Hyperspectral Analysis of Chlorophyll Content and Photosynthetic Capacity of Coral Reef Substrates
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# Hyperspectral analysis of chlorophyll content and photosynthetic capacity of coral reef substrates

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### Abstract

Few studies have assessed the biophysical properties controlling reflection and absorption of light in coral reef environments and their relationships with quantitative measures of reef health and productivity. The present article examines the relationship between spectral reflectance, photosynthetic capacity, and chlorophyll *a* from common coral reef substrates. Reflectance readings of several targets (massive corals *Montipora* sp., $n = 49$, and *Porites* sp., $n = 80$; macroalgae *Chlorodesmis* sp., $n = 24$; and sediment interspersed with benthic microalgae, $n = 35$) were obtained in situ on Heron Reef, southern Great Barrier Reef (23°27′S, 151°55′E). Measurements of photosynthetic capacity and chlorophyll content were acquired simultaneously. Linear correlations were examined between spectral reflectance at all wavelengths and both photosynthetic capacity and pigment content (Chl *a*). Reflectance plots for all targets exhibited an absorption feature centered at 675 nm, and spectral reflectance at this wavelength decreased with increasing Chl *a* levels. The strength of this correlation varied between features, being highest for *Porites* sp. and lowest for sediment, highlighting the complexities of coral reef environments and the difficulties associated with relating spectral reflectance to biophysical properties. Photosynthetic capacity did not exhibit statistically significant correlations to spectral reflectance or absorption at any wavelength. Our results demonstrate the capabilities and difficulties associated with field scale hyperspectral data for measuring select biophysical properties of coral reefs and the need for assessment of the capabilities of airborne and satellite imaging sensors for similar purposes.

Remote sensing has recently been noted for its potential contribution to monitoring and management practices of coral reefs. However, useful applications of these data are currently limited by an incomplete understanding of the interactions of light with reef features and the controlling factors of light reflection and absorption. Previous studies have used remote sensing to map large-scale reef patterns (e.g., geomorphic zonation; Ahmad and Neil 1994), whereas others have used zonation information to infer biological information (Andrefouet and Payri 2001; Roelfsema et al. 2002). However, the ability to directly derive information related to reef "health" parameters has been complicated by several issues. First is the difficulty in identifying a commonly accepted measure of reef health and second is successfully and quantitatively relating remotely sensed data to measured biophysical properties relevant to reef health. This is further complicated by the commonly cited problems associated with water depth variations and spectral similarity between common substrate types (Holden and LeDrew 1998*a*; Lubin et al. 2001; Kutser et al. 2003). The present article will address the former two issues, i.e., identifying an indicator of reef health that may be measured from remotely sensed data.

Because the relative health of coral and algae is related to the existence of photosynthesizing pigments, determination of their presence and density is important in the assessment of reef health and productivity (Myers et al. 1999). Chlorophyll *a* is the primary photosynthesizing pigment found within macroalgae, zooxanthellae (corals), and benthic microalgae (BMA) interspersed within reef sediments. Quantification of the presence of chlorophyll generally relies on extractive techniques. Determining how the presence of chlorophyll within corals, algae, and sediment affects light reflection and absorption would allow chlorophyll content estimates to be measured in a nonintrusive manner, similar to terrestrial remote sensing (Curran et al. 1991; Asner 1998). This operation will only be possible if the coral, algal, and sediment signals can be decoupled from organic content in the water column and the water's attenuation of longer visible wavelengths (>700 nm). By coupling reflectance-curve analysis with pigment analysis, additional information can be obtained about the biological composition of reef features through the interactions of incident light with the target at various wavelengths (Myers et al. 1999).

To further assess the health of photosynthesizing organisms, pulse amplitude–modulated (PAM) fluorometry has been developed as a method for measuring photosynthetic capacity, commonly expressed as $F_v/F_m$, where

$$F_v = F_m - F_o \text{ and}$$
$$F_m = \text{maximum fluorescence;}$$
$$F_o = \text{initial fluorescence (Ralph et al. 1999).}$$

This method is entirely nonintrusive and involves irradiating the target with a pulse of light (650 nm) designed to saturate the plant's photosystems, inducing a maximum fluorescent response ($F_m$). The magnitude of this response is measured
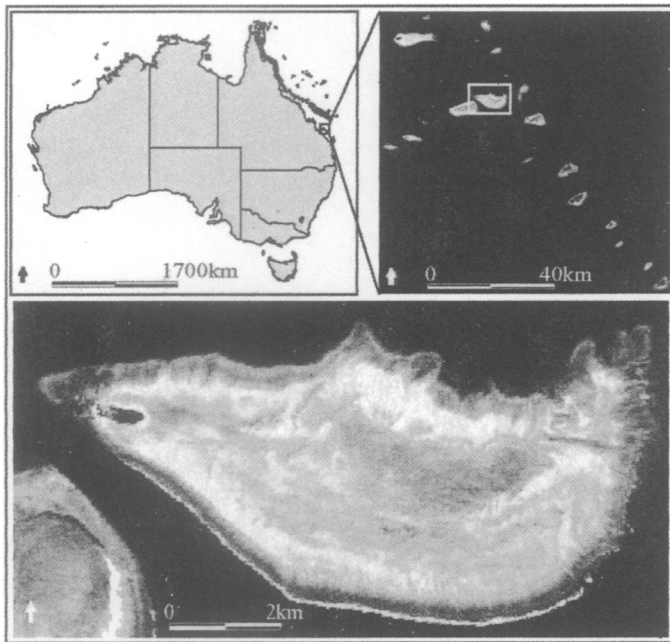
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Fig. 1. Field study site—Heron Island (23°27′S, 151°55′E). Capricorn Bunker Group, southern Great Barrier Reef, Queensland, Australia. Landsat ETM images acquired 18 and 27 May 2001. Data supply and copyright: Biophysical Remote Sensing Group, University of Queensland, GeoImage Pty Ltd. and Australian Centre for Remote Sensing.



Fig. 2. Sample collection scheme—underwater spectrometer optics, PAM, and sample core. Dark-adapting black neoprene mat is not shown.

with respect to its initial fluorescence ($F_o$), and the resultant ratio provides an indication of the photosynthetic capacity ($F_v/F_m$) of the plant (Ralph et al. 1999). This value has been shown to vary between corals at various stages of bleaching, whereby a lowering of the ratio indicates stress or a decline in photosynthetic capacity (Warner et al. 1996). The decline in photosynthetic capacity may be linked to either a loss of zooxanthellae or a loss of pigments within the zooxanthellae. In a controlled experiment, it was also shown that a decline in chlorophyll content (zooxanthellae) in *Montastrea faveolata* due to temperature stress results in increased reflectance of incident light across all regions of the electromagnetic spectrum (Schmidt et al. 1999). The development of a relationship among photosynthetic capacity, pigmentation, and spectral reflectance is therefore theoretically conceivable and potentially provides the quantitative link required for relating measurements from remotely sensed data to photosynthesis—a relevant reef health parameter.

Recent studies have evaluated the use of remote sensing in differentiating between common reef substrate types at coarse descriptive resolutions, e.g., coral, algae, and sand (Holden and LeDrew 1999; Mumby and Green 2000; Lubin et al. 2001). Yet the specific factors controlling optical differences between these features have yet to be fully understood and explained. Determining how corals and algae reflect and absorb light in different wavelengths at the coral colony scale (and their biophysical controls) will provide a sound basis for the use of airborne and satellite imaging systems to monitor biophysical properties of coral reefs. Therefore, the aim of the present study was to examine the
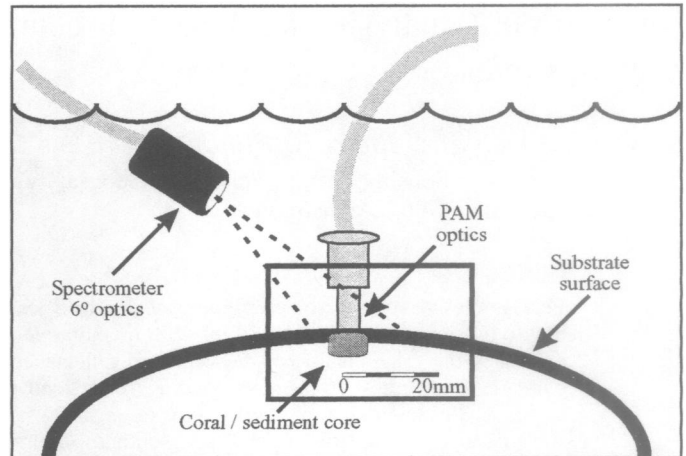
relationships among spectral response, photosynthetic capacity, and pigmentation within and between various coral reef features.

## Materials and methods

*Study site*—Heron Island is a coral cay of the Capricorn Bunker Group situated in the southern Great Barrier Reef, ~550 km north of Brisbane, Queensland, Australia (23°27′S, 151°55′E) (Fig. 1). Low tides often leave a large portion of Heron Reef either exposed or in very shallow waters, so it is possible to access most of the western portion of the reef flat and reef rim by foot. Heron Island has been the site of intensive research on coral reef ecosystems over the past 30 yr; thus, a substantial amount of historical data and literature is available for this site (Ahmad and Neil 1994; Connell et al. 1997).

The reef targets chosen for detailed analysis in the present study were selected because of their prominence and ease of access on the reef flat. These features included encrusting and massive corals *Montipora* sp. ($n = 49$) and *Porites* sp. ($n = 80$), macroalgae *Chlorodesmis fastigiata* ($n = 24$), and sediment interspersed with benthic microalgae ($n = 35$). Branching corals were not included in the present study because of their more complex structural nature and degree of self-shading potentially influencing spectral response and photosynthetic capacity measurements.

*Data collection and analysis*—An Analytical Spectral Devices FieldSpec UV-VNIR CCD spectrometer with underwater 6° field of view fore-optics was used to measure spectral radiance in 1,024 bands at 0.7-nm intervals between band centers, within a spectral range of 350–1,050 nm. The close range of spectral viewing in shallow waters (<30 cm depth) allowed us to collect spectra representative of the target with minimal water-column attenuation (Holden and LeDrew 1998b). The optics were held below the water 15 cm away from the target at a constant angle orthogonal to the plane of the sun, to avoid shading (Fig. 2). Resultant

spectral radiance signatures were calculated from an average of 36 samples with an integration time appropriate to the light field. Corresponding measurements of spectral radiance were acquired by use of the same viewing geometry from a Spectralon standard calibration panel (an assumed Lambertian surface), to enable radiance reflectance calculations (Curtiss and Goetz 1994). The time lapse between calibration panel and target reflectance measurements was minimized, to reduce discrepancies due to changing light conditions (Curtiss and Goetz 1994). Because reflectance is a relative unit, comparison between targets was afforded irrespective of insolation intensity variations, geometry, and atmospheric conditions.

The data acquired from the spectrometer resulted in a spectral reflectance curve for the target, with characteristic reflectance peaks and absorption troughs. Using the spectral response functions in ENVI for each of the Landsat 7 Enhanced Thematic Mapper and SPOT 4 visible and near-infrared bandwidths, the field spectrometer spectral reflectance curves were resampled to simulate measurements with the spectral resolution of these imaging sensors.

Target corals, algae, and sediment were dark-adapted for a period of 10 min, and a submersible PAM (diving-PAM) fluorometer was used to measure photosynthetic capacity ($F_v/F_m$) (Ralph et al. 1999). Corals and sediment were dark-adapted by placing a weighted black neoprene sheet over the sample area. Standard leaf clips were used to dark adapt algae samples. This process was undertaken primarily in an attempt to predispose all targets to the same light conditions prior to measurement of photosynthetic capacity. An 0.8-cm-diameter core was then extracted from the target, and pigment content (Chl *a, b, c* and carotenoids) was later determined by grinding the sample in 90% acetone, centrifuging, and then spectrophotometrically recording absorption in wavelengths related to pigment content (Parsons et al. 1984).

A linear correlation coefficient ($r$) was determined for the relationship between spectral reflectance in all wavebands and both $F_v/F_m$ and pigment content, specifically Chl *a*. This produced a correlogram for each target, where the wavelength of spectral reflectance was plotted as the independent variable (x axis) and $r$ as the dependent variable (y axis). The correlograms were used to establish the wavelengths of minimum and maximum sensitivity to changes in chlorophyll content and $F_v/F_m$ through the identification of the lowest and highest values of the correlation coefficient. First and second derivatives of the spectra were also calculated by use of a least-squares (Savitzky-Golay) polynomial smoothing filter of width 15 nm and order 3. The second derivative was used to locate the position of the "red edge" as the zero crossing point in the curve close to 700 nm, indicating the transition between absorption of red light and reflection of near infrared (Demetriades-Shah et al. 1990; Curran et al. 1991). Greater concentrations of chlorophyll pigments within terrestrial vegetation result in greater absorption of incident sunlight centered around the 675-nm region and widen the absorption feature toward the near-infrared wavelengths. As a result of this process, measurements of the position of the red edge have been significantly related to leaf chlorophyll content (Curran et al. 1990, 1991). It is recognized that the use of longer wavelengths such as that required for red

edge determination is restricted by water-column absorption; thus, this analytical technique will only be of use in shallow or exposed reef areas.

## Results and discussion

*Spectral characterization of coral reef substrates*—It was possible to discriminate between the selected reef features (*Montipora* sp., $n = 49$; *Porites* sp., $n = 80$; macroalgae *C. fastigiata*, $n = 24$; and sediment interspersed with benthic microalgae, $n = 35$) on the basis of their reflection and absorption of light in different wavelengths. Spectral reflectance of the sediment samples was notably higher than the corals and macroalgae in the visible wavelengths. The greatest variation in spectral response between features was found between 570 and 595 nm (Figs. 3A, 4). This finding concurs with several other published works recording this region of the spectrum as the wavelengths displaying the most variation between reef substrates (Holden and LeDrew 1998*b*; Clark et al. 2000; Kutser et al. 2000). A trough at ~675 nm in the spectral signature attributed to chlorophyll presence was observed in all signatures and was confirmed by the zero crossing point in the first derivative curve (Fig. 3B). The triple-peaked (570, 600, and 650 nm) reflectance signature reported elsewhere (Hochberg and Atkinson 2000) was observed in the *Montipora* average curve but was not evident in the *Porites* reflectance curve, highlighting the diversity of corals, their morphology, and associated pigments.

When the spectral reflectance data for each reef target were resampled to simulate that likely to be measured by broad bandwidth sensors such as Landsat ETM and SPOT, spectral differences between reflectance profiles of the targets were still evident (Fig. 4). The reflectance signatures were not processed to simulate atmospheric interference or the spatial point-spread function of each sensor; thus, it is recognized that differentiation between these features may still be difficult when satellite-borne sensors are used (Lubin et al. 2001; Kutser et al. 2003). In addition, Call et al. (2002) suggested that the wavelength regions of greatest variance in reflectance between several reef features (shallow healthy coral, deep coral, and seagrass) falls outside the spectral response function of Landsat ETM. However, the regions they suggest using are also subjected to increased atmospheric and water-column attenuation (390–440 and 705–720 nm), and they do not resample their data to simulate the spectral bandwidths of the TM sensor. Although we note that differences in the spectral response are potentially detectable using Landsat ETM and SPOT, the spatial distribution and extent of these reef features is often patchy, thus resulting in pixels containing mixtures of reef cover types, and the detection of individual features is consequently impeded in coarse spatial resolution imagery. Thus, the use of these sensors to estimate a continuous variable such as chlorophyll content may be more useful than attempts to produce categorical classes of reef "zones." The chlorophyll absorption troughs apparent in this study occur in a rather narrow portion of the spectrum and have a tendency to shift to longer wavelengths with increasing chlorophyll concentration. Unfortunately, in coarse spectral resolution data, this shift may result in an
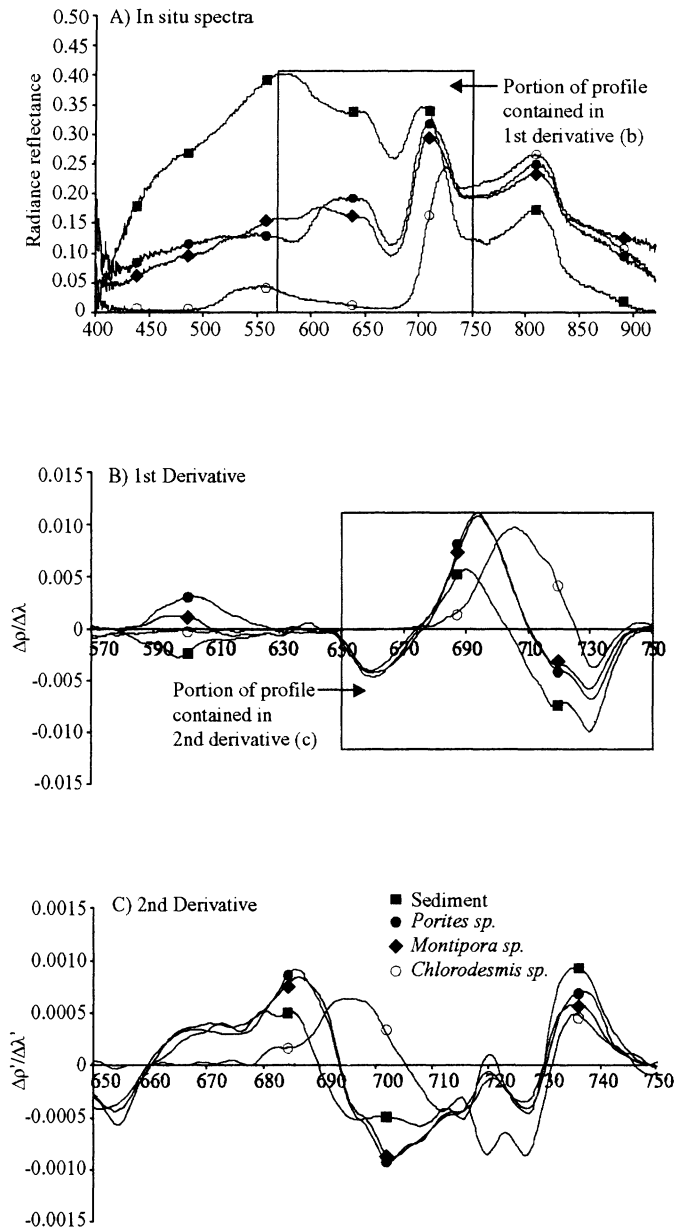
Fig. 3. (A) Average spectral signature curves (adapted from Joyce and Phinn 2000), (B) first derivative curves, and (C) second derivative curves. The horizontal axis has been rescaled for each graph to depict the most informative portion of the spectrum.



Fig. 4. Original spectra resampled to simulate the spectral response in SPOT and LANDSAT 7 ETM bandwidths.

apparent decrease in the depth of the absorption feature and thus may be misinterpreted as a feature with low chlorophyll content.

The differences observed between the spectral reflectance curves of *Chlorodesmis* sp. and the corals suggest the possibility of detecting differences in live coral and macroalgae in clear shallow waters with high spatial and high spectral resolution data, which have been identified elsewhere as a major limitation to coral reef remote sensing (Holden and LeDrew 1998a). The difference was primarily related to reflectance magnitude in the visible wavelengths, with *Chlorodesmis* being a visually dark target. The corals also displayed a shift in peak visible reflectance toward the red wavelengths, whereas the dominant peak in the reflectance
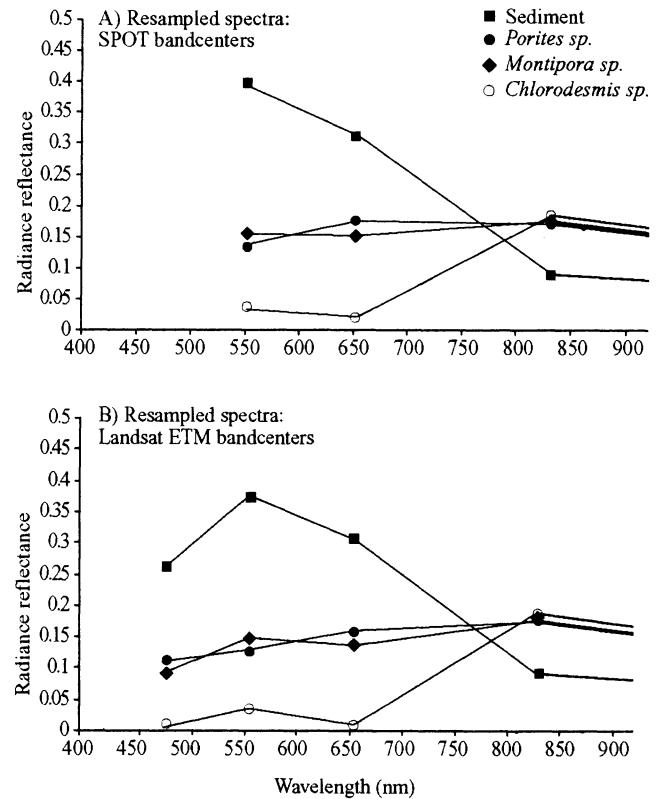
curve of *Chlorodesmis* sp. was in the green wavelengths. This example of green algae is not intended to be indicative of the spectral response of all algae on the reef, and it is recognized that brown, green, and red algae will have vastly different responses due to characteristic pigmentation. Isolation and spectral characterization of pigments unique to algae (e.g., Chl *b*) may hold the key to remote discrimination between these features.

A method proposed elsewhere as a means for discriminating among submerged sand, macroalgae, and bleached and healthy corals is the first derivative of field-based spectral reflectance (Holden and LeDrew 1999). A decision tree approach was implemented to classify targets into macroalgae, sand, bleached coral, or healthy coral on the basis of the slope (first derivative) of their spectral reflectance signature. If this approach was applied to our data set (Fig. 3), *Montipora* sp. and *Porites* sp. would have been classified as macroalgae, sediment as bleached coral, and *Chlorodesmis* sp. as sand. These conflicting results suggest that further field validation and testing of the derivative-based classification is required before a definitive method of delimitation can be ascertained by use of first-order derivatives. Possible explanations for the differences between our data and those of Holden and LeDrew (1999) may be due to variations in (1) the methods of spectra collection and calibration, (2) water optical properties, (3) the target feature, and (4) the obvious presence of benthic microalgae (seen by chlorophyll absorption) within the sediment in the present study. Although the use of derivative analysis is promising, the difficulty with relying on derivative curves to discriminate be-
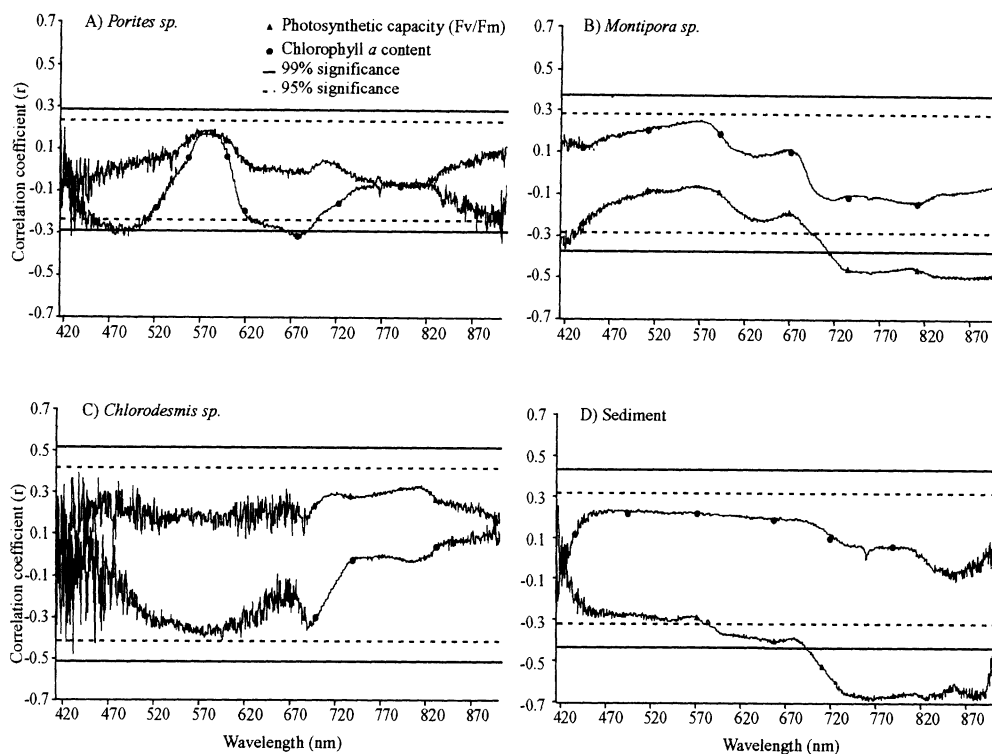
Fig. 5. Linear correlation coefficients for the relationship between spectral reflectance and chlorophyll content and photosynthetic capacity ($F_v/F_m$). (A) *Porites* sp. (adapted from Joyce and Phinn 2000), (B) *Montipora* sp., (C) *Chlorodesmis* sp., and (D) sediment.

tween different substrate types is the provision of a data set with sufficient number of bands to calculate derivatives (e.g., airborne hyperspectral CASI, HYMAP, and AVIRIS or satellite hyperspectral HYPERION, MODIS, and MERIS).

First-order derivative analysis enabled differences in the magnitude and location of slopes in the spectral reflectance curves to be measured. In terrestrial spectroscopy, the locations of points of inflection are significantly correlated to differences in pigmentation and/or structural properties between the targets (Curran et al. 1991). The only wavelengths in which *all* the reef target features exhibited noticeably different first derivative values were between 590 and 600 nm. Differences between the corals and algae were also evident at ~685 and >710 nm. The use of derivatives for feature discrimination in coral reef environments is an analysis tool still under development, and the results obtained herein and by others (Holden and LeDrew 1999; Hochberg and Atkinson 2000) suggest the potential of this method. First- and second-order derivatives provide a means to quantify the exact wavelength(s) at which absorption troughs and inflection points occur in reflectance data (Curran et al. 1991; Kokaly and Clark 1999). In addition to potential feature discrimination, the depth of the trough may then be used as a surrogate for pigment content, as is often done in terrestrial environments.

*Relationships among spectral reflectance, chlorophyll content, and photosynthetic capacity*—The linear correlation coefficients between spectral response and both Chl *a* and $F_v/F_m$ varied greatly depending on the feature of interest.

Hence, a single wavelength or portion of the reflectance spectrum cannot be considered significantly correlated or highly sensitive to the measured biophysical properties within all targets (Fig. 5). Nevertheless, a statistically significant relationship was found between spectral reflectance of *Porites* sp. and measured chlorophyll content. The portions of the spectrum found to be most sensitive to variations in chlorophyll content in *Porites* sp. were between 460 and 510 and 630 and 700 nm ($P < 0.05$). Reflectance was negatively correlated ($P < 0.01$) with Chl *a* content ~675 nm, indicating, as expected, that an increase in chlorophyll content results in decreased reflectance of incident light around this wavelength region (Curran et al. 1991; Myers et al. 1999). This corresponds with the negative (although not quantified) linear relationship between surface pigmentation and spectral reflectance in *M. faveolata* (Schmidt et al. 1999) and that between spectral reflectance and peridinin content in four different Caribbean corals, where chlorophyll content also covaried with peridinin presence (Myers et al. 1999). Although a statistically significant correlation between spectral reflectance at 675 nm and chlorophyll content in *Porites* sp. was observed, the correlation coefficient was still low ($r = 0.31$), and the degree of variation about the trend line was large (Fig. 6). Thus, development of an algorithm to accurately predict chlorophyll content by use of spectral reflectance with these data may be unreliable.

The lack of statistically significant relationships for the other targets is likely to be a combination of several factors and complications associated with (1) retrieving spectral reflectance and absorption values in which radiation transfer
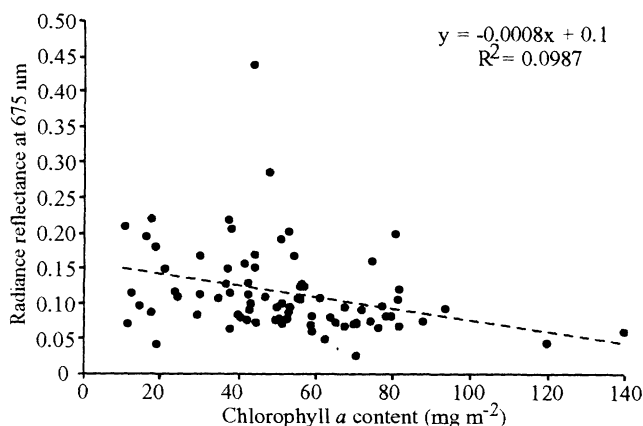
Fig. 6. Linear correlation between chlorophyll content (mg m⁻²) and radiance reflectance at 675 nm.

$y = -0.0008x + 0.1$
$R^2 = 0.0987$



Fig. 7. Mean Chl $a$ content (mg m⁻²) for each target (left side, y axis) plotted as solid bars with mean red edge location (right side, y axis) displayed as circles. Bars indicate standard error calculations.

involves underwater interactions (with the water column), (2) variations in form/structure of photosynthesising elements of corals, and (3) scale variations among the spectrometer, PAM fluorometer, and pigment measurements. These results suggest that the relationship among chlorophyll content, photosynthetic capacity, and reflectance spectra within a coral reef environment is neither direct nor causal, and a substantial amount of work is required before spectral reflectance can be used to inversely estimate reef these parameters. Future attempts to expand these methods should also select features with a greater range of chlorophyll content or with varying stages of stress—e.g., bleached and non-bleached corals—providing increased links with previous work in this area (Hardy et al. 1992). The reflectance of *Porites* sp. exhibited the greatest correlation with chlorophyll; however, it was also the group with the largest number of samples. The correlations observed indicate that a sample population with a greater range of variation in chlorophyll content is required to produce a statistically significant result and provide a greater understanding of the relationship between chlorophyll content and light absorption across the spectrum. In a similar context, the form of the correlation between the pigment content of *Porites* sp. and reflectance was as expected; however, the relationships between reflectance and pigment content of the other targets did not exhibit the strong negative correlation expected in wavelengths associated with key pigments.

Correlations between first- and second-order derivatives and chlorophyll content were typically higher than when reflectance measurements were used; however, the signal:noise ratio of these curves was considered too low to be of value in assessing their relationship with pigment content and photosynthetic capacity without substantial smoothing. Third- and fourth-order derivative analysis requires that the input reflectance profiles have been smoothed significantly to remove high-frequency variations (Hochberg and Atkinson 2000). The fourth derivative acts as a form of high-frequency enhancement filter, magnifying small absorption troughs or reflectance peaks at the expense of the original form of the reflectance spectra (Butler and Hopkins 1970; Hollas 1998). The higher order derivatives were not considered to be use-
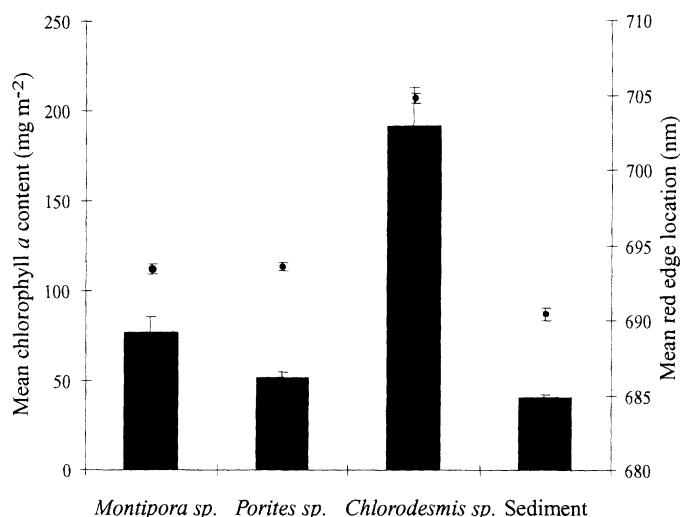
ful for establishing pigment content, because the derivative profiles were extremely noisy.

The most prominent feature of the second derivative curve was the quantification of the red edge, seen as the zero crossing point near 700 nm for all features, 690 nm for sediment, 694 nm for *Porites* and *Monitpora* sp., and 705 nm for *Chlorodesmis* sp. (Fig. 3C). The position of this inflection point is related to chlorophyll content in terrestrial plants (Curran et al. 1990), and a similar pattern was also apparent within the samples of the present study, with the red edge of low chlorophyll level samples being at shorter wavelengths than the position of high chlorophyll level samples (i.e., sediment = low chlorophyll content, *Chlorodesmis* sp. = high chlorophyll content; Fig. 7). This suggests the potential of hyperspectral remote sensing for estimating chlorophyll content and associated biological processes in marine environments and may be applied to estimating chlorophyll content on reef crests and similar structures exposed at low tides. Alternatively, this may also prove useful for laboratory-based studies of coral pigments where a nonintrusive method of data collection is desired. In the field, this method will only be useful in clear shallow waters with little suspended sediment or organic matter, such as that found in offshore coral reefs, rather than fringing reefs or inshore lagoonal reefs. The effect of varying water depths and inherent optical properties on the location of the red edge for substrate features was not assessed, although it may be possible to model differences in response and determine the true utility of this method for chlorophyll estimation.

In contrast to similar studies conducted on terrestrial vegetation, corals and sediment do not have a continuous photosynthetic surface but are a more complex association of pigments and calcium carbonate (either in the form of coral skeleton or coral sand). To obtain a more accurate signature of the photosynthesizing plant matter (zooxanthellae and BMA), characterization or removal of the calcium carbonate, and cnidarian-associated nonphotosynthetic pigments (Dove

et al. 1995) "background signature" is required. Integrating fluorescence spectra with reflectance measurements (Hardy et al. 1992; Myers et al. 1999) has been useful in characterizing the pigmentation controlling spectral absorption features, and the combination of active and passive techniques is perhaps the key to further understanding light interactions within coral reef environments.

*Research limitations*—The effects of water-column absorption were most noticeable at wavelengths longer than 720 nm, although an additional peak in reflectance in the near-infrared (806–820 nm) was apparent due to decreased water column absorption in this region relative to adjacent wavebands. Future work in this area should model the effects of varying water depths and inherent optical properties in addition to light refraction and diffusion at the air–sea interface (e.g., building on similar approaches as Lubin et al. 2001 and Kutser et al., 2003).

Wave focusing is a considerable factor that influences variation in spectral samples obtained in clear, shallow-water environments (Goodman and Ustin 2002). Although our spectral collection methods involved averaging 36 samples to obtain the reflectance curve, outlying or variable signatures may significantly influence the resultant average signature. Our current reflectance spectra measurement procedure has been modified to record one sample at a time and then retain the samples within one standard deviation of the mean for the averaging process to derive each profile. This allows the removal of signatures clearly amplified by wave-focusing effects. When obtaining spectra, we also took care to ensure that field personnel and equipment did not shade the target, as is common protocol in terrestrial environments. However, it has since been shown that shading will reduce spectral variation due to wave focusing (Goodman and Ustin 2002). Alternatively, obtaining simultaneous measurements of upwelling radiance and downwelling irradiance with a dual sensor head will also minimize similar variations due to the time difference between substrate and reference panel measurements.

One of the greatest problems with the chlorophyll measurements within the sediment is the depth to which BMA are actually found. The spectrometer and PAM take measurements typically from the upper surface of the target; however, independent field observations by the authors on Heron Reef indicate the presence of BMA to at least 25-cm depth. This would suggest that surficial measurements of chlorophyll within the sediment seriously underestimate the photosynthetic material and potential productivity within coral sands on this reef (Roelfsema et al. 2002). Another potential source of chlorophyll content underestimation on the reef may be due to the presence of endolithic algae residing within coral skeletons. The thin (1–2 mm) layer of intense green algae was noted in many of the *Montipora* sp. samples analyzed in the present study. Because this layer occurred below the calcium carbonate skeleton of the coral, its contribution to the spectral reflectance signature obtained from the coral's surface could not be determined.

Spectral absorption and reflectance in a coral reef environment are far more complex than their terrestrial counterparts, highlighting the need for more detailed and integrated research into coral reef health, condition, and process monitoring. To better map and monitor reef biophysical properties such as photosynthetic capacity and pigmentation, our results suggest that coral reef remote-sensing models need to consider spectral absorption and reflection by the underlying coral skeleton and variations in reflectance at different spatial scales.

This was an exploratory study attempting to relate spectral reflectance to quantitative measures of chlorophyll content and photosynthetic capacity. The techniques presented provide a direction for understanding and quantifying the underlying biophysical properties contributing to spectral response in a coral reef environment. Chl *a* content was significantly linearly correlated to spectral reflectance in *Porites* sp. within the spectral regions of 460–510 and 630–700 nm ($P < 0.05$). However, the range of variation about this relationship suggests that chlorophyll content cannot be considered the sole controller of light absorption at these wavelengths. Therefore, it is currently not possible to suggest a universal algorithm to predict chlorophyll content with spectral reflectance using these data. The expected pattern was not observed for the other features (*Montipora* sp., *Chlorodesmis* sp., and sediment), possibly because of a combination of factors related to the inherent difficulties in sampling in marine environments, such as accounting for water column attenuation and spectral and spatial variability. Photosynthetic capacity was not found to be significantly related to spectral reflectance in any wavelength region for any of the features sampled. Thus, we conclude that relationships between spectral response and both chlorophyll content and photosynthetic capacity are neither direct nor causal, and further work is required to fully characterize and understand the controlling factors of light reflection and absorption in reef environments.

Quantification of the relationship between spectral reflectance and chlorophyll content may provide a basis for mapping a continuous variable across the reef flat, giving an indication of photosynthetic potential. It should be noted that, with considerable refinement, an algorithm may be developed from this work, but at this stage reflectance cannot be considered a universal predictor of chlorophyll content across an entire reef flat or even within reef zones. Just as effective ocean color algorithms are restricted to deep, clear waters (case 1), this application will also be restricted by attenuation because of depth and variable dissolved and suspended materials occurring across the reef; thus, the greatest potential application of the methods described is in field-scale studies or in exposed reef areas at low tides.

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