



Steady Decline of Corals and Other Benthic Organisms in the SeaFlower Biosphere Reserve (Southwestern Caribbean)

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Coral reef decline persists as a global issue with ties to climate change and human footprint. The SeaFlower Biosphere reserve includes some of the most isolated oceanic coral reefs in the Southwestern Caribbean, which provide natural experiments to test global and/or basin-wide factors affecting coral reefs. In this study, we compared coral and other substrate cover (algae, cyanobacteria, and octocorals), along population densities of keystone urchin species from two atolls (Serrana and Roncador Banks), during 1995, 2003, and 2015/2016. We also surveyed benthic foraminifera as a water quality proxy for coral growth in the last period. A steady reduction in coral cover was clearly observed at Roncador's lagoon, but not at Serrana's reefs, with significant differences between 1995 and 2015/2016. Percent cover of fleshy algae decreased significantly also at Roncador between 1995 and 2003 but did not change notably from 1995 to 2016 at Serrana. However, both Banks exhibited a loss in crustose coralline algae from 2003 to 2015/2016. Likewise, a reduction in bottom complexity, measured as bottom rugosity, was evident between 1995 and 2003. Roncador Bank had unprecedented high octocoral densities, which increased almost threefold from 2003 to 2015. In contrast, urchin densities were low in Roncador; only *Diadema antillarum* increased from 2003 to 2016 in Serrana Bank. The Foraminifera in Reef Assessment and Monitoring (FORAM) Index (FI) in the two Banks was below the range expected for healthy coral reefs. Although both Banks follow a reduction in CCA and CA cover, Roncador Bank also faces an alarming decline in coral cover, urchins and bottom complexity (rugosity) in contrast to increases in octocoral densities and potential loss of resilience and eutrophication suggested by the FI index. These unexpected findings led us to consider and discuss potential outcomes, where these reefs deteriorate (i.e., erode and drown) providing ideal conditions for octocoral growth. Hence, it is of utmost urgency to start monitoring reef budgets, octocorals and nutrient sources.

Keywords: coral reefs, coral decline, Caribbean, algae cover, FORAM index, octocoral community, atoll, SeaFlower

INTRODUCTION

Marine biodiversity reaches its highest complexity in coral reefs. These formidable tropical ecosystems account for at least 30% of marine biodiversity at an extent of less than 1% of the planet's surface (Roberts et al., 2002). In addition to offering a seascape of indescribable beauty, they provide significant economic benefits to countries where they are found (Costanza et al., 1997), as well as providing coastal protection from storms (i.e., hurricanes) and waves (i.e., tsunamis) (Foster et al., 2013). Direct and indirect economic profit from tourism provided the exploitation of coral reef ecosystems around the world surpass 36 billion dollars a year (Spalding et al., 2017). Yet, coral reefs face unprecedented environmental challenges (Camp et al., 2018). Thermal anomalies in the oceans lead to coral bleaching and mortality (Hughes et al., 2003; Eakin et al., 2010). Of greatest concern, the increase of atmospheric carbon dioxide (CO₂) concentration alters seawater chemistry leading to ocean acidification, which includes adverse effects on the calcification rates of marine organisms including corals (Orr et al., 2005; Hoegh-Guldberg et al., 2007). These processes act in synergy with the human footprint, particularly increasing sewage and overexploitation, which reduces the resilience of marine ecosystems like coral reefs (Mumby, 2009; Graham et al., 2013; Wiedenmann et al., 2013). Failure to protect coral reefs will affect millions of livelihoods worldwide and provoke unparalleled rapid biodiversity losses in the years to come.

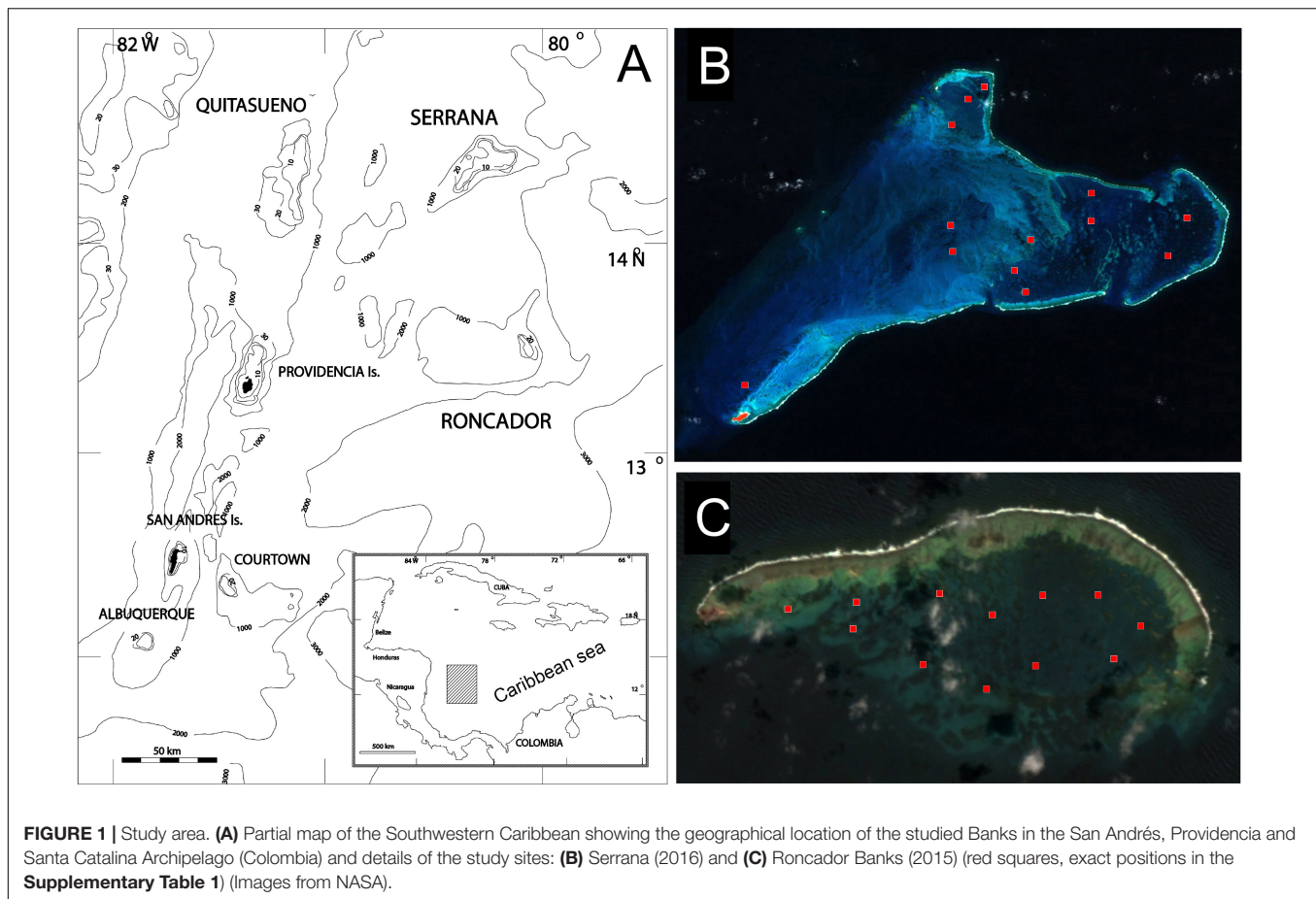
Biodiversity loss encompasses all marine coastal organisms (Hooper et al., 2012), in which coral reefs have become an emblematic instance of this global trend of ecosystem degradation. Recent trends, altering the composition of species assemblages at coastal marine environments (Dornelas et al., 2014), have raised new concerns about marine conservation because the emerging species turnover corresponds to less favorable ecosystem states in terms of productivity and services for humans (Pandolfi and Lovelock, 2014). Not understanding how marine communities react to many agents of deterioration and stress, climate change and human footprint, for example, prevents us from stopping degradation, managing and restoring vulnerable ecosystems like coral reefs (López-Angarita et al., 2014). In coral reefs, resilience and trophic functions appear greatly compromised (Jackson et al., 2001; Hughes et al., 2010). The worse-case scenario, in declining coral reefs, predicts high erosion and rising sea-levels leading to drowned reef structures with a few calcareous corals surviving and the hard bottom cover dominated by fleshy algae (Hughes et al., 2003; Hoegh-Guldberg et al., 2007, 2017; Perry et al., 2018). Are Caribbean coral reefs reaching this state?

The key players in coral reefs are set between top-down, grazing, and bottom-up, nutrient input controls (Littler et al., 2006). This relative dominance model allows an ideal coral-dominated shallow reef, including crustose coralline algae, under high grazing and low nutrient input (Littler and Littler, 2007). The worst case-scenario, under high nutrient input and low grazing, predicts a macroalgae dominated reef (Ledlie et al., 2007; Slattery and Lesser, 2014) or a sponge-dominated state, where dissolved organic matter is processed fueling higher trophic levels

(De Goeij et al., 2013; McMurray et al., 2018). Reef decline in the Caribbean can be traced back to the time of Columbus, where reduction of herbivores like green turtles started, and more recently with the extinction of the monk seal and the mass mortalities of the black sea urchins and corals (Lessios et al., 1984; Hughes, 1994; Jackson, 1997). Basin-wide, Caribbean coral cover shrunk to 10% in less than three decades (Gardner et al., 2003). A combination of thermal anomalies, leading to coral bleaching and mortality (Eakin et al., 2010), overfishing of larger herbivores like parrotfishes (Paddock et al., 2009; Mumby et al., 2012; Loh et al., 2015), human footprint (Appeldoorn et al., 2016), including coastal pollution and eutrophication (Mora, 2008), and more recent invasive species (Lesser and Slattery, 2011; Albins and Hixon, 2013), reduced the resilience of coral reefs in the Caribbean like no other region in the world (Jackson et al., 2014).

Increased nutrient and sediment load in coastal areas are recognized as major drivers of coral reef deterioration worldwide (Fabricius, 2011; Sherman et al., 2016). In addition, coastal pollution can lead to disturbances in the coral microbiome and disease-related mortality (Klaus et al., 2007; Montilla et al., 2016). Traditional methods to evaluate reef condition do not effectively reflect the current water quality in terms of nutrients, due to a delayed response by the long-lived coral community and the associated costs of long-term monitoring (Cooper et al., 2009). Recently, the benthic foraminiferal assemblage has emerged as an economic and reliable alternative to assess water quality to support growth of symbiotic and calcifying organisms on coral reefs (Hallock et al., 2003). The "Foraminifera in Reef Assessment and Monitoring (FORAM) Index" (FI), is an efficient and cost-effective measure of water and sediment quality based on the assemblage of foraminiferal shells (Hallock, 2012). On oligotrophic and clear waters with abundance of hypercalcifying mixotrophs, such as hard corals, the shells of larger (symbiont-bearing) foraminifera account for a high proportion of sediment composition (Hallock, 1999). When nutrients increase the shells of smaller heterotrophic species dominate the assemblage, if conditions lead to accumulation of organic matter, stress-tolerant or opportunistic taxa can abound (Cockey et al., 1996).

Roncador and Serrana (locally known as "Islas Cayo," hereafter referred as Banks) comprise two of the few true Darwinian atolls in the Caribbean (**Figure 1**). Surrounded by depths of over two thousand meters, these atolls enclose shallow lagoons (5–15 m), where most of the coral growth stands (Milliman, 1969; Diaz et al., 1996b). An atoll is the climax of an oceanic coral reef complex developing on an extinct volcano (Darwin, 1842). The network-like distribution of patch reefs in these lagoons respond to their positioning with respect to the lagoonal terrace, a sand Bank off the back reef, and the water motion exposure (Geister and Díaz, 1996). These Banks have the same fractal patterning formed by corals at Indo-Pacific atolls' lagoons (Blakeway and Hamblin, 2015), which remarks the singularity of this type of reef formation in Caribbean reefs. This rare coral patch formation composed mostly of *Orbicella* (instead of *Acropora* in the Indo-Pacific) species (*O. annularis*, *O. faveolata* and *O. franksi*) with some colonies attaining large sizes (Diaz et al., 1996a; Sánchez et al., 2005; Foster et al., 2013). This habitat includes a different community of benthic



organisms and fish compared to the deepest, most exposed external environments of the atolls and barrier reefs of the area (Sánchez et al., 1997a; Díaz-Pulido et al., 2004; Velásquez and Sánchez, 2015; Sánchez, 2016; Gonzalez-Zapata et al., 2018).

The SeaFlower Biosphere Reserve is the largest Marine Protected Area (MPA) in the Caribbean and the second in Latin-America (Guarderas et al., 2008). These include islands and cays, two barrier-reef systems and seven atolls similar to Roncador and Serrana (Diaz et al., 1996a; Sánchez et al., 2005). The geographic zoning of the MPA was the result of an exemplary collaboration between scientists, politicians, and community involvement since 1999 to 2005 (Friedlander et al., 2003; Sánchez et al., 2005; Schroepe, 2008; Taylor et al., 2013; Ramirez, 2016). Due to the extension of the MPA, however, the area is rarely explored beyond the larger Islands, San Andrés, Providencia and Santa Catalina (Taylor et al., 2013). Quantitative surveys of corals and other benthic organisms began with scientific expeditions led by the research groups of Invemar funded by Colciencias in 1994–1995 (Diaz et al., 1996b; Sánchez et al., 1997a, 1998; Díaz-Pulido et al., 2004), following by planning of the MPA (Coralina- Gobernación del Archipiélago de San Andrés, Providencia y Santa Catalina-The Ocean Conservancy) between 2000 and 2003 (Friedlander et al., 2003; Sánchez et al., 2005) and recently thanks to a nationwide interest (SeaFlower Expeditions: Comisión Colombiana del Océano-CCO/Dimar, Coralina, Gobernación del Archipiélago de

San Andrés, Providencia y Santa Catalina [Secretaria de Pesca y Agricultura], ColombiaBIO-Colciencias and diverse Colombian universities and ONGs). This research aimed to study trends in coral and other substrate cover between similar sites in the lagoons within Serrana and Roncador Banks, using previously available data from 1995 to 2003 and combining it with data taken during the years 2015 and 2016. In addition, we estimated the FI to assess the effect of nutrient concentration on Serrana (2016) and Roncador (2015) Banks to support recruitment and proliferation of calcifying, photosynthesizing holobionts. These surveys spanned 20 years of change in Caribbean reefs, which provide an unprecedented long-term account of ecosystem trends in some of the most isolated reefs in the region.

MATERIALS AND METHODS

Study Area

Roncador Bank is an elongated atoll of about 13 km in length (NW-SW) and 6.5 km wide. The peripheral windward reef extends without interruption along its entire length (~11 km), with considerable stretches of its crest emerging at low tides (**Figures 1A,B**). Serrana Bank is an extended Bank of triangular shape, originated from an annular atoll, which was partially dissected to leeward by subsidence of the sea floor. This

Bank measures 15.5 km in the SW-NE direction and 33.4 km in the W-N direction, where a well-developed, 50 km long, peripheral reef encloses a large lagoon basin by the N, E, and S, that connects by the W to the open sea (**Figure 1B**) (Milliman, 1969; Diaz et al., 1996a; Geister and Díaz, 1996; Díaz et al., 2000; Sánchez et al., 2005; Taylor et al., 2013). We revisited the area during September 2015 (Roncador, 12 sites: **Figure 1A**) and August 2016 (Serrana, 13 sites: **Figure 1B**). Details of sampling sites during May 1995 (Díaz-Pulido et al., 2004), April–May 2003 (Sánchez et al., 2005) and 2015/2016 (this study) are included in the **Supplementary Table 1**. The surveyed sites during 2015/2016 were positioned as close as possible to the previous expeditions using GPS coordinates (see **Supplementary Table 1**). The sheltered environments in these atolls include the highest relief environments in the lagoon and leeward terrace, with the largest coral cover and colony sizes (e.g., **Figure 2**).

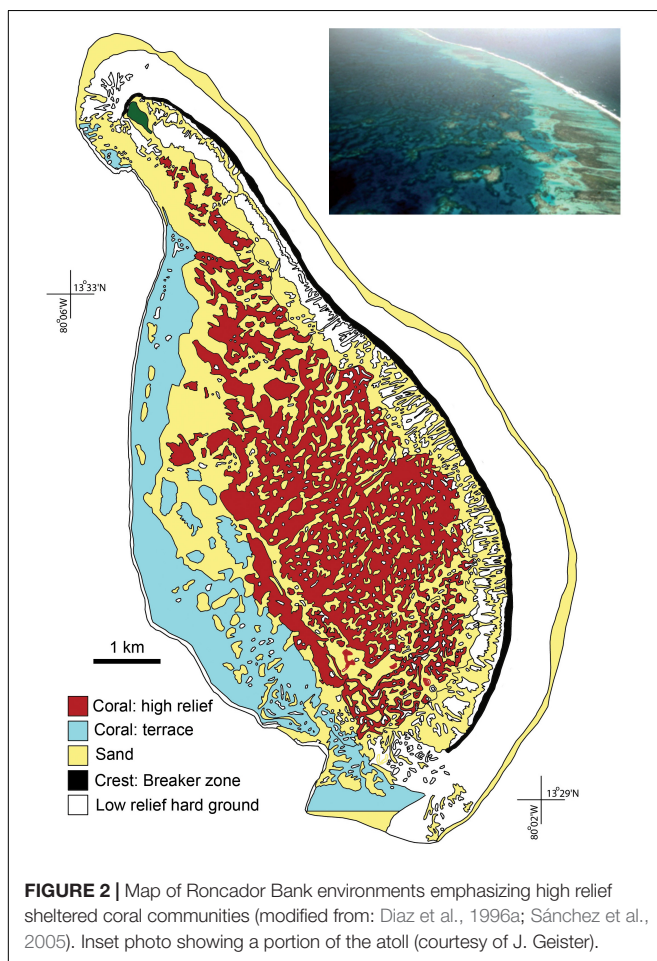
Algae and Coral Cover

Algal and coral (scleractinian) percentage cover, as well as reef rugosity values were included from two previous studies taken in 1995 and 2003 (Díaz-Pulido et al., 2004; Sánchez et al., 2005). We measured reef rugosity as an environmental variable indicator

of wave-motion energy and the chronic disturbance effect of waves (Aronson and Precht, 1995). Rugosity, a measurement of bottom topography also known as simple surface roughness index, which acts as a proxy of reef degradation (Bozec et al., 2015), was estimated from the ratio of linear length of a chain that was laid out in a straight line along the bottom following all the vertical relief to its length when stretched out 10 m (Sánchez et al., 1997b). We used a modified band transect technique (Dodge et al., 1982; Etnoyer et al., 2010) to estimate algae and coral cover during 2015 at Roncador and 2016 at Serrana. Equivalent methods for cover estimation were used in 1995 and 2003 surveys (Díaz-Pulido et al., 2004; Sánchez et al., 2005). At each site (See **Figures 1A,B** and **Supplementary Table 1** for details) a 25 m × 1 m band was surveyed using a 50 × 50 cm photoquadrat, which facilitated the quantification of the benthic components. Following the 2003 survey (Sánchez et al., 2005), the 50 × 50 cm quadrat was positioned four times in a square fashion to complete a 1 × 1 m quadrat, that was surveyed at 10 random points, to complete a total of 10 m² per band. For each site, algal and coral cover were estimated manually by digitizing the areas from the photo quadrats using ImageJ (Schneider et al., 2012; López-Angarita et al., 2014). Benthic cover was categorized as follows, hard coral (HC), crustose coralline algae (CCA), calcareous algae (CA), fleshy algae (FA), cyanobacteria (CB), other invertebrates, sponges, octocorals, rock, rubble and sand (see **Supplementary Table 1**). Hard corals included scleractinian and other hard corals such as *Millepora* spp. and *Stylaster roseus*. Algae genera for CA included *Amphiroa*, *Halimeda*, *Galaxaura* and *Penicillus*. Algae belonging to genera *Turbinaria*, *Caulerpa*, *Dyctiota*, *Lobophora*, *Mycrodictium* and *Sargassum* composed the FA category. We evaluated cover percentage differences in HC, CCA, CA, FA, CB and rugosity index (RI) per site at a mid-water reefs at Roncador (12–23 m) and shallow reefs at Serrana (2–13 m) across the 3 years of sampling, by obtaining bootstrapped ($n = 1000$ with replacement) confidence intervals (95% CI) for each mean (see **Supplementary Table 3**), to smooth confounding effects due to differences in sampling unbalanced sample sizes, repeated measures and seasonal variability. Data for cover percentage comparisons at Roncador mid-water reefs came from 8 stations (12–22 m) in 1995, 14 stations (12–23 m) in 2003 and 13 stations (8–18 m) in 2015. Likewise, data for the above comparisons at Serrana shallow reefs came from 12 stations (3–13 m) in 1995, 36 stations (2–13 m) in 2003 and 13 stations (2–11 m) in 2016.

Octocoral Densities

In situ estimates of octocoral density in the quadrats were made by counting the individual erect colonies within each quadrat and then averaging the density values of the 10 random points for each surveyed station following the same methods as in 2003 (Sánchez and Wirshing, 2005; Sánchez et al., 2005; Etnoyer et al., 2010) (see **Supplementary Table 4**). Octocoral density changes were assessed by obtaining bootstrapped ($n = 1000$ with replacement) confidence intervals (95% CI) for each mean value (see **Supplementary Table 3**) at Roncador between 2003 and 2015, and Serrana between 2003 and 2016.



FORAM Index (FI)

During the expeditions to Roncador (2015) and Serrana (2016) Banks, samples of superficial sandy sediment were collected at four different sites in each Bank (6–12 m). The samples were stored in plastic containers (20 ml), fixed with absolute ethanol, subsequently dried (>24 h, 60°C) and thoroughly mixed. From each sample, we took a 0.1 g subsample, placed it in a 90 mm-diameter petri dish and examined it using a Leica EZ4 stereoscope. We removed and counted all foraminifera until a minimum of 150 individuals were found in all the samples combined for each station, excluding heavily worn and reworked specimens. The tests were placed onto cardboard micropaleontological faunal slides, counted, identified by genus and sorted into three functional groups: symbiont-bearing, opportunistic and other small heterotrophic taxa; the proportions of each functional groups were then used to calculate the average FI (Hallock et al., 2003). The FI ranges from 1 to 10, where $FI < 2$ indicates unfavorable conditions for coral growth, $2 < FI < 4$ represents the limit for coral growth and unsuitable for recovery and $FI > 4$ permits coral growth and recovery.

Sea Urchin Densities

Sea urchin densities, namely of *Diadema antillarum* and *Echinometra viridis*, were estimated by counting the number of urchins within each quadrat along the transect, then averaging the density values for each surveyed station following the same methods as in 2003 (Coyer et al., 1993; Sánchez and Wirshing, 2005; Sánchez et al., 2005) (see **Supplementary Table 6**). We compared Sea urchin density by obtaining bootstrapped ($n = 1000$ with replacement) confidence intervals (95% CI) for each mean (see **Supplementary Table 3**) at Roncador between 2003 and 2015, and Serrana between 2003 and 2016.

RESULTS

Algae and Coral Cover

Roncador Bank mid-water reefs experienced a mean decline in CCA (10.13%) and FA (53.41%), but not HC (22.58%), from 1995 to 2015 (CCA: 2.15%, FA: 28.88%, HC: 9.85%). Mean CB increased significantly from 1995 (1.73%) to 2003 (13.20%) but decreased in 2015 (3.99%) close to its 1995 value. Mean CA did not change significantly over the three periods surveyed (6.51, 7.89, and 3.99%) at this Bank. Meanwhile, mean CCA in Serrana Bank shallow reefs from 1995 (5.05%) lowered significantly to 0.25% in 2016. During 2003 mean FA (48.53%) and HC (35.73%) reduced significantly as compared to 2003 period (FA: 25.83%, HC: 19.24%) in this Bank, but not when compared to 2016 (FA: 43.24%, HC: 20.88%). Mean CB significantly raised from 1995 (0.58%) to 2003 (9.15%) but fell back to 1.97% in 2016. (**Figure 3**, see **Supplementary Tables 1–3** for complete data sets). Cover by CA fell down from 6.5% in 1995 to 3.9% in 2015 at Roncador mid-water reefs, and from 7.3 to 3.2% at Serrana shallow reefs for the 1995–2016 period. CB reached its highest cover during 2003 at both Banks, 13.2% at Roncador and 9.2% at Serrana, while remaining below 5% at Roncador in 1995/2015 and 2% at Serrana in 1995/2016. CCA diminished from 10.1% in 1995 to 2.2% in

2015 at Roncador, and from 5.1 to 0.3% at Serrana from 1995 to 2016. FA was the highest at Roncador during 1995 with 53.4% but diminished by 24.5% in 2015, with a slight decline of 2.8% from 2003 to 2015. Similarly, HC cover at this Bank decrease from 22.6% in 1995 to 14.9% in 2003, and to 9.9% during 2016; a continuous reduction in HC cover of 12.7% over 20 years. FA at Serrana fluctuated from 48.5% in 1995 down to 25.8% in 2003 and then up to 43.2% in 2016. However, despite a 21.5% HC mean reduction at Serrana shallow reefs from 1995 to 2003, its HC cover did not differ significantly between 1995 and 2016, when reached a mean of 20.9%.

Based on the surveys performed in 1995 at Roncador Bank mid-water reefs (Díaz-Pulido et al., 2004), a total of 20.0% HC cover was attributed to *Orbicella franksi*, *Agaricia agaricites*, *O. annularis*, *Pseudodiploria strigosa*, *Colpophyllia natans*, *Siderastrea siderea*, *Montastraea cavernosa*, *Millepora alcicornis* and *Porites porites*. Comparing the datasets from the 2003 surveys taken at Roncador Bank, all previously reported species were present and dominant at mid-water reefs, with the exception of *P. astreoides* and *M. cavernosa*, but all species with an overall lower coral cover (15.5%). During 2015, the main coral species were *O. annularis*, *O. faveolata*, *A. agaricites*, *P. astreoides* and *O. franksi*. These species remained as the most abundant species despite an apparent decline of HC cover (12.7%) when compared to the 1995 dataset from Roncador Bank. On the other hand, Serrana Bank showed an apparent trend of loss and posterior recovery of HC cover. In 1995 this Bank's 32% of HC cover was represented by *Orbicella* spp., *A. agaricites*, *S. siderea*, *C. natans*, *Diploria labyrinthiformis* and *P. strigosa*. In 2003, *Orbicella* spp., *A. agaricites*, *S. siderea* along *P. astreoides* and *P. porites*, composed 15.5% of HC cover at this Bank. Lastly, in 2016 *O. annularis*, *O. faveolata*, *S. siderea*, *P. astreoides* and *Agaricia* spp. colonies composed over 17.0% of HC cover at Serrana shallow reefs, where *O. annularis* was the main responsible for the increase in mean HC cover, along the appearance of *Agaricia* spp. colonies in the quadrats.

There was an apparent decrease in rugosity at both Banks when comparing data sets between 1995 and 2003. However, there was not an apparent change in rugosity when comparing the datasets between 2003 and those taken in 2015/2016. (**Figure 4**). A 52 and 55% reduction of rugosity occurred at Roncador mid-water and Serrana shallow reefs from 1995 to 2015 and 2016, respectively.

Octocoral Densities

The density in Roncador ranged between 3.5 and 15.1 ind m^{-2} in 2003 and 11.3–68.5 ind m^{-2} in 2015, the highest value for Serrana only reached 13.9 ind m^{-2} in a survey during 2003 (see **Supplementary Table 4**). Although the octocoral densities between Roncador and Serrana showed strong spatial variation, their temporal patterns within surveyed sites are more complex. The highest value for octocoral density reported for 2003 was 15.1 ind m^{-2} , while in 2015 was 68.5 ind m^{-2} , almost 5 times the highest value in 2003. At Roncador Bank, octocoral density increased from 11.2 ind m^{-2} during 2003 to 36.4 ind m^{-2} in 2015, a 225% increment. Contrarily, Serrana Bank did not change its octocoral density over a 11-year span, with 1.9 ind m^{-2} in

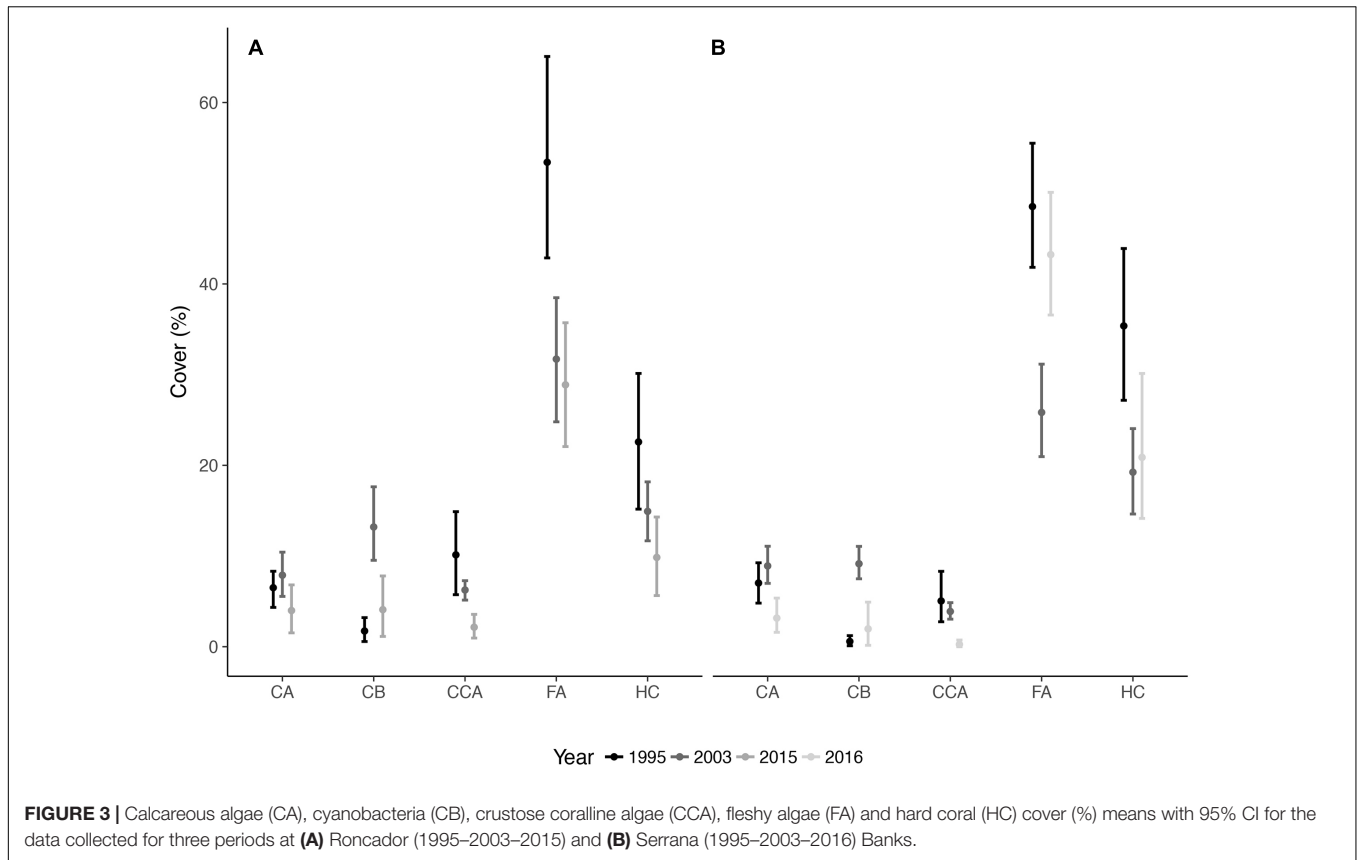


FIGURE 3 | Calcareous algae (CA), cyanobacteria (CB), crustose coralline algae (CCA), fleshy algae (FA) and hard coral (HC) cover (%) means with 95% CI for the data collected for three periods at **(A)** Roncador (1995–2003–2015) and **(B)** Serrana (1995–2003–2016) Banks.

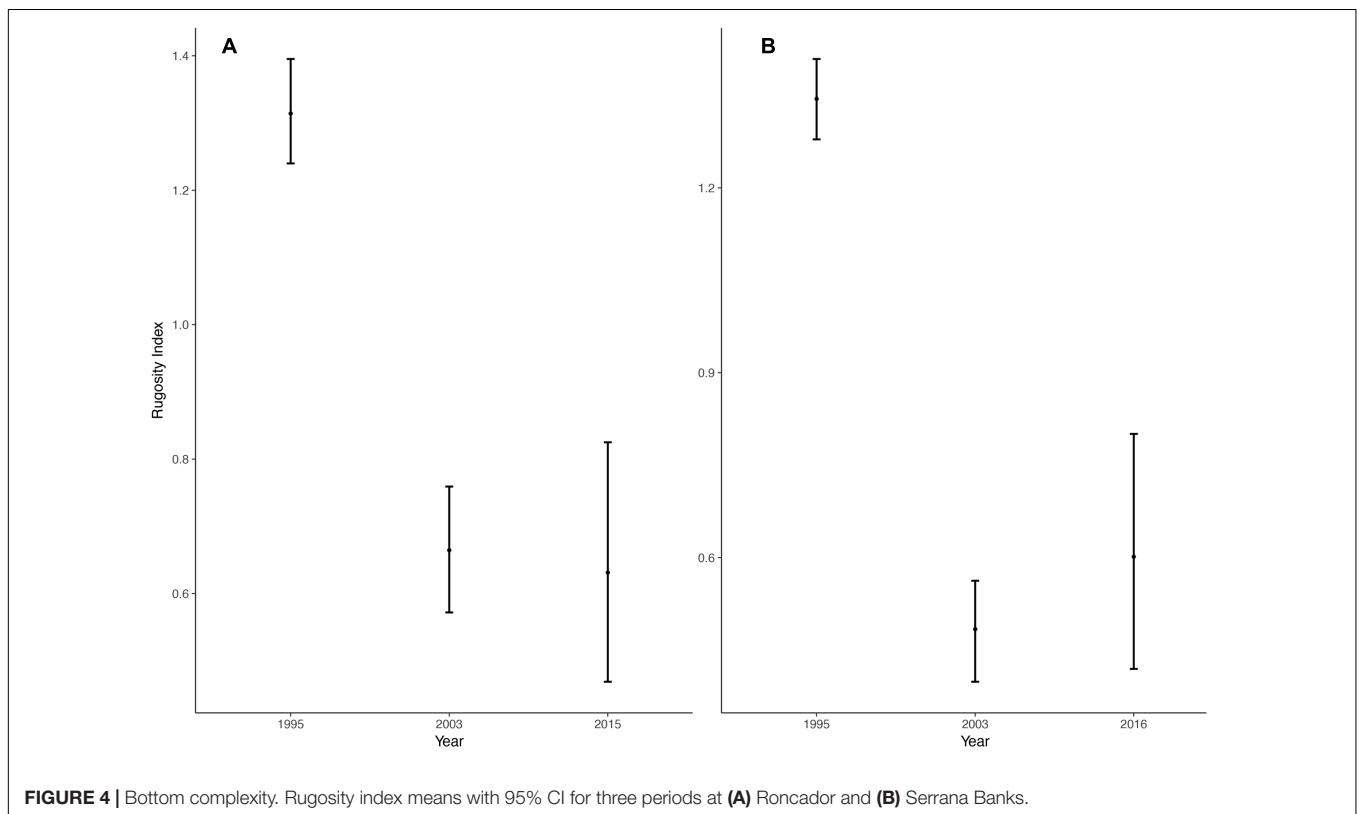


FIGURE 4 | Bottom complexity. Rugosity index means with 95% CI for three periods at **(A)** Roncador and **(B)** Serrana Banks.

2003 to 1.5 ind m^{-2} in 2016 (**Figure 5A**). In general, density values for Serrana were lower than Roncador, which included a peak value reaching 13.9 ind m^{-2} in 2003 and 6.5 ind m^{-2} in 2016. The sites where octocoral densities increased were located inside the reef lagoon. Serrana had the lowest values with low variation among sites (**Figure 5A**). Although, we did not survey densities per species, at both Banks *Antillologorgia bipinnata* was overall the most abundant gorgonian coral followed by the soft

coral *Briareum asbestinum* and plexaurid gorgonians belonging to the genera *Plexaura*, *Pseudoplexaura* and *Eunicea*.

FORAM Index (FI)

We examined a total of 8 sediment samples, counted 1363 foraminifera tests and identified 34 genera at both Banks: 7 symbiont-bearing, 3 opportunistic and 24 other small heterotrophic. The most abundant genera for each functional

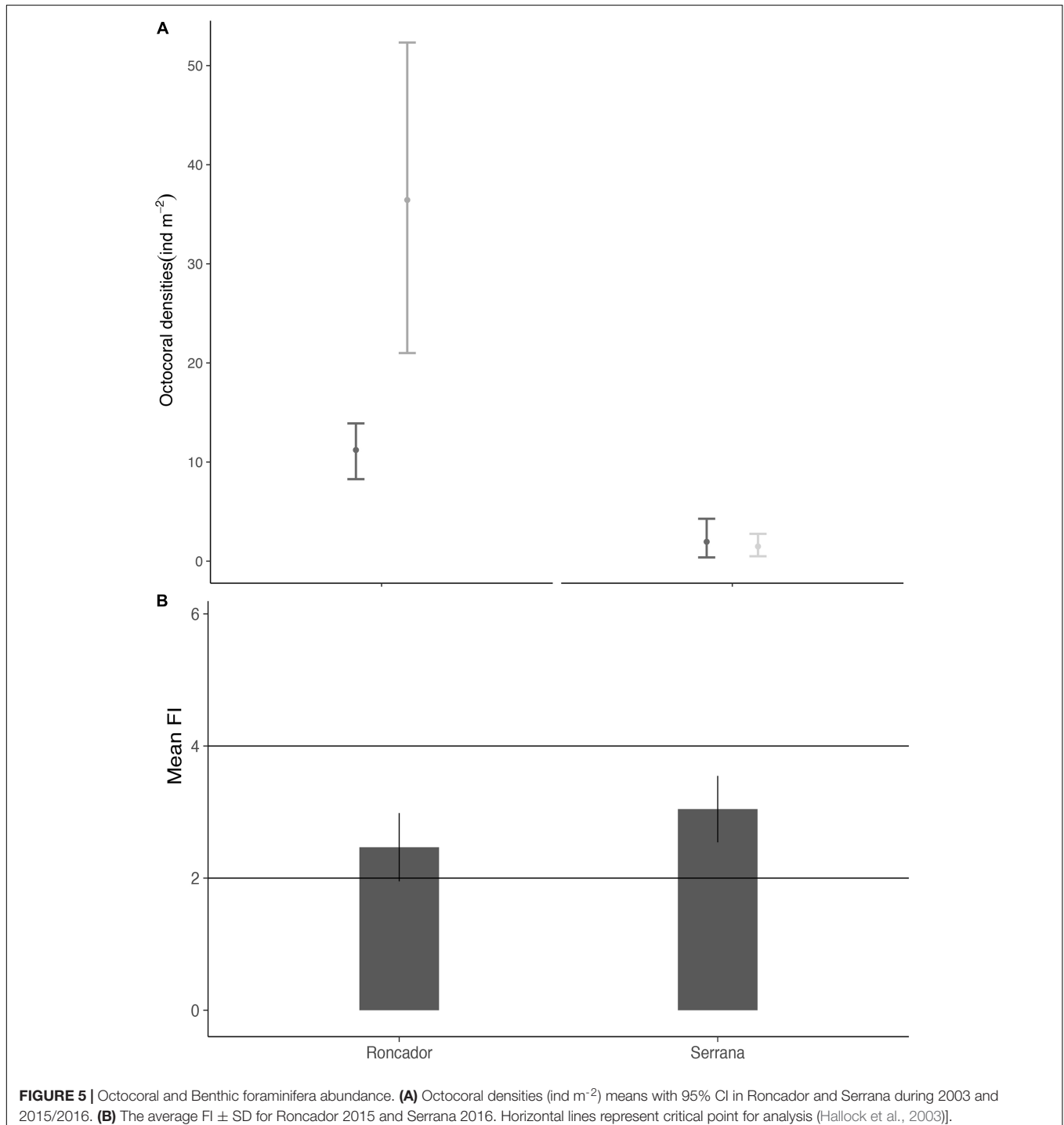


FIGURE 5 | Octocoral and Benthic foraminifera abundance. **(A)** Octocoral densities (ind m⁻²) means with 95% CI in Roncador and Serrana during 2003 and 2015/2016. **(B)** The average FI \pm SD for Roncador 2015 and Serrana 2016. Horizontal lines represent critical point for analysis (Hallock et al., 2003)].

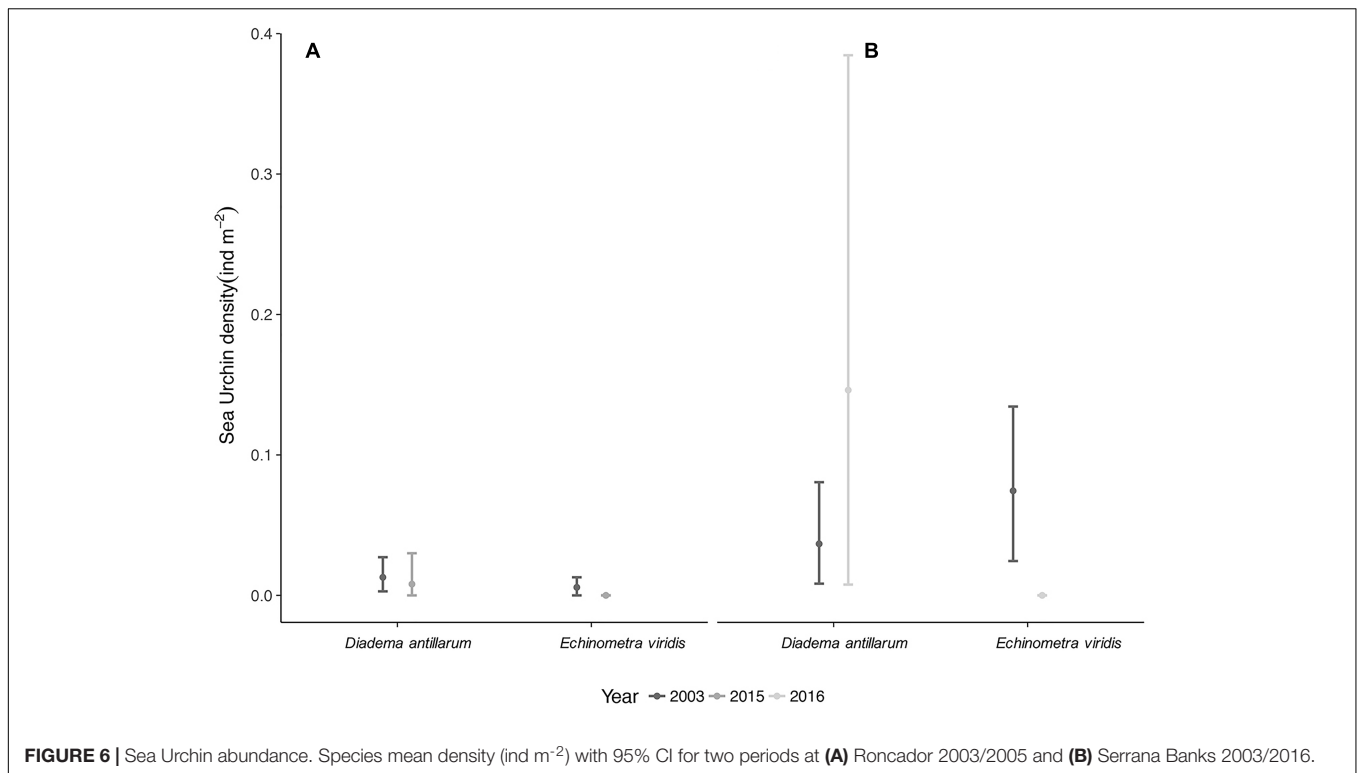


FIGURE 6 | Sea Urchin abundance. Species mean density (ind m⁻²) with 95% CI for two periods at **(A)** Roncador 2003/2005 and **(B)** Serrana Banks 2003/2016.

group were *Laevipeneroplis*, *Bolivina* and *Triloculina*, respectively (See **Supplementary Table 5**). The small heterotrophic taxa dominated the foraminifera community with 86% of all individuals, followed by 10% of symbiont-bearing and 4% of opportunistic. The average FI found for Roncador was 2.5 and 3 for Serrana (**Figure 5B**).

Sea Urchin Densities

Urchins were seldom found at both Serrana and Roncador Banks, sometimes absent in many sites during 2015 and 2016 surveys. Similar densities of the sea urchin *D. antillarum* were found at Roncador during 2003 (0.01 ind m⁻²) with respect to 2015 (0.01 ind m⁻²), while its density was higher in Serrana 2016 (0.15 ind m⁻²) than in 2003 (0.04 ind m⁻²). Despite these trends, sea urchin density did not change significantly over those periods (**Figures 6A,B**). On the contrary, no individual of *E. viridis* was recorded in Roncador 2015 and Serrana 2016, showing a reduction in its density when compared to 2003 (see **Supplementary Table 6**).

DISCUSSION

Our results demonstrate a significant reduction in CCA and HC percent cover, which included massive (*Orbicella* spp.) and encrusting/smaller (*Agaricia* spp., *P. astreoides*) reef building species, particularly at Roncador Bank mid water-reefs. Likewise, a reduction in benthic complexity (rugosity), was evident between 1995 and 2003 at both Roncador and Serrana atolls. The Banks were different in terms of gorgonian densities, whit

a nearly one order of magnitude higher in Roncador and a trend to increase. Sea urchin densities were overall low at both Banks. The FI at both Banks, a proxy of water quality and reef resilience, was below the range expected for coral reefs, which are apparently isolated from human waste water and/or sources of eutrophication (FI > 4). FI values found, between 2 and 4, corresponded to reefs with water conditions from marginal to unsuitable for recovery of coral communities after disturbance (Hallock et al., 2003). This means nutrient availability does not favor the recruitment and growth of mixotrophic and calcifying organisms like hard corals (Hallock, 2012), compromising reef health in the long term. Those values are common at fringing reefs along the continental coast of Colombia affected by constant runoff and nutrient input from pollution (Velásquez et al., 2011; López-Angarita et al., 2014). Although both Banks show a decrease in CA and CCA, Roncador Bank mid-water reefs additionally face an alarming decline in overall coral cover. The correspondence of declining CCA, FA and general coral cover, water quality and bottom complexity (rugosity) with increases in octocoral is even more alarming in an already declining reef system.

Although remote reefs represent an exemplary case to assess reef health, due to its isolation from direct human disturbances, our results evidenced a clear decline in CCA an overall HC cover from 1995 to 2015 at Roncador mid-water reefs. During the year 2003, a mass mortality of hard corals was also observed in the lagoon of Serrana Bank (Sánchez et al., 2010), whereas coral in Roncador appeared healthier that year (Sánchez et al., 2005). Rugosity for both Roncador and Serrana Banks decreased dramatically between 1995 and 2003. The 1997–1998

El Niño Southern Oscillation led to mass coral bleaching and subsequently coral mortalities as well as the appearance of numerous diseases affecting corals (Weil, 2004), which most likely also impacted the two Banks. In terms of direct external effects, these reefs face the Caribbean current, NW direction, and at least part of the year receive diluted waters influenced by fresh-water runoff from the continental coast (Beier et al., 2017). Coastal waters coming from the Colombian coast are increasingly polluted with nutrients coming from rivers, which promotes coral degradation and harmful algae blooms (Restrepo et al., 2006; Coronado-Franco et al., 2018). Moreover, direct impacts from continental eutrophic waters on these Banks are likely. Complex seasonal water circulation around the archipelago (Garay et al., 1987) can also transport nutrients from the nearby island of San Andrés, where overpopulation and eutrophication is on the rise (Gavio et al., 2010; Mancera-Pineda et al., 2014). In addition, regional currents may be introducing alien objects or drifters, which can contribute as a source or external organic and inorganic material into San Andres (Mancera-Pineda et al., 2014). The case in point of drifters demonstrates that external threats can have detrimental impacts to isolated reef sites such as Serrana and Roncador.

The models of coral degradation usually consider a shift from coral to algae dominance in degrading coral reefs (Mumby, 2009; Graham et al., 2013; Slattery and Lesser, 2014), a signal not clearly evidenced in our study area. It is important to mention that detailed observations on Serrana and Roncador reefs, made over 50 years ago (1966), describe these reef communities as both coral and CCA-dominated, which included abundant stands of species today endangered like *Acropora cervicornis* and *A. palmata*, and only mentioning a reduction on fish abundances in comparison to observation from 1945 (Milliman, 1969). Coral and CCA percent cover decreased at Roncador mid-water reefs whereas only CCA decreased at Serrana shallow reefs which kept CCA, FA and HC close to their values in 1995. A pattern unexpected in an area devoid of direct human influence, which follow the world-wide decline of marine wilderness (Jones et al., 2018) and coral reef degradation (Bruno and Valdivia, 2016). The rise of slimy cyanobacterial mats, as those observed in these Caribbean reefs, comprise another phase shift related to increases in both eutrophication and water temperature during the last 40 years (De Bakker et al., 2017). In addition, large predator fishes, such as groupers, have been depleted by unsustainable fisheries throughout the entire SeaFlower reserve (Prada et al., 2007), with Roncador bank exhibiting the lowest abundance values in the archipelago (Hooker et al., 2011). Overall, corals reefs are experimenting a more complex degradation scenario than previously thought, where even far-flung reefs seem to be unable to cope with large-scale stressor such as global warming/sea level rise and ocean acidification (Perry et al., 2013, 2018). This situation could be acting in synergy with the tectonic activity leading to subsidence in the Caribbean (Khan et al., 2017), which could be different between Serrana and Rocandor Banks. In fact, Roncador Bank has been predicted to be more vulnerable to sea-level rise impacts than Serrana (Andrade et al., 2011). In addition, the small size of Roncador Bank, together with strong water motion, coral degradation and eutrophication, makes it

prone to erosion and sediment loss, which suggest a similar reef demise as the case of Serranilla Bank (Triffleman et al., 1992). An interpretation of coral reefs declining, in both coral and algae whereas octocorals thrive, needs a more complex scenario with multiple stressors, where ocean acidification, sea-level and reef erosion should be taken into account (Pendleton et al., 2016).

A strong differentiation between octocoral densities from Roncador and Serrana Banks, on a spatial and temporal scale, was clearly found. Overall, density values in Roncador mid-water reefs were almost five times higher than those in Serrana shallow reefs, reaching up to 68.5 ind m^{-2} whereas the highest in the later was 13.9 ind m^{-2} (see **Supplementary Table 3**). These values are consistent with previous studies reporting similar ranges ($2.95\text{--}20.6 \text{ ind m}^{-2}$) for octocoral densities recently estimated in the Caribbean (Privitera-Johnson et al., 2015), except for station 17 in Roncador that showed unusually higher density than those previously reported (68.5 ind m^{-2}). Interestingly, Roncador mid-water reefs showed higher mean octocoral densities (see **Supplementary Table 4**) than those reported in many Caribbean regions (Etnoyer et al., 2010; Sánchez, 2016) and those (9 ind m^{-2}) reported for SE Sulawesi assemblages (Rowley, 2018). It is widely known that habitat complexity significantly affects the assembly of benthic communities (Sánchez et al., 1997a) and in this study we see a dramatic decrease in habitat complexity through the measured rugosity index. Since these indexes reflect the growth dynamics of hard corals and reef erosion (Bozec et al., 2015), we can conclude that the percent cover of scleractinian community has been receding in the last years, whereas changes in octocoral densities tend to increase. This is a striking pattern because if hard coral cover continues to decrease and octocorals increase, or at least remain constant; it means that their relative abundance in the community increases as well, and such trend could dominate the community in a hypothetical phase shift scenario altering the functional and trophic structure of the reef community (Norström et al., 2009; Lenz et al., 2015). These growing gorgonian assemblages can also change in composition due to the relative abundance of associate predators (e.g., *Cyphoma*) or species susceptibility to diseases (Sánchez, 2016).

In the last two decades Caribbean reefs have experienced thermal anomalies of up to 16 weeks as during 2005 and 2010, including coral bleaching throughout the province and scleractinian coral mortality, coinciding with the record of hurricanes, with four category 5 hurricanes, including Katrina (Wilkinson and Souter, 2008; Eakin et al., 2010). However, gorgonian corals (Octocorallia), one of the features of the Caribbean reef province, exhibited negligible mortality and high resilience after bleaching (Lasker and Sánchez, 2002; Lasker, 2003; Prada et al., 2010). Octocorals have also shown to be very resistant to ocean acidification in experimental settings (Enochs et al., 2016), even below saturation of Ω_{calcite} (Gómez et al., 2015). Other octocorals, such as the soft coral species of the Red Sea, have also shown resistance to high pCO_2 values due to the protective properties of their tissues (Gabay et al., 2013, 2014). In short, octocorals, due to their resistance to bleaching and acidification, together with a heterotrophic feeding strategy in most Caribbean species (Baker et al., 2015; Sánchez et al., 2019),

should be included in the list of climate change/human footprint survivors. Yet, these organisms have been rarely considered as reef-building corals, although a large colony can contribute as much calcium carbonate, at its holdfast, as a small scleractinian coral species (Kocurko, 1987). Octocoral-dominated reefs already exists at naturally acidified waters (Inoue et al., 2013). Should we consider an octocoral-algae phase shift in Caribbean reefs?

CONCLUSION

Although both Banks followed a loss in coral cover, topographic complexity (rugosity) and resilience (FI index), Roncador Bank mid-water reefs face a steady decline. These unexpected findings led us to consider the scenario of some of these reefs starting to lose complexity, whereas providing ideal conditions for octocoral recruitment, settlement, successful establishment and subsequent growth. Other SeaFlower reef complexes, like San Andrés Island, have already shown the effects of coastal erosion and eutrophication (Gavio et al., 2010). Situations predicted to increase with the human footprint and under a climate change scenario (Schönberg et al., 2017), hence bioerosion and reef budgets are rarely considered in monitoring programs (Perry et al., 2013). Serrana Bank shallow reefs, a larger reef-complex with signs of HC recovery, provides some hope in terms of its withstanding HC cover, yet a more detailed monitoring is needed.

Another concern is the apparent eutrophication of the Banks as seen in the coral/algae abundances and FORAM index. Due to lack of information, foreign sources of nutrients should not be ignored and deserve further study. Yet, a more likely scenario could be related with the cycle of dissolved organic carbon (DOC), fleshy algae and the microbial community (Pawlik et al., 2016), which maintains the algal competitive abundance and promotes coral degradation (Haas et al., 2016). Coral diseases are prevalent in the two Banks and mass mortalities have been observed in Serrana Bank (Sánchez et al., 2005, 2010). Monitoring the sources of nutrients in these Banks, along with the other components of reef resilience (i.e., herbivorous fish), can bring important information for, urgently needed, adaptive management in these deteriorating coral reefs.

The implications of high octocoral densities in Roncador are of the utmost importance for understanding the future of Caribbean reefs. First it is important to note that Roncador mid-water reefs, and even Serrana shallow reefs, show significantly lower densities of sponges as compared to continental reefs (Zea, 2001), where increased suspended particles promote sponge abundance and dominance (Valderrama and Zea, 2003; Loh et al., 2015). Novel community assemblages may include new trophic and habitat provisioning opportunities (Lugo et al., 2000) and could even transform the storm resistance regimes (Lenz et al., 2015). To fully understand the nature of octocoral densities, as well as how environmental conditions change by high octocoral abundances, it is paramount to set a baseline of recruitment survivorship and dynamics in future monitoring programs. Specifically, future studies in the area should address the hypothesis of the stock-recruitment within the octocoral canopy (Privitera-Johnson et al., 2015), which suggests that once

larvae leave the parental colonies, they will get caught up beneath the canopy of the octocoral community promoting settlement and eventually densities of adult colonies.

Caribbean atolls, such as Roncador and Serrana Banks, developed remarkable areas of high relief coral communities in their lagoons and terraces (e.g., **Figure 2**), but today live coral cover averages less than 10% at Roncador mid-water reefs, when in 1995 was 22.6%, and less than 21% at Serrana shallow reefs, when in 1995 was 35.4%. These Banks, isolated from human populations and rivers, comprised the climax of thousands of years of a reef-building process, which is disappearing in the last few decades in the absence of a clear causal explanation. The fate of these and many coral reefs in the Caribbean are beyond alarming. The need of more sophisticated means of reef monitoring, including reef budgets and nutrients (i.e., carbon sources), is urgently needed toward adaptive management of Caribbean MPAs.

AUTHOR CONTRIBUTIONS

JS conceived the study. FG-Z, LG-C, and MGn collected the samples. FG-Z, LG-C, NP, PR, LN, MGn, DV, and AS processed the imagery. MG-C analyzed the samples. MG-C, PR, LG-C, and DV performed the data analyses. JS and MG-C wrote the manuscript with contributions from LG-C and DV. All authors edited the manuscript before submission.

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SUPPLEMENTARY MATERIAL

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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