

# Reports

## Spread of *Diadema* Mass Mortality Through the Caribbean

**Abstract.** *Populations of the ecologically important sea urchin Diadema antillarum suffered severe mass mortalities throughout the Caribbean. This mortality was first observed at Panama in January 1983; by January 1984 it had spread to the rest of the Caribbean and to Bermuda. The sequence of mortality events in most areas is consistent with the hypothesis that the causative agent was dispersed by major surface currents over large distances. However, some of the late die-offs in the southeastern Caribbean do not fit this pattern. Several lines of indirect evidence suggest that the phenomenon is due to a water-borne pathogen. If so, this is the most extensive epidemic documented for a marine invertebrate.*

The black sea urchin *Diadema antillarum* is ubiquitous in shallow waters of the Caribbean. It inhabits coral reefs, sea-grass beds, mangroves, and sandy bottoms (1), reaching densities of 71 individuals per square meter (2). Its effects on the geomorphology and ecology of coral reefs are profound. *Diadema* erodes more calcium carbonate from reef framework than any other organism (3), eats live coral (4, 5), affects algal and coral community diversity (2, 5), competes with other sea urchins (6) and herbivorous fish (6, 7), and causes bare areas in sea-grass beds around the fringes of coral reefs (8). In January 1983 we became aware of mass mortality in this species on the Caribbean coast of Panama (Fig. 1); by September 1983 this mortality had extended to many other areas (9). Population densities of *D. antillarum* were reduced to 1.1 to 5.8 percent of their previous levels in Panama (10), to 1 percent in Jamaica (11), and to 0.6 percent in Curaçao (12). The causative agent has not been identified. We report that *D. antillarum* mass mortality has now affected the entire Caribbean and Bermuda and that it appears to be due to a waterborne pathogen transported by ocean currents.

To determine the geographical extent of the mortality and to test the hypothesis that the causative agent was dispersed with currents, we compiled records of the timing of outbreaks in each locality (13). Mass mortality of *D. antillarum* was first observed at Galeta Point, Panama, in mid-January 1983 (14). In approximately 3 months it had extended to the San Blas Archipelago (Fig. 2). It reached the Panama-Colombia border at the end of June and arrived in Santa

Marta, Colombia, in mid-August (15). Prevailing near-shore surface currents follow the same path (Fig. 2). At the end of June *D. antillarum* die-offs were observed on the coast of Costa Rica (16). This appearance is also in accordance with our hypothesis of a current-dispersed causative agent, because a large eddy exists from Panama to Costa Rica (17, 18). The appearance of mass mortality at the Cayman Islands in the beginning of June (19), before its arrival at Costa Rica or Colombia, is also consistent with the existing information on Caribbean surface water circulation. The main Caribbean current (20) travels past Panama toward the Cayman Islands with twice the average velocity of the eddy from Panama to Costa Rica (17). What is more, this eddy may at times reverse direction (18). Studies of Caribbean water circulation with satellite-tracked drifters (18, 21) have revealed a path of water movement from Panama to the Caymans that is interrupted by meanders and eddies at the Cayman ridge; such turbulence is likely to have carried the



Fig. 1. *Diadema antillarum* dying on the Caribbean coast of Panama during mass mortality. [M. Parker photo]

mortality laterally toward the Caymans.

That the mortality should reach the Caymans before Jamaica (11, 22) is also consistent with the hypothesis that it was carried by currents, because most of the water flowing past Jamaica travels westward, coming from the Windward Passage between Hispaniola and Cuba (23). However, an east-bound current exists from the Caymans to Jamaica in early summer (17). This current accounts for the transportation of the mortality to the western tip of Jamaica in early July (22). The mortality continued spreading eastward along the north side of Jamaica, even though the offshore surface current is in the opposite direction. It then rounded the east end of the island and spread westward along the south side (22).

Die-offs occurred almost simultaneously at Cancun, Mexico (24), and at Belize (25) in mid-July, indicating that the causative agent had traveled with the main Caribbean current to the Yucatan peninsula and subsequently followed the dividing near-shore current (26) both northward and southward. It also followed the Florida current to the northeast. The first noted outbreak in Florida was at South Key Largo in late July (27); mortality subsequently spread to North Key Largo and south to the lower Keys, reaching Looe Key in early August (28) and the Dry Tortugas in early September (29). In Florida, as in Jamaica, the progress of the phenomenon on a local scale did not follow the major offshore surface currents. Although eddies and a near-shore southward-flowing countercurrent are present in Florida, the main direction of the offshore current is northward (30).

The mortality reached the northern Bahamas in early August and Andros Island later that month (31), probably through the Florida Straits, because no die-offs had occurred in Puerto Rico (32), Grand Turk (33), or Hispaniola (34, 35) up to that time. *Diadema* mass mortality occurred at Bermuda in mid-September (36). The causative agent could have been carried northward from Florida in the Gulf Stream and then southward to Bermuda in a large "cold-core ring" (37) that formed in August at about 38°N and headed southward to within 200 miles of Bermuda (38). Thus, until September 1983 the sequence of outbreaks of *D. antillarum* mortality followed, over large distances, the pattern predicted from Caribbean surface water circulation.

After late September the agreement between Caribbean water circulation and sequence of mortality events broke down. At that time die-offs occurred at Barbados (39) upstream from any affect-

ed locality. Coastal countercurrents, although frequent along the borders of main currents (40), cannot be invoked as carriers of the causative agent from Colombia to Barbados because outbreaks did not start at Curaçao until early October (12), at Bonaire until early November (41), and at Venezuela until late November (42); they had not occurred at Tobago as of early December (43). In view of the mortality in Barbados, the subsequent die-offs in St. Lucia in early November (44) and in Martinique in mid-December (45) fit the predictions of our hypothesis. However, the pattern breaks down once again when the islands to the northwest of Martinique are considered. In late October *D. antillarum* was dying in Haiti (35); mortality then spread along the coast of Hispaniola, eastward along the south coast and then westward along the north coast (46). St. Thomas and St. John in the U.S. Virgin Islands were affected in early December (47) and Tortola and Virgin Gorda in the British Virgin Islands in early January 1984 (48). However, no *Diadema* mortality had occurred in Guadeloupe as of mid-December (45) or in St. Kitts as of early December (49). St. Croix (50) and Puerto Rico

(32) were affected in mid-January 1984. Perhaps mortality was spread from Barbados to the northwest in this uneven fashion by meanders and eddies formed in the Antillean region by the Aves Ridge (21). Perhaps the mortality agent, having entered the Central Atlantic water circulation from Florida, returned to the southeastern Caribbean at multiple points. Or perhaps the outbreaks in Barbados and Hispaniola are independent events, much as the start of the mortality in Panama must have been.

The spread of mortality by currents suggests that it is due to a water-borne agent. That *D. antillarum* kept for months in aquaria with ocean water inflow in the Discovery Bay Marine Laboratory, Jamaica (22), and in the Coral World Aquarium, St. Thomas (47), died at the same time as natural populations at these islands also supports this hypothesis. Three lines of evidence suggest that this causative agent is a pathogen, perhaps similar to the one responsible for the epizootics of the green sea urchin *Strongylocentrotus droebachiensis* at Nova Scotia (51), rather than a pollutant or a mass of water with abnormal physical characteristics. First, mortality of *D.*

*antillarum* spread from Panama through the Yucatan and Florida Straits to Bermuda without any dissipation of its severity; yet none of the other six sea urchin species (52) coexisting with it has suffered unusual mortality in any locality (10–12, 15–16, 19, 22, 27, 28, 31, 47). It is hard to imagine a pollutant so toxic that it could remain lethal over such a wide area yet so specific that it affected only one species. Second, water temperature and salinity in Panama did not undergo any abnormal fluctuations during the time of *Diadema* mass mortality (10). Third, although loss of zooxanthellae and death of some corals occurred in a few areas of the Caribbean (9), this phenomenon did not follow the spatial and temporal sequence of *Diadema* mortality events (53). Thus an explanation for the mortality of both groups based on a single factor and favoring physical fluctuations as the cause of die-offs is unlikely. *Diadema mexicanum* in the eastern Pacific, although closely related to *D. antillarum* (54), did not suffer mass mortality (10). Corals in the same area, however, were devastated during the 1983 El Niño (54, 55). Finally, the local progress of mortality in directions other than that of the prevailing offshore surface currents in northern Jamaica, the Florida Keys, the Bahamas, and northern Hispaniola also suggest a pathogen as the most probable causative agent. A pathogen that travels over areas of open water with the currents until it makes landfall at a particular point is then likely to spread with shore eddies or tidal currents or by cross-infection between adjacent populations.

Whatever the nature and mode of transmission of the causative agent of mortality may be, its effects have extended over a geographic area of approximately 3.5 million square kilometers (not counting Bermuda); this is the most widespread epidemic ever documented for a species of marine invertebrate. By comparison, the deaths of sponges in the Bahamas and Belize (56), the epizootics of sea urchins in California and Canada (51, 57), and the die-offs of starfish in the Gulf of California (58) are local phenomena. Recovery of *Diadema* populations will probably be slow because of the paucity of unaffected localities that could serve as sources of larvae. Our data show that *D. antillarum* populations in Panama are still less than 10 percent of their previous numbers 1 year after the die-offs (10). In view of the important role of *D. antillarum* in Caribbean reef ecology (1–8), the repercussions of its mass mortality are likely to be far-reaching, rivaling those of the wasting disease

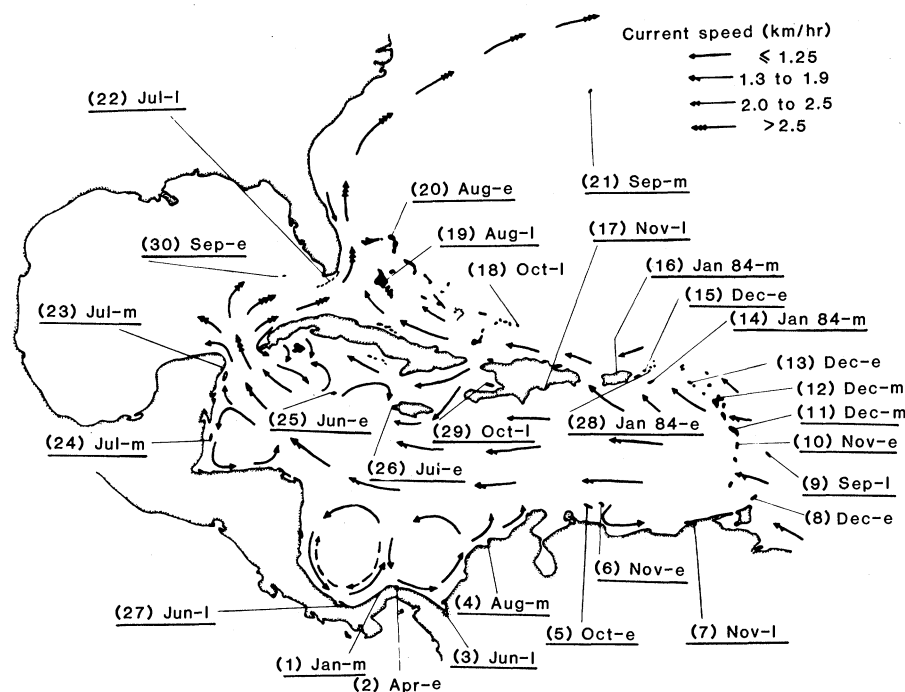


Fig. 2. Spread of *Diadema* mass mortality through the Caribbean and the western Atlantic. Underlined dates indicate the first time mortality was noted at each locality. Dates without underlining indicate the last time lack of mortality was verified in unaffected areas. e, m, and l indicate the early, middle, and late part of the month. Unless otherwise noted, dates refer to 1983. Current patterns were compiled from (17, 18, 20, 21, 40, 61). Numbers denote the following localities: 1: Galeta Point, Panama; 2: San Blas Archipelago; 3: Puerto Obaldia, Panama; 4: Santa Marta, Colombia; 5: Curaçao; 6: Bonaire; 7: Venezuela; 8: Tobago; 9: Barbados; 10: St. Lucia; 11: Martinique; 12: Guadeloupe; 13: St. Kitts; 14: St. Croix; 15: St. 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.

of the eelgrass *Zostera marina* (59) in the North Atlantic and of the mass mortality of corals in the eastern Pacific related to the El Niño (9, 54, 55).

*Note added in proof:* Mass mortality reached Tobago in mid-February (60).

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10 February 1984; accepted 26 March 1984

## The Jovian Nebula: A Post-Voyager Perspective

**Abstract.** *Voyager 1* carried a diverse collection of magnetospheric probes through the inner Jovian magnetosphere in March 1979. The ensuing data analysis and theoretical investigation provided a comprehensive description of the Jovian nebula, a luminous torus populated with newly released heavy ions drawn from Io's surface. Recent refinements in Earth-based imaging instrumentation are used to extend the *Voyager* in situ picture in temporal and spatial coverage. An analysis of [SIII] and [SII] optical emissions observed during the Jovian apparitions of 1981 through 1983 reveals three distinct torus components. Regularities have been identified in the ion partitioning and ion densities in the hot outer and inner tori, sharply defined radial structure is found in the plasma near Io, and the relative permanence of the cool inner torus is inferred. An extended cloud of neutral material is required as a source of fresh ions in the nebula.

The Io torus was extensively probed during the *Voyager 1* flyby in March 1979 with a trajectory that penetrated the Jovian magnetosphere to distances within the orbit of Io (*I*). With Io as a source of heavy ions, Jovian rotation as an energy source, and Jupiter's magnetic field as a confinement mechanism, the Io torus nevertheless exhibits many characteristics typical of ionized gas found in planetary nebulae and thus the "Jovian nebula" is also accessible to Earth-based

astronomy. This is the first astronomical nebula to be studied both by the methods of classical astronomy and by in situ measurements. Earth-based astronomy provides coverage of the entire nebula over an extended period of time, bridging the gaps between infrequent spacecraft visits to Jupiter.

The Jovian magnetic field imposes a well-defined geometry upon the Iogenic plasma distribution. Jupiter presents a nearly undistorted dipole magnetic field