

# Mass Mortality of the West-Indian Echinoid *Diadema antillarum* (Echinodermata: Echinoidea): A Natural Experiment in Taphonomy

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*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 sudden incorporation of tests and spines of large numbers of urchins into surficial reef sediments suggests that sediment composition may be altered with respect to the amount of echinoderm material present. The hypothesis that a clear record of the mass mortality might be preserved in the reef sedimentary record was tested at Bonaire, Netherlands Antilles, where the mortality was reported to have occurred in November, 1983. Samples taken along a series of reef profiles and at specific depths within surficial reef sediments were analyzed for total echinoderm content and the proportion of the echinoderm fraction composed of skeletal elements of D. antillarum. The echinoderm fraction is virtually unchanged from pre-mortality levels as reported by other workers. Echinoderms overall are minor contributors to reef sediments, and skeletal elements of Diadema account for a large proportion of the echinoderm fraction. The lack of a strong signal of the event demonstrates the inadequacy of the reef sedimentary record to preserve this short-term, ecologically significant event.*

## INTRODUCTION

Prior to 1983, the long-spined echinoid *Diadema antillarum* Philippi was often the dominant herbivore in tropical Western Atlantic reef environments,

reaching densities of 71 individuals per square meter (Sammarco, 1980; Hawkins and Lewis, 1982). As such, it was responsible for large amounts of bioerosion while grazing algae from reef surfaces (Scoffin et al., 1980; Hunter, 1977). *Diadema* also prey on living coral (Bak and van Eys, 1975; Carpenter, 1981); thus they contributed 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 that was first observed at Galeta Point, Panama, and by January, 1984, had spread to most of the Caribbean and to Bermuda (Lessios et al., 1984). The causative agent is suspected to have been 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 et al., 1984). Whatever the exact nature of the disease, its effect was catastrophic on *Diadema* populations, with mortality rates of 98–100% in Curaçao (Bak et al., 1984), 94–99% in Panama (Lessios et al., 1984) and 99% in Jamaica (Hughes et al., 1985). Sharp increases in bottom cover by noncrustose algae subsequent to the loss of *Diadema* populations have been documented in Curaçao (de Ruyter van Steveninck and Bak, 1986), St. Croix (Carpenter, 1985) and Jamaica (Hughes et al., 1985; Liddell and Ohlhorst, 1986).

The mass mortality occurred along the fringing reefs of Bonaire, Netherlands Antilles, in November, 1983 (Lessios, 1984). By August, 1984, only broken, disarticulated spines and test plates were evident in surficial reef sediments.

The sudden incorporation of innumerable urchins into reef sediments

suggests that sediment composition may be altered by an increase in the amount of echinoderm material present. Frankel (1978) reported that mass outbreaks and subsequent mass mortalities of the Crown-of-Thorns starfish *Acanthaster planci* were preserved as layers of sediment enriched in their ossicles on the Great Barrier Reef. However, Moran et al. (1986) demonstrated that Frankel's data were insufficient to draw that conclusion. The mass mortality of *Diadema* serves as a natural experiment in taphonomy; it provides an opportunity to assess the preservation potential of an event that continues to have a profound ecological impact on coral reef ecosystems in the Caribbean and tropical Western Atlantic.

Here, I document the effect of *Diadema* mass mortality on sediment composition along the fringing reefs adjacent to Bonaire. Constituent particle analyses of samples collected from a series of reef slope profiles, and from distinct intervals within surficial reef sediments, reveal that the echinoderm fraction shows no substantial enrichment above the pre-mortality levels as reported by Kobluk and Lysenko (1984). Although skeletal elements of *Diadema* account for a large proportion of the echinoderm fraction, no pre-mortality data concerning the percentage of *Diadema* skeletal elements in reef sediments exist for comparison. The lack of signature of the mass mortality illustrates the inadequacy of the near-reef sedimentary record to preserve the event.

## STUDY SITE AND SAMPLING METHODS

Samples were obtained from four localities on the leeward side of Bonaire, an island in the La Blanquilla-Aruba chain that parallels the South American coastline (Fig. 1A). The profile of the leeward fringing reef around Bonaire consists of a narrow shelf from shore to 7–12 m depth, where the slope changes abruptly to a drop-off of 20–45 degrees (Kobluk and Lysenko, 1984). The slope again changes at 30–38 m depth, coral diversity drops off and a sandy plain slopes seaward at 5–15 degrees reach-

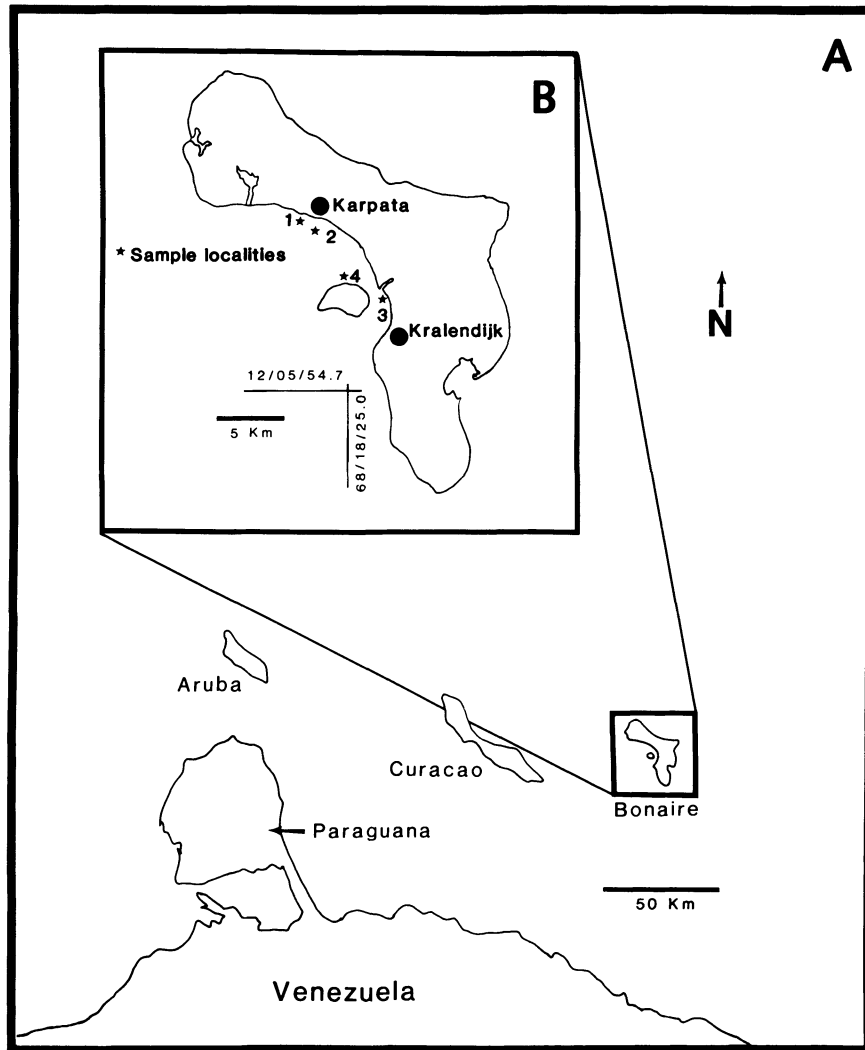


FIGURE 1—Area of study. Localities 1, 3 and 4 are reef slope profiles: locality 2 is a sand channel.

ing a maximum depth between Bonaire and Klein Bonaire of 200 m (Bak, 1975). In most places, the reef profile occurs as a series of buttresses separated by sand channels.

Surficial sediment samples were obtained at 6 m depth intervals down the reef slope at three localities and down a sand channel at one locality by a SCUBA diver (Fig. 1B). Samples from distinct horizons below the sediment-water interface were obtained from two adjacent areas at locality 1 by means of hole encasement with a calibrated length of PVC pipe and use of an air lift

device similar to that described by Shinn (1968) to remove sediment down to specific depths. To alleviate the problem of mixing sediments from different depth intervals, samples were obtained from the encased hole at each specific depth, rather than from the air lift device itself.

Samples were air-dried, sieved through a stack of A.S.T.M. standard sieves, and the 500–1000  $\mu$  size fraction of each was split on an Otto micro-splitter until sample sizes of 400–800 grains were obtained. The samples were then analyzed with a binocular

microscope to determine total echinoderm content and the proportion of the echinoderm fraction composed of skeletal elements of *D. antillarum*. Echinoderm grains can be recognized on the basis of characteristic structures (Fig. 2). For each sample, additional quantities of the 500–1000  $\mu$  size fraction were impregnated with epoxy and ground into standard thin sections, which were point-counted on a 1 mm x 1 mm grid following the method of Ginsburg (1956).

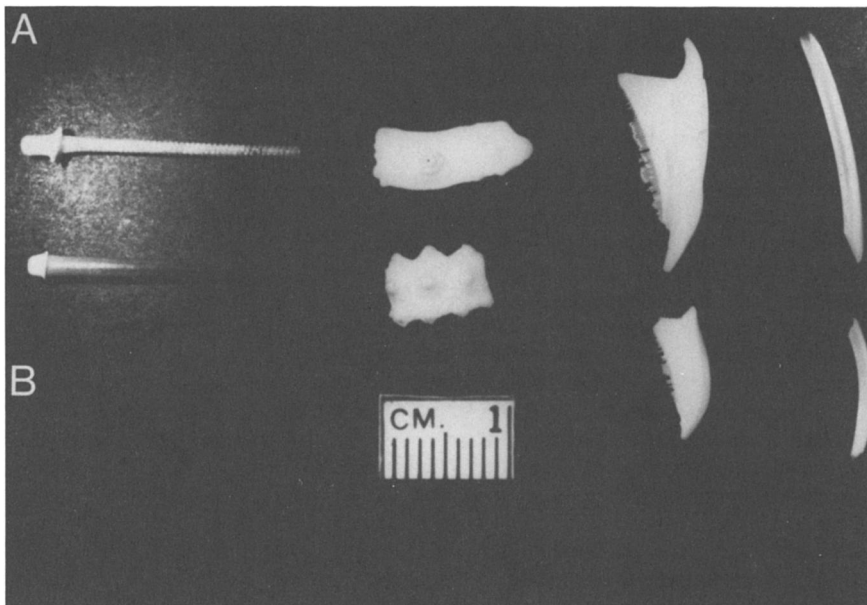
By evaluating both individual grains and thin sections, it was possible to identify not only distinctive fragments, but also echinoderm skeletal elements that had been mechanically, chemically or biologically reduced to grains of high-Mg calcite lacking any characteristic shape features. As a result, thin section point counts revealed consistently higher echinoderm percentages than grain counts because of the more accurate identification of echinoderm skeletal elements in polarized light.

*Diadema* skeletal elements have characteristic morphologies that permit recognition of spines, tubercles, teeth and components of the Aristotle's Lantern and their distinction from skeletal elements of other echinoids (see Durham and Melville, 1957; Philip, 1965 and Smith, 1984 for illustrations). Because these morphologies are rarely present in thin section, only the echinoderm fractions isolated by grain counting were analyzed for the definite presence of *Diadema* skeletal elements.

## RESULTS

Echinoderm material was present in the 500–1000  $\mu$  sediment fraction as completely disarticulated skeletal elements. Overall, this material represented only a minor fraction of reef sediments, composing from 0 to 7% of the constituents in each sample (Fig. 3). Recognition of trends is difficult, owing to the exceedingly slight variation within and between stations and low overall percentages of echinoderm material.

Thin section point counts yield consistently higher values of echinoderm percentages than grain counts (Fig. 3). At locality 1, the echinoderm fraction increases between 6 and 12 m depth,



**FIGURE 2**—Examples of characteristic morphologies with which echinoid skeletal elements can be recognized by analyzing individual grains. A) Skeletal elements of *Diadema*. B) Skeletal elements of *Echinometra*, another common regular echinoid in Bonaire.

declines at 18 m and increases to its highest value at a depth of 36 m: the base of the reef slope (Fig. 3A). This does not occur at locality 2, the sand channel, where the echinoderm fraction is highest at 18 m depth (Fig. 3B). Average percentages of echinoderm material are slightly higher in the channel than at any reef slope locality.

Point counts and grain counts reveal conflicting variation at locality 3 (Fig. 3C). The echinoderm fraction increases steadily with depth in grain counts whereas it decreases to a depth of 24 m and then increases at 30 m in samples analyzed in thin section. In thin section, the amount of echinoderm material present along the reef slope adjacent to Klein Bonaire (locality 4) decreases to a depth of 18 m and then increases at the base of the reef slope (Fig. 3D). Grain counts reveal variation of 1% or less at this locality.

Analyses of sediments collected at specific intervals below the sediment-water interface suggest that whatever variation there may be in the amount of echinoderm material is minor. Percentages increase slightly with depth in the 10 m excavation (Fig. 4A). This was also revealed by grain counts of samples

collected at the adjacent 12 m excavation but not by point counts (Fig. 4B). It should be emphasized that, as in reef slope sediments, the echinoderm fraction is quite small.

Skeletal elements of *Diadema* account for a large proportion of the echinoderm fractions isolated by grain counting, averaging 32% and ranging from 0 to 80%. Other echinoderm remains include additional regular echinoids, crinoids and ophiuroids.

## DISCUSSION

### Biostratigraphic Processes

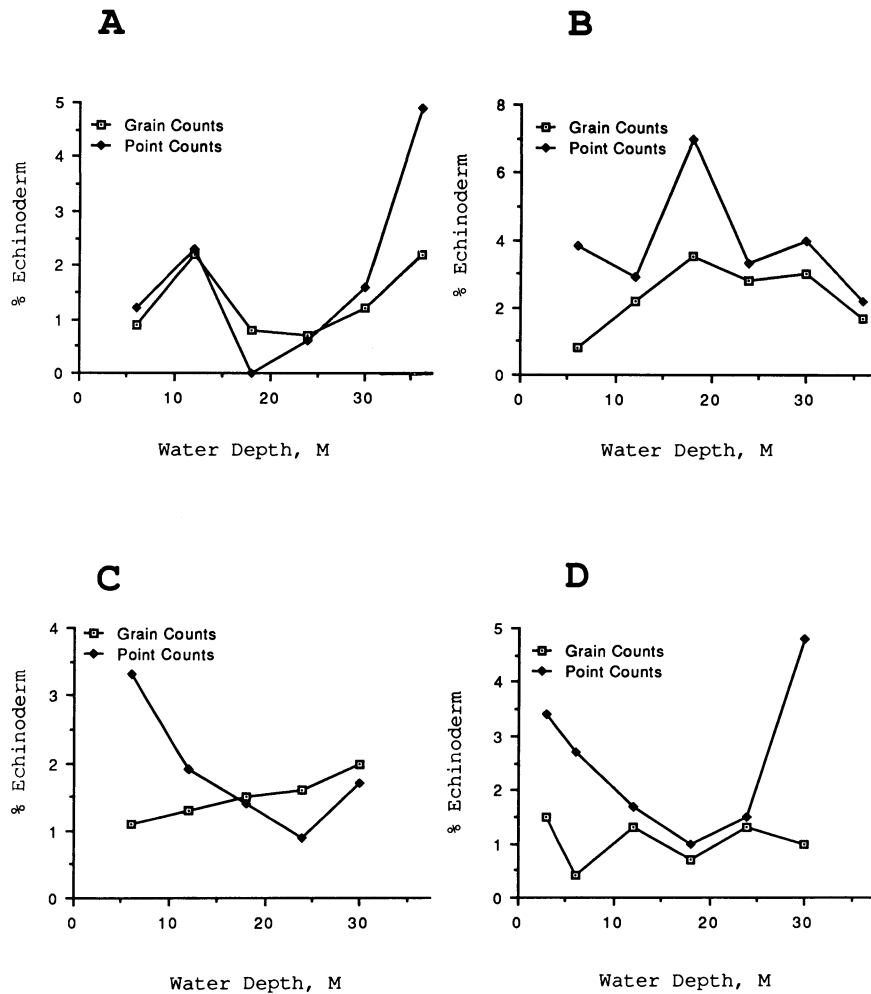
The condition of echinoderm debris in reef sediments indicates that decay and disarticulation took place quickly on the sediment surface with subsequent incorporation into the sediment. Field experiments with freshly killed *Diadema* specimens indicate disarticulation of the test within days in the absence of rapid burial (Greenstein and Meyer, 1985). Moreover, I have observed that *Diadema* in aquaria disarticulate rapidly as decay sets in. Spines fall off and the lantern and apical system collapse into the corona within a few days. In this condition, the slightest disturbance

causes the corona to disarticulate along plate sutures. These findings, along with those of Schäfer (1972), suggest that scavengers can greatly accelerate disarticulation once decay sets in. Lessios et al. (1984) reported that loss and breakage of spines accompanied the onset of the disease presumed to have caused the mass mortality. Additionally, sick *Diadema* abandoned their day-time cryptic habits and were consequently attacked by fishes that do not normally prey upon healthy individuals. Thus, it is to be expected that individuals dying during the mass mortality would be incorporated into the reef sediments as fragmented remains.

### Recognition of the Mass Mortality

No echinoderm enrichment in surface sediments occurred as a consequence of the mass mortality. A comparison of the results of this study with pre-mortality values obtained using similar methods by Kobluk and Mielczarek (1984) indicates that a slight increase in the echinoderm fraction has occurred in 4 out of 7 depth intervals (Fig. 5A). However, the overall percentages are low and do not vary substantially between the two studies. Skeletal elements of *Diadema* compose a large proportion of the echinoderm fraction. However, no data exist concerning pre-mortality proportions of *Diadema* in the sediment, making it impossible to determine what effect, if any, the mortality had on their contribution. The lack of an increase in the echinoderm fraction overall indicates that no substantial increase in the amount of *Diadema* material could have occurred.

Thus, it is highly unlikely that the slight increase in echinoderm material will constitute a recognizable signature of the mortality in the reef sedimentary record. Rather, it may be the length of time before population levels return to normal that does so. Liddell and Ohlhorst (1986) suggested that the rate of recovery of *Diadema* populations will dictate the impact of the mass mortality on the reef biota. This has been corroborated by various workers who have documented a new coral-algal equilibrium that is likely to remain as a result of the generally slow recovery of *Diadema* populations and the urchin's low



**FIGURE 3**—Percentage of echinoderm material versus depth at localities 1 through 4 (A through D, respectively) as determined by grain counts and point counts. Locality 2 (B) is the sand channel locality.

larval recruitment rate (Bak, 1985; de Ruyter van Steveninck and Bak, 1986; Lessios, 1988). These observations also apply to the signature of the event in coral reef sediments. The net effect of the slow *Diadema* recovery may be the deposition of an interval essentially barren of their remains (and therefore a lower overall echinoderm fraction). Thus, it may ultimately be the case that a decrease, rather than an increase, in *Diadema* content records the event in reef sediments. However, both bioturbation and storm processes may well obliterate any such signature. The latter point emphasizes the inadequacy of the reef environment to preserve an event that continues to have a profound

impact on coral reef ecosystems in the Caribbean and tropical Western Atlantic.

#### Distribution of Echinoderm Material

The distribution of live echinoids at regular depth intervals along the reef slope was determined by Kobluk and Lysenko (1984) prior to the mass mortality. Live echinoid abundance decreased consistently with depth (Fig. 5B). The amount of echinoderm material in the sediment generally does not reflect the distribution of live echinoids, particularly at the base of the reef slope, where live echinoid abundance is lowest and the percent contribution of echinoderms to the sediment increases

[Fig. 3A, C and D (delineated by point count data only)]. This suggests that echinoderm skeletal elements are undergoing limited transport and accumulating at the base of the reef slope. The channel sediment represents an amalgam of shelf and reef slope material. Moreover, the echinoderm fraction is composed of other common reef echinoderms and would not be expected to mirror the distribution of a single echinoderm group.

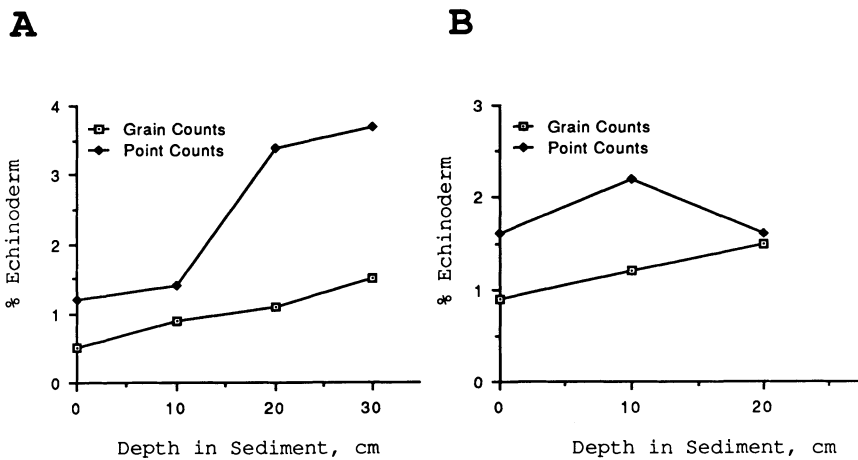
Figure 4 suggests that no "echinoderm spike" exists within surficial reef sediments; if such an enrichment was ever present, it probably disappeared quickly as a consequence of the bioturbation that occurs along the reef profile (Kobluk and Lysenko, 1984).

#### Implications for Echinoid Fossil Record

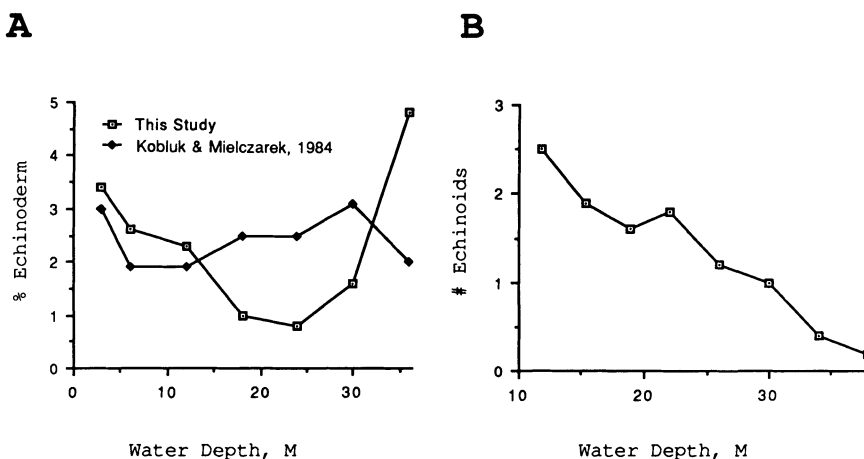
The lack of a clear mortality signature in reef sediments underscores the rapidity with which populations of *Diadema* have been reduced to essentially unrecognizable carbonate sand grains. Although less than one year elapsed between the time of mortality (November, 1983) and the time of sampling (August, 1984), the potential record of the event has been lost. However, well-preserved diadematoïd echinoids have been described. Aslin (1968) demonstrated that well preserved specimens of the regular salenioid *Acrosalenia* from the Middle Jurassic were preserved because of a rapid burial event. Rosenkranz (1971) invoked rapid sedimentation and the differing abilities to escape it as responsible for producing echinoid lagerstätten. Bloos (1973) suggested that rapid burial entombed individuals of the Middle Jurassic pedinoid *Diademopsis*. This emphasizes the likelihood that well-preserved fossil diadematoïd assemblages probably reflect truly extraordinary taphonomic events.

#### CONCLUSIONS

1. The mass mortality has not resulted in an echinoderm-rich horizon in surficial reef sediments, nor is the amount of echinoderm material in the sediment markedly greater than that reported by Kobluk and Lysenko (1984) prior to the mortality.



**FIGURE 4**—Percentage of echinoderm material versus depth at specific horizons within surficial sediments. A) Excavation in 10 m of water. B) Excavation in 12 m of water. Note that both excavations occurred adjacent to locality 1.



**FIGURE 5**—A) Comparison of the results of this study with those obtained by Kobluk and Mielczarek (1984) prior to the mass mortality. Both curves were generated using average percent echinoderm determined from three reef slope localities. Values in both studies were obtained by point counting. B) Distribution of living echinoids versus depth (Kobluk and Lysenko, 1984).

2. Preservation of the mass mortality may be contingent on the slow rate of recovery of *Diadema* populations, although it is unlikely that slight increases or decreases in the echinoderm fraction could be observed in a stratigraphic succession.
3. Once dead, individuals of *Diadema* disarticulate rapidly as a result of biostratigraphic processes. They are then incorporated into surficial reef sediments as fragmented remains.
4. Echinoderm material undergoes

limited transport along sand channels to the base of the reef slope; the distribution of echinoderm skeletal elements does not reflect that of the living echinoid fauna.

5. An "echinoderm spike" in the fossil record may well record highly unusual mass mortalities and rapid coincident or subsequent burial.

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