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Ecological studies of Geniculate coralline algae in Stillwater Cove, Carmel Bay, CA, with emphasis on *Bossiella californica* ssp. *schmittii* (Manza) Johans

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Carmel Bay, CA, with emphasis on *Bossiella californica* ssp. *schmittii*
(Manza) Johans**

Konar, Brenda, M.A.

San Jose State University, 1991

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ECOLOGICAL STUDIES OF GENICULATE CORALLINE ALGAE IN
STILLWATER COVE, CARMEL BAY, CA, WITH EMPHASIS ON
BOSSIELLA CALIFORNICA ssp. *SCHMITTII* (MANZA) JOHANS.

A Thesis

Presented to

The Faculty of the Department of Biology

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

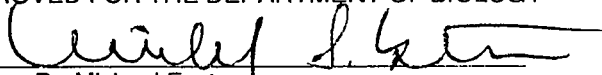
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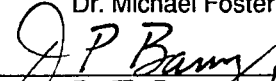
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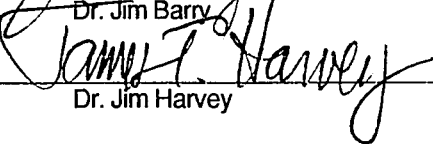
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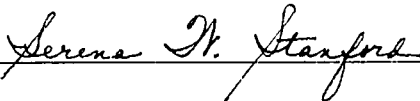


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ABSTRACT

ECOLOGICAL STUDIES OF GENICULATE CORALLINE ALGAE IN STILLWATER COVE, CARMEL BAY, CA, WITH EMPHASIS ON *BOSSIELLA CALIFORNICA* ssp. *SCHMITTII*

by Brenda Konar

Distribution and abundance of geniculate corallines were examined in a kelp forest with an understory dominated by corallines. *Calliarthron tuberosum* was most abundant, growing primarily on horizontal surfaces. *Bossiella californica schmittii* was second most abundant, found on vertical walls and cobbles. Generally, corallines were more abundant at 15 m than at 10 or 20 m.

Spring and fall recruitment and growth rates of coralline crusts and fronds were determined in clearings at 10, 15, and 20 m. These rates decreased with depth for both crusts and fronds, with some seasonal differences observed.

Aspects of demography and morphology of *Bossiella californica schmittii* were also studied. Percent cover of juvenile, adult, and senescent plants varied, with adults dominating. Adults were commonly tetrasporic, from August through April. No mortality of fronds was observed over a one year period. Plants were largest at 10 and 20 m, and most reproductive at 15 m. Intergeniculate dimensions varied little with depth. Epiphytes, particularly bryozoans, were abundant at all depths.

Where corallines were most abundant, they were smaller and more reproductive than in areas where they were less abundant. Several factors may contribute to produce these patterns, however, more studies are needed to resolve the cause of these differences.

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CHAPTER 1: DISTRIBUTION AND RECRUITMENT OF GENICULATE CORALLINE ALGAE
IN STILLWATER COVE, CARMEL BAY, CA

INTRODUCTION

The family Corallinaceae (Rhodophyta, Gigartinales) contains a large number of species, many poorly known. Corallines are grouped as geniculate (articulate) and non-geniculate (crustose) (Abbott and Hollenberg, 1987). This study concentrated on geniculate corallines. These are pink to purple algae with calcified cell walls, that live in most euphotic zones where stable surfaces are present. Geniculate corallines often form extensive mats that harbor an array of different organisms, providing a habitat similar to kelp holdfasts (Dearn, 1987). They also inhibit recruitment of other algae (particularly *Macrocystis pyrifera*) and hence may be important in structuring the kelp forest community (Reed, 1981; Wells, 1983).

Corallines occur in all oceans of the world, often dominating shallow subtidal areas and sometimes occurring deeper than other benthic algae (Johansen, 1976). Coralline abundance and distribution is affected by environmental conditions such as wave exposure, temperature, and light. For example, Johansen (1981) indicated that agitation was important in coralline growth. At subtidal sites around Monterey Bay, CA, corallines are more abundant at exposed sites than at protected sites (Devinney and Kirkwood, 1974; Harrold *et al.*, 1988). Geniculate corallines, however, tend to be more abundant in shallower waters and non-geniculates in deep (VanBlaricom and Foster, ms). Corallines generally grow better in relatively low light intensities (Pearse, 1972; Colthart and Johansen, 1973; Johansen, 1981). However, Adey (1970) found growth rates of non-geniculate corallines of the boreal-subarctic had little light dependence at temperatures below 4-6 °C., but exhibited a strong light dependence at higher temperatures.

Few researchers have investigated coralline distribution and abundance at small spatial

scales. Some qualitative studies indicate that different species of geniculate corallines inhabit different depths and substratum orientations. Deviney and Kirkwood (1974) concluded that algal species composition, including geniculate corallines, varied with depth at one exposed site. McLean (1962) found that *Calliarthron* sp. grew thicker on projecting walls that were continually exposed to wave action, and that *Calliarthron cheilosporioides* inhabited a zone from 5 m at a site in central California.

Information concerning recruitment by coralline algae to subtidal habitats is limited. Corallines recruit on artificial (Matsuda, 1989; Reed *et al.*, 1988; Hruby and Norton, 1979; Foster, 1975; Kain, 1975; Johansen and Austin, 1970), and natural surfaces (Breitburg, 1984; Reed and Foster, 1984), and can be among the first colonizers. Geniculate genera, such as *Bossiella*, *Calliarthron* and *Corallina*, can grow between 0.9 to 4.2 mm/month (Johansen and Austin, 1970; Smith, 1970; Foster, 1972; Pearse, 1972; Colthart and Johansen, 1973). Delicate species, such as *Corallina officinalis*, grew faster than more robust species, such as *Calliarthron tuberculosum* and *Bossiella orbigniana* (Colthart and Johansen, 1973). Robust species, typical of subtidal habitats in Carmel Bay, have spores which germinate and, during several months, grow slowly into substantial crusts that may become 5.0 mm in diameter before fronds appear (Johansen and Austin, 1970). Growth rates for basal crusts can be between 1.4 to 2.0 mm/month for geniculate corallines (Johansen and Austin, 1970) and 2.9 to 3.9 mm/month for non-geniculate species (Matsuda, 1989).

This study focused on the distribution of some geniculate coralline species and used clearings to examine features of crust settlement, frond production, and crust and frond growth rates in an area dominated by coralline algae. The following questions were addressed: 1) How do the distribution patterns of geniculate corallines vary with depth and substratum orientation? 2) If clearings are made in an area dominated by coralline algae, will corallines or more "weedy" ephemerals recruit? and 3) If corallines do recruit, what are the settlement and growth rates of both

basal crusts and fronds?

METHODS

This study was conducted at Stillwater Cove in Carmel Bay, California (36° 34' N, 121° 56' W), a site described by Schiel (1985), Foster and Schiel (1985), and Reed and Foster (1984). Three study areas were randomly chosen inside the cove at depths of 10, 15, and 20 m (Fig. 1). These areas were composed of large conglomerate and sandstone boulders and rock reefs surrounded by cobble fields and sand channels. The cove has a surface canopy of *Macrocystis pyrifera*, a subsurface canopy of *Pterygophora californica*, an understory largely dominated by geniculate corallines, and a primary surface of non-geniculate corallines. The site is protected from large northerly swells associated with winter storms as well as strong northwesterly winds during spring (Reed and Foster, 1984).

Distribution of the most common geniculates in the cove, *Bossiella californica* ssp. *schmittii*, *Calliarthron tuberculosum*, *Calliarthron cheilosporioides*, *Corallina vancouveriensis*, and juvenile geniculate corallines, which were unidentifiable because of size and nonreproductive status, was determined by estimating percent cover on available substrata. The ends of fifteen 10 m line transects were randomly placed in each study area. The direction of these lines was determined using random compass bearings. Percent cover of cobble, horizontal rock (slope > 45°) and vertical rock (slope < 45°), and geniculate corallines was estimated from the proportion of each substratum and geniculate type under each transect. Because geniculate corallines did not occur on sand or undercut rocks, these substratum types were excluded from analysis. Algal cover was corrected for amount of available substratum by dividing total length of each transect covered with each coralline by the total lengths of each substratum, and multiplying by 100. Comparisons of percent cover among species were made within and among depths and substratum types. Percent cover of substratum types also was compared within and among depths.

Rates of settlement and growth were determined for species that recruited into areas cleared of all biota. Plots were cleared at three sites within each of three depths (10, 15, and 20 m). Sites at each depth were between five and fifteen meters apart. At each depth, clearings of 25 cm² were made to bare rock with a pneumatic chisel. Clearings were haphazardly placed and marked individually with a numbered section of polyvinyl chloride that was attached to the substratum adjacent to the clearing with Z-spar™ A-788 Splash Zone Compound. All clearings were made on relatively smooth surfaces with slopes less than 45 degrees.

Ten clearings per site were made in March 1989, or a total of thirty clearings per depth (spring clearings). In August- 1989, five additional clearings were made at each site for a total of fifteen clearings per depth (fall clearings). Genuculate corallines surrounding the clearings were reproductive at both of these times. Data from sites within depths were combined for final comparison because there were no significant differences among the sites at each depth (see results). Fewer clearings were made in the fall because a performance curve for data collected in May, 1989 indicated that mean density of crusts vs. sample size stabilized at fifteen clearings (Fig. 2). All crusts and upright fronds, visible to the naked eye (≥ 1 mm), were counted in clearings every 8 weeks using a 16 cm² quadrat placed in the center of each cleared area. Edges of clearings were avoided to eliminate the effects of vegetative recruitment into the clearings from surrounding plants. Sampling continued until crusts had grown together or density of uprights was too high to count. Spring clearings were monitored for 48 weeks and fall clearings for 32 weeks. Densities of crusts and uprights were compared within and between depths.

Growth rates of crusts and fronds were determined within two clearings chosen randomly at each site (six clearings per depth) for each sample date. All diameters of crusts and lengths of upright plants were measured (in mm) within the 16 cm² quadrat placed in the center of each clearing. Measurements were made every eight weeks, beginning when crusts first became visible and ending when individual crusts could no longer be distinguished. Final growth rates

must be considered as minima because new crusts and fronds appeared in the clearings with time, causing the actual rates measured to be lower than if only the first recruits were measured. Growth rates of crusts and upright plants were compared among clearings, sites, and depths. Because differences in growth rates were not evident between sites within a depth (see results), data from all clearings at one site were pooled.

The cover of recruits in clearings was compared to the percent cover of corallines surrounding the clearings. Six randomly chosen clearings were selected at each depth (two from each site within a depth) and percent cover of geniculate and non-geniculate corallines was determined using a 4 cm Random Point Contact Bar. The percent cover of corallines within a 1 m radius around each of these clearings was determined with a 1 m Random Point Contact Bar (similar to that described by Foster, 1975). These bars had a string attached at each end, with five knots along their length. When a knot on the line was pulled taught away from the bar and placed on the substrate, the identity of the algae under the point was recorded. If no organisms were present at the knot, the type of substratum was noted. All knots on both sides of the bar were recorded (totaling ten points).

All data were tested for normality using Cochran's Test for Homogeneity (Zar, 1984). If data were non normal, a logarithmic transformation was used, and normality and homogeneity of variance checked again. Transformed and non-transformed data were tested for significant differences using one-factor, Model I ANOVAs and Fisher PLSD multiple comparisons. If the data were not normal after transformation, they were still examined using an ANOVA because the test is robust when there is a large sample size (Underwood, 1981). In the 8 week sampling of crust density, Cochran's Test for Homogeneity was slightly significant but ANOVA was used because all sample sizes were equal and large (Underwood, 1981).

RESULTS

The percent cover of substrata was examined at all depths as an index of the space available to coralline algae. Substrata cover (cobble, horizontal, and vertical rock) varied with depth (Fig. 3). While there were significant differences in horizontal and vertical rock with depth, greatest differences were in the abundance of cobbles. Cobble substratum was nearly four times as common at 15 and 20 m than at 10 m. Horizontal surfaces were abundant at all sites, and accounted for 60% of the substratum at 10 m, the highest by any substratum type at all three depths (Fig. 3).

Distribution and abundance of corallines varied with substratum type and depth. Overall, the most abundant species were *Bossiella californica schmittii* and *Calliarthron tuberosum*. *Calliarthron cheilosporioides*, *Corallina vancouveriensis*, and juveniles were also found, but in lower abundances (Fig. 4). Each coralline species was most abundant on a specific substratum type. At all depths, *B. californica schmittii* was more abundant on vertical rocks. Also at all depths, *C. tuberosum*, *C. cheilosporioides*, and *C. vancouveriensis* were most abundant on horizontal rocks, although of the three, *C. tuberosum* was the dominant. No clear pattern emerged in juvenile substratum preference. Juveniles, however, were more abundant on cobble surfaces at 20 m (Table 1).

Density and growth of crusts in clearings tended to be greater at shallower depths (Fig. 5). There was a significant increase in number of crusts with decreasing depth for the spring clearings at eight weeks but this difference did not persist (Fig. 5). After 16 weeks, the density of crusts at 10 m was so high that individuals could no longer be distinguished. After 24 weeks, densities at the other two depths were also too high to distinguish individuals (Fig. 5). In the fall clearings, crusts were more abundant and settled faster in shallower depths. After 8 weeks, there were significantly more crusts at 10 m than the other depths. All depths were significantly different at sixteen weeks, and these differences continued through 24 weeks (Fig. 5). After 24 weeks, the

crusts at all depths had grown together and could no longer be distinguished.

Growth rates of crusts in spring and fall clearings were similar, but growth was significantly greater at shallower depths (Fig. 6). Growth in spring clearings ranged from 0.6 mm/month at 10 m to 0.3 mm/month at 20 m, and fall clearings ranged from 5.0 mm/month at 10 m to 0.3 mm/month at 20 m (Fig. 6).

The first upright fronds were found at 10 m in 16 week old clearings. Clearings at 15 and 20 m did not produce uprights until 24 weeks. Density of all fronds tended to decrease with increasing depth during spring and fall. In spring clearings at 16 to 32 weeks, there was a significantly greater production of fronds at the 10 m site (Fig. 7). At 40 and 48 weeks, there were still significantly more fronds at 10 m, but there was also an increase at the other two depths (Fig. 7). The 48 week old geniculates at the 10 m site were too dense to be counted. Trends in frond density were similar in fall clearings, although densities were slightly higher during spring clearings. (Fig. 7).

Frond lengths during spring and fall were generally greater at shallower depths, and growth tended to be faster in the fall clearings (Fig. 8). Frond growth rates in spring clearings ranged from 0.3 mm/month at 10 m to 0.01 mm/month at 20 m. Fall rates ranged from 0.5 mm/month at 10 m to 0.03 mm/month at 20 m. Spring fronds at 40 weeks and fall fronds at 32 weeks were significantly longer at 10 m compared with 20 m. Fronds from the intermediate depth, 15 m, also had intermediate growth rates for both seasons (Fig. 8).

At each depth, percent cover of geniculate and non-geniculate corallines in the spring clearings after 48 weeks was not significantly different from natural cover found in a one meter area surrounding each clearing (1 Factor (in vs out) ANOVA, Fisher PLSD, $p \leq 0.05$, Fig. 9). Similar trends in cover were found in newly recruited clearings and in the adjacent vicinity. Although there were more geniculate than non-geniculate corallines at all depths, there was a tendency for the former to decrease, and the latter to increase, with depth (Fig. 9).

DISCUSSION

The distribution of coralline algae varied with depth and substratum orientation in Stillwater Cove. *Calliarthron tuberosum* was the dominant geniculate coralline at all depths, and was the most abundant coralline on horizontal rocks, which was the most abundant substratum (Figs. 3 and 4). *Bossiella californica schmittii* was second in abundance, and occurred primarily on vertical rocks. Johansen and Austin (1970) also found these to be the dominant species in Carmel Bay. The observed low densities of *Calliarthron cheilosporioides* on all substrata and at all depths was probably related to this plant having a higher depth distribution than sampled during this study. *Calliarthron cheilosporioides* forms a zone to a depth of about 5 m at a site a few kilometers south of Carmel Bay in central California (McLean, 1962). *Corallina vancouveriensis* and juvenile corallines were the least abundant. Like *C. cheilosporioides*, *C. vancouveriensis* also is commonly found in shallower water. It is the one coralline that can endure many hours of desiccation (Abbott and Hollenberg, 1987). Juveniles, however, were most abundant at 20 m. There may be more juveniles at this lower depth because low light may slow growth to maturity and adult size. Generally, geniculate corallines were more abundant at 15 m (Fig. 4). In agreement with Van Blaricom and Foster (ms), there was an increase in non-geniculates and a decrease in geniculates with depth (Fig. 9). Why some corallines are more successful at particular depths and on different substratum orientations is unknown.

Corallines are the obvious understory algae in this cove (Reed and Foster, 1984), and although they are slow growers, they are the most abundant colonizers. Corallines were the first and only settlers in clearings made in this coralline dominated area. The only variations seen were the actual settlement and growth rates. In contrast, Kain (1975) found variation in species recruitment in clearings made in *Laminaria* beds, especially at deeper depths. She suggested that differences in colonization were due to depth, slope, grazing, light, or available spores. Depth was

the only variable purposely manipulated in this study. Which variables associated with depth that caused these results are unknown. In this study, slope was held fairly constant. However, grazing and light were not, hence these could be part of the cause. Generally there is less light at greater depths and under more kelp canopy (Reed and Foster, 1984). *Bossiella californica schmittii* produced tetraspores from August to April, when these clearings were made (see Chapter 2). If other corallines produced spores at this time, this may explain why corallines were found so abundantly in the clearings. The clearings were not monitored long enough to identify plants to species, so many of the new recruits could have been *B. californica schmittii*. Hruby and Norton (1979) also found that species whose propagules were most abundant in the water also were the most common colonists, and patchiness in the distribution of propagules in the water was reflected on newly settled substratum. Foster (1975), however, reported that corallines recruited into an area which was dominated by corallines (61%), but they did not produce a monoculture. This may be because his work was on plates above the substratum, his site was shallower (hence more light), or because his site in southern California has a greater number of species than Stillwater Cove. The latter may have resulted in a higher diversity of propagules in the water column. Reed and Foster (1984) found various species recruited to clearings which were made under varying kelp canopies. In their study, light did influence the composition of the recruits, and their results suggest that corallines are capable of recruiting even when light is unfavorable for most other species. All of the studies mentioned were conducted at single depths. This study was done at three different depths, yet corallines were the only colonizers.

As found by Matsuda (1989) in the Ryukyu Islands, coralline settlement was similar for spring and fall clearings. In this study, corallines were the only settlers during both seasons, and colonization was always greater at shallower depths. In contrast, Emerson and Zedler (1978) found that scraping rocks in different seasons led to different algal dominants with no predictable sequence of colonization. This pattern was thought to be caused by environmental variations.

The pre-clearing dominant, *Lithothrix aspergillum*, recolonized all disturbed plots, but not in the original densities. In this study, initial settlement rates of crusts were generally higher in the spring clearings. This coincides with a previous study at 15 m in Stillwater Cove, in which the kelp canopy was at a maximum in July and minimum in March (Reed and Foster, 1984). Crusts initially appeared sooner in spring clearings as expected if differences in light were important. Seasonal differences in crust settlement rates were particularly apparent at 10 m where the kelp canopy was thickest (Fig. 5). Also as expected if light was a major controlling factor, there was more settlement and growth of crusts and appearance of fronds in the fall clearings at sixteen weeks when the kelp canopy was recovering in the spring and declining in the fall (Figs. 5, 6, and 7).

For spring and fall seasons, crusts settled and expanded in diameter faster at 10 m (Figs. 5 and 6). This is expected due to the higher light levels at shallower depths. Johansen and Austin (1970) found basal crusts appeared in less than one month. In this study, crusts may have been present after one month, but the first measurements were not made until eight weeks. Growth rates in spring clearings ranged from 0.6 mm/month at 10 m to 0.3 mm/month at 20 m, and fall clearings ranged from 0.5 mm/month at 10 m to 0.3 mm/month at 20 m (Fig. 6). This is much slower than rates found by Matsuda (1989) found in the Ryukyu Islands (2.9 to 3.9 mm/month). His study was conducted with non-geniculate corallines, which may grow faster than basal crusts of geniculate corallines. However, basal crust growth rates in this study also were slower than those found by Johansen and Austin (1970) (1.4 to 2.0 mm/month). In this study, the dominant corallines, *Calliarthron tuberosum* and *Bossiella californica schmittii* were considered robust species (particularly *B. californica schmittii*) and robust species grow more slowly than delicate species (Colthart and Johansen, 1973). Johansen and Austin (1970) also worked with *C. tuberosum*, but they were working at 5 and 11 m. The difference in light or other environmental conditions associated with depth may be the cause of the variations.

Fronds appeared sooner and grew faster at 10 m. Plants had the first protuberances at 10

m when clearings were 16 weeks old. At greater depths, fronds were not seen until 24 weeks. This differs from previous studies that found that newly settled *Calliarthron tuberosum* initiated fronds after eight weeks, and in culture, after three weeks (Johansen, 1969). The differences seen here are probably because Johansen's (1969) field plants were grown at shallower depths, and lab plants were grown under optimal conditions. Frond growth rates ranged from 0.01 to 0.5 mm/month. In other studies *Bossiella gardneri*, *C. tuberosum*, and *Corallina vancouveriensis* grew in length between 3.3 to 4.2 mm per month (Smith, 1970), and Johansen and Austin (1970) found that *C. tuberosum* grew 1.3 to 2.3 mm in length per month. Foster (1972) found geniculate corallines grew 0.9 to 1.8 mm per month on blocks in the field. In the lab, *Corallina officianalis* grew 2.2 mm per month (Colthart and Johansen, 1973), and *Bossiella orbigniana* grew 1.7 mm per month (Pearse, 1972). The differences between findings in this study and others is likely related to light, but could be due to variations in species, age, and environmental conditions. This study showed that growth declined with depth and light. None of these previous studies were done along a depth gradient. Also, the dominant species in this study were the robust *C. tuberosum* and *Bossiella californica schmittii* and robust appear to species grow slower. All of these studies were done on different species and only one, Foster (1972), was not on adult plants. Aside from depth, differences in growth rates could be due to the size differences in growth with site.

Forty-eight weeks after settlement, plants that had settled into the clearings were identical in composition and abundance to those immediately surrounding clearings (Fig. 9). "Weedy" ephemeral species were never seen; corallines were the only algae that recruited into this coralline dominated area. This system proceeded directly to a "climax community," and no successional communities existed. This is quite different from findings in intertidal studies, where it took nine weeks for *Alaria/Corallina/Bossiella* (Lee, 1966) to dominate, and slightly less than two years for a *Corallina* (Kitching, 1937) community to revert back to its climax community. This

may be due to a lack of a seed bank of ephemeral species. Corallines generally dominate Stillwater Cove and there are probably relatively few non-coralline propagules in the water column. Low light levels caused by the various canopies in this cove probably enhance the conditions for coralline recruitment.

Overall, there were more uprights at shallow water and more crusts in deep water (Fig. 9). The abundance trends for the newly recruited areas and the adjacent vicinity concur with those found by VanBlaricom and Foster (ms). The differences in species requirements or other factors that may cause this variation would be a fruitful area of future research.

CHAPTER 2: THE MORPHOLOGY AND DEMOGRAPHY OF
BOSSIELLA CALIFORNICA SSP. *SCHMITTII* (MANZA) JOHANS.
IN STILLWATER COVE, CARMEL BAY, CA

INTRODUCTION

Bossiella californica schmittii is a geniculate coralline found in the rocky subtidal from British Columbia to San Diego, Ca. with the type locality off Pt. Loma, San Diego Co (Abbott and Hollenberg, 1987). It is commonly found in the understory of *Macrocystis pyrifera* forests (Devinney and Kirkwood, 1974; Foster and Schiel, 1985; Harrold *et al.*, 1988) where it is abundant on vertical walls (see Chapter 1). *Bossiella californica schmittii* has horizontally growing fronds with a definite dorsiventral orientation. The dorsal surface contains up to fifty conceptacles on each intergenicula (Johansen, 1971). These conceptacles differ from those of other geniculate coralline genera, such as *Calliarthron* sp., because they originate in cortical rather than medullary tissue (Johansen, 1973); they are eccentric in all *Bossiella* sp. (Johansen, 1976). *Bossiella californica schmittii* produces tetraspores, bispores, and male and female gametes. Dorsal surfaces of intergenicula are dark violet, and the ventral surfaces are light pink. Intergenicula are 3-12 mm long and 10-15 mm broad with thin, flat wings bending downwards. Ventral surfaces frequently harbor an array of bryozoans and tube worms (Abbott and Hollenberg, 1987).

In Stillwater Cove, this species is most abundant at 15 m and on vertical rocks. It is found secondarily on cobble and is least abundant on horizontal rocks (see Chapter 1). Most corallines are long-lived (Johansen and Austin, 1970; Foster, 1972), but little is known about reproductive timing, growth, and mortality.

The morphology of many seaweeds changes with depth. The fronds of some algae, such

as *Callophyllis crispa* and *Phycodryas rubens* (Norall *et al.*, 1981), decrease in size and thickness with increasing depth, whereas other algae, such as *Chondrus crispus* (Mathieson and Burns, 1975) and *Ptilota serrata* (Norall *et al.*, 1981), exhibit a progressive elongation and narrowing of the thallus. Some calcareous algae may be less heavily calcified in deeper water (Gilmartin, 1960). Ford *et al.* (1983) reported that the number of conceptacles in different *Lithophyllum incrustans* populations were highly correlated with age of the plant. These morphological differences have not been examined closely for geniculate corallines. This study explored the variation in some of these variables for *Bossiella californica schmittii*, including number of fronds per plant, frond length, number of intergenicula per frond, number of conceptacles per intergeniculum, intergeniculate length and width, and conceptacle position.

Bossiella californica schmittii covers a large portion of the substratum at Stillwater Cove (see Chapter 1), and provides a significant amount of habitat for benthic and encrusting organisms. Many organisms inhabit the spaces among the fronds of corallines, but little is known about the organisms that epiphytize it (Dommasnes, 1967; Dearn, 1987). This plant harbors many invertebrates on its ventral surface, which, like those on *Macrocystis pyrifera*, may contribute to blade loss (Dixon, 1981). In this part of the study, the epiphytic cover on the ventral portion of *B. californica schmittii* was examined to determine if differences in species composition and abundance correlated with depth or intergeniculate position.

Bossiella californica schmittii commonly occurs in subtidal areas where only a few other algal species, such as *Desmarestia ligulata* var. *firma* and non-geniculate corallines, are found. Its presence in this atypical algal habitat offers refuge to many invertebrate species, providing cover and substratum. This study examined various questions concerning the ecology of this kelp forest plant. These included: 1) How is the plant distributed? 2) How old is it when it becomes reproductive? 3) When is it reproductive? 4) What are frond mortality rates? 5) Are there any differences in morphology and epiphyte cover with depth?

METHODS

Distribution and abundance of juvenile, adult, and senescent *Bossiella californica schmittii* at different depths and various substrata were examined using cover estimates. The study sites are described in Chapter 1. Fifteen ten meter line transects were surveyed at depths of 10, 15, and 20 m. Placement of transects, calculations of percent cover, and substratum sites were described in Chapter 1. Juvenile plants were non-reproductive, with small upright branches in clusters with frond lengths of less than 5 cm. Healthy adult plants were reproductive, purple fronds growing alone or in small clusters, with lengths greater than 5 cm. Senescent plants were usually solitary, white, and fragile. Percent cover of various plant types at each depth was corrected for amount of available substratum, and then compared for differences within and among depth and substratum. Depth distribution and substratum of each life stage was compared.

Age at first reproduction was determined in plants that recruited to clearings made in March, 1989 (see Chapter 1). Age of sexual maturity was determined by recording the date of appearance of conceptacles.

To determine temporal variation in the reproduction of adult plants, twenty plants from each depth were collected randomly every month from the top 0.5 m of north facing vertical walls. These were brought back to the lab, conceptacles were manually opened with a dissecting probe, and examined at 20x. All conceptacles from intergeniculum #1, 3, 5, 7, and 9 (in order from tip towards base) of the longest frond on the plant were examined. Presence and type of conceptacle product, if any, were recorded.

Frond mortality was examined by observing twenty-five adult plants at each depth for one year. Randomly chosen plants were tagged with a numbered piece of polyvinyl chloride epoxied to the substratum next to the plant with Z-spar™ A-788 Splash Zone Compound. All fronds on the

plant were measured as either $<$ or $>$ 1 cm. Fronds were counted instead of individual plants because it was sometimes difficult to differentiate individuals. In such cases, it is best to consider the population biology of the modular components (ramets) rather than genets (Chapman, 1985). These plants were remeasured after one year.

Morphological variations were compared among depths. Variations caused by growth patterns include: branch length, intergeniculum marginal dimensions, and intergeniculum thickness (Johansen, 1969). All but the latter was examined in this study because the intergenicula were commonly overgrown by epiphytes, and were thus difficult to measure. Moreover, ventral epiphytes make measurements inaccurate as they cannot be entirely removed without damaging the plant. Twenty-five plants were collected at each depth from the top 0.25 m of north facing vertical walls and examined at 20x. Number and length of fronds and number of intergenicula per frond were measured. A frond was defined as each upright portion of the plant which arose from the basal crust. Hence, one frond may have many secondary branches that come off the primary branch. The first (tip), third, fifth, and ninth intergeniculum on the longest frond of each plant were further examined for size, number of conceptacles per intergeniculum (only found on the dorsal side), and percent cover of ventral epiphytes (Fig. 10). Epiphytes on the intergenicula were recorded under random points in the micrometer of the eyepiece of a dissecting microscope. Number and length of fronds, number of intergenicula per frond, intergeniculum size (length and width), number of conceptacles per intergeniculum, and percent cover of ventral epiphytes were compared among depths and with position on the frond. Length and width of intergeniculum were examined instead of area because the length is determined by the plant while the width can be environmentally modified.

All data were treated and tested for significant differences as described in Chapter 1.

RESULTS

Abundances of life stages varied among substrata but were similar among depth. Adults of *Bossiella californica schmittii* were the most common form of this coralline in the field, and was found primarily on vertical walls (Fig. 11). Juvenile and senescent plants had similar abundances at all depths and substratum types, but were much less abundant than adults (Fig. 11).

Bossiella californica schmittii was reproductive from August to April. Tetraspores were the only dissemules found at any depth. The first reproductive plant occurred in the spring clearings at 32 weeks. It was a single 1.1 cm long frond with three intergenicula and nine tetrasporangial conceptacles. This was the only reproductive plant found in any of the clearings at 32 weeks.

No mortality was observed during the one year study period. All tagged plants were relocated at the end of the study, and all had the same number of < 1 mm and >1 mm fronds as the previous year.

The morphology of *Bossiella californica schmittii* varied with depth. The number of fronds per plant ranged from 2 to 24, with more fronds on plants at 15 m (Table 2). Lengths of fronds ranged from 0.1 to 10.0 mm, and were significantly longer at 20 m than at 15 m. Number of intergenicula ranged from 1 to 188 per frond, and maximum number of conceptacles per intergeniculum was 56. Number of intergenicula per frond was greatest at 10 and 20 m and number of conceptacles per intergeniculum was highest at 15 m (Table 2).

Intergeniculate lengths and widths varied little with depth (Table 3). For intergeniculum 3, the lengths at 20 m were less than at the other two depths. For intergeniculum 5 and 9, the widths at 15 m were significantly greater than at the other depths (Table 3).

There were some differences in the number of conceptacles with the position on the frond and with depth (Tables 4 and 5). Intergeniculum 1 and 5 had significantly more conceptacles at 15 m than at the other depths and, in general, conceptacles were most abundant on all

intergenicula at this depth. The fewest conceptacles were found at 20 m. At 10 m and 20 m, intergeniculum 1 had significantly fewer conceptacles than either intergeniculum 3 or 5. At 10 m, intergeniculum 9 had significantly fewer conceptacles than intergeniculum 3. At 15 m, intergeniculum 9 had significantly fewer conceptacles than intergeniculum 3 or 5 (Tables 4 and 5).

The cover of epiphytes on the dorsal surface of the intergenicula varied slightly with depth and position on the frond (Table 6). Bryozoans were the most abundant epiphyte at all depths and intergeniculum positions. Spirorbids were the second most abundant epiphyte, and were most abundant at 15 m. There was generally less fouling at intergeniculum 1. Miscellaneous organisms included non-geniculate corallines, fleshy red algae, sponges, tunicates, cup corals, anemones, and barnacles.

DISCUSSION

Juvenile and senescent plants were rarely seen during this study, but adult plants were common at all depths and substrata. Adults were most abundant at 15 m and on vertical substrata (Fig. 11). Plants on vertical surfaces appear to settle on small rock outcroppings on walls and not necessarily on a vertical plane. Why this plant does so well in this habitat where few other algae can survive is unknown. *Calliarthron tuberculosum* is the dominant coralline at all three depths and yet it is rarely found on vertical surfaces (see Chapter 1). The fronds of *Bossiella californica schmittii* are stiffer than *C. tuberculosum*. This may enable *B. californica schmittii* to survive the harsh environmental conditions which may be found on vertical walls.

The first reproductive frond occurred in a clearing that was 8 months old and the frond was 1.1 cm long. All reproductive plants were scored as adults in the distribution study. This suggests that the lack of juveniles may result from rapid maturation. In another study, *Calliarthron tuberculosum* reached maturity after 11 months (Johansen and Austin, 1970). Non-geniculate corallines have shown raised conceptacles after one month (Matsuda, 1989). Observed differences in the timing of new conceptacles could be due to timing of settlement and/or reproduction, environmental conditions, or species differences. Non-geniculates may become mature before geniculates because the latter must produce fronds that bear reproductive structures.

Bossiella californica schmittii was reproductive during a large portion of the year (August through April). Zonate tetraspores were the dominant type of disseminules at Stillwater Cove. Bisporos were seen only during one month, and were very rare (< 1% of the plants examined). Carpospores and spermatia were never seen. Johansen and Austin (1970) found spermatia and carpospores in this plant only a few kilometers away at Pt. Lobos, Carmel Bay, California, but even at this site, tetraspores dominated.

All tagged plants at all depths survived, and none showed signs of senescence. This was expected because corallines are slow growers, and have been projected from other studies to live a long time. *Calliarthron tuberculosum* grew to its maximum average size of 10 cm after 4 to 5 years at Pt Lobos, California (Johansen and Austin, 1970). *Calliarthron* sp. in southern California have been calculated to grow to 10 to 20 cm (average maximum height) in five to ten years (Foster, 1972). These, however, do not represent maximum longevity, but are ages of average maximum height. Thus far, no mortality studies have been conducted. However, the lack of change in numbers of fronds < and > 1 mm during this study has a number of possible implications. Plants could lose fronds at a rate equal to the rate of replacement, though this loss rate must be very low given data on adult coralline growth rates. If this were true, however, Plants would have to lose one > 1 mm frond at the same time that a < 1 mm frond became > 1 mm and a new < 1 mm frond arose. If this were the case, the entire plant could be very long-lived as all lost fronds are replaced by new ones. More probable is that the plant stops growing at a certain size and is again probably very long-lived. Either of these phenomena may result in the few actual senescent plants were seen in the field. In the distribution part this study, discolored plants were scored as senescent but they may not have been dying plants. *Asterina miniata*, an abundant seastar found in Stillwater Cove, exudes its stomach over plants and discolors them (pers obs). Change in color of these plants may be temporary, and the plant may still be healthy. Therefore, there may be no actual senescent plants in this cove. More work needs to be done on frond growth vs. size, mortality, and the pigments associated with coralline algae to resolve these issues.

There were greater numbers of fronds per plant at 15 m compared to the other depths, but fronds were longer at 20 m and there were more intergenicula per frond at 10 m (Table 2). Because there were no significant differences in intergeniculum sizes between depths, number of fronds per plant, frond length, and number of intergeniculum per frond can be multiplied to give a relative index for total plant size. This index for 10, 15, and 20 m was 625, 530, and 645,

respectively. A small frond can have more intergenicula per frond because it has more branching. The plant size index, multiplied by the number of conceptacles per intergeniculum, gives a reproductive index. This index for 10, 15, and 20 m was 3320, 4555, and 2000, respectively. Thus, at 10 m, plants are large, but not very reproductive. At 15 m, plants are small, but they are more reproductive. Lastly, at 20 m, the plants are large, and are the least reproductive. Plants may be smaller at 15 m than at 10 m because there is less light at deeper depths. Steneck and Adey (1976) found that the amount of branching in *Lithophyllum congestum* was influenced by reduced light. The larger size of plants at 20 m was puzzling; they may be longer lived than at the other two depths, or there may be a negative correlation between reproduction and growth since these plants were the least reproductive. Plants at 20 m may be larger because they are less reproductive. Ford *et al.* (1983) found that reproductive effort (conceptacle count) in *Lithophyllum incrustans* differed among sites. Photoperiod and light intensity also may play an important role in conceptacle number in *Bossiella cretacea* (Masaki *et al.*, 1982). This also could be true for *Bossiella californica schmittii*. For reproductive measures, it was assumed that conceptacle sizes were similar at all depths. Conceptacle dimensions were not quantitatively measured, but there were no apparent qualitative differences when examined through a dissecting scope.

There were no clear trends in intergenicula size (Table 3). This may be due to the intergenicula shape being genetically determined but environmentally modified (Johansen, 1971). Erosion, secondary growth, and adverse environmental conditions may modify intergenicula shape and sometimes branch number (Johansen, 1971). The modification of intergenicula by the environment may start at such an early age that differences are quickly expressed. Width of intergenicula varied more than length in various species of *Bossiella* (Johansen, 1971). Intergenicula shape has also been shown to vary with different environments in various corallines (Munda, 1972; Johansen, 1981). The growth of the wings, and hence the width of the intergenicula, seemed to be slower during winter and in wave-exposed areas

(Johansen, 1971). However, for *Bossiella californica schmittii*, no such patterns were observed. No differences were expected in the width because this is usually modified by the environment; however, no differences were found in the lengths either. The environment could also be affecting the lengths or else there are no differences in lengths among depths. The actual role that any of these variables play in intergenicula shape is unknown and needs to be examined further.

Bryozoans were the dominant epiphyte at all intergeniculate positions and at all depths (Table 6). The newest intergeniculum was least fouled, suggesting fouling increases (at least temporarily) with age. The only depth difference was fewer spirorbids at 20 m. Foster and Schiel (1985) suggested epiphytes became particularly abundant as algal fronds became senescent. They believe that this is probably not due to epiphytes actually overwhelming plants and causing their demise, but the general deterioration of host plants at this time. Long-lived perennials such as the Fucales may shed their epidermal cells to reduce fouling, and this is the case for *Ascophyllum nodosum* (Filion-Myklebust and Norton, 1981) and *Halidrys siliquosa* (Moss, 1982). *Bossiella californica schmittii* does not follow the same trends as other perennials. The plant also does not seem to be shedding cells to remove epiphytes from its ventral side because there are so many epiphytes on this side. Almost all epiphytes were on the ventral surface, and did not seem to affect the plants health. If the dorsal side was epiphytized, then the plant would receive less light and conceptacles would be covered so reproduction could be impaired. If epiphytes are removed, the thallus beneath is a healthy pink color. In another study, Johnson and Mann (1986) suggested that the crustose coralline alga, *Phymatolithon* sp., has an unstable surface, and has the ability to slough off cells to inhibit settlement on the crust.

An additional question which resulted from this study was why corallines were generally more abundant at 15 m, yet settled and grew faster at 10 m (Chapter 1 and Fig. 12). Because *Bossiella californica schmittii* was one of the plants that recruited into clearings, it may be that all

corallines from the clearings have similar trends. The abundance and the size of *B. californica schmittii* showed opposite trends (Fig. 13). There was a higher percent cover at 15 m where plants were smaller, hence growth may have been faster at 10 m because of increased light. At 20 m, the abundance and size were intermediate between those of 10 and 15 m. Corallines might have been more abundant at 15 m even though they grew slower because there were significantly more conceptacles produced at 15 m. Plants were least reproductive at 20 m, perhaps due to less light. Higher plant cover was correlated with more conceptacles (Fig. 14). The plants might invest more energy into reproduction at 15 m, and more into growth at 10 m. Size and reproduction showed opposite trends; where plants were larger, they were less reproductive (Fig. 15). In addition to changes in reproductive effort, grazers may affect these trends; there may have been more grazers and, hence, fewer corallines at 10 m. They may have grown faster so they were not overgrazed. This, however, was unlikely because corallines are generally grazer resistant (Chapman, 1985). Lastly, there could be poorer conditions at 15 m that affect both reproduction and growth.

There is still much to learn about the demographics of coralline algae. This study has suggested some new and interesting trends, but it has also uncovered many new questions. A number of growth and reproductive characteristics of *Bossiella californica schmittii* vary with depth. Corallines recruit and grow faster at 10 m, yet there are more plants, particularly, *B. californica schmittii*, at 15 m, and these plants are more reproductive. Additional studies are needed to understand the demographics of this and other corallines.

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Table 1. Depth differences of corallines on each of the substrata. (n/s) = not significant, (*) = $p \leq 0.05$, (**) = $p \leq 0.001$, (ANOVA, $n=15$).

depth	<i>B. c. schmittii</i>		<i>C. tuberculosum</i>		<i>C. cheilosporioides</i>		<i>C. vancouveriensis</i>		juveniles			
	cobble	horiz	vert	cobble	horiz	vert	cobble	horiz	vert	cobble	horiz	vert
10 m vs 15 m	n/s	n/s	n/s	n/s	15>10**	n/s	n/s	n/s	n/s	n/s	n/s	n/s
10 m vs 20 m	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	20>10**	n/s	n/s
15 m vs 20 m	n/s	n/s	n/s	15>20*	15>20**	n/s	n/s	n/s	n/s	20>15**	n/s	n/s

Table 2. Number of fronds per plant, frond length, intergenicula per frond, and conceptacles per intergeniculum of *Bossiella californica schmittii* at three depths. \bar{x} (\pm 1 S.E., min, max, N). * = $p \leq 0.001$ (ANOVA).

Depth	# fronds/plant	frond length (mm)	# intergenicula/frond	# conceptacles/intergeniculum
10 m	* 7.8 (0.7, 2.0, 17.0, 25)	3.6 (0.1, 0.1, 8.9, 194)	* 22.3 (2.1, 1.0, 188.0, 194)	* 5.3 (1.0, 0.0, 61.0, 124)
15 m	* 11.3 (1.0, 4.0, 24.0, 25)	* 3.3 (0.1, 0.1, 9.1, 284)	* 14.2 (0.9, 1.0, 87.0, 284)	* 8.6 (1.2, 0.0, 56.0, 124)
20 m	* 8.0 (0.8, 2.0, 17.0, 25)	* 3.9 (0.1, 0.5, 10.0, 201)	* 20.7 (1.3, 2.0, 112.0, 201)	* 3.1 (0.5, 0.0, 39.0, 125)
signif. diff.	* = 15 m > 10 m and 20 m	* = 15 m > 20 m	* = 10 m and 20 m > 15 m	* = 15 m > 10 m and 20 m

Table 3. Intergenicula lengths and widths at five positions on the longest frond of Bossiella californica schmittii at three depths. * = $p \leq 0.001$ (ANOVA).

Depth	Length (mm)				Width (mm)				Significant differences
	$\bar{x} \pm 1se$	min	max	n	$\bar{x} \pm 1se$	min	max	n	
Intergeniculum # 1									
10 m	4.3 ± 0.8	1	18	25	3.4 ± 0.5	1	12	25	
15 m	5.0 ± 1.0	1	19	25	3.4 ± 0.5	1	10	25	
20 m	3.3 ± 0.4	1	8	25	2.4 ± 0.3	1	6	25	
Intergeniculum # 3									
10 m	6.3 ± 3.2	2	17	25	5.4 ± 0.6	2	15	25	
15 m	6.6 ± 0.6	3	13	25	5.2 ± 0.4	1	10	25	
20 m	4.2 ± 0.3 *	2	8	25	4.4 ± 0.3	2	8	25	* = 10 m and 15 m > 20 m
Intergeniculum # 5									
10 m	5.9 ± 0.5	2	16	25	6.7 ± 0.7 *	2	18	25	* = 10 m > 15 m and 20 m
15 m	5.9 ± 0.5	2	13	25	4.7 ± 0.4	2	9	25	
20 m	4.8 ± 0.4	2	8	25	4.9 ± 0.4	1	9	25	
Intergeniculum # 7									
10 m	4.7 ± 0.4	1	9	25	5.0 ± 0.5	1	17	25	
15 m	5.0 ± 0.4	1	8	25	4.5 ± 0.3	1	7.5	25	
20 m	4.1 ± 0.3	2	7	25	4.1 ± 0.3	2	7	25	
Intergeniculum # 9									
10 m	4.0 ± 0.5	1	10	23	4.3 ± 0.6	1	12	23	
15 m	4.5 ± 0.6	1	12	24	3.1 ± 0.4 *	1	7	24	* = 10 m and 20 m > 15 m
20 m	4.4 ± 0.2	2	6	25	4.6 ± 0.3	2	8	25	

Table 4. Number of conceptacles per intergeniculum for five positions on the longest frond of *Boswellia californica schmittii* at three depths. \bar{x} (\pm 1 S.E., max, N). (*) = $p \leq 0.01$, (**) = $p \leq 0.05$ (1-way ANOVA).

Depth	Intergeniculate Position					Position Statistics
	#1	#3	#5	#7	#9	
10 m	1.3 (0.9, 23, 25)	9.6 (3.3, 61, 25)	7.8 (2.5, 47, 25)	4.8 (8.5, 29, 25)	2.8 (1.1, 16, 23)	* = #3 > #1, ** = #5 > #1 & #3 > #9
15 m	9.8 (3.2, 56, 25)	11.5 (2.9, 49, 25)	11.9 (2.8, 45, 25)	6.3 (2.5, 53, 25)	3.3 (1.7, 30, 24)	** = #3 & #5 > #9
20 m	0.4 (0.2, 5, 25)	4.6 (1.6, 39, 25)	5.1 (1.2, 23, 25)	2.4 (0.8, 15, 25)	2.6 (0.9, 19, 25)	* = #3 & #5 > #1
Depth Stats	* = 15 m > 10 m and 20 m		** = 15 m > 20 m			

Table 5. Depth and intergeniculate position differences (2-way ANOVA)
 (n/s) = not significant, (*) = $p \leq 0.05$, (**) = $p \leq 0.01$, (***) = $p \leq 0.001$

depth	position	10 m			15 m			20 m							
		# 1	# 3	# 5	# 7	# 9	# 1	# 3	# 5	# 7	# 9	# 1	# 3	# 5	# 7
10 m	# 1														
	# 3	**													
	# 5	*	n/s												
	# 7	n/s	n/s	n/s											
	# 9	n/s	*	n/s	n/s										
15 m	# 1	**	**	n/s	n/s	*									
	# 3	***	n/s	n/s	*	**	n/s								
	# 5	***	n/s	n/s	*	**	n/s	n/s							
	# 7	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s						
	# 9	n/s	*	n/s	n/s	n/s	*	**	**	n/s					
20 m	# 1	n/s	n/s	*	n/s	n/s	**	***	***	*	n/s				
	# 3	n/s	n/s	n/s	n/s	n/s	n/s	*	*	n/s	n/s	n/s			
	# 5	n/s	n/s	n/s	n/s	n/s	n/s	*	*	n/s	n/s	n/s	n/s		
	# 7	n/s	*	n/s	n/s	n/s	*	**	**	n/s	n/s	n/s	n/s	n/s	
	# 9	n/s	*	n/s	n/s	n/s	*	**	**	n/s	n/s	n/s	n/s	n/s	n/s

Table 6. Percent cover of epiphytes at five positions on the longest frond of *Bossiella californica schmittii* at three depths. $\bar{x} \pm 1S.E.$. *, ** = $p \leq 0.001$ (ANOVA, $n=25$).
 b = brozoan, sp = spirorbid, misc = miscellaneous epiphyte, unf = unfouled
 * = sig. diff w/in a frond, ** = sig diff w/in one position at various fronds

position	bryozoan	spirorbid	misc	unfouled	sig. diff. for % epiphyte
10 m					
1	* 29.6 ± 6.7	**/* 1.6 ± 1.1	6.4 ± 4.6	* 62.4 ± 7.6	b>sp,misc ; unf>b,sp,misc
3	* 51.2 ± 7.4	**/* 9.6 ± 2.6	** 0.8 ± 0.8	* 38.4 ± 7.2	b>sp,misc ; unf>sp,misc
5	* 63.2 ± 6.4	* 13.6 ± 4.0	8.8 ± 4.2	**/* 14.4 ± 3.9	b>sp,misc,unf
7	* 52.0 ± 7.7	* 20.0 ± 4.9	4.0 ± 2.6	* 24.0 ± 5.9	b>sp,misc,unf ; sp,unf>misc
9	46.1 ± 6.2	** 11.3 ± 4.1	** 4.3 ± 2.1	* 38.3 ± 6.8	b>sp,misc ; unf>sp,misc
sig. diff. w/in frond	* = 3, 5, 7 > 1	* = 5, 7 > 1 7 > 3		* = 1 > 3, 5, 7, 9 5, 9 > 3	
15 m					
1	* 24.8 ± 7.0	**/* 8.0 ± 3.3	* 0.8 ± 0.8	* 66.4 ± 7.5	b>sp,misc ; unf>b,sp,misc
3	* 49.6 ± 6.8	** 14.4 ± 3.9	** 12.0 ± 4.6	* 24.0 ± 4.6	b>sp,misc,unf
5	* 52.8 ± 6.5	19.2 ± 4.1	9.6 ± 4.8	**/* 18.4 ± 3.6	b>sp,misc,unf
7	* 52.8 ± 6.2	17.6 ± 3.7	* 13.6 ± 5.9	* 16.0 ± 2.8	b>sp,misc,unf
9	* 47.5 ± 7.0	**/* 24.2 ± 5.5	** 3.3 ± 2.0	* 25.0 ± 5.9	b>sp,misc,unf ; sp,unf>misc
sig. diff. w/in frond	* = 3, 5, 7, 9 > 1	* = 9 > 1	* = 7 > 1	* = 1 > 3, 5, 7, 9	
20 m					
1	* 23.2 ± 5.4	**/* 0.0 ± 0.0	5.6 ± 3.6	* 71.2 ± 6.0	b>sp,misc ; unf>b,sp,misc
3	* 48.8 ± 6.9	** 4.0 ± 2.0	** 7.2 ± 3.2	* 40.0 ± 6.9	b>sp,misc ; unf>sp,misc
5	* 47.2 ± 4.9	* 9.6 ± 3.5	8.0 ± 2.8	**/* 35.2 ± 4.4	b>sp,misc,unf ; unf>sp,misc
7	* 48.8 ± 7.0	* 11.2 ± 3.8	10.4 ± 3.9	* 29.6 ± 5.4	b>sp,misc,unf ; unf>sp,misc
9	* 51.2 ± 5.7	** 7.2 ± 3.0	** 13.6 ± 4.7	* 28.0 ± 4.0	b>sp,misc,unf ; unf>sp,misc
sig. diff. w/in frond	* = 3, 5, 7, 9 > 1	* = 5, 7 > 1		* = 1 > 3, 5, 7, 9	
sig. diff. w/in position and at various fronds		** 1 : 15m>10m, 20m 3 : 15m>20m 9 : 15m>20m	** 3 : 15m>10m 9 : 20m>15m	** 5 : 20m>10m, 15m	

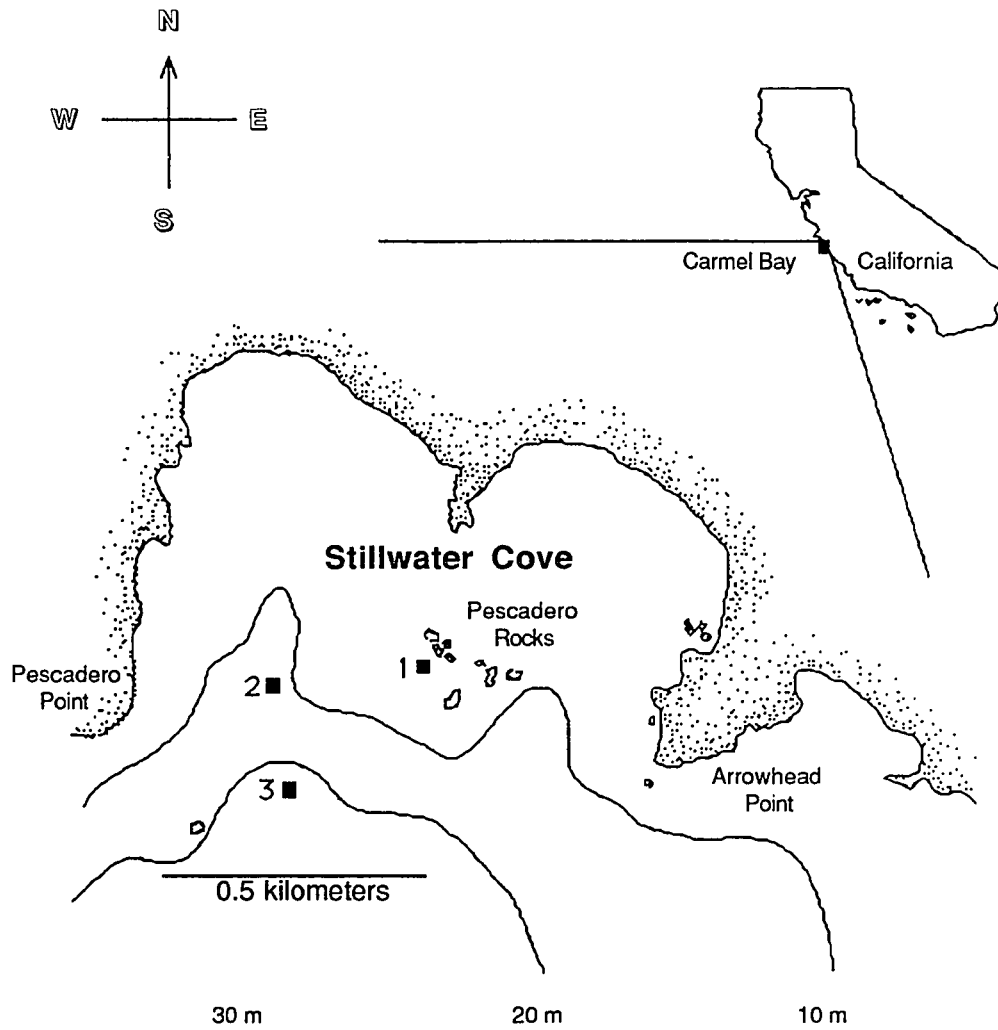


Figure 1. Study sites at Stillwater Cove, Carmel Bay, CA.

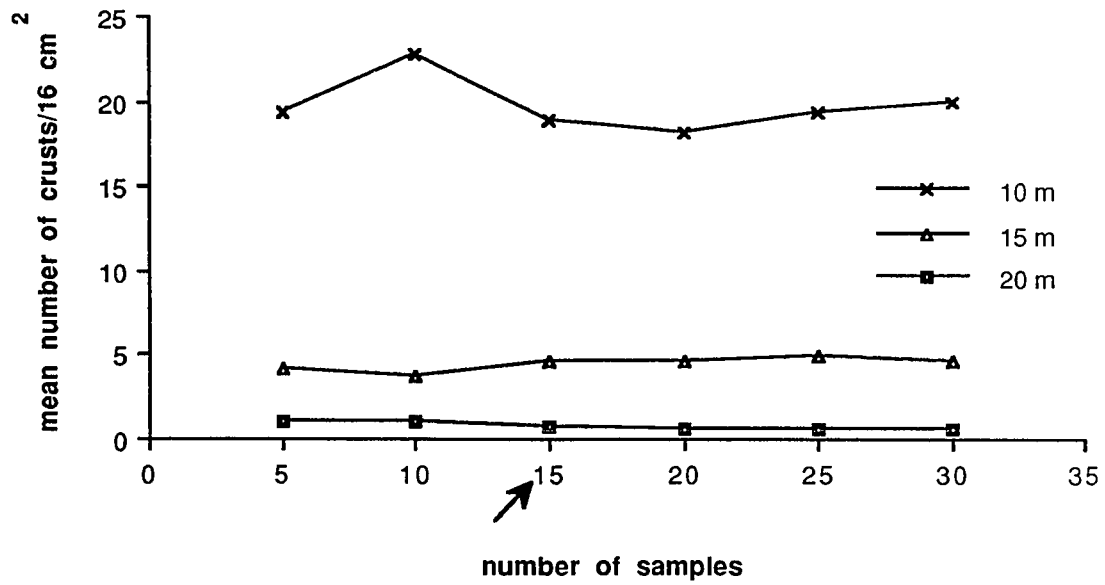


Figure 2. Performance curve to determine adequate sample size. Data were mean number of crusts per 16 cm² from surveys at eight weeks after clearings were made.

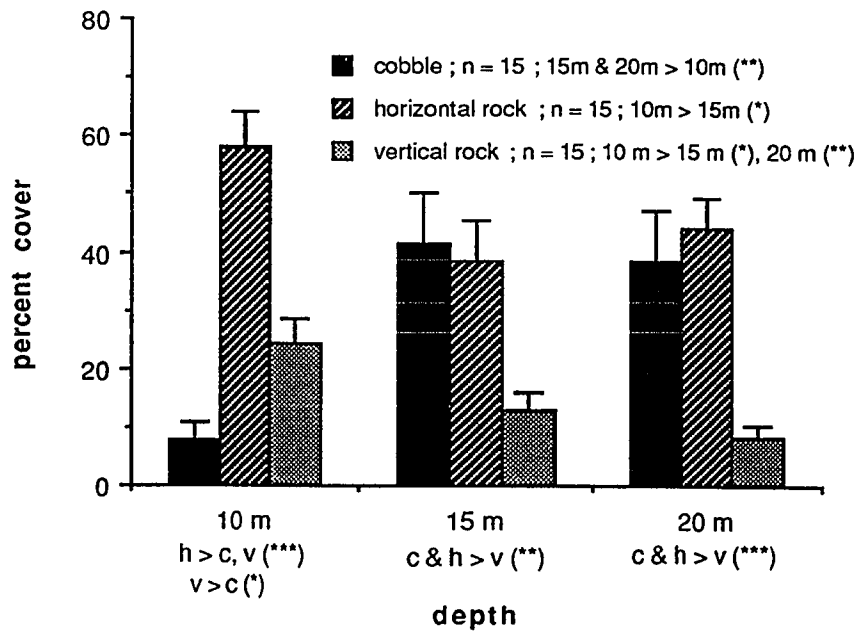


Figure 3. Percent cover ($\bar{x} \pm 1$ S.E.) of substrates at each depth. ">" next to a depth or substrate abbreviation (10 m, 15 m, 20 m, and c, h, v) indicates a significant difference (*) = 0.05, (**) = 0.01, (***) = 0.001.

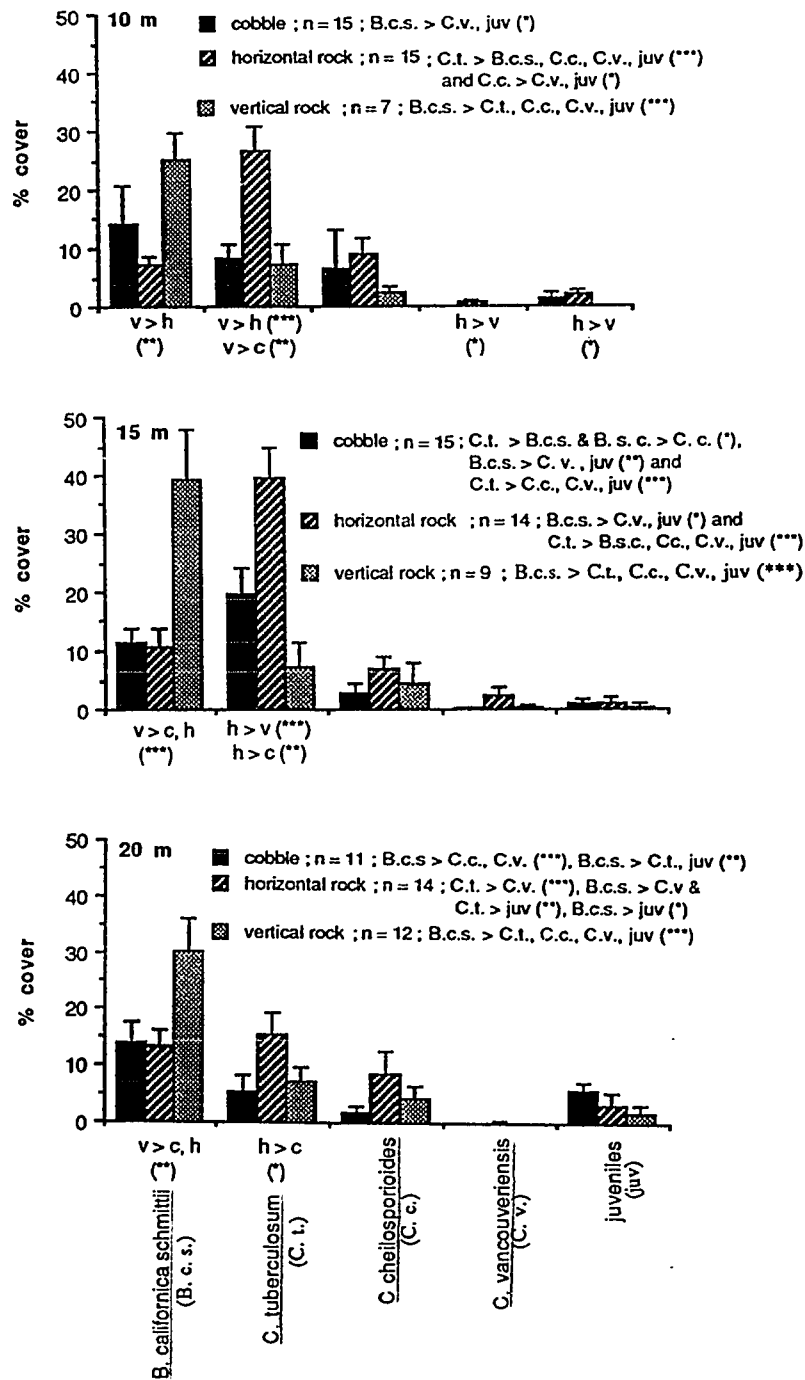


Figure 4. Percent cover ($\bar{x} \pm 1$ S.E.) of geniculate corallines at three depths. Values were corrected for availability of substratum (see text). "n" refers to the number of transects along which substrata were found. ">" next to an algal or substratum abbreviation (B.c.s., C.t., C.c., C.v. juv. and c, h, v) indicates a significant difference (*) = 0.05, (**) = 0.01, (***) = 0.001. One factor ANOVA's were run by coralline for each substratum and by substratum for each coralline.

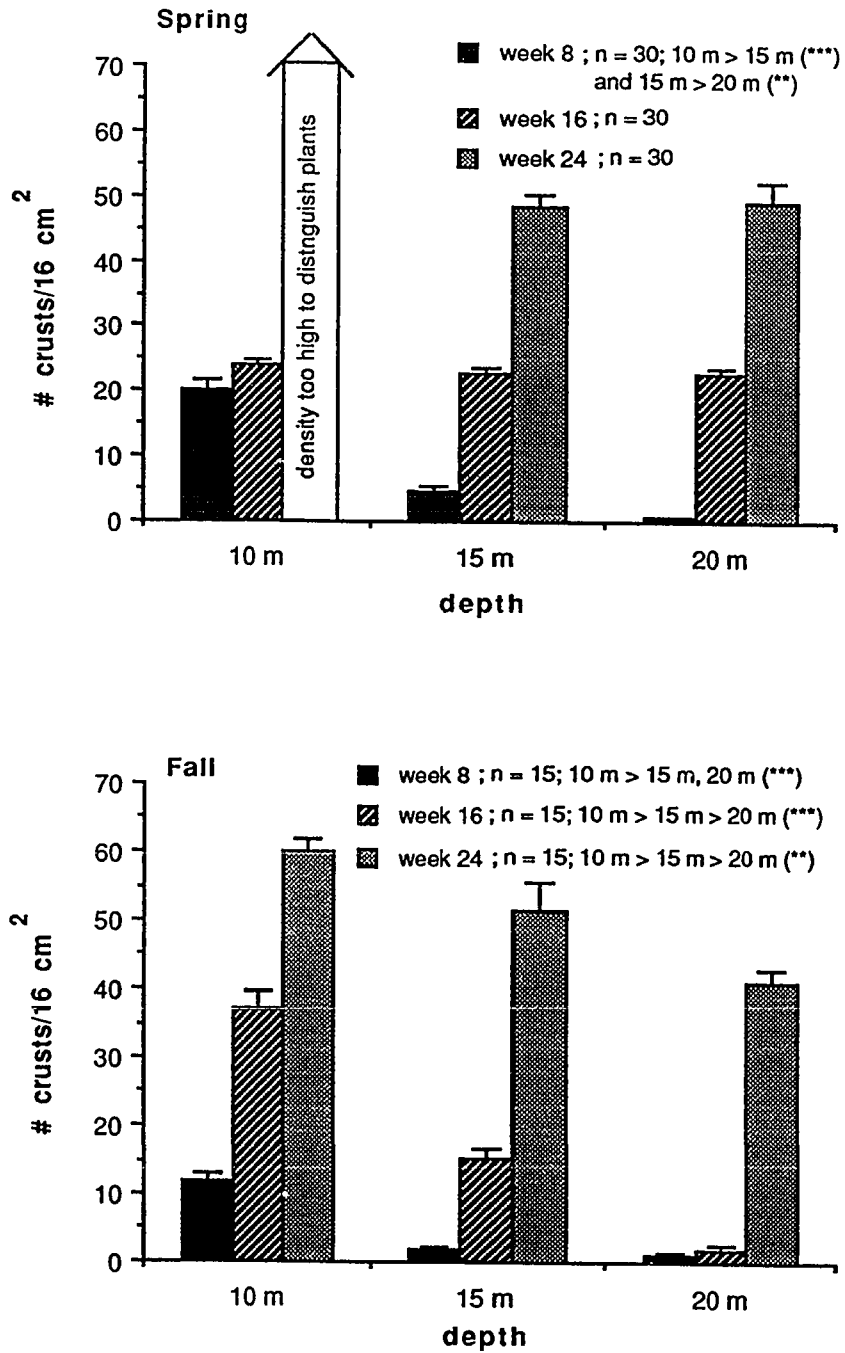


Figure 5. Crust density ($\bar{x} \pm 1$ S.E.) in 16 cm² quadrats within clearings made in spring and fall at each depth (spring, n = 30; fall, n = 15). Counts were made every 8 weeks for 24 weeks post clearing. ">" next to a depth indicates a significant difference (**) = 0.01, (***) = 0.001.

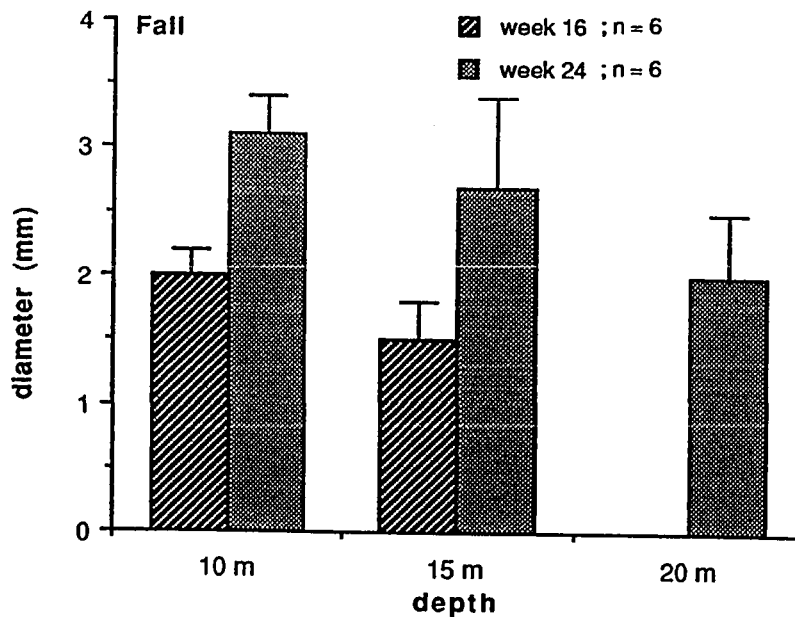
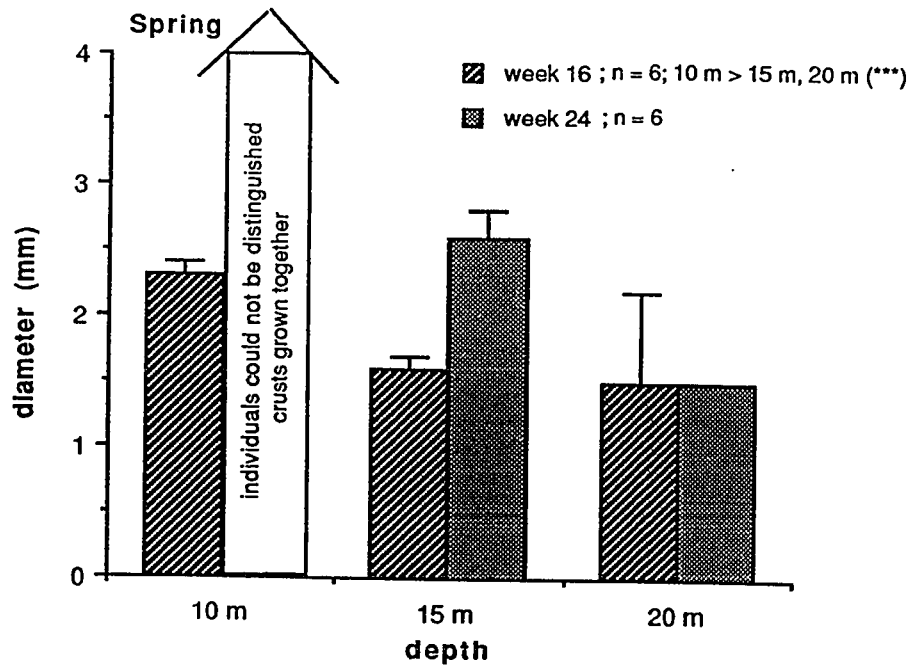


Figure 6. Diameters (mm) of spring and fall crusts in 16 cm² quadrats within clearings at each depth. Measurements were made at 16 and 24 weeks post clearing. No visible crusts were present at the 20 m site at 16 weeks. Mean and standard errors are based on 6 replicates. ">" next to a depth indicates a significant difference (***) = 0.001.

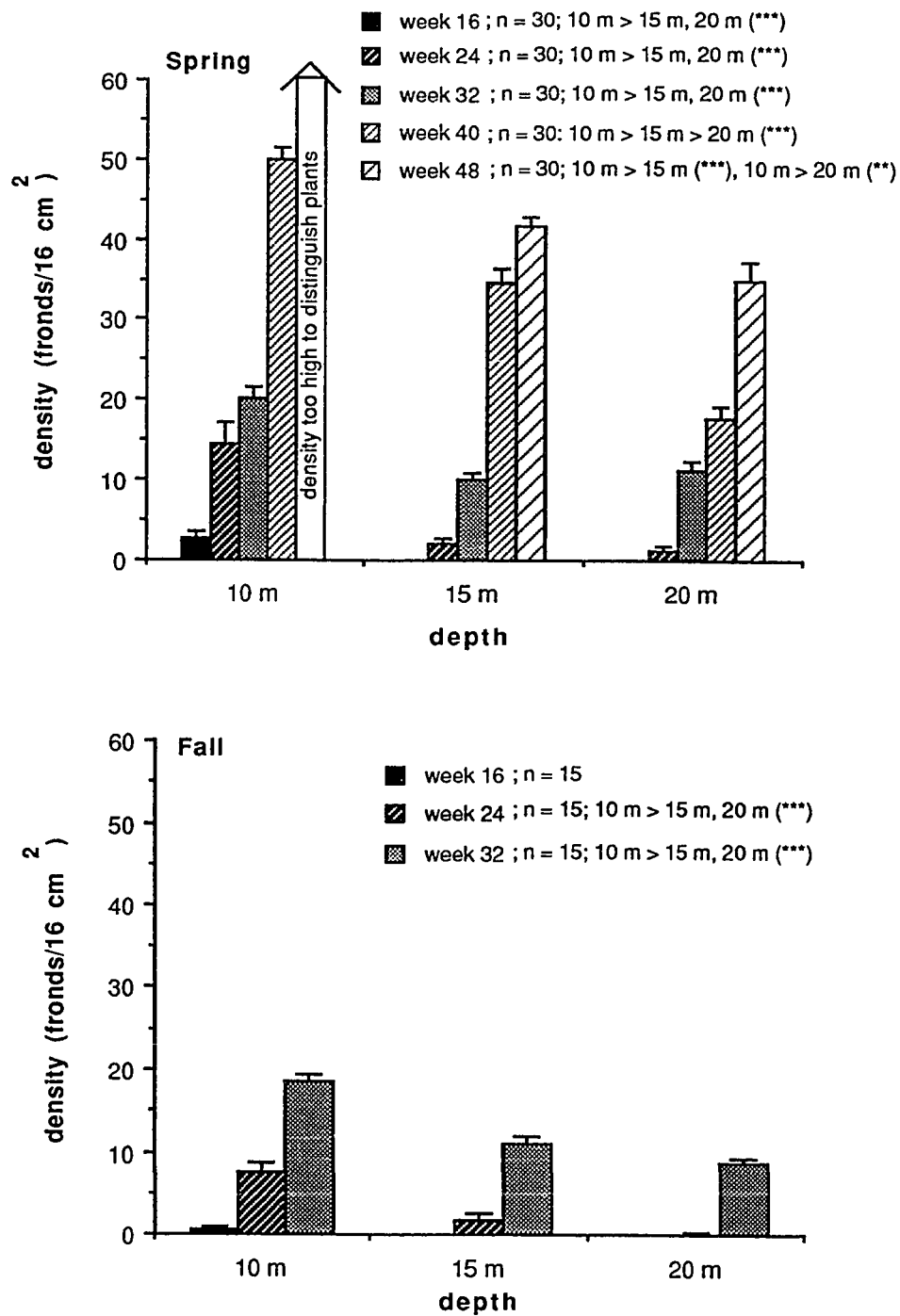


Figure 7. Densities ($\bar{x} \pm 1$ S.E.) of fronds in 16 cm² quadrats placed in spring and fall clearings at each depth (spring, n = 30; fall, n = 15). Counts were made until 48 weeks (spring) and 32 weeks (fall). First uprights appeared at 16 weeks. ">" next to a depth indicates a significant difference (**) = 0.01, (***) = 0.001.

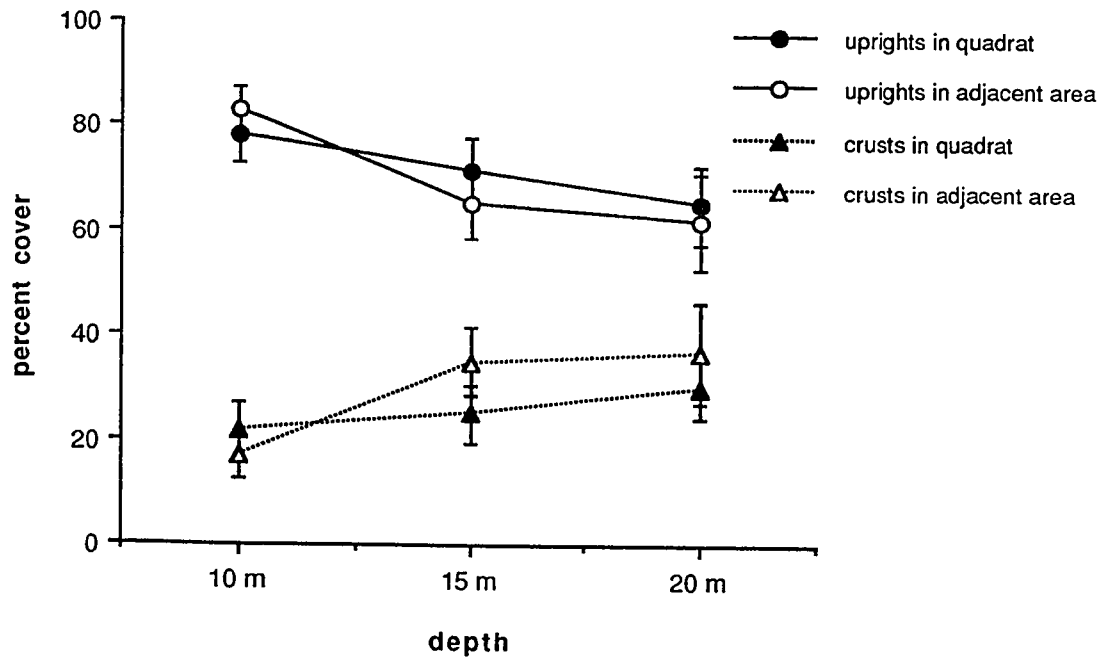


Figure 9. Comparison of frond and basal crust densities in and one meter away from clearings (after 48 weeks).

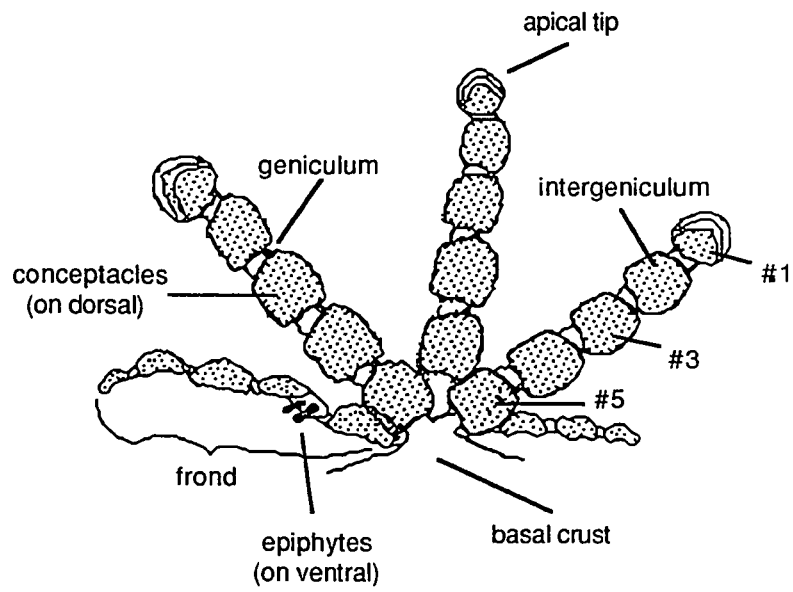


Figure 10. Morphological variables examined on
Bossiella californica schmittii

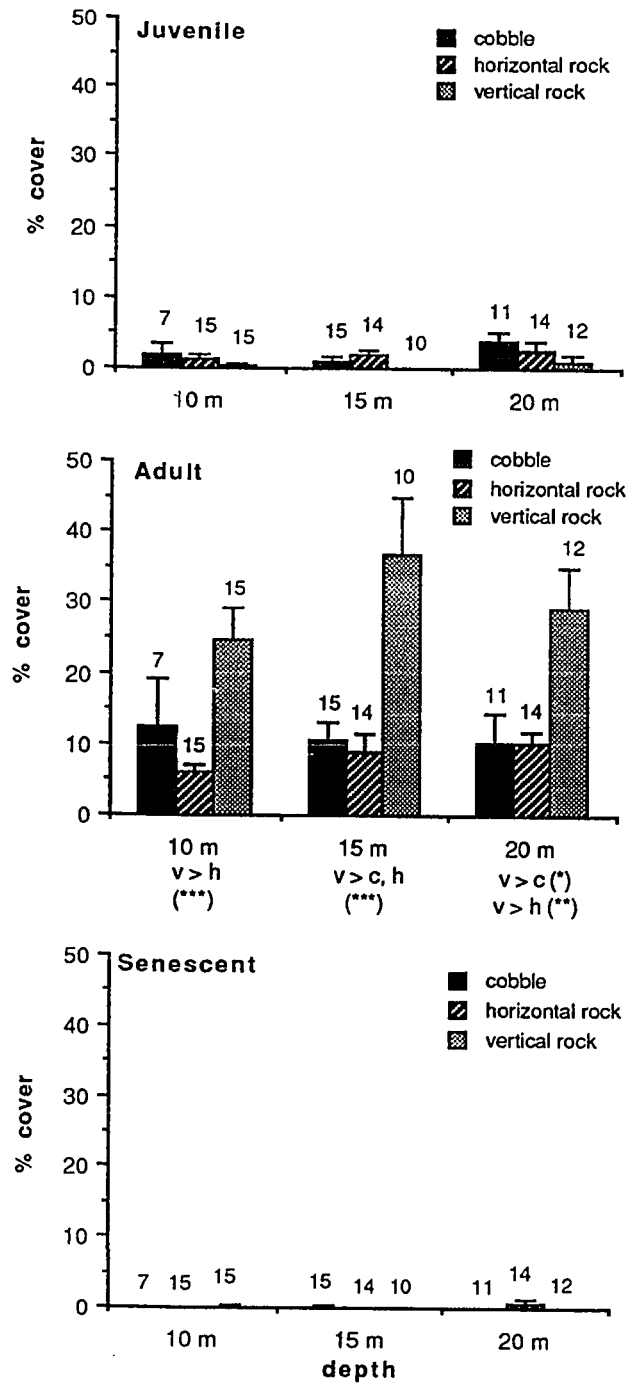


Figure 11. Percent cover (mean \pm 1 S.E.) of *Bossiella californica schmittii* plant types at 3 depths. Values are corrected for availability of substrate. The numbers above the standard error bars are the number of transects which the life stage occurred. ">" next to substrate abbreviation (c, v, h) indicates a significant difference (*) = 0.05, (**) = 0.01 (***) = 0.001.

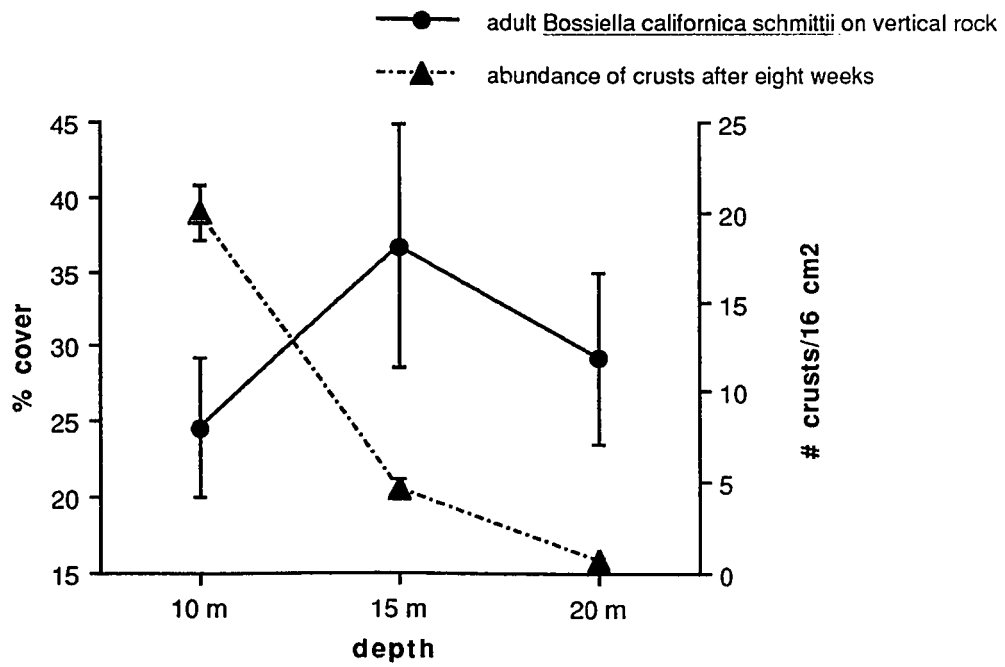


Figure 12. Comparison of % cover of adult *Bossiella californica schmittii* on vertical rocks and abundance of crusts after eight weeks in spring clearings.

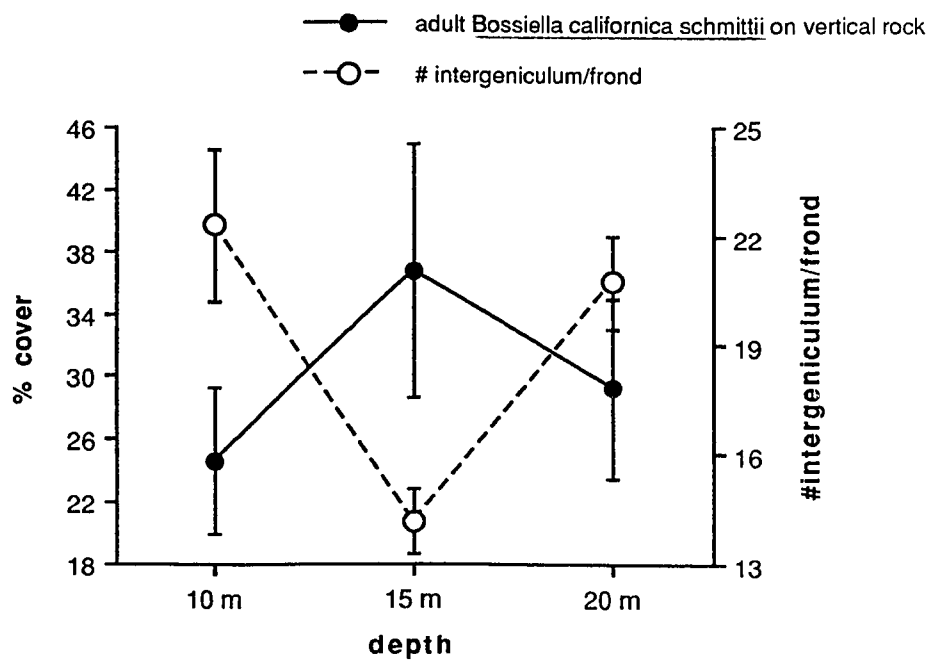


Figure 13. Comparison of % cover of adult *Bossiella californica schmittii* on vertical rocks and # intergeniculum/frond at the three depths.

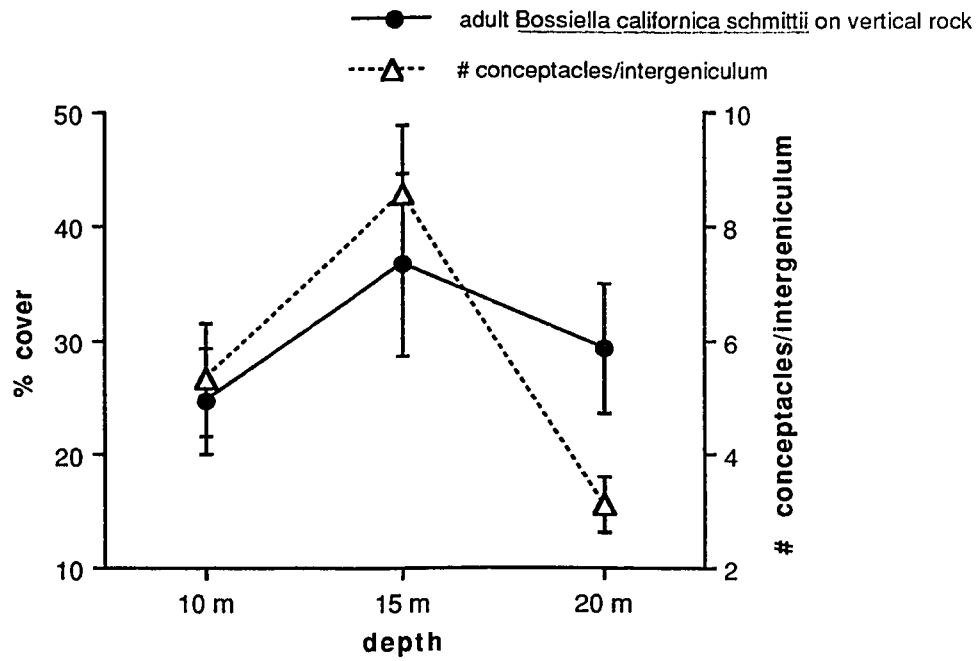


Figure 14. Comparison of adult *Bossiella californica schmittii* abundance on vertical rocks and #conceptacles/intergeniculum at the three depths.

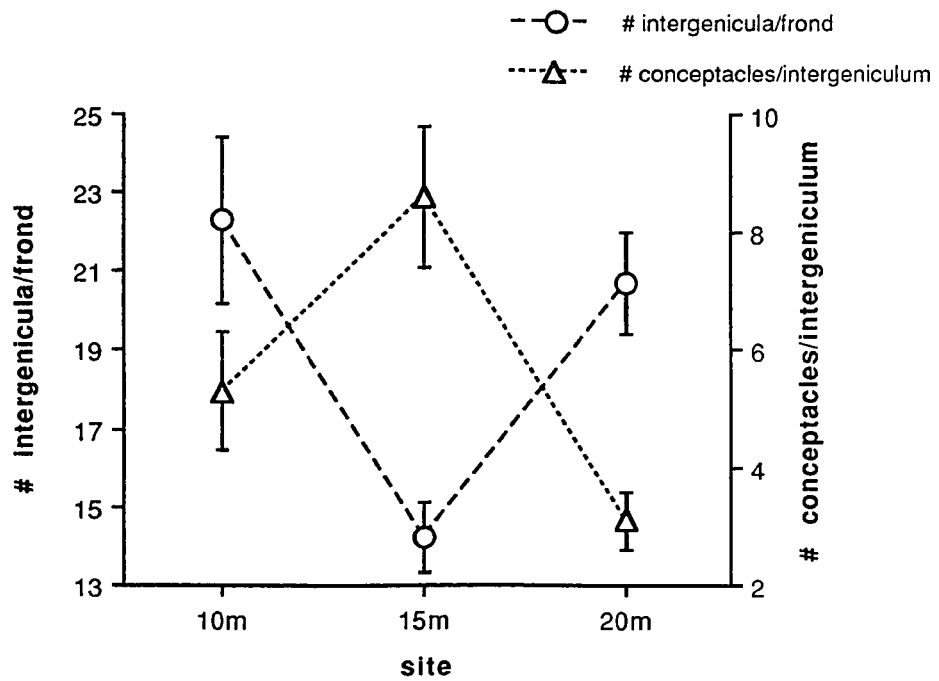


Figure 15. Comparison of # intergenicula/frond and # conceptacles/intergeniculum at the three depths.