Changes in Urchin and Kelp Densities at Anacapa Island, California

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Abstract – The densities of three species of sea urchins and the giant kelp *(Macrocystis pyrifera)* were monitored at a site near Anacapa Island, California. Although the study site had previously supported a dense kelp bed, from 1981-1983 it was dominated by urchins and coralline algae, and *Macrocystis* was restricted to a narrow band in shallow water. After limited recruitment in 1984, *Macrocystis* recruited heavily throughout the study site in 1985, resulting in an extensive kelp bed; the recruitment event was not accompanied by a sharp decline in urchin densities. However, high existing urchin densities, accompanied by unusually heavy urchin recruitment in 1985, resulted in the gradual decline of the kelp bed. By 1987, the kelp bed was again restricted to a narrow band in shallow water.

Introduction

Sea urchins can dramatically influence the structure of temperate marine communities. In some areas, overgrazing by sea urchins results in the removal of all macroscopic algae (Lawrence 1975; Breen & Mann 1976a; Hagen 1983; Himmelman *et al.* 1983; Kitching & Thain 1983). The resulting "sea urchin barrens", more appropriately termed a "crust-dominated community", can persist for years, and is dominated by urchins and encrusting coralline algae that are resistant to grazing (Mann 1977; Wharton & Mann 1981; Hagen 1983; Breitburg 1984). Crust-dominated communities are found throughout the world, including Alaska (Estes & Palmisano 1974; Simenstad *et al.* 1978; Duggins 1980), western Canada (Foreman 1977), eastern Canada (Mann & Breen 1972; Breen & Mann 1976a; Lang & Mann 1976), New Zealand (Ayling 1981; Schiel 1982), Ireland (Kitching & Thain 1983), Japan (Ohmi 1951; Noro *et al.* 1983) and Norway (Hagen 1983).

Crust-dominated communities are generally considered to be caused by increases in the intensity of urchin grazing. Two mechanisms have been proposed to explain the increased grazing. First, increases in urchin densities may result from decreased predation on urchins (Leighton *et al.* 1966; Estes & Palmisano 1974; Dayton 1975; Breen & Mann 1976b; Mann 1977; Breen 1980; Tegner 1980; Tegner & Dayton 1980; Wharton & Mann 1981; Pringle *et al.* 1982; Hagen 1983) or changing oceanographic conditions that favor urchin recruitment (Foreman 1977; Hagen 1983). Second, increased grazing may be due to changes in urchin behavior, the most important factor being the availability of drift algae. When drift abundance decreases, urchins forage more widely from protective crevices (Mattison *et al.* 1977; Dean *et al.* 1984; Harrold & Reed 1985) and graze more intensely on attached plants.

Kelp beds in southern California are very dynamic, as density can fluctuate considerably over time due to both oceanographic and biological factors (Dayton *et al.* 1984). In many cases, grazing by urchins appears to have caused the disappearance of kelp beds in southern California (Leighton *et al.* 1966; North & Pearse 1970; Dayton *et al.* 1984; Ebeling *et al.* 1985). Harrold & Reed (1985) have developed a model of the dynamics of kelp and crust-dominated communities based on a study at San Nicolas Island in the California Channel Islands. With unfavorable hydrographic conditions (such as severe storms, low nutrients, or warm temperatures), low algal

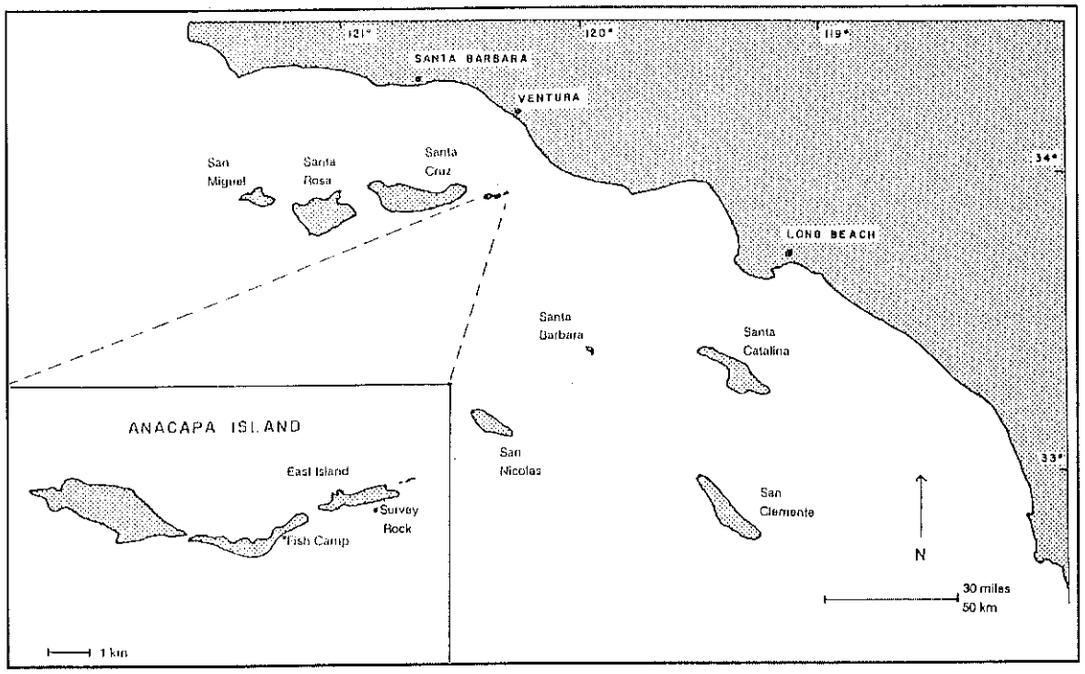

Figure 1. Location of the study site at Survey Rock on East Anacapa Island.

standing stock leads to low drift abundance and high grazing activity, which prevents high algal abundance – resulting in a crust dominated community. With favorable hydrographic conditions (such as mild storms, high nutrients or low temperatures), high algal recruitment and/or high algal standing stock leads to high drift abundance and low grazing activity on attached algae – resulting in a kelp bed. In Harrold & Reed's model extrinsic factors, the hydrographic conditions, drive the system by determining the state of the algae.

In this paper we examine fluctuations between a kelp bed and a crust-dominated community at Anacapa Island, California. From 1982-1984, conditions throughout southern California were generally unfavorable for kelp due to the high water temperatures and low nutrients associated with El Niño (Dayton & Tegner 1984; Gerard 1984; Zimmerman & Robertson 1985; Dean & Jacobsen 1986). After 1984, more favorable conditions returned and there was a general recovery of kelp beds, including the kelp at our study site. We report a widespread recruitment of kelp following El Niño that expanded the kelp bed at Anacapa Island. We also report that a crust-dominated community formed in spite of high algal standing stock and conditions that were apparently favorable for kelp, suggesting that Harrold & Reed's model should be modified to include urchin density at the time of kelp recruitment as an important parameter.

Methods

Study site: Anacapa Island is one of the four northern Channel Islands and is a small (285 ha) chain of three separate islets 8 km in length and 20 km west of Oxnard, California, USA. The study site was situated on the south side of the East Island, adjacent to Survey Rock (Fig. 1). In the mid 1960's, the kelp bed extended to nearly 700 m offshore and a depth of 34 m (Neushul *et al.* 1967). Between 1981 and 1983, kelp was restricted to a sharply-defined narrow band (50 m wide) along the

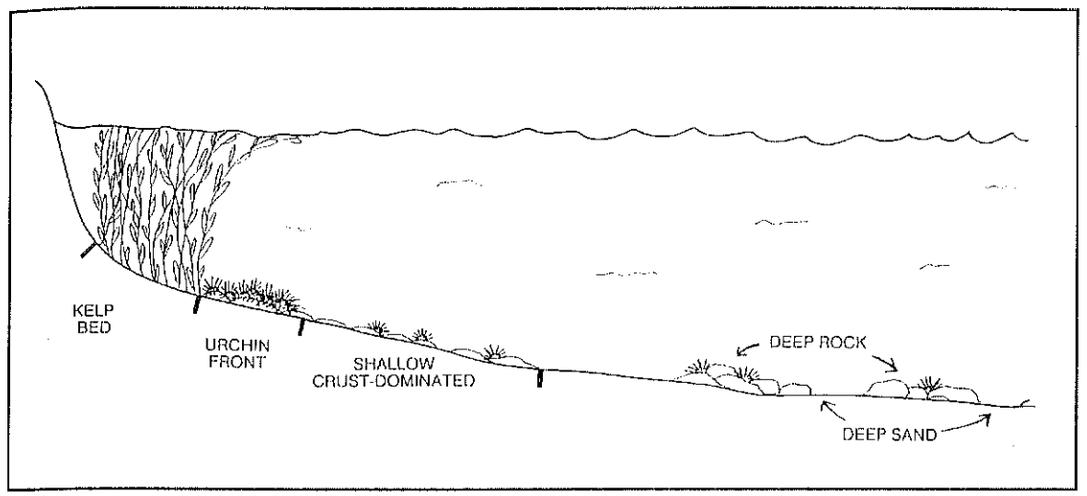

Figure 2. Diagram of the locations of the five different study areas at East Anacapa Island (not to scale). The shallow crust-dominated community extended from the edge of the urchin front to 12m deep; the deep rock and deep sand areas were between 15 and 20m deep.

shore to a depth of 8 m. Offshore of the kelp band, the site was an extensive crust-dominated area with a high density of urchins (unpubl. data).

Three species of urchins occurred at the study site: the red urchin *(Strongylocentrotus franciscanus* Agassiz), the purple urchin *(S. purpuratus* Stimpson) and the white urchin *(Lytechinus anamesus* Clark). The three urchin species exhibited different distributional patterns (Coyer *et al.* 1987). The red urchin was the most common species in the kelp bed and became less common in deeper water. The purple urchin was most common on the shallow crust-dominated community areas. The white urchin did not occur in the kelp bed and was most common in the deeper areas of the site. Only the white urchin occurred in the deep sand area.

The area studied sloped shallowly from about 5 m to 20 m. The study was restricted to rocky substrate except in the deeper portions of the site, where sandy plains that were interspersed with rocky reefs also were studied. Physical relief varied from moderate in shallow areas to low in deeper regions.

Five different habitats, or areas, were examined (Fig. 2): 1) the kelp bed, generally restricted to inshore portion of study site in relatively shallow water (although during the course of this study its area fluctuated considerably); 2) the urchin front, a narrow band (about 3 m wide) of high urchin density near the offshore edge of kelp bed (with maximum density in 1982 of 360 urchins/m^2 and mean=136/m^2, mostly of purple urchins); 3) the shallow crust-dominated community, the largest of all areas, stretching from the edge of the front to 12 m deep; 4) the deep rock crust-dominated community, between 15 and 20 m and 5) the deep sand, consisting of sand plains interspersed among the deep rock crust-dominated community.

Sampling: Urchin densities were estimated by censusing 20-101 haphazardly placed 0.25-m^2 quadrats in each of the five regions. All urchins were counted in each quadrat; because very small urchins (< 5 mm test diameter) are cryptic and difficult to see in the field, this size category may have been underestimated.

Urchin size distributions were determined from a minimum of 100 individuals from each study area. To insure unbiased sampling, the urchins were collected from the 0.25 m^2 quadrats, with all urchins being collected until 100 of that species were represented. Because

Table 1. Urchin densities in different habitats at Anacapa Island. Urchins were sampled in 0.25-m^2 quadrats; density is presented as No. of urchins/m^2.

	1984			1985			1986		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Strongylocentrotus franciscanus									
Kelp	19.0	6.03	79	3.4	0.70	81	7.5	2.60	50
Front	9.5	1.33	40	2.0	1.63	49	24.0	4.25	20
Shallow Crust-dominated	1.0	0.23	101	4.1	1.11	31	9.0	2.15	20
Deep Rock Crust-dominated	1.9	0.83	77	11.0	2.56	57	16.5	3.81	52
Deep Sand	0.1	0.11	35	0.3	0.08	50	0.2	0.11	50
Strongylocentrotus purpuratus									
Kelp	13.6	7.92	79	18.2	4.07	81	21.7	3.39	50
Front	38.4	5.00	40	58.9	7.71	49	82.4	7.32	20
Shallow Crust-dominated	30.0	12.90	101	106.6	25.79	31	87.2	9.74	20
Deep Rock Crust-dominated	4.0	3.65	77	32.0	5.19	57	61.1	4.29	52
Deep Sand	0.0	0.00	35	0.1	0.25	50	3.8	1.78	50
Lytechinus anamesus									
Kelp	0.0	0.00	79	0.0	0.00	81	0.1	0.08	50
Front	0.1	0.10	40	4.2	2.23	49	1.8	0.74	20
Shallow Crust-dominated	6.7	2.39	101	32.8	9.91	31	31.0	6.62	20
Deep Rock Crust-dominated	49.4	6.70	78	57.0	5.46	57	84.8	7.77	52
Deep Sand	61.9	8.32	35	185.6	14.71	50	174.0	14.48	50

the density of red urchins was sometimes low in the deep crust-dominated community, divers in this area carefully searched the substrate and collected every red urchin encountered until the required number had been collected. Urchin test diameters were measured at the surface with calipers.

Kelp density was estimated by counting plants >1 m tall along transects in three different areas: 1) the kelp bed; 2) the shallow crust-dominated community and 3) the deep rock crust-dominated community. The transects were 60 m long, and were delineated by permanent stakes; all plants within 1 m of either side of the transect line were included. Plants were tallied by 20 m x 1 m segments (*i.e.*, three segments along each side of the transect line), with means based on the six segments per transect. The number of stipes present 1 m from the substrate was recorded for each plant included in the transect.

Results

Urchin densities: The abundances of all three urchin species were relatively high in 1984, but increased markedly in most habitats in 1985/86 (Table 1). Densities of white urchins in 1985/86 were up to 3x higher in the deep habitats, and nearly 5x higher in the shallow barrens, compared to 1984. Purple urchin densities also were lowest in all habitats in 1984, and increased up to 3.5x in the shallow habitats and up to 15x in the deep habitats. The densities of red urchins increased substantially in all habitats except the kelp forest, where densities were highest in 1984.

The higher abundance of urchins in 1985/86 was primarily due to heavy recruitment. The proportion of urchins with test diameters <10 mm has been used as an indication of recruitment, and Figure 3 shows proportion of the population with tests <10 mm for the 5 different areas from 1984 through 1986. In 1985, both red and purple urchins recruited heavily to the study site. Red urchins recruited primarily to the urchin front region. Purple urchins recruited to all rocky habitats, and up to 60% of the population was smaller than 10 mm. Purple urchins recruited again to all habitats in 1986. Supplemental collections

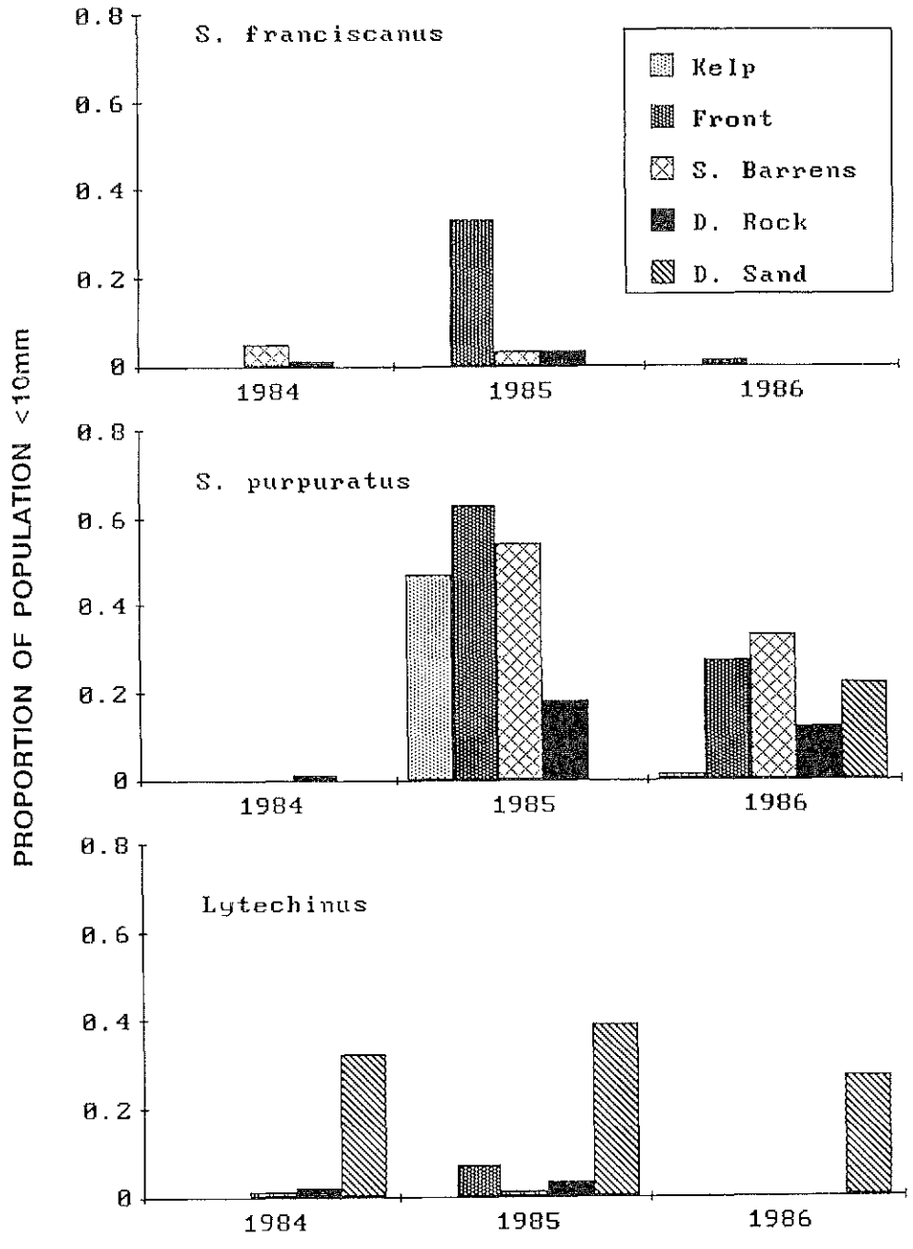

Figure 3. Urchin recruitment from 1984 to 1986. The proportion of urchins with test diameters <10 mm has been used as an indication of recruitment.

specifically directed at urchins <10 mm confirmed that urchins settled in 1986 (R. Rowley, pers. comm.) White urchins recruited in considerable number to the deep sand areas in all years, with a small additional recruitment to the front area in 1985.

***Macrocystis* density:** From 1981 through 1983, *Macrocystis* was common only in the shallowest section of the study area and was virtually nonexistant in all other areas (pers. obs.). In 1984, there was limited recruitment of *Macrocystis* in the shallow crust-dominated community (unpubl. data); however, these were primarily young plants that did not form a canopy.

In 1985, there was extensive recruitment of *Macrocystis* throughout the study site (Table 2). The kelp occurred in all areas and on nearly all available hard surfaces; density was particularly high at the deep rock crust-dominated community and the kelp bed. The recovery of the kelp bed was widespread, with the bed extending approximately 800 m offshore, and the canopy cover returned to the area of the 1960's (Fig. 4).

The extensive recruitment of *Macrocystis* in 1985 is reflected in the frequency of small plants in all three areas sampled (Fig. 5). Based on plants with 2-6 stipes, recruitment was highest in the deep rock crust-dominated area, followed by the kelp bed. Only the kelp bed area had significant densities of larger plants, although there were few plants larger than 16 stipes.

By 1986, kelp density was lower in all areas (Table 2). Some recruitment did occur in 1986, as indicated by the number of plants with 2-6 stipes, but it was much lower than in 1985 (Fig. 5). Conditions continued to be favorable for kelp growth; although the density decreased, probably as a result of shading, many of the plants in the kelp bed grew to larger sizes. However, few plants survived in the crust-dominated areas in 1986 (Fig. 5). The absence of kelp was particularly noticeable in the deep rock area, where only a few new recruits were found in spite of the fact that this area received the greatest recruitment in 1985. The holdfasts of the kelp plants remaining in the shallow and deep rock crust-dominated areas were being attacked by urchins (primarily purple and white urchins).

By February 1987, qualitative observations indicated that the study site had returned to its previous crust-dominated condition: the kelp bed was restricted to a narrow band in shallow water and *Macrocystis* was virtually absent throughout the remainder of the study site.

Table 2. *Macrocystis* density at Anacapa Island. Density was averaged for six 20x1 m segments of the 60x2 m transects in each area in 1985 - 1986; in 1984, a different method was used to determine density, so only qualitative results are presented here: ++ indicates high density; + indicates presence and - indicates absence. Density is presented as No. plants/10 m².

	Mean Density (SE)		
	1984	1985	1986
Kelp Bed	++	28.5 (1.39)	7.5 (1.36)
Shallow Crust-dominated	+	7.8 (1.22)	1.8 (2.45)
Deep Rock	-	26.2 (6.35)	0.7 (0.80)

Discussion

Kelp recruitment: Our study shows that *Macrocystis* can rapidly colonize a large area at considerable distances from adult plants. The widespread recruitment of *Macrocystis* at our study site seems at variance with previous reports that *Macrocystis* only disperses over distances of a few meters (Anderson & North 1966; Dayton *et al.* 1984; T.A Dean & F.R. Jacobsen, pers. comm.). The extensive recruitment of *Macrocystis* at our study site could be explained by: 1) long-lived gametophytes that had persisted since kelp last covered the site; 2) seeding by kelp rafts or sporogenic material that drifted over the study site, or 3) dispersal from the inshore kelp bed.

Neushul (1978) has demonstrated that gametophytes can survive for many years under ideal laboratory conditions. Recent studies of gametophyte survival under field conditions in southern California, however, suggest that very few gametophytes survive more than six weeks (Dean *et al.* 1986); *Macrocystis* had been absent from the crust-dominated areas at Anacapa for at least 3-4 years before 1984 (pers. obs.).

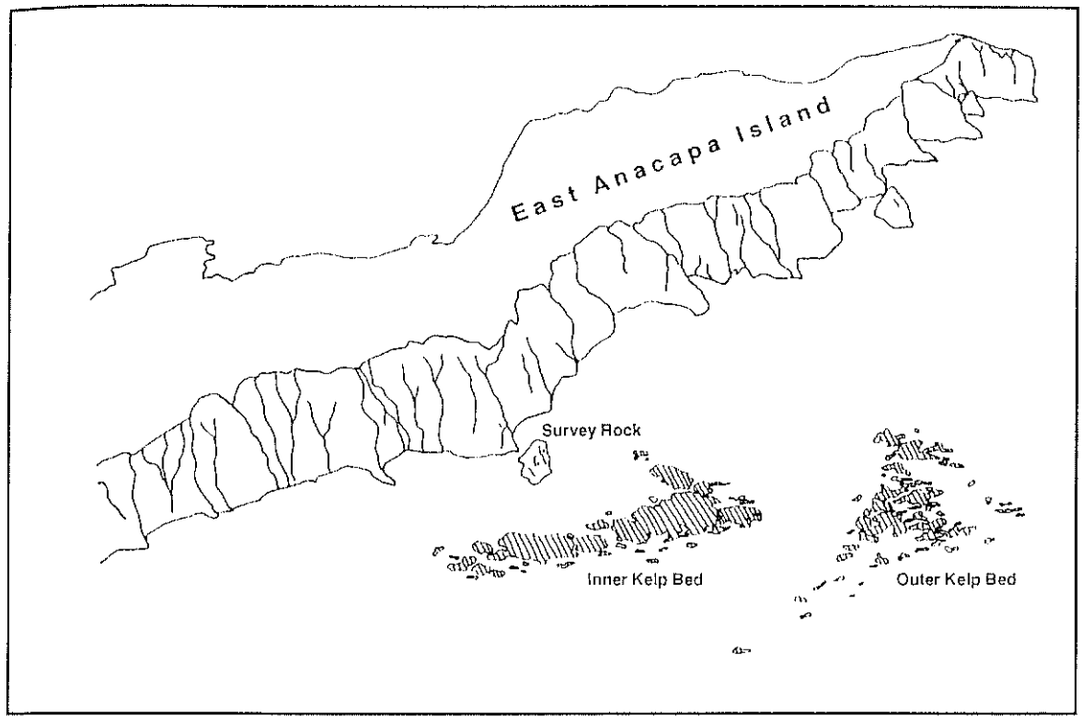

Figure 4. Diagram of kelp canopy at East Anacapa Island in July 1985. Kelp was growing on virtually all hard substrates at the site; the gap between the inshore and offshore beds was due to a wide sand channel. From 1981-1983, kelp was restricted to a narrow band along the innermost portion of the inner kelp bed. Drawn from an infrared slide by R. McPeak.

Furthermore, it seems unlikely that gametophytes could survive years of intense grazing by urchins, especially since Dean & co-authors (1984, 1986) have shown that white urchins graze microscopic life stages of kelps.

Drift kelp or pieces of sporophyll could certainly have provided spores to the crust-dominated areas. Dayton & co-authors (1984) report kelp recruitment due to spores dispersed by drifting kelp plants. At Anacapa, the drift plants could have originated from either the inshore bed or other kelp beds around the island. If the recruitment was due to drift kelp, the extent of coverage was remarkable, since kelp recruitment occurred on nearly all rocky areas in 1985. In contrast, Dayton & co-workers (1984) report a "recruitment swath" (*i.e.*, a band of young *Macrocystis* plants in a kelp-free area) rather than complete coverage.

Finally, it is possible that *Macrocystis* spores from the inshore kelp bed could disperse considerably farther than normal under severe storm or current conditions. Although we cannot thoroughly evaluate this possibility, it is interesting to note that one deep rocky ridge at our study site had conspicuously few kelp plants, in spite of a high density of *Macrocystis* on an adjacent ridge that was farther offshore. It seems more likely that the ridge without kelp would be missed by drift plants than by widely dispersing spores from the inshore bed.

Whatever the mechanism, there have been several other reports of colonization of areas at considerable distances from adult kelp plants. Several artificial structures have developed kelp beds shortly after being emplaced in spite of being located several km from the nearest kelp beds (Turner *et al.* 1969; Fager 1971; Davis *et al.* 1982). Naples Reef, a natural reef 6 km from the nearest kelp bed, changed rapidly from a crust-dominated community to a kelp bed following severe storms in 1983 (Ebeling

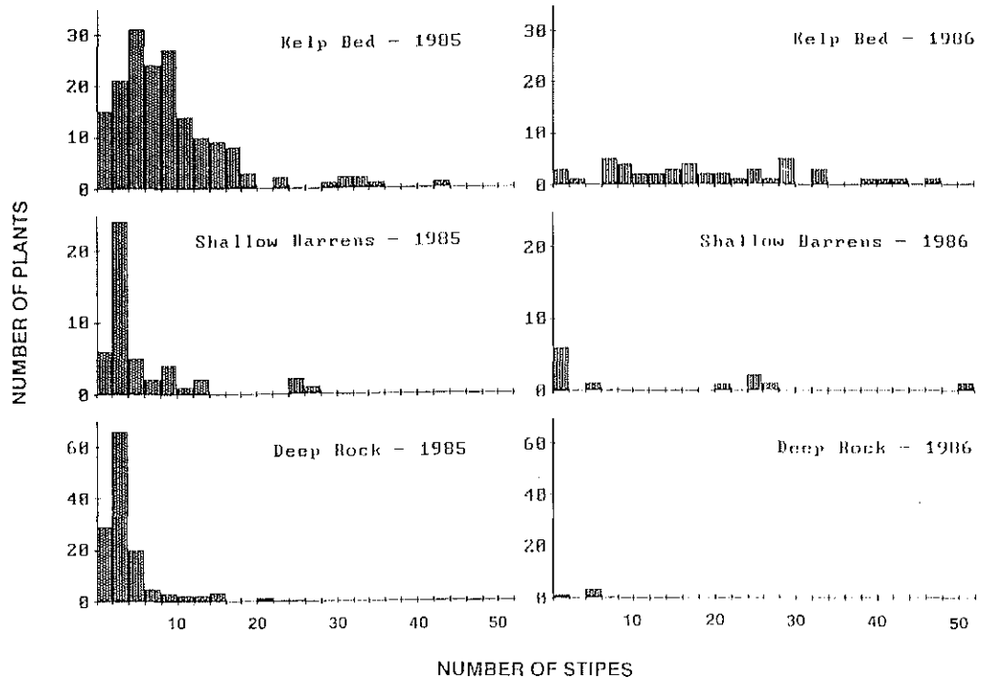

Figure 5. Size distribution of *Macrocystis* in the kelp bed, shallow crust-dominated community, and deep rock crust-dominated community in 1985 and 1986. Number of stipes were counted for all plants taller than 1m in transects.

et al. 1985). These examples, in conjunction with our observations at Anacapa Island, indicate that long-distance dispersal of *Macrocystis* is a normal, although perhaps infrequent, phenomenon. By providing for the rapid development of kelp beds at distant sites, long-distance dispersal may play an important role in the dynamics of southern California kelp forests.

Dynamics of kelp beds and crust-dominated communities: Kelp beds in southern California exhibit a wide range of dynamic behaviors. Dayton & co-authors (1984) note that, although kelp beds exhibit persistence and resistance to invasion by other algal species, most are eventually perturbed or invaded. Indeed, many kelp beds in southern California have exhibited periods of loss and renewal (see southern California Edison 1982). Harrold & Reed (1985) report rapid transitions (within 4 years) between kelp beds and crust-dominated communities at San Nicolas Island.

Changes in kelp density have recently been studied by Ebeling & co-workers (1985) at Naples Reef, a relatively isolated mainland reef near Santa Barbara, California. In 1980, a large storm removed all the kelp from the reef. In the absence of drift algae, urchins left their crevices to graze on attached algae. From 1980-1983, *Macrocystis* was absent from Naples Reef. A second large storm devastated the urchins in 1983, after which the kelp returned to the reef.

The kelp bed at our study site at East Anacapa Island has a history of rapid disappearance and reappearance (Neushul 1981). In 1964-1965, the bed extended from shallow water out to nearly 700 m offshore, into water 34 m deep. By 1966 the kelp had completely disappeared, and Neushul noted high densities of urchins on the rock surfaces. In 1967, the kelp again covered the entire site.

Nearly 20 years after Neushul's observations, the kelp bed at East Anacapa exhibited similar fluctuations in kelp density, except the crust-dominated community predominated. Urchin density remained high from our initial observations in 1981 through 1986 (unpubl. data). From 1981-1983, *Macrocystis* was absent from most of the study site. Kelp recruitment in 1984-1985 created a dense bed throughout the study site in spite of the high urchin densities, but by 1987 most of the study site again lacked kelp.

In some ways, the recent history of the kelp bed at Anacapa Island resembles that of Naples Reef. In both areas, urchins dominated the site, then kelp beds were created rapidly by extensive *Macrocystis* recruitment, in spite of the absence of nearby adult kelp plants. However, the mechanisms leading to kelp recruitment on the two reefs were fundamentally different; unlike Naples Reef, kelp returned to Anacapa in spite of high urchin densities.

The density of urchins at Anacapa, even during the year of kelp recruitment, was considerably higher than that reported for other "urchin barrens" in southern California. Harrold & Reed (1985) report a density of only 9.5 *Strongylocentrotus franciscanus*/m^2 at San Nicolas Island. Ebeling & co-authors (1985) report a density of 23 urchins/m^2 (both *S. franciscanus* and *S. purpuratus)* during the "barrens period" at Naples Reef, when urchins were apparently preventing kelp recruitment. By comparison, the mean density of all urchins in the shallow crust-dominated community at Anacapa ranged from 37.7/m^2 in 1984, when kelp first recruited to the site, to 143.5/m^2 in 1985. *Macrocystis* was able to recruit in spite of these high densities.

Hagen's (1983) model of the dynamics of kelp beds and crust-dominated communities suggests that kelp beds can recover from the crust-dominated state only if there is a decrease in urchin populations. Studies by Miller (1985) and Ebeling & co-workers (1985), which document kelp bed recovery after urchin densities decreased, support this model. Declines in urchin densities may be due to mass mortalities (Hooper 1980; Miller & Colodey 1983; Ebeling *et al.* 1985) or the reintroduction of predators (Breen *et al.* 1982; Duggins 1980).

Harrold & Reed (1985), however, have demonstrated that kelp beds can recover from the crust-dominated state without a corresponding decline in urchin densities. At their study site on San Nicolas Island, favorable hydrographic conditions resulted in the return of the kelp bed even though urchin densities were unchanged. Our data also indicate that kelp recruitment can be independent of urchin densities.

However, even when hydrographic conditions are good for kelp, a kelp forest will not necessarily persist. Because kelp recruitment may be independent of urchin density, high pre-existing urchin densities may limit, and eventually eliminate, a kelp forest. At Harrold & Reed's study site, kelp recruitment was independent of urchin density, and subsequent production of drift algae was sufficient to allow urchins to return to protected crevices, thereby reducing grazing intensity. At Anacapa, where urchin abundances were much higher when *Macrocystis* recruited, the drift algae produced by the new kelp bed apparently was not sufficient to reduce grazing intensity. As a consequence, the urchins grazed directly on the kelp plants, and the extensive new kelp bed disappeared rapidly. Thus, the state of a kelp bed is determined by an interaction between hydrographic conditions and existing urchin densities.

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