THE EFFECTS OF THE ADULT CANOPY ON THE GROWTH AND SURVIVORSHIP OF YOUNG *PTERYGOPHORA CALIFORNICA* PLANTS IN A CENTRAL CALIFORNIA KELP FOREST

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ABSTRACT

Following a large scale physical disturbance an adult canopy of the understory alga *Pterygophora californica* was shown to have no effect on the growth and survivorship of newly recruited sporophytes. The intense winter storms of 1982-83 removed all of the *Macrocystis pyrifera* canopy and much of the *P. californica* canopy (sporophylls and entire adult plants) from the study site, resulting in increased light levels. At light levels sufficient for the recruitment of young sporophytes, the adult canopy did not affect the subsequent growth or survivorship of these plants. Under these conditions, the range of young sporophyte densities studied had no effect on growth and survivorship.

Age distribution patterns of plants present at the beginning of this study suggested that recruitment had not occurred beneath the adult *P. californica* canopy for at least 6 years at this site. Age classes of the adult plants were clumped, suggesting that once canopies were reduced and sufficient light was available for recruitment to occur, recruitment continued for several years before a canopy developed enough to reduce light and once again inhibit recruitment. Differences in the age of plants among separate populations at this site may be attributed to localized variation in canopy cover as a result of the differential effects of small scale physical and biological (grazing) disturbances. Periods of maximum stipe elongation (March - August) alternated with periods of reproductive development (September - February). By the end of their second year all plants had

sporophylls and 50% of these had reproductive sori. Once stipe lengths were ~20 cm mortality rates decreased and remained constant.

The results of this study differed from others where the removal of algal canopies have resulted in increased recruitment and growth of plants. These findings illustrate the importance of periodic disturbances, and the dynamic nature of this kelp forest community.

INTRODUCTION

Community structure in both terrestrial forests and marine algal communities can be affected by plants that form shade-producing canopies. In terrestrial systems long-lived canopy trees often reduce available light, suppressing plant growth and making it difficult for new age classes to enter the canopy (Harper 1977, Connell 1978). Canopies formed by algae in marine communities have a similar effect, though often surface canopy plants, such as *Macrocystis pyrifera*, can be outcompeted by understory algae (Dayton et al. 1984, Reed and Foster 1984).

Competitive interactions between canopies are reflected in demographic patterns. Specific demographic information on recruitment, growth and survivorship is necessary for an understanding of canopy-understory interactions (Harper 1977, Schiel 1985a). Demographic patterns may be affected by physical-chemical conditions including light, temperature, nutrient availability and physical disturbance. Biological factors such as grazing, propagule production and dispersal, growth characteristics, and inter- and intraspecific competition may also regulate demographic patterns (e.g. Dean et al. 1986). Several studies have investigated these various factors, especially echinoid grazing, and the effects of the overlying kelp canopy on community structure (for review see Dayton 1985, Schiel and Foster 1985). Others have addressed the dynamics of recruitment, growth, and survivorship of various populations of marine algae through the development of survivorship curves and life tables (Rosenthal et al. 1974, Gunnill 1980, Coyer and Zaugg-Haglund 1982, Chapman and Goudey 1984, Dayton et al. 1984, DeWreede 1986, Gunnill 1986). In contrast to the consistent observations of density-dependence and self-thinning in terrestial plants (Harper 1977), evidence for density effects on the growth and survivorship of algal recruits is equivocal (for review see Foster and Schiel 1985).

The stipitate laminarian alga *Pterygophora californica* Ruprecht is an important and abundant species in central California kelp forests. It commonly occurs in dense single-species stands that form a thick subsurface canopy in giant kelp (*Macrocystis pyrifera* (L.) C.A. Agardh) forests in central California. This canopy can reduce light to levels that inhibit new *P. californica* and *M. pyrifera* recruitment, as well as invasion by other species (Dayton et al. 1984, Reed and Foster 1984). The question then is: what factors lead to an individual plant becoming a member of the adult canopy? I addressed this question by obtaining demographic information on the timing of recruitment, growth and survivorship of newly recruited *P. californica* plants in areas with and without adult *P. californica* canopies. The data gathered were also utilized to evaluate overall patterns of distribution and abundance of *P. californica*.

This study describes the post recruitment development and survivorship of *Pterygophora californica* in a central California kelp forest. Experimental manipulations of the adult canopy and bottom cover of algae were carried out to simulate large-scale disturbances, and evaluate the effects the adult canopy had on recruitment, growth and survivorship of *P. californica*. Specific questions addressed were: 1) Does the presence of an adult canopy affect the growth, survivorship and reproductive characteristics of young *P. californica* ? 2) Do different densities of natural recruitment have an effect on subsequent growth and/or proportional survivorship?

MATERIALS AND METHODS

Study site and organisms

This study was done in Stillwater Cove within Carmel Bay in central California (36°34' N, 121°56' W)(Figure 1). This cove is described in detail by Reed and Foster (1984). Opening to the south, the cove is normally protected from the large northerly swells associated with winter storms, as well as the strong northwesterly winds of spring. The substrate consists of sandstone, conglomerate and lava (Simpson 1972). An extensive surface canopy of *Macrocystis pyrifera* can fill the cove during spring and summer but it is usually thinned by storms during fall and winter (Reed and Foster 1984). The algal assemblage of this kelp forest is typically characterized by four layers of perennial algae: a surface canopy of the giant kelp *M. pyrifera*; an understory canopy of *Pterygophora californica* ~1.5 m in height; a bottom canopy composed mostly of articulated corallines ~10 cm height; and a layer of encrusting coralline algae on bedrock. Except for seasonal blooms of *Desmarestia* spp., non-calcareous algae comprise only a small portion of the understory (Reed and Foster 1984). Large sea urchins *Strongylocentrotus franciscanus*, and *S. purpuratus* are rare at this site due to predation by the sea otter *Enhydra lutris*.

Pterygophora californica is often found in dense stands, averaging 7 adult plants per m^2 (Dayton et al. 1984, Reed and Foster 1984, Hymanson et al. in prep.). In Stillwater Cove it usually has a stiff, woody stipe one to two meters long which terminates in a single lanceolate blade with numerous equal sized lateral sporophylls beneath it (Figure 2). The blades are rarely long enough to touch the substratum. The sporophylls develop sori in the late summer and fall. Blades are often torn away by winter storms. *Pterygophora californica* is known to live up to 14 years and develop annual rings in the stipe (Frye 1918, DeWreede 1984, Hymanson et al. in prep.). The life history of *P. californica* is similar to that of other laminarian algae with a heteromorphic alternation of generations between the large asexual (2N) sporophytes and the microscopic (1N) gametophytes (McKay 1933).

Macrocystis pyrifera plants were absent from the study sites during the course of this study. They often form a surface canopy at this site which can reduce subsurface light levels to <1% of surface irradiation (Reed and Foster 1984). *M. pyrifera* was eliminated from Stillwater Cove by the unusually severe winter storms of 1982-1983 associated with an El Nino oceanographic event (Dayton and Tegner 1984, Schiel unpubl. data). The few *M. pyrifera* plants that recruited into the study sites subsequent to 1983 were counted and removed to minimize interspecific effects.

Experimental design and analysis

Adult *Pterygophora californica*, in dense single-species stands, has been shown to inhibit algal recruitment and thereby affect community structure. An experiment was designed to examine the effects of the *P.*

californica canopy and the bottom canopy of algae on the growth and survivorship of young *P. californica* recruits (Figure 3).

Two pairs of adjacent, flat terraced rocks in Stillwater Cove at depths of ten to thirteen meters were chosen as the study sites. The pairs were separated by a distance of 60 m. Dense stands of *Pterygophora californica* present at these sites indicated that they were suitable habitat for this alga (Table 1). Water depths surrounding the terraces were 15 to 18 meters.

In November 1982, *Pterygophora californica* was removed just above the holdfast from one of each pair of terraces (P-). *P. californica* plants on the other two terraces were left untouched (P+). Twelve 2 x 2 m quadrats were randomly selected and permanently marked with concrete nails and bicycle tape on each of the four terraces and all the enclosed *Pterygophora californica* plants were counted (Figure 3, Table 1). No two quadrats were within a meter of each other. Three different substratum treatments were randomly assigned to quadrats within each terrace: (1) four quadrats were chipped down to bare rock; (2) articulated corallines were cut and scraped from four other quadrats, leaving only encrusting coralline algae; (3) the remaining four 2 x 2 m quadrats were left untouched as controls (Figure 3).

To characterize the effects that the adult canopy had on light, measurements from a Licor 192 S underwater photosynthetically active quantum sensor were taken in June 1983 in each of the forty eight 2 x 2 m quadrats and compared to the LI 190 S surface sensor to calculate the percent of surface light reaching the bottom. Measurements were taken between 1100 and 1200 hours on a clear sunny day. Horizontal water visibility was 10 m.

It was necessary to follow individual plants to obtain information on growth and survivorship. In July 1983, fourteen 0.5 x 0.5 m permanent quadrats were established around areas where recruits occurred within the 2 x 2 m quadrats on the P- terraces. These 0.25 m^2 quadrats were used in order to enclose a range of plant densities. Grid coordinates were used to map and identify individuals (n=135) for subsequent study. So few plants recruited on the P+ terraces at this time that it was not feasible to map them. Stipe lengths were measured from just above the haptera to the base of the meristem (Figure 2). Sporophylls were counted and the number with sori noted. These measurements were continued at bimonthly intervals. At the conclusion of the experiment in January 1985, stipe diameter and terminal blade length of all mapped individuals were measured. Stipe diameter was taken 10 cm above the holdfast in order to standardize the measurement and reduce variability associated with haptera growth (Hymanson et al. in prep.). If stipe length was less than 10 cm, stipe diameter was measured at 5 cm.

To evaluate canopy effects on the growth of 1983 cohort plants, measurements were taken in February 1984 of all 1983 recruits found in the 48 2 x 2 m quadrats. These were analyzed with a two-way ANOVA using sites (I, II) and canopies (P+, P-) as factors.

Pterygophora californica successfully recruited on all four terraces in the spring of 1984. In March, 22 new 0.5 x 0.5 m permanent quadrats were established around areas where recruits occurred within the larger 2 x 2 m quadrats on all four terraces. No 1983 recruits contacted these new 0.25 m^2 quadrats. Quadrats were located within all three of the original substratum treatments, which were still significantly different in amount of coralline algal cover (Schiel unpubl. data), to evaluate the effects of these treatments. Individual plants were mapped. Initial measurements were of total length when individual stipes were less than 5 mm and difficult to measure precisely. The development and fate of 411 individuals from all four terraces were followed until January 1985.

The survival of the adult plants originally found in each 2 x 2 m quadrat on the P+ terraces was followed for the duration of the experiment.

Growth and survivorship of recruits were compared among sites, densities, canopy and substrate treatments (Figure 3). Stipe lengths of the 1984 cohort plants, measured in March and again in December, were compared with a two-way ANOVA using sites (I, II) and canopies (P+, P) as factors. Twenty plants from the 1984 cohort were randomly selected from each canopy treatment at each site for these 1984 growth analyses. The distribution of plants did not allow whole 0.25 m^2 quadrats and substratum treatments to be used in this analysis, therefore they were analyzed separately. To evaluate density effects on stipe length, quadrats were divided into three groups, based on naturally-occurring densities (<7,7-20, and >20 per 0.25 m^2), and tested with a one-way ANOVA. Cochran's C test was used to test for variance homogeneity for all ANOVAs. Log transformations were used for growth data and arcsine transformations for survivorship data when needed. All tests were termed significant at $P<.05$.

Five sets of plants were measured and analyzed for morphological comparisons. In January 1985, ten plants each from the adult canopy, the subadult canopy (which was mostly comprised of 1983 recruits) and the

1984 recruits were randomly collected from each of the four terraces, outside the 2 x 2 m quadrats (n = 120). To evaluate relationships between a plant's age, biomass and meristic characteristics, measurements of stipe length, diameter, number of sporophylls, number of sporophylls with sori and area of sori were taken. Plants were aged by counting stipe rings 1 to 3 cm above the haptera. Annual bands of dark rings are visible in polished sections (DeWreede 1984, Hymanson et al. in prep). The stipe, blades and sori of each plant were dried and weighed. Regression analyses were used to assess the relationships between: (i) stipe diameter, number of sporophylls, and number of rings on stipe length, (ii) number of rings, number of sporophylls, and stipe diameter on number of sporophylls with sori, (iii) number of rings and stipe diameter, (iv) sori area and sori weight, and (v) stipe dry weight and blade dry weight. Sporophylls, sori and terminal blade were weighed together to obtain blade dry weight. Regressions were performed separately for the 1983 and 1984 cohorts. Tests for normality were made with the Q-Q correlation (Gnanadesikan 1977). ANOVA significance tests were used, and r^2 calculated for each regression.

RESULTS

Historical perspective

Dense *Macrocystis pyrifera* and *Pterygophora californica* canopies had been present at Stillwater Cove since at least 1980 (Reed and Foster 1984). The severe winter storms of 1982-83 (December to February) removed nearly all the *M. pyrifera* plants from the study site and most of the blades from *P.*

californica plants. Adult *P. californica* mortality had occurred as the density of adult, canopy-forming plants at the beginning of this study was $3/m^2$ compared with $7/m^2$, in 1978-79 at the same site (Reed and Foster 1984)(Table 1). Sporophytes of these species generally recruit in the spring at Stillwater Cove (Reed and Foster 1984). Water clarity was very poor during this time period in the spring of 1983 (pers. obs.). Zoospores released from the sporophylls of these plants can take less than 50 days to develop into visible sporophytes given enough light and nutrients (Foster 1975, Dean and Deysher 1983, Dean et al. 1986, Deysher and Dean 1986). The low number of recruits of these two species in Stillwater Cove in the spring of 1983 appeared to have been a result of the physical disturbance associated with storms (Schiel unpubl. data).

Macrocystis pyrifera plants were rare in Stillwater Cove during the summer of 1983. The adult *Pterygophora californica* canopy was sparse and the number of adults was declining (Figure 4). By the spring of 1984 both canopies were reestablishing in Stillwater Cove, though they were not nearly as extensive as in the years prior to the winter of 1982-83. Large numbers of small recruits (sporophytes) of *P. californica* and to a lesser degree *M. pyrifera* were observed at the study site in mid-March 1984. By the summer of 1984 *M. pyrifera* formed a dense surface canopy over much of Stillwater Cove. Fall and winter storms thinned this *M. pyrifera* canopy.

Light

Light readings were analyzed for differences between sites, canopies and treatments. The presence or absence of a canopy (P+ or P-) accounted for

83.3% of the variation (Table 2). There was a difference between sites but this accounted for only 7% of the total variation (Table 2). On the P+ terraces a mean of 10.6% ± 4.1% S.D. of the surface light reached the bottom, compared to 16.3% ± 2.7% in the P- areas. The actual (mean) amount of irradiation reaching the bottom on the P- terraces was 300.7 ± 47.0 S. D. $\mu E\ m^{-2}\ s^{-1}$, while on the P+ terraces it was 184.5 ± 74.5 $\mu E\ m^{-2}\ s^{-1}$. Although these measurements were taken during the seasonal period of maximum understory canopy cover (Reed and Foster 1984), the *Pterygophora californica* canopy in June 1983 was particularly sparse due to severe winter storms.

1983 Cohort

Site (I,II) and treatment (P+, P-) effects were statistically significant when measurements of all 1983 recruits, taken in February 1984, were analyzed (Table 3). Biologically these may not have been important as the mean stipe lengths on 3 of the 4 terraces ranged from 27.1 to 30.0 cm (Table 3). The other terrace had a mean stipe length of 15.7 cm and fewer plants (Table 3). This variation in size was probably due to differences in timing of recruitment. The signifigance of the interaction term suggests that the effect of the adult *Pterygophora californica* canopy on the stipe length of young recruits depends on a plant's location.

Growth curves show that 1983 plants had a period of maximum stipe elongation from March to September (Figure 5).

Canopy and density effects on growth

The adult *Pterygophora californica* canopy of ~3 plants per m^2 had no effect on juvenile growth rates. The first measurements in March 1984 showed significant differences in stipe lengths between canopies. In addition to this average difference between treatments, the effect of the adult canopy on size depends upon a plant's location, resulting in a significant interaction term (Table 4). Plants may have recruited on different days resulting in significant differences in size at an early age. By December 1984 there were no significant differences in stipe length for any of the factors (Table 4). Mean stipe lengths on the 4 terraces in December ranged from 200 to 244 mm (Figure 5).

Quadrats were divided into three groups, based on naturally occurring densities (<7, 7-20, >20) of juveniles, to examine density effects on growth. There were no significant differences in stipe length, or in any other morphological characteristics (Table 5). The density of 1984 plants in the 0.5 x 0.5 m quadrats ranged between 1 and 58 in December 1984. Thirty-five plants were randomly selected from each density level as the number of quadrats for each group was unequal.

Growth curves for both years showing mean stipe length over time depicted an increased rate of stipe elongation during the spring and summer months. Differences in stipe lengths of plants from the 1984 cohort were used (September - March n=190, December - September n=164) to determine growth rates. The mean growth rate was 1.2 mm per day from March to September, and 0.3 mm per day from September to December. The regression analyses done for both time periods indicated there was no relationship between initial plant size and growth rates of mapped plants. (Table 6).

Survivorship

Plant survivorship of the 1984 cohort was not affected by canopy treatments (P+, P-) and did not vary between sites (I,II)(Table 7). The number of 1984 recruits in the 0.25 m^2 quadrats surviving in December 1984 was divided by the number present in March 1984. Results from a two-way ANOVA with sites (I,II) and canopies (P+, P-) as factors were not significant (Table 7).

The substratum did not significantly affect survivorship of mapped 1984 plants. Six 0.25 m^2 quadrats from each substratum treatment (bare rock, articulated coralline removal and controls) were randomly selected. The number of plants found in December 1984 was divided by the initial number in March 1984 and these percentages were compared with a one-way ANOVA (Table 8). An additional analysis found no significant difference in survivorship between plants which settled on encrusting coralline algae versus articulated coralline algae in twenty-one 0.25 m^2 quadrats (Table 9). Over 85% of all mapped plants were initially found settled on these two types of substratum. Many plants initially found on articulated coralline algae were able to grow haptera down to solid substratum.

To test for density-dependent survivorship final density and proportional survivorship were regressed against initial densities. Final and initial densities were related ($r^2 = .50$, $P<.001$), and proportional survivorship was not significantly related to initial density (Table 10).

Yearly counts of *Pterygophora californica* plants present at the beginning of the study, on the P+ terraces in the 2 x 2 m quadrats, showed a steady decline of the adult population from January 1983 to December 1984. Mean densities fell from 11.7 to 4.7 per 4 m^2 (Figure 4). Survivorship curves and an ANCOVA for these adults, as well as 1983 and 1984 cohorts, showed that after three months of visible growth (stipe length ~ 20 cm) juveniles and adults have similar survivorship curves (Figure 6, Table 11). These were similar to curves for plants from a site in southern California (Dayton et al. 1984).

Dry weight analysis and reproductive characteristics

Five sets of plants were analyzed for morphological similarities. Adult canopy plants (>2 yrs.), subadult plants (mostly 1983 recruits), and 1984 recruits were collected from the terraces outside of the 2 x 2 m quadrats in January 1985. Measurements from the 1983 and 1984 mapped plants were also used.

There were significant relationships between stipe length and diameter for all groups of plants except the subadults, although the coefficient of determination (r^2) varied greatly (Tables 12 and 13). The number of sporophylls was related to stipe length only for the 1983 and 1984 cohort plants. The number of sporophylls related directly to stipe diameter in all cases except the adult plants. As the number of sporophylls on a plant increased, the percent of sporophylls with reproductive sori also increased. The stipe dry weight was significantly correlated with blade dry weight for all except the adult plants.

Ring counts could only be made on the three harvested groups. For all except the adult group there appeared to be a direct relationship between the number of rings and the number of sporophylls. Except for the 1984 recruits, the number of rings a plant had was directly related to stipe diameter. Only with the adult plants did the number of rings exhibit a direct relationship with stipe length.

The number of rings adult plants had differed significantly between terraces (Figure 7, Table 14). Age classes appeared clumped on each of the terraces. No plants on any of the terraces were less than 6 years old suggesting that recruitment has not occurred beneath the canopy for that amount of time. These results and the 2 years of recruitment which occurred beneath the adult canopy during this study suggest that recruitment of sporophytes may continue for several years after a disturbance has thinned the *P. californica* canopy.

In all groups, as the percentage of sporophylls with sori on a plant increased so did the mean weight of the sori. Sorus area was directly related to sorus weight.

The percentage of plants with sporophylls was increasing in both the 1983 and 1984 cohorts throughout the course of this study (Figure 8). In both cohorts sori began to develop in September each year. For the plants in the 1983 cohort the percentage of sporophylls with sori reached a peak (9.5%) in February 1984. This fell to 0% by midsummer, and then increased to 61% by December 1984 (Figure 8).

DISCUSSION

In this study the presence or absence of the understory algal canopy of *Pterygophora californica* had no effect on the growth and survivorship of young *P. californica* recruits. These results contradict the general paradigm that removal of algal canopies results in increased recruitment and growth of plants beneath them (for review see Foster and Schiel 1985). Differences in the results of this study and those of others were due to the increase in available light beneath the adult *P. californica* canopy following blade removal and adult mortality by a large scale physical disturbance, the unusually severe winter storms of 1982-83.

The giant kelp *Macrocystis pyrifera* often forms a dense surface canopy and can reduce irradiance beneath it by over 90% (Neushul 1971, Dean et al. 1973, Reed and Foster 1984). Understory algal canopies can also reduce light levels to <1% of surface irradiance (Kastandiek 1982, Reed and Foster1984, Santelices and Ojeda 1984, Dayton et al. 1984). Within a giant kelp forest the surface canopy and/or the understory canopy can independently, or in combination, reduce light levels and inhibit algal recruitment (Reed and Foster 1984).

A large scale physical disturbance, associated with an El Nino oceanographic event, that occurred at the beginning of this experiment, removed all the *M. pyrifera* canopy from the study area and reduced adult *P. californica* densities by 50% (Reed and Foster 1984)(Table 1). These storms also removed nearly all the blades from the remaining plants, so that what remained of the adult canopy had no effect on the growth and survivorship of young *P. californica* recruits. Although light levels beneath the adult canopy were less than those in areas from which the adult plants had been removed (10.6 vs. 16.3% of surface irradiation), the absolute amount of irradiation reaching the bottom beneath the *P. californica* canopy (184.5 ± 74.5 $\mu E\ m^{-2}\ s^{-1}$) exceeded the saturation level for growth of juvenile *M. pyrifera* (Dean and Jacobsen 1984) and kelps in general (Luning 1980).

In this experiment the adult *P. californica* canopy had no effect on the morphology of plants or development of reproductive structures (Tables 12 and 13). As in other studies periods of increased stipe elongation (March - August) alternated with the seasonal development of reproductive structures (September - February)(1983)(Figures 5 and 8). Fifty percent of the plants had sporophylls by the end of their first year and all of the plants had them by the end of the second year.

Over the range studied, the density of *P. californica* recruits did not change the growth or survivorship rates of the plants. Others have observed increased stipe elongation and etiolation in *P. californica* plants growing at higher densities (Hymanson et al. in prep., Reed unpubl. data).

The age estimates from ring counts of plants present at the beginning of this study suggested that *P. californica* had not successfully recruited at this study site for at least 6 years (Figure 7). Age classes from each of the 4 terraces studied were clumped together into 3-6 year classes so it appeared that once conditions were favorable for recruitment, recruitment continued for several years before the *P. californica* and/or the *M. pyrifera* canopy developed enough to reduce light levels and once again inhibit recruitment.

Small scale disturbances may have accounted for the differences between the age classes of adult plants found on the 4 terraces used during this study (Table 14). *Macrocystis pyrifera* is more susceptible to removal by storms and is generally shorter-lived than *P. californica* (Rosenthal et al. 1974, Littler and Littler 1980, Reed and Foster 1984). The bottom canopy of articulated coralline algae has been shown to inhibit algal recruitment, although in this study it did not affect the growth and survivorship of plants 1 cm and greater in size. Interactions between these canopies would add another level of complexity to understanding under what conditions successful recruitment of *P. californica* occurs. Although the effects of grazing were not conspicuous at this study site, small sea urchins, gastropods, seastars, seahares and amphipods may prey upon small recruits and weaken adult plants. Senescence may affect susceptibility to grazing and physical disturbances. These factors, which vary in space, time and intensity, interacting at various levels probably lead to the mosaic pattern of age structures found among the terraces. However the basic processes of canopy reduction leading to increased levels of light, and increased algal recruitment and growth were probably the same.

Before this study it was known that understory algal canopies inhibited laminarian algal recruitment under certain conditions (Reed and Foster 1984, Dayton et al. 1984). This study has shown under what natural conditions recruitment does occur beneath an adult canopy. A large scale physical disturbance removed all of the *M. pyrifera* canopy and much of the *P. californica* canopy, blades and whole plants, from the study site at the beginning of this experiment. This made a limited resource, light, available which allowed the recruitment of young sporophytes to occur beneath the adult *P. californica* canopy. Once enough light was available beneath the *P. californica* canopy, what remained of the adult canopy had no effect on the continued growth and survivorship of young recruits. Varying densities of young recruits had no effect on their growth and survivorship under these conditions. This study illustrates the importance of periodic disturbances to recruitment events, and the dynamic nature of the understory kelp system.

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TABLE 1: Mean (± S.D.) densities of *Pterygophora californica* in the 48 2 x 2 m permanently marked quadrats prior to the removal experiment (P+ = *Pterygophora* control, P- = *Pterygophora* removal).

Site	I		II	
Canopy treatment	P+	P-	P+	P-
Density ($4m^{-2}$) of *Pterygophora californica*	11.4 ± 4.0	10.8 ± 1.5	12.0 ± 3.6	10.3 ± 1.5

TABLE 2: Analysis of light readings taken in each of the 48 2 x 2 m quadrats in June 1983 (ANOVA).

Source of Variation	DF	SS	MS	F-Stat
Sites	1	0.277	0.277	3.874
Canopies	1	2.477	2.477	34.637
Treatments	2	0.128	0.128	1.785
Site x Canopy	1	0.050	0.050	0.697
Site x Treatment	2	0.161	0.080	1.123
Canopy x Treatment	2	0.077	0.039	0.540
Site x Canopy x Trt.	2	0.198	0.099	1.384
Residual	36	2.575	0.072	
Total	47	6.070		

$F_{.05(1)2,36} = 4.13$

$F_{.05(1)1,36} = 3.28$

TABLE 3: Analysis of stipe length measurements, taken in February 1984, of all 1983 cohort plants found in the 48 2 x 2 m permanently marked quadrats.

Site and Canopy Treatment	mean stipe length (cm) ± S.E.	
Site I with *Pterygophora*	15.7 ± 1.9	n=15
Site I without *Pterygophora*	29.0 ± 1.6	n=52
Site II with *Pterygophora*	30.0 ± 1.9	n=42
Site II without *Pterygophora*	27.2 ± 0.9	n=195

ANOVA Table
Sites x Canopies

Source of Variation	DF	SS	MS	F-Stat
Among subgroups	3	2478.485	826.162	
Sites	1	1361.044	1361.045	10.11
Canopies	1	955.054	955.054	7.09
Interaction	1	2262.065	2262.065	16.80
Within groups	300	40399.617	134.665	
Total	303	42878.102		

$F_{.05(1)1,\infty} = 3.84$

TABLE 4: Growth (stipe length) analysis of the 1984 cohort.

ANOVA Table
March 1984

Source of variation	DF	SS	MS	F-Stat
Among subgroups	3	27.7459	9.2486	
Sites	1	0.3184	0.3184	0.2710
Canopies	1	15.5808	15.5808	13.2576
Interaction	1	11.8467	11.8467	10.0803
Within groups	76	89.3176	1.1752	
Total	79	117.0635		

$F_{.05(1)1,76} = 3.97$

ANOVA Table
December 1984

Source of variation	DF	SS	MS	F-Stat
Among subgroups	3	0.5756	0.1919	
Sites	1	0.2437	0.2437	0.4947
Canopies	1	0.0356	0.0356	0.0723
Interaction	1	0.2962	0.2962	0.6012
Within groups	76	37.4420	0.4927	
Total	79	38.0176		

$F_{.05(1)1,76} = 3.97$

TABLE 5: Density effects on growth (stipe length) of the 1984 cohort.

ANOVA Table

Density <7, 7-20, >20 /0.25 m^2

Source of variation	DF	SS	MS	F-Stat
Among groups	2	8.96933e + 06	4.48467e + 04	3.0216
Within groups	102	1.51386e + 06	1.48418e + 04	
Total	104	1.60356e + 06		

$F_{.05(1)2,102} = 3.09$

TABLE 6: Incremental growth (stipe length) analysis of the 1984 cohort.

Relationship	Regression Equation	r^2	$P(\beta = 0)$
Initial stipe length in March (mm) versus August-March/#days	growth (mm/day) = 0.64 + 0.03 initial length	0.01	N. S.
Stipe length in August (mm) versus December-August/#days	growth (mm/day) = -0.33 + 0.00 initial length	0.03	N. S.

TABLE 7: Survivorship analysis of the 1984 cohort (December 'n' 1984/March 'n' per 0.25 m^2).

ANOVA Table
Sites x Canopies

Source of variation	DF	SS	MS	F-Stat
Among substrates	3	0.9475	0.3158	
Sites	1	0.2757	0.2757	1.4930
Canopies	1	0.5560	0.5560	3.0106
Interaction	1	0.1158	0.1158	0.6270
Within groups	16	2.9549	0.1847	
Total	19	3.9025		

$F_{.05(1)1,16} = 4.49$

TABLE 8: Survivorship analysis of substratum (bare rock, articulated coralline removal, control) treatments of the 1984 cohort (December 'n'/March 'n' per 0.25 m^2).

ANOVA Table

Source of variation	DF	SS	MS	F-Stat
Among groups	2	0.0981	0.0490	0.4450
Within groups	15	1.6527	0.1102	
Total	17	1.7507		

$F_{.05(1)2,15} = 3.68$

TABLE 9: Comparison of survivorship of plants initially found settled on articulated corallines versus encrusting corallines (December 'n'/ March 'n' per 0.25 m^2).

Variable	Encrusting coralline	Articulated coralline
Mean:	0.447	0.362
Standard deviation:	0.328	0.316
Paired observations:	21	
t-statistic:	1.950	Hypothesis:
Degrees of freedom:	20	$H_0: \mu 1 = \mu 2$
$t_{.05(2)20}$	2.086	$H_a: \mu 1 \neq \mu 2$

TABLE 10: Proportional survivorship compared to initial density with regression analysis.

Relationship	Regression Equation	r^2	$P(\beta = 0)$
Final density (December) versus Initial density (March)	Dec. density = −0.59 + 0.45 March density	0.50	<.001
Proportion surviving in December versus Initial density (March)	(December 'n'/March 'n' per 0.25 m^2) = 0.61 − 0.003 March density	0.02	N. S.

TABLE 11: Comparison of mortality rates for plants older than three months (~20cm)(X = age, Y = % survivorship)(ANCOVA).

By Age Group	Regression Equation	$P(B_1 = B_2 = B_3 = B_4) < .25$
Adult canopy	y = 0.98 - 0.05x	
1983 cohort	y = 0.98 - 0.02x	
1984 cohort	y = 0.87 - 0.04x	
Dayton et al. (1984)	y = 0.69 - 0.05x	N. S.

TABLE 12: Summary of morphological measurements and dry weights of collected and mapped plants (mean ± S.E.).

	Adult (n = 40)	Subadults (mostly 1983 recruits) (n = 40)	1983 Cohort (n = 75)	1984 Recruits (n = 38)	1984 Cohort (n = 180)
Number of Rings	10.6 ± 0.6	4.4 ± 0.3	—	1.5 ± 0.1	—
Stipe Length (cm)	104.7 ± 4.5	42.1 ± 2.0	46.8 ± 2.2	26.9 ± 1.1	22.2 ± 0.9
Stipe Diameter (cm)	24.6 ± 0.5	13.4 ± 0.3	10.8 ± 0.5	6.7 ± 0.2	5.0 ± 0.2
Nos. of Sporophylls	31.3 ± 1.0	15.0 ± 0.9	13.2 ± 1.0	5.1 ± 0.4	2.2 ± 0.2
Nos. of Sporophylls with Sori	26.7 ± 1.1	8.8 ± 1.1	4.0 ± 0.5	1.1 ± 0.3	0.4 ± 0.1
Stipe Weight (gm)	134.7 ± 9.5	16.4 ± 1.8	—	2.3 ± 0.2	—
Blade Weight (gm)	128.2 ± 6.9	45.5 ± 6.3	—	5.1 ± 0.9	—
Sori Area (cm^2)	2768.7 ± 156.3	679.0 ± 122.6	—	30.6 ± 12.1	—
Sori Weight (gm)	65.7 ± 3.8	17.2 ± 3.3	—	0.7 ± 0.3	—

TABLE 13: Morphological measurements regression analyses.

Stipe Length (X) versus Stipe Diameter (Y)

Group	Regression Equation	r^2	$P(B = 0)$
Adults (n = 40)	y = 1.48 + 0.01x	0.59	<.001
Subadults (n = 40)	y = 1.16 + 0.00x	0.06	N. S.
1983 cohort (n = 75)	y = 4.54 + 0.01x	0.39	<.001
1984 recruits (n = 38)	y = 0.48 + 0.01x	0.16	<.025
1984 cohort (n = 180)	y = 1.45 + 0.02x	0.76	<.001

Stipe Length versus Number of Sporophylls

Group	Regression Equation	r^2	$P(B = 0)$
Adults	y = 30.07 + 0.01x	0.00	N. S.
Subadults	y = 17.88 - 0.07x	0.02	N. S.
1983 cohort	y = 1.69 + 0.02x	0.28	<.001
1984 recruits	y = 5.87 - 0.03x	0.01	N. S.
1984 cohort	y = 1.22 + 0.02x	0.39	<.001

Stipe Diameter versus Number of Sporophylls

Group	Regression Equation	r^2	$P(B = 0)$
Adults	y = 26.50 + 1.94x	0.01	N. S.
Subadults	y = -8.63 + 17.60x	0.45	<.001
1983 cohort	y = -6.23 + 1.81x	0.67	<.001
1984 recruits	y = -3.33 + 12.60x	0.40	<.001
1984 cohort	y = -2.82 + 1.02x	0.55	<.001

Number of Sporophylls versus Number of Sporophylls with Sori

Group	Regression Equation	r^2	$P(B = 0)$
Adults	y = -1.11 + 0.89x	0.72	<.001
Subadults	y = -7.55 + 1.09x	0.77	<.001
1983 cohort	y = -1.10 + 0.38x	0.68	<.001
1984 recruits	y = -2.12 + 0.06x	0.51	<.001
1984 cohort	y = 0.19 - 0.08x	0.37	<.001

Number of Rings versus Stipe Length

Group	Regression Equation	r^2	$P(B = 0)$
Adults	y = 62.39 + 3.99x	0.27	<.001
Subadults	y = 39.88 + 0.51x	0.01	N. S.
1984 recruits	y = 29.90 - 1.98x	0.07	N. S.

TABLE 13: Morphological measurements regression analyses, continued.

Number of Rings versus Number of Sporophylls

Group	Regression Equation	r^2	$P(\beta = 0)$
Adults	$y = 32.28 - 0.09x$	0.00	N. S.
Subadults	$y = 8.42 + 1.49x$	0.24	<.005
1984 recruits	$y = 3.22 + 1.22x$	0.22	<.005

Number of Rings versus Stipe Diameter

Group	Regression Equation	r^2	$P(\beta = 0)$
Adults	$y = 1.98 + 0.05x$	0.23	<.005
Subadults	$y = 1.05 + 0.07x$	0.33	<.001
1984 recruits	$y = 0.62 + 0.03x$	0.05	N. S.

Number of Sporophylls with Sori versus Sori Weight

Group	Regression Equation	r^2	$P(\beta = 0)$
Adults	$y = -9.62 + 2.83x$	0.64	<.001
Subadults	$y = -5.15 + 2.53x$	0.73	<.001
1984 recruits	$y = -0.11 + 0.74x$	0.77	<.001

Sori Area versus Sori Weight

Group	Regression Equation	r^2	$P(\beta = 0)$
Adults	$y = 6.97 + 0.02x$	0.76	<.001
Subadults	$y = 0.47 + 0.02x$	0.85	<.001
1984 recruits	$y = 0.00 + 0.02x$	0.98	<.001

TABLE 14: Differences in number of rings in adult plants collected from the 4 terraces (ANOVA).

ANOVA Table

Source of variation	DF	SS	MS	F-Stat
Among groups	3	348.60	116.20	24.52
Within groups	37	4.73	4.73	
Total	40	353.33		

$F_{.001(1)3,37} = 6.67$

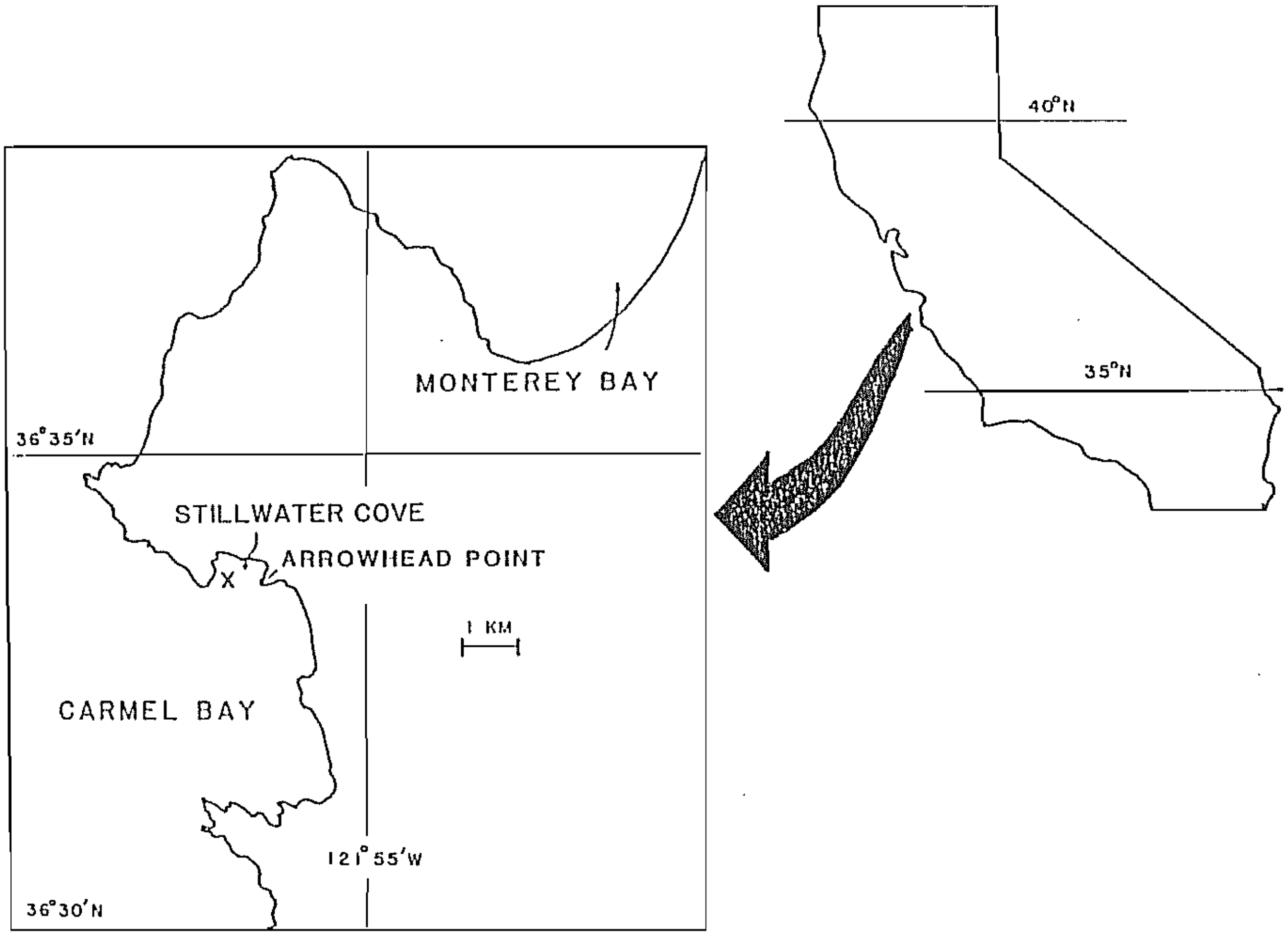

Figure 1: Map showing the location of the study sites in California.

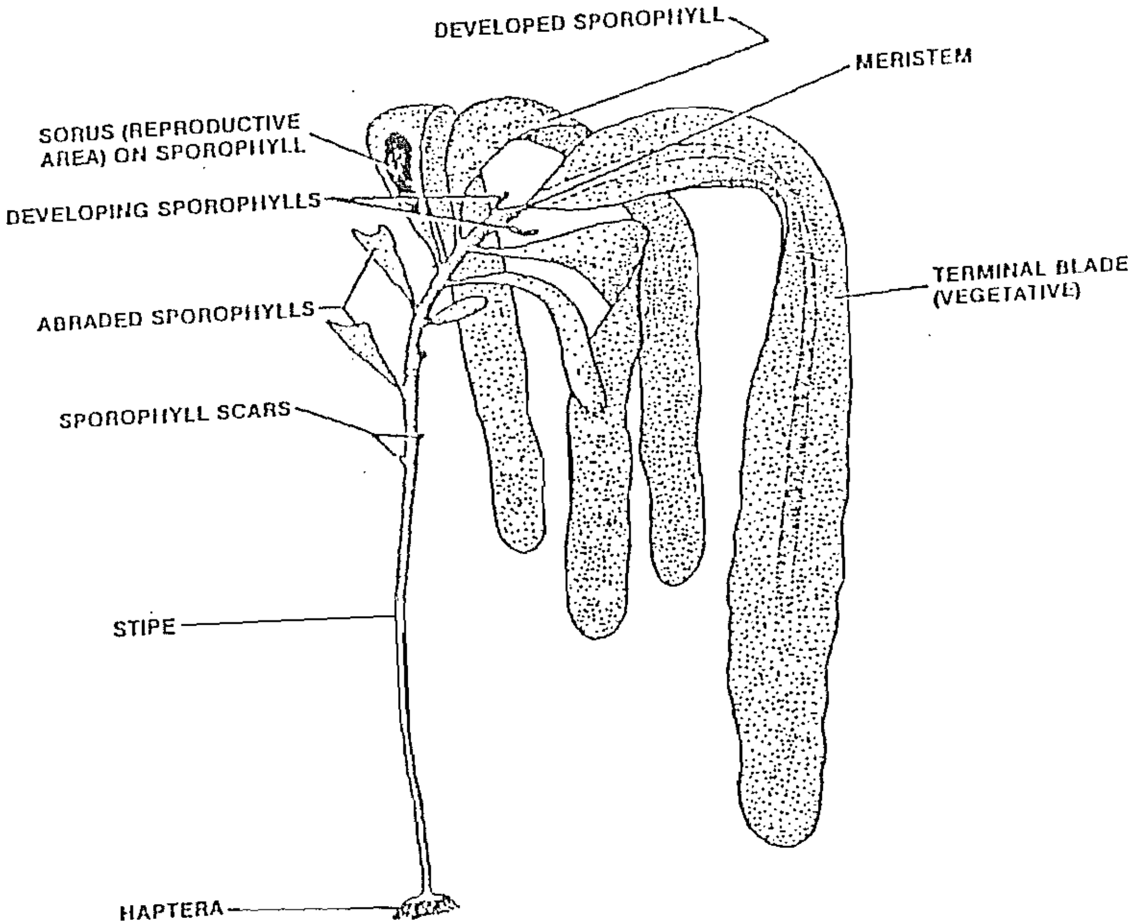

Figure 2: The *Pterygophora californica* sporophyte (after Dawson and Foster 1982).

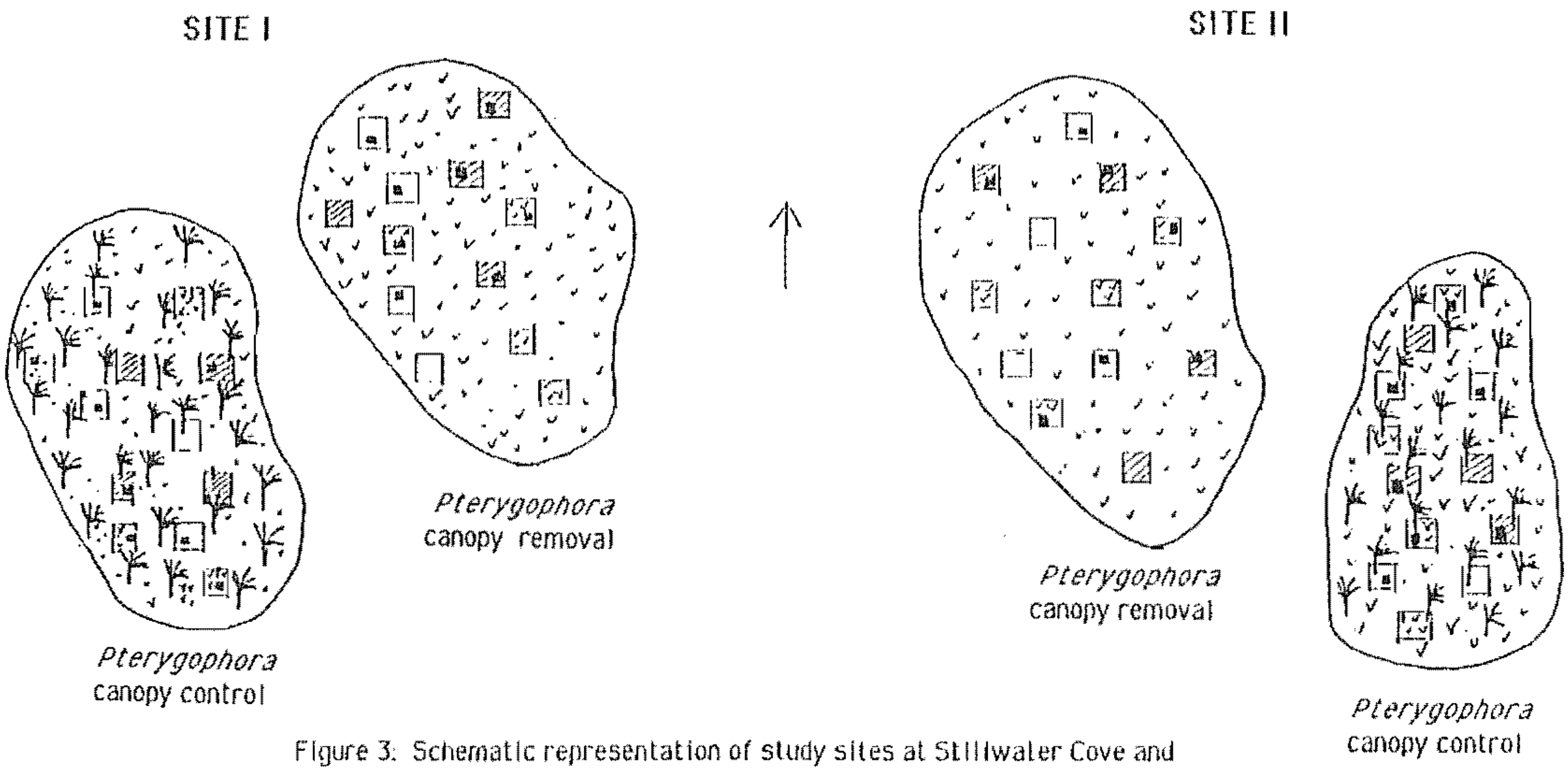

Figure 3: Schematic representation of study sites at Stillwater Cove and experimental design with 2x2 m quadrats. Sites were ~60 m apart and each terrace was ~20 x 50 m (not to scale).

- bare rock
- articulated coralline removal
- control with articulated corallines
- 0.5 x 0.5 m quadrats
- <u>Pterygophora</u> plants
- articulated corallines

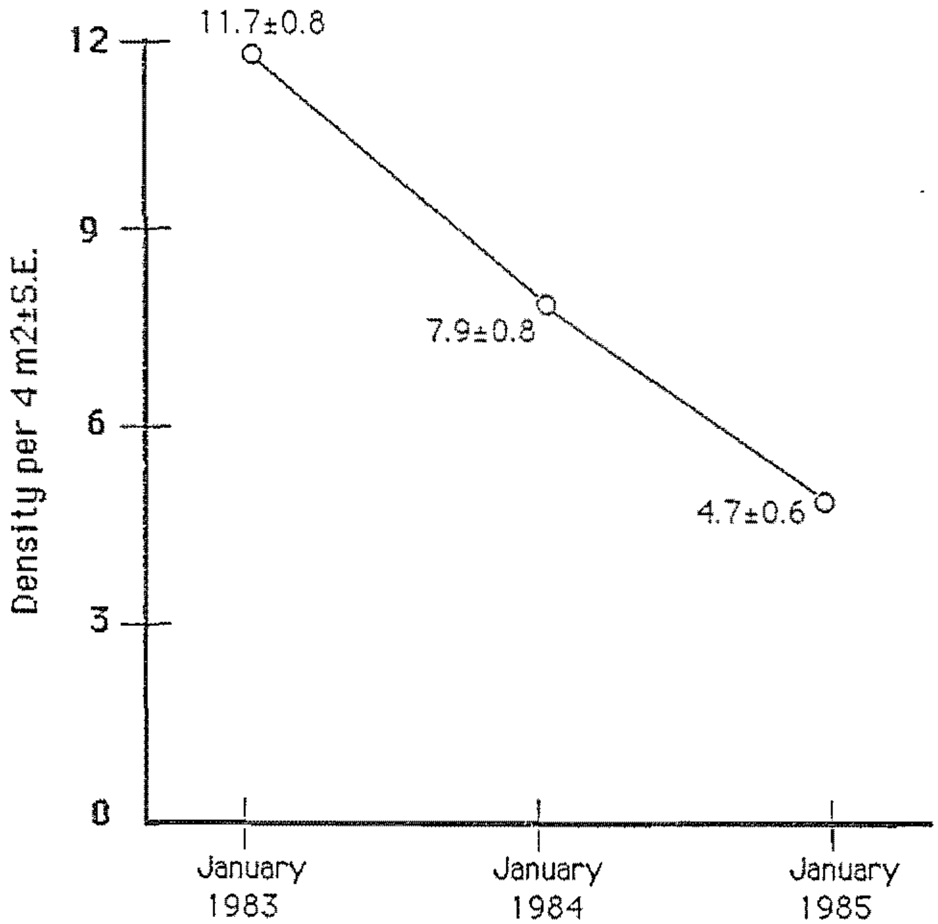

Figure 4: Mean number of original adult Pterygophora plants in each 2 x 2 m quadrat on the terraces with canopies(n = 24 each year).

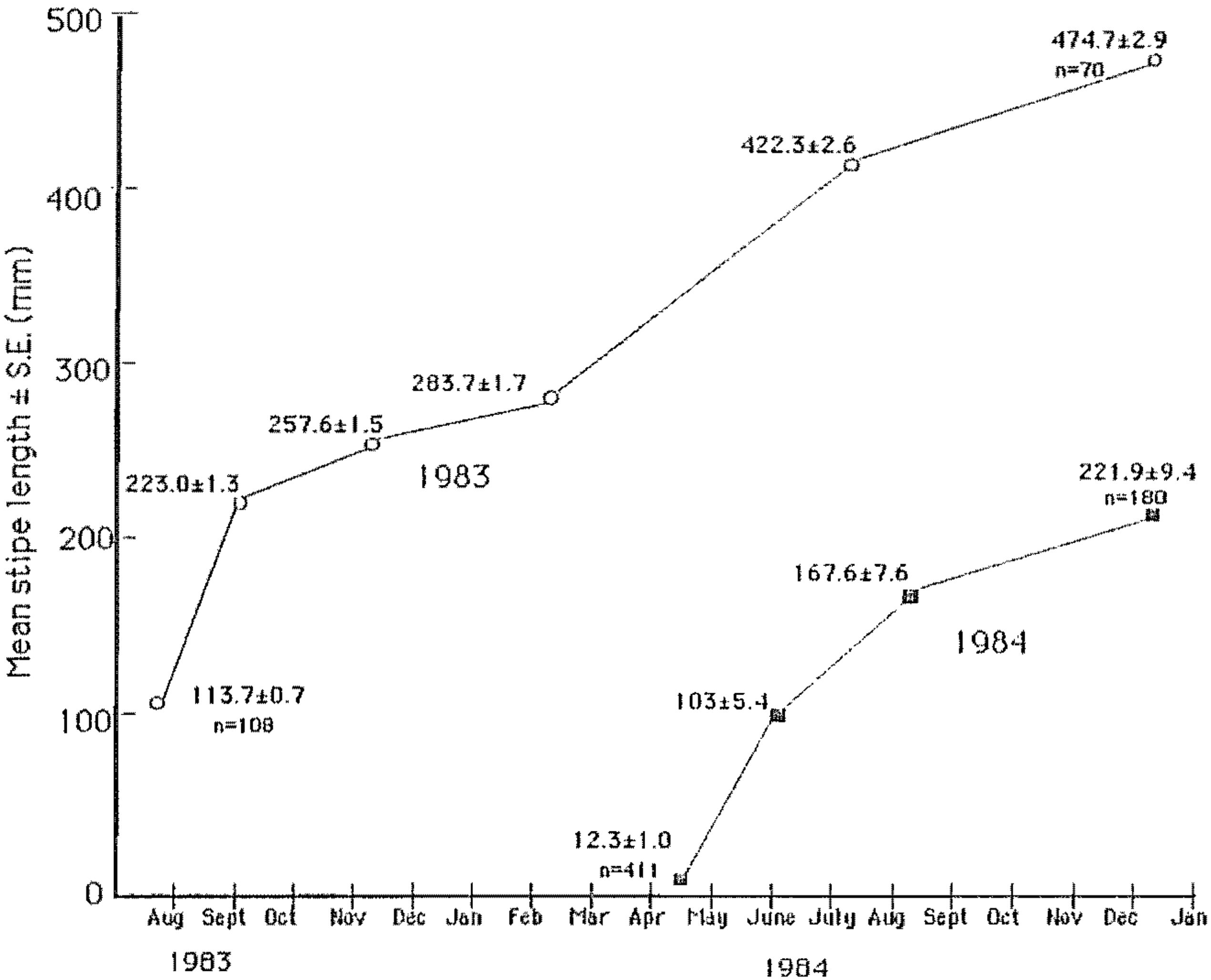

Figure 5: Growth curves for 1983 and 1984 cohorts from mapped plants in 0.25 m^2 quadrats.

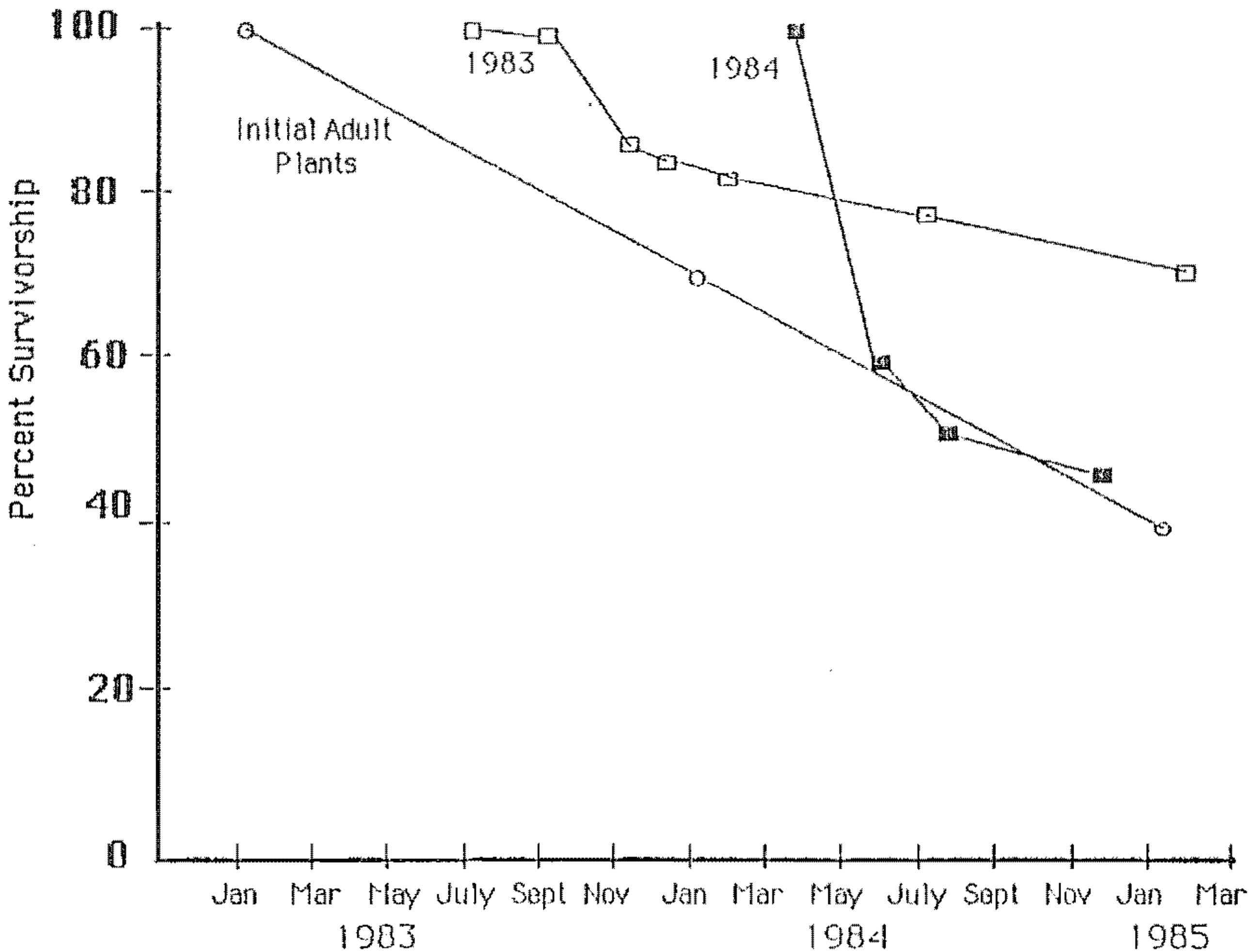

Figure 6: Percent survivorship (N_t/N_0) of adult plants initially found in the 2x2 m quadrats, and all mapped 1983 and 1984 cohort plants in 0.25 m^2 quadrats.

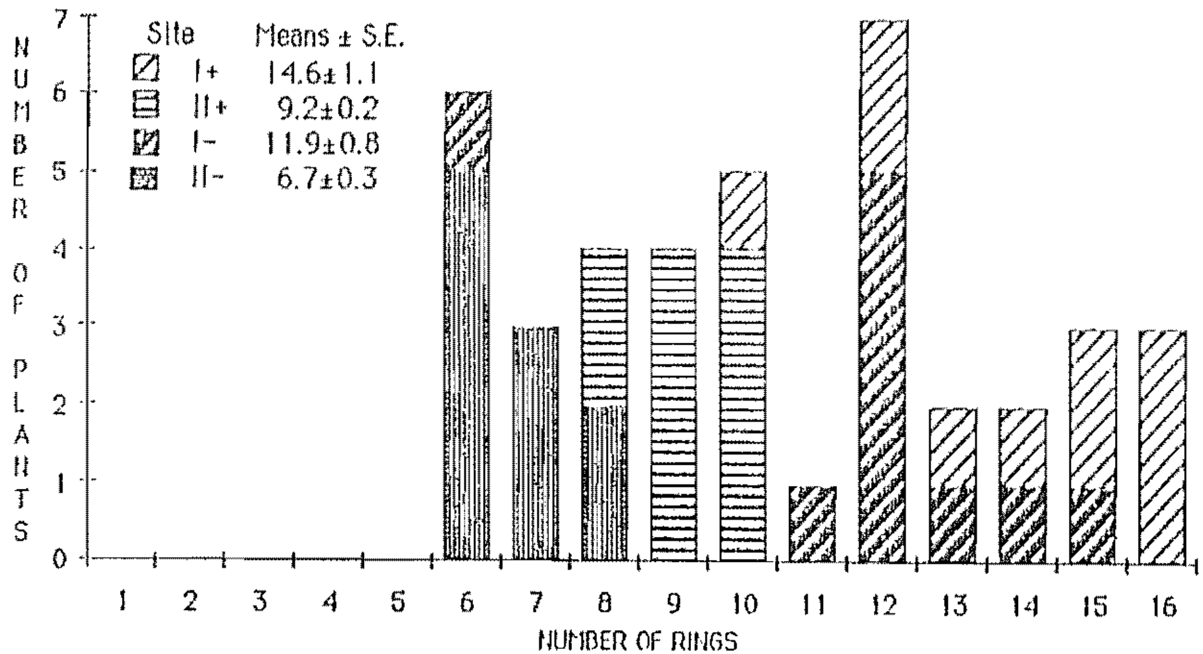

Figure 7: Ring frequency of adult canopy plants, which were present when this study began. Ten were collected from each of the 4 terraces outside of the 2x2 m quadrats.

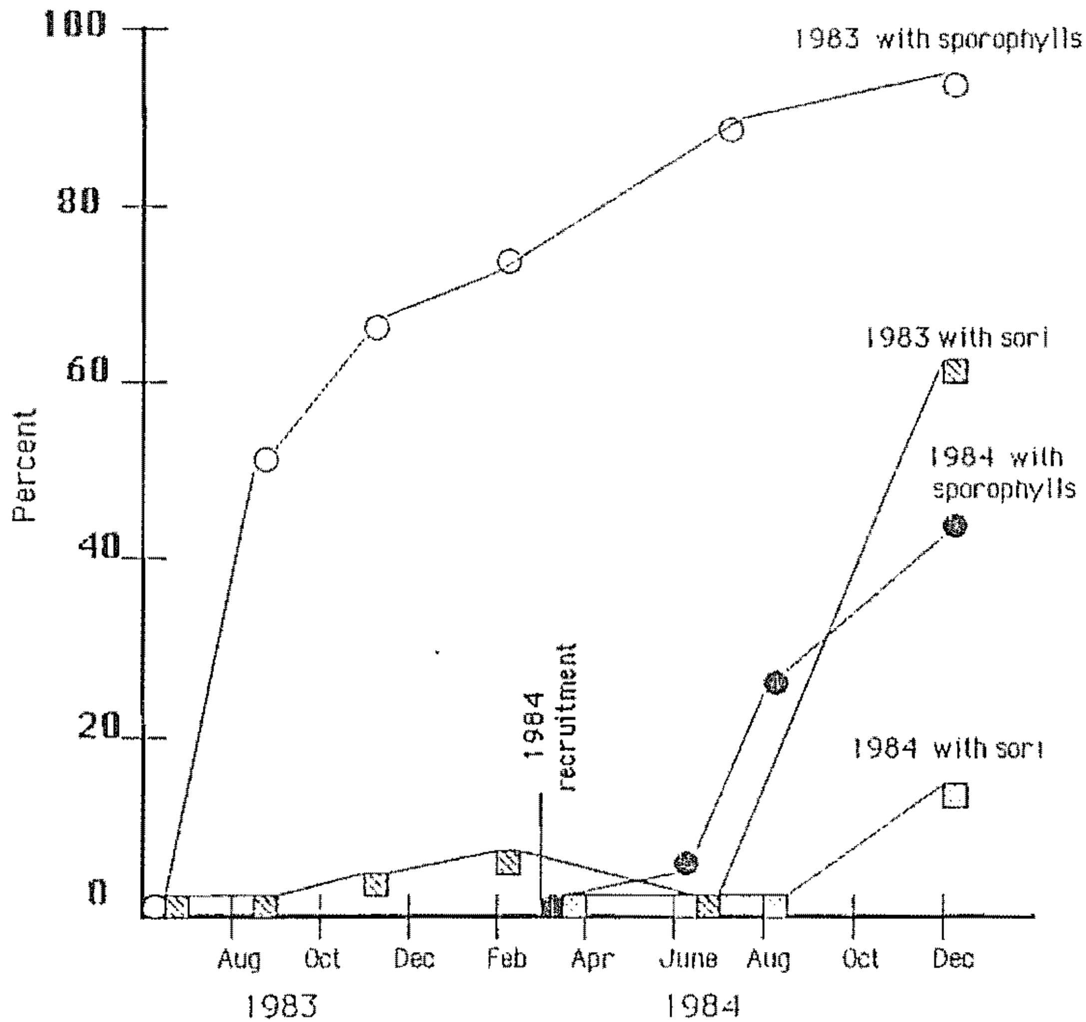

Figure 8: Percentages of 1983 and 1984 cohort plants with sporophylls or sori.