



Photoacclimation mechanisms of corallimorpharians on coral reefs: Photosynthetic parameters of zooxanthellae and host cellular responses to variation in irradiance

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ABSTRACT

Rhodactis rhodostoma and *Discosoma unguja* are the most common corallimorpharians on coral reefs in the northern Red Sea, where individuals of *R. rhodostoma* form large aggregations on intertidal reef flats and those of *D. unguja* occupy holes and crevices on the reef slope. Aside from these contrasting patterns of microhabitat, little is known concerning their mechanisms of photoacclimation to environmental conditions. We demonstrate here that different mechanisms of photoacclimation operate in both species and that these differences explain, in part, the contrasting patterns of distribution and abundance of these common corallimorpharians. Experimental exposure of the species' respective polyps to the synergistic effects of ultraviolet and photosynthetically active radiation revealed that endosymbiotic zooxanthellae protected the host *R. rhodostoma* from photooxidation damage. Zooxanthellae do so by reducing their chlorophyll pigment and cellular abundance, as well as by adjusting their efficiency of light absorption and utilization according to the level of irradiance. The host photoprotects its endosymbionts from harmful ultraviolet radiation (UVR) by synthesizing enzymatic antioxidants against oxygen radicals. In contrast, individuals of *D. unguja* utilize a behavioral mechanism of photoacclimation in which they physically migrate away from exposed areas and towards shaded habitats and thus avoid the damaging biological effects of UVR. We conclude that a combination of physiological and behavioral mechanisms appear to control microhabitat segregation between these corallimorpharian species on tropical reefs. These various mechanisms of local adaptation to environmental conditions may be largely responsible for the wide distributional ranges of some corallimorpharians, and may enable these common reef organisms to tolerate environments that are highly variable, both spatially and temporally.

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1. Introduction

Corallimorpharians are non-calcifying, evolutionarily important relatives of stony corals (Medina et al., 2006), although the exact relationship between Corallimorpharia and the Scleractinia remains under debate (Fukami et al., 2008). Increased understanding of the ecophysiology of corallimorpharians can provide insights into the evolution of corals from Mesozoic to recent forms (Stanley and Fautin, 2001) and their ability to survive drastic climatic changes.

Coral reefs are among the most vital and biologically diverse ecosystems on the planet. Despite their great value, both ecological and socio-economical, however, coral reefs are severely threatened by anthropogenic global climate change (IPCC, 2001; IPCC, 2007). The

steady rise in atmospheric CO₂ has led to higher sea surface temperatures (SST) (Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2002, 2007) and lower pH levels. Increasing atmospheric CO₂ has been postulated to deplete the ozone layer (Austin et al., 1992), leading to an increase of ultraviolet radiation (UVR) on the oceans' surfaces (Harley et al., 2006). Understanding the protective mechanisms used by marine organisms to mitigate the damage caused by UVR is particularly urgent today, as the thinning of atmospheric ozone by greenhouse gases has magnified the intensity of UVR reaching the sea surface in some areas (McKenzie et al., 1998). In clear tropical seawater, UVR penetrates to ecologically important depths (Gleason and Wellington, 1993). UVR radiation breaks down dissolved organic carbon (Hader et al., 2007), which is responsible for short-wavelength absorption in the water column. In addition, oceanic warming and acidification results in faster degradation of dissolved and particulate organic carbon (DOC, POC), thereby enhancing the penetration of UVR into the water column (Sinha and Hader, 2002). Short-term increases in UVR intensity under calm, clear water conditions may expose

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marine algae and invertebrates to photophysiological effects of UVR stress (Gleason and Wellington, 1993). As a result, the productivity of marine ecosystems may be greatly and adversely affected (Sinha and Hader, 2002).

Tropical reef-building corals and other photosynthetic marine invertebrates live in habitats where solar irradiance may be extremely high (Shick et al., 1996; Lesser, 2000; Banaszak and Lesser, 2009). Several studies have implicated exposure to elevated solar radiation, including both photosynthetically active radiation (PAR, 400–700 nm, Hoegh-Guldberg and Smith, 1989; Lesser and Shick, 1989) and UVR (290–400 nm, Lesser and Stochaj, 1990; Kinzie, 1993; Baruch et al., 2005; Lesser and Shick, 1989), as a major contributor to coral bleaching stress. In particular, UVB (290–320 nm) suppresses photosynthesis while simultaneously increasing the risk of damage to DNA, proteins, and membrane lipids (Greenberg et al., 1989; Lyons et al., 1998; Baruch et al., 2005), partly through the production of reactive oxygen species (ROS) (Lesser, 1989; Lesser and Lewis, 1996; Shick et al., 1996; Jokiel et al., 1997; Tchernov et al., 2004). While the photophysiological effects of UVR stress in some hexacorallians (scleractinians, actinarians and zoanthids) have been studied extensively, corallimorpharians have been almost completely overlooked in this context.

Like many marine invertebrates, some corallimorpharians harbor endosymbiotic dinoflagellate algae, also known as zooxanthellae (den-Hartog, 1980; Lajeunesse, 2002; Kuguru et al., 2007, 2008). Zooxanthellae play a critical role in host nourishment via the translocation of photosynthates (Muscatine et al., 1981). Recent studies have demonstrated that zooxanthellae are made up of eight broad clades (designated A–H), each of which contains multiple, closely related molecular types that exhibit a range of physiological responses and tolerances (reviewed in Coffroth and Santos, 2005; Stat et al., 2006). The specific *Symbiodinium* type(s) that an organism harbors may affect its distribution and reaction to extreme environmental conditions (Robison and Warner, 2006). In the Red Sea, the common corallimorpharians *Rhodactis rhodostoma* and *Discosoma unguja* both host *Symbiodinium* type C1 in shallow waters (1–6 m), and types D1a and C1 in deeper waters (18–20 m) (Kuguru et al., 2007, 2008). A recent study in Australia (Jones et al., 2008) indicated that both clades C1 and D1 may confer equal thermotolerance to host corals. Both of the above corallimorpharian species, when transplanted from their original habitats to either shallower or deeper water, shuffle their symbiont types, a mechanism that may contribute to their occupation of a wide bathymetric range on coral reefs (Kuguru et al., 2008). However, individuals of *D. unguja* are more susceptible to light stress than are those of *R. rhodostoma*, and tend to occur in deeper, more shaded habitats (Kuguru et al., 2008). The mechanisms employed by these two corallimorpharians to photoacclimatize to microhabitats on the coral reef that differ in level of irradiance (UVR + PAR) are not yet understood.

The success of corals and other reef invertebrates that have essentially transparent tissues but manage to thrive in shallow water indicates that they have developed effective mechanisms for UVR protection. There are substantial differences between closely related species in their ability to escape the damaging effects of UVR in this high-energy waveband (Sinha and Hader, 2002). The ability of scleractinian corals and other reef organisms to survive environmental changes depends on their physiological mechanisms of acclimatization (Gates and Edmunds, 1999). Many symbiotic cnidarians display rapid modifications in behavior, morphology, and physiology that enable them to photoacclimate to changing light conditions, thus demonstrating considerable biological flexibility. Shallow reef organisms exposed to high levels of solar UVR have evolved several types of photoacclimation mechanisms to cope with light stress, including: (1) behavioral avoidance, such as migrating away from intense light (Gleason et al., 2006) and into shaded microhabitats (crevices and holes on the reef); (2) mechanisms to control internal cellular damage, such as development of free-radical quenching agents like

carotenoids, xanthophyll pigments, and antioxidants [both enzymatic, i.e., superoxide dismutase (SOD) and catalase; and non-enzymatic, i.e., vitamin E (Lesser, 2006)]; (3) changes in tissue structure and morphology (Brown et al., 1994; Loya et al., 2001; Kuguru et al., 2007; Mass et al., 2007); and (4) sunscreens in the form of UV-absorbing compounds (UVAC), also known as mycosporine-like amino acids (MAAs) (Shick et al., 1999; Banaszak et al., 2000). These mechanisms of photoacclimation vary among species of symbiotic host cnidarians, partly because their zooxanthellae comprise a highly divergent group of dinoflagellates (Coffroth and Santos, 2005) with a broad range of genotypic and phenotypic responses to light (Iglesias-Prieto and Trench, 1994, 1997; Savage et al., 2002; Robison and Warner, 2006), which in turn influence their ecological distributions (Lajeunesse, 2002; Iglesias-Prieto et al., 2004).

In addition, variation among host species in traits such as behavior [e.g., polyp retraction (Brown et al., 1994), and contraction/expansion (Brown et al., 2002)], gastrodermal tissue structure (Kuguru et al., 2007), skeletal structure (Mass et al., 2007), and light absorption by fluorescent proteins (Salih et al., 2000), all potentially modulate the available light and, thereby, impact the photochemical response of their endosymbionts. While species-specific patterns of photoacclimation have been elucidated for marine algae (Huner et al., 1996), stony corals (Falkowski and Dubinsky, 1981; Warner and Berry-Lowe, 2006), and actinian sea anemones (Stoletzki and Schierwater, 2005), almost nothing is known about mechanisms of response to light stress in corallimorpharians.

The corallimorpharians *R. rhodostoma* and *D. unguja* are both common on coral reefs in some areas of the Indo-Pacific, and are successful recolonizers of shallow habitats following disturbances such as bleaching, which kill stony corals and other zooxanthellates (Chadwick-Furman and Spiegel, 2000; Kuguru et al., 2004; Work et al., 2008). They occupy contrasting microhabitats on the reef: individuals of *R. rhodostoma* form large aggregations on intertidal reef flats while those of *D. unguja* occupy holes and crevices deeper on the reef slope (Muhando et al., 2002; Kuguru et al., 2008). Effects of UVR are expected to be highly pronounced in the Red Sea, which is classified as an oligotrophic class II water body, representing one of the most optically clear water bodies in the world (Stambler, 2005). Thus, understanding differences in mechanisms of UVR acclimation between these two corallimorpharians may provide insights into their bathymetric distributional patterns and predict the extent to which they can withstand climate change. The objective of the present study was to experimentally assess the photoacclimation mechanisms of these two corallimorpharian species in response to increased PAR and UVR in terms of the photosynthetic parameters of their zooxanthellae density and the cellular responses of their tissues.

2. Materials and methods

2.1. Study site and polyp collection

This study was conducted during the period January–August 2007 at the Interuniversity Institute for Marine Sciences (IUI), in Eilat, Israel, in the northern Red Sea (29°30'N, 34°55'E). Polyps of the corallimorpharians *R. rhodostoma* and *D. unguja* were collected on coral reefs adjacent to the IUI at depths of 3–20 m, and attached to polyvinyl chloride (PVC) bases using underwater epoxy. Care was taken to ensure that the replicate polyps were located at least 10 m apart from each other, to avoid collecting individuals that originated asexually from the same parent colonies. Following a one-month acclimation period in outdoor aquaria (irradiance of 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PAR), equivalent to that at 18–20 m depth, flow-through seawater at 120 L h^{-1}), the polyps were transferred to experimental aquaria for treatments (see below, modified after Kuguru et al., 2007, 2008).

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