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14. Using the rate-dependent strength-scaling law from K. R. Housen and K. A. Holsapple [*ibid.* **84**, 226 (1990)] 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  $3.8 \times 10^{-18} \text{ km}^{-2} \text{ year}^{-1}$ . 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.
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# Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef

Terence P. Hughes

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.

Coral reefs are renowned for their spectacular diversity and have significant aesthetic and commercial value, particularly in relation to fisheries and tourism. However, many reefs around the world are increasingly threatened, principally from overfishing and from human activities causing excess inputs of sediment and nutrients such as pollution, deforestation, reef mining, and dredging (1). There is a pressing need to monitor coral reefs to assess the spatial and temporal scale of any damage that may be occurring and to conduct research to understand the mechanisms involved.

Here I describe dramatic shifts in reef community structure that have largely destroyed coral reefs around Jamaica. The results presented here summarize the most comprehensive reef monitoring program yet conducted in the Caribbean, in which annual censusing has been carried out for 17 years at multiple sites and depths along 300

km of coastline. In addition, Jamaican reefs are among the best studied in the world, with a wealth of information available on marine ecology and reef status since the 1950s (2). These long-term observations provide a basis for evaluating the role of rare events such as hurricanes and for quantifying gradual trends in coral cover and diversity over a decadal time scale.

Jamaica (18°N, 77°W) is the third largest island in the Caribbean and lies at the center of coral diversity in the Atlantic Ocean (2). Over 60 species of reef-building corals occur there, four of which are spatial dominants: branching elkhorn and staghorn corals, *Acropora palmata* and *Acropora cervicornis*, which form two distinctive zones on the shallow fore-reef; massive or platelike *Montastrea annularis*, the most important framework coral; and encrusting or foliose *Agaricia agaricites* (3). Reefs fringe most of the north Jamaican coast along a narrow (<1 to 2 km) belt and occur sporadically on the south coast on a much broader (>20 km) shelf. Sea-grass beds and mangrove are

often closely associated with reefal areas and provide significant nurseries for commercially important reef fisheries (4). Similar ecosystems, with minor variations in community composition, occur throughout the Caribbean (2).

Jamaica's population growth trajectory is typical of most Third World countries (Fig. 1). The population was less than half a million before 1870, then doubled by 1925 and again by 1975, rising to 2.5 million today. Exponential growth continues, with a further 20% increase expected in the next 15 years (5). Environmental changes on land are conspicuous, with virtually all of the native vegetation having been cleared for agriculture and urban development. Major transformations are also occurring on Jamaica's coral reefs.

## 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-

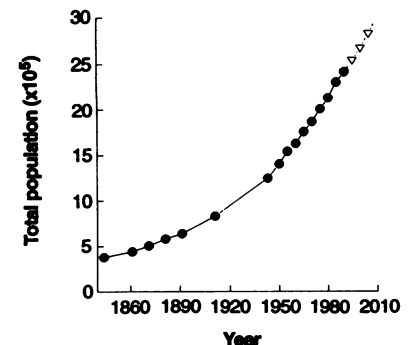


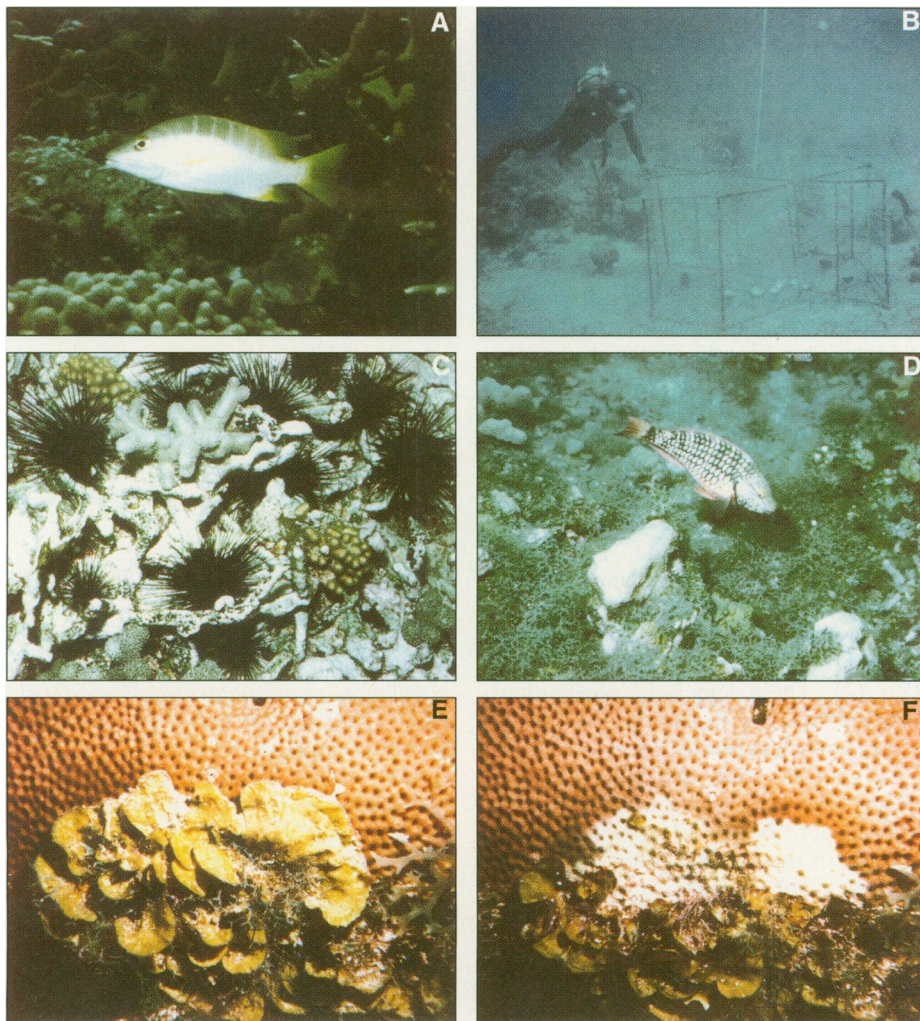
Fig. 1. Population growth of Jamaica, based on numerous sources (5).

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), ballistids (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

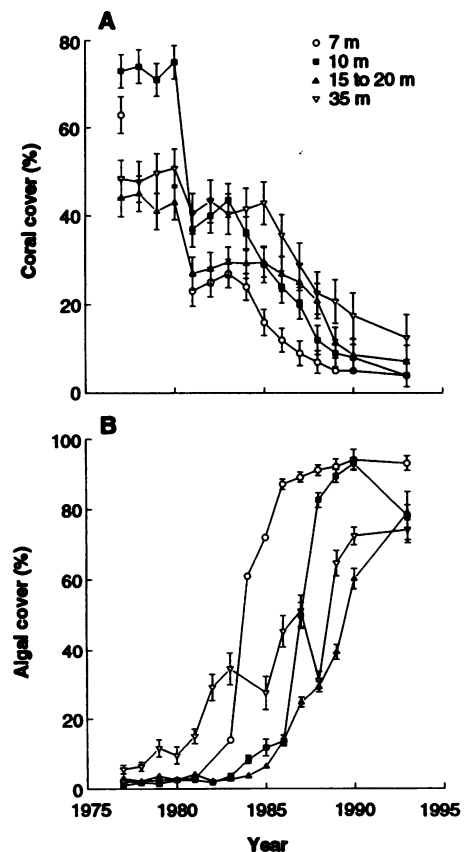
minimum reproductive size. Indeed, because adult stocks on the northern coast of Jamaica have been sharply reduced for several decades, populations today may rely heavily on larval recruitment from elsewhere in the Caribbean (7). This sequence of changes was repeated more recently along the southern 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 re-

duction 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 the 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.

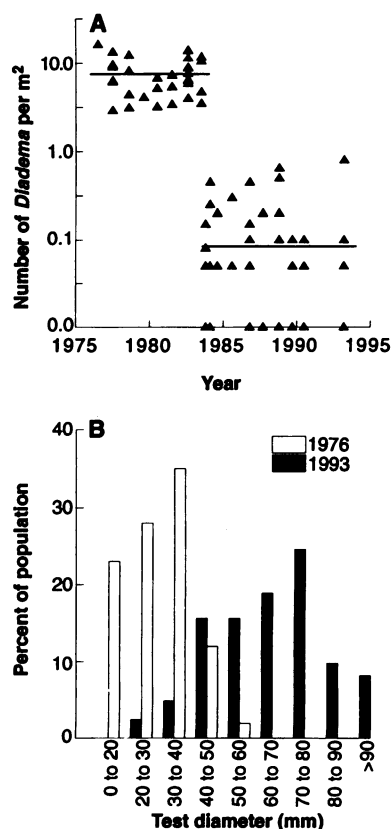
classes became uncommon, indicative of low rates of recruitment (Fig. 4B). Individuals today are large, well fed, and have well-developed gonads. However, densities may be too low for effective spawning success because fertilization in *Diadema* is strongly density-dependent (21).

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-lying 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.

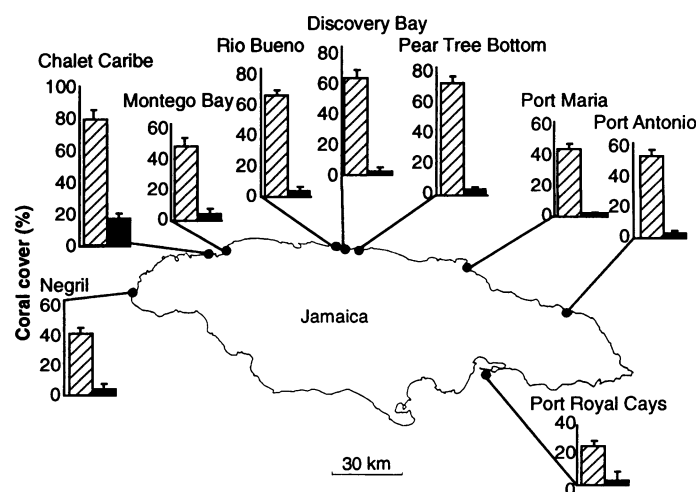
The scale of damage to Jamaican reefs is enormous. Censuses at sites 5 to 30 km

## 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



**Fig. 4.** Long-term dynamics of the echinoid *Diadema antillarum* on Jamaican reefs. (A) Abundances over time based on estimates at 14 sites along >100 km of coastline over nearly two decades. Note the 99% drop in 1983 (from a mean of 9 to 0.09 per square meter), with no recovery after 10 years. (B) Population structure of *Diadema* (33) before and after the 1983 die-off.



**Fig. 5.** Large-scale changes in community structure at fore-reef sites along >300 km of the Jamaican coastline, surveyed in the late 1970s (1977, hatched bars) and the early 1990s (1993, solid bars) (34).

apart along >300 km of coastline in 1977 to 1980 and again in 1990 to 1993 show a decline in coral cover from a mean of 52 to 3% and an increase in cover by fleshy macroalgae from 4 to 92% (Fig. 5). Indeed, the classic zonation patterns of Jamaican reefs, described by Goreau and colleagues just two to three decades ago (3), no longer exist. A striking phase shift has occurred from a coral-dominated to an 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 reefs were already extensively damaged by the late 1970s (from direct and indirect effects of overfishing) to the extent that the synergistic effects of two subsequent hurricanes and the *Diadema* die-off were sufficient to cause a radical phase shift to algae (Fig. 6). Paradoxically, the changes have occurred although reef systems have demonstrable robustness on a geological time scale. For example, coral reefs have continued to flourish despite major fluctuations in sea level occurring on a time scale of  $10^3$  to  $10^5$  years (26). However, the ability of coral reefs to cope with such disturbances in the past is no guarantee of continued resilience in the face of unprecedented and much more rapid anthropogenic stresses. It is highly probable that global reef growth is currently being outpaced by reef degradation (1), with unknown consequences for the future.

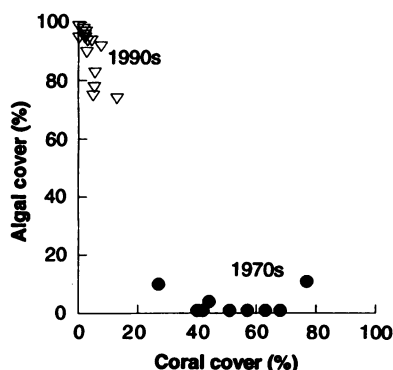


Fig. 6. Large-scale community phase shifts on Jamaican reefs, from coral- to algal-dominated systems (34).

A great deal has been learned about the functioning of coral reefs from the litany of disasters described here, and the opportunity should be seized to implement scientifically based management procedures that would facilitate processes of recovery. Clearly, the Jamaican reef system needs more herbivory to allow coral recruitment to resume (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.

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32. Coral and algal abundance (percent cover) shown here were measured from annual photographs of 10 to 20 permanent 1-m<sup>2</sup> plots at each depth (7, 10, and 15 to 20 m at Rio Bueno; 35 m at Pinnacle 1). All corals (approximately 38,000 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 algae. 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 ( $\pm$ SE) estimated from 20 random transects at each of the 7-, 10-, 15- to 20-, and 35-m stations in Fig. 3A was 5.0  $\pm$  0.8, 5.4  $\pm$  1.2, 5.6  $\pm$  0.9, and 12.8  $\pm$  2.4, 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 1993 with 20 transects, with the addition of five more north coast sites.
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