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THE EFFECT OF LIFE HABIT
ON THE
PRESERVATION POTENTIAL OF ECHINOIDS

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ABSTRACT

Live (biocoenoses) and dead (taphocoenoses) populations of regular and irregular echinoids inhabiting shallow water environments of San Salvador and Lee Stocking Island, Bahamas (and elsewhere in the Caribbean) have been censused over the last five years to test Kier's (1977) hypothesis that the relatively poor fossil record of the regular echinoid is the result of taphonomic bias. In general, results reveal that distributions of living regular echinoids are not reflected by accumulations of their carcasses, while the reverse is true for irregular taxa: subfossil material is more often asssociated with living populations suggesting that irregulars may have relatively greater likelihood of preservation.

Population distributions of four regular echinoid taxa (*Diadema antillarum, Eucidaris tribuloides, Echinometra lucunter* and *Tripneustes ventricosus*) were systematically studied in reef and near-reef environments. Although these taxa are common components of the benthic fauna, the distributions of the biocoenoses were patchy. High abundance of living individuals (densities approaching 60/m^2) of *Echinometra* was not correlated with an increase in subfossil material even though previous work has indicated the remarkable durability of the corona relative to other regular echinoid taxa. *Tripneustes, Diadema* and *Eucidaris* occurred in lower abundances than *Echinometra* and were associated with limited amounts of skeletal remains >2 mm in size.

Shallow-burrowing irregular echinoids selected for study included two mellitid sand dollars (*Mellita quinquiesperforata* , *Leodia sexiesperforata*), and the spatangoid *Meoma ventricosa*. In contrast to the results obtained for regular echinoids, more subfossil material comprised the taphocoenoses, the majority of it occurring on the sediment surface: the latter observation suggesting that the shallow infaunal life mode does not guarantee that biostratinomic processes won't affect skeletal material.

Multivariate analyses of census data reveal that live echinoid distribution is likely related to substrate: the regular echinoids under study occurred on hard or rubbly substrates that inhibit burrowing, while the irregular echinoids occurred in soft substrates of clean carbonate sand. In Fernandez Bay, *Echinometra* and *Tripneustes* were most common closest to shore (between 0 m and 18 m from the shoreline), while *Diadema* and *Eucidaris* occurred farther out (between 28 m and 138 m). *Mellita* and *Leodia* occurred farthest from shore (between 46 m and 1566 m). However, echinoid carcasses do not reflect the same pattern: regular taxa, though rare, are restricted to the same areas in which living counterparts occur. Conversely, the irregular echinoid taphocoenosis has undergone some transport: carcasses possess a wider distribution than their living counterparts. Results of this study suggest that Kier's (1977) hypothesis, while essentially correct, requires modification: 1) Skeletal durability may be more important than life habit in determining preservation potential; 2) Regular echinoid fragments, although rare in the fossil record are useful tools for paleoenvironmental reconstruction based on the fidelity with which they reflect the distribution of a once-living fauna; 3) The poor fossil record of the regular echinoid may also be an artifact of taxonomic bias; finally, 4) As is the case with regular echinoids, exceptionally well-preserved assemblages of mellitid and shallow-burrowing spatangoids must be viewed as the result of extrinsic processes rather than intrinsic traits.

INTRODUCTION

In recent years, the utility of taphonomic field studies in enhancing our understanding of the fossil record has been demonstrated for many invertebrate and vertebrate groups following the pioneering studies of Schäfer (1972). Donovan (1991) provides an excellent review of this literature for many important fossil groups. Field and laboratory studies of taphonomy have historically been used to make predictions concerning preservation potential that may then be applied to the fossil record, and are generally subdivided into studies of decay rates and processes (see for example Meyer, 1971; Liddell, 1975; Plotnick, 1986; Allison, 1986, 1988; Allmon, 1985; Alexander, 1986; Kidwell & Baumiller, 1990; and Greenstein, 1991); or the relationship of live and dead assemblages (see for example the classic works of Cadée, 1968; Boucot, 1953 and Schopf, 1978 and more recent work by Davies *et al*, 1989a, 1989b and Kidwell & Bosence, 1991). More recently, field-based studies have demonstrated that different depositional environments produce distinct taphonomic signatures on subfossil material (for example Parsons, 1989; Meldahl & Flessa, 1990 and Staff & Powell, 1990a, 1990b). Results of the latter may then be applied to fossil material to maximize the information yielded by taphonomic data collected. Although the emphasis of each approach is different, these types of studies are similar in that they generate hypotheses based on observations in modern environments that may be tested using the fossil record. Here I work essentially in reverse: testing the hypothesis that a macroevolutionary pattern observed in the fossil record is predominantly the result of taphonomic bias by utilizing a comparative study between live and dead assemblages in modern marine environments.

Over the last three decades, research concerning the taxonomy and evolutionary history of echinoids has consistently revealed an important fact: more species of irregular echinoids have been described from fossils than have regular echinoids. Moreover, the number of specimens of fossil irregular echinoids far outnumbers that of regulars (Kier, 1977). Consequently, irregular echinoids outnumber regular echinoids in every stage beginning with the Aptian (mid-Cretaceous) after their apparent origination in mid-Jurassic time. Kier (1977) suspected that these differences in abundance and diversity were largely the result of taphonomic bias because the opposite pattern exists in modern marine

Table 1 -- An update of the data presented by Kier (1977). Numbers in parentheses are echinoid species described through 1969 as compiled by Kier (1977). I have compiled the number of new fossil and living species described in each order through 1990 by checking citations in the Zoological Record. Updated values are next to those in parentheses. To mitigate variation in stratigraphic resolution, Jurassic and Cretaceous stages have been combined at the series level.

Interval	Regular	Irregular	% of all species that are regular
Recent	(474) 491	(426) 469	(53) 51
Plio-Pleistocene	(63) 66	(220) 237	(22) 22
Miocene	(184) 192	(924) 971	(17) 17
Oligocene	(54) 61	(343) 356	(14) 15
Eocene	(301) 309	(1,014) 1,041	(23) 23
Paleocene	(25) 28	(83) 97	(23) 22
U. Cretaceous	(697) 719	(1137) 1191	(38) 38
L. Cretaceous	(292) 299	(321) 333	(44) 47
U. Jurassic	(421) 428	(99) 105	(81) 80
M. Jurassic	(328) 339	(114) 117	(74) 74
L. Jurassic	(127) 128	(11) 11	(94) 92

environments: there are presently more extant species of regular echinoids than irregular echinoids. An update of Kier's (1977) data reveals that this is still the case (Table 1). Kier further suggested the taphonomic bias to be the result of differences between irregulars and regulars in both life habit and skeletal durability. Regulars are epifaunal and, relative to many irregulars, have a fragile skeleton; irregulars are infaunal and generally have a more durable skeleton. Thus the contrast between the groups in the fossil record is the result of better preservation potential of irregular echinoids rather than a macroevolutionary phenomenon. Although this conclusion was presented 15 years ago and continues to serve as a working hypothesis for researchers interested in macroevolutionary patterns, paleoecologic reconstructions and echinoid taphonomy, no data to test this hypothesis have been presented.

If irregular echinoids are indeed more likely to be preserved than regulars, one would expect living assemblages of irregulars to be associated with larger accumulations of subfossil material -- carcasses in various states of degradation but nonetheless recognizable -- than living assemblages of regulars. Consequently, the distribution of irregular echinoid carcasses will reflect that of living populations, whereas the distribution of living populations of regular echinoids will not be paralleled by subfossil material. Nebelsick (1992) used regular and irregular echinoid fragments taken from bulk samples to delineate various facies in the Northern Bay of Safaga (Red Sea). Gordon & Donovan (1992) demonstrated the utility of regular echinoid fragments in delineating reef and near-reef facies exposed in the Pleistocene of Jamaica. These studies suggest that preservation of regulars may not be as tenuous as Kier suggested. The purpose of this study is to test Kier's (1977) hypothesis by systematically examining living and subfossil assemblages of irregular and regular echinoids in shallow reef and near-reef environments. Results suggest that populations of irregular echinoids are associated with more subfossil material than populations of regulars. However, when present, carcasses of regular echinoids more accurately reflect the distribution of their living counterparts than do carcasses of irregular echinoids. Although the taphonomic bias suggested by Kier is appparently at work in the environments studied, it may also be the result of taxonomic methodology: fragments of regular echinoids are potentially very useful tools for paleoenvironmental analysis.

STUDY SITES AND CENSUS METHODS

Fieldwork was based at three separate marine labs: The West Indies Laboratory, St. Croix, U.S.V.I., Caribbean Marine Research Center, Lee Stocking Island, Bahamas and The Bahamian Field Station, San Salvador, Bahamas. Localities were selected on the basis of their diverse and abundant populations of echinoids and the accessibility of reef and near-reef environments. Censuses of echinoid populations were conducted while using SCUBA at circular stations or along transects constructed in shallow water adjacent to the three islands.

St.Croix

Smuggler's Cove is located along the northeast coast of St. Croix and is protected from open ocean energy by a bank barrier reef. The area was selected because several reef and near-reef environments supporting populations of several different regular echinoid taxa are present within a relatively short distance. A 720 m transect line was constructed heading due North from the Smuggler's Cove dock (Fig. 1). At stations 60 m apart, a 1 m² quadrat was

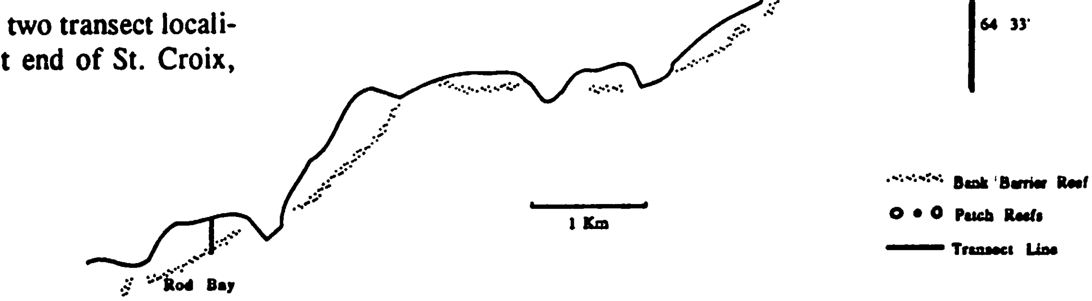

Figure 1 -- Location of the two transect localities established on the east end of St. Croix, U. S. Virgin Islands.

placed adjacent to the transect line; live and dead echinoids within the quadrat were counted and the condition of the dead material was recorded. The quadrat was then flipped over and another square meter was studied. This process was repeated ten times at each station resulting in a census of a 1 x 10 m² "column" situated perpendicular to the transect line and occurring every 60 m. Each column represented one census station and was numbered according to its distance from the beginning of the transect line. Thus 13 stations representing a total of 130 m² were examined along the transect. Echinoids were counted in a rocky shoreline zone, *Callianassa*-dominated sandy areas, *Thalassia*-dominated grassbeds, patch reef, reef tract and shallow (water depth 1.5 m) and deep (water depth 12 m) forereef environments. Water depth from shore to the reef tract in Smuggler's Cove reached a maximum of 6 m.

Populations of regular echinoids were observed to be particularly diverse and abundant in Rod Bay, the second census locality on St. Croix (Fig. 1). A 50 m transect was constructed and a population census was conducted using the methodology outlined above at stations 10 m apart; a total of 60 m² were examined. Within the transect, rocky shoreline, *Thalassia*-dominated seagrass beds, a zone of coral-algal rubble and very small patch reefs were encountered. Maximum water depth along the transect was 1 m.

Lee Stocking Island

Lee Stocking Island is one of the Exuma Cays, a chain of cays stretching over 160 km in the central portion of the Bahamas archipelago (Fig. 2). Two separate populations of irregular echinoids (*Leodia sexiesperforata* and *Meoma ventricosa*) were studied adjacent to Lee Stocking Island at Perry Deep Reef and a large sand plain due west of Children's Cay (Fig. 2). These echinoids were chosen because they burrow to relatively shallow depths in the substrate (Chesher, 1969; Bell & Frey, 1969) Because both populations were limited to environments dominated by substrates composed of calcareous sand, census methodology followed that of Scheibling (1982): stations 10 m in diameter (approximately 78.5 m²)were delineated on the bottom. The uppermost 10-15 cm of sand within the station was overturned to expose any live echinoids present. This depth exceeds the normal burrowing depth of both echinoids (Chesher, 1969; Bell & Frey, 1969; Salsman & Tolbert, 1965). Live and dead echinoids were counted and the condition of dead material was recorded. One station was censused at Perry Deep Reef in a water depth of 20 m. Two

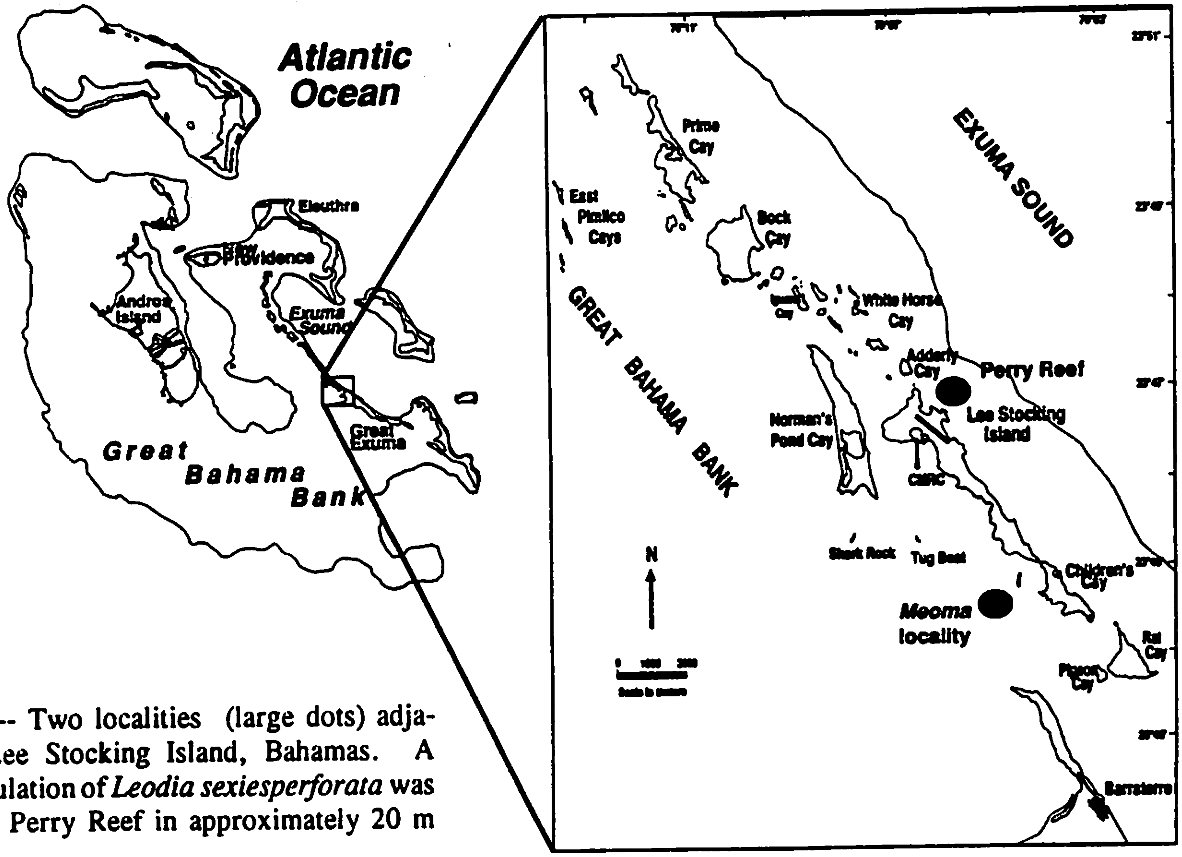

Figure 2 -- Two localities (large dots) adjacent to Lee Stocking Island, Bahamas. A small population of *Leodia sexiesperforata* was present at Perry Reef in approximately 20 m of water.

census stations were examined adjacent to Children's Cay in a maximum water depth of 3 m.

San Salvador

Census work was done at three sites along the western (leeward) margin of San Salvador (Fig. 3). All censuses were conducted using the same method described above for St. Croix although transect line length and intervals between census stations along the transect lines varied according to the dimensions of the site. In addition, any time a sand substrate was encountered, the sand within the quadrat was overturned to a depth of 10-15 cm to expose shallow-burrowing irregular echinoids.

Rocky Point.

A small bay, just south of Rocky Point, is known locally as "sand dollar beach" because of a population of abundant mellitid sand dollars (*Leodia sexiesperforata*) present in the sand. Since the time the census was conducted (June, 1988) the population has apparently been reduced for reasons that are as yet unknown. Determination of whether reduction of the population is part of a normal ecological cycle (e.g Salsman & Tolbert, 1965) is presently hampered by recent restrictions on access to the area. A 90 m transect line was constructed in the bay bearing due west from the shoreline. Census stations were placed at 10 m intervals to 30 m with additional stations censused at 60 and 90 m along the transect. The substrate underlying the entire transect area was clean carbonate sand. A total of 60 m^2 were examined in a maximum water depth of 3 m.

Fernandez Bay.

Two sites were chosen in Fernandez Bay, a large bay located along the central portion of San Salvador's west coast (Fig. 3). Collectively the sites represent a wide variety of substrates supporting populations of several regular and irregular echinoid taxa that were censused at relatively small intervals from shore to the edge of the shelf, where the bottom drops off abruptly to bathyal depths. Substrates encountered at the census sites included rocky shoreline, smooth bedrock overgrown with an algal "turf", coral rubble, patch reef, sand with sparse sea grass (dominated by *Thalassia*) and clean sand. All transect lines were constructed bearing due west from the shoreline. The sand plain that comprises the shelf offshore from Bamboo Point begins 46 m from shore at the base of a ledge of bedrock. Census stations were examined at

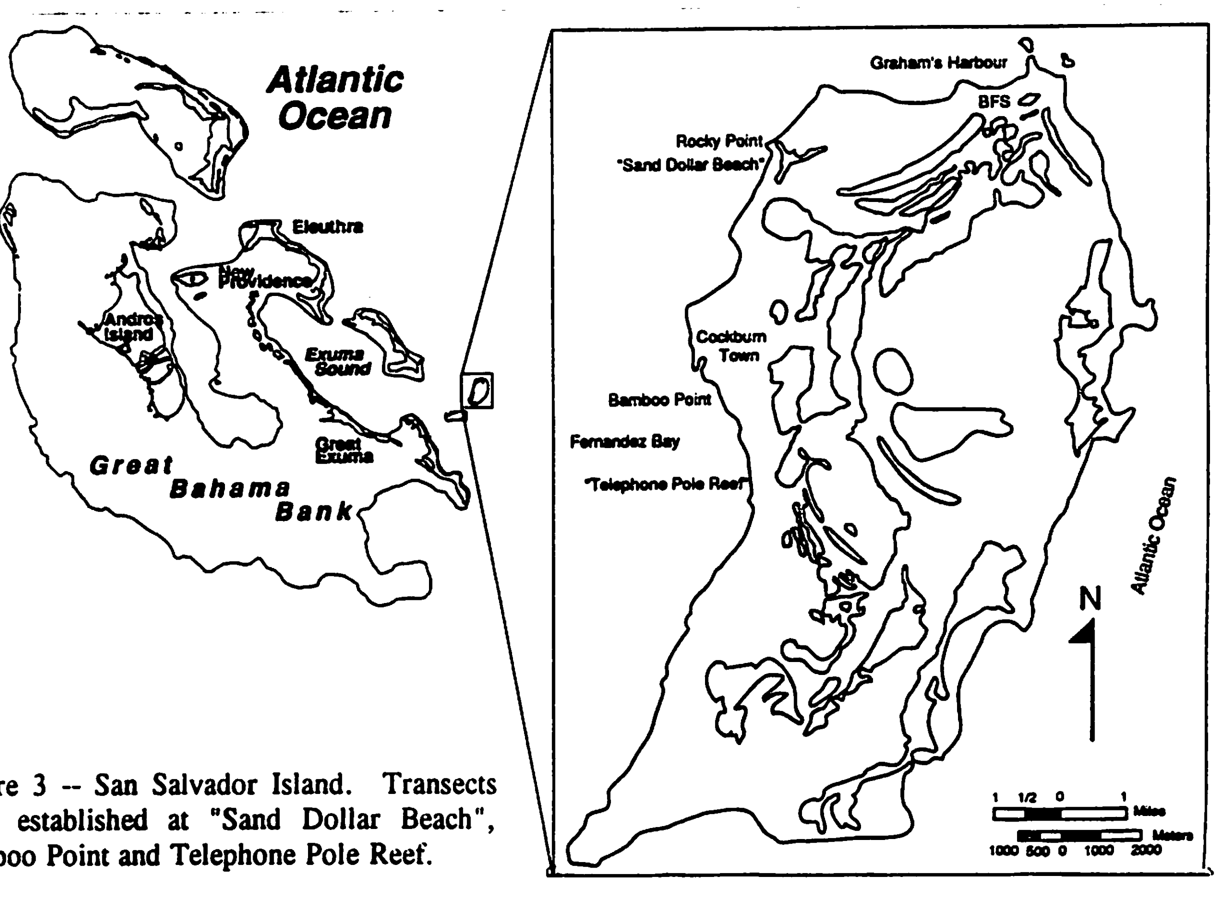

Figure 3 -- San Salvador Island. Transects were established at "Sand Dollar Beach", Bamboo Point and Telephone Pole Reef.

30 m intervals along the transect line to 106 m, and then at 50 m intervals to the edge of the shelf, 256 m offshore. A total of 60 m² were examined. At Telephone Pole Reef, a total of 130 m² were studied along a 168 m transect line that began at the mean high tide mark. Census stations were placed at 0 m, 4 m, 6 m, 8 m, 16 m, 18 m, 28 m, 38 m, 48 m, 78 m, 108 m, 138 m and 168 m along the transect line.

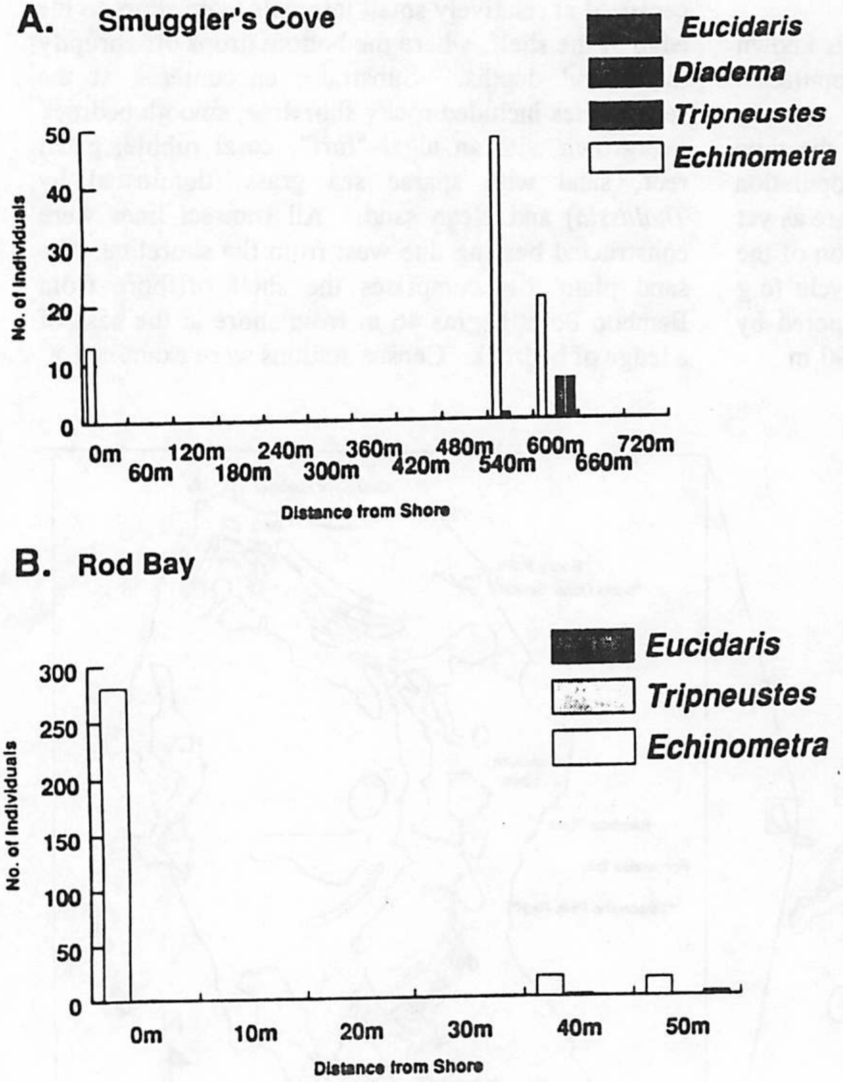

Figure 4 -- Results of censuses at Smuggler's Cove and Rod Bay. Only living echinoids were present at both localities. Note the number of individuals along the Y axis refers to the number occurring in 10 m² censused at each station.

RESULTS AND DISCUSSION

Regular Echinoids

Regular echinoids were observed along both transects offshore of St. Croix and at the Telephone Pole Reef locality on San Salvador. They were represented by four taxa in the environments studied: *Diadema antillarum* Philippi (Family Diadematidae), *Eucidaris tribuloides* Lamarck (Family Cidaridae), *Echinometra lucunter* Linnaeus (Family Echinometridae) and*Tripneustes ventricosus* Lamarck (Family Toxopneustidae). Although these echinoids are generally recognized as ubiquitous in shallow reef and near-reef environments (Kier & Grant, 1965), their distribution was patchy where populations were present. In general, little macroscopic subfossil material was associated with live populations. Raw data for all localities are presented in Appendix I.

St. Croix.

Few living echinoids, and no dead echinoids, were present in Smuggler's Cove and live echinoid occurrences were concentrated at three of the 13 transect stations. *Echinometra lucunter* were observed in low numbers (average of 1.3 per square meter) in five of the ten quadrats analyzed at transect Station 0 (Fig. 4A) along the rocky shoreline. No additional echinoids were observed until the reef tract was reached at Station 540, where live individuals of *E. lucunter* were again observed, in slightly higher numbers (average of 4.8 per square meter) in eight of the ten quadrats counted. One live *Tripneustes ventricosus* was also present. Highest echinoid diversity, but low abundance, occurred at Station 600, in the shallow forereef environment; *D. antillarum*, *E. lucunter* and *E. tribuloides* were all present. No intact or partial coronal material was observed anywhere along the transect.

Examination of the echinoid fauna in Rod Bay yielded comparable results (Fig 4B): no dead material was associated with living individuals. Live echinoids were present at three of the six transect stations analyzed. Relatively high numbers of live *Echinometra* were present in all 10 of the quadrats analyzed at Station 0, averaging 28.1 per square meter. One *Tripneustes* was also present. Individuals of *Echinometra* occurred, in low abundance (average of 1.9 per square meter), in five of the ten quadrats studied at Station 40; two *Tripneustes* were present in one quadrat. Finally, echinoids were present on a small patch reef encountered at Station 50. Low numbers of *Echinometra* (average of 1.7 per square meter) were counted in five of the ten quadrats, while two *Eucidaris* were observed in each of two quadrats.

San Salvador.

Regular echinoids exhibited a patchy distribution along the transect constructed at Telephone Pole Reef (Fig. 5).

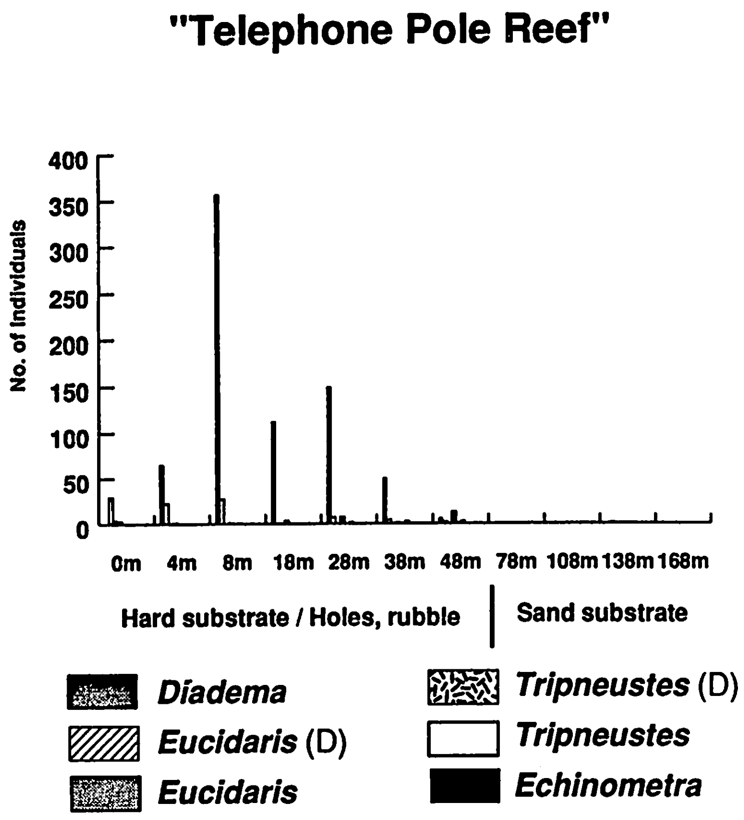

Figure 5 -- Results of census at Telephone Pole Reef. Note the high numbers of *Echinometra* and overall low numbers of regular echinoid carcasses. On this scale, the occurrence of *Diadema* remains does not register.

A population of abundant living *Echinometra lucunter* occupied numerous holes excavated in beachrock in the shallow (0.10 m) subtidal zone close to shore. Individuals were first observed at station zero, and averaged 1.0 individual/m^2. Abundance was concentrated along the first 38 m of the transect before dropping off precipitously. Maximum abundance reached an average of 35.6 individuals/m^2 at station eight, where one of the quadrats yielded 129 living individuals. No intact or partial carcasses were associated with the living population.

Populations of living *Tripneustes ventricosus* were also concentrated at the shoreward end of the transect (Fig. 5). Live *T. ventricosus* were first observed at station 0 largely underneath pieces of coral rubble that had accumulated in larger pockets in the beachrock. Maximum average abundance (5.4 individuals/m^2) was lower than that of the *E. lucunter* population and occurred at station 0. Abundance generally decreased offshore, dropping abruptly at 18 m along the transect. Subfossil material was rarely associated with live individuals (Fig. 5). A total of eight carcasses, in various states of degradation, were observed during the census. Five carcasses were noted at station 0, occurring as fragments of corona smaller than an interambulacrum (2), coronal fragments larger than an interambulacrum (2) and one freshly killed individual with some spines still attached. Coronal fragments smaller than an interambulacrum were recorded once from station four and twice from station 48.

Diadema antillarum was the least abundant living echinoid observed during the survey. This may in part be the result of continued slow recovery after the pan-Caribbean demise of *Diadema* populations during 1983-84 (Lessios et al., 1984). Live individuals were observed along the central portion of the transect. Maximum average abundance reached 0.3 individuals/m^2 at stations 38 and 48. One occurrence of macroscopic remains, a cluster of long spine segments and pyramids of the Aristotle's Lantern was observed at station 48.

Like *Diadema*, living individuals of *Eucidaris tribuloides* had relatively low abundance. Average abundances were higher along the central portion of the transect and were intermediate between *Diadema* and *Tripneustes*. *Eucidaris* were first observed at station 0 and maintained low abundance along the transect, reaching a maximum of 1.2 individuals/m^2 at station 48.

Macroscopic skeletal remains were also exceedingly rare, occurring at station 48 as a cluster of complete spines.

The overall paucity of remains of regular echinoids suggests that, in these environments, they are relatively rapidly reduced to grains of carbonate sand (see Kidwell & Baumiller, 1990 and Greenstein, 1990; 1991 for further discussion of regular echinoid biostratinomy). Even as bioclastic particles, however, their contribution to the sand-size fraction of the sediment is so slight that echinoderms in general are included in a "miscellaneous" or "other" category in most constituent particle analyses of modern carbonate sediments (see for example Illing, 1954; Ginsburg, 1956). Kobluk and Lysenko (1984) determined that echinoderms comprised only 3-4% of the constituents of reefal sediments >2 mm in size in Bonaire: a figure that was not significantly raised by the sudden incorporation into the sediment of innumerable echinoid carcasses following mass mortality of *Diadema* populations in 1983-84 (Greenstein, 1989). Constituent particle analysis of sediments previously obtained from the transects in Smuggler's Cove and Rod Bay indicated that the echinoderm fraction did not exceed 3.2% and averaged 1.2% (Greenstein, 1990). Similarly, reefal sediments collected from Andros Island, Bahamas yielded an average of 1.2% echinoderm material in the >2 mm size fraction (Greenstein and Meyer, 1990).

Thus, although results of this study indicate that the presence of regular echinoid populations is likely to be best reflected by examining the sand-size fraction of surficial sediments rather than searching for macroscopic material, previous research demonstrates that the amount of echinoderm material that size is too low to draw conclusions concerning the distribution of various taxa: an increase or decrease of less than 1% is hardly conclusive evidence for the presence or absence of a particular taxon. Rather, low amounts of echinoderm material in the sediments can only suggest that echinoids and other echinoderms common in these environments (ophuiroids, asteroids) were present but subsidiary to the major sediment contributors (corals, molluscs and, in lagoons, calcareous algae).

These results appear to contrast with those of Nebelsick (1992) who found that bulk samples obtained from similar environments in the Northern Bay of Sagafa contained a sufficient quantity of fragments of irregular and regular echinoid fragments (>2 mm size fraction) to distinguish between various facies using statistical analysis. Direct comparison is difficult, however, since the amount of fragmented material contributed by each echinoid taxon is given as a weight percent of the entire echinoid fraction. No data are presented to indicate the amount of echinoderm material relative to other sediment constituents.

Irregular Echinoids

Irregular echinoids observed in this study included two mellitid sand dollars: *Mellita quinquiesperforata*, *Leodia sexiesperforata* and the spatangoid *Meoma ventricosa*. Substrate type has been shown to be one of the most important controls on echinoid distribution (Kier & Grant, 1965; Ebert, 1971; Smith, 1984). Consequently, occurrences of living irregular and regular echinoids were mutally exclusive: irregulars inhabited the unconsolidated sand substrates examined adjacent to Lee Stocking Island and offshore from Rocky Point and Bamboo Point, San Salvador while regulars occurred on substrates that inhibited burrowing (solid rock, dense seagrass, large pieces of coral rubble or reef surfaces) present at the localities discussed above.

Lee Stocking Island.

Few irregular echinoids were observed during the census adjacent to Perry Deep Reef (Fig. 6).

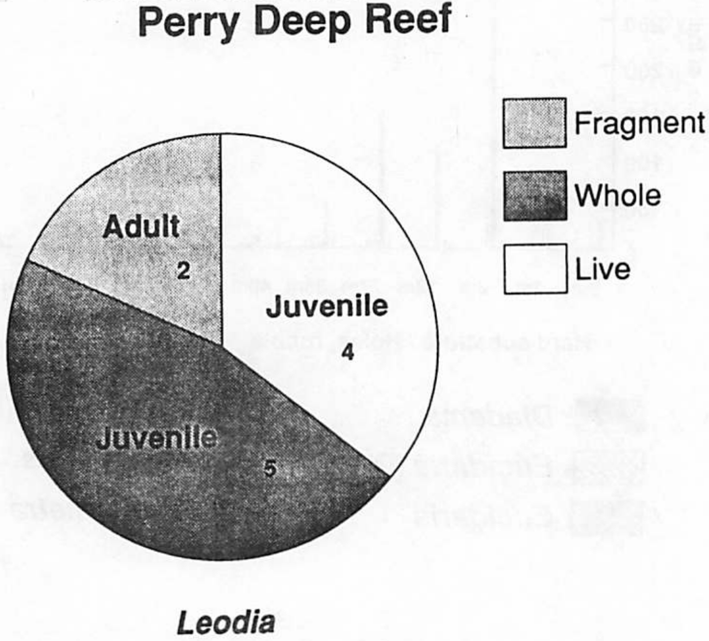

Figure 6 -- Results of census of a circle 10 m in diameter. Sand was overturned to 10-15 cm depth.

Careful examination of the upper 15 cm within a 10 m diameter circle yielded four living juvenile *Leodia sexiesperforata*. Subfossil material associated with the individuals included five intact coronas of juvenile *Leodia* and two adult *Leodia* represented by skeletal fragments (Fig. 7).

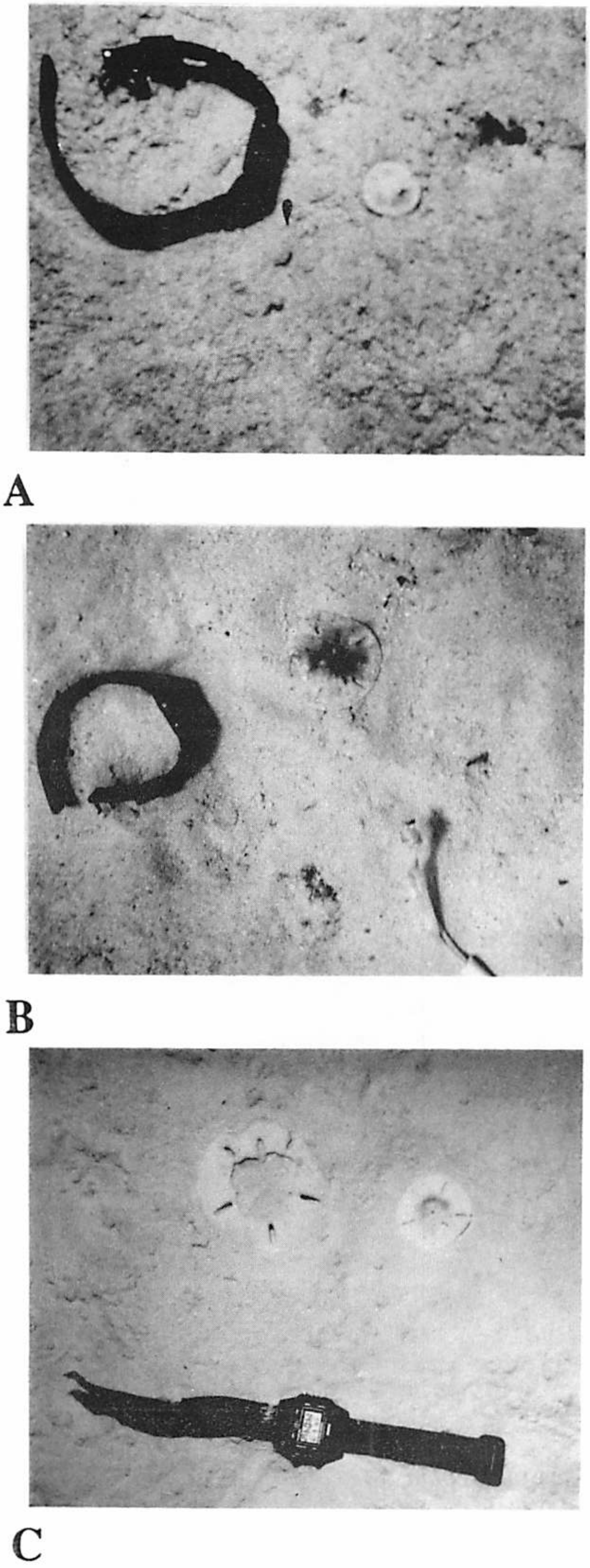

Figure 7 -- Condition of carcasses of *Leodia* observed at Perry Reef: A) Juvenile; B) Complete adult, note Batophora growing from apical end; C) two carcasses missing apical end.

Interestingly, all intact tests of *Leodia* occurred on the sediment surface. This supports Smith's (1984) observation that irregular echinoids, when placed under stress, come to the surface and are therefore unlikely to be buried alive. Thus, an infaunal life habit *per se* does not necessarily prevent post-mortem exposure on the sediment surface and consequent increase in preservation potential.

The two census localities in the sand patch adjacent to Children's Cay yielded an abundant population of live *Meoma ventricosa*. Moreover, a great deal of subfossil material was present (Fig. 8).

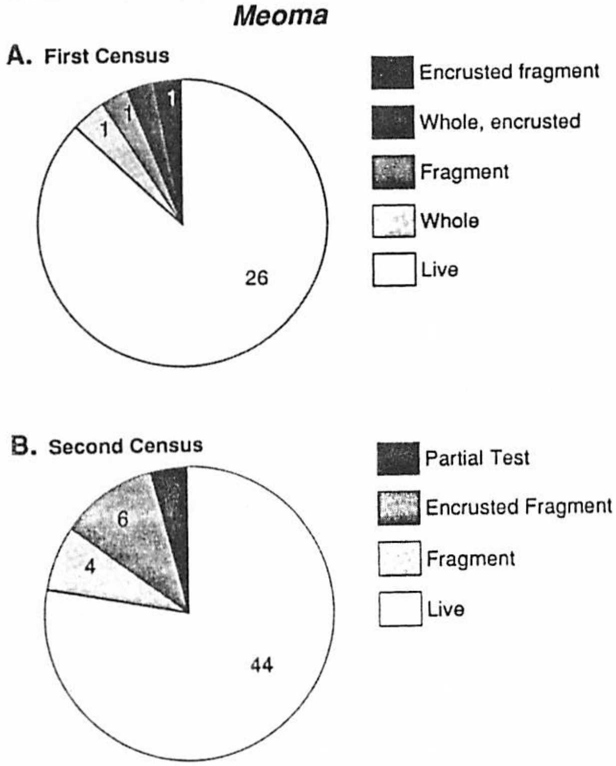

Figure 8 -- Results of censuses of two circles 10 m in diameter in a lagoonal environment west of Children's Cay, Lee Stocking Island.

A total of 70 live individuals were observed at the two localities. Four carcasses were associated with 26 live individuals at the first census site, while 12 carcasses were associated with 44 live indivuals at the second site. The condition of the material varied from intact coronas to encrusted fragments (Fig.9). Encrusted and non-encrusted material (roughly indicative of post-mortem residence time on the sea floor) was present in approximately equal proportions (Fig. 8A, B). Virtually all of the carcasses were observed on the substrate: digging beneath the sediment yielded only living individuals.

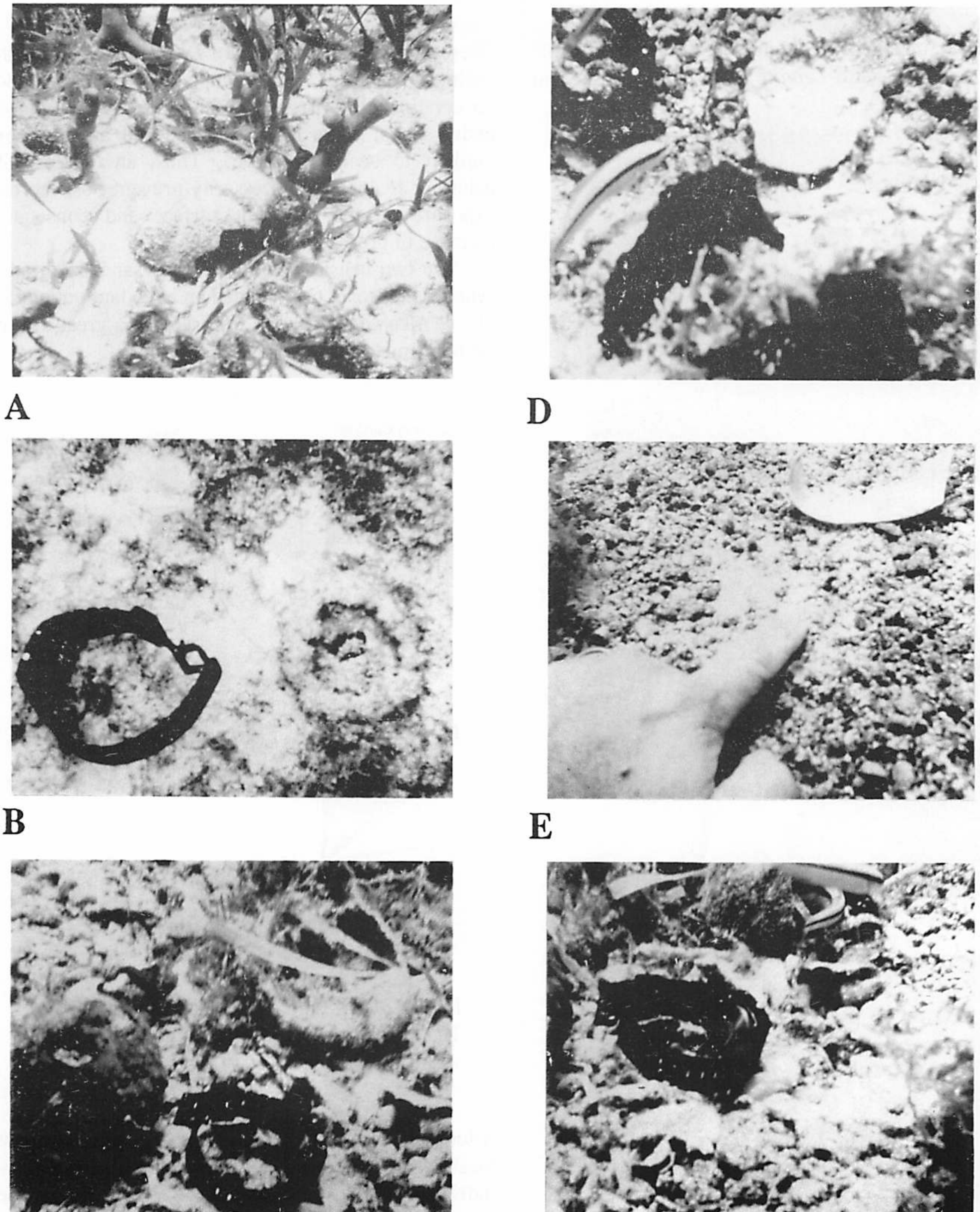

Figure 9 -- Condition of carcasses of *Meoma* observed offshore of Children's Cay: A) Unencrusted large aboral fragment; B) Heavily-encrusted aboral fragment, oral view; C) Encrusted aboral fragment; D) Smaller, encrusted fragment; E) Unencrusted fragments; F) Small, encrusted fragments (just below the watchband).

San Salvador.

Subfossil material associated with the population of *Leodia sexiesperforata* offshore from Rocky Point occurred as either intact coronas or fragments. A total of 21 live individuals were observed along the transect and associated with 27 occurrences of macroscopic remains (Fig. 10A). Live abundance was highest at station 30: a total of eight individuals (note this is an average of only 0.8 individuals/m²). Carcasses were present at all stations except station 90 and reached their maximum abundance at station 10 (13 were observed, average of 1.3/m²).

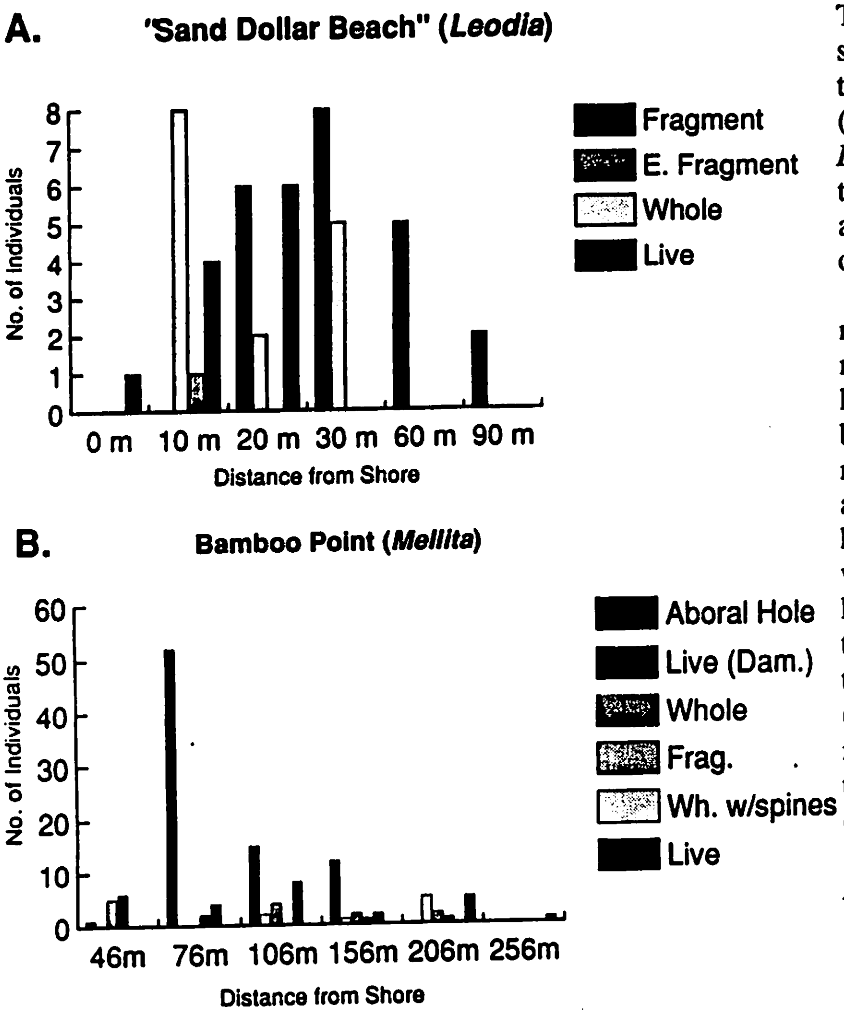

Figure 10 -- Results of censuses conducted at "Sand Dollar Beach" (A) and Bamboo Point (B). Note how the distribution of the taphoncoenosis is offset from that of the biocoenosis at each locality.

Irregular echinoids observed offshore from Bamboo Point included a small population of *Leodia* present at station 76 and a larger population of *Mellita quniquiesperforata* present in relatively high abundances at stations 76, 106 and 156 and low abundance at station 46 (Fig. 10B). The highest number of individuals occurred at station 76, where a total of 54 sand dollars were observed: 40 *Mellita* and 14 *Leodia*. Fragmented material associated with the living population included whole and fragmented coronas. A total of 21 occurrences of subfossil material, distributed relatively evenly among stations 46, 76, 106 and 156, were observed. Maximum abundance reached 6 carcasses at station 106.

Living irregular echinoids were not observed along the transect at Telephone Pole. This was due to the fact that no sand substrates were encountered over the length off the transect. However, carcasses of *Mellita* (four at station 138, two at station 16) and *Leodia* (one at station 138) were present on the sediment surface. With the exception of a whole corona of *Mellita* at station 138, all other occurrences were coronal fragments.

The presence of a substantial quantity of remains of irregular echinoids relative to regulars indicates that carcasses are surviving long enough on the sea floor to potentially become incorporated into the sedimentary record. As a consequence, there is general agreement between the distribution of the living fauna and that of subfossil material, whereas the total absence of remains of regular echinoids in several environments adjacent to St. Croix contradicts the existence of four taxa, one having particularly high abundance (*E. lucunter*). Offshore of San Salvador, few remains of regular taxa were found. Additionally, no macroscopic fragments of regular echinoids occurred in areas bereft of live individuals (see Fig. 5). The fragments of *Leodia* and *Mellita* observed along the transect at Telephone Pole Reef on substrates unlikely to be inhabited by burrowing echinoids suggest that these forms are more able to survive at least limited post-mortem transport (recall that a sand substrate was within approximately 100 m from the end of the transect line at Telephone Pole Reef). Results from Sand Dollar Beach and Bamboo Point further support this conclusion. Examination of Figure 10A indicates the live population is concentrated offshore at station 30, while the amount of subfossil material is highest closer to shore suggest ing post-mortem transport. Examination of Figure 10B indicates that carcasses are present both landward and seaward of the live population: limited post-mortem transport has occurred.

While skeletal durability is certainly a factor in producing these patterns (see Smith, 1984 on the effects of skeletal microstructure on coronal strength), the role of environment in determining preservation potential is particularly evident when one considers the results obtained from observation of populations of *Echinometra* offshore of St. Croix and San Salvador and the population of *Meoma* offshore of Lee Stocking Island. Populations of *Echinometra* had the highest abundance of any echinoid observed in this study. However, subfossil material was lacking even though the echinometrid corona is significantly more resistant to breakage than the other regular echinoids observed (Greenstein, 1991). If live abundances of *Meoma* are calculated as individuals/m², abundances at the two census stations are lower than those observed for *Echinometra* (0.33 and 0.56 individuals/m², respectively) but associated with many carcasses in various states of degradation. Moreover, like other spatangoid echinoids,

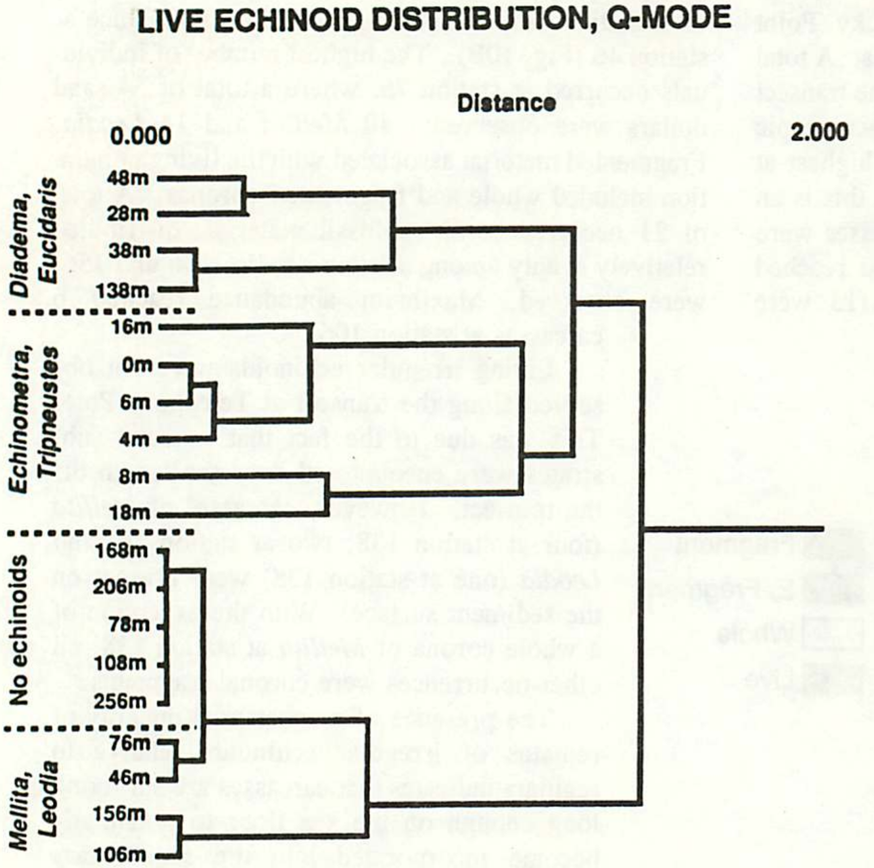

Figure 11 -- Results of Q-mode cluster analysis of the live echinoid fauna present in Fernandez Bay (data obtained from Bamboo Point and Telephone Pole Reef were combined for the analysis).

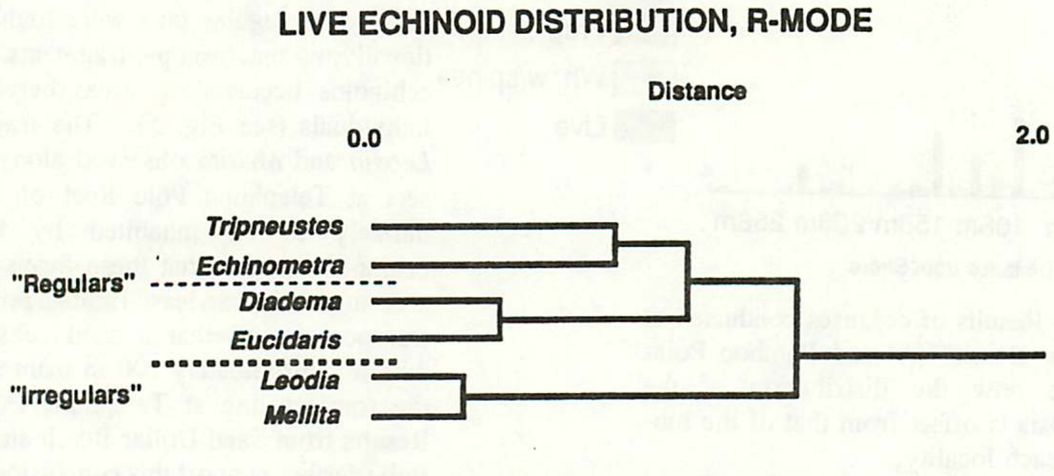

Figure 12 -- Results of R-mode cluster analysis of the live echinoid fauna present in Fernandez Bay.

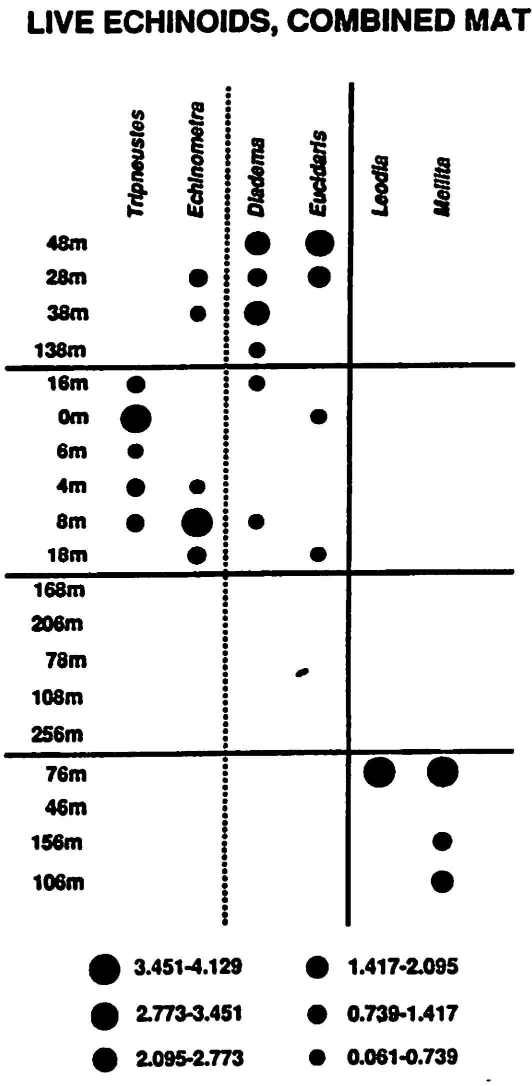

Figure 13 -- Two-way cluster analysis of the Fernandez Bay data set. Note how the echinoids are distributed along the transect. Numbers given in legend refer to Z-transformed data.

Meoma possesses a relatively fragile skeleton. Clearly, beginning the post-mortem interval in the semi-protected environment present west of Children's Cay allows for longer residence time (and, all else being equal, greater likelihood of preservation) of subfossil material than along the rocky shoreline of Fernandez Bay.

Implications for the Fossil Record

Results of the censuses suggest that Kier's (1977) hypothesis, although essentially correct, needs modification:

1. For the two clypeasteroid and one spatangoid echinoid observed in this study, skeletal durability may be a more important factor affecting preservation potential than life habit. Most whole and fragmented carcasses of the irregular echinoids were observed to occur on, rather than in, the substrate. This material is consequently vulnerable to biostratinomic processes. Thus the infaunal life mode does not necessarily guarantee that an echinoid begins its post-mortem interval removed from the taphonomically active zone (TAZ; see Davies et al., 1989a; 1989b). Recall that these echinoids are generally shallow burrowers (Chesher, 1969; Salsman & Tolbert, 1965). This conclusion cannot be extended to deeper- burrowing forms.

2. The paucity of subfossil material of regular echinoids does not limit their utility as paleoenvironmental indicators. In light of the census results, isolated occurrences of macroscopic subfossil material, although rare, may be the only evidence that regular echinoids were present in a particular environment. That this material is useful in delineating different reefal facies has been demonstrated by Gordon & Donovan (1992) working with material from the Pleistocene Falmouth Formation of Jamaica.

Further analysis of the data presented here corroborates their work. To further assess the relationship between the live and dead populations, the data collected from the Bamboo Point and Telephone Pole Reef localities were combined and subjected to cluster analysis. The sites were combined so that all of the subenvironments could be incorporated and the relationships between live and dead populations of both regular and irregular echinoids explored. The census data were standardized using a Z-transformation to mitigate wide variation in the numbers of echinoids counted. Similarity was measured using the Pearson Correlation Coefficient, and clustering of samples was done using the average linkage method. Live and dead echinoids were analyzed separately.

Results of Q-mode analysis reveal that samples from the combined transects cluster into four groups at relatively low distance values (Fig. 11). Three of these clusters are formed based on the presence of various echinoid taxa, while the fourth simply reflects transect stations where no living echinoids were encountered. Comparison of the echinoids on the basis of their distribution among transect stations (R-mode analysis, Fig. 12) reveals that the four regular taxa observed have distributions more similar to each other than they do to that of the irregular echinoids. This is not surprising given the substrate preferences discussed above. Moreover, since live irregular echinoids were not observed along the transect at Telephone Pole Reef, this separation represents the two transect locations in Fernandez Bay. Combining Q- and R-mode matrices illustrates how live populations are distributed in Fernandez Bay (Fig. 13). *Echinometra* and *Tripneustes* populations occur closest to shore (stations 0 through 18) while populations of *Diadema* and *Eucidaris* inhabit substrates further from shore (stations 28 through 138). The irregular echinoids inhabit the sand substrates that are generally farther from shore (stations 46 through 156 at Bamboo Point).

Analysis of the regular echinoid taphocoenosis (*sensu* Fursich, 1990) using the same methods reveals that it is more restricted within the area where live individuals occur. Q-mode analysis results in three distinct clusters and one station not included in a cluster (Fig. 14).

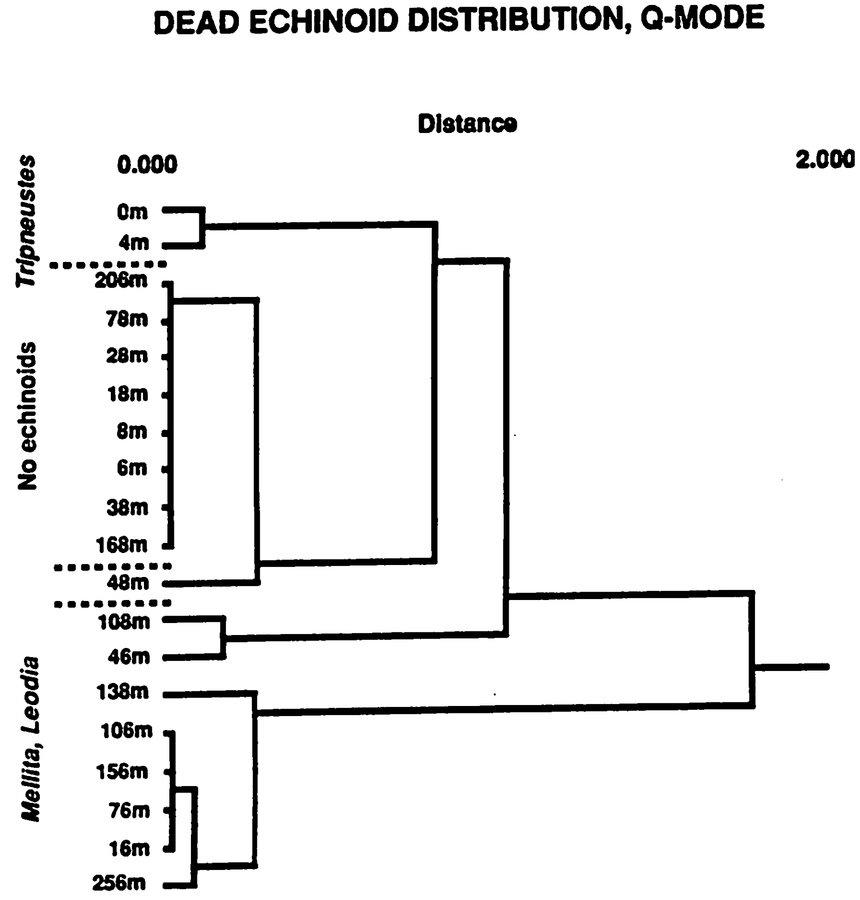

Figure 14 – Results of Q-mode cluster analysis of the taphocoenosis present in Fernandez Bay (data from Telephone Pole Reef and Bamboo Point were combined for the analysis). Note the limited range of occurrence of carcasses of the regular taxa and the expanded range of occurrence of carcasses of irregular taxa.

As with the biocoenosis, one of the clusters simply represents stations where no echinoid carcasses were observed. R-mode analysis reveals that subfossil material is distributed among the samples in essentially the same way as are living taxa (Fig. 15). Combining the matrices (Fig. 16) and comparing the result with that for the living fauna (Fig. 13) reveals the range restriction that has occurred to the regular echinoid taphocoenosis. Along the transect, the 18 m range of living *Echinometra* and *Tripneustes* populations is reflected by a narrower range of subfossil material of *Tripneustes* only (stations 0 and 4). Similarly, the range between stations 28 through 138 observed for living *Diadema* and *Eucidaris* is reflected by carcasses at station 48 only. The reverse has occurred to the irregular echinoid taphocoenosis: the range of the live fauna (stations 46 through 156) is expanded by the distribution of subfossil material, from station 16 through station 256. Although these results are logical given differences in skeletal durability between the echinoids, the implication for the fossil record is counterintuitive: rarer occurrences of fragmented regular echinoid material should more faithfully represent once living populations whereas more common occurrences of irregular material may have undergone more (albeit limited) transport and are therefore less likely to accurately reflect the distribution of the biocoenosis.

3. Differences between regular and irregular echinoids in both abundance and diversity over geologic time are also the result of taxonomic methodology. Results of this study as well as those of Nebelsick (1992) and Gordon & Donovan (1992) suggest that regular echinoid fossil material usually occurs as fragmented remains that are not likely to be useful to taxonomists for purposes of classification. Smith (1990, p. 79) states that intact coronal material, including lantern, tooth structure and lantern muscle attachment structure are crucial characteristics in defining and recognizing major taxonomic groups. Moreover, even at lower taxonomic levels certain skeletal elements are required for classification.

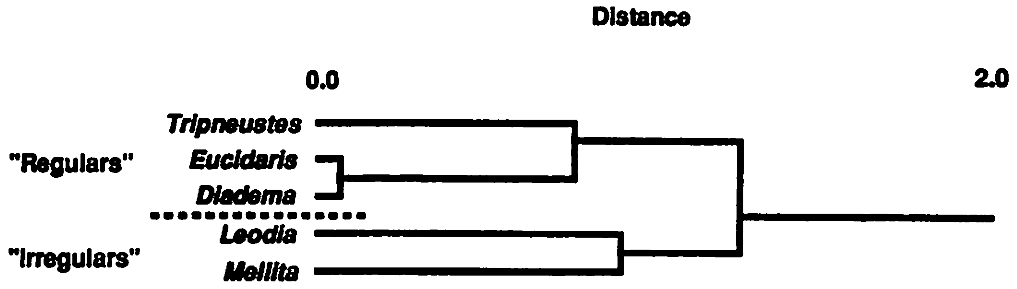
DEAD ECHINOID DISTRIBUTION, R-MODE

Figure 15 -- Results of R-mode cluster analysis of the taphocoenosis present in Fernandez Bay. Note that the echinoid taxa still tend to occur together.

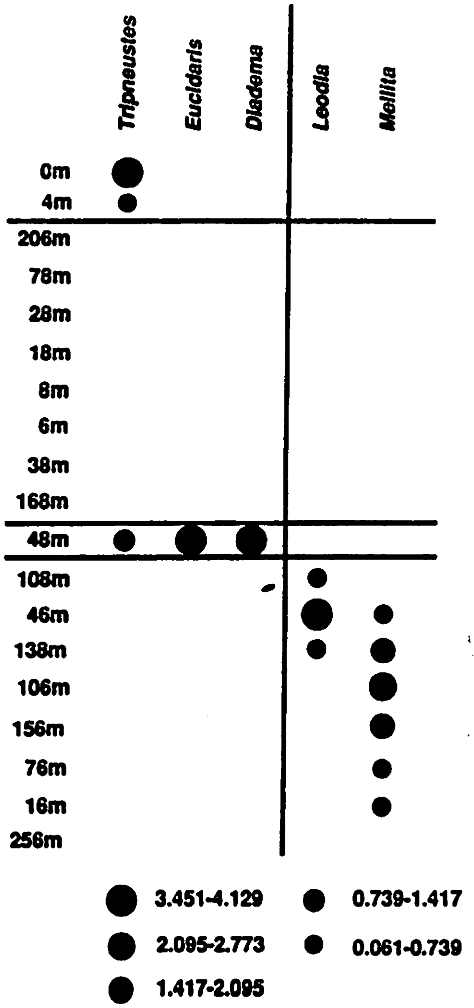
DEAD ECHINOIDS, COMBINED MATRIX

Figure 16 -- Two-way cluster analysis of the Fernandez Bay taphocoenosis. Numbers in legend refer to Z-transformed data.

without exception, coronal morphology is important for distinguishing between fossil forms in each family of regular echinoid represented by the taxa observed, although at different taxonomic levels (see Durham *et al.*, 1966). Identification of this aspect requires more of the skeleton than an isolated coronal plate or small coronal fragment. Thus, Kier's (1977) measure of abundance and diversity using the number of described species and museum specimens underestimates the abundance of regular echinoids in the fossil record.

4. Finally, the nature of taphonomic bias in the echinoid fossil record should not be reduced to differences between regulars and irregulars of intrinsic traits such as skeletal durability and life habit. The fact that very large accumulations of irregular echinoid carcasses were not observed at any of the study areas suggests that rich accumulations of fossil clypeasteroids (e.g. the Late Eocene of the southeastern U. S., see Carter, 1990) are not simply time-averaged samples accumulated from populations with low abundance, but represent populations that contained extraordinarily high numbers of individuals. However, high population densities alone may not result in fossil echinoids either. A survey of live and dead echinoids present on the west Florida shelf (Serafy, 1979) revealed that high population densities of *Mellita* (although an average of over 15,000 living individuals recovered during winter months using a box dredge and otter trawl cannot accurately be compared to the data presented here) did not correspond with a large amount of subfossil material. Similarly, Salsman and Tolbert (1965) observed population densities averaging 136 individuals/m^2 during a 12 month survey of transects

established offshore of Panama City, Florida. They also reported that mounds 10-15 cm high and composed of several hundred individuals formed during the summer months as a consequence of a large die-off of the population. These mounds were observed to be dismantled and the carcasses comprising them fragmented over the following three months. By late fall, no indication of the accumulation remained. Thus, as is the case with regular echinoids, exceptionally rich deposits of irregular echinoids must be viewed as resulting from a taphonomic process extrinsic to the echinoids themselves rather than a result of attributes intrinsic to these animals (durable skeleton, infaunal life habit).

CONCLUSIONS

In addition to serving as predictive tools for assessing taphonomic bias in the fossil record, field studies of taphonomy can serve to test hypotheses that are generated by observations based on fossil data. Specifically, Kier's (1977) hypothesis that, because of life habit and test construction, taphonomic biasing has particularly influenced the fossil record of regular echinoids has been corroborated with some qualifications.

1. The distribution of living populations of four taxa of regular echinoids adjacent to St. Croix and San Salvador Islands is patchy. With the exception of *Echinometra lucunter*, live individuals occur in relatively low abundance.

2. Subfossil material was not associated with the regular echinoid biocoenosis at two localities censused adjacent to St. Croix. Limited numbers of carcasses, occurring as fragments, were associated with populations in Fernandez Bay.

3. A small population of *Leodia sexiesperforata* (total of four individuals) inhabiting a sand substrate adjacent to Perry Reef (Lee Stocking Island) was associated with subfossil (mainly juvenile) material.

4. A large population of *Meoma ventricosa* (total of 70 individuals) censused at two adjacent localities offshore of Children's Cay occurred with a relatively high number of carcasses in various states of degradation (16).

5. Populations of *Mellita quinquiesperforata* and *Leodia sexiesperforata* occupying two distinct localities along the lee coast of San Salvador are associated with relatively large amounts of carcasses in varying states of degradation. The taphocoenosis at both localities has been subjected to transport.

6. The occurrence of the majority of irregular [illegible] carcasses on the substrate indicates that their [illegible] mode does not automatically result in removal from biostratinomic processes post-mortem.

7. Multivariate analysis of census data reveals that the echinoids under study show a distinct distribution form onshore to offshore in Fernandez Bay: *Tripneustes* and *Echinometra* occupy hard substrates close to shore, *Diadema* and *Eucidaris* occupy hard substrates farther from shore, while *Mellita* and *Leodia* are restricted to sandy substrates.

8. Subfossil material of regular echinoids, although rare, more faithfully represents the distribution of the biocoenosis than does subfossil material of irregular echinoids. This is primarily the result of the inability of the regular echinoid carcass to survive even limited transport.

9. Fragments of regular echinoids in the fossil record should be useful indicators of paleoenvironments.

10. The taphonomic bias suggested by Kier (1977) may also be the result of taxonomic methodology: fragmented fossil material is less useful for purposes of classification than relatively complete material.

11. As is the case with regular echinoids in general, well-preserved assemblages of clypeasteroid echinoids must be viewed as resulting from a taphonomic process extrinsic to the echinoids themselves rather than a result of intrinsic attributes such as life habit and skeletal durability.

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Raw data obtained in this study. For all localities, substrate abbreviations are as follows: RS = rocky shoreline; RU = rubble zone; PA = pavement; GR = sea grass beds; CA = abundant *Callianassa* mounds; SA = clean sand; RF = reef. The first number listed represents live individuals counted in a 10 m^2 area. A second number indicates the number of carcasses counted in that same area.

Smuggler's Cove, St. Croix

Station # (m from shore)	Substrate	*Echinometra*	*Diadema*	*Eucidaris*	*Tripneustes*
0	RU	13	0	0	0
60	GR	0	0	0	0
120	CA	0	0	0	0
180	GR	0	0	0	0
240	CA	0	0	0	0
300	CA	0	0	0	0
360	SA	0	0	0	0
420	CA	0	0	0	0
480	CA	0	0	0	0
540	RF	48	0	0	1
600	RF	21	7	7	0
660	SA	0	0	0	0
720	SA	0	0	0	0

Rod Bay, St. Croix

Station # (m from shore)	Substrate	*Echinometra*	*Diadema*	*Eucidaris*	*Tripneustes*
0	RS	281	0	0	1
10	GR	0	0	0	0
20	GR	0	0	0	0
30	GR	0	0	0	0
40	RU	19	0	0	2
50	RF	17	0	4	0

Sand Dollar Beach, San Salvador, Bahamas

Station # (m from shore)	Substrate	*Leodia sexiesperforata*
0	SA	0,1
10	SA	0,13
20	SA	6,8
30	SA	8,5
60	SA	5
90	SA	2

Bamboo Point, Bahamas

Station # (m from shore)	Substrate	*Mellita quinquiesperforata*	*Leodia sexiesperforata*
46	SA	2,2	0,5
76	SA	40,2	14
106	SA	21,6	0
156	SA	14,4	0
206	SA	0	0
256	SA	0,1	0

Telephone Pole Reef, Bahamas

Station # (m from shore)	Substrate	*Tripneustes*	*Echinometra*	*Eucidaris*	*Diadema*
0	RS	54,5	10	3	0
4	RS	22,1	65	1	0
6	RS	14	8	0	0
8	RS	27	354	1	1
16	RU	20	3	1	1
18	PA	0	112	3	0
28	PA	7	139	7	2
38	PA	4	50	1	3
48	PA	3,2	6	12,1	3,1
78	PA	0	0	0	0
108	PA	0	0	0	0
138	SA	1	0	0	1
168	RF	0	1	0	0

Note -- carcasses of *M. quinquiesperforata* occurred at stations 16 (2) and 138 (4), while carcasses of *L. sexiesperforata* occurred at station 138 (1).

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