Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing

Eric J. Hochberg, Marlin J. Atkinson, Serge Andréfouët

Abstract

Coral reef benthic communities are mosaics of individual bottom-types that are distinguished by their taxonomic composition and functional roles in the ecosystem. Knowledge of community structure is essential to understanding many reef processes. To develop techniques for identification and mapping of reef bottom-types using remote sensing, we measured 13,100 in situ optical reflectance spectra (400–700 nm, 1-nm intervals) of 12 basic reef bottom-types in the Atlantic, Pacific, and Indian Oceans: fleshy (1) brown, (2) green, and (3) red algae; non-fleshy (4) encrusting calcareous and (5) turf algae; (6) bleached, (7) blue, and (8) brown hermatypic coral; (9) soft/gorgonian coral; (10) seagrass; (11) terrigenous mud; and (12) carbonate sand. Each bottom-type exhibits characteristic spectral reflectance features that are conservative across biogeographic regions. Most notable are the brightness of carbonate sand and local extrema near 570 nm in blue (minimum) and brown (maximum) corals. Classification function analyses for the 12 bottom-types achieve mean accuracies of 83%, 76%, and 71% for full-spectrum data (301-wavelength), 52-wavelength, and 14-wavelength subsets, respectively. The distinguishing spectral features for the 12 bottom-types exist in well-defined, narrow (10–20 nm) wavelength ranges and are ubiquitous throughout the world. We reason that spectral reflectance features arise primarily as a result of spectral absorption processes. Radiative transfer modeling shows that in typically clear coral reef waters, dark substrates such as corals have a depth-of-detection limit on the order of 10–20 m. Our results provide the foundation for design of a sensor with the purpose of assessing the global status of coral reefs.

Published by Elsevier Science Inc.

Keywords: Coral reef; Spectral reflectance; Remote sensing; Radiative transfer

1. Introduction

Coral reef benthic ecosystems are collections of distinctive communities, which are distinguished by their characteristic assemblages of organisms and substrates (Stoddart, 1969). A benthic community’s structure is defined by its component set of organisms and substrates; hereafter, we refer to these fundamental elements of the community as “bottom-types.” Several reef communities may share bottom-types in common, but the bottom-types’ proportional contributions vary both between and within communities. From this viewpoint, all reef communities are simply combinations of some comprehensive set of bottom-types. Quantification of benthic community structure is central to understanding coral reef ecosystem function. Community structure determines rates of reef metabolism (Kinsey, 1985) and indicates reef status (Connell, 1997). Different bottom-types are important in life history strategies of reef-dwelling organisms, e.g., as recruitment sites for coral larvae (Miller et al., 2000) and juvenile fish (Light & Jones, 1997), and as habitat for adult fish (Chabanel et al., 1997). Reef community structure exhibits tremendous spatial heterogeneity over scales of centimeters to hundreds of meters and, in contrast to phytoplankton and macrophyte communities, is inherently stable on time scales of months to years (Buddemeier & Smith, 1999). Reports of reef degradation worldwide (Wilkinson, 2000) are now fueling interest in—and debate over the causes of—temporal shifts in community structure on longer time scales.

Conventional methods for determining benthic community structure include the use of in situ quadrats, line transects, and manta tows (Miller & Müller, 1999). These are not feasible means for accurate determination of bottom-type spatial distributions over large areas (Ginsburg, 1994). Digital remote sensing is the most cost-effective approach for acquiring such data (Mumby, Green, Edwards, & Clark, 2001).
there is surprisingly scant information on spectral reflectance \((R)\) for reef bottom-types globally. The following is a brief review of the literature concerning \(R\) for coral reef benthos.

Maritorena, Morel, and Gentili (1994) made in vitro reflectance measurements of carbonate sand, \textit{Sargassum} sp., \textit{Turbinaria} sp., \textit{Boodlea} sp., \textit{Porolithon onkodes}, and \textit{Corallinaea} sp., but did not examine spectral differences between the bottom-types. Miyazaki and Harashima (1993) and Miyazaki, Nakatani, and Harashima (1995) made both laboratory and in situ measurements of \(R\) for nine corals, rocks, and sand. They visually inspected the spectra and concluded there were minimal differences between those three benthic community types. Mazel (1996) examined the contribution of fluorescence to \(R\), for which he had \(\sim 300\) in vivo measurements for 25 coral specimens (10 species). Holden and LeDrew (1998) made a statistical investigation on a total of 22 in situ reflectance measurements, representing bleached and non-bleached \textit{Acropora}, dead coral rubble, and algae-covered dead corals. They applied cluster, principal components and derivative analyses to show that statistically significant spectral differences could be detected between healthy \textit{Acropora} and bleached/dead \textit{Acropora}. Holden and LeDrew (1999) measured 133 in situ \(R\)'s in Fiji and Sulawesi, Indonesia for bleached coral, healthy massive corals, healthy branching corals, dead coral debris, and algae-covered surfaces. They performed 181 individual univariate \(t\)-tests (one for each wavelength measured) for each of the classes and determined that there is no significant spectral difference between geographic locations within each class. Similar statistics indicated there is also no spectral difference attributable to coral morphology, but that there is a difference due to coral health. Myers, Hardy, Mazel, and Dustan (1999) reported on five in situ \(R\)'s for bleached and pigmented coral (\textit{Montastrea cavernosa}), a red crustose alga, a brown algae, and a red alga (\textit{Rhizocephalus phoenix}) at Lee Stocking Island, Bahamas. Their objective was not to discriminate between the bottom-types but to demonstrate an empirical relationship between pigmentation and \(R\). In Kanehoe Bay, Oahu, Hawaii, Hochberg and Atkinson (2000) measured a total of 247 in situ \(R\)'s of three coral species (\textit{Montipora capitata}, \textit{Porites compressa}, \textit{Porites lobata}), five algal species (\textit{Dictyosphaeria cavernosa}, \textit{Gracilaria salicornia}, \textit{Halimeda} sp., \textit{Porolithon} sp., \textit{Sargassum echinocarpum}), and three sand communities (fine-grained carbonate sand, sand mixed with coral rubble, coral rubble). They used derivative analysis and the multivariate techniques of stepwise wave-length selection and linear discriminant analysis to show that spectral separation of basic bottom-types (coral, algae, and sand) is possible with as few as four non-contiguous narrow wavebands. In the lagoon of Rangiroa, French Polynesia, Clark, Mummy, Chisholm, Jaubert, and Andréfouët (2000) measured \(\sim 1800\) in situ \(R\)'s for 94 reef targets, including coral (\textit{Porites}, \textit{Pocillopora}, and others), encrusting and turf algae, and sand. Using derivative analysis, they determined that it is possible to distinguish among these three states of coral mortality: live coral, coral dead for 6 months, and coral dead
for >6 months. Joyce and Phinn (2002) analyzed $R$ from corals with three distinct morphologies (open branching, closed branching, and table) and determined that the three are distinguishable by the differing amount of shadow each morphology generates. Finally, Minghelli-Roman, Chis-holm, Marchioretti, and Jaubert (2002) measured $R$ for 152 coral colonies in the Red Sea and were able to discriminate between 14 genera of hard and soft corals using ratios of only six wavebands. Hedley and Mumby (2002) provide a review of coral reef $R$ and its biological basis.

These studies represent the greater part of the current state of knowledge of $R$ for coral reef bottom-types. In their review, Hedley and Mumby (2002) conclude that “there is a great deal of uncertainty and inconsistency in the reported spectral features that can be employed to discriminate reef benthos.” This is attributable to the fact that the total number of measurements has been few, methods have been dissimilar (producing data of varying quality), and objectives have focused on very localized measurements for a few species. That is, the database of $R$ for coral reefs is small, and the data within are nonuniform. As a result, deterministic, reef-up remote sensing of bottom-types remains impractical, which in turn precludes quantitative remote sensing of reef community structure. If remote sensing technology is to be applied to reef-up assessment of reef community structure, the first step must be to evaluate the degree to which fundamental bottom-types can be spectrally discriminated.

Our goals are (1) to characterize spectral reflectance for reef bottom-types worldwide and (2) to determine spectral separabilities of the bottom-types. We have used a portable spectrometer to measure 13,100 in situ $R$’s at 11 sites in four major reef biogeographic regions worldwide at water depths ranging from 0 to 15 m. We assign each measured $R$ to one of a set of fundamental reef bottom-types, which are defined primarily by function in the reef system, but also by taxonomy and by apparent color. We find that each bottom-type exhibits characteristic and distinctive features in $R$ that exist in well-defined, narrow wavelength ranges and that are conservative across biogeographic regions. Classification analysis demonstrates that the bottom-types are statistically separable and identifiable based on their reflectance spectra. We reason that features in $R$ arise primarily as a result of spectral absorption processes. Radiative transfer modeling shows that in typically clear coral reef waters, dark substrates such as corals have a depth-of-detection limit on the order of 10–20 m. Our results provide the basis for quantitative remote sensing of community structure using consistent criteria for coral reefs worldwide.

2. Methods

2.1. Classification of fundamental bottom-types

Coral reef communities are largely mosaics of coral, various algae and carbonate sand (Kinsey, 1985), and knowl-edge of their distributions is fundamental to assessment of reef status (Connell, 1997; Done, 1992, 1995). Thus, these three bottom-types form the foundation for our classification scheme. There are three basic forms of reef algae: turf algae, crustose calcareous algae, and fleshy macroalgae (Berner, 1990). Crustose calcareous algae are important reef calcifiers (Kinsey, 1985), cementing the products of disintegration of various other calcifying reef organisms, thus creating a harder skin for the reef (Berner, 1990). Turf algae and fleshy macroalgae are a major source of fixed carbon to reef primary consumers (Klumpp & McKinnon, 1989). Because of their importance to different reef processes, these three algal types form subclasses within the broader algae class.

While crustose calcareous algae are mainly Rhodophytes (Corallinaceae), algal turfs are often a mixture of Chlorophytes, Cyanophytes, Phaeophytes, and Rhodophytes (Berner, 1990) that can mix on spatial scales of <1 cm, well beyond the spatial abilities of today’s remote sensors (smallest footprint ~ 2 m). However, discounting their epiphytic communities, fleshy macroalgae—mainly Chlorophytes, Phaeophytes, and Rhodophytes—exist at a spatial scale (one-tenth to tens of meters) that may be resolvable by remote sensing. The different fleshy macroalgae taxa are preferred forage material for different reef consumers (Glynn, 1990). Furthermore, Chlorophytes, Phaeophytes, and Rhodophytes possess different photosynthetic accessory pigments (Kirk, 1994) and thus often exhibit their characteristic colors of green, brown, and red, respectively. Because they may be important to understanding energy flow through the reef system, and because there is potential that they can be discriminated based on their optical reflectance spectra, we further separate the fleshy macroalgae subclass into brown, green, and red divisions.

Soft corals and gorgonians can occupy substantial reef areas and may compete with scleractinian corals for space (Bastidas, Benzie, Uthicke, & Fabricius, 2001; Ben-Yosef & Benayahu, 1999; Fabricius, 1997). Seagrass is essential habitat in the life histories of many reef species and can cover extensive back-reef and lagoonal areas (Enriquez, Merino, & Iglesias-Prieto, 2002). The spread and deposition of terrigenous sediments can be deleterious to reefs near high islands (Watanabe, Nakamura, Samarakoorn, Mabuchi, & Ishibashi, 1993). Because of their respective importances to coral reef systems, each of these reef bottom-types is included in the classification scheme.

Examination of the data set has revealed two basic modes of coral $R$: one mode is associated with corals that are visually (to humans) brown, red, orange, yellow, or green, while the other mode is associated with corals that appear purple, blue, pink, or gray. These patterns of association occur across taxonomic lines and in all oceans. Thus, we divide scleractinian corals into two subclasses, which, for lack of better terminology, we label “brown” and “blue.” Lastly, the bleached coral subclass is included due to the prevalence in recent years of reports of coral bleaching.
worldwide (Wilkinson, 2000). Fig. 1 summarizes the overall classification scheme adopted for this study.

2.2. Spectral measurements and processing

We measured 13,100 $R$’s at the following sites in the Atlantic, Indian, and Pacific Oceans (Fig. 2): (1) St. Croix, USVI; (2) Puerto Rico; (3) Florida Keys; (4) Oahu, Hawaii; (5) Maui, Hawaii; (6) Rangiroa, French Polynesia; (7) Moorea, French Polynesia; (8) Palau; (9) Bali, Indonesia; (10) Mayotte, Comoros; (11) the Waikiki Aquarium (Indo-Pacific corals grown in aquaria). The 11 sites represent four major reef biogeographic regions as defined by Veron (1995): Caribbean, Hawaiian Islands, Central Pacific, and Indo-west Pacific.

The spectral reflectance $R$ (implicitly a function of wavelength) of a material is defined as the ratio of the reflected radiant flux to the incident radiant flux (Morel & Smith, 1993). In our case, $R$ is the fraction of incident light flux that is reflected by the different bottom-types. We measured and processed in situ $R$ for visible wavelengths (400–700 nm) following methods described in Hochberg and Atkinson (2000). The sampling unit consisted of a 30-m-long fiber optic cable (400 µm diameter) attached to an Ocean Optics S2000 portable spectrometer (wavelength range 330–850 nm, with ~0.3-nm sample interval and ~1.3-nm optical resolution), which in turn was operated by a laptop computer. The fiber optic cable tip collected light over a solid angle of ~0.1 sr, which at a distance of 10 cm projected to a circular area of 10 cm². For each single measurement of $R$, a diver pointed the collecting tip of the fiber optic cable at the desired bottom-type and depressed a button at the end of a 30-m-long trigger cable, prompting the computer to store the spectrum (in units of digital counts). Immediately thereafter, the diver pointed the collecting tip at a Spectralon diffuse reflectance target (same depth as the target bottom-type) and triggered the storage of its spectrum. In this manner, both spectra could be acquired within 1–2 s. To maximize the signal-to-noise ratio, a 10% reflectance target was used for dark substrates (e.g., corals, algae), and a 99% reflectance target was used for bright substrates (i.e., carbonate sand). To ensure a constant ambient light field between the two measurements, the Spectralon was placed immediately adjacent to the target bottom-type, and the diver’s position was held constant for the 1–2 s required for the measurements. Measurement depths ranged between 0 and 15 m. For shallow (<5 m) samples, we shaded both target bottom-type and Spectralon to minimize the influence of wave focusing (light “flashes”). We employed a submersible flashlight (Underwater Kinetics Sunlight C8) to supplement flux at red wavelengths for deeper (>5 m) samples.

We corrected all spectra for baseline electrical signal, then calculated $R$ as the ratio of digital counts measured over the bottom-type to the digital counts measured over the Spec-
tralon (corrected to 100% reflectance) for each pair of measurements. Note that this is the ratio of two radiance measurements: our calculation of $R$ assumes that both the bottom-type and Spectralon are diffuse reflectors (see Hochberg & Atkinson, 2000). We linearly interpolated $R$ to 1-nm intervals over the wavelength range 400–700 nm, then filtered the result using the Savitsky–Golay method (Savitsky & Golay, 1964; Steiner, Termonia, & Deltour, 1972).

2.3. Spectral characterization

We examined spectral shapes by numerically calculating second-derivative spectra following the Savitsky–Golay method (Savitsky & Golay, 1964; Steiner et al., 1972) and identifying the wavelength locations of local maxima (peaks). Note that derivative analysis merely exaggerates spectral shapes, highlighting features present in zero-order
spectra; derivative analysis does not add information not already contained in zero-order spectra (Talsky, 1994). For each bottom-type, we compared spectral shapes between biogeographic regions by computing the frequencies of occurrence of the second-derivative peaks. It became apparent that each bottom-type exhibited its own remarkably consistent features in $R$ across all biogeographic regions. Therefore, to describe global $R$ for each bottom-type, we combined spectra from all regions and computed the 2.5, 25, 75, and 97.5 percentile spectra, as well as the overall mean spectrum. We further computed the frequencies of occurrence of second-derivative peaks for global $R$ in each bottom-type.

2.4. Spectral separability

To determine the spectral separability of the bottom-types, we performed a classification analysis following the partition method (Rencher, 1995): we used half of the $R$’s in each class to train linear classification functions (LCFs), and the other half to test classification accuracy (LCFs are linear combinations of variables with a different set of variable coefficients for each bottom-type. The variable coefficients are calculated considering both the magnitude and shape of the training spectra. An unknown spectrum is predicted to belong to the bottom-type for which it has the highest LCF value). Training and test spectra were chosen using a pseudo-random number generator. We calculated classification rates as the number of individual $R$’s in the predicted class divided by the total number of $R$’s in the actual class, multiplied by 100. The values in such a classification table are equivalent to a table of Producer’s Accuracies (Congalton, 1991).

Finally, we investigated whether full-resolution spectra (i.e., 400–700 nm at 1-nm intervals) are necessary for

![Fig. 4. Biogeographic consistency in $R$ for fleshy green algae (left) and brown hermatypic coral (right). Each panel shows the frequency of occurrence of second-derivative local maxima for a given biogeographic region. The second-derivative describes the shape of $R$; positive extrema in the derivative correspond to peaks or shoulders in $R$. Consistency in the wavelength locations of second-derivative local maxima between biogeographic regions indicates that $R$ also has consistent spectral shapes across biogeographic regions.](image-url)
spectral separation of the bottom-types. We used a multivariate stepwise selection procedure (Rencher, 1995) to find the subset of wavelengths that best separates the 12 classes (stepwise selection discards those wavelengths that are statistically redundant for separating the bottom-types). The selection produced a list of 52 wavelengths, which appeared to aggregate in clusters of wavelengths. Consequently, we further simplified the wavelength set by finding the mean wavelength in each cluster, resulting in a 14-wavelength list. We repeated the classification analysis using the same training and test R’s, but undersampled to the 52-wavelength and 14-wavelength sets.

3. Results

There are features in R that are common to all bottom-types (Fig. 3). Low values at blue and green wavelengths are largely the result of absorption by photosynthetic and photoprotective compounds (Bidigare, Ondrusek, Morrow, & Kiefer, 1990; Dove, Takabayashi, & Hoegh-Guldberg, 1995; Salih, Larkum, Cox, Küh, & Hoegh-Guldberg, 2000). Similarly, higher values at red wavelengths indicate lack of absorption or presence of active fluorescence (Mazel, 1995). Chlorophyll absorption is readily apparent near 675 nm, and the effect of strong near-infrared reflectance is apparent at 700 nm. Except for carbonate sand, all bottom-types have low average R, generally falling in the range 0–30%, and all have either peaks or shoulders near 600 and 650 nm. Finally, all bottom-types exhibit wide variations in the magnitude of R, while maintaining the same relative shape.

In brown corals, R has the triple-peaked pattern described by Hochberg and Atkinson (2000), which is marked by a prominent positive reflectance feature near 570 nm (Fig. 3). Healthy blue coral R is characterized by an absorption feature (local minimum) near 580 nm and a plateau between 600 and 650 nm. The presence of fluorescent pigments (Salih et al., 2000) in the coral tissue is sometimes apparent as subtle positive features at blue and green wavelengths in both healthy coral classes (though not apparent in Fig. 3). The shape of bleached coral R resembles that of carbonate sand more closely than that of either healthy coral class, but the magnitude is intermediate between that of the healthy corals and carbonate sand. Encrusting calcareous and turf algae have spectral shapes similar to that of red fleshy algae. These algae are characterized by two broad, positive features in R over the ranges 435–490 and 500–565 nm. Brown fleshy algae R also exhibits the first feature at 435–490 nm, but lacks the second. Both green fleshy algae and seagrass have a single broad reflectance feature centered at 550–560 nm. Soft/gorgonian coral R resembles that of brown coral. Terrigenous mud is characterized by a very low R, increasing nearly linearly from 1% at 400 nm to 8% at 700 nm, and exhibiting a minimal chlorophyll absorption feature near 675 nm. Finally, carbonate sand has a very high R, with minimum values of 20% at 400 nm and reaching maximum values of 80% at 700 nm.

In all bottom-types, locations of second-derivative peaks are consistent across biogeographic regions. Fig. 4 is an example showing fleshy green algae and brown hermatypic coral. This consistency in peak location results from each bottom-type having a suite of pigments that is conservative throughout the world, and it is spectral absorption by these pigments that ultimately determines the shape of R. Fig. 5 shows the frequencies of second-derivative peak wavelengths for all bottom-types across all biogeographic regions.

![Fig. 5. Differences in spectral features between coral reef bottom-types. Each row corresponds to 1 of 12 bottom-types and shows the frequency of occurrence of second-derivative local maxima across all biogeographic regions. Brighter grays (to white) indicate higher frequencies of occurrence (see color bar at bottom). In each bottom-type, spectral features occur in tight wavelength bands, indicating worldwide consistency in R. All bottom-types exhibit features near 600 and 650 nm, while most differences between bottom-types occur at wavelengths ≤ 570 nm. Notably, >90% of brown hermatypic corals and soft/gorgonian corals have a feature near 570 nm, but all algal classes lack this feature.](image-url)
Notably, brown hermatypic coral and soft/gorgonian coral each have a strong feature near 570 nm, exhibited by no other class. Nearly all peaks occur in narrow wavelength ranges, sometimes as broad as 20 nm, but often on the order of 10 nm.

In the classification analysis, mean accuracy (average of correct classification rates) was 83% (Table 1A) (we report mean accuracy, rather than overall accuracy, due to the wide differences in samples sizes between classes). In all instances of significant confusion between two bottom-types (arbitrarily defined as a misclassification rate ≥ 10%), the confusion was one-way. Soft/gorgonian corals were misclassified as brown coral, but the reverse was not true. Most classification errors occurred within, not between, broader bottom-types. That is, algae tend to be misclassified as other algae, and corals tend to be misclassified as other corals.

### Table 1
Classification rates (%) for 12 basic coral reef bottom-types using in situ R with different waveband sets: full-resolution (301-wavelength at 1-nm intervals), 52-wavelength, 14-wavelength

<table>
<thead>
<tr>
<th>Predicted class</th>
<th>Algae</th>
<th>Coral</th>
<th>Other</th>
<th>Sediment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fleshy</td>
<td>Non-fleshy</td>
<td>Bleached</td>
<td>Blue</td>
</tr>
<tr>
<td>Brown</td>
<td>92.4</td>
<td>0.0</td>
<td>1.3</td>
<td>2.5</td>
</tr>
<tr>
<td>Green</td>
<td>4.7</td>
<td>81.3</td>
<td>2.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Red</td>
<td>7.4</td>
<td>0.0</td>
<td>85.7</td>
<td>4.4</td>
</tr>
<tr>
<td>Non-fleshy</td>
<td>14.6</td>
<td>0.2</td>
<td>1.7</td>
<td>70.6</td>
</tr>
<tr>
<td>Turf</td>
<td>12.7</td>
<td>0.9</td>
<td>2.3</td>
<td>6.8</td>
</tr>
<tr>
<td>Coral</td>
<td>3.8</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Blue</td>
<td>0.0</td>
<td>0.4</td>
<td>3.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Brown</td>
<td>0.9</td>
<td>0.0</td>
<td>2.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Non-fleshy</td>
<td>1.1</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Turf</td>
<td>0.8</td>
<td>5.3</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Coral bleached</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Blue</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Brown</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Classification rates are the number of individual R’s in the predicted class divided by the total number of R’s in the actual class, multiplied by 100. Diagonal elements (in bold) represent correct classification rates, and off-diagonal elements represent misclassification rates. Misclassification rates ≥ 10% are italicized. Predicted classification rates (i.e., rows) sum to 100% (or near to 100% due to roundoff error).
The same patterns are present in both the 52-wavelength and 14-wavelength classification rates (Table 1B and C). Generally, with fewer wavelengths, misclassification rates increase. Mean classification accuracy is 76% and 71% for the 52-wavelength and 14-wavelength cases, respectively.

Table 2 lists the 52- and 14-wavelength sets used in the subset analyses.

4. Discussion

\( R \) as reported here is a combination of the light flux not absorbed by the bottom-types and the light fluorescent by the bottom-types. Coral and zooxanthellae (unicellular algae living endosymbiotically within coral-host tissue) pigments have been shown to fluoresce (Dove, Hoegh-Guldberg, & Ranganathan, 2001, Dove et al., 1995; Mazel, 1995, 1996; Myers et al., 1999; Salih et al., 2000), and our data have indications of that fluorescence. However, it is largely spectral absorption by pigments that determines the overall spectral shape of \( R \). We demonstrate this by performing a simple modeling exercise: we create a relative absorption spectrum for brown coral (Fig. 6A) by summing the absorption spectra of five zooxanthellae pigments (chlorophyll \( \alpha \), chlorophyll \( c \), \( \beta \)-carotene, diadinoxanthin, peridinin), which

Table 2

<table>
<thead>
<tr>
<th>52-wavelength subset</th>
<th>14-wavelength subset</th>
</tr>
</thead>
</table>

The 52-wavelength subset was identified by multivariate stepwise selection as those wavelengths that, without redundancy, provide greatest separation of the 12 bottom-types. The 14-wavelength subset was identified interactively as average wavelengths of clusters from 52-wavelength subset. Wavelengths listed in nanometers.

The same patterns are present in both the 52-wavelength and 14-wavelength classification rates (Table 1B and C). Generally, with fewer wavelengths, misclassification rates increase. Mean classification accuracy is 76% and 71% for the 52-wavelength and 14-wavelength cases, respectively.

Fig. 6. Model of relative reflectance for brown coral using absorption spectra weighted by relative concentrations reported in literature. See text for details of calculations. (A) Relative spectral absorptions by the five pigments in the model, and the total relative absorption. \( \text{chl } \alpha = \text{chlorophyll } \alpha \), \( \text{chl } c = \text{chlorophyll } c \), \( \beta \)-\text{car} = \( \beta \)-carotene, diadin = diadinoxanthin, per = peridinin. (B) Normalized reflectance for modeled and measured coral spectra. (C) Second derivative of (B).
have been weighted by their relative concentrations in corals, as reported in the literature (Andersen, Bidigare, Keller, & Latasa, 1996; Cottone, 1995; Fang, Liao, & Liu, 1995; Kleppel, Dodge, & Reese, 1989; Myers et al., 1999). We convert to relative reflectance by taking the base-10 logarithm of the inverse of relative absorption (Talsky, 1994), then normalizing by the result’s vector length. For comparison, we average 4308 brown coral R’s and normalize that spectrum by its vector length. The normalized spectra (Fig. 6B) are relative (as opposed to absolute) reflectances and represent spectral shape independent of magnitude. The modeled and in situ spectra compare favorably, each showing the same triple-peaked pattern characteristic of brown corals. Comparison of the second derivatives of the relative reflectances confirms that both spectra have the same basic shape (Fig. 6C). Furthermore, the R we have measured for brown coral (and soft/gorgonian corals) is the inverse pattern of spectral absorption by peridinin-containing dinoflagellates (Johnsen, Samset, Granskog, & Sakshaug, 1994), the group to which zooxanthellae belong. Thus, we conclude

Fig. 7. Model of $R_{rs}$ for three water masses: pure water (no chlorophyll or sediment), clear reef water (0.3 mg m$^{-3}$ chl a and 0.3 g m$^{-3}$ carbonate sediment), and turbid reef water (1 mg m$^{-3}$ chl a and 3 g m$^{-3}$ carbonate sediment). (A) Total $R_{rs}$ over coral bottom. (B) Total $R_{rs}$ over black bottom. (C) Coral bottom contribution to $R_{rs}$, calculated as the difference between (A) and (B). (D) Coral bottom contribution to $R_{rs}$, calculated as (C)/(A) × 100.
that, while fluorescence does contribute to $R$ in specific cases, the shape of $R$ for brown coral is primarily determined by zooxanthellae pigment absorption.

The concept that absorption is the primary determinant of $R$ can be extended to other reef bottom-types. For example, the absorption feature near 580 nm in blue corals indicates the presence of pocilloporphin in the coral host (Dove et al., 1995). Thus, $R$ in blue corals results from a combination of absorptions by zooxanthellae and host pigments. Encrusting calcareous algae, turf algae, and red fleshy algae exhibit similar $R$’s because the dominant (or sole) components of these bottom-types all belong to the taxonomic division Rhodophyta and therefore share the same suite of absorbing pigments. Bleached coral has $R$ similar to that of carbonate sand due to loss of zooxanthellae combined with a decrease in zooxanthellar and host pigmentation, resulting in optical exposure of the coral carbonate skeleton (Kleppel et al., 1989). Finally, $R$ for carbonate sand itself shows the combined effects of absorption by calcium carbonate sand grains and chlorophyll in benthic microalgae (Roelfsema, Phinn, & Dennison, 2002).

The fact that absorption by pigments is responsible for the shape of $R$ in reef bottom-types is expected. The same principle has been the basis for remote sensing of ocean
color for more than 20 years (Gordon & Clark, 1980; Morel & Prieur, 1977). It has been demonstrated that there is a link between induced fluorescence of reef benthic organisms and their pigment compositions and concentrations (Hardy, Hodge, Yungel, & Dodge, 1992; Myers et al., 1999). Based on those studies and our results, it may now be appropriate to develop the field of “coral reef color.”

We have presented Fig. 4 as a qualitative example showing that the shape of $R$ is geographically invariant. Unfortunately, we cannot statistically explore this issue, since, despite our large sample size, we do not have sufficient numbers of measurements for each bottom-type in each biogeographic region for appropriate multivariate tests (Rench, 1995). However, the peaks of second-derivative spectra are consistent between regions (e.g., Fig. 4), which indicates that the shapes of zero-order $R$ are also consistent (Talsky, 1994). Geographic invariance in $R$ is attributable to the facts that (1) absorption is a fundamental process that is independent of biogeography and (2) the pigments responsible for absorption also exist independently of biogeography. Geographic invariance of $R$ within bottom-types has a corollary: differences between bottom-types are also geographically invariant. This is the biooptical basis for the spectral separation achieved here through classification analysis.

Previous studies have demonstrated the feasibility of using high-resolution remote sensing to assess coral reef status (e.g., percent of live and dead corals) in localized settings using extensive ground-truthing and unsupervised classifications (e.g., Mummy, Chisolm, Clark, Hedley, & Jaubert, 2001), but generalizations of methods have not been possible. For example, the results obtained by Mummy et al. (2001) at Rangiroa (Tuamotu Archipelago, French Polynesia) are not reproducible at nearby Moorea (Society Islands, French Polynesia), even using data from the same hyperspectral imaging system, due to the influence of fleshy brown algae at Moorea (Andréfouët, unpublished data; Mumbay, personal communication). That $R$ for a given bottom-type has the same shape regardless of geography ultimately provides the foundation for development of global discrimination/classification algorithms.

It is important to note that $R$ is a convolution of magnitude and relative shape, and both components contribute to spectral separation between the bottom-types. An example is the comparison between carbonate sand and bleached coral: both bottom-types exhibit the same relative spectral shape, because the dominant optically absorbing component in each is the mineral calcium carbonate. However, carbonate sand has much higher overall reflectance because bleached coral (1) actually retains some pigmentation in the zooxanthellae and coral host and (2) maintains its three-dimensional structure which creates shadows, while (3) the benthic microalgal community resident on sand generates a smaller pigment absorption signature than that of bleached coral, and (4) sand has a more two-dimensional structure. More subtly, several of the bottom-types share many second-derivative features (e.g., fleshy red algae and non-fleshy turf algae), but do exhibit slight differences in both the wavelengths at which the features occur (Fig. 5) and their absolute magnitudes (Fig. 3). The implication is that discrimination of bottom-types based on these subtle spectral differences requires relatively high spectral resolution, with maximum bandwidths on the order of 10–20 nm.

For each of the three different wavelength sets used in the classification analysis, the greatest occurrence of error is soft/gorgonian coral misclassified as brown hermatypic coral. In a region where soft/gorgonian corals are common (e.g., many sites in the Caribbean), a remote sensing study that considers only spectral variables may produce significant overestimates of hermatypic coral cover. For many of the world’s reefs, however, soft/gorgonian corals are not a dominant benthic component and often occupy different reef zones than hermatypic corals (Fabricius & Alderslade, 2001). Thus, an applied remote sensing study should also make use of knowledge-based algorithms, employing ecological (i.e., spatial) as well as spectral variables (e.g., Andréfouët & Roux, 1998).

Our results represent an upper limit to spectral classification accuracy, because in situ $R$ is independent of absorption and scattering within the atmosphere and water column. These radiative transfer processes spectrally alter the reef-surface signal before it is received by the remote sensor, and continued research is necessary to develop methods for inverting their effects. One important factor that has yet to be explored in detail (except see Maritorena et al., 1994) is the depth at which the bottom is no longer detectable. Considering only the water column and seafloor, this depth-of-detection limit ($z_{lim}$) is a function of $R$ and of the water column’s optical properties. Because both $R$ and water column optical properties are functions of wavelength, so is $z_{lim}$. We have explored the behavior of $z_{lim}$ with respect to water column optical properties using the radiative transfer model HydroLight 4.1 (C.D. Mobley and L.K. Sundman, Sequoia Scientific, Redmond, WA, USA). We use a four-component model (pure water, chlorophyll-bearing particles, colored dissolved organic matter covarying with chlorophyll, and suspended calcareous sediment) to simulate remote sensing reflectance ($R_{rs}$, water-leaving radiance divided by downwelling irradiance) for three water masses: pure water (no chlorophyll or sediment), clear reef water (0.3 mg m$^{-3}$ chl $a$ and 0.3 g m$^{-3}$ carbonate sediment), and turbid reef water (1 mg m$^{-3}$ chl $a$ and 3 g m$^{-3}$ carbonate sediment). We execute the model for water depths in the range 0–30 m with the bottom boundary specified as a coral bottom (our average brown coral spectrum, Fig. 7A) and as a perfectly absorbing bottom (flat spectrum of 0% reflectance across all wavelengths, Fig. 7B). $R_{rs}$ over a coral bottom is comprised of a bottom component and a water column component, while $R_{rs}$ over a black bottom expresses only the water column component (Maritorena et al., 1994). By subtracting the latter from the former, we estimate the contribution of the coral bottom to total $R_{rs}$ (Fig. 7C), and by dividing this value by total $R_{rs}$ and multiplying by 100, we obtain the coral bottom contribution to total $R_{rs}$ as a
percent (Fig. 7D). This value represents the relative signal-to-noise level for the coral bottom, where noise is the water column contribution to \( R_{rs} \).

Fig. 8 shows the coral 5% and 10% signal levels as functions of wavelength for the three water masses. In theory, these lines are exact; we choose not to draw the 0% signal line because, in practice, a radiometer pointed downward at a reef will have difficulty resolving lower signal levels (i.e., sensor signal-to-noise issues). Thus, these lines approximate functional \( z_{lim} \). It is no surprise that \( z_{lim} \) is much shallower for turbid water than for clear water. It also should be noted that most reef areas of interest in studies of community structure lie well within the clear reef water \( z_{lim} \) and that reef waters, especially outer reef slopes, are often more clear than our clear reef water case. Finally, these results are generally valid for all the bottom-types except carbonate sand, because all have roughly the same magnitude \( R \) as brown coral.

The wavelength dependence of \( z_{lim} \) in clear reef water indicates that remote sensing of coral reefs is best achieved at wavelengths shorter than about 580 nm. This of course results from the rapid rise in attenuation at longer wavelengths due to absorption by water. There is potential for this effect to interfere with remote discrimination of reef bottom-types: the characteristic 570 nm feature in \( R \) of brown hermatypic coral is at the cusp of increasing attenuation, and the attenuation feature tends to produce a strong shoulder in \( R_{rs} \) in this wavelength region for all water clarities and all bottom compositions. The strength of the effect and the depth at which it becomes apparent vary with water clarity. As long as the bottom is not past \( z_{lim} \), however, there is potential for inverse radiative transfer modeling to remove the effect, thus allowing accurate identification of bottom-type.

With regard to the specific classification technique, we have achieved high classification accuracy rates with simple LCFs. With further tuning of our classifiers, it is possible to achieve even higher levels of accuracy. More sophisticated classifiers such as quadratic classification functions or multivariate density estimators will likely increase classification accuracy of the “pure” bottom-type spectra, and others may afford the ability to deconvolve spectrally mixed signals.

LCFs with full 1-nm-resolution spectra (i.e., 301 contiguous wavelengths) demonstrate high spectral separability of the classes. Existing satellite sensors, however, do not approach this degree of spectral resolution, and this fact limits their abilities to discriminate between the 12 bottom-types that we have defined. A repeat of our classification analysis using appropriate sensor wavebands resulted in mean classification accuracies of 41%, 45%, and 47% for the satellite sensors SPOT-HRV (Systeme Pour l’Observation de la Terre—High Resolution Visible), Ikonos and Landsat-ETM+ (Enhanced Thematic Mapper Plus), respectively. At 78%, only the airborne sensor AVIRIS (Airborne Visible Infrared Imaging Spectrometer, visible wavebands only) has a mean classification accuracy commensurate with that of full-resolution spectra. Fortuitously, in the near future, satellite sensors will begin to match the spectral capabilities of AVIRIS.

Alternatively, advancing technology has made it feasible to design a satellite sensor with the purpose of addressing specific questions in global coral reef science. Such a sensor would possess particular wavebands explicitly chosen for the task at hand, and it is important to determine classification accuracies for these more realistic waveband sets. For classification of the three more general bottom-types—algae, coral, and sand—LCFs using four 20-nm-wide wavebands achieved an overall accuracy of 91% (Hochberg & Atkinson, 2003). Coupling this waveband set with radiative transfer models indicates that this spectral separation is achievable to

![Fig. 8. Functional depth-of-detection limits \((z_{lim})\) for the three water masses. Below \( z_{lim} \) inverse radiative transfer calculations are unable to reconstruct bottom reflectance signatures. At a given wavelength, \( z_{lim} \) is a function of water clarity and magnitude of bottom reflectance. These cases of \( z_{lim} \) are computed for the brown hermatypic coral bottom in Fig. 7D, but these results are extendable to other bottom-types, because most have \( R \) at approximately the same order of magnitude as coral.](image-url)
This demonstrates the utility of employing characteristic R as the basis for space-borne coral reef remote sensing. Such simplified waveband combinations ease satellite engineering constraints (i.e., a sensor with fewer wavebands is easier to design and operate), facilitating lower cost remote sensing solutions to the problem of global coral reef study and monitoring.

We have found measurement of R for any bottom-type to be extremely repeatable. The R's we have measured are consistent in shape and magnitude with those reported by other researchers using a similar methodology: near-simultaneous measurement of incident and reflected light fluxes (Andréfouët et al., 2001; Clark et al., 2000; Hochberg & Atkinson, 2000; Holden & LeDrew, 1998, 1999; Joyce & Phinn, 2002; Lubin, Li, Sustan, Mazel, & Stammes, 2001; Maritorena et al., 1994; Miyazaki & Harashima, 1993; Myers et al., 1999). We have shown that basic reef bottom-types have characteristic R, that within each bottom-type, the shape of R is consistent across biogeographic regions, and that the bottom-types are spectrally separable from each other. Our results provide the basis for other research efforts aimed at detailed ecological interpretation of global coral reef remote sensing imagery. Given that coral reefs around the world are believed to be in peril, and that current in situ sampling methods are incapable of providing the synoptic information required for assessment of the world’s coral reef resources, the need for a reef-monitoring satellite is now greater than ever.

Acknowledgements

We are grateful for field assistance from Shannon Atkinson, Mark Carmichael, Steve Dollar, Jim Falter, Jim Fleming, Michael Guidry, Mika Hochberg, Brian Lapointe, Jennifer Liebeler, Claude Payri, Russell Perkins, Brendalee Phillips, Michel Pichon, Ann Tarrant, Bernard Thomassin, and Robert Tomasetti. Logistic support for field operations was provided by the US NOAA/NOS Biogeography Program, the US National Park Service, and the US Geological Survey. Our most effusive gratitude goes to S.V. Smith for his comments and suggestions. This work was funded by NASA award numbers NAG5-7513, NAG5-5276 and NAG5-10908, and NOAA award number NA07-OA0571. This is SOEST contribution 6053, HIBM contribution 1147, and IMaRS contribution 0041.

References


Fabricius, K. E., & Alderslade, P. (2001). Soft corals and sea fans: a comprehensive guide to the tropical shallow-water genera of the Central-


