Coral Reefs
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RESEARCH

Interspecific variation in demographics reveals ecological winners and losers in a highly disturbed coral reef system

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Abstract The resilience of many coral reef communities has been diminished in the Anthropocene. Nowhere is this more evident than in southeast Florida, where coral cover rarely recovers following increasingly frequent disturbances and has resulted in community change to resilient taxa such as octocorals. Understanding community dynamics and the demographic mechanisms of populations that underpin them, may provide insight into the barriers to coral recovery and the future for benthic community structure. We leveraged 20 years of data to test for spatiotemporal variation in benthic community structure and region-wide demographic changes in four stony coral and three octocoral species. From 2003 to 2023, multiple acute disturbances induced significant reconfigurations of benthic community structure, most notably repeated coral loss and macroalgal gains. Interspecific differences in demography suggest variability in resilience, which facilitates the presence of ecological winners and losers. *Siderastrea siderea* (stony coral) and *Antillogorgia americana* (octocoral) exhibited high resilience, fueled by booms in recruit density. However, *S. siderea* size frequency distributions (SFDs) were heavily skewed with few large colonies, suggesting limited growth and survival. *Porites astreoides* (stony coral) and *Gorgonia ventalina* (octocoral) populations grew steadily from 2013 to 2023, facilitated by consistent recruitment and growth, which was reflected in lognormal SFDs, indicative of transition between size classes. The reef-building stony corals *Meandrina meandrites* and *Montastraea cavernosa* emerged as ecological losers due to substantial mortality from heat stress and disease and limited recovery. Due to the restricted size (*S. siderea* and *P. astreoides*) or planar morphologies (*A. americana*, *Eunicea flexuosa* (octocoral), *G. ventalina*) of the winners, they contribute little to benthic cover. As a result, benthic community structure is becoming increasingly homogenous, with much of the remaining spatial variation dependent upon whether a site has more sediment/turf algae or macroalgae/cyanobacteria, which combined constitute over 80% of the benthic cover and further reduce stony coral recovery potential.

Keywords Scleractinian corals · Octocorals · Size structure · Recruitment · Community dynamics · Southeast Florida coral reef ecosystem conservation area

Introduction

Anthropogenic and natural disturbances are increasingly exerting pressures on coral reef ecosystems worldwide, resulting in widespread coral mortality, impaired growth, and reduced fecundity (Bellwood et al. 2004; Bauman et al. 2013; Vercelloni et al. 2020; Emslie et al. 2024). Under low to moderate levels of disturbance, coral reefs can be expected to recover (Wilkinson et al. 1999; Graham et al. 2015), but on reefs that experience frequent or prolonged disturbances, the cumulative impact of coral loss may diminish recovery capacity and promote changes in community composition (Connell et al. 1997; Bellwood et al. 2004; de Bakker et al. 2017). Many reefs have undergone dramatic benthic community changes, classically involving the replacement

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of Scleractinian corals with non-reef-building biota, especially macroalgae, turf algae, and octocorals (McManus and Polsenberg 2004; Ruzicka et al. 2013; Reverter et al. 2021; Tebbett et al. 2023), leading to reduced ecological functionality and provisioning of ecosystem services (Bellwood et al. 2004; Alvarez-Filip et al. 2009; Mudge and Bruno 2023). However, the fate of disturbed communities is complex and the extent to which community reorganization occurs is contingent upon species-specific responses to disturbance and demographic performance (Gouezo et al. 2019; Pratchett et al. 2020; Sommer et al. 2024). Given that the magnitude and frequency of disturbances is predicted to increase under current climate change scenarios (Hughes et al. 2017; Setter et al. 2023; Emslie et al. 2024), there is an urgent need to elucidate the factors that influence coral reef community change and recovery in order to project ecosystem trajectories and implement effective conservation action.

Long-term monitoring, especially that collects demographic information, has emerged as a critical tool for illuminating the underlying ecological processes shaping community structure (Edmunds and Riegl 2020; Pisapia et al. 2020; Edmunds 2024a; Sommer et al. 2024). The recovery, and thus persistence, of stony coral assemblages following disturbance relies in part on several key demographic processes including recruitment of new individuals and the growth or propagation of surviving colonies (Pratchett et al. 2015; Gouezo et al. 2019). However, these processes may be highly variable across spatiotemporal scales due to heterogeneity of biotic and abiotic environmental conditions (e.g., sedimentation, substrate availability, temperature, competition) (Edmunds 2022), but also across taxa owing to differences in life-history traits (e.g., reproductive mode, fecundity, growth rate, size-specific mortality) and susceptibility to disturbance (Meesters et al. 2001; Kuffner et al. 2006; Graham et al. 2011; Lachs et al. 2021; Schlesinger and Loya 2021; Harper et al. 2023). For example, broadcast spawning coral species, such as siderastrids, exhibit stochastic recruitment patterns that are minimally impacted by heat stress, whereas brooding coral species, such as poritids, display lower and more consistent recruitment that is negatively associated with high temperatures (Harper et al. 2023). Further, coral reefs are dynamic systems facing at least one acute disturbance approximately every two to seven years (Connell et al. 1997; Hughes et al. 2018; Vercelloni et al. 2020; Jones et al. 2022): decadal monitoring captures impacts across disturbance events, which is essential for understanding the trajectories of long-lived species such as corals that will likely encounter multiple disturbances within their lifespan (Montefalcone et al. 2020; Pisapia et al. 2020; Emslie et al. 2024). Thus, long-term monitoring datasets can provide a comprehensive view of community and population dynamics across multiple disturbances and on ecologically relevant time scales, potentially revealing valuable insights into the mechanisms contributing to community change and vulnerabilities to future population viability.

Here, we utilize more than two decades of long-term monitoring data collected within the Kristin Jacobs Coral Reef Ecosystem Conservation Area (Coral ECA) in Southeast Florida, a marginal (27.1° N to 25.6° N), highly urbanized subtropical reef system located near the northern terminus of hermatypic coral distribution in the Western Atlantic Ocean (Toth et al. 2021). Several acute disturbances, particularly repeated heat stress events in 2014 and 2015, an outbreak of stony coral tissue loss disease (SCTLD; prevalent from 2014 to 2017), and hurricanes in 2005, 2017 and 2022, have impacted the region and led to substantial declines in coral cover and density (Hayes et al. 2022; Jones et al. 2022). This, coupled with chronic local pressures, particularly high nutrient load and sedimentation from multiple sources including riverine input, port development, coastal construction and reclamation activities (Lapointe and Clark 1992; Miller et al. 2016; Whitall et al. 2019), has resulted in limited coral recovery and contributed to the proliferation of macroalgae and octocorals (Jones et al. 2022; Duran et al. 2024; Jones and Gilliam 2024a). In this study, we aimed to understand (1) how benthic community structure has changed in relation to these major acute disturbances, specifically testing for temporal and spatial variability in community structure, and (2) how demographic mechanisms (recruitment, survival, and size structure) influence region-wide stony coral and octocoral assemblages. We analyze demographics of four stony coral species and three octocoral species in the context of their response to disturbance pressure, then discuss the implications of our findings for the future of stony coral and octocoral assemblages in Southeast Florida and, potentially, the larger Caribbean basin.

Methods

Benthic community long-term monitoring and demographic data collection

Benthic community data have been collected annually in the Coral ECA since 2003 at repeatedly monitored sites as part of the Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP). This study utilizes data from 18 SECREMP sites. From 2003 to 2009, eight sites were monitored, in 2010 four additional sites were added, and in 2013 six further sites added, such that from 2013 to 2023, 18 sites were monitored. At each site, four 22 m long permanently fixed belt transects are monitored following methods detailed in Hayes et al. (2023). Briefly, benthic community structure was quantified using photographic data collected along each transect where ~ 60 abutting images, each 40 cm wide, were taken at a fixed distance from the substrate, covering ~ 8.8 m^2 of hardbottom per transect. Images were analyzed using PointCount'99 to determine percent substrate coverage (Dustan et al. 1999); for each image, benthic taxa were identified at 15 randomly placed points, for a total of 900–1000 points per transect. Benthic taxa were categorized as stony corals (Scleractinians and milleporids), octocorals, sponges, macroalgae (grouped with cyanobacteria), zoanthids, turf algae/substrate, or other taxa (e.g., hydroids, anemones, etc.). Broad taxonomic groups were used following previous analyses for the region (e.g., Ruzicka et al. 2013; Jones et al. 2022).

Stony coral demographic data was quantified along each 22 m × 1 m belt transect. From 2013 to 2017, all stony coral colonies ≥ 4 cm diameter were identified to species and the colony diameter and height were measured. From 2018 onward, all colonies ≥ 2 cm were identified to species and measured, and every visible colony < 2 cm, considered recruits as detailed in Jones and Gilliam (2024a), was identified to species and abundance tallied per transect. Stony colony boundaries were carefully followed to avoid including isolates of larger colonies or colonies with live tissue < 2 cm diameter due to shrinkage from partial mortality. Colonies greater than 2 cm and less than 4 cm were considered juveniles (Stein and Ruzicka 2021; Hayes et al. 2022; Jones and Gilliam 2024a). On the first 10 m of each belt transect, octocoral demographic data were collected for three locally abundant species, *Antillogorgia americana*, *Eunicea flexuosa,* and *Gorgonia ventalina*, where each colony was identified to species and the height measured. Target octocorals were later divided by height into recruits and adults using growth estimates from Borgstein et al. (2020), with recruits below the size estimated to < 1 year old (similarly to stony coral recruits). *Antillogorgia americana* recruits were considered to be ≤ 6 cm; *E. flexuosa* recruits, ≤ 4 cm; *G. ventalina* recruits, ≤ 5 cm.

Study species

Four common stony coral species (termed target stony coral species)—*Meandrina meandrites*, *Montastraea cavernosa*, *Porites astreoides,* and *Siderastrea siderea*—were chosen for detailed demographic study here due to differing resistance to disturbance, primarily SCTLD (NOAA 2018), and life-history strategies, and because they have been previously studied in the Coral ECA (e.g., Jones et al. 2023; Jones and Gilliam 2024b). *Meandrina meandrites* is a submassive, gonochoric broadcast spawning species that is highly susceptible to SCTLD. *Montastraea cavernosa* is a massive, hermaphroditic broadcast spawning species with intermediate susceptibility to SCTLD and is the primary contemporary reef builder in the Coral ECA. *Porites astreoides* is a competitive, weedy, brooding species, with high clonality in the Coral ECA (Shilling et al. 2023) and low susceptibility to SCTLD. *Siderastrea siderea* is a massive, gonochoric broadcast spawning species with intermediate susceptibility to SCTLD that has demonstrated boom-or-bust patterns of recruitment in the Coral ECA (Harper et al. 2023).

Three common arborescent octocoral species (termed target octocoral species)—*Antillogorgia americana*, *Eunicea flexuosa,* and *Gorgonia ventalina*—were chosen for detailed demographic study due to morphological differences (sea plume, sea rod, sea fan), confidence in field identification, and comparability with similar studies elsewhere (e.g., Cant et al. 2024). *Antillogorgia americana* is a plumose, pinnate octocoral, which can reach ~ 150 cm height. *Eunicea flexuosa* is a bushy/candelabrum-shaped sea rod that can reach ~ 100 cm height. *Gorgonia ventalina* is a sea fan that can reach ~ 100 cm height.

Statistical analysis

Multivariate statistical analysis of spatiotemporal variation in benthic community structure was conducted in Primer 7 (Clarke and Gorley 2006). Benthic community structure was quantified per transect per year, and Bray–Curtis similarity coefficients were calculated on square root transformed data. Data were square root transformed to reduce the importance of the most abundant taxa (turf algae/sediment) and to allow rarer taxa to influence the similarity calculation. Spatial and temporal variation in benthic community structure were analyzed using a two-way Permutational Analysis of Variance (PERMANOVA, Anderson 2001; McArdle and Anderson 2001) with year and site as fixed factors. A type 3 PERMANOVA, based on 9999 permutations of residuals under a reduced model, was used with transects as replicates ($n = 1088$). Post hoc pairwise analysis was used to assess temporal changes across periods with major acute disturbances (e.g., 2013 to 2018) and inter-disturbance periods (e.g., 2006 to 2013). Temporal variation in dispersion (i.e., spatial variation) was analyzed using PERMDISP, which assesses the homogeneity of within-group multivariate dispersion. Non-metric multidimensional scaling plots were created in RStudio (R Core Team 2023) to visualize spatiotemporal variation in benthic community structure and dispersion. Convex hulls of the target years, 2003, 2006, 2013, 2018 and 2022, were created and overlaid.

Univariate analyses of temporal variation in stony coral and octocoral recruit and adult abundance from 2013 to 2023 were conducted in RStudio. For each species, generalized linear mixed models (GLMMs) were created using the package glmmTMB (Brooks et al. 2017; Table S1). Abundance per transect was fitted as the response for stony coral and octocoral adult species. Abundance was summed by site for stony coral and octocoral recruits due to low abundance on some transects. Year was fitted as a categorical fixed factor and transect nested within site or site as a random intercept to account for hierarchical structure of the data. Each model was fitted with three possible distributions, Poisson (log link), Negative Binomial 1 (log link) or Negative Binomial 2, and the best fitting model was selected using the Akaike Information Criterion (AIC). Model validation was performed using the package DHARMa with residual diagnostics, including overdispersion and heterogeneity, conducted on the fitted model (Hartig 2022). Model validation indicated no problems. Post hoc pairwise assessment was conducted using the package emmeans and the Tukey method, where differences in the response variable were analyzed between levels of the fitted factor based on model predictions (Lenth 2019). Emmeans linear contrasts were used to assess significant variation in levels of a fixed effect against the mean value. Between-year differences in post hoc analyses were considered significant at $p < 0.05$.

Size frequency distributions of the log10-transformed maximum colony diameters and heights were constructed for all target stony coral and octocoral species. The mean colony diameter and height (mean of the colony diameter or height of each colony per transect), log10-transformed coefficient of variation (coefficient of variation (CV) = log10(standard deviation)/log10(mean)), log10-transformed skewness, and log10-transformed kurtosis were calculated per site per year. GLMMs were created for each response metric using glmmTMB and analyzed in relation to the species and year. Species and year were both fitted as categorical fixed factors, while site was fitted as a random intercept. Stony corals and octocorals were analyzed independently. Mean colony diameter and height and kurtosis were fitted with Gamma (log link) distributions. Coefficient of variation (CV) and skewness were fitted with Gaussian (identity link) distributions. Model selection was conducted on all possible combinations (year x species, year + species, year, species and the null model) and the minimum adequate model was selected using the AIC. Model validation was conducted in the same way as the previously described analyses. Model validation indicated heteroscedasticity in all stony coral metrics and octocoral mean colony height, CV, and kurtosis, and a dispersion parameter was added to the fitted model to account for interspecific variation. Despite this, the stony coral diameter fitted model still indicated heterogeneity and each species was modeled independently. Temporal autocorrelation was detected in the fitted models of stony coral CV and kurtosis and octocoral mean colony height, and a first-order autocorrelation structure was fitted. Post hoc pairwise assessment of retained factors in the fitted model were conducted in the same way as the previously described univariate analyses.

Results

Benthic community structure

Benthic community structure varied significantly between sites (PERMANOVA, Pseudo-$f = 93.6$, $p = 0.0001$) and significantly changed temporally (PERMANOVA, Pseudo-$f = 30.1$, $p = 0.0001$) and spatiotemporally (PERMANOVA, Pseudo-$f = 2.5$, $p = 0.0001$; Table S2). Spatial variability in benthic community structure also exhibited significant temporal change (PERMDISP, $f = 4.5$, $p = 0.0001$). Following every major acute disturbance period, the benthic community structure changed significantly (Fig. 1), but dispersion did not always. Between 2003 and 2006, there were relative declines in octocoral, stony coral, zoanthid, and turf algal/sediment cover and increases in macroalgal/cyanobacterial cover following thermal stress and hurricanes in 2005 (PERMANOVA, $t = 3.3$, $p = 0.0002$). Dispersion did not change (PERMDISP, $t = 0.3$, $p = 0.8$). During the following inter-disturbance period from 2006 to 2013, both the centroid position and dispersion changed, although this was largely due to the addition of sites, where some had increased turf algal cover and some macroalgae and zoanthid cover (PERMANOVA, $t = 2.1$, $p = 0.02$; PERMDISP, $t = 2.5$, $p = 0.02$). Following repeated thermal stress events in 2014 and 2015, the SCTLD outbreak that began in 2014, and Hurricane Irma in 2017, benthic community structure significantly changed again (PERMANOVA, $t = 4.2$, $p = 0.0001$), with relative declines in stony coral, zoanthid, sponge, and octocoral cover. Spatial variability in benthic community structure did not change significantly (PERMDISP, $t = 1.3$, $p = 0.2$), but while in 2013 some sites had higher stony coral, sponge, or octocoral cover, in 2018 spatial variability was largely related to whether a site had more turf algae or macroalgae (Figure S1). Finally, from 2018 to 2022, the benthic community structure changed and spatial variability declined significantly (PERMANOVA, $t = 3.4$, $p = 0.0001$; PERMDISP, $t = 3.6$, $p = 0.0003$), with a relative increase in macroalgal/cyanobacterial cover and greater similarity in benthic community structure between sites.

Recruit and adult density

Two distinct patterns of temporal change in stony coral density were evident (Fig. 2). Adult *Siderastrea siderea* and *Porites astreoides* density doubled and increased 70%, respectively, from 2013 to 2023. Conversely, there was substantial *Montastraea cavernosa* and *Meandrina meandrites* mortality from 2015 to 2016, primarily from SCTLD, but also heat stress, such that adult density declined 45% and 94% respectively, with slow/no subsequent recovery.

After a 22% decline in *S. siderea* adult density from 2013 to 2016 (Tukey pairwise, $z = 3.6$, $p = 0.01$), following

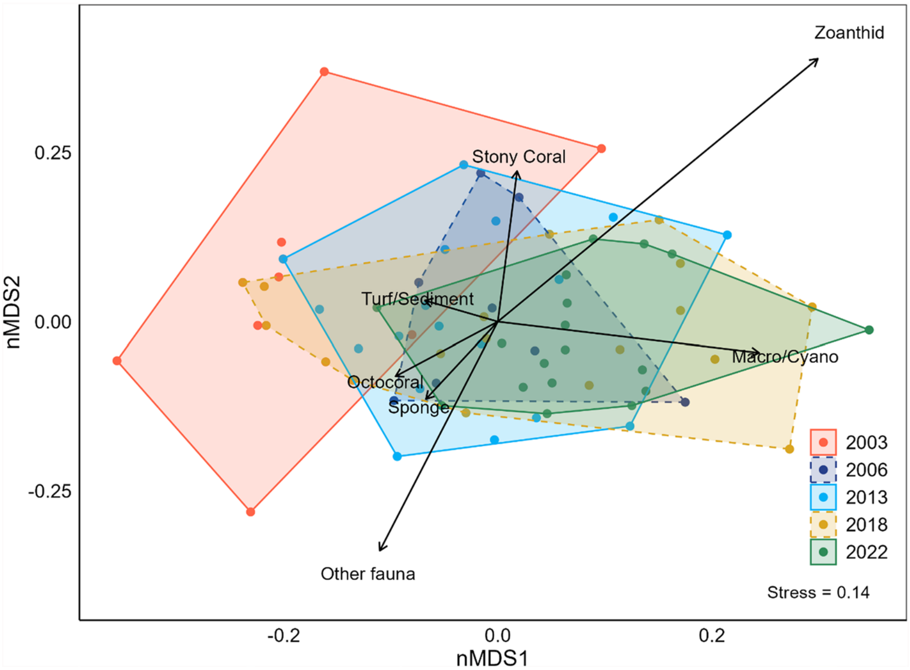

Fig. 1 Non-metric multidimensional scaling (nMDS) plot depicting spatiotemporal variation in benthic community structure. Each point represents each site per year. Similarity is based upon Bray–Curtis similarity matrix after square root transformation. Convex hull is the minimum distance surrounding all sites in a year. Solid outlines indicate years prior to a major disturbance/at the end of the inter-disturbance period. Dashed outlines indicate years following major acute disturbances. Vectors represent benthic taxa

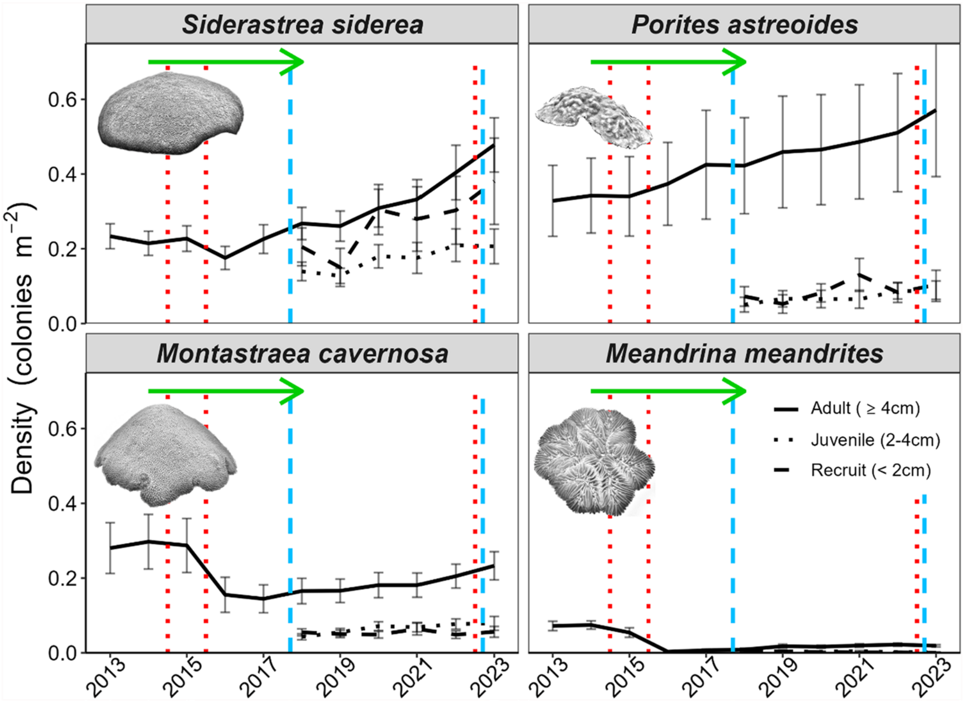

Fig. 2 Temporal changes in target stony coral species recruit (*dashed line*), juvenile (*dotted line*) and adult (*solid line*) density. *Vertical lines* denote major acute disturbances, where *red dotted line* = bleaching event, *blue dashed line* = hurricane. *Green arrow* shows temporal duration of stony coral tissue loss disease (SCTLD), which was prevalent from 2014 through 2017 and has been endemic since

back-to-back heat stress events, density recovered quickly and continued to increase, such that adult *S. siderea* density (mean ± SE unless stated) was twice as high in 2023 (0.48 colonies $m^{-2} \pm 0.07$) as in 2013 (Tukey pairwise, $z = 11.3$, $p < 0.0001$). The significant increase in adult density from 2018 to 2023 (Tukey pairwise, $z = 9.6$, $p < 0.0001$) and 50% increase in juvenile density was largely fuelled by recruitment. Recruit density (mean = 0.27 recruits m^{-2} $yr^{-1} \pm 0.03$) was three times higher than the other stony coral species and particularly high in 2020, when it was twice as high as the previous year (Tukey pairwise, z = 4.7, $p < 0.0001$), and in 2023 (linear contrasts, $p = 0.003$).

Porites astreoides adult density consistently increased from 2013 (0.33 colonies $m^{-2} \pm 0.1$) to 2023 (0.57 colonies $m^{-2} \pm 0.2$; Tukey pairwise, $z = 10.1$, $p < 0.0001$). Recruit density was low (mean = 0.09 recruits m^{-2} $yr^{-1} \pm 0.01$), but relatively stable, being significantly below and above the mean in 2019 (linear contrasts, $z = -3.9$, $p = 0.00007$) and 2021 (linear contrasts, $z = 3.6$, $p = 0.0009$), respectively. Juvenile density consistently increased from 0.05 colonies $m^{-2} \pm 0.02$ in 2018 to 0.09 colonies $m^{-2} \pm 0.03$ in 2023.

Montastraea cavernosa adult density declined significantly from 2015 to 2016 (Tukey pairwise, $z = 7.4$, $p < 0.0001$), then slowly but significantly increased in the inter-disturbance period beginning in 2018 (0.17 colonies $m^{-2} \pm 0.03$) until the end of the study (0.23 colonies $m^{-2} \pm 0.04$), despite bleaching and two hurricanes impacting south Florida in 2022 (Tukey pairwise, $z = 4.2$, $p = 0.001$). *Montastraea cavernosa* recruit density was low (0.05 recruits m^{-2} $yr^{-1} \pm 0.004$), but consistent, not varying temporally, and resulted in juvenile density doubling from 2018 (0.04 colonies $m^{-2} \pm 0.02$) to 2023 (0.08 colonies $m^{-2} \pm 0.02$).

Meandrina meandrites adult density was four times lower in 2023 than in 2013 (Tukey pairwise, $z = 6.5$, $p < 0.0001$), due to the significant decline in density from 2015 to 2016 (Tukey pairwise, $z = 6.2$, $p < 0.0001$), and minimal recovery. Recruit density was exceptionally low (0.002 recruits m^{-2} $yr^{-1} \pm 0.0006$), as was juvenile density (0.003 colonies m^{-2} $yr^{-1} \pm 0.0006$) and did not vary temporally. Consequently, adult density was just 0.02 colonies $m^{-2} \pm 0.003$ in 2023.

Each octocoral species had distinct temporal patterns (Fig. 3). *Antillogorgia americana* adult density fluctuated, but substantially increased overall (Tukey pairwise, $z = 8.1$, $p < 0.0001$), fuelled by a boom in recruit density. *Antillogorgia americana* adult density increased significantly from 2014 to 2016 (Tukey pairwise, $z = 5.0$, $p < 0.0001$), declined slightly from 2016 to 2018, likely due to Hurricane Irma, then increased substantially from 2018 to 2022 (Tukey pairwise, $z = 9.2$, $p < 0.0001$), particularly from 2019 to 2020 (Tukey pairwise, $z = 5.5$, $p < 0.0001$). Recruit density during this period was significantly above the mean in 2019, 2020, and 2021 (linear contrasts, $z > 3.4$, $p < 0.01$), being twice the mean when it peaked in 2020 (0.51 recruits $m^{-2} \pm 0.05$). After peaking in 2022 (3.19 colonies $m^{-2} \pm 0.24$), adult density declined significantly in 2023 (Tukey pairwise, $z = 5.4$, $p < 0.0001$), after the Coral ECA experienced multiple acute disturbances in the second half of 2022. Despite that, density was still over four times higher than any stony coral species.

Eunicea flexuosa was resilient, declining significantly below the mean in 2018 following Hurricane Irma (linear contrasts, $z = 3.3$, $p = 0.01$), but recovering quickly despite low recruit density (0.03 colonies m^{-2} $yr^{-1} \pm 0.003$). Recruit density was significantly higher than the mean in 2023 (linear contrasts, $z = 2.9$, $p < 0.05$). Recruit and adult density were otherwise consistent, but adult density did vary widely spatially (GLMM, conditional $R^2 = 0.85$, marginal $R^2 = 0.007$).

Gorgonia ventalina adult density steadily increased from 2013 to 2023 (Tukey pairwise, $z = 5.6$, $p < 0.0001$), with consistent recruitment supplemented by two years, 2021 and 2023, where recruit density was 50% above the mean (linear contrasts, $z = 3.0$, $p = 0.01$). In those years, there were 0.14 recruits $m^{-2} \pm 0.03$. *Gorgonia ventalina* adult density did not vary temporally otherwise, but, like *E. flexuosa,* varied widely spatially (GLMM, conditional $R^2 = 0.71$, marginal $R^2 = 0.03$).

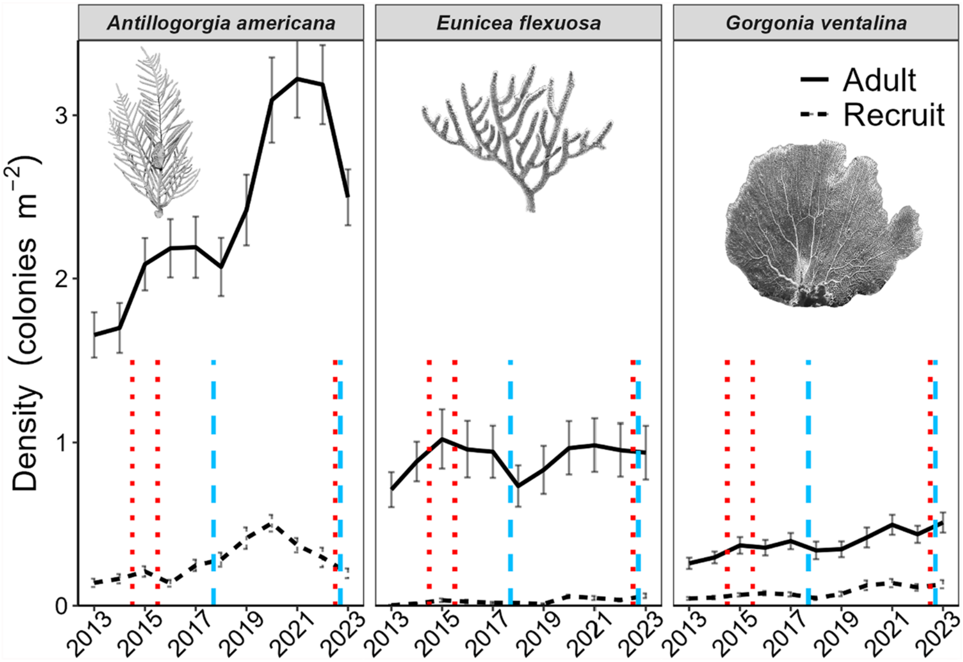

Fig. 3 Temporal changes in target octocoral species recruit (*dashed line*) and adult (*solid line*) density Vertical lines denote major acute disturbances, where *red dotted line* = bleaching event, *blue dashed line* = hurricane

Size structure

Mean colony diameter, coefficient of variation (CV), skewness, and kurtosis all varied significantly temporally and interspecifically in the target stony corals (Table S3). Temporal changes in size frequency distributions generally reflected the interspecific changes in density, with gradual changes in *S. siderea* and *P. astreoides* and abrupt temporal changes in *M. cavernosa* and *M. meandrites* (Fig. 4). *Siderastrea siderea* size frequency distributions had strong positive skew (1.1 ± 0.2 in 2023), which became increasing strong from 2013 to 2023 (Tukey pairwise, t = -3.5, $p = 0.02$) as mean colony diameter declined significantly (Tukey pairwise, $z = -5.0$, $p < 0.0001$) with the influx of recruits. *Siderastrea siderea* kurtosis also increased significantly from 2013 to 2023 (Tukey pairwise, $z = -3.5$, $p = 0.02$) and was strongly leptokurtic in 2023 (3.9 ± 0.5). *Porites astreoides* had no skew (mean = 0.00 ± 0.3) and relatively low CV (20.3 ± 0.4) throughout the study period. While *P. astreoides* mean colony diameter declined significantly from 2013 to 2023 (Tukey pairwise, $z = 6.4$, $p < 0.0001$), kurtosis declined significantly from 2014 to 2019 (Tukey pairwise, $t = 3.2$, $p < 0.05$) and remained platykurtic (~ 2) from then on, suggesting transition between size classes.

Montastraea cavernosa and *M. meandrites* mean colony diameters, which initially were the largest of the study species (24.3 cm ± 3.4 and 22.4 cm ± 3.1, respectively) declined following the 2014–2017 disturbance period, significantly declining from 2015 to 2018 (Tukey pairwise, z = 7.5, $p < 0.0001$) and from 2015 to 2016 (Tukey pairwise, z = 7.5, $p < 0.0001$), respectively. There was no significant increase in mean colony diameter of either species subsequently, with the 2023 means 60% and three times smaller than in 2013 (14.9 ± 3.4 and 7.0 cm ± 0.4). *Montastraea cavernosa* coefficient of variation remained high throughout the study period, with some large colonies remaining, and kurtosis was roughly lognormal throughout (mean = 2.8 ± 0.1), but skewness increased significantly from 2013 to 2023 (Tukey pairwise, $t = 4.2$, $p = 0.002$) and was strongly positive (0.9 ± 0.2) in the final year. *Meandrina meandrites* CV was only significantly greater than the mean in 2013 (linear contrasts, $t = 3.3$, $p = 0.01$) and after all large colonies (> 10 cm diameter) had died by 2016, kurtosis, which was already lower than all other species (Tukey pairwise, $p < 0.0001$), dropped to 0.5 and did not increase significantly.

Octocoral size frequency distributions were comparatively consistent temporally and all were platykurtic (2.2 to 2.7), with no to marginally negative skew (Fig. 5). Only temporal changes in mean colony height varied interspecifically, but accounted for little variation (GLMM, conditional $R^2 = 0.09$, marginal $R^2 = 0.05$; Table S1). *Antillogorgia americana* mean colony height was significantly lower than the mean in 2019, 2020, and 2021 (linear contrasts, $p < 0.0001$), when recruitment was high, and in 2022 (linear contrasts, $p = 0.04$), but increased significantly from 2021 to 2023 (Tukey pairwise, $z = 5.8$, $p < 0.0001$). *Eunicea flexuosa* and *G. ventalina* mean colony heights all declined from 2013 to 2023 (Tukey pairwise, $p < 0.01$), but the change was only from 25.9 cm ± 1.4 to 19.7 cm ± 1.6 and 16.2 cm ± 2.6 to 14.5 cm ± 1.5, respectively. CV increased significantly

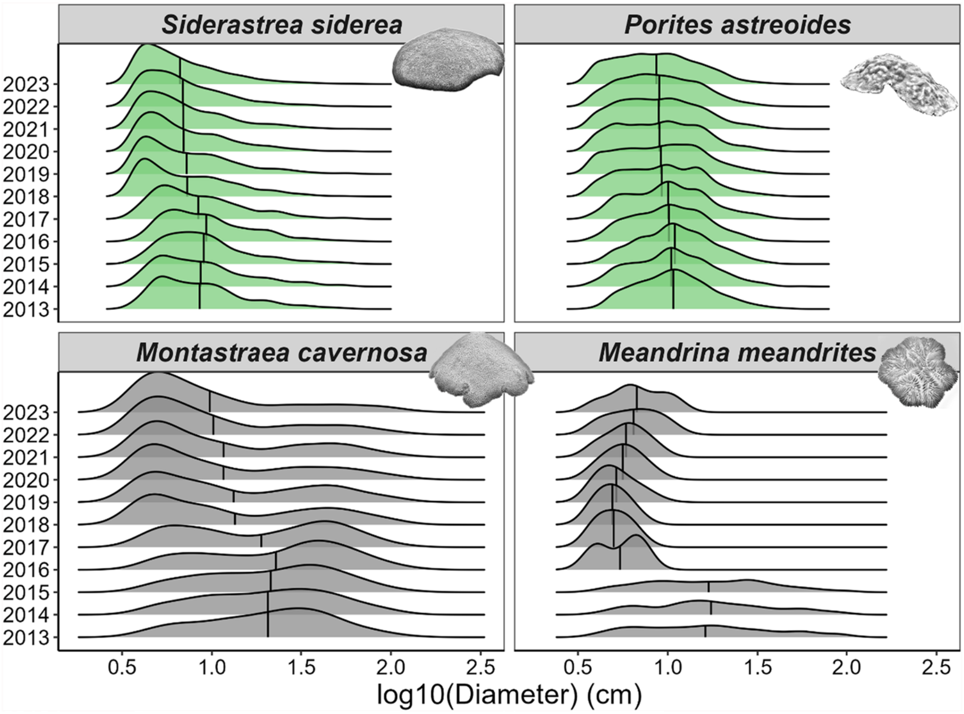

Fig. 4 Temporal variation in size frequency distributions using log10 transformed maximum colony diameter, separated by species. Within each panel, histograms are separated by year. Frequency estimated by kernel density estimate, which uses kernel smoothing (the weighted average of the observed data) for probability density estimation (using a smoothed histogram) for each species. Colors denote predicted ecological performance (*green* = 'winner", *gray* = "loser"). Solid vertical line within histograms represents the mean size per species per year

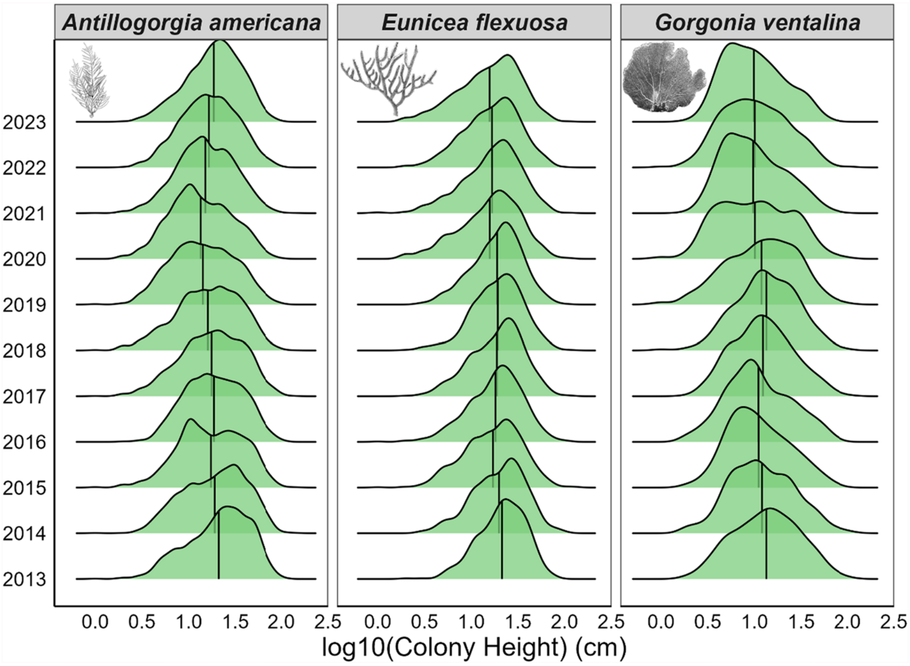

Fig. 5 Temporal variation in size frequency distributions using log10 transformed maximum colony height, separated by species. Within each panel, histograms are separated by year. Frequency estimated by kernel density estimate, which uses kernel smoothing (the weighted average of the observed data) for probability density estimation (using a smoothed histogram) for each species. Colors denote predicted ecological performance (*green* = 'winner", *gray* = "loser). Solid vertical line within histograms represents the mean size per species, per year

from 2013 to 2015 for all species (Tukey pairwise, $t = 3.9$, $p = 0.005$) and was particularly high in 2020 (linear contrasts, z = 7.0, $p < 0.0001$). It was significantly higher in *G. ventalina* than *E. flexuosa* (t = 2.5, $p = 0.04$). Skew and kurtosis did not significantly change temporally, but significantly varied by species. Skew was significantly more negative in *A. americana* (-0.2 ± 0.003) and *E. flexuosa* (−0.2 ± 0.03) than *G. ventalina* (−0.04 ± 0.04; Tukey pairwise, $p = 0.001$). Kurtosis was significantly higher in *A. americana* than *E. flexuosa* (Tukey pairwise, $z = 4.3$, $p = 0.0001$) and *G. ventalina* (Tukey pairwise, z = 6.4, $p < 0.0001$), and significantly higher in *E. flexuosa* than *G. ventalina* (Tukey pairwise, z = 2.8, $p = 0.02$).

Discussion

Acute disturbances are a major driver of community change on coral reefs (Hughes et al. 2017; Jones et al. 2022; Edmunds 2024a) and their frequency is increasing such that there may be insufficient time for coral assemblages to recover between successive events (Lough et al. 2018). Here, we leverage more than two decades of long-term monitoring data to examine the impact of the Coral ECA's disturbance history on spatiotemporal changes in benthic community structure and the underlying demographic processes influencing these changes. From 2003 and 2023, multiple acute disturbances, including thermal bleaching events, hurricanes, and a severe disease outbreak, each induced significant reconfigurations of benthic community structure, most notably repeated coral loss and macroalgal gains, with increased spatial homogeneity in community structure over time. We also identified interspecific differences in demographics for target stony corals and octocorals, suggesting taxon-specific variability in resilience which facilitates the presence of ecological "winners" and "losers" (Loya et al. 2001; Riegl et al. 2017; Edmunds 2024a). The identity of these losers, in particular reef-building corals and large stony coral colonies, highlights why recovery in coral coverage in the Coral ECA is so limited (Jones et al. 2022) and underpins the reconfiguration of benthic community structure which is mirrored throughout the Western Atlantic and Caribbean (Roff and Mumby 2012; Jackson et al. 2014; Walker et al. 2024).

Benthic community structure significantly changed after both major acute disturbance periods and reconfigured, rather than recovered, during the following inter-disturbance period. Relative declines in all faunal taxa were observed from the start of this study, 2003, to 2006, following the first of three multi-disturbance periods, bleaching and hurricanes in 2005. The thermal bleaching event in 2005 was the strongest on record at the time (Eakin et al. 2010) and Hurricanes Katrina and Wilma both brought tropical cyclone strength winds to the region, in August and October, respectively (Wilkinson and Souter 2008). Subsequently, no major disturbances impacted the Coral ECA for seven years, within the range of time required for moderate stony coral recovery on isolated reefs (Gilmour et al. 2013; Adjeroud et al. 2018; Gouezo et al. 2019), but as is commonplace in the Western Atlantic (Jackson et al. 2014; Tebbett et al. 2023; Walker et al. 2024) recovery was limited (Jones et al. 2022). Spatial variability did increase from 2006 to 2013, but this was largely related to the addition of sites. Some sites had higher stony coral, octocoral or zoanthid cover than the regional mean, but recovery in stony coral cover was not evident in site-level trajectories or in the region-wide centroid position, highlighting the recovery constraints imposed by the local environmental pressures on recruitment (Speare et al. 2019; Duran et al. 2024), colony growth (Jones et al. 2023), and survival (Jones and Gilliam 2024a). The 2014–2017 acute disturbance period included repeated thermal bleaching in 2014 and 2015 (Eakin et al. 2019), the devastating SCTLD outbreak, which began in the Coral ECA in 2014 and peaked in 2016 (Precht et al. 2016; Walton et al. 2018; Hayes et al. 2022), and Hurricane Irma in 2017. The severity and variety of disturbances led to relative declines in all major faunal taxa, including an 85% decline in stony coral cover at the most impacted site (Jones and Gilliam 2024a). The subsequent inter-disturbance period again saw minimal recovery in benthic community structure and a decline in dispersion. Together, these suggest increasing homogenization across the region, with much of the remaining spatial variation dependent upon whether a site has more turf algal or macroalgal cover, which combined constituted over 80% of the benthic cover in 2022.

Interspecific variation in target stony coral and octocoral resilience resulted in winners and losers, determined in part by life-history strategy. Of the winners, *Siderastrea siderea*, *Antillogorgia americana,* and *Eunicea flexuosa* were resilient, with adult density recovering quickly following the 2014–2017 multi-disturbance period. *Siderastrea siderea* adult density declined from 2013 to 2016, but recovered within a year and was twice as high in 2023 as in 2013. Mortality primarily occurred from 2015 to 2016 following the second marine heatwave and peak SCTLD period (Hayes et al. 2022), suggesting initial bleaching/SCTLD resistance before environmental conditions became too intense or that whole colony mortality was slow. *Siderastrea siderea* are considered stress tolerant (Colella et al. 2012; Toth et al. 2019; Edmunds 2024b), but are moderately susceptible to SCTLD (NOAA 2018; Meiling et al. 2021) and bleaching (Alemu and Clement 2014). Heat stress in the Coral ECA was more intense in 2015 than in 2014 (Jones et al. 2020), when El Niño was stronger (Eakin et al. 2019), and, while reports detailing the relationship between SCTLD progression rates and thermal stress are mixed (Precht et al. 2016; Muller et al. 2020; Sharp et al. 2020; Jones et al. 2021; Williams et al. 2021; Hayes et al. 2022), it still appears plausible that heat stress reduced resistance and increased mortality. The subsequent increase in *S. siderea* adult density, particularly from 2019 onwards, was striking and is likely associated with a large spawning event observed in the middle and lower Florida Keys in 2018 (Harper et al. 2023). Boom-bust recruitment patterns have been documented in branching species in the Pacific (Holbrook et al. 2018; Morais et al. 2021) and *S. siderea* appears to have employed a similar strategy, although due to slow growth these do not result in concomitant increases in coral cover.

Antilligorgia americana adult density followed a similar pattern to *S. siderea*, although the primary cause of declines appears to be related to storm action rather than temperature and disease. *Antillogorgia* spp. are resistant to bleaching (Pelosi et al. 2021) and *A. americana* density increased following each marine heatwave. However, *A. americana* adult density declined from 2017 to 2018, following Hurricane Irma, and 2022, following Hurricanes Ian and Nicole, highlighting their vulnerability to physical disturbance (Yoshioka and Yoshioka 1991; Lasker et al. 2020; Cant et al. 2024). After Hurricane Irma, recovery was rapid, recovering to pre-disturbance density within a year regionally, although varying spatially. Further booms in recruit density in 2019, 2020, and 2021 fueled population growth until 2022, when multiple disturbances (thermal heat stress and hurricanes) again affected the Coral ECA. While our data suggest that under the current disturbance regime *A. americana* will continue to be a winner, the variety of disturbances which are intensifying and becoming more frequent under climate change suggest they may be vulnerable in the future (Cant et al. 2024). Future monitoring will capture whether another pulse of high *A. americana* recruit density will again enable rapid recovery following the significant decline in adult density at the end of the study.

The general stability in *Eunicea flexuosa* adult density and rapid recovery following slight decline from 2017 to 2018 suggest the population may be at equilibrium. Like *A. americana*, *E. flexuosa* rarely bleach (Prada et al. 2010), but are susceptible to physical disturbance (Lasker et al. 2020). Polyp bailout, which could stimulate recovery, has been observed in *E. flexuosa* under stressful conditions (Wells and Tonra 2021), but recruit density was generally low and fluctuated little temporally, suggesting the reattachment of autotomized branches to the substrate (Lasker 1984) was primarily responsible for recovery from 2018 to 2019. Further investigation, including population growth modeling, is needed to determine whether the *E. flexuosa* population is at equilibrium. Reaching equilibrium is thought to be rare on dynamic systems such as coral reefs (Connell 1978; Lasker 1991), but populations tend toward them (Mumby et al. 2007) and *E. flexuosa* has demonstrated a propensity to recover toward equilibrium in the US Virgin Islands (Cant et al. 2024). The limited fluctuation in recruit or adult density seen in our study, even if at low density, coupled with a relatively stable, lognormal size frequency distribution, suggests a healthy *E. flexuosa* population in the ECA.

The other winners in our study, *Porites astreoides* and *Gorgonia ventalina,* exhibited steady population growth from 2013 to 2023 facilitated by consistent recruitment, which was reflected in platykurtic size frequency distributions with limited skew, indicative of transition between size classes. Increases in *P. astreoides* density have been common throughout the wider Caribbean in recent decades (Green et al. 2008; Estrada-Saldivar et al. 2019; Edmunds 2024a, b), but reports of localized *P. astreoides* population decline in recent years (e.g., Edmunds et al. 2021) highlights their vulnerability to climate change. We found little evidence of that here, with adult density consistently increasing, steady recruit density, and a transition from leptokurtic to platykurtic size frequency distributions. While some studies consider colonies created through fission as distinct, we did not, suggesting colonies identified as recruits here are from sexual reproduction or parthenogenesis, as has been suggested to readily occur in the population (Shilling et al. 2023), rather than partial mortality induced fission (Edmunds et al. 2021). This study strengthens our previous suggestion that the temperature regime in the region will continue to favor *Porites* spp. (Jones et al. 2020).

Gorgonia ventalina adult density was substantially lower than the other target octocoral species throughout the study and elsewhere in the Caribbean (e.g., Edmunds 2020), but the population still doubled from 2013 to 2023 due to consistent recruitment. Further, *G. ventalina* was the only octocoral species whose density did not significantly decline below the mean at any point, suggesting resistance to both heat stress and hurricane impacts. Previous studies have shown some susceptibility to wave action (Edmunds 2020; Cant et al. 2024), but the morphological flexibility of *G. ventalina* allows it to sway with moderate surge and our study sites were all below five meters depth, likely buffering them from the most severe effects. Severe *Gorgonia* sp. population declines in the mid-1990s were largely attributed to fungal infection by aspergillosis (Kim and Harvell 2004; Smith and Weil 2004), but disease prevalence was rarely observed. As with *P. astreoides*, size frequency distributions were platykurtic with no skew, suggesting a healthy population, albeit one with few large individuals.

The two largest stony coral species in this study, *Meandrina meandrites* and *Montastraea cavernosa*, emerged as ecological losers. Massive, stress-tolerant species are conventionally presumed to be winners under climate change (Loya et al. 2001; Baum et al. 2023), but both species were severely affected by SCTLD (Hayes et al. 2022) and heat stress duration (Jones et al. 2020). As a result, they experienced 94% and 45% declines in adult density, respectively, and all large *M. meandrites* colonies and most large *M. cavernosa* colonies died. Repeated bleaching can turn winners into losers (Grottoli et al. 2014), which may have played a role here, but the decline in *M. meandrites* in particular is emblematic of SCTLD's lethality. While thermal stress alone often results in high partial colony mortality in larger colonies (Colella et al. 2012; Speare et al. 2022), disease can kill whole colonies, substantially reducing recovery potential (Koester et al. 2020). *Montastraea cavernosa* juvenile and adult density did increase from 2018 to 2023, but recruit density was low and hence recovery was slow, as with reef-building species worldwide subject to severe disturbance (Gouezo et al. 2019; Pratchett et al. 2020). Connectivity to other regions and the remnant population may continue to maintain population growth until the next major acute disturbance (Sturm et al. 2022), but the dearth of large colonies and the growth constraints within the Coral ECA (Jones et al. 2023) suggest functional recovery will be limited under current conditions. There was minimal *M. meandrites* recovery, with only 20 recruits observed across six years of surveys from 2018 to 2023, presumably originating from outside of the Coral ECA, as has been demonstrated to occur in *M. cavernosa* (Sturm et al. 2022). *M. meandrites* adult density did increase by 83% from its lowest point in 2015 to 2023, but this only translated to 30 colonies observed in the study area at a density of 0.01 colonies m^{-2}, making sexual reproduction unlikely. *M. meandrites* was among the most common species in the Coral ECA prior to the multi-disturbance period, but may now be functionally extinct, like the confamilial *Dendrogyra cylindrus* (Jones et al. 2021).

Most large stony coral colonies died between 2014 and 2018, and underlying chronic pressures have since maintained stony coral populations composed almost entirely by small colonies (Jones and Gilliam 2024b), which contribute little to cover. Skewed size frequency distributions dominated by small colonies is indicative of highly disturbed reefs (Bauman et al. 2013; Riegl et al. 2017; Pisapia et al. 2020), but counters predictions that marginal reef systems select for large colonies (Chong et al. 2023). This is in part due to the extent of whole colony mortality, but also hints particularly at the constraints to growth and survival of *S. siderea*, the most abundant species in the Coral ECA and a reef-builder in the Florida Keys and Caribbean (Jones et al. 2023; Jones et al. 2024a, b). Despite the small size of most *S. siderea* colonies, there is evidence that many of them are reproductively active (St Gelais et al. 2016), which may enable continued population growth, but adding little to habitat complexity. The *M. meandrites* population was composed almost entirely of colonies below putative reproductive size and while *M. cavernosa* size frequency distributions from 2018 onwards were mesokurtic, they were heavily positively skewed with few large colonies. Only *P. astreoides* size frequency distributions were not skewed, remained stable, and suggested transition between size classes throughout the study.

Comparatively, the octocoral target species were able to maintain lognormal size frequency distributions indicative of healthy populations (Bak and Meesters 1998; Pisapia et al. 2020), albeit with very few colonies that approach their maximum height. The only temporal changes, in mean colony size and coefficient of variation, were associated with pulses in recruitment and accounted for minimal variation. Whereas stony coral growth in the Coral ECA is constrained (Jones et al. 2023), skewing size frequency distributions, the capacity of octocorals for fast, vertical growth likely allows them to escape many pressures (Lasker et al. 2020), principally sediment, turf algae, and macroalgae, which affect stony corals (Box and Mumby 2007; Speare et al. 2019; Duran et al. 2024). Combined, the ability of *A. americana*, *E. flexuosa,* and *G. ventalina* to resist and/or recover rapidly from multiple disturbances and maintain size structure during the 11-year study will likely allow these three species to continue to be winners under current environmental conditions. The extent to which the populations grow to form true octocoral forests (Lasker et al. 2020) may determine any further reconfiguration in benthic community structure.

Spatial variability was high in benthic community structure and temporal changes in most target species. While we accounted for site level variation in all models, it is important to note that our conclusions highlight the regional reconfiguration and increasing homogenization of the Coral ECA. By 2022, most spatial variation in benthic community structure related to whether a site had more turf algae/sediment-laden turf algae or macroalgae rather than sites with high stony coral cover, which relates to environmental conditions (Jones and Gilliam 2024a) and physical disturbances (Williams et al. 2013). It seems likely that recruit density and hence recovery in the Coral ECA is also heavily influenced by these factors (Speare et al. 2019, 2023; Duran et al. 2024) and identifying and addressing the local chronic pressures which reduce recovery potential (Jones et al. 2022; Jones and Gilliam 2024a) is crucial.

The identity and size structure of the stony coral winners and losers highlight why coral cover recovery is so limited within the Coral ECA and why benthic community structure is dominated by turf algae and macroalgae. Three of the four target stony coral species are massive/submassive reef-builders in the Caribbean; but, the populations of two, *M. meandrites* and *M. cavernosa,* were significantly reduced by disturbances, and the third, *S. siderea* is size-constrained (Jones et al. 2023; Jones and Gilliam 2024b), despite substantial recruitment (Harper et al. 2023) and a doubling in adult density over this 11-year demographic study. Only the competitive, submassive-encrusting species *P. astreoides* has a size structure which reflects a relatively healthy population, and its growth is also constrained by partial mortality (Jones et al. 2023). While each target octocoral species was resilient and emerged as a winner under current environmental conditions, each species has a predominantly planar growth form which adds little to two-dimensional cover. Instead, this reconfigured, marginal reef system will continue to be dominated by sediment, turf algae, macroalgae, and cyanobacteria, which hinder stony coral population growth (Kuffner et al. 2006; Box and Mumby 2007; Speare et al. 2019; Duran et al. 2024), with the remaining spatial variation predominantly dependent upon whether a reef site has more turf algae and sediment or macroalgae and cyanobacteria.

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Author's contribution NPJ and DSG conceived the study and developed study design. DSG secured funding. NPJ conducted data analyses and data visualization. NPJ and SEL wrote the manuscript, and all authors edited and contributed to the final version.

Data availability All raw data are available at https://myfwc.com/research/habitat/coral/cremp/data/ Code for data analysis and visualizations is available at https://github.com/nj350. All data are available at https://myfwc.com/research/habitat/coral/cremp/data/

Code availability Code for data analysis and visualizations is available at https://github.com/nj350

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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