



Quantifying exceptionally large populations of *Acropora* spp. corals off Belize using sub-meter satellite imagery classification

¹ Geology Department,
Washington & Lee University,
204 W Washington St.,
Lexington, Virginia 24450.

² Geology Department,
Macalester College, 1600 Grand
Avenue, Saint Paul, Minnesota
55105.

³ Department of Biology & Earth
Sciences, Otterbein University, 1
South Grove Street, Westerville,
Ohio 43081.

⁴ Department of Geosciences,
Smith College, 44 College Lane,
Northampton, Massachusetts,
01063.

⁵ Department of Geography and
Environmental Sustainability,
University of Oklahoma, 100
East Boyd Street, Norman,
Oklahoma 73019.

* Corresponding author email:
<greerl@wlu.edu>.

James Busch¹
Lisa Greer^{1*}
David Harbor¹
Karl Wirth²
Halard Lescinsky³
H Allen Curran⁴
Kirsten de Beurs⁵

ABSTRACT.—Caribbean coral reefs have experienced dramatic declines in live coral cover in recent decades. Primary branching framework Caribbean corals, *Acropora cervicornis* (Lamarck, 1816) and *Acropora palmata* (Lamarck, 1816), have suffered the greatest collapse. Coral Gardens, Belize, is one of few remaining, and perhaps the largest, refugia for abundant, healthy, but undocumented populations of both *Acropora* species in the Caribbean Sea. In the present study, GeoEye-1 multispectral satellite imagery of a 25 km² reefal area near Ambergris Caye, Belize, was analyzed to identify live *Acropora* spp. cover. We used a supervised classification to predict occurrence of areas with live *Acropora* spp. and to separate them from other benthic cover types, such as sandy bottom, seagrass, and mixed massive coral species. We tested classification accuracy in the field, and new *Acropora* spp. patches were mapped using differential GPS. Of 11 predicted new areas of *Acropora* spp., eight were composed of healthy *Acropora* spp. An unsupervised classification of a red (Band 3):blue (Band 1) ratio calculation of the image successfully separated *Acropora* corals from other benthic cover, with an overall accuracy of 90%. Our study identified 7.58 ha of reef dominated by *Acropora* spp. at Coral Gardens, which is one of the largest populations in the Caribbean Sea. We suggest that Coral Gardens may be an important site for the study of modern *Acropora* spp. resilience. Our technique can be used as an efficient tool for genera-specific identification, monitoring, and conservation of populations of endangered *Acropora* spp.

Date submitted: 5 June, 2015.
Date accepted: 5 February, 2016.
Available online: 14 March, 2016.

Caribbean coral reefs have experienced significant decline in live coral cover in recent decades (Gardner et al. 2003, Bellwood et al. 2004, Carpenter et al. 2008, Miller et al. 2009, Eakin et al. 2010). The framework-building corals, such as *Acropora palmata* (Lamarck, 1816) and *Acropora cervicornis* (Lamarck, 1816), were prolific

throughout the Caribbean Sea during the Pleistocene and Holocene (Jackson 1992, Greenstein et al. 1998, Wapnick et al. 2004, Pandolfi and Jackson 2006, Greer et al. 2009, Riegl et al. 2009a). These key reef-building corals have experienced massive population decline since the 1980s and now rank among the most decimated of Caribbean scleractinians (Aronson and Precht 2001, Miller et al. 2002, Bruckner 2003, Vollmer and Palumbi 2007). Many researchers believe that *Acropora* spp. may not recover without active restoration efforts (Young et al. 2012). The mortality of *Acropora* corals has been attributed primarily to white band disease (WBD; Gladfelter 1982, Aronson and Precht 2001), or overfishing (e.g., Jackson et al. 2014), and susceptibility of *Acropora* spp. to WBD has been linked to recent increases in global sea-surface temperature (Bruno 2015, Randall and Van Woesik 2015). This drastic decline of *Acropora* spp. throughout the Caribbean led to *A. cervicornis* and *A. palmata* becoming the first two coral species listed as threatened under the US Endangered Species Act (NOAA 2005, NMFS 2006). Understanding the recent decline and lack of recovery of *Acropora* corals is important because in addition to being significant Caribbean reef-framework builders, the structural complexity and high growth rates of *Acropora* spp. make them ecologically valuable for western Atlantic marine ecosystems (Precht et al. 2010, Williams and Miller 2012).

Acropora corals survive in abundance in few remaining places (Aronson and Precht 2001, Miller et al. 2009). With rare exception, reports of extant *Acropora* spp. (*A. cervicornis* in particular) are limited to small, isolated, or non-reef building colonies. Vargas-Ángel et al. (2003) documented between 0.1 and 0.8 ha of non-reef forming *A. cervicornis* off Fort Lauderdale, Florida, with between 5%–28% live coral cover. Lidz and Zawada (2013) reported isolated small *A. cervicornis* colonies spaced over a large region (average of 0.002 colonies m⁻²) on Pulaski Shoal, Dry Tortugas, Florida, and Larson et al. (2014) reported *A. palmata* densities of 0.02–0.28 colonies m⁻² with high live coral cover off Veracruz, Mexico. Lirman et al. (2010) documented approximately 2 ha of prolific reef-forming *A. cervicornis* off northern Dominican Republic, perhaps the largest quantified population reported in recent years. Keck et al. (2005) reported the presence of extensive *A. cervicornis* populations at Smith Bank and Cordelia Shoal, Roatán, Honduras, which Purkis et al. (2006) and Riegl et al. (2009b) documented in greater detail using remote sensing techniques. In a short note, Macintyre and Toscano (2007) commented on the return of *A. palmata* to Belize, but to our knowledge, no efforts to quantify the extent of *Acropora* spp. off Belize have been published. With the exception of Purkis et al. (2006) and Riegl et al. (2009b), the studies above relied on video, photography, or field observations using a variety of underwater survey methods to characterize *Acropora* spp. populations. Colony or population size, where estimated, were determined by methods ranging from visual estimates to estimates from digital photography, or measuring tapes and handheld GPS (see also Walker et al. 2012). Other attempts to precisely document *Acropora* spp. cover in detail have been smaller in scale (e.g., Huntington and Miller 2014).

Coral Gardens (formerly also known as Mitchell Rocks) is located south of Ambergris Caye and north of Caye Caulker in the shallow (<7 m water depth) back reef off coastal Belize (Fig. 1). The Holocene abundance of *Acropora* spp. and the recent general decline of these corals off Belize have been well documented by Aronson et al. (2002, 2004). Anecdotal reports suggest *Acropora* corals were well established at Coral Gardens in the past (prior to the 1980s Caribbean die-off). It is unclear what

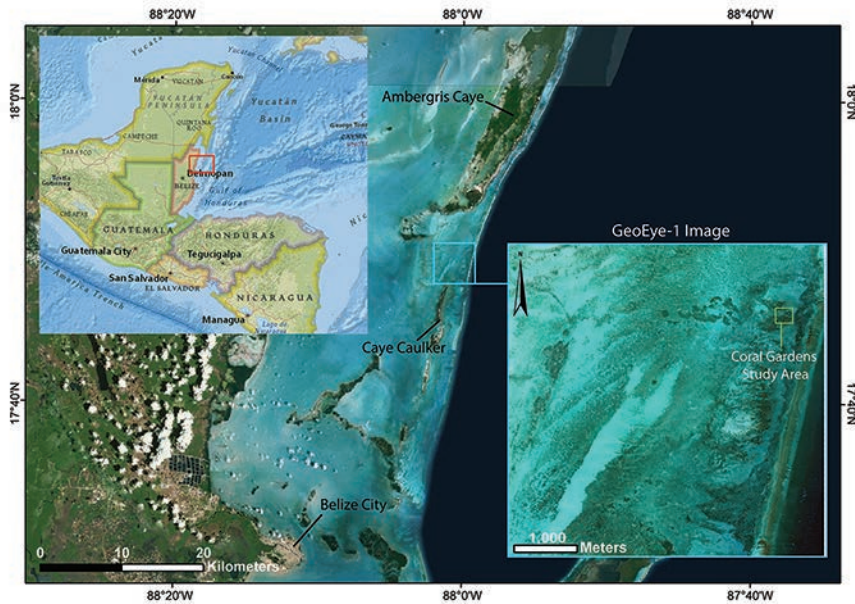


Figure 1. Location of Coral Gardens, Belize and the GeoEye-1 image of the area (outlined in blue). Basemap imagery courtesy of ESRI, DigitalGlobe, GeoEye, I-cubed, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, Swisstopo, the GIS User Community, National Geographic, DeLorme, HERE, UNEP-WCMC, NASA, ESA, METI, NRCAN, GEBCO, NOAA, Increment P Corp.

their extent has been in time or space, or the degree to which live *Acropora* spp. have declined in recent decades (K Mattes and M Gannon, Belize Marine TREC, pers comm; HA Curran, Smith College, pers comm). An extensive literature review suggests that no long-term studies of the abundance, extent, or persistence of *Acropora* spp. exist for Coral Gardens prior to a study by Greer et al. (2015) and associated short contribution papers. In that investigation, Greer et al. (2015) established five permanent survey transects across Coral Gardens and quantified live coral cover as well as additional habitat characteristics over a 4-yr period (2011–2014) using field observation techniques. Given the lack of high-resolution and larger-scale quantitative information on the spatial extent of endangered *Acropora* spp. at Coral Gardens and elsewhere, we suggest that a more efficient and reliable method for identifying and monitoring the few remaining *Acropora* reefs is critical for long-term protection of these now rare habitats.

Here, we develop a satellite imagery classification technique in ArcGIS®, which, with high accuracy, specifically identifies *Acropora* corals at Coral Gardens. Image classification is the process of extracting information about the spectral character of observed features. Two conventional methods for data extraction are supervised classification, where the operator defines the classes (features) to be identified in the imagery using “training areas” and unsupervised classification, where numerical methods break pixel values into clusters and automatically define classes in the image based on statistical relationships of pixel values, with no operator involvement (Aranoff 2005). One of the most common uses of image classification is to identify and/or differentiate objects or areas of interest in satellite imagery.

Landsat satellite imagery was first used for coral reef applications in the early 1970s (Smith et al. 1975). Subsequently, a multitude of new sensor platforms have been developed. Advantages and disadvantages of many of the platforms have been assessed for coral reef specific applications (Mumby et al. 2004). Techniques previously employed by others to characterize marine benthic habitats and coral reef communities include hand-held or boat-towed optical reflectance spectrometry and hyperspectral remote sensing (Holden and LeDrew 1998, Hochberg and Atkinson 2000, Hochberg et al. 2003, Louchard et al. 2003, Kutser and Jupp 2006, Suffianidris et al. 2009, Leiper et al. 2012), boat-based digital imaging (Lidz et al. 2008, Lidz and Zawada 2013), airborne and space imaging (Andréfouët et al. 2001, 2003, Mumby and Edwards 2002, Hochberg and Atkinson 2003, Rowlands et al. 2008, Mishra et al. 2006, Tamondong et al. 2013), combinations of optical reflectance spectrometry and airborne hyperspectral imaging (Leiper et al. 2014), combinations of spectral modeling and space imaging (Lubin et al. 2001), integrated satellite imagery and ecological time-series data (Purkis and Riegl 2005), and the multifaceted integration of satellite, aerial, ground, and acoustic methods (Purkis et al. 2008, Rowlands et al. 2012).

Airborne and satellite imagery are attractive ways to remotely identify and monitor coral populations. Diver-operated field surveys can be logistically challenging, costly, time intensive, or even impossible for remote, dangerous, or politically unstable locations. While remote sensing methods can have drawbacks as well (cost of image acquisition and water depth limitations, addressed later), they can significantly expand the spatial range of coral monitoring efforts. The spectral and spatial resolution, and cost of satellite or airborne platforms are all important to consider when choosing the best approach to map a particular reef site. For a researcher simply trying to distinguish coral from other bottom cover, the most important consideration is likely spatial resolution. Spatial resolution is particularly important to identify small populations of rare *Acropora* spp. in imagery. However, if the goal of the study is to differentiate specific species of coral and map their distributions, then spectral and spatial resolution both must be prioritized and the chosen sensor must be capable of resolving the spectral signatures of small species-specific areas. Relatively few studies have been specifically designed to distinguish *Acropora* spp. from other species of corals (Purkis et al. 2006, Collier and Humber 2007, Collin and Planes 2012), and the scientific literature provides no previous studies that aimed to do so using an easily replicated methodology with widely available proprietary software.

The purpose of this study was to: (1) quantify *Acropora* coral cover near Coral Gardens using GeoEye-1 imagery and ArcGIS® software; (2) devise a semi-exportable classification methodology for discriminating *Acropora* corals from other benthic cover that is user friendly, time efficient, and cost-effective; (3) document the largest quantified population of *Acropora* spp. in the Caribbean Sea to date; and (4) establish a baseline for long term monitoring at Coral Gardens for future studies that emphasize reef conservation and stewardship of endangered *Acropora* spp.

METHODS

LIVE ACROPORA CORAL COVER AT CORAL GARDENS.—Large populations of live *Acropora* spp. populations were identified for our study in the field at Coral Gardens in summer 2013. Five transects across large patches of living *A. cervicornis*, ranging from 12 to 35 m in length, were chosen from locations of dense shallow-water (<7

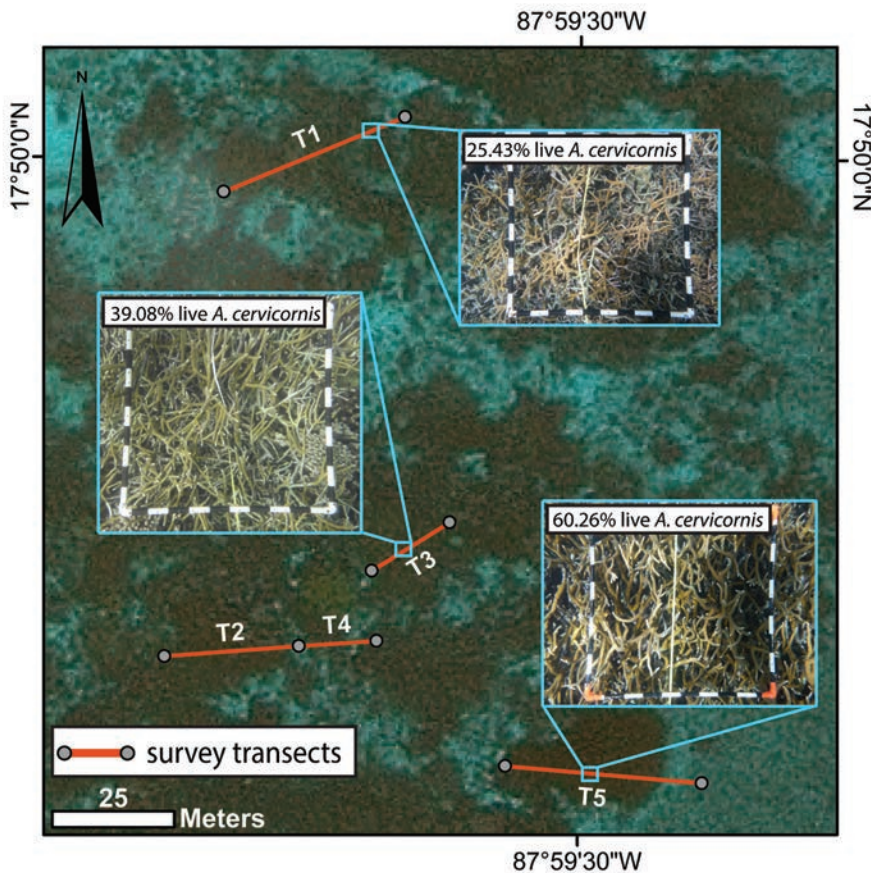


Figure 2. Locations of the survey transects from the Greer et al. (2015) study area with underwater photographs showing examples of calculated live *Acropora cervicornis* coral cover for 1 m² quadrats.

m depth) *Acropora* coral documented in diver surveys (Greer et al. 2015, and present study). *Acropora cervicornis* was virtually monospecific across all transects. Live *A. cervicornis* coral was assessed by quantifying live coral tissue coverage from 130 scaled photographs of 1-m² quadrats from the transects using ImageJ and MatLab (Fig. 2). The exceptional health and size of the *Acropora* spp. populations provided the motivation to acquire satellite imagery for the purpose of identifying additional, previously unidentified, *Acropora* spp. populations in the greater Coral Gardens region. The area of the longest transect, T5 (35 m), was used as a representative example of *Acropora* spp. coral cover for the initial image classification methodology described below.

INITIAL IMAGE CLASSIFICATION.—We chose GeoEye-1 multispectral satellite imagery of a 25 km² area near Ambergris Caye, Belize (collected 25 August, 2011), to analyze for live *Acropora* coral cover in the greater Coral Gardens region. The GeoEye-1 multispectral pansharpened imagery (from DigitalGlobe™) was selected because it is relatively inexpensive and has sub-meter spatial resolution (0.50 m). DigitalGlobe™ implemented the pansharpening and a standard geometric correction to the image.

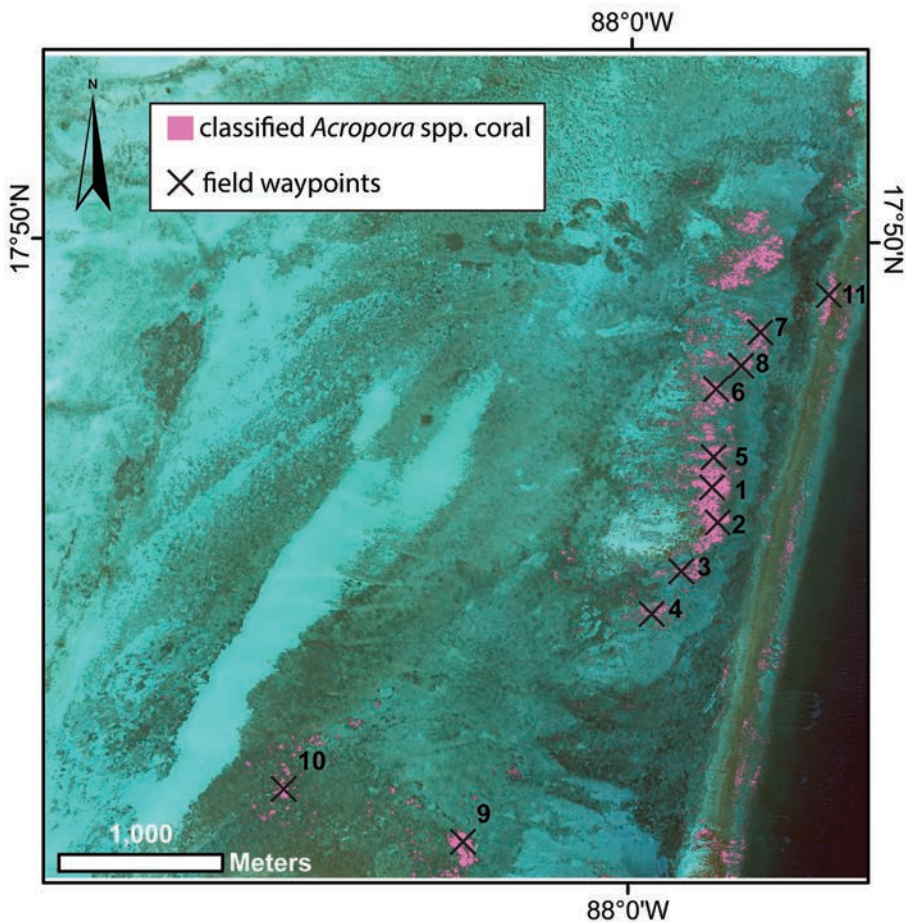


Figure 3. Locations of the 11 identified new areas of *Acropora cervicornis*, *Acropora palmata*, and *Acropora prolifera* that were ground-truthed (waypoints) during field assessment of the supervised classification.

The imagery has blue (450–510 nm), green (510–580 nm), and red (655–690 nm) visible light bands and one near IR band (780–920 nm). ArcGIS® was chosen for imagery analysis because it is a widely-available, full-feature GIS program. The image was not atmospherically corrected because such a correction requires more advanced proprietary software and image processing experience, and a goal of our study was to create an easily replicable method for non-specialists.

A supervised classification using red (Band 3), green (Band 2), and blue (Band 1) was chosen for the initial purpose of identifying *Acropora* spp. at Coral Gardens based on the populations of *Acropora* spp. previously surveyed and described above. Because we had quantitative data on live coral cover, these locations were the most obvious choice as training regions from the greater Coral Gardens region for the supervised classification. The training area for the supervised classification was drawn as a polygon across *Acropora* corals in the center of transect T5. For the purpose of visual comparison, training areas were also drawn as one polygon each in locations of other representative benthic cover: dense seagrass, moderate seagrass, light seagrass and sand, mixed coral species and seagrass, sand and rubble. These locations

were chosen solely based on interpretation of the visual appearance of benthic cover as they appeared in the image. We used the results of this classification to qualitatively identify 11 new potential areas dominated by *Acropora* spp. (Fig. 3). All potential sites of *Acropora* spp. were outside, and did not overlap our training area (T5) and did not overlap any of the locations of *Acropora* spp. surveyed by Greer et al. (2015).

FIELD VERIFICATION.—In 2014, snorkelers visited each of the 11 sites identified during initial classification and observed live coral cover, water depth, orientation of live coral, species of corals present, and height of the tallest live coral. Ground-truth points of newly documented *Acropora* corals were recorded using a Trimble GeoExplorer® XT 6000 differential GPS. Additional ground-truth points of non-*Acropora* spp. benthic cover, such as environments dominated by sparse seagrass, medium seagrass, dense seagrass, sandy bottom, and other mixed massive corals, were collected at eight sites using direct observation methods in the field to help refine the method of spectrally distinguishing live *Acropora* corals from other benthic cover. The GPS data were post-processed using Pathfinder Office® software with a differential correction from a reference base station in Quintana Roo, Mexico. The resulting horizontal precision is 0.1 to 0.4 m.

UNSUPERVISED BAND 3:BAND 1 IMAGE CLASSIFICATION.—Following the groundtruthing of the supervised classification in the field as described above, the classification scheme was refined to improve the accuracy of distinguishing *Acropora* corals from other benthic cover. The new classification scheme was designed to be completely independent from the initial supervised classification and any training area data so it could be replicated by other researchers attempting to identify *Acropora* spp. in new locations without previously collected field observations. The three *Acropora* spp. [*A. cervicornis*, *A. palmata*, *Acropora prolifera* (Lamarck, 1816)] are spectrally indistinguishable using our methods so they are treated at genus level in our study. The initial supervised classification successfully discriminated *Acropora* coral, but incorrectly identified some areas of seagrass and populations of mixed massive corals as *Acropora* spp. Therefore, *Acropora* coral, seagrass (primarily *Thalassia testudinum* K. D. Koenig and *Syringodium filiforme* Kützing), and mixed massive coral cover dominated by *Orbicella* spp., *Siderastraea* spp., *Agaricia* spp., and *Porites* spp. were identified as the most important benthic units for refining the classification scheme. The spectral signature of each benthic unit was extracted from the image, compared, and examined at ground-truth locations. The spectral signatures were generated by compiling statistics for each Band at the ground-truth locations, which included mean value, maximum value, minimum value, and standard deviation. Spectral response curves were also generated for each of the three benthic units using Exelis ENVI® software to visualize the spectral similarities and differences between *Acropora* coral, mixed massive coral species, and dense seagrass (Fig. 4). The three benthic units have very similar minimum, maximum, and mean values for Band 3, as well as similar spectral response curves, making them spectrally very similar. However, a unique inverse reflectance relationship between red Band 3 (655–690 μm) and blue Band 1 (450–510 μm) was observed in a spectral profile across a section of *Acropora* reef (Fig. 5). To capture the inverse relationship between Band 3 and Band 1 for *Acropora* spp., a Band 3:Band 1 ratio calculation was performed to examine whether the statistical relationship was specific to *Acropora* coral and could distinguish the *Acropora* coral from other types of coral and benthic

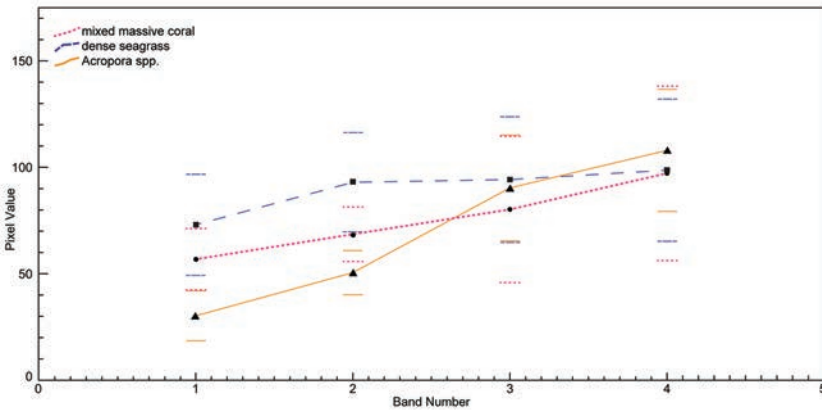


Figure 4. Spectral response curves generated for *Acropora* spp. coral, mixed massive coral species, and dense seagrass using the mean pixel values calculated within mapped reference areas for each benthic unit with error bars showing standard deviation.

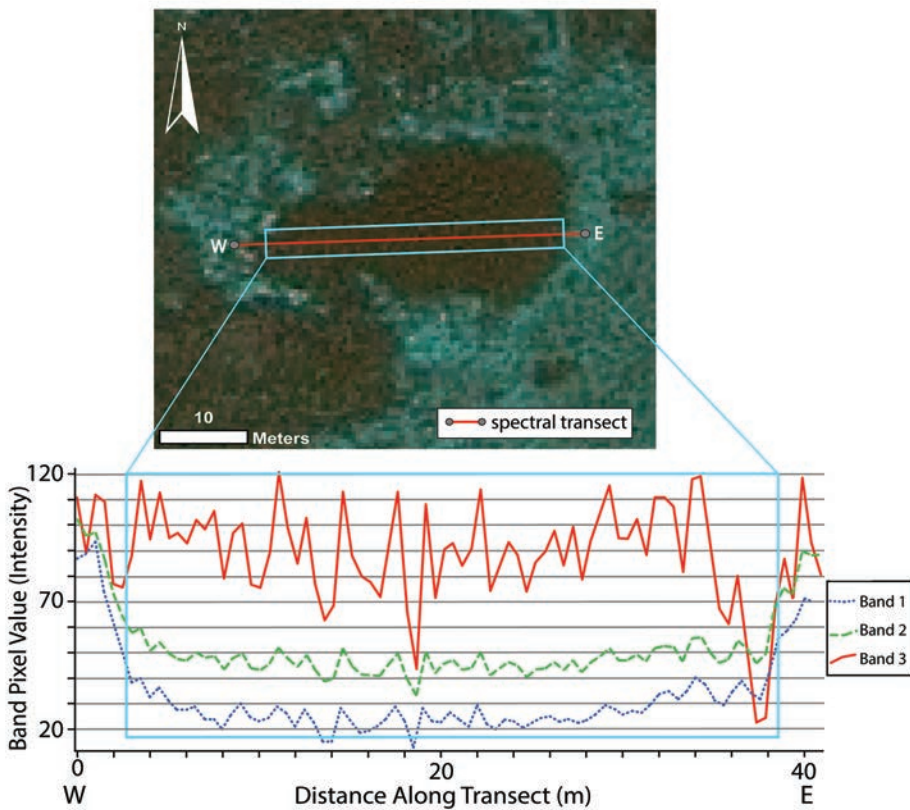


Figure 5. Pixel values for the blue, green, and red bands from a transect drawn across part of the study area by Greer et al. (2015) that has an average live *Acropora cervicornis* coral cover of 53.11% at T5.

cover. An ArcGIS “ISO Cluster” unsupervised classification (a modified iterative optimization clustering procedure) with a maximum of 50 classes was performed on the Band 3: Band 1 ratio image. Of the 49 classes produced, a single class populated the *Acropora* spp. reference areas [class number 49; range: 0.0161–0.5758, mean = 0.2866 (SD 0.0464)]. This result agrees with field observations that *Acropora* spp. have a distinct color from other corals and habitat, even underwater (e.g., Figs. 2, 6). Other band ratios and derived variables including principal components were attempted, but did not yield results that effectively discriminated *Acropora* spp. coral from the other types of benthic cover.

CLASSIFICATION ASSESSMENT.—The differentially corrected GPS ground-truth points for *Acropora* spp., mixed massive corals, and seagrass with underwater photography and the GeoEye-1 imagery to accurately map these single benthic units as polygons in ArcMap. These “reference areas” mapped as polygons around the ground-truth points formed the basis of a quantitative accuracy assessment of the supervised classification and ratio classification methods. The *Acropora* reference area was mapped as rectangles that included survey transects from Greer et al. (2015), as well as a polygon that encompassed the perimeter of the patch reef surveyed at transect T5 (Fig. 6A). The mixed massive coral reference area was the largest non-Acroporid stand of coral observed in the field (Fig. 6B). It was composed of mixed coral species dominated by large *Orbicella* spp., *Siderastrea* spp., and various brain corals, as well as smaller *Agaricia* spp., *Porites* spp., and *Millipora* spp., allowing the area to be easily identified and mapped in the imagery based on the GPS points and underwater photography that was collected in the field. The seagrass reference area was composed almost exclusively of dense seagrass growing on a featureless sandy bottom (Fig. 6C).

Because the seagrass reference area was significantly larger than the mixed massive coral and *Acropora* coral reference areas, we subsampled it so the area for accuracy assessment would be similar for the three reference areas and the larger dense seagrass reference area would not statistically skew results. To select a subset of the seagrass cells, we generated random raster cells within the area to produce an area equivalent to the mean size of the *Acropora* area and mixed massive coral areas. For the purposes of our study, we assumed that 100% of a given area was composed of its respective benthic cover in each mapped reference area. At Coral Gardens, average live coral cover is 29.85% (Greer et al. 2015, and the present study) and areas that were ground-truthed and mapped as coral also include small patches of macroalgae and dead coral rubble.

An error matrix shows the correct vs incorrect classifications for the initial supervised classification and the ratio classification and leads to calculations of the producer error (error of omission, type II error), consumer error (error of commission, type I error), overall accuracy, and \hat{k} statistic (Jensen 1996). Consumer error describes the probability that *Acropora* coral on the map will be correct, whereas producer error describes the probability that a reference area was correctly interpreted by the classification. The \hat{k} statistic provides a measure of classification accuracy adjusted for the probability that an entity was identified correctly by chance. The “overall accuracy” is the proportion of correctly classified pixels to the total number (Aranoff 2005). In the error matrix, seagrass and mixed massive coral reference areas are combined into a binary classification, yielding either *Acropora* spp., or non-*Acropora* coral.

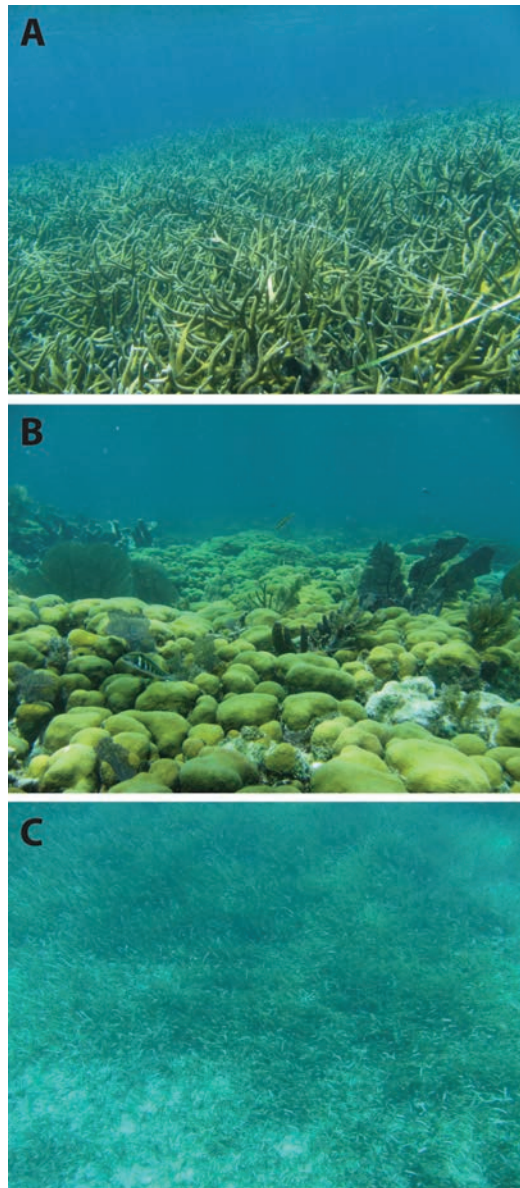


Figure 6. Underwater photographs of the reference areas for (A) *Acropora* spp. coral, (B) mixed massive coral, and (C) dense seagrass used in the accuracy assessment.

TOTAL AREA CALCULATION OF LIVE *ACROPORA* CORAL.—The total area of live *Acropora* coral reef was calculated by isolating the only class of the 49 classes produced from the ratio classification that populated the *Acropora* reference area. A depth criteria of 7 m was used to mask out erroneous classifications in deeper water (>7 m). The depth criteria was established by examining depth measurements collected by divers in the field and previously existing bathymetric maps. The total area was then calculated as the summation of all the classified *Acropora* pixels in the isolated class from the ratio classification. No minimum mapping unit was established

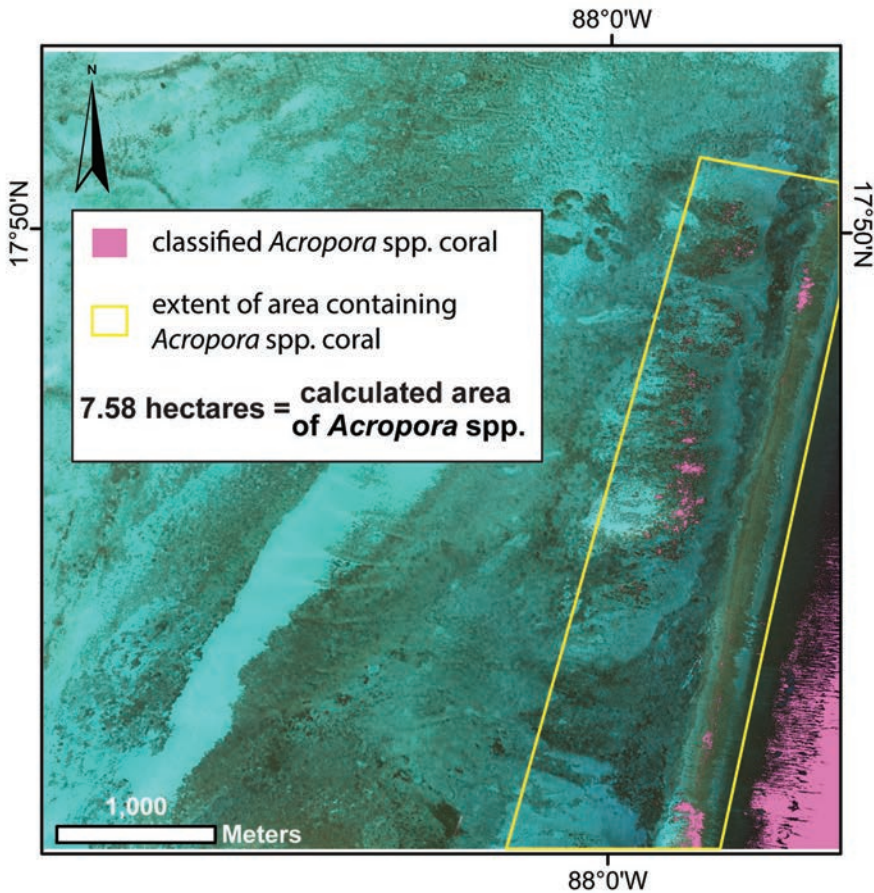


Figure 7. Total area of *Acropora cervicornis*, *Acropora palmata*, and *Acropora prolifera* coral contained within the yellow bounding box calculated from the ratio classification results. Note that the classified *Acropora* spp. outside the yellow box is falsely identified (in deep water) and was not counted in the 7.58 ha calculation.

because the accuracy assessment suggested an accuracy close to the map resolution (0.5 m) and many patches of live *Acropora* coral observed in the field were not much larger than several square meters.

RESULTS

The average live coral cover at Coral Gardens (living tissue in only two dimensions) from photographic data at T5 was 53.11% live monospecific *Acropora cervicornis* ($n = 35$ m² quadrats) with a range of 27.54%–64.33% live coral cover per quadrat. This number does not reflect the living coral below a two-dimensional surface cover. The remaining percent cover was composed of coralline and fleshy algae, bare coral skeletons, and empty or unresolved space (interior canopy).

We identified a total of 7.58 ha of living *Acropora* spp. in the shallow (<7 m depth) reef crest and back-reef area of Coral Gardens using our final unsupervised ratio classification method (Fig. 7). Most visually-assessed sites were dominated by *A. cervicornis*, but *A. palmata* was not uncommon. Water depth was assessed using

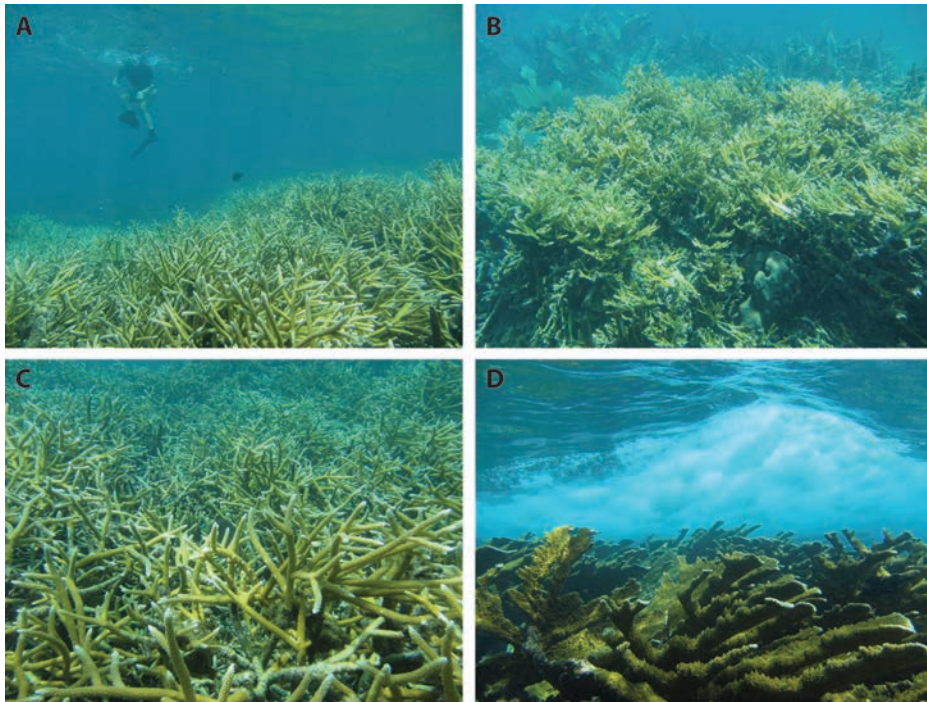


Figure 8. Dense *Acropora* spp. coverage discovered during the field assessment of the supervised classification. Locations are in UTM Northings and Eastings: (A) 394384.387, 1969991.250 (*Acropora cervicornis*); (B) 394524.711, 1971149.383 (*Acropora prolifera*); (C) 394564.166, 1971087.790 (*A. cervicornis*); (D) 395271.140, 1971685.381 (*Acropora palmata*).

bathymetric maps and field depth measurements of the reef crest and back reef areas. The deep water (>7 m, and offshore of the reef crest) false identifications in both the supervised classification and ratio classification were not used in abundance calculations or the accuracy assessment because they reflect limitations of satellite imagery and can be eliminated using a depth criteria of >7 m, although most false positive data are likely from significantly deeper areas. Therefore, the total *Acropora* spp. coral area calculation used here only included the reef crest (approximately 0 to 7 m depth, usually much shallower than 7 m) and shallow water patch reef areas (<7 m). Mapped shallow water populations based on the ratio classification show that *Acropora* corals populate a relatively thin but long stretch of the back reef and lagoonal area around Coral Gardens (Fig. 7). Ground-truthing revealed that the reef crest areas are dominated by *A. palmata*, but lagoonal areas are strongly dominated by *A. cervicornis* with some *A. palmata* (and the hybrid *A. prolifera*) present. Patches vary in connectivity, shape, and size. The largest patches are close to 2 ha in size and the smallest appear as scattered isolated patches of only a few square meters. Field assessment of the initial supervised classification led to the discovery of large and numerous previously-undocumented patches of *Acropora* coral (Fig. 8) proximal to 9 of the 11 areas visited for field verification of the supervised classification. *Acropora* spp. health and live coral cover at these sites appeared comparable to the original transect locations. Only two were falsely identified as *Acropora* spp. (Fig. 3), and consisted of large areas of seagrass. The supervised classification occasionally falsely grouped mixed massive coral with *Acropora* spp. and overestimated the size

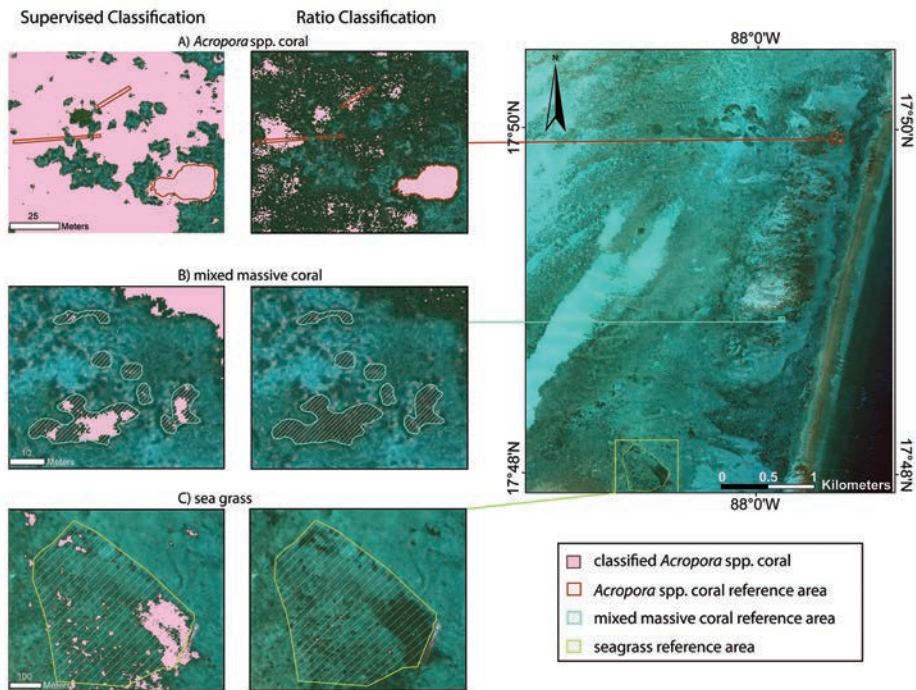


Figure 9. Comparison between the initial supervised classification and the ratio classification of *Acropora cervicornis*, *Acropora palmata*, and *Acropora prolifera* corals at each reference area.

of some *Acropora* patches (Fig. 9). Moreover, deeper water areas of the image were falsely classified as *Acropora* spp. (lower right, Fig. 7). The ratio classification eliminated false identifications of mixed massive coral and reduced false identifications in large areas of seagrass. However, in the northern area of dense *Acropora* coral, more patches of coral went unidentified.

The error matrices show that the ratio classification improved both overall accuracy and the \hat{k} percentage, but yielded mixed results for consumer and producer error for identification of *Acropora* coral (Table 1). The decreased consumer error in the ratio classification indicates that *Acropora* coral occurs in nearly 100% of the classified cells. However, the increased producer error in the ratio classification shows that more of the field-observed *Acropora* coral was missed than in the supervised classification. Despite the mixed results for consumer and producer error, the overall accuracy of the ratio classification for *Acropora* spp. coral was nearly 90%.

DISCUSSION

ACROPORA SPP. ABUNDANCE PROXIMAL TO CORAL GARDENS.—Our study quantified one of the largest extant *Acropora* spp. populations currently known in the Caribbean Sea. The 7.58 ha of mostly reef-forming *Acropora* spp. documented at Coral Gardens exceed the approximately 2 ha of *A. cervicornis* estimated to be present off the northern Dominican Republic coast (Lirman et al. 2010) and numerous other smaller, non-reef forming *Acropora* spp. populations documented by others (Vargas-Ángel et al. 2003, Walker et al. 2012, Lidz and Zawada 2013, Huntington and

Table 1. Error matrices for the (A) initial supervised classification and the (B) ratio classification. Consumer error (error of commission) is the probability that *Acropora* coral on the map will be correct and producer error (error of omission) describes the probability that a reference area was correctly interpreted by the classification. The \hat{k} statistic measures classification accuracy adjusted for the probability that a pixel was identified correctly by chance. The overall accuracy is the proportion of correctly classified pixels to the total number of pixels.

Reference area	Classified area		Total (m ²)	Consumer error	Producer error	\hat{k}
	Not <i>Acropora</i> coral (m ²)	<i>Acropora</i> coral (m ²)				
A. Error matrix for supervised classification						
Not <i>Acropora</i> coral	720.30	177.52	897.82	98.05%	80.23%	
<i>Acropora</i> coral	14.30	535.11	549.42	75.09%	97.40%	
Total	734.60	712.63	1,255.41			73.39%
Overall accuracy = 86.75%						
B. Error matrix for ratio classification						
Not <i>Acropora</i> coral	896.79	1.02	897.82	86.03%	99.89%	
<i>Acropora</i> coral	145.59	403.83	549.42	99.75%	73.50%	
Total	1,042.39	404.85	1,300.62			77.34%
Overall accuracy = 89.87%						

Miller 2014, Larson et al. 2014). *Acropora* spp. abundance at Coral Gardens may even rival total area coverage off Roatán, where extensive *A. cervicornis* reefs have been documented (Keck et al. 2005, Purkis et al. 2006, Riegl et al. 2009b). While our imagery analysis is only for one location, we hope it will serve as a template or starting point for additional *Acropora* spp. surveys in the future, including other locations.

IMAGERY CLASSIFICATION.— Field assessment results indicated that the initial supervised classification method was successful in identifying populations of *Acropora* spp. coral, but in some instances seagrass and mixed massive coral zones were misidentified as *Acropora* spp. (Fig. 9). This likely occurred because seagrass, mixed massive coral, and *Acropora* spp. coral have mean green (Band 2) and red (Band 3) values that are within the standard deviation, making them more likely to be grouped together by the ArcMap® maximum likelihood supervised classification algorithm (Fig. 4). The ratio classification method resulted in a significant decrease of false positive classification of seagrass and mixed massive coral as part of the *Acropora* spp. class, suggesting it successfully captures the unique difference in red Band 3 and blue Band 1 values of *Acropora* spp. While our ratio classification methodology is relatively straightforward and accessible to non-specialists, it did not falsely identify any habitats in the mixed massive coral reference area and successfully separated *Acropora* spp. from other coral types (Fig. 9). The ratio classification is also advantageous because it is a commonly-used technique that is easily applicable in a variety of software platforms.

It should be noted that part of the *Acropora* spp. training area polygon used for the initial supervised classification partially overlaps the reference area for *Acropora* coral used in the accuracy assessment. Therefore, the accuracy of the initial supervised classification for identifying only *Acropora* spp. is potentially biased due to the supervised classification automatically identifying the pixels within the training area as *Acropora* spp. However, because this reference area is the largest and most homogenous stand of *Acropora* spp. identified in the field, it still serves as the best

representative area to assess classification accuracy. Therefore, the accuracy calculated for the ratio classification should be the focus of the accuracy assessment, since the unsupervised classification operates completely independent from any operator identification of training areas and proves to be the most easily replicable and accurate method implemented.

The increase of false negative classification for the ratio classification method (producer error decrease from 97% to 74%) may reflect the inaccuracy of the null hypothesis for the *Acropora* spp. reference area, which states that 100% of the area is live coral cover. Although the reference areas are along transects with documented high density *Acropora* coral cover, coral cover is heterogeneous and some areas along transects have far lower live *Acropora* cover than the average at T5 of 53.11%. Areas of low live coral tissue abundance may result in less classified live *Acropora* spp. cover (Fig. 2). Therefore, the increase in false negatives for the supervised classification method may actually be a more accurate reflection of the amount of live *Acropora* cover. Given the inability to map live coral in the field with a high degree of spatial accuracy as well as the limit of spatial resolution in the imagery, it would be extremely difficult to assess the accuracy of the classification at such a fine scale.

All Coral Gardens *Acropora* spp. patches occurred at a water depth of no more than 7 m with little turbidity and surface waves. Our method cannot be assumed to be accurate for populations that live in deeper water due to the limitations of multispectral satellite imagery and the effects of light attenuation with water depth (see false identifications of *Acropora* spp. at depth in bottom right of Fig. 7). However, most documented reef-forming populations of *Acropora* coral are found at shallow water depths similar to Coral Gardens (Goreau 1959, Tunnicliffe 1981, Riegl et al. 2009a). Therefore, we suggest that our method, when constrained to shallow water habitats, could be effective for identifying *Acropora* spp. elsewhere in the Caribbean region. It is also important to note that environmental conditions of Coral Gardens are well suited to high-resolution satellite imagery acquisition because of minimal turbidity and relatively calm water conditions at this site. Also, the acquisition of GeoEye-1 imagery was such that the percent cloud cover (4%) was minimized and the sun angle elevation was ideal (66.65°) to produce a high-quality image. The quality of imagery acquired and subsequent classification attempts in areas of high turbidity, greater water depth, and higher wave activity might be less successful, but the use of a ratio classifier may reduce the impact of illumination, water depth, or turbidity. Other studies have developed successful tools to further decrease the impacts of reflectance and water column properties using more sophisticated techniques when water depth can be constrained (e.g., Purkis and Riegl 2005). Furthermore, because the image was not atmospherically corrected, it should be noted that if the imagery is not collected under similar ideal conditions in future studies, it could be subject to atmospheric noise that could degrade the effectiveness of the method.

The error matrices also show the tradeoff inherent between the initial supervised and refined ratio classification methods, with the initial supervised classification identifying more of the *Acropora* coral than exists in the imaged study area, and the ratio classification identifying the *Acropora* spp. more accurately (Table 1). We suspect many field researchers would prefer the map to more accurately show *Acropora* spp. even if about 10% is missing, rather than have a map with false positive identifications that would lead to wasted time in the field. Hence, the ratio classification

method may hold more value to field researchers trying to identify *Acropora* corals prior to a field study.

The purposes of our study were to document *Acropora* coral cover at Coral Gardens and to create an easily replicatable, time efficient, and inexpensive method for identifying *Acropora* spp. using remote sensing. We used methods commonly implemented in imagery analysis using ArcGIS® software, a widely available and user-friendly program, making our method more accessible to non-specialists. The present study successfully mapped possibly one of the largest accumulations of *Acropora* spp. documented in the Caribbean region today, quantifying >7.5 ha of living *Acropora* spp. reef habitat. We hope that our methods can be useful in quantifying *Acropora* spp. abundance at other Caribbean sites, particularly sites that are difficult to access and monitor on site. If preserving *Acropora* spp. habitat is a goal, our method might prove useful in future management of *Acropora* spp. reefs.

ACKNOWLEDGMENTS

This work was supported by the National Science Foundation under Grant No. NSF-REU #1358987 and the Keck Geology Consortium as well as the Washington and Lee University Department of Geology, Office of the Provost, and the R Preston Hawkins IV Geology Fund. We thank K Mattes and M Gannon at Belize Marine TREC for logistical support of this project. We are grateful for the support of the Belize Fisheries Department, M Alamilla of the Hol Chan Marine Reserve, and J Azueta of the Belize Ecosystems Management Unit for granting permission for this work. We thank three anonymous reviewers for thoughtful reviews.

LITERATURE CITED

- Andréfouët S, Muller-Karger FE, Hochberg EJ, Hu C, Carder KL. 2001. Change detection in shallow coral reef environments using Landsat 7 ETM+ data. *Remote Sens Environ.* 78:150–162. [http://dx.doi.org/10.1016/S0034-4257\(01\)00256-5](http://dx.doi.org/10.1016/S0034-4257(01)00256-5)
- Andréfouët S, Kramer P, Torres-Pulliza D, Joyce KE, Hochberg EJ, Garza-Pérez R, Mumby PJ, Riegl B, Yamano H, White WH, et al. 2003. Multi-site evaluation of IKONOS data for classification of tropical coral reef environments. *Remote Sens Environ.* 88:128–143. <http://dx.doi.org/10.1016/j.rse.2003.04.005>
- Aranoff S. 2005. *Remote sensing for GIS Managers*. Redlands, CA: ESRI Press. p. 58–61, 272–273.
- Aronson RB, Precht WF. 2001. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia.* 460:25–38. <http://dx.doi.org/10.1023/A:1013103928980>
- Aronson RB, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM. 2002. The expanding scale of species turnover events on coral reefs in Belize. *Ecol Monogr.* 72:233–249. [http://dx.doi.org/10.1890/0012-9615\(2002\)072\[0233:TESOST\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9615(2002)072[0233:TESOST]2.0.CO;2)
- Aronson RB, Macintyre IG, Wapnick CM, O’Neil MO. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology.* 85:1876–1891. <http://dx.doi.org/10.1890/03-0108>
- Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. *Nature.* 429:827–833. <http://dx.doi.org/10.1038/nature02691>
- Bruckner AW. 2003. *Proceedings of the Caribbean Acropora Workshop: potential application of the US Endangered Species Act as a conservation strategy*. Silver Spring, Maryland: NOAA Technical Memorandum NMFS-OPR-24. 199 p.
- Bruno JF. 2015. Marine biology: the coral disease triangle. *Nat Clim Chang.* 5:302–303. <http://dx.doi.org/10.1038/nclimate2571>
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortés J, Delbeek JC, DeVantier L, et al. 2008. One-third of reef-building corals face elevated

- extinction risk from climate change and local impacts. *Science*. 321:560–563. <http://dx.doi.org/10.1126/science.1159196>
- Collin A, Planes S. 2012. Enhancing coral health detection using spectral diversity indices from worldview-2 imagery and machine learners. *Remote Sens*. 4:3244–3264. <http://dx.doi.org/10.3390/rs4103244>
- Collier JS, Humber SR. 2007. Time-lapse side-scan sonar imaging of bleached coral reefs: a case study from the Seychelles. *Remote Sens Environ*. 108:339–356. <http://dx.doi.org/10.1016/j.rse.2006.11.029>
- Eakin CM, Morgan JA, Heron SE, Smith TB, Liu G, Alvarez-Filip L, Yusuf Y. 2010. Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS ONE*. 5:e13969. <http://dx.doi.org/10.1371/journal.pone.0013969>
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. *Science*. 301:958–960. <http://dx.doi.org/10.1126/science.1086050>
- Gladfelter WB. 1982. White-band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bull Mar Sci*. 32:639–643.
- Goreau TF. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology*. 40:67–90. <http://dx.doi.org/10.2307/1929924>
- Greenstein BJ, Curran HA, Pandolfi JM. 1998. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western north Atlantic and Caribbean province: a Pleistocene perspective. *Coral Reefs*. 17:249–261. <http://dx.doi.org/10.1007/s003380050125>
- Greer L, Lescinsky H, Wirth K. 2015. Multi-level characterization of acroporid coral populations at Coral Gardens, Belize: a refugia identified. Proceedings of the 28th Annual Keck Research Symposium. Union College, Schenectady, New York, USA. Available from: http://www.keckgeology.org/keckwp/wp-content/uploads/http://www.keckgeology.org/28th-keck-symposium-volume/28thSymVol_Belize_Greer.pdf
- Greer L, Jackson JE, Curran HA, Guilderson T, Teneva L. 2009. How vulnerable is *Acropora cervicornis* to environmental change? Lessons from the early to middle Holocene. *Geology*. 37:263–266. <http://dx.doi.org/10.1130/G25479A.1>
- Hochberg EJ, Atkinson MJ. 2000. Spectral discrimination of coral reef benthic communities. *Coral Reefs*. 19:164–171. <http://dx.doi.org/10.1007/s003380000087>
- Hochberg EJ, Atkinson MJ. 2003. Capabilities of remote sensors to classify coral, algae, and sand as pure and mixed spectra. *Remote Sens Environ*. 85:174–189. [http://dx.doi.org/10.1016/S0034-4257\(02\)00202-X](http://dx.doi.org/10.1016/S0034-4257(02)00202-X)
- Hochberg EJ, Atkinson MJ, Andréfouët S. 2003. Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing. *Remote Sens Environ*. 85:159–173. [http://dx.doi.org/10.1016/S0034-4257\(02\)00201-8](http://dx.doi.org/10.1016/S0034-4257(02)00201-8)
- Holden H, LeDrew E. 1998. Spectral discrimination of healthy and non-healthy corals based on cluster analysis, principal components analysis, and derivative spectroscopy. *Remote Sens Environ*. 65:217–224. [http://dx.doi.org/10.1016/S0034-4257\(98\)00029-7](http://dx.doi.org/10.1016/S0034-4257(98)00029-7)
- Huntington BE, Miller MW. 2014. Location-specific metrics for rapidly estimating the abundance and condition of the threatened coral *Acropora cervicornis*. *Restor Ecol*. 22:299–303. <http://dx.doi.org/10.1111/rec.12057>
- Jackson JBC. 1992. Pleistocene perspectives of coral reef community structure. *Am Zool*. 32:719–731. <http://dx.doi.org/10.1093/icb/32.6.719>
- Jackson J, Donovan M, Cramer K, Lam V. 2014. Status and trends of Caribbean coral reefs: 1970–2012. Washington: Global Coral Reef Monitoring Network.
- Jensen JR. 1996. Introductory digital image processing: a remote sensing perspective. Upper Saddle River, NJ: Prentice-Hall. 318 p.
- Keck J, Houston RS, Purkis S, Riegl BM. 2005. Unexpectedly high cover of *Acropora cervicornis* on offshore reefs in Roatán (Honduras). *Coral Reefs*. 24:509. <http://dx.doi.org/10.1007/s00338-005-0502-6>
- Kutser T, Jupp DLB. 2006. On the possibility of mapping living corals to the species level based on their optical signatures. *Estuar Coast Shelf Sci*. 69:607–614. <http://dx.doi.org/10.1016/j.ecss.2006.05.026>

- Larson EA, Gilliam DS, Padierna ML, Walker BK. 2014. Possible recovery of *Acropora palmata* (Scleractinia: Acroporidae) within the Veracruz Reef System, Gulf of Mexico: a survey of 24 reefs to assess the benthic communities. *Rev Biol Trop.* 62:75–84. <http://dx.doi.org/10.15517/rbt.v62i0.15903>
- Leiper I, Phinn S, Dekker AG. 2012. Spectral reflectance of coral reef benthos and substrate assemblages on Heron Reef, Australia. *Int J Remote Sens.* 33:3946–3965. <http://dx.doi.org/10.1080/01431161.2011.637675>
- Leiper IA, Phinn SR, Roelfsema CM, Joyce KE, Dekker AG. 2014. Mapping coral reef benthos, substrates, and bathymetry, using compact airborne spectrographic imager (CASI) data. *Remote Sens.* 6:6423–6445. <http://dx.doi.org/10.3390/rs6076423>
- Lidz BH, Brock JC, Nagle DB. 2008. Utility of shallow-water ATRIS images in defining biogeologic processes and self-similarity in skeletal scleractinia, Florida reefs. *J Coast Res.* 24:1320–1338. <http://dx.doi.org/10.2112/08-1049.1>
- Lidz BH, Zawada DG. 2013. Possible return of *Acropora cervicornis* at Pulaski Shoal, Dry Tortugas National Park, Florida. *J Coast Res.* 29:256–271. <http://dx.doi.org/10.2112/JCOASTRES-D-12-00078.1>
- Lirman D, Bowden-Kerby A, Schopmeyer S, Huntington B, Thyberg T, Gough M, Gough Y. 2010. A window to the past: documenting the status of one of the last remaining ‘megapopulations’ of the threatened staghorn coral *Acropora cervicornis* in the Dominican Republic. *Aquat Conserv: Mar and Freshwat Ecosystems.* 20:773–781.
- Louchard EM, Reid RP, Stephens FC, Davis CO, Leathers RA, Downes TV. 2003. Optical remote sensing of benthic habitats and bathymetry in coastal environments at Lee Stocking Island, Bahamas: a comparative spectral classification approach. *Limnol Oceanogr.* 48:511–521. http://dx.doi.org/10.4319/lo.2003.48.1_part_2.0511
- Lubin D, Li W, Dustan P, Mazel CH, Stamnes K. 2001. Spectral signatures of coral reefs: Features from space. *Remote Sens Environ.* 75:127–137. [http://dx.doi.org/10.1016/S0034-4257\(00\)00161-9](http://dx.doi.org/10.1016/S0034-4257(00)00161-9)
- Macintyre IG, Toscano MA. 2007. The elkhorn coral *Acropora palmata* is coming back to the Belize barrier reef. *Coral Reefs.* 26:757. <http://dx.doi.org/10.1007/s00338-007-0268-0>
- Miller MW, Bourque AS, Bohnsack JA. 2002. An analysis of the loss of acroporid corals at Looe Key, Florida, USA: 1983–2000. *Coral Reefs.* 21:179–182.
- Miller J, Muller E, Rogers C, Waara R, Atkinson A, Whelan KRT, Patterson M, Witcher B. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs.* 28:925–937. <http://dx.doi.org/10.1007/s00338-009-0531-7>
- Mishra D, Narumalani S, Rundquist D, Lawson M. 2006. Benthic habitat mapping in tropical marine environments using Quickbird multispectral data. *Photogramm Eng Remote Sensing.* 72:1037–1048. <http://dx.doi.org/10.14358/PERS.72.9.1037>
- Mumby PJ, Edwards AJ. 2002. Mapping marine environments with IKONOS imagery: enhanced spatial resolution can deliver greater thematic accuracy. *Remote Sens Environ.* 82:248–257. [http://dx.doi.org/10.1016/S0034-4257\(02\)00041-X](http://dx.doi.org/10.1016/S0034-4257(02)00041-X)
- Mumby PJ, Skirving W, Strong AE, Hardy JT, LeDrew EF, Hochberg EJ, David LT. 2004. Remote sensing of coral reefs and their physical environment. *Mar Pollut Bull.* 48:219–228. <http://dx.doi.org/10.1016/j.marpolbul.2003.10.031>
- NMFS (National Marine Fisheries Service). 2006. Endangered and threatened species: final listing determinations for elkhorn coral and staghorn coral. *Fed Regist.* 71:26852–26861.
- NOAA (National Oceanic and Atmospheric Administration). 2005. Endangered and threatened wildlife and plants; 12-month finding on a petition to list elkhorn coral, staghorn coral, and fused-staghorn coral as threatened or endangered. *Fed Regist.* 70:13151–13152.
- Pandolfi JM, Jackson JBC. 2006. Ecological persistence interrupted in Caribbean coral reefs. *Ecol Lett.* 9:818–826. <http://dx.doi.org/10.1111/j.1461-0248.2006.00933.x>
- Precht WF, Aronson RB, Moody RM, Kaufman L. 2010. Changing patterns of microhabitat utilization by the threespot damselfish, *Stegastes planifrons*, on Caribbean reefs. *PLoS ONE.* 5:e10835. <http://dx.doi.org/10.1371/journal.pone.0010835>

- Purkis SJ, Riegl B. 2005. Spatial and temporal dynamics of Arabian Gulf coral assemblages quantified from remote-sensing and in situ monitoring data. *Mar Ecol Prog Ser.* 287:99–113. <http://dx.doi.org/10.3354/meps287099>
- Purkis SJ, Myint SW, Riegl BM. 2006. Enhanced detection of the coral *Acropora cervicornis* from satellite imagery using a textural operator. *Remote Sens Environ.* 101:82–94. <http://dx.doi.org/10.1016/j.rse.2005.11.009>
- Purkis SJ, Graham NAJ, Riegl BM. 2008. Predictability of reef fish diversity and abundance using remote sensing data in Diego Garcia (Chagos Archipelago). *Coral Reefs.* 27:167–178. <http://dx.doi.org/10.1007/s00338-007-0306-y>
- Randall CJ, Van Woessik R. 2015. Contemporary white-band disease in Caribbean corals driven by climate change. *Nat Clim Chang.* 5:375–379. <http://dx.doi.org/10.1038/nclimate2530>
- Riegl B, Bruckner A, Coles SL, Renaud P, Dodge RE. 2009a. Coral reefs: threats and conservation in an era of global change. *Ann NY Acad Sci.* 1162:136–186. <http://dx.doi.org/10.1111/j.1749-6632.2009.04493.x>
- Riegl B, Purkis SJ, Keck J, Rowlands GP. 2009b. Monitored and modeled coral population dynamics and the refuge concept. *Mar Pollut Bull.* 58:24–38. <http://dx.doi.org/10.1016/j.marpolbul.2008.10.019>
- Rowlands GP, Purkis SJ, Riegl BM. 2008. The 2005 coral-bleaching event Roatán (Honduras): use of pseudo-invariant features (PIFs) in satellite assessments. *J Spatial Sci.* 53:99–112. <http://dx.doi.org/10.1080/14498596.2008.9635139>
- Rowlands GP, Purkis SJ, Riegl BM, Metsamaa L, Bruckner A, Renaud P. 2012. Satellite imaging coral reef resilience at regional scale: a case-study from Saudi Arabia. *Mar Pollut Bull.* 64:1222–1237. <http://dx.doi.org/10.1016/j.marpolbul.2012.03.003>
- Smith VE, Rogers RH, Reed LE. 1975. Automated mapping and inventory of Great Barrier Reef zonation with Landsat data. Ocean 75 conference record, Institute of Electrical and Electronics Engineers, Inc, New York.
- Suffianidris M, Jean KS, Zakariya R. 2009. Hyperspectral discrimination and separability analysis of coral reef communities in Redang Island. *J Sustainability Sci Manage.* 4:36–43.
- Tamondong AM, Blanco AC, Fortes MD, Nadaoka K. 2013. Mapping of seagrass and other benthic habitats in Bolinao, Pangasinan using Worldview-2 satellite image. *International Geoscience and Remote Sensing Symposium (IGARSS).* 6723091:1579–1582.
- Tunncliffe V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis*. *Proc Natl Acad Sci USA.* 78:2427–2431. <http://dx.doi.org/10.1073/pnas.78.4.2427>
- Vargas-Ángel B, Thomas JD, Hoke SM. 2003. High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. *Coral Reefs.* 22:465–473. <http://dx.doi.org/10.1007/s00338-003-0336-z>
- Vollmer SV, Palumbi SR. 2007. Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: implications for the recovery of endangered reefs. *J Hered.* 98:40–50. <http://dx.doi.org/10.1093/jhered/esl057>
- Walker BK, Larsen EA, Moulding AL, Gilliam DS. 2012. Small-scale mapping of indeterminate arborescent acroporid coral (*Acropora cervicornis*) patches. *Coral Reefs.* 31:885–894. <http://dx.doi.org/10.1007/s00338-012-0910-3>
- Wapnick CM, Precht WF, Aronson RB. 2004. Millennial-scale dynamics of staghorn coral in Discovery Bay, Jamaica. *Ecol Lett.* 7:354–361. <http://dx.doi.org/10.1111/j.1461-0248.2004.00586.x>
- Williams DE, Miller MW. 2012. Attributing mortality among drivers of population decline in *Acropora palmata* in the Florida Keys (USA). *Coral Reefs.* 31:369–382. <http://dx.doi.org/10.1007/s00338-011-0847-y>
- Young CN, Schopmeyer SA, Lirman D. 2012. A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and western Atlantic. *Bull Mar Sci.* 88:1075–1098. <http://dx.doi.org/10.5343/bms.2011.1143>



