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MULTISPECIES CONSIDERATIONS OF RESOURCE MANAGEMENT IN SOUTHERN CALIFORNIA KELP BEDS

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ABSTRACT

Southern California kelp beds, especially those around major metropolitan centers, have suffered from severe episodes of sea urchin overgrazing in the last four decades. The proposal that increases in sea urchin populations leading to this destructive grazing were caused by release from predation by the sea otters is rejected on the basis of historical data. While fluctuations in standing crop have been observed, some kelp beds in this region continue to flourish in the absence of either otter predation or human control of urchins. Abalones, spiny lobsters, and sheephead are other species whose populations have been reduced by fishing and which, by virtue of their trophic relationships with urchins, could be expected to control urchin distribution and abundance patterns. Studies of giant kelp mortality in the Point Loma kelp bed off San Diego provide evidence for the role of lobster and sheephead predation in controlling urchin populations. These biological interactions provide a mechanism for the maintenance of southern California kelp bed communities in a stable configuration after the demise of the sea otter from this region.

INTRODUCTION

Sea urchins are well known for their abilities to control the distribution and abundance of marine plants; and especially where their preferred foods are large kelps, these herbivores can be the major structure-determining factor in nearshore communities. In his recent review, Lawrence (1975) cites reports from several parts of the world where urchins appear to have overgrazed their food supply, leading to urchin-dominated barren grounds. Mann and his associates have documented the decline of kelp beds in St. Margaret's Bay, Nova Scotia, in the face of intense grazing pressure by Strongylocentrotus droebachiensis (this work is reviewed by Mann, 1977). This increase in urchin grazing was apparently caused by heavy fishing of an important urchin predator, the lobster Homarus americanus.
The urchins, sustained by drift from algal refuges too shallow for urchin grazing, prevent algal recolonization in deeper water. Because of the persistence of this association, Mann (1977) has proposed the hypothesis that the urchin-dominated barren grounds of Nova Scotia are not representative of cyclic changes in the abundance of kelp and associated herbivores but instead are a new, stable configuration of the system. In other words, he is suggesting that overfishing a predator of the major grazer has so perturbed the community that it will not be able to recover to its previous, long-persisting state.

The decline of kelp beds in southern California predates that documented for Nova Scotia by many years; and here as well, sea urchin grazing has received much of the same. I would like to consider the resiliency of these kelp bed communities and the applicability of Mann's hypothesis to southern California. This will entail first a discussion of the history of this ecosystem and the changes which have taken place as a result of human impact on the nearshore environment. Secondly, my own research has dealt with the natural history and population dynamics of two sea urchins, Strongylocentrotus purpuratus and especially S. franciscanus, which is now the object of a commercial fishery. These two sea urchins are the most important consumers of kelps in southern California; control of their populations is fundamental to the persistence of kelp beds in this region.

SOUTHERN CALIFORNIA KELP BEDS: A BRIEF HISTORICAL PERSPECTIVE

The giant kelp, Macrocystis pyrifera, is the most prominent alga of southern California kelp beds. Several other kelps contribute to the diversity of these assemblages, but Macrocystis is most important in terms of biomass and its contribution to the spatial structure of the community. Its holdfast, fronds, and canopy furnish food, substrate, or shelter for a variety of organisms. These beds are the location of valuable fisheries for abalone, spiny lobster, fin fish, and most recently, sea urchins. The surface canopy, which forms large offshore beds often covering several km², is easily harvested and has been an important resource since the early part of this century (Leighton, Jones, and North, 1966; North, 1971).

When potash supplies became a national concern about 1910, Congress authorized a survey of west coast kelp resources. The beds were mapped during the period of 1911 to 1912 and the total area of kelp beds in southern California (San Diego to Point Conception) was estimated at
253 km² (North, 1971). North (IMR, 1963) has used these data to assess subsequent changes, especially the decline of large kelp beds around the two major metropolitan centers of southern California. During the decade of 1940-1950, productive beds around the Palos Verdes peninsula (the site of the Los Angeles County sewer outfall) deteriorated to the point that little or no harvesting was conducted. A decade later, the same changes took place in the Point Loma kelp bed off San Diego (see Leighton, Jones, and North, 1966, for historical variation of the Point Loma beds). In both cases, the historical data indicated that those portions of the beds close to sources of waste disposal were affected first (IMR, 1963).

Early investigations of these once productive beds revealed an abundance of grazers, particularly sea urchins (IMR, 1963). North and his co-workers described barren rock bottoms where grazing pressure prevented algal recolonization. Perhaps the coup de grâce was delivered to these communities by the warm-water years of 1957-1959 when abnormally high temperatures prevailed throughout the year. Offshore island beds produced normally in 1957; but by 1958 these were affected, as were the beds along the coast. By 1959, North reports that most of the canopies in kelp beds of southern California had deteriorated and many beds had virtually disappeared (IMR, 1963).

Several authors have proposed that this apparent population explosion of S. purpuratus and S. franciscanus associated with the decline of kelp beds along the coast of southern California (North and Pearse, 1970) was caused by a decrease in predation by the sea otter, Enhydra lutris (McLean, 1962; North, 1965, Lowry and Pearse, 1973). Leighton, Jones, and North (1966) consider the otter to be the only predator capable of controlling urchin populations in California. Sea urchins are a preferred food of sea otters (Ebert, 1968), and otter predation of urchins has been documented as having major effects on kelp community structure in Alaska (Estes and Palmisano, 1974; Dayton, 1975). As the now protected otter has begun to reoccupy part of its former range in central California, urchin densities have decreased and the herbivores are now restricted to deep crevices beyond the reach of the otters (Lowry and Pearse, 1973).

The problem with this hypothesis for the control of urchin populations is that otters were probably gone from southern California 130 to 150 years ago (Ogden, 1941). Hunting is known to have continued up to the time of the Gold Rush in 1848 and sporadically after that; but this most likely took place north of Point Conception where sea
conditions and the coastline are considerably rougher and where in fact a remnant population did survive (Woodhouse, Cowen, and Wilcoxon, 1977). Furthermore, the abalone (another preferred food of the sea otter; Ebert, 1968) fishery dates back to the 1850's around San Diego (Cox, 1960), and large kelp beds were documented in 1913 (North, 1971). According to North, the major decline of surface canopies did not begin until the 1940's (IMR, 1963). These historical data strongly suggest that factors other than otter population have controlled urchin populations in southern California.

SEA URCHINS AND THEIR INTERACTIONS WITH OTHER SPECIES

Since sea urchins can be considered a foundation species (Dayton, 1972) in these communities, any factors which affect their birth or death rates are likely to be important to the maintenance of community structure. I have been studying sea urchin recruitment, competition, and mortality patterns to determine what disturbances may have prevented urchin domination in the past. An obvious consideration is those species which, in addition to sea otters, have been fished.

While several benthic invertebrates graze on attached or drift Macrocystis (Leighton, 1971), the abalones, by virtue of their physical size (Haliotis rufescens attains sizes up to 30 cm; Cox, 1960) and the magnitude of their populations, require consideration as competitors of the sea urchins. Seven species are found in southern California; all are subject to both sport and commercial fisheries. While abalone shells are common in Indian middens dating back more than 7,000 years, the recorded history of the abalone fishery in California begins with the Chinese in the early 1850's (Cox, 1960). These immigrants, collecting primarily green and black abalones in shallow water around San Diego, built up an industry to over 4.1 million pounds per year in 1879. When coastal counties made it unlawful to fish for abalone in shallow water, Japanese hard hat divers, later followed by Caucasians, took their place subtidally and extended the fishery throughout the state (Cox, 1960).

While landing records indicate that all commercial species have suffered major declines in standing stock, data are presented in Figure 1 for the pink abalone, H. corrugata, the second most valuable species, because the northern limit of its range is Point Conception (Cox, 1960). Interpretation of these data is not yet confused by the range extension of the sea otter. The pink abalone's range was opened to commercial fishing in 1943. After 1952, the catch declined
Figure 1. Commercial pink abalone, Haliotis corrugata, landings. Data are compiled from various California Department of Fish and Game sources.
as virgin stocks were depleted (Cox, 1960). The average catch of recent years is a small percentage of peak yields.

The abalones, especially those found subtidally, share very similar food (Leighton, 1966) and habitat preferences with the two strongylocentrotids. Under optimal conditions, both groups feed on drift algae carried by currents and surge. While urchins are well known to attack attached plants when drift becomes limiting, red, pink, and white abalones have also been observed foraging on Macrocystis holdfasts (Leighton, 1971; personal observations).

Considering that these herbivores share both food and habitat resources and that abalone standing stocks have been greatly reduced by fishing, it is tempting to speculate that the urchin population growth may have been caused in part by a release from competition. It has been suggested that abalones out-compete urchins for space (Lowry and Pearse, 1973) but that where food is limiting, urchins may be able to displace abalones by differences in feeding habits (Shepherd, 1973). We have been conducting studies of exploitive competition between red urchins, *S. franciscanus*, and red abalones, *H. rufescens*, in the laboratory (Tegner, unpublished data). Under conditions of limited food supply, the urchins have proven to be superior exploiters capable of scavenging all the food they need for growth, despite the presence of abalones. Red urchins and red abalones exhibit virtually identical resistances to starvation. Behavioral observations support the contention that urchins are better foragers. When presented with the scent of Macrocystis, starved abalones assume feeding posture and wait for the food to drift to them; starved urchins move toward the source of the scent (Tegner, unpublished data).

Field observations of habitat partitioning suggest that abalones may be superior in interference competition in the presence of adequate food supply (Lowry and Pearse, 1973; personal observations). Manipulations of the densities of these two herbivores are planned to study competition for space. The effects of this hypothesized interaction may be most obvious where predators (urchins and abalones share many of the same predators) restrict the herbivores' foraging patterns.

More clearly than competition, predation is important for regulating the abundances of the two strongylocentrotids. Sea urchin predators in southern California today include three asteroids (*Pycnopodia helianthoides*, *Astrometis sertulifera*, and *Dermasterias imbricata*), cancer crabs (*Cancer antennarius*, *C. productus*), the spiny lobster (*Panulirus interruptus*), the horn shark (*Heterodontus*...
franciscii, and three labrids of which the California sheephead (Pimelometopon pulchrvm) is most important (Leighton, Jones, and North, 1966; Winget, 1968; Rosenthal and Chess, 1972; Tegner and Dayton, in preparation). Two of these predators are subject to fishing pressure. Spiny lobsters are taken by both commercial fishermen and sport divers; sheephead are a sport fish taken by anglers and spear fishermen. Commercial lobster landings data are presented in Figure 2. Data are not available for the sport catch of either species.

To analyze urchin predation patterns, 200 m² transects were established at three depths (10, 15, and 20 m) in the Point Loma kelp bed. Urchin populations were censussed and the tests of dead sea urchins collected as often as possible. While we were not able to visit these areas with sufficient regularity to establish rates of predation, some interesting patterns emerged (Tegner and Dayton, in preparation). Morphological differences between purple and red urchins suggest different susceptibilities to predation. *S. purpuratus* is smaller, with a maximum test diameter in this area of about 70 mm, and has short spines relative to its test size. *S. franciscanus* reaches about 140 mm locally, has long spines relative to its test size, and has a considerably thicker test than *S. purpuratus*. While all of the predators cited take purple urchins, only the spiny lobster and sheephead prey on adult *S. franciscanus*.

Male sheephead feed on large red urchins by turning the animal over and using dog-like teeth to puncture the oral surface. The oral surface of the urchin is bitten in a regular, characteristic pattern (which allows identification of the predator when such tests are found) to give the fish access to the soft tissues inside. The advantage of long spines is seen in how these predators handle *S. purpuratus*: the purple urchins are attacked from any angle and often the entire test is consumed (Tegner and Dayton, in preparation). Sea urchins are the major dietary constituent of sheephead larger than 30 cm (McCleneghan, 1968, unpublished M.Sc. thesis)

Winget (1968) reported that the spiny lobster, *P. interruptus*, feeds on sea urchins but assumed that only *S. purpuratus* was taken. Molluscs were most heavily consumed, followed by sea urchins and crabs. Because of the problems of observing a skittish, nocturnal predator in the field, we conducted feeding tests in the laboratory. The lobster was capable of handling full-size red urchins, generally by inverting its prey and using its third maxillipeds and anterior walking legs to pierce the test (Figure 3). Irregular holes, occasionally in the aboral surface, were made in most tests; however, some urchins were consumed by
Figure 2. Commercial spiny lobster, *Panulirus interruptus*, landings. Data are compiled from various California Department of Fish and Game sources.
The spiny lobster, *Panulirus interruptus*, using its anterior walking legs and third maxillipeds to break into the surface of the red sea urchin, *Strongylocentrotus franciscanus*.

Figure 3a. The spiny lobster, *Panulirus interruptus*, using its anterior walking legs and third maxillipeds to break into the surface of the red sea urchin, *Strongylocentrotus franciscanus*. 
Figure 3b. Recovered tests of *S. franciscanus* following consumption of soft parts.
simply removing the peristomial membrane. Again, *S. purpuratus* were attacked from any angle and the entire test consumed (Tegner and Dayton, in preparation).

Sheephead (and lobsters to some degree) are far more common at offshore locations such as San Clemente Island and Tanner Bank. Several effects can be noted in the urchin populations of these areas. Compared to the coastline, the short-spined purple urchins are more cryptically located and the purple to red urchin ratio is much lower. Size-frequency distributions of red urchin populations suggest that the predators are having a major impact on the 30 to 60 mm size class where recruits are no longer sheltered by the spine canopies of adult urchins (Tegner and Dayton, 1977; in preparation). While the effects of increased predation can be observed in these urchin populations, some episodes of overgrazing have been reported for San Clemente Island (McPeak, pers. comm.). It should be noted that extensive abalone and lobster fisheries are conducted there so large lobsters are not common.

Thus, competition with abalones and predation by spiny lobsters and sheephead are proposed as biological interactions which may have regulated sea urchin abundances in the past. In 1971, a commercial fishery began harvesting sea urchins around the Northern Channel Island; this fishery spread to San Diego in the second half of 1976. Only the red urchin is large enough to be commercially feasible for the export market at this time. The fishery has grown rapidly; about 12 million pounds were landed in 1977 (Figure 4). The value of this resource suggests that major episodes of red urchin overgrazing in the future are unlikely.

**RESILIENCY OF THE POINT LOMA KELP BED**

Given these biological interactions which may have controlled urchin population after the demise of the sea otter, I would like to go back to the question of the resiliency of southern California kelp bed communities by considering our study areas off San Diego. After the *Macrocytis* canopy of the Point Loma kelp bed reached a recorded low in 1960, a program of urchin control by quicklime was organized and started late in 1962. In 1963, the City of San Diego moved its sewer outfall to deeper waters. By 1964, considerable restoration of the canopy had occurred (Leighton, Jones, and North, 1966). Today, after extensive urchin control efforts by the Kelp Habitat Improvement Program and Kelco, the Point Loma bed once again covers a large area. From a low of 0.03 sq. mi. in 1960, the canopy has grown to 3.2 sq. mi. in 1978 (McPeak, pers. comm.).
Figure 4. Commercial red sea urchin, *Strongylocentrotus franciscanus*, landings. Data are compiled from various California Department of Fish and Game sources.
In recent years, certain areas of the Point Loma bed have remained unstable, suffering major losses of canopy and requiring continual urchin control (McPeak, pers. comm.). Other areas of the bed have exhibited fairly stable canopies; these have varied in percent cover with time but have not gone through drastic declines. My colleague, Paul Dayton, has been studying Macrocystis mortality in the Point Loma kelp bed since 1970 at sites which Kelco has graciously allowed us to study in an unharvested state. These are the same three sites where I have been following sea urchin predation. All three sites have significant urchin populations within or adjacent to Dayton's plant transects. The deeper two sites are characterized by extensive vertical relief, reefs and boulders, while the third is mostly flat pavement rock with a few low ledges and boulders. The amount of vertical relief appears to be important to urchin populations for two reasons. First, vertical relief makes it easier for urchins to snare and hold down drift kelp, especially in surge conditions. Where urchins can be sustained by drift kelp, they are less likely to attack attached plants. Secondly, both lobsters and sheephead are dependent upon vertical relief, forming caves or ledges. The nocturnally foraging lobsters require shelter from sheephead, among other predators, during daylight hours, and the sheephead need a place to sleep at night. Sheephead are common and lobsters are present at both of the study areas with extensive vertical relief. I have never observed either predator at the third site. Dayton's Macrocystis data indicate that 100% of the observed mortalities at both sites with extensive vertical relief was caused by entanglement with other drifting plants. At the flat site, 50-70% of the kelp mortality was due to urchin grazing and the remainder was caused by entanglement. Macrocystis densities at all three sites have shown considerable variation over the years of the study but only the flat site went through a virtually complete loss of plants (Dayton, in preparation). It is interesting to note that although no urchin control measures were used, a massive Macrocystis germination restored the canopy in a little over a year.

This episode provides further evidence in support of a relationship between Macrocystis and urchin settlement which affects urchin population size proposed by Pearse, Clark, Leighton, Mitchell, and North (1970). They observed that barren mode populations of S. franciscanus apparently consisted of continuously recruiting small animals but that after an area became reforested with Macrocystis, the size frequency distribution of the population shifted to the right as the animals present grew and recruitment declined. They proposed that filter feeding organisms associated with the canopy were effectively minimizing larval settlement. The
largest pulse of red urchin recruitment observed at our flat site in three years of study was after the Macrocytis canopy was eliminated by grazing. After the canopy returned, recruitment rates went back down. At another location, settling experiments detected red urchin recruitment at both edges of a dense 100 m canopy, but almost no settlement was observed at a reef inside the bed (Tegner and Dayton, in preparation). Thus, in an indirect manner, Macrocytis apparently affects the population size of a major grazer.

Eight years of relatively stable canopies and Macrocytis mortality caused only by entanglement with drifters indicate that sea urchin populations were being controlled in these two areas of extensive vertical relief. At both sites, red urchin recruitment was observed in all three years of this study at fairly constant rates (Tegner and Dayton, in preparation). Predation was also significant in these areas, suggesting that these urchin populations have been in a steady state. Our sampling program at the third site, which underwent an episode of urchin overgrazing, ruled out the possibility of increases in urchin abundance caused by recruitment but did not test for immigration. While one explanation of this episode would be an increase in urchin populations, an alternate hypothesis would be a decrease in the supply of drift kelp. This grazing episode took place during the time of year when Point Lorna is most susceptible to surge conditions which can make it very difficult for the urchins to trap drift. At any rate, Macrocytis rapidly recolonized the area and the grazing cycle was completed.

Other examples of cycles of sea urchins overgrazing their food source, followed by algal recolonization, are available. Foreman (1977) documents a massive outbreak of S. droebachiensis in the Strait of Georgia where a combination of environmental factors favored urchin recruitment. His results indicated that S. droebachiensis undergoes periodic outbreaks which are responsible for localized perturbations of the kelp community and that about 8 to 12 years are required to complete the cycle. North (1971) records algal recolonization after urchin grazing has destroyed kelp beds when urchin concentrations are reduced by starvation or migration. Pearse, Costa, Yellin, and Agegian (1977) document two incidences of localized mass mortalities of S. franciscanus caused by disease, another mechanism which could complete cycles of urchin grazing. We have observed similar outbreaks of disease at Point Lorna.
DISCUSSION

Whether the conditions of 1960 were evidence of a massive cycle of urchin grazing or represented a new stable configuration of these ecosystems is subject to debate. The kelp beds around the major metropolitan centers of Los Angeles and San Diego may well have deteriorated so far that these areas could not have recovered on their own; since extensive urchin control efforts were expended in both areas, the question cannot be answered. The Point Lorna bed showed significant recovery one year after urchin control measures were started (Leighton, Jones, and North, 1966); but it took seven years of effort until the first growing bed stabilized at Palos Verdes in 1974 (Wilson, Haaker, and Hanan, 1978). However, Palos Verdes is the site of the largest sewer outfall in southern California, and large-scale ecological changes have occurred in this area (Grigg and Kiwala, 1970).

Of more biological interest is the history of kelp beds less heavily impacted by waste disposal. Rosenthal, Clarke, and Dayton (1974) reported on a bed off Del Mar, California, which has undergone major fluctuations in relative kelp harvest. During their six-year study, there was a pronounced oscillation in Macrocystis standing crop, apparently caused by storms. There was little indication that urchin grazing contributed to kelp mortality. Other beds, in coastal areas distant from metropolitan centers or offshore island sites, have recovered from the warm-water years to become major producers of kelp without either otter predation or human activities to control urchins (McPeak, pers. comm.). A notable example is the large bed around San Nicholas Island. The higher priced shellfish, abalones and lobsters, are both harvested intensively; but since San Nicolas is the farthest of the Channel Islands from any mainland port, urchin divers have only recently begun to investigate this area. Local areas of the San Nicolas bed have undergone cycles of urchin overgrazing leading to losses of Macrocystis standing crop; but, as we have observed at Point Loma in recent years, the large beds of this island have persisted (McPeak, pers. comm.).

The persistence of kelp beds in southern California well over a century after the demise of the sea otter from this region clearly indicates that other factors have controlled sea urchin populations and thereby maintained the structure of this community in a stable configuration. Southern California kelp beds have suffered from urchin grazing, environmental perturbations such as the warm-water years, sewage disposal, and heavy human use. Natural recovery from such stresses in many areas illustrates the resilience of the ecosystem. However, continued problems, such as at Palos Verdes, suggest that there are limits to the ability of the
system to resist and recover from severely disturbed conditions. Hopefully, our recognition of these limits is a major step toward protection of the nearshore environment.

I have proposed biological interactions, predation by spiny lobsters and sheephead, and possibly competition with abalones, as the factors which have controlled sea urchin abundance and distribution patterns since the time of the sea otters in southern California. These interactions provide mechanisms for the maintenance of kelp community structure and are fundamental to the system's resilience to external perturbations. The populations of spiny lobsters, abalones, and to a lesser degree, sheephead, have all been reduced by fishing. A knowledge of the functional relationships between these species and sea urchins would have predicted that external perturbations favorable to urchins and/or unfavorable to Macrocystis could lead to the destructive overgrazing episodes of the late fifties. The biology and history of this complex community underscore the need for a multispecies approach to the management of resources.

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