

# Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality

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**ABSTRACT:** Growth of newly settled purple sea urchins *Strongylocentrotus purpuratus* was studied using laboratory rearing of individuals at natural densities, size-frequency analysis of a recently settled cohort collected in field samples, and mark-recapture techniques with individuals injected with tetracycline. In the laboratory, sea urchins were reared on crustose coralline algae as characteristic of a sea-urchin barren ground (barrens), and on foliose red algal turf as characteristic of a kelp bed. Growth in a barrens was compared with growth in a kelp-bed habitat using all 3 methods. Field work was done at 2 subtidal sites near Santa Barbara, California, USA, from 1985 through 1987. *S. purpuratus* in the laboratory grew at similar rates for the first 50 d after settlement regardless of substrata (0.29 to 0.45 mm mo<sup>-1</sup>), and in the field grew slightly, but significantly, faster in the barrens (0.42 mm mo<sup>-1</sup>) than in the kelp-bed (0.31 mm mo<sup>-1</sup>). At roughly 50 d of age and 0.8 to 1.2 mm test diameter, sea urchins switched from feeding by surface scraping to grazing on fleshy algae. Thereafter, growth was significantly faster in the presence of macroalgae (0.56 to 1.67 mm mo<sup>-1</sup>), than in habitats or treatments without fleshy algae (0.12 to 0.27 mm mo<sup>-1</sup>). Based on these results, *S. purpuratus* diameter at 1 yr old was estimated to be 3.6 mm in barrens and 17 mm in kelp-bed habitats. Newly settled sea urchins suffered higher mortality in the kelp bed than in the barrens, but individuals at slightly greater ages showed no detectable difference in mortality between the 2 habitats. The attainment of a threshold size for switching diets and increasing growth rate (if algae is available) may be a critical event in a sea urchin's life-history.

## INTRODUCTION

The period of growth immediately following larval settlement and metamorphosis can be critical to the successful recruitment to adulthood of many marine invertebrates. Early post-settlement mortality of marine invertebrates shows great variability (Loosanoff & Engle 1940, Coe 1956, Keough & Downes 1982, Young & Chia 1982, Wetthey 1985), is often very high (Loosanoff 1964, Muus 1973, Highsmith 1982, Sebens 1983, Luckenbach 1984, Connell 1985, Watzin 1986, Dauvin & Gentil 1989), and can limit the size of resulting populations (Highsmith 1982, Young & Chia 1982, Connell 1985, Elmgren et al. 1986). Such mortality is commonly size-related, with surviving individuals eventually reaching sizes at which the risk of mortality is reduced (Birkeland 1974, Highsmith 1982, Sebens 1983, Watzin 1986). A faster growth rate during the early post-settlement period reduces the time that an individual remains at high risk. Thus, growth rate

becomes a factor influencing successful recruitment to adulthood.

Studies of growth during this period are also important because population studies often estimate cohort strength based on the smallest recruits easily sampled. The age of these recruits is based on growth rate estimates made by back-extrapolating growth rates measured for larger animals. Such studies rarely include data on the growth rates of newly settled individuals (for sea urchins, Ebert 1967, 1968, Tegner & Dayton 1981, Ebert 1983, Himmelman et al. 1983; but see Raymond & Scheibling 1987).

One reason that data on growth rates of newly settled individuals is rarely included in estimates of the age of recruits is that little is known about the early post-settlement life of mobile marine invertebrates such as sea urchins. The difficulties involved in following the fate of mobile, microscopic individuals in the field have resulted in a paucity of information on the growth or mortality of newly settled individuals (Barker 1979,

Sarver 1979, Switzer-Dunlap & Hadfield 1979, Highsmith 1982, Luckenbach 1984, Elmgren et al. 1986, Highsmith & Emlen 1986, Watzin 1986, Raymond & Scheibling 1987, Zann et al. 1987, Dauvin & Gentil 1989).

Sea urchins are the dominant herbivores in many algal communities and can exert profound effects on community structure (Lawrence 1975, Ebeling et al. 1985). They are also the basis of a large and growing fishery along both coasts of North America: landings in California alone were worth 13.7 million dollars in 1987 (Tegner 1989). In spite of this growing importance, it is not known what factors are necessary for successful recruitment into adult sea urchin populations (Ebert 1983, Tegner & Levin 1983, Harrold & Pearse 1987, Raymond & Scheibling 1987, Hart & Scheibling 1988, Rowley 1989).

To better understand the factors influencing recruitment into adult sea urchin stocks, the growth and mortality of newly settled purple sea urchins *Strongylocentrotus purpuratus* Stimpson were examined. Growth and mortality were studied in the field in both kelp-bed and sea-urchin dominated barren-ground (barrens) habitats, and in the laboratory on substrata representative of each of the 2 habitats.

## STUDY SITES AND METHODS

Most of the field work was conducted between 1985 and 1987 by SCUBA diving at Naples Reef, an isolated outcrop of shale located 1.6 km offshore and 23 km west of Santa Barbara, California (34°25' N, 119°57' W; Ebeling et al. 1985). Study sites included a low-relief saddle area, which has remained a barrens since at least 1984 (pers. obs.), and an adjacent area of higher relief, which has supported a stand of the giant kelp *Macrocystis pyrifera* and associated benthic cover for the same period. The barrens was ca 1000 m<sup>2</sup> in area, at a depth of 10 to 12 m, and was dominated by crustose coralline algae. The coralline algae at this site were identified by R. S. Steneck and reported in Breitburg (1984), and include the genera *Lithothamnium*, *Lithophyllum*, and *Pseudolithophyllum*. The kelp bed covered ca 10 500 m<sup>2</sup>, was 1 to 2 m shallower, and was dominated by a turf of foliose red algae (commonly *Rhodomenia californica*, *Gigartina* spp. and *Gymnogongrus* sp.) and associated invertebrates.

Densities of *Strongylocentrotus purpuratus* differed greatly between the 2 sites. The barrens was maintained by a high density of small, exposed sea urchins, while the kelp bed supported fewer, larger sea urchins, mostly sheltered in cracks and crevices (Rowley 1989).

To take advantage of a clear and abrupt border between kelp-bed and barrens habitats, Coal Oil Point,

8 km east of Naples Reef, was chosen for a mark-recapture study. Marked sea urchins were transplanted in 1983 to sites located on either side of the barrens/kelp bed boundary at 8 m depth.

Water temperatures were recorded daily at the intake to the UCSB Marine Laboratory seawater system and are reported as mean  $\pm$  1 standard deviation of the midpoints between daily minimum and maximum values. The laboratory is located 12 km east of Naples Reef and 4 km east of Coal Oil Point.

**Growth in the laboratory.** To obtain newly settled individuals, larvae of *Strongylocentrotus purpuratus* were reared in the laboratory and settled on several types of natural substrata (Rowley 1989). Approximately equal numbers of such individuals were added to the following treatments: (1) Coralline algae – small cobble rocks (5 to 7 cm maximum dimension) encrusted with crustose coralline algae; (2) Coralline algae + kelp – identical to Treatment 1, except that kelp *Macrocystis pyrifera* blades were cut into 1 to 2 mm pieces and added throughout rearing; (3) Turf – small rocks covered with foliose red algae including *Rhodomenia californica*, *Gigartina* spp., and *Gymnogongrus* sp.; (4) Bare rock – rock pieces without visible algae, but presumably supporting a natural microbial (bacterial) film.

These individuals (3 to 5 d old initially) were maintained for 100 d in the laboratory on the natural substrata in flowing seawater. The only food available was the natural growth on these substrata, and the kelp added to the kelp addition treatment. Water temperature in the laboratory generally stayed within 1°C of field water temperatures.

All substrata were collected at Naples Reef and cleaned of mobile invertebrates before use. Each treatment had ca 64 cm<sup>2</sup> projected surface area of substratum, resulting in initial sea urchin densities of roughly 15 to 40 ind. 200cm<sup>-2</sup>, which is within the range of densities recorded in the field (Rowley 1989). Sea urchins that settled on algal turf or rock were reared on the same substratum, with their numbers augmented with individuals chosen haphazardly from those settled on coralline algae. The 2 coralline algal treatments used only sea urchins that had settled on coralline algae. Two replicates of each treatment were reared.

Sea urchin sizes were recorded as test diameters measured in  $\mu$ m. All data were transformed to log (diameter) because the change in biomass with diameter is better described logarithmically than by an arithmetic function (Tessier 1960). Day 50 corresponded to a shift in diet and a major acceleration in growth in the 2 fleshy-algae treatments. For this reason data for 0 to 50 d were analyzed separately from data for 50 to 100 d.

Statistical analysis was complicated by inability to measure individual growth rates: there is no method developed for marking newly settled sea urchins. This ruled out the use of analysis of individual variance or covariance. To compare change in size of sea urchins in the 4 treatments over the 2 time periods, the mean sizes were adjusted to be equal at the beginning of each time period. Significant differences in mean sizes at the end of each period were tested for using a single-factor analysis-of-variance with Scheffe' comparisons of means (Sokal & Rohlf 1981). This was done separately for each period: 0 to 50 and 50 to 100 d. Because the 2 replicates within any treatment were not significantly different (2-tailed t-tests, each  $p > 0.05$ ), the replicates were pooled for analysis.

**Size-frequency analysis.** To collect newly settled sea urchins from kelp-bed and barrens habitats, pieces of the reef shale were broken free, complete with resident flora and fauna. Samples were collected haphazardly and each was immediately sealed in a plastic bag. The anesthetic magnesium chloride was used to ease the removal of small sea urchins and other microinvertebrates from the samples (L. G. Harris pers. comm., Rowley 1989). This was added in excess (ca  $100 \text{ g l}^{-1}$ ) to each bag. After the fauna were obviously anesthetized (ca 2 h) all mobile animals were rinsed off each sample, collected onto a  $243 \mu\text{m}$  mesh filter and preserved with 5% buffered formalin. Any sea urchins found were identified and measured ( $\pm 20 \mu\text{m}$ ). Several samples of each type of substratum were destructively searched very thoroughly after being rinsed, and no sea urchins were found that had been missed by the magnesium chloride sampling. Each substratum was mapped onto a clear plastic sheet from which the area sampled was measured (Rowley 1989). Numbers of each sea urchin species on each type of substratum for each date sampled were plotted in size-frequency histograms. The sea urchins collected were estimated to be 5 to 17 d old (post-settlement) when first sampled on 9 May 1986 (Rowley 1989).

In order to statistically compare estimates of cohort growth and mortality it was necessary to know the size limits of the cohort for each date. The size limits used for this analysis were set by eye based on the 95% confidence limits of a presumed normal distribution of sizes around the mean, using probability paper analysis as a graphic aid (Harding 1949, Cassie 1954). The limits were adjusted to exclude a presumed younger cohort indicated by new settlement apparent in both habitats on 2 June. See 'Discussion' for a justification of the cohort size limits.

Using these estimates of cohort size limits, calculations are made of the change in mean size of sea urchins in the cohort over time, which is interpreted as growth. Growth rates are compared between the 2

habitats using a 2-tailed t-test of slopes of the linear regressions of  $\log_{10}$  (sea urchin test diameter) versus time (Snedecor & Cochran 1967).

The density of sea urchins in the cohort was calculated for each sample and standardized to reflect a sample size of  $200 \text{ cm}^2$ , which is close to the size of the samples taken. Since samples included all microhabitats, and individuals were too small to emigrate from the study site, the change in density over time was a measure of the mortality of sea urchins within the cohort. Mortality rates between the 2 habitats were compared using a 2-tailed t-test of slopes of the linear regressions of  $\log_{10}$  (sea urchin density) versus time (Snedecor & Cochran 1967).

**Tetracycline mark-recapture study.** In order to compare growth of slightly larger sea urchins between kelp-bed and barrens habitats, 2 to 10 mm diameter *Strongylocentrotus purpuratus* were marked, released, and recaptured. Sea urchins were collected from the barrens at Coal Oil Point, brought into the laboratory, and injected with tetracycline hydrochloride (modification of the method of Ebert 1977, 1980, 1982). Individuals were injected through the peristomial membrane with 0.01 to 0.05 ml of a solution of  $2 \text{ g tetracycline HCl l}^{-1}$  seawater, using either a small hypodermic needle or a micropipette injection system. The sea urchins were held in a bath of  $0.05 \text{ g tetracycline HCl l}^{-1}$  seawater for 1 d prior to and 1 d after being injected. After marking, sea urchins were divided into groups of 20 individuals, randomly assigned to treatments and transplanted to the field sites. Seven groups were transplanted to sites in the barrens and 2 groups to sites in the kelp bed. Each field site was marked with a metal post glued into the rock. To maintain natural densities where possible, 20 small sea urchins were removed from around the post before individually placing the marked sea urchins within a  $0.25 \text{ m}^2$  circle centered on the post. This procedure retained natural densities in the barrens habitat, but resulted in higher than normal densities in the kelp bed, where small sea urchins were naturally rare. After periods of 44 to 126 d, all sea urchins within a  $1 \text{ m}^2$  circle centered on each post were collected, and their tests were cleaned in a dilute solution of sodium hypochlorite.

Tetracycline is incorporated at sites of active calcium deposition and fluoresces under ultraviolet light (Kobayashi & Taki 1969), so the growth sutures of the sea-urchin tests were marked. Following growth, the lines of incorporated tetracycline parallel the sutures and are separated by sea-urchin test material added since marking (Fig. 1). Thus, growth can be measured as a function of the distance between the fluorescent lines at the level of the greatest diameter (ambitus) of the test. The distance between fluorescent lines was measured for 3 sutures, and the mean of these measurements was multiplied by the total number of sutures in a test (20) to

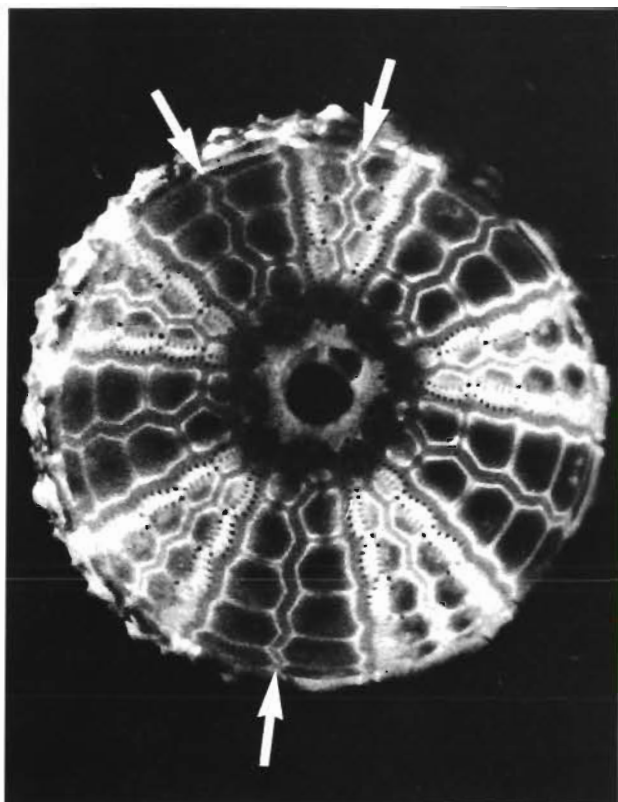


Fig. 1. *Strongylocentrotus purpuratus*. A tetracycline-marked sea urchin photographed under fluorescent light. The oral surface of the test has been removed, revealing the inside of the aboral surface. The growth sutures do not appear, but are located between the parallel, fluorescent tetracycline lines.

Three sets of fluorescent lines are marked with arrows

estimate the change in circumference of the test since marking. This was converted to change in diameter and standardized to reflect growth per 30 d. Differences in growth between habitats were tested for using a single factor analysis of variance and means were compared using SNK tests (Sokal & Rohlf 1981). Since there were no statistically significant differences between replicates within treatments (2-tailed t-tests; overall  $p > 0.05$ ), replicates were pooled for analysis. The effect of size on growth rate was examined using linear regressions of growth rate versus initial size.

An alternate method would be to measure the tetracycline marks at the point of maximum separation of the fluorescent lines, instead of at the ambitus of the test. Because the position of the ambitus shifts during ontogeny, this point differs slightly from the position of the ambitus at the end of the outplant period. This method results in growth rate estimates 25% higher than the estimates presented here, and increases the estimated sizes at Yr 1 by 19%. The ambitus measure was used because preliminary studies suggested that it was the more accurate.

## RESULTS

### Study sites

Naples Reef barrens supported a density of  $135 \pm 62$  ind.  $m^{-2}$  (mean  $\pm$  95% CI) *Strongylocentrotus purpuratus* compared to  $23 \pm 7$  ind.  $m^{-2}$  in the kelp bed ( $p < 0.001$ ). The Coal Oil Point site had an *S. purpuratus* density of  $84 \pm 67$  ind.  $m^{-2}$  in the barrens and  $6 \pm 15$  ind.  $m^{-2}$  in the kelp bed ( $p < 0.05$ ) (Rowley 1989).

### Growth in the laboratory

In the laboratory, *Strongylocentrotus purpuratus* grew at a rate of 0.29 to 0.45 mm  $mo^{-1}$  on all substrata over the first 50 d, with no significant differences in growth between treatments ( $F_{3,54} = 1.165$ ;  $p = 0.33$ ) (Fig. 2; Table 1). During this period the sea urchins

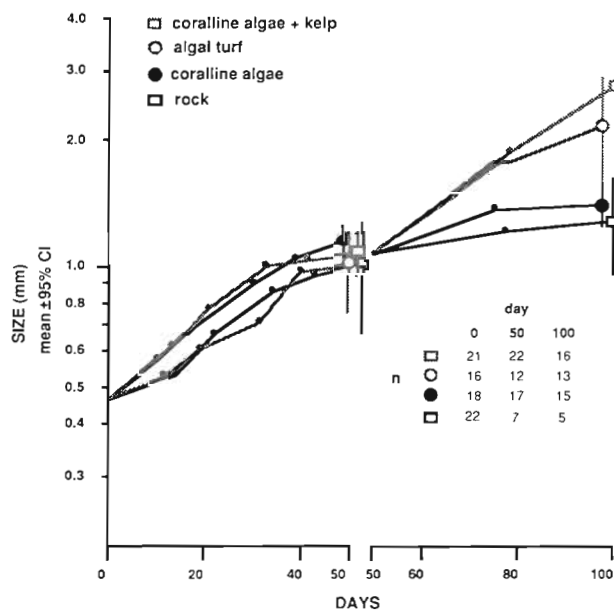


Fig. 2. *Strongylocentrotus purpuratus*. Growth of newly settled sea urchins at natural densities on substrata in the laboratory. Mean sizes at the beginning of each time period (0 to 50, 50 to 100 d) were adjusted to be equal (see text). Numbers of urchins found on each treatment are indicated for Days 1, 50, and 100

apparently fed by superficial scraping of the substrata because each sea urchin was surrounded by a small area from which the surface film (from rock or foliose algae) or the epithallial cell layer (from coralline algae) had been removed, apparently by the sea urchins' grazing.

Sea urchins in the coralline + kelp treatment were first observed holding and eating pieces of kelp on Day

Table 1. *Strongylocentrotus purpuratus*. Summary of growth rates of small sea urchins as determined in this study, and compared to published data. Statistical comparisons were made only within a particular method and age range – as shown by the brackets. Within each comparison, different letters in the 'Stats' column denote significant differences ( $p < 0.05$ ) in growth rate

Sizes sampled (approximate)	Growth rate (mm mo <sup>-1</sup> )	Stats	Method	Food available	Lab/field	Source
0.5–1.0 mm	0.3	a	Individual measurement (0–50 d)	Algal turf	L	This study
	0.4	a		Coralline algae + kelp	L	This study
	0.5	a		Coralline algae	L	This study
	0.3	a	Size-freq. analysis	Microbial film on rock	L	This study
	0.3	b		Algal turf (kelp bed)	F	This study
	0.4	a		Coralline algae (barrens)	F	This study
0.8–2 mm	0.6	a	Individual measurement (50–100 d)	Algal turf	L	This study
1–3 mm	1.2	a		Coralline algae + kelp	L	This study
1–1.5 mm	0.2	b		Coralline algae	L	This study
1 mm	0.1	b		Microbial film on rock	L	This study
2–10 mm	1.64	b	Tetracycline mark recapture	Algal turf (kelp bed)	F	This study
2–10 mm	0.25	a		Coralline algae (barrens)	F	This study
5–9 mm	1.8–2.6		Individual measurements	Microbial film	L	Pearse et al. (1970)
5–20 mm	2.3		Individual measurements	Kelp	L	Pearse et al. (1986)
10–60 mm	1.7		Individual measurements	Kelp	L	Pearse et al. (1970)
15–60 mm	0–2.1		Tetracycline mark recapture	Kelp	F	Ebert (1977)

30. The proportion feeding on kelp increased until by Day 50 nearly all individuals were eating kelp. Similarly, the sea urchins on algal turf substrata began eating the fleshy red algae during the same period.

During the second period (50 to 100 d), the sea urchins grew at similar, rapid rates in the 2 treatments containing foliose algae (turf, and coralline algae + kelp) at a rate of 0.56 to 1.16 mm mo<sup>-1</sup> (Fig. 2; Table 1). In both treatments without fleshy algae (coralline algae and rock) sea urchins grew at significantly slower rates, 0.12 to 0.23 mm mo<sup>-1</sup>, with little difference in growth on the 2 substrata ( $F_{[3,45]} = 24.5$ ;  $p < 0.001$ ) (Fig. 2; Table 1).

Although growth rates on coralline algae and rock were nearly constant over the 2 periods, the growth rates on fleshy algae increased substantially during the second period (Fig. 2).

Water temperatures during rearing (8 March to 15 June 1986) averaged  $13.5 \pm 1.2^\circ\text{C}$ .

#### Growth of the size-frequency cohort in the field

The size-frequency histograms of *Strongylocentrotus purpuratus* from both barrens and kelp-bed habitats (Figs. 3 and 4) show a clearly defined mode on 9, 13, and 20 May, and 2 June 1986. The mode is less clearly defined on 19 and 24 June 1986. New settlement is evident in the kelp-bed histogram for 2 June, and the size limits used in the analyses were adjusted to exclude those individuals (see arrows in Figs. 3 and 4).

Growth rates of newly settled *Strongylocentrotus purpuratus* in the field were very similar to rates measured in the laboratory from 0 to 50 d (Table 1). In the field, however, the difference between the treatments was statistically significant, with growth faster in the barrens (0.42 mm mo<sup>-1</sup>) than in the kelp bed (0.31 mm mo<sup>-1</sup>) ( $t_{[556]} = 6.23$ ;  $p < 0.01$ ) (Fig. 5; Table 1).

The sensitivity of these results in respect to the specific cohort size limits used was explored by recal-

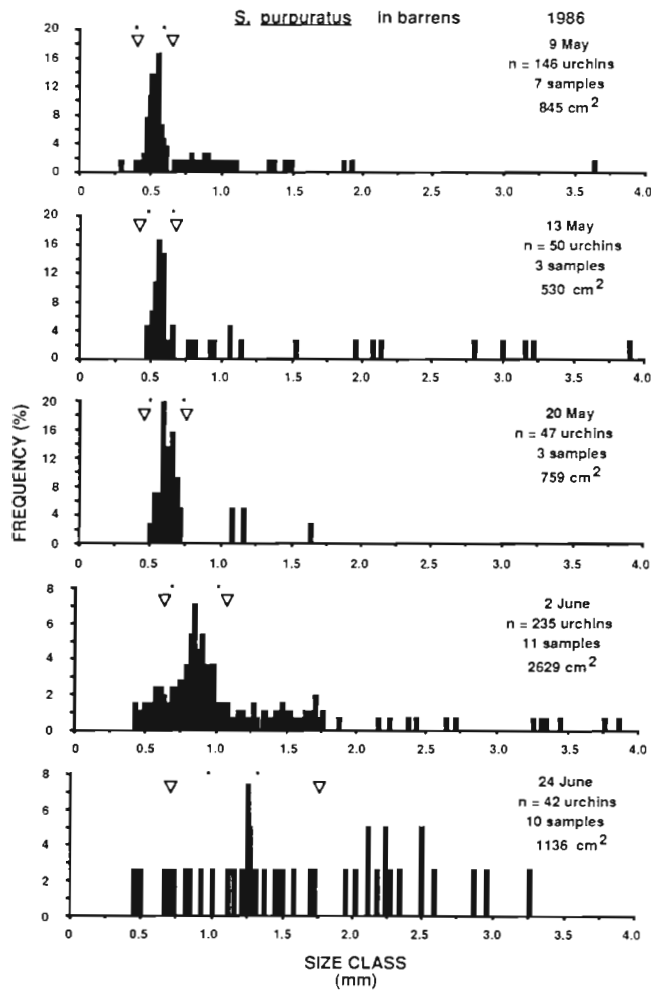


Fig. 3. *Strongylocentrotus purpuratus*. Size-frequency histograms of newly settled sea urchins in the barrens. Arrows mark the subjectively-determined cohort size limits, asterisks mark the limits set by comparison with laboratory growth data

culating the growth and mortality comparisons using (1) size limits determined independently based on the laboratory growth data (paired asterisks in Fig. 3 and 4), and (2) an expansion of the field-based size limits suggested by the data (unpaired asterisk in Fig. 4). These changes made little difference in either the direction or statistical significance of the results (see 'Discussion').

Water temperatures during the sampling period (9 May to 25 June 1986) averaged  $14.2 \pm 1.2^\circ\text{C}$ .

#### Growth of tetracycline-marked sea urchins in the field

Marked sea urchins were recovered from all outplant sites. Recovery rates ranged from 15% (3/20) to 55% (11/20) with no significant difference between the 2 habitats ( $p > 0.05$ ). Neither recovery rates nor growth rates varied significantly with increasing time in the

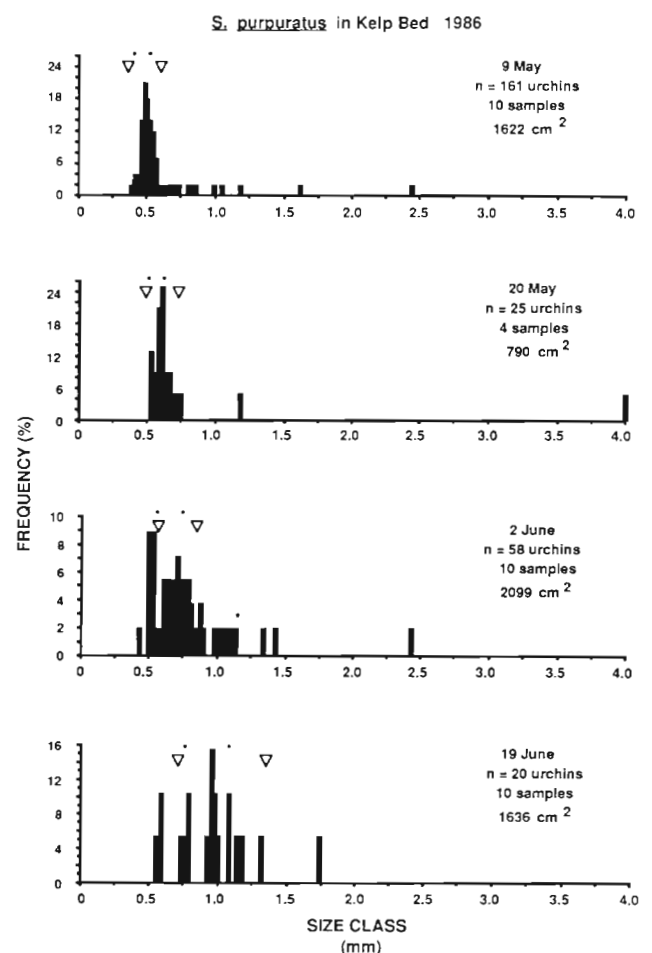


Fig. 4. *Strongylocentrotus purpuratus*. Size-frequency histograms of newly settled sea urchins in the kelp bed. Symbols as in Fig. 3. Single asterisk marks the extended upper size limit (see 'Discussion')

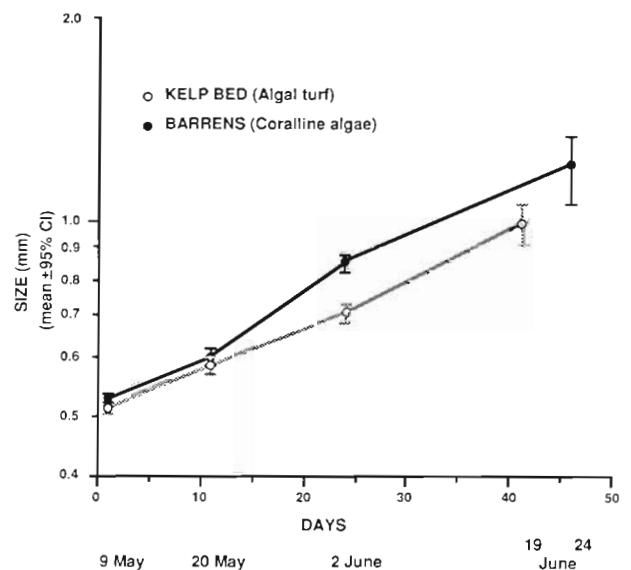


Fig. 5. *Strongylocentrotus purpuratus*. Growth of a cohort of newly settled sea urchins in kelp bed and barrens



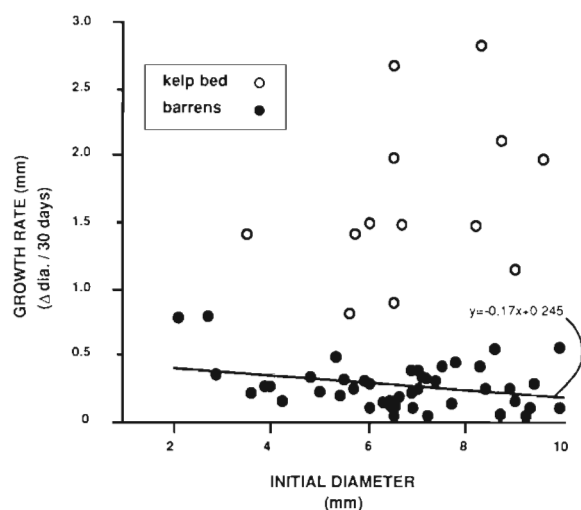


Fig. 6. *Strongylocentrotus purpuratus*. Growth rates of 2 to 10 mm diameter sea urchins in kelp bed and barrens, as determined by tetracycline marking. Formula for the regression of the barrens data is shown ( $p < 0.05$ )

field. There were no significant differences in growth rates among the 7 barrens sites, or between the 2 kelp-bed sites, but growth in all barrens sites was significantly different than growth in either kelp-bed site ( $F_{(8,59)} = 33.33$ ;  $p < 0.001$ ).

In contrast to growth of newly settled sea urchins, growth rates of these larger (2 to 10 mm) individuals were significantly faster in the kelp-bed than in the barrens habitat. This resulted from a dramatic increase in growth at larger sizes (2 to 10 mm) in the kelp-bed habitat (average growth rate of  $1.67 \text{ mm mo}^{-1}$ ), with no comparable change in the barrens ( $0.27 \text{ mm mo}^{-1}$ ) (Fig. 6; Table 1). Within the 2 to 10 mm size range tested, growth rate tended to decrease with increasing size in the barrens (slope of the regression significantly different than zero;  $p < 0.05$ ) but not in the kelp bed (Fig. 6).

Water temperatures during the outplant (11 August 1983 to 24 January 1984) averaged  $17.3 \pm 2.0^\circ\text{C}$ .

### Mortality

Mortality of the newly settled *Strongylocentrotus purpuratus* in the field cohort was higher in the kelp bed than in the barrens (Fig. 7) ( $t_{(62)} = 2.06$ ;  $p < 0.05$ ). Mortality was highest at the beginning of the sampling period, when the difference in mortality between habitats was also greatest. Ancillary samples taken in the barrens on 13 May (using different methods and not presented here) suggest that the highest mortality may have occurred very soon after 9 May, with densities on 13 May as low as later sampled on 20 May. Whether the same pattern held for the kelp bed is not known.

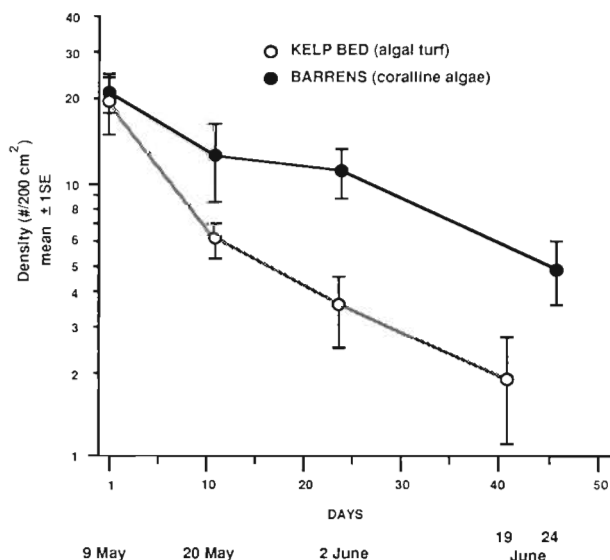


Fig. 7. *Strongylocentrotus purpuratus*. Mortality (change in density) of a cohort of newly settled sea urchins in kelp bed and barrens

## DISCUSSION

### Rationale of size-frequency analysis

The long-standing problem of how to distinguish modes or cohorts within a size-frequency histogram has been approached in several ways (Harding 1949, Cassie 1954, Macdonald & Pitcher 1979, Grant et al. 1987). However, all these approaches are at least partially subjective, or require sample sizes that are often unrealistically large (Grant et al. 1987). Since in this analysis there is generally only one mode present, the main difficulty involves setting the size limits of that mode. My approach has been to set the size limits to the mode subjectively (see 'Methods'), and support those limits with the following comparisons.

(1) To explore the sensitivity of my results to the specific cohort size limits used, a second set of size limits was created based on the 99 % confidence limits to sea urchin sizes derived from the coralline and turf treatments of the laboratory growth data. For example, the mean size of sea urchins grown on coralline algae in the laboratory was computed for each sampling date along with the 95 % and 99 % confidence limits. The data were then adjusted slightly so that the mean size of the laboratory sea urchins on Day 1 equalled the mean size on the field cohort in the barrens on 9 May. This single adjustment was used for all comparisons of all dates. The 9 May barrens size-frequency histogram (Fig. 3) shows a very clear mode with easily-defined limits. The best fit to these observed limits was the 99 % confidence interval of the laboratory data, so the 95 %

confidence limits were discarded and the 99 % limits were used. The second field sample was taken 4 d later (13 May) and so corresponds to Day 5 of the laboratory data. Therefore the 99 % confidence limits for Day 5 were interpolated from the laboratory graph and positioned on the size-frequency histogram of field data for 13 May. Size limits based on the laboratory data were similarly estimated for all treatments and dates. The limits so defined are shown by the asterisks in Fig. 3 and 4.

The independently-derived size limits based on the 99 % confidence limits of the laboratory growth data are similar to the subjectively-determined limits. The main difference between them is that the laboratory data are less variable. This is not surprising given the more constant conditions in the laboratory. The similarity in the ranges of sizes enclosed by these 2 sets of limits suggests that the variation in sea urchin sizes reflected by the subjective limits is a realistic estimate of natural variation of sizes in a cohort of sea urchins. The correspondence in the position of these 2 sets of size limits reflects the nearly identical growth rates measured in the field and laboratory.

The 2 methods of setting the cohort size limits gave similar results; there were no differences between the 2 methods in the ranking of growth or mortality rates in the 2 habitats. All results presented are significant to at least a 0.05 probability level using either method, with the exception that the significance of the difference between mortality rates in the kelp bed and barrens was reduced to  $< 0.10$  using the laboratory-defined limits. The results from the subjectively-defined cohort limits based exclusively on field data are presented here because they are the more conservative in terms of recognizing a difference in growth rate between habitats.

(2) The data from 19 and 24 June (see Figs. 3 and 4) show the least well defined modes and thus the most subjectively determined limits. However, all the results remain the same, in both rank order and statistical similarity, even if the size limits for 19 and 24 June are expanded to include the entire size scale (0 to 4.0 mm).

(3) Modes of the kelp-bed data of 20 May and 2 June appear to be skewed to the right, while the data from 9 May were not (see Fig. 4). This suggests that some individuals may be outgrowing the main cohort, beyond the cohort size limits. That a few individuals can show accelerated growth appears reasonable in light of the observed rapid growth of larger individuals on turf and in the kelp bed. Yet increasing the upper size limit for 2 June to include these outliers (to the unpaired asterisk in Fig. 4) did not alter either the rank order or statistical similarity of the results.

Thus the results presented appear to be robust in respect to relevant changes in the cohort size limits.

## Growth

The growth of newly settled *Strongylocentrotus purpuratus* may constitute 2 distinct stanzas separated by a transition in feeding mode. During the initial period from settlement to roughly 50 d old (0.8 to 1.2 mm diameter) feeding appears to be limited to surface scraping. Growth in the laboratory is similar on kelp-bed or barrens substrata; growth in the field is slightly faster in the barrens. Sea urchins in the laboratory removed either the surface film and filamentous epiphytes from algal turf, or a crustose, pale layer presumably of epithallial cells from coralline algae. Sea urchins did not hold or feed on available pieces of kelp or algal turf for most of this period.

After reaching an apparent threshold size of 0.8 to 1.2 mm diameter (30 to 50 d old), sea urchins first began feeding on kelp or algal turf, if available. In the laboratory, individuals first held pieces of kelp on Day 30; by Day 50 most sea urchins were feeding in this way in treatments where fleshy algae were available.

Once a sea urchin reaches this threshold size or age and begins eating fleshy algae, the food supply available to it increases enormously. Thus growth in the kelp bed (or on algal turf) was as much as 6 to 7 times faster than in the barrens for sea urchins beyond the threshold size and up to at least 10 mm in diameter.

For sea urchins beyond the threshold size living in the barrens, neither food supply nor growth rate shows such an increase. In fact, food may become increasingly limiting at larger sizes, as suggested by the negative relationship between size and growth rate in the barrens.

The growth rates measured here (summarized in Table 1 and Fig. 8) are very similar to results obtained by Raymond & Scheibling (1987) for newly settled green sea urchins *Strongylocentrotus droebachiensis* Muller in Nova Scotia, Canada.

A similar pattern of slow growth soon after settlement with more rapid growth following a transition to the adult diet was described for the asteroid *Acanthaster planci* (L.) (Yamaguchi 1973, Zann et al. 1987). Newly settled *Acanthaster* feed by everting their stomachs onto substrata and digesting the microbial or algal film. At larger sizes they switch to the adult diet of feeding on coral polyps and growth rate increases (Yamaguchi 1973, Zann et al. 1987).

The size of sea urchins at an estimated age of 1 yr is a measure commonly used in studies of recruitment and community organization (for sea urchins, Ebert 1967, 1968, Tegner & Dayton 1981, Ebert 1983, Himmelman et al. 1983). Estimates of the size of *Strongylocentrotus purpuratus* at Year 1 have ranged from 16.5 mm, based on the smallest peak in a size-frequency graph (Ebert 1967), to 25 mm, based on back-extrapolation of Ebert's



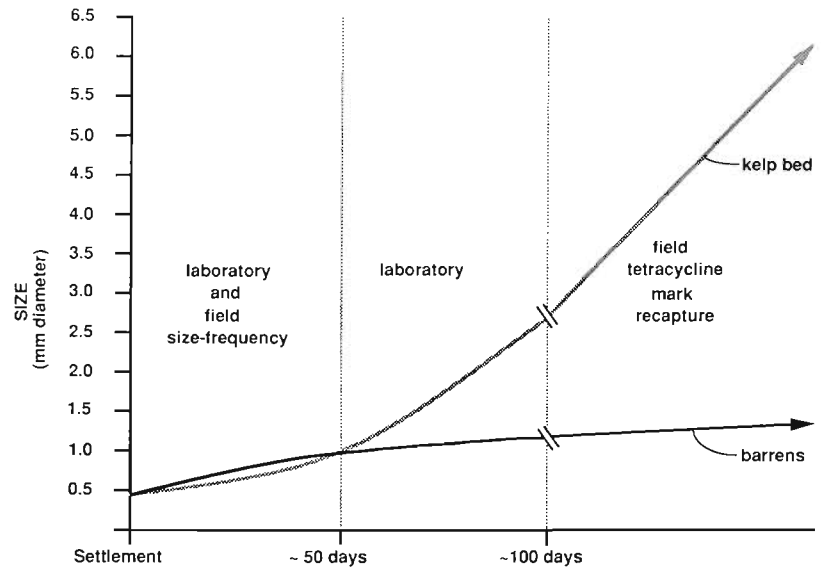


Fig. 8. *Strongylocentrotus purpuratus*. Composite graph of the growth of sea urchins in the kelp bed (or on fleshy algal turf) and in the barrens (or on crustose coralline algae). Approximate age ranges over which growth was measured, and the different methods used, are shown in the 3 sections

(1977) estimate of growth of larger sea urchins (Tegner & Dayton 1981), and 20 to 38 mm based on preliminary analysis of growth rings in sea urchins' tests (Pearse et al. 1970). Each of these methods has limitations: (1) the size-frequency data used did not include sea urchins smaller than 2 to 3 mm, (2) the growth of larger sea urchins differs from the growth of newly settled individuals (this paper) and (3) use of growth lines for ageing sea urchins has since been criticized by Ebert (1988).

Estimates of the sizes of sea urchins at 1 yr of age were calculated using the average growth rate in the laboratory from 0 to 50 d ( $0.375 \text{ mm mo}^{-1}$ ), and the average growth rate with fleshy algae present from 50 to 100 d ( $0.9 \text{ mm mo}^{-1}$ ). Other growth rates used are from Table 1. These calculations provide a Year 1 estimate of 3.6 mm for a sea urchin in a barrens [ $0.4 \text{ mm at settlement} + (0.375 \text{ mm mo}^{-1} \times 1.6 \text{ mo}) + (0.25 \text{ mm mo}^{-1} \times 10.4 \text{ mo})$ ], or 17 mm for an individual in a kelp bed [ $0.4 \text{ mm} + (0.375 \text{ mm mo}^{-1} \times 1.6 \text{ mo}) + (0.9 \text{ mm mo}^{-1} \times 1.1 \text{ mo}) + (1.64 \text{ mm mo}^{-1} \times 9.3 \text{ mo})$ ] (Table 1). These values agree well with the estimate of 16.5 mm for sea urchins in tidepools presumably eating macroalgae (Ebert 1967), but are somewhat smaller than the others.

The range of estimates of size at Year 1 does not appear to be due to geographic variation in growth rates. While the higher estimates are all from warmer locations, where growth is presumably faster if temperature dependent, a large body of physiological research (reviewed by Vernberg 1962) has documented latitudinal compensation, with organisms at higher latitudes and colder temperatures showing metabolic rates similar to related organisms in more tropical regions. Dehnel (1955) extended this to growth rates by documenting faster growth in snail larvae at higher

latitudes. That sea urchin growth may show little variation with latitude is suggested by the results of Raymond & Scheibling (1987). They found no effect on growth rates of newly settled green sea urchins *Strongylocentrotus droebachiensis* of a large difference in rearing temperatures ( $5$  vs  $16^\circ\text{C}$ ). Also, Swan (1966) reported that both purple sea urchins *S. purpuratus* and red sea urchins *S. franciscanus* grew at nearly identical rates at Friday Harbor, Washington and San Diego, California, USA.

Yamaguchi (1975) explored the consequences of estimating the growth of marine invertebrates based solely on measured of adults without consideration of an early 'lag phase' of growth such as is described here. He concluded, in part, that failure to recognize the uniqueness of early growth... 'would lead to a serious underestimate of age or overestimate of early growth'. While this conclusion was challenged by Ebert (1982), my results support Yamaguchi's interpretation (pointed out to by T. A. Ebert pers. comm.), and the differences between my estimates and the others may reflect the bias caused by estimating growth of newly settled invertebrates based on study of larger individuals.

The general growth pattern described here – of a threshold size at which a juvenile switches to a different (adult) mode of feeding – applies to a variety of invertebrate taxa (abalone: Morse et al. 1979, Shepherd & Turner 1985; *Aplysia*: Sarver 1979; starfish: Birkeland et al. 1971, Yamaguchi 1973, 1974, 1975, Barker 1979, Zann et al. 1987). Young of several of these taxa associate with crustose coralline algae (Barnes & Gonor 1973, Yamaguchi 1973, Barker 1979, Morse et al. 1979, Shepherd & Turner 1985, Zann et al. 1987), presumably because such algae slough the epithelial cell layer thereby providing food for these surface-feeding micro-grazers (Steneck 1986). However, few of these species feed predominantly

on coralline algae as adults, and so must switch to their adult food source. Since this switch may strongly affect growth rate (and thereby, indirectly, mortality), the attainment of a size at which the switch can occur may be a critical event in the life-history of these species.

### Mortality

Mortality of newly settled sea urchins was higher in the kelp-bed than in the barrens habitat. Yet, due to faster growth, the kelp-bed sea urchins more rapidly reached the larger sizes at which the risk of mortality, is, presumably, reduced. Thus at least 2 conflicting tendencies affect the relative numbers of sea urchins in kelp-bed and barrens habitats, and the present data cannot weigh their relative importance. My results are consistent with the standing hypothesis that numbers of adults are lower in the kelp bed because of higher mortality there (Ebert 1975, 1982, Tegner & Dayton 1977, 1981, Cowen 1983, Ebert 1983, Himmelman et al. 1983, Pearse & Hines 1987, Rowley 1989).

### Mariculture and fisheries

The presence of a size threshold for a change in diet such as described here should be considered in planning transplants of hatchery-reared individuals to augment field stocks or to grow-out facilities, as is done with both sea urchins and abalone (Tegner 1989). Delaying such transplants until seed animals are above the threshold size for eating macroalgae should help ensure more rapid growth and reduced mortality.

### CONCLUSIONS

The growth rate data presented here are the first to follow the growth of sea urchins from metamorphosis through sizes commonly sampled in field studies. While each method used (laboratory rearing, field size-frequency, and field tetracycline marking) is internally consistent, and comparisons within each data set robust, these growth rates should be considered first approximations awaiting confirmation by further study of newly settled individuals. Despite these limitations, these results clearly point out that the patterns of growth and mortality of newly settled invertebrates can be complex, and may not be accurately described by observations of the growth and mortality of larger macroscopic individuals. Therefore, studies focused specifically on the ecology of early life-history stages are essential to our understanding of the mechanisms regulating natural populations in both space and time.

Studies of adult recruitment and community processes necessarily differ in scale from studies of settlement and early post-settlement biology, and there is often little common ground between these 2 types of research. Determination of a threshold size at which the growth process changes abruptly between juvenile and adult patterns could provide the needed common ground; a naturally-defined lower size goal for studies of large juveniles and adults, and an upper size goal for studies of settlers and small juveniles.

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