Limnol. Oceanogr., 50(1), 2005, 265–271

Coral bleaching following wintry weather

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Abstract

Extensive coral bleaching occurred intertidally in early August 2003 in the Capricorn Bunker group (Wistari Reef, Heron and One Tree Islands; southern Great Barrier Reef). The affected intertidal coral had been exposed to unusually cold (minimum = 13.3°C; wet bulb temperature = 9°C) and dry winds (44% relative humidity) for 2 d during predawn low tides. Coral bleached in the upper 10 cm of their branches and had less than 0.2×10^6 cell cm^{-2} as compared with over 2.5×10^6 cell cm^{-2} in nonbleached areas. Dark-adapted quantum yields did not differ between symbionts in bleached and nonbleached areas. Exposing symbionts to light, however, led to greater quenching of Photosystem II in symbionts in the bleached coral. Bleached areas of the affected colonies had died by September 2003, with areas that were essentially covered by more than 80% living coral decreasing to less than 10% visible living coral cover. By January 2004, coral began to recover, principally from areas of colonies that were not exposed during low tide (i.e., from below dead, upper regions). These data highlight the importance of understanding local weather patterns as well as the effects of longer term trends in global climate.

The majority of Scleractinian coral live in a mutualistic endosymbiosis with single-celled dinoflagellate algae of the genus *Symbiodinium.* Together, these two organisms are responsible for a major component of the structure (framework) and function (primary productivity) of tropical reef systems. In recent years, the abundance of coral colonies on reefs worldwide has been rapidly declining under the pressure of human-derived stresses (Bryant et al. 1998; Wilkinson 2000; Hughes et al. 2003). Among these stresses, climate change has assumed a major importance as ocean temperatures have warmed and major periods of symbiotic dysfunction, called mass bleaching events, have been triggered. These events are undocumented prior to the 1970s but have been expanding since then in frequency, severity, and geographic scale (Hoegh-Guldberg 1999). Since their advent, there have been six major periods of bleaching across the planet. The frequency in some areas is even higher. Mass coral bleaching events, which have been reported as the worst yet in each case, have affected coral populations on the Great Barrier Reef twice since 1997 (1998, 2002). In each case, coral bleaching has spread to more than 50% of the Great Barrier Reef Marine Park (Berkelmans and Oliver 1999; Berkelmans 2002; Dennis 2002).

Understanding how variability in the physical environment affects coral reefs is a priority if we are to truly understand the ramifications of the changing global climate. Mass coral bleaching events are triggered by periods in which sea temperatures rise above the long-term averages for a particular region. Plant–animal endosymbioses are very sensitive to changes in temperature, which result in an increased sensitivity of the dinoflagellate symbiont to photoinhibition (Iglesias-Prieto et al. 1992; Warner et al. 1996; Jones et al. 1998), cellular damage, and eventually disintegration. The mechanism that underlies the earliest stages of coral bleaching is very similar to that seen during thermal stress in higher plants (Jones et al. 1998; Salvucci and Crafts-Brandnera 2004), leading to the conclusion that coral bleaching is at least in part a result of thermal stress occurring within the photosynthetic processes of the dinoflagellates. Warm seas, often only 1–2°C above the long-term averages, can be detected by satellite measurements and used to predict (with more than 95% accuracy) mass coral bleaching events several weeks in advance (Strong et al. 2000).

Reduced temperatures also intensify photoinhibition in higher plants (Aro et al. 1990; Lyons 1973; Greer and Laing 1991; Long et al. 1994) in a similar way to that that occurs at elevated temperatures. Reduced temperatures lead to a re-

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Acknowledgments

We thank Efrat Fine for laboratory assistance; Mark Davy, Paul Fisher, Sascha Thyer, and the Stanford Australia Program class of 2003 for field assistance; and David Logan, Michael Phillips, and Collette Bagnato for collecting meteorological and field data.

duction in the rate at which the quenching of Photosystem II (PSII) develops (Krause 1992), leading to an accumulation of active oxygen species and cellular damage. Cold temperatures have also been observed to trigger the loss of dinoflagellate symbionts from anemones and coral (Shinn 1966; Coles and Jokiel 1977; Steen and Muscatine 1987). In a previous study, Saxby et al. (2003) established that cold stress creates similar physiological symptoms in coral to those seen when they are heat stressed. Saxby et al. (2003) demonstrated that water temperatures of 12°C for 12 h or more led to the complete loss of photosynthetic efficiency by PSII and death of exposed coral. Exposure of coral to 14°C revealed a light-dependent response, in which (as with elevated temperature) thermal stress in low light had little effect while coral exposed to 14°C and full sunlight were heavily impacted. In the latter case, photosynthetic efficiency was reduced and the coral became bleached in 24 h. These observations match those of Jones et al. (1998) and other research groups for elevated thermal stress, with the enhancement of the effect by light giving insight into where the damage due to low or high thermal stress occurred.

This paper investigates cold stress on reefs that manifested itself as a mass bleaching event in the intertidal areas of the Capricorn–Bunker group (southern Great Barrier Reef) in the austral winter of 2003. The measurements made during this event confirm the conclusions of Saxby et al. (2003) and previous workers. In addition, this study highlights the importance of understanding the impact of the variability in weather patterns as well as the overall shift that has been occurring due to climate change.

Materials and methods

Heron Island is a platform reef (approximately 8 km^2) located within the Capricorn–Bunker group of reefs on the southern Great Barrier Reef (23°26′60″S, 151°55′0″E). Large areas of the intertidal flat at Heron Island were found to be bleached in the austral winter, being first observed on 5 August 2003. In addition to the exploration of environmental data, measurements were made of the condition of the coral and their fate over 5 months following the event.

Changes in coral cover—With the advent of bleaching in the reef flat at Heron Island in early August 2003, the Capricorn–Bunker group of reefs was surveyed from the air to assess the scale of the bleaching event.

Two 50-m permanent belt transects were set to follow the progression and patterns of bleaching and recovery on the reef flat on the northern side of Heron Island. Permanent belt transects were established that were oriented north to south (perpendicular to the shore line) or east to west (parallel to the shore line). These sites were photographed using a digital camera (Nikon Coolpix 5000) over a measuring tape. Photography was carried out during high tide to have sufficient distance between the camera and the studied substrate and in order to minimize observer impact on the surveyed reef. Each exposure covered 1 m^2 of substrate. The pictures were analyzed using the point-intercept method by placing a transparency marked with 16 randomly marked points over each image on the computer screen. The substrate underlying the points was scored according to three categories: healthy, bleached, or dead coral. We then calculated percentage of each of the categories for each survey date. The same procedure was repeated during September and October 2003 (6 and 10 weeks after the first set of photography, respectively) and during early February 2004 (6 months after the first set of measurements).

Environmental data—Temperature data for Heron Island was obtained from three sources.

1. Average sea surface temperature for the period 30 July–4 August (1600 h) of the Capricorn Islands group was retrieved from NOAA-16 AVHRR Satellite (downloaded at the Australian Institute of Marine Science), pixel size = 1 km.
2. A set of data loggers that were deployed at Heron Island reef crest. One logger was positioned approximately 10 m from the low-tide mark on the southern side of Heron Island. A second logger was deployed midway across the intertidal flat and a third was deployed off the reef crest in 5-m depth at low tide. In each set of data loggers, there were sensors for temperature, light, and pressure (depth/tides).
3. A log of weather observations by the Heron Island Research Station staff, performed twice daily. These included meteorological parameters, such as sea temperature, air temperature, humidity, wind speed, precipitation, cloudiness, and tides. These parameters have been logged since 1967.

Physiological measurements—Twelve fragments, approximately 5 cm long, from four colonies of *Acropora aspera* were sampled for area density of symbiotic dinoflagellates on 5 August 2003. They were taken as follows: Four were taken from the upper 10 cm (bleached section) of the colonies, four from 10 cm under the bleached part, and four from 20 cm under the bleached section. In the lab, the tissue of each fragment was removed using an air gun. The resulting slurry was homogenized and diluted to a total volume of 50 ml. A volume of 10 μl was sampled out twice from every test tube and put onto a hemocytometer (upper and lower fields). Two hemocytometer fields were photographed using a fluorescent microscope (Olympus BX5) and a digital camera. Counting of the fluorescent symbiotic dinoflagellates was performed from the digital images using Blob Analysis in MATROX 2.1 software (Matrox Electronic Systems). The software counts the number of fluorescent objects in the photo under predefined conditions of size and area. The number of cells was calculated for the total 50-ml volume.

Surface area was measured by dipping each fragment in hot wax (65°C) for 10 s. It was then cooled to room temperature to allow the wax to solidify. After weighing the fragments, they were dipped for 10 s in wax again at the same temperature and weighed again after it solidified. The net weight (weight 2 − weight 1) was multiplied by a coefficient of 0.038, which was obtained by using the same coating method on cylinders with known surface area and calibrating against a regression coefficient. The number of cells was then calculated per square centimeter coral surface area.

Photosynthetic efficiency—The portable Diving-Pulsed Amplitude Modulated (PAM) Fluorometer (Walz Gmbh)

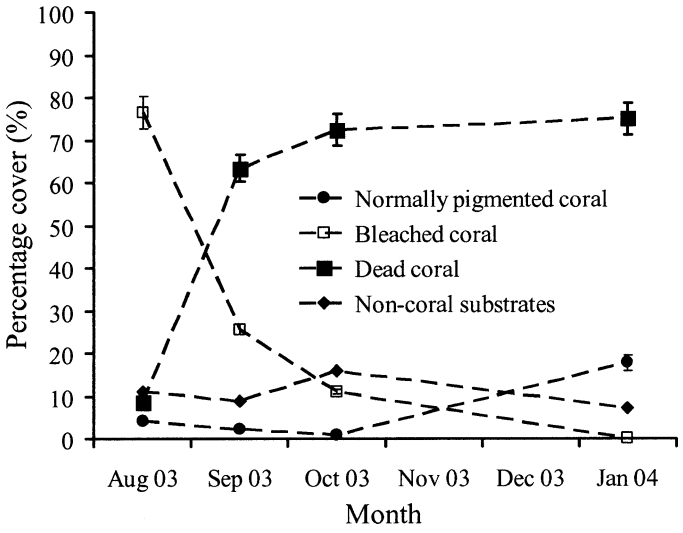

Fig. 1. Changes in coral cover over the period August 2003–January 2004.

was used to explore the photosynthetic capacity of dinoflagellates inhabiting the tissue of *A. aspera* colonies during the bleaching event. The PAM light meter was precalibrated against a quantum sensor of a Li-Cor LI-189 light meter. In each measurement, the tip of the PAM main optical fiber was placed on the coral surface. In situ measurements were performed on 5 August, right after the initial observation of bleaching and on 26 August (3 weeks after the onset of bleaching). Both measurements were undertaken at 2200 h (low tide; total darkness). Dark-adapted maximal quantum yield (Fv/Fm) was measured for three sections of each of five branches (note: branches were taken from five separate colonies): (a) upper 10 cm (bleached section) of the colonies, (b) 10 cm under the bleached section, and (c) 20 cm under the bleached section. Four saturation pulses were done on each of these sections. Quantum yields were also measured after incubating branches in light (1 min continuous actinic light before saturation pulse; 1,000 μmol m^{-2} s^{-1}). This was done on five bleached and five nonbleached fragments of *A. aspera.* At the end of these measurements, rapid light curves of photosynthesis versus irradiance were done on five bleached and five nonbleached fragments of *A. aspera.* Rapid light curves were done by measuring the quantum yield of symbionts after illuminating branches from each of the colonies for 10 s at each one of a series of eight irradiances.

Results

Inspection of bleaching at Heron Island revealed that most of the visual impact on coral was restricted to the upper portions of colonies, which had been presumably exposed at low tide (for photographs, see Hoegh-Guldberg and Fine 2004). Affected areas stretched as far as the eye could see along the reef crest at Heron Island. Aerial inspection by helicopter revealed extensive bleaching around the entire reef crest at Heron and the intertidal areas of neighboring Wistari Reef and One Tree Island.

Changes in coral cover—Monthly surveys done after first observing mass bleaching in the intertidal areas of Heron

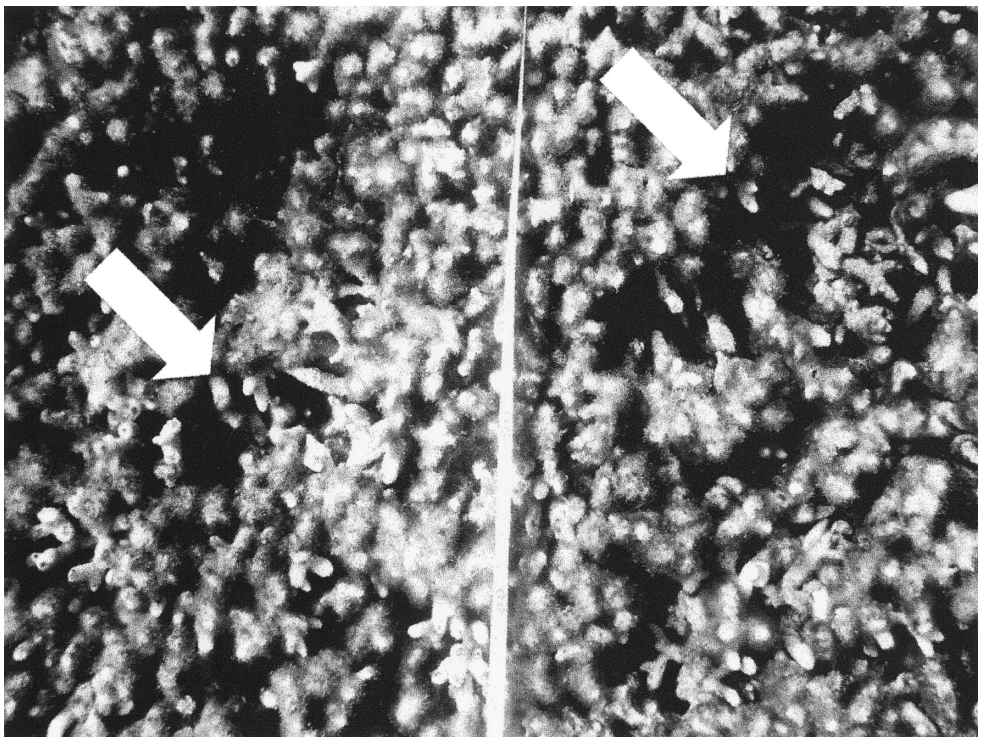

Fig. 2. Photograph taken on 24 January 2004 of areas severely bleached in early August 2003. Regrowth of coral out of crevices is evident, as indicated by arrows. Transect tape is shown running down middle of photograph.

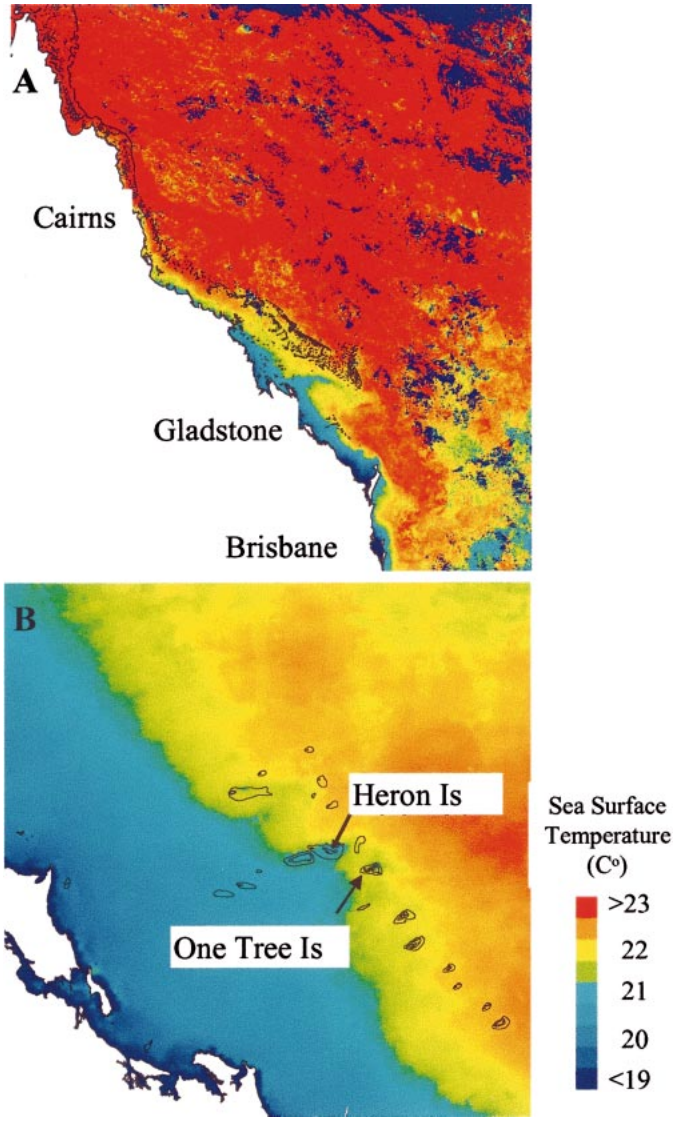

Fig. 3. (A) Average sea surface temperature (30 July–4 August 2003). The coolest water of the Great Barrier Reef during this period is along the southern coast. (B) Average sea surface temperature of the Capricorn (30 August–4 September 2003). Note the cool water engulfing Heron Island. Data sets in both A and B from NOAA-16 AVHRR data downloaded at the Australian Institute of Marine Science.

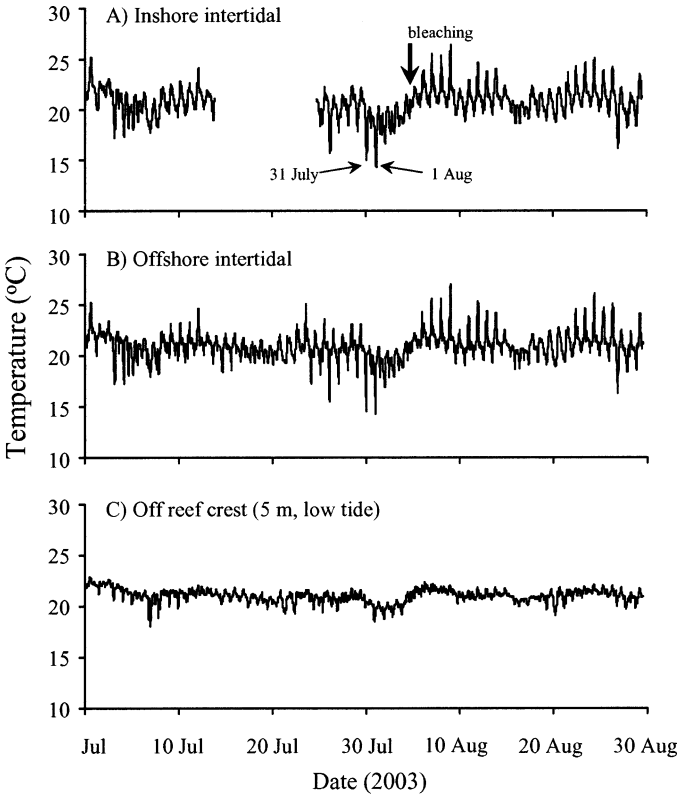

Fig. 4. Data retrieved from loggers placed in the intertidal areas of Heron Island. Water temperatures for loggers positioned (A) within 10 m of the shoreline of Heron Island on the intertidal flat. Missing data in July are due to logger failure. Arrows indicate the extremely cold days of 31 July and 1 August 2003. (B) Midway across the intertidal flat, and (C) off the reef crest in 5-m depth at low tide.

Island revealed that the affected areas of bleached coral mostly died (Fig. 1). By September, areas that had greater than 80% coral cover prior to the bleaching event (due mainly to one species, *A. aspera*) had less than 30% living coral cover. By October, living coral represented less than 12%. By early January 2004, coral cover had begun to recover (17.8%), with coral tissue growing out of regions that were shaded as well as not being exposed at low tide (Fig. 2).

Environmental data—Waters along the inshore region of the southern Great Barrier Reef were cool by comparison with other regions within the Reef and ranged between 19°C and 21°C. Average sea surface temperature (30 July–4 August 2003) retrieved from the NOAA-16 AVHRR dataset revealed that the coolest water for the Great Barrier Reef lay along the southern coastal regions. A tongue of relatively cool water (21°C) extended out from the coast to the seaward side of the platform reef on Heron Island (Fig. 3A,B). This patch of cool water bathed Wistari and Heron Island but did not reach as far as One Tree Island, which was approximately 0.5–1.0°C warmer.

The satellite data were validated by data loggers that were located in intertidal and reef crest areas associated with bleached areas (Fig. 4A–C). Sea temperatures just off the reef crest (5 m; Fig. 4C) averaged 21.0°C ± 0.02°C, with a maximum value of 22.7°C and a minimum of 18.1°C. These values match the values reported within the satellite data (Fig. 3). The two loggers based in the intertidal also revealed similar average temperatures of 21.0°C ± 0.06°C and 21.0°C + 0.05°C for inshore and offshore intertidal locations, respectively (Fig. 4A,B). The range of values was much larger for both than sea temperatures measured by the logger located off the reef crest. In this case, minimum values of 14.4°C and 14.5°C and maximum values of 26.3°C and 27.0°C were recorded for inshore and offshore intertidal sites, respectively. Importantly, the minimum values for sea temperature off the reef crest occurred 3–4 d before bleach-

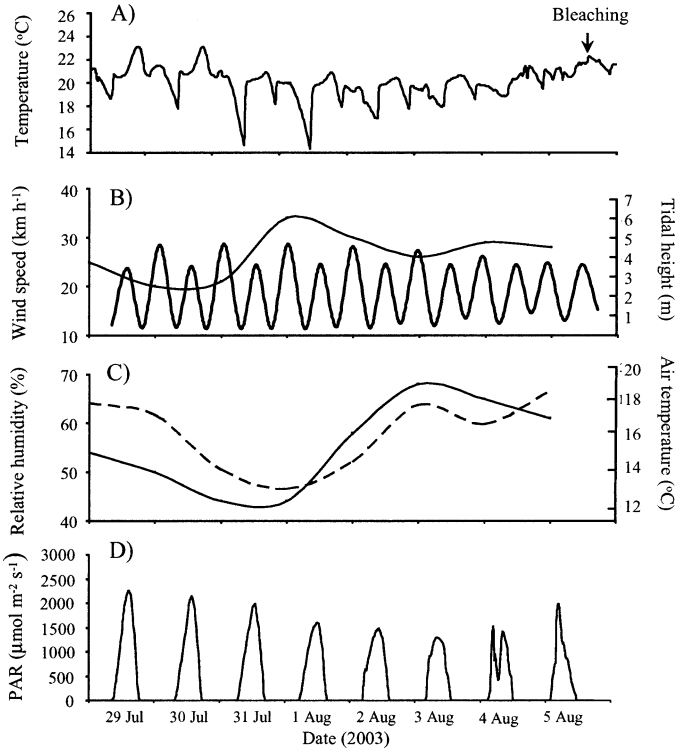

Fig. 5. Detail of (A) water temperature and (D) light data taken from data loggers positioned midway across the reef crest at Heron Island (29 July–5 August). Meteorological data collected by Heron Island Research Station for the same period is also shown. (B) Wind speed (left axis, solid line) and tidal height (right axis, solid high-frequency sinusoidal line), and (C) relative humidity (left axis, solid line) and air temperature (right axis, dashed line). Accompanying data and comments for records are shown in Table 1.

ing was first reported on the intertidal regions of Heron Island.

Detailed examination of dates revealed that the coldest days (Fig. 5A) coincided with predawn low tides and were typified by high winds (Fig. 5B), low humidity and air temperatures (Fig. 5C) on cloudless days (Table 1, Fig. 5D). Significantly, this is the only time in the history of daily weather records on Heron Island (from 1967 to 2004) in which observers used the word ''freezing'' to describe the conditions (Table 1). Air temperature ranged from 13.3°C to

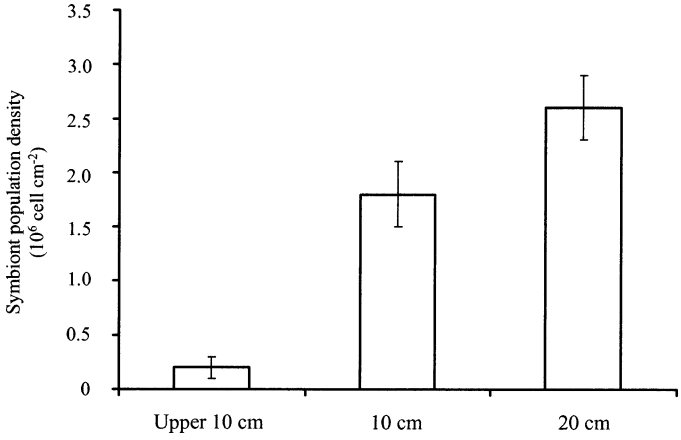

Fig. 6. Symbiont density as a function of distance along branches of *Acropora aspera* (shown) on 5 August 2003. Upper portions (left hand in this diagram) were visibly bleached relative to lower portions (right hand in this diagram).

23.4°C over the period 26 July–5 August 2003. From these data, it is possible to calculate a wind chill of 9°C for coral exposed at low tide during these conditions (based on the coldest day, 1 August, in which air temperatures dropped to 13.3°C and wind speed increased to 0.040 km h^{-1}). This would have been accentuated by the very low humidities (44%) that accompanied these conditions.

Physiological condition of cold-stressed coral—Bleaching was most pronounced in affected colonies in the upper 10 cm of the branch tips. Symbiont density decreased in the upper 10 cm to less than 0.2×10^6 cell cm^{-2} and increased away from the affected zone to over 2.5×10^6 cell cm^{-2} (Fig. 6). The lower values were similar to the values obtained by Dove (2004) for control *A. aspera.* Dark-adapted photosynthetic efficiency did not correlate with the extent of bleaching down the branches (Fig. 7A). A major difference in quenching behavior was revealed when quantum efficiency was measured at successively higher light levels (Fig. 7B). This confirmed the observation of low-light–adapted yields in the bleached regions as compared with those measured in the nonbleached regions (Fig. 7C). In this case, symbionts remaining in the bleached areas quenched the photosynthetic efficiency of PSII by a much larger amount

Table 1. Daily weather data collected by Heron Island Research Station over the period 26 July–5 August.

Date	Rain (mm)	T_{max} (°C)	T_{min} (°C)	Remarks from research personnel
26 Jul 03	0	18.3	15.4	Little cumulus to the north
27 Jul 03	0	19.3	14.7	No cloud
28 Jul 03	0	18.6	15.4	Cumulus and alto cumulus on horizon
29 Jul 03	0	20.4	18.3	Scattered cumulus and stratus
30 Jul 03	0	21.3	17.6	Cold, minute amount of cumulus
31 Jul 03	0	20.4	14.4	Freezing, minute amount of cumulus
1 Aug 03	0	17.4	13.3	Freezing, tiny amount of cumulus
2 Aug 03	0	18.8	14.9	Freezing, tiny amount of cumulus
3 Aug 03	0	20.7	18.2	Freezing, mostly cumulus
4 Aug 03	6.4	21.1	17.1	Varied cloud cover, rain surrounding
5 Aug 03	1	23.4	19	Mostly alto cumulus

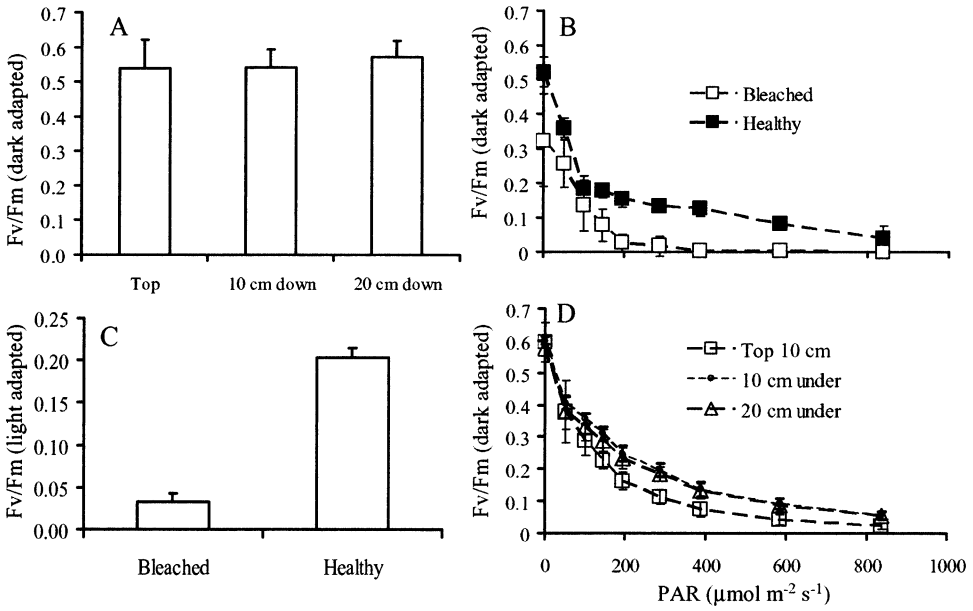

Fig. 7. Physiological state of symbionts in *Acropora aspera* as a function of distance down the branches. (A) Dark-adapted yield at three different sections of *A. aspera* branches measured soon after 2200 h on 5 August 2003. (B) Light-adapted yield (after 1 min of 1,000 μmol photons m^{-2} s^{-1}) for bleached and unbleached *A. aspera*. (C) Quantum yield of PSII of symbionts in *A. aspera* as a function of light level on 5 August 2003. (D) Measurements repeated for symbionts in *A. aspera*, 3 weeks after the onset of bleaching (26 August 2003). Symbols indicate different positions on the colony: top section, 10 cm down from tip and 20 cm down from the tip are shown.

as light levels increased. Three weeks later, this behavior was much less pronounced (Fig. 7D).

Discussion

Sea temperature has a major influence over survivorship of reef-building coral and their symbionts and is considered to be a major determinant of their latitudinal distribution (Kleypas et al. 1999). While coral can sustain seasonal variability in sea temperature that may be more than 12°C (Kleypas et al. 1999), small excursions above geographically associated maxima or thresholds leads to syndromes associated with stress (Harvell 1999; Hoegh-Guldberg 1999). One of these syndromes, coral bleaching, has increased enormously in magnitude and frequency over the past 30 years. A combination of elevated sea temperature and exposure time predicts mass coral bleaching with great certainty (Hoegh-Guldberg 1999; Strong et al. 2000; Hoegh-Guldberg 2001), with high values leading to mass mortality events. Estimates of mortality from mass coral-bleaching events range from zero to an almost total loss of reef-building coral from affected areas. An average of 17.7% of the living coral in six major coral reef regions of the world was killed during one of the warmest years on record, 1998. The range of mortality estimates is perhaps the most interesting detail hidden within the average. While some regions (e.g., Australia and Papua New Guinea) lost small amounts (3%), regions like the Arabian Gulf and the Wider Indian Ocean lost 33% and 46%, respectively during the single event in 1998.

Cold temperatures can also be a problem for reef-building coral. While some coral are adapted for colder conditions (e.g., down to 11.5°C in the case of the temperate hermatypic coral *Plesiastrea versipora*; Kevin and Hudson 1979), downward excursions have a similar impact on reef-building coral in laboratory experiments. The massive coral *Montastrea annularis* is killed by water temperatures of 14°C for more than 9 h (Mayer 1914), while many coral species appear able to tolerate 15°C for short periods (Roberts et al. 1982). Saxby et al. (2003) revealed similar responses from the hardy intertidal coral *Montipora digitata* at Heron Island. In this case, 16°C and 12°C lead to a progressive reduction of photosynthetic efficiency (Fv/Fm) of algal symbionts in *M. digitata* over 6 h of exposure to these temperatures in the light. In both cases, incubation in the dark over the next 12 h did not lead to recovery of Fv/Fm, suggesting chronic photodamage had occurred. In subsequent experiments, Saxby et al. (2003) showed that coral became bleached and did not recover when exposed to temperatures as low as 12°C for over 12 h.

The lower threshold of *M. digitata* from the Heron Island in the laboratory was 12–14°C for exposure times of 1–2 d (Saxby et al. 2003). In the light of these conclusions for what is considered to be a fairly hardy coral, the observation of a bleaching event on 5 August is not surprising. Coral were exposed at low tide to reduced temperatures at night (down to 13.3°C) with 0.030–0.035 km h^{-1}, low humidities, and clear sunny conditions during the day. Affected areas of the colonies (upper 10 cm) were exposed to air at night time during these periods. Combining the effect of high winds and low humidities, coral tissue was exposed to surface temperatures of 9°C (wet bulb temperature) for several hours. Based on the observations of Saxby et al. (2003), exposure to the sunlit conditions of the intertidal while experiencing these low temperatures would have led to chronic photo-

inhibition as light levels increased. This damage appears to have been repaired by 5 August, as measurements of the quantum efficiency of PSII under darkness revealed similar values for symbiotic dinoflagellates in bleached and unbleached coral (Fig. 7). The quantum efficiency of PSII in symbionts left in bleached areas was considerably lower when measured after incubation in the photosynthetically active radiation (1,000 μmol m^{-2} s^{-1}). In this case, symbionts left in the bleached areas exhibited extensive quenching when exposed to the light. One explanation for this is that light levels within the skeletons were much higher due to greater reflection of light within the polyp calices after the majority of symbionts had left (Roberto Iglesius-Prieto, UNAM, pers. comm.). This highlights the important observation that light stress (and hence the effect of anything that affects the speed at which excitations are processed) will have proportionately higher effects on coral that are partially or fully bleached.

This paper highlights the importance of downward as well as upward excursions of air and water temperatures for reef-building coral and their symbionts. While day-to-day variability in local weather patterns is hard to attribute to climate change, global climate-change models do project complex changes to local weather patterns that may involve localized downward trends in local sea and air temperatures (IPCC 2001). Understanding these changes may be as important as appreciating the direct effects of an upwardly moving temperature signal on important ecosystems such as coral reefs.

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Received: 5 May 2004
Accepted: 1 September 2004
Amended: 26 September 2004