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Tolerance of endolithic algae to elevated temperature and light in the coral *Montipora monasteriata* from the southern Great Barrier Reef

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Summary

Photosynthetic endolithic algae and cyanobacteria live within the skeletons of many scleractinians. Under normal conditions, less than 5% of the photosynthetically active radiation (PAR) reaches the green endolithic algae because of the absorbance of light by the endosymbiotic dinoflagellates and the carbonate skeleton. When corals bleach (loose dinoflagellate symbionts), however, the tissue of the corals become highly transparent and photosynthetic microendoliths may be exposed to high levels of both thermal and solar stress. This study explores the consequence of these combined stresses on the phototrophic endoliths inhabiting the skeleton of *Montipora monasteriata*, growing at Heron Island, on the southern Great Barrier Reef. Endoliths that were exposed to sun after tissue removal were by far more susceptible to thermal photoinhibition and photo-damage than endoliths under coral tissue that contained high concentrations of brown dinoflagellate symbionts. While temperature or light alone did not result in decreased photosynthetic efficiency of the endoliths, combined thermal and solar stress caused a major decrease and delayed recovery. Endoliths protected under intact tissue recovered rapidly and photoacclimated soon after exposure to elevated sea temperatures. Endoliths under naturally occurring bleached tissue of *M. monasteriata* colonies (bleaching event in March 2004 at Heron Island) acclimated to increased irradiance as the brown symbionts disappeared. We suggest that two major factors determine the outcome of thermal bleaching to the endolith community. The first is the microhabitat and light levels under which a coral grows, and the second is the susceptibility of the coral-dinoflagellates symbiosis to thermal stress. More resistant corals may take longer to bleach allowing endoliths time to acclimate to a new light environment. This in turn may have implications for coral survival.

Key words: bleaching, endolithic algae, thermal stress, photoacclimation, photoinhibition, coral, *Montipora monasteriata, Symbiodinium.*

Introduction

Corals, the framework builders of reefs, live in close association with a range of phototrophic species including intracellular dinoflagellates and skeletal-dwelling endolithic microalgae and cyanobacteria. Microendoliths and especially the siphonaceous green algae *Ostreobium* Bornet and Flahault (Jeffrey, 1968; Lukas, 1974; Le Campion-Alsumard et al., 1995) inhabit the calcareous skeleton of many reef-building corals (Highsmith, 1981; Le Campion-Alsumard et al., 1995). These endoliths lie under the coral tissue and appear as dense green bands or zones within the external skeleton (Highsmith, 1981). The endolithic community lives in a protected environment within the coral skeleton (Shashar et al., 1997) where less than 5% of the photosynthetically active radiation (*PAR*) may be able to penetrate and reach these zones (Halldal, 1968; Shibata and Haxo, 1969; Schlichter et al., 1997) because of to its absorbance by the unicellular endosymbiotic algae (zooxanthellae) and the inorganic skeleton itself (Kanwisher and Wainwright, 1967).

Coral bleaching involves the disruption of the association between coral hosts and their endosymbiotic photosynthetic algae. It is a stress response that results in abrupt decreases in the population density of symbiotic dinoflagellates after changes to the physical and chemical environment surrounding corals. These changes may include low salinity (Goreau, 1964; Egana and DiSalvo, 1982); low or high photosynthetic radiation (Vaughan, 1914; Yonge and Nichols, 1931; Hoegh-Guldberg and Smith, 1989; Jones et al., 1998); elevated ultraviolet radiation (Gleason and Wellington, 1993; Lesser et al., 1990); toxins, e.g. cyanide (Jones and Hoegh-Guldberg, 1999), copper ions (Jones, 1997), diuron and atrazine (Jones et al., 2003); microbial infection, e.g. *Vibrio* (Kushmaro et al., 1996) and temperature (high: Jokiel and Coles, 1977, 1990; Coles and Jokiel, 1978; Hoegh-Guldberg and Smith, 1989; Glynn and D'Croz, 1990; low: Saxby et al., 2003). More recently, global episodes of mass coral bleaching have occurred that are linked to elevated seawater temperature (Goreau and Hayes, 1994; Glynn, 1991, 1993; Brown, 1997; Hoegh-Guldberg, 1999). These responses are exacerbated by

high irradiance due to the effect of elevated sea temperatures on the ability of symbiotic dinoflagellates in affected corals to process light excitations.

While the response of corals and symbiotic dinoflagellates to thermal/irradiance stress have been the focus of a wide range of studies, microendolithes have been largely overlooked. Several lines of information suggest, however, that endolithic algae may be important for the survival of bleached corals (Fine and Loya, 2002). Furthermore, it is most likely that the phototrophic endolithic community has influenced measurements and interpretations of aspects such as symbiont pigment concentrations (Kleppel et al., 1989) and photosynthetic efficiency (Fine et al., 2004). Understanding endoliths response to temperature and light stress is of great importance if we wish to better understand holobiont (corals and their many associates) during and following stressful events.

We hypothesised that endoliths will survive increased temperature as long as the loss of symbiotic dinoflagellates lags behind the temperature stress, hence the deterimental combination of light and temperature stress is avoided. We have also hypothesised that exposure to the combined effect of temperature and light stress, will affect the rate of recovery from photoinhibition.

We extend previous studies that have largely concentrated on the ability of *Ostreobium sp.* to harvest light and photosynthesise in dim environments (Halldal, 1968; Schlichter et al., 1997; Fork and Larkum, 1989; Koehne et al., 1999) by examining the response of an endolith phototrophic community (consisting mainly of the green algae *Ostreobium sp.*) within the coral *Montipora monasteriata* Forskal exposed to extreme solar and thermal stress. We also examine the protective effect of the dinoflagellates during stressful events and the following recovery of the endoliths. Our results confirm a complex interaction between endolithic algae, symbiotic dinoflagellates and their coral hosts.

Materials and methods

Corals used in this study were collected on the reef crest (at 1–2 m at low tide) off the southern shore of Heron Island (23°27′ S, 151°54′ E) and the northern edge of neighbouring Wistari reef during 2003 and early 2004. These reefs are located within the Capricorn-Bunker group of reefs on the southern section of the Great Barrier Reef.

The response of phototrophic endoliths to temperature and light stress

The portable underwater Pulse Amplitude Modulated (PAM) fluorometer (Diving-PAM, Walz Gmbh, Effeltrich, Germany) was used to examine the photosynthetic efficiency of endolithic algae inhabiting the skeletons of the coral *Montipora monasteriata* Förskal under elevated light and temperature. To examine possible synergistic effect of temperature and light on the photosynthetic performance of phototrophic endoliths in *M. monasteriata* we exposed corals to two levels of temperature and irradiance in aquaria with sea water flow-through at Heron Island Research Station. Pieces from five colonies of *M. monasteriata* were collected at Wistari Reef, from an environment with *PAR* of 200–300 μmol m^{-2} s^{-1} (at midday low tide), and cut into fragments (3×3 cm–5×5 cm) using a band saw (fragments from different colonies were mixed).

Fragments were acclimated in a tank with water flow-through and natural irradiance of 250 μmol m^{-2} s^{-1} (at midday) for 48 h prior to the experiment (Fig. 1). Coral tissue was removed from half of the surface area of 72 fragments (randomly picked from our pool of fragments) using an air gun, to expose the endoliths to increased irradiance. Twelve fragments were put in each aquarium: six that had their tissue removed from half their surface area and six that were left intact. Photosynthetic efficiency (F_v/F_m, where F_v is the variable fluorescence, F_m is the maximal fluorescence) was measured after adapting the corals to the dark for 30 min on the intact and exposed sections at the beginning of the experiment The fragments were then subjected to one of four treatments (three aquarium tank were included within each treatments); in treatment 1, fragments were exposed to sunlight (similar to habitat light levels, 300–350 μmol m^{-2} s^{-1} at midday) and heated to 31°C over 24 h to inflict both thermal and light stress; in treatment 2, fragments were exposed to sunlight and a temperature of 25°C; in treatment 3, fragments were shaded (50–100 μmol m^{-2} s^{-1} at midday) and heated to 31°C and in treatment 4, they were shaded and exposed to temperature of 25°C. 24 h after the beginning of the experiment the tissue from the intact half of each fragment and from three out of six of the intact fragments was removed using an air gun. At this point, measurement of dark-adapted F_v/F_m was repeated for the intact and exposed sections. The temperature in all treatments was stabilized at 25°C from 24 h onwards, and a daily measurement of F_v/F_m (dark-adapted) was performed on each of the fragments to examine their recovery from the heat/light stress. This was carried out for 6 days from the end of the heat stress (7 days from the beginning of the experiment, Fig. 1).

Since no significant difference was found between the F_v/F_m of fragments from different aquaria within a treatment, we analysed the results after pooling them together.

Two-way ANOVA was performed after transformation of log(x+1) to examine whether light level (sunlight/shaded) and temperature (25°C/31°C) affect the photosynthetic efficiency.

ANCOVA analysis was performed after transformation of log(x+1) to test the hypothesis that recovery of dinoflagellates and endolites varied following the different treatments.

Photosynthetic efficiency in exposed versus *shaded endoliths*

We measured the diurnal changes in photosynthetic efficiency of the endolithic phototrophs under high and low irradiance. Three fragments of *M. monasteriata* (10 cm×10 cm,) were ground using an industrial grinder (in seawater) on their underside until the green band of the endolithic phototrophes was exposed. Coral tissue was

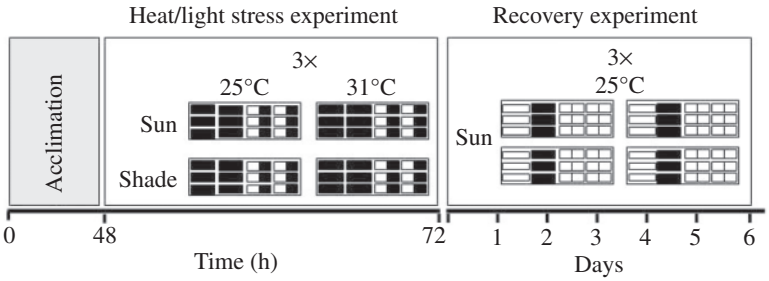

Fig. 1. Diagram of experimental design for measuring the effect of heat and light stress and following recovery, demonstrating the number of fragments of coral in each aquarium, number of aquaria in each treatment and duration of each stage of the experiment. Black and white rectangles represent intact and bare coral skeleton fragments, respectively.

removed from half of the surface of the fragment (Fig. 2A,B) using an air gun. Two fibre optic cables from two PAM fluorometers were mounted under the coral fragment using 'coral clips' (Walz Gmbh), one facing the intact tissue section and one under the exposed bare skeleton where tissue had been removed. The underside and sides of the coral fragment were covered with black plasticine to allow light penetration through the upper part only (i.e. through the dinoflagellates, coral tissue and skeleton, or the coral skeleton only where tissue was removed). Measurements were undertaken in aquaria under natural irradiance similar to that experienced by the colonies within their habitat on the reef (200–300 µmol m^{-2} s^{-1} at midday). PAR was monitored using the external light meter of the PAM fluorometer. Two horizontal grooves were drilled into the endoliths green band (one under intact and one under the exposed section) and the coral sections carefully washed to remove any remaining skeletal dust. The light sensor of the PAM fluorometers was inserted into each of the grooves (Fig. 2B) so that it faced upwards and then the groove was sealed using black plasticine. The light sensor was pre-calibrated against a Li-Cor quantum sensor (LI-189; Li-Cor, Lincoln, NE, USA). Measurements of both PAR and dynamic photosynthetic efficiency were taken over a 24 h period.

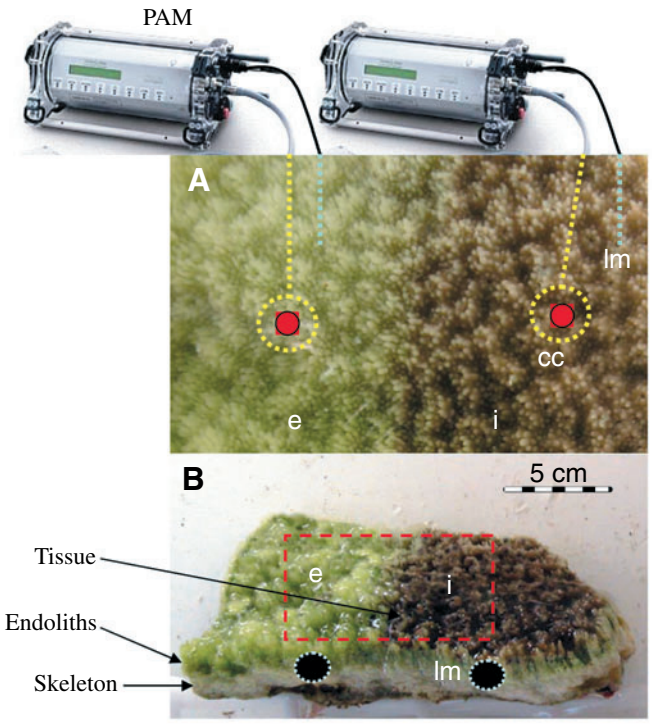

Fig. 2. Illustration of experimental setting for diurnal light and F_v/F_m measurements in *Montipora monasteriata*. (A) Top view of the intact (i), and exposed (e) parts of the skeleton; the position of the coral clip (cc) and the light meter (lm) can be seen. The coral clip and light meter were mounted underneath or inside the endolithic algae layer hence the broken line. Note the green pigment of the endoliths in the exposed part. (B) Side view showing the two grooves drilled for each of the pulse amplitude modulated (PAM) light meters can be seen between the skeleton and the endolithic algae layer. Two PAM fluorometers were used simultaneously.

Mass bleaching occurred in the reef flat and crest of Heron island in March 2004, after unusually high sea temperatures were experienced in the Coral Sea and Great Barrier Reef in February and March 2004. We collected five partially bleached colonies of *M. monasteriata* during this event as well as performing measurements on the photosynthetic capacity of the phototrophic endoliths under healthy and bleached sections of each colony. Rapid light curves (RLC) were measured on dark-adapted corals to investigate the photosynthetic performance of the endoliths and the endosymbiotic dinoflagellates in bleached and healthy sections. To do this, optic fibre sensors were positioned on the coral surface so that the tips were 3 mm from the coral tissue surface. RLC consisted of dynamic yield measurements being performed after each of a series of eight irradiances (lasting 10 s each). The effective photosynthetic yield Y of photosystem II (PSII) was derived from the Genty equation $Y=(F_m'-F)/F_m'$ (Genty et al., 1989), where F is the fluorescence under a given irradiance and F_m' is the maximal fluorescence in light-adapted dinoflagellate symbionts after the application of a short flash (0.8 s) of PAR that was saturating for photosynthesis (approx. 6000 µmol photons m^{-2} s^{-1}).

Results

The photosynthetic efficiency (F_v/F_m) was significantly higher in dark-adapted coral dinoflagellates from the intact half of each fragment at 25°C than at 31°C [Fig. 3A; two-way ANOVA with repeated measures (RM), LSD; $P<0.001$]. They were not different prior to heating (two-way RM-ANOVA; $P>0.05$). The lowest dark-adapted F_v/F_m was seen in dinoflagellates from fragments that were exposed to both elevated temperature and light, although these were not significantly different from dinoflagellates in heated yet shaded fragments (two-way RM-ANOVA, LSD; $P>0.05$) due to high

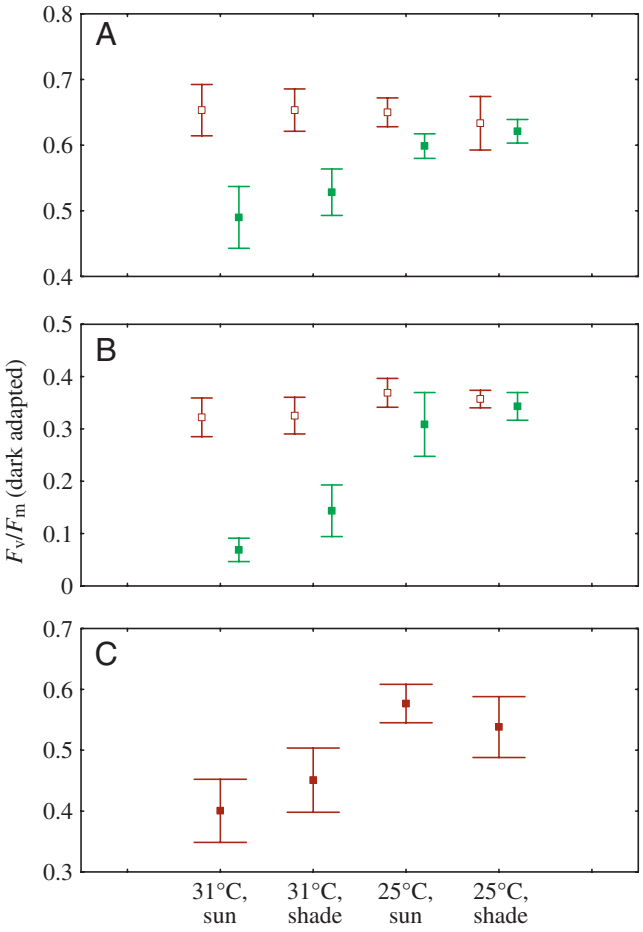

Fig. 3. Maximal photosynthetic quantum yields (F_v/F_m, mean ± 95% confidence limits) of (A) dinoflagellates, (B) exposed endoliths and (C) endoliths under intact tissue. Each was examined under four combinations of temperature and light in the beginning of the experiment (red open squares) and 24 h later (green filled squares). In C (under intact tissue) only the endpoint F_v/F_m could be measured, after removal of coral tissue (red-filled squares).

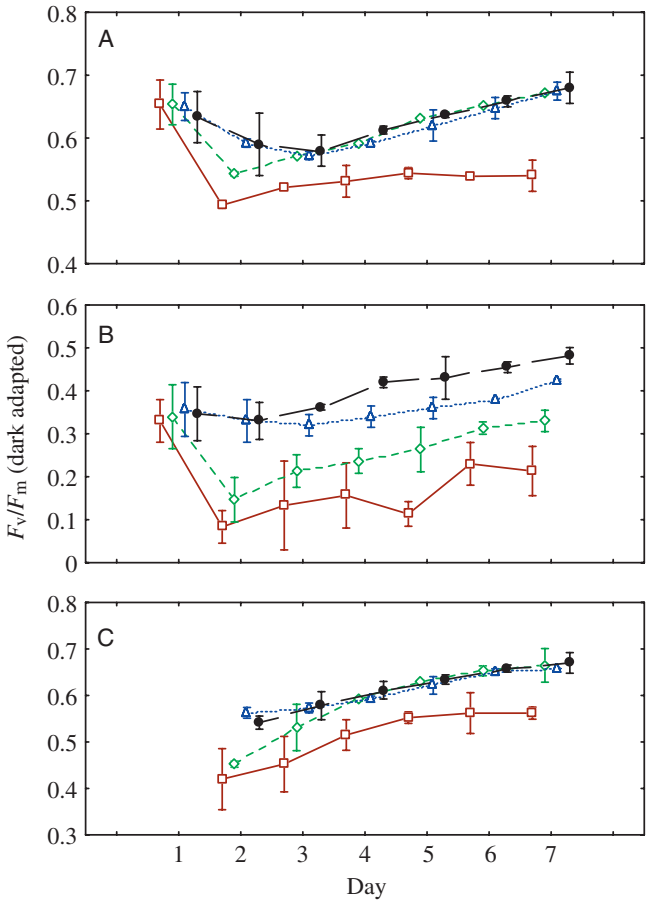

Fig. 4. Recovery of (A) dinoflagellates, (B) exposed endoliths and (C) endoliths under intact tissue, as reflected by F_v/F_m (values are means ± 95% confidence limits during 6 days following the heating experiment). Fragments were exposed to one of four treatments: 31°C in the sun (red squares), 31°C in shade (green diamonds), 25°C in the sun (blue triangles) and 25°C in shade (black circles). Please note that day 1 is still within the heating experiment.

variability within each treatment (Fig. 3A). Both heated treatments were significantly lower, however, than F_v/F_m of the same fragments in the beginning of the experiment (two-way ANOVA with repeated measures, LSD; $P<0.001$). Dark-adapted F_v/F_m of dinoflagellates did not differ from the intact half of treated fragment and fragments that were all covered with coral tissue (two-way RM-ANOVA, LSD; $P>0.05$). This demonstrates that our technique of removing the tissue off half the fragment did not adversely affect the rest of the dinoflagellates hosted in the tissue on the other half.

The photosynthetic performance of the endoliths (Fig. 3B,C) revealed a similar pattern to that seen in dinoflagellates. That is, there was a significant difference between F_v/F_m measured at time 0 and that measured 24 h after, fragments were exposed to 31°C (two-way RM-ANOVA, LSD, $P<0.001$) but no significant difference between time 0 and 24 h after, of fragments at 25°C (two-way RM-ANOVA, $P>0.05$). The lowest dark F_v/F_m was seen in heated and sun-exposed endoliths (Fig. 3B), which was significantly lower than the F_v/F_m of endoliths from the other three treatments (two-way RM-ANOVA, LSD, $P<0.001$). Endoliths from fragments that were heated in the shade and those kept at normal temperatures but exposed to sunlight had significantly higher dark-adapted F_v/F_m values than endoliths that were exposed to sun and heated (two-way ANOVA with repeated measures, LSD, $P<0.001$). Endoliths under the dinoflagellates (at 24 h) demonstrated significantly higher maximum dark-adapted F_v/F_m than endoliths that were exposed after tissue removal (two-way RM-ANOVA, LSD; $P<0.001$; Fig. 3C). These changes persisted even after longer periods of darkness, implying that the exposed endoliths had experienced chronic photoinhibition. Endoliths under dinoflagellates from fragments that were kept at 25°C (ambient temperatures) and exposed to sunlight showed the highest maximum dark-adapted F_v/F_m, followed by endoliths in shade at control temperatures (25°C) and heated (31°C) in the shade. The lowest values were always found under the combination of

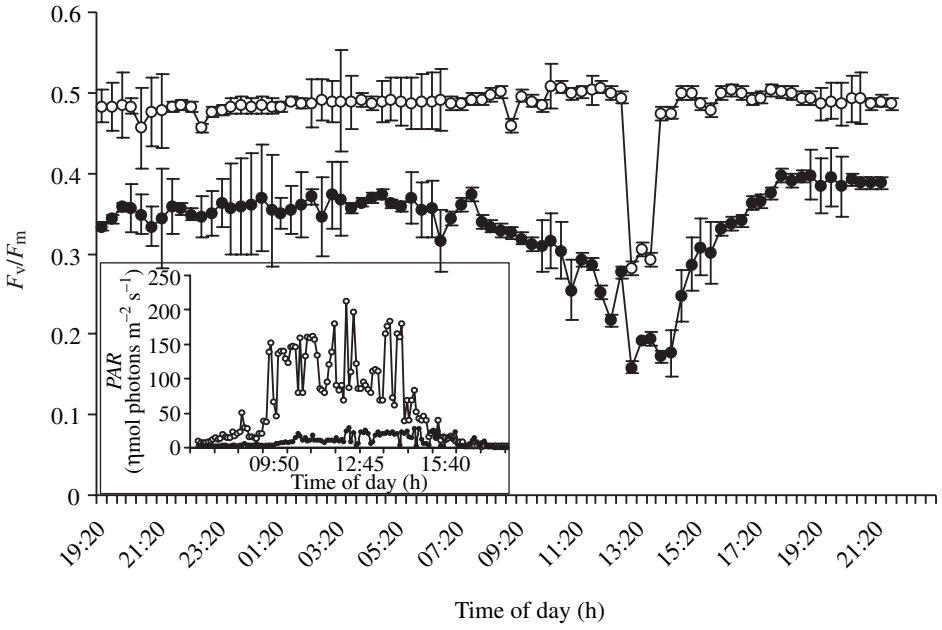

Fig. 5. A 24 h cycle of F_v/F_m of exposed endoliths (filled circles) and endoliths under intact tissue (open circles) (mean ± S.D., N=4) as recorded every 20 min in the skeletons of *M. monasteriata*. The inset shows the average (N=3 days) light intensities inside the skeleton, under intact tissue (filled circles) and in exposed skeleton (open circles) during the days of the experiment.

elevated temperature (31°C) and normal sunlight. The recovery of dinoflagellates following heating revealed that elevated temperature and sunlight can adversely affect the capability of dinoflagellates to recover from photodamage (r^2=0.98; P<0.001; Fig. 4A). Even after a week, fragments that were exposed to 31°C and normal sunlight had not recovered fully whereas dinoflagellates from other treatments (including those exposed to 31°C in shade) recovered (ANCOVA, GLM analysis P<0.001; Fig. 4A).

Endoliths exposed to 31°C and normal sunlight exhibited a similar pattern of photosynthetic efficiency to the dinoflagellate symbionts and had not recovered after a week (ANCOVA; GLM analysis P<0.001; Fig. 4B). Endoliths from other treatments, however, recovered to their initial level, even reaching a higher dark-adapted values of F_v/F_m, possibly because of their photoacclimation to the increased irradiances after removal of the tissue and dinoflagellates. Endoliths that were shaded by the coral tissue and dinoflagellates recovered very rapidly under all treatments (ANCOVA, GLM analysis P<0.001; Fig. 4C).

Diurnal cycle

Comparison between the diurnal cycle of endoliths exposed to sun for 24 h (after tissue removal) with those under healthy coral tissue revealed that the dark-adapted F_v/F_m of the exposed endoliths was constantly lower (Fig. 5). This corresponded with the irradiance measured within the skeleton habitat of these endoliths after tissue removal. Irradiance in the skeletons under dinoflagellates and coral tissue reached 25 μmol m^{-2} s^{-1} at midday while irradiance within the skeletons after tissue removal reached 200 μmol m^{-2} s^{-1} at midday (Fig. 5 inset).

The dynamic (i.e. not dark-adapted) F_v/F_m of phototrophic endoliths from both healthy and exposed sections of the colony showed distinct changes over the course of the day, dropping from 0.5 to less than 0.3 by noon for endoliths under dinoflagellates and coral tissue. Dynamic F_v/F_m in endoliths in exposed skeletons decreased from 0.35 to less than 0.2 by noon. The lowest values of dynamic F_v/F_m always coincided with the highest irradiance. F_v/F_m began to increase again as light levels began to decrease in the early afternoon and had returned to their pre-dawn values 2 h after the initial drop in efficiency. Recovery of F_v/F_m after midday high irradiance was at a lower rate in exposed endoliths than endoliths under healthy tissue.

Endolithic algae of bleached corals on the reef crest

Exposed endoliths had significantly higher photosynthetic efficiencies than those under more pigmented parts of partially bleached colonies found on the Heron Island reef crest during the 2004 bleaching event (maximum dark-adapted F_v/F_m was 0.44 and 0.53 respectively; Fig. 6). Photosynthetic efficiencies

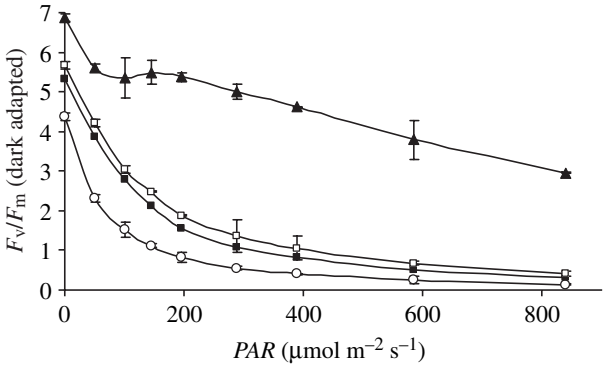

Fig. 6. Rapid light curves of partially bleached colonies of *M. monasteriata* in March 2004. Curves are shown for dinoflagellates in a healthy area (triangles), and in a bleached area of the colony (open squares), and endoliths under a bleached area (filled squares) and under a healthy area (open circles).

of dinoflagellates in more pigmented parts of the colony were significantly higher than those in the bleached parts of the same colony (max F_v/F_m of 0.69). Endoliths under bleached areas had a max F_v/F_m of 0.58 whereas endoliths under more pigmented areas (under dinoflagellates) demonstrated significantly lower quantum efficiency under all irradiances during RLCs than endoliths under bleached parts of the colony, implying photoacclimation of the latter (Regression analysis r^2=0.99, P<0.001, Fig. 6).

Discussion

Episodes of mass coral bleaching have been increasing in frequency and severity over the past two decades, with episodes being mostly triggered by warmer than normal summer temperatures (Hoegh-Guldberg, 1999). Heat stress increases the susceptibility of the photosynthetic apparatus to photoinhibition in the symbiotic algae within affected corals by blocking the ability to process excitations captured by the light reactions of photosynthesis (Iglesias-Prieto et al., 1992; Jones et al., 1998; Warner et al., 1996, 1999). During mass bleaching events, endolithic algae are exposed to similar levels of thermal stress as the overlying coral tissue (and dinoflagelate symbiont). They may, however, be exposed to an order of magnitude change in irradiance (depending on habitat and skeletal ultrastructure) as the overlying coral tissues lose the brown colouration of the dinoflagellate symbionts. Revealing the response of microendoliths to thermal stress and increased irradiance is essential for better understanding the consequences to the coral-algal complex (holobiont) and changes in the microendolith community following recovery or mortality of the coral host (Le Campion-Alsumard, 1995; Diaz-Pulido and McCook, 2002).

In the present study we demonstrate that the response of phototrophic microendoliths to thermal and irradiance stress is similar to that of the symbiotic dinoflagellates. As in symbiotic dinoflagellates, the combined affect of temperature and light on the microendoliths is detrimental to the ability of the organisms to process captured light excitations (Warner et al., 1996, 1999) and recovery from the combined damage may take several days to weeks, depending on intensity and period of exposure. The combined effects of elevated temperature and irradiance were much higher in both dinoflagellates and endoliths, causing a decrease of 25% and 80% in dark-adapted F_v/F_m, respectively. Increased temperature or irradiance alone causes the F_v/F_m of exposed endoliths to decrease by 53% or 14%, respectively. Elevated temperature in this case caused a more severe photoinhibition than increased irradiance following exposure. This finding was reinforced by the higher performance of endoliths in areas of the skeleton covered by tissue and symbionts, as compared to exposed areas. The former demonstrated a decrease in F_v/F_m when incubated in 31°C as compared with their equivalent fragments that were incubated in the ambient temperature of 25°C (Fig. 3C).

Our findings suggest that if a coral is shaded or does not lose all of its endosymbiotic dinoflagellates during bleaching, conditions are less stressful and promote a more rapid recovery of the skeletal endoliths. These results match those of Fine et al. (2004), who demonstrated that the endolithic algae of shade adapted Mediterranean coral, *Oculina patagonica*, rapidly photoacclimate to increased irradiance during repetitive bleaching events. In the Mediterranean, temperature stress on the holobiont may prevail for 3 month and coral colonies may remain bleached for almost 8 months of the year.

The recovery of phototrophic endoliths was also found to be delayed by the combined effect of thermo/solar stress (Fig. 4). Intact endoliths that were under the protection of dinoflagellates during the extreme thermal stress, showed a rapid increase in F_v/F_m when tissue was removed at the end of the thermal stress, suggesting photoacclimation to increased irradiance. This may explain the observations from previous studies in which endolithic algae bloom after bleaching (Diaz-Pulido and McCook, 2002; Fine and Loya, 2002; Fine et al., 2004) or coral death (Le Campion-Alsumard, 1995).

Our observations suggest that outcome for endoliths after stressful conditions depends to a large extent on two major parameters. These are (1) the microhabitat the coral lives in (reef-flat, reef-crest, overhang) and (2) the response time of the coral host and endosymbiont to the stress and recovery. In coral species that respond quickly to the thermal/solar stress and consequently bleach or die rapidly, the endoliths will be exposed to the combined effect and photo-damage may significantly prolong recovery time. In short events or in the case of more tolerant coral species, this may allow rapid recovery and photoacclimation of the endoliths, even if the coral eventually bleach after the thermal stress is over. This is supported by our observations in a natural bleaching event where endoliths under the bleached section of the coral showed higher F_v/F_m, and hence photoacclimation, than endoliths under more normally pigmented parts of the same colony (Fig. 6).

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 appear sensitive to changes in temperature, which result in an increased sensitivity of the dinoflagellate symbiont to photoinhibition (Iglesias-Prieto et al., 1992; Fitt and Warner, 1995; Iglesias-Prieto, 1995; Warner et al., 1996; Jones et al., 1998), cellular damage and eventually disintegration (but see Takahashi et al., 2004). Our findings suggest that increased sea water temperature leads to increased sensitivity to photoinhibition of the phototrophic microendoliths and that heat stress is amplified by the presence of *PAR*.

The endolithic-reef-building coral relationship is considered to be an ectosymbiosis (Schlichter et al., 1995) yet the symbiosis does not break down following thermal stress as does coral-dinoflagellate symbioses. Healthy photoacclimated endolithic communities may be beneficial to bleached coral as pointed out by Fine and Loya (2002), showing that endolithic algae in bleached areas of a coral colony can be a significant source of photoassimilates. Photoassimilates released from the phototrophic endolithic algae reach the coral tissue and, the

dissolved organic substances can be taken up by the coral utilised (Schlichter et al., 1995).

We suggest that the response of the holobiont to stress is a result of the combined responses of each of its components (host zooxanthellae and endoliths) to the stress factor.

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