

Solar radiation modulates bleaching and damage protection in a shallow water coral

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ABSTRACT: Corals have been shown to bleach through the combined effects of elevated sea temperature and high solar radiation. In this study, cores from the west and east sides of a hemispherical shallow reef coral, *Goniastrea aspera*, were exposed to ambient and elevated water temperature treatments, combined with varying natural solar radiation regimes for periods of 3 d at different times of the year. At elevated temperature, the loss of zooxanthellae from east-side cores was directly related to the dose of solar radiation (measured as photosynthetically active radiation [PAR], 400 to 700 nm). Elevated temperature (+4°C) was responsible for 35 % of the total loss, and PAR dose for up to a further 14 %. Zooxanthellae from cores from both the east and west sides exhibited chronic photoinhibition (a reduction in maximal photochemical yield [F_v/F_m]) in both the ambient and elevated temperature treatments, which was directly related to the PAR dose. The chronic photoinhibition was consistently greater in the elevated temperature treatment, and also in the east cores relative to the west. These results quantify the direct contribution of solar radiation to both chronic photoinhibition and loss of zooxanthellae. The differences in both loss of zooxanthellae and photoinhibition between the different faces of the coral colony can be directly attributed to differences in prior experience, whereby the west sides of the coral had been exposed to higher natural solar radiation throughout the year, thus conferring greater tolerance to the effects of elevated temperature and solar radiation.

KEY WORDS: Solar radiation · Bleaching · Corals · PAR · Zooxanthellae · Photoinhibition · Photoprotection

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INTRODUCTION

Understanding the interaction between elevated temperatures and solar radiation in eliciting zooxanthella or pigment loss (bleaching) from corals is fundamental to the interpretation of bleaching susceptibility of corals and reefs worldwide. While the interplay between these 2 environmental factors has been widely acknowledged in the literature (see Fitt et al. 2001 for review), the contrasting influences of solar radiation on reef corals have rarely been addressed. It is clearly established that solar radiation acts as a damaging influence, eliciting bleaching, both in its own right (Coles & Jokiel 1978, Hoegh Guldberg & Smith 1989, Brown et al. 1994) and also in concert with elevated temperatures

(Hoegh Guldberg 1999). However, it has also been demonstrated that regular exposure of corals to moderately high irradiance can actually improve bleaching tolerance both to damaging solar radiation and to elevated temperature (Dunne & Brown 2001, Brown et al. 2002a) through a mechanism of cross-protection from solar to temperature stresses. Solar radiation, therefore, has the potential to both damage and protect corals, depending on environmental circumstances.

To date there is only 1 instance of direct evidence for the influence of solar radiation on changes in zooxanthella density in corals (Le Tissier & Brown 1996). Earlier, Coles & Jokiel (1978) reported visible reductions in pigmentation in *Montipora verrucosa* from Hawaii in several temperature treatments (ambient, elevated and

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cooled) when exposed to full solar radiation in shallow experimental tanks. From measurements of chlorophyll *a* (chl *a*) concentration they showed that at elevated temperature and in full sun, there was a loss of chl *a* specifically due to solar radiation. Hoegh Guldberg & Smith (1989) also demonstrated a reduction in chl *a* per zooxanthella in *Stylophora pistillata* at Lizard Island, Australia, exposed to full sunlight at ambient temperature for 8 h, but with no loss of zooxanthellae. Brown et al. (1994) reported visible bleaching in *Goniastrea aspera* at Ko Phuket, Thailand, as a direct result of high solar radiation in the field without any effect of temperature, and this has subsequently been shown to involve loss of zooxanthellae (Le Tissier & Brown 1996).

In the present study the direct relationship between solar radiation and zooxanthella loss was quantified in *Goniastrea aspera* at elevated and ambient temperatures and varying solar radiation scenarios. The focus here was on photosynthetically active radiation (PAR) dose, because evidence from earlier field studies (Brown et al. 1994, Dunne & Brown 2001), and work by Fitt & Warner (1995) and Hoegh Guldberg (1999) on corals, and more recently in macroalgae and phytoplankton (Hader 2006), has demonstrated the importance of this waveband in natural solar radiation compared to the shorter wavelengths of ultraviolet radiation (UVR), which are present at much lower intensity, in both photoinhibition and coral bleaching.

In addition to zooxanthella loss, which is considered to be an advanced stage of the bleaching process, this study also examined the influence of PAR on the maximal photochemical yield (the photosynthetic quantum yield in a dark-adapted coral; F_v/F_m) of zooxanthellae in *Goniastrea aspera*, since there are already several examples of the detrimental interaction of light and temperature on F_v/F_m in reef corals under dim- and bright-light conditions in the laboratory (Fitt & Warner 1995, Jones et al. 1998, Bhagooli & Hidaka 2003, 2004).

The protective influences of solar radiation on west faces of hemispherical *Goniastrea aspera* colonies have been described in earlier work (Brown et al. 1994, 2000, 2002a). These west surfaces receive significantly higher natural PAR doses than the east faces at certain times of the year, and this differential exposure confers improved thermal tolerance (and reduced bleaching) when the colonies are subject to elevated sea temperatures (Brown et al. 1994, 2002a). Similar effects have been noted in *Montastraea annularis* and *M. faveolata*, where shallow colonies bleached preferentially on shaded surfaces, but, in these cases, bleaching patterns were defined by the environmental tolerances of different symbiotic zooxanthella clades harboured by the coral colony (Rowan et al. 1997). In contrast, the inshore *G. aspera* colonies at this study location (Ko Phuket, Thailand) host only a single zooxanthella

clade, and bleaching patterns cannot be attributed to zooxanthella genetics as in other coral species (Brown et al. 2002a). This clade was originally described in Brown et al. (2002a) as Clade E, but has since been renamed Clade D (Douglas 2003).

Goniastrea aspera therefore provides a useful model for evaluating the damaging and protective roles of PAR on corals. The present study examined the responses (zooxanthella loss and maximal photochemical yield [F_v/F_m]) of east- and west-side cores to different natural solar radiation scenarios at ambient and elevated water temperatures, during a series of outdoor laboratory experiments between February 2000 and February 2001.

MATERIALS AND METHODS

Study site. The study site was located on the southeast tip of Ko Phuket, Thailand, in the Andaman Sea (7° 48' N, 98° 25' E). Physical characteristics of the location (Site A in Brown et al. 1994) are described in detail in Scoffin et al. (1992) and Brown et al. (1996). At this site, a wide intertidal reef flat extends for a distance of up to 200 m from the shore, where it terminates in a shallow fore-reef extending to a depth of 5 m. The reef flat is dominated by massive coral species, including *Goniastrea aspera*.

Continuous solar radiation measurements and computation. Long-term solar radiation (400 to 700 nm PAR) was recorded on a horizontal plane every minute, averaged and logged every 30 min using a 2π -cosine-corrected quantum sensor (Macam Photometrics) located above water 1.5 km from the study site. This sensor was calibrated annually under natural sunlight using a scanning spectroradiometer (Dunne & Brown 1996). The long-term downwelling PAR at the depth of the coral colonies on the reef flat was computed as described in Brown et al. (1999a).

Irradiance and temperature experiments. A total of 5 temperature/irradiance experiments were conducted, each lasting 3 d. Experiments were carried out in February 2000 (in ambient light and in shade), April and November 2000, and February 2001. On each occasion, coral cores were randomly assigned to each of 2 adjacent aquaria (10 l volume) exposed to natural solar radiation. Cores were held vertically at a uniform depth of 10 cm in running seawater (3 to 4 l min⁻¹). Water temperature in each aquarium was measured by calibrated thermocouples and logged every minute. In the heated tank, the water temperature was computer controlled continuously throughout the experiment and heated by a 3 kW immersion heater. Circulatory pumps were also placed in the aquaria to ensure thorough mixing.

Solar radiation falling on the corals was recorded continuously throughout each experiment using a 2π -cosine-corrected PAR sensor (Macam Photometrics) placed at the same depth as the tops of the cores. The PAR sensors were recalibrated using a scanning spectroradiometer in natural sunlight prior to each experiment. All readings were corrected for the immersion effect. Irradiance was logged every minute. The solar radiation conditions for each experiment are summarised in Table 1.

The median ambient temperatures for the different experiments ranged from 28.51 to 29.77°C, and the range for the elevated temperature treatments was from 33.03 to 33.81°C. Anticipating that the highest irradiance would be expected in February, with lower irradiances at other times of the year, 2 experiments were run in February 2000—one under ambient irradiance and the other under a neutral density filter that reduced the ambient irradiance by two-thirds. In this way the performance of corals under high and low irradiances in February could be compared with that of corals at other times of the year.

In each experiment, coral cores (25 mm diameter) were collected from each of the east and west surfaces of 15 to 19 colonies of *Goniastrea aspera* on the inner reef flat at the same depth. The zooxanthella density and chl *a* pigment content of 5 core pairs (east and west baseline) were determined immediately, and 2 sets of 10 to 14 core pairs were each incubated for 68 h in the aquaria maintained with running seawater—one at ambient temperature and the other at elevated temperature. Zooxanthella density samples were also sacrificed at the end of the 3 d experiment, with cores being fixed and decalcified following Le Tissier & Brown (1996). Zooxanthellae from 5 subsamples were counted in a Neubauer haemocytometer, and densities were normalised to core surface area,

computed from the core diameter measured with vernier calipers prior to fixation. Baseline chl *a* pigment samples were processed as described in Brown et al. (2002b) and Ambarsari et al. (1997) and analysed by reverse-phase high-performance liquid chromatography.

Maximal photochemical yield (dark-adapted F_v/F_m) was measured before dawn prior to the start of the experiments and every 24 h thereafter, using a Waltz Mini-PAM fluorometer (blue LED 470 nm) with a 5 mm diameter fibre optic held in a fixed-geometry measuring head (25° from the vertical, 5 mm from the end of the fibre optic to the coral). During measurement, the cores were removed from the tanks in their holder (ca. 10 to 14 cores each) for about 30 s. F_0 (minimal fluorescence) was measured (measuring pulse 0.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$) followed by a saturation pulse of 18 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to record F_m (maximal fluorescence).

Statistical analyses. Data for percentage zooxanthella loss, although normally distributed for each experiment date, were heteroscedastic between dates. A weighted least-squares regression was therefore used to examine relationships between zooxanthella loss and water temperature, and PAR dose, and to remove the heteroscedasticity. F_v/F_m data were normal and homoscedastic, and were examined using parametric regression to determine any relationship between changes in F_v/F_m and the PAR dose. Analysis of covariance (ANCOVA) was employed to test for differences in the regression slopes and intercepts. For assessing changes over season in baseline zooxanthella densities and chl *a* pigment samples, analysis of variance (ANOVA) followed by Student-Newman-Keuls (SNK) analysis was employed. Paired 2-tailed *t*-tests were used for comparison of baseline zooxanthella densities and chl *a* pigments in east and west sides. In all cases, α was set to 0.05.

Table 1. Dates, solar radiation (photosynthetically active radiation [PAR]) conditions and number of coral core samples used in the maximal photochemical yield (F_v/F_m) and zooxanthella loss experiments. All treatments were full sun, apart from Expt 2 (neutral density filter)

Expt	Date	Solar radiation underwater (PAR)		F_v/F_m sample number Ambient and Heated	Zooxanthella loss	
		Mean irradiance 11:00–13:00 h ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Total dose (mol m^{-2})		Ambient	Heated
1	21–23 Feb 2000	2208	165.38	10 East & 10 West in each treatment	5 East & 5 West	5 East & 5 West
2	25–27 Feb 2000	676	57.69	10 East & 10 West in each treatment	5 East & 5 West	5 East & 5 5 West
3	7–9 Apr 2000	2033	128.77	12 East & 12 West in each treatment (6 on last day)	5 East & 5 West	6 East & 6 West
4	13–15 Nov 2000	1199	100.76	12 East & 12 West in each treatment (6 on last day)	6 East & 6 West	6 East & 6 West
5	7–9 Feb 2001	1401	96.42	14 East & 14 West in each treatment (8 on Days 2 & 3)	6 East & 6 West	8 East & 5 West

RESULTS

Long-term solar radiation

The daily underwater PAR dose from January 2000 to February 2001 is shown in Fig. 1. The record is split into the morning and afternoon components, representing in broad terms the different doses experienced by the west (afternoon) and east (morning) facing surfaces of the hemispherical coral colonies. The pattern that emerges is of west sides of colonies being subjected to a consistently higher daily PAR dose throughout the year, with the greatest difference in the dry season (December to April).

Comparisons of baseline zooxanthella densities and chl *a* pigment concentrations between sides and at different times of the year

There were no significant differences in zooxanthella densities between east and west baseline cores for any experimental date apart from February 2001, when east cores contained slightly fewer zooxanthellae ($p < 0.01$) than west cores (Table 2). No significant differences were detected in baseline chl *a* pigment concentrations between east and west cores at any time (Table 2). In terms of comparisons of baseline zooxanthella densities over the period 2000 to 2001, the only significant difference was for February

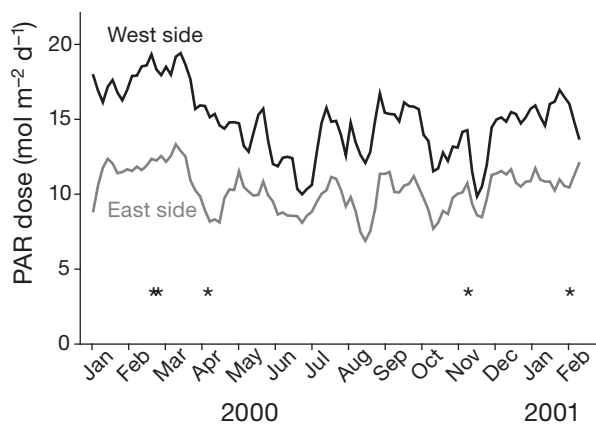


Fig. 1. *Goniastrea aspera*. Downwelling photosynthetically active radiation (PAR) dose underwater at the depth of coral colonies on the reef flat at Ko Phuket, Thailand. Plots are the daily averages from January 2000 to February 2001 split at 12:00 h local time when the sun reaches its zenith. A 16.5 d smoothing filter has been applied for clarity. *: dates of the experiments

Table 2. Mean values (see Table 1 for number of samples) for zooxanthella density ($\times 10^7 \text{ cm}^{-2}$) and chlorophyll *a* concentration per cell ($\mu\text{g cell}^{-1}$), and standard deviations (in parentheses) for baseline cores from east and west sides of colonies on the experimental dates

	Feb 2000		Apr 2000		Nov 2000		Feb 2001	
	East	West	East	West	East	West	East	West
Zooxanthella density	1.82 (0.38)	2.00 (0.31)	1.34 (0.15)	1.23 (0.22)	1.37 (0.25)	1.38 (0.25)	1.28 (0.11)	1.58 (0.19)
Chlorophyll <i>a</i> concentration	3.8 (1.8)	3.4 (1.3)	4.98 (1.49)	4.98 (1.01)	5.35 (0.91)	3.89 (1.49)	4.91 (1.42)	5.76 (0.78)

2000, when both east and west cores had slightly higher zooxanthella densities ($p < 0.05$) than at any other experimental date. No significant differences were detected in baseline chl *a* pigment concentrations in cores at any experimental date over the 12 mo period.

Patterns of zooxanthella loss

Zooxanthella loss only occurred in samples from the east sides of the corals at elevated temperatures. There was no significant relationship between this percentage zooxanthella loss and the elevated treatment temperatures, thereby excluding the possibility that any slight differences in water temperature between experiments had any effect.

Percentage zooxanthella loss in the east sides at elevated temperature was positively related to the total 3 d PAR dose ($r^2 = 0.988$, $p < 0.001$, $n = 29$). A best fit of the data (Fig. 2) was made to a power function represented by:

$$\% \text{ zooxanthella loss}^{0.5} = 5.827 + (4.19 \times 10^{-5}) \times \text{PAR dose}^2$$

At the low PAR doses, there was a large data spread for zooxanthella loss, which reduced markedly at the highest doses. The shape of the curvilinear relationship at low PAR doses suggests that elevated temperature was responsible for approximately 35% of the overall zooxanthella loss in east-side cores (Fig. 2). The regression line in Fig. 2 has been extended to demonstrate that the model remains realistic at lower and higher PAR doses, which may occur naturally. Solar radiation compounded the zooxanthella loss so that, at the highest experimental PAR dose (165 mol m^{-2} , equivalent to an average daily dose of $55 \text{ mol m}^{-2} \text{ d}^{-1}$, and a mean irradiance of $2200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ during the 2 h either side of solar noon), it accounted for a further 14%, whilst, for doses $< 57 \text{ mol m}^{-2} \text{ d}^{-1}$, the additional loss was very small ($< 2\%$). At the lower PAR doses, the coral cores in the experimental treatments were

receiving daily doses ($19 \text{ mol m}^{-2} \text{ d}^{-1}$) comparable to (see Fig. 1) and peak irradiances ($676 \mu\text{mol m}^{-2} \text{ s}^{-1}$) well below those routinely experienced on the reef flat during a normal tidal cycle (Brown et al. 2002a).

Maximal photochemical yield (F_v/F_m)

There were no significant differences in F_v/F_m of cores sampled before each experiment between different times of the year in each respective side (east and west). However, F_v/F_m was consistently lower in west-side cores compared to the east at the beginning of the experiment at every date (2-tailed t -tests; all p -values < 0.001). Since all cores had been subject to identical handling, this difference must have reflected field conditions, and was confirmed by additional field measurements. This initial depression in F_v/F_m varied between sampling dates from 0.019 in February 2001 to 0.073 in February 2000 (full sun) (Fig. 3). Over the course of each experiment (3 d) F_v/F_m declined in the ambient tanks, except for the west cores in November 2000 and February 2001 (regression slopes not significant), whilst in the shaded experiment in February 2000 it rose for both west and east cores (Fig. 3). In the elevated-temperature treatments, there was reduction in F_v/F_m in both west and east cores on all experiment dates that was consistently greater than for the ambient tanks (all ANCOVA, $p > 0.001$). There was also an effect of side, such that at high PAR doses (April 2000 and February 2000 [full sun]; 128.8 and 165.4 mol m^{-2} , respectively), there was a greater reduction in F_v/F_m in the east compared to the west cores (ANCOVA, $p <$

0.028 and $p < 0.0001$, respectively). For PAR doses in the middle of the range in November 2000 and February 2001 (100.8 and 96.4 mol m^{-2}), there was no difference in the slopes of the lines, and in February 2000 (shaded) there was again a greater depression in east sides (ANCOVA, $p < 0.0001$) (Fig. 3).

To investigate the effect of PAR dose on F_v/F_m independent of experiment date, the dose for each day of the experiments was plotted against the change in F_v/F_m for that day. In each case (west and east, ambient and elevated temperature), there was a significant negative regression (all data between $p = 0.012$ and 0.0019). Since the regressions for the west and east ambient treatments and the west and east elevated treatments both had the same slope and intercept (ANCOVA), the data for each treatment were pooled. The pooled regression lines are shown in Fig. 4. There was no significant difference between the slopes of these lines, but the intercepts were significantly different (ANCOVA, $p < 0.0001$). In 4 instances of low PAR dose at ambient temperature, F_v/F_m increased (samples from the west sides from February 2000 and from the west and east from February 2001). The fact that this analysis of the daily data did not discern a difference between east and west sides may appear to contradict the effect of side detected from the individual experiments. However, this is likely to have been a consequence of combining the data from all experiments, where the lack of difference in 2 of the 5 experiments has reduced the 'power' of this regression analysis.

DISCUSSION

The effect of prior environmental experience on bleaching susceptibility has been well recognised (see Coles & Brown 2003), and it was anticipated that this factor would have a marked influence on the results obtained in the present study. Previous studies, including one at the same location (Ko Phuket; Brown et al. 1999a), have shown that there are seasonal variations in zooxanthella density, algal pigment concentrations (Stimson 1997, Brown et al. 1999a, Fagoonee et al. 1999, Fitt et al. 2000) and F_v/F_m (Warner et al. 2002), with higher values at times of the year when sunlight and sea temperature were reduced. Prior to and during the period of these experiments at Ko Phuket in 2000 to 2001, solar radiation did not follow the previous reported pattern for this location where east and west surfaces of the coral normally receive similar PAR doses from May to December (Brown et al. 2002a). Instead, the west sides of *Goniastrea aspera* colonies consistently received higher daily PAR doses during the whole year compared to east

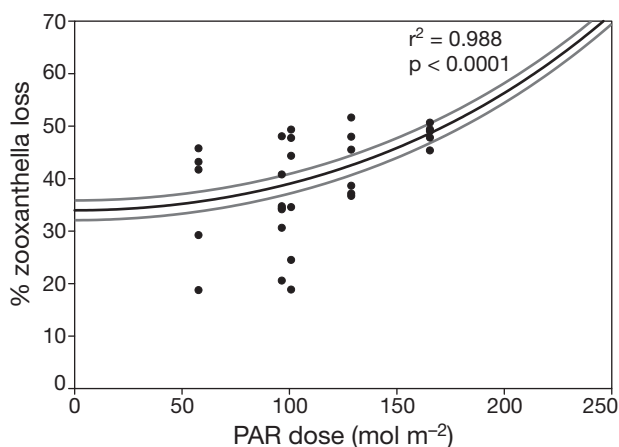


Fig. 2. Weighted least-squares regression for percentage loss of zooxanthellae in east side cores at elevated temperature and photosynthetically active radiation (PAR) dose accumulated over the course of each experiment (3 d). Regression line has been extended down to a PAR dose of 0 (no sunlight) and up to 250 mol m^{-2} ; 95% prediction intervals are also shown (grey lines)

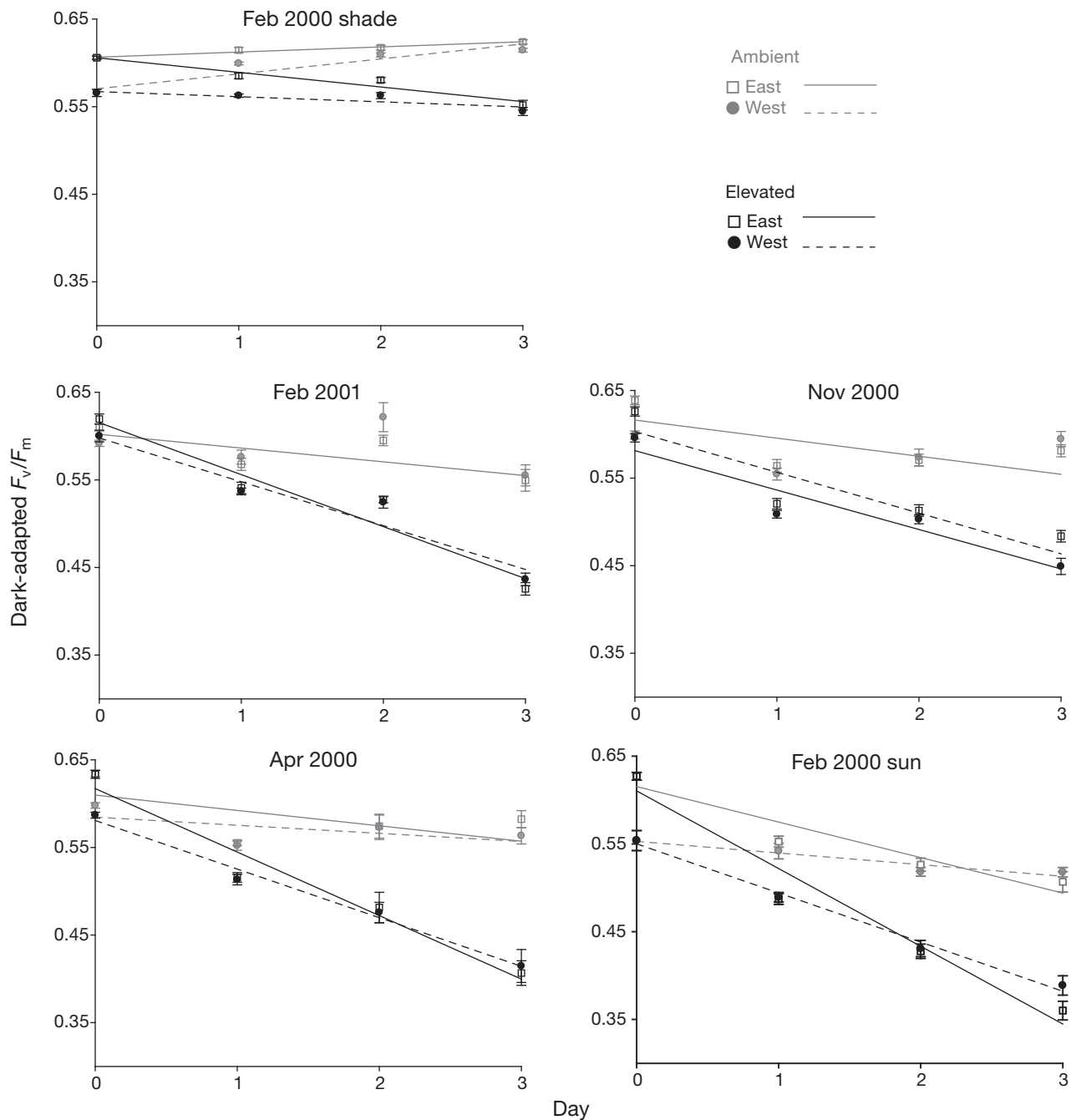


Fig. 3. Matrix of maximal photochemical yield (F_v/F_m) measured on each day of the experiment before dawn. Experimental dates are placed in order of increasing solar radiation dose, from the shaded experiment in February 2000 (top left) to the full sun experiment, also in February 2000 (bottom right). Regression lines are shown where these were significant. Data points are means \pm SE

sides (Fig. 1), and the notable seasonal depression in PAR, which normally occurs during the wet season (May to October), was not as marked. This was reflected in a lack of significant differences in baseline zooxanthella density, chl a pigment concentrations and F_v/F_m values in coral samples collected at the end of the dry season (April) and the end of the wet season

(November). Clearly, while seasonality in environmental factors and associated photo-physiological parameters might be expected at this site, there are circumstances when meteorological and tidal influences combine to reduce this effect. The period 2000 to 2001 was one such example, rendering shallow-water corals in an apparently similar photo-physiological state

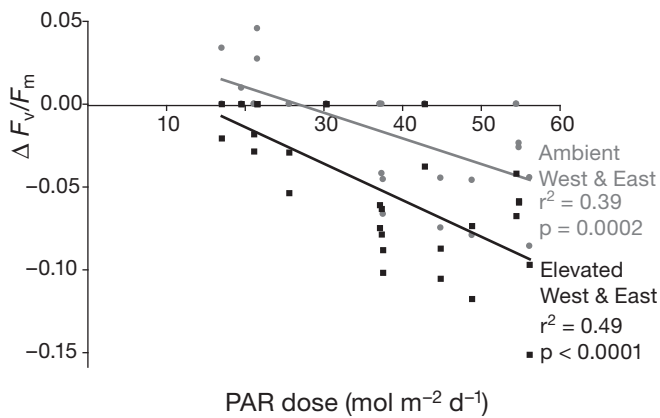


Fig. 4. *Goniastrea aspera*. Relationship between daily photosynthetically active radiation (PAR) dose and change in maximal photochemical yield (F_v/F_m). Data for each treatment from different sides (east and west) have been pooled (see 'Results — Maximal photochemical yield [F_v/F_m])

throughout the year, regardless of slight differences in ambient sea temperatures. In the present experiments, comparison of coral responses to varying PAR dose at different times of the year was also justified by the setting of upper and lower limits (sun and shade experiments) for the solar radiation dose at the same date (February 2000).

Solar radiation (PAR dose) modulated both zooxanthella loss and chronic photo-inhibition (depression in F_v/F_m) at elevated temperatures in the present study. In biological terms, the power relationship between zooxanthella loss and the accumulated PAR dose at elevated temperature (Fig. 2) is a realistic model for *Goniastrea aspera* living on the reef flat, since at the lower experimental PAR doses, these corals were experiencing comparable or more benign conditions than in their natural surroundings. The relationship between PAR dose and zooxanthella loss also corroborates earlier results from much longer-term field studies in which the strongest statistical relationship for zooxanthella loss was found to be with the PAR dose in the 24 h preceding sampling (Brown et al. 1999a). It is also interesting to note, in the present experiments, the large data spread in zooxanthella loss at low PAR doses, which becomes much reduced at higher doses. This effect might be explained in terms of phenotypic plasticity, where cores from different colonies are able to display a wide variation in the effectiveness of their defences at low stress levels, but under more extreme conditions such variation becomes much more restricted as defences are breached and a switch occurs to apoptosis and necrosis. Such generalized organism responses under stress are discussed in detail by Goldring et al. (2006).

PAR dose also had a major effect on reducing F_v/F_m in *Goniastrea aspera* at ambient and elevated temperatures, being more marked for any given PAR dose, at elevated temperature. A similar interaction between temperature and light has been observed by Fitt & Warner (1995), who reported that F_v/F_m in *Montastraea annularis* exposed to 32°C, declined faster when corals were exposed to ambient natural light compared to low light, and also by Jones et al. (1998) working with shaded and illuminated surfaces of *Stylophora pistillata* at 28 and 33°C under varying artificial light. In another experiment, high artificial light (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) had a much greater negative effect on F_v/F_m of 5 species of Indo-Pacific corals maintained at 34°C than medium light (170 $\mu\text{mol m}^{-2} \text{s}^{-1}$) or darkness (Bhagooli & Hidaka 2003). Effects on zooxanthellae isolated from these coral species were similar, but much more pronounced, with reduced F_v/F_m values at high, medium and low (70 $\mu\text{mol m}^{-2} \text{s}^{-1}$) light levels.

There were clear differences in zooxanthella loss between the east and west sides of corals in all experiments, irrespective of time of year, with no significant loss of zooxanthellae in west sides at either ambient or elevated temperatures. East sides of colonies, however, showed significant loss of zooxanthellae in all experiments at elevated temperature throughout the year, confirming their increased susceptibility to bleaching compared with the west cores. In terms of chronic photo-inhibition, cores from both west and east sides showed a significant decline in F_v/F_m at elevated temperatures, though east cores showed a more marked reduction than west at high PAR doses (Fig. 3). At ambient temperatures both east and west cores displayed a reduction in F_v/F_m at the highest PAR doses. East cores, but not the west, also showed a reduction in F_v/F_m at a moderate PAR dose. Taken together these results have interesting implications. Firstly, they confirm the superior tolerance of west sides of corals, over the east sides, to both increased PAR alone, and the combined effects of PAR and elevated temperature, as a consequence of greater exposure of western surfaces of colonies to increased solar radiation, as discussed in Brown et al. (2002a). Secondly, they demonstrate the equal susceptibility of zooxanthellae of both east and west sides to the combined effects of PAR and temperature at high PAR doses, and the superiority of zooxanthellae from west sides when the light stress is only moderate. This pattern of susceptibility differs markedly from that of zooxanthella loss, under the same experimental conditions, where only east sides showed any significant reductions. The explanation probably lies in the fact that F_v/F_m is solely a measure from functioning zooxanthellae, whereas zooxanthella loss is dependent on both the coral host and its symbionts (Gates et al. 1992). The zooxanthellae in *Gonias-*

trea aspera at this site belong to Clade D (Brown et al. 2002a, Douglas 2003), which has already been shown to be particularly temperature tolerant (Rowan 2004). It is clear from the present study that, as well as possessing this background tolerance, zooxanthellae from west sides also have improved photoacclimatory ability compared to those from the east sides of coral colonies. Earlier evidence suggests that this may be achieved, in part, by improved photo-protection through more efficient xanthophyll cycling (Brown et al. 1999b). Thirdly, the results show that in terms of bleaching susceptibility, the coral host plays an important role. Despite zooxanthellae from east and west sides showing equal chronic photo-inhibition at high PAR and combined temperature and PAR stresses, bleaching did not occur on west sides, probably as a result of superior host defences (increased stress proteins and antioxidant enzymes), which have been demonstrated in earlier work (Brown et al. 2002b).

The results of the present study quantify the damaging role of PAR on zooxanthella loss and chronic photo-inhibition in *Goniastrea aspera*, while simultaneously highlighting the protective benefits of regular exposure of corals to sub-lethal doses of solar radiation on bleaching susceptibility. Ultimately the interaction between solar radiation and elevated temperature, and its effect on coral bleaching susceptibility, is complex, involving the duration and degree of these stresses as well as the scope of both the coral host and its symbiotic zooxanthellae to acclimatise to altered environmental conditions.

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