Corals of the genus *Porites* are a locally abundant component of the epibiont community on mangrove prop roots at Calabash Caye, Turneffe Atoll, Belize


Mangrove prop roots support diverse epibiont communities, but they are generally regarded as inhospitable for corals. However, recent reports have documented corals thriving on mangrove roots in the U.S. Virgin Islands and Cuba, and it has been proposed that mangroves may provide a refuge from environmental conditions that trigger coral mortality on nearby reefs. It also raises interesting questions about the potential evolutionary significance of coral populations in mangrove forest. We investigated diverse mangrove habitats for the presence of corals at Calabash Caye, Belize, part of a recently designated marine reserve on Turneffe Atoll. Here we present data on the distribution, size and morphology of 127 colonies of branching *Porites* found in a survey of 1858 meters of mangrove prop roots fringing three qualitatively distinct bodies of water: a high-flow channel, a moderate-flow creek, and a low-flow mangrove pond. The distribution of *Porites* was highly clumped, with 108 colonies occurring in a 178-meter stretch of shoreline along the high flow channel. Colony morphology varied widely, from bushy colonies with more than 40 branch tips per 1000 cm$^3$ of ecological volume, to spindly colonies with fewer than 10 branch tips per 1000 cm$^3$, to new recruits that have not yet developed distinct branches. Comparisons of the same coral-bearing roots in 2013 and 2014 revealed that colonies can experience substantial growth in a year’s time. We also document a much more diverse coral fauna living in the mangroves at Crooked Creek, a high flow environment on the western edge of Turneffe Atoll. The data described here contribute to an emerging picture of mangroves as potentially important habitat for corals, while suggesting that different types of mangrove habitat vary in their suitability for different species of coral. Future studies are needed to identify the critical environmental features of mangrove habitats that support coral, to further characterize those corals that can utilize mangrove habitat, and to investigate potential connectivity between coral populations in mangroves and nearby reef habitats.
Corals of the genus *Porites* are a locally abundant component of the epibiont community on mangrove prop roots at Calabash Caye, Turneffe Atoll, Belize.

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Keywords: coral; mangrove; epibiont; *Porites*,

Running Head: *Coral epibionts of mangrove roots in Belize*
Abstract

Mangrove prop roots support diverse epibiont communities, but they are generally regarded as inhospitable for corals. However, recent reports have documented corals thriving on mangrove roots in the U.S. Virgin Islands and Cuba, and it has been proposed that mangroves may provide a refuge from environmental conditions that trigger coral mortality on nearby reefs. It also raises interesting questions about the potential evolutionary significance of coral populations in mangrove forest. We investigated diverse mangrove habitats for the presence of corals at Calabash Caye, Belize, part of a recently designated marine reserve on Turneffe Atoll. Here we present data on the distribution, size and morphology of 127 colonies of branching *Porites* found in a survey of 1858 meters of mangrove prop roots fringing three qualitatively distinct bodies of water: a high-flow channel, a moderate-flow creek, and a low-flow mangrove pond. The distribution of *Porites* was highly clumped, with 108 colonies occurring in a 178-meter stretch of shoreline along the high flow channel. Colony morphology varied widely, from bushy colonies with more than 40 branch tips per 1000 cm$^3$ of ecological volume, to spindly colonies with fewer than 10 branch tips per 1000 cm$^3$, to new recruits that have not yet developed distinct branches. Comparisons of the same coral-bearing roots in 2013 and 2014 revealed that colonies can experience substantial growth in a year’s time. We also document a much more diverse coral fauna living in the mangroves at Crooked Creek, a high flow environment on the western edge of Turneffe Atoll. The data described here contribute to an emerging picture of mangroves as potentially important habitat for corals, while suggesting that different types of mangrove habitat vary in their suitability for different species of coral. Future studies are needed to identify the critical environmental features of mangrove habitats that support coral, to further characterize
those corals that can utilize mangrove habitat, and to investigate potential connectivity between
coral populations in mangroves and nearby reef habitats.
Introduction

Mangroves can promote the health and taxonomic richness of nearby coral reefs through a number of mechanisms, including stabilizing sediments, increasing water clarity, and serving as a nursery for juvenile fishes and invertebrates that will migrate to the reef as adults [1, 2]. Additionally, mangrove prop roots support diverse communities of sessile epibionts, some of which can co-occur in nearby reef habitats [2]. For example, at seven Caribbean localities, coral reefs and nearby mangrove ecosystems were found to support overlapping but distinctive assemblages of sponges, implying that some sponge species can disperse between reef and mangrove [3], representing yet another mechanism whereby mangroves impact the biodiversity of nearby coral reefs.

To date, the abundance and distribution of scleractinians in mangroves has received relatively little study [4], but based on recent published reports from the U.S. Virgin Islands [5-7] and Cuba [8], there is emerging evidence to suggest that mangroves could represent a significant habitat for corals. Rogers reported 28 coral species growing on or among mangrove prop roots in Hurricane Hole, St. John (Table 1) [5]. A follow-up study quantified the abundance of two reef-building corals — *Colpophyllia natans* and *Diploria labyrinthiformis* — revealing that some specimens in the mangroves survived an outbreak of disease and bleaching that caused high mortality in nearby reef habitats [6]. Based on this finding, the authors suggested that mangroves may provide a refuge from conditions that promote bleaching on the reef because of differences in key environmental parameters e.g., shading from mangrove trees [7]. Alternatively, corals could become locally adapted to conditions in the mangroves. As poorly flushed mangrove habitats tend to experience higher temperatures than nearby reefs, mangroves could harbor populations of heat tolerant individuals whose larvae could replenish nearby reefs following
heat-related coral mortality [7]. More recently, Hernández-Fernández reported 11 species of hermatypic corals living on mangrove roots at Jardines de la Reina National Park in Cuba, all inhabiting roots that were also occupied by crustose coralline algae [8].

To evaluate the potential importance of mangroves as a habitat for corals, we conducted a systematic survey for corals on the prop roots of *Rhizophora mangle* at Calabash Caye, Turneffe Atoll, Belize. Here, we present data on the abundance, distribution, size, colony morphology, and year-to-year survival of corals along 1858 meters of mangrove prop roots fringing both banks of a high-flow channel, a moderate-flow creek, and a low-flow mangrove pond. In all, we found 127 coral colonies occupying mangrove roots at Calabash, all branching members of the genus *Porites*. Their distribution was highly clustered, with 108 colonies located in a single 178-meter stretch of shoreline. An incipient longitudinal study of 60 randomly sampled mangrove roots at Calabash revealed that roots bearing corals are relatively rare, but that corals inhabiting mangrove roots exhibit a high survival rate over a year’s time. Given that the coral fauna we characterized at Calabash was substantially less diverse than that reported in the U.S. Virgin Islands and Cuba, we also investigated coral species richness at Crooked Creek, a high flow environment along the western edge of Turneffe Atoll—there, we found representatives of eight scleractinian genera, in contrast to the single genus we found at Calabash. We discuss the implications of these findings for the importance of mangroves as a coral habitat in Turneffe Atoll, and for the hypothesis that mangroves may represent a refuge for reef corals suffering from the impacts of climate change.

Methods

Study sites
In November and December of 2013 and 2014, we surveyed the mangrove roots fringing three contiguous bodies of water at Calabash Caye, a small mangrove on the eastern (windward) face of Turneffe Atoll (Fig. 1). From north to south, these sites were: (1) a mangrove pond in the interior of Little Calabash (17°17'18.87"N, 87°48'43.46"W); (2) the channel separating Little Calabash from Calabash Caye (17°17'12.88"N, 87°48'41.86"W); and (3) a narrow creek connecting the channel with a mangrove pond in the interior of Calabash (17°17'10.50"N, 87°48'44.94"W). These three sites—henceforth referred to as (1) Seahorse Pond, (2) Calabash Channel, and (3) Calabash Creek—differed qualitatively with respect to current judged by in-water observers: the pond exhibited the lowest current, the channel exhibited the highest current, and the creek exhibited an intermediate current. At all three sites, the banks were continuously lined with prop roots of *Rhizophora mangle*, and the roots located furthest from the bank were densely occupied by a diverse epibiont community including macroalgae, sponges, tunicates, bivalves, anemones, and corals. From November 16-December 15, 2014, nine data loggers (HOBO Pendant® model 8K) were deployed to record hourly measurements of water temperature at seven locations along the survey site (Fig. 1B, a-g). We also performed visual surveys for corals on mangrove prop roots at Crooked Creek (17°19'45.00"N, 87°55'4.10"W), for comparison with the mangroves at Calabash (Fig. 1C). Crooked Creek is a high-flow channel on the western edge of Turneffe Atoll located approximately 12 km WNW of Calabash. The research was conducted under Aquatic Scientific Research Permit 000047-13 issued by the Belize Fisheries Department and signed by Fisheries Officer James Azueta.

*Targeted coral surveys*
In November of 2014, along three discontinuous sections of shoreline at Calabash Caye spanning 1858 meters (Fig. 1; red lines), the mangroves were systematically inspected for the presence of corals by three observers who slowly snorkeled in sequence past the fringing prop roots. Each root that harbored at least one coral was marked above the waterline using colored zip ties, and its location was determined using a handheld GPS device (Garmin; GPSmap 76CSx). Every coral colony was photographed from above and from one side using an underwater digital camera (Pentax WG-10). In each photograph, a centimeter rule was held in approximately the same plane as the center of the coral, so that each colony’s dimensions could be estimated from the photographs.

**Transect-based sampling of mangrove roots**

In November 2013, we established six 30m transects along the shorelines of Calabash Channel and Calabash Creek (Fig. 1B; 1-6). On each transect, a unique combination of colored zip ties was used to mark ten mangrove prop roots at regular intervals (3, 6, 9, 12, 15, 18, 21, 24, 27 and 30 m from the start of the transect). Video and still photography were used to record the macroscopic epibionts inhabiting each of these 60 marked roots. The same 60 roots were photographically re-sampled in November 2014. The still photos and videos were analyzed by five independent observers to identify corals living on the roots.

**Species identification**

Corals were identified based on gross colony morphology by observers on site and from photographs. In the case of the branching *Porites*, which proved to be the only type of coral we observed at Calabash, we did not attempt to identify individual colonies to species. Caribbean
branching *Porites* are thought to compose a monophyletic group, but the number of species constituting the complex is unclear. A recent molecular phylogenetic analysis of this clade based on the mitochondrial control region and 10 nuclear loci failed to resolve the three nominal species: *P. divaricata*, *P. furcata*, and *P. porites* [9]. Given this uncertainty, we refer to all of these specimens as branching *Porites*, to differentiate them from sympatric crustose/massive congeners such as *P. astreoides*.

**Characterization of colony size and morphology**

The length, width, and height of each branching *Porites* found at Calabash Caye were measured on site. From these linear dimensions, the ecological volume of each colony was calculated according to the formula of Shaish et al. [10]. Branch tips were counted from photographs aided by ImageJ [11]. Branch density was then calculated by dividing the number of branch tips by the ecological volume.

**Analysis of spatial distribution**

Distances between corals were estimated from GPS coordinates. Using the estimated distances between colonies within each contiguous stretch of shoreline, we applied the Clark-Evans test [12] modified for dispersion along one dimension [13] to determine if the average distance between nearest neighbors differed from null expectations.

**Results**

**Number and distribution of corals at Calabash Caye**
Representative photographs of coral colonies on red mangrove prop roots at Calabash Caye are shown in Fig. 2. In all, 127 coral colonies were identified along the 1858 meters of shoreline surveyed at Calabash Caye (Fig. 3). All of the corals identified appeared to be branching members of the genus *Porites*. However, twenty (15.7%) of the colonies were recent recruits that did not yet have any branches.

The corals exhibited a highly clustered distribution, with 85% (108/127) of the *Porites* colonies occurring on 26 prop roots in a 178-meter stretch along the north side of Calabash Channel (Fig. 3A, B). Single colonies were found on 9 of these roots, but multiple colonies were found on the other 17 roots, with as many as 18 colonies on a single root (Fig. 3B). Along the eastern edge of Calabash Creek and the southern side of Calabash Channel (Fig. 3A; blue line), corals were identified on 11 prop roots. Most of these roots bore a single coral, but three colonies were found on one root and five on another (Fig. 3C). Only two coral-bearing roots were found on the western edge of Calabash Creek (Fig. 3A; green line), each with only 1 colony per root.

No corals were found along the 821 m of shoreline surveyed within Seahorse Pond. According to the Clark-Evans test, the corals along the 1110 m shoreline encompassing Seahorse Pond and the north side of Calabash Channel were more tightly clustered than would be expected by chance (p<0.001; Table 2), while those located along the 550 m shoreline encompassing the south side of Calabash channel and the eastern edge of Calabash Creek were not (p=0.184).

We determined the size of the colonies using two metrics: the number of branch tips and the ecological volume [10]. The number of branch tips ranged from zero to 120 (mean = 9.9), with more than half of all corals having ≤3 branch tips (Fig. 4A). The ecological volume ranged from 0.25 to 8008 cm$^3$ (mean = 366.3; Fig. 4B). The two parameters were positively correlated ($r^2=0.39; p<0.0001; $Fig. 4C), but the number of branch tips varied substantially among colonies.
at higher ecological volumes. For example, the colony in Fig. 4D occupies about 73% of the ecological volume of the colony in Figure 4E (960 vs. 1320 cm$^3$), but it has over 8x as many branch tips (65 vs. 8).

To examine the distribution of *Porites* colonies by size, we divided all corals into four size categories based on branch number (0; 1-10; 11-40; >40) and four categories based on ecological volume (1-10; 10-100; 100-1000; 1000-10000 cm$^3$; Fig. 5). Regardless of whether colonies were categorized according to branch number or ecological volume, the categories were not distributed equally among shoreline regions (for branch number: $\chi^2(6) = 40.05, p<0.005$; for ecological volume: $\chi^2(6) = 25.49, p<0.005$). Nearly all of the colonies lacking branches (19/20) were found in the western section of the north shore of Calabash channel (Fig. 5A, B). By contrast, nearly all of the colonies with >40 branches (4/5) were found in the stretch of shoreline encompassing the eastern bank of the creek and the southern bank of the channel (Fig. 5A, C).

In addition to our targeted search for corals living on mangrove roots, we undertook a longitudinal, transect-based survey of mangrove roots at Calabash, which would allow us to estimate the frequency of mangrove roots bearing corals along stretches of shoreline where corals were observed. Of the 60 roots we surveyed in both 2013 and 2014 (labeled 1-6 in Fig. 1B), 57 did not bear any corals in either 2013 or 2014; the roots lacking corals included 20 of 20 roots sampled along the east bank of Calabash Creek, 20 of 20 along the south shore of Calabash Channel, and 17 of 20 (85%) along the north shore of Calabash Channel. In both 2013 and 2014, one root along the north shore of Calabash Channel was found to harbor a single coral colony (Fig. 6A, B), while a second root was found to harbor 4 coral colonies (Fig. 6C-E). In our 2013 survey, we identified a single unbranched colony on root 2-7. This colony cannot be seen in the images recorded in 2014.
Given their comparable locations on the same mangrove roots, we conclude the colonies found in 2013 are the same colonies identified in 2014 (Fig. 6), and therefore, it is possible to make inferences about change in colony shape and size in the intervening year. Among the five corals we can compare between years, there are colonies that appear to have lost branches and colonies that appear to have gained branches. In the single coral located on root 1-9 (the ninth root sampled on transect one) a substantial section of the colony appears to have been lost between 2013 and 2014 (see dashed line in Fig. 6A). By contrast, coral 1 on root 2-3 appears to have erupted new branches near its point of attachment with the mangrove root (compare dashed circles in Fig 6C and 6E).

Species diversity of corals at Crooked Creek

To determine whether the coral diversity on mangroves at Calabash Caye was representative of Turneffe Atoll, we surveyed the mangroves lining Crooked Creek, a high-flow channel on the western edge of Turneffe Atoll (Fig. 1C). In sharp contrast to Calabash Caye, at Crooked Creek, we were able to tentatively identify nine coral species in addition to branching *Porites* (Table 1). These included *Porites astreoides*, *Dichocoenia stokesii*, *Orbicella faveolata* and *Siderastrea siderea* (Fig. 7). Fire coral (*Millepora alcicornis*), a member of the cnidarian class Hydrozoa, was also abundant at Crooked Creek (Fig. 7) but absent from the mangroves we surveyed at Calabash.

Discussion

Mangroves are generally regarded as unsuitable habitat for scleractinians, and, as a result, few studies have focused on the abundance and diversity of corals living on or among mangrove prop roots [5, 7, 8]. There are a handful of references to corals occupying mangrove roots in
general studies on mangrove biodiversity [14-17]. For example, in their authoritative analysis of
mangrove epibionts at four cays off the coast of southern Belize, Farnsworth and Ellison
included two corals among the species list in the appendix (*Porites astreoides* and *Diploria
strigosa*), but they did not mention corals in the text [16]. In their biotic survey of the Pelican
Cays, McIntyre et al. reported corals inhabiting mangrove roots at five sites [4]. In one mangrove
pond, the prop roots supported a few colonies of *Agaricia* sp., while in another pond, a single
large colony of *Siderastrea siderea* was found inhabiting mangrove roots. In three other sites,
“corals” were listed among the members of the mangrove root community, but no species were
identified by name [4]. In a biotic survey of Twin Cays, also in southern Belize, Rützler and co-
workers reported corals occupying mangrove prop roots at three of 20 observation stations. The
species identified on mangrove roots were *Diploria strigosa*, *Porites astreoides*, and *P. porites*
[17].

In contrast to these general studies of mangrove biodiversity, recent studies in St. John and
Cuba have focused explicitly on corals. These studies have demonstrated that diverse coral
assemblages can thrive on and among mangroves [5-8], thus raising the question of how
important mangroves might be for particular coral species. Mangroves could prove critical to the
long term health of certain coral populations, perhaps especially during periods of extreme
environmental stress on nearby reef habitats [6, 7]. If this proves true, we may begin to regard
mangroves as part of the ecological niche for some coral species [18]. Alternatively, mangroves
may represent marginal habitat for corals with little impact on regional abundance or species’
resilience, even for those species that occur in mangroves regularly.

Understanding the importance of mangroves as coral habitat will require studies on coral
abundance and diversity from many more sites. Given the existing data (Table 1), it appears that
corals are widespread on mangroves, but mangrove coral assemblages can differ substantially between sites. At Calabash Caye, all of the corals we identified were branching *Porites*, representing at most two nominal species (*P. divaricata* and *P. furcata*), making it the least diverse mangrove coral fauna so far described. The most diverse site described to date, Hurricane Hole, boasts 34-36 distinct species (depending upon whether *P. divaricata, furcata,* and *porites* prove to be valid species)[7]. Of note, the published studies from Hurricane Hole do not specify in every instance whether a particular species was found attached directly to mangrove prop roots, on the peat shelf immediately below mangrove prop roots, or on some other substratum in one of the mangrove lined bays and creeks that were studied [7]. This distinction is potentially important when identifying suitable habitat for a given species. Intermediate levels of coral diversity were observed at five sites in Cuba (4-9 species; [5, 7]) and at Crooked Creek, where we observed 10-12 different species (depending upon resolution of the branching *Porites*). Branching *Porites* have been reported at every mangrove site where corals have been systematically surveyed (Table 1), which suggests that this may among those corals most tolerant of the mangrove forest environment.

With existing data we cannot ascertain definitively why some mangrove sites have high coral diversity, some sites have low coral diversity, and some sites are lacking corals entirely. The biodiversity of mangrove epibiont communities is driven by a combination of processes operating at different scales [16]. Key environmental parameters such as light, flow, and the abundance of predators can vary substantially between adjacent prop roots and even within a single root.

However, based on this study and previous studies on mangrove epibiont communities, it appears that flow is likely to be a major determinant of a mangrove site’s suitability for corals.
While a detailed analysis of water flow was beyond the scope of our study, we observed a qualitative difference in the current between Seahorse Pond, where we found no corals, and Calabash Channel, where we found 85% of the corals identified in our study. Within Seahorse Pond, there was no perceptible current, at least none sufficient to displace a snorkeler or a small buoy. The stillness of the water was further evidenced by a nearly ubiquitous layer of fine sediment covering the sessile epibionts on the mangrove roots, a layer that was easily dislodged by the current from a passing snorkeler. By contrast, in the channel, snorkelers had to actively swim against the current to maintain their positions relative to the bank, and the sessile epibionts inhabiting the mangrove roots were not covered in sediment. Other recent studies on low flow mangrove sites are consistent with the absence of corals in the low-flow Seahorse Pond. Ruiz et al. characterized more than 59,000 macroinvertebrate epibionts inhabiting prop roots in a low-flow coastal mangrove pond in Mexico, and did not report a single coral specimen [19], and Yates et al. reported finding no corals in the most interior portion of three embayments at Hurricane Hole [7].

Another factor that we suspect is impacting coral diversity in the mangroves is the fine-scale topography of the shoreline. Along the northern bank of Calabash Channel where we observed many branching *Porites* but no other species, there was a pronounced undercut in the peat bank, and the overhanging prop roots effectively shaded a habitat of mixed peat bank. By contrast, at Crooked Creek, the coral-bearing areas were characterized by a shallow, well-lit peat bank and carbonate platform that was occupied by numerous coral colonies, some of which extended from the bank to the prop roots (Fig. 7A, F). This microhabitat is similar to that depicted in the photographs of mangrove corals in St. John [5, 7] and Cuba [8]. We suspect that the broad, shallow, well-lit shelf observed at these sites can support a more diverse coral
assemblage by providing a larger settlement area for corals and by allowing some species to colonize the mangrove fringe that might not be well suited to settle and/or grow to substantial size directly on the prop roots themselves.

To understand the importance of mangrove populations for the regional abundance of corals—and whether mangroves might serve as refuges during periods of environmental stress—we will require data on the growth, health, reproductive output, and temporal variability of coral populations living in mangroves, as well as their relationship to populations in nearby reef habitats. The current study begins to address these needs by obtaining baseline data on the size and location of individual mangrove corals. By identifying a range of colony sizes, and documenting the persistence of individual colonies from year-to-year, we have shown that branching *Porites* can settle, survive, grow, and presumably reproduce in the channel and creek habitats at Calabash Caye. We are in the process of acquiring additional longitudinal data (1) to track the growth and survival of individual corals, (2) to determine how these life history traits might be impacted by microhabitat, (3) to determine how this population fluctuates over time, (4) to determine whether it is self-sustaining or requires constant immigration from adjacent “core” habitats, and (5) to determine whether this site may export larvae to nearby reef and seagrass habitats.

Branching *Porites* appear particularly adept at colonizing mangroves, and we suspect that phenotypic plasticity is critical to their ability to tolerate a range of environments, from high irradiance sites in shallow reefs, to shaded locations in the mangroves. The colony form of branching corals has been shown to be strongly impacted by features of the physical environment, particularly water flow and irradiance [20]. It is therefore noteworthy that our study has detected substantial variation in colony form among branching *Porites* in the
mangroves at Calabash, namely a 10-fold difference in the number of branch tips found in corals at a similar ecological volume. At this time, we lack the data necessary to determine the relative contributions of fixed genetic differences and phenotypic plasticity to the range of colony forms we observed. To address this question, we are currently working to determine the genetic relatedness and characterize the microhabitat of colonies exhibiting alternative morphologies. We are also monitoring the development of recent recruits to document their growth patterns, and how growth relates to microhabitat. Finally, we are conducting reciprocal transplants to directly test the capacity for phenotypic plasticity.

Going forward, we hope that this study will contribute to our understanding of the importance of mangrove habitats for coral resilience. Future studies will be required to determine if the utilization of mangroves by corals is predictable and deterministic or stochastic. If we discover that mangrove populations make important contributions to the long-term survival of some coral species, and that the type of mangrove habitat utilized by these corals is predictable, this information could prove vitally important to marine resource managers in the design of marine protected areas.

**Acknowledgments**

This research was conducted by students and faculty participating in the Marine Semester offered by the Boston University Marine Program (BUMP) and Biology Department. The research was conducted at the Calabash Caye Field Station (CCFS), Environmental Research Institute, University of Belize. We are grateful to the staff of BUMP (D. Brown, J. Hammer-Mendez, J. Perry, and J. Scace), the staff of CCFS (M. Alamina, V. Alamina, A. Cherrington, N. Craig, C. Encalada, J. Hall, J. Morey) and colleagues from UB (L. Cho-Ricketts, E. Garcia) for
their technical expertise and logistical support. We are grateful to J. Azueta and I. Majil at the
Belize Fisheries Department for assistance in obtaining research permits. We thank J. Lang for
assistance in identifying corals. EAR was supported by a summer research fellowship from the
Undergraduate Research Opportunities Program at Boston University.
References


Table 1 (on next page)

Species diversity of corals in mangrove habitats of the Caribbean
**Table 1. Species diversity of corals in mangrove habitats of the Caribbean**

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<td>34-36</td>
<td>5</td>
<td>4-5</td>
<td>6-7</td>
<td>7-9</td>
<td>6-7</td>
<td>1-2</td>
<td>10-12</td>
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</table>

1 referred to as *Montastrea faveolata*; 2 a range is given depending on whether branching *Porites* are counted as one species or multiple species; 3 not all corals found on mangrove roots in this study were identified by species. US Virgin Islands [5]: HH=Hurricane Hole; Cuba [8]: BS=Boca Stone; LA=Las Auras, M-n=Mariflores north, M-s=Mariflores south, Ni=Nicola; Belize: TC=Twin Cays [4]; Ca=Calabash Caye [the current study]; CC=Crooked Creek [the current study].
**Table 2** (on next page)

Clark-Evans analysis of dispersion
Table 2. Clark-Evans analysis of dispersion

<table>
<thead>
<tr>
<th>Shoreline</th>
<th>Corals</th>
<th>Span</th>
<th>( R_A )</th>
<th>( R_E )</th>
<th>( R_A/R_E )</th>
<th>( \sigma_{RE} )</th>
<th>C</th>
<th>p</th>
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</thead>
<tbody>
<tr>
<td>N. Channel(^1)</td>
<td>108</td>
<td>1100m</td>
<td>1.66 m</td>
<td>5.09 m</td>
<td>0.33</td>
<td>0.49</td>
<td>6.99</td>
<td>&lt;0.001</td>
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<td>S. Channel(^2)</td>
<td>14</td>
<td>550m</td>
<td>10.00 m</td>
<td>16.18 m</td>
<td>0.62</td>
<td>3.92</td>
<td>1.57</td>
<td>0.116</td>
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</tbody>
</table>

\(^1\) includes Seahorse pond; \(^2\) includes eastern shore of Calabash Creek; \( R_A \) = actual mean nearest-neighbor distance; \( R_E \) = expected mean nearest-neighbor distance; \( \sigma_{RE} \) = the standard error of the mean distance to nearest neighbor in a randomly distributed population with a known density; \( c \) = the standard variate of the normal curve.
Overhead view of study sites

(A) The locations of mangrove roots that were inspected for the presence of corals are shown for (B) Calabash Caye and (C) Crooked Creek. At Calabash Caye, the survey area was divided between three discontinuous stretches of mangrove: (1) the shoreline of Seahorse Pond which is contiguous with the northern shoreline of Calabash Channel; (2) the eastern edge of Calabash Creek which is contiguous with the southern shore of Calabash Channel; (3) the western edge of Calabash Creek. In panel B, the white diamonds labeled a-g indicate the approximate locations of temperature loggers, and the white lines labeled 1-6 indicate the approximate locations of 30m transects. In panel C, the red lines indicate the shoreline that was surveyed for corals.
Representative photographs of *Porites* inhabiting prop roots

The images depict a specimen that has not yet developed any branches (A) as well as larger colonies with eight (B) or more than 20 (C) branches. A 5-cm scale bar is shown in each photograph.
3

Plot of coral locations

(A) Along three stretches of shoreline (yellow, blue, and green lines), we identified 40 prop roots bearing corals (circles). (B-D) The graphs indicated the number of corals found at each point along the three transects.
Coral dimensions

(A) Number of corals with a given number of branches. (B) Number of corals with a given ecological volume. (C) Linear regression of branch number versus ecological volume. Photographs of two of the individual corals represented in this plot (red circles) are shown (D-E).
Geographic distribution of coral size classes at Calabash

(A) All corals along three stretches of shoreline (B-D) were placed into one of four size categories based upon the number of branch tips and one of four size categories based upon ecological volume. The pie charts indicate the proportion (and number) of corals in each size category for branch tips and for ecological volume for each stretch of shoreline. The same color scheme is used as in Fig. 3.
Visual comparison of the same coral colonies in 2013 and 2014

The single coral observed on mangrove root 1-9 is shown in 2013 (A) and 2014 (B). The corresponding sections of the coral colony are given the same number in each panel (1-3). The arrow indicates what appears to be the identical sponge species in the same location relative to the colony in both photographs. The dashed line in (A) indicates a region of the colony that was lost between 2014 and 2014 (B). The five corals observed on root 2-3 are shown for both 2013 (C, D) and 2014 (E). The presumed correspondence between colonies, based on their relative locations along the root, is indicated by the numbering (1-5). The dashed circles on colony 1 in 2013 (C) indicate protuberances near the base of the colony that appear to be located in the same relative positions as the bases of two erupting branches in 2014 (E). The asterisks (C, D) indicate branches that have experienced breakage.
Coral diversity at Crooked Creek

Representative photos of corals observed at Crooked Creek. (A) PA: *Porites astreiodes*; (B) bP: branching *Porites*; DS: *Dichocoenia stokesii*; (C) PA: *Porites astreiodes*; (D) OF: *Orbicella faveolata*; SS: *Siderastrea siderea*; (E) MA: *Millepora alcicornis* (a hydrozoan); (F) DS: *Dichocoenia stokesii*;