Potential Habitat of *Acropora* spp. on Reefs of Florida, Puerto Rico, and the US Virgin Islands

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Original research article

Potential Habitat of *Acropora* spp. on Reefs of Florida, Puerto Rico, and the US Virgin Islands

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HIGHLIGHTS

- Potential habitat for *Acropora palmata* is currently well defined.
- Potential habitat for *Acropora cervicornis* is more variable than that for *A. palmata*.
- Additional habitat in Florida is included in the new potential habitat maps.
- The maps refine spatial coverage to more manageable areas in Puerto Rico & the USVI.
- The methodology for mapping the extent of habitats of *Acropora* spp. is described.

ABSTRACT

Elkhorn and staghorn corals (*Acropora palmata, Acropora cervicornis*) were listed in 2006 as threatened under the Endangered Species Act. The goal of this study was to create model potential-habitat maps for *A. palmata* and *A. cervicornis*, while identifying areas for possible re-establishment. These maps were created using a database of reported field observations in combination with existing benthic habitat maps. The mapped coral reef and hardbottom classifications throughout Florida, Puerto Rico, and the US Virgin Island reef tracts were used to generate potential-habitat polygons using buffers that incorporated 95% and 99% of reported observations of *Acropora* spp. Locations of 92% of *A. palmata* observations and 84% of *A. cervicornis* observations coincided with mapped coral reef or hard-bottom habitat throughout the study area. These results indicate that potential habitat for *A. palmata* is currently well defined throughout this region, but that potential habitat for *A. cervicornis* is more variable and has a wider range than that for *A. palmata*. This study provides a novel method of combining data sets at various geographic spatial scales and may be used to inform and refine the current National Oceanic and Atmospheric Administration critical habitat map.

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Objective Statement: The primary objective of this study was to model locations of potential habitat throughout the ranges of *Acropora* spp. within US jurisdictions (Florida, Puerto Rico, and the US Virgin Islands). The second objective was to compare the extent of potential habitat and *Acropora* spp. observations between main geographic regions.

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1. Introduction

Corals of the genus *Acropora* have epitomized coral reefs worldwide because of their typical distribution in shallow water (making them more accessible and therefore more familiar) and characteristic branching morphologies. Two species occur in the western Atlantic and Caribbean region, *Acropora cervicornis* (Lamarck 1816) and *Acropora palmata* (Lamarck 1816).

The precipitous decline of *Acropora* spp. in the western Atlantic and Caribbean is a primary issue of discussion in coral reef conservation. Their formal listing as threatened in 2006 (Federal Register, 2006) highlighted the concern for these historically important reef-building corals, bringing attention to the overall decline in reef-building corals over the past several decades. Fortunately for conservation and management purposes, their distribution in shallow water makes their habitats relatively accessible and amenable to mapping techniques based on satellite or aircraft-based remote sensing.

1.1. Recent threats to *Acropora* populations

During the past three decades many western Atlantic coral communities, including *Acropora* spp. populations, have been affected by a series of disturbances. The most notable of these include the spread of white-band disease (WBD) through Atlantic and Caribbean *Acropora* populations beginning around 1976 (Gladfelter, 1982; Porter et al., 2001), a cold-water event in 1976–1977 (Davis, 1982; Lessios, 1988; Lirman et al., 2011; Porter et al., 1982; Roberts et al., 1982), a region-wide *Diadema* (sea urchin) die-off in 1983 (Lessios, 1988), widespread mass-bleaching events in 1983 (Jaap, 1985; Lang et al., 1992; Hoegh-Guldberg, 1999), and numerous hurricanes (Lirman and Fong, 1996). In addition, the increase in frequency of such disturbances has limited recovery of extensive *Acropora* thickets in most of the western Caribbean.

The spread of WBD is widely considered one of the most significant disturbances affecting *A. palmata* and *A. cervicornis*. White-band disease was first documented in the early 1970s at Buck Island National Reef Monument in St. Croix, US Virgin Islands (Gladfelter et al., 1977). Prior to the spread of the disease, areas of the reef in St. Croix were composed of more than 50% live *A. palmata* (Mayor et al., 2006). Unfortunately, and as is the case for many populations throughout the species range, the combination of WBD and other disturbances has reduced populations more than 90% (Mayor et al., 2006). Similarly, WBD drastically reduced *A. cervicornis* populations in both the shelf lagoon and spur-and-groove zones of the Belizean Barrier Reef, where in some locations coverage dropped from ~70% to close to zero in just seven years (Aronson and Precht, 1997). Additionally, gene flow between populations has been found to be restricted, negatively contributing to the influence of WBD on many populations (Baums et al., 2010; Hemond and Vollmer, 2010; Vollmer and Palumbi, 2007). As in many locations, the losses of these two reef-building species have had lasting and widespread effects on reefs throughout Florida, Puerto Rico, and the US Virgin Islands (Rogers et al., 2008a,b).

Human population growth poses a variety of local threats to coral reef ecosystems, including nutrient enrichment, diminished water clarity, inhibition of calcification by phosphates, biotic replacement, and increased bioerosion (Hallock and Schlager, 1986; Simkiss, 1964; Smith et al., 1981; Weiss and Goddard, 1977). Nevertheless, significant thickets of *A. cervicornis* have been reported in shallow nearshore waters off of populous Fort Lauderdale, Florida (Thomas et al., 2000; Vargas-Angel et al., 2003), at or near the northern latitudinal limits of the species. These populations are believed to be among the largest and northernmost in the continental USA and are a potential source of propagules for replenishment of threatened populations in south Florida habitats (Vargas-Angel and Thomas, 2002). Extensive populations of *A. palmata* are notably absent from southeast Florida coastal habitats, although isolated colonies have been found (Banks et al., 2008). Unfortunately for these populations, the reefs of southeast Florida are located outside formal marine management zones, unlike the reefs in the Florida Keys and Dry Tortugas (Causey et al., 2002).

In the US Virgin Islands, many locations have vast stands of dead *A. palmata*, but small areas with dense live *A. palmata* do exist (Rogers et al., 2008a,b; Zitello et al., 2009). Unfortunately, no reefs in the US Virgin Islands exhibit densities of *A. palmata* as high as those recorded in the 1960s and 1970s (Rogers et al., 2002). In many areas of Puerto Rico, the fire coral *Millepora* spp. has replaced *A. palmata* as the dominant reef-crest coral species (Ballantine et al., 2008).

1.2. Habitat requirements of Atlantic and Caribbean *Acropora* spp.

Habitat requirements for *A. palmata* and *A. cervicornis* are well known. *A. palmata* has sensitive environmental requirements including clear, well-circulated water of normal marine salinity, a solid substrate, and moderate water temperatures (optimally 25–29 °C, without extreme seasonal variation) (Jaap et al., 1989). The presence of a solid substrate such as coral reef or hard bottom is vital for the attachment of coral recruits during settlement (Harrison and Wallace, 1990). Before the 1970s, in much of the Caribbean *A. palmata* was the dominant coral in wave-exposed and high-surge reef zones, typically at depths of less than 10 m (Adley and Burke, 1976). At the same time, *A. cervicornis* was found at shallow to medium depths, as deep as 30 m in clear water (Fenner, 1988). *A. cervicornis* thickets in shallow reef flats and patch reefs were common before the 1980s (Dustan, 1985; Shinn et al., 1989). However, the full extent of historical and current distributions, as well as potential habitat for these two species in the western Atlantic and Caribbean, has not been fully documented.

Recent studies of both species found *A. cervicornis* distribution to be wider than that of *A. palmata*, with colonies found on a variety of habitats, including mid-channel and offshore patch reefs, as well as inner reef-tract sites (Miller et al., 2008). Following spatially extensive surveys performed in 2007, Miller et al. (2008) estimated that there were 14 ± 12 million *A.
cervicornis colonies and 1.6 ± 1.4 million A. palmata colonies in the Florida Keys. Most of these colonies, however, have not been documented, nor has their location been verified by observation.

1.3. Previous research

Wirt et al. (2013) used reported observations of A. palmata and A. cervicornis to generate potential-habitat maps for the species along the Florida reef tract. The study found that locations of 99% of A. palmata and 84% of A. cervicornis observations coincided with previously mapped coral reef or hard-bottom habitat. A main conclusion of that research was that potential habitat for A. palmata is currently well defined in Florida, while A. cervicornis, habitat is more variable and has a wider range (Wirt et al., 2013).

1.4. Objectives and potential significance

The objectives of this study were:

(1) to evaluate the accuracy of reported Acropora spp. observations and current benthic habitat maps of Florida, Puerto Rico, and the US Virgin Islands;

(2) to use reports of existing colonies of A. palmata and A. cervicornis and current benthic habitat maps to model the distribution of potential habitat in Florida, Puerto Rico, and the US Virgin Islands; and,

(3) to create potential-habitat maps showing areas in which these species exist, as well as areas that would be suitable for their re-establishment.

The results of this research will help define where conservation actions will be most effective. With existing populations mapped, the results will also aid in preventing destruction of the limited areas in which these species occur. This study also provides a model for developing future critical habitat maps, which will be necessary if other coral species are designated as threatened or endangered.

2. Methods

2.1. Field area

This study focused on the reef tracts of Florida, Puerto Rico, and the US Virgin Islands (St. Thomas, St. John, and St. Croix). The Florida reef tract extends from Martin County through the Dry Tortugas, and both species are present throughout. In Puerto Rico, the reef tract encircles the island, but Acropora spp. is most prevalent off the southwest and northeast coasts. In St. Croix, Acropora spp. is concentrated along the north and northeast coasts of the island. Acropora spp. locations are distributed relatively evenly along the reef tract on all sides of St. Thomas and St. John (Fig. 1).

2.2. Data

The Florida Fish and Wildlife Conservation Commission’s (FWC) Fish and Wildlife Research Institute (FWRI) received Acropora spp. location data in Florida, Puerto Rico, and the US Virgin Islands, as described by Wirt et al. (2013). Due to errors discovered in the original Florida data set, the data here represent a reanalysis of the Florida region. Observations of Acropora spp. were reported from surveys conducted between 1996 and 2012 by a range of groups, agencies, and institutions.

While locations of surveys that did not detect Acropora spp. are important, they were not addressed in this study. All results pertain to locations where surveys detected one or both species of Acropora.

2.3. Benthic habitat maps

Recently, benthic habitat maps created by FWRI, the National Park Service (NPS), Nova Southeastern University, and the National Oceanic and Atmospheric Administration (NOAA) were combined to create the Unified Florida Reef Tract Map, which provides a seamless spatial representation of the Florida reef tract benthos. The classification system used accommodates and integrates various classification schemes while retaining the original information. The original maps used to build the Unified Florida Reef Tract Map were created using a combination of IKONOS imagery, aerial photography (digital and analog), and LiDAR (Baumstark, 2013).

Benthic habitat maps used for Puerto Rico and the US Virgin Islands were digitized from aerial photography acquired in 1999 by the NOAA Biogeography Branch. This project mapped the insular shelf between the shoreline and the shelf edge throughout Puerto Rico and the US Virgin Islands (Kendall et al., 2001). While these two mapping projects (Florida and the Caribbean) used different classification schemes, the goal of this study was to extract only mapped coral reef and hard-bottom areas, which in this study allowed for the use of multiple classification schemes. Information on benthic habitat maps used for this study, including the year and minimum mapping unit for each map, is provided in Table 1.
Fig. 1. Regions of focus in this study, with locations of Acropora spp. observations.

Table 1
Details of the multiple benthic habitat maps used for this study.

<table>
<thead>
<tr>
<th>Location</th>
<th>Year</th>
<th>Year of source imagery</th>
<th>Agency</th>
<th>Minimum mapping unit (acre)</th>
<th>Area covered (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. Thomas/St. John/St. Croix</td>
<td>2001</td>
<td>1999</td>
<td>NOAA Biogeography</td>
<td>1</td>
<td>490</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>2001</td>
<td>1999</td>
<td>NOAA Biogeography</td>
<td>1</td>
<td>1600</td>
</tr>
<tr>
<td>Florida</td>
<td>2013</td>
<td>2001–2012</td>
<td>FWRI</td>
<td>0.5–1</td>
<td>9102</td>
</tr>
</tbody>
</table>

2.4. Determination of Acropora habitat

ArcGIS software was used to overlay the Acropora spp. observation database on the benthic habitat maps. Observations of Acropora spp. located entirely within mapped coral reef or hardbottom were identified. The various classifications, which were considered coral reef and hardbottom in each of the benthic habitat maps, are shown in Table 2. In situ observation data points that fell outside of mapped reef or hardbottom were extracted and further examined. For each point not on a coral reef or hardbottom classification, the type of substrate was identified from the underlying benthic habitat maps.

2.5. Buffer generation

Buffers of various widths were created around mapped coral reef and hardbottom to compensate for errors associated with lower-resolution habitat maps (Tveite and Langaas, 1999). The frequency of points included within each buffer distance was determined. Buffers were created at 1-m increments until 95% and 99% of all points were included. This process was automated by creating a program using ArcGIS’s ModelBuilder, which created a set of 10 buffers at a time at 1-m increments for each benthic habitat map.

Observations were then separated into four regions, Florida, Puerto Rico, St. Thomas/St. John, and St. Croix, based on the benthic habitat map to which they corresponded. The percentage of points within each buffer size was calculated to determine the cumulative distribution of the four regions. A Kolmogorov–Smirnov (K–S) test for goodness of fit (Sokal and Rohlf, 1981) was performed to determine whether any of the four regions differed significantly from the overall cumulative...
Table 2
Coral reef and hardbottom classifications used for the benthic habitat maps in this study.

<table>
<thead>
<tr>
<th>Classification</th>
<th>Florida</th>
<th>Puerto Rico</th>
<th>St. Croix</th>
<th>St. Thomas/St. John</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggregate reef</td>
<td>×</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colonized bedrock</td>
<td></td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Colonized pavement</td>
<td></td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Colonized pavement with sand Channels</td>
<td>×</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Linear reef</td>
<td>×</td>
<td></td>
<td>×</td>
<td></td>
</tr>
<tr>
<td>Patch reef (aggregated)</td>
<td>×</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Patch reef (individual)</td>
<td></td>
<td>×</td>
<td></td>
<td>×</td>
</tr>
<tr>
<td>Pavement</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reef rubble</td>
<td>×</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ridge</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scattered coral/rock in unconsolidated</td>
<td>×</td>
<td>×</td>
<td></td>
<td>×</td>
</tr>
<tr>
<td>Spur and groove reef</td>
<td>×</td>
<td></td>
<td>×</td>
<td>×</td>
</tr>
</tbody>
</table>

Table 3
Number of observations of Acropora spp. by region of the Florida reef tract after erroneous points were removed from the database.

<table>
<thead>
<tr>
<th>Observation</th>
<th>Florida</th>
<th>Puerto Rico</th>
<th>St. Croix</th>
<th>St Thomas/St. John</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora palmata presence</td>
<td>3885</td>
<td>1901</td>
<td>2900</td>
<td>5594</td>
<td>14,280</td>
</tr>
<tr>
<td>A. cervicornis presence</td>
<td>3832</td>
<td>54</td>
<td>40</td>
<td>146</td>
<td>4,072</td>
</tr>
<tr>
<td>Total presence</td>
<td>7717</td>
<td>1955</td>
<td>2940</td>
<td>5740</td>
<td>18,352</td>
</tr>
</tbody>
</table>

percentage distribution ($\infty = 0.05$). The K–S test was performed for \textit{A. palmata} and \textit{A. cervicornis} individually and for both species combined.

2.6. Potential-habitat map generation

Based on the frequencies recorded in the various buffer sizes and the results of the K–S tests, potential habitat was delineated for each of the four regions by merging the appropriate buffered coral reef and hardbottom polygons. These polygons were then clipped to appropriate depth limits, using USGS FLaSH bathymetry in Florida and isobaths from National Geospatial-Intelligence Agency Digital Nautical Charts in Puerto Rico and the USVI. These potential habitat maps are models representing habitats in which \textit{Acropora} spp. would be expected to be found, based on mapped habitats of previously observed colonies.

Potential habitat was determined and mapped for each species and for both species together, and at two confidence levels, 95% and 99%. A total of six potential-habitat maps were created. Potential habitat was determined based on the buffer distance where exactly 95% and 99% of observations were included, as well as the results of the K–S test. The \textit{Acropora} spp. and \textit{A. cervicornis} potential habitat maps were clipped to a 30 m depth limit to represent the maximum depth range of \textit{A. cervicornis}, while the \textit{A. palmata} potential habitat maps were clipped to a 10 m depth limit.

3. Results

A total of 18,732 locations of \textit{Acropora} spp. presence in Florida, Puerto Rico, and the US Virgin Islands were reported to the database. Of those records, 380 (2%) were clearly erroneous and removed based on unreasonable locations in relation to bathymetry and coastline. For example, observations located on land or at depths greater than 50 m were assumed to be erroneous and were removed. A total of 18,352 recorded \textit{in situ} observations of \textit{Acropora} spp. presence were retained for use in this study (Table 3).

3.1. Habitats of observed Acropora spp.

A total of 17,069 observations coincided with previously mapped coral reef or hardbottom, accounting for 93% of the observations. \textit{A. palmata} had the highest percentage of occurrence on previously mapped coral reef or hardbottom in the St. Croix region and the lowest in Florida. \textit{A. cervicornis} had the highest percentage of occurrence on mapped reef or hardbottom in Puerto Rico and the lowest in Florida. Overall, observations of both species combined were most often located on mapped reef or hardbottom in St. Croix. In that region, 99% of all observations were located on mapped reef or hardbottom (Fig. 2). In all regions except Puerto Rico, both \textit{A. palmata} and \textit{A. cervicornis} were observed outside mapped reef or hardbottom. While 100% of \textit{A. cervicornis} observations in Puerto Rico occurred on mapped reef or hardbottom, the limited number of observations (54) was not enough to increase the percentage of both species combined over that at St. Croix. The substrate associated with observations not on mapped reef or hardbottom is detailed by region in Figs. 3–6.
3.2. Buffer generation

The buffer sizes at which 95% and 99% of points were included are detailed for each species by region in Table 4. The benthic habitat maps for St. Croix required no buffer to include 95%–99% of Acropora spp. observations, while those for Florida required a buffer as wide as 490 m to include 99% of A. cervicornis observations. Fig. 7 compares the percentage of points included within each buffer distance by region. Most observations of A. cervicornis were recorded in Florida, and very few occurred in other regions. Therefore, the percentage of points across all regions is mostly influenced by the observations in Florida, as seen in Fig. 7(b).

Results of the K–S test (Table 5) suggest that, for both species combined, the distribution in each region is significantly different from that across all regions combined. Distributions of A. palmata observations in St. Thomas, St. John, and Puerto Rico are not significantly different from those of the entire study area combined, but the distributions of A. palmata in St.
Fig. 4. Associated substrate of *A. palmata* observations in Puerto Rico.

Fig. 5. Associated substrate of *Acropora* spp. observations in St. Croix.

Table 4

<table>
<thead>
<tr>
<th></th>
<th>St. Thomas/St. John</th>
<th>Puerto Rico</th>
<th>St. Croix</th>
<th>Florida</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>95%</td>
<td>99%</td>
<td>95%</td>
<td>99%</td>
<td>95%</td>
</tr>
<tr>
<td><em>A. palmata</em> (m)</td>
<td>2</td>
<td>15</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td><em>A. cervicornis</em> (m)</td>
<td>2</td>
<td>22</td>
<td>0</td>
<td>0</td>
<td>86</td>
</tr>
<tr>
<td>Both species (m)</td>
<td>2</td>
<td>15</td>
<td>0</td>
<td>10</td>
<td>0</td>
</tr>
</tbody>
</table>

Croix and Florida are significantly different. No distribution of *A. cervicornis* in any region is significantly different from distributions in the entire study area.
Fig. 6. Associated substrate of *Acropora* spp. observations in St. Thomas/St. John.

### Table 5
Results of K-S goodness of fit test comparing distributions in each region to distributions of the full reef tract.

<table>
<thead>
<tr>
<th>Region</th>
<th>A. cervicornis</th>
<th>A. palmata</th>
<th>Acropora spp.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>$D_{max}/D_{0.05}$</td>
<td>n</td>
</tr>
<tr>
<td>Florida</td>
<td>3816</td>
<td>0.01/0.02</td>
<td>3384</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>54</td>
<td>0.15/0.19</td>
<td>1901</td>
</tr>
<tr>
<td>St. Croix</td>
<td>40</td>
<td>0.07/0.22</td>
<td>2900</td>
</tr>
<tr>
<td>St. Thomas/St. John</td>
<td>146</td>
<td>0.11/0.11</td>
<td>5594</td>
</tr>
</tbody>
</table>

*Designates significance.*

### Table 6
Buffer distances used for potential-habitat maps.

<table>
<thead>
<tr>
<th>Region</th>
<th>A. cervicornis</th>
<th>A. palmata</th>
<th>Acropora spp.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>95% 99%</td>
<td>95% 99%</td>
<td>95% 99%</td>
</tr>
<tr>
<td>Florida (m)</td>
<td>97</td>
<td>468</td>
<td>11 259</td>
</tr>
<tr>
<td>St. Croix (m)</td>
<td>97</td>
<td>468</td>
<td>0 0</td>
</tr>
<tr>
<td>Puerto Rico (m)</td>
<td>97</td>
<td>468</td>
<td>0 37</td>
</tr>
<tr>
<td>St. Thomas/St. John (m)</td>
<td>97</td>
<td>468</td>
<td>0 37</td>
</tr>
</tbody>
</table>

### 3.3. Generation of potential-habitat maps

Table 6 presents the buffer distances used for the six potential-habitat maps. The final maps were created by merging the buffered benthic-habitat maps for each region to create a single representation of *Acropora* spp. potential habitat. While these maps are best suited for use with GIS, Figs. 8–11 nevertheless provide useful visual comparisons between the 95% potential habitat maps created in this study and the previously designated NOAA critical-habitat maps. Merging maps from multiple data sources, as is done here, has been useful in other studies (Giglio et al., 2010). While regions in the backcountry of the Florida Keys (Florida Bay and Biscayne Bay) have been mapped as hardbottom, they were excluded from all potential habitat maps because no observations were recorded there. Moreover, this area is not suitable habitat for *Acropora* spp. due to high turbidity and variability in salinity and water temperature (Roberts et al., 1982; Shinn et al., 1989).
Fig. 7. Percentages of points included for various buffer distances by region (a) percentages of *A. palmata* (b) percentages of *A. cervicornis* (c) percentages of both species combined.

4. Discussion

The results of this study provide the methodology for mapping the extent of habitats known to support or likely capable of supporting *A. palmata* and *A. cervicornis* throughout US jurisdictions. At the time of listing of the species, NOAA designated critical habitat maps throughout the species range within US territory (Federal Register, 2008). The current critical habitat maps cover large areas of reef tract in Florida, Puerto Rico and the US Virgin Islands (Figs. 8–11). These results will aid in refining these critical-habitat maps for the species and in accurately representing habitat necessary for their re-establishment.

Ideally, all observations of *Acropora* spp. would be located on previously mapped coral reef or hardbottom. In this study approximately 7% of observations were located outside of these classified bottom types. Most of these points (673) were *A. palmata*, but that accounted for only 5% of the *A. palmata* observations. There were fewer *A. cervicornis* locations in the database, so the 610 observations located outside of mapped coral reef or hardbottom accounted for a higher percentage (15%). This reflects more extensive potential habitat for *A. cervicornis*, because habitat for *A. palmata* is less variable and more often limited to reef margins. These results are comparable to those of Wirt et al. (2013), who found 1% of *A. palmata* and 7% of *A. cervicornis* observations outside of mapped reef or hardbottom. A key question can be addressed using this data set: Do the data points that do not fall on mapped coral reef or hardbottom reflect mapping error, the potential of *Acropora* spp. to occupy habitats other than coral reef or hardbottom, or still other phenomena?
Fig. 8. 95% Acropora spp. potential habitat compared to previously determined NOAA critical habitat around Florida.

Fig. 9. 95% Acropora spp. potential habitat compared to previously determined NOAA critical habitat around Puerto Rico.

Low spatial resolution of benthic habitat maps could result in observations outside of mapped coral reef or hardbottom; for example, a small patch reef encompassing an area smaller than the minimum mapping unit would not be mapped differently than the surrounding habitat. Temporal variability of the habitats could have the same result. Areas of thin
Fig. 10. 95% *Acropora* spp. potential habitat compared to previously determined NOAA critical habitat around St. Croix.

Fig. 11. 95% *Acropora* spp. potential habitat compared to previously determined NOAA critical habitat around St. Thomas and St. John.

sediment-cover where hardbottom occurs intermittently both spatially and temporally within seagrass and sand could be mapped as potential habitat or completely overlooked.

Habitats have changed since the benthic habitat maps were created, which also could have resulted in outlying points. Recent hurricanes affecting south Florida, Puerto Rico, and the US Virgin Islands, such as Katrina, Wilma, Otto, and Kyle, were
strong enough to alter habitats. Strong hurricanes dislodge and move hard substrate (Geister, 1980) and expose hardbottom, creating *Acropora* spp. habitat in previously uninhabitable regions. This problem can be resolved only by more frequent mapping, especially after significant storms.

The present database is a compilation of reported observations from many groups, agencies, and individuals. A number of errors could occur in data acquisition, including errors in recording latitude and longitude and those in simple data handling. The most likely error would be in data recording, but the fact that 95% of the *A. palmata* records fell on previously mapped reef or hardbottom indicates that the data set is highly reliable. Any point-pattern data may be spatially biased towards accessible areas, resulting in errors of omission (false negatives) or commission (false positives, Rondinini et al., 2006). This data set is no exception and is subject to errors of omission because a complete census of *Acropora* spp. does not exist (Pressey, 2004). While the potential habitat in this study contains inherent commission errors, these errors are generally seen as less 'costly' for conservation and management actions than errors of omission (Guisan and Zimmermann, 2000).

The number of reports of *A. cervicornis* outside of mapped reef or hardbottom reflects the greater range of habitats available to this species. Larvae can recruit to habitats dominated by sand or seagrass so long as there is hard substrate upon which it can settle, such as a shell or a small outcropping of hardbottom. *A. cervicornis* is also common on inshore and offshore patch reefs, which are more difficult to map than are the reef crests, where *A. palmata* is more commonly found. Additionally, *A. cervicornis* has been found to be spatially and temporally dynamic, with patches capable of moving tens of meters in a few years time (Walker et al., 2012). This dynamic nature of *A. cervicornis* supports the use of a buffer around coral reef and hardbottom habitat, as used in this study, in order to account for possible movement into adjacent areas.

Field surveys are needed to examine sites at which discrepancies occur between mapped habitat and observations. The results of such surveys can provide guidance in determining whether it is feasible to better define the potential habitat for *A. cervicornis*. But since 95% of the reported observations of *A. cervicornis* occur within 99 m of previously mapped coral reef or hardbottom, the current maps should be suitable for delineating critical habitat. Therefore, future mapping efforts should focus on reef areas for which habitat maps do not yet exist, such as those outside the Dry Tortugas.

This study confirms that *A. cervicornis* has a wider habitat range than *A. palmata* throughout Florida, Puerto Rico, and the US Virgin Islands. This difference is especially apparent offshore southeast Florida, where *A. cervicornis* appears to be thriving outside mapped coral reef areas and at latitudes considered marginal for hermatypic corals. The documentation of a wider range of habitat for *A. cervicornis* than for *A. palmata* indicates that different management strategies may be needed for the two species.

When the species were listed as threatened, NOAA designated critical-habitat maps throughout the species range within US territory. The newly generated potential-habitat maps were compared with NOAA's mapped critical habitat. Overall, the new potential-habitat maps are more refined in spatial coverage than the current critical-habitat maps. An important aspect of the new potential-habitat maps concerns the southeast coast of Florida. The northern extent of the NOAA-designated critical habitat is in the southern portion of Palm Beach County, whereas the northern extent of all versions of the new potential-habitat maps is farther north, in the southern portion of Martin County. While no observations were located in Martin County, 10 observations of *A. cervicornis* were located north of the NOAA critical habitat in Palm Beach County. The caveat associated with this extended region is that it is defined only by the presence of mapped hardbottom. The northernmost extent of *Acropora* spp. is still not precisely known, but all *A. cervicornis* observations in this study were located south of 26.682°N. The northern extension of potential habitat within Palm Beach County exhibits additional areas of reef and hardbottom available for *Acropora* spp. settlement. However, settlement of *Acropora* spp. in southern Martin County is unlikely due to unique hydrodynamics present in this region. A recent study by Walker and Gilliam (2013) suggests the unlikelihood of northern expansion of tropical coral communities into the Martin County region due to frequent and intense upwelling events that occur north of the Bahamas Fault Zone (Klitgord et al., 1984; Pitts, 1999; Pitts and Smith, 1997; Smith, 1983). Coral communities north of this fault zone are restricted to cold tolerant species such as *Siderastrea* and *Oculina* (Colella et al., 2012; Lirman et al., 2011; Walker and Gilliam, 2013).

Defined potential habitat around the Dry Tortugas is confined to the extent of the currently mapped reef and hardbottom in the region. NOAA's critical-habitat map extends farther outside of Dry Tortugas National Park and, therefore, encompasses regions that are believed to be *Acropora* spp. habitat. But the current potential-habitat map does not include these regions due to the limited extent of the mapped reef and hardbottom in the region.

Throughout the Caribbean regions (Puerto Rico and the US Virgin Islands), the new potential-habitat maps do not encompass additional *Acropora* spp. habitat. Instead, they reduce the coverage to more manageable areas, areas in which *Acropora* spp. is likely to be found. But the number of observations of *A. palmata* greatly exceeds that of *A. cervicornis*. This is likely a result of the concentration of surveys on linear reef zones rather than on patch reefs, where *A. cervicornis* is commonly found. Therefore, the unevenness of these observations throughout this region may have resulted in the exclusion of some potential *A. cervicornis* habitat. Clearly, more observations of *A. cervicornis* are needed to improve the accuracy of the potential-habitat maps.

Multiple potential-habitat maps were produced from the results of this study that will have value in a number of management efforts. In general, the 95% *Acropora* spp. potential-habitat maps may be best suited for general purposes, because their boundaries were determined based on the presence of both species. However, the 99% *A. cervicornis* potential-habitat map could be used when the maximum area of potential habitat is desired, given the wider range of *A. cervicornis*. Alternatively, the species maps can be used individually, recognizing the different environmental requirements of the two species relative
to light availability and water movement. These maps show suitable substrate that could be available for the settlement of *Acropora palmata* and *A. cervicornis*, and do not assign any type of threat potential or probability of survival facing potential transplants.

### 4.1. Possibilities for future research

The potential for future work related to this study is extensive. More extensive in-water surveys are needed to clarify any anomalous observations in relation to mapped habitat. This study also revealed the need for additional mapping efforts in the Dry Tortugas, where a large portion of habitat is currently unmapped.

Determining the benthic habitat required for these species is only the first step in determining true critical habitat. Other factors, such as water transparency, water quality, and temperature, are also important determinants of suitable habitat for the re-establishment of the species. The next step should be to incorporate these parameters into the potential-habitat maps to more specifically identify critical habitat for Atlantic and Caribbean *Acropora* spp. The results of this and future studies can also provide the framework for determining critical habitat for other species of coral.

Future work could also examine habitats where *Acropora* spp. was once found but from which it has since disappeared. The detection of these locations could provide the opportunity to identify which environmental parameters are now different from those at locations where *Acropora* spp. is still present. This may improve understanding of the most crucial environmental parameters necessary for these species’ survival.

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