

10-28-2014

Dynamics and Survival of Coral and Octocoral Juveniles following Disturbance on Patch Reefs of the Florida Reef Tract

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Dynamics and Survival of Coral and Octocoral Juveniles following Disturbance on Patch Reefs
of the Florida Reef Tract

by

Lucy Ann Bartlett

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
College of Marine Science
University of South Florida

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Date of Approval:
October 28, 2014

Keywords: Florida Keys; Scleractinia; Octocorallia; recruitment; disturbance; fate-tracking

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ACKNOWLEDGMENTS

I would like to thank everyone who has helped me in completing my thesis research over the past three years. My advisor, Dr. Pamela Hallock Muller has provided essential guidance and knowledge to keep me focused and on track and I am so grateful to her for that. I would also like to thank my committee members, Dr. Alison Moulding, Dr. Kate Lunz and Dr. Kendra Daly for their valuable input and wisdom.

I am grateful to the Florida Fish and Wildlife Coral Reef Evaluation and Monitoring Project (CREMP) researchers, my coworkers, who have spent long hours underwater with their faces pressed close to the substrate searching for tiny juvenile corals. Vanessa Brinkhuis has been invaluable to me during this process, ready and willing to answer any question, big or small and I can't begin to express how thankful I am to have had her guidance. Michael Colella and Rob Ruzicka have been especially helpful and provided much assistance and direction as well. This project would not have been possible without them. Thank you all!

Funding for this project was provided by the Environmental Protection Agency (EPA).

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ABSTRACT

Over the past several decades, rapid decline in adult stony-coral (comprising the Orders Scleractinia and Anthomedusae, specifically Family Milleporidae) cover has occurred concurrent with an increase in adult octocoral (Octocorallia/gorgonian) cover along the Florida Reef Tract. In January 2010, the Florida Keys experienced extremely cold air and water temperatures, below the lethal threshold for many reef organisms including corals. Very high stony-coral mortality occurred on some patch reefs. The newly-available space created by this disturbance event provided the opportunity for recruitment and settlement of new coral larvae and other reef organisms.

The goal of this study was to examine post-disturbance recruitment and survival of juvenile stony corals and octocorals on patch reefs in the Middle and Upper Florida Reef Tract. Permanent quadrats were established at eight patch-reef sites. Stony-coral and octocoral juveniles, visible to the naked eye and having a maximum 4 cm diameter for stony corals or 4 cm height for octocorals, were identified, measured, and photographed to track each colony through spring and fall for two years. Juvenile densities increased significantly over that time; octocoral density increased with higher significance ($p < 0.001$) than stony-coral density ($p = 0.019$). Overall, 48% of all juveniles observed over the course of this study were stony corals and 52% were octocorals. Stony-coral juveniles dominated the Middle-Keys sites, while octocorals dominated the Upper-Keys sites. The stony-coral juveniles were dominated by hardy and weedy, opportunistic species such as *Siderastrea siderea* (46%) and *Porites astreoides* (19%),

whereas juveniles of massive, late-successional species such as *Orbicella annularis* were nearly absent (<3%). The octocoral juveniles were dominated by *Antillogorgia* spp. (25%) and *Gorgonia* spp. (21%).

Opportunistic and/or hardy organisms are re-populating patch-reef sites, whereas slower growing, massive stony-coral species are declining. When a reef environment is plagued with chronic stressors, such as terrestrial runoff, overfishing, high temperature fluctuations and turbidity, the succession process may be inhibited following acute disturbances such as cold-water events. Patch reefs of the Florida Reef Tract now appear to be caught in a perpetually disturbed state, which supports opportunistic and hardy taxa and inhibits recovery of slower-growing climax taxa that dominated until the past few decades.

INTRODUCTION

DISTURBANCE AND MULTIPLE STRESSORS

In a coral reef community, stony corals (comprising the Orders Scleractinia and Anthomedusae, specifically Family Milleporidae) produce limestone skeletons that contribute to the reef structure. This framework provides habitat, protection and food for many kinds of organisms. The presence and health of stony corals on a reef are strong indicators of the health of the entire reef ecosystem (Veron 2000). Coral reefs around the world continue to decline in response to multiple stressors, including those caused by humans and those occurring naturally. Often natural disturbances such as hurricanes, high sea-surface temperatures [especially those associated with El Niño Southern Oscillations (ENSOs)] or cold-water events can cause mass mortality in coral communities (Baker et al. 2008).

Historically, disturbance is considered to be a natural part of both terrestrial and aquatic ecosystems, facilitating natural selection as well as spatial and temporal heterogeneity. Disturbance may impact the dominant species in a community, allowing for diversification of the recovering community (Porter et al. 1981). Sousa (1984) defined the role of disturbance in natural communities as a “discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established” (p. 356). Connell (1978) further described the “Intermediate Disturbance Hypothesis,” which states that high diversity ecosystems, such as coral reefs and

rainforests, are maintained not in a state of equilibrium, but in a state of resurgence from repeated disturbance. For a given reef's community composition to recover from disturbance, new corals must replace those killed.

Recruitment, or the arrival of new individuals into populations, is an essential step toward the replenishment of a community. Coral-reef community structure has historically recovered by means of coral recruitment in the years following disturbance. Coral larvae must overcome numerous pre-settlement and post-settlement obstacles to successfully survive to adulthood. However, anthropogenic influence is transforming the role of disturbance and recruitment in shaping reef communities. Today, corals are threatened by chronic, anthropogenic stressors, such as pollution, overfishing and terrestrial runoff, as well as by the much more daunting and overarching issues of climate change and ocean acidification. These “man-made” stressors are stunting the ability of corals to recover following natural disturbance (Hughes and Connell 1999, Graham et al. 2011).

CORAL TO OCTOCORAL SHIFTS IN COMMUNITY DOMINANCE

Researchers have studied coral-reef community recovery following disturbance in many different areas of the world. The results of the majority of these studies have described a shift in community dominance to other benthic organisms, usually fleshy macroalgae (Hughes 1994, Hoegh-Guldberg 1999, McCook 1999, Hughes et al. 2007). This shift has been described as a phase shift (Maliao et al. 2008). Very few studies have examined alternative-state phase shifts in which octocorals (gorgonians), sponges or other sessile reef organisms have taken over dominance of a reef (Hallock et al. 1993, Norström et al. 2009).

In the Florida Keys, such an alternative-state shift is being observed; long-term monitoring data have shown an increase in octocoral abundance, concomitant with the decline in stony-coral abundance (Ruzicka et al. 2013). The Florida Fish and Wildlife Research Institute's Coral Reef Evaluation and Monitoring Project (CREMP) has been monitoring coral reefs of the Florida Reef Tract since 1996. This long-term dataset has shown that stony corals of the Florida Reef Tract have continued to decline for more than a decade [Fig. 1, from Ruzicka et al. (2011) Fig. 12]. Yet, unlike patterns seen in other areas of the world, significant increases in macroalgae cover have not been observed here. Interestingly, CREMP has identified an overall increase in octocoral cover concurrent with the loss of stony corals (Ruzicka et al. 2013). Is this negative correlation between stony-coral cover and octocoral cover evidence of a phase-shift to an octocoral-dominated state on the Florida Reef Tract?

An example of a rapid coral-octocoral phase shift was observed on Aldabra Atoll, Seychelles, following the 1998 coral-bleaching event; coral mortality immediately following the event reached 66% at 10 m depth and 38% at 20 m depth (Stobart et al. 2005). Despite high levels of coral recruitment following the event, coral cover had not recovered significantly five years after the event. Results showed no significant increase in macroalgae cover, but did show a significant increase in octocoral cover.

Differences to be noted between the CREMP data and the Aldabra study are the time frame, reef framework and presence of direct human influence. The Florida Reef Tract is a very large area that has experienced gradual community shift over several decades, whereas Aldabra Atoll experienced a rapid change prompted by an acute disturbance event. The Florida Reef Tract is a large bank reef complex comprised of multiple reef types, including hardbottom, patch reefs, shallow and deep forereefs, and exists just miles from the populated Florida Keys.

Aldabra Atoll consists of a single reef type, and exists far from human influence. Perhaps Aldabra Atoll may ultimately experience recovery of stony-coral cover with more time. On the other hand, the presence of chronic stressors may be influencing both the gradual change seen in the Florida Keys, as well as the lack of coral recovery seen on Aldabra Atoll. It is unclear what this trend may mean for the future of coral reefs of the Florida Reef Tract; however, it is certain that reproduction and recruitment of juvenile stony corals and octocorals will be essential in determining the future patterns of benthic composition on these precious reefs.

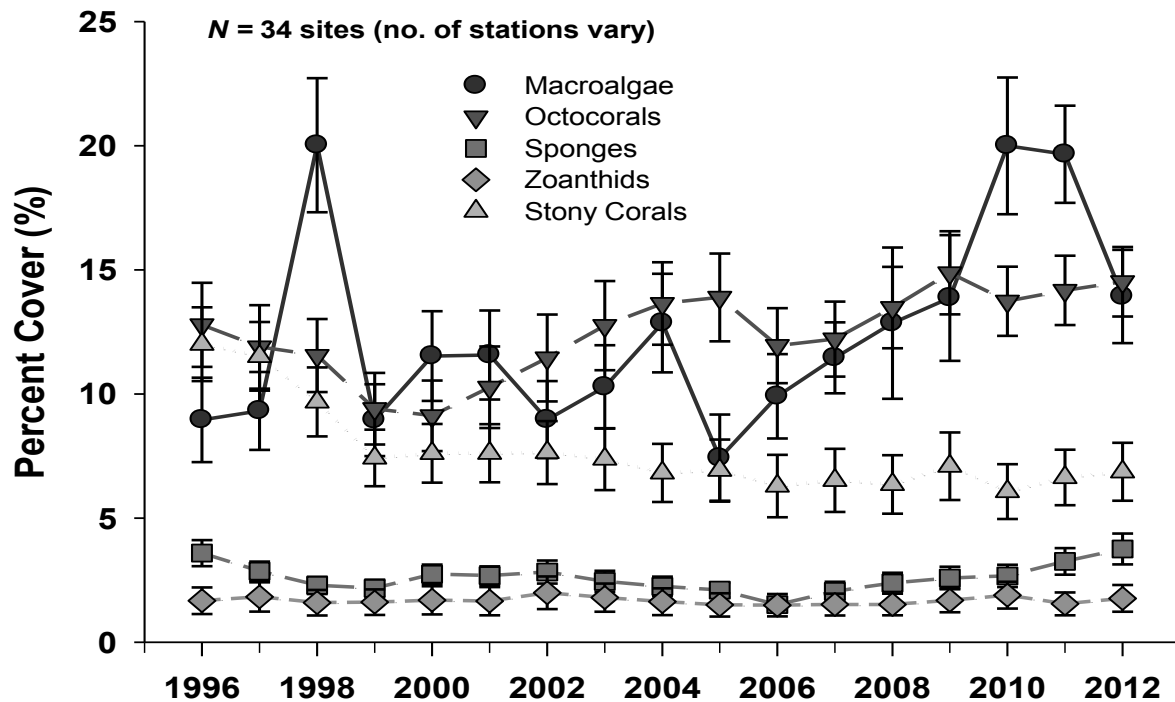


Figure 1. Mean-annual percent cover of four major benthic taxa from 1996-2008. Mean percent cover is pooled from 97 stations in the Florida Keys. A mixed model regression indicates a decreasing trend for stony corals and sponges ($p < 0.001$), an increasing trend for octocorals ($p < 0.001$), and no trend for macroalgae ($p > 0.05$). [Fig. 12, Ruzicka et al. 2011 (CREMP 2009 final report)].

REPRODUCTION AND RECRUITMENT

For coral reefs to persist in the presence of chronic stressors, the continued reproduction by stony corals and the recruitment of offspring to reef environments are imperative. Stony corals reproduce using multiple methods. Sexual reproduction is accomplished by broadcast spawning or brooding, with the release of eggs and sperm or pre-fertilized larvae, respectively, into the water column. Massive species often found on reefs of the Florida Reef Tract, such as *Orbicella* (formerly *Montastraea*) spp., *Diploria* spp., *Colpophyllia natans* and *Siderastrea siderea*, are broadcast spawners, reproducing only once a year in synchrony with the late summer lunar cycle (Szmant 1986). Some octocoral species also reproduce in this way. The success of sexual reproduction via spawning is a function of reef connectivity and is highly dependent on physical characteristics of the water column, including tides and currents (Richmond and Hunter 1990). Non-massive coral species, such as *Porites* spp., *Agaricia* spp. and *Siderastrea radians*, are internal brooders, reproducing many times a year (Szmant 1986, Moulding 2005). There are also many octocoral species that utilize this method of reproduction. Brooded planulae are larger and more developed when they enter the water column, so they are ready to settle sooner and, hence, often closer to the parent colony than larvae formed in the water column from broadcast spawning colonies (Richmond 1997). Asexual reproduction is accomplished primarily by fragmentation in which a portion of the coral colony breaks off and is established as a new colony on open substrate nearby (Veron 2000). This form of asexual reproduction is most common in stony-coral species with branching growth morphologies and in octocorals. Many genera of stony corals are able to reproduce both sexually and asexually. For example acroporids, once the dominant coral on Florida reefs, utilize fragmentation as their primary mode of reproduction, but are also broadcast spawners (Szmant 1986).

Sexual reproduction may provide the best opportunity for successful recruitment of stony corals under certain environmental circumstances; however, near the edge of a species range, or when densities of sexually viable adult colonies are low, asexual reproduction may take over as the dominant means of reproduction for the same species (Richmond and Hunter 1990). The Florida Reef Tract exists near the northern latitudinal limit of coral-reef development and is often subjected to environmental extremes. Both sexual and asexual reproduction are important to coral populations of the Florida Reef Tract. Sexual reproduction provides genotypic complexity, which can protect against disease outbreaks and extreme environmental fluctuations (Reusch et al. 2005). Asexual reproduction provides a means by which superior genotypes can proliferate and can allow an organism to survive when sexual reproduction fails (Foster et al. 2007). Recruitment of larvae to an area is determined by both biotic factors, including competition and predation, and abiotic factors such as currents and substrate availability (Moulding 2005). Disturbance events that kill adult corals and other sessile fauna also create open substrate, providing the opportunity for new recruitment (Porter et al. 1981). Can it be expected then, that a more severe disturbance event, which creates more open substrate, would facilitate recruitment in general?

Enhanced recruitment does not always mean enhanced community recovery. In the Aldabra Atoll case, although researchers observed increased recruitment following the 1998 mass-bleaching event, coral cover did not increase. Newly settled coral recruits (spat) often demonstrate very low survival rates within the first year of settlement and many die before reaching adulthood (Veron 2000). Thus, sufficient space to settle, availability of larvae and conditions conducive to post-settlement growth and survival of spat are all essential for

successful recovery of a coral community following disturbance (Dunstan and Johnson 1998, Miller et al. 2000).

The reproductive strategies and conditions necessary for successful recruitment are very similar between stony corals and octocorals. Many gorgonians are thought to be gonochoric brooders (Brazeau and Lasker 1989). Brooding can occur internally, as occurs with stony corals, or externally, on the surface of the female colony as occurs with the species *Briareum asbestinum*. Others are broadcast spawners, releasing both sperm and egg into the water column for fertilization as occurs with *Gorgonia ventalina* (Fitzsimmons-Sosa et al. 2004). For broadcast spawning species of both stony corals and octocorals, fertilization can be highly variable and dependent upon numerous factors for success, including synchrony of release, population density and aggregation of adults, water-flow and currents (Brazeau and Lasker 1989). As with stony corals, octocorals spawn in synchrony with the lunar cycle, usually following a full moon, though not necessarily synchronous across species (Fitzsimmons-Sosa et al. 2004). The flexible branching growth morphology of octocorals facilitates asexual reproduction through a number of methods, giving octocorals a unique advantage following disturbance events. As with branching stony corals, fragmentation of a larger colony can establish one or more new colonies (Lasker 1984). Other forms of asexual reproduction that have been recorded in octocorals are simple fission (Benayahu and Loya 1986) and partial mortality causing division into two separate colonies (Farrant 1987). These methods of asexual reproduction are not unique to octocorals, as some branching forms of stony corals are also able to reproduce via these methods. However, many species of stony corals with plate or boulder growth morphologies are at a disadvantage when it comes to asexual reproduction. The ability to proliferate by means of vegetative growth and development of new colonies from runners or

stolons is unique to octocorals (Lasker 1983). Asexual reproduction via parthenogenesis has also been reported in at least two octocoral species (Brazeau and Lasker 1989). The ability for vegetative growth allows octocorals to aggregate in high densities and to colonize space quickly (Benayahu and Loya 1987). This can provide an advantage following a disturbance event, allowing them to out-compete more slowly reproducing organisms, such as spawning stony corals, for the newly available space.

STUDY AREA: THE FLORIDA REEF TRACT

The Florida Reef Tract (Fig. 2) is the only shallow-water coral-reef system in North America. It extends from Soldier Key in a disjointed arc along the Florida Keys archipelago out to the Dry Tortugas (Jaap 1984). The reef formation here is a spur-and-groove system with limestone reef structure separated by sand grooves oriented perpendicular to land (Shinn 1963). Several reef habitat types reach from 25 m to 13 km offshore, including hard bottom and patch reefs closest to land, and shallow and deep bank reefs that form the spur-and-groove pattern further offshore (Jaap 1984). Seaward of the reef lie the Straits of Florida and the Florida Current. The Florida Current originates from the Caribbean and Loop Currents and brings warm water up from the tropics, helping to protect the outer reefs from cold-water events that can occur in winter months. The Florida Current also carries coral larvae from distant reefs, promoting genetic diversity (Jaap 1984). Closer to land and in shallower waters, the patch reefs and hard-bottom communities often experience greater temperature and salinity fluctuations (Jaap 1984, Soto et al. 2011).

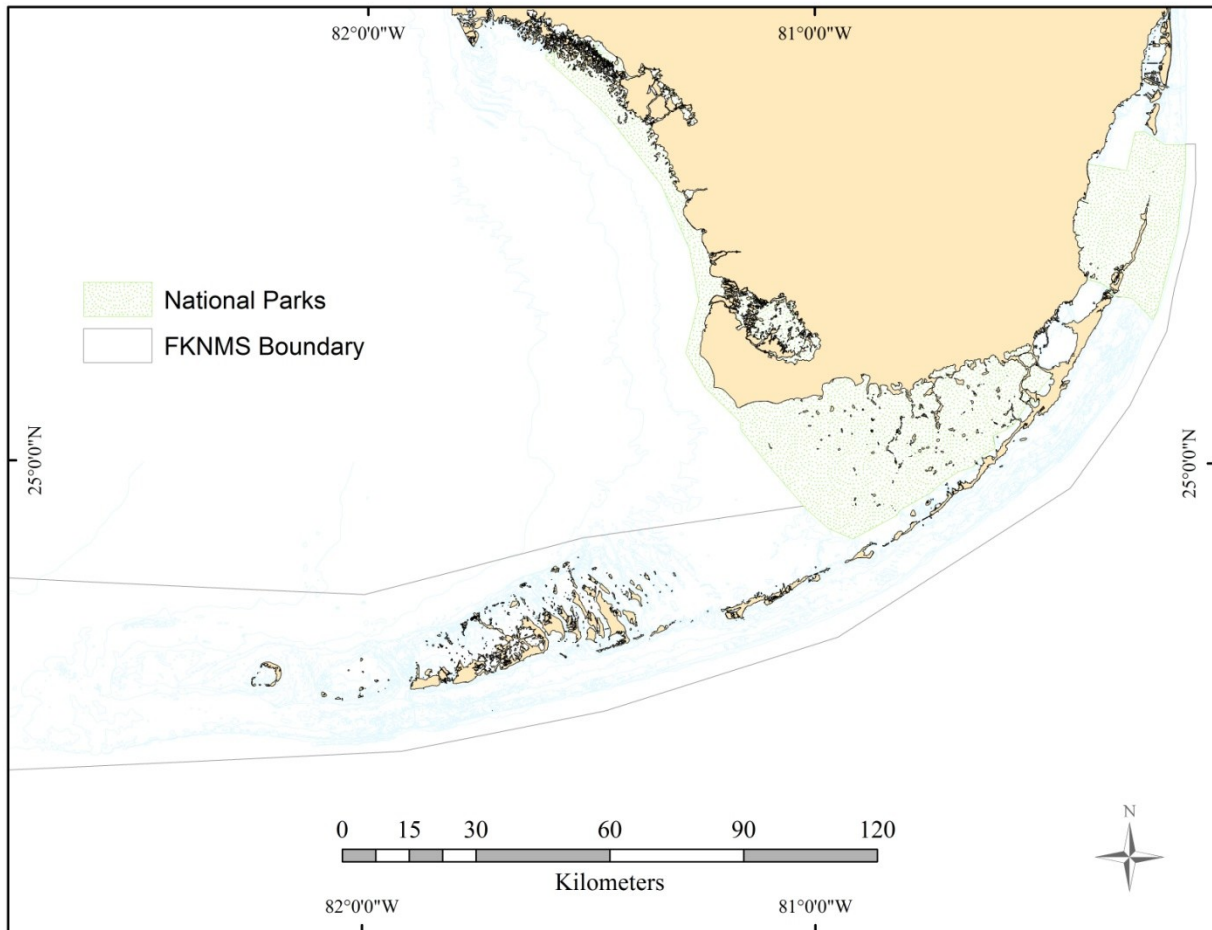


Figure 2. Map of the Florida Reef Tract.

Patch Reefs

Patch reefs are isolated reefs that exist landward of barrier or bank reefs in the calm, sometimes turbid waters of the inner shelf. Along the Florida Reef Tract, patch reefs are often circular or oval in shape and occur at depths of 3-6 meters; however, they can also be expansive with several meters of vertical relief (Brock et al. 2004, Colella et al. 2012). Patch reefs are the most numerous type of reef in the Florida Reef Tract (Ginsburg et al. 2001).

The major reef-building corals of Florida patch reefs are *Montastraea cavernosa*, *Orbicella* spp., *Diploria* spp., *Colpophyllia natans* and *Siderastrea siderea* (boulder star corals,

brain corals and massive starlet corals). Community composition of these patch reefs can be quite variable, with some reefs completely dominated by a single species of coral such as *Orbicella* spp. and others consisting of a diverse variety of coral species (Ginsburg et al. 2001).

Florida Reef Tract patch reefs are located between the outer bank reefs and the keys, in an area commonly known as Hawks Channel. Their close proximity to land exposes them to more direct anthropogenic effects such as terrestrial runoff, pollution (Lapointe et al. 1990, Chiappone and Sullivan 1996, Fabricius 2005), fishing, boating and diving (Ginsburg et al. 2001). The waters of Hawks Channel display higher concentrations of nutrients, more turbidity and faster light attenuation than waters further offshore (Lirman and Fong 2007). Despite the poorer water quality associated with these reefs, patch reefs often have higher stony-coral cover, higher coral-growth rates and lower partial-mortality rates than their offshore counterparts (Lirman and Fong 2007). These observations suggest that the corals living on these patch reefs are acclimated to lower water quality and may be resilient to chronic stressors, such as sedimentation and eutrophication, which are common to the waters of Hawks Channel. Hence the corals here may have better potential to recover following an acute disturbance event such as high or low water-temperature exposure (Soto et al. 2011). Thus, these unique reef environments are important to local conservation efforts (Brock et al. 2006, Lirman and Fong 2007, Wooldridge and Done 2009). More research must be done on Florida Keys patch reefs to determine the level of resilience and the potential benefits for the reef tract.

DISTURBANCE IN THE FLORIDA KEYS: 2010 COLD-WATER EVENT

In January of 2010, patch reefs suffered a devastating loss when a prolonged influx of cold Arctic air caused sea-surface temperatures on the Florida Reef Tract to drop below the

lethal threshold for many benthic fauna, including corals. Water temperature not only reached well below 16°C, but stayed low for several days (Lirman et al. 2011, Colella et al. 2012).

CREMP researchers evaluated the impact of this cold-water event on the benthic fauna of patch reefs in the upper and middle Florida Keys.

Supplementary to yearly monitoring of several patch reefs, four patch reefs (Dustan Rocks, West Turtle Shoal, Burr Fish and Thor) were surveyed for benthic mortality, using a combination of percent cover and demographic techniques. Averaged over the four sites between 2009 and 2010, all benthic taxa studied (stony corals, octocorals, macroalgae and sponges) declined significantly in percent cover (Fig. 3). Varying levels of mortality were observed between sites, with two of the patch reefs suffering extremely high loss of coral cover (Dustan Rocks and Burr Fish) and the other two patch reefs experiencing significantly less coral-cover loss (West Turtle Shoal and Thor).

Similarly variable patterns of coral-cover loss were observed during yearly monitoring in May-June of 2010 on the remaining CREMP patch-reef sites in the Upper and Middle Florida Keys. It is unclear what caused the conspicuous differences in response to the cold-water event between patch reefs. Differences in duration of exposure to the cold water, depth of the reef or community composition and structural complexity could have influenced the degree of coral mortality (Colella et al. 2012).

Whatever the cause, the reefs that suffered the highest levels of mortality from this event had much more open substrate following the event. Will this open substrate be colonized by macroalgae, as seen with many reef environments around the world? Or, will octocorals move in

and take over the open space? Or, a third possibility, will stony corals successfully recruit to these areas?

OBJECTIVES AND HYPOTHESES

To examine community composition following the 2010 cold-water event, this study took advantage of the documented responses of selected patch reef sites. The distinct difference in stony-coral mortality among sites provided a unique opportunity to quantify and track the success of recruitment and juvenile survival of stony corals and octocorals in the years following the disturbance. This study fate-tracked stony-coral as well as octocoral juvenile abundance and survival on eight patch reefs, in the Upper and Middle Florida Keys, for a two-year period following the event. The inclusion of octocoral juveniles in the study allowed for an assessment of patch-reef susceptibility to the octocoral phase shift that appears to be occurring on the offshore reefs in the Florida Keys.

The objectives of this study were to: (1) measure, quantify and describe abundance of juvenile stony corals and octocorals at study sites over time; (2) describe differences in juvenile survival and in new recruitment among study sites and between octocorals and stony corals; and (3) compare juvenile abundance and survival of both taxa at high-mortality patch reefs versus at low-mortality patch reefs.

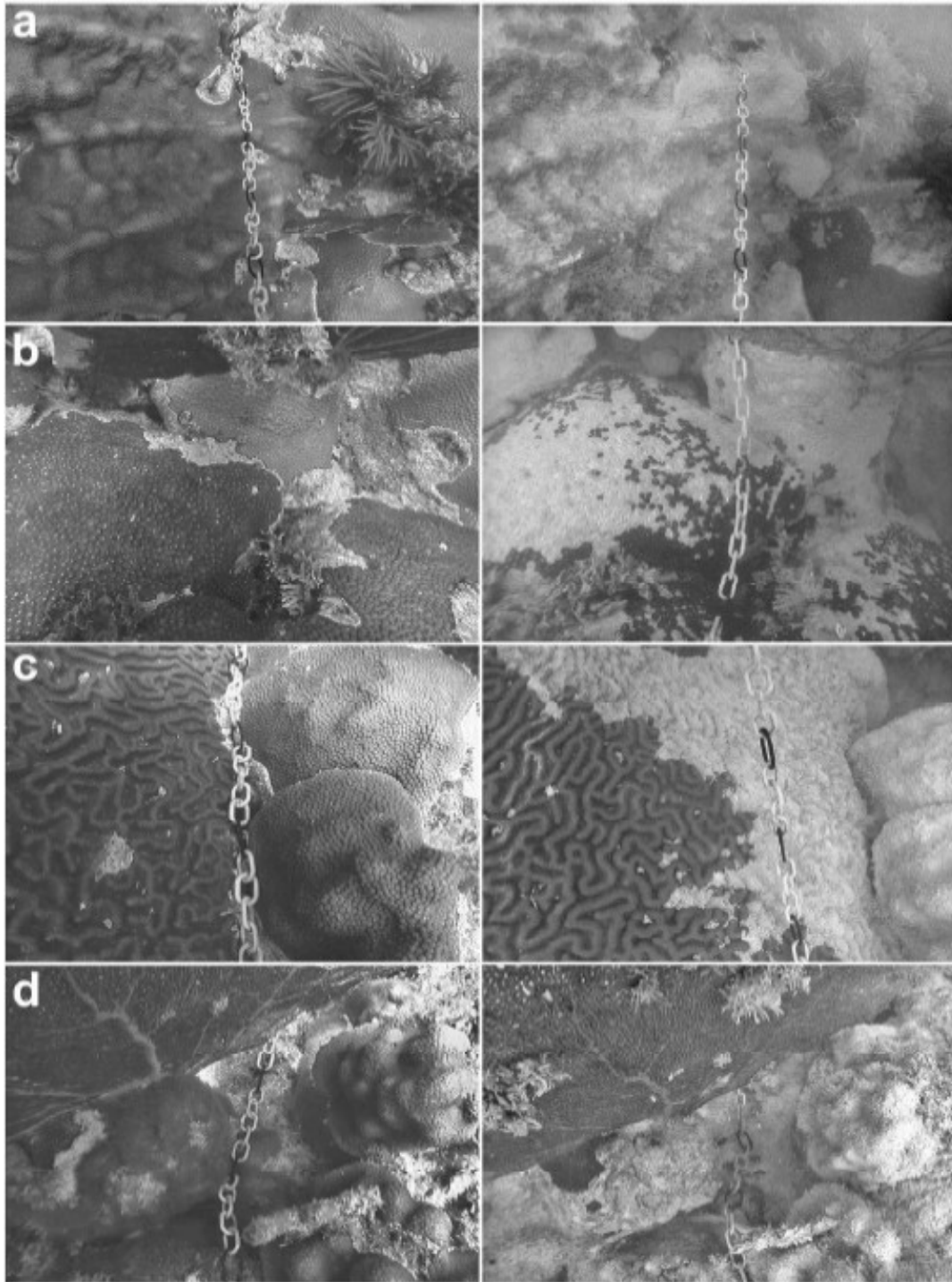


Figure 3. Photos in the left column are before and photos in the right column are the same location after the cold-water event (from Colella et al. 2012).

Classification of patch reefs as high-mortality sites or low-mortality sites was based on loss of stony-coral cover from 2009 to 2010 (Fig. 4, 5). High-mortality sites demonstrated a significant loss of coral cover of $>5\%$ ($p < 0.05$), whereas the decline in coral cover on the low-mortality sites was ≤ 0.006 . I hypothesized that high-mortality sites would experience more new recruitment as well as higher juvenile abundance and survival. This hypothesis was based on the possibility that extreme coral-cover loss could result in increased availability of open substrate, which should attract recruits (Graham et al. 2011). Results may be complicated, however, by the fact that, prior to the disturbance, high-mortality sites displayed much higher coral cover than the low-mortality sites. In other words, following the event, coral cover was very similar on both high and low mortality sites. Furthermore, site-level differences between patch reefs, such as community composition, species richness and topographic/structural complexity, may influence recruitment patterns to individual patch reefs. For example, in 2009 before the cold-water event, Admiral Patch was dominated by a monotypic stand of *Orbicella* spp., accounting for 33% of the total benthic cover. In 2010, after the cold-water event, Admiral Patch suffered mass-mortality of *Orbicella* spp., with a recorded 0% cover (CREMP 2009, 2010 data). Other patch reefs, such as Porter Patch that maintained greater species diversity and coral cover, were essentially uninfluenced by the cold-water event. Hence, recruitment may prove to be driven by site-level environmental and structural differences rather than by availability of new substrate.

My second hypothesis was that recruitment and survival of octocorals would exceed that of stony corals. Octocorals are affected by many of the same stressors as stony corals; in fact, octocorals also suffered extreme mortality due to the 2010 cold-water disturbance event (Colella et al. 2012). However, octocorals have been increasing in abundance and cover on CREMP sites over the past decade (Ruzicka et al. 2013). This study will compare octocoral and stony-coral

recruitment and survival following an acute disturbance event in an environment facing multiple chronic stressors.

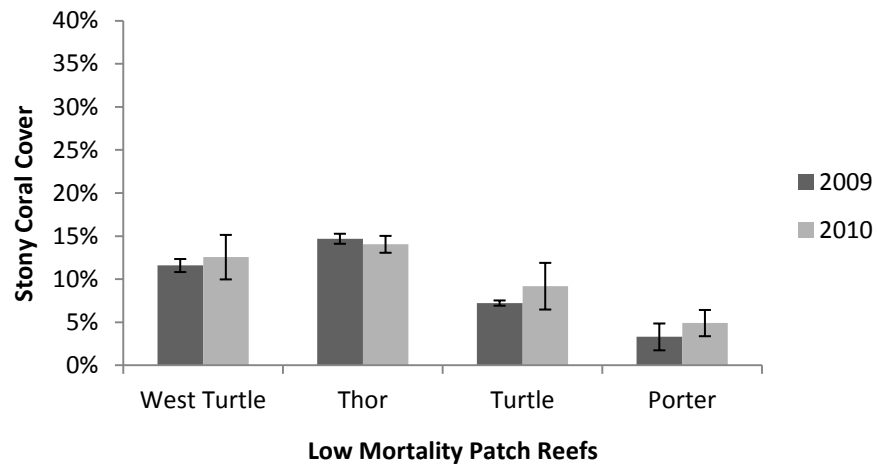


Figure 4. Percent stony-coral cover in 2009 and 2010 at low-mortality patch reef sites (error bars are standard error of the means). Cover values from CREMP data.

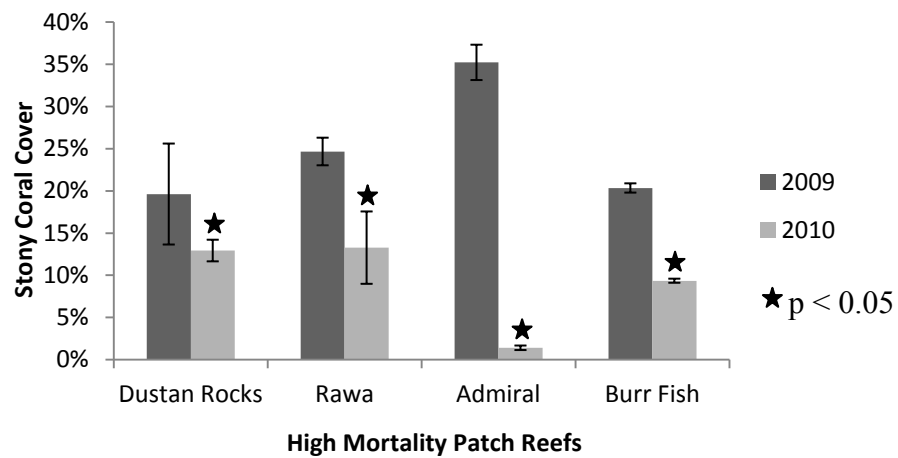


Figure 5. Percent stony-coral cover in 2009 and 2010 at high-mortality patch-reef sites (error bars are standard error of the means). Significant loss ($P = <0.05$) of stony-coral cover was recorded on all four patch reefs. Cover values from CREMP data.

METHODS

SITE DISTURBANCE MORTALITY CLASSIFICATION

Eight patch-reef sites were included in this study: four in the Upper-Keys region and four in the Middle-Keys region (Fig. 6). All sites chosen for this project were previously established CREMP yearly monitoring locations, where historical adult stony-coral demographic and benthic-cover data were available (e.g., Ruzicka et al. 2013). In each region, two sites were categorized as “high mortality” and two sites as “low mortality” following the 2010 cold-water event. A site was considered to have high mortality if stony-coral cover declined by at least five percent (-5.0%) between years or low mortality if cover declined by less than one percent (-1.0%) between years. In the Middle Keys, Dustan Rocks and Rawa were classified as high-mortality sites, and West Turtle Shoal and Thor as low-mortality sites. In the Upper Keys, Admiral and Burr were high-mortality sites and Porter and Turtle were low-mortality sites. High versus low mortality was determined by the difference in percent coral cover between 2009 and 2010, as determined by CREMP surveys (Figs 4, 5).

Rawa, Admiral and Burr suffered declines of more than 10% from 2009 to 2010 (-11.4, -33.8, -11.0%, respectively). The greatest loss of coral cover for the low-mortality sites was seen on Thor (-0.6%). Three of the low-mortality sites (West Turtle Shoal, Turtle and Porter) appeared to have gained coral cover. However, this observation likely resulted from the loss of canopy due to octocoral mortality and not to an actual gain in stony-coral cover, as the CREMP

methodology for determining benthic cover also measures canopy cover of octocorals (Ruzicka et al. 2011). This study included the four patch reefs (West Turtle Shoal, Dustan Rocks, Thor and Burr) examined by Colella et al. (2012) immediately following the disturbance.

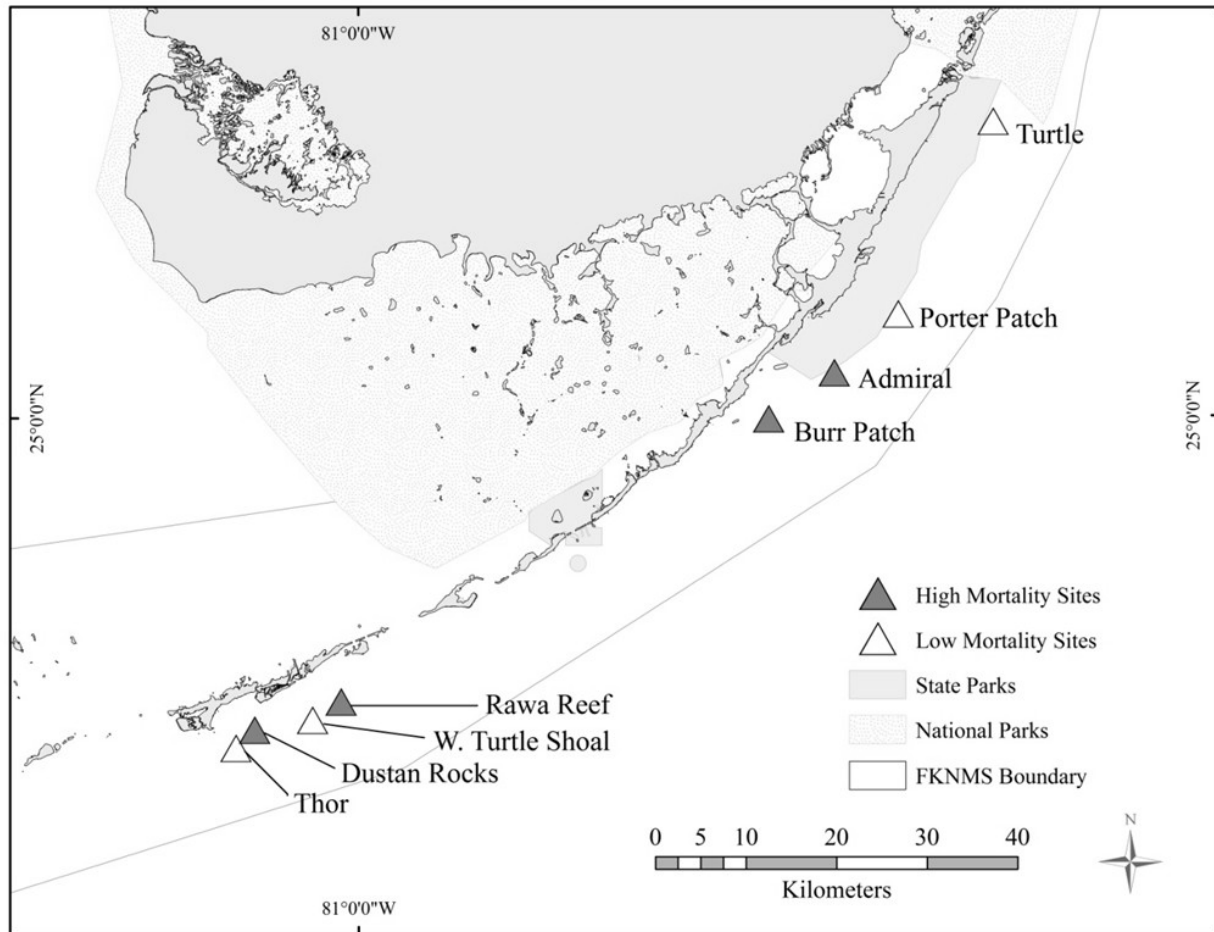


Figure 6. Map of the Middle and Upper Florida Keys with locations of recruitment-study sites. Red triangles represent high-mortality sites and black triangles represent low-mortality sites.

PLOT SETUP AND SAMPLING

Plots were established within two existing CREMP stations per site (8 sites). Stations were 22 m long by 2 m wide and were demarcated by two permanent station markers (Ruzicka et al. 2011). Thirty-two randomly-placed, permanent 0.25 m² quadrats were established at each site

(16 per station). Three small (~7.6 cm long) masonry nails were inserted into the substrate, and flagging tape was tied to each nail, to delineate three out of four corners of each permanent quadrat (Fig. 7). Photos were taken of each quadrat to aid in relocation for subsequent surveys. Stony-coral and octocoral juveniles, visible to the naked eye and having a maximum 4 cm diameter for stony corals or 4 cm height for octocorals, were identified, measured, mapped and photographed in March/April and September/October in two successive years. The 4 cm dimension was selected for two reasons: 1) CREMP adult-demographic surveys only include colonies ≥ 4 cm, and 2) previous studies have found 4 cm to be an appropriate size cut-off for juvenile corals (Loya 1976, Bak and Engel 1979, Moulding 2005).

Stony corals were identified to species, and octocorals were identified to genus. In situ identification of octocorals to the species level is difficult when dealing with adult colonies and nearly impossible for many juveniles. Identification to genus can also be very challenging at times. Consequently the “unknown” octocoral category was used by observers when a juvenile was either too small to identify confidently, was obscured by another benthic flora or fauna, or was unidentifiable for some other reason.

Study setup and deployment of demarcating nails occurred in fall of 2011. Due to inclement weather, surveys did not begin until spring of 2012. Individual colonies ≤ 4 cm were fate-tracked and re-measured during each of the four survey periods to obtain temporal survival and new recruitment data. Surveyors fate-tracked juveniles over time, assigning an S, for each juvenile that “Survived” from one survey to the next, a D for each juvenile that “Died” and an A for each juvenile that grew to >4 cm, or became an “Adult”.

It was often very difficult to distinguish between new recruits and remnant tissue isolates of larger colonies. Surveyors used their best judgment to exclude remnant isolates from the survey. In addition, making the distinction between sexual and asexual recruits was very difficult in most circumstances. To preserve consistency in data collection methodology, surveyors were instructed to include any colony less than 4 cm, regardless of reproductive method.



Figure 7. Permanent quadrat setup within CREMP stations. Left. Full quadrat with three nails and pink flagging tape to delineate corners. Right. For each quadrat, one nail was tagged with a numbered aluminum tag to distinguish permanent quadrats.

STATISTICAL ANALYSES

Data were pooled for all sites and survey periods to calculate overall taxonomic composition. Representation of >3% of the total assemblage (for stony corals and octocorals separately) was used as the cutoff for species/genera inclusion in data analyses. Seven stony-coral species and seven octocoral genera met that criterion.

Juvenile sizes (diameter for stony coral and height for octocoral) were grouped into classes of 10 mm size increments (0-10 mm, 11-20 mm, 21-30 mm, 31-40 mm, and 41+). Only colonies that had been previously recorded as juveniles (≤ 40 mm) and subsequently grew >40

mm in a later survey were included in the 41+ mm size class. Size data were separated into stony-coral and octocoral datasets and pooled into high and low-mortality groupings. A series of Kruskal-Wallis One Way Analyses of Variance (ANOVA) on Ranks were performed in SigmaPlot 11.0 to identify relationships, first, between site mortality-classification groups and, second, between study periods. Each size class was analyzed for differences in abundance over time (all sites pooled). Mortality classification groups were also analyzed in this way, but lacked sufficient replication to achieve the desired statistical power; hence, size-class data are reported here with all sites pooled for each survey period.

Relative frequencies of stony-coral and octocoral juvenile colonies were calculated for each of the 1024 quadrats surveyed overall. Abundance data were tested for normality using a Shapiro-Wilk test in Sigmaplot. Despite attempts at transformation, the data were found to be non-normal with unequal variances, so non-parametric statistical testing was used for all analyses.

Abundance data were then pooled for all survey periods, with stations as replicates, to compare abundance among high and low-mortality patch-reef sites. Mann-Whitney Rank Sum tests were performed for stony-coral and octocoral juvenile abundances. Comparisons resulting in a p-value <0.05 were considered significant relationships. To more specifically identify differences between the sites, ANOVA on Ranks was used. Though statistical testing was done on raw abundance values, the results are expressed as density/m² as it allows for more useful visual representation of the data. Tukey HSD (honestly significant difference) Multiple-Comparison test was done to identify which sites had significant relationships. Linear-regression analysis was completed in Sigmaplot to identify a relationship between stony-coral and octocoral abundance among sites.

Plymouth Routines in Multivariate Ecological Research PRIMER-E Ltd., Plymouth (PRIMER) was used for the following multivariate analyses. CLUSTER analysis on stony-coral and octocoral juvenile abundance was performed in PRIMER v6 using Bray-Curtis resemblance matrix on untransformed data. Dispersion weighting was used to account for differences in variance structure of species counts due to spatial clumping of some species (Clarke et al. 2006). SIMPROF analysis was used to check for structure in the data and identify where clusters were significant. A non-metric Multi-Dimensional Scaling (MDS) plot was created to visually display the relationships among sites. Non-metric Multi-Dimensional Scaling plots map the sites in 2D space, with proximity between sites representing similarity and a stress level of <0.2 indicating a useful representation of the relationship (Clarke and Warwick 2001). Analysis of similarity (ANOSIM) test was used to demonstrate where the dissimilarities were strongest among sites. Similarity percentages (SIMPER) analysis was used to quantify similarity within and among sites based on abundance of octocorals and stony corals. This statistical procedure was repeated using taxa-composition data to more specifically identify which species/genera were contributing to within and among site similarities. Dispersion-weighting was used to down weight individual species/genera counts.

To assess for a relationship between adult and juvenile stony-coral assemblages, similar procedures to those outlined for the juvenile abundance data were accomplished in PRIMER v6. Adult stony-coral densities (colonies/m²) for each of the eight patch reef sites were acquired from 2011 and 2012 CREMP demographic survey data. Juvenile densities were calculated by dividing abundance values by the study area (4 m²/station). Multi-Dimensional Scaling (MDS) analysis was performed on Bray-Curtis similarities of averaged data to create a two dimensional spatial visualization of relationships among adult and juvenile population densities of stony

corals. In PRIMER v6 the RELATE test was used to compare the adult and juvenile Bray-Curtis similarity matrices. The RELATE test uses the Spearman Rank Correlation Coefficient (Rho), with a Rho of +1 or -1 representing the highest correlation possible and with a p-value of <0.05 representing a significant result. SIMPER analysis showed which sites had the greatest adult-juvenile assemblage similarity overall.

Temporal abundance of stony corals and octocorals were examined, with all sites pooled and with quadrats as replicates, to yield a sample size of $n=256$ and to allow for robust statistical testing. Analyses were also done with stations as replicates; however, stations only provided 16 replicate sampling units. To gain resolution and statistical power in temporal abundance data analyses, it was necessary to scale down to the quadrat level to elucidate relationships. A Kruskal-Wallis ANOVA on Ranks was done in SigmaPlot 11.0 to determine if there were significant changes in octocoral and stony-coral juvenile abundances over the four survey periods. A Tukey post-hoc test was used to identify which survey periods differed from others.

Densities were calculated from total quadrat-abundance data for each site and were plotted over time. ANOVA on Ranks was done for each site to identify which sites had significant increases in juvenile abundance over time.

To fate-track each colony, juveniles that survived from one survey to the next were labeled as Survivors (S), while juveniles that survived and also grew over 40 mm were labeled as Adults (A). The Survivors (Ss) and Adults (As) were pooled to create a group that represented total survivors (SA) and percent survival was calculated. To analyze the overall survival of stony-coral versus octocoral juveniles, survival data were pooled for all sites and for survey periods 2-4 (Survey period 1 represented the baseline, Time 0). A Mann-Whitney Rank Sum test

was performed to determine if juvenile survival was greater for stony corals or octocorals overall.

To identify differences in survival among the different patch-reef sites, survey periods were pooled and stations were used as replicates. Kruskal-Wallis ANOVA on Ranks was performed on octocoral and stony-coral percent survival to identify significant differences in survival among sites. All analyses were attempted using quadrats as replicates as well; however, there were many missing values and zero values, hence the statistical analyses were more robust with stations as replicates.

Temporal changes in survival among surveys 2-4 were tested using a Kruskal-Wallis ANOVA on Ranks for both stony corals and octocorals. Survival among the seven stony-coral and seven octocoral taxa was described by pooling all sites and survey periods and calculating the median percent survival (stations as replicates). Survival was plotted against density for all species/genera to identify any correlations between the two measures.

All sites were pooled to compare new recruitment (N) between survey periods 2-4. Survey period 1 served as a baseline to establish initial abundance at each site and was omitted from the analysis. Kruskal-Wallis ANOVA on Ranks was used to compare new recruitment for octocorals and stony corals, separately, over time. Proportions were calculated by dividing the number of new recruits for each survey by the total number of recruits for each survey. Hence for this study, the term recruitment refers to the percent of each assemblage comprised of, and recorded as, new-recruits (R). Recruitment was compared between octocorals and stony corals using a Mann-Whitney Rank Sum Test with all sites and survey periods pooled. This procedure was repeated for taxa.

RESULTS

JUVENILE ASSEMBLAGE DYNAMICS

Species/Genera Composition

Seven stony-coral species made up at least 3% of the overall juvenile stony-coral assemblage on patch-reef sites: *Siderastrea siderea* (46%, Fig. 8a), *Porites astreoides* (19%, Fig. 8b,), *Siderastrea radians* (6.3%), *Agaricia agaricites* (4.7%), *Stephanocoenia intersepta* (4.6%), *Porites porites* (4.4%) and *Montastraea cavernosa* (3.7%). These seven species were selected for inclusion in statistical analyses. *Siderastrea siderea* made up almost half of all stony corals observed, and *P. astreoides* made up almost a fifth. These two species dominated the stony-coral juvenile assemblage, making up 65% of all stony-coral juveniles in the study. The hydrocoral species, *Millepora alcicornis*, was the next closest to the 3% threshold (2.7%). Small specimens of *Orbicella* spp. were occasionally recorded (2.5%), but many of these colonies were likely remnant tissue isolates of larger colonies with partial mortality. Surveyors attempted to exclude remnant tissue isolates, when obvious; however, in many circumstances differentiation was very difficult. Ten percent of the stony-coral assemblage was comprised of other species, each making up <1% of the total.

Octocoral genera with $\geq 3\%$ species composition were: *Antillogorgia* (formerly *Pseudopterogorgia*, 25%), *Gorgonia* (21%), *Eunicea* (19%), *Erythropodium* (14%), *Muriceopsis* (4.0%), *Pseudoplexaura* (3.0%) and *Briareum* (3.0%). The four most abundant octocoral genera (*Antillogorgia*, *Gorgonia*, *Eunicea* and *Erythropodium*, Fig. 9a-d, respectively) made up almost

80% of all octocorals seen, but unlike the stony corals, percent composition was more evenly distributed among these four genera. *Eunicea flexuosa* (formerly *Plexaura flexuosa*) was included in the *Eunicea* genus. The Unknown octocoral category included 5.2% of all juvenile octocoral observations and was used by observers when a juvenile was too small to identify confidently, was obscured by another benthic flora or fauna, or was unidentifiable for some other reason. This category was not included in the analyses. Consequently, seven octocoral genera and seven stony-coral species were selected for use in statistical analyses.

Size Distribution

At both high and low-mortality sites, stony corals were most abundant in the three smallest size classes (0-10, 11-20 and 21-30 mm) (Fig. 10, data pooled for all survey periods). Low-mortality sites demonstrated higher variability in juvenile sizes in these smallest size classes. Low-mortality sites also displayed slightly higher abundance, with each size class having at 1-4 more colonies/m² than on high-mortality sites. The very limited number of colonies in the largest size classes may reflect the limited temporal span of the study.

Octocoral size distributions showed similar patterns to stony corals, with overall more variability and higher abundance on the low-mortality sites (Fig. 11). The difference in abundance between the two mortality groups is much more distinctive with octocorals: low mortality-sites had 4-12 more colonies/m² in every size class than high-mortality sites. Octocorals also displayed a decrease in abundance in the two larger size classes, similarly to the stony-coral size distribution (non-significant).

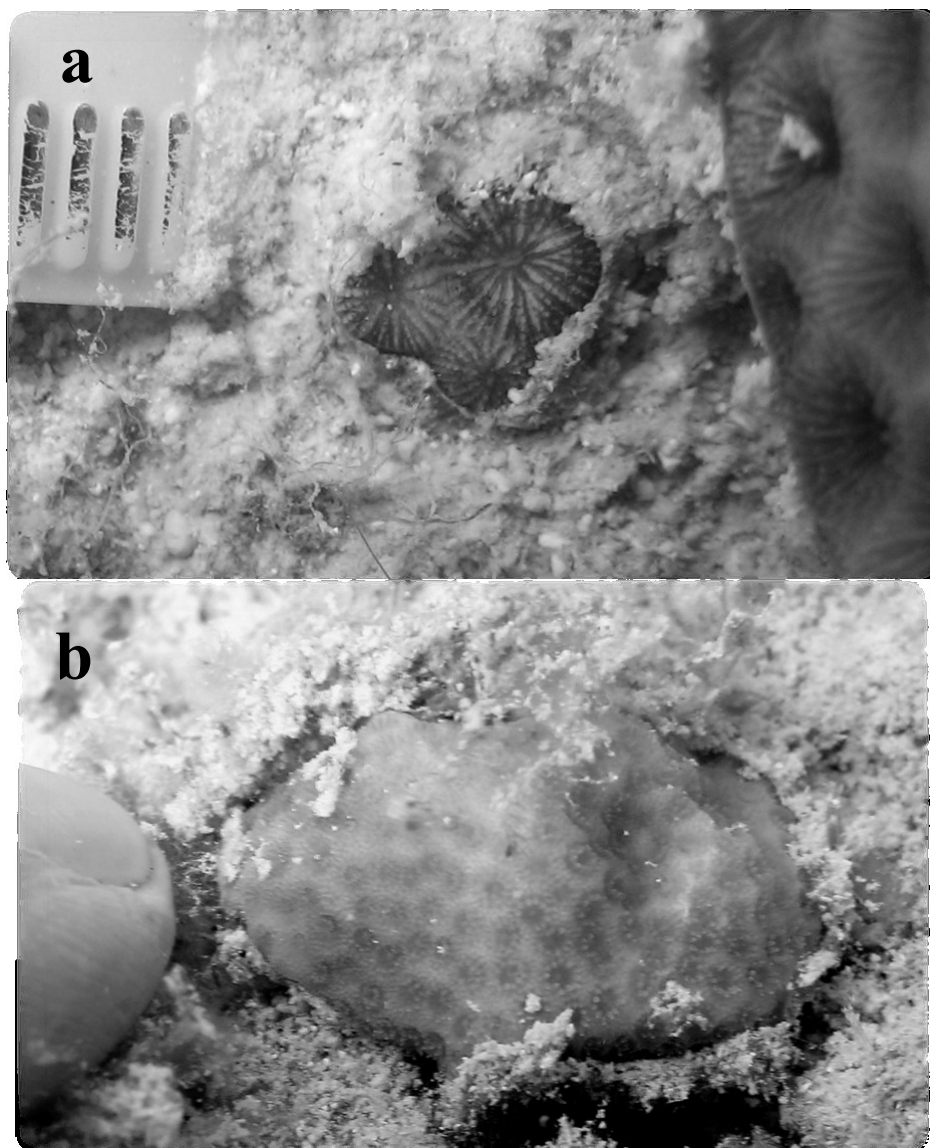


Figure 8. The two most abundant stony-coral species (66% of all stony-coral juveniles found): a) *Siderastrea siderea* three polyp juvenile colony about 4 mm in diameter. Tick marks on the ruler in the photo are millimeters; b) *Porites astreoides* juvenile colony with diver finger for scale.

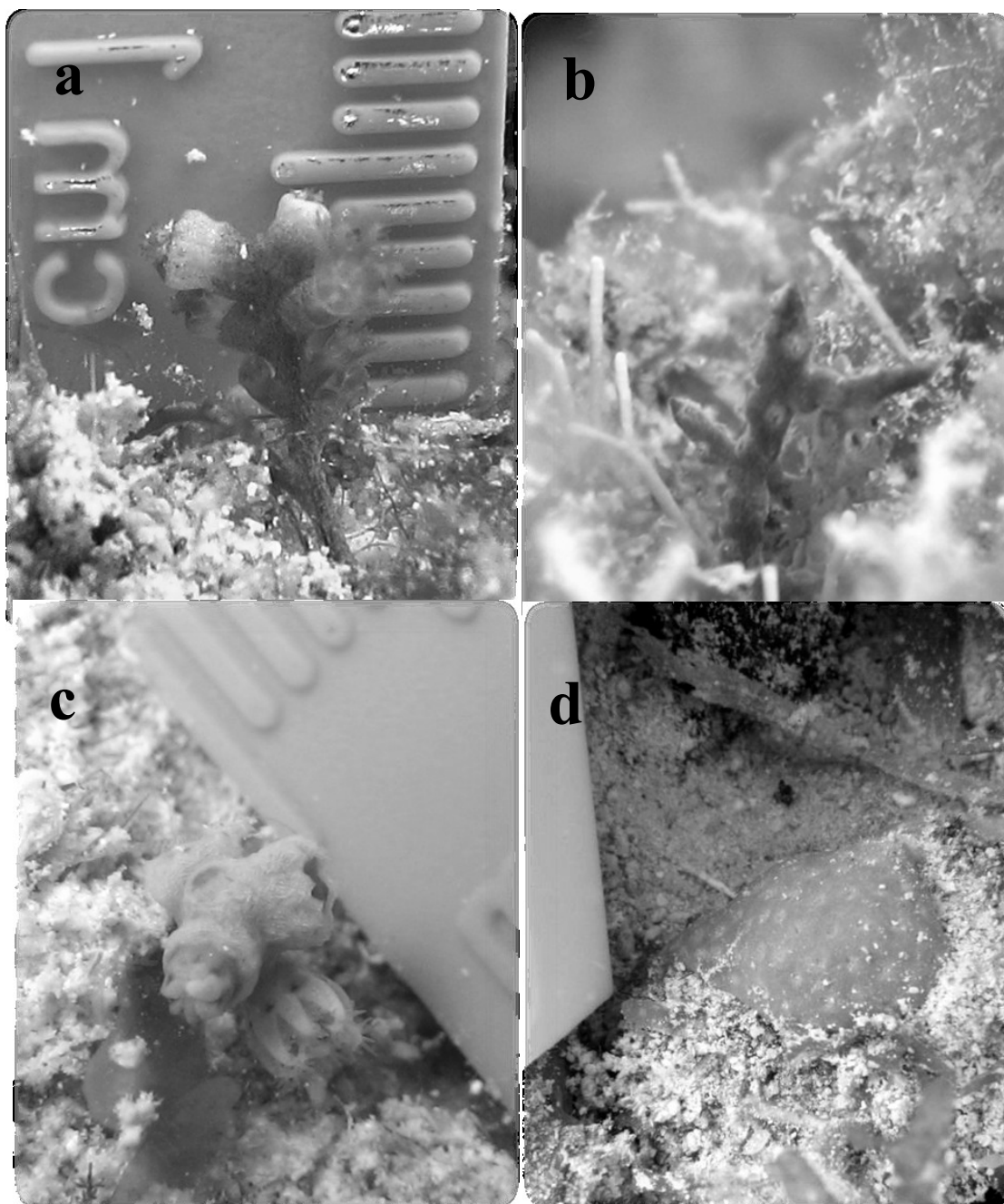


Figure 9. Four most abundant octocoral genera (80% of all octocoral juveniles found): a) *Antilloorgia* (formerly *Pseudopterogorgia*) approximately 7 mm tall; b) *Gorgonia* amidst turf algae fronds; c) *Eunicea* five polyp colony approximately 3 mm in height; d) *Erythropodium*, encrusting octocoral genus.

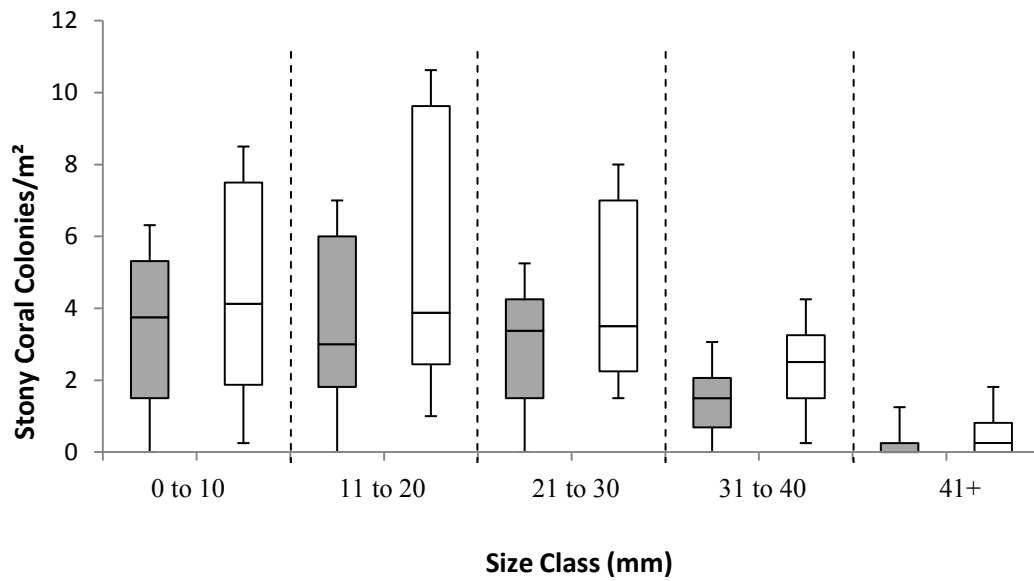


Figure 10. Stony-coral size-class distribution of juvenile density (non-significant, pooled for all survey periods). Gray boxes are high-mortality sites and white boxes are low-mortality sites. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

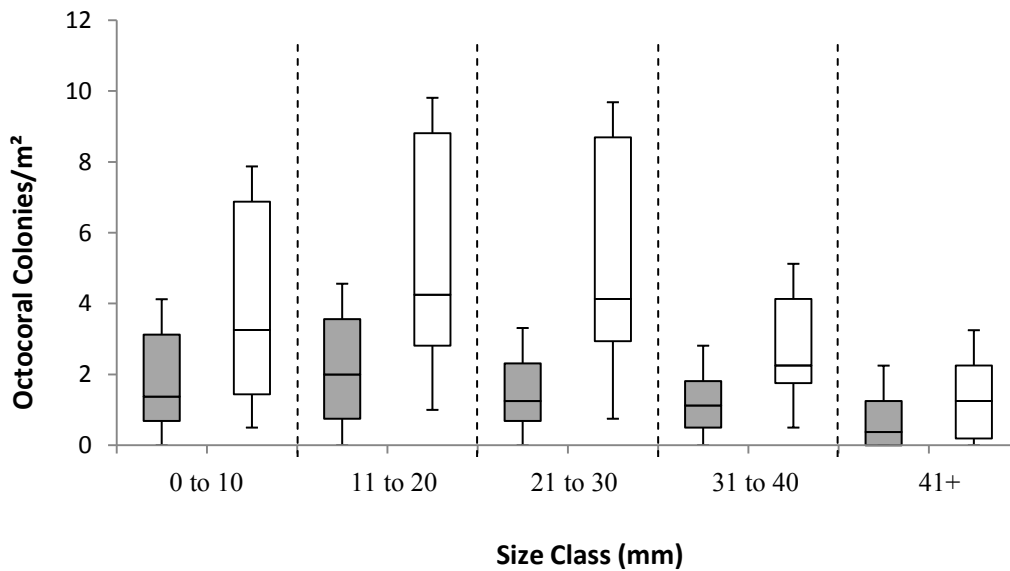


Figure 11. Octocoral size-class distribution of juvenile density (non-significant, pooled for all survey periods). Gray boxes are high-mortality sites and white boxes are low-mortality sites. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

Overall juvenile density exhibited an increasing trend over time within the smallest size class (0-10 mm, all sites pooled) for both stony corals and octocorals. High variability limited further in-depth analyses of mortality-classification groups or individual sites. With all sites pooled, stony-coral density showed a slight (not significant) increase over time in the smallest size class (Fig. 12). The remaining size classes showed little to no change in stony-coral density over the four survey periods (Table 1). Octocorals also showed the greatest increase over time in the smallest size class (0-10 mm, 4 colonies/m²) with a significant increase occurring between fall of 2012 and fall of 2013 (surveys 2 and 4, $p=0.019$, Kruskal-Wallis ANOVA on ranks, Fig. 13). Octocoral density also showed a slight increase over time in the 11-20 mm size class (Table 2), whereas stony corals did not.

Table 1. Stony-coral median density (colonies/m²) in each size class (mm) over time.

Survey	0 to 10	11 to 20	21 to 30	31 to 40
Spring 2012	3	3	3	2
Fall 2012	4	3	4	2
Spring 2013	4	4	3	2
Fall 2013	5	3	4	2

Table 2. Octocoral median density (colonies/m²) in each size class (mm) over time.

Survey	0 to 10	11 to 20	21 to 30	31 to 40
Spring 2012	2	2	2	2
Fall 2012	1	3	3	2
Spring 2013	3	3	3	2
Fall 2013	5	5	3	2

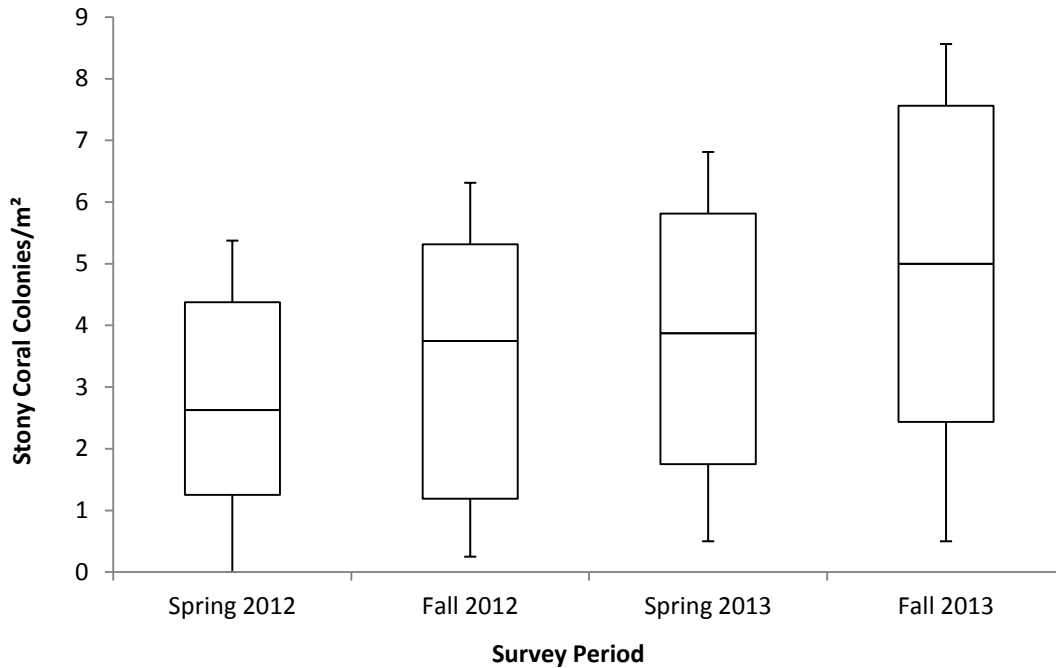


Figure 12. Temporal stony-coral density within the 0-10 mm size class, showing a slight, though non-significant increase over time (all sites pooled). Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

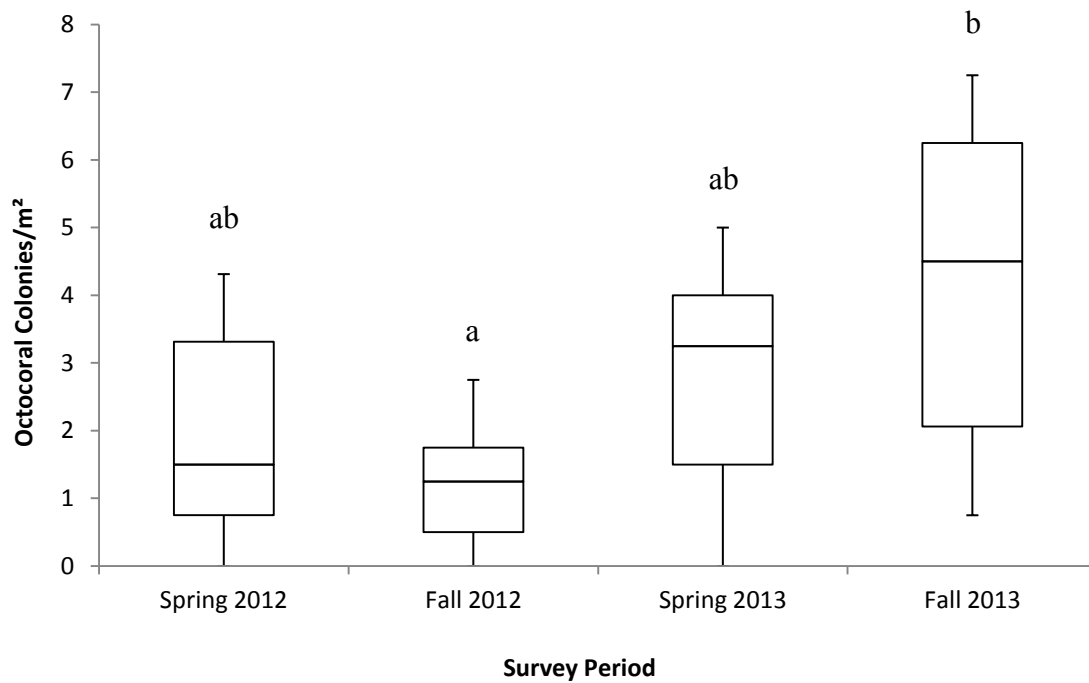


Figure 13. Temporal octocoral density within the 0-10 mm size class. A significant difference was found between Fall 2012 and Fall 2013 ($p=0.019$, all sites pooled). Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

Abundance

Juvenile-abundance data for both stony corals and octocorals were non-normally distributed (Shapiro-Wilk, $p < 0.001$). The distribution curves were skewed to the right (positive skew), with the highest frequencies occurring at the smallest abundance values. For both taxa, median frequencies were higher for low-mortality sites than for high-mortality sites (Fig. 14), that is, 3 (low) versus 2 (high) stony-coral juveniles per 0.25 m^2 per site and 4 (low) versus 1 (high) octocoral juveniles per 0.25 m^2 per site. The most frequent abundance value was zero. With all sites and survey periods pooled, there were a total of 1024 replicate sampling units (quadrats). Recruitment was highly spatially variable. Almost a quarter (22%) of all quadrats (226/1024) had zero stony-coral juveniles present and just over a quarter (28%) had zero octocoral juveniles present (288/1024). High-mortality sites had 3-4 times more quadrats where no juveniles were recorded than the low-mortality sites (Fig. 14). Otherwise, frequency distributions of stony corals and octocorals were similar for high and low-mortality sites.

A Mann-Whitney Rank-Sum Test was performed on stony-coral abundance, pooling temporal data and using stations as replicates to compare high and low-mortality sites (Fig. 15: represented here as median density). Low-mortality sites demonstrated higher stony-coral abundance than high-mortality sites; however, the relationship was found to be marginally insignificant ($p = 0.053$). The test was repeated for octocoral abundance, with low-mortality sites showing significantly higher octocoral abundance than high-mortality sites ($p < 0.001$, Fig. 15).

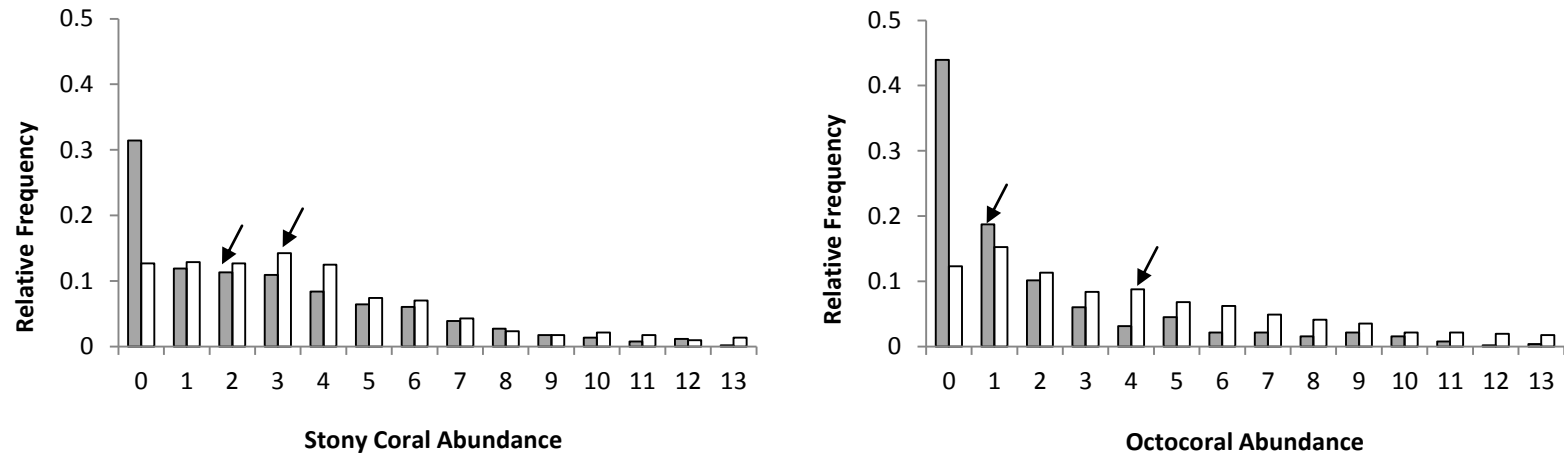


Figure 14. Relative-frequency distributions for stony-coral (left) and octocoral (right) abundance by 0.25 m² quadrat (all sites and survey periods pooled). Both distributions are skewed to the right, with highest frequencies occurring at lower abundance values. Abundance data are not normally distributed (Shapiro-Wilk, $p < 0.001$). Gray bars are high-mortality sites and white bars are low-mortality sites. Arrows indicate median values.

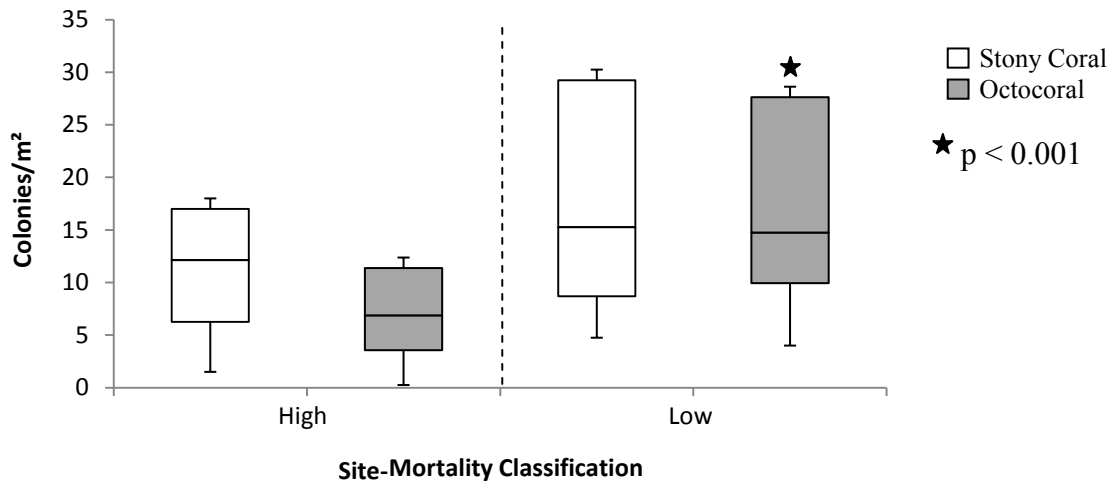


Figure 15. Juvenile density (colonies/m²) by site mortality classification (high vs. low). White boxes are stony-coral density and gray boxes are octocoral density. The star represents a significant difference ($p < 0.001$); octocoral abundance was significantly higher on low-mortality sites than on high-mortality sites. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

The relationship shown in Figure 15 was not consistent throughout all sites in each mortality-classification group. A site by site comparison (Tables 3, 4) showed that certain sites contributed to this pattern more than others. Stony-coral and octocoral juvenile abundances were pooled for all survey periods to compare abundance among sites (stations as replicates). Boxplots (Figs 16, 17) show median density of juveniles per square meter. Overall, West Turtle (30 colonies/m²) demonstrated the highest density of stony corals followed by Thor (24 colonies/m², Fig. 16). Admiral (3 colonies/m²) and Porter (5 colonies/m²) had the lowest densities of stony corals. Turtle had more than double (50 colonies/m²) the number of octocoral juveniles of any other site (Fig. 17). The two sites that demonstrated the lowest stony-coral density showed the second and third highest octocoral densities (Admiral with 16 colonies/m², and Porter with 15 colonies/m²). An inverse relationship between octocoral and stony-coral

juvenile density was apparent when Turtle was omitted from analyses, though the relationship was not statistically significant ($p=0.346$, Fig. 18).

Table 3. Difference of Ranks between sites for stony-coral abundance (survey periods pooled). Bold values represent significant relationships ($p < 0.05$).

	Dustan	Thor	W. Turtle	Rawa	Turtle	Admiral	Porter	Burr
Dustan								
Thor	153							
W. Turtle	243.5	90.5						
Rawa	129.5	23.5	114					
Turtle	68	85	175.5	61.5				
Admiral	165.5	318.5	409	295	233.5			
Porter	100	253	343.5	229.5	168	65.5		
Burr	123.5	29.5	120	6	55.5	289	223.5	

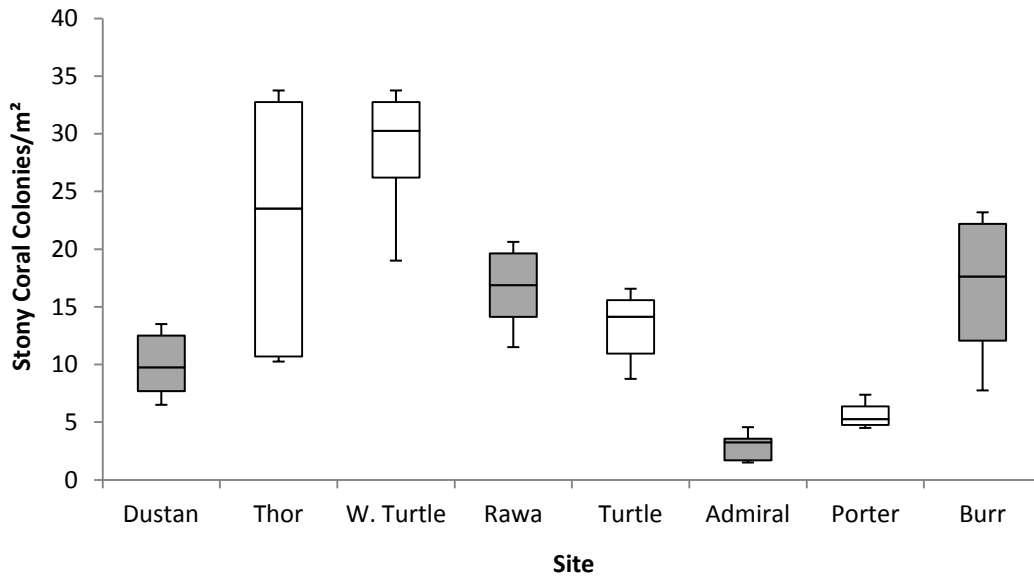


Figure 16. Box plot of median densities (colonies/m²) of stony-coral juveniles by site. Data pooled for all survey periods (n=8). Gray bars are high-mortality sites and white bars are low-mortality sites. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

Table 4. Difference of Ranks between sites for octocoral abundance (survey periods pooled). Bold values represent significant differences ($p < 0.05$).

	Dustan	Thor	W. Turtle	Rawa	Turtle	Admiral	Porter	Burr
Dustan								
Thor	66.5							
W. Turtle	49	17.5						
Rawa	135	201.5	184					
Turtle	305	238.5	256	440				
Admiral	189	122.5	140	324	116			
Porter	195	128.5	146	330	110	6		
Burr	21.5	88	70.5	113.5	326.5	210.5	216.5	

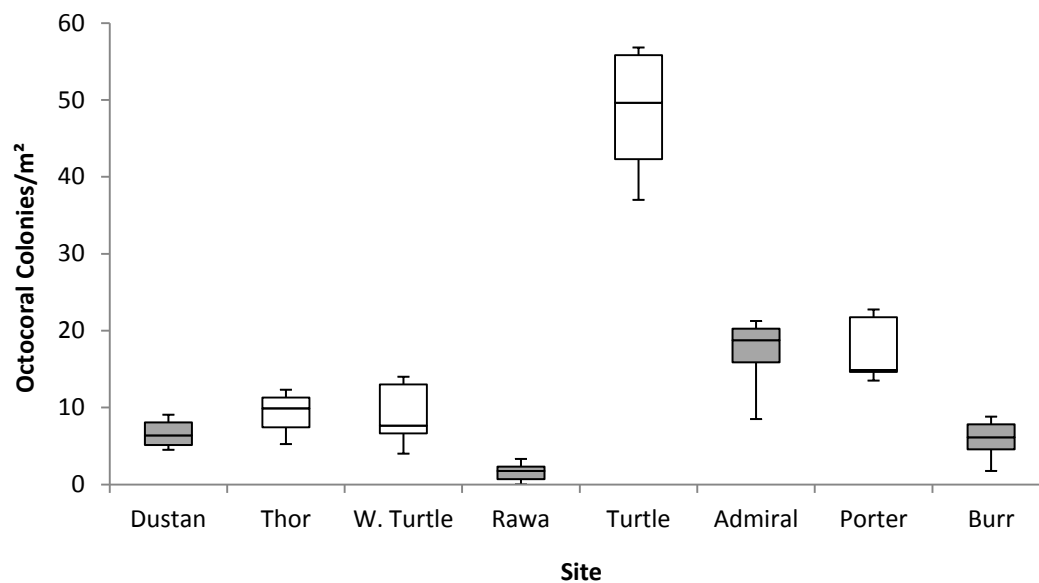


Figure 17. Box plot of median densities (colonies/m²) of octocoral juveniles by site. Data pooled for all survey periods (n=8). Gray bars are high-mortality sites and white bars are low-mortality sites. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

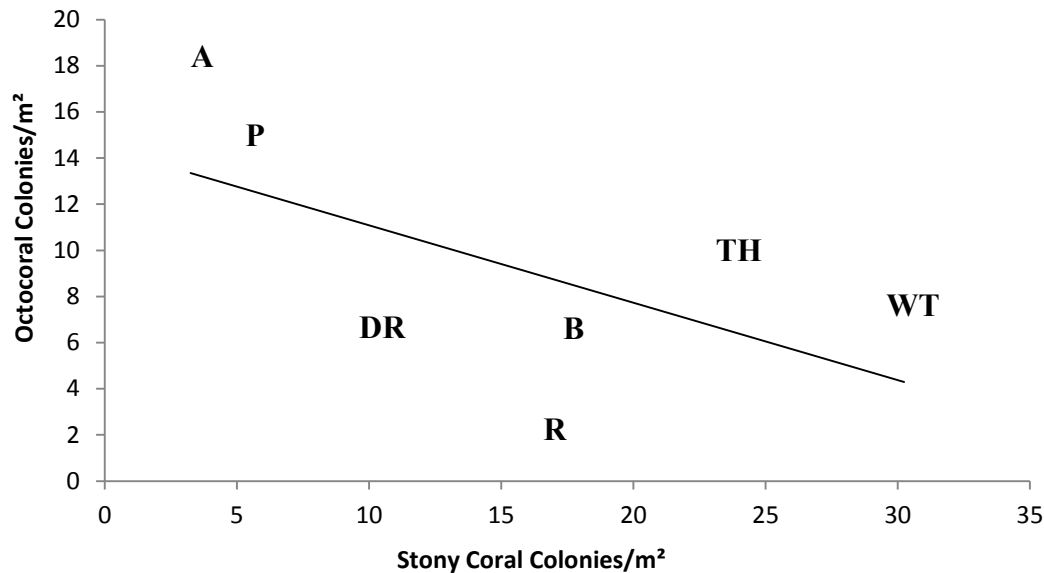


Figure 18. Scatter-plot of median octocoral versus stony-coral juvenile densities for each site (excluding Turtle), with linear regression line ($p=0.346$, data pooled for all survey periods). Letters represent sites (A=Admiral, P=Porter, DR=Dustan Rocks, R=Rawa, B=Burr, TH=Thor, WT=West Turtle).

SITE CLUSTER, MDS AND SIMPER ANALYSES

Stony Corals and Octocorals

CLUSTER and SIMPROF analyses were performed in PRIMER on untransformed Bray-Curtis similarities of stony-coral and octocoral abundance data (pooled for all survey periods with stations as replicates) to evaluate abundance among sites. The resulting dendrogram (Fig. 19) revealed that the three northern-most sites, Turtle, Porter and Admiral, grouped separately from the rest of the sites (SIMPROF $p<0.05$). All four Middle-Keys sites and the southernmost site in the Upper Keys (Dustan Rocks, Thor, West Turtle, Rawa and Burr, respectively) formed one large cluster, which exhibited 60% similarity. Turtle was distinct (<60% similarity) from Porter and Admiral, which were >60% similar. Except for two samples from Admiral, the other samples from Admiral were very similar (>80%) to all samples from Porter. MDS analysis

further demonstrated that total juvenile assemblages were distinct among these three clusters (Fig. 20), while the ANOSIM test demonstrated where the dissimilarities were strongest among sites (Table 5).

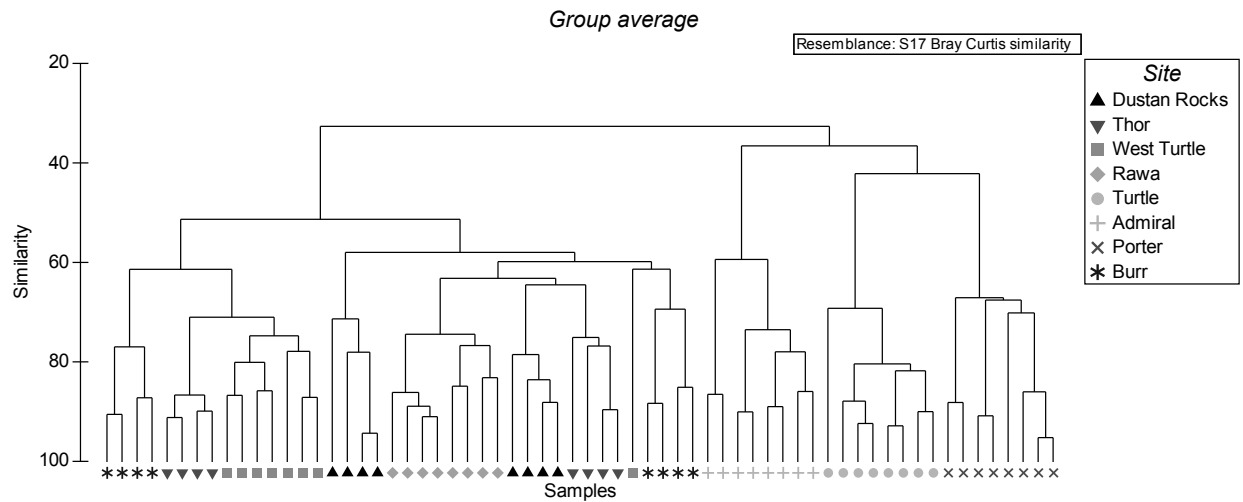


Figure 19. Dendrogram of Bray-Curtis similarities of juvenile stony-coral and octocoral abundance among sites, survey periods pooled (eight samples per site).

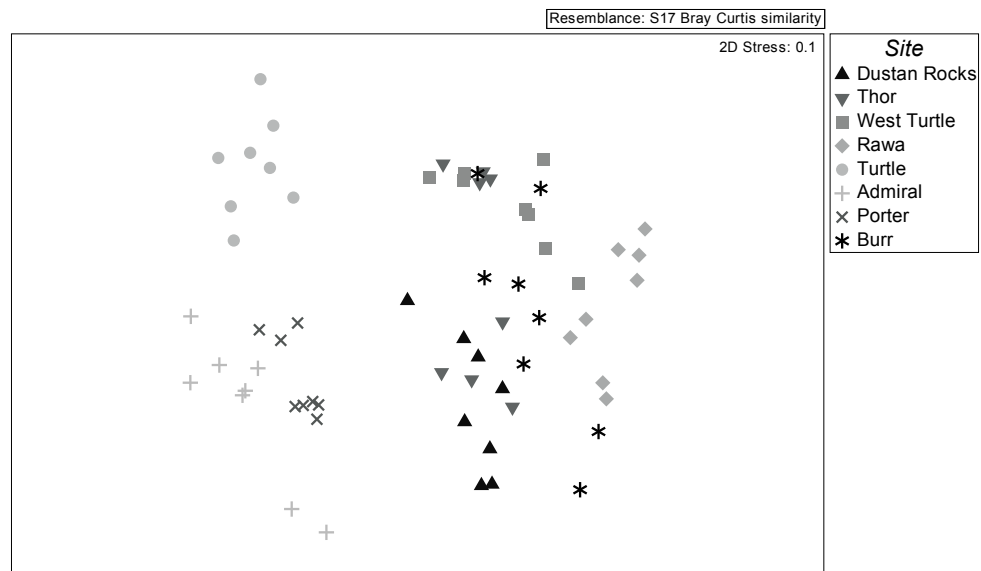


Figure 20. MDS plot of Bray-Curtis similarities of juvenile stony-coral and octocoral abundances among sites, survey periods pooled (eight samples per site).

	Dustan	Thor	W Turtle	Rawa	Turtle	Admiral	Porter	Burr
Dustan Rocks								
Thor	0.2							
West Turtle	0.8	n.s.						
Rawa	0.7	0.5	0.7					
Turtle	1.0	1.0	1.0	1.0				
Admiral	0.9	0.9	1.0	1.0	0.9			
Porter	0.9	0.8	1.0	1.0	1.0	0.2		
Burr	0.2	n.s.	0.2	0.2	0.9	0.9	0.8	

Table 5. ANOSIM R-Statistic dissimilarity matrix for all sites ($p < 0.05$, n.s represents an insignificant result). An R-statistic of 1.0 represents the highest level of dissimilarity possible while an R-statistic of 0 suggests that sites are very similar.

SIMPER analysis showed that the within-site similarity for all sites ranged from 69-88%. Stony corals contributed most (60-94%) to within-site similarity for sites in the larger cluster, which were the Middle-Keys sites and the southernmost Upper-Keys site (Dustan Rocks, West Turtle, Thor, Rawa and Burr). Octocorals contributed most (75-87%) to the within-site similarity in the two smaller clusters, which contained Turtle alone and Admiral and Porter together (Table 6). Stony-coral juveniles dominated the Middle-Keys sites and Burr, while octocorals dominated the remaining Upper-Keys sites.

Table 6. SIMPER results by site, showing average percent within-site similarity for each site, average density (colonies/m²), and percent contribution for taxa contributing to similarity within each site.

Dustan Rocks Average similarity: 80%			Thor Average similarity: 73%			West Turtle Average similarity: 84%			Rawa Average similarity: 84%		
Taxa	Density	Contrib%	Taxa	Density	Contrib%	Taxa	Density	Contrib%	Taxa	Density	Contrib%
Stony	10	60	Stony	24	65	Stony	30	79	Stony	17	94
Octo	7	40	Octo	10	35	Octo	9	21	Octo	2	6.4

Turtle Average similarity: 87%			Admiral Average similarity: 78%			Porter Average similarity: 87%			Burr Average similarity: 69%		
Taxa	Density	Contrib%	Taxa	Density	Contrib%	Taxa	Density	Contrib%	Taxa	Density	Contrib%
Octo	50	79	Octo	16	87	Octo	15	75	Stony	19	77
Stony	14	21	Stony	3	13	Stony	5	25	Octo	6	23

By Taxa

CLUSTER analysis of untransformed Bray-Curtis similarities of abundance data for taxa (species/genera, pooled for all survey periods with stations as replicates) revealed similar results (Fig. 21), while adding a layer of detail to the site groupings. The three northernmost sites, Turtle, Porter and Admiral, each clustered separately from one another at <45% similarity. Porter and Turtle grouped more closely to one another, where previously Admiral and Porter had grouped closely. All remaining sites clustered, as before, into one larger group with >45% similarity. MDS analysis provided a two dimensional visualization of the resemblance among clusters (Fig. 22). Inclusion of taxon-composition data in the SIMPER analysis revealed that Turtle, Porter and Admiral were dominated by three different genera of octocoral.

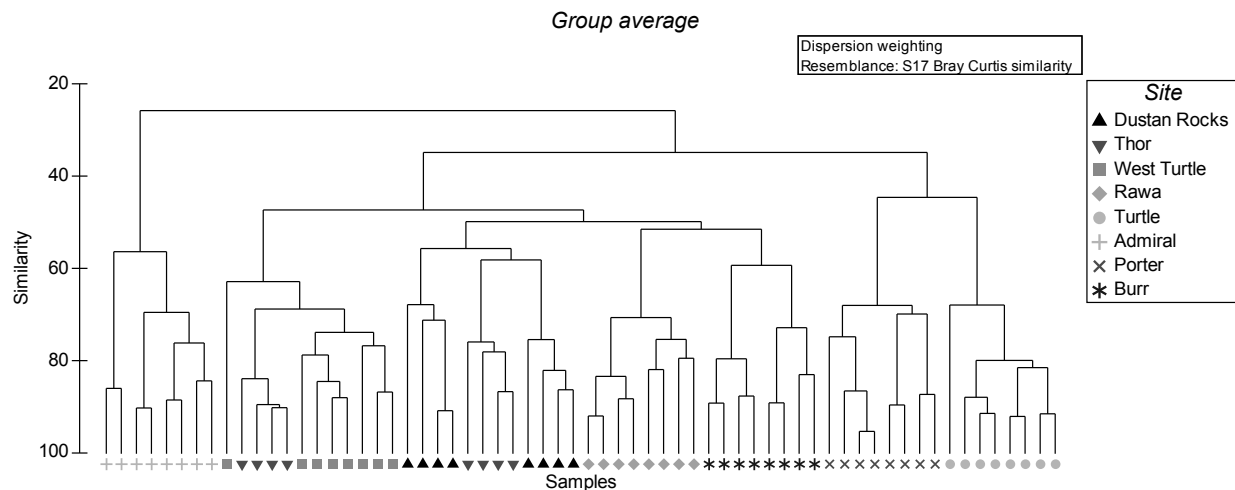


Figure 21. Dendrogram of Bray-Curtis similarities of dispersion weighted juvenile abundance of all species/genera among sites, survey periods pooled (eight samples per site).

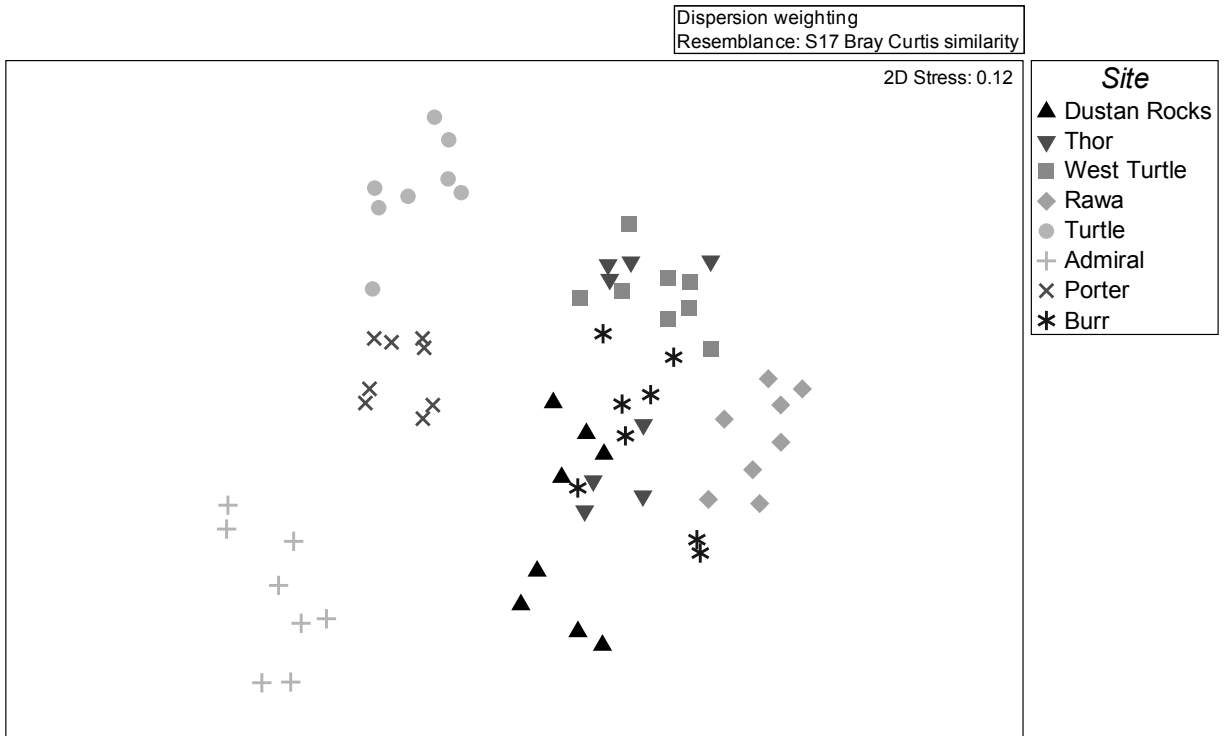


Figure 22. MDS plot of Bray-Curtis similarities of dispersion weighted juvenile abundance of all species/genera among sites, survey periods pooled (eight samples per site).

SIMPER analysis showed that the within-site similarity for all sites ranged from 62-80%. The stony coral *S. siderea* contributed most (33-56%) to within site-similarity on sites in the larger cluster (Dustan Rocks, West Turtle, Thor, Rawa and Burr). Three octocoral genera, *Antillogorgia*, *Gorgonia* and *Eunicea*, each contributed most to the within-site similarity on Turtle (44%), Admiral (66%), and Porter (35%), respectively (Table 7). Results are consistent with the MDS analysis results reported above, separating sites into four distinct clusters. Table 8 shows median density of each taxon, for each site, with the shaded values representing the dominant taxon. It is clearly apparent that the most abundant taxa were also top contributors to within-site similarity (Tables 7, 8).

Table 7. SIMPER results by site showing average percent similarity for each site, the top three taxa of stony corals and octocorals contributing to within group similarity, density (colonies/m²) and percent contribution for those taxa. The column to the far right shows percent cumulative contribution to within site similarity.

Within Group Similarity

Site	Avg % Similarity	Taxon 1	Density	%cont	Taxon 2	Density	%cont	Taxon 3	Density	%cont	% cum
Dustan Rocks	69	<i>S. siderea</i>	6	48	<i>Antillogorgia</i>	3	20	<i>Eunicea</i>	2	13	80
Thor	67	<i>S. siderea</i>	12	41	<i>P. astreoides</i>	4	16	<i>Erythropodium</i>	3	14	71
West Turtle	74	<i>S. siderea</i>	11	33	<i>P. astreoides</i>	6	18	<i>S. intercepta</i>	2	8	60
Rawa	78	<i>S. siderea</i>	8	56	<i>M. cavernosa</i>	2	15	<i>P. astreoides</i>	2	13	85
Turtle	79	<i>Antillogorgia</i>	23	44	<i>Eunicea</i>	5	11	<i>S. siderea</i>	6	10	65
Admiral	70	<i>Gorgonia</i>	12	66	<i>Antillogorgia</i>	3	19	<i>S. siderea</i>	1	8	93
Porter	71	<i>Eunicea</i>	6	35	<i>Gorgonia</i>	2	14	<i>Antillogorgia</i>	2	10	59
Burr	62	<i>S. siderea</i>	9	47	<i>P. astreoides</i>	2	17	<i>A. agaricites</i>	1	8	71

Table 8. Median density (colonies/m²), per site, for the top seven stony-coral species and top seven octocoral genera. Shaded values are the dominant taxon for that site. Species and genera coding are (listed in *Appendix A*) the first letter of the genus and the first three letters of the species for stony corals and the first four letters of the genus for octocorals.

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

Adult Stony-Coral Demographics

Adult densities (colonies/m²) for seven species of stony corals (*S. siderea*, *P. astreoides*, *S. intercepta*, *P. porites*, *M. cavernosa*, *A. agaricites* and *S. radians*) were acquired from CREMP demographic data for 2011 and 2012 (Table 9). Adult octocoral data were not available for all study sites, so octocorals were removed from the juvenile data to allow for direct comparison. Multi-dimensional scaling (MDS) analysis of dispersion-weighted and averaged Bray-Curtis similarities provided a spatial visualization of similarities among adult and juvenile densities of stony corals (Fig. 23). Site clustering was very similar to the juvenile MDS results (RELATE Spearman Rank Correlation Rho = 0.7, p<0.001), with all Middle-Keys sites and Burr clustering together, while Porter and Admiral clustered separately. One main difference that resulted from removing octocorals from the analysis is that Turtle grouped with the larger cluster, instead of by itself and this was true for both juveniles and adults. Juvenile and adult assemblages from the same sites tended to cluster together. Porter (X symbol) provides an example of a site where adult and juvenile assemblages clustered more closely to each other than to other sites.

Table 9. Median (2011 and 2012 data) density (colonies/m²), per site, for seven adult stony-coral species. Shaded values are the dominant species for that site. Species coding are (listed in *Appendix A*) the first letter of the genus and the first three letters of the species.

Site	SSID	PAST	SMIC	PPOR	MCAV	AAGA	SRAD
Dustan Rocks	4	1	3	0	2	0	0
Thor	2	2	2	1	1	0	0
West Turtle	8	1	3	2	1	1	0
Rawa	4	0	1	0	1	0	0
Turtle	3	2	0	2	0	2	0
Admiral	0	0	0	0	0	0	0
Porter	1	1	0	1	0	0	0
Burr	4	0	1	0	0	0	0

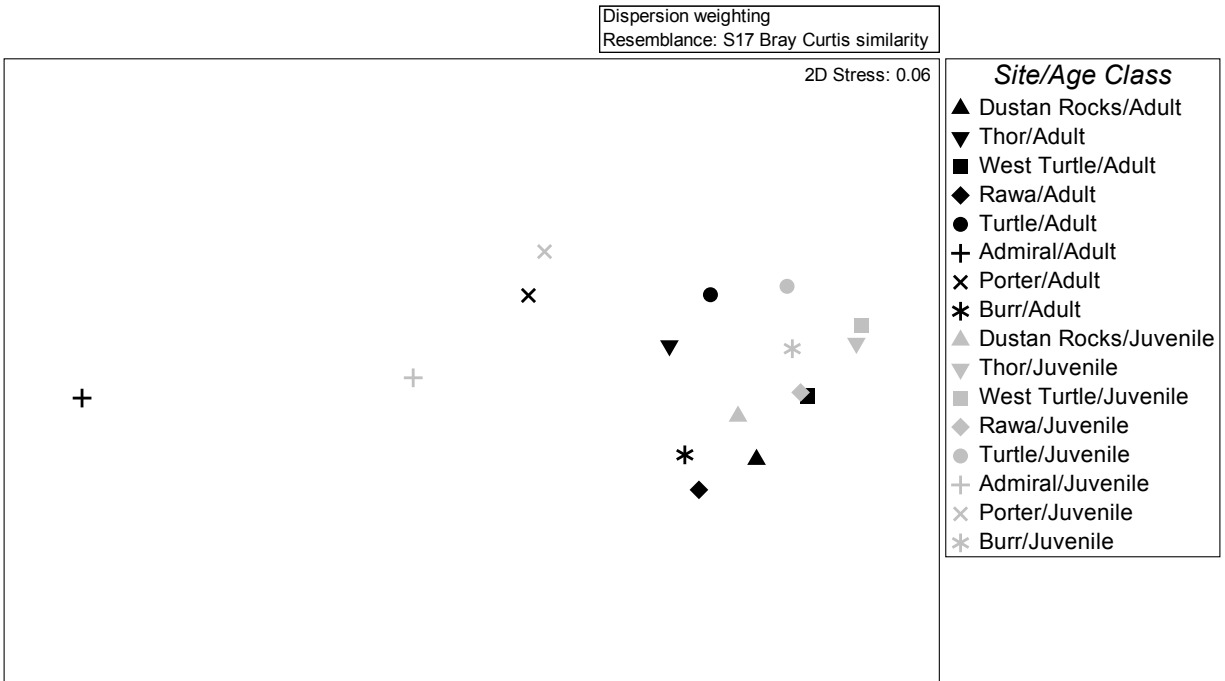


Figure 23. MDS plot of stony-coral adult and juvenile densities of 7 species among sites with survey periods pooled (juveniles-eight samples per site, adults-four samples per site). Solid black shapes are adult-density sites and gray shapes are juvenile-density sites.

SIMPER analysis showed that adult-juvenile within-site similarity ranged from 30-72%. West Turtle showed the greatest similarity between adult and juvenile stony-coral assemblages, while Admiral demonstrated the least similarity (Table 10).

Table 10. Percent similarity between adult and juvenile stony-coral densities on each site.

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

TEMPORAL ANALYSES

Abundance

Stony-coral juvenile abundance (all sites pooled, quadrats as replicates) showed only a slight increase between the first survey period (spring 2012) and the last (fall 2013, $p=0.019$, Tables 11, 12). Octocoral abundance differed significantly among survey periods ($p<0.001$, Table 13). Data from surveys 1 and 2 (spring 2012 and fall 2012) revealed significantly fewer juvenile octocorals than survey 4 (fall 2013, Table 14). Overall, octocoral abundance increased more dramatically than stony-coral abundance. Neither relationship was found to be significant when using stations as replicates. When stations were used as replicates instead of quadrats, this only yielded 16 replicate sampling units per survey period, which reduced the power to detect change. Using quadrats as the sampling units provided 256 replicates, which increased the power to detect change.

Table 11. Kruskal-Wallis One-Way Analysis of Variance on Ranks of untransformed stony-coral abundance (quadrats as replicates).

Survey	N	Missing	Median	25%	75%
1	256	0	2	1	4
2	256	0	3	1	5
3	256	0	3	1	6
4	256	0	3	1	6

H = 9.9 with 3 degrees of freedom. (**P = 0.019**)

Table 12. All Pairwise Multiple-Comparison Procedures (Tukey Test) on overall stony-coral abundance (quadrats as replicates).

Comparison	Diff of Ranks	q	P<0.05
4 vs 1	20675	4.37	Yes
4 vs 2	9237	1.95	No
4 vs 3	7465	1.58	No
3 vs 1	13210	2.79	No
3 vs 2	1773	0.38	No
2 vs 1	11438	2.42	No

Table 13. Kruskal-Wallis One-Way Analysis of Variance on Ranks of untransformed octocoral abundance (quadrats as replicates).

Group	N	Missing	Median	25%	75%
1	256	0	1	0	4
2	256	0	1	0	5
3	256	0	2	0	5
4	256	0	3	0.25	7

H = 19.2 with 3 degrees of freedom. (P = <0.001)

Table 14. All Pairwise Multiple-Comparison Procedures (Tukey Test) on overall octocoral abundance (quadrats as replicates).

Comparison	Diff of Ranks	q	P<0.05
4 vs 1	26558	5.61	Yes
4 vs 2	21995	4.65	Yes
4 vs 3	12172	2.57	No
3 vs 1	14386	3.04	No
3 vs 2	9823	2.08	No
2 vs 1	4563	0.96	No

Densities of juvenile stony corals and octocorals were calculated from total quadrat-abundance data for each site. Stony-coral juvenile density at each site is shown below (Fig. 24) over the four survey periods (spring 2012, fall 2012, spring 2013 and fall 2013). The highest density of stony-coral juveniles occurred at West Turtle for all four survey periods, the lowest at Admiral. While most of the sites did not show an increase in juvenile densities of stony corals over this time, an increase was apparent at West Turtle and Burr.

Juvenile octocoral density was highest at Turtle and was also relatively high at Admiral and Porter (Figs 25, 26). Turtle showed double the octocoral density of any other site (Fig. 25), so it was removed from the scatter plot (Fig. 26) to reveal differences among other sites. The lowest octocoral juvenile density occurred at Rawa. An inverse relationship between stony-coral and octocoral densities was evident, as the sites with the lowest stony-coral density were also the sites with some of the highest octocoral density. This is especially apparent at Admiral and

Porter. Unlike with stony corals, every site except Rawa showed a slight, but apparent increase in octocoral density over time.

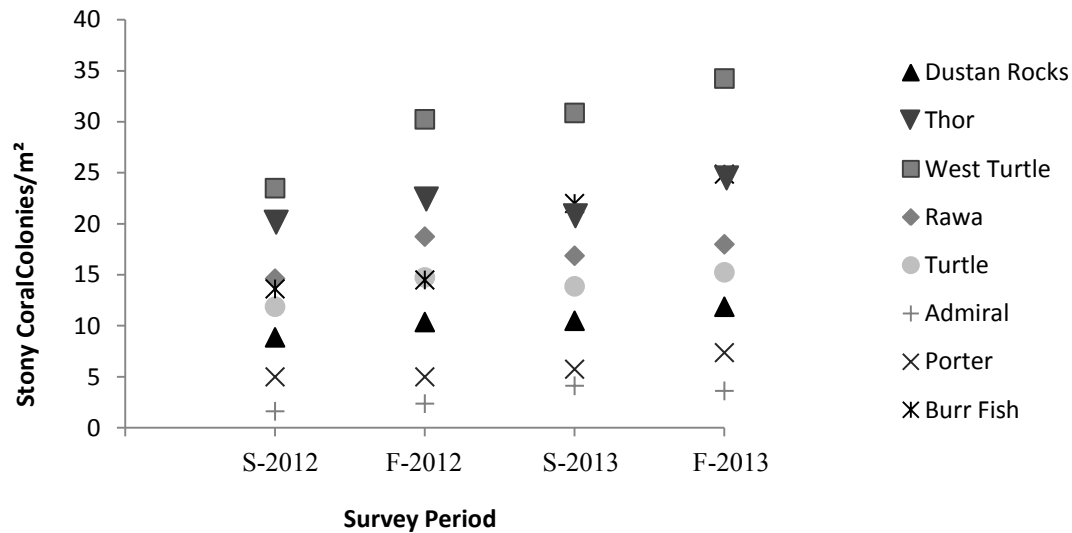


Figure 24. Scatter-plot of stony-coral juvenile density (total colonies/m²) on each site over four surveys.

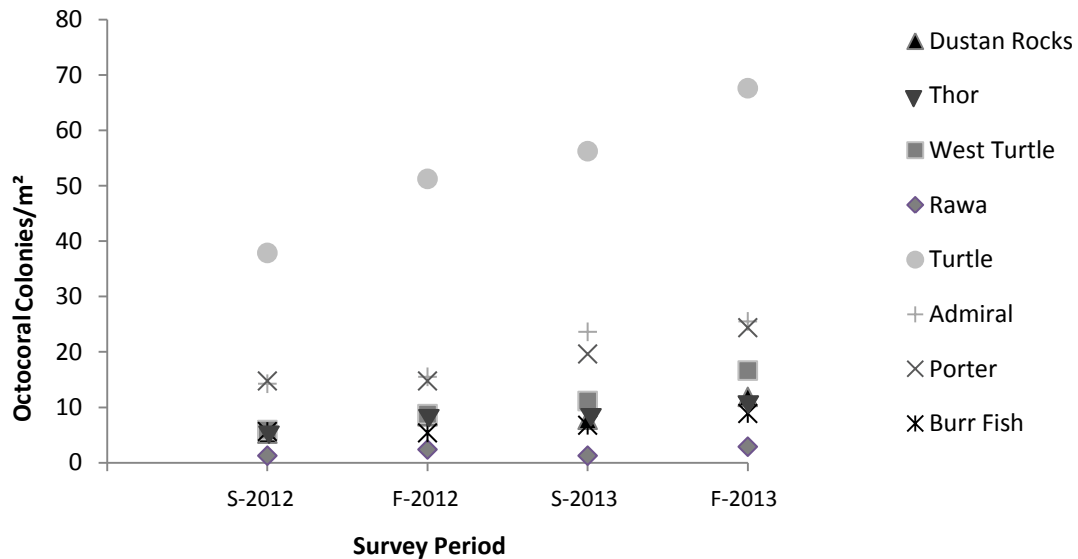


Figure 25. Scatter-plot of octocoral juvenile density (total colonies/m²) on each site over four surveys.

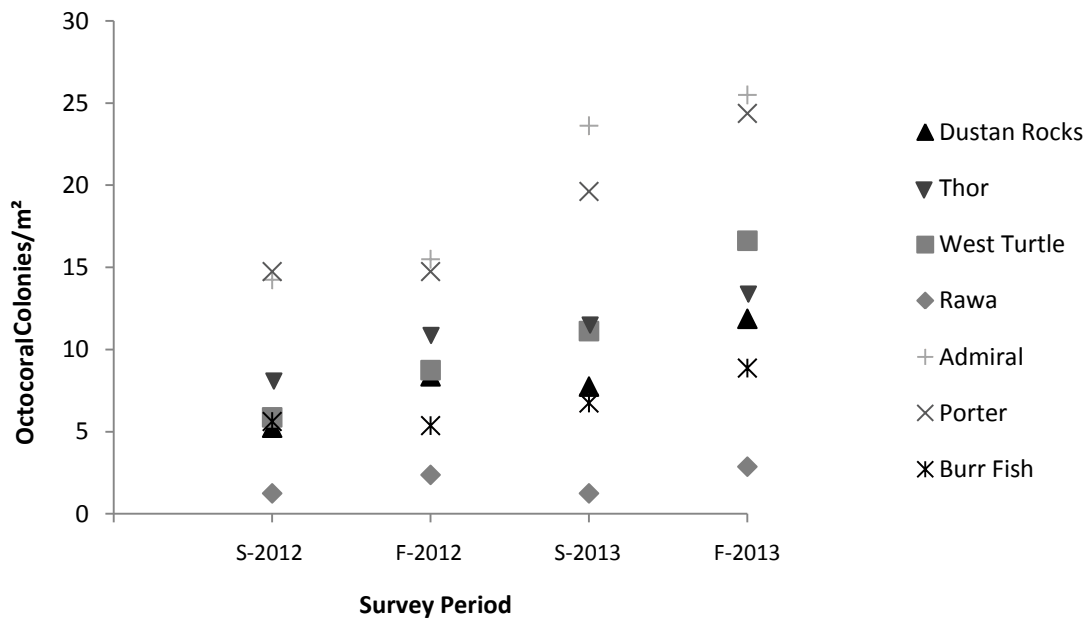


Figure 26. Scatter-plot of octocoral juvenile density (total colonies/m²) on each site (except Turtle) over four surveys.

For stony corals, there were no significant differences in juvenile abundance over time at any of the sites. Significant increases in octocoral abundance over time occurred at Turtle, Porter and West Turtle ($p=0.004$, 0.008 , 0.045 , respectively, Tables 15, 16, 17). A Tukey post-hoc test revealed that significant differences occurred exclusively between surveys 1 and 4 for Turtle and West Turtle (Tables 18, 19); however, at Porter significant differences also occurred between surveys 2 and 4 (Table 20).

Table 15. Kruskal-Wallis ANOVA results for Turtle showing a significant difference in octocoral abundance among survey periods (quadrats as replicates).

Turtle					
Survey	N	Missing	Median	25%	75%
1	32	0	8	5	13
2	32	0	12	8	18
3	32	0	11	9	20
4	32	0	17	10	21

H = 13.5 with 3 degrees of freedom. (**P = 0.004**)

Table 16. Kruskal-Wallis ANOVA results for Porter showing a significant difference in octocoral abundance among survey periods (quadrats as replicates).

Porter					
Survey	N	Missing	Median	25%	75%
1	32	0	4	1	6
2	32	0	3	2	5
3	32	0	5	3	7
4	32	0	6	4	9

H = 12.0 with 3 degrees of freedom. (**P = 0.008**)

Table 17. Kruskal-Wallis ANOVA results for West Turtle showing a significant difference in octocoral abundance among survey periods (quadrats as replicates).

West Turtle					
Survey	N	Missing	Median	25%	75%
1	32	0	1	0	2
2	32	0	1	1	3
3	32	0	1	1	5
4	32	0	4	1	5

H = 8.07 with 3 degrees of freedom. (**P = 0.045**)

Table 18. All Pairwise Multiple-Comparison Procedures (Tukey Test) results for Turtle showing the significant difference between surveys 1 and 4.

Turtle			
Comparison	Diff of Ranks	q	P<0.05
4 vs 1	1075	5.12	Yes
4 vs 2	486	2.32	No
4 vs 3	381	1.82	No
3 vs 1	694	3.31	No
3 vs 2	105	0.50	No
2 vs 1	589	2.81	No

Table 19. All Pairwise Multiple-Comparison Procedures (Tukey Test) results for Porter showing the significant difference between surveys 1 and 4 and between surveys 2 and 4.

Porter			
Comparison	Diff of Ranks	q	P<0.05
4 vs 2	880	4.19	Yes
4 vs 1	860	4.10	Yes
4 vs 3	435	2.07	No
3 vs 2	446	2.12	No
3 vs 1	425	2.03	No
1 vs 2	20.5	0.10	No

Table 20. All Pairwise Multiple-Comparison Procedures (Tukey Test) results for West Turtle showing the significant difference between surveys 1 and 4.

West Turtle			
Comparison	Diff of Ranks	q	P<0.05
4 vs 1	816	3.89	Yes
4 vs 2	452	2.15	No
4 vs 3	325	1.55	No
3 vs 1	492	2.34	No
3 vs 2	127	0.61	No
2 vs 1	365	1.74	No

Survival

Overall, with all sites and survey periods pooled, survival was higher for stony corals than for octocorals, with median survival of 78% and 64%, respectively ($p < 0.001$, Fig. 27). Octocoral survival was more variable (0-70%), while stony-coral survival had a much narrower range (40-85%) of variability.

Comparisons among sites revealed that juvenile octocoral survival was significantly higher on Porter than on Rawa ($p = 0.028$). Stony-coral juvenile survival was very similar among all sites ($p = 0.631$). The highest survival of both stony corals and octocorals occurred at Porter (Fig. 28). The lowest survival of octocorals occurred at Rawa, while the lowest survival of stony corals occurred at Admiral.

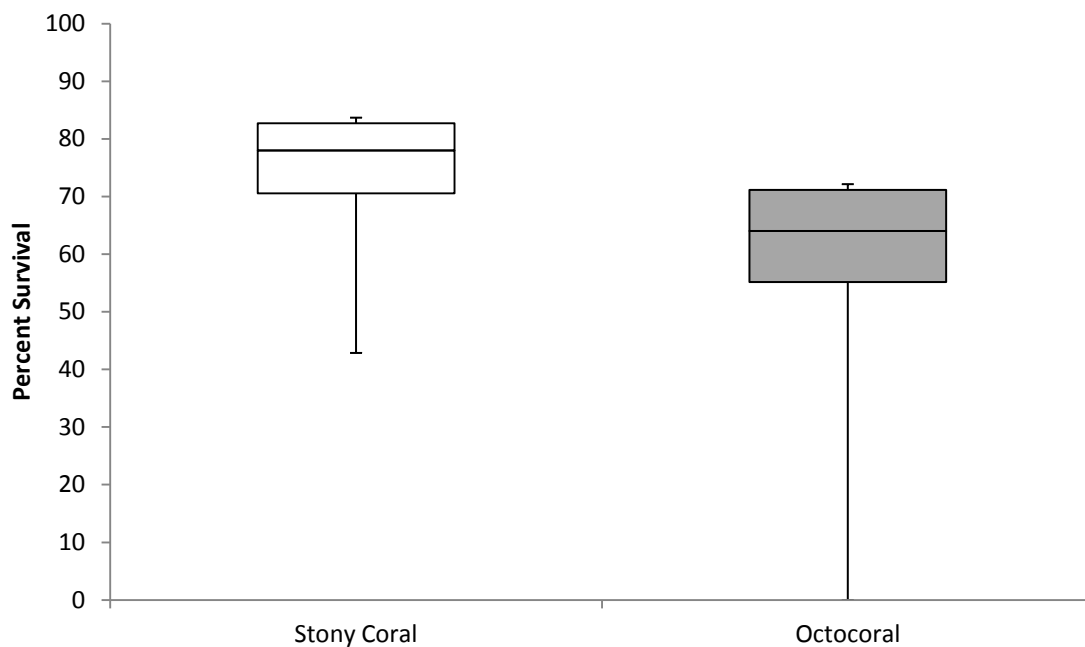


Figure 27. Overall percent survival was greater for stony corals than for octocorals ($p < 0.001$). Survival data were pooled for all survey periods and sites. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

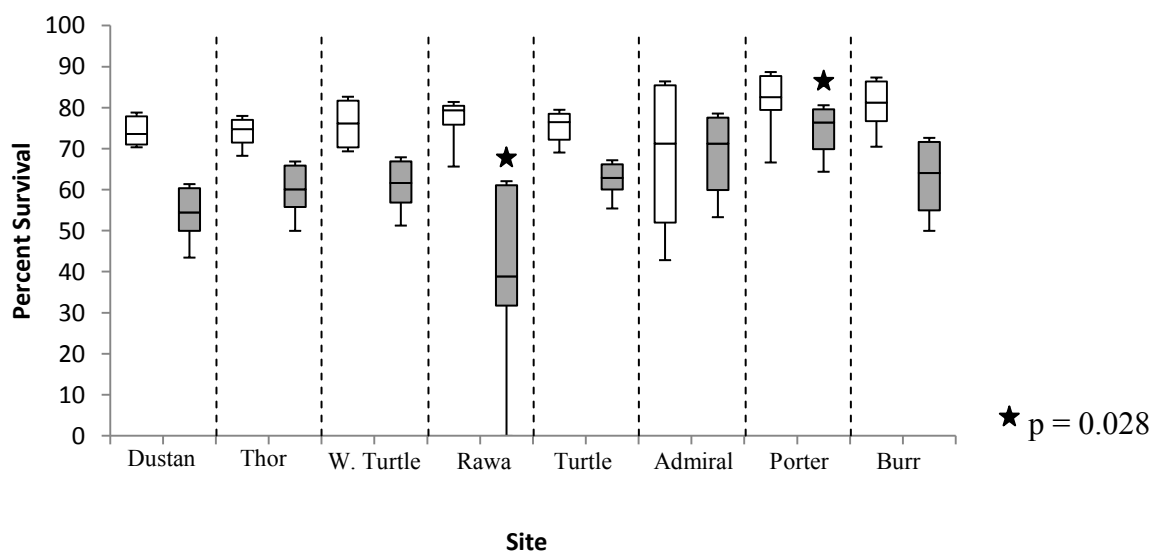


Figure 28. Boxplot of stony-coral and octocoral percent survival on each site (stations as replicates). Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values. White boxes are stony-coral survival and gray boxes are octocoral survival.

Octocoral survival varied significantly between survey periods 2 and 3 (Table 21, $p=0.003$). Median octocoral survival was highest for survey 2 (68%), dropped over 10 percent for survey 3 (55%), then rebounded for survey 4 (61%). Stony-coral survival showed a slight, though insignificant increase (Table 21, $p=0.191$) over survey periods 2-4 (76, 77 and 80%).

Table 21. Octocoral and stony-coral survival among survey periods (2-4). Stations as replicates.

<u>Octocorals</u>					<u>Stony Corals</u>				
Survey	N	Median	25%	75%	Survey	N	Median	25%	75%
2	16	68*	65	78	2	16	76	70	80
3	16	55*	50	64	3	16	77	70	85
4	16	61	57	73	4	16	80	75	85
H = 11.6 with 2 degrees of freedom. (*P = 0.003)					H = 3.31 with 2 degrees of freedom. (P = 0.191)				

The species of stony coral with the highest juvenile survival was *S. radians* with 100% median survival overall (Table 22). In general, stony-coral species had higher survival than octocoral genera, with the exception of the octocoral genus *Briareum* (92%). *Briareum* is different from many of the other octocoral species in that it is one of the few encrusting octocorals that grows in a mat along the substrate. Interestingly, the most abundant stony-coral species, *S. siderea*, also had the lowest survival out of all stony corals (65%, Fig. 29). This was also true for octocorals, as the species with the highest overall abundance, *Antillologorgia*, demonstrated the lowest survival (40%) overall.

Table 22. Median-percent survival by species/genera. All sites and surveys pooled (stations as replicates).

Taxa	N	Missing	Median	25%	75%
<i>S. radians</i>	47	19	100	61	100
<i>Briareum</i>	47	24	92	33	100
<i>M. cavernosa</i>	48	21	83	55	100
<i>S. intersepta</i>	48	17	79	67	100
<i>P. astreoides</i>	48	1	78	58	86
<i>P. porites</i>	45	20	67	50	82
<i>A. agaricites</i>	48	14	67	50	100
<i>S. siderea</i>	48	0	65	53	80
<i>Pseudoplexaura</i>	47	20	65	25	100
<i>Erythropodium</i>	48	7	56	30	90
<i>Gorgonia</i>	48	2	50	31	75
<i>Eunicea</i>	48	2	50	33	66
<i>Muriceopsis</i>	48	27	50	10	82
<i>Antillogorgia</i>	48	3	40	23	59

New Recruitment

New recruitment was compared over three survey periods (2-4) for both octocorals and stony corals. No significant differences were found between survey periods for either taxonomic group (Tables 23, 24). Octocorals showed a slight increase in the number of new recruits found over time, while stony corals showed a decrease in new recruitment during the third survey, then an increase during the fourth survey. Comparison of new recruitment between octocorals and stony corals was done with all sites and survey periods pooled, for each taxonomic group. While no significant difference was found between the raw numbers of new recruits, the proportional data showed a significant relationship, with higher percentage of the octocoral-juvenile assemblage comprised of new recruits ($p < 0.001$, Fig. 30). Nearly 50% of the octocoral juveniles recorded were new recruits, whereas only 30% of the stony-coral juveniles were new recruits.

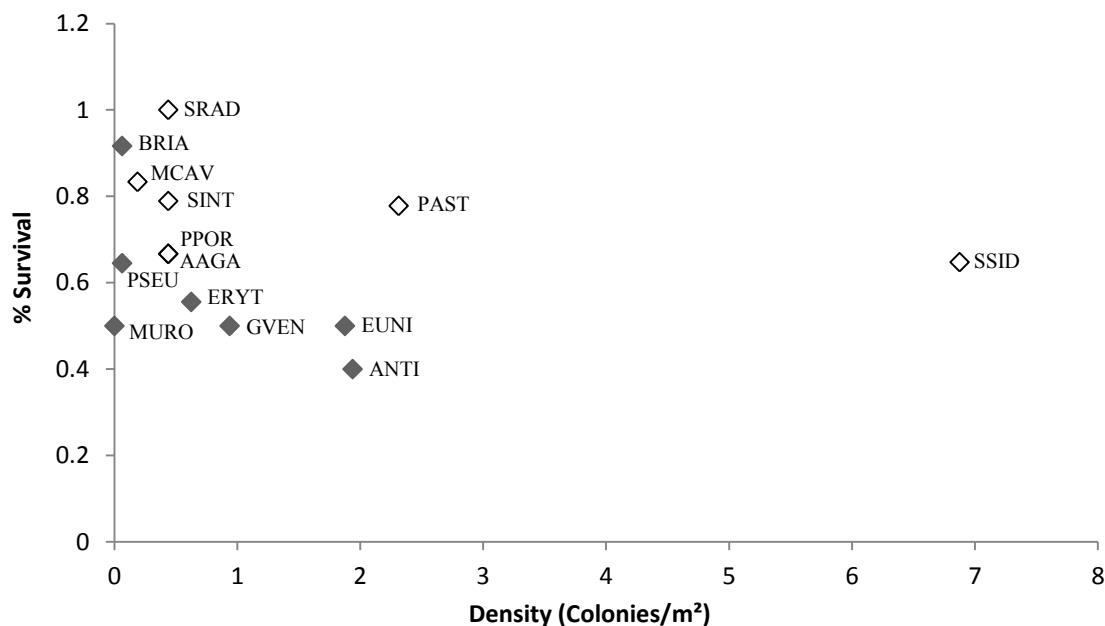


Figure 29. Scatter-plot of median juvenile density and % survival for each of the seven stony-coral species and seven octocoral genera (see Appendix I for species/genera codes). White markers are stony corals and gray markers are octocorals.

Table 23. Stony-coral median recruitment for each survey period (except survey 1). In parentheses next to median values are the percentages of the total stony-coral juvenile assemblage.

Survey	N	Missing	Median	25%	75%
2	16	0	19 (35%)	10	32
3	16	0	13 (28%)	8	24
4	16	0	20 (28%)	9	29

H = 0.638 with 2 degrees of freedom. (P = 0.727)

Table 24. Octocoral median recruitment for each survey period (except survey 1). In parentheses next to median values are the percentages of the total octocoral juvenile assemblage.

Survey	N	Missing	Median	25%	75%
2	16	0	16 (48%)	10	23
3	16	0	22 (47%)	14	54
4	16	0	29 (50%)	17	47

H = 3.59 with 2 degrees of freedom. (P = 0.166)

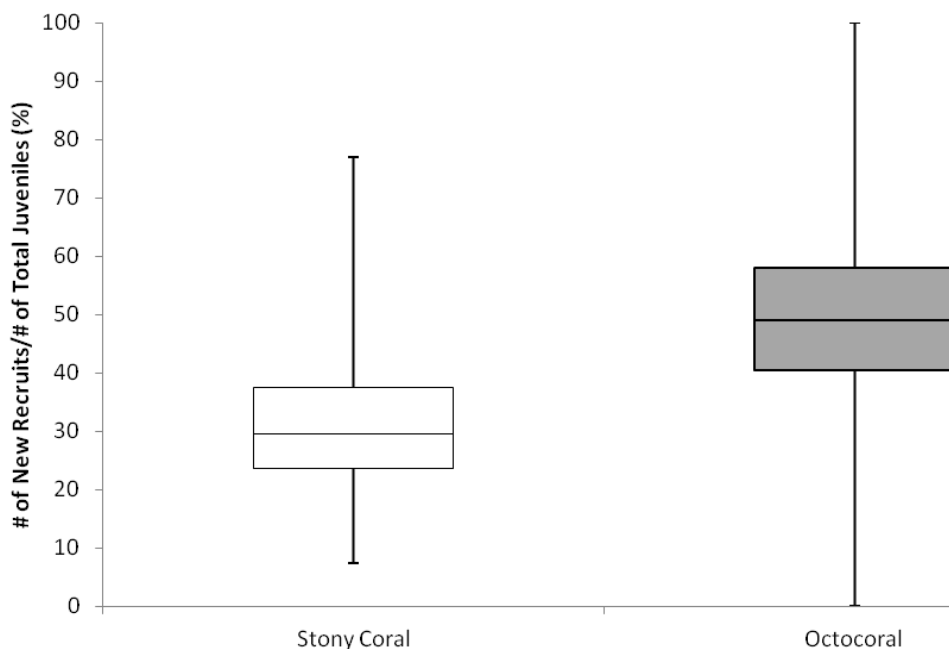


Figure 30. Percent recruitment for stony corals and octocorals ($p < 0.001$). Data pooled for all sites and survey periods. Box center-lines represent medians, box ends are first and third quartiles, whiskers are minimum and maximum values.

Recruitment data showed that some of the octocoral and stony-coral taxa with the lowest survival also demonstrated high recruitment. Recall that for this study, recruitment represents the proportion of new recruits relative to total recruits for a particular taxon. *Antilloporgia* had the highest recruitment (60%), with over half of its population comprised of new recruits (Table 25). Overall, octocorals had higher recruitment than stony corals. Of the stony corals, *Siderastrea siderea* (35%), *P. porites* (33%) and *A. agaricites* (33%) demonstrated the highest recruitment.

Table 25. Median-percent recruitment by taxa. All sites and survey periods pooled (stations as replicates).

Taxa	N	Missing	Median	25%	75%
<i>Antillogorgia</i>	48	3	60	42	77
<i>Eunicea</i>	48	2	50	35	67
<i>Muriceopsis</i>	48	27	50	15	80
<i>Gorgonia</i>	48	2	45	25	69
<i>Erythropodium</i>	48	7	44	18	68
<i>Pseudoplexaura</i>	47	20	36	0	73
<i>S. siderea</i>	48	0	35	20	46
<i>P. porites</i>	45	20	33	19	43
<i>A. agaricites</i>	48	14	33	0	50
<i>Briareum</i>	47	24	25	0	63
<i>P. astreoides</i>	48	1	23	14	41
<i>S. intersepta</i>	48	17	22	0	33
<i>M. cavernosa</i>	48	21	14	0	45
<i>S. radians</i>	47	19	0	0	35

DISCUSSION

JUVENILE ASSEMBLAGE TRENDS

Stony-Coral and Octocoral Abundance

Overall juvenile abundance was similar between stony corals and octocorals with all sites and survey periods pooled. However, abundance differed between site mortality-classification groups and more specifically in site-to-site comparisons. Low-mortality sites displayed higher abundance of both stony-coral and octocoral juveniles than the high-mortality sites. Therefore, results fail to support the hypothesis that newly available substrate on high-mortality sites would facilitate recruitment.

An alternative hypothesis suggests that the presence of healthy adult colonies may be an important driver for coral recruitment. Low mortality sites did not experience severe and sudden loss of coral cover and hence, corals existing there had less partial mortality (Colella et al. 2012), which may have facilitated recruitment. One possible method by which healthy adult coral communities might attract recruits is through chemical signaling. It has been documented that reef invertebrates, such as adult communities of barnacles, can attract larvae by releasing chemical settlement cues into the water column (Hay 2009). Coral larvae are thought to actively select suitable substrate for settlement (Fadlallah 1983). Chemical signaling has been found to be an important driver of coral larval settlement and metamorphosis (Morse and Morse 1996,

Ritson-Williams et al. 2009). Biofilms associated with crustose coralline algae (CCA) produce chemical signals that promote settlement and induce metamorphosis of coral larvae (Morse et al. 1996, Heyward and Negri 1999, Webster et al. 2004). Adult coral colonies may produce similar chemicals that signal coral larvae to settle. Macroalgae and cyanobacteria have also been found to chemically inhibit settlement of corals (Kuffner et al. 2006).

A second method by which a healthy adult coral population may attract recruits is through self-seeding by means of asexual reproduction or internally brooding planulae. A disturbed community may lack the healthy adult colonies to accomplish self-seeding. Past studies have shown that self-seeding by means of brooding is a dominant method of reproduction in the Florida Reef Tract (Chiappone and Sullivan 1996). Multidimensional scaling (MDS) results showed that adult and juvenile assemblages grouped closely to each other on certain sites and more loosely on others, indicating that self-seeding may be an important reproductive strategy in some areas.

However, MDS results showed no pattern indicating that site-mortality classification influenced site clustering. This may be due to the fact that stony-coral cover was very similar on high and low-mortality sites following the disturbance event. In fact, CREMP data show that high-mortality sites had higher coral cover than low-mortality sites before the cold-water event. The mortality event eliminated cold-sensitive species of stony coral such as *Orbicella* spp. from high-mortality sites, while they were already lacking on low-mortality sites (Colella et al. 2012).

A closer look at differences in abundance among sites showed that mortality classification was not necessarily the most appropriate way to group sites. While juvenile abundance varied greatly by site, a pattern was apparent. There was a slight inverse relationship

between octocoral and stony-coral abundance. Sites with high octocoral abundance tended to have low stony-coral abundance and vice versa. A regional pattern was observed, in which abundance of juvenile stony-corals was greatest in the Middle Keys, while abundance of juvenile octocorals was greatest in the Upper Keys.

The regional pattern observed between octocoral and stony-coral abundance was apparent in the cluster, MDS and Simper results. The Middle-Keys sites and the southernmost Upper-Keys site, Burr, all grouped together. Within this cluster, sites were dominated by the stony coral *S. siderea*. The northernmost site, Turtle, formed its own group, while Admiral and Porter grouped together. Each of the three northernmost sites, Turtle, Admiral and Porter, were dominated by octocorals of three distinct genera (*Antillogorgia*, *Gorgonia* and *Eunicea*, respectively). The site clustering shows a distinct regional pattern with one exception, Burr Patch. Burr Patch did not fit the regional pattern, as it was dominated by *S. siderea*, more similarly to Middle Keys sites than Upper Keys sites. Regional/latitudinal trends have been observed in past studies on the Florida Reef Tract (Miller et al. 2000, Moulding 2005), where density of juvenile stony corals increased in a south-westerly direction down the reef tract.

There are certain environmental factors that differ between the Middle- and Upper-Keys regions that could be driving this pattern. Middle-Keys patch reefs lie close to tidal connections with Florida Bay and, hence, experience higher turbidity levels, more temperature and salinity fluctuations and higher inputs of terrigenous materials (Ginsburg and Shinn 1964, Montague and Ley 1993). Connections to Florida Bay become less frequent moving toward the Upper-Keys region. The last large connection to the bay lies near Upper Matecumbe Key. Burr Patch is the southernmost Upper-Keys site in this study, occurring just west of Plantation Key (Fig. 6) and is

the closest of all Upper-Keys sites to tidal connections. Burr Patch was categorized as a high-mortality site, experiencing heavy stony-coral cover loss from the 2010 cold-water event. Its location and relative proximity to the northernmost connection to Florida Bay may explain the similarity in juvenile assemblage to Middle-Keys sites. The regional trend in site clustering is a strong indication that juvenile abundance was not influenced by stony-coral cover loss, but by regional trends in hydrodynamics.

Species Composition

Middle-keys sites and Burr Patch were dominated by *S. siderea*, which was also the most abundant stony-coral species observed overall (46%). It was the most dominant stony coral at every site for almost every survey (61 out of 64 times) throughout the study. *Siderastrea siderea* dominated the juvenile assemblage in a previous in-situ coral recruitment study in the area as well (Smith et al. 2008). This massive coral species reproduces via broadcast spawning and is quite hardy, able to survive under a wide range of temperature fluctuations (Colella et al. 2012).

Siderastrea siderea has the ability to stay at very small sizes for many years, stunting its growth in a sense through fission, in which discontinuous coral tissue results in physiological separation of part of the colony (Elahi and Edmunds 2007). In other coral species (*A. agaricites*, *O. annularis*) partial mortality, fission and fusion are methods that confound any simple relationship between size and age (Hughes and Jackson 1980). The abundance of *S. siderea* in this study may represent some older colonies that have undergone fission and remained <4 cm. *Siderastrea siderea* colonies are not reproductively viable until reaching 100 cm² surface area (Soong 1993); however, it is unclear whether small, older colonies, that were once larger, are able to reproduce. Nonetheless, the ability to withstand temperature fluctuations and the

tendency to remain in a smaller size class for a longer period of time are most likely responsible for the abundance of *S. siderea* in this study.

The second most common stony-coral juvenile overall was *P. astreoides* (19%), a small brooder, that can reach reproductive maturity at 70 cm² (Soong 1993). *Porites astreoides* is sensitive to temperature fluctuations (Mayor 1914, Colella et al. 2012), but is also known to be a very fecund and weedy (Bak and Engel 1979, Chornesky and Peters 1987) coral species, able to come in quickly and colonize space following disturbance.

The overall juvenile assemblage was essentially devoid of *Orbicella* spp. The few small *Orbicella* colonies found were most likely remnant tissue isolates of older, larger colonies with partial mortality. Previous studies have documented very little *Orbicella* spp. recruitment on the Florida Reef Tract (Miller et al. 2000, Moulding 2005). The breeding method and life history characteristics of *Orbicella* spp. do not support high recruitment rates, but instead high survival rates of settled juveniles (Szmant 1986, Moulding 2005). *Orbicella* spp. can be described as a climax or late-successional species that may take longer to recover following disturbance, but should eventually gain dominance if disturbances are infrequent (Hutchinson 1953, Horn 1974, Hudson 1981).

If disturbances are frequent, however, early-successional, opportunistic species will maintain dominance. Opportunistic or fugitive species have been described by Grassle and Grassle (1974) as having wide abiotic-tolerance ranges, fast growth rates and the ability to colonize a disturbed area quickly. Both *S. siderea* and *P. astreoides* have certain characteristics that define them as opportunistic. *Siderastrea siderea* can tolerate a wide range of temperature and environmental fluctuations, but is a slow-growing, massive broadcast spawner. In this study,

the high tolerance for environmental fluctuations clearly outweighs the slow growth and reproductive mode of *S. siderea*, to make it the most abundant stony-coral juvenile on patch-reef sites. *Porites astreoides* is a smaller, brooding species that reaches maturity sooner, but has a low tolerance for temperature fluctuations. Even though *P. astreoides* is one of the first species to be influenced during a cold-water disturbance, it is also quick to recover (Green et al. 2008).

Octocorals in general are intolerant of fluctuations in environmental conditions outside their normal range (Bayer 1981, Prada et al. 2010, Colella et al. 2012). However, octocorals are also fast-growing, opportunistic organisms, which are able to quickly colonize newly available substrate. Hence, one would expect to have higher abundances of octocoral juveniles on recently disturbed patch reefs than on undisturbed patch reefs. Results did not support this expectation. Octocoral juvenile abundance instead followed the regional pattern described above, in which stony corals dominated the Middle-Keys sites and octocorals dominated the Upper-Keys sites.

Why was juvenile species composition not influenced by site-mortality classification? In terrestrial plant ecology, when disturbance events are frequent, an ecosystem may stay in a non-equilibrium state, in which a mixed community of strong competitors (known as climax or late successional species) and opportunistic species are intermingled (Hutchinson 1953, Horn 1974). I propose that the combined influence of chronic and acute stressors may be holding patch-reef sites in a state of perpetual disturbance, preventing succession of species composition from proceeding. Certain stressors, including temperature and salinity fluctuations, are inherent to patch reefs of the Florida Reef Tract as they exist closer to land than other reef types. Other stressors caused by humans, such as pollution, fishing, boating and sewage runoff, may have a greater impact on patch reefs due to their proximity to land. The combined effect of

anthropogenic and natural stressors can have devastating effects (Hughes et al. 2007). More research needs to be done to identify specific anthropogenic stressors and determine how they influence this area so that they can be managed and reduced. If multiple stressors are in fact holding patch reefs in perpetual disturbance, comparisons between sites impacted by the cold-water event and those un-impacted may not be appropriate, since all of the sites in this study are in a state of frequent disturbance.

Size Distribution

The size distributions of both stony corals and octocorals were dominated by smaller colonies (0-30 mm), with fewer juveniles in the largest size class (31-40 mm). This may have been a function of the limited duration of the study. Juveniles that recruited to study sites after the disturbance event may not have had sufficient time to grow and reach the largest juvenile size class. If this was the case, results would show this pattern for high-mortality sites, but not for low-mortality sites. However, the decrease in juvenile abundance at the 31-40 mm size class was present in both mortality-classification groups, though more dramatically on the high-mortality sites. Additionally, one would expect this pattern to be absent for octocorals, since octocorals are faster growing and would have had sufficient time to reach the 31-40 mm size class. However again, this is not the case, as results show a decrease in abundance for both stony corals and octocorals in the largest size class. The only deviation from this pattern was observed on high-mortality sites, where octocoral sizes were quite evenly distributed among size classes and abundance was lower than on low-mortality sites in every size class.

Another more likely explanation for the size-class trend is that ecosystem pressures caused mortality before juveniles could reach the largest size class (Hughes 1984). If this is the

case, the decrease in abundance in the largest size class would be seen on all sites, and for both stony corals and octocorals, which is what the data showed. In a natural community, organism size is often inversely related to frequency within a population (Ogden 1970). The oldest, largest individuals are also often the fewest in number, having undergone numerous competitive and predatory interactions over many years. The apparent decrease in abundance in the largest juvenile size class may be a function of this overarching ecological rule and nothing more. In addition, certain corals have been found to remain in a smaller size class by means of partial mortality, fragmentation and fission (Hughes and Jackson 1980).

Although it is unclear what caused the drop in abundance in the largest juvenile size class, results demonstrate the importance of future investigation into post-settlement survival of juvenile corals.

FATE-TRACKING TEMPORAL TRENDS

Abundance

Temporal results showed an increase in both octocoral and stony-coral abundance throughout the two-year study (all sites pooled). Significant increase in abundance was observed between the first survey (spring of 2012) and the last survey (fall 2013), for both stony corals ($p=0.019$) and octocoral ($p<0.001$); however, the significance level was much higher for octocorals. Observer error may have influenced the magnitude of the recorded increase in abundance over time, as surveyors undoubtedly improved their ability to locate juveniles over the course of the study. Even so, there was an obvious and highly significant increase in abundance of juvenile octocorals between the first and last surveys.

A closer look at temporal abundance among sites revealed that stony-coral abundance was relatively stable on most sites, whereas octocoral abundance increased over time on the majority of study sites, with significant increases on three sites, Turtle, Porter and West Turtle. The observed increase in abundance was not influenced by site mortality classification. Octocoral juveniles increased in abundance much more rapidly than stony corals. Hence, temporal results support the hypothesis that octocoral juveniles are better suited to quickly take advantage of available space than stony corals. The fact that CREMP data show decadal trends of increasing octocoral cover throughout the Florida Reef Tract supports this finding. Environmental conditions may be either promoting success of fast-growing, fast-recruiting organisms and/or inhibiting establishment of late-successional organisms in both the juvenile and adult life stages.

Turtle and Porter, the two sites that displayed significant increases in octocoral abundance over time ($p < 0.001$), also displayed the highest octocoral abundance overall. An anomalously high density of octocorals (50 colonies/m²) was recorded at Turtle Patch, over double the density on any other site. Turtle Patch is the northernmost site in the study and most geographically separate from the other sites. The unique latitudinal position of Turtle Patch may have contributed to its impressive abundance of juvenile octocorals. More research is needed in this region to evaluate assemblage trends in juvenile octocorals and to test environmental parameters for possible distinctions from other areas of the reef tract.

Survival and New Recruitment

Overall, stony corals demonstrated higher survival than octocorals. Octocoral survival ranged from 0-70% while stony-coral survival ranged from 40-85%. Octocoral survival

demonstrated more volatility over time, with a significant drop in survival between the second (fall 2012) and third (spring 2013) survey periods (68 to 55%), then rebounding somewhat by the fourth (fall 2013) survey period (61%). The decreased survival observed for the spring 2013 survey, relative to the fall surveys, indicates the possibility of reduced survival in winter months. Stony-coral survival was more stable over time, with a slight increase in survival over the three survey periods (76, 77 and 80%).

Overall, a higher percentage of the assemblage of juvenile octocorals was made up of new recruits than for stony corals. Nearly 50% of all octocoral juveniles were classified as new recruits, whereas only 30% of stony-coral juveniles were classified as new recruits. New recruitment did not differ over time for either taxonomic group. Results support the idea that octocorals are faster growing and more opportunistic than stony corals in general (Sorokin 1991), octocorals showing more volatility, lower survival and higher recruitment overall.

The taxa with the highest abundances also tended to have lower survival and higher recruitment than other species. *Siderastrea siderea*, the species with the highest abundance overall (46% of total stony-coral species composition), had the lowest survival (65%), and highest recruitment (35% classified as new recruits) of the seven stony-coral species that were commonly encountered. *Antillogorgia*, the octocoral genus with the highest abundance demonstrated the lowest survival overall (40%) and the highest recruitment overall (60% classified as new recruits). Select stony corals that demonstrated some of the lowest survival and highest recruitment, *P. astreoides*, and *A. agaricites*, were also the top contributors to stony-coral juvenile abundance overall. This trend supports the idea that the most abundant taxa were also the most opportunistic.

Opportunistic organisms tend to have faster growth rates, more efficient reproduction/recruitment, and lower survival rates. Out of the top seven stony-coral species, three were broadcast spawning species, *M. cavernosa*, *S. intercepta* and *S. siderea*, while the remaining four species were brooders, *P. astreoides*, *P. porites*, *A. agaricites* and *S. radians*. Often species that reproduce via brooded planulae have opportunistic life history characteristics, as brooding facilitates faster settlement (Szmant 1986) and limits the risk of mortality associated with longer dispersal time. Unlike broadcast spawners that only reproduce once a year, brooders reproduce multiple times per year and when brooded larvae are released, the fertilization process has already been completed within the parent colony; hence larvae are larger and able to settle immediately. The taxa with the highest abundance and recruitment in the juvenile assemblage also demonstrated the lowest survival and vice versa.

Opportunistic organisms are populating patch-reef sites, whereas slower growing, massive stony-coral species are declining. For example, *M. cavernosa* demonstrated the third highest survival (83%), and the lowest recruitment (14% classified as new recruits) overall, though it made up only 3.7% of the total stony-coral juvenile assemblage. The taxa that reproduce via brooding were more successful at recruiting to patch-reef sites. This trend has been apparent in adult assemblages throughout the Florida Reef Tract and Caribbean for several decades; slow-growing, massive, broadcast spawning species are declining (Hudson et al. 1994), while smaller, fast-growing, brooding species are increasing (Dustan and Halas 1987). *Siderastrea siderea* is a major exception to this trend; nonetheless, its high tolerance for environmental fluctuations and ability to reproduce asexually through fission gives this hardy species its distinct advantage in marginal reef environments.

THE FATE OF FLORIDA PATCH REEFS

Patch-reef sites are the closest reef environment to land and to Florida Bay; hence, they experienced the coldest water temperatures during the 2010 cold-water event. Species composition on a particular reef was a major factor in determining the mortality suffered on that reef. Species such as *Orbicella* spp. are very sensitive to temperature fluctuations (Mayor 1914, Voss 1973, Roberts et al. 1982), whereas other species such as *S. siderea* are very hardy and can thrive in a wide range of sea-surface temperatures (Mayor 1914, Colella et al. 2012). Admiral Patch suffered the highest overall mortality, because it was a nearly monotypic *Orbicella* spp. stand before the 2010 cold-water event killed almost 100% of its stony-coral assemblage. The lack of species diversity and limited number of cold-tolerant species present on this site exacerbated the disturbance impacts. Patch-reef sites that suffered the highest mortality also had higher stony-coral cover to begin with than the low-mortality sites. The majority of the “excess” stony-coral cover seen on the high mortality sites before the disturbance was comprised of *Orbicella* spp. and other cold-intolerant species (Colella et al. 2012).

The future of patch reefs may mirror the species composition on reefs that experienced very little impact from the cold water. The question is, will the future of Florida reefs be dominated by opportunistic, weedy organisms, or will the specialized, slow-growing, slow-reproducing organisms, with higher survival rates, eventually regain dominance?

Terrestrial ecologists have consistently documented that, following a disturbance event, there is a succession to re-colonization of an area (Horn 1974, Glitzenstein et al. 1986).

Succession, or secondary succession, is a process by which the most opportunistic organisms colonize an area quickly following disturbance and the more specialized organisms often take longer, but eventually gain dominance of that environment (Sousa 1979). When a reef environment is plagued with chronic stressors, such as terrestrial runoff, overfishing, high temperature fluctuations and turbidity, the succession process may be inhibited, as is described by Connell's Intermediate Disturbance Hypothesis (Connell 1978). Succession may only progress when there is enough time between disturbance events. Numerous stressors now influencing the Florida Reef Tract, especially patch reefs, may be keeping the reefs in a perpetually disturbed state, not allowing succession to progress. If this is the case, two types of organisms may thrive: opportunistic species, which settle and grow quickly, and hardy species, which are better equipped to handle disturbance in the presence of existing chronic stressors.

It appears as though succession has stalled on the Florida Reef Tract, with increasing octocoral cover concurrent with declining stony-coral cover. This study is far too short-term to truly describe the succession that may or may not occur on the patch reef-sites in the future; however, it has provided valuable information on the juvenile stony-coral and octocoral assemblages on these sites. It is important to conservation efforts to understand which species are best able to survive disturbance events, as well as which species are most capable of taking advantage of open substrate created by such mortality events.

CONCLUSIONS

Patch reefs have been identified as resilient to chronic stressors occurring naturally and caused by human influence. Before the 2010 cold-water event, the highest coral cover, highest growth rates and lowest incidences of partial mortality on the reef tract were found on patch reefs (Lirman and Fong 2007). Patch reefs are essential to the Florida Reef Tract. As the most numerous type of reef, they may act as a source of larvae to seed the offshore bank reefs, as well as to serve the local and national economies as popular fishing and snorkeling areas. It is imperative to gain a better understanding of the reproduction and recruitment processes on these reefs, as these processes are critical to the persistence of coral reefs in the future.

The results of this study point toward one of two future outlooks for the reef. One being that species succession will continue very slowly over many years, if disturbance is infrequent. In this scenario, the results of this study represent the beginning of the succession process, in which opportunistic, faster-recruiting and faster-growing organisms are most abundant. In the future, populations of the slow-growing, massive broadcast-spawning species may eventually recover and increase in abundance. This may prove be a very slow process, which is further inhibited in the Florida Reef Tract by numerous stressors.

A second, alternative explanation for the results is that the process of biotic homogenization is occurring on these patch reef sites and throughout the keys (Dustan and Halas 1987). Biotic homogenization is the process by which an environment becomes dominated by a

few species that either are able to withstand disturbance in the face of chronic stressors, or are fugitive and able to recover quickly following disturbance. Biotic homogenization has been observed in many ecosystems throughout the world and occurs as a outcome of human manipulation and influence on the environment (McKinney and Lockwood 1999). In Florida, the overall shift in community structure to an octocoral-dominated state (Ruzicka et al. 2013), as well as the short-term dynamics of recovering assemblages outlined in this study, support this prediction. Though octocorals suffered as much mortality as stony corals following the cold-water-disturbance event, they have the ability to re-colonize disturbed areas faster than stony corals. Certain species of stony corals, such as *S. siderea*, were resilient to cold-water, whereas other species were very sensitive to temperature fluctuations (*P. astreoides*), but were able to recover more quickly following disturbance.

With human population on the rise and environmental impact increasing with every passing year, ecosystems around the world are changing, the species making up those ecosystems are either declining or adapting. Perhaps the massive, broadcast-spawning species of coral like *Orbicella* spp. are quickly becoming a thing of the past in the Florida Keys. Corals that once were dominant on the Florida Reef Tract are being replaced by smaller, faster-growing, opportunistic “winners” (McKinney and Lockwood 1999).

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APPENDICES

APPENDIX A. STONY CORAL SPECIES CODES, REPRODUCTIVE METHODS AND GROWTH RATES.

Stony Coral Species	Code	Reproduction Method	References	Growth Rates (mm/yr)	References
<i>Siderastrea siderea</i>	SSID	broadcast spawner	Fadlallah 1983	1.0-4.6	Elahi et al. 2007; Hubbard & Scaturo 1985
<i>Porites astreoides</i>	PAST	internal brood	Fadlallah 1983; Vaughan 1910	1.9-3.5	Gladfelter et al. 1978; Hubbard & Scaturo 1985
<i>Stephanocoenia intercepta</i>	SMIC	broadcast spawner	Lueg et al. 2012	1.5-2.1	Hubbard & Scaturo 1985
<i>Porites porites</i>	PPOR	internal brood	Goreau et al. 1981	36.0	Lewis et al. 1968
<i>Montastrea cavernosa</i>	MCAV	broadcast spawner	Szmant 1991	2.0-11.0	Huston 1985; Hubbard & Scaturo 1985
<i>Agaricia agaricites</i>	AAGA	internal brood	Fadlallah 1983	0.8-2.7	Huston 1985; Edmunds 2007
<i>Siderastrea radians</i>	SRAD	internal brood	Fadlallah 1983	1.3-2.1	Edmunds 2007

APPENDIX B. OCTOCORAL GENERA CODES, REPRODUCTIVE METHODS AND GROWTH RATES.

Octocoral Genera	Code	Reproductive Method	References	Growth Rates (cm/yr)	References
Antillogorgia	ANTI				
<i>Antillogorgia americana</i>	-	broadcast spawner	Fitzsimmons-Sosa et al. 2004; Yoshioka 1979		
<i>Antillogorgia acerosa</i>	-	broadcast spawner	Yoshioka 1979	4.0-6.9	Yoshioka 1979
Gorgonia	GORG				
<i>Gorgonia ventalina</i>	-	broadcast spawner	Fitzsimmons-Sosa et al. 2004	7.0-37.4	Cary 1914
Eunicea	EUNI				
<i>Eunicea flexuosa</i>	-	broadcast spawner	Beiring & Lasker 2000; Fitzsimmons-Sosa et al. 2004	2.2-26.9	Yoshioka & Yoshioka 1991; Cary 1914
Erythropodium	ERYT				
<i>Erythropodium caribaeorum</i>	-	broadcast spawner	Lindquist & Hay 1996		
Pseudoplexaura	PSEU				Brazeau & Lasker 1992
<i>Pseudoplexaura porosa</i>	-	broadcast spawner	Kapela & Lasker 1999; Lasker et al. 1996		
Briareum	BRIA				
<i>Briareum asbestinum</i>	-	surface brooder	Brazeau & Lasker 1990	16.6	Brazeau & Lasker 1990
Muriceopsis	MUR O				
<i>Muriceopsis flavida</i>	-	broadcast spawner	Fitzsimmons-Sosa et al. 2004		

APPENDIX C. SITE CHARACTERISTICS AND COVER VALUES.

Site	Region	Mortality Classification	Depth (m)	2012 CREMP % Cover						
				Cyanobacteria	Macroalgae	Octocoral	Stony coral	Porifera	Zoanthidea	Substrate
Dustan Rocks	Middle	High	6.1	1	10	6	2	1	0	80
Rawa	Middle	High	6.4	1	44	4	7	1	0	42
West Turtle	Middle	Low	7.0	0	16	15	12	2	1	54
Thor	Middle	Low	6.1	1	14	14	4	3	0	63
Admiral	Upper	High	1.5	1	18	5	13	1	5	58
Burr Fish	Upper	High	4.9	1	2	14	17	8	9	48
Porter	Upper	Low	4.6	3	14	40	9	3	0	30
Turtle	Upper	Low	4.9	0	4	16	15	10	4	48

APPENDIX D. SITE PHOTOS.

