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Dynamics of Stony Coral and Octocoral Juvenile Assemblages Following Disturbance on Patch Reefs of the Florida Reef Tract

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Abstract

In January 2010, reefs in the Upper and Middle Florida Keys experienced prolonged exposure to extremely cold water temperatures, below lethal thresholds for many reef organisms including corals. We examined post-disturbance juvenile assemblages of stony corals and octocorals on eight patch reefs, four of which were categorized as high impact and four as low impact, based on declines in stony-coral cover following disturbance. We established permanent quadrats to conduct field surveys in spring and fall of 2012 and 2013. Overall, juvenile abundances of both stony corals and octocorals were greater on low-impact sites, suggesting that those sites had higher recruitment and juvenile survival than high-impact sites. Juvenile assemblages also showed a regional pattern, with more stony corals on Middle Keys sites and more octocorals on Upper Keys sites. The stony-coral juvenile assemblage was dominated by *Siderastrea siderea* (46%) and *Porites astreoides* (19%), whereas previously abundant species such as *Orbicella annularis* were nearly absent (<3%). Octocoral juveniles were dominated by *Antillogorgia* spp. (25%), *Gorgonia* spp. (21%), *Eunicea* spp. (19%) and *Erythropodium caribaeorum* (14%). Overall, post-disturbance juvenile assemblages displayed a wide range of octocoral genera, but only a few select stony-coral species, which exhibited either opportunistic or hardy life-history characteristics.

Keywords: recruitment, *Siderastrea siderea*, *Porites astreoides*, *Antillogorgia*, *Gorgonia*, *Eunicea*

1. Introduction

Coral reefs around the world continue to decline in response to compounding stressors, including those caused by humans and those occurring naturally. Often, natural disturbances such as hurricanes and thermal anomalies (especially those associated with El Niño Southern Oscillations (ENSOs) or cold-water events) can cause mass mortality in coral communities [1, 2]. For the past several decades, chronic anthropogenic disturbances, including reduced water quality, pollution, terrestrial runoff, and coastal development, have been exacerbating the impacts of natural disturbances by contributing to stressful environmental conditions that inhibit reef-community recovery [3–5]. Corals are thereby threatened by local anthropogenic stressors coupled with the challenges of warming seas and ocean acidification [6]. The additive and synergistic effects of these stressors can prevent reef-building corals from recovering following natural disturbances [1, 4, 5, 7]. This complex disturbance regime is readily evident in the history of coral communities of the Florida Keys [8–13].

The Florida reef tract was historically dominated by stony-coral species such as the branching *Acropora* spp. and the massive *Orbicella* spp., which have undergone dramatic declines in the last several decades [10, 14, 15]. In many documented cases around the world [16–19], macroalgae have taken over reefs following decline in stony-coral cover. In the Florida reef tract, octocorals and sponges, rather than macroalgae, have assumed the role of spatial opportunists and are replacing stony corals on many reefs [13, 20]. In other areas of the Caribbean where stony corals have declined, octocorals have maintained similar densities [21].

Octocorals, like macroalgae, are opportunistic, with higher recruitment and growth rates than stony corals [22–25]. Although octocorals do not confer the same ecosystem services as stony corals, they do offer more structural attributes than macroalgae. Octocorals found in the Florida Keys span a range of functional groups. Some grow as fans and plumes, creating canopies that provide habitat and protection for reef organisms [26], while encrusting species protect reef framework from bioeroding grazers such as parrot fish [27].

The Florida reef tract, off southeast Florida and the Florida Keys, is near the northern limit of coral-reef development and occasionally experiences environmental extremes, like the cold-water event that occurred in January 2010 [28–30]. In addition, nearshore patch reefs of the Florida reef tract are exposed to fluctuations in temperature and salinity and to greater variability in turbidity and light attenuation [31, 32]. Their proximity to land also potentially exposes these reefs to more direct anthropogenic effects such as terrestrial runoff, pollution [33–35], and fishing, boating and diving [31]. Despite this, prior to the 2010 cold-water event, patch reefs demonstrated the highest coral cover, highest growth rates and lowest incidences of partial mortality on the reef tract and hence had been identified as resilient to a variety of acute and chronic stressors [32].

In January 2010, patch reef communities were profoundly impacted when a prolonged influx of Arctic air caused sea-surface temperature to drop below the lethal threshold for many benthic organisms. Water temperature fell well below the 16°C lethal threshold for stony corals and remained low for several days [28, 36–38]. The event caused extreme, yet spatially inconsistent mortality among stony corals of the nearshore patch reefs in the Upper and Middle Florida Keys [28].

In the present study, we quantified juvenile abundance to determine if coral-recruitment success and post-settlement survivorship would provide early indications of recovery on these patch reefs. We chose four patch reefs that were severely impacted by the cold-event (high-impact sites) and four patch reefs that were essentially unchanged in community composition (low-impact sites) to create a balanced study design. The study compared juvenile communities of stony corals (comprising the orders Scleractinia and Anthomedusae, specifically family Milleporidae) and octocorals on patch reefs that endured significant losses of coral cover (high impact) with those that were less impacted (low impact). We included octocoral juveniles in the study to assess for susceptibility of patch reefs to documented increases in octocoral cover concurrent with declines in stony-coral cover occurring throughout the Florida reef tract. In addition, we used Coral Reef Evaluation and Monitoring Project (CREMP) data to compare macroalgal cover before and after the event to investigate the prospective role of macroalgae in stony-coral decline and recovery in this setting. We had four overarching questions: (1) Does coral recruitment differ between high-impact and low-impact sites? (2) Does coral recruitment differ between stony corals and octocorals? (3) Is there a difference in recruitment between the Upper and Middle Florida Keys? and (4) Did macroalgal cover increase following the cold-water event and if so, did it influence coral recruitment?

2. Methods

2.1. Site selection and survey protocol

Eight patch reef sites were selected for this study: four in the Upper Keys region (Admiral, Porter, Burr and Turtle) and four in the Middle Keys region (Dustan Rocks, West Turtle, Rawa and Thor) (**Figure 1**). All sites were selected from annual monitoring locations in the Coral Reef Evaluation and Monitoring Project (CREMP), for which historical demographic and benthic cover data were available for adult stony corals and macroalgae [13, 15, 39]. In each region, two reefs were categorized as high impact and two reefs as low impact (reference sites) based on the difference in percent stony-coral cover between 2009 and 2010 (**Figure 2**). A site was considered to be high impact if there was a 6% decrease in absolute stony-coral cover from summer 2009 to summer 2010, whereas low-impact sites decreased in cover by less than 1% or had slight gains during this time period [37].

Although all eight study sites were categorized as patch reef habitat, they differed in certain characteristics, including structural complexity, topography, depth and species composition. For example, Admiral reef was at least 3 m shallower than any other sites and was unique in that nearly all coral cover was previously comprised of massive *Orbicella annularis* colonies, which were decimated by the cold-water event [28]. Porter patch reef was structurally less complex than most of the other sites, with little rugosity and higher octocoral cover. The remaining sites, Dustan Rocks, Rawa, West Turtle, Thor, Burr and Turtle reefs, had similar depths and structural complexity and were representative of typical mid-channel patch reefs located in the Florida Keys.

Thirty-two randomly placed, permanent 0.25 m² quadrats were established at each patch reef. Sixteen quadrats were placed along each 22-m-long by 2-m-wide CREMP monitoring

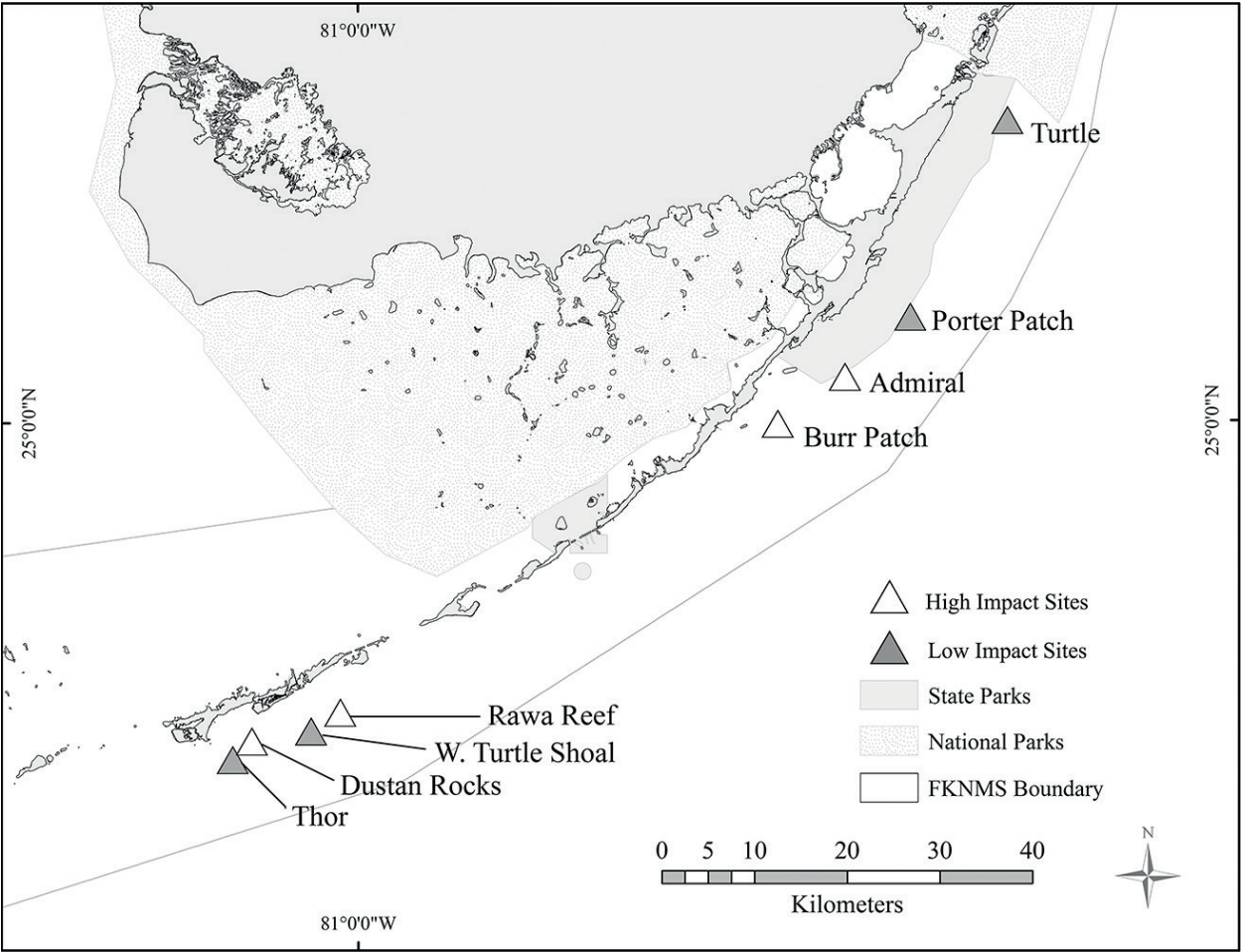


Figure 1. Map of the Middle and Upper Florida Keys with locations of recruitment study sites. White triangles represent high-impact sites, and gray triangles represent low-impact sites.

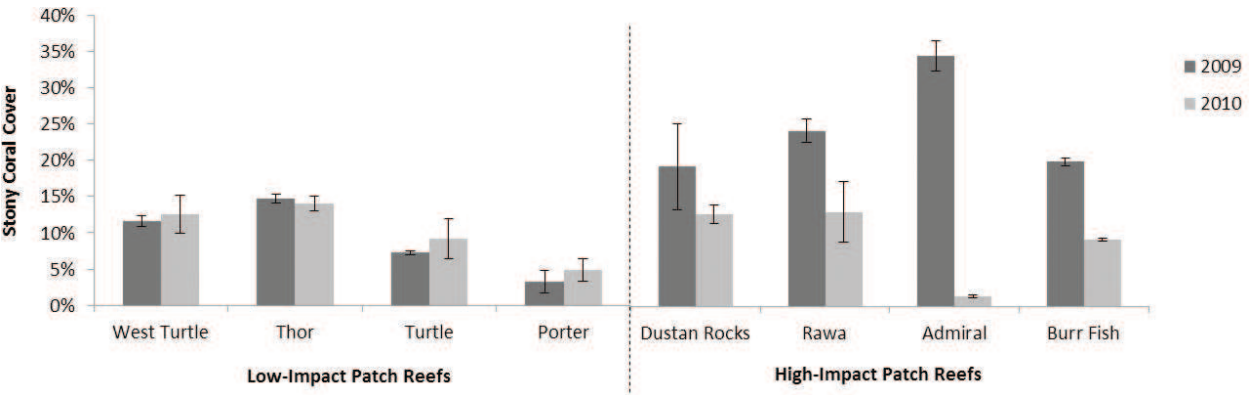


Figure 2. Percentage of stony coral cover in 2009 and 2010 at eight patch reef sites (error bars are standard error of the means). Extreme loss ($\geq 6\%$) of stony coral cover was recorded on four patch reefs (high-impact sites). Cover values from CREMP data.

transect [40], and two transects were used per site. Quadrat locations within transects were randomly determined by subdividing the belt transect into 0.5 m by 0.5 m squares, numbering them (1–176), and using a random number generator to choose quadrat location. To avoid placing quadrats in locations where the substrate was unsuitable for coral settlement, more

than 50% of the quadrat could not be comprised of living coral or sand. When a quadrat location did not meet these criteria, the next random number was selected. Three small (~7.6 cm long) masonry nails were inserted into the substrate and marked with flagging tape to delineate three corners of each quadrat to aid in relocation.

Photographs were taken of each quadrat and used as a visual aid for relocation. For the survey, all stony corals having a maximum diameter ≤ 4 cm and all octocoral juveniles with a maximum height ≤ 4 cm were identified, measured, mapped and photographed in March/April and September/October in 2012 and 2013. The 4-cm dimension for scleractinians was selected based on studies that found 4 cm to be an appropriate size cutoff for juveniles [41–43]. For octocorals, a 4-cm-height cutoff was applied because several gorgonian species can exceed 4 cm in height in a single year [24, 25]. This conservative threshold was applied so that octocorals under 4 cm in height were considered less than a year old to aid in distinguishing between year classes (e.g., juveniles identified in the first year of surveys would presumably be larger than 4 cm in the second year). Stony corals were identified to species, and octocorals were identified to genus. When identification was not possible, the colony was designated as either unknown stony coral (UNKS) or unknown octocoral (UNKO). The unknown categories were used by observers when a juvenile was too small to identify confidently, was obscured by another benthic organism, or was unidentifiable for some other reason.

2.2. High-impact vs. low-impact reefs

To compare the juvenile abundance of stony corals and octocorals at high-impact and low-impact sites, we built a generalized linear mixed model assuming a negative binomial distribution in SAS v9.3 (SAS Inc., Cary, NC). We included coral type (stony and octocoral) and site category (high-impact vs. low-impact) as well as their interaction as fixed factors. The negative binomial distribution was used in place of Poisson to account for over-dispersion (i.e., variance being unequal to mean) [44]. To account for the subsampling nature of data collection, we included random effects for multiple transects per site, as well as multiple quadrats per transect. As sites were repeatedly sampled, we incorporated a repeated-measures variance structure into the statistical model to account for potential autocorrelation, but removed it when the effect was estimated to be zero. We used a means comparison to determine which relationships were significant. Comparisons resulting in a p value < 0.05 were considered statistically significant. Sites ($n = 8$) and survey periods ($n = 4$) were pooled, and relative frequencies of stony-coral and octocoral juvenile colonies were calculated to illustrate differences in high-impact versus low-impact site-frequency distributions as well as to highlight the high frequency of quadrats with very few or zero recruits found within them.

We employed a Before-After-Control-Impact analysis framework [45–47] to assess the impact of the 2010 cold-water event on macroalgae (including cyanobacteria) using the CREMP long-term monitoring database from 2007 to 2012. The 2007–2009 samples represented the “before” dates, while 2010–2012 represented “after.” We built a linear mixed model to incorporate period (before vs. after), impact class (high impact vs. low impact), and their interaction, as well as random terms for year, site, and the year-by-site interaction. Model residuals were examined to ensure they met the assumptions of normality and homogeneity of variance. All analyses were performed in SAS v9.4.

To assess the impact of percent cover of macroalgae on juvenile abundance, we used the CREMP long-term monitoring data for each of the sites, and the spring juvenile abundance counts. Spring counts were used because they were done at about the same time of year as the CREMP surveys. We summed juvenile abundance across quadrats to enable us to compare to percent cover data at the transect level. We built generalized linear mixed models assuming a negative binomial distribution, separately for octocoral and stony-coral juvenile abundance. We included site category (high or low impact) as a categorical fixed factor and macroalgal percent cover as a continuous fixed factor.

2.3. Spatial patterns

To test for relationships among sites and to elucidate any regional differences in community assemblages, we used PRIMER v6 (PRIMER-E Ltd., Plymouth, UK) for the following multivariate analyses. We performed a CLUSTER analysis on abundances of stony-coral and octocoral juveniles using a Bray-Curtis resemblance matrix on untransformed data. We applied dispersion weighting to account for differences in variance structure of species counts due to spatial clumping [48]. We conducted a SIMPROF analysis to check for structure in the data and identify where clusters were significant. We then created a nonmetric multidimensional scaling (MDS) plot to visually display the relationships among sites. Nonmetric MDS plots map the sites in two-dimensional space, with proximity between sites representing similarity and a stress level of <0.2 indicating a useful representation of the relationship [49]. We used an analysis of similarity (ANOSIM) test to demonstrate where the dissimilarities were strongest among sites.

To assess relationships between adult and juvenile stony-coral assemblages, we used similar procedures to those outlined above for juvenile abundance. We acquired adult stony-coral densities (colonies/m²) for each of the eight patch reef sites from 2011 and 2012 CREMP demographic survey data. We omitted octocoral data from this analysis since adult octocoral data were not available for all sites. We calculated stony-coral juvenile densities by dividing the total abundance by the study area (4 m²/station). We then performed an MDS analysis on Bray-Curtis similarities of square-root-transformed, dispersion-weighted and averaged data to create a two-dimensional spatial visualization of relationships among adult and juvenile assemblage densities of stony corals. We used the PRIMER v6 RELATE test to compare the adult and juvenile Bray-Curtis similarity matrices. The RELATE test uses the Spearman Rank Correlation Coefficient (Rho), with a Rho of +1 or -1 representing the highest possible correlation and with a p value of <0.05 representing a significant result. SIMPER analysis showed which sites had the greatest overall similarity between adult and juvenile assemblages.

2.4. Species compositions

To determine which species of stony corals and genera of octocorals were most abundant for all quadrats, data were pooled for each site and survey period to calculate overall taxonomic composition (**Table 1**).

Stony coral species	% of total	Octocoral species	% of total
<i>Siderastrea siderea</i>	46.2	<i>Antillologorgia</i> spp.	24.5
<i>Porites astreoides</i>	19.1	<i>Gorgonia ventalina</i>	20.7
<i>Siderastrea radians</i>	6.3	<i>Eunicea</i> spp.	18.9
<i>Agaricia agaricites</i>	4.7	<i>Erythropodium caribaeorum</i>	14.3
<i>Stephanocoenia intercepta</i>	4.6	<i>Muriceopsis</i> spp.	4
<i>Porites porites</i>	4.4	<i>Pseudoplexaura</i> spp.	3
<i>Montastraea cavernosa</i>	3.7	<i>Briareum asbestinum</i>	3
<i>Millepora alcicornis</i>	2.7	<i>Muricea</i> spp.	1.8
<i>Orbicella</i> spp.	2.2	<i>Plexaura</i> spp.	1.5
<i>Dichocoenia stokesii</i>	0.94	<i>Plexaurella</i> spp.	1.3
<i>Scolymia cubensis</i>	0.85	<i>Pterogorgia</i> spp.	0.14
<i>Colpophyllia natans</i>	0.83	Unknown octocoral	6.8
<i>Eusmilia fastigiata</i>	0.74		
<i>Pseudodiploria strigosa</i>	0.41		
<i>Mycetophyllia lamarckiana</i>	0.37		
<i>Oculina diffusa</i>	0.27		
<i>Diploria labyrinthiformis</i>	0.24		
<i>Agaricia fragilis</i>	0.07		
<i>Favia fragum</i>	0.07		
<i>Solenastrea bournoni</i>	0.04		
Unknown stony coral	1.3		

Table 1. Juvenile stony coral and octocoral total percent species composition.

3. Results

3.1. High-impact vs. low-impact reefs

We found a significant interaction between coral type (stony corals vs. octocorals) and impact class (high impact vs. low impact) for juvenile abundance ($F_{1,1982} = 27.1$, $P < 0.001$). Both octocorals and stony corals were present in greater abundance at the low-impact sites (**Figure 3**). The difference in juvenile abundance between high- and low-impact sites was more pronounced for octocorals than that for stony corals. For both stony corals and octocorals, median frequencies for low-impact sites were higher than those for high-impact sites as well (**Figure 4**). The most frequent abundance value recorded within a single quadrat was zero. There were three to four times more quadrats (approximately 1 m²) where

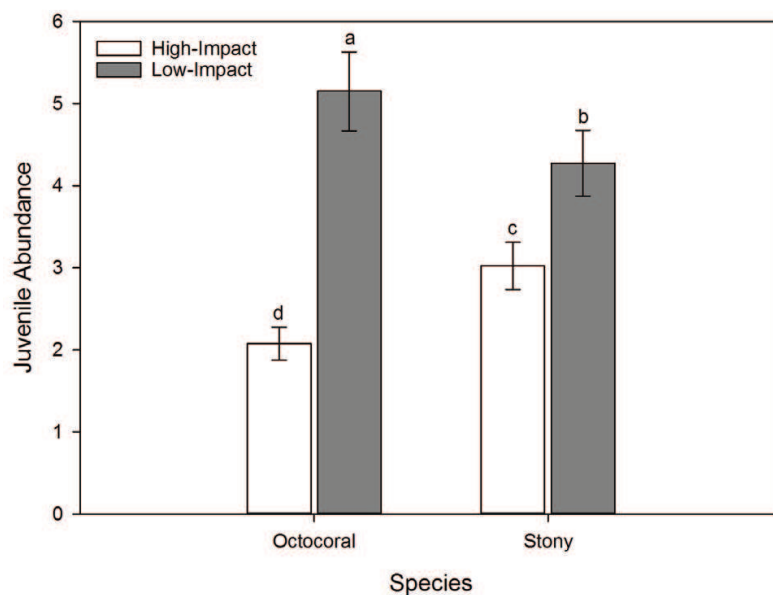


Figure 3. Juvenile coral abundance (least-squares mean \pm SEM) per quadrat (0.25 m²) by coral type (stony coral vs. octocoral). White bars are high-impact sites, and gray bars are low-impact sites. Means sharing any common letters are not significantly different ($P < 0.001$): octocoral and stony coral abundance was significantly lower on high-impact sites.

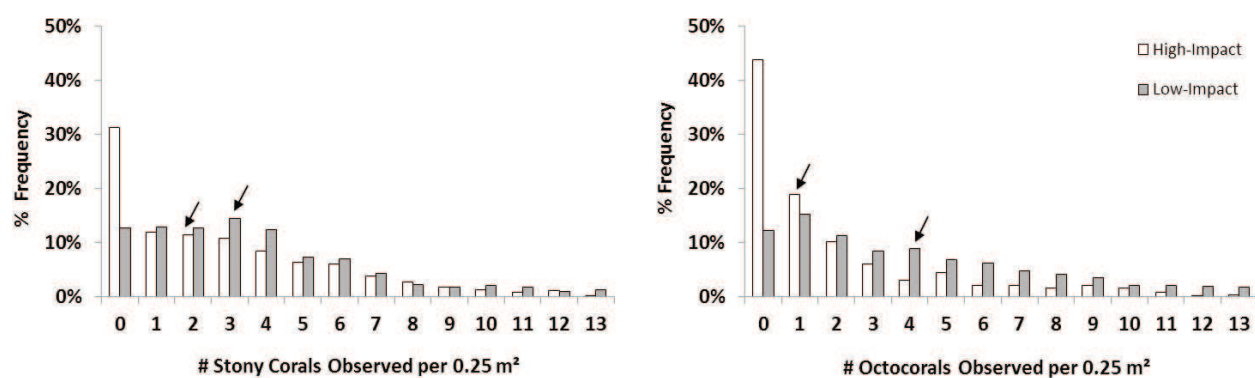


Figure 4. Relative-frequency distributions for stony coral (left) and octocoral (right) abundance by 0.25 m² quadrat (all sites and survey periods pooled). Both distributions are skewed to the right, with highest frequencies occurring at lower abundance values. Abundance data are not normally distributed (Shapiro-Wilk, $p < 0.001$). White bars are high-impact sites, and gray bars are low-impact sites. Arrows indicate median values.

no juveniles were recorded on high-impact sites than on low-impact sites. Otherwise, frequency distributions of stony corals and octocorals were similar for high-impact and low-impact sites.

The BACI analysis revealed macroalgal cover increased following the 2010 cold-water event. There was a clear influence of time period ($F_{1,86} = 15.6$, $P = 0.0002$), indicating that macroalgal cover was more abundant post-disturbance. However, there was no difference between

impact classes ($F_{1.86} = 1.87$, $P = 0.175$), suggesting that this increase was not influenced by a level of coral mortality. The lack of a significant interaction term also indicates that changes in macroalgal cover were influenced more by reef-tract wide processes and high annual variability, which overshadowed any differences that would have been associated with post-event mortality ($F_{1.86} = 1.10$, $P = 0.298$, **Figure 5**). Additionally, we found no effect of macroalgal cover on juvenile coral abundance for either stony corals (**Table 2**) or octocorals (**Table 3**).

3.2. Spatial patterns

The three northernmost sites (Turtle, Porter and Admiral reefs) had different juvenile assemblages than the remaining sites (**Figure 6**, SIMPROF $P < 0.05$). On these three sites, juvenile assemblages were dominated by octocorals, whereas assemblages on the remaining sites were dominated by stony corals. The stony coral *S. siderea* was the most abundant juvenile on all four Middle Keys sites as well as the southernmost Upper Keys site, Burr Patch. Juvenile assemblages on the three northernmost sites (Turtle, Porter and Admiral) were dominated by three different octocoral genera *Antillologorgia*, *Eunicea* and *Gorgonia*, respectively (**Table 4**). Cluster analysis demonstrated that the spatial pattern was based on regional differences rather than site-impact category.

Similarities among post-disturbance adult and juvenile scleractinian assemblages by site were evaluated using CREMP demographic data for 2011 and 2012. Site clustering was very similar to the juvenile MDS plot (RELATE Spearman Rank Correlation $\rho = 0.7$, $p < 0.001$), with all Middle Keys sites and Burr displaying similar adult and juvenile scleractinian assemblages,

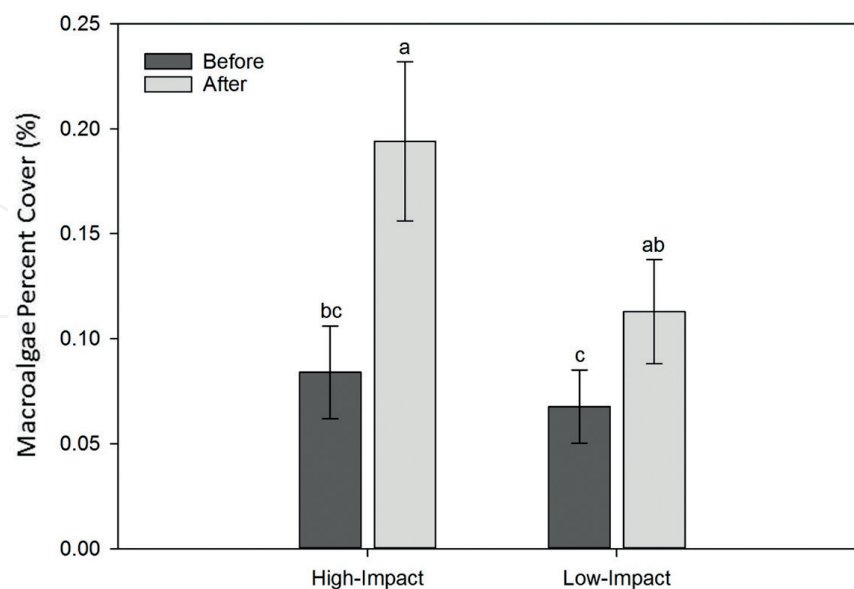


Figure 5. Macroalgae percent cover (least-squares mean \pm 95% CI) by impact class (high vs. low impact) and time period (before and after 2010 bleaching event). Means sharing any common letters are not significantly different ($P > 0.05$).

Effect	Num DF	Den DF	Estimate	Standard error	F value	Pr > F
Site category	1	15	–	–	0.21	0.655
Macroalgae	1	15	–0.880	0.895	97	0.341

Site category (high impact vs. low impact) included as a categorical fixed factor and macroalgal cover as a continuous fixed factor.

Table 2. Model results showing impact of macroalgal cover on stony coral juvenile abundance.

Effect	Num DF	Den DF	Estimate	Standard error	F value	Pr > F
Site category	1	15	–	–	3.29	0.0896
Macroalgae	1	15	0.264	0.996	0.07	0.794

Site category (high impact vs. low impact) included as a categorical fixed factor and macroalgal cover as a continuous fixed factor.

Table 3. Model results showing impact of macroalgal cover on octocoral juvenile abundance.

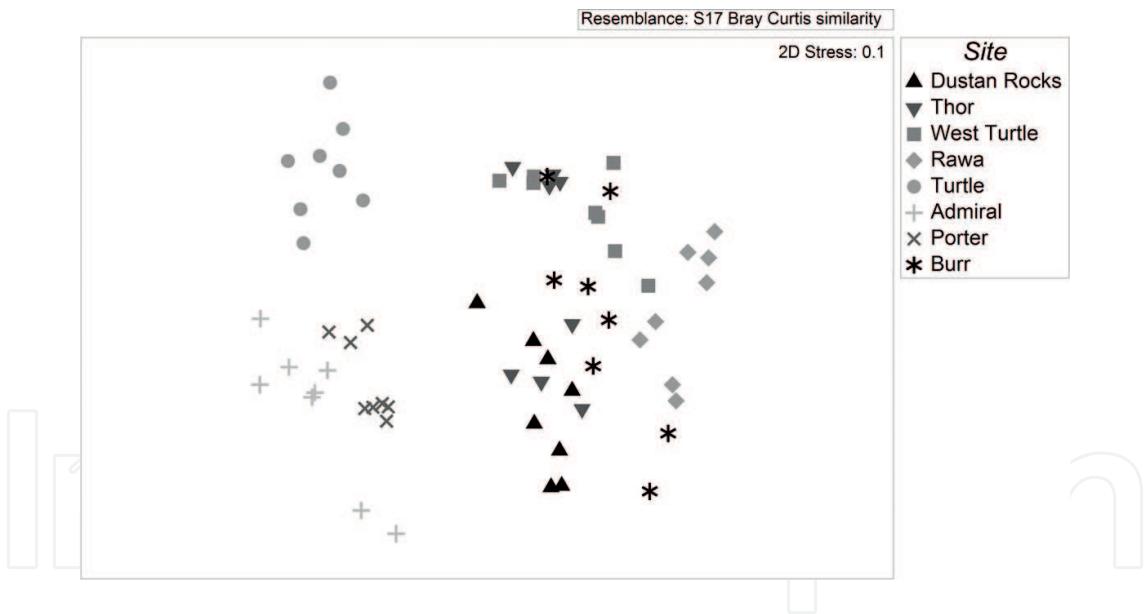


Figure 6. MDS plot of Bray-Curtis similarities of juvenile stony coral and octocoral abundances among sites, survey periods pooled (eight samples per site).

while Porter and Admiral displayed different assemblages (Figure 7). A main difference that resulted from removing octocorals from the analysis was that Turtle grouped with the larger cluster, instead of remaining distinct. This was true for both juveniles and adults, suggesting that the stony-coral assemblage on Turtle reef was actually quite similar to that at the Middle Keys sites. Juvenile and adult assemblages from the same sites tended to be similar. SIMPER analysis showed that within-site similarity between adults and juveniles ranged from 30 to

Site	SSID	PAST	SINT	PPOR	MCAV	AAGA	SRAD	ANTI	GORG	EUNI	ERYT	PSEU	BRIA	MURO
Turtle	6	5	0	1	0	1	0	23	5	5	1	5	2	2
Porter	1	1	0	0	0	1	1	2	2	6	2	1	0	0
<i>Admiral</i>	1	1	0	0	0	0	0	3	12	1	0	0	0	0
<i>Burr</i>	9	3	0	0	0	1	1	1	1	1	1	0	0	2
<i>Rawra</i>	8	2	1	1	2	0	0	0	0	0	0	0	0	0
W. Turtle	11	6	2	2	2	2	1	2	1	2	1	0	0	0
<i>Dustan</i>	6	1	1	0	0	0	1	3	1	2	0	0	0	0
Thor	12	4	3	1	0	0	0	2	1	2	3	0	1	0

Bolded values are the dominant species for that site. Sites are listed from northernmost to southernmost with high-impact sites in italics. Species and genera coding is the first letter of the genus and the first three letters of the species for stony corals (SSID-*Siderastrea siderea*, PAST-*Porites astreoides*, SINT-*Stephanocoenia intersepta*, PPOR-*Porites porites*, MCAV-*Montastraea cavernosa*, AAGA-*Agaricia agaricites*, SRAD-*Siderastrea radians*) and the first four letters of the genus for octocorals (ANTI-*Antilloorgia*, GORG-*Gorgonia*, EUNI-*Eunicea*, ERYT-*Erythropodium*, PSEU-*Pseudoplexaura*, BRIA-*Briareum*, MURO-*Muriceopsis*).

Table 4. Median densities (colonies per m², per site) for top seven juvenile stony coral species (left side) and top seven juvenile octocoral genera (right side).

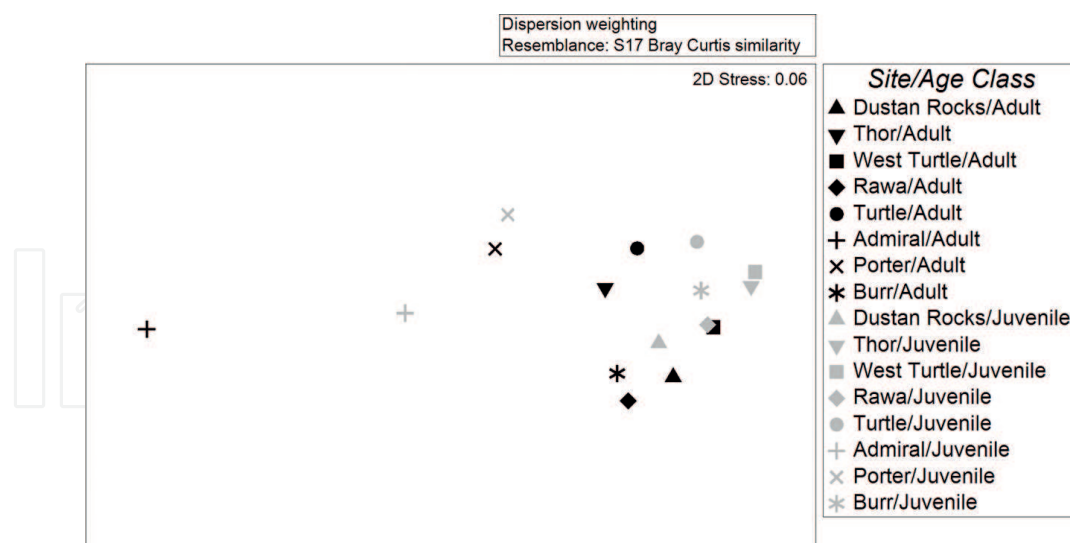


Figure 7. MDS plot of stony-coral adult and juvenile species densities among sites with survey periods pooled (juveniles—eight samples per site, adults—four samples per site). Data were dispersion-weighted, square-root-transformed and averaged.

72%. West Turtle and Porter reefs showed the greatest similarity between adult and juvenile assemblages, while Admiral showed the least similarity (**Table 5**).

3.3. Species compositions

The most abundant stony-coral species were *Siderastrea siderea* (46.2%), *Porites astreoides* (19.1%), *Siderastrea radians* (6.3%), *Agaricia agaricites* (4.7%), *Stephanocoenia intersepta* (4.6%), *Porites porites* (4.4%) and *Montastraea cavernosa* (3.7%) (**Table 1**). *Siderastrea siderea* made up nearly half of all stony corals observed, and *P. astreoides* made up almost one-fifth. Combined, these two species comprised over 65% of the stony-coral juvenile assemblage, in the study. Ten percent of the stony-coral assemblage was made up of other species, each accounting for

Site	%Similarity
W. Turtle	72
Porter	67
Turtle	67
Dustan	66
Burr	61
Rawa	60
Thor	55
Admiral	30

Table 5. Percent similarity between adult and juvenile stony-coral densities on each site (SIMPER test in PRIMER v6).

<1% of the total, with the exception of fire coral, *Millepora alcicornis*, which made up 2.7%, and *Orbicella* spp., which made up 2.1% (**Table 1**).

The most abundant octocoral genera were *Antillologorgia* (formerly *Pseudopterogorgia*, 24.5%), *Gorgonia* (20.7%), *Eunicea* (19.0%), *Erythropodium* (14.3%), *Muriceopsis* (4.0%), *Pseudoplexaura* (3.0%) and *Briareum* (3.0%) (**Table 1**). The four top octocoral genera (*Antillologorgia*, *Gorgonia*, *Eunicea* and *Erythropodium*) made up almost 80% of all octocorals seen, but unlike the stony corals, percent composition was more evenly distributed among these four genera. The unknown octocoral category included 6.8% of all juvenile octocoral observations and was included in analyses comparing total stony-coral abundance to total octocoral abundance, but was not included in species and genera analyses.

4. Discussion

With increasing frequency and intensity of perturbations impacting coral reefs around the world, an understanding of recovery processes is crucial. While coral-reef response to disturbances involving warm-water bleaching events, hurricanes and nutrient stress is well documented [4, 50, 51], comparatively less is known of recovery from cold-stress events [29, 30]. This study examined juvenile assemblages following the cold-water mass-mortality event in 2010, which resulted in one of the greatest losses of reef-building corals in the Florida Keys in modern time [28, 36, 38]. We found fewer stony coral and octocoral juveniles on the high-impact sites (**Figures 3 and 4**), suggesting that recruitment to severely degraded reefs was impaired. Unlike in many documented cases of abated coral recovery, here, macroalgae was not implicated for impairing coral recovery as we found no significant difference in macroalgal cover between high- and low-impact sites following the event (**Figure 5**). In addition, we observed a regional trend in which juvenile stony corals were more abundant on the Middle Keys reefs, while juvenile octocorals were more abundant on the northernmost Upper Keys reefs (**Figure 6, Table 4**). Moulding [43] found similar results in 2004, with higher stony-coral recruit density in the Middle Keys than in the Upper Keys. During our study, only *Siderastrea siderea* and *Porites astreoides* accounted individually for >10% of the juveniles recorded and together totaled 65%. Of the juvenile octocorals identified, four genera accounted for >10% individually and together totaled 78% of those recorded (**Table 1**). Results suggest that recovery will be slower in areas where disturbance impacts were greatest and that post-mortality species composition will be influenced by regional differences in settlement and survival, as well as by differences in species life-history characteristics.

4.1. High-impact vs. low-impact reefs

The level of mortality on a reef negatively correlated with recruitment. Partial and complete colony mortality on high-impact sites [28] appeared to have dampened recruitment and/or juvenile survival. Higher abundance and cover of living coral are important drivers of coral recruitment [52–54]. However, percent cover on high-impact sites was comparable to cover on low-impact sites following the cold-water event. This suggests that the magnitude of mortality and post-event conditions on a reef had more influence on recruitment than total

percent cover. Thus, regardless of the similarities in coral cover following the disturbance, severe mortality on high-impact sites placed these reefs at a clear reproductive disadvantage for recruitment of both octocorals and stony corals.

Massive scleractinian species often found on reefs of the Florida reef tract, such as *Orbicella* (formerly *Montastraea*) spp., *Diploria* spp., *Colpophyllia natans* and *Siderastrea siderea*, reproduce via broadcast spawning, releasing gametes only once a year in synchrony with the late summer lunar cycle [55]. The success of sexual reproduction via spawning is a function of reef connectivity and is highly dependent on physical characteristics of the water column, including tides and currents [56]. Nonmassive coral species, such as *Porites* spp., *Agaricia* spp. and *Siderastrea radians*, are internal brooders, reproducing many times a year [43, 55]. Brooded planulae are larger and more developed upon release into the water column, settle sooner and presumably, closer to the parent colonies than larvae produced by broadcast spawning corals, which require the fertilization of gametes in the water column after release [57]. The reduced size of the overall coral population in addition to the suboptimal condition of surviving adult corals at the high-impact reefs would have likely lowered successful reproduction, while low-impact sites may have benefited from the local supply of brooded planulae from the relatively healthy colonies still present on those reefs. In addition, coral larvae may actively select suitable substratum for settlement via chemical signals produced by adult colonies and associated flora such as crustose coralline algae (CCA) [58–60], and this process may have been disturbed on high-impact sites. It is unclear which stage of the reproduction cycle was influenced most by the mortality event; however, our results show that stony-coral percent cover alone did not explain the observed differences in juvenile abundances.

While macroalgal cover increased on high-impact sites in the years following the cold-water anomaly, there was no difference in macroalgal cover between high- and low-impact sites, suggesting that this increase reflected the natural variability in macroalgal cover along the Florida reef tract [13] and that the production of macroalgae is independent of coral-mortality event-driven processes [61, 62]. Additionally, we found no effect of macroalgal cover on juvenile coral abundance for either stony corals or octocorals. Our ability to discern differences in macroalgal cover between high- and low-impacts sites was likely limited by low replication (e.g., only two CREMP transects per site were used to match pooled quadrat data) and high annual variability in cover (e.g., high inter-site variability). Macroalgae can interfere with coral recruitment through either competition for space or more direct methods involving allelopathy [63, 64]. Macroalgae colonize a reef quickly following disturbance, taking advantage of the vacant space [17–19]. However, here the increase in macroalgal cover on high-impact sites did not differ significantly from cover on low-impact sites and did not influence juvenile assemblages; thus, it seems factors other than macroalgal or stony-coral cover drove recruitment in this study. Potential factors include the magnitude of the loss of live coral cover, the post-event condition of the surviving reef community, and the regional location of a particular reef, all of which could influence larval supply, settlement rates and post-settlement survival.

4.2. Spatial trends

A strong regional trend was observed, in which juvenile stony corals dominated the Middle Keys sites and Burr Patch (the southernmost site in the Upper Keys), whereas juvenile octocorals dominated the three northernmost sites, Turtle, Admiral and Porter. While this trend was unanticipated, there are certain environmental factors that differ between the Middle and

Upper Keys regions that could have influenced this pattern. Middle Keys patch reefs lie close to tidal connections with Florida Bay and so experience greater turbidity, greater fluctuations in temperature and salinity, and higher inputs of terrigenous materials [65–67]. Connections to Florida Bay become less frequent toward the Upper Keys. Burr Patch is the southwesternmost Upper Keys site in this study and is the closest of all Upper Keys sites to tidal connections. Its location and proximity to the northernmost connection to Florida Bay may explain its similarity in juvenile assemblage to the Middle Keys sites. It is still unclear, however, how such a hydrodynamic difference between regions would facilitate such a pattern. We were unable to compare adult to juvenile octocoral assemblages, due to lack of adult demographic data, but such a comparison may help to explain the observed spatial patterns in the data.

The regional pattern we observed in the site clustering is a strong indication that post-disturbance juvenile abundance was influenced by regional differences in hydrodynamics. Site-specific differences in structural complexity, topography and reef structure also may have influenced these results. While each of the eight study sites are designated as patch reefs, such reefs are inherently diverse, with different depths, structural complexities and species compositions such that site-level differences undoubtedly influenced results. In fact, species compositions of adult assemblages did prove similar to juvenile species compositions at certain sites (**Figure 7, Table 4**), including West Turtle, Porter and Turtle (72, 67 and 67% similarity among adult and juvenile assemblages, respectively). In 2010, Kuffner et al. [68] found a strong influence of “reef effect” on variance of the biological community structure in Biscayne National Park and suggested prior residents on a reef, or “priority” effects were important in determining future benthic-community structure. It seems likely similar effects may be at play here.

Additionally, the location of the Florida reef tract near the northern latitudinal limit for coral-reef accretion may help explain the reduction in stony-coral juveniles and the proliferation of octocoral juveniles on the northernmost study sites. Results corroborate regional trends observed on the Florida reef tract [43, 69], where the density of juvenile stony corals increased in a southwesterly direction down the reef tract. This is an important finding, and further investigation is needed to elucidate the causes behind this pattern.

4.3. Species composition

Species-abundance data suggest that specific life-history traits play a major role in which species recruit to and survive on patch reefs. Known ecological traits of *Siderastrea siderea* and *P. astreoides* likely influenced successful recruitment and survival. *Siderastrea siderea* can tolerate a wide range of temperature and environmental fluctuations [28, 36, 37] but it is slow-growing, can reach massive sizes and reproduces typically once a year via broadcast spawning [55, 70]. In this study, the high tolerance of environmental fluctuations clearly outweighs the slow growth and reproductive mode of *S. siderea*, making it the most abundant stony-coral juvenile observed on study patch reefs. *Porites astreoides* is a smaller, weedy, brooding species that can reproduce prolifically, multiple times a year, and reaches maturity sooner but that is less tolerant of temperature fluctuations [41, 71–73]. Even though *P. astreoides* was nearly extirpated at some of the high-impact sites [28] during the cold-water event, the species can quickly recover after disturbances [74]. Our results are consistent with those of van Woesik et al. [75] which indicated that *S. siderea* and *P. astreoides* have also had high recruitment rates on outer bank reefs in the Florida Keys. In this study, each species demonstrated a different, yet successful, method of recruitment to patch reefs.

The overall juvenile assemblage was essentially devoid of *Orbicella* spp. (<3% of the juvenile stony-coral species composition). *Orbicella* spp. are very sensitive to temperature fluctuations [70, 76, 77]. The few small *Orbicella* colonies found were most likely surviving tissue remnants of older, larger colonies that had undergone near-complete mortality. In recent years, recruitment by *Orbicella* spp. on the Florida reef tract has been poor [43, 69, 75]. *Orbicella* spp. reproduce only once per year in synchrony with the late summer lunar cycle via broadcast spawning [55]. Their breeding method and life history characteristics do not support high recruitment rates, but rather high survival rates of settled juveniles [43, 55]. This reproduction method is apparently not the best for present conditions along Florida reef tract.

Octocorals were an important part of the coral juvenile assemblage on all of our patch reef sites. Relative to stony corals, less is known about reproduction in octocorals. Many gorgonians are thought to be gonochoric brooders [78]. Brooding can occur internally, as occurs with stony corals, or externally, on the surface of the female colony as occurs with the species *Briareum asbestinum* [79]. Others are broadcast spawners, releasing both sperm and egg into the water column for fertilization as occurs with *Gorgonia ventalina* [80, 81]. As with stony corals, octocorals spawn in synchrony with the lunar cycle, usually following a full moon, though not necessarily synchronous across species [80].

Relative to stony corals, octocorals are weedy, fast-growing, opportunistic organisms that can quickly colonize newly available substrate, outcompeting stony corals for suitable settlement space [24, 80]. The flexible-branching morphology of octocorals facilitates asexual reproduction through a number of methods, giving octocorals a unique advantage following disturbance events. The ability for vegetative growth allows octocorals to aggregate in high densities and to colonize space quickly [82, 83]. This can provide an advantage following a disturbance event, allowing them to outcompete more slowly reproducing organisms, such as spawning stony corals, for the newly available space. Octocoral extension rates are also orders of magnitude higher than those of stony corals [22–25].

The most abundant octocoral genus that we recorded was *Antillogorgia* (25%), which includes several species, many of which have fast growth rates [23] and often colonize quickly following disturbances. Octocorals were most abundant on Admiral, Porter and Turtle, the northernmost sites in the study. Overall, octocorals exhibited a wider range of successfully recruiting genera than did stony corals, which may promote higher species diversity in future assemblages. The successful recruitment of octocorals may further promote the ongoing shift in community structure to an octocoral-dominated state, which has been observed in adult assemblages throughout the Florida Keys [13]. More research is needed on the changing role of octocorals in reef ecosystems of the Florida reef tract.

5. Conclusions

Our results support previous findings that Florida stony-coral populations struggle to recover after major perturbations. Patch reefs were considered one of the last refuges for corals on the Florida reef tract that could potentially serve as a larval source for repopulating the highly depauperate outer bank reefs [32]. The 2010 cold-water event decimated many major framework-building corals that had previously shown resistance to a variety of acute and chronic

stressors impacting Florida Keys reefs. Short-term recovery thus far has been defined by recruitment and survival of opportunistic and hardy stony-coral species and octocorals. If early results persist, composition of the scleractinian assemblages on these patch reefs will be homogenized by the few coral species that are successfully recruiting in the Florida Keys, or, as documented elsewhere in Florida and the Caribbean, modern reefs will be dominated by associated coral-reef fauna (e.g., octocorals) interspersed with the few corals that are resilient to disturbances. A better understanding of local hydrodynamics, reproductive timing and dispersal mechanisms of both octocorals and stony corals is needed to provide insight into potential drivers of the spatial patterns observed in this study as well as the changing ecological role of octocorals on the Florida reef tract.

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