

**A peer-reviewed version of this preprint was published in PeerJ on 14 December 2017.**

[View the peer-reviewed version](https://doi.org/10.7717/peerj.4119) (peerj.com/articles/4119), which is the preferred citable publication unless you specifically need to cite this preprint.

Pizarro V, Rodríguez SC, López-Victoria M, Zapata FA, Zea S, Galindo-Martínez CT, Iglesias-Prieto R, Pollock J, Medina M. 2017. Unraveling the structure and composition of Varadero Reef, an improbable and imperiled coral reef in the Colombian Caribbean. PeerJ 5:e4119 <https://doi.org/10.7717/peerj.4119>

# Unraveling a resilient reef: structure and composition of Varadero, an imperiled coral reef in the Colombian Caribbean

Valeria Pizarro <sup>Corresp., 1</sup>, Sara C Rodríguez <sup>2</sup>, Mateo López-Victoria <sup>2</sup>, Fernando A Zapata <sup>3</sup>, Sven Zea <sup>4</sup>, Claudia T Galindo-Martínez <sup>5</sup>, Roberto Iglesias-Prieto <sup>5</sup>, Joseph Pollock <sup>5</sup>, Monica Medina <sup>5</sup>

<sup>1</sup> Ecomares NGO, Cali, Valle, Colombia

<sup>2</sup> Department of Natural Sciences and Mathematics, Pontificia Universidad Javeriana, Cali, Valle, Colombia

<sup>3</sup> Department of Biology, Universidad del Valle, Cali, Valle, Colombia

<sup>4</sup> Centro de Estudios en Ciencias del Mar - CECIMAR, Universidad Nacional de Colombia - Sede Caribe, Santa Marta, Magdalena, Colombia

<sup>5</sup> Department of Biology, Pennsylvania State University, State College, Pennsylvania, United States

Corresponding Author: Valeria Pizarro

Email address: [valeria.pizarro@ecomares.org](mailto:valeria.pizarro@ecomares.org)

Coral reefs supply millions of people with ecosystem goods and services, especially those living along tropical coastlines. Unfortunately, these ecosystems are disappearing at an alarming pace. In the Caribbean, the rate of coral loss is high (5.5 – 9.2% per year) and constant. In 2013, a healthy coral reef was discovered in one of the least expected places within the Colombian Caribbean: at the entrance of Cartagena Bay, a highly-polluted system that receives industrial and sewage waste, as well as high sediment and freshwater loads from an outlet of the Magdalena River (the longest and most populated river basin in Colombia). Here we provide the first characterization of Varadero Reef's geomorphology and biological diversity. We also compare these characteristics with those of a nearby reference reef, Barú Reef, located in an area much less influenced by the described polluted system. Below the murky waters, we found high coral cover of 45.1% ( $\pm 3.9$ ; up to 80% in some sectors), three species of lobster, eight of sea urchin, a fish community composed by 61 species from 24 families, and the typical zonation of a Caribbean fringing reef. All attributes found correspond to a reef that, according to current standards should be considered in "good condition". Current plans to dredge part of Varadero threaten the survival of this reef and could hinder efforts to uncover the underpinnings of this reef's remarkable resilience. There is, therefore, an urgent need to describe the location and characteristics of Varadero as a first step towards gaining acknowledgement of its existence and garnering inherent legal and environmental protections.

# 1 Unraveling a resilient reef: structure and composition of 2 Varadero, an imperiled coral reef in the Colombian 3 Caribbean

4 Valeria Pizarro<sup>1</sup>, Sara Catalina Rodríguez<sup>2</sup>, Mateo López-Victoria<sup>2</sup>, Fernando A. Zapata<sup>3</sup>, Sven  
5 Zea<sup>4</sup>, Claudia Tatiana Galindo-Martínez<sup>5</sup>, Roberto Iglesias-Prieto<sup>5</sup>, F. Joseph Pollock<sup>5</sup>, Mónica  
6 Medina<sup>5</sup>

7 <sup>1</sup> Fundación Ecomares, Cali, Valle, Colombia

8 <sup>2</sup> Department of Natural Sciences and Mathematics, Pontificia Universidad  
9 Javeriana Seccional Cali, Valle, Colombia

10 <sup>3</sup> Department of Biology, Universidad del Valle, Cali, Valle, Colombia

11 <sup>4</sup> Departament of Biology, Universidad Nacional de Colombia, Santa Marta, Magdalena,  
12 Colombia, [sezeas@unal.edu.co](mailto:sezeas@unal.edu.co)

13 <sup>5</sup> Department of Biology, Pennsylvania State University, State College, Pennsylvania, USA

14 Corresponding Author:

15 Valeria Pizarro<sup>1</sup>

16

17 Calle 5B # 4-139, Santa Marta, Magdalena, Colombia

18

19 Email address: [valeria.pizarro@ecomares.org](mailto:valeria.pizarro@ecomares.org)

## Abstract

Coral reefs supply millions of people with ecosystem goods and services, especially those living along tropical coastlines. Unfortunately, these ecosystems are disappearing at an alarming pace. In the Caribbean, the rate of coral loss is high (5.5 – 9.2% per year) and constant. In 2013, a healthy coral reef was discovered in one of the least expected places within the Colombian Caribbean: at the entrance of Cartagena Bay, a highly-polluted system that receives industrial and sewage waste, as well as high sediment and freshwater loads from an outlet of the Magdalena River (the longest and most populated river basin in Colombia). Here we provide the first characterization of Varadero Reef's geomorphology and biological diversity. We also compare these characteristics with those of a nearby reference reef, Barú Reef, located in an area much less influenced by the described polluted system. Below the murky waters, we found high coral cover of 45.1% ( $\pm$  3.9; up to 80% in some sectors), three species of lobster, eight of sea urchin, a fish community composed by 61 species from 24 families, and the typical zonation of a Caribbean fringing reef. All attributes found correspond to a reef that, according to current standards should be considered in "good condition". Current plans to dredge part of Varadero threaten the survival of this reef and could hinder efforts to uncover the underpinnings of this reef's remarkable resilience. There is, therefore, an urgent need to describe the location and characteristics of Varadero as a first step towards gaining acknowledgement of its existence and garnering inherent legal and environmental protections.

## Introduction

Coral reefs provide important ecosystem services (Moberg & Folke, 1999), but many currently face unprecedented pressure from multiple natural and anthropogenic factors (Wilkinson, 2008). Caribbean reefs have been particularly impacted, with coral cover decreasing from an average of 50% to 10% in just four decades (Jackson et al., 2014). Coral cover loss has resulted in a phase shift from coral to macroalgal domination with a concurrent increase in sponge abundance (e.g., Rose and Risk, 1985; Szmant, 2002; Ward-Paige et al., 2005; Chaves-Fonnegra et al., 2007; Maliao et al., 2008; Jackson et al., 2014).

Coral reef ecosystems, built mainly by scleractinian corals, typically thrive within a narrow range of environmental conditions characterized by low sedimentation rates, low nutrient

availability (i.e., oligotrophic waters), high light penetration, warm waters (e.g., around 28 °C) and salinity between 33 and 36 psu (Kleypas, McManus & Meñez, 1999; Díaz et al., 2000; Sheppard, Davy & Pilling, 2009). Although reefs can be found outside these ranges in “extreme” environmental conditions, such reefs are typically dominated by a low number of resistant specialist species. Some examples include reefs under higher water temperatures in the Persian Gulf and Hawaii (Oliver & Palumbi, 2009; Riegl & Purkis, 2012), reefs under low pH waters in Japan and Papua New Guinea (Fabricius et al., 2011; Inoue et al., 2013), and reefs under high salinity such as those at the Arabian Sea where salinity can exceed 45 psu and temperatures regularly top 34 °C (Rezai et al., 2004).

In 2013, a reef was discovered under unexpected conditions below a thick layer of highly turbid water at the mouth of Cartagena Bay, Colombia (López-Victoria et al., 2015). This reef, known as Varadero, is located south of Tierra Bomba Island, at the mouth of the highly-polluted Bay. The man-made “Canal del Dique” dumps industrial and sewage waste as well as discharges of sediment from the Magdalena River into the vicinity of Varadero. With a drainage basin covering 24% of Colombia’s surface area (27.3 million hectares), the Magdalena River feeds approximately  $144 \times 10^6$  tons of suspended solids into Cartagena Bay each year. This enormous sediment load has contributed to the demise of the Bay’s once vibrant coral reefs (Restrepo et al., 2006). Paradoxically, Varadero Reef has not only survived, but thrived with up to 80% coral cover dominated by large *Orbicella* spp. colonies, the major reef building corals in the Caribbean (López-Victoria et al. 2015).

Despite its close proximity to the city of Cartagena, Colombia (> 1 million inhabitants), Varadero Reef remained concealed due to perception that local environmental conditions were incompatible with reef growth. High levels of sedimentation and turbidity have previously been shown to drive coral bleaching and disease that can ultimately lead to coral death (Bruno et al., 2003; Harvell et al., 2007; Pollock et al., 2014). Here we provide a preliminary characterization of Varadero Reef, including its geomorphology (i.e., size, shape and location) and biological diversity (i.e., coral, fish and sponge community composition). We also compare these characteristics with those of a nearby reference reef, Barú Reef, located 4.5 km south of Varadero, in a location much less influenced by runoff from the Canal del Dique and the city of Cartagena.

Current plans to dredge part of Varadero threaten the survival of this reef and could hinder researchers' ability to gain insights into the factors that have allowed corals to thrive under such unusual conditions. There is, therefore, an urgent need to describe the location and characteristics of Varadero as a first step towards gaining acknowledgement of its existence and garnering inherent legal and environmental protections.

## Materials & Methods

In order to supplement the brief, general description of Varadero Reef reported by López-Victoria et al. (2015), detailed geomorphological and biological surveys were performed between 2014 (March) and 2015 (March and October). During the March 2015 field trip, Reef's geographic extent was assessed by two researchers diving along the border of the Reef with a GPS, recording in tracking mode, attached to an accompanying buoy. This information was downloaded using GIS software (Garmin BaseCamp). Subsequently a map of the Reef was produced. The Reef's coral diversity was characterized by two coral experts performing three replicate profiles starting in the deepest zone (in direction to open sea) towards Cartagena Bay (shallowest zone). The methods of Geister (1977) were employed, which include annotations of coral community composition at multiple depths. All profiles were compared and compiled to obtain a detailed profile of the Reef's coral community structure and diversity.

The vertical attenuation coefficients ( $K_d$ ) were determined at both sites using the cosine corrected sensor of a diving pulse modulated fluorometer (PAM) (Waltz, Germany). The PAM sensor was calibrated against a traceable reference sensor LiCor (USA). A diver operating the PAM maintained the instrument in a horizontal position and triggering the data collection system of the fluorometer at different depths. The maximum excitation pressure over photosystem II ( $Q_m$ ) was calculated in both sites using the effective quantum yield of photosystem II at apparent noon ( $\Delta F/F_m'$ ) and the maximum quantum yield of charge separation at dusk ( $F_v/F_m$ ) (Iglesias-Prieto et al., 2004).

A detailed benthic community assessment was also conducted to evaluate sessile and mobile species composition, fish diversity and abundance, and sponge richness. To allow comparison of Varadero with a nearby reef that reflected typical Caribbean reef environmental conditions, a reef on the Barú Peninsular (from now on Barú Reef) was also surveyed. At each reef, five

stations were established and two 30 m transects were deployed in the same landscape unit (i.e., reef type and depth). Quadrats (50 by 50 cm) were placed every three meters on each side of the transect and photographed for a total of 20 photo-quadrats per transect. Each photograph was analyzed using Coral Point Count 4.1 software (Kohler & Gill, 2006), which randomly places 50 points within the quadrat for a randomly stratified methodology (Kohler & Gill, 2006; Dumas et al., 2009; Andersen et al., 2012). The benthic component below each point was identified and categorized as coral (identified to coral species), sponge (identified to sponge species), algal overgrown dead coral, sand/rubble or other invertebrates (e.g., tunicates, gorgonians or zoanthids). Mobile reef invertebrates were also assessed using the same benthic transects. A visual census was performed of all sea urchins, conchs, and lobsters within a 1 m band of the transect. Macroalgal communities were characterized by randomly selecting five photoquadrats per transect, randomly placing 10 points within each quadrat (using Coral Point Count 4.1), and categorizing any observed macroalgae as fleshy, coralline or turf. Fleshy algae were identified to genus level. To compare Varadero and Barú Reefs, species richness, abundance and composition were tested for normal distributions (Shapiro-Wilk's test) then compared using a two sample Student's t-test in the software PAST version 3.14 (Hammer, Harper, & Ryan, 2001).

During exploratory dives, sponges were visually identified while swimming over the reef. Photographs and small samples were also taken for later spicule examination in cases when sponges could not be readily distinguished in the field. Species lists were made for both Varadero and Barú Reefs, separately for the upper terrace (down to 10 – 13 m) and slope (below 10 – 13 m) zones. Sponge species present within each of the 2 x 30 m band transects in the shallow terrace zone of Varadero (n = 7 transects) and Barú (n = 4 transects) were also recorded. This sampling scheme permitted calculation of gross abundances as percent frequency of occurrence (number of transects in which a sponge was present/total transects) and species richness per transect. Data on total coral and sponge cover obtained in 10 phototransects (covering 5 m<sup>2</sup> each, see above) in the upper terrace of each locality were also analyzed for trends in cover of sponges vs. corals vs. available substratum using simple correlation analysis. For sponge identification in the laboratory, small fragments of each collected sponge were digested in commercial bleach to obtain free spicules, which were observed under a light microscope. Species were identified using specialized literature and extensive local knowledge/experience (see Zea, 1987; Zea et al., 2014).



Overall fish diversity and community composition were visually assessed. In order to compile fish species lists for each reef, a team of three divers recorded all fishes observed while exploring the general reef areas of Varadero and Barú during a total of 8 dives on each reef (approximately 1-hour per dive), in 2014 and 2015. In 2015, 22 visual censuses were performed along 30 x 2 m belt-transects ( $n = 15$  at Varadero and  $n = 7$  at Barú) to characterize fish community composition. All individuals observed within each belt transect were counted and these counts were used to estimate mean species richness, diversity (Shannon's  $H'$ ), dominance (Simpson's  $D$ ) and evenness (Pielou's  $J'$ ). These community variables were compared between Varadero and Barú using a two sample Student's  $t$ -test, after establishing that the data met assumptions of normality and homoscedasticity with Shapiro-Wilk's and  $F$  tests, respectively. All tests were performed using PAST 3.14 (Hammer, Harper & Ryan, 2001).

To assess species abundance differences between sites, a regression analysis of mean species abundance was performed along with paired Student's  $t$ -tests. Given the different sampling efforts between the two localities, a sample-based rarefaction procedure was carried out to compare fish species richness between Varadero and Barú. Finally, a non-Metric Multidimensional Scaling (nMDS) analysis was carried out using Jaccard's similarity index (based on species occurrence) and the Bray-Curtis similarity index [based on the  $\log(x + 1)$  transformed abundance data] to examine differences in assemblage structure between the two localities based on species composition and abundance, respectively. The nMDS analysis was complemented with analyses of similarity (ANOSIM) based on either Jaccard or Bray-Curtis similarity. All statistical analyses and calculation of community indices were performed using the software PAST 3.11 (Hammer, Harper & Ryan, 2001).

## Results

### *Geomorphology and optical properties*

Located between the Bocachica navigation channel and the island of Barú, Varadero Reef has an area of approximately 1.12 km<sup>2</sup> (Figure 1). The Reef has two contrasting zones, the first (0.44 km<sup>2</sup>) is a well-developed reef where scleractinian coral colonies dominate the substratum. The second (0.68 km<sup>2</sup>) is a carbonated terrace with scattered corals, octocorals, a few other benthic species and sand patches with seagrasses (Figure 1c, Figure 2). The largest seagrass beds were



observed near the islands of Draga and Abanico (Figure 1c). Analyses of the vertical attenuation coefficients of the water in both sites indicate significant vertical stratification. We identify an upper layer with high attenuation values located between the surface and 3-5 m depth. Comparisons between the attenuation coefficients of the first layer at both sampling sites indicate significantly ( $p < 0.001$  ANOVA) higher attenuation values for Varadero Reef ( $0.336 \pm 0.050 \text{ m}^{-1}$ , average  $\pm$  SE,  $n = 32$ ) relative to Barú Reef ( $0.243 \pm 0.053 \text{ m}^{-1}$ ,  $n = 11$ ). In some cases, we identify a second layer with  $K_d$  values ranging between 0.193 and  $0.051 \text{ m}^{-1}$  at depths above the limit of the first layer between three to five meters (Figure 3). Depending on the depth profile of the reef, some corals were completely contained within the first optical layer (Figures 2-3). We recorded the maximum excitation pressure of photosystem II for *Orbicella faveolata* colonies growing in the shallow parts of both reefs. In both cases corals were exposed to irradiances high enough to induce significant levels of photoprotection at noon with  $Q_m$  values of  $0.208 \pm 0.109$ , average  $\pm$  SE,  $n = 25$  at 4.5 m depth and  $0.249 \pm 0.052$ ,  $n = 25$  at 6.0 m depth for Varadero and Barú Reefs respectively.

#### *Coral and benthic community*

In total, 42 scleractinian coral and four fire coral species (Families Milleporidae and Stylasteridae) were identified at Varadero (Table S1). These species include several threatened species such as the acroporids (*Acropora cervicornis* and *A. palmata*). Depth profiles indicate that Varadero Reef's calcareous matrix starts at around 27 to 35 m depth (Figure 2). At greater depths, moving towards open sea, the sand bottom has small patches of sponges and black corals (Anthipatharia). Coral cover from 27 to 35 m until approximately 10 to 12 m is relatively low (1 to 5%) and the reef slope is around  $45^\circ$ . Coral communities at this depth range are dominated by *Agaricia* spp. (*A. lamarcki*, *A. grahamae*), *Madracis* spp. and *Helioceris cucullata*. At 25 m and shallower, small plate-like growth forms of *Siderastrea siderea*, *Montastraea cavernosa* and *Mycetophyllia aliciae* were observed. Besides corals, tube and branching sponges, encrusting algae and cyanobacteria are present. Beginning at 18 m and shallower, small patches of *Undaria tenuifolia* start to appear, becoming more abundant until they dominate the landscape between 12 and 10 m. Between 12 and 10 m, live coral cover increases to 40 – 45%, the slope reduces to  $25 - 30^\circ$  and other scleractinian species are present, including *Porites astreoides*, *H. cucullata*, *Colpophyllia natans*, *Madracis auretenra*, *Scolymia cubensis*, and *O. faveolata* becomes more

common. At 10 – 12 m depth, growth morphologies of typically massive species are plate like and small (~ 10 – 40 cm maximum diameter). *M. auretenra* also form scattered monospecific patches in this area.

At approximately 8 m, the slope decreases to 10 – 15°, corals are more abundant and larger (up to 2 – 3 m diameter), but the main coral matrix is still dominated by *U. tenuifolia* and in some areas is mixed with *P. divaricata*. The morphology of typically massive coral species is a mix of massive and plate. The most common species are *O. faveolata*, *O. annularis*, *Meandrina meandrites*, *Pseudodiploria strigosa*, *M. ferox*, *M. cavernosa* and *S. siderea*. At this depth, it is possible to find *A. cervicornis*. At 6 m, coral cover increases to 50 – 60%, massive corals become dominant (especially *Orbicella* spp.), and patches of *U. tenuifolia* and *P. divaricata* can be found in sand patches. Between 5 and 3 m, massive corals dominate the reefscape, *O. faveolata* and *O. annularis* colonies with diameters exceeding 5 m are common and the slope decreases to almost 0°. Other common coral species include *U. agaricites*, *C. natans*, *U. tenuifolia*, *P. strigosa*, *P. astreoides*, *P. divaricata*, *S. cubensis*, *S. siderea*, *M. aliciae*, *Millepora complanata*, *M. alcicornis*, and *M. striata*. Live coral cover is higher than 50% and colonies of *A. cervicornis*, *A. palmata* and *A. prolifera* are found scattered throughout the Reef. This area of high coral cover which is dominated by large colonies of *Orbicella* spp. continues until around 3 m. At this depth, coral colony size and abundance decreases. Common coral species, between 3 and 2 m depth include *P. divaricata*, *O. faveolata*, *A. tenuifolia*, *P. astreoides*, *Favia fragum*, *P. strigosa*, *P. clivosa*, *M. cavernosa*, *S. siderea*, *A. fragilis*, as well as the milleporids *Millepora complanata* and *M. striata*. Most of the massive coral species' growth morphologies change to crustose, and the reef slope is less than 10°. Calcareous terraces appear at 2 m. In this area, dispersed corals (*P. clivosa*, *S. radians* and *S. siderea*), octocorals, and sand patches are common. Towards the Bay, close to the islands of Abanico and Draga, seagrasses (i.e., *Thalassia testudinum* and *Halodule wrightii*) are common.

Varadero Reef's benthos between 3 and 15 m is dominated by live coral ( $45.1 \pm 3.9\%$ ) and algae-overgrown dead coral ( $47.5 \pm 4.0\%$ ; average  $\pm$  SE). Sand and rubble ( $4.6 \pm 0.6\%$ ), sponges ( $0.7 \pm 0.1\%$ ) and other invertebrates (gorgonians, zoanthids, etc.) ( $1.8 \pm 0.9\%$ ) are also observed. 38 coral species (scleractinian and fire corals) were identified. The most abundant species are *O. faveolata* (38.1%), *U. agaricites* (28.8%), *O. annularis* (14.4%) and *U. tenuifolia* (12.2%) (Table

S1). Similar to Varadero, the most common benthic components at Barú Reef are algae-overgrown dead coral ( $56.9 \pm 2.7\%$ ) and live coral ( $38.1 \pm 3.2\%$ ). The other benthic categories assessed show low percentage cover of sand and rubble ( $3.4 \pm 1.6\%$ ), sponges ( $0.8 \pm 0.2\%$ ) and other invertebrates ( $0.9 \pm 0.3\%$ ). In total, 35 coral species were identified, and, similar to Varadero, the most common were *O. faveolata* (25.6%), *U. agaricites* (11.3%), *O. annularis* (10.4%) and *U. tenuifolia* (4.5%) (Table S1).

### *Sponge community*

In total, fifty sponge species were observed at Varadero (38 species) and Barú (31 species) Reefs. The upper shallower terraces (between 3 and 10 m depth), which were more thoroughly documented through more dives and transects, hosted a total of 43 species. Upper terraces were more sponge species rich at Varadero (36 in total) than Barú (25 in total), although the number of species per transect were not significantly different (t-Student test,  $p = 0.86$ ),  $10.0 \pm 1.23$  species per transect (mean  $\pm 1$  standard error,  $n = 7$  transects) for Varadero, and  $10.5 \pm 2.36$  for Barú ( $n = 4$  transects) (Table S2). Eight species were observed in greater than 50% of terrace transects on both reefs, *Mycale laevis*, *Niphates erecta*, *Ircinia felix*, *Monanchora arbuscula*, *Lissodendoryx colombiensis*, *Haliclona wallentinae*, *Cliona laticavicola* and *Scopalina ruetzleri*. None of these common species were exclusive to either reef, and when reef-specific species were observed, they were typically comprised of single occurrences. Visually, sponge abundance was similarly low in both Varadero and Barú Reef terraces though there were sponge patches growing on dead coral. Mean coral cover estimated from phototransects was slightly but not significantly higher in Varadero than in Barú ( $45.1 \pm 14.3\%$  vs.  $38.1 \pm 12.0\%$  respectively, t-Student test,  $p = 0.18$ ,  $n = 10$  transects per site, Figure 4). Sponge cover was equally low and similar between the two localities ( $0.66 \pm 0.21\%$  and  $0.80 \pm 0.25\%$  respectively, t-Student test,  $p = 0.52$ ). Moreover, correlations between per-transect total coral and sponge cover, although negative as expected, were not significant (Varadero,  $r = -0.42$ ,  $p = 0.22$ ; Barú,  $r = -0.06$ ,  $p = 0.86$ ). Mean sponge cover was also not significantly correlated with the availability of dead coral substratum (covered with turf and macroalgae, Varadero,  $r = 0.42$ ,  $p = 0.23$ ; Barú,  $r = 0.36$ ,  $p = 0.30$ ), which was higher in Barú ( $56.9 \pm 18.0\%$ ) than in Varadero ( $51.4 \pm 16.3\%$ ).

### *Fish community*

A total of 61 fish species from 24 families was observed at Varadero Reef compared to 44 species from 22 families observed at Barú. While a total of 67 species were observed at both sites combined, 38 species were common to both. Twenty four species were observed at Varadero only, while six species were observed exclusively at Barú. Overall, Jaccard's coefficient of similarity considering the full fish species list of each site was 0.57 (Table S3). The number of species per family was similar between Varadero and Barú ( $r = 0.90$ ,  $p < 0.001$ ,  $n = 26$  families) and at both sites damselfishes (Pomacentridae) were the most species rich (8 and 7 species at Varadero and Barú, respectively), followed by wrasses (Labridae; 5 species at each site), groupers (Serranidae; 5 and 4 species, respectively) and parrotfishes (Scaridae; 4 species at each site; Table S3).

Considering only data from visual censuses, a total of 834 individuals belonging to 36 species were observed at Varadero, while only 519 individuals of 32 species were observed at Barú. Correcting for differences in sampling effort, sample-based rarefaction indicated that, for the same number of samples, species richness was slightly greater at Barú than at Varadero (Figure S1). Nonetheless, mean species richness within transects at Varadero did not differ significantly from mean species richness at Barú (Table 1). Except for the total number of individuals per transect, which was on average significantly greater at Barú than at Varadero, none of the other community parameters (Simpson's Dominance  $D$ , Shannon's Diversity  $H'$ , and Pielou's Evenness  $J'$ ) differ significantly between Varadero and Barú ( $p > 0.05$ ) (Table 1). Even though there was a highly significant positive correlation between the abundance of species common to both sites (considering only species observed in transects at both sites;  $r = 0.95$ ,  $p < 0.001$ ,  $n = 26$  species), a paired Student's  $t$ -test indicated that mean abundance was significantly greater at Barú than at Varadero (mean difference = 0.78,  $t = -2.51$ ,  $p = 0.019$ ).

Results of the nMDS analysis showed that there was a great deal of overlap in fish assemblage structure between Varadero and Barú considering either species composition alone (based on Jaccard's similarity; Figure 5a) or species abundance and composition (based on Bray Curtis's similarity; Figure 5b). ANOSIMs based on these two similarity measures indicated that the fish assemblage at Varadero did not differ significantly from that at Barú (Jaccard-based ANOSIM,  $R = 0.03$ ,  $p = 0.37$ ; Bray-Curtis-based ANOSIM,  $R = -0.06$ ,  $p = 0.69$ ).

## Discussion

Caribbean coral reefs are declining rapidly due to anthropogenic activities (e.g., overfishing, pollution, etc.), climate change and the synergies between these factors. Caribbean reefs have experienced declines in coral cover (and increases in macroalgae and sponge cover), and reduction in the abundances of sea turtles, sharks and fish populations since the 1970s (Jackson et al. 2014). Reef deterioration has not been equal throughout the Caribbean with few regions still holding coral cover higher than 30% (Gardner et al., 2003). Most areas with relatively high coral cover are under some conservation/management program and have experienced little anthropogenic influence from land-based pollution and fisheries (Jackson et al., 2014). Moreover, regional and global risk assessments correlate reefs' vulnerability to their proximity to man-made stressors (Burke et al., 2011). The discovery of an apparently healthy reef in Varadero adjacent to the major population center of Cartagena, Colombia, apparently runs counter to the prevailing dogma.

The development of coral reefs under "sub-optimal" conditions (e.g., high sedimentation, nutrients) does not appear to be a widespread phenomenon, though a few disparate cases have been recently reported. These anomalous reef ecosystems can be found in warm waters (Liddell & Ohlhorst, 1987; Spalding & Brown, 2015), upwelling-influenced areas (Bayraktarov et al., 2013), high latitudes (Harriot & Banks, 2002) and naturally turbid waters (Anthony, 2006; Smithers & Larcombe, 2003). Under extreme conditions, corals have adapted and/or acclimatized to the high temperature variance, and heterotrophic feeding is their dominant feeding mode (Teece, et al., 2011; Hughes & Grottoli, 2013). Additionally, the shading from elevated turbidity decreases photo-oxidative damage produced during warm-water stress (Lirman & Fong, 2007; Manzello et al., 2015).

Most of the reefs subjected to ongoing or temporal sedimentation have growth constraints due to the limitation on light penetration. Perry and Larcombe (2003) predicted that reef framework development in turbid environments might be restricted or absent, limiting coral distribution to shallow waters. Correspondingly, the portions of Varadero Reef with highest coral cover are currently constrained to the shallower portions of the reef, where they appear to be autotrophic as indicated by their relatively high  $Q_m$  values. Environmental conditions at Varadero Reef have changed drastically since the Spaniards arrived several centuries ago. As described by Restrepo

et al. (2017), before the opening of the Canal del Dique during the 16<sup>th</sup> century in the colonial period, and subsequent modifications in the 19<sup>th</sup> Century, Cartagena Bay had no river inputs and coral reefs and seagrass beds flourished inside the Bay (Martínez et al., 2010). The massive arrival of waters from the Magdalena River via the Canal del Dique, after the three major modifications to the channel in 1925, 1951 and 1984 (Mogollon, 2013), drastically changed conditions within the Bay from clear, warm-waters to a tidal estuarine environment (Restrepo et al., 2017). The dispersion patterns of the turbid plume of the Canal del Dique in the Cartagena Bay are highly variable depending on the hydrodynamic and meteorological conditions (Lonin et al., 2004). In this context, the optical properties of the water at Varadero Reef could experiment dramatic short-term changes depending on the prevailing hydro-meteorological conditions. The description of the variability in the optical properties of the water column is key to understand the energy and calcification balance of the coral community.

Varadero Reef is highly influenced by local stressors including eutrophication, agro-chemical runoff, port and industry development, and tourism activities. The main stressor being land-based pollution that flows into the Bay through the Canal del Dique (Mogollón, 2013). In addition to the influx of large volumes of fresh water, sediment loads arriving into the Bay can top 150 million tons per year (Restrepo et al., 2006). Varadero Reef appears to be a relic of the reef formations that dominated Cartagena Bay and adjacent coastal regions during the pre-Columbian period. Despite these challenging environmental conditions, our results on reef structure and species composition demonstrate that Varadero Reef is a functional ecosystem, fully developed and similar to those found on nearby reefs (e.g., Barú and Rosario Archipelago) and Caribbean reefs more broadly (Zea, 2001; Claro & Cantelar-Ramos, 2003; Pattengill-Semmens & Semmens, 2003; Valderrama & Zea, 2003; Alvarado-Chacon, Pizarro, & Sarmiento-Segura, 2011; Kramer, Marks, & Turnbull, 2014).

The existence of Varadero, a “paradoxical reef” (López-Victoria et al., 2015), is a call for scientists and managers to start looking in unexpected places for similar reefs. More importantly, Varadero may hold information on reef coral resilience, resistance, and adaptations to high sedimentation and turbidity. In this context, Varadero could serve as a natural laboratory and potentially provide source material for reseeded future reef environments. Current reef degradation challenges the initial goal of restoration ecology, meaning that returning to a pre-



disturbance state might be not possible and/or practical under present climate change (van Oppen et al., 2017). Tolerance to warmer and acidified waters, greater fluctuations in salinity and exposure to nutrients, herbicides and other pollutants are critical coral resilience traits. Our observations and preliminary results of ongoing research indicate that some of these traits can be found at Varadero, but further research is needed.

If the dredging for a new shipping channel is authorized by government authorities (Agencia Nacional de Licencias Ambientales – ANLA), we estimate that 25% of the reef will be directly affected and around 50% will be indirectly affected. The environmental impacts of this dredging include sediment stress (suspended and deposited), release of toxic contaminants, noise contamination, and complete destruction of benthic organisms within the dredge path (Rogers, 1990; Erftemeijer et al., 2012; Roberts, 2012). Depending on the intensity, duration and frequency of increased turbidity and sedimentation, the impacts on corals may include: smothering and burial, shading, bleaching, disease (Pollock et al. 2014), and decreased survival and recruitment success of coral larvae (Erftemeijer et al., 2012). Additionally, a recent review on the effect of dredging on fish suggests the potential for elevated fish mortality, especially in early life stages (eggs and larvae) (Wegner et al, 2017). The destruction of Varadero Reef would be a loss for the scientific community, for local stakeholders and for Colombia, a country struggling to emerge from a 50-year civil war conflict.

## Acknowledgements

We would like to thank the community of Bocachica, specially the Eight Brothers with whom we did all our fieldwork in Varadero and Barú. This community has welcomed and teach us about their uses of Varadero Reef and other nearby areas. Additionally, to all the people including the crew of Oregon State University from Terra, that have spread the word about Varadero Reef.

## References

- Alvarado-Chacon E, Pizarro V, Sarmiento-Segura A. 2011. Formaciones arrecifales. In Zarza-Gonzalez E. ed. *El entorno ambiental del Parque Nacional Natural Corales del Rosario y de San Bernardo*. Cartagena de Indias: Parques Nacionales Naturales de Colombia, 109-123.
- Andersen PK, Borgan O, Gill RD, Keiding N. 2012. *Statistical models based on counting processes*. New York: Springer Science & Business Media.
- Anthony K. 2006. Enhanced energy status of corals on coastal high-turbidity reefs. *Marine Ecology Progress Series* 319:111-116.



- Bayraktarov E, Pizarro V, Eidens C, Wilke T, Wild C. 2013. Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling. *PLoS ONE* 8: e80536 DOI:10.1371/journal.pone.0080536.
- Bruno JF, Petes LE, Drew Harvell C, Hettinger A. 2003. Nutrient enrichment can increase the severity of coral diseases. *Ecology letters* 6:1056-1061.
- Burke L, Reyntar K, Spalding M, Perry A. 2011. *Reefs at risk revisited*. Washington D.C.: World Resources Institute.
- Chavez-Fonnegra A, Zea S, Gomez M. 2007. Abundance of the excavating sponge *Cliona delitrix* in relation to sewage discharge at San Andrés Island, SW Caribbean, Colombia. *Boletín de Investigaciones Marinas y Costeras* 36:63-78.
- Claro R, Cantelar-Ramos K. 2003. Rapid assessment of coral communities of María la Gorda Southeast Ensenada de Corrientes, Cupa (part 2: fishes). *Atoll Research Bulletin* 496:278-293.
- Díaz JM, Barrios LM, Cendales MH, Garzon-Ferreira J, Geister J, Lopez-Victoria M, Ospina GH, Parra-Velandia F, Pinzón J, Vargas-Angel B, Zapata FA, Zea, S. 2000. *Áreas coralinas de Colombia*. Santa Marta: Serie Publicaciones Especiales No. 5.
- Dumas P, Bertaud A, Peignon C, Leopold M, Pelletier D. 2009. A “quick and clean” photographic method for the description of coral reef habitats. *Journal of Experimental Marine Biology and Ecology* 368:161-168.
- Erfteimeijer P, Riegl B, Hoeksema B, Todd P. 2012. Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin* 64:1737-1765.
- Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, De'ath G, Okazaki R, Muehllehner N, Glas MS, Lough JM. 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* 1:165-169.
- Gardner T, Cote I, Gill J, Grant A, Watkinson A. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958-960.
- Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. *Proceedings of the 3rd International Coral Reef Symposium* 1:23-29.
- Hammer O, Harper D, Ryan P. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4:1-9.
- Harriot V, Banks S. 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21: 83-94.
- Harvell D, Jordán-Dahlgren E, Merkel S, Rosenberg E, Raymundo L, Smith G, Weil E, Willis, B. 2007. Coral disease, environmental drivers, and the balance between coral and microbial associates. *Oceanography* 20:172-195.
- Hughes A, Grottoli A. 2013. Heterotrophic compensation: a possible mechanism for resilience of coral reefs to global warming or a sign of prolonged stress? *PLoS ONE* 8:e81172.
- Iglesias-Prieto, R., Beltrán V. H., LaJeunesse, T. C., Reyes-Bonilla, H., Thomé, P. E. 2004 Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. *Proc. R. Soc Lond. B* 271:1757-1763.
- Inoue S, Kayanne H, Yamamoto S, Kurihara H. 2013. Spatial community shift from hard to soft corals in acidified water. *Nature Climate Change* 3:638-687.
- Jackson J, Donovan M, Cramer K, Lam W. 2014. *Status and trends of Caribbean coral reefs: 1970-2012*. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN.
- Kleypas J, McManus J, Meñez L. 1999. Environmental limits to coral reef development: where do we draw the line? *American Zoologist* 39:146-159.

- 423 Kohler K, Gill S. 2006. Coral Point Count with Excel extensions (CPCe): a visual basic program  
424 for the determination of coral and substrate coverage using random point count  
425 methodology. *Computers & Geosciences* 32:1259-1269.
- 426 Kramer P, Marks K, Turnbull T. 2014. Assessment of Andros Island reef system, Bahamas (part  
427 2: fishes). *Atoll Research Bulletin* 496:100-123.
- 428 Liddell W, Ohlhorst S. 1987. Patterns of reef community structure, North Jamaica. *Bulletin of*  
429 *Marine Science*, 40: 311-329.
- 430 Lirman D, Fong P. 2007. Is proximity to land-based sources of coral stressors an appropriate  
431 measure of risk to coral reefs? An example from the Florida Reef Tract. *Marine Pollution*  
432 *Bulletin* 54:779-791.
- 433 Lonin S, Parra C, Andrade C, Thomas Y.-F. 2004. Patrones de la pluma turbia del Canal del  
434 Dique en la Bahía de Cartagena. *Boletín Científico CIOH* 22:77-89
- 435 López-Victoria M, Rodríguez-Moreno M, Zapata FA. 2015. A paradoxical reef from Varadero,  
436 Cartagena Bay, Colombia. *Coral Reefs* 34:231.
- 437 Malaio R, Turingan R, Lin J. 2008. Phase-shift in coral reef communities in the Florida Keys  
438 National Marine Sanctuary (FKMNS), USA. *Marine Biology* 154:841-853.
- 439 Manzello D, Enochs I, Kolodziej G, Carlton R. 2015. Recent decade of growth and calcification  
440 of *Orbicella faveolata* in the Florida Keys: an inshore-offshore comparison. *Marine Ecology*  
441 *Progress Series* 521:81-91.
- 442 Martínez J, Yokoyama Y, Delgado A, Matsuzaki H, Rendon E. 2010. Late Holocene marine  
443 terraces of the Cartagena region, southern Caribbean: the product of neotectonism or a  
444 former high stand in sea-level? *Journal of South American Earth Sciences* 29:214-224.
- 445 Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. *Ecological*  
446 *Economics* 29:215-233.
- 447 Mogollón JV. 2013. *El Canal del Dique: historia de un desastre ambiental*. Bogotá: El Áncora  
448 Editores.
- 449 Pattengill-Semmens C, Semmens B. 2003. Status of coral reefs of Little Cayman and Grand  
450 Cayman, British West Indies, in 1999 (part 2: fishes). *Atoll Research Bulletin* 496:226-247.
- 451 Perry C, Larcombe P. 2003. Marginal and non-reef-building coral environments. *Coral Reefs*  
452 22:427-432.
- 453 Pollock FJ, Lamb JB, Field SN, Heron SF, Schaffelke B, Shedrawi G, Bourne DG, Willis BL.  
454 2014. Sediment and turbidity associated with offshore dredging increase coral disease  
455 prevalence on nearby reefs. *PLoS ONE* 11: e0165541.
- 456 Restrepo J, Escobar J, Otero L, Franco D, Pierini J, Correa I. 2017. Factors influencing the  
457 distribution and characteristics of surface sediment in the Bay of Cartagena, Colombia.  
458 *Journal of Coastal Research* 331:135-148.
- 459 Restrepo J, Zapata P, Díaz JM, Garzón-Ferreira J, García C. 2006. Fluvial fluxes into the  
460 Caribbean Sea and their impact on coastal ecosystems: the Magdalena River, Colombia.  
461 *Global and Planetary Change* 50: 33-49.
- 462 Rezai H, Wilson S, Claereboudt M, Reigl B. 2004. Coral reef status in ROPME Sea area. In  
463 Wilkinson C, ed. *Status of coral reefs of the world*. Townsville, Australia: Australian  
464 Institute of Marine Science, 155-170.
- 465 Riegl BL, Purkis SJ. 2012. Coral reefs of the Gulf: adaptation to climatic extremes in the world's  
466 hottest sea. In: Riegl BL & Purkis SJ, eds. *Coral reefs of the Gulf: adaptation to climatic*  
467 *extremes*. USA: Springer Science & Business, 1-4.

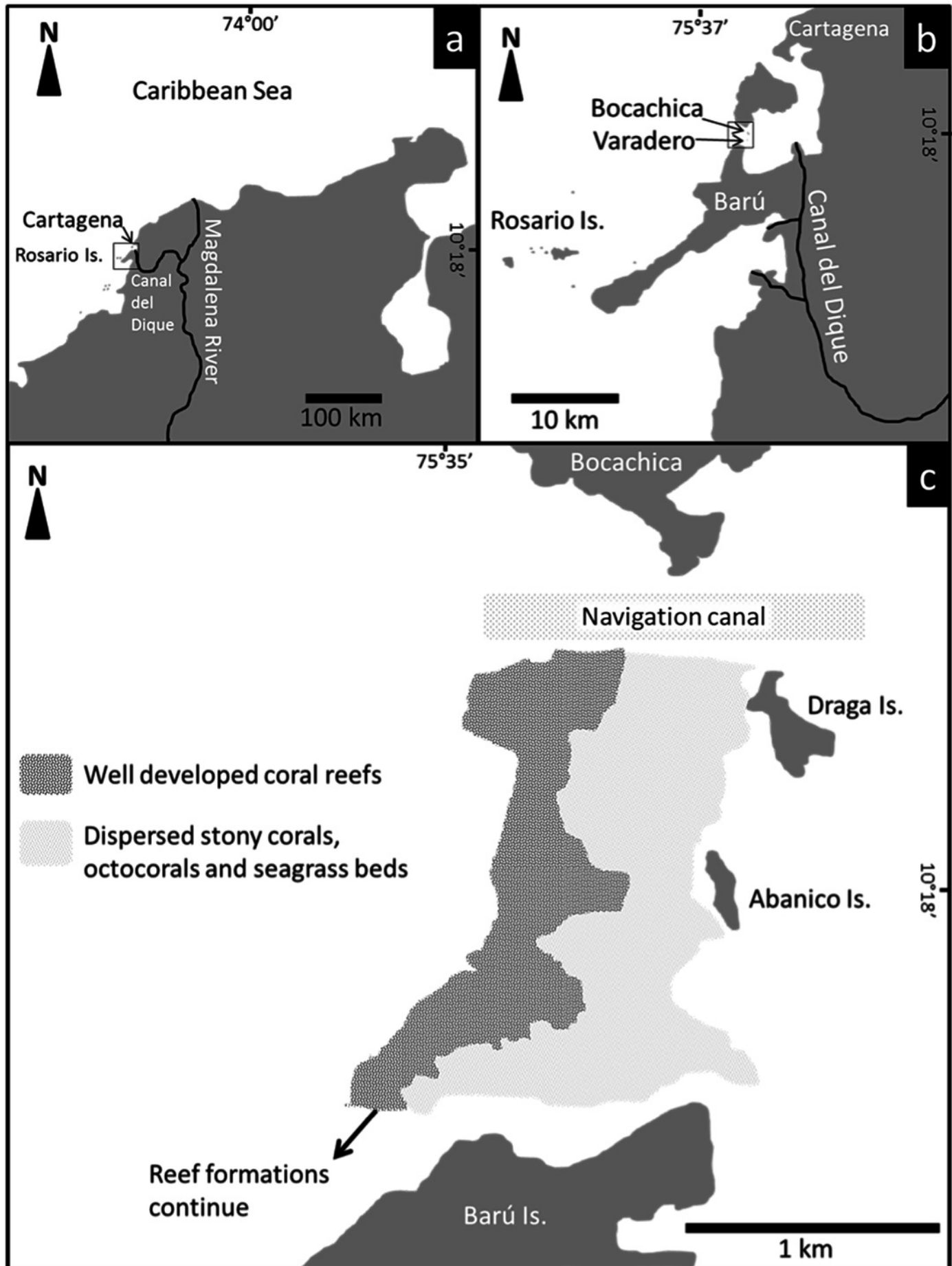
- 468 Roberts D. 2012. Causes and ecological effects of resuspended contaminated sediments (RCS) in  
469 marine environments. *Environment International* 40:230-243.
- 470 Rogers C. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology*  
471 *Progress Series* 62:185-202.
- 472 Rose C, Risk M. 1985. Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* head on  
473 an organically polluted portion of the Grand Cayman. *Marine Ecology* 6:345-363.
- 474 Oliver TA, Palumbi SR. 2009. Distributions of stress-resistant coral symbionts match  
475 environmental patterns at local but not regional scales. *Marine Ecology Progress Series*  
476 378:93-103.
- 477 Smithers S, Larcombe P. 2003. Late Holocene initiation and growth of nearshore turbid-zone  
478 coral reef: Paluma shoals, central Great Barrier Reef, Australia. *Coral Reefs* 22:499-505.
- 479 Sheppard CRC, Davy SK, Pilling GM. 2009. The Biology of Coral Reefs. United Kingdom:  
480 Oxford University Press.
- 481 Spalding M, Brown B. 2015. Warm-water coral reefs and climate change. *Science* 350: 769-771.
- 482 Szmant A. 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline?  
483 *Estuaries* 25:743-766.
- 484 Teece M, Estes B, Gelsleichter E, Lirman D. 2011. Heterotrophic and autotrophic assimilation of  
485 fatty acids by two scleractinian corals, *Montastraea faveolata* and *Porites astreoides*.  
486 *Limnology and Oceanography* 56:1285-1296.
- 487 Valderrama D, Zea S. 2003. Esquemas de distribución de esponjas arrecifales (Porifera) del  
488 noroccidente del Golfo de Úraba, Caribe Sur, Colombia. *Boletín de Investigaciones Marinas*  
489 *y Costeras* 32:37-56.
- 490 van Oppen M, Gates RD, Blackall LL, Cantin N, Chakravarti LJ, Chan WY, Cormick C, Crean  
491 A, Damjanovic K, Epstein H, Harrison P, Jones TA, Miller M, Pears RJ, Peplow LM, Raftos  
492 DA, Schaffelke B, Stewart K, Torda G, Wanchenfeld D, Weeks A, Putnam HM. 2017.  
493 Shifting paradigms in restoration of the world's coral reefs. *Global Change Biology*  
494 doi:10.1111/gcb.13647.
- 495 Ward-Paige C, Risk M, Sherwood O, Jaap W. 2005. Clionid sponge survey on the Florida Reef  
496 Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* 51:570-579.
- 497 Wegner A, Harvey E, Wilson S, Rawson C, Newman S, Clarke D, Saunders BJ, Browne N,  
498 Travers MJ, Mcilwain JL, Erteneijer PA, Hobbs J-PA, Mclean D, Depczynski M, Evans RD.  
499 2017. A critical analysis of the direct effects of dredging on fish. *Fish and Fisheries* 1-19.  
500 DOI: 10.1111/faf.12218.
- 501 Wilkinson C. 2008. *Status of coral reefs of the world: 2008*. Townsville, Australia: Global Coral  
502 Reef Monitoring Network and Reef and Rainforest Research Center.
- 503 Zea S. 1987. Esponjas del Caribe colombiano. Dictyoceratida, Dendroceratida, Verongida,  
504 Haplosclerida, Poecilosclerida, Halichondrida, Axinellida, Demosporida y  
505 Homosclerophorida. *Catálogo Científico* 1-286.
- 506 Zea S. 2001. Patterns of sponge (Porifera, Demospongiae) distribution in remote, oceanic reef  
507 complexes of the southwestern Caribbean. *Revista de la Academia Colombiana de Ciencias*  
508 25:597-592.
- 509 Zea S, Henkel TP, Pawlik JR. 2014. The Sponge Guide: a picture guide to Caribbean sponges.  
510 Available at [www.spongeguide.org](http://www.spongeguide.org) (accessed March 2016).

# Figure 1

Location and distribution of Varadero Reef.

Figure 1. Location and distribution of Varadero Reef. The reef continues to the South towards Barú Island.

*\*Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

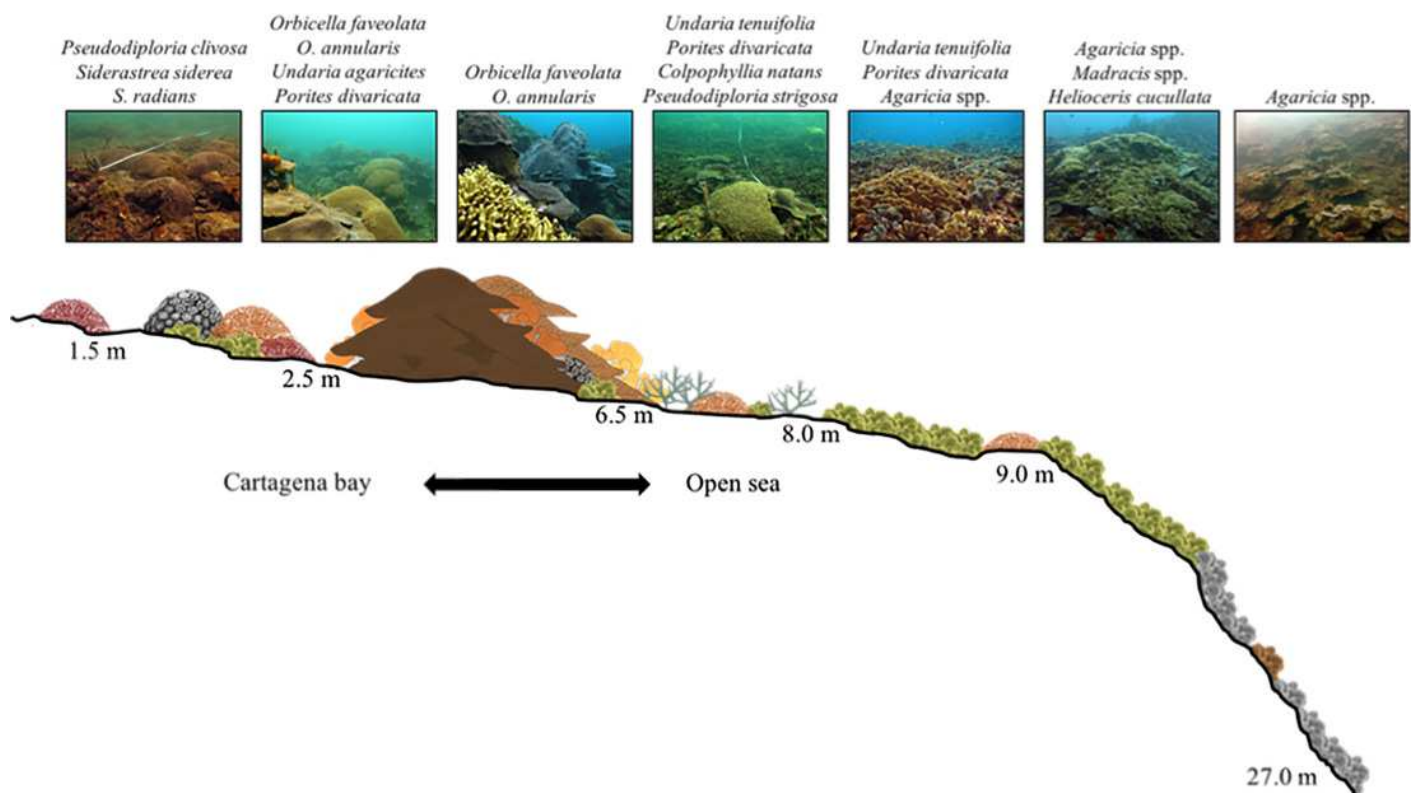




# Figure 2

## Varadero Reef profile

Figure 2. Profile of Varadero Reef showing the typical zonation and coral composition. Top panels correspond to each sector of the reef and the dominant scleractinian coral species/genus (Credit: coauthors).

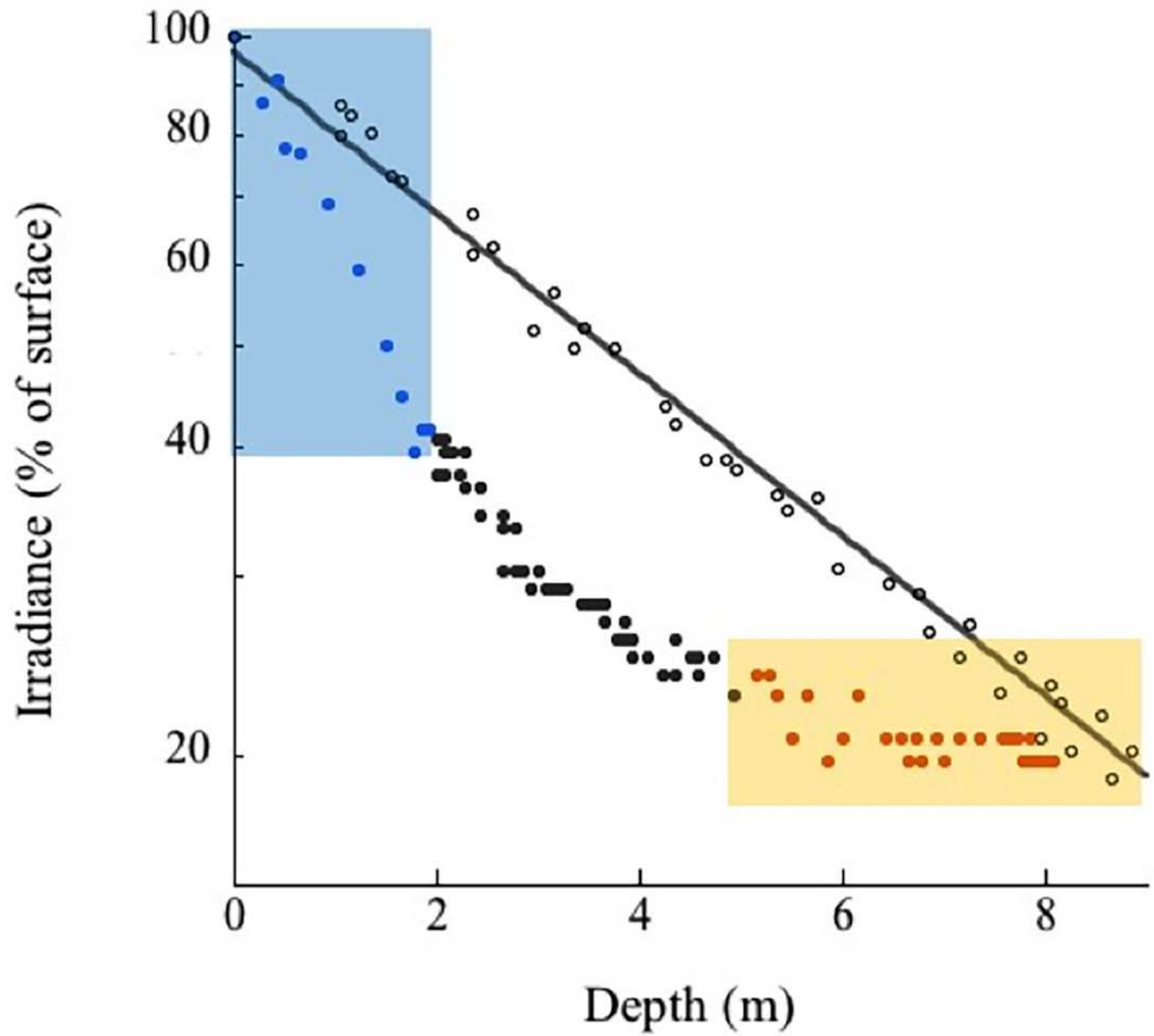


# Figure 3

Varadero Reef optical properties.

Figure 3. Analyses of the variations in the optical properties of the water column in Varadero Reef (solid circles) indicate the presence of highly stratified water masses. The blue symbols in the blue shaded area highlight the upper layer with  $K_d$  values of  $0.488 \text{ m}^{-1}$ , the black symbols indicate transition region with  $K_d$  of  $0.19 \text{ m}^{-1}$  whereas the orange symbols in the shaded area indicate the presence of very clear waters with  $K_d$  values of  $0.041$ . For comparison the monotonic vertical attenuation for the Rosario Island is presented (open circles) with  $K_d$  values of  $0.165 \text{ m}^{-1}$ .

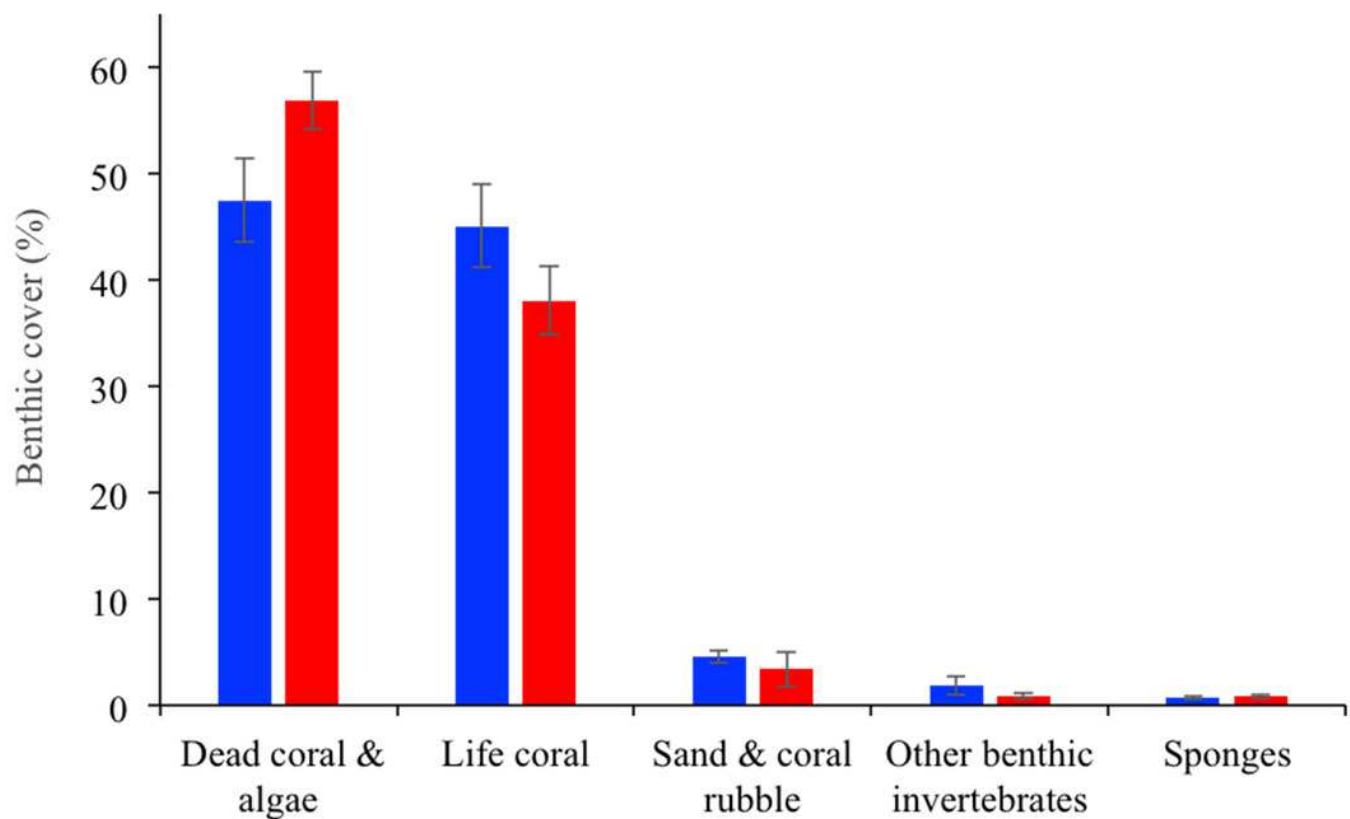




# Figure 4

Varadero and Barú benthic cover.

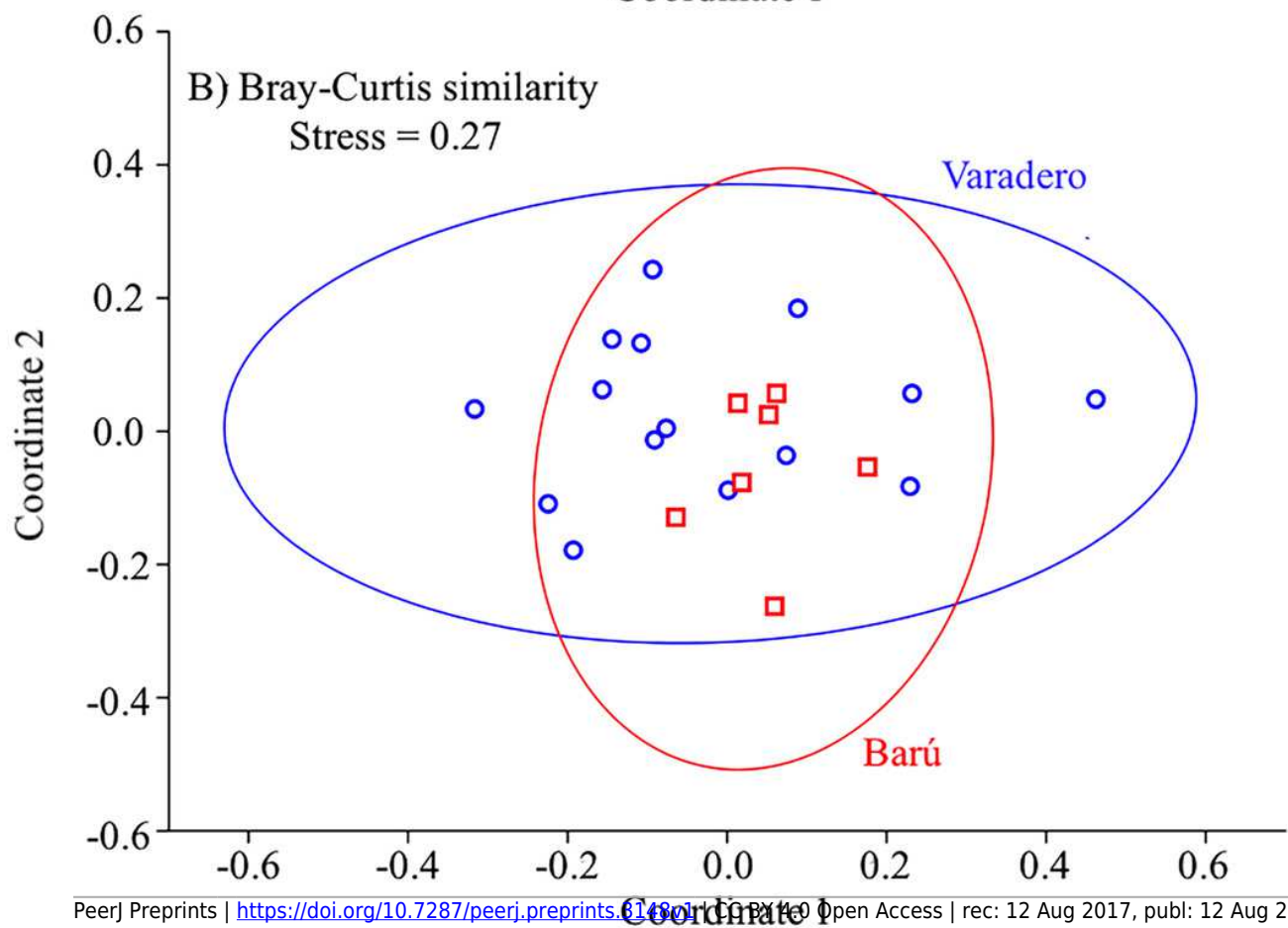
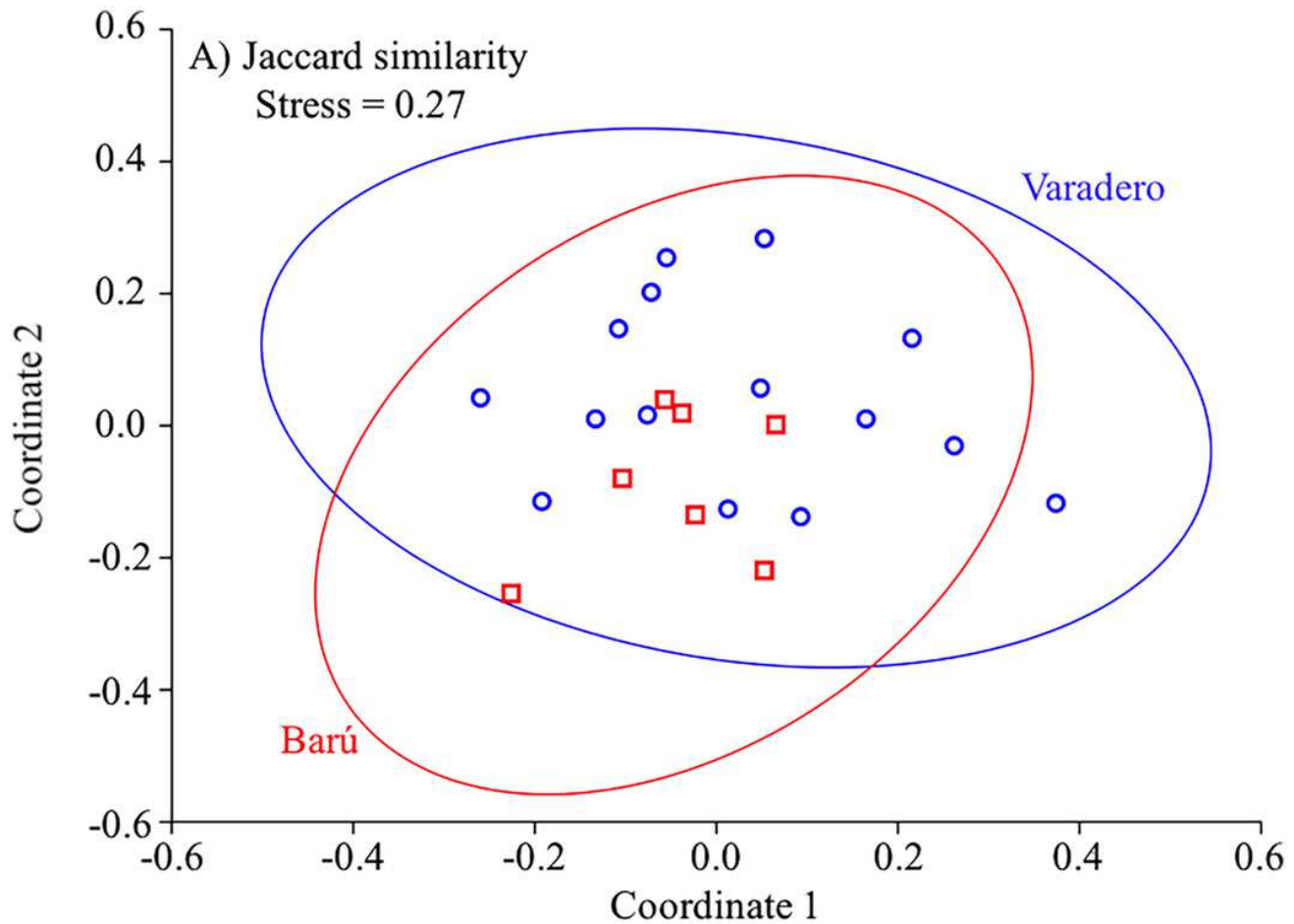
Figure 4. Average benthic coverage Varadero (blue) and Barú (red) Reefs. Error bars indicate standard error.



# Figure 5

Fish presence-absence and abundance data for Varadero and Barú Reefs.

Figure 5. Non-metric multidimensional scaling analysis biplots based on A) presence-absence data (Jaccard's similarity) and B) abundance data (Bray-Curtis's similarity) for fish visual censuses made at Barú (red) and Varadero (blue) Reefs.



# **Table 1** (on next page)

Fish assemblage at Varadero and Barú Reefs.

Table 1. Fish assemblage attributes estimated through visual censuses on 30 x 2 m belt transects made at Varadero and Barú Reefs.

Community attribute	Varadero (n = 15)		Barú (n = 7)		t	p
	Mean	± SD	Mean	± SD		
Species richness	12.4	3.0	15.0	2.4	-1.99	0,06
Number of individuals	55.6	15.9	74.1	14.4	-2.62	0,02
Dominance (Simpson's D)	0.18	0.05	0.16	0.04	0.94	0,36
Diversity (Shannon's H')	2.0	0.3	2.2	0.2	-1.36	0,19
Evenness (Pielou's J')	0.81	0.07	0.80	0.04	0.27	0,79

1