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Bleaching and Reef Community Change in Jamaica: 1951-1991[1]

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SYNOPSIS. Coral reefs have deteriorated at an accelerating pace during 40 years of ecological study at 11 sites around Jamaica. This is due to a variety of causes, whose effects are analyzed by comparing sites with known and divergent histories of environmental change. Degradative factors include overgrowth by algae, sponges, and soft corals, eutrophication by sewage nutrients, reduced herbivory due to overfishing and natural causes, hurricanes, sedimentation, diver and boat damage, and coral bleaching. These stresses have very different histories and gradients at different sites, allowing separation of their effects. Mass coral bleaching is apparently a novel phenomenon of the past decade. Non-parametric statistical analysis of relative stresses at the 11 sites shows that its pattern in space and time is unrelated to previously existing stresses.

METHODS

Diving as a long-term ecological research tool was started in Jamaica in 1951 by the late Thomas F. Goreau. Its use by his colleagues and students may make Jamaican reefs the longest directly observed submarine ecosystem. During the 1950s and 1960s reefs all around Jamaica were photographed, mapped, bathymetrically profiled, and their species and ecology described (Goreau, 1956, 1959; Goreau and Goreau, 1973; Goreau, unpublished). Detailed field notes provide unique baseline data for evaluating changes during the 1970s and 1980s. Before dying in 1970, T. F. Goreau started the Port Royal Marine Laboratory on the South Coast and the Discovery Bay Marine Laboratory on the North Coast. Over 500 subsequent publications from those labs are well known, but these important contributions are not reviewed here as many focus on single sites or species, over relatively short periods.

Reefs were studied with numerous colleagues by a variety of methods, including snorkeling, SCUBA diving, photography, photographic quadrats, line transects, sonar profiling, side-scan sonar (P. Goreau, 1990), drilling, and other techniques. Direct field observations have been repeated as frequently as circumstances permitted, and supplemented by detailed discussions with large numbers of individual divers, fishermen, and scientists with long and reliable knowledge of particular sites. The primary technique used is detailed and sustained observation of species distributions, natural history, and environmental history. The focus has been on corals, the major producers of reef framework, along with algae, which now dominate biomass at many sites. Large areas of reefs are surveyed by snorkeling long distances, observing coral and algal species abundance and distribution patterns (*e.g.,* Table 1), and supplemented by close-up observation of all corals and algae during dives at representative sites based on snorkel surveys. Species lists can be used to record numbers, variants, and distribution patterns of individual species. Species distribution patterns are inferred from what are effectively thousands of observations. Interactions between species and environmental gradients affecting coral cover and growth rates are noted. Coral growth rates in Jamaica have been studied by repeated observation, photography, respirometry (Goreau, 1956, 1963; Porter, 1985), radio-isotopes (Goreau and Goreau,

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[1] From the Symposium on *Long-Term Dynamics of Coral Reefs* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1991, at Atlanta, Georgia.

TABLE 1. *Negril coral abundances and bleaching.*[1]

Coral species	Aug. 1960	Nov. 1991	Bleaching
*Millepora complanata**	common	common	2
*Millepora squarrosa**	not reported	not seen	–
*Millepora alcicornis**	not reported	common	2
Stylaster roseus	uncommon	uncommon	–
Stephanocoenia michelinii	deeper water	uncommon	–
Acropora palmata	abundant	rare	1
Acropora cervicornis	common	rare	1
Acropora prolifera	not reported	not seen	–
Madracis decactis	uncommon	not seen	–
Madracis mirabilis	common	common	1
Madracis pharensis	not seen	not seen	–
Madracis formosa	not seen	not seen	–
*Agaricia agaricites**	common	common	1
Agaricia tenuifolia	not reported	not seen	–
Agaricia undata	not reported	common	2
*Agaricia fragilis**	common	common	3
*Agaricia lamarcki**	not reported	common	3
Agaricia grahamae	not reported	not seen	–
Helioseris cucullata	common	not seen	–
*Siderastrea siderea**	common	common	9
*Siderastrea radians**	common	common	6
*Porites porites**	uncommon	uncommon	1
Porites furcata	common	common	2
Porites divaricata	not reported	uncommon	–
*Porites astroides**	abundant	abundant	2
Porites branneri	not reported	not seen	–
*Favia fragum**	common	common	4
*Diploria strigosa**	common	common	3
*Diploria clivosa**	common	common	2
*Diploria labyrinthiformis**	common	common	1
*Manicina areolata**	common	common	3
*Colpophyllia natans**	common	common	2
*Montastrea annularis**	common	common	2
*Montastrea cavernosa**	common	very common	7
Solenastrea hyades	not seen	not seen	–
Astrangia solitaria	common	not seen	–
Phyllangia americana	common	not seen	–
Oculina diffusa	not seen	not seen	–
Oculina valenciennesii	not seen	not seen	–
*Meandrina meandrites**	common	common	5
Dichoecenia stokesi	common	common	3
*Dendrogyra cylindrus**	rare	rare	1
Mussa angulosa	common	uncommon	–
Isophyllia sinuosa	common	common	2
Isophyllastrea rigida	common	common	3
Mycetophyllia lamarckana	common	common	2
Mycetophyllia ferox	not reported	not identified	–
Mycetophyllia aliciae	not reported	not identified	–
Mycetophyllia danaana	not reported	not identified	–
Mycetophyllia reesi	not reported	not identified	–
*Eusmilia fastigiata**	common	common	1
Tubastrea coccinea	not seen	not seen	–
Scolymia lacera	not reported	uncommon	1
Scolymia cubensis	not reported	not seen	–
Cladocora arbuscula	not reported	not seen	–

1959, 1960), sclerochronology (Dodge *et al.*, 1974; Goreau, 1977; Huston, 1985; Teal, 1986; Goreau *et al.*, 1988; Goreau and Dodge, unpublished), non-destructive *in situ* growth measurements (Goreau and Macfarlane, 1990), and other techniques.

Many species which are relatively uncommon, have broad distribution ranges, or are sporadic in distribution, provide little environmental information. Some have puzzling patterns: the brown alga *Turbinaria turbinata* was very common, vanished for no obvious cause, and was later replaced by *Turbinaria tricostata.* A number of species tend to be more abundant in certain areas which are shallow, deep, rough, calm, near to or away from freshwater, or are more tolerant or intolerant of sediment, nutrient, or temperature stress (Goreau, 1959). Changes in the abundances of these indicator species can be strongly indicative of changing environmental conditions. Some algae are strong indicators of herbivory because of different feeding preferences of major herbivores (Sammarco, 1982*a, b*; Lewis, 1986; Liddell and Ohlhorst, 1986; Hughes *et al.*, 1987; Goreau and Goreau, 1988). The red alga *Liagora* is normally very rare but quickly becomes dominant over large areas for about a year after hurricanes. Many algae are sharply zoned along stress gradients, making them useful for characterizing degree of eutrophication stress from external nutrients. Sewage stimulates green algae such as *Enteromorpha, Ulva, Chaetomorpha,* and other species capable of polyphosphate storage, which dominate near sewage outfalls. With distance green, red, and then brown algae generally predominate. In submarine springs with high nitrate and low phosphorus contents, red algae, including *Ceramium, Acanthophora,* and *Hypnea* co-dominate with greens like *Cladophora* and *Bryopsis.* Algal overgrowth of the reef is seen in reef habitats where nitrate is as low as a few micromoles per liter (Lapointe *et al.*, 1988). Good indicator species of sediment and sewage stress are also found among some sponges which are zoned along stress gradients (Goreau, 1992).

This paper summarizes general island-wide changes over the past 40 years seen by repeated direct observation, focusing on eleven sites (Fig. 1). These sites, about a fifth of those examined, were chosen because they are representative of larger areas or have strong gradients in various stress factors. Their ecological history has been followed over all or most of the period. Although all stresses probably act to some degree at all sites, their intensity and duration vary greatly among sites, allowing effects of major stresses to be separated.

COMPARATIVE ENVIRONMENTAL HISTORIES OF SITES

1) Hellshire

Hellshire is the most intensely and longest stressed reef site in Jamaica. Over a million people, or half the island's population, live nearby. Kingston Harbour outflow is pushed directly towards these reefs by currents. These reefs are exposed to the most polluted waters in Jamaica, into which almost all the country's industrial wastes, commercial pollutants, ship traffic, hydrocarbons, and sewage effluents flow. The area is strongly affected by high turbidity from erosion of deforested mountains around Kingston, and by sediment plumes from the Yallahs River to the East during rainy seasons. Dredging

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[1] Coral species as listed in T. F. Goreau, 1960, generally ammended for later species name changes. There still remains taxonomic uncertainty in certain genera, particularly *Agaricia, Montastrea,* and *Mycetophyllia.* Underlined species have either undergone largest reductions in abundance, or are the most abundant species which were highly bleached. Species marked by asterisks have been greatly affected by bleaching in Jamaica during severe episodes, and may have largely recovered at the time of the survey (late November 1991, after strong storms had lowered water temperatures). Relative abundances were noted on long transects by SCUBA or snorkelling. Bleaching frequency was estimated on a 10 point scale, where – indicates the species was not seen or too rare for bleaching frequency to be meaningful, 1 indicates that at least one of those seen were bleached, and 10 indicates that all coral heads showed signs of bleaching over part or all of their surface. Most species not seen bleached were very rare or are small solitary coral species which lack symbiotic algae. Estimates are pooled based on all observations, and are probably accurate to within plus or minus 10%.

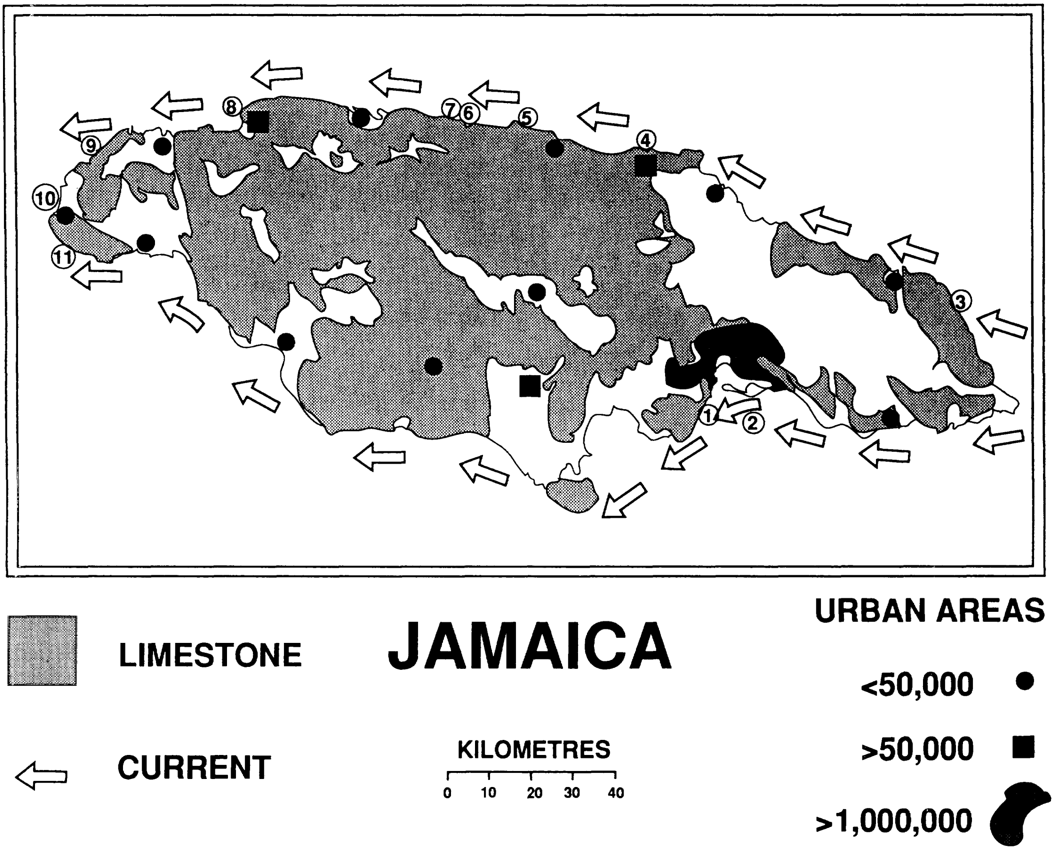

FIG. 1. Map of Jamaica showing sites discussed in text. Major population centers are indicated by size. Coastal current directions are indicated by arrows. North is at top. Map by Dr. Peter D. Goreau.

for airport construction and ship channel maintenance has caused episodic impacts from resuspended sediment plumes. In the early 1950s the reefs of Hellshire were subject primarily to high turbidity, and had probably been so for at least three centuries. Dominant corals were those adapted to high energy and high turbidity. Open exposure to the east causes heavy wave activity under all but calmest conditions. Much damage occurred after Hurricane Charlie in 1951 (Goreau, 1956). During the 1950s these reefs were gradually overgrown by algae, and by the mid 1960s were largely dead.

2) Port Royal Cays

The Port Royal Cays, a few kilometers east of Hellshire, are reefs around small sandy islands on the sediment-impacted South coastal shelf (Goreau and Burke, 1966). Strong westward currents place them upcurrent of the harbour mouth, so they receive only a tiny fraction of the land-derived pollution in the Hellshire area. Being near the ship channel entrance, they are presumably affected by ship-derived hydrocarbon emissions. Although off the driest part of the island (less than 70 cm rain per year), turbidity is high due to current-transport of eroded soils, resuspended sediment, and flocculent organic particles. Turbidity is especially high during rainy seasons, since the area is downcurrent from the mouth of the Yallahs River, which drains some of the steepest and most erodible soils in Jamaica. Catastrophic landslides have occurred, with one town completely buried by slumping of a mountainside in 1692. Deforestation by the current coffee boom is once again pushing up to the crests of the highest mountains in the island, deforested and then abandoned during the coffee boom which ended in the early 1800s, and likely to increase erosion further. These reefs were strongly affected by Hurricane Charlie, but large banks of *Acropora* occurred in the 1950s, especially in southern parts (Goreau, 1956). Following hurricane rains in 1963, extensive local bleaching occurred (Goreau, 1964). Very little *Acropora* is now to be seen, sediment stress is very high, the coral fauna is primarily made up of sediment-tolerant corals, and the sponge and gorgonian biomass exceeds that of corals. Mass coral bleaching has only slightly affected these reefs. During the 1989 bleaching event, when around 80% of corals along the north coast were bleached, frequency of bleaching in the Cays was no more than 5%, and water temperatures were noticeably colder on the south coast reefs.

3) Eastern Portland

These reefs lie along the most exposed coasts on the island, subject to full force of hurricanes and tropical storms arriving over open water. Wave action is dangerously strong at most times, and reflected by massive boulders and slumped reef blocks underwater (Goreau, 1956; Goreau and Goreau, 1973). The corals are a veneer of wave-adapted species rather than a true constructional reef framework. This area is upstream from all human influence in Jamaica, and lies near the rainiest part of the island (over 7 meters per year, around 2 centimeters per day). The area is virtually uninhabited, densely-forested limestone mountains with little soil. Tourism is extremely low due to isolation, poor roads, and heavy rains. Rivers draining non-limestone areas to the southwest contribute minor sediment, and the major freshwater influence is from strong groundwater springs, driven by high rainfall and steep hydraulic gradients. Nitrate contents of these springs are only one tenth that of limestone aquifers on the north coast (Lapointe and Goreau, in preparation). The area has bleached synchronously with reefs all along the North Coast of Jamaica, and sites in Cayman, Florida, and the Bahamas. Little deterioration has been noted in this area except for mass bleaching.

4) Ocho Rios

These reefs were among the first to have species composition and zonation described in detail (Goreau, 1956, 1959). There is no surface drainage, but strong groundwater springs occur underwater and on land, containing very high levels of nitrate (UNDP, 1974; Goreau et al., 1988). In the early 1950s these were among the best reefs in Jamaica, with vigorous reef growth, high species diversity, and stunning underwater caves and canyons (Goreau, 1956, 1959). Tourism was minor, and the town had only a handful of wooden buildings, some shorefront cottages, no more than a few hundred people, and trees covered the hills down to the beach. By the late 1950s hotels had expanded rapidly and most of the reef was dying from sediment stress as hills were deforested, buildings constructed, and reef sediment dredged on a large scale for landfill to create hotel land and port facilities above the previously living back reef. Expanding employment turned Ocho Rios into one of the country's largest towns (around 50,000), resulting in urban commercial and slum areas. Treatment facilities are inadequate to deal with all raw sewage, and much passes directly into the bay. Remaining reefs in the bay are largely dead and overgrown with algae. Mass bleaching has taken place in heavily used tourist resort reefs to the east and west of the town center.

5) Runaway Bay

Reefs here have vigorous coral growth on a steep limestone slope, producing caves, canyons, and vertical drop offs. There is little local surface drainage, but submarine springs occur. Two small rivers less than 10 km upcurrent are fed by high nitrate groundwater springs, known from dye studies to be fed by rivers disappearing underground in central Jamaica. Their waters are normally clear but turn muddy for days to weeks after flood rains a few times per decade, so sediment stress is rare. Population densities are moderate, the area being primarily used for low-density holiday villas or pasture. The resort area receives less than 3% of the island's visitors, and the town is small. Septic tanks release nutrients into groundwater, with some primary and secondary treatment by larger hotels. Reefs remain in fairly good condition in deeper areas, but there is considerable anchor and diver damage at tourist dive sites and in shallow back reef areas from high density pleasure boat traffic. The area has been heavily affected by mass bleaching. Algal overgrowth of reefs is moderately severe, with large amounts of *Lobophora, Dictyota,* and *Halimeda,* on the fore reef and *Peysonnelia* in caverns.

6) Discovery Bay

Discovery Bay reefs were analogous to those of Runaway Bay, with extremely well developed *Acropora* zones on the shallow fore reef until these were destroyed by Hurricanes Allen (Woodley *et al.,* 1981; Porter *et al.,* 1981; Knowlton *et al.,* 1990) and Gilbert. *Acropora* are now slowly regenerating in deeper water (10 to 25 meters). Discovery Bay is sheltered by reefs and had well developed back reef habitats with highly productive submarine spring communities (Goreau *et al.,* 1986). Species diversity has been affected by overfishing, which has severely reduced catches of most fish species, and by inadequately controlled collection of organisms by visitors to the Discovery Bay Marine Lab, especially in the west back reef zone, often used for ecological studies. There is very little tourism in Discovery Bay, a few holiday villas, a small town focused on bauxite mining offices, and a small dock for bauxite ships. Anchor and diver damage is minor. Sediment stress is apparent mainly within the hundred meters next to the bauxite dock. The nearest corals are largely dead, and fine-grained red bauxite mud has promoted dominance by sediment-tolerant *Madracis, Porites* and other genera. Sediment stress is confined to a very small part of the bay as there is no surface drainage or nearby rivers. Algal overgrowth has been severe in the last decade, with major coral overgrowers being *Lobophora variegata* in deep water, *Ceramium nitens* on the reef crest, and *Chaetomorpha linum* in the back reef. During this period fore-reef algal bottom cover and biomass has changed from being very minor (except for *Halimeda* and *Dictyota*) to exceeding that of corals. Much of this was due to the sharp reduction of the major sea urchin herbivore, *Diadema antillarum* following massive disease-induced mortality in 1983 (Liddell and Ohlhorst, 1986; Hughes *et al.,* 1987). However algal overgrowth has continued to increase despite lack of significant further change in herbivores. Strong growth response of local algae to nitrate concentrations similar to those introduced into reef waters by submarine springs (Lapointe *et al.,* 1988), concentric zonation of algae around springs, and their spread outwards from them indicates that algal populations are undergoing eutrophication from nutrients in groundwater sources. Local freshwater-induced bleaching has not been noted at Discovery Bay, but mass bleaching has been severe. Growth rates of bleached and unbleached populations of different color morphs of *Montastrea annularis* were followed from 1987 to 1991. Bleached corals cease growth (Goreau and Macfarlane, 1990), and many are being overgrown by algae, especially in damselfish territories (Goreau, in preparation).

7) Rio Bueno

This site is only a few miles downcurrent from Discovery Bay. There is no tourism, a very small old town in ruins, and a former sugar port whose heyday had passed by 1850. Reef growth is exceptionally vigorous, and submarine relief is spectacular. Conditions differ from nearby Discovery Bay since a large river enters the bay. Its source is an inland spring derived from rivers vanishing into sinkholes in central Jamaica. The watershed is largely forested, with small farms in valleys, and some cattle grazing. River water is usually clear or green, but turns red following heavy rains. There is a strong freshwater stress gradient in the bay, and strong but episodic sediment stress. These reefs underwent severe local bleaching following Hurricane Gilbert, being affected by muddy freshwater flows for several weeks. Reefs upcurrent from the river mouth were not affected. Rio Bueno reefs have also been affected by mass bleaching, and thus have bleached now for five years in a row (1987–1991). Bleached *Siderastrea siderea* colonies are unable to clean themselves of sediment filling their calices, and many large colonies appear to be succumbing. Several species of *Montastrea* and *Agaricia* which bleach strongly at Discovery Bay have brightly colored populations in Rio Bueno which are not affected. Hurricane impacts varied greatly at different sites after Hurricane Allen and Gilbert (T. Hughes, personal communication).

8) Montego Bay

Reefs to the north and east of Montego Bay are free from sediment influence, but to the west they are affected by high sediment loads from the Great River, which drains interior sugar plantations and small farms. The town, one of the largest in Jamaica with 70,000 people, was a major sugar port for 300 years, and its hotels receive over a third of all visitors to the island. Tourism began in the late 1940s, but most visitor growth, hotel construction, and population growth has been within the last 15 years. Extensive dredging and landfill dumping in the 1960s on top of reefs created port facilities and caused extensive sediment damage. Tourism and population growth greatly exceeded sewage treatment capacity, and much raw sewage flows straight into the bay. Around half the coral in shallower areas is dead, and most of the rest is strongly stressed by sediment or algal overgrowth. Bleaching has been severe at better sites near resort areas, and algal overgrowth is a general problem, as elsewhere along the North Coast. Spectacular relief provides good diving at deeper upcurrent reef sites, but anchor and diver damage are clear at many locations due to mass diving operations and heavy pleasure boat activities. Port facilities for cruise ships result in illicit garbage dumping and hydrocarbon releases. The area is the second most polluted after Kingston, but with an intensity that is probably at least an order of magnitude lower due to the smaller population and negligible industry.

9) Western Hanover

These reefs are among the richest and most pristine in Jamaica and show minimum disturbance. Coastal population densities are low, based on subsistence farming and fishing, and the area is one of the poorest on the island. Tourism is almost absent. Coral reefs, except just downstream from river mouths, have extremely high species diversity, large colonies, morphologies indicating vigorous growth, and high biomass. Coral growth rates are the most rapid measured in Jamaica (Goreau *et al.,* 1988). Reefs are affected primarily by fishing and by mass bleaching. Sediment stress is confined to local river mouth sites, where local bleaching may also have occurred. Algal overgrowth appears relatively low. Because these may be some of the best reefs in Jamaica they need to be closely monitored for long term and short term changes, and protected before they are damaged by external stresses.

10) Negril

Reefs at Negril include offshore bank reefs, lagoonal patch reefs, and fringing reefs on rocky shores. Negril was the most isolated and unpopulated part of Jamaica until 1960, when a road was built first providing land access to the 12 km long beach. In that year canals were dug to drain swamps which blocked landward access to the beach, and large amounts of organic peat sediment is discharged onto reefs at both ends of the bay. The area has transformed since 1960 from entirely unpopulated to the island's third major resort area: the beach is now almost continuous resorts. Boat and diving traffic is very heavy. Diver and anchor damage are high, but have been nearly eliminated by installation of moorings and education efforts by dive operators. Sewage treatment is inadequate to deal with existing hotel outputs, so much is discharged raw into the bay. Septic tanks are used by local residents in the hills. Detailed ecological surveys of the Negril area in 1960 (Goreau, 1960), before the advent of tourism, allow comparison of current conditions with undisturbed ones (Table 1). Formerly abundant *Acropora* reefs are now almost entirely dead. Areas near sewage inputs have been killed by algal overgrowth. In 1986 algal overgrowth of corals was confined near river mouths, but five years later affected the entire bay. Reefs near drainage canals are strongly affected by sediment and brown, peat-stained freshwater from swamps, which depress coral growth by reducing light levels (Dallmeyer *et al.,* 1982). Peat debris forms organic sediments which are easily resuspended. A petroleum spill was caused by rupture of a storage tank into Negril River in late 1991 (K. Thacker, personal communication). Study of coral cores from Negril showed a small, but statistically significant decline in growth rates from 1940 to 1980 (Hendry *et al.*, 1992). A regional survey of coral growth rates in Negril in 1986 found growth rates to be declining at much faster rates between 1970 and 1985, and rates of decrease were directly proportional to growth, so fastest growing corals were slowing most rapidly (Goreau *et al.*, 1988). Expanding sediment stress was the likely cause of growth reduction, since algal overgrowth was then confined near river mouths. Since 1986, mass bleaching or local bleaching has occurred every year. Bleaching of *Montastrea annularis* in November 1991 was about half as frequent in the most stressed parts of Negril Bay as in nearby areas free from sediment, freshwater, sewage, and boat damage (Goreau, 1992). Many colonies were brightly colored and unbleached, and several species have colors in common, which are unusual in other parts of Jamaica, that may indicate bleaching-resistant algal symbionts. By the end of 1991 most Caribbean reef species were still present, but corals were being steadily overgrown. With the exception of stable coral-sponge symbionts (Goreau and Hartman, 1966), corals were losing ground wherever they contacted sponges, algae, soft corals, and *Millepora* (Goreau, 1992). Some encrusting sponges are especially effective at overgrowing corals, but large masses of algae are also responsible, especially *Sargassum hystrix, Lobophora variegata,* and several *Dictyota* and *Halimeda* species in deeper water. In 1960 the inshore area was almost devoid of algae, but in 1991 masses of *Chaetomorpha linum* up to 2 or 3 meters long smothered large areas of seagrass and patch reefs. Algal species composition, zonation, and spread outwards from sewage inputs suggest eutrophication. Without prompt tertiary sewage treatment, algae and sponges are likely to overgrow most of the bay's reefs within a few years, as in Hellshire, Ocho Rios, and Montego Bay.

11) Western Westmoreland

The coastline in this area has only recently been connected by road, and is one of the least populated and developed shorelines in Jamaica. Reefs are not affected by stresses from Negril Bay because of strong current flow. Reef growth is vigorous but shallow. The shore line is rocky, with few beaches. The exposed location and large amounts of *Acropora* rubble indicate past hurricane damage. Species diversity is very high and most unbleached corals are healthy. Fishing is limited by low population, strong currents, and distance from fishermen's beaches. Algal biomass is moderate, and algal overgrowth does not appear to be a problem, except *Lobophora,* which may be influenced by groundwater spring inputs and reduced *Diadema* abundance. Algal species diversity is fairly high and dominated by relatively oligotrophic brown and green algal species. The area has been affected by mass bleaching events. In November 1991, after one of the mildest mass bleaching events to date, nearly half the corals were bleached, including virtually all the dominant *Montastrea cavernosa* and *Siderastrea siderea.* The former were bleached to grey. Most of the latter bleached to blue colors, but about a tenth had partial bleaching: pale polka-dots on a dark brown background. Bleaching to white was rare. A small proportion of other abundant corals such as *Montastrea annularis, Diploria, Agaricia,* and *Mycetophyllia* species were partially bleached. Bleaching was about twice as common as in Negril Bay at the same time, in marked contrast to the high anthropogenic stresses at the latter area. Almost all species of hermatypic corals had at least some partially bleached individuals (Table 1), but these estimates are certainly too low because most bleached corals were in recovery phases, and many had recovered in previous weeks after a long period of very hot, calm weather was ended by a severe storm with record floods.

DISCUSSION

Of the many stress factors operating at each site, only two, hurricane damage and epidemic mortality of *Diadema,* have had

TABLE 2. *Estimated magnitudes of reef stress factors at each site.**

Site	RI	SS	SD	SW	PO	OF	DR	CC	BD	AL	SC	LB	MB
1	M	0	VH	VH	VH	VH	VH	L	L	VH	H	H	L
2	H	0	VH	L	M	VH	0	M	H	M	H	H	L
3	L	VH	L	VL	0	M	0	VL	0	L	L	0	VH
4	M	H	M	H	M	VH	VH	VH	VH	VH	H	0	VH
5	VL	M	L	L	L	VH	VL	H	H	H	L	0	VH
6	0	H	VL	L	L	VH	H	M	L	H	L	0	VH
7	VH	0	VH	L	L	H	0	L	0	M	M	VH	VH
8	H	VL	H	H	H	VH	VH	VH	VH	VH	M	M	H
9	M	L	M	VL	VL	VH	0	VL	0	L	L	L	VH
10	H	0	VH	M	M	H	0	L	VH	H	H	L	M
11	0	H	VL	VL	0	M	0	VL	0	L	L	0	VH

* Relative reef stresses listed are rivers (RI), submarine springs (SS), sedimentation (SD), sewage (SW), industrial pollution (PO), overfishing (OF), dredging (DR), curio collection (CC), boat, anchor and diver damage (BD), algal overgrowth (AL), sponge and soft coral overgrowth (SC), local bleaching (LB), mass bleaching (MB). Factors are ranked as absent (0), very low (VL), low (L), moderate (M), high (H), or very high (VH).

fairly uniform island-wide impacts. The others show great variability between sites. Table 2 shows the relative importance of 13 stress factors at the 11 sites. The factors reflect magnitude of, and proximity to, stresses from rivers (RI), submarine springs (SS), terrigenous sedimentation (SD), sewage (SW), industrial pollution (PO), overfishing (OF), dredging (DR), curio collection (CC), boat, anchor and diver damage (BD), algal overgrowth (AL), sponge and soft coral overgrowth (SC), local bleaching (LB), mass bleaching (MB). These factors ranked as none (0), very low (VL), low (L), moderate (M), high (H), or very high (VH). Values are assigned based on direct observations at all sites over 4 decades, photographs, and discussions with individuals working in each area. The latest observations are used, but some sites have been examined at different times and with differing frequency. Values generally represent the entire area and include the full range of habitats in each. Many factors vary considerably from place to place within each area, including for example both upstream and downstream reef areas at sites with river inputs, or sites near and far from sewage outfalls. Many stress factors are strongly episodic, so rankings are based on maximum impacts observed, which have happened at different times in different places, for example dredging or population growth impacts such as sewage. Rankings are internally consistent, but relative and somewhat subjective, so it is possible that other observers with the same field experience might rank some of them slightly differently. The relative importance of these factors should only be compared by non-parametric statistics.

The non-parametric Spearman rank order correlation coefficients and their statistical significances for all pairs of factors in Table 2 are shown in Table 3. Considering correlations to be significant at the 0.05 probability level, to be strong at the 0.01 level, and very strong at the 0.001 level, the pair interactions of factors are:

1) *Significantly positive:* RI-SC, SW-CC, OF-DR, SS-MB, PO-DR, OF-CC, PO-SD, PO-CC, DR-CC, BD-SC.

2) *Strongly positive:* RI-LB, PO-BD, SC-SD, PO-SC, SW-DR, CC-BD, SW-BD, CC-AL, SW-SC, BD-AL.

3) *Very strongly positive:* RI-SD, LB-SD, SW-PO, SW-AL, PO-AL, DR-AL.

4) *Significantly negative:* PO-SS, SC-SS, SD-MB, LB-MB.

5) *Strongly negative:* RI-SS, PO-MB, SC-MB.

6) *Very strongly negative:* SD-SS, LB-SS.

Some of these correlations are related to common patterns of human activity in certain areas. For example, erosion, pollution, sewage, dredging, boat and anchor damage, and curio collection stresses correlate with each other because they are most intense near cities and resort areas. Proximity to rivers is not a direct measure of terrigenous sedimentation impact because South Coast

TABLE 3. *Spearman rank order correlation coefficients and probabilities for all factors listed in Table 2.*[1]

	RI	SS	SD	SW	PO	OF	DR	CC	BD	AL	SC	LB	MB
RI	—	**	***	NS	NS	NS	NS	NS	NS	NS	*	**	NS
SS	−0.782	—	***	NS	*	NS	NS	NS	NS	NS	*	***	*
SD	0.904	−0.906	—	NS	*	NS	NS	NS	NS	NS	**	***	*
SW	0.406	−0.467	0.546	—	***	NS	**	*	**	***	**	NS	NS
PO	0.528	−0.633	0.679	0.947	—	NS	*	*	**	***	**	NS	**
OF	0.068	−0.224	0.153	0.497	0.584	—	*	*	NS	NS	NS	NS	NS
DR	−0.115	0.075	−0.031	0.768	0.650	0.642	—	*	NS	***	NS	NS	NS
CC	0.192	−0.099	0.122	0.675	0.641	0.661	0.710	—	**	**	NS	NS	NS
BD	0.304	−0.246	0.311	0.743	0.742	0.476	0.539	0.812	—	**	*	NS	NS
AL	0.206	−0.262	0.309	0.956	0.866	0.592	0.889	0.794	0.779	—	NS	NS	NS
SC	0.671	−0.654	0.817	0.767	0.821	0.240	0.268	0.384	0.614	0.581	—	NS	**
LB	0.832	−0.899	0.879	0.355	0.528	0.159	−0.082	0.002	0.002	0.136	0.556	—	*
MB	−0.501	0.731	−0.730	−0.583	−0.771	−0.265	−0.154	−0.176	−0.466	−0.406	−0.741	−0.623	—

[1] Figures below the diagonal are correlation coefficient values between factors, and their significances are indicated above the diagonal. Correlations which are not significant are shown as NS, while those significant at the 0.05 level are shown as *, at the 0.01 level as **, and at the 0.001 level as ***. Underlined significance symbols have negative correlations, others are positively correlated.

sites are fairly distant from rivers, but undergo severe episodic sedimentation when extremely high erosion occurs in upcurrent watersheds during flood rains.

The positive significant Spearman correlations support field observations along stress gradients which suggest that rivers and sedimentation are related to local bleaching and shifts towards sponge, gorgonian, and soft coral dominance. Sedimentation appears to have caused species shifts rather than eliminated coral reefs, even at sites where sediment stress has continued for over 300 years. Sewage is strongly associated with pollution and algal overgrowth. Nutrient inputs stimulate algal overgrowth of corals, and have caused expanding rings of dead or overgrown coral reef framework around major nutrient sources to the coastal zone.

The negative correlations in Table 3 are also especially revealing, as all significant negative correlations involve either mass bleaching or submarine springs. All significant correlations of mass bleaching and of submarine springs are negative, except only for their mutual correlation, which is positive. Submarine springs are most common at less-populated and less stressed sites (except for Ocho Rios) where mass bleaching is especially prevalent. Submarine springs generally carry little or no sediment. A natural "stress," they appear to have minor negative impacts on reefs unless nutrient levels are excessive.

Mass coral reef bleaching has a unique pattern. It first appeared in Jamaica in 1987, followed by repeated events in 1989, 1990, and 1991 (Table 4). Mass bleaching did not occur in Jamaica from 1951 through 1986, and it is not possible that it could have happened without our knowledge because of frequent field work and regular contact with divers and fishermen around the island. The only year since 1987 without mass bleaching was 1988, but local bleaching occurred that year. Hurricane Gilbert, whose eye passed the length of the island, generated floods which caused local bleaching at sites such as Rio Bueno. The distribution of mass coral bleaching in space and time is entirely unlike patterns of other known stresses, which all show clear environmental stress gradients increasing towards obvious sources like towns and rivers. In contrast, mass bleaching has been intense all around the north, east, and west of Jamaica, but only mild or rare on the south coast, site of most sediment, sewage, and pollution inputs to the coastal zone. Detailed study of bleaching along freshwater, sediment, and sewage stress gradients in western Jamaica during late 1991 showed unpolluted reefs had higher coral cover and lower algal, sponge, and soft coral overgrowth than chronically stressed reefs, but frequency of bleaching was about half as high in the most stressed areas than at pristine sites (Goreau, 1991). This implies that the standard local anthropogenic stresses are not a cause of bleaching, and that corals which are routinely subject to them appear to be less susceptible to the stresses which cause mass bleaching. In contrast, the intensity of bleaching in Jamaica is extremely similar to high sea surface temperature anomalies since 1987, recorded by both *in situ* temperature measurements and by satellite radiometer data (Goreau *et al.*, 1992). This suggests that many Jamaican reefs may have only passed their temperature tolerance thresholds in the last decade.

TABLE 4. *Coral bleaching in Jamaica, 1951–1991.*[1]

Year	Hurricane	Local bleaching	Mass bleaching
1951	Charlie	?	
1952			
1953			
1954	+		
1955	+		
1956			
1957			
1958	+		
1959			
1960			
1961			
1962			
1963	Flora	x	
1964	+		
1965			
1966	+		
1967			
1968			
1969			
1970			
1971			
1972			
1973	+		
1974			
1975			
1976			
1977			
1978			
1979	+		
1980	Allen	?	
1981			
1982			
1983			
1984			
1985			
1986			
1987			**
1988	Gilbert	x	
1989			**
1990			**
1991			**

[1] Major hurricanes whose eye hit Jamaica directly are named. Minor hurricanes or those hitting peripherally are marked by +. Reported local freshwater bleaching is indicated by x, and possible occurences which were not reported are indicated by ?. Mass regional bleaching along North Coast reefs are shown by **.

CONCLUSIONS

Major observed changes in Jamaican coral reef community structure and health from 1951 to 1991 suggest:

1) Clear signs of reef degradation in terms of changing reef community composition, coral cover, or coral growth rates are present at all sites;

2) The rate and character of reef degradation depends on the type, intensity, and duration of stresses;

3) Hurricanes have played a major role in eliminating *Acropora palmata* and *Acropora cervicornis* zones which previously dominated most shallow reefs all around the island;

4) The intensity and extent of reef stress from sewage, sediment, pollution, overfishing, boat anchor, and divers have steadily increased;

5) Algal overgrowth of corals is a seriously escalating problem in most Jamaican reefs;

6) This is due to a combination of reduced herbivory due to overfishing and disease, and to increased fertilization by nutrients derived from inappropriate land and sewage management practices;

7) Increased sediment and organic mat-

ter loading correlates with coral overgrowth by sponges and soft corals;

8) Local bleaching occurred in shallow reefs downstream from rivers after major hurricanes;

9) Mass bleaching did not take place before 1987;

10) The primary deep water reef building species in the genera *Montastrea, Siderastrea, Diploria, Agaricia,* along with other less abundant genera, are among those most strongly impacted by mass bleaching in the past decade;

11) The spatial and temporal distribution of bleaching is opposed to that of all major reef stress patterns;

12) Bleaching is most frequent on reefs which previously escaped degradation because they were remote from local stresses;

13) The spatial and temporal patterns of mass bleaching correlate with mean monthly open sea water temperatures above 30°C;

14) All stresses act to reduce coral area coverage and/or coral growth rates;

15) The net impact of all stresses is accelerating decline of reef health around the island, especially during the last five years.

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REFERENCES

Dallmeyer, D., J. Porter, and J. Smith. 1982. Effects of particulate peat on the behaviour and physiology of the Jamaican reef building coral *Montastrea annularis.* Mar. Biol. 68:229–233.

Dodge, R., R. Aller, and J. Thompson. 1974. Coral growth related to resuspension of bottom sediments. Nature 247:574–577.

Goreau, P. 1990. Side scan sonar survey of the coral and sediment distribution south of Scott's Cove, S.W. Jamaica. Proc. Assoc. Marine Labs. Carib. 23:187–188.

Goreau, S. and T. J. Goreau. 1988. Fish mariculture potential of Jamaican back-reef springs. Proc. Assoc. Island Marine Labs. Carib. 21:35.

Goreau, T. F. 1956. *A study of the biology and histochemistry of corals.* Ph.D. Diss., Yale University, New Haven.

Goreau, T. F. 1959. The ecology of Jamaican reefs. I. Species composition and zonation. Ecology 40: 67–90.

Goreau, T. F. 1960. Report on a biological survey of the offshore regions bordering upon the Negril Green Island area. Negril Area Land Authority, Jamaica.

Goreau, T. F. 1963. Calcium carbonate deposition by coralline algae and hermatypic corals in relation to their roles as reef builders. Ann. N.Y. Acad. Sci. 109:127–167.

Goreau, T. F. 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. Science 145:383–386.

Goreau, T. F. 1969. Post Pleistocene urban renewal in coral reefs. Micronesica 5:323–326.

Goreau, T. F. and K. Burke. 1966. Pleistocene and Holocene geology of the island shelf near Kingston, Jamaica. Mar. Geol. 4:207–225.

Goreau, T. F. and N. Goreau. 1959. The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. Biol. Bull. 117:239–250.

Goreau, T. F. and N. Goreau. 1960. The uptake and distribution of labelled carbon in reef building corals with and without zooxanthellae. Science 131: 668–669.

Goreau, T. F. and N. Goreau. 1973. The ecology of Jamaican coral reefs. II. Geomorphology, zonation, and sedimentary phases. Bull. Mar. Sci. 23: 399–464.

Goreau, T. F. and W. Hartman. 1966. Sponge: Effect on the form of reef corals. Science 151:343–344.

Goreau, T. J. 1977. Coral skeletal chemistry: Physiological and environmental regulation of stable isotopes and trace metals in *Montastrea annularis.* Proc. Roy. Soc. London B 196:291–315.

Goreau, T. J. 1991. Coral reef health in the Negril area: Survey and recommendations. *In* D. Quirolo and K. Thacker (eds.), *Protecting Jamaica's coral reefs: Final report of the Negril Reef mooring buoy workshop and installation project.* Reef Relief, Key West, Florida.

Goreau, T. J., R. Dodge, and P. Goreau. 1988. Decline of coral growth rates at Negril, Jamaica. Proc. Assoc. Island Marine Labs. Carib. 21:43.

Goreau, T. J., P. D. Goreau, S. H. Goreau, A. H. Macfarlane, P. V. Devi Prasad, B. Lapointe, and J. Ryther. 1986. Jamaican back reef springs: Aspects of their ecology and mariculture potential. Proc. Assoc. Island Marine Labs. Carib. 19.

Goreau, T. J., B. Lapointe, J. O'Connell, P. Goreau, and A. Macfarlane. 1988. Groundwater nutrient inputs to Jamaican reefs. Proc. Assoc. Island Marine Labs. Carib. 21:40.

Goreau, T. J. and A. Macfarlane. 1990. Reduced growth rate of *Montastrea annularis* following the 1987–1988 coral bleaching event. Coral Reefs 8:211–216.

Goreau, T. J., R. Hayes, J. Clark, D. Basta, and C. Robertson. 1992. Elevated sea surface temperatures correlate with Caribbean coral reef bleaching. *In* R. A. Geyer (ed.), *A Global Warming Forum: Scientific, Economic, and Legal Overview.* CRC Press, Boca Raton, Florida.

Hendry, M., J. Woodley, C. Holmes, and R. Miller. 1992. Coral growth records from Negril, Jamaica: Growth band timing, the effect of swamp drainage alteration and a correlation with rainfall. Coral Reefs. (In press)

Hughes, T., D. Reed, and M. J. Boyle. 1987. Herbivory on coral reefs: Community structure following mass mortalities of sea urchins. J. Exp. Mar. Biol. Ecol. 113:39–59.

Huston, M. 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19–25.

Knowlton, N., J. Lang, and B. Keller. 1990. Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. Smithsonian Contr. Mar. Sci. 31:1–25.

Lapointe, B., J. O'Connell, A. Macfarlane, and T. J. Goreau. 1988. Photosynthesis of algae in Jamaican back-reef spring communities. Proc. Assoc. Island Marine Labs. Carib. 21:36.

Lewis, S. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs 56:183–200.

Liddell, W. and S. Ohlhorst. 1986. Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. J. Exp. Mar. Biol. Ecol. 95:271–278.

Porter, J. 1985. The maritime weather of Jamaica: Its effects on annual carbon budgets of the massive reef-building coral *Montastrea annularis.* Proc. 5th Intl. Coral Reef Symp. 6:363–379.

Porter, J., W. Fitt, H. Spero, C. Rogers, and M. White. 1989. Bleaching in reef corals: Physiological and stable isotopic responses. Proc. Nat. Acad. Sci. 86: 9342–9346.

Porter, J., J. Woodley, G. Smith, J. Neigel, J. Battey, and D. Dallmeyer. 1981. Population trends among Jamaican reef corals. Nature 294:249–250.

Sammarco, P. 1982*a*. Effects of grazing by *Diadema antillarum* Phillipi (Echinodermata: Echinoidea) on algal diversity and community structure. J. Exp. Mar. Biol. Ecol. 65:83–105.

Sammarco, P. 1982*b*. Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. J. Exp. Mar. Biol. Ecol. 61:31–55.

Teal, L. 1986. Growth patterns and fluorescent banding in the hermatypic coral *Montastrea annularis,* Jamaica, West Indies. Thesis, Geology Department, Middlebury College, Vermont.

United Nations Development Programme. 1974. Development and management of water resources: Jamaica, Dry Harbour Mountains—North Coast Basin. AGL:DP/JAM/70/512/Tech. Rept. 3. UNDP-FAO, Rome.

Woodley, J., E. Chornesky, P. Clifford, J. Jackson, L. Kaufman, N. Knowlton, J. Lang, M. Pearson, J. Porter, M. Rooney, K. Rylaarsdam, V. Tunnicliffe, C. Wahle, J. Wulff, A. Curtis, M. Dallmeyer, B. Jupp, M. Koehl, J. Neigel, and E. Sides. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755.