

## Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals

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Severe tropical storms can cause widespread mortality in reef corals<sup>1,2</sup>. The Caribbean staghorn coral, *Acropora cervicornis*, although dependent on fragmentation for asexual propagation<sup>3-5</sup>, is particularly vulnerable to hurricane damage<sup>6,7</sup>. The most important agents of post-hurricane mortality are assumed to be high wave energy<sup>6</sup> and change in salinity<sup>8</sup>, factors which typically soon diminish in intensity. We report here that there was substantial delayed tissue and colony death in *A. cervicornis* on a Jamaican reef damaged by Hurricane Allen. This previously undocumented degree of secondary mortality, sustained for 5 months and unrelated to emersion<sup>9</sup>, was over one order of magnitude more severe than that caused by the immediate effects of the storm. The elimination of >98% of the original survivors suggests potentially complex responses to catastrophes, involving disease<sup>10,11</sup> and predation, which may explain the widely variable rates of reef recovery previously reported<sup>12-15</sup>.

Hurricane Allen passed within 65 km of the reefs of Discovery Bay on 6 August 1980 (refs 7, 16). This storm, the strongest recorded for the Caribbean, generated massive waves (>6-12 m) but little rain<sup>7</sup>. The large mounds of the delicately branching *A. cervicornis*, which had dominated the West Fore Reef between 6 and 20 m depth<sup>4,17</sup>, were extensively fragmented<sup>7,16</sup>. To assess the long-term effects, we surveyed all pieces of *A. cervicornis* having living tissue in three haphazardly chosen 1-m<sup>2</sup> areas of moderate to severe damage at 8 ( $n = 125$ ) and 14 ( $n = 129$ ) m depth on Dancing Lady Reef 3-9 days after the storm. These pieces were all detached by the hurricane, the skeletal break often (53%) occurring where there had been no living tissue<sup>4</sup>. Although the once open network of branches was compacted, much of the surviving tissue was not smothered by direct contact with other fragments or the underlying solid reef base. The median number of living or partially living branches per fragment was 3 (range 1-19), and 53% of the fragments had at least one living axial (terminal) polyp (median = 1, range 0-17). The median total length of living tissue in these quadrats was 916 (range 457-1,250) cm m<sup>-2</sup>, ~40% of 1977 estimates<sup>18</sup>. We individually tagged each living staghorn in the six quadrats and returned at irregular intervals to re-examine them.

Mortality continued at an unexpectedly high rate (Fig. 1). For censuses made within 4 weeks of the storm, there were highly significant differences at both depths (after tagging) between surviving and dead colonies in the lengths (when tagged) of their longest living branches ( $P < 0.001$ , Mann-Whitney U test), but this difference showed reduced significance by 7 weeks ( $P < 0.03$ ) and was absent by 12 weeks ( $P > 0.1$ ). The relationship between the total number and presence of axial polyps on the longest living branch and survival was not strong ( $0.05 > P > 0.01$  at any depth for one census only). Other attributes (depth, branching order<sup>19</sup>, number of live branches, orientation of longest living branch and relative height of fragment off bottom) showed no significant relationship with survival. Five months after the storm, we found only four living colonies within the six

quadrats, and median total length of living tissue was reduced, from 916 to 10 (range 0-26) cm m<sup>-2</sup>. Thus there had been a nearly 100-fold long-term decrease in living colonies from the original post-storm number. Examination of other areas on Dancing Lady and other Discovery Bay reefs indicated that our quadrats were not atypical.

Two 18-m<sup>2</sup> transects were established near the shallow and deep sites following the death of most of the originally tagged corals by January 1981. Surveys of these transects showed that, in some areas, tissue mortality still exceeded new growth (indicated by lengthening branches and production of new axial polyps) nearly 1 yr after the hurricane. At 8 m depth there was a 26% reduction in live tissue (from 27 to 20 cm m<sup>-2</sup>) between mid-March and late July, while at 14 m depth there was an increase of 11% (from 26 to 29 cm m<sup>-2</sup>). In both transects the number of living fragments had declined during this interval (from 25 to 17 at 8 m, and from 23 to 17 at 14 m).

There are many possible explanations for this delayed mortality. Fragmentation might (1) facilitate continuing abrasion by the rolling of free fragments<sup>12</sup>; (2) decrease the 'three-dimensionality' of the reef, resulting in smothering or easier access for benthic predators of corals<sup>4</sup>; or (3) increase the susceptibility or exposure of colonies to disease<sup>10,11</sup>. *A. cervicornis* could be particularly susceptible to these processes because of its growth form, sensitivity to stress (for example, extreme temperature<sup>20,21</sup> and low salinity<sup>8</sup>), and its apparently high vulnerability to disease<sup>11</sup> (perhaps partly a consequence of its tendency to form large stands, hence increasing the potential for epidemics<sup>22</sup>). Differential initial mortality of staghorn coral and its predators, competitors<sup>23</sup>, prey and pathogens could upset pre-storm relationships, leading to the coral's sharp decline. Some of these mechanisms seem to have had no major effect: we observed little evidence of burial by sediment or continuing mechanical abrasion, even on days with large swells. There was no obvious, long-term increase in competition with algae; species which showed 'blooms' within a month of the hurricane<sup>7</sup> have since died back.

During the first few months, much of the mortality was probably related to continuing disease and fragmentation stress. Unusual amounts of tissue exfoliation, resembling that termed<sup>10</sup> 'white band disease' were observed in some colonies of *A. cervicornis* for 2 months before the hurricane<sup>7</sup>. This exfoliation continued after the storm, and could not be reliably distinguished from predation (see below) for at least 1 month. Although a relationship between fragmentation and disease has been reported for *A. cervicornis* in Curacao<sup>11</sup>, we found no persistent relationship between survival and fragment length, orientation or elevation. There is, moreover, some evidence for delayed post-hurricane mortality in species of *Acropora* not showing extensive tissue loss beforehand (*Acropora palmata* in Jamaica<sup>7</sup> and *Acropora prolifera* in St Croix; R. D. Clarke, personal communication).

By January 1981 mortality was primarily related to the activities of species that were previously important sources of

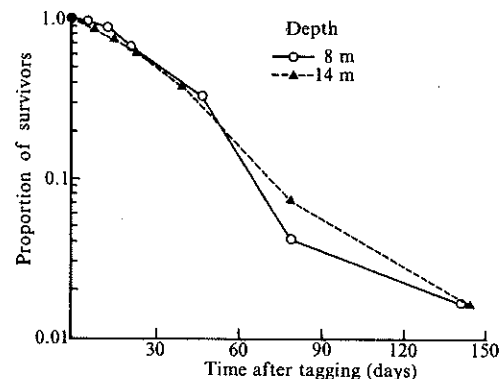


Fig. 1 Proportion of fragments surviving as a function of the time elapsed after tagging. Each fragment had one or more patches of living tissue, and was tagged 3-9 days after the hurricane.

**Table 1** Estimates of mean predator densities (per m<sup>2</sup>) before and after Hurricane Allen

Species	Depth, Location	Density (m <sup>-2</sup> )	
		(Before hurricane)	(After hurricane)
<i>Diadema antillarum</i>	8 m, DL	13.5 (30)	8.4 (16)
<i>Diadema antillarum</i>	14 m, DL	6.0 (30)	2.6 (25)
<i>Eupomacentrus planifrons</i>	14 m, DL	1.8 (30)	1.3 (25)
<i>Coralliophila abbreviata</i>	9 m, LTS	0.6 (40)	0.3 (25)
<i>Coralliophila abbreviata</i>	14 m, DL	0.6 (40)	0.1 (200)

Reefs surveyed were Dancing Lady (DL) and LTS (reef immediately west of DL); numbers in parentheses indicate numbers of 1-m<sup>2</sup> areas examined. The only values available for before the hurricane are based on surveys by Kaufman<sup>24</sup> (1977; *Diadema*, *Eupomacentrus*) and L. S. Land (unpublished results, 1975; *Coralliophila*), but these seemed to be representative of pre-storm conditions in 1980. 'After' densities were assessed in February–March 1981.

mortality in Discovery Bay. Predation by the snail *Coralliophila abbreviata*<sup>4,24,27</sup> has been particularly severe in shallow water; 1-m<sup>2</sup> quadrats along the transect at 8-m depth containing living staghorn and snails in May showed a median decrease by July in total staghorn length of 27.5 cm, whereas quadrats containing coral but no *C. abbreviata* showed a median increase of 2 cm ( $P < 0.01$ , Mann–Whitney U test). Disturbance by the urchin, *Diadema antillarum*<sup>24,25</sup>, and the damselfish, *Eupomacentrus planifrons*<sup>24</sup>, has also contributed to the observed coral deaths. In March, densities of these species were generally lower but within an order of magnitude of pre-storm estimates (Table 1), in contrast to the 100-fold decrease suffered by the staghorn. Thus predation pressure per colony of surviving *A. cervicornis* is now substantially higher.

Several important points emerge from this study. First, future studies of catastrophic damage to reefs (and other ecosystems) should be started as soon as possible after the event. By 5 months, for example, many tagged dead pieces had eroded calices, thus this characteristic<sup>14</sup> could not by then be used to distinguish between pieces dying before and after the storm<sup>26</sup>. Second, the geographical and temporal scale over which catastrophes occur could critically influence subsequent events. For example, destabilization of relationships between corals and their predators is more likely to occur when the area of coral destruction is great; adult predators of limited mobility, unable to emigrate from decimated regions, will continue to feed in

areas where new coral growth can no longer keep pace with predation. The resulting drop in coral abundance will be particularly severe if predators do not succumb rapidly to starvation. Similarly, when substantial coral mortality (for whatever reason) occurs only rarely, the relative abundances of associated reef organisms are more likely to be strongly shifted<sup>28</sup>. Thus survival probabilities and regeneration rates observed after routine levels of fragmentation (experimental or natural<sup>4,5,11</sup>) may tell us little of the reef's potential for recovery from unusually extensive damage<sup>13</sup>.

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