

Microhabitat use and photoacclimation in the clownfish sea anemone *Entacmaea quadricolor*

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Many reef-building corals photoacclimate by increasing levels of chlorophyll per microalgal cell with depth, but mechanisms of photoacclimation in coral reef sea anemones remain poorly understood. We determined variation in ambient irradiance and patterns of abundance, microhabitat use, chlorophyll and microalgal cell concentrations in clownfish sea anemones Entacmaea quadricolor from 0 to 43 m depth on a coral reef at Aqaba, Jordan, northern Red Sea. In shallow areas, anemones occupied shaded reef microhabitats exposed to significantly lower irradiance than in the adjacent open water, but on the deep reef slope they occupied unshaded habitats. Anemone abundances were the highest observed thus far in the Red Sea, and peaked at mid depth on the reef slope. Microalgal abundance in anemone tentacles increased four-fold from the shallow to deep reef, while chlorophyll-a concentrations per algal cell did not vary significantly with depth. We conclude that E. quadricolor photoacclimates using two major mechanisms: (1) occurrence in shaded microhabitats when shallow, thus reducing exposure to high irradiance, and (2) increasing microalgal abundance with depth, thereby enhancing photosynthetic efficiency at low irradiance.

Keywords: irradiance, microalgae, coral reef, Gulf of Aqaba, Jordan, Red Sea, *Symbiodinium*

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INTRODUCTION

Photoacclimation is an important process for photosynthetic organisms on coral reefs because they experience extremes of irradiance over a narrow depth range in this tropical habitat (Mass *et al.*, 2010; Dubinsky & Falkowski, 2011). Photosynthetically active radiation (PAR) can reach high and even damaging levels near the sea surface, where rates of photosynthesis level off due to light intensities that either inhibit or saturate photon receptors (Mass *et al.*, 2010). Many coral reef cnidarians use photoprotective substances such as mycosporine-like amino acids (MAAs) as sunscreen against the damaging effects of intense ultraviolet radiation (UVR) in shallow tropical waters (Shick *et al.*, 2003). On coral reefs, high PAR and UVR act synergistically with elevated water temperatures to cause bleaching in some stony corals (Lesser, 1996; Anderson *et al.*, 2001). Giant sea anemones also bleach more in shallow areas exposed to high irradiance than in deeper reef areas (Hobbs *et al.*, 2013). Shallow reefs that occur in waters with high concentrations of dark brown leachate from rotting sea grasses, such as those in some reef lagoons, may exhibit reduced bleaching due to shading effects of the dissolved pigments (Iluz *et al.*, 2008). At the other extreme, diminishing levels of irradiance with depth set the lower limits of coral reef growth at about

40–70 m depth, depending on water clarity (Fricke & Schuhmacher, 1983; Jarrett *et al.*, 2005; Grigg, 2006). Many reef corals are limited to shallow areas on reefs due to their inability to survive at low irradiance on the deep reef slope (Fricke & Schuhmacher, 1983). Cnidarians that survive in low light employ a variety of mechanisms to capture the sparse photons that reach the deep reef slope. Some alter the body shape and skeletal growth patterns of the host animal to become more flattened (Fricke & Schuhmacher, 1983). Others alter their microhabitat use with depth, occupying shaded reef areas such as crevices and vertical walls when shallow, but occurring more on open horizontal areas when deep (Chadwick-Furman & Loya, 1992; Kuguru *et al.*, 2010). In addition, many stony corals increase the concentration of chlorophyll-*a* per endosymbiotic microalgal cell (*Symbiodinium* zooxanthellae; Blank & Trench, 1986) with increasing depth and decreasing irradiance (Falkowski & Dubinsky, 1981; Dubinsky *et al.*, 1990; Stambler *et al.*, 2008; Mass *et al.*, 2010). This photoacclimation mechanism results in higher densities of photon receptors in coral tissues, and allows them to maintain a steady rate of photosynthesis regardless of irradiance intensity (Stambler, 2008). Reef cnidarians express these mechanisms most extremely near their shallow and deep range limits, where irradiance reaches extreme levels.

Many reef-building corals have been examined for photoacclimation mechanisms, but little is known about this process in soft-bodied cnidarians on tropical reefs, including the photosynthetic sea anemones (Actiniaria), soft corals and sea fans. A few species that form clonal aggregations of

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small polyps have been examined; the sea anemone *Aiptasia pulchella* and the corallimorpharians *Rhodactis rhodostoma* and *Discosoma unguja* all vary microalgal cell abundances in their tissues and chlorophyll content per microalgal cell with irradiance levels on reefs (Muller-Parker, 1987; Kuguru et al., 2007, 2010). Some temperate sea anemones also adjust their concentrations of microalgal cells with irradiance level (Muller-Parker & Davy, 2001). Giant sea anemones are conspicuous organisms on many tropical reefs and play major ecological roles as symbiotic hosts to obligate cleaner shrimps in the Caribbean Sea (Huebner et al., 2012), and to both fish and shrimps in the Indo-Pacific region (Fautin & Allen, 1997; Chadwick et al., 2008; Huebner & Chadwick, 2012). Information concerning their photoacclimation mechanisms is important for understanding how they are able to occupy diverse microhabitats on reefs.

Irradiance attenuates with water depth, at exponential rates that vary with factors such as inorganic and organic particle concentrations, plankton abundance and other contributors to water turbidity (reviewed in Mass et al., 2010). The northern Red Sea receives some of the strongest solar irradiance on earth due to its situation in a desert region that usually lacks cloud cover and thus receives low rainfall, sediment and nutrient inputs (Stambler, 2008). These factors contribute to low light attenuation in coastal waters of the northern Red Sea, where the euphotic zone extends to at least 90 m depth (Stambler, 2005), and three-dimensional coral structure and thus reef development occur to about 60 m depth (Fricke & Schuhmacher, 1983). Below this depth, only minute amounts of light penetrate into the twilight zone, defined as 50–150 m deep (Brokovich, 2008). Depth–irradiance curves exist for some parts of the Red Sea (Fricke & Schuhmacher, 1983; Stambler, 2008; Mass et al., 2010), but not for Jordanian coral reefs at the northern tip of this enclosed sea.

Individuals of the bulb-tentacle sea anemone *Entacmaea quadricolor* are the preferred hosts of the Red Sea endemic anemonefish (clownfish) *Amphiprion bicinctus* (Huebner et al., 2012). These anemones occur throughout the Red Sea region on coral reefs (Chadwick & Arvedlund, 2005; Huebner et al., 2012). Photoacclimation mechanisms in *E. quadricolor* over their wide depth range of at least 0–65 m (Brokovich et al., 2008; Bridge et al., 2012) may be complicated by several factors. Firstly, small clonal individuals of this species may be limited to shallow reef areas, and thus may photoacclimate across a narrower range of irradiance than do large solitary ones in parts of the Indo-Pacific, where both forms are found (Dunn, 1981; Fautin, 1986; Srinivasan et al., 1999; Scott et al., 2011; Bridge et al., 2012). However, northern Red Sea individuals of *E. quadricolor* all belong to the solitary, non-clonal form (Chadwick & Arvedlund, 2005; Brokovich et al., 2008). Secondly, the tentacles in members of this species may exhibit either a digitiform or bulbous morphology, or sometimes both in one individual (Dunn, 1981; Fautin & Allen, 1997; Huebner et al., 2012). Tentacle bulbs may form when the anemones are exposed to high irradiance (Delbeek, 2002), but other factors such as clownfish presence also appear to affect tentacle morphology (Huebner et al., 2012), and this influence varies among geographic regions (Dunn, 1981). Finally, Red Sea individuals of *E. quadricolor* host microalgal cells belonging to more than one variant of Clade C1 *Symbiodinium* (Roopin et al., 2011). Thus, body form, tentacle shape and microalgal type all may interact with photoacclimation processes in this

anemone, and these relationships deserve examination in future studies.

Here we describe an initial study on photoacclimation mechanisms by the bulb-tentacle anemone *E. quadricolor*, in which we present information on variation over a wide depth range (0–43 m) in the abundance, microhabitat use, microalgal cell content and chlorophyll-*a* concentrations of individuals on coral reefs at Aqaba, Jordan, northern Red Sea.

MATERIALS AND METHODS

Levels of irradiance

This study was conducted from June 2008 to June 2010 on coral reefs adjacent to the Marine Science Station (MSS), Aqaba, Jordan, in the Gulf of Aqaba, northern Red Sea (29.458°N 34.977°E; for site details see Huebner et al., 2012). In 2008, SCUBA divers measured levels of downwelling irradiance (photosynthetically active radiation, PAR) at 1–3 m depth intervals in open water adjacent to the coral reef using an irradiance meter (LI COR LI-185B) encased in an underwater housing. The PAR measurements were taken on 18 June 2008 during the period of maximum daily irradiance (12:00–13:00 hours; reported in absolute units, after Levy et al., 2003; Stambler et al., 2008; Mass et al., 2010) at 0–42 m depth. The vertical attenuation coefficient (K_d) of PAR was determined from a best-fit curve to these data (after Stambler, 2005). Irradiance also was measured in reef microhabitats occupied by individuals of the bulb-tentacle sea anemone *Entacmaea quadricolor* that were sampled for microalgal cell and chlorophyll-*a* concentrations (see below), by placing the light sensor adjacent to the outermost tentacle tips of each anemone in the field (after Muller-Parker, 1987).

Anemone abundance and microhabitat use

In 2008, the abundance and microhabitat use of individuals of *E. quadricolor* was determined on a coral reef slope that contained a marked study site near the MSS. This site was selected because it was a well-developed coral reef interspersed with sand patches (see maps in Mergner, 1981; Maniere & Jaubert, 1984; Mergner et al., 1992; Khalaf et al., 2006) and contained abundant sea anemones (Mergner & Schuhmacher, 1974; Huebner et al., 2012). All detected individuals of *E. quadricolor* were counted in three haphazardly-placed belt transects of 2 × 25 m each (50 m²) parallel to shore at each of nine 5 m depth intervals that extended from 0 m to 45 m depth on the reef slope. As part of a separate demographic study on the mid-slope, we quantified microhabitat use by all individuals (N = 72) that occurred at six 16 m depth (after Huebner et al., 2012). For each individual, we recorded the orientation of the oral disc as facing upwards (oriented horizontally) or sideways (oriented vertically), and the type of substrate contacted by the anemone tentacles (rock, sand).

Chlorophyll and microalgal cell concentrations

To assess concentrations of microalgal cells *Symbiodinium* in the tentacle tips of *E. quadricolor*, in June 2008, divers haphazardly selected 46 individuals from 3 m to 43 m depth. One tentacle tip (2–3 cm length, after Muller-Parker, 1987; Kuguru et al., 2008; Roopin et al., 2011) was clipped

from each selected anemone and transported to the nearby MSS. Tentacle samples were blotted to remove excess water, and wet mass measured to 1 mg. Microalgal cells were separated from the animal tissue by homogenizing the samples and centrifuging the homogenate to obtain an algal pellet, then the algae were resuspended in filtered seawater, and a haemocytometer (Hausser Scientific) was used to determine microalgal cell abundances at $200\times$ magnification (after Muller-Parker, 1984; Stambler & Dubinsky, 2005; Kuguru *et al.*, 2010). Only three replicates per tentacle sample were examined due to limited time at the field site; previous studies on microalgae in this anemone have shown that this level of replication is sufficient to detect significant variation among treatments (Roopin & Chadwick, 2009; Roopin *et al.*, 2011).

Chlorophyll concentrations were not assessed from samples collected in 2008 due to equipment limitations onsite. During a subsequent field season in June 2010, divers haphazardly selected 22 anemones over a wide depth range of 0.1–43 m. From each selected anemone, they collected a tentacle sample that was processed for microalgal abundance analysis as described above. Acetone (90%) was added to a subsample of the microalgal suspension, stored overnight at 4°C for chlorophyll extraction, re-centrifuged, and Chl *a* concentrations determined using a Spectronic Genensys 5 spectrophotometer (Thermo Electron Corporation, Waltham, MA, USA; after Stambler & Dubinsky 2005; Kuguru *et al.*, 2008; Mass *et al.*, 2010), based on the equations of Jeffrey & Humphrey (1975). All data are presented as means plus one standard deviation unless otherwise indicated.

RESULTS

During 2008, the irradiance level in open water near the coral reef was high at the water surface ($1800\ \mu\text{M}\ \text{quanta}\ \text{m}^{-2}\ \text{s}^{-1}$), and decreased exponentially with depth to only $150\ \mu\text{M}$

$\text{quanta}\ \text{m}^{-2}\ \text{s}^{-1}$ at 42 m depth, or 8.3% of surface irradiance (Figure 1A). The attenuation coefficient K_d was $0.058\ \text{m}^{-1}$. Levels of PAR in reef microhabitats occupied by individuals of *Entacmaea quadricolor* varied within each depth and decreased significantly with depth, ranging from 50 to $700\ \mu\text{M}\ \text{quanta}\ \text{m}^{-2}\ \text{s}^{-1}$ (Figure 1A). In shallow areas (3–20 m depth), PAR in anemone microhabitats was significantly lower than that in open water (Mann–Whitney *U*-test, $U = 3.90$, $P < 0.001$). Many anemones on the shallow reef occurred in shaded microhabitats such as under overhangs and in crevices. In contrast, on the deep reef slope (21–43 m depth), many anemones occupied unshaded microhabitats where PAR did not differ significantly from that in adjacent open water ($U = 101.5$, $P = 0.07$).

Individuals of *Entacmaea quadricolor* occurred throughout the examined depth range, and their abundance varied significantly with depth (Kruskal–Wallis test, $H = 19.21$, $P < 0.05$). They were significantly more common at mid-depths on the reef slope (6–20 m) than in either shallower or deeper areas (multiple comparisons tests, $P < 0.05$; peak abundance = 93.3 ± 30.9 individuals per $1000\ \text{m}^2$, or roughly 1 individual per $10\ \text{m}^2$ at 10–15 m depth, Figure 1B), where they received about $100\text{--}500\ \mu\text{M}\ \text{quanta}\ \text{m}^{-2}\ \text{s}^{-1}$ PAR (Figure 1A). On the mid-slope, their oral discs mostly faced sideways (oriented vertically, 72.2%, $N = 72$ anemones examined) with their bases deep in reef holes. Most individuals contacted reef rock (65.3%) or occurred at the rock/sand interface (26.4%), with only a few individuals surrounded by sand (8.3%).

The abundance of microalgal cells within sea anemone tentacles also varied widely among individuals within each depth, but increased significantly with depth (Linear regression, $r = 0.76$, $P < 0.001$, Figure 2A). Microalgal concentration was lowest near the water surface ($5.07 \pm 2.59 \times 10^7$ cells g^{-1} tentacle wet mass, $N = 10$ at 3–10 m depth) and increased about four-fold with depth, reaching $20.31 \pm 5.57 \times 10^7$ cells g^{-1}

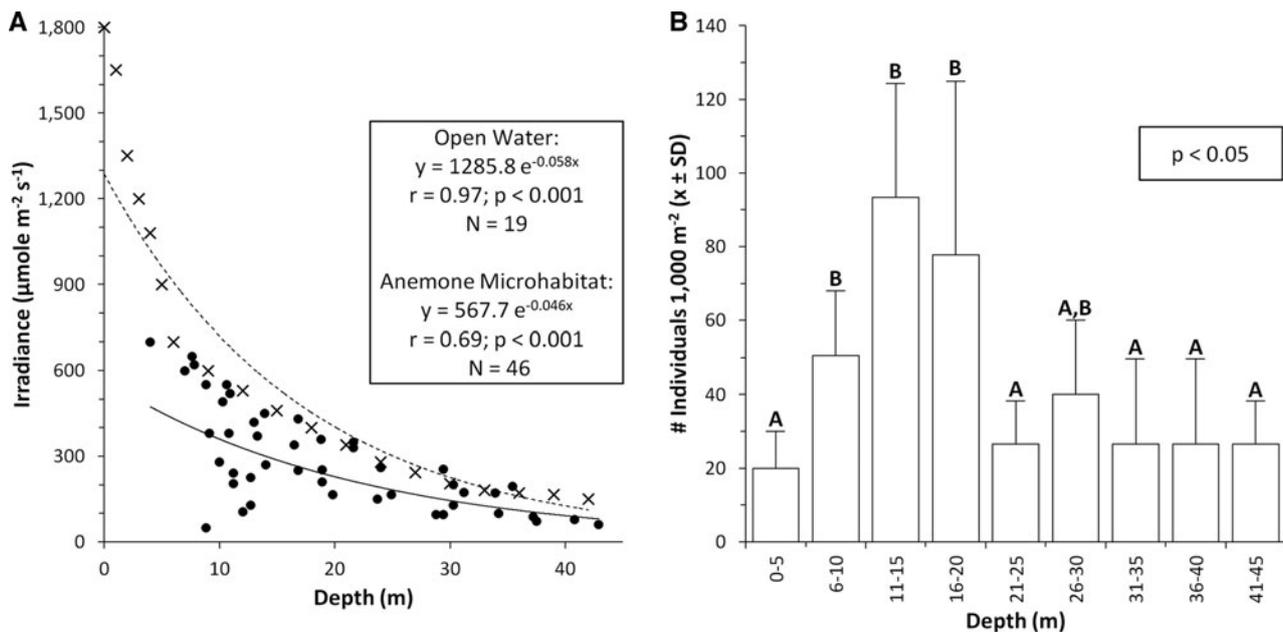


Fig. 1. Levels of photosynthetically active irradiance (PAR) and abundances of bulb-tentacle sea anemones *Entacmaea quadricolor* on a coral reef adjacent to the Marine Science Station in Aqaba, Jordan, northern Red Sea. Variation in: (A) downwelling PAR with depth, in open water near the reef (circles) and in reef microhabitats occupied by sea anemones (x); (B) anemone abundance with depth. Different letters above columns indicate significant differences in abundance among depths. See text for details.

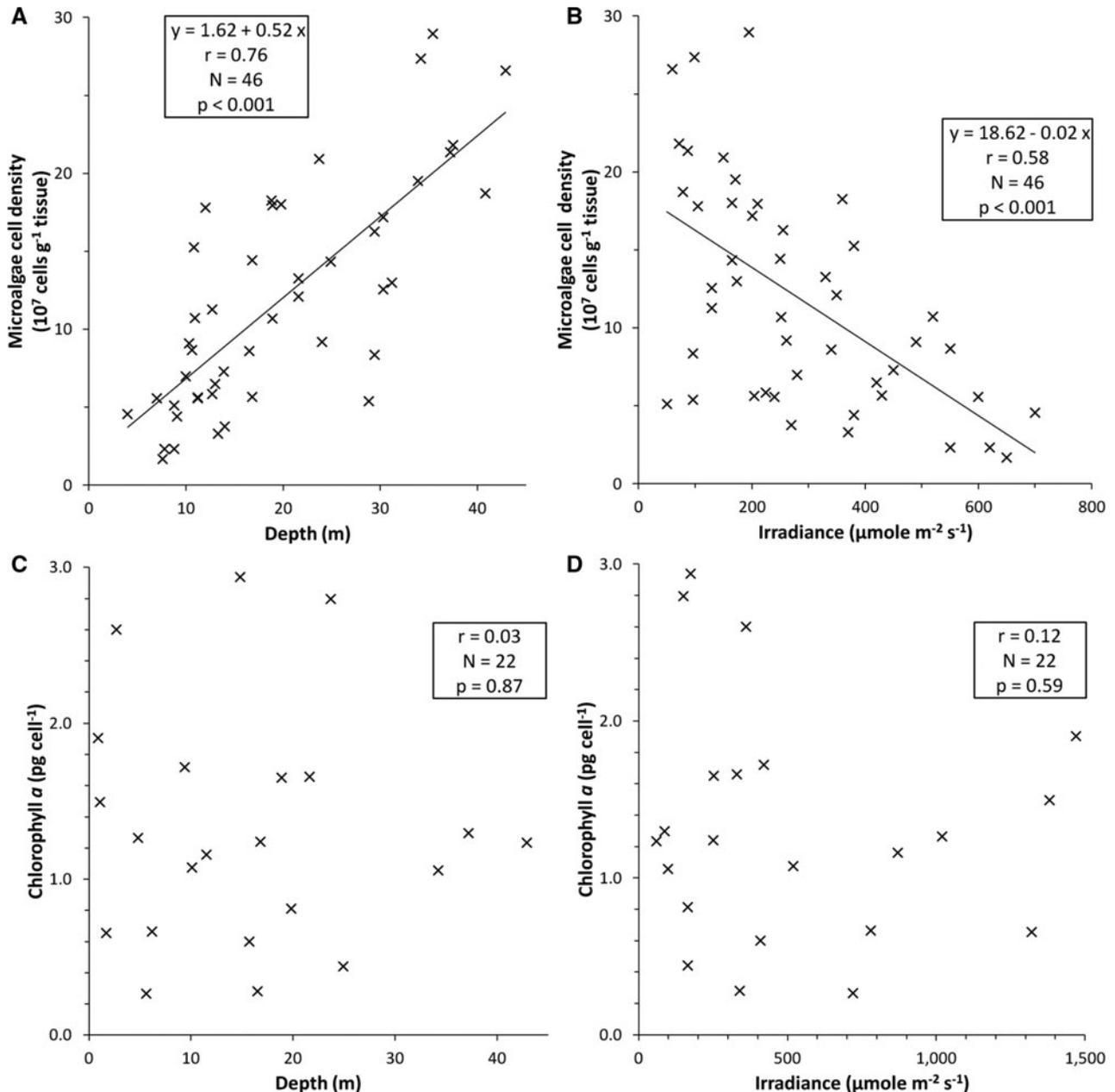


Fig. 2. Densities of endosymbiotic microalgae *Symbiodinium* and chlorophyll per microalgal cell within the tentacles of bulb-tentacle sea anemones *Entacmaea quadricolor* on a coral reef adjacent to the Marine Science Station in Aqaba, Jordan, northern Red Sea. Variation in: (A) abundance of microalgal cells in anemone tentacles with depth; (B) abundance of microalgal cells with levels of irradiance; (C) chlorophyll-*a* concentrations per microalgal cell with depth; (D) chlorophyll-*a* concentrations per microalgal cell with irradiance.

($N = 11$) at 30–43 m depth (Figure 2A). Microalgal concentration in anemone tentacle tips decreased significantly with the level of PAR in anemone microhabitats (Linear regression, $r = 0.58$, $P < 0.001$, Figure 2B), but the relationship was looser than that between microalgal abundance and water depth. Some anemones contained few microalgae even at low irradiance (Figure 2B).

Chlorophyll-*a* concentrations per microalgal cell in anemone tentacles (1.31 ± 0.76 pg cell⁻¹, range = 0.27–2.94 pg cell⁻¹, $N = 22$ anemones) likewise varied widely among individuals within each depth, but did not vary significantly with either depth or PAR level (Linear regressions, $r = 0.032$ and 0.122 , $P = 0.87$ and 0.59 , respectively, Figure 2C, D). Similar to the pattern of microalgal cell

abundance, some anemones contained little chlorophyll even at low irradiance or in deep areas (Figure 2C, D).

DISCUSSION

We demonstrate that the giant sea anemone *Entacmaea quadricolor* inhabits a wide depth range on northern Red Sea coral reefs and appears to photoacclimate to exponentially decreasing PAR with depth, using two major mechanisms. Firstly, shallow individuals occupy shaded reef holes, thus exposing themselves to lower levels of irradiance, including damaging UVR, than in open water. Secondly, individuals increase the abundance of endosymbiotic microalgal cells in their tissues

about four-fold on the deep vs shallow reef slope, thereby greatly enhancing their photosynthetic efficiency as irradiance decreases with depth. The microalgae within these anemones do not appear to increase their per-cell chlorophyll concentrations with depth, in contrast to most stony corals (Dubinsky *et al.*, 1990; Stambler *et al.*, 2008; Mass *et al.*, 2010) and other reef cnidarians (Muller-Parker, 1987; Kuguru *et al.*, 2007, 2010).

The depth profile of PAR observed here (attenuation coefficient $K_d = 0.058 \text{ m}^{-1}$) is almost identical to those reported from other sites in the northern Red Sea, where $K_d = 0.054 \pm 0.006 \text{ m}^{-1}$ (Stambler, 2005), but one recent study revealed even greater light penetration in open water in this region ($K_d = 0.004$; Stambler, 2008). Thus, values from both Israel and Jordan at the northern tip of the Gulf of Aqaba confirm that high water transparency occurs near coral reefs on both sides of this steep, narrow gulf, and that shallow reef organisms here are exposed to some of the highest levels of irradiance on earth (Stambler, 2005, 2008; Mass *et al.*, 2010). Slight deviations from a smooth curve in our light profile may have occurred due to limited accuracy of the diving depth gauge ($\pm 0.1 \text{ m}$), refraction of light due to surface waves, variation in absorption across the water column, and changes in surface intensity during the sampling period, which extended over 1 h during a SCUBA dive.

The vertical oral disc orientation and occupation of shaded reef microhabitats by shallow individuals of *E. quadricolor* (which also occurs at Eilat; Roopin *et al.*, 2011) is similar to both the orientation behaviour and microhabitat use of some mobile fungiid corals (Chadwick-Furman & Loya, 1992) and corallimorpharians (Kuguru *et al.*, 2010) on nearby reefs. These patterns indicate that in shallow water, some mobile cnidarians orient their oral discs away from downwelling irradiance and occupy shaded microhabitats, potentially as protective mechanisms against the damaging effects of high irradiance (reviewed in Muller-Parker & Davy, 2001; Mass *et al.*, 2010). In contrast, on the deep slope ($>20 \text{ m}$ depth), similar levels of PAR in anemone microhabitats and adjacent open water indicate that individuals do not appear to prefer shaded areas when ambient irradiance is low. The oral disc orientations of the anemones were not recorded in deep water, so variation in their orientation behaviour with depth remains unknown.

The high abundance of individuals of *E. quadricolor* measured here (up to 1 individual per 10 m^2 at 10–15 m depth) is more than ten times that on reefs nearby in Israel (~ 6 individuals per 1000 m^2) and more than 100 times that on reefs in Egypt (<1 individual per 1000 m^2 ; Chadwick & Arvedlund, 2005). Thus, coral reefs at Aqaba support much greater abundances of this anemone than do all other reef areas examined in the Gulf of Aqaba, possibly due in part to the relatively pristine condition of many Jordanian coral reefs (Mergner, 1981; Khalaf & Abdallah, 2003; Khalaf *et al.*, 2006). Individuals of the obligate anemonefish *Amphiprion bicinctus* also occur at high abundances of up to 3 individuals per 100 m^{-2} on some reefs at Aqaba (Khalaf *et al.*, 2006). At protected sites in the Philippines, giant anemones including *E. quadricolor* occur at abundances of 2–6 individuals per 1000 m^{-2} (Shuman *et al.*, 2005), which are lower than those in Jordan, but similar to abundances of giant anemones on Egyptian coral reefs (Chadwick & Arvedlund, 2005). Interestingly, recent studies have documented high abundances of *E. quadricolor* on mesophotic reefs at 50–65 m

depth on the Australian Great Barrier Reef (Bridge *et al.*, 2012), which are similar to the values reported here, and even higher abundances at 10–15 m depth in southern Australia (Scott *et al.*, 2011).

The depth distributional patterns of *E. quadricolor* are similar throughout the Gulf of Aqaba, in that individuals occur at all depths on the reef slope, but are most abundant at $<15 \text{ m}$ depth (Chadwick & Arvedlund, 2005). The decrease in anemone abundance at very shallow depths (0–5 m) in Aqaba may relate to the high per cent cover of coral competitors (30–50%) near the reef crest on Jordanian reefs (Mergner & Schuhmacher, 1974; Mergner, 1981; Mergner *et al.*, 1992) in contrast to lower coral abundances on most shallow reefs in Israel (Wielgus *et al.*, 2003; Ben-Tsvi *et al.*, 2011) and Egypt (Hawkins & Roberts, 1994; Hassan *et al.*, 2002). Photoinhibition effects on the anemones at high irradiance in very shallow water also may limit their shallow abundances, and cause them to inhabit shaded habitats in shallow areas. Irradiance patterns can change temporally, both daily and seasonally. The angle of the sun to the reef may influence the shading of anemones within hole and crevice habitats, so that anemones shaded at mid-day may be exposed to direct sunlight earlier or later in the day. By measuring irradiance during the summer at mid-day, we revealed patterns of anemone shading during both a season and time of day with high irradiance, when photoinhibition effects may be most intense. In Australia, giant anemones (mostly *E. quadricolor*) that host anemonefish are most abundant at mid-depths on the reef slope, although in some areas they also are abundant on the deep slope (Bridge *et al.*, 2012). These anemones may reach their physiological optimum at moderate levels of irradiance (about $400\text{--}600 \mu\text{M}$ quanta $\text{m}^{-2} \text{ s}^{-1}$), because very low or high irradiance may cause sub-optimal photosynthetic performance in this and other giant anemones such as *Heteractis crispa*, which exhibits the same depth distributional pattern (Chadwick & Arvedlund, 2005). The anemonefish *Amphiprion bicinctus* occupies large individuals of *E. quadricolor* to 65 m depth in the twilight zone, and is one of the few pomacentrids to extend this deep in the Red Sea (Brokovich, 2008; Brokovich *et al.*, 2008). In Australia, the coral reef pomacentrid *Chrysiptera rollandi* also occurs deep on the reef slope (to 40–50 m), but in contrast to anemonefish, its depth distribution does not relate to the availability of preferred habitat such as a host sea anemone (Hoey *et al.*, 2007). Variation with depth in other physical factors such as water motion, and in biological processes such as predation and competition, also may in part cause these depth distributional patterns (for example, competition with corals near the water surface at Aqaba, see above). However, photoacclimation responses to irradiance appear to be major contributors to the depth-distributional pattern of *E. quadricolor* in the Red Sea.

The increase with depth in microalgal abundance in the tissues of *E. quadricolor* is similar to the pattern observed in other sea anemones (reviewed in Muller-Parker & Davy, 2001) and corallimorpharians (Kuguru *et al.*, 2007, 2010), and in a few species of stony corals (Titlyanov *et al.*, 2001; Stambler *et al.*, 2008). In contrast, most stony corals increase chlorophyll concentration per microalgal cell with decreasing irradiance and increasing depth (Falkowski & Dubinsky, 1981; Dubinsky *et al.*, 1990; Mass *et al.*, 2010). The four-fold increase in microalgal abundance with depth observed here greatly enhances the photosynthetic efficiency

of *E. quadricolor*, and appears to allow for the maintenance of large body size in deep individuals. Symbiotic sea anemones such as *E. quadricolor* may depend heavily on photosynthate from their endosymbiotic microalgae, which can provide up to 100% of anemone metabolic energy needs and be important for the maintenance of body size (Muller-Parker & Davy, 2001). Individuals of this species on nearby reefs at Eilat do not vary their microalgal abundance with depth between 5 and 20 m, but their microalgal levels decrease significantly with irradiance in the microhabitats they occupy (Roopin *et al.*, 2011). The latter depth range may be too narrow to detect microalgal trends with depth; however, in shallow water the anemones occur in reef holes, thereby reducing their exposure to high irradiance near the water surface, resulting in the trend with irradiance but not depth. Results obtained here for Aqaba also are similar to those from Eilat, in that shallow individuals harbour concentrations of about $5-20 \times 10^7$ microalgal cells g^{-1} tentacle wet mass at both sites (Roopin *et al.*, 2011; Figure 2A). The microalgal concentrations reported here also are similar to those in the tissues of other sea anemone species (Stambler & Dubinsky, 1987) and in starved individuals of *E. quadricolor* under laboratory conditions, but are lower than for anemones exposed to ammonia supplements or anemonefish in the laboratory, where microalgae can reach $>30 \times 10^7$ cells g^{-1} (Roopin & Chadwick, 2009). These patterns demonstrate that exposure to both high nutrients and low irradiance can enhance concentrations of microalgae in the tissues of these sea anemones.

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