

Patterns of Fluorescent Protein Expression in Scleractinian Corals

DAVID F. GRUBER^{1,2}, HUNG-TEH KAO², STEPHEN JANOSCHKA², JULIA TSAI³, AND VINCENT A. PIERIBONE⁴

¹*The Institute for Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey 08901;*

²*Division of Biology and Medicine, Brown University, Providence, Rhode Island 02912;* ³*New York University School of Medicine, New York, New York 10016;* and ⁴*The John B. Pierce Laboratory, Cellular and Molecular Physiology, Yale University, New Haven, Connecticut 06519*

Abstract. Biofluorescence exists in only a few classes of organisms, with Anthozoa possessing the majority of species known to express fluorescent proteins. Most species within the Anthozoan subgroup Scleractinia (reef-building corals) not only express green fluorescent proteins, they also localize the proteins in distinct anatomical patterns. We examined the distribution of biofluorescence in 33 coral species, representing 8 families, from study sites on Australia's Great Barrier Reef. For 28 of these species, we report the presence of biofluorescence for the first time. The dominant fluorescent emissions observed were green (480–520 nm) and red (580–600 nm). Fluorescent proteins were expressed in three distinct patterns (highlighted, uniform, and complementary) among specific anatomical structures of corals across a variety of families. We report no significant overlap between the distribution of fluorescent proteins and the distribution of zooxanthellae. Analysis of the patterns of fluorescent protein distribution provides evidence that the scheme in which fluorescent proteins are distributed among the anatomical structures of corals is nonrandom. This targeted expression of fluorescent proteins in corals produces contrast and may function as a signaling mechanism to organisms with sensitivity to specific wavelengths of light.

Introduction

Fluorescence of living corals has been recognized for many years (Catala, 1959; Burns *et al.*, 1967; Kawaguti, 1969; Schlichter *et al.*, 1986; Mazel, 1995; Hoegh-Guldberg and Jones, 1999; Zawada and Jaffe, 2003). It has been

discovered that the fluorescence is due to the coral's production of a wide spectrum of unique proteins (Mazel, 1995; Matz *et al.*, 1999; Myers *et al.*, 1999; Dove *et al.*, 2000; Lukyanov *et al.*, 2000; Mazel *et al.*, 2003). However, the role or function that fluorescence plays among these organisms, which has been historically been debated (Kawaguti, 1944), remains undetermined (Oswald *et al.*, 2007).

The first fluorescent protein discovered, green fluorescent protein (GFP), was found in the bioluminescent marine hydroid *Aequorea victoria* (synonym, *A. aequorea*) (Shimomura *et al.*, 1962). GFP-like fluorescent proteins have since been identified in a number of members of the cnidarian phylum, including corals, anemones, hydroids, pennatulids, and corallimorpharians (Shagin *et al.*, 2004). In some cases multiple different fluorescent proteins have been isolated from a single Anthozoa species, and proteins with different spectral properties have been reported from the same animal (Kelmanson and Matz, 2003; Sun *et al.*, 2004; Kao *et al.*, 2007). However, outside of Cnidaria, fluorescent proteins have been isolated only from some species of copepod (phylum Crustacea)—*Pontellina plumata*, *Pontella meadi*, *Chiridius poppei*, and *Labidocera aestiva* (Shagin *et al.*, 2004)—and from amphioxus (phylum Chordata)—*Branchiostoma floridae*, *B. lanceolatum*, and *B. belcheri* (Deheyn *et al.*, 2007). Fluorescent proteins have not been found in the terrestrial environment, although nonfluorescent structural homologs exist (Hopf *et al.*, 2001). In *Aequorea* and *Obelia*, GFP is localized in photocytes to convert blue bioluminescent light to green (Morin and Hastings, 1971), but how fluorescent proteins function and are distributed in nonbioluminescent organisms is less clear.

Most scleractinian corals engage in an obligate mutualistic symbiosis with photosynthetic dinoflagellates, belonging predominantly to the genus *Symbiodinium*, that reside in the animal's gastrodermal cells. These dinoflagellates, com-

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* To whom correspondence should be addressed. E-mail: David_Gruber@baruch.cuny.edu

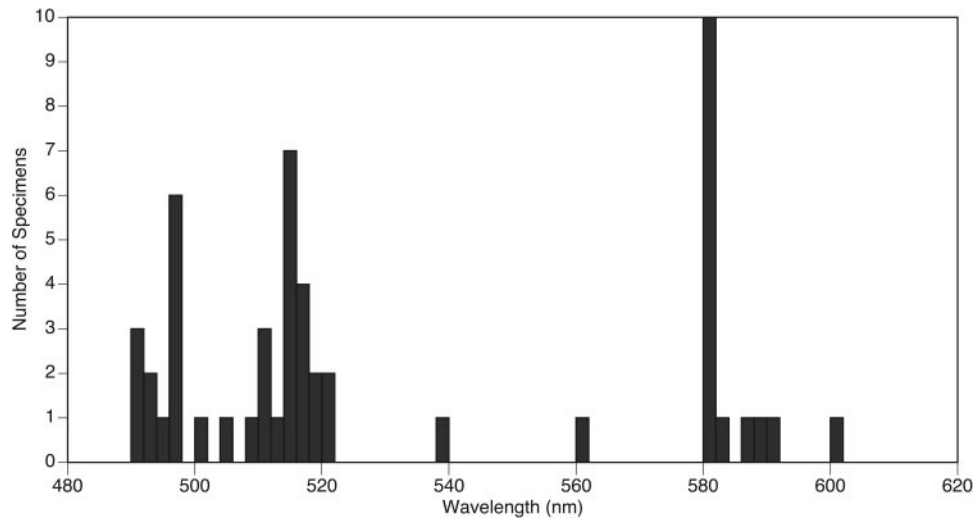


Figure 1. Distribution of *in situ* peak fluorescent emission spectra of coral specimens ($n = 51$).

monly referred to as zooxanthellae, supply complex carbohydrates, amino acids, sugars, and peptides (or photosynthate) to their coral hosts. It is estimated that up to 95% of the coral's carbon requirement is provided by zooxanthellae (Muscatine, 1967, 1977; Falkowski *et al.*, 1984; Sutton and Hoegh-Guldberg, 1990). In return, the zooxanthellae are protected from predation and obtain nutrients excreted by the coral.

Various theories have been proposed to explain the function of fluorescent proteins in coral. Fluorescent proteins convert the abundant high-energy (violet, blue, and green) photons in sunlight to lower energy and possibly aid photosynthesis in the coral's algae symbionts (Schlichter and Fricke, 1990). However, this theory has been challenged by the argument that the trivial process of transferring photons between the fluorescent proteins present in the coral cells and the photosynthetic machinery of algal cells is far too inefficient to impact photosynthesis significantly (Mazel *et al.*, 2003). Fluorescent proteins have been shown to have a photoprotective role and may shield the coral and zooxanthellae from excess sunlight (Salih *et al.*, 2000). Fluorescent proteins also absorb reactive oxygen species, including H_2O_2 (Inouye and Tsuji, 1994; Bou-Abdallah *et al.*, 2006) that are dangerous byproducts of photosynthesis (Tchernov *et al.*, 2004). Additionally, studies have suggested that fluorescent proteins may act to produce light that enhances coloration at depth (Mazel, 1995; Myers *et al.*, 1999; Dove *et al.*, 2000; Lukyanov *et al.*, 2000; Mazel and Fuchs, 2003).

Most fluorescent protein homologs absorb blue or green light and emit green or red, respectively. Mazel and Fuchs (2003) found that fluorescent light from some highly fluorescent corals represents a considerable component of the animal's exitant light spectrum. However, the expression level of fluorescent proteins in *Montastrea cavernosa* has been shown to vary greatly, and expression levels do not correspond to the coral's daylight coloration (Kao *et al.*, 2007). These results led us to hypothesize that patterns of fluorescent protein expres-

sion may not be related to the coral's visual appearance under natural light conditions but instead function as a signaling mechanism to specific organisms capable of detecting the wavelengths emitted by the coral.

Materials and Methods

We examined the fluorescence of 33 scleractinian coral species found on the northern Great Barrier Reef. Reef fluorescence was examined on night dives using a GENII intensified night vision scope contained in an underwater housing (Ikelite). The intensifier screen was imaged with a black-and-white camera and the image recorded on a Sony TRV900 camcorder. The night vision scope was outfitted with longpass interference filters (see below) and, for illumination, a bright light cannon (HD lamp) outfitted with bandpass excitation filters. Corals were collected at locations around Lizard Island, Australia, in water depths ranging from 1 to 30 m. Samples were photographed *in situ* with a Nikon Coolpix 5000 camera in an Ikelite housing using an Ikelite DS125 electronic flash. White balance and color was corrected against standard Kodak targets. The emission spectrum was obtained by illuminating the coral samples with a high intensity discharge lamp fitted with the excitation filters and recording fluorescence spectra with a fiber optic probe connected to a spectrophotometer (Ocean Optics USB2000, Ocean Optics, Dunedin, FL).

Macro photography

Samples of coral were placed in a narrow photography tank against a thin plate glass front. Fluorescent macro images (2180×1800 pixel; Nikon Coolpix 5000) were produced in a dark room by covering the flash (Ikelite DS125 or Vivitar 185) with interference bandpass excitation filters (Chroma Tech., Rockingham, VT). Longpass and bandpass emission filters (Chroma Tech.) were attached to

Table 1

Coral specimens collected

Species	Family	Depth (m)	GenBank accession #	Previous noted fluorescence
<i>Montipora spongodes</i>	Acroporidae	5.2	—	—
<i>Acropora tenuis</i>	Acroporidae	ND	AY646074	Unpublished
<i>Acropora millepora</i>	Acroporidae	2.1	AY646070	Unpublished
<i>Acropora latistella</i>	Acroporidae	ND	—	—
<i>Acropora samoensis</i>	Acroporidae	ND	—	—
<i>Acropora humilis</i>	Acroporidae	ND	—	—
<i>Acropora</i> sp.	Acroporidae	ND	AB128822	(Karasawa <i>et al.</i> , 2004)
<i>Acropora</i> sp.	Acroporidae	ND	AB128822	(Karasawa <i>et al.</i> , 2004)
<i>Montipora</i>	Acroporidae	ND	AB209967	(Kogure <i>et al.</i> , 2006)
<i>Astreopora</i> sp.*	Acroporidae	5.2	—	—
<i>Leptastrea pruinosa</i>	Faviidae	3.7	—	—
<i>Favia complanata</i>	Faviidae	4.0	—	—
<i>Goniastrea australensis</i>	Faviidae	6.1	—	—
<i>Favia pallida</i>	Faviidae	7.0	—	—
<i>Favia favius</i>	Faviidae	7.9	AB193293	Unpublished
<i>Leptastrea bewickensis</i>	Faviidae	4.9	—	—
<i>Cyphastrea microphthalma</i>	Faviidae	1.2	—	—
<i>Goniastrea</i> sp.*	Faviidae	6.7	—	—
<i>Echinopora mammiformis</i>	Faviidae	6.4	—	—
<i>Favia pallida</i>	Faviidae	1.5	—	—
<i>Favia</i> sp.	Faviidae	4.0	AB193293	Unpublished
<i>Favia pentagona</i>	Faviidae	5.8	—	—
<i>Favia veroni</i>	Faviidae	4.6	—	—
<i>Favia</i> sp.	Faviidae	9.1	AB193293	Unpublished
<i>Caulastrea tumida</i>	Faviidae	3.7	—	—
<i>Goniastrea pectinata</i>	Faviidae	4.0	—	—
<i>Favia rotumana</i>	Faviidae	5.8	—	—
<i>Platygyra lamellina</i>	Faviidae	4.6	—	—
<i>Favia marshallae</i>	Faviidae	1.8	—	—
<i>Favia</i> sp.	Faviidae	1.8	AB193293	Unpublished
<i>Caulastrea echinulata</i>	Faviidae	ND	—	—
<i>Fungia cyclolites</i>	Fungiidae	ND	—	—
<i>Merulina scabricula</i>	Merulinidae	0	—	—
<i>Merulina</i> sp.*	Merulinidae	2.1	—	—
<i>Merulina ampliata</i>	Merulinidae	6.1	—	—
<i>Lobophyllia hemprichii</i>	Mussidae	2.4	AY765217	(Wiedenmann <i>et al.</i> , 2004)
<i>Lobophyllia hemprichii</i>	Mussidae	5.8	AY765217	(Wiedenmann <i>et al.</i> , 2004)
<i>Lobophyllia hemprichii</i>	Mussidae	4.0	AY765217	(Wiedenmann <i>et al.</i> , 2004)
<i>Lobophyllia hemprichii</i>	Mussidae	4.3	AY765217	(Wiedenmann <i>et al.</i> , 2004)
<i>Lobophyllia hataii</i>	Mussidae	7.0	—	—
<i>Lobophyllia pachysepta</i>	Mussidae	1.8	—	—
<i>Acanthastrea faviaformis</i>	Mussidae	6.1	—	—
<i>Acanthastrea rotundoflora</i>	Mussidae	2.4	—	—
<i>Galaxea fascicularis</i>	Oculinidae	4.6	AB107915	(Karasawa <i>et al.</i> , 2003)
<i>Galaxea fascicularis</i>	Oculinidae	6.1	AB107915	(Karasawa <i>et al.</i> , 2003)
<i>Porites</i> sp.	Poritidae	2.4	DQ206391	Unpublished
<i>Goniopora</i> sp.	Poritidae	8.8	AF383156	(Gurskaya <i>et al.</i> , 2001)
<i>Porites</i> sp.	Poritidae	10.7	DQ206391	Unpublished
<i>Porities</i> sp.	Poritidae	1.8	DQ206391	Unpublished
<i>Porites</i> sp.	Poritidae	1.8	DQ206391	Unpublished
<i>Psammocora superficialis</i>	Siderasteidae	2.7	—	—

Entries in bold represent the first identification of fluorescence in that species. *Asterisk indicates the first report of fluorescence in that genus.

the front of the camera. A variety of excitation/emission filter pairs were tested on each sample: ex. 400–450 nm, em. 450 LP; ex. 450–500 nm, em. 510 LP; ex. 500–550 nm, em. 555 LP; ex. 550–600 nm, em. 600 LP; ex. 600–650 nm, em. 655 LP; and ex. 650–700 nm, em. 700 LP.

Micro photography and colocalization analysis

To determine the relative colocalization of fluorescent proteins and zooxanthellae, additional fluorescence and bright field microscopic images (Nikon CoolPix 5000) of 31

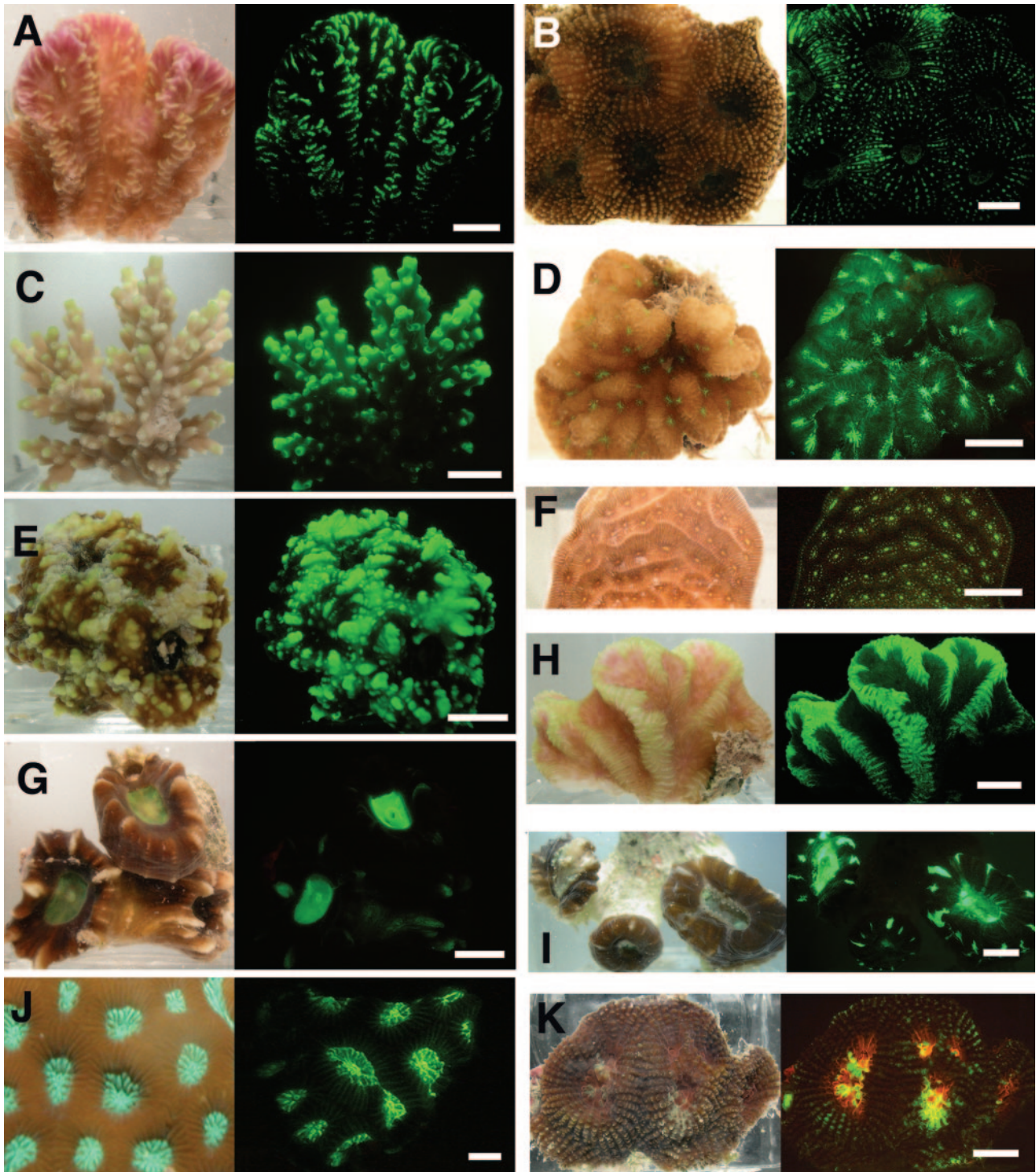


Figure 2. Scleractinian corals with highlighted fluorescent protein distribution. Pairs of images taken with white light illumination (left) and blue illumination (450–500 nm) and green fluorescent emission (right; 500–550 nm). (A) *Merulina scabricula*, (B) unknown, (C) *Acropora* sp., (D) unknown, (E) *Favia rotumana*, (F) *Agaracia* sp., (G) *Merulina* sp., (H) *Caulastrea tumida*, (I) *Caulastrea echinulata*, (J) *Goniastrea australensis*, (K) *Favia favius*. Scale bar = 5 mm.

live samples were taken on a Zeiss epifluorescent Axioskop microscope equipped with a 50-W mercury lamp and GFP (ex. 470/30 nm and em. 525/50) and RFP (ex. 530/30, em.

605/70) filters. Five samples that were either bleached or azooxanthellate were removed. In-focus areas were isolated and a 95% threshold was applied, using Photoshop ver. 8.0

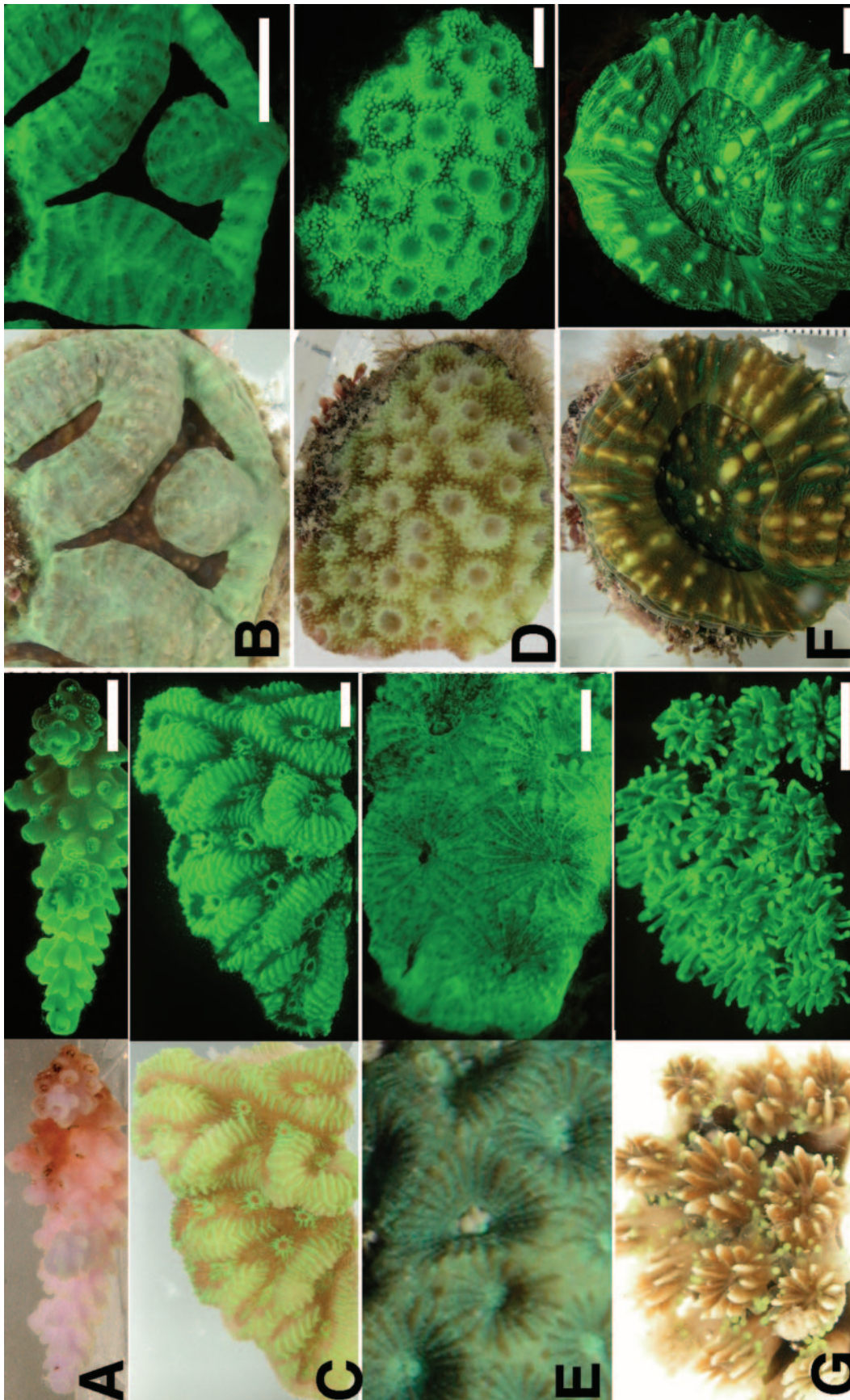
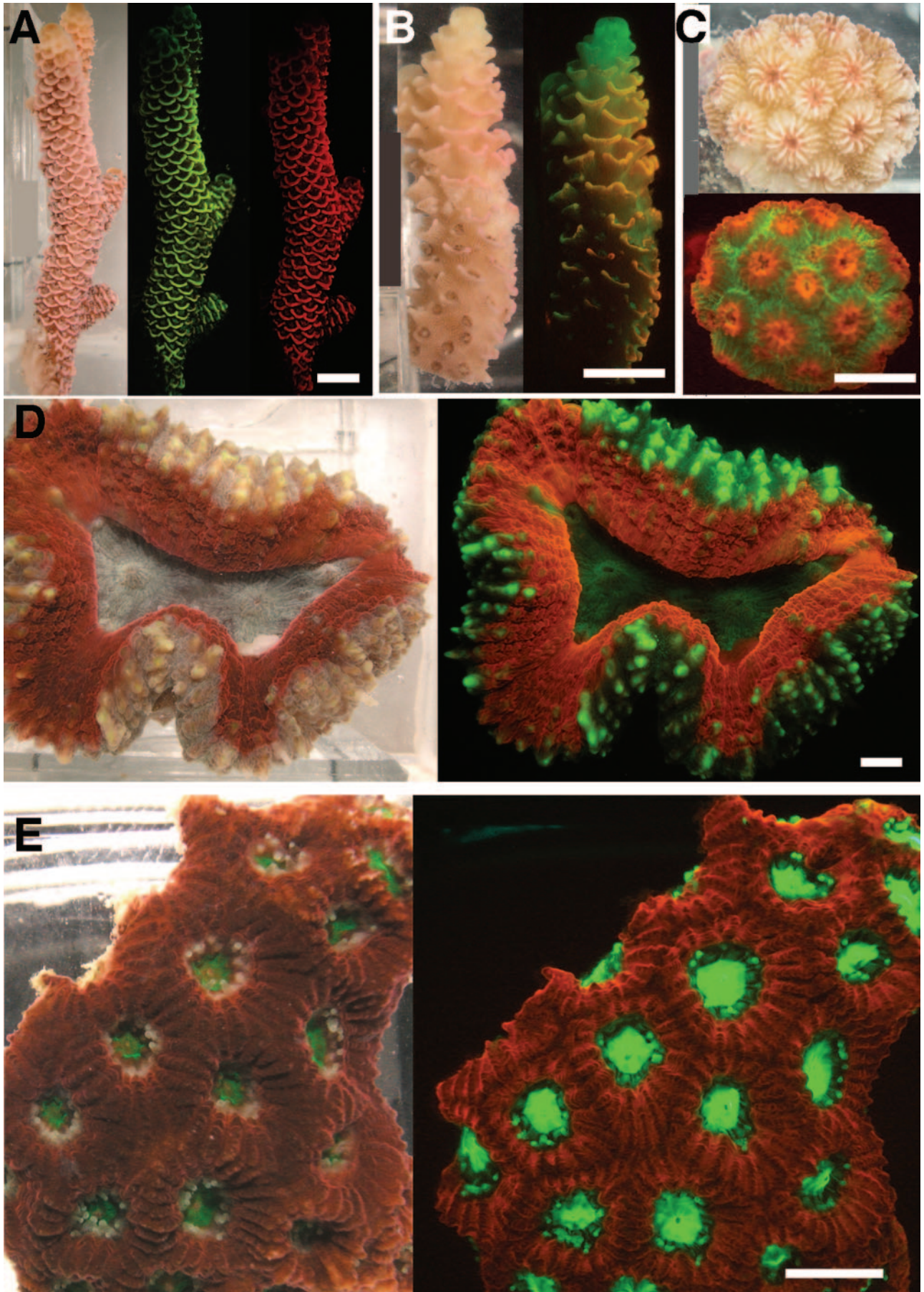


Figure 3. Scleractinian corals with uniform fluorescent protein distribution. (A) *Acropora latistella*, (B) unidentified, (C) *Merulina ampliata*, (D) *Astreopora* sp., (E) *Favia veroni*, (F) *Lobophyllia* sp., (G) *Galaxea fascicularis*. Scale bar = 5 mm.



(Adobe Systems), to minimize background noise. For each sample, the percentage of total zooxanthellate surface area coincident with red, green, or red + green coral fluorescence and the correlation coefficient, also called Pearson's coefficient (PC; Pearson, 1896; Bolte and Cordelieres, 2006), were calculated using ImageJ ver. 1.38 public domain software (U.S. National Institutes of Health).

Anatomical distribution of fluorescent proteins

In a separate analysis, the distribution of fluorescence in anatomical structures of 51 coral specimens was scored from macroscopic photographs using white light and fluorescence blue and green excitation light and an appropriate emission filter. Six structures of the coral were assayed: oral disc, tentacles, costae, septa, calice, and coenosarc. Structures were scored as red/orange, red/orange/green, green, or none. The presence of fluorescence in all pairings of structures was determined and normalized as probabilities.

Results

Visible fluorescence

We observed fluorescence clustered into three excitation/emission profiles (Fig. 1): cyan to green fluorescence (490–509 nm peak) induced by violet (400–450 nm) excitation light; green fluorescence (510–525 nm peak) induced by blue (450–500 nm) excitation light; and red fluorescence (580–600 nm peak) induced by blue/green excitation light (500–550 nm). In some samples, mixtures of these colors produced orange fluorescence. We used a range of other excitation (500–700 nm) and emission filter pairs, but except for the signature emitted by chlorophyll, we did not detect visible fluorescence in this region of the spectrum. We did not examine blue or violet fluorescence.

Distribution of coral fluorescence

We examined 51 scleractinian coral specimens taken from varying depths and representing 33 species from eight families (Table 1). These corals displayed distinct fluorescence compartmentalization distributed among three categories: *highlighted*, *uniform*, and *complementary*.

Those with a *highlighted* pattern varied in fluorescent distribution, but invariably resulted in the concentration of

fluorescence in anatomical regions of the coral polyp or the underlying calcium carbonate skeleton (Fig. 2). For example, corals often concentrated fluorescent protein to the oral disc or the tentacles (Fig. 2f, g, j) while other areas of the coral exhibited no fluorescence. This pattern was present across all scleractinian coral families examined, including Acroporidae, Mussidae, Faviidae, Fungiidae, Merulinidae, Oculinidae, Siderasteidae, and Poritidae. The fluorescent patterns were mainly constant among species, whereas the fluorescence intensity often varied.

Uniform fluorescence distribution occurs when fluorescent protein expression is distributed evenly across coral polyp cells (Fig. 3) and exhibits no targeting of the fluorescent protein to a specific component (*i.e.*, tentacle, mouth, oral disc, trunk, septa/costae, or coenosteum) of the animal's body. This pattern was predominantly observed among green fluorescent corals, with rare occurrences of red. Uniform fluorescence does not provide fluorescence contrasting of coral structures, but does highlight the coral colony against a nonfluorescent background.

Complementary fluorescence occurs when green and red fluorescent proteins are targeted to differing anatomical regions of the coral, often with distinct boundaries between green and red fluorescence (Fig. 4). In some cases, the fluorescent proteins produced visible coloration under sunlight irradiance; however, in many cases coloration did not coincide with the fluorescent patterning of the animal (Fig. 4c, d).

Differences in green and red fluorescence

We report that corals often differentially targeted red and green fluorescence to specific anatomical structures. For example, green fluorescence might be targeted to the mouth or oral disc and red targeted to the coenosarc, the tissue that joins the coral to the neighboring polyp (Figs. 3e and 4e). In other specimens, the inverse pattern was observed (Fig. 3c). The distribution of red fluorescence, while highly varied, was often coincident with the green fluorophores (Figs. 4–6), producing an orange color. Red fluorescence was rarely found alone, but in those few cases it exhibited both highlighted and uniform patterns (Fig. 5). Using violet (450–500 nm) and blue (500–550 nm) excitation light, it was also possible to identify corals that targeted different

Figure 4. Examples of corals expressing complementary patterns of green and red fluorescence. (A) Overlapping distribution of green and red fluorescence in *Acropora* sp. (B) Branching coral *Acropora latistella*. The branch tip colonies are predominately green while the more proximal ones exhibit both green and red fluorescence (producing orange fluorescence). (C) Juvenile *Cyphastrea microphthalma* colony with polyps exhibiting red fluorescent mouth and septa and green fluorescent coenosarc. (D) Large mature *Lobophyllia* sp. polyps with red fluorescence and green fluorescent highlights of the septa/theca. (E) *Goniastrea* sp. with bright green mouth and red coenosarc. Scale bar = 5 mm. Figure B, C, D, and E are reprinted by permission of the publisher from *Aglow in the Dark: The Revolutionary Science of Biofluorescence*, by Vincent Pieribone and David F. Gruber, published by The Belknap Press of Harvard University Press, Cambridge, MA: Copyright ©2005 by the President and Fellows of Harvard College.

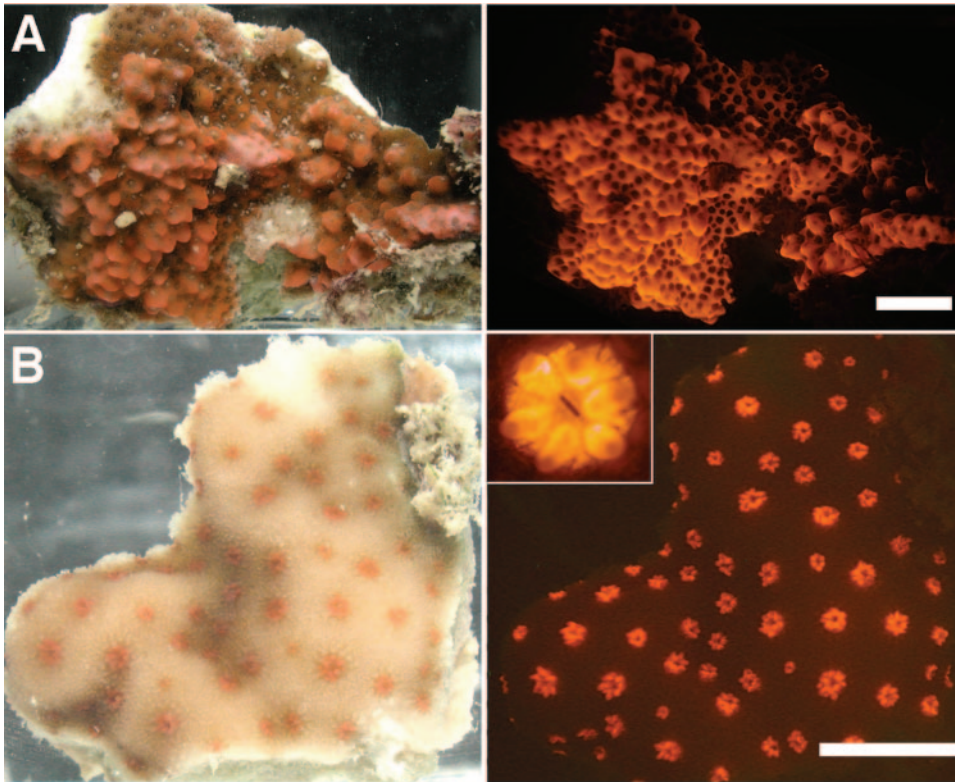


Figure 5. Two corals with exclusively red fluorescence. (A) White-light image of *Montipora spongodes* (left) and red fluorescence (right) induced by green excitation light (500–550 nm). Red fluorescence exists mostly in the coenosarc around the tiny polyps. (B) White-light and red-fluorescent image of a sample of *Porities* sp. exhibiting bright red fluorescent tentacles. Insert: Micrographs of red fluorescent tentacles from coral in B. Scale bar = 5 mm.

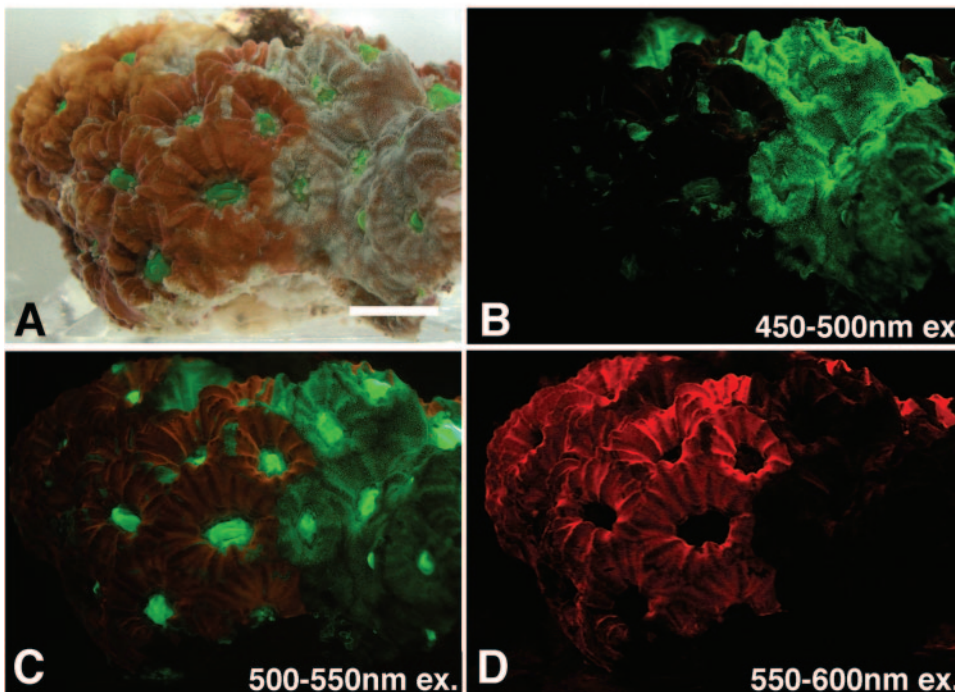


Figure 6. Different colonies from the same coral, *Favites pentagona*, exhibit differential fluorescent protein distribution. (A) A white-light image of the coral piece reveals two distinct color morphs. Colonies on the left have green mouths and red theca/septa, while colonies on the right have grey theca/septa. (B) Fluorescent excitation with violet light (400–450 nm ex./ 500 nm LP em.) reveals the presence of a specific fluorescent protein within the theca/septa. Note the absence of green fluorescence in the mouth region. (C) Illumination with blue light (500–550 nm ex./550 LP em.) reveals the bright green fluorescence in mouth of all colonies, green theca/septa fluorescence on the right-hand colonies, and red fluorescence in the theca/septa of the left-hand colonies. (D) Illumination with green light (550–600 nm ex./610 nm LP em.) shows the discrete localization of red fluorescent protein to theca/septa in some colonies. Scale bar = 5 mm.

green fluorescent proteins to different polyp structures. For example, *Favites pentagona* targeted violet-excited green fluorescence to the coenosarc of some colonies while targeting blue-excited green fluorescence to the mouth region (Fig. 6). This coral also expressed red fluorescence on some areas of the coenosarc. We cannot rule out the possibility

that the orange/red fluorescence detected in some of these corals may in fact be derived from phycobiliproteins (Lesser *et al.*, 2004). A recent finding (Lesser *et al.*, 2007) that chemical uncoupling of PSII energy transfer increases fluorescence in the >570 nm range further supports the presence of significant amounts of cyanobacteria in coral. How-

ever, the degree to which cyanobacteria contribute to coral fluorescence is contested (Oswald *et al.*, 2007).

Association of fluorescent proteins and zooxanthellae

To determine the degree to which fluorescence is associated with the localization of zooxanthellae, we calculated the proportion of total zooxanthellate surface area coincident with fluorescence and computed the Pearson coefficient (PC) (see Materials and Methods). PC values range from -1 to 1 , where -1 represents a complete negative correlation between data sets, 1 represents positive correlation, and zero represents no correlation.

In our analysis of 26 high-resolution images of various coral species (Table 2), neither measure suggested that zooxanthellae were correlated with fluorescent protein distribution. On average, 60.9% (SD = 27.3%) of the zooxanthellate surface area colocalized with fluorescence, with a mean PC of -0.11 (SD = 0.19). Analysis of zooxanthellate localization to either green or red fluorescence, independently, also did not result in a correlation (56.1% of total

zooxanthellae surface area colocalized with green fluorescence, PC = -0.12 ; 56.2% with red fluorescence, PC = 0.0). Among specimens exhibiting a strong positive or negative correlation, one *Acropora* sample displayed high colocalization (PC = 0.39) and samples of *Leptastrea bewickensis* and *Astreopora* sp. displayed strong negative correlations (PC = -0.40 and -0.50 , respectively). It should be noted that this analysis examines the zooxanthellate/fluorescent protein distribution only from a random group of corals found around Lizard Island on the Great Barrier Reef. While many studies have examined the diversity and biogeography of zooxanthellae (Rowan *et al.*, 1997; Baker, 2003), the anatomical distribution of zooxanthellae in coral tissue has rarely been examined, except for a report that zooxanthellate density is relatively constant in coral tissue at 10^6 to 2×10^6 cells/cm (Muscatine *et al.*, 1985).

Correlated anatomical expression of fluorescent proteins

We sought to determine whether the distribution of fluorescent proteins across anatomical structures was nonrandom across coral species. To answer this question we performed pair-wise comparisons of structures (Fig. 7) and calculated the normalized probability that corals with fluorescence (red or green or both) in one structure exhibit fluorescence in another. Coral polyps were subdivided into oral disc (M), coenosarc (Cs), tentacles (Ten), costae (Co), calice (Ca), and septa (Ss). Although in most cases the probability of co-expression was close to 0.5, six pairs (between four structures) showed a negative probability. Whereas these structures contained fluorescence at equivalent probability, fluorescence in one of the structures resulted in a significantly reduced probability that fluorescence would be found in the other structure. The color or colors of the fluorescence did not affect the outcome of the analysis. This finding indicates that the targeting of fluorescent proteins is nonrandom and, given that those structures in the low probability pairs were all juxtaposed to each other, the net result is that fluorescent and nonfluorescent structures create visual contrast. This is evident in the corals in Figures 2g, j, k; 4a, c, d, e; 5b; and 6. This contrasting pattern was present in specimens from all depths and across the majority of coral taxa studied in this report. In addition, several structures appeared to consistently co-express a particular fluorescence color. For example, green fluorescence in the coralite was often paired with green fluorescence in the coenosarc, and green mouth fluorescence was often paired with green calice fluorescence. Our sample size was not large enough to support a phylogenetic association of fluorescence distribution.

Discussion

The present study reveals that many Indo-Pacific scleractinian corals express green or red fluorescent proteins, or

Table 2

Zooxanthellae and fluorescence colocalization

Specimen	% Zooxanthellate surface area colocalized with coral fluorescence	% Coral surface area exhibiting fluorescence	Pearson's Coefficient
<i>Acropora</i> sp.	67.6	46.6	0.39
<i>Caulastrea tumida</i>	73.6	70.1	0.08
<i>Astreopora</i> sp.	54.5	65.5	-0.34
<i>Acanthastrea rotundoflora</i>	95.0	94.8	0.00
<i>Favia veroni</i>	77.9	80.8	-0.04
<i>Psammocora superficialis</i>	64.3	77.1	-0.25
<i>Porites</i> sp.	77.6	86.3	-0.18
<i>Porites</i> sp.	12.0	13.3	-0.02
<i>Leptastrea bewickensis</i>	2.0	12.2	-0.40
<i>Merulina</i> sp.	73.3	81.2	-0.09
<i>Cyphastrea microphthalma</i>	77.6	72.1	0.09
<i>Astreopora</i> sp.	53.7	80.9	-0.50
<i>Montipora spongodes</i>	93.2	91.4	0.03
<i>Echinopora mammiformis</i>	84.3	85.3	-0.02
<i>Goniastrea</i> sp.	77.6	85.5	-0.18
<i>Goniastrea pectinata</i>	67.4	72.4	-0.05
<i>Acropora millepora</i>	38.5	49.9	-0.14
<i>Lobophyllia pachysepta</i>	53.7	70.0	-0.21
<i>Galaxea fascicularis</i>	77.3	82.5	-0.11
<i>Fungia cyclolites</i>	69.2	84.3	-0.36
<i>Favia</i> sp.	8.2	11.9	-0.08
<i>Acropora latistella</i>	87.4	85.4	0.02
<i>Platygyra lamellina</i>	65.6	67.8	-0.03
<i>Merulina scabricula</i>	9.6	29.3	-0.13
<i>Favia rotumana</i>	87.9	90.0	-0.02
<i>Lobophyllia hemprichii</i>	35.2	46.7	-0.36
Avg.	60.9	66.7	-0.11
St. Dev.	27.3	25.3	0.19

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