Effects of Cyclone ‘Joy’ on nearshore coral communities of the Great Barrier Reef

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ABSTRACT: The rain associated with tropical Cyclone ‘Joy’, in late 1990 and early 1991, led to the third largest recorded flood in central Queensland, Australia. This study examined the effects of floodwaters on nearshore coral communities, in 3 regions of the Great Barrier Reef. The Keppel Island reefs (23° 10’ S) were affected by extreme floodwaters which damaged corals to an average depth of 1.3 m below low water datum. Mortality was highest for shallow Acropora spp. and pocilloporids; faviids were most tolerant. The most widespread effect on deeper colonies of Acropora spp. was gross swelling and lysis of the epidermal cells and loss of zooxanthellae from the gastrodermis (bleaching). Shallow waters around Middle Reef (19° 09’ S) experienced moderate floodwaters and significant mortality occurred to colonies of Acropora spp.; other corals were not damaged. The Whitsunday Island reefs (20° 20’ S) were subjected to minor floodwaters and shallow corals suffered little damage, however deep-water pocilloporids died, possibly because of low incident light during the tropical depression.

KEY WORDS: Cyclones, Floods, Coral damage

INTRODUCTION

Tropical storms, such as cyclones, hurricanes and typhoons, are among the most severe physical disturbances to affect coral reefs (Ball et al. 1967, Stoddart 1969, Woodley et al. 1981, Harmelin-Vivien 1994). Effects may include the removal of reef matrix, scouring and fragmentation (Van Woesik et al. 1991, Done 1992) or, once tropical storms make landfall, nearshore salinities may decline dramatically, following intense rainfall and flooding. This can cause coral bleaching (the expulsion of endo-symbiotic zooxanthellae) and can lead to extensive mortality of the shallow reef corals (Hedley 1925, Rainford 1925, Goreau 1964, Glynn 1993 for review). Damage may also result from sediment taken into suspension by storm currents causing sandblasting and burial of reef organisms (Ball et al. 1967, Hubbard et al. 1991), or through changes in turbidity, decreasing available light and increasing the energetic allocation toward the removal of sediment particles (Rogers 1983).

In mid-December 1990, an intense low pressure system developed in the Coral Sea off the North Queensland coast, Australia (15° S) (Fig. 1). On 19 December Cyclone ‘Joy’ (barometric pressure of 995 hPa) entered the Great Barrier Reef province. Its minimum central pressure dropped to 940 hPa on 23 December while it was located approximately 100 km east of Cairns (16° 40’ S, 146° 30’ E). Wind gusts at times exceeded 200 km h⁻¹. For the next 3 d the cyclone weakened and moved steadily south, crossing the coast on 26 December near Townsville where it degenerated into a tropical depression.

Rainfall was highest in the region between Proserpine (20° S) and Rockhampton (23° S) where over 2000 mm fell between 23 December and 7 January 1991 (Fig. 1). High rainfall associated with tropical low pressure systems continued to the end of March 1991. This led to extensive flooding of the central Queensland coastal plain. The flood was the third largest in more than 100 years. The effects of the tropical depres-
reefs on 2 January 1991. Salinities were low for 15 d. During the flood peak, salinities around the islands were in the order of 7 to 10 ppt at the surface, 15 to 28 ppt at 3 m, 31 to 34 ppt at 6 m, and 33 to 34 ppt at 12 m (Brodie & Mitchell 1992).

Middle Reef. Middle Reef is located in Cleveland Bay, 19°09' S, 146°50' E, approximately 4 km offshore from Townsville (Fig. 2b). The Ross River, with a catchment area of 1815 km², discharges directly into Cleveland Bay. Discharge from Ross River peaked in mid-February at 31873 Ml d⁻¹, averaging at 15000 Ml d⁻¹ for January and February. On 8 and 12 February 1991, surface salinity was 20 ppt and 20.5 ppt at 2.5 m (Great Barrier Reef Aquarium, M. Townsend pers. comm.).

Whitsunday Islands. The Whitsunday Islands are located 20 km from the mainland at 20°20' S and 148°57' E (Fig. 2c). The islands were not influenced by direct river runoff. Although the Proserpine River flows into Repulse Bay, immediately to the south of the Whitsunday Islands, the construction of a large dam 57.7 km up river (completed in December 1990, just prior to the heavy rains) precluded substantial river runoff (dam catchment area 260 km², holding capacity 500000 Ml). Therefore the Whitsunday reefs were subjected to only direct rainfall and localised runoff.

Fig. 1. Map of Queensland, Australia, depicting the track of tropical Cyclone ‘Joy’ and associated rainfall, where isobars signify mm of rain from 23 December 1990 to 7 January 1991. The catchment area of the Fitzroy River is depicted by dashed lines

sion on the coral reefs where studied at 3 nearshore locations, the first receiving extreme floodwaters (Keppel Islands), the second moderate floodwaters (Middle Reef), and the third receiving slight surface dilutions (Whitsunday Islands) (Fig. 1).

SITE DESCRIPTION

Keppel Islands. The Keppel Islands are located at 23°10' S, 150°59' E (Fig. 2a), 33 km from the mouth of the Fitzroy River, which has a catchment area of 140000 km² (Fig. 1). In December, the river typically discharges an average of 480857 Ml d⁻¹ (mean for the period 1965–1990). During the flood, discharge peaked at 1250000 Ml d⁻¹, causing a 9 m rise in river height. The first floodwater plume spread over the

METHODS

Keppel Islands. A total of 8 fixed sites were established with steel pins on the reef edge, between low water datum and 2 m, in October 1989 (Fig. 2a). At least 3 compass bearings were taken from prominent headlands nearby to facilitate site relocation. Each site measured 20 × 10 m with the long axis parallel to the reef crest. The size, identity and abundance of all corals were recorded by subdividing each site into 5 × 5 m plots and allocating a size class to each colony based on maximum diameter: class 1: 1 to 10 cm; class 2: 11 to 50 cm; class 3: 51 to 100 cm; class 4: 101 to 300 cm; class 5: >301 cm. Sites were re-examined in February 1991 (by RVW). Each site was searched systematically for corals that exhibited bleaching and/or partial or total colony mortality. Colony depth (relative to low water datum) and the level of bleaching (partial or total) was recorded.

Histopathology. Terminal polyps from 10 partially bleached colonies (5 Acropora formosa, 2 A. secale, 1 A. latistella, 1 Pocillopora damicornis and 1 Seriat-
**Porites hystrix** were collected from 2 leeward locations in the Keppel Islands (Clam Bay and Barren Island) in February 1991 at depths ranging from 1 to 6 m. With material intended for histology, an attempt was made to sample the border between normal and bleached tissue. All tissues were fixed in 10% seawater/formalin in the field and decalcified with formic acid (0.5 to 5%) over a period of several weeks in the laboratory. The remaining soft tissues were embedded in paraffin wax, cut to a thickness of 5 to 6 μm and stained with Haematoxylin and Eosin, Periodic Acid Schiff and Trichome (by JSG).

**Middle Reef.** A total of 6 fixed sites were established with steel pins in July 1990 (Fig. 2b). Each site measured 20 × 8 m. The 20 m central axis was placed parallel to the reef crest at 2 m below low water datum (LWD). In order to calculate estimates of coral cover, 6 haphazardly positioned 20 m line transects were laid and the intercepts of coral species and other benthos were recorded. All sites were resurveyed after the floods, in June 1991. Mean percent cover estimates were used for comparative analyses after an arcsin transformation. Two-way analysis of variance (ANOVA) was used to determine whether changes had occurred on Middle Reef, using the within subgroups variance as the error mean square.

**Whitsunday Islands.** A monitoring program was initiated in November 1990 for the eastern Whitsunday Islands (Fig. 2c). A total of 9 sites, on 4 islands, were surveyed for coral abundance and composition using the line transect intercept technique, as for Middle Reef. Sites measured 80 × 10 m with the long axis parallel to the reef crest. Four replicate 20 m line transects were laid, almost contiguously, at each of 4 depths; 0 m LWD (reef flat), 3, 6, and 10 m. These depths were chosen to encompass the 4 major habitats identified by a pilot study. Sites were not marked with steel pins but were relocated to within 50 m of the original positions, using compass bearings off prominent headlands (RVW pers. obs.). All sites were resur-
veyed in May 1991. Changes in total coral cover were analysed via a 3-factor ANOVA, with the 3 main effects fixed, following the fixed factor model in Sokal & Rohlf (1995). Calculations were undertaken on total length of each taxa per transect, transformed to log_{10}(x + 1).

RESULTS

Keppel Islands

Leeward reefs supported large stands of arborescent Acropora species (A. formosa, A. microphthalma), colonies of A. millepora, and some favid and Porites spp. Zonation was indistinct and slopes were primarily covered in monospecific stands. Coral cover was high at most sites (≥54.3%, SE 9.9%), particularly at Site 2 (Middle Island), supporting 94% coral cover, principally Acropora formosa. In contrast, the reef at Site 6 (Humpy Island) supported 19% cover. Windward reefs supported more species than leeward reefs (Van Woesik 1991).

Mortality after the flood was most apparent on leeward reefs with large reef flats (Fig. 3). In contrast, windward reefs had low (~5%) coral mortality. Approximately 85% of the shallow (<1.3 m) leeward corals were dead and overgrown by turf algae in early February 1991, suggesting that mortality had taken place shortly after inundation by the first floodwaters. A narrow band of bleached coral was evident between 1.3 and 1.7 m LWD, and mortality was most pronounced above this depth (Fig. 3). Below this depth most corals were alive, although the reefs usually extended only a further 1.5 m onto sand, except at Barren Island, a further 7 km offshore. Barren Island was more akin to a windward reef, supporting narrow reef flats and steep slopes (Fig. 3). This reef showed minor effects, with some shallow Acropora and pocilloporid colonies having bleached.

Mortality was most extensive for Acropora spp., Pocillopora damicornis and Seraiatopora hystrix. Colonies of Montipora spp. were partially bleached, appearing more resistant than Acropora spp. to floodwaters. Some survival was apparent above 1.3 m for the favids Leptastrea, Cyphastrea, Goniatrea, Favites, and Favia spp., the dendrophyllids Turbinaria spp. (T. peltata, T. frondens, T. reniformis), the poritids Porites lutea, P. lobata, P. australis, and the siderasterids Psammocora contigua and Coscinaraea columna (Table 1).

All specimens collected for histological examination had partial bleaching. Fragments collected from deeper water had more soft tissue intact (particularly Seraiatopora hystrix collected from Barren Island). Least affected colonies showed hypertrophy and lysis of the epidermal cells, together with the secretion of large amounts of mucus. More severe damage led to loss of

![Leeward Reef](granite_island_reef.png)

![Windward Reef](carbonate_island_reef.png)

Table 1. Field observations on coral species exposed to floodwaters on Keppel Island reefs above 1.3 m LWD, February 1991

| Alcyonacea: Capnella sp. |
| Partially bleached (and appeared to recover completely) |
| Scleractinia: Favia favus, Portites australiensis, P. lutea, P. lobata, Goniopora spp., Montipora spp., Galaxea fasciculans, Hydnophora pilosa, Favia rotumana |
| Alcyonacea: Sarcophyton spp., Efstatbouria spp., Xenia sp., Alcyonium spp. |
| Totally bleached or dead |
| Scleractinia: All Acropora spp. and pocilloporids |
| Alcyonacea: Nephthids |
zooxanthellae from the gastrodermis, and the formation of bacterial emboli in the subepidermis. The most damaged colonies showed necrosis of the epidermis, gastrodermis, mesogleal filaments and tentacles (Fig. 4). Some resilience to conditions was evident in deeper Acropora spp. by hyperplasia of border areas (i.e. increase in number of cells).

Middle Reef

Reef slopes were shallow and coral communities extended to 4–5 m. There was little variation in composition with depth. In 1990, hard coral cover was high, ranging from 80% on the windward edge (east) to 20–40% on the leeward edge (Table 2). Coral commu-

Fig. 4. (a) Cross section of a normal Acropora formosa colony, showing oral ectoderm (E), aboral gastroderm (G) and calicoblastic layer (CL). Mucus secreting cells are interdispersed with tall, columnar epithelium. Zooxanthellae are concentrated in the gastrodermis (stain: H&E). (b) Hypertrophy of the epidermal layer showing margination of nuclear material (N) and the loss of numerous zooxanthellae (Z) from the gastrodermis (H&E). (c) Mucus (M) in the epidermal/subepidermal layers of a hyposaline-stressed Acropora (Periodic Acid Schiff and Trichome). (d) Ovoid, gram negative, bacterial (B) colonies on the subepidermal region. One colony has breached the integrity of the epithelium (E) and another lies between the epidermis and gastrodermis. Note a lack of inflammatory response (H&E). (e) Death of a polyp — rupturing of epidermal cells (E) and shedding of mucus and cellular debris (CD) to the external surfaces (H&E). (f) Advanced decay — necrotic debris consisting of degenerating cell wall and nuclear material. Pyknotic nuclei (PN) resemble dark, basophilic staining bodies (H&E). All panels x200
nities were composed primarily of fast-growing corals at Sites 1, 2, 3 and 5: Montipora spp. (M. tuberculosa group), Acropora spp. (A. latistella, A. nobilis, A. formosi), Turbinaria reniformis at Site 4, and Porites spp. at Site 6.

The post-flood survey was conducted 4 mo after the passage of Cyclone 'Joy'. Significant increases in dead coral cover were evident ($p < 0.001$, Table 3a), where an *a posteriori* Least Significant Difference (LSD) test showed that the mean cover of dead coral was significantly greater after the cyclone, primarily because of the significant mortality in colonies of Acropora spp. (A. latistella, A. tenuis, and A. digitifera) at Sites 1, 2, 3 and 5 (Fig. 5a). However, there was no discernible net change in live coral cover 4 mo after the flooding (Table 3b) because the loss of Acropora spp. was the same as the growth in Montipora spp. between observation periods (Fig. 5b). Nevertheless, shifts in community composition and relative abundances had occurred.

### Whitsunday Islands

Well developed reefs in the eastern Whitsunday Islands supported corals in 4 distinct habitats. (1) The reef flat had low coral cover ~8% composed of Montipora spp., Turbinaria spp., Pavona varians, Goniatrea spp., Porites spp., Acropora millepora and Acropora valida. (2) The reef crest supported monospecific stands of massive Porites spp., Acropora spp. and Sinularia spp. (soft coral). Coral cover was ~25%. (3) The upper slope, from 3 to 6 m, supported diverse communities (classified as the acroporid/pocilloporid/poritid zone), and a coral cover which ranged from 15 to 65%. (4) The lower slope, from 6 to 10 m, supported pectiniid, mussid and agariciid corals with ~30% coral cover (Table 4).

There was no significant difference in the amount of (total) live coral cover between the observation periods (Table 5a). There was however a significant increase in dead coral cover ($p < 0.0001$), and a significant ($p < 0.0001$) interaction effect between time and site.

<p>| Table 2. Change in mean percent coral cover between July 1990 and June 1991, at 6 sites, on Middle Reef, Queensland, Australia. Standard error is given in brackets. <em>-</em> 0% coral cover |
|---|---|---|---|---|---|---|</p>
<table>
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<tr>
<th>Year</th>
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<th>Site 5</th>
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<td>82.8 (9.6)</td>
<td>37.5 (10.0)</td>
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<td>40.5 (7.0)</td>
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<td>30.2 (7.4)</td>
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Table 3. Two-way analysis of variance (ANOVA) for changes in (a) dead coral and (b) live coral cover on Middle Reef before and after the 1991 floods

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<th>F-value</th>
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Table 5. Three-way analysis of variance (ANOVA) for changes in live coral, dead coral and pocilloporidae corals in the Whitsunday Islands before and after the floods, where all 3 main effects are fixed

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<tr>
<td>Error</td>
<td>216</td>
<td>0.1460</td>
<td></td>
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<td>(b) Dead coral</td>
<td></td>
<td></td>
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<tr>
<td>Time (Factor A)</td>
<td>1</td>
<td>47.461</td>
<td>79.84</td>
<td>0.0001</td>
</tr>
<tr>
<td>Site (Factor B)</td>
<td>8</td>
<td>5.5671</td>
<td>9.37</td>
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<tr>
<td>Habitat (Factor C)</td>
<td>3</td>
<td>3.6030</td>
<td>6.06</td>
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<tr>
<td>Interactions</td>
<td></td>
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<tr>
<td>A x B</td>
<td>8</td>
<td>4.6704</td>
<td>7.86</td>
<td>0.0001</td>
</tr>
<tr>
<td>A x C</td>
<td>3</td>
<td>1.9137</td>
<td>3.22</td>
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</tr>
<tr>
<td>B X C</td>
<td>24</td>
<td>1.1026</td>
<td>1.85</td>
<td>0.0114</td>
</tr>
<tr>
<td>A x B x C</td>
<td>24</td>
<td>1.1907</td>
<td>2.00</td>
<td>0.0050</td>
</tr>
<tr>
<td>Error</td>
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<td>0.5944</td>
<td></td>
<td></td>
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<tr>
<td>(c) Pocilloporidae</td>
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<td></td>
<td></td>
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<tr>
<td>Time (Factor A)</td>
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<td>0.3667</td>
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<td>Habitat (Factor C)</td>
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<td>18.32</td>
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<td></td>
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<tr>
<td>A x B</td>
<td>8</td>
<td>1.527</td>
<td>1.51</td>
<td>0.1549</td>
</tr>
<tr>
<td>A x C</td>
<td>3</td>
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<td>0.50</td>
<td>0.6884</td>
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<td>B X C</td>
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<td>1.69</td>
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<tr>
<td>Error</td>
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<td>1.0124</td>
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</table>

DISCUSSION

The Fitzroy River plume flowed predominantly northeast over the denser saline waters and became diluted with increased distance from the rivermouth (Table 5b). The latter suggests mortality between the observation periods was strongly dependent on location. Although there was no significant overall mortality recorded for pocilloporids (Table 5c), when Sites 3 and 4 were analysed separately there was a significant decline in pocilloporid cover between observation periods ($F=6.70$, df = 1, 63, $p=0.013$; Fig. 6). Mortality was highest in *Seriatopora hystrix*, the needle-like pocilloporid, which was dominant on the lower slopes. No significant changes were detected for other coral families i.e. Acroporidae, Poritidae, Mussidae, Pectinidae, Faviidae and soft corals, although their distribution patterns varied among habitats (Table 4).

Table 4. Change in mean percent coral cover (SD in brackets) between November 1990 and May 1991, at 4 depths in the Whitsunday Islands, Queensland, Australia. Sixteen 20 m line transects were measured at each depth.

<table>
<thead>
<tr>
<th>Family</th>
<th>Year</th>
<th>Reef flat</th>
<th>Reef crest</th>
<th>Upper slope &lt; 6 m</th>
<th>Lower slope 6-12 m</th>
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</thead>
<tbody>
<tr>
<td>Acroporidae</td>
<td>1990</td>
<td>2.1 (2.0)</td>
<td>15.8 (17.3)</td>
<td>10.4 (11.5)</td>
<td>5.3 (3.0)</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>4.8 (4.6)</td>
<td>11.0 (14.3)</td>
<td>12.4 (12.6)</td>
<td>4.8 (3.0)</td>
</tr>
<tr>
<td>Pocilloporidae</td>
<td>1990</td>
<td>0.7 (1.1)</td>
<td>21.2 (2.2)</td>
<td>8.7 (15.3)</td>
<td>7.9 (11.9)</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>0.9 (0.6)</td>
<td>1.8 (1.7)</td>
<td>5.5 (6.2)</td>
<td>1.8 (2.5)</td>
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<tr>
<td>Faviidae</td>
<td>1990</td>
<td>0.5 (0.4)</td>
<td>2.3 (2.3)</td>
<td>3.2 (2.2)</td>
<td>2.7 (1.7)</td>
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<tr>
<td></td>
<td>1991</td>
<td>0.5 (0.6)</td>
<td>1.7 (1.6)</td>
<td>2.8 (2.9)</td>
<td>3.1 (2.6)</td>
</tr>
<tr>
<td>Portitidae</td>
<td>1990</td>
<td>1.3 (0.9)</td>
<td>15.1 (14.6)</td>
<td>9.6 (10.6)</td>
<td>7.9 (7.9)</td>
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<td>1991</td>
<td>3.5 (6.4)</td>
<td>14.1 (14.7)</td>
<td>12.4 (10.9)</td>
<td>9.7 (10.0)</td>
</tr>
<tr>
<td>Pectinidae</td>
<td>1990</td>
<td>-</td>
<td>1.3 (1.6)</td>
<td>3.0 (3.1)</td>
<td>5.3 (3.5)</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>0.2 (0.7)</td>
<td>1.3 (1.7)</td>
<td>2.5 (2.7)</td>
<td>5.7 (4.9)</td>
</tr>
<tr>
<td>Mussidae</td>
<td>1990</td>
<td>0.3 (0.4)</td>
<td>0.8 (0.9)</td>
<td>0.8 (0.6)</td>
<td>0.5 (0.7)</td>
</tr>
<tr>
<td></td>
<td>1991</td>
<td>0.3 (0.3)</td>
<td>0.7 (1.0)</td>
<td>0.8 (0.7)</td>
<td>1.1 (1.0)</td>
</tr>
</tbody>
</table>

(LeX & Mitchell 1992). River plumes are usually restricted to nearshore waters of the Great Barrier Reef (Wolanski & van Senden 1983, King & Wolanski 1991). Extensive coral mortality was apparent on leeward reefs of the Keppel Islands. Windward reefs were only marginally affected. Shallow *Acropora* spp. (*A. formosa*, *A. microphthalma*, *A. latistella, A. millopora*, *A. valida*) and pocilloporids (*Pocillopora damicornis, Seriatopora hystrix*) were most susceptible. Coral mortality did not extend beyond 1.7 m. Coral mortality may have resulted from either one or a combination of effects, including low salinity (Rainford 1925, Hoegh-Gulberg & Smith...
specific indicators of stress which could have been exacerbated by heavy sediment load and low light conditions in the water column (Rogers 1979).

Necrosis of important structural components such as mesogleal filaments and tentacles was the direct result of lysis, leaving behind cellular debris and pyknotic nuclei. The mechanism by which bacterial emboli developed in the subepidermis was unknown, although these have been reported in anemones *Ceriantheopsis americanus* exposed to dredge spoil (Peters & Yevich 1989). The ability of corals to recover from medium term exposure to floodwaters, was evident by the presence of hyperplasia in the border tissues. What cellular processes prevented stress in favids is unknown, although the reduced exposure of the body wall to the external environment, largely a consequence of their morphology, may increase resistance. Previously, Muthiga & Szmant (1987) reported on the resistance of the Atlantic species *Siderastrea siderea* to reduced salinities, a species similar to many favids. These authors suggested that polyps retract in response to environmental extremes (not only in hypo-saline conditions), to produce ‘blanching’. This term was recently coined by Brown & Ogden (1993) to describe (temporary) visible paling without loss of photosynthetic pigments or zooxanthellae (Brown et al. 1994).

Shallow communities on Middle Reef exhibited mortality only in colonies of *Acropora* spp. (*A. latistella, A. valida, A. digitifera* and *A. tenuis*). Pocilloporids were rare. No net change in coral cover was evident, although a shift in community composition occurred. Cover of *Montipora* spp. had increased considerably between sampling periods, compensating for the loss of *Acropora* spp.

In the Whitsunday Islands, the upper slope communities showed no detectable change in coral cover or signs of necrosis. Deep water pocilloporids, specifically *Seriatopora hystrix*, were most affected and were observed undergoing necrosis *in situ* during the tropical depression (M. Stafford-Smith pers. comm.). Analyses of all sites showed no significant (overall) coral mortality; however, significant mortality was apparent when sites with abundant pocilloporid cover were analysed independently. These results emphasize that subtle changes to corals can be masked by the patchy distributions of associated organisms.

The small polyps of *Seriatopora hystrix* suggest that autotrophy (Porter 1976), via photosynthesis by the endo-symbiont, is the primary source of energy. Respiration rates of *Seriatopora hystrix* increase as light intensity decreases, implying colony stress (Hoegh-Gulberg & Smith 1989). Light extinction coefficients (*k*) are generally high in the Whitsunday Islands (*k* = 0.410; S. Blake pers. comm.) because of the high turbidity characteristic of the area. Further reductions in
light during the tropical depression were caused by overcast skies and plankton blooms (Brodie & Mitchell 1992). Long periods of low light on deep reef slopes increase the light extinction coefficient below 5% surface light, where autotrophs (such as Seriatopora hystrix) may not be able to survive. Other corals, such as musssids and pectinids, which are more heterotrophic, may have been able to compensate their energy requirements at these depths.

Coral bleaching and mortality have been previously reported from both the Indo-Pacific and Caribbean regions in association with stormwater runoff, varying from minor damage (Orr 1993), to extensive coral bleaching because of moderate floodwater (Goreau 1964), and massive reef mortality during extreme events (Yonge & Nichols 1931, Goodbody 1961, Jokiel et al. 1993). Mayer (1918) and Jokiel et al. (1993) both reported the susceptibility of species of Montipora and Pocillopora to floodwaters, and Jokiel et al. (1993) noted the unusual resilience of Porites compressa, where apparent death was followed by the subsequent regeneration of tissue. The present study also found intense effects on acroporids and pocilloporids but less severe effects on both Montipora and Porites spp. (Table 1). Porites spp. appeared resistant (as opposed to resilient) to floodwater, as only partial bleaching was observed, from which they recovered in 2 mo (RVW pers. obs.). Notably, Jokiel et al. (1993) reported on Porites compressa, a coral with digitate morphology, whereas the Porites spp. on the Keppel Islands were predominantly massive colonies (P. lutea, P. lobata, and P. australiensis). Hedley (1925) and Rainford (1925) described the effect of the 1918 flood on the Whitsunday reefs, which was the most extensive flood on record for the area. Both Hedley and Rainford reported absolute coral mortality above 2 to 3 m. Their descriptions are similar to those reported here for the Keppel Islands, although the 1991 effects were less severe and restricted to corals in waters shallower than 1.7 m.

Hypothetically, disturbance events of this nature may allow species that are more resistant to floodwaters, such as Porites spp. and favids, to dominate the Keppel Island reefs, especially since partially bleached Porites and favids recovered. However, extensive discharge from the Fitzroy River occurs regularly. A flood of this intensity has a recurrence interval of approximately 50 yr, although floods with half the flow rate occur approximately every 8 yr (Bureau of Meteorology Report 1991). A high disturbance frequency may sustain the reef communities at a primary or recovering stage in succession, where opportunistic corals, such as Acropora spp., dominate through history. Furthermore, remnant survivors on the lower slopes were Acropora spp., and the southern Great Barrier Reef region is dominated by Acropora spp. (Van Woesik 1991), increasing the likelihood that similar communities will again dominate.

Floods associated with Cyclone 'Joy' caused differential coral mortality and shifts in community composition which were dependent on both the intensity of floodwater discharge and types of coral communities present. Acropora and pocilloporid colonies were most susceptible to the floodwaters and associated conditions. In contrast, colonies with massive morphology generally exhibited only partial bleaching and recovered rapidly. A history of the frequency and intensity of such events may be traced through proxy cues in the skeleton of massive colonies (Isdale 1984, Risk et al. 1992). In a regional context, integrating isotopic stratigraphy studies, from massive corals, with real-time responses of coral communities subjected to extreme events, may allow not only the reconstruction of historical ocean-atmospheric variability but also the turnover frequency of associated communities (Williams & Bunkley-Williams 1990, Glynn 1993).

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