

Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef

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ABSTRACT: Despite extensive research into the coral bleaching phenomena there are very few data which examine the population biology of affected species. These data are required in order to predict the capacity of corals to respond to environmental change. We monitored individual colonies of 4 common coral species for 8 mo following historically high sea-surface temperatures on the Great Barrier Reef in 1998 to compare their response to, and recovery from, thermal stress and to examine the effect of bleaching on growth and reproduction in 2 *Acropora* species. *Platygyra daedalea* and *P. lobata* colonies took longer to bleach, longer to recover and longer to die. In contrast, *Acropora hyacinthus* and *A. millepora* colonies bleached quickly and most had either recovered, or died, within 14 wk of the initial reports of bleaching. Whole colony mortality was high in *A. hyacinthus* (88%) and *A. millepora* (32%) and partial mortality rare. In contrast, most colonies of *P. daedalea* and *P. lobata* lost some tissue and few whole colonies died. The mean proportion of tissue lost per colony was $43 \pm 6.6\%$ and $11 \pm 1.1\%$ respectively. Consequently, observed hierarchies of species susceptibility will depend critically on the time since the onset of stress and must consider both whole and partial colony mortality. Colony mortality was highly dependent on visual estimates of the severity of bleaching but independent of size. Growth rates of *Acropora* colonies were highly variable and largely independent of the severity of bleaching. *A. hyacinthus* was more susceptible to bleaching than *A. millepora* with 45% of surviving colonies gravid compared to 88%. High whole-colony mortality combined with a reduction in the reproductive output of surviving *Acropora* suggests that recovery to former levels of abundance is likely to be slow.

KEY WORDS: *Acropora* · Coral reef · Disturbance · *Platygyra* · Population biology · *Porites* · Recovery · Stress response · *Stylophora*

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INTRODUCTION

Coral bleaching is occurring with increasing frequency and severity on reefs around the world (Williams & Bunkley-Williams 1990, Glynn 1996, Goreau et al. 2000). Bleaching can be triggered by a range of stresses such as high UV radiation (Gleason &

Wellington 1993), reduced salinity (Goreau 1964, van Woesik et al. 1995) bacterial infection (Kushmaro et al. 1997) and combinations of different stresses (Brown et al. 1995). However, thermal stress seems responsible for most large-scale bleaching events (Goreau & Hayes 1994, Hoegh-Guldberg 1999, Goreau et al. 2000). 1998 was the hottest year on recent record, and the geographic scale and severity of the coral bleaching that ensued has led to concerns about the future of coral reefs in the face of global climate change (Hoegh-Guldberg 1999, Wilkinson et al. 1999, Glynn 2000). Some climate models of sea-surface temperatures (SST)

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predict that the current thermal tolerances of most reef-building corals on the Great Barrier Reef (GBR) will be exceeded within the next few decades and large-scale bleaching will occur annually on the GBR by the year 2030 (Hoegh-Guldberg 1999). Assuming that these models of temperature change are correct, the future of reefs will depend on the capacity of corals to acclimatize or adapt to increased temperatures.

Despite extensive research into coral bleaching there are very few data with which to predict the capacity of coral to respond to changing environmental conditions (Brown 1997, Buddemeier & Smith 1999). Most field studies have examined changes in the structure of assemblages rather than providing the necessary detail on the population biology of affected species (Bak & Meesters 1999). Mortality in corals is generally size-specific, and rates of whole-colony mortality decrease as the size of the colony increases (Connell 1973, Sakai 1998a). Furthermore, partial mortality often accounts for a greater proportion of tissue loss within populations than whole-colony mortality (Hughes & Jackson 1985). In addition, larger colonies produce more eggs per unit area (Hall & Hughes 1996, Sakai 1998b) and consequently make a disproportionate contribution to the reproductive output of the population. Thus, to quantify the effect of disturbance on coral populations, it is necessary to determine which individuals are affected and to measure both whole-colony and partial mortality. The only effective way to do this is to follow individual colonies through time (Brown et al. 1994).

Bleaching, like many other types of stress, is known to have important sub-lethal effects on colonies. Zooxanthellae have been estimated to provide 30% of the total nitrogen and 91% of carbon needs of the coral host (Bythell 1988). Consequently, when the density of zooxanthellae is reduced during bleaching, the coral

loses an important source of energy (Porter et al. 1989). Sub-lethal effects of bleaching include a reduction in stored energy (Fitt et al. 1993), reduced growth (Goreau & MacFarlane 1990, Leder et al. 1991) and tissue biomass (Szmant & Gassman 1990), and a reduction in the rate of regeneration from injury (Meesters & Bak 1993). However, few studies have followed recovery in sufficient detail to determine how growth and reproductive output are affected by the severity of bleaching (van Woessik 2001). Szmant & Gassman (1990) suggested that the reproductive output of *Montastrea annularis* was dependent on the severity of bleaching and how quickly corals recovered. Unbleached *M. annularis* colonies and colonies that recovered within 6 mo produced gametes. In contrast, colonies that remained bleached did not produce gametes (Szmant & Grassman 1990). Similarly, the egg size and polyp fecundity in experimentally bleached colonies of the soft coral *Lobophytum compactum* was reduced for 20 mo (Michalek-Wagner & Willis 2000). However, it remains to be tested whether these results are generally applicable to other coral species.

In this study, we observed tagged colonies of 4 scleractinian species, *Acropora hyacinthus*, *A. millepora*, *Platygyra daedalea* and *Porites lobata* at regular intervals for 8 mo to compare the patterns of response to, and recovery from, historically high SST on the GBR in January 1998. In particular, we aimed to quantify the extent of mortality in these populations and to test whether mortality was size-specific and influenced by the severity of bleaching. Furthermore, we aimed to determine whether the growth rate and reproductive output in the 2 acroporid species could be predicted from a visual estimate of colony condition.

MATERIALS AND METHODS

Study sites. This study was conducted on the fringing reef on the leeward side of Orpheus Island, and on the windward side of Pelorus Island. Both islands are continental islands of the Palm Islands group (18° 46' S, 146° 15' E) in the Central Section of the GBR Marine Park. These sites were amongst the worst affected by bleaching on the GBR following a sharp rise in sea-surface temperature in the early months of 1998 (Baird & Marshall 1998, Berkelmans & Oliver 1999). Data loggers maintained by the GBR Marine Park Authority demonstrated that these sites experienced an identical thermal regime in the weeks leading up to bleaching and in the following 3 mo (Fig. 1).

Species response to and recovery from high SST. On 24 March 1998, all living colonies of *Acropora millepora* (n = 37) and *A. hyacinthus* (n = 28) in a 20 m × 40 m area between 3 to 4 m deep on the fring-

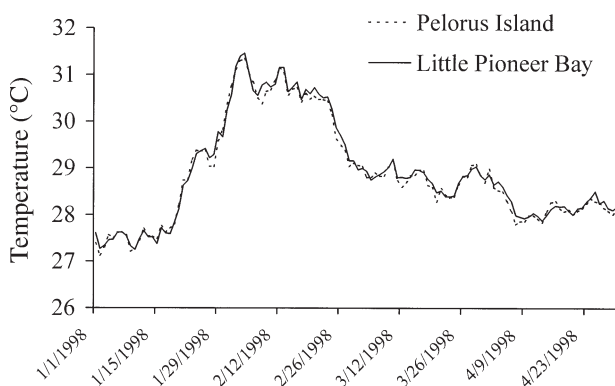


Fig. 1. Mean daily sea surface temperatures recorded at 3 m depth at each of the 2 study sites from 1 January 1998 to 31 May 1998 (data from the Great Barrier Reef Marine Park Authority)

ing reef at the SE corner of Pelorus Island were tagged to examine the patterns of response to, and recovery from, high SST. Similarly, all colonies of *Platygyra daedalea* ($n = 28$) and *Porites lobata* ($n = 14$) at 3 to 4 m depth in an area 50 m \times 10 m were tagged at Little Pioneer Bay on Orpheus Island. The extent of colony bleaching was classified into 6 categories following the scheme of Gleason (1993): no bleaching, 1 to 10, 11 to 50, 51 to 99, 100% bleached, and dead. Colonies appearing uniformly pale were classified with those 1 to 10% bleached. The extent of colony bleaching was estimated on 6 occasions: 6, 10, 14, 20, 28 and 40 wk following the initial report of bleaching at these sites on 10 February 1998 (Hoegh-Guldberg 1999).

The influence of colony size and bleaching severity on colony mortality. A number of different approaches were used to examine the influence of colony size on the patterns of mortality depending on the response of the species to stress. In *Platygyra daedalea*, few whole colonies died but most lost some tissue. Consequently, linear regression was used to test whether there was a correlation between tissue loss and colony size. The size of *P. daedalea* colonies was determined from the maximum diameter (e.g. Babcock 1991) of colonies at the initial census, which ranged from 10 to 40 cm. Partial mortality was defined as the proportion of tissue lost within each colony, estimated to the nearest 5%, at the time of the final census. Values ranged from zero (escape from injury) through various amounts of injury (partial mortality) to 100% (whole-colony mortality) (e.g. Hughes & Jackson 1985). In the *Acropora*, there was very little partial mortality: the whole-colony either lived or it died. Consequently, Pearson's χ^2 statistic was used to test whether colony fate after 40 wk (i.e. alive or dead) was independent of colony size at the initial census (i.e. large or small). The projected area of the acroporids was estimated from digitized photos of the colonies and ranged from 133 to 3078 cm² in *A. millepora* and 438 to 9900 cm² in *A. hyacinthus*. Two size classes were defined to maintain adequate sample sizes for analysis. The size class boundaries were 500 cm² in *A. millepora* and 3000 cm² in *A. hyacinthus*.

To examine whether a visual estimate of bleaching severity was a good guide to colony mortality, the analyses were similarly determined by the response of the species. In the *Acropora*, Pearson's χ^2 statistic was used to test whether whole-colony mortality was independent of the maximum bleaching severity observed during the study. Two bleaching categories were defined to maintain adequate sample sizes for analysis: moderately (0 to 50% of the colony affected, or the whole-colony pale) and severely (51 to 100%) bleached. In *Platygyra daedalea* and *Porites lobata* 1-way ANOVA was used to test whether the mean proportion of tissue lost per colony (estimated as described

above) differed among bleaching categories. In *P. daedalea* 3 bleaching categories were defined: 0 to 50, 51 to 99, and 100% bleached. In *P. lobata* 2 categories were defined: 0 to 50 and 51 to 99% bleached. The values for the proportion of tissue lost per colony were log₁₀-transformed to satisfy the assumption of homogeneity of variance.

Bleaching and the reproductive output and growth of *Acropora*. To determine whether the growth of colonies was affected by the severity of bleaching, the size of the *Acropora* colonies was estimated as described above on 3 occasions: 6, 20 and 40 wk after the initial reports of bleaching. The growth of each colony was expressed as a proportion of initial size, and colonies were categorized as moderately or severely bleached as described above. To test whether severely affected *A. millepora* grew less than moderately affected colonies, a *t*-test was used to compare the mean proportional area change. The non-parametric Mann-Whitney *U*-test was used to test whether there was a difference between the growth of severely affected and moderately affected *A. hyacinthus*.

To determine whether surviving *Acropora millepora* and *A. hyacinthus* colonies produced gametes, 3 branches were broken from the center of each colony to avoid sterile zones on the periphery (Wallace 1985), just prior to spawning in November 1998. The branches were preserved in 10% seawater formalin and decalcified in 10% formic acid. The presence or absence of eggs was determined by dissection. To confirm the presence of mature testes, the decalcified branches were embedded in wax, sectioned to 10 microns, stained with Mallory's Heidenham Trichome and examined under HP microscope. Pearson's χ^2 statistic was used to test whether the presence of eggs was independent of the severity of colony bleaching. The χ^2 statistic was not calculated when >20% of the cells had an expected value <5. To confirm that colonies released eggs, the colonies were sampled again in December following the mass spawning period. The proportion of the population gravid in 1998 was then compared to 2 previous years of data collected from this site. These data were obtained by haphazardly selecting 20 colonies of each species and sampling up to 3 branches from the center of the colony. The colony was scored as gravid if pigmented eggs were visible in any of the branches (e.g. Baird et al. 2002).

RESULTS

Patterns of response and recovery

The response to high SST in the acroporids was rapid and dramatic. At the time of the first census, 6 wk after

the initial report of bleaching at these sites, all *Acropora* colonies were affected and mortality was high with 70% of *A. hyacinthus* and 10% of *A. millepora* colonies dead (Fig. 2). Furthermore, many of the surviving colonies were severely (i.e. >50%) affected, with 80% of *A. hyacinthus* and 30% of *A. millepora* completely bleached (Fig. 2). In contrast, only 60% of *Platygyra daedalea* colonies were affected and only

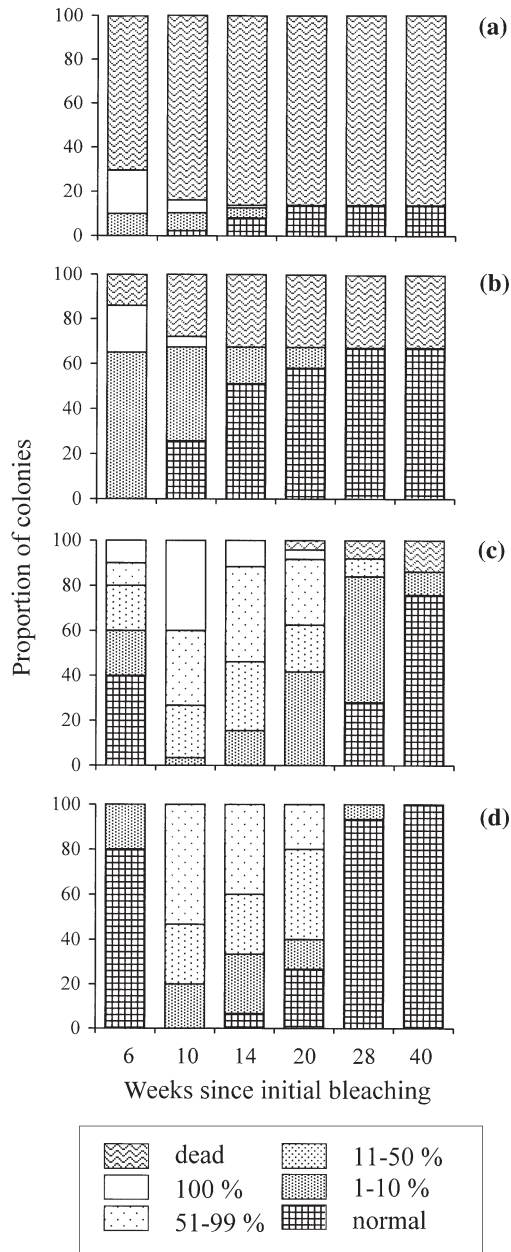


Fig. 2. (a) *Acropora hyacinthus*, (b) *A. millepora*, (c) *Platygyra daedalea*, (d) *Porites lobata*. Proportion of colonies in the 4 coral species in each of 6 bleaching categories on 6 occasions between March 1998 and November 1998

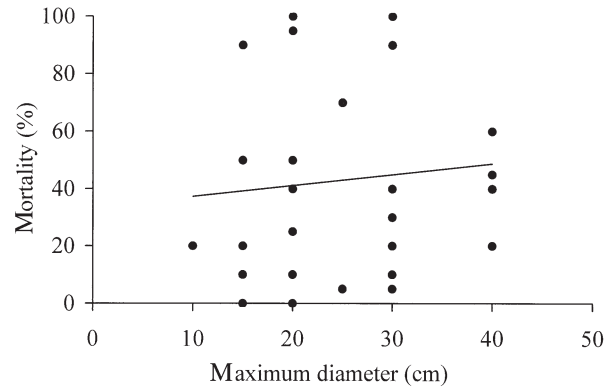


Fig. 3. *Platygyra daedalea*. Proportion of tissue lost (mortality) in colonies of different sizes

10% were completely bleached (Fig. 2). Most *Porites lobata* colonies were unbleached with only 20% of colonies affected (Fig. 2). No whole-colony mortality was recorded in the non-acroporid species in the initial census.

Between 6 and 10 wk, mortality remained high in the *Acropora*, with 50% of *A. hyacinthus* and 20% of *A. millepora* colonies dying. However, many of the surviving acroporid colonies had recovered and few remained severely affected (Fig. 2). In contrast, the extent of bleaching in most *Platygyra daedalea* and *Porites lobata* colonies had increased. All colonies of these species were now affected and 65% of *P. daedalea* and 50% of *P. lobata* were severely bleached (Fig. 2).

After 14 wk, when SSTs had returned to seasonal averages (Fig. 1), most surviving *Acropora* had recovered and no further mortality was recorded in either species. Most colonies of *Porites lobata* recovered gradually. No *P. lobata* bleached completely and none died (Fig. 2). *Platygyra daedalea* colonies took longer to recover than colonies of the other species, and 60% of colonies remained bleached for 4 to 6 mo. The first whole-colony mortality was recorded at 26 wk, a second at 30 wk and 2 more at 40 wk (Fig. 2). Interestingly, 50% of the *P. daedalea* colonies that died had recovered normal pigmentation.

Patterns of mortality

Acropora hyacinthus was highly susceptible to bleaching with 88% whole-colony mortality. This compared to 32% in *A. millepora* and 13% in *Platygyra daedalea*. No whole-colony mortality occurred in *Porites lobata*. However, while whole-colony mortality was lower in *P. daedalea* and *P. lobata*, most surviving colonies lost some tissue. For example, 88% of *P. daedalea* colonies lost

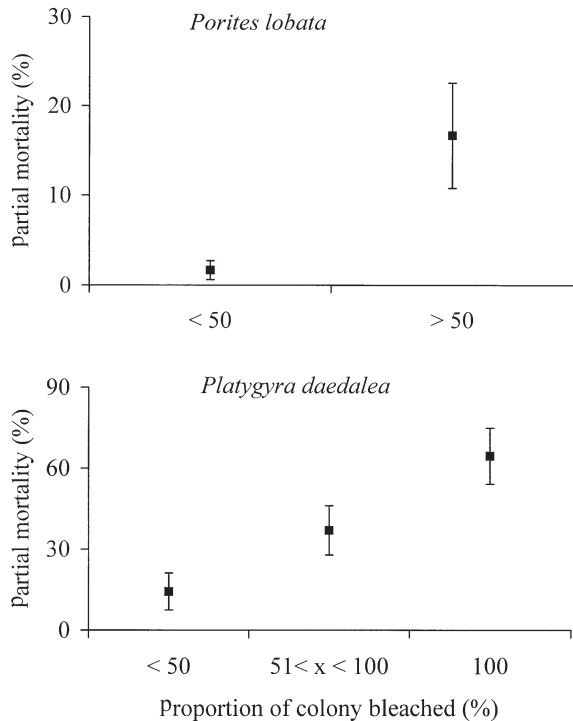


Fig. 4. *Porites lobata* and *Platygyra daedalea*. Proportion of tissue lost in colonies suffering different amounts of bleaching

tissue, and the mean loss of tissue per colony was $42 \pm 6.6\%$ (SE). Partial mortality was substantially lower in *P. lobata*: only 1 colony lost more than 20% tissue, and 40% of the colonies recovered completely. In contrast, partial mortality was rare in the acroporids: colonies either survived intact, or died.

Mortality was equally high in large and small colonies of *Acropora hyacinthus*: 40% of colonies survived in both size classes ($\chi^2 = 0$, $p = 1.0$, $n = 14$). Survivorship of *A. millepora* was independent of colony size ($\chi^2 = 3.07$, $p = 0.08$): 90% of small colonies ($n = 18$) and 60% of large colonies ($n = 19$) survived. Similarly, there was no correlation between colony size and partial mortality in *Platygyra daedalea* (Fig. 3: $r^2 = 0.008$, $F_{(1,27)} = 0.227$, $p = 0.638$).

Mortality was highly dependent on the severity of bleaching. All moderately affected *Acropora hyacinthus* colonies survived ($n = 6$), compared to only 25% of severely bleached colonies ($n = 22$) ($\chi^2 = 8.3$, $p = 0.004$). Similarly, 92% of moderately affected *A. millepora* colonies survived ($n = 25$), compared to only 42% of severely bleached colonies ($n = 12$) ($\chi^2 = 10.3$, $p = 0.002$). The mean partial mortality of *Platygyra daedalea* colonies increased as bleaching severity increased ($F_{(2,26)} = 8.53$, $p = 0.001$; Fig. 4) and mean partial mortality was higher in severely bleached colonies of *Porites lobata* than in moderately bleached colonies ($F_{(1,13)} = 28.64$, $p = 0.0001$). Nonetheless, there

was some variation in the extent of mortality in colonies bleached to a similar extent. For example, partial mortality in colonies >50% bleached ranged from 0 to 60% in *P. lobata* and from 5 to 100% in *P. daedalea*. The proportion of tissue lost never exceeded the proportion of tissue bleached.

Growth and reproductive output of acroporids

Growth rates of acroporid colonies were highly variable and largely independent of the severity of bleaching. The size of moderately affected colonies of *Acropora hyacinthus* increased between 6 and 40 wk after bleaching (Fig. 5). In contrast, most severely bleached colonies shrank. However, due to considerable variation in growth between colonies within each category, this difference was not significant (Mann-Whitney $U = 5$, $p = 0.068$). The size of moderately bleached *A. millepora* colonies increased by $20\% \pm 11.31$ between 6 and 40 wk (Fig. 5). In contrast, no increase in size was recorded in the severely affected colonies (Fig. 5). However, due to the considerable variation in growth between colonies within each group, this difference was not significant ($t = 0.797$; $p = 0.435$).

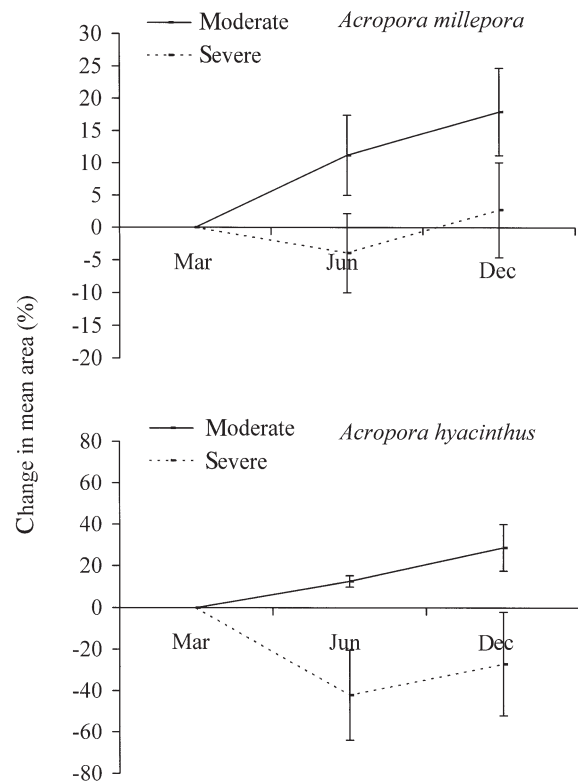


Fig. 5. *Acropora millepora* and *A. hyacinthus*. Change in mean colony area as a proportion of initial area in moderately (0 to 50%) and severely (51 to 100%) bleached colonies

Table 1. *Acropora millepora* and *A. hyacinthus*. Proportion of colonies gravid in November 1998 and in 2 previous years unaffected by bleaching at Pelorus Island

Species	Year	Fecund	Empty	n
<i>Acropora hyacinthus</i>	1996	95	5	20
	1997	100	0	20
	Bleaching 1998	45	55	11
<i>Acropora millepora</i>	1996	100	0	20
	1997	90	10	20
	Bleaching 1998	88	12	25

The reproductive output of *Acropora hyacinthus* was more susceptible to bleaching than *A. millepora*. Only 20% of severely affected *A. hyacinthus* colonies (n = 5) produced eggs and testes compared to 60% of moderately affected colonies (n = 6). The overall proportion of *A. hyacinthus* colonies gravid in 1998 was substantially lower than in the 2 previous years when no bleaching was recorded (Table 1). In contrast, a similar proportion of moderately (90%, n = 19) and severely (80%, n = 5) bleached *A. millepora* colonies were gravid. The overall proportion of *A. millepora* colonies gravid in 1998 was not substantially different from that in 1996 and 1997 (Table 1).

DISCUSSION

The response and recovery of the 4 species examined reveal that the bleaching phenomenon is highly dynamic (see also McClanahan et al. 2001). In particular, there was a pronounced difference among species in the time taken to respond to the thermal stress. The most likely explanation for this phenomenon is differences among species in respiration rate. Faster-growing species, such as the *Acropora*, are generally assumed to have a higher respiration rate than the slower-growing massives, and a high correlation between respiration rate and coral susceptibility to thermal stress has long been recognized (Jokiel & Coles 1990, but see Gates & Edmunds 1999). Alternatively, Jones et al. (2000) have suggested that poritids and faviid corals can withdraw their polyps into deeper shaded regions, thus protecting algae from further light exposure. Whatever the mechanistic explanation for this pattern, it is clear that the rank order of susceptible species, and estimates of the severity of a particular bleaching event, will depend critically on the time elapsed since the onset of stress.

A dynamic response was also apparent between colonies of the same species. In the *Acropora* the appearance of individual colonies changed markedly between census only 4 wk apart. For example, 20% of

acroporid colonies recorded as pale at 6 wk were completely bleached 4 wk later. Similarly, 25% of *Acropora* completely bleached at 6 wk had recovered 4 wk later. Consequently, it is vitally important to census a colony promptly, regularly and with little delay between censuses to establish its bleaching history. A marked difference in response to thermal stress between nubbins of *Pocillopora damicornis* has also been noted under experimental conditions (Berkelmans & Willis 1999). Our results confirm that this is likely to be a regular feature of the ecology of many species in the field.

Important differences were evident in the patterns of mortality among the studied species. The *Acropora* had high rates of whole-colony mortality and little partial mortality. In contrast, rates of whole-colony mortality were low in *Platygyra daedalea* and *Porites lobata*. In these species, the majority of tissue was lost through partial mortality, a feature typical of many coral populations (Highsmith 1982, Hughes & Jackson 1985, Bythell et al. 1993). Consequently, estimates of whole-colony mortality would have vastly underestimated the impact of bleaching on *P. daedalea* and *P. lobata*. Indeed, the proportion of tissue lost from partial mortality in the *P. daedalea* population (44%) was greater than the proportion of tissue lost from whole-colony mortality in *A. millepora* (34%). Thus, in terms of tissue loss, *P. daedalea* was more severely affected than *A. millepora*, a result we would not have predicted from accepted patterns of species susceptibilities (e.g. Marshall & Baird 2000, McClanahan et al. unpubl.). This demonstrates the importance of quantifying loss of tissue through partial mortality when constructing hierarchies of species susceptibilities. These rates of mortality are higher than previously attributed to bleaching on the GBR (e.g. Harriott 1985, Fisk & Done 1986, van Woesik et al. 1995) and similar to some of the major disturbances on the GBR such as *Acanthaster planci* (Moran 1986) and cyclones (Connell et al. 1997). For these species at this location, with the possible exception of *P. lobata*, this was not a trivial event and the mortality of *A. hyacinthus* is comparable to some of the worst cases of bleaching elsewhere in the Indo-Pacific (e.g. Brown & Suharsono 1990, Glynn et al. 2001, Mumby et al. 2001) and the Caribbean (Williams & Bunkley-Williams 1990).

High rates of whole-colony mortality in the acroporids will have important implications for the recovery capacity of these populations. High rates of whole-colony mortality are rare following other disturbance such as hurricanes, where large corals in particular, frequently survive as remnants or fragments (Woodley et al. 1981, Highsmith 1982). In such cases, recovery to former levels of abundance is swift because surviving remnants and fragments regenerate relatively quickly (Connell et al. 1997, Smith & Hughes 1999). In contrast,

recovery to former levels of abundance of the *Acropora* at these sites will depend on successful larval recruitment, which is likely to be considerably slower.

One possible explanation for the difference in the patterns of mortality among these species is the relative degree of physiological integration. Characteristics indicating higher levels of physiological integration include polyp dimorphism, intra-tentacular budding and a complex colony morphology (see Soong & Lang 1992). The *Acropora* are the most highly integrated of the Scleractinia: they are the only genera with polyp dimorphism (Veron 1986) and one of the few scleractinians with a continuous extension of the coelenteron between polyps throughout the colony (Gladfelter 1983). We hypothesize that in species with polyps that are physiologically independent, only polyps directly affected by both heat and light respond, as predicted by the photoinhibition model of coral bleaching of Jones et al. (1998). The result is that bleaching within the colony is patchy. This was the response in *Platygyra daedalea* and *Porites lobata* (Fig. 2). In contrast, in taxa where there is a high level of integration between polyps the damage is not contained. We recorded very few *Acropora* in which patches of the tissue were bleached and other areas normal (Fig. 2): the whole colony was pale or completely bleached. The Alcyonacea and Milleporidae are other anthozoan taxa with high degree of colony integration, such as polyp dimorphism (Bayer 1973). These taxa also suffered high levels of whole-colony mortality in the 1998 bleaching event on the GBR (Fabricius 1999, Marshall & Baird 2000) and elsewhere in the Indo-Pacific (Glynn & de Weerd 1991, McClanahan 2000, Loya et al. 2001).

The death of a number of *Platygyra* colonies following the recovery of normal pigmentation demonstrates that it is important to follow colonies for some time after recovery in order to quantify rates of mortality. Possible sources of mortality include an increase in both the incidence of disease (Baird 2000) and the abundance of the coral predator *Drupella rugosa* (Baird 1999) at these sites in the months following bleaching. Secondary mortality from predation is often a feature of catastrophic disturbance, such as hurricanes, particularly when predators remain relatively unaffected compared to prey (e.g. Knowlton et al. 1981).

Mortality was independent of the size of colonies. This lack of an escape in size is a feature that distinguishes mortality following thermal stress from many other sources of mortality on reefs. Other sources of mortality emanate from point sources, e.g. competition with neighbors, injury from predation or objects tossed about in storms (Jackson & Hughes 1985). In contrast, the scale of a thermal anomaly is much larger, with

temperature elevated relatively evenly over a relatively large scale from which size cannot provide an escape. Indeed, recent experimental and theoretical work predicts that large size may actually be deleterious when corals are exposed to thermal stress (Nakamura & van Woesik 2001) and field evidence indicates that the mortality rates of coral recruits (i.e. 2 to 20 mm diameter) were unaffected by bleaching (Mumby 1999). Similar rates of mortality between large and small colonies will have important implications for the rates of recovery of these affected species. The reproductive output in many coral populations is often dominated by a few large individuals (e.g. Babcock 1991, Hall & Hughes 1996). Consequently, bleaching may have a more dramatic effect on the reproductive output of populations than other types of disturbance because a relatively higher proportion of large colonies will be removed.

Visual estimates of the maximum extent of bleaching were an excellent indicator of colony mortality. Similarly, Gleason (1993) found rates of mortality in acroporids dependent on the degree of bleaching. Visual estimates of bleaching have recently been criticized on the grounds that they cannot distinguish between the various mechanisms of bleaching (i.e. pigment loss or loss of zooxanthellae) (Fitt et al. 2001). While this specific criticism is certainly valid, our results demonstrate that a properly conducted visual census can predict, with a high degree of confidence, the fate of individual colonies.

Growth rates in the *Acropora* were highly variable with no clear trend apparent between bleaching severity and growth. A more rigorous measure, such as the proportional loss of zooxanthellae (Jones 1997), or tissue biomass (e.g. Fitt et al. 2000) may be required to predict the effect of bleaching on colony growth. Furthermore, the ability to test for significant difference between the groups was affected by the low sample size resulting from the high mortality of severely bleached colonies.

Bleaching caused a substantial decrease in the reproductive output of the *Acropora* populations, primarily as a result of a significant decline in colony abundance. The reproductive output of *A. hyacinthus* was more sensitive to bleaching than *A. millepora*, both because a higher proportion of the population was killed and because the number of surviving colonies gravid was lower. Assuming that all colonies would have survived in the absence of high SST, the number of gravid *A. hyacinthus* colonies at this site was only 6% of that in 1997. Similarly, the number of gravid *A. millepora* colonies was 63% of that in 1997. Recent work on the GBR has demonstrated that recruitment rates are drastically reduced when the proportion of the population fecund falls below 80%

(Hughes et al. 2000). Consequently, a 37% reduction in the proportion of the population gravid is likely to significantly reduce the rates of recruitment.

A number of features of the population response to bleaching outlined in this study suggest that recovery of populations from bleaching is likely to be slower than from many other types of catastrophic disturbance. As a consequence of high whole-colony mortality, particularly in the *Acropora*, recovery will rely on successful larval recruitment, which is likely to be reduced both by a reduction in the abundance of gravid colonies and the loss of a higher proportion of large colonies than would be expected in other types of disturbance. However, even in the most severely affected species, some colonies survived and these surviving colonies reproduced, providing the capacity for these population to adapt to changing thermal regimes (e.g. Glynn et al. 2001). Whether these populations do adapt will depend on many factors including the frequency and severity of future bleaching episodes (Hoegh-Guldberg 1999).

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