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Variation in Coral Recruitment and Juvenile Distribution Along the Southeast Florida Reef Tract

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Thesis of
Leah M. Harper

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Environmental Sciences

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

December 2017

Approved:
Thesis Committee

Major Professor: Nicole Fogarty

Committee Member: Joana Figueiredo

Committee Member: Daniel Gleason

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

VARIATION IN CORAL RECRUITMENT AND JUVENILE DISTRIBUTION
ALONG THE SOUTHEAST FLORIDA REEF TRACT

By

Leah M. Harper

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

Marine Environmental Science

Nova Southeastern University

Thesis of

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ABSTRACT

Coral recruitment in Southeast Florida is being outpaced by mortality, resulting in population declines in many species. Identifying the coral species most likely to recruit and survive on Southeast Florida reefs and evaluating spatial variation in recruitment and survivorship is crucial for managing decreasing coral populations. This study focuses on 12 sites in Broward and Miami-Dade counties that have served as long-term stations for monitoring adult coral cover and demographics. At each site, thirty-two 225cm^2 grooved terracotta settlement tiles were attached to the substrate in winter of 2015 and retrieved in winter of 2016 to evaluate scleractinian and octocoral recruitment rates. Thirty-two corresponding 0.25 m^2 quadrats were surveyed *in situ* for corals <4cm during fall of 2016 to evaluate densities of juvenile scleractinians and octocorals. The densities of recruits and juveniles were compared with adult densities to estimate recruitment success and relative juvenile survivorship. Results suggest that taxa that are tolerant of marginal environmental conditions, such as Poritidae, Siderastreidae, and Octocorallia, exhibit signs of recruitment success and/or juvenile survivorship. Scleractinian recruitment was not variable spatially, but juvenile densities varied on site-level spatial scales, suggesting that differential survivorship structures adult scleractinian communities. This study will inform reef management and restoration efforts within Southeast Florida by identifying sites and species with potential to recover from disturbance through natural recruitment processes.

Keywords: scleractinian, octocoral, recruitment, survival, resilience, settlement

INTRODUCTION

Coral reefs perform vital ecosystem services. Their structure supports the biodiversity that draws snorkelers and tourists and bolsters coastal economies (Moberg and Folke 1999) and millions of people rely on coral reef fisheries for food and livelihood (White et al. 2000, Barnes-Mauthe et al. 2013, Gomes et al. 2014). The protection that coral reefs provide shorelines is critical for low-lying coastal communities facing rising sea levels and intense tropical storms (Elliff and Kikuchi 2017, Elliff and Silva 2017). Between providing shelter for sandy beaches and a tourist attraction in their own right, the world's coral reefs are worth almost $36 billion to the tourism sector, with nearly one third of reefs worldwide contributing directly to the tourism economy of the adjacent country (Spalding et al. 2017).

Worldwide, coral reefs are facing an array of global anthropogenic stressors. Global warming is causing sea surface temperatures to rise, and oceans absorb approximately 25% of global carbon dioxide emissions leading to a chemical reaction that acidifies seawater (Doney et al. 2009, Gattuso and Hansson 2011). Higher temperatures cause corals to release their endosymbiotic dinoflagellates in mass bleaching events (Brown 1997, Hughes et al. 2003), while ocean acidification hinders the calcifying abilities of corals (Hoegh-Guldberg et al. 2007). By 2008, the combined effects of these stressors and other localized impacts had led to a 19% decline in coral reefs (Wilkinson and Souter 2008), causing one third of reef-building corals to be classified as having an elevated extinction risk (Carpenter et al. 2008). Even coral reefs with the highest level of protection are approaching ecological extinction (Pandolfi et al. 2005). Mass extinction of coral reef communities has been predicted to occur by 2050 (Burke et al. 2011).

The majority of reefs worldwide are affected by human exploitation (Halpern et al. 2008). Some of these impacts cause direct physical damage to reef structures, such as destructive fishing, anchor damage, and ship groundings (Davis 1977, Smith 1988, Fiege et al. 1994, Glynn 1994, Edinger et al. 1998, White et al. 2000). Sedimentation from dredging projects and coastal construction is a widespread local stressor that can cause diminished productivity, reduced growth, and mortality in various scleractinian coral

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species (Rogers 1990, Abelson et al. 1999, Bastidas et al. 1999, Erftemeijer et al. 2012, Restrepo et al. 2016, Stubler et al. 2016, Bessell-Browne et al. 2017). Another common stressor is eutrophication of coral reef waters from terrestrial fertilizer runoff and sewage input, which increases turbidity and can lead to increased macroalgal cover (Bell 1992, Edinger et al. 1998, Fabricius 2005, Reopanichkul et al. 2009). Macroalgae in turn inhibits coral recovery by causing polyp damage that reduces fecundity of some scleractinian species (Foster et al. 2008), inhibiting scleractinian recruitment (Birrell et al. 2008), and outcompeting small corals for space and light (Box and Mumby 2007). As climate change increases the frequency of tropical cyclones (Knutson et al. 2010), coral reef damage from storms (Rogers et al. 1983, Mallela and Crabbe 2009, Lugo-Fernández and Gravois 2010) may increase as well. Mass physical damage from storms can be costly for corals. Even if a storm does not result in mortality, corals must divert energy to reattachment and regeneration, initiating a complex immune response to prevent colonization by pathogenic microbes (van de Water et al. 2015).

Caribbean reefs are particularly vulnerable. Species diversity in the Caribbean is historically lower than in the Pacific (Veron 1995). For example, the scleractinian coral genus *Acropora* includes over 100 species in the Indo-Pacific (Wallace and Willis 1994), while the Caribbean has only 2 species and a hybrid (Van Oppen et al. 2000) and hosts only 62 scleractinian coral species total (Spalding et al. 2001). Additionally, the Caribbean has experienced a more drastic decline in scleractinian coral, including crucial reef-building species. Mean coral cover on Caribbean reefs has decreased from 50% in the 1970's to 10% in 2002 (Gardner et al. 2003). Compared with reefs worldwide, a larger proportion of Caribbean coral species are classified as having a high risk of extinction (Carpenter et al. 2008). Overfishing, hurricane damage, coral disease, and mass mortality of grazers (e.g. *Diadema antillarum*) have been suggested to contribute to phase shifts on Caribbean reefs from scleractinian coral dominance to macroalgae dominance (Levitan 1988, Hughes 1994, Nugues and Szmant 2006).

When a population's death rate exceeds its birth rate, the population will decline. For coral reefs to subsist or recover, corals must reproduce and recruit to reefs at a rate equal or greater than the rate at which colonies are dying. Caribbean reefs experiencing increased mortality rates (due to disease, bleaching, etc.) would require drastic increases

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in recruitment and post-settlement survival for populations to persist and degradation to be reversed. However, Caribbean reefs are experiencing recruitment failure. Long-lived and slow-growing species (most Caribbean reef-builders) have lower levels of recruitment than small, short-lived, disturbance-resistant ("weedy") species. and thus are expected to eventually collapse (Hughes and Tanner 2000). Quantifying and understanding coral recruitment and post-settlement survival, particularly in areas where the coral decline has been more drastic, such as the high-latitude Southeast Florida reef tract, is critical for developing effective conservation strategies (Maynard et al. 2015).

Reproduction and successful recruitment are essential for the Southeast Florida reef system to recover from frequent disturbances. Corals can reproduce sexually and asexually. Fragments of boulder-forming species are sometimes able to reattach, but these species often rely on sexual reproduction to propagate (Szmant 1986). Branching corals reproduce sexually, but are also structurally adapted for asexual reproduction and tend to live in dynamic environments where branch breakage is probable, allowing these fast-growing species to dominate their reef zones when conditions are favorable (Highsmith 1982). Like branching scleractinians, octocorals frequently propagate via fragmentation (Lasker 1984, Coffroth and Lasker 1998). While reproduction by fragmentation contributes to increase coral cover, and builds reef framework and rugosity, the formation of new genotypes through sexual reproduction is essential to colonize distant disturbed areas or new habitat, and increase genetic diversity. A higher genetic diversity provides more opportunities for local adaptations to occur and could result in increasingly stress-resistant populations (Baums 2008).

Scleractinian corals reproduce sexually by brooding or broadcast spawning. Broadcast spawning describes the release of positively buoyant gametes into the water column for external fertilization. This mode of reproduction requires spawning synchrony (Szmant 1986). The larvae of broadcast-spawners take two to ten days to become competent to settle and metamorphose, depending on species, with some species surviving in the water column over 200 days when denied access to appropriate substrate (Graham et al. 2008). Most of the large-sized, framework-building scleractinian species in the Caribbean reproduce by broadcast spawning (*Agaricia tenuifolia* is an exception). Of the ESA-listed threatened Caribbean species, only one (*Mycetophyllia ferox*)

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reproduces through brooding (Szmant 1986, Richmond and Hunter 1990). Brooding corals release only sperm and rely on internal fertilization, with maternal polyps releasing competent or nearly-competent planulae (Duerden 1902). Brooded larvae are more likely than broadcast-spawned larvae to recruit locally, though high rates of local retention have been observed through both reproductive mechanisms (Sammarco and Andrews 1988, Ayre and Hughes 2000, Miller and Ayre 2008, Underwood et al. 2009, Figueiredo et al. 2014). The Caribbean has higher abundances of brooding corals than broadcast spawning corals, though the region's brooding species are typically limited to small adult sizes (Szmant 1986, Richmond and Hunter 1990). Because coral larvae tend to develop faster and have higher mortality rates in higher temperatures, models predict that local retention of broadcast-spawned coral larvae will increase as the climate warms (Figueiredo et al. 2014). Due to a combination of high proportion of brooding corals and warming seas, Caribbean reefs are likely to depend heavily on local stocks for population replenishment.

The mechanism of reproduction employed by a coral has implications for the recruitment rates of its larvae. In the Caribbean, broadcast-spawning corals such as *Orbicella* spp., *Pseudodiploria* spp., *Diploria* sp., and *Acropora* spp. historically have dominated the structural framework of reefs yet, for at least the past three decades, have exhibited low rates of recruitment compared with brooding corals such as *Porites astreoides* and *Agaricia agaricites* (Bak and Engel 1979, Rylaarsdam 1983, Rogers et al. 1984, Smith 1992). Observations of low recruitment but high adult cover of broadcast spawning species led to the hypothesis that these corals produce fewer juveniles that have higher long-term survivorship (Rogers et al. 1984, Smith 1992).

Octocoral reproduction and larval ecology is poorly understood compared with scleractinian reproductive ecology. Some octocoral species reproduce in synchronized spawning events (Brazeau and Lasker 1989, Fitzsimmons-Sosa et al. 2004) while others are brooders (Brazeau and Lasker 1990). Octocorals are thought to respond to many of the same settlement cues as scleractinians (Lasker and Kim 1996), but octocoral settlement behavior and their broader recruitment patterns have rarely been described (Lasker 2013, Lasker and Porto-Hannes 2015). The study of octocoral recruitment

patterns and population distributions has been limited, largely because of difficulty identifying recruits (Jamison and Lasker 2008).

As with scleractinians, larvae of brooding octocorals are often retained locally. *Pseudopterogorgia elisabethae* and *Briareum asbestinum* are Caribbean surface brooding octocorals with negatively buoyant planulae that are retained on the colony surface until competency. Planulae of *B. asbestinum* settle immediately and near the natal colony (Brazeau and Lasker 1990), while planulae of *P. elisabethae* are more likely to be transported tens of meters from the natal colony (Gutierrez-Rodriguez and Lasker 2004). Broadcast-spawning octocorals are thought to have wider ranges of dispersal than brooding octocorals (Jamison and Lasker 2008) since their larvae take longer to settle. For example, most larvae of Caribbean broadcast-spawner *Antillogorgia americana* were shown to take over a month to settle in a laboratory setting, in some cases delaying settlement up to 58 days (Coelho and Lasker 2016). Octocoral recruit populations tend to mirror adult populations in terms of species composition, while different species compositions are frequently reported between recruit and adult scleractinian populations (Yoshioka 1996).

Once planktonic coral larvae are competent to settle, they attach themselves to suitable substrata, and metamorphose to adopt a sessile benthic lifestyle (Babcock and Heyward 1986, Ritson-Williams et al. 2009). Selecting an appropriate place to settle can increase a coral's survival potential, whether by large-scale determinants (finding a healthy reef) or small-scale (finding a promising microhabitat) (Babcock and Mundy 1996, Harrington et al. 2004). Settlement and metamorphosis are mediated by external cues. These cues can be physical (e.g., light, pressure, sediment, temperature) or chemical (e.g. exudates from other organisms) in origin (Gleason and Hofmann 2011).

Several species of crustose coralline algae (CCA) act as settlement cues for coral larvae (Morse et al. 1988, Raimondi and Morse 2000, Doropoulos et al. 2012). The CCA species facilitating settlement vary among coral species; not all CCA species provide a settlement cue for all scleractinian corals. Certain species of CCA may actually inhibit scleractinian settlement (Ritson-Williams et al. 2014), and the CCA species that most effectively facilitate settlement may not be the most abundant on reefs (Harrington et al.

2004, Ritson-Williams et al. 2014, Ritson-Williams et al. 2016). Furthermore, decreases in CCA cover have been reported along with decreased coral cover for some places in the Caribbean; in Bonaire and Curacao CCA cover decreased from 6.4 to 1% over a 40-year period (de Bakker et al. 2017).

Bacterial biofilms have also been shown to facilitate settlement, both in conjunction with and in the absence of CCA. Some CCA species may harbor specific bacterial communities required for settlement or metamorphosis by specific coral species (Negri et al. 2001, Sneed et al. 2015).   One study of multiple Caribbean species suggests that brooding coral species may be more likely than broadcast-spawning species to settle on surfaces that have biofilm but lack the specific CCA species that increase settlement rates (Ritson-Williams et al. 2016).

Settlement location and success can be influenced by light intensity and wavelength and substrate complexity. Experiments using unconditioned plastic items (e.g. cable ties) suggest that larvae of *Porites astreoides* and *Acropora palmata* preferentially settle on red surfaces, demonstrating their ability to seek out substrata reflecting light wavelengths of 550 nm or greater (Mason et al. 2011). *Porites astreoides* planulae have also been shown to avoid areas exposed to elevated ultraviolet radiation (Gleason et al. 2005). Planulae that may benefit from settling in a habitat comparable to their parental habitat can use light levels as an indicator of similar depth (Mundy and Babcock 1998). A deep-water population of *Pseudodiploria strigosa* was shown to produce larvae that preferentially settle in light conditions that mirror deep habitats, even though *P. strigosa* is also common in shallow water (Strader et al. 2015). Larvae of various species have also been shown to prefer substrata conditioned with biofilms from the same depth as the parental habitat (Baird et al. 2003). Scleractinian corals have been shown to preferentially settle on irregular surfaces or in cryptic microhabitats (e.g. tile undersides) (Carleton and Sammarco 1987). In coral culture, lab-reared larvae have been demonstrated to preferentially settle in grooves in the provided substrate, with species-specific preferences in substrate angle (Petersen et al. 2005). Providing refuges in upward-facing substrates in field experiments has been shown to increase the proportion of recruits settling in upward-facing habitats (Edmunds et al. 2014).

Patterns of settlement may be mediated by adult distributions, though evidence suggests that these effects are caused more by local retention than by adult-seeking behavior of planulae (Vermeij 2005). In a survey of nine sites at Moorea, French Polynesia, the abundance of scleractinian juveniles was positively correlated with the abundance of adults, though the correlation was driven by only four of the six dominant, broadcast-spawning genera (Penin et al. 2007). Recruits of the Caribbean brooding species *Siderastrea radians* were shown to settle near adult colonies on small spatial scales (2500cm^2 quadrats) at low adult *S. radians* densities, up to 10% adult cover at which settlement rates were saturated. The research was conducted on the wreck of the Benwood in the FL Keys, which is densely populated with *S. radians* adults and few other species (Vermeij 2005, Vermeij and Sandin 2008).

Macroalgae and cyanobacteria can inhibit coral recruitment. Several species of macroalgae and cyanobacteria were found to reduce *Porites astreoides* settlement, and two were found to decrease post-settlement survival. In the same experiment, the cyanobacteria *Lyngbya majuscula* was found to decrease recruitment and survival of *Briareum asbestinum*, a common Caribbean octocoral (Kuffner et al. 2006). Macroalgal turfs have also been found to reduce overall scleractinian recruitment in field experiments (Vermeij et al. 2009, Arnold et al. 2010, Webster et al. 2015, Doropoulos et al. 2016). Severe macroalgae blooms can lead to widespread recruitment failure (Doropoulos et al. 2014). As the pH of oceans decreases, calcifying benthic organisms such as CCA may be impeded, increasing the competitive advantages of macroalgae and leading to higher macroalgae cover which threatens coral recruitment (Crook et al. 2016).

Octocorals and corals compete for space on the reefs. Adult octocorals employ chemical tactics to defend themselves from scleractinian corals using allelopathic agents to induce tissue necrosis in neighboring scleractinians and overgrowing scleractinian tissue. Conversely, scleractinians cause tissue necrosis in octocorals, forcing the octocorals to secrete a protective layer of polysaccharides to defend themselves. The degree of harm and susceptibility varies among species (Sammarco et al. 1985). The effects of adult octocoral presence on scleractinian settlement or, conversely, adult scleractinian presence on octocoral settlement have rarely been studied. However, species of adult Pacific soft corals have been shown to prevent some, but not all,

scleractinian genera from recruiting to substrate in their immediate proximity (Atrigenio and Alino 1996, Maida et al. 2001). It is possible that a dense canopy of octocorals could impede scleractinian settlement.

Coral recruits are vulnerable to many stressors and post-settlement mortality is often high, although rates vary spatially and temporally (Table 1). Survivorship also varies between species with different reproductive strategies. In the Caribbean, three broadcast spawning coral species were found to have lower survival rates than the two brooding species they were compared with. The broadcast spawners' eight-week survival ranged from 10% (*Acropora cervicornis*) to 23% (*Pseudodiploria strigosa*), with survival dropping to 0% (*A. cervicornis* and *A. palmata*) and 4% (*P. strigosa*) after 22 months. In contrast, 36% of *Favia fragum* recruits and 6% of *Agaricia agaricites* recruits (both brooding corals) survived after 20 months (Ritson-Williams et al. 2016).

For coral larvae, locating appropriate settlement substrate can play a pivotal role in determining post-settlement survival. Some CCA species have effective defenses, such as epithallial cell sloughing and overgrowth, to prevent fouling by organisms including coral recruits (Keats et al. 1997).   Settling on a species of CCA that is less likely to use these mechanisms (e.g. *Titanoderma prototypum*, found in both the Caribbean and Pacific), can therefore enhance survival prospects for recruits (Harrington et al. 2004). CCA species are strong competitors, and competition for space with CCA is an important mechanism determining juvenile coral assemblages and survival outcomes (Buenau et al. 2012). Several species of CCA are capable of completely overgrowing scleractinian coral spat, directly causing coral mortality (Harrington et al. 2004). Less is known about octocoral post-settlement survivorship rates and mediating factors. *Plexaura kuna* was found to have low post-settlement survival over the short term with only 40% of lab-settled recruits that were transplanted back to the reef surviving the first two weeks (Lasker et al. 1998). In a study of Florida Keys patch reefs, which used fate-tracking to evaluate survivorship of juveniles up to 4cm (height for octocorals, diameter for scleractinians), octocorals were found to have lower survivorship overall than scleractinians (Bartlett 2014).

Table 1: Previous studies assessing recruit and juvenile coral survivorship. Studies refer to total scleractinian survivorship unless otherwise noted.

Study	Location	Mortality (~1 year unless noted)
Bak and Engel 1979	Curacao and Bonaire	30% (6 months)
Rylaarsdam 1983	Jamaica	54%
Smith 1992	Bermuda	14.3% (*Diploria* spp.) 31.5% (*Porites astreoides*)
Lasker and Kim 1998 (octocoral)	San Blas Islands, Panama	60% (*Plexaura kuna*) after 2 weeks
Wilson and Harrison 2005	Solitary Islands, Australia	97.2-99.8% (3 broadcast spawning species)
Penin et al. 2010b	Moorea, French Polynesia	39.4% (juveniles >1cm)
Trapon et al. 2013	Moorea and Trunk Island, Australia	52.9%
Bartlett 2014	FL Keys	22% (scleractinian corals) 36% (octocorals) (pooled 6 month periods)
Humanes and Bastidas 2015	Los Roques Archipelago, Venezuela	22-49% (after 4 months)

Mortality rates decrease as coral recruits grow (Trapon et al. 2013). Before reaching less vulnerable size classes, recruits run a gauntlet of threats including predation, competition, and smothering by sediments (Bak and Engel 1979, Arnold et al. 2010). From the coral life-history perspective, predation is one of the earliest factors modulating survival outcomes. Indiscriminately grazing invertebrates such as *Diadema antillarum* cause high mortality in the smallest recruit size classes (Sammarco 1980, Rylaarsdam 1983). Larger grazers and corallivores, such as butterflyfishes and

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parrotfishes, have also been observed to damage or kill juvenile corals (Penin et al. 2010, Penin et al. 2010b). Corals that settle in microhabitat refuges, such as indentations in the substrate, have greater likelihood of survival. For example, after a 29-day experiment, juvenile *Porites lobata* individuals located in full crevices exhibited over 90% survival. In contrast, only 28% of juveniles attached to exposed surfaces survived (Gallagher and Doropoulos 2016).

Though herbivorous grazers pose an incidental threat to juvenile corals, removing grazers leads to increases in macroalgae, a significant benthic competitor in degraded reef systems (Mumby et al. 2016). Competition with macroalgae decreases survival of scleractinian corals in their first weeks and months post-settlement (Birrell et al. 2008, Arnold et al. 2010, Olsen et al. 2014, Webster et al. 2015). By shading scleractinian juveniles or abrading them via direct contact, macroalgae can restrict growth and survival (Box and Mumby 2007). Allelopathic chemicals found on the surfaces of macroalgae species are to impede or kill scleractinian corals (Rasher et al. 2011).

Caribbean scleractinian taxa exhibit differential rates of recruitment and post-settlement mortality, reflecting different life history strategies (Szmant 1986, Hughes and Tanner 2000). Recruitment rates of broadcast-spawning Caribbean species have been lower than recruitment rates of brooding species for decades or longer, even in areas dominated by broadcast-spawning adults (Bak and Engel 1979, Rylaarsdam 1983, Rogers et al. 1984, Hughes and Jackson 1985, Tomascik 1991, Smith 1992, Arnold et al. 2010, Humanes and Bastidas 2015). Brooding corals tend to exhibit high post-settlement mortality which is compensated by large numbers of recruits (Rylaarsdam 1983, Smith 1992). Broadcast-spawning, massive species such as *Diploria* spp. and *Orbicella* spp. are longer-lived and have comparatively low post-settlement mortality rates (Smith 1992). Therefore, scleractinian coral recruit community composition may differ from juvenile and adult community compositions once differential mortality acts to alter taxonomic ratios. Quantifying recruit and juvenile abundances separately to the highest possible taxonomic resolution can clarify the shifts in community composition between life stages, providing insight into differential mortality rates and life history strategies.

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Two field research methods are commonly employed to quantify coral recruits and juveniles: settlement tiles and *in situ* surveys, with each method having advantages and disadvantages. Settlement tiles (or "settlement plates") allow researchers to remove previously placed tiles from the site to examine them closely under a microscope, decreasing the probability that small recruits will be overlooked (Table 2). Juvenile octocorals can be removed from the tiles for identification on the molecular level (Jamison and Lasker 2008). Settlement tiles are often bleached to remove tissue and reveal corallite structures of scleractinians that are evaluated for morphological characteristics (e.g. Harriott and Fisk 1987). This process allows for more accurate identifications and for identification of juveniles to a higher taxonomic resolution. Bleaching also removes algae and other overgrowing organisms, so that even recruits that died shortly after they began producing skeletal material can be located and possibly identified. When examining settlement tiles in the lab, high quality photographs of live and bleached coral recruits can be produced using microscopy, allowing for long-distance collaboration on recruit identification efforts. Furthermore, when using settlement tiles to quantify recruitment, researchers can be sure that recruits found on the tiles were produced during the time the tile was deployed. The drawback of using settlement tiles is that they are unable to mimic the natural substrate exactly, so information on recruitment gleaned from tiles may not accurately reflect the settlement and juvenile survival that is happening on natural reef substrate. To more closely approximate natural substrate, tiles must be given sufficient time to condition and become colonized with biofilms and CCA (Crook et al. 2016).

Table 2: Previous studies using settlement tiles to assess coral recruitment in the Caribbean and Atlantic.

Settlement Tiles				
Study	**Location**	**Tile Type**	**Settlement Rate (Recruits per m2 per month)**	**Settlement Orientation Preference**
Rogers et al. 1984	St. Croix	*Acropora palmata* plates	1.27	89% underside
Tomascik 1991	Barbados	Terracotta	17.75	100% underside
Vermeij 2006	Curacao	Formica settlement "frames"	0.1 (12m), 0.3 (30m) in first year of deployment	94% underside (when including azooxanthelate corals and *Madracis*, 0.05% underside when excluded) Frames at 12 and 30m
Rubin et al. 2008	SE FL	Terracotta	0.1	all tiles vertical
Malella and Crabbe 2009	Tobago	Ceramic	0-9	preference for vertical tiles
Arnold et al. 2010	Bonaire	Terracotta	8	only surveyed underside: 83% within 1.5cm of edge
Arnold and Steneck 2011	Belize	Terracotta	20.25	only quantified underside
Green and Edmunds 2011	St. John	Terracotta	12.67	not available
Edmunds et al. 2014	St. John	Smooth terracotta (quantified underside), smooth acrylic plate (quantified top), acrylic plate with drilled refuges (quantified top)	~5.3 (estimated from pooled data)	94% underside, 6% upper refuges, 0% upper smooth surfaces

Humanes and Bastidas 2015	Venezuela	Terracotta	30-236	not available
Fieseler, unpublished data	Belize	Terracotta, homogenous grooves top on top and bottom	7.2 scler.,1.9 octo (May '15-Sept '16); 5.4 scler., 4.3 octo (Nov '15-Jan '17)	95% underside (May 15-Sept 16); 43% underside (Nov 15-Jan17; includes 3 sites at 30m depth)
Fogarty and Piniak unpublished data	Dry Tortugas	Elevated terracotta arrays One side smooth, one side homogenous grooves; vertical and horizontal orientation	1.4	61% grooved, 34% smooth surface, 4% sides, 58.1% horizontal tiles (42% upper, 58% lower) and 42% on vertical tiles

Settlement tiles have been used to evaluate variation in recruitment patterns through time and space (Vermeij 2006, Green and Edmunds 2011), to measure settlement after disturbances (Tamelander 2002, Rubin et al. 2008, Salinas-de-Leon et al. 2013), and to compare rates of sexual and asexual recruitment (López-Pérez et al. 2007). Settlement tiles are frequently attached to a structure that elevates them above the reef (Maida et al. 1994, López-Pérez et al. 2007, Rubin et al. 2008). These structures can be designed to reduce or eliminate the effects of predation by stacking tiles mounted on stainless steel bolts and separating them by spacers (Maida et al. 1994). This method can have a drawback in that structures with vertical relief are more likely to topple over at some point during the study, especially in high energy areas, resulting in loss of data. An alternative strategy is to attach the tiles directly to the substrate (Edmunds et al. 2014). Attaching the tiles parallel to the substrate has another advantage in that it more closely mimics the natural contours of the reef.

Unglazed terracotta is a common and well-established material used in settlement tile studies (Atrigenio and Alino 1996, Adjeroud et al. 2007, López-Pérez et al. 2007, Arnold and Steneck 2011, Green and Edmunds 2011, Salinas-de-Leon et al. 2013, Sawall et al. 2013, Edmunds et al. 2014, van Woesik et al. 2014, Humanes and Bastidas 2015). Other materials employed as settlement tiles include ceramic tiles, pieces of coral rubble,

formica plates, marine blocks, and limestone tiles (Harriott and Fisk 1987, Maida et al. 1994, Vermeij 2006, Rubin et al. 2008, Burt et al. 2009, Salinas-de-León et al. 2011, Roeroe et al. 2013). Tile types are typically selected based on a combination of convenience, cost-effectiveness, and ease of comparison with other studies.

In situ juvenile surveys allow researchers to estimate recruitment to natural, heterogeneous substrates (Table 3). These are often performed using a series of haphazardly placed quadrats to designate survey areas (e.g. Bak and Engel 1979). While settlement tiles are typically used to identify the species that recruit to an area in a given timeframe, juvenile surveys are used to answer to determine which species comprise the juvenile population, often defined as corals <4cm in diameter. Juvenile surveys typically cover a larger spatial area than settlement tiles, and provide a snapshot of the juvenile population at a moment in time. One caveat of *in situ* juvenile surveys is that estimating the ages of juveniles is virtually impossible, as individual corals often have different growth rates. Corals frequently fuse, split, or experience partial mortality, so size is not always related to age (Hughes and Jackson 1980). An assessment of a juvenile population (<4cm) could potentially include corals that are decades old. Additionally, precision of identification is limited without the use of microscopy. Surveyors can take quality photos to save and share, but cannot view or photograph the skeletal structure under the tissue. Therefore, some key diagnostic characteristics are often obscured.

Another caveat of *in situ* juvenile census studies is that it is time-consuming to accurately quantify the surface area studied. A square meter quadrat placed over highly rugose substrate will include much more than a square meter of surveyed settlement substrate. Also, while settlement tiles provide a "blank slate" for recruitment, usually with only early-successional colonizers present at the time of coral settlement, juvenile census quadrats may include areas of substrate that are unavailable to coral settlers. These can include adult coral colonies, sponges, or areas of loose sediment. Studies using juvenile censuses have typically attempted to select areas for quadrat placement that have a significant proportion of available substrate, avoiding sand patches or large monospecific patches of adult coral (e.g. Bak and Engel 1979).

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Table 3: Previous studies that used *in situ* census techniques to assess recruit and juvenile coral densities in the Caribbean and Atlantic.

In Situ Census Studies				
Study	**Location**	**Size Limit**	**Density of Juveniles (in m⁻²)**	**Additional Objectives (if any)**
Dustan 1977	Carysfort Reef, FL Keys	Counted new recruits on cleared natural substrate	1.2-4.9	Assessed recruitment *in situ* to cleared vs uncleared plots
Bak and Engel 1979	Curacao	<4cm	15	Determined variations in depth and habitat (3-37m)
	Bonaire	<4cm	18	
Rylaarsdam 1983	Jamaica	<5cm	76-274	
Rogers et al. 1984	St. Croix	<4cm	0-80	Determined variations in settlement patterns across depths at either side of a submarine canyon
Hughes and Jackson 1985	Jamaica	Counted new recruits ~5-10mm	1.2-4.2	Studied population dynamics: recruitment, growth, population cover, size frequency, and mortality
Chiappone and Sullivan 1996	FL Keys	<4cm	1.18-3.74	Quantified relationships between juveniles and adults across depths and habitats
Carpenter and Edmunds 2006	St. Croix	<4cm	2-45	Assessed how *Diadema* presence affects recruitment
	Grenada		9-28	
	Bonaire		7-11	
	Barbados		8-34	
	Belize		4-8	
	Jamaica		5-27	

				Determined how damselfish grazing on turf algae affects recruitment and survivorship
Arnold et al. 2010	Bonaire	≤ 4cm	17 (grazing territory), 25 (ungrazed)	Determined how damselfish grazing on turf algae affects recruitment and survivorship
Stein 2012	SE FL	<4cm	1.6-5.1	Examined variations in juvenile density across habitat types and between bioregions
Bartlett 2014	FL Keys	≤4cm	11-14 scler., 8-15 octo	Examined post-disturbance recruitment and survival at patch reefs
Buglass et al. 2015	Tobago	≤5cm (lg taxa), ≤2cm (sm taxa)	5.4	Determined resilience after mass bleaching

Most studies have utilized either settlement tiles or *in situ* surveys to assess recruitment and juvenile survivorship, while few have used both (e.g. Rogers et al. 1984, Penin and Adjeroud 2013, Chong-Seng et al. 2014. Employing both methods simultaneously can improve understanding of the relationships between the recruit and juvenile populations. Tiles are used to determine which species are recruiting, and *in situ* censuses are used to determine which of those are present in the juvenile population. Evaluating relationships between recruit and juvenile densities across sites can provide information about which sites and species demonstrate higher potential for survival. This information can then inform management efforts by pointing to sites and species with limited capacity to recover from disturbances.

The subtropical reefs of Southeast Florida have been the focus of few studies compared with reefs in the Florida Keys and elsewhere in the Caribbean. Coral recruit and juvenile populations have been assessed only recently (Rubin et al. 2008, Stein 2012) and not simultaneously. The present study utilized both settlement tiles and *in situ* censuses to assess the taxa that are recruiting to the Southeast Florida reef tract, how recruitment varies across latitudes and depths within the region, and how the recruit population found on settlement tiles differs from the juvenile and adult populations.

Some agencies have established monitoring programs at permanent sites to document further changes to coral reef communities. One such program was established by the Florida Fish and Wildlife Conservation Commission (FWC) in 1996 throughout the Florida Keys (Coral Reef Evaluation and Monitoring Project, "CREMP") and 2003 in Southeastern Florida (Southeast Florida Coral Reef Evaluation and Monitoring Project, "SECREMP"). CREMP and SECREMP monitoring sites support a variety of data collection methods, including demographic surveys, video transects, and benthic cover assessments of diverse taxa. These datasets combine to form a useful assessment of the benthic ecosystem in the region as the environment changes through time. However, coral recruitment is a missing piece in these datasets. Documenting coral recruitment rates on long-term monitoring transects will provide for a more complete picture of population dynamics, decline, and potential for resilience. The present study aims to provide an understanding of coral recruitment dynamics and subsequent juvenile survival at twelve SECREMP-monitored sites in Broward County and Miami-Dade County, FL. Simultaneously, collaborators will follow similar monitoring methods throughout the Florida Keys. The combination of these monitoring programs will culminate in a better understanding of coral recruitment processes along almost the entirety of the Florida reef tract.

The Florida reef tract extends from Dry Tortugas National Park (24.6285˚N, 82.8732˚W) to the St. Lucie inlet in Martin County (27.1489˚N, 80.1373˚W) (Banks et al. 2007), making it among the longest barrier reefs in the world. Florida reefs are more degraded and less protected by local and federal governments than nearby reefs in the Bahamas and Cuba (Pandolfi et al. 2005). Seven scleractinian coral species native to Florida are listed as threatened by the Endangered Species Act: *Acropora cervicornis, Acropora palmata, Orbicella annularis, Orbicella faveolata, Orbicella franksi, Dendrogyra cylindrus,* and *Mycetophyllia ferox* (NOAA 2014). These species appear to be experiencing recruitment failure possibly in part because of the Allee effect, with low population densities making fertilization less likely (Stephens et al. 1999). Even in the Florida Keys where coral population densities are slightly higher, threatened species may be failing to recruit. Williams et al. (2008) monitored a 2,250 m^2 area of the Florida Keys for three years and found only two sexually produced *A. palmata* recruits of

detectable size. Florida's reefs have been impacted by mass bleaching events (Wagner et al. 2010, Gilliam 2014) and disease outbreaks throughout Southeastern Florida and the Keys (Richardson 1998, Porter et al. 2001, Williams and Miller 2005, Sutherland et al. 2010, Gilliam 2014, Precht et al. 2016). While scleractinian cover is declining, recent monitoring suggests an increase in octocoral cover in the Florida Keys (Ruzicka et al. 2013). Octocorals do not contribute to reef framework, but they add spatial heterogeneity to the reefs.

The northern extension of the Florida reef tract is comprised of limestone ridges that are parallel to shore, forming three major reef terraces that are progressively deeper with distance from shore. These terraces are separated by gradually sloped sand channels (Goldberg 1973, Banks et al. 2007). Each terrace was constructed by *Acropora palmata* or *Orbicella* (formerly *Montastraea*) and *Diploria* species during the Holocene epoch, and drowned as they were unable to keep up with rising sea level (Lighty 1977). These reefs are considered relict structure, as live coral cover is too low to promote active accretion (Moyer et al. 2003).

Southeast Florida's reefs are dominated by octocorals, macroalgae, and sponges. Scleractinian coral cover on Southeast Florida reefs has been reported to average only 3%; a few shallow sites with "exceptionally high" cover exhibited cover up to 15% (Sathe et al. 2008). However, more recent reports suggest declines in scleractinian cover over the past decade, with a decrease from 2.5% to 1.5% cover between 2015 and 2016 (Fig 1, Gilliam et al. unpublished data). The most recent declines can largely be attributed to disease (Precht et al. 2016). Meanwhile, octocoral cover has fluctuated but changes remain statistically insignificant (Gilliam 2014). Due to their dominance in the region and contribution to the spatial heterogeneity of the reef tract, combined with the lack of existing information about their population dynamics and recruitment patterns, octocorals are included in the present assessment of recruit and juvenile populations in Southeast Florida.
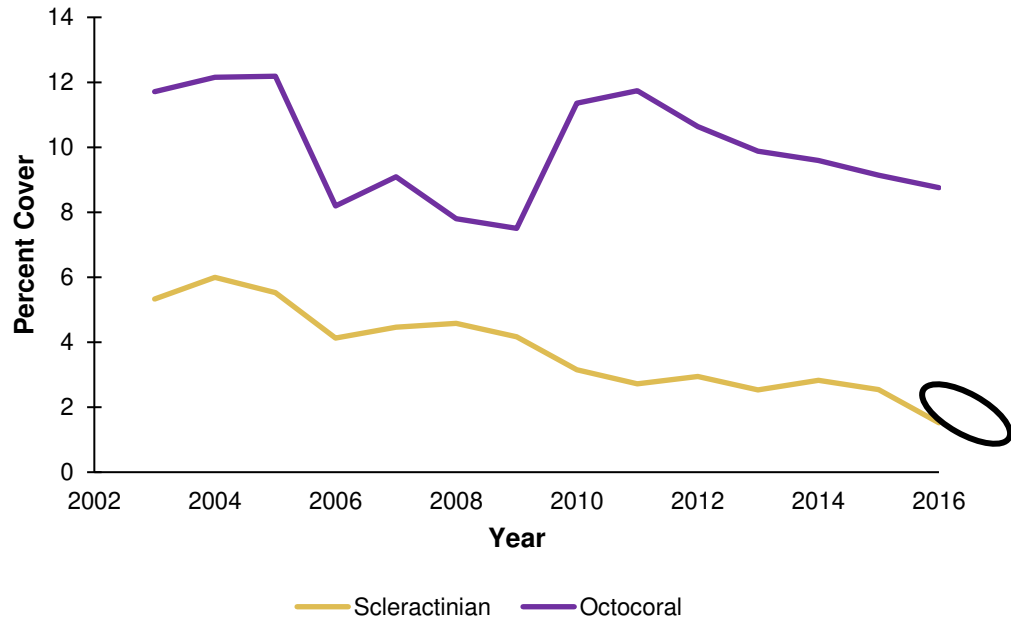
Figure 1. Trends in octocoral and scleractinian cover reported by SECREMP since its initiation in 2003. Octocoral cover has fluctuated, showing the potential for fast recoveries (e.g. 2009-2010), while scleractinian cover has declined more steadily. The 2015-2016 decline from 2.5% to 1.5% scleractinian cover is circled.

Southeastern Florida's reefs are among the highest latitude (25.5°-27.25°) reefs in the Atlantic (Moyer et al. 2003). Because the coral reefs adjacent to mainland Florida are among the most northerly reefs, they can be subject to extreme cold-water events resulting in high mortality (Walker et al. 1982). Rates of scleractinian recruitment have been reported to decrease with increasing latitude (Hughes et al. 2002). Low scleractinian recruitment and recruit survival rates have been reported on some high-latitude reef systems, such as in Hong Kong (Chui and Ang 2010). However, while recruitment to the sub-tropical reef system off Lord Howe Island, Australia, was comparable to rates from the Great Barrier Reef, there was a different taxonomic distribution between the two areas (Harriott 1992). Previous studies conducted in Southeast Florida suggest lower recruitment rates compared with tropical Caribbean reefs (Rubin et al. 2008, Stein 2012), while the high-latitude reefs of Bermuda have comparable recruitment rates to the Caribbean (Smith 1992).

The coral reefs of Southeast Florida are located just offshore from the population centers of Ft. Lauderdale and Miami. The effects of high latitude, such as cooler winter temperatures and increased turbidity, and proximity to population centers inflict

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additional stress upon this coral reef ecosystem (Sathe et al. 2008). In 2015, the combined populations of Broward and Miami-Dade counties was 4.6 million (U.S. Census Bureau). Population growth in the area was rapid through the 20th century, with increases averaging 90% for every decade from 1900 to 1980 (Smith 2005). The urban development processes undertaken by humans in this region since the 1950's have largely lacked consideration for environmental sustainability, and thus contributed to coastal erosion and the degradation of the reef ecosystem (Finkl and Charlier 2003).

Anthropogenic stressors to the Southeast Florida reef tract impact water quality, sedimentation levels, and the structural integrity of the reef. Southeast Florida's major cities pump over 1.5 million cubic meters of treated sewage per day from six outfalls in Palm Beach, Broward, and Miami-Dade counties. The effluent from these outfalls enters the ocean between 1500 and 5800 m offshore, on the third reef tract at approximately 30 m depth (Koopman et al. 2006). Nitrogen from these and other land-based sources of sewage have been implicated in contributing to harmful macroalgal blooms that have directly impacted reef corals (Lapointe et al. 2005). The region's ocean-access inlets have been found to carry fecal contaminants to the reef on outgoing tides, deteriorating water quality of the coral reef habitat (Futch et al. 2011). Southeast Florida hosts three major ports, which were found to impact a total of 312.5 ha of coral reef environment (Walker et al. 2012). Since then, the Port of Miami has been expanded. During expansion, over 1,100 ha of coral habitat were found to be covered by turbidity plumes observed using satellite images (Barnes et al. 2015). Efforts to widen eroded beaches through nourishment projects are another source of increased sediment levels on Southeast Florida's reefs (Jordan et al. 2010).

Physical damage to Southeast Florida's reef structures occurs in conjunction with both commercial and recreational boat use. Damage from ship groundings and anchor drags is often not quantified, but an impact area of six hectares has been reported for known events directly related to port activity (Walker et al. 2012). Broward County's Port Everglades anchorage, which is located between two reef terraces, was the epicenter of six anchor drag incidents and eleven ship groundings between 1993 and 2006, resulting in damage to over 4.4 ha of reef (Collier et al. 2008). Scleractinian recruitment to a damaged site following a ship grounding in Broward County was found to be low,

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suggesting limited potential for recovery from reef destruction in this region (Rubin et al. 2008). Hurricanes and tropical storms have also caused localized damage to Southeast Florida's reefs. Hurricane Andrew caused extensive breakage in *Acropora* populations in 1992, and Tropical Storm Gordon subsequently transported rubble and sediment that smothered many *Acropora* fragments and other small corals (Litinan and Fong 1995).

The study described herein assessed recruitment to the Southeast Florida reef tract during the reproductive season of 2015 and surveyed juvenile populations present in fall of 2016. In late September of 2014, after an unusually warm summer and widespread coral bleaching, early signs of a disease outbreak were observed in the southern part of the region near Virginia Key (25.7466˚ N, -80.0999˚ W). By the summer of 2015 the disease, classified as white-plague, had spread north throughout Broward County. White-plague impacted *Meandrina meandrites, Dichocoenia stokesii*, and *Eusmilia fastigiata* most heavily, resulting in an estimated mortality of 97% or greater throughout the region (Precht et al. 2016). The disease also affected previously abundant (Sathe et al. 2008, Gilliam 2014) populations, including *Pseudodiplora strigosa* and *Diploria labyrinthiformis* (>75% mortality) and *Montastraea cavernosa* (38% mortality) (Precht et al. 2016). By 2016, the disease was prevalent in the Upper Keys (Brinkhuis and Huebner 2016). This unprecedented disease outbreak likely reduced the reproductive output of corals in the region and may have played a role in shaping recruitment patterns in this study if source populations of coral larvae are local.

To understand the resilience of this region and specific taxonomic groups, as well as to evaluate where the population bottleneck may exist, this study poses three research questions:

1. What is the taxonomic distribution of scleractinian and octocoral recruit and juveniles? Answering this question will help to determine which taxa are most successful in terms of recruitment and juvenile survivorship, suggesting their potential to be resilient to disturbances.
2. Do recruit and juvenile abundances vary spatially? Answering this question will help to determine whether certain habitats and sites may have more resilient coral communities than others.

3. How do adult, recruit, and juvenile density relate to one another in scleractinians and octocorals (and within the most common scleractinian families)? Answering this question will help to determine whether these relationships elucidate differences in recruitment success and juvenile survivorship between scleractinians and octocorals, and between specific scleractinian taxa. Rather than fate tracking individual coral recruits, examining juvenile densities relative to recruit densities can allow for inferences regarding post-settlement survivorship.

This study is part of a larger collaborative effort that spans the entire Florida reef tract from Broward County to Key West. While my thesis focuses on the recruit and juvenile populations of Southeast Florida, results produced in this study will be useful in the future to compare recruitment rates from 30 sites across the world's third largest barrier reef.

METHODS

2.1 Study Sites

Recruitment tiles were deployed at four sites in Broward County ("BC" sites) and eight in Miami-Dade County ("DC" sites) (Table 4). These sites were selected due to the convenience of pre-existing transects installed for SECREMP. Because SECREMP maintains a long-term monitoring dataset using these transects at each site, recruitment data could be directly compared to adult population data. Sites were selected to represent the nearshore, inner, middle, and outer reef portions (Gilliam et al. 2014) and include three different depth ranges- six sites were within a 5-8m depth range, three were 15m deep, and three were 20m deep. To compare between broad reef zones, sites were grouped into "inshore" and "offshore" categories. "Inshore" sites were all located in nearshore and first reef habitats, and ranged from 5-10 m depth. "Offshore" sites were located on the second and third reef terraces, at 15-20 m. Inshore sites are nearer to anthropogenic sources of nutrient and sediment pollution, such as beaches, fertilizer runoff, and nutrient-enriched inlet waters. Because they are shallower, they also are subject to more wave energy. Offshore sites are further from land, but nearer to nutrient

input from sewage outfalls. Each site consisted of four stations, and each station included two transects 20-22m in length. Stations were oriented with both transects running north to south. All sites except DC1, DC2, and DC3 were set up with stations positioned in a two by two matrix. At DC1, DC2, and DC3, the stations were oriented in a row (Fig. 3).

2.2 Hardware Installation

Preliminary hardware installation procedures were conducted between October 2014 and February 2015. During this phase, each site was visited by a dive team. Dive teams located the SECREMP posts and used 2m aluminum station poles designed to fit over posts to accurately place transect tapes over two transects (one east and one west) at each station. Divers haphazardly placed four quadrats along the left side of the east transect and along the right side of the west transect at each station (Fig 3). Quadrat locations were based on the feasibility of installing nails in at least two corners and availability of substrate (less than 50% live coral cover within the quadrat). As near as possible to one of the outer corners of each quadrat, the divers installed receiving hardware (a drywall anchor and lag screw) for attaching tiles later. Tile locations were selected based on feasibility of drilling (i.e., divers will avoid locations with soft sand or live cover as substrate) (Fig 4).

Table 4: Sites listed with their depth, habitat, and location.

Site	Depth (m)	Habitat	County
BC1	8	Nearshore	Broward
BC2	15	Middle Reef	Broward
BC3	20	Outer Reef	Broward
BC4	8	Inner Reef	Broward
DC1	8	Inner Reef	Dade
DC2	15	Middle Reef	Dade
DC3	20	Outer Reef	Dade
DC4	15	Outer Reef	Dade
DC5	8	Inner Reef	Dade
DC6	5	Nearshore	Dade
DC7	20	Middle Reef	Dade
DC8	5	Nearshore	Dade
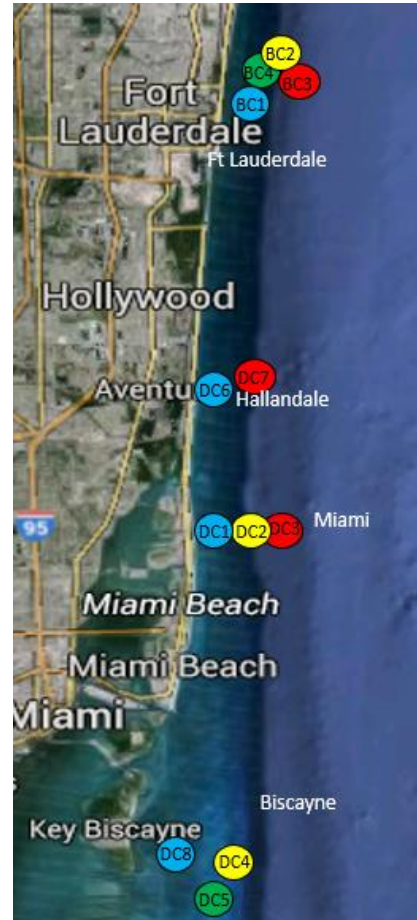
Figure 2. SECREMP sites where settlement tiles were deployed and juvenile censuses conducted. Blue circles represent nearshore reef, green are first reef, yellow are middle reef, and red are third reef.

Dive teams hammered nails securely into the substrate in at least two corners of each quadrat to mark its location. Using a pneumatic drill attached to a SCUBA cylinder, divers drilled holes into the substrate where each tile would be placed. A ribbed plastic drywall anchor (1/2" length) was inserted into the drilled hole. A stainless steel bolt was screwed into the anchor using a wrench (Fig 4).
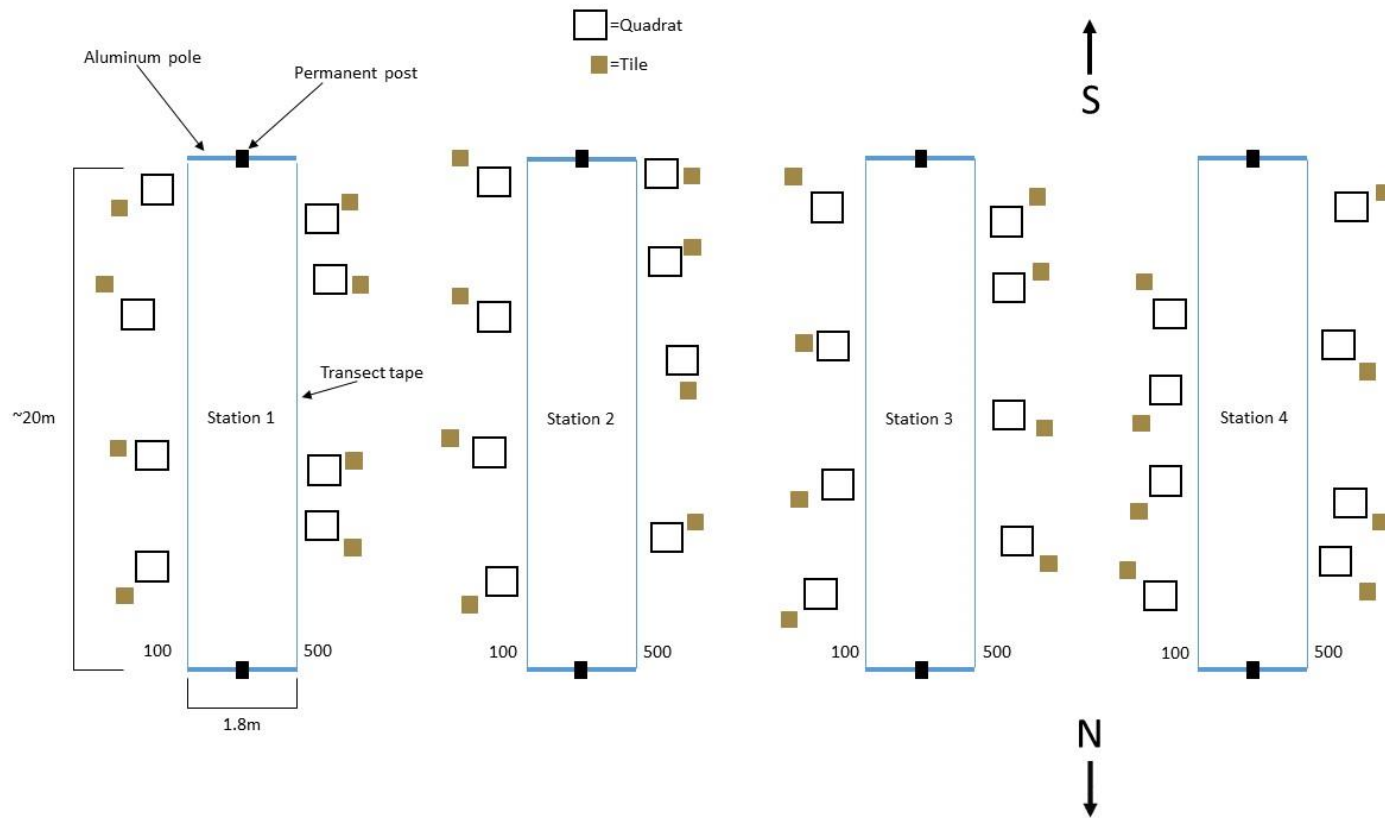
Figure 3. Sites DC1, DC2, and DC3 have four stations oriented in a row as depicted above. Sites DC4, DC5, DC6, DC7, DC8, BC1, BC2, BC3, and BC4 have four stations oriented in a two by two matrix. Quadrat and tile depictions represent the random placement choices influenced by substrate and complexity variations at each site.

Tiles were deployed
between February
and April 2015. I
used unglazed
terracotta tiles which
were attached
parallel to the
substrate and
anchored with a
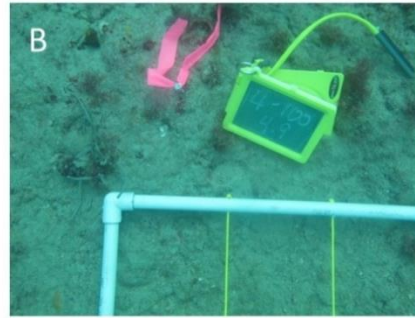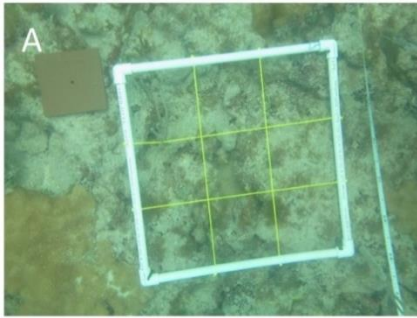
Figure 4. (A) Quadrat and tile placed along transect, nails installed. (B) Screw installed and marked with flagging tape.

drywall anchor and screw to minimize risk of tile loss. Tiles were grooved to provide refuge on exposed surfaces, maximizing recruitment

potential on all sides (Edmunds et al. 2014). To ensure that the grooves were exposed on both sides, tiles were paired and positioned with grooved sides facing out.

Dive teams brought 32 tile pairs to each site, and attached them to the substrate using the previously installed screws (Fig. 5).

Figure 5. Tile attached to substrate with screw; shown approximately three months after deployment.

2.3 Juvenile Census

In Fall 2016, dive teams returned to each of the 12 study sites to conduct juvenile censuses. PVC quadrats were placed in the locations marked by the nails along either side of the transect of each station at each site. Two photographs were taken of each quadrat during the census: a photo of the quadrat with its associated tile, and a photo in which the quadrat fills the entire frame. One diver surveyed each quadrat, spending as much time as necessary to scan all the area within the quadrat for juvenile corals. Area under the PVC frame was included in the survey, as was any substrate overhanging the quadrat area. Juveniles found on rubble were also included, but unattached fragments of octocorals found within the quadrat were not.

In this study, scleractinian corals less than 4cm in diameter and octocorals less than 4cm in height were considered juveniles (Bak and Engel 1979, Rogers et al. 1984). Corals that were less than 4cm but appeared to consist of living tissue remaining from a larger adult colony were recorded as isolates. Juveniles were identified to the highest possible taxonomic resolution. The majority of scleractinian corals were identified to species. Most octocorals were identified to genus unless the juvenile was clearly a member of one of the SECREMP target species (*Eunicea flexuosa, Eunicea calyculata, Antillogorgia americana, Gorgonia ventilina,* and *Pseudoplexaura porosa*). Juveniles were measured to the nearest millimeter using calipers or a ruler. The diameter of scleractinian corals and the height of octocorals were recorded, and juveniles were evaluated for partial mortality and bleaching.

Juvenile identifications were confirmed whenever possible using photographs taken in the field. Corals recorded as isolates in the juvenile census were excluded from data analysis. *Briareum asbestinum* juveniles were excluded from the data due to difficulty in distinguishing the erect and encrusting forms at small sizes. However, *B. asbestinum* could not be excluded from the recruit data because it cannot be reliably distinguished from other octocoral species as single-polyp recruits.

2.4 Tile Retrieval and Wet Scans

Tiles were retrieved between 11.5 and 13.5 months after deployment. This range was due to weather and boat availability which limited the timing of fieldwork. Before each tile was unscrewed from the substrate, a photograph was taken of the upper surface, and after removal a photograph was taken of the lower surface. Tiles were kept separate from one another on egg crate trays equipped with bolts to hold tiles in place. Once aboard the research vessel, tiles were held in coolers filled with seawater.

Tiles were returned as quickly as possible to the laboratory and were kept in seawater throughout the wet scanning process. Ten photographs were taken of each tile: one photo in which the upper surface of the tile fills the entire frame and one photo of each of the four quadrants of the upper surface of the tile. These photos were repeated for the lower surface to capture the entire tile. The upper and lower surfaces of each tile pair were examined under a dissecting microscope for spat of hard and soft corals. Tile sides were examined for any corals visible to the naked eye, but could not be scanned using the microscopes due to the size of the tiles. Octocoral recruits found during wet scans were removed from the tile and placed in a labeled vial of 96% molecular grade ethanol. Identifications were recorded when possible; however very few octocoral recruits were large enough to identify visually. Scleractinian corals found during the wet scans were photographed whenever initial identification was not possible, and their locations on the tile were recorded for later relocation. Scleractinian recruits were defined as any individuals that had settled and metamorphosed on the tile such that a recognizable skeleton was formed, regardless of whether they were alive or dead at the time of tile retrieval. Octocoral recruits were defined as any individuals attached to the tiles (excluding obviously encrusting octocorals) whether tissue was damaged or intact.

Only the live scans were used to locate octocorals, as the bleach eliminated all traces of octocoral tissue. After the wet scanning process was complete, tiles were submerged in a 10% bleach solution for approximately 48 hours, to remove all live tissue and reveal scleractinian skeletons.

2.5 Dry Scans and Identification

After tiles were bleached and dried, they were scanned a second time to locate any scleractinian recruit skeletons that were missed during the wet scans, and to verify identifications. All skeletons were photographed and their locations were noted. Recruits were identified to the highest possible taxonomic resolution. Diagnostic characteristics for scleractinian coral recruits included macromorphological features, such as calice diameter and number of septal cycles, and micromorphological features, such as septal morphology (Budd and Stolarski 2011). Here, the recruitment rate (recruits/m^2/month) is reported, which allows for comparison with studies that used settlement tiles over different periods of time.

2.6 Adult Monitoring (SECREMP)

SECREMP adult demographic data was used to compare recruit and juvenile densities to adult densities at the same transects. Adult data was collected by Gilliam et al. during the summer of 2015, overlapping with the timeframe that settlement tiles were deployed on those sites. Adult demographic data consists of four 22m x 1m belt transects for each site (octocorals are only surveyed over the first 10m of transect). All scleractinians 4cm in diameter or greater are recorded in SECREMP surveys. Octocorals as small as 1cm in height are recorded in SECREMP surveys, so some overlap with the juvenile population occurs in these data. However, the SECREMP protocol covers more area, and surveyors spend less time scanning for small octocorals.

2.6 Statistical Methods

2.6.1 Taxonomic Distribution of Recruits and Juveniles

To assess whether scleractinians or octocorals were more prevalent as recruits and juveniles, t-tests, or if parametric assumptions were not met, Wilcoxon tests, were used.

Descriptive statistics were used to determine the most prevalent scleractinian and octocoral families in the recruit and juvenile studies.

2.6.2 Spatial Parameter Modeling

To assess the influence of spatial parameters on the number of recruits found on settlement tiles and then number of juveniles found in quadrats, generalized linear models were used. The recruit data had four spatial variables: location on tile (top or bottom), site, region (Ft. Lauderdale, Hallandale, Miami, Biscayne), and inshore vs, offshore sites. The juvenile data had three spatial variables: site, region, and inshore vs. offshore sites. Initial assessments identified overdispersion in the data, meaning that variances exceeded those predicted by a theoretical model, precluding the use of a conventional Poisson regression. Instead, a negative binomial regression model was used, which estimates an overdispersion parameter that accounts for excessive variability in the data. Similar to Poisson regression, the negative binomial model employs a log link function to model the mean of the response variable (here, coral counts) against a variable (here, location on tile, site, region, and zone). A candidate set of five single-parameter negative binomial regression models was selected (four for the juvenile data) to include separate models for location on tile, site, region, and zone, and an interaction term for region and zone. Akaike's Information Criterion (AIC) (Akaike 1973, Hurvich and Tsai 1989) determined the ranking of support for each model. The precision (significance) of each parameter estimate was assessed by examining 95% confidence intervals. Parameters with a 95% confidence interval that did not overlap zero were considered important predictors (i.e. statistically significant). Models were fit in R v. 3.4.1 (R Core Team 2017). To assess whether tile microhabitats had different settlement densities, T-tests or Wilcoxon tests (if parametric assumptions were not met) were used. To determine whether differences in recruit and juvenile densities existed between sites, one-way ANOVAs or, if parametric assumptions were not met, Kruskal-Wallis tests were used. To assess whether inshore and offshore sites differed in recruit, juvenile, or adult densities, T-tests or, if parametric assumptions were not met, Wilcoxon tests, were used. If significant effects/differences were found, Tukey's post-hoc tests, or, if parametric assumptions were not met, non-parametric multiple comparisons post-hoc tests were performed using R packages "pgirmess" and "multCompView."

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2.6.3 Comparing Recruit, Juvenile, and Adult Densities

Life history stage data had to be compared at the transect level because the SECREMP demographic methods do not include any smaller unit of replication. Prior to conducting any statistical tests, the datasets were tested for the parametric assumptions of normality and homogeneity of variances. Normality was determined using the Shapiro-Wilk test and Bartlett's test was used to test for homogeneity of variances. To assess whether differences existed between adult, recruit, and juvenile densities, one-way ANOVAs, or, if parametric assumptions were not met, Kruskal-Wallis tests, were used. If significant effects/differences were found, Tukey's post-hoc tests or non-parametric multiple comparisons post-hoc tests were performed using R packages "pgirmess" and "multCompView." To determine whether relationships existed between adult and recruit, recruit and juvenile, and juvenile and adult data, sites were used as replicates. Pearson Correlation tests, or, if parametric assumptions were not met, Spearman Correlation tests, were used. Data was transformed using log(x+1) transformations to meet parametric assumptions when necessary.

RESULTS

Scleractinians exhibited significantly higher recruitment rates than octocorals ($W=318850$, $p<0.0001$) The overall rate of scleractinian recruitment was 0.7 recruits/m^2/month and the rate of octocoral recruitment was 0.5 recruits/m^2/month. Scanning the tiles after bleaching revealed a 276% increase in the total scleractinian coral count compared with live scans. In the *in situ* juvenile census, the mean density of scleractinian juveniles found in quadrats was 5.9/m^2, while the mean density of octocoral juveniles was 7.5/m^2.

3.1 Taxonomic Distribution of Recruits and Juveniles

A total of 764 tiles were recovered between March and May of 2016 (Appendix 1 is a table of recruits found on tiles at each site). Most octocoral recruits had only developed a single polyp at the time of tile retrieval and very few were identifiable to family or genus. Scleractinian recruits ranged in size from approximately 0.5-10mm in

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diameter. A total of 182 scleractinian recruits and 120 octocoral recruits were located. Total settlement area included both the upper and lower tile surfaces and was calculated based on tile length, width, and height, as a surface area of $285cm^2$. Because two sites had smaller sample sizes than the rest (as a result of dislodged tiles), recruitment was standardized by converting the number of recruits to density (i.e. number of recruits.m^{-2}.

Among scleractinians, recruits from the Poritidae family comprised 46.7% of the recruit population found across all sites, followed by Siderastreidae at 23.1%. While identifying recruits confidently to a higher taxonomic resolution than family was not possible in this study, based on the species composition of the adult and juvenile populations, and the morphology of larger and more well-developed recruits, I assume that the majority of the poritid recruits reported were *Porites astreoides* (based on prevalence in the adult community and the "mustard yellow" tissue color observed in most live recruits), the majority of the siderastreid recruits were *Siderastrea siderea* (based on prevalence in the adult community and calice shape of large recruits)*,* and the majority of the agariciid recruits *Undaria agaricites* (based on prevalence in adult community, shape of corallite outer margins, and color of tissue on larger live recruits). The faviid recruits reported in this study appear to include *Montastraea cavernosa* recruits and members of the *Diploria* and/or *Pseudodiploria* genera, based on corallite size at the time of budding, septal dentition, and columella development. A single recruit that did not fall into one of these four families was identified to species as *Madracis decactis.* Due to small size, structural damage, or ambiguous corallite morphology, 18% of scleractinian recruits could not be identified. Resolution of octocoral identification was limited due to size and similarities between taxa; therefore, all octocorals were grouped together for this portion of the study.

In the *in situ* censuses, a total of 561 scleractinian juveniles were observed in quadrats. Siderastreids were the dominant scleractinian, and 91% of siderastreid juveniles were identified to species as *Siderastrea siderea*.   The majority of poritid juveniles were identified as *Porites astreoides*. All faviid corals reported were broadcast-spawning, boulder-forming species. *Montastraea cavernosa* was the most dominant faviid, with 71 juveniles reported. Other faviids included *Solenastrea bournoni* (8 juveniles),

Diploria/Pseudodiploria (5 juveniles)*,* and *Orbicella* (2 juveniles). No *Colpophyllia natans* juveniles were reported in 2016. "Other Scleractinians" included *Stephanocoenia intersepta, Dichocoenia stokesii, Meandrina meandrites, Eusmilia fastigiata* (one juvenile) and mussid juveniles (Appendix 2 is a table of juveniles identified to family at each site; Appendix 3 shows the number of juveniles of each species identified across all sites). A total of 716 octocorals were observed in quadrats (Appendix 4). Plexaurids were the dominant family among octocorals, with 89% of the Plexaurids identified to genus *Eunicea*.

3.2 Spatial Parameter Modeling

The most plausible single-parameter model of scleractinian recruitment was the microhabitat (location on tile) model, while best-approximating single-parameter model of octocoral recruitment was scaled to the site level. Both were weighted as the only plausible models for the data out of the candidate models provided. Juveniles exhibited most of their variation on the site scale. The best-fitting single-parameter model of scleractinian juvenile distribution was based on site (weighted 100%). The best fitting model of octocoral juvenile distribution was also based on site and was 166 times more plausible than the next-best fit (region) (Appendix 5, AIC scores and weights of model selection).

3.2.1 Microhabitat spatial scale (orientation on tiles)

There was significantly higher density of settlement on the top tile of the tile pairs than the bottom in both scleractinians and octocorals (W=57332, p<0.0001 and W=69740, p=0.0257, respectively). This was evident in parameter estimates from the negative binomial regression model of settlement location (Table 5), followed by paired contrasts. Eighty-four percent of scleractinian recruits were found on top tiles, and 78% of octocorals were on top tiles. Of poritid recruits, 85% were found on top tiles, and 100% of siderastreid recruits were on top tiles. Only agariciid recruits had more representatives on bottom tiles than tops (83%), though the difference was not statistically significant (Wilcoxon, p=0.056) (Fig 6).
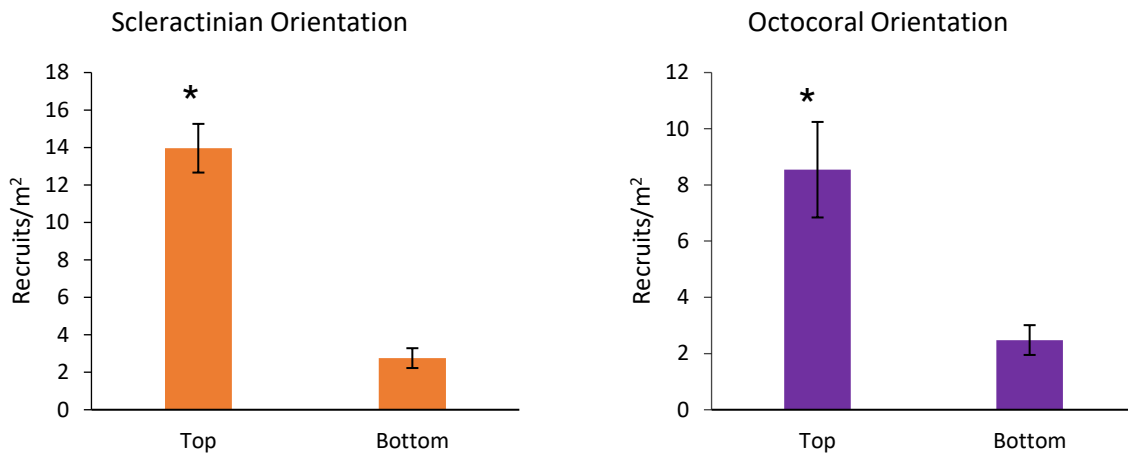
Figure 6. Mean density of scleractinian and octocoral recruits on tops and bottoms of tiles. Bars represent mean densities ± S.E. Asterisks represent significance (p<0.05). N=382

Table 5: Parameters estimates, standard errors (SE), and 95% confidence interval based on the negative binomial regression models relating coral recruit counts on settlement tiles to location on tiles. This model was best-fitting of all candidate models for scleractinian recruits, but not for octocoral recruits.

	Scleractinian Location Model			**Octocoral Location Model**		
Parameter	**Estimate**	**SE**	**Confidence Interval**	**Estimate**	**SE**	**Confidence Interval**
Intercept	-2.54	0.19	(-2.94)-(-2.19)	-2.65	0.26	(-3.16)-(-2.15)
Top	1.24	0.33	0.6-1.89	1.62	0.21	1.22-2.06

No data was collected for juvenile microhabitat distribution (i.e., exposed vs. cryptic). Most quadrats had low substrate complexity and limited cryptic microhabitat space, so performing a similar comparison of juvenile distributions would have required normalizing for exposed and cryptic surface areas and was beyond the scope of this study.

3.2.2 Site-level spatial scale

Recruits

Overall, scleractinian recruit abundance did not vary across sites, as supported by the parameter estimates from the model using site as a spatial variable, followed by paired contrasts (all p-values greater than 0.05) (Fig. 7). Scleractinian recruit density was lowest at DC3 and highest at DC6 and DC7. Octocoral recruit densities ranged from 0-10.2 recruits/m^2, with one statistically significant exception. The best-approximating model of spatial variation in octocoral recruitment was the model that used site as the variable. Octocoral density differed at the site DC8 (negative binomial regression paired contrasts p<0.001) (Fig. 8), where a total of 78 octocoral recruits were found on 32 tile pairs, for a mean octocoral recruit density of 42.8/m^2. Octocoral recruits from DC8 represent 65% of the total octocoral recruits found in this study.
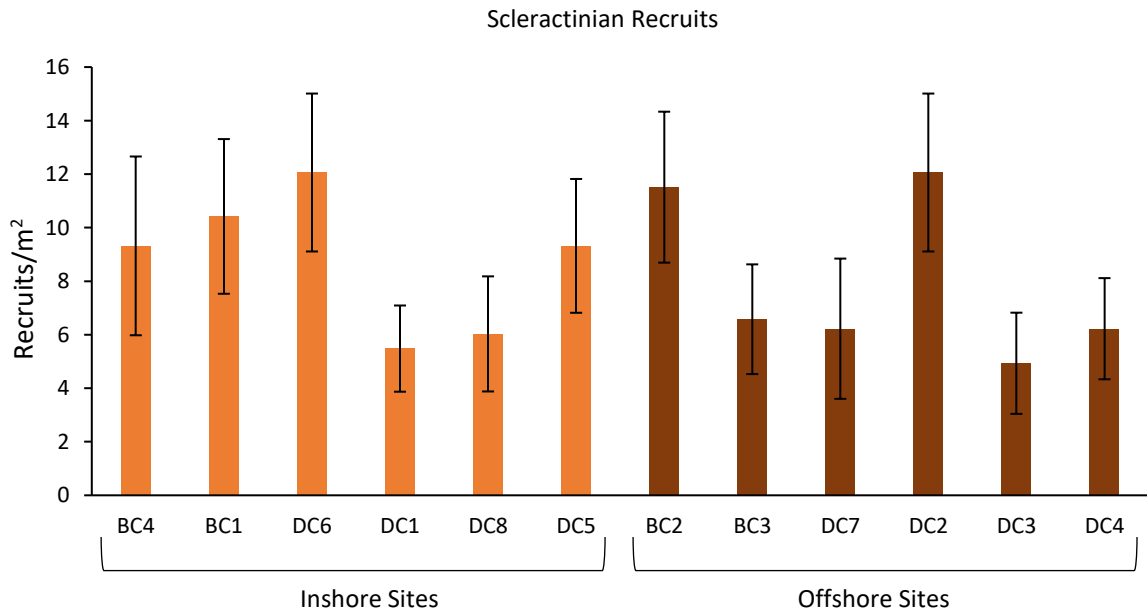
Figure 7. Bars represent mean density ± S.E. of scleractinian recruits. Inshore and offshore sites are arranged by latitude from north to south.
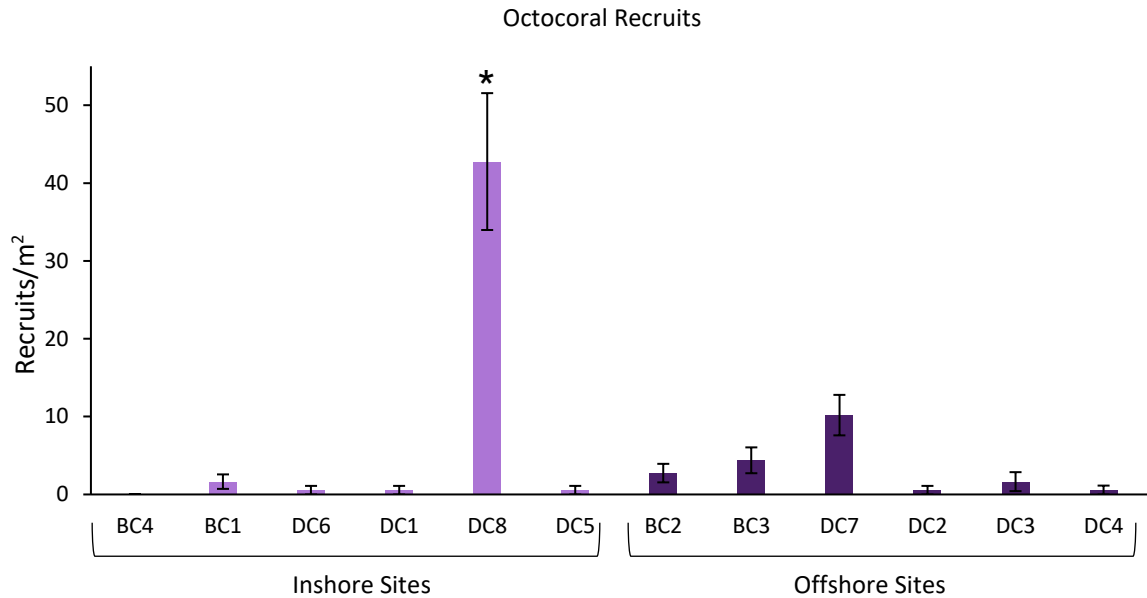
Figure 8. Bars represent mean density ± S.E. of octocoral recruits. Inshore sites are represented by lighter bars and offshore sites are represented by darker bars. Inshore and offshore sites are arranged by latitude from north to south.

Juveniles

Juvenile scleractinian abundance varied among sites according to a negative binomial regression model of juvenile counts (Fig. 9, Appendix 6 is a table of parameter estimates). Mean scleractinian juvenile density ranged from $1.3/m^2$ (DC3) to $11.5/m^2$ (BC4). Octocoral abundance also varied across sites, with DC8 having significantly higher density than the rest (Fig. 10, Appendix 6). Mean octocoral densities ranged from $4.1/m^2$ (DC7) to $14.0/m^2$ (DC8). No trend in density across the latitudinal gradient was apparent for scleractinians or for octocorals. Sites located in the same regional clusters exhibited significantly different scleractinian densities despite their proximity, with BC4 having significantly higher scleractinian juvenile density than BC1 in the Ft. Lauderdale region, and DC5 having significantly higher scleractinian juvenile density than DC8 in the Biscayne region. A significantly higher octocoral density was observed at DC8 compared with DC5, despite proximity. The second-reef site DC2 had significantly higher scleractinian density than third-reef site DC3, even though they are both located in the Miami site cluster, 700m apart from one another.

Scleractinian Juveniles
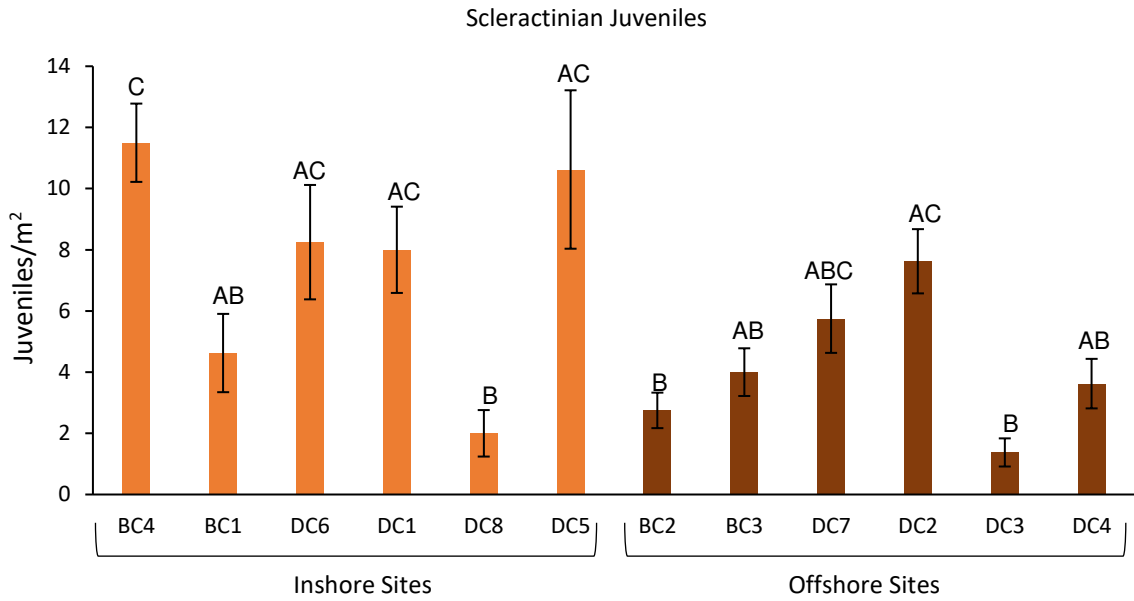
Figure 9. Bars represent mean density ± S.E. of scleractinian juveniles. Inshore sites are represented by lighter bars and offshore sites are represented by darker bars. Inshore and offshore sites are arranged by latitude from north to south. Letters represent significant differences

Octocoral Juveniles
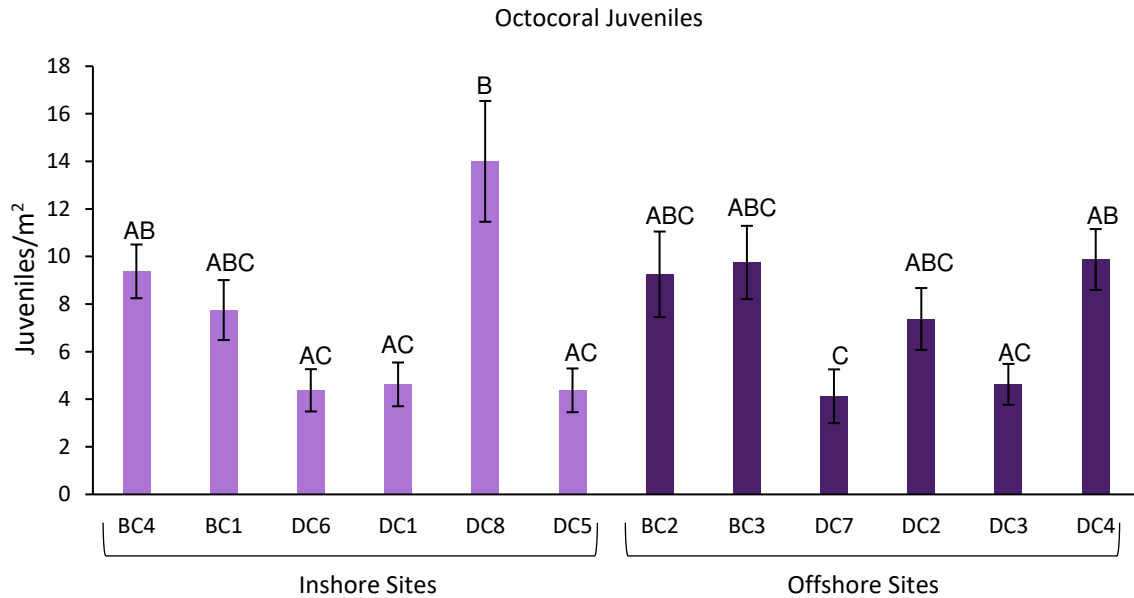
Figure 10. Mean density ± S.E. of octocoral juveniles per site. Inshore sites are represented by lighter bars and offshore sites are represented by darker bars. Inshore and offshore sites are arranged by latitude from north to south.

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Regional Stony Taxa Distribution of Recruits
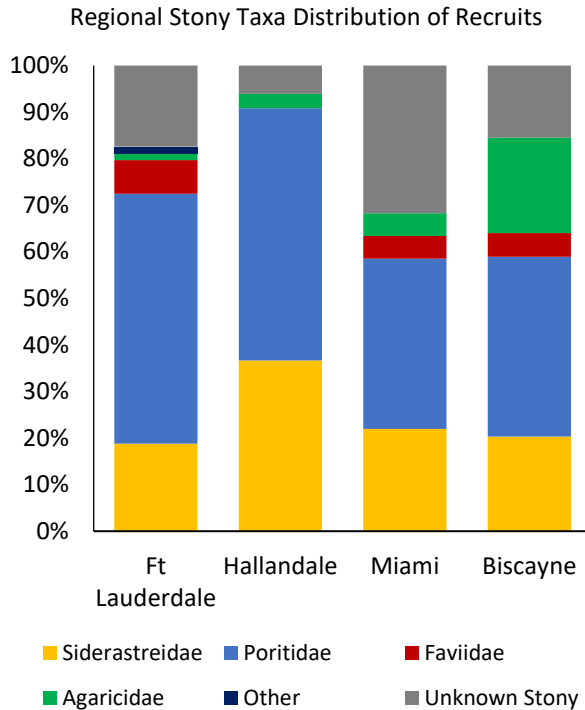
Figure 11. Percentage of recruit population comprised of each identified family, by regional cluster. Regions are ordered by latitude from north to south.

3.2.3 Regional Scale

No significant variation was observed in scleractinian recruit density across the four latitudinal regions (χ^2=0.6243, df=3, p=0.8909). This was supported by paired contrasts performed based on the negative binomial regression model with region as the variable, as well as a non-parametric post-hoc test. Individual families did not vary in density among the four regions. Poritidae was the dominant family in each region followed by Siderastreidae (Fig 11). Octocoral recruitment was variable between regions according to paired contrasts, with the Biscayne and Hallandale regions having significantly higher likelihood of octocoral recruitment (Appendix 7, table of paired contrast p-values). This is probably due to the influence of the high octocoral recruitment at DC8 in the Biscayne region and the moderate recruitment at DC7 in the Hallandale region, with very low octocoral recruitment recorded at all other sites (Fig 10). The Hallandale and Biscayne are located north and south, respectively, of the Miami cluster. The sites DC7 and DC8 have little similarity in complexity or species composition. Scleractinian juvenile density did not significantly vary between the four latitudinal regions (χ^2=4.7584, df=3, p=0.1904), supported by a lack of significant paired contrasts for the negative binomial regression with region as the independent variable. Latitudinal patterns in the octocoral juvenile distribution were difficult to discern because of the lack of taxonomic resolution and high percentage of unidentified octocorals (Fig 12).

Octocoral juvenile densities were more variable among regions, with the Ft. Lauderdale and Biscayne regions (the northernmost and southernmost, respectively) having the highest octocoral densities ($\chi^2=30.207$, df=3, p<0.0001), supported by paired contrasts (Appendix 7). Plexauridae was the dominant family of octocoral juveniles due to the prevalence of the genus *Eunicea*. Octocorals too small to identify were common. Thirty-six percent of the octocoral juveniles recorded were 4mm in height or less, and of those 86% were recorded as "unknown octocoral." Other reasons for unidentified octocorals include ambiguous morphology and severe tissue damage.
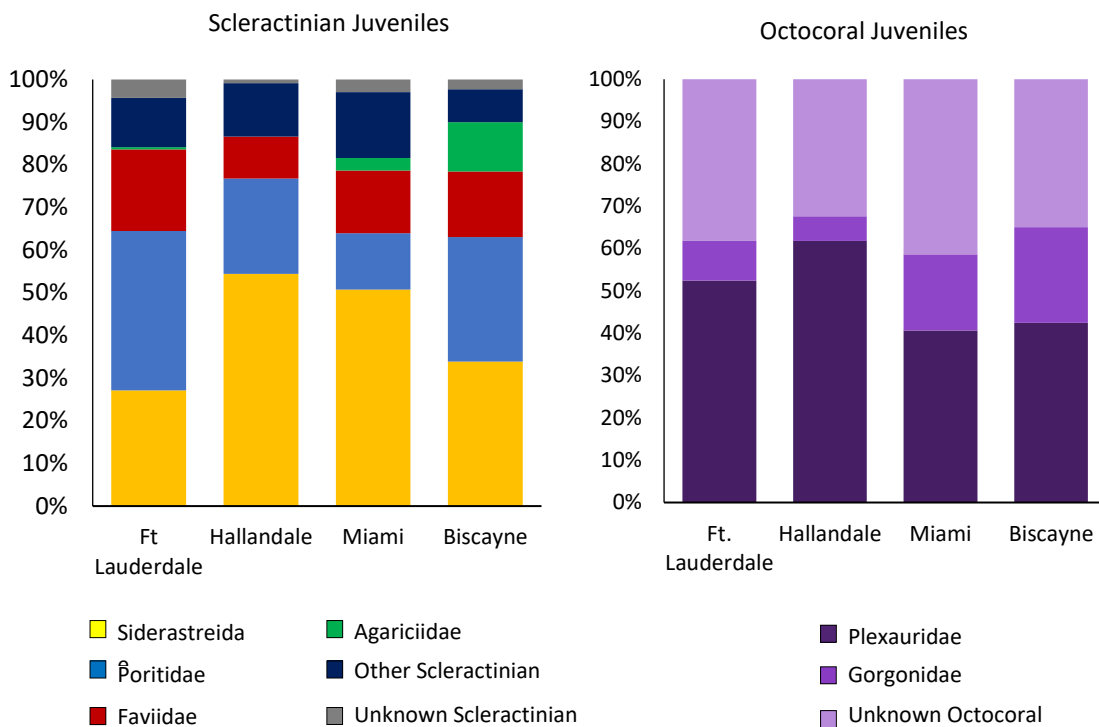
Figure 12. The taxonomic composition of the scleractinian and octocoral juvenile populations of each region (listed by latitude from north to south) is expressed as a percentage of the total. "Other scleractinians" were corals that did not fall into the families Siderastreidae, Poritidae, Faviidae, and Agaricidae, and "Unknown Scleractinians" were any scleractinians which the observer could not identify.

3.2.4 Inshore vs. Offshore Sites

The SECREMP data for the twelve study sites (normal when log(x+1) transformed) suggest that the inshore study sites have significantly higher adult scleractinian densities than offshore sites (t=-7.0548, df=38.044, p<0.0001), and no significant difference was found between octocoral densities at offshore and inshore sites (t=0.25238, df=45.994, p=0.8019). In contrast, no significant difference was observed in scleractinian recruitment between offshore and inshore sites for scleractinians, and the abundance of octocoral recruits was significantly higher at inshore sites (Table 6, Fig 15).

Table 6: Parameter estimates, standard errors (SE), and lower and upper 95% confidence limits based on the negative binomial regression models relating coral recruit counts on settlement tiles to zone (inshore/offshore) of tile deployment. During model fitting, the offshore parameter was arbitrarily selected as the statistical baseline.

	Scleractinian Recruit Ishore/Offshore Model			Octocoral Recruit Inshore/Offshore Model		
Parameter	**Estimate**	**SE**	**Confidence Interval**	**Estimate**	**SE**	**Confidence Interval**
Intercept	-1.49	0.13	(-1.74)-(-1.24)	-2.36	0.25	(-2.84)-(-1.87)
Inshore	0.1	0.18	-0.25-0.45	0.84	0.32	0.21-1.47

Consistent with the adult demographic data reported by SECREMP, scleractinian juvenile density was significantly higher at inshore sites than offshore sites (W=14772, p=0.0004), while juvenile octocoral density did not significantly differ between offshore and inshore zones (W=18546, p=0.9147). The nonparametric analyses were mirrored by results of modeling efforts (Table 7). These results suggest that the distribution of juveniles between inshore and offshore reefs may be more similar to the adult distribution than the recruit distribution.

Table 7: Parameter estimates, standard errors (SE), and lower and upper 95% confidence limits based on the negative binomial regression models relating coral juvenile counts in quadrats to zone (inshore/offshore) of quadrat location. During model fitting, the offshore parameter was arbitrarily selected as the statistical baseline.

Parameter	Scleractinian Juvenile Inshore/Offshore Model			Octocoral Juvenile Inshore/Offshore Model		
	Estimate	SE	Confidence Interval	Estimate	SE	Confidence Interval
Intercept	0.05	0.10	-0.14-0.23	0.63	0.08	0.48-0.78
Inshore	0.58	0.13	0.33-0.83	-0.02	0.11	-0.23-0.20

3.6 Comparing Recruit, Juvenile, and Adult Densities

3.6.1 Relationships in Scleractinians and Octocorals

Because transects serve as replicates in the adult data, tiles and quadrats from the recruit and juvenile studies were pooled into their respective transects for comparison. All data were converted to density (i.e. number of individuals.m^{-2}). Nonparametric analyses were used because the recruit data, with transects as replicates, were not normally distributed (W=0.87157, p<0.0001). Scleractinian density was significantly higher in the recruit and juvenile populations than in the adult population, which had a mean density of 1.4 colonies/m^2 (χ^2=60.895, df=2, p<0.0001, Fig. 13). Mean density of scleractinian recruits (8.2/m^2) was not significantly different from the density of scleractinian juveniles (5.8/m^2). Octocoral density was significantly different across life history stages (χ^2=49.365, df=2, p<0.0001, Fig. 13). Density was highest in adult octocoral populations (11.3/m^2), followed by juvenile populations (7.5/m^2). The lowest density was found in the recruit population, at 5.5 colonies/m^2. The mean ratio of scleractinian juveniles per scleractinian recruit was 3.1 juveniles.recruit^{-1}, while the mean ratio of octocoral juveniles/octocoral recruit was 6.0 juveniles.recruit^{-1}.
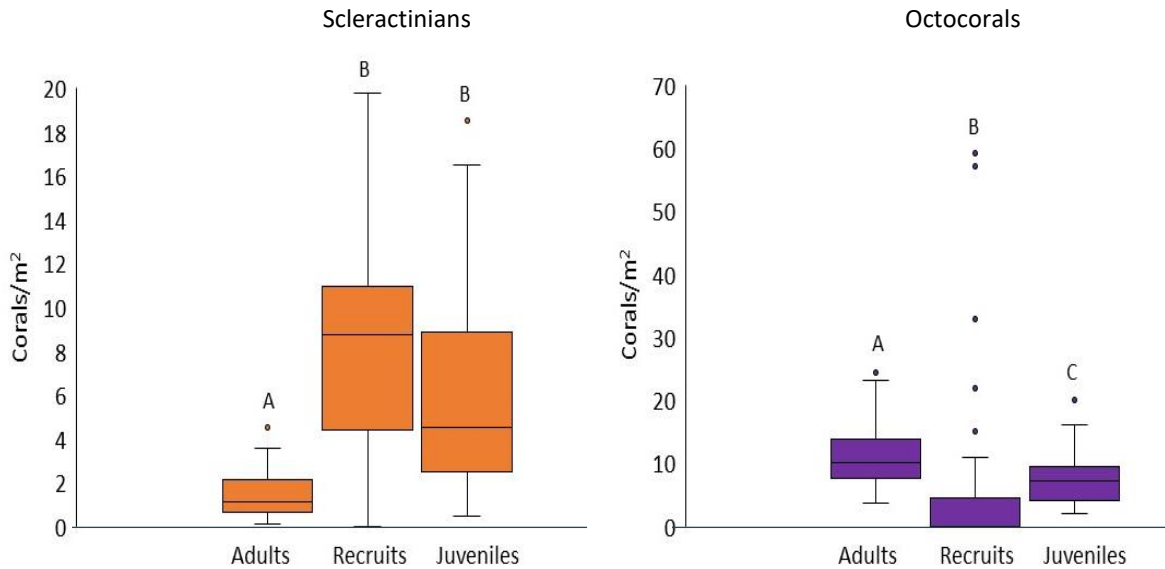
Figure 13. Box and whisker plots of adult, recruit, and juvenile mean transect densities of scleractinians and octocorals. Letters designate significantly different (p<0.05) groups as reported by a non-parametric multiple comparisons post-hoc test.

3.6.2 Relationships Within Common Scleractinian Families: Poritidae and Siderastreidae

Poritidae was the most common family represented in the settlement tile study. When poritid densities are compared across life history stages, the adult, recruit, and juvenile populations are significantly different in density (χ^2=15.839, df=2, p=0.0004, Fig. 14). Significantly more recruits were observed than adults or juveniles (3.9 recruits/m^2 compared with 1.6 juveniles/m^2 and 0.5 adults/m^2). Siderastreid corals also varied in density across life history stages, though they follow a different pattern than poritids (χ^2=18.754, df=2, p<0.0001, Fig. 14). In this study, a significantly higher density of juvenile siderastreids was observed compared with adults and recruits (Fig 14). While poritid adults are dominant at inshore sites and siderastreids dominant at offshore sites, at both inshore and offshore sites siderastreid corals increase in relative density as they progress from the recruit to the juvenile life stage. The ratio of *Siderastrea* juveniles to *Siderastrea* recruits was higher than the ratio of *Porites* juveniles to *Porites* recruits at both inshore sites and at offshore sites (Fig 16).

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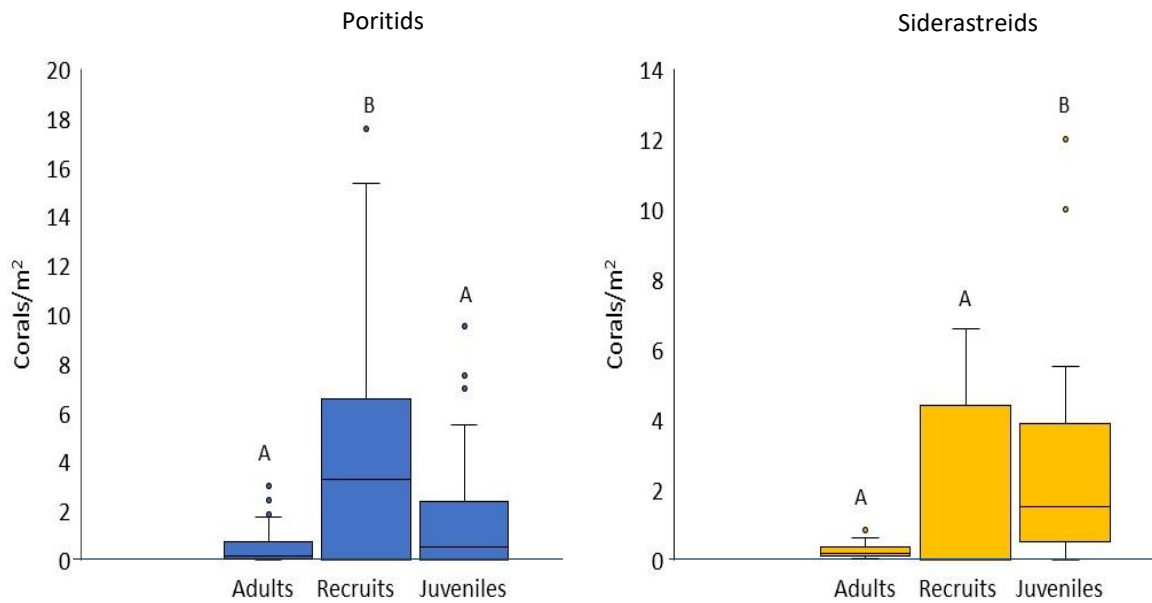
Figure 14. Box and whisker plots of adult, recruit, and juvenile mean transect densities of poritids and siderastreids in which center lines represent medians, box ends represent first and third quartiles, whiskers represent minimum and maximum values, and dots represent outliers in the data. Letters designate significantly different (p<0.05) groups as reported by a non-parametric multiple comparisons post-hoc test.

3.6.3 Differences Between Inshore and Offshore Sites

Offshore and inshore sites lie at different depths and are subject to different suites of stressors. To determine whether these areas exhibit different relative recruitment and juvenile survivorship trends, densities of adults, recruits, and juveniles were compared separately within offshore and inshore sites. When tiles and quadrats were pooled into transects for comparison with adult data, the trends in relative density of corals at offshore and inshore sites across life stages were the same as when tiles and quadrats were treated as replicates. Octocoral densities did not differ between offshore and inshore study sites at any life stage (recruits: W=72442, p=0.7200; juveniles: W=18546, p=0.9147; adults: t=0.2524, df=45.994, p=0.8019). Meanwhile, scleractinian adults exhibited higher density at inshore sites than offshore (t=-7.0548, df=38.044, p<0.0001),

recruit densities did not differ (W=72232, p=0.7182), and juveniles had significantly higher densities at inshore sites (W=14772, p=0.0004) (Fig 15). The mean ratio of recruits per adult on a transect (recruit density divided by adult density for each transect) is higher on average at offshore sites (t=4.3908, df=36.252, p<0.0001), while the number of juveniles per recruit at each transect did not differ between inshore and offshore sites (W=167, p=0.0545).
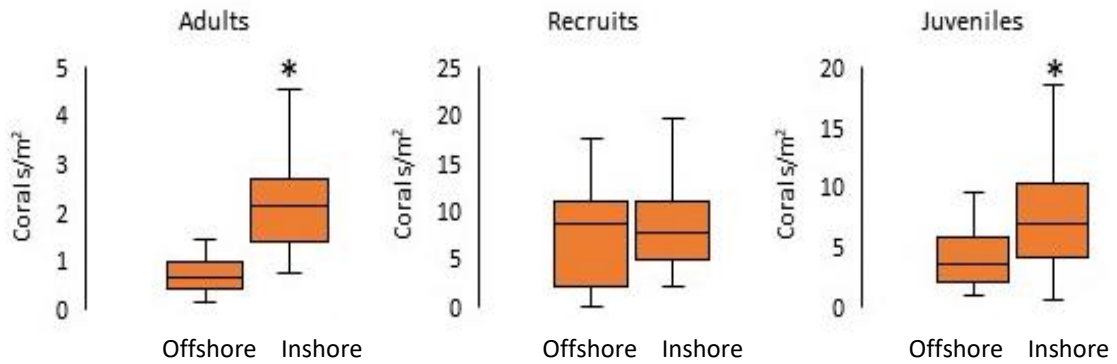
Figure 15. Box and whisker plot of scleractinian density between offshore and inshore sites across life stages. Asterisks represent significance (p<0.05). Transects were treated as replicates.
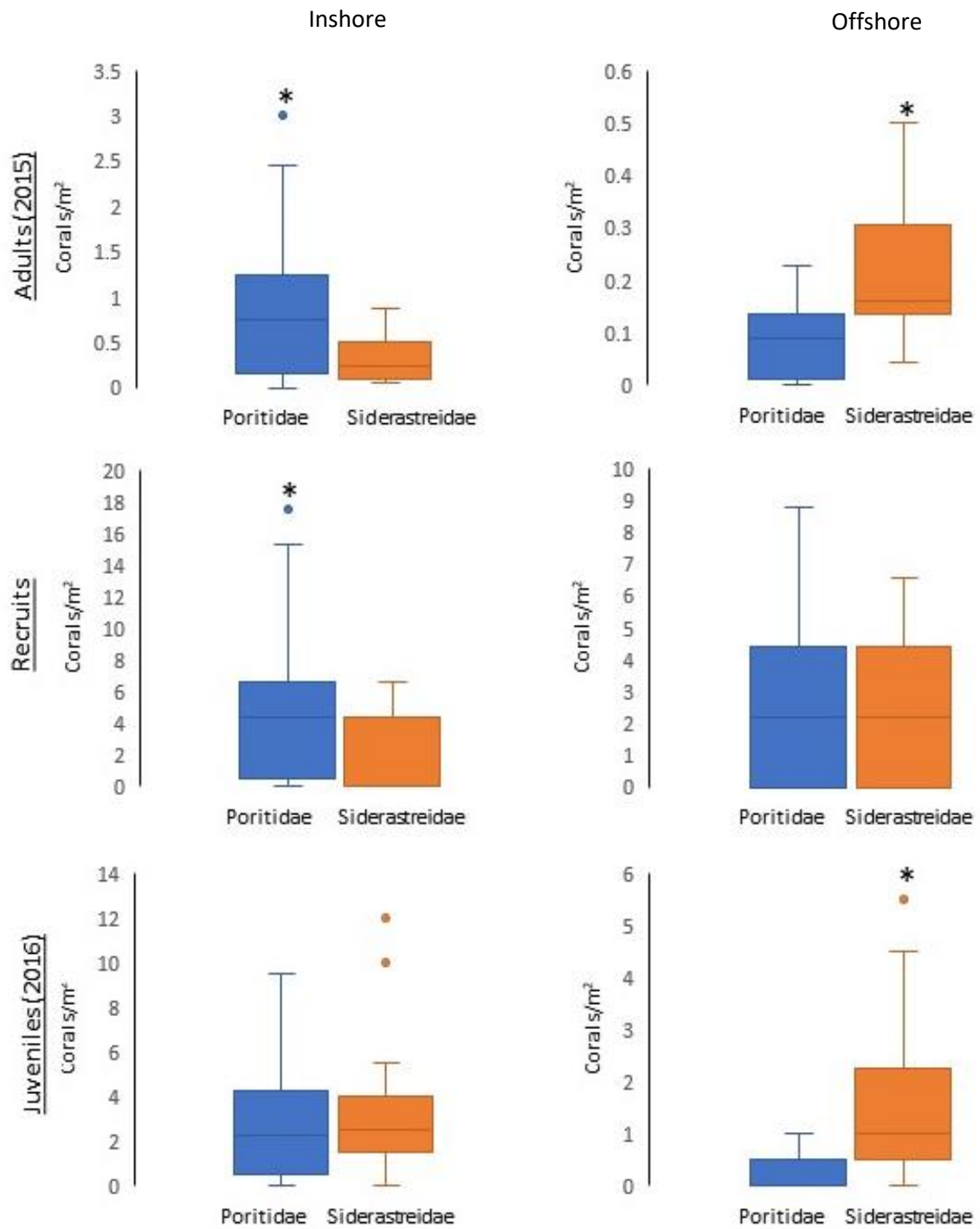
Inshore

Offshore

Figure 16. Box and whisker plots showing the relative density of Poritidae and Siderastreidae as adults, recruits, and juveniles at inshore and offshore sites. Center lines are median values, box ends are the first and third quartiles, and whiskers are minimum and maximum densities (by transect). Asterisks indicate significance (p<0.05).

3.6.3 Correlations Between Adult, Recruit, and Juvenile Densities

Scleractinian density were normally distributed when log(x+1) transformed. No significant relationship was found between scleractinian adults and scleractinian recruits at the site level (Pearson's Correlation, p=0.2697). Furthermore, juvenile scleractinian density were not significantly correlated with recruit density, even though the juveniles censused in 2016 were expected to reflect any relative increases in density resulting from recruits from the 2015-2016 reproductive season (while tiles were deployed) (Pearson's Correlation, p=0.202). However, significant relationships existed between scleractinian juvenile and adult data (Pearson's Correlation, p<0.001, r=0.83, respectively) (Fig. 17).
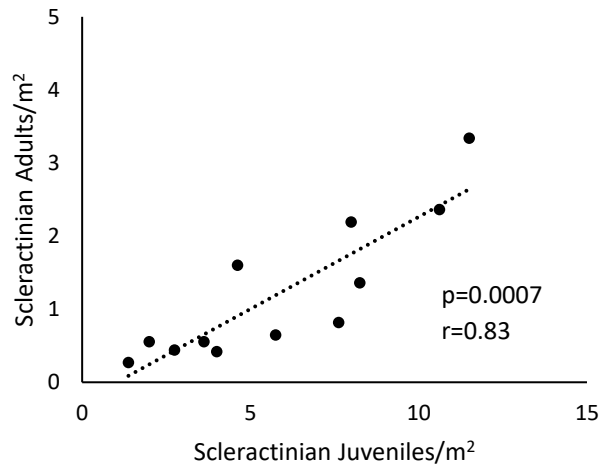
Figure 17. Relationship between adult and juvenile scleractinian densities per site.

Significant relationships across all life stages at the family level only existed for poritids. Recruit density was positively correlated with adult density (p=0.0018, ρ=0.80, Table 8), juvenile densities positively correlated with adult densities (p<0.0001, ρ =0.92), and recruit densities positively correlated with juvenile densities (p=0.0026, r=0.78).

Table 8: Relationships between recruit, juvenile, and adult datasets are shown, with sites treated as replicates. (S)=Spearman's Rank Correlation, (P)=Pearson's Product Moment Correlation, asterisk denotes log(x+1) transformed data. Significant correlations include correlation coefficient (r) and are boxed. The extension below shows the breakdown of the "Other" taxa where relationships were significant.

	Relationships Between Datasets on Site Level		
	2015 Adult, Recruit	**Recruit, 2016 Juvenile**	**2016 Juvenile, 2016 Adult**
Agariciidae	p=0.1955 (S)	p=0.0833 (S)	p=0.1485 (S)
Poritidae	p=0.0018 (S) r=0.7993	p=0.0005 (S) r=0.84	p<0.0001 (S) r=0.92
Faviidae	p=0.6487 (S)	p=0.3880 (S)	p=0.4765 (S)
Siderastreidae	p=0.1869* (P)	p=0.7413 (P)	p=0.5232* (P)
Other	N/A	N/A	p=0.03613* (P) r=0.6075
Total Scleractinian Corals	p=0.2697 (P)	p=0.2020 (P)	p=0.0007474* (P) r=0.8339
Octocorals	p=0.6664 (S)	p=0.4256 (S)	p=0.1266 (P)

	2016 Juvenile, 2016 Adult
Stephanocoenia intersepta	p=0.2546 (S)
Mussidae p	p=0.3435 (S)

Dichocoenia stokesii	p=0.01639 (S) r=-0.6733
Eusmilia fastigiata	p<0.0001 (S)
Meandrina meandrites	p=0.2457 (S)

The "Other Scleractinians" group also exhibited significant correlations between juvenile and adult populations for both 2015 (p=0.0146, r=0.68) and 2016 (p=0.0361, r=0.61, log(x+1) transformed). After separating the "Other" group into categories of higher taxonomic resolution, significant relationships were found for *D. stokesii* (p=0.0164, ρ=-0.6733) and *E. fastigiata* (p<0.0001, ρ=1). However, the relationship for *D. stokesii* was negative. Also, in 2016, *E. fastigiata* was only found at one site (DC2) in the juvenile and adult populations, after suffering high rates of mortality from disease. Because sample sizes for each of these taxa were low in the context of this study (N<15 for each taxon in the juvenile population), it is difficult to draw conclusions from these relationships.

Octocoral recruit data was non-normally distributed when sites were used as replicates (Shapiro-Wilk p<0.05), while juvenile and adult data were normal when log(x+1) transformed. The density of juvenile octocorals is not significantly correlated to the density of adult octocorals (Pearson's, p=0.1266). Octocoral recruit densities were also not significantly correlates with adult octocoral densities (Spearman's, p=0.6664). However, a small but statistically significant negative correlation was observed between scleractinian adult density and octocoral recruit density (p=0.0353, ρ=-0.6, Fig. 18). No relationship was observed between scleractinian recruit density and adult octocoral density (Pearson's, p=0.9879).
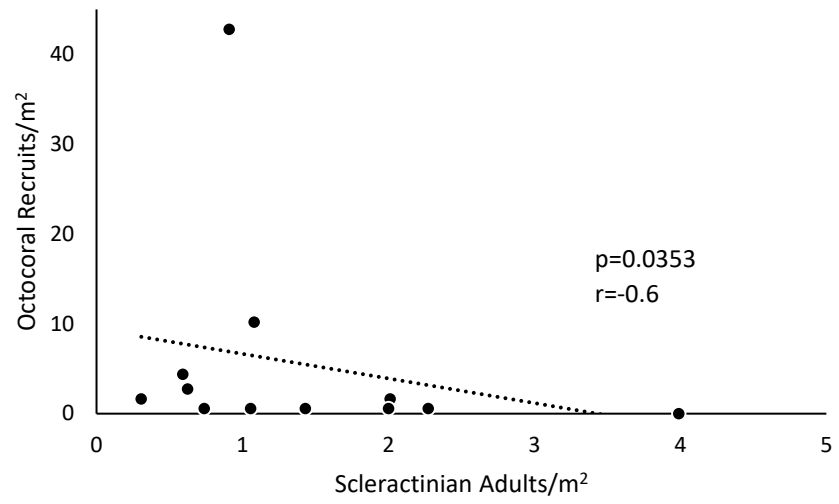
Figure 18. Scatterplot depicting negative correlation between scleractinian adult density (x axis) and octocoral recruit density (y axis).

DISCUSSION

Two broad ecological patterns emerge after examining one year of coral recruitment and juvenile data in Southeast Florida. First, taxa that are tolerant of marginal conditions exhibited evidence of successful recruitment, juvenile survivorship, or both. Second, a spatial uniformity in recruitment throughout the region, coupled with a patchy distribution of juveniles, suggests that differential post-settlement survivorship is a major factor in structuring adult populations. Unlike studies on other sites, this study found that, in Southeast Florida, 84% of scleractinian recruits settled on the exposed upper settlement tile surfaces. This trend may be unique to high latitude reef systems, or even specifically to Southeast Florida, and challenges the existing tenet that cryptic recruitment is driven by sedimentation, predation, or filamentous algae (Birkeland et al. 1981, Babcock and Mundy 1996, Doropoulos et al. 2016, Ricardo et al. 2017). The results of this study provide insight into the recruitment dynamics in the region and the potential for juvenile survivorship and eventual coral reef recovery.

The overall rate of scleractinian recruitment found in this study (0.7 recruits/m^2/month) is seven times higher than was reported in a 2008 settlement tile study in Southeast Florida (Table 2), which reported an overall recruitment rate of 0.1 recruits/m^2/month across five sites [two sites damaged by ship groundings and three control sites (Rubin et al. 2008)]. One possible explanation for this disparity is that Rubin et al. (2008) did not bleach their tiles but rather sampled frozen recruits for genetic analysis. Scanning only once for live or frozen recruits increases the likelihood that sediment, algae, and other organisms obscure small recruits, resulting in a less reliable settlement scan. Conducting a second scan after bleaching the tiles allows for recruits that were overgrown or smothered at the time of the live scan to be located, allowing for a more accurate assessment of total settlement. In this study, a 276% increase in scleractinian recruits was discovered after tiles were bleached.

A study conducted in Belize using similar methods found much higher scleractinian and octocoral recruitment (Fieseler and Harper, unpub. data) than reported in the present study of Southeast Florida. From May 2015 to September of 2016, 3.8 scleractinians/m^2/month and 1 octocoral/m^2/month recruited to tiles deployed at four sites

directly east of Carrie Bow Caye at depths of 5m, 10m, 20m, and 30m. During a second tile deployment from November of 2015 to January of 2017, 1.2 scleractinians/m^2/month and 0.9 octocorals/m^2/month recruited to tiles deployed at two 30m sites at Carrie Bow Caye and four sites (5m, 10m, 15m, and 20m) at Ranguana Caye. These recruitment rates are approximately two to four times those observed in the present Southeast Florida study (0.7 scleractinians/m^2/month and 0.4 octocorals/m^2/month). The Belizean barrier reef is located further offshore than Southeast Florida's barrier reef and receives less anthropogenic impact. The Belize reef system is also located in the tropics, compared with Southeast Florida's high latitude, subtropical reef system. Its remote location and comparatively stable environment mean that the Belize barrier reef likely hosts healthier reefs with higher adult scleractinian cover and diversity than Southeast Florida. For reference, mean coral cover at the Smithsonian Institute's long-term monitoring stations at Carrie Bow Caye is 12.4% (Jones et al., unpub. data), while mean coral cover across at the twelve SECREMP sites used in this study is 1.9% (Gilliam et al., unpub. data). Also, agariciid corals were the dominant recruits in Belize (49-53%). Species within the family Agariciidae planulate multiple times per year (Van Moorsel 1983) and have been found to recruit at high densities (Arnold and Steneck 2011). The higher prevalence of Agariciidae recruits in Belize and the wider Caribbean, but not in Southeast Florida, may explain part of the disparity in recruitment rates.

One difference between this study and previous recruitment studies that used settlement tiles is that more octocorals and scleractinians settled on the upper, exposed surfaces of the tiles than on the cryptic undersides. Typically, >90% of recruits are found on tile undersides in locations throughout the Caribbean, such as Barbados (Tomascik 1991) and St. John (Edmunds et al. 2014), although using tiles with microhabitat refuges on upper surfaces has been shown to increase the proportion of settlement to the top surface (Edmunds et al. 2014). Studies that include sites deeper than 10m tend to reveal a shift in settlement orientation from undersides to upper surfaces with increasing depth (Bak and Engel 1979, Birkeland et al. 1981, Rogers et al. 1984, Babcock and Mundy 1996, Vermeij 2006). For example, in a companion study on the Mesoamerican Barrier Reef in Belize, the same grooved terracotta tiles were used. One hundred percent of

recruits settled on tile undersides at 5m, 97% at 10m, 82% at 20m and only 51% at 30m (Fieseler and Harper, unpub. data).

The shift in settlement orientation with increasing depth has been hypothesized to be caused by the light attenuation at depth limiting the growth of filamentous algae or by sediment scouring from shallow water surge (Birkeland et al. 1981, Babcock and Mundy 1996). However, even corals at the shallowest sites in Southeast Florida (<10m) settled predominately on exposed surfaces, and macroalgae cover on the Southeast Florida reef tract fluctuates but tends to be higher than scleractinian coral cover (Gilliam 2014). Additionally, most tiles in my study were coated with filamentous algae and sediment, regardless of deployment depth. Corals are sensitive to light levels and can preferentially settle in areas with appropriate light intensity (Mundy and Babcock 1998). Ultraviolet radiation (UVR, 280-400nm) influences the behavior and survival or coral larvae (Gleason and Hofmann 2011). Intense UVR has been shown to be detrimental to coral larvae, and many species use mycosporine-like amino acids to protect against the harmful impacts of UVR (Wellington and Fitt 2003, Gleason et al. 2005). The waters of Southeast Florida are likely more turbid than the waters of tropical Caribbean reefs due to a combination of natural and anthropogenic influences, such as dredging, beach renourishment, and nutrient runoff that enhances microalgal growth. The diminished light intensity caused by the suspended sediments in the water may prompt coral larvae to behave more consistently with larvae settling on deep reefs elsewhere in the Caribbean. While in other locations exposed surfaces may receive too much UVR to be appealing to coral larvae, the UVR reaching upper surfaces of tiles in Southeast Florida may be appropriate for larval settlement. Because exposed surfaces more often than cryptic surfaces are affected by sedimentation, predation, and algal growth, the trend of settlement to exposed surfaces in Southeast Florida may have implications for the post-settlement survivorship outcomes of juvenile corals.

Calculating overall density of juveniles in quadrats allows for comparison with other studies that used *in situ* census techniques (Table 3). The mean density of scleractinian juveniles found in quadrats was $5.9/m^2$, while the mean density of octocoral juveniles was $7.5/m^2$. The present study reports a higher density of scleractinian juveniles than a 2012 study of the Southeast Florida reef tract (Stein 2012). Densities in the 2012 study

ranged from 1.6-5.1 juveniles/m^2, while the range among sites reported in the present study is 1.4-11.5 juveniles/m^2. Whether the difference between the two studies is the result of an increase in the juvenile population in the region or differences in sample site selection and survey intensity is unclear. Compared to juvenile population on a Caribbean-wide scale, the Southeast Florida sites in the present study are scleractinian juvenile depauperate: historical densities of 15 and 18 juveniles/m^2 were reported in Curacao and Bonaire, respectively (Bak and Engel 1979) and 0 to 80 juveniles/m^2 in St. Croix (Rogers et al. 1984). More recently, 8 to 34 juveniles/m^2 were reported in Barbados (Carpenter and Edmunds 2006), and 17 to 25 juveniles/m^2 in Bonaire (Arnold et al. 2010) (Table 3). This disparity could indicate low recruitment, low survivorship, or both, for Southeast Florida's scleractinian populations.

The taxa that were found to exhibit the clearest evidence of recruitment success and post-settlement survivorship in Southeast Florida were Poritidae, Siderastreidae, and Octocorallia. All three were common in both the recruit and juvenile study results. These taxa demonstrated the capacity to recruit at high densities, the potential for high survivorship (surmised by an increase in density from the recruit to the juvenile stages), or both. All three have been reported to be tolerant of marginal conditions. Siderastreids and tolerant of extreme temperatures (Kemp et al. 2016, Okazaki et al. 2017), siderastreids and poritids are tolerant of chronic sedimentation (Lirman et al. 2008), and octocorals are tolerant of the influences of chronic rainfall (Edmunds and Lasker 2016, Tsounis and Edmunds 2017).

Poritids, which are brooding corals, were the most abundant recruits in Southeast Florida during the 2015-2016 recruitment season. Settlement studies using tiles consistently show that recruit demographics are dominated by brooding corals throughout the Caribbean: typically Poritidae (Green and Edmunds 2011) or Agariciidae (Rogers et al. 1984, Arnold and Steneck 2011). Poritid corals accounted for almost half of the recruits recorded in this study. *Porites astreoides* (the most abundant poritid in Southeast Florida) has the reproductive advantage of being able to planulate multiple times per year (Chornesky and Peters 1987). Additionally, recent research found that 100% of *Porites astreoides* individuals sampled near the Ft. Lauderdale region study sites in 2015 reproduced asexually through parthenogenesis (Vollmer and Fogarty, unpub. data).

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Implications of parthenogenic reproduction on *P. astreoides* dispersal, post-settlement survival, and population fitness are still unclear. However, it is possible that this alternative strategy is enhancing reproductive success, contributing to *P. astreoides*' dominance in the recruit population.

The second most common family of recruits reported in this study was Siderastreidae. Locally, the Siderastreidae family is comprised of the broadcast-spawning, boulder-forming *Siderastrea siderea*, and the small brooder *Siderastrea radians* (Gilliam 2014). These two species have very similar corallite morphologies and are difficult to distinguish as recruits, yet occupy different ecological niches as adults. SECREMP reports indicate higher densities of *S. siderea* adults at the study sites, but coral recruit distributions do not necessarily mirror adult distributions (Penin and Adjeroud 2013). At this stage it is impossible to conclude which siderastreid species is more represented in the recruit population.

Siderastrea siderea was the most common juvenile found in quadrats in this study. *Siderastrea siderea* has been shown to dominate at small size classes throughout the Florida Reef Tract (Stein 2012, Bartlett 2014). However, *S. siderea* juveniles were rare (<5% of total population) in other *in situ* studies in the Netherlands Antilles (Bak and Engel 1979, Carpenter and Edmunds 2006), Belize (Carpenter and Edmunds 2006), and St. Croix (Rogers et al. 1984, Carpenter and Edmunds 2006). The trend of *S. siderea* prevalence in Florida but not in the wider Caribbean may be explained by the wide thermal tolerance of this species that allows it to perform well in marginal habitats. *Siderastrea siderea* was found to be resistant to thermal stress when subjected to elevated temperatures (30.3˚C) (Okazaki et al. 2017) and was unaffected by a 2010 cold-water anomaly in the Florida Keys that dropped water temperatures to more than 11˚C below normal temperature minimums and caused high mortality among other common species, including *Porites astreoides* (Kemp et al. 2016). Its tolerance of unstable environmental conditions likely provides *S. siderea* with a competitive advantage that may explain why it is a dominant juvenile in the marginal habitats of Southeast Florida and the Florida Keys, yet much less abundant in juvenile populations elsewhere in the Caribbean where it may be outcompeted. The low light irradiance at depth caused by turbid water in Southeast Florida is probably not a driving factor in their distribution because *S. siderea*

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is found across a wide depth range including shallow (<5m) water, suggesting light tolerance.

   Porites astreoides was the second most common species found in the juvenile population, followed by the broadcast-spawning (Birkeland 1996) faviid species *Montastraea cavernosa*. *Montastraea cavernosa* is the dominant framework-building coral in the region (Moyer et al. 2003) and the highest contributor to total scleractinian cover (Sathe et al. 2008). It has been previously hypothesized to have a low-recruitment, high-survival life history strategy (Bak and Engel 1979, Rylaarsdam 1983, Rogers et al. 1984). Bak and Engel found only five *M. cavernosa* juveniles in their 1979 study for a density of 0.07 juveniles/m^2. The present study found a density of 0.76/m^2, despite the impact of the disease outbreak, which afflicted an estimated 38% of *M. cavernosa* adults on the first reef line in the Miami-Dade region in 2015 (Precht et al. 2016). Additionally, several of the faviid corals that recruited to the tiles may be *M. cavernosa*. Local *M. cavernosa* recruitment success and juvenile survivorship may be higher than elsewhere in the Caribbean due to reduced benthic competition in Southeast Florida. Southeast Florida's *M. cavernosa* recruits and juveniles could also be a sink population for larvae from the Florida Keys. The abundance of *M. cavernosa* juveniles may be a sign of greater potential to recover from disturbances compared with other disease-susceptible species.

   Comparison of poritid and siderastreid densities across life stages suggests that these taxa, while both demonstrating signs of recruitment and survivorship success in Southeast Florida, may exhibit different life history strategies. The Siderastreidae family was found at higher densities in the juvenile stage than in the adult or recruit stages, while the Poritidae family was found at higher densities in the recruit stage than the adult or juvenile stages (Fig. 15). When an adult population has a higher density than the subsequent recruit population, it suggests reduced adult fecundity or fertilization success, high mortality in the earliest life history stages, or high dispersal out of the study area. When an adult population has a lower density than the subsequent recruit population, it suggests high adult fecundity and fertilization success, increased survival in the earliest life history stages or local retention, or an influx of larvae from another location. Therefore, Siderastreidae and Poritidae recruit populations, which are equal to or denser

than the respective adult populations, may be benefiting from high adult fecundity, advantages in early survivorship, high local retention, or high influx of larvae from upstream sources, such as the Florida Keys. Poritids have been among the families thought to exhibit high recruitment and low survivorship (Smith 1992). Siderastreids have demonstrated low recruit and juvenile populations relative to adult populations in other locations(Bak and Engel 1979, Rylaarsdam 1983, Rogers et al. 1984, Carpenter and Edmunds 2006), so their recruitment success in Florida may be unique to the region.

Because juvenile demographics are the result of several years of recruitment, higher observed density of juveniles than recruits may be caused by high recruitment and/or low post-settlement mortality during the previous year(s), or by frequent fragmentation or larger colonies. Lower observed density of juveniles than recruits may be caused by post-settlement mortality and/or low recruitment year(s). The present study does not fate track juveniles and only includes one year of recruitment data, so it is impossible to disentangle the effects of post-settlement survivorship from the effects of prior recruitment success. However, preliminary recruit data from a second recruitment year is consistent with the first years' data. Differences in juvenile density compared to recruit density are probably at least in part the result of differential survival outcomes (e.g. (Smith 1992, Ritson-Williams et al. 2016)). Based on this supposition, I hypothesize that siderastreid and faviid recruits, which increase in density from the recruit to the juvenile life stages, have higher survival rates than poritid recruits, which decrease. Southeast Florida's current population of siderastreid corals appears to be exhibiting both high settlement success and high post-settlement survivorship relative to other taxa.

The difference in relative densities at offshore and inshore sites of the two dominant families in the region, Poritidae and Siderastreidae, may be evidence of higher post-settlement survivorship of siderastreids in both habitats (Fig. 16). As adults, Poritidae dominates at inshore sites and Siderastreidae dominates at offshore sites. As recruits, poritids are found at significantly higher densities than siderastreids at inshore sites, while their densities at offshore sites are the same. This evidence suggests the ratio of recruits per adult is greater in poritids than siderastreids in both inshore and offshore habitats. As juveniles, siderastreids dominate the offshore sites, and are comparable to poritids at inshore sites, suggesting that siderastreids may have greater survivorship to the

juvenile stage in both inshore and offshore habitats. Siderastreids have been documented to be more resistant to temperature fluctuations than poritids (Kemp et al. 2016, Okazaki et al. 2017) which could enhance their early survival. However, this conclusion contradicts results from a study which fate-tracked juvenile corals on Florida Keys patch reefs and found higher survivorship of *Porites astreoides* than *Siderastrea siderea* (Bartlett 2014). There are many environmental differences between the reefs of Southeast Florida and the patch reefs of the Florida Keys that could lead to different survivorship trends. Florida Keys patch reefs have higher adult coral density than the Southeast Florida study sites (1-16 corals/m^2 at patch reefs vs. 0.5-3 corals/m^2 at study sites in Southeast FL) (Gilliam et al. unpub. data, Ruzicka et al. unpub. data). Competitive dynamics and resource availability may differ between these two regions, and the benthic habitat in Southeast Florida may be more conducive to siderastreid survival. It is also possible that high siderastreid recruitment in past years is responsible for its high relative juvenile densities. Greater understanding of the interannual variation in recruitment and survivorship is needed to draw a conclusion.

An alternative explanation for the higher numbers of siderastreid juveniles per recruit compared with poritids is that the timing of tile deployment could have inflated poritid recruit densities. *Porites astreoides*, which comprises >75% of the juvenile Poritidae population reported in this study, reproduces in April, May, and June (Chornesky and Peters 1987, McGuire 1998). Since the tiles were deployed between March and early May of 2015 and retrieved between February and March of 2016, poritid planulae were exposed to tiles that had been conditioned for approximately two to ten weeks. At that point, tiles were in an early-successional state, and likely had limited colonization by sponges, ascidians, and encrusting gorgonians. The sediment layer on top of the tile was probably inshore, since there was little time for it to accumulate. By the time *Siderastrea siderea,* which comprises >90% of the juveniles observed in this study, spawned in the fall (St.Gelais et al. 2016), the tiles had been conditioned for seven to nine months. Some of the upper tile surfaces (where all siderastreids settled) had been colonized by poritids, erect and encrusting octocorals, macroalgal turfs, and occasional sponges and ascidians. Tiles likely had accumulated most of the thick sediment layer that was apparent when they were retrieved and scanned. Arnold and Steneck (2011)

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proposed a "recruitment window" for corals that lasts from about 9 to 14 months after a surface is opened for recolonization post-disturbance or after a bare tile is deployed. The *S. siderea* settlement period falls within that timeframe, so if the timing of the "recruitment window" holds true in southeast Florida, the timing of tile deployment should have allowed optimal *S. siderea* settlement. However, their research was conducted in Belize, where less sediment may accumulate on tile surfaces. Thick sediment layers that accumulate within a matter of months may alter the timing of the "recruitment window" for the corals of Southeast Florida. Future investigation of recruitment patterns could include deploying a subset of tiles in early July, only three months before *S. siderea* spawning occurs, to determine whether the relative settlement success for siderastreids compared with poritids is enhanced.

In Southeast Florida, octocorals exhibited evidence of possible advantages over scleractinians in terms of post-settlement survivorship. When all study sites and families were pooled, no significant difference was observed between scleractinian recruit and juvenile densities. Because the juvenile populations include many cohorts of recruits, this result implies that post-settlement mortality is occurring. Adult scleractinian density was lower than recruit and juvenile densities, suggesting high mortality rates in the recruit and juvenile life stages for taxa that recruited to tiles. Meanwhile, octocoral density was greatest in adults followed by juveniles and recruits (Fig. 13). While this trend seems to suggest higher post-settlement survival in octocorals than scleractinians, early post-settlement survival success in Caribbean octocorals has been observed to be poor (Lasker et al. 1998), even when compared with scleractinian survival (Bartlett 2014). Another explanation for the relative abundance of juvenile octocorals compared with recruits, even when post-settlement survival rates are hypothesized/assumed to be low, is that vegetative propagation could cause an inflated "juvenile" population that may be partially comprised of small clonal fragments from nearby adults. In a study of clonal reproductive strategies in Caribbean octocoral, *Plexaura kuna*, as few as three genotypes were identified on a reef, with clones greatly comprising most of the local abundance (Coffroth and Lasker 1998). However, while some octocoral species have morphologies that facilitate fragmentation, others seem less apt to fragment (Lasker 1984), and more research is needed to determine the extent to which vegetative reproduction contributes to

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Southeast Florida's octocoral population. The higher juvenile octocoral densities relative to recruit densities could also be the product of interannual variation in recruitment leading to high juvenile abundance in the juvenile census. Lastly, there is an overlap in sampling size classes between octocorals on settlement tiles, in quadrats (many small octocorals are recorded that could be from the same recruit cohort as found on tiles), and in adult surveys (no size minimum). The juvenile data could include octocorals that should have been classified as recruits, and the adult data could include may include some individuals that should be classified as juveniles. Future analyses should be conducted with size class under consideration.

While octocoral juvenile densities were greater than octocoral recruit densities overall and at most individual sites, the site DC8 was an exception that demonstrates the capacity of octocorals to recruit at high densities. DC8 had a significantly higher abundance of octocoral recruits than other sites, with a mean density of 42.8 octocoral recruits/m^2, accounting for 65% of the octocoral recruits in the entire study. The nearest inshore site to DC8 geographically (DC5, 3.8km away) had a single octocoral recruit (0.5 octocoral recruits/m^2). Despite their proximity, these sites have different adult species assemblages and structural complexity, resulting in two distinctly different habitats (Gilliam 2014).

The site DC8 had the highest juvenile and adult octocoral density of all study sites, and the abundance of octocoral recruits was higher than at other sites, even relative to the adult and juvenile octocoral abundances. One potential explanation for the high numbers of octocorals found on these tiles is that DC8 has several large sand patches, and was also impacted by the dredging of Port Miami, which increased sediment loads on the benthos (Barnes et al. 2015). Since tiles provided hard substrate in an area where stable substrate may be scarce, octocoral larvae may have preferentially settled on tiles, resulting in an inflated density of recruits. It is not well understood if octocoral larvae prefer to settle on tiles versus the natural benthos. An alternative hypothesis is that while a large influx of octocoral larvae is occurring throughout the site, juvenile densities are lower than recruit densities because of high post-sediment mortality on the natural substrate. Many of the octocorals recruiting to the benthos could be smothered by

sediment before reaching the juvenile stage. The elevated tile substrate may enhance post-settlement survival of octocorals when sedimentation is high.

The high abundance of adult and juvenile octocorals relative to recruits may be evidence of a successful life history strategy that results in high proportions of successful propagation. This apparent success under the current environmental conditions in Southeast Florida could support the conclusions of recent research that suggests a phase shift is occurring from scleractinian dominance to octocoral dominance in the Caribbean (Ruzicka et al. 2013, Edmunds and Lasker 2016, Tsounis and Edmunds 2017). The statistically significant negative relationship between adult scleractinian density and octocoral recruitment could be considered evidence for this shift (Fig. 18). Perhaps octocoral recruits are opportunistically settling in scleractinian-depauperate areas because they have the capacity to thrive in these marginal conditions. As environmental conditions deteriorate with anthropogenic climate change and increased local impacts, octocoral communities have been predicted to become more prevalent as they are more resilient to chronic stressors than scleractinian communities (Tsounis and Edmunds 2017).

Less tolerant, ESA-listed threatened species were rare in both components of this study. The absence of as recruits and juveniles of threatened corals *Acropora, Orbicella,* or *Dendrogyra* genera suggests that genetic diversity will tend to decrease and recovery is unlikely without input of larvae from a source outside the region. As of 2016, *Dendrogyra cylindrus* was rapidly approaching local extinction in Southeast Florida (Kabay 2016), and there were no living adult *Orbicella* colonies within any of the 22m^2 belt transects surveyed by SECREMP at any of the 12 study sites (Gilliam et al., unpub. data). While some *Orbicella* colonies remain living in Southeast Florida, Allee effects resulting from low densities make successful fertilization unlikely within local *Orbicella* populations and nearly impossible for *Dendrogrya*. Nineteen *Acropora cervicoris* colonies were recorded at the study sties in 2016 SECREMP surveys (Gilliam et al., unpub. data). Even though Broward County has one of the most genetically diverse *A. cervicornis* populations in Florida (Drury et al. 2017), based on the results of this study they do not appear to be yielding sexually produced recruits. The absence of *Orbicella* and *Acropora* recruits in this study also suggests that Southeast Florida's threatened

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populations are unlikely to be re-seeded by larvae from the Florida Keys or elsewhere in the Caribbean, though more understanding of interannual variation in recruitment rates is necessary to make this conclusion.

The recruitment failure of these threatened species may not be a new phenomenon. In a 1979 study that censused juvenile corals (<40mm diameter) over 75m^2 of reef across different habitats in Curacao and Bonaire, a total of one *M. ferox*, two *Acropora* spp. and four *Orbicella* spp. juveniles were identified, with no *D. cylindrus* representatives (Bak and Engel). Other studies conducted in the Caribbean before the acceleration of coral decline also recorded low recruit and juvenile densities of these species relative to their adult populations. It was hypothesized that *Orbicella* spp. have low recruitment but high survival rates relative to other species, and that *Acropora* spp. rely more on fragmentation than sexual reproduction to propagate (Rylaarsdam 1983, Rogers et al. 1984). While there is precedent for low recruitment of these species, their apparent recruitment failure in Southeast Florida is evidence of their limited potential to recover from mass mortality events such as the 2014-2015 disease outbreak (Precht et al. 2016).

Diploria and *Pseudodiploria* species and *Colpophyllia natans* are not ESA-listed, but may struggle to recover after Florida's disease outbreak or other local disturbances. In the disease outbreak evaluation, 83% of *Diploria labyrinthiformis* and 84% of *Pseudodiploria strigosa* adult colonies were afflicted or killed (Precht et al. 2016). *Colpophyllia natans* affliction was reported at 93%. *Diploria* spp. are among the corals that have exhibited low recruitment and high survival in past studies (Smith 1992). We identified only five *Diploria/Pseudodiploria* individuals in the juvenile census (a density comparable to that reported in Bak and Engel 1979), and only one *C. natans* juvenile. These populations may struggle to recover through natural recruitment processes in Southeast Florida, compared with taxa such as Poritidae, Siderastreidae, and Octocorallia, which have been shown to be tolerant of marginal conditions and exhibited evidence of successful recruitment and survivorship within the region.

The second major conclusion of this study is that in Southeast Florida, recruits are dispersed evenly over the spatial parameters evaluated, but survivorship through the

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juvenile stage is a critical factor in structuring the spatial structure of adult coral communities. Scleractinian recruit densities were not significantly different among study sites, nor did they differ between inshore and offshore sites. Octocoral recruit densities, however, were variable on the site-level scale. Overall scleractinian and octocoral recruit densities also did not differ between the four regional clusters. Meanwhile, scleractinian and octocoral juvenile densities were highly variable among sites, which may be explained by localized distributions of factors affecting survivorship, including macroalgae and sedimentation. Sites located within 0.7 km of one another and at approximately the same depth (DC3 and DC2) were found to exhibit stark differences in scleractinian juvenile density (1.2 juveniles/m^2 and 6.8 juveniles/m^2, respectively). Meanwhile, sites located distances greater than 50 km from one another, such as BC4 and DC5, had no significant difference in recruit density. Octocorals also exhibited variation in juvenile density between nearby sites. Greater variation in coral assemblages on small spatial scales than on regional spatial scales has been previously reported in Florida and elsewhere in the Caribbean (Aronson 2001).

While scleractinian recruit densities did not differ between inshore and offshore habitats, inshore sites had significantly greater scleractinian juvenile densities than offshore sites (Fig 16), suggesting that post-settlement mortality of scleractinian recruits may be higher at the offshore study sites than at the inshore study sites. One reason that survivorship may be higher at inshore sites may be that more light could allow for more energy production by corals' symbiotic algae, leading to higher growth rates and less time spent in the most vulnerable size classes. Other reasons may include lower grazing pressure or lower cover of cyanobacteria or macroalgae at inshore sites. Cyanobacteria and macroalgae cover were higher at inshore sites in 2016, but higher at offshore sites in 2015 (Gilliam et al., unpub. data). SECREMP samples for cyanobacteria and macroalgae cover once per year, but algal cover likely fluctuates throughout the year. Therefore, while these two benthic competitors contribute to coral recruit mortality, quantifying their role in the mortality observed in this study is not possible. Finally, sediment is unlikely to explain disparity in survivorship between inshore and offshore sites because the inshore sites on the nearshore hard bottom and first reef line are believed to be more heavily impacted by sedimentation stress due to their proximity to shore. Higher juvenile

densities at inshore sites may also be the product of a recruitment event or series of events occurring in nearshore hardbottom and first-reef habitats within the last few years that was not reflected in recruit cohort that settled on tiles.

The lack of variability in scleractinian recruit densities, coupled with high variability in scleractinian juvenile densities, suggests that differential survival outcomes occur on local (site level) scales. A few possible ecological factors may contribute to the observation of high variation in juvenile density on local, but not regional, spatial scales. Macroalgae and cyanobacteria blooms can harm juvenile corals, decreasing post-settlement survival (Box and Mumby 2007). These blooms tend to be ephemeral, localized, and do not follow a noticeable pattern or latitudinal gradient (Gilliam 2014), so the variable juvenile densities observed may reflect differential survival outcomes caused by harmful local algae blooms. Another possible explanation might be that different species of crustose coralline algae can impact survival outcomes positively or negatively (Harrington et al. 2004, Buenau et al. 2012), and therefore juvenile coral distributions could be related to the distributions of CCA species. More characterization of CCA species distributions in Southeast Florida would be necessary to determine if CCA could be modulating survival outcomes in the region. Localized sedimentation stress and differences in grazing pressure could also contribute to local-scaled post-settlement mortality.

Healthier reefs with higher densities of adults are typically expected to have higher rates of recruitment (Reyes and Yap 2001), however this was not observed. This can be due to high local retention of larvae (Sammarco and Andrews 1988, Ayre and Hughes 2000, Miller and Ayre 2008, Underwood et al. 2009) or conspecific cues signaling quality settlement substrate (Da-Anoy et al. 2017). However, when all scleractinian taxa were pooled, there was no relationship between adult and recruit density at the site level. Poritidae was the only family that exhibited a positive relationship between adult density and recruit density (Spearman's, p=0.0018). This relationship probably exists because Caribbean poritids are brooding corals (Szmant 1986) and brooded larvae are competent upon release and thus tend to have high local retention (Sammarco and Andrews 1988, Ayre and Hughes 2000, Holstein et al. 2014). Agariciids are also brooders (van Moorsel

1983) and thus should exhibit high local retention, but the number of agariciid recruits reported in this study was too small to evaluate statistically (N=12).

The absence of a relationship between overall adult densities and recruit densities could mean that most coral larvae are dispersing further than the site-level scale. However, with total scleractinian adult densities ranging from 0.3 to 4 adults/m^2, many species at the study sites could be failing to reproduce altogether because of the Allee effect (Knowlton 2001). Fecundity of adult scleractinians can be affected by stress (Paxton et al. 2016) and may be low in the region due to temperature or sedimentation stress, disease, or other factors. Recruits were not counted in this study until they developed a recognizable skeleton. Therefore, it is also possible that many more corals attached to the substrate but suffered mortality within the first hours or days post-settlement. This early-stage mortality is difficult to quantify and may not occur proportionately across sites.

If post-settlement survival is high, greater juvenile densities should be expected in 2016 at the sites where high recruit densities settled during the 2015-2016 recruitment season. Overall scleractinian and octocoral recruit density were not significantly correlated with juvenile density recorded the subsequent year Poritidae was the only taxon which recruit and juvenile densities were positively correlated. The correlation within the Poritidae family is likely a result of the high local retention of *Porites* species, which seems to have led to uneven spatial distributions across the reef tract and dominance at inshore sites (Gilliam 2014). Higher survival of poritid corals is an unlikely explanation because their recruit densities were significantly higher than juvenile densities, suggesting high post-settlement mortality (Fig. 14). The absence of correlation between recruit and juvenile densities of other taxa suggest that most scleractinian and octocoral families are subject to high post-settlement mortality.

Across the three life history stages examined, the only positive correlation found for scleractinian densities was between juvenile and adult densities, implying that sites with high scleractinian juvenile densities also have high scleractinian adult densities. Sites with conditions conducive to maintaining healthy adult scleractinian communities likely also have conditions conducive to juvenile survivorship. However, this conclusion

is not supported by individual coral families. The only groups within the scleractinian taxon for which significant relationships existed were Poritidae and the "Other Scleractinian" category (Table 8).   Poritid adult density also correlated with poritid recruit density. *Porites astreoides* populations have been found to be highly fragmented on small spatial scales (Holstein et al. 2014), and the site-level correlations reported in this study are evidence that self-seeding of *Porites* populations is common. The fragmented distributions of abundant *Porites astreoides* corals in Southeast Florida is the driving factor in shaping the strong relationship between juvenile and adult scleractinian corals.

CONCLUSIONS

The relationships between the densities of recruit, juvenile, and adult corals observed in this study provide some insight into where population bottlenecks impeding reef recovery may be occurring. Minimal variation was observed in scleractinian recruit density across sites and depths, while juvenile densities varied even on small, site-level spatial scales. In scleractinian corals, the highest density is observed among recruits, with a drop-off in density approaching the juvenile stage. Recruit density does not correlate with adult density at the site level, but juvenile density does. These results suggest that differential post-settlement survival likely plays a greater role than recruitment in structuring adult scleractinian communities. Therefore, early post-settlement survival, rather than recruitment, is more likely to dictate the relative resilience potential of reef sites across the Southeast Florida reef tract. This conclusion is consistent with results found in French Polynesia (Penin and Adjeroud 2013) and the Seychelles (Chong-Seng et al. 2014). The former study found that juvenile, but not recruit, assemblages correlated closely with adult assemblages, and the latter found very little spatial variation in recruitment, with much more "patchy" distributions of juvenile corals.

This study used recruit and juvenile distributions to examine the potential for resilience of different reef sites and common species in Southeast Florida. The region is unique in the microhabitat distribution of coral recruits on artificial settlement tiles, with most recruits settling on exposed surfaces. While this may be due to reduced light from

high turbidity, further research is needed to evaluate the role of light in determining coral settlement location. Optimal light levels for growth and survival may differ for coral recruits and adults, and are not necessarily the same for all species. Implications of high rates of settlement on exposed surfaces should also be thoroughly explored, as this trend could result in elevated recruit mortality (Doropoulos et al. 2016).

Southeast Florida is also unique in its juvenile species assemblage when compared with other regions of the Caribbean, with siderastreids dominating the juvenile population and exhibiting evidence of relatively high survival rates. The prevalence of siderastreids on Southeast Florida's reefs could be promising for the future; modeling efforts predicted that *Siderastrea siderea*-dominated reefs may remain stable even in temperature and pCO_2 conditions predicted for 2100 (Okazaki et al. 2017). Octocorals also appear to be employing successful propagation and survival strategies, with densities increasing from younger to older life history stages. Already considered tolerant of marginal conditions, octocorals may increase in abundance relative to scleractinians due to their apparent capacity to recover from disturbances and their potential to recruit at extremely high densities (e.g., DC8).

The phase shift from scleractinian to octocoral dominance has been described in the Caribbean (Ruzicka et al. 2013, Tsounis and Edmunds 2017), yet understanding of octocoral reproduction, dispersal, settlement, and survival is still limited. Research is needed to determine the timing of spawning for many species. Investigating the ability of octocoral larvae to selectively settle on suitable substrate and the ability of adults to propagate clonally would help to explain their spatial distributions. Additionally, research on the potential competitive interactions between octocorals and scleractinians during different life stages will be important if a phase shift progresses.

This study provides evidence that low recruit survivorship is a bottleneck that structures adult coral populations. To increase management efficacy, more data is needed to determine the primary causes of post-settlement mortality within the Southeast Florida region. The current monitoring data are sampled for on a yearly basis, but the environmental factors that kill coral recruits are likely to occur on finer temporal scales. Monthly sampling of a subset of quadrats would be useful for understanding the

fluctuations in macroalgae, cyanobacteria, and sediment cover. Further research should also include an assessment of herbivory and corallivory in the region, to determine how grazing rates differ between Southeast Florida's reef habitats. In addition to supporting insight into what factors kill coral recruits, these studies could help to elucidate the reasons for apparently different rates of post-settlement survival between study sites of similar habitat qualities. Managers can employ this knowledge to limit the causes of recruit mortality to increase juvenile survivorship. For example, managing for reduced macroalgae cover and reduced sedimentation may improve early coral survivorship outcomes. Future management efforts in Southeast Florida should focus on investigating methods to enhance post-settlement survival, loosening the population bottlenecks that are limiting recovery.

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APPENDICES

Appendix 1: The number of recruits on settlement tiles by family. N=total number of tile pairs scanned per site.

Site	N	Poritidae	Siderastreidae	Faviidae	Agariciidae	Other Scleractinian	Unknown Scleractinian	Total Scleractinian	Total Octocoral
BC1	32	6	4	2	1	0	6	19	3
BC2	32	7	8	2	0	0	4	21	5
BC3	32	7	1	1	0	1	2	12	8
BC4	32	17	0	0	0	0	0	17	0
DC6	32	16	5	0	0	0	1	22	1
DC7	30*	2	7	0	1	0	1	11	18
DC1	32	8	1	0	0	0	1	10	1
DC2	32	5	6	2	2	0	7	22	1
DC3	32	2	2	0	0	0	5	9	3
DC4	30	6	0	0	2	0	3	11	1
DC5	32	9	1	0	6	0	1	17	1
DC8	32	0	7	2	0	0	2	11	78
Totals		**85**	**42**	**9**	**12**	**1**	**33**	**182**	**120**

*30 tiles were scanned for scleractinians and 26 were scanned for octocorals

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Appendix 2: Scleractinian juveniles from census, totaled by family level.

Site	Poritidae	Siderastreidae	Faviidae	Agariciidae	Other Stony	Unknown Stony	Total Stony
BC1	2	23	7	0	1	4	37
BC2	2	7	9	0	4	0	22
BC3	1	8	7	0	12	4	32
BC4	63	12	12	1	4	0	92
DC6	23	43	0	0	0	0	66
DC7	2	18	11	0	15	1	46
DC1	17	34	9	2	3	0	64
DC2	1	29	10	2	17	3	61
DC3	0	6	2	0	2	1	11
DC4	7	4	11	1	5	1	29
DC5	30	28	9	14	9	0	85
DC8	1	12	0	0	1	2	16
Totals	**149**	**224**	**86**	**20**	**74**	**16**	**561**

2016 Scleractinian Juveniles

Siderastrea siderea	203
Siderastrea radians	21
Porites astreoides	122
Porites porites	27
Montastraea cavernosa	71
Pseudodiploria/Diplora sp.	5
Colpophyllia natans	1
Solenastrea bournoni	8
Orbicella sp.	2
Stephanocoenia intersepta	40
Dichocoenia stokesii	8
Meandrina meandrites	6
Eusmilia fastigiata	1
Mussidae family	9
Agariciidae family	20
Unknown Stony Coral	16

2016 Octocoral Juveniles

Pseudoplexaura sp.	21
Eunicea sp.	306
Plexaurella sp.	5
Plexaura sp.	1
Muriceopsis sp.	0
Muricea sp.	11
Antillogorgia americana	42
Gorgonia ventalina	18
Antillogorgia sp.	36
Pterogorgia sp.	0
Unknown Octocoral	276

Appendix 3. Juvenile abundances identified to highest taxonomic resolution. Discrepancies between the following and the family-level counts in Table 8 are explained by corals that were only identified to genus or another subgroup (when the majority within that genus were identified to species) and thus were moved to the "Unknown" category. "Antillogorgia sp." may include Antillogorgia americana juveniles that were not identified to species during the survey.

Appendix 4: Octocoral juveniles totaled by family level.

Site	Plexauridae	Gorgonidae	Unknown Octocorals	Total Octocorals
BC1	50	0	12	62
BC2	22	8	44	74
BC3	49	1	28	78
BC4	31	18	26	75
DC1	19	5	13	37
DC2	21	14	24	59
DC3	14	5	18	37
DC4	37	15	27	79
DC5	13	10	12	35
DC6	17	3	15	35
DC7	25	1	7	33
DC8	46	26	40	112
Totals	**344**	**106**	**266**	**716**

Appendix 5: Model parameters (Model), number of parameter (K), log likelihood (logLik), AICc, ΔAICc, and weights for the candidate set of negative binomial regression models relating coral counts to the spatial parameters. All models included an intercept.

	Model	**K**	**LogLik**	**AICc**	**ΔAICc**	**w**
Scleractinian Recruits	Location on Tile	3	-426.42	858.9	0	1
	Intercept-only	2	-460.49	925	66.12	0
	Zone (Inshore vs. Offshore)	3	-494	926.7	67.83	0
	Region	5	-459.57	929.2	70.33	0
	Zone*Region	9	-456.69	933.6	74.75	0
	Site	13	-454.36	935.2	76.34	0
Octocoral Recruits	Site	13	-230.29	487.1	0	1
	Zone*Region	9	-254.91	528.1	40.99	0
	Region	5	-274.55	559.2	72.11	0
	Location	3	-288.83	583.7	96.62	0
	Zone	3	-292.52	591.1	104	0
	Intercept-only	2	-295.81	595.6	108.56	0
Scleractinian Juveniles	Site	13	-593.81	-593.81	0	1
	Zone	3	-628.88	-628.88	49.22	0
	Zone*Region	9	-635.84	-625.84	55.56	0
	Intercept-only	2	-639.01	-639.01	67.45	0

	Region	5	-638.06	-638.06	71.68	0
Octocoral Juveniles	Site	13	-677.61	1382.2	0	0.994
	Region	5	-691.13	1392.4	10.23	0.006
	Zone*Region	9	-690.25	1399	16.79	0
	Intercept-only	2	-206.31	1416.7	34.46	0
	Zone	3	-706.3	1418.7	36.47	0

Appendix 6: Parameter estimates, standard errors (SE), and lower and upper 95% confidence limits based on the negative binomial regression models relating coral juvenile counts by site. This model was best-approximating for both scleractinians or octocorals.

	Scleractinian Site Model			Octocoral Site Model		
Parameter	Estimate	SE	Confidence Interval	Estimate	SE	Confidence Interval
Intercept	0.11	0.21	-0.3-0.51	0.63	0.17	0.29-0.96
BC2	-0.49	0.32	-1.13-0.14	0.21	0.24	-0.25-0.67
BC3	-0.11	0.3	-0.71-0.47	0.26	0.23	-0.2-0.72
BC4	0.94	0.26	0.43-1.47	0.22	0.24	-0.24-0.68
DC1	0.58	0.27	0.05-1.12	-0.49	0.26	-1.01-0.03
DC2	0.53	0.27	0-1.07	-0.02	0.24	-0.5-0.46
DC3	-1.18	0.39	(-1.98)-(-0.45)	-0.49	0.26	-1.01-0.03
DC4	-0.21	0.31	-0.82-0.38	0.27	0.23	-0.18-0.73
DC5	0.86	0.27	0.35-1.39	-0.54	0.27	(-1.07)-(-0.02)
DC6	0.61	0.27	0.08-1.15	-0.54	0.27	(-1.07)-(-0.02)
DC7	0.25	0.28	-0.31-0.81	-0.6	0.27	(-1.13)-(-0.08)
DC8	-0.81	0.35	(-1.51)-(-0.14)	0.62	0.23	0.18-1.07

Appendix 7: Differences for each paired contrast of octocoral recruit and juvenile counts by region, standard errors (SE), lower and upper 95% confidence limits, and p-values (z-statistic = Difference/ SE) associated with each paired contrast. FTL=Ft. Lauderdale, HAL=Hallandale, MIA=Miami, BIS=Biscayne.

Octocoral Recruits					Octocoral Juveniles				
	Diff	SE	zstat	p-value		Diff	SE	zstat	
					pvalue				
FTL - BIS	-1.908	0.380	-5.015	0.000	FTL - BIS	-0.050	0.131	-0.379	0.981
HAL - BIS	-1.027	0.407	-2.525	0.054	HAL - BIS	-0.796	0.180	-4.420	0.000
MIA - BIS	-2.783	0.540	-5.150	0.000	MIA - BIS	-0.530	0.150	-3.530	0.002
HAL - FTL	0.881	0.453	1.945	0.204	HAL - FTL	-0.746	0.173	-4.302	0.000
MIA - FTL	-0.875	0.576	-1.520	0.418	MIA - FTL	-0.481	0.142	-3.379	0.004
MIA - HAL	-1.756	0.594	-2.958	0.016	MIA - HAL	0.265	0.188	1.409	0.489