

A Preliminary Quantitative Survey of the Echinoid Fauna of Kealakekua and Honaunau Bays, Hawaii¹

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DURING 8 DAYS in early August and October, 1968, the members of an expedition from the University of Hawaii examined the distribution and abundance of sea urchins in two bays along the Kona (leeward) Coast of the Island of Hawaii (Fig. 1): Kealakekua Bay (19° 28' N; 155° 55' W) and Honaunau Bay (19° 25' N; 155° 55' W). The major sampling effort was expended in Kealakekua, the larger of the two bays. The expedition was part of a program to survey the biota of Kealakekua. Information gathered from this survey will form a baseline for assessing changes that may be brought about by the activities of tourists and shoreline residents. At the present time, there is a small village on Kealakekua (Napoopoo) plus a small number of homes at the middle and south ends of the bay. The north end, by Captain Cook Monument, is uninhabited. At Honaunau Bay there is a small village, Honaunau, and the City of Refuge National Historical Park. Bay-related activities of people resident along the shorelines are fishing, principally with nets and handlines, and domestic-waste pollution. Some sea urchins are taken for food, but not in great numbers. Tourist activities include the collection of slate-pencil sea urchins (*Heterocentrotus mammillatus*) for their spines and the removal of snails and small coral heads. Tourists appear to be concentrated in Kealakekua Bay at Kaa-waloa Cove by Captain Cook Monument. Boats bring visitors from Kailua-Kona and, during the summer months, make two trips per day carrying up to 120 passengers per trip. Honaunau has no tourist boats and so possibly is not used as extensively. The area near Cook's Monument was selected for intensive sampling because of the high tourist density.

The August survey party consisted of Dr. J. Branham, E. Brecknock, J. McVey, and the

author; in October, the team consisted of E. Brecknock and D. Kelso.

ORGANISMS

Edmondson (1946) lists 14 regular urchins found as members of shallow-water benthic assemblages in Hawaiian waters. Eleven of these were found in Kealakekua and Honaunau bays and are listed below. The classification of Hyman (1955) is used.

Order Cidaroidea

Family Cidaridae

Chondrocidaris gigantea A. Agassiz

Euclidaris metularia (Lamarck)

Order Diadematoidea

Family Diadematidae

Diadema paucispina A. Agassiz

Echinothrix calamaris (Pallas)

E. diadema (Linnaeus)

Family Toxopneustidae

Tripneustes gratilla (Linnaeus)

Family Echinometridae

Colobocentrotus atratus (Linnaeus)

Echinometra mathaei (de Blainville)

E. oblonga (de Blainville)

Echinostrephus aciculatus A. Agassiz

Heterocentrotus mammillatus (Linnaeus)

METHODS

Five areas were examined within Kealakekua Bay, and single sites were selected within Honaunau Bay and 1 mile south of Honaunau (Fig. 1). From north to south, the sampling areas will be called: Napoopoo Light, Kaawaloa Cove, Napoopoo Breakwater, Ashihara Cottage, Palemano Point, Honaunau Bay, and 1 mile south of Honaunau.

Urchin densities in Kealakekua were anticipated to be less than one animal per square meter. A plotless method of sampling was

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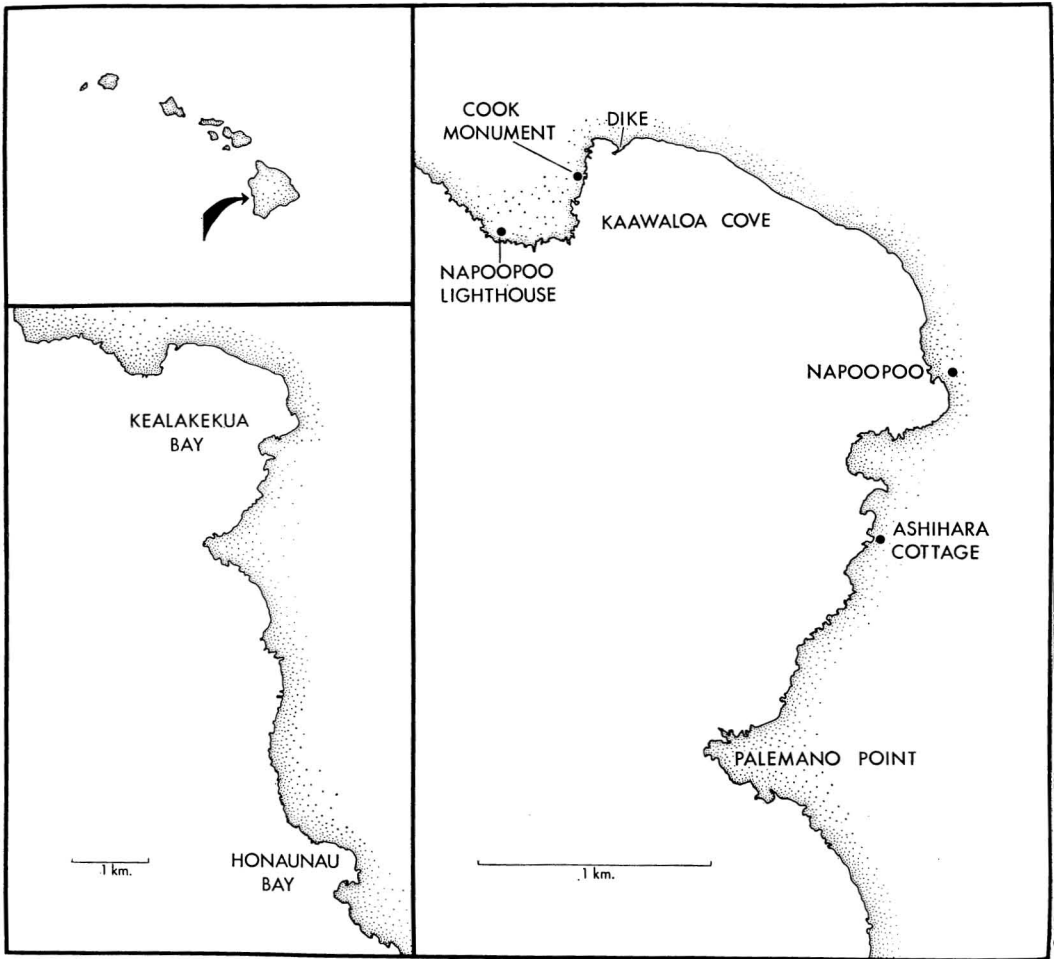


FIG. 1. Outline of Kealakekua and Honaunau bays, indicating their position in the Hawaiian chain.

selected, rather than quadrats, because I felt that an appropriate quadrat with such densities would be so large that it would be cumbersome for divers, or would have to be constructed at each sampling site. The quarter method of forest sampling (Cotton and Curtis, 1956) was modified for underwater use by divers with SCUBA. A concrete block or smooth lava stone weighing about 7 kg was used as the body of the sampling device. A cross of orange Glolite tape (such as used by construction survey teams) was attached to the block either with epoxy glue or small concrete-studs. A threaded stud was driven into the center of the cross and a snap-swivel placed over the stud. A nut and washer prevented the swivel from coming off, but still

allowed the swivel to move freely around the stud. A 50-foot stainless steel tape was attached to the snap. In each quadrant, a diver measured to the nearest sea urchin and recorded both distance and species. Data were written on white plastic slates. The plastic is distributed by Transparent Products Corporation (1727-43 W. Pico Boulevard, Los Angeles, California 90015) as no. VS-5300-08 pp, matte surface on both sides, and 0.02" thick. It is available in 20" × 40" sheets that are easily cut. Three divers were used, and generally each was able to measure between eight and 13 points per dive. Initial points were haphazardly selected at the deepest portion of the transect. Divers were taken by boat or swam to the area above the deepest

portion of the transect. Each diver was then given a concrete block and the first point was wherever he landed on the bottom. Subsequent points were taken along a line towards shore at 20- to 25-foot (7- to 8-meter) intervals.

Densities were calculated by first summing all the individual distances without regard to species, determining the mean distance, standard deviation, and standard error, and converting these into meters. The mean distance was then squared, and used to estimate the mean area containing one urchin. Confidence intervals were set by adding or subtracting one standard error from the mean and redetermining the mean area by squaring the result. This procedure is similar to handling data on which a square-root transformation has been performed (Sokol and Rohlf, 1969). For example, the mean distance off the breakwater at Napoopoo was $7.56 \pm .69$ feet.

$$\begin{aligned} 7.56 \pm .69 \text{ ft} \times 0.3048 \text{ m/ft} &= 2.30 \pm .21 \text{ meters} \\ 2.30^2 &= 5.29 \text{—the mean distance squared} \\ (2.30 + .21)^2 &= 6.30 \text{—the mean plus 1 SE squared} \\ (2.30 - .21)^2 &= 4.37 \text{—the mean minus 1 SE squared} \end{aligned}$$

The reciprocals of each of these squares give an estimate of the mean number of animals per square meter plus or minus 1 SE of the mean of the distance measurements.

$$\begin{aligned} 1/5.29 &= .19 \text{—the mean} \\ 1/6.30 &= .16 \\ 1/4.37 &= .23 \end{aligned}$$

$$\bar{x} = .19 + .4 \text{ or } -.03 \text{ animals per square meter}$$

The number of each species per square meter was calculated by multiplying the total density by the relative densities of the species. Relative density is defined as the number of a given species divided by total number of individuals in the sample. For a further discussion of the quarter method, see Cottom and Curtis (1956).

The initial August survey indicated higher densities than anticipated, so sampling in October was done with 1-meter-square quadrats. Sampling was initiated as in quarter-method sampling. The quadrat for the first sample was placed at the greatest depth; the next sample was taken by simply turning the quadrat over, thus advancing 1 meter up the slope. The result was a set of quadrats forming a 1-meter-wide band transect from deep water to the shore.

Echinometra sp. and *Colobocentrotus* were

not included in the quarter method of sampling in August, but were included in the quadrat counts.

In analyzing urchin distribution and abundance, several parameters were estimated, which were also used in a phytosociological description (Curtis and McIntosh, 1950, 1951). These parameters are defined as:

Relative frequency = number of occurrences of one species as a percentage of the total number of occurrences of all species.

Relative density = number of individuals of one species as a percentage of the total number of individuals of all species.

Relative weight = total wet weight of one species as a percentage of the total wet weight.

These relative values will be used to compare the species composition of different areas, and are descriptive additions to the estimates of absolute density (number of individuals per square meter).

Relative frequency and density were determined directly from the quadrat counts or from the points of the quarter method; however, because individuals were not weighed when counted, certain calculations were required to estimate weight. Animals were collected at several locations to determine the size structure of the populations. A sample (generally about 100 individuals) was taken by collecting as many animals from one location as possible. It must be stressed that the size distributions represent animals exposed enough to be seen by a swimmer. This obviously introduces a bias in favor of large individuals, and animals under 1 cm were probably inadequately sampled, although the diver efficiency indicated by Larsson (1968) may mean that sampling was not adequate even for animals as large as 4 cm.

Size distributions (Figs. 2 and 3) were constructed for *Heterocentrotus*, *Echinobrix calamaris*, and *Diadema* in Kaawaloa Cove, for *Triploneustes* at Palemano Point, and for *Heterocentrotus* at Honaunau Bay. Because *Echinometra* lives in holes in the coral and is generally difficult to extract, the sampling technique for this species was different from that used for the other urchins. Individuals were measured in place in a series of 1-meter quadrats in the corner of Kaawaloa Cove. The urchins were

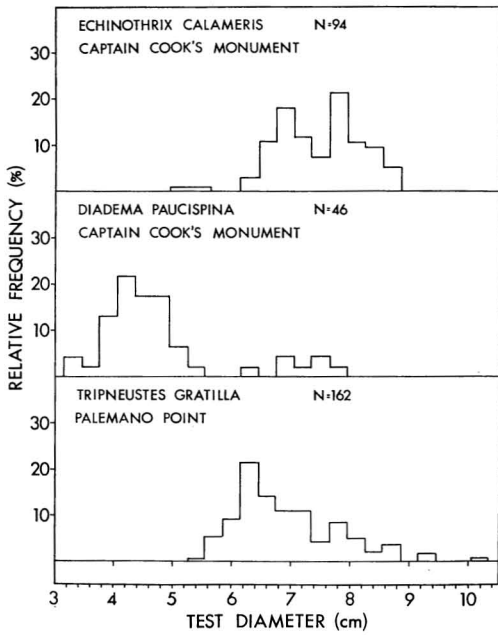


FIG. 2. Relative frequency as a function of test diameter in selected urchin species.

measured under water with vernier calipers and the individuals assigned to 1-cm size classes.

Size distributions were converted into weights by first determining a mathematical expression relating wet weight to a linear measurement. A series of animals was weighed and measured: *Heterocentrotus* from Kealakekua Bay; *Echinothrix diadema* from Kapapa Island, Oahu; *Tripneustes* from Kaneohe Bay and Makua Beach, Oahu; and *Echinometra mathaei* from the Blowhole, Oahu.

Log-log plots of wet weight vs. diameter were not linear. It was discovered that the exponent required to raise a linear measurement to its wet weight was a function of that linear measurement, but that the relationship was non-linear (Fig. 4). For *Echinothrix* and *Tripneustes*, the exponent increased with increasing size. For *Heterocentrotus* the exponent decreased with increasing size. This relationship appears to be determined by the contribution of the spines to the total weight of an individual. The spines of *Tripneustes* and *Echinothrix* are relatively large in a small individual, and relatively small in a large individual. The result is that a greater percentage of the total weight is made

up of spines in a small animal, and relatively less in a large individual. The opposite is true for *Heterocentrotus*, where small individuals have relatively less of their total weight made up by spines than do large individuals. The possibility of allometric relationships between test size and relative thickness or test height and test diameter cannot be ruled out. These morphological features, however, were not examined, and, as a first approximation, the changing contribution of the spines to total weight appears to be paramount. *Tripneustes* showed the least weight variation at a given size, and *Heterocentrotus* showed the greatest variation. This difference again may be related to the relative contribution of the spines to total weight. A single lost or broken spine in *Heterocentrotus* would change the weight more than removing all of the spines of a *Tripneustes* of similar size.

Several methods were used to develop an expression that would describe the size-dependent exponent. No method was found that was satisfactory for all species. The "Walford method" (Ricker, 1958) of fitting growth data to the von Bertalanffy growth equation was used to approximate exponent values for a given size.

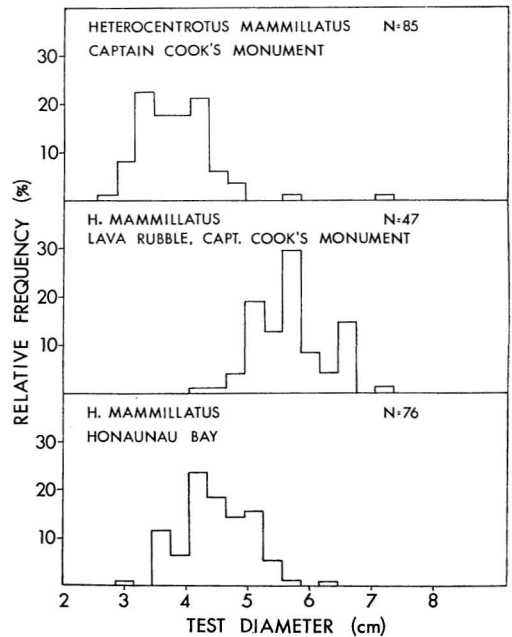


FIG. 3. Relative frequency of the urchin *Heterocentrotus mammillatus* as a function of test diameter.

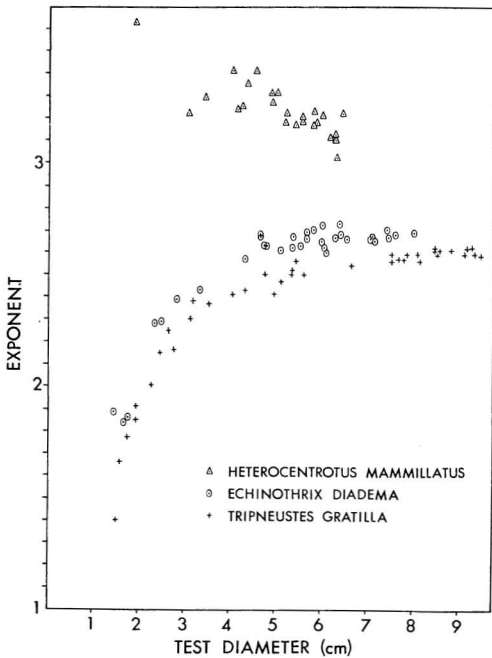


FIG. 4. Exponent (x) required to convert urchin test diameter (D) into wet weight in the expression wet weight = D^x (diameter in centimeters and weight in grams).

Size classes were set up with a 1-cm interval, and the mean exponent (x) at a diameter ($d + 1$ cm) was plotted as a function of the exponent at size d . This is comparable to Walford's length at ($t + 1$) as a function of length at time t . The maximum exponent determined in this manner was used as a trial value in the plot of $\ln(x_{\max} - x_d)$ as a function of d . The straightness of such a plot is a function of the value

selected for x_{\max} (Ricker, 1958). The value of x_{\max} was adjusted to give the straightest line by a computer program that maximized the correlation coefficient. The constants derived from the regression of $\ln(x_{\max} - x_d)$ on d were used to write an expression relating the value of an exponent to the animal size. The general form of the expression is:

$$x_d = x_{\max} (1 - e^{-K(d-d_0)}) \quad (1)$$

and, then to determine wet weight in grams,

$$W_d = d^x \quad (2)$$

where W_d is wet weight at a given size and d is test diameter.

A second method of finding exponents was by selecting constants from a regression of $\log_{10} x_d$ on $\log \log d$.

$$W_d = d^{k(\log d)^b} \quad (3)$$

A third method was by using constants from a regression of $\ln \ln W_d$ on $\ln \ln d$.

$$W_d = e^{k(\ln d)^b} \quad (4)$$

Generally, the best fit was obtained from expression 3 (Table 1). No attempt was made to determine a general expression relating wet weight to size for *Echinometra*. The size distribution of *Echinometra mathaei* in Kaawaloa Cove had a small mean and small standard deviation (mean diameter = $2.4 \pm .7$ [SD] cm). It was felt that an adequate estimate of weight did not require the establishment of a general expression. Nine small *Echinometra* were collected from rocky pools near the Blowhole, Oahu. Size range was from 2.27 cm to 3.74 cm.

TABLE 1
REGRESSION EQUATIONS RELATING LINEAR TEST MEASUREMENTS IN CENTIMETERS (D) TO WET WEIGHTS IN GRAMS (W_T)

SPECIES	AREA OF COLLECTION	N	EXPRESSION
<i>Heterocentrotus mammillatus</i>	Kealakekua Bay, Hawaii	26	$W_t = D^{3.063(\log D) - .1491}$
<i>Echinothrix diadema</i>	Kapapa Island, Oahu	35	$W_t = D^{2.839(\log D)^{.2462}}$
<i>Tripneustes gratilla</i>	Kaneohe Bay, Oahu and Makua Beach, Oahu	307	$W_t = D^{2.688(1 - e^{-.769(D - .500)})}$ $W_t = e^{2.194(\ln D)^{1.250}}$ $W_t = D^{2.620(\log D)^{.1482}}$

NOTE: Equations are listed for each species in order of adequacy in relating wet weight to test diameter. Goodness of fit was determined by eye. Greatest length was measured in *Heterocentrotus*; diameters were measured in *Tripneustes* and *Echinothrix*. All animals were collected during August 1968.

Wet weight of a 2.4-cm individual was determined graphically and found to be 8.2 grams. Average weights for the other urchin species were found by calculating the weight of each class in the size distribution and multiplying this by the relative frequency of the class. The sum of weight times frequency for all classes is an estimate of the weight of an average individual, and was used to estimate the weight of a given density of urchins and to calculate relative weights.

For a species where no size distribution was constructed, weights were approximated by the urchin that most closely resembled it in size. *Eucidaris* and *Echinostrephus* were approximated by *Echinometra*; *Chondrocidaris* was approximated by *Heterocentrotus*. All relative weight values were based on the size distributions indicated above: all *Echinobrix* populations were assumed to be like the one measured in Kaawaloa Cove; all *Tripneustes* populations were assumed to be like the one measured at Palemano Point; and so forth. The relative weight values are subject to the errors inherent in these approximations of size structure. A problem developed in the underwater identification of the two species of *Echinobrix*, so that there is doubt surrounding the actual field records; both *E. diadema* and *E. calamaris* were present, but data are pooled to avoid conveying inconsistencies.

RESULTS

Total Urchin Density

The initial stage of quarter data analyses was to combine distance measurements at the points into statistically homogeneous subsets of the entire sample. Because transects were made up a physical cline (depth) in all but the Napoopoo breakwater transect, an analysis procedure was selected that would permit separation of the transect into subsets showing similar densities. Beginning at the bottom of the transects, distance measurements from adjoining pairs of points were pooled, yielding subsets of eight measurements each (four measurements per point). For example, measurements from points one and two were pooled, those from points three and four were pooled, etc. Cottom, Curtis, and Hale (1953) showed that the mean values

of the four measurements at the points are normally distributed so the means of the subsets were tested for homogeneity by analysis of variance. The subsets were combined where non-significance of difference ($p > .05$) was indicated by Duncan's multiple range test (Walpole, 1968). This procedure gave a single subset for the entire transect, or the transect was broken into several homogeneous subsets (Table 2).

Data gathered from the use of quadrats were processed differently. In Kaawaloa Cove, quadrats were segregated by 10-foot depth intervals and the quadrats for the five transects were combined on this basis. Statistical analysis involved the calculation of means and variances at each 10-foot level (Table 3). A single mean was calculated for areas showing low urchin densities (Napoopoo Light and 1 mile south of Honaunau).

Analysis of Species Composition in Each Area

AREA 1, BETWEEN NAPOOPOO LIGHT AND KAAWALOA COVE: Of the sites sampled, this area and the transect 1 mile south of Honaunau were the most exposed to waves. The bottom sloped rapidly away from the shore with several vertical ledges of 15 to 20 feet (5 to 7 meters). Near shore, in the surf, the rocks were relatively barren, with only a few *Colobocentrotus*. At a depth of about 30 feet (10 meters) the bottom was covered with coral heads. Below this depth, the bottom dropped to 28 fathoms at an angle of about 30°. Three quarter-method transects and a single transect using quadrats were run in this area. Transects were perpendicular to the shore and started at a depth of about 80 feet (25 meters). Of all regions sampled by the quarter method, distances to urchins from the center point were greatest in this area. When no urchin could be found in a quadrant within a radius of 50 feet, the value of 50 feet was recorded and the species called "blank." This region and the transects at Napoopoo breakwater were the only areas where blanks were recorded. Other areas fulfilled the requirements of the quarter method with an urchin recorded for every quadrant. The means of the distance measurements of the three transects were not homogeneous by an analysis of variance ($F_{(2,81)} = 11.22, p < .01$). Means of two transects,

TABLE 2
URCHIN DENSITY ESTIMATES BASED ON THE QUARTER METHOD OF SAMPLING

AREA	SUBSET*	NUMBER OF MEASUREMENTS	DISTANCE (m) MEAN \pm 1 SE		DENSITY** (no./m ²)	
1. Napoopoo Light	A	72	4.77 \pm .56	.03	<u>.04</u>	.06
	B	12	11.7 \pm 1.0	.006	<u>.007</u>	.009
2. Kaawaloa Cove	A†	8	7.26 \pm 2.32	.01	<u>.02</u>	.04
	B	16	2.08 \pm .26	.20	<u>.23</u>	.30
	C	32	1.62 \pm .17	.31	<u>.38</u>	.47
	D	4	3.61 \pm .52	.06	<u>.08</u>	.10
	E	176	.64 \pm .03	2.22	<u>2.45</u>	2.73
	F	8	.84 \pm .16	1.01	<u>1.43</u>	2.16
	G	8	1.28 \pm .16	.49	<u>.61</u>	.80
3. Napoopoo Breakwater	A	76	2.30 \pm .21	.16	<u>.19</u>	.23
4. Ashihara Cottage	A	48	.92 \pm .10	.96	<u>1.18</u>	1.48
	B	20	1.86 \pm .24	.15	<u>.29</u>	.72
5. Honaunau Bay	A	92	.68 \pm .05	1.87	<u>2.14</u>	2.48
	B	40	.96 \pm .10	.99	<u>1.08</u>	1.25

* Subsets determined by analysis of variance and Duncan's multiple range test. Full explanation given in text.

** The mean is underlined and bracketed by estimates based on 1 SE of the mean distance. See text for sample calculation.

† Spatial relationship of the subsets in Kaawaloa Cove is shown in Figure 5. Relationships of subsets in other areas are described in the text.

however, formed a homogeneous subset by Duncan's least significant range test. The two transects that were combined bracketed the statistically distinct transect. The variation between the two subsets accordingly cannot be attributed to a cline and is probably due to chance. The larger subset contained 72 distance measurements with 14 percent blanks. The smaller subset contained 12 measurements and had 33 percent blanks. Because the quarter method requires

that the individuals be randomly dispersed, it was necessary to determine whether the urchins were indeed randomly distributed in the areas that were sampled. The estimate of density using the quarter method is too low in aggregated populations and too high in regularly dispersed populations (Greig-Smith, 1964). If a population is randomly dispersed, then the distance measurements, if grouped into classes, should follow a Poisson distribution. Deviation

TABLE 3
ESTIMATE OF URCHIN DENSITY FOR KAAWALOA COVE

DEPTH (feet)	NUMBER OF QUADRATS	MEAN DENSITY (number per square meter)	r^2	DEVIATION FROM A POISSON (chi ²)	d.f.	SIGNIFICANCE
0.1-10.0	26	5.4	20.1	8.19	2	p < .05
10.1-20.0	27	5.7	5.5	0.65	2	N.S.
20.1-30.0	28	3.5	8.3	14.3	2	p < .01
30.1-40.0	25	2.1	3.7	0.29	1	N.S.
40.1-50.0	25	1.8	1.7	0.05	1	N.S.
50.1-70.0	22	1.1	0.9	0.04	1	N.S.

NOTE: Estimate based on 1-square-meter quadrats arranged in band transects perpendicular to the shore. *Echinometra* is not included in estimate.

from randomness was examined for each subset of measurements by first constructing five frequency distributions using 0.5, 1, 2, and 4 feet, and the mean distance as interval widths. It was felt that construction of five distributions would be similar to selecting five quadrat sizes for examining dispersion. The choice of a single interval size for construction of the frequency distribution would be analogous to arbitrarily selecting a quadrat size for sampling, and so interval size would influence statements concerning pattern and interpretation of the density estimate using the quarter method. In the case of the Napoopoo Light transects, the 72-value subset indicated that urchins were aggregated at all interval widths. Using a 1-foot interval, significance of difference was at the .01 level ($\chi^2_{(7)} = 74.1$) and the variance-mean ratio was 13.4, which indicates that the deviation of the observed distribution from the expected Poisson distribution was due to aggregation, rather than regular dispersion. When the mean distance was used as the interval size (15.7 feet, rather than 1 foot), the resulting distribution was still significantly different from a Poisson ($\chi^2_{(2)} = 45.5$, $p < .01$); however, the variance-mean ratio was only 1.7. The decrease in the variance-mean ratio with increasing interval size suggests that the animals appeared less aggregated when a large sampling unit was used. This decrease in the ratio may also mean that the animals occurred in large clumps or in aggregates of small clumps.

The 12-value subset was too small to analyze by grouping values into a frequency distribution; however, the variance-mean ratio of the distance measurements was 3.7, again indicating aggregation. Estimates of density for the two subsets are $.04 \pm .02$ or $-.01$ urchins per square meter for the 72-point subset and $.007 \pm .002$ or $-.001$ urchins per square meter for the 12-value subset (Table 2). Because the urchins were not randomly dispersed, these density estimates are low.

Densities estimated from quadrats are higher. The single transect by the lighthouse gave a density estimate of $.67 \pm .24$ (SE) animals per square meter, not including *Echinometra* and $.83 \pm .27$ urchins per square meter, including *Echinometra*. Aggregation, however, was still indicated with a variance-mean ratio of 2.

Echinobrix and *Heterocentrotus* were the dominant urchins, according to the quarter method, with relative weights (percentage of urchin biomass) of 65.5 and 29.4, respectively (Table 4). *Tripneustes*, *Eucidaris*, and *Echinostrephus* were similar with relative weights all less than 5 percent. Relative weights determined from the quadrats were similar, although *Heterocentrotus* had a somewhat lower value and *Echinobrix* had a somewhat higher value: 20 for *Heterocentrotus* and 75.9 for *Echinobrix*. *Tripneustes*, *Eucidaris*, and *Echinometra* were less than 5. *Echinostrephus* was not detected in the quadrat transect, and *Echinometra* was not counted when the quarter method was used. The wet weight of urchins per square meter indicated by the quarter method was 5 grams for the 72-point subset, and 1 gram for the 12-point subset. The wet weight calculated from the quadrat data was 130 grams per square meter. As indicated by forest populations (Cottom and Curtis, 1956), when individuals are aggregated, the distance measurements of the quarter method are too long, and indicate fewer individuals per unit area than are actually present. Although not documented, all divers agreed that when densities were low there was a good chance that the urchin closest to the block would not always be found. The small number of quadrats counted may also lead to an error in estimation.

AREA 2, KAAWALOA COVE: The cove appeared to be very protected from waves. The degree of protection is suggested by the fact that the bay is used for boat moorage during winter storms. Six quarter-method transects were run: three in front of Cook's Monument (one directly off the Monument, and one on each side) and three south of the Monument, and off a geologic dike (one transect directly off the dike and one on each side). Five quadrat transects were run from directly in front of the Monument to the corner of the cove between the Monument and the dike. The rate of descent was between 30° and 50°, with the highest rate directly in front of the Monument. The shallow waters, less than 4 feet deep, were different in the two areas of the cove. The area off the dike was at the base of a tallus slope, and was composed of large lava boulders that did not support a lush coral growth. Coral rubble with some living coral formed the substrate in the shallows in

TABLE 4
RELATIVE DENSITY AND RELATIVE WEIGHT OF URCHINS IN EACH AREA

AREA	SPECIES	NUMBER OF QUADRATS OR POINTS OF OCCURRENCE	NUMBER OF URCHINS	RELATIVE DENSITY (number/ total number)	RELATIVE WEIGHT†
1. Napoopoo Light (quarter)	<i>Heterocentrotus</i>	16	33	47.1	29.4
	<i>Echinothrix</i>	17	26	37.1	65.5
	<i>Tripneustes</i>	4	4	5.7	4.5
	<i>Eucidaris</i>	3	5	7.1	0.4
	<i>Echinostrephus</i>	2	2	2.9	0.2
1. Napoopoo Light (quadrat)	<i>Heterocentrotus</i>	6	9	32.1	20.0
	<i>Echinothrix</i>	10	12	42.9	75.9
	<i>Tripneustes</i>	1	1	3.6	2.8
	<i>Eucidaris</i>	2	3	10.7	0.6
	<i>Echinometra</i>	3	3	10.7	0.6
2. Kaawaloa Cove (quarter) Subset B	<i>Heterocentrotus</i>	2	2	15.4	9.8
	<i>Echinothrix</i>	3	3	23.1	41.7
	<i>Tripneustes</i>	3	7	53.8	43.6
	<i>Chondrocidaris</i>	1	1	7.7	4.9
2. Kaawaloa Cove (quarter) Subset C	<i>Heterocentrotus</i>	6	13	40.6	30.1
	<i>Echinothrix</i>	4	4	12.5	26.3
	<i>Tripneustes</i>	7	14	43.7	41.3
	<i>Chondrocidaris</i>	1	1	3.1	2.3
2. Kaawaloa Cove (quarter) Subset E	<i>Heterocentrotus</i>	42	145	84.3	69.1
	<i>Echinothrix</i>	13	21	12.2	28.5
	<i>Tripneustes</i>	1	2	1.2	1.2
	<i>Eucidaris</i>	1	1	0.6	0.0
	<i>Chondrocidaris</i>	1	1	0.6	0.5
	<i>Diadema</i>	1	2	1.2	0.7
2. Kaawaloa Cove (quadrat)	<i>Heterocentrotus</i>	103	363	49.8 (75.1)*	57.4 (59.5)*
	<i>Echinothrix</i>	41	69	9.5 (14.3)	31.1 (32.2)
	<i>Tripneustes</i>	31	37	5.1 (7.7)	7.5 (7.8)
	<i>Eucidaris</i>	9	10	1.4 (2.1)	0.0 (0.0)
	<i>Echinometra</i>	50	246	33.7 —	3.5 —
	<i>Diadema</i>	3	3	0.4 (0.6)	0.4 (0.4)
	<i>Echinostrephus</i>	1	1	0.1 (0.2)	0.0 (0.0)
	3. Napoopoo Breakwater (quarter)	<i>Heterocentrotus</i>	19	55	77.5
<i>Echinothrix</i>		8	10	14.1	31.2
<i>Tripneustes</i>		4	6	8.4	8.4
4. Ashihara Cottage (quarter) Subset A	<i>Heterocentrotus</i>	12	46	95.8	94.0
	<i>Echinothrix</i>	1	1	2.1	5.8
	<i>Eucidaris</i>	1	1	2.1	.2
4. Ashihara Cottage (quarter) Subset B	<i>Heterocentrotus</i>	5	13	65.0	41.5
	<i>Echinothrix</i>	3	6	30.0	54.5
	<i>Tripneustes</i>	1	1	5.0	4.1
6. Honaunau Bay (quarter) Subset A	<i>Heterocentrotus</i>	23	90	97.8	95.9
	<i>Echinothrix</i>	1	2	2.2	4.1
6. Honaunau Bay (quarter) Subset B	<i>Heterocentrotus</i>	10	37	92.5	86.6
	<i>Echinothrix</i>	2	3	7.5	13.4

TABLE 4 (Continued)

AREA	SPECIES	NUMBER OF QUADRATS OR POINTS OF OCCURRENCE	NUMBER OF URCHINS	RELATIVE DENSITY (number/total number)	RELATIVE WEIGHT†
7. 1 Mile	<i>Heterocentrotus</i>	4	9	45.0	52.6
South of	<i>Tripleneustes</i>	4	6	30.0	44.7
Honaunau	<i>Eucidaris</i>	1	1	5.0	0.5
(quadrat)	<i>Echinometra</i>	3	4	20.0	2.1

* Relative values do not include *Echinometra*.

† Relative weight = calculated weight of a species/calculated weight of all species.

front of the Monument. Below 4 to 5 feet, there was living coral in both areas. At depths below 30 to 40 feet (10 to 15 meters), the two areas once again differed. Off the Monument, *Porites compressa* was the principal coral found, but the heads appeared dead except for their tips; algae were abundant between the coral fingers; and there was considerable rubble, perhaps caused by anchor chains. Off the dike *Porites pukoensis* was more abundant, and more of the coral appeared to be alive.

The distance measurements of the six quarter transects were lumped to form two-point subsets in each transect. The subsets were then grouped into horizontal sets composed of similar points of all transects (i.e., all subsets formed from points one and two of all transects were grouped into a single set; all subsets formed from points three and four of all transects were grouped into a single set, etc.). Subsets within each set were tested for homogeneity of means and were combined according to Duncan's multiple range test at the .05 level. These new subsets were then tested vertically for homogeneity of means and combined when not significantly different. The resulting subsets represented regions of the transects that had similar distance measurements. Seven regions were segregated by this technique (Fig. 5). One subset, subset E, included the major portion of the sampled region and contained 43 points (172 measurements). There was one region with eight points, subset C; one with four points, subset B; three with two points, subsets A, F, and G; and one subset with only one point, subset D. A frequency distribution of the distance measurements was constructed using intervals of 1 foot. This distribution was not significantly different from a Pois-

son ($\chi^2_{(4)} = 6.75, p > .05$). However, significant difference was obtained when the interval size was 0.5 foot ($\chi^2_{(7)} = 32.2, p < .01$), which suggested that if a nonrandom pattern exists, it is of a small scale. Distributions using interval sizes of 2 and 4 feet, and the mean distance (2.1 feet) also were not significantly

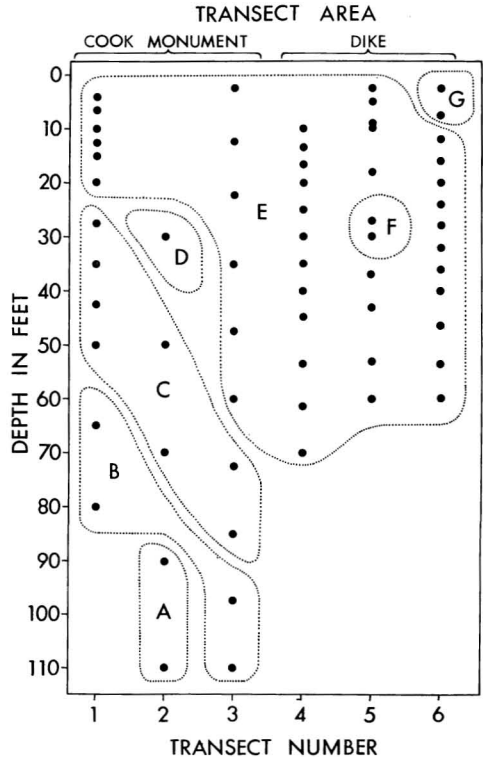


FIG. 5. Areas of equal urchin density in Kaawaloa Cove determined by the quarter method of sampling and variance analysis. Values for each area are given in Table 2.

different from Poisson distributions with similar means. Subset *B* did not indicate aggregation at any interval size. Subset *C* distances were of random length using a 0.5-foot interval ($\chi^2_{(3)} = 6.0$, $p > .05$), and nonrandom at 1-foot and 2-foot intervals ($\chi^2_{(5)} = 12.7$, $p < .05$), and ($\chi^2_{(3)} = 8.46$, $p < .05$). Mean distance (Table 2) for subset *A*, the deepest subset (100 feet), was 7.26 ± 2.32 meters, which gives a density estimate of $.02 \pm .02$ or $-.01$ animals per square meter. For subset *B*, at depths extending from 70 to 100 feet, the mean distance was $2.08 \pm .26$ meters, which gives a density estimate of $.23 \pm .07$ or $-.03$ animals per square meter. For subset *E*, the shallowest subset (average depth about 30 feet), the mean distance was $.64 \pm .03$ meters, and the density $2.45 \pm .28$ or $-.23$ urchins per square meter, indicating definite decreases in density with depth, a conclusion also reached using the quadrat data (Table 3). All species except *Tripneustes* decreased in density with increasing depth (Figs. 6 and 7). Densities were somewhat higher than indicated by the quarter method, which gave an average density for a depth range from 5 to 60 feet (2 to 20 meters). The range indicated from quadrat data, excluding *Echinometra* to make it comparable to the quarter survey, was 5.4 ± 0.9 animals per square meter at a depth of zero to 10 feet (2 to 3 meters) and $1.1 \pm .2$ per square meter at 50 to 70 feet (19 to 20 meters). If the values from quadrat sampling are weighted and

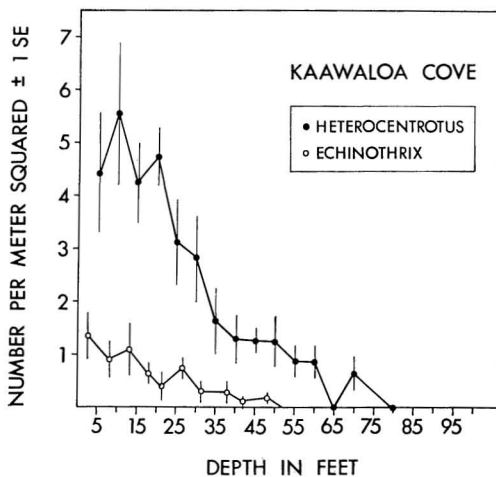


FIG. 6. Density of *Heterocentrotus* and *Echinothrix* as a function of depth in Kaawaloa Cove.

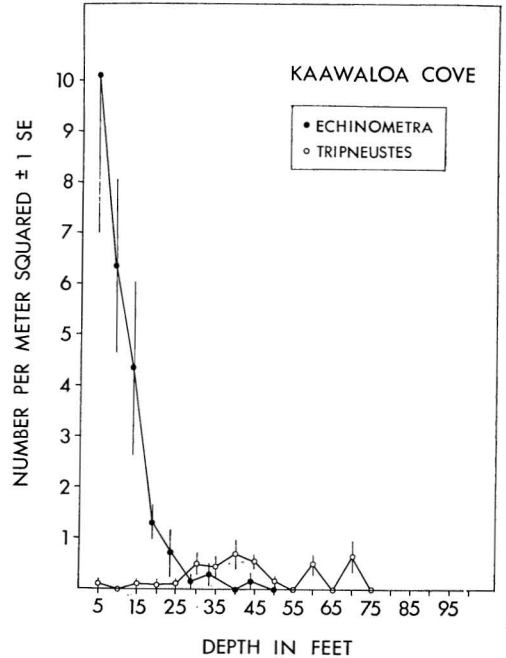


FIG. 7. Density of *Echinometra* and *Tripneustes* as a function of depth in Kaawaloa Cove.

combined in such a manner as to approximate the quarter samples of subset *E*, the density estimate is 3.7 urchins per square meter, which is higher than the quarter-method estimate of 2.45 ± 0.28 or $-.23$ and is a pattern often found when quadrat and quarter data are compared (Risser and Zedler, 1968). This difference again appears to be related to dispersion pattern. Generally, the urchins tended to be randomly dispersed within Kaawaloa Cove at any particular depth (Table 3); however, the exceptions at zero to 10 feet and 20 to 30 feet, if real, will influence the estimate of density. The safest conclusion is that the density for the major portion of Kaawaloa Cove lies between 2.5 and 3.7 urchins per square meter, exclusive of *Echinometra*, and that there are more individuals in shallow areas.

According to the quadrat data, the only species to increase with depth was *Tripneustes*. This trend was also shown by the quarter method, where subsets *B* and *C* had greater densities of *Tripneustes* than did subset *E*. Relative weights (Table 4) are similar by both sampling methods: *Heterocentrotus*, with a relative weight

of 59.5 by the quadrat sampling method, and 69.1 by the quarter sampling methods in subset *E*, contributed the most to total biomass of urchins. The next important urchin in terms of total biomass was *Echinothrix* with a relative weight of 32.2 using quadrats, and 28.5 in subset *E* of quarter sampling. All other urchins were of minor importance in shallower waters. In deeper water, in subset *B*, *Tripneustes* contributed most to the urchin biomass with a relative weight of 43.6. *Echinothrix* had nearly the same relative weight (41.7), and *Heterocentrotus* formed only 9.8 percent of the urchin biomass. In subset *C*, the relative weights were: *Heterocentrotus*, 30.1; *Echinothrix*, 26.3; and *Tripneustes*, 41.3.

The total wet weight of urchins based on quadrat sampling was a function of depth in Kaawaloa Cove (Fig. 8), approaching 1 kilogram per square meter in shallow water, and decreasing to 100 grams per square meter at 80 to 100 feet (30 meters).

AREA 3, NAPOOPOO BREAKWATER: Directly

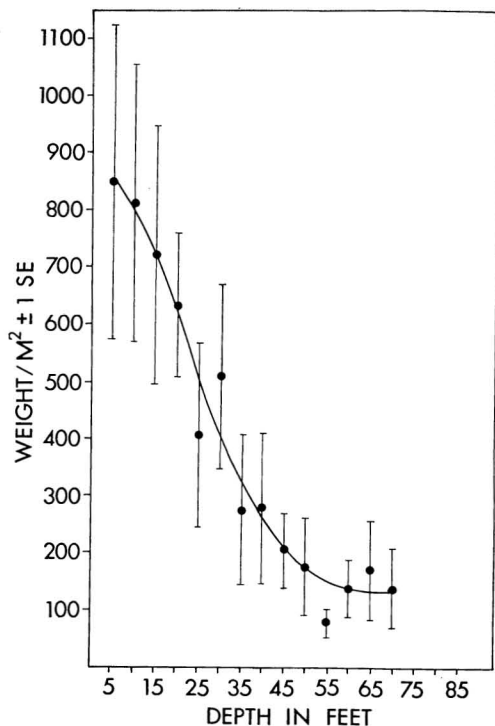


FIG. 8. Urchin biomass (wet weight) as a function of depth in Kaawaloa Cove.

in front of the breakwater at Napoopoo, the bottom consisted of large coral mounds separated by sand. Two quarter-method transects were run 100 and 200 feet from shore, and parallel to it. Water depth was 10 to 20 feet (3 to 5 meters). Analysis of variance indicated that the measured distances of the two transects were homogeneous ($F_{(1,69)} = 1.28$, $p > .05$), so distance measurements of the two transects were combined. Distance measurements grouped by 0.5 foot intervals formed a frequency distribution significantly different from a Poisson ($\chi^2_{(13)} = 224$, $p < .01$). Distributions also were significantly different from a Poisson using 1-foot and 2-foot intervals, but were not significant with a 4-foot interval, or with the interval equal to the mean of 7.56 feet ($\chi^2_{(3)} = 8.0$, $p < .05$ and $\chi^2_{(2)} = 1.7$, $p > .05$). The variance-mean ratio using a 0.5-foot interval was 5.1, which indicates aggregation. The mean distance was $2.30 \pm .04$ or $-.03$ animals per square meter (Table 2). Because the population had an aggregated dispersion pattern, this estimate of density is too low. The nature of the substrate explains the aggregation: coral heads separated by sandy areas where urchins were not found. Relative weights (Table 4) are, however, still valid in describing the composition of the urchin biomass. *Heterocentrotus* and *Echinothrix* were similar to subset *E* of Kaawaloa Cove, and *Tripneustes* was higher: 60.4 for *Heterocentrotus*, 31.2 for *Echinothrix*, and 8.4 for *Tripneustes*.

AREA 4, ASHIHARA COTTAGE. The fourth area was a lava rock shore in front of a cottage owned by T. Ashihara of Kealakekua, Hawaii. A single 17-point transect was run from about 300 feet (100 meters) offshore into a small cove in front of the cottage. Water depth was from about 30 to 5 feet (10 to 2 meters). Measured distances for two-point subsets did not form a homogeneous set for the entire transect ($F_{(8,59)} = 4.81$, $p < .01$). Two homogeneous sets could be formed using Duncan's multiple range test which separated the transect into its upper five points and lower 12 points. Within the lower 12 points, the frequency distribution of distances grouped by 1-foot intervals was not significantly different from a Poisson ($\chi^2_{(3)} = 7.59$, $p < .05$), indicating a random distribution of animals. Using 0.5-foot intervals, the

resulting distribution of distance measurements was significantly different from a Poisson ($\chi^2_{(5)} = 28.9$, $p < .01$), with a variance-mean ratio of 3.6. In the upper five points, use of a 4-foot interval size produced a frequency distribution that departed significantly from a Poisson ($\chi^2_{(6)} = 17.1$, $p < .01$); other interval sizes produced frequency distributions that were not significantly different from Poisson distributions. Accordingly, the urchins can be considered to be generally randomly dispersed, and estimates of density should be accurate. The mean distances were 0.92 ± 0.10 meters in the lower subset and 1.86 ± 0.24 meters in the upper subset. These give density estimates of $1.18 \pm .30$ or $-.22$ and $0.29 \pm .43$ or $-.014$, respectively. *Heterocentrotus* contributed most to urchin biomass in the lower subset with a relative weight of 94.0. In the upper subset, it formed 4.5 percent of the biomass. *Echinobrix* made up 5.8 percent of the biomass in the lower and 54.4 percent in the upper subset. *Euclidaris* was present in the lower and not present in the upper subset, and *Tripneustes* was in the upper and not present in the lower subset. The distribution of the urchins is interesting when compared with subset *E* in Kaawaloa Cove, where *Euclidaris* was present near the surface, and not deep, and *Tripneustes* was rare near the surface, and more abundant at lower depths.

AREA 5, PALEMANO POINT: The fifth area was a protected shelf at Palemano Point at the south end of Kealakekua Bay. A lava flow formed a flat area with rocks rising above the water surface. There were many shallow pools, some of which were sandy. The plotless method was not used here, but rather a 1-meter quadrat was employed to sample a densely aggregated population of *Tripneustes*. A total of 30 quadrats were enumerated in $1\frac{1}{2}$ meters of water. The band of urchins was about 8 meters wide and 20 meters long. Mean density within the aggregation was 4.3 per square meter; however, the range was from zero to 12. *Heterocentrotus*, *Echinobrix*, and *Echinometra* were present in the area around the *Tripneustes* bed, but were not abundant. The areas where *Tripneustes* was present were bare of algae, although algae and coral were present in surrounding areas.

AREA 6, HONAUNAU BAY: Sampling was done just north of the canoe landing at the village of

Honaunau. The bottom was principally composed of living coral. Depth ranged from 10 to 35 feet (3 to 10 meters). The bottom sloped very gently for a distance of about 100 meters from shore, where it descended rapidly to 23 fathoms. Although the average slope was small, the bottom consisted of very large coral mounds, separated by coral-filled valleys, so locally there was high relief. Some of the mounds appeared to be dead. Sampling was initiated just shoreward of the drop-off, where three plotless transects were run perpendicular to the shore.

The means of the distance measurements of the three transects did not form a homogeneous subset ($F_{(2,129)} = 4.10$, $p < .05$). Duncan's least significant range test indicated that two subsets should be formed, one with 23 points (subset *A*), and the other with 10 (subset *B*). Mean distance in subset *A* was $.68 \pm .05$ meter, and in subset *B*, it was $.96 \pm .10$ meter. These give density estimates of $2.14 \pm .34$ or $-.27$ animals per square meter, and $1.08 \pm .17$ or $-.09$. Distance measurements grouped in 1-foot and larger intervals formed frequency distributions not significantly different from a Poisson in both subsets, indicating that the urchins were randomly dispersed. Relative weight values of the two subsets were similar, although *Echinobrix* was somewhat more important in subset *B*. The values were: for *Heterocentrotus*, 95.9 in subset *A*, and 86.6 in subset *B*; and *Echinobrix* 4.1 in subset *A*, and 13.4 in subset *B*. The two subsets differed slightly in the method of selecting points. The two transects making up subset *A* were set directly perpendicular to the shore, and so points were sampled both on the tops of the coral mounds, and in the valleys between mounds. Subset *B* was taken by following a valley, and did not include points from the tops of the mounds. The conclusion is that the tops of the mounds may differ from valleys by having more animals, and there are more *Echinobrix* at the tops of mounds. Whether this is the result of the same interactions that produced zonation in Kaawaloa Cove is not known.

AREA 7, 1 MILE SOUTH OF HONAUNAU. The final area that was sampled was about 1 mile south of Honaunau Bay. A single transect using quadrats was run from a depth of 60 to 20 feet (20 to 6 meters). The bottom was lava, and the shore was exposed to the sea. The transect was

similar to the transect at Napoopoo Light with respect to wave action, exposure, and so forth. Density of *Echinothrix* was estimated to be $.67 \pm .24$ compared with $.83 \pm .19$ at the lighthouse, and with *Echinometra*, the density was $.83 \pm .27$ compared with $.93 \pm .20$ at the lighthouse. The urchins were aggregated as indicated by the variance-mean ratio of 2.0. The urchin biomass was composed of 52.6 percent *Heterocentrotus*, followed by *Tripneustes* (44.7 percent). *Echinothrix* did not appear in the sample, and its absence is a major difference between this sample and those at Napoopoo Light, where *Echinothrix* formed the major segment

of the urchin biomass by both the quarter method and quadrat sampling.

Comparison of Areas

Not only did major areas differ in absolute density of animals, but the relative contributions of different urchin species varied from region to region. To organize this information, a clustering analysis was performed which permitted similar areas to be lumped together (Table 5). The distribution of relative densities or frequencies of a species in two areas distribute themselves in a 2×2 contingency table according to chi-square (Greig-Smith, 1964, p.

TABLE 5

POSSIBLE GROUPS OF AREAS BASED ON RELATIVE FREQUENCY AND RELATIVE DENSITY OF *Heterocentrotus*, *Echinothrix*, AND *Tripneustes*

<i>Heterocentrotus</i>				
Group				
I	Honaunau A (96, 98)			
II	Ashihara A, Honaunau B, Kaawaloa E, Napoopoo Breakwater (86, 96) (83, 93) (71, 84) (61, 77)			
III	Napoopoo Breakwater, Kaawaloa Quadrats, Ashihara B (55, 75) (56, 65)			
IV	1 Mile South of Honaunau, Napoopoo Light A and B, Kaawaloa C, Napoopoo Light Quadrats (44, 56) (38, 47) (33, 41) (32, 36)			
V	Kaawaloa B (22, 15)			
<i>Echinothrix</i>				
Group				
I	Napoopoo Light Quadrats, Napoopoo Light A and B, Ashihara B, Kaawaloa B (53, 48) (41, 37) (33, 30) (33, 23)			
II	Kaawaloa B, Napoopoo Breakwater, Kaawaloa Quadrats, Kaawaloa C, Kaawaloa E (26, 14) (22, 14) (22, 12) (22, 12)			
III	Honaunau B, Ashihara A, Honaunau A, 1 Mile South of Honaunau (17, 8) (7, 2) (4, 2) (0, 0)			
<i>Tripneustes</i>				
Group				
I	1 Mile South of Honaunau, Kaawaloa C, Kaawaloa B (44, 38) (39, 44) (33, 54)			
II	Kaawaloa Quadrats, Napoopoo Breakwater, Ashihara B, Napoopoo Light A and B, Napoopoo Light Quadrats (17, 8) (13, 8) (11, 5) (9, 6) (5, 4)			
III	Napoopoo Light Quadrats, Kaawaloa E, Ashihara A, Honaunau A, Honaunau B (2, 1) (0, 0) (0, 0) (0, 0)			

NOTE: Pairs of areas tested in a 2×2 contingency table by χ^2 with Yates's correction. Numbers in parentheses are relative frequency and relative density, respectively. Areas that are underlined are members of two groups.

39). Recurrent groups were formed at the .05 level of significance. Groups of areas were formed for *Heterocentrotus*, *Echinothrix*, and *Tripneustes*. Grouping was done both by relative density and relative frequency. Relative frequency is defined as the number of occurrences of one species as a percentage of the total number of occurrences of all species (Curtis and McIntosh, 1950, 1951). Not too surprisingly, the two measures generally agreed. A group of areas for a species was formed by first ranking the relative values from high to low; then the area showing the highest value was placed with all those areas which did not differ significantly from it. The group was checked with the first group formed using relative frequency. Differences were confined to the last one or two areas assigned to a group. Only rarely, however, did the penultimate member of a group overlap with a succeeding group. The rule that was used to decide whether a terminal member should be included in two groups or should be eliminated was that, if by either relative density or relative frequency two areas were significantly different at the .01 level, they would not be placed in the same group, even though by one test, they may not have been significantly different. If they were not significantly different by one test and significant at the .05 level by the other test, they were placed together. Occasionally, the last member of a group was used as the first member of the succeeding group. Five groups of areas were segregated for *Heterocentrotus*, three recurrent groups for *Echinothrix*, and three for *Tripneustes*. No definite pattern exists for any species, although there is a tendency for *Heterocentrotus* to be densest inside protected areas, and in relatively shallow water. For *Heterocentrotus*, groups I, II, and III all have members that are either more protected or shallower or both than are the members of groups I and V. The general pattern of *Echinothrix* is that, relatively, it may be more abundant in exposed areas than *Heterocentrotus*, but the pattern is not consistent. *Tripneustes* appears to occur in greatest abundances where living coral is sparse. Group I for *Tripneustes* consists of areas that are either exposed or deep. Group III, with the lowest abundances of *Tripneustes*, has four areas that are protected from waves and have masses of living coral. Again, however, the pattern is not

consistent. There are three recurrent groups, however, that are consistent for all three species: two of these recurrent groups are from inside bays and one is outside. One group from inside a bay consisted of the Honaunau Bay transects, and the lower portion of the transect in front of the Ashihara cottage in Kealakekua Bay. The other group inside a bay was made up of the major portion of Kaawaloa Cove, and the transects at Napoopoo breakwater, both in Kealakekua Bay. The group outside bays consisted of the transects at Napoopoo Light. Other areas were variously grouped for different species. The great degree of variability in species composition was not expected and will be discussed in the following section.

General Observations on Urchins

Kier and Grant (1965) suggest that the three primary factors controlling echinoid distribution in Key Largo Coral Reef Preserve, Florida are depth, substrate, and distance from shore, with other possible influences being light penetration, wave agitation, current direction, water temperature, and food supply. In Kealakekua and Honaunau bays, there are at least six, and possibly seven, factors which must be considered, some of which are the same as those suggested by Kier and Grant; these factors are: depth, substrate, exposure to waves, food, predators, animal behavior, and chance. None of these can be assessed with the data presented; however, several reasonable suggestions can be made, and problems for further study defined.

DEPTH: There was little correlation between assemblage composition and depth. In Kaawaloa Cove, *Tripneustes* was infrequent near shore in shallow water, and showed both a higher density and higher relative weight at lower depths. It increased in numbers as other urchins decreased. Off the Ashihara cottage, *Tripneustes* was rare in the lower part of the transect and more abundant near the shore. At Palemano Point, it was the most abundant urchin in 1 meter of water. *Euclidaris* in Kaawaloa Cove was found only near the surface, but is described by Edmondson (1946) as generally being more common at depths of several fathoms. *Chondrocidaris* was found only in the deepest portions of the transects, and because transects generally were not initiated below 50 to 60 feet (20

meters), it was recorded only from Kaawaloa Cove, where some transects were begun at 110 feet. This distribution is in accord with that suggested by Edmondson (1946).

There was a striking decrease in the numbers of urchins with increasing depth in Kaawaloa Cove. The reverse, however, was true for the transect off the Ashihara cottage, where there were more animals away from shore in deeper water than were present in the shallows. It would seem that depth, *per se*, is unimportant in determining distribution. In cases where there is a correlation with depth, it is necessary to examine more environmental factors to determine the causes for observed distributions.

SUBSTRATE: Certain substrate requirements appeared to be associated with each species: crevices for *Heterocentrotus*, small ledges or large cavities for *Echinobrix*, and low relief without living coral for *Tripneustes*. Presence of coral, either living or dead, did not appear to be required for *Heterocentrotus* or *Echinobrix*. In the Ashihara transect, there was living coral away from shore, and near shore the rocks were relatively barren. In Kaawaloa Cove, dead coral increased with depth. The area at Palemano Point where *Tripneustes* was abundant also lacked living coral. *Heterocentrotus* was found both on living and dead coral, and on lava rocks. The size distribution of *Heterocentrotus* on the lava tallus by the dike in Kaawaloa Cove was skewed towards large individuals. Whether this was due to a more rapid growth rate or longer life than urchins in coral areas of Kaawaloa Cove is not known.

EXPOSURE: Exposure to the open sea is correlated with numbers of certain urchin species. Generally, density decreased from a protected bay to the exposed coast. The cluster analysis of areas segregated Napoopoo Light from the within-bay samples. However, the analysis did not group the sample gathered 1 mile south of Honaunau with the sample from Napoopoo Light, although they had similar exposure to waves. There was a higher urchin density in all areas of Kealakekua and Honaunau bays than in transects at Napoopoo Light and 1 mile south of Honaunau. Species diversity was highest in Kaawaloa Cove, but was low in Honaunau Bay, so protection from high surf does not ensure high diversity of urchin species.

Colobocentrotus was not present in Kaawaloa Cove, but was common in the surf by the lighthouse, and was observed at the top of the transect at the Ashihara cottage. *Echinometra oblonga* was rare in Kaawaloa Cove, but was more abundant in slightly more exposed conditions, such as the Ashihara transect and at the tops of the transects in Honaunau Bay. *Echinostrephus* was recorded only in Kealakekua Bay, and had a higher relative weight in samples from the lighthouse than in samples from Kaawaloa Cove. *Heterocentrotus* had higher relative weight values and higher densities in protected regions. *Echinobrix* appeared to be less sensitive to wave exposure than did *Heterocentrotus*, and therefore its relative weight value tended to increase even though its densities decreased. *Tripneustes* showed no consistent pattern with respect to exposure. At Napoopoo Light it formed a relatively unimportant fraction of the urchins with a relative weight of 4.5 by the quarter method, and 2.8 in the quadrat transect. One mile south of Honaunau, *Tripneustes* was the second most important animal with a relative weight of 44.7. In Kaawaloa Cove, in subset B, which was below 50 feet (15 meters), *Tripneustes* made up 43.6 percent of urchin biomass. According to the cluster analysis, the relative frequency and density of subset B were not significantly different from subset C, or from the transect 1 mile south of Honaunau. *Tripneustes* was most dense in the highly protected area at Palemano Point. If there is any pattern, it is probably that *Tripneustes* can survive under a wide range of surf conditions, but does best in protected areas.

FOOD: In Kaawaloa Cove, the decrease in urchin numbers with increasing depth does correlate with decreasing light, and so presumably with primary productivity. Unlike *Strongylocentrotus* (Ebert, 1968), in which biomass but not numbers appeared to be food limited, both numbers and biomass of urchins in Kaawaloa Cove correlate with decreasing primary production. Whether food was actually limiting was, of course, not determined by this study.

PREDATORS: It is difficult to assign significance to the roles of predators in the distribution and abundance of these urchins. There was only one direct observation in the field: In Kaawaloa Cove, a small (shell length 17.5 cm)

triton shell (*Charonia tritonis*) was found feeding on a slate-pencil sea urchin. When found, it was on top of the urchin, and when it was removed, a region devoid of spines was exposed. The triton was held out of water for about 15 minutes, at which time it regurgitated secondary spines of *Heterocentrotus*. Whether it would have killed the urchin is not known; however, tritons have been implicated as predators of other echinoderms (Chesher, 1969; Endean, 1968–1969). This single triton was the only one seen, and the only act of predation observed. Fishes such as triggerfish, parrotfish, and wrasses undoubtedly eat urchins. *Diodon hystrix*, a puffer fish, feeds on *Echinometra lucunter* in Puerto Rico (Glynn, 1968) and seems to be the large spiny puffer of Hawaii (Gosline and Brock, 1960), where it occurs inshore and reaches approximately 2 feet in length. Puffers were not observed in either Kealakekua or Honaunau bays, but undoubtedly occur in both.

BEHAVIOR: Behavior during two stages of the life cycle may be important in urchin distribution: larval settlement and movements of the adults. There are indications that urchins tend to settle where adults live (Moore et al., 1963; Ebert, 1968). Adult *Echinus* make seasonal migrations (Elmhirst, 1922; Stott, 1931), and movement of adult *Strongylocentrotus purpuratus* and *S. franciscanus* (Leighton, 1960), and *Paracentrotus* (Kitching and Ebling, 1961), is linked with food availability. In Kaawaloa Cove, low production rates in deep water may result in adult migration into shallow water. Adult movement would be important only for those species that do not live in cavities of their own construction. It is unlikely that the distribution of *Echinometra* or *Echinostrephus* is determined by adult behavior, and aggregation of echinoderms due to social responses is considered unlikely (Reese, 1966). The aggregated dispersion patterns that were observed may be due to environmental heterogeneity, although members of the family Diadematidae, particularly the genus *Diadema*, do respond to other members of the same species, apparently by a chemical sense (Snyder and Snyder, 1970).

CHANCE: Certain features of the distribution of urchins in this study do not appear to be associated with physical or biological factors. At Napoopoo Light, *Echinothrix* formed 65.5

percent of the biomass by the quarter method and 75.9 percent of the biomass by the quadrat method. *Echinothrix* did not occur in the transect 1 mile south of Honaunau. *Tripneustes* also had different abundances at these two stations, as described in the section on exposure, with a higher density south of Honaunau than by the lighthouse. Finally, *Heterocentrotus* was abundant at most of the sites examined along the Kona Coast, yet is generally uncommon in other areas along the Hawaiian Island chain. Whether *Heterocentrotus* was always rare in other areas is uncertain. Edmondson (1946), referring primarily to Oahu, lists *Tripneustes* and *Echinothrix* as common forms, and says that *Heterocentrotus* "frequents the outer border of the reef platform, but young specimens are sometimes seen near the shore." The impression given by Edmondson is that *Heterocentrotus* has not been a dominant element in the echinoid fauna of Oahu for the past 70 years, if it ever was. Although *Heterocentrotus* is collected to make wind chimes for tourists, and Oahu has a larger human population, there are areas both on Oahu and other islands that are at least as free of human intervention as is the Kona Coast of Hawaii. *Heterocentrotus* is even present on the Kona Coast in Kailua Bay, which receives substantial human waste pollution. The environment along the Kona Coast appears similar to that of many other areas of Hawaii. Because of the absence of clear correlations with environmental factors, it seems probable that chance has played a role in determining local distributions of such urchins as *Echinothrix* and *Tripneustes*, and, on a larger scale, in the establishment of the larger populations of *Heterocentrotus* along the Kona Coast.

Several general conclusions are warranted from this study of urchins of Kealakekua and Honaunau bays on the Kona Coast of Hawaii. First, nearly the entire shallow water regular echinoid fauna of Hawaii is represented in the bays at Kealakekua and Honaunau. In descending order of abundance, the urchins are *Heterocentrotus*, *Echinothrix*, and *Echinometra*, followed by *Tripneustes* and several minor species: *Eucidaris*, *Diadema*, *Colobocentrotus*, *Chondrocidaris*, and *Echinostrephus*. This list includes most of the shallow-water regular echinoid fauna of Hawaii. *Lytechinus*, *Pseudoboletia*, and

Centrostephenus may be present. In this respect, the bays are not unique, for the urchins appear to be generally distributed among the islands in the Hawaiian chain (Edmondson, 1946). Only the high abundance of *Heterocentrotus* is unique because, other than the Kona Coast and a few sites on Maui, such as Molokini Reef, *Heterocentrotus* is not common. A second conclusion is that urchins form a segment of the shallow-water communities that probably receives a large portion of the energy from primary production: standing crops near shore reach nearly 1 kilogram per square meter. A third conclusion is that the urchin species appear to distribute themselves into loose aggregates independently of each other, and not in definite associations, as suggested for the echinoids of Key Largo, Florida (Kier and Grant, 1965). And finally, the species respond differently to features of their environment, and either some of these features are very subtle or distributions, in part, are determined by chance.

DISCUSSION OF METHODS

Because the information in this article may be used as a baseline for future comparisons, it is necessary to make some general statements concerning the sampling techniques, because, under many conditions, the techniques determine the density estimates (Greig-Smith, 1964). Both quadrat and plotless methods used in this study assumed random distribution of individuals, and the accuracy of estimating density decreases as the populations deviate from a random dispersion pattern. The best estimates of density are for Kaawaloa Cove, part of the Ashihara transect, and Honaunau Bay, because all three of these regions had urchin populations which tended to fulfill the requirement of random dispersion. The analysis of pattern from the plotless data is a new method, and requires further examination to determine whether it is indeed valid. Pielou (1969) examined pattern, using distance measurements; however, she stated that an independent density estimate is required. Therefore, caution is required in the interpretation of the statements concerning pattern of urchins in this study. The trends, however, are probably valid, and the method of analyzing pattern in this study appears to fall

within the general assumptions of the method (Clark and Evans, 1954; Morisita, 1957; Heyting, 1968).

In regions where an aggregated dispersion pattern was indicated, the relative values of frequency and density are still valid, although the density estimate will be too low (Cotton and Curtis, 1956). If the dispersion pattern does not change, then comparisons can be made with these areas if similar sampling methods are used at later sampling dates. Although difficult to handle underwater, plotless methods that do not assume random dispersion patterns, such as the wandering-quarter (Catana, 1963), or the angle-order method (Morisita, 1957), may be required. The wandering-quarter would have to be modified for marine populations, because this method assumes that the shape of an aggregation is a circle and that clumps of individuals are randomly dispersed—two assumptions that often will not be true for benthic populations.

The method of estimating wet weights for urchin populations by utilizing size structure, density, and the relationship between a linear measurement and wet weight will probably continue to be of general use, but may more profitably be replaced by treating the component parts of an urchin (spines, test, gut, and so forth) separately, and describing weight of each of these as a function of a linear measurement similar to a method of describing growth developed by Laird (1965).

SUMMARY

1. A preliminary survey was made of the sea urchin populations of Kealakekua and Honaunau bays on the Kona Coast of Hawaii. Sampling was done using both 1-meter-square quadrats and a plotless method, the point-centered quarter method.

2. Eleven of the 14 regular urchins reported for Hawaii occurred in the samples. Within bays, the most abundant urchin was *Heterocentrotus*, followed by *Echinobrix*. Total density of all species of urchins was highest within areas protected from waves. In Kaawaloa Cove, average urchin density was between 2.5 and 3.5 animals per square meter.

3. Maximum biomass of urchins was in shallow water in Kaawaloa Cove, where it ap-

proached 1 kilogram (wet weight) per square meter. Urchins form a segment of these shallow water communities that probably receives a major portion of the energy from primary production.

4. Seven factors are suggested as possibly being important in determining urchin distribution and abundance: depth, substrate, exposure to waves, food, predators, animal behavior, and chance.

5. The urchin species appear to distribute themselves into loose aggregates independently of each other, and not into definite species associations.

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