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MASS MORTALITY OF THE WEST INDIAN ECHINOID *DIADEMA ANTILLARUM* ADJACENT TO ANDROS ISLAND, BAHAMAS: A NATURAL EXPERIMENT IN TAPHONOMY

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ABSTRACT

During 1983, populations of the common long-spined echinoid *Diadema antillarum* were decimated by disease throughout the Caribbean and as far north as Bermuda. The role of *Diadema* as a grazer of algae and agent of bioerosion is well documented. The slow rate of recovery of *Diadema* populations has been demonstrated to have had profound effects on the coral reef ecosystem. The hypothesis that the sudden incorporation of tests and spines of innumerable urchins into reef sediments would leave a clear record was tested at Andros Island, Bahamas, where the mortality was reported to have occurred in October, 1983. Sediments collected from three reef subenvironments in May, 1984 were analyzed for total echinoderm content. The echinoderm fraction shows a slight increase over pre-mortality levels reported from Bonaire, Netherlands Antilles, but it is not clear that this increase resulted from an influx of *Diadema* skeletal elements. The fragility of the *Diadema* test and post-mortem processes are suggested to be responsible for the lack of signature. The lack of a strong signal of the mass mortality event demonstrates the inadequacy of the reef sedimentary record to preserve many short-term although ecologically significant events.

INTRODUCTION

Mass Mortality

The long-spined echinoid *Diadema antillarum* Philippi is often the dominant herbivore in tropical Western Atlantic reef environments, reaching densities of 71 individuals per square meter (Sammarco, 1980; Hawkins & Lewis, 1982). As such it is responsible for large amounts of bioerosion as it grazes algae from reef surfaces (Scoffin et al., 1980; Hunter, 1977). *Diadema* also preys on living coral (Bak & van Eys, 1975; Carpenter, 1981) contributing to the control of the coral community as predators on coral recruits (Sammarco, 1980, 1982).

Beginning in January, 1983, *Diadema* suffered a widespread mass mortality (Lessios et al., 1984). The mortality was first observed at Galeta Point, Panama and by January, 1984, had spread to most of the Caribbean and to Bermuda (Figure 1). The sequence of mortality events indicates that the causative agent was generally dispersed by major surface currents over large distances until October, 1983. After that month, mortality events no longer followed a regular pattern. The causative agent is suspected to be a species-specific pathogen because the mortality spread over such a wide area without any dissipation of its severity, and no other species of sea urchin was affected (Lessios, 1984). Whatever the exact nature of the disease, its effect was catastrophic on *Diadema* populations, reducing them 98- 100% in Curacao (Bak et al., 1984), 94-99% in Panama (Lessios et al., 1985) and 99% in Jamaica (Hughes et al., 1985) where a sharp increase in bottom cover by non-crustose algae occurred within two weeks of the urchins' demise (Figure 2) (Liddell & Ohlhorst, 1986).

Urchins inhabiting the backreef, reef tract and fore-reef environments adjacent to Andros Island, Bahamas were reported dying in great numbers by the end of October, 1983 (Lessios, 1984). By May, 1984, only broken, disarticulated spines and test plates were evident in surficial reef sediments, and limited recovery of the live population had begun.

Mass mortality events affecting echinoid populations are commonly the result of prolonged exposure to elevated temperature (Glynn, 1968; Hendler, 1977), storms (Schafer, 1972) or disease (Pearse et al., 1977; Boudouresque et al., 1981; Scheibling & Stephenson, 1984). Such events occur in specific environments and on a local scale. If the current mass mortality is indeed the result of a species-specific pathogen, it represents

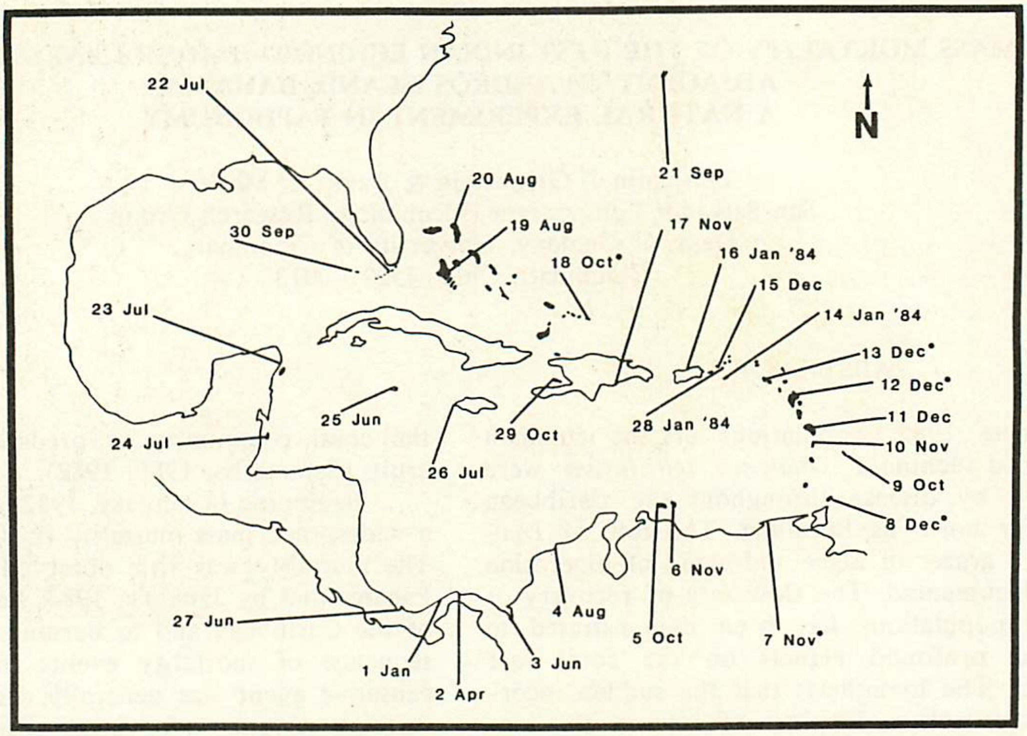

Fig. 1. Spread of Diadema *mass mortality through the Caribbean and Western Atlantic. Dates indicate the first time mortality was noted at each locality. Dates marked with a dot indicate the last time lack of mortality was verified in unaffected areas. Unless otherwise indicated, dates refer to 1983. Locality numbers: 1) Galeta Point, Panama. 2) San Blas Archipelago. 3) Puerto Obaldia. 4) Santa Marta, Columbia. 5) Curacao. 6) Bonaire. 7) Mochima, Venezuela. 8) Tobago. 9) Barbados. 10) Saint Lucia. 11) Martinique. 12) Guadeloupe. 13) Saint Kitts. 14) Saint Croix. 15) Saint Thomas and St. John. 16) Puerto Rico. 17) Santo Domingo. 18) Grand Turk. 19) Andros and New Providence Islands. 20) Grand Bahama. 21) Bermuda. 22) Florida Keys. 23) Cancun, Mexico. 24) Belize. 25) Grand Cayman. 26) Jamaica. 27) Cahuita, Costa Rica. 28) Tortola, Virgin Gorda and Salt Island. 29) Gulf of Gonave, Haiti. 30) Dry Tortugas. (after Lessios et al., 1984).*

the most extensive epidemic ever documented for a marine invertebrate (Lessios et al., 1984).

Taphonomy

A mass mortality affecting entire populations of a particular species provides a natural experiment in taphonomy, the systematic study of fossil preservation and preservational processes (see Muller, 1979, for an excellent review). More specifically, observing the result of the incorporation of large numbers of individuals in Recent reef sediments can yield information on their biostratinomy. The study of biostratinomy begins with the death struggle of an organism and ends with the final burial and arrangement of the dead or dying organism or its disarticulated remains (Muller, 1979) (Fig. 3).

The incorporation of innumerable echinoids into reef sediments suggests that sediment composition may be altered by an increase in the amount of echinoderm material present. Mass outbreaks and subsequent mortalities of the crown-of-thorns starfish *Acanthaster* have been reported preserved as layers enriched in their ossicles on the Great Barrier Reef (Frankel, 1978). Well-preserved echinoid assemblages are reported rarely in the literature (e.g Aslin, 1968; Rosenkranz, 1971; and Bloos, 1973), as are sediments composed primarily of their skeletal debris (e.g. Cherns, 1983). The mass mortality of *Diadema* provides an opportunity to assess the liklihood that an ecologically significant event will be recorded as a recognizable change in the composition of reef sediments.

STUDY AREA

Andros Island lies on the eastern margin of the Great Bahama Bank (Figure 4). The reef

Fig. 2. Overgrowth of algae occurring on the reef tract of the Florida Keys. Picture was taken in June, 1984, 11 months after the mass mortality was reported to have occurred (Photo by D. L. Meyer).

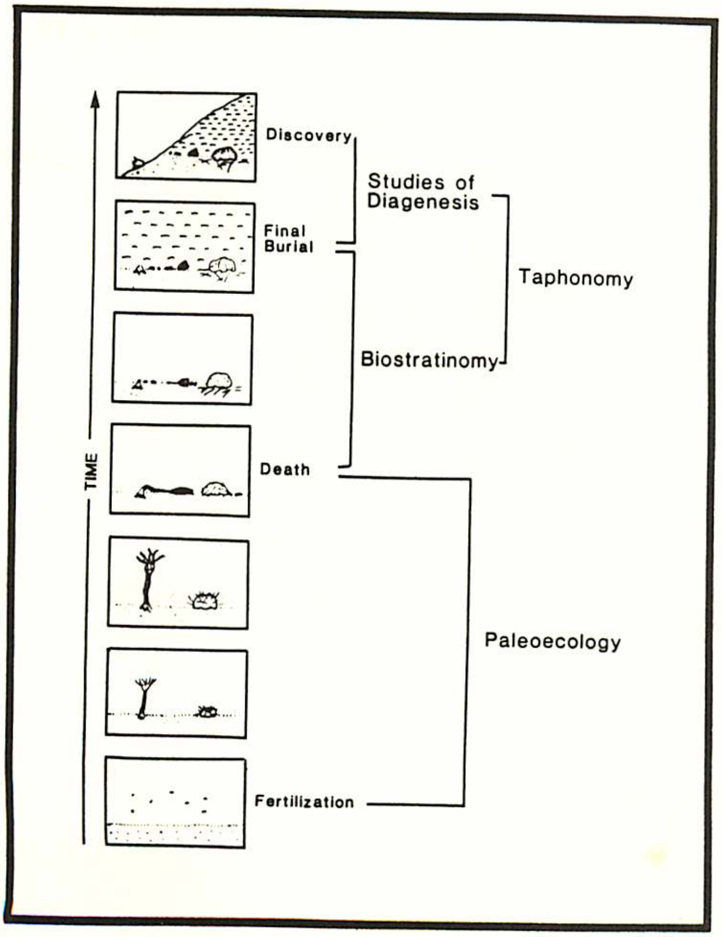

Fig. 3. Schematic illustration of the disciplines of taphonomy and biostratinomy (after Lewis, 1981).

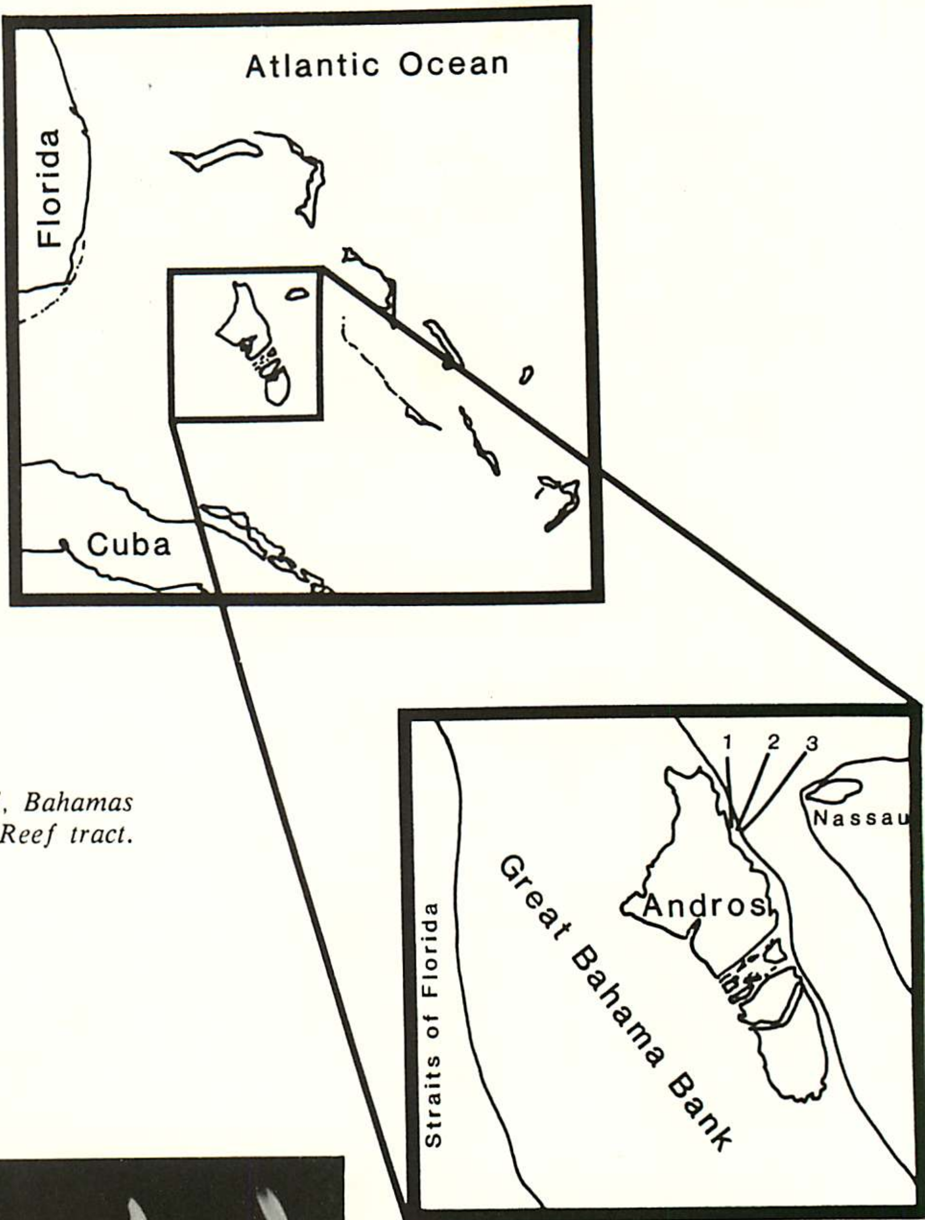

Fig. 4. Location of Andros Island, Bahamas and sample localities: 1) Backreef, 2) Reef tract. 3) Fore-reef.

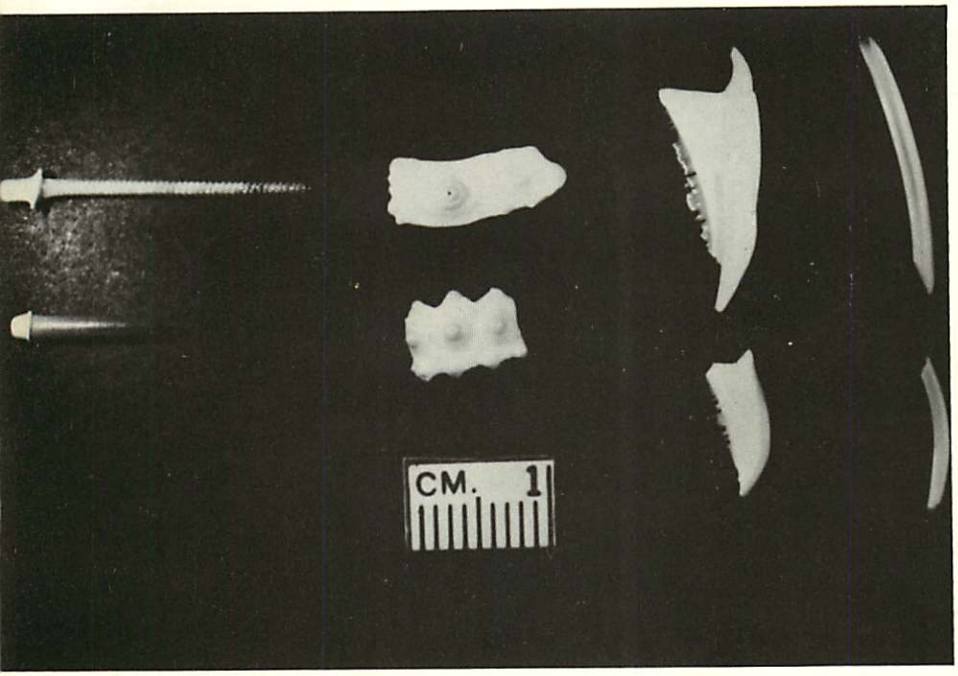

Fig. 5. Echinoid skeletal elements possessing characteristic structures include spines, parts of the Aristotle's Lantern, teeth, and test plates.

tract on the east side of Andros is quite narrow and contains islands of Pleistocene carbonate in some places. Landward of the reef tract lies the backreef environment. It is shallow (water depth less than 6 m) and subject to varying amounts of environmental energy. Seaward of the reef tract the fore-reef slopes moderately steeply to a depth of 50 m where it reaches the drop-off into the Tongue-of-the-Ocean. The three subenvironments sampled are quite narrow as a result of the islands' proximity to the drop-off.

METHODS

Samples from the three subenvironments were collected while on SCUBA (Table 1). Surficial sediments were obtained as well as sediments 5-6 cm below the sediment-water interface using a scoop. Samples were air-dried, sieved and the 500-1000 micron size fraction of each was isolated for analysis. The size fractions were split on an Otto micro-splitter until sample sizes of 400-600 grains were obtained. The samples were then analyzed under a Bausch & Lomb stereozoom microscope and all echinoderm grains identified were counted and separated from the rest of the sample. Additional quantities of the 500-1000 micron size fraction of each sample were impregnated with epoxy and ground into standard thin sections. The thin sections were then point-counted following the method of Ginsburg (1956).

Recognition of Echinoderm Grains

Echinoderm grains can be recognized under a stereo microscope on the basis of their characteristic structures (Fig. 5). Skeletal elements of less common echinoderms such as ophiuroids, crinoids and starfish can also be recognized in this manner. Thin sections were made in order to take advantage of the distinctive appearance of the stereomic microstructure and the unit extinction exhibited by echinoderm calcite in cross-polarized light. It was therefore possible to identify echinoderm skeletal elements that had been mechanically, chemically or biologically reduced to grains of high-Mg calcite lacking any characteristic shape features.

RESULTS

Echinoderms are minor contributors to reef sediments ranging from .58-3.9% of each sample (Table 2). Thin section point counts and grain counts reveal similar trends (Figure 6) and echinoderm percentages obtained by point counting are consistently higher than those obtained by counting grains. Comparison of the samples obtained by digging 5-6 cm below the sediment-water interface with those obtained from the sediment surface reveals that the amount of echinoderm material remains essentially unchanged at the backreef locality, decreases slightly at the

TABLE 1, Sample Locations

Sample	Environment	Location
1SA 1D	Backreef	1 km N. of Pigeon Key and 100 m W. of Reef tract. Water depth 3 m.
6S 6D	Reef Tract	Reef tract E. of Forfar Field Station Water depth 3 m.
3S 3D	Forereef	E. of reef tract and E. of Forfar Field Station. Water depth 20 m.
4S 4D	Forereef	Staniard Rock, SE of Pigeon Key. Water depth, 20 m.

TABLE 2

	THIN SECTION POINT COUNTS			GRAIN COUNTS		
Sample	# Echinoderm	Total Grains	% Echinoderm	# Echinoderm	Total Grains	% Echinoderm
1SA	1	172	0.58	4	406	1
1D	2	119	0.52	5	418	1.2
6S	6	196	3	5	409	1.2
6D	2	137	1.4	3	300	1
3S	3	191	1.5	9	473	1.9
3D	5	169	2.9	12	627	1.9
4S	6	153	3.9	7	556	1.3

reef tract locality and increases slightly at the fore-reef locality.

DISCUSSION

Higher echinoderm percentages revealed in thin section as compared to grain counts result from better identification of echinoderm grains in polarized light. Under reflected light, the stereomic microstructure of echinoderm grains cannot be reliably recognized. Moreover, all sediments analyzed were obtained from the active marine phreatic zone where precipitation of aragonite and Mg-calcite occurs (Longman, 1980). Grains coated by these cements lack the characteristic appearance of stereom, making their identification under reflected light unlikely. The actions of boring organisms in the active marine phreatic may further alter a grain's appearance. The unit extinction exhibited by echinoderm calcite in thin section provides the most precise means of identification. All echinoderm skeletal elements, regardless of the degree of their destruction by mechanical, chemical or biological processes, can be reliably identified.

Frankel (1978) demonstrated that mass outbreaks and subsequent mortalities of the crown-of-thorns starfish *Acanthaster* on the Great Barrier Reef, Australia, are being preserved as layers in the sediment enriched in their ossicles.

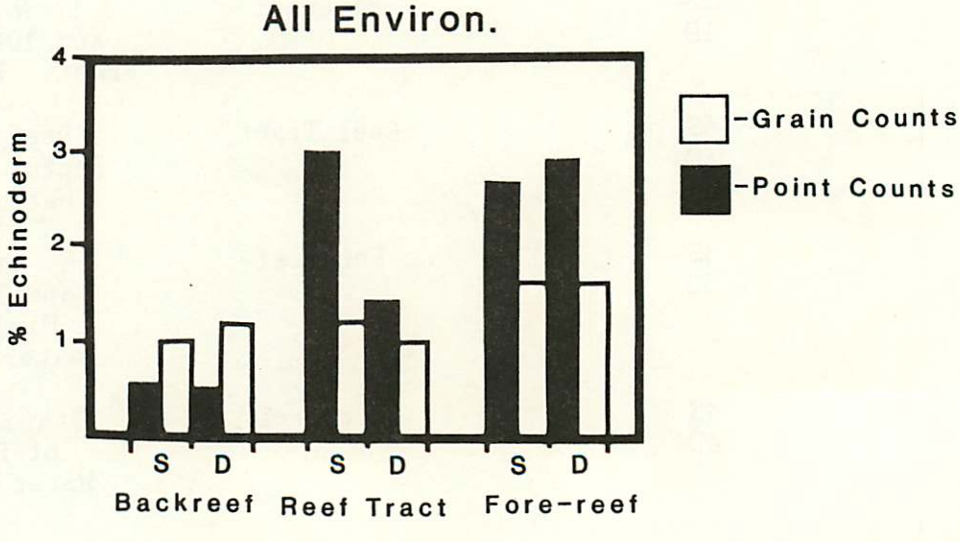

Fig. 6. Data obtained from the three reef subenvironments. In all histograms, S refers to surficial sediments and D refers to sediments collected 5-6 cm below sediment-water interface.

Comparison of surficial sediments with those 5-6 cm beneath the sediment surface does not yield a consistent pattern of "echinoderm enrichment". Sampling technique may, in part, be responsible for the lack of pattern, since sediment easily slides down the side of a hole excavated to 5 cm depth. However, recent work in the Netherlands Antilles (Greenstein & Meyer, 1985) with a sediment lift and encasing pipe also show a lack of layering of echinoderm skeletal elements suggesting that the results from Andros are accurate. The depth sampled is well within the range of burrowing organisms such as marine worms (Jacobsen, 1967; Rhoads, 1967), thalassinid shrimp (Pemberton et al., 1976) and holothurians (Mosher, 1980). Thus any layering that had occurred was rapidly disseminated as a result of bioturbation.

Comparison to Previous Work

Although no layering occurred as a result of the mass mortality, the results of this study were compared to those of constituent particle analyses conducted in the area prior to the mortality event to determine if the overall echinoderm content has increased. Because of the minor contribution echinoderm material makes to reef sediments, it is rarely reported as a separate constituent. Rather, it is included with other minor constituents in a more general category. Only if the echinoderm percentages reported in this study are greater than those of the general categories constructed by previous workers may an overall increase in echinoderm skeletal elements be suggested. Comparisons of the results of this study to those of the classic constituent particle analyses conducted in the area reveal that this is not the case (Table 3).

Kobluk & Lysenko (1984) included echinoderms as a distinct constituent in their analysis of surficial sediments collected at various depths from a fringing reef adjacent to Bonaire, Netherlands Antilles. In addition, the samples analyzed were collected between 1978-82, prior to the mass mortality event. Comparison of the results of this study to the pre-mortality values reported by these authors reveals that a very slight increase in the percentages of echinoderm material has occurred (Figure 7). A slight increase in overall echinoderm content was also reported when samples collected from the same area after the mortality event were analyzed and compared to those obtained by Kobluk & Lysenko (Greenstein & Meyer, 1985).

Recognition of the Event

It is unlikely that the slight increase of echinoderm material will constitute a recognizable signature of the mass mortality event. Liddell & Ohlhorst (1986) have suggested that the rate of recovery of the *Diadema* population will dictate the extent of the impact the mass mortality will have on the reef biota. The same may also be said with respect to the effect on reef sediments. A rapid recovery of the *Diadema* population with subsequent continued incorporation of their skeletal elements into the sediments may have the effect of masking the event entirely. If the opposite occurs, and the *Diadema* population recovers very slowly, the slight increase in echinoderm material documented by this study may then be followed by an interval of lower than normal levels as a result of the absence of *Diadema* ossicles. Thus it may not be the increase in echinoderm material resulting from the mass

Table 3. Comparison to previous work in similar environments (after Ginsburg, 1956).

THIS STUDY (2 Samples)	FLORIDA (Ginsburg, 1952) (25 Samples)	BAHAMAS (Thorp, 1937) (10 Samples)	BAHAMAS (Illing, 1954) (5 Samples)
2.2 %	9.0 %	8.0 %	4.0 %

Value reported from this study is the average percent of echinoderms obtained from sediments collected from the reef tract environment. The other values are for the percent "miscellaneous" categories of these workers. Values obtained by point counting (this study, Ginsburg, 1956) and visual estimates of percentages (Thorp, 1936, Illing, 1954).

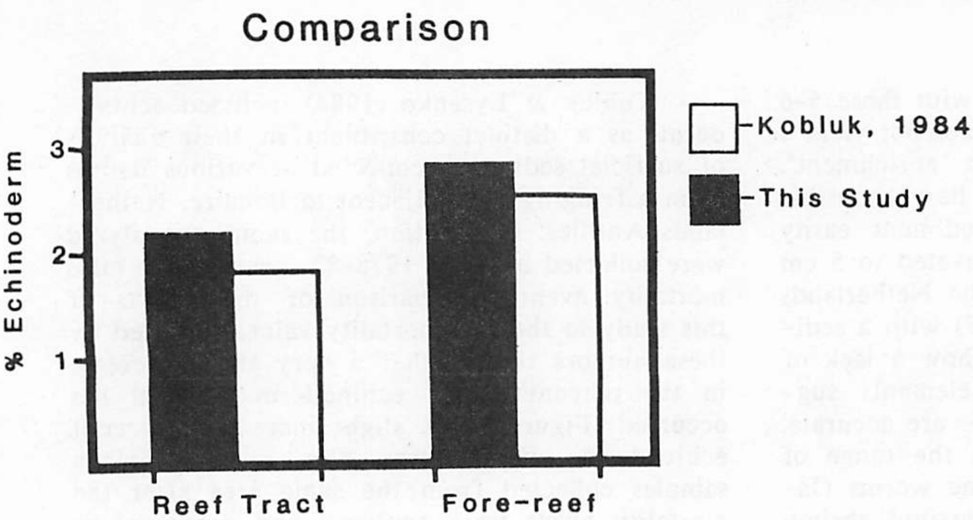

Fig. 7. Comparisons of the results of this study to those reported by Kobluk and Lysenko (1984).

mortality, but rather the duration of the interval before the population returns to normal that will determine the signature of the event in reef sediments. It should be emphasized, however, that the bioturbation processes responsible for destroying any layering of echinoderm material in the sediments are likely to be at work disseminating any "echinoderm-poor" sediments into "normal" sediments.

Application to Echinoid Fossil Record

The fact that there has been no clear signature of the mass mortality event in reef sediments underscores the rapidity with which populations of *Diadema* have been reduced to essentially unrecognizable carbonate sand grains. Although less than one year elapsed between the time the mortality was reported (October, 1983) and the reef subenvironments were sampled (May, 1984), the potential record of the event has been lost. A year is infinitesimally short geologically speaking yet there is likely to be no record of the event nor recognizable tests of *Diadema* remaining: the latter fact emphasizing that occurrences of well-preserved diadematids record truly extraordinary burial conditions.

Test plates of genera belonging to the Family Diadematidae are compounded in a manner that makes their test extremely fragile (Smith, 1984). The fragile test, coupled with an epifaunal mode of life in high energy reef environments makes preservation of these animals an exceptional event. Well-preserved echinoid assemblages must therefore be interpreted with respect to the source of the mortality as well as the processes responsible for preserving it. There are many sources of mass mortality affecting echinoids. These include disease, salinity changes, temperature changes, desiccation and storms. All of these sources will generate many dead echinoids at any given instant of geologic time. However, the mortality will only be recorded if it coincides with or is caused by an event enhancing its preservation potential. The long evolutionary history of echinoids as delineated by their fossil record should be interpreted with respect to the extraordinary conditions their preservation requires. Further work is necessary to document the taphonomic and sedimentologic aspect of fossil echinoid assemblages to ascertain the conditions of their preservation.

CONCLUSIONS

1. Thin section point counts are a more accurate means of identifying echinoderms in Recent carbonate sediments than are grain counts.

2. Echinoderms are a minor constituent of reef sediments and are therefore rarely specifically included in constituent particle analyses by recent authors. Comparison of the results of this study with those of previous workers is therefore difficult.

3. Any layering of echinoderm sediments in the three reef subenvironments sampled has been destroyed by bioturbation and/or environmental energy in less than one year.

4. The mass mortality of *Diadema antillarum* is recorded in the reef sediments adjacent to Andros by a slight increase in echinoderm content as compared to pre-mortality levels reported from Bonaire, Netherlands Antilles.

5. Preservation of the mortality event may

be contingent on the rate of recovery of the *Diadema* population, although it is unlikely that the slight increase in the echinoderm fraction documented by this study could be observed in a stratigraphic succession.

6. The reef sedimentary record may be inadequate to record this short-term but ecologically significant event.

7. Echinoid mass mortalities observed in ancient rocks are the result of extraordinary preservational events that remain poorly understood.

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