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Thesis of Shane Wever

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Science

Nova Southeastern University Halmos College of Arts and Sciences

December 2022

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HALMOS COLLEGE OF ARTS AND SCIENCES

Ship Groundings and Boulder Deployment: a study on restoration of ship grounding sites in the Kristin Jacobs Coral Reef Ecosystem Conservation Area

By

Shane Oliver Wever

Submitted to the Faculty of Halmos College of Arts and Sciences in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

December 2022

Abstract

Coral reefs are widely regarded as one of the world's most important ecosystems. These ecosystems have been in a state of rapid decline worldwide due to chronic stressors and acute disturbances. Ship groundings on coral reefs are one of the most destructive acute disturbances, damaging both the biological community and the underlying reef framework. Once disturbed, these reef ecosystems often require restoration to promote recovery. Southeast Florida is home to an extensive high latitude reef system located near a highly developed and densely populated coast. In 2006, two large commercial vessels, the Spar Orion and Clipper Lasco, grounded north of the Port Everglades entrance channel offshore Broward County, Florida. Both groundings caused substantial reef damage. Grounding site visits three and four years after the grounding events showed limited coral reef community recovery and direct management action was recommended. Stabilization efforts were completed within the vessel created bow scars at both sites in December 2015. These efforts included relocating rubble into the bow scars, capping the rubble with large limestone boulders, and grouting the boulders and rubble with concrete. The benthic community was monitored annually at fixed transects on the stabilized bow scars, remaining rubble areas, and at nearby undamaged reference reef sites, and spatiotemporal differences in benthic biological community composition and physical characteristics were examined. Results from this study showed that from 2016 to 2022, stony coral $(\geq 5 \text{ cm})$ density increased by 700% and stony coral recruit (< 5 cm) density increased by 1200% on boulder transects. In that same time, stony coral (≥ 5 cm) density increased 170% and stony coral recruit (< 5 cm) density decreased 15% at rubble transects. These results suggest boulder deployment may promote stony coral recovery following ship groundings, creating habitat more similar to un-impacted reef than unconsolidated rubble. Tis study demonstrates the value of long-term restoration monitoring to better understand reef succession after disturbance events.

Keywords: Mitigation boulders, Benthic community structure, Southeast Florida, Long-term coral reef monitoring, Restoration, Rubble, Ship groundings, Stabilization, Coral reef, Monitoring

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1. Introduction

Coral reefs are widely regarded as one of the world's most important ecosystems. They provide coastal protection for more than 100 million people (Beck et al., 2018; Ferrario, 2014), support more than 30% of total marine biodiversity (Fisher et al., 2015; Reaka-Kudla, 2005), sustain global marine fisheries production (Eddy et al., 2021; Moberg and Folke, 1999), and provide countless other geophysical and economic benefits such as ecotourism, recreation and aesthetic beauty (Allen et al., 2021; Brander et al., 2007; Quataert et al., 2015; Reguero et al., 2021). These vital ecosystems have been in a state of rapid decline worldwide for the past half century, with the Pacific Ocean losing more than 50% of its living coral (Bruno and Selig, 2007, Hughes et al., 2017) and the Atlantic Ocean, specifically the Caribbean, losing more than 80% of its corals (Jackson et al., 2014). This decline is due in part to global climate change, where increases in sea surface temperatures cause coral bleaching and can increase coral disease prevalence (Alvarez-Filip et al., 2019; Hughes et al., 2017). Coral reefs are also impacted by chronic local pressures including nutrient pollution, sedimentation, overfishing, and acute local disturbances such as dredging, anchor drags, and ship groundings (Hughes et al., 2017; Ladd et al., 2018; Precht et al., 2001; Victoria-Salazar et al., 2017; Walker et al., 2012).

Ship groundings on coral reefs are one of the most destructive acute disturbances, damaging both the biological community and the underlying reef framework (Jaap, 2000; Precht et al., 2001; Riegl, 2001) (Figures 1 and 2). Ship groundings can damage, bury, and displace sessile benthos (Jaap, 2000; 2001; Riegl, 2001), and fracture or remove three-dimensional structure, flattening the reef and creating unconsolidated rubble and sediment deposits (Jaap, 2000; Moulding et al., 2012). Unconsolidated rubble poses a threat to recovery as it is an unstable substrate that prevents successful long-term settlement of sessile organisms (Kenyon et al., 2020). Secondary impacts can include scarring, abrading, and burial of previously undamaged reef flora and fauna by rubble and sediment remobilized by hydrodynamic forces (Precht et al., 2001, Viehman et al., 2018). The destruction of both hermatypic scleractinian (reef building) coral and complex benthic structure means a direct loss of habitat for mobile organisms such as fish and invertebrates (Gilliam, 1999; Spieler et al., 2001).

1

Figure 1. Bow scar left after M/V Clipper Lasco ran aground in 2006, with a diver in the bow scar for reference.

Once disturbed, these reef ecosystems and their functions begin to decline immediately and require active restoration efforts to promote recovery (Ladd et al., 2018). Restoration efforts which may stabilize damaged areas following physical disturbance can include the removal or relocation of rubble and the deployment of structures or natural limestone boulders (Kilfoyle et al., 2013; Levrel et al., 2012; Precht et al., 2001). Rubble removal and creation of stable substrate reduces the potential for chronic sedimentation, episodic mobilization of rubble, and secondary damage caused by rubble movement (Roth et al., 2018, Viehman et al., 2018). Stabilization with materials such as limestone boulders and concrete has been shown to bind loose rubble, fill in scoured areas and replace lost rugosity (Schittone, 2010; Hudson et al., 2007), providing better habitat for recruitment and benthic community recovery (Jaap, 2000). This is particularly important in areas like southeast Florida, which has suffered major declines in coral abundance in the last few decades (Jones et al., 2020; Walton et al., 2018).

Southeast Florida is home to an extensive high latitude reef system extending approximately 170 kilometers from Martin County through Palm Beach, Broward, and Miami-Dade counties (Walker et al., 2008) in an area known as the Kristin Jacobs Coral Reef Ecosystem Conservation Area (Coral ECA) (FDEP, 2021). Florida's Coral ECA is home to developed octocoral, macroalgae, stony coral, and sponge communities (Collier et al., 2008), that facilitate the ecological foundation for vital fisheries and a tourism-based economy while providing shoreline protection, sand production, nutrient cycling, and carbon sequestration (Cesar et al., 2003; Johns et al., 2001; Lirman et al., 2013). This high latitude reef system is located near a highly developed and densely populated coast (Moulding et al., 2012) which contains three major ports: Port of Miami, Port Everglades, and Port of Palm Beach (Walker et al., 2012). The constant use of both ports and anchorages (anchoring areas outside of the port) increases as maritime shipping becomes more critical to the global economy, acting as one of the main factors in global freight transport (Corbett et al., 2010). For example, the economic value of cargo and cruise ship activity at Port Everglades increased from \$13.9 billion in 2010 to \$32.2 billion in 2019 (Martin Associates, 2020). This increase in maritime shipping and transport may lead to a greater occurrence of ship groundings and anchoring incidents on adjacent coral reefs.

Figure 2. Bow scar and rubble berm resulting from M/V Clipper Lasco grounding. Rubble berm on lefthand side, bow scar on right hand side.

Prior to the 2008 reconfiguration of the Port Everglades anchorage in Broward County, Florida (Walker et al., 2012), large ship groundings significantly impacted reefs adjacent to the Port (Walker et al., 2012). In 2006, two large commercial vessels grounded in 7-10 m of water on the Inner Reef, approximately 3 km north of the Port Everglades entrance channel and 1,300 m offshore (Continental Shelf Associates, Inc., 2006) (Figure 3). The M/V Spar Orion, a 185 m long cement freighter carrying 44 metric tons of cement, grounded May 17, 2006, and the M/V Clipper Lasco, a 170 m long bulk carrier carrying 30,000 metric tons of bauxite, grounded September 14, 2006. Both groundings caused substantial reef damage, including surficial scarring of substrate and associated biota, scraping, fracturing, and displacing substrate, and sheering, fracturing, and displacing biota (Continental Shelf Associates, Inc., 2006). In the areas where each vessel's bow made direct contact with the reef, displacement of reef substrate and accumulation of destabilized substrate (rubble), referred to as bow scars, occurred. The Spar Orion and Clipper Lasco bow impact areas were estimated to be 107 m^2 and 172 m^2 in size, respectively (Continental Shelf Associates, Inc., 2006).

Limited primary restoration efforts were made to consolidate loose rubble and reattach displaced biota immediately after the vessels were refloated in 2006 (Continental Shelf Associates, Inc., 2006). Site visits three and four years after the grounding events demonstrated limited recovery (Gilliam and Moulding, 2012). Therefore, direct management action was undertaken to stabilize the remaining unconsolidated rubble and recreate natural substrate complexity to allow for recovery as well as provide an area for future biological restoration through transplantation of stony corals and gorgonians. In 2015, the Florida Department of Environmental Protection (FDEP) Coral Reef Conservation Program carried out a restoration project to stabilize the substrate at these two grounding sites. Funds were derived from private settlements associated with the original grounding events as well as civil penalties collected through a provision of the Florida Coral Reef Protection Act (Olsen Associates, Inc., 2016). Rehabilitation and stabilization were completed in December 2015 and included relocating loose rubble from the impacted areas into their respective bow scar areas, capping the rubble in the bow scars with a single layer of large limestone boulders, and grouting with concrete (Figure 4) (Olsen Associates, Inc., 2016).

The objective of this study was to determine from long-term monitoring if the stabilization actions taken at the Spar Orion and Clipper Lasco grounding sites have improved the structural complexity such that recovery of the associated biological community may occur. To answer this question, permanent belt transects were established at sites within stabilized (boulder) and un-stabilized (rubble) grounding areas as well as adjacent un-impacted reef areas, and stony coral, gorgonian corals, and giant barrel sponge demographic were collected. Photo transects were completed to collect benthic cover data to describe the benthic biological community. Sediment depth and rugosity were used to define the physical characteristics of each habitat type and roving diver surveys were also used to observe any changes in the macroinvertebrate communities at different sites. Results from this study describe the community that developed on boulders after seven years and provide important data to guide future restoration efforts on the successes and shortcomings of boulders in site stabilization.

Figure 3. Map of the project area with study site locations north of Port Everglades, Broward County, Florida. Monitoring sites signified by circles (blue = grounding sites, red = reference reef sites). North Reference Reef site numbers and the Clipper Lasco and Spar Orion sites refer to site numbers established by Gilliam and Moulding (2012).

Figure 4. Clipper Lasco grounding site rehabilitation. Top row are images of the bow scar in 2010, middle row images are from 2016 initial surveys, bottom row images are from surveys in 2022.

2. Methods 2.1. Site Establishment

In 2016, permanent transects were established at the Spar Orion and Clipper Lasco grounding sites in the boulder stabilized bow scars and in adjacent damaged areas still dominated by rubble. The bow scar and rubble area at the Spar Orion grounding site were smaller in area (107 m²) than these areas at the Clipper Lasco grounding site (172 m²) (Olsen Associates, Inc., 2016). One boulder and one rubble transect were established with approximately 8 m between them at the Spar Orion grounding site. Two boulder and two rubble transects were established at the Clipper Lasco site with boulder transects approximately 9 m apart from one another, and similar spacing between rubble transects with 12 m separating the boulder transects from the rubble transects. Transects were tagged, and the ends of all transects were marked with permanent stakes. Four, undamaged, reference reef sites were established on the Inner Reef north of the grounding sites and assessed in 2009 (Gilliam and Moulding, 2012) (Figure 3). Each of these sites had one, 20 m x 1.5 m transect which was tagged and marked by permanent stakes. All transects were sampled as 1.5 m wide belt transects; boulder and rubble sites allowed transects 15 m in length while reference reef sites allowed for transects 20 m in length. The four reference transects and all boulder and rubble transects were sampled annually from 2016 to 2022 (Table 3).

2.1 Data Collection

At each site, the belt transects were surveyed to evaluate benthic biological communities in two ways. A population approach was employed to evaluate stony and gorgonian corals within the belt transects with species distribution, abundance, density, and size (colony diameter) measured. Secondly, photographic data were collected, and a percent benthic cover estimate was calculated for benthic communities, including stony corals, gorgonians, sponges, crustose coralline algae (CCA), zoanthids, algae, etc. These values were calculated from digital images analyzed with Coral Point Count with Excel (CPCe) software (Kohler and Gill, 2006).

						Sample	Transect
				Depth	Length	Area	Bearing
Site	Habitat	Latitude	Longitude	(f ^t)	(m)	(m ²)	$(\mathrm{^{\circ}})$
N. Reference 3	Reef	26° 08.083	80° 05.409	30	20	30	80
N. Reference 4	Reef	26° 08.355	80° 05.409	25	20	30	30
N. Reference 11	Reef	26° 08.317	80° 05.454	22	20	30	180
N. Reference 12	Reef	26° 08.070	80° 05.493	17	20	30	70
Spar Orion Boulder	Boulder	26° 07.646	80° 05.406	34	15	22.5	150
Spar Orion Rubble	Rubble	26° 07.646	80° 05.406	34	15	22.5	180
Clipper Lasco Boulder 1	Boulder	26° 07.093	80° 05.578	27	15	22.5	200
Clipper Lasco Boulder 2	Boulder	26° 07.093	80° 05.578	27	15	22.5	200
Clipper Lasco Rubble 1	Rubble	26° 07.093	80° 05.578	27	15	22.5	130
Clipper Lasco Rubble 2	Rubble	26° 07.093	80° 05.578	27	15	22.5	60

Table 1. Grounding and reference reef site locations (deg dec. min), depth (ft), transect length (m), sample area (m^2) and bearing (degrees).

Benthic community demographic data were collected within each belt transect utilizing 0.75 m² quadrats (1 m x 0.75 m). Non-overlapping quadrats were placed at each meter mark along both sides of each transect for a sample area of either 30 m^2 (40 x 0.75 m² quadrats) or 22.5 m² (30 x 0.75 m² quadrats) (Table 1). Stony corals, gorgonians, and barrel sponges (*Xestospongia muta*) were identified and measured in each quadrat. For stony corals ≥ 5 cm diameter, colonies were identified to species, condition data (bleaching and disease) were recorded, and colony diameter and colony live tissue area (live tissue length and width) were measured. For gorgonian corals ≥ 2 cm in height, colonies were identified to genus, and colony height was measured and assigned to a size class (2-5 cm, 6-10 cm, 11-25 cm, 26-50 cm, and >50 cm). Barrel sponge height and base width were measured.

Visually identifying small colonies proved difficult, so juvenile stony corals (recruits) $<$ 5 cm in diameter and juvenile (recruits) gorgonians < 2 cm in height were identified and measured in smaller 0.25 m^2 quadrats. As with adults, stony coral juveniles were identified to species and gorgonians to genus when possible. Overall, thirty quadrats were assessed at the grounding sites $(30 \times 0.25 \text{ m}$ quadrats, $7.5 \text{ m}^2)$, and 40 quadrats were assessed in the reference reef sites (40 x) 0.25 m quadrats, 10 m^2).

Figure 5. Divers using quadrats to define areas along a transect.

 A photo transect was conducted on the left side of each site transect to estimate benthic community cover. Photo transects were 0.4 m in width for a sample area of 6 m^2 (15 m transects) or 8 $m²$ (20 m transects). Each transect image was processed with CPCe software, where 15 random points were examined per image to determine percent cover for benthic functional groups. Functional groups included both biotic taxa (stony coral, gorgonian, sponge, CCA, macroalgae, and zoanthid) and substrate type (substrate, boulder, rubble, and sand). Prior to image analysis, a data quality assurance (QAQC) procedure was completed. All researchers assisting with the point count analyzed the same points on the same transect to evaluate differences among the research group. A Bray-Curtis similarity matrix was calculated on the square root (to assess variation in broad taxa ID) and fourth root (to assess variation in rarer taxa ID) transformed for inter-observer QAQC point count data. Similarity between all observers was above 90% for broad taxa (i.e., square root transformed data) and 95% for rare taxa (i.e., fourth root transformed data).

A measure of rugosity (topographical complexity of substrate) using a chain link method (Rogers et al., 1982) along the center of each transect was completed. A chain marked at both 15 m and 20 m, with links approximately 2 cm in size, was draped over and within the contours of the substrate including all the holes, crevices, and raised surfaces (including stony coral and *X. muta*) under each sample transect. The measuring tape defining each transect was used to determine the ratio of the tape length to chain length to get an index of rugosity (length of tape/length of chain). The higher the index value, the more complex (rugose) the substrate. For example, an index value of 1.0 is flat.

Sediment depth data were collected at every site every survey year. A measurement of depth (cm) was collected directly under belt transects at each meter mark using a graduated ruler.

A visual survey of macroinvertebrates was carried out within the direct area of each site. The grounding sites survey areas were approximately 15 m x 15 m, and the reference reef sites areas were approximately 20 m x 20 m. This visual survey specifically targeted *Strombus gigas* (queen conch), *Panulirus argus* (Caribbean spiny lobster), and *Diadema antillarum (*long-spined sea urchin*)* because of their ecological and economic importance.

2.3 Statistical Analysis

The purpose of this study was to compare differences between grounding and reference sites in benthic community composition, cover and demographics, and physical characteristics. The null hypothesis' tested was: 1. There is no difference between the biological community that developed on stabilized reef (boulder sites) and remaining rubble (rubble sites), 2. There was no difference in physical properties between stabilized reef (boulder sites) and remaining rubble (rubble sites). Data analysis was conducted in multiple ways to assess changes in each of the three habitats (reference reef, boulder, and rubble) over time. The "Reef" habitat in the analyses included the four northern reference reef sites, the "Boulder" habitat included the 3 boulder sites (1 Spar Orion site and 2 Clipper Lasco sites), and "Rubble" included the three rubble sites (1 Spar Orion site and 2 Clipper Lasco sites) (Table 1). Mean stony coral species density, gorgonian genus density, stony coral recruit density, gorgonian recruit density and *Xestospongia muta* density were calculated for each habitat, at each timepoint, by dividing the abundance by the

transect area (22.5 m² for grounding sites, 30 m² for reference sites). Univariate and multivariate data analyses were conducted to specifically assess whether stony coral density, stony coral colony size (diameter), stony coral community composition, gorgonian community composition, recruit (stony coral and gorgonian) community composition and benthic community composition in different habitats (reefs, boulders, and rubble) were changing in the same way over time.

All statistical analyses were conducted on the 2016 to 2022 data. Data collected preboulder deployment from the one Spar Orion site in 2009 and two Clipper Lasco sites in 2010 (Gilliam and Moulding, 2012), referred to as "Unrestored", were plotted and habitat means calculated for qualitative comparisons. Reference reef site data from 2009 were plotted and habitat means calculated for qualitative comparison in tables and trajectory figures. Univariate analyses were conducted in R (R Core Team, 2020). Generalized Linear Mixed Models (GLMM) were used to assess whether stony coral density varied between habitats, between years surveyed, and whether each habitat was changing in the same way using the function "glmmTMB" from the package of the same name (Brooks et al., 2017). A poisson GLMM was used with an offset, "Transect Length", to account for differences in transect length and random intercept "Site", to account for spatial autocorrelation and repeat measures on the same transect each year. The fixed categorical factors "Year" and "Habitat" were included in the full model, and model selection was determined using the Akaike Information Criterion (AIC) from all possible model combinations. Model validation was performed using the package "DHARMa", with residual diagnostics, including overdispersion, heterogeneity and temporal autocorrelation, conducted on the fitted model (Hartig, 2017). These diagnostic tests indicated no significant deviations from each model's respective assumptions. Post hoc, pairwise assessment of retained factors in the fitted models were conducted using the package "emmeans", where differences in the response variable are analyzed between levels of a factor (e.g., Year) or interaction (e.g., Year x Habitat) based on model predictions using Tukey adjustment to control for type 1 error (Length, 2019). Between level differences in post hoc analysis were considered significant at p < 0.05. Mean stony coral colony length (i.e., mean colony length per transect per timepoint), gorgonian density, stony coral recruit density, and gorgonian recruit density were all assessed using GLMM. Mean stony coral (\geq 5 cm) colony length was analyzed with a gamma distribution. Gorgonian (≥ 2 cm) density and stony coral recruit ($\lt 5$ cm) density analysis used a negative binomial 1 distribution, and gorgonian recruit density was analyzed with a negative

binomial 2 distribution. Specific distributions were determined using the Akaike Information Criterion (AIC). Site was included as a random intercept, while; Habitat and Year were included as fixed categorical factors. Model validation was assessed as described above and indicated no deviations of the assumptions from each respective model.

Multivariate statistical analyses were conducted in Primer 7 (Clarke and Gorley, 2006). Stony coral species density, gorgonian genus density, benthic community cover, and stony coral recruit density were assessed in relation to habitat and year. Gorgonian recruits were not assessed as there were so few at multiple sites or multiple years. Prior to generation of Bray-Curtis similarity coefficients, each dataset was square root transformed to reduce the importance of abundant taxa and allow mid-range and rarer taxa to have some influence on the similarity calculation (Clarke and Warwick, 2001). Spatiotemporal variation in the stony coral species density, gorgonian genus density, benthic community cover, stony coral recruit density from 2016 to 2022 were statistically analyzed using Permutation Analysis of Variance (PERMANOVA, Anderson, 2001; McArdle and Anderson, 2001). Type 3 PERMANOVA based on 9999 permutations of residuals under a reduced model was used to analyze each dataset with transects as replicates. Similarity matrices were assessed by the fixed spatiotemporal factors: Year and Habitat including the interaction between Year and Habitat. Multivariate results were considered significant at $p < 0.05$. If a significant difference was found for a factor using PERMANOVA, a post hoc test (PERMANOVA Post hoc) was conducted to determine differences between levels of the factor (e.g., if the stony coral community in 2016 was significantly different to that in 2022). For visual assessment of similarity between habitats and years, metric multidimensional scaling (mMDS) plots were created from the Bray-Curtis resemblance matrix of all surveys conducted. Each sample in the mMDS represents each habitat at one time point, and the distance between samples depicts the similarity in community composition (i.e., the closer a sample, the more similar the community composition). Community trajectories for each response type were visually assessed using the distance among centroids from the Bray-Curtis resemblance matrix to see how the mean community at each habitat is changing over time (Anderson, 2014). Benthic community trajectories were plotted for each habitat at the centroid position in dissimilarity space (i.e., the mean position per habitat at each timepoint) and the origin of differences between habitats visually assessed by plotting taxon vectors onto the mMDS.

Multiple diversity indices were calculated to assess spatiotemporal variation in each habitat in each year. Each array of diversity indices was calculated for stony coral species, gorgonian genus, and stony coral recruit abundance in each habitat during each survey year. Diversity indices included the Total Number of Species (S), mean abundance (N), Species Richness (Margalef's d), Evenness (Pielou's J), Shannon-Weaver Diversity (H') and Inverse Simpson's diversity $(1-\lambda)$.

Margalef's d for species richness was calculated for each habitat in each year using the following equation where S is the number of species and N is the total number of individuals in the sample:

$$
D = (S-1/\log(N))
$$

Shannon-Weaver Diversity Indices for number of species (H') were calculated for each habitat using the following equation where " p_i " is the relative abundance of species or genus "i," and "S" is the total number of species.

$$
S
$$

H' = - Σ p_i ln p_i
i = 1

Evenness for number of species (J') at each habitat in each year was calculated using the equation:

$$
J' = H'/H'max = H'/lnS
$$

where H'max is the maximum possible diversity for any given "S". While H' indicates the index of diversity, evenness indicates how close those values come to the maximum possible value for each habitat.

Inverse Simpson's diversity index was calculated for each habitat in each year using the following equation:

$$
1 - \lambda = 1 - \Sigma(n_i^*(n_i - 1)/N^*(N - 1))
$$

where, $n =$ the number of individuals in the ith species and $N =$ total number of individuals in the community.

Site rugosity indices were tested for normal distribution and homogeneity using a Shapiro Wilks test and Bartlett test, respectively. Parametric assumptions were met, and a one-way repeated measures Analysis of Variance (ANOVA) was used to test the effect of the factors Habitat and Year on rugosity indices. A GLMM was not used due to the violation of assumptions of normality and homogeneity of variance despite transformation or centering of data for rugosity and sediment depth. Mean sediment depth (cm) measures were tested for normal

distribution and homogeneity using a Shapiro Wilks test and Bartlett test as well. Sediment data did not meet parametric assumptions, so a non-parametric Kruskal-Wallis one-way ANOVA on ranks was used to test the effect of the factors Habitat and Year on sediment depth.

Macro-invertebrates were compared between habitats and years, but no statistical tests were run because there were so few, if any, macro-invertebrates at most of the grounding sites during most years.

3. Results

3.1 Rugosity

Mean rugosity index values were compared across habitats. A one-way repeated measures ANOVA sum of squares found habitat was the main cause of variation (Sum sq = 0.3683) and was shown to significantly affect the rugosity ($p < 0.0001$) (Figure 6) while year played no significant role ($p = 0.991$). Boulder sites had the highest mean (\pm SE) rugosity index each year ranging from 1.43 ± 0.01 in 2021 to 1.50 ± 0.06 in 2020 (Table 2). Rubble site mean rugosity index was significantly lower than boulder sites ($p < 0.0001$) as well as reef sites ($p < 0.0001$) and was lower every year, ranging from 1.04 ± 0.02 in 2017 to 1.18 ± 0.02 in 2020 (Table 2).

Figure 6. Box and whisker plot of rugosity index. Points represent outliers and solid black lines represent the median, the box ranges from the first quartile to the third quartile of the distribution. The "whiskers" on box plots extend to the most extreme data points.

Reef site mean rugosity index was significantly lower than boulder habitats ($p < 0.0001$), ranging from 1.20 ± 0.03 in 2016 to 1.32 ± 0.05 in 2020 (Table 2). Data from unrestored sites showed a similar rugosity index to that of rubble sites with an index of 1.06 ± 0.03 (Table 2).

Habitat	Year	Rugosity Index	Sediment Depth
Unrestored	2009/2010	1.06 ± 0.03	NA
	2009	1.20 ± 0.02	NA
	2016	1.20 ± 0.03	0.24 ± 0.07
	2017	1.24 ± 0.03	0.37 ± 0.06
Reef	2018	1.24 ± 0.05	0.23 ± 0.05
	2020	1.32 ± 0.05	0.43 ± 0.11
	2021	1.28 ± 0.01	0.33 ± 0.09
	2022	1.25 ± 0.02	0.55 ± 0.2
	2016	1.49 ± 0.07	0.19 ± 0.06
Boulder	2017	1.47 ± 0.10	0.08 ± 0.04
	2018	1.45 ± 0.01	0.35 ± 0.11
	2020	1.50 ± 0.06	0.27 ± 0.08
	2021	1.43 ± 0.01	0.23 ± 0.07
	2022	1.44 ± 0.02	0.21 ± 0.06
	2016	1.05 ± 0.01	1.52 ± 0.24
	2017	1.04 ± 0.02	0.94 ± 0.16
Rubble	2018	1.16 ± 0.03	1.4 ± 0.26
	2020	1.18 ± 0.02	1.54 ± 0.32
	2021	1.09 ± 0.03	1.63 ± 0.34
	2022	1.16 ± 0.03	2.42 ± 0.42

Table 2. Mean $(\pm SE)$ rugosity index per habitat type per year (the higher the index value the more rugose the habitat) and mean $(\pm SE)$ sediment depth.

3.2. Sediment

Sediment data did not fit parametric assumptions, so a non-parametric Kruskal Wallis test was used to define the factors affecting sediment depth. Habitat had the most significant impact on sediment depth ($p < 0.05$) followed by site ($p < 0.05$) and year ($p < 0.05$). Post hoc analysis showed mean sediment depth at boulder and reef sites were not significantly different between habitats ($p = 0.184$) while mean sediment depth of rubble habitats was significantly higher than

boulder sites ($p < 0.05$) and reef sites ($p < 0.05$). Boulder sites had the lowest mean (\pm SE) sediment depth each year ranging from 0.08 ± 0.04 cm in 2017 to 0.35 ± 0.11 cm in 2018 (Table 2). Reef site sediment depth ranged from 0.23 ± 0.05 cm in 2018 to 0.55 ± 0.20 cm in 2022 (Table 2). Rubble site sediment depth was significantly higher than reef or boulder every year ranging from 0.94 ± 0.16 cm in 2017 to 2.42 ± 0.42 cm in 2022 (Table 2). Sediment data were not collected at unrestored sites in 2009/2010.

Figure 7. Change in mean $(\pm SE)$ sediment depth (cm) overtime between habitat types.

3.3. Stony Coral Density

Stony coral density (colonies ≥ 5 cm diameter) (Appendix Tables 4, 5, and 6) varied significantly by survey year and habitat. Combined with the random effect of transect area, the model explained 56% of variation in the data (GLMM; Marginal R^2 (i.e., fixed effects only) = 0.497; Conditional R^2 (i.e., fixed and random effects) = 0.559). Colony density was significantly higher at reference reef sites every year when compared to rubble sites ($p < 0.05$). Additionally, there were significantly more colonies at reef sites than at boulder sites every year until 2022 when boulder sites and reef sites were no longer significantly different (emmeans pairwise comparisons, $p > 0.1$). Stony coral density did not significantly vary between boulders and rubble at any point ($p > 0.05$).

Figure 8. Examples of each habitat type; top images = Spar Orion boulder in 2022, middle image = Spar Orion rubble in 2022, bottom image = Reference reef site 11 in 2022.

Mean colony density was highest in 2022 in every habitat: 2.38 ± 0.32 colonies m⁻² (\pm) SE) at reference reef sites, 1.17 ± 0.15 colonies m⁻² at boulder sites and 0.80 ± 0.23 colonies m⁻² at rubble sites (Table 3). Model predictions suggested that boulder sites in 2022 had significantly higher coral density than previous years (emmeans contrast, $p = 0.0001$), with colony density increasing 700% from 2016 to 2022. Coral density at rubble sites did not significantly change over time (p > 0.05), ranging from 0.21 ± 0.12 colonies m⁻² in 2018 to 0.80 ± 0.23 colonies m⁻² in 2022, but did significantly increase after hurricane Irma from 2018 to 2022 (emmeans contrast, $p = 0.02$) (Table 2). Colony density did significantly change over time at reference reef sites with an increase in density of 1.34 ± 0.43 to 2.38 ± 0.32 from 2016 to 2022 (emmeans contrast, $p < 0.05$) (Table 3). Table 4 summarizes the mean density at each habitat in 2022 and the unrestored habitat in 2009/2010.

Habitat	Year	Abundance	Density	Length
	2016	3.33 ± 2.03	0.15 ± 0.09	6.20 ± 0.57
	2017	3.00 ± 1.73	0.13 ± 0.08	6.22 ± 0.66
Boulder	2018	3.00 ± 1.53	0.13 ± 0.07	6.67 ± 0.50
	2020	12.33 ± 2.33	0.55 ± 0.10	6.78 ± 0.27
	2021	15.00 ± 1.53	0.67 ± 0.07	6.87 ± 0.26
	2022	26.33 ± 3.48	1.17 ± 0.15	6.78 ± 0.21
	2016	40.25 ± 8.74	1.34 ± 0.29	9.03 ± 0.37
	2017	48.25 ± 10.86	1.61 ± 0.36	9.25 ± 0.36
Reef	2018	46.25 ± 6.41	1.54 ± 0.21	9.04 ± 0.32
	2020	60.50 ± 5.78	2.02 ± 0.19	8.40 ± 0.26
	2021	59.50 ± 8.57	1.98 ± 0.29	8.26 ± 0.24
	2022	71.50 ± 9.68	2.38 ± 0.32	8.33 ± 0.25
	2016	7.00 ± 3.61	0.44 ± 0.23	6.80 ± 0.53
	2017	9.00 ± 3.51	0.60 ± 0.23	6.48 ± 0.34
Rubble	2018	4.67 ± 2.73	0.31 ± 0.18	7.36 ± 0.96
	2020	10.00 ± 3.21	0.67 ± 0.21	7.33 ± 0.66
	2021	11.33 ± 4.10	0.50 ± 0.18	7.35 ± 0.51
	2022	18.00 ± 5.13	0.80 ± 0.23	6.87 ± 0.36

Table 3. Stony coral (colonies \geq 5 cm) colony mean (\pm SE) abundance (colonies), density (colonies $m⁻²$), and mean length (cm) by habitat type and year.

3.4. Stony Coral Length

Mean stony coral colony (> 5 cm diameter) length significantly varied by habitat, but not by year, and there was no significant interaction between survey year and habitat (GLMM; Marginal $R^2 = 0.614$, Conditional $R^2 = NA$). Mean colony length was significantly higher at reference sites than at boulder or rubble sites ($p < 0.05$), ranging from 8.28 ± 0.24 cm in 2021 to 9.25 ± 0.36 in 2017 (Table 3). Boulder and rubble sites were not significantly different from each other ($p =$ 0.4032).

Figure 9. Change in stony coral (colonies \geq 5 cm) colony mean density (\pm SE) over time between habitats.

Despite no significant change by year, mean colony length generally increased at boulder sites ranging from 6.20 ± 0.57 cm in 2016 to 6.87 ± 0.26 cm in 2021 (Table 2). Mean coral length fluctuated at rubble sites, ranging from 6.48 ± 0.34 cm in 2017 to 7.36 ± 0.96 cm in 2018 (Table 3). The largest colony observed in any year or habitat surveyed was a 32 cm (diameter) *Montastraea cavernosa* at a reference site in 2016 and 2017 (Table 4). The largest stony coral colony (\geq 5 cm) at boulder sites was a *Porites porites* that settled on the boulders after deployment and grew to 13 cm by 2022 (Table 5). Rubble sites had a 15 cm *Pseudodiploria strigosa* in 2016 that grew to 25 cm by 2020, lost tissue sometime between 2020 and 2021 and is now 22 cm (Table 5). Table 4 summarizes the mean colony length at each habitat in 2022 and the unrestored habitat in 2009/2010.

Table 4. Summary data (mean \pm SE) for each habitat type in 2022 and the 2009/2010 unrestored sites (The presence of a "–" signifies data weren't collected for that metric).

Table 5. Largest stony coral (colonies \geq 5 cm) species and size (diameter in cm) per habitat per year.

3.5. Stony Coral Community

Stony coral community (colony diameter \geq 5 cm) density significantly varied by habitat but did not vary significantly by year, and there was no interaction between habitat and year (PERMANOVA; Habitat: pseudo-f = 10.156, $p = 0.0001$; Year: pseudo-f = 1.415, $p = 0.6$). Post hoc analysis found the stony coral community differed significantly between rubble and reef habitats ($p = 0.0001$), between boulder and reef ($p = 0.0001$), and between boulder and rubble habitats ($p = 0.0132$). Reference reef sites generally had a higher number of stony coral species than rubble or boulder (12 to 14 species at reference reef sites, four to seven species at rubble sites, and three to nine species at boulder sites).

Stony coral species richness fluctuated between 12 and 14 species every year for the reference reefs sites and varied from four to seven in the rubble sites. The boulder sites had an increase in species richness from three in 2016 to nine in 2022 (Appendix Tables 1, 2, and 3). Several species contributed to differences between habitats in the stony coral community. Both *Montastrea cavernosa* and *Orbicella annularis* were present every year at reference reef sites but were not present in rubble or boulder sites (Appendix Tables 4, 5, and 6).

Figure 10. Change in stony coral (colonies \geq 5 cm) colony mean length (\pm SE) over time between habitats.

Agaricia agaricites was present every year at the reference reef sites with a mean density range from 0.06 ± 0.01 colonies m⁻² (mean \pm SE) in 2016 to 0.18 ± 0.08 colonies m⁻² in 2021. *Agaricia agaricites* did not appear on boulders until 2020 but persisted over time with mean density ranging from 0.10 ± 0.02 colonies m⁻² to 0.15 ± 0.03 colonies m⁻². *Agaricia agaricites* was never present at rubble sites (Appendix Tables 4, 5, and 6). *Porites astreoides* was identified in all habitats every year. *Porites astreoides* was the most abundant stony coral species at reference reef sites, with density ranging from 0.59 ± 0.18 colonies m⁻² in 2016 to 0.87 ± 0.34 colonies m-2 in 2022 (Appendix Tables 1, 2, and 3). *Siderastrea siderea* was the only other species identified in all habitats every year. *Siderastrea siderea* was the most abundant species at boulder (ranging from 0.09 ± 0.04 colonies m⁻² in 2016 to 0.49 ± 0.22 colonies m⁻² in 2022) and rubble sites (range from 0.20 ± 0.11 colonies m⁻² in 2018 to 0.41 ± 0.14 colonies m⁻² in 2022). *Siderastrea siderea* was the second most abundant species at reference reef sites in most years

(range from 0.20 ± 0.08 colonies m⁻² in 2016 to 0.45 ± 0.08 colonies m⁻² in 2022) (Appendix Tables 4, 5, and 6).

Active disease lesions identified as white syndrome, were only identified affecting two reference reef sites in 2016. Northern reference site 12 had one diseased *P. astreoides* colony and one *P. porites* colony, while northern site 4 had one diseased *Agaricia lamarcki* colony.

Diversity metrics (Table 6), MDS ordination (Figure 11), and community trajectories (Figure 12) show that stony coral diversity is consistently higher at reference reef sites than rubble, unrestored habitat, or boulder sites, but stony coral diversity at boulders is generally increasing and that evenness at boulders is higher than all other habitats (Table 6).

Table 6. Stony Coral \geq 5 cm abundance diversity indices. Total Number of Species (S), mean abundance (N), Species Richness (Margalef's d), Evenness (Pielou's J), Shannon-Weaver Diversity (H') and Inverse Simpson's diversity $(1-\lambda)$.

Sample	S	N	d	J'	H'	$1-\lambda$
Unrestored 2010	3	$\overline{2}$	3.241	0.811	0.979	1.266
Reef 2009	12	14	4.22	0.891	2.213	0.940
Reef 2016	14	16	4.695	0.843	2.173	0.913
Reef 2017	12	17	3.913	0.842	2.093	0.903
Reef 2018	13	17	3.130	0.686	1.758	0.760
Reef 2020	12	61	2.681	0.703	1.747	0.777
Reef 2021	15	60	3.426	0.680	1.841	0.790
Reef 2022	14	72	3.045	0.681	1.797	0.790
Boulder 2016	3	3	1.661	0.991	1.089	0.943
Boulder 2017	$\overline{4}$	3	2.731	0.918	1.273	1.037
Boulder 2018	5	3	3.641	0.887	1.427	1.074
Boulder 2020	7	12	2.388	0.852	1.659	0.846
Boulder 2021	9	15	2.954	0.862	1.894	0.886
Boulder 2022	9	26	2.446	0.813	1.785	0.824
Rubble 2016	$\overline{4}$	7	1.542	0.862	1.194	0.751
Rubble 2017	6	9	2.276	0.679	1.216	0.642
Rubble 2018	$\overline{4}$	5	1.947	0.742	1.029	0.688
Rubble 2020	6	10	2.171	0.596	1.068	0.543
Rubble 2021	7	11	2.471	0.670	1.304	0.645
Rubble 2022	7	18	2.076	0.766	1.490	0.723

Figure 11. Metric MDS of stony coral species (\geq 5 cm colony diameter) community density. Each point represents the stony coral community at one site surveyed at one time point. Points closer together have more similar communities based upon Bray-Curtis resemblance. Vectors represent coral species accounting for over 50% correlation between samples (Pearson's correlation coefficient). *SINT = Stephanocoenia intersepta, MCAV = Montastraea cavernosa, AAGA = A. agaricites, PAST = Porites astreoides, PPOR = P. porites, PSTR = Pseudodiploria strigosa, SSID = Siderastrea siderea.*

3.6. Gorgonian Density

Gorgonian (colonies ≥ 2 cm) density significantly varied by habitat and year with a significant interaction between habitat and year (GLMM; Marginal $R^2 = 0.490$, Conditional $R^2 =$ 0.612). In 2016, boulder sites had significantly fewer gorgonians than reef sites ($p < 0.05$) and had fewer gorgonians than rubble site although the difference was non-significant ($p > 0.05$). Effects from Hurricane Irma in 2017 seemed to be captured in the data as gorgonian density decreased significantly ($p < 0.05$) at rubble sites, dropping from 3.59 \pm 1.30 colonies m⁻² (\pm SE) in 2017 to 1.26 \pm 0.88 colonies m⁻² in 2018. There was a non-significant decrease ($p > 0.05$) on reference reef sites from 5.30 ± 1.24 colonies m⁻² (\pm SE) in 2017 to 3.93 ± 0.55 colonies m⁻² in 2018, and a non-significant decrease ($p > 0.05$) in gorgonian density at boulder sites from 0.73 \pm 0.28 colonies m⁻² in 2017 to 0.4 \pm 0.19 colonies m⁻² in 2018.

Figure 12. Metric MDS of stony coral species (\geq 5 cm colony diameter) community trajectory for each habitat. Points represent the centroid positions of the stony coral community in each habitat each year. Trajectories detail the progression of coral community change over time. Vectors represent coral species accounting for over 80% correlation between samples (Pearson's correlation coefficient). Note: Reef community trajectory starts in 2009. *SINT = S. intersepta, AAGA = A. agaricites, PAST = P. astreoides, PPOR = P. porites, MCAV = Montastraea cavernosa, SSID = Siderastrea siderea.*

Gorgonian density did not significantly change over time from 2016 to 2022 at boulder sites (ranging from 0.4 ± 0.19 colonies m⁻² in 2018 to 1.07 ± 0.51 colonies m⁻² in 2021), rubble sites (ranging from 1.26 ± 0.88 colonies m⁻² in 2018 to 3.64 \pm 1.68 colonies m⁻² in 2021) or reef sites (ranging from 3.93 ± 0.55 colonies m⁻² in 2018 to 5.63 ± 0.91 colonies m⁻² in 2020). In 2022, gorgonian densities at boulder sites were still significantly different from reef sites ($p <$ 0.05) but were not significantly different from rubble sites ($p > 0.05$). Rubble sites and reef sites were not significantly different from each other in 2022 ($p > 0.05$).

3.6. Gorgonian Community

Gorgonian (> 2 cm) abundance and density were higher at reference reef sites than rubble or boulder sites every year (Table 7). The sample year with highest mean abundance and mean

density was the same for rubble and boulder sites but different for reef sites (Table 7). Reference reef sites had the highest mean abundance and mean density in 2020 with a mean abundance of 168.70 ± 27.27 (colonies \pm SE) and a mean density of 5.63 ± 0.91 colonies m⁻². Rubble sites had the highest mean abundance and mean density in 2021 with an abundance of 82.00 ± 37.89 and a density of 3.64 \pm 1.68 colonies m⁻². Boulder sites had the highest mean abundance and mean density in 2021 with an abundance of 24.00 ± 11.53 and a density of 1.07 ± 0.52 colonies m⁻² (Table 7).

Habitat	Year	Abundance	Density
	2016	13.33 ± 2.85	0.59 ± 0.13
	2017	16.33 ± 6.36	0.73 ± 0.28
Boulder	2018	9.00 ± 4.16	0.40 ± 0.19
	2020	21.66 ± 6.57	0.96 ± 0.29
	2021	24.00 ± 11.53	1.07 ± 0.51
	2022	17.00 ± 7.23	0.76 ± 0.32
	2016	166.20 ± 30.10	5.54 ± 1.00
	2017	159.00 ± 37.23	5.30 ± 1.24
	2018	117.70 ± 16.42	3.93 ± 0.55
Reef	2020	168.70 ± 27.27	5.63 ± 0.91
	2021	159.00 ± 20.80	5.30 ± 0.69
	2022	131.70 ± 14.29	4.39 ± 0.48
Rubble	2016	51.00 ± 12.70	2.27 ± 0.56
	2017	80.66 ± 29.36	3.59 ± 1.30
	2018	28.33 ± 19.88	1.26 ± 0.88
	2020	71.00 ± 29.67	3.16 ± 1.32
	2021	82.00 ± 37.89	3.64 ± 1.68
	2022	59.33 ± 25.75	2.64 ± 1.14

Table 7. Gorgonian colony (colony > 2 cm) mean (\pm SE) abundance (colonies) and density (colonies m^{-2}) by habitat type and year.

All habitats were significantly different from one another ($p < 0.05$). Boulder sites had consistently lower gorgonian density than rubble or reference reef sites. Three genera were found in every habitat every year: *Antillogorgia spp.*, *Eunicea spp*., and *Gorgonia spp. Antillogorgia*

spp. density ranged from 0.31 ± 0.18 colonies m⁻² to 0.50 ± 0.24 colonies m⁻² at boulder sites, from 0.33 ± 0.15 colonies m⁻² to 1.62 ± 0.55 colonies m⁻² at rubble sites, and from 1.12 ± 0.24 colonies m⁻² to 1.93 ± 0.55 colonies m⁻² at reference reef sites (Appendix Tables 7, 8, 9). *Eunicea spp.* and *Gorgonia spp.* showed similar patterns with low colony density at boulder sites, moderate density at rubble sites, and the highest colony density at reference reef sites, peaking at 1.89 ± 0.20 colonies m⁻² in 2020 and 1.14 ± 0.14 colonies m⁻² in 2016, respectively (Appendix Table 7). No *Muricea spp.*, *Plexaura spp.*, or *Pterogorgia spp.* were found at boulders sites during the study.

Table 8. Gorgonian (colonies ≥ 2 cm) abundance diversity indices. Total Number of Species (S), mean abundance (N), Species Richness (Margalef's d), Evenness (Pielou's J), Shannon-Weaver Diversity (H'), and Inverse Simpson's diversity $(1-\lambda)$.

Sample	S	N	d	J'	H'	$1-\lambda$
Unrestored 2010	4	13	1.159	0.7797	1.081	0.6438
Reef 2009	7	27	1.831	0.9111	1.773	0.8392
Reef 2016	$\overline{7}$	24	1.887	0.8441	1.643	0.8094
Reef 2017	6	22	1.615	0.8705	1.56	0.7966
Reef 2018	7	21	1.981	0.8415	1.638	0.8137
Reef 2020	$\overline{7}$	25	1.871	0.8524	1.659	0.8093
Reef 2021	$\overline{7}$	25	1.874	0.8416	1.638	0.8043
Reef 2022	7	24	1.893	0.8562	1.666	0.8146
Boulder 2016	$\overline{4}$	6	1.692	0.8611	1.194	0.7745
Boulder 2017	$\overline{4}$	7	1.546	0.9415	1.305	0.828
Boulder 2018	$\overline{4}$	$\overline{4}$	2.107	0.9171	1.271	0.9144
Boulder 2020	5	8	1.882	0.8875	1.428	0.8345
Boulder 2021	$\overline{4}$	8	1.431	0.9122	1.265	0.7975
Boulder 2022	4	$\overline{7}$	1.56	0.8817	1.222	0.8025
Rubble 2016	5	12	1.596	0.8336	1.342	0.7532
Rubble 2017	6	16	1.82	0.8146	1.459	0.7637
Rubble 2018	5	8	1.964	0.7748	1.247	0.7508
Rubble 2020	5	14	1.516	0.788	1.268	0.7245
Rubble 2021	6	16	1.808	0.7906	1.417	0.7656
Rubble 2022	5	13	1.571	0.8083	1.301	0.7356

Diversity metrics (Table 8), MDS ordination (Figure 13), and community trajectories (Figure 14) show that gorgonian diversity is consistently higher at reference reefs than unrestored habitat, rubble, or boulder sites. Boulder sites have fewer species and abundance of gorgonians than other
habitat types, including the unrestored sites from 2009/2010. In general, reference reef sites had a higher abundance of all gorgonian genera than rubble, unrestored habitat, and boulder sites.

3.7 Stony Coral Recruit Density

Stony coral recruit (colonies $<$ 5 cm) density significantly varied by habitat and year with no significant interaction between habitat and year (GLMM; Marginal $R^2 = 0.348$, Conditional $R^2 =$ 0.409) (Table 9). In 2016, mean stony coral recruit density at reference reef sites was similar to rubble sites ($p = 1.000$), while boulder sites had significantly fewer recruits than both reef and rubble sites ($p < 0.05$). After Hurricane Irma in 2017, recruit density decreased significantly ($p <$ 0.05) at rubble sites, dropping from 3.23 ± 0.97 colonies m⁻² (\pm SE) in 2017 to 1.16 \pm 0.18 colonies m⁻² in 2018. There was a non-significant decrease ($p > 0.05$) on reference reef sites from 1.48 ± 0.14 colonies m⁻² (\pm SE) in 2017 to 1.41 \pm 0.2 colonies m⁻² in 2018, and a slight increase in recruit density at boulder sites from 0.64 ± 0.28 colonies m⁻² in 2017 to 0.86 ± 0.12 colonies $m²$ in 2018. In 2018 all three habitat types had similar recruit densities ($p > 0.1$) and remained similar in 2020 ($p > 0.1$).

Figure 13. Metric MDS of gorgonian genera community density. Each point represents the gorgonian community at one site surveyed at one time point. Points closer together have more similar communities based upon Bray-Curtis resemblance. Vectors represent gorgonian genus accounting for over 75% correlation between samples (Pearson's correlation coefficient). EUNI = *Eunicea spp.,* GORG = *Gorgonia spp.,* ANTI = *Antillogorgia spp.*

By 2021, boulder sites had significantly more recruits than reef sites $(p < 0.05)$ (Figure 15) but were not significantly different from rubble sites ($p > 0.05$). In 2022, boulder habitats had significantly more recruits than rubble sites ($p < 0.05$), and boulder sites had marginally higher densities than reef sites $(p=0.058)$. Reef and rubble sites maintained similar recruit densities throughout every year of the study ($p > 0.05$). Over the course of this study, boulder sites significantly increased in stony coral recruit ($<$ 5 cm) density (p $<$ 0.05), ranging from 0.44 \pm 0.18 colonies m⁻² in 2016 to 5.39 \pm 1.37 colonies m⁻² in 2022. Rubble sites fluctuated interannually but did not change significantly over time, ranging from 1.16 ± 0.18 colonies m⁻² in 2018 to 3.23 ± 0.97 colonies m⁻² in 2017. Reef sites had relatively low but consistent recruitment throughout the study, non-significantly increasing from 1.16 ± 0.15 colonies m⁻² in 2016 to 1.71 \pm 0.20 colonies m⁻² in 2022.

Figure 14. Metric MDS of gorgonian community trajectories for each habitat. Points represent the centroid positions of each habitat each year. Trajectories detail the progression of coral community change over time. Vectors represent coral species accounting for over 90% correlation between samples (Pearson's correlation coefficient). *EUNI = Eunicea spp., GORG = Gorgonia spp., ANTI = Antillogorgia spp.*

3.8 Stony Coral Recruit Community

Stony coral recruit community density significantly varied by habitat and year with a significant interaction between the two (PERMANOVA; Habitat: pseudo-f = 7.5, p = 0.0001; Year: pseudo-f = 2.4, p = 0.0003; Interaction: pseudo-f = 1.5, p = 0.03). It was not possible to model the effect of site level variability appropriately due to no stony coral recruits at multiple sites. Pairwise post hoc analysis found that the stony coral recruit community at reference reef sites was significantly different than rubble sites ($p = 0.0001$) and boulder sites ($p = 0.001$).

Table 9. Stony coral recruit (colonies < 5 cm diameter) colony mean (± SE) abundance (colonies), density (colonies $m⁻²$), and length (cm) by habitat type and year.

Reference reef sites (Appendix Table 10) generally had a higher number of stony coral recruit species than boulder sites (Appendix Table 11) and rubble sites (Appendix Table 12) (9 to 12 species at reference reef sites, 5 to 13 species at boulder sites, and 6 to 10 species at rubble sites). Reference reef sites had higher relative abundance of *Porites astreoides* and *Agaricia agaricites* recruits (Appendix Table 10). *Porites astreoides* recruit density ranged from 0.21 ± 0.05 colonies m⁻² in 2017 to 0.43 \pm 0.05 colonies m⁻² in 2016 at reference reef sites, 0.04 \pm NA colonies m⁻² in 2017 to 0.31 \pm 0.08 colonies m⁻² in 2018 at boulder sites, and from 0.04 \pm NA colonies m⁻² in 2022 to 0.16 ± 0.02 colonies m⁻² in 2021 at rubble sites (Appendix Tables 10, 11, 12). *Agaricia agaricites* recruit density at reference reef sites ranged from 0.07 ± 0.02 colonies $m²$ in 2017 to 0.18 \pm 0.12 colonies $m²$ in 2021, while *A. agaricites* did not recruit onto boulders until 2018 with a single recruit settling at each of the Clipper Lasco boulder sites. By 2021 *A. agaricites* had recruited to all three boulder sites, and by 2022 boulder sites had a mean density

of 0.10 ± 0.03 colonies m⁻² (Appendix Table 10). No *A. agaricites* recruits were found at rubble sites at any point.

Figure 15. Change in stony coral (colonies $<$ 5 cm) colony mean density (\pm SE) between habitats over time.

Siderastrea siderea was the dominant stony coral recruit at both boulder and rubble sites, contributing to the differences between habitats in the recruit community (Figure 16 and 17). Density of *S. siderea* was higher at rubble sites than reference reef sites every year and up until 2020, rubble sites had higher densities than boulder sites. *Siderastrea siderea* recruit density ranged from 0.81 ± 0.23 colonies m⁻² in 2018 to 2.21 ± 0.84 colonies m⁻² in 2017 at rubble sites (Appendix 12). *Siderastrea siderea* density at reference reef sites ranged from 0.34 ± 0.03 colonies m⁻² in 2016 to 0.46 ± 0.06 colonies m⁻² in 2022. Boulder sites had the lowest *S. siderea* density between 2016 and 2018 but increased 7-fold from 2018 to 2020 with densities ranging from 0.34 ± 0.15 colonies m⁻² in 2016 to 4.15 ± 0.84 colonies m⁻² in 2022.

Figure 16. Metric MDS of stony coral recruit species (< 5 cm colony diameter) community density. Each point represents the stony coral community at one site surveyed at one time point. Points closer together have more similar communities based upon Bray- Curtis resemblance. Vectors represent coral species accounting for over 40% correlation between samples (Pearson's correlation coefficient). *MCAV = Montastraea cavernosa, AAGA = A. agaricites, PAST = Porites astreoides, PPOR = P. porites, PDIP = Pseudodiploria species (P. clivosa and P. strigosa), SSID = Siderastrea siderea, SBOU Solenastrea bournoni.*

Porites porites was found in higher density at rubble habitats in 2016 and 2017 (although this species was only found at Clipper Lasco rubble sites) than reef sites and did not settle on boulders until 2017 (1 recruit at each site). No *P. porites* were found at rubble sites in 2018 (post Hurricane Irma), and starting in 2020, boulder sites had the highest density of *P. porites* which would then alternate between reef and back to boulder over the next two years. It should be noted that rubble sites had recruitment of "rarer" reef building species, such as *Colpophyllia natans*, *Diploria labyrinthiformis,* and *Meandrina meandrites,* before 2018 and have not had recruitment of these species since hurricane Irma, boulder sites have had recruitment of *Colpophyllia natans*, *Diploria labyrinthiformis,* and *Meandrina meandrites* since 2018 and have also had recruitment of *Eusmilia fastigiata* and one *Orbicella spp.* recruit, which was found in 2020 but not recorded

again. Boulder sites had a higher number of stony coral species recruit in 2022 (13) than the rubble sites at any point (Appendix Tables 10, 11, 12). Although stony coral recruits fluctuated over time (Table 10; Figure 17), stony coral recruit diversity was marginally higher in 2022 than 2016 in every habitat (i.e., boulders, H' $2016 = 0.841$, $2022 = 1.024$), with boulder sites having the largest increase in the number of recruit species.

Figure 17. Metric MDS of stony coral (< 5 cm colony diameter) recruit species trajectory for each habitat. Points represent the centroid positions of the stony coral recruit community in each habitat each year. Trajectories detail the progression of coral community change over time. Vectors represent coral species accounting for over 75% correlation between samples (Pearson's correlation coefficient). Note: Reef community trajectory starts in 2009. *MCAV = Montastraea cavernosa, AAGA = A. agaricites, PAST = P. astreoides, PPOR = P. porites*, SSID = *Siderastrea siderea.*

Table 10. Stony Coral \lt 5 cm abundance diversity indices. Total Number of Species (S), mean abundance (N), Species Richness (Margalef's d), Evenness (Pielou's J), Shannon-Weaver Diversity (H') and Inverse Simpson's diversity $(1-\lambda)$.

Sample	S	$\mathbf N$	$\mathbf d$	\mathbf{J}^{\prime}	H'	$1-\lambda$
Unrestored 2010	11	36	2.796	0.530	1.271	0.530
Reef 2009	9	17	2.824	0.760	1.669	0.802
Reef 2016	10	35	2.537	0.731	1.684	0.777
Reef 2017	12	42	2.938	0.741	1.842	0.821
Reef 2018	12	42	2.938	0.773	1.921	0.843
Reef 2020	12	49	2.823	0.776	1.929	0.840
Reef 2021	10	45	2.364	0.790	1.819	0.824
Reef 2022	11	51	2.540	0.773	1.852	0.824
Boulder 2016	5	10	1.737	0.523	0.841	0.440
Boulder 2017	9	14	3.005	0.596	1.309	0.597
Boulder 2018	8	19	2.363	0.701	1.458	0.726
Boulder 2020	12	80	2.513	0.433	1.075	0.445
Boulder 2021	11	114	2.113	0.385	0.923	0.365
Boulder 2022	13	121	2.501	0.399	1.024	0.404
Rubble 2016	10	39	2.457	0.520	1.197	0.507
Rubble 2017	9	73	1.867	0.542	1.191	0.520
Rubble 2018	6	26	1.535	0.583	1.044	0.501
Rubble 2020	8	43	1.861	0.559	1.162	0.526
Rubble 2021	8	45	1.835	0.572	1.189	0.518
Rubble 2022	8	33	2.002	0.614	1.276	0.584

3.9. Gorgonian Recruit Community

The gorgonian recruit community varied significantly by year, but not by habitat, and no significant interaction between habitat and year was found (PERMANOVA; Year: pseudo- $f =$ 3.4, $p = 0.007$; Habitat: pseudo-f = 1.3, $p = 0.4$; Interaction: pseudo-f = 1.3, $p = 0.2$). Many sites had no gorgonian recruits (e.g., Clipper Boulder 1 and 2 and Northern Reference (reef) site 3 in 2020, Clipper Boulder 2, Clipper Rubble 1, and Northern Reference (reef) site 12 in 2016, and the Spar Boulder in 2016 and 2017). Gorgonian recruit density was variable throughout the study with each habitat having its highest density in different years (reef = 0.37 ± 0.08 recruits m⁻² in 2018; boulder = 0.16 ± 0.12 recruits m⁻² in 2017; rubble = 0.47 ± 0.27 recruits m⁻² in 2020) (Figure 7; Table 13). Post hoc analysis found that the gorgonian recruit community differed

significantly between 2016 and 2020 ($p = 0.01$) and between 2016 and 2017 ($p = 0.02$). In 2016, only *Antillogorgia spp.* (0.25 recruits m^{-2}) and *Eunicea spp.* (0.61 \pm 0.53 recruits m^{-2}) were identified on reference reef sites (Appendix Table 10) and *Eunicea spp.* recruits at boulder sites (0.07 recruits m-2) (Appendix Table 13). In addition to *Eunicea spp.* and *Antillogorgia spp.* recruits (0.13 and 0.37 ± 0.2 recruits m⁻², respectively), one *Gorgonia spp*. and one *Muricea spp*. recruit were found at rubble sites (Appendix Table 12). Boulder sites still had low gorgonian recruit density and diversity in 2017 and 2020 (Appendix Table 14), but reference reef sites had four recruit genera in 2017 (*Antillogorgia spp.*, *Eunicea spp.*, *Gorgonia spp.,* and *Muricea spp*.) and six in 2020 (*Antillogorgia spp.*, *Eunicea spp.*, *Gorgonia spp.*, *Muricea spp.*, *Pseudoplexaura spp.,* and *Pterogorgia spp.*) (Appendix Table 10). *Eunicea* spp. density was always highest at rubble sites, ranging from 0.4 ± 0.1 recruits m⁻² to 0.1 ± 0.04 recruits m⁻² (Appendix Table 12).

Habitat	Year	Taxa	Abundance	Density	Height
	2016	Gorgonian	$0.33 \pm NA$	$0.01 \pm NA$	$2.00 \pm NA$
	2017	Gorgonian	3.67 ± 2.73	0.16 ± 0.12	2.15 ± 0.80
Boulder	2018	Gorgonian	1.67 ± 0.67	0.07 ± 0.01	0.68 ± 0.28
	2020	Gorgonian	$1.67 \pm NA$	$0.07 \pm NA$	0.88 ± 0.34
	2021	Gorgonian	$0.33 \pm NA$	$0.01 \pm NA$	$1.40 \pm NA$
	2022	Gorgonian	1.00 ± 0.58	0.04 ± 0.03	1.17 ± 0.45
	2016	Gorgonian	1.25 ± 0.63	0.04 ± 0.02	1.30 ± 0.22
	2017	Gorgonian	6.75 ± 2.78	0.23 ± 0.09	1.39 ± 0.08
Reef	2018	Gorgonian	11.00 ± 2.27	0.37 ± 0.08	1.46 ± 0.09
	2020	Gorgonian	4.00 ± 1.47	0.13 ± 0.05	2.51 ± 0.10
	2021	Gorgonian	4.50 ± 1.26	0.15 ± 0.04	2.75 ± 0.09
	2022	Gorgonian	2.25 ± 0.63	0.08 ± 0.02	2.42 ± 0.09
	2016	Gorgonian	5.00 ± 4.04	0.22 ± 0.18	1.75 ± 0.08
	2017	Gorgonian	3.33 ± 1.20	0.14 ± 0.05	1.57 ± 0.19
Rubble	2018	Gorgonian	5.67 ± 1.67	0.25 ± 0.07	0.91 ± 0.11
	2020	Gorgonian	10.67 ± 6.11	0.47 ± 0.27	0.80 ± 0.09
	2021	Gorgonian	5.00 ± 3.51	0.22 ± 0.16	1.06 ± 0.12
	2022	Gorgonian	2.33 ± 1.86	0.10 ± 0.08	0.86 ± 0.24

Table 11. Gorgonian recruit (colonies $\lt 2$ cm height) colony mean (\pm SE) abundance (colonies), density (colonies m^{-2}), and height (cm) by habitat type and year.

3.10. Benthic Biological Community Cover

Benthic biological community cover significantly varied by habitat and year with no interaction between habitat and year (PERMANOVA; Habitat = pseudo-f = 29.877 , p = 0.0001 ; Year: pseudo-f = 2.034, p = 0.0258; Interaction: pseudo-f = 1.094, p = 0.3641). Pairwise analysis found that the benthic community cover at every habitat was significantly different to each other at every timepoint throughout the study (Figure 18; $p < 0.05$). The benthic biological community did not change significantly between years overall or within any habitat ($p > 0.05$) with the exception of data compared between 2010 and 2022 ($p < 0.05$). Benthic biological community cover trajectories show clear dissimilarity between habitats (Figure 18), with higher relative cover of octocorals, stony coral, and macroalgae on reef sites, higher relative sand and rubble cover on rubble sites, and higher boulder substrate and CCA cover at boulder sites.

Figure 18. Metric MDS of benthic biological community cover trajectory. Points represent the centroid positions of each habitat each year. Trajectories detail the progression of benthic biological community change over time. Vectors represent benthic taxa accounting for over 90% correlation between samples (Pearson's correlation coefficient).

Stony coral cover was low at every site, as it was at unrestored sites in 2009/2010 (0.4% cover), ranging between 0.58% in 2016 and 1.11% in 2022 at reef sites (Appendix Table 1), 0.05% in 2016 and 0.38% in 2022 at boulder sites (Appendix Table 2), 0.11% in 2020 and 0.30% in 2016 at rubble sites (Appendix Table 3) (Appendix Table 4). Octocoral cover was lowest every year at boulder sites (Appendix Table 2), ranging from 0.05% in 2016 to 0.84% in 2022. The habitat remained defined by substrate type throughout the study. Turf algae/substrate cover was highest at reference reef sites (ranging from 49.59% in 2021 to 64.6% in 2017; Appendix Table 2); rubble and sand cover was highest at rubble sites (ranging from 2.23% to 52.08% and 12.40% to 22.92%, respectively; Appendix Table 3); which was similar to that of the unrestored sites in 2009/2010 which had 15.9% rubble and 11.8% sand (Appendix Table 4). Boulder cover was highest at boulder sites (ranging from 31.79% to 79.64%; Appendix Table 1).

Figure 19. Metric MDS of benthic biological community cover. Each point represents benthic biological community composition cover at one site surveyed at one point in time. Vectors represent benthic taxa accounting for over 50% correlation between sample (Pearson's correlation coefficient).

3.11. Barrel Sponges

No barrel sponges were found on boulders at boulder sites, but several were found on the very edge of the boulder habitat (Table 12). Rubble sites had a mean density range of 0.09 ± 0.09 barrel sponges per m⁻² in 2018 to 0.15 ± 0.12 barrel sponges per m⁻² in 2017 (Table 12). Reference reef sites had a slightly higher mean density than rubble sites with a mean density range of 0.23 ± 0.06 barrel sponges per m⁻² in 2018 to 0.47 ± 0.16 barrel sponges per m⁻² in 2022 (Table 12). Mean $(\pm$ standard error (SE)) base width was not statistically analyzed because there were so few barrel sponges in boulder and rubble sites. The last barrel sponge found at a boulder site was in 2020, and it had a base width of 25 cm. Mean base width at reference reef sites ranged from 12.33 ± 2.25 cm in 2009 to 16.88 ± 3.88 cm in 2020. Barrel sponges at rubble sites fluctuated in base width over time with a range of 20.22 ± 5.31 cm in 2021 to 29.14 ± 5.19 cm in 2022 (Table 12).

Sample	Year	Abundance	Density	Base Width
Unrestored	2009/2010	2.00 ± 2.00	0.10 ± 0.10	4.67 ± 1.23
	2009	5.25 ± 2.18	0.26 ± 0.11	12.33 ± 2.25
	2016	8.25 ± 3.17	0.28 ± 0.11	14.88 ± 1.70
	2017	7.75 ± 2.39	0.26 ± 0.08	16.01 ± 1.96
Reef	2018	7.00 ± 1.78	0.23 ± 0.06	15.75 ± 2.00
	2020	8.50 ± 2.40	0.28 ± 0.08	16.88 ± 3.88
	2021	10.00 ± 4.38	0.33 ± 0.15	14.03 ± 1.64
	2022	14.00 ± 4.93	0.47 ± 0.16	15.03 ± 1.54
	2016	0.33 ± 0.33	0.01 ± 0.01	$35.00 \pm NA$
	2017	0.67 ± 0.33	0.03 ± 0.01	32.50 ± 2.50
Boulder	2018	0.33 ± 0.33	0.01 ± 0.01	$24.00 \pm NA$
	2020	0.33 ± 0.33	0.01 ± 0.01	$25.00 \pm NA$
	2021	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2022	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2016	2.33 ± 2.33	0.10 ± 0.01	22.43 ± 4.22
	2017	3.33 ± 2.85	0.15 ± 0.12	20.50 ± 4.73
Rubble	2018	2.00 ± 2.00	0.09 ± 0.09	27.00 ± 5.61
	2020	2.33 ± 2.33	0.10 ± 0.10	23.14 ± 6.96
	2021	3.00 ± 3.00	0.13 ± 0.13	20.22 ± 5.31
	2022	2.33 ± 2.33	0.10 ± 0.10	29.14 ± 5.19

Table 12. Mean $(\pm SE)$ barrel sponge abundance, mean $(\pm SE)$ density (sponges m⁻²), and mean $(\pm S$ E) base width (cm) per habitat type per year.

3.12. Macroinvertebrates; *Panulirus argus* **(spiny lobster),** *Diadema antillarum* **(long-spined sea urchin), and** *Strombus gigas* **(queen conch)**

Spiny lobsters were identified within boulder sites during two monitoring years, in 2018 with a mean (\pm standard error (SE)) abundance of 0.33 \pm 0.33 and in 2021 (2.67 \pm 0.88), while spiny lobsters were found within rubble sites in 2018 (0.33 \pm 0.00) and in 2022 (1.00 \pm 0.00). Lobsters were identified at reef sites every year except 2018. Mean abundance ranged from 0.17 \pm 0.17 in 2016 to 2.75 \pm 1.18 in 2020. Long-spined sea urchins were not identified in rubble sites any year except for 2020 with a mean abundance of $0.33 \pm NA$. Boulder habitats had urchins at an abundance of 2.00 ± 1.53 in 2020 and 1.00 or greater the following two years (Table 13). Long-spined sea urchins were identified at reef sites every year but 2018 and ranged in abundance from 0.75 ± 0.48 in 2016 to 1.75 ± 0.85 in 2017 (Table 13). No queen conch were identified in the rubble sites and were only identified in 2017 and 2021 at boulder sites with a mean abundance of 0.33 ± 0.33 and 0.67 ± 0.33 , respectively (Table 13). Queen conch were identified every year at reef sites. Abundance ranged from 0.25 ± 0.25 in 2020 to 1.00 ± 0.71 in 2021 (Table 13).

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Table 13. Mean (± SE) *Panulirus argus* (Caribbean spiny lobster), *Diadema antillarum* (longspined sea urchin), and *Strombus gigas* (queen conch) abundance. Density was not calculated because survey area was not specifically defined.

	Year		Diadema	
Sample		Panulirus argus	antillarum	Strombus gigas
	2016	0.17 ± 0.17	0.75 ± 0.48	0.75 ± 0.48
	2017	2.50 ± 0.87	1.75 ± 0.85	0.50 ± 0.50
Reef	2018	0.00 ± 0.00	0.00 ± 0.00	0.75 ± 0.75
	2020	2.75 ± 1.18	1.50 ± 1.19	0.25 ± 0.25
	2021	1.50 ± 0.50	0.25 ± 0.25	1.00 ± 0.71
	2022	1.25 ± 0.48	0.25 ± 0.25	0.50 ± 0.50
Boulder	2016	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2017	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.33
	2018	0.33 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2020	0.00 ± 0.00	2.00 ± 1.53	0.00 ± 0.00
	2021	2.67 ± 0.88	1.00 ± 0.58	0.67 ± 0.33
	2022	0.00 ± 0.00	1.33 ± 0.33	0.00 ± 0.00
	2016	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2017	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Rubble	2018	0.33 ± 0.33	0.00 ± 0.00	0.00 ± 0.00
	2020	0.00 ± 0.00	0.33 ± 0.33	0.00 ± 0.00
	2021	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	2022	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

4. Discussion

The consolidation of rubble and deployment of limestone boulders promoted biological recovery of damaged sites following two ship groundings in southeast Florida. Results from this study demonstrated that the physical habitat created by boulders developed stony coral recruit (< 5 cm) communities faster than rubble, with both density and species richness at boulder sites increasing dramatically while these traits fluctuated at rubble sites. Significant impacts from hurricane Irma caused the stony coral recruit community at rubble sites to become restructured. Boulders also developed stony coral adult (\geq 5 cm) communities faster than rubble, increasing in stony coral density, species richness, and cover. Cover of important taxa (including stony corals,

CCA and non-*X. muta* sponges) increased on boulders while remaining relatively unchanged over time at rubble sites. Some important taxa, however, including gorgonians and *Xestospongia muta,* had limited recovery, with no recruitment of *X. muta* on boulders at any time throughout the study.

Stony coral recruit density increased 12-fold from 2016 to 2022 at boulder sites. In that same time, rubble transects decreased in stony coral recruit density and species richness. Stony coral community trajectories indicate the species richness and density on boulders are becoming more similar to the community found at reference reef sites while the stony coral community trajectories on rubble seem to be less complex, lacking many species that are developing on boulders. Higher stony coral recruitment and species richness on areas restored with boulders compared to unrestored areas was also seen at the M/V Wellwood restoration site in the Florida Keys National Marine Sanctuary (Hudson et al., 2007) suggesting stabilizing substrate provides a better chance for the stony coral community to develop long-term.

Stony corals are slow growing with many of the common southeast Florida species growing less than 1 cm/year (in terms of linear extension) (Jones, 2022). *Montastraea cavernosa,* a hermatypic scleractinian species which contributes heavily to reef complexity in Broward County, Florida (Moyer et al., 2003), was observed recruiting to boulders as well as rubble by 2022. Along with *M*. *cavernosa*, *Solenastrea bournoni* recruits were found at both rubble and boulder sites, as were other important reef building genera such as *Colpophyllia natas, Diploria labyrinthiformis* and *Pseudodiploria spp.* Development of coral communities is well-known to be a long-term (decadal) process (Hudson et al., 2007), but the presence these reef building species may have significant implications on the gradual development of site complexity with corals adding to rugosity to sites as they grow.

Stony coral recruit species richness fluctuated interannually at rubble sites, while species richness was consistent and steadily increased at boulder sites, such that recruit species richness in 2022 was nearly identical between boulder sites and reference reef sites. The persistence of sediment within rubble sites may have had significant implications on recruitment and survival leading to the fluctuation of coral density and the species present at rubble sites. When rubble habitats were subjected to strong hydrodynamic disturbances, mobilized sediment deposits likely prevented larval settlement or buried recruits that may have found suitable habitat, preventing

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consistent development of the stony coral community at rubble sites (Kenyon et al., 2020; Viehman et al., 2018). This was demonstrated after hurricane Irma when colonies of many rare species were lost (*D. labyrinthiformis*, *C. natans,* and *Meandrina meandrites),* as well as more common species like *Porites porites* (Hayes et al., 2022). Similarly, other historic groundings have seen damaged areas exacerbated by hurricanes such as the M/V Alec Owen Maitland grounding site which greatly increased in size after Hurricane Andrew in 1992 (Schittone, 2010) and the R/V Columbus Iselin grounding site where the bow scar doubled in size after Hurricane George in 1998 (Hudson and Franklin, 2005). These dramatic impacts to substrate and turnover in community demonstrates how susceptible disturbed rubble environments can be to further disturbances both natural and anthropogenic (Precht et al., 2001; Viehman et al., 2018).

Although the stony coral community on boulder sites had not recovered to that at reference reef sites by the end of the study, stony coral density had increased nearly 800%. Neither boulder sites nor rubble sites had any adult *Solenastrea bournoni* or *Montastraea cavernosa*, key reef building species in the Kristin Jacobs Coral Reef Ecosystem Conservation Area (Coral ECA) (Walker et al., 2021), with only *Porites astreoides* and *Siderastrea siderea* found in every habitat every year. Due to the slow growth of reef-building species in particular, the low diversity in the adult stony coral community at boulder sites after only seven years was not unexpected. For example, linear extension in *M. cavernosa* is only 6-7 mm yr⁻¹ in the Caribbean (Crabbe, 2009). As such, it will take several years for many massive species to grow to adult size and enable appropriate assessment of whether the stony coral community on boulders can replicate that found on the reference reefs.

Important differences in the common species were also observed within the boulder and rubble sites. *Siderastrea siderea,* an abundant species whose colonies are primarily small in the ECA (Jones, 2022), were common at both boulder (76% in 2022) and rubble (64% in 2022) sites as recruits, but adult colonies on boulders contributed much less to species abundance (28% in 2022) than on rubble (52% in 2022). High abundances of *S. siderea* recruits have been documented at other ship grounding sites on the inner reef near Port Everglades, Florida (Moulding et al., 2012) and on reefs in the Florida Keys National Marine Sanctuary (Hudson et al., 2007; Schittone, 2010). Additionally, rubble sites lacked several relatively common species

(e.g., *Agaricia agaricites* and S*tephanocoenia intersepta*) that have increased in cover and/or density on boulders and in the Coral ECA (Jones et al., 2020).

While boulder deployment promoted the development of crustose coralline algae, sponges and stony coral recruitment, very few gorgonians recruited to boulders, and no *Xestospongia muta* sponges recruited, suggesting a large part of the benthic biological community on reefs in the Coral ECA will not be replicated (Gilliam and Moulding, 2012). Gorgonians and *X. muta* are an important functional constituent of reefs in the Coral ECA creating habitat, and while *X. muta* density is relatively low, gorgonians are abundant on the inner reef (Moyer, 2003). Boulder sites lacked several gorgonian genera, both in the adult and recruit communities, which were relatively abundant at reference reef sites. Gorgonian density and community diversity were also low at rubble sites, where gorgonian recruitment is lower than at reference reef sites. Also, the few *X. muta* found at rubble sites are large, suggesting they were present prior to the groundings. This implies that gorgonian and *X. muta* recruitment potential is low in the ship grounding locations in general, but both seem unable to effectively settle on boulders. These community differences were also identified during a previous survey of multiple boulder reefs offshore southeast Florida (Gilliam, 2012). Despite this, the cover of other sponges has increased 7-fold on boulders, but remained stable at reference reef and rubble sites, as has been observed regionally (Jones et al., 2020).

5. Conclusion

Our evidence suggests that the deployment of boulders for site stabilization following ship groundings can return some ecosystem services. Most notably, boulders can promote the recovery of the stony coral community following ship groundings through securing loose rubble and unconsolidated substrate, preventing continued site damage from strong hydrodynamic disturbances. Community trajectories suggest that boulder sites are becoming more similar to reference reef sites in benthic biological and stony coral community composition than rubble sites or the unrestored grounding sites. Multiple stony coral species recruited to boulders at grounding sites, and the stony coral adult and recruit communities are more diverse at boulder sites than rubble or unrestored sites. Gorgonians and *Xestospongia muta,* however, did not

effectively recruit to boulders, and the gorgonian community on boulders remains underdeveloped in relation to reference reef sites. Due to the slow nature of coral growth and recruitment, it appears it will take several years before the full effectiveness of boulder deployment is realized. We suggest continued monitoring of these grounding sites on a yearly basis until a ten-year data set can be completed and every 5 years thereafter to define both shortterm and long-term community development. It is also suggested that monitoring take place after any major localized hurricane events.

Despite evidence that the stony coral community at boulder sites is becoming more similar to reference reefs than rubble sites, the three habitats are still defined by their initial substrate type. Rubble sites remained rubble interspersed with sand throughout the study. Rubble sites have low rugosity, and most fluctuations in the benthic biological community likely resulted from hydrodynamic forces (Viehman et al., 2018). Likewise, boulder sites still and likely will continue to look like boulders and will be visibly different than the natural reef habitat in the Coral ECA. Rugosity is 25% higher at boulder sites than at reference reef sites, despite having smaller stony coral colonies and no large *Xestospongia muta*. The increased rugosity of boulders can create differences in fish assemblages, which would likely not replicate natural reef (Harborne et al., 2011; Kilfoyle et al., 2013). We suggest a reduction of at least 50% in the size of boulders deployed as site stabilization would more appropriately reflect the physical appearance of reef in the Coral ECA. Similar stabilization projects in the Florida Keys Marine Sanctuary situated limestone boulders and cement modules within bow scars leaving one meter or less of the structure exposed above the surrounding substrate replicating the adjacent areas more similarly than the restored sites in this study (Hudson and Franklin, 2005; Hudson et al., 2007; Schittone, 2010). We recommend stabilizing substrate following ship groundings and other impact events as soon as possible to prevent further damage to the site and promote recruitment of sessile invertebrates, enhancing recovery potential. To fully understand the recovery potential of ship grounding sites stabilized with boulders, more time needs to pass for the initial recruiters on boulders to grow into a larger size class to observe what will persist on boulders and understand how an older adult community may differ from that of the natural reefs.

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Appendix

Habitat	Boulder								
Year	2016	2017	2018	2020	2021	2022			
Stony Coral (SE)	0.05 ± 0.05	0.14 ± 0.08	0.13 ± 0.06	0.21 ± 0.05	0.38 ± 0.20	0.38 ± 0.15			
Octocoral (SE)	0.05 ± 0.05	0.08 ± 0.04	0.13 ± 0.13	0.58 ± 0.29	0.28 ± 0.20	0.84 ± 0.84			
Sponge (SE)	0.81 ± 0.34	2.43 ± 0.49	5.09 ± 0.39	7.25 ± 1.11	6.89 ± 0.80	5.78 ± 0.73			
Zoanthid (SE)	0.05 ± 0.05	0.16 ± 0.16	0 ± 0	0.05 ± 0.05	0 ± 0	0 ± 0			
Macroalgae (SE)	2.7 ± 0.59	10.61 ± 5.15	8.71 ± 3.11	13.36 ± 2.47	7.85 ± 1.99	15.86 ± 1.71			
CCA (SE)	1.58 ± 0.64	15.41 ± 8.3	5.76 ± 5.67	2.17 ± 1.03	1.92 ± 0.58	3.43 ± 0.65			
Cyanobacteria (SE)	5.71 ± 2.48	0.05 ± 0.05	0.57 ± 0.19	1.69 ± 1.03	0.06 ± 0.06	0.54 ± 0.29			
Other (SE)	0.05 ± 0.05	0.04 ± 0.04	0 ± 0	0 ± 0	0.06 ± 0.06	0.05 ± 0.5			
Boulder (SE)	58.65 ± 4.16	31.79 ± 7.15	38.25 ± 7.79	48.29 ± 8.61	79.64 ± 0.44	41.07 ± 3.16			
Rubble (SE)	0.66 ± 0.66	3.63 ± 0.92	4.87 ± 2.23	1.26 ± 1.18	0.05 ± 0.05	0.21 ± 0.21			
Sand (SE)	3.06 ± 2.2	3.99 ± 1.58	0.98 ± 0.69	1.32 ± 1	2.34 ± 1.81	1.20 ± 0.68			
Substrate (SE)	26.64 ± 4.5	31.66 ± 6.68	35.51 ± 5.54	23.82 ± 8.86	0.60 ± 0.36	31.17 ± 2.17			

Appendix Table 1. Boulder sites mean percent functional group benthic cover ($% \pm SE$).

Habitat	Reef							
Year	2016	2017	2018	2020	2021	2022		
Stony Coral (SE)	0.58 ± 0.12	0.67 ± 0.16	0.66 ± 0.18	0.67 ± 0.21	0.65 ± 0.16	1.11 ± 0.18		
Octocoral (SE)	2.9 ± 0.79	2.67 ± 0.35	2.15 ± 0.47	2.72 ± 0.74	2.86 ± 0.28	4.45 ± 0.82		
Sponge (SE)	3.42 ± 0.71	4.23 ± 0.8	2.48 ± 0.6	3.61 ± 0.86	3.83 ± 1.06	5.24 ± 1.07		
Zoanthid (SE)	3.18 ± 1.51	3.42 ± 1.2	2.49 ± 0.93	3.16 ± 1.26	4.61 ± 1.13	3.09 ± 0.81		
Macroalgae (SE)	21.43 ± 4.21	20.31 ± 5.89	22.42 ± 5.81	21.08 ± 3.09	36.31 ± 6.93	25.93 ± 0.61		
CCA (SE)	0.58 ± 0.21	1.15 ± 0.56	0.79 ± 0.65	0.74 ± 0.31	0.63 ± 0.21	1.05 ± 0.52		
Cyanobacteria (SE)	0.43 ± 0.15	0.54 ± 0.33	0.22 ± 0.09	0.24 ± 0.14	0.47 ± 0.16	0.82 ± 0.28		
Other (SE)	0 ± 0	0.02 ± 0.02	0.05 ± 0.05	0 ± 0	0.50 ± 0.15	$0.03 \pm .03$		
Boulder (SE)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0		
Rubble (SE)	6.01 ± 4.43	0.52 ± 0.32	3.73 ± 3.52	2.36 ± 2.22	0.15 ± 0.15	0 ± 0		
Sand (SE)	7.03 ± 6.26	1.93 ± 1.08	5.02 ± 4.63	2.63 ± 1.94	0.87 ± 0.41	1.89 ± 1.63		
Substrate (SE)	54.43 ± 5.68	64.55 ± 6.53	60 ± 3.88	62.79 ± 3.26	49.59 ± 6.97	57.23 ± 2.47		

Appendix Table 2. Reference reef sites mean percent functional group benthic cover ($% \pm SE$).

Habitat		Rubble								
Year	2016	2017	2018	2020	2021	2022				
Stony Coral (SE)	0.3 ± 0.23	0.25 ± 0.07	0.2 ± 0.12	0.11 ± 0.06	0.28 ± 0.12	0.22 ± 0.15				
Octocoral (SE)	1.54 ± 0.92	0.91 ± 0.63	0.47 ± 0.47	1.34 ± 0.5	1.04 ± 0.54	1.69 ± 0.66				
Sponge (SE)	2.3 ± 1.24	2.86 ± 1.63	2.06 ± 1.6	2.1 ± 0.97	2.14 ± 1.31	2.29 ± 2.14				
Zoanthid (SE)	0.14 ± 0.14	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0				
Macroalgae (SE)	14.86 ± 8.85	4.42 ± 0.83	10.04 ± 3.17	5.28 ± 1.65	9.34 ± 1.83	11.02 ± 2.54				
CCA (SE)	0.23 ± 0.12	0.21 ± 0.04	0.13 ± 0.13	0.11 ± 0.11	0.44 ± 0.27	0.89 ± 0.60				
Cyanobacteria (SE)	1.08 ± 0.64	0.29 ± 0.11	0 ± 0	0.97 ± 0.89	0.11 ± 0.05	0.52 ± 0.20				
Other (SE)	0 ± 0	0 ± 0	0.07 ± 0.07	0 ± 0	0.11 ± 0.05	0 ± 0				
Boulder (SE)	0.05 ± 0.05	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0				
Rubble (SE)	11.23 ± 4.64	15.47 ± 8.16	15.14 ± 11.99	2.23 ± 2.23	52.08 ± 14.75	15.76 ± 4.37				
Sand (SE)	12.4 ± 8.03	15.75 ± 11.37	12.92 ± 6.87	15.8 ± 11.87	22.92 ± 7.72	19.90 ± 9.50				
Substrate (SE)	55.87 ± 1.08	59.85 ± 16.09	58.98 ± 13.02	72.07 ± 12.11	11.65 ± 11.08	48.25 ± 4.12				

Appendix Table 3. Rubble sites mean percent functional group benthic cover ($% \pm SE$).

Species	2016		2017		2018		2020		2021		2022	
	Abundance	Density										
A. agaricites	1.67 ± 0.33	0.06 ± 0.01	3.33 ± 0.33	0.11 ± 0.01	3.25 ± 0.85	0.11 ± 0.03	4.25 ± 1.65	0.14 ± 0.06	5.50 ± 2.53	0.18 ± 0.08	3.75 ± 1.75	0.17 ± 0.08
A. fragilis	0.00 ± 0.00	0.00 ± 0.00	1.50 ± 0.50	0.05 ± 0.02	2.00 ± 0.58	0.06 ± 0.03	1.33 ± 0.33	0.04 ± 0.01	$2.00 \pm NA$	$0.07 \pm NA$	1.33 ± 0.33	0.04 ± 0.02
A. humilis	1.50 ± 0.50	0.05 ± 0.02	0.00 ± 0.00	0.00 ± 0.00								
A. lamarcki	1.00 ± 0.00	0.02 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00
C. natans	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$						
D. labyrinthiformis	$1.00 \pm NA$	$0.03\pm NA$	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$	$2.00 \pm NA$	$0.07 \pm NA$
D. stokesii	$1.00 \pm NA$	$0.03\pm NA$	1.00 ± 0.00	0.03 ± 0.00	1.00 ± 0.00	0.03 ± 0.00	1.33 ± 0.33	0.04 ± 0.01	1.00 ± 0.00	0.03 ± 0.00	2.00 ± 1.00	0.07 ± 0.03
M. cavernosa	2.50 ± 0.50	0.08 ± 0.02	3.00 ± 0.82	0.12 ± 0.04	2.75 ± 0.48	0.09 ± 0.02	3.25 ± 1.65	0.11 ± 0.06	3.25 ± 1.31	0.11 ± 0.04	4.00 ± 1.22	0.13 ± 0.04
M. decactis	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
M. meandrites	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00						
O. annularis	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03\pm NA$	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$	$1.00 \pm NA$	$0.03 \pm NA$
O. faveolata	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00	$1.00\pm NA$	$0.03 \pm NA$
P. astreoides	17.75 ± 5.31	0.59 ± 0.18	20.50 ± 6.51	0.68 ± 0.22	21.00 ± 6.54	0.70 ± 0.22	24.50 ± 6.25	0.82 ± 0.21	23.50 ± 6.71	0.78 ± 0.22	26.0 ± 10.09	0.86 ± 0.34
P. clivosa	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00						
P. porites	5.75 ± 1.18	0.19 ± 0.04	7.25 ± 2.98	0.24 ± 0.10	5.25 ± 1.80	0.18 ± 0.06	11.00 ± 2.68	0.37 ± 0.09	9.00 ± 1.41	0.30 ± 0.05	14.0 ± 4.02	0.47 ± 0.13
P. strigosa	1.00 ± 0.00	0.03 ± 0.00	$1.00 \pm NA$	$0.03\pm NA$	$1.00 \pm NA$	$0.03\pm NA$	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.03\pm NA$
S. bournoni	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
S. intersepta	4.00 ± 1.47	0.13 ± 0.05	5.67 ± 1.67	0.19 ± 0.06	6.00 ± 2.08	0.20 ± 0.07	5.50 ± 2.40	0.18 ± 0.08	5.25 ± 2.02	0.18 ± 0.07	5.75 ± 2.25	0.19 ± 0.08
S. radians	$1.00 \pm NA$	$0.03 \pm NA$	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$3.00 \pm NA$	$0.10 \pm NA$	0.00 ± 0.00	0.00 ± 0.00
S. siderea	6.00 ± 2.48	0.20 ± 0.08	8.50 ± 1.66	0.28 ± 0.06	6.25 ± 0.85	0.20 ± 0.03	9.00 ± 1.08	0.30 ± 0.04	9.25 ± 1.31	0.31 ± 0.04	13.75 ± 2.25	0.46 ± 0.08
Total # species	14		12		13		12		15		13	

Appendix Table 4. Stony coral (colonies \geq 5 cm) species mean (\pm SE) abundance and density (colonies m⁻²) per year at reference reef sites.

Species	2016		2017		2018			2020	2021		2022	
	Abundance	Density	Abundance	Density	Abundance	Density	Abundance	Density	Abundance	Density	Abundance	Density
A. agaricites	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.50 ± 0.50	0.11 ± 0.02	2.33 ± 0.67	0.10 ± 0.03	3.33 ± 0.67	0.15 ± 0.03
A. fragilis	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
A. lamarcki	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
C. natans	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.04 \pm NA$	$1.00 \pm NA$	$0.04 \pm NA$
D. labyrinthiformis	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
D. stokesii	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.04 \pm NA$	$1.00 \pm NA$	$0.04\pm NA$	$1.00 \pm NA$	$0.04 \pm NA$	1.50 ± 0.50	0.07 ± 0.02
M. cavernosa	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$\overline{0.00} \pm 0.00$	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
M. decactis	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
M. meandrites	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
O. annularis	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
O. faveolata	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
P. astreoides	$3.00 \pm NA$	$0.13 \pm NA$	$2.00 \pm NA$	$0.09 \pm NA$	1.00 ± 0.00	0.04 ± 0.00	1.67 ± 0.67	0.07 ± 0.03	2.33 ± 0.33	0.10 ± 0.01	2.66 ± 0.33	0.12 ± 0.01
P. clivosa	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
P. porites	0.00 ± 0.00	0.00 ± 0.00	$2.00 \pm NA$	$0.09 \pm NA$	$1.00 \pm NA$	$0.04 \pm NA$	3.33 ± 1.20	0.15 ± 0.05	3.33 ± 1.20	0.15 ± 0.05	8.00 ± 2.65	0.36 ± 0.12
P. strigosa	0.00 ± 0.00	0.00 ± 0.00	$\overline{0.00} \pm 0.00$	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$1.00 \pm NA$	$0.04 \pm NA$	$1.00 \pm NA$	$0.04 \pm NA$	$1.00 \pm NA$	$0.04 \pm NA$
S. bournoni	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	$2.00 \pm NA$	$0.09 \pm NA$	$3.00 \pm NA$	$0.13 \pm NA$
S. intersepta	1.50 ± 0.50	0.07 ± 0.02	$1.00 \pm NA$	$0.04 \pm NA$	$1.00 \pm NA$	$0.04 \pm NA$	1.50 ± 0.50	0.07 ± 0.02	1.67 ± 0.67	0.07 ± 0.03	3.50 ± 2.50	0.16 ± 0.11
S. radians	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
S. siderea	2.00 ± 1.00	0.09 ± 0.04	2.00 ± 1.00	0.09 ± 0.04	$4.00 \pm NA$	$0.18 \pm NA$	6.00 ± 4.00	0.27 ± 0.20	5.50 ± 3.50	0.24 ± 0.16	$11.00 \pm$ 5.00	0.49 ± 0.22
Total # species	3		$\overline{4}$		5			τ	5			$7\overline{ }$

Appendix Table 5. Stony coral (colonies \geq 5 cm) species mean (\pm SE) abundance and density (colonies m⁻²) per year at boulder sites.

Appendix Table 6. Stony coral (colonies \geq 5 cm) species mean (\pm SE) abundance and density (colonies m⁻²) per year at rubble sites.

 ∞ sites. **Appendix Table 7**. Gorgonian (colonies ≥ 2 cm) genus mean (\pm SE) abundance and density (colonies m⁻²) per year at reference reef

Appendix Table 8. Gorgonian (colonies ≥ 2 cm) genus mean (\pm SE) abundance and density (colonies m⁻²) per year at boulder sites.

Appendix Table 9. Gorgonian (colonies ≥ 2 cm) genus mean (\pm SE) abundance and density (colonies m⁻²) per year at rubble sites.

Appendix Table 10. Stony Coral recruit (colonies $<$ 5 cm) species mean (\pm SE) abundance and density (colonies m⁻²) per year at reference reef sites.

Appendix Table 11. Stony Coral recruit (colonies $<$ 5 cm) species mean (\pm SE) abundance and density (colonies m⁻²) per year at boulder sites.

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63 **Appendix Table 12.** Stony Coral recruit (colonies $<$ 5 cm) species mean (\pm SE) abundance and density (colonies m⁻²) per year at rubble sites.

Appendix Table 13. Gorgonian (colonies < 2 cm) genus mean (\pm SE) abundance and density (colonies m⁻²) per year at reference reef sites.

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Appendix Table 14. Gorgonian (colonies < 2 cm) genus mean $(\pm SE)$ abundance and density (colonies m⁻²) per year at boulder sites.

Appendix Table 15. Gorgonian (colonies $\lt 2$ cm) genus mean $(\pm SE)$ abundance and density (colonies m⁻²) per year at rubble sites.

