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RESEARCH ARTICLE

Adaptation strategies of the corallimorpharian *Rhodactis rhodostoma* to irradiance and temperature

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Abstract Corallimorpharians may dominate some habitats on coral reefs and compete with stony corals for access to light, yet little is known concerning their photosynthetic traits. At Eilat in the northern Red Sea, we observed that the abundance of individuals of the corallimorpharian *Rhodactis rhodostoma* decreased significantly with depth on the reef slope. Field and laboratory experiments revealed that they employ several mechanisms of photoadaptation to high irradiance on the shallow reef flat. Their endosymbiotic microalgae (zooxanthellae) varied significantly in both abundance and chlorophyll content with level of irradiance. Use of a diving pulse amplitude modulated fluorometer revealed that the zooxanthellae of *R. rhodostoma* effectively disperse excess light energy by expressing significantly higher values of non-photochemical quenching and maximum excitation pressure on photosystem II when experimentally exposed to high light (HL) versus low light (LL). Host corallimorpharian tissues mediated this response by shielding the algal symbionts from high irradiance. The endoderm of host tentacles thickened significantly and microalgal cells were located further from the mesoglea in HL than in LL. The clades of zooxanthellae hosted by the corallimorpharians also varied with depth. In shallow water, all sampled individuals hosted clade C zooxanthellae, while in deep water the majority hosted clade D. The photosynthetic output of individuals of *R. rhodostoma* was less affected by HL than was that of a stony coral examined. When exposed to both high temperature (HT) and HL, individuals of *R. rhodostoma* reduced their maximum quantum yield, but not when exposed to HL at low temperature (LT). In contrast, colonies of the scleractinian coral *Favia favus* reduced their photosynthetic output when exposed to HL in both temperature regimes. After 2 weeks of HT stress, *R. rhodostoma* polyps appeared to bleach completely but re-established their zooxanthella populations upon return to ambient temperature. We conclude that mechanisms of photoadaptation to high irradiance employed by both the endosymbiotic zooxanthellae and host corallimorpharians may explain in part the abundance of *R. rhodostoma* on some shallow reef flats. The ability to survive for weeks at HT while bleached also may allow corallimorpharians to repopulate shallow reef areas where scleractinians have been killed by thermal stress.

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Introduction

Corallimorpharians occur in a wide range of marine habitats and may dominate hard substrata in both

temperate (Chadwick 1991) and tropical regions (den Hartog 1980). On coral reefs, they form aggregations at depths of up to 65 m (S. Einbinder, personal communication) but highest abundances typically occur near the water surface (<0.5 m depth, den Hartog 1980; Chadwick-Furman and Spiegel 2000; Muhando et al. 2002). Some corallimorpharians replicate asexually, aggressively damage competitors, and withstand physical disturbances better than do stony corals (Chadwick 1991; Muhando et al. 2002). Due in part to these traits, they may rapidly occupy recently opened space following natural and anthropogenic disturbances on coral reefs (den Hartog 1977; Langmead and Chadwick-Furman 1999; Kuguru et al. 2004). As such, chronically damaged coral reefs may become dominated by some opportunistic species of corallimorpharians.

Anatomical and molecular evidence reveals that members of the order Corallimorpharia (Cnidaria: Anthozoa) are closely related to scleractinian corals (Daly et al. 2003) and may have originated due to skeletal loss by some scleractinians (Medina et al. 2006). However, while numerous studies exist on biochemical and physiological responses to environmental stressors in some orders of anthozoans (reviewed in Baker 2003), similar responses of corallimorpharians are poorly understood. Like many marine invertebrates, some corallimorpharians harbor endosymbiotic dinoflagellate algae (zooxanthellae) (den Hartog 1980; Hamner and Dunn 1980; LaJeunesse 2002). Zooxanthellae play a vital role in host nourishment via translocation of photosynthates (Muscatine et al. 1981). Zooxanthellae comprise many strains or species that belong to eight major clades and exhibit a range of physiological responses and tolerances (reviewed in Coffroth and Santos 2005). The *Symbiodinium* clade(s) that an organism harbors may affect its distribution, reaction to extreme environmental conditions, and ability to survive and recover after a disturbance (reviewed in Baker 2003). Only a few species of corallimorpharians have been examined for associated zooxanthella clades and have been found to harbor members of clade C (LaJeunesse 2002; LaJeunesse et al. 2004).

Irradiance and temperature are major environmental parameters that influence the distribution and abundance of cnidarians on coral reefs (Falkowski and Dubinsky 1981; Fitt et al. 2001). Increases in the levels of both factors have contributed to frequent bleaching events on coral reefs during the past two decades (Loya et al. 2001; Muhando et al. 2002). While the effects of these factors on reef-building corals have been well studied, the impacts of thermal and light stress on other groups of reef cnidarians have been mostly overlooked. Individuals of *Rhodactis rhodostoma* are one of the most common corallimorpharians on coral reef flats in the Indo-Pacific region, and may become especially abundant following bleaching and other disturbances that kill stony corals (Chadwick-Furman and Spiegel 2000; Kuguru et al. 2004). We investigated responses of individuals of *R. rhodostoma* to variation in irradiance and temperature to better understand the mechanisms that allow members of this species to become abundant on shallow reef flats. We hypothesized that individuals of this species (1) decrease significantly in abundance with depth, (2) withstand high irradiance without decreasing their photosynthetic output, (3) survive at high temperature (HT) for long periods while bleached, (4) shield their zooxanthellae from high irradiance, and (5) harbor different clades of zooxanthellae at different depths on the coral reef.

Methods

Study site and depth distribution

This study was conducted during January 2004 to March 2005 on coral reefs adjacent to the Interuniversity Institute for Marine Science (IUI) near Eilat at the northern tip of the Gulf of Aqaba, Red Sea (29°30′N, 34°55′E). To determine the depth distribution of the corallimorpharian *R. rhodostoma*, 20 quadrats of 1 m^2 each were deployed haphazardly at each of three depths: reef flat (0.5 m), shallow slope (3 m), and deep slope (18 m). The number of polyps of this species in each quadrat was determined while snorkeling or scuba diving.

Photophysiology

Polyps of *R. rhodostoma* were selected haphazardly at 3–20 m depth, collected, and glued to PVC bases using underwater epoxy. Selected polyps were each at least 10 m apart to avoid collecting individuals that originated asexually from the same aggregation. Following a 2-week acclimation period in outdoor flow-through (120 l h^{-1}) seawater aquaria, the polyps either were returned to the reef for field experiments or transferred to laboratory treatments.

For the field experiments, four corallimorpharians were attached by their PVC bases to underwater frames and acclimated at each of three depths (5, 10, and 20 m) on the coral reef for 1 month. Following acclimation, we used an underwater pulse amplitude modulated (PAM) fluorometer (the Diving PAM,

Walz, Germany; Hoegh-Guldberg and Jones 1999; Winters et al. 2003; Iglesias-Prieto et al. 2004) to measure photosynthetic parameters in each coral-limorpharian. PAM fluorometry induces chlorophyll fluorescence in vivo to estimate the potential quantum yield of photosystem II during photosynthesis, a parameter that correlates with more traditional measures of photosynthetic rate such as CO_2 uptake and O_2 evolution (Beer et al. 1998). At 1 h after sunset, the PAM was used to record the nocturnal maximum quantum yield of photosystem II (F_v/F_m), where F_v = variable fluorescence and F_m = maximum fluorescence for the dark adapted sample. This period of darkness is sufficient to maximize the frequency of open reaction centers in photosystem II (Winters et al. 2003). At noon, the midday effective quantum yield $[(F_m' - F)/F_m' = \Delta F/F_m']$ also was measured where F_m' = maximum fluorescence for the light adapted sample and F = initial fluorescence for the light adapted sample (after Genty et al. 1989; Schreiber et al. 1994). Based on these measurements, we calculated for each polyp the maximum midday excitation pressure [$Q_m = 1 - (\Delta F/F_m'$ at noon)/(F_v/F_m at 1 h after darkness), after Maxwell et al. 1994, 1995; Iglesias-Prieto et al. 2004].

A stress experiment on photosynthetic responses to variation in light and temperature was performed on 16 individuals each of the corallimorpharian *R. rhodostoma* (3–4 cm diameter each) and for comparison the massive scleractinian coral *Favia favus* (4–5 cm diameter each) in an outdoor running seawater table. Eight individuals of each species were photoadapted for 1 month under each of two treatments created by layers of plastic netting shades: (1) high light (HL), 30% shade with a maximum midday irradiance of 1,160 µmol photons m^{-2} s^{-1} and (2) low light (LL), 90% shade with a maximum midday irradiance of 350 µmol photons m^{-2} s^{-1}. These treatments mimicked irradiance at 5 and 20 m depth, respectively, which encompasses most of the depth range of individuals of *R. rhodostoma* (Chadwick-Furman and Spiegel 2000) and *F. favus* (Sheppard and Sheppard 1991). The diffuse attenuation co-efficient (K_d), an indicator of the penetration of solar irradiance in seawater, was 0.0726 as measured in situ at the time of the experiment using an LI-192 underwater quantum sensor lowered from a boat. Irradiances were measured using quantum sensors (LI-190SA, LiCor, USA) connected to a data logger (LI-1400, LiCor, USA).

Within each of the two light treatments, four individuals of each species were subjected to a gradual rise in temperature over 14 days by applying a heater until 6°C above mean ambient seawater temperature was reached (=HT treatment, 31°C), after which polyps were maintained at this temperature for a further 18 days. During the entire period, a chiller (TECO, Italy) was used to maintain the remaining animals at 25°C, a temperature identical to that of seawater at 4 m depth on the adjacent coral reef (=low temperature, LT). Submersible temperature loggers (HOBO temperature Pro, Onset Computers, USA) monitored the temperatures in each treatment. The LT treatment of 25°C equaled mean summer temperature on the shallow reef at Eilat (Loya 1985). The HT treatment of 31°C was a few degrees above the maximum summer temperature in very shallow water of 28°C, and was selected to mimic a possible warming event in this region.

Four experimental treatments were maintained, each containing four individuals of each species: high light and high temperature (HLHT), high light and low temperature (HLLT), low light and high temperature (LLHT), and low light and low temperature (LLLT). The temperature treatment areas were separated from each other using Styrofoam insulation sheeting, and each was supplied with a separate inflow of running seawater at a rate of 60 l h^{-1} (after Zakai et al. 2006). The water also was well mixed within each treatment by a small aquarium pump at a rate of 600 l h^{-1}. Due to the technical constraints of maintaining a large number of chambers at different temperatures and irradiances, the experimental individuals were grouped within each treatment. This lack of replication of chambers within treatments is standard for laboratory physiological experiments, and is based on previous studies which have demonstrated the validity of results for cnidarians using this method (reviewed in Chomski et al. 2004).

During each of 18 days in the stress experiment when the HT treatments were maintained at 31°C, F_v/F_m was measured for all individuals using the PAM at 1 h after sunset. To assess the photo-protective abilities of the corallimorpharian polyps following the above treatments, non-photochemical quenching (NPQ) [NPQ = $(F_m - F_m')/F_m'$, after Hoegh-Guldberg and Jones 1999], also was measured for individuals in all treatments at the end of the experiment.

Individuals were subjected to the stress experiment for a total of 32 days (14 days of gradual temperature rise plus 18 days at HT), during which the corallimorpharians exposed to the HLHT treatment became bleached as evidenced by their white appearance. We then lowered the temperature back to ambient and monitored the corallimorpharians for an additional month during which we recorded F_v/F_m at 1 h after sunset each day. Photographs were taken of each

individual before, during, and after bleaching when microalgae repopulated the corallimorpharians.

After 32 days in the stress experiment, before recovery, and after 30 days in the field treatments, 6–8 tentacles were removed from each corallimorpharian polyp to determine zooxanthella abundance and chlorophyll *a* (chl *a*) content. Tentacles were examined because they are major photosynthetic organs in anthozoans and have been used widely to assess variation in photosynthetic parameters such as zooxanthella abundance and chl *a* levels (Dunn et al. 2002, 2004). The group of tentacles from each polyp was blotted on absorbent tissue paper to remove all excess water. Then their wet mass was determined accurately using an electronic microbalance with an error of ±0.0002 g (wet mass per group of 6–8 tentacles = 0.10 ± 0.02 g, $x \pm$ SE). Each group of tentacle tips then was homogenized in 2 ml of filtered seawater and the resulting slurry was centrifuged (after Dunn et al. 2002, 2004). In the zooxanthella-containing aliquots we measured (1) chl *a* content (overnight extraction in 90% acetone, absorbance readings at 664 and 630 nm; Jeffrey and Humphrey 1975), and (2) zooxanthella abundance (cells counted under a light microscope using a hemocytometer, modified after Warner et al. 2002). Algal pigment and abundance were normalized per wet mass of tentacle tissue.

Anatomy

Following 32 days in the stress experiment, 6–8 tentacle tips also were removed from each corallimorpharian polyp for histological examination. The tentacle tips were relaxed in 7% $MgCl_2$ for 3 h, fixed in 10% formalin for 24 h, washed in 70% ethanol prior to storage in a refrigerator at 4°C (after Chadwick-Furman et al. 2000), and then sent to Tel Aviv University for histological sectioning. Anatomical parameters (diameter of zooxanthella cells, tentacle endoderm thickness, and minimal distances between algal cells and tentacle mesoglea) observed in the histological sections from each treatment were quantified using image analysis (UTHSCSA Image tool, version 3.0, 2002).

Symbiodinium clades

Tissue samples were obtained from ten polyps of *R. rhodostoma* each located at least 10 m apart at each of two depths on the coral reef slope: shallow (0–4 m) and deep (18–20 m). A few tentacle tips were removed from each polyp, preserved in 100% acetone (Fukatsu 1999), and shipped to Auburn University, USA. Total nucleic acids were extracted from the tissues according to Coffroth et al. (1992), and *Symbiodinium* small subunit (18S) ribosomal DNA (rDNA) was amplified by PCR using the primers ss5 (5′-GGTTGATCCTGCC AGTAGTCATATGCTTG-3′) and ss3z (5′-AGCACT GCGTCAGTCCGAATAATTCACCGG-3′) according to Rowan and Powers (1991a). PCR products were digested with the *Taq*I restriction enzyme to generate restriction fragment length polymorphisms (RFLPs) as described in Rowan and Powers (1991a). RFLP analysis of 18S-rDNA PCR products separates *Symbiodinium* into several large clades [i.e., *Symbiodinium* A, B, C (Rowan and Powers 1991a, b), D (Carlos et al. 1999), and E (*Symbiodinium californium*; LaJeunesse and Trench 2000; LaJeunesse 2001)], and allows simple and rapid identification of the symbiont clade. Digestion products were separated on 2% sodium-borate agarose gels and visualized with ethidium bromide under UV light. RFLP patterns were compared with cloned standards or to the literature to assign each sample to one of the established *Symbiodinium* 18S-rDNA RFLP clades. Samples of extracted DNA used in this study are available upon request to the corresponding author.

Statistical analyses

Variation in the number of corallimorpharian polyps, and in the zooxanthella abundance, chlorophyll pigment concentration, Q_m and F_v/F_m of polyps with depth in the field were analyzed using one-way ANOVAs. The combined effects of light and temperature on zooxanthella abundance, chlorophyll pigment concentration, and NPQ in the stress experiment were analyzed using two-way ANOVAs. Effects of light and temperature on daily values of F_v/F_m were determined using repeated measures two-way ANOVAs, with time as the repeated measure. Effects of high and low irradiance on zooxanthella diameter, endoderm thickness and distance of zoozanthellae from the mesoglea were determined using *t*-tests. Proportional data were arcsine transformed prior to statistical analysis. All data met the parametric test assumptions of homogeneity of variances (Leven's test) and normality (normal probability plots). Significant differences among treatment groups were determined post-hoc using Student–Newman–Keuls tests.

Results

Abundance of the corallimorpharian *R. rhodostoma* decreased significantly with depth on the coral reef at Eilat (one-way ANOVA, $F_{(2,0.05)} = 305.62$, $P < 0.001$, Fig. 1). In contrast, both the abundance of zooxanthellae

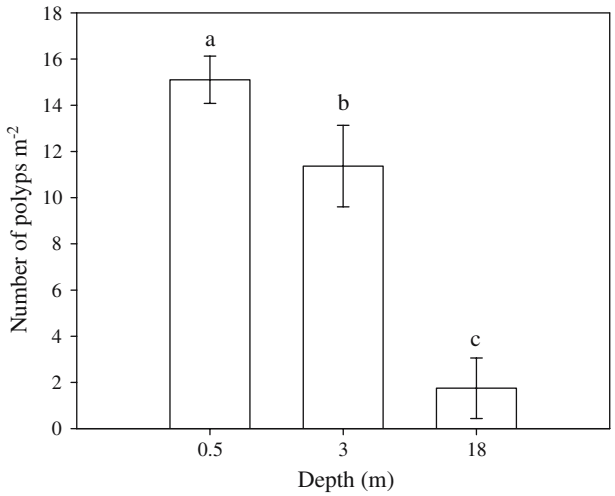

Fig. 1 Variation in abundance of the corallimorpharian *Rhodactis rhodostoma* with depth on a coral reef at Eilat, northern Red Sea. Data are presented as means ± SE of polyp abundance in 20 1 m^2 quadrats examined at each depth. Depths with different *superscript letters* are significantly different at $P < 0.05$ (Student–Newman–Keuls post-hoc tests following ANOVA analysis, see text for details)

and the concentration of chl *a* within transplanted corallimorpharians increased significantly with depth (one-way ANOVAs, $F_{(2,0.05)} = -19.17$, $P < 0.001$ for zooxanthella abundance and $F_{(2,0.05)} = 4.93$, $P < 0.05$ for chl *a* concentration, Fig. 2a, b, respectively). Excitation pressure on photosystem II (Q_m) in transplanted polyps was significantly higher in shallow than in deep water, but did not differ from either at mid depth (one-way ANOVA, $F_{(2,0.05)} = 3.25$, $P < 0.05$, Fig. 2c). Maximum quantum yield (F_v/F_m) did not vary significantly with depth in the transplanted individuals (one-way ANOVA, $F_{(2,0.05)} = 1.28$, $P = 0.31$, Fig. 2d).

In the laboratory experiment, similar results were observed as for polyps transplanted in the field. Both the abundance of zooxanthellae and the concentration of chl *a* within polyps decreased significantly in HL versus LL, equivalent to light levels at 5 and 20 m depth on the reef, respectively (Fig. 3a). Both parameters also decreased significantly at HT versus LT, and there was no interaction effect between light and temperature (Table 1). In the HLHT treatment, both zooxanthella abundance and chl *a* concentration decreased to almost 0 (Fig. 3a), and polyps appeared bleached (Fig. 4a).

The corallimorpharians had significantly higher values of NPQ at HLLT than they did in any of the other laboratory treatments (Fig. 3b). NPQ increased significantly with light level in both temperature treatments (Table 1). Exposure of the polyps to HT depressed the effect of HL on NPQ (Fig. 3b), possibly due to the almost complete absence of zooxanthellae in polyps by the end of the experiment in this treatment (HLHT, Figs. 3a, 4a).

After approximately 1 week in the stress experiment, individuals of *R. rhodostoma* in both HT treatments began to decrease their maximum quantum

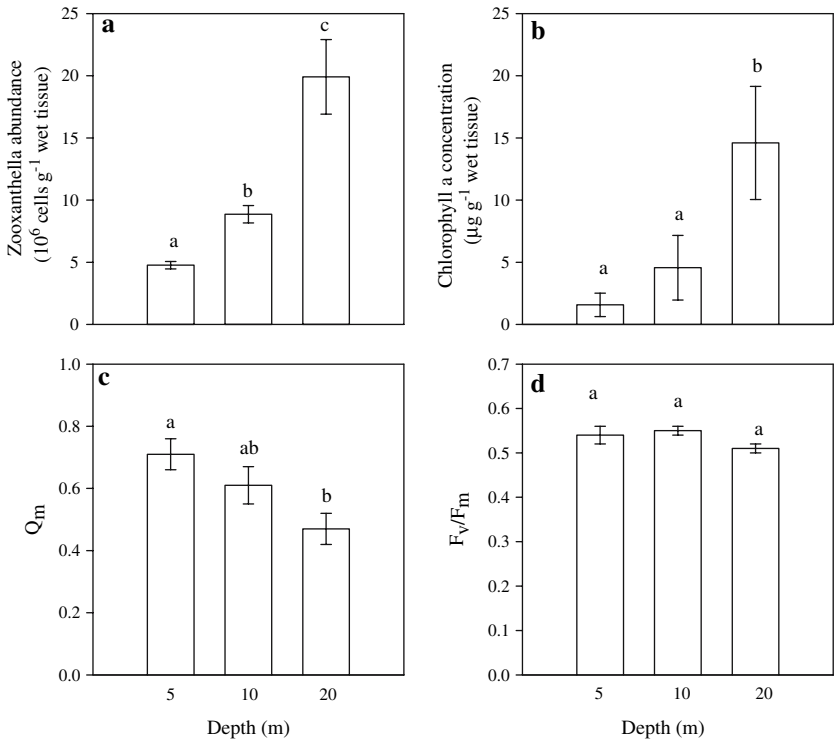

Fig. 2 Variation in photosynthetic traits of the corallimorpharian *Rhodactis rhodostoma* with depth on a coral reef at Eilat, northern Red Sea: **a** zooxanthella abundance, **b** chlorophyll *a* concentration, **c** excitation pressure over photosystem II (Q_m), and **d** maximum quantum yield (F_v/F_m). Data are presented as means ± SE, $n = 5$ polyps examined per depth. Depths with different *superscript letters* are significantly different at $P < 0.05$ (Student–Newman–Keuls post-hoc tests following ANOVA analysis, see text for details)

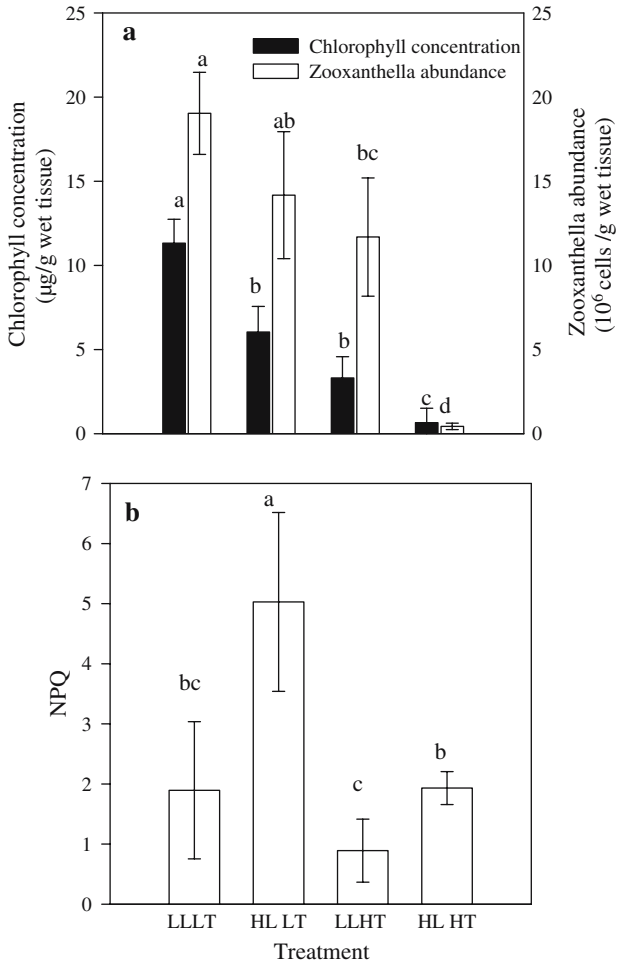

Fig. 3 Variation in **a** zooxanthella abundance and chlorophyll concentration and **b** levels of non-photochemical quenching in polyps of the corallimorpharian *Rhodactis rhodostoma* exposed to a stress experiment of four combinations of light and temperature treatments under laboratory conditions: low light and low temperature, high light and low temperature, low light and high temperature, and high light and high temperature. Data are presented as means ± SE, $n = 4$ polyps per treatment after 18 days of exposure. Treatments with different *superscript letters* are significantly different at $P < 0.05$ (Student–Newman–Keuls post-hoc tests following ANOVA analysis, see text for details)

yields (Fig. 5a). By the end of the experiment, individuals in the HLHT treatment had significantly lower maximum quantum yields than those in all other treatments (Table 2; Fig. 5a), and became bleached (Fig. 4a). Polyps in the LLHT treatment also significantly decreased in maximum quantum yield, but not as drastically as those in the HLHT treatment, indicating an added effect of HL when exposed to HT (Fig. 5a). Polyps in both of the LT treatments did not significantly decrease their maximum quantum yields over the course of the experiment; there was no significant effect of light level in the LT treatments (Table 2; Fig. 5a).

In contrast, individuals of the scleractinian coral *F. favus* significantly reduced their maximum quantum yields at HL in both temperature treatments (Fig. 5b). At LL, the corals did not reduce their maximum quantum yields in either of the temperature treatments (Fig. 5b; Table 2). As in the corallimorpharians, the combination of HLHT created the largest depression in maximum quantum yield (Fig. 5a, b).

After the temperature decreased, individuals of the corallimorpharian recovered significantly in terms of maximum quantum yield (Fig. 5c; Table 2) and became pigmented again, indicating repopulation by endosymbiotic zooxanthellae (Fig. 4b).

Under LLLT, the corallimorpharian tentacles contained histologically discernible layers of ectoderm, mesoglea, and endoderm with zooxanthella cells located near the thin mesogleal layer (Fig. 6a). In contrast, at HLLT, the mesogleal layer was significantly thicker and the zooxanthella cells were significantly larger and located further distant from the mesoglea than in the LLLT treatment (Fig. 6b; Table 3). In both HT treatments, the tissue layers became disorganized, the zooxanthellae degenerated, and many empty vacuoles appeared (Fig. 6c, d). This tissue disintegration prevented statistical analysis of mesogleal thickness and zooxanthella size and position in either HT treatment.

Individuals of *R. rhodostoma* on the coral reef at Eilat contained algal symbionts belonging to *Symbiodinium* clade C or D (Fig. 7). All polyps ($n = 7$) sampled from shallow water (0–4 m depth) harbored clade C, while in deep water (18–20 m depth) most polyps (73%, $n = 11$) hosted clade D and a minority (27%) contained clade C. None of the polyps examined from either depth contained both clades C and D.

Discussion

We demonstrate here that the corallimorpharian *R. rhodostoma* employs multiple mechanisms of photoacclimation, including: (1) variation in both zooxanthella abundance and chlorophyll concentration with depth, (2) dispersal of excess light energy via NPQ by the zooxanthellae at HL, (3) host-mediated shading of zooxanthellae from HL by thickening of the endodermal layer and movement of algal cells away from the mesoglea, and (4) variation in the genetic identity of harbored zooxanthella clades with depth.

The decrease in abundance of this species with depth observed here is similar to the pattern observed for these corallimorpharians on other coral reefs in the northern Red Sea (Chadwick-Furman and Spiegel

Table 1 Two-way ANOVAs of photosynthetic parameters with temperature and light treatments in a stress experiment on the corallimorpharian *Rhodactis rhodostoma* under laboratory conditions at Eilat, northern Red Sea

Photosynthetic parameter	Source of variation	*df*	Mean square	*F*	*P*
Chlorophyll *a* concentration	Temperature	1	179.47	26.98	***
	Light	1	62.82	9.44	**
	Temperature × light	1	6.86	1.03	ns
	Error	12	6.65		
Zooxanthella abundance	Temperature	1	4.44×10^{14}	6.87	*
	Light	1	2.60×10^{14}	4.01	ns
	Temperature × light	1	0.41×10^{14}	0.63	ns
	Error	12	0.65×10^{14}		
Non-photochemical quenching	Temperature	1	16.80	4.34	ns
	Light	1	17.41	4.50	*
	Temperature × light	1	4.38	1.13	ns
	Error	12	3.87		

ns not significant
$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

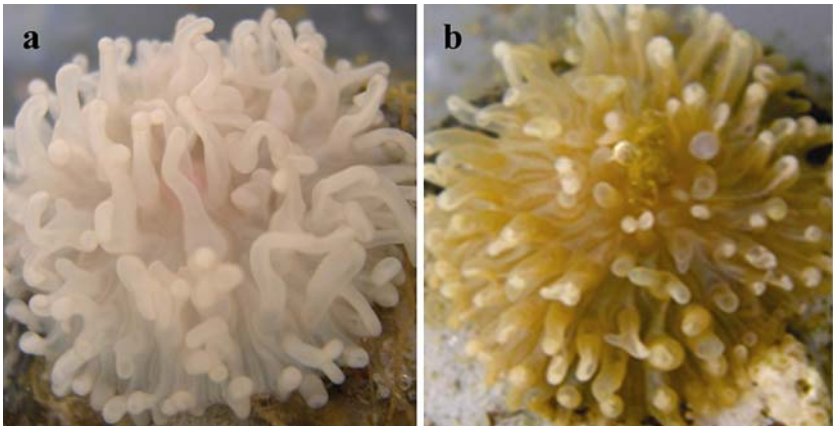

Fig. 4 Photographs of a representative individual of the corallimorpharian *Rhodactis rhodostoma* under laboratory conditions following exposure to **a** a stress experiment of 18 days of high light and high temperature, and **b** a recovery experiment of 14 days after seawater temperature was returned to ambient (25°C). Note *bleached appearance* in (**a**) and same polyp with *brown pigmentation* in (**b**) indicating recovery of zooxanthellae

2000) and Tanzania (Muhando et al. 2002; Kuguru et al. 2004). The high abundance of *R. rhodostoma* on shallow coral reef flats indicates an ability to withstand extremely high levels of irradiance. The diverse mechanisms of photoacclimation described above may in part explain this depth distributional pattern.

The increase in chl *a* concentration and zooxanthella abundance with depth shown here for polyps of *R. rhodostoma* also occurs in some scleractinian corals as photosynthetic compensation for exposure to LL conditions (Falkowski and Dubinsky 1981; Titlyanov et al. 2000). Thus at very high levels of irradiance on shallow reef flats, individuals of this corallimorpharian are able to reduce both the pigment content per algal cell and the total number of zooxanthella cells they contain.

Our fluorescence-based measurements of F_v/F_m, Q_m, and NPQ also show that the algal symbionts of this corallimorpharian effectively disperse excess energy in HL environments. While polyps of *R. rhodostoma* do not vary significantly in maximum quantum yield F_v/F_m with depth, some stony corals for example *Stylophora pistillata* at Eilat decrease F_v/F_m in shallow water, indicating chronic photoinhibition in the corals when growing at 2 m as compared to 11 m depth (Winters et al. 2003). Values of Q_m approach 1.0 in the corallimorpharians, indicating that under maximum irradiance many of the PSII reaction centers in their zooxanthellae are closed and thus that some photoinhibition occurs at HL (Iglesias-Prieto et al. 2004). Since F_v/F_m does not decrease in the shallow growing corallimorpharians, these high Q_m values could be attributed to a midday drop in effective quantum yield due to high levels of midday irradiance in shallow water. These corallimorpharians also exhibit high levels of NPQ at high irradiance, another indicator of their ability to disperse excess light energy.

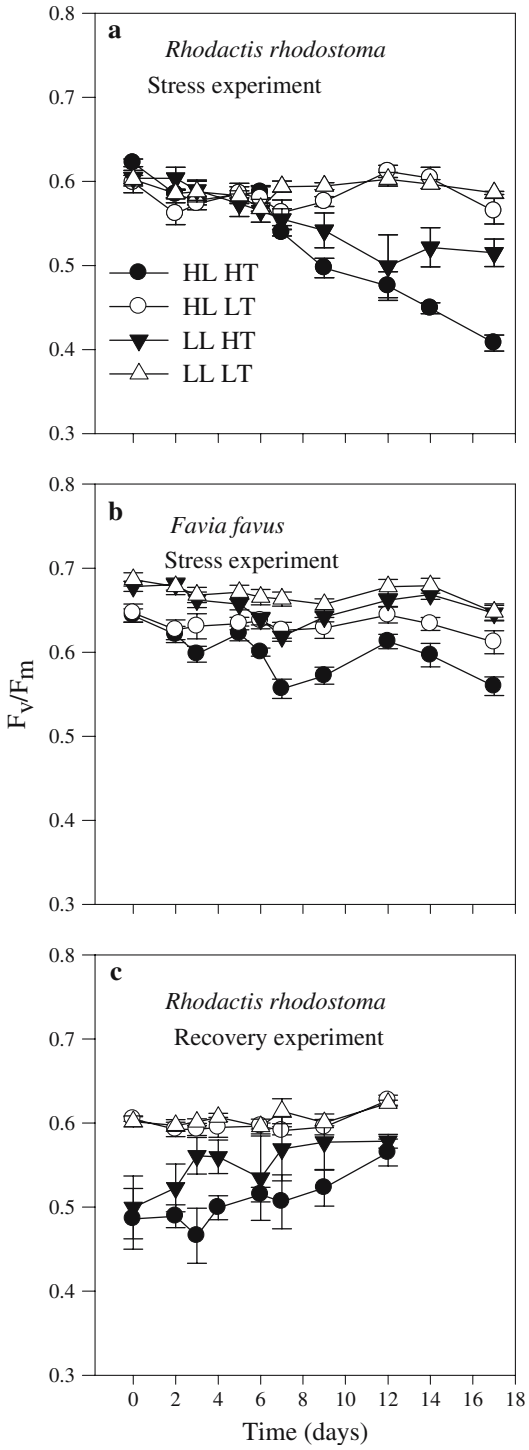

Fig. 5 Variation in maximum quantum yield (F_v/F_m) over time among laboratory treatments applied to cnidarians. **a** The corallimorpharian *Rhodactis rhodostoma* in a stress experiment with four combinations of light and temperature: low light and low temperature, high light and low temperature, low light and high temperature, and high light and high temperature. **b** *R. rhodostoma* in a recovery experiment after temperature in the two HT treatments was reduced back to ambient (25°C = LT). **c** The massive scleractinian coral *Favia favus* in a stress experiment with the above four combinations of light and temperature. $N = 4$ corallimorpharians and five corals per treatment. Data are presented as means ± SE

While individuals of *R. rhodostoma* appear to photoadapt to high irradiance, they are sensitive to HT as known for many stony corals (Warner et al. 1999; Fitt et al. 2001; Loya et al. 2001; Bhagooli and Hidaka 2003; Rowan 2004). In contrast, the stony corals *F. favus* (Fig. 5b), *S. pistillata*, and *Pocillopora damicornis* (G. Winters, unpublished data) all show lowered photosynthetic potential (expressed as F_v/F_m) mostly as a function of irradiance (up to 70% of full sunlight) and less as a function of temperature (up to 31°C). Our study area in the northern Red Sea is exposed to one of the highest irradiances on earth (e.g., http://www.eosweb.larc.nasa.gov/sse/; Winters et al. 2003). Thus, if photosynthetic sensitivity to light is the norm in this area as indicated by the above corals, the corallimorpharian *R. rhodostoma* is unusual in showing more sensitivity to temperature than to light.

The tissue modifications observed here in *R. rhodostoma* that shade the zooxanthellae from excess light are similar to those employed by the zoanthid *Palythoa caribaeorum*, in which a thick epidermis is produced that sunscreens the algal symbionts (LaJeunesse 2002). Similar tissue modifications when exposed to HL have not been observed in the more closely related scleractinian corals, but occur in some actinian sea anemones in response to heat stress (Dunn et al. 2002, 2004). At HT, we also observed a loss of functioning zooxanthellae and degeneration of host tissue similar that observed in some stony corals, especially in combination with high irradiance (Brown et al. 1995; Warner et al. 1999; Dunn et al. 2002; Bhagooli and Hidaka 2003; Rowan 2004). The recovery of these corallimorpharians from exposure to several weeks of HT stress contrasts with responses known for some stony corals which may die from this type of exposure (Muhando et al. 2002). During extended periods of bleaching and while deprived of photosynthates from zooxanthellae, the corallimorpharian *R. rhodostoma* may utilize alternate nutritional strategies. In scleractinian corals, endolithic algae can serve as an alternate source of photosynthate and contribute to host survivorship following coral bleaching and prior to repopulation by zooxanthellae (Fine and Loya 2002). However, corallimorpharians do not possess a calcareous skeleton so this option is not available to them. The experimentally bleached corallimorpharians in our treatments may have survived by preying on zooplankton (Elliott and Cook 1989), absorbing dissolved organic material (Schlichter 1982), and/or relying on energy reserves or materials recycled from degraded cells (Cikala et al. 1999). Their ability to survive bleaching may contribute to the opportunistic life history strategy exhibited by some members of this

Table 2 Repeated measures two-way ANOVAs with time as the repeated measure of variation in photosynthetic yield (maximum quantum yield, F_v/F_m) with temperature and light in the coral-limorpharian *Rhodactis rhodostoma* and the scleractinian coral *Favia favus* under laboratory conditions at Eilat, northern Red Sea

Species and experiment	Source of variation	*df*	Mean square	*F*	*P*
R. rhodostoma; stress experiment	Temperature	1	0.070	36.18	***
	Light	1	0.008	3.97	ns
	Temperature × light	1	0.002	1.02	ns
	Error	12	0.002		
	Time	10	0.006	11.05	***
	Time × temperature	10	0.010	20.10	***
	Time × light	10	0.001	2.23	*
	Time × temperature × light	10	0.001	1.86	ns
	Error	120	0.001		
F. favus; stress experiment	Temperature	1	0.008	1.26	ns
	Light	1	0.068	11.07	**
	Temperature × light	1	0.000	0.08	ns
	Error	16	0.006		
	Time	10	0.005	10.33	***
	Time × temperature	10	0.001	1.18	ns
	Time × light	10	0.002	4.53	***
	Time × temperature × light	10	0.001	1.18	ns
	Error	160	0.001		
R. rhodostoma; recovery experiment	Temperature	1	0.178	38.04	***
	Light	1	0.020	4.36	ns
	Temperature × light	1	0.012	2.54	ns
	Error	12	0.005		
	Time	7	0.004	3.27	**
	Time × temperature	7	0.001	1.00	ns
	Time × light	7	0.002	1.24	ns
	Time × temperature × light	7	0.001	0.43	ns
	Error	84	0.001		

In stress experiments, individuals were subjected to variation in levels of temperature and light. In the recovery experiment, temperature was returned to ambient. See text for details

ns not significant

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

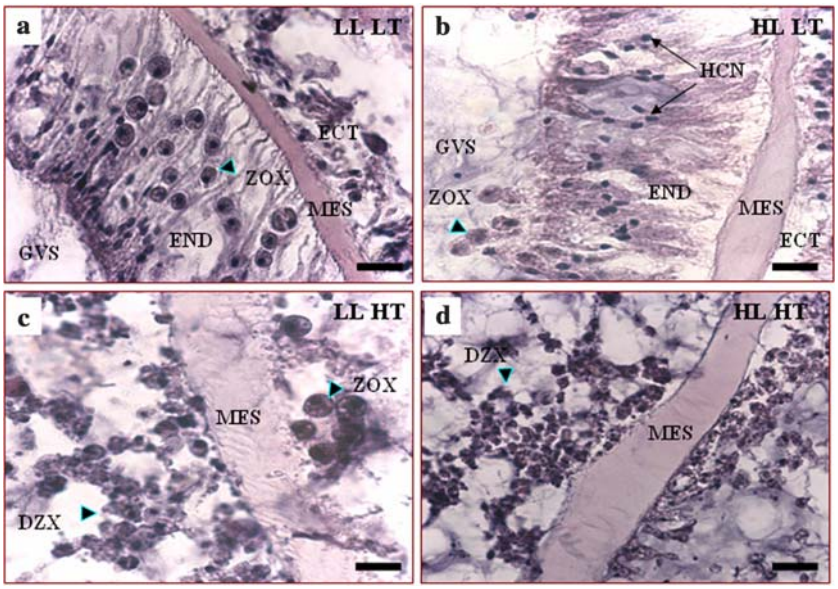

Fig. 6 Photomicrographs of tentacle tissue sections from the corallimorpharian *Rhodactis rhodostoma* in a stress experiment after 18 days of exposure to four combinations of light and temperature treatments under laboratory conditions: **a** low light and low temperature, **b** high light and low temperature, **c** low light and high temperature, and **d** high light and high temperature. *ZOX* zooxanthella, *HCN* host cell nucleus, *DZX* degenerated zooxanthella, *MES* mesoglea, *END* endoderm, *ECT* ectoderm, *GVS* gastrovascular space. Scale bars are 10 μm each

genus (den Hartog 1977; Langmead and Chadwick-Furman 1999; Kuguru et al. 2004).

This is the first study to document the types of zooxanthella clades harbored by corallimorpharians in the Red Sea, and the first to detect clade D zooxanthellae in anthozoans in the northern Red Sea. Our results are similar to those of LaJeunesse (2002) and LaJeunesse et al. (2004) in that clade C was associated with some of the corallimorpharians. However, the *Symbiodinium* clades detected here in individuals of *R. rhodostoma* differed from those reported for soft and stony corals at Eilat, which harbor either clade A or C (Barneah et al. 2004; Karako-Lampert et al. 2004). In the southern Red Sea, most stony corals also contain clades A and C, while very few (1.5%) contain clade D (Baker et al. 2004). In terms of both the lack of clade A and strong

Table 3 Variation in anatomical characteristics of tentacle tissue in the corallimorpharian *Rhodactis rhodostoma* between experimental laboratory treatments of high versus low light at ambient seawater temperature

	Zooxanthella diameter (μm)	Endoderm thickness (μm)	Distance of zooxanthellae from mesoglea (μm)
High light	7.11 ± 0.09	102.93 ± 2.50	56.71 ± 2.22
Low light	6.82 ± 0.09	75.22 ± 1.10	28.42 ± 1.46
Level of significance	$P < 0.01$	$P < 0.0001$	$P < 0.0001$

$N = 4$ polyps sampled per treatment. Data are presented as means ± SE. Levels of significance were determined using *t*-tests. See text for details

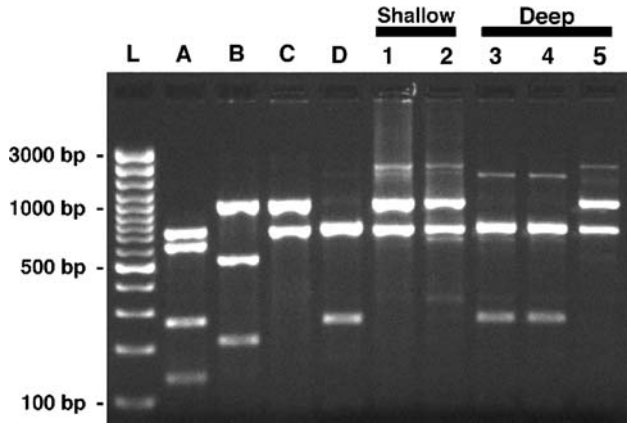

Fig. 7 Diversity of zooxanthella clades in the corallimorpharian *Rhodactis rhodostoma* collected from shallow (0–4 m) and deep water (18–20 m) on a coral reef at Eilat, northern Red Sea. *Symbiodinium* cladal identity was determined by digesting PCR-generated algal small subunit ribosomal DNA with the restriction enzyme *Taq*I to generate restriction fragment length polymorphism patterns. *L* represents DNA size ladder, *A* represents *Symbiodinium* Clade A standard, *B* represents *Symbiodinium* Clade B standard, *C* represents *Symbiodinium* Clade C standard, *D* represents *Symbiodinium* Clade D standard. *Lanes 1–5* are zooxanthellae from representative individuals of *R. rhodostoma* in shallow (*lanes 1* and *2*) and deep water (*lanes 3–5*)

presence of clade D, our results are more similar to those of Toller et al. (2001) for zooxanthellae in stony corals of the Caribbean Sea, where clade C dominates at all depths and clade D occurs only in deep water. Most of the scleractinians and alcyonaceans in the Red Sea that harbor clade C zooxanthellae transmit them horizontally, in that the zooxanthellae are acquired from the surrounding environment with each new host generation and not directly from host parents (Barneah et al. 2004; Karako-Lampert et al. 2004). Individuals of *R. rhodostoma* also likely acquire their zooxanthellae from the environment since they broadcast gametes that do not contain algal cells (Chadwick-Furman et al. 2000).

Variation among clades of zooxanthellae in their physiological responses to environmental conditions such as irradiance and temperature may result in the dominance of different clades at different depths (reviewed in Baker 2003; Iglesias-Prieto et al. 2004; but see also Coffroth and Santos 2005; Kinzie et al. 2001; Lajeunesse et al. 2003; Tchernov et al. 2004). Ongoing reciprocal transplantation experiments are aimed at investigating the extent to which the zooxanthella clades associated with in this corallimorpharian are depth and light dependent (B.L. Kuguru et al., in preparation).

We conclude that the corallimorpharian *R. rhodostoma* is able to produce large aggregations on some shallow reefs in the highly irradiated northern Red Sea partly due to photoacclimation strategies contributed by both the host cnidarian and microalgae to the holobiont. Clonal replication of polyps and high sexual reproductive output also likely contribute to the rapid expansion of aggregations on the reef flat (Chadwick-Furman and Spiegel 2000; Chadwick-Furman et al. 2000). While these corallimorpharians alter their anatomy to screen their zooxanthellae from excess irradiance, the latter photoadapt physiologically by dissipating excess light through NPQ and by avoiding chronic photoinhibition as reflected in maintained high F_v/F_m values. Variation in zooxanthella clades with depth also may contribute to photoadaptation of the holobiont to variation in irradiance levels. Individuals of this corallimorpharian can survive extended bleaching and recover fully, likely by altering their mode of nutrition when aposymbiotic. Thus in comparison with some stony corals, individuals of *R. rhodostoma* exhibit diverse traits for survival in HL environments. These characteristics may allow members of this species to repopulate some shallow reef areas that have been denuded from stony corals following thermal stress events.

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