

**Associations between three irregular urchins  
and cone-and-funnel topography in a  
tropical soft-bottom community**

by

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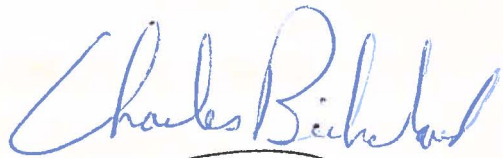
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Habitat characteristics and densities of three species of irregular urchins were measured in Apra Harbor, Guam. The densities of *Maretia planulata*, *Metalia dicrana* and *Fibularia ovulum* in the microhabitat defined as cone-and-funnel topography were analyzed at 10, 20 and 30 m in depth. Urchins were sampled to measure densities for each depth with respect to characteristics of the cone-and-funnel topography including: depth of anoxic layer, sediment granulometry, sediment organics and mean distance between sediment cones. Secondly, growth rates for *Maretia planulata* were measured along a sediment gradient. Sediment organic content was also analyzed. Laboratory experiments demonstrated that growth rates for *Maretia planulata* were not significantly different at 10, 20 and 30 m depths, but densities for each species, organic content and cone densities were significantly different across the depth gradient. Densities of *Maretia planulata* and *Metalia dicrana* densities were more similar across depth gradients and not between microhabitats. *Fibularia ovulum* densities were generally grouped with respect to either the cone microhabitat or the funnel microhabitat. Physical differences (organic content, anoxia, and sediment granulometry) and other niche partitioning may regulate densities of these macroinvertebrates along the depth gradient.

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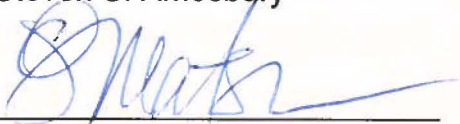
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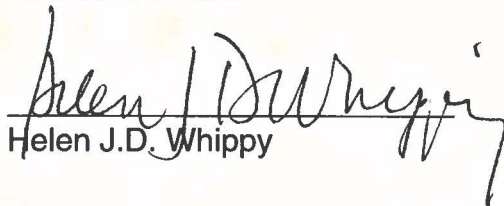
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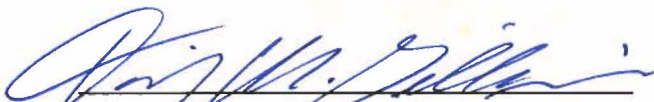


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## INTRODUCTION

Growth, distribution and mortality studies for echinoderms have focused mainly on holothurians and regular echinoids (McPherson 1965; Ebert 1975, 1982; Taki 1978). Spatangoid urchins have been largely overlooked in studies of benthic community structure or associations with other infauna (Woodin 1976). Because of their occasional abundance and role as marine bioturbators, they may be locally important in community function (Commito 1985; Tsuchiya 1986; Norris 1991). Community and population structure for infaunal macrobenthic organisms can be better understood when more basic ecological information is obtained. I examined density-related associations between *Maretia planulata* (Lamarck) (Echinodermata: Spatangidae), *Metalia dicrana* Clark (Echinodermata: Brissidae) and *Fibularia ovulum* Lamarck (Echinodermata: Clypeasteridae) and the “cone-and-funnel topography” (Fig. 1) in Apra Harbor, Guam. In addition, interactions between the echinoids and other macrofauna, the association with the microhabitat defined as cone-and-funnel topography and the roles these bioturbators play in the community are documented.

Bioturbation and sediment restructuring by benthic infauna affect sediment chemistry, particle sorting, spatial distribution of organic matter and the transfer of reduced compounds from depth to the oxygen-rich surface sediments (Myers 1977; Brenchley 1981; Mooi 1990). Organisms known to burrow and form cones include thalassinid shrimp (e.g., *Callinassa* sp.) and large worms (e.g., *Arenicola* sp.). Production of feces has been used to estimate sediment turnover rates (Suchanek 1985). Rates of fecal deposition for *Callinassa* were between 500 and 2500 pellets/burrow/day (approximately 4 - 20 g), containing between 2.9 and 3.7% organic carbon (Waslenchuk et al.



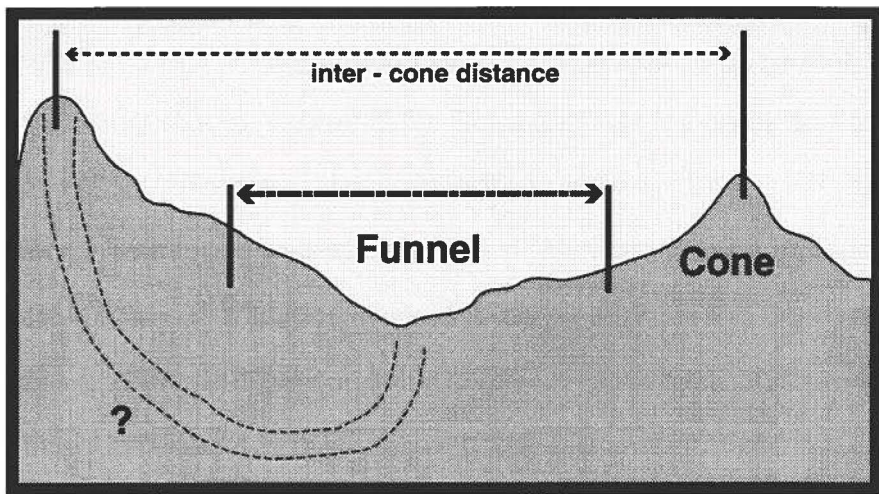
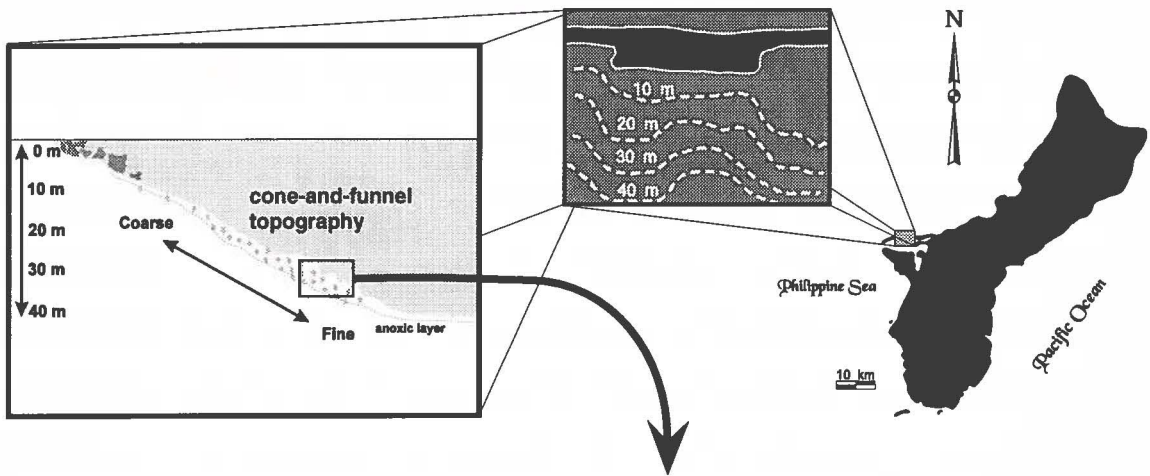


Figure 1. Study site.

1983). Although the bioturbated topography in Apra Harbor has not been traced to a specific organism, this major bioturbator creates a large number of cones and funnels.

Most research on infaunal, nearshore, macrobenthic organisms has been done in temperate regions (Moore 1958; Ambrose 1984; Warwick et al. 1987; Ferrand et al. 1988). Population densities of the major infauna have been used in evaluating trophic structure interactions and distribution patterns in some communities. Associations among some burrowing species and sessile tube dwellers and microinfauna have been described (Eckman 1985; Kristensen 1985), but associations between burrowing urchins and other macroinfauna have been largely overlooked.

The distribution of many populations is influenced by sediment granulometry (Rhoads and Young 1970; Birkeland 1971; Ferber and Lawrence 1976; Myers 1977; Telford and Mooi 1986; Telford et al. 1985, 1987; Mooi 1990). Differences in sediment particle size distribution can affect marine soft-bottom macrofaunal communities in various ways, such as the depth of habitable sediment and the energetic requirements for movement and ventilation.

Sediment processing and burrowing activities within these communities may alter redox profiles, spatial distribution patterns and the pattern of deposition of organic-rich particles. Yager et al. (1993) demonstrated that biogenic "negative relief" (funnels) can affect fluid dynamics and therefore cause patchy accumulation of organic-rich flocs. This can significantly influence the food supply of the macroinfaunal organisms that live near or in these areas of increased bottom relief. Yager demonstrated that a funnel's effectiveness in collecting particles depends on the diameter, depth, fluid density, bed roughness and particle density. These factors vary in importance in affecting the

number of particles that can be removed from a moving column of water. Yager also hypothesized that some organisms may build a better funnel under a given flow field.

If deposition to the funnels increases the availability of food material, do other organisms increase in abundance? Are there associations between biogenic relief and other deposit feeding organisms? Increased relief created by another organism's burrow (cone-and-funnel) may influence populations of associated infauna along a gradient of increasing relief. The density of the cone-and-funnel topography that dominates the study site at Apra Harbor, was found to increase along the depth gradient. In this study, I investigated growth, population density and microhabitat associations among three species of irregular urchins that dominate the macro-infaunal population, *Maretia planulata*, *Metalia dicrana* and *Fibularia ovulum*, and measured the topographical relief created by an infaunal worm. Associations between a cone-and-funnel building organism and other cohabitants have not been investigated previously from this point of view.

*Maretia planulata* and *Metalia dicrana* (Fig. 2) are irregular urchins that exhibit pronounced secondary bilateral symmetry (Lawrence 1987). These two species fall under the feeding mode category of irregular urchins that have no Aristotle's lantern but which occupy deeper substrata in the habitat. They feed with specialized tube feet, oral spines and a body morphology that assists in directing food-laden sediment into the mouth.

*Metalia dicrana* are characterized by a more globiferous test and comparatively shorter spines than *Maretia planulata*. *Maretia planulata* exhibit an arched, low test that is flattened dorsally and is less heart-shaped than other members of the genus (Mortensen 1951). Spines of *Maretia planulata* are

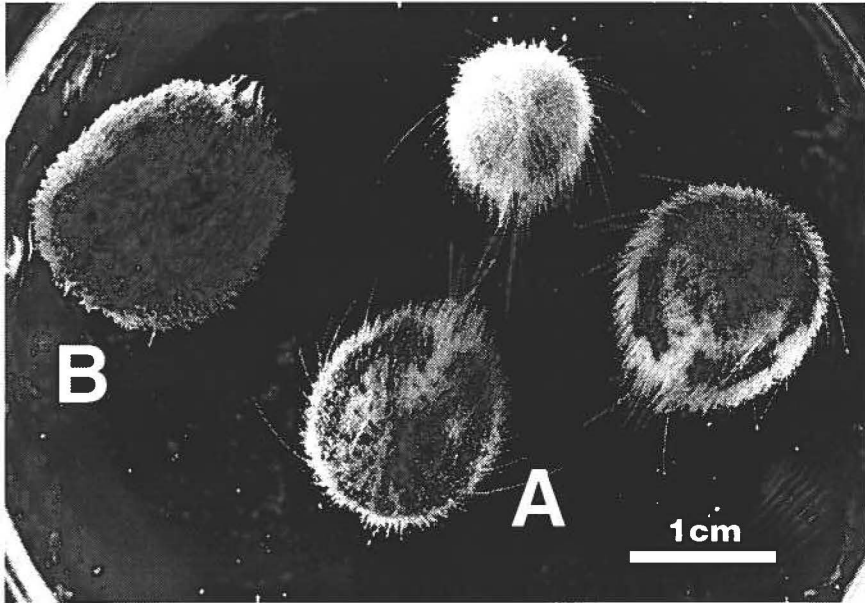


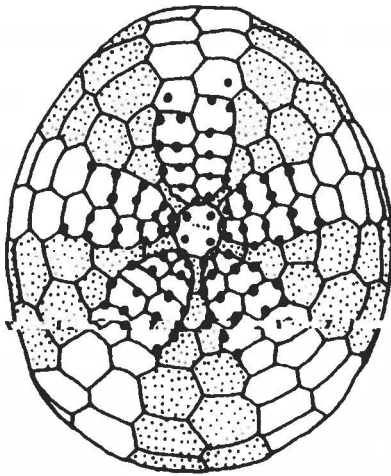
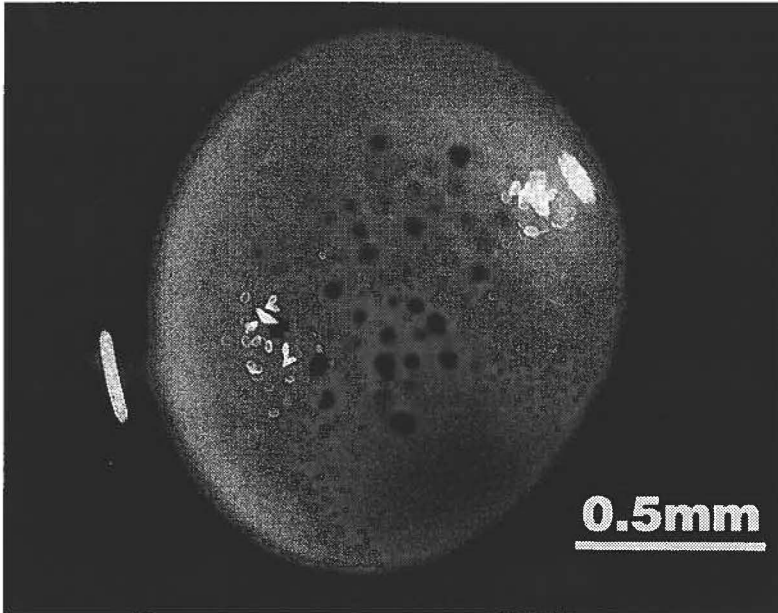
Figure 2. A) *Maretia planulata*. B) *Metalia dicrana*.

comparatively long, curved backward and distally thorny. *Metalia dicrana* individuals possess dark, globose pedicellaria while *Maretia planulata* individuals do not. Some *Fibularia* also possess globiferous pedicellaria. This is unique within the clypeasteroids, in that only members of the genus *Fibularia* possess globiferous pedicellaria (Lawrence 1987). Also, variability within the species has been noted by others (Mortensen 1951). At the study site in Apra Harbor, Guam, many individuals of *Maretia planulata* have distinct brownish bands along the top edges of their tests. Other individuals are completely white. In the Indian Ocean, individuals are primarily white or pinkish white (Mortensen 1951).

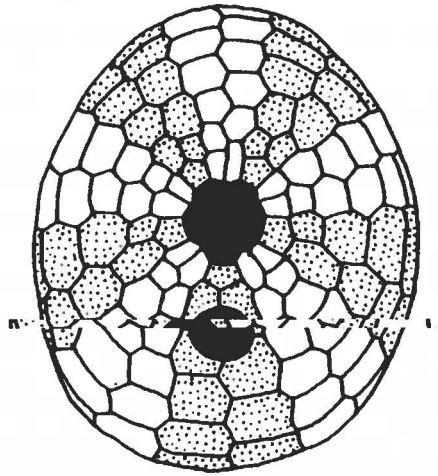
*Maretia planulata* can be found from the intertidal zone down to a depth of 60 m throughout the waters of the tropical and sub-tropical Indo-West Pacific, East Africa (Mozambique to Madagascar), Fiji, the Gilbert Islands, the Mariana Islands, and Sagami Bay, Japan. *Metalia dicrana* occurs in the South China Sea, the Malay region, the Philippines, Fiji and Samoa (Mortensen 1951).

*Fibularia ovulum* is one of the smallest echinoid species either extant or extinct (Fig. 2a). Individuals range in size from 0.2 to 5.0 mm in diameter (Mooi 1987). The general body form (ovoid) of *F. ovulum* is not consistent with the generally unidirectional movement of burrowing, irregular echinoids.

In order to describe this habitat and the biological interactions within it, I measured sediment cone densities at 10, 20 and 30 m, the distribution of *Fibularia ovulum*, *Maretia planulata* and *Metalia dicrana* in and near the sediment cones and whether this association related to sediment grain size, anoxia or density of the cones at each depth. I presupposed the following null hypotheses regarding these issues. There will be a significant difference in the depth to the anoxic layer for the three depths. There will be a significant



**Aboral**



**Oral**

Figure 2a. *Fibularia ovulum* (sketch from Mooi 1987).

difference in the density of the cones among the three depths. There will be significant differences in the relative densities of these three species of urchins within the cones and the funnels. I proposed that *Fibularia ovulum* would be associated with the cones, specifically with increasing depth and cone density. Also, I proposed that *Maretia planulata* and *Metalia dicrana* would be more associated with the funnels across the depth gradient. These associations between *Maretia planulata*, *Metalia dicrana* and *Fibularia ovulum* and the sediment cones were analyzed by measuring densities for each species of urchin per unit volume of sediment and depth. Secondarily, I quantified growth for *Maretia planulata* in the lab along the depth gradient and analyzed sediment organics at 10, 20 and 30 m depths. Growth of *Maretia planulata* as well as sediment organics were measured over a 60 day period. The null hypothesis was that there would be significant differences in the growth rate for *Maretia planulata* kept in the sediment from the different depths. Also, I hypothesized that there would be a significant difference in the relative amounts of organic matter within the substratum at each depth.

## MATERIALS AND METHODS

### Preliminary Distribution of *Maretia planulata* and *Metalia dicrana*, Sediment Analysis and Growth

The study area is located south of Glass Breakwater (a large, ~ 2 miles long, boulder and cobble, man-made jetty) inside the northern perimeter of Apra Harbor, Guam (Fig. 1). Wave action is erratically light to heavy, largely due to the passing of ships. A coral community now exists on the boulders that occur down to approximately 7.5 m. Cobbles and smaller boulders can be found below the coral zone, from 12 to 15 m out into the harbor basin.

A transect was established due south (normal to the shore) from the shore. Sediment samples were collected at 1.5 m depth intervals along the transect (down to 15 cm in the sediment) with a 50 cc syringe made into a core sampler. Four sieves (2.0, 0.850, 0.600, 0.425 mm), were used to fractionate the 100 g dry samples.

Sediment anoxia was estimated by placing a graduated Plexiglas™ panel into the sediment at each of 10, 20 and 30 m depths. Ten replicates were conducted for each depth. All sediment was removed from the down slope side of the panel and the depth of the sediment anoxic layer was recorded. Sediment anoxia was estimated to begin where the sediment was darkest and did not change over the next 2 to 3 cm.

A preliminary survey of the size range of *Maretia planulata* was conducted on 21 - 33 individuals collected in a framed sieve at each 1.5-m depth increment. Total length (longest test length) for each urchin was measured according to Chesher (1968) i.e., along the axis from the periproct to anterior tip of the test.



Growth experiments were conducted using only *Maretia planulata*. *Metalia dicrana* and *Fibularia ovulum* did not live for extended periods in the lab sediment tanks. Laboratory growth experiments were conducted from April 17 to June 18, 1992. Bulk sediments were collected in the field from 10, 20 and 30 m (down to 15 cm) and placed in separate partitions within laboratory tanks equipped with a flow-through seawater system. Urchins from depths of 18 to 25 m were used for this experiment. Urchins were randomly selected and nine groups of ten urchins were placed into the appropriate cages for each depth treatment. Cages consisted of a prefabricated plastic box with lid. The boxes and lids were constructed of perforated plastic (2 x 12 mm holes) and measured 20 cm x 30 cm x 45 cm. Cages were filled 15 cm deep with sediment, the lid was attached and the cages were placed into the sediment partition that corresponded to the appropriate depth/sediment treatment. Each depth treatment contained sediment collected from that depth in the field. Sediment samples were collected from each cage, at the beginning of the experiment (day 1) and at the end (day 60), and analyzed for organic content. Growth was also recorded for the urchins.

Organic content was measured on sediments collected from laboratory treatments and the field. Samples were collected on day 1 and day 60 for both treatments. Triplicate sediment samples from laboratory cage experiments and field sediment samples were collected using a core sampling device, as above. All sediment samples were dried at room temperature, treated with 20% HCl to dissolve carbonates, and the remaining material was collected onto preweighed glass fiber filters, dried, weighed, combusted at 500°C for 2 h, and reweighed. The weight loss after combustion was used as an estimate of LOI (loss on ignition).

Sediment Cones and Associations by *Maretia planulata*,  
*Metalia dicrana* and *Fibularia ovulum*

The densities of *Maretia planulata*, *Metalia dicrana* and *Fibularia ovulum* per unit volume of sediment were quantified at depths of 10, 20 and 30 m. These depths were chosen to correspond to the depth regime where all three species co-occurred. Densities between the cones were quantified by positioning the 0.5 m<sup>2</sup> quadrat into the sediment a known depth (15 cm) and hand excavating all sediment into sieves for counting of individuals. A volumetric comparison of the density of urchins (0.5 m<sup>2</sup> X 15 cm vs. volume of cone) in cone vs. funnel volumes of sediment was then conducted. Cone volume was defined as any pile of sediment having a shape that is obviously biogenous in origin (possessing fecal castings or having the appearance of recent excavation) and was more than 10 cm in height above the surrounding substratum. Funnel volume was defined as the area between cone bases. Individuals of *Fibularia ovulum* were collected using a core sampling tube (100 cc). These samples were collected from the apex of the cones and from the funnel areas surrounding the cones.

Ten cone and ten funnel samples for each depth were obtained along a transect established at isobaths of each depth. The cones used in this analysis were chosen randomly along the transect using a random number table and selected from either side of the transect (odd = left, even = right). The 0.5 m<sup>2</sup> quadrat was placed around each cone and cone height and base diameter were measured. The cones were then excavated by hand and all urchins identified and counted *in situ*. Cone densities were determined by measuring the distance between the apex of a cone and the apex of the next closest cone for 15 to 30 cones selected randomly. The mean distance between the apices was then used to estimate cone density at each depth.

## RESULTS

### Preliminary Distribution of *Maretia planulata* and *Metalia dicrana*, Sediment Analysis and Growth

During preliminary surveys, *Maretia planulata*, *Metalia dicrana* and *Fibularia ovulum* were encountered and identified as range extensions for the three species and new records for Guam (Kerr et al. 1992). Results of the sediment size analysis at each depth are shown in Figure 3. Mean number of individuals per 0.5 m<sup>2</sup> was found to be significantly greater ( $F_{[1,69]}=33.735^{***}$ ) for *M. planulata* than *M. dicrana*. Mean densities of *Fibularia ovulum* were found to be higher than *Maretia planulata* or *Metalia dicrana* at all depths.

The Mean size of *Maretia planulata* also increased significantly ( $F_{(0.025)[1,236]}=5.405$ ) with depth (Fig. 4). A significant difference in organic content of sediment was found along the depth gradient ( $p>0.005$ , Table 1). The sediment organic content in the lab samples for each depth increased. While in the field samples, LOI did not change. The depth, site and day interaction were found to be significantly different at the  $p=0.043$  level. All other sources of variation were found to be significant below the 0.005 level. Depth, time and site are plotted against amount of organic material lost on ignition (Fig. 5). Depth to the sediment anoxic layer was 0.8 cm ( $\pm 0.1$  SD) for 10 m, 1.7 cm ( $\pm 0.01$  SD) for 20 m and 5.1 cm ( $\pm 0.5$  SD) for 30m.

Although sediment organics were significantly different for the three depth treatments on day 1, they were not found to be significantly different on day 60 in the lab. Lab trials demonstrated that growth rates, over a 60 day period, were the same for individuals of *Maretia planulata* grown in 10 m, 20 m and 30 m depth sediment (Fig. 6). The slopes of the regressions calculated

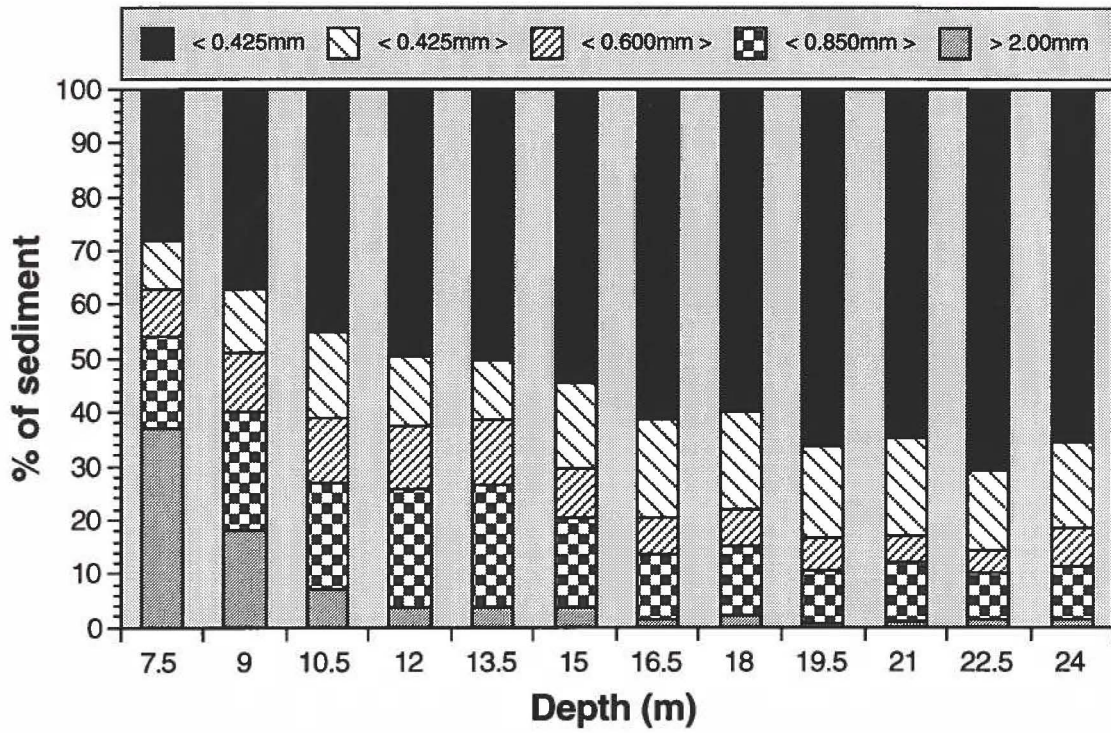


Figure 3. Results of sediment size analyses.

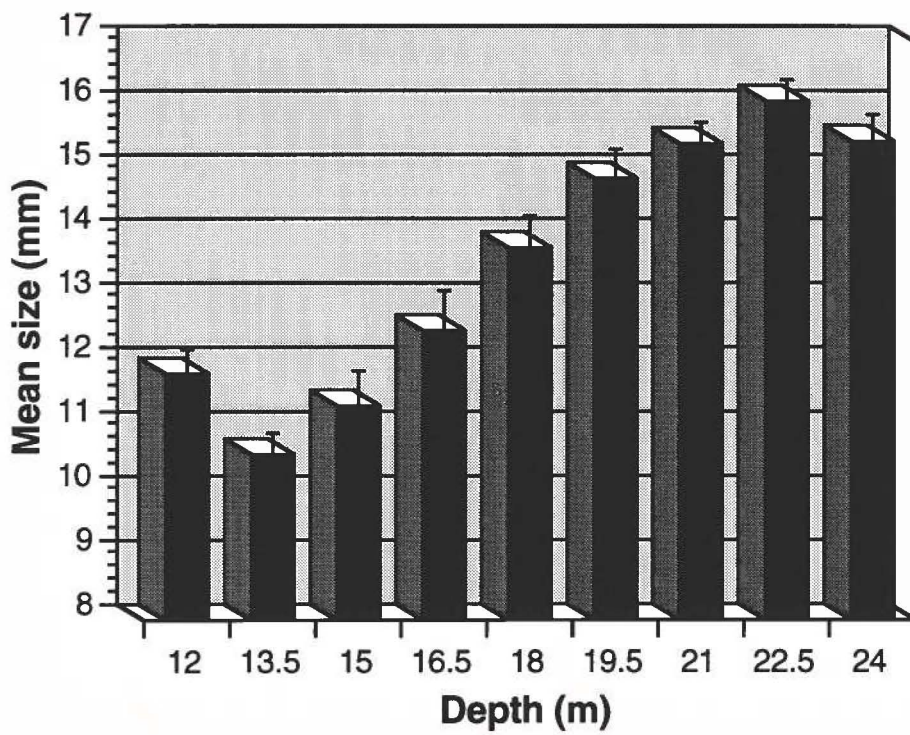


Figure 4. Mean size of *Maretia planulata* from 12 to 24 m in depth.

Table 1. ANOVA results for organic analysis

Source of Variance	DF	MS	F	P
Depth	2	0.034	89.407	<0.005
Site	1	0.019	51.758	<0.005
Day	1	0.022	58.307	<0.005
Depth•Site	2	0.001	3.457	0.048
Depth•Day	2	0.006	15.325	<0.005
Site•Day	1	0.018	46.767	<0.005
Depth•Site•Day	2	0.001	3.591	0.043

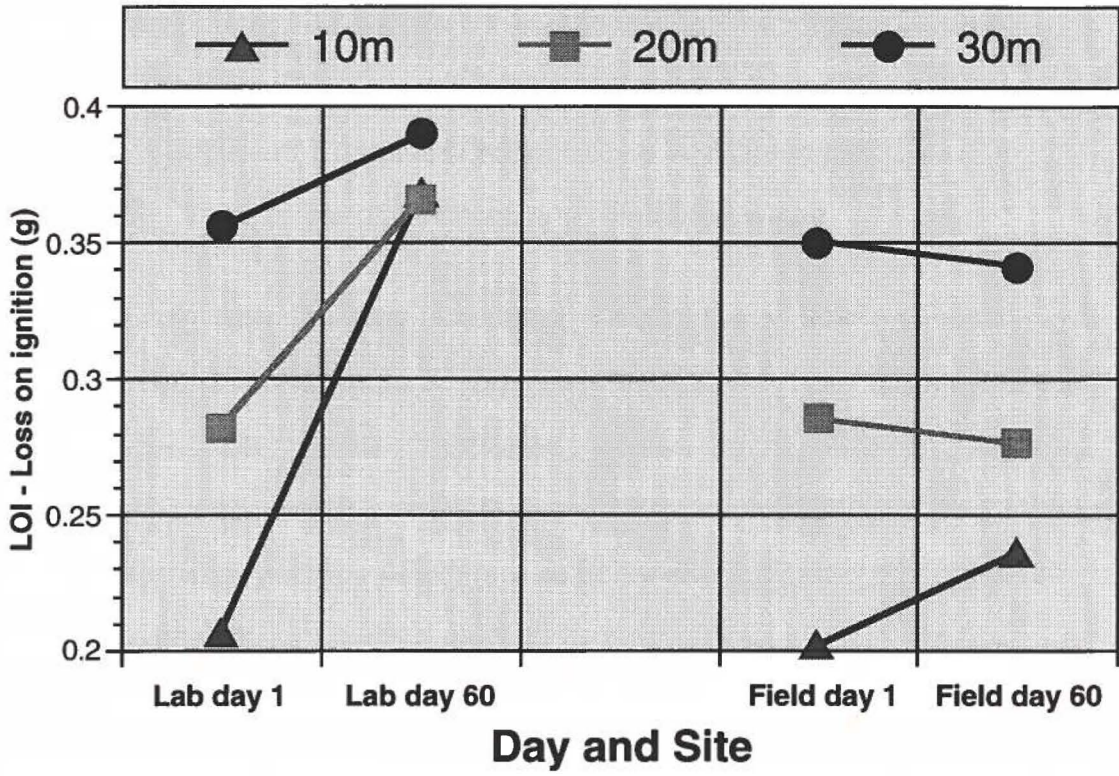


Figure 5. Depth vs. time and site for sediment organics.

for growth within each treatment (10 m, 20 m and 30 m sediment) were not found to be significantly different using ANCOVA ( $F_{[7,141]}=1.199$ ,  $p>0.25$ ). Initial and final mean sizes for individuals of *Maretia planulata* were not found to be significantly different among the three different sediment types (ANOVA).

Sediment Cones and Associations by *Maretia planulata*,  
*Metalia dicrana* and *Fibularia ovulum*

Results from the analysis of the density of the sediment cones at each depth can be found in Figure 7. One-way ANOVA was used to determine if the densities were significantly different between depths. The distances between cones were used to estimate densities for each depth (Fig. 7) and these data support that the mean sediment cone density is significantly different among depths ( $F_{(0.001)[2,90]}=78.2$ ,  $p<0.001$ ).

Mean number of *Fibularia ovulum*, *Metalia dicrana* and *Maretia planulata* for each depth and microhabitat can be inferred from Figures 8, 8a and 8b. Densities for each species of echinoid were analyzed using the Games and Howell multiple comparison test (Sokal and Rohlf 1981). Some densities for the three species of urchins were found to be not significantly different at the 95% level. Densities for *Maretia planulata* and *Metalia dicrana* were found to be more stratified within each depth and densities for *Fibularia ovulum* were found to be more stratified across the cone or the funnel microhabitats.



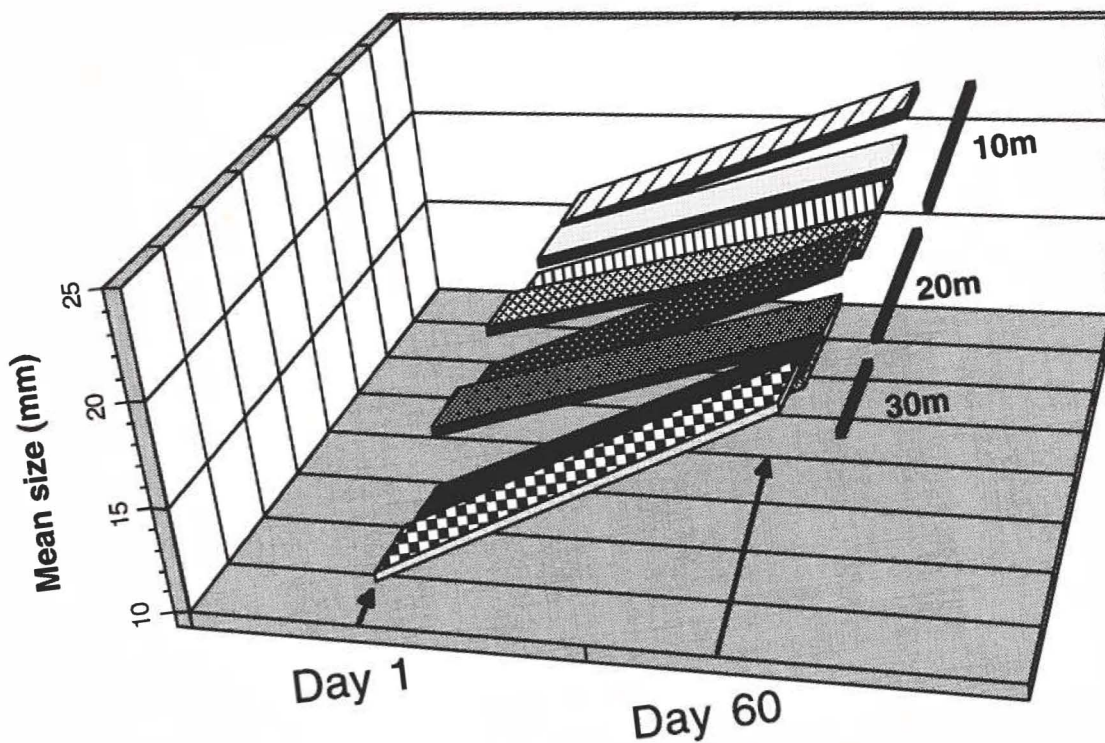


Figure 6. Mean growth in lab for *Maretia planulata* for 60 days in 10, 20 and 30 m sediments.

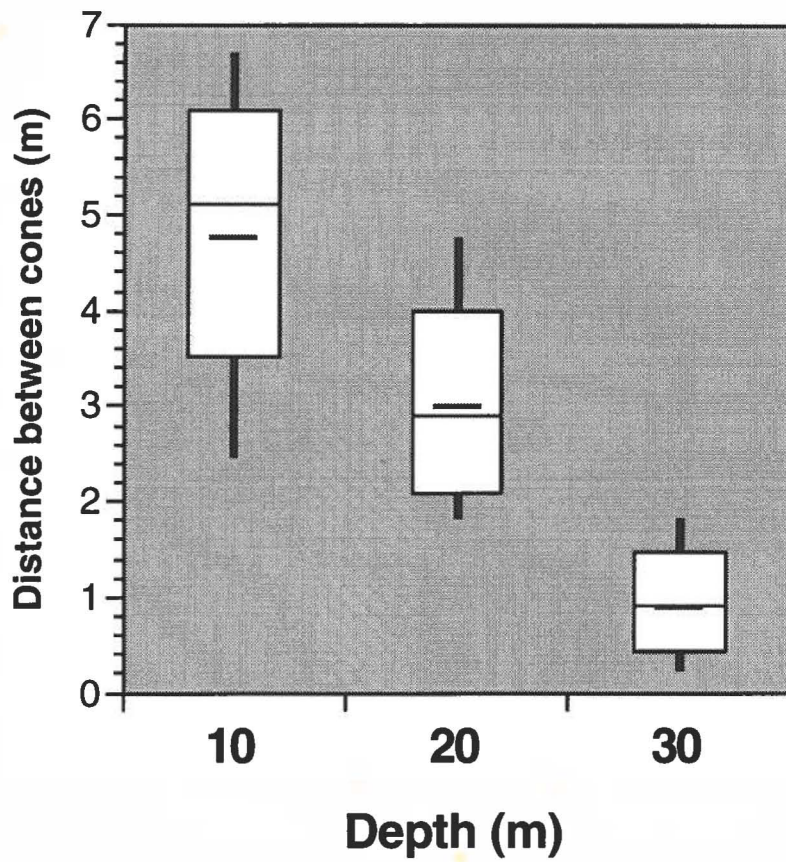


Figure 7. Mean distance between cones for 10, 20 and 30 m depths. Mean (small horizontal line), median (large horizontal line) and quartiles (stems).

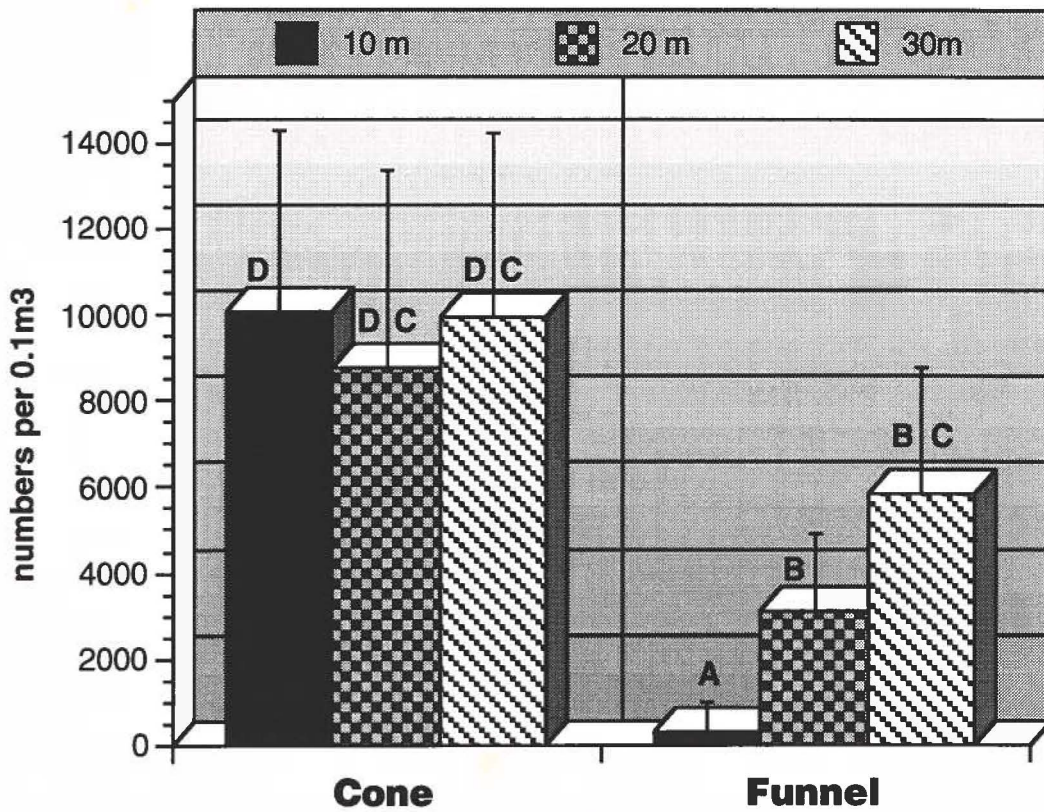


Figure 8. Mean numbers ( $\pm 1$  SD) of *Fibularia ovulum* per 0.1m<sup>3</sup> at each depth and in both microhabitats. Matching letters indicate that the densities are not significantly different at the 95% level using Games and Howell multiple comparisons test.

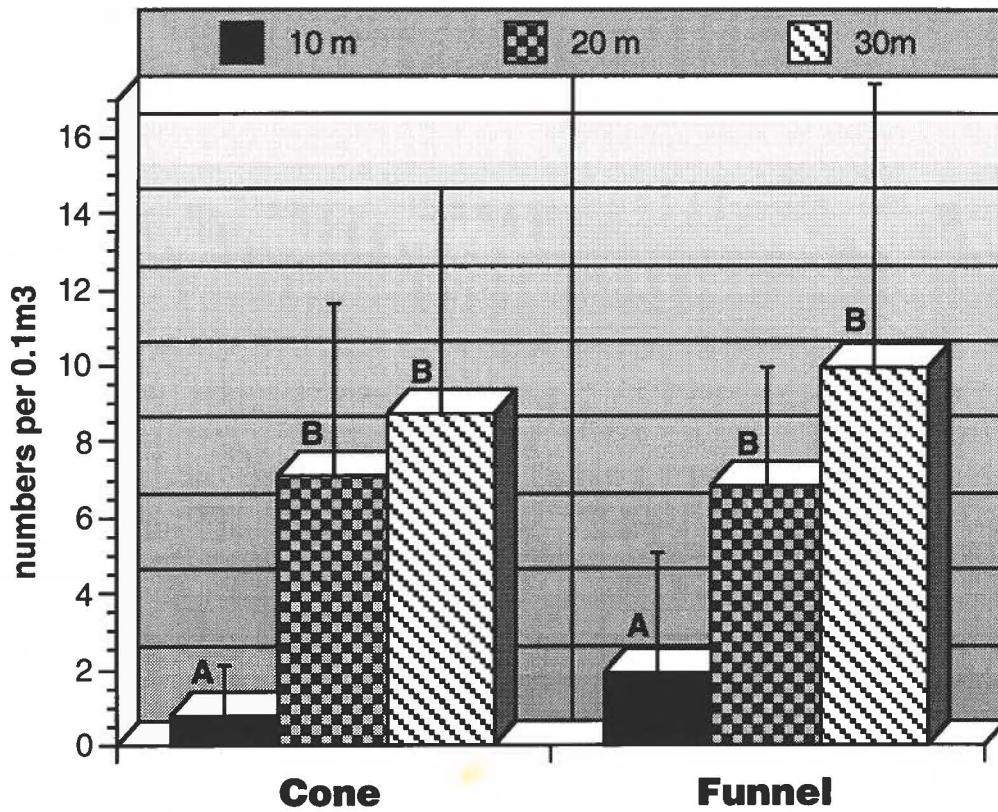


Figure 8a. Mean numbers ( $\pm 1$  SD) of *Metalia dicrana* per 0.1m<sup>3</sup> at each depth and in both microhabitats. Matching letters indicate that the densities are not significantly different at the 95% level using Games and Howell multiple comparisons test.

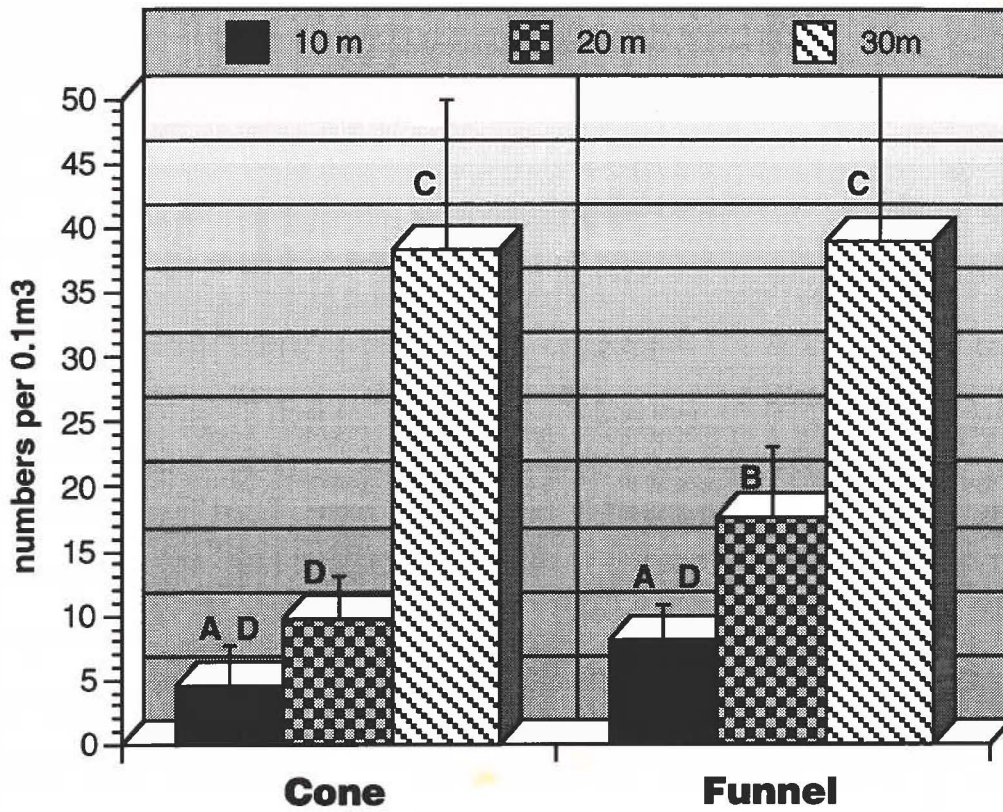


Figure 8b. Mean numbers ( $\pm 1$  SD) of *Maretia planulata* per  $0.1\text{m}^3$  at each depth and in both microhabitats. Matching letters indicate that the densities are not significantly different at the 95% level using Games and Howell multiple comparisons test.

## DISCUSSION

### Preliminary Distribution of *Maretia planulata* and *Metalia dicrana*, Sediment Analysis and Growth

The preliminary work demonstrated that the irregular urchin, *Maretia planulata*, is found in greater abundance than *Metalia dicrana*, within Apra Harbor, Guam. Tsuchiya et al., (1989) studied the distribution of shallow subtidal macrobenthic animals at Sichang Island, Thailand (a similar site), and showed a different distribution of *M. planulata* with respect to another infaunal irregular urchin, *Brissus latecarinatus*, and other species found there, including *Metalia dicrana*. Densities of *M. planulata* at Sichang Island were determined to be “extremely low”. Only two other species of infaunal echinoids have been found throughout the present study. The densities of these two species are very low compared to *Maretia planulata* or *Metalia dicrana*. Only one individual of *Clypeaster reticulatus* has been found and individuals of *Fibularia ovulum* are found primarily near and among the fecal castings of the burrow-forming organism in Apra Harbor. *F. ovulum* is a very small echinoid (<2.0 mm length) and is therefore unlikely to compete directly with *Maretia planulata* for sediment resources (R. Mooi, pers. comm., California Academy of Sciences).

The site investigated by Tsuchiya et al., (1989) contained nine species of urchins. Six species of urchins overlapped with *B. latecarinatus* in position along the transect and five species were found within the sediment. These data suggest that at Sichang Island the greater number of species of infaunal echinoderms may affect the densities of both *M. planulata* and *M. dicrana*.

Sediment size and composition of sediment at both Sichang Island and Apra Harbor study sites were found to be similar (Choonhabandit and Tsuchiya 1989).

Sediment particle size range is an important regulating factor in the distribution of these two species. A correlation was found between depth, particle size and population density of both species (Fig. 3). Both *Maretia planulata*, *Metalia dicrana* and *Fibularia ovulum* exist within the same general habitat, yet differences in the distribution of the three species were found. Abundances for these urchins may be regulated by a minimum or maximum sediment size, organic content or water depth. Studies have shown that sediment size and organic content are generally correlated (Levinton et al. 1984; Sanders 1968). Feeding efficiency and therefore growth, within the sediment, may be differentially affected along the sediment size gradient (Fig. 4). Differences in morphology (such as spine and/or test morphometrics) and energetic requirements may also be an important factor in determining the distribution of these two species in the shallower depths.

Sediment surface irregularities caused by macrobenthic burrowers such as *B. latecarinatus*, *M. planulata* and *M. dicrana* have been proposed as regulating factors in communities such as Sichang Island (Tsuchiya et al. 1986) and benthic communities in general (Dayton 1984). *M. planulata* was observed to be more active in disturbing the sediment at the present study site than *Metalia dicrana* or *Fibularia ovulum*. *Metalia dicrana* was found to be less mobile and inhabited generally deeper areas within the sediment. Individuals of *Fibularia ovulum* were found near the surface of the sediment and generally inhabited sediment near the tops of the sediment cones. Bioturbation by these three species at Apra Harbor may affect community structure. Organisms that

are unable to recruit, because of disturbances produced by the other species, have been found to be excluded from similar habitats (Woodin 1976; Roberts, Suchanek and Wiseman 1981; Branch and Pringle 1987; Sutherland 1990).

Figure 5 shows that the day 1 sediment organics for 10, 20 and 30 m depth treatments were found to be different along a depth gradient. By day 60, the sediments had equilibrated and the resulting organic contents were approximately the same. In the field, organic content for the three treatments were again different along a depth gradient. But after 60 days, these sediments did not reach an equivalent maximum in the amount of organic matter per gram of sediment.

Nowell, Jumars and Eckman (1980) demonstrated how animal tracks and fecal pellet production by infaunal residents influenced the entrainment velocity of marine sediments: biological activities caused either binding or destabilization of marine sediments. These biological effects are quite variable and depend on "organism density, sediment composition and the activities of co-inhabitants". A more recent study by Yager et al. (1993) investigated enhanced particle deposition to pits. In an experimental flume study, particle residence times, particle concentrations and particle fluxes to pits from the main flow were all significantly influenced by pit shape/size and flow regime. Therefore, compared to smooth flat benthic surfaces, a cone-and-funnel type benthos increases particle residence times and increases the surface area to which particles can adhere. Mean distance between cones decreases with depth (Fig. 7), therefore a greater amount of organic matter may become entrained in the deeper depths at the study site (Fig. 5 and Table 1). The data also suggested that an optimum pit density can be calculated to estimate a theoretical maximum amount of sediment entrainment for a specific benthic profile.



Sediment Cones and Associations by *Maretia planulata*,  
*Metalia dicrana* and *Fibularia ovulum*

As relationships between the various biotic factors are quantified, they provide a better understanding of organismal interactions at the population, community and ecosystem levels. Organismal associations in soft-bottom habitats have shown that the feeding mode of one organism may enhance the availability of food resources for other organisms (Johnson 1971; Yingst 1976; Connell 1983; Aller and Aller 1992). Meyers et al. (1987) demonstrated that interstitial meiofauna could be associated with the tubes and burrows of macrofaunal tube builders. The study showed how the traditional, simple 2-layer model of marine sediments (aerobic vs. anaerobic) cannot be used to entirely describe the structure of these complex communities. The proposed association between the tube builders and the associated meiofauna also demonstrates the potential complexity of these interactions (Driscoll 1975). The associations between *Maretia planulata*, *Metalia dicrana*, *Fibularia dicrana* and the sediment cones are evidence that such associations exist along a habitat gradient.

Densities of urchins for each depth and microhabitat were compared and charted from the Games and Howell data (Figs. 8, 8a and 8b). Densities for *Fibularia ovulum* are more similar within the microhabitats. Densities of *F. ovulum* in the cones at 10, 20 and 30 m were found to be not significantly different. In addition, densities within the funnels were found to be not significantly different at the 20 and 30 m depths. Densities for *F. ovulum* at 30 m (cones and funnels) and 20 m cones were also grouped at the 95% level. This was the only instance of trans-microhabitat similarity for densities of *F. ovulum*.

Games and Howell analysis for *Metalia dicrana* densities formed two distinct groups. Densities at 10 m for both the cone and funnel microhabitats and densities for both 20 m (cone and funnel) and 30 m (cone and funnel) were found to be not significantly different at the 95% level. Results from the analysis of *Maretia planulata* densities were similar to those of *Metalia dicrana* in that depth was more prominent as a grouping factor. Densities for *M. planulata* were found to be not significantly different for both extremes in depth, 10 m and 30 m, for both the cone and funnel microhabitats.

Figures 8, 8a and 8b show that there may be habitat specific characteristics that affect the mean densities of each species of urchin. Cone densities change significantly with depth (Fig. 7). As cone densities change with depth, relative particle flux may also change with depth. With increased numbers of cones per unit area, more particles can be removed from the water column and remain on the substratum. Field and laboratory experiments also demonstrated that although there are initially significant differences in sediment organic content, growth rates for *Maretia planulata* were not significantly different for each of 10, 20 and 30 m depth treatments (Norris 1993). These data suggest that these differences in organic content do not statistically correspond to increased growth rates for *Maretia planulata* (Fig. 6).

Habitat modifications caused by the sediment cones may facilitate the assemblages of urchins at the different depths. A positive relationship exists between the quantity of organic matter at the deepest habitat depth (30 m) and the number of sediment cones per unit area. Mean number of urchins peak between 20 and 30 m in depth (Norris 1991) and drops to zero between 35 and 40 m. At 25 m the habitat may be modified in a way that facilitates the existence of a maximum number of urchins (Valderhaug 1984).

Abundance and size distribution for *Maretia planulata* also suggest that densities of urchins may play a role in structuring these size classes. Maximum mean size may be differentially influenced at each depth by a combination of urchin density, organic content and sediment size/anoxia (Fig. 4). The habitat extremes, 7 and 40 m, may be sufficiently biologically and physically unfavorable to support the existence of the larger densities of *Maretia planulata* found at 25 m. Anoxia has been proposed as a potential factor in maintaining this distribution pattern (Mangum and Winkle 1973; Rosenberg et al. 1991). A shallow anoxic layer translates into less habitable sediment for aerobic organisms. The increasing depth to the anoxic layer, that characterizes the sediment in the middle depths, suggests that the larger number of urchins may be altering the sediment. The shallower depths have a shallower aerobic sediment layer and therefore less habitat space. Grab samples and exploratory dives also suggest that the deeper areas of Apra Harbor (40 - 50 m) are similar to the shallowest habitats (10 m) with respect to anoxia and densities of urchins.

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