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## Hurricane Allen's Impact on Jamaican Coral Reefs

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The relative importance of environmental processes that affect the distribution of organisms varies with the intensity and frequency of the processes (1). Exposure to wave energy exerts an influ-

ence on community composition of reef corals, and thus on coral reef structure (2), both directly and through its influence on biological interactions. Reefs differ in their exposure to both routine wave energy and hurricanes (3, 4), but, because hurricanes occur irregularly and comparatively rarely, it is hard to assess their relative importance. While hurricanes can cause violent disturbance to coral reefs with extreme short- (5) and long-term (3, 4, 6-9) effects, very little is known of their immediate consequences for previously investigated populations (10). In this article, we present data on the types and magnitudes of damage done by Hurricane Allen to the well-studied coral reefs of north Jamaica.

We believe that these observations are

of unusual value for the following reasons. First, Jamaican coral reefs are among the best known in the world as a result, in particular, of the studies of T. F. Goreau, his associates, and subse-

quent researchers at the Discovery Bay Marine Laboratory of the University of the West Indies (11). Second, many of these people were at the laboratory during or soon after the storm, and they collected data comparable to those taken previously on routine patterns and processes. Third, these factors, combined with the severity of Hurricane Allen,

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created a natural experiment of Goreau's thesis (7) that structural and taxonomic differences between reefs on Jamaica's north and south coasts were due to differences in hurricane frequency. In the last half-century, while Port Royal on the south coast experienced 11 hurricanes, Discovery Bay on the north has seen only four; the last severe hurricane was in 1917 (12).

On 6 August 1980, Hurricane Allen, the strongest storm recorded in the Caribbean, passed close to the north coast of Jamaica (Fig. 1), severely damaging its reefs (13). Winds reached 285 kilometers per hour at the center (14), and approximately 110 km/hr in Discovery Bay, where waves over 12 meters (15) were seen breaking (Fig. 2) in water 15 m deep on the East Fore Reef (Fig. 1, location E). These waves, and the dislodged material that they carried, devastated the shallow reefs in Discovery Bay (Figs. 3 and 4). Dense stands of *Acropora palmata* colonies (1 to 3 m high), which had dominated the reef between 0 and a depth of 5 m, were leveled. The breaker zone and reef flat were transformed from constructional reefs into a gently sloping rubble rampart, which emerged here and there as islands where none had been before. Physical disturbance extended even to a depth of 50 m, where some platelike colonies of *Agaricia* spp. were damaged, and the sediment normally covering their bases was temporarily washed away. Everywhere damage was inflicted not only by violently moving water (16) but also by the solid objects that it dislodged: rolling corals (Fig. 4, A and C), suspended fragments (Fig. 4B), and scouring sand (Fig. 4D). The types and magnitudes of damage varied with reef location, depth, and topography and differed between taxa according to their location, form, and

construction. We consider first the effects of spatial factors and then describe the immediate impact on common organisms and their subsequent responses over the following 7 months.

### Spatial Patterns of Damage

Damage was patchy on several scales, varying regionally around Jamaica, locally between reefs and reef zones, and within zones. Not all patchiness can be easily explained, but a number of patterns emerge. The northeast coast of Jamaica, which was closest to the hurri-

cane track (Fig. 1), suffered most heavily (17). West of this region, at Discovery Bay (Fig. 1), damage was more severe on the exposed East Fore Reef than on the West Fore Reef (Fig. 1, location C), where breaking waves were only half as high (15), and damage was much less severe in back reef areas sheltered by the reef crest. For example, wholesale tumbling and shattering of head corals occurred locally at depths of 14 m on the East Fore Reef (Fig. 4A); similar devastation did not occur below a depth of 7 m on the West Fore Reef or at any depth within Discovery Bay. Similarly, increases over routine frequencies of death

and injury of arboresecent gorgonians (18) were greater among exposed, shallow colonies at Gorgo City (Fig. 1, location B) than among those in the protected West Back Reef (Fig. 1, location G), where no significant increase in injury was seen (Table 1, rows 1 and 2;  $\chi^2$  values for the increase in death and injury at Gorgo City are 149 and 33).

At any single locality, dissipation of wave impact depended on aspects of the local reef profile, including depth, slope, and shelf width. Shallow fore-reef areas were generally more severely damaged than deep ones. We see this most directly by comparing the same species on the same reefs at different depths. For example, head corals were more frequently toppled in sand channels in 10 m of water than in 14 m (Table 1, compare rows 5 and 6;  $\chi^2$  for numbers toppled and not toppled after Hurricane Allen = 4.75,  $P < .05$ ). Similarly, densities of the urchin *Diadema antillarum* were reduced more in shallow areas (Table 1, rows 13 to 17). Similar decrease in damage with increasing depth is evident for all corals combined (Table 1, compare rows 8 and 9).

Sloping or level reef surfaces were more severely affected than vertical ones. At West Rio Bueno (Fig. 1, location A), where the reef is vertical below a depth of 8 m, little mortality was seen in marked quadrats of largely foliaceous corals at depths of 10, 15, and 20 m (Table 1, rows 10 to 12), in contrast to the toppling of the more massive head corals observed at comparable depths on the sloping West Fore Reef (Table 1, rows 5 to 7). A broad terrace dissipated more wave energy than a narrow one. In the southwest corner of the broad East Fore Reef (Fig. 1, location F) more *A. palmata* colonies remained erect at a depth of 3 m than on the narrow West Fore Reef where they were leveled.

Distribution of damage also depended on small-scale position effects. At the West Fore Reef, massive corals in sand channels were more likely to be overturned than those in adjacent reef lobes (Table 1, compare rows 5 and 6 with row 7;  $\chi^2 = 44$ ,  $P < .001$ ). Surviving large, massive corals provided shelter for more fragile organisms in their lee, but those that toppled left paths of damage (19). Corals seaward or shoreward of sand patches suffered abrasion, as evidenced by white paths of corals with stripped skeletons; some paths were as much as 10 m long. On vertical walls in West Rio Bueno (Fig. 1, location A), damage by falling sand and skeletal debris was much greater below sand channels and chutes than that in the marked quadrats between them.

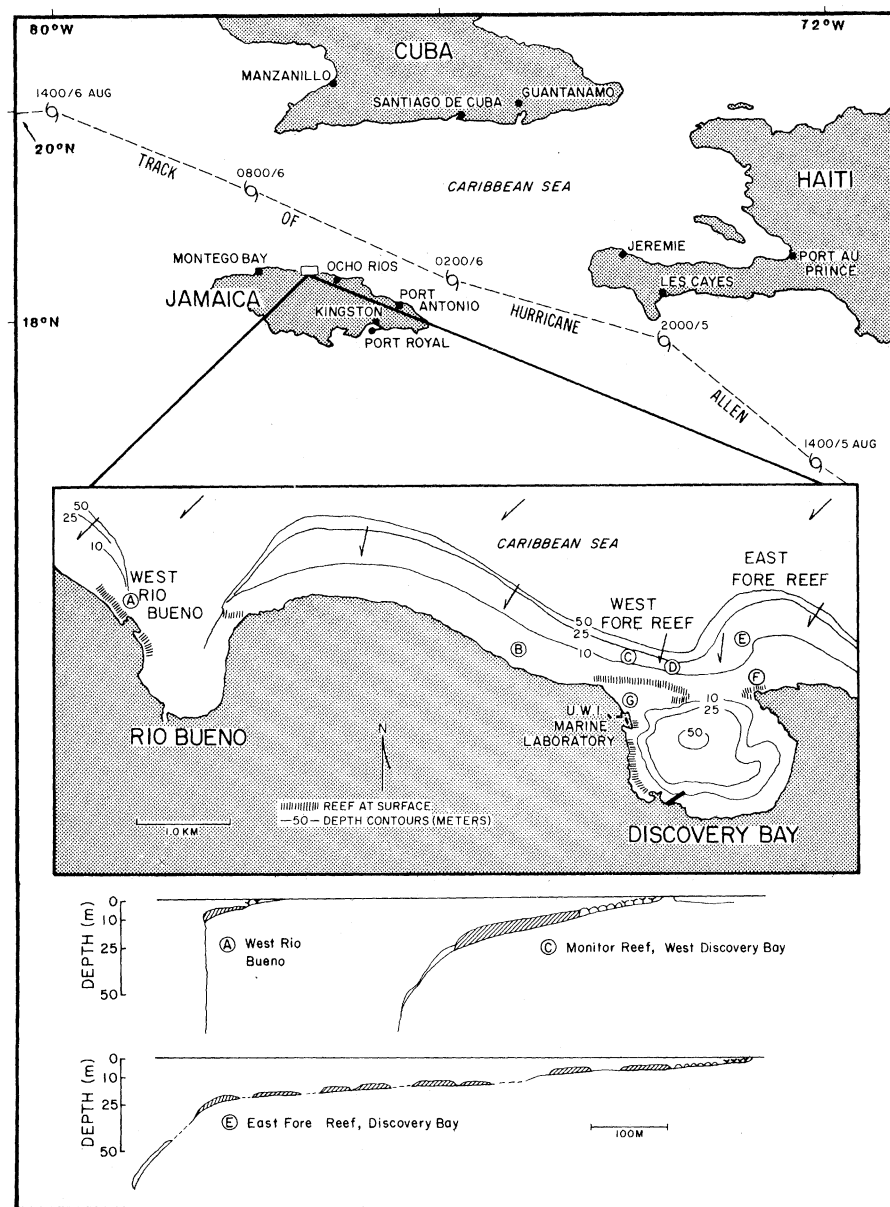


Fig. 1. Track of Hurricane Allen on 5 and 6 August 1980. Inset shows coastline and submarine shelf in the vicinity of Discovery Bay, Jamaica. The 120-m depth contour, not shown, would be almost coincident with that for 50 m. Arrows approximate wave directions on the morning of 6 August. Study sites referred to in text, from west to east: A, West Rio Bueno; B, Gorgo City; C, West Fore Reef including Arena, Pinnacle Two, Monitor, Long-Term Sampling, Dancing Lady, and Zingaro reefs, all within 0.4 km; D, West Fore Reef including Upper Buoy and Pinnacle One reefs, both within 0.1 km; E and F, East Fore Reef; and G, West Back Reef. Sketch profiles of three sites are shown at the bottom.

## Damage to Sessile Taxa

Within any zone, the amount and type of damage inflicted upon sessile organisms was greatly influenced by their shapes, sizes, and mechanical properties. Damage to gorgonians, corals, and sponges ranged from partial to complete mortality (20) and was caused by abrasion, burial, and the tearing or fracture of tissue and skeleton. The fate of detached colonies and fragments, and thus the ultimate consequences to populations, of Hurricane Allen, varied widely between taxa.

Among gorgonians at Gorgo City, for example, 51 percent of colonies were killed by detachment, abrasion, and burial in sand or coral fragments. Many detached colonies died ultimately from abrasion or from transport onshore or over the drop-off at a depth of 50 m. Of surviving, attached colonies, 98 percent had lost polyps through abrasion or branch fracture (Table 1, rows 1 and 2).

Differences in damage to different growth forms (7) were particularly striking for corals, whose skeletal morphologies include branching, foliaceousness, encrusting, and head forms. As reported previously (5), branching species were more susceptible to hurricane damage than were massive heads (Fig. 4B). In an extreme example, at a depth of 6 m on



Fig. 2. Waves of Hurricane Allen breaking on East Fore Reef at Discovery Bay (Fig. 1, location E) at 0700, 6 August 1980. Wave heights were calculated to be 12 m; trees on shoreline are 15 m high. [Photograph by C.M.W.]

Monitor Reef on the West Fore Reef (Fig. 1, location C, and Fig. 3) the planar living areas of branching *Acropora* spp. were reduced by up to 99 percent (Table 2, rows 1 to 3), whereas colonies of foliaceous and encrusting *Agraricia agaricites* were reduced by only 23 percent (Table 2, row 6), and massive *Montastrea annularis* by only 9 percent (Table 2, row 12). Comparable patterns were evident elsewhere. At a depth of 14

m on the West Fore Reef (Fig. 1, location C), *A. cervicornis* was reduced to 40 percent of its 1977 coverage (21); virtually all colonies were broken free, and horizontal transport of live fragments was recorded for distances of up to 6 m. In the same area, only 2 percent of the encrusting colonies of *A. agaricites* present after the storm were detached fragments, and total tissue recently lost for those remaining was only 3 percent (22).

Table 1. Damage to organisms from Hurricane Allen in relation to location on the reefs on the basis of survey data from before and after the storm. Abbreviations: WFR, West Fore Reef; EFR, East Fore Reef.

| Row               | Organism                                   | Depth (m) | Location            | Data type          | Before | After | After/before | Reference |
|-------------------|--|-----------|---------------------|--------------------|--------|-------|--------------|-----------|
| <i>Gorgonians</i> |  |           |                     |                    |        |       |              |           |
| 1                 | Arborescent                                | 7         | Gorgo City          | Dead (%)           | 2      | 51    | 25.5         | (18)      |
| 2                 | Arborescent                                | 7         | Gorgo City          | Injured (%)        | 51     | 98    | 1.9          | (18)      |
| 3                 | Arborescent                                | 1         | West Back Reef      | Dead (%)           | 0      | 7     | ∞            | (18)      |
| 4                 | Arborescent                                | 1         | West Back Reef      | Injured (%)        | 95     | 76    | 0.8          | (18)      |
| <i>Corals</i>     |  |           |                     |                    |        |       |              |           |
| 5                 | Head (mainly <i>Montastrea annularis</i> ) | 10        | WFR, sand channel   | Standing (No.)     | 26     | 9     | 0.35         | (41)      |
| 6                 | Head (mainly <i>M. annularis</i> )         | 14        | WFR, sand channel   | Standing (No.)     | 28     | 18    | 0.64         | (41)      |
| 7                 | Head (mainly <i>M. annularis</i> )         | 10, 14    | WFR, reef lobe      | Standing (No.)     | 128    | 119   | 0.93         | (41)      |
| 8                 | All (mainly <i>Acropora palmata</i> )      | 4         | WFR, reef lobe      | Cover (%)          | 51     | 12    | 0.24         | (42)      |
| 9                 | All (mainly foliaceous)                    | 33        | WFR, reef lobe      | Cover (%)          | 64     | 64    | 1.00         | (42)      |
| 10                | All (mainly foliaceous)                    | 10        | West Rio Bueno wall | Cover (%)          | 71     | 71    | 1.00         | (43)      |
| 11                | All (mainly foliaceous)                    | 15        | West Rio Bueno wall | Cover (%)          | 33     | 32    | 0.97         | (43)      |
| 12                | All (mainly foliaceous)                    | 20        | West Rio Bueno wall | Cover (%)          | 33     | 32    | 0.97         | (43)      |
| <i>Urchins</i>    |  |           |                     |                    |        |       |              |           |
| 13                | <i>Diadema antillarum</i>                  | 5         | EFR                 | No./m <sup>2</sup> | 9.3    | 0.1   | 0.01         | (44)      |
| 14                | <i>D. antillarum</i>                       | 8         | WFR, reef lobe      | No./m <sup>2</sup> | 13.3   | 6.1   | 0.46         | (44)      |
| 15                | <i>D. antillarum</i>                       | 11        | WFR, reef lobe      | No./m <sup>2</sup> | 9.5    | 8.4   | 0.88         | (44)      |
| 16                | <i>D. antillarum</i>                       | 10        | West Rio Bueno wall | No./m <sup>2</sup> | 6.3    | 3.8   | 0.60         | (44)      |
| 17                | <i>D. antillarum</i>                       | 20        | West Rio Bueno wall | No./m <sup>2</sup> | 1.5    | 0.9   | 0.60         | (44)      |
| <i>Fish</i>       |  |           |                     |                    |        |       |              |           |
| 18                | <i>Eupomacentrus planifrons</i>            | 8         | WFR, reef lobe      | No./m <sup>2</sup> | 0.7    | 0.9   | 1.29         | (44)      |
| 19                | <i>E. planifrons</i>                       | 11        | WFR, reef lobe      | No./m <sup>2</sup> | 0.7    | 0.8   | 1.14         | (44)      |
| 20                | <i>E. planifrons</i>                       | 18        | WFR, reef lobe      | No./m <sup>2</sup> | 0.6    | 1.1   | 1.83         | (44)      |
| 21                | <i>E. planifrons</i>                       | 10        | West Rio Bueno wall | No./m <sup>2</sup> | 0.6    | 0.5   | 1.20         | (44)      |
| 22                | <i>E. planifrons</i>                       | 20        | West Rio Bueno wall | No./m <sup>2</sup> | 0.0    | 0.0   |              | (44)      |



Fig. 3. Photostation on Monitor Reef (Fig. 1, location C; depth 6 m) before (September 1978) and 19 days after Hurricane Allen (each photograph 1/4 m<sup>2</sup>). (A) Branching *Acropora palmata* (upper right), *A. prolifera* (lower left), and *A. cervicornis* (lower right) before Hurricane Allen. (B) The same quadrat after the hurricane showing total destruction of *Acropora* spp. (C) *Acropora palmata* overtopping massive *Montastrea annularis* before Hurricane Allen. (D) The same quadrat after the hurricane showing removal of *A. palmata* and lesions on *M. annularis*. [Photographs by J.E.N., J.W.P., and J.D.W.]

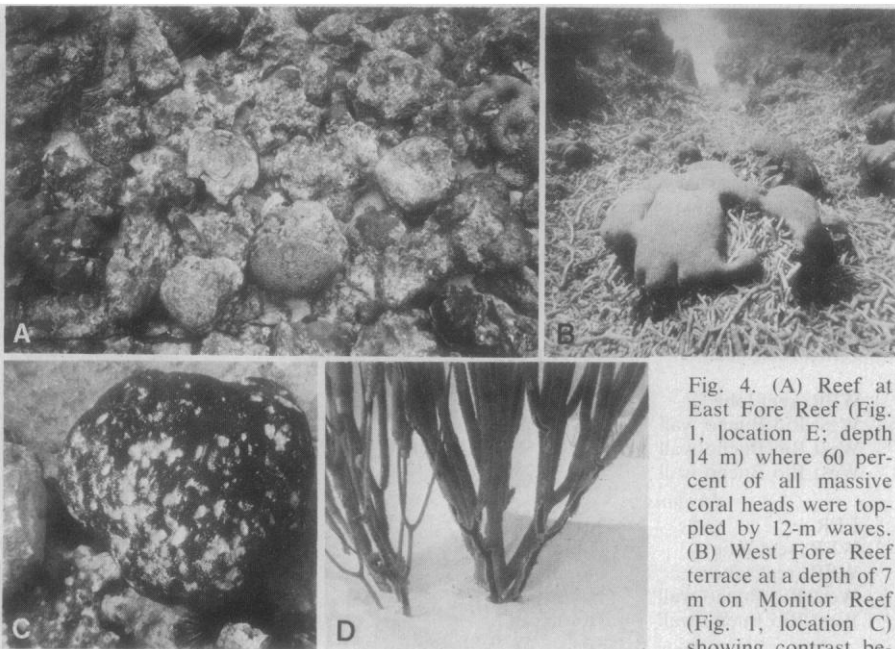


Fig. 4. (A) Reef at East Fore Reef (Fig. 1, location E; depth 14 m) where 60 percent of all massive coral heads were topped by 12-m waves. (B) West Fore Reef terrace at a depth of 7 m on Monitor Reef (Fig. 1, location C) showing contrast between the fates of branching and massive corals. (C) Detached and gouged head of *Siderastrea siderea* at Gorgo City (Fig. 1, location B; depth 7 m). (D) Polyp loss on a gorgonian, *Plexaurella* sp., by abrasion and burial in sand at Gorgo City; note shattered calcareous skeleton of *Millepora* sp. encrusting branches in left foreground. [Photographs by J.D.W. (A), J.W.P. (B), and C.M.W. (C) and (D)]

Within broadly defined morphological classes, stouter forms were less likely to be injured. At depths of 6 m, the massively branching *A. palmata* suffered less than the more delicately branching *A. prolifera* and *A. cervicornis* (Table 2, compare row 1 with rows 2 and 3). Thick plates of *M. annularis* at depths of 33 and 40 m were hardly affected (Table 2, rows 10 and 11), while some thin plates of *Agaricia* spp. at 50 m were broken or overturned.

Damage to sponges also varied with shape. At a depth of 15 m on the East Fore Reef (Fig. 1, location E) nearly one half of all ropelike forms were broken off at the base, and many of those still attached were injured (Table 2, rows 13 and 14). About a third of all other sponges were seriously damaged (Table 2, row 15).

Colony size is another factor that affected partial mortality of corals. At Gorgo City (Fig. 1, location B), large encrusting colonies of *A. agaricites* were more likely to suffer some damage than were small ones, but injuries to small colonies were proportionately more severe in extent (Table 2, rows 7 to 9; *G* tests,  $P < .005$ ). Similar patterns of routine partial mortality before Hurricane Allen have been described for foliaceous corals on the wall at West Rio Bueno (23) (Fig. 1, location A).

Injury to sessile organisms also varied with mechanical characteristics of the skeleton. Skeletons of corals are brittle, and branching corals were readily fragmented. For example, before Hurricane Allen, *A. cervicornis* on the West Fore Reef was highly branched (24), but afterward the broken organisms had, on the average, only one living side branch (Fig. 4B), and median live tissue length per fragment was only 15 percent of 1978 values (Table 2, rows 4 and 5; differences between values before and after the hurricane were significant at  $P < .001$ , Mann-Whitney *U* test) (25). The advantage of flexibility was evident among gorgonian branches encrusted by the hydrocoral *Millepora* spp. (26) at Gorgo City (Fig. 1, location B). Although gorgonian branch fracture increased during Hurricane Allen ( $\chi^2 = 40$ ), branches often proved more resilient than the overlying rigid *Millepora*, which shattered and fell off, reexposing gorgonian axes (Fig. 4D). Many nonencrusting *Millepora* colonies were sheared off at the substratum. The fate of exposed massive sponges was also related to their texture; tough ones like *Ircinia* spp. often appeared unaffected, whereas almost all soft, crumbly forms, such as *Neofibularia nolitangere*, were destroyed.

## Recovery of Surviving Sessile Organisms

Among sessile organisms, there were marked differences in survivorship and repair after initial injury. Most *Acropora* spp. fragments that were alive 1 to 2 weeks after Hurricane Allen died over the next few months. Of 254 fragments of *A. cervicornis* that were tagged within 9 days after the hurricane at depths of 8 and 14 m on the West Fore Reef, only four were living 5 months later (21). Of 54 fragments of *A. palmata* tagged at depths of 2, 4, and 6 m on the West Fore Reef (Pinnacle Two Reef, Fig. 1, location C) within 4 weeks after the hurricane, only 28 percent were alive at 16 weeks. In both cases, initial survivors had significantly larger areas of live tissue than those that died (Mann-Whitney *U* test,  $P < .001$ ) (21, 24, 27). In massive and encrusting corals small lesions generally healed, but large ones sometimes led to increased mortality (28). After 7 months, many semierect and wedged gorgonian colonies were still alive. The degree of polyp regeneration varies widely between injured colonies. Many detached sponges also died, but ropy sponges lying on hard substrata were often able to reattach; at Upper Buoy on the West Fore Reef (Fig. 1, location D) and on the East Fore Reef (Fig. 1, location E) 75 percent of 52 of these ropy sponges and 73 percent of 26 had reattached within 3 weeks. Among nonropy

sponges that remained attached, exposed sponges were more likely to have begun to repair injuries after 2 to 3 weeks than were cryptic sponges (43 percent of 72 versus 24 percent of 17 at Upper Buoy and 35 percent of 153 versus 0 percent of 29 at the East Fore Reef;  $\chi^2 = 7.03$ ,  $P < .005$ ).

## Disturbance to Motile Organisms

Motile organisms were also affected by Hurricane Allen. The impact of the hurricane on populations of the urchin *Diadema antillarum* and the damselfishes *Eupomacentrus planifrons* (three-spot) and *Microspathodon chrysurus* (yellowtail) is of potentially great importance because these herbivores are known to have considerable influence on Discovery Bay coral reef communities (29). Densities of *D. antillarum* were significantly reduced in shallow water, especially in areas of extreme disturbance, where the urchins were almost exterminated (Table 1, rows 13, 14, and 16; Mann-Whitney *U* tests comparing values before and after the hurricane,  $P < .001$ ). In deeper water, however, there were no significant reductions in density (Table 1, rows 15 and 17; Mann-Whitney *U* tests,  $P > .05$ ). Densities of damselfishes, in contrast, were higher after the hurricane than they were in 1977 (Table 1, rows 18 to 22; the increase

is significant only for row 20, Mann-Whitney *U* test,  $P < .01$ ), indicating that the hurricane was unlikely to have seriously reduced their numbers. However, the algal lawns defended by damselfishes were eliminated on the West Fore Reef in depths shallower than 10 m, and they were partially disrupted elsewhere.

There were striking changes in damselfish behavior. Immediately following Hurricane Allen, these normally aggressive fishes showed no apparent territory or home range and often displayed submissive coloration. Territorial behavior resumed within 2 to 9 days, but there have been gradual shifts in the distributions of damselfish species, presumably because of changes in reef structure (30).

Other species also showed aberrant behavior in response to the hurricane. Schools of the striped parrot fish, *Scarus croicensis*, which normally feed heavily within *E. planifrons* territories, were unusual in that they were smaller (5 to 25 rather than 50 or more individuals), less stable in composition, and nonreproductive. Reproductive behavior was first observed 12 days after Hurricane Allen, and typical schooling behavior was resumed within 3 weeks. In the following weeks, cryptic fishes were more often seen than before, planktivorous fishes foraged closer to the reef than usual, and large predatory fishes were unusually common (31). Normally cryptic brittle stars were seen wandering about in the

Table 2. Damage from Hurricane Allen to sessile organisms in relation to morphology. Abbreviations: WFR, West Fore Reef; EFR, East Fore Reef.

| Row                                     | Structure type  | Depth (m) | Location   | Data type  | Before  | After  | After/before | Reference |
|---|---|-----------|------------|--|---------|--------|--------------|-----------|
| <i>Branching corals</i>                 |   |           |            |  |         |        |              |           |
| 1                                       | <i>Acropora palmata</i>                                       | 6         | WFR        | Plan area (cm <sup>2</sup> ) in 8 m <sup>2</sup> | 15,700  | 2,370  | 0.15         | (42)      |
| 2                                       | <i>Acropora prolifera</i>                                     | 6         | WFR        | Plan area (cm <sup>2</sup> ) in 8 m <sup>2</sup> | 18,900  | 137    | 0.007        | (42)      |
| 3                                       | <i>Acropora cervicornis</i>                                   | 6         | WFR        | Plan area (cm <sup>2</sup> ) in 8 m <sup>2</sup> | 2,630   | 99     | 0.038        | (42)      |
| 4                                       | <i>A. cervicornis</i>   | 7 to 14   | WFR        | Median Strahler branching order                  | 5       | 2      | 0.04         | (24, 25)  |
| 5                                       | <i>A. cervicornis</i>   | 7 to 14   | WFR        | Tissue per fragment (cm)                         | 117     | 18     | 0.15         | (24, 25)  |
| <i>Foliaceous and encrusting corals</i> |   |           |            |  |         |        |              |           |
| 6                                       | <i>Agaricia agaricites</i> (foliaceous and encrusting)        | 6         | WFR        | Plan area (cm <sup>2</sup> ) in 8 m <sup>2</sup> | 1,060   | 797    | 0.77         | (42)      |
| 7                                       | <i>A. agaricites</i> , < 5 cm <sup>2</sup> (encrusting)       | 7         | Gorgo City | Colonies with any damage (%), > 20%              | No data | 17, 27 |              | (45)      |
| 8                                       | <i>A. agaricites</i> , 5.1 to 10 cm <sup>2</sup> (encrusting) | 7         | Gorgo City | Colonies with any damage (%), > 20%              | No data | 42, 20 |              | (45)      |
| 9                                       | <i>A. agaricites</i> , > 10 cm <sup>2</sup> (encrusting)      | 7         | Gorgo City | Colonies with any damage (%), > 20%              | No data | 68, 3  |              | (45)      |
| 10                                      | <i>Montastrea annularis</i> (foliaceous)                      | 33        | WFR        | Cover (%)  | 51      | 50     | 0.98         | (42)      |
| 11                                      | <i>M. annularis</i> (foliaceous)                              | 40        | WFR        | Cover (%)  | 55      | 55     | 1.00         | (46)      |
| <i>Massive corals</i>                   |   |           |            |  |         |        |              |           |
| 12                                      | <i>M. annularis</i>   | 6         | WFR        | Plan area (cm <sup>2</sup> ) in 8 m <sup>2</sup> | 4,400   | 4,030  | 0.91         | (42)      |
| <i>Sponges</i>                          |   |           |            |  |         |        |              |           |
| 13                                      | Ropy  | 15        | EFR        | Injured (%)                                      | No data | 67     |              | (47)      |
| 14                                      | Ropy  | 15        | EFR        | Stump only (%)                                   | No data | 46     |              | (47)      |
| 15                                      | Nonropy   | 15        | EFR        | > 1/3 tissue lost (%)                            | No data | 31     |              | (48)      |



open for a day or two after Hurricane Allen; they also showed evidence for increased partial mortality (arm loss) as a consequence of the storm (32).

Demersal plankton responded quickly to major changes in bottom topography. Plankton samples collected over sand generally differ from those collected over reef areas (33). Ten days after Hurricane Allen, the abundance and composition of samples collected at night from a West Fore Reef sand channel that had become filled with rubble resembled those from reef areas. Over reef substrata, after the hurricane, samples collected at night showed little change when compared with samples collected in August 1979 at the same moon phase and at the same localities. Samples collected during the day, however, contained much higher numbers of predatory polychaetes after the hurricane; in 1979, only one polychaete was present in six samples, but after Hurricane Allen, there was an average of 55.5 polychaetes in four samples.

### Succession

Hurricane Allen exposed large amounts of substratum by abrasion, erosion, fracture, and death, thereby greatly increasing the surface available for recruitment and growth of sessile organisms. Even at depths of 16 m on the leeward side of the East Fore Reef, where little toppling occurred, the proportion of substratum assessed as bare or covered with filamentous algae in a 100-m<sup>2</sup> plot rose from 13 percent in 1976 (34) to 37.5 percent 6 weeks after Hurricane Allen ( $\chi^2 = 104$ ,  $P < .001$ ). Thus the hurricane set the stage for a major secondary successional sequence, succession being defined here in the broad sense of a progressive change in the fauna and flora through time.

Preliminary successional events included spectacular blooms of the green algae *Trichosolen duchassaingii*, which occurred in shallow water within a week (35). Within 2 weeks mean biomass reached 96 grams dry weight per square meter in an area of the west rear zone (Fig. 1, location G) on the basis of three 1/16 m<sup>2</sup> samples. By 1 month, however, this alga was dying, and in some areas it was succeeded by the red algae *Crouania pleonospora* and *Liagora* sp.

Ultimately we expect that corals as a group will regain at least some of their former abundance on these reefs. But corals differ in their recruitment rates, growth rates, competitive abilities, and susceptibilities to predation.

The almost total mortality of the slow-

ly sexually recruiting *A. cervicornis* (36), which is a good space competitor under the levels of wave stress routinely experienced in Discovery Bay (24, 37), should for sometime favor the growth and recruitment of the hardier, longer-lived (*M. annularis*) and more fecund (*A. agaricites*) taxa (36) which survived the storm. Thus massive and encrusting/foliaceous corals may become relatively more abundant in areas more frequently exposed to extreme wave energies.

In summary, the effects of Hurricane Allen on the reef populations were impressive for their magnitude, speed, and patchiness. Organisms were unevenly affected, and the reefs are now a mosaic of areas that differ in the amount of open space and in the relative abundance of surviving species. Consequent differing opportunities for sexual and asexual colonization may result in differing successional communities (4), and such a sequence may partly explain the heterogeneity of mature reefs (38). Overnight, Hurricane Allen created patterns of distribution and abundance of organisms that are strikingly different from preexisting states. Hurricane-induced changes in reef community composition will persist if such storms occur more frequently than the period of time required for "recovery" (3, 8, 9). In places where severe storms are rare, like north Jamaica, there may exist a repetitive, though irregular, "pulse-reset" cycle of disturbance and recovery (39). Alternatively, rare hurricanes may cause progressive shifts in community composition, and "recovery" to prestorm states thus may not occur (40). Using comparable before-and-after data, we have described the immediate effects of a major hurricane on a Caribbean coral reef. The ultimate significance of disturbances of this magnitude and rarity will largely depend on the life histories and routine interactions of the surviving organisms.

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16. Just before a 12-m high solitary wave breaks in water 15.4 m deep, the water velocity 0.6 m above the bottom is 5.4 m per second. After breaking, turbulent flows of much greater velocity will occur. Calculation after R. L. Wiegell [*Oceanographical Engineering* (Prentice-Hall, Englewood Cliffs, N.J., 1964)].
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18. Patterns of routine mortality were recorded in summer 1977 for 364 and 95 colonies along line transects in Gorgo City and the West Back Reef (Fig. 1, locations B and G). After Hurricane Allen, rapid rates of regeneration necessitated haphazard sampling of all 203 colonies encountered. Values of colony mortality exclude those killed by gradual encrustation. The species involved and their distributions are described by R. A. Kinzie [in (11)].
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32. A subsample of *Ophiocoma echinata* collected in July 1978 was matched for number and disk diameter with the post-hurricane sample from the same site ( $N = 50$ ) and showed  $10.2 \pm 4.9$  percent arm loss, compared with  $17.6 \pm 13.6$  percent (Mann-Whitney  $U$  test,  $P < .002$ ). Routine losses are probably due to predation [E. M. Sides, thesis, University of the West Indies, Kingston, Jamaica (1981)].
33. Traps are as described by J. W. Porter and K. G. Porter [*Limnol. Oceanogr.* 22, 553 (1977)] except that 110- $\mu$ m mesh plankton netting was used.
34. The 750 transect points. Data are from S. Ohlhorst [thesis, Yale University, New Haven, Conn. (1980)].
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41. Data were collected on two swims along the depth contours at Dancing Lady and Zingaro Reefs (Fig. 1, location C). All heads counted were known to be standing before the storm.
42. The 12 photostations on Monitor Reef (Fig. 1, location C) have 32 replicate 0.25-m<sup>2</sup> quadrats per station. The last census before Hurricane Allen was in 1978. Perimeters of all living corals in each photograph were traced for area calculation. Because of extensive branch overlap of *A. palmata*, actual loss at a depth of 4 m was greater than calculated.
43. Seven 1-m<sup>2</sup> quadrats (one at a depth of 10 m, four at 15 m, and two at 20 m) were photographed in late May (T. P. Hughes) and 15 August 1980.
44. Data from before the hurricane are based on surveys of 30 m<sup>2</sup> in 1977 in Discovery Bay [L. S. Kaufman, thesis, Johns Hopkins University, Baltimore (1979)] or 28 m<sup>2</sup> in July 1980 at Rio Bueno. Data were obtained 1 week (Rio Bueno), 2 weeks (West Fore Reef), and 2 months (East Fore Reef) after the hurricane over comparable areas.
45. Data are on three 1-m<sup>2</sup> quadrats involving 78 small, 24 medium, and 57 large colonies; percentages for > 20 percent damage were calculated from the subset of colonies showing tissue loss without skeletal loss due to fracture.
46. Data are based on photostation surveys covering 12 m<sup>2</sup>, as in (43) on Pinnacle One Reef.
47. For example, *Aplysina* sp., *Iotrochota birotulata*, and *Haliclona rubens*. Figures are based on a survey of a 71-m<sup>2</sup> area containing 69 attached, ropey sponges; 21 fragments of ropey sponges that had been ripped off of their bases were also found in the plot.
48. For example, *Neofibularia nolitangere*, *Ectyoplasia ferox*, *Erylus formosus*, *Ircinia strobilina* and spp., *Pseudoceratina crassa*, *Geodia neptuni*, *Ulosa hispida*, *Anthosigmella varians*, and *Agelas dispar*. Semicryptic sponges among these (for example, *Mycale laevis*) were damaged as a consequence of the movement of their substrata. Figures are based on a plot survey described in (47); the plots contained 293 non-ropey sponges.
49. We thank H. G. Davis, L. Green, G. Harvey, M. D. Hendry, I. O. Henry, L. S. Land, S. Mailer, W. Maluk, J. M. Pair, C. J. Robinson, R. Warnock, and J. Wilson for technical and field assistance, T. P. Hughes and S. Ohlhorst for unpublished field data, and S. Palumbi and two reviewers for comments. This work was supported by a Sigma Xi grant and University of Texas at Austin Subvention Fund award to E.A.C.; NSF grant OCE 78-19674 to J.B.C.J. and J. E. Winston; NSF grant BNS-7904747 to N.K.; University of California Berkeley Regents Junior Faculty Fellowship to M.A.R.K.; NSF grants OCE 77-26781, OCE 80-05940, and DEB 79-23519 to J.W.P.; Inter-University Council, London, studentship to M.C.R.; Institute of Ocean Sciences, Sidney, British Columbia, Canada, to V.J.T.; NSF grant OCE 79-12674 to C.M.W. and J.B.C.J.; and American Museum of Natural History, Lerner Fund for Marine Research grant to J.L.W. Contribution 228 of the Discovery Bay Marine Laboratory, University of the West Indies.

## Colonization Lessons from a Tropical Forest

Nigel J. H. Smith

In 1970, the Brazilian government announced plans to integrate the Amazon region with the rest of the country. The forest-clad region was to be crisscrossed by a web of pioneer roads with the east-west Transamazon Highway serving as the backbone for the system. The 3300-kilometer Transamazon slices across the forest blanketing the southern interflaves of Amazonia, starting in Estreito on the Tocantins River and finishing in Cruzeiro do Sul near the Peruvian border (Fig. 1). The entire road was opened with bulldozers by 1975. Plans called for settling 1 million families on 100-hectare farms along the highway by 1980.

The Transamazon Highway was designed to accomplish three main goals. First, this two-lane dirt road would provide a safety valve for the poverty-stricken Northeast, a region with 30 million inhabitants increasing by 1 million a year. The 1970 drought that seared the

backlands of the region and uprooted some 3 million people triggered the government's decision to build the Transamazon. Second, the highway would help fill a demographic void in a region occupying half of Brazil's territory but containing only 4 percent of the nation's

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**Summary.** The decade-old Transamazon Highway provides a useful stage for examining some of the major issues related to frontier conquest and the impact of pioneer settlement on one of the world's richest biomes. The highway project is an ambitious colonization scheme and the lessons that can be drawn from it, ranging from the environmental effects of stripping back the tree cover to the spread of diseases, will be useful in guiding development policy in other tropical regions.

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population. The Brazilian government was reluctant to leave such an immense space vulnerable to the covetous eyes of foreign concerns, and saw the Transamazon Highway as placing an indelible stamp of sovereignty on a land surrounded by an ever-increasing population and experiencing a growing scarcity of natural resources. Finally, the highway

would create access to mineral and timber reserves that would fuel the country's spectacular 10 percent annual economic growth.

The Transamazon scheme has largely failed on all three counts. With the colonization phase of the highway now completed, only 8000 families have been settled by INCRA (Instituto Nacional de Colonização e Reforma Agrária), the federal agency responsible for administering the project. Even allowing for the estimated 1600 families that have settled spontaneously at the end of side roads and in forest reserves, the highway scheme has clearly not even come close to achieving the colonization target.

Although three-quarters of the colonists were supposed to be northeasterners, only 40 percent of the settlers have come from that parched region. The hu-

mid valleys of the Transamazon have accommodated 23,000 *nordestinos*, but since the highway was built, the population of the Northeast has grown by 6 million. The Transamazon has thus absorbed less than 1 percent of the region's population growth. The failure of the highway to relieve the demographic pressures and social strife in the North-

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