Multi-year coral recruitment study across the Florida Reef Tract reveals boom-or-bust pattern among broadcast spawners and consistency among brooders

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ABSTRACT: Scleractinian coral populations are in global decline, and successful recruitment is fundamental to community persistence and recovery, but recruitment may vary by coral reproductive mode. Using settlement tiles, we assessed coral recruitment over 3 consecutive years across 4 regions (~300 km) of the Florida Reef Tract (FRT) to determine whether spatio-temporal variation differs between brooding and broadcast spawning corals and whether coral recruit distributions correlate with adult coral live tissue area, site temperature, or depth. We deployed 32 tiles to each of 30 sites with depths ranging from 2 to 18 m; tiles were retrieved and replaced annually. From 2016–2018, we counted 11 633 scleractinian coral recruits, most of which belonged to the Siderastreidae, Agariciidae, Poritidae, and Faviidae families. Faviid recruits were rare (<1 %). While recruitment of brooding agariciids and poritids was relatively stable across the 3 yr, recruitment of broadcast spawning siderastreids increased an unprecedented 70.7-fold from 2017 to 2018, in a boom that spanned 19 sites across the FRT. Elevated temperature during the preceding reproductive season was a significant predictor of low recruitment for all groups except siderastreids and faviids, and recruitment of brooding taxa was positively linked to adult confamilial live tissue area. For siderastreids, adult live tissue area was also related to recruitment, but the direction of the relationship differed by year and region. The unprecedented high recruitment of siderastreids in Florida, preceded by 2 yr of comparatively low recruitment, demonstrates that broadcast-spawning scleractinians are among the marine taxa capable of employing boom-and-bust recruitment cycles over geographically widespread areas.

KEY WORDS: Recruitment · Settlement tile · Scleractinia · Florida Reef Tract · *Siderastrea siderea*

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1. INTRODUCTION

The importance of recruitment in maintaining populations has long been recognized for marine organisms exhibiting a bipartite life cycle of pelagic larvae and sessile adults. Retention and export are important structuring forces in open marine assemblages, but the scales over which these processes act vary by species, space, and time (Caley et al. 1996, Cowen et al. 2003, Holstein et al. 2014). While some marine invertebrate taxa can maintain locally stable recruitment year after year (Navarrete et al. 2002), others, such as scallops (Beukers-Stewart et al. 2003, Wolff et al. 2007) and the crown-of-thorns sea star *Acanthaster planci* (Uthicke et al. 2009, Wolfe et al. 2015), exhibit boom-and-bust patterns of recruit availability. High interannual variability in recruitment can confound predictions of stock fluctuation for commercially important species (Wolff et al. 2007) and can complicate efforts to conserve species with populations in local or global decline, including scleractinian corals (Hoegh-Guldberg et al. 2018, Guan et al. 2020).

The scleractinian coral populations of the western Atlantic and Caribbean have suffered unprecedented mortality from regional stressors such as overfishing, hurricane damage, disease outbreaks, and loss of grazers (Gardner et al. 2003, Alvarez-Filip et al. 2009, 2022, Jackson et al. 2014) that are further compounded by global stressors such as ocean warming (Bove et al. 2020). The dominant coral assemblages have shifted away from large, framework-building species to generally smaller, stress-tolerant species (Aronson et al. 2002, Green et al. 2008). The loss of these corals has been exacerbated in recent years by stony coral tissue loss disease (SCTLD), which emerged in 2014 near Miami, Florida (Precht et al. 2016, Walton et al. 2018). SCTLD has caused mass mortality of framework-building species including *Orbicella* spp., *Montastraea cavernosa*, *Colpophyllia natans*, and *Pseudodiploria strigosa* throughout the Florida Reef Tract (FRT) (Muller et al. 2020) and the wider Caribbean (Alvarez-Filip et al. 2022). Understanding the intrinsic and extrinsic factors driving temporal and spatial patterns in coral recruitment will help determine if recruitment can outpace mortality and ultimately lead to population recovery.

Where scleractinian recruitment has been quantified in the Caribbean, recruit distribution has been shown to vary across species and may be intrinsically linked to reproductive mode. Recruits of the mountainous *Orbicella* spp. have been rare (Bak & Engel 1979, Rogers et al. 1984, Smith 1992), and for decades or longer, Caribbean *Acropora* spp. populations have primarily reproduced through asexual fragmentation (Highsmith 1982). These framework-building genera are broadcast spawners, which release positively buoyant gametes into the water column for external fertilization (Szmant 1986) during synchronized spawning events 1 or 2 times per year (Jordan 2018). By contrast, brooding corals fertilize internally, with maternal polyps releasing competent or nearly competent planulae (Duerden 1902), often during multiple lunar cycles each year (Szmant 1986). The 2 Caribbean species that have shown high rates of recruitment are both relatively small and weedy brooders: *Agaricia agaricites*, which can planulate 6 times per year (van Moorsel 1983) and often dominates recruit cohorts in the Caribbean basin (Bak & Engel 1979, Rogers et al. 1984, Humanes & Bastidas 2015), and *Porites astreoides*, which can planulate 3–4 times per year (McGuire 1998) and can also dominate recruit cohorts in the western Atlantic (Rubin et al. 2008) and Bermuda (Smith 1992). A shift in community dominance from broadcast spawning to brooding species is significant because adult live cover is a possible predictor of recruitment rates (Bramanti & Edmunds 2016), although the relationship may be more predictable for sites and species with high local retention, and thus a closer link between stock and recruitment (Chiappone & Sullivan 1996, Ayre & Hughes 2000, Figueiredo et al. 2014).

Extrinsic factors of latitude (Hughes et al. 2002, Price et al. 2019) and depth (Rogers et al. 1984, Turner et al. 2018) are predictors of recruitment variation across spatial gradients but are likely confounded by temperature and light availability. These factors influence larval behavior during substratum selection and the ability of those recruits to survive (Ritson-Williams et al. 2009, Gleason & Hofmann 2011). Recruitment is often highest at intermediate depths: within one study that examined recruitment across a depth range of 3–40 m in the Indian Ocean, the highest recruitment rates were found at 25 m (Turner et al. 2018), and a study in St. Croix that investigated a depth gradient of 9–37 m found peak recruitment densities at 18 m (Rogers et al. 1984). However, the narrow depth range included in most studies of coral recruitment hinders our ability to interpret the effects of depth variation on settlement. Even broad spatial patterns are dynamic across time: a meta-analysis of 98 coral recruitment studies found that while recruitment was generally higher near the equator from the 1970s to 2000, recruitment in the tropics (0–20° N and S) has since been declining

while recruitment in the subtropics (20–40° N and S) has been increasing (Price et al. 2019).

While closely linked with spatial gradients of latitude and depth, temperature also fluctuates over seasonal and interannual time scales (Edmunds 2021). On the supply side, thermal anomalies can contribute to widespread coral bleaching and mortality (Welle et al. 2017, Burkepile et al. 2020), reducing adult population density or reproductive output of surviving temperature-stressed corals; decreased oocyte size from temperature stress has been observed for more than 1 yr following a bleaching event (Johnston et al. 2020). Elevated temperatures have also been shown to cause reduced fertilization success, larval survival, and settlement (Humanes et al. 2016) through mechanisms such as oxidative stress and synergistic interactions with other stressors (Ritson-Williams et al. 2016). Warming oceans can also accelerate larval development, potentially decreasing dispersal distances and resulting in high local retention of recruits, even for broadcast spawning species (Figueiredo et al. 2014). Because Caribbean brooders typically start planulating in the spring and broadcast spawners typically spawn in late summer (Szmant 1986, Jordan 2018), their larvae are subject to different environmental conditions. Larvae of broadcast spawning corals are likely subjected more to elevated temperatures, which in the Caribbean peak around many species' spawning events between July and September (Jordan 2018).

Live coral cover (measured in 2 dimensions, as derived from top-down imagery) or live tissue area (measured in 3 dimensions) are other variable extrinsic factors that could predict coral recruitment through one or more of several mechanisms. Conspecific corals could be a positive indicator of potential stock, although brooding corals are more likely to retain larvae locally (Chiappone & Sullivan 1996, Ayre & Hughes 2000, Figueiredo et al. 2014). Conspecific corals also serve as a positive indicator of past recruitment success and benevolent environmental conditions (Salinas-de-León et al. 2013). Cover or live tissue area of conspecifics, or of the scleractinian community in general, could serve as an arbiter of chemical, structural, or auditory cues that could positively influence recruitment by attracting coral larvae to a more coral-dominated reefscape (Vermeij et al. 2010); coral tissue can also suppress macroalgal proliferation via spatial competition (Ferrari et al. 2012). However, live coral cover could also depress recruitment success by limiting substratum availability or through the chemical defenses of adult coral colonies (Marhaver et al. 2013).

Our understanding of coral recruitment in the western Atlantic has been impeded by a lack of studies conducted at sufficient scales to capture the gradients of extrinsic spatio-temporal variables (e.g. region, depth, live coral cover, temperature). Instead, most western Atlantic and Caribbean coral recruitment studies have been limited to single islands, taking place over small (<10 km) spatial scales (Arnold et al. 2010, Green & Edmunds 2011, Arnold & Steneck 2011, Edmunds et al. 2014). Because successful coral recruitment is fundamental to the resilience and recovery of declining framework-building coral populations, quantifying recruitment over ecologically relevant space and time scales is a necessary component of management and restoration plans (Maynard et al. 2015, Hein et al. 2020).

We assessed variability in coral recruitment over 3 consecutive years across approximately 300 km of the FRT, including 30 reef sites within 4 regions. Specifically, we examined the following hypotheses: (1) temporal and spatial variation in recruitment rates for corals of the western Atlantic and Caribbean is intrinsically linked to reproductive mode, and (2) temporal and spatial variation in recruitment rates is altered by extrinsic factors that differ in their magnitude and predictability. We predicted that across the FRT, (1a) brooders recruit to tiles at higher densities than broadcast spawners, consistent with records from throughout the western Atlantic (Bak & Engel 1979, Rogers et al. 1984, Smith 1992, Arnold & Steneck 2011, Humanes & Bastidas 2015); (1b) the patterns of recruitment observed over time are consistent between regions and across depth gradients for both brooders and broadcast spawners; (2a) recruitment rates correlate positively with live tissue area of confamilial adults for both brooders and broadcast spawners; and (2b) recruitment rates are inversely correlated with abnormally high water temperatures that occur during the months when most scleractinians reproduce. We investigated these hypotheses in what amounts to the most spatially expansive multi-year assessment of coral recruitment yet conducted in the western Atlantic.

2. MATERIALS AND METHODS

2.1. Study sites and habitat characteristics

We selected 30 study sites across the FRT from those within the Coral Reef Evaluation and Monitoring Project (CREMP; FWRI 2022a) and the Southeast Florida Coral Reef Evaluation and Moni-

toring Project (SECREMP; FWRI 2022b), which monitor reefs in the Florida Keys and Southeast Florida (respectively) annually to assess benthic percent cover and coral demographics (Table S1 in the Supplement at www.int-res.com/articles/suppl/m721p039_supp.pdf). Because not all (SE)CREMP surveys (coral and octocoral demographic surveys and benthic percent cover) are conducted across all sites, the subset of (SE)CREMP sites chosen for this project was selected to align with the sites at which all (SE)CREMP surveys are conducted and for even allocation across habitats and regions. Our selected sites ranged from Broward County in the northeast (26.1599° N, 80.0825° W) to Key West in the southwest (24.4517° N, 81.8798° W) and were regionally stratified by Southeast Florida (n = 12), Upper Keys (n = 6), Middle Keys (n = 6), and Lower Keys (n = 6). Within Southeast Florida, 3 sites each were in 4 habitats: nearshore ridge complex, and inner, middle, and outer terraces. Within the Florida Keys, 6 sites each were in mid-channel patch reef, shallow forereef, and deep forereef habitats. The distance between nearest neighboring sites ranged from ~0.2 to 10 km.

By selecting CREMP and SECREMP sites for the investigation of coral recruitment, we were able to reference the adult scleractinian live tissue area and temperature data from those programs as potential factors that may influence recruitment rates. For both programs, corals are surveyed once per year, generally between May and September, along four ~20 m long permanent transects per site. In SECREMP prior to 2018, all scleractinian coral colonies ≥2 cm in diameter falling within a 1 m wide belt along the entire ~20 m transect were identified, measured (maximum width and height), and assessed for percent mortality (Walton et al. 2018). In CREMP prior to 2018, only the first 10 m of each transect was surveyed for corals ≥4 cm in diameter because of higher coral abundances in the Florida Keys relative to Southeast Florida. After 2018, both CREMP and SECREMP included a search for all juvenile corals <4 cm in diameter along 10 and 20 m transects, respectively. From the demographic data, the coral live tissue area per site was calculated as described in Walton et al. (2018). Because transects in Southeast Florida were 20 × 1 m (vs. 10 × 1 m in all Keys regions), live tissue area for Southeast Florida sites was divided by 2 to normalize transect area. To track changes in bottom temperature through time, 1–2 HOBO ProV2 temperature loggers were attached to the transect marker stakes at each site and replaced annually.

2.2. Tile deployment and recruit identification

To quantify coral recruitment, in 2015, 2016, and 2017, we deployed terracotta tiles (15 × 15 × 1 cm) for year-long saturations as described in Harper et al. (2021). In brief, because tiles were grooved on one surface and flat on the other, we deployed tiles as pairs, with the grooved surfaces facing outward to provide consistent rugosity for settlement on both the top and bottom. In 2015, from February to April, 32 tile pairs were deployed per site, attached directly to the substrata with drywall anchors, haphazardly arranged along 4 transects per site. These tile pairs were retrieved after about 1 yr, and subsequent deployments in 2016 and 2017 to the same locations and retrievals in 2017 and 2018 occurred for similar durations. Over the 3 yr study, 2880 tile pairs were deployed and 2778 pairs (96%) were recovered (Harper et al. 2021); most of the unrecovered tiles were displaced due to Hurricane Irma striking the Keys in 2017.

After retrieval from the reef, tile pairs were submerged in 10% sodium hypochlorite solution for 24–48 h to remove live tissue, then dried. Each tile was then scanned on the grooved surface (top or bottom when in the tile pair) and on the sides to locate scleractinian recruit skeletons (Harper et al. 2021). Recruit skeletons were identified to the family level using diagnostic morphological characteristics for scleractinian coral recruits (Budd et al. 2001, Budd & Stolarski 2011, Humblet et al. 2015). Although the taxonomic classifications of several species have since changed (Huang et al. 2011, Budd et al. 2012), recruit assignment to the family Faviidae here was based upon the species classified as 'Atlantic faviids' by Budd & Stolarski (2011). As a result, Faviidae recruits herein could be members of the current genera *Cladocora*, *Colpophyllia*, *Diploria*, *Favia*, *Manicina*, *Montastraea*, *Orbicella*, *Pseudodiploria*, and *Solenastrea*.

2.3. Statistical methods

While many recruits were unidentifiable to the family level each year, nearly all (99.9%) of the identified recruits were in the families Agariciidae, Poritidae, Faviidae, and Siderastreidae (see Section 3). Thus, statistical tests for patterns of recruitment include assessments of total scleractinian recruitment (all recruits, identified and unidentified) and of the 4 major families. Because some tiles were lost, resulting in differences in settlement area per site,

we included tile area as an offset variable in statistical tests.

To determine whether more brooders or broadcast spawners recruited to the FRT each year (Prediction 1a), we fit a generalized linear model (GLM) with a negative binomial distribution for each year within each region, regressing recruit count as the response variable against taxonomic family as a fixed factor, grouped as 'primarily brooders' (Poritidae and Agariciidae) and 'primarily broadcast spawners' (Siderastreidae and Faviiae). We evaluated the significance of differences between taxa with a Type II ANOVA using the R package 'car' (Fox & Weisberg 2019) and used the R package 'emmeans' (Lenth et al. 2023) to investigate pairwise contrasts using estimated marginal means among taxa within each year and region.

To test whether patterns of recruitment are consistent across space and time for brooders and broadcast spawners across the FRT (Prediction 1b), we tested for differences in recruitment (total, the 4 major families, and unidentified recruits) between all combinations of region and year by regressing year, region, and their interaction against recruit count by tile (offset by tile area) using a negative binomial GLM. We evaluated the significance of fixed effects with a Type II ANOVA using 'car' (Fox & Weisberg 2019), and we used 'emmeans' (Length et al. 2023) to investigate pairwise contrasts using estimated marginal means between years for total recruitment across the reef tract, between years within sites, and between region–year combinations. Then, to assess temporal differences (among the 3 yr) in total scleractinian recruitment across the FRT, we determined interannual significance with a Kruskal-Wallis test followed by Dunn's post hoc test with a Bonferroni correction using the R package 'dunn.test' (Dinno 2017), with individual settlement tiles as replicates (n = 955 in 2016, n = 956 in 2017, n = 867 in 2018). To determine whether recruitment varied temporally at the smaller spatial scale of sites (~100 m^2), we tested for year-to-year differences within each site using Kruskal-Wallis tests with tiles as replicates, and we tested for significant pairwise contrasts using Dunn's post hoc test with a Bonferroni correction.

To understand how bottom water temperature may potentially function as a predictor of scleractinian recruitment, we first needed to determine how temperature may vary across our study area and between years during the scleractinian reproductive seasons. From the temperature loggers, we determined the daily mean temperatures from April to September during the year immediately preceding each annual tile collection to capture both the most common brooder and broadcast spawner planulation, spawning, and settlement seasons for Atlantic corals (van Moorsel 1983, Szmant 1986, Edmunds et al. 2001). For days where temperature loggers failed or were lost, the mean temperature of the nearest site of similar depth (e.g. within ~2.5 m depth) from the same day was substituted as a proxy (occurred in 9% of site-days monitored). We tested for annual and regional differences in bottom temperature by regressing daily mean temperatures against region, year, and their interaction using a linear model, evaluated the significance of fixed effects using Type II ANOVA within 'car' (Fox & Weisberg 2019), and tested for significant pairwise differences in regions and years using 'emmeans' (Lenth et al. 2023). Finally, the mean temperature for each reproductive season was calculated as the mean of daily average temperatures (n = 183 d from April through September).

We investigated potential factors predicting variation in recruitment (Predictions 2a and 2b), as well as the interactions between spatial and temporal variability, using a series of negative binomial GLMs. Recruit counts on all tiles from each site within each year were summed and used as site-level replicates. For each family, we fit a full model that included year, region, depth, live tissue area of confamilial adult corals, and mean temperature for each site from April to September in the year preceding recruitment. To test whether patterns observed over time are consistent across region and depth, we allowed for interactions between year and region and year and depth. We also allowed for interactions between year and confamilial adult live tissue area as well as region and confamilial adult live tissue area, to test whether site-level spatial relationships between live tissue area and recruitment were consistent across region and year. After fitting the full model for each group, we used the 'step' function (from the R package 'stats'; R Core Team 2020) for algorithmic model comparisons to reduce each group's model to that with the lowest Akaike's information criterion (Akaike 1974). For total scleractinian recruitment, we fit the same full model, except we substituted all scleractinian live tissue area per site in place of the confamilial live tissue area. We then tested significant effects of each relevant variable with a Type II ANOVA using the R package 'car' (Fox & Weisberg 2019), and calculated Nagelkerke-adjusted R^2 for each group's reduced mode using the

R package 'PIECEWISESEM' (Lefcheck 2016). For each group with a significant relationship between adult live tissue area and recruitment identified via step-wise model selection, we further used simple linear regression to determine significant relationships between adult live tissue area and recruitment within and across regions each year. For each significant relationship, we calculated Pearson's ρ as well as the intercept. To determine the directionality of significant relationships and visualize model predictions, we used the R package 'sjPlot' (Lüdecke 2022) to produce marginal effects plots of predicted values for supported continuous variables.

3. RESULTS

We counted 11 633 scleractinian coral recruits across 3 yr long saturations (2016–2018) at 30 sites throughout the FRT. Across all 3 yr, 7825 recruits (67%) were identifiable to at least the family level, all but 8 of which belonged to the families Agariciidae (870 recruits), Poritidae (1433 recruits), Faviidae (99 recruits), and Siderastreidae (5415 recruits). Faviid recruits were difficult to identify to species, but 31 (31%) were identified as the brooding species *Favia fragum* — *Manicina areolata* is the only other known brooder in the family (Jaap 2015) — and none were suspected to belong to the endangered, broadcast spawning, framework-building genus *Orbicella*. Based upon the composition of the adult coral community at the study sites (FWRI 2022a,b) and the juvenile community (L. Huebner et al. unpub. data), in which *Siderastrea siderea* individuals were very common (93% of all siderastreid juveniles) and *S. radians* individuals were rare (6% of all siderastreid juveniles), we suspect that the majority of the siderastreid recruits were the broadcast spawning species *S. siderea*. Furthermore, the majority of larger siderastreid recruits (>1 cm) were visually identifiable as *S. siderea*. The 8 identified recruits belonging to families other than Agariciidae, Poritidae, Faviidae, and Siderastreidae were within the broadcast spawning family Acroporidae (n = 1; *Acropora* spp.), brooding family Pocilloporidae (n = 2; *Madracis decactis*), or mostly broadcast spawning family Meandrinidae (n = 5), including *Meandrina meandrites* (n = 2) and *Dichocoenia stokesii* (n = 1). Either due to their small size or damage to their skeletal structures, a proportion of recruits were unidentifiable each year: 50 in 2016 (out of n = 629; 8%), 168 in 2017 (out of n = 1279; 13%), and 3590 in 2018 (out of n = 9725; 37%).

3.1. Hypothesis 1: temporal and spatial variation in recruitment rates for corals of the western Atlantic and Caribbean is intrinsically linked to reproductive mode

3.1.1. Prediction 1a: brooders recruit to tiles at higher densities than broadcast spawners

In 2016 and 2017, recruitment of the brooding family Poritidae generally outpaced recruitment of the primarily broadcast spawning families Siderastreidae and Faviidae. In 2017, recruitment of the brooding family Agariciidae also exceeded broadcast spawner recruitment in each region except for Southeast Florida. However, in 2018, siderastreid recruitment increased to exceed brooder recruitment in all regions except the Upper Keys (Fig. 1). Siderastreid recruitment was similar across all regions in 2016 and 2017, with no differences between these years within regions, and was low relative to 2018 (Fig. 2). In 2018, the number of siderastreid recruits significantly increased within each region, with the smallest increase in the Upper Keys, followed by Southeast Florida, and with massive 53- and 435-fold increases in the Middle and Lower Keys, respectively (Fig. 2). Because of these increases, Siderastreidae became the dominant recruit family in 2018 (54% of 9725 recruits), reducing poritid and agariciid proportions to only 5 and 4% of total recruitment, respectively, although raw agariciid and poritid recruitment numbers were comparable to 2016 and 2017. Faviid recruitment was consistently low across the reef tract but was lower in Southeast Florida in 2017 and 2018 compared to the Upper Keys in 2017. The number of unidentified recruits was generally comparable across regions in 2016 and 2017 but increased across regions in 2018, especially in the Middle and Lower Keys, in a pattern that reflected the substantial increases in siderastreid recruitment (Fig. 2, Table S2).

3.1.2. Prediction 1b: the patterns of recruitment observed over time are consistent between regions and across depth gradients for both brooders and broadcast spawners

Interactions between region and year were only significant for total scleractinian recruits, and depth × year interactions were only significant for total scleractinian recruits and for siderastreids, suggesting that temporal patterns in recruitment within the other groups (agariciids, poritids, and faviids) spanned the
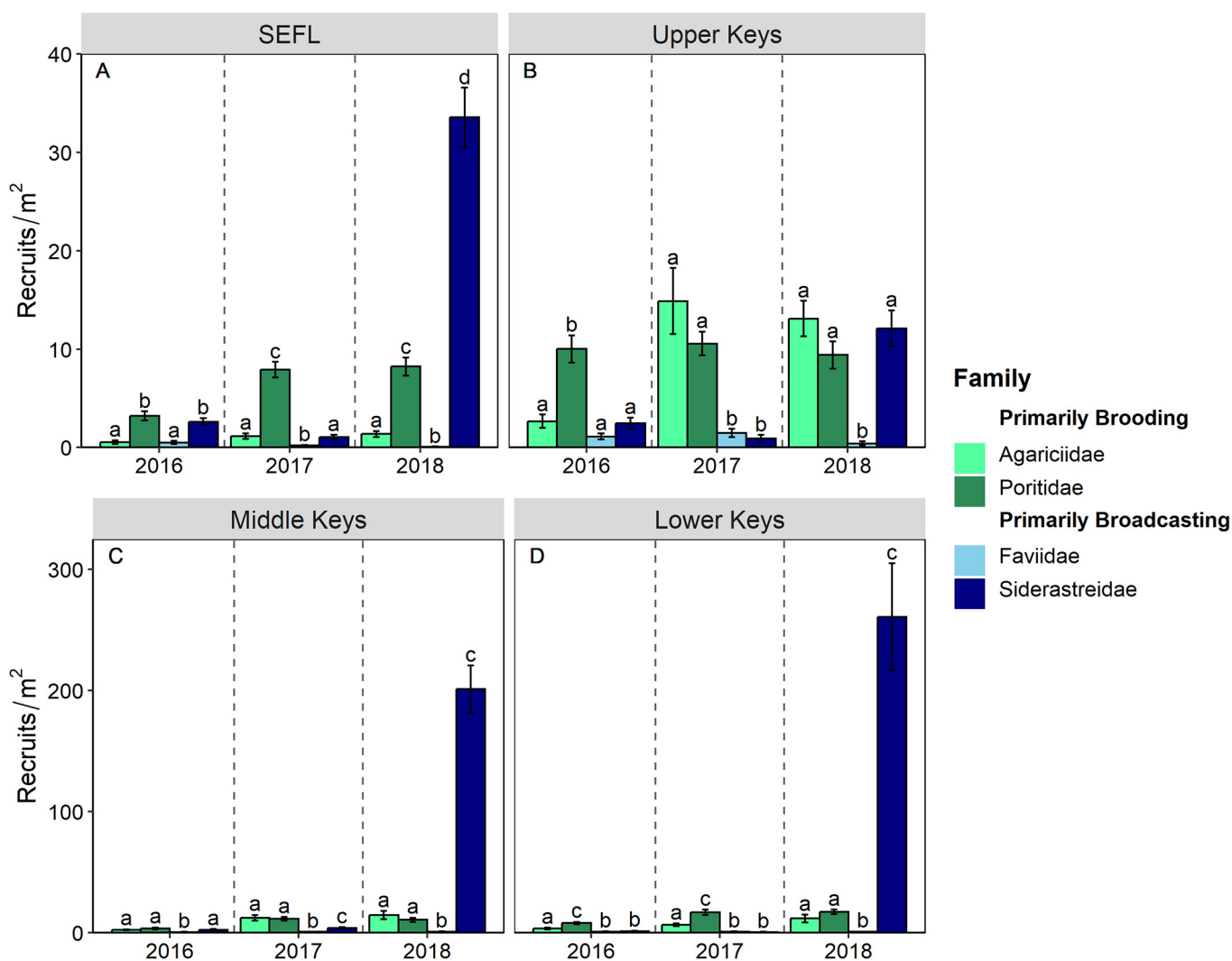
Fig. 1. Mean recruit density for the most abundant brooding families (Agariciidae and Poritidae) and the most abundant primarily broadcast spawning families (Siderastreidae and Faviidae) within each of 4 regions of the Florida Reef Tract (SEFL: Southeast Florida) during each year of a 3 yr study. Letters denote significance groups within, but not across, years nested within regions. Note that the *y*-axis is scaled differently by region

study regions and depth gradient (Table 1). Mean scleractinian recruit density across the FRT differed significantly across years (Kruskal-Wallis $\chi^2_2 = 565.5$, $p < 0.001$), with 11.5 recruits m^{-2} in 2016, 23.4 recruits m^{-2} in 2017, and 197.9 recruits m^{-2} in 2018 (Fig. 3). Within-site variation in total recruitment over the 3 yr ranged from a 1.3-fold difference at the site with the smallest change to a 402.8-fold difference at the site with the largest change. At the sites with the largest differences in recruitment between years, these changes were driven by siderastreid recruitment, which increased significantly between 2017 and 2018 at 23 of 30 sites (Dunn's $p < 0.05$; Fig. 4, Table S3). This influx of siderastreid recruits was spread

throughout the reef tract, occurring at 5 (of 6) sites in the Lower Keys, 6 (of 6) sites in the Middle Keys, 4 (of 6) sites in the Upper Keys, and 8 (of 12) sites in Southeast Florida. Additionally, recruitment of total scleractinians increased significantly at 19 sites from 2017 to 2018, all of which saw significant siderastreid increases (Fig. 4, Table S3).

The siderastreid boom was evident in CREMP and SECREMP *in situ* surveys of juvenile corals in subsequent years, where in all regions except Southeast Floria, an increase in *S. siderea* juvenile density was observed in 2020 (Upper and Middle Keys) or 2021 (Lower Keys; Fig. 5), 3–4 yr after initial settlement. At published *S. siderea* recruit growth rates (4 mm lin-
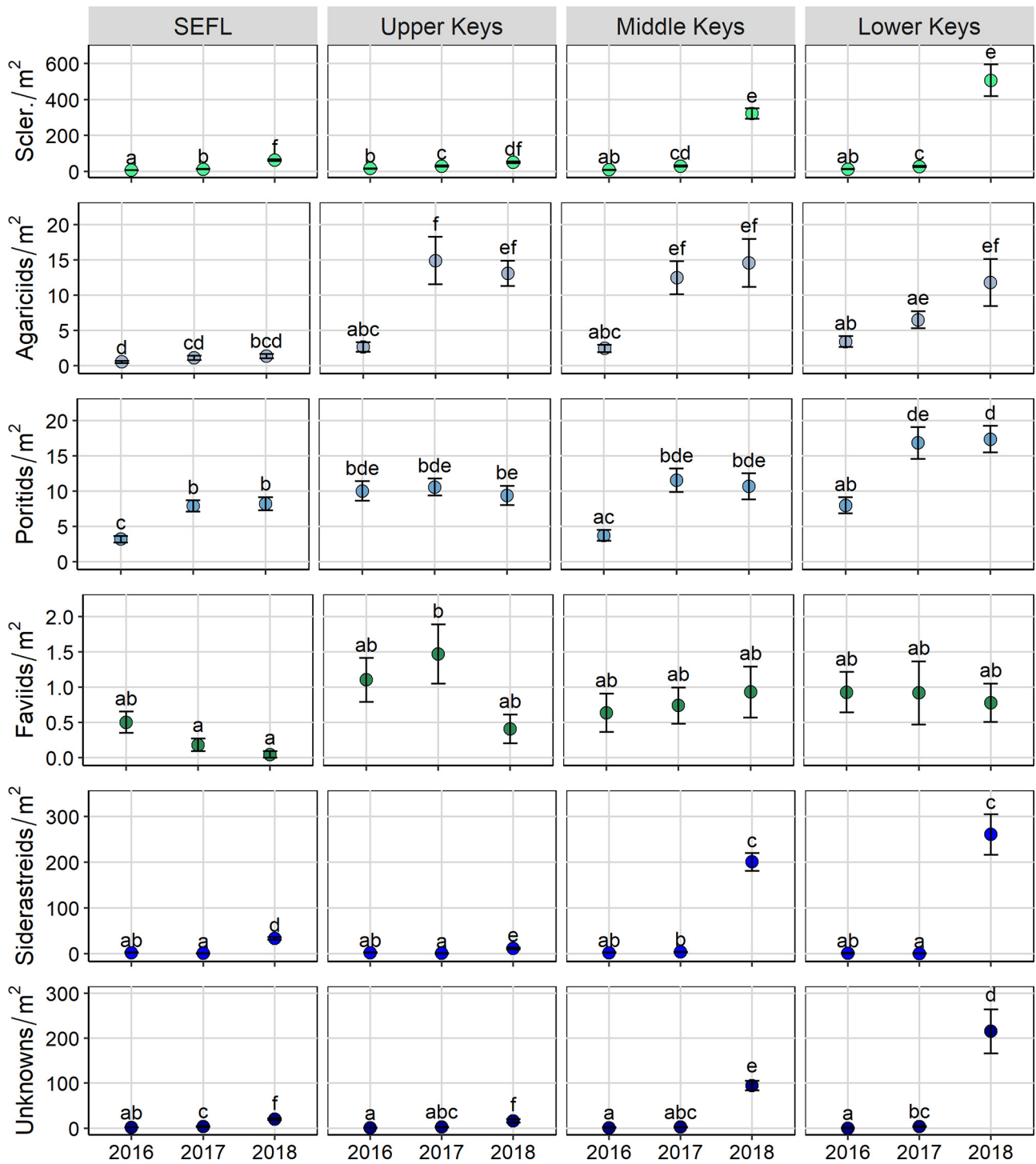
Fig. 2. Mean (±SE) recruit density on settlement tiles of total scleractinians (Scler.), family-level, and unidentified (unknown) scleractinian recruits each across 3 yr within 4 regions of the Florida Reef Tract (SEFL: Southeast Florida). Letters denote significant differences in recruit count across all region−year combinations within each taxonomic group (Tukey's HSD, p < 0.05). Note that the *y*-axis is scaled differently for each group

ear growth each year; Elahi & Edmunds 2007), juveniles could be expected to be approximately 10–15 mm in diameter in 2020–2021 and readily de-

tected during *in situ* transect surveys. Reported growth rates for *S. radians* are slightly faster (~6 mm yr^{-1}; Lirman & Manzello 2009); however, *S. radians*

Table 1. Negative binomial generalized linear models investigating the effects of year, region, depth, and live tissue area (LTA) of adult corals, and mean temperature from April to September for each site on total and family-level scleractinian recruitment across 3 yr and 30 sites within 4 regions of the Florida Reef Tract. The full model with all factors and covariates was compared to all possible combinations of reduced models using Akaike's information criterion (AIC), and the model with the lowest AIC was tested for significance using Type II ANOVA. Factors and covariates that were removed from the model with the lowest AIC are denoted 'na,' and significant p-values ($p < 0.05$) are in **bold**; the directions of significant relationships between recruitment and covariates are indicated in square brackets. All scleractinian LTA at the site was used for the total scleractinian model. LTA from confamilial scleractinians was used for the family models; spring was specified for the brooding families (Agariciidae and Poritidae) and summer for the primarily broadcast spawning families (Faviidae and Siderastreidae)

	Total Scleractinian		Agariciidae		Poritidae		Faviidae		Siderastreidae	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Year	136.1	**<0.001**	na	na	1.3	0.531	1.4	0.490	210.2	**<0.001**
Region	20.3	**<0.001**	99.4	**<0.001**	17.1	**<0.001**	32.3	**<0.001**	19.3	**<0.001**
Year × Region	17.5	**0.008**	na	na	12.5	0.052	na	na	8.3	**0.214**
Depth	0.1	0.763	7.4	**0.007 [−]**	na	na	7.9	**0.005 [+]**	11.2	**<0.001 [+]**
Year × Depth	6.9	**0.031**	na	na	na	na	na	na	16.3	**<0.001**
Confamilial LTA	22.6	**<0.001 [+]**	35.1	**<0.001 [+]**	42.0	**<0.001 [+]**	3.1	0.079	5.1	**0.024 [−]**
Year × LTA	21.4	**<0.001**	na	na	na	na	4.4	0.112	15.1	**<0.001**
Region × LTA	na	na	na	na	28.5	**<0.001**	9.2	**0.027**	22.3	**<0.001**
Mean temp.[a]	3.8	**0.050 [−]**	33.9	**<0.001 [−]**	23.2	**<0.001 [−]**	na	na	3.9	**0.049 [+]**
Model R^2	0.88		0.57		0.56		0.37		0.86	

[a]Apr–Sep, year of recruitment

juveniles were less abundant *in situ* and did not show the same pattern of increase (except for a small increase in density in the Upper Keys). For the individual sites with the highest contributions to siderastreid recruitment in our study, the spike in observed juveniles was even more pronounced, with all but one of the 10 sites with highest siderastreid recruit density on settlement tiles in 2018 showing a clear increase in *S. siderea* juvenile density in 2020 or 2021. Meanwhile, *S. radians* juveniles were uncommon or absent at these same sites (Fig. S1).
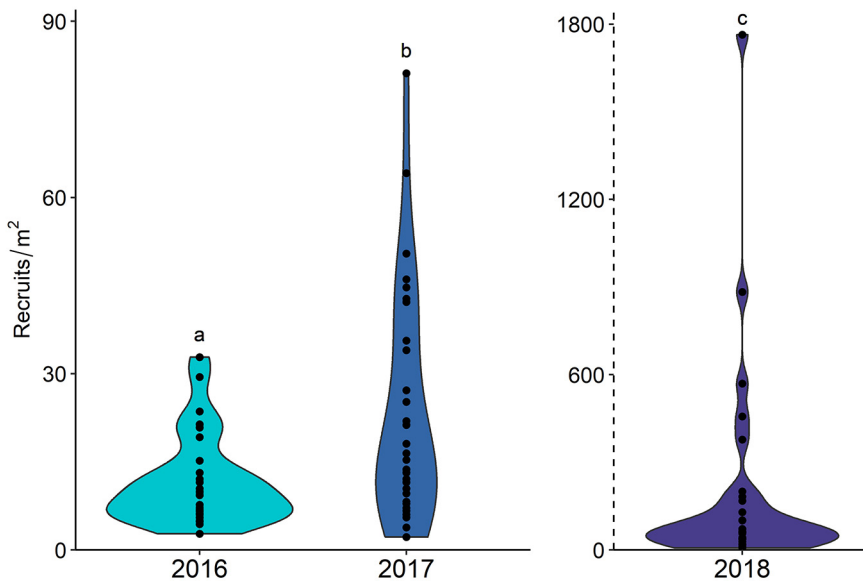

Fig. 3. Distribution of total scleractinian recruit density on settlement tiles during 2016–2018 across 30 sites in the Florida Reef Tract. Each dot within the violin plot represents density per site, calculated by pooling all recruits and dividing by total available settlement area; the shape of the violin plot indicates the distribution of the sites by recruit density. Significantly more recruits settled in each successive year of study (Kruskal-Wallis $\chi^2_2 = 565.5$, $p < 0.001$). Letters denote significance assigned by Dunn's post hoc pairwise comparisons. The 2018 plot is represented on a different axis because the maximum site-level recruit density was 22-fold greater than the maximum density in 2017

3.2. Hypothesis 2: temporal and spatial variation in recruitment rates underlying scleractinian reproductive modes are altered by extrinsic factors that differ in their magnitude and predictability

3.2.1. Prediction 2a: recruitment rates correlate positively with live tissue area of confamilial adults for both brooders and broadcast spawners

In all 3 yr, both agariciid and poritid recruitment had a significant positive linear relationship with confamilial adult live tissue area across the FRT (i.e. when all 30 sites were combined), but this relationship was only significant each year for a sub-
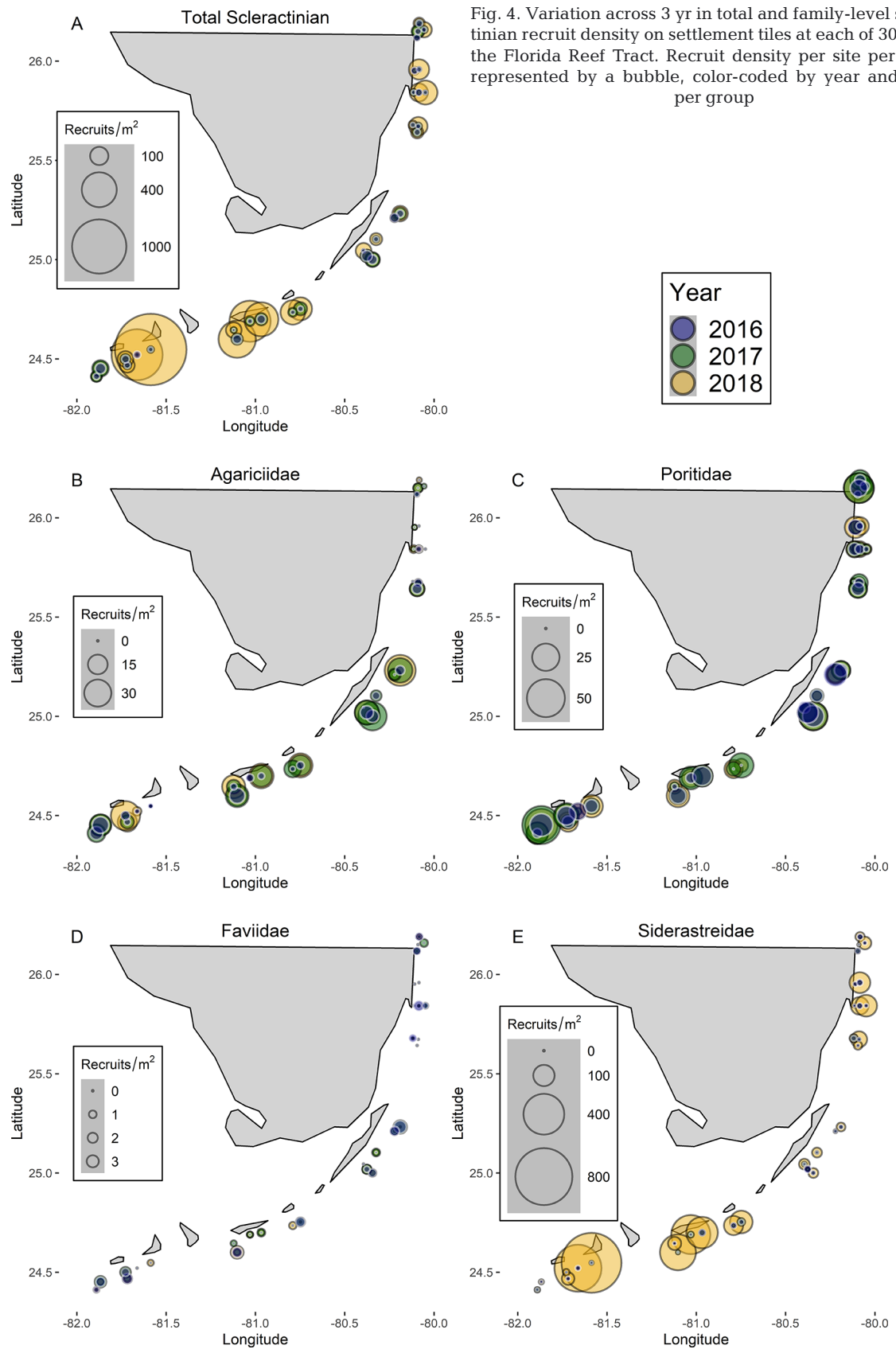
Fig. 4. Variation across 3 yr in total and family-level scleractinian recruit density on settlement tiles at each of 30 sites in the Florida Reef Tract. Recruit density per site per year is represented by a bubble, color-coded by year and scaled per group
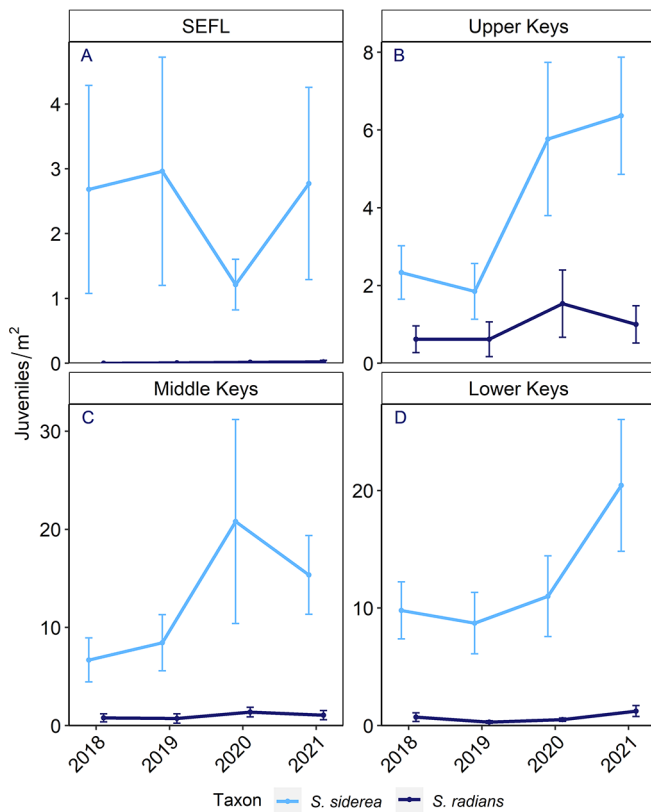
Fig. 5. Mean (±SE) density of *Siderastrea siderea* (light blue) and *S. radians* (dark blue) juveniles <4 cm in diameter recorded in the Coral Reef Evaluation and Monitoring Project (CREMP) and the Southeast Florida Coral Reef Evaluation and Monitoring Project (SECREMP) surveys in the years following the coral recruitment study, partitioned by region. Note that the scale of the *y*-axis differs by region

set of the regions (Fig. 6, Table 2). For agariciids, the linear relationship was significant every year in Southeast Florida, in 2016 and 2018 in the Middle Keys, and in 2017 and 2018 in the Upper Keys. For poritids, the relationship was significant in 2016 and 2018 in Southeast Florida and in 2017 in the Middle Keys. By contrast, siderastreids only exhibited a significant within-year linear relationship between live tissue area and recruitment in 2018, when positive relationships were identified across the reef tract and within the Upper and Lower Keys. Meanwhile, Southeast Florida exhibited a negative relationship between adult siderastreid live tissue area and recruitment (Fig. 6C, Table 2). When examined across years and accounting for covariates including depth and temperature, the overall relationship between siderastreid live tissue area and recruitment was negative, and there was a significant effect of the interaction between region and live tissue area on faviid recruitment.

3.2.2. Prediction 2b: recruitment rates are inversely correlated with abnormally high water temperatures occurring during the months when most scleractinians reproduce

We found a negative relationship between total scleractinian recruitment and the mean daily bottom water temperature from April to September that differed among years (ANOVA, $F_2 = 171.1$, p < 0.001; Fig. S2, Table S4) and was warmest in 2015 and cooler in 2016 and 2017 (Tukey's HSD, p < 0.05). The primarily broadcast spawning family, Faviidae, showed no relationship between recruitment and temperature. By contrast, for the other primarily broadcast spawning family, Siderastreidae, the relationship between temperature and recruitment was weakly supported (ANOVA, likelihood ratio $\chi^2_1 = 3.9$, p = 0.049) but positive, with predicted recruitment increasing with temperature (Fig. S3).

4. DISCUSSION

We monitored coral recruitment in 3 successive years (2016–2018) at 30 sites throughout the FRT and counted a total of 11633 scleractinian recruits with significant interannual variation in density. While year-to-year variation in recruitment is well documented (Edmunds 2017, Burt & Bauman 2020, Evans et al. 2020) the magnitude of interannual variation we recorded in this study is much greater than previously reported in both the Atlantic and Indo-Pacific. At all sites combined, the density of scleractinian recruits increased dramatically in 2018 compared to the prior 2 yr: there was a 17.2-fold increase from 2016 and an 8.4-fold increase from 2017. By contrast, other long-term studies of recruitment have commonly identified roughly 2-fold interannual variation: overall recruitment decreased by slightly more than half from the first to the second year in Abu Dhabi, United Arab Emirates (Burt & Bauman 2020), and in a 4 yr study off the Pilbara Coast, NW Australia, overall recruit density doubled between the lowest and highest year (Evans et al. 2020). Although other extreme pulses in coral recruitment have been observed, these have been at localized subsets of study sites in the Indo-Pacific (Davidson et al. 2019, Adjeroud et al. 2022), with only one recorded pulse event in the Atlantic, which was a nearly 2-fold increase of *Orbicella* spp. recruits to natural substrate across a 4 km area in St. John, US Virgin Islands (Edmunds et al. 2011).
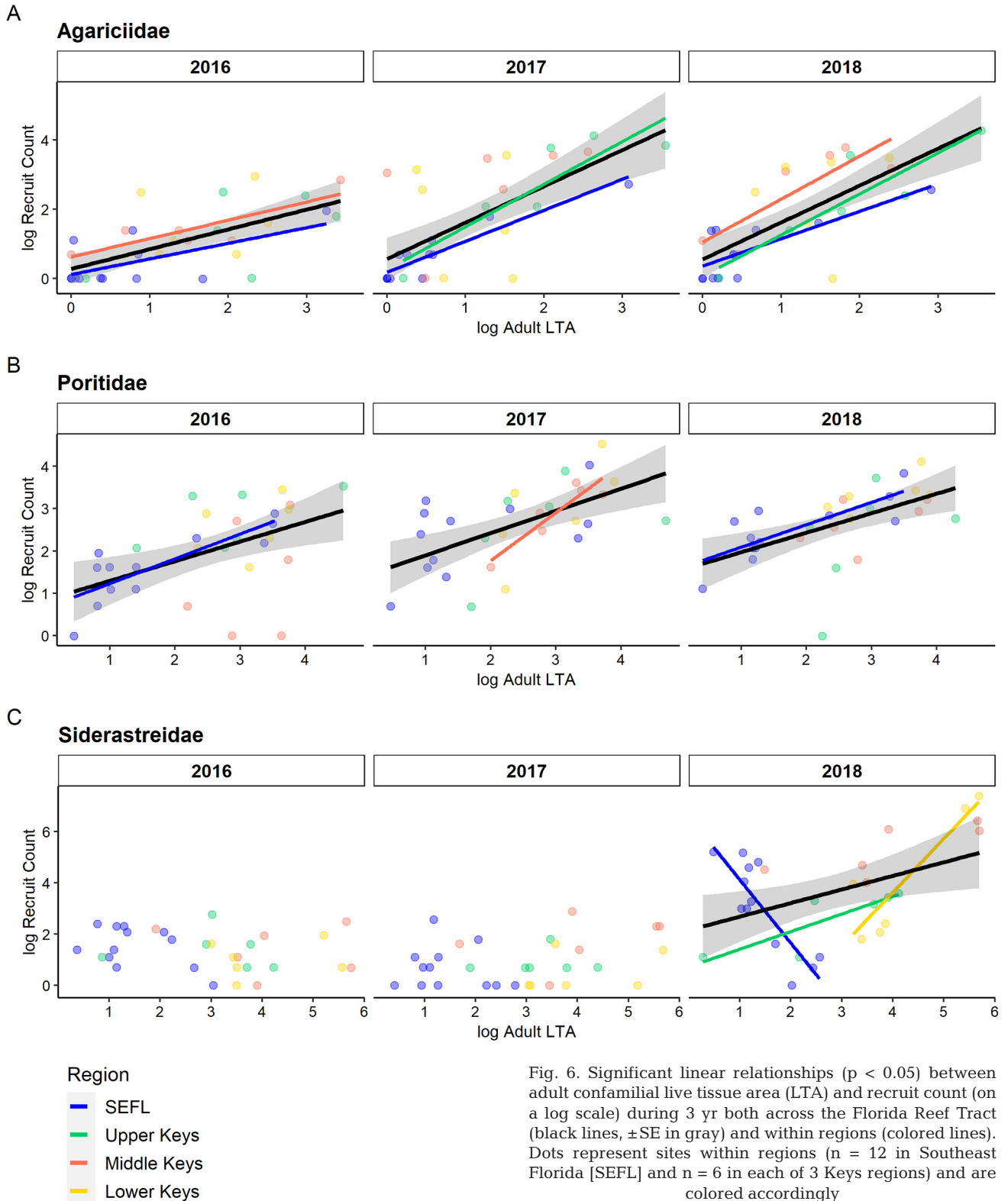
A

Agariciidae

B

Poritidae

C

Siderastreidae

Region
- SEFL
- Upper Keys
- Middle Keys
- Lower Keys

Fig. 6. Significant linear relationships (p < 0.05) between adult confamilial live tissue area (LTA) and recruit count (on a log scale) during 3 yr both across the Florida Reef Tract (black lines, ±SE in gray) and within regions (colored lines). Dots represent sites within regions (n = 12 in Southeast Florida [SEFL] and n = 6 in each of 3 Keys regions) and are colored accordingly

As western Atlantic coral communities become increasingly dominated by weedy, stress-tolerant, and mostly brooding corals (Green et al. 2008), distinguishing the rates and patterns of recruitment between brooding and broadcast spawning corals is important for predicting reef community trajectories. Identifiable recruits in our study belonged almost exclusively to the brooding families of Agariciidae

Table 2. Pearson's correlation coefficients, intercepts, and p-values of significant (p < 0.05) linear models regressing confamilial scleractinian adult live tissue area and recruitment over 3 yr within and across 4 regions of the Florida Reef Tract (SEFL: Southeast Florida). Across-region relationships are shown in **bold**

Family	Year	Region	Pearson's ρ	Intercept	p
Agariciidae	2016	SEFL	0.60	0.72	0.039
		Middle Keys	0.84	0.12	0.035
		All Regions	**0.61**	**0.23**	**<0.001**
	2017	SEFL	0.94	0.47	<0.001
		Upper Keys	0.89	0.73	0.016
		All Regions	**0.65**	**0.09**	**<0.001**
	2018	SEFL	0.78	0.22	0.003
		Upper Keys	0.90	0.92	0.015
		Middle Keys	0.84	0.15	0.036
		All Regions	**0.70**	**0.07**	**<0.001**
Poritidae	2016	SEFL	0.82	0.17	0.001
		All Regions	**0.51**	**0.18**	**0.004**
	2017	Middle Keys	0.92	0.52	0.009
		All Regions	**0.60**	**0.01**	**<0.001**
	2018	SEFL	0.80	0.00	0.002
		All Regions	**0.61**	**0.00**	**<0.001**
Siderastreidae	2018	SEFL	-0.84	0.00	0.001
		Upper Keys	0.84	0.35	0.036
		Lower Keys	0.90	0.10	0.016
		All Regions	**0.43**	**0.02**	**0.018**

and Poritidae and the primarily broadcast spawning families of Faviidae and Siderastreidae. Recruitment of the agariciids and poritids was consistent across all 3 yr and higher than that of the faviids and siderastreids in 2016 and 2017. Therefore, in those 2 years in Florida, brooders dominated recruit cohorts, consistent with records throughout the western Atlantic and Caribbean (Bak & Engel 1979, Rogers et al. 1984, Smith 1992, Rubin et al. 2008, Arnold & Steneck 2011, Humanes & Bastidas 2015) and in accordance with our first prediction that brooders recruit at higher rates than broadcasters. The patterns of agariciids and poritids (brooder) recruitment also aligned with our second prediction: while their recruitment was slightly depressed in most regions in 2016 compared to 2017 and 2018 (Fig. 2), year overall was not a significant factor predicting recruitment for either family, and no interaction was identified between region and year or depth and year (Table 1), demonstrating temporal consistency across these spatial gradients.

The link between recruitment patterns and reproductive mode for broadcast spawning corals is more difficult to discern. Faviid recruitment was low relative to all other families, and while it varied across years (Table 1) and generally increased with depth (Fig. S4), the patterns were consistent across regional

and depth gradients, evidenced by the lack of interaction between region and year and depth and year (Table 1). Although most of the members of Faviidae are broadcasters, about one-third (31%) or more of our faviid recruits were the brooding species *Favia fragum*. The general consistency in faviid recruitment, while in alignment with our second prediction of recruitment consistency over time and space, may thus have been driven by a brooding species. Further, faviid recruitment in our study year in Florida aligned with our first prediction of brooders recruiting at higher densities than broadcasters, in that a higher proportion of the faviid recruits were represented by a single brooding species than were represented by any individual member of the larger proportion of broadcasting members in the family.

Patterns of siderastreid recruitment did not align with either of our first 2 predictions on the link between recruitment variation and reproductive mode. While siderastreid recruitment did not vary within regions and varied little across regions between 2016 and 2017, it dramatically increased in 2018 by 70.7-fold compared to 2017 and 31.9-fold compared to 2016 (Fig. 2). Unlike the speciose Faviidae, Siderastreidae in Florida includes only 2 species: the brooder *Siderastrea radians* and the broadcast spawner *S. siderea*; based on recruit morphological identification, and the composition of the adult and juvenile communities (Figs. 5 & S1), the majority of our siderastreid recruits were *S. siderea*. Therefore, the more than 1000% increase in siderastreid recruits between 2017 and 2018 at 13 of 30 sites distributed across the reef tract was the result of a broadcast spawner boom, such that siderastreids dominated the recruit cohort at most sites in 2018. Due to the siderastreids, recruitment in Florida in 2018 did not align with our first prediction of brooders recruiting at higher densities on tiles. Additionally, siderastreid recruitment also did not follow our second prediction of consistency over time across depth gradients, in that we observed an interaction between year and depth in siderastreid recruitment, in which the positive association between recruitment and depth was more pronounced in 2018, when recruitment rates were elevated (Table 1). The 2018 siderastreid densities (site means range: 0.7–888.7 m^{-2}) were

unprecedented and high relative even to overall scleractinian recruitment rates reported from elsewhere in the Caribbean; for example: 50–175 m^{-2} in Bonaire (Arnold et al. 2010), 14–117 m^{-2} in St. John (Edmunds et al. 2014), and 30–236 m^{-2} in Los Roques, Venezuela (Humanes & Bastidas 2015). This massive increase in siderastreids in 2018 (Fig. 1) drove the patterns observed for total scleractinian recruitment (Figs. 2–4) and was reflected in those of the unidentified recruits (Fig. 2). The similarity of these patterns indicates that the unidentified recruits likely included many underdeveloped siderastreid individuals, meaning that our already massive siderastreid densities in 2018 were conservative estimates.

Overall, our results demonstrate a link between spatial and temporal variation in recruitment based on reproductive mode in Florida: brooding corals had consistent recruitment rates both spatially and temporally while recruitment of broadcast spawning corals reflected a boom-and-bust pattern that greatly influenced the outcomes for time and space. The brooding reproductive strategy may be more reliable than broadcast spawning because brooding corals are more likely to be able to self-fertilize (Brazeau et al. 1998, Carlon 1999, Gleason 2001) as well as conserve energy and reduce mortality risk by dispersing short distances (Szmant 1986). Additionally, brooding taxa often have more opportunities to planulate throughout the year than broadcast spawners have opportunities to spawn (Szmant 1986). These factors may reduce brooding species' reliance on favorable extrinsic factors during an isolated time period to achieve a 'successful' reproductive season. Meanwhile, broadcast spawners, as demonstrated by *S. siderea*, may be more likely to exhibit boom-and-bust patterns of recruitment similar to some other marine organisms (Uthicke et al. 2009, Sams & Keough 2012, Szuwalski et al. 2019), for which extrinsic factors such as water and weather conditions during 1 or 2 spawning events may make or break recruit output for the year.

The FRT has experienced sustained chronic pressures on coral populations that are overlaid with an increasing frequency of acute disturbances (Jones et al. 2022). These extrinsic factors were particularly variable prior to and during the 3 yr of this study: significant bleaching in the summers of 2014 and 2015 (NOAA Coral Reef Watch 2015), the start of the SCTLD outbreak in 2014 in Southeast Florida and eventual spread through the Middle Florida Keys by 2018 (Walton et al. 2018, Muller et al. 2020), and the landfall of Hurricane Irma in the Lower Keys in September 2017 (Kobelt et al. 2020). These major

stressors likely all had potential influences on coral recruitment in addition to their impact on the tissue area of adult corals. We predicted that recruitment rates would correlate positively with the tissue area of confamilial adult corals and found a positive correlation between agariciid and poritid (brooder) recruits and adult confamilial live tissue area (Fig. 6A,B, Tables 1 & 2). Abundances of juvenile brooders surveyed *in situ* have previously been found to correlate with adult conspecific abundances in the Florida Keys (Chiappone & Sullivan 1996, Moulding 2007). Because juvenile corals recorded *in situ* are often 1–3 yr old (Moulding 2007), they represent corals that have survived to detectability. Thus, the positive relationship between conspecific juveniles and adults could be interpreted as either environmental filtering, self-seeding, or a combination of the two. However, settlement tiles can detect much younger recruits, which, when bleached, include those that perished shortly after laying skeletal material. Here, the relationship between conspecific recruits and adults is more likely to be a function of short dispersal distances characteristic of brooders (Ayre & Hughes 2000, Underwood et al. 2007, Figueiredo et al. 2014, Holstein et al. 2014) and may indicate self-seeding of brooding species.

In contrast with the brooders, the recruitment of broadcast spawning siderastreids was not always correlated with confamilial adult live tissue area (Fig. 6C, Tables 1 & 2). Within the 2018 recruit cohort, the relationship between adult siderastreid live tissue area and siderastreid recruitment in the Lower Keys was characterized by high-cover, high-recruitment sites (Fig. 6C). However, further from the focal point of the recruitment boom in the Lower and Middle Keys, the strength and slope of the adult–recruit relationship declined and became significantly negative in Southeast Florida, where siderastreids largely recruited to the deeper outer reef terrace where live cover of all corals is very low (<1%; Fig. 2). Using biophysical modeling, Frys et al. (2020) identified Lower and Middle Keys patch reefs as likely source locations and the outer reefs of Southeast Florida as likely sink locations for broadcast spawned larvae. Additionally, models of *Montastraea cavernosa* larval dispersal suggested that Hurricane Irma enhanced connectivity throughout the reef tract by accelerating larval transport (Meurice et al. 2019). The September arrival of Irma is within the generally accepted spawning time frame for *S. siderea* (Szmant 1986, St. Gelais et al. 2016, Jordan 2018); therefore, the hurricane may have increased export of *S. siderea* larvae from reefs with high siderastreid cover in the Lower and Middle Keys to coral-depauperate

reefs in Southeast Florida, such as those in the outer terrace, where recruitment was significantly elevated in our 2018 cohort. Weather conditions enhancing larval export could serve as an example of environmental variables 'making' rather than 'breaking' the success of a broadcast spawning species' reproductive output and dispersal for the year. However, we cannot exclude the possibility that the entire 2018 siderastreid recruit cohort may have been imported from elsewhere in the Caribbean, as genetic connectivity has been demonstrated in *S. siderea* populations separated by up to 1200 km (Nunes et al. 2011).

Temperature has recently been identified as an extrinsic, relatively unpredictable factor modulating temporal patterns in coral recruitment (Edmunds 2021). Elevated temperature during the preceding reproductive season was identified as a negative predictor of recruitment for both brooding families Agariciidae and Poritidae. This pattern is likely the result of elevated temperatures during 2015 that were associated with low recruitment in 2016 relative to the 2 subsequent years. Establishing a causal relationship between temperature and recruitment is not possible from *in situ* studies such as this one, as many confounding variables are present (e.g. turbidity, oceanographic variables). However, elevated sea temperatures and resultant coral bleaching have been shown to reduce the abundance and size of oocytes in affected colonies (Ward et al. 2002, Howells et al. 2016, Johnston et al. 2020). Impaired stock–recruitment relationships due to adult coral fatalities from temperature stress are another possible mechanistic link between elevated temperature and depressed recruitment (Hughes et al. 2019). However, as our models accounted for confamilial live tissue area (stock), the negative relationship between temperature and recruitment that we observed for brooders is unlikely to be completely explained by depleted stocks and instead may represent the negative effects that temperature has on larvae directly (Humanes et al. 2016, Ritson-Williams et al. 2016). As global sea temperatures continue to rise, Florida reefs could become increasingly dominated by siderastreids, whose recruitment was positively but weakly related to warmer temperatures in our study. Siderastreid recruitment could be minimally affected by thermal stress because siderastreids may be more resistant or resilient to temperature-induced bleaching than other Caribbean species (Smith et al. 2013, Neal et al. 2017) and *S. siderea* is known to thrive in marginal habitats throughout much of Florida (Hine et al. 2008). Still, research into the true nature of rela-

tionships between temperature and coral recruitment is required.

The effects of both adult live tissue area and temperature were less clear for Faviidae. We found no association between faviid recruitment and temperature. There was also no identified relationship, within or across years, between faviid adult tissue area and faviid recruitment, likely in part because <1% (n = 99) of all recruits were members of the family Faviidae, and at least 31% of them were the small (<100 cm^2) brooding species *F. fragum*, the adults of which contribute a small fraction of live tissue area to the site total and contribute little to reef structure (Soong 1993). In general, Faviidae is a more speciose coral family than the others examined, such that abundant live tissue area of one faviid species is unlikely to predict recruitment of a different faviid species, and uncertainty in identifying recruits to species precludes a species-level model of faviid recruitment. Many of the reef-building, mountainous species grouped in the Faviidae family in this study, in particular *M. cavernosa*, *Orbicella faveolata*, *Colpophyllia natans*, and *Pseudodiploria strigosa*, are highly susceptible to SCTLD (Muller et al. 2020). Disease may have depressed recruitment rates as a result of compromised health and/or loss of adult live tissue area in Southeast Florida and the Upper Keys, where the disease was active during much of the study period. However, we did not identify changes in faviid recruitment across time, even as SCTLD became more prevalent throughout the study region.

Historically, the main builders of reef framework in the Florida Keys were in the genera *Orbicella* (Faviidae herein) and *Acropora* (Acroporidae; Precht & Miller 2007, Toth et al. 2019). No confirmed *Orbicella* recruits and just one *Acropora* recruit were found on 2778 tiles during our 3 yr of study. This is consistent with decades of studies in the Caribbean region that have observed p oor recruitment and low juvenile densities of these genera, especially relative to brooding species (Bak & Engel 1979, Rogers et al. 1984, Smith 1992, Williams et al. 2008). By contrast, a relatively recent assessment of recruitment in the Florida Keys recorded a high number of acroporid recruits (24) on an order of magnitude fewer tiles (240 tiles; van Woesik et al. 2014) than deployed in the current study. The acroporid recruit number documented in this earlier study may have been inflated due to the challenges of identifying very small recruits that had minimal time to develop post-settlement (1–2 mo in their study as opposed to >6 mo in our study). Additionally, the example photo in van Woesik et al. (2014) is inconsistent with photos of 2 mo old acroporids

reared in the lab from known acroporid crosses (Fig. S5). Personal communication with the authors of that publication indicated that additional photographs and voucher specimens are unavailable. While some portion of the recruits may have been misidentified, it is entirely possible that their result represents a rare, mass recruitment event for *Acropora*, providing further support for a boom-and-bust life history for broadcast spawning coral species in the Atlantic and Caribbean. Even *S. siderea*, a broadcast spawner that is one of the most abundant adult species along the FRT, was among the relatively low recruit densities (0.6–3.8 recruits m^{-2}) for siderastreids in 2016 and 2017 before booming in 2018. Therefore, it is possible that other broadcast spawning species, including the framework-building faviid and acroporid taxa, could, given the right conditions, also recruit in boom events as once observed with *Orbicella* recruits in St. John (Edmunds et al. 2011). Had we not conducted our study for a third year, we would have missed the siderastreid boom event entirely; if we had conducted our study only in the Upper Keys, we also would have missed the magnitude of interannual variation that is possible. Thus, multi-year time scales and large spatial areas of study will be required to adequately assess the frequency with which siderastreids experience boom-and-bust cycles as well as the possibility of other broadcast spawner mass recruitment events.

Our observations revealed distinctions between brooding and broadcasting taxa, suggesting that coral recruitment patterns are intrinsically linked to reproductive mode. Brooding poritid and agariciid corals recruited consistently over the 3 yr, indicating their potential to endure and recover after prolonged periods of temperature stress (*Porites astreoides*; Kemp et al. 2016) and associated bleaching (*P. porites* and *Agaricia agaricites*; Wagner et al. 2010) and a multi-year disease outbreak (Walton et al. 2018, Muller et al. 2020). Furthermore, the spatial distribution of poritid and agariciid recruits tracked predictably with the distribution of adult live coral tissue from the same families. Our results suggest that the recruitment success of broadcast spawned larvae is influenced by stochastic processes and is less predictable across space and time than recruitment of brooding species.

The broadcast spawning *S. siderea* demonstrated the ability to mass-recruit during a boom event in 2018, which resulted in siderastreids dominating the recruit cohort that year over scales of 100s of km, irrespective of local coral cover and temperature. Even though the siderastreid-dominant recruit cohort only occurred in the third year of our study, *S. siderea* are

often among the most common juvenile corals recorded *in situ* in Florida (Miller et al. 2000, Moulding 2007, L. Huebner et al. unpub. data); however, in highly disturbed habitats such as shipwreck decks, *S. radians* is occasionally more locally abundant (Vermeij & Sandin 2008). As has been hypothesized for other broadcasting taxa (Rogers et al. 1984, Smith 1992), *S. siderea* may compensate for bust recruitment years through high survivorship of recruits from boom years, resulting in their consistently high relative representation among *in situ* juvenile communities. While a few marine invertebrate species have been shown to recruit in boom-and-bust patterns (Uthicke et al. 2009, Sams & Keough 2012, Szuwalski et al. 2019), the phenomenon has been much more thoroughly described and investigated in long-lived plant species (Kelly 1994, Pesendorfer et al. 2021). High but synchronous interannual variation in seed availability, called mast seeding, has occasionally been compared to coral spawning patterns (Kelly & Sork 2002). Mast seeding has been hypothesized to be more common in plants than animals in part because plants' longer life spans dilute the consequences of missed reproductive opportunities (Kelly & Sork 2002). However, the extent to which mast seeding is driven by stochastic forces versus selective pressure is still up for debate, and research progress has been slow due to the time scales over which such interannual variation must be observed in long-lived species (Koenig 2021). Our understanding of potential patterns of boom-and-bust recruitment in corals is less advanced because coral recruitment is much more difficult to observe than mast seeding. Nevertheless, we can hypothesize that among coral taxa, those with longer life spans and broadcast spawning reproductive modes may be subjected more to both selective and stochastic processes, encouraging patterns resembling mast seeding. *S. siderea* is slow-growing and long-lived: colonies 20–58 cm in diameter sampled in the Florida Keys were aged to be between 34 and 107 yr old (Rippe et al. 2018), and several colonies in the CREMP database exceed 100 cm in diameter. Patterns of high interannual variability in reproduction may have been selected for in *S. siderea* if benefits such as optimal currents or predator satiation (Kelly and Sork 2002) outweigh the consequences of missed reproductive opportunities, ultimately yielding higher long-term recruitment.

While population genetic analysis is needed to confirm, this widespread siderastreid boom event radiating from the patch reefs of the Middle and Lower Keys may be a sign of the potential for sudden influxes of broadcast spawned larvae across a connected

FRT (Frys et al. 2020, King et al. 2023) if source populations can be identified and preserved. Future efforts to identify the factors that facilitate the spawning and recruitment of corals in the Families Acroporidae and Faviidae (as grouped herein), paired with protections for both source populations and newly settled juveniles, could generate increased recruitment of imperiled corals across the world's third largest barrier reef system.

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