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Patterns in fluorescence over a Caribbean reef slope: the coral genus *Madracis*

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Abstract

Patterns of fluorescence and colony tissue colour were studied (field observations and epifluorescence microscopy) in six species of the coral genus *Madracis* over depth from 10 to 60 m at a reef slope in Curaçao. Two functions showed up: (*1*) Decrease in number of colourmorphs ($n = 25$) with depth suggests a photo-protective function where short wavelengths (*e.g.* UV) are transformed to long wavelengths. (*2*) Green fluorescence, observed in four species over their entire depth range, transforms radiation to wavelengths useful for photosynthesis. The observed patterns in fluorescence between species did not correspond to the current taxonomic classification. Our results do not support the usefulness of fluorescence as a taxonomic tool in corals.

Additional key words: *Agaricia*; chlorophyll; colourmorph; *Montastraea*; radiation wavelength; species differences; taxonomy.

Introduction

Colour variation and fluorescence in *Anthozoa* is known since the 1920's from sea anemones (Philips 1927) and currently studied in corals for its ecological significance. Although this research is at an early stage (Mazel 1995, Salih *et al.* 1998, Hoegh-Guldberg and Jones 1999), two possible functions of the pigments responsible for colour and fluorescence have come forward. Kawaguti (1944) was the first to suggest their possible role as photoprotectants, changing short wavelength radiation (including UV radiation) into long wavelengths, thereby preventing that the former damages the organism's tissue. Later, Kawaguti (1969) suggested a second function of pigments: transforming short wavelength radiation to wavelengths that can be used by zooxanthellae for photosynthesis. This function has led to the presence of in particular substances that emit green wavelengths (GFP's; Dove *et al.* 2001) in many coral species. These two functions are also reflected in the organisation of the pigments at a cellular level (Delvoye 1995, Salih *et al.* 1998). In shallow water, pigments are found above the zooxanthellae suggesting a photo-protective function, whereas with depth the pigments lie below the zooxanthellae where they back scatter radiation that passed the overlying zooxanthellae layer. The two-fold function of fluorescence is therefore found at the physiological as well as at the cellular level: photoprotection and assistance for zooxanthellae photosynthesis (Kawaguti 1944, Salih *et al.* 1998).

Since photoprotection is an important feature in the biology of shallow water corals (Jokiel and York 1982, Jokiel *et al.* 1997), most of the research on the functional role of fluorescence has been on shallow water (<10 m) corals in the Indo-Pacific receiving high irradiances. Caribbean corals are found well below this depth (Bak 1977) and maximum coral cover is found at 10-20 m where UV-radiation is less harmful (Boelen *et al.* 1999). Green fluorescence is still present at these depths and even deeper (>50 m) (Delvoye 1995) which suggests that fluorescence in Caribbean corals is mainly determined by its assistant function in zooxanthellae photobiology. This is a hypothesis that will be investigated in this paper.

Coral fluorescence and colour result from pigments in the coral holobiont, either in the coral's tissue (animal pigments) or in the zooxanthellae (algal pigments). The presence of green fluorescence is extremely consistent over a broad taxonomical range (Delvoye 1995, Mazel 1995, Salih *et al.* 1998) and throughout the phylum *Cnidaria* (Philips 1927, Morin and Hastings 1971).

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Tissue colour can be highly variable between colonies of the same species (Veron 1995) and has been suggested as a taxonomic tool to distinguish between species (Lang 1984). Colour distinguishes species in other marine invertebrates such as brittlestars (Deheyn and Jangoux 1999) and sea anemones (Haylor *et al.* 1984).

The ecological significance of colour variation in corals is unknown and tissue colour can be a neutral side effect of pigments involved in biochemical processes or adaptive to environmental conditions. Environmental factors, such as depth (Haylor *et al.* 1984, Takabayashi and Hoegh-Guldberg 1995, Nagelkerken and Bak 1998, Vermeij and Bak 2002a), sedimentation (Gleason 1998), and radiation availability (Veron 1995) correlate to a change in colour of colonies in several coral species. In addition, colour variation corresponds to variation in life history aspects: regeneration (Nagelkerken and Bak 1998), reproduction (Richmond 1987), and growth (Takabayashi and Hoegh-Guldberg 1995). The interaction of these factors must be responsible for the large colour variation that characterises present-day reefs (Veron 1995, 2000) and questions the use of colour as a taxonomic tool.

To study the function and usefulness of tissue colour and fluorescence for taxonomic purposes we looked at the variation in tissue colour in six closely related Caribbean coral species of the genus *Madracis* over a 60 m-depth gradient. The purpose of the research is to investigate: (*1*) The patterns in fluorescence for each species. (*2*) The relation between patterns in tissue colour and fluorescence. (*3*) How tissue colour and fluorescence correlate with depth.

Materials and methods

Samples of six *Madracis* species (*M. mirabilis, M. decactis, M. pharensis, M. senaria, M. formosa, M. carmabi*; Wells 1973a,b, Vermeij and Bak 2002a,b) were collected by *SCUBA* diving from depths between 10 and 60 m at Buoy 1 on the leeward coast of Curaçao, Netherlands Antilles (12°05'N, 69°00'W). The samples were transported (shaded) to the lab within 30 min. They were kept in shaded aquariums with running seawater at the irradiance of the depth of collection. Small samples of coral were covered by a cover slip. Seawater filled the gap between the sample and the cover slip. Corals were examined under epifluorescence with a *Leitz Ortholux* microscope, equipped with a *Ploemopak* epifluorescence attachment. A 40× phase contrast objective permitted a quick change between epifluorescence and phase contrast observation of samples. A *HBO-50 Osram* high pressure mercury lamp in combination with a *BG12* and *UG5 Schott* filters (transmission peak value ≈ 375 nm) was used as a radiation source for fluorescence observation. A standard photographic attachment or a *Sony* digital camcorder (*DCV 900E*) could be fitted on the microscope. Spectra were photographed on *100ASA* black and white film (*Kodak*) and standardised against the solar spectrum. All observations were made at reef ambient temperatures (27 °C) in a darkroom. Histological analyses (Vermeij *et al.*, unpublished) showed the position of the fluorescent particles and zooxanthellae.

Results

No fluorescence was observed in *M. mirabilis* and *M. decactis* except for the red fluorescence resulting from zooxanthellae. Green-turquoise fluorescence dominated in colonies of all other species independent of depth of collection (Table 1). Radiation between 420 and 510 nm resulted in maximum excitation intensity. Although orange and yellow fluorescence were often observed, these colours resulted from the optical mixing of the red chlorophyll *a* fluorescence of the zooxanthellae and the green fluorescence of the coral host. These wavelengths are not further considered in our analyses. The emission spectra of different species were nearly identical and no relation was found between the morphological classification of the genus and patterns in tissue fluorescence. Our spectra indicate a range of emitted wavelengths (≈512-620 nm) but peaks could be distinguished within this band (Table 1).

In general, two peaks were found in addition to the red fluorescence of zooxanthellae chlorophyll that was found in all samples. The first peak has a spectral width between approximately 1 to 51 nm and was found between 520 and 587 nm. The second peak was found between 587 and 620 nm with a spectral width between 1 and 30 nm. We found low variation between colonies of the same species at the same depth in the position of peak one and two.

In *M. pharensis*, colonies occur in a large number of colour varieties. At our site we found 25 different colour-morphs (Fig. 1). The large variation arises mainly due to combinations of certain fixed characteristics, such as the possession of a green coenosarc, gray tentacles, green tentacle tips, and a red mouth field (Fig. 1). The colour variation did not necessarily correspond to variation in fluorescence pattern (Table 1). The *M. pharensis* morph with gray tentacles (morph no. 5) possesses a characteristic peak at 560 nm compared to all other *M. pharensis* morphs at 10 m. The morph with a red ring on its mouth-field (morph no. 6) does not possess a second peak and the green morph (morph no. 8) possesses a broad emission range around the position of peak 1 (Table 1).

The structures that appear yellow to green as seen by the eye under normal daylight, such as the yellow mouths or green tissue colour (Fig. 1), corresponded to areas with the high intensity of (green) fluorescence. Different distributions of the green-fluorescent substance therefore contribute, at least partially, to the large number of colour varieties in *M. pharensis*. The number of colour varieties decreased with depth (Fig. 2). Although the decrease with depth was highly significant ($r^2 = 0.97$, $p = 0.03$, $n = 5$), a stronger relation showed up between the number of colour varieties and the maximum irradiance (PAR, 400-700 nm) available at that depth ($r^2 = 0.99$, $p < 0.001$, $n = 5$).

Although we found no differences between species or depths in fluorescence patterns, the brightness of the green fluorescence increased with depth. Our experimental setting did not allow measurements on the intensity of coral fluorescence. However, subjective comparisons between pictures taken under standardised circumstances of colonies collected at different depth support the observation that fluorescence intensity increases with depth (Fig. 3).

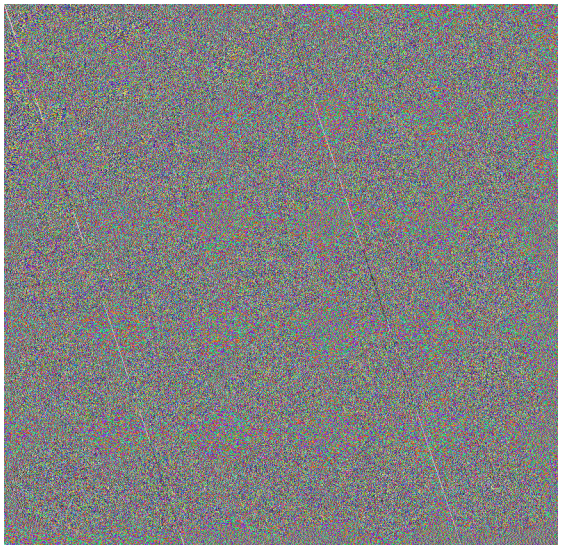

Fig. 1. The 25 colourmorphs of *M. pharensis* at Curaçao, Netherlands Antilles (12°N, 69°W).

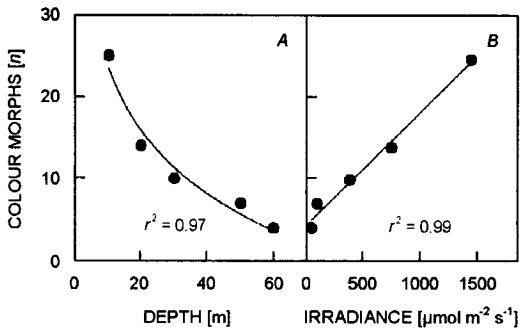

Fig. 2. Decrease in number of colourmorphs in relation to depth and irradiance.

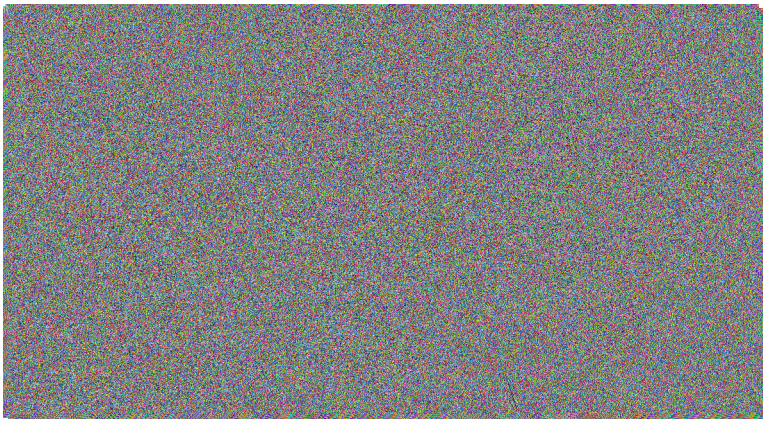

Fig. 3. Increase in green fluorescence with depth in morphotype 1 of *M. pharensis* (brown morph). Polyp diameter is 1.2 mm in all pictures.

Histological examination revealed that the layer consisting of fluorescent substances was positioned below the layer of zooxanthellae in the coral endoderm. This structural organisation was found for two other coral species (*Montastraea cavernosa*, *Scolymia cubensis*) whose fluorescence was additionally studied for comparative purposes. The position of the fluorescent layer under the zooxanthellae increases the amount of light that zooxanthellae receive by wavelength transformation and backscattering. Another strategy is found for three *Agaricid* species (*A. undata, A. lamarcki, A. agaricites*) where the layer with zooxanthellae is found below the fluorescent layer.

Table 1. Fluorescence of six *Madracis* species and five colourmorphs of *M. pharensis* collected over a 10-60 m depth range. Numbers refer to colourmorph number in Fig. 1; *n* = number of colonies sampled.

	Colourmorph	No.	*n*	Depth	Fluorescence spectrum [nm] continuum	peak 1	peak 2
Madracis pharensis	brown tissue	1	4	10	524-612	532	590
	grey tentacles	5	4	10	-	560	590
	grey with blue intra	10	3	10	525-616	537	590
	red ring on intra	6	4	10	525-616	532	-
	green tissue	8	6	10	517-617	519-570	590-615
	brown tissue	1	4	10	524-612	532	590
		1	6	20	524-612	533	590
		1	3	40	561-620	587	609
		1	4	60	514-614	535	587
	green tissue	8	6	10	517-617	520-570	590
		8	6	20	517-617	520-570	590
		8	6	40	517-623	520-570	590-620
		8	6	60	517-617	520-570	590
Madracis carmabi	-		4	20	512-620	520-555	590
	-		4	40	512-615	519-557	590
Madracis senaria	-		4	10	512-615	519-559	590
	-		2	20	512-620	520-558	590
	-		3	40	527-616	561	587-516
	-		4	60	512-615	559	590
Madracis formosa	-		5	40	522-623	-	-
	-		4	60	525-616	534	575
Madracis decactis	-		5	20	-	-	-
	-		5	30	-	-	-
Madracis mirabilis	-		5	10	-	-	-
	-		5	20	-	-	-
Agaricia undata			1	40	515-620	542	-
Agaricia agaricites			1	60	508-620	-	-
Monastrea cavernosa			1	40	510-623	-	-
			2	60	515-620	534	593

Discussion

Fluorescence: to protect or to serve? Recent quantitative studies describe two possible roles of fluorescence: improvement of photosynthesis (Schlichter 1990, Schlichter *et al.* 1994) and photoprotection (Salih *et al.* 1998). The majority highlights the supportive role of fluorescence in coral photosynthesis (Schlichter *et al.* 1986, 1994, Schlichter and Fricke 1991) rather than its photoprotective role (Salih *et al.* 1998). Also for our *Madracis* species fluorescence is related to the photosynthesis of the coral holobiont rather than to photoprotection because of several reasons.

Firstly, UV-protection is more important for corals in the Pacific than in the Caribbean since they grow in high irradiance environments on shallow reefs. Such reef systems are rare in Curaçao where coral cover gradually increases with depth with a maximum at 20-25 m for *Madracis* (Vermeij and Bak 2002). This depth corresponds to the maximum depth to which harmful UV-radiation penetrates in tropical reef waters (Boelen *et al.* 1999). Therefore, most colonies are in a position where they do not receive harmful doses of UV-radiation.

Secondly, *M. mirabilis* and *M. decactis*, two species that are generally found at well lit positions between depths of 5 and 15 m, are the only two *Madracis* species that show no fluorescence. This observation corresponds to data from Barbados and Bermuda (Logan *et al.* 1990). The presence of *Madracis* colonies at relative deep positions (>30 m) on the reef and the absence of fluorescence in the two shallow water species, *M. mirabilis* and *M. decactis*, suggest no functional role of fluorescence for photo-protective purposes.

Thirdly, supporting this hypothesis is the position of the zooxanthellae above the fluorescent layer. The position of the zooxanthellae above the fluorescent layer (contrary to the *Agaricids*) is useless if this layer has a protective function since symbiotic dinoflagellate algae

are damaged by UV radiation (Calkins and Thordardottir 1980).

The green fluorescence is present in all *Madracis* species (except *M. mirabilis* and *M. decactis*) and other coral species we studied (Table 1: *Montastraea cavernosa, Agaricia undata, A. agaricites,* Pers. obs.: *Scolymia cubensis, A. lamarcki*), but also in many other coral species (Logan *et al.* 1990, Schlichter *et al.* 1994, Mazel 1995, Manica and Carter 2000). The emission wavelengths depend on the excitation wavelength used (365-410 nm), but generally range between 430 and 590 nm (Schlichter *et al.* 1994, Mazel 1995). For *Madracis*, we found emission values ranging between approximately 512 and 620 nm. It is very difficult to translate the emission peaks directly to the pigments involved. Shifts in the position of the emission peaks are caused by small changes in the chemical environment of fluorescent molecules (*e.g.* pH; Mazel 1995) and by the native state of the pigment (Titlyanov *et al.* 1998). The only way to effectively compare fluorescence data therefore requires a standard protocol to describe and measure coral fluorescence. Accessory light-harvesting pigment-protein complexes serve as additional antennae for photosynthetic reaction centres. Carotenoids and xanthophylls implanted into the chlorophyll-protein matrix allow an organism to absorb photons in the green region of the spectrum. One of these pigments, peridinin, is an important accessory pigment in dinoflagellates, such as zooxanthellae (Dring 1982). It has a maximum absorbance in the 500-560 nm range, depending on the native state of the pigments (Titlyanov *et al.* 1980). Peridinin can transfer the absorbed radiant energy that is back-scattered from the fluorescent layer underlying the zooxanthellae onto chlorophyll *a* (Song *et al.* 1976). This suggests that fluorescence in *Madracis* has a supportive function in the photosynthesis of the coral holobiont.

Fluorescence and coral tissue colour: The presence of a large number of colourmorphs in *M. pharensis* is not reflected in different fluorescence patterns. In some morphs colour differences corresponded to variations in the overall fluorescence pattern although for other colour-morphs fluorescent patterns were identical (Table 1). Colours that appeared green and yellow to the eye *in situ* corresponded to the presence of the green fluorescent particles in the coral tissue. The various spots where green and yellow coloration was observed suggest variable production or rearrangement of fluorescent particles in different regions in the coral's tissue.

Other colours that were observed (red, blue, pink, white) were not related to fluorescent substances in the coral. Fluorescence of the substances related to these colours can, however, occur if different excitation wavelengths are used (Mazel 1995). Indeed, an experiment using a standard black-light (*Philips 4W/08 F4 T5/BLB*) resulted in bright orange fluorescence in one *M. pharensis* colourmorph (red circle around the oral area, see Fig. 1). This indicates that if only one excitation wavelength is used, fluorescence of some substances remains unseen.

The strong relation between the decreasing number of colourmorphs with decreasing irradiance, PAR and UV (Fig. 2) suggests that the pigments responsible for these colours are involved in photoprotection (Jokiel and York 1982). Green fluorescent particles should provide the optimal wavelengths for the pigments involved in photosynthesis, *e.g.* peridinin, which are conservative in nature. Transforming UV-radiation to radiation of higher wavelengths is not subjected to such restrictions: as long as the UV-radiation is transformed to longer wavelengths, the organism benefits. Green fluorescence assisting in photosynthesis is therefore more conservative than the fluorescence involved in the protection against UV-radiation. Through time mutations are therefore likely to result in more photoprotective fluorescent pigments, resulting in a large number of *M. pharensis* colourmorphs whereas photosynthetic fluorescence has only one: the green fluorescence. The universal nature of the photosynthetic apparatus has resulted in the presence of an identical green fluorescence in a large number of coral species (Logan *et al.* 1990, Schlichter *et al.* 1994, Mazel 1995, Manica and Carter 2000).

Taxonomic implications: The use of fluorescence for taxonomic purposes has been suggested more than 40 years ago (Catala-Stucki 1959). The usefulness of this approach has recently been investigated for the *Montastraea annularis* species complex (Manica and Carter 2000). The *Montastraea* morphotypes showed to be highly heterogeneous in fluorescent characteristics that could not be used to separate the species (Manica and Carter 2000). In *Madracis,* the separation of *M. decactis* and *M. pharensis* as different species is currently debated (Fenner 1993, Vermeij and Bak 2002a,b). No genetic difference was found between these two species by Diekmann *et al.* (2001). However, *M. decactis* does not show any fluorescence in contrast to *M. pharensis*. We do not think this difference is enough to distinguish the two as different species. We relate the difference in fluorescence to the different habitat preferences of the two species/morphs (Vermeij and Bak 2002a). *M. decactis* generally occurs in well lit positions on the reef whereas *M. pharensis* colonies occur in cryptic environments. The difference in radiation received is compensated by the higher photosynthetic efficiency of *M. pharensis* caused by the possession of green fluorescence. The only other species, *M. mirabilis*, which lacks fluorescence also shows preference for well lit locations on the shallow reef (<15 m). This suggests that green fluorescence has developed in relation to ecological factors, *i.e.* irradiance. Consequently, fluorescence can only be used for taxonomic purposes if the species involved do not occur in multiple (radiation) habitats. The *M. pharensis/decactis* species complex occurs in cryptic and exposed positions and

therefore fluorescence can not be used to distinguish between the two beyond the level of (eco)morphs. All other *Madracis* species show identical fluorescence patterns with no diagnostic features.

We conclude that both these functions of fluorescence, photoprotection and photosynthesis enhancement, are found in the genus *Madracis*. The first function is based on the decreasing number of colourmorphs with depth and needs further study. The second function is found in all species, except those that occur on well-lit positions on the reef, *i.e. M. decactis* and *M. mirabilis*. Fluorescence patterns do not correspond to the taxonomic classification of the genus.

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