DOCUMENTING DECADAL SPATIAL CHANGES IN SEAGRASS AND ACROPORA PALMATA COVER BY AERIAL PHOTOGRAPHY ANALYSIS IN VIEQUES, PUERTO RICO: 1937–2000

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ABSTRACT

Aerial photographs from 1937–2000 of Bahía Salina del Sur on Vieques, Puerto Rico were analyzed to detect and describe spatial changes in the areal cover of seagrass beds in Bahía Salina del Sur. The images were pre-processed to minimize noise and unsupervised classification was used to detect areas colonized by seagrass. The number of individual seagrass patches, direction, and characteristic of growth were quantified and described. Seagrass coverage increased by 85.8% over the 64-yr period and this increase was best described by a 2nd order polynomial function ($r^2 = 0.91$). Between 1937 and 2000, the spatial expression of the seagrass patchiness went through discrete episodes characterized by expansion in the number and spatial extent of small patches followed by an increase in patch size and agglomeration of small patches to form large homogeneous areas. Patch growth was limited only by proximity to boundaries (i.e., coastline and reef structures) and a fluctuating physical environment. This study suggests that the overall increase in seagrass cover was linked to the synergy of hurricane impacts, decrease in grazers, and the protective geomorphology of Bahía Salina del Sur. Decreases in areal cover only occurred in concert with known anthropogenic impacts.

Remote sensing by satellite imagery has been used extensively to develop thematic maps of benthic marine environments (Andréfouët et al., 2000; Purkis and Riegl, 2005). The even finer spatial resolution attained by aerial images makes them one of the best data sources for benthic habitat mapping and detection of change within habitats at scales of meters to tens of meters (Ekebom and Erkkilä, 2003; Chauvad et al., 1998; Mumby et al., 1998). However, as with satellite data, the spectral resolution of analogue aerial images is limited to the wavelengths detected by photographic emulsion or the digital sensor arrays (Chauvad et al., 1998), and the water absorption qualities. Consequently, aerial photography is only of value for benthic mapping in shallow waters (Pasqualini et al., 1999). Despite limitations in spectral resolution of archived analogue aerial imagery, it has repeatedly been proven successful for accurately mapping shallow coastal ecosystems (Armstrong, 1981; Yamano et al., 2000; Geerders, 2001; Lewis, 2002; Mumby et al., 2003). The combination of high spatial and temporal resolution, dating further back than any other air- or space-borne sensor, and the cost-effectiveness has allowed archived aerial photography to be used routinely to monitor changes in shallow marine environments with a high thematic accuracy (Ekebom and Erkkilä, 2003). Thus, aerial photography is often used for monitoring seagrass meadows (i.e., Armstrong, 1981; Dobson et al., 1995; Ferguson and Korfischer, 1997; Robbins, 1997; Pasqualini et al., 1999; Diersen & Zimmerman, 2003; Kendall et al., 2004; Dekker et al., 2005). Nonetheless, as with any other sensor, the development of a time-series is constrained by the availability of imagery and is only possible in areas of particular historical interest.
For the past six decades, approximately 75% of Vieques has been utilized as a U.S. Navy training facility. Aerial imagery of the area has been periodically acquired for the U.S. Navy since the 1930s. Preliminary examination of the dataset revealed an increase in area covered by seagrass meadows. Although these analogue aerial images do not provide much spectral information, they nonetheless provide the temporal resolution required to detect and document shifts in spatial patterns of seagrass and reef structures. In 2003, the U.S. Navy withdrew from Vieques and transferred the lands to the Vieques Department of Interior, and as part of the memorandum agreement, the lands were declared a National Wildlife Refuge (NWR).

Managed by the US Fish and Wildlife Service, the Vieques NWR has become the largest NWR in the Caribbean. This area represents a unique study site to: (1) evaluate the usefulness of historical aerial imagery, (2) appraise the biota that can be reliably discriminated using aerial imagery of variable quality (1937–2000), (3) quantify the changes in spatial cover of the benthic biota in Vieques over eight decades, and (4) provide an understanding of the spatial changes in benthic habitats to be used as a guideline in future management plans. This study analyzes and compares the acquired data with two different approaches: a user-delineated and an automated process.

**Materials and Methods**

**Study Location.**—Vieques (18°7′54.55″ N, 65°25′11.03″ W) is the larger (34 × 5 km) of two island-municipalities of Puerto Rico, located in the northern Caribbean Sea 20 km off the eastern end of Puerto Rico (Fig. 1). The climate is tropical maritime, exhibiting small seasonal variations. Rainfall is influenced by topography and major rainfall occurs during the summer months (May–November) when precipitation is caused mainly by disturbance embedded in the generally east-to-west trade winds (Daky et al., 2003). During this period, tropical storms and hurricanes bring the greatest amount of rainfall.

From 1941 to 2003, approximately 75% of Vieques Island was used as a military training facility by the U.S. Navy, U.S. Marine Corps, and other NATO countries. In 1941, the U.S. Navy divided the island into three main regions: the eastern side of Vieques became the Atlantic Fleet Weapons Training Facility (AFWTF), the western part the Naval Ammunitions Facility (NAF) and the center portion remained under civilian jurisdiction (Fig. 1).

The eastern most part of the AFWTF was used as testing ground for bombs, missiles, and other weapons. The activities in this area, the Live Impact Area (LIA), triggered a number of civilian and legal accusations against the U.S. Navy for environmental violations and maintaining their bombing range (Raymond, 1978; Antonius and Weiner, 1982; Rogers et al., 1983). Most of the damage inflicted by the military practice on land occurred in the LIA. A number of studies performed in this area affirm that the military practices negatively affected the benthic biota surrounding the LIA (i.e., Rogers et al., 1978; Porter, 2000), while others studies contradict this conclusion (i.e., Raymond, 1978; Dodge, 1981; Antonius and Weiner, 1982).

The study site at Bahía Salina del Sur, was selected because it is inside the LIA, resulting in a relative abundance of aerial images. The relatively arid climate in this part of the island allows for clear waters which are ideal for remote-sensing. Bahía Salina del Sur is a shallow crescent-shaped bay surrounded on land by mangrove patches, high cliffs and sandy beaches (Fig. 2). Inside the bay a dense seagrass community, composed mainly of *Thalassia testudinum* Banks & Soland. ex Koenig (turtle grass) and coral patch reefs, is enclosed by a fringing coral reef system. In the west and south of the bay *Acropora palmata* (Lamarck, 1816) stumps fringe Cayo Conejo, Roca Alcatráz, and the southeast corner of Cerro Matías. *Porites porites* (Pallas, 1766) in association with scattered *A. palmata* corals fringe the north portion of the bay. Most of this fringing reef system is presently composed of coral skeletal remains and rubble.
Aerial Images.—Archive aerial imagery dating from 1937, 1959, 1962, 1975, 1983, 1994, and 2000 were provided by the Vieques US Fish and Wildlife Service in digital format. The only information included with the images was the year of acquisition, resolution, and geo-information. The sensor, spectral resolution or even season of acquisition was unknown. This represents a significant drawback which prohibits the effective application of any radiometric, atmospheric, or water column corrections, especially important in areas such as seagrass beds where the bottom reflectance is influenced strongly by the spectral properties of the surrounding sediments (Armstrong, 1993), variable water depth, and water properties.

The quality of the seven images and characteristics (some monochromatic) varied from year to year. Earlier images were digitalized with a high resolution scanner to an 8 BIT resolution to maintain comparability with the rest of the data set. The images were also resized to the 7.5 km² study area and re-sampled to a 1 m pixel spatial resolution (cursor resolution of the data set). The images were enhanced by a histogram equalization technique and a rank-order filter. The rank-order filter is a special case of a median filter that removes salt and pepper noise and allows the user to choose the median of a nonrectangular mask (Ahmad and Sundararajan, 1987). A 10 × 10 pixel mask was applied to each image to reduce the noise and to significantly enhance the imaged seabed-characteristics of each scene (Fig. 3). The histogram equalization and filtering considerably removed the noise and visually enhanced the images. However, due to the sub-optimal quality of the earlier monochrome images, minor confusion between seagrass patches, deep sand, and patch reefs was encountered. Expert knowledge was used to assist the differentiation process. To further reduce the amount of confusion, a mask was applied to the image to “switch-off” everything except the area inside the bay, reducing the amount of necessary classes. NOAA benthic shapefiles were used to build a mask in which
only non-reefal areas inside the bay were classified (http://biogeo.nos.noaa.gov/products/benthic/htm/data.htm) (Fig. 2).

In this study seagrass meadows are defined as a vegetated marine area colonized primarily by *T. testudinum*, secondarily by *Syringodium filiforme* Kuetz. in association with algae (i.e., *Halimeda* sp., *Udotea* sp., *Turbinaria* sp., *Penicillus* sp., and *Stypopodium zonale* (Lamouroux) Howe. To quantify the increase and decrease of seagrass meadows, a k-means classification was applied to separate seagrass pixels from the surrounding sandy area pixels. Due to the differences in image noise and color, expert knowledge of the area was used to determine the classification threshold for each image. Two different processes were followed to convert the seagrass class into discrete patches: (1) a user-delineated process in which the vectors were hand drawn (Fig. 4), and (2) an automated process coded in MATLAB® (Fig. 5), in which the classified image was converted to binary form by merging all classes identified as seagrass (sparse to dense) into a single class assigned a one-value and the surrounding substrate and other non-seagrass biota to a zero-value. The number of discrete patches was determined by calculating pixel connectivity. A pixel was identified as belonging to a patch if it was connected both to a substrate (zero-value) and a seagrass (one-value) pixel. The mean area cover for each image was plotted against year to determine the trajectory of the overall change.

Classification results and interpretations were rigorously ground-truthed against a series of 700 geo-referenced control sites. These sites consisted either pf GPS-stamped photographs or spot-observations that recorded information directly relevant to the classifications (i.e., seafloor type, percentage of live coverage as relevant to spectral characteristic, species identification).
Results

Seagrass Meadows.—The area covered by seagrass increased 85.84% over the 64-yr period of study. The overall increase was characterized by 2nd order polynomial growth of 0.64 km$^2$ from 1937 to 2000 ($r^2 = 0.91$). If the period is analyzed in two sections, seagrass cover increased exponentially from 1937 to 1964 (Fig. 6). The 1975 image represents one of the two periods in which a decrease in area cover was detected (15% decrease from 1964). After 1975, the increase in seagrass areal cover was re-established and it continued its polynomial increase. Maximum cover (0.84 km$^2$) was attained in 1994, and approached the total holding capacity of the bay (1.11 km$^2$), considered to be the entire sandy, subtidal area of the bay, Fig. 4). A second decrease of 12.29% was quantified in 2000, at which time seagrass meadows constituted 66.88% of the 1.11 km$^2$ study area inside Bahía Salina del Sur.

Figure 3. The same image (A) before and (B) after noise reduction. The rank-order filter removed salt and pepper noise and significantly enhanced visibility of the seabed. Some confusion was still present in those areas affected by glinting and stitching artifacts.

Figure 4. Images were de-noised and then classified by an unsupervised k-means process. The resulting thematic maps were employed to draw polygons (maroon in image) around dense and dense–sparse seagrass patches. Seagrass areal cover increased during most of the study period, decreasing only in 1975 and 2000. The 1975 image is concurrent with the deployment of the USS Killen (arrow). Live coral cover (indicated by arrow) present in the *A. palmata* reef apparent in 1962, began to decrease in 1975 and completely disappeared by 1994. A thin band of dead *A. palmata* overgrown by algae appears in the reef fringing Roca Alcatráz in 1983 and spread throughout the *A. palmata* zone in the following years.
In addition to total area cover, the number and mean size of individual seagrass patches was calculated using the results returned by the automated delineation of habitat (Fig. 5). A patch was defined as pixels diagonally adjacent, as well as pixels in the same row or column that represented discrete seagrass units (as in Purkis et al., 2005). Relating patch size to frequency of occurrence revealed that large patches were rare and small patches were common, as is commonly observed in fragmented habitat landscapes (Connell and Keough, 1985; Li, 2000).

As seagrass area increased through time, the number of small patches (< 100 m\(^2\)) decreased and the number of medium size patches (100–1000 m\(^2\)) increased. The increase in frequency of medium size patches was due to the merging of smaller patches; the same occurred as medium size patches merged to increase the size of a larger patch.

**Coral Reefs.**—The time series revealed two key changes in coral reef cover inside Bahia Salina del Sur. Early in the time series (most apparent in 1962), the seaward side of the *A. palmata* reef, also referred to as the S5 reef in previous studies (Antonius and Weiner, 1981; Raymond, 1978) and S1 by Dodge (1981), showed a distinctive healthy, dense live coral reef band (Fig. 4: 1962 arrow). This area of live coral decreased drastically by 1975, disappearing completely by 1983. In the south, the...
mono-specific *A. palmata* reef fringing Roca Alcatráz developed into a band of dead *A. palmata* stumps overgrown by algae on the deeper landward side of the island. This band of algae continued to spread to shallower areas until it covered the entire *A. palmata* zone by 2000.

**Land Use.**—At the earliest stages of the time series, little to no land use was apparent in the area. Nonetheless, military activities are dramatically evident on the 1975 image (Fig. 4). At this time larger roads had been constructed, in conjunction with an airstrip that was later abandoned. Approximately 28,704 m² of vegetation, probably mangroves, was removed to provide direct access from the roads and airstrip to the lagoon. The impact on the land by the bombarding activities inside the LIA was evident by the amount and size of craters in this area (~964 craters per km² with an average of 5 m diameter). The number of craters caused by live impacts continued to increase throughout the time series.

**Discussion**

**Spatial Growth and Distribution of Seagrass.**—It is apparent that seagrass meadows in Bahía Salina del Sur have been following the Principle of Lateral Continuity, which states (in reference to geological beds) that “strata originally extend in all directions until they end by thinning, ending against a barrier, grading into another type of sediment or are eroded” (Costeno in Rankey, 2002). If the 1937 patches, which constitute the start of the time series, are considered as two large discrete patches (which is not unreasonable, cf. Fig. 6), their structure can be described as a continuum spreading to fill areas not constrained by a natural barrier (i.e., coastline and reef structures). Thus patches spread southward and into the center of the bay (Fig. 6A). The land acted as a barrier against spread in a north, east, or westerly direction. Once it occupied the majority of the bay (1959), the reefs and cay islands in the south began acting as barrier, impeding the patches from spreading farther. Post-1959, smaller patches started to merge and form patches of increasing size. Smaller patches were still present but were confined to the periphery of large patches and to the north and northeast of the bay. In 2000, the last image of the series, one large patch occupied 94.92% of the total seagrass area, while 135 smaller patches represented the other 5.08% which were located in close proximity to the cay islands.

A similar study of seagrass in Tampa Bay, Florida, reported that small patches fringed larger patches of continuous seagrass and that areal increase of patches could be described as a decrease in fragmentation (Robins, 1997). The only area where we did not detect an overall increase in patch size as function of decrease in patchiness and where seagrass practically disappeared in 2000, was on the northern and northeast side of the bay. Seagrass patchiness in this area was high for all years (numerous small patches), likely due to an edge and/or stress effect that did not allow development of larger patches. The patchiness in this area can probably be attributed to both the military ordnance impacts and the effluent discharges of Anones lagoon into the bay. On numerous occasions this area was reported to be the most affected by the military activities, which conceivably could cause craters and discontinuity in the seagrass beds and an increase in suspended sediments among other detrimental effects (Raymond, 1978; Antonius and Weiner, 1982; Rogers et al., 1983; Porter, 2000; ADNFEC, 2002). Anones lagoon was also reported to increase the discharge of effluents into the bay as result of the filling of the lagoon with sediments due to
the bombing activities around and inside the lagoon (Raymond, 1978; Rogers et al., 1983). Since patchiness was reduced over the entire bay, and was usually less at the edges of larger patches than in this specific area, we infer that the synergistic effect of both the military impacts and the discharges from the lagoon were likely responsible for limiting the patch size-frequency distributions by maintaining a large number of small patches.

It would be interesting to determine whether the initial increase in patchiness was associated with a shift in dominance of the different seagrass species. The influence of increasing patch-boundary length with increasing fragmentation may also be linked to changes in the impacts of grazers at the different stages of habitat fragmentation. Of course, it would be interesting to know the state of seagrass meadows prior to 1937, but unfortunately, the lack of earlier images precludes this. The Principle of Lateral Continuity may describe the spatial increase of the seagrass meadow, but does not provide a causal link to the process or processes that facilitated this increase.

Processes Associated with the Areal Increase of Seagrass Meadows.— Most decadal change studies investigating seagrass meadows have reported the decrease and, in some cases, the complete disappearance of seagrasses due to natural (Glynn et al., 1974; Armstrong, 1981 [both decrease and increase reported], Armstrong, 1993; Rodríguez et al., 1994) and mainly anthropogenic disturbances (Ziemann, 1975; Lewis et al., 1985; Hadd, 1989; Pasqualini et al., 1999; Short and Neckles,
Our study identified a second order polynomial increase ($r^2 = 0.91$) in seagrass meadows from 1937 to 2000. A similar study in Buck Island, US Virgin Islands, reported a three-fold increase in horizontal expansion of seagrass meadows and speculated that the increase may be associated with a positive impact caused by hurricane activity (Kendall et al., 2004). Hurricanes are known to negatively affect seagrass beds (Armstrong, 1981; Rodríguez et al., 1994) and algal plains (Dahl, 1973) by generating sufficiently strong currents to scour sediment from the roots, de-anchor them from the seabed, and transport them onshore (Glynn et al., 1974; Rodriguez et al., 1994). Because our study only quantified a decrease in seagrass cover in the 1975 and
2000 images, the question arises whether hurricanes could have been responsible for these declines. The Hurricane Historical Track record from NOAA databases showed no major storms or hurricanes impacting Vieques Island from 1964 to 1975 (Fig. 7). Moreover, if hurricanes have a negative impact on seagrass beds in Bahía Salinas del Sur, we would expect to see a similar decrease on the images following an impact, i.e., in 1983 and 1994 following the passage of Tropical Storm Federic (1979) and category 4 hurricanes David (1979) and Hugo (1989). However, there was no disruption in the increase in seagrass cover. The second decrease in 2000 could be attributed to the impact of category 2 hurricanes Marilyn (1995) and George (1998). Because the decrease was quantified only in the northeast section of the bay, adjacent to Anones lagoon, we assume that it was not solely due to hurricane impacts, but may also be related to an increased effluent discharge from the lagoon (discussed further in next section). In 1928, category 4 hurricane San Felipe, (8 yrs prior to the first image on the time-series), passed south of Vieques Island. We recognize that there is a possibility that this hurricane impacted the seagrass community, and resulted in the small and confined patches of 1937. However, we believe this to be unlikely given that no decrease in seagrass cover was apparent in 1994, 5 yrs after the landfall of category 4 hurricane Hugo.

Kendall et al. (2004) speculate that hurricanes may in fact stimulate seagrass growth under certain conditions by enhancing pollination, seed dispersal, and vegetative propagation. This provides a plausible explanation as to why, in certain areas, seagrass continued to increase even during periods of increased hurricane activity. We believe that the geomorphology of Bahía Salina del Sur could provide the necessary conditions for this phenomenon to occur. The southern islands (Cayo Conejo and Roca Alcatráz) and their associated reef systems, and the *A. plamata* reef located in the southeast of the bay, could provide sufficient protection from strong currents to mitigate the detrimental effect of passing hurricanes while waves and currents would still be able to affect the bay and (according to Kendall et al.’s (2004) hypothesis) stimulate horizontal growth. Other seagrass meadows located in unprotected areas in Vieques Island, have been negatively affected by hurricane impacts (i.e., the areas of Esperanza and Escollo de Arenas; Rodríguez et al., 1994), lending support for our hypothesis that the geomorphology of the Bahía Salina del Sur has protected the seagrass meadows from the devastating effects of hurricanes.

An alternative or contributing explanation for the increase in seagrass cover could be the decline in the abundance of seed predators, herbivorous fishes, or sea turtles (Kendall et al., 2004). In a similar decadal change study in La Parguera, on the south-west coast of Puerto Rico, Armstrong (1981) reported a decrease in seagrass due to a population explosion of grazers. Armstrong also referred to a study in the Florida Keys (Camp et al., 1973 in Armstrong [1981]) in which the grazing activities of the urchin *Lytechinus variegatus* (Lamarck, 1816) resulted in the destruction of seagrass beds. A decrease in grazers might therefore have the opposite effect (a similar hypothesis is expressed by García et al., in press). Other than anecdotal observation of local fishermen, no data are available that quantified changes in grazing fauna in the bay. Only one study (ADNFEC, 2002) quantified fish populations in the AFWTF. However, this study did not offer any comparisons with previous years, nor did it contain any samples from Bahía Salina del Sur. Therefore, this hypothesis cannot be evaluated.
Processes Involved in the Areal Decrease of the Seagrass Meadows and Acropora palmata.—The 1975 image represents the first period in which a decrease in seagrass area cover was quantified. Contrary to our expectation, the decrease was not associated with hurricane impacts but coincided with the deployment and sinking of the USS Killen, an old destroyer that was used as bombing target in the bay. After the wreck was deployed in the bay, a sand halo of more than 100 m developed around it. By 1983, the halo had reduced to ~20 m width, increasing on the downstream side of the wreck, but nonetheless twice the width of halos around other reef patches inside the bay. By 1994, it was reduced to the same width of the other halos inside the bay (~10 m). The USS Killen was a 2050-t Fletcher-class destroyer used in WWII that after decommissioning was used for weapons tests in the Central Pacific (Department of the Navy, 2002; Geo-Marine, 2003). It was then transferred to the AFWTF to be used as a target and sunk in Bahía Salina del Sur in 1975. Porter (2000) reported that the USS Killen contained 150–200 sealed 55-gal barrels with unknown contents, thus the halo could either have been caused by the movement of the ship during rough seas or due to the leaks of any unknown materials from the barrels. It has been speculated that the barrels could contain toxic material and could have played a role in the degradation of seagrass surrounding the wreck. The use of toxic materials (i.e., napalm, Agent Orange, depleted uranium among others) was reported on Vieques (Porter, 2000; Ithier-Guzmán and Pyrtle, 2004) and some toxic markings were identified on numerous barrels (Porter, 2000). However, a study conducted for the AFWTF in 2002 concluded that the barrels inside the wreck were unlikely sources of contaminants (Deslarzes et al., 2002), although it is worth noting that the study was conducted after the sand halo was reduced to an average size and did not take into consideration the marked decrease in seagrass cover immediately after the USS Killen was deployed. A second decrease in seagrass cover was quantified in 2000. It was characterized by a decrease in density from sparse to very sparse cover in the northeastern sector of the bay. This area was reported as the most severely impacted by military activity, since increased sediment discharge into Bahía Salina del Sur resulted from the filling of Anones Lagoon with material mobilized during bombing activities (Raymond, 1978; Rogers et al., 1983). As previously mentioned, seagrass cover in this particular area never increased as a function of increasing patch size. Nevertheless, patchiness was higher in the area between Bahía Salina del Sur and Anones Lagoon, and by 2000, the density decreased to such an extent that even though seagrass is still present in this area, it is currently so sparse, that it would been omitted from the classification. Therefore, due to the characteristics and location of the decline, we hypothesize that the decrease was primarily a consequence of increasing sediment discharge and possible temperature anomalies in this very shallow area. The impact of live ammunition was also reported to cause craters in the seagrass meadow (Rogers et al., 1978; Porter, 2000) but the spatial resolution of our dataset precluded distinguishing naturally occurring patches from craters.

The decline of healthy coral cover, most notably by A. palmata, in Bahía Salina del Sur has been blamed on military activities (Rogers et al., 1978; Porter, 2000) and/or natural disturbance (Raymond, 1978; Dodge, 1981; Antonius and Weiner, 1982). Studies concur that military activities had a detrimental effect on some P. porites reefs near the headlands and directly or indirectly affected the two A. palmata reefs in closest proximity to land targets (Raymond, 1978; Rogers et al., 1978; Macintyre, 1983; Porter, 2000), but there is no consensus as to effects on the health of the entire
reef system inside the LIA. Rogers et al. (1978) and later Porter (2000) blamed degradation of the reefs on military activities and identified an inverse correlation between coral health and distance from the center of the bombing range. Antonius and Weiner (1982) considered most damage to be caused by natural factors. Dodge (1981) identified both extreme temperature variations and hurricane impacts as a direct threat to the reefs inside Bahía Salina del Sur. Although hurricanes apparently do not represent a major threat to seagrass beds inside the bay, their impact on the reefs can vary between no effect and total destruction over distances of just a few meters (Lugo et al., 2000). The decrease in coral cover in Vieques was concurrent with observations of White Band Disease in Puerto Rico (Lugo et al., 2000), which tends to appear following hurricane impacts and amplifies mortality (Bak and Criens, 1981). Thus, diseases may have overwhelmed the ability of corals to regenerate (Lugo et al., 2000) and may have ultimately caused the demise of *A. palmata* in the area.

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