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Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach, Kenya

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Abstract

Studies were carried out on the inner and outer coral reefs at Diani Beach on the Kenya coast to assess the distribution, density and behaviour of *Echinometra mathaei* (de Blainville). Transects 1 m wide were run on the two reefs in April, June and September, 1970. Test measurements on representative samples from the animal populations on both reefs were also taken. Direct observations on specimens of *E. mathaei* in selected rock pools on the outer reef were made to determine their movement, gregariousness, homing and feeding behaviour. Population density was higher on the inner reef furthest from the sea at low tide than on the outer reef. On the submerged inner coral reef at low tide, *E. mathaei* occurred mainly exposed on the seaweeds, but, on the exposed outer reef, its main niches were crevices in rock pools and under coral ledges. Size-frequency distributions revealed that smaller individuals occurred on the inner reef and larger ones on the outer reef. The growth rate of *E. mathaei* was estimated from the positions of modal values, calculated from size-frequency distributions. No gregarious or homing behaviour was observed and, once settled in a suitable crevice, *E. mathaei* showed little movement.

Introduction

Although the reproductive biology of the Indo-Pacific echinoid *Echinometra mathaei* has been studied (Pearse, 1968, 1969), there is very little information available on its ecology and behaviour. Such information is necessary for understanding the part played by this echinoid in contributing significantly to the food chain and its effect on the marine intertidal region.

On a world basis, *Echinometra mathaei* ranges in distribution from central Japan to southern Australia; and from Clarion Islands off Mexico to the Gulf of Suez (Mortensen, 1943). Throughout its distribution area, this echinoid has been noted to occupy a variety of habitats. Along the western shore of the Gulf of Suez, it has been observed to occur mostly in the open on dead coral blocks and rubble (Pearse, 1969). In many other areas, it has been found partially hidden, nestled under coral ledges on the reef or nearly completely hidden under rocks or in deep crevices or holes in coral blocks.

At Diani Beach, Kenya, *Echinometra mathaei* is the dominant echinoid. It occurs both on the inner coral reef which is always submerged by tidal water at low tide, and on the outer coral reef which is usually exposed to the air at low tide.

Materials and methods

Diani Beach is situated at approximately latitude 4°S on the coast of Kenya (Fig. 1) and is, therefore, a typical tropical coastal shore. It is long and narrow, separated from the main body of the Indian Ocean by a fringing coral-reef platform about 0.9 km wide. The reef extends the entire length of the beach and can be divided into an inner reef (Fig. 1*B* and Fig. 2) consisting mainly of dead coral and rubble, and an outer reef (Figs. 1*C* and 2) consisting of dead and living corals.

The surface of the inner reef varies from regions of sandy bottom to areas of coral rubble sometimes covered with seaweeds. It is about 0.6 m lower than the outer reef, and is, therefore, always submerged, as much as 0.9 m in deep channels at low tide.

The surface of the outer reef is very uneven, resulting in areas which become completely uncovered, areas with water about 5 to 10 cm deep, and areas with large and small, shallow and deep pools at low tide. Opposite Jadini Hotel area (Fig. 1), the outer reef platform is divided by a narrow channel of water at low tide into southern and northern sections. The two sections are similar, but the southern one is about 0.3 m lower than the northern one and, therefore, is exposed for less time each day. The northern section is exposed for $2\frac{1}{2}$ h during low water neap tides (LWN) and for $5\frac{1}{4}$ h during low water spring tides (LWS). The southern section is exposed for 2 h at LWN and for $4\frac{3}{4}$ h at LWS.

Seaward, the outer reef platform drops off quite sharply, and there are many crevices in the coral. Wave action is strong, and there is not much sand. It would require diving to determine whether echinoids occur here.

Between land and the inner reef the shore consists of bare sand (Fig. 1*A* and Fig. 2) which is always exposed to air at low tide and is devoid of echinoderms.

Three transects each in April, June, and September of 1970, were run across the inner coral reef and the two sections (north and south) of the outer reef opposite Jadini Hotel (Fig. 1). A landmark was used to ensure sampling along the same transect in subsequent months. A 1 m^2 wooden quadrat was dropped along each transect at 10 m intervals on the inner reef and

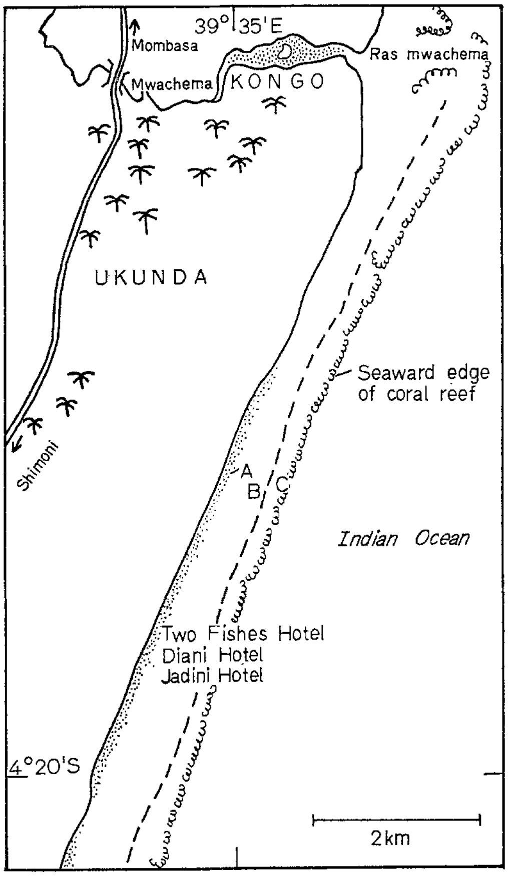

Fig. 1. Map of Diani Beach showing surrounding land and main zones of the intertidal habitat. *A* sandy beach; *B* inner coral reef; *C* outer coral reef

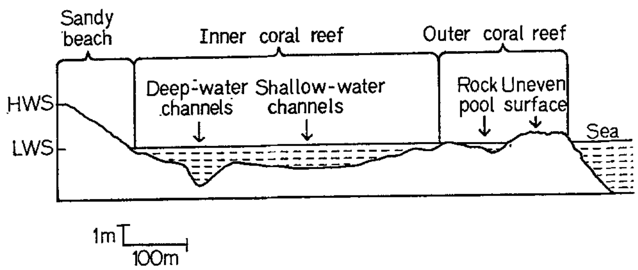

Fig. 2. Profile of seashore at Diani Beach from shore line to seaward edge of outer coral reef platform at low tide

at 5 m intervals on the northern outer reef and the southern outer reef comprising a total of 30 quadrats each and named, landward, middle and seaward positions. The numbers of *Echinometra mathaei* in each quadrat were counted and their density estimated for inner and outer reefs as well as for landward, middle and seaward positions in each transect.

Caliper measurements of test lengths were taken on 59, 31 and 61 echinoids in April, June, and September, respectively from the inner reef; and on 40, 74 and 42 echinoids in April, June, and September, respectively from combined outer reef areas. Size frequency analyses were made to determine size distributions of *Echinometra mathaei* from each area.

Field observations were also made on the behaviour of *Echinometra mathaei* in regard particularly to niche preferences, movement patterns, gregariousness, homing and feeding habits. Five selected rock pools on the northern outer reef were used to study movement patterns. The number and position of specimens in each pool were noted and each specimen was then marked with red paint[1] on the surface spines. Observations were made every day at low tide from April 18 to May 3, noting any intruders in the pools and whether or not any of the residents in each pool changed their positions. Specimens which had not changed their positions for the two weeks were carefully removed from their crevices by dragging them along the substrate in order to minimize their disorientation and placed at the center of the sandy bottom of the pool. Observations were then made on their movement and note taken of any specimens which returned to their original crevices.

In another empty pool in a nearby area, specimens of *Echinometra mathaei* were introduced in a cluster to determine whether they are gregarious. This pool contained suitable habitats, but was unoccupied by sea urchins, presumably because it was often exposed to air.

In addition, gut contents of a few specimens from all areas were microscopically examined to determine their food types in the environment. Observations on actual feeding were also made and specimens were considered to be feeding if they had material between their teeth.

Results

Abundance and size

A total of 931 specimens of *Echinometra mathaei* were counted along the three transects in the three months studied. Of these, 479, 303 and 149 were counted on the inner reef, the southern outer reef and the northern outer reef, respectively. The mean number of *E. mathaei*/m^2 on the three reefs sampled in April, June, and September was 5.3, 3.4, and 1.7 for the inner reef, the southern outer reef and the northern outer reef, respectively (Fig. 3). This difference in frequency was highly significant ($F = 10.2$, $P < 0.01$). Differences between landward, middle and seaward positions along the transects were also significant ($F = 4.3$, $P < 0.05$). The mean number of *E. mathaei*/m^2 on landward and

[1] Artist's paint mixed with a solution of shellac in alcohol adhered and dried quickly in air on the spines of the echinoids; it remained throughout the time of observation.

middle positions of the inner reef which are less exposed to the ocean waves was 4.13 for each position, while for the seaward section which is more exposed to the waves it was only 2.10 — almost twice as many individuals/m^2 in samples away from the seaward side of the reef (Fig. 3). This analysis also revealed that the difference in the number of specimens/m^2 between seaward, middle and landward positions depended upon the reef being sampled ($F = 2.5$, $P < 0.05$) and is less on the outer reef than on the inner reef. No significant differences were detected between the different samples taken at different times.

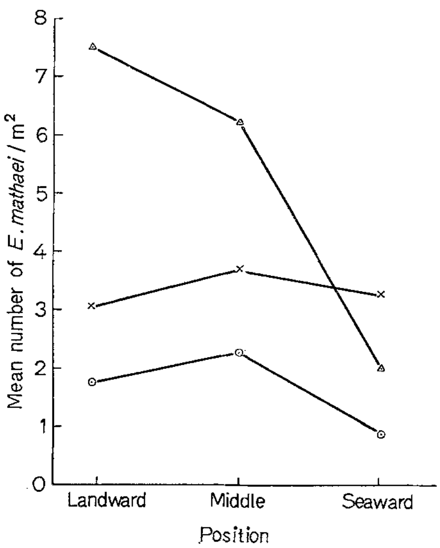

Fig. 3. *Echinometra mathaei.* Mean distribution at different positions along transect lines taken across. △: inner reef; x: outer reef (south); ⊙: outer reef (north). (Error mean square = 96.6)

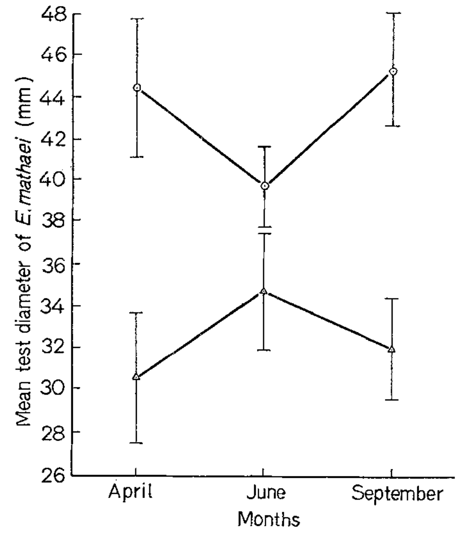

Fig. 4. *Echinometra mathaei.* Size frequencies of urchins from △: inner and ⊙: outer coral reefs at Diani Beach in April, June and September. Vertical limits: 95 % confidence intervals

Fig. 4 shows the mean size differences between *Echinometra mathaei* on the inner and combined outer reefs in April, June, and September. Smaller specimens

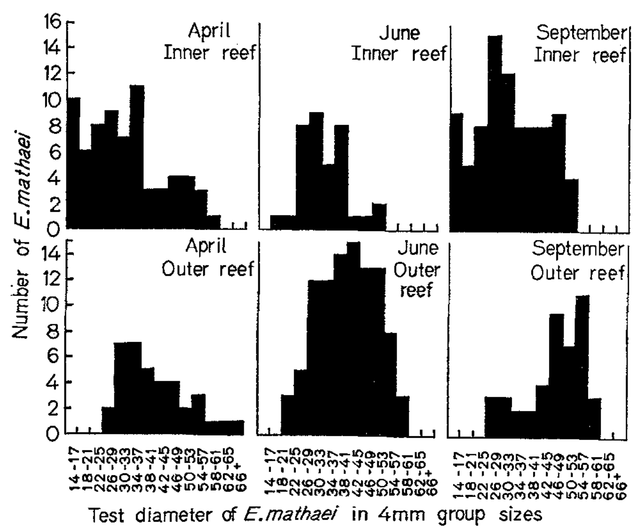

Fig. 5. *Echinometra mathaei.* Size frequencies of urchins from inner and outer reefs at Diani Beach in 4 mm size groups for April, June and September, 1970, showing occurrence of young and adult populations

with mean test lengths of 31.08, 34.80 and 32.08 mm in April, June, and September, respectively, occurred on the inner reef. Larger specimens with mean test lengths of 44.33, 39.65 and 45.43 mm in April, June, and September, respectively, were found on the outer reef. These differences were highly significant ($F = 19.2$, $P < 0.01$). Differences between sizes of *E. mathaei* when reefs were compared in terms of time were also significant ($F = 6.2$, $P < 0.05$), but no significant differences existed when months alone were compared.

Fig. 5 shows size-frequency distributions of echinoids in each sample from the inner and combined outer reefs in April, June, and September. The distributions were unimodal. On the inner reef, the modes in April, June, and September were at size-groups 34 to 37 mm, 30 to 33 mm and 26 to 29 mm, respectively; corresponding modal values on the outer reef occurred at size-groups 30 to 37 mm, 38 to 41 mm and 46 to 49 mm in April, June, and September, respectively. Thus, on the inner reef, modal values for June and September showed a decrease in the April value; the reverse occurred on the outer reef.

Behaviour

In studies on movement patterns, only 2 individuals out of 176 observed in various pools moved from one pool to another about 3 m away in the two weeks of observation. In another two pools, 3 individuals in one, and 1 individual in the other appeared to have merely changed to new quarters within the same pool. The rest remained firmly attached to the sides or in crevices in their pools. Of those that moved, none was seen moving during daytime at low-water tides. It is doubtful that they would voluntarily move about at high tide, as the water is extremely turbulent. It can only be concluded that those which moved either did so during the night low-tide period, or were carried by water currents at high tide.

When individuals were removed from positions which they had occupied for 2 weeks and were placed in the center of the pool, they immediately protruded their podia and rapidly moved towards the edge of the pool. In 1 h most specimens travelled a distance of 2 to 3 m, and by the end of the day all had returned to the sides of the pools into crevices similar to the ones they had previously occupied. None returned to its original crevice or home even after three weeks following the experiment.

Specimens introduced in a small empty pool together moved apart and continued moving until they occupied a crevice. Once in a crevice they stopped moving. Whenever *Echinometra mathaei* came in contact they would always move away from each other. The separation movement was initiated by the active podia of the moving specimen touching the spines of the stationary one. The stationary specimen then extruded its podia to touch the spines of the approaching specimen. As soon as the spines of the latter were touched it bent its spines away from the area. Podia on the opposite side of its test became active and it moved away in that direction. All moving specimens in search of a sheltered crevice picked up shells and other debris which they deposited on their tests, a behaviour also noticed in the exposed specimens on the inner reef. The *E. mathaei* in crevices and on the sides of rock pools not directly reached by sunlight did not cover themselves with debris, thus confirming observations made by MORTENSEN (1943) and MOORE (1966) that this is a protective measure against strong light among sea urchins. The introduced specimens did not appear to be affected by exposure, elevated temperatures or increased illumination in their new habitat.

Feeding

Most of the specimens examined contained unidentified algae in their guts. This appeared to be the predominant food, although many specimens also contained unidentified animal tissues and varying amounts of fine calcareous material, probably coral remains. Of the 157 *Echinometra mathaei* examined, 37% fed on algae, 11% had bits of shell material between their teeth and the remainder were not feeding.

Discussion

The East African coast lies in the zone of the northeast and southeast trade winds. The former blow from November to March and the latter from May to October, with April comprising a transition period. TALBOT (1964) showed that the southeast trade winds are twice as strong as the northeast winds and that the resulting wave action has devastating effects on reef animals. March to June is the rainy season in East Africa, with the rain being brought by the southeast winds. During this study, it rained almost everyday in April and June and for 13 days in September. The clarity of the water after it had rained suggested that run-off from the land has little effect on the inshore environment at Diani Beach.

PEARSE (1968, 1969) suggested that sea temperatures are important in regulating the reproductive periodicity of *Echinometra mathaei*. He believed this species to be reproductively active when temperatures are about 18° to 20 °C, and that it spawns continuously throughout the year within the tropics. Water temperatures at Diani Beach ranged from a minimum of 27 °C taken at dawn to 29 °C taken at midday, on a sunny day in April. The average monthly temperatures of inshore surface waters for the entire East African coast range from 24.8° to 29.1 °C (NEWELL, 1959). Tropical marine animals, in general, tolerate these temperatures without difficulty (MORGANS, 1959), and it is unlikely that the small range in temperature variations at Diani Beach had any effect on the distribution and behaviour of *E. mathaei*.

The *Echinometra mathaei* population reached its maximum density (5.3/m²) on the inner coral reef, where it occurred exposed on blocks and, sometimes, although not as frequently, on bare coral surface, and was thus less protected against wave action and predators. Less violent waves would allow the larvae of *E. mathaei* to settle more easily on the inner reef than on the outer one, and the sublittoral nature of the former region would also reduce dangers of exposure to the sun and air (CLARK and BOWEN, 1949). Thus, reduced effect of wave action and exposure on the inner relative to the outer reef, probably account for the highly significant difference in population densities between these two areas. In support of the wave-action hypothesis, differences between landward, middle and seaward positions along the inner reef transects were significant. The population was twice as dense on the landward and middle sections of the inner reef as on the seaward side. These differences were less significant between the southern and northern areas of the outer reef (Fig. 3).

Very small differences in the length of exposure time between two areas can produce a great difference in the distribution of inshore marine organisms. During both LWN and LWS tides, the northern part of the coral reef is exposed 30 min longer than the southern part. Presumably this is one of the reasons for the significant differences in the mean population densities of *Echinometra mathaei*/m² observed between the northern and southern sections of the outer reef. Higher population densities on the southern section of the outer reef, which is further away from the seaward edge than the northern section, also supports the hypothesis that *E. mathaei* tends to settle in relatively calm and sheltered intertidal waters rather than in turbulent ones.

Other unmeasured factors, such as food supply and breeding patterns, may also modify the distribution of *Echinometra mathaei* at Diani Beach, but the above observations strongly indicate that wave action may be one of the major factors involved. Protection against wave action, particularly for the smaller specimens, availability of food and cover, or some other unknown factors could be important cues for the observed differences in habitat selection or survival by *E. mathaei* of different sizes.

The occurrence of smaller specimens of urchins on the sheltered inner reef and larger ones on the exposed outer reef is contrary to observations made by other workers. EBERT (1968) found smaller urchins on the exposed areas of the shore and larger individuals on sheltered areas. He attributed this to the breakage of more spines by turbulent waves in the former areas and, hence, more energy expension for repairs than in the latter areas, where energy was directed into test growth. Our results indicated that this problem might be more complex than this; thus, further observations seem necessary.

On the inner reef, modal values for June and September occurred at successively reduced size-groups from that in April (Fig. 5), possibly due to the entry of the growing smaller urchins of size-groups 14 to 25 mm test lengths found on that reef. It could not be due to age structure, since the data shows that maximum size in *Echinometra mathaei* at Diani Beach must occur well beyond the 40 mm test length. MCPHERSON (1969) made observations in Florida, USA, on a different species of the same genus, *E. lucunter* LINNAEUS, and found that, under natural conditions, adult populations were consistently larger than 40 mm in test length. On the outer reef, where urchins in size-group 14 to 25 mm test length were almost absent, modal values for June and September were successively above that in April. It is thus estimated that *E. mathaei* at Diani Beach has a growth rate of about 5 to 10 mm in three months. At this rate, most of the April 14 to 25 mm size-group population on the inner reef will be in the 26 to 35 mm range by June and September. This population will lower the modal values in June and September if it is present in large enough numbers.

The growth rate of 5 to 10 mm in three months is not unusual among echinoids. *Echinometra viridis* AGASSIZ in Florida grew at the rate of 5 mm in three months in aquaria (MCPHERSON, 1969); and *Salmacis bicolor* AGASSIZ, which occurs in the same habitat on the outer reef with *E. mathaei* at Diani Beach, has also been reported to have a growth rate of 4 to 5 mm or more in three months (AIYAR, 1935). The actual growth rate in *E. mathaei*, however, remains unknown until determined by studies similar to those of SWAN (1961, 1966) and EBERT (1968) on growth rates in other echinoids, correlated with environmental factors.

Echinometra mathaei individuals did not seem to home at all, and their positions in the habitat seemed to be the result of chance. The attraction for crevices would be selectively advantageous since it serves to hide them from predators, reduce desiccation and light intensity, and provide protection against turbulent waves. Boring into rocks and other hard material by echinoids is well established (REESE, 1966), and probably some of the burrows and crevices in which specimens of *E. mathaei* were found on the outer reef were made by the urchins themselves.

For an animal displaying little movement, a gregarious habit would be disadvantageous, since food supply would become a problem. This may explain the lack of gregariousness among the individuals observed. There are, of course, some stationary animals which exhibit gregariousness in the intertidal region, especially among certain bivalve molluscs, but their feeding methods are completely different from that of *Echinometra mathaei* which grazes on the surface it occupies (REESE, 1966). Findings on gut contents confirmed that, like most sea urchins, *E. mathaei* is omnivorous, feeding on plants, animals and even dead coral (MOORE, 1966).

Summary

1. Transects 1 m wide were run across the inner and outer north and south coral reefs at Diani Beach, Kenya; each transect was divided into three equal positions: landward, middle and seaward. The number of *Echinometra mathaei* (DE BLAINVILLE) in each quadrat was counted and their density estimated. Test measurements on representative samples of urchin populations on the different reefs were taken to determine size-frequency distributions. Observations on several behavioural aspects to determine patterns, niche preferences, homing and gregariousness, and feeding habits, were also made.

2. *E. mathaei* was denser on the inner than on the outer coral reef. Population density was also higher on the southern outer reef than on the northern outer reef. These differences, which were significant, are probably due to the much greater effect of wave action and exposure on the outer reef than on the inner reef. Exposure would contribute more to the difference between southern and northern portions of the outer reef, since the southern portion is exposed for less time at each low tide than the northern one. The fact that the mean number of *E. mathaei*/m^2 on landward and middle positions of transects on the inner reef which are less subjected to wave action was much higher than that on the seaward position, supports the wave-action hypothesis.

3. Size frequency analyses revealed that larger specimens of *E. mathaei* occurred on the outer reef and smaller ones on the inner reef due to unknown factors. Differences in positions of modal values in the April, June, and September distributions on the inner reef were probably due to the growing small urchins found on this reef which would enter the population of the next size-group in three months. Growth rate of *E. mathaei* is, therefore, about 5 to 10 mm in three months.

4. Over the short term, *E. mathaei* appears to stay in one position. On the inner reef, urchins occurred more often exposed on coral rubble covered with seaweeds than in crevices or sides of pools, whereas, on the outer reef, the main niches were crevices, rock-pool sides and under coral projections. When removed from their crevices the urchins did not home but moved towards and entered any crevice.

5. Diet of *E. mathaei* was chiefly algae and detritus.

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