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Diurnal photosynthetic response of the motile symbiotic benthic foraminiferan *Marginopora vertebralis*

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ABSTRACT: Movement of the symbiont-bearing foraminiferan *Marginopora vertebralis* and photophysiological response to diurnal fluctuations in irradiance were investigated in field and laboratory experiments. The abundance of *M. vertebralis* from both light-exposed and sheltered habitats was determined 5 times during the day, from pre-dawn to post-dusk. *M. vertebralis* abundance was significantly higher in sheltered compared to exposed habitats at midday under high irradiance, and this movement enabled the algal symbionts to avoid excessive photoinhibition. The diurnal changes in photosynthetic efficiency were not consistent with the typical midday solar maximum downregulation of photosystem II observed in other photoautotrophs and was likely due to the negatively phototactic capacity of the foraminifera. To confirm the light-dependent movement of foraminifera, individuals in exposed and sheltered habitats were exposed to the photosynthetic inhibitor 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) in the laboratory. The lack of movement in DCMU-exposed specimens confirmed light-dependent movement and subsequent disruption of signalling between the host foraminiferan and the algal symbionts. Analysis of chlorophyll and xanthophyll pigments, as well as symbiont density, indicated that under high irradiance, foraminiferal symbionts have the capacity to reduce light stress by activating photoprotective mechanisms. The negatively phototactic behaviour prevented chlorophyll degradation, symbiont loss and bleaching, suggesting that it is the primary mechanism for controlling light exposure in these foraminifera. This behaviour provides a competitive advantage over other sessile organisms in avoiding photoinhibition and bleaching by moving away from over-saturating irradiance, towards less damaging light fields.

KEY WORDS: Phototaxis · Chlorophyll fluorescence · Symbiotic algae · *Symbiodinium*

INTRODUCTION

Benthic symbiont-bearing foraminifera are single-celled organisms that harbour a variety of groups of endosymbiotic microalgae in their test chambers, including dinoflagellates, diatoms, unicellular chlorophytes, unicellular rhodophytes and cyanobacteria, and are also capable of chloroplast husbandry (Goldstein 1999, Lee 2006). The dominant tropical larger foraminiferan *Marginopora vertebralis* Quoy & Gaimard predominantly hosts several clades of dinoflagellates from the genus *Symbiodinium* (Clades C, F, G, H) (Ross 1972, Pawlowski et al. 2001, Garcia-Cuetos et al. 2005, Pochon & Pawlowski 2006, Lee et al. 2009).

Relationships between larger foraminifera and algal symbionts are varied and complex (Goldstein 1999). The host foraminiferan receives numerous

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benefits from its algal symbionts: photosynthetic energy, enhanced calcification and removal of metabolites (Hallock 1999). In return, foraminifera provide their symbionts with a stable microenvironment and a nutrient supply in the form of dissolved nitrogen and phosphorus (Goldstein 1999). As a result of this symbiotic relationship, benthic larger foraminifera are found in well-lit shallow waters of coral reefs (Nobes et al. 2008). The symbiont-bearing foraminiferan *Marginopora vertebralis* is commonly found on sandy substrates and attached to the calcifying macroalga *Halimeda* (Severin 1987, Sinutok et al. 2011).

Foraminifera have a useful feature not shared by all algal symbiont-bearing organisms in that they are motile. Khare & Nigam (2000) showed that pseudopodially mediated movement of benthic foraminifera on glass varied from 2 to 8 mm h^{-1}. Despite the reliance of algal symbionts on sunlight to obtain energy for photosynthesis and calcification, exposure to high irradiances can lead to reduced photosynthetic efficiency and, potentially, to photoinhibition, similar to algae and higher plants (Franklin et al. 1996, Winters et al. 2003). Nobes et al. (2008) showed no difference in growth rate during exposure to a wide range of irradiances (1200, 375, 60 µmol photons m^{-2} s^{-1}) for the high-light species *Amphistegina* spp. and *Calcarina* spp., while in the low-light species *Heterostegina depressa*, growth rate was highest under low light (60 µmol photons m^{-2} s^{-1}). Nobes et al. (2008) found that in all 3 species, decreasing irradiance caused an increase in the initial slope (α) of electron transport and a decrease in minimum saturating irradiance (I_k), suggesting that these species can rapidly acclimate to changes in light conditions. In contrast, Hallock (1981) showed that the growth rates of the benthic foraminifera *A. lessonii* and *A. lobifera* were greater under higher irradiance (140 µmol photons m^{-2} s^{-1}) compared to low irradiance (32 and 14 µmol photons m^{-2} s^{-1}).

The capacity for movement in response to light (i.e. phototactic behaviour) has been observed in benthic symbiotic foraminifera under various light conditions (Zmiri et al. 1974, Lee et al. 1980, Murray 2006). *Amphistegina lobifera* showed positive phototaxis under low irradiance (1.4 to 13.5 µmol photon m^{-2} s^{-1}) and negative phototaxis under higher irradiances (>150 µmol photons m^{-2} s^{-1}), which may have had the potential to cause photoinhibition (Lee et al. 1980). Foraminifera may therefore be able to avoid photoinhibition by moving away from over-saturating light environments (e.g. uncovered substrate) to areas with more suitable light intensities (e.g. within seagrass or macroalgal foliage) (Lee & Bock 1976, Severin 1987, Murray 2006). Sessile organisms such as corals may respond to higher irradiances by decreasing symbiont density or chlorophyll content to maintain optimum photosynthetic rates (Fagoonee et al. 1999, Fitt et al. 2000, Rodolfo-Metalpa et al. 2008) and by inducing photoprotective mechanisms such as polyp retraction (Brown et al. 2002) and dissipation of excess energy through non-photochemical quenching (NPQ) (Brown et al. 1999, Hill et al. 2012). Over-saturating irradiance can also lead to the expulsion of symbiotic algae from corals or a reduction in photosynthetic pigment concentration, resulting in coral bleaching (Fitt et al. 2001, Hill et al. 2004, Lesser & Farrell 2004). In the foraminiferan *Amphistegina*, high light causes damage to the algal symbionts and results in bleaching (Hallock et al. 2006). The phototactic behaviour of foraminifera provides a competitive advantage over their sessile counterparts by enhancing their ability to cope with variable irradiance. Another factor that influences movement of foraminifera is heterotrophic feeding, where the speed of movement is influenced by temperature and the need to search for food (Gross 2000, Murray 2006). The pseudopodia are used in both gathering food and digestion (Murray 2006). In symbiont-bearing foraminifera, heterotrophic feeding makes an important contribution to the protist's energy requirements, although Röttger et al. (1980) found that *A. lessonii* did not grow in the dark even when it was fed with algae, detritus, bacteria, protozoa and fungi. Along with the findings of Lee et al. (1991), this suggests that larger foraminiferan growth is dependent on light.

When a high level of photosynthetically active radiation (PAR) is applied, downregulation or photoinhibition of the photosynthetic apparatus within the symbiotic algae may occur (Brown et al. 1999, Jones & Hoegh-Guldberg 2001, Hill & Ralph 2005). Downregulation of photosynthesis involves photoprotective processes and can be defined as short-term photoinhibition and the reversible loss of photosynthetic efficiency of photosystem II (PSII) and photosynthetic electron transport rate (Jones & Hoegh-Guldberg 2001, Larkum et al. 2006). Photoprotection can reduce the potential for damage by dissipating excess solar energy as heat via the xanthophyll cycle, a form of NPQ (Demmig-Adams & Adams 1992, Hill & Ralph 2005). In addition, less energy is used in photochemical reactions, which results in decreasing the photosynthetic efficiency of PSII (e.g. maximum quantum yield [F_V/F_M] and effective quantum yield [$\Delta F/F_M'$]) (Hill & Ralph 2005). In comparison, long-term photoinhibition results in irreversible photodamage to PSII and a long-term reduction in F_V/F_M

and requires the resynthesis of damaged photosynthetic proteins (Brown et al. 1999, Jones & Hoegh-Guldberg 2001, Hill & Ralph 2005, Hill et al. 2011).

We aimed to investigate foraminiferal movement in response to diurnal fluctuations in light intensity and identify associated changes in the photosynthetic response of symbiotic algae. We assessed the capacity for movement in benthic larger foraminifera, quantified the degree of potential stress and investigated whether migration was dependent on light. Field observations and manipulative experiments were performed. The photosynthetic inhibitor 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) was used to eliminate the photosynthetic function from symbionts to test the hypothesis that foraminiferal movement is controlled by symbiont photosynthesis.

MATERIALS AND METHODS

Field observations

Field observations were carried out at the Heron Island reef flat on the southern Great Barrier Reef, Australia (151° 55′ E, 23° 27′ S), in November 2009. To observe the movement of *Marginopora vertebralis* in their natural habitat, the proportion of foraminifera exposed to direct irradiance was assessed to determine the number of individuals that moved to exposed or sheltered locations. Exposed foraminifera were defined as individuals living on the surface of a *Halimeda opuntia* thallus and exposed to direct sunlight. Sheltered foraminifera were those individuals living within the shaded, cryptic habitat of an *H. opuntia* thallus. The abundance of exposed and sheltered individuals was determined in 10 quadrats (10 × 10 cm) 5 times over the day, from pre-dawn to post-dusk (04:30, 09:00, 12:00, 15:00 and 19:00 h), for 3 consecutive days. Water temperature and light intensity at the sampling depth in the subtidal reef flat was recorded every 10 and 5 min, respectively, for 3 consecutive days using submersible data recorders (Odyssey). Relative to the position of the foraminifera, the high tides during field observations occurred at 08:45 and 20:47 h at 2.9 and 2.1 m depth, respectively, and the low tides occurred at 02:14 and 15:15 h at 0.3 and 0.6 m depth, respectively.

To investigate the photosynthetic performance of the exposed and sheltered foraminifera in the field, rapid light curves (RLCs) were performed at the same time each day, using a 6 mm diameter fibre-optic on a pulse-amplitude modulated (PAM) fluorometer (DIVING-PAM, Walz) (n = 5). RLCs with 10 increasing actinic light intensities (0, 44, 78, 112, 153, 214, 303, 435, 634 and 950 µmol photons m^{-2} s^{-1}) were applied, with 0.8 s saturating flashes (>4500 µmol photons m^{-2} s^{-1}) between each actinic light intensity every 10 s. Effective quantum yield of PSII ($\Delta F/F_M'$; Schreiber 2004), maximum relative electron transport rate ($rETR_{max}$), minimum saturating irradiance (I_k) and initial slope (α) of RLCs were calculated using the curve fitting protocols outlined in Ralph & Gademann (2005) with SigmaPlot Version 10.0 (SPSS).

Laboratory experiment

Laboratory experiments were run to determine whether foraminiferal movement is controlled by algal symbiont photosynthesis. *Marginopora vertebralis* individuals were collected by hand from the Heron Island reef flat and maintained in outdoor 1 l aquaria with flow-through seawater (pH 8.1, 26°C, salinity 33). The movement of foraminifera was investigated in 4 experimental treatments: exposed, sheltered and with and without the photosynthetic inhibitor DCMU (0.25 µM). Four independent tanks were used for each treatment, and 10 foraminifera were placed in each independent tank, which was gently bubbled using pipette tips connected to air pumps. To test whether foraminiferal movement was controlled by symbiont photosynthetic activity, DCMU was added to the seawater to eliminate photosynthetic function in the symbiotic algae (ter Kuile et al. 1989). In the presence and absence of DCMU, foraminifera in exposed treatments were placed on a sandy substrate, while those in the sheltered treatments were given access to thalli of *Halimeda opuntia* for shading. The horizontal migration (number of foraminifera exposed to direct sunlight in each treatment) was determined 5 times per day, from pre-dawn to post-dusk (04:30, 09:00, 12:00, 15:00 and 19:00 h). Water temperature and light intensity were recorded in each tank, as detailed above for field observations.

PSII photochemical efficiency was determined through measures of chlorophyll *a* fluorescence using a DIVING-PAM fluorometer. Steady state light curves (SSLCs; Kramer et al. 2004, Sinutok et al. 2011) with 1 irradiance step (372 µmol photons m^{-2} s^{-1}) applied for 300 s and 0.8 s saturating flashes (>4500 µmol photons m^{-2} s^{-1}) every 30 s were performed at 04:30, 09:00, 12:00, 15:00 and 19:00 h after 10 min of dark adaptation. The maximum quantum yield of PSII (F_V/F_M), effective quantum yield of PSII (Y(II)), capacity for photoprotection (non-photochem-

ical quenching [Y(NPQ)] and level of photoinhibition (non-regulated heat dissipation [Y(NO)] were determined from each SSLC (Kramer et al. 2004, Ulstrup et al. 2006, Hill et al. 2012).

Photosynthetic pigment concentration from the foraminiferal symbionts (chlorophylls *a* and c_2) was determined using the standard spectrophotometric method of Ritchie (2006) at the end of the 3 d experiment. Chlorophylls *a* and c_2 were extracted by homogenising samples in 3 ml of 90% acetone at 4°C for 24 h. Samples were centrifuged at 1500 *g* for 10 min, and the supernatant was placed into a quartz cuvette in a spectrophotometer (Varian), with absorbance measured at 630 and 664 nm.

Four foraminifera from each treatment were collected for initial and final xanthophyll pigment determinations at 04:30 h on the first day and at 19:00 h on the final day (Day 3) and were immediately snap frozen and stored in liquid nitrogen. Reverse-phase HPLC was used to detect the concentration of the xanthophyll pigments diatoxanthin (Dt) and diadinoxanthin (Dn) as described in Hill et al. (2012). Dn is de-epoxidised to Dt, which is a photoprotective mechanism to avoid long-term photodamage (Falkowski & Raven 2007). Xanthophylls were extracted by crushing the samples (n = 4) with a mortar and pestle in 100% acetone, leaving for 24 h at 4°C and filtering through GF/C filter paper (Whatman) and a 0.2 µm PTFE 13 mm syringe filter (MicroAnalytix). The extracted samples were stored in amber-coloured HPLC glass vials at −80°C overnight (Van Heukelem & Thomas 2001). The HPLC consisted of a pump system with inline degasser, programmable autoinjector, temperature-controlled autosampler, temperature-controlled column oven compartment, photodiode array detector and Empower Pro software (Waters). The pigments were detected using a photodiode array detector at 450 nm and 665 nm with 20 nm bandwidth (Van Heukelem & Thomas 2001). Calibration and quality assurance were performed by external calibration standards (DHI). Peaks were integrated using Empower Pro software with manual confirmation. The de-epoxidation state of xanthophyll pigments was calculated as the relative proportion of Dt to the total xanthophyll pool (Dt+Dn) (Ulstrup et al. 2008, Hill et al. 2012). Dt, Dn and the total xanthophyll pool (Dt+Dn) were expressed as weight per fresh weight (µg g^{-1}).

At the end of the experiment, algal symbionts were isolated from the foraminifera by crushing the foraminiferal test with a glass rod in 3 ml of 0.2 µm filtered seawater (n = 4). Symbiont density was determined as the number of cells per mm^2 using a haemocytometer. Four replicate counts were made per sample and were averaged for each replicate.

Statistical analysis

To determine any significant differences among treatments in foraminiferal abundance, number of foraminifera in sun-exposed regions and chlorophyll fluorescence parameters (F_V/F_M, Y(II), Y(NPQ), Y(NO), $\Delta F/F_M'$, $rETR_{max}$, I_k, α) over time, repeated-measures ANOVA tests were performed. One-way ANOVA tests were used to compare treatments at the initial and final time points for chlorophyll *a* and c_2 concentrations, xanthophyll pigments and ratios, and symbiont density (SPSS Version 17). All tests were performed with a significance level of 95%, and Tukey's honestly significant difference post hoc tests were used to identify the statistically distinct groups. If data did not meet the assumptions of normality (Kolmogorov-Smirnov test) and equal variance (Levene's test), the data were transformed using $\log_{10}$ or square root.

RESULTS

Field observations

Irradiance on the Heron Island reef flat from 16 to 18 November 2009 reached a maximum of 1117 ± 46 µmol photons m^{-2} s^{-1} at solar noon (12:53 h). The sea surface temperature fluctuated over the day, with a low of 23.6 ± 1°C at pre-dawn and a maximum of 28.8 ± 0.5°C at 13:05 h (all means ± SE; Fig. 1a). Observations of the number of sun-exposed versus sheltered foraminifera in the field revealed significant differences over the sampling time ($p = 0.027$; Fig. 1b). Foraminifera were most abundant in sheltered habitats at 12:00 and 15:00 h (1.5 ± 0.2 and 1.6 ± 0.2 cm^{-2}; $p = 0.002$ and 0.001; Fig. 1b), while at 04:30 h, foraminifera were most abundant in sun-exposed areas when the habitat experienced very low irradiances (at or close to 0 µmol photons m^{-2} s^{-1}) ($p = 0.005$). The number of individuals in the sun-exposed habitat decreased compared to sheltered habitats at 12:00 and 15:00 h (0.7 ± 0.1, 0.6 ± 0.1 cm^{-2}).

RLCs (all means ± SE) revealed that the highest initial quantum yield measurement of PSII occurred before sunrise in the foraminifera located on exposed surfaces of *Halimeda* at 04:30 h (0.618 ± 0.017), and the lowest occurred at 09:00 h (0.441 ± 0.035) ($p < 0.001$; Fig. 2a). $\Delta F/F_M'$ in sheltered foraminifera sig-

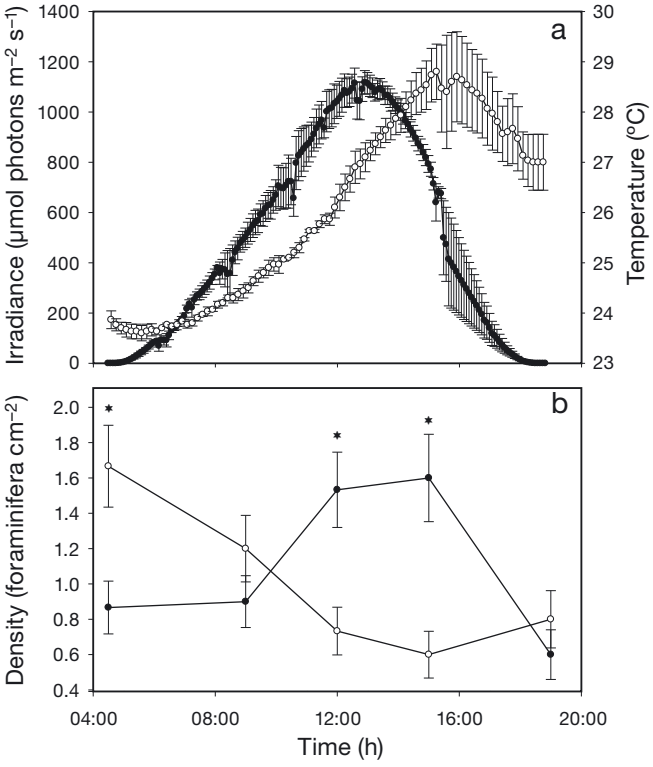

Fig. 1. (a) Irradiance (●; µmol photon m^{-2} s^{-1}) and seawater temperature (○; °C) on the Heron Island reef flat from 04:30 to 19:00 h. Means (±SE; n = 3) from 3 consecutive days. (b) Density (ind. cm^{-2}) of exposed (○) and sheltered (●) foraminifera on the Heron Island reef flat from 04:30 to 19:00 h. Means ± SE (n = 10). *: significant difference

nificantly decreased from 0.663 ± 0.018 at 04:30 h to 0.566 ± 0.025 at 09:00 h ($p < 0.001$; Fig. 2a). At 09:00 and 12:00 h, $\Delta F/F_M'$ was significantly lower in exposed individuals than in those in sheltered habitats ($p < 0.001$; Fig. 2a). There was no significant difference in $rETR_{max}$ among times of day within either habitat ($p > 0.05$; Fig. 2b), although a significantly higher $rETR_{max}$ was observed in sheltered foraminifera (12.2 ± 2.2 µmol electrons m^{-2} s^{-1}) than in those exposed to direct sunlight (5.5 ± 1.4 µmol electrons m^{-2} s^{-1}) at 09:00 h ($p < 0.05$; Fig. 2b). Minimum saturating irradiance (I_k) was not significantly different between exposed and sheltered foraminifera (88 ± 15 compared to 129 ± 10 µmol photons m^{-2} s^{-1}), except at 09:00 h, where sheltered individuals had a higher I_k (182 ± 32 µmol photons m^{-2} s^{-1}) compared to those exposed to direct sunlight (91 ± 22 µmol photons m^{-2} s^{-1}; Fig. 2c). Initial slope (α) was significantly greater for sheltered foraminifera at all time points except 15:00 h ($p = 0.002$; Fig. 2d). In both exposed and sheltered foraminifera, significantly higher α values were found at 15:00 h compared to other time points (Fig. 2d). There were no significant differences in relative electron transfer rate (rETR) between sheltered and exposed foraminifera at 04:30, 15:00 and 19:00 h ($p > 0.05$; Fig. 3a,d,e). There was significantly higher rETR in sheltered foraminifera at 09:00 h ($p = 0.038$; Fig. 3b). Interestingly, a greater rETR was found in exposed foraminifera at 12:00 h ($p = 0.021$; Fig. 3c).

Laboratory experiment

To investigate the dependence of foraminiferal movement on symbiont photosynthesis, the horizontal movement of foraminifera in both the sun-exposed and sheltered treatments (with and without DCMU) was recorded. The water temperature fluctuated over the day, with a low of 24.1 ± 0.1°C at predawn and a maximum of 27.1 ± 0.1°C at 11:15 h, and irradiance reached a maximum of 1580 ± 67 µmol photons m^{-2} s^{-1} at 09:23 h (Fig. 4a). The shade provided by *Halimeda* thalli reduced ambient irradiance by 70 to 90%. The number of foraminifera exposed to the sun in the sheltered treatment (without DCMU) significantly decreased at 09:00 h from 04:30 h ($p = 0.001$), reaching the lowest abundance at 12:00 and 15:00 h. A significant increase was observed at 19:00 h compared to 12:00 and 15:00 h ($p < 0.001$; Fig. 4b); however, the number of foraminifera exposed at 19:00 h was still significantly lower than at 04:30 h. In comparison, when treated with DCMU, the number of sun-exposed foraminifera in the sheltered treatment declined after 04:30 h and showed no subsequent change up to 19:00 h even though movement within the shaded habitat was observed (Fig. 4b). Foraminifera were also observed to move in both exposed treatments (with and without DCMU); however, as no source of shade was provided, the number exposed to the sun remained constant and was significantly higher than the counts in the sheltered treatments ($p < 0.001$).

F_V/F_M and Y(II) showed the same response in diurnal oscillation in both exposed and sheltered treatments within each of the 2 DCMU treatments. In the absence of DCMU, F_V/F_M and Y(II) significantly decreased from 04:30 to 12:00 h ($p < 0.001$; Fig. 5a,b) and showed a significant recovery by 15:00 h. F_V/F_M and Y(II) were close to zero and constant over time in the presence of DCMU ($p > 0.05$; Fig. 5a,b). Within the + and − DCMU treatments, there were no significant differences in Y(NO) and Y(NPQ) between both exposed and sheltered treatments ($p > 0.05$; Fig. 5c,d). However, Y(NO) was higher and Y(NPQ) was lower in DCMU-treated foraminifera ($p < 0.001$;

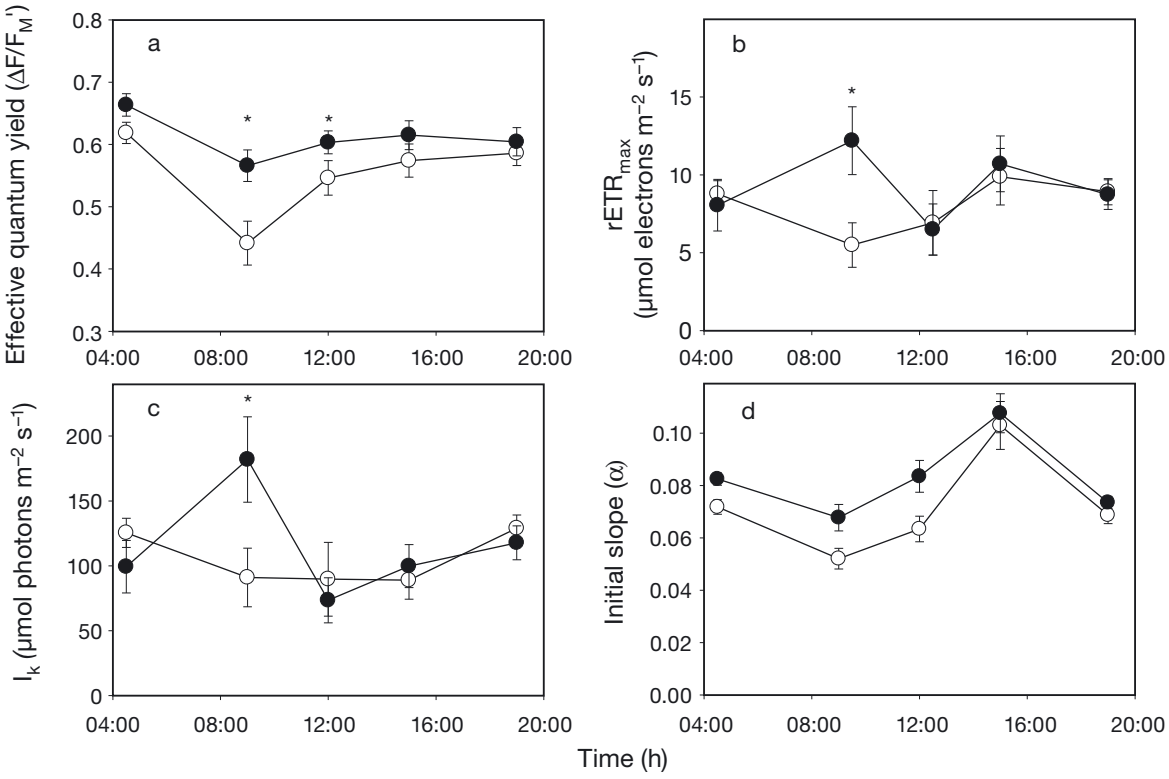

Fig. 2. (a) Effective quantum yield of PSII ($\Delta F/F_M'$), (b) maximum relative electron transport rate ($rETR_{max}$; µmol electrons m^{-2} s^{-1}), (c) minimum saturating irradiance (I_k; µmol photons m^{-2} s^{-1}) and (d) initial slope of rapid light curves (α) of exposed (O) and sheltered (●) foraminifera on the Heron Island reef flat from 04:30 to 19:00 h. Means ± SE, n = 5. *: significant difference

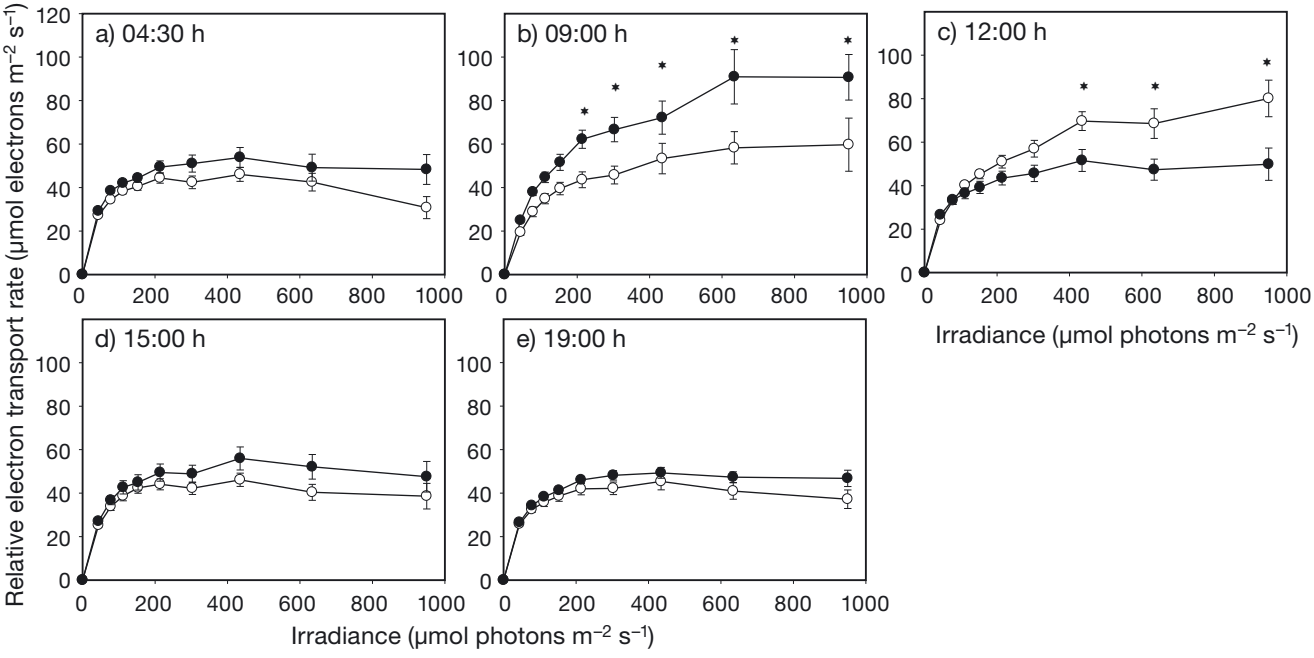

Fig. 3. Rapid light curves (relative electron transport rate vs. irradiance) from exposed (O) and sheltered (●) foraminifera at 10 irradiance steps (0 to 950 µmol photons m^{-2} s^{-1}) on the Heron Island reef flat from (a) 04:30 h, (b) 09:00 h, (c) 12:00 h, (d) 15:00 h and (e) 19:00 h. Means ± SE, n = 5. *: significant difference

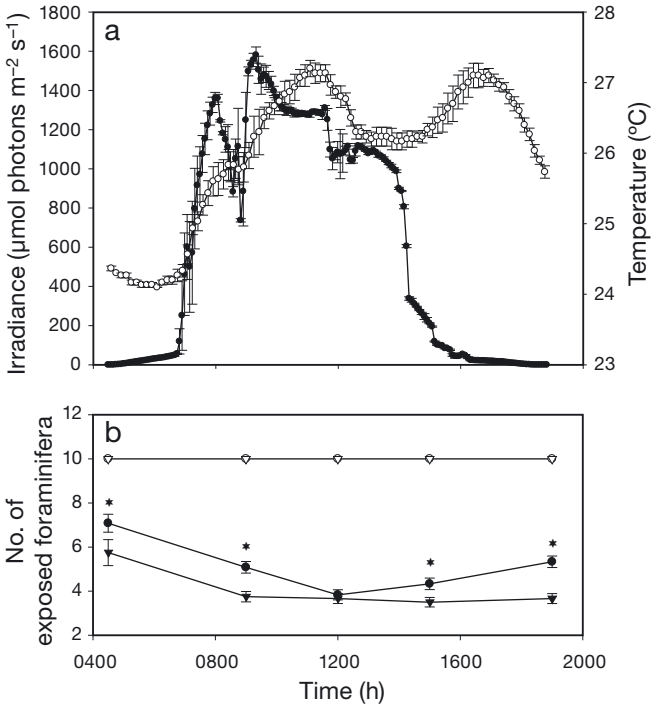

Fig. 4. (a) Irradiance (●; µmol photons m^{-2} s^{-1}) and seawater temperature (○; °C) from 04:30 to 19:00 h in the laboratory experimental treatments. Means (± SE; n = 3) from 3 consecutive days. (b) Number of foraminifera in sun-exposed (○), sheltered (●), sun-exposed with 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) (▽) and sheltered with DCMU (▼) treatments from 04:30 to 19:00 h. Means ± SE, n = 4). *: significant difference

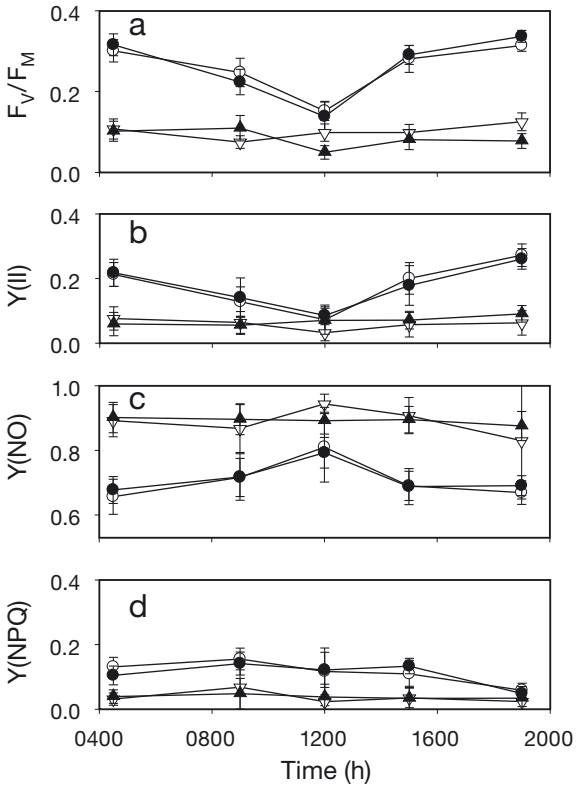

Fig. 5. (a) Maximum quantum yield of PSII (F_V/F_M), (b) effective quantum yield of PSII, Y(II), (c) non-regulated heat dissipation yield, Y(NO), and (d) non-photochemical quenching yield, Y(NPQ), from foraminifera in sun-exposed (○), sheltered (●), sun-exposed with 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) (▽) and sheltered with DCMU (▼) treatments from 04:30 to 19:00 h. Means ± SE, n = 4

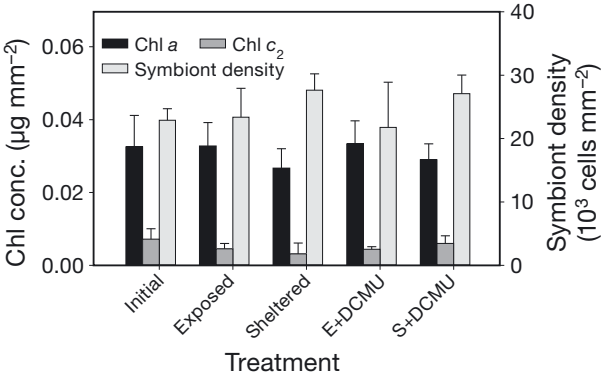

Fig. 6. Chlorophyll *a* and c_2 concentrations (Chl conc.) and symbiont density in foraminifera before experimentation (initial) and at the end of the experiments on Day 3 in sun-exposed, sheltered, sun-exposed with 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) (E+DCMU) and sheltered with DCMU (S+DCMU) treatments. Means + SE, n = 4

Fig. 5c,d). No significant change occurred over time in either Y(NO) or Y(NPQ) ($p > 0.05$; Fig. 5c,d).

Chlorophyll *a* and c_2 concentrations within *Marginopora vertebralis* and algal symbiont density were constant (over the 3 d) in all 4 treatments (± shelter, ± DCMU; $p > 0.05$; Fig. 6). In addition, measurements of xanthophyll pigments also revealed no significant change in Dt/(Dt+Dn) between the initial (Day 1 at 04:30 h) and final (Day 3 at 1900 h) time points in exposed and sheltered foraminifera in the absence of DCMU ($p > 0.05$; Fig. 7a). However, a significantly lower Dt/(Dt+Dn) was observed in foraminifera exposed to DCMU for 3 d compared to the initial measurement ($p < 0.001$; Fig. 7a). A significantly greater Dt+Dn pool was found in exposed foraminifera on Day 3 without DCMU, compared to all other treatments and the initial measurement ($p = 0.031$; Fig. 7a), while there were no significant differences in the Dt+Dn pool between initial measurements and other treatments ($p > 0.05$; Fig. 7a). The concentration of each individual pigment was greater in exposed foraminifera without DCMU, compared to initial measurements ($p = 0.029$ and 0.038 for Dt and Dn, respectively; Fig. 7b). Individual pigment concentrations within each treatment were otherwise stable ($p > 0.05$; Fig. 7b), and Dn was the main contributor to the increase in the total pool size.

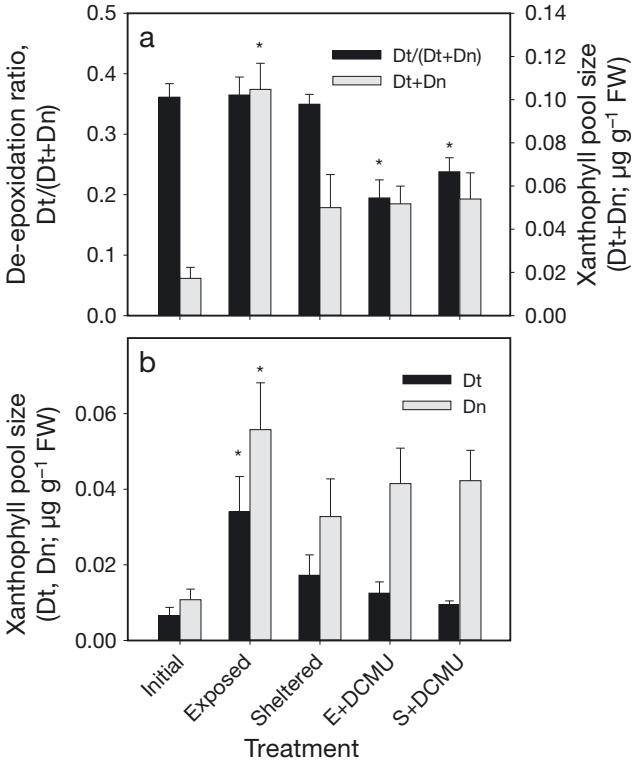

Fig. 7. (a) De-epoxidation ratio, i.e. diatoxanthin to total pool of diatoxanthin and diadinoxanthin; Dt/(Dt+Dn), and total pool size of diatoxanthin and diadinoxanthin (Dt+Dn; µg g^{-1} fresh weight, FW). (b) Diatoxanthin and diadinoxanthin (µg g^{-1} FW) from foraminifera initially and in sun-exposed, sheltered, sun-exposed with 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) (E+DCMU) and sheltered with DCMU (S+DCMU) treatments. Means + SE, n = 4. *: significant difference

DISCUSSION

Our results demonstrate for the first time the capacity for movement in the benthic symbiotic foraminiferan *Marginopora vertebralis* in response to diurnal changes in irradiance. This movement was directed and had beneficial effects on symbiont photosynthetic performance. From observations in the field, *M. vertebralis* abundance was found to be significantly higher in sheltered areas at midday under high irradiance, indicating that an over-excitation of the photosynthetic light reactions is likely to be the main driver influencing this phototactic movement of benthic symbiotic foraminifera. Although the speed of movement in foraminifera is influenced by temperature (Gross 2000) and our study did not measure the rate of movement, the temperature and number of exposed foraminifera in the laboratory (Fig. 4) may indicate that the diurnal movement of foraminifera observed in our study is independent of temperature.

The effective quantum yield of PSII ($\Delta F/F_M'$) in exposed *Marginopora vertebralis* declined by 30% when the light intensity reached 500 µmol photons m^{-2} s^{-1} at 09:00 h, indicating a reduction in photosynthetic efficiency due to high irradiance (White & Critchley 1999, Ralph & Gademann 2005). However, $\Delta F/F_M'$ in exposed individuals significantly increased at 12:00 and 15:00 h, despite increasing incident irradiance. This is likely to be a consequence of the motile capacity of *M. vertebralis*, with the possibility that individuals measured in exposed areas may have recently moved into this space and not received the full morning of direct sunlight. With a lower cumulative photon dose, the individuals that only recently entered sun-exposed habitats would have had less photoinhibition or downregulation of photosynthesis and could thus be operating with a higher photosynthetic efficiency. Similar to the exposed individuals, $\Delta F/F_M'$ in sheltered ones declined at 09:00 h, indicating that sheltered individuals experienced some, but less severe, light stress than the exposed ones. The decline in $\Delta F/F_M'$ in sheltered *M. vertebralis* at 09:00 h could also be due to some of the exposed individuals moving to sheltered regions after 09:00 and 12:00 h, but tracking of individuals would be needed to confirm this.

Understanding the light history and influence of photosynthesis in foraminiferal symbionts could identify associated changes in the photosynthetic response of symbiotic algae. RLCs have been used to quantify the light history and acclimation state of photosynthetic marine phototrophs (Ralph & Gademann 2005). In general, low-light-adapted and high-light-adapted sessile organisms (such as seagrass, macroalgae and coral) show distinctly different patterns in RLC parameters (I_k, α, $rETR_{max}$), with high-light-adapted phototrophs exhibiting a higher I_k, higher rETR and lower α due to a slower decline in $\Delta F/F_M'$ with increasing light intensity (Ralph & Gademann 2005). The minimum saturating irradiance (I_k; Ralph & Gademann 2005) in our study (60 to 210 µmol photons m^{-2} s^{-1}) was higher compared to the benthic diatom-bearing foraminifera *Amphistegina* spp., *Calcarina* spp. and *Heterostegina depressa* from Edward Island, Australia (Nobes et al. 2008), as well as the chlorophyte endosymbiont foraminifera *Archaias angulatus* Fichtel and Moll and *Cyclorbiculina compressa* d'Orbigny from the Conch and Tennessee reefs in the Florida Keys, United States (Walker et al. 2011). In Nobes et al. (2008), the benthic diatom-bearing foraminifera received a midday irradiance of 1200 µmol photons m^{-2} s^{-1} and exhibited an I_k of 43 µmol photons m^{-2} s^{-1}, while the

chlorophyte endosymbiont foraminifera *A. angulatus* and *C. compressa* from 1 to 2 m and 10 to 30 m depth, respectively, received a midday irradiance of 1200 to 1500 µmol photons m^{-2} s^{-1}, with an I_k of 85.7 and 122, respectively (Walker et al. 2011). This indicates that the dinoflagellate-bearing foraminiferan *Marginopora vertebralis* from Heron Island (0.3 to 2 m depth; maximum irradiance 1163 µmol photons m^{-2} s^{-1}) was photoadapted to a higher light intensity. Another study which observed the benthic diatom-bearing foraminifera *Baculogypsina sphaerulata* Parker and Jones and *Calcarina gaudichaudii* d'Orbigny and the dinoflagellate-bearing foraminiferan *M. kudakajimensis* Gudmundsson from a nearshore, intertidal reef flat at Ikei Island (Ryukyu Island, Japan) demonstrated that the algal symbionts were photoadapted to high light and did not experience photoinhibition up to irradiances of 1500 µmol photons m^{-2} s^{-1} (Fujita & Fujimura 2008). These differences could be related to variability in morphology (thickness of the test), light reflection of the test (porcelaneous versus hyaline tests), light history (deeper versus shallower species), migration behaviour (movement rate) and symbiont consortium (diatoms versus dinoflagellates) (Röttger & Krüger 1990, Fujita 2004, Nobes et al. 2008). High-light adaptation enables a greater capacity to cope with high light intensities (Ralph & Gademann 2005) and results in smaller and slower photoinhibitory effects (Shick et al. 1995) and faster recovery (Henley et al. 1991, Hanelt et al. 1993).

The diurnal pattern in $\Delta F/F_M'$ observed in *Marginopora vertebralis* during our study was not consistent with the more commonly observed solar maximum downregulation of PSII photochemical efficiency seen in other phototrophs (Häder et al. 1999, Winters et al. 2003). Instead, we found some recovery of $\Delta F/F_M'$ at midday, where the maximum light intensity occurred. We suggest this unusual response arose due to the capacity for movement in foraminifera. This ability is likely to provide a means to reduce the effect of light stress by moving away from direct sunlight once irradiance becomes over-saturating. In addition, because the same individuals were not measured at each time of sampling, at 12:00 h, those which recently moved into sunlight would have had a higher photochemical efficiency compared to individuals which had received direct sunlight for the whole morning. In the laboratory experiment, however, the downregulation of photochemistry was observed in both the exposed and sheltered treatment, as significant reductions in photosynthetic efficiency [F_V/F_M and Y(II)] were found at midday, when high irradiance occurred (Fig. 5a,b). The recovery of F_V/F_M and Y(II) in the afternoon, when irradiance declined, indicated that the symbionts of *M. vertebralis* can recover from saturating irradiances by activating photoprotective mechanisms.

To confirm that light-dependent movement occurs in *Marginopora vertebralis*, we recorded the location of individuals in aquaria from sun-exposed and sheltered treatments. When provided with shelter in *Halimeda* thalli, individuals moved horizontally into shaded areas once irradiance exceeded 1400 µmol photons m^{-2} s^{-1}. Once irradiance dropped below 20 µmol photons m^{-2} s^{-1} at 19:00 h, individuals moved into exposed areas. It is likely that individuals moved into the shaded areas to avoid over-saturating light that could cause photoinhibition, which may result in bleaching (Talge & Hallock 2003). Chlorophyll concentration and symbiont density in foraminifera are influenced by temperature, pH, spectral quality and the quantity of PAR (Williams & Hallock 2004, Schmidt et al. 2011, Sinutok et al. 2011, Uthicke et al. 2012). Exposure to high light intensity alone may also lead to bleaching (Talge & Hallock 2003). As the endosymbionts play a vital role in calcification and growth of the host, expulsion of endosymbionts and bleaching would constitute a negative effect to host condition and potentially result in mortality. However, our results showed that chl *a* and c_2 concentrations and symbiont density were constant over all treatments, suggesting that no chlorophyll degradation, symbiont loss or bleaching occurred (Fig. 6). Foraminiferal movement is also known to occur during heterotrophic feeding activity (Gross 2000, Murray 2006). Although feeding was not quantified in these experiments, the search and detection of food on *Halimeda* surfaces may have been an additional factor, although secondary to irradiance, as this involved the movement of individuals towards *Halimeda* thalli.

The exposed and sheltered *Marginopora vertebralis* treated with the photosynthetic inhibitor DCMU did not show significant movement during the day except in the sheltered treatment from 04:30 to 09:00 h, where +DCMU individuals moved into shade. Adding DCMU blocks the electron transport in PSII (Ridley 1977), so that photosynthesis in the algal symbionts is inhibited. There was some movement at dawn before complete PSII inhibition occurred, but once PSII was damaged due to the presence of the DCMU in light (Ridley 1977), then movement ceased. The lack of movement between the sheltered and exposed areas once photosynthesis was inhibited would indicate that there was light-driven communication between the symbiotic partners and that the host movement was tightly coupled to

photosynthesis. We therefore suggest that host behaviour can be influenced by the photosynthetic activity of the algal symbionts. Our study is consistent with Zmiri et al. (1974), who observed that no negative phototactic responses in *Amphistegina radiata* occurred under low-light conditions (<2 µmol photons m^{-2} s^{-1}). Positive and negative phototaxis was also observed in *A. lobifera* when exposed to low light (1.35 to 13.5 µmol photon m^{-2} s^{-1}) and higher light levels (>150 µmol photons m^{-2} s^{-1}), respectively (Lee et al. 1980). It has been suggested that phototactic behaviour is the primary mechanism for modulating light exposure in symbiont-bearing foraminifera (Fujita 2004, Williams & Hallock 2004). In the symbiont-bearing foraminifera *Peneroplis antillarum*, *P. planatus*, *Sorites orbiculus* and *Neorotalia calcar*, phototactic behaviour within a certain range of light intensity has been suggested to play a role in the small-scale distribution across a reef, with foraminifera shifting position to gain an optimal light environment for the algal symbionts (Fujita 2004). This behaviour provides an advantage in avoiding photoinhibition and bleaching by moving away from oversaturating irradiance to more optimal light fields or increasing light availability when light conditions are sub-saturating.

Adding DCMU caused a reduction in de-epoxidation in both exposed and sheltered treatments because a proton gradient, which is an important process in xanthophyll cycle activation, was not present across the thylakoid membranes (Ridley 1977). The proportion of Dt to the total xanthophyll pool (Dt+Dn) shows the de-epoxidation of xanthophylls, Dn to Dt, which is a photoprotective mechanism to avoid long-term photodamage (Falkowski & Raven 2007). Our result showed that there were no significant differences in the degree of de-epoxidation between exposed and sheltered treatments and initial measurements. This may be explained by the time of sample collection for HPLC pigment analysis (04:30 and 19:00 h), which may not have detected any midday, high-light-induced de-epoxidation of xanthophyll pigments. However, the total quantity of xanthophyll pigments (Dt+Dn) was significantly higher in exposed *Marginopora vertebralis* compared to sheltered ones and the initial pool (Fig. 7a,b). The increase in the xanthophyll pools was caused by increases in both Dt and Dn, indicating that light stress induces the synthesis of photoprotective pigments as a mechanism for photoprotection. The symbionts of *M. vertebralis* therefore have the capacity to reduce the photosynthetic pressure from saturating irradiances by activating photoprotective mechanisms.

Our results indicated that the phototactic behaviour in foraminifera provides a competitive advantage over co-existing sessile coral reef organisms (such as coral and macroalgae) by enhancing their ability to cope with over-saturating irradiance and adjusting their light environment. By attaching to macroalgae (Hallock 1981) or seagrasses (Severin 1987), foraminifera can move upward to the top of the plants when requiring more light (positive phototaxis) and move downward or horizontally to shaded areas to avoid excess light (negative phototaxis). This behaviour would help avoid long-term photoinhibition, loss of photosynthetic pigments and digestion of zooxanthellae from the foraminiferal host (bleaching) that could occur under prolonged high-light stress (Talge & Hallock 2003). In addition, by harbouring a mixed community of endosymbionts which can vary their photophysiology and susceptibility to bleaching under different light and temperature conditions (e.g. *Symbiodinium* sp. Clades A, C, D, F, G, H; Garcia-Cuetos et al. 2005, Pochon & Pawlowski 2006, Ulstrup et al. 2008, Fay et al. 2009), the phototactic behaviour along with the mixed community of endosymbionts would provide enhanced growth and fitness of the holobiont in shallow coral reef habitats (Hallock 2000). We suggest that the motility of the benthic symbiotic foraminiferan *Marginopora vertebralis* is light related and controlled by the photophysiology of the symbiont. Therefore, the phototactic behaviour is the primary mechanism for modulating the light exposure in symbiont-bearing foraminifera and provides benefits to the foraminiferan host.

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