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LOCAL VARIATIONS OF GROWTH, FEEDING, REGENERATION AND SIZE STRUCTURE IN A NATURAL POPULATION OF THE SEA URCHIN, *STRONGYLOCENTROTUS PURPURATUS* (STIMPSON)

by

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I would like to thank Dr. Peter W. Frank for his help during the past four years. Many parts of this study are direct or indirect results of his suggestions.

To Timmy and Chris, two urchins
of a different color.

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INTRODUCTION

> I here salute the echinoderms as a
> noble group especially designed to puzzle
> the zoologist.
> Libbie H. Hyman, 1955

Although echinoid populations have been much exploited in physiology and embryology, they have been relatively neglected by ecologists. Few studies of growth rates of urchins have been conducted, and those in the literature often lack critical information on local variations in growth. These will be examined in detail in the Discussion. Probably the major reason critical information on growth has not been gathered for urchins in the field has been the lack of an adequate method of marking individuals. Methods cited in the literature are elastic bands around the test (Moore 1935); nylon line or brass wire wrapped around the test, small squares of rubber balloon placed on the spine tips, and plastic-covered wire or brass wire threaded through holes drilled in spines (Sinclair 1959); and plastic discs on stainless steel wire pushed through the test (McPherson 1965). All of these methods are useful for short time periods only. The development of a suitable marking procedure was probably one of the major factors in making this study possible.

The urchin examined here, *Strongylocentrotus purpuratus* (Stimpson), is a regular echinoid of the family Strongylocentrotidae, distinguished from other common littoral members of the genus on the eastern Pacific coast (*S. dröbachiensis and S. franciscanus)* by the slight difference between primary and secondary spines (this at once distinguishes it from *S. franciscanus* in which primary spines are much larger than secondary spines) and at least eight pore pairs on typical aboral ambulacral plates (this separates it from *S. dröbachiensis*). The purple urchin, according to Ricketts and Calvin (1962), ranges from Alaska to Cedros Island, Baja California; however, Boolootian (personal communication 1964) states that purple urchins north of Puget Sound probably are *S. echinoides*. The urchin examined in this study occurs along the south central Oregon coast and is, without doubt, *S. purpuratus*.

The purple urchin is mainly an herbivore using algae as its chief food source. To an extent it is also an opportunistic feeder. It either grazes on attached algae or catches floating debris. Urchins may move to large pieces of food such as dead fish. The sexes are separate; spawning is during February and March (Ricketts and Calvin 1962), or no definite season may exist, with some individuals able to spawn at any season, and possibly individuals being able to spawn more than once during the year (Giese et al. 1959). In rocky areas, the animals may be very common and reach densities of over $100/m^2$. In the areas discussed here, urchins appear to be the major herbivore and, therefore, of considerable importance with respect to energy flow through the ecosystem.

The present study examines local growth variation in a population of urchins at Sunset Bay, Oregon. Differences in the rates of growth as well as differences in size structure are shown. Some of the conditions associated with different growth rates are examined. This, to be sure, is in terms of correlation rather than causation, and definite conclusions concerning cause can not be made; however, a reasonable picture of growth and growth regulation can be constructed. Methods of study of urchin populations are developed which are applicable to the study of other echinoids and possibly to other populations.

AREAS AND METHODS

The area studied was the south side of Sunset Bay, Oregon, lat. N. 43° 20', near the city of Coos Bay, Oregon. The south side of the bay is formed of tipped beds of sandstone dipping sharply to the east and striking north and south. Differential weathering has produced a series of ridges, flat areas and channels seaward and a relatively flat area shoreward with a boulder field at the north end (Fig. 1). The flat area south of the boulder field is where growth of the turban snail *Tegula* was studied by Frank (1965). The urchin beds investigated are shown in Fig. 2. Three locations were of major interest and are referred to as: *Postelsia* zone, high eel grass area, and boulder field. Relatively, the eel grass area is the highest intertidally, the *Postelsia* zone next and the boulder field lowest. A species list of the more common algae in each location is given in Appendix I.

The general procedure for the study of growth rates was to measure and mark animals in the three areas and to measure these again at later dates. The first marking method consisted of slipping pieces of spaghetti tubing over the tips of spines (suggested by Dr. Cadet Hand ca. 1960). Using this technique, 14 animals were marked at Sunset Bay on 8 December 1962. On 22 January 1963, three animals were recovered. The marked spines apparently deteriorated around the mark and could be easily broken. The method was discarded. A second unsuccessful method which was field tested used plastic dart tags manufactured by the Floy Tag & Manufacturing Company, Seattle, Washington. The company shortened a standard dart tag used for fish and six of these were

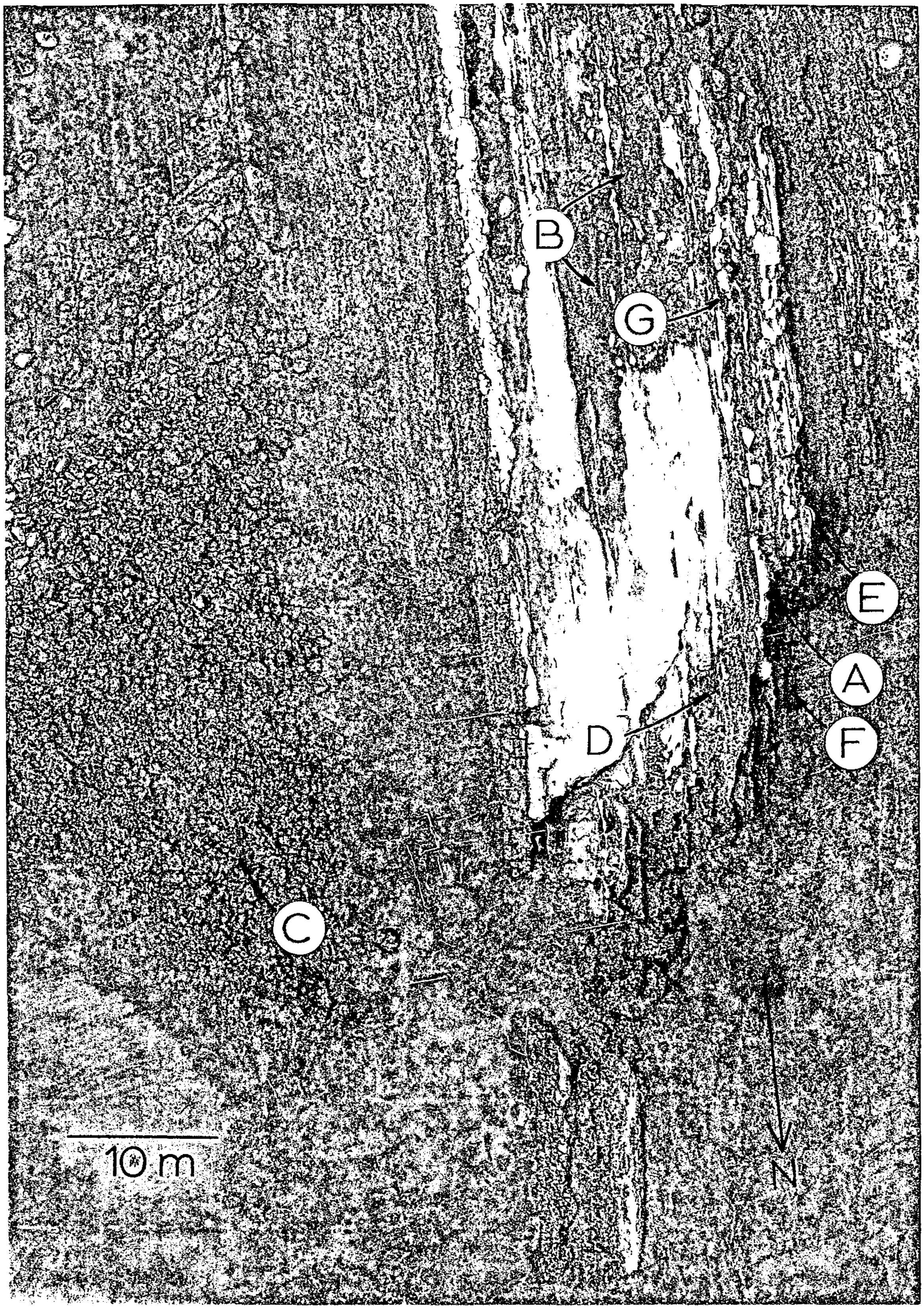
Figure 1

Aerial photograph of the south side of Sunset Bay showing general topography. The outlined area includes all regions of this study and is shown in a vertical projection in Fig. 2.

Figure 2

Aerial photograph of the south side of Sunset Bay showing the areas where animals were studied.

Letter	Name used in text
A	*Postelsia* zone
B	Eel grass area
C	Boulder field
D	High area above and north of *Postelsia* zone
E	South and below *Postelsia* zone
F	North and below *Postelsia* zone
G	West and north of eel grass area


B
G
E
A
D
F
C
10 m
N

planted at Sunset Bay in animals with test diameters of 2.1 to 7.6 cm. The date of marking was 26 January 1964. On 23 February 1964, all marked animals had disappeared. The marking method which proved to be successful was developed during the summer of 1963. It consisted of inserting 0.025 mm diameter (4-lb. test) nylon monofilament line through two holes in the test, marking the line with colored pieces of vinyl tubing, and fastening the ends of the line with a square-knot and a drop of Dekophane (a methacrylate glue) or Duco cement. A piece of the vinyl tubing was slipped over the knot. Insertion of the line was accomplished with a 22-guage, 2-inch hypodermic needle mounted on a shaft and used in a high speed drill. The method, as reported (Ebert 1965), used a needle with a side hole in the base to allow the line to be threaded after the holes were drilled in the test. This was discarded in the summer of 1964 when it was found that the monofilament could simply be inserted into the tip of the needle after drilling through the test, pushed down as far as possible and the needle pulled out. Threading in this manner required no groove in the shaft holding the needle or hole in the base.

There were apparently no serious effects of marking. The holes in the test sometimes healed and held the line securely. Often, however, the holes remained open and the line could be freely moved even after a year in the field. A small calcareous deposit filled with granular pigmented (echinochrome) material was often formed on the inside of the test around the monofilament line. The most serious consequence of marking was the apparent decrease in growth rate of the marked ambulacrum. This decreased the precision of estimating the diameter and also yielded a slightly lower growth rate estimate for the entire animal. The increase in standard error is shown in Appendix V along with changes in size of representative animals which show the slower growth of the marked ambulacrum.

During the summer of 1963, 131 animals were marked and returned to a tide pool in the eel grass area. In 1964, only six of these marked urchins were recovered. It was found in September 1963 that an animal could chew through the monofilament line if the loop was long enough to reach its mouth. This probably accounts for the poor recovery of animals marked in 1963. In the summer of 1964, 500 animals were marked, using smaller loops; these were distributed among the *Postelsia* zone, the eel grass area and the boulder field. Samples of animals were measured from the three areas in December 1964, April 1965 and July 1965, approximately one year after the original marking. Additional animals were marked and placed in the three areas in July 1965. Samples were again measured in November 1965 and March 1966. Measurements of test diameter were made with knife-edged vernier calipers. Five measurements were made per animal from the center of each ambulacrum to the center of the opposite interambulacrum. Standard errors of such measurements are given in Appendix V. A comparison of measurements of animals before and after cleaning in NaOCl is given in Table 1.

When it became apparent that there were differences in growth rates among animals from the three areas, a search was begun to determine some of the factors responsible for these differences.

Table 1

Check on the accuracy of measurement of test diameter of living urchins. Animals were collected at Sunset Bay 25 June 1964, marked and measured, killed and bleached in NaOCl and again measured. Means are from five measurements and are in centimeters.

Measured alive		Measured after cleaning	
Mean	± SE	Mean	± SE
5.19	0.014	5.18	0.011
5.38	0.006	5.37	0.008
5.16	0.023	5.53	0.004
5.15	0.007	5.15	0.008
4.98	0.017	4.99	0.005
5.08	0.013	5.07	0.009
4.83	0.008	4.81	0.001
5.74	0.015	5.72	0.009

Because the areas are very close together, the assessment of factors influencing growth, to an extent, is simplified. Such variables as temperature, salinity, oxygen tension, turbidity, pH and concentrations of trace ions were assumed to be approximately the same for all the animals studied. Because of differences in tidal levels there are, of course, local changes in these variables; but, because of the proximity of the areas, these factors were ignored.

Environmental components which were investigated were wave exposure and food.

Population density was not measured in Sunset Bay because of the difficulties caused by the highly irregular relief. Visually, the three major areas seemed to have about the same numbers of animals. Typically, unless there is actual physical contact, density of a population is assumed to simply indicate differences in the amounts of food gathered. Attempting actually to measure the food intake of the urchins eliminated this problem.

Food gathered per day was estimated by feeding pieces of tattooed algae to samples of animals in each of the three areas and collecting the animals 24 hours later, dissecting out the gut and determining the amount between the mouth and the tattoed piece of algae. Samples of 10 animals from each area were collected eight times during the period September 1964 to October 1965. When collected, the animals were killed and fixed in the field with an injection of 100% formalin. The amount used varied with the size of the animal but ranged between 3 and 7cc. This amount of formalin was necessary to prevent autolysis of the stomach ("small intestine" of Hyman 1955). Animals were preserved in 5% formalin in sea water until ready for dissection. They were then washed in fresh water for 24 hours, damp dried and measured. Animals were dissected in the following manner. A cut was made around the peristome, and the membrane removed. A strong pair of forceps was inserted around an ambulacrum (one arm of the forceps inserted on the inside and one on the outside of the test). Care was taken to avoid rupturing the gut. A small piece of test was broken out, and the procedure repeated for another ambulacrum. After five slots were completed, one in each ambulacrum, a small spatula was used to break the mesentaries holding the gut and the gonads to the interambulacral areas. As areas of interambulacrum were freed, the plates were removed by breaking them off with a strong forceps. After reaching the ambitus, it was usually possible to free the gut and gonads from the test without further breaking of plates. The freed mass was placed, oral side down, into a white dissecting tray. The gonads were separated from the gut for weighing. The small intestine was disarticulated from the large intestine and the entire digestive tract was spread out. The esophagus and lantern were placed with the spines and pieces of test. Small sections of gut were cut off, starting at the junction of intestine and esophagus. These were placed in a water-filled Syracuse dish, opened, and the contents examined for the presence of the tattooed algae. When the marked *Hedophyllum* was found it was removed and discarded, and the contents between it and the mouth were placed in a 50 ml beaker. Gut contents after the tattooed algae were weighed separately. The gut wall was dried with the test plates and spines. Beakers were placed in a drying oven at 110-115° C for at least 24 hours, cooled in a $CaCl_2$ desiccator and weighed to the nearest 10 mg on a Mettler balance. After weighing, the dried gonads were discarded. The tests and gut contents were treated with 5% sodium hypochlorite (commercial bleach) to remove organic material. Usually at least two treatments with NaOCl were required. After treatment the samples were washed and again dried and weighed. Gut content samples were then treated with HCl to remove $CaCO_3$, washed, dried and again weighed. The information gathered from each animal included: diameter and height (three measurements of each with vernier calipers to the nearest 0.1 mm), gonad dry weight, total organic weight other than gonad weight, calcite weight and weight of food, $CaCO_3$ and silicious sand before and after the marked algae.

Physical abrasion in each area was estimated by an examination of spine breaks and tubercle morphology. A sample of animals was collected in August 1964 from the three locations and, after cleaning the animals in NaOCl, washing and drying, a spine sample was impregnated with a mixture of 22 parts terpineol and 1 part methyl salicylate as suggested by Deutler (1926; originally from Becher 1914). Impregnation was facilitated by placing spines in the oil mixture under a vacuum. Spines were viewed with transmitted light under a compound microscope. Breaks were measured with an ocular micrometer.

More detailed work with internal structure of the spines was done by making thin mid-sagittal sections in essentially the manner of Carpenter (1847, 1870) and Deutler (1926). After bleaching in NaOCl, washing and drying, the spines were dipped in xylene, placed on a slide and covered with Canada balsam. They were then heated on an electric hot-plate to boil away the xylene and cooled. When hard, the preparations were suitable for making thin sections by grinding on a glass plate with #220 followed by #600 carborundum grinding compound. Water was used as the liquid medium for grinding. The slide was tilted during grinding to insure production of a median section. After grinding one side, the slide was returned to the hot-plate, the balsam remelted and the spine turned over, recooled and grinding completed. The preparation was cleaned with xylene before a cover slip was added.

Before June 1963, organic material was not removed from the spines before grinding. This caused the spines to become extremely brittle, and most of them fractured during the grinding process. Removal of as much organic material as possible with NaOCl facilitated the handling of spines with a minimum of damage. NaOCl was used by Swan (1952) and is essentially the "Eau de Javelle" of Deutler (1926).

Sections were made of test plates to examine the "growth zones" as a possible means of determining age. Separation of the plates required first boiling the tests in water. These were then disarticulated and the plates dried and mounted on slides in approximately the same manner as the spines. Rough grinding was greatly facilitated by the use of a Dremel Moto-tool with a small drum-sander bit.

Photographs were produced from the finished slides simply by placing them in the negative holder of a photographic enlarger and projecting onto high-contrast paper. All slides were projected with the same magnification so direct measurements could be taken from the negative prints.

Certain studies were carried out in the laboratory. A circulating sea water system was constructed in an 11°C controlled temperature room. The basic plan of construction followed the system built at the University of California at Riverside by Lars H. Carpelan (Strong 1962). Experiments on regeneration of spines and growth of animals were carried out using this system.

Work during the summers of 1963, 1964 and 1965 was based at the Oregon Institute of Marine Biology at Charleston. The Institute is 3 miles north of Sunset Bay.

Further detailed explanations of techniques will be given where appropriate in the results.

RESULTS

The results will be divided into two major parts: a section on growth of spines and plates and deposition of pigments, and a second section describing size distributions of animals at Sunset Bay, growth rates of animals from three major areas of study (the *Postelsia* zone, the eel grass area and the boulder field) and some factors which may be important in determining differences in growth rates.

Growth and Repair of Spines

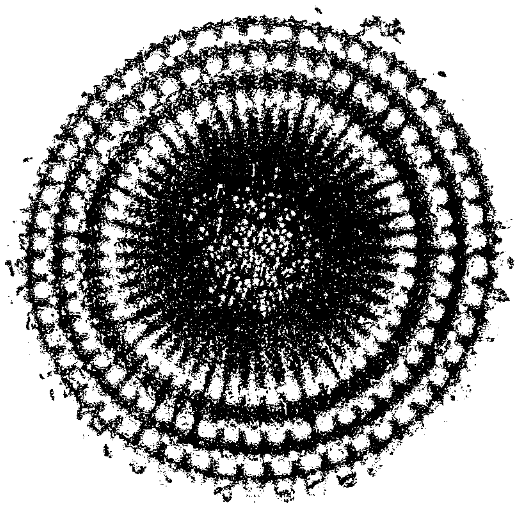
The calcareous portions of urchins are internal, of porous construction and filled with living organic material (Hyman 1955). The microscopic structure of spines was apparently first examined by Valentin (1842) and that of the test apparently first by Lovén (1874). Spine sections have been described for many species of urchins by various authors (Carpenter 1847, 1870; Mackintosh 1879, 1883a and b; Kříženický 1917; Deutler 1926; Mortensen 1928-1951), but the "rings" or "cycles of wedges" which appear in cross section (Figs. 3 and 4) have not been properly interpreted. Carpenter (1847, 1870) and Swan (1952) have suggested that these cycles may be formed like the annual growth layers in woody perennial plants. Deutler (1926) calls them "Wachstumzonen" and suggests periodic formation. Borig (1933) recognized that cycles ended at sharp discontinuities, but still concluded that "cycles" were formed periodicly. He felt that after breaking, the spine would not regenerate a new tip until the next "Wachstumperiode" when a new tip and a new cycle would be formed. Cycles would be added even though no break had occurred.

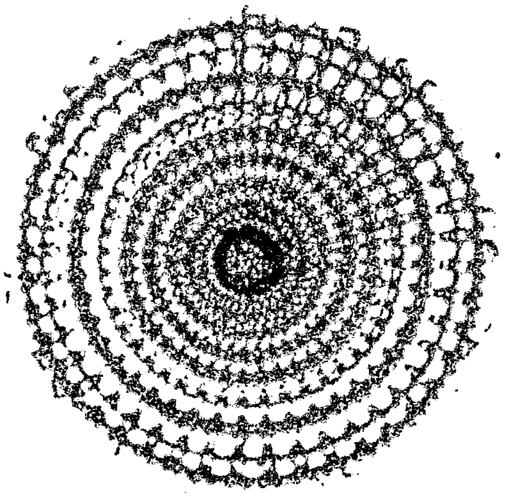
Figure 3

Cross section of a spine of *Strongylocentrotus purpuratus* showing 4 cycles of wedges (large calcite crystals) and fine crystalline meshwork with dense pigmentation. The central area with wide meshes probably indicates that the spine has been totally regenerated.

Figure 4

Cross section of *S. purpuratus* spine showing 10 cycles of wedges.





Examination of several hundred longitudinal sections of *S. purpuratus* spines, during the summer of 1963, led to the hypothesis that cycle formation was the result of breakage and regeneration. This was proposed because: spines always have a cycle of wedges on the outside and if the cycles were formed only at certain periods during the year, at some time one would expect to find the fine crystalline meshwork on the outside (this is never the case); and in longitudinal section, cycles are always distally terminated at a sharp discontinuity which suggests a break (Figs. 5 and 6).

On 4 May 1964, a sample of urchins was collected from Sunset Bay, brought back to the University of Oregon and placed in aquaria of aerated sea water at 11° C. On 6 May, four urchins were individually marked with nylon monofilament and returned to the tanks. On 8 May, the tips of all primary spines in the interambulacrum nearest the mark were removed and placed on a card in the order of removal. The position of the mark was recorded to insure proper matching of the tips with the spines at a later date. Figure 6 shows one such pairing after two months of regeneration. A new tip and a new cycle have formed.

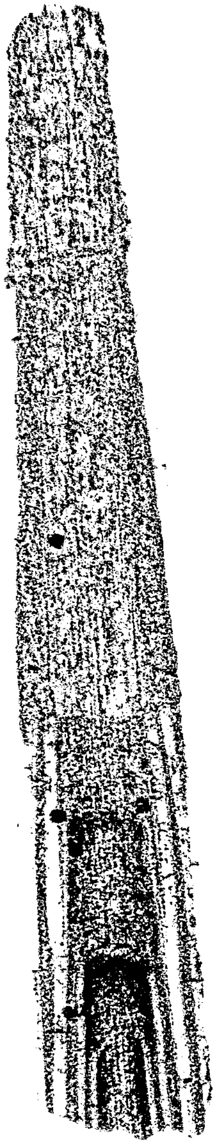
If a spine breaks many times during the life of an animal, older animals should have more breaks per spine, and there should be a general correlation between size and number of cycles in original spines, i.e. those spines which have never been totally regenerated. Indeed, this is the case. Spines from animals taken from Sunset Bay on 8 December 1962 and 22 January 1963 were ground in longitudinal

Figure 5

Longitudinal section of a primary spine of *Strongylocentrotus purpuratus* showing the calcite crystals (the "cycles of wedges" in cross section) terminating at sharp discontinuities. Note the partial "cycles" near the top of the spine.

Figure 6

Matched spine tip and spine (with regenerated tip) showing the addition of a "cycle". Regeneration time was two months.



section and examined for the presence of a green core. It was felt that green cores indicated original spines as suggested by Swan (1952). Of 33 animals, only 12 showed at least one green-cored spine of the three or four spines sampled. Because of the effort involved in preparing longitudinal sections, no further slides were made when a spine with a green core was found for any animal. As shown in Table 2, there is a positive correlation between test diameter and number of cycles in the spines.

Regeneration of entire spines has been demonstrated with *Echinus* (Chadwick 1929), *Psammechinus* (Hobson 1930), *Arbacia* (Jackson 1939) and *Strongylocentrotus* (Swan 1952).

Swan (1952) showed at Friday Harbor, Washington, that when a spine of *Strongylocentrotus* was removed completely from the test, the associated tubercle became dull after a period of time and could be distinguished from shiny tubercles of spines that had not been removed. Because this could be a useful measure of the amount of spine loss, the length of time for a tubercle to become dull and again shiny was determined.

On 16 July 1964, spines were removed from the interambulacrum opposite the madreporite of each of 70 urchins at Sunset Bay. After treatment, the animals were placed into a deep tidepool about 15 m south of the eel grass area and at approximately the same intertidal level. Urchins were collected periodically and the tests cleaned in NaOCl. Tubercles became dull in one week and apparently returned to the shiny condition in about three months. However, after three months, many animals appeared to be new in the pool, so it is

Table 2

Number of cycles in the spines of urchins collected from Sunset Bay on 8 December 1962 and 22 January 1963.

Test diameter (cm)	No. of cycles
7.71	9
6.20	8
6.20	8
4.69	6
4.57	8
3.51	6
2.65	6
2.41	5
2.41	5
2.20	6
2.11	5
2.09	5

correlation coefficient r = 0.91

possible that the last sample did not represent animals that had originally been treated. The experiment was repeated in 1965. On 28 July 1965, animals were collected and marked with nylon monofilament. After the primary spines in the interambulacrum opposite the marked ambulacrum had been removed, the animals were returned to the deep tide pool at Sunset Bay that had been used in 1964. Tubercles were dull after one week as in 1964. A sample taken on 8 November 1965 showed dull tubercles; however, samples from 2 February and 18 February had shiny tubercles. Because tubercles were in very poor condition in November and in fairly good condition in February, an estimate of five months for restoration of the shiny condition does not seem unreasonable.

Growth Lines in the Plates of the Test

Plates of the test, both coronal and genital, have been used (Deutler 1926; Moore 1935; 1937) in attempts to determine the ages of urchins. Growth of echinoids, by addition of material around individual plates and by addition of new plates, has long been known. It is mentioned by Agassiz (1874) and was probably understood by Valentin (1842). The incorporation of pigments into the growing meshwork to form growth zones was apparently first pointed out by Agassiz (1904). Deutler (1926) examined thin sections of plates of *Echinus esculentus*, but because of technical difficulties switched to the method of impregnating the skeletal parts with terpineol and methylbenzoate as discussed by Becher (1914). He suggested that the colored material was the result of different diets at different times of year and that animal migration could account for this. Moore (1935) examined the growth lines in genital plates and decided that lines were annual, were produced by echinochrome pigment, and that this was the result of different foods at different times of year. Awerinzew (1911) found that feeding red algae to *Strongylocentrotus dröbachiensis* caused the animals to become red. With this background, I also attempted to determine the ages of animals from test plate morphology.

Figs. 7 and 8 show thin sections of coronal plates which indicate a large number of lines. If only major lines are chosen, the results indicated in Appendix II for 29 December 1963 animals are produced. There appears to be more than one line per year.

Genital plates from animals collected 30 November 1963 were ground and the lines examined. The results, however, were not at all interpretable. The maximum number of lines was four in an animal 6.76 cm in test diameter. Four other animals of about the same size (6.41 to 7.50 cm) each had 3 major lines in the genital plates. The number of lines in the genital plates and the major lines of the coronal plates do not seem to be correlated.

An attempt was made to determine the pigment involved in producing the lines in the plates. The methods used were modified from Fox and Scheer (1941). The absorption maximum for an acidic extraction in diethyl ether was about 480 mμ. The carotinoid echinone has a maximum of 490 mμ and one maximum of beta-carotene is 483 mμ (Fox and Scheer 1941). Although the observed maximum was closest to beta-carotene there is some doubt whether this was the only pigment because,

Figure 7

Negative print of thin sections of coronal plates of two purple urchins showing "growth lines." Plates are arranged in sequence from aboral to oral. In the larger animal (above) the small plate at the extreme right is aboral. The aboral end of the smaller urchin (below) is at the left. The test diameters were 1.47 and 3.92 cm. Relative size has been preserved in printing Figs. 7 and 8.

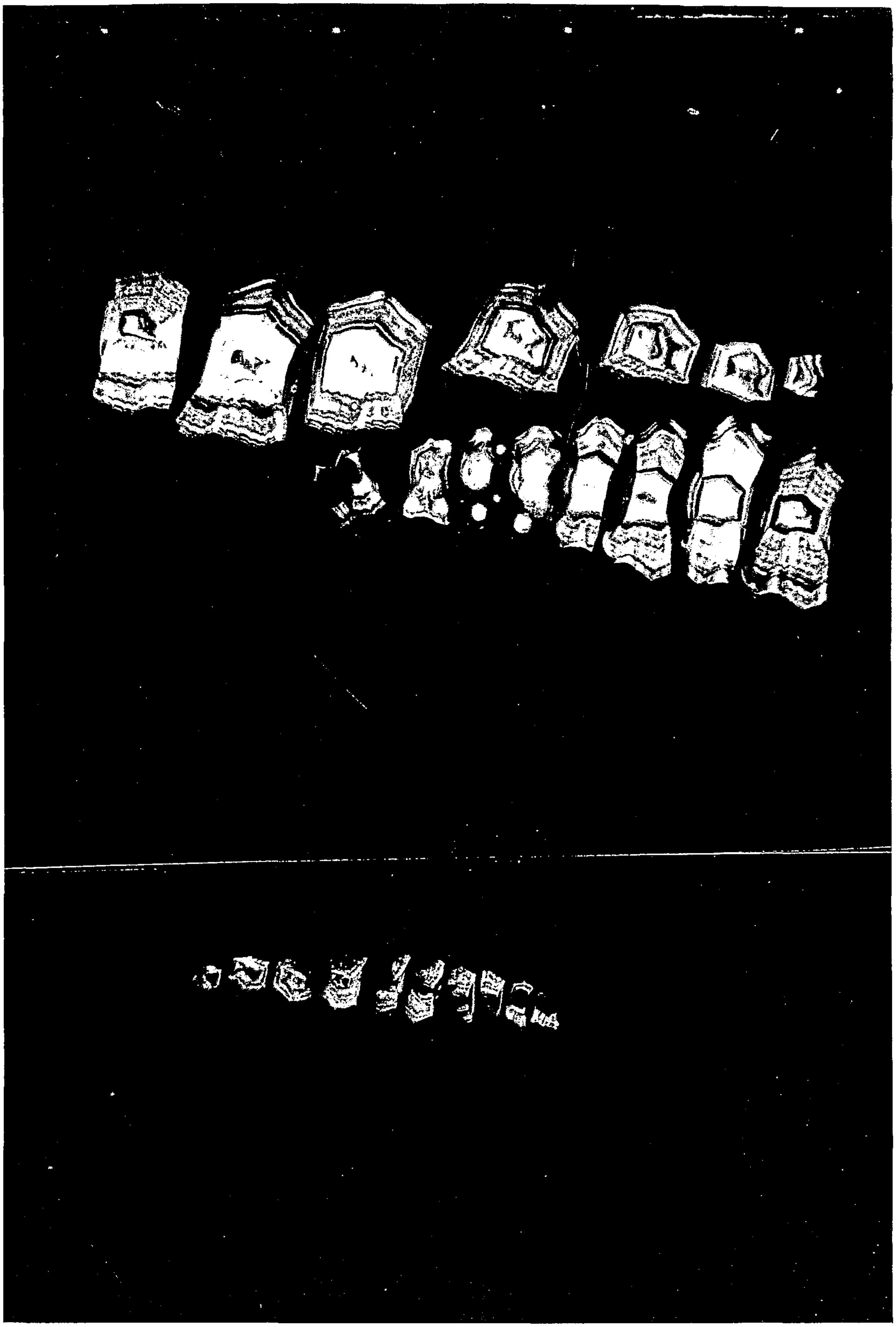
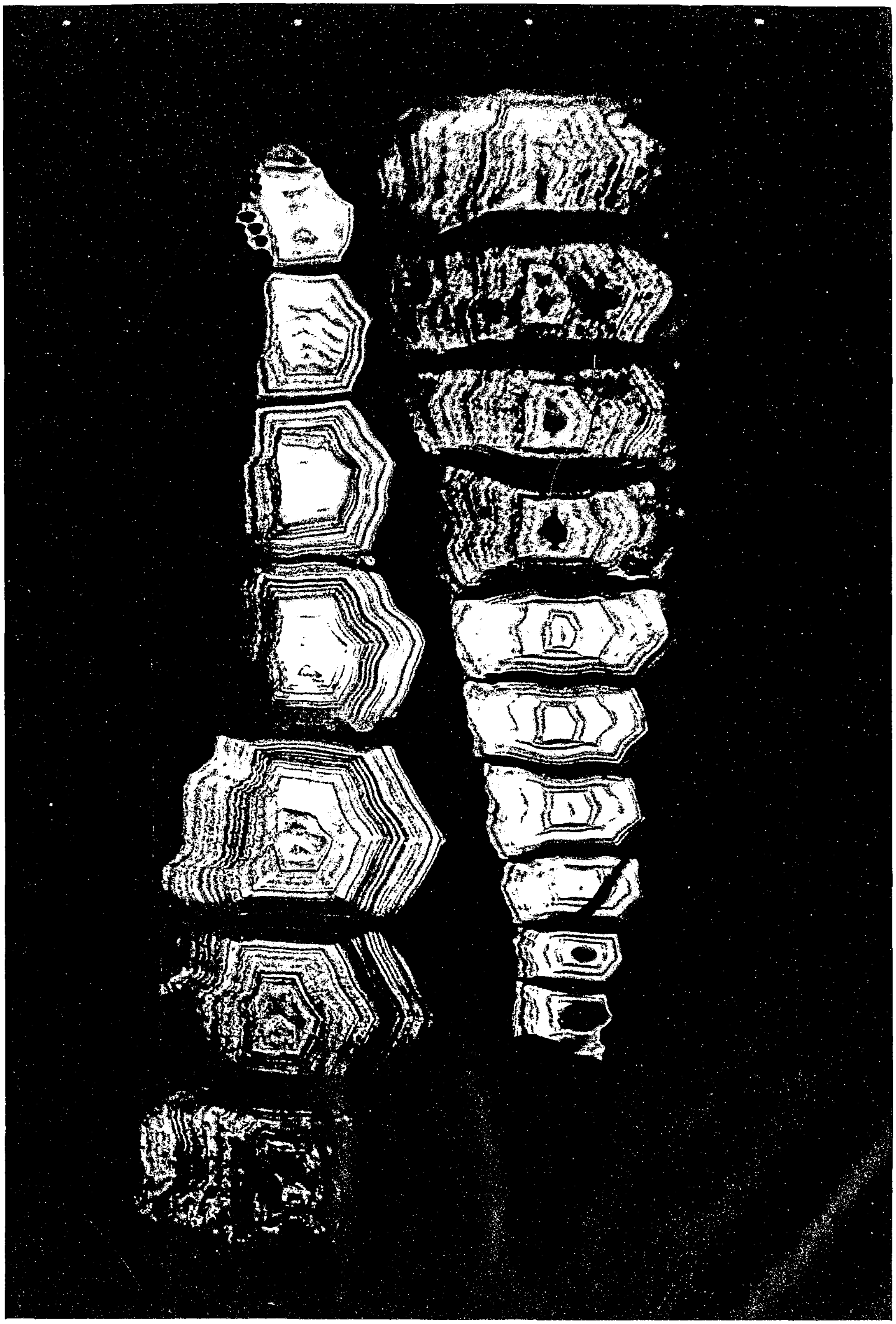


Figure 8

Negative print of coronal plates of an animal 6.86 cm in diameter. Aboral is at the top and left, oral is right and at the bottom. The nature of growth is evident: addition of material around each individual plate and addition of new plates at the aboral end.



when treated with KOH, there was a color shift toward yellow and in a diethyl ether - KOH (in water) partition, part of the yellow pigment became hypophasic which suggests a xanthophyll (Fox and Scheer 1941). In *Strongylocentrotus purpuratus*, the "growth lines" in the test are thus not the result of echinochrome as is suggested for *Echinus* by Moore.(1935). It may or may not be the "red pigment" Deutler (1926) found in the plates of *Colobocentrotus*. The suggestion that the pigment in the test is a carotinoid is, in itself, interesting because Vevers (1963) states, "In echinoids carotinoid is principally, if not exclusively, restricted to the gonads, although the marked sensitivity of these forms suggests that is may be present in the skin." The pigment apparently must be bound to the calcite crystals because it is not removed by NaOCl treatment.

Summary of Results on the Investigation of Spine and Plate Growth

The cycles in the spines represent breaks and subsequent regenerations. Other conditions being the same, large animals can be expected to have more breaks in their spines than do small animals. After a spine has been removed from an urchin, the associated tubercle becomes dull in about one week and again gains its shiny luster in about five months. Growth of the spines is a dynamic process with controlled deposition and uptake of calcite. The pigment causing "growth zones" in the coronal plates appears to be a carotenoid but no explanation has been offered for its deposition, and the relationship of the lines to age is obscure.

Description of the Size Distributions of Urchins at Sunset Bay

Samples of 300 animals were measured on 8, 9 and 10 August 1964 from each of the three major areas. Single measurements from the center of an ambulacrum to the opposite interambulacrum were made with vernier calipers having knife-edged jaws. The results are shown in Fig. 9 and Table 3. The distributions in all three areas are bimodal; moreover, the modes are not in the same positions in all distributions, but shift to the right as samples from the *Postelsia* zone, eel grass area and boulder field are compared. The shift in the positions of the modes suggests differences in growth rates.

In July 1965, samples of animals were again measured in the three areas. In addition to these, several other locations were examined. These are indicated on the map of the bay (Fig. 2) and the distributions are shown in Fig. 9 and Table 3. The relative positions in the intertidal are shown at the bottom of Table 3.

A general correlation exists between intertidal position and size. The mean sizes of small animals in the lowest areas (Fig. 2C, E and F; Fig. 9v to viii) are greater than in the intermediate regions (Fig. 2B, G; Fig. 9iv, ix) which are greater than in the highest region (Fig. 2D; Fig. 9x). When the second modes are compared (large animals), the correlation with intertidal position is not as good. The largest are still found in the lowest areas but the smallest are in an intermediate area (Fig. 9ix). The general impression is that high intertidal areas are less favorable than low areas. Urchins in high pools (such as shown in Fig. 9x) would receive less debris than urchins lower down

Figure 9

Size distributions of animals at Sunset Bay for 1964 and 1965. To be used together with Table 3. Arrows indicate an arbitrary separation of Modes I and II (Table 3).

Area	Map location (Fig. 2)	Distribution
Postelsia zone 1964	A	i
Postelsia zone 1965	A	ii
Eel grass area 1964	B	iii
Eel grass area 1965	B	iv
Boulder field 1964	C	v
Boulder field 1965	C	vi
South and below *Postelsia* zone 1965	E	vii
North and below *Postelsia* zone 1965	F	viii
West and north of eel grass area 1965	G	ix
High area above and north of *Postelsia* zone	D	x

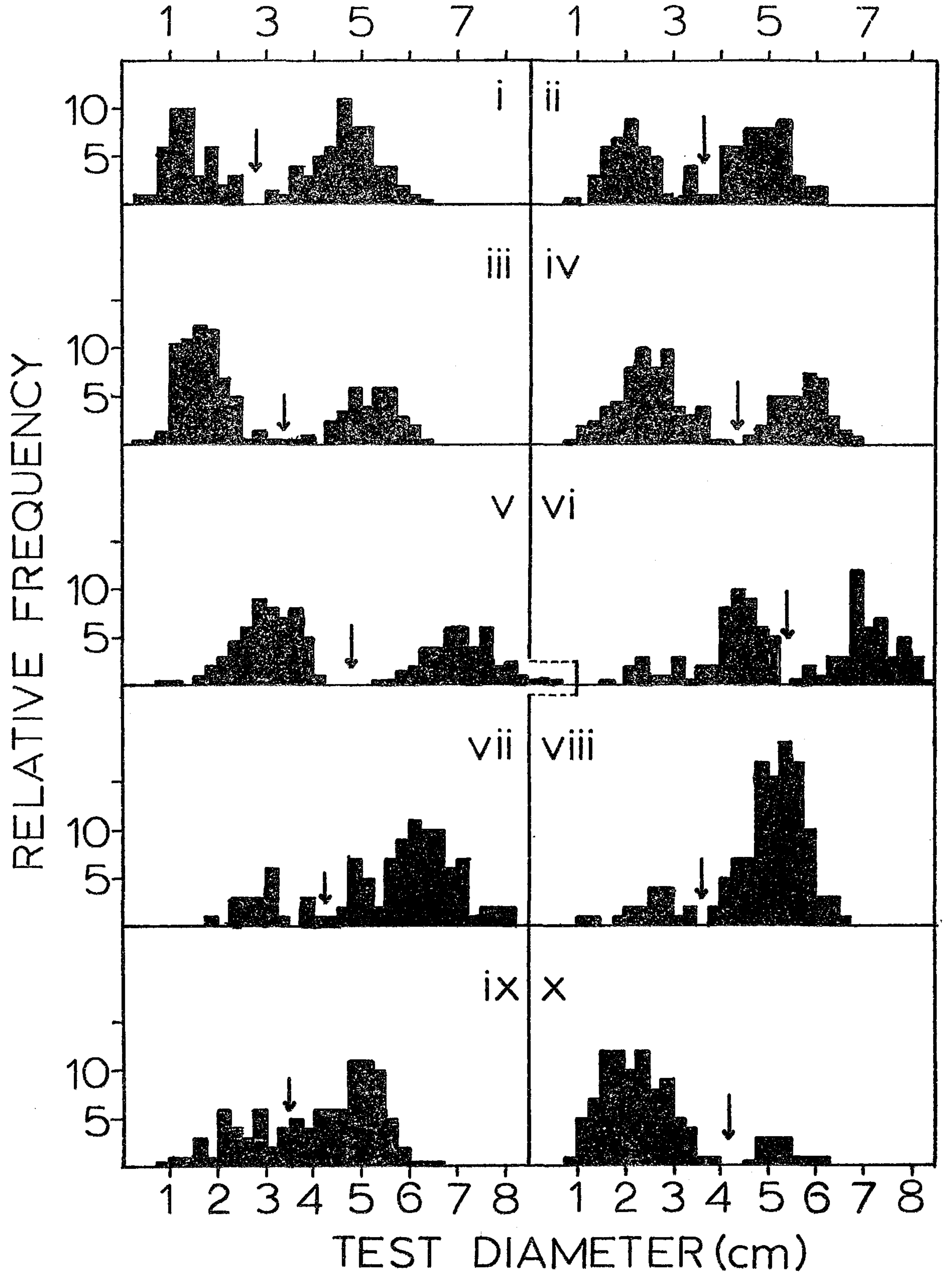

1
3
5
7
1
3
5
7
i
ii
iii
iv
v
vi
vii
viii
ix
x
10
5
RELATIVE FREQUENCY
1 2 3 4 5 6 7 8
1 2 3 4 5 6 7 8
TEST DIAMETER (cm)

Table 3

Positions and importance of modes in size distributions of animals at Sunset Bay.

Distribution (Fig. 9)	Date	Number of Animals		Mean ± SD		Relative Importance	
		Mode I	Mode II	Mode I	Mode II	Mode I	Mode II
i	8-8-64	131	172	1.38 ± 0.43	4.68 ± 0.45	43.2%	56.8%
ii	7-22-65	69	86	2.21 ± 0.57	4.92 ± 0.59	38.7	61.3
iii	8-10-64	200	111	1.62 ± 0.49	5.18 ± 0.40	64.3	35.7
iv	7-9-65	145	93	2.44 ± 0.65	5.69 ± 0.65	60.9	39.1
v	8-9-64	175	136	2.95 ± 0.61	7.08 ± 0.63	56.3	43.7
vi	7-29-65	92	84	4.07 ± 0.69	7.15 ± 0.69	52.0	48.0
vii	7-28-65	21	83	3.00 ± 0.53	6.16 ± 0.85	20.2	79.8
viii	7-28-65	22	100	2.50 ± 0.56	5.20 ± 0.60	18.0	82.0
ix	7-23-65	73	145	2.39 ± 0.65	4.80 ± 0.66	33.5	66.5
x	6-28-65	194	27	2.08 ± 0.80	5.28 ± 0.42	87.8	12.2

Relative intertidal positions starting with the lowest: E and F, C, A, B and G, and D.

because of the differences in lengths of time the animals would be covered by moving water. There would also be extremes of temperature and salinity with associated changes in oxygen tension.

Examination of the distributions indicates that there are differences in the relative importance of the two modes. There is a decrease in relative importance of the large animals from low to high intertidal. Changes in importance of the first mode in the three major regions from 1964 to 1965 are shown in Fig. 9 and Table 3. The relative decrease in all three cases is about 4%. This suggests that differential survival can not explain differences in the relative importance of the two modes. It is possible, chance factors causing mass mortality in the high areas could explain the intertidal differences. Drastic changes in salinity during heavy winter rains could kill large numbers of animals, as could extremely high termperatures during low summer tides. Under laboratory conditions, small animals are more tolerant of extreme conditions than are large animals. Urchins over 7 cm could not be maintained in the circulating sea water system described earlier, although small animals could be kept with no trouble. Four small animals (0.5 cm to 1.2 cm) were kept for three months in a 1-gal. jar at 11° C without aeration, food or changed water. At the end of this time, three animals were still alive (one had been eaten by the others), and the salinity was so high that crystals were forming in the water. There is no question that there is a loss of tolerance with increased size. This may be very important in explaining the changes in importance of large animals with changes in intertidal position. If only extremes of temperature or salinity cause mass mortality, it is possible that no such extremes occurred during 1964-65, and so the mortalities for the year were the same in the three major areas. If information were available for several years, differences might indeed exist.

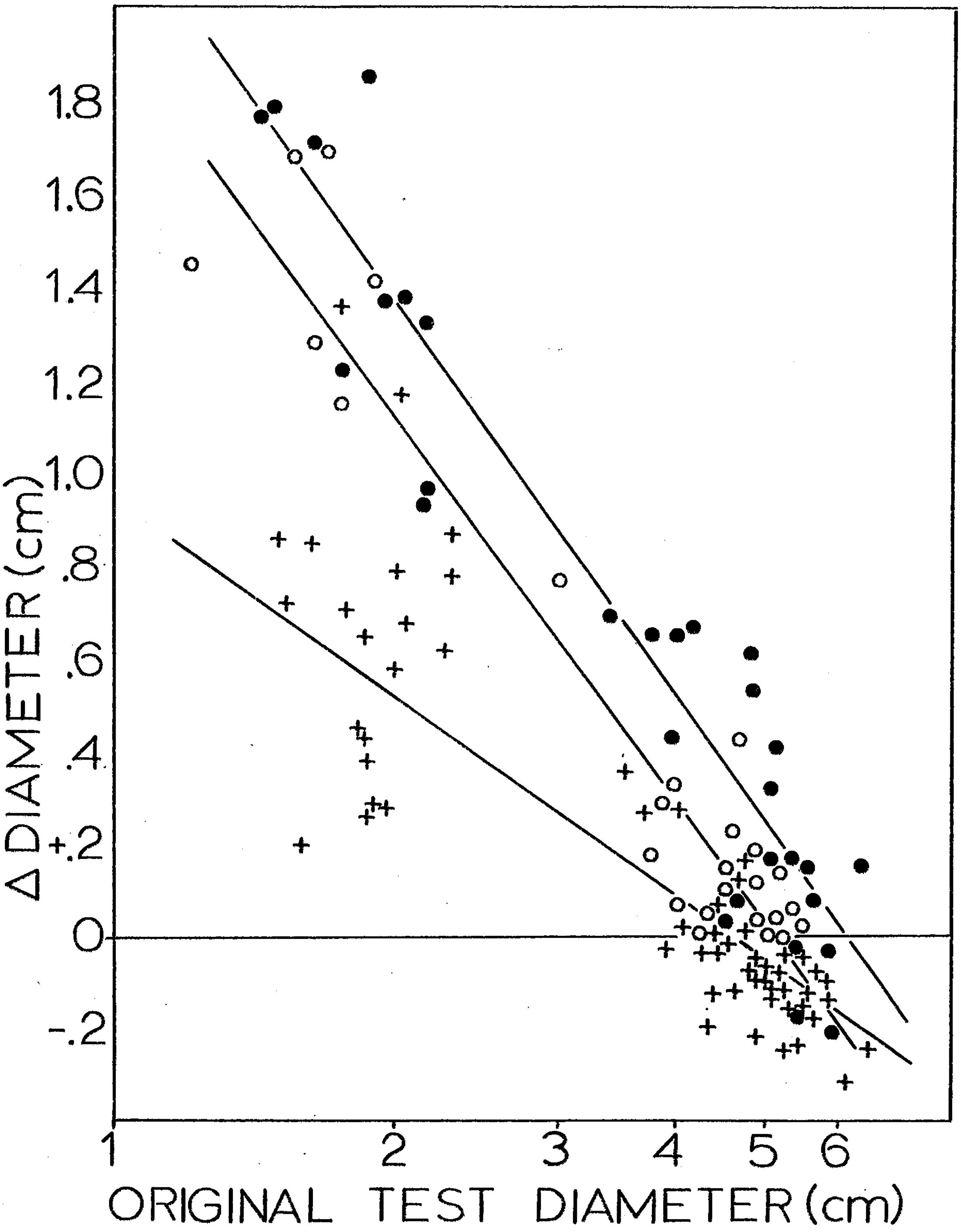
Examination of Growth Rates in the Three Major Study Areas

As can be deduced from the size distributions, differences in growth rates exist among animals of three major study areas. This was conclusively demonstrated with marked animals placed in the three areas in the summer of 1964. Changes in the diameters of these animals confirmed that differences in growth rates existed and, quite unexpectedly, that urchins are able to decrease in diameter. Examination of Fig. 10 shows that animals grow most slowly in the *Postelsia* zone, most rapidly in the boulder field and at an intermediate rate in the eel grass area. Each point represents the mean of five measurements of diameter, both for the initial diameter in 1964 and for the change in diameter as measured in the summer of 1965. Lines in Fig. 10 are least squares regressions. The test for the significance of difference was by regression analysis (Dixon and Massey 1951, pp. 216-219). The 0 intercept for the boulder field animals is 6.13 cm; it is 5.11 cm for animals in the eel grass area and 4.64 cm in the *Postelsia* zone. Animals showing negative growth in the eel grass area have not been plotted in Fig. 10 simply because of the congestion of points but are shown in Fig. 10A. The maximum amount of shrinkage observed was slightly more than 3 mm and was in an animal from the *Postelsia* zone.

Figure 10

Diameter changes over a 1-year period in each of the three major areas determined from marked animals. Each point represents from 3 to 5 original diameter measurements (the mean is plotted) and 5 measurements 1 year later. Standard errors for representative changes in diameter (Δd) are given in Appendix V. Negative values for eel grass animals are not shown. For these see Figure 10A.

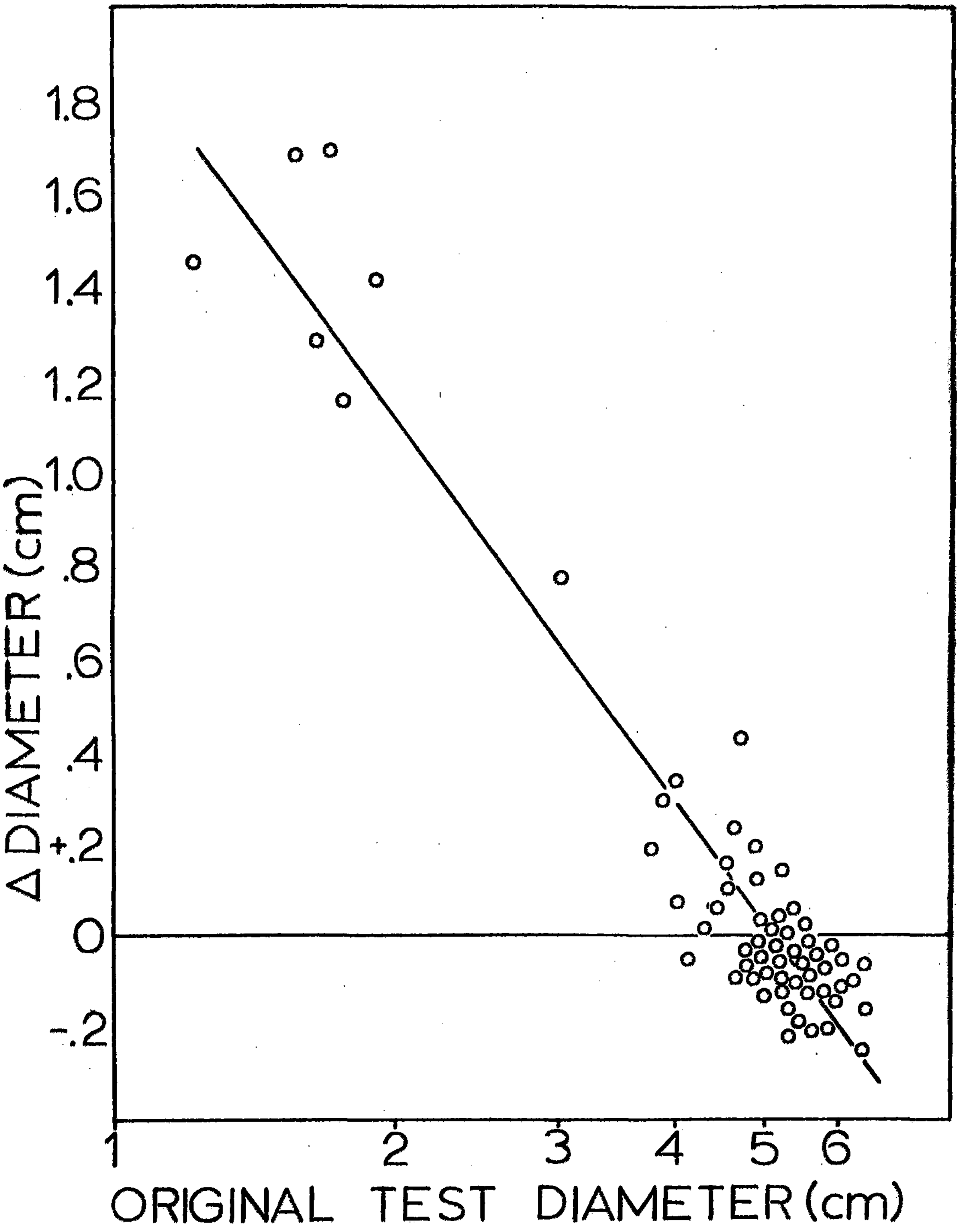
+	*Postelsia* zone
o	eel grass area
●	boulder field



1.8
1.6
1.4
1.2
1.0
.8
.6
.4
+.2
0
-.2
Δ DIAMETER (cm)
1
2
3
4
5
6
ORIGINAL TEST DIAMETER (cm)

Figure 10A

Diameter changes of marked animals in the eel grass area.


1.8
1.6
1.4
1.2
1.0
.8
.6
.4
+.2
0
-.2
Δ DIAMETER (cm)
1
2
3
4
5
6
ORIGINAL TEST DIAMETER (cm)

The ability of echinoids to resorb calcite was shown in the previous section on spine growth; shrinkage of animals would therefore simply indicate the uptake of calcite from around each individual plate in the test. The ability to take up calcite in such a manner that the test would not be weakened was also indicated in the section on spine growth where a highly ordered rearrangement of calcite was shown to take place to maintain "cycles of wedges" on the outside of the spine.

Seasonal differences in growth are shown in Table 4. Growth apparently was greatest from July to December, least during the winter and increased during the period from March to June. Low numbers of recaptures unfortunately do not permit differences among the three areas to be resolved during the winter and spring.

In summer 1965, animals were again marked and placed in all three areas. A total of 201 urchins were gathered from the eel grass area, marked and distributed in the following manner: 67 to the eel grass area, 62 to the *Postelsia* zone and 72 to the boulder field. As shown in Table 4, there is apparently no difference between growth in 1964 and 1965. Short-term effects of marking were examined by comparing the growth of animals marked in 1964 with those marked in 1965. The two time periods examined, July to November 1965 and November 1965 to March 1966, are not significantly different with respect to time of marking (Table 4). Possible effects of handling animals were assessed by comparing the diameter changes of animals recaptured only once after marking with animals recaptured twice and three times. Handling apparently has no effect (Table 4).

Table 4

Analysis of growth information gathered from marked animals in the *Postelsia* zone (PZ), eel grass area (EG) and boulder field (BF). Comparison by regression analysis (Dixon and Massey 1951, pp. 216-19)

Dates	Number of animals examined			Significance of difference	Regression equations
	PZ	EG	BF	among areas	
7-64 to 12-64 (summer and fall)	58	33	32	$F_{4,117} = 22.82$, $p<.01$	PZ $y = -0.92x + 1.07$[a] EF $y = -1.47x + 1.53$ BF $y = -1.37x + 1.58$
12-64 to 4-65 (winter)	32	8	6	$F_{4,40} = 1.65$, $p>.05$	$y = -0.18x + 0.61$
4-65 to 7-65 (spring and summer)	34	32	6	$F_{4,66} = 7.14$, $p<.05$	PZ $y = -0.32x + 0.76$ EG $y = -1.10x + 1.30$ BF $y = -0.85x + 1.16$
7-65 to 11-65 (summer and fall)	24	60	8	$F_{4,86} = 10.83$, $p<.05$	PZ $y = -0.27x + 0.73$ EG $y = -1.13x + 1.35$ BF $y = -0.68x + 1.20$
11-65 to 3-66 (winter)	15	43	3	$F_{4,55} = 4.13$, $p>.05$	$y = -0.17x + 0.61$
7-64 to 7-65 (one year Fig. 10 and 10A)	63	71	30	$F_{4,158} = 36.4$, $p<.01$	PZ $y = -1.43x + 0.94$ EG $y = -2.77x + 1.97$ BF $y = -2.83x + 2.28$

---

[a] x = original diameter in logs, y = change in diameter (Δd) for the specified time period

Table 4 (cont.)

Dates	Number of animals examined			Significance of difference
	Area	1964	1965	between years
Summer and fall 1964 with summer and fall 1965	PZ	58	24	$F_{2,78} = 7.22, p>.05$
	EG	33	60	$F_{2,89} = 2.44, p>.05$
	BF	32	8	$F_{2,36} = 1.61, p>.05$
Winter 1964 with winter 1965	all areas	47	61	$F_{2,104} = 0.16, p>>.05$

Assessment of short term effects of marking by comparing animals in the eel grass area marked in 1964 ("old") with animals marked in 1965 ("new").

	"old"	"new"	between animals newly marked and those marked the previous year
7-65 to 11-65	24	36	$F_{2,56} = 2.29, p>.05$
11-65 to 3-66	16	27	$F_{2,39} = 0.02, p>>.05$

Table 4 (concluded)

Assessment of effect of handling animals on growth by comparing animals marked in 7-64 and not remeasured until 7-65 with animals recaptured and measured twice and three times.

	Area	Once	Twice	3x	among numbers of times recaptured
7-64 to 7-65	PZ	11	25	22	$F_{4,52} = 1.71$, $p>.05$
	EG	22	38	12	$F_{4,66} = 4.01$, $p>.05$

Growth data from individuals marked in summer 1963, although limited, are shown in Table 5. As previously indicated, tag loss could account for the poor recovery of animals in June 1964. The general information at least does not contradict the results obtained in 1965.

Examination of the shifts in positions of the modes in the size distributions (Fig. 9) from 1964 to 1965 and calculations of the positions of modes for age classes based on the growth rates established from marked animals, indicates that good settling occurred only in 1963 and that 1962, 1961, 1960 and possibly 1959 were years of poor settling. The years 1964 and 1965 were observed to be poor for settling.

Associated with the differences in growth rates in the three areas are differences in gonad production and organic material (exclusive of the gonads). A "gonad index" such as used by Lasker and Giese (1954), Bennett and Giese (1955), Greenfield et al. (1965) was not used to describe gonad development because the relationship between total size and gonad size is not linear as, indeed, has been shown by Moore et al. (1963a). Moreover, when both calcite weight and gonad weight are converted to logarithms, the regressions do not pass through the origin, so that use of a ratio is invalid if samples of different sized animals must be compared (as is the case in this study). Moreover, the individual samples in this study have such great variability in gonad development that regressions for a particular season are somewhat meaningless with the numbers of animals used.

Table 5

Growth data for urchins in the eel grass area, 1963-64. After one year, only 6 animals were recovered of 131 marked. Measurements are in centimeters.

Animal	Date	Mean diameter ± SE	No. of measurements
1	7-24-63	5.88	1
	11-30-63	5.67 ± 0.007	2
	6-25-64	5.56 ± 0.034	3
2	7-63	5.34	1
	11-63	5.19 ± 0.023	3
	6-64	5.05 ± 0.025	4
3	7-63	5.64	1
	6-64	5.53 ± 0.010	4
4	7-63	6.00	1
	11-63	5.82	1
	6-64	5.81 ± 0.028	4
5	7-63	5.98	1
	6-64	5.93 ± 0.030	4
6	7-63	4.04	1
	11-63	3.94 ± 0.021	2
	6-64	4.02 ± 0.018	4

The less precise analysis based on maximum development seems to be more appropriate (Fig. 11). The trends as shown in Table 6, however, are probably valid or at least they seem to be in the expected direction; they indicate greatest production in the boulder field and least in the *Postelsia* zone. There is a suggestion of a major gonad build-up in fall. Some spawning animals, however, have been observed in both winter and summer; possibly the suggestion of Giese et al. (1958) that there is no definite season is correct.

There are differences in amounts of organic material (other than gonads) among the animals with respect to time as well as area. The pooled data for each season (Table 7) represent about 60 animals per sample with about 20 per area or 10 per area for each of the two collecting dates of a season. Samples were pooled in the follow manner: fall is 23 September 1964 and 23 October 1965; winter is 30 November 1964 and 29 January 1965; spring is 15 March 1965 and 11 April 1965; and summer is 27 June and 31 July 1965. Regression analysis was used to test the adequacy of a single regression to describe animals in the three areas for each season. Only in summer was there a significant difference (Table 7). In summer, animals of the *Postelsia* zone had less organic material for a given size than did animals from the other two areas (Fig. 12). Eel grass and boulder field urchins were not significantly different (Table 7). There was more organic material in samples in fall than in summer, less in winter and spring and an increase again during summer. Animals from the *Postelsia* zone apparently do not recover as rapidly as do urchins

Figure 11.

Gonad size as a function of total calcite weight. All dates are pooled.

+ *Postelsia* zone

o eel grass area

● boulder field

A conversion table for calcite weight into test diameter and wet weight is given in Table 13.

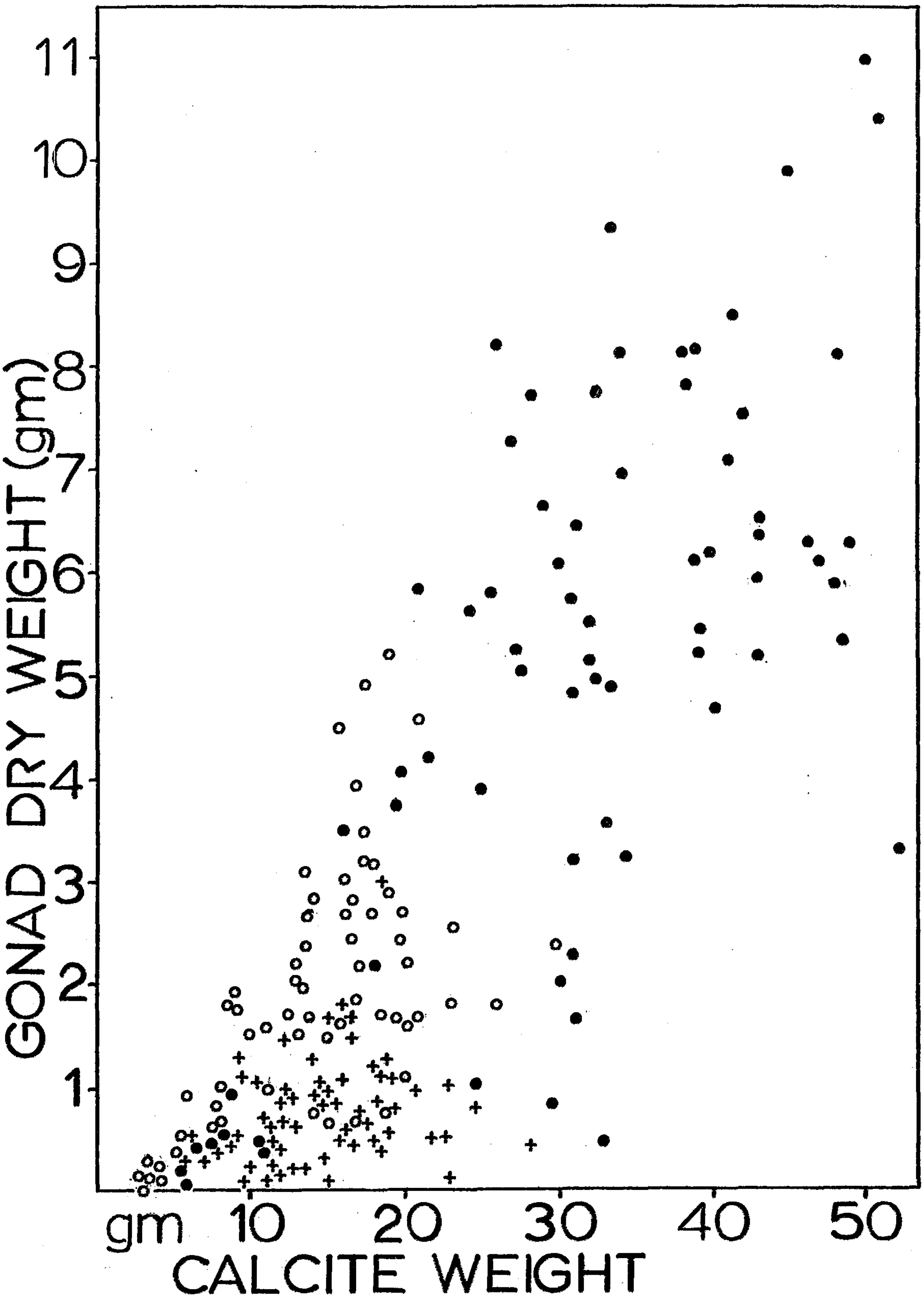

GONAD DRY WEIGHT (gm)
11
10
9
8
7
6
5
4
3
2
1
gm
10
20
30
40
50
CALCITE WEIGHT

Table 6

Differences in gonad development among the three major areas. Values for each area are the numbers of animals with gonads from 0 to 49% and 50 to 100% maximum size (determined from Figure 11).

Season	*Postelsia* zone		Eel grass area		Boulder field	
	0-49%	50-100%	0-49%	50-100%	0-49%	50-100%
Fall	20	0	10	10	1	15
Winter	20	0	9	10	4	13
Spring	18	1	12	8	11	9
Summer	19	0	13	5	9	11

Table 7

Regression analysis of organic material in animals from the *Postelsia* zone (PZ), eel grass area (EG) and boulder field (BF).

Season	No. of animals			Significance of difference between areas	Regression equations
	PZ	EG	BF		
Fall	20	19	16	$F_{4,49} = 4.22$, $p>.05$	$y = .120x + 0.33$[a]
Winter	20	19	17	$F_{4,50} = 2.3$, $p>.5$	$y = .100x + 0.21$
Spring	19	20	19	$F_{4,52} = 0.23$, $p>.05$	$y = .100x + 0.10$
Summer	19	19	20	$F_{4,52} = 21.13$, $p<<.01$	PZ $y = .077x + 0.35$
	--	19	20	$F_{2,35} = 7.73$, $p>.05$	EG and BF $y = .107x + 0.25$

Fall, winter and spring should not be described with a single line. ($F_{4,163} = 15.98$, $p<.01$)

Winter and spring can be described with one line ($F_{2,110} = 2.46$, $p>.05$; $y = 0.101x + 0.14$).

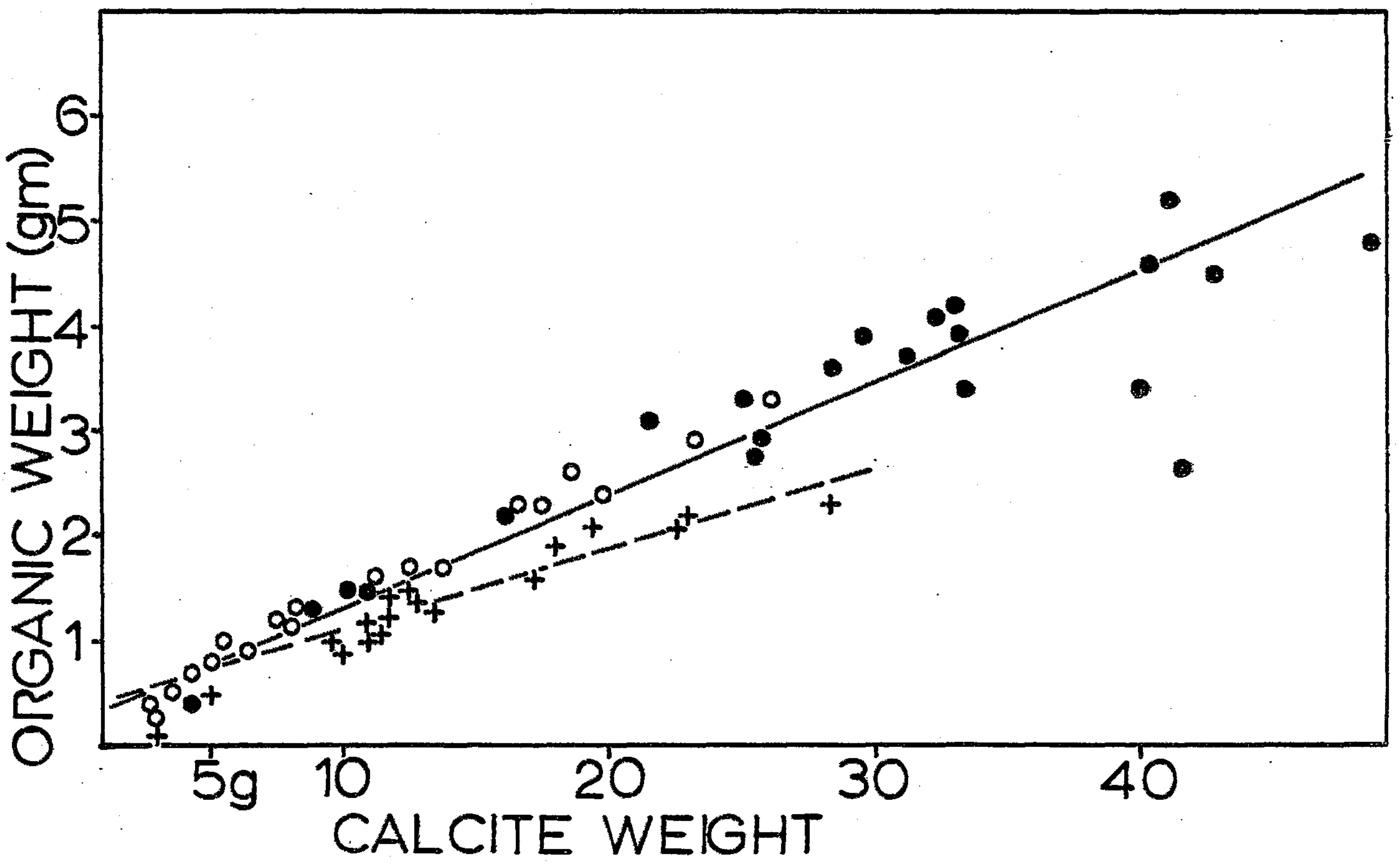
[a] x = calcite weight in grams, y = total organic dry weight in grams (other than gonad dry weight and gut contents).

Figure 12.

Organic weight (gut wall and tissues of the test, spines and tube feet) in the summer as a function of total calcite weight. Lines are least squares regressions. Other seasons are given in Table 7.

+	*Postelsia* zone
o	eel grass area
●	boulder field

A conversion table for calcite weight into test diameter and wet weight is given in Table 13.


ORGANIC WEIGHT (gm)
1
2
3
4
5
6
5g
10
20
30
40
CALCITE WEIGHT

in the other two areas. A cycle of stored glycogen in the wall of the gut was found in *S. purpuratus* in California by Lawrence et al. (1965). The changes in organic weight shown among animals at Sunset Bay probably represent this cycle of stored food.

As indicated in Methods, two general features of the environment are to be considered as possibly important in determining the rate of growth and ultimate size of individuals: surf exposure, which could regulate growth by requiring energy expenditure for spine repair and replacement, and food availability.

Effects of Spine Breakage on Growth

During the spring and summer of 1964, an experiment was conducted to test whether breakage of spines could have an effect on increase in test diameter. On 24 May 1964, 46 age-class I animals were collected at Sunset Bay. On 25 May, the urchins were divided into two groups and measured. Spines were cut to within several millimeters of the base in one group and the animals were returned to aquaria and maintained at 11° C. Individuals were again measured on 21 June, 29 July and 25 August. Urchins were transported from Eugene to the Oregon Institute of Marine Biology at Charleston on 16 June. At first, animals were kept in wooden and glass aquaria but they did not seem to adjust properly. On 21 June, the animals were measured (the spines of the experimental group were not again broken) and the animals were moved to a plastic wading pool with rocks and kept in running sea water. Spines of the experimental animals were again broken on 29 July. For the entire experiment animals were fed the brown alga

Hedophyllum. By the end of 97 days, the control and experimental means had diverged sufficiently that they were statistically distinct (Table 8). This indicates that spine breakage and subsequent repair can have an effect on the increase in test diameter of an urchin and that, other environmental factors remaining constant, animals which must repair spines will increase in diameter, or "grow" in the sense of this study, more slowly than animals which do not have to expend energy in this fashion.

Breakage of Spines in the Field

The first method was to measure breaks in spines. A total of 85 animals were examined: 30 from the *Postelsia* zone, 24 from the eel grass area and 21 from the boulder field. Five spines from each animal were impregnated with an oil of the same refractive index as calcite, as described in Methods, and viewed by transmitted light. Fig. 13 shows the maximum break measured for each spine as a function of test diameter. The only relationship is that larger animals show larger breaks. The three areas are not significantly different (Fig. 13). There is a suggestion that if a force great enough to break a very large spine were applied to a somewhat smaller spine, the spine would be ripped completely from the test. Conditions apparently are severe enough in all areas that a linear relationship between diameter of maximum break and test diameter is maintained throughout the range of observations. Under less severe conditions, a curve should be produced which would approach a break diameter characteristic of the set of conditions i.e. the less severe the conditions the smaller

Table 8

Effect of spine breakage and regeneration on increase in test diameter. Experimental animals had spines broken on day zero and after 65 days. Diameter means are from 3 measurements and are in centimeters.

Date	Time in days	Experimental		Control	
		No. of animals	Mean diameter ± SE	No. of animals	Mean diameter ± SE
5-25-64	0	23	1.61 ± 0.05	23	1.64 ± 0.05
6-21-64	27	23	1.61 ± 0.05	22	1.66 ± 0.06
7-29-64	65	22	1.87 ± 0.09	23	2.05 ± 0.07
8-20-64	87	22	1.87 ± 0.09	23	2.10 ± 0.07

After 87 days the variances of the two samples were still the same ($F_{21,22} = 1.92$, $p > .05$)

The means are significantly different by a t-test ($t = 1.98$, $df = 43$, $p < .05$).

Figure 13.

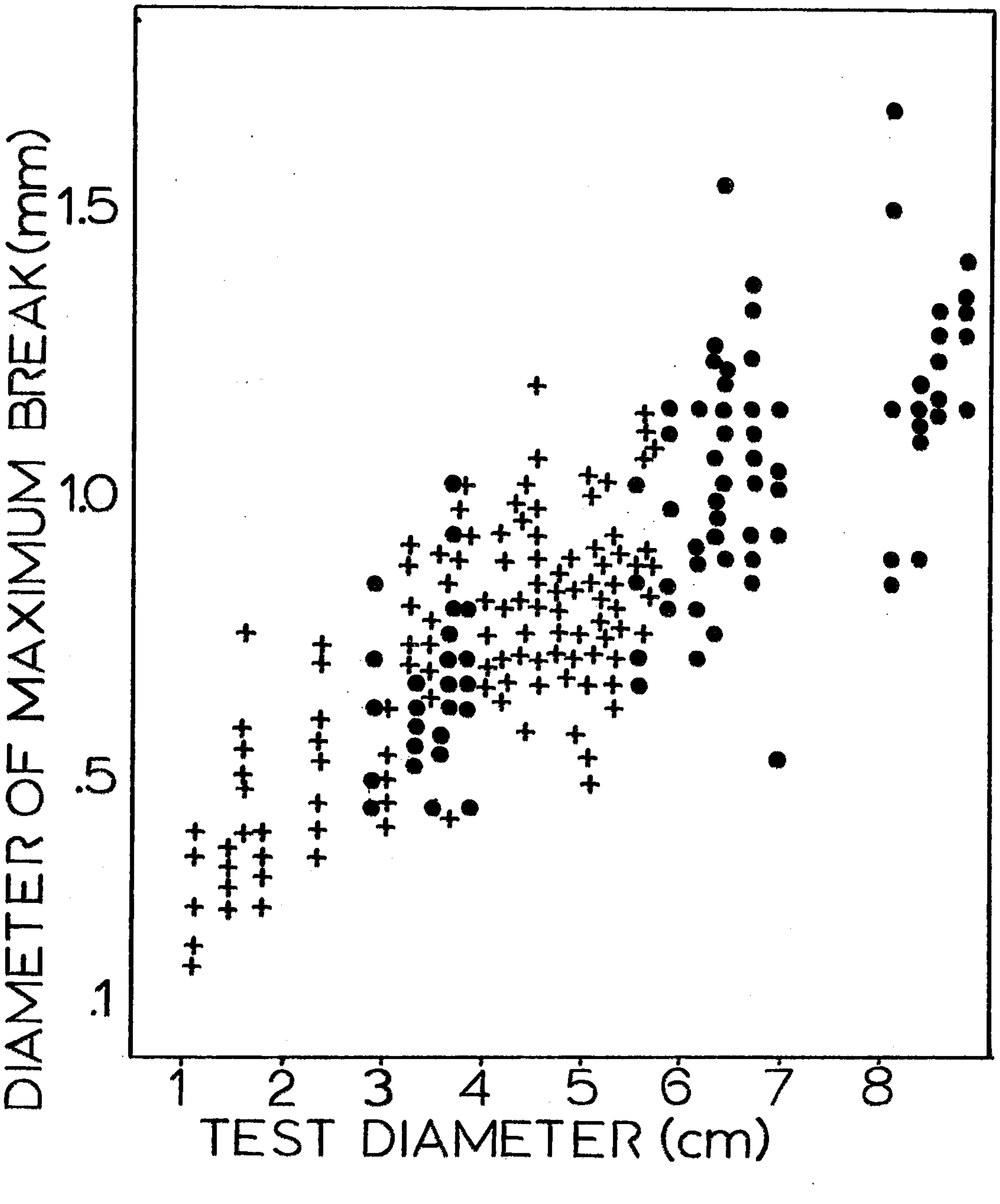
Maximum break seen within a spine as a function of size of animal. Five spines are shown for each animal. Some points in the center of the distribution and eel grass animals have not been plotted.

The three areas are not significantly different by regression analysis ($F_{4,374} = 4.34, p>.05$). The regression equation is:

$y = 0.118x + 0.18$ where x = test diameter in centimeters and

y = maximum break in millimeters.

+	*Postelsia* zone
●	boulder field


DIAMETER OF MAXIMUM BREAK (mm)
1.5
1.0
.5
.1
1
2
3
4
5
6
7
8
TEST DIAMETER (cm)

the maximum break. It is expected that subtidal populations will show this.

Complete Removal of Spines under Field Conditions

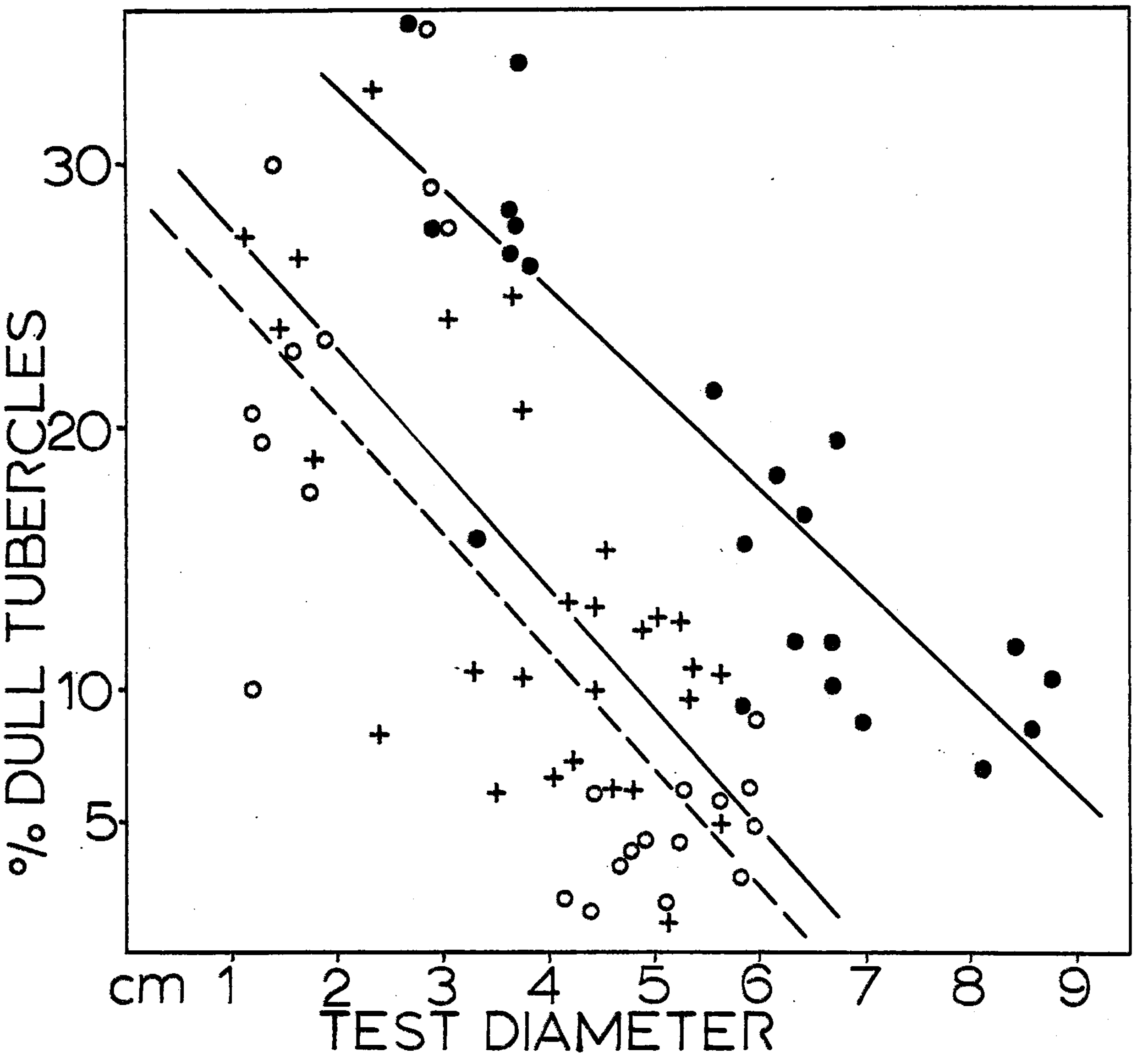
As shown in Methods, when a spine is completely removed from the test the associated tubercle becomes dull in about one week and, with regeneration of the spine, becomes shiny again in from three to five months. Primary interambulacral tubercles from samples of animals collected in August 1964 were examined and recorded as either shiny or dull. The "percent dull tubercles" of an animal represents an accumulation of spines ripped from the test over a 3- to 5-month period. For any given test diameter, the animals of the boulder field show a greater number of lost spines than do urchins of the other two areas (Fig. 14). Furthermore, smaller animals lose relatively more spines than do large animals. This is not too surprising considering that a force just strong enough to rip a primary spine from a small animal would only break a primary spine on a large individual. Spine breakage and regeneration are apparently, in this case, not adequate contributors to size regulation; the area with the greatest amount of spine loss also shows the highest growth rate. Although spine breakage was shown to be important in regulating growth rates in the laboratory (Table 8), it must be concluded that there are more important factors involved in regulating urchin growth in the particular areas at Sunset Bay. It is possible, however, that situations do exist where spine breakage in the field could be important.

Figure 14.

Percent dull tubercles as a function of test diameter. All primary interambulacral tubercles were examined for each animal.

The three areas are significantly different by regression analysis ($F_{4,68} = 39.72$, $p << .01$).

+	*Postelsia* zone $y = -4.58x + 32.12$
o	eel grass area $y = -4.49x + 29.50$
●	boulder field $y = -3.74x = 39.72$


30
20
10
5
% DULL TUBERCLES
cm 1
2
3
4
5
6
7
8
9
TEST DIAMETER

Amounts of Food Eaten per Day

A second possible factor causing growth differences is the amounts of food eaten in the three areas. This was examined, as described in Methods, using tattooed algae. A major problem with this technique was that it was not possible to tell without dissection whether an animal had indeed eaten the marked food. This possibly could have been obviated by using isotope labeling. The success of recovery of marks was very variable and is shown in Table 9. Generally, the animals in the boulder field were less likely to ingest the marked algae than were animals in either the eel grass area or the *Postelsia* zone. The highest and most consistant success was in the *Postelsia* zone. In the July and October 1965 samples, none of the animals from the boulder field had a mark. This makes comparisons with the other areas impossible for these time periods. Fig. 15 shows the variability in the food gathered in one day. The boulder field data are presented in Table 10. Data for the critical summer months are missing for both the boulder field and the eel grass area. The rest of the year, with the number of animals dissected and the degree of variability within a single sample, does not show significant differences in the amounts of food eaten in 24 hours between the *Postelsia* zone and the eel grass area (Table 11). The positive correlation indicated by the Corner Test (Table 11) simply means that large animals probably eat more than small animals and is not very profound. In retrospect, the degree of variability is expected because urchins are opportunistic in their feeding habits. Thus on any day, an individual may or may

Table 9

Recovery success of tattooed pieces of algae 24 hours after feeding to animals in the field.

Date	*Postelsia* zone		Eel grass area		Boulder field	
	No. with mark	No. without	No. with mark	No. without	No. with mark	No. without
9-23-64	5	5	9	1	2	4
11-30-64	7	3	6	3	4	2
1-29-65	8	2	6	4	2	9
3-15-65	9	0	10	0	5	5
4-11-65	7	3	7	3	6	4
6-27-65	9	0	6	3	3	7
7-31-65	8	2	1	9	0	10
10-23-65	9	1	6	3	0	10
total	62	13	51	26	22	51
Percent success	82.7		66.2		30.1	

Figure 15.

Rate of feeding as a function of size as determined from feeding animals tattooed algae. See Table 11 for statistical analysis. The line was fit by least squares regression.

A conversion table for calcite weight into test diameter and wet weight is given in Table 13.

+	*Postelsia* zone
o	eel grass area

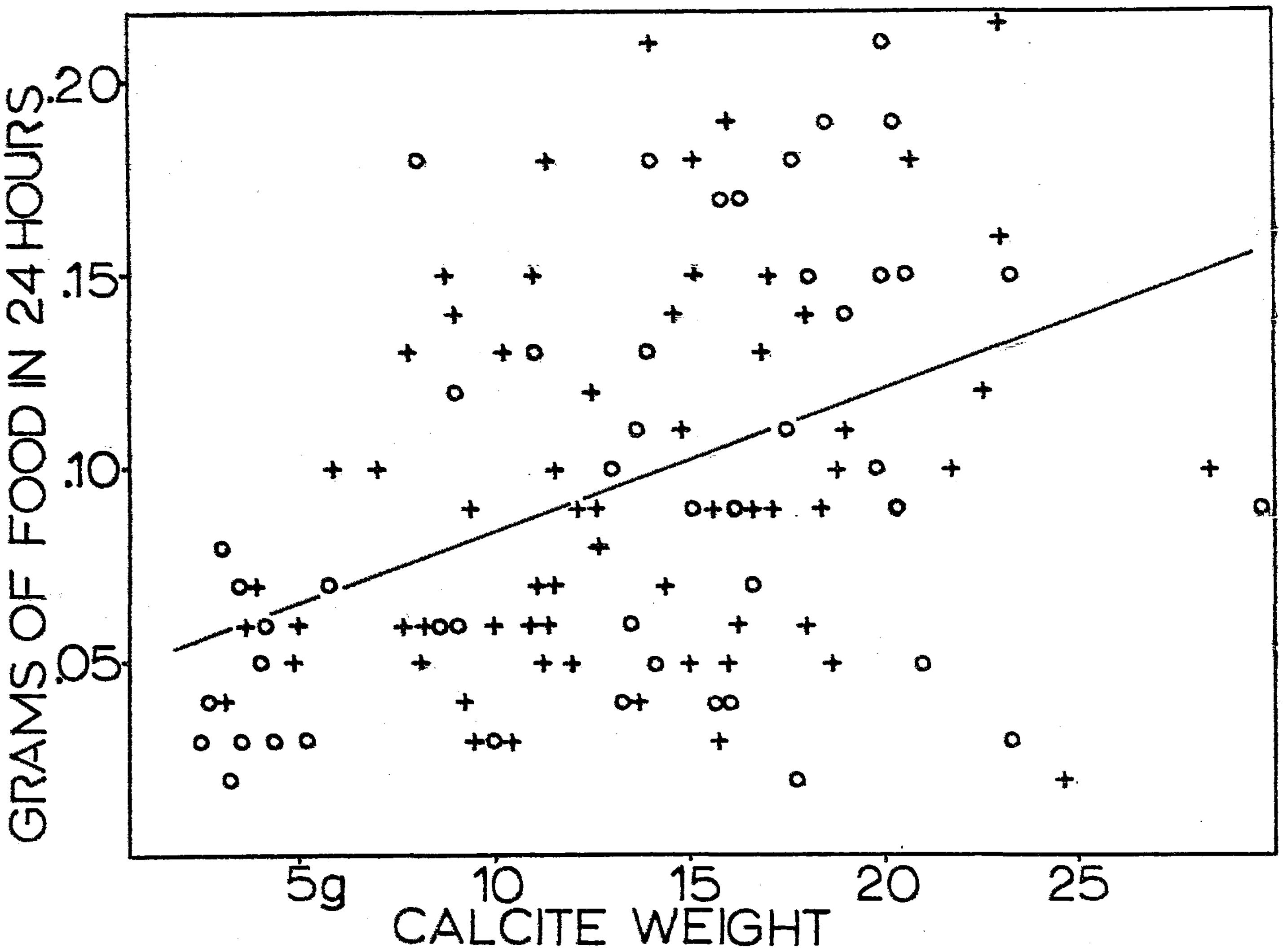

GRAMS OF FOOD IN 24 HOURS
.20
.15
.10
.05
5g
10
15
20
25
CALCITE WEIGHT

Table 10

Rate of feeding of animals in the boulder field. The material eaten in 24 hours was determined by tattooed algae fed one day before collecting. All values are in grams.

Date	Total calcite weight	organic material eaten in 24 hours
9-23-64	34.1	.36
	31.2	.52
11-30-64	48.3	.48
	39.9	.17
	38.8	.65
	19.6	.34
1-29-65	27.6	.17
	5.6	.03
3-15-65	32.0	.02
	30.8	.04
	8.4	.03
	7.3	.04
	5.4	.02
4-11-65	38.8	.31
	31.0	.12
	18.1	.13
	5.9	.10
	4.7	.11
	3.5	.04
6-27-65	49.1	.52
	33.4	.19
	10.5	.05
7-31-65	None	
10-23-65	None	

Table 11

Regression analysis of the organic material eaten in 24 hours by animals in the *Postelsia* zone (PZ) and eel grass area (EG) where x = calcite weight in grams and y = dry weight of organic material eaten in 24 hours as determined by use of tattooed algae.

Season	Area	No. of animals				Significance of difference
		Fall	Winter	Spring	Summer	among seasons
All 4	PZ	14	15	16	17	$F_{6,54} = 2.88$, $p>.05$
	EG	15	10	16	7	$F_{6,40} = 1.61$, $p>.05$
	PZ	EG				between areas
	62	48				$F_{2,106} = 1.13$, $p>.05$

By analysis of variance the slope of the least squares regression is not significantly different from zero ($F_{1,108} = 0.198$, $p>.05$).

Using a Corner test (Tate and Clelland 1957), a positive association is suggested (Quadrat sum = 23, $p>.01$).

not catch a large piece of floating debris. This means that increased precision could be gained either by increasing the numbers of animals in a sample (probably by at least a factor of 4 or 5) or by increasing the number of days between the feeding of the tattooed algae and collecting the animals. This latter method would, however, increase the length of time of food in the gut and so increase loss of weight by digestion.

The total amount of organic material in the gut for a given size is presented in Table 12. The amounts are about the same for all seasons except winter, when the amount is lower. This suggests that, if differences in amounts of food eaten do exist among the areas, there would have to be differences in the rates of turnover of the gut contents. Possibly a study of gut content turnover times using radioisotope labeling could lead to a relatively simple estimate of feeding rates.

Distribution of inorganic components of the gut contents is shown in Figs. 16 and 17. Confidence intervals are two standard errors of the mean of the ratios after casting out extreme values (all values are given in Appendix III). The actual interval can not be taken too seriously, particularly for animals in the boulder field, since ratios are not normally distributed. Thus, although the central values (*Postelsia* zone and eel grass area) can be manipulated without a transformation, the extremes (the boulder field ratios) should not be used without transforming (e.g. arc-sine). The general impression is that the inorganic components (carbonates

Table 12

Regression analysis of total organic material in the gut of animals from the *Postelsia* zone (PZ), eel grass area (EG) and boulder field (BF).

Season	No. of animals			Significance of difference	Regression equations
	PZ	EG	BF	among areas	
Fall	20	19	14	$F_{4,47} = 2.72$, $p > .05$	
Winter	20	17	17	$F_{4,48} = 3.84$, $p > .05$	$y = 0.011x + o.12$[a]
Spring	19	20	20	$F_{4,53} = 0.16$, $p > .05$	
Summer	19	19	20	$F_{4,52} = 1.34$, $p > .05$	
				among seasons	
All seasons	78	75	71	$F_{6,216} = 8.49$, $p < .01$	
Spring, summer and fall	58	58	54	$F_{4,164} = 0.56$, $p > .05$	$y = 0.022x + 0.03$

[a] x = calcite weight in grams, y = dry weight of organic material from the gut in grams.

Figure 16

Silicous sand in the gut as a function of time. Extreme values were removed before means and standard errors were calculated (see text and Appendix III). Each point is the mean ± 2SE for samples of eight to ten animals.

+	*Postelsia* zone
o	eel grass area
●	boulder field

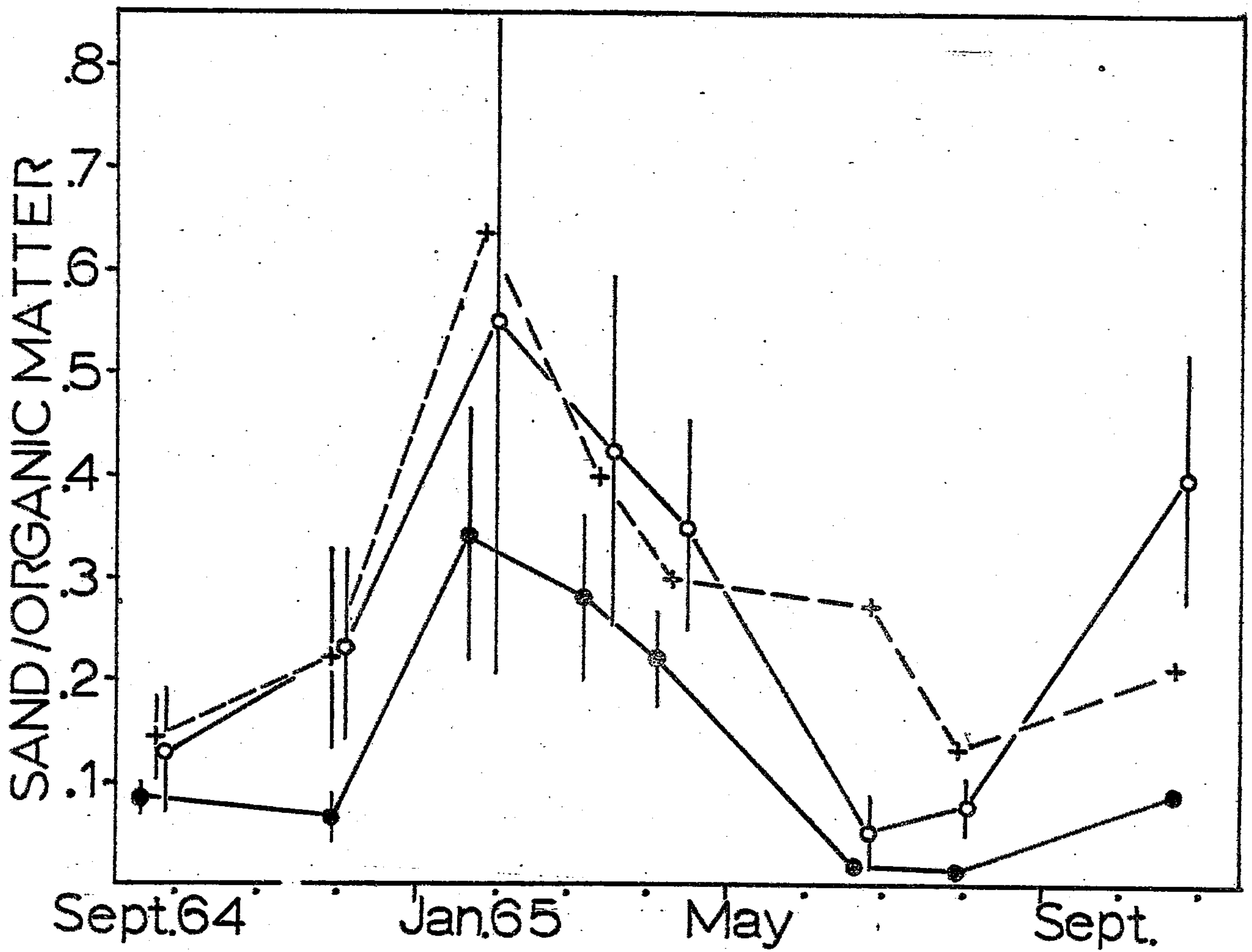
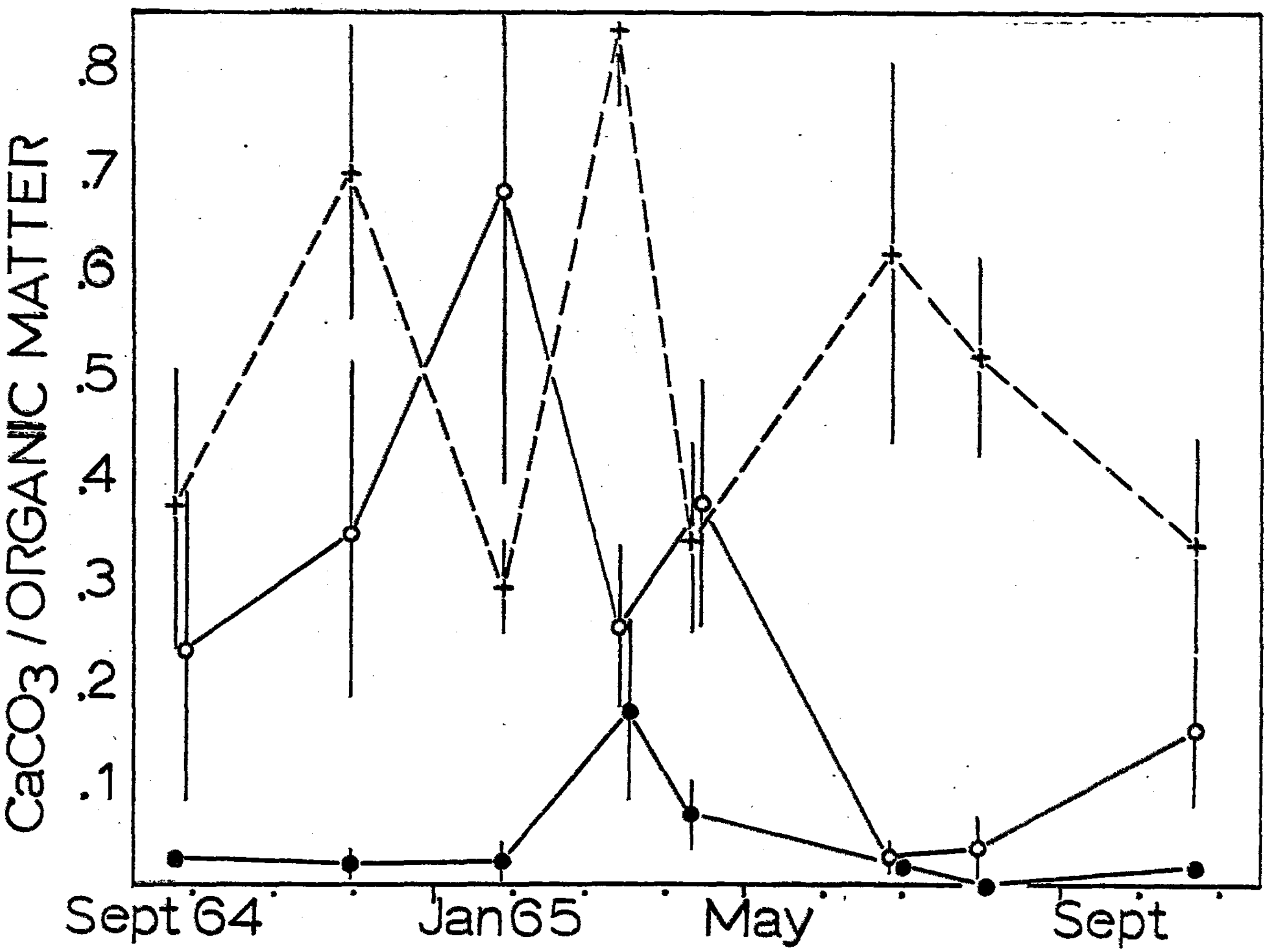

SAND/ORGANIC MATTER
.8
.7
.6
.5
.4
.3
.2
.1
Sept.64
Jan.65
May
Sept.

Figure 17.

$CaCO_3$ in the gut as a function of time. Extreme values were removed before means and standard errors were calculated (see text and Appendix III). Each point is the mean ± 2SE for samples of eight to ten animals.

+	*Postelsia* zone
o	eel grass area
●	boulder field


CaCO3 / ORGANIC MATTER
.8
.7
.6
.5
.4
.3
.2
.1
Sept 64
Jan 65
May
Sept

and silicates) act very differently. Silicious sand (Fig. 16) appears to be about the same in all three areas with an increase during the fall, reaching high values during the winter, dropping during the spring and reaching low values during the summer. The high values during the winter possibly reflect increased surf conditions which would carry larger volumes of sand or, with the winter rains, increased stream run-off (a small stream enters Sunset Bay). Urchins apparently keep their bases clean by eating the sand. It is also possible that this could indicate decreasing amounts of food available during the winter so that sham feeding would increase the amounts of sand.

The seasonal changes in amounts of $CaCO_3$ (Fig. 17) indicate that during the fall and winter the *Postelsia* zone and the eel grass area animals are essentially the same. The boulder field animals have much lower amounts of carbonates in the gut for all times of year. The only value which approaches those observed in the other two areas occurs during the winter when values may be the same as in the eel grass area and *Postelsia* zone. Values in the eel grass area drop during the spring and are low, essentially the same as in the boulder field animals, during the summer. Lewis (1958) found that *Tripneustes esculentus* Leske refused to eat algae with a high $CaCO_3$ content. Forster (1959) suggests that *Lithothamnion*, an encrusting coralline, may not be browsed on heavily. Coralline forms appear to survive under conditions of high urchin densities (North 1963; Forster 1959). Kawamura (1965) showed an increase in calcareous algae in the gut was associated with decreased gonad production. I should like to conclude from this that the amounts of $CaCO_3$ in the gut contents of Sunset Bay animals reflects general food availability; if given a choice, urchins would rather eat something other than corallines, but under conditions of low food they will accept algae high in $CaCO_3$. This would mean that animals in the *Postelsia* zone have low amounts of food essentially all year, animals in the eel grass area have small amounts during the fall and winter, have increasing amounts during the spring and are well fed during the summer. Animals in the boulder field generally are well fed but do have less food during the winter.

Another method of estimating amounts of food, which yielded very similar results, was by measuring the quantities of debris held by animals in the three areas. The rationale is that, for an opportunistic feeder dependent upon debris, before food can be eaten it must first be caught and held. Measuring the amounts held, although not indicating the actual amounts eaten, does give an indication of food availability. Table 13 gives a summary of such information gathered in July 1965 and March 1966. A more complete analysis is given in Appendix IV. During the summer, animals in the boulder field were holding more algae than animals in the other two areas. The *Postelsia* zone urchins had the least. A comparison with the amounts of algae eaten in 24 hours (Fig. 15) indicates that animals in the *Postelsia* zone are holding about the maximum amount they would eat in one day (using the conversion values in Table 13, a 100-g urchin

Table 13

Food held by urchins during summer and winter. Values for each season are dry weights of food in grams per 100 g urchin wet weight. Detailed analysis is presented in Appendix IV.

Area	Time	
	July 1965	March 1966
Postelsia zone	0.26	0.008
Eel grass area	0.42	0.019
Boulder field	0.70	0.021
Below *Postelsia* zone and north (Fig. 2 F)	0.12	
Below *Postelsia* zone and south (Fig. 2 E)	0.41	

Conversion table for comparing Table 13 with Fig. 15

Test diameter	Total wet weight	Calcite weight
3.75 cm	25 g	7.0 g
4.75	50	13.5
5.90	100	24.5
7.65	200	ca. 46.0

would be 5.90 cm in test diameter and would have 24.5 g of calcite). Using this as a base, animals in the eel grass area have 1.6 times the amount they would eat in one day and urchins of the boulder field have 2.7 times the required amount. In the sample taken in March 1966, food is very low in all areas, but lowest in the *Postelsia* zone. Although particular details are somewhat different, the basic picture is the same as indicated by the amounts of $CaCO_3$ in the gut contents.

Seasonal differences in food are due to the equivalent differences in algal production and growth. During the summer, the intertidal supports a lush growth of many algal species which die during the fall leaving the rocks relatively barren during the winter. Algal growth resumes during the spring. Local differences seem to be correlated with local topography: areas of high local relief seem to have more food which grows on the tops or sides of the ridges, hangs down and supplements floating debris. This appears most impressively in the boulder field where animals stay at the bases of the boulders and have large quantities of algae hanging over them. In flat areas such as the eel grass area little or no supplementary food hangs over the animals. The amounts of algae which grow on the boulders or ridges are controlled by the factors limiting algal settling and growth. This accounts for the small amounts of algae hanging in the *Postelsia* zone even though it is an area of high relief.

Food quality has been shown to be important in determining growth rate in *Strongylocentrotus* by Swan (1958, 1961). Differences in assimilation efficiency with different algae have been demonstrated by Fuji (1962). Differences in the algal composition of the three areas are indicated in Appendix I for algae collected in the areas, and also in Appendix IV, which shows the debris held by urchin samples. Differences do exist, and quality may play a part in determining growth of these animals; however, generally it appears that differences in food quantity can explain the differences observed in Sunset Bay.

Decrease in Gut Contents with Gonad Growth

Fuji (1962) indicated that, when spawning approaches, there is a decrease in feeding rate. A similar correlation is shown in Fig. 18 and 20. The total weight of organic material in the gut is plotted against the percent maximum gonad weight. The general suggestion is that, up to a certain point, gut contents and gonad size are directly related; beyond this, increases in gonad size are associated with decreasing gut contents. The implication from Fuji's work is that this is behavioral; however, in dissecting the animals in this study, my impression was that this response was due to physical crowding inside the test. With maximum gonad development, there simply is not enough room for maximum gut expansion. The variability of the values in all three figures is so great that any single one is not very convincing; however, the trend is the same in all three therefore, even though this in itself is not proof, it does **strengthen** the suggestion that there is first a direct relationship between gonad size and gut contents, a critical point is reached, and any further gonad

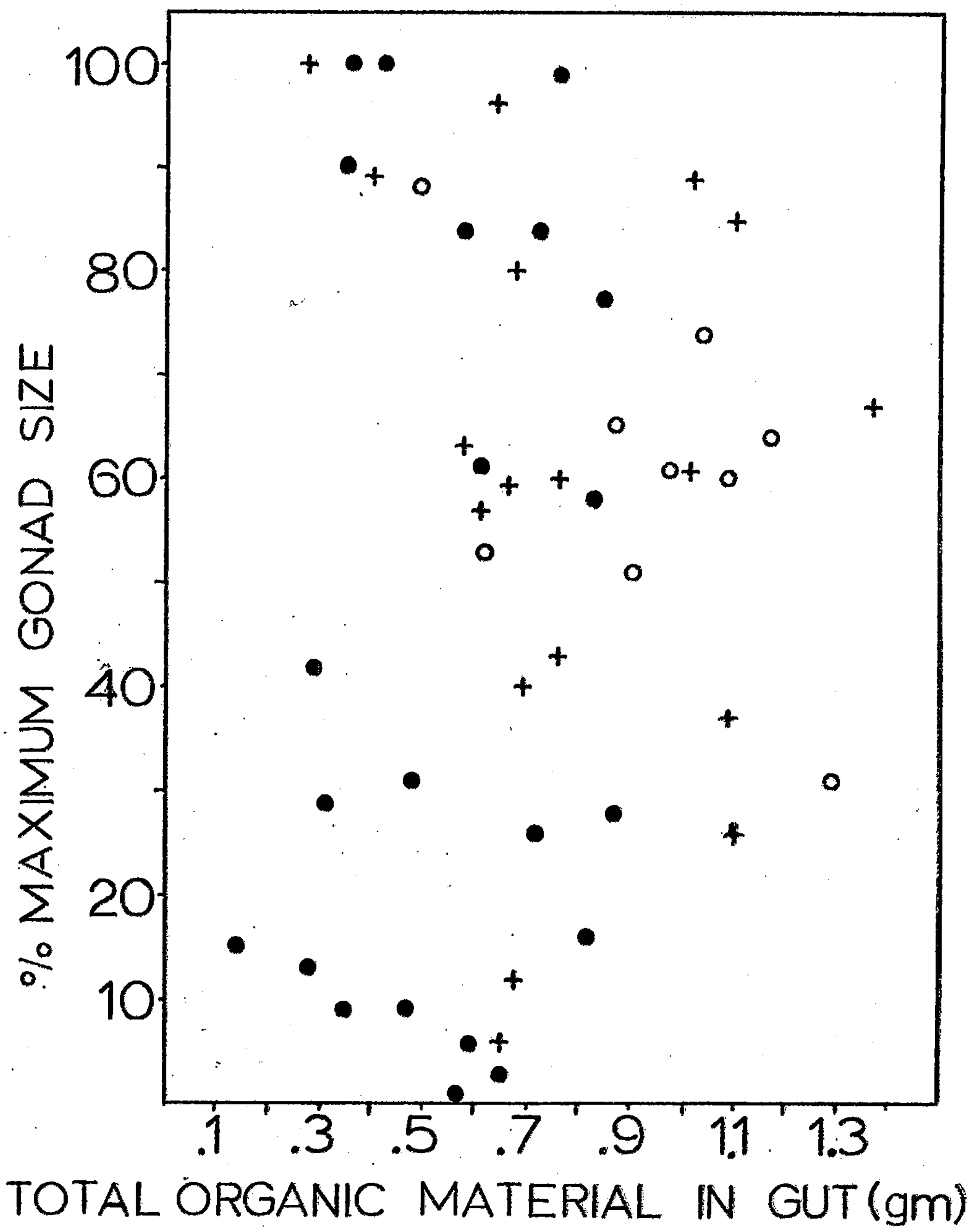
Figure 18.

Relationship between gonad development and amount of organic material in the gut. All seasons pooled.

● 21 to 30 g total calcite weight

+ 31 to 40 g total calcite weight

o 41 to 50 g total calcite weight



% MAXIMUM GONAD SIZE
100
80
60
40
20
10
.1
.3
.5
.7
.9
1.1
1.3
TOTAL ORGANIC MATERIAL IN GUT (gm)

Figure 19

Relationship between gonad development and amount of organic material in the gut. All seasons pooled.

● 11 to 20 g total calcite weight

Note change of scale.

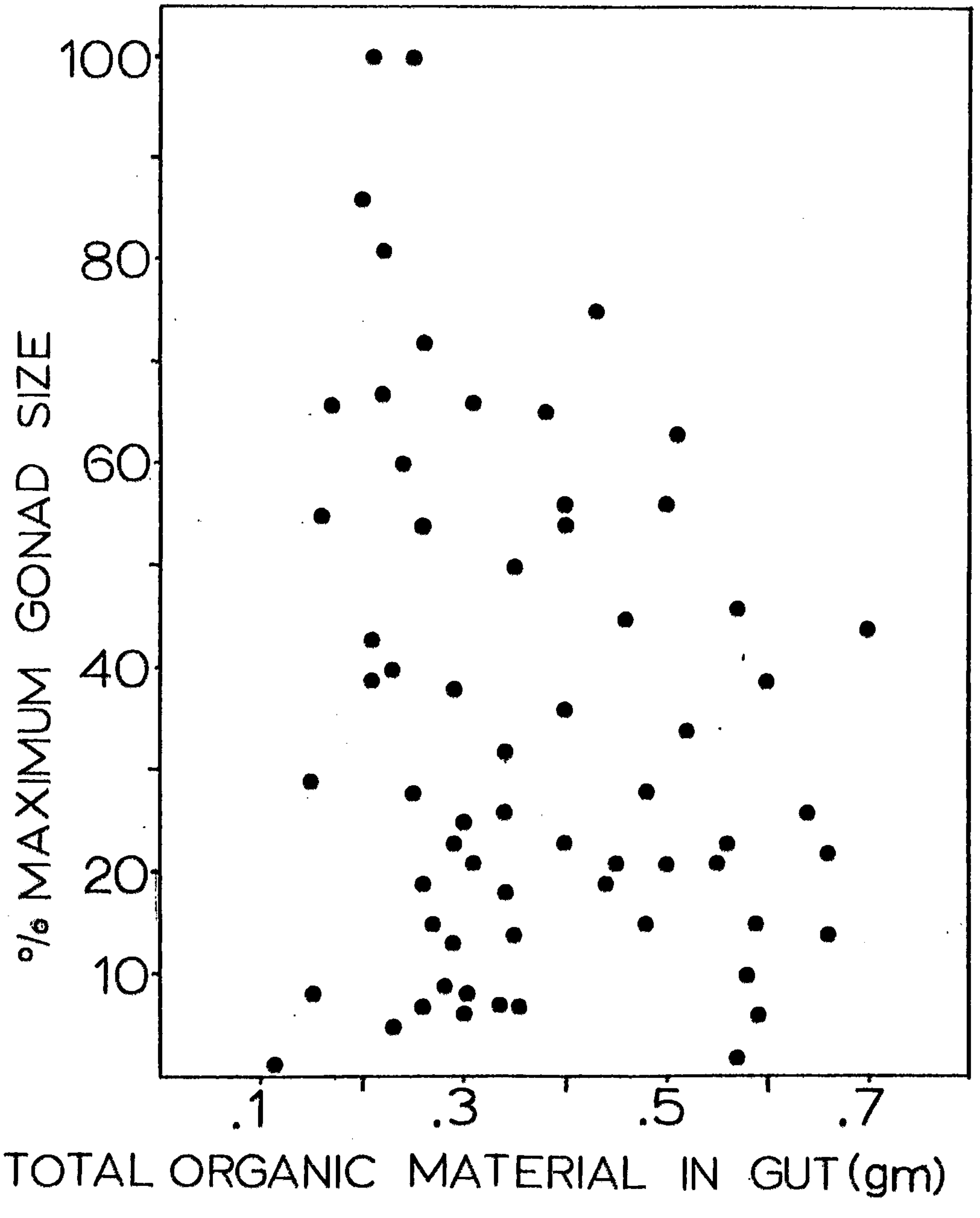
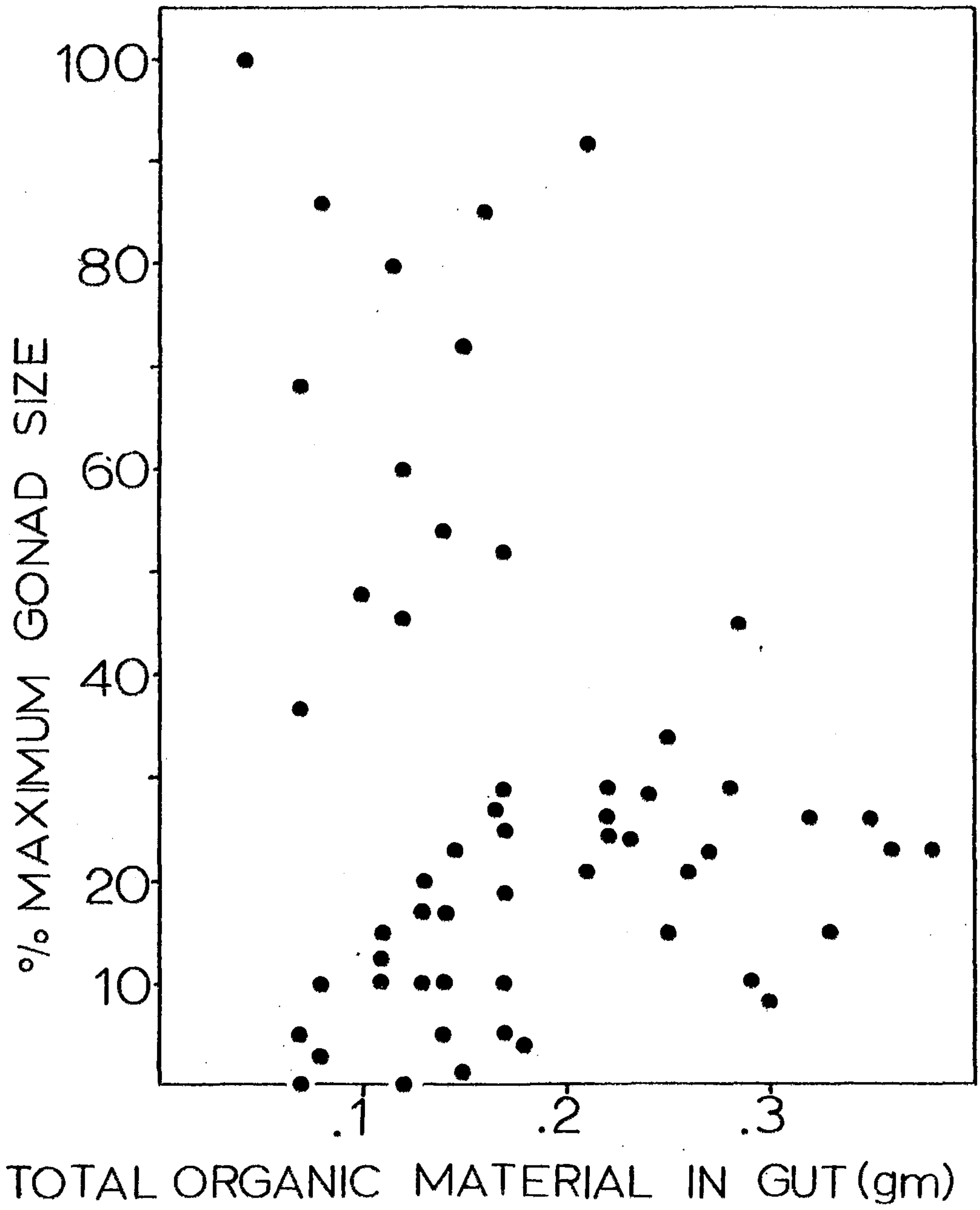

100
80
60
40
20
10
% MAXIMUM GONAD SIZE
.1
.3
.5
.7
TOTAL ORGANIC MATERIAL IN GUT (gm)

Figure 20.

Relationship between gonad development and amount of organic material in the gut. All seasons pooled.

● 1 to 10 g total calcite weight

Note change of scale.


100
80
60
40
20
10
% MAXIMUM GONAD SIZE
.1
.2
.3
TOTAL ORGANIC MATERIAL IN GUT (gm)

development limits the amount of food which can be held in the gut. This relationship will tend to further obscure the results of feeding estimates from field data and may be a contributing cause to the variability of feeding rates determined from tattooed algae.

Summary of Investigation on Size and Growth

Differences in size distributions of the purple sea urchin, *Strongylocentrotus purpuratus* (Stimpson), exist locally at Sunset Bay, Oregon. These differences generally can be accounted for by differences in growth rates. A given size does not indicate a certain age because of the wide spectrum of growth rates and the ability of the animals to shrink. Animals clustered around the second mode of the size distributions are, therefore, of many age classes and there is little hope of separating them. Possible reasons for the differences in growth were examined in this study. Spine breakage and regeneration were discarded as likely because the area with the greatest amount of spine loss also showed the highest growth rate. Food differences were examined; although the data are not conclusive, they strongly suggest that differences in the amounts of food exist among the three areas. In summer, during the maximum algal production, animals in the boulder field take in much more food than do animals in either of the two other areas. This apparently is the basis for differences in the rates of growth and ultimate sizes that were observed.

DISCUSSION

Studies of echinoid ecology typically have delt with only one or two aspects of the animals; no one has attempted to analyze a number of variables, particularly on a local level. A recent study by Kawamura (1964, 1965a and b), however, does require special mention. A number of urchin populations are being studied and the results from 1962 through 1964 have been reported (Kawamura 1964, 1965; Kawamura and Taki 1965). Differences in growth rates were observed from year to year along with changes in gut contents and gonad sizes. The study does not attempt to explain observed differences or deal with populations as local as those reported in Sunset Bay. Many of Kawamura's findings, however, are in agreement with those of this study.

Growth information reported in the literature has been based on animals held in cages (Lewis 1958; Swan 1961; Moore _et al_. 1963a and b; McPherson 1965); aquaria (Aiyar 1935; Bull 1939; Moore _et al_. 1963a and b; McPherson 1965); and size distributions (Soot-Ryen 1924; Schorygin 1928; Grieg 1928; Elmhirst 1922; Crozier 1920; Moore 1935; Moore _et al_. 1963 a and b; Lewis 1958; Swan 1961; McPherson 1965; Kawamura 1964). Only one investigator (McPherson 1965) successfully attempted marking individuals but his method was unsuitable for animals smaller than 6 cm. A summary of the information concerning growth of echinoids is given in Appendix II.

As indicated above, most estimates of growth have been based on positions of modes in size distributions. This tends to underestimate the true ages of animals because, as has been shown, settling success is not the same for every year; entire age classes can, therefore, be missing. In the studies indicated in Appendix II the first few years of growth probably are reasonably accurately determined especially in cases where observed for a number of years (Kawamura 1964; Lewis 1958; Moore et al. 1963a).

Laboratory studies of growth, although not giving an accurate picture of growth in the field, give an indication of a possible rate and longevity for the species studied. The best reported work of this type is that of Bull (1939) on *Psammechinus miliaris*. It is interesting to note the apparently slow rate of growth in these aquarium animals. At the end of 6 years, Bull's urchins were about 3.9 cm in test diameter. In the field, Lindahl and Runnström (1929) found animals over 13 cm. In the same area with these large animals, the small animals showed a model class of 2.25 cm. Bull's animals at the end of one year were 2.0 cm. Most of the distributions presented by Lindahl and Runnström had animals over 5 or 6 cm and a first mode at about 2.0 cm. It seems reasonable that the animals around 2 cm were one year old and the possibly situations existed for *Psammechinus* very similar to those in Sunset Bay for *Strongylocentrotus*, giving rise to different rates of change in size (such as observed for animals in the *Postelsia* zone and the eel grass area in Fig. 10). Although initial growth may be quite similar in a number of areas, ultimate sizes could be very different. This would mean that the animals observed by Lindahl and Runnström (1929) may or may not be older than the aquarium animals of Bull. In general, the rate of growth and apparent longevity are similar to the findings for

S. purpuratus in the present study.

The work of Moore et al. on *Lytechinus variegatus* (1963a) is a composite of the work of a number of Moore's students and is presented in a somewhat confused and confusing manner. It probably is an adequate picture of the growth rate of these urchins over a 5-year period; however, the data do not really support their conclusion that the normal life span is only 2 years. All that can really be stated is that the animals grow rapidly the first year and approach maximum size during the second year.

The impression one gets from examining the many distributions of Lindahl and Runnström (1929) is that, even with the complication of migrating animals, there are differences in the rates of growth in different areas because of the shifts in the first mode from area to area. North et al. (1963) give a large number of distributions for *Strongylocentrotus purpuratus*, *S. franciscanus*, *and Lytechinus anamesus* in California. They point out that there is very substantial geographical variation and say "presumably the populations did not all arise from a single favorable year for the larvae or other stage in the life histories." An interesting example of size constancy in a given area is presented:

> A cobble bottom offshore from Imperial Beach at one time supported a kelp area designated by the Dept. of Fish and Game as Bed N. 1. The last recorded harvest from Bed 1 was in 1939. [Conrad] Limbaugh (personal communication) dived in the area about ten years ago (1953) and reported barren rocks with an abundance of young, long-spined *S. franciscanus*. North found the same conditions in early 1957 and little changes [sic] could be found when the area was visited July 12, 1963.

North et al. (1963) point out that the expected growth rate for the small *S. franciscanus* at Imperial Beach was 2 cm per year (based on rates determined in the laboratory). In other areas studied by this group, animals were also small with modes for large *S. purpuratus* of 2 to 4 cm. Distributions of urchins in most areas had modes of about 2.5 to 3 cm. North terms these "urchin limited environments". Gut contents indicated that very little food was available in the areas. A photomicrograph published in the work shows gut contents from an animal collected at Pt. Loma in January 1963 with only sand and unidentifiable amorphous matter in the gut. Under low food conditions, animals move, but they remain stationary when well fed (North et al. 1963). North suggests that regulation of urchin size in the areas he and his co-workers examined may be similar to regulation of size in populations of the gastropod *Littorina* (North 1954) where there was either environmental selection for a particular size or animals migrated to the type of environment which, for some reason, favored the particular size (North does not suggest the possibility of growth differences). In light of the present study it seems more likely that animals were growing very slowly in these "urchin limited" areas and had a very small "optimum" size (corresponding to the size showing zero growth in Fig. 10 of this study). Geographic differences are simply differences in growth rates and optimal sizes.

The work with "growth zones" is difficult to evaluate mainly because no adequate explanation for their formation has been advanced. Deutler (1926) suggests different diets during summer and winter and animal migration to account for the different diets. Moore (1937) also believed that differences in pigment deposition could be accounted for by differences in food. The pigment Moore discusses is echinochrome which, structurally, is a naphtoquinone (Kuhn and Wallenfels 1939). Echinochromes, carotenes and xanthophylls are present in urchins (Fox and Scheer 1941) but no red pigments related to the phycobilins of red algae. There may be a connection between large amounts of food, growing, and producing pigment, but it is highly doubtful that as close a relationship as Deutler (1926), Moore (1937) and Awerinzew (1911) suggest exists. It is possible, on the contrary, that starving may be associated with the increased pigment as was found in starfish by Vevers (1949). This pigment, of course, was not echinochrome but the phenomenon suggests that the production of a pigment does not always have to be associated with intake of food.

Granting, however, the periodic production of echinochrome the question is: are the results of aging studies reasonable? Examination of the growth information for the Isle of Man (Moore 1935) based on "growth lines" in the genital plates, indicates what appears to be an increasing growth rate with increasing size (see Appendix II). This is highly unlikely, and, if true, would be unique unless representing the beginning of a log phase of growth which in this case is also unlikely.

A possible explanation for the presence of echinochrome pigmentation in the plates could be a response to minor injury. Areas of irritation show an increased amount of echinochrome. The urchins that were first marked in December 1962 with pieces of vinyl "spaghetti" tubing showed increased echinochrome deposition in the calcite meshwork underneath the plastic sleeves. A second example of response to injury is in the marking method presently used (Ebert 1965). Here, there is an accumulation of the pigment around the monofilament inside the test, with denser accumulations at the points on the test where the line passes through. General observation of animals in the field indicates that there is an accumulation around areas of injury on the test (punctures, cracks or abrasions). Echinochrome deposition in the genital plates could simply be a response to mild injury on the surface during storms. This would lead to a larger number of lines in large animals and could, if large animals were more resistant to injury (a stimulus must be greater to elicit a response in larger animals as indicated for spine breakage in Fig. 13) account for the apparent increase in growth rate indicated by Moore (1935).

An age of 35 years for *Colobocentrotus* determined from "growth zones" (Deutler 1926) seems somewhat high but may be correct. I do doubt, however, that each "growth zone" in the coronal plates is equivalent to one year. As indicated for *S purpuratus*, at least for small sizes, more than one line is deposited per year. The results shown in Appendix II give a growth rate somewhat higher than suggested by marked animals and do not consider shrinkage as a possibility which, of course, is not considered by any of the authors mentioned.

Because a carotenoid was suggested as responsible for the growth lines in the plates of *S purpuratus* it is necessary to return to the suggestion of Moore (1935), Deutler (1926) and Awerinzew (1911) that food is at the basis of the growth lines because, typically, animals are not able to produce beta-carotene and must get this from plant sources. However, according to DeNicola (1954), urchin embryos may be able to synthesize beta-carotene. DeNicola's work, at least, suggests the possibility that adults could also produce this product. The point is unresolved, but periodic deposition of a substance obviously occurs. The real question is whether it is correlated with an annual cycle. This has not been answered by the present study, but the problems resulting from shrinkage suggest caution in interpretation of the lines. It is possible that they are related to the number of times an animals has had to shrink; in which case, lines would indicate winter conditions and major lines would be severe conditions which might not recur every year.

A fairly constant feature of studies showing size distributions for a number of areas is the variation in position of modes and maximum size. McPherson (1965) shows this for *Tripneustes ventricosus* at three localities near Miami, Florida. He suggests that this could be due to differences in growth rates or settlement times. His distributions for Boca Raton compared with Virginia Key show a shift in the bimodal distributions similar to the shifts seen in the distributions of animals at Sunset Bay, Oregon. Moore (1937) shows unimodal curves for *Echinus esculentus* from four stations along the

British coast. He states that there "appears to be a definite increase in the size of urchins southwards". The implication from the work over several years at the Isle of Man is that sea water temperature is important in determining rate of growth for any particular year (Moore 1935). Kristensen (1957), working with cockles, states that regional variation of size in relation to temperature is generally slight and often not readily recognizable. Hallam (1965), in his review of environmental causes of stunting in invertibrates, concludes that "temperature does not therefore seem to be a particularly significant factor in stunting, at least at the species level." It is very likely that the distributions of *Echinus* along the British coast are not regulated by temperature.

Food availability as a factor in determining growth rates has been observed among intertidal suspension feeders such as *Cardium edule* and *Mytilus edulis* (Kristensen 1957; Hancock and Simpson 1961). A direct relationship between the growth and the period of immersion (time available for feeding) was observed but it was not determined that this, in fact, was the cause for increased growth. Subtidally, there seems to be some question concerning food availability. Fox (1957) suggests that there is more than enough food available for the large organisms of the sea. The evidence of North et al. (1963) would certainly argue against this, not only for urchins, but also for other herbivores or opportunistic feeders.

The importance of food quality has been pointed out by Moore et al. (1936b) for the growth of the gastropod *Nucella (=Purpura)* *lapillus* which attains a greater size on a diet of *Mytilus* than on *Balanus*. Similar findings were reported for the starfish *Pisaster ochraceus* in Puget Sound by Paine (1965). Suggestions of importance of food quality in sea urchins have been made by Fuji (1962) and demonstrated by Swan (1961).

It has been suggested in this study that the effect of food availability on the urchins of Sunset Bay is to regulate the sizes of individuals without, apparently, influencing the numbers of animals. This poses the problem of what does regulate the numbers of urchins. Predation is a possibility but is difficult to demonstrate. Predators include the sunflower-star *Pycnopodia helianthoides* (observed eating urchins at North Cove of Cape Arago and reported to be predators of urchins by Ricketts and Calvin (1962). Wolf eels (*Anarhichas lupus*) are cited as predators by Barsukov (1956) and are present on the Pacific coast of North America. One was seen at Sunset Bay by a SCUBA diver, John Palmer (personal communication), but apparently they are not abundant enough to be a major factor in controlling urchin populations. Occasionally, sea gulls were observed eating urchins. One was observed at Sunset Bay dropping an urchin onto rocks and then coming down to eat the contents. Broken urchins high on rocks were usually assumed, misanthropically, to have been caused by small children of all ages. It is, however, possible that many of these could have been from sea gulls. Gulls may, in fact, be the major predators on intertidal populations, although local and exotic tourists have been observed removing animals, sometimes in large numbers. This leaves the subtidal relatively untouched except by *Pycnopodia*. I should like to propose that regulation of numbers, for the most part, is by physical factors acting initially on very early stages and later excluding very large animals from high areas either by high temperature or low oxygen tensions. These factors would eliminate large animals during times of physical extremes.

The general picture of urchin populations that can be presented from the study of animals at Sunset Bay is that urchins are capable of a wide spectrum of growth rates which vary with existing physical and biotic conditions. Animals are capable not only of increasing in size but also of shrinking. This yields an accumulation of animals at a size which indicates the optimal size for the set of conditions. Animals are apparently long lived and reach ages of at least ten years and possibly twice this. Mortality is low and, after the first year, population size is apparently controlled by a combination of storms, extremes of temperature, salinity and oxygen tension, and low level predation. Evidence from the literature suggests that other urchin species may be adapted to intertidal and sublittoral conditions by essentially the same mechanisms and controlled in the same ways.

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Appendix I

Species list of algae collected from
the *Postelsia* zone, the eel grass area, and the boulder
field. Sunset Bay, Oregon, Summer 1964.

Postelsia zone (Fig. 2 A)

Postelsia palmiformis Ruprecht 1852

Hedophyllum sessile (Agardh) Setchell 1899

Gigartina papillata Setchell 1899

Hymenena sp.

corallines

Area below *Postelsia* zone (Fig 2 E and F)

Costaria costata (Turner) Saunders 1895

Cystoseira osmundacea (Menzies) C. Agardh 1820

Nereocystis luetkeana (Mertens) Postels and Ruprecht 1840

Erythrophyllum delesserioides J. Agardh 1872

Iridaea sp.

Odonthalia floccosa (Esper) Falkenberg 1901

Ptilota sp.

Plocamium violaceum Farlow 1877

Laurencia spectabilis Postels and Ruprecht 1840

Opuntiella californica (Farlow) Kylin 1925

Pterosiphonia sp.

Hymenena sp.

Cryptopleura sp.

corallines

Appendix I (cont.)

Eel grass area (Fig. 2 B)

Phyllospadix torreyi Wats.

Cladophora sp.

Spongomorpha sp.

Ulva sp.

Monostroma zostericola Tilden 1900

Fucus furcatus Agardh

Leathesia difformis (Linne) Areschoug 1846

Soranthera ulvoidea Postels and Ruprecht 1840

Heterochordaria abietina (Ruprecht) Setchell and Gardner 1924

Farlowia mollis (Harvely and Bailey) Farlow and Setchell

Rhodomela larix (Turner) C. Agardh 1822

Microcladia borealis Ruprecht 1851

Gigartina papillata Setchell 1899

Cumagloia andersonii (Farlow) Setchell and Gardner 1917

Odonthalia floccosa (Esper) Falkenberg 1901

Halosaccion glandiforme (Gmelin) Ruprecht 1851

Iridaea sp.

Ceramium pacificum (Collins) Kylin 1925

C. eatonianum (Farlow) DeToni 1903

Smithora naiadum (Anderson)

corallines

Appendix I (concl.)

Boulder field (Fig. 2 C)

Cladophora sp.

Ulva sp.

Fucus furcatus Agardh

Hedophyllum sessile (Agardh) Setchell 1899

Egregia menziesii (Turner) Areschoug 1878

Bangia vermicularis Harvery 1858

Iridaea heterocarpa Postels and Ruprecht 1840

I. flaccidum (Setchell and Gardner)

Gigarina canaliculata Harvey 1841

G. cristata (Setchell) Setchell and Gardner 1933

G. papillata Setchell 1898

Odonthalia floccosa (Esper) Falkenberk 1901

Microcladia borealis Ruprecht 1851

Halosaccion glandiforme (Gmelin) Ruprecht 1851

Rhodomela larix (Turner) C. Agardh 1822

Ceramium eatonianum (Farlow) DeToni 1903

Polysiphonia hendryi Gardner 1927

Pterosiphonia sp.

Appendix II

A summary of growth information on echinoids.

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.	
Colobocentrotus stratus	Reunion	Deutler (1926)	"growth zones" in the test	an animal 6.5 cm in test diameter was judged to be 35 years old.	
Echinus esculentus	Millport, Scotland	Elmhirst (1922)	size distributions	6 months	2 cm
				1 year	4
				2	4 - 7
				3	7 - 9
				4	9 - 11
				7 - 8	15 - 16
	Isle of Man, England. "chickens" area	Moore (1935)	size distributions	1	2.2
				2	3.4
				3	5.2
			"growth lines" in genital plates	1	1.6
				2	2.8
				3	4.0
				4	5.5

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.	
E. esculentus (cont.)	Isle of Man, England, breakwater on side of Port Erin Bay		"growth lines" in genital plates	1	-
				2	-
				3	5.5
				4	7.5
				5	8.0
				6	9.0
				7	10.5
Lytechinus variegatus	Miami, Florida	Moore et al. (1963a)	size distributions	1	5.0 - 5.5
				2	7.0
				normal life span about 2 years	
Mellita sexies-perforata	Bermuda	Crozier (1920)	size distributions	1 year	3.0 cm
				2	6.0
				3	8.0
				4	10.0
				normal life span about 4 years	

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.	
Psammechinus miliaris	Cullercoats, Northumberland, England	Bull (1939)	aquaria	metamorphosed	0.10
				6 months	0.33
				1 year	2.00
				2	2.62
				3	2.92
				4	3.03
				5	3.70
				6	3.87
	Kristineberg Zoological Station, Sweden	Lindahl and Runnström (1929)	no actual determinations of age but several size distributions are presented	sizes that appear to be 1 year old are: 0.7, 0.8, 2.0 and 2.4 cm.	
Salmacis bicolor	Madras, India	Aiyar (1935)	aquaria	3 months	0.4 - 0.5
				6	1.3
				1 year	1.6
Tripneustes ventricosus (=T. esculentus)	Barbados, West Indies Federation	Lewis (1958)	size distributions and cages	1 year	5 - 8 cm

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.
T. ventricosus (cont.)	Bimini, Bermuda	Moore *et al.* (1963b)		suggest that animals in a high pool at Bimini grow more slowly than animals at Barbados (Lewis 1958) because in June the mean diameter was 2.48 cm compared with 7.5 cm in Barbados
	Miami, Florida	McPherson (1965)	size distributions	about 8 cm in one year
Strongylocentrotus dröbachiensis	New Hampshire and Maine	Swan (1961)	size distributions	1 year 0.8 - 1.0 cm 2 2.4 - 2.6 3 4.0 - 4.2 4 4.6 - 5.4
	Ramfjorde, Norway	Soot-Ryen (1924)	size distributions	1 1.2 - 2.2 2 2.2 - 3.3 3 3.3 - 4.0 4 4.0 - 5.2 5 5.2 - 6.0

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.	
S. dröbachiensis (cont.)	Barents Sea, U. S. S. R.	Schorygin (1928)	size distributions	1	1.2 - 2.0
				2	2.1 - 3.1
				3	3.2 - 4.1
				4	4.2 - 5.2
				5	5.3 - 6.0
	Folden and Bals Fjords, Norway	Grieg (1928)	size distributions	1 year	0.5 - 0.6 cm
				2	1.5
				3	2.4 - 3.2
				4	4.07
				5	5.07

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.
S. dröbachiensis (cont.)	Friday Harbor, Washington	Swan (1961)	cages	At beginning of experiment three groups of animals were set up with 12, 10 and 4 individuals. One year later 11, 9 and 1 animals remained. No conclusions were drawn other than animals at Friday Harbor grew faster than animals at New Hampshire. Based on Swan's growth observations the following estimates seem reasonable. 1 year --- 2 3.0 cm 3 5.6 4 --- 5 + 7.6

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.
S. echinoides	Friday Harbor, Washington	Swan (1961)	cages	Three groups of animals were set up with 17, 20 and 8 individuals. One year there were 15, 14 and 7 still alive. The following age classes are my estimates. 1 year --- 2 2.6 cm 3 4.2 4 5.5
Strongylocentrotus franciscanus	Friday Harbor, Washington	Swan (1961)	cages	Two size classes were set up with 15 and 14 individuals. After one year all were still present. The age class estimates are mine. 1 year 2.9 cm 2 4.9

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.
S. intermedius	North region of Rebun Island on the coast of Funadomari, Japan	Kawamura (1964)	size distributions	1 1.00 cm and less 2 1.00 - 2.99 3 3.00 - 4.00
S. purpuratus	Friday Harbor, Washington	Swan (1961)	cages	Two size classes with 2 and 12 individuals were set up. After one year 2 and 10 remained. The age class estimates are mine. 1 year 1.5 cm 2 2.6 - 3.0 3 4.2 - 4.6
	Sunset Bay, Oregon, high eel grass area, 29 December 1963	This study	"growth zones" in coronal plates	1 1.5 ± 0.04 SE 2 2.8 ± 0.02 3 4.0 ± 0.56 4 5.1 ± 0.26 5 6.0 ± 0.24

Appendix II (cont.)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.	
S. purpuratus (cont.)	Sunset Bay, Oregon, high eel grass area, 1964-65	This study	size distributions	1 year	1.62 (mode)
				2	2.44
			marked animals	1	1.94
				2	3.09
				3	3.68
				4	4.06
				5	4.33
				6	4.52
				7	4.66
				8	4.77
				9	4.86
				10	4.91
	Sunset Bay, Oregon, *Postelsia* zone, 1964-65	This study	size distributions	1	1.38
				2	3.21

Appendix II (concluded)

Species	Location	Authority	Method of age determination	Age or growth information. Unless otherwise specified, time is in years and size is in centimeters.	
S. purpuratus (cont.)	Sunset Bay, Oregon, *Postelsia* zone, 1964-65 (cont.)	This Study	marked animals	1	0.95
				2	1.76
				3	2.36
				4	2.78
				5	3.09
				6	3.34
				7	3.54
	boulder field, 1964-65		graphic method which assumes that the first mode of the 1964 size distribution is 1-year's growth and the second mode is the point of zero growth	1	2.95
				2	4.26
				3	5.02
				4	5.53
				5	5.89
				6	6.15
				7	6.35
				8	6.50
				9	6.61
				10	6.69
	eel grass area, 1964-65		determined by the graphic method explained above	1	1.62
				2	2.76
				3	3.38
				4	3.80
				5	4.10
				6	4.33
				7	4.51
				8	4.65
				9	4.76
				10	4.85

Appendix III

Inorganic components of the gut contents showing extreme values. Numbers are $CaCO_3$ or silicous sand weight divided by weight of organic material in the gut contents. * indicates extreme values that were cast out before calculations were performed. (see Figs. 16 and 17.)

Postelsia Zone

Date	$CaCO_3$	sand	Date	$CaCO_3$	sand	Date	$CaCO_3$	sand
9-64	.36	.22	11-64	.88	.12	1-65	.47	.56
	.44	.06		.50	.32		.12	.82
	.36	.17		.89	.21		* .11	.08
	*1.06	.16		.71	.25		.37	1.31
	.32	.06		.46	.16		.17	.21
	* .04	* .00		.87	.13		.24	.32
	.77	.20		.88	* .08		.20	*3.33
	.42	* .23		* .30	.28		.40	* .05
	.20	.16		.37	* .44		* .78	1.09
	.08	.11		*1.07	.32		.36	.71
3-65	* .39	.38	4-65	.40	* .55	6-65	.89	.36
	1.08	* .08		.12	.44		.38	.31
	.62	* .97		* .52	.52		.23	* .11
	1.04	.50		.49	.49		.61	* .39
	.43	.43		.17	.23		*1.46	.38
	.82	.21		.39	.18		* .10	.27
	.63	.56		* .00	* .00		.73	.17
	.69	.52		.38	.14		.98	.14
	*1.43	.19		.32	.21		.49	.29
				.42	.18			

Appendix III (cont.)

Postelsia Zone (cont.)

Date	$CaCO_3$	sand	Date	$CaCO_3$	sand	Date	$CaCO_3$	sand
7-65	.13	* .00	10-65	.36	.09			
	1.14	.14		.23	.38			
	.79	.24		.13	* .03			
	.32	.00		.50	.21			
	.30	.02		* .06	.06			
	* .13	.07		.62	.31			
	.32	* .32		* .64	.09			
	.72	.23		.23	* .50			
	.59	.21		.28	.43			
	*1.37	.17		.21	.13			

Eel Grass Area

9-64	*1.00	.21	11-64	.23	.34	1-65	*1.60	.30
	.03	.15		* .00	.15		.39	.28
	* .00	* .00		.40	* .00		* .13	.69
	.60	.04		*1.05	.24		1.03	.28
	.00	.02		.35	.06		1.19	.44
	.40	.25		.78	* .78		.33	*7.07
	.10	.23		.42	.48		.80	* .20
	.29	.08		.17	.11		.33	1.33
	.40	* .32		.05	.26			
	.02	.06						

Appendix III (cont.)

Eel Grass Area (cont.)

Date	CaCO$_3$	sand	Date	CaCO$_3$	sand	Date	CaCO$_3$	sand
3-65	.18	.41	4-65	.32	.22	6-65	* .00	.09
	.21	.21		.50	.40		.02	.12
	* .52	1.00		.17	.69		.01	.03
	.10	*1.35		.48	.19		.06	.04
	* .00	* .00		.08	.32		.03	.04
	.17	.28		* .08	* .08		.00	* .00
	.33	.33		.59	.24		* .08	* .18
	.44	.56		.29	.29		.05	.09
	.25	.25		.53	.47		.00	.00
	.35	.35		* .86	*1.98			
7-65	* .00	.12	10-65	.08	.20			
	.00	.04		.20	.27			
	.00	.0		.29	* .19			
	.00	* .00		.24	* .90			
	.23	* .15		* .31	.38			
	.07	.07		.21	.36			
	.00	.08		* .00	.43			
	.00	.00		.05	.40			
	.00	.11		.00	.75			
	* .35	.12						

Appendix III (cont.)

Boulder Field

Date	$CaCO_3$	sand	Date	$CaCO_3$	sand	Date	$CaCO_3$	sand
9-64	* .03	.15	11-64	* .00	* .00	1-65	.03	.26
	.03	* .02		.02	* .16		.00	.37
	* .00	.04		.00	.03		.00	.27
	.02	* .17		.04	.09		.00	* .05
				.02	.07		.00	.10
				* .04	.08		.08	.50
							.00	.53
							.00	.09
							.11	.67
							.03	* .90
								.31
3-65	* .00	* .05	4-65	.09	.27	6-65	.01	.01
	.40	.40		.02	* .03		.04	* .00
	.24	.42		.09	*1.04		.03	.01
	* .95	* .57		.01	.14		.03	* .13
	.18	.35		.10	.73		.02	.00
	.05	.19		.01	.05		.01	.00
	.26	.30		* .00	.05		.09	.00
	.02	.15		.03	.16		* .00	.00
	.02	.15		* .16	.18		* .09	.09
	.21	.29		.04	.39		.03	.05

Appendix III (concl.)

Boulder Field (concl.)

Date	$CaCO_3$	sand	Date	$CaCO_3$	sand	Date	$CaCO_3$	sand
7-65	.01	* .00	10-65	* .08	* .00			
	.00	.01		* .00	.04			
	* .00	.02		.00	* .21			
	.00	.01		.05	.10			
	.00	* .05		.01	.03			
	.00	.00		.01	.12			
	* .33	.04		.03	.10			
	.00	.03		.02	.10			
	.00	.00		.02	.19			
	.00	.00		.00	.03			

Appendix IV

Algae held by samples of urchins in five areas at Sunset Bay.

All weights are in grams.

Boulder field, 29 July 1965 Size distribution shown in Fig. 9 vi.

Number of animals in sample = 176, wet weight = 18,103,

mean = 102.8 g.

Species	Wet weight	Dry weight
Red algae		
Iridaea sp.	173.53	36.75
Gigartina sp. (mainly *G. papillata*	129.79	30.74
Rhodomela larix	12.34	2.37
Odonthalia floccosa	9.70	1.91
Porphyra sp.	2.68	0.35
Cryptopleura sp.	4.71	0.39
Rhodomenia sp.		
Ceramium sp.	1.66	0.30
Pterochondria woodii		
Endocladia muricata		
Plocamium sp.		
Pterosiphonia sp.		
Ptilota sp.		
Laurencia spectabilis		
Brown algae		
Fucus furcatus	150.35	31.09
Hedophyllum sessile	22.55	3.10

Appendix IV (cont.)

Boulder field, 29 July 1965 (cont.)

Species	Wet weight	Dry weight
Brown algae (cont.)		
Alaria valida	12.65	2.75
Egregia menziesii	6.50	0.83
Desmarestia sp.	1.19	0.17
Cystoseira osmundacea		
Soranthera ulvoidea		
Heterochordaria abietina		
Scytosiphon lomentaria		
Green algae		
Ulva sp.	51.25	9.96
Cladophora sp.	1.69	0.50
Diatoms		
mainly *Navicula* sp.	2.31	0.48
Angiosperms		
Phyllospadix torreyi	26.25	5.40
Total weight	606.84 g	126.61 g

Eel grass area, 30 July 1965

Number of animals in sample = 104, wet weight = 3,412, mean = 32.8 g.

Red algae		
Gigartina papillata	2.74	0.80

Appendix IV (cont.)

Eel grass area, 30 July 1965 (cont.)

Species	Wet weight	Dry weight
Red algae (cont.)		
Rhodomela larix	2.34	0.50
Coralline algae	1.87	0.95
Iridaea sp.	0.78	0.23
Brown algae		
Fucus furcatus	15.64	3.68
Hedophyllum sessile *Soranthera ulvoidea*	0.48	0.08
Green algae		
Ulva sp.	16.13	3.71
Spongomorpha sp.	2.77	1.02
Cladophora sp.	2.02	0.83
Angiosperms		
Phyllospadix torregi	1.57	0.40
Animals		
3 crabs 1 large *Pugettia* sp. 1 small *Pugettia* sp. 1 small *Hemigrapsus* sp.	6.91	2.14
Total weight	53.63 g	14.46 g

Appendix IV (cont.)

Postelsia zone, 29 July 1965

Number of animals in sample = 70, wet weight = 3,397, mean = 48.5 g.

Species	Wet weight	Dry weight
Red algae		
Hymenena sp.	0.40	0.08
Brown algae		
Hedophyllum sessile	65.60	8.83
Misc. algae and angiosperms		
Gigartina sp.	0.10	0.01
Plocamium sp.		
Ectocarpus sp.		
Phyllospadix torreyi		
Total weight	66.10 g	8.97 g

Area below the *Postelsia* zone and north, 29 July 1965, size distribution shown in Fig. 9 viii. Number of animals in sample = 122, wet weight = 8,438, mean = 69.1 g.

Red algae		
Iridaea sp.	10.16	1.96
Cryptopleura sp.	9.76	2.47
Polyneura sp.	7.84	2.00
Opuntiella californica	6.74	1.86
Plocamium sp.	1.42	0.15

Appendix IV (cont.)

Area below the *Postelsia* zone and north, 29 July 1965 (cont.)

Species	Wet weight	Dry weight
Red algae (cont.)		
Erythrophyllum delesserioides *Constantinea simplex* *Polysiphonia* sp.	0.86	0.18
Brown algae		
Hedophyllum ?	4.74	0.62
Cystoseira osmundacea	1.54	0.31
Misc. algae		
Diatoms *Fucus furcatus* *Ulva* sp.	0.84	0.17
Angiosperms		
Phyllospadix torreyi	0.90	0.23
Total weight	44.80	9.95

Area below the *Postelsia* zone and south, 29 July 1965, size distribution shown in Fig. 9 vii. Number of animals in sample = 104, wet weight = 7,571, mean = 72.8 g.

Read algae		
Iridaea sp.	46.29	10.00
Cryptopleura sp.	7.69	2.04
Microcladia borealis	4.18	0.87

Appendix IV (cont.)

Area below the *Postelsia* zone and south, 29 July 1965 (cont.)

Species	Wet weight	Dry weight
Red algae, (cont.)		
Opuntiella californica	2.62	0.94
Coralline algae	1.32	0.82
Rhodomela larix	0.84	0.24
Polyneura sp.	0.30	0.17
Odonthalia sp.		
Polysiphonia sp.		
Brown algae		
Egregia menziesii	128.02	15.82
Misc. algae		
Porphyra sp.	0.30	0.09
Ulva sp.		
Angiosperms		
Phyllospadix torreyi	2.06	0.52
Total weight	191.56	30.99

Appendix IV (cont.)

Boulder field, 4 March 1966

Number of animals in sample = 34, wet weight = 4,007, mean = 117.9 g.

Species	Wet weight	Dry weight
Red algae		
Gigarina sp. *Phorphyra* sp.		0.26
Misc.		
Bryozoan		0.03
Hydroid (mainly chitinous material)		0.56
Total weight		0.85 g

Eel grass area 4 March 1966

Number of animals in sample = 49, wet weight = 1,563, mean 31.9 g.

approx. 99% *Phyllospadix* 1% *Porphyra* sp. and *Ulva* sp.	0.30
Total weight	0.30

Postelsia zone, 4 March 1966

Number of animals in sample = 42, wet weight = 1,913, mean = 45.5 g.

Red algae	
Coralline algae	0.04

Appendix IV (concluded)

Postelsia zone, 4 March 1966 (cont.)

Misc.

approx. 90% dead *Phyllospadix* 10% *Iridaea* sp., live *Phyllospadix*, *Pterosiphonia* sp., and *Schizymenia* ? or *Dilsea* ?	0.11
Total weight	0.15

Appendix V

Effect of marking on growth of the test. The statistic Δd is the change in test diameter without respect to area, time of measurement or original diameter. Original diameter in centimeters is d_o and the diameter after a variable time period of from two months to one year is d_i. Time is most variable for intermediate values of Δd. At the extremes of growth (greatest shrinkage and greatest increase) time is mainly one year. Most means are from five measurements. Animals less than 2.00 cm were usually measured only three times; therefore, comparisons of standard errors of animals less than 2.00 cm with animals larger than 2.00 cm will give conservative estimates of difference.

Δd	d_o		d_i		Δd	d_o		d_i	
	Mean ±	SE	Mean ±	SE		Mean ±	SE	Mean ±	SE
-.30 to -.21	5.47 ±	.029	5.24 ±	.009	-.10 to -.01	5.54 ±	.014	5.53 ±	.005
	4.92	.018	4.71	.011		5.42	.013	5.37	.019
	6.15	.019	5.84	.009		2.93	.015	2.90	.005
	6.53	.046	6.24	.009		4.96	.009	4.91	.015
	6.35	.019	6.10	.007		5.17	.015	5.07	.013
	5.29	.015	5.08	.020					
MEAN	5.79	.024	5.54	.011		4.80	.017	4.76	.011

Appendix V (cont.)

Δd	d_o		d_i		Δd	d_o		d_i	
	Mean	± SE	Mean	± SE		Mean	± SE	Mean	± SE
+.10 to +.19	1.88	± .004	2.06	± .008	+.30 to .39	4.67	± .008	4.97	± .010
	5.81	.009	5.93	.021		1.79	.003	2.11	.007
	4.87	.012	4.97	.010		3.79	.006	4.14	.011
	3.91	.004	4.08	.009		4.05	.033	4.39	.044
	5.15	.010	5.30	.019		1.91	.015	2.23	.005
MEAN	4.32	.008	4.47	.012		3.24	.013	3.57	.007
					- - - -				
+.50 to .59	2.82	.009	3.40	.017	+.70 to .79	1.91	.011	2.62	.008
	2.59	.006	3.14	.010		1.54	.003	2.26	.016
	4.91	.005	5.44	.012		2.37	.003	3.11	.007
	2.49	.017	2.99	.022		1.79	.005	2.53	.013
	1.92	.008	2.49	.010		2.51	.029	3.25	.031
MEAN	2.95	.009	3.49	.014		2.02	.010	2.75	.015

Appendix V (cont.)

Δd	d_o	d_i	Δd	d_o	d_i
	Mean ± SE	Mean ± SE		Mean ± SE	Mean ± SE
+.90 to 1.09	1.57 ± .002	2.51 ± .029	1.30 to 1.79	1.77 ± .008	3.13 ± .015
	2.02 .009	2.93 .032		1.22 .008	2.67 .029
	1.90 .005	2.86 .015		1.50 .020	3.29 .020
	1.89 .010	2.92 .027		2.20 .012	3.52 .035
	1.93 .037	2.94 .014		1.46 .007	3.23 .009
MEAN	1.86 .013	2.83 .023		1.63 .011	3.17 .022

Appendix V (concluded)

Growth of three animals from the eel grass area with three to five measurements in centimeters for each date. * indicates the diameter with the marked ambulacrum.

Date / Animal	7-64	12-64	7-65	11-65	3-66
1	1.57, 1.56 1.57	2.53, 2.55 2.48, 2.49	*3.12, 3.31 3.24, 3.29 3.29	*3.57, 3.74 3.66, 3.69 3.68	*3.57, 3.77 3.68, 3.72 3.72
2	1.78, 1.76 1.78		*2.85, 2.96 2.89, 2.95 2.97	*3.20, 3.35 3.24, 3.25 3.34	
3	1.91, 1.94 1.91	2.52, 2.49 2.51, 2.46 2.48	*3.31, 3.37 3.26, 3.35 3.37	*3.79, 3.97 3.96, 3.82 3.92	*3.85, 3.93 3.92, 3.87 3.96

Typed By: Sadri

(Sadri Secretarial Service)