

Changes in zooxanthellar densities and chlorophyll concentrations in corals during and after a bleaching event

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ABSTRACT: In January 1994 a coral bleaching event occurred on the reefs of Magnetic Island (Australia) immediately after a period of anomalously high air temperatures. Average daily water temperature increased by 2°C over 1 wk, reaching 34°C (reef flat) and 32°C (reef slope). Bleached corals were observed soon afterwards, suggesting the bleaching event was temperature related. Bleached (light tan coloured) and unbleached (dark brown coloured) colonies of staghorn coral *Acropora formosa* sampled during and after the bleaching event had lower zooxanthellar densities and higher chlorophyll *a* (chl *a*) concentrations per zooxanthella than the same colonies sampled 10 mo after the bleaching event. Significant increases in zooxanthellar chl *a* concentrations were measured in 2 colonies which were sampled and found to be losing zooxanthellae during the event. Intrinsic differences in the densities, chlorophyll concentrations and zooxanthellar cell sizes between neighbouring colonies of the same species resulted in intraspecific variability in coral discoloration during the bleaching event.

KEY WORDS: Bleaching · Chlorophyll · Coral · Temperature · Zooxanthellae

INTRODUCTION

Coral bleaching is considered a stress reaction to abnormal environmental conditions. The extent, timing and severity of many natural bleaching events has been closely correlated with elevated seawater temperature (Glynn 1984, Cook et al. 1990, Fitt et al. 1993, Brown et al. 1995, Hoegh-Guldberg & Salvat 1995).

Bleached corals sampled after warm-water bleaching events invariably have lower densities of symbiotic algae (zooxanthellae) than unbleached, normal coloured colonies (Yonge & Nicholls 1931, Hoegh-Guldberg & Smith 1989a, Kleppel et al. 1989, Porter et al. 1989, Fitt et al. 1993). Analyses of zooxanthellar chlorophyll concentrations have produced an equivocal picture. Kleppel et al. (1989) and Porter et al. (1989) report that bleached colonies of *Agaricia lamarckii* and

Montastrea annularis have lower zooxanthellar chlorophyll *a* (chl *a*) concentrations than normal coloured colonies. Hoegh-Guldberg & Smith (1989a) and Fitt et al. (1993) report that bleached corals (*Seriatopora hystrix* and *M. annularis*) have higher zooxanthellar chl *a* concentrations. The reason for this discrepancy is unclear.

Another puzzling aspect of coral bleaching is the intraspecific variability of the response. Bleached corals are often observed beside individuals of the same species showing no signs of colour loss (Fisk & Done 1985, Oliver 1985, see photographs in Ghiold & Smith 1990). Manipulative experiments and field observations with *Porites porites* have indicated that some of the variability may be related to the differential susceptibility of clonal coral genotypes (Edmunds 1994). Differences in the thermal tolerance of the zooxanthellae and diversity of zooxanthellar genotypes between or within colonies have also been suggested as a source of the inter- and intraspecific variability of bleaching (Rowan & Powers 1991, Fitt & Warner 1995).

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In January 1994, a bleaching event occurred on the fringing reefs of Magnetic Island (Great Barrier Reef region, Australia). In this work, a description of the hydro-meteorological conditions over the bleaching period is given, including an analysis of air temperatures and *in situ* seawater temperatures. Evidence is presented from corals sampled during and after the event to suggest that bleaching can occur through loss of zooxanthellae without decreases in zooxanthellar chl *a* concentrations. An examination is made as to why some colonies of Pacific staghorn coral *Acropora formosa* bleached whilst other neighbouring colonies did not. This includes an analysis of zooxanthellar densities, chl *a* concentrations and zooxanthellar cell sizes.

MATERIALS AND METHODS

Magnetic Island (19° S, 147° W) is a continental island situated ~8 km N of the mainland city of Townsville (Fig. 1). Fringing reefs occur on the SE side of the island as assemblages of coral and algae overlying platforms of accumulated non-biogenic sediments. The fringing reefs are situated in turbid waters: underwater visibility ranges from approximately <0.2 to 10 m.

Signs of bleaching on reefs at Magnetic Island were first observed by the Great Barrier Reef Marine Parks Authority (GBRMPA) Research and Monitoring Section on 16 January 1994. Scuba-diving instructors from a commercial diving outlet based on Magnetic Island also observed discolouration of corals in mid January

1994, but observed no discolouration of corals in late December 1993. It is likely the bleaching event started in the first 2 wk of January 1994.

Hydro-meteorological conditions. Air temperatures (accuracy 0.1°C) recorded at the Townsville Bureau of Meteorology (TBM) were obtained for the period 20 December 1993 to 2 February 1994. The TBM weather station is located on the Australian mainland (19.15° S, 145.46° E), ~10 km S of Magnetic Island (Fig. 1). Seawater temperatures at Geoffrey Bay between 20 December 1993 and 2 February 1994 were measured *in situ* by waterproof platinum RTD thermocouple sensors (accuracy ±0.1°C) and recorded onto data loggers. Water temperatures were measured on the reef flat (1 m depth; GBRMPA Research and Monitoring Section), and reef slope (5 m depth; Stobart 1994). The average, maximum and minimum daily temperatures were determined from recordings every 0.5 h (reef flat) and every 1 h (reef slope), from all available data loggers (n = 1 or 2 loggers at each site).

Sampling of corals. On 28 January 1994, 5 'brown-tipped' branches (see Oliver 1984) were sampled from one bleached (light tan coloured) colony (Colony 1) of a staghorn coral, *Acropora formosa* (Dana 1846), at 5 to 6 m depth in Nelly Bay, Magnetic Island (Fig. 1, Table 1). Five brown-tipped branches were also taken from a neighbouring colony of *A. formosa* (Colony 3) at the same depth which appeared a normal dark brown colour typical of the species at Magnetic Island. Five days later (2 February 1994) and 10 mo later (1 December 1994), a further 5 brown-tipped branches were sampled from the same colonies. The zooxanthellar density and zooxanthellar chl *a* concentrations were determined in the branch tips. All brown-tipped branches involved in this study were selected randomly from the respective colonies.

On 14 February 1994, 2 colonies of *Acropora formosa* at 5 to 6 m depth in Nelly Bay which the zooxanthellar densities prior to the bleaching event were known (Jones 1997) were located. One of the colonies (Colony 2) had bleached to a light tan colour and the other colony (Colony 4; ~3 m away) showed no signs of colour loss. At 2 to 4 wk intervals for the remainder of the year 5 brown-tipped branches were sampled from each of the 2 colonies and the zooxanthellar density, zooxanthellar chl *a* concentration and zooxanthellar cell size determined.

In the second week of February 1994, 4 bleached colonies of *Acropora formosa* and 5 colonies which showed no signs of colour loss were tagged for later studies (see Table 1). All colonies were located at 5 to 6 m depth on the reef slope at Nelly Bay and separated from each other by 3 to 10 m. In December 1994, 10 mo after the bleaching event, 5 brown-tipped branches were excised from each of the colonies and the zoo-

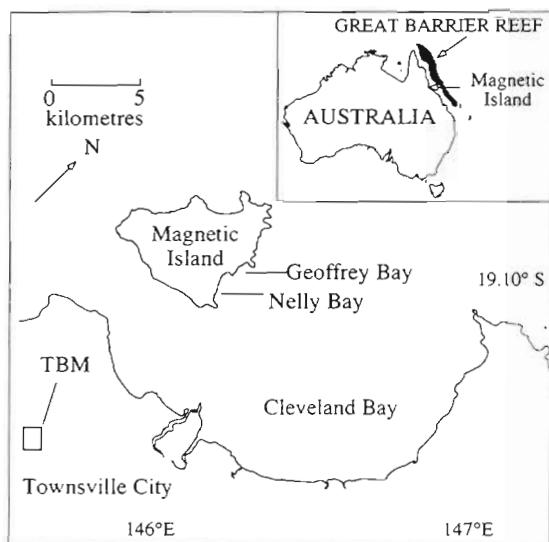


Fig. 1. Nelly Bay (coral sampling) and Geoffrey Bay (seawater temperature measured), on Magnetic Island, and the Townsville Bureau of Meteorology (TBM; air temperatures measured) on the adjacent mainland (Australia)

Table 1 Sampling dates of bleached and 'normal' coloured colonies of *Acropora formosa* (Magnetic Island, Great Barrier Reef region, Australia)

Sampling date (1994)	Bleached colonies	'Normal' coloured colonies
28 January	Colony 1 sampled	Colony 3 sampled
2 February	Colony 1 re-sampled	Colony 3 re-sampled
14 February	Colony 2 sampled, 4 bleached colonies (including Colony 1) tagged for later studies (see December 1994)	Colony 4 sampled, 5 'normal' coloured colonies (including Colony 3) tagged for later studies (see December 1994)
14 February to 1 December	Repetitive sampling of Colony 2	Repetitive sampling of Colony 4
28 November to 1 December	4 colonies which bleached sampled (see 14 February)	5 colonies which did not bleached sampled (see 14 February)

xanthellar density, zooxanthellar chl *a* concentration and zooxanthellar cell sizes determined.

Processing of corals. All coral samples were frozen for 1 h before being transported to the laboratory packed in ice. Within 3 h of collection, tissues were removed from the skeletons with a jet of 0.45 μm filtered seawater using a WaterPik™ (Johannes & Wiebe 1970). Small subsamples of the tissue homogenate were taken for analysis of zooxanthellar densities, chl *a* concentration (see Jones 1997 for methods) and zooxanthellar cell size (the largest linear diameter of 50 zooxanthellae from each of the tips, measured using a calibrated ocular micrometer at 1000 \times magnification under oil immersion). Zooxanthellae volume was calculated by assuming the cells to be spherical. The total number of zooxanthellae was normalised to the number of polyps recorded by visual census (Muscatine et al. 1991).

Data are presented as mean \pm 95% confidence intervals (CI). Data were analysed ($\alpha = 0.05$) using Type I ANOVA (JMP 1994) and Student's *t*-test. Dunnett's test of significance was used to compare the nature of significant differences between bleached and unbleached colonies. Prior to all analyses, assumptions of normality (Shapiro-Wilk's test) and homogeneity of variance (Welch's test) were tested.

RESULTS

Hydro-meteorological conditions

There were 2 periods of elevated air temperatures in the Magnetic Island area in January 1994 (Fig. 2). The first period (4 to 11 January) included the highest maximum air temperature (44.3°C, 7 January) recorded at the Townsville Bureau of Meteorology (TBM) since records began in 1942. The second period (~19 to 23 January) included the second highest minimum (night time) air temperature (29°C, 22 January) since records began in 1942. In late January average daily

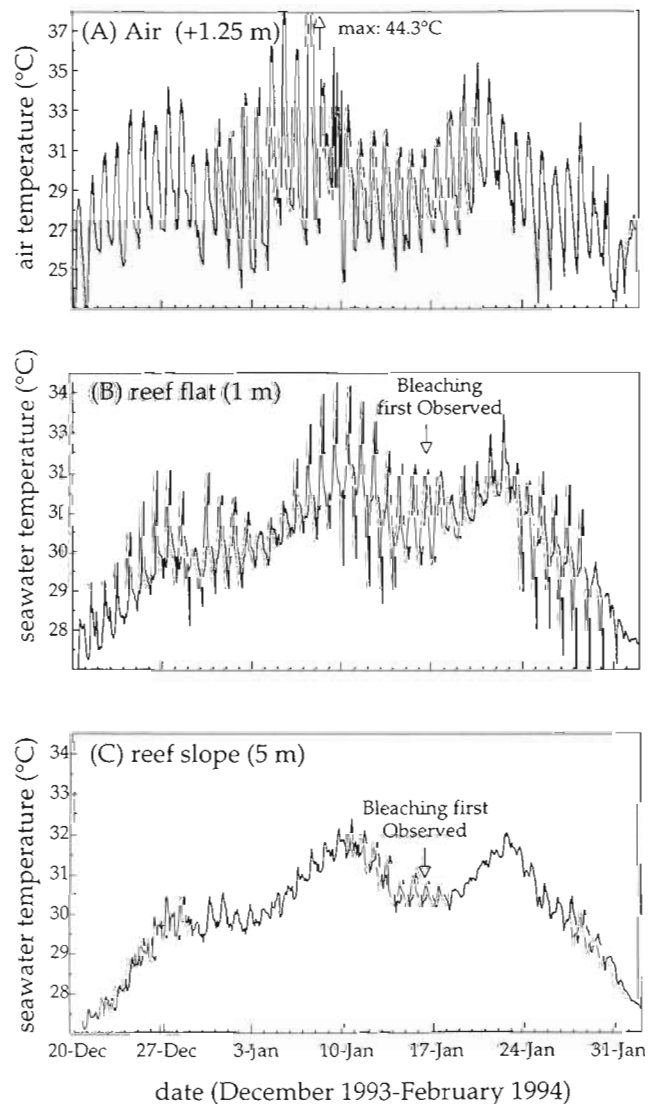


Fig. 2. (A) Air temperature (recorded every 3 h at the Townsville Bureau of Meteorology), (B) seawater temperature on the reef flat (recorded every 0.5 h at 1 m depth at Geoffrey Bay, Magnetic Island), and (C) seawater temperature on the reef slope (recorded every 1 h at 5 m depth at Geoffrey Bay) over the period 20 December 1993 to 2 February 1994

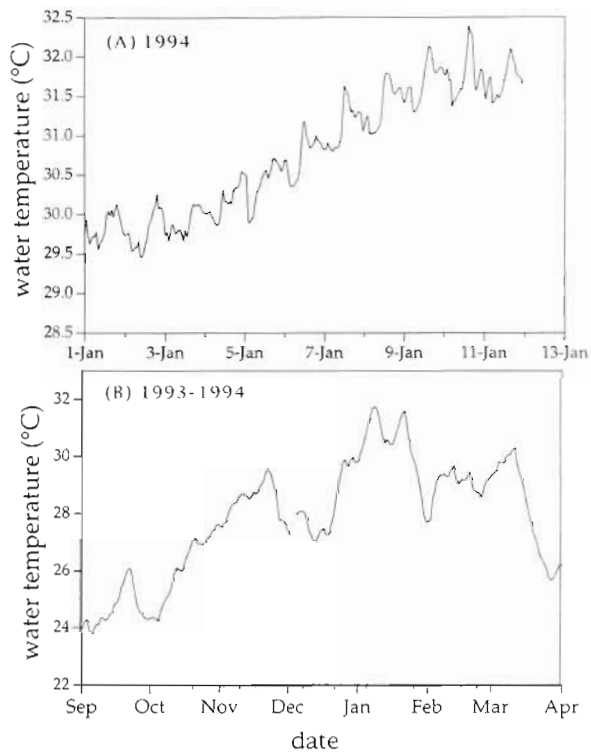


Fig. 3. Average daily seawater temperature (A) from 1 to 12 January 1994 and (B) from September 1993 to April 1994 recorded every 1 h on the reef slope (5 m depth) at Geoffrey Bay. Bleached corals were first observed at Magnetic Island on 16 January 1994

air temperatures fell sharply to $<25^{\circ}\text{C}$ during storm activity associated with a decaying cyclone. January 1994 was the warmest month recorded at the TBM since 1942 (average temperature = 29.7°C).

There were 2 periods of elevated seawater temperatures at Magnetic Island in January 1994, from 7 to 13 January and 19 to 24 January (Fig. 2). During these periods the average daily seawater temperature on the reef flat and slope exceeded 31°C . Maximum seawater temperature recorded on the reef flat (34.3°C , 9 January) and reef slope (32.4°C , 10 January) occurred 2 to 3 d after the record in maximum air temperature. The average daily seawater temperatures on the reef slope increased from 30°C to 32°C over an 8 d period before bleached corals were first observed (Fig. 3). Average daily seawater temperatures fell rapidly in late January to $\sim 28^{\circ}\text{C}$ in early February 1994 (Figs. 2 & 3).

Over the period 6 to 11 January, the maximum daily seawater temperature occurred close to the predicted daytime low water (Fig. 4), and average daily seawater temperatures increased as the tides changed from neaps to springs (see also Fig. 2). The maximum seawater temperature, and the highest average daily seawater temperature in January 1994, occurred on 9 Jan-

uary (reef flat) and 10 January (reef slope), when the spring tides were at their lowest and when low water occurred in the early afternoon. After 11 January the tides changed back towards neaps, the daytime low water occurred in the late afternoon at $\sim 16:00$ h, and the average daily seawater temperatures decreased (Figs. 2 & 4).

Zooxanthellar densities and chl *a* concentrations

The zooxanthellar density in 2 colonies of *Acropora formosa* (Colony 1, bleached, and Colony 3, normal coloured) decreased by 27 and 25% respectively between 28 January and 2 February 1994 (Fig. 5; Student's *t*-test, $p < 0.05$). Zooxanthellar chl *a* concentration in both colonies increased by 32 and 14% respectively (Student's *t*-test, $p < 0.05$) over the same period. Both colonies were sampled again in December 1994 (10 mo after the bleaching event). At that time the zooxanthellar densities had increased 3-fold (bleached colony) and 1.8-fold (normal coloured colony; Student's *t*-test $p < 0.05$).

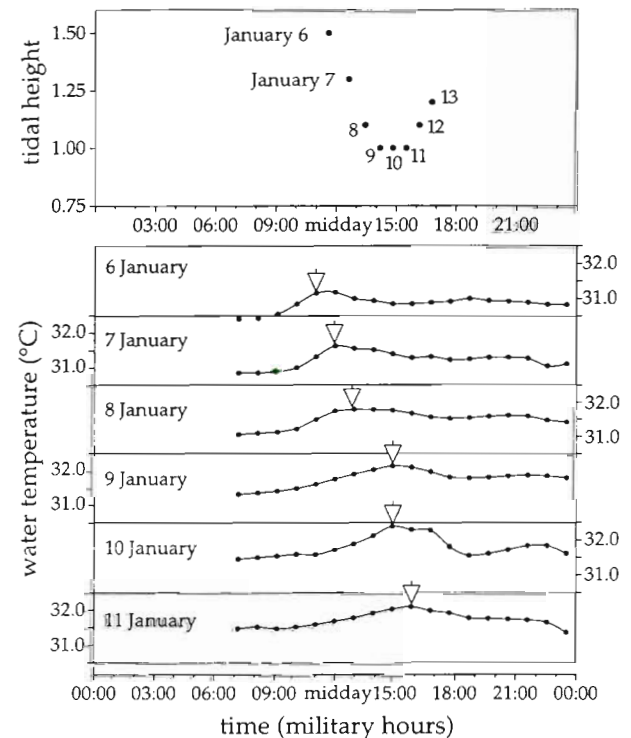


Fig. 4. Predicted times of daytime low water at Magnetic Island (m above chart datum) from 6 to 13 January 1994, and daily seawater temperature profiles on the reef slope (recorded every 1 h at 5 m depth) at Geoffrey Bay, Magnetic Island. Y-axis scales on the temperature profiles range from 30 to 32.5°C . Arrows indicate maximum daily seawater temperature in each profile

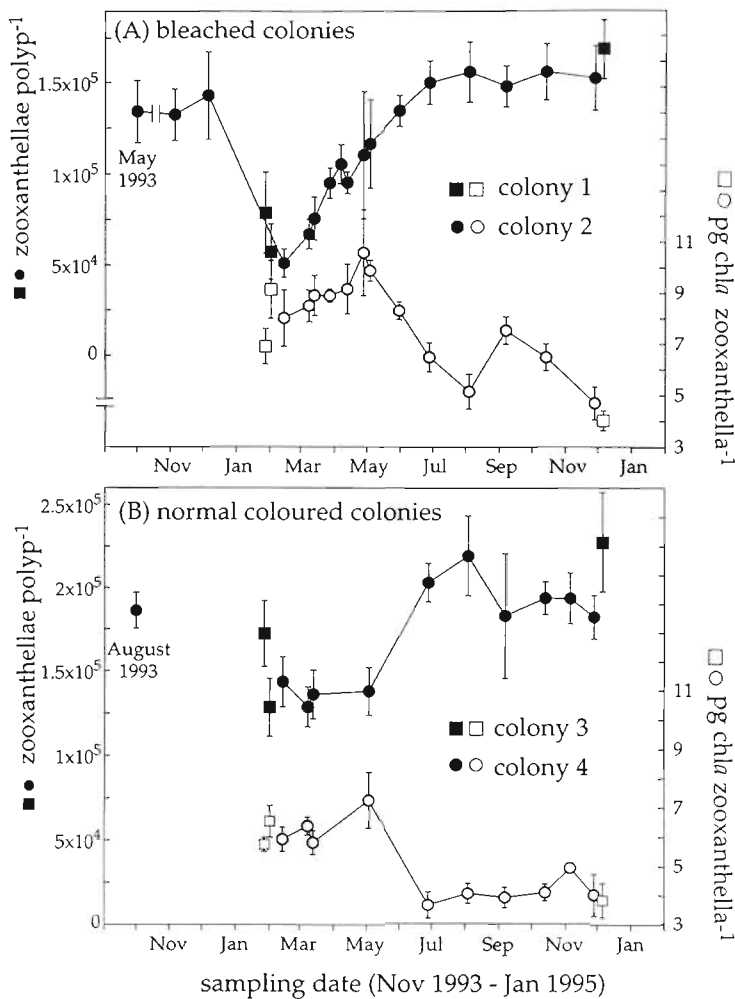


Fig. 5. *Acropora formosa*. Mean zooxanthellar density polyp⁻¹ (■, ●), and pg chl *a* zooxanthella⁻¹ (□, ○) in the terminal 40 to 50 mm of branch tips from (A) 2 bleached (light tan coloured) colonies and (B) 2 normal (dark brown) coloured coral colonies. Colonies 1 and 3 (bleached and unbleached respectively) were sampled during the bleaching event and again in December 1994. $\bar{x} \pm 95\%$ CI, $n = 5$ branch tips per data point

On 14 February 1994, 2 colonies of *Acropora formosa* (Colonies 2 and 4) were located in which the zooxanthellar densities had been measured prior to the bleaching event. One of the colonies had bleached to a light tan colour (Colony 2) and the other colony (Colony 4) appeared a normal dark brown colour. The zooxanthellar density in both colonies at the time of sampling was markedly lower than before the bleaching event (Fig. 5). From mid February until late April 1994, both the zooxanthellar density and zooxanthellar chl *a* concentration increased in both colonies. By early May 1994 the bleached colony had regained its normal colouration. From this point onwards the zooxanthellar density continued to increase to a steady-state level of $\sim 1.5 \times 10^5$ zooxanthellae polyp⁻¹ (bleached colony) and

$\sim 1.8 \times 10^5$ zooxanthellae polyp⁻¹ (normal coloured colony; Fig. 5).

If the zooxanthellar density and zooxanthellar chl *a* concentrations in the 4 colonies in December 1994 are considered to be representative of 'normal' levels, then the colonies lost 65 and 66% (bleached colonies) and 44 and 48% (normal coloured colonies) of their zooxanthellar complement during the bleaching event. Zooxanthellar chl *a* concentrations were significantly higher when each of the colonies were first sampled than they were in December 1994 at the end of the study (Student's *t*-test $p < 0.05$).

There was a significant inverse relationship between chl *a* concentration and zooxanthellar density using the data collected from the colonies of *Acropora formosa* over the study period ($p < 0.05$, $r = 0.68$; Fig. 6).

The mean zooxanthellar cell volume in Colony 2 (bleached) was significantly larger than that in Colony 4 (unbleached) when first sampled (Fig. 7; ANOVA, $p < 0.05$). There was no change in the mean zooxanthellar volume in either colony over the course of the year.

Ten months after the bleaching event, the zooxanthellar density, zooxanthellar chl *a* concentration and zooxanthellar cell size were determined in 4 colonies which were known to have bleached and 5 colonies which were known to have shown no signs of colour loss. Bleached colonies had regained their colouration by May 1994, and there was no difference in colour between the 2 groups of colonies at the time of sampling (December 1994). There was no significant difference in chl *a* concentration per polyp between the 2 groups (ANOVA, $p > 0.05$; Fig. 8). However, there were significant differences in zooxanthellar densities, chl *a* concentrations per zooxanthella and zooxanthellae cell size between the bleached and unbleached groups (Fig. 8; ANOVA, $p < 0.05$). Colonies which bleached had fewer zooxanthellae which were larger and had more chl *a* per zooxanthellae than colonies which did not bleach.

DISCUSSION

Hydro-meteorological conditions

The 1994 bleaching event at Magnetic Island is a clear example of a warm-water bleaching event. Average daily seawater temperatures increased by 2°C in

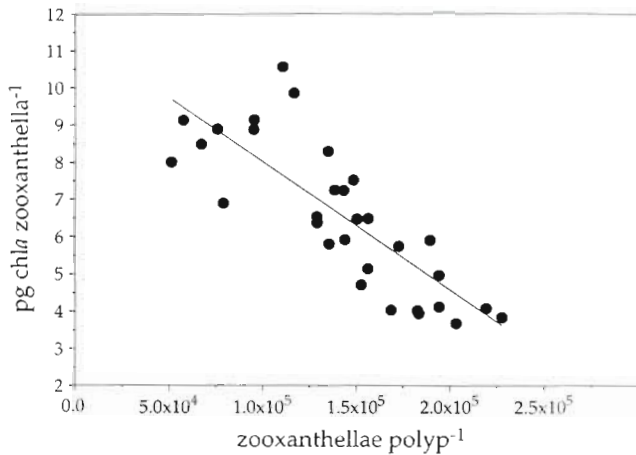


Fig. 6. *Acropora formosa*. Relationship between zooxanthellar chl *a* concentration and zooxanthellar density in colonies sampled during and after a bleaching event. Each value represents the mean of 5 branch tips from each colony

1 wk, reaching 32°C (reef slope) and 34°C (reef flat), and bleached corals were observed soon afterwards. Unlike bleaching events in the Pacific which appear related to large scale oceanographic features (Hoegh-Guldberg & Salvat 1995), the 1994 bleaching event Magnetic Island was caused by a period of anomalously high air temperatures (see also Jones et al. 1997 in this volume).

An interesting feature of the event was the tidal modulation of the daily heating cycle on the reef. Over a 1 wk period before bleached corals were first observed, the maximum daily seawater temperature coincided with the daytime low water, and average daily seawater temperatures increased during the change from neap tides to spring tides (Fig. 4). Coral bleaching has been observed following sub-aerial exposure or extreme low tides (Yamazato 1981, Brown et al. 1994); however, neither were corals sub-aerially exposed, nor were daytime low tides extreme during the 1994 bleaching event at Magnetic Island. A different tidal regime could have led to a more intense or benign bleaching event. It follows that variations in tidal range and timing of daytime low water may contribute to between-reef variability in coral bleaching during periods of regionally elevated air temperatures.

Zooxanthellar densities and chl *a* concentrations

The results of this study suggest that, for a taxon of *Acropora*, loss of zooxanthellae can occur without decreases in zooxanthellar chlorophyll concentrations during a warm-water bleaching event (Fig. 5). In fact, in the 2 colonies which were losing zooxanthellae dur-

ing the bleaching event, the zooxanthellar chl *a* concentrations actually increased (Fig. 5; see below).

Decreases in zooxanthellar densities in corals without decreases in zooxanthellar chl *a* concentrations have also been reported in corals sampled after natural bleaching events (Hoegh-Guldberg & Smith 1989a, Fitt et al. 1993) and in corals exposed to elevated seawater temperatures during laboratory manipulations (Hoegh-Guldberg & Smith 1989a, Glynn et al. 1992, Fitt & Warner 1995). However, Kleppel et al. (1989) and Porter et al. (1989) report both lower zooxanthellar chl *a* concentrations and lower zooxanthellar densities in corals (*Agaricia lamarckii* and *Montastrea annularis*) sampled after bleaching events. In both of these cases, corals were collected between 2 and 6 mo after bleaching was first observed (see Jaap 1988, Ogden & Wicklund 1988). Given these delays, the decrease in zooxanthellar chlorophyll concentrations reported by Kleppel et al. (1989) and Porter et al. (1989) may represent the result of (1) sustained periods of elevated seawater temperatures, (2) water temperatures higher than those measured during the present study, or (3) secondary effects of the loss of zooxanthellae.

An increase in zooxanthellar chl *a* concentration was measured in the 2 colonies sampled and found to be losing zooxanthellae during the bleaching event (Fig. 5). Unfortunately this result could not be verified by further sampling from additional colonies because of the abrupt end to the bleaching event in early February 1994 following decreased water temperatures and increased cloud cover during storms associated with a decaying cyclone. However, the finding is consistent with all 4 colonies involved in the study having higher zooxanthellar chl *a* concentrations when first

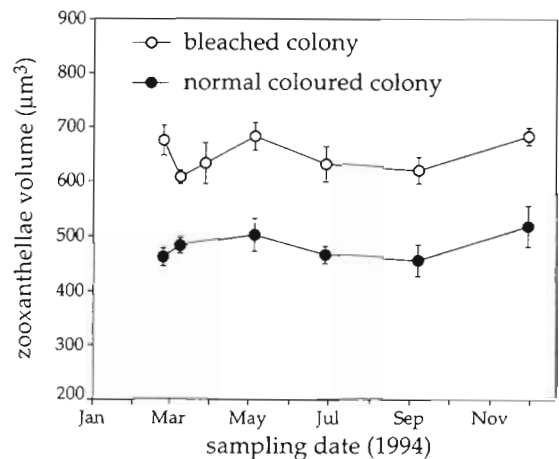


Fig. 7. *Acropora formosa*. Zooxanthellar cell size in a bleached colony (Colony 2, ○) and neighbouring unbleached colony (Colony 4, ●) after a bleaching event. Each value represents the mean zooxanthellar cell size in 5 separate tips (50 zooxanthellae measured per tip) from each colony ($\bar{x} \pm 95\%$ CI)

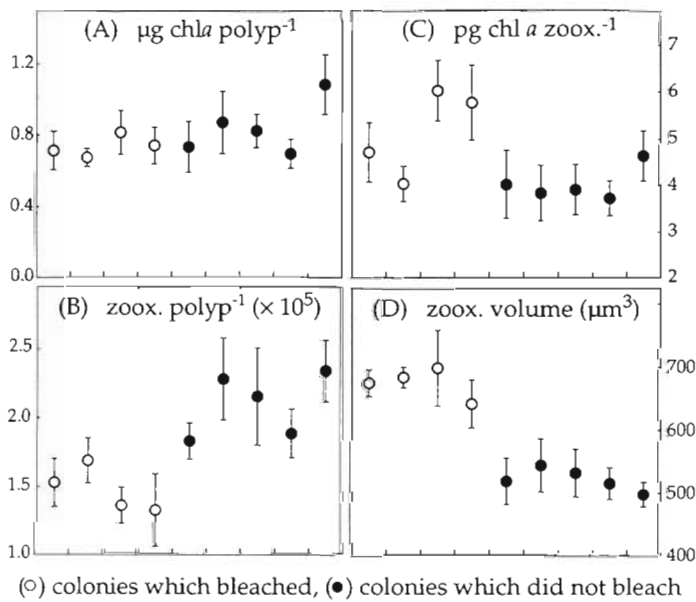


Fig. 8. *Acropora formosa*. (A) Areal chl *a* concentration, (B) zooxanthellar density, (C) zooxanthellar chl *a* concentration, and (D) zooxanthellar size in 4 colonies which bleached (○) and 5 colonies which did not bleach (●) in January 1994. All colonies were sampled in early December 1994, 10 mo after the bleaching event. $\bar{x} \pm 95\%$ CI, $n = 5$ tips from each colony

sampled compared with levels 10 mo after the bleaching event (and immediately before the next summer period).

Recently, Le Tissier & Brown (1996) also measured increases in zooxanthellar chl *a* concentrations in corals (*Goniastrea aspera*) during stress-related loss of zooxanthellae following sub-aerial exposure. They suggest the increase in zooxanthellar chlorophyll concentration occurred because of either (1) greater loss of zooxanthellae from the apical tissues (thereby leaving 'dark-adapted' zooxanthellae located in the lower tissues) or (2) breakdown products of chlorophyll and other pigments interfering with the absorption peak used to compute chl *a* concentrations (Le Tissier & Brown 1996). Alternatively, the increase may be related to the nutrient status of the algal symbionts. As discussed in Hoegh-Guldberg & Smith (1989b) and Fitt et al. (1993) the inverse relationship between zooxanthellar density and zooxanthellar chl *a* concentration (Fig. 6) is the opposite of that expected from a photoadaptive response to zooxanthellar self-shading as zooxanthellar densities increase. The chl *a* concentration of unicellular algae is also a reliable indicator of nutrient status (Rees 1991), and the relationship may signify nutrient limitation at higher zooxanthellar densities (Hoegh-Guldberg & Smith 1989b, Fitt et al. 1993, Jones & Yellowlees

1997, Jones & Steven 1997). The increase in zooxanthellar chl *a* concentration during the bleaching event observed in this study may represent a response of the remnant zooxanthellar population to increased nutrient availability through decreased competition.

Whether the increase in zooxanthellar chl *a* concentration during the bleaching event is an artefact of chlorophyll breakdown products, or represents genuine changes in the zooxanthellar chl *a* concentration as a result of bleaching remains unclear. Marked decreases in photosynthetic performance have been measured in zooxanthellae (both in culture and *in hospite*) during exposure to elevated seawater temperatures (Iglesias-Prieto et al. 1992, Fitt & Warner 1995). These changes have occurred without decreases in zooxanthellar chl *a* concentrations. However, chlorophyll can act as a photosensitising agent in the presence of molecular oxygen and sunlight to produce active oxygen species (Asada & Takahashi 1987, Lesser & Shick 1989). Increased zooxanthellar chlorophyll concentrations may further promote the production of active oxygen species for which many components of the cell are targets (Lesser & Shick 1989).

Intraspecific variability in the bleaching response

Both bleached and unbleached colonies of *Acropora formosa* lost zooxanthellae during the bleaching event (Fig. 5). Szmant & Gassman (1990) and Brown et al. (1995) also report that corals can lose significant quantities of zooxanthellae without discolouring. Some of the intraspecific variability in the bleaching response may therefore have been due to the higher level of zooxanthellae loss from the colonies which bleached (65 and 66%) as opposed to the normal coloured colonies (44 and 48%), and the level of zooxanthellae loss required for the colonies to discolour (i.e. >50% of the algal standing stock).

Nevertheless, there did appear to be intrinsic differences between the bleached and normal coloured colonies of *Acropora formosa* sampled over the course of the year. Colony 2, which bleached, had significantly larger zooxanthellae (Fig. 7) after the bleaching event, and naturally lower zooxanthellar densities both before the bleaching event, and at the end of the recovery period (Fig. 5). Ten months after the bleaching event, the other colonies of *A. formosa* known to have bleached also contained inherently fewer zooxanthellae which were larger and had more chl *a* per cell than the colonies known to have not bleached (Fig. 8).

There are several lines of evidence to suggest that these represent intrinsic differences between the 2 groups and are not the result of the bleaching event itself. Firstly, the zooxanthellar densities in 2 of the colonies had recovered to a steady-state level ~5 mo after the bleaching event (Fig. 5) and the colonies were sampled a further 5 mo later. Secondly, the difference in zooxanthellar density between the bleached (Colony 2) and normal-coloured (Colony 4) colonies in December 1994 was evident before the bleaching event occurred. Thirdly, there was no change in the zooxanthellar cell size measured over the course of the year, despite marked changes in zooxanthellar density and chl *a* concentration, and seasonal changes in water temperature and light levels.

Significant morphological, biochemical, physiological, behavioural and genetic differences have been documented in zooxanthellae from different hosts (Schoenberg & Trench 1980a, b, Rowan & Powers 1991, Banaszak et al. 1993) and within individual hosts (Rowan & Knowlton 1995). Schoenberg & Trench (1980b) noted distinct variations in dimensions of recently divided vegetative cells of cultured zooxanthellae isolated from a number of different hosts. Categories of zooxanthellae based on size agreed remarkably well with categories based on isozyme patterns (Schoenberg & Trench 1980a, b). The zooxanthellae of *Acropora formosa* at Magnetic Island have not been subject to taxonomic review; however, juvenile colonies acquire zooxanthellae from the external environment, as opposed to from parental inheritance in oocytes. The former process is potentially more prone to the formation of different host-zooxanthellar partnerships. Whether the differences in the size of the zooxanthellar symbionts between the neighbouring colonies of *A. formosa* represent different zooxanthellae taxa is the subject of continuing study.

The results of the present study suggest that loss of zooxanthellae can occur without decreases in zooxanthellar chlorophyll concentrations in *Acropora formosa* during a warm-water bleaching event. Colonies of *A. formosa* begin to discolour when they have lost >50% of their zooxanthellae. Intrinsic differences in the densities, chlorophyll concentrations and zooxanthellar cell sizes between neighbouring colonies may result in intraspecific variability in coral discolouration during a bleaching event.

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