Population dynamics of the sea urchin Strongylocentrotus purpuratus in a Central California kelp forest: recruitment, mortality, growth, and diet

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Population dynamics of the sea urchin *Strongylocentrotus purpuratus* in a Central California kelp forest: recruitment, mortality, growth, and diet

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Abstract. The population dynamics of *Strongylocentrotus purpuratus* inhabiting dense mats of geniculate coralline algae in a shallow central California *Macrocystis pyrifera* forest was examined. Sea otters had occupied the area for over two decades. Sea urchin density and size distribution were sampled during 1984–1986 to determine recruitment and mortality patterns. Growth rates were obtained from tetracycline-labeled individuals and changes in size-frequency modes. Periodic collections were made to examine gut contents and the relationship of diet to food availability. The interaction of recruitment and mortality resulted in a dynamic population structure. Mean densities ranged from 6.5 to 12.7 urchins 0.25 m^{-2}. The population consisted primarily of urchins up to 40 mm in test diameter in a size distribution which changed from unimodal to bimodal and back over the 2 yr study. Mortality was temporally variable and related to test diameter. Growth rates were somewhat lower than most previous reports for the species and suggested that most of the population was made up of 1 and 2 yr-old individuals. Diet consisted largely of geniculate coralline algae, with fleshy brown algae becoming important when available as drift. This study showed high densities of small urchins can exist in a California kelp forest inhabited by sea otters, but regular recruitment may be necessary to maintain such populations.

Introduction

Sea urchins have the greatest potential of any kelp forest grazer for shaping community structure, and their ecology has been examined in numerous studies (see review by Harrold and Pearse 1987). The sea otter *Enhydra lutris* can play an important role in kelp forests by limiting sea urchin size and abundance to levels below those at which destructive grazing can occur (Lowry and Pearse 1973,

Estes and Palmisano 1974, Dayton 1975, Estes et al. 1978, Duggins 1980, Breen et al. 1982, VanBlaricom 1984, Laur et al. 1988). In spite of this, there have been few studies examining urchin populations, other than their density and size distribution, in areas where sea otters have become reestablished.

Estes et al. (1978) found that in the western Aleutian Islands, at islands where sea otters had been at equilibrium density for several decades, sea urchin (*Strongylocentrotus polyacanthus*) densities were relatively low in shallow water but increased with depth, and test diameters were generally limited to <30 mm. At islands where sea otters were absent, urchins were large (some >100 mm), and very abundant in shallow water; density and size decreased with increasing depth. At Attu Island, at sites where an expanding sea otter population has been foraging for several years, high densities of small urchins have persisted (Estes et al. 1989), perhaps as a result of high recruitment rates. Sea urchin recruitment in the western Aleutians may be regular and high relative to California (Estes personal communication).

In California, Lowry and Pearse (1973) sampled sea urchin abundance and size distribution at Hopkins Marine Life Refuge (HMLR) after sea otters had occupied the area for over a decade. *Strongylocentrotus franciscanus* were quite rare, but *S. purpuratus* occurred at densities of 0.21 m^{-2}, with a mean test diameter of 29 mm. Both species were restricted to crevices. Other surveys in California have indicated that sea otters limit urchin populations to low densities of small and cryptic individuals (McLean 1962, Foster et al. 1979, Foster and VanBlaricom 1986, Laur et al. 1988). This may be particularly true at sites where sea urchin recruitment is low. Pearse and Hines (1987) found that between 1972 and 1981 there was only one large urchin recruitment event at HMLR. *S. purpuratus* densities rose from approx 2 to 50 10 m^{-2}, but then declined again to low levels over the course of a year, possibly due to predation by the sunflower star *Pycnopodia helianthoides*.

The present study examined a population of *Strongylocentrotus purpuratus* living in a central California kelp

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forest. Sea otters have foraged in the area for almost 30 yr (E. E. Ebert 1968). The urchins inhabit dense mats of geniculate coralline algae which provide the dominant bottom cover in the area. Such coralline mats are a common feature in the shallow sublittoral along the central California coast (Foster and VanBlaricom 1986, Harrold et al. 1988).

The objective of this study was to examine the influence of recruitment, growth, and mortality on the population structure of subtidal urchins within the sea otter range in California. In addition, the influence of the coralline mat habitat on diet was examined.

Materials and methods

Study site

Stillwater Cove in Carmel Bay, California, USA, opens to the south, and so is protected from northwest winter swells (Reed and Foster 1984). Most of the work was conducted on a shallow reef near the center of the cove, southwest of Pescadero Rocks (Fig. 1). The reef rises abruptly on the seaward side from a depth of 12 m at its base to 5–8 m on top. The rise is more gradual on other sides. The substrate is hard sandstone and basalt and, although the surface topography is irregular, cracks and crevices are rare.

A dense mat of geniculate coralline algae, consisting mainly of Calliarthron tuberculosum, C. cheilosporioides, and Bossiella californica ssp. schmittii, covers up to 100% of the bottom. This mat

Fig. 1. Location of study site in central California, USA, and other sites referred to in text

provides a habitat for high densities of small crabs, snails, sea stars, and sea urchins (Dearn 1987). The fucalean alga Cystoseira osmundacea is common on the reef and forms a dense canopy of reproductive fronds in summer. Giant kelp, Macrocystis pyrifera, forms a canopy along the seaward edge and scattered individuals occur along with sparse groves of the understory kelp Pterygophora californica over the rest of the reef. Patches of fleshy red algae, most notably Cryptopleura (= Botryoglossum) farlowianum are also common.

Population structure

The density and size distribution of Strongylocentrotus purpuratus on the reef were sampled in December 1984, April, June, and July 1985, and Semptember 1986. Random 0.25 m² quadrats were thoroughly searched and the number of S. purpuratus found and their test diameters (measured to the nearest millimeter) were recorded. Additional size distribution data were gathered in September 1984 and September 1985 by measuring urchins collected for growth studies.

The empirically derived equation

$$w \text{ wt (g)} = 0.0007 \, [\text{test diam (mm)}]^{2.87}, \tag{1}$$

$n = 56, r^2 = 0.988$, was used to estimate a mean biomass (g 0.25 m^{-2}) from size distributions when sea urchin density was known.

Size-frequency data were analyzed graphically (Cassie 1954) to help define cohorts and to find means of cohort modes to aid in formulating a growth equation.

Mortality

Size-specific mortality of 1 + yr-old urchins was calculated between successive size-frequency samples using a modification of Sainsbury (1982a, b). After correcting for differences in sampling effort, an expected size distribution (for no mortality) was calculated by applying the growth equation (Eq. 6) to the initial size distribution of the sample pair. A standard deviation of 1.28 mm per year of growth (chosen as a minimum based on growth variation observed in the tetracycline-marked urchins) was used in calculating the expected distribution. Finally, the size classes in both the measured and the expected size distributions were grouped into 5 mm increments in order to smooth erratic frequencies resulting from sampling error. For each 5 mm size class, i, survival, s_i, over the time interval between the samples was then calculated as

$$S_i = N_{mi}/N_{ei}, \tag{2}$$

where N_{mi} is the number of urchins actually measured in the ith 5 mm size class, and N_{ei} is the expected number of urchins in the same size interval. The instantaneous mortality rate for the size class (Z_i) was calculated as

$$Z_i = -\log_e (S_i) \, / \, t, \tag{3}$$

where t is the time in years between samples. The annual mortality rate for the size class (M_i) was then calculated as

$$M_i = 1 - e^{z_i}. \tag{4}$$

Sea otter scats collected at Cypress Point (Fig. 1) in 1982 (Faurot et al. 1986) were examined for urchin remnants in order to determine what sizes of urchins were commonly eaten by local otters. An equation relating the length of compass parts of the Aristotle's lantern (the complex jaw structure in regular echinoids) to test diameter was empirically derived so that diameters could be reconstructed:

$$\text{diameter}_{(mm)} = [0.392 \, \text{compass}_{(mm)}]/0.114; \tag{5}$$

$n = 52, r^2 = 0.958$. Compass parts were used instead of demipyramids (Estes et al. 1989) because they were more often found unbroken in the scats.
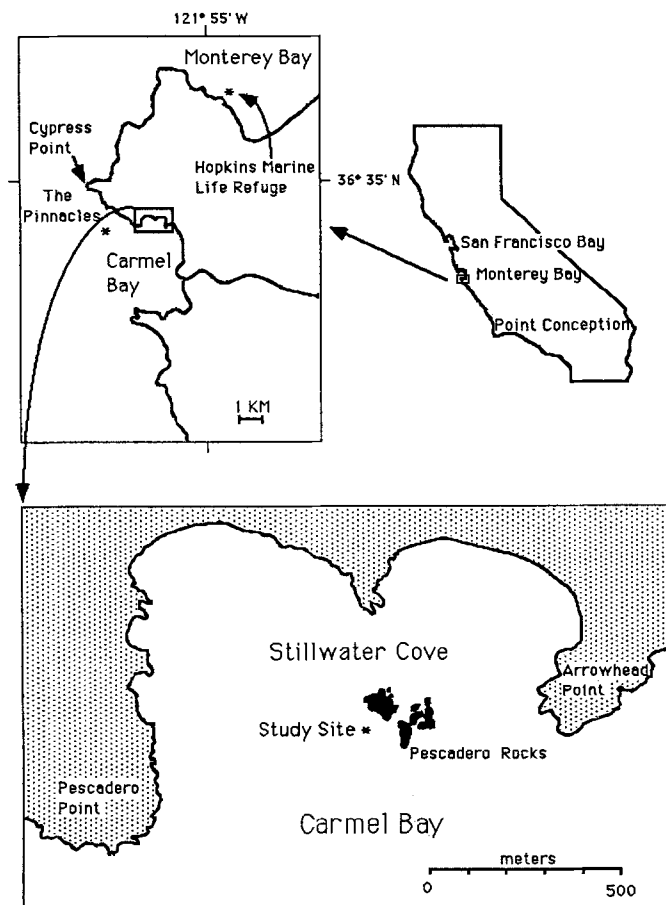
Growth

Growth rates of urchins in the population were determined by marking individuals with tetracycline and by following the movement of size-frequency modes through time. Tetracycline produces a fluorescent mark on the actively growing portions of skeletal elements in sea urchins (Kobayashi and Taki 1969, Pearse and Pearse 1975, Ebert 1977, 1980a, 1982, Russell 1987) and these marks indicate the size of the skeletal part at the time of tagging. Demipyramids (jaws) of the Aristotle's lantern were used since they do not require grinding to reveal the fluorescent marks (Ebert 1982).

In September 1984, 244 *Strongylocentrotus purpuratus* collected from the Stillwater Cove population were injected in the laboratory with 0.1 mg tetracycline HCl per gram sea urchin (Pearse and Pearse 1975). The tetracycline solution consisted of 10 mg tetracycline per ml sea water. The urchins were then separated into six groups of similar size distribution which were randomly assigned to six marked sites on the reef. The following day, they were returned to the field, where they were placed into the coralline mat in the area immediately surrounding the marker at the designated site. The urchins bore no external marks or tags and were not caged or restricted in any way.

One year later, the six sites were searched for sea urchins, and 385 were returned to the laboratory, where they were dried, cleaned in 5% sodium hypochlorite, and examined for fluorescent tetracycline marks with an ultraviolet light (Blak-ray®). The jaw length and test diameter of each urchin was recorded. Jaw lengths were measured using a dissecting scope with an ocular micrometer. Jaw growth of marked urchins was determined and subsequently converted to growth in test diameter as described by Ebert (1980a).

The Richards' function (Richards 1959), a more flexible form of the Von Bertalanffy equation, was used to describe growth of urchin jaw parts:

$$S_t = S_\infty [(1 - be^{-Kt})^{-n}], \qquad (6)$$

where S_t is the size at time t, S_∞ is the asymptotic size, b is a scaling factor equal to $(S_\infty^{-1/n} - S_0^{-1/n})/S_\infty^{-1/n}$, where S_0 is the size at settlement (0.1 mm was used as the jaw length at settlement here), $K(\text{yr}^{-1})$ is the growth-rate constant, and n is a shape parameter. When $n = -1$, the equation is equivalent to the Von Bertalanffy equation. The initial jaw lengths (J_t) and jaw lengths one year later (J_{t+1}), for recaptured urchins, were used in a computer program developed by Ebert (1980b) which searches for the Richards' function growth parameters (n, K and S_∞) that minimize the sum of squared errors (SSE) for a Walford plot of initial and final sizes. The computer program was used in conjunction with size-frequency data to arrive at a growth equation which fits the population.

Diet

Temporal trends in diet were determined by examining the guts of urchins collected over a 13 mo period. Food availability was sampled along with these collections so that the type and abundance of attached and drift algae in the immediate vicinity of each urchin examined was known. Urchins ≥ 15 mm in diameter were collected from randomly placed 0.25 m² quadrats. Preliminary work indicated that gut contents of smaller urchins were difficult to identify. Sampling continued until 25 urchins were collected, requiring 3 to 6 quadrats per sampling period. Immediately after collection, the urchins were injected with 0.3 to 0.5 ml formalin to fix gut contents and later were frozen to await dissection. These collections were made in October and December 1984, and January, April, June, August, and November 1985.

The percent cover of attached algae in the vicinity of the collected urchins was sampled using a random-point contact technique (Foster 1982). Twenty haphazardly spaced points were sampled from within a 1 m² frame placed surrounding the 0.25 m² quadrat from which the urchins were collected. Attached algae above (within 0.5 m of the substrate) or below these points were recorded. Since layering occurred and more than one species could be recorded for

a point, total cover often exceeded 100%. To assess the fleshy algae available as drift, all detached thalli and pieces of fleshy macroalgae were collected from within the 1 m² quadrat. These were later sorted and weighed.

Gut contents were analyzed using the method of Harrold and Reed (1985) with the following modifications. Individual guts were not subsampled and the number of pieces (>0.5 mm) of coralline, fleshy red, and fleshy brown algae in each of five (rather than three) randomly selected squares in a 1 cm² grid in a petri dish were counted. The amount of each food type was then calculated as the percent of the total number of food pieces counted in the five squares.

Temporal variation in the relative amount of coralline algae in the gut contents was tested for significance using a single-factor nested ANOVA with quadrats nested within months. In order to test the hypothesis that time of year, test diameter or food availability had a significant influence on diet, a stepwise multiple regression was run using the percent of coralline algae in the gut as the dependent variable. Seven independent variables were tested: month, test diameter, percent cover of geniculate coralline, fleshy red, and brown algae, and the mass of fleshy red and brown drift algae. The stepwise multiple regressions were run using the SAS statistical software package (SAS Institute Inc., Cary, North Carolina) utilizing the STEPWISE procedure and the MAXR technique. The C_p statistic, a measure of total squared error, was used to evaluate which independent variables to retain (Mallows 1973, Daniel and Wood 1980, SAS Institute Inc. 1985). Percent cover and percent of gut contents data were arcsine-transformed prior to statistical testing in order to normalize the distribution. Data on drift algal biomass were square-root transformed, since the variance had a linear relationship to the mean (Sokal and Rohlf 1981). Untransformed means and variances were used in Fig. 7.

Results

Population parameters

The size-frequency data show that *Strongylocentrotus purpuratus* recruitment at Stillwater Cove occurred several times throughout the study. Urchins as small as 3 mm were present in all except the June–July sample, where 5 mm was the smallest found (Fig. 2). The September 1984 sample consisted mostly of one large mode centered around 24 mm. This mode will be referred to as the 1983 cohort, since growth-rate calculations indicate that it is probably the result of a recruitment in the spring of 1983. In the December–January sample, recruitment of a 1984 cohort became obvious. This event was foreshadowed by the small mode present in the previous (September 1984) sample. Noticeable recruitment also occurred in 1985 (although not obvious in 1985 samples) and 1986, since distinctive cohorts are apparent at 3 to 7 mm and 9 to 19 mm in the September 1986 sample (Fig. 2). The 1984 cohort dominated the population structure within 6 mo of its recruitment. Although obviously bimodal in December 1984 and April 1985, the size distribution was virtually unimodal by June–July 1985, consisting almost entirely of the 1984 cohort. The 1983 cohort appears to have become essentially extinct over the previous few months. During 1984 and 1985, sampled test diameters ranged from 3 to 40 mm, with at least 90% of each sample consisting of urchins <30 mm. By September 1986, however, >50% of the sample was in a large mode centered at 30.5 mm. This shift apparently resulted from survival and growth of members of the 1984 cohort.
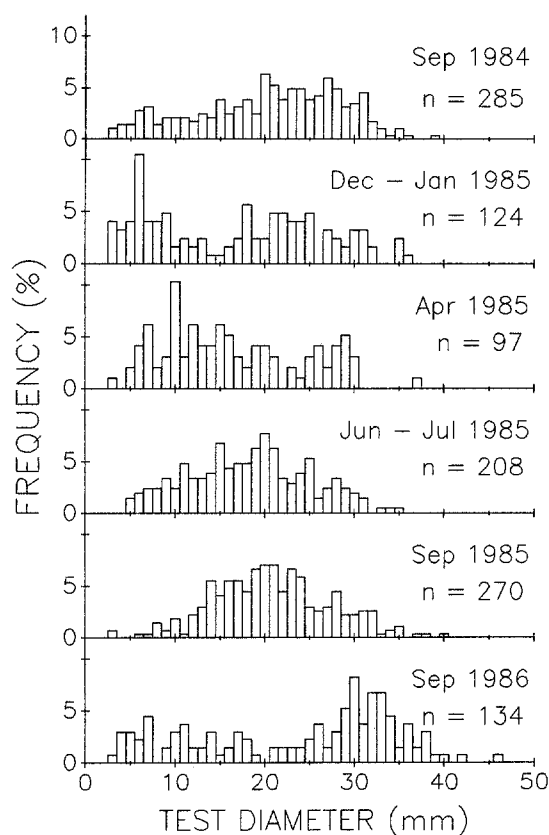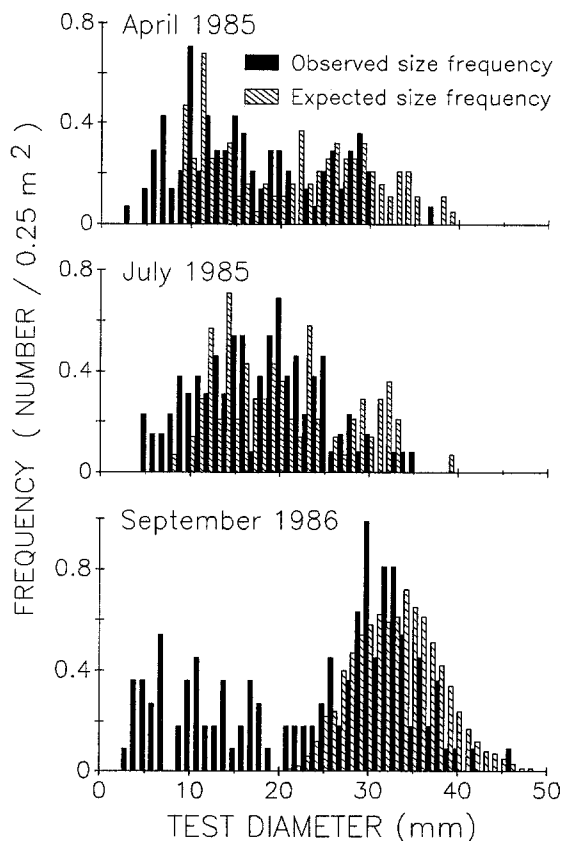
Fig. 2. *Strongylocentrotus purpuratus.* Size-frequency distribution at Stillwater Cove over time. Dates and sample sizes are shown. Note growth of cohort which appeared in September 1984, and loss of previous cohort during course of study

Table 1. *Strongylocentrotus purpuratus.* Summary of sample size, mean density and biomass data. Values in parentheses are standard errors

Month	No. of 0.25 m² quadrats	Density (nos. 0.25 m⁻²)	Biomass (g 0.25 m⁻²)
Dec. 1984/Jan. 1985	19	6.5 (0.81)	26.5
Apr. 1985	14	7.0 (0.92)	27.7
June 1985	13	7.5 (0.98)	33.6
July 1985	13	8.5 (1.42)	33.2
Sep. 1986	11	12.7 (2.21)	121.3

Mean densities rose slightly from 6.5 to 8.5 urchins per 0.25 m² during 1984 and 1985 and urchin biomass rose from 26.5 to 33.2 g per 0.25 m² during this period as growth of the recruits compensated for the loss of the previous cohort (Table 1). When density was again sampled in September 1986, however, it had nearly doubled to >12 urchins per 0.25 m². This is significantly higher than the previous densities measured (ANOVA $p < 0.05$ and Student-Newman-Keuls test). In addition, biomass had more than tripled since July 1985, increasing from 32.2 to 121.3 g per 0.25 m². Density was not measured in September 1984 or September 1985. Size frequencies for those months resulted from samples taken for growth studies.

Fig. 3. *Strongylocentrotus purpuratus.* Observed and expected size frequencies for those samples for which density was measured. Difference between observed and expected frequencies was result of recruitment (on left) and mortality (on right). Expected size frequencies for each period were derived by applying the growth equation (Eq. 6) to each size class in the sample from the previous period

Mortality

Mortality rates were much higher for the 1983 cohort than for the 1984 cohort of the same age, and mortality appeared to affect smaller sizes. The expected (zero mortality) size distributions for April and July 1985 and September 1986 are plotted with the observed distributions in Fig. 3. The observed densities of individuals >30 mm (test diameter) were considerably less than expected in the 1985 samples, indicating relatively high mortality for these sizes in the 1983 cohort. In contrast, the 1986 sample indicated moderate mortality in the 35 to 40 mm range and higher mortality >40 mm for the 1984 cohort. Annual mortality rates of 94 to 100% were calculated for sizes 31 to 35 mm and 36 to 40 mm in the 1983 cohort in the winter and spring of 1985, and overall annual mortality rates of 85.6 and 92.5% were calculated for sizes >20 mm for these samples (Table 2).

In contrast, the maximum annual mortality rate for the 1984 cohort was 72.2% for the 41 to 45 mm size group, and the total annual mortality for sizes >30 mm was only 24.7% (Table 2). Both cohorts displayed a similar pattern of increasing mortality rates with larger test diameter (the 26 to 30 mm size class during the December/January–April 1985 interval is an unexplained exception; $M = 18.7\%$: Table 2).

Table 2. *Strongylocentrotus purpuratus.* Size-specific mortality between sampling dates. Z: instantaneous mortality coefficient; S: % survival during time interval (t) between samples; M: % annual mortality. Dividing line separates 1983 cohort (data to left) from 1984 cohort (data to right). md > pd: measured density exceeds predicted density (these size classes were not used to calculate total); 0: measured density was zero; 00: measured and predicted densities were zero
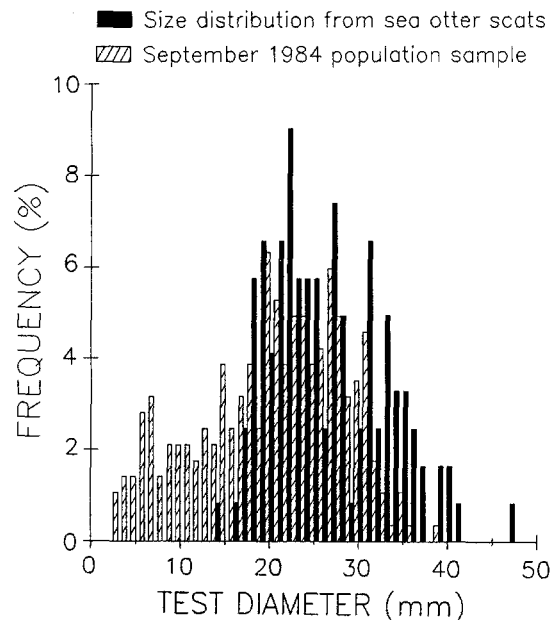
Size and mortality parameters	Dec./Jan. 1985	Apr. 1985	July 1985	Sep. 1986
	$t = 0.29$ yr	$t = 0.25$ yr	$t = 1.24$ yr	
21–25 mm				
Z	2.11	md > pd		
S	54.3%	md > pd		
M	87.8%	md > pd		
26–30 mm				
Z	0.21	0.85	md > pd	
S	94.2%	29.2%	md > pd	
M	18.7%	56.6%	md > pd	
31–35 mm				
Z	0	5.11	0.10	
S	0.0%	27.9%	88.4%	
M	100.0%	99.4%	9.5%	
36–40 mm				
Z	2.85	0	0.48	
S	43.8%	0.0%	55.2%	
M	94.2%	100.0%	38.8%	
41–45 mm				
Z	00	00	1.48	
S	00	00	16.0%	
M	00	00	72.2%	
Total for 21–45 mm				
Z	1.94	2.78	0.28	
S	57.0%	52.2%	70.3%	
M	85.6%	92.5%	24.7%	

■ Size distribution from sea otter scats
▨ September 1984 population sample

Fig. 4. *Strongylocentrotus purpuratus.* Size frequency of sea urchins reconstructed from 19 sea otter scats collected from Cypress Point in 1982, compared to size frequency from Stillwater Cove population from September 1984 sample ($n = 285$). Test diameters for scat samples were calculated from lengths of compass parts of Aristotle's lanterns: ≤ 5 compass parts of identical size in a scat were assumed to represent one urchin, resulting in a sample size of 122 sea urchins

The apparent difference in the sizes affected by mortality in the two cohorts is at least partially explained by the disparity in the time intervals between samples. Actual mortality could occur at any time between consecutive samples, so a longer interval (such as between July 1985 and September 1986) would show mortality affecting larger size classes, since growth over the time interval would be greater (up to 15 mm rather than 2 to 4 mm between closer samples).

Of the 23 sea-otter scats examined, 19 contained measurable compass parts, representing an estimated 122 urchins ranging from 14 to 47 mm in diameter. Urchins 18 to 35 mm made up most of the sample (Fig. 4) and it is apparent that by September 1984 most of the 1983 cohort had outgrown its size refuge from sea otter predation.

Growth

A geometric mean functional regression (Ricker 1973) of the $\log_e$ transformations of jaw length and test diameter

results in an equation of the form:

$$D = \alpha J^{\beta}, \tag{7}$$

where J and D are jaw length and test diameter, respectively (Ebert 1982). In this population, $\alpha = 2.734$ and $\beta = 1.263$ ($r^2 = 0.903$, $n = 385$).

Of the 385 sea urchins collected in September 1985, 15, ranging from 22 to 37 mm in diameter, bore fluorescent marks from tetracycline. Ebert's (1980 b) Richards' function computer program yielded a best-fit (sum of squares error = 1.86) shape parameter of $n = 0.37$, with $K = 1.951$ and the asymptotic jaw length, $J_\infty = 8.35$ mm for these individuals. Although the resulting curve is a good fit to the tetracycline data (Fig. 5 a), it is unrealistic when plotted beyond these, predicting almost no growth in test diameter over the first several years (Fig. 5 b). This situation is probably due to the scatter and narrow size range of the growth data. In an effort to find parameters which better described growth in this population, the September 1985 and September 1986 means of the 1984 cohort modes were used as presumed Age 1 yr (17.5 mm) and Age 2 yr (30.5 mm) test diameters. These corresponded to jaw lengths of 4.35 and 6.75 mm, respectively. The shape parameter, n, was then estimated by applying Ebert's program to the jaw growth data and providing trial n's until an equation was produced that predicted jaw lengths similar to those of the September 1985 and September 1986 modes. The parameters $n = -0.79$, $K = 0.326$, and $J_\infty = 12.05$ mm result in Age 1 yr and Age 2 yr jaw lengths of 4.41 and 6.75 mm, respectively, and still yield a good fit (SSE = 2.29) to the tetracycline data (Fig. 6 a).

The parameters for jaw growth can be converted to those describing test diameter growth by solving for the
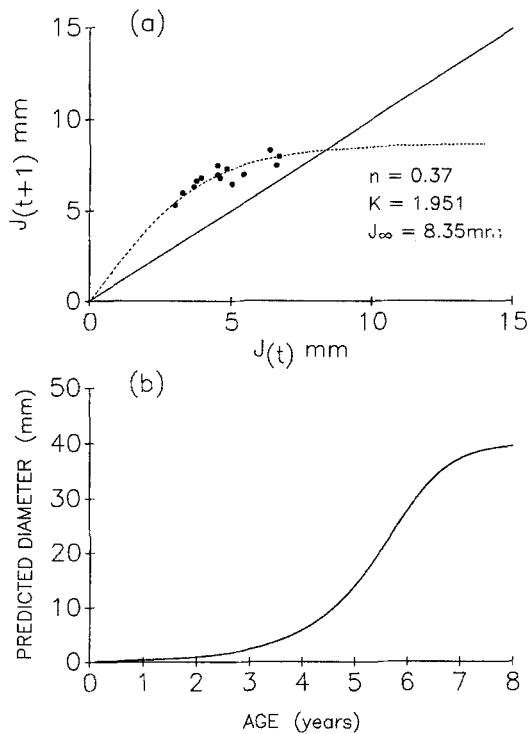
Fig. 5. *Strongylocentrotus purpuratus.* (a) Walford plot of growth of tetracycline-marked demipyramids and curve resulting from least-squares estimate of the Richards' function-shape parameter, n, $=0.37$; $J_{(t)}$ is the jaw length of urchins at the time of tagging, $J_{(t+1)}$ is the jaw length 1 yr later, K is growth rate constant, and J_∞ is asymptotic jaw length; diagonal line represents no growth. (b) Growth curve for test diameter growth derived from above shape parameter, n, and relationship of test diameter to jaw length
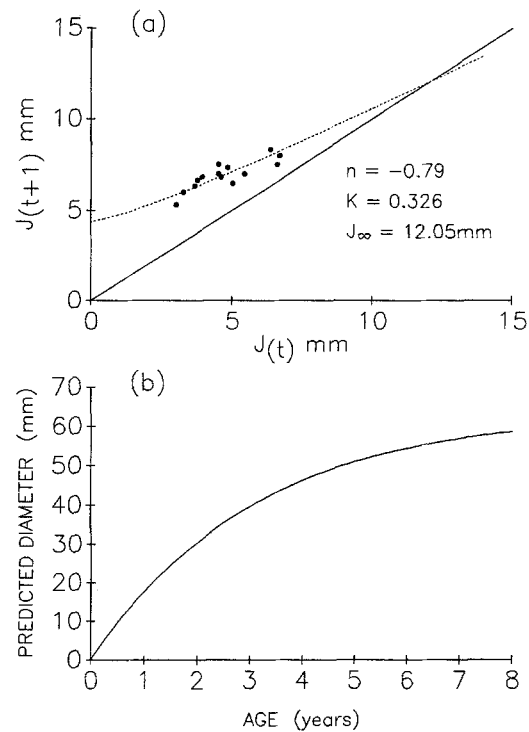
Fig. 6. *Strongylocentrotus purpuratus.* (a) Walford plot of tetracycline data and curve resulting from adjusting growth equation to correspond to movement of size-frequency modes over time. Shape parameter, n, $= -0.79$. (b) Growth curve for test diameter growth derived from above shape parameter, n, and relationship of test diameter to jaw length

asymptotic test diameter, D_∞, and the shape parameter for test growth, n_D (Ebert 1982):

$$D_\infty = \alpha J_\infty^\beta, \tag{8}$$

$$n_D = \beta n_J. \tag{9}$$

The resulting parameters for test diameter growth are $n = -1.0$, $K = 0.326$, and $D_\infty = 63.29$ mm, and the curve is a Von Bertalanffy type.

Virtually identical growth parameters result without using size-frequency modes if the J_t and J_{t+1} jaw lengths are converted to test diameters and Von Bertalanffy test growth is assumed. A Walford plot of the derived D_t and D_{t+1} values results in the growth parameters $K = 0.327$ and $D_\infty = 63.38$ mm.

Using $K = 0.326$, and $D_\infty = 63.29$ mm, predicted annual test diameters for the first 4 yr of growth are 17.8, 30.5, 39.6, and 46.2 mm (Fig. 6b). This suggests that in 1984 and 1985, approx 90% of the population may have been less than 2 yr-old and, even in 1986, none may have been as old as 4 yr.

Diet and food availability

Geniculate coralline algae were the dominant food items during all times of the year. Of 159 urchin guts examined over 13 mo, 44 contained >90% coralline algae. At least

50% coralline algae was found in 109 guts, and only 8 guts were completely free of corallines. Mean monthly abundance in guts ranged from 40.0% in August to 94.6% in December (Fig. 7a).

Fleshy brown algae were the second most abundant food items in the guts, with fleshy red algae making up most of the remainder. Brown algae occurred in 122 of 159 guts. They accounted for at least 10% of the items in 75 of the guts and at least 50% of the items in 32 of these. Mean monthly percent in guts ranged from 0% in December to 37.3% in August (Fig. 7a).

Fleshy red algae appeared in the guts of 122 of the 159 urchins examined. Only 45 of these, however, contained 10% or more fleshy red algae and only 9 had 50% or more. Mean monthly percent in guts ranged from 4.1% in October to 22.3% in August (Fig. 7a).

The nested ANOVA found that temporal variation in the relative amount of coralline algae in the guts was significant ($p < 0.05$). Spatial variation was highly significant ($p < 0.0001$), however, and error variation accounted for about 59% of the variance (Table 3). This suggests that small-scale patchiness in food availability may tend to overshadow larger scale patterns.

The percent cover of geniculate coralline algae remained high throughout the year, with seasonal means ranging from 81.7 to 98.8% (Fig. 7b). In contrast, the percent cover of brown and fleshy red algae fluctuated
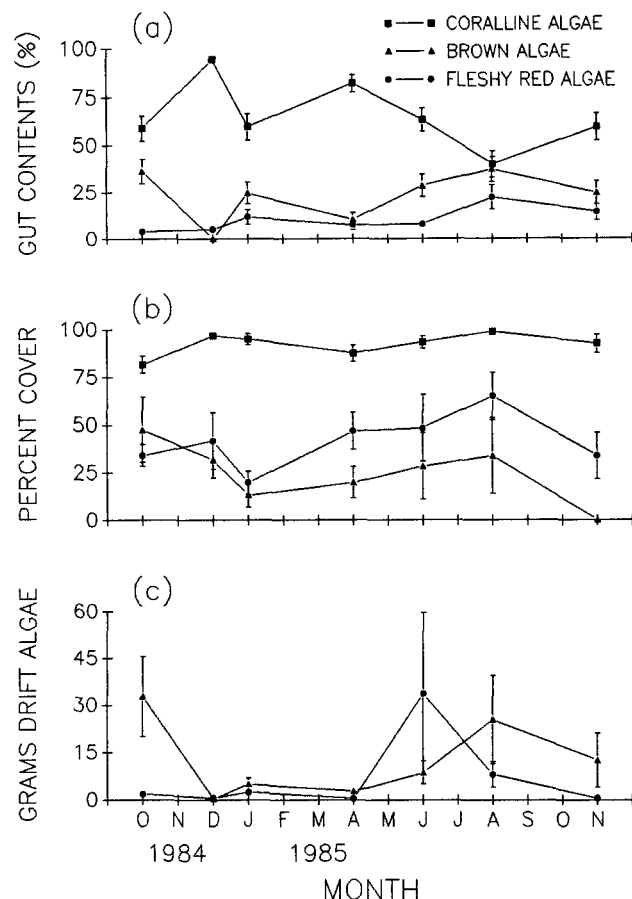
Fig. 7. *Strongylocentrotus purpuratus.* Temporal trends in diet and food availability (untransformed $\bar{x} \pm 1$ SE). (a) Percent gut contents ($n = 14$ sea urchins in December, $n = 23$ to 25 in other months); (b) percent cover of attached algae; (c) biomass (g m^{-2}) of fleshy algal drift [$n = 3$ to 6 quadrats per sampling period in (b) and (c)]

Table 3. *Strongylocentrotus purpuratus.* Results of nested-model II ANOVA, examining temporal and spatial differences in relative amount of coralline algae in gut contents. Quadrats are nested within month. Satterthwaite's approximation for unequal sample sizes was used to calculate F^* and the subgroups' degrees of freedom (**) for finding critical value of F^*. MS: mean square

Source	DF	MS	F	p	% of variation
Months	6	3785.37	3.32 (2.62)*	<0.05	15.77%
Quadrats	25 (20)**	1139.55	2.94	<0.0001	25.11%
Error	127	388.00			59.12%
Total	158	635.93			

Table 4. *Strongylocentrotus purpuratus.* Stepwise multiple-regression results for relative amounts of coralline algae in gut contents and two independent variables. MS: mean square; $R^2 = 0.200$

Source	DF	MS	F	$p > F$
Regression	2	10064.90	19.54	0.0001
Error	156	515.05		
Total	158			

Variable	Parameter estimate	F	$p > F$
Intercept	85.794	105.67	0.0001
Diameter	−0.729	4.44	0.0368
Brown drift algae	−4.672	33.06	0.0001

significantly, with higher cover in summer months than in winter, and with red algae usually more abundant (Fig. 7b).

Fleshy drift algae were markedly seasonal, with drift highest in summer and fall and usually low in winter and spring. Brown algae usually made up the bulk of the drift (Fig. 7c).

The stepwise multiple-regression analysis arrived at a highly significant model, with brown algae drift and test diameter inversely correlated with the relative amount of coralline algae in the guts sampled. However, the low r^2 value indicuates that much of the variation remains unexplained (Table 4). Drift of brown algae was highly significant in this regression.

Discussion

The density of the *Strongylocentrotus purpuratus* population examined in this study is the highest reported from within the established range of the sea otter in California, but part of this difference probably resulted from more careful searching for small urchins in the present study. The September 1986 density of 12.73 per 0.25 m^2 was

~ 240 times greater than that found by Lowry and Pearse (1973) at HMLR, 10 times greater than that measured there after a large recruitment in 1976 (Pearse and Hines 1987), and 3 times greater than that measured in August 1986 at a deforested deep reef site (The Pinnacles: Fig. 1) ~ 2 km southwest of the Stillwater Cove site (Watanabe and Harrold 1991). The densities reported in the present study were within the range of densities measured for green urchins (*S. polyacanthus*) at sea otter-foraged sites in the western Aleutians at Amchitka Island, but substantially less than those found at Attu Island (Estes et al. 1978, 1989, Estes unpublished data). Densities of sea urchins measured at sites where translocated sea otter populations have spread and foraged in southeast Alaska (Estes et al. 1989), British Columbia (Breen et al. 1982, Watson 1990), and Washington (Kvitek et al. 1989) were considerably lower, perhaps as a result of limited sea urchin recruitment.

The size distribution of *Strongylocentrotus purpuratus* from the Stillwater Cove population ranged up to 46 mm, but in most samples the maximum test diameter was 30 to 40 mm. The size distribution from September 1986 was very similar to that of the Outer Pinnacles population in August 1986 (Watanabe and Harrold 1991), but was much more restricted than the size distribution from HMLR, where large individuals of 40 to 60 mm consistently occurred during the 1970s but were typically confined to cracks and crevices (Pearse and Hines 1987). The Stillwater Cove population was also very similar in size range to the green urchin populations found at sites on

Attu Island, where sea otters have foraged for ~20 yr but where cracks and crevices are rare (Estes et al. 1989).

During the course of this study, four cohorts of varying strengths could be identified. In September 1984, the size distribution was dominated by a cohort which, based on growth rates for this site, probably recruited in the spring of 1983. By December 1984, a second cohort had recruited and already accounted for 43% of the population. This increased to 74% of the population by the fall of 1985, following substantial mortality of the 1983 cohort. More moderate recruitments in 1985 and 1986 were apparent in the September 1986 sample (Fig. 2). Together with the high densities measured, these data indicate that several successful recruitments of *Strongylocentrotus purpuratus* had occurred at Stillwater Cove, at least since 1983.

It is unknown if successful recruitment of *Strongylocentrotus purpuratus* is typical at Stillwater Cove. No density or size-structure data are available prior to 1983, although the presence of small *S. purpuratus* in the coralline mat has been observed since 1976 (Foster et al. 1979, Reed 1981, Foster personal communication). There was only one detectable recruitment at HMLR between 1971 and 1981 (Pearse and Hines 1987), but there was a large recruitment there in 1983 and one or two subsequently (Watanabe personal communication). If there is a consistent difference in echinoid recruitment success between Stillwater Cove and HMLR, it could result from small-scale oceanographic differences which effect larval supply or from site-related post-settlement processes. Alternatively, recruitment levels could typically be similar at the two sites and the recruitment events observed at Stillwater Cove and noted above for HMLR could have been a response to greatly reduced kelp canopies following severe winter storms in 1983 and 1984.

Recruitment is affected by both presettlement and postsettlement processes. Advection of larvae by offshore currents associated with coastal headlands has been proposed by Ebert and Russell (1988) as an important physical factor which may explain some latitudinal variations in settlement along the California and Oregon coasts. *Macrocystis pyrifera* canopies may reduce settlement either through altered current flow or the consumption of larvae by associated filter-feeding invertebrates or planktivorous fish (Bernstein and Jung 1979, Gaines and Roughgarden 1987, Duggins 1988). Understory kelp canopies can also influence larval settlement by the mechanisms of shading, reduced flow, or increased sedimentation (Duggins et al. 1990). Finally, Rowley (1989) has shown that differential postsettlement mortality can be important in determining recruitment patterns.

Survival of juvenile urchins is probably enhanced by the refuge from predation provided by the coralline mat. Watanabe (1984) showed that dense algal cover can inhibit sea star predation on *Tegula* spp. The coralline mat is likely to have a similar effect on sea star predation on small urchins. Kelp forest fishes known to feed on juvenile urchins such as the black surfperch (*Embiotica jacksoni*) (Quast 1968), the rubberlip surfperch (*Racochiles toxotes*) (Quast 1968), and the señorita (*Oxyjulis californica*) (McCleneghan 1968, Tegner and Dayton 1977) were

frequently observed picking at the coralline mat. The dense mat probably provides some protection from these predators as well. However, predation on juvenile urchins by small crabs which inhabit the coralline mat at high densities (Dearn 1987) could be an important unmeasured factor (Harrold et al. 1991).

Mortality rates calculated for age 1+ yr cohorts show year- to-year variation as well as a relationship to size. In 1985, the 1983 cohort incurred high mortality during the winter and spring months. Mortality in the 1984 cohort the following year was considerably lower. Mortality of the 1983 cohort appeared concentrated in individuals >20 mm.

Predation was probably the cause of the observed mortality. The maximum size of urchins in the population (46 mm test diameter) was considerably less than those attainable by this species (100 m). Storm-related mortality is unlikely, since 1985 was a mild winter and even severe storms are unlikely to have a direct impact on urchins in the coralline mat. No diseased urchins (sensu Pearse et al. 1977) were seen during this study, and no outbreaks of urchin diseases have been reported in this area in over a decade. Finally, both broken tests with spines intact, and whole cleaned tests were found, indicating predation by at least two different predators.

The sea star *Pycnopodia helianthoides* and the sea otter are the most probable predators involved. Although densities of *P. helianthoides* were not measured, it was common to encounter one or more on a given dive. *P. helianthoides* ingests its prey whole and then egests the hard parts a few days later (Herrlinger 1983). The leather star *Dermasterias imbricata* consumes *Strongylocentrotus purpuratus* in the same manner (Rosenthal and Chess 1972), but was only occasionally encountered on the reef. Although Duggins (1983) found that *P. helianthoides* at Torch Bay, Alaska, preyed exclusively on sea urchins which were greater than 40 mm in diameter, this apparently was related to the fact that large (40 to 80 mm) sea urchins were common and available. At HMLR, Pearse and Hines (1987) found no difference between the size distribution of the *S. purpuratus* population (mostly less than 40 mm diam) and the size distribution of empty tests which were assumed to result from predation by *P. helianthoides*. At Stillwater Cove, as at HMLR, the smallest empty tests observed were <10 mm in diameter, indicating that size selection was not a factor in predation by *P. helianthoides* here.

Sea otters are known to be size selective in their foraging (Estes and VanBlaricom 1988, Estes et al. 1989). They typically consume small urchins whole (Kenyon 1969) and hard parts are passed through in the scats (Faurot et al. 1986). Based on sea urchin parts found in the sea otter scats examined, 20 to 35 mm urchins are common in local sea otters' diets. Interestingly, the size distribution of urchins from Cypress Point sea otter scats is almost identical to that reported by Estes et al. (1989) for sea otter scats from Attu Island, and the maximum size in the two urchin populations is also very similar.

Since individual sea otters may have quite different prey preferences, and since one sea otter can easily consume over 30 small urchins in a foraging bout (Lyons
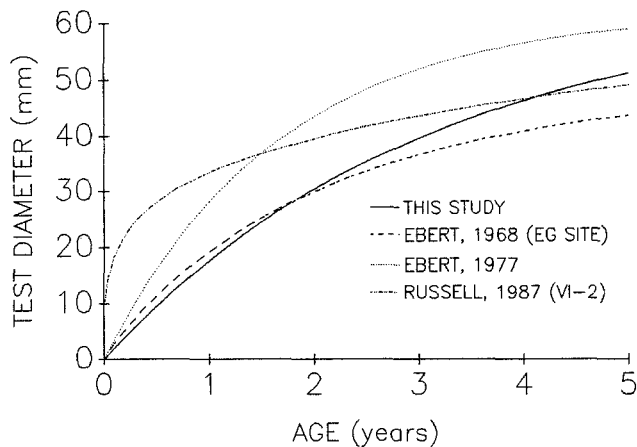
Fig. 8. *Strongylocentrotus purpuratus*. Comparison of idealized growth curves from present and from previous studies. Curves drawn from equations in T. A. Ebert (1968: Site EG), Ebert (1977), Russell (1987: Site VI-2), and from present study. Ebert (1968) gave equations for three sites, of which growth at Site EG most closely resembled that at Stillwater Cove; Ebert (1977) gave equation for only one site; Russell gave growth equations for eight sites, of which Site VI-2 is representative

1989), the activity of one or a few sea otters may locally affect prey densities (Riedman and Estes 1988). The change in observed mortality between 1985 and 1986 could thus be the result of the movement of a few individual otters from the area. Although both sea stars and sea otters preyed upon the population, sea otter predation is the most likely explanation for the observed patterns of mortality and, unlike Pearse and Hines (1987), predation by *Pycnopodia helianthoides* was probably not as important.

Growth rates in this study are much lower than some previously found for *Strongylocentrotus purpuratus* (Ebert 1977, Russell 1987) but are similar to those found by T. A. Ebert (1968) in an intertidal (*Phyllospadix* sp. bed in Oregon (Fig. 8). The estimated size of 17.8 mm at Age 1 yr compares favorably with Rowley's (1990) estimate of 17 mm for a 1yr-old *S. purpuratus* in a kelp forest. There are some problems comparing growth curves from these different studies. T. A. Ebert (1968) used external tags, and this technique could have reduced growth rates (Ebert 1977). In addition, growth rates from most previous studies are based on the growth of larger urchins and several different growth equations have been used. T. A. Ebert (1968) used a logarithmic growth equation, Ebert (1977) used a Von Bertalanffy equation, and Russell (1987) used the Richards' function.

These problems aside, however, it appears that the urchins in the Stillwater Cove population are growing at a rate below that reported in most earlier studies. Considering the large proportion of coralline algae in their diet, this is not surprising. T. A. Ebert (1968) found that, of the three populations he examined, those with the highest proportion of coralline algae in their guts had the slowest growth rates. Reduced growth rates have also been found for urchins fed coralline algae in laboratory experiments (North 1964, Boolootian 1966, Leighton 1971, Rowley 1990, Kenner unpublished data). Coralline algae are low

in caloric value (Vadas 1977) and their assimilation is low in *S. purpuratus* (Leighton 1971).

The continuous presence of very small urchins (3 to 4 mm) indicates that either several low-level recruitment events occurred at different times of the year (Harrold et al. 1991), or that there may be a small proportion of very slow-growing individuals in the population. Such variation in growth could result from genetic or microhabitat differences. Regardless of the cause, this kind of variation suggests that caution is necessary when applying empirically-derived growth equations at the population level.

If the derived growth equation is valid for the majority of the population, the growth curve and size distribution for the population indicate a young age structure. The majority of the population appears to be in the 0 to 1 yr and 1 to 2 yr age-classes. Over 90% of the population may be this young, with a few individuals as old as 4 yr. Unless recruitment prior to 1983 was very low, this age structure indicates high mortality of larger urchins in past years also.

The patterns of food availability and diet demonstrate the opportunistic character of urchin feeding. Coralline algae, which are low in preference and food value (Leighton 1971), were the most abundant and the least spatially and temporally variable food. Consequently, they made up the bulk of the urchins' diet. The availability of brown drift algae was responsible for most of the explained variation observed in the diet. Apparently, when encountered brown algae were taken in preference to coralline algae.

There was significant temporal variation in the abundance of coralline algae in the diet, with a higher proportion of coralline algae in the guts during the winter. T. A. Ebert (1968) also found a higher occurrence of coralline algae in *Strongylocentrotus purpuratus* guts during winter months. This trend probably reflects the seasonal abundance of drift algae. The abundance of fleshy brown drift algae was negatively correlated with coralline algae in the diet. Drift abundance is typically higher in summer and fall (Gerard 1976, Harrold and Reed 1985) (Fig. 7c) when kelp biomass is high and water motion is low. In addition, the fucoid *Cystoseira osmundacea* forms a dense floating canopy of reproductive fronds at the site. These fronds, which may account for 80% of the plants' biomass, are shed in late summer (Schiel 1985). These structures accounted for at least 30 to 40% of the fleshy brown portion of gut contents in August and October and at least 20% in November. There is some senescence of *Macrocystis pyrifera* fronds in late summer as well, contributing to the abundance of drift biomass at that time.

The fact that there was a significant negative relationship between test diameters and percent of corallines in guts suggests that small urchins may be at a disadvantage in obtaining drift algae. Alternatively, urchins which rely more on coralline algae for food may grow slower and therefore be smaller than those which eat more fleshy algae. Both explanations seem plausible and there is not sufficient data to resolve them here. As mentioned above, a diet of coralline algae is likely to result in

slower growth. However, Himmelman (1986) found that, in *Strongylocentrotus droebachiensis*, small urchins (<15 mm) tend to be less mobile and do not respond to the presence of macroalgae.

Previous studies have shown that urchins in food-poor areas are more mobile than those able to catch sufficient drift algae without moving (Lees 1970, Mattison et al. 1977, Dean et al. 1984, Harrold and Reed 1985). Tagged individuals from this population exhibited movements of up to 141 cm d^{-1} in the field, with a mean movement rate of 21.1 cm d^{-1} (Kenner 1987). In contrast, Lees (1970), using similar techniques, measured a mean movement rate of 5.1 cm d^{-1} for *Strongylocentrotus purpuratus* in a food-limited site. The dense coralline mat may prevent the usual means of drift capture. Small pieces of drift algae do, however, entangle in the mat. Movement may therefore be necessary in order to encounter drift algae in the mat.

Poor food quality has been found to result in low reproductive output (Pearse 1980, Keats et al. 1984). In the present population, however, gonad indices did not seem obviously depressed and followed a typical seasonal cycle (Kenner 1987). In addition, urchins in this population actually became fertile at a smaller size (16 to 22 mm) (Kenner and Lares 1991) than the 25 to 35 mm previously reported for this species (Gonor 1972). The presence of a substantial number of reproductive individuals demonstrates that this population, and probably others within the range of the sea otter, is reproductively viable, even though it lacks large individuals.

In spite of predation by sea otters, regular recruitments and the protection provided by the geniculate coralline mat allowed the development of a high-density population of *Strongylocentrotus purpuratus*. The coralline mat also influenced the feeding and movement habits of the population, resulting in slow-growing, mobile urchins. Lack of suitable crevice space may preclude the survival of larger urchins, but individuals became reproductive at a small size. Since the population consisted mostly of Age 1 yr and Age 2 yr classes, variations in recruitment strength and in patterns of mortality led to rapid changes in population structure.

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