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REPORT

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Spectral reflectance of coral

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Abstract Spectral reflectance (R) of corals is a fundamental parameter to coral reef remote sensing. We explore general trends as well as geographic and taxonomic variabilities of coral R using a data set consisting of 5,199 R's measured in situ at depths of up to 15 m for 195 coral colonies at 11 sites worldwide. Coral R ranges in magnitude from ~0.5% at 400 nm to near 100% at 700 nm; mean coral R rises from ~2.5% at 400–500 nm to ~8% between 550 and 650 nm. All corals measured in this study exhibit one of two basic shapes of R, which we label the "brown" and "blue" modes. We postulate that brown-mode R is determined by pigment absorption solely by zooxanthellae, while blue-mode R arises through expression of a non-fluorescing coral-host pigment. Taxonomic and geographic variabilities are approximately equal to global variability, both in magnitude and shape, indicating that coral R is independent of taxonomic or geographic differences. We reason that this is to be expected, since R is determined by pigments that are conservative across geographic and taxonomic boundaries.

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Introduction

Sea-floor spectral reflectance (R) is a central parameter to coral reef remote sensing for two reasons. First, R represents the bottom boundary for radiative transfer in optically shallow water (e.g., Maritorena et al. 1994). As a result, R is important for—and is often the objective of—solving the inverse radiative transfer problem presented by passive remote sensing. Second, R is a function of an object's structure and material composition; thus R serves as a link between optics and the makeup of the sea floor (e.g., Lyzenga 1978). Accordingly, image classification and generation of thematic maps ultimately rely on differences in R between benthic classes (e.g., Andréfouët et al. 2001; Hochberg et al. 2003).

The most commonly stated reason for developing coral reef remote sensing techniques is to assess and/or to monitor the status of these ecosystems (Green et al. 1996; Kuchler et al. 1988). The most important parameters for such assessment are the relative bottom covers of hermatypic corals, various algae, and sediments (Connell 1997; Done 1992, 1995). Thus, remote sensing of reef status should focus on these bottom-types. Several local-scale investigations of coral reef R indicate that these fundamental reef classes are spectrally distinct from each other (Andréfouët et al. 2001; Clark et al. 2000; Hedley and Mumby 2003; Hochberg and Atkinson 2000; Holden and LeDrew 1998, 1999; Kutser et al. 2003; Louchard et al. 2003; Lubin et al. 2001). Recently, Hochberg and Atkinson (2003) and Hochberg et al. (2003) have confirmed this at the global scale using a set of R's collected on reefs around the world. These studies have focused primarily on the spectral separabilities between relatively broad reef classes such as coral and algae. However, among these studies there seems to be little consensus of the spectral variability within these broad classes.

Holden and LeDrew (1999), through repeated univariate *t*-tests and principal-component analysis, determined that there is no significant difference in *R* between corals from Fiji and Indonesia and that *R* does not vary significantly with coral colony morphology. Conversely, Joyce and Phinn (2002) reported that different morphologies impart different degrees of variance to coral *R*, which in turn may enable spectral discrimination of those morphologies. Lubin et al. (2001) suggested that four Caribbean coral species are in fact distinguishable from each other, based on visual inspection of mean *R*'s for the species. Kutser et al. (2003) illustrated variability in spectral shape and magnitude for *Acropora hyacinthus* with mean spectra taken from six individual colonies. Computing spectral slopes among selected wavebands, Minghelli-Roman et al. (2002) demonstrated spectral separability between 14 genera of Red Sea corals. Finally, Andréfouët et al. (2001) and Hochberg et al. (2003) each made brief mention of corals exhibiting either "blue" or "brown" modes of *R*.

To date, those studies detailing trends and variabilities of coral *R* have been conducted at the local scale (except Holden and LeDrew 1999). In this study, we utilize a unique database to explore coral *R* at colony and species levels, and at local, regional, and global scales. We should note that these data were collected for the purpose of determining spectral separabilities between corals and non-coral organisms and substrates on reefs worldwide. Because of this experimental design, and despite the very large overall sample size, the data are not sufficient for making definitive statistical comparisons, for example, between coral taxa or study sites. However, our data set does encompass a wide variety of coral taxa and locales. Thus, it is possible to describe trends and variabilities in coral *R*, which is the aim of this report.

Materials and methods

Details of spectral measurements are given in Hochberg and Atkinson (2000) and Hochberg et al. (2003). Briefly, we employed a portable fiber optic spectrometer (Ocean Optics S2000) to measure light upwelling from a given reef target (e.g., a coral or portion of a coral) and from a calibration target of known *R* (Spectralon diffuse reflectance target). The calibration target was placed at the same depth as the reef target and thus was exposed to the same ambient light field. Measurement distances were held constant between the calibration and reef targets, generally ~10 cm from each. Taking the ratio of reef target (reflected) intensity to calibration target (incident) intensity, we computed reef target *R*. Because water column effects on the ambient light field were equal for both targets, this computed *R* was solely a property of the reef target.

In all, our database currently contains 5,199 *R*'s measured in situ at depths of up to 15 m for 195 coral colonies at the following sites (Fig. 1): (1) St. Croix, U.S. Virgin Islands; (2) Puerto Rico; (3) Florida Keys; (4) Oahu, Hawaii; (5) Rangiroa, French Polynesia; (6) Moorea, French Polynesia; (7) Palau; (8) Heron Island, Great Barrier Reef, Australia; (9) Bali, Indonesia; (10) Mayotte, Comoros; and (11) the Waikiki Aquarium (Indo-Pacific corals grown in aquaria). These sites represent four major coral biogeographic regions as defined by Veron (1995): Caribbean, Hawaiian Islands, Central Pacific, and Indo-west Pacific. *R*'s in this study are reported at 1-nm intervals over the range 400–700 nm, for a total of 301 wavelengths. To facilitate comparisons of spectral shapes without the effects of spectral magnitudes, normalized spectra were computed through division of each spectrum by its vector length, computed over the 301β wavelength dimensions.

Results

General features

The top panels of Figs. 2 and 3 show mean *R* for 143 corals in our database (those identified taxonomically). All exhibit relatively depressed *R* between 400 and 500 nm, higher *R* between 550 and 650 nm, a narrow chlorophyll absorption feature near 675 nm, and very rapidly increasing *R* at wavelengths greater than 680 nm. Magnitude of *R* ranges from ~0.5% at blue wavelengths to near 100% at 700 nm. Overall mean *R* (not shown) rises from ~2.5% at 400–500 nm to ~8% between 550 and 650 nm. Some individual colonies exhibit apparent fluorescence features at wavelengths in the range 450–520 nm (see Discussion).

Brown and blue corals

The most obvious trend in the data is that corals exhibit one of two modes of *R*. The more common of the two is the triple-peaked pattern first commented on by Myers et al. (1999). This pattern is characterized by depressed reflectance between 400 and 550 nm and by positive reflectance features (i.e., local maxima or shoulders) near 575, 600, and 650 nm. Because this pattern is expressed by corals that visually appear brown, red, orange, yellow, or green, we label this the "brown coral" mode. The top panel of Fig. 2 shows mean *R* for 106 brown coral colonies from reefs worldwide (Table 1 lists represented taxa and locations). Despite variations in absolute magnitude between colonies, the 570–600–650 nm pattern is clearly apparent. This is borne out in normalized *R* shown in the bottom panel of Fig. 2. In this case, all but a few spectra have very similar values over the range 550–700 nm, and all spectra again exhibit the triple-peaked pattern.

The less common mode of *R* is exhibited by those corals visually appearing purple, blue, pink, or gray, hereafter referred to as "blue corals." In this mode, the 575 nm feature is generally absent, leaving a plateau-like shape between 600 and 650 nm. The top panel of Fig. 3 illustrates this mode of *R* for 37 coral colonies from reefs worldwide, and the bottom panel shows the same spectra normalized to their vector lengths (Table 1 lists represented taxa and locations). In some colonies it appears that the 575 nm feature of brown corals simply has shifted to shorter wavelengths, while in other colonies there is a strong absorption feature in the region 560–570 nm.

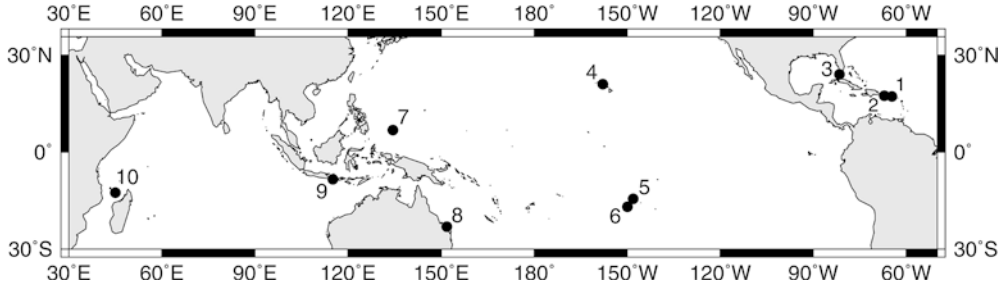

Fig. 1 Locations of study sites, shown as *circles*: (*1*) St. Croix, U.S. Virgin Islands; (*2*) Puerto Rico; (*3*) Florida Keys; (*4*) Oahu, Hawaii; (*5*) Rangiroa, French Polynesia; (*6*) Moorea, French Polynesia; (*7*) Palau; (*8*) Heron Island, Great Barrier Reef, Australia; (*9*) Bali, Indonesia; (*10*) Mayotte, Comorros; and (*11*) the Waikiki Aquarium (not shown)

Colony-scale variability

All corals exhibit some degree of variation between *R*'s measured at different locations on the colony. The primary variation is in magnitude rather than shape. As an example, we present *R* for three coral colonies, one a massive *Porites lobata* (Fig. 4A) and the others branching *P. compressa* (Fig. 4B–C), measured under identical lighting conditions in a shallow outdoor tank at the Hawaii Institute of Marine Biology. Greater variation in the *P. compressa* colonies is likely due to shadows produced by the branches coupled with the spectrometer field of view, which encompassed variable amounts of branch tips and branch bases. It is clear from the normalized *R* data in Fig. 4D–F that each respective coral has a very consistent shape of *R* regardless of measurement location on the colony.

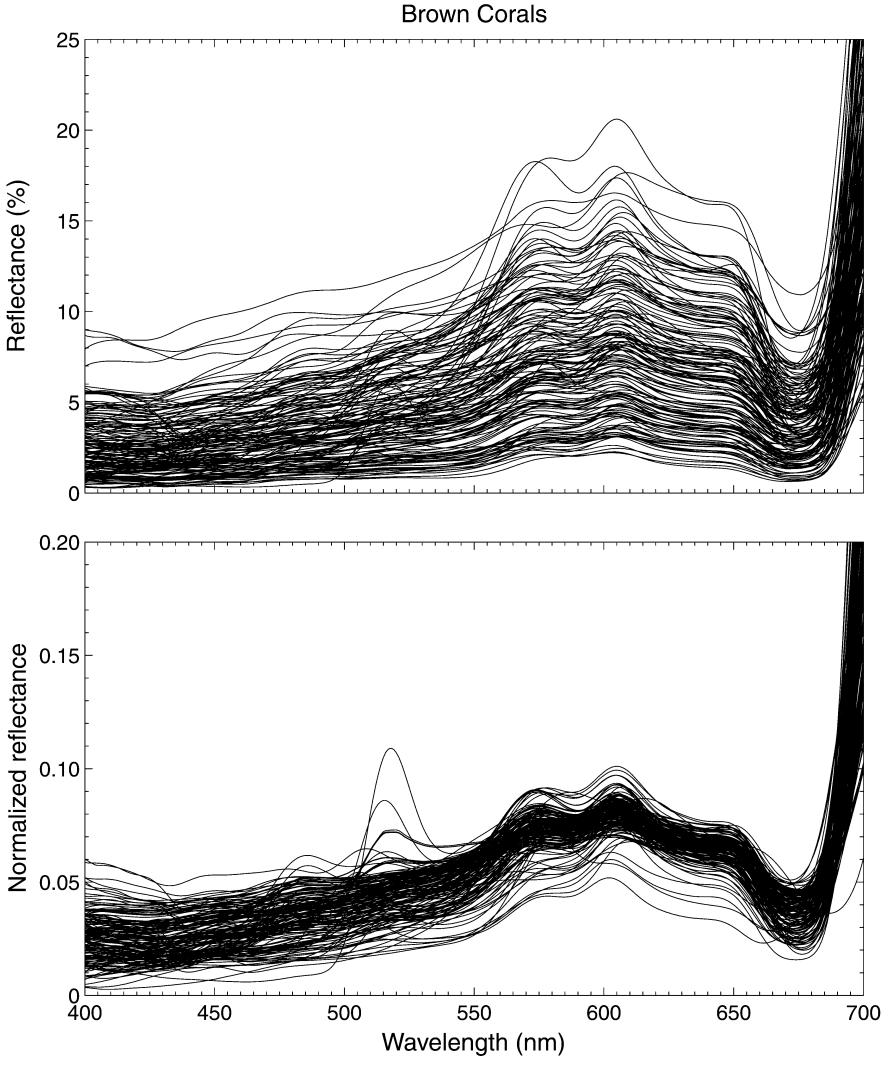

Fig. 2 Top: Mean *R* for each of 106 brown coral colonies worldwide, illustrating range in magnitude and shape of *R*. Bottom: Normalized mean *R* for the same colonies, highlighting the triple-peaked pattern at 570, 600, and 650 nm characteristic of brown-mode *R*. See Table 1 for list of taxa and measurement locations

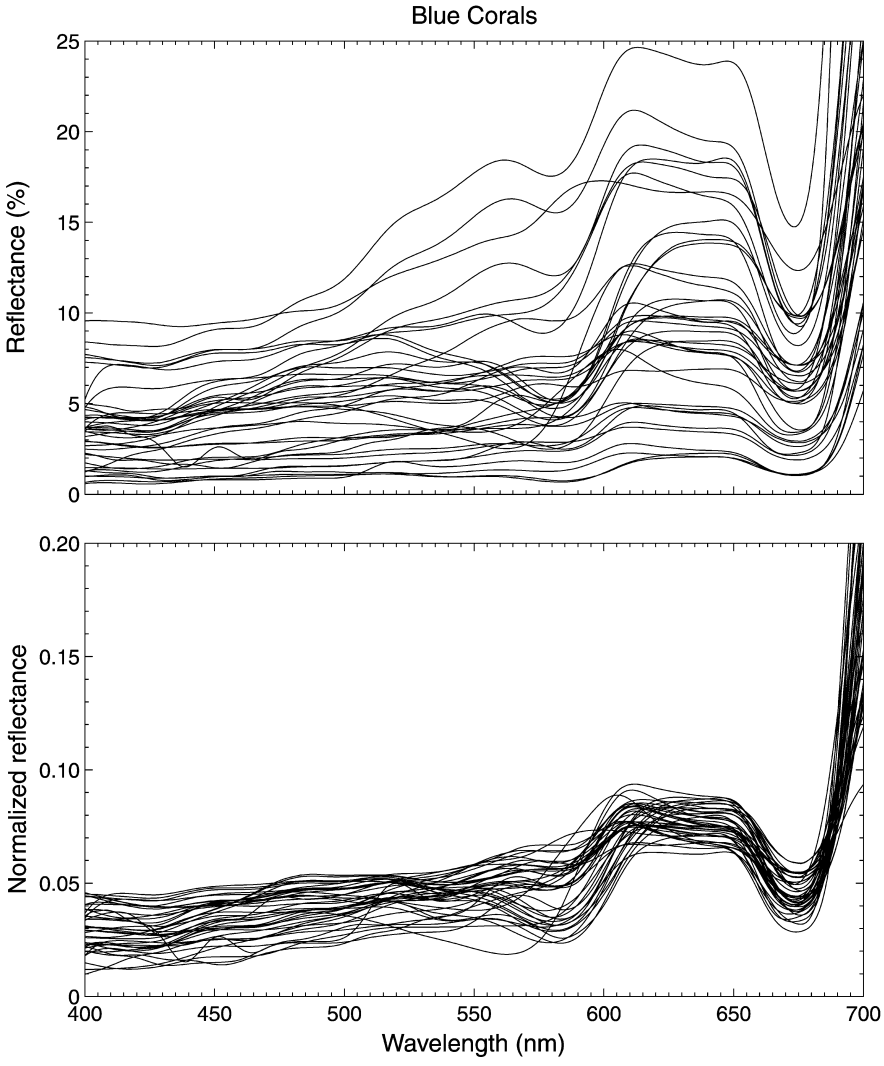

Fig. 3 Top: Mean *R* for each of 37 blue coral colonies worldwide, illustrating range in magnitude and shape of *R*. Bottom: Normalized mean *R* for the same colonies, highlighting the plateau-shaped pattern between 600 and 650 nm characteristic of blue-mode *R*. See Table 1 for list of taxa and measurement locations

Taxonomic variability

Figure 4 also indicates that conspecifics and congeners exhibit wide variabilities in the magnitude of *R*. For example, the *P. compressa* in Fig. 4B has a minimum *R* near the maximum *R* of the *P. compressa* in Fig. 4C. In contrast, the *P. lobata* in Fig. 4A has *R* with relatively small variability, falling at the intersection of the two *P. compressa* colonies. Thus, the magnitude of *R* for these two *Porites* species ranges at the least between 1 and 15%. The shapes of *R* for the two *P. compressa* colonies, however, appear strikingly similar (Fig. 4E–F): in each, the first peak of the triple-peaked pattern falls near 575 nm and is slightly higher than the 600 nm peak (which falls nearer to 610 nm), and the 650 nm feature is more of a shoulder than a peak. In contrast, normalized *R* for the *P. lobata* colony reveals that the first peak is actually near 570 nm and much lower than the 600 nm feature (Fig. 4D).

Conspecifics can also exhibit wide variation in the shape of *R*. Figure 5A and B show absolute and normalized *R*, respectively, for six *Porites rus* colonies measured on a fringing reef flat at Tiahura, Moorea, French Polynesia. All six colonies were within 20 m of the others, all were at the same depth of ~1 m, and all were measured on the same day. Here, the shape of *R* varies from that of a clearly brown coral with a well-defined triple-peaked pattern to that of a clearly blue coral with a strong absorption feature near 570 nm. *Acropora digitifera* from the reef flat at Ajanguoua Reef, Mayotte, Comoros shows a comparable trend. In this case, absolute *R* ranges between 4 and 12% (Fig. 5C), but the shape of normalized *R* also ranges between blue and brown (Fig. 5D).

Geographic variability

The spectra in Figs. 4 and 5 also demonstrate that local variability within and between taxa is nearly of the same order as the global variability in Figs. 2 and 3. Figure 6A is an example showing ten mean *R*'s for *Montastrea annularis* measured at different sites in the

Table 1 Coral species exhibiting brown and blue modes of spectral reflectance

Brown coral species	Blue coral species
Acropora aspera[j]	*Acropora digitifera*[j]
Acropora austera[k]	*Acropora grandis*[k]
Acropora cytheria[k]	*Acropora hyacinthus*[g]
Acropora digitifera[j]	*Acropora irregularis*[g]
Acropora elseyi[k]	*Acropora nana*[k]
Acropora humilis[j]	*Goniastrea retiformis*[j]
Acropora hyacinthus[g,k]	*Montipora digitata*[k]
Acropora micropthalma[k]	*Montipora* sp.[f]
Acropora nasuta[h,j]	*Pocillopora meandrina*[k]
Acropora nobilis[g]	*Pocillopora* sp.[e]
Acropora palmata[a]	*Porites astreopora*[j]
Acropora sp. (several)[f,g,h,i,j,k]	*Porites cylindrica*[h]
Anacropora forbesi[k]	*Porites lutea*[f,g,h]
Caulastrea furcata[k]	*Porites rus*[f]
Diploria strigosa[a,b]	*Porites* sp. (several)[e,f,j]
Euphyllia ancora[k]	*Siderastrea radians*[a]
Euphyllia glabrescens[k]	*Siderastrea siderea*[b,c]
Favid sp.[e]	Unidentified coral (several)[e,g]
Goniopora sp.[k]	
Heliopora sp.[k*]	
Hydnophora rigida[k]	
Montastrea annularis[a,b,c]	
Montastrea cavernosa[a,b]	
Montipora capitata[d]	
Montipora digitata[k]	
Montipora sp.[h]	
Pavona sp. (several)[f,g]	
Pocillopora sp.[g]	
Pocillopora verrucosa[f]	
Porites astreoides[a,b]	
Porites compressa[d]	
Porites cylindrica[g]	
Porites lobata[k]	
Porites lutea[f,g]	
Porites porites[b]	
Porites rus[f,g]	
Porites sp. (several)[e,f,i,j]	
Siderastrea siderea[a,b,c]	
Unidentified coral (several)[g,i]	

These lists represent 106 and 37 brown and blue coral colonies, respectively, that have been taxonomically identified. Approximately 52 coral colonies in our database have not been taxonomically identified. Study sites include [a]St. Croix, U.S. Virgin Islands; [b]Puerto Rico; [c]Florida Keys; [d]Oahu, Hawaii; [e]Rangiroa, French Polynesia; [f]Moorea, French Polynesia; [g]Palau; [h]Heron Island, Great Barrier Reef, Australia; [i]Bali, Indonesia; [j]Mayotte, Comoros; and [k]the Waikiki Aquarium. **Heliopora* is a non-Scleractinian coral

Caribbean: two from the Florida Keys, three from Puerto Rico, and five from St. Croix, U.S.V.I. While all exhibit the brown mode of *R*, there is variability in both magnitude and shape of *R* (Fig. 6C). In fact, the St. Croix individuals exhibit the widest variability, having both the darkest and brightest *R*, as well as differing degrees of apparent fluorescence near 510 nm. The Florida and Puerto Rico individuals fall within the range defined by the St. Croix individuals, and two of the Puerto Rico specimens also exhibit fluorescence features near 510 nm.

Figure 6B shows mean *R* for *Porites* sp. at each site in our database (except Florida). In these data, the only noticeable trend is that *Porites* from Rangiroa appears to have brighter mean *R* than those from other locales. Conversely, *Porites* from the other French Polynesian site, Moorea, has mean *R* near the middle of the overall distribution. Oahu shows the darkest mean *R* in this set. Normalized *R* (Fig. 6D) suggests that *Porites* at St. Croix, Puerto Rico, Oahu, and the Waikiki Aquarium predominantly exhibit brown mode *R*, while *Porites* from the other sites are predominantly blue mode.

Discussion

Pigments and *R*

Ultimately, coral *R* is determined by spectral absorption and fluorescence properties of multiple pigments residing at various locations in a coral colony, including the zooxanthellae and ectodermal and endodermal host tissues (Dove et al. 1995; Fox 1972; Kawaguti 1944). Variability in each of these pigment sources contributes to the complexity in shape and magnitude of coral *R*.

Zooxanthellae are peridinin-containing dinoflagellates and thus contain the major pigments chlorophyll *a*, chlorophyll *c*, *β*-carotene, diadinoxanthin, and peridinin (Gil-Turnes and Corredor 1981). Chl c_2 and peridinin in particular are unique to Dinophyta (Prezelin 1987). Zooxanthellae pigments span a wide range of concentrations, ranging from 4–18 μg chl *a* per cm^2 of coral surface and 1.8–7 pg $cell^{-1}$ (as reviewed in Myers et al. 1999). Variations in pigment concentrations are associated with changes in zooxanthellae density or alterations of concentration within the zooxanthellae, which are both functions of environmental conditions and/or coral taxon (Hedley and Mumby 2002; Myers et al. 1999). Generally, aquatic photosynthetic organisms express an inverse relationship between light levels and chlorophyll concentration, with organisms in high light environments typically having reduced concentrations (Falkowski and Raven 1997). Xanthophyll cycling causes diatoxantin and diadinoxanthin to fluctuate with changing light conditions, and their concentrations typically decrease in low light (Brown et al. 1999). Changing environmental factors such as salinity, temperature, and nutrients also cause decreases in pigment concentrations and/or expulsion of zooxanthellae from the coral host. Another source of concentration variability exists between different coral species: Myers et al. (1999) found chl *a* concentrations of 0.9–5.4 μg cm^{-2} and peridinin concentrations of 0.4–4.2 μg cm^{-2} in seven different coral species at similar depths. Same-species pigment studies could determine whether relationships exist between pigment concentrations and coral taxa.

Different genetic clades of zooxanthellae may also possess different typical pigment concentrations. LaJeunesse (2002) found prominent ecological zonation present in several of the more abundant zooxanthellae clades, and it is conceivable that relative pigment

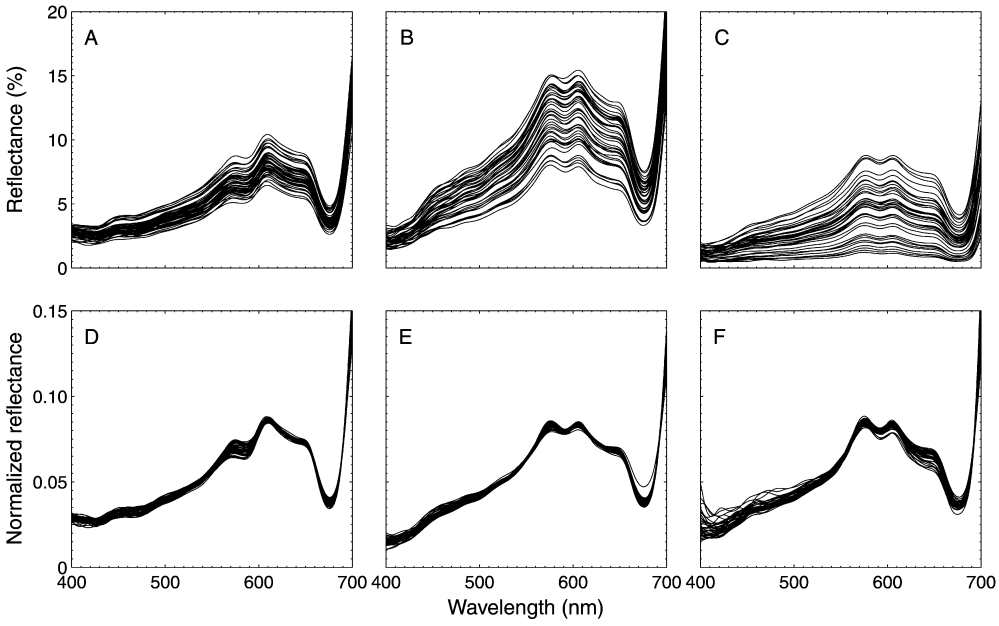

Fig. 4 Absolute *R* for one (**A**) *Porites lobata* and two (**B** and **C**) *P. compressa* colonies, measured in a shallow outdoor tank at the Hawaii Institute of Marine Biology, Oahu. (**D**), (**E**), and (**F**) show normalized *R* corresponding to the data in (**A**), (**B**), and (**C**), respectively

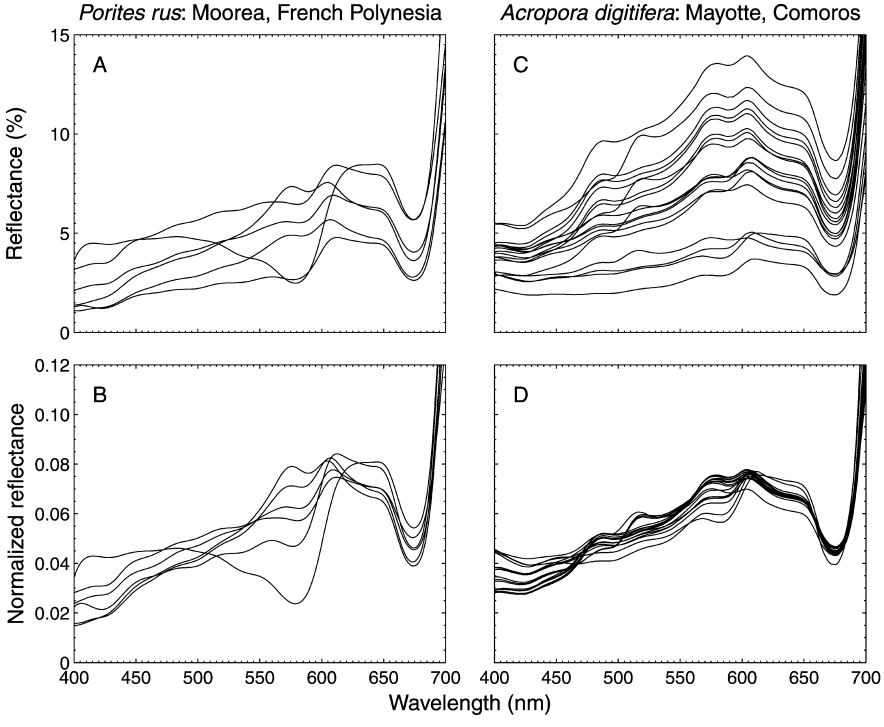

Fig. 5 Mean (**A**) absolute and (**C**) normalized *R* for six *Porites rus* colonies, measured on a fringing reef flat at Tiahura, Moorea, French Polynesia; and mean (**B**) absolute and (**D**) normalized *R* for 18 *Acropora digitifera* colonies, measured on a barrier reef flat at Ajanguoua Reef, Mayotte, Comoros. These data illustrate intra-specific variability in both the magnitude and shape of *R* and suggest a continuum between brown- and blue-mode corals

concentrations of the clades drives this zonation. One clade (A) has been found to possess measurable quantities of mycrosporine-like amino acids (MAA, UV-protective compounds, Banaszak et al. 2000). To date, however, the pigments of different zooxanthellae clades have only been investigated in culture, and this potential source of variability requires further study.

Because they are ubiquitous in healthy corals, zooxanthellae pigments form the basis for coral *R*, but coral-host pigmentation can also generate spectral variations at ultraviolet and visible wavelengths (Hedley and Mumby 2002). Green fluorescent proteins (GFP) absorb and fluoresce light at shorter and longer wavelengths, respectively, contributing to striking, human-perceived colorations (Dove et al. 2001; Mazel and Fuchs 2003; see below). Other GFP-like pigments only absorb and do not fluoresce (Dove et al. 1995; Lukyanov et al. 2000). The fluorescing and non-fluorescing GFP's are characterized by a variety of different wavelengths of energy excitation/emission and absorption, respectively (Labas et al. 2002; Salih et al. 2000). The genetic and molecular structure of several GFP's have been charac-

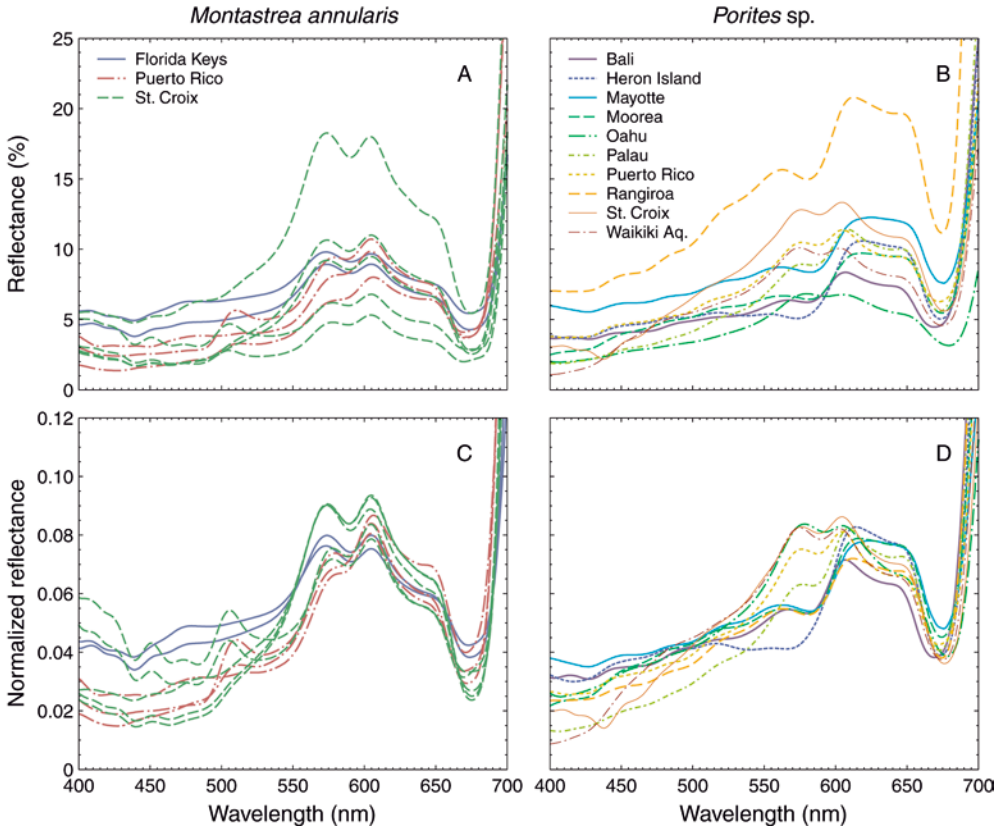

Fig. 6 Panels **A** and **C** show mean absolute and normalized *R*, respectively, for 10 *Montastrea annularis* colonies at three sites in the Caribbean. All exhibit brown-mode R, and some show apparent fluorescence features near 510 nm. Panels **B** and **D** show mean absolute and normalized *R*, respectively, for all *Porites* sp. measured at each of the 10 sites around the world. *Porites* in the Caribbean, Oahu, and the Waikiki Aquarium show only brown-mode *R*, while those at the remaining sites are predominantly blue mode

terized by Dove et al. (1995, 2001) and Matz et al. (1999), and many more have been spectrally characterized (Dove et al. 2001; Mazel 1990; Mazel 1995, 1996; Mazel and Fuchs 2003; Mazel et al. 2003; Salih et al. 2000). In five studies reviewed by Hedley and Mumby (2002), six out of ten coral species contained more than one, and often as many as three, host pigments. Several ecological functions have been ascribed to GFP's (Dove et al. 2001; Salih et al. 2000), but their concentrations have been found to be constant over a gradient of high to low light (Mazel et al. 2003).

Both zooxanthellae and coral-host pigment densities are known to vary across all spatial scales considered in this study. Thus, it is not surprising that coral *R* also shows variability at these scales. An important next step is to further the work of Myers et al. (1999) in linking pigments and coral *R*. Such research is fundamental to developing the field of coral reef color and may aid performance of coral reef thematic mapping algorithms.

Brown and blue corals

Myers et al. (1999) suggested, and Hochberg et al. (2003) demonstrated through a simple model, that absorption by zooxanthellae pigments can produce the 575 nm feature characteristic of brown-mode *R*. If, as mentioned above, coral-host pigments serve no ecological function, their concentrations may exhibit little temporal or spatial variation, and their contributions to *R* may be useful for differentiation between coral taxa (Hedley and Mumby 2002). Such might be the case with the non-fluorescing GFP (so-called "pocilloporin") described by Dove et al. (1995), which exhibits an absorption peak near 560 nm. We postulate that this pigment, or a similar one (e.g., Lukyanov et al. 2000), is responsible for the apparent absorption feature in that spectral region in blue-mode *R*. As we have shown, many coral taxa exhibit both blue- and brown-mode *R*, but Veron's (2000) comprehensive descriptions of corals worldwide indicate that some taxa only have colorations consistent with brown-mode *R*. Given an unknown blue-mode spectrum, it should therefore be possible to eliminate brown-mode-only taxa from a list of potential identifications.

Conversely, confusion may arise among and between those corals exhibiting both brown- and blue-mode *R*. Figure 5 illustrates this point: there are intermediate spectra among the six *P. rus* and 18 *A. digitifera* colonies. By our model, these represent the variable expressions of absorption by varying concentrations of a coral-host pigment, which indicates that the blue and brown modes are not mutually exclusive. Rather, they are end-members of a continuum that depends on the concentration of the coral-host's pigmentation relative to the concentrations of zooxanthellar photosynthetic pigments. In this case, lack of ecological function for the GFP would ultimately hinder discrimination between taxa due to a lack of predictability. In fact, our data are a corollary to the lack of a GFP-*versus*-depth gradient (Mazel et al. 2003): there is no pattern of coral-host

Table 2 List of studies with illustrations depicting blue- and/or brown-mode coral *R*

Reference	Modes Represented
Andréfouët et al. (2001)	Blue, brown
Clark et al. (2000)	Brown
Fuchs (2001)	Brown
Hedley and Mumby (2003)	Brown
Hochberg and Atkinson (2000)	Brown
Holden and LeDrew (1998)	Brown
Holden and LeDrew (1999)	Blue, brown
Joyce and Phinn (2002)	Brown
Joyce and Phinn (2003)	Blue, brown
Kutser et al. (2003)	Brown
Louchard et al. (2003)	Brown
Lubin et al. (2001)	Brown
Mazel and Fuchs (2003)	Brown
Mazel et al. (2003)	Brown
Minghelli-Roman et al. (2002)	Brown
Myers et al. (1999)	Brown
Yamano et al. (2003)	Brown

pigments expressed in *R* among conspecifics growing in apparently the same environment (Fig. 5).

Our modes of categorizing coral *R* are supported through examination of nearly all spectra published by other researchers for locations throughout the world. Table 2 lists those papers and the coral spectral mode(s) which they present. A few of the listed studies require further discussion. First, the single healthy coral *R* presented by Myers et al. (1999) only extends to 600 nm, and only the 575 nm feature is visible. It is therefore impossible to determine whether the coral (*Montastrea cavernosa*) truly exhibits the full triple-peaked brown mode. Second, among other brown corals, Joyce and Phinn (2002) present *R* for an unspecified table coral which apparently exhibited only a very strong reflectance feature near 570 nm and a shoulder near 650 nm. Thus, the authors conclude that this coral did not follow the triple-peaked pattern established by Hochberg and Atkinson (2000). However, though the 600-nm feature is obscured, it is still visible as a shoulder in the spectrum, and this sample is still identifiable as a brown coral. Finally, Minghelli-Roman et al. (2002) present several *R*'s for *Porites* sp. and *Echinopora* sp. measured at depths of 5–20 m, with neither genus exhibiting either the brown or blue mode of *R*, pointing to the possible existence of other modes. However, the authors' methods relied on modeled rather than measured values for incident light, and their exponential attenuation model would generate greater errors with increasing water depth. This is the likely reason that, in this case, *R* is strongly dependent on depth, which is especially evident at wavelengths >600 nm where light attenuation by the water column is strongest. Thus, as the most shallow spectra for *Porites* and *Echinopora* are at 5 m depth, the shapes of *R*'s in that study may arise through modeling errors. Interestingly, the only *R* presented by Minghelli-Roman et al. as measured in very shallow water (*Turbinaria* sp. at 10 cm, presumably insensitive to modeling artifacts) is a good example of brown-mode coral.

Finally, we should make clear that our categorizations of blue- and brown-mode are intended merely to describe the basic shape of coral *R*. We do not mean to suggest color-blindness on the part of the diver/observer: visually green corals are not brown, and pink corals are not really blue. Mazel and Fuchs (2003) provide a very good description of the perceived color of corals. In this framework of human perception, visually green corals have brown-mode *R* with a GFP fluorescence contribution near the wavelengths to which green cones in the human eye are sensitive. Similarly, a pink coral may arise from low concentrations of the blue-mode non-fluorescing GFP coupled with low zooxanthellae densities, resulting in greater optical exposure of the coral's carbonate skeleton, which in turn generates a visually brighter scene. Of course, these biooptical model "suggestions" must be verified through further studies. The key point, however, is that there are two basic modes of coral *R*, which, for lack of more elegant terminology, we have labeled blue and brown.

Colony-scale variability

Intra-colony variation in both absolute and normalized *R* may indicate differences in pigment concentrations across the colony's surface. This might be the case at blue wavelengths (400–500 nm) in normalized *R* of the second *P. compressa* colony in Fig. 3F: this is the region of peak photosynthetic pigment absorption and thus is also the region where variations of those pigments would be most expressed in *R*. Additionally, fluorescence by GFP's commonly occurs at wavelengths between 450 and 520 nm (e.g., Matz et al. 1999; Salih et al. 2000), and differential concentrations of GFP's may produce spectral variability in this range. Clark et al. (2000) also noted high intra-colony variability in general and thus considered closely spaced but non-overlapping spectral measurements to be independent.

Taxonomic variability

Table 1 shows that the *R*'s in our database agree well with observations on coral coloration reported in Veron (2000). All species with the triple-peaked *R* are known to exhibit some variation of brown coloration, such as brown, red, orange, yellow, cream, or green. Similarly, all species with blue-mode *R* are known to have some purple, blue, pink, or gray coloration. Table 1 lists as blue or brown several species that are known to exhibit both colorations, sometimes simultaneously, and especially among the genus *Acropora*. In no instances do measurements of a species in Table 1 express an *R* mode against reported colorations (e.g., *Acropora palmata* only exhibits brown-mode *R* in our database). At the family level, our spectral database contains blue and brown representatives for the Acroporidae, Faviidae, Pocilloporidae, Poritidae, and Siderastreidae, while we

have only brown representatives of the Agariciidae, Euphyllidae, and Merulinidae.

Geographic variability

Our geographic exploration of coral *R* has not revealed any identifiable trends. The few mean *R*'s in Fig. 6 do not constitute unbiased samples of the *M. annularis* populations in the three locales, or of the *Porites* sp. populations at sites worldwide. Without evidence to the contrary, for example, we must assume that *M. annularis* populations in Florida and Puerto Rico have variability in *R* at least equal to that of the St. Croix population. Overall, these taxa and the taxa not illustrated here all show local and regional variabilities in shape and magnitude on the level of the global data.

Fluorescence contributions

Fluorescence by coral-host pigments has become an area of active research, especially as it pertains to coral physiology (e.g., Dove et al. 2001; Fuchs 2001; Labas et al. 2002; Lukyanov et al. 2000; Matz et al. 1999; Mazel 1996; Mazel and Fuchs 2003; Mazel et al. 2003; Salih et al. 2000). Only Mazel (1996), Fuchs (2001), and Mazel and Fuchs (2003) have investigated the contribution of fluorescence by these pigments to overall coral *R*. Though our measurements were passive and did not specifically target fluorescence, our database does contain several clear examples of coral-host pigment fluorescence, occurring in most taxa and at all geographic locations sampled. As an example, we present *R*'s for four *Acropora* colonies from the Waikiki Aquarium and Moorea (Fig. 7). These individuals show apparent fluorescence peaks at 487, 488, 501, 516, 518, 519, and 522 nm. The features at 487–488 nm and 516–518 nm are near the wavelengths of fluorescence reported elsewhere (e.g., Fuchs 2001; Mazel 1996; Salih et al. 2000). Most fluorescence features have subtle or moderate influence on the shape of *R*. In our data set, only *Acropora* colonies growing in artificial light at the Waikiki Aquarium or on the very shallow (~0.1 m) reef flat at Mayotte exhibit striking fluorescence contributions to reflectance (as the individual in Fig. 7). In all such cases, the fluorescence occurs in the range 515–520 nm and is very similar in shape to that presented by Fuchs (2001). Our data support his assessment that this level of fluorescence is "likely on the high side" and is not representative of the general coral population. There is no evidence in our data that fluorescence by coral-host pigments affects the basic shapes of blue or brown mode *R*, that is, the plateau and triple-peaked patterns. It is possible that coral-host fluorescence near 575 nm (Mazel 1995, 1996) enhances that feature in brown coral *R*, but Myers et al. (1999) and Hochberg et al. (2003) have demonstrated that fluorescence need not be invoked to explain the presence of this feature.

Coral *R* in perspective

We have stated that the current data set does not permit rigorous statistical exploration of topics including discrimination between coral taxa and between corals from different locales or regions. The reason is that the data were not collected to address these questions, which presents two problems. First, the appropriate techniques for exploring multivariate differences between groups

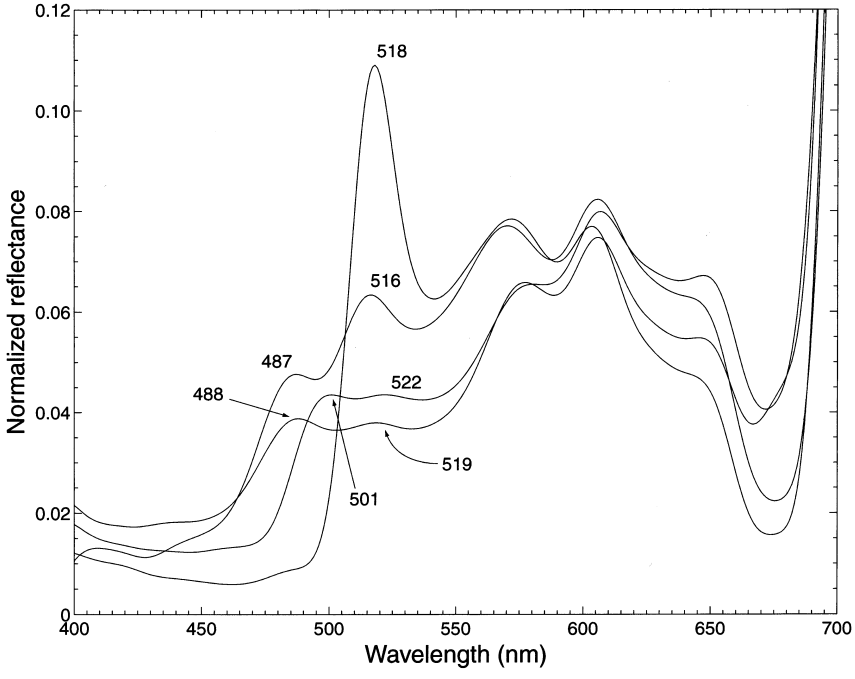

Fig. 7 Normalized *R* for four *Acropora* sp. colonies at the Waikiki Aquarium and Moorea, French Polynesia. These are representative of corals worldwide that show fluorescence features, and the wavelengths of the fluorescence peaks here match those reported elsewhere. In our database, the very strong fluorescence peak at 518 nm is only present in *Acropora* sp. grown under artificial lights or on very shallow reef flats

(e.g., MANOVA) require sample sizes (n) to be significantly larger than the number of variables under consideration (p). In our case, we have $p = 301$ variables (wavelengths), but in most cases $n =$ several 10's of R. Second, in those cases where we do have $n > p$, those n spectra arise from only a few (2–10) individual coral colonies. As mentioned earlier, two *Montastrea annularis* colonies cannot be considered representative of all *M. annularis* in Florida. It is true that R's measured several centimeters apart on the same coral colony may be considered as independent with respect to surface geometry and pigment composition (Clark et al. 2000), but 10's of R's from a single colony are clearly more correlated than R's from different colonies, even of the same species (Fig. 3). To answer the question of whether two coral taxa are spectrally distinguishable from each other, it will be necessary to make a much more rigorous sampling of their respective populations.

We developed our spectral library to determine (1) whether reef-building corals are spectrally discriminable from other reef components and, if so, (2) how to achieve that discrimination. Thus, we sampled the *population of all corals*, without regard to taxonomy. For this study, we have considered only this coral component of our spectral library. A total of 195 is a very small number compared to the number of all coral colonies in the world, but our data do serve as an unbiased sample of coral R worldwide. Our sample is by far the most complete to date and is corroborated by data from other studies (Table 2). With our data, we have seen that coral R exhibits wide variability in magnitude, ranging from near zero to as high as 25% at red wavelengths (600–650 nm). Corals also express considerable variability in the shape of R, most apparent through effects of absorption and fluorescence by coral-host pigments on the basic shape generated by zooxanthellae. For brown-mode corals, these effects are secondary, while coral-host pigmentation is a requirement for basic blue-mode R. Though not definitively, the data indicate that these zooxanthellae and coral-host generated variabilities are present across both taxonomic and geographic boundaries. That is, the variabilities exist in all observed taxa and at all geographic scales.

To be clear, these variabilities never obscure the basic shapes of blue- and brown-mode R (Figs. 2 and 3). In fact, coral R is readily distinguishable from that of other reef bottom-types (Hochberg et al. 2003). This indicates significant spectral differences between corals and other bottom types that are independent of coral groupings (e.g., taxa), which further implies that variability in coral R must not be random. In this respect, corals share a high degree of similarity in R. At the same time, it is possible that coral groups themselves are distinguishable from each other. Discrimination between corals and other bottom types may rely on spectral features that are independent of those features that might discriminate between coral groups. For example, blue and brown corals have significant spectral separability from each other, though not as clear as that between corals and algae (Hochberg and Atkinson 2003). More investigation (with sampling designed for the task) is required to statistically determine the degrees to which various coral groupings are spectrally discernable.

Variable coral R presents an as yet unrecognized implication for spectral mixing in coral reef remote sensing. It has long been known that components of reef communities are inherently mixed on spatial scales of cm to 10's of meters. Accordingly, remote sensing studies have targeted whole communities (often termed "habitats") rather than their fundamental components: the bottom types (e.g., Mumby and Edwards 2002). With the development of spectral libraries for reefs, there is potential for quantification of the bottom types through unmixing of remotely sensed signals, for example through linear spectral unmixing (e.g., Hedley and Mumby 2003). Since such methods rely on definitions of spectral end members, a question arises: Which spectrum should be chosen as the end member? All coral R's in our database represent equally pure coral, all *Acropora* R's represent equally pure *Acropora*, and so on. Clearly, the solution is that end members must not be modeled as points in spectral space, but as distributions. Spectral libraries such as that presented here are fundamental to modeling these distributions of R. This is a well-established concept among the terrestrial remote sensing community which should be realized by the coral-reef remote-sensing community.

As mentioned in Hochberg et al. (2003), the similarity of coral R across taxonomic and geographic boundaries is to be expected, since the pigments that drive R are conservative across those boundaries. The spectral contrast between coral and algae is sufficient to discriminate 97% of all corals from all algae (Hochberg and Atkinson 2003). This spectral contrast is detectable by high-spectral-resolution imaging systems: the spectral response of AVIRIS has been found to afford discrimination of 97% of all corals from all algae, and a hypothetical sensor with four 20-nm-wide wavebands centered at 480, 510, 540, and 570 nm has been shown to discriminate 88% of all corals from all algae. It is clear that coral reflectance features have potential for use in identification and enumeration of coral cover using remote sensing techniques. This is especially promising with the advent of space-borne, hyperspectral sensors such as Hyperion, but further investigation is required to link in situ measurements of R to remotely sensed data, which is impacted by radiative transfer effects in both the atmosphere and water column.

It is widely suggested that reef communities around the world are currently undergoing a phase shift, with previously coral-dominated areas being permanently replaced by algae (e.g., Wilkinson 2000). Accurate assessment of the status of coral reefs of the world requires a data set that has significant global coverage and is uniform (Ginsburg 1994). Maps of the world's reef communities would enable investigation into the fundamental spatial and temporal variabilities of the relative distributions of coral and algae, which is the basic requirement to truly understand reef

status (Connell 1997; Done 1992, 1995). Space-borne remote sensing is the only currently viable option to produce the necessary data. The unique spectral reflectance characteristics of coral provide the foundation to remote sensing of coral cover worldwide.

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