Use of *in situ* and airborne reflectance for scaling-up spectral discrimination of coral reef macroalgae from species to communities

Serge Andréfouët[1,4,*], Claude Payri[2,4], Eric J. Hochberg[3], Chuanmin Hu[1], Marlin J. Atkinson[3], Frank E. Muller-Karger[3]

[1]Institute for Marine Remote Sensing, College of Marine Science, University of South Florida, 140, 7th Av. South, St Petersburg, Florida 33701, USA

[2]Université de la Polynésie Française, Laboratoire Terre-Océan, BP 6570, Faaa-Aéroport, Tahiti, French Polynesia

[3]University of Hawaii, Hawaii Institute of Marine Biology, PO Box 1346, Kanehoe, Hawaii 96744, USA

[4]*Present address:* Institut de Recherche pour le Développement, BP A5, 98848 Nouméa cedex, New Caledonia

ABSTRACT: In principle, *a priori* knowledge of organism-scale spectral signatures for key ecological end-members is a basic requirement for identifying coral reef benthic communities using hyperspectral remotely-sensed imagery. Spectral signatures of end-members are now relatively well known for predominant reef taxa (coral, algae) and for the background of the living communities (e.g. sediments). What remains unclear is whether the criteria for spectral discrimination between end-members at the millimeter or centimeter scale remain valid when attempting to process images at several meters resolution. In other words, is it possible to scale-up spectral criteria of identification from species/organisms to communities? We address this issue with *in situ* and 'compact airborne spectrometer imager' (CASI) hyperspectral measurements of the tropical marine flora of 2 South Pacific Ocean coral reefs. Targets were the dominant algal species and communities encountered in the shallow (0 to 3 m) barrier and fringing reefs of Moorea Island and the outer margin of the rim of Rangiroa Atoll (French Polynesia). Stepwise wavelength selection and linear discriminant analysis highlighted the key non-redundant wavelengths necessary to achieve good separation between the predefined ecological groups. Comparison of the wavelengths identified from *in situ* and airborne measurements allowed definition of a subset of common wavelengths that were robust to changes in spatial scale and still provided excellent discrimination and classification accuracy between the ecological groups. These results suggest that continuous spectral signatures acquired *in situ* at the centimeter scale can be used to select key discrete wavelengths for remote-sensing observations of communities at the meter scale despite the spatial heterogeneity in benthic cover and the resulting spectral mixing.

KEY WORDS: CASI · Remote sensing · Hyperspectral · Atmospheric correction · Macroalgae · Coral reef · Atoll · Moorea · Rangiroa

INTRODUCTION

Over the past 8 yr, our knowledge on the spectral reflectance of coral reef benthos has risen from virtually nil to an overwhelming abundance of spectral libraries, generally acquired using hand-held spectrometers that are convenient enough to be used in the field (Yamano et al. 2002, Hochberg et al. 2003, Kutser et al. 2003, Louchard et al. 2003). Using these spectral libraries, current remote-sensing research aims to unmix remotely-sensed community-scale or habitat-scale spectra to retrieve the percent cover of individual end-members (live corals, dead corals, algae, sediments, etc.) at different depths (Hochberg & Atkinson 2003,

Hedley et al. 2004). The ultimate goal is to remotely sense coral reef 'health' by separating algae from live coral, or dead coral from live coral over large areas and quantifying their cover (e.g. Hochberg & Atkinson 2000, Mumby et al. 2001). A less challenging goal is the identification of the main benthic communities contributing to the structure of the reefs in order to estimate, for instance, the extent of habitats of economically important species (Long et al. 1993, Andréfouët et al. 2004), or to budget biogeochemical processes (Andréfouët & Payri 2001).

Knowledge of organism-scale spectral signatures for key ecological end-members is a basic requirement for identifying benthic communities and their status by hyperspectral remotely-sensed imagery (Clark et al. 2000, Hochberg & Atkinson 2003). Spectral signatures of end-members are now relatively well known for primary reef benthos (coral, algae) and for the background of the living communities (e.g. sediments). The vast majority of these spectra represent the reflective properties of a few square centimeters of homogeneous tissue or substrate at best. Because remote-sensing pixels cover larger areas, and because reef end-members form inherently mixed communities at these larger scales, it is unclear whether the criteria for spectral discrimination between end-members at the millimeter or centimeter scales hold when attempting to process images at several meters resolution. In other words, is it possible to 'scale-up' spectral criteria of identification?

It has previously been assumed that if a set of wavebands allows spectral discrimination between algae and coral at a few square centimeters, then the same set would be valid at larger spatial (and ecological) scales and for various sites of investigation. This hypothesis led to good results in Kaneohe Bay, Hawaii (Hochberg & Atkinson 2000). However, its general validity is questionable, since benthic objects in coral reefs spatially aggregate to form a virtually infinite number of combinations of intricate heterogeneous 3-dimensional mosaics, even at a few square meters resolution. It is therefore very possible that criteria for discrimination between species of cyanobacteria, brown, green and red algae, corals, soft corals, sponges, and different types of sediments based on *in situ* measurements will not be optimal for all communities.

The study of spectral separability has 2 applications. (1) At the organism scale, non-destructive optical measurements may provide precise information on the physiological properties of the target and its adaptation to different environments (e.g. photoacclimation of *Hydrolithon onkodes:* see Payri et al. 2001). Different signatures may indicate different physiologies. (2) Knowledge on the spectral separability of benthic objects is useful for designing and optimizing coral reef

remote-sensing applications (Atkinson et al. 2001). The need for prior identification of the discriminatory wavebands is still critical, despite the availability of hyperspectral sensors providing an almost continuous signal from 350 to 700 nm (the spectral domain most useful in shallow and subsurface waters). Indeed, the technical limitations of many airborne (and space) sensors necessitate an operational compromise between spatial resolution and spectral resolution. For instance, it is sometimes only possible to achieve sub-meter or meter-scale spatial resolution in the multispectral mode, not in the hyperspectral mode. Thus, preliminary knowledge of discriminatory wavebands is critical. Excluding wavebands that provide redundant information may also facilitate post-acquisition processing.

In this study, our goal was to assess the robustness of waveband selection using reflectance measurements at both organism and community levels. For this purpose, we used *in situ* species-level measurements (cm resolution) and airborne 'compact airborne spectrometer imager' (CASI) hyperspectral community-level measurements (meter resolution) from two shallow reefs in French Polynesia. We focused on the rich algal species and communities of these 2 reefs (Pichon 1985, Payri 1987). Algal cover is substantial, if not dominant, on many reefs worldwide, comprising various communities controlled by hydrodynamics, depth, light, substrate, water quality, or nutrient gradients. With the increasing number of reports of algal blooms, and of settlement and spread of invasive species in reefs (e.g. Russel & Balazs 1994, Stiger & Payri 1997), there is also a need to assess with precision whether spectral discrimination between algae species and between algae communities is possible. The detection of changes in reefs and reef health status will probably motivate many future applications, but economic objectives (e.g. biomass estimation of algae interesting for biotechnology applications) or fundamental objectives such as assessment of the coralline algae contribution to reef calcification (Payri 1997) also motivate our research. The feasibility of large-scale benthos assessment with a focus on algae is of interest for many ecologists.

Algae in temperate environments and seagrass in tropical environments have received some attention (Jakubauskas et al. 2000, Wittlinger & Zimmerman 2000, Dekker et al. 2001 [review], Fyfe 2003), but previous hyperspectral studies in tropical coral reefs have preferentially targeted live, bleached and dead corals (Hedley & Mumby 2002 [review], Minghelli-Roman et al. 2002, Hochberg et al. 2003). For coral reefs, several studies have presented spectral signatures of macroalgal species (Maritorena et al. 1994, Myers et al. 1999, Andréfouët et al. 2001, Lubin et al. 2001, Kutser et al. 2003, Karpouzli et al. 2004) or have considered algal morphotypes (fleshy, turf, encrusting) and groups

(Phaeophyceae, Chlorophyceae and Rhodophyceae) (Hochberg et al. 2003), but very few studies have addressed the community level (Mumby et al. 1997, Hochberg & Atkinson 2000, Purkis & Pasterkamp 2004). In their review, Hedley & Mumby (2002) pointed out that '*it is clear that intra-specific spectral variation is considerable in macroalgae, but currently there is insufficient information to assess the extent to which this compromises the spectral discrimination of species.*' We agree that more data are needed for this important benthic compartment at the species and community levels, and have chosen algae species and communities to address the scaling problem.

MATERIALS AND METHODS

Study sites. We selected 2 reef configurations typical of Pacific Ocean reef flats, namely the carbonate atolls of the Tuamotu Archipelago and the volcanic islands of the Society Archipelago. These were selected because of their obvious differences, to cover 2 different configurations. Both are well-known research sites. These 2 environments represent the dominant shallow algae communities encountered in French Polynesia (Payri

et al. 2000). Bays, rocky volcanic shorelines, estuaries, or deeper lagoon floors or outer slopes were not considered since these 2 reef flats represent the majority of the productive coral reef areas present in the South Pacific islands and atolls.

Site 1—Tivaru, Rangiroa: The Tivaru reef flat located on the northwestern side of Rangiroa atoll (Fig. 1) is very shallow (not more than 50 cm depth), which is typical for Pacific atoll-rim flats. It presents (1) a coralline algal crest dominated by *Hydrolithon onkodes* on the oceanic side, (2) a back reef with alternation of patches of fossil crest and pools of corals mixed with algae, and (3) a lagoon-facing pavement that is either bare with scattered coral heads, or encrusted by coralline algae and algal turf mainly composed of the geneculate coralline *Jania adhearens*, *Amphiroa annulata* and *A. fragilissima*. Fig. 2 illustrates the spatial structure of this section of the Rangiroa outer rim. Algal flora is dominated by *H. onkodes*, but 4 different algae-dominated communities are recognizable (Table 1). We also include the different coral pavements in our analysis.

Site 2—Tiahura, Moorea: In contrast to the Rangiroa reef flat, Tiahura reef on the northwestern coast of Moorea Island (Fig. 1) provides a greater diversity and
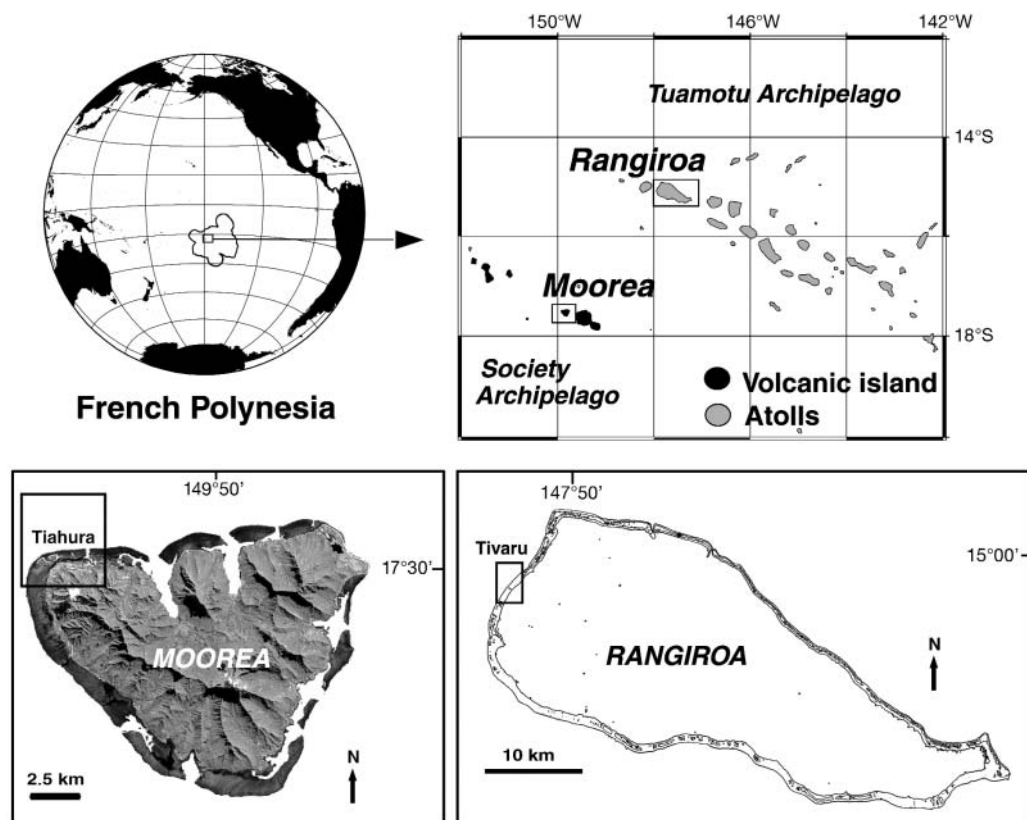

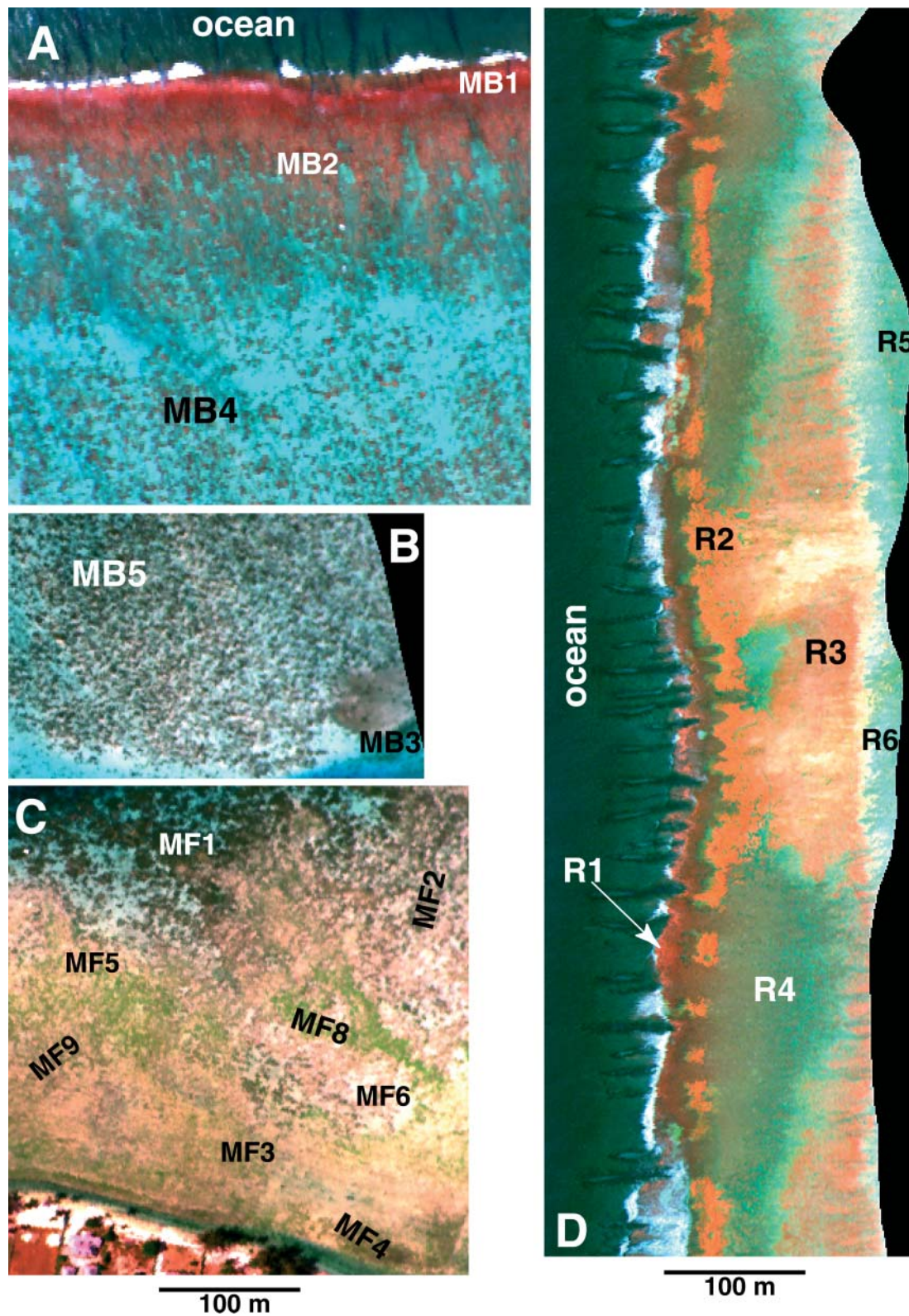Fig. 1. Location of Moorea Island and Rangiroa Atoll

Fig. 2. Structure of studied reef sites and location of main algae communities; zones labeled as in Table 1. (A) Algal crest, back-reef and large patches in Moorea barrier reef. (B) Small coral patches and Rhodoliths patch in Moorea barrier reef. (C) Moorea fringing reef communities. (D) Rangiroa coralline crest and back reef. Structure of each reef is revealed by these RGB (red-green-blue) composites obtained with CASI bands: for (A) and (C) R = 700, G = 554 and B = 435 nm; for (B) R = 674, G = 575 and B = 449 nm; for(D) R = 700, G = 562 and B = 436 nm

Table 1. Algae present in each reef zone. Footnotes give composition of turfs and of rare algae on fringing reef (Rare f.a.)

				Dominant algae	Secondary algae
Rangiroa:	**Reef flat and crest**	R1	Crest	*Hydrolithon onkodes*	*Hydrolithon gardineri* *Sporolithon* spp.
		R2	Fossil crest	Rhodymeniales/Ceramiales assemblages *Hydrolithon onkodes*	
		R3	*Lobophora variegata*	*Lobophora variegata* Rhodymeniales/Ceramiales assemblages *Microdictyon* spp.	*Liagora ceranoides*
		R4	Coral	*Hydrolithon onkodes* *Halimeda* spp. *Microdictyon* spp. *Hydrolithon onkodes*	*Caulerpa pickerengii* *Dictyota friabilis* *Hydrolithon gardineri*
		R5	Pavement	*Jania adhaerens, Gelidium pusillum* on *Hydrolithon onkodes*	
		R6	Bare pavement		
Moorea:	**Barrier reef**	MB1	Crest	*Turbinaria ornata* *Sargassum sociale* *Sargassum mangarevense*	*Amphiroa fragilissima* *Jania adhaerens* *Laurencia flexilis* *Hydrolithon onkodes* *Mastophora pacifica* *Mesophyllum erubescens* *Caulerpa webbiana* *Chlorodesmis fastigiata* *Codium geppii* *Dictyosphaeria cavernosa* *Dictyota hamifera*
		MB2	Back-crest	*Sargassum sociale* *Sargassum mangarevense* *Turbinaria ornata*	*Amphiroa* spp. *Jania* spp. *Mesophyllum erubescens* *Boodlea kaeneana* *Chlorodesmis fastigiata* *Halimeda* spp. *Microdictyon umbilicatum* *Dictyopteris repens* *Dictyota hamifera* *Lobophora variegata*
		MB3	Rhodolith patch	*Neogoniolithon frutescens* *Hydrolithon reinboldii* *Anabaena torulosa*	
		MB4	Large patches	*Sargassum mangarevense* *Turbinaria ornata* *Amansia rhodantha* Turf[a]	*Actinotrichia fragilis* *Galaxaura fasciculata* *Gelidiopsis* spp. *Hydrolithon onkodes* *Lithophyllum flavescens* *Lithophyllum insipidium* *Lithophyllum kotschyanum* *Halimeda incrassata* *Halimeda minima* *Neomeris vanbosseae* *Valonia* fastigiata *Ventricaria ventricosa* *Lobophora variegata*
		MB5	Small patches	*Turbinaria ornata* *Sargassum mangarevense* *Dictyota* spp.	*Halimeda incrassata* *Hydrolithon onkodes* *Lithophyllum* spp. turf *Gelidiopsis* spp.
		MB6	Pavement		*Valonia aegagropila* *Turbinaria ornata* *Dictyota divaricata*
	Fringing reef	MF1	Large channel patches	Turf[a] *Turbinaria ornata*	Rare f.a.[b] *Galaxaura filamentosa*
		MF2	Compact, small, dead patches	Turf[a] *Turbinaria ornata*	Rare f.a.[b]
		MF3	Micro-atolls	*Padina boryana* *Halimeda incrassata* *Hydrolithon onkodes* *Acanthophora spicifera* *Turbinaria ornata*	Rare f.a.[b]
		MF4	*Halimeda* spp. complex	*Halimeda opuntia*	*Acanthophora spicifera*
		MF5	Sand rubble with *Padina*	*Padina boryana* *Dictyota divaricata*	*Hydrolithon reinboldii* *Halimeda incrassata*
		MF6	Sand with Cyanobacteria	*Phormidium* spp.	*Halimeda incrassata*
		MF7	Sand and rubble		*Hydrolithon reinboldii*
		MF8	*Boodlea* spp. bloom	*Boodlea kaeneana*	
		MF9	Mixed fringing community	*Padina boryana* *Halimeda opuntia* *Acanthophora spicifera* *Boodlea kaeneana* *Halimeda incrassata*	
		MF10	Grazed turf on dead structures	Turf[a] *Hydrolithon onkodes*	*Padina boryana* *Turbinaria ornata*

[a]Turf composition: *Ceramium* spp., *Polysiphonia* spp., *Lophosiphonia* spp., *Heterosiphonia* spp., *Champia, Sphacelaria, Enteromorpha clathrata*
[b]Rare fringe algae: *Hydrolithon onkodes, Caulerpa racemosa, Caulerpa serrulata, Caulerpa sertularoides, Halimeda distorta, Halimeda incrassata, Halimeda opuntia, Chnoospora implexa, Dictyota divaricata, Hydroclathrus clathratus, Phormidium* spp., *Symploca hydnoides, Spyridia filamentosa*

patchiness of communities, habitats and ecological niches. The composition and dynamics of the algae community of Tiahura reef have been well studied (Payri 1987, 1997, Gattuso et al. 1997). In shallow areas (<2 m) encountered along the 800 m of reef from the shore to the algal crest, we observed 6 zones on the barrier reef (Fig. 2A,B) and 10 zones on the fringing reef (Fig. 2C) (Table 1). On the fringing reef, the main algal zones were the summit of the large coral heads at the edge of the channel, heterogeneous assemblages of various algae (mostly *Padina boryana*, *Halimeda* spp., *Acanthophora* sp.), different zones of dead structures (continuous coral framework and isolated micro-atolls) covered partly by turf algae and diverse assemblages, sandy areas rich in cyanobacteria, large *Padina boryana* and *Halimeda incrassata* beds close to shore, and sand/rubble zones. Moreover, a bloom of the green algae *Boodlea kaeneana* occurred during the acquisition of CASI data. On the barrier reef, the main algal zones were the belt of brown algae *Turbinaria ornata* and *Sargassum mangarevense* along the crest, the heterogeneous coral–algae back-reef framework, various zones of coral patches of different sizes and densities, zones of accumulation of the coralline rhodolithes *Neogoniolithon frutescens* and *Hydrolithon reinboldii* (overgrown by the cyanobacterium *Anabaena torulosa* at the time of the surveys), and areas of bare pavement with scattered brown algae.

Acquisition of *in situ* reflectance spectra of representative algae. There are 425 taxa of benthic marine algae inventoried in French Polynesia (Payri & DeN'Yeurt 1998). Collection of *in vivo* or *in vitro* reflectance spectra for each of the species in the coral reef environment would be an unjustified and daunting task. Reflectance spectra are likely to be similar for many of these species because of their similar pigmentations (Beach et al. 1997). Also, such a task would be irrelevant from a remote-sensing standpoint, since a large number of taxa are rare, hidden in crevices or spatially imbricate over a few square centimeters. Therefore, we selected *a priori* the most conspicuous and abundant species in the 2 reefs (Table 2) and insured that the Cyanophyceae, Phaeophyceae, Chlorophyceae and Rhodophyceae were all represented. We also included substrata (dead *Porites* spp., pavement, rubble) colonized by algal turfs. The algal turf sampled was a complex assemblage of filamentous forms including mainly red algae such as

Ceramiales (*Polysiphonia* spp., *Ceramium* spp., *Corallophila apiculata*, *Herposiphonia* spp.), Rhodymeniales (*Gelidiopsis* spp., *Coelothrix irregularis*, *Champia* spp.), the brown algae *Sphacelaria* spp. and the green alga *Enteromorpha clathrata*.

Hochberg & Atkinson (2000) provided a scheme to measure radiance reflectance and assess benthos spectral separability. Underwater *in situ* reflectance (*R*) spectra were measured on Rangiroa and Moorea in April 1999 using the same instrument and protocol detailed in Hochberg & Atkinson (2000) and Hochberg et al. (2003). Briefly, using an Ocean Optics S2000, we measured the upwelling radiance of the target, and then normalized the result by the upwelling radiance measured from a lambertian Spectralon plaque of known reflectance (10%). If we assume that the benthic target is also lambertian, this ratio provides the reflectance *R*. Both measurements were obtained within 2 to 3 s. For some algae, taxa that could not be measured in the field in French Polynesia for diverse reasons (e.g. battery failure, unsuitable conditions), we included spectra from Palau, Micronesia (Table 2), measured in July 2000 following the same methods. Reflectance spectra were filtered using the Savitski-Golay algorithm and resampled at 2 nm spectral resolution (for details see Hochberg et al. 2003).

Table 2. Algae species selected for *in situ* reflectance measurements and their locations. Zones as in Table 1 and Fig. 2

Zone	Algae
Rangiroa	
R5	*Jania adhaerens*, *Gelidium pusillum* on *Hydrolithon onkodes*
R1	*Hydrolithon onkodes*
R3	*Lobophora variegata*
R2	Rhodymeniales
R3	Rhodymeniales and *Lobophora variegate* complex
Moorea	
MB2	*Sargassum mangarevense*
MB2, MB4, MF1	*Turbinaria ornata*
MB3	*Neogoniolithon frutescens*, *Hydrolithon reinboldii*, *Anabaena torulosa* complex
MB4	*Lithophyllum flavescens*
MB4	*Lithophyllum insipidium*
MB4	*Hydrolithon onkodes*
MF8	*Boodlea kaeneana*
MF5	*Padina boryana*
MF3	*Acanthophora spicifera*
	Ceramium spp., *Polysiphonia* spp. turf complex
MB4, MF1	*Lophosiphonia* spp., *Heterosiphonia* spp., *Champia* spp.
	Sphacelaria spp., *Enteromorpha clathrata*
MF10	Grazed turf
Palau	
	Halimeda spp.
	Dictyota spp.

A total of 14 groups of *in situ* reflectance spectra (overall total = 616) were obtained and processed in overall 1999, including individual algae species and complexes that could not be measured separately (Table 2).

Acquisition and processing of airborne CASI data. CASI images were acquired in May 1998 for Rangiroa and in November 1998 for Moorea. For each of the sites, several modes were used, providing various combinations of spectral and spatial resolution. Here, we considered the hyperspectral data acquisitions. These consisted of 21 bands evenly distributed between 400 and 700 nm for Moorea at 1 m^2 spatial resolution, and 54 bands evenly distributed between 400 and 700 nm for Rangiroa at 2.7 m^2 spatial resolution. We traded a lower spatial resolution for a better spectral resolution for Rangiroa because the coral community cover was less heterogenous. Flight altitude was 500 m. Weather conditions were ideal, with clear sky and no wind. There were small waves breaking along the reefs, but the crests were not completely obscured by foam. The Rangiroa crest was exceptionally calm during data acquisition; community description and ground-truthing (Fig. 2) were made simultaneously or a few days after the overflight.

CASI images were acquired and pre-processed by Hyperspectral Data International. CASI calibration was made by the ITRES company on an annual basis. The accuracy of radiometric calibration of the CASI is estimated to be ±2% from 470 to 700 nm and ±5% between 400 and 470 nm (Babey & Soffer 1992). We extracted 230 total at-sensor radiance spectra (L_t) from 16 locations in Moorea and 182 spectra from 14 locations in Rangiroa (Table 1). Each location represented a different community in Moorea. In Rangiroa, several community types were represented in multiple locations, providing duplicates and some mixed zones as well.

To transform the total radiance spectra into remote-sensing reflectance (R_{rs}), it is necessary to remove the reflected sky radiance and atmospheric effects and normalize by the downwelling irradiance (Mobley 1999, Toole et al. 2000, Hu & Carder 2002). Thus

$$R_{rs} = \frac{L_t - L_{sky} - L_{atm}}{tE_d}$$

and

$$L_{sky} \approx t\rho \frac{E_{ds}}{r}$$

where L_t is the total at-sensor radiance, L_{sky} is the radiance accounting for the reflected sky light, L_{atm} is the atmospheric path radiance (light scattered to the sensor before reaching the sea surface), t is the diffuse transmittance from the sea surface to the sensor, ρ is the sea surface Fresnel reflectance, E_d is the down-welling irradiance above the water surface, E_{ds} is the diffuse component of E_d, and r is the ratio between E_{ds} and nadir sky radiance. L_{atm} and t were computed using 6S software (Vermote et al. 1997). ρ was set at 0.02 taking the incident viewing angle (note that this incident angle is not the solar angle, but the nadir sky angle, i.e. 0°) and calm sea surfaces into consideration. E_d and E_{ds} were taken from the spectral solar irradiance model of Gregg & Carder (1990) after spectral binning to match CASI wavebands, and account for the extra-terrestrial irradiance attenuation due to Rayleigh and aerosol scattering, oxygen, ozone and water-vapor absorption. Here, typical values for oceanic atmospheres have been used. To estimate L_{sky}, we used the ratio r of Aas & Hokedal (1999). These authors provided r for only 7 bands, thus we interpolated to retrieve the sky radiance between 400 and 700 nm.

Statistical analysis of *in situ* and airborne spectra. Our goal was to characterize the spectral separability between benthic objects. Thus we applied well-known methods (Rencher 1995) to identify the key spectral bands and build linear discriminant functions (Hochberg & Atkinson 2000, Karpouzli et al. 2004).

To determine which wavelength best separates the algal groups at species or community levels, we used the technique of stepwise selection of wavelength (SSW) and discriminant function analysis (DFA), detailed in Rencher (1995) and Hochberg & Atkinson (2003). SSW discarded the wavelengths that were redundant for separating the predefined groups (Renche 1995). Individual wavelengths were selected based on partial p-values resulting from successive multivariate partial *F*-tests. We considered only wavelengths significant at p < 0.05. For the *in-situ* spectra, non-redundant wavelengths too close together for a remote-sensing application were merged to provide a separation of at least 8 nm between wavelengths. In contrast to Hochberg & Atkinson (2000), we did not discard wavelengths >600 nm because water depth was not considered a limiting factor in this study, since most algae communities were in shallow reef flats (0 to 1 m depth in Rangiroa, 0 to 3 m in Moorea). These non-redundant wavelengths were used to build the linear discriminant functions (LDF) that best separated the different algal groups (Rencher 1995). Then, to visualize the actual discrimination operated by the linear discriminant functions, we projected individual spectra into the planes that best separated the predefined groups.

R and R_{rs} spectra from Rangiroa and Moorea were both analyzed with the SSW and DFA methods.

Scaling of spectral discrimination from species to community scale. The non-redundant wavelengths identified from *in situ* and CASI measurements by SSW were compared to identify a subset of common

wavelengths. We assumed that wavelengths emerging from both *in situ* and CASI data would be sufficiently robust for a change in spatial and ecological scales, and that the other wavelengths could be discarded. In addition, the set of common wavelengths would be sufficiently robust for a change in measurements, since *in situ* data are radiance reflectance and airborne data are remote-sensing reflectance. To test this hypothesis, we used these common wavelengths to conduct a new DFA analysis of the CASI data and to observe the degradation in the classification compared to the DFA analysis conducted with the full set of non-redundant CASI wavelengths. For Moorea, where all species are encountered, we used the 616 *in situ* spectra available, while for Rangiroa we used only the local spectra, since algae are much more specific on the atoll crest and reef flat. The analysis is summarized in Fig. 3.

Classification accuracy. To quantify the loss of discrimination when using a subset of wavelengths, we assessed the accuracy of the classifications for the different groups of communities or algae. To avoid bias in assessing classification accuracy, especially for small sample sizes, it is necessary to have a set of training data, which are used to construct the classification

rule, and a set of validation data used to evaluate the rule. Typically, a complete data set is split into 2 roughly equal parts, with one part used for training and the other for validation. However, partitioning the sample in this manner has at least 2 disadvantages. First, it requires large samples that may not be available (as in our case); second, it does not evaluate the classification function used in practice, i.e. the estimate of error based on half the sample might vary considerably from that based on the entire sample.

In this study, we employed an improved version of the sample-splitting procedure termed 'the holdout method' (also called cross-validation) (Rencher 1995). With the holdout method, all but 1 observation is used to compute the classification rule, and this rule is then used to classify the omitted observation. This procedure is repeated for each observation, so that for a sample size of N, each observation is classified by a rule based on the other N – 1 observations. Withholding a single spectrum from the computation of a classification rule means that the rule is not biased by the variability engendered by that spectrum. Each time a different spectrum is withheld, the classification rule is independent from that spectrum, and each
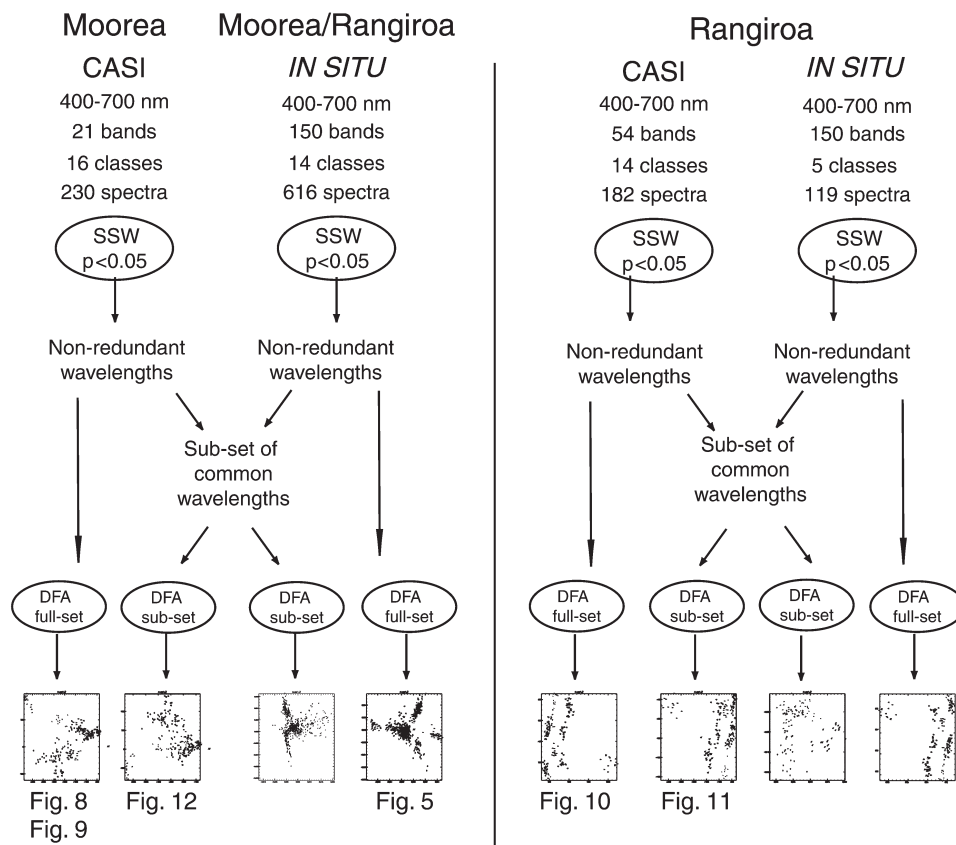

Fig. 3. Diagrams summarizing *in situ* and CASI data and their analysis for full set and subset of wavelength. DFA: discriminant function analysis; SSW: stepwise selection of wavelength

newly computed rule is independent from all others. Although computationally more demanding, the hold-out method has the advantage that, with only a single spectrum withheld, the classification rule is as close as possible to the rule that would be built using all spectra in the data set, thus minimizing the variance in the error rate estimate.

Classification results are in the form of an error matrix that shows how the spectra from one reference class are attracted to other classes, and how a reference class attracts spectra from other classes. A summary is provided by the overall accuracy, which is simply the ratio of correctly classified spectra to the total number of spectra.

RESULTS

In situ reflectance and species level discrimination

The differences between the mean reflectances of the main algae species are shown in Fig. 4 for Moorea and Rangiroa. Rubble, pavement, turfs and coralline spectra acquired on Moorea are available elsewhere (Andréfouët et al. 2001). The full set of *in situ* reflectance spectra highlights the continuum of algae color encountered in the field (inset in bottom graph of Fig. 4). Generally, the coralline and red algae covering Rangiroa reef flat provide brighter and less diverse spectra than the dominant brown and green algae of Moorea reefs. Considering the 616 spectra, the SSW analysis identified 16 non-redundant wavelengths (p < 0.05), including 6 above 600 nm (Table 3); overall classification accuracy was 92.0% (Table 4). Considering only the Rangiroa spectra, the SSW analysis identified 11 non-redundant wavelengths optimized for the atoll communities; overall accuracy was 94.1% (Table 4). Using the 616 spectra, the reconnaissance achieved using only the 2 first linear discriminant functions is presented in Fig. 5. The groups of the brown, green and coralline *Hydrolithon onkodes* algae are clearly separated. The complex Rhodolithes/*Anabaena torulosa* is intermediate between the green algae and the cluster formed by dead structures, pavement and rubbles. The red algae stretch between *H. onkodes* and the cluster pavement/rubble. Other linear functions help to discriminate between the main clusters in Fig. 5. For instance, the group of brown algae (*Padina boryana*, *Turbinaria ornata*, *Sargassum* spp. and *Dictyota* spp.) can be separated using different LDFs (data not shown).

Airborne R_{rs} spectra and community-level discrimination

The parameters used to transform L_t into R_{rs} are provided in Table 5 for Moorea. They are of the same magnitude for Rangiroa (not shown). The range and spectral shape between 400 and 700 nm of the various correcting variables provided by the models are of minor influence. Spectral binning to match the CASI bandwidths also attenuates effects that could have an influence at higher spectral resolution. The small influence of the atmosphere is explained by the low altitude of the flight. Sky-reflected radiance is also a very small factor in consideration of the larger amplitude of the shallow targets (0 to 3 m). This warrants further sensi-
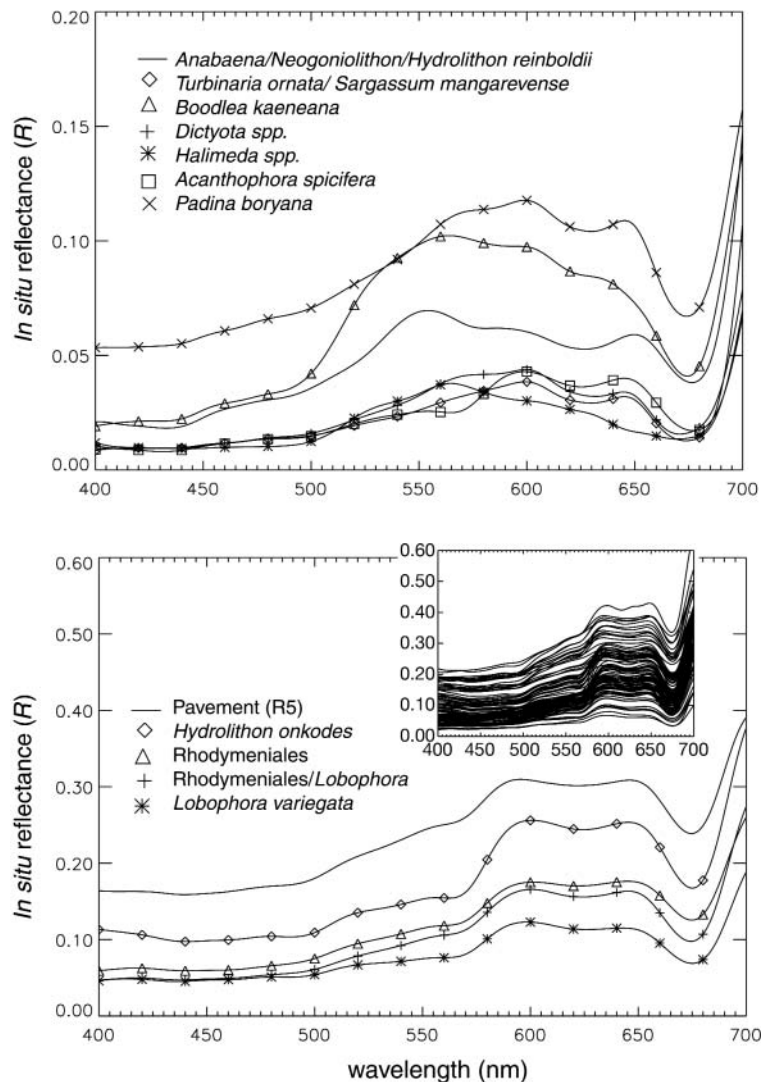

Fig. 4. Mean *in situ* reflectance spectra for some dominant algae in Table 2. Top: Moorea (see also Andréfouët et al. 2001 for rubble, pavement and turf spectra); bottom: Rangiroa. Note different ordinate scales. Each alga appears well separated by mean reflectances, but inset (representing all Rangiroa samples) highlights actual continuum of reflectance

Table 3. Wavelengths (nm) identified by stepwise selection of wavelengths (SSW) for *in situ* and CASI reflectance, for Moorea and Rangiroa. Last 2 columns show common wavelengths for *in situ* and CASI measurements

In situ reflectance		CASI reflectance		Common wavelengths	
Moorea + Rangiroa	Rangiroa only	Moorea	Rangiroa	(Moorea)	Rangiroa
699	700	691	699	645	682
688	684	675	694	630	665
664	664	660	688	584	614
644	658	645	682	554	592
628	612	630	671	539	580
606	594	615	665	450	535
584	578	599	654	406	
572	534	584	648		
554	456	569	614		
540	434	554	608		
518	400	539	592		
500		524	580		
475		509	568		
450		480	546		
432		465	535		
405		450	529		
		435	473		
		406	462		
			440		
			418		

Table 4. Overall accuracy (%) achieved in different configurations (full set and subset of wavelengths) for each site

Configuration	Moorea		Rangiroa	
	in situ	CASI	*in situ*	CASI
No. of classes	14 species	16 communities	5 species	14 communities
Full set of wavelengths	92.0% (16 bands)	90.9% (18 bands)	94.1% (11 bands)	83.5% (20 bands)
Subset common wavelengths	85.9% (7 bands)	86.1% (7 bands)	93.3% (6 bands)	76.4% (6 bands)

Table 5. Coefficients used to convert CASI total radiance to remote-sensing reflectance for Moorea image. See 'Materials and methods — Acquisition and processing of airborne CASI data' for parameter explanations

Wavelength (nm)	t	E_{ds} $W\,m^{-2}\,nm^{-1}$	E_d $W\,m^{-2}\,nm^{-1}$	r	L_{atm} $W\,m^{-2}\,nm^{-1}\,sr^{-1}$	L_{sky} $W\,m^{-2}\,nm^{-1}\,sr^{-1}$
406	0.992	0.301	0.963	4.086	0.00305	0.00146
421	0.993	0.283	1.004	4.206	0.00271	0.00134
435	0.993	0.265	1.032	4.309	0.00242	0.00122
450	0.994	0.289	1.230	4.430	0.00251	0.00130
465	0.995	0.270	1.253	4.607	0.00229	0.00117
480	0.995	0.249	1.250	4.706	0.00202	0.00105
494	0.996	0.227	1.225	4.757	0.00176	0.00095
509	0.996	0.210	1.219	4.813	0.00156	0.00087
524	0.996	0.193	1.200	4.875	0.00137	0.00079
539	0.996	0.183	1.216	4.950	0.00126	0.00074
554	0.997	0.170	1.203	5.017	0.00112	0.00068
569	0.997	0.158	1.185	5.035	0.00102	0.00063
584	0.997	0.143	1.136	5.043	0.00092	0.00057
599	0.997	0.133	1.112	5.051	0.00084	0.00052
615	0.997	0.128	1.134	5.059	0.00076	0.00051
630	0.998	0.119	1.106	5.068	0.00069	0.00047
645	0.998	0.110	1.066	5.075	0.00062	0.00043
660	0.998	0.100	1.020	5.078	0.00056	0.00039
675	0.998	0.097	1.032	5.078	0.00052	0.00038
691	0.998	0.081	0.904	5.078	0.00044	0.00032

tivity analysis, but it is unlikely that the influence of sky-reflected light will be as critical as it is for deep-water environments (Mobley 1999, Hu & Carder 2002).

R_{rs} spectra are provided in Fig. 6. Moorea spectra had shapes typical of shallow underwater targets due to water attenuation above 570 nm, while Rangiroa spectra showed very little water attenuation except for the pavement (R6) submerged at ~50 cm depth. Elsewhere, the communities were subsurface, which is typical of Tuamotu atolls' outer reef flats. Except for communities with a large proportion of sand or bare pavement, the spectra peak at 0.03 sr^{-1} around 575 nm. The shape of the deepwater R_{rs} spectrum (Fig. 7) is correct (e.g. Mobley 1999), with the chl *a* fluorescence peak at 680 nm visible on a log-scale plot. The range of values seems a bit high for Moorea, but is in agreement with spectra published for the same location (Maritorena & Guillocheau 1996). Rangiroa R_r spectra, computed at higher spectral resolution than Moorea, suggest a lack of accurate correction since atmospheric absorption features are visible. These artifacts can be attributable to a calibration problem (especially in the blue) or an underestimation of the atmospheric path radiance (also more critical in the blue).
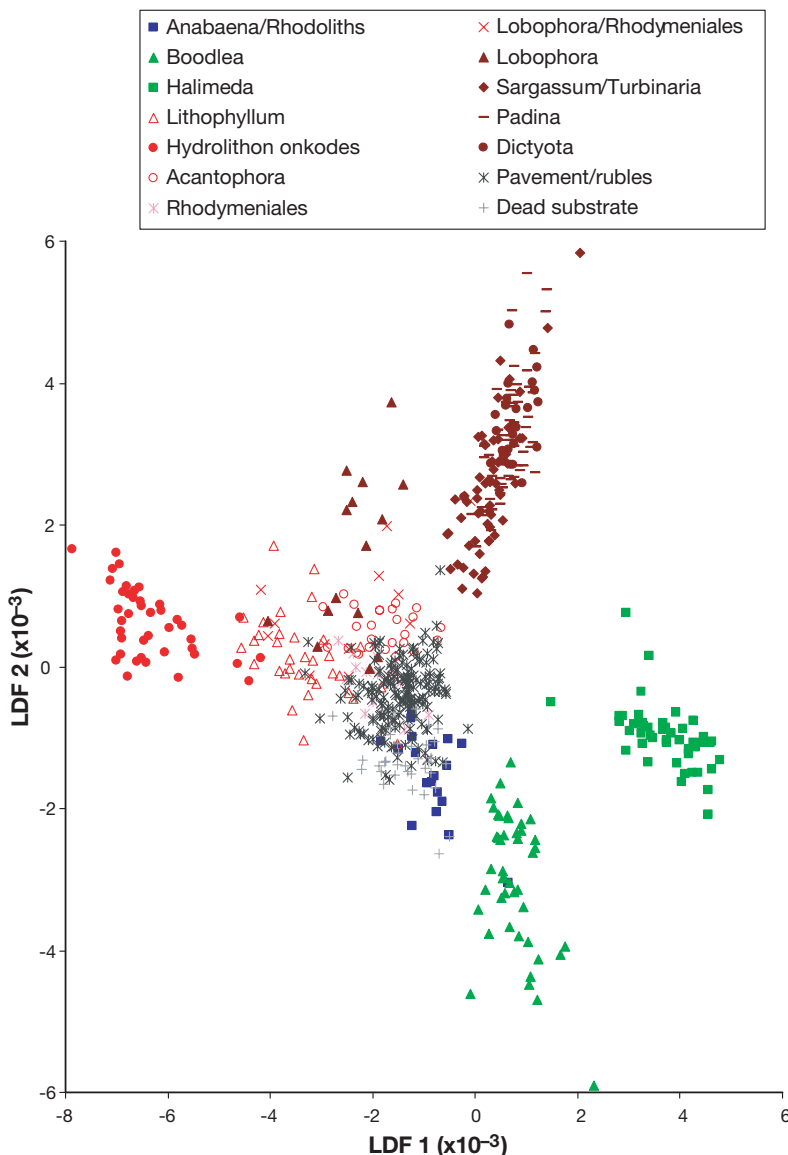
Fig. 5. Moorea and Rangiroa: 616 *in situ* reflectance spectra projected in plane formed by Linear Discriminant Functions (LDFs) 1 and 2, computed from 16 non-redundant wavelengths in Table 3. Full species names in Table 1

Comparisons between ranking of *in situ* reflectance and remote-sensing reflectance reveal different patterns (Figs. 4 & 6). For instance, *Lobophora variegata* is at the lowest range of *in situ* reflectance as a species, but is intermediate in R_{rs} as a community (R3). The opposite is found for *Hydrolithon onkodes*. This reflects the influence of background at the community scale. For instance, the *L. variegata*-dominated community (R2, Table 1) is brightened by the pavement in the background, while Community R1 (Table 1) is entirely covered by its dominant species *H. onkodes*.

For Moorea and Rangiroa CASI data, 18 and 20 wavelengths were identified respectively by SSW

(Table 3), providing classification accuracies of 90.9 and 83.5% respectively (Table 4). Discrimination of the 16 algae communities of Moorea is presented using the 3 first linear functions (Figs. 8 & 9). The third function is critical for separating the MB2 back-crest coral/algae assemblage, rich in corals (~25% cover), *Turbinaria ornata* and *Sargassum mangarevense*, from other locations dominated only by the same algae, such as the tops of large dead patches. In Rangiroa, all groups were clearly differentiated using only the first 2 linear discriminant functions. The apparent lower accuracy (83.5%) is explained by the fact that we have kept each ground-truthing site separate. Thus, similar communities overlapped (e.g. the 3 *Hydrolithon onkodes* sites: Fig. 10), and decreased the overall accuracy. The plots also show that mixed classes fall between the pure classes. This result encourages unmixing algorithms using spectral endmembers.

Robustness of spectral separability between species and community levels

Using only the subset of common non-redundant wavelengths identified in both *in situ* and CASI measurements, we observed excellent discrimination and classification accuracy between the algal groups at both sites. For Rangiroa, these common bands were centered at {682, 665, 614, 592, 580, 535 nm}. The overall accuracy of CASI spectra ranged from 83.5% down to 76.4% (Table 4). For Moorea, the key wavebands were centered at {645, 630, 584, 554, 539, 450, 406 nm}. Overall accuracy of CASI spectra decreased from 90.9% down to 86.1% (Table 4). The discrimination remained visually excellent for Rangiroa communities using the first 2 linear discriminant functions (Fig. 11 and Table 3). Conversely, 8 of the 16 Moorea communities suffered accuracy loss. The most significant degradation was for the MB2 back crest coral/algae assemblage (Fig. 2) with a loss of 15% accuracy, while the MB3 rhodolith patch (Fig. 2) decreased from 100% accuracy down to 66% (Fig. 12).

DISCUSSION

We used species-level spectra only for algae, and considered communities dominated by the same species. Under these conditions, our results suggest that
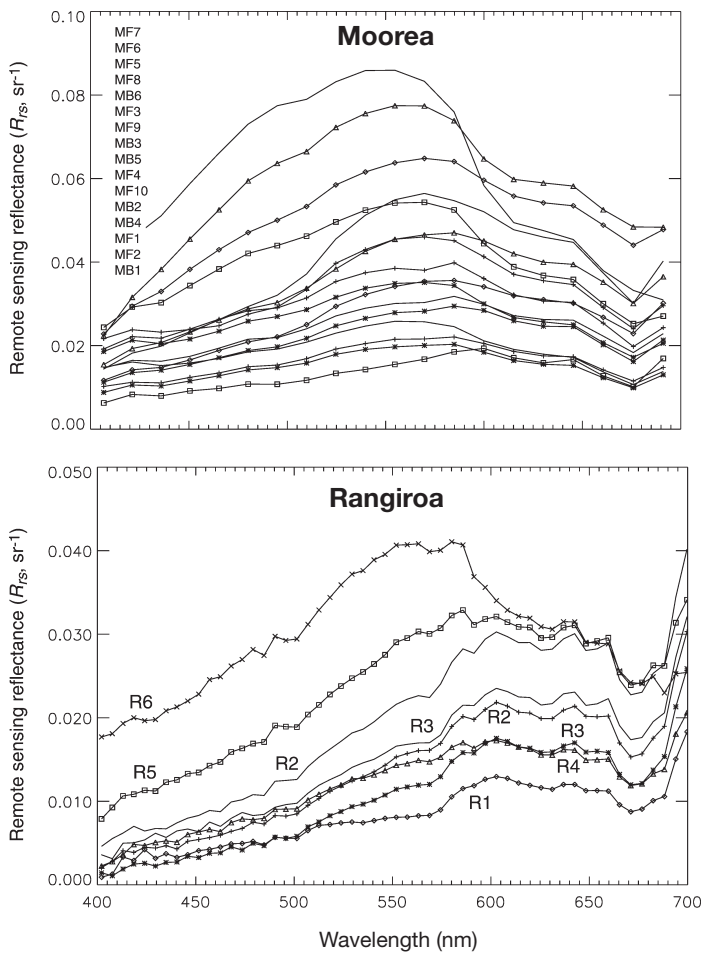
Fig. 6. Average CASI remote-sensing reflectance (R_{rs}) spectra for each community in Moorea (top graph) and Rangiroa (bottom graph); zones labeled as in Table 1. For Moorea, zones are listed by decreasing R_{rs} at 524 nm
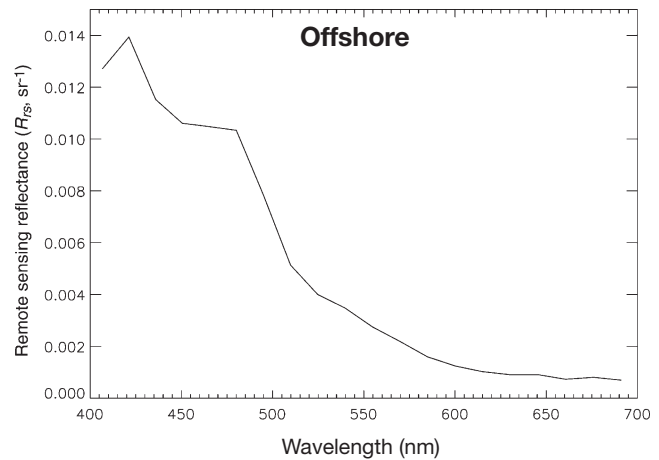

Fig. 7. Remote-sensing reflectance (R_{rs}) spectrum of deep, clear-blue waters offshore Moorea (see also Maritorena & Guillocheau 1996 for spectra from same location)

utilizing species-level reflectance to define wavebands and apply them directly for community-level discrimination using R_{rs} is effective, despite increased spatial heterogeneity and spectral mixing. Classification accuracies decrease when using fewer wavebands, but the rates remain excellent (Table 4).

The major caveat to generalizing our results would be the importance of the depth factor. Rangiroa results can be generalized with confidence to most Pacific atoll-rim communities, since coralline pavement communities occur mostly in shallow waters. On the other hand, results for more ubiquitous Moorea communities would be more questionable in deeper water. Several of the spectral bands identified at Moorea were longer than 600 nm and these would be less informative in water depths greater than few meters. For deeper waters, only wavebands that are still informative at depth could be used. Some degradation in the classification results could thus be expected, but Hochberg &

Atkinson (2000) showed that even with only 4 bands below 584 nm, results were acceptable, although they tested only the level of very ecologically broad communities (coral, algae and sediment). We emphasize that, despite the lack of bathymetric correction of the R_{rs} spectra, spectral scaling is effective, indicating that accurate bathymetric correction of R_{rs} data in the 0 to 3 m range of depth is not strictly necessary when using R data. However, beyond 3 m, it is likely that water correction will be required to improve the classification results (Purkis & Paterkamp 2004). Nevertheless, shallow-reef flats are very extensive in the Indo-Pacific areas. They represent, in terms of surface area, most of the productive coral reef system at many locations. In addition, they are likely to be more vulnerable to storms, bleaching, pollution or human activities. Therefore, they are prime targets for remote-sensing investigations, and our conclusion that depth correction can be omitted for these areas when using hyperspectral data is of potential importance.

Working at the ecological end-member level (corals, algae, sediments) has many conceptual merits. For instance, comparisons between sites are theoretically easier, since the end-members are ubiquitous. However, this approach, by systematically breaking the ecological system into 'atomic' units, may hide entities that have an ecological meaning only as a whole. For instance, modes in the inorganic or organic productivity of coral reefs have been expressed by Kinsey (1985) in terms of communities. Also, a large lone brown *Porites* sp. coral head, with some brown algae (*Turbinaria ornata*) on top, on a sandy bottom covering half a pixel may have the same mixed and unmixed signature as a pixel comprised of 50% sand and 50% numerous small rocks covered by the same algae and

Fig. 8. Moorea: 230 CASI remote-sensing reflectance projected in plane formed by LDFs 1 and 2, computed from 18 non-redundant wavelengths (Table 3); zones labeled as in Table 1. Poorly classified clusters correspond to mixed brown algae communities (e.g. coral-brown algae or turf-brown algae), and are close to end-member MB1 (algal crest, covered by brown algae *Turbinaria ornata-Sargassum mangarevense*) (see also Fig. 9). Full species names in Table 1; cyano: cyanobacteria
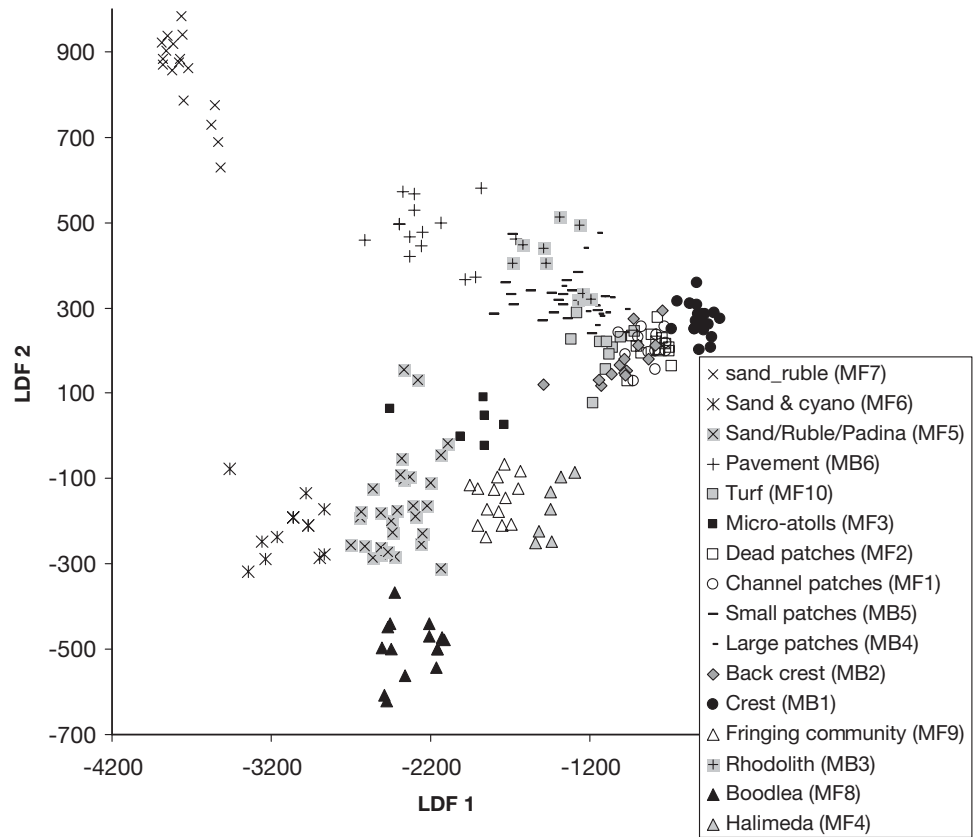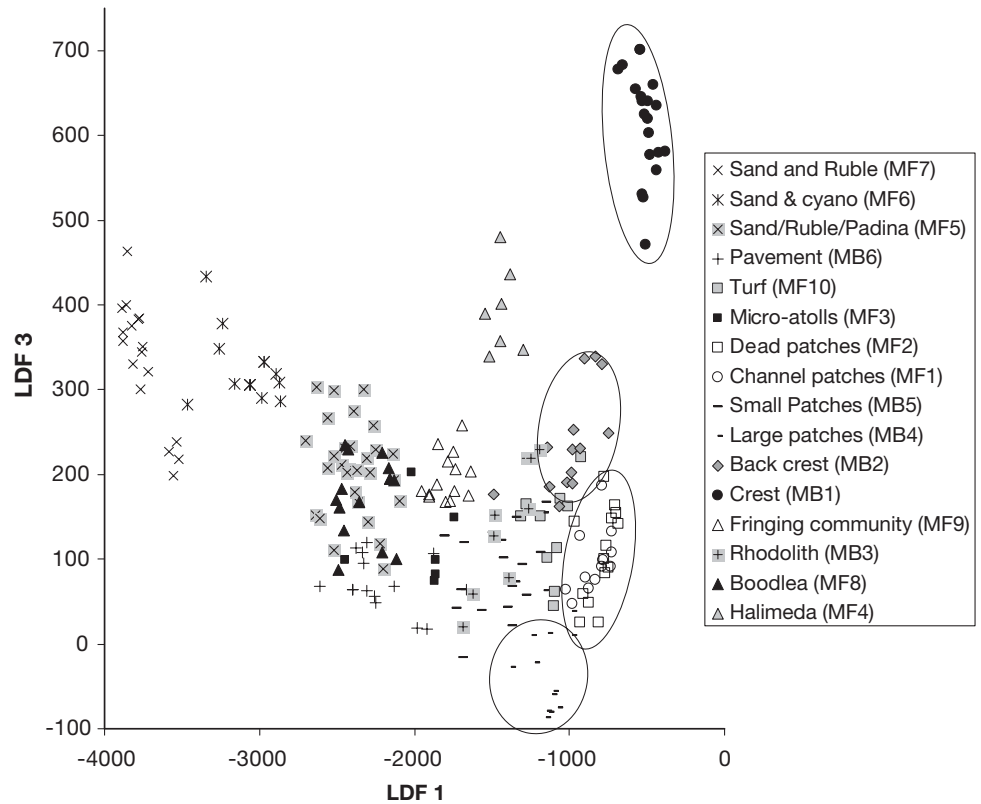

Fig. 9. Moorea: 230 CASI remote-sensing reflectance spectra projected in plane formed by LDFs 1 and 3, computed from 18 non-redundant wavelengths (Table 3); zones labeled as in Table 1. LDF 3 allows discrimination within mixed brown algae communities (see Fig. 8). Note separation achieved for MB2 (◆), area with highest coral cover on Moorea barrier reef; circled data points: groups poorly separated by LDFs 1 and 2 (Fig. 8). Full species names in Table 1; cyano: cyanobacteria
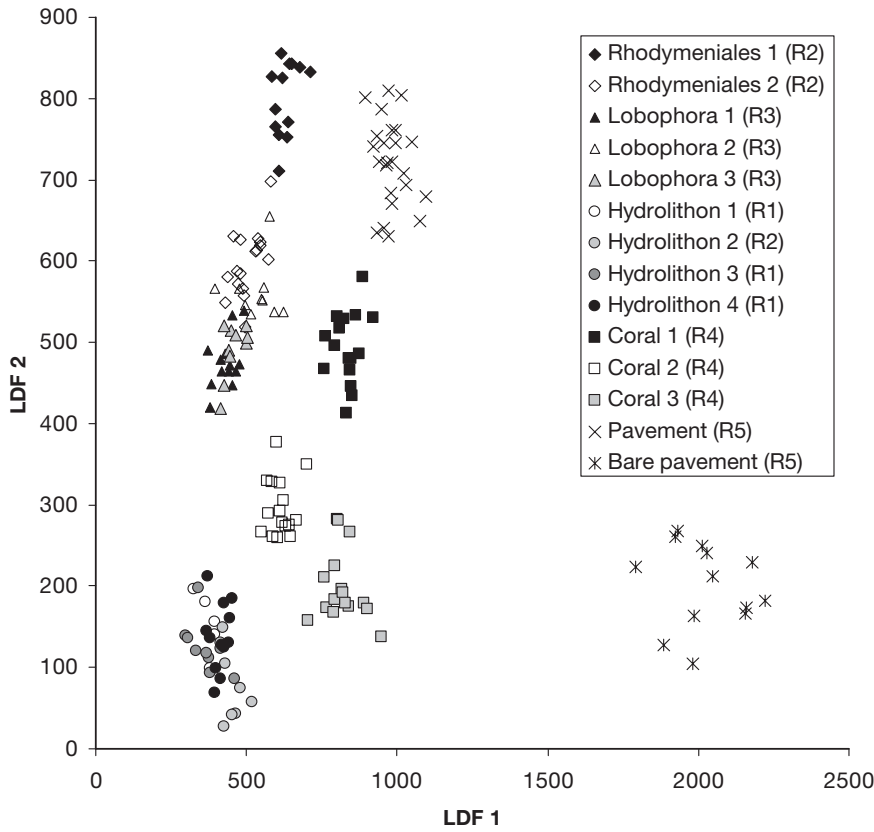
Fig. 10. Rangiroa: 182 CASI remote-sensing reflectance spectra projected in plane formed by LDFs 1 and 2, computed from 20 non-redundant wavelengths (Table 3). Zones and full species names in Table 1
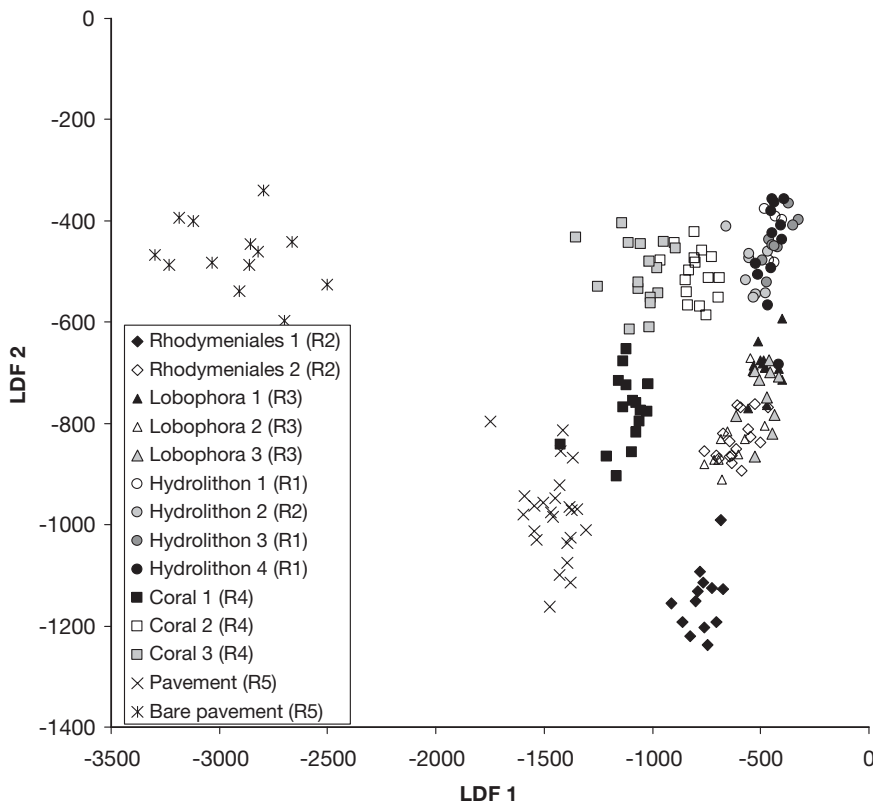

Fig. 11. Rangiroa: 182 CASI remote-sensing reflectance spectra projected in plane formed by LDFs 1 and 2, computed from 6 non-redundant wavelengths (Table 3). Zones and full species names in Table 1
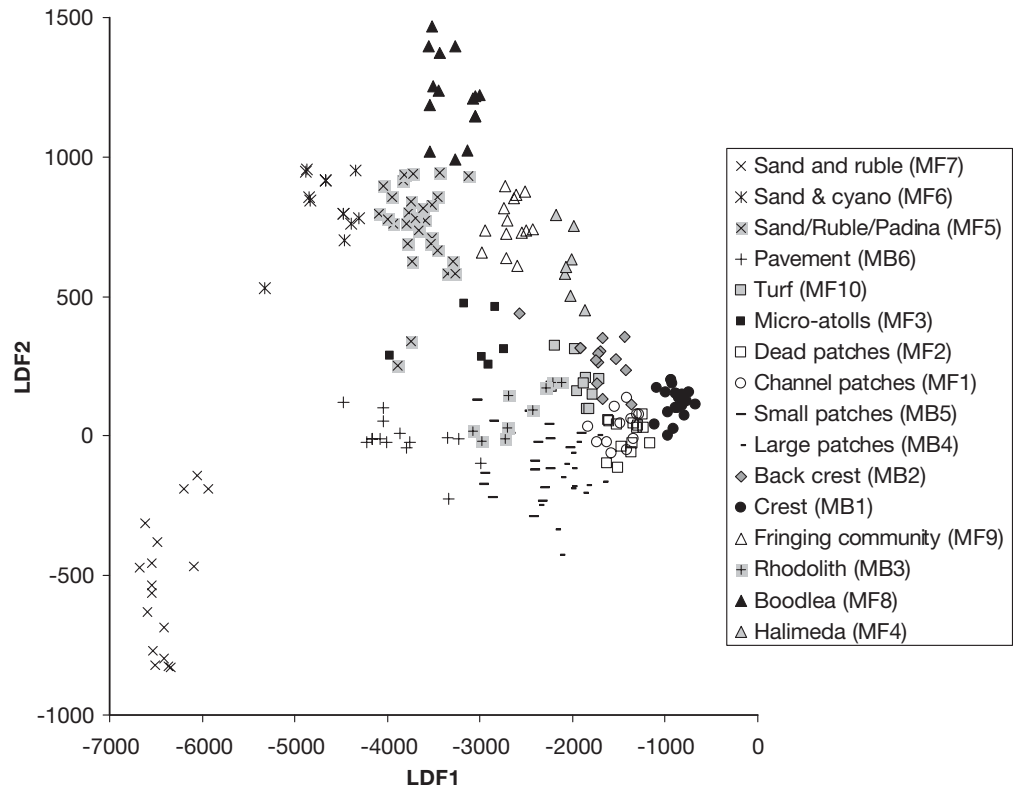
Fig. 12. Moorea: 230 CASI remote-sensing reflectance spectra projected in plane formed by LDFs 1 and 2, computed from 7 non-redundant wavelengths (Table 3). Zones and full species names in Table 1

encrusted by some brown *Montipora* spp. These 2 types of bottom do not have the same ecological functions within the reef system (e.g. as a habitat for fishes) and spectral unmixing will not differentiate the spatial arrangements of the end-members within a pixel. Thus, it may be more useful to try to differentiate them as a community or habitat-type.

For many ecological applications, we believe it is not necessarily useful to attempt to break the community into end-members. The community-level approach often implies a local classification scheme (or typology) requiring expensive costly and time-consuming field work, and the results for one locale are not comparable with those from another locale. Although we were recently faced with this fact in a multi-site evaluation of new space sensors for coral reef habitat mapping (Andréfouët et al. 2003), we nevertheless believe that the community-level approach may better highlight the specificities and reef processes of a particular site, which in itself may be of importance in a conservation context. For this reason, we believe that a knowledge of the spectral separability at the community level *and* at the end-member level are required for future reef-science applications. We believe that both scales are important, but because of the current advance in algorithm development, we also believe that at this stage reef science can take immediate advantage of integrated community-scale measurements.

We consider this a pilot study. It is an objective confirmation that it is possible to scale from species-level to community-level algorithms in the real world using real data, not simulations. However, similar tests need to be made. Inter-site comparisons taking their specific features into account are necessary to fully understand which methods work and what results can be consistently expected. We recently compared habitat classification results for 10 different sites representative of reef morphology and habitat types worldwide, using 4 m-resolution, spaceborne, multispectral data ('IKONOS images'). The pooled results show clear trends in accuracy, but local specificities are important and modulate the general trends (Andréfouët et al. 2003). Similar strategies should be applied for community-scale assessments using hyperspectral measurements. Nevertheless, the current study has demonstrated that using spectral libraries at the organism scale to interpret airborne imagery at the community scale is likely to provide accurate classification results, when the main species of the area covered by the imagery are present in *in situ* data.

CONCLUSION

Our goals were 2-fold: (1) operational remote-sensing application, to test the robustness of optical

criteria of separability between 2 ecological and spatial scales; (2) to increase our knowledge on the spectral discrimination of tropical algae species and communities from 2 French Polynesian reefs with very different structures. This study is the first to explicitly address the problem of spatial scaling of spectral measurements in shallow aquatic environments. Even if our results are considered local, they clearly suggest that it is possible and effective to generalize optical criteria from species level to community level, and thereby refine the design of hyperspectral missions, whether airborne or spaceborne. Rather than acquiring full-spectrum data, keying on pre-selected wavebands will provide better image signal-to-noise ratios and allow increases in spatial resolution. Similar to the global-scale comparative studies recently achieved at the species-level using *in situ* measurements (Hochberg et al. 2003) and at the habitat level using satellite images (Andréfouët et al. 2003), we suggest that a worldwide well-stratified study targeting the current 'missing link' (i.e. community scale) using airborne data is required to complete our knowledge of the optical properties of coral reefs. With this knowledge, the design of multi-scale space missions aimed at surveying and understanding coral reef functions and status will be greatly improved.

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