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LONG-TERM CHANGES AND SPECIES INTERACTIONS IN A SEA URCHIN-DOMINATED COMMUNITY AT ANACAPA ISLAND, CALIFORNIA

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ABSTRACT

Densities of sea urchins, other benthic invertebrates, and macroalgae were monitored annually from 1981 to 1998 at Anacapa Island, California. Although the study site was formerly dominated by a dense kelp (*Macrocystis*) forest, kelp and other macroalgae have largely been absent since 1986 due to urchin overgrazing. White sea urchins (*Lytechinus pictus*) were very abundant in the mid-1980s but are now nearly absent. Purple sea urchins (*Strongylocentrotus purpuratus*) have increased since 1993 while abundances of red urchins (*S. franciscanus*) have remained at relatively constant and low levels. Coexisting invertebrates are mainly sessile filter-feeders resistant to the effects of urchin grazing, such as coelenterates (*Balanophyllia elegans* and *Corynactis californica*) and tube-dwelling polychaetes (*Chaetopterus variopedatus* and *Spirobranchus spinosus*). Benthic community structure has changed substantially at the study site in recent years. The ophiuroid *Ophiothrix spiculata* has become abundant (>1,300/m²) in deeper areas since 1994, apparently causing declines in *B. elegans* and other sessile species. Macroalgae is unlikely to recover unless ophiuroid and echinoid populations decline, and the oceanographic regime shifts to an extended period of cool water/high nutrients favorable for kelp recruitment and growth.

Keywords: California, Anacapa Island, *Strongylocentrotus* spp., *Ophiothrix spiculata*, disturbance, sessile invertebrates, urchin barrens, giant kelp forest.

INTRODUCTION

The structure of temperate marine communities can be greatly influenced by biological disturbance caused by the intense grazing activity of sea urchins. Destructive grazing by sea urchins on forests of laminarian kelps is a well documented phenomenon (Paine and Vadas 1969; Lawrence 1975), and a variety of mechanisms have been identified

that explain some of the causes of overgrazing (see review by Foster and Schiel 1985). In some cases, the immediate effects on the epibenthic community are not only reductions in macroalgal biomass, but also dramatic declines in algal and invertebrate diversity in the resulting "barrens" (Breen and Mann 1976; Foreman 1977). Extensive cover of crustose (non-geniculate) coralline algae is a common feature of rock substrata subjected to moderate levels of chronic urchin grazing and may persist even after grazing intensity subsides (Breitburg 1984). Recovery to a condition of kelp abundance and reduced grazing can be facilitated by physical oceanographic conditions favorable for kelp growth (Harrold and Reed 1985), and reductions in urchin populations by physical disturbance, disease, predation, or lack of recruitment (Duggins 1980; Ebeling et al. 1985).

The overgrazing phenomenon itself has been documented in temperate communities worldwide, but the long-term changes to the epibenthic community in areas with sustained levels of urchin habitation are less well known. Ayling (1981) investigated one such community in New Zealand over a 3 yr period and found a relatively diverse assemblage of sponges, tunicates, coelenterates, and ephemeral algae co-occurring with the urchin *Evechinus chloroticus*. Many of these taxa were able to persist by being opportunistic settlers and rapid colonizers, small and relatively tough to eat, or toxic and unpalatable to grazers. Long-term monitoring at several sites in the northern Channel Islands has also documented a range of epibenthic diversity in areas that have been impacted by chronic urchin habitation (Richards et al. 1997).

In this paper, we report changes in the abundances of algae and invertebrates that occurred over an 18 yr period in two adjacent epibenthic assemblages at Anacapa Island: one characterized by extensive cover of crustose coralline algae and subjected to chronic grazing by four urchin species, and the other initially dominated by macroalgae. Urchin species present include the red urchin (*Strongylocentrotus*

franciscanus), the purple urchin (*S. purpuratus*), and the crowned sea urchin (*Centrostephanus coronatus*) primarily on the crust-dominated rock reef, and the white urchin (*Lytechinus pictus*) on rock and sand/shell debris substrates at depths >10 m. The present study is a continuation of earlier work by Ambrose et al. (1993) on changes in urchin and kelp density at this study site, but here we emphasize changes in the attached epibenthic assemblage. The study period encompassed a range of oceanographic conditions including two major El Niño episodes. In the kelp-dominated assemblage, macroalgae gradually declined over the study as echinoid grazing persisted and kelp recruitment diminished. The urchin-coraline dominated assemblage largely persisted throughout the study with the exception of a 2 yr period of macroalgal colonization from 1984 to 1985. We report on a relatively rich epibenthic assemblage that was adapted to, and in some cases, enhanced by the chronic biological disturbance of grazing. Toward the end of the study, however, an episodic increase in ophiuroid densities dramatically reduced the abundance of most sessile organisms at depths >12 m.

METHODS AND MATERIALS

Study Site

Anacapa Island, one of the four northern Channel Islands, is a small (285 ha) chain of three separate islets 8 km in length and 20 km from the southern California mainland. The study site was situated on the south side of the East Island, adjacent to Survey Rock. In the mid 1960s, the kelp bed extended nearly 700 m offshore to a depth of 31 m (Neushul et al. 1967). By the early 1980s, kelp was restricted to a narrow (ca. 50 m) band along the shore to a depth of 8 m, and urchins and crustose coralline algae largely dominated the deeper offshore areas (Ambrose et al. 1993).

Mean monthly sea surface temperatures at Anacapa Island from 1982 to 1992 varied from a low of 14°C in March to a high of 19°C in August (Engle 1994). Minimum and maximum temperatures measured at a depth of 12 m at Survey Rock from 1994 to 1997 ranged from 11°C to 21°C. In summer the site is exposed to occasional south swells that result in considerable subtidal surge, particularly in the shallow kelp bed area. Winter storm swells from the northwest also subject the site to indirect wave exposure. Tidal currents generally flow from west to east with peak velocities >50cm/sec.

Sampling

Benthic invertebrates were enumerated by divers in 30 randomly located 0.25 m² quadrats along each of two permanent 60 m transects. One transect was located at depth of ca. 8 m on predominantly rocky substrate within the existing kelp forest. A second transect was positioned on an adjacent rock reef at a depth of ca. 12 m in an area largely dominated by sea urchins and devoid of macroalgae. We refer to these as the "kelp" and "urchin-coraline" transects,

respectively, to designate their primary community type during the initial years of the study. Taxa comprised of separate individuals were counted in each quadrat when practical. Encrusting invertebrates and algae were generally quantified as percent cover. The transects were surveyed annually in June or July from 1981 to 1998 (urchin-coraline) and 1983 to 1998 (kelp).

Five permanent photoplots (0.15 m²) also were established on rock substrate at a depth of 18 m from 1986 to 1998 to follow changes in invertebrate cover through time. Two photographs were taken of each quadrat annually; one undisturbed, and a second with all motile invertebrates removed to expose organisms and substrates that may have been covered in the first photograph. Transparencies were scored for percent cover of taxa using a point contact method (Littler 1980). Transparencies were projected against a field of 50 points per plot and all taxa that intersected points were tallied. Taxa that were present but not contacted were given a cover of 0.5%. Some species sampled by the photographic point contact method were combined into broader taxonomic categories because the resolution of the photographs precluded accurate identifications of all taxa. Spiculate brittle stars, *Ophiothrix spiculata*, became unusually abundant on deep rock reefs in the later years of the study. The photoplot data were primarily used in the present analysis to examine changes in the cover of sessile invertebrates and *O. spiculata*.

We quantified the condition of an abundant cup coral (*Balanophyllia elegans*) relative to the density of *O. spiculata* using another method. Measurements were done in 1995, the first year that ophiuroid densities substantially increased at the 18 m depth. After a 0.25 m² quadrat was haphazardly placed on the rock substrate, the number of *B. elegans* with and without retracted tentacles (in a non-feeding position) was counted. The total number of *O. spiculata* was then counted by removing each individual from the quadrat. The data were analyzed with a Model I least squares regression on untransformed data using ophiuroid density as the independent variable and percent of corals with retracted tentacles as the dependent variable.

Multivariate Community Analysis

Multivariate statistical methods are useful for examining spatial and temporal variation in biological communities (Green 1979; Gauch 1982). We used a principal components biplot (Digby and Kempton 1987) to portray the relative variation within the kelp and urchin-coraline communities through time, and to identify the taxa groups that contributed to the temporal patterns. Twelve taxa were analyzed for changes from the kelp transect and 13 taxa were analyzed from the urchin-coraline transect (Table 1). These taxa represented several of the common invertebrates and algae from each transect. The positions and lengths of the vectors represent the relative contribution of each taxon to the dispersion pattern of the component scores for the survey years. Data from the kelp and urchin-coraline transects were analyzed separately.

Table 1. Taxa used in multivariate principal components analyses. Taxon abbreviations listed are those shown in bi-plots of taxa scores and annual survey scores. (Figures 8 and 9; kelp transect and urchin-coralline transect, respectively).

Taxon	Abbreviation	Taxon description	Kelp transect	Urchin-coralline transect
<i>Astrangia lajollaensis</i>	<i>A. lajolla.</i>	Aggregating cup coral		X
<i>Balanophyllia elegans</i>	<i>B. elegans</i>	Solitary cup coral		X
Arborescent bryozoans	bryoz.	—	X	
<i>Corynactis californica</i>	<i>C. cal.</i>	Clonal anemone	X	X
<i>Cystoseira neglecta</i>	<i>C. neg.</i>	Perennial brown alga	X	
<i>Chaetopterus variopedatus</i>	<i>C. vario.</i>	Annelid worm	X	X
Crustose coralline algae	crust. cor.	—	X	X
Ephemeral brown algae	eph. brn.	—	X	X
Erect coralline algae	erect cor.	—	X	
<i>Lytechinus pictus</i>	<i>L. pict.</i>	Sea urchin		X
<i>Macrocystis pryerifera</i>	<i>M. pyrif.</i>	Perennial brown alga	X	
<i>Ophiothrix spiculata</i>	<i>O. spic.</i>	Brittle star		X
<i>Sagartia catalinensis</i>	<i>S. cat.</i>	Clonal anemone	X	X
<i>Strongylocentrotus franciscanus</i>	<i>S. fran.</i>	Sea urchin	X	X
<i>Sargassum muticum</i>	<i>S. muticum</i>	Perennial brown alga		X
<i>Strongylocentrotus purpuratus</i>	<i>S. purp.</i>	Sea urchin	X	X
<i>Spirobranchus spinosus</i>	<i>S. spin.</i>	Annelid worm		X
<i>Serpulorbis squamigerous</i>	<i>S. squam.</i>	Vermetid gastropod	X	

RESULTS

Algae and Echinoids

A well-developed surface kelp canopy was present on the kelp transect in 1983, but perennial macroalgal abundance (measured as percent cover in permanent quadrats, including *Macrocystis*) steadily declined through 1988, with minimum coverages thereafter (Figure 1). Macroalgae were scarce on the urchin-coralline transect except during 1984 to 1985 when *Macrocystis*, *Cystoseira*, and other perennial brown algae increased substantially (Figure 1). Crustose coralline algae gradually increased on the kelp transect from a low of 1.2% in 1986 to nearly 40% in 1997 as urchin grazing continued and the cover of perennial macroalgae declined. Crustose coralline algal cover on the urchin-coralline transect averaged 28.9% from 1981 to 1998, but declined to less than 15% cover in 1984 and 1997. Ephemeral algae, comprised mainly of filamentous red algae, brown algae, and diatom chains, increased substantially on the kelp transect from near absence in the mid-1980s to nearly 30% in 1998. The greatest cover of ephemeral algae (23.2%) on the urchin-coralline transect was recorded in 1984 when urchin abundance was relatively low and conditions were favorable for algal growth.

Densities of the three predominate urchin species fluctuated on both the kelp and urchin-coralline transects over the duration of the study (Figure 2). *Strongylocentrotus purpuratus* was the most abundant echinoid on the kelp transect and was nearly five times more abundant than *S. franciscanus*. *S. franciscanus* fluctuated less than the other

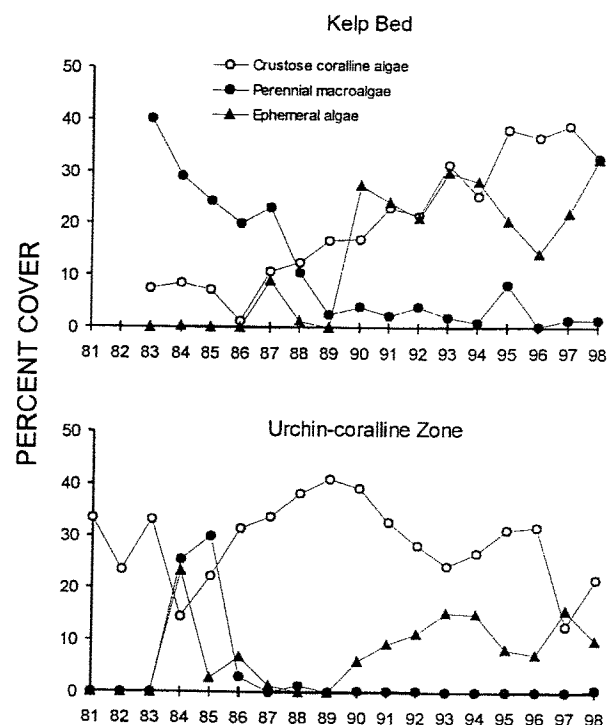


Figure 1. Percent cover of crustose coralline algae, perennial macroalgae, and ephemeral algae from 1981 to 1998. $n = 30$, 0.25 m^2 quadrats sampled in June or July of each year.

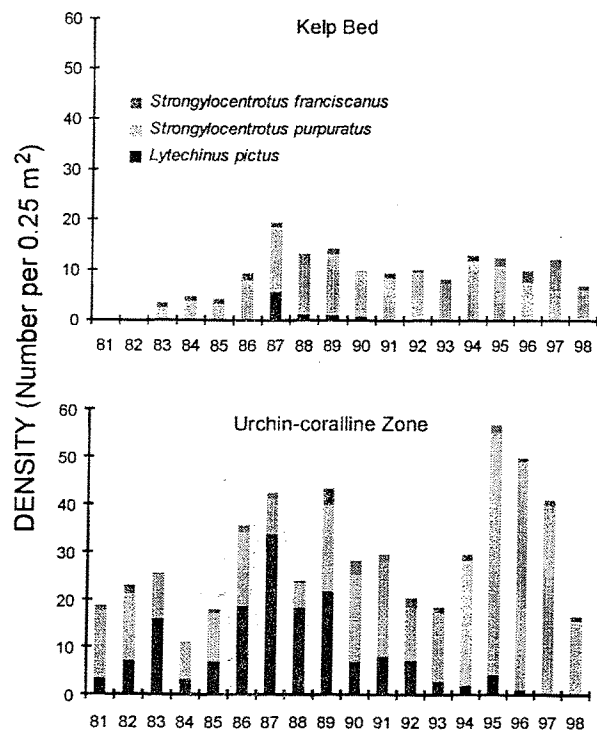


Figure 2. Mean densities of three sea urchin species from 1981 to 1998. $n = 30$, 0.25 m^2 quadrats sampled in June or July of each year.

species and was at low densities of ca. 1-3/0.25 m^2 throughout the study. *Lytechinus pictus* was largely absent in the kelp until a recruitment pulse occurred in 1987, but their numbers declined to near zero in subsequent years. *Centrostephanus coronatus*, a relatively rare species at Survey Rock, was not recorded in any kelp transect quadrats, but qualitative observations confirmed its presence at very low densities elsewhere in the kelp forest.

L. pictus was considerably more abundant on the urchin-coraline transect than on the kelp transect, attaining maximum densities of over 30/0.25 m^2 in 1987 (Figure 2). However, a subsequent long-term decline in the species resulted in minimal densities of only 0.1/0.25 m^2 in 1998. *S. purpuratus* maintained densities of ca. 10-20/0.25 m^2 from 1981 to 1994, but doubled in density from 1995 to 1998. *S. franciscanus* was present on the urchin-coraline transect at low densities throughout the study. *C. coronatus* was absent from the urchin-coraline transect until a settlement event in late 1997 resulted in subsequent densities of 0.6/0.25 m^2 in July 1998.

Other Invertebrates

From 1983 to 1989, the sessile invertebrate community on the kelp transect was comprised of a moderately diverse assemblage (ca. 40 quantified taxa) including coelenterates, tube-dwelling polychaetes, bryozoans, vermetid gastropods, and tunicates. After 1989, the cover of the clonal coelenterates *Corynactis californica* and *Sagartia catalinensis* increased (Figure 3). *Chaetopterus variopedatus*, a tube-dwelling polychaete, also increased

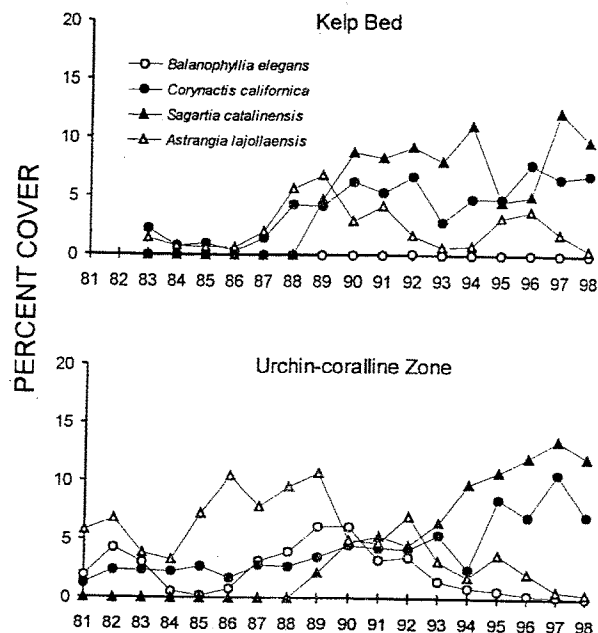


Figure 3. Percent cover of four coelenterate species from 1981 to 1998. $n = 30$, 0.25 m^2 quadrats sampled in June or July of each year.

rapidly after 1989 (Figure 4). Arborescent bryozoan species (*Bugula californica*, *Diaporecia californica* and *Thalamoporella californica*) were most abundant from 1984 to 1986 and then declined thereafter (Figure 5). Tunicates (*Euherdmania claviformis* and *Pycnoclavella stanleyi*) were also abundant during the early years of the study but declined substantially from 1989 to 1998. *Serpulorbis squamigerous*, a tube-dwelling vermetid gastropod, increased gradually from 1983 to 1988 and then remained nearly unchanged through 1998 (Figure 4).

The urchin-coraline transect also had a moderately diverse macroinvertebrate assemblage. Coelenterates comprised a common taxonomic group on this transect (Figure 3). One of the most numerous was the solitary orange cup coral, *Balanophyllia elegans*. Highest densities of nearly 50/0.25 m^2 occurred in 1989 to 1990, with low densities of <5/0.25 m^2 in 1984 to 1986 and 1994 to 1998. *B. elegans* was scarce in the kelp forest throughout the entire study. Other abundant coelenterates along the urchin-coraline transect were *C. californica* and *S. catalinensis*, which increased over the same period as on the kelp transect. Tube-dwelling polychaetes, particularly *C. variopedatus* and *Spirobranchus spinosus*, were also abundant on the urchin-coraline transect for much of the study (Figures 4 and 5). Arborescent bryozoans, present on the kelp transect, were absent on the urchin-coraline transect.

Motile macro-invertebrates, other than echinoids and ophiuroids (see below), were infrequent in the quadrats and few temporal trends in abundance were evident. For example, abundances were relatively constant from 1983 to 1998 for the gastropod *Cypraea spadicea* and the holothuroid *Parastichopus parvimensis*, ranging from 0.1 to 0.3/0.25 m^2 .

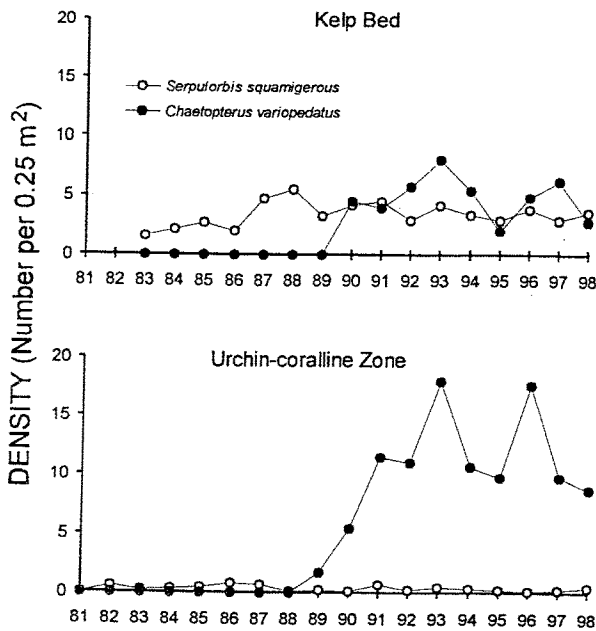


Figure 4. Mean densities of *Serpularia squamigerous* and *Chaetopterus variopedatus* from 1981 to 1998. n = 30, 0.25 m² quadrats sampled in June or July of each year.

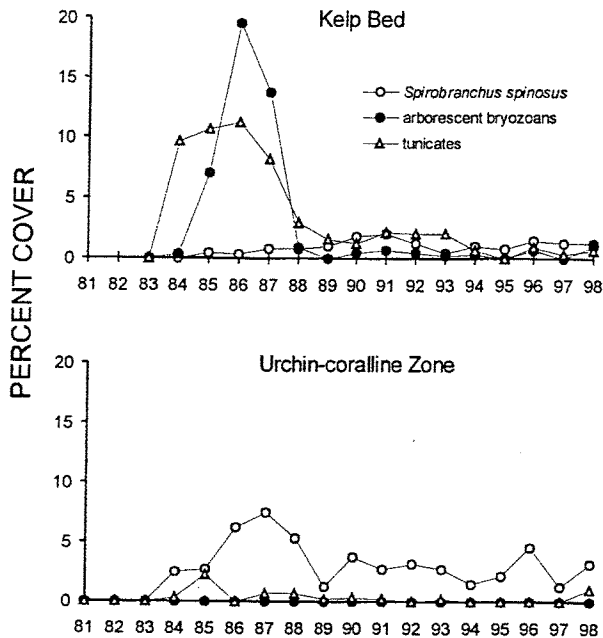


Figure 5. Percent cover of *Spirobranchus spinosus*, arborescent bryozoans, and tunicates from 1981 to 1998. n = 30, 0.25 m² quadrats sampled in June or July of each year.

Ophiuroid Studies

Ophiothrix spiculata increased substantially in the deep reef photoplots (18 m depth) from 1995 to 1998, increasing in cover to nearly 85% in 1997 (Figure 6). The average density of *O. spiculata* on the rock reef surrounding the photoplots, as determined by haphazard quadrat counts in 1996 to 1998, was approximately 350/0.25 m². As

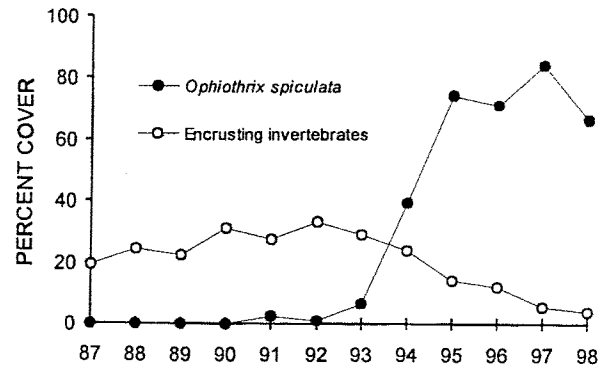


Figure 6. Percent cover of *Ophiothrix spiculata* and sessile encrusting invertebrates from photo-quadrats (18 m depth). n = 5, 0.15 m² quadrats sampled with 50 random points per quadrat.

coverages increased, much of the underlying sessile invertebrate fauna declined to near absence (Figure 6). Analysis of the photoplots revealed that *B. elegans* had been one of the most conspicuous sessile invertebrates from 1986 to 1996. *S. spinosus* and *C. variopedatus* were also common in the plots until *O. spiculata* densities increased. *O. spiculata* was first recorded on the urchin-coraline transect (12 m depth) in 1996 and had an average cover of approximately 15% in 1997, followed by a decline in 1998.

In a sample of twelve 0.25 m² quadrats haphazardly located in the deep reef area in 1995, there was no significant correlation between the density of *O. spiculata* and the density of *B. elegans* ($r^2 = -0.32$). There was, however, a significant positive relationship between the density of *O. spiculata* and the condition of *B. elegans* as measured by percent polyp retraction ($r^2 = 0.68$, $p < .01$; Figure 7).

Multivariate Community Analysis

Continual community changes on the kelp transect from 1983 through 1989 were followed by a relatively stable

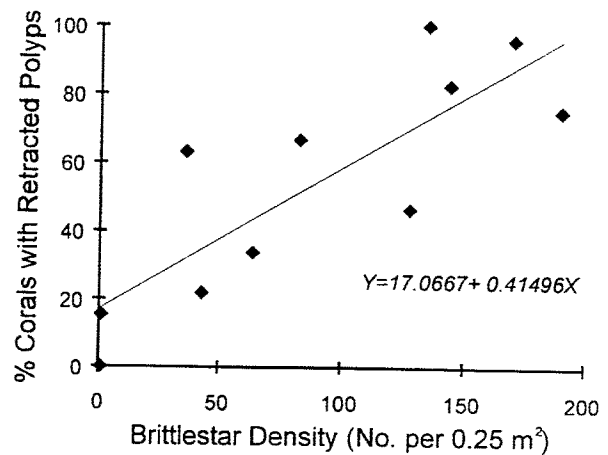


Figure 7. Regression of brittle star (*Ophiothrix spiculata*) density and cup coral (*Balanophyllia elegans*) condition, as measured by percent of cup corals with retracted polyps. Data were obtained in 1995 from a sample of 12 haphazardly located 0.25 m² quadrats (-18m depth).

community from 1990 through 1998. The community composition that existed through much of the 1990s was contrasted with the composition of the community from 1983 through 1989 on the first component axis of the biplot which accounted for 56% of the variation within the data (Figure 8). Changes from 1983 through 1989 were contrasted on the second component axis which accounted for 16% of the residual variation. By associating the taxa vectors on the biplot with the component scores, the analysis showed that the community from 1983 through 1985 was distinguished by relatively greater abundances of the kelps *Macrocystis pyrifera* and *Cystoseira neglecta*. Erect corallines and arborescent bryozoans defined community composition through 1986 and 1987, and by 1988 through 1989 urchins dominated the community. These changes were contrasted with the community that existed through much of the 1990s and was dominated by coralline and ephemeral brown algae, and the sessile invertebrates, *Corynactis californica* and *Chaetopterus variopedatus*.

In the urchin-coraline analysis, the years from 1981 to 1983 and 1986 to 1988 were clustered, with *Lytechinus pictus* and *Astrangia lajollensis* the predominant taxa (Figure 9). A brief recurrence of macrophytes, represented by *Sargassum muticum*, defined the post-1983 El Niño years, 1984 to 1985. From 1989 to 1992 crustose coralline algae, *Balanophyllia elegans* and *Spirobranchus spinosus* were the most abundant taxa in the urchin-coraline area. The years 1993 to 1998 were clustered on Axis 1 and were separated from the earlier years by relative increases in *S. purpuratus*, *C. variopedatus*, *Corynactis californica*, *Ophiothrix spiculata*, and ephemeral brown algae.

DISCUSSION

The kelp forest and urchin-coraline transects at Survey Rock were considerably different from one another in

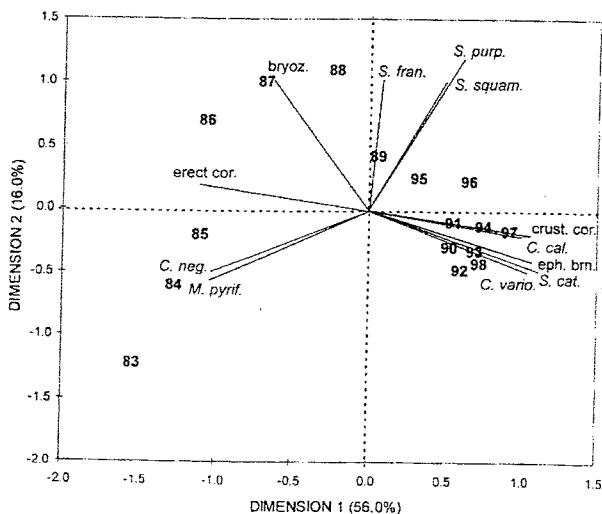


Figure 8. Principal components analysis bi-plot of kelp bed assemblage from 1983 to 1998. Refer to Table 1 for complete names of taxa abbreviations.

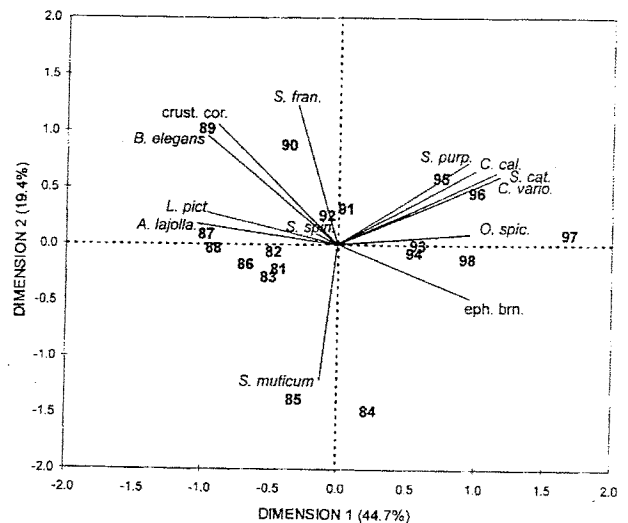


Figure 9. Principal components analysis bi-plot of urchin-coraline zone assemblage from 1981 to 1998. Refer to Table 1 for complete names of taxa abbreviations.

the early 1980s. When the study first began in 1981, the urchin-coraline area (12 m depth) had likely been dominated by urchins for many years. Except for a temporary increase in kelp from 1984 to 1985, the only other report of persistent kelp cover at Survey Rock was in 1967 (Neushul et al. 1967). *Macrocystis* and other macroalgae at the shallow kelp bed transect (8 m depth) declined during the 1980s and remained at low levels during the 1990s. By 1998, both areas were obviously urchin dominated, although the characteristics of their epibenthic assemblages differed due to the length of time exposed to urchin grazing as well differences in depth, wave exposure, and bathymetric relief.

Lytechinus pictus declined substantially in the urchin-coraline area from 1987 to 1998. This may have been attributable to a combination of poor recruitment and mortality from disease during the extended episodes of warmer water during this period. Of the three common urchin species at Survey Rock, *L. pictus* is the most susceptible to echinoderm wasting disease (J. Engle, pers. obs.), although we only observed diseased urchins infrequently at the study site. *L. pictus* is common in the deeper epibenthic shelf assemblage of southern California and population declines have been documented following El Niño episodes (Thompson et al. 1993). It is unclear why *L. pictus* reached unusually high densities in shallow-water habitats at Survey Rock and elsewhere in southern California (Richards et al. 1997) during 1986 to 1989. The unusual abundance of small *Centrostephanus coronatus*, an echinoid with tropical affinities, at Survey Rock in 1998 was a biological indicator of the strong El Niño episode that affected the eastern Pacific in 1997.

Densities of *Strongylocentrotus purpuratus* and *S. franciscanus* did not change substantially over time in the kelp bed, yet macroalgae declined from 1983 to 1988 and were replaced by ephemeral algae as urchins moved out of

crevices and grazed epibiota. With poor macroalgal growth and recruitment, the persistent urchin grazing altered the kelp bed community structure. Foreman (1977) found that ephemeral algae benefited from moderate levels of urchin grazing, colonizing areas in the initial phases of recovery after urchin grazing "fronts" moved through an area. The changes in sessile invertebrates and algae in the Survey Rock kelp forest occurred gradually over a period of several years, as evidenced by the multivariate analysis. Species richness increased in the kelp bed after macroalgae declined. One explanation for the increase may be related to the heterogeneous substrate relief in the kelp forest. Many crevices, vertical walls and rock shelves provided micro-habitats that protected some sessile invertebrates from grazing disturbances, while loss of overstory kelps and other bushy algae created space for ephemeral species and invertebrates resistant to urchin grazing.

Ayling (1981) found that colonial invertebrates such as tunicates and sponges were successful invertebrate guilds at a site in New Zealand heavily grazed by echinoids. He suggested that the biological disturbance resulted in selective pressures for long-lived colonial species that could rapidly regenerate when parts of the colonies were lost to grazing. Clonal coelenterates were also successful at Survey Rock, and some solitary sessile species benefited from the chronic disturbance. One of those species was the solitary cup coral *Balanophyllia elegans*. In the urchin-coralline area, Coyer et al. (1993) demonstrated that the density of *B. elegans* increased with decreasing macroalgal cover as growth and survival were negatively affected by surge-induced brushing from foliose algae. Resulting coral polyp retraction led to overgrowth of the corals by filamentous and crustose algae. Watanabe and Harrold (1991) also found that *B. elegans* increased at a study site (depth range from 17 to 30 m) in central California after it was overgrazed by urchins. In the kelp bed, *B. elegans* never attained high densities even after macroalgae declined to near absence. This may be due to the limited dispersal capabilities of *B. elegans* which reproduces by means of crawling planula larvae that generally settle <1 m from the adult (Gerrodette 1981), or could reflect adverse nearshore environmental conditions. Dayton et al. (1984) noted that *B. elegans* in San Diego reached high densities in urchin barrens, then declined after urchins were experimentally removed. Other sessile invertebrates presumably were able to withstand grazing by passive defenses such as calcareous tubes (*Spirobranchus spinosus*, *Serpulorbis squamigerus*, *Dodecaceria fewksii*), inhabiting crevices (*Chaetopterus variopedatus*), or protective cnidocytes (*B. elegans*, *Corynactis californica* and *Sagartia catalinensis*).

High densities of the ophiuroid *Ophiothrix spiculata* from 1995 to 1998 resulted in dramatic community changes on rock reefs >12 m. Gregariousness, or massive aggregations, in epibenthic ophiuroids is thought to be a response to a combination of factors including favorable environmental conditions, gregarious settlement of their planktotrophic larvae, enhanced feeding stability in strong currents, or im-

proved fertilization success during broadcast spawning (see review by Hendler 1991). In our study, densities of several hundred *O. spiculata* per square meter were common, and often exceeded 1,000/m² with nearly total coverage of the substrate.

Warner (1971) found that aggregations of *O. fragilis* in the English Channel persisted for several years and that underlying epibenthic fauna was not significantly affected. This was clearly not the case in the present study, which demonstrated over a 4 yr period that nearly all sessile taxa declined in response to chronic ophiuroid coverage. Before the rock reef became colonized with ophiuroids, urchin grazing released *B. elegans* from the disturbances of algal brushing and enhanced cup coral density. The dense aggregations of ophiuroids caused chronic polyp retraction in *B. elegans* and branchial plume retraction in *S. spinosus*, apparently resulting in mortality in much the same manner as was caused by brushing algae in experiments by Coyer et al. (1993); however, *B. elegans* also declined on the urchin-coralline transect where *O. spiculata* cover was low or absent. It is likely that sessile epifauna will recover when *O. spiculata* aggregations dissipate, provided that urchin densities are high enough to prevent inhibition by foliose algae. *Corynactis californica* was one sessile filter feeder that was not negatively affected by *O. spiculata*. Ophiuroids avoided direct contact with *C. californica* because of their potent nematocysts (Chadwick 1991). *O. spiculata* experimentally placed on an adjacent *C. californica* colony responded with rapid escape movements and, in some cases, autonomy of one or more arms.

The effects of increased coverage of *O. spiculata* on epibenthic biota likely were widespread along the southern shorelines of Anacapa, eastern Santa Cruz, and Santa Barbara islands. High densities of ophiuroids have also been observed during reconnaissance surveys at these locations (J. Engle, unpublished data), and along some permanent transects monitored by the Channel Islands National Park Service (D. Kushner, pers. comm.). These shorelines were also influenced by strong tidal currents that would be favorable for ophiuroid feeding aggregations.

Many of the changes we have described at Survey Rock were less evident on the northern shoreline (opposite side) of Anacapa Island, although *Macrocystis* declines, urchin overgrazing, and ophiuroid aggregations were noted at various locations (J. Engle, unpublished data). The north side is protected from southern swells, and much of the subtidal zone is protected from human harvesting of fish and invertebrates. The relative contributions of physical characteristics and human impacts on differences in benthic community composition at Anacapa Island are not known and were not investigated in the present study.

Urchin overgrazing may have been a rare occurrence about 200 years ago when a major predator, the sea otter, was common in southern California. Dense aggregations of large urchins are not known to occur in central California or Alaska where sea otters are present (Reidman and Estes 1988), although aggregations of smaller *S. purpuratus* can

co-occur with otters (J. Blecha, unpublished data). In the absence of sea otters, however, urchins do not always cause the development of crust-dominated assemblages on shallow rock reefs; instead, there is good evidence that urchin overgrazing and the consequent shifts in benthic community structure between urchin-coraline and kelp-dominated assemblages are part of the natural variation in a dynamic community (Cowen et al. 1982; Foster and Schiel 1985). The rapid increases and persistence in ophiuroid density at Survey Rock introduce another component to the dynamics, namely the role of episodic events. Such events underscore the unattainable goal of accurately predicting benthic community composition considering variable periods in hydrographic cycles, changing invertebrate settlement patterns, and complex interactions between species (Gray and Christie 1983). In the main, however, changes in structure at Survey Rock appear to have been driven by a combination of warmer water and poor nutrient conditions unfavorable for kelp growth, coupled with pulses of successful recruitment in purple urchins and brittle stars. Secondary changes resulted from species interactions and the accommodation to chronic grazing disturbances. Significant kelp bed recovery at the study site is unlikely until the oceanographic regime in the Southern California Bight shifts to an extended period of cooler water, and both urchin and ophiuroid populations decline.

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SOURCES OF UNPUBLISHED MATERIALS

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- David Kushner, Channel Islands National Park Service, 1901 Spinnaker Drive, Ventura, CA 93001.