

AN ABSTRACT OF THE THESIS OF

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Title: Turf Assemblage of a *Macrocystis* Kelp Forest: Experiments on Competition and Herbivory.

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Early and later successional stages of the assemblage of turf algae and sessile animals of a *Macrocystis* kelp forest were studied off San Nicolas Island, California from 1980 through 1981, and 1983 through 1984. Kelps were manipulated to determine if differences in illumination could account for dominance by turf algae or sessile animals. Caging and algal-removal experiments were conducted to determine if the effects of herbivory and competition could account for the low or variable recruitment and abundance of foliose turf algae. Plots were covered for different time intervals up to 1 year to determine if survival of overgrowth could explain the prevalence of competitively subordinate crustose coralline algae.

Increased cover and recruitment of turf algae and decreased cover and low recruitment of sessile animals were correlated with the removal of canopy. In the presence of canopy, existing cover of crustose algae and sessile animals changed little over time; sessile animals recruited at significantly higher levels than algae on cleared

plots.

Patiria (a common invertebrate grazer) removed certain ephemeral algae and appeared to slow recruitment by other algae, but had little effect on mature turf algae. These effects appeared dependent on a high density of *Patiria*.

Algal recruitment on caged and open, near-bare plots was negligible, but sessile animals recruited heavily to these plots. These results were correlated with low illumination caused by a dense and persistent surface canopy of *Macrocystis*.

Established foliose red algae increased significantly in caged plots compared to open plots implying effects due to herbivory. No changes in cover were associated with turf algal-algal competition on these plots; a major decline in cover of all arborescent turf algae was correlated with low illumination.

On covered plots, crustose coralline algae alternately survived, died, and recruited at different sampling points, resulting in only a slight change in abundance after 12 months of coverage. Other sessile organisms also survived while covered, but declined substantially compared to crustose coralline algae.

Patterns of distribution and abundance of turf algae and sessile animals were correlated with the *Macrocystis* canopy, as it affects illumination at the substrate. No pervasive effects were attributed to grazing by large invertebrates. Herbivory, probably by fishes, was a plausible explanation for the low abundance of foliose red algae. The ability of crustose coralline algae to survive and recruit under conditions of overgrowth was shown to be a contributing factor for the prevalence of these algae.

Turf Assemblage of a *Macrocystis* Kelp Forest: Experiments on
Competition and Herbivory

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Turf Assemblage of a *Macrocystis* Kelp Forest:
Experiments on Competition and Herbivory

INTRODUCTION

Concepts of succession have intrigued terrestrial forest ecologists for much of this century. But in the past, the complexity of biotic interactions and physical disturbances that act to delay, advance or return succession to some previous state, proceeded separately from and were rarely incorporated into successional theory (Drury and Nisbet 1973, Connell and Slatyer 1977, Cattelino et. al. 1979, McIntosh 1981). Presently, ambitious but workable studies have investigated the effects of biotic interactions and physical disturbance as integral components of ecological succession in marine communities (e.g., Dayton 1975b, Lubchenco and Menge 1978, Sousa 1979). The practicality of studying marine communities to elucidate concepts of ecological theory is apparent from the number of investigations of the past 20 years. Marine communities found on rocky habitat are unique in that ecologically complex interactions occur among and between algae and sessile or slow-moving animals. The significance of these interactions can often be determined by properly designed, small-scale experiments. Until recently, these studies were primarily conducted in intertidal habitats as compared to subtidal habitats, because of accessibility. But, increasing use of and improvements to SCUBA have facilitated investigations of rocky and soft-bottom subtidal habitats.

Kelp forest communities may be appropriate systems for testing hypotheses of community succession that are applicable to terrestrial forest communities. Tests of

these hypotheses in terrestrial forests are usually stymied because of the difficulty in manipulating the taller vegetative layers and the longevity of different seral stages. The time necessary for observable results may exceed the average life span of a biologist, and therefore, many of the conclusions reached tend to be based on extrapolations (Drury and Nisbet 1973). In kelp forests, the competitively dominant upper vegetative layers, which are typically the kelps, are more easily manipulated than terrestrial trees, and turnover of these dominant layers can occur in a very brief time span compared to terrestrial forests (Neushul 1971). Kelp forests may be comparable to terrestrial forests in stratification of vegetative layers, diversity of species, and complexity of trophic levels and food webs (see reviews in North 1971; Foster 1975a, Dayton et al. 1984).

San Nicolas Island, California, was identified as a possible site for translocation of California sea otters (*Enhydra lutris*) by the U.S. Fish and Wildlife Service (USFWS) in the late 1970's. Several studies (some continuing) were conducted at sites around the island in order to determine structure, change and causes of change in different marine communities prior to the proposed re-establishment of otters. As part of the USFWS effort, I made preliminary observations on San Nicolas Island from May through August 1979, and initiated questions about structure and change within a kelp forest community. Because of the ecological importance of kelp forests to sea otters, studies of this component of the marine systems around San Nicolas Island were particularly important to the research needs of the USFWS.

The kelp forests around San Nicolas Island are almost exclusively *Macrocystis pyrifera*. Much of these kelp forests were found at depths that indicated that the presence or absence of the surface canopy of *Macrocystis* might affect illumination within the kelp forest, and in turn might affect turf species (sessile organisms that paved

the substrate or that grew no greater than 40cm in height). Physical disturbances resulting from exposure of the island to turbulent oceanic conditions observably caused a substantial loss and, therefore, absence of surface canopy; biotic factors, such as herbivory, possibly contributed to this removal of surface canopy. The formation of canopy that decreases light to underlying algae has been documented as a form of competition in marine kelp communities, but probable effects on the turf assemblage inclusive of both algae and sessile animals have not been studied thoroughly. Sessile animals are commonplace on both vertical and horizontal surfaces in *Macrocystis* kelp forests. In 1980, I proposed to investigate structure and causes of change in structure of the turf assemblage of a kelp forest. I initially suggested that the presence or absence of canopy might affect changes in abundance and distribution not only of turf algae, but also sessile animals, which might require spatial resources similar to algae.

Investigations on these initial questions were conducted from summer 1980 through 1981, and follow-up questions were researched from late 1982 through 1984.

I recognized that the removal of *Macrocystis* might have affected other physical and biological aspects of the study area other than illumination. For example, water movement, nutrient and spore deposition, and species-utilization were all potentially affected by the removal of *Macrocystis*. Although none of these factors were investigated, the location of the removal site within and surrounded by the remaining kelp forest was assumed to minimize these potential effects. Additionally, when the different potential effects of *Macrocystis*-removal were considered, and the results interpreted from the the different studies, the most plausible explanation for changes in cover were correlated with differences in illumination.

Studies were confounded by natural disturbances that substantially affected

experiments. Because of open exposure, San Nicolas Island was vulnerable to severe oceanic conditions that not only affected kelp forests, but also determined access to the study area. No piers existed on San Nicolas Island, and during turbulent wind and sea conditions, access through the surf was impossible for periods up to 3 weeks at a time. Severe oceanic conditions were characteristic of the winters of 1981 and 1983 on San Nicolas Island. The effects of the winter of 1981 had an apparent impact on experiments conducted during that time period; the winter of 1983 did not have long-term effects on the turf assemblage or kelp forest in general, and did not affect studies conducted that year. In contrast, the winter of 1984 was milder than observed in previous years and those mild conditions had a profound effect on experiments conducted in 1984.

The first chapter of this thesis addresses questions pertaining to changes in the turf assemblage that were correlated with differences in illumination within the kelp forest, as determined by the presence or absence of *Macrocystis*. As a result of this initial study, further questions were raised concerning distribution and abundance of conspicuous species or groups of species that could not solely be explained by the presence or absence of canopy. Chapters 2 and 3 document investigations of the causes of low abundance of foliose red (Rhodophyta) algae in established turf assemblages, the variable distribution of algae in early successional stages of the turf assemblage, and the high density of competitively subordinate crustose coralline algae. The thesis is written in manuscript format, and the three chapters are presented as independent papers.

Chapter 1.

Correlations Between Canopy Cover of a *Macrocystis* Kelp Forest and the Structure of the Turf Assemblage

Abstract

The effects of the surface canopy on the turf assemblage found on horizontal substrate were investigated in a kelp forest located off San Nicolas Island, California. Percent cover of both turf (no greater than 40cm tall in the adult form) algae and sessile animals was estimated from summer 1980 to fall 1981, and again in fall 1982 on 2 sites, to determine structure and change of the turf assemblage. To determine the effects of canopy on structure of the turf assemblage, *Macrocystis* was experimentally removed from 1 site from fall 1980 through fall 1981, and not manipulated on the other site. The turf assemblage was studied in 2 successional stages at each site: the existing assemblage as found on intact plots, and on plots cleared to bare substrate. Additional plots were cleared at different times of the year to determine if season of clearing affected the composition or pattern of recruitment of different groups of species.

Sessile animals and algae were equally abundant on horizontal substrate. Increased cover of turf algae and either decreased cover or low recruitment of sessile animals occurred on both intact and cleared plots on the canopy-removal site; increases in crustose and articulated coralline algae were documented that were correlated with greater illumination. On the canopied site, cover of crustose algae and sessile animals changed little over time on intact plots; an increase in arborescent turf algae in the spring was associated with a partial loss of surface canopy of *Macrocystis* as a result of storms, and subsequent decreases in cover of these algae were correlated with the return of a full surface canopy. On cleared plots on the canopied site, sessile animals recruited at significantly greater levels of cover than algae. Higher numbers of kelp recruits and greater biomass of understory kelps on the canopy-removal site compared to the

canopied site further substantiated effects correlated with the surface canopy.

Ephemeral algae that recruited to cleared plots were rare on intact plots, and perennial algae occupied cleared plots relatively early after substrate was cleared. A bryozoan that was uncommon on intact plots was the dominant sessile animal that recruited to the cleared plots. Other sessile animals recognized from intact plots were slow to colonize on cleared plots. Natural disturbances and variable recruitment on cleared plots made actual stages of succession difficult to discern.

Species composition changed little when substrate was cleared at different times of the year, but differences in patterns of recruitment were observed. Ephemeral algae recruited more quickly in the spring and summer than in fall and winter, and sessile animals recruited more quickly in early fall than in other seasons.

Kelp canopy, as it affected illumination at the substrate, was correlated with and appeared ultimately responsible for observed patterns of distribution and relative abundances of turf algae and sessile animals in this kelp forest.

Introduction

The formation of canopy that decreases light to underlying species is a well-documented form of competition in plant assemblages in natural communities (e.g., Tomlinson and Zimmerman 1978, Harper 1977, West et al. 1981). Marine kelp forests are particularly appropriate for study of the effects of canopy on community structure because kelp forests are more easily manipulated than terrestrial forests, can develop quickly, and can undergo a turnover of the canopy-forming population in as few as 8 - 12 months (Neushul and Haxo 1963, Neushul 1971, Rosenthal et al. 1974, Dayton et al. 1984).

A number of studies have documented the light-inhibiting effects of kelp canopy on the structure of kelp assemblages (Dayton 1975a, Pearse and Hines 1979, Duggins 1980, Kirkman 1981, Kastendiek 1982, Moreno and Sutherland 1982, Dayton et al. 1984, Reed and Foster 1984, Santelices and Ojeda 1984). The effects of canopy on turf assemblages within kelp forests, however, have not been studied thoroughly. Turf was defined as the collective assemblage of algae and sessile animals, which were no greater than 40cm tall and which paved or grew close to the substrate. With one exception (Foster 1975a), most studies investigating effects of kelp canopy on turf assemblages report changes in abundance of foliose algae without addressing possible effects on other components of the turf assemblage (Pearse and Hines 1979, Reed and Foster 1984, Santelices and Ojeda 1984). For example, sessile animals are commonplace on both vertical and horizontal surfaces in *Macrocystis* kelp forests (Woolacott and North 1971, Aleem 1973, Rosenthal et al. 1974, Foster 1975a,b, pers. obs.). Changes in abundance and distribution of turf algae related to canopy might affect sessile animals

that require similar spatial resources. Foster (1975a) predicted that in the presence of both herbivores and predators, sessile animals could outcompete algae under low light conditions, and that algae could outcompete sessile animals under moderate light conditions.

Competition for space between sessile animals and algae has been demonstrated or suggested in studies of intertidal communities (e.g., Dayton 1975b, Lubchenco and Menge 1978, Paine and Suchanek 1983). Most subtidal studies of competition that involved sessile animals were conducted in habitats that were typically devoid of arborescent algae, e.g., vertical walls, undersurfaces, and also certain tropical habitats (e.g., Jackson 1977, Osman 1977, Buss and Jackson 1979, Woodin and Jackson 1979, Russ 1980, 1982, Sebens 1986). Relative abundances of both algae and sessile animals on natural, horizontal substrate in kelp forests have rarely been quantified.

In addition to the possible effects of light inhibition by canopy on turf assemblages, holdfasts of *Macrocystis* can overgrow and possibly kill underlying turf organisms. The subsequent loss of adult *Macrocystis* (and their holdfasts) due to physical or biotic disturbance can create near-bare patches of substrate in turf assemblages. The presence or absence of canopy might affect early stages of succession by favoring recruitment by sessile animals or algae to these bare patches. Subsequently, the presence or absence of canopy cover might determine dominance by sessile animals or algae in later successional stages. The persistence of early colonizing organisms depends largely on the longevity of those colonizers and possibly their resistance to displacement by later colonizing species (Connell and Slatyer 1977).

This study examined whether changes, i.e., succession, in the turf assemblage of a *Macrocystis* forest were correlated with the kelp canopy over that assemblage. Factors

such as predation, nutrient availability, and physical disturbances might also regulate or cause changes in turf assemblages. But previous studies strongly indicated that differences in illumination at the substrate caused by the presence or absence of canopy might prevail in shifting dominance in a turf assemblage between sessile animals and algae. The purposes of this study was to determine the structure of the turf assemblage on natural, horizontal substrate in a *Macrocystis* kelp forest, while testing the effects of differences in illumination on that structure, and to determine if illumination affecting newly established turf assemblages could influence the outcome of later successional stages. In the form of a priori hypotheses, I asked first, if dominance by sessile animals or algae in later or on-going stages of succession was correlated with the presence or absence of kelp canopy, and secondly, if dominance by sessile animals or algae in primary and early stages of succession was correlated with the presence or absence of kelp canopy.

Study Area

The study was conducted on San Nicolas Island (33.15N 119.31W), about 128km off the nearest coastal point of Southern California (Fig.1.1). The water tends to be cooler and the winds more persistent around San Nicolas Island than the other Channel Islands and the California coastline east and south of San Nicolas Island (pers. comm., San Nicolas Island Weather Service, USDOC). During the time of the study (1980 - 1982), water temperatures ranged from 10° - 14° C on the study site, with occasional fluctuations beyond this range. Swells generated by tropical storms were common on the south side of the island in summer. In winter, swell from north Pacific storms were

predominantly from the north and west. Except for very small coves, there was no protected coastline on San Nicolas Island. Natural loss of *Macrocystis* was apparent in the beach wrack following swells greater than about 2.0m. The clarity of the water on the study area was good, and visibility was estimated consistently at 8+m during most of the study. Low illumination within kelp forests due to turbidity was rarely observed, and extended planktonic blooms were not observed.

Kelp forests around San Nicolas Island occurred exclusively on sandstone reefs. These reefs varied in size from several hectares to several hundred hectares, and were separated by sand substrate. The reefs were generally flat on top with either abrupt or gradual relief, and interspersed with crevices, rock pinnacles and boulders. The microtopography of the substrate was pocketed, probably from the abrasive action of sea urchins over time, and in places permeated with tunnels excavated by the boring clam, *Penitella* sp.

The kelp forests around San Nicolas Island had a floating canopy almost entirely of *Macrocystis pyrifera*. *Egregia* sp. formed a surface canopy in isolated areas at depths of <3 - 4m. The kelps *Eisenia arborea* and *Laminaria* sp. formed an open understory and were common in these kelp forests. *Pterygophera* sp. was generally uncommon, but groves of this species could be found in sand channels bordering kelp forests. The Fucal *Cystoseira* sp. and *Sargassum* sp. were present around the island, but were generally uncommon.

The study area was located in a kelp forest 150m off the south shore of San Nicolas Island at 9 - 11m below the surface. Study sites were established on a homogeneously flat area of the reef that was about 60m E-W (parallel to the island) and 30m N-S. The study area was abutted by large boulders and crevices on one side, a sand channel that

was 3 - 4m from the top of the reef on another side, and bordered by ledges on the N and S (Fig.1.1). Generally, this kelp forest appeared typical for San Nicolas Island, but there were areas off the west and north sides of the island that were characteristic of urchin barrens (Harrold and Reed 1985).

General Methodology

The study area was accessed using SCUBA. Two permanent 10m x 10m sites, about 35m apart, were established on an area of the reef that was relatively flat, contained no boulders, and no crevices >0.50m wide. The sites were marked with stainless steel eyebolts at the corners. Eyebolts were affixed into drilled holes with underwater epoxy. Twenty permanent 0.25m² (50cm x 50cm) plots were established within each site. The plots were marked with eyebolts that were placed 1.5m - 2.0m apart; 5 plots were placed along 4 equally spaced transect lines (Fig.1.1). The plots were situated on as similar substrate as possible, i.e., kelp holdfasts, crevices and other irregularities were avoided.

Composition and abundance of species were quantified on each 0.25m² plot using a 100 random point sampling method. An adjustable, double-layered, acrylic table was centered, leveled, and attached with elastic cords to the plot eyebolts. Percent cover was estimated by contacting species with a rod passed through each of 100 holes in the table. This study identified 2 categories of cover: primary cover, consisting of organisms or the parts of organisms (e.g., holdfasts) that paved or adhered directly on the substrate (including some sedentary animals), and secondary cover, consisting of the arborescent structure of organisms that grew no greater than 40cm above the

substrate in the adult state, such as foliose algae and hydroids. This approach to sampling did not account for species occupying primary cover that may have been overgrown by other turf species; overgrown species were underestimated. For example, the shell of the sessile tube snail, *Serpulorbis sp.*, was commonly overgrown and encrusting species were tabulated as primary cover when contacted on the shell. There was stratification of organisms forming secondary cover; the taller algae grew 20 - 25cm in height, while other arborescent algae and animals were rarely taller than 10cm. Multiple contacts of different organisms at sampling points were not common, but secondary cover could exceed 100%. Organisms contacted were identified to species or grouped into the lowest recognized taxa (called species-groups in text) if identification to species was not possible in situ. Urchins most often appeared entombed in the substrate and were categorized as primary cover when contacted. Large, mobile invertebrates were tabulated and not disturbed. Bare substrate, sand and the calcified remains of algae and animals that adhered to the substrate were also tabulated. Sand >2cm deep was tallied as primary cover when contacted to minimize disturbance to the plots.

After the 40 (20 per site) plots were sampled in July - August 1980, *Macrocystis* was removed on and 5m - 8m around one site. The understory was open, but kelps were trimmed or removed around all plots on that site in order to prevent shading of turf species. Recruits of *Macrocystis* (about 3 - 5cm tall) were counted and removed from the canopy-removal site as necessary throughout the study to prevent the reformation of canopy. Kelp recruits were counted and removed from all 0.25m² plots to avoid overgrowth by these species. Counts of kelp recruits on both sites were compared in order to substantiate if differences in light intensity affected these algae. A General

Electric DW-68 light meter was used to measure illumination at the substrate on the 2 sites. This was a simple method of light measurement, and the results were used only as an index to compare light intensity on the 2 sites at specific time intervals (Appendix 1). The removal of canopy was ended in December 1981. The plots on both sites were sampled in December 1982 in order to extrapolate patterns of change in the turf assemblage following the cessation of canopy removal.

The canopied and canopy-removal sites were not replicated because of personnel and time constraints, and therefore, inferences drawn from statistical tests are restrictive in their interpretations. Analyses were performed on the mean percent cover of common species and species grouped into common affinities. The trend of these means was compared between the canopied and canopy-removal sites, using profile analysis (Morrison 1976, pgs. 153 - 160). Means were graphed over time, and profile analysis examined if the line segments of the graphed means were parallel when compared between the 2 sites. If the changes in means were parallel, further analysis examined if the graphed means were significantly different between the 2 sites. If the means were not significantly different, a final test determined if the means were different from sampling period to sampling period. These 3 tests of profile analysis were referred to as parallelism, equal levels and equal means, respectively. Profile analysis was performed using the Systat Program (Systat, Inc. Evanston, Ill.). Within-site changes in percent cover were examined using 1-way ANOVA, and the Newman-Keuls test was used for separation of means. For statistical analyses, percent cover data were normalized using square root transformations (Steele and Torrie 1980). All results were evaluated at the 0.05 level of significance. All references to cover are mean percent cover unless otherwise stated.

Hypothesis 1 was based on observations of differences in relative cover of algae and sessile animals in areas around San Nicolas Island that appeared to have established kelp forests (based on size of *Macrocystis* holdfasts) as compared to areas with sparse surface canopy or developing *Macrocystis*. These variations in relative cover of turf assemblages were also observed at different depths within kelp forests, further substantiating a possible effect due to differences in illumination. The possibility that dominance of turf assemblages by algae or sessile animals might have to occur during early stages of succession of the turf assemblage, in order to be expressed in later stages, was addressed in Hypothesis 2.

Methods and Results

Structure and Succession of the Existing Turf Assemblage

Hypothesis 1. When removal of kelp canopy over the existing turf assemblage is maintained, turf algae increase in response to greater illumination, and sessile animals decrease, e.g., overgrowth by algae occurs. In the continued presence of canopy, relative percent cover of turf algae and sessile animals remain essentially constant except for seasonal fluctuations.

Methods. Following the sampling of all 40 plots in July - August 1980, 10 plots were randomly selected on both the canopied site and on the canopy-removal site. The plots were sampled again just prior to the removal of canopy in early October 1980. Two of the 10 plots on the canopy-removal site were excluded from the results because of substantial recruitment of kelps that occurred on those plots between monitoring

periods. The first 2 plots on the canopied site that kelp recruited were subsequently excluded from the results.

Results. The turf assemblage occupying open, flat habitat, was characterized by crustose coralline algae, small patches of bryozoans and sponges, a sessile tube-snail, articulated coralline algae, and foliose red (Rhodophyta) algae. Embedded urchins and small sea cucumbers that appeared to be sedentary were also common. (Table 1.1). Many species were sampled (particularly animals) during the study, but most species were represented by a small number of organisms. Only 46 of the 152 species or species-groups that were identified formed >1 percent cover during any sampling of the intact plots, and 13 of those 46 species accounted for >1 percent cover during all sampling periods (Table 1.1). Percent cover estimates were conservative, because sand covered a substantial area of the 0.25m² plots and filled the depressions of the pocketed substrate (Fig.1.2). Sand-filled pockets were not used as habitat by many sessile animals and algae. Decreasing cover of sand might have exposed some algae or sessile animals that were previously buried under sand, but bare substrate was most commonly found under >2cm of sand. Decreases in cover of sand from fall 1980 to spring 1981 were similar on both sites, but changes in primary cover of algae or sessile animals were markedly different between the 2 sites during that same period (Fig.1.3).

Removal of the *Macrocystis* canopy had little effect on species richness. During 1980 and 1981, an average of 25 species was tallied on both canopied and canopy-removal sites, with no significant ($P>0.05$) changes over time in number of species sampled ($F = 0.93$ and $F = 0.31$, respectively).

Percent Primary Cover

Primary cover of algae and sessile animals were similar during the study (Fig.1.3).

On the canopied site, a slightly greater percent primary cover of sessile animals than algae occurred over time, except for spring 1981 and fall 1982. On the canopy-removal site, sessile animals formed more primary cover before and just after the initial removal of canopy in October 1980, but a significant ($P < 0.05$) increase in cover of algae ($F = 13.24$) and concomitant decrease in cover of sessile animals ($F = 3.45$) occurred in spring 1981. This reversal of relative abundance continued throughout 1981 on the canopy-removal site. Primary cover of algae and sessile animals on both sites was similar by fall 1982 after *Macrocystis* was allowed to grow on the canopied site in December 1981 (Fig.1.3).

Primary cover of algae increased significantly ($P < 0.05$) on both the canopy-removal ($F = 13.24$) and canopied ($F = 4.19$) sites between fall 1980 and spring 1981 (Fig.1.4a). On the canopy-removal site, primary cover of algae was significantly ($P < 0.05$) greater in all 1981 samples compared to the 1980 samples. On the canopied site, primary cover of algae was significantly ($P < 0.05$) greater than the other sampling periods only in spring 1981, which coincided with a natural loss of *Macrocystis* canopy on that site. In January 1981, storms dislodged *Macrocystis* around the island, and 40 - 50 percent of the surface canopy was lost on the canopied site. The surface canopy regrew to >80 percent cover on the canopied site by mid-May 1981. This loss of canopy probably facilitated growth of algae on the canopied site that was similar to that on the canopy-removal site. Algae forming primary cover were mainly crustose coralline algae that were thin and smooth in texture, and that covered the substrate throughout the study area. Increases in cover of crustose coralline algae appeared to occur on bare substrate resulting from decreasing sand cover and also on calcified remains of sessile organisms, but overgrowth of live sessile organisms was

rarely observed.

The overall trend of percent primary cover of all sessile animals was not significantly different from fall 1980 to fall 1981 when compared between the 2 sites. But, there was a significant ($P < 0.05$) decline in primary cover of sessile animals on the canopy-removal site between late fall 1980 and spring 1981 ($F = 3.45$), whereas little change occurred on the canopied site ($F = 0.30$, $P > 0.05$) (Fig.1.5a). Most changes in primary cover of individual species of sessile animals were slight and not significant, probably because of the low number of individuals contacted per species. The major groups of sessile animals represented on the study area that could be affected by increasing cover of algae were sponges, bryozoans and tunicates. Initially, primary cover of all sponges was greater on the canopy-removal site compared to the canopied site, but declined to a level lower than the canopied site (Fig.1.5b). A slight increase in cover of all sponges occurred over time on the canopied site. Cover of bryozoans declined significantly ($P < 0.05$) on both canopied ($F = 7.42$) and canopy-removal ($F = 9.30$) sites, but the decline was greater on the canopy-removal site from fall 1980 to spring 1981 (Fig.1.5c). Cover of bryozoans continued to decline from spring to fall 1981 on the canopy-removal site, but little change occurred on the canopied site during that time. Significant changes in cover occurred among *Membranipora fusca* (specimens taken included *Cryptosula sp.*), which was the most common bryozoan on the intact plots; cover of other species of bryozoans did not change significantly on either site. As a group, tunicates were uncommon, with little change in cover noted over time on either the canopied or canopy-removal site (Fig.1.5d). Other faunal species that formed primary cover were either uncommon or difficult to detect with the sampling method used and were probably not affected ultimately by illumination at the substrate. For

example, the extensive tube shells of *Serpulorbis* sp., were commonly overgrown by other turf species with no apparent harm to the organisms. Burrowing echinoderms and anenomes were generally found attached to substrate in sand-filled pockets, and could avoid the affects of overgrowth by arborescent algae. Purple urchins were common on the study area, but they were often entombed laterally in pockets of the substrate and not contacted. Estimates for purple urchins were probably low (Table 1.1); 3.83 urchins per 0.25m^2 ($n = 95$, s.d. = 3.46) were estimated during a random sampling of flat substrate on the study area.

Percent Secondary Cover

Percent secondary cover of algae changed in a significantly different manner over time when compared between the canopied and canopy-removal sites (Fig.1.4b). Secondary cover of algae increased significantly ($P < 0.05$) on the canopied ($F = 17.11$) and canopy-removal ($F = 21.33$) sites. Changes in secondary cover of algae were similar on both sites through spring 1981, with greater cover on the canopied site. On the canopied site, secondary cover of algae stabilized during the summer, but by fall 1981, declined to levels not significantly ($P > 0.05$) different from 1980 levels. Increases in cover of arborescent turf algae between fall 1980 and spring 1981, followed by no change or decreases in cover by summer were correlated with the loss and regrowth of the *Macrocystis* canopy on the canopied site mentioned above (Fig.1.4b). In contrast, levels of secondary cover of algae were significantly greater in 1981 than 1980 and increased continually from spring to fall 1981 on the canopy-removal site ($P < 0.05$).

This pattern of change in secondary cover was similar for the 2 more common genera of arborescent algae present on the study area, the articulated coralline algae *Calliarthron chielosporioides* and *Corallina officinalis* var. *chilensis* (Fig.1.4c,d,e).

Other articulated coralline algae formed <5 percent secondary cover. *Calliarthron* and *Corallina* were greater in cover on the canopied site compared to the canopy-removal site by spring 1981; both species declined to levels not significantly ($P>0.05$) different from 1980 levels by fall 1981. On the canopy-removal site, cover of *Calliarthron* and *Corallina* increased to significantly ($F=5.34$ and $F=4.59$ respectively, $P<0.05$) greater levels by spring and summer 1981 and remained at those levels into fall 1981.

Foliose red algae were not as common as articulated coralline algae, and changes in cover of these algae were similar over time on the canopied and canopy-removal sites (Fig.1.4f). On the canopied site, an increase in cover of foliose red algae occurred in spring 1981, but was only significantly ($P<0.05$) greater than that measured in early fall 1980. In contrast, cover of foliose red algae increased significantly ($P<0.05$) on the canopy-removal site through spring and summer 1981, and decreased by fall 1981 to a level comparable to 1980 levels. Cover of the most common foliose red alga, *Rhodomenia californica*, changed in a similar manner on both sites, but a substantially greater rate of increase occurred on the canopy-removal site from spring to summer 1981 (Fig.1.4g). The other common red alga, *Plocamium* sp. declined notably in spring 1981 on the canopy-removal site and later on the canopied site (Fig.1.4h). In Feb 1981, diatoms (mainly *Licmophora* sp.) coated the blades of *Plocamium* on the canopy-removal site. The cell wall and sporiferous tissue found on these blades were impregnated with diatoms which may have caused the decline of this species.

Other species of arborescent algae were either rare or too patchy to detect change on either site. *Ulva* sp., *Giffordia* spp., *Colpomenia* sp. *Pachydictyon* sp., *Dictyota* sp., *Platythamnion* spp., and *Tiffaniella* sp., which all appeared to have an ephemeral life history, were not sampled on the study sites in 1980, but were sampled in spring 1981.

These algae ranged from 1 - 5 percent secondary cover and were more abundant on the canopy-removal site. By fall 1981, these algae were sampled on plots on the canopy-removal site but were not found on plots on the canopied site.

Most species of arborescent animals that formed secondary cover were low in abundance, and some used arborescent algae for habitat. Arborescent species of hydroids (e.g., *Aglaophenia* sp.) and bryozoa (e.g., *Hippodiplosia* sp. and *Thamnoporella* sp.) were typically epiphytic on articulated coralline algae. Sessile animals forming secondary cover declined steadily from 11 to 3 percent cover on the canopied site, and from 8 to <1 percent cover on the canopy-removal site. These arborescent sessile animals probably were affected by high water motion associated with swell (Rosenthal et al. 1974) or predation, and not by differences in light intensity.

Primary Succession on Cleared Plots

Hypothesis 2. With removal of kelp canopy, ephemeral algae rapidly colonize cleared substrate compared to sessile animals; recruitment by perennial algae is enhanced by greater illumination and ephemeral algae are replaced. In the presence of canopy, ephemeral algae and sessile animals colonize cleared substrate about equally; recruitment of perennial algae is slow compared to the canopy-removed site.

Methods. The 10 remaining 0.25m² plots on the canopied and canopy-removal sites (those not used to test Hypothesis 1) were cleared to bare substrate. Hand tools were used to meticulously remove several millimeters of substrate without altering the microtopography. The plots were wire-brushed a final time prior to the removal of *Macrocystis* from one site in October 1980. Three of 10 plots on both sites were excluded from the results because of substantial recruitment of kelps that occurred on

those plots between monitoring periods.

Due to time and personnel constraints, cover of organisms recruiting to cleared plots was roughly estimated with a 0.25m^2 sampling frame from October 1980 to February 1981. The frame was grided with nylon lines that crossed at 25 points. Species found under each crossing line were tabulated and multiplied ($\times 4$) to provide an estimate of percent cover. After February, the random point method was applied, using the acrylic table. Statistical comparisons were restricted to data collected using the random point method. Cleared plots were sampled in October, November, and December of 1980; February, March, June, August and November 1981; and December 1982.

Very little information was available on life histories of turf algae. In this study, the term ephemeral identified algae that recruited rapidly, declined substantially in cover during the study, and were rare or absent on intact plots. Perennial algae were known from intact plots, fluctuated little in percent cover, or were known to have a perennial life history.

A different set of plots was cleared at 3 intervals 12 - 14 weeks apart to determine if the time of year space was available might affect the composition and abundance of early colonizers on cleared substrate. One 0.125m^2 (one-eighth of a square meter) plot was cleared at each corner of the 2 sites (4 per site) starting in February 1981, and the procedure repeated in May and August 1981; 24 plots in all were cleared (Fig.1.1). The seasonally cleared plots were sampled using a sampling frame in March, April and May 1981, followed by using 50 random points on the acrylic table in June, August and December 1981. The 50 points were multiplied by 2 to provide an estimate of percent cover.

Results. A uniform, periphytic film of diatoms and other organic matter formed on all plots 1 to 2 weeks after the substrate was cleared (Fig.1.6). Soon after this film appeared, similar kinds of organisms recruited to cleared plots at about the same time on both sites. In the first 5 months, growth of ephemeral algae was visibly more pronounced on plots on the canopy-removal site, but patchy in distribution on plots on both sites. Patchy distribution of ephemeral algae was probably due to variable recruitment and several forms of disturbances on the cleared plots. *Patiria* sp. (asteroid) was the most common of large invertebrates that were attracted to the cleared plots, particularly on the canopy-removal site (Fig.1.7). *Patiria* either grazed or dislodged the periphytic film and filamentous ephemeral algae. Other disturbances were observed that probably affected cleared plots on both sites equally; for example, fish often rubbed against the exposed substrate of the cleared plots (removing recruiting organisms), and sand displaced by water motion either scoured or buried the periphytic film. Percent cover of filamentous, ephemeral algae fluctuated, i.e., these algae could recruit again soon after being disturbed. Recruitment accelerated in late February and early March 1981. These changes were probably in response to favorable seasonal changes, such as oceanic upwelling and increasing day length. Recruiting organisms which contributed >1 percent cover from March 1981 to December 1982 are listed in Table 1.2.

Percent Primary Cover

Primary cover of ephemeral algae changed in a similar manner over time on the cleared plots on both sites, but cover was significantly ($P < 0.05$) greater on the canopy-removal site (Fig.1.8a). From October 1980 to May 1981, ephemeral algae consisted of thickly clumped patches of arborescent, filamentous algae. By July 1981, a fleshy, encrusting form of the brown algae, *Dictyota* sp. and *Pachydictyon* sp. recruited

to cleared plots. Perennial algae were found on cleared plots by December 1980 and increased at similar measures of percent cover on both sites (Fig.1.8a). Perennial algae forming primary cover were mainly the same type of crustose coralline algae found on the intact plots.

Primary cover of algae was substantially greater than primary cover of sessile animals on cleared plots on the canopy-removal site (Fig.1.9). In contrast, similar recruitment of algae and sessile animals occurred on plots on the canopied site. Changes in cover of sessile animals were similar (parallel) over time on cleared plots on both sites, but the abundance of that cover was significantly greater on the canopied site. Two weeks after the plots were cleared, trace numbers (<1 percent) of barnacles and anenomes (immature *Epiactis* sp. that drifted in) were the first visible animals encountered. By 3 weeks, hydroids accounted for about 10 percent and <1 percent cover on plots on the canopied and canopy-removal sites, respectively, but were scarce by December 1980. Five to 8 weeks after the plots were cleared, bryozoans, which appeared to be primarily *Parasmittina* sp., recruited to the plots. *Parasmittina* sp. accounted for >95 percent of the sessile animals that recruited to the cleared plots in 1981, and was still the most common sessile animal by December 1982. None of the other major groups of sessile animals became established on the plots during 1980 and 1981. For example, tunicates were observed in trace numbers from May to November 1981 on plots on the canopied site, but not on the canopy-removal site. Sponges did not recruit or invade on plots on either site during 1980 and 1981. Both tunicates and sponges had recruited to the plots by December 1982.

Percent Secondary Cover

From March to November 1981, cover of ephemeral algae on cleared plots of the

canopy-removal site was significantly ($P < 0.05$) greater than on the canopied site (Fig. 1.8b). Tall (about 3 - 5cm) filamentous ephemeral algae often grew in thick, clumped patches rather than uniformly on the plots, and the large measure of cover was due in part to more than 1 contact per species per sampling point. Increased percent cover of ephemeral algae on the canopied site was probably enhanced by the aforementioned loss of *Macrocystis* canopy in January 1981. When sampled, cover of ephemeral algae declined significantly ($P < 0.05$) after May 1981 on plots on the canopied site and after July 1981 on the canopy-removal site. Changes in cover of ephemeral green (Chlorophyta) algae were similar (parallel) over time on both sites, but percent cover of these algae was significantly ($P < 0.05$) greater on plots on the canopy-removal site compared to the canopied site ($F = 100.18$). Changes in cover of ephemeral red (Rhodophyta) algae were not significantly ($P > 0.05$) different between sites, although greater cover of these algae occurred on plots on the canopy-removal site compared to the canopied site from March to November 1981. Changes in cover of ephemeral brown (Phaeophyta) algae were significantly different ($F = 4.48$, $P < 0.05$) over time. Except when sampled in February 1981, cover of ephemeral brown algae was greater on cleared plots on the canopy-removal site compared to the canopied site. The effects of *Patiria* and other disturbances on filamentous brown algae resulted in highly variable measures of cover (Fig. 1.8b).

Secondary cover of perennial algae was found on cleared plots on both sites by February 1981. Perennial algae were markedly greater in cover on cleared plots on the canopy-removal site compared to the canopied site from May to November 1981 (Fig. 1.8b). The increase in cover of perennial algae continued during 1981 on the canopy-removal site, but peaked in May and declined by November 1981 on the

canopied site. This pattern applied to most species of foliose algae that recruited to the cleared plots, and was similar to the pattern of change observed on the intact plots on both sites. Also similar to the intact plots was the greater percent cover of articulated coralline algae on the cleared plots of the canopied site compared to the canopy-removal site (Fig. 1.8c). Likewise, cover of articulated coralline algae continued to increase on plots on the canopy-removal site during 1981 and declined from July to November 1981 on the canopied site. Unlike the intact plots, articulated coralline algae on the cleared plots consisted mostly of *Lithothrix* sp. that appeared to have an ephemeral life cycle.

Succession on Seasonally Cleared Plots

Variability of recruitment was well-documented on the 0.125m² plots cleared in February 1981. By mid-March, filamentous brown and green algae covered 75 percent of 1 plot and 10 - 30 percent of the other plots on the canopied site and 45 - 85 percent of plots on the canopy-removal site. By mid - April, *Ulva* sp. covered 50 percent of 1 plot (canopy-removal site), and 1 - 15 percent on all other plots; *Colpomenia* sp. covered 70 percent of 1 plot (canopied site) and 1 - 5 percent of all other plots. Only trace measures of *Colpomenia* and *Ulva* of the above species were found on those plots by early May. Recruitment by groups of species was more uniform when random-point sampling was conducted in June, August and December.

The time of year the plots were cleared affected the rate of recruitment but not the composition or pattern of recruitment. Recruitment and growth of algae were more rapid and pronounced on the 0.125m² plots cleared in February and May and sampled

in August than that observed during similar time intervals on the 0.25m^2 plots cleared in October 1980, or the 0.125m^2 plots cleared in August and sampled in December 1981 (Table 1.3). Composition of species or groups of species found on the 0.125m^2 plots was the same as that listed in Table 1.2. The pattern of recruitment on 0.125m^2 plots on the 2 sites was similar to what occurred on the 0.25m^2 cleared in October 1980 (Table 1.3). Greater recruitment of ephemeral algae occurred on the plots on the canopy-removal site compared to plots on the canopied site. However, in June and August, secondary cover of perennial algae was greater on the canopied site compared to the canopy-removal site. The high percent cover of ephemeral algae on plots on the uncanopied site may have delayed recruitment by perennial algae; by December, cover of perennial algae was greater on the canopy-removal site compared to the canopied site. Cover of algae was similar on plots cleared in February and May, and sampled in August. By August, ephemeral algae might have been still recruiting on the plots cleared in May, whereas cover of ephemeral algae peaked or started to decline on the plots cleared in February. When sampled in December, cover of perennial algae on the plots cleared in May was equal to or greater than plots cleared in February and August, further substantiating more favorable conditions for recruitment in the summer months.

Sessile animals, which consisted mainly of the bryozoan *Parasmittina* sp., were more abundant on seasonally cleared plots on the canopied site as compared to the canopy-removal site (Table 1.3). This pattern was similar to the 0.25m^2 plots cleared in October 1980. Sessile animals appeared to recruit or grow more slowly in the spring and summer compared to the fall. Primary cover of sessile animals on the plots cleared in February were greater than plots cleared in May. However, in December, cover of sessile animals was substantially greater on the plots cleared in August than on the plots

cleared in February or May.

Correlated Effects of Light on Kelp Recruitment

Differences in the number of kelp recruits on the canopied and canopy-removal sites was correlated with differences in light intensity on the 2 sites. From October 1980 through February 1981, few visible kelp sporophytes were removed from the canopy-removal site. In March 1981, recruitment of *Macrocystis* accelerated, and sporophytes were removed every 2 weeks from the canopy-removal site. Recruitment of sporophytes peaked to 904 in June on the canopy-removal site and declined to 291 in July and to 17 in September 1981. Recruitment of sporophytes on the canopy-removal site may have been greater if adult plants were present on the site just prior to March 1981. Recruitment of *Macrocystis* on the canopied site was not as pronounced as on the canopy-removal site, but was substantial probably because of a loss of surface canopy due to winter storms in January 1981. Eighty new sporophytes were found on the canopied site in March 1981, and by 30 April, 35 of those sporophytes were part of the surface canopy. Five hundred-thirty *Macrocystis* were counted on the canopied site in October 1981, but 152 of those were in poor condition. By December 1981, 315 *Macrocystis* remained, of which 159 were in poor condition. Most of the plants in good condition were among 150 sporophytes tagged in summer 1981 after becoming part of the surface canopy. Eighty-eight percent of those plants survived to December 1981, indicating that mortality was highest among those plants that failed to achieve canopy status before or just after the *Macrocystis* canopy closed in early summer 1981.

Greater recruitment and biomass of understory occurred on the canopy-removal site compared to the canopied site. Recruitment of understory kelps on the canopy-removal site was high, but substantial recruitment also occurred on the canopied site that was possibly related to the loss of surface canopy mentioned above (Fig.1.10). In October 1981, 20 *Eisenia* sp. were taken at random from the canopy-removal site, blotted dry and weighed; 20 *Eisenia* of comparable (± 5 cm) stipe-length were taken from the canopied site. The biomass of *Eisenia* from the canopy-removal site (mean = 1.231kg, s.d. = 0.450) was significantly ($P < 0.05$) greater than the biomass of *Eisenia* from the canopied site (mean = 0.647kg, s.d. = 0.344) ($F = 30.86$). These differences between the 2 sites in numbers and biomass of understory were correlated with differences in illumination.

Discussion

Changes in the structure of different successional stages of the turf assemblage were correlated with differences in light intensity; these differences appeared to be determined primarily by the surface canopy of *Macrocystis*. Most of the changes observed supported the proposed hypotheses. When the surface canopy was removed, there was a significant increase in primary cover of algae and decrease in sessile animals in existing turf assemblages. In the presence of canopy, there was little change over time in primary cover of algae and sessile animals. On plots where the turf assemblage were cleared and the canopy removed, ephemeral algae occurred at significantly greater levels compared to similar plots on the canopied site, and primary cover of algae occurred at markedly greater levels than sessile animals. On the canopied site,

significantly greater recruitment of sessile animals occurred as compared to the canopy-removal site, and sessile animals and algae recruited in comparable measures of cover.

Changes in secondary cover of arborescent algae that were correlated with differences in light intensity were subtle or not clear-cut, primarily because of the high initial increase in cover of articulated coralline algae on the canopied site, similar changes in foliose red algae on both sites, and the effects of large invertebrates on filamentous algae on cleared plots, particularly on the canopy-removal site. The partial loss of *Macrocystis* canopy in late winter and early spring probably facilitated recruitment and growth of algae on the canopied site. The decline in algal abundance later in the study occurred soon after the regrowth of the surface canopy by late spring. Therefore, these changes were considered supportive of the proposed hypotheses.

Crustose coralline algae were the most common species forming primary cover in the turf assemblage, but they were probably the most commonly overgrown turf species in this and other marine communities (pers. obs., Buss 1980, Quinn 1982, Sebens 1986). Crustose coralline algae appeared to have several strategies for survival and persistence; they can survive and probably recruit beneath species when overgrown (Sebens 1986, Chapter 3). Disturbances observed in this kelp forest, such as frequently high water motion or predation, had little effect on exposed crustose coralline algae but removed turf and kelp species that could overgrow these algae. Such advantages to otherwise competitively subordinate species, due to disturbance of dominant species, have been demonstrated experimentally in intertidal studies (e.g., Paine and Vadas 1969, Dayton 1971, Menge 1976, Lubchenco 1978, Lubchenco and Menge 1978, Hixon and Brostoff 1983). High water motion also displaced sand and

exposed bare substrate that was apparently occupied more rapidly by crustose coralline algae than other species. This rapid occupation by crustose coralline algae on cleared and intact plots might have occurred from high spore settlement, because of suggested slow growth rates for these algae (Littler 1972). However, observations indicated that crustose coralline algae grew at faster rates than has been suggested. Recruitment of crustose coralline algae was equally uniform on cleared and intact plots on both sites, despite the occurrence of potentially dominant species. These algae increased in cover on intact plots on the canopy-removal site by occupying calcified remains of sessile organisms and bare substrate resulting from decreasing sand cover. Crustose coralline algae recruited on cleared plots in the presence of high recruitment of sessile animals and ephemeral algae on the canopied site and canopy-removal site, respectively. The ability of these algae to occupy available substrate was thought to be opportunistic because crustose coralline algae had no apparent defenses against encroachment by other species. But the smooth surface of these algae, movement of sand across that surface, and frequent water motion may have inhibited recruitment of spores of some species (Charters et al. 1973, Devlinny and Volse 1978).

Excluding crustose coralline algae, arborescent turf algae are considered the subordinate competitors for light in the hierarchy of kelp forest algal assemblages mainly because of their size disadvantage (e.g., Pearse and Hines 1979, Dayton et al. 1984, Reed and Foster 1984, Santelices and Ojeda 1984). The persistence of turf algae in this kelp forest appeared facilitated by reoccurring gaps in the kelp canopy, caused by frequently strong water motion that damaged or dislodged *Macrocystis*. Dislodged plants can entangle and dislodge other *Macrocystis*, further increasing gap size (Rosenthal et al. 1974, Dayton et al. 1984). In terrestrial systems, gaps in the canopy

are suggested as means of persistence by competitively subordinate species in tropical rain forests (e.g., Hartshorn 1978, Vasquez-Yanes 1976) and temperate forests (Collins et al. 1985).

The open understory of kelps on the study area indicated that these kelps did not continually shade turf algae. Although understory kelps responded positively to increased light conditions that might result in continual shading of turf algae, understory kelps were probably more susceptible to physical disturbance. Dayton et al. (1984) suggested that turf algae persisted in areas too disturbed for understory kelps to survive for long periods of time, i.e., areas of shallow depths. The potential for high loss and recruitment of overstory and understory kelps was evident because of frequently high water motion associated with the open exposure of San Nicolas Island. Winter storms and summer swell that generate high water motion were probably important to the recruitment and persistence of turf algae in this and also other kelp forests (Reed and Foster 1984). During physically milder periods, low light due to the surface canopy affected recruitment and biomass of understory kelps, probably contributing to the open understory.

There was no indication that turf algae in this kelp forest could in turn inhibit developing kelp sporophytes (Dayton et al. 1984, Reed and Foster 1984). No species of turf algae formed a dense canopy that might shade developing sporophytes. Harris et al. (1984) suggested that a dense mat of turf algae actually could be beneficial to kelp sporophytes by hiding them from herbivores. Resolution of whether turf algae positively or negatively effect kelp sporophytes awaits further study.

The increase in cover of articulated coralline algae on the canopied site did not clearly support the proposed hypotheses, but the loss of *Macrocystis* canopy probably

influenced that increase. Also, bleaching of the tips of the fronds of articulated coralline algae was observed on the canopy-removal site in spring 1981, indicating possibly a negative initial response to the greater light intensity. This condition did not occur on the canopied site, and was not observed on the canopy-removal site by summer. The subtle effects of different light intensities on articulated coralline algae on the 2 sites were most apparent from summer to fall when articulated coralline algae increased in cover on the canopy-removal site but declined in cover on the canopied site. The response of articulated coralline alga, *Calliarthron* sp., to levels of illumination on both sites contributed to its dominance in the turf assemblage. Other factors include its tough morphology and long life span (Johansen 1974, Johansen and Austin 1970).

Coralline algae seemed equal to or more responsive than foliose algae to changes in cover that were correlated with differences in light intensity. Other researchers investigating the effects of greater light intensity on turf algae emphasized increases in the abundance of foliose algae following the removal of kelp canopy, but did not emphasize increases in the coralline algae (Pearse and Hines 1979, Reed and Foster 1984). The results of this study seemed inconsistent with studies that reported greater rates of photosynthesis and productivity by foliose algae as compared to crustose or articulated coralline algae (Colthart and Johansen 1973, Littler and Murray 1974, King and Schramm 1976, Arnold and Murray 1980, Dawes 1981). The decline in cover of foliose algae from summer to fall on both sites may have been partially due to lower light conditions expected in the fall season, but a later study demonstrated that the generally low abundance of foliose red algae was also due to herbivory (Chapter 2, see also Foster 1975a). That study also showed declines in turf algae that were correlated with low illumination due to a dense and persistent surface canopy. The surface canopy

occurred throughout the winter and spring, further substantiating the probable importance of gaps in the canopy to turf algae, particularly during those time periods.

There was not an explicit pattern of species by species or group by group replacement of ephemeral algae by perennial algae on the cleared plots. The high percent cover of ephemeral algae on the canopy-removal site may have interfered with settlement by perennial algae. This could account for similar percent cover of crustose coralline algae that recruited to 0.25m² cleared plots on both sites, and to the initial lower percent cover of perennial algae on the 0.125m² plots on the canopy-removal site. Both external disturbances and variable settlement appeared to affect abundance and distribution of ephemeral algae, and any direct effects of ephemeral algae on perennial algae were unknown. Ephemeral algae that recruited to cleared plots were uncommon on intact plots, probably because they were short-lived, affected more by external disturbances or they were unable to invade established turf assemblages.

Most of the common perennial species of algae that recruited to the cleared plots were common on the intact plots, except for *Gigartina* sp. The rare occurrence of *Gigartina* in later successional stages indicated that other factors, possibly herbivory, affected its abundance (Foster 1975a). Perennial species of algae were capable of recruiting during the early months of succession on the cleared plots. Perennial foliose red algae and crustose coralline algae recruited soon after the plots were cleared, followed by perennial articulated coralline algae.

Except for the sessile bryozoan *Parasmittina* sp., recruitment of sessile animals appeared to be a slow and gradual process. The low number of individuals per species on intact plots indicated that recruitment by many sessile animals was variable and patchy over time and space. *Parasmittina* sp. was able to occupy space quickly when

conditions were less favorable for algae to recruit, i.e., on the canopied site or during the fall season. The high recruitment of *Parasmittina sp.* on cleared plots but comparatively low abundance on intact plots indicated that this species occupied space opportunistically. Either *Parasmittina sp.* was not very effective in maintaining space among later successional colonizers or died-off before those colonizers became well-established.

Illumination at the substrate and the different times of the year substrate was cleared were correlated with the quantity of algae or sessile animals that recruited, but had little effect on composition of species that recruited or the succession of groups of species. The same types of species recruited at different times of the year to cleared plots on both sites. Early spring and summer were the better seasons for recruitment and growth of algae, but many of the common species could recruit year round (see also Foster 1975b). Conversely, there were indications that fall and winter may be the better time of year for recruitment of sessile animals, possibly because of low recruitment of algae.

The changes in cover of organisms that were correlated with differences in light intensity indicated that competition among algae and also between algae and sessile animals might be responsible. Low light at the substrate caused by the surface canopy was a form of competitive inhibition of resources necessary for recruitment and growth of turf algae and subsurface kelps. The reduced pressure of competing with turf algae for space probably facilitated the maintenance of sessile animals on intact plots and recruitment on cleared plots on the canopied site. Sessile animals in turn might interfere with recruitment by turf algae or overgrow crustose algae. On the canopy-removal site, higher growth by articulated coralline algae on intact plots may have inhibited other turf algae: a later study failed to prove or disprove competition between turf algae, because

of deterioration of turf algae that was correlated with low illumination at the substrate (Chapter 2). Certain ephemeral turf algae recruited faster to cleared substrate, possibly interfering with recruitment by perennial algae and sessile animals. Further, arborescent algae could encroach on sessile animals (e.g. Dayton 1975b). Finally, the more intense grazing by macroinvertebrates on cleared substrate on the canopy-removed site probably removed both ephemeral algae and sessile animal that settled. Grazing probably had a greater impact on sessile animals that recruited more slowly than algae under the greater light intensity.

When turbidity and depth do not prevail, the surface canopy may determine patterns of abundance and distribution of turf assemblages by affecting illumination at the substrate. Obviously, more research is needed to establish how the spatial relationship between turf algae and sessile animals is organized. Light appears to play an important role, but it was uncertain whether differential recruitment or competition were more important to the structural patterns observed. Sessile animals are an important component of turf assemblages on horizontal substrate, and need to be considered in schemes of structure and organization of kelp forest communities.

Table 1.1. The range of mean percent cover of algae and sessile or sedentary turf species (or species- groups) that formed >1 percent cover on 0.25m² intact plots on the canopied and canopy-removal sites, San Nicolas Island, Ca., 1980 - 1982. Species that were greater than 1 percent cover for all sampling periods indicated by *. n is the total number of species or species-groups sampled for that phylum.

<u>Species</u>	<u>Range of Mean Percent Cover</u>
<u>Rhodophyta</u> (red algae, n = 31)	
crustose coralline algae *	19.7 - 35.9
crustose fleshy algae	1.1 - 4.0
<i>Calliarthron cheilosporioides</i> *	7.0 - 26.2
<i>Calliarthron tuberculosum</i>	0.0 - 1.0
<i>Corallina officinalis</i> var. <i>chilensis</i> *	1.1 - 12.1
<i>Bossiella orbignana</i>	0.0 - 2.5
<i>Rhodymenia californica</i> *	1.0 - 17.1
<i>Plocamium cartilagineum</i> *	0.1 - 5.4
<i>Gelidium robustum</i>	0.0 - 2.5
<i>Gigartina</i> sp.	0.0 - 1.0
<i>Nienburgia andersoniana</i>	0.0 - 1.6
<i>Cryptopleura</i> spp.	0.0 - 1.4
<i>Platythamnion</i> sp. (also	
<i>Pterisiphonia</i> spp., <i>Plenosporium</i> sp.)	0.0 - 1.2
<i>Tiffaniella snyderiae</i>	0.0 - 1.1
<u>Chlorophyta</u> (green algae, n = 8)	
<i>Cladophora graminea</i>	0.0 - 1.9
<i>Codium fragile</i>	0.0 - 1.0
<u>Phaeophyta</u> (brown algae, n = 16)	
<i>Giffordia</i> spp. (also <i>Ectocarpus</i> sp.)	0.0 - 2.4
<i>Dictyota binghamiae</i>	0.0 - 5.6
<i>Pachydictyon coriaceum</i>	0.0 - 1.1
<u>Mollusks</u> (n = 5)	
<i>Serpulorbis squamigerus</i>	1.9 - 11.0
<u>Echinoderms</u> (n = 6)	
<i>Cucumaria fisheri</i> *	3.9 - 10.0
<i>Lissothuria nutriens</i>	0.2 - 1.8
<i>Pachythyone rubra</i> *	3.4 - 15.4
<i>Eupentacta quinquesemita</i>	0.4 - 2.9
<i>Strongylocentrotus purpuratus</i> *	0.6 - 3.1
<i>S. franciscanus</i>	0.0 - 2.5

Table 1.1. Continued.

<u>Bryozoans</u> (n = 17)	
<i>Membranipora fusca</i> (also, <i>Cryptosula</i> sp.) *	2.0 - 10.0
<i>Parasmittina</i> sp. (also <i>Microporella</i> sp. and 1 unknown) *	2.5 - 5.6
<i>Schizoporella</i> sp. (also <i>Fenestrulina</i> sp.)	0.2 - 1.2
Unknown, encrusting (i.d. # 303)	0.1 - 1.8
Unknown, encrusting (i.d. # 305)	0.2 - 1.0
<i>Thamnoporella</i> sp.	0.0 - 5.1
<i>Cellaria</i> sp.	0.1 - 4.4
<i>Crisia</i> sp. (also <i>Begula</i> sp., but rare on horizontal substrate)	0.1 - 3.4
<i>Hippodiplosia</i> sp.	0.0 - 1.1
<u>Tunicates</u> (n = 25)	
<i>Synocium parvustis</i>	0.0 - 2.4
<i>Aplidium californica</i>	0.0 - 1.2
<i>Trididemneum opacum</i>	0.0 - 1.0
<u>Cnidarians</u> (n = 9)	
<i>Anthopleura</i> sp. *	0.6 - 5.0
<i>Tealia lofotensis</i>	0.0 - 1.0
<i>Epiactis prolifera</i>	0.0 - 1.6
<i>Balanophyllia elegans</i> (also <i>Astrangia</i> sp., but rare)	0.4 - 1.5
Unknown (i.d. # 503)	0.0 - 1.6
<u>Hydriods</u> (n = 6)	
<i>Aglaophenia struthionides</i>	0.0 - 2.5
<u>Sponges</u> (n = 29)	
<i>Hymenamphiastra cyanocrypta</i>	0.0 - 3.5
<i>Microcladia parthena</i>	0.1 - 2.0
<u>Other</u>	
Annelids (n = 5)	
Crustaceans (n = 2, barnacles)	

Table 1.2. Range of mean percent cover of algae and sessile or sedentary animals that recruited to cleared 0.25m² plots on the canopied and canopy-removal sites, San Nicolas Island, California, from March 1981 to November 1981.

<u>Ephemeral Algae</u>	<u>Range of Mean Percent Cover</u>
<u>Chlorophyta</u>	
<i>Derbesia</i> sp.	0.0 - 1.0
<i>Ulva</i> sp.	0.0 - 6.6
<i>Cladophora</i> spp.	0.0 - 18.86
<u>Phaeophyta</u>	
<i>Giffordia</i> spp., <i>Ectocarpus</i> sp.	0.0 - 23.29
<i>Colpomenia</i> sp.	0.0 - 2.86
<i>Dictyota</i> sp.	0.0 - 11.29
<i>Pachydictyon</i> sp.	0.0 - 3.29
<i>Zonaria</i> sp.	0.0 - 2.29
<u>Rhodophyta</u>	
<i>Tiffaniella snyderiae</i>	3.7 - 24.71
<i>Lithothrix</i> sp.	0.1 - 14.87
<i>Platythamnion</i> spp. (also	
<i>Pterisiphonia</i> spp., <i>Plenosporium</i> sp.)	0.1 - 4.29
<i>Plenosporium</i> sp.	0.0 - 3.57
<i>Pterisiphonia</i> spp.	0.0 - 3.57
<u>Perennial Algae</u>	
<u>Rhodophyta</u>	
crustose coralline algae	
<i>Gigartina</i> sp.	1.9 - 18.71
<i>Rhodomenia californica</i>	1.9 - 11.86
<i>Gelidium robustum</i>	0.6 - 8.71
<i>Corallina</i> sp.	0.7 - 5.14
<i>Calliarthron</i> sp.	0.0 - 3.29
<u>Sessile Animals</u>	
<u>Bryozoans</u>	
<i>Parasmittina</i> sp.	2.9 - 24.86
Unknown, encrusting (i.d. # 303)	0.0 - 1.71
<u>Echinoderm</u>	
<i>Pachythyone</i> sp.	2.3 - 6.43

Table 1.3. Mean percent cover of major groups of algae and sessile animals on 125m² plots cleared at 12 - 14 week intervals on the canopied and canopy-removal sites during 1981, San Nicolas Island, California.

<u>Species-Group</u>		<u>Canopied Site</u>		<u>Canopy-Removal Site</u>	
		<u>mean % cover</u>	<u>s.e.</u>	<u>mean % cover</u>	<u>s.e.</u>
<u>Sampled in June</u>					
(cleared)					
<u>Primary Cover</u>					
ephemeral algae	Feb	12.7	1.8	20.7	7.0
perennial algae	Feb	2.0	1.2	4.7	1.7
sessile animals	Feb	1.3	1.3	0.7	0.7
<u>Secondary Cover</u>					
ephemeral algae	Feb	56.7	3.7	81.3	10.7
perennial algae	Feb	9.3	4.4	3.3	2.4
<u>Sampled in August</u>					
(cleared)					
<u>Primary Cover</u>					
ephemeral algae	Feb	11.3	4.3	20.7	2.9
	May	9.0	2.6	15.5	4.6
perennial algae	Feb	5.3	2.7	16.0	1.1
	May	0.5	0.5	16.0	8.7
sessile animals	Feb	11.3	3.5	1.3	1.3
	May	3.0	1.0	0.5	0.5
<u>Secondary Cover</u>					
ephemeral algae	Feb	28.7	7.1	86.7	15.9
	May	28.5	2.2	78.0	7.0
perennial algae	Feb	10.0	6.4	2.0	1.1
	May	6.5	4.5	7.0	5.2

Table 1.3. Continued.

Sampled in December
(cleared)Primary Cover

ephemeral algae	Feb	8.0	1.7	24.7	7.9
	May	0.5	0.5	9.5	4.8
	Aug	2.0	0.8	4.0	1.2
perennial algae	Feb	7.3	1.8	17.3	4.1
	May	3.0	1.7	23.0	2.5
	Aug	2.0	0.8	11.0	4.2
sessile animals	Feb	19.3	5.9	2.7	1.3
	May	14.0	2.4	2.0	1.4
	Aug	37.0	10.4	1.5	1.0

Secondary Cover

ephemeral algae	Feb	16.0	5.0	46.0	3.5
	May	5.5	3.2	30.0	6.1
	Aug	7.0	5.2	48.0	8.8
perennial algae	Feb	6.7	3.5	22.7	7.7
	May	8.0	4.3	21.5	14.3
	Aug	1.5	1.0	9.0	6.5

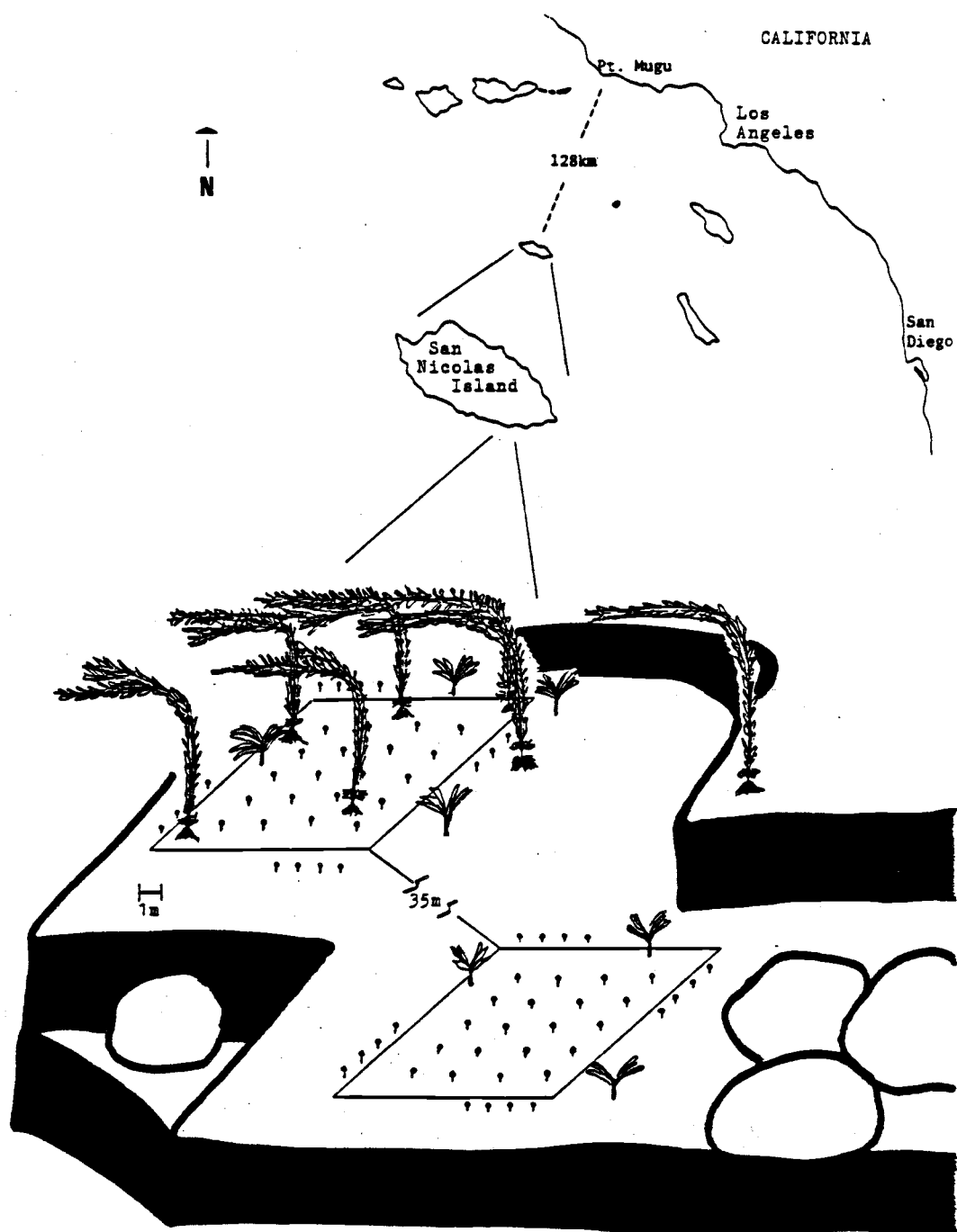
Cleared
Feb 1981 (plots = 3)
May 1981 (plots = 4)
Aug 1981 (plots = 4)

Sampled
June Aug Dec
Aug Dec
Dec

Figure

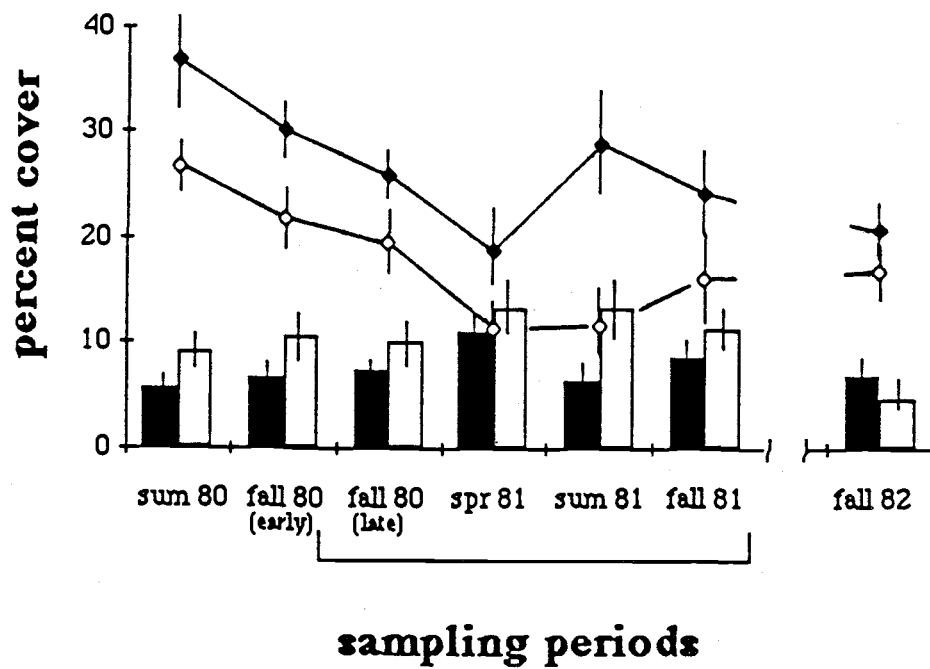
- 1.1. Study area, San Nicolas Island, California, and layout of canopied and canopy-removal sites, 1980 - 1982. The cleared and intact 0.25m^2 plots were designated with eyebolts within these sites, and seasonally cleared 0.125m^2 plots were located at corners of each site.

Figure 1.1



Figure

- 1.2. Mean percent cover of sand and bare substrate on the intact 0.25m^2 plots on the canopied and canopy-removal sites, San Nicolas Island, California, 1980 - 1982. Bars are ± 1 standard error. Bracket denotes canopy-removal period.

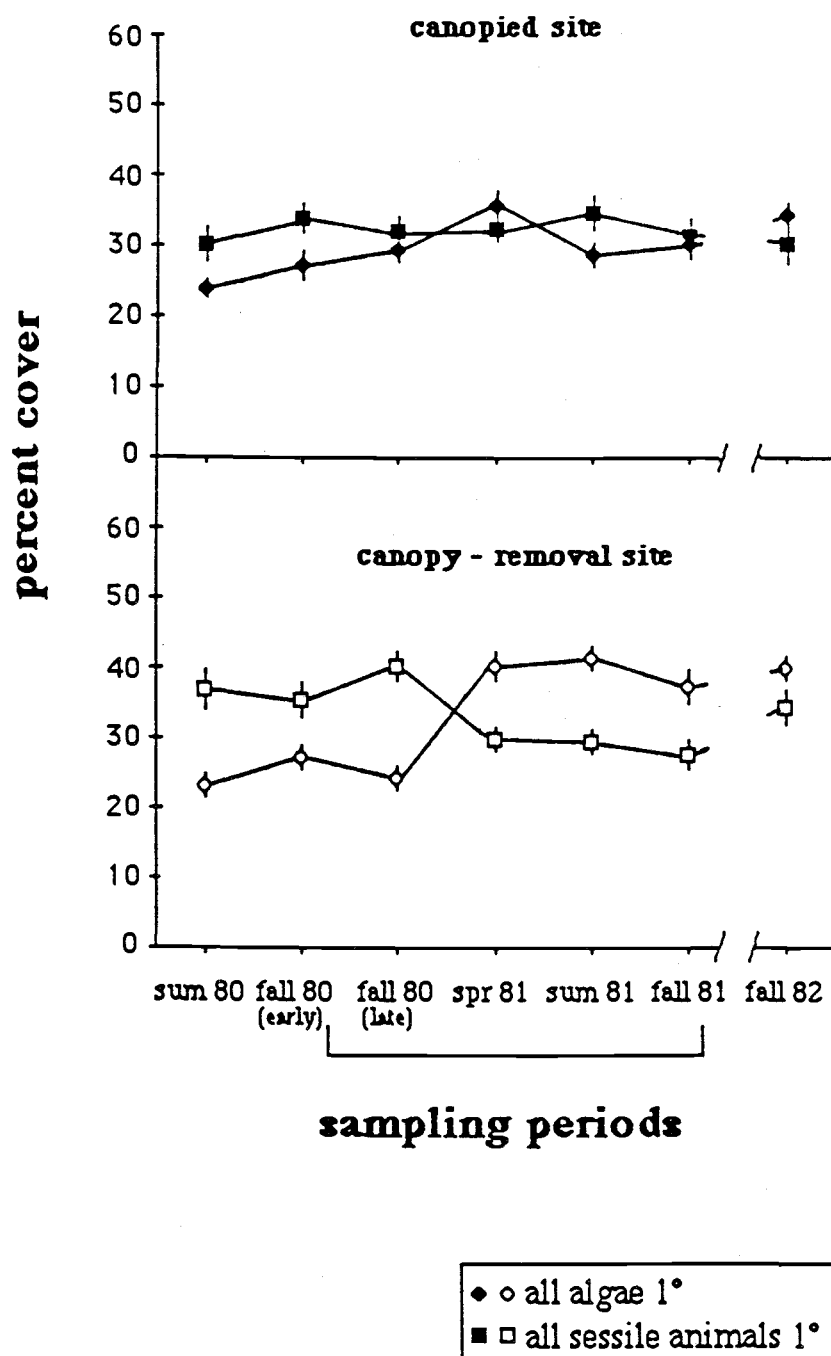
Figure 1.2.

- ◆ sand, canopied site
- sand, canopy-removal site
- bare, canopied site
- bare, canopy-removal site

Figure

- 1.3. Mean percent primary cover of algae and sessile animals on intact 0.25m^2 plots on the canopied and canopy-removal sites, San Nicolas Island, California, 1980 - 1982. Bars are ± 1 standard error, and bracket denotes canopy-removal period.

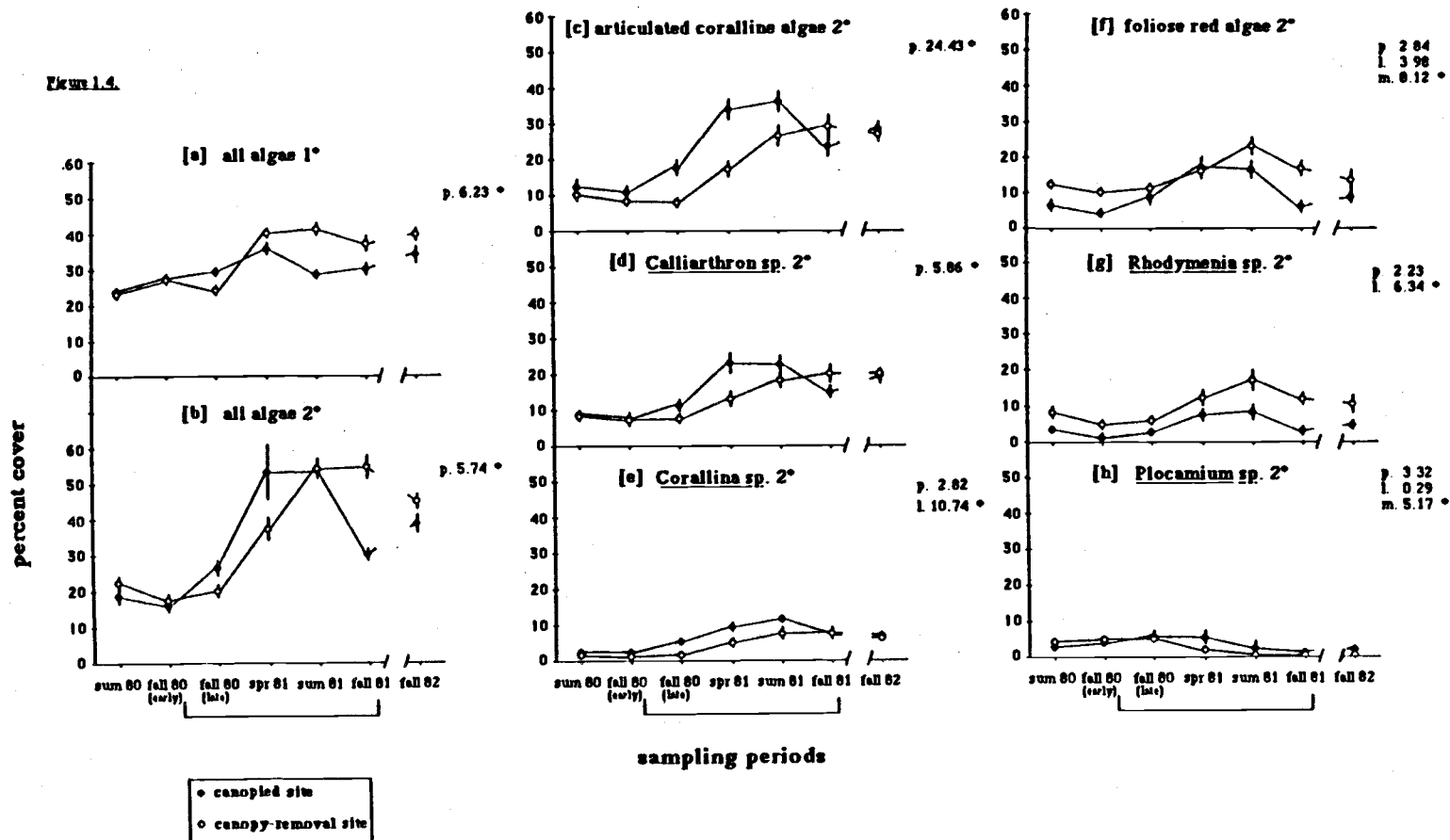
Figure 1.3.



Figure

- 1.4. Mean percent primary (1°) and secondary (2°) cover of all algae, the major groups of algae, and the most common species of algae on intact 0.25m² plots on the canopied and canopy-removal sites, San Nicolas Island, California, 1980 - 1982. Bars are ± 1 standard error. The F - values for the tests of profile analysis are p = parallelism, l = levels, m = means. * P < 0.05. Bracket denotes canopy-removal period.

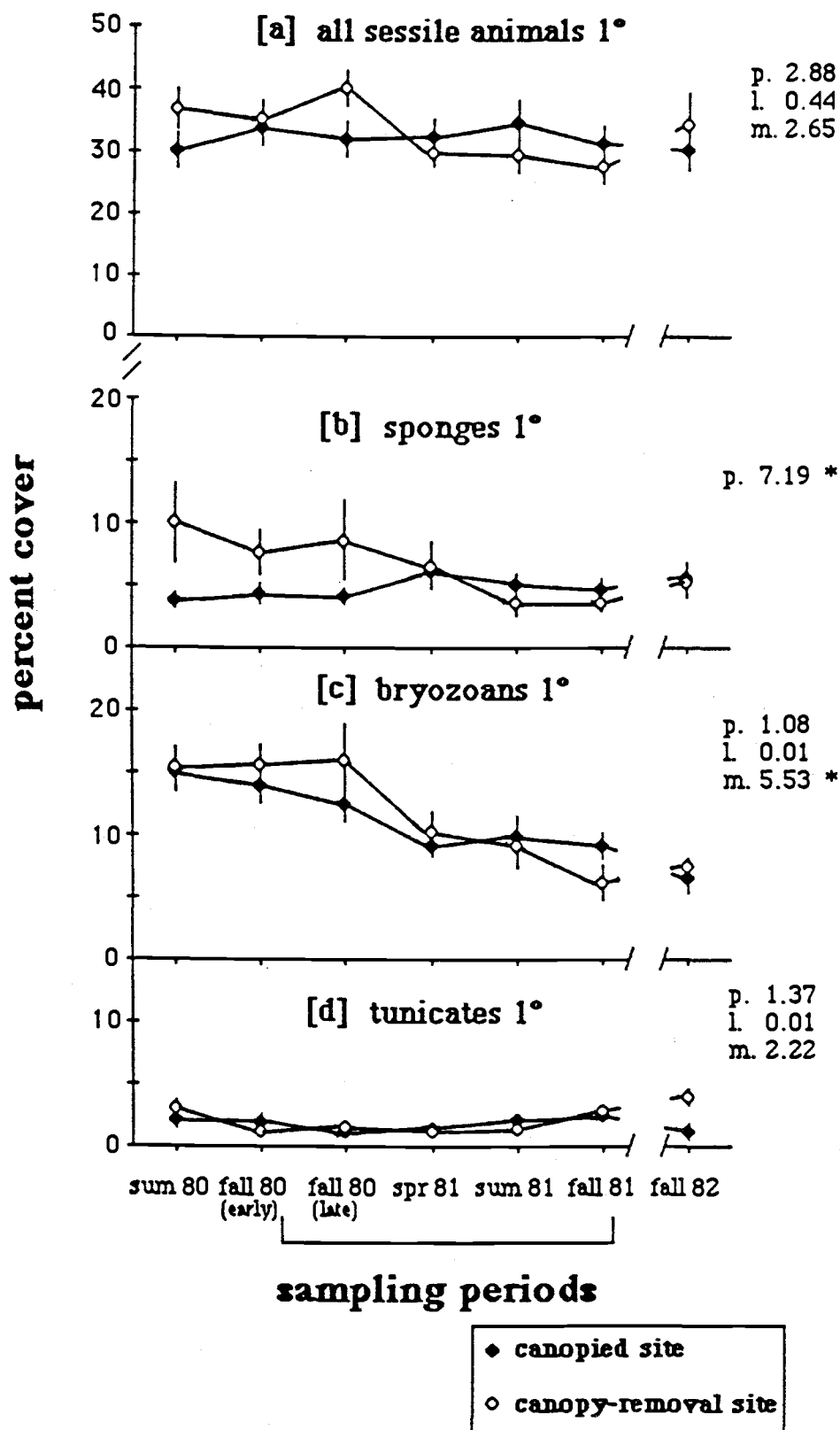
Figure 1.4.



Figure

- 1.5. Mean percent primary (1°) cover of all sessile animals, and 3 major groups of sessile animals on intact 0.25m² plots on the canopied and canopy-removal sites, San Nicolas Island, California, 1980 - 1982. Bars are ± 1 standard error. The F - values for the tests of profile analysis are p = parallelism, l = levels, m = means. * P < 0.05. Note different scales of the graphs. Bracket denotes canopy-removal period.

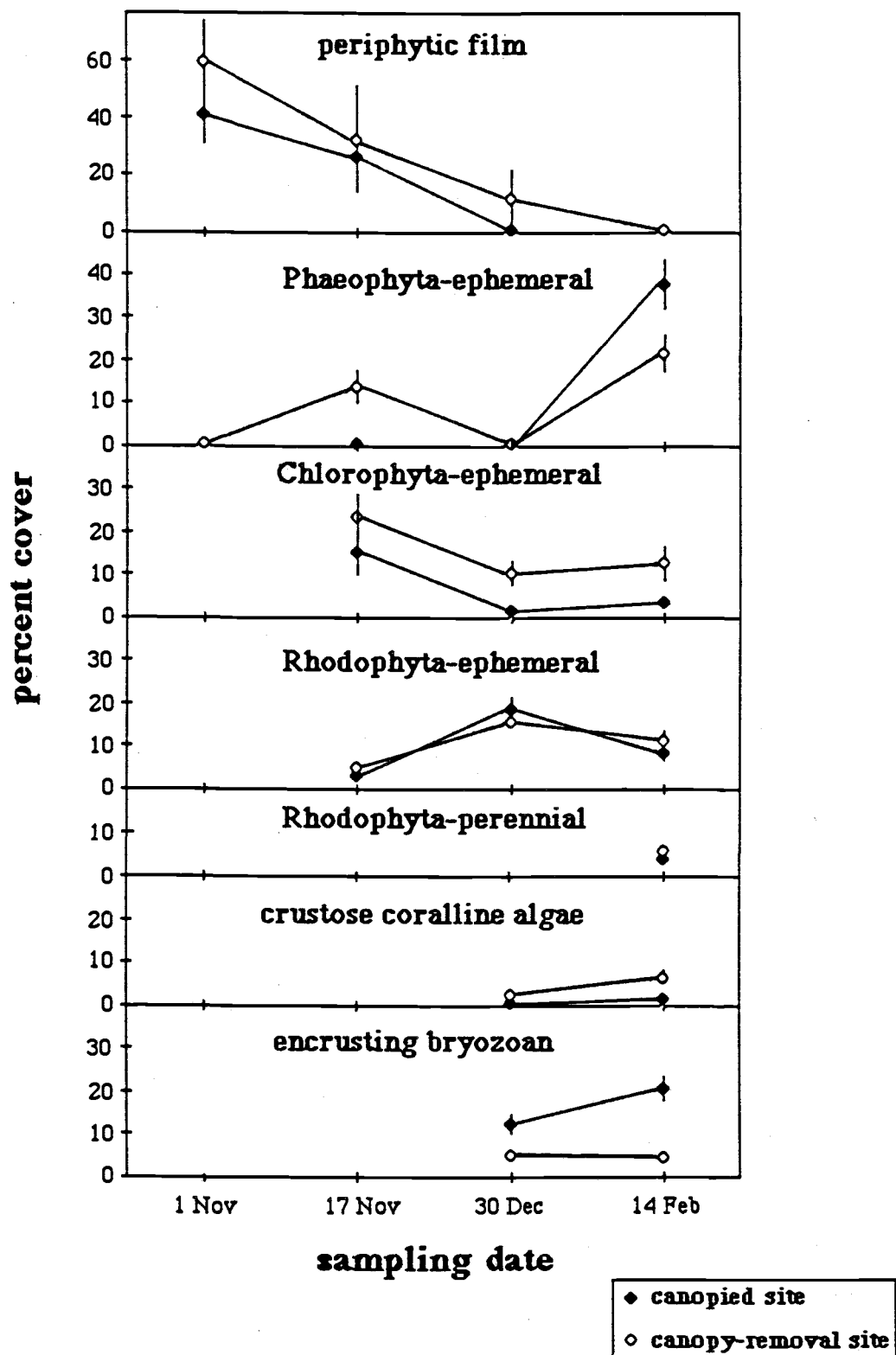
Figure 1.5.



Figure

- 1.6. Mean percent cover of early recruitment to cleared 0.25m^2 plots on the canopied and canopy-removal sites, San Nicolas Island, California. Cover was estimated from November 1980 to February 1981 by using a grided sampling frame. Bars are ± 1 standard error.

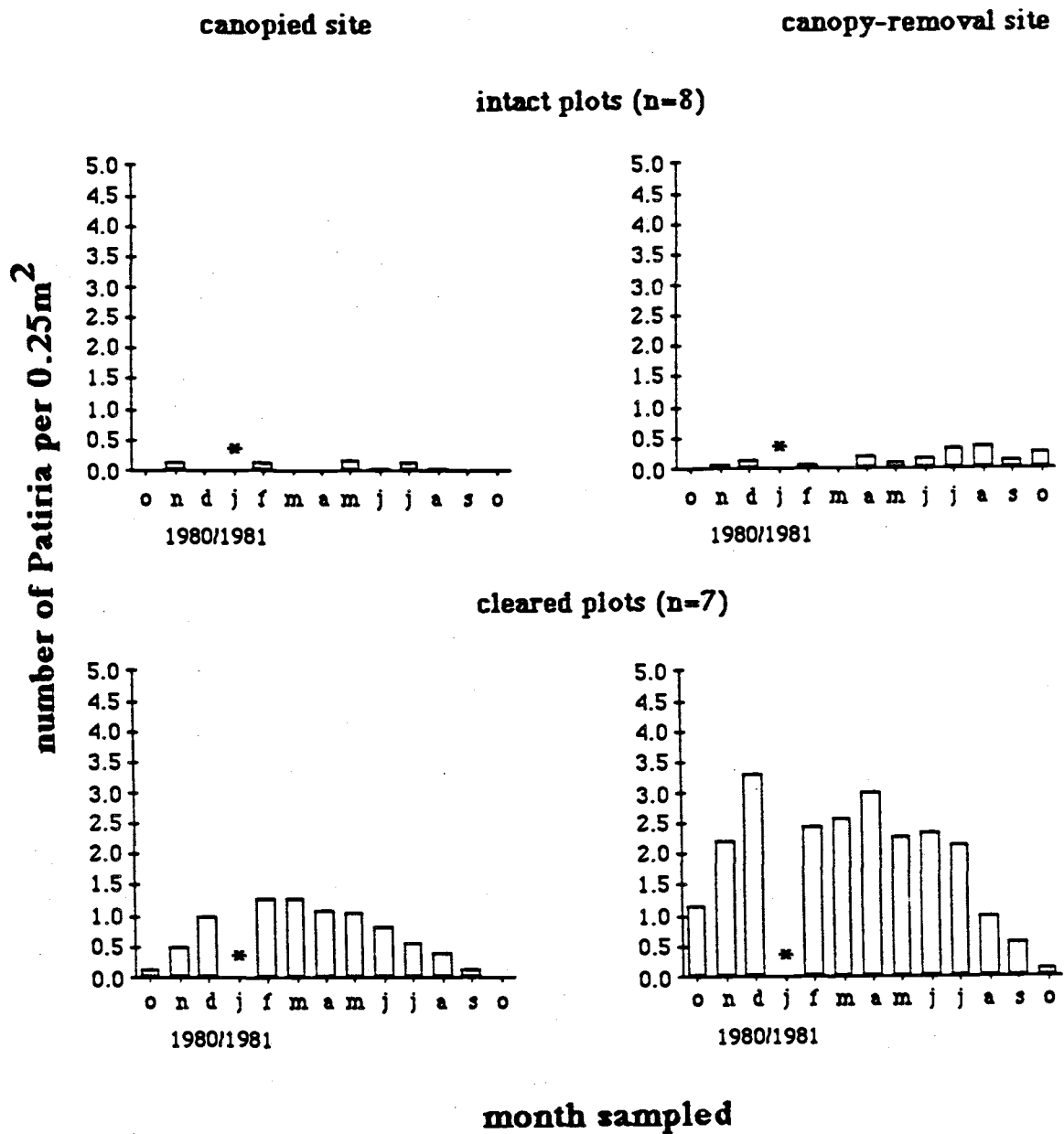
Figure 1.6.



Figure

- 1.7. Average number of *Patiria miniata* found on 7 cleared and 8 intact 0.25m² plots the canopied and canopy-removal sites, San Nicolas Island, California, between October 1980 and October 1981. *Patiria* were counted 2 or 3 times per month from March to August 1981, and 1 time per month otherwise.

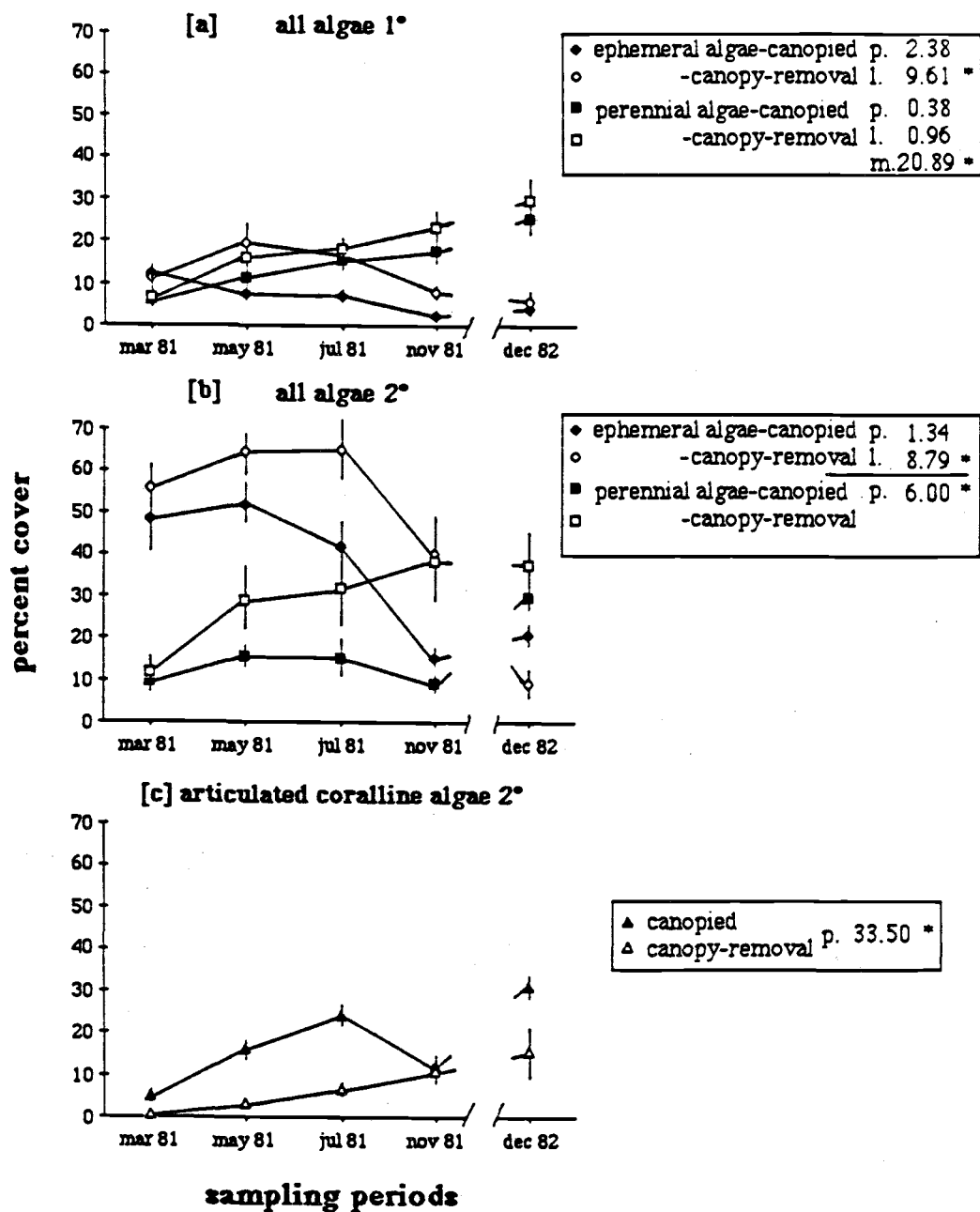
Figure 1.7.



Figure

- 1.8. Mean percent primary (1°) and secondary (2°) cover of ephemeral and perennial algae, and all articulated coralline algae on cleared 0.25m² plots on the canopied and canopy-removal sites, San Nicolas Island, California. 1980 - 1982. Bars are ± 1 standard error. The F-values for the tests of profile analysis are p = parallelism, l = levels, m = means. * P < 0.05.

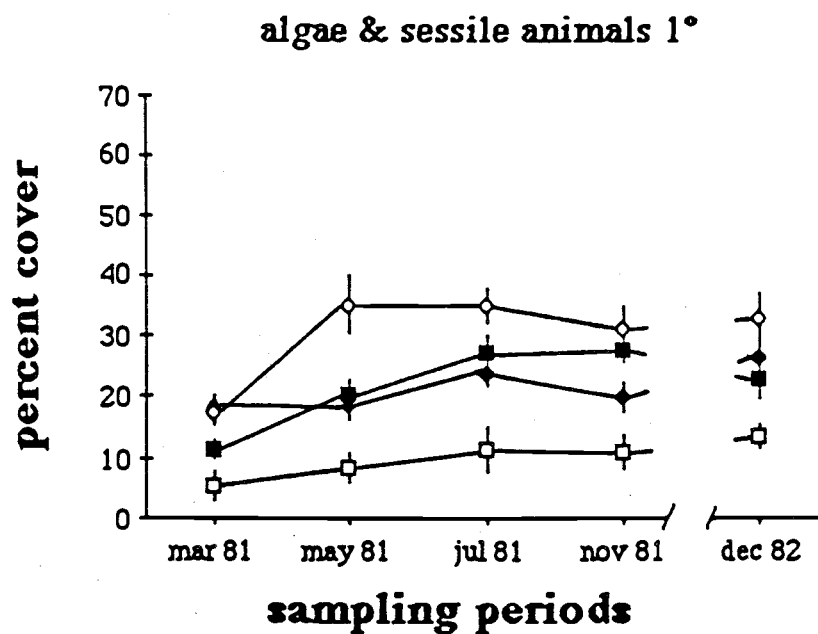
Figure 1.8.



Figure

- 1.9. Mean percent primary (1°) cover of all algae and all sessile animals on cleared 0.25m^2 plots on the canopied and canopy-removal sites, San Nicolas Island, California. 1980 - 1982. Bars are ± 1 standard error. The F - values for the tests of profile analysis are p = parallelism, l = levels, m = means. * $P < 0.05$.

Figure 1.9.

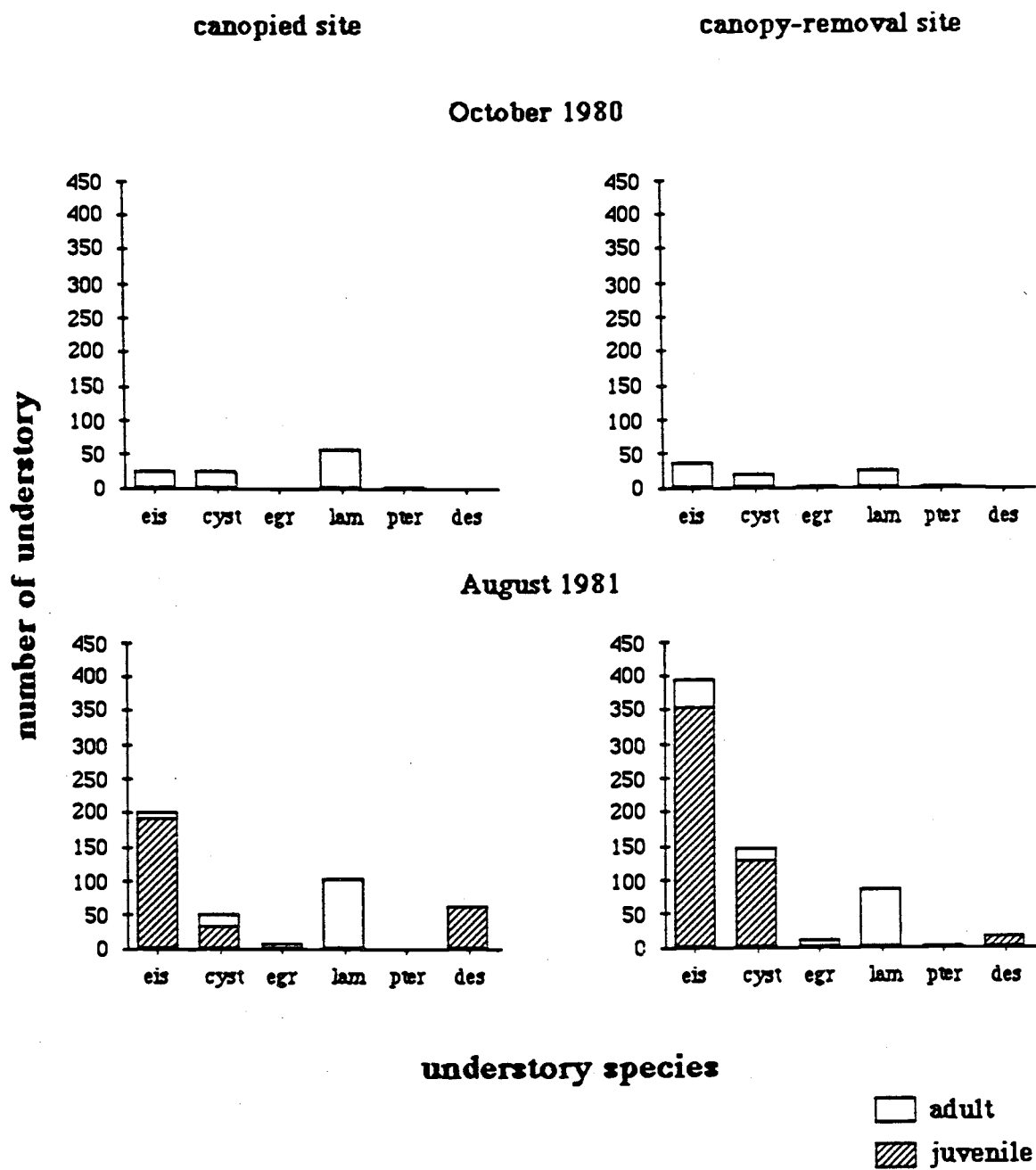


◆ algae	canopied site	p. 2.77
■ animals		l. 0.14
○ algae	canopy-removal site	m. 6.59 *
□ animals		p. 4.41 *
■ animals		p. 3.21
□ animals		l. 11.68 *

Figure

- 1.10. Number of understory kelps counted on the canopied and canopy-removal sites, San Nicolas Island, California, in October 1980 and August 1981. No juvenile kelps were found in October 1980. Eis = *Eisenia*; Cyst = *Cystoseira*; Egr = *Egregia*; Lam = *Laminaria*; Pter = *Pterygophera*; Des = *Desmarestia*.

Figure 1.10.



Chapter 2.

Experiments on Herbivory and Competition: The Prevailing Effects of Canopy on the Turf Assemblage of a *Macrocystis* Kelp Forest

Abstract

Variable distribution and abundance of recruiting algae, and low abundance of established populations of foliose red algae were characteristic patterns of the turf assemblage of a *Macrocystis* kelp forest located off San Nicolas Island, California. To examine the effects of mobile, herbivorous invertebrates on recruiting algae, *Patiria miniata* (asteroid) was fenced in and out of units containing cleared plots from June 1981 to March 1982. Additionally, *Patiria* were excluded from and included on caged, near-bare plots from June through August 1983. In a follow-up study, all large herbivores were excluded from caged versus uncaged, near-bare plots from September 1983 to December 1984. To examine the effects of herbivory on established turf algal assemblages, large herbivores were excluded from caged plots that were compared to adjacent uncaged plots from June 1983 to December 1984. On 5 of those caged and adjacent uncaged plots, the dominant turf alga, *Calliarthron cheilosporioides*, was removed to examine possible effects of algal-algal competition.

On the fenced, cleared plots, a density of 3 - 4 *Patiria* per 0.25m² was effective in removing filamentous brown (Phaeophyta) and green (Chlorophyta) algae, and slowed recruitment by other forms of brown algae. *Patiria* appeared to have little effect on foliose algae once a certain size of plant was attained, and red (Rhodophyta) algae actually were more abundant on plots containing *Patiria*. *Patiria* caged on near-bare plots had no significant effect on algal recruitment after 3 months, possibly because of the lower density (1) of *Patiria* on these plots.

When the effects of all large herbivores on early succession were examined, algal recruitment on caged and uncaged, near-bare plots was negligible from September 1983

to August 1984. From January to August 1984, low algal recruitment on these plots was associated with very low illumination at the substrate, caused by a dense and persistent surface canopy of *Macrocystis*. In contrast, sessile animals recruited heavily to these plots during this same time period.

Cover of foliose red algae found in established turf assemblages increased significantly in caged plots compared to uncaged plots in December of both 1983 and 1984, indicating an effect due to herbivory. From January to August 1984, a substantial decline in cover of all arborescent turf algae was correlated with low illumination at the substrate. No changes in cover of turf algae were associated with the removal of *Calliarthron* sp.

Although some effects due to herbivory were demonstrated, no pervasive, long-term effects on the turf assemblage were attributed to grazing by *Patiria*. Possible effects due to all large herbivores on early succession were not evident apparently because of the effects of the *Macrocystis* canopy cover. Herbivory, probably by fishes, was shown to be a feasible explanation for the low abundance of foliose red algae in established turf assemblages, but these effects were also diminished by canopy cover. By affecting illumination at the substrate, the presence of a dense surface canopy of *Macrocystis* was associated more with patterns of distribution and abundance of turf algae than herbivory.

Introduction

Studies of the structure of natural communities invariably lead to questions concerning what forces cause observed patterns of distribution and abundance of species. One aim of ecologists is to identify which forces are most significant in determining these observed patterns. These forces include biotic interactions and qualities of the environment that significantly influence the maintenance of community structure or cause predictable changes. Biotic interactions are inherent in communities, but the significance of the effects of these interactions on structure may vary greatly between communities or within communities over space and time (Connell 1975, Lubchenco and Menge 1978, Foster 1982). Moreover, continual or recurrent physical disturbances can directly influence structure in communities, or mitigate or intensify the effects caused by biotic forces (Menge 1978, 1983, Paine and Levin 1981, Sousa 1984).

Predation (including herbivory) and competition are biotic interactions that probably occur in most natural communities. Herbivory is well-documented as a significant organizing influence on structure of communities in many terrestrial and marine systems (see reviews by Harper 1977, Lubchenco and Gaines 1981). However, the role of competition as a pervasive force in the organization of communities has been questioned (Salt 1984, Strong, Jr. et al. 1984). One integral component of the concept of competition is that dominant species can maintain subordinate species at low abundance, unless the abundance of the dominant species is restricted by predation or physical disturbance (e.g., Paine 1974, Dayton 1975, Lubchenco 1978).

The light-inhibiting effect of canopy on the structure of a turf assemblage was

studied in a *Macrocystis* kelp forest located off San Nicolas Island, California (Chapter 1). Turf was defined as the collective assemblage of algae and sessile animals, which were no greater than 40cm tall and which paved or grew close to the substrate. In this kelp forest, changes in cover of turf algae were correlated with differences in light intensity (illumination), produced by the presence or experimental removal of the kelp canopy. Substantial increases in cover of articulated coralline algae were associated with a greater intensity of light, but only subtle increases occurred in cover of foliose red (Rhodophyta) algae under the same experimental treatment. Also, Recruitment of algae to cleared plots of substrate appeared affected by factors in addition to light intensity: herbivory and/or algal - algal competition were suspected of further depressing the abundance of foliose algae in both early and later successional stages.

The effects of urchins on community structure are the best documented of species-specific herbivory in temperate kelp forests and tropical coral reefs (Lawrence 1975). In the San Nicolas Island kelp forest, urchins were not suspected of exerting enough grazing pressure to affect overall structure of the turf algal assemblage, except near crevices and ledges (pers. obs., Cowen 1983, also Dayton et al. 1984). This did not apply to all habitats around San Nicolas Island (Harrold and Reed 1985). The effects of other large herbivores, including fishes, on community structure are not well-documented, except in some tropical studies (e.g., Randall 1965, Ogden and Lobel 1978, Choat 1982, Hatcher and Larkum 1983, Hay 1984a,b). Grazing by *Patiria miniata* (asteroid), and also by less common *Parastichopus parvimensis* (large holothuroid) and *Astraea undosa* (wavy turban snail) removed turf organisms that recruited to experimentally cleared plots (Chapter 1). But exact effects of these invertebrates on structure of early recruitment in the turf assemblage were not known.

Other large invertebrate grazers that occurred in this kelp forest were known to consume some species of turf algae (Leighton 1966). Fishes may affect structure of algal assemblages in temperate kelp forests, but few studies have demonstrated that possibility (Choat 1982). Fishes may be significant consumers of brown (Phaeophyta) kelp sporophytes and other macroalgae in temperate kelp forests (Choat 1982, Harris et al 1984). Stomach contents of opaleye (*Girella nigricans*), halfmoon (*Medialuna californiensis*) and senorita (*Oxyjulis californica*) sampled off Del Mar, Ca., contained mostly macroalgae (Quast 1968, 1971). These fishes were common in the kelp forests off San Nicolas Island.

Arborescent turf algae in the San Nicolas Island kelp forest consisted mainly of the articulated coralline alga, *Calliarthron cheilosporioides*, foliose red algae and other articulated coralline algae. *Calliarthron sp.* was more resistant to physical or biotic disturbances and grew larger than other turf algae observed. *Calliarthron sp.* also may have a competitive effect on foliose algae and other articulated coralline algae by dominating available space, shading (e.g., Reed and Foster 1984) or by "whiplashing" other surrounding species (Velimirov and Griffiths 1979).

This study investigated the possible roles of herbivory and competition on the structure of the turf assemblage of a *Macrocystis* kelp forest. The following questions were addressed: what effect do large herbivores have on the composition, abundance and distribution of early recruiting organisms in the turf assemblage? What effect do herbivores have on the abundance and distribution of foliose red algae in established turf assemblages? Does the dominant turf alga, *Calliarthron cheilosporioides*, determine or contribute to the comparatively lower abundance of foliose turf algae, and also of other articulated coralline algae?

Methods and Results

Investigations were conducted in the aforementioned *Macrocystis* kelp forest located off San Nicolas Island, California. This kelp forest was described in Chapter 1, and was under study or observation periodically from 1980 through 1984.

Effects of *Patiria* on Early Recruitment

Methods. A preliminary study was conducted to determine if grazing by *Patiria* affected composition and abundance of early recruitment in the turf assemblage. In June 1981, an 18m x 10m area was established and divided into 3 equally-sized 6m x 10m units. Within each unit, 3 50cm x 50cm (0.25m²) plots were established at about 2m intervals and cleared to completely bare substrate. A 45cm-high fence, made of Dupont vexar netting (0.75in. x 0.75in. mesh, Conweb OV 1581, Consolidated Net and Twine Co., Seattle, Wash.) and supported by steel rods, was placed around 2 of the 3 units. Fifty *Patiria* were fenced within one unit; *Patiria* were fenced out of one unit; 1 unit was not fenced. On the inclusion unit, 5 *Patiria* were placed on each plot and the other 35 placed randomly on the unit at the start of the study. No *Patiria* were observed on the unfenced unit at the start of the study. *Patiria* on the plots were counted once per month from August - December 1981, and again in March 1982. Because of a limited-sized area in which to establish this experiment, 1 plot on each unit was situated at the edge of a 0.50m vertical drop-off. This provided an opportunity to examine edge-effects on early recruitment.

The 100 random point sampling method described in Chapter 1 was used in August and November 1981, and March 1982 to estimate percent cover of recruiting species. Species were categorized into 2 forms of cover: primary cover, i.e., grew directly on or paved the substrate; and secondary cover i.e., grew arborescently. Algae capable of growing >40cm (Phaeophyta: orders Laminariales and Fucales) were counted and removed when detected.

Results. *Patiria* counted monthly from August 1981 - December 1981, and in March 1982, averaged 3.72 (s.d. = 0.58) per plot on the inclusion unit, and 0.88 (s.d. = 0.50) *Patiria* per plot on the unfenced unit. On one occasion, 4 *Patiria* were found and removed from the exclusion unit; the plots did not appear to have been disturbed by their presence.

Percent cover of filamentous brown (Phaeophyta) and green (Chlorophyta) algae was lower on plots with *Patiria* compared to those without *Patiria* (Fig.2.1a,b). These algae were either consumed or displaced by *Patiria*. By November 1981 and March 1982, filamentous brown algae accounted for less than 2 percent cover on any of the plots. Recruitment of brown algae was dominated by the foliose brown algae, *Dictyota* sp. and *Pachydictyon* sp. These 2 species were probably reduced by *Patiria* on the inclusion unit, although no effect was evident once these algae grew greater than about 5cm tall. The leafy, green alga, *Ulva* sp., was common on the plots by November, but did not appear to be affected by *Patiria*. *Ulva* was rare in this kelp forest, and was not observed at >2 - 3cm tall on the plots. I removed substantially more recruits of species of Laminariales and Fucales (algae that could grow >40cm tall) from plots on the exclusion unit than the other 2 units. In August 1981, when numbers of these algae were highest, 240 recruits were removed from plots without *Patiria*, compared to 26

recruits removed from plots with *Patiria*; 55 recruits were removed from unfenced plots. Recruitment of these algae declined substantially after August.

Recruitment of foliose red algae was patchy and slower than filamentous brown or green algae. Foliose red algae that appeared first were minute forms that were uncommon in later successional assemblages of turf algae (Fig.2.1c, Chapter 1). These were followed by *Rhodymenia sp.*, which was the most common of foliose red algae in later successional turf assemblages, and *Gigartina sp.* *Gigartina* was common in early successional assemblages, but rare in later successional assemblages. Most red algae did not appear affected by *Patiria*, and, in fact, a significantly ($P < 0.05$) greater percent cover of foliose red algae occurred on plots with *Patiria* compared to those without *Patiria* and the unfenced plots ($F = 5.74$). Recruitment of coralline algae appeared unaffected by the presence of *Patiria* (Fig.2.1d,e).

Heavy recruitment by sessile animals on 3 plots (1 plot in each unit) situated at the edge of a vertical drop probably accounted for some of the large variability in cover of turf organisms in Fig.2.1 (Fig.2.2a). These sessile animals, mostly barnacles and colonial tubeworms, were eaten by *Pisaster gigantea* (asteroid) on the plots with *Patiria* and the unfenced plots. Two *Pisaster* were repeatedly observed on one unfenced plot, and *Patiria* were not observed on that plot when *Pisaster* were present. Brown algae did not successfully recruit to or remain on plots located along the ledge after sessile animals became dominant (Fig.2.2b). Brown algae did not appear to recruit well on the hardened outer-structures of live sessile animals or on the calcified remains of those consumed by *Pisaster*. In contrast, red algae eventually colonized on these 3 plots at similar rates as the remaining 6 plots (Fig.2.2c). Cover of crustose coralline algae was reduced mainly because of overgrowth by sessile animals.

Herbivory on Near-Bare Plots

Methods. The inclusion and exclusion of *Patiria* on fenced plots was ended in March 1982 and a follow-up study was conducted between June and August 1983 to determine if *Patiria* affected recruitment on patches created by the loss of *Macrocystis*' holdfasts. Ten large, mature *Macrocystis*' holdfasts were randomly selected and removed. The underlying substrate was cleared of any accumulation of sand and wire-brushed to remove remnants of holdfasts. Brushing had no visible effect on surviving (i.e., unbleached) crustose coralline algae which remained under the holdfasts. No arborescent algae occurred on this substrate, but a few small patches of sponges and some anenomes were found. Remains of calcified sessile organisms were common on this substrate, and some were removed with a hammer to approximate bare substrate on all plots. Some bleached shells were removed that appeared empty but contained live *Serpulorbis* sp. A 20cm buffer was cleared around the 50cm x 50cm plots. Each of the 10 plots were covered with a 70cm x 70cm x 35cm high cage. Cages were made of a PVC (0.50in dia) box-shaped frame, and covered with Dupont Vexar netting (0.75in x 0.75in). Cages were bolted to the substrate at the corners and were removable. One *Patiria* was placed in each of 5 randomly selected caged plots in early June 1983. The cages were removed, cleaned and reinstalled every 6 weeks to remove fouling. The plots were sampled using the 100 random point sampling method described in Chapter 1. Algae that were capable of growing >40cm tall were counted and removed when detected.

After 3 months, no differences were apparent between the plots with *Patiria* and

those without (see results). Therefore, the experiment was redesigned to examine the effects of excluding all large herbivores (blocked by the 0.75in mesh size) including *Patiria*, on recruiting turf algae compared to cleared, uncaged plots. The cages were removed from the 10 plots, the substrate re-brushed, and 10 additional, mature *Macrocystis*' holdfasts were randomly selected and removed, and the underlying substrate prepared as described above. Cages were placed randomly on 10 of the 20 plots and the remaining 10 plots were uncaged. Dupont Vexar, 30cm in width, was strung in a vertical plane above and diagonally across the uncaged plots to affect water motion in a manner similar to the cages. The cages were removed, cleaned and reinstalled every 6 weeks to remove fouling organisms. Light meter readings indicated that illumination at the substrate was not changed measurably by the presence of the cages.

These 20 plots became operational in September 1983, and were sampled using the 100 random point sampling method in January, May, August and December 1984. One-way ANOVA ($P=0.05$) was used to compare mean percent cover of algae in caged versus uncaged plots at each sampling date.

Results. The caged inclusion and exclusion of *Patiria* on holdfast-removal plots had no observable effect on recruiting species 3 months after exposing and brushing the plots (Fig 3). There were no significant differences ($P>0.05$) in primary cover of sessile animals, and secondary cover of red or brown algae between the *Patiria* inclusion and exclusion cages. Only trace (<1 percent) measures of green algae were observed during this period. The lack of significant difference and the high percent cover of brown algae may have reflected the density of 1 *Patiria* per 0.25m^2 area. Also, many *Patiria* on and around the study area showed signs of infection from a wasting

disease first recognized on San Nicolas Island in 1981. The uncertainty of the outcome of the disease and of how many *Patiria* were necessary to affect early succession warranted that the experiment be redesigned to exclude all large herbivores.

From September 1983 to August 1984, cover of major groups of algae and sessile animals compared between the caged, herbivore-exclusion plots and uncaged plots was not significantly different ($P > 0.05$) (Fig.2.4). In January 1984, the growth of arborescent turf algae was negligible, except for the brown algae *Dictyota sp.* and *Pachydictyon sp.* But cover of sessile animals was high and similar on both the caged, herbivore-exclusion plots and uncaged plots sampled between January and August 1984. By December 1984, secondary cover of red algae was still negligible, but secondary cover of brown algae was significantly ($P < 0.05$) greater on the uncaged plots compared to the caged, herbivore-exclusion plots. These particular brown algae, *Dictyota sp.* and *Pachydictyon sp.*, were probably not affected in the adult form by herbivores, and the difference was probably because of variable recruitment. High recruitment of these brown algae was associated with a decline in sessile animals on the uncaged plots measured in December 1984 (Fig.2.4).

Little or no growth of arborescent algae on the holdfast-removal plots was correlated with low illumination at the substrate. From January 1984 to July 1984, the *Macrocystis* canopy over the study area was more dense than observed from 1980 through 1983. Ten light readings taken randomly on the study area averaged 25.0 (footcandles) in August 1983, 7.8 in January 1984, 2.9 in May 1984, 3.0 in July 1984, and 16.1 in December 1984. This compared with a reading of >70.0 (off the scale of the light meter) outside the kelp bed at a similar depth of 9m. Observations of the surface canopy on the study area in February and April 1984 suggested that the

denseness of the surface canopy probably was consistent from winter to summer 1984. Severe, prolonged oceanic swell, which lasted 7 days, was observed in August; this was the first physical disturbance that summer to cause substantial thinning of the surface canopy.

Herbivory and Competition on Established Turf Assemblages

Methods. Plots were established on areas where both foliose and articulated coralline turf algae were common and 2 plots could be placed adjacently to examine the effects of herbivory and competition on established turf algal assemblages. Ten such areas were selected, and 2 plots were placed at random within each area as follows: a 70cm x 70cm x 35cm cage, constructed and attached as described above, was placed over half of each selected area; the other half was left uncaged. The uncaged plot was marked with 4 stainless steel rods cemented 70cm apart in a square pattern. I assumed that if water motion was substantially disrupted by the cage, the adjoining uncaged plot would also be affected.

Five caged plots and their adjoining uncaged plots were randomly selected to determine the effects of herbivory. These uncaged plots were the true control for these experiments. To determine if the removal of the dominant alga could have an effect on the abundance of foliose red algae, *Calliarthron* sp. was removed from the 5 remaining caged plots and their adjoining uncaged plots. *Calliarthron* was removed after the cages were in place through 2 periods of severe oceanic swell to assure that the cages could withstand high water motion.

The plots of established turf assemblages were photographed in June, July, August

(*Calliarthron*-removal plots only) and December 1983, and June, August, and December 1984 with a Nikonos II camera. The camera and 2 opposing electronic strobes were mounted on a frame that established a consistently aligned 50cm x 50cm photographic reference area within the 70cm x 70cm plot.

The established turf algal assemblages were sampled from projected 35mm color images. Percent cover of different algae was measured and calculated from the 50cm x 50cm areas by outlining the images of different species of algae with a digitizer (GTCO Corporation, Rockville, Md) on-line with an IBM PC XT computer. This method calculated near absolute measures of turf algae forming secondary cover.

For each sampling period, mean percent cover of foliose red algae was compared between treatments and control using one-way ANOVA ($P=0.05$). Two-way ANOVA was not used to test for effects over sampling dates because of the uncontrolled effect of low illumination at the substrate that affected the outcome of the experiment over time. The Student-Newman-Keuls means separation test was used to compare means when a significant difference was detected. Mean percent cover of articulated coralline algae at each sampling date was compared between caged, herbivore-exclusion plots and uncaged plots with *Calliarthron* intact, and caged, herbivore-exclusion plots and uncaged plots with *Calliarthron* removed. All data were normalized by square root transformation (Steele and Torrie 1981).

The cages were removed, cleaned and reinstalled every 6 weeks to remove fouling organisms. Light meter readings indicated that illumination at the substrate was not changed by the presence of the cages. Algae capable of growing >40cm were counted and removed when detected.

Results. Cover of foliose red algae and articulated coralline algae compared

between caged, herbivore-exclusion plots and uncaged plots were not significantly ($P>0.05$) different in July 1983 (Figs.5,6). In August, after the removal of *Calliarthron* from randomly selected plots, cover of articulated coralline algae remaining was not significantly ($P>0.05$) different between caged and uncaged plots ($F=0.02$). By December 1983, cover of foliose red algae on the caged plots was significantly ($P<0.05$) greater compared to the uncaged plots (Fig.2.5). Comparison of means of percent cover of foliose red algae showed no significant ($P>0.05$) difference between caged plots with *Calliarthron* intact and removed, or uncaged plots with *Calliarthron* intact and removed, indicating no effect due to the removal of *Calliarthron*. As documented in previous studies, cover of foliose red algae in general declined on all plots from July - December 1983 (i.e., from summer to winter), but the decline was slight on the caged plots, and substantially greater on the uncaged plots. This was true for most foliose red algae that were identified, particularly *Rhodomenia californica*, which was the most abundant foliose red alga. *Cryptopleura* spp., which previously had rarely been encountered in established turf assemblages, increased slightly on the caged plots from July 1983 to December 1983.

Changes in cover of articulated coralline algae were nominal by December 1983. The removal of *Calliarthron* sp. had no apparent effect on cover of other articulated coralline algae, mainly consisting of *Corallina officinalis* var. *chilensis* (Fig.2.6). No significant ($P>0.05$) differences in cover of articulated coralline algae were found between caged, herbivore-exclusion plots and uncaged plots in the presence or absence of *Calliarthron* sp.

Percent cover of foliose red algae declined to <1.50 percent on all caged, herbivore-exclusion plots and uncaged plots by June 1984, and remained at low cover

into August 1984 (Fig.2.5). Likewise, cover of articulated coralline algae declined substantially during the same period on both caged and uncaged plots (Fig.2.5). The decline in turf algae was correlated with low illumination at the substrate, caused by the persistence of the dense surface canopy of *Macrocystis* reported above.

By December 1984, foliose red algae had increased on most caged, herbivore-exclusion plots and uncaged plots (Fig.2.5). More cover of foliose red algae was found on the caged plots compared to the uncaged plots; the difference between the caged plots with *Calliarthron* removed and the uncaged plots was significant ($P < 0.05$). *Rhodomenia* appeared to recruit from stolons that were found embedded among sessile animals, particularly sponges. In a previous study (Chapter 1) and in July 1983 of this study, *Cryptopleura corallinara* was uncommon and found only epiphytically on articulated coralline algae, and *C. violacea* was rare. Neither species was observed with blades > 1 - 2cm in length. When protected from herbivory in this study, *C. violacea* was more common growing on *Corallina* sp. with *C. corallinara*, and also on the substrate, and had blades > 10 cm in length. The larger size of *C. violacea* appeared susceptible to damage by high water motion, but recruited or regrew within weeks after being damaged.

Articulated coralline algae also increased on most caged, herbivore-exclusion plots and uncaged plots from August to December 1984. In December 1984, there was no significant ($P > 0.05$) difference in cover of articulated coralline algae between caged and uncaged plots with *Calliarthron* intact (Fig.2.6), but in the caged plots with *Calliarthron* removed, articulated coralline algae were significantly ($P < 0.05$) lower in cover than that observed in the uncaged plots with *Calliarthron* removed. These were the same caged plots with significantly greater cover of foliose red algae compared to the uncaged plots.

Closer examination of the turf algae showed that the foliose red algae, *Cryptopleura* spp., grew on and around the articulated coralline alga, *Corallina officinalis* var. *chilensis*. Cover of *Corallina* sp. on the caged plots was less than that observed on the uncaged plots, and growth of *Corallina* sp. appeared inhibited by a heavy epiphytic load of *Cryptopleura* spp. This expansive growth of *Cryptopleura* spp. was not evident on the uncaged plots and had not been observed previously on the study area.

Discussion

Patiria consumed or displaced filamentous brown and green algae and probably reduced recruitment of nonfilamentous algae characteristic of early successional stages. There was no indication that filamentous algae survived over a longer interval of time when *Patiria* was excluded. Once *Dictyota* and *Pachydictyon* became established, these species clearly brushed the substrate surrounding them and might have displaced some filamentous algae from the *Patiria*-exculsion plots. *Patiria* may facilitate recruitment by foliose red algae on early successional plots by removing colonizing brown algae. Most species of recruiting red algae were apparently not affected by the presence of *Patiria*, and, in fact, *Tiffaniella* sp. was often found growing in a medium of sand particles mixed with mucous from the everted stomach of *Patiria*. *Patiria* might affect later stages of succession in the kelp forest by reducing the number of sporophytes of kelps that recruit to bared patches. However, the formation of dense canopies of *Macrocystis* and other kelps appeared most responsible for reduced recruitment of their progeny in this and other kelp forests (Chapter 1, Reed and Foster 1984, Pearse and Hines 1979).

Grazing by *Patiria*, *Parastichopus* sp. and *Astraea* sp. was most apparent on early

successional patches that were created naturally by the loss of *Macrocystis*' holdfasts, and on sand-scoured substrate close to sand channels. These invertebrates might contribute to observed patterns of abundance of certain turf algae, but were probably not a major force that determined patterns of succession of early recruiting turf algae in this study. *Patiria* affected early successional recruitment in this and a previous study (Chapter 1), but the significance of that effect appeared dependent on a density of several *Patiria* per 0.25m² area. *Patiria*, *Parastichopus* and *Astraea* were generally patchy in distribution, low in density, or displayed feeding habits that reduced their effects on established turf assemblages. *Patiria* were particularly patchy in distribution after a dieoff from disease around San Nicolas Island in 1981 through 1983 (pers obs., Harrold pers. comm.). *Parastichopus* and *Astraea* were less common in this kelp forest than *Patiria*.

The distribution and abundance of early successional algae was probably affected as much by physical disturbance or the biology of these algae as by herbivory. This kelp forest was located in the shallow subtidal (9m) and was unprotected from oceanic swell. Most filamentous brown and green turf algae appeared susceptible to being dislodged by frequently high water motion or sand-scouring. Therefore, the effects of grazing were probably greatest on these algae during mild oceanic periods, or similarly in kelp forests in protected areas. The life histories of early recruiting algae may have been equally as important as physical disturbance. The rare occurrence of early recruiting species as long-time survivors on cleared plots and in established turf assemblages indicated that the longevities of many of these species were probably short. Most species of brown and green algae occupied disturbed substrate opportunistically, and generally were uncommon in established turf assemblages in this

kelp forest (Chapter 1). The life histories of many algae identified from the turf assemblage are virtually unknown, and this information is essential to understanding succession in the assemblage.

Other large invertebrates found on the study area either used specific habitats or were not common and were not considered significant herbivores during the time of this study. Purple urchins (*Strongylocentrotus purpuratus*) found on open, horizontal substrate were generally entombed in pockets, and red urchins (*S. franciscanus*) were either entombed or inhabited ledges or crevices. Red urchins observed at night generally did not venture from protective habitat. Red and purple urchins outside of protective habitat were preyed on by Sheephead fish (*Semicossyphus pulcher*), and this predator probably curtailed the movement of urchins (pers. obs., Cowen 1983). Also, urchins and abalones, which were also found mainly in crevices and along ledges, were harvested heavily by commercial divers. Sea hares (*Aplysia californica* and *A. vaccaria*) were observed browsing on kelp sporophytes, but were rare and observed only during a 2-month period in 4 years of observation on the study area. *Pugettia producta* (kelp crab) and *Norrisia norrisii* (Norris snail) were common, but found only on kelps during the study. Most of these large invertebrates have demonstrated a feeding preference for *Macrocystis* (Leighton 1966), and the availability of *Macrocystis* and other kelps, particularly as detritus, made it unlikely that these animals substantially affected turf algal assemblages.

The effects of urchins on community structure in subtidal studies, and urchins and other herbivorous invertebrates in intertidal studies, were generally dependent on large numbers of grazers unrestricted in their movements (e.g., Estes et al. 1978, Harrold and Reed 1985, Paine and Vadas 1969, Dayton 1975, Lubchenco 1978, Lubchenco

and Menge 1978, Petraitis 1983). Many of the herbivorous invertebrates in this kelp forest were restricted in their movements or lacked the density necessary to substantially affect structure of turf algal assemblages.

From winter to summer 1984 the retention of surface canopy, decreasing cover of turf algae, and increasing cover of sessile animals were opposite that of previous observations (Chapter 1). A dense canopy of *Macrocystis* and subsequent low illumination appeared to have a substantial effect on experiments that examined herbivory and competition on near-bare plots and established turf assemblages. Any possible effects herbivores might have had on plots created by the experimental removal of *Macrocystis*' holdfasts were abated because of the lack of algal recruitment to those plots. Oceanic and atmospheric conditions were milder than previously observed (from 1980 - 1983) on this San Nicolas Island kelp forest in winter through early summer 1984. These mild weather conditions probably allowed *Macrocystis* to form a dense and persistent canopy. During these seasons, suitable illumination at the substrate is probably important to the recruitment and growth of most species of turf algae (Foster 1975b, Chapter 1). The correlated effects of low illumination caused by the surface canopy on underlying algae have been reported in several studies (e.g., Chapter 1, Reed and Foster 1984, Pearse and Hines 1979). Other possible causes of low turf algal abundance, e.g., herbivory or low nutrient levels in the water column, were not suspected because of the lack of any significant differences between caged and uncaged plots, and the healthy appearance of *Macrocystis*. Little or no recruitment by turf algae and mild oceanic conditions were probably beneficial to recruitment by sessile animals (Chapter 1, Rosenthal et al. 1975). The high percent cover of sessile animals may have in turn delayed recruitment of algae once light increased. These sessile animals, mainly

bryozoa, tunicates and sponges, were similarly abundant on caged and uncaged plots, indicating that predation on these species did not affect their distribution during the study.

Herbivory appeared either directly responsible for or contributed to the low abundance of foliose red algae in turf assemblages. In 1983, *Rhodomenia californica* did not decline substantially in cover on caged plots from summer to winter as observed on uncaged plots (and in the previous study, Chapter 1), indicating that herbivory probably caused much of that decline. Also, cover of *Rhodomenia* was greater on the caged plots compared to the uncaged plots in winter 1984, after the *Macrocystis* canopy was thinned by swell. The recruitment of *Rhodomenia* from stolons indicated that stoloniferous growth may have been an effective means of surviving both physical and biotic adversities. The foliose red algae, *Cryptopleura* spp. were more abundant when protected from herbivory. Epiphytic growth of *Cryptopleura* spp. probably interfered with the growth of *Corallina* on the caged plots and may contribute to causes of low abundance of *Corallina* in this kelp forest (Chapter 1). Herbivory apparently reduced the abundance of *Cryptopleura*, which in turn might be beneficial to *Corallina*.

Fishes were suspected to be the primary herbivores on established turf algal assemblages, because large invertebrates probably had little impact because of reasons discussed above. The diets and habits of fishes were not investigated, but opaleyes and halfmoons were present during all visits to the kelp forest. These fishes were observed feeding on *Ulva* sp., *Gigartina* sp., and minute red algae listed in Figure 1c, e.g., *Pterisiphonia* sp. and *Platythamnion* sp. These algae were common on plots cleared experimentally, and fishes may have caused their low abundance in later successional turf assemblages.

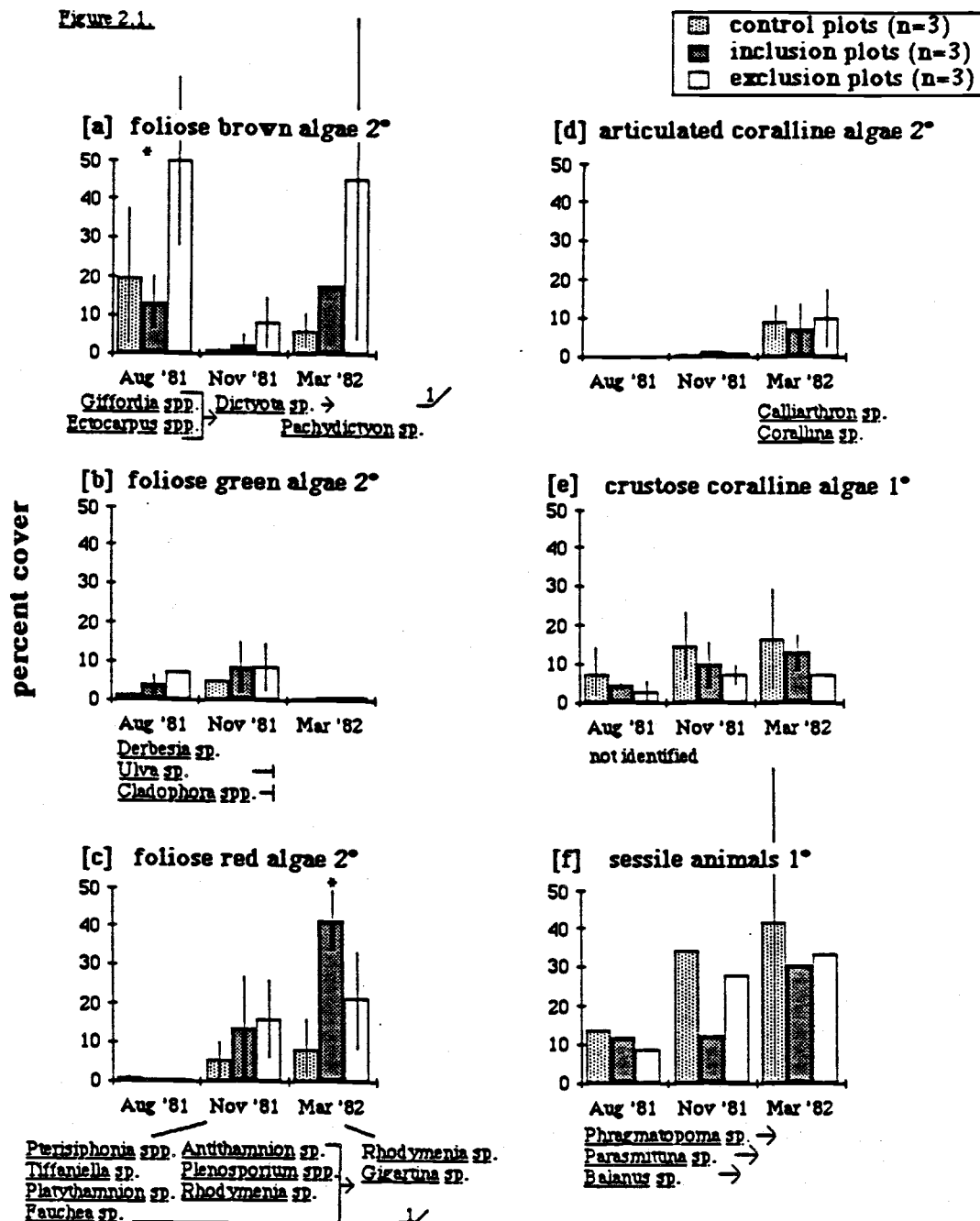
No effect could be attributed to competitive exclusion of other turf algae by *Calliarthron cheilosporioides*. While competitive exclusion by *Calliarthron* was not proved, the persistence of the surface canopy of *Macrocystis* may have resulted in the lower abundance of *Calliarthron* and effectively offset competition by this alga. Previous study provided only subtle indications that low illumination could affect abundance of *Calliarthron* and direct loss of *Calliarthron* occurred from overgrowth by *Macrocystis* (Chapter 1). In the current study, the *Macrocystis* canopy was several layers thick, with no substantial loss of canopy during the winter and spring months. The subsequent prolonged low illumination at the substrate was correlated with severe deterioration of *Calliarthron*.

The structure of this turf assemblages appeared determined predominantly by the interaction of physical disturbance and *Macrocystis*. Herbivory or competition within the turf assemblage were not disproved as major organizing forces, but other events appeared to prevail over these biotic interactions during 1984. Exclusion of light to the substrate by *Macrocystis* was probably the predominant biotic structuring element. The magnitude of the effects of the surface canopy appeared ultimately controlled by the presence or absence of physical disturbance that affected *Macrocystis*.

Figure

- 2.1. Mean percent cover of major groupings of algae and sessile animals forming primary (1°) or secondary (2°) cover on cleared 0.25m² plots in kelp forest study area located off San Nicolas Island, California, from August 1981 to March 1982. Plots were cleared in fenced areas from which *Patiria* were excluded and included, and not manipulated in a third, unfenced area (control). Species consisting of >1 percent cover are listed in descending order of magnitude under date sampled; arrows indicate carryover of species from one sampling date to next, and vertical line indicates species not found in subsequent sampling date. Bars are \pm standard deviation. Bars excluded where SD > mean. * P < 0.05.

Figure 2.1.

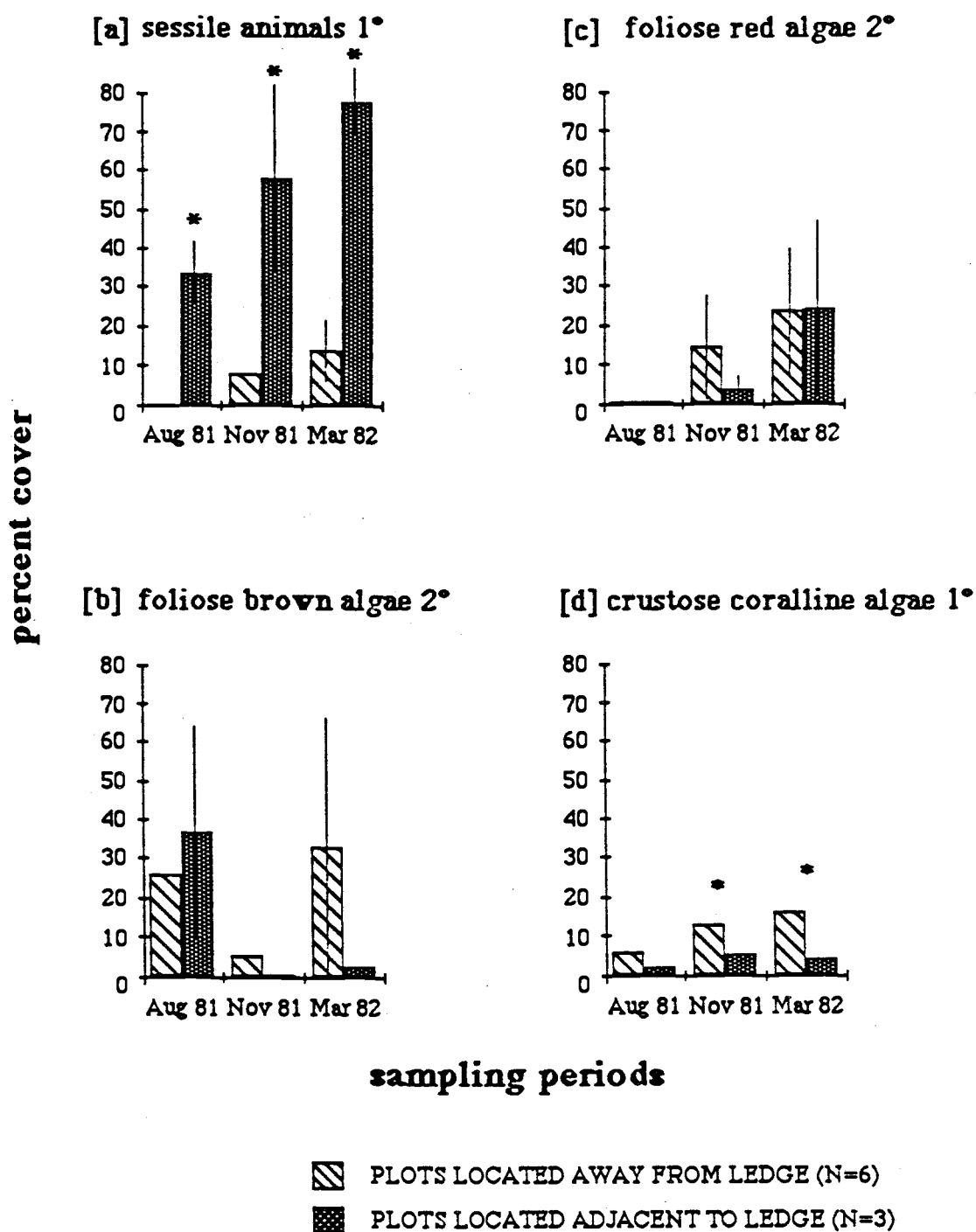


SPECIES THAT HAD A MEAN PERCENT COVER >1 ARE LISTED UNDER DATE SAMPLED, IN DESCENDING ORDER OF ABUNDANCE.

Figure

- 2.2. Mean percent cover of major groupings of sessile animals and algae forming primary (1°) or secondary (2°) cover on cleared 0.25m² plots adjacent to a ledge (N=3), as compared to cleared 0.25m² plots away from ledge (N=6), in kelp forest study area located off San Nicolas Island, California, from August 1981 to March 1982. Common species forming cover are given in Fig. 1. Bars are ± 1 standard deviation. Bars excluded where SD > mean. * P < 0.05.

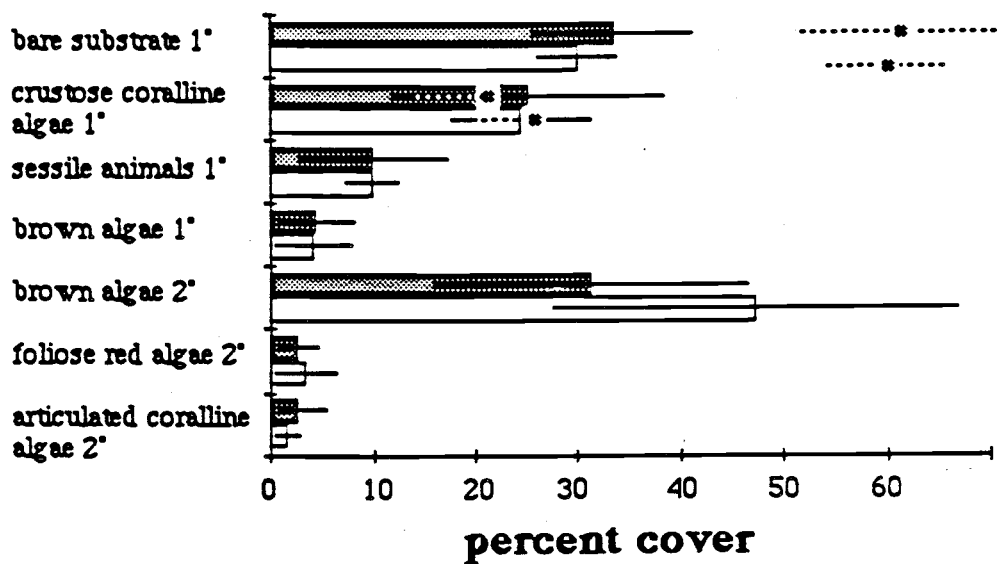
Figure 2.2.



Figure

- 2.3. Mean percent bare substrate and cover of major groupings of sessile animals and algae forming primary (1°) or secondary (2°) cover on near-bare 0.25m² plots 2 months after plots were established. Ten plots were established June 1983, by removal of *Macrocystis*' holdfasts in kelp forest study area located off San Nicolas Island, California. *Patiria* were caged in 5 of these plots and caged out of 5 plots. Not shown is cover of calcified remains. Bars are standard deviation. No significant differences were found within major groupings provided. # indicates means at start of experiment.

Figure 2.3.



■ CAGED PLOTS-PATIRIA INCLUDED (N=5)
 □ CAGED PLOTS-PATIRIA EXCLUDED (N=5)

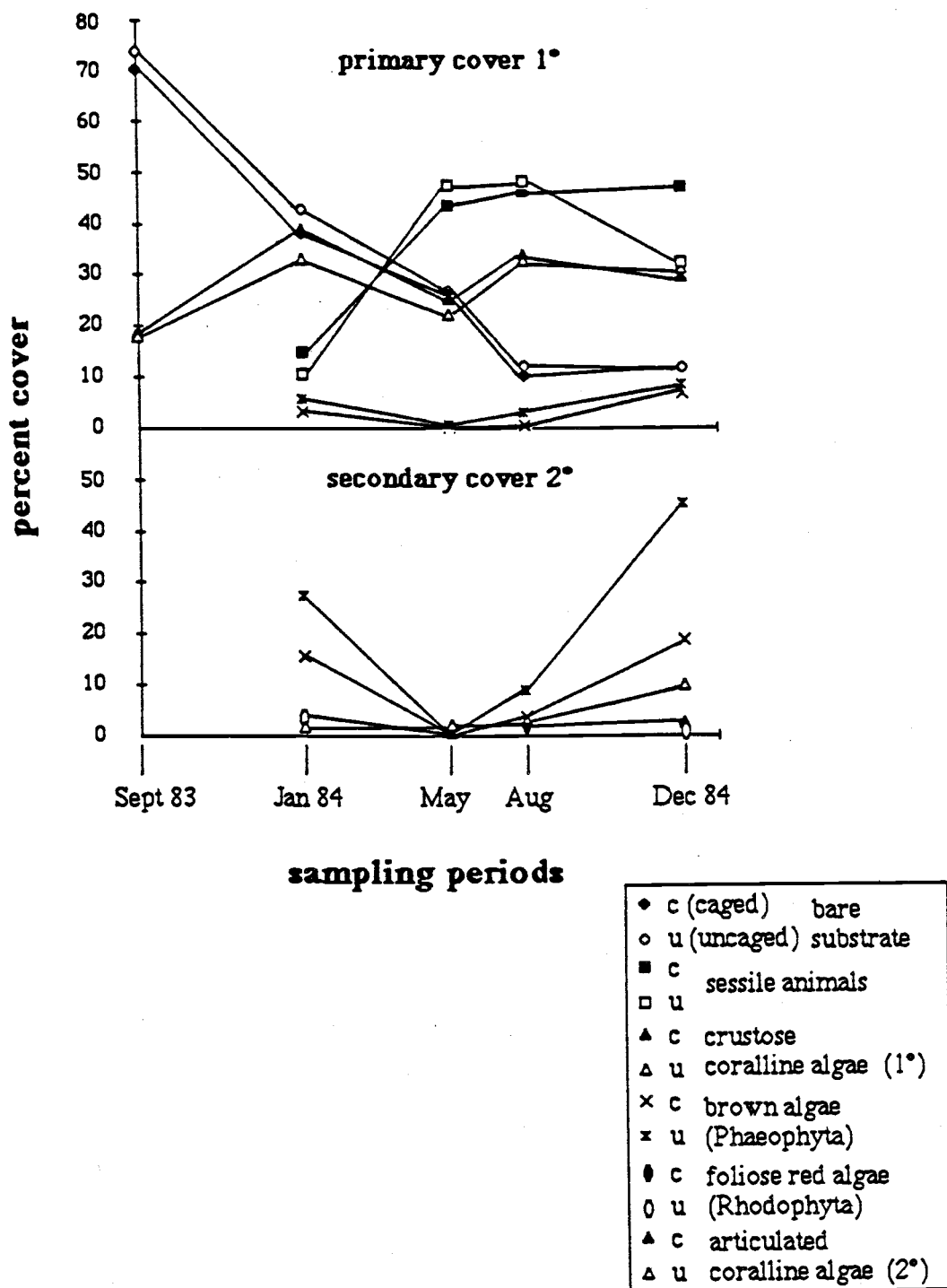
#

measure at start of experiment-June 1983

Figure

- 2.4. Mean percent cover of bare substrate and major groupings of sessile animals and algae forming primary (1°) or secondary (2°) cover on 10 caged and 10 open 0.25m² plots, September 1983 to December 1984. Near-bare plots were established by removal of *Macrocystis*' holdfasts in kelp forest study area located off San Nicolas Island, California.

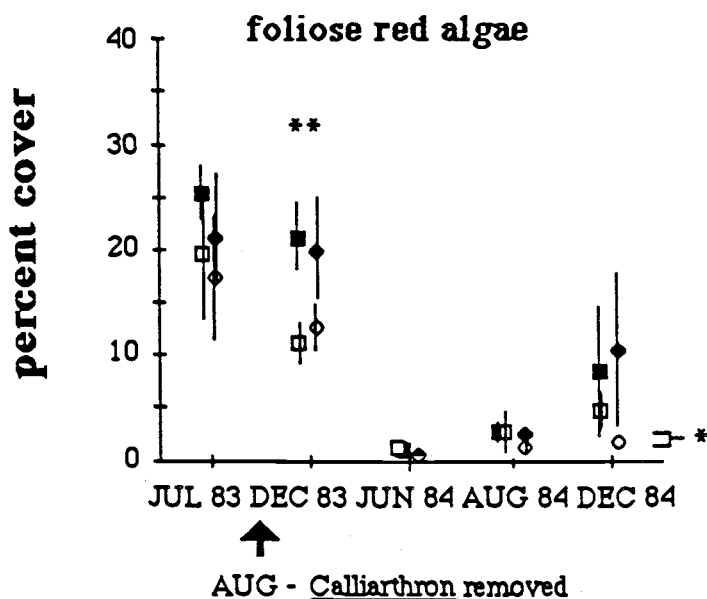
Figure 2.4.



Figure

- 2.5. Mean percent secondary (2°) cover of foliose red algae on 10 caged and 10 open 0.25m² plots in kelp forest study area located off San Nicolas Island, California, July 1983 to December 1984. *Calliarthron* was removed from 5 caged and 5 control plots in September 1983. Species of foliose red algae identified in situ are provided; means for *Rhodomenia* sp. for July and December 1983 may include other species that were not distinguishable in photographic images. Bars are ± 1 standard deviation; bars are excluded when SD > mean. * P < 0.05.

Figure 2.5.



- HERBIVORE EXCLUSION - Calliarthron INTACT (n=5)
- OPEN - Calliarthron INTACT (n=5)
- ◆ HERBIVORE EXCLUSION - Calliarthron REMOVED (n=5)
- OPEN - Calliarthron REMOVED (n=5)

PERCENT COVER OF SPECIES WITH MEAN >1:

<u>date</u>	<u>species</u>	<u>caged \bar{x}</u>	<u>open \bar{x}</u>
Jul 83	<u>Rhodymenia californica</u>	21.78	17.19
Dec 83	<u>R. californica</u>	18.00	11.09
	<u>Cryptopleura spp.</u>	2.30	0.94
Jun 84	-----		
Aug 84	<u>R. californica</u>	2.51	1.87
Dec 84	<u>R. californica</u>	6.72	2.61
	<u>Cryptopleura spp.</u>	2.47	0.01

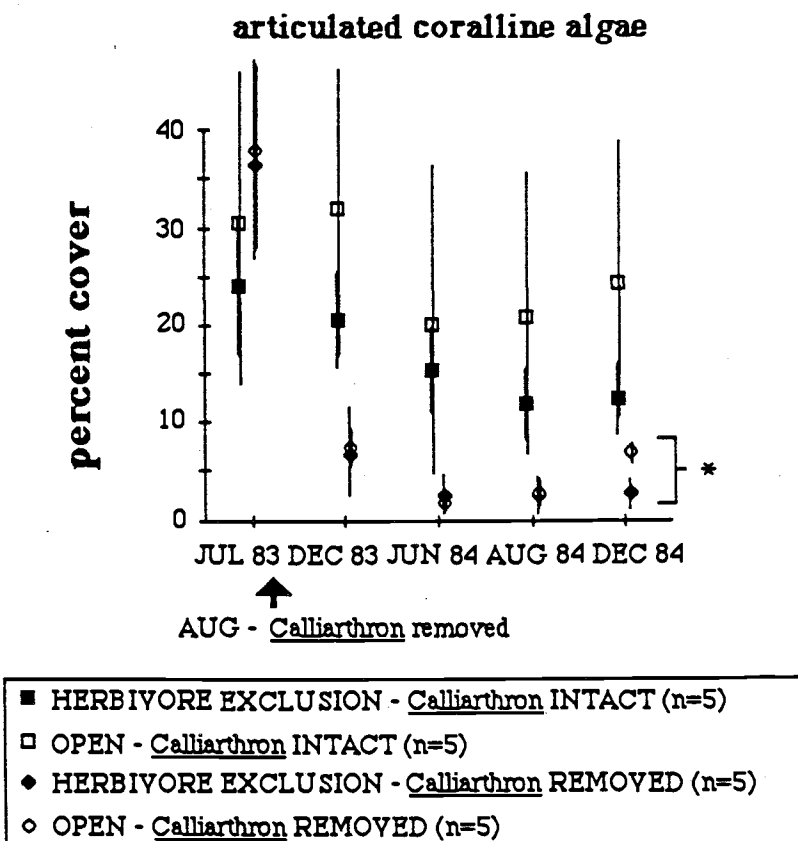
OTHER SPECIES IDENTIFIED:

Gelidium robustum
Plocamium cartilagineum
Botryocladia pseudodichotoma
Fauchea laciniata
Nienburgia andersoniana
Gigartina sp.

Figure

- 2.6. Mean percent secondary (2°) cover of articulated coralline algae on 10 caged and 10 open 0.25m² plots in kelp forest located off San Nicolas Island, California, July 1983 to December 1984. *Calliarthron* was removed from 5 caged and 5 control plots in September 1983. Common species identified are provided, with means of those species of >1 percent mean cover. Bars are \pm 1 standard deviation; bars are excluded when SD > mean. * P < 0.05.

Figure 2.6.



PERCENT COVER OF SPECIES WITH MEAN > 1:

<u>date</u>	<u>species</u>	■ \bar{x}	□ \bar{x}	◆ \bar{x}	◇ \bar{x}
Jul 83	<u>Calliarthron cheilosporioides</u>	20.07	25.22	30.46	31.52
	<u>Corallina officinalis</u> var. <u>chilensis</u>	3.67	5.27	5.81	6.41
Dec 83	<u>C. cheilosporioides</u>	19.75	27.22		
	<u>C. officinalis</u>	0.61	4.74	6.53	7.32
Jun 84	<u>C. cheilosporioides</u>	15.00	18.21		
	<u>C. officinalis</u>	0.08	1.66	2.30	1.52
Aug 84	<u>C. cheilosporioides</u>	11.59	18.79		
	<u>C. officinalis</u>	0.08	1.97	2.53	2.69
Dec 84	<u>C. cheilosporioides</u>	12.20	20.80		
	<u>C. officinalis</u>	0.03	3.39	2.63	6.83

Other species identified:

Calliarthron tuberosum
Bosiella orbigniana
B. californica

not distinguishable from C. cheilosporioides
 in photographic images, but not found > 5
 percent cover in situ

Chapter 3.
Surviving Overgrowth and Patterns of Change in the Turf Assemblage
of a *Macrocystis* Kelp Forest

Abstract

Overgrowth was a common form of competition affecting the turf assemblage (sessile organisms that grew no greater than 40cm in height) of a *Macrocystis* kelp forest located off San Nicolas Island, California. *Macrocystis* was the most conspicuous species that overgrew large areas of the turf assemblage, although overgrowth was observed between different turf organisms. Crustose coralline algae were the prevalent cover found in this turf assemblage, but also appeared to be the most commonly overgrown organisms. To determine if crustose coralline algae could survive overgrowth and thus, explain their prevalence, "artificial holdfasts" were placed on 26 of 31 plots randomly established within the kelp forest. The turf assemblage was sampled at exact points on these plots before the placement of and after removal of the artificial holdfasts at 5, 8 and 12 months.

The originally sampled population of crustose coralline algae declined between 43 and 50 percent on exact points on the covered plots, primarily due to mortality. However, crustose coralline algae recruited to new points while covered, which resulted in a net 10 percent decline in cover of these algae after 12 months of coverage. Overgrowth by sessile animals caused most of the decline in cover of crustose coralline algae on uncovered, control plots. Sessile animals, mostly encrusting bryozoans, declined in cover on the covered plots and increased sharply in cover on the control plots. Bryozoans and sponges recruited while covered, but their recruitment was slight compared to that of crustose coralline algae. Components of arborescent turf algae were able to survive coverage for up to 8 months, and propagate from those components when uncovered. Articulated coralline algae survived coverage better than did foliose

algae.

Changes in cover of sessile organisms represented a dynamic process of overgrowth or mortality, and concurrent recruitment among the turf assemblage. While abundance of some turf organisms appeared to be relatively stable, this study demonstrated continual changes in the distribution of these organisms. The ability of crustose coralline algae to survive and recruit despite coverage by *Macrocystis* and other turf organisms was a plausible explanation for the prevalence of these algae.

Introduction

Overgrowth is a common form of competition among sessile marine organisms (Buss and Jackson 1979). Several different forms of direct interference competition between sessile organisms have been grouped under overgrowth, e.g., allelopathy and shading (Jackson and Buss 1975, Stimson 1985, Sebens 1986), but direct physical smothering is probably the more familiar form known (e.g., Rutzler 1970, Dayton 1971, Stebbing 1972, Connell 1976, Karlson 1978, Woodin and Jackson 1979, Russ 1982). Patterns of overgrowth seem to follow hierarchies of dominant species that can consistently overgrow subordinate species (e.g., Connell 1961, Dayton 1971, Paine 1974, Menge 1976, Osman 1977, Quinn 1982, Sebens 1986); the waxing and waning of species in an interplay of competitive networks or loops (Buss and Jackson 1979), or species being overgrown by species they had in turn overgrown (reversals) (Jackson 1979, Russ 1982).

A common assessment from studies of overgrowth is that larger species are usually more successful in overgrowing smaller species. Smaller species must possess strategies that further their survival and persistence in the presence of larger species. These strategies may incorporate opportunistic and rapid recruitment, rapid growth, short life span, or wide dispersal of propagules that can survive long periods until conditions improve for development, i.e., some variation of a theoretical *r* - selected species (MacArthur and Wilson 1967). Strategies may also include use of refuges from predators that are temporally or spatially more accessible to smaller species than to larger ones (e.g., Lubchenco and Menge 1981). Also, smaller species may be more resistant to moderate levels of physical or biotic disturbances than larger, dominant

species (e.g., Connell 1971, Hay 1981, Lubchenco 1978, Lubchenco and Menge 1978, Lubchenco and Cubitt 1980, Menge 1983).

In the competitive hierarchies of marine communities found on rocky substrate, large, fast-growing arborescent algae tend to be the better competitors, followed by thick, fast-growing sessile animals, followed by thick, slow-growing sessile animals (Dayton 1975b, Buss 1980, Quinn 1982, Russ 1982). Thin, encrusting organisms are considered the more subordinate species in these hierarchies. Competition theory assumes that subordinate species are killed, damaged or substantially inhibited developmentally by dominant species (Birch 1957). Overgrowth by direct, physical smothering would seem to provide unrefutable support of this assumption. Some sponges and crustose coralline algae have been known to survive overgrowth, but the effects of overgrowth on their development or recruitment are not well-known (Rutzler 1970, Sara 1970, Kay and Keough 1981, Sebens 1986).

Thin, smooth, crustose coralline algae (Rhodophyta, Cryptonemiales) were the predominant cover in the turf assemblage of a *Macrocystis pyrifera* kelp forest studied from 1980 to 1984 off San Nicolas Island, California (Chapter 1). Turf was defined as sessile organisms that pave the substrate (primary cover) or grow to <40cm in height in the adult form (secondary cover). Crustose coralline algae were commonly overgrown by most sessile organisms observed in the kelp forest. Crustose coralline algae formed 17.40 mean percent cover (s.d. = 5.37) before, and 31.93 mean percent cover (s.d. = 7.09) after the upper layer of organisms on 16 0.25m² plots were removed. Most of this additional cover of crustose coralline algae was found under other sessile organisms, or under a shallow layer of sand in the pocketed sandstone substrate.

From the aspect of size alone, the spread of *Macrocystis*' holdfasts was the most

obvious form of overgrowth that affected the turf assemblage in this kelp forest off San Nicolas Island. The presence of near-bare patches that approximated the dimensions of holdfasts of *Macrocystis* was further evidence of the effects on the turf assemblage. The substrate in these patches was occupied primarily by crustose coralline algae, but it was unclear whether these algae had colonized these open patches more rapidly than other organisms or propagated clonally from algae that had survived under or near the holdfast.

The purpose of this study was to investigate the effects of different intervals of coverage on turf species or groups of species by using artificial holdfasts, and to examine changes in cover of these species after coverage was terminated. I asked if the prevalence of crustose coralline algae was due to their ability to survive overgrowth or their ability to occupy open substrate rapidly after coverage was ended.

Methods

The kelp forest was accessed using SCUBA. In December 1983, 35 43cm x 43cm plots were randomly established along a line that transected the kelp forest. The plots were established on relatively flat substrate, and crevices, boulders, and large holdfasts of kelps were avoided. I also avoided establishing plots on substrate lacking arborescent organisms, which might indicate recent disturbance to that substrate. Holes were drilled into the corner of each plot and threaded brass rods epoxied into those holes. Exact points within a 0.125m^2 (35.35cm x 35.35cm) area of the plots were systematically sampled using a grid that fit exactly over the four rods. The grid had 49 crosshairs, and species found under the crosshairs were identified and tabulated. Sand

>2cm deep was not removed to identify what was beneath it. After the 35 plots were sampled, 5 plots were randomly chosen as controls, and "artificial holdfast" plates were placed on 26 plots (4 plots were excluded because they were damaged or could not be relocated). The plates consisted of a 42cm x 42cm pad of reinforced foam rubber 5cm thick, backed by a 43cm x 43cm sheet of galvanized steel. The foam pad was similar in texture to a *Macrocystis* holdfast and partially adapted to the contour of the substrate. The foam pads were larger than 0.125m^2 to compensate for compression from water pressure. The plates fit over the threaded rods and were firmly bolted down on the plots. Ten randomly selected plates were removed at 5 months (May) and the plots sampled in May, August and December 1984; 10 more were removed at 8 months (August) and sampled in August and December 1984, and the final 6 were removed and sampled at 12 months (December 1984).

Several assumptions based on observations and other studies of overgrowth were made when sampling the plots. An organism at a given point that was replaced by a thicker organism at a later sampling interval was presumed to be overgrown; if replaced by a thinner organism it was presumed to have died or abandoned that point. In either case, the organism was identified as replaced. An organisms at a given point that was covered by sand or another organism and then reappeared at that point was presumed to have survived that coverage. When bare space or calcified remains occurred at a given point formerly occupied by an organism, mortality was assumed. Organisms were identified as recruits when they appeared at points that were formerly bare, contained calcified remains or other organisms. Organisms that were unaffected by overgrowth by other turf organisms, mainly *Serpulorbis* sp. (sessile tube-snail) in this kelp forest, were treated as substrate when other organisms were sampled on them. Organisms

were identified to species or the lowest taxonomic category possible in situ, and then grouped into higher taxonomic units for comparisons. Percent cover was derived by dividing the count of a species or species-group by the total number of points sampled for a given treatment. Changes over time in percent cover were derived from counts of organisms forming primary cover on exact points on the plots. Changes in percent cover of arborescent algae were approximate because of variable positioning of fronds over the substrate. Proportionate changes in cover of higher taxonomic units from when first sampled in December 1983 to when the plates were removed were compared between treatments using a chi-square variance test for the homogeneity of the binomial distribution (Snedecor and Cochran 1973, pgs. 240 - 242), because exact points were sampled on the plots. By using this sampling method, it was possible to observe changes in both abundance and distribution of different turf species.

In order to provide an index of the quantity of turf assemblage affected by of *Macrocystis* ' holdfasts, *Macrocystis* were counted and tagged on a 10m x 10m site periodically from 1980 to 1984. Counts and measurements were done when time permitted from other planned investigations of the turf assemblage and there was no planned schedule of collecting this information. The diameter of holdfasts of 50 randomly selected *Macrocystis* were measured 5 times during this time period, except for July 1980 when only 10 plants were measured. An estimate of substrate covered by *Macrocystis*' holdfasts was calculated by multiplying the mean area covered times the number of plants on the site.

Results

Percent cover of crustose coralline algae on the treated and control plots was not significantly different prior to treatment ($P>0.05$). These measures were similar to the estimate of cover of crustose coralline algae based on 100 random points sampled on 8 0.25m^2 plots in December 1983 (Fig.1a). The change in cover of the originally sampled population of crustose coralline algae was not significantly ($P>0.05$) different on the treatment plots covered for 5, 8, and 12 months, but there was a significant ($P<0.05$) difference in the total populations of crustose coralline algae found (Fig.1b-d). The originally sampled populations declined from 43 - 50 percent on all treatments (Fig.1b-d). In comparison, the decline in the total population of crustose coralline algae covered for 8 months (26%) was greater than that found on the plots covered for 5 months (14%), but the decline that occurred on the plots covered for 12 months (10%) was less than the plots covered for 5 and 8 months.

The change in cover of crustose coralline algae on the control plots was similar to changes that occurred on the treatment plots, but the cause of these changes was different. Crustose coralline algae on control plots appeared to decrease primarily because of overgrowth by sessile animals, but concurrently, crustose coralline algae re-emerged at points where they had previously been overgrown by sessile animals. Increasing or decreasing sand cover accounted for less than 5 percent of the changes in percent cover of crustose coralline algae on the control plots. Mortality was lower on the control plots compared to the treatment plots (Fig.1a-d).

Mortality accounted for the major proportion of decline in crustose coralline algae on the treatment plots, and mortality increased with duration of the treatments (Fig. 1b-d). White, flaking remains of crustose coralline algae were identified as dead. When uncovered, other crustose coralline algae were lighter in color, particularly those

identified from the original population. After the plates were removed at 5 and 8 months, the return of darker coloration to those algae indicated that the light color did not signify mortality.

While mortality was greater on the treatments plots than the control plots, comparisons of the original and total populations of crustose coralline algae implied that some algae survived and recruited under the plates (Fig.1b-d). Crustose coralline algae had ample substrate on which to recruit, probably because of the mortality of other turf organisms, although some turf organisms also survived under the plates. The amount of sand found on the treatment and controls in December 1983 was not significantly different ($P>0.05$), but a buildup of sand occurred on the treatment plots while the plates were in place. Therefore, changes in cover of crustose coralline algae were affected more by changes in sand cover on the treatment plots than control plots following removal of the plates (Fig.1a-d).

Plots uncovered after 5 months increased in total cover of crustose coralline algae between May and August, but continued to decline on the control plots (Fig.1a,b). Increases in cover of crustose coralline algae after the plates were removed reflected the greater availability of bare substrate or calcified remains of turf organisms compared to the control plots. From August to December 1984, cover of the total population of crustose coralline algae increased on previously covered and control plots (Fig.1a-c); the increase was greater on the treatment plots compared to the control plots. Crustose coralline algae on the control plots probably had to compete for space with established sessile animal populations. More bare or calcified substrate was available on the treatment plots for recruitment by both sessile animals and crustose coralline algae.

Most changes in cover of crustose coralline algae due to overgrowing or receding

sessile animals were caused by colonial, encrusting bryozoans (mainly *Membranipora* sp. and *Parasmittina* sp.). Cover of encrusting bryozoans were significantly ($P < 0.05$) different on treatment and controls plots prior to treatment, which implied more variable distribution than crustose coralline algae. Cover of encrusting bryozoans increased 358 percent on the control plots from December 1983 to May 1984 (Fig.2a). About one-third of those bryozoans recruited on crustose coralline algae and half recruited on bare or calcified substrate. The remaining bryozoans overgrew other sessile animals, which were mainly different species of bryozoans, and a fleshy crustose red algae that was uncommon on the study area. Mortality and decreases due to replacement equally affected encrusting bryozoans on the control plots by May 1984. Although mortality declined in August and December 1984, decreases due to replacement probably represented mortality; replacement was by crustose coralline algae that probably had survived overgrowth by encrusting bryozoans (Fig.2a). Encrusting bryozoans not replaced by crustose algae were overgrown by other sessile animals. Two-thirds and about one-quarter of the encrusting bryozoans lost in August 1984 and December 1984, respectively, were overgrown by other sessile animals. Encrusting bryozoans appeared unable to survive overgrowth by other turf organisms.

Changes in the cover of encrusting bryozoans on the treatment plots were very different from those changes that occurred on the control plots (Fig.2b-d). Covering encrusting bryozoans apparently killed many bryozoans: calcified remains or bare substrate were present where bryozoans had occurred or encrusting bryozoans were replaced by crustose coralline algae. When the plates were removed, the decline in cover of the originally sampled population of encrusting bryozoans were significantly ($P < 0.05$) different (88%, 89%, 100%), but the total populations sampled were not

significantly ($P>0.05$) different (72%, 61%, 71%; Fig.2b-d). Smaller declines in the total population indicated that recruitment of encrusting bryozoans continued after the plates were in place. Bryozoans appeared to recruit into pockets in the substrate, but did not survive direct contact with the foam pads. Mortality increased the longer the plates were in place and was probably greater than inferred, as one-quarter to more than one-half of encrusting bryozoans were replaced by crustose coralline algae. Plots uncovered after 5 months (May) and sampled in August 1984 indicated that sand covered a large proportion of encrusting bryozoans, and they might have survived coverage by sand. Although this supports observations, the original occupants of those points might also have died and been replaced by other recruiting bryozoans.

Recruitment of encrusting bryozoans was rapid after the plots were uncovered (Fig.2b,c). Similar to the control plots, more than one-third (uncovered in August and sampled in December) to almost one-half (uncovered in May and sampled in August) of that recruitment happened on crustose coralline algae.

Cover of sponges and tunicates was low on the control and treatment plots (Fig.3a,b) as compared to encrusting bryozoans. The originally sampled population of sponges declined by 57% on the plots covered for 5 or 8 months and 93% on the plots covered for 12 months. However, the total population of sponges increased on the plots covered for 5 months, were nearly unchanged on the plots covered for 8 months, and declined by 53% on the plots covered for 12 months (Fig.3b). The total population of sponges on the control plots essentially did not change until after August 1984.

Therefore, the greater total population of sponges occurred because of better recruitment under the plates than on the controls, but mortality of the originally sampled population was high after 12 months of coverage. As with bryozoans, mortality of sponges usually

occurred at points of contact with the foam pad. Sponges recruited into the pockets of the substrate and were in good condition when the plates were removed. A small percentage of tunicates did survive and recruit under the plates covered for 5 months, but no recruitment or survival of tunicates was found under the plates after 8 and 12 months (Fig.3c).

With the exception of *Serpulorbis* sp. (sessile tube snail) and holdfasts of arborescent turf algae, other groups of organisms directly covering substrate were not abundant. These included anenomes, sedentary or burrowing holothuroids, serpulids, and molluscs, some of which were capable of escaping encroaching holdfasts. Changes in cover of *Serpulorbis* ranged from 9 to 12% on the control plots (Fig.3d). The lower measures occurred in May and August 1984, when overgrowth by other sessile organisms was common. This overgrowth probably had no harmful effect on *Serpulorbis*. The shells of *Serpulorbis* were bleached white on the treatment plots when uncovered, but the animals usually were not dead. Individual *Serpulorbis* can form an extensive (up to 125mm) calcified tube but occupy a small section of the tube. Live *Serpulorbis* were found in bleached tubes under *Macrocystis*' holdfasts that were probably several years old (Chapter 2). The death of organisms overgrowing *Serpulorbis* accounted for the greater measures of *Serpulorbis* when the plates were removed after 5 and 8 months, but there were also new recruits of *Serpulorbis* found under the plates.

Cover of holdfasts of arborescent turf algae declined on the control plots from December 1983 to May 1984 (Fig.3e). Overgrowth of these holdfasts by sessile animals, which was unlikely harmful to the rest of the plants, accounted for two-thirds of that decline; the remaining one-third of these holdfasts were dead. The changes in

percent cover of these holdfasts that occurred by August represented a process of overgrowth (one-fifth), re-exposure after overgrowth (two-fifths), and recruitment to new points (two-fifths). Similar changes were observed by December 1984. On the treatment plots, percent cover of these holdfasts declined slightly after 5 months of coverage, and substantially after 8 and 12 months of coverage (Fig.3e). The holdfasts sampled when the plates were removed were all of articulated coralline algae that were bleached in color. Return of color to these holdfasts at subsequent sampling dates (August and December) indicated that these plants were still viable after 5 and 8 months of coverage. Stolons of *Rhodomenia sp.* were found on the treatment plots after 5 and 8 months of coverage, but not after 12 months of coverage.

Cover of the upright components of arborescent turf algae declined on both control and treatment plots (Fig.4a,d). On the control plots, the fronds of articulated coralline algae were bleached and sloughing by May 1984, probably because of very low illumination at the substrate. The surface canopy of *Macrocystis* was dense throughout winter and spring 1984 (Chapter 2). From August to December 1984 the surface canopy thinned, and algae increased on previously covered and control plots, probably in response to increased illumination at the substrate.

The decline in cover of articulated coralline algae on the treatment plots covered for 5 and 8 months (70% and 75%, respectively) was not significantly ($P>0.05$) different, but the decline in cover after 12 months (97%) was significantly ($P<0.05$) greater than those declines. After the plots were uncovered at 5 and 8 months, cover of articulated coralline algae increased on those plots, and were found in the approximate area where sampled in December 1983. This increase in cover appeared due to regeneration of plants identified in December 1983 more than recruitment of new individuals.

Articulated coralline algae found under the plates after 5 and 8 months were bleached and deteriorating, but more fronds were intact on these plants than on the control plots. This implied that water motion might have removed deteriorating fronds on the control plots, whereas the fronds were held in place on the treated plots.

Cover of foliose red algae declined 80% on the control plots by May, and declined 91% on the treated plots after 5 months (May)(Fig. 4d). Cover of foliose red algae was less than 1 percent on the plots after 8 months, and no foliose red algae were sampled or found on the plots covered for 12 months. Stolons of *Rhodomenia sp.* were found on the plots uncovered after 5 and 8 months, and some of the recruitment of foliose red algae that occurred on these plots following the removal of the plates propagated from these stolons. Deteriorated remnants of *Gelidium sp.* were also found on plots covered for 5 months, and recruitment of *Gelidium* occurred at or near these remnants.

High recruitment and loss of *Macrocystis* occurred on the study area from 1980 through 1984 (Fig. 5). High-water motion during winter storms and summer swell accounted for most losses of surface-reaching *Macrocystis*. The formation of a dense canopy of *Macrocystis* during the mild winter through summer 1984 either inhibited recruitment of *Macrocystis* (Chapter 2) or resulted in high mortality of existing recruits that did not reach surface canopy by summer and fall (Chapter 1). The conditions of dense canopy and mild oceanic conditions appeared to facilitate recruitment by sessile animals, while inhibiting recruitment or growth of turf algae. An estimated 6 to 12 percent of the substrate on the 10m x 10m site was covered by holdfasts of *Macrocystis* (Fig.5). This cover was not directly related to the number of plants on the site because only a few large plants could occupy an area which could support many smaller plants.

Discussion

Crustose coralline algae are competitively subordinate but form the dominant cover on rocky substrate in many marine communities (Adey 1969, Adey and Vasser 1975, Steneck 1983). Their prevalence has been attributed to resistance to biotic or physical disturbance (Bakus 1966, Paine and Vadas 1969, Adey and Vasser 1975, Lawrence 1975, Vadas 1977, Menge and Lubchenco 1981, Steneck 1983). Moreover, herbivory on epiphytic algae that can grow on crustose coralline algae, has been suggested as necessary to the survival of crustose coralline algae (Paine and Vadas 1969, Adey and Macintyre 1973, Steneck 1983).

This study showed that crustose coralline algae have yet other mechanisms for survival and dominance in marine systems where overgrowth by other sessile organisms is common. Crustose coralline algae not only survived but recruited new individuals after total coverage for periods up to 12 months, substantially beyond the time interval of survival suggested by Sebens (1986). Further, in previous study, viable crustose coralline algae were found under large *Macrocystis* holdfasts (Chapter 2). The size of these holdfasts, most of which were approximately 50cm in diameter, indicated that these *Macrocystis* were probably several years old. Sebens (1986) suggested that certain crustose algae covered by sessile animals might obtain nutrients from animal waste products, but this does not explain how crustose coralline algae under the plates obtained photosynthates. Acquisition of photosynthates for survival and recruitment under the plates might have occurred from lateral translocation through the thallus from connecting crusts that were exposed to light (see Wetherbee 1979). The moderately fast occupation (relative to other sessile organisms in the kelp forest) of substrate by

crustose coralline algae in this and previous study (Chapter 1,2) implied faster growth of these algae than suggested from other studies (Adey 1970, Adey and Vasser 1975). These findings were not viewed as contrary to researchers that suggest that predation on overgrowing organisms is necessary to the survival of crustose coralline algae or to growth-rate studies. But rather, these findings indicate a substantial gap in our understanding of the biology of different species of crustose coralline algae and the effects of different physical environments on their biology.

The survival and regeneration of arborescent turf algae from holdfasts and stolons provided insight into strategies that turf organisms may possess under conditions of low illumination and overgrowth. Turf algae found within established kelp forests probably have to endure extended periods of low illumination, with occasional greater illumination associated with disturbance and loss of the surface canopy. Survival of turf algae under the plates demonstrated that some component of the plants can survive at least 8 months with no light and subsequently regenerate. Similar strategies for survival have been suggested for algae exposed to periodically severe herbivory (Lubchenco and Gaines (1981). Further, the physical force or pressure of being overgrown as mimicked by the plates was not enough to kill all arborescent algae by 8 months. If turf organisms are not removed when *Macrocystis* holdfast are dislodged by physical disturbance, then these results indicate that certain algae and sessile animals can survive relatively long intervals of coverage.

The encrusting turf species sampled on the control plots in this study were a dynamic assemblage with organisms being recruited on bare substrate or overgrown by other organisms. Other increases in cover occurred at points where organisms were overgrown and survived after the overgrowing species disappeared. Concurrently,

other organisms were overgrown, covered by >2cm of sand or were absent and presumed dead at specific points on the plots. Although a dynamic process in changes in distribution of species, these effects could be mutually exclusive and result in relatively constant cover or abundance of sessile organisms within a small area over time. This was substantiated by random sampling on undisturbed plots from 1980 through 1981 which indicated a relatively constant percent cover of crustose organisms over time (Chapter 1). The result of the dynamic process among turf organisms was therefore negligible when compared to the pervasive effects of overgrowth by *Macrocystis*' holdfasts. Counts and measures of *Macrocystis* implied that the area (6 - 12%) of turf assemblage affected by overgrowth was not substantially large. But, the effects of overgrowth by *Macrocystis* were probably a continual process in this San Nicolas Island kelp forest. Additionally, dislodged *Macrocystis* plants can drag across the substrate, or entangle with other *Macrocystis* plants and cause their dislodgement (Rosenthal et al. 1974). The resulting mass of holdfasts can scour the substrate and causes further damage to turf assemblages (pers. obs.).

Previous investigations of this San Nicolas Island kelp forest showed that changes in cover of turf species appeared mainly correlated with illumination at the substrate (Chapter 1, 2). Differences in illumination could favor sessile animals or turf algae in the turf assemblage. Further, caging experiments showed that herbivores could affect the abundance and distribution of foliose algae (Chapter 2). Smaller but more encompassing effects on the turf assemblage that could be caused by *Macrocystis* holdfasts were demonstrated in this study. The effects of overgrowth by *Macrocystis* on the turf assemblage contributed to the prevalence of crustose coralline algae. Also, other biotic and physical forces, e.g., predation and coverage by sand, probably

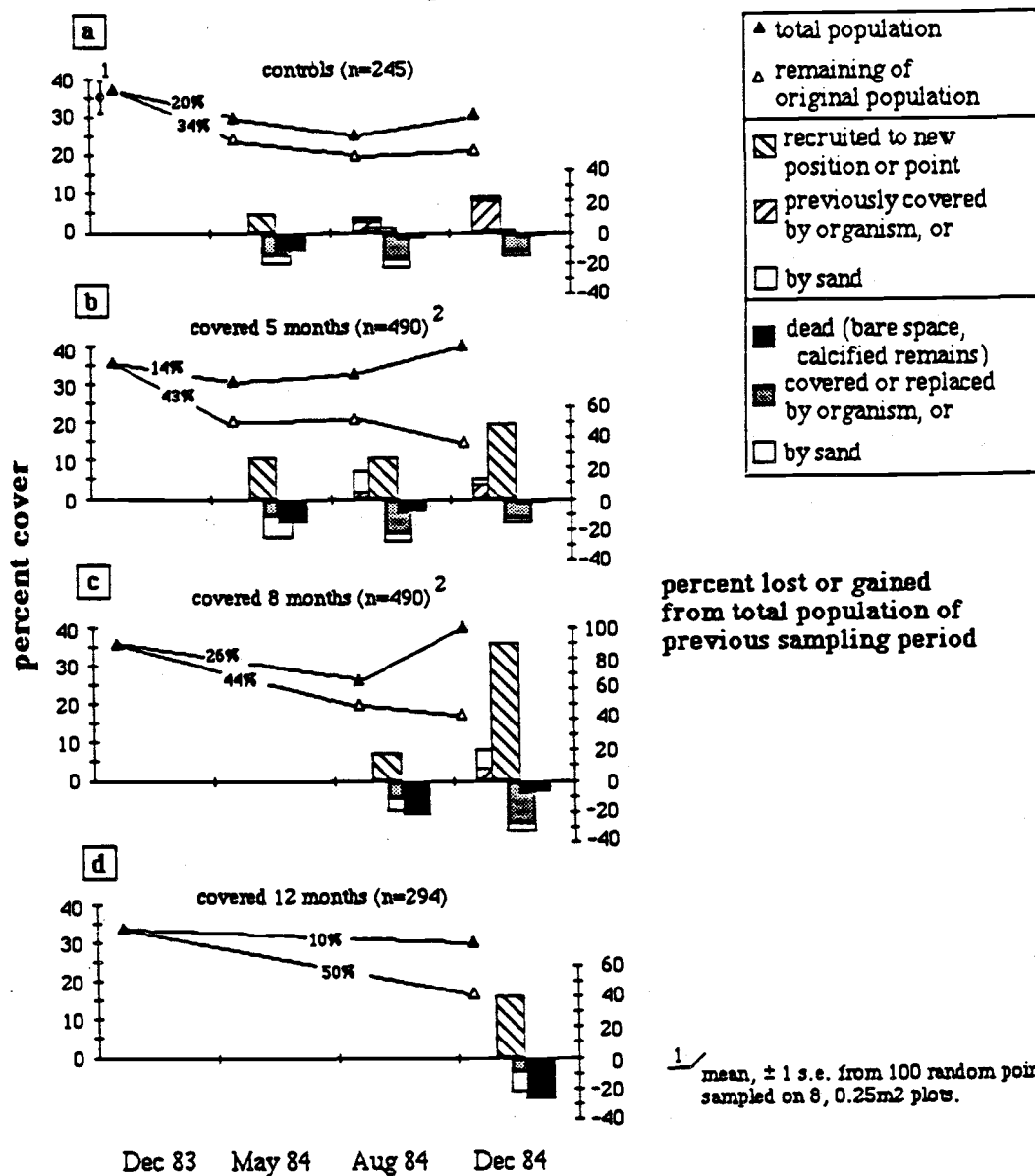
affected other sessile organisms more than crustose coralline algae. Consistently in these studies, crustose coralline algae persisted as the most abundant organisms of the turf assemblage.

Figure

- 3.1. Percent cover of crustose coralline algae sampled at exact points on 0.125m² plots from December 1983 to December 1984, in a *Macrocystis* kelp forest, San Nicolas Island, California. Plots were either controls or covered for 5, 8 and 12 months. Shown are the percent change from first to second sampling period, and percent of those individuals that recruited or disappeared because of mortality, overgrowth, or burial by sand.

Figure 3.1

Crustose Coralline Algae

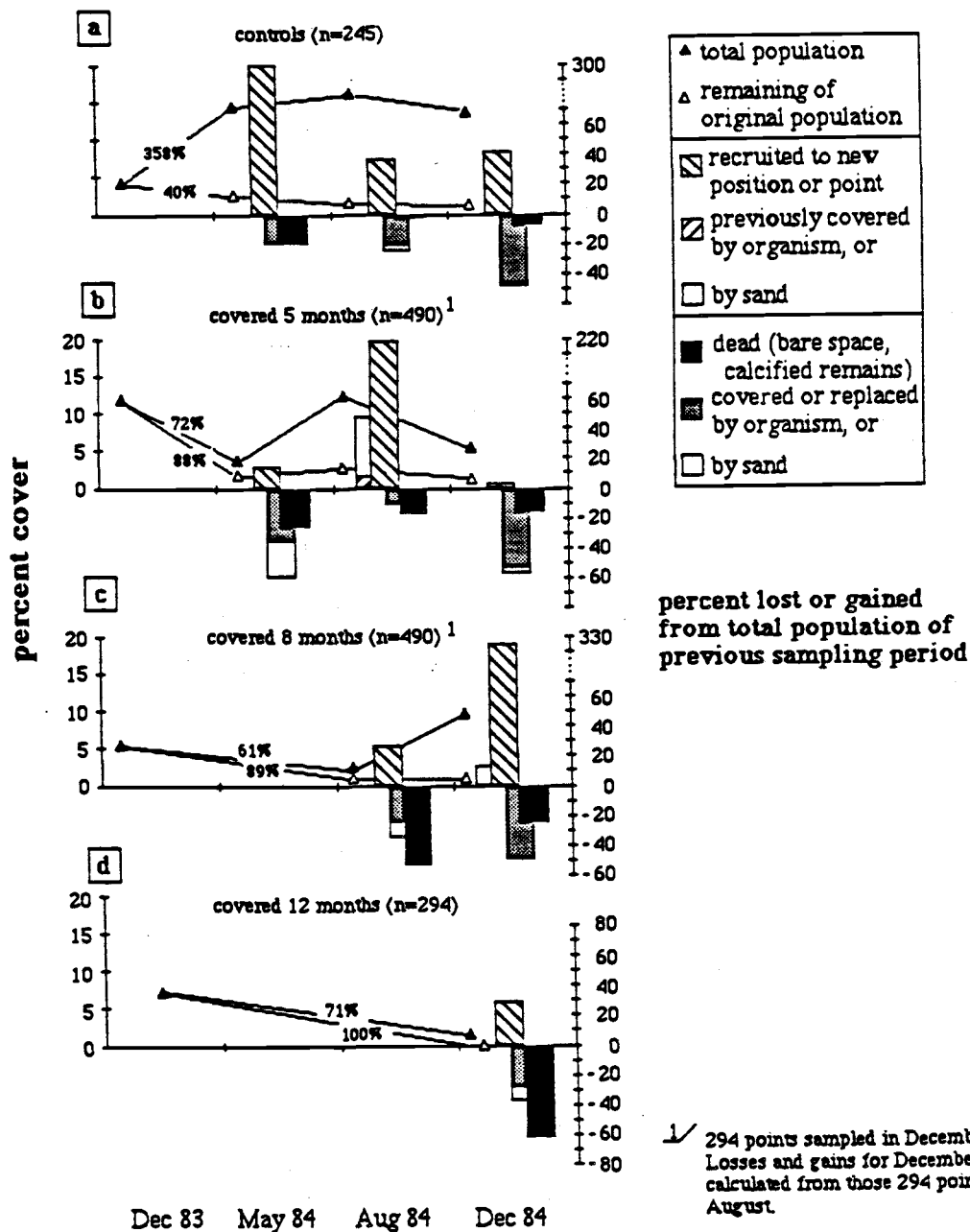


Figure

- 3.2. Percent cover of encrusting bryozoans sampled at exact points on 0.125m^2 plots from December 1983 to December 1984, in a *Macrocystis* kelp forest, San Nicolas Island, California. Plots were either controls or covered for 5, 8 and 12 months. Shown are the percent change from first to second sampling period, and percent of those individuals that recruited or disappeared because of mortality, overgrowth, or burial by sand.

Figure 3.2.

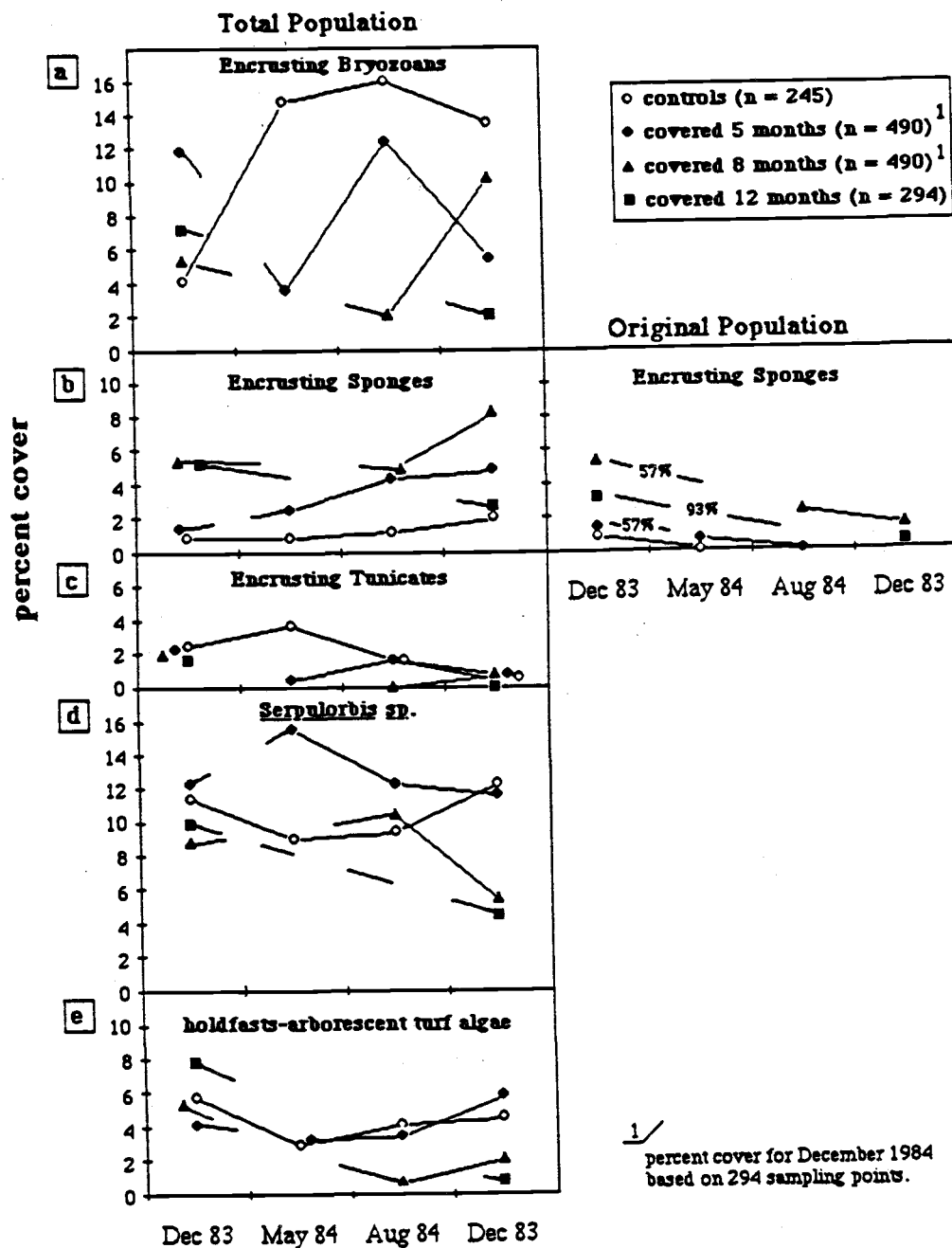
Encrusting Bryozoans



Figure

- 3.3. Percent cover of the common organisms that encrusted or paved the substrate at exact points on 0.125m^2 plots from December 1983 to December 1984, in a *Macrocystis* kelp forest, San Nicolas Island, California. Plots were either controls or covered for 5, 8 and 12 months. Shown are the percent changes from first to second sampling period.

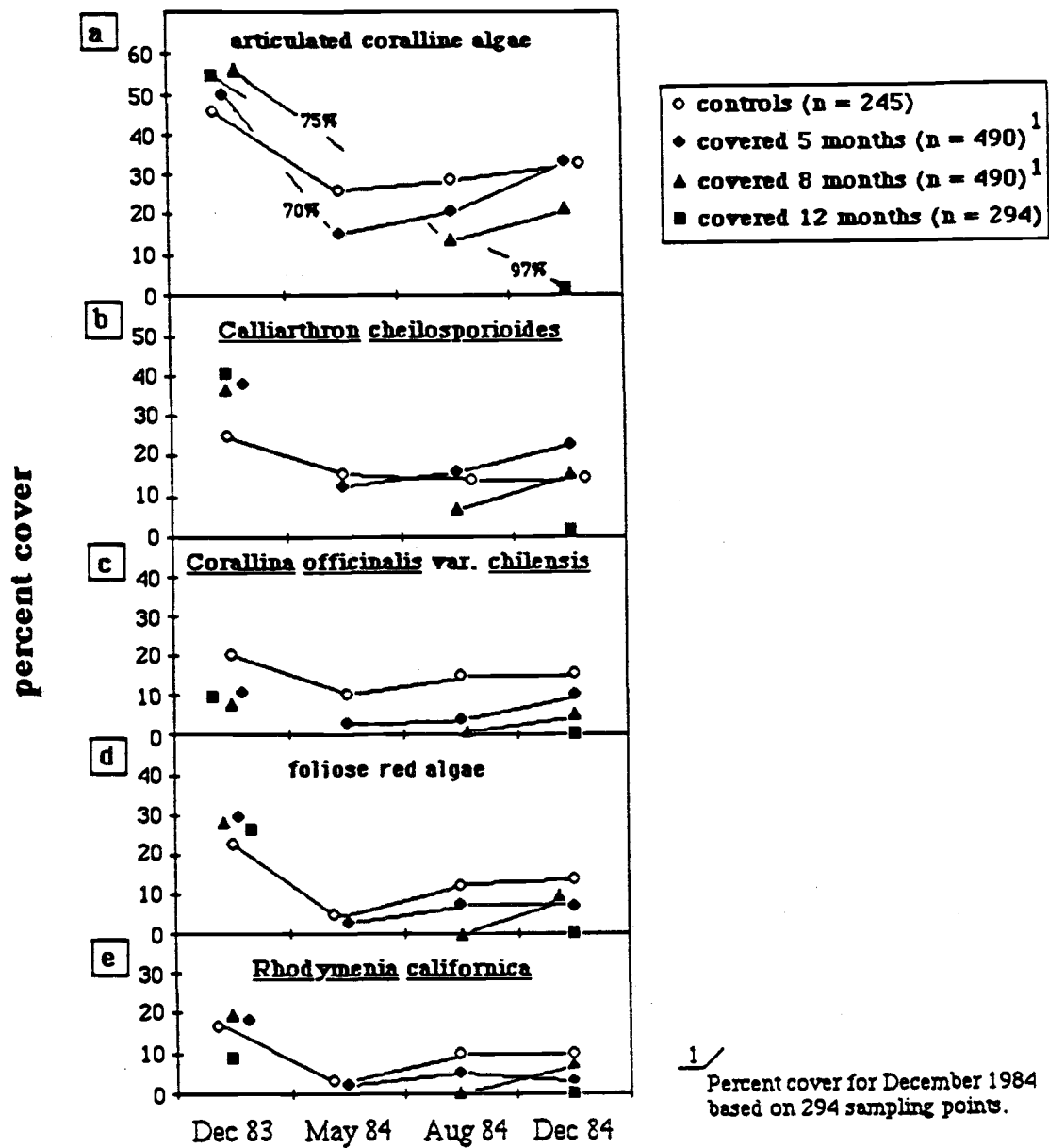
Figure 3.3.



Figure

- 3.4. Percent cover of the common turf algae that grew arborescently on 0.125m^2 plots from December 1983 to December 1984, in a *Macrocystis* kelp forest, San Nicolas Island, California. Plots were either controls or covered for 5, 8 and 12 months. Shown are the percent changes from first to second sampling period.

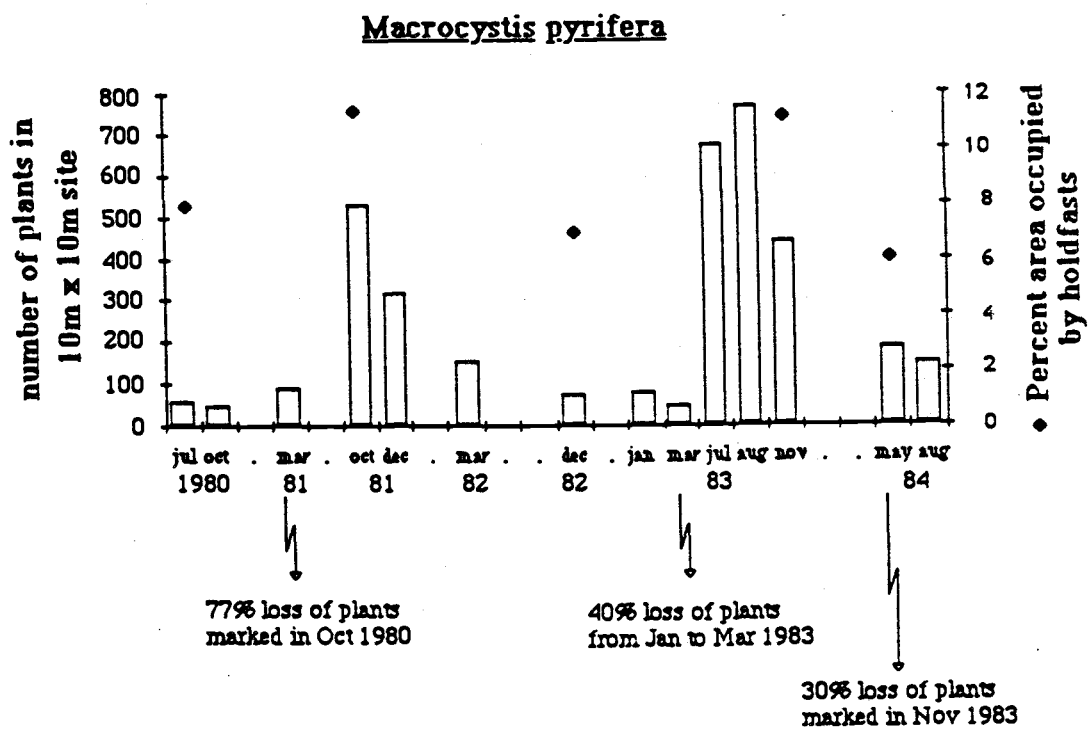
Figure 3.4



Figure

- 3.5. Number of *Macrocystis* counted periodically from 1980 to 1984 on a 10m x 10m site within a *Macrocystis* kelp forest, San Nicolas Island, California. The holdfasts of 50 randomly selected plants were measured on 5 occasions between 1980 and 1984, except for July 1980 when 10 plants were measured. To estimate the percent of substrate covered by *Macrocystis*, the average area covered by those measured holdfasts were multiplied by the number of plants found on the site at that time.

Figure 3.5.



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APPENDIX

Appendix 1.1. Light readings (in footcandles) recorded on the canopied and canopy-removal sites during 1980 and 1981, San Nicolas Island, California. These light readings served only as an index for this study, and were considered an approximate measure. The General Electric DW-68 light meter had a maximum reading of 70 footcandles. Five readings were taken on each site and averaged. Readings off the scale were given a value of 70. Three or more readings of >70 constituted a measure of >70 for that date. Except where indicated, light readings were taken on sunny days, and as close to noon as possible.

<u>Date</u>	<u>Canopy-removal site</u>	<u>Canopied site</u>
14 August 1980	5.90	5.10
11 October 1980	8.75	7.50
(Canopy-removed)		
12 October 1980	66.17	--
22 October 1980	47.50	5.70
22 April 1981 (fog)	27.67	12.17
23 April 1981 (sunny)	>70.00	46.33
15 July 1981	>70.00	19.67
22 October 1981	49.33	5.50