Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline

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ABSTRACT: Long-term data on density, size structure and microhabitat of 2 species of sea urchins in the Hopkins Marine Life Refuge, Pacific Grove, California (USA), are presented for the period 1972–1981. Densities of *Strongylocentrotus franciscanus* remained very low (ca 1 urchin m^{-2}) throughout the study period, whereas the population of *S. purpuratus* had one substantive recruitment event in 1975–76 when densities increased 25-fold from about 2 to about 50 urchins $10m^{-2}$. New recruits initially were found throughout the algal-invertebrate turf, but soon they became concentrated in shallow cracks. As the urchins outgrew the cracks they invaded kelp holdfasts. They grew to 20 to 40 mm test diameter within 1 yr, and their biomass reached nearly 500 g $10m^{-2}$. In winter 1976–1977, densities declined rapidly by more than 50 %, probably as result of predation by the sea star *Pycnopodia helianthoides* and/or mortality from disease. Most of the remaining sea urchins were restricted to deep crevices, and their densities continued to decrease slowly to about 6 urchins $10m^{-2}$ in 1981. Sea urchins in the Hopkins Marine Life Refuge of central California appear to recruit at very low levels during most years. Moreover, the single episodic recruitment event observed during our decade-long study led to only a temporary increase in population density, and most of the recruits were killed 1 yr after they settled.

INTRODUCTION

Sea urchins are important grazers that can regulate the abundance, distribution and species composition of marine plants in a variety of habitats (reviewed by Lawrence 1975, Dayton & Tegner 1984, Foster & Schiel 1985, Schiel & Foster 1986, Harrold & Pearse 1987). However, the population dynamics of sea urchins are not well understood. Recent attention has focused on population regulation by 3 major sources impacting large juveniles and adults: (1) human fishing and 'pest control' (e.g. Tegner 1980, Bernstein & Welsford 1982); (2) predation by sea otters (reviewed in VanBlaricom & Estes 1987), fishes (Tegner & Dayton 1981, Cowan 1983, Hay 1984), sea stars (reviewed by Harrold & Pearse 1987), and decapods (Tegner & Dayton 1981, Tegner & Levin 1983, Scheibling 1984, Vadas et al. 1986); (3) disease (reviewed by Jangoux 1984, 1987a, b, c, Harrold & Pearse 1987). Recruitment in sea urchin populations has received considerably less attention.

However, populations of some species experience light or virtually no recruitment in some years and heavy recruitment in other years; after an episode of heavy recruitment, cohorts often can be followed for several years as they grow and either join the adult size classes or are slowly thinned (reviewed by Ebert 1983, Harrold & Pearse 1987).

These observations indicate that once sea urchins attain a size that can be observed in the field as recruits, they have passed the major limitations to growing to adulthood. Thus, recruitment rather than adult mortality may be limiting the population because larval transport to the population is variable (Cameron & Rumrill 1982, Ebert 1983) and/or most mortality occurs in the larval and very early juvenile stages (Highsmith 1982).

The sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus* are common in intertidal and shallow rocky habitats along the west coast of North America (Durham et al. 1980), and their populations have provided examples of regulation at both recruitment and later life stages. Ebert (1983) proposed that both species exhibit a latitudinal cline in the predictability of

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recruitment, with infrequent recruitment success in the north but more regular, frequent recruitment in the south. However, variability in the size-structure of populations of *S. purpuratus* along the coast from central California to Oregon indicates that there may be considerable geographic variation in recruitment success, even within the northern portion of the hypothetical cline (T. A. Ebert & M. P. Russell, San Diego State University, pers. comm.).

The present paper provides long-term data for populations of *Strongylocentrotus purpuratus* and *S. franciscanus* at an intermediate latitude in central California, USA. The study site is within the established range of sea otters *Enhydra lutris*, which are important predators on large sea urchins (reviewed in VanBlaricom & Estes 1987). Lowry & Pearse (1973) provide an initial description of these sea urchin populations in 1972–73, when densities were low and consisted mostly of adults inhabiting deep crevices more-or-less inaccessible to sea otters. One hypothesis for the population dynamics of these sea urchins is that intense predation by sea otters on the sea urchins as they outgrow or move out of their crevices balances substantial annual recruitment, as apparently occurs with abalones cohabiting the crevices (Hines & Pearse 1982). Alternatively, low levels of recruitment, punctuated by episodic high levels once every few years or less often, may introduce animals to the system, and those remaining in crevices might survive many years, as Ebert (1983) found for intertidal populations in Oregon. Episodic mortality from disease or storms also could strongly influence the populations. In this paper we use long-term data on the density, size structure and microhabitat distribution of the sea urchins to distinguish between these modes of population dynamics. In addition, we evaluate the impacts of the major potential sources of mortality for the populations: sea otters, sea stars, and disease.

STUDY AREA AND METHODS

This study was conducted within a 40 m by 40 m area in the Hopkins Marine Life Refuge at Pacific Grove, California, USA. The biota and general characteristics of the area are described by Pearse & Lowry (1974). Irregular granodioritic outcrops at about 10 m depth support a diverse community of sessile animals and algae dominated by the giant kelp *Macrocystis pyrifera*. All sampling was done using SCUBA gear Densities, size structures and microhabitat distributions of sea urchin populations were estimated at irregular intervals from 1972 to 1981. Populations were monitored intensively at about bimonthly intervals from October 1975 through September 1978. At other times, only one or two samples were taken each year (none for

1974), but careful field observations during research on other aspects of the kelp community indicated that more frequent sampling was not warranted.

Densities were estimated by counting all sea urchins found within 10 to 25 circular 10 m² plots located by coordinates selected from a random number table. Size frequency distributions of the populations were estimated by measuring with a vernier caliper the test diameters of the first 10 urchins encountered in each random plot (if fewer than 10 individuals were encountered in a plot, all were measured). Biomass distributions of the populations were derived from a curve of the wet weight *versus* test diameter plotted for 80 individuals ranging in diameter from 5 to 48 mm. Microhabitat distributions were determined for most of the population censuses by tallying the individuals by substrate category (crevices, algal-invertebrate turf, and holdfasts of *Macrocystis*) as the urchins were encountered in the circular plots.

Although sea urchins in the study area were cryptic and often difficult to see, standardized search efforts were used in sampling. The same group of experienced divers took samples throughout the study period. Although the plots were not sampled destructively (e.g. by tearing out algae and rolling very large rocks), minimizing disruption of the habitat, great care was taken to search each plot systematically and thoroughly for as much as an hour per plot, depending on its substrate heterogeneity. All crevices and kelp holdfasts were explored visually and by feel. Small, easily movable rocks and shells were examined on all sides. Several checks were conducted to assess the accuracy of our sampling efforts. First, all sea urchins were removed from 10 plots. The same plots were then resampled for missed individuals; less than 6 % of the sea urchins were missed in the first sample of any plot. The size frequency distribution of the individuals found in the second samples did not differ significantly from that of the first collections (Kolomogorov-Smirnov test, p > 0.05). Second, in October 1976 the densities of sea urchins in the standard census were compared with the number of individuals found in 20 independent, randomly located 0.1 m² plots that were sampled by chiseling off the algal-invertebrate turf and collecting it with an airlift suction device fitted with a 0.9 mm mesh bag. Mean densities of sea urchins in the two sampling methods were not significantly different (p > 0.05). Third, during November 1975, December 1976, September 1978, June 1979, and August 1981, 6 to 9 randomly selected holdfasts of *Macrocystis* were pried from the substrate, placed in plastic bags and taken to the laboratory for dissection. The number of sea urchins per holdfast was not significantly different from the number found in holdfasts during the standard searches (paired t-test, p > 0.05). Finally, in August

1981 the circular plots were sampled in the standard way and then destructively by tearing out algae, opening as many crevices as possible, and rolling all rocks and boulders. Destructive sampling did not reveal significantly more sea urchins (paired t-test, p > 0.05). Based on size-frequency distributions of sampled sea urchins (see 'Results'), sea urchins smaller than 5 mm were not detected in our standard samples, and urchins 5 to 10 mm in size were detectable but sampled with variable error. However, we are confident that sea urchins with diameters greater than 10 mm were sampled with < 6 % error.

From January 1977 to June 1979, densities and size frequencies of empty sea urchin tests were also recorded in the 10 to 25 circular plots in the same manner as the live animals.

Densities of sea stars were sampled at the same times as the sea urchins by using the same counting methods.

All ANOVA and ANCOVA tests were run on log-transformed data; however, arithmetic means and standard errors were plotted in the figures. Homogeneity of variances and slopes were tested (p > 0.05) before proceeding with ANOVA.

RESULTS

Densities of *Strongylocentrotus franciscanus* remained low and did not change significantly (Fig. 1; ANOVA, p > 0.05); mean density of the means (± standard error) for the 10 yr period was 1.0 ± 0.8 ind $10m^{-2}$. Too few individuals of *S. franciscanus* were found to allow detailed analysis of size frequency or microhabitat distributions of the population. However, almost all the urchins were large (45 to 60 mm test diameter) and found in deep crevices. The few smaller individuals (5 to 20 mm diameter) found at different times of the year occurred in the algal-invertebrate turf and shallow cracks.

Densities of *Strongylocentrotus purpuratus* were also low at about 2 ind $10m^{-2}$ from 1972 to October 1975 (Fig. 1). The diameters of these urchins ranged from about 9 to 51 mm, with most individuals being between 16 and 34 mm (Fig. 2). Moreover, the calculated biomass of these urchins was very low, < 30 g wet weight $10m^{-2}$ (Fig. 1). In November 1975, many small individuals < 10 mm diameter were found nestled in small cracks and covered with bits of shell and debris. Although difficult to detect because of their small size and cryptic habit, nearly 3 times as many were counted in November 1975 as were counted a month earlier (Fig. 1), and the presence of the new recruits was clearly indicated in the size structure of the population (Fig. 2). By late January 1976, most of the new recruits were 10 to 20 mm diameter, and they were easier to detect and count. The density of *S. purpuratus* had increased significantly to 50 ind $10m^{-2}$ by that time, and almost all of them were new recruits. The biomass of urchins had increased to 318 g wet weight $10m^{-2}$. Densities remained unchanged at the increased level of 46 to 56 urchins $10m^{-2}$ from April to October 1976 (ANOVA,
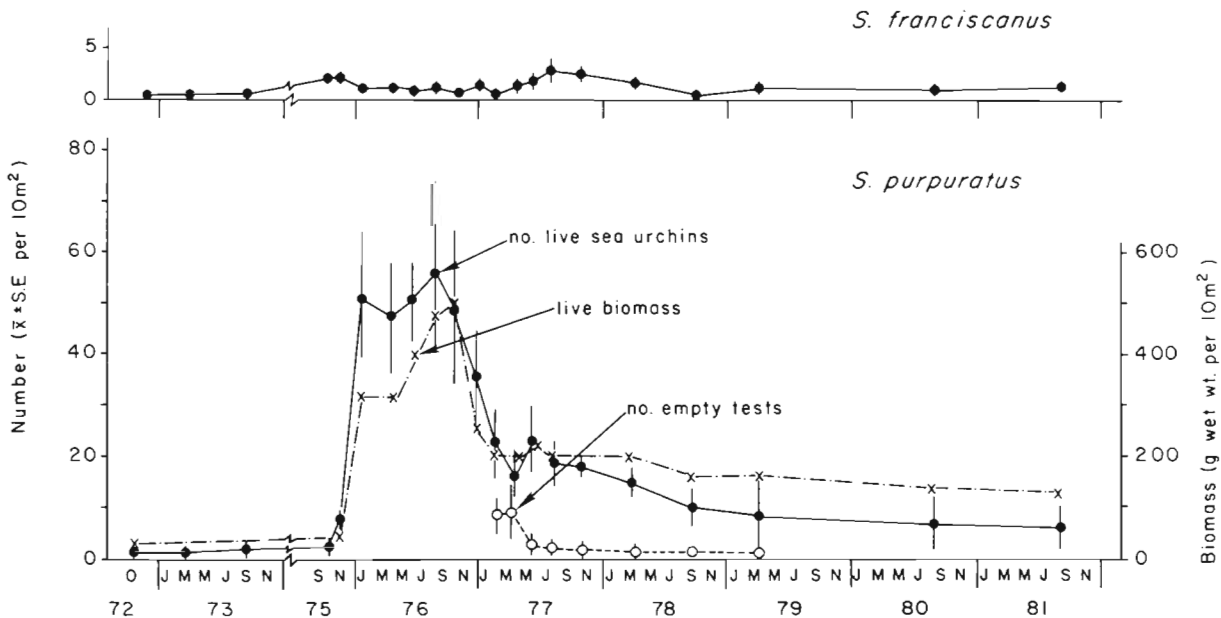

Fig. 1. *Strongylocentrotus* spp. Long-term variations of *S. franciscanus* and *S. purpuratus* in the Hopkins Marine Life Refuge from 1972 to 1981. Densities of live sea urchins of both species, densities of empty tests of *S. purpuratus,* and calculated biomass of *S. purpuratus* are plotted for each sample of 10 to 25 circular 10 m² plots. Data for 1972 and March 1973 from Lowry & Pearse (1973)

p > 0.05). The size of the urchins in the cohort increased steadily during that time, and by October 1976, nearly 1 yr after first being detected, most of the cohort was 18 to 36 mm diameter. As a result of this growth, the biomass increased to nearly 500 g wet weight $10m^{-2}$.

The density of *Strongylocentrotus purpuratus* declined significantly and rapidly from December 1976 to April 1977, to about 20 urchins $10m^{-2}$ (ANOVA,
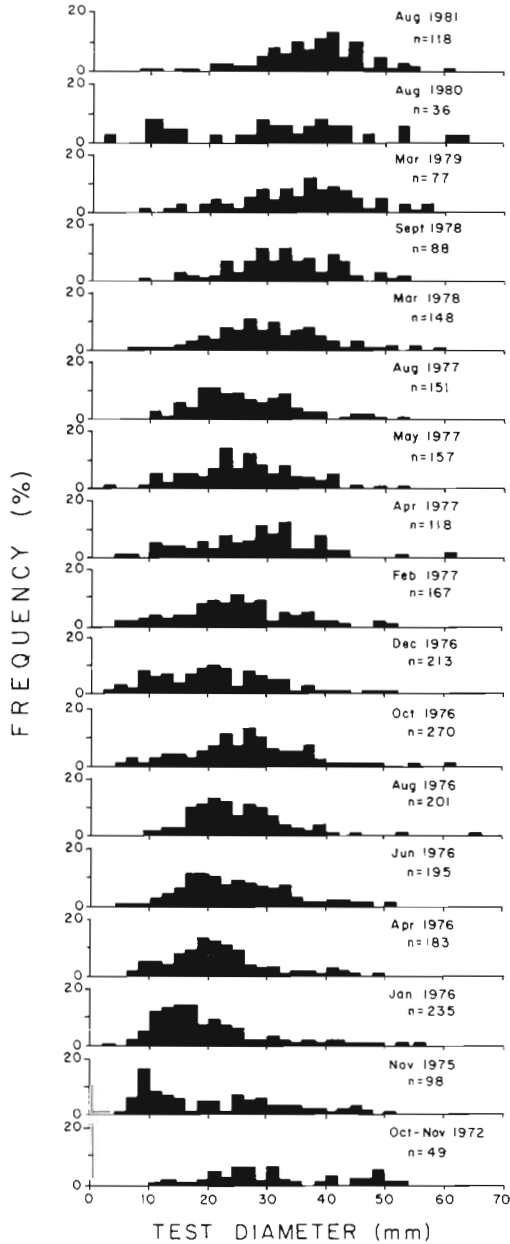
p < 0.05). The rate of decline was about 30 ind $10m^{-2}$ in 120 d, or about 0.25 urchins $10m^{-2} d^{-1}$. Urchin biomass also declined sharply to about 200 g wet weight $10m^{-2}$ in April 1977. Numerous whole, clean empty tests of *S. purpuratus* were observed in the study area beginning in December 1976, when the decline began. All tests found in the circular plots were collected and their diameters measured on the succeeding sampling dates. In February and April 1977, a mean of 8 tests $10m^{-2}$ were collected. About 2 tests $10m^{-2}$ were found during the rest of 1977, and fewer than 1 test $10m^{-2}$ in September 1978 (Fig. 1). Size frequencies of neither live sea urchins nor empty tests changed significantly among sampling dates from February and August 1977 (Kolomogorov-Smirnov tests, p > 0.05). Size distribution of empty tests was nearly identical to that of live urchins (Kolomogorov-Smirnov test, p > 0.05) (Fig. 3).

From May 1977 through August 1981, densities of *Strongylocentrotus purpuratus* declined steadily and gradually to about 6 urchins $10m^{-2}$ (Fig. 1). Because the 1975 cohort continued to grow (Fig. 2), the biomass dropped even more gradually, from a mean of 227 g wet weight $10m^{-2}$ in May 1977 to 135 in 1981 (Fig. 1). A low level of recruitment was observed in October–December 1976, making up about 5 % of the population (Fig. 2) and constituting a density of about 2 recruits $10m^{-2}$. Growth of these recruits could be followed into May 1977, but by August 1977, they were indistinguishable from the 1975 cohort. Most of the sea urchins in September 1978 belonged to the 1975 cohort; but 2 yr later in August 1980, the cohort could not be distinguished (Fig. 2). No other substantial recruitment occurred during the 1972–1981 period.

From 1972 to October 1975, the population of *Strongylocentrotus purpuratus* occurred almost entirely within deep cracks and crevices, as described by Lowry & Pearse (1973). Recruits in the 1975 cohort were first observed in the algal invertebrate turf, mainly in shallow (1 to 5 cm deep) cracks and at the interface between rock and sand, where they remained during
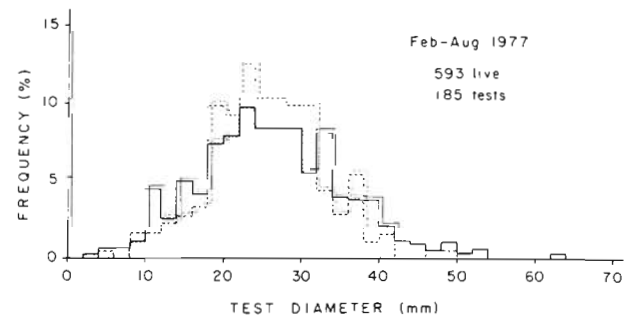

Fig. 2. *Strongylocentrotus purpuratus*. Population size structure in the Hopkins Marine Life Refuge from 1972–1981. Note the growth of the cohort of sea urchins that recruited in November 1975. Month and number of sea urchins measured are shown for each sample

Fig. 3. *Strongylocentrotus purpuratus*. Size structure of live individuals (open) and empty, intact tests (stippled) measured in the Hopkins Marine Life Refuge from February to August 1977
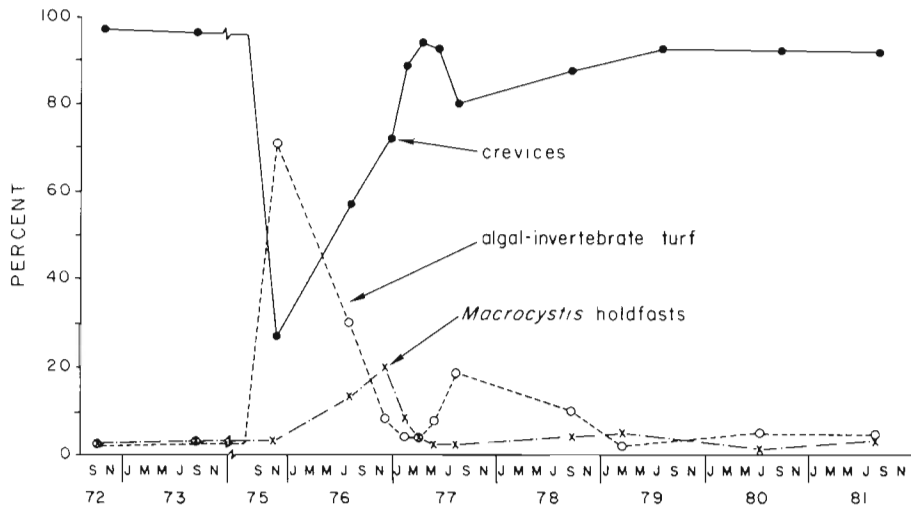
Fig. 4. *Strongylocentrotus purpuratus*. Microhabitat distributions in the Hopkins Marine Life Refuge from 1972–1981. Percentages shown of the individuals counted and measured on most sampling dates that were found in deep crevices (●), algal-invertebrate turf covering the rocks (○), and holdfasts of the kelp *Macrocystis pyrifera* (X)

the first half of 1976 (Fig. 4). However, by Jun 1976 the size of many of the sea urchins exceeded the size of the shallow cracks. Many protruded conspicuously from the cracks; others were found outside the cracks nestled in holes in encrusting mats of the vermetid gastropod *Petaloconchus montereyensis*. As the cohort grew during the period of highest densities, more and more urchins were found in deeper crevices and in holdfasts of giant kelp *Macrocystis pyrifera* (Fig. 4). The frequency of sea urchins in kelp holdfasts increased during summer and fall, until about 20 % of the population were in holdfasts in December 1976; at that time a mean of about 7 sea urchins were found per holdfast. The burrowing activity of the sea urchins appeared to weaken the kelp holdfasts substantially; many of the holdfasts had large cavities within them and the divers could extract sea urchins by pushing their hands into these cavities. The rapid decline of the population during winter–spring 1977 was accompanied by a decrease in the infestation of holdfasts, and after April 1977 <5 % of the population (<1/holdfast) were found within kelp holdfasts (Fig. 4).

In the latter half of 1977 many of the remainder of the 1975 cohort outgrew the shallower crevices and spilled out around the edges, creating 'halos' barren of algae around the crevice openings (see dip in percentage of crevice sea urchins, Fig. 4). After 1978 nearly all of the urchins were restricted to deep crevices, as during 1972–1975.

Although densities of the 5 most common species of sea stars fluctuated considerably throughout the study period (Fig. 5), there was no evidence of episodic recruitment or changes in numbers corresponding closely with those seen with *Strongylocentrotus purpuratus*. Individuals of *Patiria miniata* were most abundant with about 40 ind 10m^{-2}. Densities of *Pisaster giganteus* and *Orthasterias koehleri* fluctuated between

about 0.5 and 1.5 ind 10m^{-2}. *Pycnopodia helianthoides* and *Dermasterias imbricata* were the least abundant, averaging about 0.3 to 0.4 ind 10m^{-2}

DISCUSSION

The single major recruitment event we recorded in 10 yr of sampling indicates that the population of *Strongylocentrotus purpuratus* in our study area usually recruits at low levels and experiences rare episodic
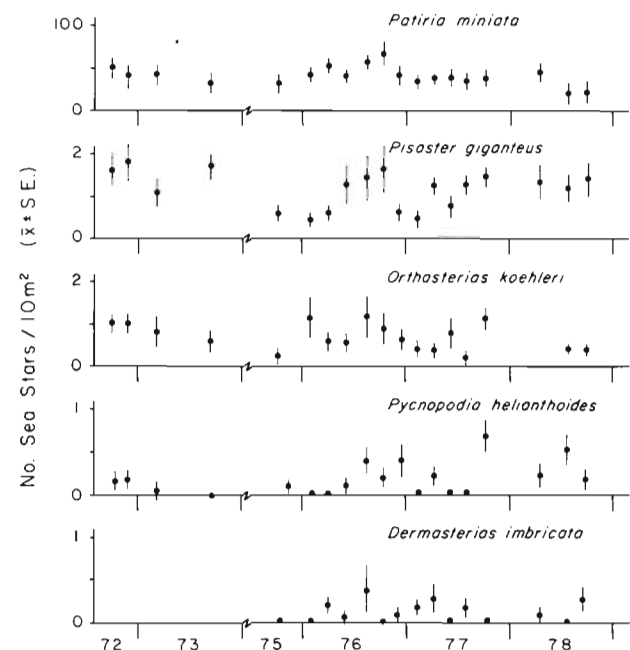

Fig. 5. Densities of 5 species of sea stars in the Hopkins Marine Life Refuge, 1972–1978. Data shown for each sample of 10 to 21 randomly selected circular 10 m^2 plots

recruitment events. Similar patterns of recruitment have been noted for intertidal populations of *S. purpuratus* in Oregon and Washington by Ebert (1983) and Paine (1986), respectively. The population of *S. franciscanus* did not experience even one major recruitment event in our study area during the 10 yr. In contrast, populations of both species recruit at high levels every year in Baja and southern California (Pearse et al. 1970, Ebert 1977, 1983, Tegner & Dayton 1981). Although there is an apparent north-south recruitment pattern (Ebert 1983), the factors causing year-to-year variation do not act uniformly over the entire coast; Ebert's (1983) Oregon population did not show a recruitment episode in 1975 when ours did. In addition, the size structure of intertidal populations of *S. purpuratus* varies considerably along the coast from central California to Oregon, with populations near capes and headlands usually lacking the small, recently-recruited individuals that are common at sites in between (T. A. Ebert & M. P. Russell, San Diego State University, pers. comm.).

Ebert (1983) was unable to detect significant correlations between recruitment patterns and those of water temperatures, water run-off from the land, and upwelling indexes. Similarly, the 1975 recruitment event at our study site was not correlated with changes in surface water temperature in the Hopkins Marine Life Refuge or in weekly coastal upwelling indexes for 36° N, 122° W (ANCOVA, p > 0.2). This finding contrasts with the significant negative correlation found between upwelling and recruitment of the intertidal barnacle *Balanus glandula* settling less than 100 m inshore of our study site (Roughgarden et al. 1987). Moreover, unlike recruitment of *B. glandula*, which is detectable every year with large variances, that of the sea urchins in our study is undetectable during most years. The underlying mechanisms controlling these species, both with pelagic larvae, might be very different.

Kelp forests substantially modify current patterns by restricting flow into them (Jackson & Winant 1983), and there is limited evidence that such current patterns influence the distributions of sea urchin recruits within kelp forests (Tegner & Dayton 1981) Moreover. variation in predation by juvenile rockfishes associated with the kelp forest canopy influences the number of barnacle larvae that pass through the kelp forest and settle on inshore rocks (Gaines & Roughgarden 1987, Roughgarden et al. 1987); similar predation in the kelp canopy on sea urchin larvae could influence sea urchin recruitment. Nevertheless, the only year during our study that showed substantially reduced kelp abundance was 1974, not 1975 when we observed heavy recruitment of sea urchins (Gerard 1976, Pearse & Hines unpubl.). Early post-larval mortality from filter-feeders and micropredators such as peracarideans also

has been shown to potentially limit recruitment in some echinoid populations at or just after settlement (Highsmith 1982); however, we do not have data on fluctuations in the abundance of the complex array of these species in our study system.

When first noticed in November 1975 the sizes of the recently recruited sea urchins were between about 7 and 15 mm test diameter with a strong mode between 8 and 10 mm (Fig. 2). The spawning period of *Strongylocentrotus purpuratus*, as well as *S. franciscanus*, is in spring (Pearse 1981), and larvae are in the plankton for 2 to 3 mo before settling and metamorphosing into juveniles about 1 mm in diameter (Strathmann 1978). Thus, the 7 to 15 mm diameter recruits we detected in November probably settled the previous late spring and early summer. By October 1976, the frequencies suggest that these urchins had increased in diameter to between about 20 and 40 mm, with a major mode between 26 and 30 mm. Such a rate of growth may be maximal in the system when there is an unlimited supply of food. Laboratory-maintained urchins in Santa Cruz at ambient sea water temperatures and fed an unlimited supply of blades of the kelp *Macrocystis pyrifera* increased in size from a mean of 10 mm in November to 28 mm the following October (Pearse et al. 1986). Similar rates of growth were found for well-fed, laboratory-reared individuals of *S. purpuratus* in southern California (Pearse et al. 1970), for caged individuals of *S. purpuratus* supplied with an abundance of food in Washington (Swan 1961), in the fastest-growing, apparently best-fed intertidal populations of *S. purpuratus* in Oregon (Ebert 1968), and in intertidal populations of *S. purpuratus* in British Columbia, southern California, and Baja California (Russell 1987).

In areas where sea otters are present, their predation usually limits densities of large sea urchins to levels well below those that could substantially impact algal growth; such predation restricts the microhabitat distribution of the sea urchins to deep crevice refuges (Lowry & Pearse 1973, VanBlaricom & Estes 1987). However, our observations suggest that heavy recruitment of sea urchins could lead to considerable change in a kelp forest community, even in an area foraged by sea otters. Within 1 yr after the 1975 recruitment, many sea urchins had burrowed into the kelp holdfasts. The resident sea otters were not seen feeding on the sea urchins, even though many were protruding accessibly from shallow cracks. The 1975 cohort was still quite small (20 to 40 mm diameter), probably too small to serve as prey for sea otters. If the population had not declined dramatically, it seems probable that the sea urchins in the holdfasts eventually would have dislodged many of the kelp plants, greatly reducing the algal component of the system. Presumably, if this had happened, the sea urchins would still grow to a size

large enough to be fed upon by sea otters, their numbers would then have been greatly reduced by sea otter predation, and subsequent algal recruitment and growth would eventually return the system to a dense kelp forest. On the other hand, a portion of a large recruitment of both *Strongylocentrotus purpuratus* and *S. franciscanus* in 1984 on the south side of the Monterey Peninsula survived in deeper water (25 to 30 m), grazed nearly all the algae, and by mid 1986 had produced a sea urchin-dominated 'barren' area within the range of sea otters (J. M. Watanabe & C. Harrold, Monterey Bay Aquarium, pers. comm.).

The cause(s) of the rapid decline of the population of *Strongylocentrotus purpuratus* at our study site during winter 1976–77 is not clear. Number, size structure, and intact condition of the fragile, empty sea urchin tests found during this period indicate that predators that damage tests during feeding were not responsible. Lobsters and fish species that commonly prey on sea urchins in southern California are rare in central California, and they inflict characteristic damage to the tests (Tegner & Dayton 1981, Tegner & Levin 1983). Similarly, crabs (e.g. adult *Loxorhynchus crispatus* and *Cancer* spp.) were present only in very low densities (Hines 1982), and they damage tests during predation. Sea otters that are common in the study area also break open the tests when they feed on sea urchins. The study site is a marine preserve, where human collecting is illegal and very limited. We know that emigration of sea urchins from the study area did not occur, because the 11 hectare kelp forest is surrounded by wide sandy areas (Pearse & Lowry 1974), where migrating sea urchins would have been observed easily.

Two possible sources could have killed the sea urchins and left their tests intact: sea stars and disease. The sea stars *Pycnopodia helianthoides*, *Dermasterias imbricata*, and *Patiria miniata* were present in the study area (Fig. 5), and they are known in other areas to prey on sea urchins, leaving intact tests (Harrold & Pearse 1987); other sea stars present (*Pisaster giganteus* and *Orthasterias koehleri*) are not known to feed on sea urchins. Although *P. miniata* were very abundant at about 40 ind 10m^{-2}, we never saw these sea stars feed on a sea urchin in many hundreds of observations during the population decline or in thousands of observations over the entire study period. Nor did we ever see escape responses invoked in individuals of *Strongylocentrotus purpuratus* by *P. miniata*, as reported by Schroeter et al. (1983) for *Lytechinus anemesus* in southern California. *D. imbricata* occurred at low densities of about 0.4 ind 10m^{-2} during the sea urchin decline. Although this species has been reported to feed on sea urchins in southern California (Rosenthal & Chess 1972), it preys almost exclusively on anthozoans in the region of our study area (Annett & Pierotti 1984),

and we never saw one feed on a sea urchin during our 10 yr study period.

Individuals of *Pycnopodia helianthoides* also were not common in our study area (densities of about 0.3 ind 10m^{-2}). Moreover, we only noted a few instances of individuals of this species feeding on sea urchins during the study period. However, because they ingest their prey whole rather than humping over it while digesting it extraorally like most other sea stars, such feeding could have escaped notice. Herrlinger (1983) examined the stomach contents of over 200 individuals of *P. helianthoides* in our study area in 1980–81, after the period of high sea urchin density, and he found about 1 % of the prey were sea urchins. Leighton (1971) reported that individuals of this species can consume up to 1.5 urchins d^{-1}. Such a high feeding rate would require a density of only 0.16 sea stars 10m^{-2} (half that observed in our study area) to cause the measured decline at 0.25 urchins 10m^{-2} d^{-1}. Conversely, the observed density of 0.3 individuals of *P. helianthoides* 10m^{-2} would have to feed at a rate of only 0.83 urchins d^{-1} to cause the decline. It seems possible that predation by *P. helianthoides* might have caused the decline, even though we did not observe high incidences of predation.

Disease has caused dramatically rapid declines in sea urchin populations in the Caribbean (*Diadema antillarum*), Nova Scotia (*Strongylocentrotus droebachiensis*), and central California (*S. franciscanus*), leaving clean intact tests of the same size structure as the live population (reviewed by Jangoux 1984, 1987a, b, c, Harrold & Pearse 1987). Disease-caused mass mortality in central California killed 60 to 95 % of the sea urchins in at least 2 localized populations during winter and spring 1976 in the Santa Cruz area, ca 35 km north and upstream of the prevailing currents from our study site (Pearse et al. 1977). Although many similar populations adjacent to the afflicted ones did not exhibit mass mortalities (Pearse et al. 1970, Yellin et al. 1977), sea urchin disease in Nova Scotia and in the Caribbean is known to be transported long distances by currents (Miller & Colodey 1983, Lessios et al. 1984, Scheibling & Stephenson 1984). Therefore, disease from the Santa Cruz area could have been transported down-current to the population of *S. purpuratus* in Pacific Grove by fall and winter 1976–77. However, despite careful bi-weekly observations in our study site during the population decline, we observed only very low incidences of diseased sea urchins that were similar to incidences seen in 'undiseased' populations in the Santa Cruz area (Yellin et al. 1977, Gilles & Pearse 1986).

If the populations of sea urchins in our study site are representative, and the population dynamics of *Strongylocentrotus purpuratus* and *S. franciscanus* there are

characterized by low levels of recruitment punctuated by episodic highs, they apparently are also characterized by highly variable levels of mortality. Low predation rates may be typical for low density, stable populations found in crevice refuges within the established range of sea otters (e.g. Lowry & Pearse 1973). Very high mortality occurs when sea otters move into new habitats and consume all exposed large sea urchins, by mass mortality caused by disease, or when sea stars feed on newly recruited small sea urchins, as most likely happened in the present study. These patterns of recruitment and mortality cannot be discerned without long-term data.

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