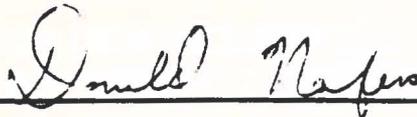


AN ABSTRACT OF THE THESIS OF James Bruce Neill for the Master of Science in Biology presented 18 July, 1985.

Title: Burrow Defense in the Sea Urchin Echinometra mathaei (Blainville) on an Indo-West Pacific Reef Flat.

Approved:



Donald M. Nafus, Chairman, Thesis Committee

Burrow defense of the rock-boring echinoid Echinometra mathaei (Blainville) was investigated in two different reef-flat habitats on Guam (Mariana Islands). Outer reef-flat inhabitants more commonly defend resident burrows than do individuals occurring in the inner reef flat. Urchins transplanted from the outer reef flat to the inner reef flat do not alter defensive tendencies. Individuals transplanted from inner reef-flat regions to the outer reef flat do not defend burrows. Recolonization rates of empty burrows in inner reef-flat regions are five times higher than in outer reef-flat regions. Burrow colonists range in maximum test diameter from 1.6 cm to 4.9 cm. Residents of the outer reef flat are unable to retain occupied burrows in the presence of larger intruders. Behavioral differences in burrow defense provides evidence supporting the splitting of E. mathaei into two species.

**BURROW DEFENSE IN THE SEA URCHIN ECHINOMETRA MATHAEI
(BLAINVILLE) ON AN INDO-WEST PACIFIC REEF FLAT**

BY

James Bruce Neill

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requirements for the degree of**

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TO THE OFFICE OF THE GRADUATE SCHOOL AND RESEARCH

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INTRODUCTION

During diurnal periods of inactivity, echinoids commonly inhabit burrows or crevices which protect them from predation (Nelson and Vance, 1979; Carpenter, 1984) and shelter them from wave energy (Khamala, 1971; Russo, 1980; Lawrence and Sammarco, 1982). Recently, the tropical Caribbean echinoid Echinometra lucunter and the temperate eastern Pacific echinoid Strongylocentrotus purpuratus were shown to exclude conspecifics from their burrows through aggressive interactions such as pushing or biting. Strongylocentrotus purpuratus defends its burrow by physically pushing an intruder out (Maier and Roe, 1983). Echinometra lucunter pushes conspecifics away and also bites intruders using the Aristotle's lantern apparatus (Grünbaum et al., 1978).

The rock-boring echinoid Echinometra mathaei (Blainville) occurs throughout the Indo-West Pacific in shallow-water habitats (Clarke and Rowe, 1971). In reef margins and outer reef-flat areas they excavate tubular burrows in the calcium carbonate substrates (Grünbaum et al., 1978; Russo, 1977; Russo, 1980; Lawrence and Sammarco, 1982; Tsuchiya and Nishihira, 1984). In quieter, inner reef-flat areas, their burrowing behavior is not as well represented (Tsuchiya and Nishihira, 1984). Preliminary investigations in Hawaii (Ogden, unpubl. data) showed that E. mathaei will defend its burrow from conspecifics by pushing but no biting behavior was observed.

In the Indo-West Pacific there are at least two forms of Echinometra and there has been some controversy as to the number of species in this region. Mortensen (1921), recognizes two species (E. mathaei and E. oblonga), whereas Clarke and Rowe (1971), recognize only one species (E. mathaei). Embryologic data suggest that the separation of these two species is valid (Mortensen, 1921). Russo (1977) reports that the two species from Hawaii roughly segregate by habitat types. E. oblonga occur in regions of high wave assault, whereas E. mathaei is most common in calmer waters. In Okinawa, Tsuchiya and Nishihira (1984), report two distinct types of E. mathaei occurring on reef flats. These types differ in spine coloration and occupy different habitats. Individuals with white-tipped or solid white spines are classified as type A and are found predominantly in back-reef habitats, rarely occurring in outer reef-flat regions. Type A individuals occur in crevices, on flat rock substrates, and in a variety of sheltered sites (Tsuchiya and Nishihira, 1984). This form frequently occurs within spine contact of conspecifics. Those individuals having spines of a solid brown or green color are type B and are found predominantly on outer reef flats. This form occurs more frequently in burrows, rarely being found within spine contact of conspecifics. Lewis and Storey (1984) recently reported a similar microhabitat distribution for E. lucunter morphs in Caribbean coral reefs. In this paper I refer to all members of the genus Echinometra

found on Guam as E. mathaei but differentiate between inner and outer reef-flat forms.

The purpose of this investigation was to address three basic components of territoriality in the sea urchin Echinometra mathaei: 1) Is intraspecific burrow defense dissimilar between the types of Echinometra occurring in inner and outer reef flats, and if so, do transplanted individuals alter their defensive behaviors according to the environment they are put in? 2) Does the size of an individual affect its ability to successfully defend its burrow from conspecifics? 3) What are the rates of echinoid colonization of empty E. mathaei burrows in inner and outer reef-flat habitats, and what are the sizes of the colonists?

LITERATURE REVIEW

Most Indo-West Pacific reef-flat platforms exhibit distinctive zonation; this zonation is partly regulated by current velocities which generally decrease shoreward concomitantly with increasing depth (Odum and Odum, 1955; Kinsey, 1979). Biotic communities subject to various current regimes fall into discernible zones in terms of community structure, primary productivity, and calcification rates (Lewis, 1977; Kinsey, 1979).

A typical fringing reef flat can be divided into (at least) three major zones, the reef margin, outer reef flat, and inner reef flat (Figure 1). Some important characteristics that commonly differ in these habitats are wave assault, current velocity, subaerial exposure, benthic fauna, and rates of primary productivity. All of these factors have been shown to influence biota inhabiting these regions (Denny et al., 1985; Russo, 1977).

Outer reef flats of Pacific coral reefs generally support high rates of primary production and calcification (Kinsey, 1979) and are exporters of organic materials and calcium carbonate. Outer reef flats are typically subject to high-energy wave inundation (Denny et al., 1985), which is often associated with fast current velocities.

Outer reef-flat communities grade shoreward into inner-reef habitats characterized by increasing amounts of loose rubble and sand, and by lower rates of primary production and calcification (Kinsey, 1979). Although not universally true, current velocities are typically

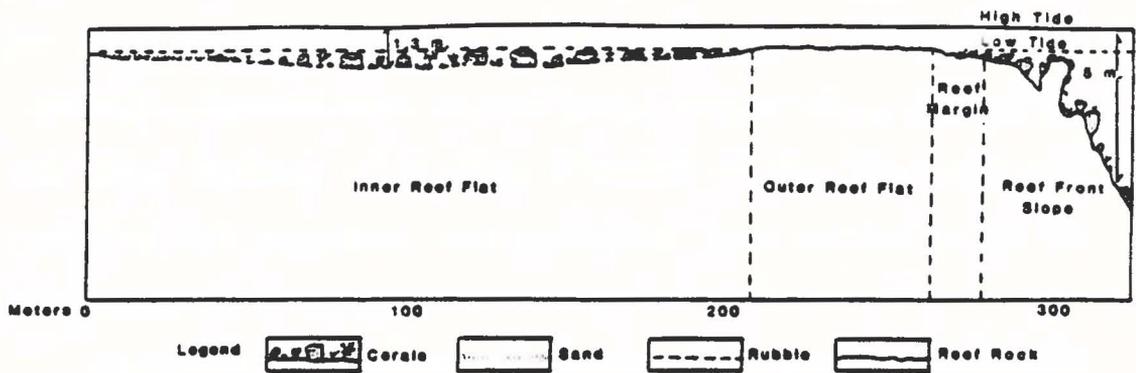


Figure 1. Vertical profile of the Piti reef platform showing zonation patterns, types of substrate and water depths. Vertical exaggeration x10. Adapted with permission from Randall and Eldredge, 1982.

lower on inner reef-flat areas than on outer reef flats; this is in part because of the increased water depth in these regions. Deeper back-reef environments are often depositional environments as substrate is removed from the reef margin and carried by wave action into these habitats. The biota occurring on the inner reef flat commonly lack physiologic and behavioral traits serving to provide strong adhesion to the substrate surface.

The ecology of shallow-water echinoids has been studied in many geographic locations throughout the world. Research has been conducted on many aspects of echinoid ecology including feeding habits (Lawrence, 1975; Ogden, 1976; Vadas, 1977; Nelson and Vance, 1979; Vance, 1979; Larson et al., 1980; Vadas and Ogden, 1982), and their effects on surrounding communities as herbivores (Paine and Vadas, 1969; Camp et al., 1973; Ogden et al., 1973; Sammarco et al., 1974; Sammarco, 1977; Ogden and Lobel, 1978; Carpenter, 1981; Sammarco, 1982; Sammarco and Williams, 1982; Vadas et al., 1982; Carpenter, 1984). Much research has also investigated them as predators, (Bak and van Eys, 1975; Sammarco, 1980), and as agents of bioerosion, (Ogden, 1977; Russo, 1980). To date, most echinoid research has been conducted in the Atlantic, Caribbean, and eastern Pacific regions (including most of the works cited above).

Investigations of Indo-West Pacific echinoid fauna are limited in number; nonetheless a significant amount of knowledge has been generated in the last 60 years. Previous research efforts have covered the topics of taxonomy (Mortensen, 1943; Clarke and Rowe, 1971),

behavior (Pearse and Arch, 1969; Pearse, 1969), bioerosion (Russo, 1980), embryonic development and growth rates (Mortensen, 1921; Ebert, 1975 respectively), and general descriptive ecology (Khamala, 1971; Russo, 1977; Tsuchiya and Nishihira, 1984; among others).

In general, Echinometra mathaei are fairly common throughout Indo-West Pacific reefs. They occur in a variety of shallow-water habitats from subtidal reef-front slopes to reef moats. Within these habitats, they occur in coral rubble and among cobble-sized sediments (Pearse, 1969), under ledges and inside crevices (Khamala, 1971; Tsuchiya and Nishihira, 1984), and in burrows excavated (at least partially) by residing individuals (Khamala, 1971; Russo, 1980; Tsuchiya and Nishihira, 1984). Burrowing individuals remain close to their burrows and may never leave them (Tsuchiya and Nishihira, 1984). Investigations dealing with the feeding habits of E. mathaei suggest that they ingest algal and animal tissue (Khamala, 1971; Tsuchiya and Nishihira, 1984) which settles in their burrow as drift material (Russo, 1980).

Territoriality was first formally described among birds in the early 1920's (Etkin, 1971), although it has been recorded by man since the mid-seventeenth century (Klopfer, 1969). Early investigations of territoriality focused primarily on birds, mammals, and reptiles and explored the adaptive values of acquisition and defense of a territory. In recent research concerning territoriality, there is a strong bias towards terrestrial vertebrate fauna which, in part, results from the

ease with which terrestrial vertebrates are individually recognized and observed in the field (Klopfer, 1969).

Territoriality occurs among a wide variety of invertebrates including spiders, insects, and marine representatives (Itô, 1980). In insects, territoriality is known from only a few major groups; the most thoroughly studied of these are the odonates (Itô, 1980), which exhibit territoriality as larvae and adults. In marine invertebrates, territorial behaviors have been described for gastropods, annelids, and crustaceans.

The ability to retain a territory is often associated with superior aggressive abilities of dominant individuals (Klopfer, 1969). Individual size differences of participants commonly affect the outcome of aggressive encounters (Caldwell and Dingle, 1979). Size advantages can reflect many factors which may increase with age such as increased physical strength, greater level of experience, and an elevated position in (social) dominance hierarchies (Alcock, 1984). Although size advantages have been shown to exist, there is often an advantage to current territory holders; such home-field advantages allow small individuals to successfully retain an area from larger intruding individuals (Alcock, 1984).

In 1964, Brown introduced the idea of economic defendability which stimulated much research on the economics of territoriality (reviewed by Davies and Houston, 1984). The propensity to defend a given area has often been found to be dependent on the value of the area to an inhabitant; this is the basic foundation upon which territory

economics is based (Davies and Houston, 1984). The value of a territory can be based on the resource potential within the area, costs of attaining the territory, or costs of optional strategies. The values of costs and benefits (in terms of genetic fitness) are well-suited to evolutionary cost-benefit analyses, and not surprisingly, many recent analyses have been conducted on territoriality utilizing game theory and the concept of evolutionary stable strategies (reviewed in Alcock, 1984, and Davies and Houston, 1984).

In summary, within a given reef-flat platform there are distinct habitats, and the benthic organisms occurring in these habitats are subject to different sets of environmental factors. In fact, closely related echinoid inhabitants of reef flats have apparently evolved different habitat preferences in response to different sets of selective pressures; this differentiation of autecologies appears to be similar in different geographic locations suggesting that these traits are of high adaptive value to individuals subject to similar environmental conditions. Moreover, behavioral patterns (such as the propensity for territoriality) could be expected to vary between organisms which occur in different habitats, and could also vary within co-occurring organisms depending on the physiologic state (e.g., size) of the individuals.

MATERIALS AND METHODS

Description of Study Site

Territoriality in Echinometra mathaei was investigated on a reef-flat platform on the western coast of Guam (Mariana Islands). The study site is located directly south of the eastern tip of Cabras Island (Figure 2). This reef flat has been well described in the recent past (Marsh, 1974; Marsh and Doty, 1975; Marsh and Doty, 1976; Marsh et al., 1977; Randall and Eldredge, 1982). Throughout most of the year, the area is subject to intense wave energy and associated strong currents. The depth of the study site ranges from 0.2 m to 2.0 m, depending on the tidal height and the presence of offshore winds. Within the reef-flat platform, two distinct habitat types were chosen in which to investigate burrow defense in E. mathaei (Figure 2).

The first habitat type (H1) is directly adjacent to Cabras Island on the outer reef flat (Figure 2). This area is contained within the inner algal zone designated by Marsh (1974). The topography of this region (Figure 3a) is for the most part flat and barren, having a vertical relief of generally less than 30 cm (Marsh, 1974). This habitat is subject to intense wave energy and extremely high currents; Randall and Eldredge (1982), reported current velocities of 0.42 to 1.0 meter/sec. in this area. The coral-algal community is poorly developed, with corals being primarily represented by fist-sized massive Porites colonies and small, scattered Pocillopora damicornis colonies. The depth in this habitat ranges from a few centimeters (during low spring tides) to over a meter during high spring tides. The

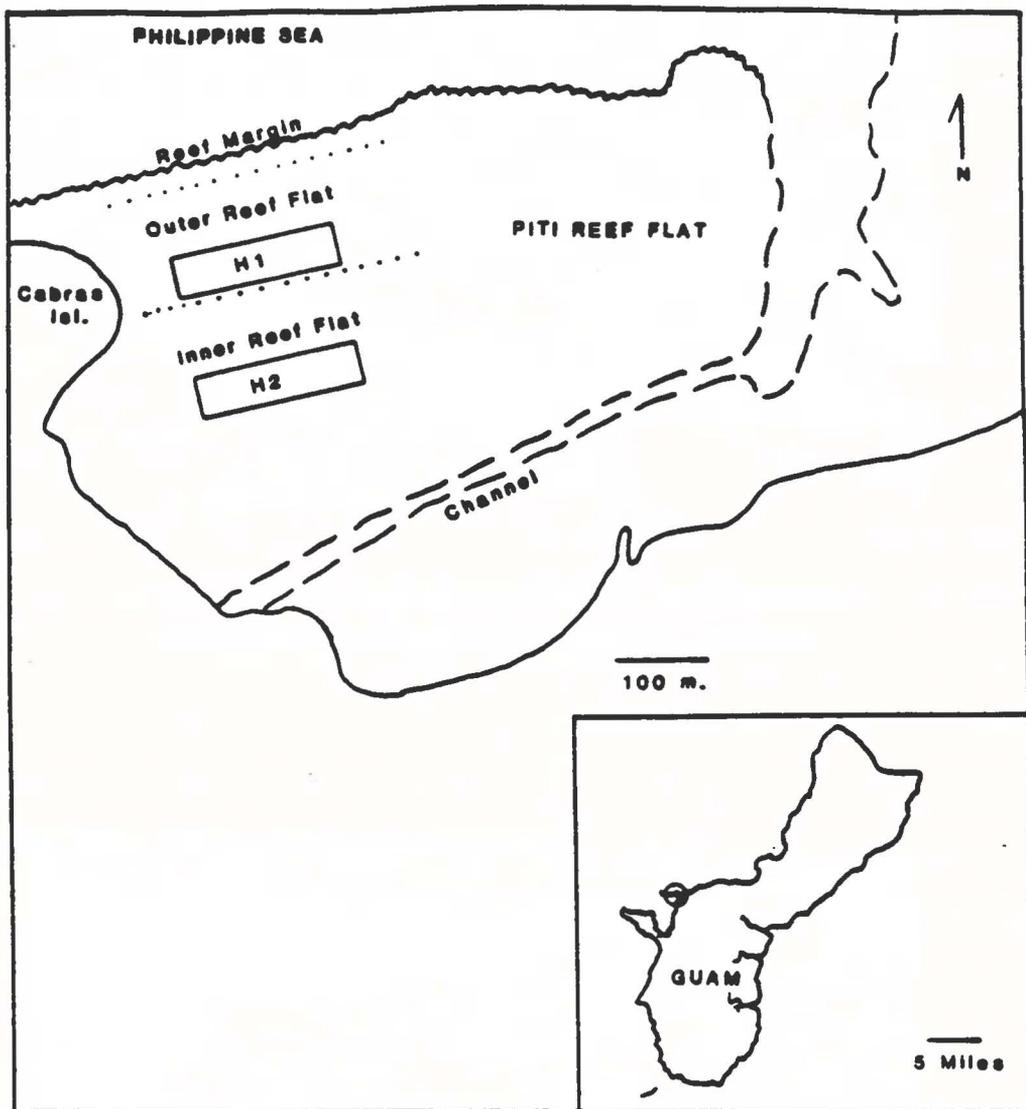


Figure 2. Map of Piti reef-flat platform, showing zonation and specific study areas (H1 and H2). Adapted with permission from Marsh, 1974.



Figure 3a. Photograph of Site H1. Note barren topography and tagged Echinometra burrows.

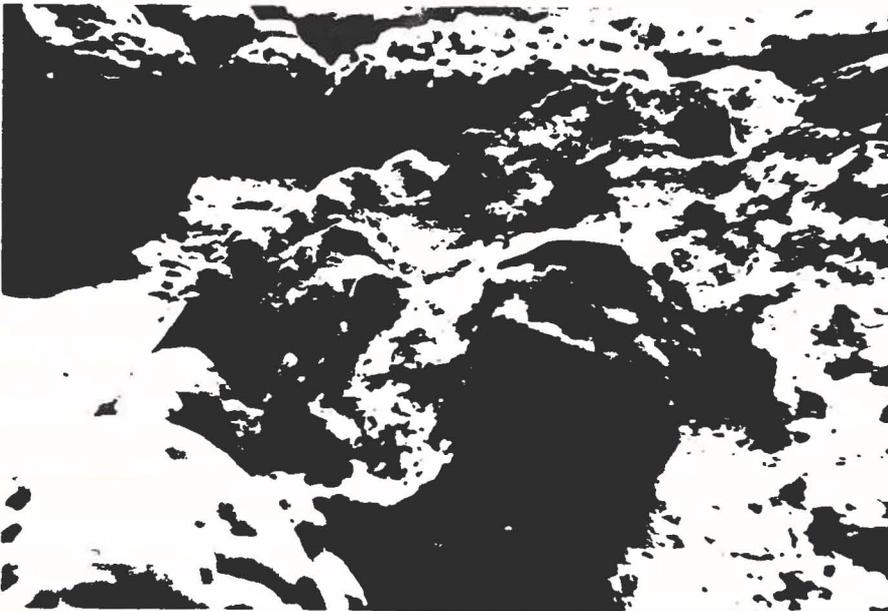


Figure 3b. Photograph of Site H2. Note topographic relief and tagged Echinometra burrow.

most conspicuous faunistic component in this habitat is E. mathaei. This area supports the highest density E. mathaei community on Guam's reef-flat platforms (R. Randall, pers. comm.).

The second habitat type (H2) is located in the inner reef-flat region 150 m south of the eastern tip of Cabras Island (Figure 2). This habitat is within the coral zone described by Marsh (1974). This region is subject to high velocity unidirectional current flow (Marsh, 1974), but does not receive as much wave assault as does H1. The topography in this habitat (Figure 3b) is more complex, with vertical relief often being up to or greater than one meter (Marsh, 1974). The substrate in H2 is dominated by consolidated reef pavements often covered with a thin vernier of scattered cobble and sand-sized particles; scattered patches of coral rubble (primarily Acropora sp.) are also common. Resting on the substrate are numerous large Porites (primarily P. lutea and P. australiensis) microatoll formations which have been vertically truncated by aerial exposure during low spring tides; the tops of these microatolls are commonly a meter above the underlying substrate. In this habitat the echinoid fauna is also very conspicuous but more diverse than in H1; the most common representatives are Diadema setosum, D. savygnii, Echinothrix diadema, and Echinometra mathaei.

Experimental Protocol

Controlled behavioral trials were conducted to elucidate the parameters of burrow defense under investigation. All trials were conducted in an identical manner. Trials were conducted between the hours of 1600 and 1830. This time period was selected because of its

temporal proximity to nocturnal periods of activity, yet all behavior could accurately be observed without utilizing artificial light and possibly disrupting normal behavior. In all experiments, an urchin (the intruder) was placed outside of a burrow containing a resident urchin (the defender); all intruding urchins were placed so that the intruder encountered the defender quickly after entering the burrow. Encounters were monitored from a distance of 0.3 m to 1.0 m for a period of fifteen minutes or until the encounter was over. An encounter was considered complete when the individuals were either no longer in spine contact or they ceased movements and spine interaction. The outcome of incomplete trials was checked the following day. In each trial, the following parameters were recorded: the sizes of the participants, temporal duration of the interaction, mechanisms of defensive behaviors, outcome of the interaction, and the distance, the intruder was displaced.

Test diameter was measured (to 0.1 cm) for all experimental sea urchins using plastic calipers; measurements were made for each urchin at its MTD (maximum test diameter). Because Echinometra mathaei are oval in shape this measurement actually represents maximum test length rather than test diameter per se, but MTD is commonly used when classifying echinoid sizes (e.g., see Carpenter, 1984); this terminology is adopted here to help retain uniformity among classifications of echinoid size measurements.

Experimental echinoids were classified by size into one of three groups. Those with a MTD \leq 2.5 cm were classified as small, those with a MTD between 2.6 cm and 4.5 cm were classified as medium and

individuals with a MTD > 4.5 cm were considered large individuals. This grouping was used to facilitate field work and for the purpose of discussion; actual MTD values were used for the evaluation of experimental results.

Echinoid burrows were measured in each habitat. The length of the burrows as well as the height at the burrow entrance were measured with a fiberglass measuring tape.

To test for differences in territorial behavior between the Echinometra types occurring in different habitats a total of 108 behavioral trials were conducted. Fifty-four trials were carried out in each habitat with naturally occurring defenders matched against experimentally placed intruders. All individuals used as intruders were collected immediately prior to the trials. Intruders were collected from the same habitat in which the trial was conducted. The intruders were collected some 50 m downstream from the site of experimental trials so it is improbable that the intruder and defender had encountered one-another in the recent past.

To test for plasticity in defensive behaviors, 15 individuals were transplanted from H1 to H2 and from H2 to H1. Behavioral trials were conducted on these individuals utilizing the naturally occurring 'type' as the experimental intruder. Medium and small individuals were used in transplant trials. In all transplant trials, the defender and intruder were of similar sizes (within 1.0 cm MTD). The experimental protocol was identical to that used in the trials previously described.

The ability of individuals to successfully defend burrows from larger intruders was tested in reef margin inhabitants only. In these

trials, 20 resident urchins were removed from their burrows and transplanted into unoccupied burrows 20 m downstream. The burrows used to house transplanted individuals were previously emptied of resident echinoids. After a period of twenty-four hours, other reef margin inhabitants were introduced into the burrows. Differences in the sizes between intruder and defender pairs tested in the size trials ranged from 0 cm to 4.8 cm.

To investigate recolonization of empty *Echinometra mathaei* burrows, 30 resident individuals were simultaneously removed from their burrows. Each burrow was numbered and tagged (Figures 3a & b). Tags were constructed from galvanized steel sheeting, numbered, and fastened to the substrate adjacent to each burrow with a 5-cm cement nail. Each burrow was subsequently monitored at 3-day intervals for a period of 30 days (yielding 10 samples for each burrow). Each echinoid colonist was identified and its MTD measured; colonists were removed from the burrows on each sampling day.

Calculations

Differences between the frequency of successful defense trials between individuals from the two habitat types were tested for with a chi-square test for goodness of fit of proportions; this test was also applied to data comparing individuals transplanted from one habitat type to the other.

To test for plasticity in defensive behaviors of individuals from a given habitat, Fisher's exact test (P), was used to evaluate differences in the number of successful trials between naturally

occurring individuals and those which had been transplanted to the opposite habitat type.

To determine the effects of size differences between defenders and intruders, a value of size differential was calculated using the following equation:

$$\text{Size Differential (cm)} = \text{MTD}_{\text{defender}} - \text{MTD}_{\text{intruder}}$$

The size differential was regressed on the duration of the defensive trial using a least-squares linear regression. The relationship between size differential and encounter duration was tested with a Mann-Whitney U test. The frequency of successful trials as a function of size differential (as either a positive or negative value) was tested with a Wilcoxon's two-sample test (U_S).

To evaluate recolonization rates of empty burrows by Echinometra mathaei, a t-test was used to test for differences between the two habitats. A Kruskal-Wallis (H) test was used to test for differences in the sizes of E. mathaei colonists between the two habitats.

The linear regression between size differential and trial temporal duration was conducted using the SAS statistical package REG. The paired comparisons t-test and the Kruskal-Wallis test were carried out utilizing Sokal and Rohlf Statistical Programs for an IBM PC-XT.

RESULTS

Of 54 trials conducted on outer reef-flat inhabitants, 48 individuals evicted the intruder within a period of fifteen minutes and all resident urchins had successfully displaced intruders within a period of 24 hours. The median encounter duration was 1.9 minutes (S.E. = 0.74). Those trials in which the intruder was not displaced within 15 minutes from the burrow fall into one of two general categories. The first of these occurred in four of the unsuccessful trials; in these situations the size of the defender was smaller than or equal to that of the intruder and the intruder wedged itself in the burrow entrance so that the defender was unable to physically displace it. The second type of unsuccessful defense (observed in two trials) occurred when the intruder quickly retreated from the defender after making spine contact. Once outside of spine contact with the defender these individuals flattened their spines against the side of the burrow thereby avoiding further contact with the defender; in both of these instances the intruder was smaller than the resident individual (by 0.8 cm and 3.5 cm). Vigorous spine waving between two individuals was noted only in the four cases in which a defender was unable to displace an intruder firmly lodged inside the burrow; in all other cases the defender merely pushed the intruder out of the burrow. No biting was observed in these trials and burrow occupants were never displaced by intruders.

Inner reef-flat inhabitants were less successful at excluding conspecifics from their burrows. Of the 54 trials conducted in this

habitat, only 26 individuals successfully displaced intruders. In 24 of the unsuccessful trials the defender was larger than the intruder; in the remaining four unsuccessful trials the defender was smaller than the intruder. The median encounter duration was 15.0 minutes (S.E. = 1.07). After 24 hours, 20 of the unsuccessful defenders had displaced the intruders; in the 8 remaining unsuccessful trials both individuals had vacated the burrows 24 hours later. Spine waving by both individuals was noted for 32 of the 54 trials conducted in this habitat; individuals that exhibited spine waving behaviors were not limited to those occupants unable to displace intruders. Raw data from the inner and outer reef-flat trials are given in Appendix 1.

Patterns of burrow defense differ between individuals in the two habitat-types. Outer reef-flat inhabitants were more successful in burrow defense than occupants of the inner reef flat ($\chi^2 = 5.96; 1df$). Observations reveal that outer reef-flat inhabitants exhibited little spine waving and quickly pushed intruders out of their burrows. It appeared that aggressive behaviors of inner reef-flat inhabitants commonly involved vigorous spine waving and pivoting inside the burrow 90° (changing the defender orientation in the burrow from parallel to perpendicular relative to the linear axis of the burrow) towards the intruder, often without linear movements.

In trials testing for plasticity of defensive behaviors, outer reef-flat inhabitants did not exhibit defensive plasticity whereas inner reef-flat inhabitants did. Raw data for transplant trials are given in Appendix 2. Of the 15 individuals transplanted from the outer reef flat

to the inner reef flat, 14 were successful in defending their burrows against inner reef-flat intruders within the 15-minute period. In one trial a defender was unable to displace an intruder after it had become tightly wedged inside the burrow, but on the following day the original defender was the only individual remaining in the burrow. This pattern of burrow defense is not different from defense in non-transplanted individuals of the outer reef flat ($P = 0.523$).

None of the 15 individuals transplanted from the inner reef flat to the outer reef flat were successful in evicting outer reef-flat intruders from their newly acquired burrows within a 15-minute period. This is significantly different from the natural trials conducted in the inner reef flat ($P = 0.0003$). After a period of 24 hours, 11 of the original transplants had been displaced from the experimental burrows by outer reef-flat individuals; 4 of the inner reef-flat individuals had successfully displaced the intruding outer reef-flat individuals. In these experiments, as in the natural trials, only inner reef-flat inhabitants waved their spines.

There was a significant relationship between the size differential of two individuals and the ability to successfully defend a burrow in outer reef-flat inhabitants (Table 1). Defenders were unable to retain burrows in the presence of larger individuals, whereas defenders could successfully evict smaller intruders. Of six trials in which a defender was smaller than the intruder, all six were displaced by the intruder; five within 15 minutes and the other within 24 hours. The single small defender that successfully defended its burrow was

Table 1. Results of size trials conducted on outer reef-flat inhabitants. The two individuals in each trial were of different sizes. Successful trials are those in which the intruder was displaced within 15 minutes; in unsuccessful trials, the defender was unable to remove an intruder within 15 minutes. Values followed by (+) indicate trials in which the outcome (24 hours later) was opposite of the outcome of the 15 minute trial. All trials were conducted in neutral burrows. Total N = 20. D_{MTD} = size of defender; I_{MTD} = size of intruder (in cm).

| | No. of Trials | Successes | Failures |
|---------------------|---------------|-----------|----------|
| $D_{MTD} > I_{MTD}$ | 13 | 12 | 1+ |
| $D_{MTD} < I_{MTD}$ | 6 | 1+ | 5 |
| $D_{MTD} = I_{MTD}$ | 1 | 0 | 1 |
| $U_s = 81^{**}$ | | | |

** - $p < .01$ level

evicted by the larger intruder within 24 hours. There was a significant relationship between the size differential (between the defender and intruder, respectively) and the duration of the defensive trial ($U_3 = 67.5$). A linear regression of encounter duration as a function of size differential yielded an $r = -1.4$ (Figure 4). Raw data from the size trials are given in Appendix 3.

Recolonization experiments (Figure 5), showed a significantly higher rate of Echinometra mathaei recolonization in the inner reef flat than in the outer reef flat. Raw data for recolonization experiments is given in Appendix 4. The mean rate of recolonization in the outer reef flat was 0.5 individual/3-day interval/30 burrows, whereas the mean rate was 2.7 individuals/3-day interval/30 burrows for the inner reef-flat habitat ($t = 2.478; 18$ df). The size of the colonists did not significantly differ between the two habitats ($H = 1.5641; 1$ df). The median colonist size for the outer reef-flat region was 3.0 cm (S.E. = 0.30 cm) while the median size of inner reef-flat colonists was 3.5 cm (S.E. = 0.21 cm). The size (MTD) range for colonists in the outer reef flat was between 2.8 cm and 4.1 cm. Inner reef-flat colonists ranged from 1.6 cm to 4.9 cm in MTD.

When small individuals (≤ 2.5 cm MTD) were transplanted from their burrows to larger ones, they usually did not remain in these burrows. This phenomenon was noted for both types of Echinometra mathaei. Of 10 small outer reef-flat individuals transplanted to large burrows (within the outer reef flat), only three were found in the burrows the following day. Of 20 small inner reef-flat inhabitants

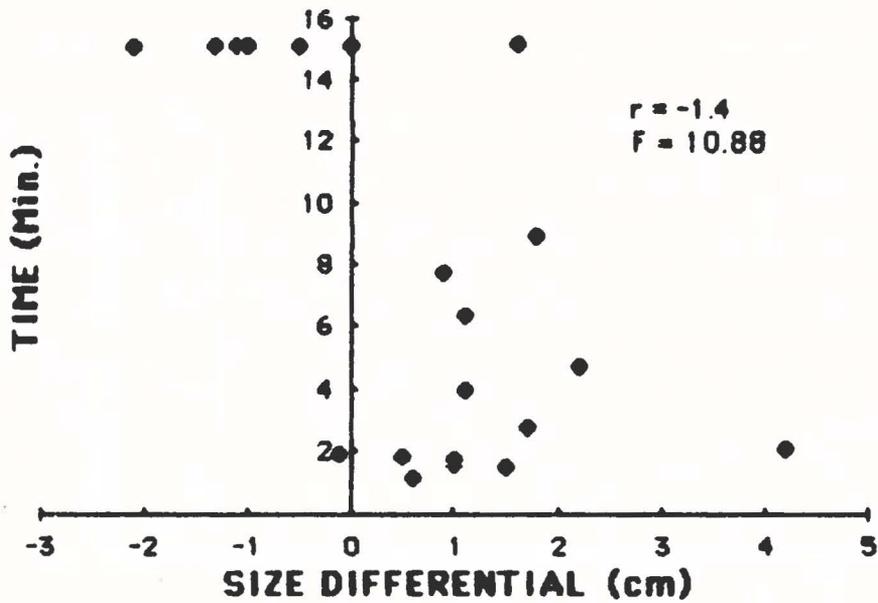


Figure 4. Temporal duration of defensive trials as a function of the size differential between the intruder and defender. $p |F| \ll .01$.

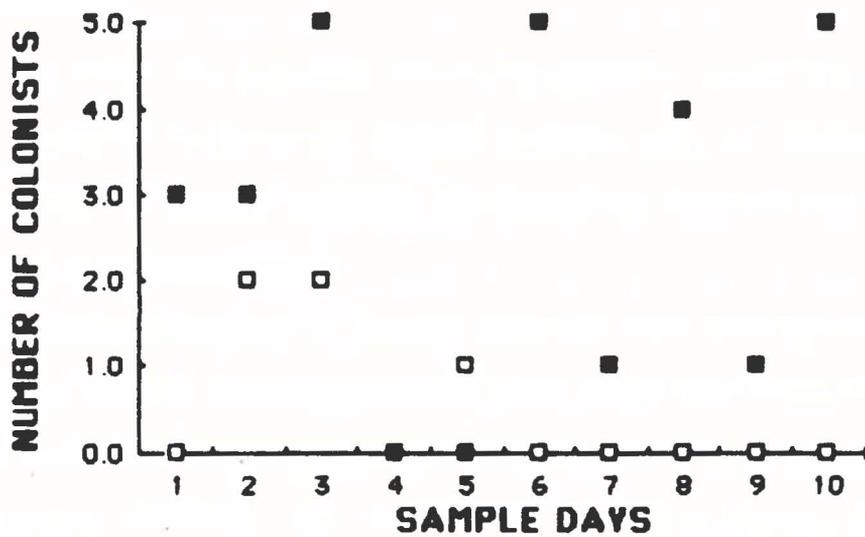


Figure 5. Recolonization rates for the inner and outer reef flats. Solid squares represent the inner reef flat and hollow squares represent the outer reef flat. Each value represents the total number of colonists from 30 burrows on each sampling day.

transplanted to large burrows in the outer reef flat region, only 7 were found in the burrows the following day. In both of these instances, the transplants were not replaced by other individuals, and it is assumed that they vacated the burrows, as opposed to have been displaced by other individuals.

In all trials the stimulus initiating agonistic behaviors by the defender appeared to be spine contact between the two individuals, although tube foot contact could not be accurately observed and cannot be ruled out as a stimulus also.

The echinoid burrows in the two sites differed from one another. The burrows found in the outer reef flat were larger than those found in the inner reef flat. In both areas the resident echinoids were engaged in excavating burrows, as evidenced by white areas in the calcium-carbonate substrate directly beneath the oral surface of the resident individual. The burrows in the outer reef-flat region were long and gutter-shaped in cross section, whereas the majority of those in the inner reef-flat region were shorter and more tubular in cross-section (Figure 3a and 3b). The mean burrow length in the outer reef flat was 18.7 cm (S.E. = 1.31), in the inner reef flat the mean burrow length was 7.8 cm (S.E. = 0.98). The sizes (length and width) of burrows from each habitat are given in Appendix 5.

DISCUSSION

Differences in burrow defense between individuals of Echinometra mathaei inhabiting outer reef-flat habitats and those inhabiting inner reef-flat regions were apparent. Outer reef-flat inhabitants exhibited rigorous burrow defense, whereas inner reef-flat inhabitants did not.

There appears to be no flexibility in defensive behaviors of outer reef-flat individuals transplanted to the inner reef flat. Because of the extreme nature of the selective pressures present on outer reef flats (Denny et al., 1985), it is not surprising that rigid behavioral repertoires would be strongly favored in this habitat. There was a low degree of burrow defense among inner reef-flat inhabitants transplanted to the outer reef flat. Possibly inner reef-flat individuals will only defend burrows that they have (at least partially) excavated. On the other hand, outer reef-flat inhabitants will defend burrows into which they were recently transplanted.

Large burrows appear unsuitable for habitation by small echinoids in outer reef-flat regions; when they are transplanted into large burrows, they commonly leave them within 24 hours; larger echinoids do not. Small individuals inhabiting the outer reef flat were unable to retain burrows in the presence of larger individuals (Figure 4), which is consistent with the results of previous research on other echinoid species (Grünbaum et al., 1978; Maier and Roe, 1983).

The results of this investigation support the suggestions of other investigators that Echinometra mathaei is represented by two

types (Tsuchiya and Nishihira, 1984), or two distinct species (Mortensen, 1943; Russo, 1977). On Guam, E. mathaei have similar coloration patterns to the types described by Tsuchiya and Nishihira, (1984), appear to conform to the size differentials proposed by Russo (1977), and segregate by habitat types as described by Russo (1977) and Tsuchiya and Nishihira (1984). My investigation suggests that there are behavioral differences between two types of E. mathaei occupying different habitats on the same reef platform. Echinometra oblonga (or Type B individuals described by Tsuchiya and Nishihira, 1984) occur in outer reef flats and on reef margins and exhibit strong tendencies for burrow defense. Echinometra mathaei (apparently equivalent to the Type A individuals described by Tsuchiya and Nishihira, 1984) occur in quieter, inner reef-flat areas and do not defend burrows as commonly as outer reef-flat inhabitants. This difference in behaviors may have a genetic basis, although long-term transplant experiments and other research are needed to substantiate this claim.

Biting was not observed in any of the trials conducted in this investigation. In all trials, resident echinoids remained relatively affixed to the burrow walls (with the oral surface in contact with the burrow walls). Conspecific biting was noted during the collection and storage of experimental individuals.

The Piti reef platform is subject to heavy fishing pressures (M. Molina, pers. comm.) which have probably reduced the populations of potential echinoid predators. Nonetheless, there are many predators

known to prey on echinoids in this area. Some of these include fishes such as balistids, monacanthids, tetraodontids, diodontids, scarids and labrids, crustaceans (principally diagenid hermit crabs), and occasional shorebirds. Because of the close proximity of these two habitats (and the high degree of mobility characteristic to echinoid predators), it is unlikely that echinoid predator populations vary significantly between these habitats. Thus, a reduced risk of predation could easily be a selective advantage favoring the evolution of burrowing behaviors (as suggested by Grünbaum et al., 1978), but it is unlikely that differing predatory pressures account for the observed differences in echinoid defensive behaviors.

Echinoid inhabitants of outer reef-flat platforms are subject to a number of environmental factors which would strongly favor the evolution of rigorous burrow defense. Such factors include vulnerability to dislodgement by wave energy and high current velocities (Grünbaum et al., 1978; Maier and Roe, 1983), a dense, patchily distributed food resource such as algal drift material (Russo, 1980). In quieter, inner reef-flat areas, vigorous burrow defense may not be an adaptive strategy for echinoids because of several environmental factors inherent to these habitats. In such (inner reef-flat) areas there is a reduced susceptibility to dislodgement by waves or high velocity currents. The quantity of algal drift material is probably lower than on the outer reef-flat (as reported by Russo, 1977) because of decreased current speeds, a loss of laminar flow and the

lack of fleshy algae inhabiting the inner reef-flat region acting as sources of algal drift material.

The Caribbean echinoid Echinometra lucunter has also recently been shown to segregate by habitat type; distinct morphological differences are found between individuals occurring in the two habitats (Lewis and Storey, 1984). This habitat segregation appears to occur in environments similar to those in which E. mathaei types segregate. The occurrence of such habitat segregation on coral reefs in the Indo-West Pacific and Caribbean could provide insights into genetic and evolutionary processes present in all tropical coral reefs.

CONCLUSIONS

Burrow defense was investigated in the rock-boring echinoid Echinometra mathaei occurring in different habitats on a single reef-flat platform on Guam. Defensive behaviors are compared between individuals from the two habitats.

Outer reef-flat inhabitants more commonly defend resident burrows than do inner reef-flat inhabitants. Outer reef-flat individuals defend their burrows by pushing intruders out of the burrow, and vigorous spine waving is uncommon. Individuals from the inner reef flat commonly limit burrow defense to spine waving and pivoting 90° inside their burrows. Distinct ecological factors inherent to these environments could help to make burrow defense advantageous to outer reef-flat inhabitants, yet disadvantageous for inner reef-flat forms.

Echinoids transplanted from the outer reef flat to the inner reef flat do not exhibit plasticity in defensive behaviors. Defensive plasticity is exhibited by inner reef-flat forms; they do not defend burrows when transplanted to the outer reef flat.

In the outer reef flat, defenders were unable to retain burrows from larger intruders, although defenders were commonly able to evict intruders that were smaller than themselves.

Recolonization rates in the inner reef flat are five times higher than on the outer reef flat. Burrow colonists in the two areas are of similar sizes. The colonists in the two habitats ranged in size from 1.6 cm MTD to 4.9 cm MTD.

These findings support previous investigations that claim Echinometra mathaei segregates by habitat-type and that individuals occurring in each habitat are sufficiently different from one another to be classified as distinct species (Mortensen, 1921).

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APPENDIX I

Data from defense trials conducted on naturally occurring burrow holders. Trials 1-54 were conducted in the outer reef-flat habitat (H1). Trials 55-108 were conducted in the outer reef flat. Duration of the encounter is given in (0.1) minutes. MTD_d refers to the maximum test diameter (cm) for the defender. MTD_i refers to the maximum test diameter (cm) for the intruder. Distance displaced is measured in centimeters. A period (.) represents missing values

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD_d</u> | <u>MTD_i</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|---------------------------|---------------------------|---------------------------|
| 1 | 3.66 | 5.7 | 5.7 | 13 |
| 2 | 5.51 | 5.4 | 5.9 | 25 |
| 3 | 3.33 | 5.1 | 5.0 | 3 |
| 4 | 3.83 | 4.9 | 5.0 | 5 |
| 5 | 1.00 | 4.6 | 4.7 | 4 |
| 6 | 15.00 | 4.5 | 5.4 | 5 |
| 7 | 1.80 | 4.6 | 4.5 | 4 |
| 8 | 1.50 | 4.6 | 5.2 | 7 |
| 9 | 0.16 | 5.6 | 5.2 | 2 |
| 10 | 15.00 | 2.9 | 3.0 | 2 |
| 11 | 1.00 | 3.3 | 2.6 | 4 |
| 12 | 1.50 | 2.8 | 3.2 | 3 |
| 13 | 15.00 | 3.5 | 3.5 | 2 |
| 14 | 15.00 | 3.0 | 3.2 | 3 |
| 15 | 15.00 | 3.6 | 2.8 | 0 |
| 16 | 1.40 | 3.0 | 2.8 | 2 |
| 17 | 0.75 | 3.7 | 3.8 | 2 |
| 18 | 6.33 | 3.2 | 3.8 | 3 |
| 19 | 3.58 | 5.8 | 4.4 | 10 |
| 20 | 4.66 | 5.5 | 4.5 | 12 |
| 21 | 3.83 | 5.0 | 3.7 | 6 |
| 22 | 1.53 | 5.1 | 3.0 | 11 |

APPENDIX 1 (Cont.)

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD₀</u> | <u>MTD₁</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|------------------------|------------------------|---------------------------|
| 23 | 3.02 | 4.9 | 4.3 | 11 |
| 24 | 1.92 | 4.7 | 4.3 | 5 |
| 25 | 1.83 | 4.9 | 3.0 | 6 |
| 26 | 2.25 | 5.9 | 2.6 | 3 |
| 27 | 0.62 | 5.2 | 2.6 | 6 |
| 28 | 0.36 | 1.9 | 2.5 | 1 |
| 29 | 0.08 | 4.5 | 1.8 | 7 |
| 30 | 1.83 | 2.5 | 2.0 | 3 |
| 31 | 0.07 | 3.3 | 2.0 | 2 |
| 32 | 3.66 | 2.2 | 2.5 | 2 |
| 33 | 1.83 | 2.7 | 2.0 | 2 |
| 34 | 2.56 | 2.8 | 2.3 | 2 |
| 35 | 0.50 | 2.7 | 1.9 | 2 |
| 36 | . | 2.2 | 2.4 | 1 |
| 37 | 1.53 | 5.8 | 1.5 | 3 |
| 38 | 1.12 | 5.0 | 1.3 | 3 |
| 39 | 15.00 | 4.8 | 1.3 | 0 |
| 40 | 0.41 | 6.1 | 2.3 | 6 |
| 41 | 2.30 | 5.4 | 1.2 | 4 |
| 42 | 1.70 | 4.8 | 2.0 | 3 |
| 43 | 2.35 | 5.6 | 2.4 | 3 |
| 44 | 6.00 | 4.9 | 2.3 | 11 |
| 45 | 4.20 | 5.1 | 1.5 | 5 |
| 46 | 3.33 | 3.2 | 1.5 | 4 |
| 47 | 1.05 | 3.0 | 1.2 | 4 |
| 48 | 1.66 | 3.2 | 1.3 | 4 |
| 49 | 2.50 | 3.9 | 0.8 | 5 |
| 50 | 0.82 | 2.7 | 1.2 | 2 |
| 51 | 4.83 | 3.9 | 1.1 | 2 |
| 52 | 1.08 | 4.3 | 1.2 | 1 |

APPENDIX 1 (Cont.)

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD_d</u> | <u>MTD_i</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|------------------------|------------------------|---------------------------|
| 53 | 2.58 | 3.4 | 1.4 | 3 |
| 54 | 1.33 | 3.8 | 1.2 | 2 |
| 55 | 15.00 | 4.8 | 4.7 | 0 |
| 56 | 15.00 | 5.0 | 4.9 | 0 |
| 57 | 15.00 | 5.3 | 5.1 | 0 |
| 58 | 15.00 | 5.2 | 5.0 | 0 |
| 59 | 4.00 | 5.0 | 4.8 | 1 |
| 60 | 15.00 | 5.2 | 4.8 | 0 |
| 61 | 2.00 | 4.9 | 4.7 | 4 |
| 62 | 15.00 | 4.9 | 4.6 | 0 |
| 63 | 15.00 | 4.8 | 4.6 | 0 |
| 64 | 15.00 | 5.0 | 4.0 | 0 |
| 65 | 15.00 | 4.6 | 3.7 | 0 |
| 66 | 1.66 | 5.6 | 3.3 | 5 |
| 67 | 2.00 | 4.1 | 3.2 | 6 |
| 68 | 15.00 | 5.2 | 3.1 | 0 |
| 69 | 15.00 | 5.8 | 2.7 | 0 |
| 70 | 15.00 | 5.3 | 3.1 | 0 |
| 71 | 15.00 | 4.7 | 4.2 | 0 |
| 72 | 15.00 | 4.7 | 2.6 | 0 |
| 73 | 2.00 | 2.8 | 2.6 | 4 |
| 74 | 3.33 | 2.1 | 2.2 | 8 |
| 75 | 15.00 | 3.2 | 2.7 | 0 |
| 76 | 3.42 | 3.1 | 1.7 | 2 |
| 77 | 3.33 | 4.3 | 1.6 | 4 |
| 78 | 6.33 | 3.5 | 2.6 | 6 |
| 79 | 1.00 | 2.6 | 2.8 | 3 |
| 80 | 1.83 | 2.8 | 1.1 | 3 |
| 81 | 1.33 | 3.1 | 2.6 | 4 |
| 82 | 1.67 | 1.9 | 1.8 | 3 |
| 83 | 2.33 | 2.8 | 2.1 | 2 |

APPENDIX 1 (Cont.)

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD_d</u> | <u>MTD_i</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|------------------------|------------------------|---------------------------|
| 84 | 0.75 | 2.1 | 1.8 | 1 |
| 85 | 1.92 | 2.5 | 1.1 | 2 |
| 86 | 2.33 | 3.2 | 2.0 | 3 |
| 87 | 1.83 | 2.8 | 2.3 | 4 |
| 88 | 4.33 | 3.2 | 0.8 | 3 |
| 89 | 2.17 | 4.8 | 0.8 | 8 |
| 90 | 3.50 | 3.6 | 1.8 | 10 |
| 91 | 15.00 | 4.2 | 3.8 | 0 |
| 92 | 15.00 | 4.2 | 2.8 | 0 |
| 93 | 15.00 | 3.9 | 3.6 | 0 |
| 94 | 15.00 | 3.8 | 5.1 | 0 |
| 95 | 15.00 | 3.4 | 4.7 | 0 |
| 96 | 15.00 | 3.9 | 4.7 | 0 |
| 97 | 15.00 | 1.7 | 1.6 | 1 |
| 98 | 15.00 | 4.6 | 1.5 | 2 |
| 99 | 15.00 | 2.8 | 3.6 | 1 |
| 100 | 15.00 | 3.9 | 2.8 | 0 |
| 101 | 0.91 | 3.2 | 2.7 | 3 |
| 102 | 15.00 | 3.2 | 2.8 | 0 |
| 103 | 4.17 | 2.6 | 1.4 | 9 |
| 104 | 4.75 | 3.9 | 3.2 | 9 |
| 105 | 2.62 | 4.1 | 3.8 | 8 |
| 106 | 15.00 | 4.6 | 3.2 | 0 |
| 107 | 15.00 | 4.6 | 4.6 | 0 |
| 108 | 15.00 | 3.4 | 2.8 | 0 |

APPENDIX 2

Data from transplant trials. Duration of the trial is given in (0.1) minutes. MTD_d refers to the maximum test diameter (cm) for the defender. MTD_i refers to the maximum test diameter (cm) for the intruder. Distance displaced is measured in centimeters.

INNER REEF FLAT INDIVIDUALS

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD_d</u> | <u>MTD_i</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|---------------------------|---------------------------|---------------------------|
| 112 | 15.00 | 2.7 | 2.8 | 1 |
| 113 | 15.00 | 2.6 | 2.8 | 0 |
| 114 | 15.00 | 3.2 | 3.4 | 0 |
| 115 | 15.00 | 2.6 | 2.5 | 0 |
| 116 | 15.00 | 3.5 | 3.3 | 0 |
| 117 | 15.00 | 3.4 | 3.7 | 0 |
| 118 | 15.00 | 3.4 | 3.2 | 2 |
| 135 | 15.00 | 3.5 | 3.5 | 5 |
| 136 | 15.00 | 3.8 | 3.5 | 3 |
| 137 | 15.00 | 5.9 | 5.2 | 0 |
| 138 | 15.00 | 2.8 | 2.7 | 0 |
| 139 | 15.00 | 3.8 | 2.8 | 0 |
| 140 | 15.00 | 5.2 | 4.9 | 0 |
| 141 | 15.00 | 4.4 | 3.8 | 0 |
| 142 | 15.00 | 3.6 | 3.2 | 2 |

OUTER REEF FLAT INDIVIDUALS

| | | | | |
|-----|------|-----|-----|---|
| 122 | 3.00 | 3.9 | 4.6 | 2 |
| 123 | 1.83 | 4.6 | 4.0 | 4 |
| 124 | 3.33 | 5.6 | 4.8 | 6 |
| 125 | 1.83 | 5.2 | 4.4 | 4 |
| 126 | 7.50 | 5.2 | 4.6 | 6 |
| 127 | 1.83 | 4.7 | 4.3 | 3 |
| 155 | 0.83 | 5.1 | 5.1 | 3 |

APPENDIX 2 (Cont.)

APPENDIX 2 (Cont.)

OUTER REEF FLAT INDIVIDUALS (Cont.)

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD_d</u> | <u>MTD_i</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|------------------------|------------------------|---------------------------|
| 156 | 15.00 | 5.3 | 5.1 | 2 |
| 157 | 3.67 | 3.1 | 3.2 | 7 |
| 158 | 1.33 | 3.1 | 2.8 | 3 |
| 159 | 0.38 | 3.0 | 2.9 | 2 |
| 160 | 3.67 | 3.5 | 3.2 | 8 |
| 161 | 2.42 | 2.6 | 2.8 | 4 |
| 162 | 1.70 | 5.2 | 5.0 | 2 |
| 163 | 2.23 | 4.8 | 4.5 | 4 |

APPENDIX 3

Size trials conducted on outer reef-flat inhabitants. Duration of the trial is given in (0.1) minutes. MTD_d refers to the maximum test diameter (cm) for the defender. MTD_i refers to the maximum test diameter (cm) for the intruder. Distance displaced is measured in centimeters.

| <u>Trial No.</u> | <u>Trial Duration</u> | <u>MTD_d</u> | <u>MTD_i</u> | <u>Distance Displaced</u> |
|------------------|-----------------------|---------------------------|---------------------------|---------------------------|
| 119 | 15.00 | 2.4 | 4.5 | 0 |
| 120 | 1.07 | 4.0 | 3.4 | 3 |
| 121 | 15.00 | 3.9 | 5.2 | 0 |
| 128 | 4.63 | 5.3 | 3.1 | 12 |
| 129 | 8.83 | 6.0 | 4.2 | 9 |
| 130 | 2.00 | 5.0 | 0.8 | 2 |
| 131 | 2.67 | 5.5 | 3.8 | 4 |
| 132 | 7.67 | 4.6 | 3.7 | 6 |
| 133 | 6.33 | 5.2 | 4.1 | 7 |
| 134 | 15.00 | 5.8 | 4.2 | 0 |
| 144 | 15.00 | 4.0 | 5.1 | 0 |
| 145 | 1.67 | 4.6 | 3.6 | 3 |
| 146 | 1.83 | 4.3 | 4.4 | 4 |
| 147 | 15.00 | 4.8 | 4.8 | 0 |
| 148 | 1.75 | 4.2 | 3.7 | 6 |
| 149 | 15.00 | 3.6 | 4.6 | 0 |
| 150 | 1.42 | 5.2 | 3.7 | 4 |
| 151 | 1.50 | 4.0 | 3.0 | 5 |
| 152 | 3.87 | 5.7 | 4.6 | 9 |
| 153 | 15.00 | 3.4 | 3.9 | 0 |

APPENDIX 4

Echinometra mathaei recolonization rates for inner and outer reef-flat habitats. Each value represents the total number of colonists in 30 empty burrows. Samples were conducted every three days for a period of 30 days.

| Sample Number | Outer Reef Flat | Inner Reef Flat |
|---------------|-----------------|-----------------|
| 1 | 0 | 3 |
| 2 | 2 | 3 |
| 3 | 2 | 5 |
| 4 | 0 | 0 |
| 5 | 1 | 0 |
| 6 | 0 | 5 |
| 7 | 0 | 1 |
| 8 | 0 | 4 |
| 9 | 0 | 1 |
| 10 | 0 | 5 |