The conclusions we have drawn are tentative since they are based on the analysis of a small number of records. We expect that the investigation of other records which exhibit Faraday rotation, and an analysis of the Jupiter-Earth relationship at times when Faraday rotation is present, will provide more conclusive evidence on the radiation generation mechanism at Jupiter.

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Mass Expulsion of Zooxanthellae from Jamaican Reef Communities after Hurricane Flora

Abstract. *Very extensive bleaching of coral reef communities occurred after severe flood rains over eastern Jamaica. The loss of color was due to the mass expulsion of zooxanthellae from the tissues of* Millepora, *Scleractinia, Zoanthidea, and Actiniaria living in the shallow reef zones. The polyps of the bleached individuals continued to expand and feed in their normal fashion. It is believed that expulsion of the zooxanthellae was induced by contact with water of lowered osmotic pressure on the surface of the sea, rather than by sedimentation or fouling. Regeneration of the depleted zooxanthellar populations was very slow; many of the bleached colonies survived well despite the near total absence of zooxanthellae from their tissues for over 2 months.*

Flood rains accompanying the near passage of hurricane Flora between 5 and 7 October 1963 caused severe damage of an unusual kind in Jamaican coral reefs. The inundation of the shallow parts of inshore habitats by fresh water flood run-off induced wholesale bleaching of Scleractinia, *Millepora*, Zoanthidea, and Actiniaria through the expulsion of their zooxanthellae. The damage was confined to very shallow reef communities and appears to be due entirely to physiological injury; mechanical destruction as such was slight, since during this period the eye of the hurricane was over central Cuba, more than 200 km away, and there was no storm surge. The track of this hurricane is shown on the inset in Fig. 1.

From 5 to 7 October the eastern half of Jamaica received approximately 550 mm of rain. The rivers reached flood level within hours and produced the worst inundations in the memory of the populace. The sea off the south coast was discolored to the horizon with reddish mud; large patches of floating detritus were sighted by ships' crews 50 km SSE of Kingston. On 8 October the marine station of the University of the West Indies at Port Royal reported nearly fresh water to a depth of more than 2.5 m off the laboratory's jetty. The floods receded by 9 October, but rivers remained in spate because of continued heavy rainfall over the center of the island. In the Port Royal area, the salinity decreased to less than 3 per mil on 9 October and remained below 30 per mil for more than 5 weeks. Salinity values recorded by B. Wade at two localities near the entrance to Kingston Harbor are shown in Table 1.

In Kingston Harbor, a land-locked bay, the accumulation of fresh water caused widespread mass killing of bottom communities which in turn fouled large areas outside with their decomposition products. For almost a week this contaminated water was observed drifting slowly out to sea over the coral reefs south and southeast of the entrance to Kingston Harbor. The normal easterly trade wind pattern did not become reestablished until 20 October. There can be no doubt that the unusually calm windless weather after Flora hindered the dispersal of the diluted sediment-laden surface water and prolonged the physiological stresses to which these reef communities were subjected. Most of the studies described in this paper were made on the coral reefs of the Port Royal region shown on the map in Fig. 1. This area was one of the worst affected because of its proximity to the outlet of Kingston Harbor and to the mouths of the Rio Cobre and Ferry rivers. At the height of the cloudburst innumerable temporary gullies, some of which are shown on the map, also poured large volumes of fresh water into the harbor. Moreover, immense amounts of sediment were brought to the sea by the Hope and Cane rivers, 13 and 14 km east of Port Royal.

Five days after the flood rains, most of the reef tract was overlain by foul-smelling, dark greyish-green water littered with floating debris and patches of slime. Owing to the turbidity it was possible to see only corals at the surface, the majority of them bleached to a striking bone-white color, whereas some others were covered by greyish-black ooze. At Maiden and Lime cays the water was a little clearer, and direct underwater observations could be made. These showed that the bleached corals had not been killed, as was at first assumed, but were alive and in good condition although their tissues had been rendered colorless by loss of nearly all the zooxanthellae. Most of the bleached colonies had a clean and healthy appearance; the polyps were expanded to a normal degree and were responsive to tactile stimulation; the dactylozoids of bleached *Millepora* had unimpaired stinging powers.

The appearance of killed individuals was very different: soon after death they became covered by thick greenish-brown slime, and the coenosarc disintegrated into mucous blebs that trailed off in strings and patches; subsequent decomposition turned the dead colonies dark mottled grey; last, the bare coralla became overgrown by brownish-green filamentous algae. None of the corals killed by these inundations became bleached. Indeed the difference in appearance between dead and living but decolorized individuals was always very marked (Fig. 2).

Wherever it occurred the zone of bleaching was well defined and extended from the surface to depths ranging from 0.5 to a maximum of about 3 m, depending on the locality. In mixed communities some species consistently bleached to a greater extent and to somewhat greater depths than others, but below 2.5 to 3 m the color and appearance of the reef were unchanged. In many cases the lower border of the bleached zone cut across tall coral colonies so that their shallow portions were decolorized, whereas the deeper parts remained normal.

Bleaching occurred only in shallow-water species associated with zooxanthellae, that is, in hydrocorals (*Millepora*), and hexacorals (Scleractinia, Zoanthidea, and Actiniaria), but not in octocorals (Gorgonacea). The failure of the octocorals to bleach is not understood; it is possible that their intensely pigmented cortical spicules masked any color changes resulting from loss of zooxanthellae. We observed that the Gorgonacea in the affected regions suffered much greater mortality than other coelenterates, indicating that these animals are more sensitive and may have sustained fatal damage before the zooxanthellae could be expelled.

Consistent differences in susceptibility to bleaching were noted in the different species. This is shown in Table 2, where 20 of the commonest species in which bleaching was observed are listed in order of their sensitivity, those most easily decolorized being placed first. The relative sensitivity was estimated visually by comparing the degree of bleaching, and the depth to which it took place, in localities where these species occurred together and had been exposed to about the same environmental stress. Invariably the most susceptible, that is, the first to bleach, was *Millepora complanata*, followed closely by *Palythoa caribbaea* and *Montastrea annularis*. By far the most resistant species was the colonial zoanthidean anemone *Zoanthus sociatus* which survived, with only slight bleaching of the outer tentacular ring, in extreme shallow water on the inshore flats at Gun Cay; in this area all other reef biota were destroyed to a depth of over 3 m by the flood rains. In other less damaged localities, *Zoanthus* suffered little or no loss of zooxanthellae.

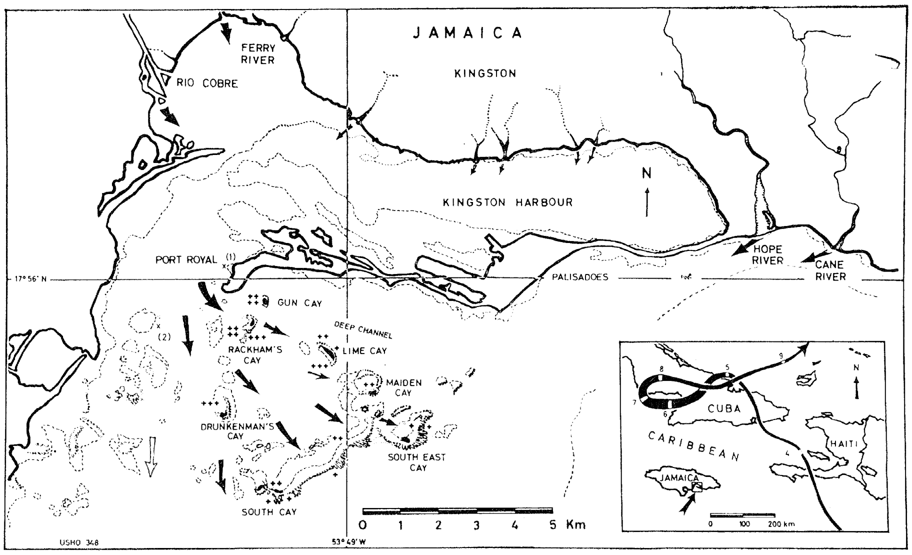

Fig. 1. Location of the reefs on which detailed underwater observations were carried out after hurricane Flora. The plus signs indicate the severity of the flood damage: +, bleaching to about 0.5 m and no mortality; ++, bleaching to about 1.5 m with low mortality; +++, bleaching to about 2.0 m with 25 to 50 percent mortality; ++++, mortality greater than 50 percent and all surviving forms fully bleached except *Zoanthus sociatus*. The sites of major fresh water discharge into the sea and the spread of the flood waters over the reefs are shown by large arrows. Church Shoal and the South Channel (see Table 1) are marked by *1* and *2*. Inset shows the path of hurricane Flora through the Caribbean between 4 and 9 October 1963. The location of the Port Royal area is indicated by an arrow. The thickened part of the hurricane track indicates the position of the storm center over Cuba at the time that flood rains were falling in eastern and central Jamaica.

Follow-up studies have been made. At Lime Cay some species were showing a faint yellowish-brown tinge as early as 16 October, and by 20 October, 13 days after the flood rains, it was already difficult to find bleached individuals that did not show at least a slight regeneration of the zooxanthellae, especially in their shaded parts. The fastest initial recoveries occurred in *Palythoa* and *Acropora*, but *Montastrea* and *Millepora* were much slower. In the reef corals, full recovery of the depleted zooxanthellar populations appears to be very slow; 14 weeks after the floods, many of the bleached colonies were still much paler than normal although they appeared to be healthy in other respects. Similar slow recoveries were noted by Yonge and Nicholls (*1*) on the Great Barrier Reef among corals bleached as a result of unusually high temperatures. Observations are being continued on the Port Royal reefs to determine the time required by the various bleached species to regain their normal complement of zooxanthellae.

Mass expulsion of zooxanthellae was experimentally induced by Yonge and Nicholls (*1, 2*) in reef corals subjected to starvation and high temperatures which depress metabolism, and darkness which prevents photosynthesis. These authors also recorded bleached but living corals in reef flats and shallow pools exposed to abnormally high temperatures coinciding with full-moon spring tides at Low Isles, Australia, in February 1929. Histological examination of these corals showed that the bleaching was due to loss of zooxanthellae. Squires (*3*) reported scattered "bone white" corals in shallow reefs off the mouth of the Rewa River in Viti Levu, Fiji, but did not state whether the bleached parts of these colonies were still alive. In Jamaica I have observed temporary and reversible bleaching in healthy, normal-looking corals under natural conditions on the fore-reef slope at depths below 30 m and also in well-fed, growing colonies of *Meandrina meandrites* which had been kept in tanks for more than 18 months in my laboratory. It is likely

Fig. 2. Underwater photograph of moderate to severe osmotic damage in a reef near Lime Cay, taken at a depth of 1.5 m 10 days after hurricane Flora. In this reef, between 40 and 60 percent of the corals above a depth of 2 m were killed, and most of the remainder were bleached. The blackened dead colonies on the left stand out in strong contrast to the living but bleached colonies on the right. The fact that the killed branches of staghorn coral, *Acropora cervicornis*, are somewhat deeper than the bleached fronds of the elkhorn coral *A. palmata* suggests that the former is less resistant to lowered osmotic pressure than the latter.

that corals can temporarily extrude most of their zooxanthellae under certain conditions without permanent ill effects even when not exposed to abnormal environmental stresses.

The conditions responsible for the extensive bleaching of the Port Royal reefs are not well known because the salinity, temperature, sediment burden, and so forth, in the reefs during and immediately after the flood rains of 5 to 7 October were not recorded. Furthermore, the area was exposed not only to muddy water of low salinity but also to fouling as a result of the mass killing of bottom communities in adjacent Kingston Harbor (*4*). However, I believe that fouling by decaying matter was not a primary factor because strong bleaching also occurred in reefs off the northeast coast of Jamaica which were exposed only to fresh water uncontaminated by decomposition products.

The question of the heavy sedimentation as a possible bleaching agent can now be examined. Sedimentation is said to be a major mechanical cause of death in reef corals (*5*), and it also reduces light penetration, thereby cutting down zooxanthellar photosynthesis (*6*). Although all the bleached reefs examined must have been covered by very muddy water for various lengths of time, we observed no unusual silting in even the most seriously damaged localities. If, on the other hand, the bleaching had resulted from the general lack of light penetration to the sea bottom due to muddy water on the surface, then it is to be expected that the loss of zooxanthellae would have been greater in the deep reef zones than in the shallow ones. This was not the case; maximum bleaching occurred only in the most superficial zones and not in the deeper ones. It is therefore unlikely that mechanical choking or reduction of light penetration by sediment, or both, were primary factors in the bleaching of the reefs during the time available.

Expulsion of zooxanthellae seems to have occurred only in those colonies that were in direct contact with the diluted surface water layer. This is suggested by the fact that the zone of bleaching always cut horizontally across reef communities without regard to topography or ecology. Furthermore, the depth of the bleaching was much greater in reefs near the entrance to Kingston Harbor, where the thickness of the fresh water layer was greatest, than in the more distant reefs where surface dilution was less. At Rackham's Cay and Gun Cay, both 1 km from Port Royal, extensive bleaching and killing took place to between 2.5 and 3.0 m; at Lime Cay, 3 km from Port Royal, the depth of bleaching was about 2 m and the mortality was much less; at South-East Cay and South Cay, distant 6.0 and 6.5 km from Port Royal, bleaching occurred to a depth of less than 1 m and there was very little mortality. The geographic distribution of these localities is shown in Fig. 1.

The long time taken for regeneration of a normal complement of zooxanthellae in the bleached corals is unexpected and raises some fundamental questions about reproduction and turnover of these algae within their hosts. Our observations showed that there were essentially no differences in the zooxanthellar regeneration rates of corals bleached in only one part of the colony and those bleached throughout. This suggests that there was little movement of zooxanthellae from normal to neighbouring bleached polyps even when linked by a common coenosarc, and that such regeneration as occurred probably came from the few healthy zooxanthel-

Table 1. Changes in salinity near Port Royal, Jamaica, after hurricane Flora.

Date	Depth (m)	Salinity (per mil)	
		Church Shoal*	South Channel*
9 Oct.	0	8.5	7.0
11 Oct.	0	10.0	12.5
11 Oct.	0.5	35.0	29.0
11 Oct.	1.0	36.5	34.0
11 Oct.	2.5	37.0	
11 Oct.	5.0	37.0	
18 Oct.	0	16.0	30.0
18 Oct.	0.5	34.0	30.5
24 Oct.	0	20.0	22.0
31 Oct.	0	19.0	30.0
14 Nov.	0	24.0	32.0

* See map in Fig. 1 for position of these localities.

Table 2. Bleaching response of Jamaican shallow water reef organisms exposed to decreased salinity, in order of decreasing sensitivity. Species marked (*) are Hydrozoa, order Milleporina. Species marked (†) are Zoantharia, order Zoanthidea. Species marked (‡) are Zoantharia, order Actiniaria. Species not marked are Zoantharia, order Scleractinia (Madreporaria).

*Millepora complanata** >> *Palythoa caribbaea*† >> *Montastrea annularis* > *Manicina areolata* > *Colpophyllia natans* > *Acropora prolifera* > *Acropora cervicornis* > *Porites furcata* > *Isophyllia sinuosa* > *Acropora palmata* > *Montastrea cavernosa* > *Porites astreoides* > *Diploria strigosa* > *Favia fragum* > *Diploria clivosa* > *Stephanocoenia michelinii* > *Stoichactis helianthus*‡ > *Siderastrea siderea* > *Siderastrea radians* > *Zoanthus sociatus*† lae which had not been expelled. It is not known whether there was reinfection of the bleached corals by motile zoospores such as those described by Freudenthal (*7*) for *Symbiodinium microadriaticum*. Even in those colonies that lost only part of their zooxanthellae, as shown by their light yellowish-brown color, return to normal took between 6 and 10 weeks; if turnover rates are of the order postulated by Odum and Odum (*8*) regeneration of the zooxanthellae should have occurred in less than 2 weeks.

The effect of wholesale depletion of zooxanthellae upon a reef community is difficult to evaluate, for the functional relationship of these algae to their coelenterate hosts differs from group to group and in most cases is still imperfectly understood (*9*). Among the reef-building Milleporidae and Scleractinia, all of which are carnivores specialized for feeding on plankton (*10*), the most important consequence of the loss of zooxanthellae would be a general lowering of the skeletal calcification rate in the affected zones of the reef. It has been shown (*11*) that the calcium deposition rate of reef corals is much greater in bright light than in darkness, and that this effect occurs only in the presence of zooxanthellar photosynthesis. In the absence of the zooxanthellae, the calcification rate of reef corals falls to very low levels and becomes independent of the light intensity (*12*).

The possible consequences of zooxanthella depletion on the Actiniaria (for example, *Stoichactis*) and the Zoanthidea (*Palythoa* and *Zoanthus*) are a matter for speculation since there is little information about the function of the zooxanthellae in these noncalcareous forms. No signs of starvation were noted in bleached *Stoichactis* and *Palythoa* even 4 to 6 weeks after they had lost their zooxanthellae. Indeed I often saw such individuals actively feeding, the former on small fish and pteropods, the latter on smaller zooplankters. Evidently, like the reef corals, these two forms do not depend on zooxanthellae for the bulk of their nutritional requirements. On the other hand, *Zonathus sociatus* was the only form that could retain most of its zooxanthellae even when exposed to an osmotic stress so severe as to kill all other reef biota; it was also the only species which I never observed to feed on zooplankton, or any other food offered to it. This evidence supports the suggestion that *Z. sociatus* may be nutritionally dependent on the photosynthetic products of its zooxanthellae.

The most probable cause of the large-scale bleaching in the Port Royal reefs was contact with low-salinity surface water, but as yet nothing is known of the concentration range necessary to produce expulsion of zooxanthellae from millepores, corals, zoanthids and actinians. According to Wells (*13*) the optimum salinity for reef corals is about 34 to 36 per mil; salinities as low as 27 per mil are tolerated, but influxes of fresh water for even short periods of time are said to be fatal. The extreme rapidity with which zooxanthellae were extruded in the inundated parts of the reef suggests that exposure to reduced salinity under controlled conditions may constitute a practical method for speedy production of healthy bleached colonies for experimental purposes.

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Silica Source in Soil Solutions

Abstract. *Heat of solution of silica in soil saturation pastes was calculated from silica solubilities and agreed with values for solid silicic acid. The immediate source of silica in soil solutions apparently is solid silicic acid. The solution of silica from soils exhibited three stages of constant silica solubility.*

Silica and silicates form a major portion of the mineral matter of most soils. Although soil minerals have been extensively studied, confusion and uncertainty exists concerning the forms and properties of silica in soil. McKeague and Cline (*1*) have reviewed the extensive literature on silica in soils. They concluded that the silica in soil solutions exists almost entirely as monosilicic acid (H_4SiO_4). Furthermore the source of the silica was presumed to be a disorganized surface layer on quartz and perhaps other silicates. This study was undertaken to secure more definite information on the solubility of silica in soils.

Silica was determined colorimetrically in solutions extracted from saturated soil pastes prepared in a standard manner (*2*) with silica-free distilled water. Extraction was performed in a pressure extraction apparatus at 7.0 kg/cm^2 (gage) in a temperature-controlled water bath at 5°, 15°, 23° (room temperature), 40°, and 55°C. Samples were placed in the bath in sealed containers for 16 hours and then transferred to the extractor, which was placed in the water bath for at least 20 minutes to return the samples to the bath temperature.

Table 1. Heat of solution of silica computed from silica solubility in soil saturation pastes.

Soil type	Great soil group	Heat of solution (kcal/mole)
Unnamed loam*	Sierozem	4.2
Unnamed loam	Sierozem	4.2
Unnamed silt loam	Sierozem	4.0
Placeritos silt loam	Alluvial	4.2
Humboldt silty clay loam	Humic-Gley	4.2
Carson clay*	Humic-Gley	5.0
Carson clay	Humic-Gley	5.2

* Virgin site, all others irrigated fields. Samples represent the top 6 inches of the soil in all cases.