

Photoprotection of Symbiotic Dinoflagellates by Fluorescent Pigments in Reef Corals



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ABSTRACT

The symbiotic algae of reef-building corals are vulnerable to the high irradiances typical of shallow tropical coral reefs. Whilst the protective properties of ultraviolet (UV) absorbing compounds, the mycosporine-like amino acids, are well known for their role in screening out UVB radiation, they have only a limited protection against the effects of the longer wavelengths of UVA and blue light. Many corals are not only brightly coloured but also show an intense turquoise or green autofluorescence under UV light due to the presence of pigment chromatophores. Despite some early speculation that coral autofluorescence may play a role in photoprotection, very little is known of the function of such animal-based colours in corals. Using confocal imaging, we have mapped the three-dimensional morphology of the fluorescent granules in corals. Their aggregation in cellular layers above the layers of symbiotic dinoflagellates suggests solar screening of the endosymbionts. By comparing their distribution between light- and shade-acclimated corals, we provide evidence that fluorescent granules of corals function as screens against high UVA/blue irradiances by absorbing these wavelengths as well as by reflecting a large proportion of visible light (photosynthetically active radiation, PAR). A second function for these granules is also proposed in shade-acclimated corals in which they are present below or among the symbiotic dinoflagellates. In these corals, fluorescent pigments appear to have an alternative light enhancement role and their presence below or among symbiotic dinoflagellates indicates that they may amplify the available light and thereby enhance photosynthesis through fluorescent coupling, back scattering and reflection.

INTRODUCTION

The brilliant colours of reef corals are well known (e.g. Takabayashi & Hoegh-Guldberg, 1995; Dove *et al.*, 1995). Equally spectacular is the intense turquoise or green fluorescence that often adorns the tissues of reef-building corals, and is stimulated by either UV or visible light (Phillips, 1927; Catala, 1959; Logan *et al.*, 1990; Schlichter *et al.*, 1994; Mazel, 1995). The function of the fluorescence of coral tissues is still very poorly understood, despite some remarkably astute early speculations that it may play a role in photoprotection (Kawaguti, 1944) and/or in the enhancement of light available for photosynthesis of coral's symbiotic algae (Kawaguti, 1969). According to Kawaguti, short wavelength radiation may be absorbed by the host's tissue pigments, transformed into longer wavelengths via their fluorescence, and utilised by symbiotic dinoflagellates in corals living under light-limited conditions. The hypothesis that coral fluorescence enhances the photosynthesis of the symbiotic dinoflagellates was substantiated recently by the discovery of light-amplifying fluorescent pigments in the deep-water coral *Leptoseris fragilis* (Schlichter *et al.*, 1986; Fricke *et al.*, 1987; Schlichter & Fricke, 1991). The fluorescent granules in this species were found in gastrodermal (hereafter referred to as endodermal) chromatophores underlying the symbiotic dinoflagellates, thereby increasing the probability of light absorption by wavelength transformation and back-scattering.

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A survey of Red Sea corals from a variety of depths also revealed the presence of fluorescent chromatophores in 17 out of 71 symbiotic species studied, many of which were collected from relatively shallow depths (Schlichter *et al.*, 1994). Multilobed chromatophores were found to be packed with fluorescent granules (0.5-1.0 μm in diameter) and located mostly in host endoderm (gastrodermis), with only a few coral species showing ectodermal (epidermal) fluorescent chromatophores. In both cases, their function in photoacclimation was suggested to be linked to light enhancement for photosynthesis of symbiotic dinoflagellates, and not for photoprotection. Thus, while a number of studies found strong evidence to support Kawaguti's (1969) hypothesis that coral tissue fluorescence has a function in improving photosynthetic performance, there has been little evidence to support his other prediction that the fluorescent tissue pigments may screen corals from the intense solar radiation.

Effective screening against excess light is probably an important survival requirement for shallow water reef-building corals. Whilst light is essential, both for corals and their symbiotic algae (symbiotic dinoflagellates), too much light can be a major problem in the high light reef habitats (Jokiel, 1980). Algal photosynthesis is very vulnerable to high solar irradiances, which may cause photoinhibition with subsequent increased concentration of reactive oxygen species and even coral bleaching (Lesser *et al.*, 1990; Shick *et al.*, 1995; Warner *et al.*, 1996; Lesser, 1997). In line with this expectation, significant impacts of even moderate irradiances on photosynthetic performance have been recently described for shallow-water *Stylophora pistillata* (Hoegh-Guldberg & Jones, 1998). Short wavelength solar radiation penetrates to considerable depths (Jerlow, 1950) and is detrimental not only to photosynthesis, but can also damage tissue DNA and proteins of marine invertebrates and algae (Shick *et al.*, 1991). To date, most studies of the solar screening compounds in coral tissues have centred on the mycosporine-like amino acids (MAAs) (Dunlap *et al.*, 1988). However, although they effectively block UV radiation shorter than 360 nm (mainly UVB at 280-320 nm), they have a limited protection against the effects of the longer wavelengths of UVA (360-400 nm) and high intensity blue light (400-500 nm). Both these wavelengths have been implicated in damage to Photosystem II (PSII) and ultimately in coral bleaching (Fitt & Warner, 1995). Despite this, there are no studies that show how the protection from the UVA/blue irradiance spectrum is achieved by shallow water corals. In the present study we investigated whether or not coral polyp fluorescence may have a function in screening out excess light for corals growing in shallow reef habitats. We show that there is strong evidence that these pigments may be functioning in screening out excess light, particularly from the UVA/blue light portion of solar radiation.

METHODS

Sample collection and preparation

Corals were collected from the reefs at One Tree Island at the southern end of the Great Barrier Reef, Australia (latitude 23°30'S; longitude 152°06'E) in March 1997 and from various fringing and patch reefs close to Hurghada (Egyptian Red Sea) in July 1997. Small pieces were broken from coral colonies of species in both high and low light habitats. In particular, colonies were collected from the high light habitats of the intertidal reef flats and reef slopes at 1 - 5 m depths, as well as from the dim light habitats of the reef slopes at 10 - 22 m depths and from under reef overhangs. Some colonies were sampled on their outer or light-acclimatised portions, as well as from their lower or more shade-acclimatised portions. Samples were kept frozen until analysis, or chemically fixed (2.5% glutaraldehyde and 0.1M phosphate buffer,

pH 7.2) and stored in 0.1M phosphate buffer at 4°C. Live corals were transported to the University of Sydney and kept in tanks with circulated seawater at 22-24°C. Since glutaraldehyde-fixed tissue is itself autofluorescent, a small piece of each sample was broken off and frozen before treatment with glutaraldehyde and was subsequently used for the comparison of the intensity and the colour of fluorescence between fixed and unfixed samples.

Fluorescence and confocal microscopy

Tissue fluorescence in frozen, chemically fixed and live coral pieces was examined using an Axiophot Photomicroscope (Zeiss, West Germany) equipped with fluorescence illuminator with a 3-lens collector and HBO 50 high pressure mercury lamp. Excitation of tissue fluorescence was achieved by light from selected UVA/blue wavelengths by means of the selected dichroic filter sets (Table 1). Overall examination of each sample was first made using low-power x2.5 objective to determine the degree of fluorescence of branch tips, corallite rims, polyps, tentacles and coenosarc.

Table 1. Filter sets used for analysis of tissue autofluorescence of the coral samples.

Excitation	Exciter filter	Chromatic beam splitter	Barrier filter
UVA	G 365 nm	FT 395 nm	LP 420 nm
Violet	BP 395-440 nm	FT 460 nm	LP 470 nm
Blue	BP 450-490 nm	FT 510 nm	LP 520 nm

Confocal Laser Scanning Microscopy (CLSM) was subsequently used to make a more detailed examination of the morphology and localisation of the fluorescent cellular structures in excised live, frozen and chemically fixed coral tissues. CLSM allows rapid imaging of cellular structure and provides high resolution images using unsectioned material by recording a series of two-dimensional images taken at incremental depths from the surface of the specimen. A Bio-rad MRC 600 confocal laser scanning microscope (Bio-rad Microscience Ltd, Hemel Hempstead, England) equipped with a 15 mW krypton-argon mixed gas laser was used in this study. Small tissue pieces were excised from polyp tentacles, placed on well-slides and were imaged by excitation or reflection in three modes. Initially, blue light at 488 nm from laser in fluorescence mode was used to image the fluorescent granules and chromatophores. Their reflective properties were identified and imaged using the reflection mode of 647 nm laser line using the K1 K2 filter block and the 488 nm line using the reflection filter block. Confocal imaging of the algal symbionts (symbiotic dinoflagellates) was achieved by excitation of their chlorophyll at 488 nm and observing the chlorophyll autofluorescence at the wavelengths longer than 585 nm. Confocal multiple imaging using these three different modes of optical sectioning was made at increasing depths and reconstructed into three-dimensional images by VoxelView Ultra 2.1.2 (Vital Images Pty Ltd, Fairfield, Iowa, USA) on a computer workstation (Silicon Graphics Indigo, Silicon Graphics Pty Ltd, Mountain View, California, USA). This enabled visualisation and localisation of the various reflective and fluorescent (UVA and blue light absorbing, white light reflecting) cellular structures in coral tissues. All colours were added by VoxelView Ultra 2.1.2.

RESULTS

Fluorescence microscopy

A variable degree of turquoise, blue or green autofluorescence of coral tissues was present in all of the samples examined by fluorescence microscopy. Tissue fluorescence, therefore, was found to be common in both high light- and low light-acclimated corals.

The majority of coral species collected from reef flat areas were found to be intensely autofluorescent on excitation by all of the tested wavelengths, thereby, showing a pronounced ability to absorb light of these wavelengths. Moreover, a number of coral species, particularly Acroporids (e.g. *Acropora hyacinthus*, *A. palifera*, *A. nobilis*) were found to have both intensely fluorescent morphs as well as non-fluorescent morphs, which were almost indistinguishable in appearance under visible light. Greenish colouration or dark brown colouration of morphs under visible light was generally associated with the presence of a large number of fluorescent pigments. Pale brown or beige morphs were mostly lacking in fluorescent pigments, as were brightly pink or blue colonies (pocilloporin, Takabayashi & Hoegh-Guldberg, 1995; Dove *et al.*, 1995).

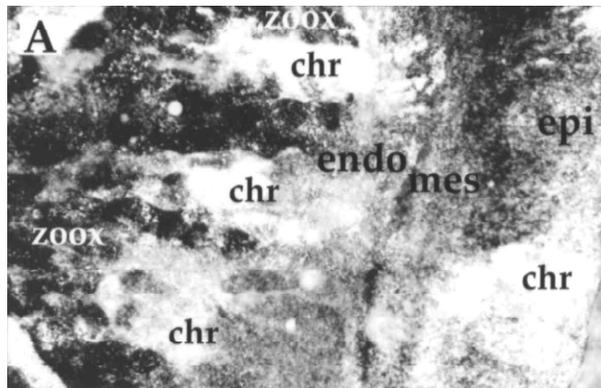
The fluorescence intensity and colour were found to vary, not only between different coral species and different colonies, but also among parts of the same colony. There was also some variability in the wavelengths that induced the most intense fluorescence, with excitation by UVA/blue light at 395 - 440 nm generally producing the strongest fluorescence in the majority of samples, followed by blue light at 450 - 490 nm and by UVA at 365 nm. The majority of samples showed strong fluorescence under both 395 - 440 nm and 450 - 490 nm but a small number of coral species were intensely fluorescent on excitation with one and not the other. The intensity and colour of fluorescent granules was found not to be substantially affected by glutaraldehyde fixation, particularly in corals which were strongly autofluorescent (quantitative data to be published elsewhere).

Confocal microscopy

Although most tissues of the examined corals were weakly fluorescent, most of the intense fluorescence was found to originate from the fluorescent pigment granules (FPGs), either scattered in endodermal (gastrodermal) or epidermal (ectodermal) layers or packed into clusters within large multi-lobed chromatophores (Figures 1 & 2) or inside epidermal columnar cells (Figure 3). Although the sizes, the amount and the density of granules in different corals was highly variable, they were found to be present in all of the coral samples examined (12 families, 52 species, 205 samples) (Table 2).

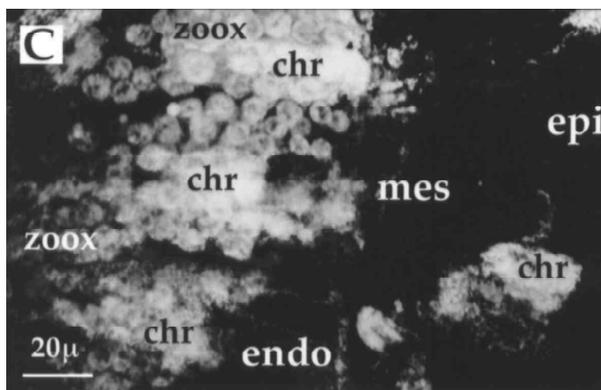
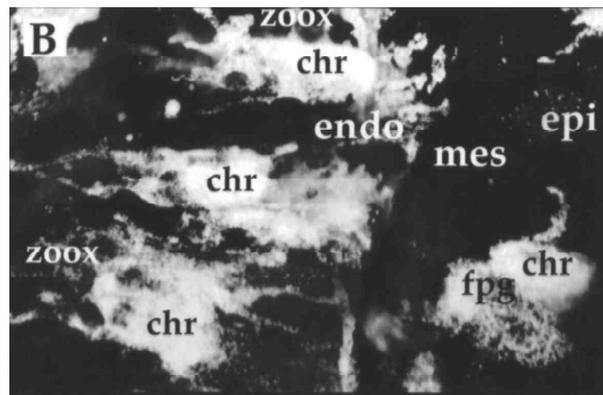
FPGs were generally round or oval in structure and 0.5-1.2 μm in diameter, similar to those described by Schlichter *et al.* (1985). The least autofluorescent species examined in the present study belonged to Pocilloporidae (*Pocillopora damicornis*, *Stylophora pistillata*, *Seriotopora hystrix*). Their FPGs were generally sparsely scattered in either endodermal or epidermal tissues. Many other species, particularly faviids, agariciids and the more fleshy poritids such as *Goniopora* spp., were found to have dense fluorescent chromatophore layers. CLSM optical imaging of these chromatophores by 488 and 647 nm laser lines in reflection mode revealed that they were also highly reflective (Figure 1A) and comparative analysis of their integrated pixel intensity (quantitative data to be published elsewhere) showed a 40-80% higher reflectance than that of adjacent cells.

Protoprotection of zooxanthellae



(A) Imaging in reflection mode of 488 nm laser line reveals cellular parts with high blue light reflectivity which are mainly composed of chromatophores filled with pigment granules.

(B) Excitation by 488 nm blue laser line reveals large clusters of fluorescent granules with emission at 520 nm inside chromatophores and their long extensions.



(C) Dense layers of symbiotic dinoflagellates as imaged by the red autofluorescence of their chloroplasts by excitation of chlorophyll at 488 nm and emission at wavelengths longer than 585 nm.

Figure 1. Reconstruction of the serial optical sections through tissues of light-acclimated live *Goniopora tenuidens* collected from One Tree Island reef flat and imaged in three modes (in reflection mode at 488 nm, in emission mode at 520 nm and in emission wavelengths longer than 585 nm) with excitation by 488 nm laser line on the same area of tissue. Large chromatophores with fluorescent granules form dense screens in the ectodermis (epidermis) and endodermis (gastrodermis), above symbiotic dinoflagellates.

(*e*pi - oral epidermis; *m*es - mesogloea, *e*ndo - endodermis (oral gastrodermis), *z*oox - symbiotic dinoflagellate, *f*pg - fluorescent pigment granules, *chr* - pigment chromatophores)



Figure 2. 3-D reconstruction of serial sections through tissues of *Acropora formosa* from the One Tree Island reef flat showing the surface screen of fluorescent granules (fpg) above symbiotic dinoflagellates (zoox). The reconstruction was made by merging the images obtained by blue light excitation and emission of fluorescent granules at 520 nm and by the emission of chlorophyll of symbiotic dinoflagellates at wavelengths longer than 585 nm.

Similar to the findings of Schlichter *et al.* (1994), FPGs were found located either in cells of the epidermis or endodermis, and in some cases, in both tissues. The significant finding of the present study was that their localisation in tissues was generally related to the light environment of corals. Examination of corals from the reef flat, the shallower upper slope or of samples taken from the sunlit outermost (i.e. light-acclimated) parts of colonies, revealed that most of the FPGs were concentrated above the endodermal symbiotic dinoflagellates (Table 2, Figure 4). In these cases, FPGs formed large clusters within the epidermal layer, which in shallow water corals was found to be much thicker than in corals from deeper slopes. Fluorescent pigments in shallow water corals were also frequently found within both the epidermal and the outer part of the endodermal layers, but again located above the symbiotic dinoflagellates and distributed in such a way as to form thick pigment screens.

In contrast, examination of fluorescent pigments in corals collected from deeper slopes, from under overhangs and from shaded parts of coral colonies, revealed that the FPGs were concentrated below and/or among the layers of algal symbionts. The outer epidermal layer in such samples was found to be very thin and in the majority of cases lacking any fluorescent pigments. Where FPGs were present in this layer, they were widely scattered and did not form pigment screens.

The fluorescent granules were also found to be concentrated in certain body parts of the shallow water corals examined. Dense aggregates were found in samples taken from the tips of branches of acroporids and in most samples taken from the edges of the encrusting or plate-like corals examined, e.g. *Montipora* spp., *Porites* spp., many faviids, as well as agariciids, mussiids and pectiniids. The FPGs were also frequently found to be concentrated in the centre of coral polyps, overlying and surrounding the mouth area or overlying the bottom of the valleys in coral species with fused corallites and cerioid, flabellate or meandroid polyps.

A common morphological feature of almost all shallow water corals examined was the presence of FPG clusters concentrated in their polyp tentacle tips. This was especially prominent in corals with large polyps such as *Goniopora* spp, but was also evident in species with small polyps, such as members of the Poritidae, Acroporidae and Pocilloporidae. Many corals with polyps containing symbiotic dinoflagellate polyps were generally found to have dense layers of FPGs around the corallite rims, polyp tentacles and mouths, while their numbers in the coenosarc between the polyps was often reduced. Alternately, in a few coral species whose polyps are naturally devoid of symbiotic dinoflagellates, the FPGs formed a thick uninterrupted epidermal layer in the coenosarc tissues between the corallites as well as within the epidermis of corallite walls. The endosymbionts in such species (e.g. *Acropora horrida*, *A. tortuosa*) were found to be restricted to the gastrodermis beneath these fluorescent parts of corals i.e between the corallites and their walls (Figure 3).

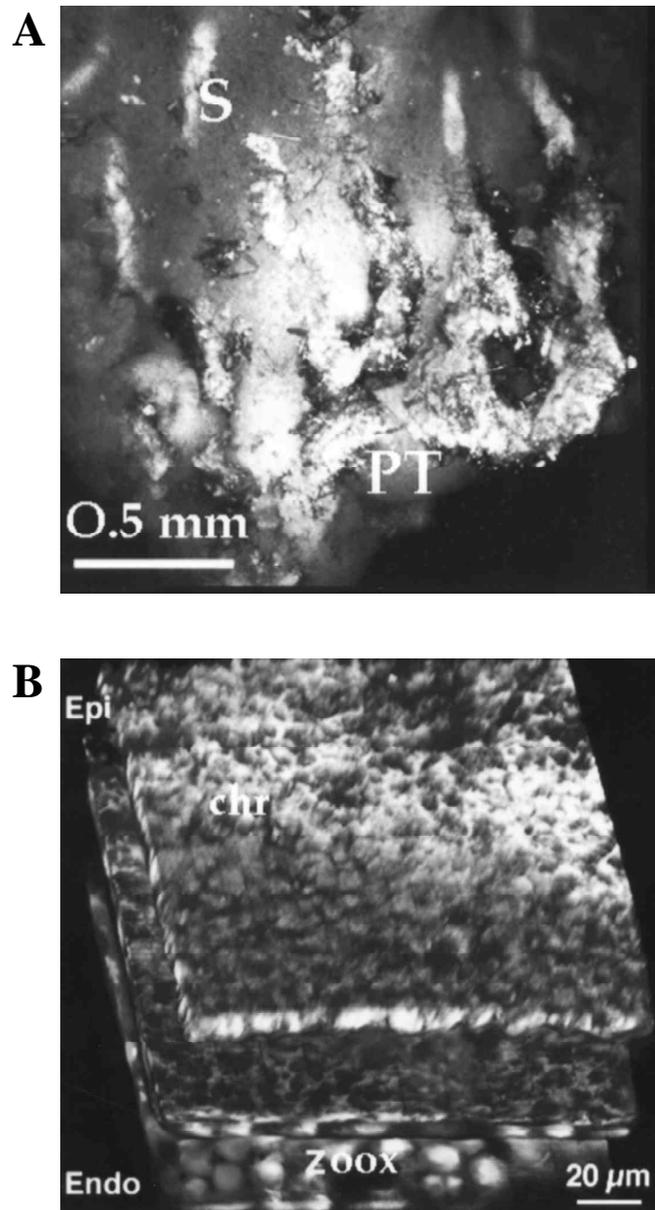


Figure 3. Tissue fluorescence of intertidal *Acropora horrida*.
(A) Edge of corallite polyp cup with highly reflective skeleton (visible due to 488 nm reflection imaging) and blue light absorbing and fluorescing epidermal cells. The coral polyp is retracted inside the corallite cup.
(B) Detail of A, showing highly fluorescent columnar epidermal cells of the corallite wall which screen the symbiotic dinoflagellate layers below.
(*chr* - chromatophores in the columnar epidermal cells, *Endo* - endodermis, *Epi* - epidermis, *PT* - polyp corallite tip, *S* - reflective skeletal ridges, *zoox* - symbiotic dinoflagellates).

Table 2. Comparative analysis of the relative amounts of fluorescent pigment granules (FPGs) in high light- and low light adapted-corals. FPGs were located in host tissues concentrated above algal layers (+) or mostly below (-) or dispersed below and among the algae (+/-). The FPGs were assessed as being 'few', when only sparse scattered granules were present; as 'medium' when they were intermittently scattered and in places formed clusters; and as 'dense', when they formed thick layers of chromatophore clusters, filled the columnar epidermal cells or formed thick pigment granules screens. (GBR=Great Barrier Reef; RedS = RedS)

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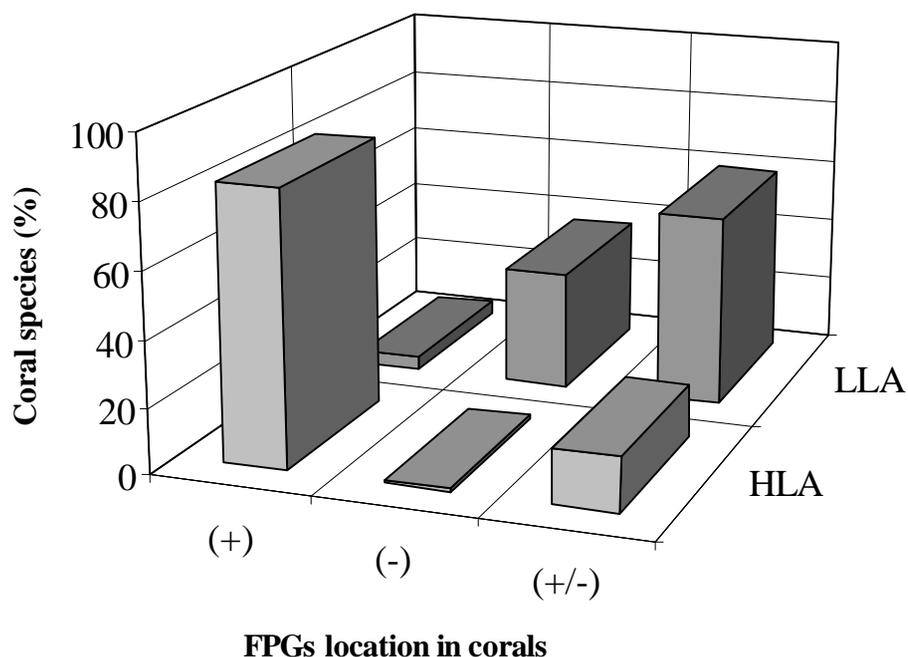


Figure 4. Percentage of corals with fluorescent pigments distributed above (+), below (-) and among (+/-) the symbiotic dinoflagellates in low light-acclimated (LLA) and high light acclimated corals (HLA).

DISCUSSION

In this study, fluorescent pigments were found to be present in tissues of the majority of corals from shallow water intertidal habitats, as well as in corals from lower light, shaded or deeper water habitats. The location of these pigments in animal tissues relative to the position of algal symbionts, however, was found to be clearly different in high light- versus shade-acclimated corals. The FPGs were mainly located above the symbiotic algae in the epidermis and outer parts of the endoderm (gastrodermis) in high light-acclimated corals but were among and/or below the algae in the endoderm in shade-acclimated corals. This distribution strongly suggests that FPGs have a role in modifying the light environment of the symbiotic dinoflagellates of both light- and shade-acclimated corals.

It recent years it has become evident that corals and their symbiotic algae may be vulnerable to the effects of high solar radiation. This vulnerability is often expressed in the field as a localised solar bleaching response, measured either as a reduction of symbiotic dinoflagellates, as a loss of photosynthetic pigments, or a combination of these processes, which occurs in the light-facing upper branch faces or in other unshaded parts of coral colonies (Goenaga & Armstrong, 1988; Goreau & Macfarlane, 1990; Brown *et al.*, 1994; Le Tissier & Brown, 1996). Moreover, while elevated temperature has been found to be the main cause of large scale coral bleaching events (e.g. Glynn, 1990), solar radiation was also implicated in mass bleaching (Harriott, 1985; Oliver, 1985). It has been known for some time that corals can protect themselves from UV radiation by synthesising MAAs (absorption maxima at 310-360 nm), mainly as protection against UVB radiation (Dunlap & Chalker, 1986; Dunlap *et al.*, 1988). Although UVB is biologically more damaging than UVA (Cullen & Neale, 1993), proportionally UVA constitute

the greater part of the solar fluxes, causing more damage to algal photosynthetic processes (Bothwell *et al.*, 1994). The results of our study suggest that the fluorescent pigments found to be present in almost all shallow water corals may supplement the role of MAAs by blocking some of the UVA portion of UV radiation.

More recently, visible (400-700 nm) solar radiation has been increasingly recognised as an additional factor which may be detrimental to corals and their symbiotic algae (Brown *et al.*, 1994; Lewis, 1995). Severe degradation of symbiotic dinoflagellates and degradative structural signs of oxidative damage in their chloroplasts were shown to occur in corals screened from all UV radiation and exposed to several hours of realistically high visible light (Salih *et al.*, 1998). Recent work at One Tree Island has shown that symbiotic dinoflagellates from at least one coral (*Stylophora pistillata*) are photoinhibited for most of the year, despite the high latitude location of these reef systems (Hoegh-Guldberg & Jones, 1998). In these studies, symbiotic dinoflagellates were found to have a number of photoprotective mechanisms for dealing with the potentially damaging effects of high irradiances. Among these are non-photochemical quenching of excess excitations and the induction of electron flow to oxygen. The key observation here is that these mechanisms have the capacity to accommodate excess photons up to a point, beyond which damage to the photosynthetic components of the symbiotic dinoflagellates begins to occur. The results of the present study show that the host can provide additional photoprotection for the cells of the algal symbiont. The positioning of the FPG screens above symbiotic dinoflagellate layers in most shallow water corals can screen out UVA/blue radiation. The demonstration that FPGs are also highly reflective to blue and red light wavelengths provides further support to this idea.

The retraction of polyps during the exposure to high irradiances is known to be a protective behavioural response of corals leading to increased shading of symbiotic dinoflagellates from solar radiation, lowering of their photosynthetic rates, and reduction of photoinhibition (Lasker, 1981; Brown *et al.*, 1994). Our finding of sunlight reflecting and UVA/blue light absorbing tentacle 'plugs' in shallow water corals suggests that corals may have a much greater solar screening capability for their symbionts during polyp retraction than was previously known. Consequently, the enhancement of UVA/blue light absorption, overall light reflectance and scattering by fluorescent granules in host tissues may provide the symbiotic dinoflagellates with an efficient protection from high solar radiation of shallow reef habitats.

The fluorescent pigments may also have certain protective functions for the coral host's benefit. Their concentration in certain parts of corals suggests that these pigments function in protecting the more vulnerable host tissues from solar radiation damage. The FPGs were found to be particularly dense in: (i) areas of rapid growth, such as branch tips of arborescent or edges of plate-like corals; (ii) tissues overlying the reproductive organs, in the area of the mouth in the middle of single polyps or in the middle of the fused polyps in valleys; (iii) polyp tentacle tips, which on polyp retraction, form a photoscreening 'plug' over the rest of the coral; and (iv) rims of polyp-cups of corals with polyps having symbiotic dinoflagellate. Such a distribution of the FPGs strongly suggests photoprotection of sensitive tissues from UVA radiation of rapidly growing branch tips, of underlying reproductive parts (gonads or even brooded larvae), and of retracted whole polyps by their FPG-laden tentacle tips and rims of polyp-cups. Depending on the solar zenith angle, up to 60% of the biologically deleterious effects of UV radiation, such as DNA damage, can be attributed to the more abundant and more penetrating UVA (Peak & Peak, 1988). Moreover, high visible light levels have been shown to detrimentally

affect not only the symbionts but also the metabolic responses of corals (Lewis, 1995). The tentacle tip 'shields' or 'plugs' may consequently also protect the coral host from overheating due to solar radiation, and possibly from UVA damage.

Our study revealed common interspecific differences in the amounts of fluorescent pigments found in corals growing under similar environmental conditions. Some reef flat species possess only sparsely scattered FPGs (e.g. *Goniastrea retiformis*), while other species have very dense FPG layers (e.g. *G. australiensis*). There were also intraspecific differences in the amounts of fluorescent pigments, with several species occurring as fluorescent and non-fluorescent morphs, found growing side by side (e.g. reef flat *Acropora palifera*). This resembles the same situation discovered for the presence and absence of the pigment compound, pocilloporin (Takabayashi & Hoegh-Guldberg, 1995; Dove *et al.*, 1995). The intraspecific variability in the presence of FPG may provide clues into the variability that has been observed, especially given the important secondary role that light appears to play in coral bleaching.

The inferred functional significance of these chromatophores in shallow water corals is clearly different from that in the low light-acclimated corals. The presence of the FPG layer below the symbiotic dinoflagellates of corals from dim habitats is consistent with a role in the enhancement of photosynthetic performance by shifting shorter wavelengths via fluorescence, into longer, more photosynthetically usable wavelengths (Kawaguti, 1969; Schlichter *et al.*, 1994). Our finding that the FPGs are highly reflective further supports the hypothesis that these pigments may enhance photosynthesis of algal symbionts by light reflection and backscattering. Physiological studies are now required to explore this very interesting area. The results of our morphological analysis of fluorescent pigments in high and dim light acclimated corals indicate differences in the use of FPGs, and provide insights into how corals may modify the irradiance environment surrounding their symbiotic algae.

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