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DISTRIBUTION, ABUNDANCE AND FOOD OF SEA URCHINS ON A LEEWARD HAWAIIAN REEF

Nancy B. Ogden, John C. Ogden and Isabella A. Abbott

ABSTRACT

The distribution, abundance and food of nine species of sea urchins along a 180-m transect on a leeward Hawaiian reef were studied in relation to algal distribution and habitat. *Echinometra mathaei* was dominant, comprising 50 to 98% of the urchin populations along the transect. Its peak average density was 70.3 urchins·m⁻² at 120 m from shore on a calcareous pavement (1.5 m deep) with scattered, small coral colonies. Although the distribution of all urchin species overlapped, all of the other species reached their peak densities shoreward of *E. mathaei*. The next most abundant urchin was *E. oblonga* (9.3·m⁻² at 110 m from shore) followed by *Tripneustes gratilla* (3.7·m⁻² at 90 m). Total urchin densities reached a peak average of 73.9·m⁻² at 110 m. Two *Ulva* species, two *Pterocladia* species, *Grateloupia hawaiiiana* and *Acanthophora spicifera* (5-100 cm tall on the rocks inshore) were the most abundant macroalgae. They became dramatically reduced in size and, except for *Pterocladia* and *Ulva*, in abundance, from 80 m offshore to the end of the transect. Out of a total of 43 species of macroalgae and 71 species of microalgae (excluding four species of crustose corallines) recorded on the transect, 19 and 14 species respectively were found in the 70 urchin guts examined. Generally, urchins selected food in relationship to its abundance, and there was evidence of a dependence upon drift algae.

The study of ecologically similar species provides biologists with the opportunity to examine the mechanisms which permit coexistence and the maintenance of associations of these potential competitors. The mechanisms may include partitioning of limiting resources, such as food and space (Carpenter, 1986; Gladfelter and Johnson, 1983). If resources are not limiting, coexistence may occur through selective predation on dominant species (Paine, 1966; 1974; Dayton, 1971) or non-selective disturbances, keeping communities in non-equilibrium conditions (Levin and Paine, 1974; Connell, 1978; Sousa, 1984). Coexistence may also be a result of patterns of recruitment leading to differing associations over time or among comparable sites (Shulman et al., 1983).

Our earlier studies of sea urchins in St. Croix (Ogden et al., 1973; Abbott et al., 1974; Abbott, Ogden and Abbott, unpubl.) showed a distinct ecological separation between three common species of Caribbean sea urchins, *Diadema antillarum* Philippi, *Echinometra lucunter* L., and *Tripneustes ventricosus* Lamarck which differ in habitat, food, and activity patterns. Furthermore, where urchins co-occurred, there were distinct intra- and inter-specific mechanisms to separate individuals and partition space (Grünbaum et al., 1978).

D. P. Abbott (unpubl.) previously identified a site on the leeward coast of the island of Maui, Hawaii where nine species of sea urchins could be found in shallow water within a short distance of shore on a rock and coral reef. This site seemed to present an ideal opportunity to examine the potential ecological and behavioral mechanisms leading to partitioning of food and space in ecologically similar species. We had three goals for our field work: (1) to describe and map the distribution and abundance of urchins along a transect; (2) to examine the diet of as many species as possible in relationship to available food, and (3) although time-limited, we also hoped to do some inter- and intra-specific behavioral studies. These studies might suggest mechanisms explaining the coexistence of these potential competitors.

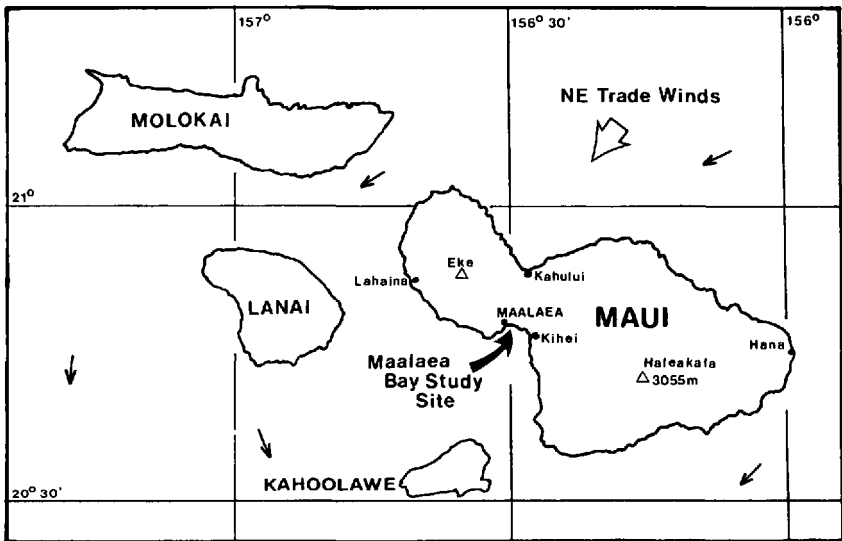


Figure 1. Map of Maui with nearby Hawaiian Islands. The study site is marked with an arrow; other arrows show the wind direction and water currents.

The nine urchin species present, in order of abundance, were: *Echinometra mathaei* de Blainville, *Echinometra oblonga* de Blainville, *Tripneustes gratilla* Linnaeus, *Echinothrix calamaris* Pallas, *Heterocentrotus mammillatus* Linnaeus, *Echinothrix diadema* Linnaeus, *Diadema paucispinum* A. Agassiz, *Echinostrephus aciculatus* A. Agassiz, and *Pseudoboletia indiana* Michelin. The latter three species were rare and received only limited attention.

DESCRIPTION OF THE STUDY SITE

Maalaea Bay, Maui (Fig. 1) is protected from the Northeast Trade Winds and the North Equatorial current by the volcano Eke to the west and by the alluvial isthmus to the north between Eke and the volcano Haleakala to the east. Gentle to moderate wave surge, characteristic of the summer season, was present. Tides ranged from a low of 0.05 m to a high of 0.5 m, and there was a gentle current to the east. Underwater visibility varied from less than 1 m to 10 m. Air temperatures varied from 25°C to 27°C and there was little rainfall.

On 2 August 1978, a 180-m transect line flagged every 10 m was set into place along a 120-degree compass course from the east end of the seawall at Island Sands Condominium (approx. Lat. 20°47'N, Long. 156°38'W, 0.5 mi east of Maalaea). The transect ran over an inshore, shallow, volcanic rock, rubble area with scattered sand pockets (Fig. 2). Between 107 m and 150 m offshore there was a calcareous pavement covered with algal turf and full of holes and grooves where urchins reached peak densities. Beyond 150 m the bottom was deeper and more irregular with mounds and ridges of dead and living coral forming poorly developed spurs and grooves. Live coral coverage (Fig. 3) varied from less than 1% (very scattered) at 60 m on the rocks to 55% at the end of the transect 180 m offshore. Beyond the end of the transect at 200 m there was sandy bottom approximately 4 m deep.

Algal distribution (Fig. 2) over the transect varied from prolific macrospecies inshore (0–80 m) to low turfs and crustose coralline algae variously covered with microalgae and a film of diatoms. The rocky bottom inshore was dominated by the macroalgae *Ulva fasciata* Delile and *Pterocladia capillacea* (Gmelin) Born. et Thur. followed by *Ulva reticulata* Forssk., *Grateloupia hawaiiiana* Dawson, *Acanthophora spicifera* (Vahl) Borg., *Amphiroa* spp., and *Pterocladia caerulescens* (Kuetz.) Santelices in that order. *Ulva fasciata* reached lengths of 100 cm, but more commonly was 7–8 cm long. *Grateloupia hawaiiiana* (4–10 cm high) was variously present between 10 and 70 m, but only scattered small plants were found 160 m offshore. Macroalgal cover in the rocky inshore area was inversely proportional to crustose coralline and microalgal cover.

At 80 m, there was a sudden shift from luxuriant macroalgae to algal mats and turf and urchins

first became abundant. Farther offshore, only crustose corallines, turfs (macroalgae grazed to less than 2 cm) and "microturfs" consisting of microalgae commonly 5–10 mm tall were present. An occasional large, isolated alga possibly inaccessible to grazers, or inedible, could be found among the corals near the end of the transect. *Pterocladia caerulescens* was abundant at 70 m and, in reduced form, was the most abundant macroalga in the turfs beyond 80 m, followed by *Ulva* and *Hypnea*, particularly on the calcareous pavement. *Ceramium byssoideum*, a small *Jania*, and a small, creeping *Chondria* (or *Laurencia*) and *Gelidium pusillum* were the most consistently present microalgae on the calcareous pavement.

Eighteen pre-weighed clod cards (plaster of Paris molds 40–50 g in weight attached to waterproof cards and dissolving in direct proportion to water movement; Doty, 1969; Russo, 1977) were tied to the reef in pairs at 90, 100, 110 and 120 m and one at 160 m. Clod card weight loss in 24 h varied from 47 to 55% with an average of 53%, indicating no significant difference in water movement over the transect.

METHODS AND MATERIALS

Distribution and Abundance of Algae and Urchins

Algal distribution (Fig. 2) along the transect was estimated with a 0.25-m² quadrat. Lengths of major macroalgae, large enough to be identified in the field, were measured with a centimeter rule. Smaller microalgae were collected and identified in the laboratory.

Urchin distribution was determined by placing a steel reinforcing rod as a center and swinging a 3-m chain to circumscribe a 6-m diameter circle in which all species of urchins were counted except *Echinometra* spp. Four such counts were made for each 10-m section of the transect. *Echinometra* spp. were counted by 12 haphazard, 0.25-m² quadrats per 10-m section of the transect. Urchin test diameters (longitudinal lengths in irregular urchins) were measured with Vernier calipers.

Diet.—Diet was determined by examination of the gut contents of 70 urchins collected along the transect, mostly in the morning, and immediately frozen. The gut contents were examined under a dissecting microscope and the components were estimated as percentages of total contents, including sand, sediment and animal material. The gut contents of each species were averaged for each 10-m section of the transect (Fig. 2, III).

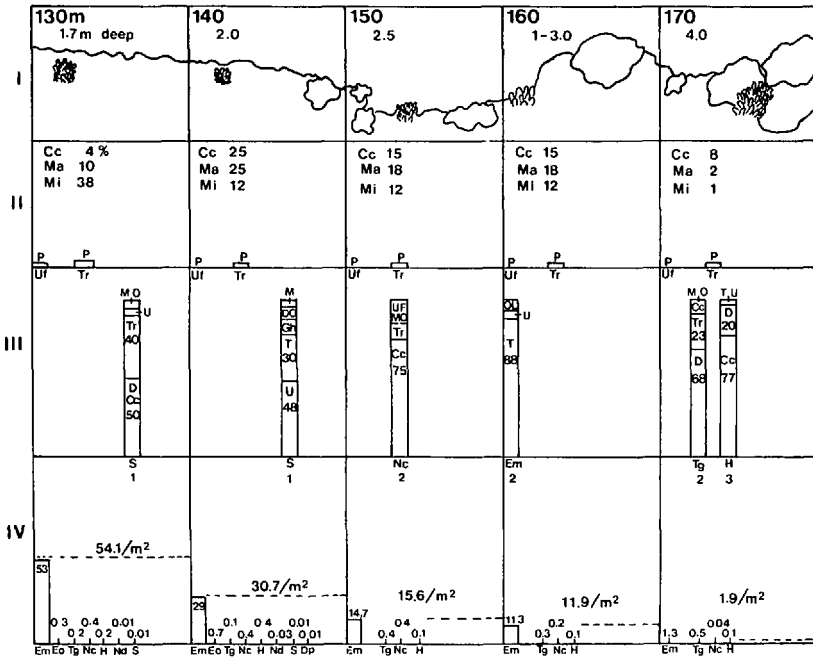
RESULTS

Echinometra mathaei was widely distributed over the transect, making up over 50% of the total number of urchins in the rocky area and over 90% on the calcareous pavement (Fig. 3). It reached a peak average density of 70.3 · m⁻² (range 8–128 · m⁻²) 120 m offshore in holes and grooves on the calcareous pavement at a water depth of 1.5 m. The highest density recorded in a single quadrat was 128 · m⁻² between 110 and 120 m. *E. mathaei* was never observed in contact with other urchins and when disturbed by a conspecific experimentally placed nearby, there was immediate pushing and the intruder retreated.

Echinometra oblonga, occupying the same habitat but easily distinguished from its congener by its dark color and stout spines, was the second most abundant urchin on the transect. It reached a peak average density of 13 · m⁻² (range 0–32 · m⁻²) at 100 m, slightly shoreward of *E. mathaei*.

Tripneustes gratilla was third most abundant on the transect and occupied exposed sites, able to hold on well in heavy wave surge. Each specimen had a homesite, distinguished as a patch about the size of the test cleared of algae. *T. gratilla* reached a peak average density of 3.7 · m⁻² (range 2.9–4.4 · m⁻²) at 90 m, in an area of large rocks (50 cm to 1 m diam) where crustose corallines (Fig. 4) and microalgae (Fig. 3) reached peak areas of coverage. It was noted that a lush diatom film covered 88% of the crustose corallines while macroalgae (Fig. 4) were uncommon in this area.

Urchin Distribution and Abundance.—*Echinothrix calamaris* ranked fourth in abundance with a peak average density of 0.9 · m⁻² (range 0.6–1.3 · m⁻²) at 110 m. It was locally more abundant (2–4 · m⁻²) on the shoreward cliff-like edge of the



of the items in the gut (averaged where more than one of each species was collected for the 10-m section). Row IV: Average urchin densities m^{-2} for each species, plus the average urchin population for each 10-m section. Key: (AM) Amphiroa, (AS) *Acanthophora spicifera*, etc.

calcareous pavement and tended to concentrate in depressions on the pavement where it was in close association with and occasionally touching, *Heterocentrotus*. *E. calamaris* was observed to occupy depressions which gave protection almost to the full height of the spines. Homesites were cleanly grazed, as well as a surrounding area two to four times the diameter of the test. Usually *E. calamaris* was well separated from its conspecifics, but some specimens were contiguous. When experimentally placed in contact with each other (in eight trials) both urchins waved their spines and the intruder moved or was pushed away.

Heterocentrotus mammillatus ranked fifth in abundance, but no peak was determined on the transect. It ranged in density from 0 to $0.9 \cdot m^{-2}$. Densities were particularly low on unconsolidated substrate. It tended to favor depressions on the reef associated with pinnacles, corals, between rocks or where the relief was at least equal to the height of its spines which often overlapped or touched the spines of other species. Juveniles were found under rocks. On two occasions single small red shrimp were found associated with *Heterocentrotus* spines. There was considerable test color variation from white in one case to red orange to brownish red. On some individuals the large spines, dark red-orange by day, changed to pale pink almost white at night, even when placed under a light.

Echinothrix diadema ranked sixth in abundance, but like *Heterocentrotus*, no peak density was established. It ranged in density from 0 to $0.14 \cdot m^{-2}$. *Echinostrephus aciculatus*, *Diadema paucispinum* and *Pseudoboletia indiana* were not found in sufficient numbers to establish densities. *Echinostrephus* was found in deep holes, two individuals on the seaward portion of the calcareous pavement and

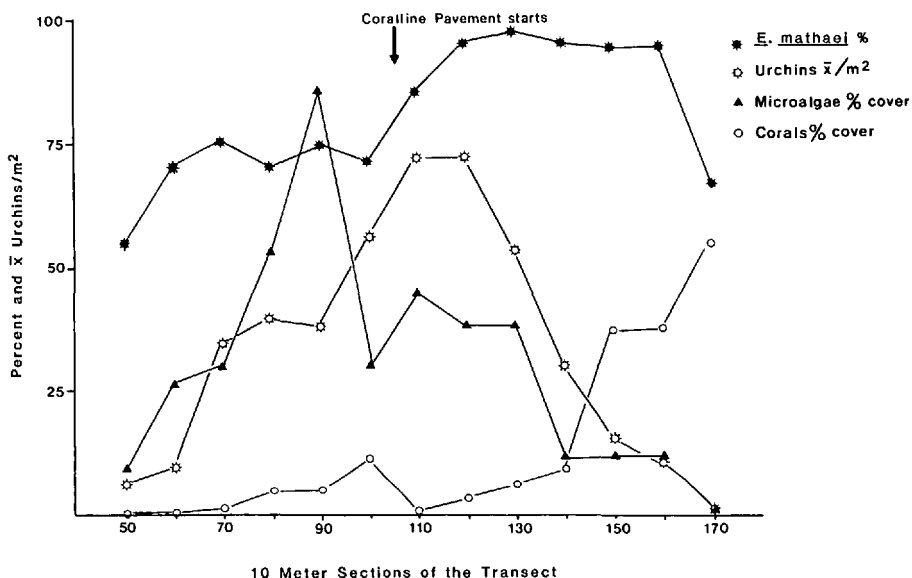


Figure 3. Average urchin densities in relation to estimated percent microalgal cover and live coral cover. *E. mathaei* plotted as the percent of the average total of urchins · 10-m.

one at 110 m. Four *Diadema* and one *Pseudoboletia*, the latter covering itself with pebbles, were found.

Size.—Test diameters of 112 *E. mathaei* measured ranged from 1.0–5.3 cm with an average of 3.1 cm. There was no difference between the average size of 80 *E. mathaei* and 25 *E. oblonga* at 120 m. *Tripneustes* test diameters averaged from 9 cm at 50 to 60 m among lush macroalgae, to 7 cm on the pavement at 100 and 140 m.

Diet.—Urchin feeding times were difficult to determine. About half of the *E. mathaei* guts were mostly empty and half were mostly full despite the time of day they were collected. The only time that fresh material was noted in the guts was in the late morning. Fresh material was also noted in the guts of *E. calamaris* and *Tripneustes* collected at this time. Seventy-five percent of a sample of 48 *Tripneustes* were observed to be actively feeding between 0945 and 1100. None of the *Heterocentrotus* had full guts.

The different species of urchins could not be easily separated by food preferences. Crustose corallines were found in the guts of all nine species examined and were a major item in the guts of both species of *Echinometra*, *E. calamaris* and *Heterocentrotus* (Fig. 2, III). Likewise *Pterocladia* and *Ulva* were found in the guts of all nine species of urchins (in 70% of the total number of urchin guts with food in them). At 40 m *Grateloupia*, *Amphiroa* and *Pterocladia* were the most abundant algae, with *Ulva* being common. The five guts of three urchin species examined from there (Fig. 2, III) contained primarily *Grateloupia*, secondarily *Ulva* then *Pterocladia*. *Amphiroa* was apparently avoided. At 60 m it was noted that the two *Tripneustes* collected for gut examination were in an area where *Ulva fasciata* and *Acanthophora* were abundant. The gut contents, averaged for the two, yielded 40% *Ulva*, 30% *Pterocladia*, 13% *Acanthophora* and 17% other species of algae.

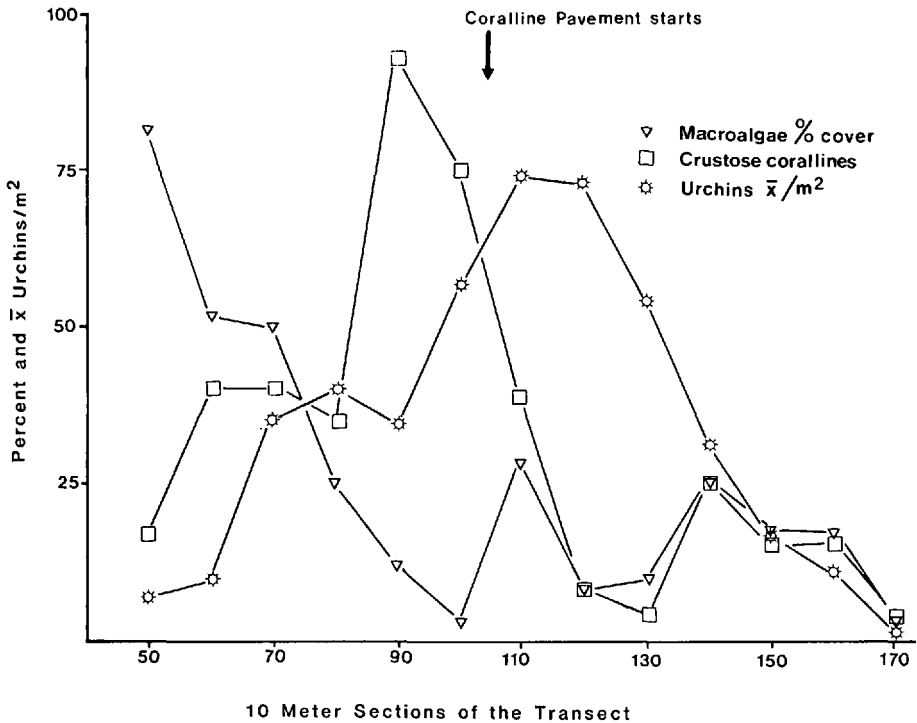


Figure 4. Average urchin densities in relation to estimated % macroalgae and crustose corallines.

Pterocladia was also abundant in that section of the transect, but its location with regard to the two urchins was not noted. At 110 m all of the algae in the guts of the six *E. mathaei* were known to be within the quadrat from which they were collected except *Acanthophora* which made up 3% of the gut contents of one individual. The reduced amount of fleshy algae in the guts of *Heterocentrotus* at 170 m agrees with the reduced amount of benthic and drift algae available. Two *Tripneustes* from 170 m contained only algae that could be found there, especially *Pterocladia caerulescens* found abundantly in one.

In general the urchins ate the algae which were most abundant around their homesites or in the drift. *Pterocladia*, *Ulva*, and *Grateloupia*, which were abundant inshore (both attached and drift), were the most significant items in the guts of the inshore urchins examined (Fig. 2), except for *Heterocentrotus*, *Pseudoboletia* and one *E. mathaei* which primarily consumed crustose corallines in an area where they were also abundant. About 19 species of macroalgae (out of 43 species recorded) and 14 species of microalgae (out of 71 recorded) were noted in the gut contents overall. *Tripneustes* on the calcareous pavement consumed little macroalgae, feeding largely upon sand with its microflora.

The burrow of a small (1.3 cm) *E. mathaei* (120 m) was collected along with the urchin. The fecal pellets consisted of well digested *Pterocladia caerulescens*, *Ceramium*, and crustose corallines. The burrow cavity was lined with 30% crustose corallines (1–3 spp.) with the bottom worn down to bare calcareous substrate. There were no visible toothmarks on the crustose corallines in the home burrow, but an adjacent unoccupied burrow had well-grazed *Hydrolithon*. Seven species of algae extended 0.5–1.5 cm into the burrow. Algae grazed from the top border

of the burrow were *Pterocladia caerulescens*, *Coelothrix*, *Dictyota* and the same species of *Ceramium* that was found in the gut. Two additional species of *Ceramium* were among the algae extending into the burrow. The bottom of the burrow had curious 1 mm high calcareous projections some of which had been freshly removed. These fragments were also found in the fecal pellets.

A second *E. mathaei* (5.1 cm diam) 50 m offshore was collected along with its burrow. The bottom half of the burrow was worn down to the dead coral skeleton. The roof (there were two openings large enough for the urchin to exit from), upper sides and outside were lined with the crustose corallines *Porolithon onkodes* (Heydr.) Fosl. and *Hydrolithon reinboldii* Weber van Bosse and Fosl. Outside of the largest opening were *Pterocladia caerulescens*, *Ulva*, *Ceramium*, *Jania*, and *Cladophora*. The *E. mathaei* from the burrow had 50% crustose corallines, 35% *Pterocladia* and 15% *Ulva* in its gut. In both cases what was found in the gut was within the burrow or within easy reach of it.

An *Echinostrephus* burrow (130 m offshore) was lined inside and out by *Hydrolithon reinboldii*. There were nine species of algae growing on the crustose coralline outside of the burrow. The urchin's gut had 50% crustose corallines, 40% *Pterocladia caerulescens*, 5% *Ulva* and 5% *Griffithsia* and *Ceramium*. The crustose coralline was in the burrow and the *Ceramium* was within easy reach. The *Pterocladia*, *Griffithsia* and *Ulva* were probably nearby or they could have been captured from the drift.

Drift algae are probably an important component of the diets of most of the urchins. Both species of *Ulva*, *P. capillacea*, *Grateloupia hawaiiiana*, *Acanthophora spicifera* and *Ahnfeltia* (from the splash zone nearby) were particularly susceptible to fragmentation. A total of 43 species of macroalgae were available as a source of drift algae. Some microalgal species, particularly *Ceramium* mats, can also be dislodged by wave action. In a brief survey of *Tripneustes* 22 (81%) out of 27 inshore individuals were carrying *Ulva fasciata* while only 3 (14%) out of 21 further offshore were found carrying it. Only 5 out of the total 48 were carrying *Ulva reticulata*; it was recognized in the guts of 2 *Tripneustes* at 40 m. The closely grazed *Ulva* offshore and most of the *Ulva* in the urchin guts was thought to be *Ulva fasciata*. *Ulva* was found in 7 (54%) out of 13 *Tripneustes* examined and most of those were from inshore areas. Similarly, 8, or 30%, of 27 individuals (40–70 m offshore) were carrying *Grateloupia* on their tests and 2 more were found eating it. Beyond its area of abundance only one individual (120 m) was found eating *Grateloupia* and none were carrying it.

In addition to *Tripneustes*, *E. calamaris* and *E. mathaei* were observed holding drift algae. At 100 m one *E. calamaris* was observed with a 13 cm fragment of *Ulva fasciata* and two others were holding *Pterocladia* fragments. In this area where macroalgae were all reduced to turfs, many *E. mathaei* among the rocks were holding large pieces of *Ulva fasciata* which must have come by drift from elsewhere.

In 16 trials with *E. calamaris*, *Ulva fasciata* was caught by all but one on the first try and five urchins were eating the material within 5–10 min. The surge helped the animals capture the drift algae. *Pterocladia* was caught more readily than *Ulva* in four trials. *Heterocentrotus* was never observed holding drift algae. Twelve trials with *E. mathaei* and one with *E. oblonga* resulted in all animals readily capturing and eating the drift alga.

DISCUSSION

The four most important factors determining urchin abundance on the Maalaea transect are substrate, wave energy, depth and food availability. From 10 to 30

m substrate and depth appear to limit the inshore presence of urchins. The rocks give less protection than a hole in a calcareous pavement and low tides would expose the urchins to drying or subject them to overheating. The outer limit appears to be food availability as algal cover diminishes to its lowest level, perhaps due to the increased densities of herbivorous fishes. Wave energy is important for algal growth, transport of drift material and removal of wastes from the urchins. At about 40 m, where water depth becomes 1 m and percent macroalgal cover is at its highest, urchins appear. They reach peak densities, dominated by *Echinometra mathaei* and *E. oblonga*, in holes and grooves on the calcareous pavement. Other studies of the distribution and abundance of Hawaiian sea urchins (Doty, 1969; Kelso, 1970; Russo, 1977), show a similar dominance of these two species. Russo (1977), working on the northwest coast of Oahu, determined that *E. oblonga* dominate *E. mathaei* in higher wave energy situations and that these *Echinometra* are totally dependent on drift algae and detritus carried to them by wave action. It is not clear whether he considered the possibility of grazing on crustose corallines. He obtained an isolated density of 175 *Echinometra* spp. \cdot m⁻² with an average of 97.5 \cdot m⁻² for the seaward portion of the reef and an average of 46.5 \cdot m⁻² for the whole reef area examined. Doty (1969), working in Honaunau Bay, Hawaii Island, found *E. mathaei* greater in abundance than *E. oblonga*, with a peak average of slightly less than 60 \cdot m⁻² at a depth of about 2 m. *E. oblonga* had a peak average density of about 6 \cdot m⁻² with an isolated high density of 436 very small individuals \cdot m⁻². In spite of the numerical abundance of *Echinometra*, Doty determined that *Heterocentrotus* was of greater importance in Honaunau Bay in terms of biomass. It dominated the deeper areas with a peak average density of about 4 \cdot m⁻² at about 7 m deep.

All of the nine species of urchins are grazers, feeding upon a variety of algae, except *Heterocentrotus* which seems to specialize in crustose corallines, taking in other algae only incidentally. The algae eaten by the other eight species of urchins are those that are most abundant on the transect: *Ulva*, *Pterocladia*, *Grateloupia* and crustose corallines. *Tripneustes* and *E. calamaris* beyond the macroalgal zone (Fig. 2) ingested more sand than crustose corallines. Most of the offshore *Tripneustes* had sand in their guts. Only one inshore *Tripneustes* was found eating sand. It is trapped by microalgae and ingested along with them, but also collects in pockets on the coralline pavement. Sand may aid in the grinding of other gut contents, but also carries with it many microorganisms.

Fifty percent of the guts of *E. mathaei* and *E. oblonga* examined were mostly empty. Possibly they were not collected at the right time of day. Abbott et al. (1974) found that grazing activity of *E. lucunter* in the Caribbean was low during the day and high during the night, between 1700 and 2300. Another possibility is that since *Echinometra* depend upon drift algae (Kelso, 1970; Russo, 1977), they feed much less during the quieter summer months when availability of drift material is likely to be lower than in winter. Abbott et al. (1974) found that 55% of the diet of *Echinometra lucunter* in the Caribbean was drift material.

It is obvious that drift material is utilized by urchins on the transect, but it is also evident that the urchins consume attached algae. Of the inshore *Tripneustes*, 89% carried drift material, while only 14% of those farther out did. However, urchins beyond the macroalgal zone usually began eating drift material within minutes of capture.

Behavior can be important in determining patterns of distribution but only a few of the urchin species examined were highly mobile. Both species of *Echinometra* moved within their burrows, but one square meter areas cleared of all urchins had only 6% repopulation after 10 days and most of that was thought to be due to overlap of the cleared areas with adjacent burrows. Abbott et al. (1974)

found that *E. lucunter* moved an average of 7 cm from their burrows during an 18-h period of observation. Movement was less during periods of heavy wave action and approximately 20% of the urchins did not move at all.

Experiments showed that *Tripneustes* were relatively active, with 31% repopulation of 10 m diameter cleared areas after 10 days. *Heterocentrotus* tagged with flagging tape moved up to 600 cm from homesites with an average move of 96 cm in 24 h. The other urchins on the transect were more stationary. *Echinothrix calamaris* was observed to move, but mostly away from a crowded situation. It seemed to require a larger homesite than *Echinometra*. Although not tested, perhaps its aggressiveness can explain its ability to compete with *Echinometra*.

Other factors of importance in distribution and abundance patterns, such as predation and recruitment, were not examined. We found approximately 35 species of fishes on the transect, but the labrids and balistids, potential urchin predators, were not abundant. We found one *Tripneustes* which had been preyed upon. All of the urchins on the transect are considered edible in Hawaii, but only *Tripneustes* is regularly collected for food. Following our study, several fishermen were seen collecting *Tripneustes* from the transect area. They apparently come every few months, and must be an important influence on *Tripneustes* abundance in the area.

E. mathaei and *E. oblonga* apparently compete for the same type of habitat. The greater abundance of *E. oblonga* in high energy situations suggests the possibility that its larvae are more capable of attaching under conditions of heavy surge. Its test with more stout spines appears to be an adaptation to such conditions. Perhaps *E. mathaei* outcompetes *E. oblonga* in calmer situations because it is more aggressive. In the Caribbean, *E. lucunter* was found to actively defend its burrow against conspecifics by pushing and biting (Grünbaum et al., 1978).

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Dr. D. P. Abbott and the inspiring times we worked together in the field in Hawaii and in the Caribbean. D.P.A. had the Maalaea Bay site in mind for a study for many years, and spoke of it often while we worked together at West Indies Laboratory on Caribbean sea urchins. In 1978, we happily gathered in Maui for the month of August. D.P.A. was the driving force of the project, wading across the transect wearing his Ifaluk diving goggles, bending at the waist to peer below the water surface, and keeping us excited with new observations, correlations, and possibilities. He kept a loose leaf naturalist's notebook with intertwined observations, sketches, and passages from the literature which made this paper possible to write nearly 10 years later.

We are grateful to Mr. and Mrs. M. Buckman for the use of their car and condominium in Kihei. Thanks go to S. Weil for providing us with the pre-weighed clod cards and to L. Hodgson and N. Nicholson for assistance in field work. We are grateful for the continuing support of our colleagues and the staff of our respective universities. The field work was supported in part by a grant from the American Philosophical Society. This paper is Contribution Number 177 of the West Indies Laboratory, Fairleigh Dickinson University, St. Croix, U.S. Virgin Islands.

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DATED ACCEPTED: August 16, 1988.

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