Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef

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Many coral reefs have been degraded over the past two to three decades through a combination of human and natural disturbances. In Jamaica, the effects of overfishing, hurricane damage, and disease have combined to destroy most corals, whose abundance has declined from more than 50 percent in the late 1970s to less than 5 percent today. A dramatic phase shift has occurred, producing a system dominated by fleshy macroalgae (more than 90 percent cover). Immediate implementation of management procedures is necessary to avoid further catastrophic damage.

14. Using the rate-dependent strength-scaling law from K. R. Housen and K. A. Holsapple (Icarus 84, 226 (1989)) and an rms collision velocity of 3.92 km/s (11) and assuming that half of the energy is partitioned into disruption of the target, we find that blocks 30 to 100 m in diameter can be disrupted by impactors that are 1.3 to 4 m in diameter. The adopted collision probability (11) is 3.8 x 10^{-10} km^{-2} year^{-1}. Assumption of a power-law exponent of ~4.0 for small projectiles yields 30 million to 80 million years for block lifetime against disruption (possibly younger if there are enhanced collisions by Koronis family asteroids) These results are in accord with meteorite exposure ages (22), which suggest that meter-sized objects survive a few tens of millions of years.

15. P. Thomas et al., J. Geophys. Res. 84, 8457 (1979); (4). Because recognizability of lineaments can be strongly influenced by the single azimuth of illumination, our knowledge of lineament orientations may be strongly biased.

16. Using the Holsapple scaling law (K. A. Holsapple, Annu. Rev. Earth Planet. Sci. 21, 333 (1993)) with an expermentally measured gravitational self-compression term (plus other assumptions) as in (14), we estimate that Ida can be shattered by a projectile 1.7 km in diameter. Ida is in the size range at which the collisional energy needed to shatter it is comparable to that needed for fragments to escape from Ida's gravity. Thus, the lifetime against disruption is about the same as the lifetime against shattering. Here we assume that Ida responds to collisions as if it were a strong rocky body; the uncertainties in the lifetime of 1.5 billion years are at least a factor of 2, mostly because of the uncertainties in (i) the effective strength and (ii) the asteroid size distribution at sizes between 1 and 25 km.

17. R. W. Carlson et al., Eos 74 (no. 43), 384 (1993).
23. We thank the Galileo project and the National Aeronautics and Space Administration (NASA) for support; in particular, the Galileo Flight Team, led by W. O'Neil, N. Amsman, L. Mandano, and D. Adams. The Ida mosaic was constructed by L. Wainio's group and we wish to recognize H. Mortensen. We also acknowledge D. J. Tholen, P. R. Binzel, P. Magnusson, A. Barucci, S. Mattioli, R. Sullivan, R. Pappardello, P. Gehrels, J. M. Pettit, J. Moore, W. F. Bottke, M. Nolan, E. Fyean, W. Merline, B. E. A. Mueller, E. Asphaug, B. Carolich, P. Lee, D. Simonelli, R. Wagner, P. J. Gudee, J. Yoshimizu, and R. Hasegawa. A portion of this research was carried out at the Jet Propulsion Laboratory, California Institute of Technology, under contract with NASA. The National Optical Astronomy Observatories are operated by the Association of Universities for Research in Astronomy, Inc. (AURA), under cooperative agreement with the National Science Foundation.

Overfishing (1960s to Present)

Chronic overfishing is an ever increasing threat to coral reefs worldwide as coastal populations continue to grow (for example, Fig. 1) and exploit natural resources (6). Extensive studies in Jamaica by Munro (7) showed that by the late 1960s fish biomass had already been reduced in preceding dec-
ades by up to 80% on the extensive (but narrow) fringing reefs of the north coast, mainly a result of intensive artisanal fish-trapping (Fig. 2). By 1973, the number of fishing canoes deploying traps on the north coast was approximately 1800 (or 3.5 canoes per square kilometer of coastal shelf), which was two to three times above sustainable levels (7). The taxonomic composition of fish has changed markedly over the past 30 to 40 years. Large predatory species, such as sharks, lutjanids (snappers), carangids (jacks), balistids (triggerfish), and serranids (groupers) have virtually disappeared, while turtles and manatees are also extremely rare. The remaining fish, including herbivores such as scarids (parrotfish) and acanthurids (surgeonfish), are small, so that fully half of the species caught in traps recruit to the fishery below the minimum reproductive size. Indeed, because adult stocks on the northern coast of Jamaica have been sharply reduced for several decades, populations today may rely heavily on larval recruitment from elsewhere in the Caribbean (7). This sequence of changes was repeated more recently along the southern coast of Jamaica. There, the broader coastal shelf has become increasingly accessible to a modernizing fishing fleet, with the number of motorized canoes almost doubling from the 1970s to the mid-1980s (8). Despite this increased fishing effort, the catch from the south coast remained the same over this 15-year period (that is, the catch per unit effort declined by half). The species composition of the fishery has also changed markedly, indicative of severe overfishing nationwide (6-8).

The ecological effects of the drastic reduction in fish stocks on Jamaica’s coral reefs as a whole were not immediately obvious. Throughout the 1950s to the 1970s the reefs appeared to be healthy; coral cover and benthic diversity were high (3) (Figs. 2 and 3). There were relatively few macroalgae throughout this period despite the paucity of large herbivorous fish as a result mainly of grazing by huge numbers of the echinoid Diadema antillarum (9, 10). The major predators of adult Diadema are fish (for example, ballistids, sparids (porgies), and batrachoidids (toadfish) (11) that are now rare in Jamaica. Other fish (such as scarids and acanthurids) compete strongly with Diadema for algal resources, as evidenced by competitor removal experiments (12). Therefore, the unusually high abundance of D. antillarum on overfished reefs such as Jamaica’s was almost certainly a result of the over-exploitation of reef fisheries. Hay (13) investigated this hypothesis on a geographic scale and found that densities of echinoids were much greater on overfished than on pristine reefs throughout the Caribbean. A mass mortality of Diadema in 1983 had far-reaching consequences, in part because of the prior reduction (for several decades) of stocks of herbivorous and predatory fish.

Fig. 2. (A) Healthy reefs are characterized by a high degree of habitat heterogeneity, which provides habitat for fish and invertebrates. (B) A Z-shaped fish trap commonly used throughout the Caribbean (7). (C) Removal of fish is likely to have promoted population growth of the echinoid Diadema antillarum, which became the dominant macroherbivore on overfished reefs throughout the Caribbean (13). (D) After the mass mortality of Diadema from disease in 1983, spectacular algal blooms ensued on overfished reefs. In Jamaica, abundance of macroalgae has increased steadily for the past decade (see Fig. 3B). (E and F) Macroalgal overgrowth and preemption of space for larval recruitment has caused a dramatic decline in abundance of corals. Here, a massive coral has been partially smothered by Lobophora (E), killing tissue overlying the white coral skeleton as revealed by peeling away the algae (F).

Fig. 3. Degradation of Jamaican coral reefs over the past two decades. Small-scale changes in (A) coral cover and in (B) macroalgal cover over time at four depths near Discovery Bay (32).
Hurricane Damage (1980)

Hurricanes, typhoons, or cyclones are predictable, recurrent events and an integral part of the natural dynamics of a coral reef (14). The regeneration of a healthy reef system is facilitated by rapid colonization of larval recruits, but in Jamaica this crucial recovery mechanism has been hindered by human influences (that is, by overfishing, which contributed to a prolonged macroalgal bloom causing recruitment failure in corals).

Extensive damage was inflicted on Jamaican coral reefs by Hurricane Allen, a category 5 hurricane that struck in 1980, following a period of almost four decades without a major storm (15). Damage was greatest at shallow sites (Fig. 3A). The hurricane smashed shallow-water branching species, most notably the elkhorn and staghorn corals (Acropora palmata and A. cervicornis). In addition, beds of the soft coral Zoanthus, which occupied large areas of the inner reef flat, were damaged by A. palmata rubble pushed shoreward by storm waves. Corals with more robust morphologies or living in deeper water (>10 to 15 m, Fig. 3A) were much less susceptible to physical destruction, so the hurricane increased the relative abundances of species with encrusting or massive-shaped colonies (15, 16). Immediately following Hurricane Allen, there was a short-lived algal bloom (primarily composed of the ephemeral Rhodophyte Liagora) probably caused by a pulse of nutrient release from terrestrial runoff and suspended reef sediments and from a temporary depression of herbivory by Diadema and other herbivores. Within a few months, however, the algae disappeared and substantial coral recruitment began (16). Recruitment by Acropora was minimal and broken fragments survived poorly (17), but other corals, notably brooding agaricids and Porites, settled in large numbers onto free space generated by the hurricane (18). For the next 3 years up to 1983, cover increased slowly as the reef began to recover (Fig. 3A). However, recovery from Hurricane Allen was short-lived and was soon reversed by biological events that were less selective and ultimately more destructive and widespread than even this powerful hurricane.

Disease and Algal Blooms (1983 to Present)

The echinoid species Diadema antillarum suffered mass mortality from a species-specific pathogen throughout its entire geographic range from 1982 to 1984 (18). In Jamaica, densities of Diadema were reduced by 99% from pre-die-off estimates of close to 10 per square meter on shallow fore-reefs, and there has been no significant recovery in the subsequent 10 years (Fig. 4A). Before 1983, Diadema were small (19-21), presumably because of food limitation caused by the prevailing high densities of this species (20). Following the die-off, the mean and maximum size of individuals increased greatly, whereas individuals in smaller size classes became uncommon, indicative of low rates of recruitment (Fig. 4B). Individuals today are large, well fed, and have well-developed gonads. However, densities may be too low for effective spawning success because fertilization in Diadema is strongly density-dependent (21).

Without Diadema, and with the continued depression of herbivorous fish from trapping, the entire reef system of Jamaica has undergone a spectacular and protracted benthic algal bloom that began in 1983 and continues today at all depths (up to 40 m or deeper) (Fig. 3B). Before the echinoid die-off, cover of fleshy macroalgae was typically less than 5% except intertidally, within damsel fish territories, or in very deep water (>25 m) where Diadema were scarce (9, 10, 13) (Fig. 3B). In the initial stages of the bloom, algae were small and ephemeral, but within 2 to 3 years weedy species were replaced by longer lived, late successional taxa (notably Sargassum, Lobophora, Dictyota, and Halimeda) that formed extensive mats up to 10 to 15 cm deep (10, 22). As a result of this preemption of space, larval recruitment by all species of corals has failed for the past decade (16). Most adult colonies that survived Hurricane Allen have been killed by algal overgrowth, especially low-growing species with encrusting or platelike morphologies (16). Additional mortality occurred following bleaching events in 1987, 1989, and 1990 (23). The most abundant coral on the fore-reef today is mound-shaped Montastrea annularis, but even this robust, dominant species has declined to 0 to 2% cover at a depth of 10 m in 1993 (24).

This decline in a long-lived coral such as Montastrea is particularly significant because it is resistant to hurricanes and is the chief frame-builder of Jamaican reefs. Its slow recruitment and growth rate (25) ensure that the decline of the past 10 years will not be reversed for many decades.

The scale of damage to Jamaican reefs is enormous. Censuses at sites 5 to 30 km
Jamaican reefs, from coral- to algal-dominated system (Fig. 6).

**Implications and Prospects for the Future**

This spectacular sequence of events highlights the dynamic and complex nature of coral reefs; points to the fundamental importance of fish, herbivory, and recovery of the reefs from physical disturbance to their functioning; and provides a clear demonstration of how quickly (one to two decades) a seemingly healthy coral reef can be severely damaged on a spatial scale similar to the size of most tropical island-nations (hundreds of kilometers). Although it was not widely recognized at the time, Jamaica's past is no guarantee of continued resilience (1). Sequential hurricanes and the Diadema die-off were sufficient to cause a radical phase shift to algae (27). Herbivorous fish (mostly juvenile scarids) responded immediately to the Diadema die-off by changing their spatial distribution and increasing their grazing rates in shallow water (28). However, this behavioral response is unlikely to be reflected later in increased fish abundance because of continued overfishing. Clearly, current stocks of herbivorous fish are not capable of reducing algal abundance in the absence of Diadema (Fig. 3B). Similarly, other echinoids have not increased in abundance to compensate for the loss of Diadema (10, 29). Recovery of Diadema has not yet taken place and is likely to be slow if densities have fallen below some threshold level required for successful spawning (21). Even a full recovery of Diadema would leave the reef reliant once more on a single dominant herbivore and vulnerable to a recurrence of disease. Future hurricanes will reinforce rather than reverse the phase shift, as illustrated by the more recent impact of Hurricane Gilbert in 1988. Also a Category 5 hurricane, it swept much of the algal covering off the reef and caused further damage to corals. However, the algae recovered fully within a few weeks of Hurricane Gilbert (Fig. 3B), mainly from regenerating filaments and holdfasts, long before successful recruitment of corals could resume. Thus, further hurricanes are likely to act in a ratchet fashion, further depressing coral abundances and favoring the phase shift to algae (Fig. 6).

There is an urgent need, therefore, to control overfishing, a call that had first been made by Munro 20 years ago (7), before more recent events demonstrated the key role of fish and echinoid herbivores in the overall functioning of Jamaica's coral reefs. On the basis of our knowledge of the demography and life histories of fish (7, 8, 30) and corals (25, 31), it will take far longer to rebuild stocks than the two to three decades it has taken to destroy them. Severe, long-term damage has already occurred, and the trajectories of coral and algal abundance (Figs. 3 and 6) predict a gloomy future unless action is taken immediately.

**REFERENCES AND NOTES**


24. Based on estimates of coral cover in 1993 at Rio Bueno, Discovery Bay, and Ocho Rios (spanning 40 km of the north Jamaican coast), Twenty replicate 10-m line-intersect transects were run at a depth of 10 m at each site.


27. There is no evidence that the nationwide algal bloom in Jamaica was caused by increased nutrients, because it occurred throughout the Caribbean immediately following the Diadema die-off (16, 20), usually far from sources of pollution. Some groundwater input does occur into the shallow margins of the back-reef at Discovery Bay, which enhances nitrates and reduces salinity close to the shore (C. F. D’Elia, K. L. Webb, J. W. Porter, Bull. Mar. Sci. 31, 903 (1981)). These conditions produce localized areas around submarine springs, typically 2 to 3 m in diameter, which contain characteristic brackish-water algal assemblages (dominated by Chelostomophora, Enteromorpha, and Ulva) that are quite unlike those occurring on the reef further offshore. None of the sites in Figs. 3 to 6 are located close to urban areas or point sources of pollution, with the exception of the Port Royal cays on the south coast near Kingston.


29. Densities of Echinometra viridis, Eucidaris tribuloides, Lytocidaris williamsii, and Trypheusstriatus ventrifrons in 1973 were reported for two Jamaican patch reefs by P. W. Sammarco [J. Exp. Mar. Biol. Ecol. 01, 31 (1982)]. The combined total then was 27.5 and 54.0 per square meter, respectively. By 1986, the combined total had fallen two- to threefold (10). In 1993, mean densities (number per square meter ± SE) on these same reefs were 14.0 ± 1.5 and 14.4 ± 1.2.


32. Coral and algal abundance (percent cover) shown here were measured from annual photographs of 10 to 20 permanent 1-m² plots at each depth (7, 10, and 15 to 20 m at Rio Bueno; 35 m at Pinnacle 1). All corals (approximately 30,000 records over 17 years) were traced and digitized to obtain relative abundances, while algal cover was estimated by superimposing a grid of dots on each image (100 per square meter) and counting those covering alga. The small-scale trends reported here for permanent plots mirror almost exactly the results from a larger scale program that was based on replicate 10-m line-intercept transects. For example, in 1993 mean coral cover (±SE) estimated from 20 random transects at each of the 7-, 10-, 15-, and 20-m stations in Fig. 3A was 5.0 ± 0.8, 5.4 ± 1.2, 5.6 ± 0.9, and 12.8 ± 4.4, respectively. Reef degradation at an even larger scale is shown in Fig. 5.

33. Data for 1976 are from (19), based on a random collection of 97 Diadema antillarum from the East Back Reef at Discovery Bay, Jamaica. Data for 1993 are based on 207 individuals from the same site.

34. Coral and macroalgal cover in Figs. 5 and 6 is based on 5 to 10 10-m line-intercept transects run at 10 m from 1976 to 1980 (mostly in 1977 and 1978) on fore-reefs at Negril, Chalet Caribe, Rio Bueno, Discovery Bay (two locations), Pear Tree Bottom, Port Maria, Port Antonio (on the north coast), and Port Royal (on the south coast). These measurements were repeated in 1990 to 1995 with 20 transects, with the addition of five more north coast sites.

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