

Population Structure, Recruitment and Mortality of Two Sea Urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a Kelp Forest

M. J. Tegner and P. K. Dayton

Scripps Institution of Oceanography, University of California, San Diego, Mail Code A-001, La Jolla, California 92093, USA

ABSTRACT: The red sea urchin *Strongylocentrotus franciscanus* and the purple sea urchin *S. purpuratus* are important members of southern California kelp bed communities. We investigated their population structures in terms of patterns of recruitment and mortality at 3 sites in the Point Loma kelp forest near San Diego, California, USA. Recruitment was annual and substantial at all sites. Several predators consume adult *S. purpuratus* but only the spiny lobster *Panulirus interruptus* and the California sheephead fish *Semicossyphus pulcher* (a large labrid) prey on large *S. franciscanus*. Urchin test collections, small scale urchin distribution patterns and grazing mortality of the giant kelp *Macrocystis pyrifera* suggest that lobsters and sheephead, both of which are harvested, control urchin populations. In the presence of these predators, the size-frequency distributions of *S. franciscanus* populations are bimodal, apparently because juveniles (up to 40 mm) are protected by the spine canopies of adults, urchins of intermediate size (50–80 mm) are very vulnerable to predators and large adults (> 90 mm) attain a partial refuge in size. The population structure of *S. purpuratus* is unimodal, evidently because this species is less dependent on the spine canopy association and its short spines and smaller adult test dimensions do not allow it a refuge in size from predation.

INTRODUCTION

While the impact of sea urchin grazing on the distribution and abundance of marine plants is widely known (e.g. Leighton, 1971; Lawrence, 1975; Mann, 1977), the population biology of these herbivores is poorly understood (Tegner, 1980). Sea urchins feed on the giant kelp *Macrocystis pyrifera*, the dominant brown alga which contributes most of the structure, biomass and primary productivity to the diverse and economically important southern California kelp forest community (North, 1971). Numerous organisms feed on giant kelp but sea urchins are the most important herbivores in terms of the frequency and severity of destructive overgrazing. Leighton (1971) reported extensive damage or complete destruction of certain kelp beds in southern California by sea urchin grazing. Over the last 20 years, kelp research and management projects have continually expended considerable resources to reduce sea urchin populations as part of kelp restoration activities (Wilson et al., 1977).

The two larger, more abundant and most destructive of the southern California species of sea urchins are the

giant red urchin *Strongylocentrotus franciscanus* and the purple urchin *S. purpuratus* (Leighton, 1971). In the early 1970's an export market was developed for sea urchin roe (Kato, 1972). This fishery has grown rapidly with landings exceeding 16 million pounds in 1980 (D. Parker, California Department of Fish and Game, pers. comm.). At the present time, only red urchins are large enough to make the labor-intensive roe processing economically feasible. However, purple urchins are also harvested for extensive use in developmental biology teaching and research. Thus, these urchins not only play disproportionately important grazing roles in the southern California kelp forest community but also have considerable economic value of their own (Tegner, 1980).

The present paper describes the population structure of both species of sea urchins and considers patterns of recruitment and mortality that probably caused the observed size structures. We previously reported that juvenile red urchins are found almost exclusively under the spine canopy of adult red urchins, an association that strongly influences the settlement and survival of juveniles (Tegner and Dayton, 1977). Here we

present size-frequency data and additional information on recruitment and mortality from 3 locations in the Point Loma kelp forest. Experiments were conducted to test the apparent effects of a large kelp canopy and its associated predators on urchin recruitment. Spiny lobsters *Panulirus interruptus* and the California sheephead *Semicossyphus pulcher* (= *Pimelometopon pulchrum*) are shown to be important predators of these 2 species of urchins. An hypothesis is proposed to explain the observed population structures and mechanisms for the natural controls of red and purple urchin populations.

STUDY AREAS AND METHODS

This study was conducted in the Point Loma kelp forest offshore of San Diego, California (Lat. 32° 42' N; Long. 117° 16' W). A large stand of the giant kelp *Macrocystis pyrifera*, measuring approximately 1 × 11 km, is located on a broad, gently sloping, pavement-like submerged terrace paralleling the shoreline (Turner et al., 1968). Our 3 study areas are located in depths of about 18, 15 and 12 m and are respectively about 2, 1.5 and 1 km from shore. These 3 study sites, which are mapped in Bernstein and Jung (1979), exhibit different relationships to the *Macrocystis* canopy. The 18 m site was established to be at the outer edge of the kelp bed; the actual boundary varied over a few tens of meters seaward of the transect with fluctuations in *Macrocystis* populations. The 15 m site is in the center of the bed, approximately 0.5 km from both seaward and landward edges. However, the study area is located adjacent to a large hole of several hundred m² in the surface canopy associated with the presence of lower standing kelps which exclude *Macrocystis* (Dayton, unpubl.). The 12 m site, established at the landward edge of the bed, was generally surrounded by several hundred meters of canopy on 3 sides. The bottom topography of the 2 deeper sites is heterogeneous with extensive vertical relief, consisting of large rocky outcrops, boulders, siltstone pavement and occasional sand channels. In contrast, the shallow site is largely pavement rock with only a few low ledges or boulders contributing to the minimal relief.

Size-frequency distributions of *Strongylocentrotus franciscanus* and *S. purpuratus* were sampled approximately monthly between November, 1974 and August, 1977 at all 3 study areas, although rough weather frequently prohibited winter diving at the 12 m site. One m² quadrats were haphazardly placed over rock piles where urchins were abundant, the rocks were turned and all urchins removed. Test diameters were measured with vernier calipers. The size-frequency data were analyzed first on the basis of all animals

collected and secondly, on the basis of those less than 90 mm to avoid the bias resulting from the commercial sea urchin fishery, which took urchins larger than 90 mm during the period of this study. Intensive urchin harvesting began at Point Loma in 1976; decreases were observed in the proportions of large animals at the 15 and 12 m sites from 1976 on (Table 1).

An experiment to test the effects of a large *Macrocystis* canopy on *Strongylocentrotus franciscanus* recruitment was conducted at the 15 m site. Adjacent to the urchin study area is a large stand of giant kelp; a 100 m transect joining the northern and southern boundaries of this stand has been used for studies of *Macrocystis* and its associated epiphytes (Bernstein and Jung, 1979; Dayton, unpubl.). Several boulder reefs, about 3 m long, were established outside the northern edge and under the center of the canopy and stocked with adult urchins in July, 1976. Eleven months later, the reefs were disassembled and all the urchins were measured.

Strongylocentrotus purpuratus eggs were obtained, fertilized and reared to the 3-d pluteus stage using standard methods (Hinegardner, 1967). To determine whether filter feeders epiphytic on *Macrocystis* are affecting sea urchin distributions, eggs and plutei were presented to the filter feeders in small dishes and observed under a dissecting microscope.

Suspected predators of larger urchins were observed in the field and laboratory to learn how sea urchin populations at Point Loma are affected by predation. We determined whether suspected predators really ate red and purple sea urchins and, if they did, we described the mode of attack and what, if anything, remained of the urchin tests. Observations of sheephead feeding behavior were made at Cortez Bank, San Clemente and San Nicholas Islands, offshore locations where large fish are common and exhibit little fear of divers. Nocturnal predators such as lobsters were offered mixtures of various size and species combinations of red and purple urchins in aquaria. Tanks were surveyed daily for the number of urchins and any test remains.

To study predation patterns in the field, permanent transects (100 × 2 m) were established at each site in areas where urchins were abundant. Visible urchins were censused at the beginning of the study. All sea urchin tests in each 200 m² area were collected at approximately monthly intervals from November, 1974 to August, 1977. Tests sufficiently intact to handle were measured with vernier calipers and the condition of the tests were compared with the test remains from the feeding trials. The resulting predation patterns were compared with predator densities, habitat structure, urchin distribution patterns and kelp mortality data from each site.

RESULTS

Population Structure

Size-frequency distributions of the 2 sea urchins show striking differences in population structure between the red (Figs 1, 2 and 3) and purple (Figs 4 and 5) species; moreover, there are differences in the red urchin populations between sites. Single collections suggested that red urchin populations are bimodal, with peaks around 25 and 110 mm; this proved to be a highly consistent pattern at 18 and 15 m but not at 12 m. This bimodality is illustrated in Fig. 1 where the data have been presented by year for the 18 m site (the 15 m site is similar). The modes are about the same

that our sampling program was not biasing the results, we collected urchins from a series of randomly chosen m^2 and adjacent 100 m^2 quadrats near San Clemente Island. Red urchin population structure is also bimodal near San Clemente Island and we could take large samples without disrupting study areas. Both quadrat sizes consistently had bimodal population structures. Nocturnal observations further suggest that the ambits of urchins in habitats with adequate food supply are too limited for the observed bimodality to be caused by emigration or immigration; a 100 m^2 quadrat is an adequate sample size for animals with low mobility.

In contrast to the deeper sites, the size-frequency distribution of *Strongylocentrotus franciscanus* from the shallow site at Point Loma (Fig. 2) was quite variable with no consistent bimodality. In 1976, there was a distinct peak in the 50 to 80 mm size range; this is the region of the nodes between the 2 peaks of the populations at the 18 and 15 m sites. When all of the data from each site are summed, the bimodal nature of the 2 deeper populations contrasts with the more even structure of the 12 m site (Fig. 3). The *S. franciscanus* population structures at 18 and 15 m are significantly different from 12 m ($\chi^2 = 109, 71$ respectively, both $\ll .005$).

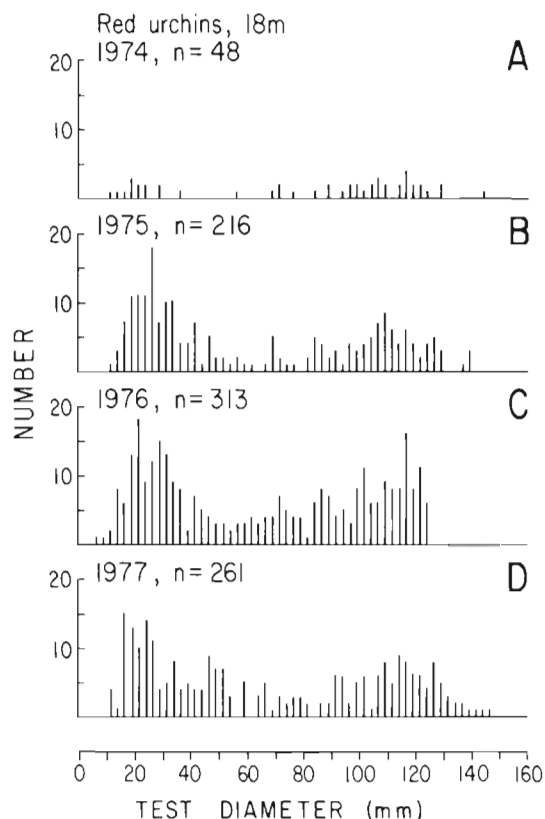


Fig. 1. *Strongylocentrotus franciscanus*. Size-frequency distributions of red urchin test diameters sampled at 18 m during 1974 (A), 1975 (B), 1976 (C) and 1977 (D)

each year; because the growth rates are known (Ebert, 1977; Tegner, unpubl.), we conclude that the modes cannot be explained by unusually strong year classes. Since these collections were small (2–4 m^2 per site per month) and quadrats haphazardly located, one possible explanation of the bimodality is that intermediate sized urchins occupy different habitat and thus were not adequately sampled by our methods. To make sure

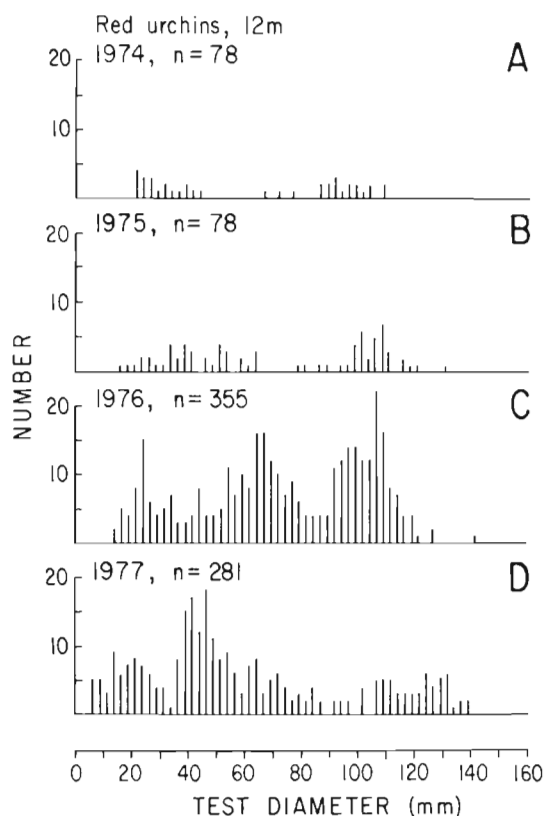


Fig. 2. *Strongylocentrotus franciscanus*. Size-frequency distributions of red urchin test diameters sampled at 12 m during 1974 (A), 1975 (B), 1976 (C) and 1977 (D)

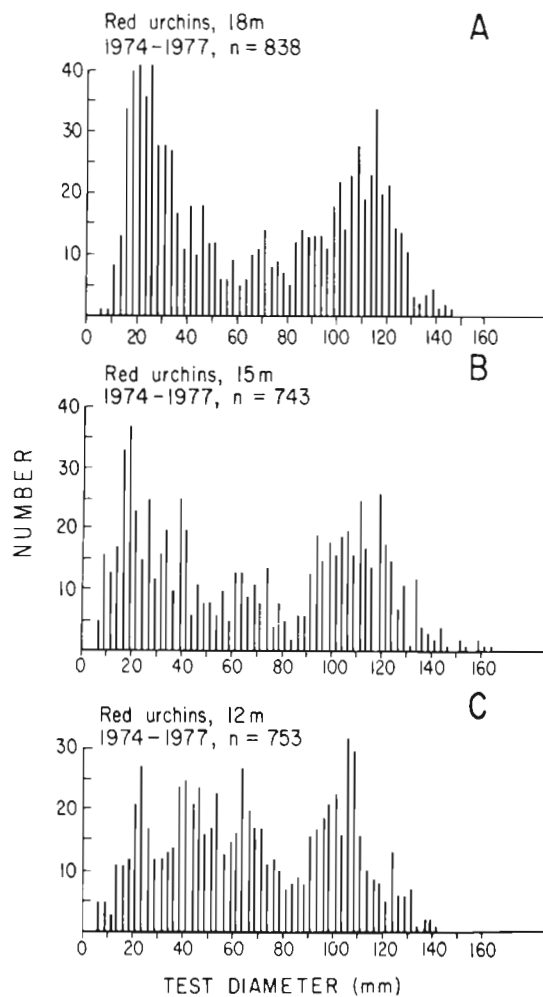


Fig. 3. *Strongylocentrotus franciscanus*. Size-frequency distributions of red urchin test diameters sampled from November 1974 through August 1977 at 18 m (A), 15 m (B) and 12 m (C)

Strongylocentrotus purpuratus population structures were similar at all 3 study areas as well as between years. The annual data for the 15 m site are in Fig. 4, the composite data for all sites in Fig. 5. There was no evidence of a bimodal size-frequency distribution for purple urchins.

Recruitment

Table 1 summarizes the *Strongylocentrotus franciscanus* collections by size categories – first, on the basis of all individuals collected and secondly, on the basis of those less than 90 mm avoid the bias resulting from the commercial sea urchin fishery. Intensive harvesting of urchins larger than 90 mm began at Point Loma in 1976 and decreases were observed in the proportion

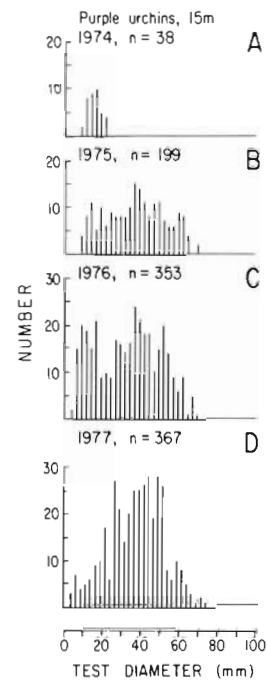


Fig. 4. *Strongylocentrotus purpuratus*. Size-frequency distributions of purple urchin test diameters sampled at 15 m during 1974 (A), 1975 (B), 1976 (C) and 1977 (D)

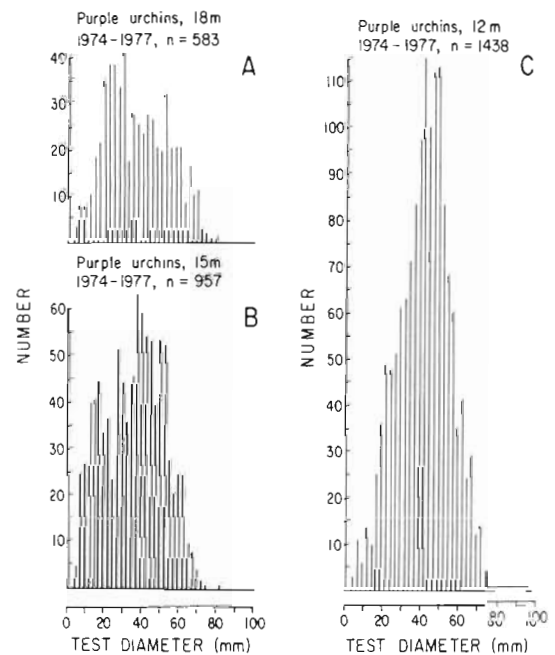


Fig. 5. *Strongylocentrotus purpuratus*. Size-frequency distributions of purple urchin test diameters sampled from November 1974 through August 1977 at 18 m (A), 15 m (B) and 12 m (C)

of large urchins at the 15 and 12 m sites after 1975. For the 3 years studied, recruitment of red sea urchins was regular and substantial in magnitude. As *S. francis-*

Table 1. *Strongylocentrotus franciscanus*. Analysis of size-frequency distributions of red urchin populations from 3 depths for 1975, 1976 and 1977. Data computed on the basis of total number (N) of urchins and on number less than 90mm to remove bias resulting from commercial urchin fishery

Depth (m)	Year	N	Based on total N				Based on N < 90 mm		
			% < 30 mm	% 30–59 mm	% 60–89 mm	% ≥ 90 mm	% < 30 mm	% 30–59 mm	% 60–90 mm
18	1975	216	32	23	11	34	49	35	17
	1976	313	27	20	18	35	42	30	28
	1977	261	28	23	10	39	45	38	16
15	1975	133	32	12	9	47	61	23	17
	1976	375	26	23	11	41	43	39	19
	1977	214	24	18	20	38	38	29	32
12	1975	78	13	33	10	44	23	59	18
	1976	355	12	20	28	39	20	33	47
	1977	281	21	40	16	22	28	51	21

canus juveniles attain a size of 30 to 40 mm during their first year (Ebert, 1977; Tegner, unpubl.), the 30 mm size category represents the young of the year. Of the total number of urchins less than 90 mm, the young of the year (i.e. animals less than 30 mm test diameter) averaged 45 % (range 42 to 49 %) at 18 m, 47 % (range 38 to 61 %) at 15 m and 24 % (range 20–28 %) at 12 m. Thus recruitment rates at the shallow site were considerably lower in every year sampled, averaging about half of that observed at the two deeper areas.

The consistency of this pattern from one year to the next supports an hypothesis (Pearse et al., 1970) that tall algae such as *Macrocystis* can effectively prevent recruitment into urchin populations. Pearse and co-workers observed that *Strongylocentrotus franciscanus* populations in areas devoid of macroalgae consisted of continually 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 urchins present grew and recruitment declined. The 18 m and 15 m sites are both close to areas of open water whereas the 12 m site was generally surrounded by several hundred meters of canopy on 3 sides. The largest pulse of *S. franciscanus* recruitment observed at the 12 m site was in September of 1976 after the *Macrocystis* canopy was virtually eliminated by urchin grazing the previous spring. This was followed by a dense *Macrocystis* settlement and a decline in the number of urchin recruits.

We used the large stand of *Macrocystis* near the urchin study area at 15 m to test the effects of a large canopy on red urchin recruitment. Reefs were established under the center and at the northern edge of a 100 m wide canopy, all juvenile urchins removed and the reefs stocked with adult urchins. Eleven months later, 2 young of the year *Strongylocentrotus francis-*

canus were found on the reef underneath the canopy. Of the reefs outside the canopy, 2 controls with no urchins present at the start of the experiment had 2 and 20 recruits. The reef originally stocked with adult purple urchins had 36 red urchin recruits. Unfortunately, the reef which started out with adult red urchins was apparently fished but because we know that red urchins recruit to red urchin spine canopies at about 8 times the rate that they recruit to purple urchin canopies (Tegner and Dayton, 1977), we can safely conclude that red urchin recruitment was considerably higher outside the *Macrocystis* canopy. Large numbers of small urchins were also observed on the reef system at the southern edge of the canopy. Storms during the fall of 1978 and winter of 1979 opened the canopy and red urchins recruited to the reef near the center of the transect.

Pearse et al. (1970) proposed that canopy-associated filter feeders, by eating urchin eggs and larvae, were responsible for the decline in urchin recruitment. The common members of the epiphyte community on *Macrocystis* include the 3 bryozoans *Membranipora membranacea*, *Hippothoa hyalina* and *Lichenopora buskiana*; the serpulid polychaete *Spirorbis spirillum*; and the hydroids *Obelia* sp. and *Campanularia* sp. (Bernstein and Jung, 1979). All 3 of the bryozoans exhibited active feeding behavior. They would grab the particles with their tentacles and attempt to insert them into their mouths. Eventually the particles always were released, apparently too large for the ectoprocts to handle. The considerably larger *Spirorbis* successfully ingested both eggs and 3 d old larvae, so at least one of these epiphytes has the potential for affecting urchin distributions. However, since mature plutei are considerably larger (about 700 μ m versus 240 μ m for the 3 d old plutei; A. Cameron, pers. comm.), even *Spirorbis* may not be able to affect urchin settlement.

Predation

Occasionally, we are able to locate *Pycnopodia helianthoides* by following a trail of clean, intact *Strongylocentrotus purpuratus* tests. *Pycnopodia* generally swallows its prey, but digestion can take place internally or externally (Mauzey et al., 1968). Observations of *Pycnopodia* and other asteroids in the process of feeding on sea urchins and of tests adjacent to these predators indicate that the test generally remains intact or sometimes will be split cleanly on the vertical axis. *Pycnopodia* densities are very low at Point Loma. However, the size of this asteroid here generally exceeds 0.5 m total diameter and once in an area, individuals tend to remain for several days suggesting that they are capable of influencing the distribution and abundance of sea urchins. Other local asteroids known to eat urchins include *Astrometis sertulifera* (Leighton, 1971), *Dermasterias imbricata* (Rosenthal and Chess, 1972) and *Patiria miniata* (Dayton, unpubl. observations). Leighton (1971) reported that *Pycnopodia* and *Astrometis* consumed the contents of about 1.5 juvenile sea urchins (any local species) per day in laboratory experiments.

Winget's (1968) study of spiny lobster gut contents at Point Loma indicated that sea urchins (species not specified) were a major dietary component with the frequency of occurrence varying seasonally from 44 to 91 %. Urchins were utilized in approximately the same proportions by all size classes of lobsters. Since this predator is difficult to observe closely in the field as it is highly mobile and nocturnal, feeding observations were conducted in aquaria. Spiny lobsters were capable of feeding on both *Strongylocentrotus purpuratus* and *S. franciscanus*. While only the larger lobsters could handle large *S. franciscanus*, the largest urchins were successfully eaten. The mode of attack and the resulting test were functions of predator and prey size. For example, a large lobster (112 mm carapace length) consumed an entire 49 mm *S. purpuratus*; only a few spines and urchin fecal pellets remained. The lobster picked up the urchin and held it dorso-ventrally using its anterior walking legs and third maxillipeds. The ambital region was inserted into the lobster's mandibles. A few spines were bitten off and then a hole was made in the test. Rotating the urchin like an apple, the lobster consumed the entire animal.

The longer spines of *Strongylocentrotus franciscanus* led to a different mode of attack. The same large lobster used his anterior walking legs and third maxillipeds to turn a 90 mm urchin over, to puncture and remove the peristomial membrane and Aristotle's Lantern, and to enlarge slightly the peristomial opening by removing some of the test. These same appendages were then employed as a sort of conveyor belt, passing

the soft parts of the urchin to the lobster's mouth. The remaining test had an asymmetrical hole in the oral surface and most of the spines were intact. In other trials, individuals of *S. franciscanus* were eaten in their entirety or some fraction thereof, spines were sometimes clipped off and/or eaten, and some tests were punctured through the aboral surface. In other instances, tests were recovered intact after lobster predation with only the peristomial membrane gone (Fig. 6).

Horn sharks *Heterodontus francisci* eat bivalves, asteroids and echinoids (Taylor, 1972). To examine feeding patterns of this nocturnally foraging shark, 4 urchins of each species were added during the day to a large tank containing several sharks. The purple urchins were all eaten in 24 h; the red urchins were not eaten during the 2 weeks of the experiment (D. A. Bodznick, pers. comm.). We conclude that horn sharks, relatively rare at Point Loma, are not an important source of mortality for *Strongylocentrotus franciscanus*.

Because sheephead are hunted by spear fishermen, the few remaining large animals tend to be wary of divers, and thus are difficult to observe along the mainland where spear fishing pressure is intense. For example: large males, when seen at Point Loma tend to hover just inside the limits of visibility, whereas at San Clemente Island and Cortez Bank, similar size fish closely follow divers working with urchins and attempt to take prey from the diver's samples. As was observed with lobsters, the mode and result of sheephead predation vary with the size and species of sea urchin as well as the size of the fish. At offshore locations where sheephead are common, virtually all *Strongylocentrotus purpuratus* as well as small and mid-sized *S. franciscanus* are found under adults, under rocks or in crevices.

When a rock was turned exposing a number of urchins, the small juveniles and purple urchins were always removed first leaving the larger individuals of *Strongylocentrotus franciscanus*. Small urchins of both species were plucked off the substrate and eaten whole. The fish placed their protruding lips around the lateral margin of large purple urchins. Male sheephead easily grasped and removed the short-spined purple urchins in this manner; the smaller females had to do more butting to dislodge the urchins. In these trials with large sheephead, the purple urchins were generally swallowed in 1 to 3 gulps, as the echinoids were crushed in the fishes' throats. Smaller fish turned the urchins over and made a characteristic circular incision in the oral surface of purple tests similar to that observed with *S. franciscanus* (Fig. 6). Two modes of attack on larger red urchins were observed, and both suggested that the sheephead were deterred by these urchins' longer spines. Generally, the fish attempted to dislodge the urchin from the substrate by butting the

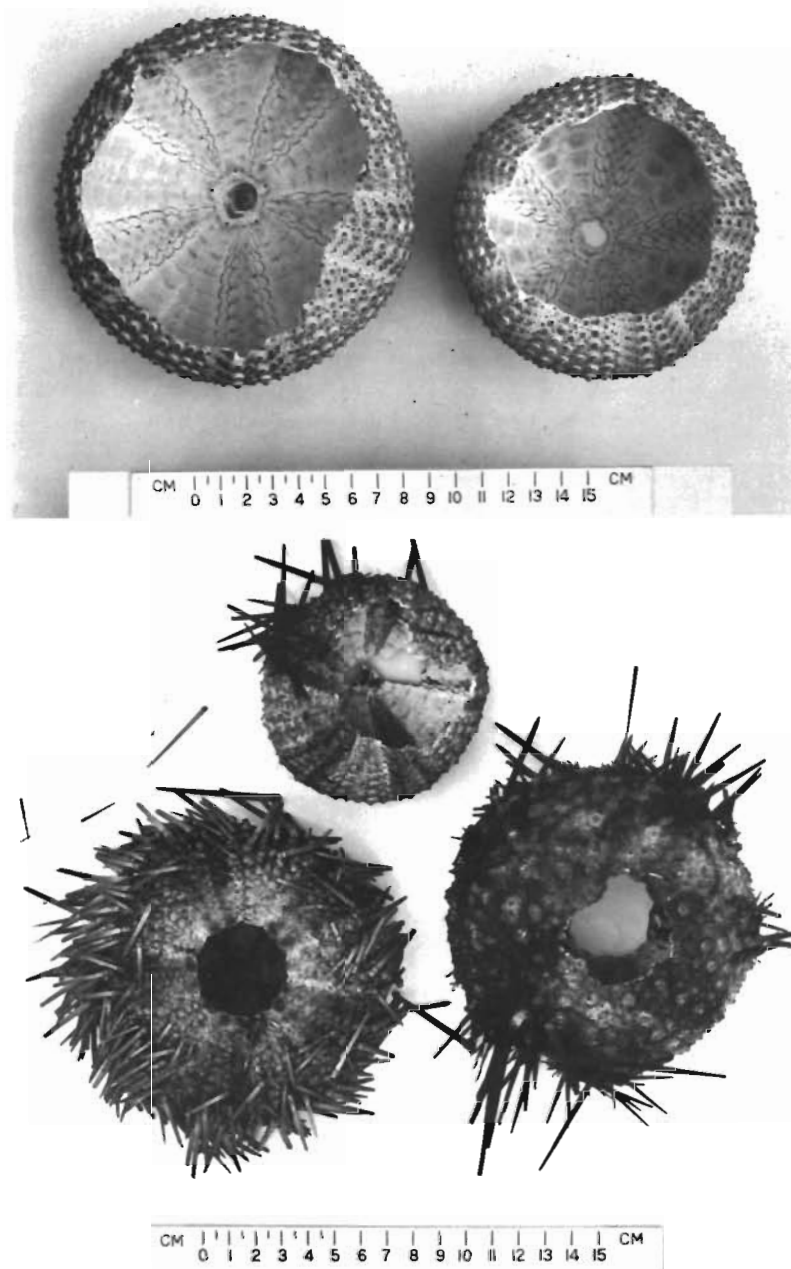


Fig. 6. *Strongylocentrotus franciscanus*. Top: Characteristic damage to tests of red urchins by sheephead wrasses *Semicossyphus pulcher* which generally break a large, symmetrical hole in the oral surface. Bottom: Spiny lobsters *Panulirus interruptus* may break holes in the oral or aboral surfaces of the test or may simply remove the peristomial membrane

urchin around the lower lateral margin with its head. On several occasions apart from these trials we have noticed sheephead with sea urchin spines imbedded in their foreheads. Once dislodged, the urchin was turned over and attacked in the region of the peristomial membrane. The Aristotle's Lantern was removed and the mouth opening enlarged to allow access to the gonads. The approximately symmetrical circular incision (Fig. 6) removing most of the oral surface of the

test is very characteristic of sheephead predation. The second mode of attack was only observed once. A large male sheephead grabbed an approximately 60 mm *S. franciscanus* by the dorsal spines and bashed it against a rock until the test was shattered.

As discussed previously, juvenile red and purple urchins seek shelter under the spine canopies of adult red urchins (Tegner and Dayton, 1977). When the observer removes the adults, an action mimicking the

commercial fishery, the underlying juveniles are exposed. On one occasion when we were attempting to collect juvenile urchins at Cortez Bank, sheephead were able to get the small urchins before the divers. In a series of adult removal trials at San Clemente Island, some juveniles were rapidly eaten and others crawled out of sight to safety. It is of interest to note that large, male sheephead often came in to inspect the scar of a removed urchin, but did not feed on the juveniles. Once the male left the immediate area, smaller female sheephead rushed in and ate the urchins. The fate of juvenile sea urchins, abalones and other inhabitants of the spine canopy association after fishing of the adult urchin, depends in part upon how much cover, e.g. substrate rugosity or foliose algae, is available.

These observations of predator feeding behavior illustrate some of the limitations of attempting to understand the role of predation in sea urchin population dynamics by collecting tests. The condition of the test is sometimes an ambiguous indication of the mode of death. An intact test, for example, is likely due to starfish predation, but also could have resulted from lobster predation, disease, or starvation although the latter two possibilities can generally be ruled out by an observer. Pearse et al. (1977) attributed 2 localized mass mortalities of *Strongylocentrotus franciscanus* in central California to disease. Many urchins, especially smaller individuals, are eaten in their entirety or the remaining fragments are too small to evaluate. Furthermore, smaller tests, if still intact after predation, are more likely to be broken apart by physical forces. These factors indicate that test collection data are strongly biased toward observing the mortality of larger individuals. No attempt was made to determine how long tests survive after the death of the urchin, since this would be expected to vary considerably with the size and species of urchin, the predator and its size, and weather conditions; but for most urchins, the period would be in the order of several weeks. The size of patches of encrusting coralline algae, bryozoans, polychaete and vermetid gastropod tubes growing on one 116 mm *S. franciscanus* test from San Clemente

Island suggested that the urchin, which was probably killed by a lobster, had been dead for at least 3-6 months (R. Osman, pers. comm.). Finally, there are periods of inclement weather when regular sampling is not possible. This is especially a problem at our shallowest site at Point Loma where large swells can scour the bottom clean of small objects such as urchin tests. All of the above problems place strong limits on our inferences of rates of predation, but the patterns which emerge are useful to consider.

The data from the test collections are summarized in Table 2. A total of 126 transects were conducted over the 34-month period yielding 879 tests sufficiently intact to estimate diameter. Of the recovered tests 25 % were *Strongylocentrotus franciscanus*, the remainder were *S. purpuratus*. The densities of each species at the beginning of the sampling period are also given in Table 2. Purple and red urchins were found in similar densities at the 18 and 12 m sites but reds outnumbered the smaller species at the 15 m area. Thus, these data indicate that *S. purpuratus* are being consumed well out of proportion to their relative abundances.

The condition and size-frequency distributions of the tests by area are represented in Figs 7 and 8. While these data do not represent the total urchin mortality because of the differential survivorship of smaller tests, several conclusions can be drawn. Of the 217 *Strongylocentrotus franciscanus* tests collected, 96 % were broken, indicating predation by sheephead or lobsters. We are not classifying (Fig. 7) the broken tests as to likely predator (Fig. 6) because some of the data were collected before we learned to differentiate the test damage caused by sheephead from that caused by lobsters. In contrast, 56 % of the *S. purpuratus* tests were broken and 44 % were cleaned of spines and intact, suggesting predation by starfish. The fact that only 4 % of the collected *S. franciscanus* were intact compared to almost half the *S. purpuratus* tests suggests that starfish are deterred by the longer spines of the red urchin in areas where *S. purpuratus* are abundant. Furthermore, the modal size of purple urchins consumed by starfish is 40 mm vs 50 mm for broken

Table 2. *Strongylocentrotus franciscanus* and *S. purpuratus*. Sea urchin test collections from predation transects at 3 depths

Depth (m)	Number of transects	<i>S. franciscanus</i>			<i>S. purpuratus</i>		
		Density* (m ⁻²)	Number broken	Number unbroken	Density (m ⁻²)	Number broken	Number unbroken
18	59	2.4	93	5	3.7	219	119
15	41	12.3	100	3	3.8	80	58
12	26	0.3	16	0	0.3	70	116
Totals	126		209	8		369	293

* Densities determined by visual censuses which underestimate cryptic individuals in transect areas

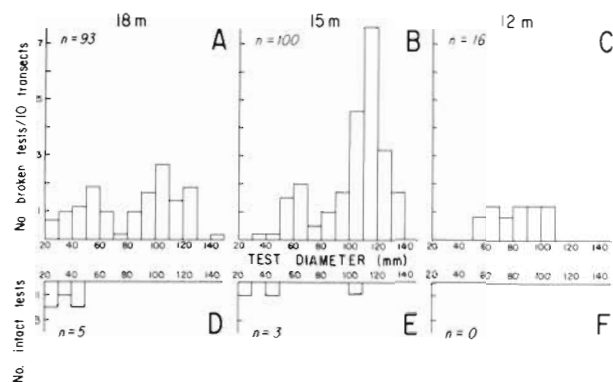


Fig. 7. *Strongylocentrotus franciscanus*. Size-frequency distributions of broken and intact red urchin tests collected between November 1975 and August 1977 at 18 m (A), 15 m (B) and 12 m (C)

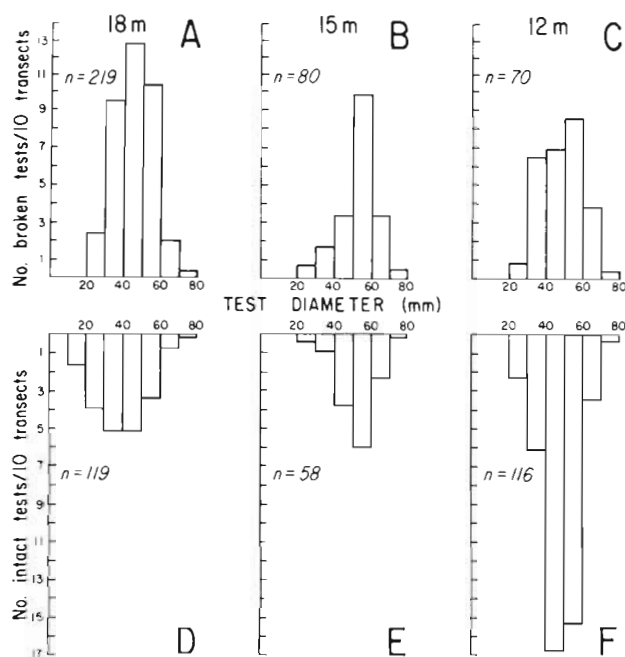


Fig. 8. *Strongylocentrotus purpuratus*. Size-frequency distributions of broken and intact purple urchin tests collected between November 1974 and August 1977 at 18 m (A), 15 m (B) and 12 m (C)

tests which may indicate that some size selection is going on by the different predators.

The patterns of broken *Strongylocentrotus franciscanus* tests reflect the habitat heterogeneity and red urchin population structure at each site. The 2 deeper sites have extensive vertical relief and both lobsters and sheephead are commonly observed there. The 12 m site is largely flat pavement with a few low lying ledges or rock piles which apparently do not provide adequate daytime shelter for lobsters or night sleeping caves for sheephead. On 2 occasions, small lobsters

were observed here out in the open, suggesting that occasional foraging by lobsters (and possible sheephead) coming from shelter outside the study area is at least partially responsible for the broken tests which were observed. Most of the mortality at the shallow site can be accounted for by starfish predation. The red urchin populations at 18 and 15 m are both bimodal in size structure and the node between the two peaks is from about 50 to 80 mm test diameter. There are peaks on the graph of broken *S. franciscanus* tests from 40 or 50 to 70 mm from both the two deeper sites (Fig. 7) suggesting that predation may be responsible for the observed bimodality. The red urchin population structure at 12 m does not exhibit the bimodal pattern, predators are rare, and recovered test sizes reflect the more uniform population structure.

If predation is important to these urchin populations, one would expect to see differences in small scale distribution patterns between areas where the predators are abundant and where they are rare. To compare small scale distribution differences (Table 3), a m^2 quadrat was placed over rock piles containing urchins. An observer counted the 'exposed' urchins, individuals which could be seen without disturbing the habitat, which presumably reflect what a visual predator 'sees'. The habitat was then systematically disrupted to collect all urchins. No attempt was made to determine lobster densities since there is considerable variation in numbers due to apparent seasonal onshore-offshore migration and the commercial fishery. Lobsters are commonly observed and traps have been set at the 18 and 15 m sites annually. Department of Fish and Game statistics indicate that the La Jolla-Point Loma coastline is a very productive area for *Panulirus interruptus* (Odemar et al., 1975). Sheephead, the other important

Table 3. *Strongylocentrotus franciscanus* and *S. purpuratus*. Small scale sea urchin distribution patterns related to urchin predators

Depth (m)	18	15	12
Number of m^2 sampled	9	7	10
<i>S. franciscanus</i> density (m^{-2})	27	18	21
% <i>S. franciscanus</i> <60 mm	42	41	27
% <i>S. franciscanus</i> cryptic	52	26	5
<i>S. purpuratus</i> density (m^{-2})	46***	29	60
% <i>S. purpuratus</i> cryptic	84***	64	63
Lobster presence	yes	yes	no
Sheephead ranges (1975)*	14-43	8-11	0
Sheephead at m^2 (1980)**	8	8	0

* Ranges in numbers of sheephead encountered by divers swimming the predation transects of 1975

** Maximum number of sheephead attracted to area of the m^2 collections in 1980

*** Determined for 8 m^2 only

visual predator, were enumerated in two different ways. First, to get a rough idea of sheephead density, an observer repeatedly swam the length of the 100 m predation transects at each site counting all visible sheephead. Because sheephead are attracted to divers and these censuses were quite variable between different days, the data are reported as ranges rather than densities. Secondly, the maximum number of sheephead attracted to the m² collections is reported as a reflection of the local environment.

The results (Table 3) show a clear decreasing trend for *Strongylocentrotus franciscanus* to be cryptic in their small scale distribution pattern as the number of sheephead decreases and with the loss of lobster presence in the habitat. At the sheephead and lobster-free shallow site, even the more vulnerable red urchins less than 60 mm in size are largely exposed. This exposure figure is not caused by a lack of hiding places at the more physically uniform 12 m site; most of the short-spined purple urchins remain cryptic. The ratio of purple to red urchins is considerably higher at the shallow site but Schroeter's (1978) demonstration of fencing behavior whereby red urchins can win contests for food or space by using their longer spines would indicate that the purples are not excluding the reds for limited shelter space. These variations of small scale urchin distribution patterns with changing lobster and sheephead populations suggest that these predators are important to the control of urchin populations, especially *S. franciscanus*, at Point Loma.

DISCUSSION

The data we have presented suggest a far more dynamic nature to the population biology of red and purple sea urchins than previously observed. Settlement of young urchins has generally been reported to be patchy and not to occur every year (examples: *Lytechinus variegatus*, Moore et al., 1963; *Centrostephanus coronatus*, Lissner, 1978). Studies of several red urchin populations in British Columbia showed a scarcity of 1 and 2 year old individuals, presumably the result of low and sporadic settlement (Bernard and Miller, 1973; Breen et al., 1976, 1978). Ebert (1968), following *Strongylocentrotus purpuratus* populations in Oregon, found only 1 good year for urchin settlement between 1960 and 1967. Dayton (1975) concluded that from 1959 through 1970 *S. purpuratus* recruited only in 1959, 1963 and 1970 along the Oregon and Washington coasts. Leighton et al. (1966) concluded that settlement of both red and purple urchins was not a frequent occurrence in southern California and suggested that conspicuous recruitment may occur at intervals of 1 to 4 years. In contrast, we have observed

substantial annual settlement at each of our 3 study areas for the 3 years of the study. The first year size class (0–30 mm) averaged 29 % (range 27 to 32 %) of the total *S. franciscanus* population at the 18 m site and 27 % (range 24 to 32 %) at the 15 m site. The shallow site exhibited a consistently lower rate of recruitment, averaging 15 % and ranging from 12 to 21 %. If we assume that purple urchins grow about 25 mm in their first year on the bottom (Ebert, 1977), it is apparent by inspection of Fig. 4 that *S. purpuratus* recruited annually in substantial numbers at 15 m. Settlement was observed annually at the other two sites as well, but similar to *S. franciscanus*, the magnitude of *S. purpuratus* recruitment was lower at 12 m.

The location of the 12 m site, with 2 to 3 km of *Macrocystis* canopy to the north and south and at least several hundred m to the west, is probably responsible for the consistently reduced recruitment. Water movements in the Point Loma kelp bed are driven by both longshore and inshore-offshore currents. Irrespective of the dominant current pattern, water along the central portion of the inner edge of the kelp bed is more likely to have been filtered through the mass of the bed than water along the outer edge (Jackson, 1976). Settlement and predation are 2 mechanisms which could reduce larval concentrations at the inshore site. Since red and purple urchin larvae spend a minimum of 2 months in the plankton (Strathman, 1978), the larvae are likely to originate from a source outside the Point Loma kelp bed. If mature urchin larvae receive cues from the kelp bed which induce settlement and metamorphosis, one would expect to find the highest concentrations of newly settled urchins near the exterior edges of a large bed with progressive decreases in abundance going into the bed. Bernstein (1979) proposed that the kelp bed acts as a filter of larvae of *Membranipora membranacea* and he was able to demonstrate order of magnitude declines in larval abundances from the outer edge to the center and again to the inner edge of the bed.

Pearse et al. (1970) proposed that filter feeders encrusting the kelp fronds provided a mechanism for predation to reduce larval abundances in the inner part of the bed but our data argue against this hypothesis. Predators more likely to affect the distribution of urchin larvae are the diurnal, planktivorous fishes. Juveniles of 3 species, the blacksmith *Chromis punctipinnis*, the kelp perch *Brachyistius frenatus*, and the senorita *Oxyjulis californica*, feed on a size range of small plankters which includes mature urchin larvae (Hobson and Chess, 1976). These fish are found in association with *Macrocystis*; blacksmith in particular are concentrated near the upcurrent or seaward edge of kelp forests (Hobson and Chess, 1976; Bray, 1978).

These 2 proposed mechanisms for the reduction of

urchin recruitment at the inshore edge of the kelp bed are not mutually exclusive; it is likely that both settlement and predation are affecting larval supply significantly. However, the localized disruptions of canopy observed at the 15 and 12 m sites which were followed by pulses of recruitment argue more strongly for the predation hypothesis.

Doubtlessly, a wide variety of microcarnivores prey on newly settled urchins, and predation at this stage is probably an important determinant of urchin population size. While recognizing this, our efforts have been devoted to understanding the impact of predation on the larger size classes. Despite the fact that we were not able to determine rates, the predation patterns emerging from these data have general implications for the structure of southern California kelp-bed communities.

The literature lists several predators of larger sea urchins in southern California. These include the 3 asteroids *Astrometis sertulifera*, *Dermasterias imbricata* and *Pycnopodia helianthoides*; the spiny lobster *Panulirus interruptus*; the horn shark *Heterodontus francisci*; and the 3 labrids, California sheephead *Semicossyphus pulcher*, rock wrasse *Halichoeres semicinctus* and senorita *Oxyjulis californica* (McCleneghan, 1968; Winget, 1968; Leighton, 1971; Rosenthal and Chess, 1972; Taylor, 1972). Most previous studies focused on the predators; only Leighton and coworkers were concerned with the natural regulation of sea urchin populations. They felt that the sea otter *Enhydra lutris*, currently found in the central portion of the state, is the only effective controlling agent of sea urchin populations in California (Leighton et al., 1966).

Of the 3 labrids, the sheephead is the most important predator of larger urchins at Point Loma. The rock wrasse is known to feed on *Strongylocentrotus* sp. (McCleneghan, 1968) but is rare here. Senoritas, while abundant in this region, are members of a microcarnivorous 'pickertype' guild (Bray and Ebeling, 1975). They have been observed picking small urchins out of coralline algae (Tegner and Dayton, 1977) and to have 2–3 mm urchins in gut contents (McCleneghan, 1968; Hobson, pers. comm.) but *Oxyjulis californica* certainly does not eat larger urchins. The California sheephead is the second most commonly encountered fish species in kelp beds in the San Diego region (Quast, 1968). These large fish have canine-type incisors suited for puncturing hard shelled prey. A study of sheephead gut contents conducted in the San Diego region indicated that they feed primarily on echinoderms (mean weight percent = 85 %, frequency of occurrence = 91 %) of which almost all were sea urchins, probably all *Strongylocentrotus* spp. (Winget, 1968).

From our examination of all the known predators of

adult urchins present in the Point Loma kelp bed today, several conclusions can be drawn. First, whereas all of the predators take large purple urchins, only lobsters and sheephead appear to prey on large red urchins. Secondly, purple urchins suffer much higher mortality relative to their abundance at each of our study sites. This higher susceptibility to predation is reflected in the comparative small scale distribution patterns; *Strongylocentrotus purpuratus* populations are more cryptic than *S. franciscanus* at all 3 locations. The differential susceptibility to predation should not be entirely unexpected. Adult red urchins are typically about twice the test diameter of adult purple urchins and are characterized by considerably longer spines in relation to body size than *Strongylocentrotus purpuratus*. Three of the urchin-eating asteroids at Point Loma are fairly small, *Astrometis*, *Dermasterias* and *Patiria*, and would not be likely to attack large *S. franciscanus*. In their extensive study of *Dermasterias* prey at Point Loma, Rosenthal and Chess (1972) found purple urchins to constitute 47 % and red urchins a negligible amount of this sea star's diet. Small juveniles probably accounted for the observed incidences of red urchin predation similar to Leighton's (1971) findings. As was pointed out by Moitza and Phillips (1979), very small red urchins (to about 20 mm) have spine lengths similar to purple urchins of the same test diameter and thus would be expected to have similar susceptibilities to predation. *Pycnopodia*, on the other hand, is a large predator and feeds on large *S. franciscanus* in the Pacific Northwest (Mauzey et al., 1968). Our data indicate a negligible rate of asteroid predation on red urchins versus a substantial one on the shorter spined *S. purpuratus*. Recent laboratory studies support our observations. Moitza and Phillips (1979) demonstrated that, despite the fact that *Pycnopodia* detect and pursue red and purple urchins at equal rates, *S. franciscanus* is able to fend the predator off with its long spines resulting in a starfish diet of almost 98 % *S. purpuratus* when presented with equal numbers of each species. Moitza and Phillips conclude that *Pycnopodia* does not prefer purple urchins, rather *S. purpuratus* has a less effective defense against predation.

In field trials of sheephead feeding patterns conducted at San Clemente Island, large purple urchins were always consumed before large red urchins. This pattern held even for big male sheephead whose large teeth would be expected to reduce the effort required to handle the prey. Considering the difference in potential benefits to the predator (the gonads of large ripe purple urchins range up to about 20 g in weight; red urchins can exceed 200 g; Tegner, unpubl.), the apparent deterrent of the red urchins' spines is impressive. Sheephead are very abundant at San Clemente

where more than 40 individuals were attracted to m² collections at 2 locations. An analysis of small scale distribution patterns at San Clemente similar to the one conducted at Point Loma indicated that 60 % of the red and 84 % of the purple urchins were cryptic (Tegner, unpubl.).

Laboratory observations of lobsters feeding on urchins further support a differential susceptibility to predation. Purple urchins could be attacked from any direction; the longer spines of red urchins required the predator to use some method to get around them to puncture the test. If the lobsters were presented with a mixture of the 2 species in aquaria, purple urchins were generally eaten first (Tegner, unpubl.). The test collection data corroborate the sheephead and lobster feeding observations. Of the broken tests, 63 % were purple urchins despite the bias caused by the greater probability of small tests being completely destroyed. Comparing the densities of visible urchins (Table 2), it is apparent that purples were being consumed well out of proportion to their relative abundance.

Schroeter (1978) examined the relationship between red and purple sea urchins in the inter- and shallow subtidal at Santz Cruz Island. He concluded that the observed distribution patterns were the result of red urchins excluding purple urchins from the more desirable habitat. While competitive interactions may be important at some times or places, our data suggest that the differential susceptibility to predation is a far more important factor regulating purple urchin distributions. Red and purple urchins coexist at high densities (Table 3) in the same boulder piles at our subtidal sites and predation pressure appears to account for the differences in small-scale distribution patterns.

In conclusion, the data indicate that sea urchin recruitment took place annually and at substantial rates at the 3 sites studied in the Point Loma kelp forest. Predation rates could not be determined but the test collections suggest that predation was an important factor. In view of the longstanding problem of destructive overgrazing of kelp forests at Point Loma by red and purple urchins, it is interesting to consider what these results indicate about the control of sea urchin populations. Both red and purple sea urchins normally feed on detached pieces of drifting algae. A kelp-free zone up to about 1 m wide around the base of urchin reefs indicates that they also make limited feeding forays. When food supply becomes limiting, whether due to drops in production or increased urchin demand, urchins will attack attached *Macrocystis* plants feeding on sporophyll, stipe and holdfast tissue until the plant is severed at the apex of the holdfast. Under severely food-limited situations, urchin fronts form which move through the kelp bed until the entire

stand is destroyed and all edible flora gone (Leighton, 1971).

Dayton (unpubl.) monitored *Macrocystis* survivorship at Point Loma from 1970 to 1978 at the same sites where we studied sea urchin mortality. At the 18 and 12 m sites the same transects were used for both studies; at 15 m our transect ran along an urchin reef adjacent to the studied stand of kelp. All of the observed giant kelp mortality at the 18 and 15 m sites was caused by storm related detachment or entanglement with drifting kelp plants. In contrast, a period of intense urchin grazing eliminated virtually all of the *Macrocystis* at the 12 m site during the spring of 1976. Although no urchin control measures were taken, a massive germination restored the giant kelp canopy in a little over a year. Urchin grazing again decimated the canopy in late 1978. *Macrocystis* densities at all 3 sites showed considerable variation over the years of the study, but only the 12 m site suffered virtually complete losses of plants and only the 12 m site sustained damage from urchin grazing.

Thus, despite large standing stocks and substantial recruitment rates at the 18 and 15 m sites, urchin populations were better regulated than at the 12 m site where recruitment and standing stocks were low. Urchin populations at the deeper 2 sites did not exhaust their drift food supply and attack attached plants. From this we infer that predation was controlling the urchin populations at 18 and 15 m, but not at 12 m in steady state condition. The 2 deeper sites are characterized by extensive vertical relief which shelters lobsters and sheephead; the shallow site is largely flat pavement and these predators are absent. Starfish are present at all 3 locations. Thus, we believe that lobsters and sheephead, both of which are taken by sport and commercial fishermen, are predators capable of controlling red and purple sea urchin populations.

The size-frequency distributions suggest how this control works. *Strongylocentrotus franciscanus* populations are strongly bimodal in the presence of lobsters and sheephead. We hypothesize that the first mode is due to the protection of the juveniles (up to about 40 mm) by the spine canopy association (Tegner and Dayton, 1977). As the urchins become too large to receive shelter from adults, they enter the intermediate and most vulnerable size category, the node between the 2 peaks (about 50 to 80 mm). As indicated by the predation studies, large urchins attain a partial refuge from predation. The lobster feeding experiments demonstrate that survival of small urchins is significantly enhanced by the presence of adults and that, when offered a choice between mid-sized and large urchins, the lobsters consistently choose the smaller prey despite having the capability to handle the largest urchins (Tegner, unpubl.). The second mode is

big despite heavy predation on intermediate sized urchins because several year classes are accumulated here as growth rates slow down (Bernard and Miller, 1973; Ebert, 1977; Tegner, unpubl.), whereas the first peak is largely constituted by the first year class (Ebert, 1977; Tegner, unpubl.). In contrast to juvenile red urchins, small purple urchins are found in a variety of micro-habitats; purple urchins do not utilize the spine canopy association to nearly the same degree or extent of time (Tegner and Dayton, 1977). Furthermore, sheephead feeding trials suggest that the short-spined purple urchins attain little if any refuge in size from larger predators; large purple urchins are in the same size category as the heavily preyed upon mid-sized red urchins. Thus, there is no reason to expect a bimodal size-frequency distribution. This was borne out by the data from all 3 sites.

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