FOOD AVAILABILITY, SEA URCHIN GRAZING, AND KELP FOREST COMMUNITY STRUCTURE

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Abstract. Unlike most previously reported kelp forests, which exhibit long-term persistence over large spatial scales, the kelp forest community on the west end of San Nicolas Island, California, occurs as a dynamic patchwork of barren areas characterized by grazing sea urchins and an algal assemblage consisting of upright and encrusting coralline algae, and kelp-dominated areas characterized by high densities of perennial brown algae, including the giant kelp Macrocystis pyrifera. In this study we examine the factors that regulate the grazing activity of sea urchins (Strongylocentrotus franciscanus), which in turn determines the structure of this community. In the barren area, drift algae were sparse, sea urchins were poorly nourished, occupied open, unprotected microhabitats, and actively grazed the substratum. In the kelp-dominated area, drift algae were abundant, sea urchins were well nourished, moved little, occupied cracks and crevices, and probably fed on drift algae. Early in the study substantial recruitment of brown macroalgae occurred in both sites, and the barren area gradually transformed into a kelp-dominated area. Concomitant with this change, the abundance of drift algae in the barren area increased. Urchins in this area abandoned open microhabitats for protected crevices and pockets, and sea urchin grazing intensity was reduced to levels characteristic of the kelp-dominated area. From these observations we present a qualitative model in which the transformation from one configuration to another is triggered by a behavioral switch in the mode of feeding of red sea urchins. This switch is controlled by the availability of drift algae, which in turn is dependent upon the abundance of attached macroalgae. The adult algal standing stocks appear to be regulated by prevailing hydrographic conditions, which are either favorable or unfavorable for kelp recruitment, survivorship, and growth. In this model grazing intensity is independent of urchin density and therefore provides a new view of how kelp forest communities function.

Key words: benthic ecology; grazing; kelp forest; plant/herbivore; sea urchins.

INTRODUCTION

Plant-herbivore interactions have been shown to be important structuring elements in a wide variety of systems in both terrestrial (Harper 1977, Morrow and LaMarche 1978, Rausher and Feeny 1980, Cumming 1982) and marine (Lubchenco and Gaines 1981, Gaines and Lubchenco 1982) environments. Although these systems and their component species are quite diverse, one feature common to all is the potential for two alternative states, one with high and one with low ratios of plant/herbivore biomass. This is certainly true for kelp forest communities found in temperate seas throughout the world. Regardless of their geographic location, these productive and complex communities are often susceptible to sea urchin grazing, which in many cases completely denudes the substratum of all macroalgae, forming barren grounds (see Lawrence 1975 for review, Breen and Mann 1976, Estes et al. 1978, Bernstein et al. 1981, and others). Intensive grazing by sea urchins not only impacts the algal assemblage but has been shown to have cascading effects on the rest of the community as well (Kitching and Ebling 1961, Estes and Palisano 1974, Estes et al. 1978). A second property shared by many kelp forest systems is that barren grounds frequently occur adjacent to ungrazed areas which are characterized by high abundances of mature kelps and other algae. The boundaries between these “kelp-dominated” areas and barren areas are distinct and not associated with any detectable difference in the character of the substratum in the two areas (Lawrence 1975). This phenomenon is widespread, having been reported from Great Britain (Kitching and Ebling 1961), Nova Scotia (Breen and Mann 1976, Chapman 1981), Alaska (Duggins 1980, 1983), central California (Pearse and Hines 1979), southern California (Leighton 1971) and New Zealand (Choat and Schiel 1982). Finally, these alternate community types show long-term persistence; transitions from one state to the other occur on a time-scale of decades and over large spatial scales (several square kilometres) (Mann 1977, Simenstad et al. 1978). These transitions are generally attributed to changes in the abundance of sea urchin grazers as a result of changes in predation pressure (Breen and Mann 1976, Mann 1977, Estes et al. 1978), storms (Harris et al. 1984), or disease (Pearse and Hines 1979, Miller and Coleody 1983).

Since 1980 we have been investigating the dynamics of a kelp forest that contrasts rather markedly with this general view. Located on the southwest end of San Nicolas Island in the Southern California Island group, this kelp forest is composed of barren and kelp-dominated patches that are unstable, appearing and disappearing over small temporal and spatial scales. Our

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studies indicated that the mechanism driving the sys-
tem involved a behavioral switch in the mode of feed-
ing of sea urchins but was independent of sea urchin
density. It is the purpose of this study to investigate
the factors that regulate sea urchin grazing intensity in
this kelp forest, and to determine what role these fac-
tors play in regulating kelp forest community structure.

Our approach was first to quantify and monitor over
time the densities of perennial brown algae and sea
urchins at permanent sites established in barren and
kelp-dominated areas. Second, we assessed the modes
of grazing by red sea urchins in the two types of hab-
itats. This included monitoring drift algal food abun-
dance, daily movement, diets, reproductive condition,
and microhabitat distributions of sea urchins. Natural
changes in all these parameters over time suggested a
qualitative model to explain the mechanisms of patch
maintenance and formation.

STUDY SITE AND METHODS

The study was done in the shallow (11 m depth)
subtidal zone off the southwest end of San Nicolas
Island, Ventura County, California (Fig. 1). The bot-
tom is composed of sandstone and shale pavement cut
by numerous crevices and ledges and strewn with large
boulders. In the summer of 1980, two permanent sam-
pling stations, each consisting of a 50-m transect marked
by stainless steel eyebolts at 5-m intervals, were estab-
lished. One of the transects (hereafter referred to as the
barren site) runs through a barren area and ends at the
boundary between it and an adjacent kelp area. The
other transect (hereafter referred to as the kelp site)
begins at the boundary and runs through a kelp-dom-
inated area.

Typically a barren area at San Nicolas Island is char-
acterized by an algal assemblage consisting primarily
of erect and encrusting coralline algae. Stipitate brown
algae including the surface canopy species *Macrocystis
cyprifera* (hereafter referred to as *Macrocystis*) are con-
spicuously absent. Red (*Strongylocentrotus franciscanus*)
and purple (*S. purpuratus*) sea urchins are abun-
dant and they often occur in open habitats, suggesting
that they are actively grazing (Mattison et al. 1977,
Russo 1979, Bernstein et al. 1981). Unlike barren areas,
kelp-dominated areas possess a well-developed surface
canopy of *Macrocystis* under which a lush brown algal
understory is found. As in barren areas, encrusting cor-
alline algae cover much of the bottom. Sea urchins are
abundant in kelp-dominated areas but they are usually
clumped in crevices and pockets, suggesting that they
are not actively grazing but feeding on drift algae (Low-
ry and Pearse 1973, Mattison et al. 1977, Bernstein et
dives outside of our study areas revealed that the above
descriptions are an accurate reflection of barren and
ekelp-dominated areas throughout much of the shallow
subtidal on the western end of the island.

The densities of large mobile invertebrates and mac-
roalgae were estimated from 2 x 10 m permanent
swaths set perpendicular to the 50-m transect at ran-
domly determined intervals. In addition, the holdfast
diameters of all *Macrocystis* plants taller than 1 m were
measured in situ using large calipers. Four swaths were
sampled in the barren area and six in the kelp area.
Sampling of the two sites began in August 1980, and
continued until the end of the study. The sites were
sampled twice per year, in the spring and fall.

The abundance of drift algae (all detached macro-
algae lying on the bottom) was estimated from collec-
tions made within 10 randomly placed 10-m² plots in
both the barren and kelp sites. The drift material was
placed in mesh bags and carried to the surface, where
it was transferred to sealed plastic bags. The algae were
then taken to the laboratory where they were sorted
into one of four categories: *Macrocystis*, other brown
algae, fleshy red algae, and erect coralline algae. Wet
mass of each category was determined.

Two additional permanent stations were set up in
the barren and kelp sites near the transects in order to
assess the modes of grazing shown by red sea urchins.
Although purple urchins are important grazers at other
locations around San Nicolas Island, they primarily
occupy pockets and crevices at our study sites and have
never been observed actively grazing. Consequently,
we focused our work on red urchins. Daily movement
(a reliable indicator of urchin grazing: Lees 1970, Mattison et al. 1977) was measured using the polar coordinate method described by Mattison et al. (1977). The position of tagged urchins was determined with a fiberglass measuring tape attached to the center of a fixed protractor. Twenty-five urchins in each area were tagged by slipping short lengths of numbered plastic straws over the spines. Some error is associated with this method: swell-induced surge pushes the tape from side to side, and the bearing can vary as much as 10°. The resulting error in estimated urchin position can be substantial. To quantify this error the positions of three stationary objects were recorded along with the positions of the urchins within each site. Ninety-five percent confidence limits were computed for both distance and bearing measurements of these points over the 3 d of measurements. The change in bearing or radius for individual urchins from one day to the next was considered to be zero if it was within the 95% confidence limits of measurements of the stationary objects. Data on sea urchin movement, along with drift algal abundance, diets, and gonad indices (see below), were collected at ≈3 mo intervals from April 1981 to October 1982.

Diets and gonad indices were determined from 10 individuals randomly collected from each of the two sites. Soon after the urchins were brought to the surface from 2 to 12 mL of formaldehyde (depending on the size of the urchin) were injected into the animals through the peristomal membrane. After 24 h (to allow fixation of the gonads, gut tissues, and gut contents) the animals were dissected and the alimentary tracts removed and placed in jars of 5% Formalin for analysis later. The gonads were removed, blotted on a paper towel, and damp-weighed to the nearest 0.1 g. Gonad indices were computed as gonad mass/urchin mass × 100. Gonad indices could not be computed directly from the wet mass of the whole animal because the fixation procedure resulted in substantial and variable fluid loss. Therefore whole-animal wet masses were estimated from a test diameter-wet mass regression analysis performed in July 1982. For this analysis 19 red sea urchins were collected haphazardly from both barren and kelp-dominated habitats on the west end of the island. The animals were taken back to the laboratory alive and abundance, diets, and gonad indices (see below), were collected at ≈3 mo intervals from April 1981 to October 1982.

The basic structure of the algal assemblage in the barren site changed substantially during the 2.5 yr of the study (Fig. 2). Although the densities of some species of brown algae fluctuated in the kelp site as well, the overall character of the kelp site remained the same. In August 1980, the densities of all adult stipitate brown algae were lower in the barren site than in the kelp site. In fact, there were no Cystoseira osumdacea, Eisenia arborea, Laminaria spp. (hereafter the generic names only will be used), large (>1 m tall) Macrocystis, or young laminariales (plants not sufficiently differentiated to identify genus and species) counted in the barren site at this time (Fig. 2A–G). The densities of all stipitate brown algae in the barren area increased throughout the study, and by October 1982, the composition and abundance of these species were similar at the two sites. The density of red sea urchins at the barren site fluctuated over time (Fig. 2H), but linear regression analysis showed that the slope of the line relating sea urchin density to time was not significantly different from zero (P > .25, F test for the presence of regression, Sokal and Rohlf 1969:430–432). The density of red urchins at the kelp-dominated site increased slightly over time (Fig. 2H), with a regression coefficient of +0.03 (P < .05, F test for the presence of regression). The increase was slight, however, and had no detectable impact on urchin grazing activity (see Sea Urchin Movement).

In April 1981, recruitment of young laminariales and small Macrocystis was observed in both areas. In the barren site small Macrocystis showed an increase in density in April 1981 and then declined (Fig. 2B), while the density of large Macrocystis steadily increased (Fig. 2C). This pattern probably resulted from high mortality of recruits and the subsequent growth of survivors into the larger size-classes. The increasing holdfast diameters of Macrocystis in the barren site support this

Three independent subsamples were taken from each specimen. Each subsample was placed in a Petri dish and suspended in water ≈1 cm deep. The Petri dish was placed over a 1 × 1 cm grid on the stage of a dissecting microscope, and the number of pieces of each category of alga in three grid squares were counted. The average size of coralline algae pieces tended to be smaller than the other types, which could result in an overestimate of the contribution of coralline algae to the diet. However, corallines made such a small contribution to the diet that any bias was considered negligible.

The microhabitat distribution of red sea urchins in the two habitat types was determined by scoring all urchins within a 1 m wide swath along the 50-m transects as occupying “cryptic” (cracks, crevices, pockets, against ledges) or “open” (flat substratum, not as above) microhabitats.

**Results**

**Abundance of attached algae and sea urchins**

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view (Fig. 3). Young laminariales and small *Macrocystis* showed a similar pattern in the kelp site. However, the increase in the density of large *Macrocystis* plants was not as dramatic as in the barren site (Fig. 2C). This, together with the declining mean holdfast diameters over time in this area (Fig. 3), suggests that some recruitment did occur as smaller (younger) plants replaced larger (older) ones.

**Drift abundance**

The composition and relative abundance of drift algae were greatly influenced by both the immediately surrounding flora and the time of year. In the kelp site, where attached algal biomass was high, drift biomass was also high. Brown algae, consisting primarily of *Macrocystis*, were the major component of drift at this site, accounting for 87–98% of the total drift biomass (Fig. 4A). Fleshy red and erect coralline algae were much less abundant and comprised the remainder of the drift. Drift biomass was highest in the summer months when water motion is low and senescent fronds accumulate on the forest floor. Lows in drift biomass were observed in winter and early spring when water motion tends to be higher and drift is transported out of the kelp forest. Gerard (1976) reported a similar pattern in drift algal abundance for a kelp forest in central California.

Initially in the barren site when attached algal biomass was low, drift abundance was also low and consisted primarily of erect coralline algae (Fig. 4B). In
Fig. 3. Holdfast diameters of *Macrocystis* > 1 m tall located in 20-m² swaths, plotted over time. Variability is expressed as ±1 se. Sample size ranged from 4 plants (when sampling first began and the abundance of *Macrocystis* plants > 1 m high in the barren site was low) to 135 plants. Data prior to April 1981 were obtained using different techniques and were not plotted.

contrast to the kelp site, brown algae were a very small component of the drift at this time. By July 1982, however, an increase in brown algal drift was observed (Fig. 4B). These drift algae were probably produced by the plants that initially appeared in April 1981. No temporal trends were recorded in the abundance of coralline algal drift except that it was consistently higher in the barren than in the kelp site.

**Sea urchin movement**

Red sea urchins in the barren site showed higher rates of movement than urchins in the kelp site for the first 10 mo of observations (Fig. 5). During this time urchins from both areas showed higher rates of movement in winter and spring and lower movement rates in the summer and fall. By July 1982 movement rates of urchins in the barren area fell dramatically to a level resembling that of urchins in the kelp area. Movement rates remained low in both sites on subsequent sampling in October 1982.

Two-way analysis of variance was used to examine the significance of the differences in movement rates between sites and over time (Table 1). It is clear that both factors significantly affected movement rates. The significant interaction term probably stems from the drop in movement rate that occurred in the animals from the barren area but not in animals from the kelp-dominated area.

Sea urchin movement was therefore inversely correlated with the temporal pattern of the combined biomass of *Macrocystis* and other brown algal drift at both sites (barren site: $r = -0.870$; kelp site: $r = -0.833$; $P < .05$). Movement and drift abundance were inversely correlated on a spatial scale as well. Movement rates of urchins at the barren site were higher than those at the kelp site through February 1982 (Fig. 5), when the abundance of drift brown algae in the barren site was lower than in the kelp site. As drift abundance at
FIG. 5. Mean distance moved per 24 h for red sea urchins (Strongylocentrotus franciscanus). Variability is expressed as ±1 se.

this site increased after February 1982, movement rates of urchins in the barren area fell. The inverse relationship between movement rates and drift abundance suggests that grazing activity is at least in part a function of the abundance of drift brown algae. Previous work that supports this idea is based on between-site comparisons (Lees 1970, Mattison et al. 1977, Russo 1979). Our study supports this idea not only with between-site comparisons but also by demonstrating a significant inverse relationship between urchin movement and drift algal abundance over time.

Sea urchin diets

The diets of urchins from both sites were composed primarily of brown algae (Fig. 6) although fleshy red algae initially constituted a higher proportion of the diet in urchins from the barren site. By December 1981, however, the diets of the two groups of urchins were indistinguishable.

Although the origin of the brown algae in the diets of urchins from the barren site is uncertain, it probably consisted of newly settled plants rather than drift, since there was a large number of kelp recruits and a small amount of kelp drift in the barren site during this time. Gut contents of urchins from other barren sites where no algal recruitment had occurred consisted of only coralline algae (C. Harrold and D. C. Reed, personal observation). Brown algae accounted for an even greater proportion of the diet of urchins from the monitored barren site as the abundance of Macrocystis and other brown algal drift increased. In the kelp site, the source of brown algae in the diets of urchins was probably drift, since the abundance of brown algal drift was high and grazing activity (as indicated by movement rates) was low. In addition, urchins at this site remained in crevices and other protected microhabitats (see below).

Gonad indices

The gonad indices of red sea urchins from the barren site were initially lower than those from the kelp site but increased to similar values by February 1982 (Fig. 7). The gonad indices of kelp-site urchins remained high and constant during this time. In April 1982 gonad indices of both groups of urchins fell, probably the result of springtime spawning. Thereafter the gonads of both groups increased in size.

The relative size of the gonads of sea urchins has been shown to be a reliable index of their nutritional well-being (Bennett and Giese 1955, Fuji 1967, Pearse 1969, Pearse et al. 1970). More recently, the gonad indices of red sea urchins from different sites have been shown to be related to the amount of algal food available to them (Pearse 1980). The effect can be very localized, as Dean et al. (1984) found that differences in food abundance between sites separated by only a few metres can result in different gonad indices. In Fig. 7 the standard errors of the mean gonad indices are small, indicating that within-habitat variation in food abundance was not great. We believe that initially the kelp site urchins had larger gonads than barren site urchins because drift algae were more available to the former animals. Barren site urchins had sufficient food for prespawning gonad growth but not for maintenance of large gonads year round. Gonad indices were similar

| Table 1. Two-way analysis of variance on movement data for red sea urchins (Strongylocentrotus franciscanus) at both study sites. |
|---|---|---|---|
| Source of variation | Degrees of freedom | F value | Probability |
| Time | 6 | 5.37 | <.0001 |
| Site | 1 | 20.28 | <.0001 |
| Time x site interaction | 6 | 5.79 | <.0001 |

FIG. 6. Composition of the diet of red sea urchins (Strongylocentrotus franciscanus) over time. N = 10 animals for each sample. Variability is expressed as ±1 se.
after spawning in April 1982 because the two groups of animals had similar amounts of food (in the form of drift brown algae) available to them after this time.

**Microhabitat distribution**

Red sea urchins from both stations occupied primarily protected habitats on all four sampling dates, but between-site and between-date differences did occur (Fig. 8). In April and August 1981, a higher proportion of urchins in the barren site occupied open habitats than in the kelp site ($G = 45.3$ and 59.5 for April and August 1981, respectively; $df = 1$, $P < .005$ in both cases), but by July 1982 there was no significant difference ($G = 0.232$ and 0.054 for July 1982 and April 1983, respectively; $df = 1$, $P > .005$). This resulted from a shift of barren-site urchins to protected microhabitats.

Different modes of feeding by sea urchins have been correlated with their microhabitat distribution (Leighton et al. 1965, Lowry and Pearse 1973). We suggest that the differences in microhabitat distribution of urchins at the two sites in April and August 1981 was related to differences in the abundance of drift algae, and that the shift of urchins in the barren area to more protected microhabitats resulted from the increase in abundance of drift brown algae after April 1982. To test the idea that microhabitat distribution and availability of drift algae are causally related, we performed an experiment in which we tried to initiate the reverse of the results reported above. For example, if drift algal abundance is reduced, urchins in crevice habitats should shift to more open habitats as they begin grazing. To reduce the abundance of drift algae we removed all *Macrocystis* plants from a 40 x 40 m plot near our study site in Oct 1982. We felt that a clearing of this size was adequate to reduce drift abundance within the area because our data indicate that the abundance of drift is correlated with abundance of attached algae in the immediate vicinity (Fig. 4). This strong correlation is due to the fact that most of the drift algae in kelp areas are senescent *Macrocystis* fronds, which sink to the bottom before they become detached from the source plant. Once on the bottom, these plants are rapidly entrapped by urchins. Therefore, except in times of severe water turbulence, these drift algae are not moved far from where they grew. Mattison et al. (1977) also suggested that local distribution of drift is determined by the standing stocks of attached algae nearby. We decided not to sample drift at this time because our previous data indicate a strong positive correlation between algal standing stocks and drift biomass. The microhabitat distribution of red sea urchins was monitored before and after the removal using the techniques described in Methods. Urchins in the kelp site served as controls. At the time of the removal 89% of the urchins in the *Macrocystis* removal site occupied cryptic habitats. Six months later (unusually severe and frequent storms prevented sampling before this time) <50% of the animals remained in cryptic habitats. The difference in distribution of urchins between these two sampling dates was highly significant ($G = 94.2$, $df = 1$, $P < .005$). In the kelp site, virtually all the urchins remained in cryptic microhabitats for the duration of the study. We conclude that reduction in the abundance of drift algae due to the removal of *Macrocystis* resulted in a shift of urchins towards more open microhabitats and presumably to an active mode of grazing.

**DISCUSSION**

The kelp forest community on the west end of San Nicolas Island differs from systems previously reported in two important aspects. First, our system is very dynamic. We witnessed the transition of a barren area into a kelp area within 1.5 yr, and other evidence sug-
suggests that the opposite transition has taken place at other sites around the island within the last 4 yr (R. McPeak, personal communication; C. Harrold and D. C. Reed, personal observation). This “patch instability” contrasts with previous studies of kelp forest systems in which these alternate community types show long-term persistence (Mann 1977, Simenstad et al. 1978). Second, we found that the intensity of grazing was independent of sea urchin density. Previous work has shown that changes in the abundance of urchins as a result of disease (Pearse and Hines 1979), changes in predation pressure (Breen and Mann 1976, Mann 1977, Estes et al. 1978), or behavioral responses to predators (Duggins 1983) are important in determining which of these two alternate configurations exists at a particular point in time. In our study, urchin densities in the two sites were similar and remained essentially unchanged throughout the study. Sea urchins in the kelp-dominated site exerted no grazing pressure on the system because the high abundance of drift algae in this site satisfied their nutritional requirements (as indicated by their high gonad indices). These animals occupied crack and crevice habitats and fed on passing drift algae. At the beginning of the study the biomass of drift algae in the barren site was not sufficient to keep urchins well fed (as indicated by their low gonad indices). As a result, they actively grazed the substratum, preventing the establishment of macroalgal growth. High algal recruitment occurred in April 1981, and some of the plants survived urchin grazing. By the following year they were large enough to produce drift algae. Once drift algae became available to the urchins, they switched from an active, grazing mode of feeding to a sedentary drift-feeding mode. This reduction in grazing pressure enhanced the establishment of kelps, so that the former barren area took on the appearance of the kelp area. Thus our study shows that sea urchins maintain barren areas with depauperate macroalgal assemblages by intensive grazing (as indicated by movement rates) and that increased availability of drift algae can depress urchin grazing below the point where brown macroalgae can become established.

Other workers have also demonstrated that the urchin density/kelp abundance relationship is too simplistic and that other factors such as availability of alternate food resources (Duggins 1981) and water turbulence (Choat and Schiel 1982, Cowen et al. 1982, Foster 1982) are also important. In particular, Dean et al. (1984) showed that the formation of high-density urchin aggregations was a prerequisite to destructive grazing by S. franciscanus in a southern California kelp bed. They suggested that 2 yr of declining kelp abundance resulted in a reduction in the availability of drift algae to sedentary urchins which stimulated them to begin moving, ultimately leading to the formation of motile urchin “fronts.” Although urchin fronts have been associated with overgrazing in other kelp forest systems (North and Pearse 1970, Leighton 1971, Bernstein et al. 1981; reviewed in Lawrence 1975), they were not observed in our study site.

From our observations we propose a qualitative model to summarize our view of how this kelp forest community functions. Standing stocks of attached algae in barren areas are low, and as a result drift abundance is low (top portion of Fig. 9). The nutritional status of the urchins deteriorates because algal food resources are scarce. This stimulates increased grazing activity which in turn inhibits algal recruitment and maintains low standing stocks of attached and drift algae. Thus, barren areas are maintained through a cycle of intense grazing which reduces the food supply which in turn stimulates grazing. In contrast, the high standing stocks of attached algae in kelp-dominated areas result in high drift biomass (bottom portion of Fig. 9). Sea urchins remain in cryptic habitats and feed on drift algae. The animals are well nourished (as indicated by high gonad indices) and have no tendency to roam about and graze. Thus, in the absence of grazing, high algal standing stocks are maintained as successful recruitment balances mortality.

The obvious question which remains to be answered is how these distinct habitat types arise. Although
changes in the abundances of algae observed in this study and observations of other students of kelp forest systems suggest a plausible mechanism of patch formation. In our model each of the two habitat types is maintained by a sequence of processes that are intrinsic to the community. Because the sequences are cyclic, each habitat persists in the absence of input from outside the system. Thus, kelp-dominated habitat would persist were it not for occasional disturbances such as severe storms, which remove entire plants from the bottom. As these plants are transported out of the forest they may entangle other plants, which are also torn loose (Rosenthal et al. 1974). Consequently, drift production is locally reduced, and sea urchins abandon their sedentary habits and begin grazing. The impact of storms is intensified if they are followed by periods when conditions are unfavorable for algal recruitment and growth (low nutrient levels, warm temperatures). Thus, hydrographic events extrinsic to the kelp forest community can initiate events that transform a kelp-dominated area into a barren area. The reverse process can also occur. In some years environmental conditions may be especially favorable for high algal recruitment and growth: benign storms and periods of relatively clear water, high nutrients, and low temperatures. Under these conditions the effects of sea urchin grazing in barren areas can be overwhelmed and some plants may escape predation and become established. Drift production subsequently increases, and sea urchin grazing slows down, allowing further recruitment and growth. Hydrographic events can thus initiate the sequence of events depicted in the lower portion of Fig. 9, resulting in the transformation of a barren area into a kelp area.

This model may explain how the transformation of the barren area into a kelp area took place. Substantial algal recruitment was observed in April 1981, at both study sites and at other sites around San Nicolas Island (Fig. 2A and B; C. Harrold and D. C. Reed, personal observation). In addition, the densities of adult Macrocystis and other kelps have been increasing since this time (Fig. 2C). One year later brown algal drift abundance in the barren site was higher than in previous months, and sea urchin movement rates, and presumably grazing pressure, were lower. Sedimentation, light, temperature, and nutrients all influence the timing of successful recruitment of Macrocystis (Dean and Deysher 1983), but we were unable to sample these parameters, and available hydrographic data are not of sufficient resolution to relate to this recruitment event. However, storm activity in the winter of 1981–1982 was low, which would increase the survivorship of young plants.

We have not witnessed the transformation of a kelp-dominated area into a barren area, but the preliminary results from the Macrocystis removal experiment suggest that storm-induced plant removal may in fact reduce food availability to the point where active sea urchin grazing is initiated. This phenomenon has also been reported for an offshore reef in southern California where storm-induced plant removal caused intense sea urchin grazing, resulting in the formation of barren grounds (Harris et al. 1984).

Our model is clearly oversimplified in that numerous other factors that cause switching from one state to another are excluded. For example, disease outbreaks in urchin populations would likely shift the community to kelp dominated. In areas where effective urchin predators are abundant, barren areas may never develop. But we feel that within the framework of the geographic location of our study site and the hydrographic and biological conditions that prevailed during our study, the parameters indicated in our model could, by themselves, control which of the two alternate states exists at a given point in time. We have thus identified an important element in the regulation of kelp forest community structure.

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