Coverage Increases of *Porites astreoides* in Grenada Determined by Shifts in Size-Frequency Distribution

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Abstract: Despite coral community collapse, the mustard hill coral (*Porites astreoides*) is a species currently experiencing success throughout the Caribbean. The inshore reefs of Grenada were selected to study the influence of benthic factors on the abundance, size, and coverage of *P. astreoides* colonies. Surveys of reef communities along established 30 m transects were conducted at eight sites in 2014 and 2017 using a 0.5 m² quadrat. Coral Point Count was used to annotate the images, estimating the coverage of scleractinian corals, sponges, algae, and benthic substrates. Coverage, size, and abundance of *P. astreoides* colonies were quantified using the area measurement tool in ImageJ standardized against the quadrats. There were significant differences in benthic community assemblages between islands, selected sites, and between years. From 2014 to 2017 there was a significant decrease in the mean abundance of *P. astreoides* colonies and significant increases in mean colony size and coverage. The presence of *P. astreoides* colonies was significantly correlated with: rubble (−), sand (−); pavement (+); macroalgae (−); coralline algae (+); sponges (varying response); gorgonians (−); massive corals (+); and branching corals (−). *P. astreoides* follows similar recruitment patterns as other scleractinian corals. Observed changes in *P. astreoides* populations appear to indicate a recovery event following a disturbance, potentially tropical storm Chantal in 2013.

Keywords: mustard hill coral; *Porites*; Grenada; population dynamics; monitoring

1. Introduction

Mirroring the state of global tropical reef ecosystems, coral reefs in the Caribbean have experienced dramatic declines in the last several decades, with live coral cover declining more than 80% since the 1970s [1,2]. The combined impacts of stressors such as rising sea temperatures, ocean acidification, overfishing, pollution, loss of herbivorous species, and disease outbreaks have been largely responsible for this decline [3–6]. Declines have not however impacted all scleractinian species in the Caribbean equally. They have been concentrated along select life-history or morphological lines, leading a shift towards non-framework building species [7]. These diverging responses among scleractinian species have led to changes in reef dynamics, with an as yet unclear impact on reef functionality [8]. Scleractinian species in the Caribbean can be broadly characterized as having one of four life history strategies based on colony morphology, growth rate, and reproductive method [9]. These life history strategies are: (1) weedy (high recruitment, brooding reproduction); (2) stress tolerant (large colonies, slow growing, broadcast spawning); (3) competitive (framework, fast-growing, broadcast spawning); and (4) generalist...
(mix of traits of all other categories) [9]. Competitive species such as *Acropora palmata* or *A. cervicornis*, historically responsible for much of the complex framework building on Caribbean reefs, have experienced the most dramatic declines since the 1970s [10,11].

Non-framework building scleractinian species with a weedy life history strategy have proven successful in the region, in an era of rapid environmental change and have been among the few ‘winners’ on Caribbean reefs [12]. Species exhibiting this life history strategy, such as the mustard hill coral (*Porites astreoides*), have increased in mean percent cover on Caribbean reefs and now account for 16–72% of all living coral in Caribbean reef communities [13–15].

*P. astreoides* is found throughout the Caribbean, along the coasts of Florida, Bermuda, Brazil, and along the coasts of West Africa. It is most abundant at depths of 0.5 m – 15 m and tolerates a wide range of thermal, physical, and water quality conditions [16]. *P. astreoides* populations are dominated by medium and large-sized colonies and colony survival is typically high, making it highly unlikely for large colonies to reduce in size once they have reached certain growth stages [15]. *P. astreoides* has a brooding reproductive strategy and is capable of either sexual or asexual reproduction, facilitating a high rate of colony production [17].

For highly abundant species such as *P. astreoides*, it is presently unclear which factors influence population dynamics in the reef communities of the Caribbean, particularly at a local scale. It is also unclear what level of resilience a weedy life history strategy confers on a species to continued changes, necessitating regular updates on population status in the region [18]. To assess short-term temporal changes in *P. astreoides* populations and the extent of influence a gradient of interspecific and substrate factors may have on coverage, the present study quantified changes in *P. astreoides* coverage, abundance, and colony size, as well as coverage of other benthic features at eight near-shore reefs in the coastal waters of Grenada and Carriacou in 2014 and 2017.

### 2. Materials and Methods

#### 2.1. Study Sites

Surveys were conducted at eight sites in the nearshore waters of Grenada and Carriacou in the Fall of 2014 and 2017. Four previously established study sites [19] were selected to complement a published dataset from Grenada [20,21] and four sites were also established on the nearby island of Carriacou (Figure 1, Table 1) [14,22].

**Table 1.** Benthic survey site names, site code for figures, locations, GPS coordinates, and similarity of species assemblages at study sites between 2014 and 2017 with *p*-values. Sites with values closer to 0 have similar species assemblages, those with values closer to 1 have very different species assemblages. All results are based on 200 permutations.

| Island   | Site Name      | Site Code | GPS Coordinates         | R    |
|----------|----------------|-----------|-------------------------|------|
| Grenada  | Dragon Bay     | DRAG      | 12°5’6.00”N 61°45’45.36’’W | 0.958* |
| Grenada  | Flamingo Bay   | FLAM      | 12°5’30.36”N 61°45’30.60’’W | 1.00*  |
| Grenada  | Northern Exposure | NORTH   | 12°2’22.14”N 61°46’4.74’’W | 0.990*  |
| Grenada  | Quarter Wreck  | QUART     | 12°1’40.98”N 61°47’0.84’’W | 0.990*  |
| Carriacou| Sandy Island   | SAND      | 12°29’7.77”N 61°29’2.00’’W | 0.656*  |
| Carriacou | Whirlpool     | WHIRL     | 12°29’2.50”N 61°29’31.35’’W | 0.927*  |
| Carriacou | Jackadam      | JAD       | 12°29’46.25”N 61°28’4.11’’W | 0.937*  |
| Carriacou | Seaview       | SEAV      | 12°26’44.13”N 61°29’59.70’’W | 1.000*  |

* denotes significant differences at *p* = 0.05.
The sites on Carriacou were chosen to mirror those in Grenada in that they were approximately equivalent distances from shore, found at similar depths, had benthic community assemblages that appeared similar during initial visual assessments, and were all frequented by the recreational dive industry. All surveyed sites were comprised of shallow patch reefs on the leeward side of each island. Each site was marked with 1 m rebar stakes that were driven into coral rubble at the ends of 30 m long transects running across patch reefs in the nearshore waters of Carriacou. Each site in Grenada and Carriacou had four transects running parallel to each other spaced 5 m apart. All transects ranged in depth from 9.4 m to 12.2 m. Sites on Carriacou were established in the last week of August 2014 with the authorization of the Grenada Ministry of Forestry, Fisheries and Agriculture.
2.2. Benthic Community Assessment

Images were captured in Fall 2014 and 2017, every 0.5 m, using a standardized 0.5 m² quadrat along each transect using a camera at a distance approximately 0.5 m above the benthos (including coral colonies that extend upwards). Images were imported into CPCe (Coral Point Count with Excel extensions) for image analysis [23]. A species accumulation curve was generated for the dataset from one full site [24]. The data were fit to a Shepard plot with a non-metric fit of 0.97 and a linear fit of 0.841. Eighteen points per image were distributed in a stratified random pattern (3 × 3 grid with 2 points distributed randomly per cell). This number of points per quadrat has been known to sufficiently capture the coverage of major benthic groups [24, 25]. Individual points were identified to the species level for hard coral and to the genus level for gorgonians. Algae were classified as macroalgae (fleshy), turf, or coralline. Remaining benthic cover types were identified as sponges (encrusting and massive), zoanthids, or non-living (sand, pavement, rubble, and dead coral).

Percent cover of major benthic groups were arcsine square root transformed to satisfy the assumption of normality required for ANOVA. Nested ANOVA using sites nested within Island were used to test for differences in arcsine percent cover of coral, macroalgae, gorgonian, sponge, and non-living cover separately within each year. Two-way ANOVA were used to test for differences in the same benthic cover groups between years. Significant differences between groups were further investigated using a Welch’s t-test with a Bonferroni correction where appropriate.

Hard coral species abundance matrices were generated using the images processed in CPCe. Abundance data were square root transformed to remove potential bias due to very rare or very abundant species and Bray-Curtis dissimilarity matrices were generated for each year. Differences in Bray-Curtis dissimilarities between sites were assessed using ANOSIM within a year. A two-way PERMANOVA with site and year as factors was used to test for differences between the same sites over time. General linear mixed models were used to test for differences in species composition of the scleractinian coral community between islands and years. All statistical analyses were conducted in the base R environment Version 3.6.2 [26] or using the ‘vegan’ package [27].

2.3. P. astreoides Population Dynamics

The area measuring tool in ‘ImageJ’ standardized against the 0.5 m² quadrat in each image was used to assess the number of P. astreoides colonies, their respective size, and absolute coverage. Colonies found completely within the borders of the quadrat, or those qualitatively assessed as being 90% within the quadrat were counted. Images taken nearby were examined to ensure an accurate measurement of colonies with any overlap of the quadrat. Changes in mean percent cover, mean abundance, and mean colony size (cm²) of P. astreoides by year and island were assessed using a two-way ANOVA. A Kolmogorov-Smirnov two-sample t-test was used to assess differences in size-frequency distributions of mean colony size between years. Site-specific changes between 2014 and 2017 were assessed using Welch’s t-tests. A Grubbs’ test was used on each variable to identify and remove any potential outliers from the subsequent correlation analyses. Percentage values of coverage were arcsine transformed. A scatterplot analysis of residuals vs. predicted values for all factors that were not significant in the Grubbs’ test was used to ensure homoscedasticity. Based on sample size calculations with predicted correlation coefficients of 0.2 [28], only predictors present in a minimum 123 quadrats, out of a total of 240 quadrats for each site, in each year (a potential maximum of four analyses), were included in the correlation. Pearson correlations were used to assess associations between the coverage of P. astreoides and habitat type (sand, rubble, and pavement), as well as biotic factors (scleractinian coral species, sponges, algae, and gorgonians; Table 2). Unless otherwise stated all statistical differences are at p < 0.05.
Table 2. Interspecific and substrate factors tested for inclusion in the correlation analyses.

| Factor                        |          | Factor                        |          |
|-------------------------------|----------|-------------------------------|----------|
| Acropora cervicornis          | Mycetophyllia aliciae | Acropora palmata              | Mycetophyllia danaana |
| Acropora prolifera            | Mycetophyllia ferox   | Agaricia agaricites           | Mycetophyllia lamarckiana |
| Agaricia fragilis             | Oculina diffusa      | Agaricia grahamae             | Orbicella annularis |
| Agaricia lamarcki             | Orbicella faveolata  | Agaricia tenuifolia           | Orbicella franksi |
| Agaricia undata               | Porites branneri     | Colpophyllia breviserialis    | Porites divaricate |
| Colpophyllia natans           | Porites furcata      | Dendrogyra cylindrus          | Porites furcata  |
| Dichocoenia stellaris         | Scolymia cubensis    | Dichocoenia stokes            | Siderastrea laceri |
| Diploria clivosa              |                   | Diploria strigosa             | Siderastrea siderea |
| Diploria labrinthiformis      |                   | Eusmilia fastigiata           | Solenastrea bourroni |
| Favia fragum                  |                   | Isophyllia sinuosa            | Solenastrea hyades |
| Leptoseris cucullata          |                   | Madracis decactis             | Stephanocoenia michelinii |
| Madracis mirabilis            |                   | Manicina areolata             | Tubastraea aurea   |
| Manicina areolata             |                   | Meandrina meandrites          | Coralline algae   |
| Millipora alcicornis          |                   | Millipora complanata          | Gorgonians        |
| Millipora squarrosa           |                   | Millipora squarrosa           | Macroalgae        |
| Montastraea cavernosa         |                   | Mussa angulosa                | Sponges           |
|                               |                   |                               | Zoanthids         |
|                               |                   |                               | Sand              |
|                               |                   |                               | Rubble            |
|                               |                   |                               | Pavement          |

3. Results

3.1. Benthic Community Assessment

Hard coral species abundance matrices were generated using the images processed in CPCe. Most sites experienced a minor, non-significant decrease in mean coral cover between 2014 and 2017, except for a significant decrease at Jackadam (19.14% ± 3.51 to 12.38% ± 3.29), which drove the significant decrease in coral cover between years (Figure 2). Mean coral cover in 2014 was 21.08% ± 6.21 (average ± SE) for all study sites and decreased to a mean of 17.45% ± 5.67 in 2017. Within each year, mean percent coral cover was not significantly different between islands. The only sites that were significantly different within a year (post-hoc test with Bonferroni correction) were Seaview and Jackadam in 2017.

There was a significant decrease in mean macroalgal cover in all sites from 2014 to 2017 (36.56% ± 14.90 to 27.88% ± 13.91). This change was driven by a significant decrease in Carriacou (41.62% ± 16.33 to 29.44% ± 16.00) at all four sites (Figure 2). Macroalgal cover was 28.91% ± 11.84 and did not change significantly in Grenada. In Carriacou, macroalgal cover was significantly higher at Jackadam than at Seaview for both 2014 and 2017 and there was a significant decrease at both sites between surveys. In Grenada, Dragon Bay had significantly higher macroalgal cover than Flamingo Bay in 2014, but not in 2017, as Flamingo Bay experienced a significant increase. Quarter Wreck and Northern exposure also experienced a significant decrease in macroalgal cover (Figure 2).
Figure 2. Mean (±SD) of percent coral and macroalgal cover at study sites in Carriacou and Grenada in 2014 and 2017. (*) denotes a significant difference ($p < 0.05$) at a single site between years while letters denote a significant difference ($p < 0.05$) between sites in a given year.

Mean gorgonian cover for all sites was 3.82% ± 6.47 and did not change significantly between years. There were significant differences in gorgonian cover between islands (not shown). Flamingo Bay and Sandy Island had significantly higher cover than all other sites on their respective islands. Mean gorgonian cover was 18.12% ± 8.6 at Flamingo Bay versus 1.92% ± 1.09 on Grenada and 4.18% ± 4.5 at Sandy Island versus 0.85% ± 0.78 on Carriacou. Mean sponge cover for all sites was 2.67% ± 3.66 and did not change significantly between years or islands within a year (not shown).

Site and island had a significant (ANOSIM) effect on predicting similarity of benthic species assemblages. The high dissimilarity ($R$) values obtained suggest that, for most sites, the majority of the variation in Bray-Curtis dissimilarity can be explained by site grouping. Island had a significant effect in predicting community dissimilarity in both 2014 and 2017. Between-years analysis using PERMANOVA showed a significant effect of time only. All sites were significantly different from the previous year when assessed using ANOSIM (Table 1).

A total of 25 unique hard coral species were identified in the photo quadrats using the stratified random method (Table 3). Of these, the most commonly observed species in Carriacou in both 2014 and 2017 were $P$. astreoides, $P$. divaricata and $O$. annularis. In Grenada, the hard coral species assemblage was dominated by $M$. mirabilis, $P$. astreoides, and $O$. annularis in 2014 (Table 3) and $M$. mirabilis, $P$. astreoides, and $P$. divaricata in 2017. The proportions of $O$. annularis, $P$. porites, and $P$. divaricata in the hard coral species assemblage changed significantly between years and islands using a general linear mixed model (Table 3).
Table 3. Mean (±SD) relative proportion of hard coral species colony counts in Carriacou (CAR) and Grenada (GND) in 2014 and 2017.

| Taxon                        | CAR 2014    | CAR 2017    | GND 2014    | GND 2017    |
|-----------------------------|-------------|-------------|-------------|-------------|
| Agaricia agaricites         | 0.037 ± 0.003 | 0.046 ± 0.004 | 0.014 ± 0.002 | 0.016 ± 0.002 |
| Agaricia lamarcki           | 0.000 ± 0.000 | 0.003 ± 0.001 | 0.000 ± 0.000 | 0.001 ± 0.000 |
| Colpophyllia natans         | 0.005 ± 0.001 | 0.092 ± 0.005 | 0.000 ± 0.000 | 0.039 ± 0.004 |
| Diploria labyrinthiformis   | 0.013 ± 0.002 | 0.021 ± 0.003 | 0.004 ± 0.001 | 0.005 ± 0.001 |
| Diploria strigosa           | 0.081 ± 0.005 | 0.006 ± 0.001 | 0.035 ± 0.003 | 0.001 ± 0.001 |
| Eusmilia fastigiata         | 0.000 ± 0.000 | 0.001 ± 0.001 | 0.002 ± 0.001 | 0.001 ± 0.001 |
| Madracis decactis           | 0.000 ± 0.000 | 0.019 ± 0.003 | 0.000 ± 0.000 | 0.015 ± 0.002 |
| Madracis mirabilis          | 0.100 ± 0.005 | 0.102 ± 0.006 | 0.250 ± 0.007 | 0.253 ± 0.008 |
| Meandrina meandrites        | 0.015 ± 0.002 | 0.017 ± 0.002 | 0.007 ± 0.001 | 0.005 ± 0.001 |
| Millipora alpicornis        | 0.033 ± 0.003 | 0.040 ± 0.004 | 0.014 ± 0.002 | 0.013 ± 0.002 |
| Millipora complanata        | 0.018 ± 0.002 | 0.000 ± 0.000 | 0.003 ± 0.001 | 0.000 ± 0.000 |
| Millipora squarrosa         | 0.000 ± 0.000 | 0.003 ± 0.001 | 0.000 ± 0.000 | 0.001 ± 0.001 |
| Montastrea cavernosa        | 0.039 ± 0.004 | 0.032 ± 0.003 | 0.036 ± 0.003 | 0.026 ± 0.003 |
| Oculina diffusa             | 0.000 ± 0.000 | 0.001 ± 0.001 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| * Orbicella annularis       | 0.147 ± 0.006 | 0.122 ± 0.006 | 0.169 ± 0.006 | 0.094 ± 0.005 |
| Orbicella favolata          | 0.003 ± 0.001 | 0.000 ± 0.000 | 0.005 ± 0.001 | 0.000 ± 0.000 |
| Orbicella franksi           | 0.000 ± 0.000 | 0.020 ± 0.003 | 0.000 ± 0.000 | 0.074 ± 0.005 |
| Porites astreoides          | 0.221 ± 0.008 | 0.199 ± 0.008 | 0.212 ± 0.007 | 0.211 ± 0.007 |
| * Porites divaricata        | 0.029 ± 0.003 | 0.178 ± 0.007 | 0.056 ± 0.004 | 0.163 ± 0.007 |
| * Porites porites           | 0.174 ± 0.007 | 0.000 ± 0.000 | 0.118 ± 0.005 | 0.005 ± 0.001 |
| Siderastrea siderea         | 0.077 ± 0.005 | 0.089 ± 0.005 | 0.072 ± 0.004 | 0.070 ± 0.005 |
| Solenastrea bouroni         | 0.000 ± 0.000 | 0.007 ± 0.002 | 0.000 ± 0.000 | 0.004 ± 0.001 |
| Stephanocenia michelinii    | 0.006 ± 0.001 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |

* denotes significance between years and islands at $p = 0.05$.

3.2. *P. astreoides* in Grenada

Mean percent coverage of the mustard hill coral increased at all eight sites, but significant increases were only observed at Flamingo Bay in Grenada, and at Whirlpool and Jackadam in Carriacou (Figure 3). Absolute colony coverage ranged from 0% to 38.9% in surveyed quadrats. Mean colony size of *P. astreoides* increased significantly at all sites in Carriacou and Grenada (Figure 4). Colony sizes from all surveyed quadrats ranged from 0.2 cm² to 1600 cm². Rates of colony size increases over the three years range from +87% to +329%. Mean colony abundance of *P. astreoides* significantly decreased at all sites in Carriacou and Grenada (Figure 5). *P. astreoides* colony abundance within a quadrat ranged from 0 to 134. There was a significant shift in the size frequency distribution (Kolmogorov-Smirnov 2-sample tests) of *P. astreoides* towards fewer, larger colonies at both islands from 2014 to 2017 (Figure 6).

Significant correlations between *P. astreoides* coverage and other biotic factors were identified in Carriacou and Grenada for both 2014 and 2017 (Table 4). Coverage of *P. astreoides* was significantly associated with sand (−), rubble (−), and coralline algae (+) in all analyses, (Table 4). Coverage was positively associated with sponges in Carriacou, and negatively associated in Grenada, although this was not statistically significant in Grenada in 2017 (Table 4). Coverage of *P. astreoides* was significantly associated with macroalgae (−) in all four correlation analyses (Table 4) and was significantly associated with gorgonians (−) in all three analyses that were possible (Table 4). *Siderastrea siderea* and *O. annularis* were the only scleractinian species present in all four analyses and no significant correlations were found with *P. astreoides* (Table 4). *Porites divaricata* was present in three of four analyses and was negatively correlated with *P. astreoides* coverage, although this was only significant in one of the three analyses (Table 4). Other scleractinian species were only present in one or two of the analyses with varying correlation relationships and statistical significance (Table 4).
Figure 3. Mean percent cover of *P. astreoides* in 2014 and 2017 in Carriacou and Grenada. (*) denotes significance (*p* < 0.05) between years.

Figure 4. Mean colony size (cm$^2$) of *P. astreoides* in 2014 and 2017 in Carriacou and Grenada. (*) denotes significance (*p* < 0.05) between years.
Figure 5. Mean colony abundance of *P. astreoides* per quadrat in 2014 and 2017 in Carriacou and Grenada. (*) denotes significance ($p < 0.05$) between years.

Figure 6. Size-frequency distribution of *P. astreoides* colonies in Carriacou (top) and Grenada (bottom) in 2014 (dark grey bar; solid line) and 2017 (light grey bar; dashed line). * Indicates significance at $p < 0.05$. 
Table 4. Magnitude of the relationship between *P. astreoides*, scleractinian coral species, biotic factors, and habitat type. Pearson correlation coefficients indicated by r. * Indicates significance at \( p = 0.05 \).

| Carriacou | Grenada |
|-----------|---------|
|           | 2014    | 2014    |
| Factor    | r       | p-value | Factor    | r       | p-value |
| Rubble    | −0.168  | 0.0001 *| Rubble    | −0.101  | 0.002 * |
| Pavement  | 0.193   | 0.0001 *| Sand      | −0.122  | 0.0001 *|
| Sand      | −0.168  | 0.0001 *| *Madracis auretenra* | −0.127  | 0.0001 *|
| *Diploria strigosa* | 0.159   | 0.0001 *| *Orbicella annularis* | 0.047   | 0.148   |
| *Orbicella annularis* | −0.031  | 0.345   | *Porites divaricata* | −0.006  | 0.844   |
| *Porites porites* | −0.118  | 0.0001 *| *Porites porites* | −0.048  | 0.143   |
| *Siderastrea siderea* | 0.013   | 0.685   | *Siderastrea siderea* | −0.063  | 0.054   |
| Gorgonians | −0.095  | 0.003 * | Gorgonians | −0.156  | 0.0001 *|
| Sponges   | 0.259   | 0.0001 *| Sponges   | −0.128  | 0.0001 *|
| Macrolgae | −0.288  | 0.0001 *| Macrolgae | 0.071   | 0.03 *  |
| Coralline Algae | 0.199   | 0.0001 *| Coralline Algae | 0.099   | 0.002 * |

| 2017 | 2017 |
|------|------|
| Factor    | r       | p-value | Factor    | r       | p-value |
| Rubble    | −0.196  | 0.0001 *| Rubble    | −0.073  | 0.027 * |
| Sand      | −0.145  | 0.0001 *| Sand      | −0.114  | 0.001 * |
| *Colphophyllia natans* | 0.126   | 0.0001 *| *Madracis auretenra* | −0.101  | 0.002 * |
| *Orbicella annularis* | −0.044  | 0.179   | *Orbicella annularis* | −0.03   | 0.364   |
| *Porites divaricata* | −0.078  | 0.017 * | *Orbicella franksi* | 0.088   | 0.008 * |
| *Siderastrea siderea* | −0.026  | 0.417   | *Porites divaricata* | −0.049  | 0.141   |
| Sponges   | 0.199   | 0.0001 *| *Siderastrea siderea* | −0.017  | 0.61    |
| Macrolgae | −0.238  | 0.0001 *| Gorgonians | −0.14   | 0.0001 *|
| *Coralline Algae* | 0.116   | 0.0001 *| Sponges   | −0.057  | 0.083   |

4. Discussion

In this study, we were able to provide insight into factors relating to the success and population dynamics of *P. astreoides*. From 2014 to 2017, populations of this species were found to shift from being dominated by many smaller colonies, to fewer, larger and more mature colonies. Given the magnitude of changes in abundance and size of colonies (coupled with moderate coverage increases) over such a short timeframe, it is likely we observed the population dynamics of *P. astreoides* during and after a large-scale recruitment event, with a recent tropical storm in 2013 (Chantal) potentially acting as a trigger [29]. *P. astreoides* colonies were found to be positively associated with coralline algae, and pavement, while negatively associated with sand, rubble, and macroalgae. This mirrors the recruitment patterns found in other scleractinian species, with substrate type and algal status playing a critical role. In addition, recruitment patterns between *P. astreoides* and other scleractinian coral species were found to be potentially predicted by life-history strategy, being positively associated with massive corals, and negatively associated with branching corals.

The composition of Caribbean coral reefs has been relatively stable for much of the last 150,000 years, with species from all life history strategies persisting [29,30]. In the last
several decades, increases in anthropogenic stressors and environmental impacts have resulted in up to 80% reductions in Caribbean live coral cover [1,2,31,32]. Communities once dominated by framework building corals are now primarily comprised of macroalgae and non-framework building species such as P. astreoides [7,33]. Prior species data for Carriacou and the nearby Tobago Cays show communities comprised of relatively similar species assemblages with the notable exception of acroporids [34,35]. In 1976, scleractinian coral cover in Carriacou was estimated at 30%, with A. palmata comprising approximately 10% of this value, with present densities being so low that the method used in the present study did not reflect their presence [34]. This lack of acroporids is attributed to their region-wide decline since the 1980s, with their near absence being noted in the nearby Tobago Cays in 1999 [35,36]. The percent coral cover values obtained in the present study for Grenada are slightly higher than those reported in recently published literature for the same study sites [20,21]. No significant differences in coral cover were detected between the islands. Unfortunately, there is a lack of extensive historical data for Carriacou and the only available published data is more than 40 years out of date and/or in the nearby Tobago Cays [34], hence the need for the present study. Statistically sound comparisons between the previous and present studies are not possible, however, broader comparisons can be made. The composition of the hard coral assemblages and the relatively low percent cover of hard corals combined with the high percent cover of macroalgae suggests that the current reefs of Carriacou and Grenada are stressed [2]. Non-reef building species such as Porites spp. now dominate these coral communities.

Size-frequency distributions (2014 vs. 2017) in Grenada and Carriacou revealed substantial increases in colony size of P. astreoides at all sites from 2014 to 2017, with a shift towards fewer, larger colonies in 2017. Although, large colonies (>400 cm²) observed in 2014 were still present in 2017. These increases ranged from +87% to +329% across the eight sites in only three years’ time. Moderate increases in mean percentage cover of P. astreoides was also observed at all sites, with statistical significance only found in Flamingo Bay, Whirlpool, and Jackadam. Although increasing in colony size and coverage, significant declines in P. astreoides abundance was observed at all sites. Considering the mean increase in colony size, coupled with a drop in colony abundance and low coverage increases, these results provide a further indication that this study observed the recruitment dynamics of P. astreoides [37]. First, local populations were dominated by juvenile colonies of P. astreoides (<40 cm²) in both 2014 and 2017 (Figure 6). Second, the large number of small colonies in 2014 could be reflective of a large-scale recovery event following a disturbance that took place prior to monitoring, such as tropical storm ‘Chantal’ that affected Grenada and Carriacou eight months prior to the first survey in 2014 [38]. Regional hurricane events in the windward islands of the Caribbean have been observed to negatively impact recruitment in scleractinian coral species, with it persisting at reduced levels [39]. These results corroborate previous research demonstrating that P. astreoides populations, much like other weedy coral species, are largely influenced by recruitment [18,40].

In addition to recruitment, which is thought to be the main explanation for the observed pattern, it is also possible that colony fusion likely played some role in the aforementioned trends observed in P. astreoides colonies. We maintain this possibility as increases in colony size do not correspond with the known growth rate of this species. The upper end of radial growth rates for P. astreoides has been estimated at ~5.78 mm year⁻¹, comparable to other scleractinian corals, with colonies reaching maturity at eight to ten years of age [40,41]. Thus, for a 40 cm² colony to more than triple in size through growth alone over three years as observed (i.e., Flamingo Bay), radial extension of more than 8 mm year⁻¹ would be required, exceeding known growth rates. Colony fusion has been observed in P. astreoides populations following hurricane Hugo in the Buck Island Reef National Monument [42]. Colony fusion rates year⁻¹ as a share of the total population were observed to have increased from a mean of 0.4% to 4.1% following this disturbance [42]. Fusion is known to occur in the species and juvenile P. astreoides colonies are highly likely to be genetically related to one another since inbreeding through self-
fertilization is common [41,43]. Asexual recruits are often found in close proximity and have irregular growth forms [37], an occurrence frequently noted observed in our image analysis (Figure 7). Yet, as we did not directly measure colony fusion in our study, this is an important aspect that future studies should consider when exploring populations of *P. astreoides*.

![Figure 7. Portion of a quadrat photo from the ‘Seaview’ site on Carriacou in 2014. *P. astreoides* is abundant, with many colonies growing in close proximity to one another.](image)

In our study, *P. astreoides* colonies were significantly correlated with pavement (+), sand (−), rubble (−), macroalgae (−), and coralline algae (+) as observed with other scleractinian species [10,44–46]. Sandy and rubble substrates are habitat ‘sinks’ for coral recruits; the former results in poor attachment and smothering [46–48], while rubble can facilitate initial attachment and growth, but is easily shifted, destroying colonies [45–49]. Conversely, *P. astreoides* larvae can settle and thrive on pavement as this substrate is resistant to physical disturbance [45,46].

The negative relationship between *P. astreoides* coverage and macroalgae observed in the present study was expected. Scleractinian corals globally are unable to compete with macroalgae, resulting in shifts from coral-dominated communities to those dominated by macroalgae [44,50,51]. Herbivorous species are essential to clear macroalgae [44,52], however, not all herbivores impact *P. astreoides* success equally. Ocean surgeonfish grazing increased growth of *P. astreoides*, but parrotfish have no impact [52]. Herbivorous fish biomass in Grenada and Carriacou is ‘poor’ [53] and herbivorous invertebrates, such as *Diadema antillarum*, are also now largely absent from reef communities in Grenada [21]. Though not directly assessed in this study, high abundances of urchins were observed in transects with the low levels of macroalgae. Unlike macroalgae, coralline algae does not outcompete coral recruits, and attracts their settlement with chemical signatures in the water [46,54]. In the present study, a positive relationship was observed between *P. astreoides* and coralline algae coverage.

Varying responses of *P. astreoides* coverage to sponges were observed in the present study. Sponges were not classified by individual species or growth form, a potential source of this unclear relationship. The negative association between *P. astreoides* and gorgonians observed in the present study was expected as the elongate form of gorgonians can block essential sunlight for many scleractinian colonies [55]. Negative relationships have been observed between gorgonians and scleractinian corals, which has resulted in the classification of coral framework reefs being habitats distinct from gorgonian plains [53,55]. Care should be taken when considering this result as gorgonian cover was based on their respective presence in the image, not just the area where each colony was attached to the substrate.
Scleractinian species that were significantly positively correlated with *P. astreoides* had a massive colony growth pattern (both stress tolerant and generalist), while species that were significantly negatively correlated had a branching growth pattern (only weedy). Weedy corals with a shared life history strategy may compete with each other in disturbed environments [56]. Large colony size is typical of stress-tolerant species, with a greater reserve of polyps from which to draw energy, often increasing the resilience of these colonies to changes over time [57].

*P. astreoides* continues to be one of the more successful coral species in Grenada and the Caribbean at large and may continue to experience success in the future. *P. astreoides* faces similar settlement and competitive challenges as other coral species and its life-history strategy may be partially responsible for its success on a regional scale. Further work is required to assess the magnitude and range of environmental stressors this species can tolerate and the role colony fusion plays may play in the recovery dynamics of its' populations, especially in the context of rapid climate change.

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**References**

1. Gardner, T.A.; Côté, I.M.; Gill, J.A.; Grant, A.; Watkinson, A.R. Long-Term Region-Wide Declines in Caribbean Corals. *Science* 2003, 301, 958–960. [CrossRef]
2. Jackson, J.B.C.; Donovan, M.K.; Cramer, K.L.; Lam, W. *Status and Trends of Caribbean Coral Reefs: 1970–2012*; International Union for the Conservation of Nature: Gland, Switzerland, 2014.
3. Hughes, T.P.; Baird, A.H.; Bellwood, D.R.; Card, M.; Connolly, S.R.; Folke, C.; Grosberg, R.; Hoegh-Guldberg, O.; Jackson, J.B.C.; Kleypas, J.; et al. Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* 2003, 301, 929–933. [CrossRef]
4. Castillo, K.D.; Ries, J.B.; Weiss, J.M.; Lima, F.P. Decline of forereef corals in response to recent warming linked to history of thermal exposure. *Nat. Clim. Chang.* 2012, 2, 756–760. [CrossRef] [PubMed]
5. Okazaki, R.R.; Towle, E.K.; Hooidonk, R.; Mor, C.; Winter, R.N.; Piggot, A.M.; Cunning, R.; Baker, A.C.; Klaus, J.S.; Swart, P.K.; et al. Species-specific responses to climate change and community composition determine future calcification rates of Florida Keys reefs. *Glob. Chang. Biol.* 2017, 23, 1023–1035. [CrossRef] [PubMed]
6. Anthony, K.R.; Marshall, P.A.; Abdulla, A.; Beeden, R.; Bergh, C.; Black, R.; Eakin, C.M.; Game, E.; Gooch, M.; Graham, N.; et al. Operationalizing resilience for adaptive coral reef management under global environmental change. *Glob. Chang. Biol.* 2015, 21, 48–61. [CrossRef] [PubMed]
7. Perry, C.T.; Steneck, R.S.; Murphy, G.N.; Kench, P.S.; Edinger, E.N.; Smithers, S.G.; Mumby, P. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Glob. Chang. Biol.* 2015, 21, 1153–1164. [CrossRef]
8. Van Woesik, R.; Sakai, K.; Ganase, A.; Loya, Y. Revisiting the winners and the losers a decade after coral bleaching. *Mar. Ecol. Prog. Ser.* 2011, 434, 67–76. [CrossRef] [PubMed]
9. Darling, E.S.; Alvarez-Filip, L.; Oliver, T.A.; McClanahan, T.R.; Côté, I.M. Evaluating life-history strategies of reef corals from species traits. *Ecol. Lett.* 2012, 15, 1378–1386. [CrossRef]
10. Schutte, V.G.W.; Selig, E.R.; Bruno, J.F. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar. Ecol. Prog. Ser.* 2010, 402, 115–122. [CrossRef]

11. Rodríguez-Martínez, R.; Banaszak, A.T.; McField, M.D.; Beltrán-Torres, A.U.; Álvarez-Filip, L. Assessment of Acropora palmata in the Mesoamerican Reef System. *PloS ONE* 2014, 9, e96140. [CrossRef]

12. Green, D.; Edmunds, P.; Carpenter, R. Increasing relative abundance of Porites astreoides on Caribbean reefs mediated by an overall decline in coral cover. *Mar. Ecol. Prog. Ser.* 2008, 359, 1–10. [CrossRef]

13. Medina-Valmaseda, A.E.; Rodríguez-Martínez, R.E.; Álvarez-Filip, L.; Jordan-Dahlgren, E.; Blanchon, P. The role of geomorphic zonation in long-term changes in coral-community structure on a Caribbean fringing reef. *PeerJ* 2020, 8, e10103. [CrossRef]

14. Eagleson, R. Spatial Distribution of Benthic Habitats and Ecological Patterns of the Mustard Hill Coral (Porites Astreoides) in the Nearshore Waters of Grenada. Master’s Thesis, University of Guelph, Guelph, ON, Canada, 2019.

15. Edmunds, P. Population biology of Porites astreoides and Diploria strigosa on a shallow Caribbean reef. *Mar. Ecol. Prog. Ser.* 2010, 418, 87–104. [CrossRef]

16. Baumann, J.H.; Townsend, J.E.; Courtney, T.A.; Aichelman, H.E.; Davies, S.W.; Lima, F.P.; Castillo, K.D. Temperature Regimes Impact Coral Assemblages along Environmental Gradients on Lagoonal Reefs in Belize. *PloS ONE* 2016, 11, e0162098. [CrossRef]

17. Goodbody-Gringley, G.; de Putron, S.J. Brooding Corals: Planulation Patterns, Larval Behavior, and Recruitment Dynamics in the Face of Environmental Change. In *The Cnidaria, Past, Present and Future*; Springer International Publishing: Cham, Switzerland, 2016; pp. 279–289.

18. Edmunds, P.J.; Didden, C.; Frank, K. Over three decades, a classic winner starts to lose in a Caribbean coral community. *Ecosphere* 2021, 12, e03517. [CrossRef]

19. Horricks, R.A.; Herbinger, C.M.; Lillie, B.N.; Taylor, P.; Lumsden, J.S. Differential protein abundance during the first month of regeneration of the Caribbean star coral Montastrea cavernosa. *Coral Reefs* 2018, 38, 45–61. [CrossRef]

20. Anderson, R.; Morrall, C.; Nimrod, S.; Balza, R.; Berg, C.; Jossart, J. Benthic and fish population monitoring associated with a marine protected area in the nearshore waters of Grenada, Eastern Caribbean. *Rev. Biol. Trop.* 2012, 60, 71–87. [CrossRef]

21. Anderson, R.A.; Morrall, C.B.; Nimrod, S.B.; Balza, R.A.; Berg, C.; Jossart, J.A. Marine Protected Area Monitoring in the Nearshore Waters of Grenada, Eastern Caribbean: Benthic Cover and Fish Populations. *Rev. Biol. Trop.* 2014, 62, 273–286. [CrossRef]

22. Horricks, R.A. Tissue Regeneration of Artificially Induced Lesions in the Caribbean Great Star Coral (Montastrea Cavernosa) in the Nearshore Waters of Grenada. Ph.D. Thesis, University of Guelph, Guelph, ON, Canada, 2017.

23. Kohler, K.E.; Gill, S.M. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral substrate coverage using random point count methodology. *Comput. Geosci.* 2006, 32, 1259–1269. [CrossRef]

24. Dumas, P.; Bertaud, A.; Peigon, C.; Léopold, M.; Pelletier, D. A “quick and clean” photographic method for the description of coral reef habitats. *J. Exp. Mar. Biol. Ecol.* 2009, 368, 161–168. [CrossRef]

25. Alquezar, R.; Boyd, W. Development of rapid, cost effective coral survey techniques: Tools for management and conservation planning. *J. Coast. Conserv.* 2007, 11, 105–119. [CrossRef]

26. Team, R.C.R. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2019; ISBN 17513243. ISBN 9780080554501.

27. Oksanen, J. Vegan: Ecological Diversity. 2016, p. 12. Available online: https://www.semanticscholar.org/paper/Vegan%3A-ecological-diversity-Oksanen/6d1f21af6a90af203ab680657c215000e292cea6 (accessed on 27 November 2020).

28. Bonett, D.G.; Wright, T.A. Sample size requirements for estimating Pearson, Kendall and Spearman correlations. *Psychometrika* 2000, 65, 263–288. [CrossRef]

29. Greenstein, B.J.; Curran, H.A.; Pandolfi, J.M. Shifting ecological baselines and the demise of Acropora cervicornis in the western North Atlantic and Caribbean Province: A Pleistocene perspective. *Coral Reefs* 1998, 17, 249–261. [CrossRef]

30. Toth, L.T.; Stathakopoulou, A.; Kuffner, I.B.; Ruzicka, R.R.; Colella, M.A.; Shin, E.A. The unprecedented loss of Florida’s reef-building corals and the emergence of a novel coral-reef assemblage. *Ecology* 2019, 100, e02781. [CrossRef]

31. Burke, L.; Maidens, J. *Reefs at Risk in the Caribbean*. Island Press: Washington, DC, USA, 2004; ISBN 1559632574.

32. Neal, B.P.; Khen, A.; Treibitz, T.; Beijbom, O.; O’Connor, G.; Coffroth, M.A.; Knowlton, N.; Kriegman, D.; Mitchell, B.G.; Kline, D. Caribbean massive corals not recovering from repeated thermal stress events during 2005–2013. *Ecol. Evol.* 2017, 7, 1339–1353. [CrossRef]

33. Aronson, R.B.; MacIntyre, I.G.; Wapnick, C.M.; O’Neill, M.W. Phase Shifts, Alternative States, and the Unprecedented Convergence of Two Reef Systems. *Ecology* 2004, 85, 1876–1891. [CrossRef]

34. Goodwin, M.; Cole, M.; Stewart, W.; Zimmerman, B. Species density and associations in Caribbean reef corals. *J. Exp. Mar. Biol. Ecol.* 1976, 24, 19–31. [CrossRef]

35. Deschamps, A.; DesRochers, A.; Klomp, K.D. St. Vincent. A Rapid Assessment of the Horseshoe Reef, Tobago Cays Marine Park, St. Vincent, West Indies (Stony Corals, Algae and Fishes). *Atoll Res. Bull.* 2003, 496, 438–459. [CrossRef]

36. Lewis, J.B. A preliminary description of the coral reefs of the Tobago Cays, Grenadines, West Indies. *Atoll Res. Bull.* 1975, 178, 1–9. [CrossRef]

37. Smith, S.R. Patterns of Coral Recruitment and Post-Settlement Mortality on Bermuda’s Reefs: Comparisons to Caribbean and Pacific Reefs. *Am. Zool.* 1992, 33, 663–673. [CrossRef]
38. Votaw, G.S.; Rosa, L.; Snell, W.; Anselmi, C.; History, S. Tropical Storm Chantal; National Weather Service: Washington, DC, USA, 2013.
39. Mallela, J.; Crabbe, M. Hurricanes and coral bleaching linked to changes in coral recruitment in Tobago. Mar. Environ. Res. 2009, 68, 158–162. [CrossRef]
40. Madin, J.S.; Anderson, K.D.; Andreasen, M.H.; Bridge, T.C.; Cairns, S.D.; Connolly, S.R.; Darling, E.S.; Diaz, M.; Falster, D.S.; Franklin, E.C.; et al. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Sci. Data 2016, 3, 160017. [CrossRef]
41. Chornesky, E.; Peters, E. Sexual Reproduction and Colony Growth in the Scleractinian Coral Porites Astreoides. Biol. Bull. 1987, 172, 161–177. [CrossRef]
42. Bythell, J.C. Assessment of the Impacts of Hurricanes Marilyn and Luis and Post-Hurricane Community Dynamics at Buck Island Reef National Monument; Technical Report; US Department of Interior, National Park Service: Washington, DC, USA, 1997. [CrossRef]
43. Kraus, D.A.; Gleason, D.F.; Morgan, M.E. Self-Fertilization in Brooding Hermaphroditic Caribbean Corals: Evidence from Molecular Markers. J. Exp. Mar. Biol. Ecol. 1998, 231, 225–238. [CrossRef]
44. Vega Thurber, R.; Burkepile, D.E.; Correa, A.M.S.; Thurber, A.R.; Shantz, A.A.; Welsh, R.; Pritchard, C.; Rosales, S. Macroalgae Decrease Growth and Alter Microbial Community Structure of the Reef-Building Coral, Porites Astreoides. PLoS ONE 2012, 7, e44246. [CrossRef]
45. Cameron, C.M.; Pausch, R.E.; Miller, M.W. Coral Recruitment Dynamics and Substrate Mobility in a Rubble-Dominated Back Reef Habitat. Bull. Mar. Sci. 2016, 92, 123–136. [CrossRef]
46. Ritson-Williams, R.; Arnold, S.; Paul, V. Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. Mar. Ecol. Prog. Ser. 2016, 548, 127–138. [CrossRef]
47. Ross, C.; Ritson-Williams, R.; Olsen, K.; Paul, V.J. Short-Term and Latent Post-Settlement Effects Associated with Elevated Temperature and Oxidative Stress on Larvae from the Coral Porites astreoides. Coral Reefs 2013, 32, 71–79. [CrossRef]
48. Olsen, K.; Sneed, J.; Paul, V.J. Differential larval settlement responses of Porites astreoides and Acropora palmata in the presence of the green alga Halimeda opuntia. Coral Reefs 2016, 35, 521–525. [CrossRef]
49. Fava, F.; Ponti, M.; Scinto, A.; Calcina, B.; Cerrano, C. Possible effects of human impacts on epibenthic communities and coral rubble features in the marine Park of Bunaken (Indonesia). Estuarine Coast. Shelf Sci. 2009, 85, 151–156. [CrossRef]
50. Gilby, B.L.; Maxwell, P.S.; Tibbetts, I.; Stevens, T. Bottom-Up Factors for Algal Productivity Outweigh No-Fishing Marine Protected Area Effects in a Marginal Coral Reef System. Ecosystems 2015, 18, 1056–1069. [CrossRef]
51. Olsen, K.; Paul, V.J.; Ross, C. Direct effects of elevated temperature, reduced pH, and the presence of macroalgae (Dictyota spp.) on larvae of the Caribbean coral Porites astreoides. Bull. Mar. Sci. 2015, 91, 255–270. [CrossRef]
52. Burkepile, D.E.; Hay, M. Impact of Herbivore Identity on Algal Succession and Coral Growth on a Caribbean Reef. PLoS ONE 2010, 5, e8963. [CrossRef] [PubMed]
53. Atlantic and Gulf Rapid Reef Assessment. Grenada’s Coral Reef Report Card; Ocean Research and Education Foundation: Key Largo, FL, USA, 2016; Available online: http://caribnode.org/documents/85 (accessed on 15 November 2017).
54. Done, T.J. Coral Community Adaptability to Environmental Change at the Scales of Regions, Reefs and Reef Zones. Am. Zool. 1999, 39, 66–79. [CrossRef]
55. Williams, S.; Mumby, P.; Chollett, I.; Cortés, J. Importance of differentiating Orbicella reefs from gorgonian plains for ecological assessments of Caribbean reefs. Mar. Ecol. Prog. Ser. 2015, 530, 93–101. [CrossRef]
56. Riegl, B.; Purkis, S.J. Coral population dynamics across consecutive mass mortality events. Glob. Chang. Biol. 2015, 21, 3995–4005. [CrossRef]
57. De Barros, M.M.L.; Pires, D.D.O. Colony size-frequency distributions among different populations of the scleractinian coral Siderastrea stellata in Southwestern Atlantic: Implications for life history patterns. Braz. J. Oceanogr. 2006, 54, 213–223. [CrossRef]