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Growth Rates of the Sea Urchin *Strongylocentrotus Purpuratus* Related to Food Availability and Spine Abrasion

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mental results to nature depends completely on whether strong preferences occur in nature. These experiments shed no light on this question, but they do emphasize its importance to ecology.

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GROWTH RATES OF THE SEA URCHIN *STRONGYLOCENTROTUS PURPURATUS* RELATED TO FOOD AVAILABILITY AND SPINE ABRASION

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Abstract. A population of the purple sea urchin *Strongylocentrotus purpuratus* Stimpson was studied at Sunset Bay, Oregon. Three sub-populations had different size-frequency distributions. Such differences in size resulted from differences in growth rate and ultimate size. Two environmental components were examined as possibly causing the different rates of growth: a component of "weather" which broke spines, and food availability and consumption. These two components are important in determining growth rate and ultimate size of these animals.

INTRODUCTION

Interest in ecology concerning the problem of regulation or limitation of population biomass needs little documentation. General points of view may be found in Slobodkin (1961), Andrewartha (1961), Nicholson (1954) and Hairston, Smith, and Slobodkin (1960). Most attention has been directed towards forms where limitation is by loss or death of individuals or changes in reproductive capacity; however, biomass also can be regulated by changes in the rates of growth and maximum sizes attained, as indicated in experiments using *Lucilia* (Ulyett 1950) and in a natural population

of the limpet *Patelloidea* (Hodgkin 1960). In both of these studies, food appeared to be a resource in short supply. The following study of a natural population of sea urchins bears directly on the problem of biomass limitation, and, although by no means exhaustive in treatment, indicates the functional roles of a component of "weather" and relative shortage of food in determining the rates of growth and ultimate sizes attained within a population.

I should like to thank Peter W. Frank for his encouragement during this work and for reading and criticizing the manuscript. The growth analysis was done at the University of Oregon Statistical Laboratory and Computing Center on an

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I.B.M. 1620 computer. Portions of the work were supported by NSF Grant GB-977 to Peter Frank.

Animals and areas

Strongylocentrotus purpuratus Stimpson is a regular echinoid of the family Strongylocentrotidae and ranges along the Pacific coast of North America from Alaska to Cedros Island, Baja California, Mexico (Ricketts and Calvin 1962). Over this range it forms a conspicuous element of the benthic fauna and gives the impression in many areas of being the dominant organism. Primarily, it appears to be an herbivore and utilizes algae as its chief food source; however, it is also opportunistic and grazes on attached algae or animals, catches floating debris and moves to large pieces of food such as dead fish.

The area in which these animals were studied was the south side of Sunset Bay, Coos County, Oregon, 43° 20' N. This side of the bay is formed of beds of sandstone which strike north and south and dip sharply to the east. Weathering has produced a series of ridges, flat areas and channels seaward and a relatively flat region towards shore with a boulder field at the north end. Urchins were studied primarily in three areas (Fig. 1)



FIG. 1. Aerial photograph of the south side of Sunset Bay. The top of the picture is south. The three study areas are indicated: boulder field (B), eelgrass area (E), and *Postelsia* zone (P). The scale line is accurate only in the region of the study areas. Tidal height is approximately datum.

which will be referred to as the *Postelsia* Zone, the eelgrass area, and the boulder field. The *Postelsia* zone was a seaward face with small ridges, ledges and pools where urchins inhabited small cavities. Above the urchins was a zone of the sea palm, *Postelsia palmaeformis* Ruprecht 1852, a brown alga found in areas "exposed to full force of the surf" (Smith 1944, p. 142). Two areas were studied in the *Postelsia* zone. One was a pool approximately 2 m long, $\frac{1}{2}$ m wide and $\frac{1}{4}$ m deep. Animals from this pool were measured to produce size distributions and to gather information on rates of feeding. Animal density determined in March 1967 was 140 per m^2 based on two, $\frac{1}{2}\text{-m}^2$ quadrats (actual numbers were 82 and 64). About 2 m from this pool was an area of smaller pools, ridges and ledges. This area was planted with tagged animals to determine growth rates.

The boulder field consisted of blocks of weathered sandstone up to 1–1.5 m diameter and in parts of the field these were several deep. In this region urchins generally did not live in cavities but rather, at low tide, were found at the bases of the boulders. The entire field was protected seaward by a ridge running north and south (Fig. 1). Animal density in March 1967 was 85 per m^2 based on two $\frac{1}{2}\text{-m}^2$ quadrats (actual numbers were 36 and 45). An area about 4 m in diameter was planted with marked urchins to study growth rates. Animals from about 10 m southeast of this area were used for constructing size distributions. In the region between these two areas, sea urchins were used for determining rates of feeding. The eelgrass area has been previously described (Ebert 1967a). Two pools were used in this area. One was approximately 1.1 m above 0 tide and had a surface area of 1.2 m^2 and a maximum depth of 0.25 m. This pool was used to hold tagged individuals. Seven meters further south, another larger (approx. 5 m^2) pool with a maximum depth of .65 m at low tide was used as a source of animals for constructing size distributions and for determining rates of feeding. Animal density in this pool in March 1967 was 200 per m^2 based on four $\frac{1}{2}\text{-m}^2$ quadrats (actual numbers were 115, 94, 85 and 105).

Relatively, the eelgrass area was the highest intertidally (Zone 2 of Ricketts and Calvin 1962), the *Postelsia* zone next (Zone 3) and the boulder field lowest (also Zone 3). The dominant types of vegetation in each area were as follows: in the *Postelsia* zone, *Postelsia palmaeformis*, *Hedophyllum sessile* (Agardh) Setchell 1899, *Gigartina papillata* Setchell 1899, *Hymenocys* sp. and coral-ines; in the eelgrass area, *Phyllospadix scouleri* Hook, *Cladophora* sp., *Spongomorpha* sp., *Ulva*

sp., *Fucus furcatus* Agardh, *Rhodomela larix* (Turner) C. Agardh 1822, *Microcladia borealis* Ruprecht 1851, and *Odonthalia floccosa* (Esper) Falkenberg 1901; and in the boulder field, *Hedophyllum sessile*, *Egria menziesii* (Turner) Areschoug 1878, *Iridaea heterocarpa* (Postels and Ruprecht 1840), *I. flaccidum* (Setchell and Gardner), *Gigartina canaliculata* Harvey 1841, *G. cristata* (Setchell) Setchell and Gardner 1933, *G. papillata* and *Fucus furcatus*. A more complete list is given elsewhere (Ebert 1966). The specific areas were originally selected for study because the subpopulations of urchins appeared to have different size structures with the smallest animals in the *Postelsia* zone and the largest in the boulder field.

Description of the size distributions of urchins at Sunset Bay

Once a year in summer from 1964–1967, size distributions were constructed for each subpopulation by gathering all animals from a small area. Single measurements were taken from the center of an ambulacrum to the opposite interambulacrum. The distributions for all years except 1967 were distinctly bi- or tri-modal (Fig. 2). In 1963, large numbers of newly settled animals were

observed under rocks and particularly under large urchins. The first mode in each distribution of 1964 is this 1963 age class. The positions of this mode in the three distributions indicated that differences in the second mode were possibly due to differences in growth rate rather than age structure. Fusion of this first mode of 1964 with the second mode of large animals by 1967 showed this to be correct. It is also evident that 1963 had exceptionally heavy settling and that other years during the study showed much lower settling success. Also, based on the positions of the modes, it is apparent that 1960 to 1962 and possibly 1959 were years of poor settlement. Such "spotty" settlement is by no means unique in *S. purpuratus* and is found in *Lytechinus* (Moore et al. 1963) and in cockles (Kristensen 1957).

Graphic analysis (Harding 1949) yielded mean values for the component distributions that made up the entire population. The approximation of true means for each component is better for the single age classes than for mixed ages. The determination of means for the small urchins consequently is more accurate than for the larger animals. Accordingly, growth rates for small animals can be adequately determined from the shifts of modes from 1964 to 1967, but shifts of modes

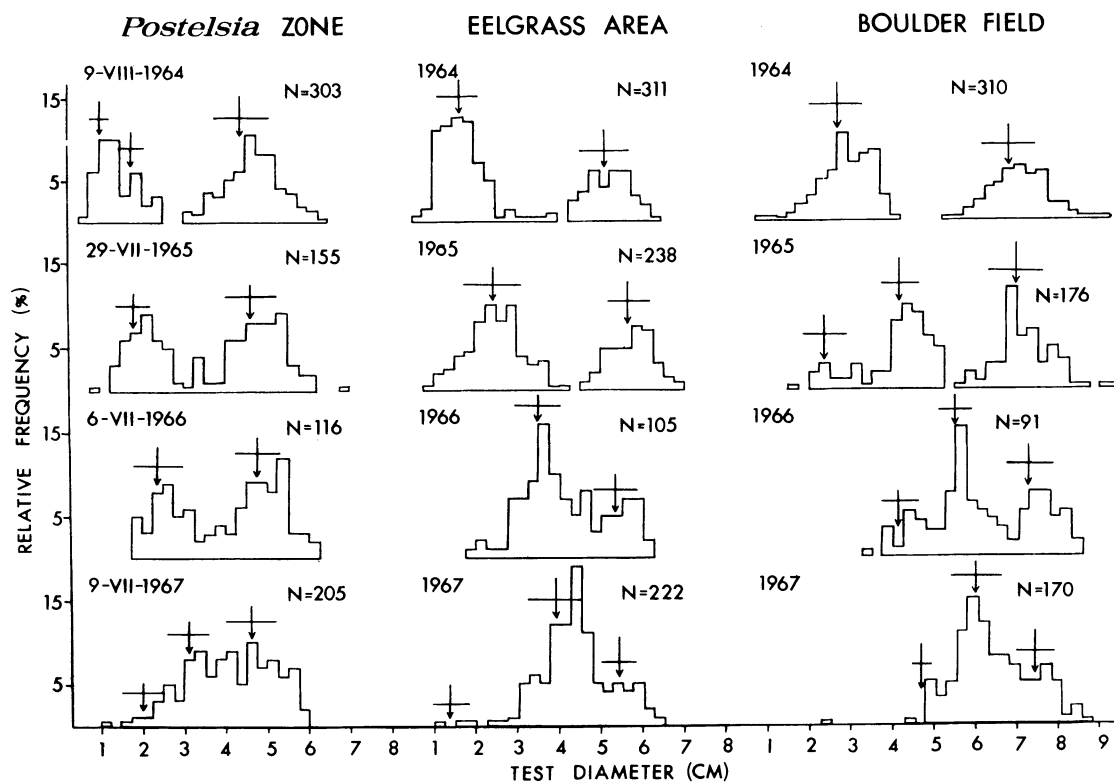


FIG. 2. Size distributions of animals in each of the three areas from 1964 through 1967. Arrows indicate the mean sizes of component distributions and horizontal lines through arrows are standard deviations as determined graphically (Harding 1949).

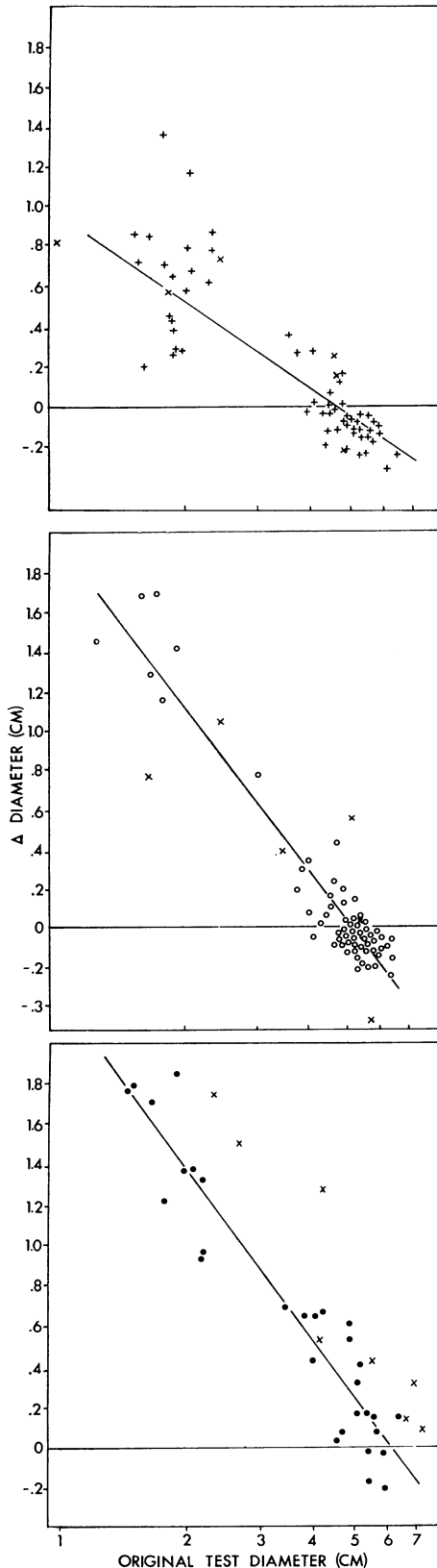


FIG. 3. Diameter changes of marked sea urchins in

for large individuals give questionable values for determining growth rates. Growth rates of large individuals can be better approximated from tagged individuals.

Growth rates determined from tagged animals

In the summer of 1964, 505 animals were gathered at Sunset Bay and tagged using the method previously described (Ebert 1965). Of these, 484 with test diameters from 0.9 to 6.5 cm were collected in the eelgrass area and 21 large individuals with diameters between 6.5 and 8.5 cm were collected in the boulder field. After tagging, the animals were measured five times from the center of each ambulacrum to the opposite interambulacrum. The urchins were distributed among the three areas as follows: in the *Postelsia* zone, animals were placed in cavities, small depressions or under small ledges; in the eelgrass area urchins were placed in cavities within a pool and in the boulder field the animals were placed around the bases of rocks. No attempt was made to assign a definite number per unit area but rather they were placed in sites where urchins either were or had been living. Measurements were again taken in December 1964, March 1965 and July 1965, approximately 1 yr after tagging. Test diameter was again estimated from five measurements.

Of the 505 animals marked in 1964, 164 were recovered in 1965: 63 in the *Postelsia* zone, 71 in the eelgrass area and 30 in the boulder field. Growth rates in the three areas were different (Fig. 3). Animals in the boulder field attained a given size more rapidly than animals in the other two areas. Urchins living in the *Postelsia* zone increased in diameter the least. Variability in growth was greatest for animals living in the *Postelsia* zone; this may have been due to the greater heterogeneity of the living space in this region as previously indicated. The growth equations that can be derived from the regressions of Figure 3 are: $-1.43 \log x_t + x_t + 0.94 = x_{t+1}$ in the *Postelsia* zone; $-2.77 \log x_t + x_t + 1.97 = x_{t+1}$ in the eelgrass area; and $-2.83 \log x_t + x_t + 2.28 = x_{t+1}$ in the boulder field where x_t is the original test diameter in centimeters and the time interval is 1 yr. The above equations are corrected from the form previously published (Ebert 1967a). Growth rate was not constant for the entire year. It was highest during the period from July to December 1964, lowest from December to March and intermediate from March to July.

each area. Time is one year from June 1964 to June 1965. The X's in each graph represent values determined from the shifts in the modes of size distributions (Fig. 2).

Growth of tagged animals in the *Postelsia* zone and eelgrass area is in general agreement with the growth indicated by shifts in the positions of the modes. Growth of marked animals is definitely different from that of unmarked individuals in the boulder field. The area selected for tagged animals was about 10 m northwest of the place where urchins were gathered to determine size distributions, and although the areas appeared to me to be the same, they were not. Unmarked animals grew more rapidly than tagged individuals. Growth of tagged animals in the boulder field is in close agreement with results obtained for caged animals at Friday Harbor, Washington, that were supplied with an abundance of food (Swan 1961).

The positions of the modes of large animals in 1965 (Fig. 2) corresponds with the size of 0 growth determined from tagged individuals from 1964 to 1965 (Fig. 3). In the *Postelsia* zone the 0 growth intercept is 4.54 cm, and the 1965 modal size of large animals is 4.64 ± 0.60 (SD); for the eelgrass area the values are 5.14 cm for the 0 intercept and 5.70 ± 0.52 (SD) for modal size; in the boulder field the 0 intercept is 6.39 cm and the modal size is 6.98 ± 0.67 (SD). The ultimate size attainable in each area is obviously different. I interpret the correspondence of the modal size class and the point of 0 growth to mean that each area has an "optimum" size set by local conditions and that animals grow to this size, enlarge in diameter during "good" years and shrink back to a smaller size (Ebert 1967a) during "poor" years. An "optimum" size is also indicated for *S. intermedius* (Fuji 1967).

Variation in growth rates could be brought about either by genetic factors or by responses to the environment. Essentially all tagged animals come from the eelgrass area, and so a certain amount of control is present. Also, changes in the relative heights of the 1963 age class in the sub-populations indicates that early mortality was the same in all areas and so it is unlikely that there was selection for genetic characters asso-

ciated with growth rate differences. At the present time it is reasonable to assume that, genetically, the subpopulations were indistinguishable. The following analysis suggests the importance of two components of the environment in determining rates of growth.

Exposure as a component of the environment

Animals in the *Postelsia* zone appeared to be more exposed to wave action than urchins in the two other areas. In the boulder field, the animals appeared least exposed. This correlated well with the rates of growth and "optimum" size. Maximum size as a function of exposure has been shown to be inversely related in clams (Brown, Clark, and Gleissner 1938). The nature of the exposure effect at Sunset Bay that is suggested is that animals living in exposed areas would have more spines broken or totally removed. Energy expended on repair would be greater in exposed than in protected areas, and less energy would be directed into test growth. The number of times a spine has been broken can be determined by examining the internal morphology of the spines (Ebert 1967b), and total removal of a spine can be detected by examining tubercles on the test (Swan 1952). Before differences in amounts of regeneration among subpopulations could be meaningfully interpreted, however, it was first necessary to demonstrate that spine breakage could affect the rate of test growth.

On May 24, 1964, 46 small animals were collected at Sunset Bay, brought to the University of Oregon, Eugene, and kept in aerated sea water at 11°C. Thereafter until the experiment terminated, the sea urchins were maintained under somewhat different conditions at various times. However no other systematic differences existed between experimental and control animals. On May 25, the urchins were divided into two groups and measured. In one group, spines were cut to within 2 or 3 mm of the milled ring (the site of muscle attachment). For the entire experiment,

TABLE 1. Effect of spine breakage and regeneration on growth. Experimental animals had spines broken on day 0 and after 65 days. Numbers are 23 animals in each group

Date	Time in days	Experimental			Control	
		Diameter Avg (cm) \pm SD	Wt. before clipping Avg (g) \pm SD	Wt. after clipping Avg (g) \pm SD	Diameter Avg (cm) \pm SD	Weight (g)
5-25-64.....	0	1.61 \pm .32	2.19 \pm 1.24	2.00 \pm 1.16	1.64 \pm .26	2.25 \pm 1.02
6-21-64.....	27	1.61 \pm .32	2.19 \pm 1.30	—	1.66 \pm .27	2.45 \pm 1.17
7-29-64.....	65	1.87 \pm .43	3.49 \pm 2.38	3.25 \pm 2.18	2.05 \pm .30	4.33 \pm 1.91
8-20-64.....	87	1.87 \pm .44	—	—	2.10 \pm .32	—

Failure of the seawater system terminated the experiment. When found, the animals were moribund or dead and had lost spines. Because of this no weights were taken on 8-20-64.

animals were fed the brown alga *Hedophyllum sessile*, either fresh or reconstituted from dried material. Initially, the mean diameters were 1.6 cm in both groups (Table 1). The weights of the animals averaged 2.19 g in the experimental group before the spines were clipped and 2.00 g after. Animals in the control averaged 2.25 g. On June 21 animals were again weighed and measured. No change in mean diameter of animals in the experimental group could be detected, although the mean weight had increased and the animals averaged as much as at the beginning of the experiment (2.19 g). Spine regeneration was noted to have taken place. The control group had increased slightly in both diameter and weight. Spines of the experimental group were not clipped at this time. Spines were again clipped on July 29 when the urchins had a mean diameter of 1.87 cm and averaged 3.49 g. An average of 0.2 g of spines (wet weight) was removed from each animal. The experiment was terminated August 20 because of failure of the sea-water system where the animals were kept. When the animals were found they were moribund or dead and had lost spines. Because of this, animals were not weighed. Test diameters of the animals were measured. Variances could not be distinguished ($F_{21,22} = 1.92$, $P > 0.05$); however, the means were distinct ($t = 1.98$, $df = 43$, $P < 0.05$).

Although individuals were not distinguished during the experiment, an estimate of individual weight changes was made by ranking values for each date and assuming that relative positions did not change. When the change in weight from May through July was considered as a function of the original weight, large animals increased more rapidly than did small individuals. The curve was straightened by plotting the logarithm₁₀ of the change in weight. The means of the experimental and control groups were significantly different by regression analysis ($F_{1,41} = 10.22$, $P < .01$) as was the difference between the two regression lines ($F_{2,40} = 6.61$, $P > .01$). The addition of material in an animal of a given size was greater in the control group than in the experimental group. The experiment suggests that breakage of spines has two effects: one due to channeling calcite into spine repair, the other, less defined, due to slowing the rate of calcite production. Such a decrease in production rate could result from a decreased ability to hold algae affecting feeding efficiency, decreased uptake of nutrients through surface digestion (Pequignat 1966) or even decreased absorption of dissolved organic matter (suggested as a possibility by Leighton, Jones, and North 1966). A combination of these is not ruled out.

The significant conclusion is that spine breakage can result in a decrease in the rate of test growth. Variation in breakage among subpopulations would indicate variations in the amount of energy required from the urchin's total budget for repair and consequently would be important in explaining variation in test growth.

Variation in numbers of breaks in the spines of animals in the field

In August 1964, 85 animals were collected at Sunset Bay: 30 from the *Postelsia* zone, 24 from the eelgrass area and 21 from the boulder field. An attempt was made to gather representatives of all sizes. The animals were cleaned in NaOCl, washed and dried. Five of the largest spines from each animal were impregnated with a mixture of 22 parts terpeneol and 1 part methyl salicylate as suggested by Deutler (1926, originally from Becher 1914). This oil mixture has the same refractive index as calcite and permits internal morphology to be examined without grinding thin sections. Impregnation was facilitated by placing the spines in a vacuum after which they could be viewed with transmitted light under a compound microscope. Breaks were measured with an ocular micrometer. Calculations of quantities lost and regenerated were based on the diameters of the breaks observed in the spines (see Ebert 1967b).

Small urchins in all three areas are apparently similar with respect to number of breaks evident in the spines at a particular size (Fig. 4). If large animals are examined there are differences among the areas with respect to the number of breaks as a function of size. Large animals in the *Postelsia* zone had more breaks per spine than did urchins in the other two areas. Urchins in the boulder

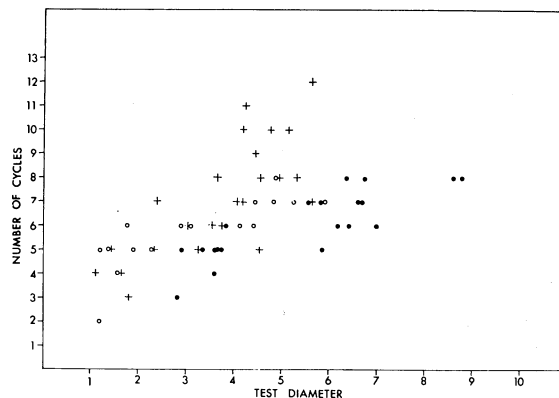


FIG. 4. Number of cycles in large primary spines as a function of test diameter. Each point is the mean of five spines. The three areas are *Postelsia* zone (+), eelgrass area (o) and boulder field (●).

field had the fewest breaks per spine. If, however, number of cycles in spines is plotted as a function of age rather than of size, urchins in all areas were about the same: at age 10 yr, urchins in all areas averaged 7 breaks per spine, at 5 yr the average is 6 cycles per spine, and at 2 yr, urchins in the *Postelsia* zone averaged 4 cycles, in the eelgrass area 5–6 cycles and in the boulder field 5 cycles. Because the urchins at a given age were larger in the boulder field than in the other two areas, a break severe enough to add a regeneration line all the way to the milled ring removed more calcite than did a break in a spine of an urchin of similar age found in the *Postelsia* zone. This will be considered in more detail in the section on total calcite production.

Complete regeneration of spines and variation among urchins of the three areas

In the field, animals not only experience spine breakage but also total removal of spines. In determining the effects of "exposure," regeneration of complete spines must be considered as well as simply spine breakage. Presumably, total removal of spines affects growth in the same manner as does breakage. Total removal of spines can be estimated from cleaned tests by examining tubercle morphology. Swan (1952) showed that when a spine of *S. purpuratus* was completely removed, the associated tubercle became dull and could be distinguished from the shiny tubercles with spines. No rates, however, were given for the loss of shiny luster after a spine was removed or for regaining a shiny luster after spine regeneration. Because such rates were necessary for converting numbers of dull tubercles on an animal into amounts of spines regenerated per year, the following experiment was conducted.

In July 1964, spines were removed from one interambulacrum of each of 70 animals which were then replaced in a tide pool about 15 m south of the eelgrass pool at Sunset Bay. Urchins were collected every day until the tubercles were dull, which required 1 week. Urchins were then collected every month. The tubercles were again shiny in about 4 months. At this time, however, originally treated animals were not easily distinguished from animals in the pool that had not been treated, so the experiment was repeated in 1965 using marked individuals. Again 1 week was required for the tubercles to become dull. After 6 months the tubercles were shiny. The previous sample had been at 4 months when tubercles were still dull. An estimate of 5–6 months for restoration of the shiny luster is reasonable.

Using the sample of 85 animals collected in

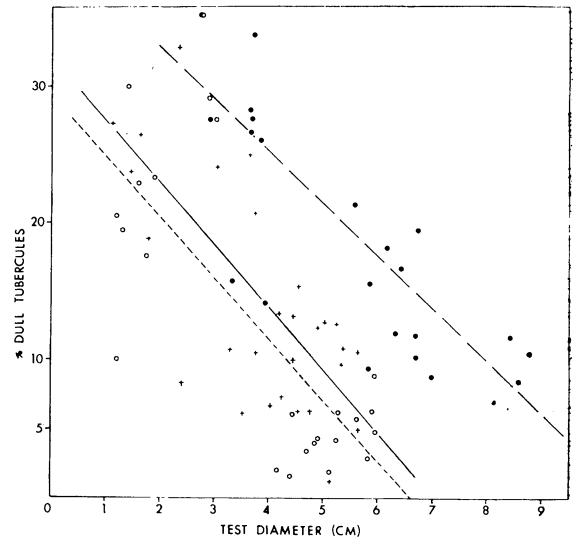


FIG. 5. Percent dull tubercles as a function of test diameter. All primary interambulacral tubercles were examined for each animal. The long-dashed line is the boulder field, the solid line is the *Postelsia* zone and the short-dashed line is the eelgrass area.

August 1964, all primary tubercles of the interambulacra were examined and the numbers that were dull and shiny were recorded. There was a negative association between size and the percentage of dull tubercles (Fig. 5). This is interpreted to mean that during a given time period, small urchins lost more spines than did large animals. This could be brought about if large spines were more strongly attached to the test than were small spines. A particular force great enough completely to rip a spine from a small animal would only break the tip of a primary spine of a large urchin. For any given size, animals in the boulder field had more dull tubercles than did animals in the other two areas. Animals in the eelgrass area had the fewest. Thus urchins in the boulder field lost more spines than did animals in the other two areas and accordingly must have expended more energy in spine replacement.

The component of "weather" which breaks spines or removes them from the test is more severe in the boulder field than in the two other areas contrary to a priori reasoning. This may result from the differences in living space. In the *Postelsia* zone and the eelgrass area, animals live in cavities whereas the urchins of the boulder field were at the bases of the rocks, not in cavities. Although it has been shown that spine breakage and subsequent repair do have an effect upon increase in test diameter, in Sunset Bay such an environmental factor cannot be of major importance in determining differences in growth of the test, but rather would be a modifying force.

The second environmental component examined was the amount of available food. Three methods were employed to estimate the amounts of food in each area: a) using tattooed algae to estimate the quantities eaten in 24 hr, b) gut analysis for differences in quantities of calcareous material, and c) measurement of the amounts of algae held on the spines and tube feet by animals in each area.

Amounts of food eaten in 24 hr in each area

Amounts of food eaten per day in each area were estimated for eight dates from September 1964 to October 1965. A blade of the brown alga *Hedophyllum sessile* was marked with commercial black tattooing ink using a cork with pins shoved through it as the tattooing tool. The blade was coated with ink and the tool was tapped against the surface. After marking, the blade was washed to remove excess ink, cut into small pieces (about $\frac{1}{4}$ cm²) and dried. When feeding was to be estimated, the small algal pieces were reconstituted usually with fresh water. A small group of about 15 individuals was selected in each area and all of these urchins were fed single pieces of marked food. The only disturbance to the animals was touching them with the algae. At the next lower low tide, about 24 hr later, the areas were revisited and 10 urchins from the center of the group were collected. Because no external marks were used to distinguish fed urchins, memory was depended upon to recall animals which had been fed. By selecting individuals from the center of the group, it was felt that all animals collected had been offered a piece of marked algae the previous day. The animals were killed and fixed in the field with an injection of 100% formalin. The amount used varied with the size of the urchins but ranged between 3 and 7 cc. This amount was required to prevent autolysis of the small intestine (terminology of Hyman 1955). Formalin fixation also prevented loss of gut contents by defecation and loss of gametes through spontaneous spawning or "bleeding" during dissection. Other tissues also were toughened thus facilitating dissections. Fixation, furthermore, was necessary because of the time required for dissections. Usually no more than about 30 animals could be processed in 1 week. Animals were preserved in 5% formalin in sea water until ready for dissection, at which time they were first washed in fresh water for 24 hr, damp dried and measured. Animals were then dissected by cutting around the peristome, removing the membrane, and using strong forceps to break away the test plates. Care was taken to avoid rupturing the gut. After

plates were removed as far as the ambitus, the gut and gonads usually could be freed from the test. The gonads were separated from the gut for weighing, and the small intestine was disarticulated from the large intestine and spread out. The esophagus and Aristotle's lantern were placed with the spines and pieces of the test for future weighings. Small sections of gut were cut off, starting at the junction of the small intestine and esophagus, and placed into a water-filled Syracuse dish where the contents were examined for the tattooed algae. When the marked *Hedophyllum* was found, it was removed and discarded. The gut contents oral and anal to the mark were dried and weighed separately. Drying was done in an oven at 110–115°C for 24 hr after which the fractions were cooled in a CaCl₂ desiccator and weighed to the nearest 10 mg. The tests and gut contents were treated with 5% NaOCl to remove the tissue washed in fresh water, dried and again weighed. Gut contents were then treated with HCl to remove CaCO₃, washed, dried and weighed. The information gathered from each animal included: diameter and height (three measurements each), gonad dry weight, total tissue weight other than gonads, calcite weight, and weight of food material and CaCO₃ oral and anal to the marked algae. In the following sections, gonad indices, dry tissue weights, gut contents, and amounts of food eaten in 24 hr all are based on these eight samples of urchins.

Results using the technique to estimate feeding rate were variable in success of recovery of the mark. A major difficulty was the inability to tell without dissection whether an animal had indeed eaten the marked food. Success of recovery varied both with the area and with season (Table 2). The highest recovery rates for the boulder field and eelgrass area were during the winter samples. Poorest recovery was during the summer and fall of 1965. The highest and most consistent success was met with animals from the *Postelsia* zone. For comparing areas and seasons, a ratio was established: $100 \times$ dry weight in grams of organic matter between the mouth and the marked algae divided by the test diameter squared. Urchins at Sunset Bay were primarily debris feeders, catching pieces of algae floating in the water. The ability to catch algae would be a function of surface area and so proportional to the square of the diameter. The factor of 100 was introduced to avoid masses of zeros when the values were graphically displayed (Fig. 6).

I interpret Figure 6 to mean that during the late winter and early spring little food was ingested. Food consumption of animals with 5.00 cm test diameter would have been about 0.05 g

TABLE 2. Recovery success of tattooed algae fed to animals in the field

Season	Postelsia zone		Eelgrass area		Boulder field	
	No. with mark	No. without	No. with mark	No. without	No. with mark	No. without
Fall (9-23-64; 10-23-65)	14	6	15	4	2	14
Winter (11-30-64; 1-29-65)	15	5	12	7	6	11
Spring (3-15-65; 4-11-65)	16	3	17	3	11	9
Summer (6-27-65; 7-31-65)	17	2	7	12	3	17

(dry weight) of algae/day in all three areas. On the graph this is equivalent to the value 0.21 ($0.21 \times 5^2/100 = 0.05$). In June, the animals of the boulder field and eelgrass area were similar and a 5.00 cm animal would have contained 0.39 g of food matter between the mouth and the mark. Animals in the *Postelsia* zone accepted the tattooed algae more readily and the samples from both June and July were pooled to determine a summer rate of feeding. For a 5.00 cm animal in this area, 0.22 g/day would have been eaten. During July, because of poor recovery of marks, little can be said concerning the boulder field and eelgrass area, although the single animal recovered from the eelgrass area which had a mark had eaten more than any other urchin examined from the eelgrass area for all other sampling dates. In the fall, i.e., the September 1964 sample combined with that of October 1965, the values for a 5.00 cm animal were 0.72 g/day in the boulder field and 0.39 g/day in the eelgrass area and the *Postelsia* zone. Generally, the animals in the boulder field ate more than did the animals of the *Postelsia* zone and eelgrass area. The urchins of the *Postelsia* zone and eelgrass area were generally similar but, during the summer, the values were higher in the eelgrass area. This correlates well with algal production during the year. A lush algal cover is present during the summer which breaks down during the fall. The rocks are relatively barren during the winter and early spring before the new growth of algae begins.

The differences in success of recovering animals which had eaten the tattooed algae shows that they were most likely to accept and eat a small piece of algae in the *Postelsia* zone and least likely in the boulder field. This may indicate that more food was available in the boulder field and a small

piece of algae was too small a stimulus to elicit holding and feeding. The degree of hunger has been shown to be related to previous feeding in *S. intermedius* (Fuji 1967).

The marked algae in the gut generally were in the second loop or "large intestine." This rate of movement from the small intestine to the large intestine in 1 day has also been observed in *S. intermedius* (Fuji 1967). According to Farmanfarmanian and Phillips (1962), the major portion of digestion takes place in the small intestine. This means that the weight of food between the marked *Hedophyllum* and the mouth is a low estimate of what was actually eaten in 1 day. The food in the large intestine may be completely digested and the food near the mouth would be in the initial stages. The small intestine appeared to be the likely site of the major portion of digestive enzymes because, without an injection of formalin into the urchin, the lining of the small intestine was severely autolyzed.

Fuji (1962), working with *S. intermedius*, showed that different algae were eaten at different rates. For a 5.00-cm animal the rates varied from about 0.42 g dry wt. of *Laminaria japonica*/day to 0.09 g dry wt. of *Rhodomenia palmata*/day. Moreover, there were seasonal variations in the rate of feeding. The 0.42 g/day of *Laminaria* was in June. When tested in January 5.00 cm *S. intermedius* ate only 0.26 g/day. Leighton (1966) working with *S. purpuratus* from La Jolla, California, showed that when urchins were presented with an abundance of different species of algae, they consistently ate more of certain species. On a wet weight basis, *S. purpuratus* ate more *Macrocystis* from a mixed collection of algae than any other alga. The second choice was *Laminaria*. Leighton's values can be converted to dry weights, using values from Ebert (1966) and approximating the relationships between dry and wet weight as 7.96 for *Egregia*, *Macrocystis*, *Eisenia*, and *Pterygophora*; 7.35 for *Laminaria*; 4.97 for *Cystoseira* and 3.82 for *Gigartina*. With these conversions of wet to dry weight, Leighton's mean value of algae eaten by 10 adult urchins/day is 0.42 g. These urchins ranged from 4 to 6 cm test diameter (Leighton, personal communication). The values of Leighton (1966) and Fuji (1962) compare favorably with the values observed in the field at Sunset Bay. The amounts of food ingested in the boulder field, in the fall of 1964, however, were almost twice those observed as a maximum by Fuji and Leighton.

The variability in amounts measured in animals at Sunset Bay can be ascribed to differences in food preference (Fuji 1962, and Leighton 1966) differences in assimilation rates for the different

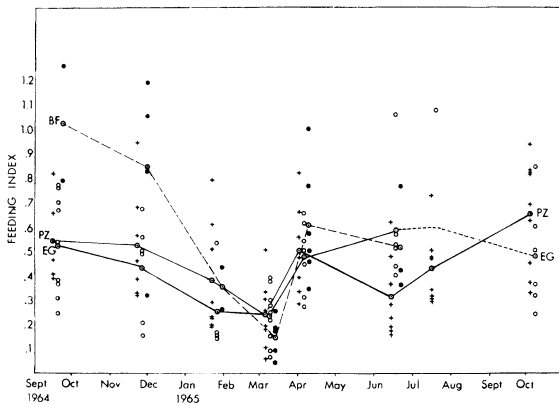


FIG. 6. Estimate of quantity of food eaten in 24 hr from tattooed algae. The weight of organic matter between the tattooed algae and the mouth divided by the animal's diameter squared is plotted as a function of time of year. The lines connect mean values for each sample.

algae (Fuji 1962) and to the stochastic nature of food reception. In any 24-hr period, an urchin may or may not catch a large piece or several pieces of algae. No attempt was made at gut analysis by algal species; however, urchins usually had more than two kinds of algae in the gut between the mouth and the tattooed algae, although it was not uncommon for a single algal species to form over 90% of the total eaten in 24 hr. Size of the algal "bits" would greatly influence the estimate for any 24-hr period, so the variability in Figure 6 is in part explained. Moore and McPherson (1965) indicated the importance of temperature in feeding rate in *Lytechinus*, as did Fuji (1967) with *S. intermedius*. Moore and McPherson, however, also showed that the optimum temperature for greatest feeding shifted during the year to coincide with the ambient temperature, and that the absolute rate at ambient temperature for winter and summer was the same. Temperature is probably unimportant in determining changes of rates of feeding in *S. purpuratus*.

Variation in amounts of calcium carbonate in gut contents of urchins from the three areas

A second method for estimating available food is suggested by the feeding preferences of sea urchins. Lewis (1958) found that *Tripneustes esculentus* refused to eat algae high in calcium carbonate. Forster (1959) suggested that *Lithothamnion*, an encrusting coralline alga, was not heavily browsed by *Echinus esculentus*. Coralline algae appear to survive even where densities of urchins are high. This has been observed in *S. purpuratus* by North et al. (1963) and in *E. esculentus* (Forster 1959). Differences in amounts of CaCO_3 in gut contents would indicate possible

differences in quantity and quality of available food.

Seasonal changes in the amounts of CaCO_3 in the gut contents were evident in the eight samples of urchins collected from September 1964 to October 1965. Primarily, the calcareous material was coralline algae with some gastropod shell fragments. To compensate for differences in the total gut contents, a ratio of the dry weights of CaCO_3 to food material in the gut was used in comparisons. Values in the three areas ranged from 0 to 7.07, i.e. 0–7 times as much CaCO_3 as food material in the gut. During the winter and spring, animals of the *Postelsia* zone and eelgrass area were similar and had mean CaCO_3 /food ratios ranging between 0.25 and 0.85. During this same period the boulder field urchins had less calcareous matter in the gut with mean ratios between 0.02 and 0.18. During the summer the urchins of the *Postelsia* zone still had relatively large quantities of coralline algae in their guts with average ratios of 0.5–0.6. Animals of the boulder field and eelgrass areas were similar with mean ratios of 0–0.05. In the fall, the *Postelsia* zone animals averaged the highest mean ratios of 0.38 and 0.35. The urchins of the boulder field were low with mean ratios of 0.01 and 0.02. Animals of the eelgrass area were intermediate and showed average ratios of 0.23 and 0.15. Seasonal changes in amounts of CaCO_3 in the gut contents indicated that urchins in the *Postelsia* zone contained relatively large quantities for all seasons. During the winter and spring samples the urchins of the *Postelsia* zone and eelgrass area were similar. They were different during the summer when animals in the eelgrass area contained very little CaCO_3 . The amounts of calcareous material in the gut contents of eelgrass animals increased during the fall. Mean ratios were consistently low in the boulder field, but the highest values here occurred during the winter.

Kawamura and Taki (1965) showed that an increase in calcareous algae in the gut contents of *S. intermedius* was associated with decreased gonad production. In the laboratory, *S. purpuratus* that were fed calcareous algae grew more slowly and showed only small increases in general size than when fed noncalcareous forms (North 1964, Boolootian 1966). I conclude from this that the high values of CaCO_3 in the gut contents of animals in the *Postelsia* zone at Sunset Bay indicate less available food, that the low values of CaCO_3 in the gut contents of urchins in the boulder field indicate greater amounts of available food, and that the urchins in the eelgrass area have intermediate amounts.

Amounts of algae held by urchins in the Postelsia zone, eelgrass area, and boulder field

On July 29, 1965 samples of sea urchins were gathered from each area. The sampling procedure was to pick a small area up to 1-1½ m² and gather all individuals within the area. Care was taken that no algae held by the spines and tube feet of the animals were lost. The algae were carefully removed and saved; the total samples of urchins were weighed and returned to their areas. In the boulder field, 176 animals were collected which weighed a total of 18,103 g. The dry weight of the algae held by the urchins was 126.61 g. In the eelgrass area 104 urchins were taken; these weighed 3,412 g and held 14.46 g of food. In the *Postelsia* zone, the sample of urchins weighed 3,397 g and held 8.97 g dry weight of food. For comparison, the values can be expressed as dry weights of food held by an animal 5.00 cm test diameter (wet weight 62 g.) Such a value for the boulder field is 0.43 g; for the eelgrass area, 0.26; and for the *Postelsia* zone, 0.16 g. The species composition of the food items varied among the three areas as did food item diversity: 28 different items in the boulder field, 12 items in the eelgrass and only five in the *Postelsia* zone. In the *Postelsia* zone the major species was the brown alga *Hedophyllum sessile* (Agardh) Setchell 1899, which comprised 99% of the total food weight. In the eelgrass area the brown alga *Fucus furcatus* C. A. Agardh 1820 formed 25% of the total weight and the green alga *Ulva* sp. formed 26%. Three algae were of high importance in the boulder field: *Fucus furcatus* comprised 25%, and two red alga genera, *Iridophycus* (both *I. flaccidum* S. & G. 1937 and *I. splendens* S. & G. 1937), 29%, and *Gigartina* (mainly *G. papillata* (C. A. Agardh) J. G. Agardh 1846), 24% respectively. Although these values do not show what actually was eaten they do indicate the availability of food items.

Samples of animals were again gathered on March 4, 1966. In the boulder field, 34 animals were collected which weighed 4,007 g and held 0.85 g of potential food. Only 0.26 g of this was algal; the rest was chitinous, dead hydroid and bryozoan material. The diversity of food items held was much lower at this time compared with the summer. In the boulder field only four items were held: a hydroid, a bryozoan and two algae, *Gigartina* and *Porphyra*. In the eelgrass area, 49 urchins were collected with a wet weight of 1,563 g. They held three food items: *Phyllospadix*, *Porphyra*, and *Ulva*. *Phyllospadix* was approximately 99% of the sample. In the *Postelsia* zone, 42 animals were collected which weighed

1,913 g. The dry weight of material held weighed only 0.15 g and consisted of six different items: approximately 90% of the sample was dead (brown and gray) *Phyllospadix*, the remaining 10% was *Iridaea*, live (green) *Phyllspadix*, *Pterosiphonia*, and *Schizymenia*(?) or *Dilsea*(?). Converted to dry weights, a 5-cm animal in the *Postelsia* zone held 0.005 g, in the eelgrass area 0.012 g, and in the boulder field 0.013 g if the total weight of all material is considered, but 0.004 g if only the algae are taken. These low values are not the total amount available because the urchins would have eaten some food they had captured during the previous 24-hr period as indicated by the experiments with tattooed algae; however, the amounts held do indicate that food is scarce.

The quantities held during the summer are "unused" fractions of the amounts actually captured. In the boulder field and possibly in the eelgrass area, food was thus abundant during the summer. The amounts held by a 5.00-cm animal in the respective areas were 0.43 g and 0.26 g. Leighton (1966) showed, with the food items he presented, that the maximum amount eaten when food was superabundant was 0.42 g per day; Fuji (1962) using *S. intermedius* found the highest feeding rate with *Laminaria* in June to be 0.42 g per day, Moore et al. (1963) in preliminary work with *Lytechinus* showed a rate of feeding for animals 2.3 cm and 6.5 cm. By linear extrapolation, the rate of feeding of a 5.0 cm animal would be 0.2 g of *Thalassia* per day. A comparable plant for *Strongylocentrotus* is *Phyllospadix*. Fuji (1962) showed a June feeding rate of 0.1 g per day. Both of these rates were from laboratory studies, and so represent feeding when food is superabundant. That this is a maximum, however, is questioned by Moore and McPherson (1965) who show that *Lytechinus* is sensitive to current and feeds better in moving water. As a result, the amounts eaten in the laboratory may not indicate maximum for the field under conditions of unlimited food as indicated by the very high values shown from tattooed algae in *S. purpuratus*. Moore et al. (1963) and Moore and McPherson (1965) suggest that *Lytechinus* is at least capable of eating the entire net production of a *Thalassia* bed but that food is not limiting, because they have never observed grass patches which appeared to have been heavily grazed. The conclusion, however, in light of the subpopulations at Sunset Bay is that the urchins in the field experience a "relative shortage of food" (Andrewartha 1961) and that the biomass is indeed limited by food.

The general conclusion from the examination of available food and feeding is that a) food is not

equally distributed among the three areas; b) there is more food available in the boulder field than in the eelgrass area and *Postelsia* zone; c) animals have less than they would eat as indicated from laboratory studies.

Growth in crowded and uncrowded conditions

The effects of food availability on growth is further demonstrated by data gathered at Sunset Bay by Frank (unpublished). In 1964, age class I animals were placed in two pools in the eelgrass area. The pool farthest south was approximately 1 m wide, 2 m long and $\frac{3}{4}$ m deep and located near the pool used for determining size distributions. It had been cleared of all urchins in 1961, had not been repopulated and supported a lush growth of attached algae. In the summer of 1964, 59 animals were placed here. The other pool used by Frank was much smaller: only about $\frac{1}{2}$ m in diameter and about $\frac{1}{4}$ m deep and at the level of the pool used for tagged animals. In 1964, 142 animals were placed there. The mean test diameter of the animals in the two pools was $2.5 \text{ cm} \pm .35(\text{SD})$. In the summer of 1965, the mean diameter of animals in the small pool was $3.4 \pm .5(\text{SD})$ and the mean diameter of animals in the larger pool was $4.75 \pm .5(\text{SD})$. The means were distinct ($t = 13.7$, $P < .01$). The obvious difference between the two pools was the difference in quantity of attached algae. Differences in density and size have been observed in *Lytechinus* (Moore et al. 1963). Animals at a mean density of 2 per m^2 averaged 6.5 cm diameter. At a mean density of 43 per m^2 , animals averaged 2.3 cm diameter. The authors indicate that this was an age difference; however, it is certainly possible that they were observing differences in rates of growth.

At this point, for *S. purpuratus* at Sunset Bay, it is strongly suggested that food is indeed limiting growth rate. This suggestion is further strengthened by the following analysis of production of component parts of the urchins: a) calcite, b) gonads, and c) tissues and organs other than gonads.

Total calcite production of urchins in the three areas

To determine the total calcite production for individuals in each area, it was necessary to a) determine change in test weight during 1 yr b) correct the net change in spine weight by the additional breaks that occurred during the year and c) correct the net change in spine weight for total removal and replacement of spines.

A plot of total calcite weight (y) as a function

of test diameter (x) gave the following regression: $\log y = 2.66 \log x + \log 0.2$. Spine weight (y) was related to test diameter by: $\log y = 2.45 \log x + \log 0.1$. Change in net weight during 1 yr was determined from these equations and the growth equations from marked animals.

To relate calcite weight lost to the diameter of a spine tip that was broken off it was necessary to determine the density of the spines. Volumes were calculated for 12 spine tips cut at the milled ring. The formula used to estimate volume was that of a truncated cone: $V = \pi h (r_1^2 + r_1 r_2 + r_2^2)/3$ where h is the length and r_1 and r_2 are the radii of the two ends. The mean density of the 12 spines that had been cleaned in NaOCl was 1.66 mg/mm^3 . This value is lower than the density of calcite (2.7–2.9, Handbook of Chemistry and Physics, 48th ed.) because of the fenestrated nature of the echinoderm skeleton. The angle between the spine at the base of the milled ring and a line drawn to the tip was calculated to average 87.7° . Using this angle, the density of 1.66, and the diameters of breaks measured in the individual spines, I estimated the gross production of five spines per individual for the sample of 85 animals gathered in August 1964. To make use of such values to estimate general production of spines, the mean values were expressed as ratios of calculated gross production divided by the observed spine weight. The ratios are plotted as a function of test diameter in Figure 7.

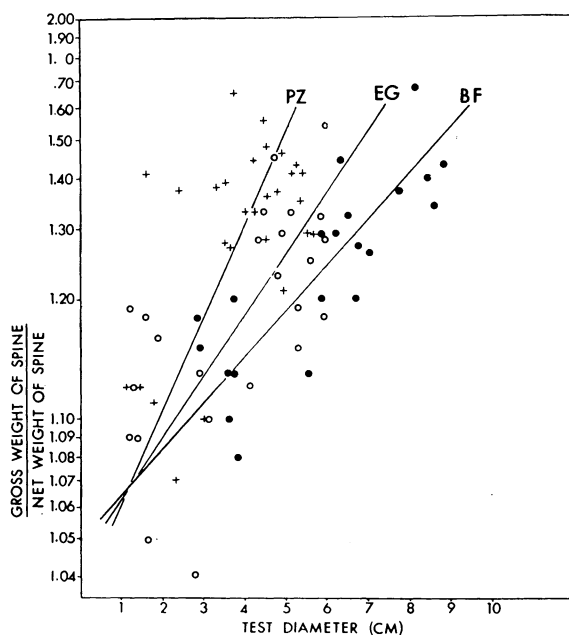


FIG. 7. The ratio of gross/net spine weight plotted as a function of test diameter. See text for the method of calculating gross spine weight.

There is great variability in the ratios, but the values are generally positively correlated with size: large urchins have large ratios, which means that a large spine required relatively more production than did a small spine. A ratio of 1 would mean that no breakage had occurred and that all the calcite produced was present in the spine. There are differences among the three areas. The points are generally highest for the urchins of the *Postelsia* zone and are lowest for animals of the boulder field. The ratios for urchins in the eelgrass area were intermediate. The lines in Figure 7 were fitted by eye. Using the growth equations determined from marked animals, and the equation presented above that related size to spine weight, the net weights of spines could be corrected for breaks using the ratios of Figure 6 and the difference between year n and $n + 1$ would then be the amount of production of individual spines during that year.

To correct for the spines that were completely removed, urchin sizes were first calculated based on a 6-month period, which is an estimate of the length of time required for a tubercle to become shiny after spine loss. Spine loss was assumed generally constant during the year and so the weight of spines multiplied by the percentage dull tubercles would be equal to the amount totally lost and being repaired. The two estimates were summed, added to the production indicated for broken spines and general increase in spine size, and added to the change in test weight. This value was taken as an estimate of total calcite production by an individual urchin for 1 yr. Table 3 shows such values determined for individuals living for 10 yr in each of the three areas.

On an individual basis, calcite production is almost four times greater during the second year of growth in the boulder field than in the *Postelsia* zone. During this same period an animal in the boulder field produced about 1.5 times as much

calcite as did an urchin in the eelgrass area. At the end of 10 yr, however, urchins in the boulder field produced only three times the weight produced by animals in the *Postelsia* zone and eelgrass area. At the point of no increase in size, animals in each area still produce calcite to replace spine loss. These values are estimated as 1 g per animal year in the *Postelsia* zone, 0.4 g per animal year in the eelgrass area and 3 g per animal year in the boulder field. This is an underestimate of actual loss of calcite because it is based only on total loss of spines. With the method used to determine the amounts regenerated by broken spines, no estimate can be made for annual production because there is no change in size, and so no apparent addition from repair of breaks.

Annual production varied with animal size (Fig. 8). The curves for the three areas show the rate of change in calcite production with high values at different sizes in the three areas. Greatest addition of calcite was at about 1.5 cm in the eelgrass area, 3 cm in the *Postelsia* zone and 3.5 cm in the boulder field. The size of maximum calcite production is determined by the rate of growth and the changes in the amounts of spines lost either in part or totally. Total production per animal was different in the three areas, lowest in the *Postelsia* zone and highest in the boulder field.

Differences in organic production

In addition to differences in individual production of calcite, urchins in the three areas showed variation in the production of tissue material, both gonads and weight of other organs. Tissue content of the spines, test, lantern and gut was determined by subtracting the dry weight of these elements after treatment with NaOCl from the dry weight before treatment. For comparison of the three areas, the following "gonad index" was calculated: $100 \times \text{gonad dry weight}/d^2h$; where

TABLE 3. Calcite production (g/animal yr) for animals ranging from 1 yr to 10 yr old in the three areas

Age	<i>Postelsia</i> zone			Eelgrass area			Boulder field		
	spines (g)	test (g)	gross (g)	spines (g)	test (g)	gross (g)	spines (g)	test (g)	gross (g)
1-2.....	0.7	0.7	1.4	1.7	1.8	3.5	2.8	2.5	5.3
2-3.....	0.9	0.6	1.5	1.7	1.6	3.3	3.1	2.3	5.4
3-4.....	1.0	0.6	1.6	1.6	1.2	2.8	3.3	2.0	5.3
4-5.....	1.0	0.6	1.6	1.4	1.1	2.6	3.4	1.7	5.1
5-6.....	1.1	0.5	1.6	1.3	0.8	2.1	3.3	1.4	4.8
6-7.....	1.1	0.5	1.5	1.2	0.6	1.8	3.3	1.2	4.5
7-8.....	1.1	0.4	1.5	1.1	0.5	1.6	3.3	1.0	4.3
8-9.....	1.1	0.4	1.5	1.0	0.4	1.4	3.3	0.8	4.0
9-10.....	1.1	0.3	1.4	0.9	0.3	1.2	3.3	0.6	4.0
terminal size.....	1.1	0.0	1.1	0.4	0.0	0.4	3.3	0.0	3.3

Terminal size is 4.5 cm in the *Postelsia* zone, 5.1 cm in the eelgrass area, and 6.4 cm in the boulder field.

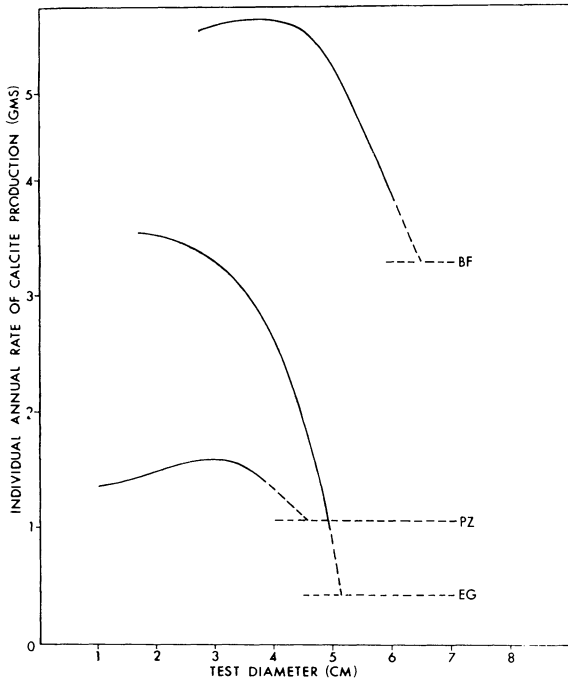


FIG. 8. Annual calcite production as a function test diameter. As plotted the graph should be read: an animal of a stated size will produce the indicated amount of calcite during the coming year. The horizontal dashed lines are the amounts of production of animals that are not increasing in test diameter and represent the amounts of calcite lost through total removal of spines. These estimates are accordingly low and do not include the amounts lost through abrasion or breakage at the point of zero growth.

d is test diameter and h is height in centimeters. There is a slight bias in such a gonad index which yields relatively higher values for large individuals. A plot of "gonad index" as a function of test diameter yielded a positive association by a Corner test (Tate and Clelland 1957) for animals of the eelgrass area (quadrat sum = 15, $P < 0.01$). For the other two areas, the association was not significant but the quadrat sum was positive in both cases. For animals of all areas combined, the association was significant (quadrat sum = 16, $P < 0.01$). This is probably the same association that would be found with other indices that have been proposed (Lasker and Giese 1954, Greenfield et al. 1958). The index of Moore et al. (1963) yielded higher values for intermediate size animals.

Gonad development appears to be generally the same in the boulder field and the eelgrass area (Fig. 9). In the *Postelsia* zone development was much less. A cycle of gonad size is apparent and is similar to those reported by several workers and summarized by Boolootian (1966). Gonads increased in size during the fall and decreased

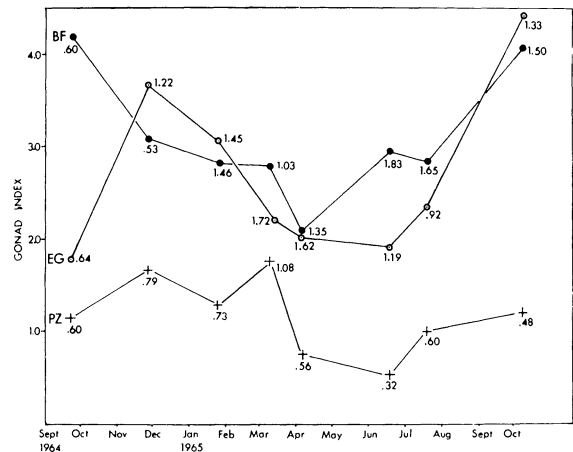


FIG. 9. A gonad index as a function of time. The "index" is $100 \times \text{gonad dry weight/diameter}^2 \text{ height}$. Each point is the mean of usually 10 animals and the numbers are one standard deviation.

during the winter. By summer most urchins had small gonads. The cycle may not have been synchronized in the three areas. In 1964 the major buildup occurred in the boulder field before it took place in the eelgrass area and growth during the summer began earlier in the boulder field. Because of the degree of variation, this interpretation must be very tentative. The trends are, however, probably valid and the gonad production in the *Postelsia* zone is indeed less than in the other two areas.

It is interesting to speculate concerning the meaning of the cycle because it is often assumed that the decrease in gonad size indicates spawning. However, the possibility cannot yet be ruled out that decrease in size simply indicates metabolism of a storage product during times of low food, and that spawning may not occur in all individuals in a single year or may not take place in any individual for several years. Shrinkage of the gonad during starvation has been demonstrated in *S. purpuratus* (Lasker and Giese 1954).

There are differences in amounts of tissue other than gonads and gut contents in animals with respect to time and area. During the winter, urchins of a given size in all three areas had similar quantities of organic matter in the gut, spines and test. A single regression line was adequate to describe the relation between dry weight of tissue material and calcite weight for all three areas ($F_{4,50} = 2.3$, $P > 0.05$). The same is true for spring ($F_{4,52} = 0.23$, $P > 0.05$). Furthermore, the two seasons could not be distinguished ($F_{2,110} = 2.46$, $P > 0.05$; $y = 0.101x + 0.14$, where y is dry organic weight and x is calcite weight both in grams). During the summer the animals of

the *Postelsia* zone contained less tissue material than did the urchins of the two other areas. A single regression did not satisfy all points ($F_{4,52} = 21.13$, $P < 0.01$). The animals of the eelgrass area and boulder field, however, could not be distinguished ($F_{2,35} = 7.73$, $P > 0.05$). The regression equation for the *Postelsia* zone during the summer is $y = 0.077x + 0.35$; that for the eelgrass area and boulder field is $y = 0.107x + 0.25$. The values from the fall were not significantly different among areas ($F_{4,49} = 4.22$, $P > 0.05$; $y = 0.120x + 0.33$); but the values for fall, winter and spring were significantly different ($F_{4,163} = 15.98$, $P < .01$). The changes in tissue weight shown in the areas can be described as a cycle with low values during the winter and spring, an increase during the summer but with animals in the *Postelsia* zone still showing relatively less weight, and urchins in all areas showing high values during the fall. An annual cycle of stored glycogen in the wall of the gut has been reported for *S. purpuratus* in California by Lawrence, Lawrence, and Holland (1965). The changes in tissue weight shown among animals at Sunset Bay probably represent this cycle of stored food. A similar cycle has been reported by Fuji (1967) for the gut weight in *S. intermedius*.

The data on algae held by urchins, the contents of CaCO_3 in the gut, the amounts of food eaten per day in each area, and the variation in success of accepting tattooed algae all indicate that the least amounts of food were available in the *Postelsia* zone, most in the boulder field and intermediate in the eelgrass area. These differences correlate very well with the general productivities of urchins in the three areas. The cause and effect relationship between available food and productivity of the urchins is strengthened by the differences in growth rates of crowded and uncrowded urchins. I conclude that the productivities, growth rates and ultimate sizes attained by urchins at Sunset Bay are determined by available food. Such rates are modified by the amounts of spine breakage and repair. Other modifying factors, of course, are not ruled out.

DISCUSSION

The results presented indicate the importance of a relative shortage of food in limiting growth rate and ultimate size of sea urchins in the three subpopulations at Sunset Bay. Furthermore, the modifying effect of a component of "weather" that breaks spines is demonstrated. Such a conclusion is interesting in light of the statement by Hairston, Smith, and Slobodkin (1960) that the usual condition is for populations of herbivores not to

be limited by their food supply or weather but rather by predators. In fairness the term "usual," and the fact that the paper was intended to relate primarily to terrestrial communities should be emphasized. This food limitation may be of general importance, however, considering that these urchins form such a conspicuous element of the benthic fauna. It also appears evident that food is not a limiting factor to numbers but only to biomass. Such a conclusion would be consistent with the observed ability of these animals to decrease in size and with the observation of the intertidal region where numbers appear to be limited by suitable places in which to live, i.e. pools, or bases of boulders. The general distribution pattern of urchins at Sunset Bay showed fewer animals per square meter at the low intertidal level of the boulder field and higher densities in the eelgrass area where urchins were confined to pools. From the data presented, the boulder field is a better place in which to live for an individual urchin. The problem becomes, why are there not more urchins in the boulder field? Limitation of numbers is obviously not due to food, as indicated by the larger amounts available to urchins in this region by all methods used. Differential mortality must be ruled out as determining different densities because this would mean that more empty "spaces" would develop in the boulder field than in the eelgrass area or *Postelsia* zone, and that when a heavy settling occurred there would be relatively more individuals settling in the region with the most empty spaces. The heavy settling of 1963 showed relatively equal numbers of new animals in the three areas examined. The most reasonable explanation is that there are fewer suitable places to live per square meter in the boulder field than in a tide pool in the eelgrass area. An alternate explanation, however, would be that settlement is density dependent and animals preferentially settle where there are adults. This would be consistent with the observations of Moore et al. (1963) on transplanted *Lytechinus* populations and a phenomenon not uncommon in marine organisms (Knight-Jones 1951, Wilson, 1956). The sides and tops of boulders are apparently unsuitable as no urchins were found in these positions. The range of "suitability" for growth is obviously great, as shown by the very different productivities and growth rates of the animals in this study. It is further apparent that the urchins grow to the capacity of their "suitable space" with respect to food and physical abrasion. This is shown by the differences in optimum size in the three areas discussed. Because of their ability to shrink, as conditions change from year to year, urchins would

be expected to increase or decrease in diameter to adjust to the carrying capacity of the environment rather than to decrease or increase in numbers. The actual number of urchins living in a pool at one time would, of course, be dependent upon the amount of settlement over the past several years. Given a longevous animal, numbers may decline over periods of many years and the population not go to extinction. All that is required is occasional settling success. The result is that numbers within a "suitable space" may be limited by purely physical factors, the "weather," and yet biomass is dependent upon food availability which is, in turn, determined by local topography and currents.

The results are of more practical interest with regard to the sea urchin population of the southern California coast (North et al. 1963, Leighton et al. 1966). The populations have increased greatly over the past decade following destruction of the offshore kelp beds. The urchins in these populations have very little organic matter in their gut contents and are small animals of only 2–4 cm. This finding is consistent with the idea of limitation of ultimate size by a shortage of food. The numbers are great with densities of 200 /m² or more, a density similar to that of animals in selected areas of Sunset Bay. What is different, however, is that the regions appear in published photographs to be relatively homogeneous with urchins at high density over large areas. A possible interpretation is that the destruction of kelp increased the number of "suitable places in which to live" which was then followed by an increase in urchin numbers. Food limited the rate of growth and ultimate size and the resulting populations had small test diameters. Such a population once started in an area would not be eliminated by shortage of food but rather could respond to decreasing food supply by shrinking of individuals.

The general conclusion is that *Strongylocentrotus purpuratus* is regulated in size and number not by a single factor but rather by the complex of factors proposed by Andrewartha (1961), components of weather, food, a place in which to live, and other animals in this case, of the same species.

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THE RELATIONSHIP BETWEEN SPECIES DIVERSITY AND STABILITY: AN EXPERIMENTAL APPROACH WITH PROTOZOA AND BACTERIA¹

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Abstract. Small experimental communities of bacteria and Protozoa were designed to test the widely held hypothesis that higher species diversity brings about greater stability. Three species of bacteria, three species of *Paramecium* and two species of protozoan predators, *Didinium* and *Woodruffia*, were used. The communities were maintained by regular additions of the appropriate combinations of species of bacteria. Stability was measured as persistence of all species and as a tendency to maintain evenness of the species abundance distribution. The measures were in essential agreement. Stability at the *Paramecium* trophic level was increased by increasing diversity at the bacterium level, but three species of *Paramecium* were less stable than two. An important finding was that one pair of *Paramecium* species consistently showed greater stability without the third species than with it. This finding indicates that there were significant second-order effects, with two species having an interaction that was detrimental to the third species. We conclude that much more experimental and observational work is necessary before the nature of any functional relationship between diversity and stability can be claimed with confidence.

INTRODUCTION

A widely held opinion is that increased species diversity leads to increased stability within ecological systems. This opinion has almost reached the status of an axiom since the demonstration of its theoretical validity by MacArthur (1955). We do not challenge MacArthur's conclusions

for the restricted conditions that he postulated and agree that they follow logically and mathematically from his premises. It is not clear, however, that the same formal properties would obtain in a more realistic community in which there is overlap in food species among different species of the same trophic level. Such an extension of MacArthur's conclusions would have to be reconciled with the equally logical and experimentally verifiable conclusions of Volterra (1926), Lotka (1932), and Gause (1934) concerning the outcome of competition.

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