Coral bleaching reduces reproduction of scleractinian corals and increases susceptibility to future stress.

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ABSTRACT

Extensive bleaching of corals occurred at Heron Island Reef during the 1998 mass bleaching event on the Great Barrier Reef, Australia. Two hundred coral colonies were labelled and sampled on the reef flat at Heron Island in March 1998 (when approximately 80% of corals growing in the intertidal reef flat were bleached). These included both bleached and unbleached colonies of many species. Bleached colonies of all sampled species had lower densities of symbiotic dinoflagellates and lower chlorophyll *a* concentrations per surface area of coral tissue than unbleached colonies. Samples of the colonies were decalcified and polyps dissected to determine fecundity. There were significantly fewer eggs present in the bleached than unbleached colonies in all sampled species. In many species, no eggs were present in the bleached colonies. Eggs that were present were also significantly smaller in the bleached than the unbleached colonies of the majority of species sampled. There were also significantly fewer polyps containing eggs and testes in the bleached than the unbleached colonies. The percentage of tissue made up by lipids in the bleached colonies was significantly lower than that of the unbleached colonies in some species. By July 1998, 23% of the sampled colonies had died and many of the previously bleached colonies had regained their colour, suggesting visually that they had recovered. However, previously bleached colonies in November 1998 still had fewer eggs and reproductive polyps than colonies that had been previously unbleached. In July of the following year, in the middle of the Australian winter, many of the corals that had bleached the year before bleached again and more colonies had died. In contrast, none of the previously unbleached colonies bleached at this time. In November 1999, just prior to the spawning period, there were large areas of coral on the reef slope that were noticeably pale. These pale colonies were sampled along with adjacent normally pigmented corals and the pale colonies were almost entirely devoid of eggs. During the 1998 bleaching event approximately 80% of the reef slope colonies were bleached, so it is likely that these pale colonies were previously bleached colonies. These data suggest that bleaching has adverse and long-lasting effects on coral reproduction and that previously bleached colonies may be more susceptible to future stress.

Keywords Corals, Bleaching, Reproduction, Stress, Climate change.

Introduction

Scleractinian corals harbour symbiotic dinoflagellates that can translocate up to 95% of their photosynthetic production to the coral host (Muscatine 1990). In addition to the photosynthetic energy that they supply to the host, symbiotic dinoflagellates also supply critical compounds and nutrients such as amino acids, complex carbohydrates and small peptides (Muscatine 1973, Trench 1979, Swanson and Hoegh-Guldberg 1998). The density of symbiotic dinoflagellates fluctuates throughout the year with changes in season (Stimson and Kinzie 1991, Jones 1995, Fagonee et al. 1999, Fitt et al. 2000) and in some conditions densities of symbiotic dinoflagellates are dramatically reduced and corals will "bleach" and become pale (Hoegh-Guldberg and Smith 1989).

Bleaching is triggered by a variety of stressors including increased or decreased in salinity (Goreau 1964, Egana and DiSalvo 1982), elevated copper concentrations (Jones 1997), exposure to cyanide (Jones and Steven 1997, Jones and Hoegh-Guldberg 1999), bacterial infection (Kushmaro et al. 1996), increased light (Brown 1994) and elevated seawater temperature (Jokiel and Coles 1977, Coles and Jokiel 1978, Hoegh-Guldberg and Smith 1989, Fitt and Warner 1995, Brown et al. 1995).

Elevated sea temperatures are responsible for mass bleaching events (Porter et al. 1989, Hoegh-Guldberg 1999, Wilkinson et al. 1999) with six major global events having occurred since 1979.

In 1998 the most severe and extensive bleaching on record occurred (Hoegh-Guldberg 1999, Wilkinson et al. 1999). Bleaching affected coral reef ecosystems in all parts of the world including areas that had not previously recorded mass bleaching and mortality. There was widespread coral mortality in many areas, with India, Sri Lanka, Kenya, Tanzania, Maldives and the Seychelles amongst the worst affected areas (Wilkinson et al. 1999) and, in some areas, almost all coral species were affected.

Coral species utilise a variety of reproductive modes including brooding of larvae and broadcast spawning of gametes for external fertilisation (Harrison et al. 1984). For broadcast spawning corals, reproduction involves a long gametogenic cycle in which eggs and testes develop in the months prior to a mass-spawning event. Eggs and testes are externally fertilised and the resulting larvae develop until they are competent to settle (Harrison and Wallace 1990). Larvae then swim to the substratum and attach themselves before metamorphosing into coral spat. Coral reproduction is particularly sensitive to stress (Harrison and Wallace 1990) and measures of reproductive output or fecundity can be used as indicators of reactions to various stressors such as mechanical damage (Ward 1995), nutrients (Tomascik and Sander

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1987, Ward and Harrison 1997, Ward and Harrison 2000) and oil (Guzman and Holst 1993).

This study aimed to investigate the effects of the 1998 bleaching event on the reproduction of scleractinian corals and to examine the recovery process of these corals in the two years following bleaching.

Methods

Fieldwork was done at Heron Island in the Capricorn-Bunker group of islands on the southern Great Barrier Reef, Australia (23°26'S, 151°55'E). The study site was located on the intertidal reef flat on the southwest side of Heron Island.

Bleaching in 1998

A total of 200 bleached and unbleached colonies of 14 species were located and tagged with coded plastic tags in March 1998. In March, July and November 1998 paired samples were cut from each colony. One sample from each pair was fixed in formalin for fecundity analysis while the other was frozen for analysis of the population density and quality of the symbiotic dinoflagellates.

Coral tissue was removed from frozen samples and densities of symbiotic dinoflagellates, concentrations of chlorophyll *a* per surface area and per symbiotic dinoflagellate were calculated using methods detailed in Jones et al. (2000). Formalin preserved samples were decalcified in hydrochloric acid until all skeletal material had dissolved, then placed into ethanol for storage. Individual polyps were dissected under a dissecting microscope so that individual eggs and testes could be counted and measured. Two measurements were taken from each egg, a "length" and "width" measurement. The mean egg diameter was calculated as the mean of these two measures. The egg size of the polyp was the mean of the individual egg diameters.

Where present, testes were counted for the testes number and the length and width of each testis was measured and multiplied together. The sum of these calculations for each polyp was called the "testes total" for that polyp. The percentage of reproductive polyps was also scored. At least 20 polyps per colony were checked for the presence of eggs and/or testes.

In November 1999, at the end of spring and just prior to the expected spawning period colonies were sampled along a large area (> 500 m) of the reef slope, as approximately 80% of these colonies appeared pale. More than 200 colonies were examined for reproductive activity by looking for pigmented eggs in the branches. A subsample of both pale colonies and, when available, normally pigmented but adjacent colonies was taken and the density of symbiotic dinoflagellates and the percentage of reproductive polyps were calculated (using the methods described above).
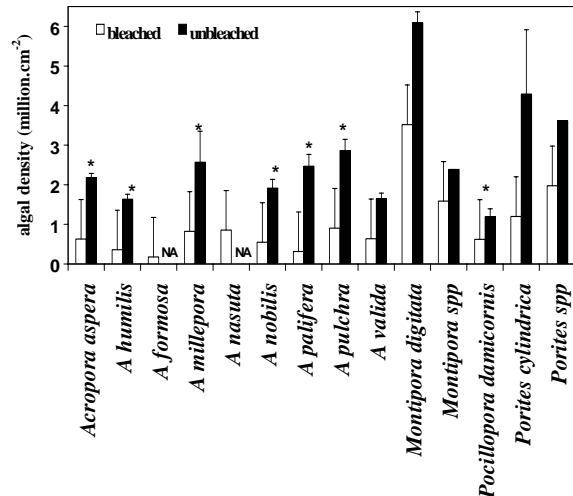

Fig. 1. The density of symbiotic dinoflagellates per cm^2 surface area in bleached and unbleached coral colonies from Heron Island sampled during the 1998 bleaching event. Error bars represent standard errors of the mean (SEM).

Results

1998 Bleaching event

Bleaching reduced the reproductive condition of corals in addition to the number of symbiotic dinoflagellates per cm^2 surface area of tissue when compared to unbleached colonies (Fig. 1). It is noteworthy that the 1998 bleaching event resulted in a reduction of up to 90% in the density of symbiotic dinoflagellates in some coral species.

In late March, 1998, about five weeks after the bleaching event, unbleached colonies of acroporid corals were in the early stages of their gametogenic cycles. In this geographic region, eggs are generally visible in acroporid colonies in early February.

Bleached colonies of many important reef flat species contained no eggs (*Symphyllia* sp, *Montipora* spp, *Acropora humilis*). *Montipora* spp represents many species of *Montipora*, none of which contained any eggs. In other prolific reef flat species there were significantly lower numbers of eggs present in bleached than unbleached corals and these included *Acropora aspera*, *Acropora palifera*, *Acropora pulchra* and *Montipora digitata* (Fig. 2).

Colonies of faviid species (*Platygyra daedalea, Favia* spp, *Goniastrea* spp) did not contain eggs when sampled in March 1998 as expected because these corals have a 5-6 month gametogenic cycle. All available colonies of *Acropora formosa* and *Acropora nasuta* were bleached, hence no comparisons can be made with non-bleached colonies of these species.
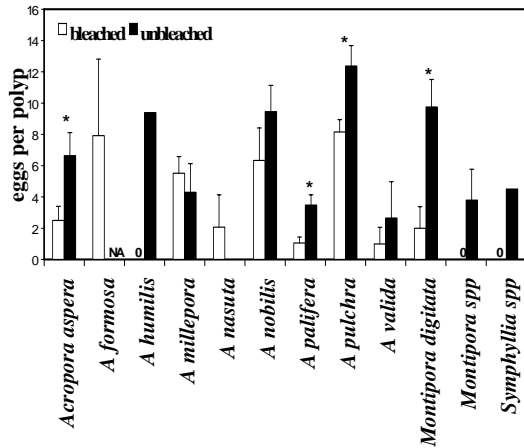
Fig. 2. The mean number of eggs present in polyps from bleached and unbleached corals at Heron Island sampled at the end of March 1998, 6 weeks after the 1998 bleaching event. Error bars are SEM.

The percentage of reproductive polyps was also compared and unbleached colonies of *Acropora aspera, Acropora humilis, Montipora digitata, Symphyllia* sp and *Montipora* spp had a significantly greater percentage of reproductive polyps than bleached colonies (Fig. 3). Unbleached colonies of many species in this study had percentages of reproductive polyps well below 100% (Fig. 3) and generally lower than in unbleached colonies.
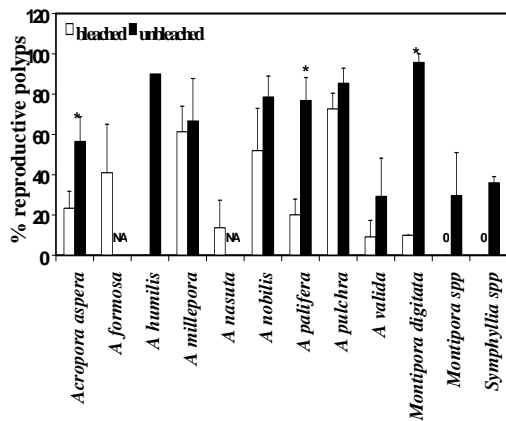

Fig. 3. The percentage of reproductive polyps present in bleached and unbleached corals at Heron Island sampled at the end of March 1998, 6 weeks after the 1998 bleaching event. Error bars are SEM.

When corals were sampled again in July 1998, 23% of the sampled colonies had died and many of the previously bleached colonies had regained their colour and appeared visually to have recovered. However, when sampled again in November, the previously bleached colonies of most species still had significantly fewer reproductive polyps and significantly fewer eggs and smaller eggs per polyp (Fig 4). There was also less testes material present in those colonies that were previously bleached (Fig. 5).
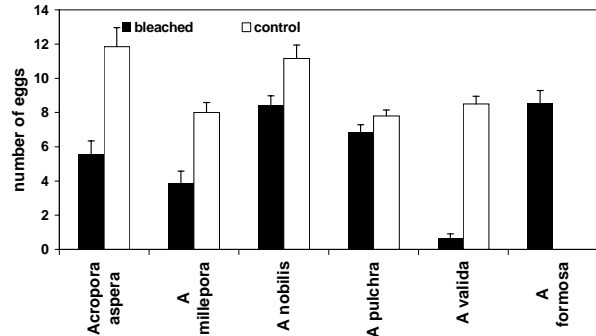

Fig. 4. The number of eggs present per polyps in bleached and unbleached corals at Heron Island sampled in November 1998, just prior to the spawning period and nine months after the 1998 bleaching event. Error bars are SEM.
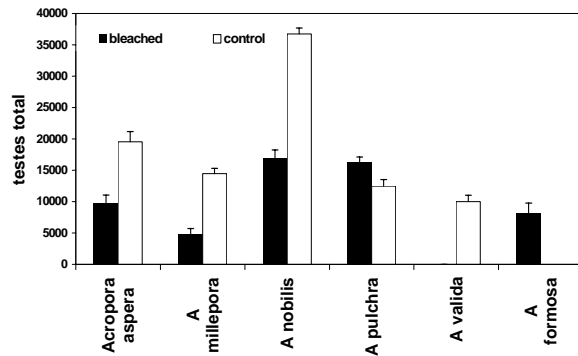

Fig. 5. The percentage of reproductive polyps present in bleached and unbleached corals at Heron Island sampled in November 1998, just prior to the spawning period and 9 months after the 1998 bleaching event. Error bars are SEM.

Many colonies bleached again in the winter of 1999 (July). Bleaching in winter is not a common phenomenon on the Great Barrier Reef and there had been no abnormally cold temperatures leading up to this bleaching (T. Saxby and Hoegh-Guldberg, unpublished). Corals that bleached at this time were corals that had bleached during the 1998 bleaching event and previously unbleached colonies did not bleach at this time. Those corals that had previously bleached had lower percentages of reproductive polyps than those that had not previously bleached (Fig 6).
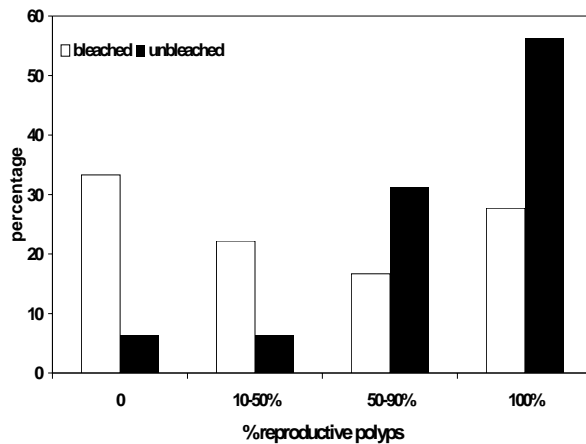
Fig. 6. The percentage reproductive polyps found in corals that had previously bleached or not bleached in March 1998 . Many corals bleached again in July 1999

In November 1999, only a small number of pale colonies on the reef slope contained no eggs whilst the normally pigmented colonies contained normal numbers of eggs. Pale colonies had reduced densities of symbiotic dinoflagellates and low percentages of reproductive polyps (Fig. 7).
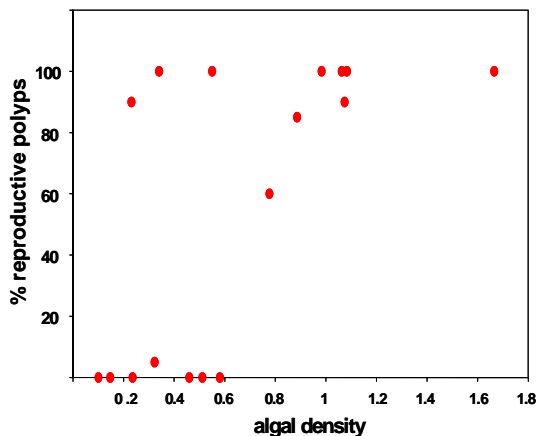

Fig. 7. The percentage reproductive polyps graphed against the density of symbiotic dinoflagellates for corals on the reef slope at Heron Island in November 1999, 21 months following the 1998 bleaching event.

Discussion

The reproduction of corals at Heron Island was severely affected by mass bleaching that occurred in response to changes in water temperature in 1998. Bleaching reduced the amount of reproductive material present in most reproductively active scleractinian coral species on the reef flat at Heron Island in March 1998 with bleached colonies of some species containing no eggs. There were fewer polyps containing reproductive material in the bleached colonies than the unbleached colonies and these polyps contained fewer eggs. Although

these results show dramatic changes in reproduction for bleached colonies, they are probably an underestimate of the effects of bleaching as many of the "unbleached" colonies with apparently normal colouration, were probably also partially bleached. Their densities of symbiotic dinoflagellates were relatively low and they had lower than usual percentages of reproductive polyps. The comparison between the two categories of colonies still stands. Those that were less affected by the thermal stress of the 1998 bleaching event had higher densities of reproducing polyps.

Colonies of many species sampled in November 1998 had fewer and smaller eggs present in the previously bleached colonies than the unbleached colonies, although most of these colonies had regained their normal colouration lost during the bleaching event. They also had reduced amounts of testes material. These data, along with observations of many previously bleached colonies rebleaching in winter of 1999, suggest that observations of returned colouration following bleaching events are not sufficient evidence to suggest that corals have recovered.

Mass coral bleaching has been reported to affect coral reproduction. Szmant and Gassman (1990) examined a limited number of corals (due to marine park restrictions) following a bleaching event in Florida in 1987 and found that bleached colonies did not complete gametogenesis in the season following the bleaching event. They also found that bleached colonies had 30% less tissue carbon and 44% less tissue nitrogen biomass per skeletal surface area than unbleached colonies. Severe bleaching also occurred on the West Australian coast in 1998 and was followed by a year of failed recruitment at Scott Reef (L. Smith, Australian Institute of Marine Science, pers comm.).

The failure or decrease in reproductive activity of bleached corals is probably due to the reduction of energy available to the coral with the loss of a great percentage of its symbiotic dinoflagellates. Bleached colonies in this study lost up to 90% of their symbiotic dinoflagellate population and hence probably the majority of their photosynthetic food energy source. In addition to the loss of cells, remaining symbiotic dinoflagellates in 1998 have been shown to have greatly reduced photosynthetic yields (Jones et al. 2000).

Reproduction is usually the most sensitive measure of performance (Begon et al. 1986) and coral reproduction can be negatively affected by a variety of stressors (Harrison and Wallace 1990). Damaging corals through fragmentation or dislodgement can reduce their fecundity (Kojis and Quinn 1981, Szmant-Froelich 1985, Ward 1995), as can lesions on the coral branches (van Veghel and Bak 1994). Coral reproduction can be sensitive to pollutants in the water such as heavy metals and oil (Rinkevich and Loya 1977) and to increased levels of sediment and turbidity (Kojis and Quinn 1984).

The results of this study are disturbing in light of projections of an increasing frequency of mass bleaching events under steadily increasing seawater temperatures (Hoegh-Guldberg 1999). Small increases in temperature and bleaching have been shown to have very detrimental

effects on coral reproduction, although these effects may not be immediately obvious to the observer. The reproductive status of corals must be considered in addition to more simplistic visual means of determining if a reef has "recovered" or not following a bleaching event. Most of the corals in this study had regained their colour by five months following bleaching but were not reproducing normally nine months after bleaching and many appeared susceptible to future bleaching by bleaching during the winter of the following year. Bleaching clearly caused this reduction in reproductive activity. The other possible explanation is that corals that don't reproduce at high rates may be more susceptible to bleaching, but this is not the case. In previous years, there have not been large percentages of the corals on the reefs in this region that do not contain eggs by late March (personal observations).

Successful coral reproduction is vitally important for the continued existence of coral reefs as it provides new recruits to replace corals that die or break from predation, storm damage, algal competition, disease and the myriad of human activities such as diver and boat damage, agricultural and urban runoff and pollutants, cyanide and blast fishing and removal of corals for collection, dredging and building materials. With the current frequency of bleaching events with their associated coral mortality, it is even more important that the surviving corals reproduce successfully.

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