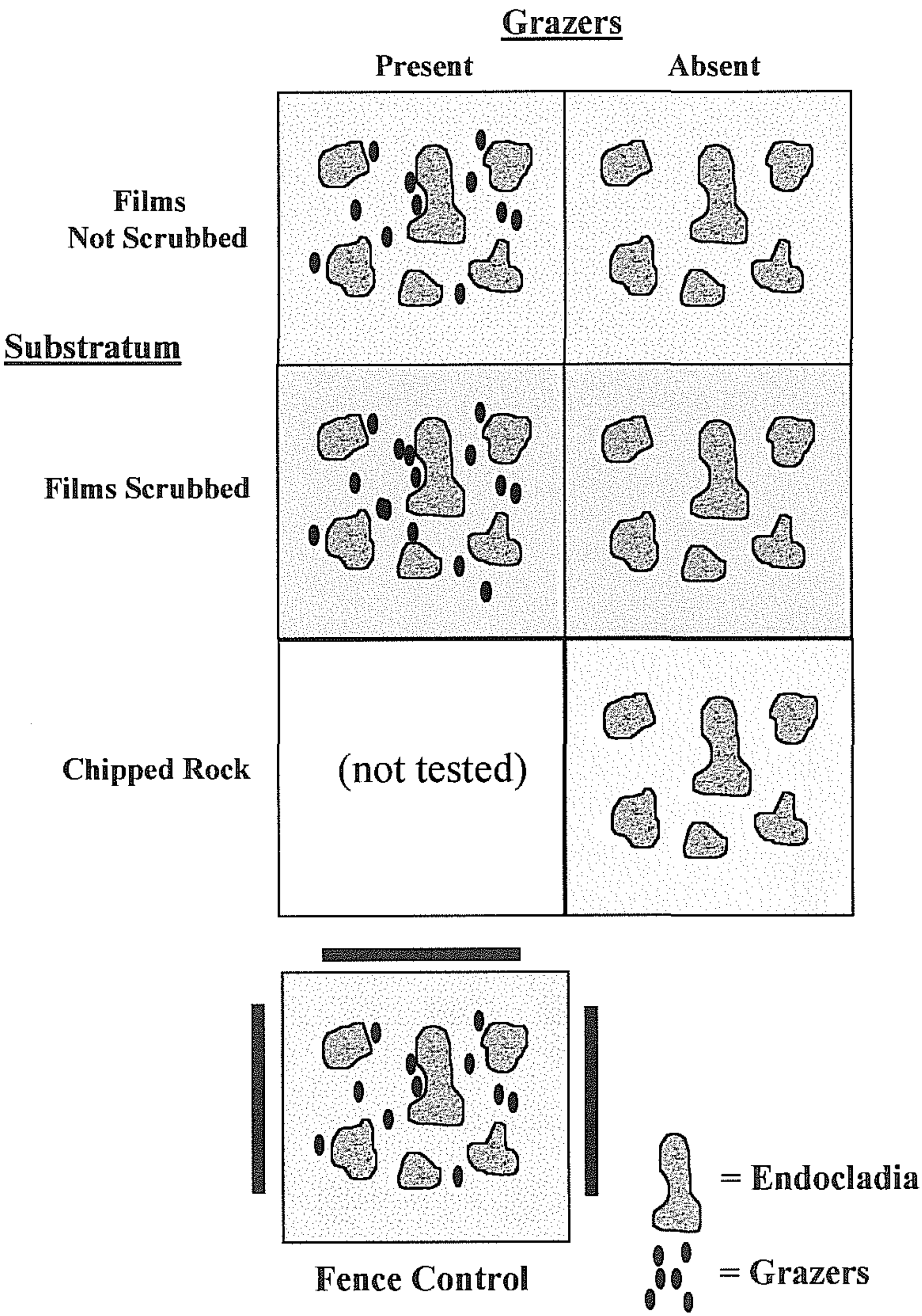


Fig. 2. Experimental design for grazer, film and substratum effects.

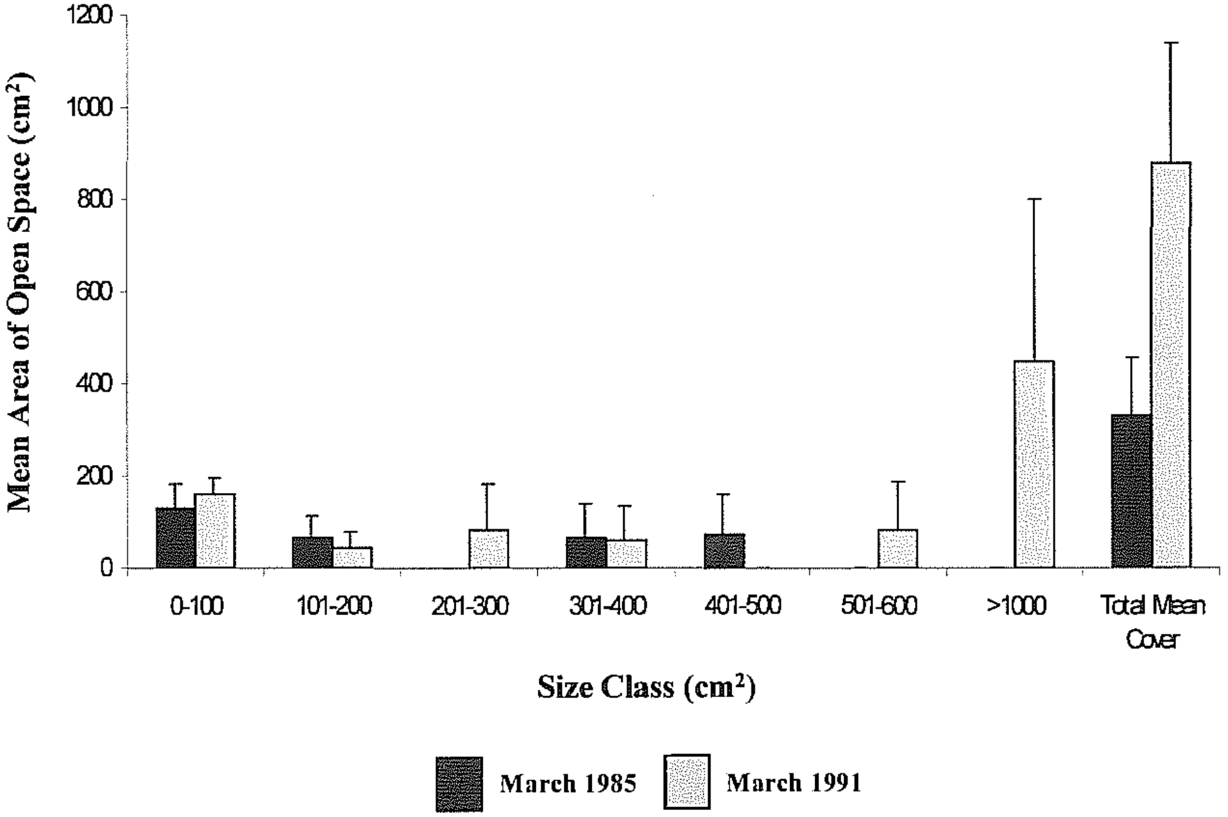


Fig. 3. Amount of mean area (w/SE) per size class of open space for March 1985 and March 1991; n = 6. Total mean cover for all size classes is shown on the right.

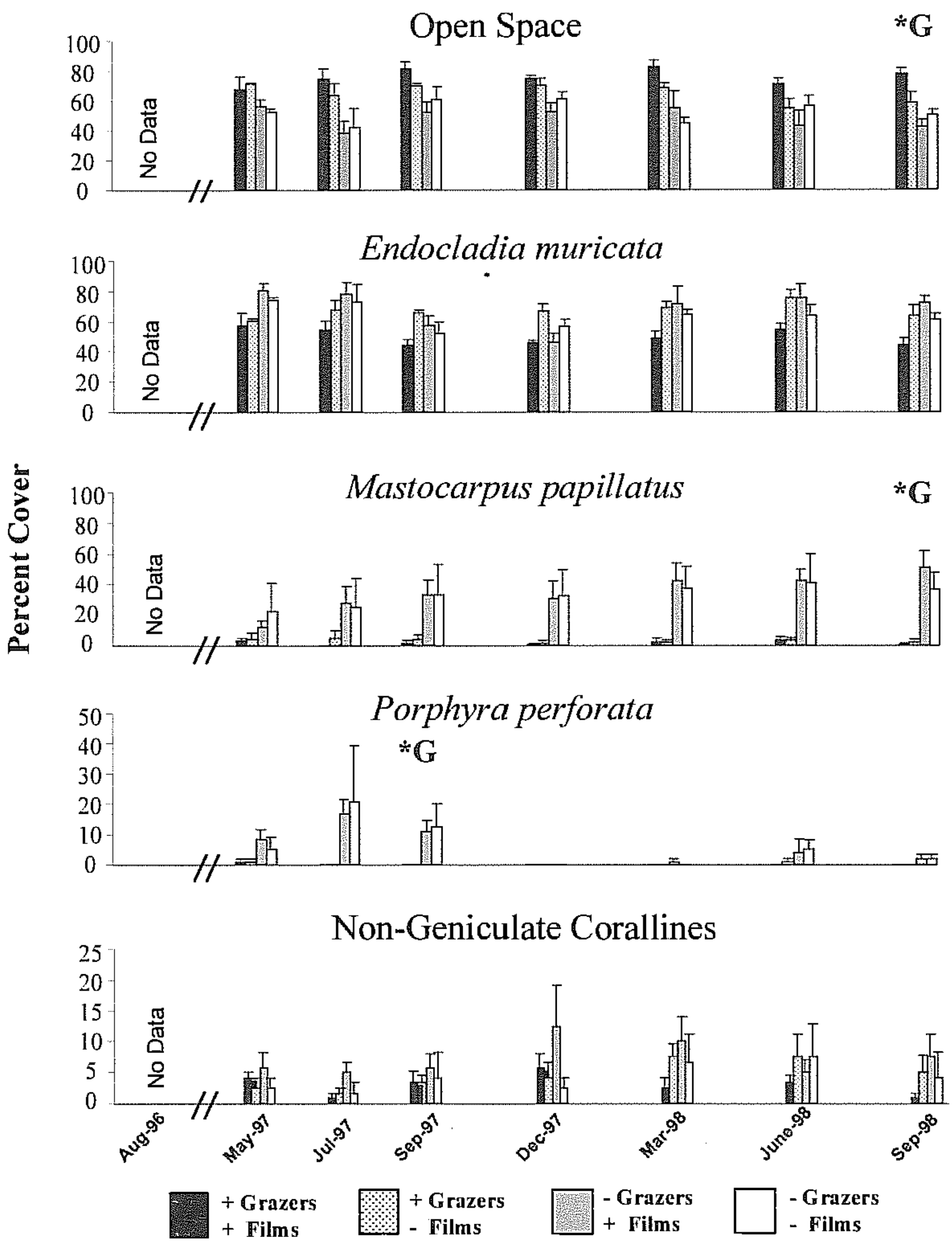


Fig. 4. Experiment 1: mean cover (w/SE) of Open Space, *Endocladia muricata*, *Mastocarpus papillatus*, *Porphyra perforata* and non-Geniculate Corallines in grazer and film treatments; n = 4. Only those species with cover that exceeded 10% at any sampling are shown. *G represents a statistically significant difference in cover due to grazers.

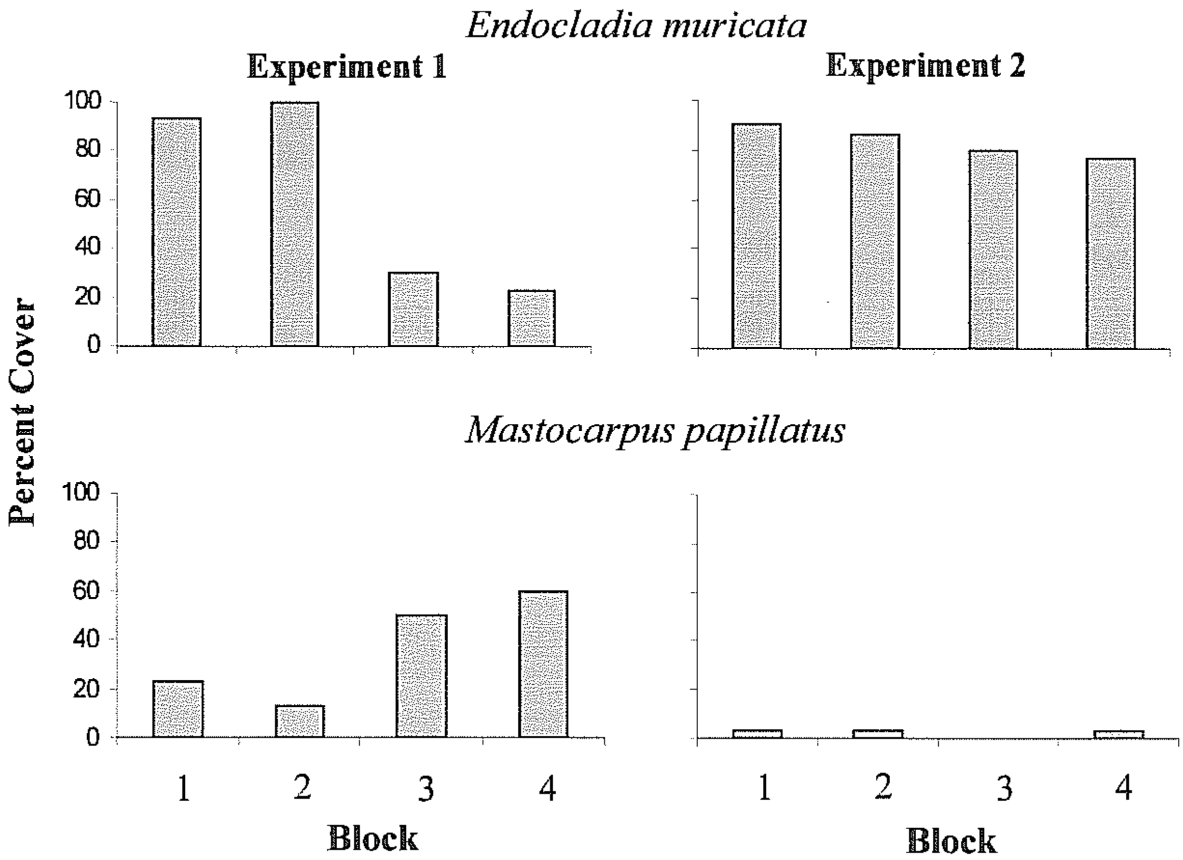


Fig. 5. Cover per block for *Endocladia muricata* and *Mastocarpus papillatus* in the -Grazers/-Films treatment for Experiment 1 andExperiment 2 in September 1998.

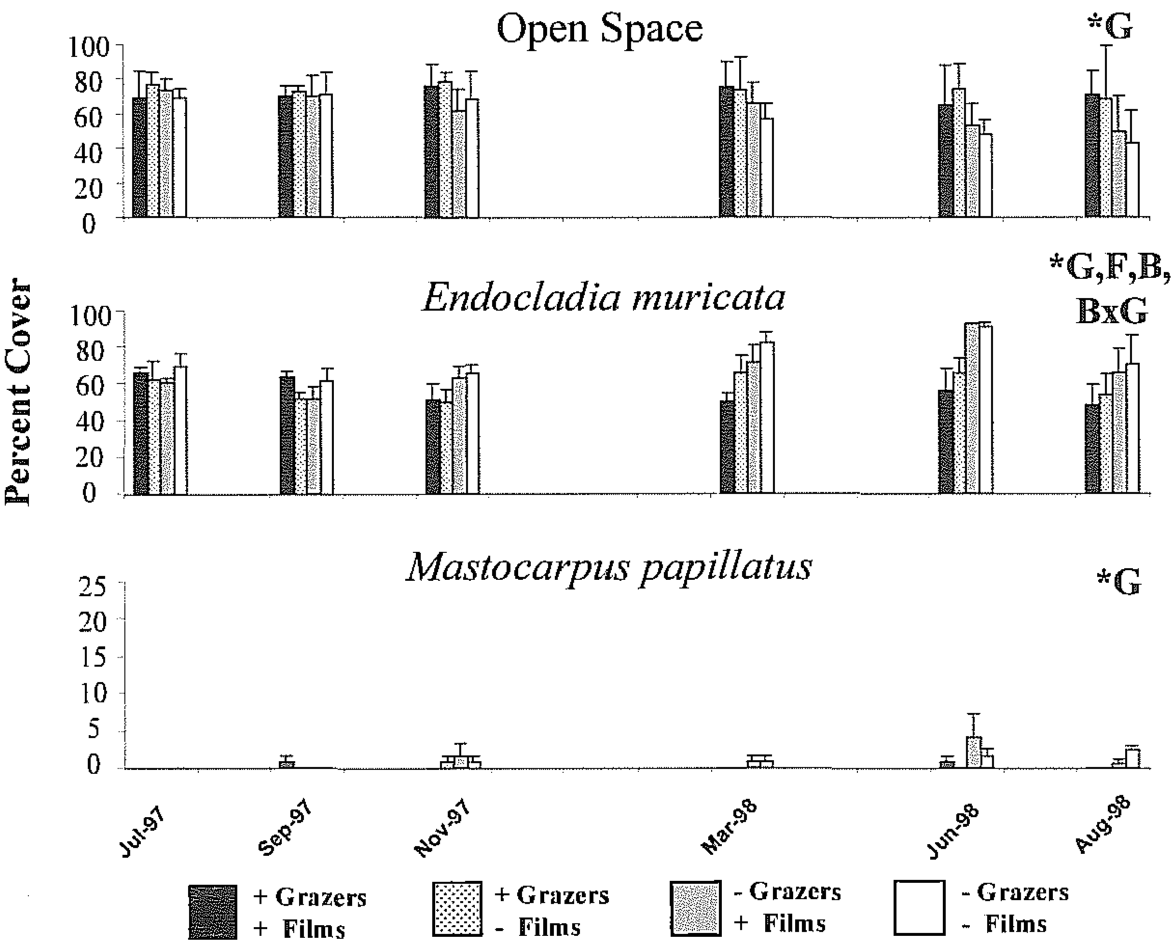


Fig. 6. Experiment 2: mean cover (w/SE) for Open Space, *Endocladia muricata* and *Mastocarpus papillatus* in grazer and film treatments; n = 4. *M. papillatus*, open space and those species with cover that exceeded 10% at any sampling are shown. *G,F,B and BxG represents a statistically significant difference in cover due to grazers, films and block, and a block x grazer effect on this date.

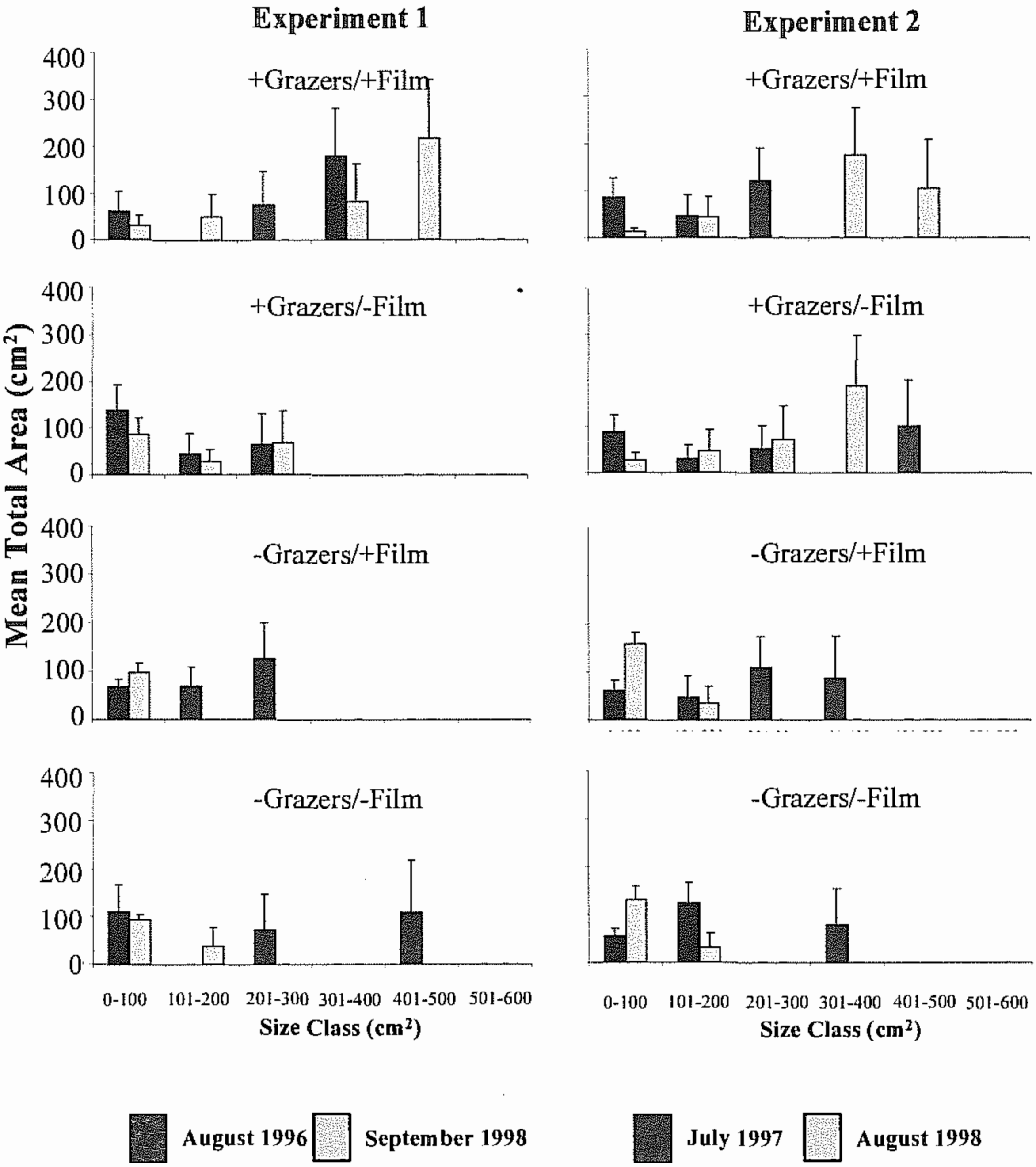


Fig. 7. Mean total area (w/SE) per size class of open space for Experiments 1 and 2. Bars represent the mean total area (cm^2) in each size class.

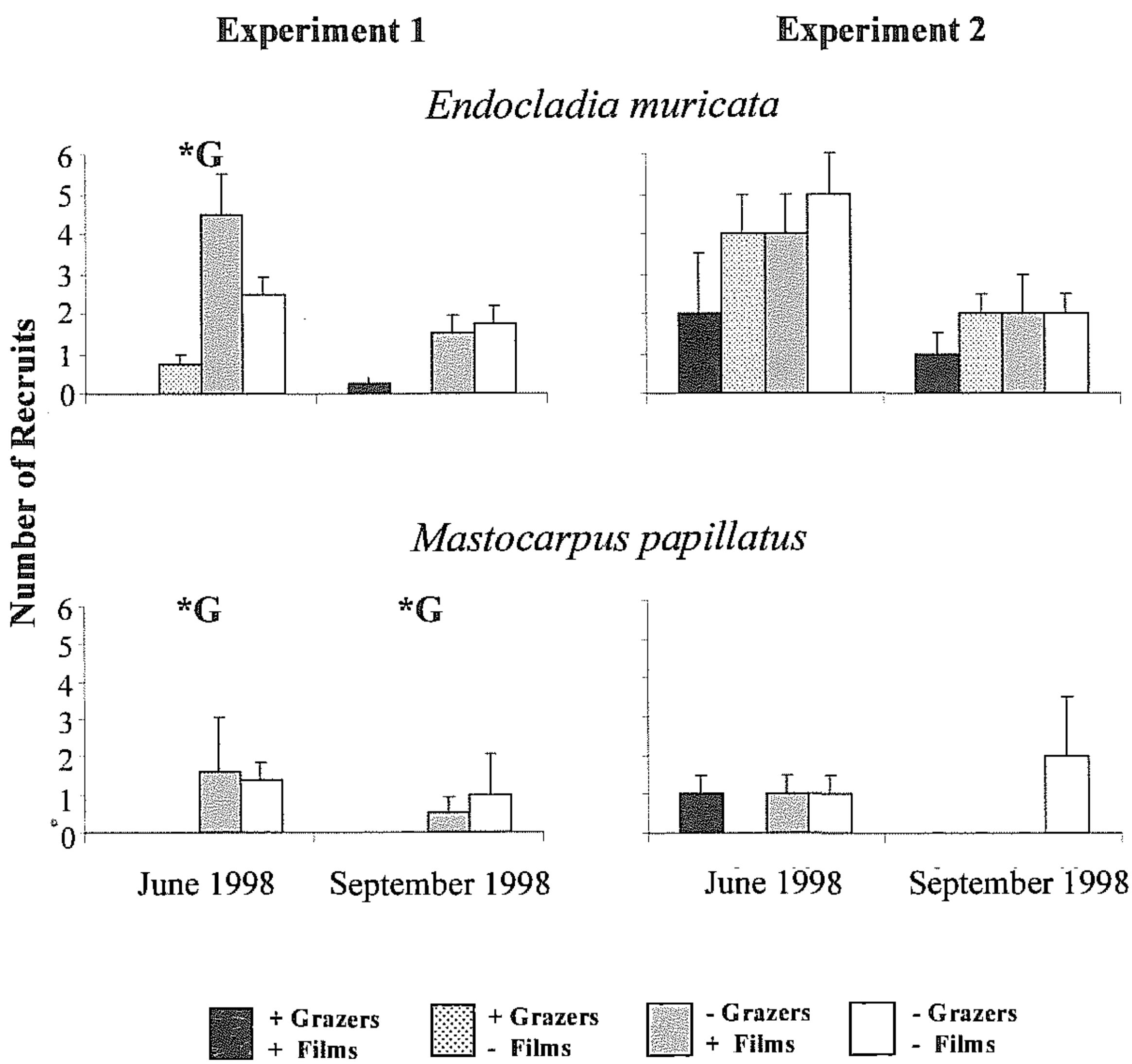


Fig. 8. Mean number of recruits (w/SE) for *Endocladia muricata* and *Mastocarpus papillatus* for Experiment 1 and 2; n = 4. *G Represents a statistically significant difference in recruit abundance due to grazers on the given date.

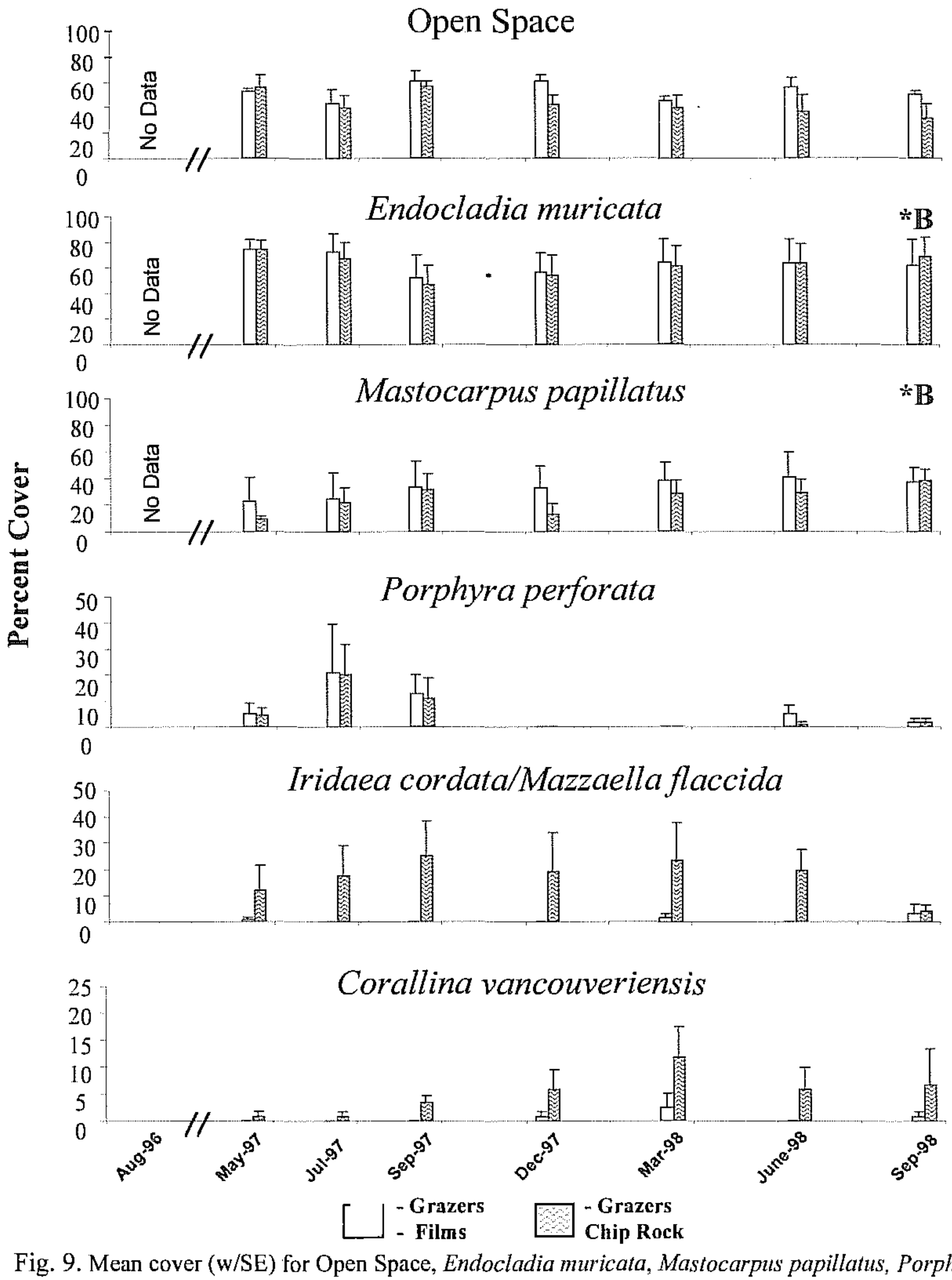


Fig. 9. Mean cover (w/SE) for Open Space, *Endocladia muricata, Mastocarpus papillatus, Porphyra perforata, Iridaea cordata/Mazzaella flaccida* and *Corallina vancouveriensis* in substratum condition treatments; n = 4. Only those species with cover exceeding 10% at any sampling are shown.
*B represents a significant block effect on this date.

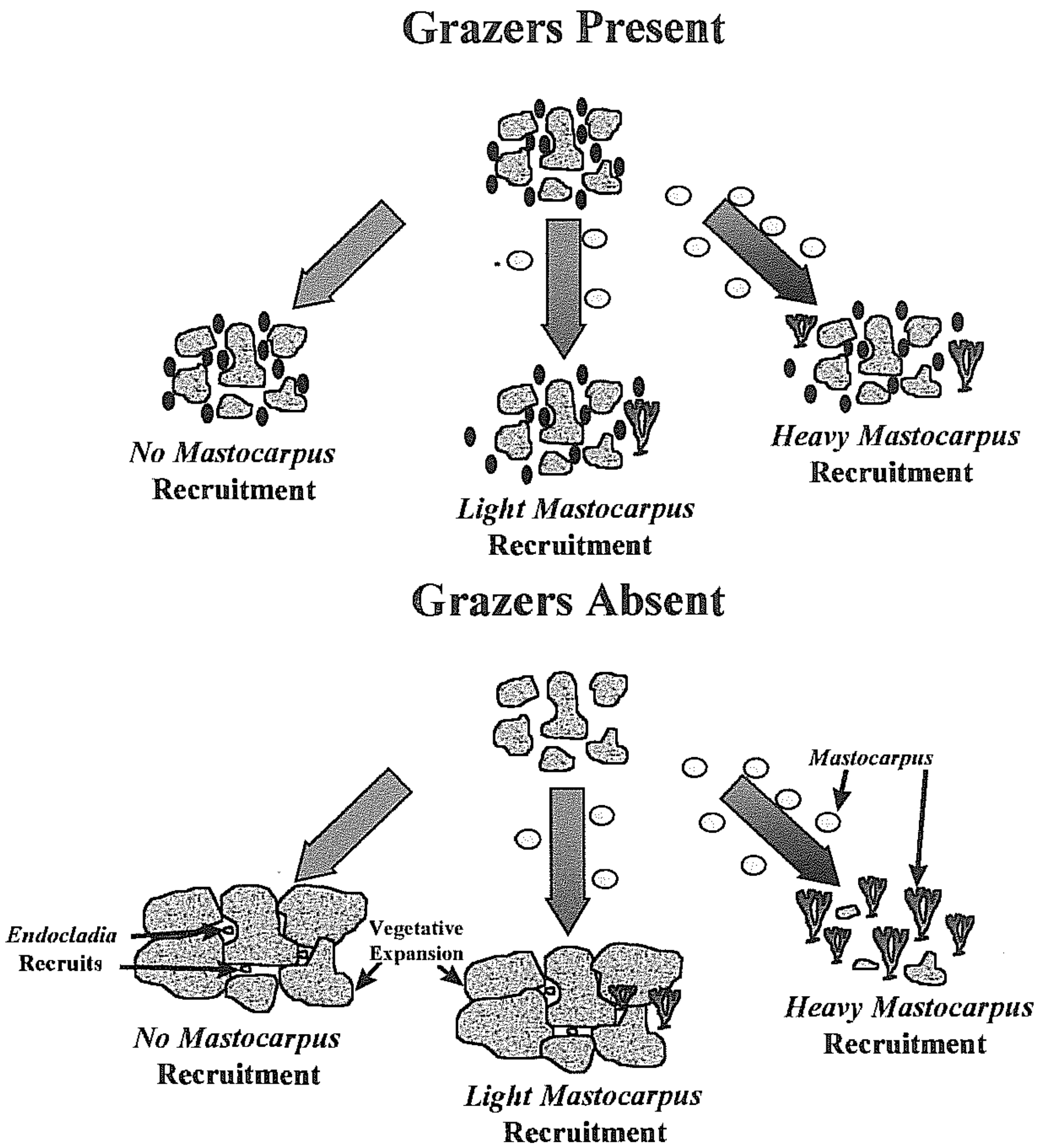
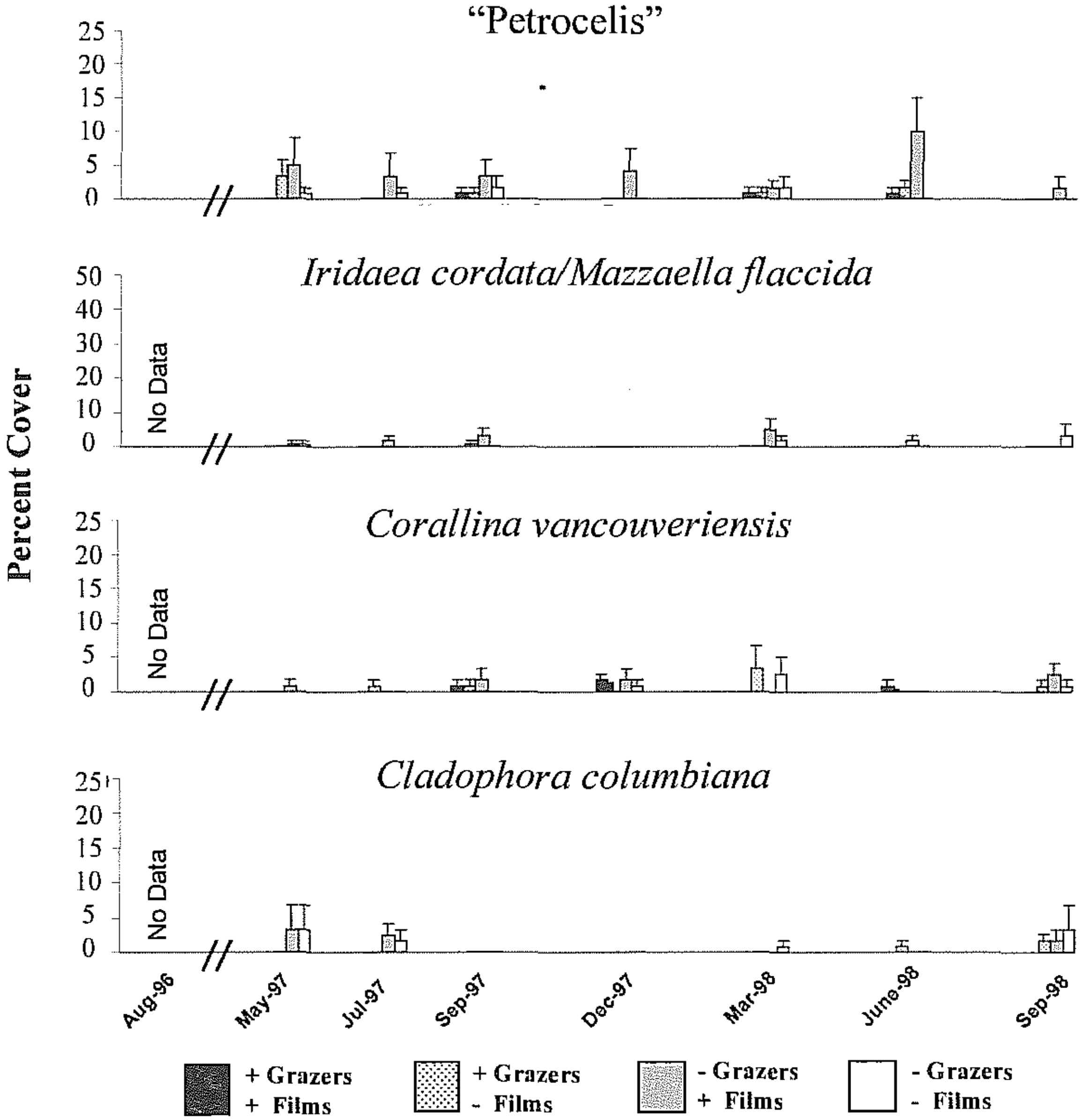


Fig. 10. Model demonstrating the effects of recruitment and grazers on the *Endocladia muricata* assemblage at Point Pinos, Pacific Grove, CA. Model assumes constant recruitment of *Endocladia*. In the presence of grazers, no *Mastocarpus* recruitment results in the persistence of open space and dominance but not expansion of *Endocladia*. Light and heavy *Mastocarpus* recruitment with grazers present result in a few species colonizing open spaces. Grazers by preventing heavy colonization of their habitat, indirectly mediate competition among algae. When grazers are removed from the system, no or light *Mastocarpus* recruitment resnlts in the vegetative and/or reproductive expansion of *Endocladia* into open space. When heavy *Mastocarpus* colonization occnrs, *Endocladia* cover declines, likely from shading or whiplash.

Appendix A. Example of a 3-way ANOVA with the variables grazers (G), films (F) and block (B).

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
G$	0.000809	1	0.000809	23.040827	0.017207
F$	0.000041	1	0.000041	1.162064	0.359994
B	0.000210	3	0.000070	1.997128	0.292175
B*G$	0.000089	3	0.000030	0.845011	0.553416
B*F$	0.000183	3	0.000061	1.741057	0.330007
F$*G$	0.000315	1	0.000315	8.982046	0.057807
Error	0.000105	3	0.000035		



Appendix. B1. Experiment 1: mean cover (w/SE) for "Petrocelis", *Iridaea cordata/Mazzaella flaccida, Corallina vancouveriensis and Cladophora columbiana* in grazer and film treatments; n = 4. Species with cover less than 10% are shown.

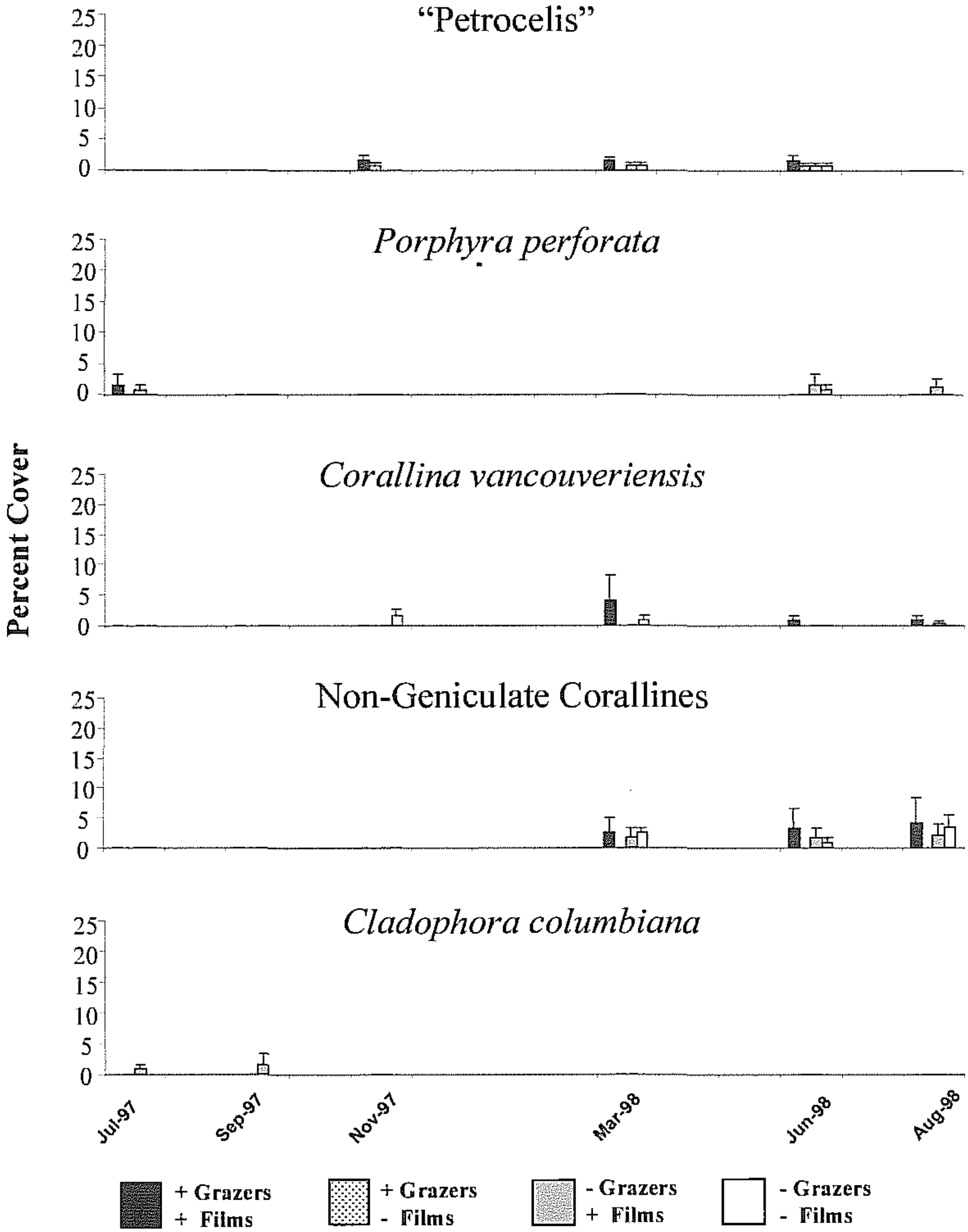
Appendix B2. Experiment 1 Three-way ANOVA's for change in algae due to grazers and films. Species listed have cover less than 10 percent. Bold values are significant.

Ephemeral Algae

Species	**Parameter**	**df**	**SS**	**F-statistic**	**P-value**
Iridaea cordata and *Mazzaella flaccida*	Grazers	1	0.000070	1.877269	0.264
	Films	1	0.000070	1.877269	0.264
	Block	3	0.000111	1.000000	0.500

Perennial Algae and Open Space

Species	**Parameter**	**df**	**SS**	**F-statistic**	**P-value**
"Petrocoelis"	Grazers	1	0.000042	1.000000	0.391
	Films	1	0.000042	1.000000	0.391
	Block	3	0.000125	1.000000	0.500
Corallina vancouveriensis	Grazers	1	0.000121	2.833114	0.191
	Films	1	0.000004	0.083443	0.791
	Block	3	0.000648	5.045757	0.108
Cladophora columbiana	Grazers	1	0.000042	0.237170	0.660
	Films	1	0.000139	0.792404	0.439
	Block	3	0.000625	1.185078	0.446



Appendix. C1. Experiment 2: mean cover (w/SE) for "Petrocelis", *Porphyra perforata, Cladophora columbiana* in grazer and film treatments; n = 4. Species with cover less than 10% are shown.

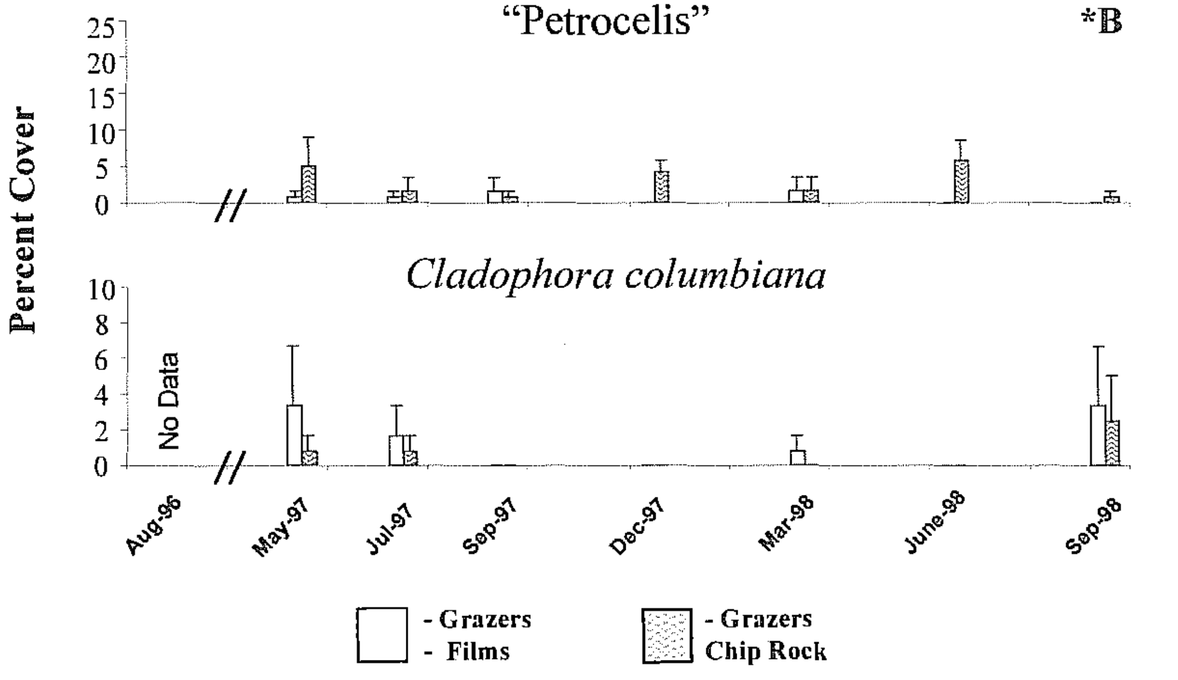
Appendix C2. Experiment 2 Three-way ANOVA's for change in algae cover due to grazers and films. Species listed have cover less than 10 percent. Bold values are significant.

Ephemeral Algae

Species	**Parameter**	**df**	**SS**	**F-statistic**	**P-value**
Porphyra perforata	Grazers	1	0.000070	1.877269	0.264
	Films	1	0.000021	0.561366	0.508
	Block	3	0.000631	5.673114	0.094

Perennial Algae and Open Space

	Parameter	**df**	**SS**	**F-statistic**	**P-value**
Corallina vancouveriensis	Grazers	1	0.000021	1.000000	0.391
	Films	1	0.000021	1.000000	0.391
	Block	3	0.000062	1.000000	0.500
Non-Geniculate Corallines	Grazers	1	0.000005	0.025297	0.884
	Films	1	0.000005	0.025297	0.884
	Block	3	0.000608	1.000000	0.500



Appendix. D1. Mean cover (w/SE) for "Petrocelis" *and Cladophora columbiana* in substratum condition treatments; n = 4. Species with cover less than 10% are shown. *B represents a block effect

Appendix D2. Two-way ANOVA's for change in algae and open space cover on newly exposed and weathered substrata. Species listed have cover less than 10 percent. Bold values are significant.

Perennial Algae and Open Space

Species	Parameter	df	SS	F-statistic	P-value
"Petrocoelis"	Substratum	1	0.000040	1.000000	0.391
	Block	3	0.000121	1.000000	0.500
Cladophora columbiana	Substratum	1	0.000003	1.000000	0.391
	Block	3	0.001785	190.440000	0.001
Non-Geniculate Corallines	Substratum	1	0.000200	1.948052	0.257
	Block	3	0.001681	5.459416	0.098