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ENVIRONMENT-INDUCED COLOUR CHANGES IN THE MASSIVE CORALS *DIPSASTRAEA SPECIOSA* AND *DIPLOASTREA HELIOPORA*

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ABSTRACT. — Environment-dependent variation in the morphological, physiological or behavioural expression of a genotype is termed phenotypic plasticity. Twelve colonies of both *Dipsastraea speciosa* and *Diploastrea heliopora*, two common Indo-Pacific massive corals, were tested for plastic responses by transplanting palm-sized fragments (clone-mates) over six stations (three reefs × two depths) in Singapore's southern waters. After 15 weeks, there were no major changes in colour among the fragments transplanted to the shallow stations, with the typical grey of *Diploastrea heliopora*, and the bright green oral discs of the *Dipsastraea speciosa* polyps, clearly represented. The fragments at the two deepest stations, however, changed dramatically. The oral discs of *Dipsastraea speciosa* lost their bright green pigmentation and the surrounding tissue turned pale brown. The response from *Diploastrea heliopora* was even more pronounced, with yellow-pinks and pale greens replacing its usual grey pigmentation. Plasticity in colour was evident for both species, and probably light-induced, however, further work is required to determine whether such changes are adaptive.

KEY WORDS. — acclimatisation, colour, depth, phenotypic plasticity, reef, sediment, Singapore

INTRODUCTION

Even though it is well known that corals exhibit a wide range of colours within and among species, their function remains largely unexplored (Takabayashi & Hoegh-Guldberg, 1995; Salih et al., 1998). The most vivid colours, the brilliant greens, blues, and reds, are host (animal) based and related to Green Fluorescent Proteins (GFPs), probably pocilloporins (Dove et al., 2001; Shagin et al., 2004; Oswald et al., 2007; Gruber et al., 2008). These are generally found in the epithelial cells of the coral polyp (Salih et al., 2000; Mazel et al., 2003), usually above the zooxanthellae in high light environments and below them in low light environments (Schlichter et al., 1994; Salih et al., 1998; Dove et al., 2001). They have also been found in close association with zooxanthellae in the gastroderm (Oswald et al., 2007). In addition, a family of non-fluorescent proteins known as chromoproteins (CPs) contributes to the bright purple and blue colours displayed by some species (Dove et al., 2001; Shagin et al., 2004). The brown colour common to most corals is attributed to their algal symbiont: zooxanthellae (Hochberg et al., 2003). The algal pigments enable the zooxanthellae to utilise light of different wavelengths for photosynthesis. Of the spectrum that makes up photosynthetically active radiation (PAR), 400–550 nm is absorbed by chlorophyll *a*, chlorophyll *c*, and the carotenoid peridinin, whereas 650–700 nm is absorbed almost entirely by chlorophyll *a* (Falkowski et al., 1990). The host pigments are believed to have at least two, non-exclusive, purposes, i.e., to protect the coral from harmful ultra-violet radiation (UVR) (Salih et al., 2000; Dove et al., 2001), and to absorb UVR and re-emit the energy at longer wavelengths that can be photosynthesised (Schlichter & Fricke, 1990). It has also been proposed that GFPs have a role in attracting zooxanthallae, which are drawn to green light (Hollingsworth et al., 2005).

Short UVR wavelengths are damaging to coral reef epifauna (Jokiel, 1980). Of the ultra-violet spectrum, UV-A (320–400 nm) is considered the least deleterious, UV-B (280–320 nm) is highly biocidal, but the majority of the lethal UV-C (200–280 nm) does not reach Earth's surface (Jokiel & York, 1982). Corals taken from deep water, where less UVR penetrates, tend to be more sensitive to UVR than those acclimatised to the shallows (Falkowski et al., 1990). Elevated UVR causes greater photosynthetic activity and production of O_2, which results in a proportionate increase in production of reactive oxygen species (ROS) (Jamieson et al., 1986). These ROS collectively lead to a condition known as photo-oxidative stress, causing damage to DNA, membrane proteins, enzymes, lipids, and photosystem components (Lesser, 2006), eventually causing coral bleaching (Downs et al., 2002). UVR photo-inhibition is a result of chloroplast damage (Jokiel & York, 1982) and photo-pigment destruction (Wood, 1987). GFPs are thought to be part of a broad antioxidant defence system as they neutralise O_2, a ROS (Bou-abdallah et al., 2006). Further, GFPs may also directly convert excess UVR into radiation at wavelengths less detrimental to the zooxanthellae (Dove et al., 2001). They are, however, not physical barriers to UVR (D'Angelo et al., 2008).

As the variation in both host and zooxanthellae pigment types and quantities can often be correlated to light character and intensity, they are believed to be photo-adaptive (Jokiel & York, 1982; Chalker et al., 1983; Titlyanov, 1991; Salih et al., 1998). Light is directly linked to the expression of pigment proteins, causing either an increase or decrease in concentration of different pigments when intensity is increased (D'Angelo et al., 2008). Jokiel & York (1982) found more near-UV absorbing substances (identified as mycosporinelike amino acids [MAAs] by Dunlap & Chalker [1979]) in *Pocillopora damicornis* in high UVR environments. The green and brown morphs of *Porites astreoides* (Caribbean coral) have different depth distributions with the green morphs, more abundant in shallow (≤2 m) waters, better able to endure UVR (Gleason, 1993). The green morphs have more MAAs which block 310–360 nm but are transparent to PAR. Total concentrations of MAAs decreased with depth in 10 species of coral from Hawaii and Belize (Banaszak et al., 1998), and UVR had a significant positive effect on the quantity of MAAs present in colonies of the coral *Porites compressa* (Kuffner, 2001).

It has also been suggested that other animal pigments absorb UVR and fluoresce the energy as longer wavelengths suitable for photosynthesis (Falkowski et al., 1990), possibly giving the host coral a competitive edge in low light environments (Schlichter et al., 1994). Wavelength tranformance in the deep-water (95–145 m) coral *Leptoseris fragilis* is believed to help this species survive in extremely low light conditions (Schlichter & Fricke, 1990, Kaiser et al., 1993). In 17 out of 71 zooxanthellate species, Schlichter et al. (1994) detected autofluorescent chromatophores transforming 365–410 nm wavelengths into 430–500 nm. Zooxanthellae and the autofluorescent chromatophores are often found densely packed in the oral area (Schlichter & Fricke, 1990; Schlichter et al., 1994). However, Gilmore et al. (2003) and Mazel et al. (2003) disagree that GFPs enhance photosynthesis, as there is no observable photon transfer between GFPs and zooxanthellae. Although widespread, the specific function that GFP serves in the coral host has yet to be determined conclusively (Mazel et al., 2003; Field et al., 2006; Oswald et al., 2007).

In zooxanthellae, pigmentation usually increases in each cell with depth, but the actual number of cells can increase or decrease (Falkowski et al., 1990, Kaiser et al., 1993; Iglesias-Prieto & Trench, 1994). Zooxanthellae densities decreased with depth while content of pigment per cell increased in *Leptoseris fragilis* (Kaiser et al., 1993), *Fungia repanda*, and *Fungia echinata* (Masuda et al., 1993). In the pocilloporid *Stylophora pistillata*, the density of zooxanthellae and their pigmentation concentration both increased under 30% and 8% surface PAR, but at 0.8% surface PAR zooxanthellae were lost through degradation (Titlyanov et al., 2001). Zooxanthellae with higher levels of pigment become more efficient light harvesters at greater depth, but why their density should change is less clear (Titlyanov et al., 2001).

Even though Salih et al. (1998) and Schlichter et al. (1994) explain where pigments are concentrated in the coral tissue, few authors describe in detail how study corals actually look in differing environments, or before and after transplantation. During a large study to test for morphological plasticity in two massive coral species: *Dipsastraea speciosa* and *Diploastrea heliopora* (Todd et al., 2004), dramatic changes in pigmentation were observed. Photographs of these changes were published by Todd et al. (2002a), but with very little accompanying explanatory text. Here we discuss in greater depth, the colour changes, their probable causes, and their potential functional significance.

MATERIAL AND METHODS

The methods for the transplant part of this study are described in full in Todd et al. (2004). In brief: in May 2000, fragments of *Dipsastraea speciosa* (formerly *Favia speciosa*; Budd et al., 2012) and *Diploastrea heliopora* were reciprocally transplanted among three reefs: Cyrene Reef, Pulau Hantu, and Raffles Lighthouse. Cyrene Reef is a submerged reef close to Singapore Island (4 km), heavily impacted by sediment originating from nearby dredging of shipping lanes, reclamation activities, and river discharge. Pulau Hantu is a small island, 7.5 km from Singapore Island. As a result of the many surrounding islands and reefs, Pulau Hantu has the calmest waters of the three study reefs. Raffles Lighthouse is situated 15 km offshore with open sea to the south and is the least affected by sedimentation (but possibly exposed to more wave action).

Two stations were established at each reef, one deep and one shallow (the depths of each station are provided in Fig. 1). Four colonies of both species were sampled randomly from each of the three reefs. From every colony, six fragments (clone-mates) were excised and distributed randomly throughout the six stations (3 reefs × 2 depths). At each station, 24 fragments (12 of each species), with their tissue-covered surface facing upwards, were attached to rectangular aluminium racks at a height of ~0.45 m above the substrate. Fifteen weeks after the corals fragments were moved to their new habitats, 2:1 photographs were taken of all specimens in situ and with a Nikonos V camera loaded with Fujichrome 'Velvia' colour slide film (ASA 50). Flash lighting and distance from the coral was fixed for all photographs taken. The resultant images were grouped by genotype and examined for phenotypic change.

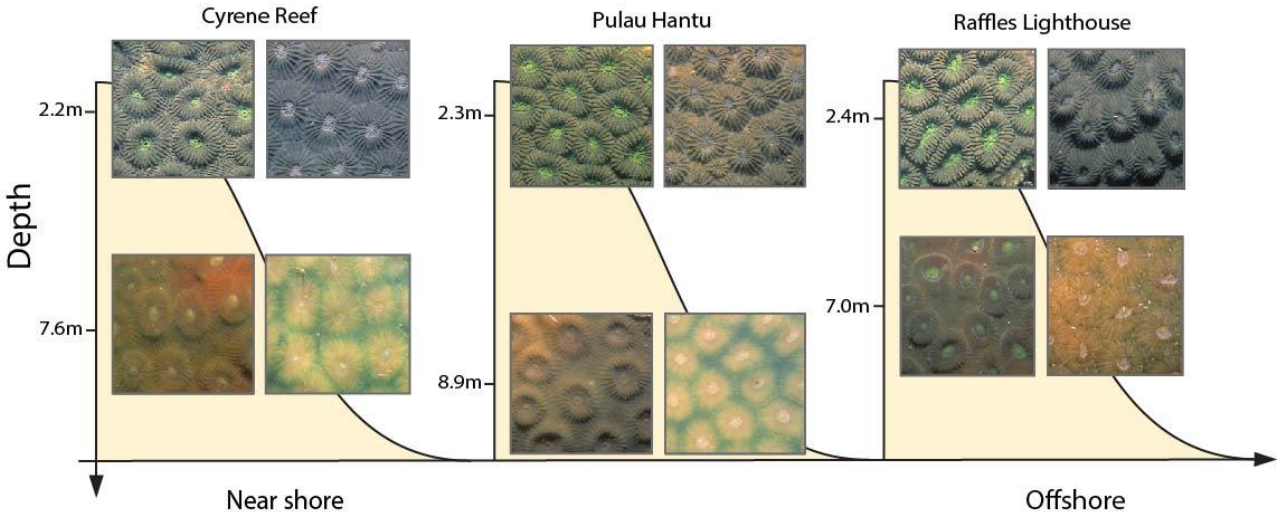

Fig. 1. Fragments (clone-mates) of *Dipsastraea speciosa* and *Diploastrea heliopora* were reciprocally transplanted across six stations (3 reefs × 2 depths). The depth (below mean sea level) of each station is provided on the y-axis. These representative images were taken 15 weeks later. For each pair of images, *Dipsastraea speciosa* is always on the left and *Diploastrea heliopora* is always on the right. Note: For each species, all six fragments originated from the same donor colony.

RESULTS

After 15 weeks of transplantation, the shallow water fragments at Cyrene were most similar to how *Dipsastraea speciosa* and *Diploastrea heliopora* appeared in their 'natural' environment. There was no obvious change in pigmentation, with the typical grey of *Diploastrea heliopora*, and the bright green oral discs of the *Dipsastraea speciosa* polyps, clearly represented (Fig. 1). The fragments at the deep station, however, changed dramatically. The oral discs of *Dipsastraea speciosa* lost their bright green pigmentation and the surrounding tissues turned pale brown. The response from *Diploastrea heliopora* was even more pronounced, with very little of its characteristic grey pigmentation remaining. The coral also appeared to have lost its undulating topography.

At Pulau Hantu (shallow station), the lateral and vertical expansion of polyps discerned by the morphometric analysis of cleaned skeletons by Todd et al. (2004) was clearly visible (Fig. 1). Furthermore, six buds could be seen growing in between mature *Diploastrea heliopora* polyps, as described by Todd et al. (2002b). The topography of this fragment also appeared rugged when compared to Cyrene Reef (shallow station). At the deep station, the oral discs of *Dipsastraea speciosa* were only distinguishable from the surrounding tissue by their shape in relief, not by their colour. The polyps appeared lacklustre. Similar to Cyrene Reef (deep station), the tissue of *Diploastrea helipora* had a translucent quality.

For the fragments transplanted to the shallow station at Raffles Lighthouse, the polyps of both species, and particularly those of *Diploastrea heliopora*, were more exsert than at Cyrene Reef (shallow station) and pigmentation was strong for both species (Fig. 1). At the 7 m station (the least deep and least sediment-impacted of the deep stations), the loss of pigmentation was not so dramatic compared to the other deep sites, for example, the green oral discs of *Dipsastraea speciosa* were still visible and colours in the *Diploastrea heliopora* fragments were more pronounced.

DISCUSSION

The timing and nature of this survey enabled observations to be made that were not feasible later on as, by the end of 30 weeks when the experiment was terminated, many of the deep fragments at Cyrene Reef and Pulau Hantu were severely degraded, making comparisons of all six cogeners impossible. The images presented here, taken after 15 weeks and representative of the overall results, illustrate both physiological and morphological plasticity in *Dipsastraea speciosa* and *Diploastrea heliopora* (Todd et al., 2002a), with changes in colour especially clear. The changes in morphology that occurred have been described in detail elsewhere (Todd et al., 2004; Todd, 2008), therefore, only the induced changes in pigmentation will be considered here.

Kawaguti (1937) suspended clone-mates of *Pavona praetora* at 1-m intervals to a depth of 10 m in the sea near Palao, South Pacific (underwater visibility 6–7 m). After three weeks the specimens had turned yellowish near the surface, reaching a maximum in brown colouration at 4 m and becoming paler again between 4–10 m. The pattern of colouration observed by Kawaguti (1937) is similar to that of *Dipsastraea speciosa* in the present study if the deep station at Raffles Lighthouse is considered an intermediate site for light (being shallower and in less sedimented waters

than the other two deep sites). Fig. 1 illustrates how the fragments transplanted to 7 m at Raffles Lighthouse were darker than those moved to shallow and deep stations elsewhere. As an increase in UVR and PAR reduces the photosynthetic capabilities of symbiotic algae (Lesser, 2000), the amount of photosynthetic pigments and therefore intensity of these browns usually decreases with increased UVR and PAR (Oswald et al., 2007; Torres et al., 2007). Correspondingly, fragments of *Dipsastraea speciosa* at shallow stations appeared less brown compared to the fragments from the deep stations.

Lewis (1974) found juveniles of *Favia fragum* were almost colourless after 12 weeks of dark incubation and Miller (1995) noted that whereas exposed colonies of *Oculina arbuscula* were brown, those living under overhangs were white. These finding are analogous to the changes in *Diploastrea heliopora*, which displayed an inverse relationship between pigmentation and depth (Fig. 1), i.e., a mid-grey colouration in the shallows, changing to light ruddy-brown at Raffles Lighthouse (deep station), finally turning to pale yellow-pink, with inter-polyp areas of mid-green, at the greatest depths. Titlyanov et al. (2001) found, as a result of zooxanthellae degradation, a net loss of chlorophyll per polyp for *Stylophora pistillata* in extremely low light (0.8%). A similar loss of zooxanthellae in *Diploastrea heliopora* and *Dipsastraea speciosa* may explain the paleness of fragments transplanted to the deep stations at Cyrene Reef and Pulau Hantu, where conservative estimates of light penetration to are, respectively, 1.13% and 0.58% surface PAR (Todd et al., 2004). Being located slightly shallower and with greater light penetration, the fragments at Raffles Lighthouse (deep station) displayed a darker brown colour compared to colonies at Cyrene and Pulau Hantu, which had distinctive pale green inter-polyp areas (Fig. 1). The increasing intensity of these green lines with decreasing light seems to suggest a photo-enhancement role to assist zooxanthellae photosynthesis under reduced light conditions. The cause for the loss of zooxanthallae with increasing depth is less clear, but may be because the zooxanthellae type hosted by the coral could not survive at such low light levels.

At Raffles Lighthouse (deep station), *Dipsastraea speciosa* appeared to be gaining pigmentation whereas *Diploastrea heliopora* seemed to be losing it. This may have been related to their different depths of origin. Around Singapore, *Dipsastraea speciosa* is common between 3–6 m, but *Diploastrea heliopora* is more frequently found in depths of <3 m. Therefore, the deep station at Raffles Lighthouse, with irradiance levels of only ~1.55% surface PAR (Todd et al., 2004), may be more detrimental to *Diploastrea heliopora* than *Dipsastraea speciosa.* Contrary to this argument, at the termination of this experiment (15 weeks after these images were taken) *Diploastrea heliopora* appeared to have experienced less tissue loss than *Dipsastraea speciosa* at all the deep stations.

Dipsastraea speciosa around Singapore is characterised by its bright green oral disc (probably due to GFPs). If the pigment causing this colouration aided photosynthesis through auto-fluorescence, then it could be expected to be more apparent, or at least equally apparent, in low light. Instead, the intensity of the green diminished with depth, suggesting that it is an UVR absorbing and/or reflecting pigment that is redundant in deeper waters where UVR levels were reduced. Only the deep station at Raffles Lighthouse still supported *Dipsastraea speciosa* with green oral discs, again probably due to more light penetrating here than the deep stations at Cyrene Reef and Pulau Hantu.

Since the sites differed primarily in the amount of light reaching the fragments, it would seem that pigment levels in *Dipsastraea speciosa* and *Diploastrea heliopora* are regulated by light intensity. For both species, there was a change in colouration from predominantly beige (for *Dipsastraea speciosa*) and grey (for *Diploastrea heliopora*), to various intensities of brown, yellow and green.. The increase in depth may have reduced the expression of certain host pigments responsible for the colours at the shallow stations, possibly because of reduced need for protection from UVR, thereby allowing the brown colour of the symbionts to be displayed more prominently. Zooxanthellae density may also have affected the intensity of the colours exhibited. It is not known, however, whether the concentration of photo-pigments in zooxanthellae increased, or only became visible due to the absence of host pigments masking their colours. It would be insightful to know the quantities of each pigment, and the density of zooxanthellae, in the various clone-mates before and after transplantation but, unfortunately, these data were not collected. Plasticity in colour is evident in both species and probably light-induced, however, further work is required to determine whether such changes are adaptive.

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