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Population dynamics of the threatened staghorn coral, Acropora cervicornis, and the development of a species-specific monitoring protocol

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NOVA SOUTHEASTERN UNIVERSITY HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

POPULATION DYNAMICS OF THE THREATENED STAGHORN CORAL, *ACROPORA CERVICORNIS*, AND THE DEVELOPMENT OF A SPECIES-SPECIFIC MONITORING PROTOCOL

By

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Abstract

Historically, *Acropora cervicornis* was found in high densities on many Caribbean, Florida, and Gulf of Mexico reefs. A disease outbreak in the late 1970s and 80s caused up to 99% loss of *A. cervicornis* cover at some sites, leaving populations sparsely distributed throughout its range and typically found as isolated colonies. Even though populations are depauperate causing a decrease in sexual reproduction, its fast growth rate and ability to reproduce through asexual fragmentation affords this species the potential for quick recovery and population growth. However, limited to no natural recovery has been documented. Many of these populations are poorly studied because most monitoring programs are not designed to capture *A. cervicornis'* unique life history characteristics. Its patchy distribution, complex growth form, frequent fragmentation, and dislodgment present a challenge for long term tracking. Furthermore, its ability to exist from small isolated colonies to semi-continuous patches spanning hectares makes defining individuals to assess abundance, survival, health, and growth a difficult task. The aim of this dissertation was to develop a species-specific monitoring protocol to describe the abundance and cover of *A. cervicornis* and the effects of disease, predation, and disturbance events across space and time. The monitoring protocol was developed and used across three sub-regions of the Florida Reef Tract (Broward County, Middle Keys, and Dry Tortugas). Several permanent 3.5 m radial plots were installed across multiple sites in each sub-region. A species census, percent cover, and demographic data of a sub-set of colonies were collected three times per year (winter, summer, and fall) from 2008-2016. These results were then used to assist in designing and testing optimal outplant strategies. Outplanting occurred at seven sites in Broward County, FL between 2012- 2015. Experiments were designed to assess the effects outplant colony density, host genotype, colony size, and attachment technique had on colony survival, growth, and health. The monitoring protocol was successfully used for identifying spatial and temporal patterns and trends in cover, disease, and predation on *A. cervicornis* across a range of population sizes. Percent cover of living *A. cervicornis* declined significantly during the duration of the project. Disease prevalence and occurrence was highest during the summer. Colony size and volume increased with depth and were the largest in the

Broward County sub-region. Disease caused the most mortality, however fireworms were the most prevalent cause of recent mortality. Disease and predation were more prevalent on masses (individuals larger than 1.5 m in diameter). The outplant experiments showed that colony survival and health were greatest when colonies had greater than 15 cm in total tissue and in densities less than 1 col/m^2. Host genotype and outplant site had variable effects on survival and growth. Outplanted colonies quickly acclimated to their environment and increased colony abundance within sites by fragmentation. Prevalence of disease and predation were lower on outplanted colonies than wild colonies. Frequent disturbances such as tropical storms, hurricanes, and disease events caused increased, prolonged, and widespread mortality and fragmentation, however periods void of disturbances resulted in recovery and growth. Therefore, reducing the effects of climate change and determining and decreasing the causes of disease could promote species recovery. In the meantime, population enhancement by outplanting is a viable way to assist species conservation and recovery.

Keywords: Coral Recovery, Species Specific Monitoring, Threatened Species, Transient Corals, Population Recovery, Disease, Predation, Fragmentation

General Introduction

Acropora cervicornis *Background*

In previous decades, *Acropora cervicornis* colonies were typically found in high densities and were referred to as thickets, fields, stands or patches lining the fore reef of many Caribbean, Florida, and Gulf of Mexico reefs. *Acropora cervicornis* is one of the most important corals in terms of contributing to habitat complexity and reef framework, playing a significant role in the reef community (Goreau 1959; Goreau and Goreau 1973; Adey and Burke 1977; Neigell and Avise 1983). The mainly monotypic stands are generally found in high wave energy areas of shallow depths (0-30 meters) on fore and back reefs, atop spurs, and octocoral dominated reefs (Davis 1982; Bruckner 2002; *Acropora* Biological Review Team 2005). Its fast growth rate and natural ability to fragment allows it to spread across habitats quickly under optimal conditions, forming dense patch-like structures and providing habitat to a multitude of vertebrate and invertebrate species. The habitat diversity and ecological benefits provided by the structure of *A. cervicornis* colonies are virtually irreplaceable within the natural marine community.

More recently (since the 1980's) populations within Florida have become regionally isolated, existing most commonly as individual colonies or much smaller patches separated by kilometers or more, due to an unprecedented white band disease event (Gladfelter 1982; Bythell et al. 1989; Bythell et al. 1993; Aronson and Precht 2001; *Acropora* Biological Review Team 2005). This dramatic decline and lack of recovery lead to the listing of the two Atlantic *Acropora* species, *A. cervicornis* and *A. palmata,* as threatened under the United States Endangered Species Act (US ESA; (NOAA 2006)), critically endangered on the International Union for Conservation of Nature (IUCN) Red list (Aronson et al. 2008a,b).

Acropora cervicornis, along with all Caribbean corals, have many environmental and biological factors affecting their density, cover, and health. Environmental factors that have caused change in the population structure and distribution of *A. cervicornis* include major disturbances including tropical storms or hurricanes, ocean temperature changes, pollution, and land-use conversion caused by humans (Knowlton et al. 1981; Woodley et al. 1981; White et al. 2008; Roth et al. 2013; Bright et al. 2016; Miller et al.

2016b) The most commonly reported biological stressors to *A. cervicornis* are white band disease and rapid tissue loss (Antonius 1977; Peters et al. 1983; Peters 1997; Williams and Miller 2005; Miller et al. 2014b), fireworm, snail and damselfish predation (Marsden 1962; Antonius 1977; Brawley and Adey 1977; Kaufman 1977; Hayes 1990; Knowlton et al. 1990; Williams and Miller 2005; Miller et al. 2014a; Schopmeyer and Lirman 2015), and colony fragmentation (Gilmore and Hall 1976; Shinn 1976; Highsmith et al. 1980; Tunnicliffe 1981; Knowlton et al. 1990).

Due to the confounding effects of disease, genotypic isolation, bleaching, storms, anthropogenic stressors, some historic populations have never recovered (Miller et al. 2002; Wilkinson 2008), while others might be considered as maintaining or possibly returning (Vega-Zepeda et al. 2007; Miller et al. 2008; Zubillaga et al. 2008; Lirman et al. 2010; Lidz and Zawada 2013; Miller et al. 2016a). There are the rare occurrences that populations within a few regions have survived this period and are continuing to succeed. Many of the largest known patches currently in existence within the entire Florida Reef Tract are found in Broward County, Florida, the northern most extent of the species range (Vargas-Ángel et al. 2003; Walker et al. 2012a; D'Antonio et al. 2016). Only a few other known large living patches of *A. cervicornis* have been documented within the species range: Punta Rusia, Dominican Republic (Bruckner 2002; Lirman et al. 2010), Roatan, Honduras (Keck et al. 2005; Riegl et al. 2009), Antigua (Ecoengineering Caribbean Limited 2007; Wilkinson 2008), Belize (Busch et al. 2016) and Veracruz, Mexico (Larson et al. 2014). These locations are of particular interest as to how they continued their existence through multiple disease events, hurricanes, cold water, and numerous anthropogenic events that decimated other populations (Hughes and Connell 1999). As a threatened species, it is important to examine the effects that predation, disease, and fragmentation have on these remaining populations so progress can be made in first stabilizing the existing population, and eventually restoring this species back to a self-sustaining population throughout the species range.

Acropora cervicornis *Recovery Potential*

Atlantic *Acropora* species awareness and restoration projects have grown in popularity and size since they were first listed as threatened in 2006. It been acknowledged

that without assistance this species will not recover (Mercado-Molina et al. 2015b; Mercado-Molina et al. 2015a; Miller et al. 2016a). Unique to many, if not all, *Acropora spp.*, is the ability to reproduce both sexually and asexually. This is a beneficial characteristics especially when resources are limited (habitat or food), population levels are low, genetic diversity is of concern, and may even aid in adapting to small scale environmental change or even large scale changes such as climate change. Furthermore, for a threatened species asexual reproduction is extremely advantageous as it can occur year round and makes it well suited for restoration activities. However, habitat suitability plays a factor in the success of a fragment reattaching to the substrate, high sedimentation and energy will decrease the likelihood that the fragments will attach, no matter how fast it can grow. There are three major drawbacks in asexual reproduction for this species 1) lack of increase in genetic diversity, 2) decrease in long distance dispersal and 3) reduction in colony size. Because there is no cross fertilization occurring during asexual reproduction the same genetic composition of the host will not increase, but production of ramets will occur. This is a drawback because disease, bleaching, and predation may be genotype specific, research in this field is still up and coming, but initial findings for white band disease in the Atlantic *Acropora* show that some genotypes may be resistant to being infected (Vollmer and Kline 2008). Therefore, by limiting the diversity of the species may lead to future population declines from one outbreak event. Long distance dispersal and wide species range is a benefit for most species. Much like the previous example, a wide species range will limit the impact that events listed above will have on the survival of the species as a whole (for example a storm will not decimate the entire population only a portion). If the range of the species is limited to begin with and only reproduces through fragmentation, range expansion will be very limited even if habitat is available. Dispersal of fragments can also limit population expansion, the larger the size the higher the survivorship, however the larger the fragments the shorter the distance traveled. Furthermore, fragmentation of a colony always reduces the size of the colony. If reduced or fragmented enough the ability for the colony or fragment to reproduce sexually will be impacted (Szmant-Froelich 1985; Szmant 1986). Soong and Lang (1992) determined that many species have a minimum reproductive size, including both of the Caribbean Acropora species. Therefore, continual asexual reproduction through fragmentation of the same

colony or population may be decreasing the size of the colonies to a size that would be limiting the ability to potential reproduce sexually (Kojis and Quinn 1985; Szmant 1986; Smith and Hughes 1999; Lirman 2000). In addition, Okubo (2009) reported that colonies following transplantation (asexual reproduction) displayed skip years in their sexual reproductive cycles. While asexual reproduction appears to be the only option when so many of the species are faced with extinction, we also must consider their ability to reproduce sexually when evaluating restoration projects and long-term species recovery.

Because of the dramatic decline in population density the potential for species recovery through sexual reproduction is further reduced from an already low rate of settlement (Vargas-Ángel et al. 2006). Experts suggest that *A. cervicornis* colonies of various host genotypes should be within 0.5 m to 10 m of each other to maximize the likelihood of fertilization (Acropora Coral Conservation/ Restoration Workshop Final Report, 2009). Even though gene flow (with the possibility of some fine scale differences within 2 km (Vollmer and Palumbi 2007)) and genotypic diversity was found to be high across the Florida Reef Tract (Baums et al. 2010; Hemond and Vollmer 2010) populations are so depauperate that recovery by sexual reproduction within natural populations is not realistic. A majority of the *Acropora* restoration projects are propagating corals via asexual reproduction. The goal behind these restoration projects is to create genetically diverse outplant sites that will contribute to the sexual reproduction of the species. Many in situ restoration programs are now teaming with land-based nursery programs or larval ecology experts to further explore the possibility of gamete collection and lab rearing of sexually produced larvae for use in restoration. While current genetic diversity is high for *Acropora* throughout the Greater Caribbean and Florida, (Baums et al. 2010; Hemond and Vollmer 2010; Drury et al. 2017b), maintaining or increasing the diversity must be considered for successful restoration of this species and included in outplanting and restoration plans (Baums 2008). However, the role of genotypic diversity in terms of successful sexual reproduction, competition, growth, survivorship, and predator and disease resistance is still relatively unknown (Vollmer and Kline 2008; Baums et al. 2013; Lirman et al. 2014; Drury et al. 2016; Drury et al. 2017a; Goergen et al. 2017; Lohr and Patterson 2017; O' Donnell et al. 2017; Goergen and Gilliam 2018).

Research Needs to Support and Inform Species Recovery

Remaining *A. cervicornis* populations are sparsely distributed throughout the Caribbean and typically found as isolated colonies. As a transient (i.e. colonies suffer frequent fragmentation and complete colony dislocation) species, demographic monitoring of individual colonies or populations has been difficult (Smith et al. 2005; Williams et al. 2006). Monitoring efforts have long existed for other sessile benthic organisms (stony corals, sponges and gorgonians), but none of which have been able to capture long-term monitoring of *A. cervicornis* colonies or populations for reasons such as an inability of the sampling methodology to adequately capture its complex growth form, frequent fragmentation and dislocation, and patchy distribution. Because of the species' patchy distribution, most monitoring efforts miss populations entirely unless they are targeted (Bruckner and Hourigan 2002). It is difficult to adequately capture data appropriate for colony growth and survival because of the species' unique ability to quickly shift across life history stages and across sites (Walker et al. 2012b; Miller et al. 2016a). These large patches are rare and are difficult to survey due to the continuous coral coverage, making it difficult or impossible for repetitive monitoring. However, these populations are unique and need to be monitored to fully understand the population dynamics of this threatened species.

Previous to *A. palmata* and *A. cervicornis* being listed as an ESA threatened species, a group of *Acropora* biologists, state, territorial and federal agencies, and ESA experts held a workshop to 'obtain recent information on the status of *Acropora* throughout the wider Caribbean and determine appropriate strategies to conserve these critical resources' (Bruckner 2002) and to identify information and research needs to 'better understand and address the threats these species face, and predict the likelihood of recovery.' A multitude of research needs were identified throughout this process, many of which involve the need to increase our understanding of species specific threats and how to effectively manage, monitor, assess, and restore these species. Below is a summary of the research needs that I addressed during my dissertation:

1. More scientific information is needed on the demographic variables of *A. cervicornis* such as: survival, growth, and frequency distribution by age (population dynamics).
2. Develop a monitoring protocol that addresses the impacts of environmental and anthropogenic factors, can be used from local to regional scales, and includes fate tracking of colonies at various stages of succession.
3. Coral diseases and coral predators need far more study. Causes, impacts, and transmissions need to be identified. Potential for predator removal programs needs to be evaluated.
4. Restoration will have limited success unless the drivers causing population declines are understood and addressed.
5. Restoration efforts need to consider appropriate site selection and the potential benefits must be weighed against the probability of natural recovery.
6. Improve our understanding of the population declines, was it cyclical and recovery will occur or do the current anthropogenic stressors inhibit this recovery?

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Dissertation Objectives

In response to the research needs identified through the *Acropora* workshop I addressed the following objectives during my dissertation:

1. Develop a species specific protocol to effectively monitor, evaluate, and compare *Acropora cervicornis* across the species range.
2. Characterize the population dynamics of *Acropora cervicornis* across multiple regions using the species specific protocol.
3. Determine how the cover and/or density of *Acropora cervicornis* influence the dynamics of a population in terms of predation, disease, fragmentation, growth, and survival within natural and outplanted populations.

The outcomes of these objectives were disseminated through the chapters of this dissertation and four publications:

1. Goergen, E.A., Moulding, A.L., Walker, B.K., and Gilliam, D.S. (In Prep). Identifying causes of temporal changes in *Acropora cervicornis* populations and the potential for recovery. Frontiers in Marine Science.
2. Goergen, E.A., Lunz, K.S., and Gilliam, D.S. (In Prep). Spatial and temporal differences in *Acropora cervicornis* colony size and health. Coral Reefs.
3. Goergen, E.A., and Gilliam, D.S. (In Prep). *Acropora cervicornis* colony residence and retention rates implications for long-term monitoring.
4. Goergen, E.A., and Gilliam, D.S. (2018). Outplanting technique, host genotype, and site affect the initial success of outplanted *Acropora cervicornis*. PeerJ 6, e4433. doi: 10.7717/peerj.4433.

Acropora cervicornis Monitoring Protocol

Monitoring is defined as a collection and analysis of repeated information over time to evaluate changes in species cover, composition, abundance, and causes of mortality, and ultimately direct resource managers' decisions about management plans (Shampine 1993; Elzinga et al. 1998; Spellerberg 2005). However, if data collected during monitoring projects are not appropriately detecting changes, it could lead to mis-management of a species. To help ensure more accurate data collection for comparison across regions of a specific species, a detailed monitoring protocol tailored to that specific species could be utilized (Geoghegan 1996). A protocol can also help ensure that standardized, quality data are being collected (Oakley et al. 2003) if it is collected in a consistent manner (Beard et al. 1999). Furthermore, a monitoring protocol is a critical tool for measuring management success and management of resources.

The development of a species specific monitoring protocol is especially important for *A. cervicornis* because of its current threatened status. In addition, the United States Endangered Species Act requires the implementation of a system to effectively manage threatened or endangered species. A protocol that can be used range-wide will assist scientists and managers in comparing populations of multiple regions, identifying key mechanisms contributing to population growth or decline, measuring management success, and developing conservation plans.

There are many types of monitoring including: resource monitoring, habitat monitoring, baseline studies, measuring trends, research, and long term ecological studies (Elzinga et al. 1998; Vaughan et al. 2001; Spellerberg 2005). There are pros and cons to each monitoring effort, and the type of monitoring to be used comes down to the objectives of interest. This particular monitoring protocol was designed for implementing a long-term ecological study, which is geared towards documenting the rates and types of change in response to natural processes and provide the ability to evaluate species management. The goals of this protocol are to document the changes of *A. cervicornis* within permanent

plots with respect to natural factors such as water temperature, hurricanes, storms, predators, and diseases and may be used to inform management directions.

Williams et al. (2006) developed a monitoring protocol originally designed to capture demographic data for both Atlantic *Acropora* species. However, after implementing this protocol with *A. cervicornis* there were obvious changes that needed to be made, mainly due to the difference in colony morphology, complex growth form, and frequency of colony disappearance. Therefor as part of my dissertation I developed a protocol that can adequately assess the growth, succession, condition, and health of populations ranging in size from isolated colonies to patches. The results of utilizing this protocol are found in chapters 1-3. The full monitoring protocol is found in the supplemental material of this dissertation.

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Chapter 1: Identifying causes of temporal changes in *Acropora cervicornis* populations and the potential for recovery

Abstract

Corals, specifically the Atlantic staghorn coral, *Acropora cervicornis*, are under major threat as disturbance events such as storms and disease and predation outbreaks increase in frequency. Since its population declines due to a wide spread disease event in the early 1980s, limited long-term monitoring studies describing the impact of current threats and potential recovery have been completed. The aim of this study was to document the impacts of environmental (tropical storms, increased wind) and biological (disease and predation) threats on *A. cervicornis* to further understand its population dynamics and potential for recovery. Two high-density *A. cervicornis* patches (greater than 1 hectare each) were surveyed tri-annually (winter, summer, fall) from 2008-2016. *Acropora cervicornis* percent cover, canopy height, census of individuals, and prevalence and occurrence of disease, predation, and bleaching were evaluated within permanent 3.5 m radial plots. Temporal variability was observed in mean percent live cover at both patches and resulted in an overall loss of tissue. Frequent disturbances such as tropical storms, hurricanes, and disease events, caused increased, prolonged, and widespread mortality. Periods void of disturbance allowed for recovery and growth. Prevalence and occurrence of disease and predation were highly variable between monitoring events. They were also found to be significantly higher on masses (individuals ≥ 1.5 m) than on colonies and during summer surveys (June-August). These data indicate that substantial length of time between major disturbance events are necessary for recovery and growth of this species. The implication of these results is that given the current rates of growth, recruitment, and storm frequency, natural species recovery is unlikely unless, large scale issues like climate change and ocean warming, which affect the intensity and frequency of disease and predation are addressed.

Keywords: Demographic monitoring, time series, disease, fireworm, long-term monitoring, Florida

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Introduction

Acropora cervicornis is a fragile, vulnerable, and dynamic species that has been known to change in abundance and/or cover quickly (e.g., weeks to years) in response to disease outbreaks, tropical disturbances, or climatic events (Shinn 1976; Antonius 1977; Davis 1982; Knowlton et al. 1990; Schopmeyer et al. 2012; Miller et al. 2014b) and was frequently found lining the fore reef of many Caribbean, Florida and Gulf of Mexico coral reefs. Its fast growth rate and ability to reproduce asexually allow it to propagate quickly across a site, forming mainly monotypic stands referred to as thickets, fields, stands, or patches (Davis 1982; Bruckner 2002; *Acropora* Biological Review Team 2005). *Acropora cervicornis* plays a significant role in the coral reef community by contributing to reef complexity and habitat framework (Goreau 1959; Goreau and Goreau 1973; Adey and Burke 1977; Neigell and Avise 1983). The habitat diversity and ecological benefits provided by the structure of *A. cervicornis* colonies are virtually irreplaceable within the natural marine community.

A. cervicornis populations became spatially and regionally isolated following a multi-decadal white band disease outbreak starting in the 1970's which left the surviving populations most commonly distributed as individual colonies or much smaller patches (Gladfelter 1982; Bythell et al. 1989; Bythell et al. 1993; Aronson and Precht 2001; *Acropora* Biological Review Team 2005). This dramatic decline lead to its listing as threatened under the United States Endangered Species Act (US ESA; (National Marine Fisheries Service 2006)) and as critically endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Aronson et al. 2008). Since this dramatic decline, recovery has been limited with few known high cover populations remaining throughout the species' range (Vargas-Ángel et al. 2003; Keck et al. 2005; Grober-Dunsmore et al. 2006; Lirman et al. 2010; Walker et al. 2012; Busch et al. 2016). One region where numerous large patches of *A. cervicornis* exist today is within the Southeast Florida Coral Reef Ecosystem Conservation Area and more specifically in Broward County, FL, at the northern-most extent of this species' range (Vargas-Ángel et al. 2003; Walker et al. 2012; D'Antonio et al. 2016).

However, little data exist on the temporal and spatial variability of the demography and ecology of *A. cervicornis* (Mercado-Molina et al. 2015; Goergen et al. In Prep), and we are only beginning to define the impact disease and predation have on the persistence of this species outside of large scale catastrophic events (Williams and Miller 2006; Miller et al. 2014a; Miller et al. 2014b; Goergen et al. In Prep). To fully understand the population dynamics of this threatened species and to further inform restoration and conservation efforts, these data need to be evaluated over the long-term.

To address these questions, two patches (>1 hectare each), BCA and Scooter, formally known as Dave and Oakland I patches, respectively (Vargas-Ángel et al. 2003) were used to evaluate temporal patterns in species abundance, percent cover, and the presence, prevalence, and occurrence of disease, predation, and bleaching. These analyses will further our understanding of the dynamics of the threats affecting remaining, future, and restored populations.

Methods

Two large semi-continuous patches of *A. cervicornis*, BCA and Scooter, were surveyed three times per year during Winter ((WS) February/March), Summer ((SM) June-August), and Fall ((F) October/November) from Summer 2008 through Fall 2016. These monitoring periods will be referenced by the season followed by the last two digits of the year throughout the rest of this paper (e.g., SM09 is Summer 2009). An additional survey was completed 10 September 2012, following the passing of Tropical Storm Isaac (TSI12) on 26 August 2012. Prior to the initial survey (June 2008), the boundary of each patch was mapped using a handheld GPS. Plots were installed in a grid with spacing appropriate to cover the patch and the surrounding area to account for possible patch growth or movement (Walker et al. 2012). Thirty-two plots each separated by30 m were installed at BCA, and 31 plots were installed at Scooter with 23 m separation.

Monitoring methodologies were modified from a previously developed *Acropora* spp. demographic monitoring protocol (Williams et al. 2006). Radial plots 7 m in diameter (38.48 m^2), marked by a permanent center pin and tag designated the survey

area. Temporary transect lines, 7 m in length were laid perpendicular to each other across the center of each plot defining the survey area during monitoring events. Condition characteristics and a species census were completed in all plots. Condition characteristic data included: 1) estimates of percent cover of live *A. cervicornis*, 2) the presence and relative ranking of tissue loss caused by white band disease, rapid tissue loss (Williams and Miller 2005), and predation by the bearded fireworm (*Hermodice carunculata)*, three-spot damselfish (*Stegastes planifrons)*, and the coralivorous snail (*Coralliophila abbreviata)*, and 3) presence and severity of bleaching. Maximum *A. cervicornis* canopy height was measured within the plot boundary. During the species census, all *A. cervicornis* individuals were counted and categorized as either a loose fragment, colony (well defined boundary of continuous skeleton (dead or alive), attached, <1.5 m diameter) or a mass (difficult to define boundary, typically >1.5 m in diameter). Beginning in F10, individuals that showed signs of disease were quantified to obtain disease prevalence of colonies and masses. Presence of disease was not quantified on loose fragments because the cause of recent mortality on fragments could not be identified confidently. All individual areas (occurrences) of recent mortality within the plot boundary were counted based on cause (rapid tissue loss, white band disease, fireworm, and snail); recently dead areas separated by living tissue were counted as separate occurrences. The occurrence of damselfish predation and bleaching were not recorded because of the difficulty in defining and enumerating individual gardens and areas of bleaching.

Meteorological data were obtained from multiple on-line resources to better describe the conditions during tropical disturbances and aiding in identifying other causal events. Storm track, wind swath data, and individual storm reports were downloaded from the National Hurricane Center (www.nhc.noaa.gov). Wind data for 2008 were collected from the National Centers for Environmental Information Fort Lauderdale Airport station (www.ncdc.noaa.gov), which is located approximately 3 km inshore and 10 km from the study sites; however, in 2009 a closer station was established on the ocean approximately 6.5 km south of the study sites. Therefore, 2009-2016 were downloaded from the National Data Buoy Center station PVGF1- Port Everglades

Channel, FL (www.ndbc.noaa.gov). Rainfall data were obtained from the South Florida Water Management Districts Hollywood Station (2008- Oct 2014) and S36-RR Station (Nov. 2014-2016; my.sfwmd.gov). Temperature (°C) was recorded every two hours using Onset Hobo Pendant® Temperature/Light loggers or TidbiT® v2 Temperature loggers attached to a permanent pin at each patch. Data were recorded from June 2008 at BCA and February 2010 at Scooter until the end of the study. Loggers were exchanged every 3-6 months. Unfortunately, a series of faulty loggers at Scooter resulted in missing data from 27 February 2014 to 10 August 2016.

Data analysis

Plots in which *A. cervicornis* were never recorded during the duration of the study were not included in the analysis (n=5 for BCA). Data were pooled within each monitoring event by patch providing event means. For annual analyses, the three monitoring events completed during that calendar year were pooled; the TSI12 event was included in 2012 for a fourth event for that year. For the seasonal analyses, all years were pooled within each season; monitoring event TSI12 was included in the summer season.

Percent cover was estimated for each plot during each event and was used to calculate mean cover by patch. Trends in mean percent cover of living *A. cervicornis* (PCL) were analyzed using Time Series Analyses followed by decomposing the components and analyzing the decomposed trend component with a linear regression (R Core Team 2017). Simple linear regressions were used to analyze the annual trend observed in PCL. One-way analysis of variance (ANOVA) was used to assess the differences in PCL between seasons. Post-hoc comparisons were performed using Tukey's HSD tests. Kruskal-Wallis test by ranks were used to explore absolute change in PCL. When significant, Multiple Comparisons 2-tailed post-hoc tests were performed to determine significance between factor levels.

The total abundance of fragments, colonies, and masses in each individual plot were averaged by patch for each event, year, and season. The trend in mean abundance

of fragments, colonies, and masses was analyzed using a Poisson regression for both between monitoring events and years. In addition, to determine differences in mean abundance and absolute change in abundance between seasons, Kruskal-Wallis test by ranks followed Multiple Comparisons 2-tailed post-hoc tests were used.

The presence of disease and predation was analyzed through the prevalence of plots with each condition. During each event, researchers documented the presence or absence of white disease, fireworm predation, damselfish predation, snail predation, and bleaching. A sum of the total number of plots with each condition was divided by the total number of plots providing a prevalence for each condition for each event. Mean prevalence of plots with each condition were calculated annually and seasonally. These data indicate how wide-spread each condition was at each patch. Prevalence of white disease was also calculated per plot by dividing the number of colonies or masses with disease by the total number of colonies or masses in each plot. Disease prevalence was analyzed using binomial (plot prevalence) and quasi-binomial (colony and mass prevalence) generalized linear models between monitoring event, years, and seasons. When the model identified significant factors, post-hoc multiple comparisons with a Bonferroni correction were employed to define specific contrasts of factor levels.

The occurrence of white disease, fireworm predation, snail predation, and bleaching were summed by their occurrence on colonies or masses per plot. Mean number of occurrences of each condition per plot was calculated per monitoring event, year, and season. These data were analyzed using Kruskal-Wallis ANOVAs, and when significant, Multiple Comparisons 2-tailed post-hoc tests with a Bonferonni correction were performed.

Individual plot canopy height was used to calculate a mean canopy height per patch for each event. These data were analyzed across all events using linear regression analyses for both between monitoring events and annual changes.

Results

Across the 8 years of the study, abundance and health of *Acropora cervicornis* were surveyed within 27 plots at BCA and 31 plots at Scooter, five plots at BCA never had *A. cervicornis*. The center pin was not located for two plots at Scooter following the SM15 and F15 events because of *A. cervicornis* overgrowth and were not included following these events.

Disturbance events

Tropical storm force winds, identified by the predicted area of the wind swath published by NOAA (http://www.nhc.noaa.gov), impacted southeast Florida during six named storm events (Table 1). Each storm had different conditions (temperature change, wave height, rainfall, and wind speed) and relate to the range of impacts at each patch. The passing of all storms, except Hurricane Sandy at BCA, resulted in mean PCL losses ranging from 1.5- 50% for both patches. The largest PCL losses by area were 78 m^2 for BCA during monitoring event WS09 and 116 m^2 for Scooter during TSI12. Besides named storms, additional high energy periods during the study were identified by elevated mean daily wind speeds greater than the average sustained wind produced by a tropical storm, 12.78 kts (Table 2). Additional losses of >20% relative mean cover per patch were observed between events not associated with named storms at at least one patch during: WS10, F11, SM15, F15, WS16, and SM16.

Cover Characteristics

PCL decreased for both patches during the study, although only BCA had a significant, decreasing linear trend (r^2 =0.5013, F (3,20) = 6.702, $p< 0.001$; Scooter: r^2 =0.07924, F (3,20) = 0.5738, $p>0.05$; Fig. 1). PCL within individual plots at BCA ranged from 0 to 70%, with an overall study mean of 8.6 ± 0.38% (±SE). PCL was greater at Scooter with an overall mean of 16.0 ± 0.48% but had a similar range from 0 to 75%. Fluctuation in cover was observed at both patches between monitoring events, years, and seasons with the greatest increases for both patches in 2013 and during the summer (Figs. 1 & 2). However, these gains were not enough to outweigh the total losses, and by area BCA experienced a net loss of 144 m^2 of living *A. cervicornis* and Scooter 173 m^2. The

greatest PCL losses occurred following system-wide disturbance events such as tropical storms, hurricanes, or disease events (Table 1, Fig. 2).

The absolute change in mean PCL varied between monitoring events at both patches (X^2=106.88 and 174.28, df=24, p<0.001 BCA and Scooter, respectively; Fig. 2). The largest increases were observed from the winter to summer monitoring events where average increases in percent cover per plot were 1.4 and 1.9% at BCA and Scooter, respectively (Fig. 2- yellow bars). When all years were pooled, 74% (BCA) and 68% (Scooter) of the plots had a mean PCL increase during the summer monitoring events. A negative percent change in mean PCL was observed for a majority of the fall to winter and summer to fall monitoring periods. The magnitude of change was larger at Scooter for 60% of the monitoring events, and BCA and Scooter differed in gain or loss of tissue during 6 monitoring events (Fig. 2).

Mean canopy height at BCA ranged from 38 to 55 cm and had an overall mean of 45.6 ± 0.74 cm (±SE). Mean canopy height at Scooter ranged from 32 to 48 cm and had an overall mean of 43.2 ± 0.50 cm. Monitoring event had a significant effect on the absolute change in canopy height (BCA- r^2 =0.1069, F (16,408) = 3.051, p<0.001; Scooter- r^2 =0.1907, F (16,470) = 6.923, p<0.001). Canopy height varied across the study increasing during summer events and decreasing towards the end of the study, as indicated by a large portion of the plots having negative change in height for the final events (Fig. 3).

Species Census

A total of 4,692 colonies were counted at BCA (density of 0.18 ± 0.01 col/m^2) and 11,894 at Scooter (0.40 ± 0.01 col/m^2) across the entire project. Mean colony abundance at Scooter exhibited a significant decreasing trend (p<0.001), with moderate but significant seasonal variation (X^2=17.097, p<0.001) whereas BCA remained relatively stable with only a few monitoring events having significant deviations from the mean (p<0.001), but had no significant seasonal change (X^2=1.5795, p>0.05; Fig. 4). On average, 70 colonies were lost at Scooter and 20 at BCA between each summer and fall

monitoring event. Significant increases in mean colony abundance were observed in the summer at Scooter and the winter events at both patches ($p<0.05$). The mean number of masses per plot for both patches was less than 4 (Fig. 4). Counts of masses increased at Scooter from 2008 to 2010 and then remained stable. The most masses counted during one monitoring event was at Scooter with 119 masses during SM11. Significant seasonal changes in the abundance of masses were observed at Scooter, with greatest changes observed in the summer ($p<0.05$).

Nearly 18,000 fragments were counted at the patches during the study. Total fragments counted per monitoring event ranged from 15 to 359 at BCA (plot average= 6.3 ± 0.31 fragments) and 80 to 1,313 at Scooter (17.6 ± 0.73 fragments). Two major fragmentation events occurred at Scooter, WS10 and WS15, where total fragment counts were over 1,000. Four additional events (TSI12, F15, WS16, and F16) had counts 30% over the patch mean. Fragment counts at BCA were highest during TSI12 and WS16 where total fragment counts were over 300. Differences were found between the annual means of fragment counts, with 2010, 2015, and 2016 as high years at Scooter and 2012 and 2016 at BCA. Mean fragment counts differed significantly between seasons (Fig. 4); on average there were 88 and 243 fewer fragments counted in the summer than in the previous winter at BCA and Scooter, respectively ($p<0.05$).

Condition Characteristics

The most prevalent condition recorded for both patches, when all seasons and years were pooled, was fireworm predation followed by white disease, damselfish predation, snail predation, then bleaching. Two white diseases were observed at both patches, rapid tissue loss and white band disease, but because the distinction between them is uncertain, they were pooled as white disease for analyses. Similar annual and seasonal patterns were found between patches for all conditions, although prevalence rates were higher at Scooter for all conditions besides damselfish predation and bleaching. Overall mean prevalence of plots at BCA and Scooter, respectively was 44.1 ± 1.88 SE% and 72.0 ± 1.6% for fireworm predation, 44.3 ± 1.88% and 66.6 ± 1.68% for

disease, 38.8 ± 1.84% and 33.2 ± 1.67% for damselfish predation, 6.6 ± 0.94% and 17.9 ± 1.36% for snail predation, and 6.2 ± 0.91% and 3.4 ± 0.65% for bleaching.
Disease prevalence oscillated during the study, resulting in monitoring event, year, and season as significant factors in explaining prevalence of disease (glm, <0.001; Figs. 5 & 6). The presence of disease increased at times when water temperatures were warmer and following disturbance events. The highest (or near highest) disease prevalence was observed during TSI12, and highest number of occurrences was during SM15 (Figs. 5 & 6). The year 2013 had the lowest mean maximum temperatures and significantly lower disease prevalence (Tukey, $p<0.01$) and occurrence counts. Disease was more widespread (present in more plots) at Scooter than BCA (Figs. 5 & 6), and when present, it was recorded as the primary cause of recent mortality 58 ± 5% and 57 ± 4% of the time at BCA and Scooter, respectively. Overall mean prevalence of disease was higher on masses 36 ± 2.5% and 41 ± 1.9% than on colonies 8 ± 0.8% and 7 ± 0.5% for BCA ($X^2=37.525$, $p<0.001$) and Scooter ($X^2=88.801$, $p<0.001$), respectively. Nearly three times the occurrence counts occurred on masses than colonies (BCA: $X^2=58.352$, $p<0.01$; Scooter: $X^2=121.4$, $p<0.001$).

Fireworm predation affected 40-90% of the plots at Scooter with mean occurrence counts ranging from 1-10 recently predated tips on colonies and 1-44 tips on masses per plot. Prevalence of plots with fireworm predation was lower at BCA, affecting fewer than 70% of the plots during any monitoring event. However, BCA had similar mean occurrence counts on colonies (1-8 tips) as Scooter, but much fewer on masses (2-14 tips). When present, it was recorded as the primary cause of mortality in 30 ± 5% and 41± 4% plots on average for BCA and Scooter, respectively. Prevalence of fireworm predation was significantly higher in 2015 at both BCA and Scooter (Tukey, $p<0.001$) and significantly lower in 2013 at Scooter (Tukey, $p<0.001$). Summer prevalence at Scooter was significantly higher than fall and spring (Tukey, $p<0.001$), and occurrence counts were the lowest in the fall on both colonies and masses (Fig. 5 & 6).

Snail predation was not observed at every monitoring event and increased significantly in prevalence towards the end of the study (2013-2016) at Scooter (glm,

p<0.01). Prevalence was between 0 and 40% of plots at BCA and 0 to 60% at Scooter. Although snail predation was affecting close to half of the plots when present, mean occurrence counts were less than three per plot, affecting masses significantly more than colonies (Kruskal-Wallis p<0.001), and when present, was only the primary cause of mortality in 3 ± 2% and 12 ± 4% of plots on average at BCA and Scooter, respectively.

Damselfish predation was present during all events and was more wide-spread at BCA than Scooter. It was the primary condition when present in 48 ± 5% and 34 ± 5% of the plots on average at BCA and Scooter, respectively. Damselfish predation significantly increased during the study for Scooter (glm, p<0.05). No seasonal trends were detected in the prevalence of damselfish predation.

Bleaching was not present during all events and was significantly higher during the fall for BCA (Tukey, p<0.001) and summer for Scooter (Tukey, p<0.01). Bleaching was more prevalent at BCA than Scooter, affecting up to 70% of the plots (Figs. 5& 6). Masses were more affected by bleaching than colonies.

Temperature

Monthly mean temperature increased during the study (Fig. 7). The maximum monthly mean ranged between 29.2 and 30.8° C. The warmest month was August for all years except 2008 when July was the warmest. Mean daily temperatures were above 31° C for 1 day in 2010, 5 days in 2011, 10 days in 2014, and 11 days in 2015. Minimum monthly mean increased during the study, ranging from a low in 2009 of 21.5° C to a high in 2014 of 23.9° C. From January 2012 through 2016, only 5 days fell below 22° C, whereas from January 2009 through December 2011 there were 83 days below 22° C.

Discussion

Presented here is a portion of the one of the longest continuous demographic-based monitoring dataset, specifically targeting long-term monitoring of the threatened coral *A. cervicornis*. Published studies on the demography of this species are either sporadic across many years, missing short-term temporal changes and drivers of mortality

and recovery, or cover only a few years, missing long-term trends and important life history characteristics such as impacts from destructive events that may not occur during the time frame of the study. This study included 8 years of observations of two high density populations and documented temporal variation in: PCL, fragment, colony, and mass abundance, and prevalence and occurrence of disease and predation. Environmental disturbances and disease caused significant decreases in PCL and total abundance of colonies. Disease was constantly present and increased during the summer, following Tropical Storms, and on masses. Predation by fireworms, snails, and damselfish caused minimal mortality when compared to disease, but their chronic presence is concerning for species growth, reproduction, and possible transmitter of disease. Unfortunately, the overall health of the two patches deteriorated significantly over the 8 years of this study. Mean cover of living *A. cervicornis* decreased by over 50% at both patches (17-3% BCA; 26-7% Scooter) due to the increasing prevalence of predation and disease and the high frequency of disturbances such as tropical storms, hurricanes, high energy events, and a widespread disease event affecting the Florida Reef Tract (Precht et al. 2016).

Disturbances during the study disrupted the demography of *A. cervicornis*. During these periods we documented an increase in disease and predation (typically during the summer) and an increase in fragmentation (during the fall and winter). In fact, the two largest fragmentation events were subsequently followed by an increase in disease prevalence. Exposed skeleton from fragmentation could increase disease susceptibility (Knowlton et al. 1981). In the best-case scenario, we would have expected to see a shift from fragment to colonies and eventually to masses across the study. However, our data indicate that fragment survival and attachment rate may be very low, but similar to what has been previously reported (Highsmith et al. 1980; Knowlton et al. 1981; Heyward and Collins 1985; Knowlton et al. 1990; Dollar and Tribble 1993; Miller et al. 2016a). These rates were not enough to replace the loss of tissue caused by disturbance events. The frequency of disturbance events varied between years; however, during years of few or no disturbances such as 2013, both patches exhibited signs of recovery with increased PCL. This relatively mild year, with lowest maximum mean

water temperatures, average wind speeds, and above average rainfall, resulted in the lowest prevalence of both disease and fireworm predation at both patches. This year could be a model year for conditions that allowed for population recovery.

Coral diseases are known to peak when there have been significant or prolonged changes in water temperature, sedimentation, pollution, predator lesions, or for unexplainable reasons (Harvell et al. 1999; Harvell et al. 2007). Our data indicate that the diseases affecting *A. cervicornis,* while continuously observed in background levels, may also be exacerbated by increased water temperatures and disturbance events. It is also likely that fireworms and snails may be acting as vectors or reservoirs for pathogens as there is a relationship between the prevalence of disease and predation at both sites (Williams and Miller 2005; Gignoux-Wolfsohn et al. 2012; Miller et al. 2014a; Bright et al. 2015). Above average air temperatures from May through mid-October 2009 caused SST to remain high through October, resulting in over 80 days at or above 30° C. This increased duration of warmer waters preceded one of the highest prevalence of disease (70-94% of plots) and predation (80-90% of plots) recorded for this study, and prevalence remained high for the next two monitoring events, leading to a major decrease in live tissue at Scooter (-121 m^2). Live tissue at BCA at this time also decreased but only slightly (-20 m^2), and the prevalence of disease and predation were elevated but lower than Scooter.

The occurrence of disease was significantly higher in 2015 during a widespread disease event affecting the entire Florida Reef Tract (Miller et al. 2016b; Precht et al. 2016). These two patches of *A. cervicornis* were not spared from this outbreak, but were affected on different time scales. Increased presence of disease was maintained at Scooter into the following year, and while there was a decrease in occurrences, prevalence indicated that disease was still present across the entire patch at greater than average prevalence rates. BCA however, had a slight reprieve from disease and a small increase in percent cover, until Hurricane Matthew passed by in October 2016, further reducing PCL at both sites. Prevalence of disease may have been lower at BCA simply due to the sparseness of tissue remaining.

Predation by fireworms and snails varied radically during the study by years, seasons, and sites. The variability was similar to what Miller et al. (2014a) reported across two years at multiple sites. While prevalence levels were chronic, the mean tissue lost per colony has been described as 3% (Goergen et al. In Prep). Fireworms typically feed on the live branch tips of colonies, removing the growing end, and stunting branch growth. Regrowth and repair over the consumed area is unlikely (Berkle 2004; Miller et al. 2014a). Increased occurrence and prevalence of fireworm and snail predation towards the end of the study could be severely damaging for the future growth of the species because predation may become more focused due to the lack of tissue available, leading to the removal of more growth tips from the same colonies. Moreover, fireworms have been a proven vector of a bleaching pathogen (Sussman et al. 2003), which is of great concern because colonies with predation lesions may be more likely to become diseased (Miller et al. 2014a) and both fireworms and snails have been associated with increased disease prevalence (Knowlton et al. 1990; Miller et al. 2014a; Bright et al. 2016). Therefore, it may be advantageous to manage both snail and fireworm populations to increase the health and growth of *A. cervicornis*.

Not only do the presence of disease and predation have a spatial and temporal component, they were also variable across different life history stages, affecting masses more than colonies. The prevalence of disease for this study ranged from 0 to 37% on colonies (mean approximately 7%) which was similar to previous reports across the species' range (Lirman et al. 2010; Miller et al. 2014b; Goergen et al. In Prep). However, on masses (what others may consider large colonies, thickets or patches) prevalence was higher, with a range of 2 to 84% (mean 38%), than previously reported (Vargas-Ángel et al. 2003; Ladd et al. 2016; Goergen and Gilliam 2018). Because of this discrepancy, high density patches may not be able to persist long-term under modern day conditions. While healthy populations do still exist (Walker 2017) the loss of cover may be a cyclical event linked to population growth (density) and age. While we were unable to age the patches anecdotal observations of patch structure and successional stages such as height and extant of old dead structure and abundance and size of *Agaricia* spp. colonies on dead

structure, indicate that BCA is older and experienced cover decline prior to Scooter. Therefore, as populations grow and potentially expand into high density patches, disease and predation are likely to increase after some time, causing substantial mortality subsequently weakening the skeleton and increasing the likelihood of fragmentation. This process could be detrimental to the persistence of the dense patches unless the fragmentation of a patch can shift to an alternate stable state such as isolated colonies; however, we found very low reattachment success of loose fragments. On the other hand, signs of recovery were present in this study in 2013 when predation and disease prevalence were minimal, maximum water temperatures were lower, and there were only a few days of elevated winds. Unfortunately, reducing water temperatures and wind speeds is out of our direct control, however active management of predators may be a feasible task. This may be even more prudent in high density areas where disease is more prevalent. Because we still don't know the etiology and transmission mechanisms of these diseases (spreading could be occurring through water movement or fish) by abating disease where it is most abundant will benefit the rest of the marine community.

Extreme changes in cover may not indicate a total loss of *Acropora cervicornis* tissue at the site. Its high frequency of fragmentation and dislodgement (Goergen et al. in prep) and fast growth rate allow for fast propagation across sites if conditions are conducive (Highsmith et al. 1980). In previous research we have shown that the centroids of the densest portions of these patches are indeed shifting (Walker et al. 2012). This shift in live cover is evident in the monitoring plots surrounding the high density areas in the direction of the centroid shift. However, increases in cover in these plots is very minimal (less than 5%) and is in no way equivalent to what was lost in the other plots. In addition, it was most common for plots to decrease in live cover and simultaneously increase in dead skeleton, indicating high mortality and not extreme movement that could support the notion that the population is just shifting spatially. However, there is evidence that propagation is still occurring through colony fragmentation and dislodgement. Propagation through fragmentation has the potential to support the existence of this species in low levels but gains do not keep up with the mortality observed. Despite there being evidence of reef recovery from the propagation

of *A. cervicornis* through fragmentation in the Florida Keys in the 1970's (Gilmore and Hall 1976; Shinn 1976), current ocean conditions and the increase in frequency of disturbance events will make it difficult for *A. cervicornis* to recover naturally. Population enhancement by way of outplanting colonies in low density aggregations from nurseries could have a positive effect on this species' long-term sustainability while larger environmental issues are tackled (Miller et al. 2016a; Goergen and Gilliam 2018; Hughes et al. 2018).

Overall, our results confirm that *A. cervicornis* is greatly affected by extreme environmental conditions, disease, and predation. Unfortunately, our data also indicate that prevalence of disease, predation, and fragmentation are increasing and having an even greater detrimental effect on the long-term persistence of this species. As oceans continue to warm (Hughes et al. 2018), warm water driven factors such as bleaching, disease, and predation will increase in frequency and likely intensity. Without time for recovery and growth between these major events, this species will not recover naturally. Of concern is the relationship between disease and predation prevalence and occurrences on masses, which is implying density driven mortality and indicating a cyclical component to the existence of the species. As populations become denser and age, disease and predation become more widespread causing populations to decline to remnant patches of isolated colonies. Furthermore, under modern day reef condition and the frequent occurrences of storms and elevated winds, paired with seasonal and sometimes chronic disease and chronic predation, the ability for a population to grow into these large patches may be difficult. However, these populations are of upmost importance to the continued existence of the species providing an abundance of larvae during spawning and through fragmentation these populations are likely a source to local expansion through propagation of fragments. Therefore, we suggest specific management actions such as the management of predator populations; this may not only lead to improved growth of colonies by reducing the number of damaged growth ends, but could also lead to a reduction in disease due to their abilities to be vectors of pathogens. This may be even more prudent in high density areas where disease is more prevalent, because the etiology of these diseases is still unknown, and they could also be

spreading by water movement or fish, by abating disease where it is most abundant would benefit the rest of the marine community. Furthermore, supporting population enhancement by advising practitioners to outplant at lower densities would also improve the health and longevity of *A. cervicornis.* While colonies may eventually grow together, outplanting them further apart provides more time for growth and healthy colonies to spread across the reef.

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Table 1. Tropical disturbance metadata for southeast Florida including days impacted (based on elevated wind levels), monthly average wind speed, rainfall and wave height (calculated using the Beaufort Scale) for the month the storm occurred, overall mean sustained wind, rainfall and wave height across impact days, maximum daily average wind and wave height, maximum speed of wind gusts, rainfall, and wave height, and the change in in situ water temperatures during and following the storm and the duration of the change. nc= no change observed; na=not applicable.

					Wind (kt)			Rain (cm/day)			Wave Height (m)*			Temperature (°C)	
Storm Name	Date	Approximate Distance from Storm (km)	Category	Impact Days	Monthly Average	Storm Sustained Average (max)	Max Storm Gusts	Monthly Average	Storm Average	Storm Max	Monthly Average	Storm Average (max)	Storm Max	Change	Duration of Deviation
Fay	19 Aug 2008	135	TS	4	7.2	12.3 (16.5)	27.8**	1.05	3.8	9.1	0.6	1 (2)	3.5	3.21	10
Bonnie	24 July 2010	75	TS	5	7.37	12.1 (16.4)	31.8	0.94	0.7	2.8	0.6	1 (2)	4.5	nc	na
Irene	25 Aug 2011	294	H	3	6*	10.5 (11.4)	34.8	0.63	1.2	3.5	0.2	0.6 (1)	5.5	nc	na
Isaac	26 Aug 2012	287	TS	6	7.4	13.8 (20.8)	46.3	0.65	3.3	10.2	0.6	1.5(2.5)	7	1.1	10
Sandy	26 Oct 2012	309	H	9	9.9	15.7 (20.3)	45.7	0.81	0.3	1.6	1	1.5(2.5)	7	1.8	10
Matthew	6 Oct 2016	127	H	3	12.1	12.3 (14.2)	38.7	0.40**	0.8	1.7	1	1 (1.5)	6.5	nc	na

* 7 days were missing from dataset

** Data were from a source different than the rest of the storms. Max gust were not recorded so fastest 2 min speed was used.

Table 2. Number of days between monitoring events in which the wind speed was greater than the average wind speed (12.78 kts) observed in southeast Florida for the 6 tropical disturbances occurring during the study. na= not enough data were available or the monitoring period did not exist (ie 2008).

	2008	2009	2010	2011	2012	2013	2014	2015	2016
Fall to Winter	na	19	13	6	10	0	11	9	19
Winter to Summer	na	na	8	3	5	0	3	3	3
Summer to Fall	na	4	4	14	18	6	3	7	18

Figures

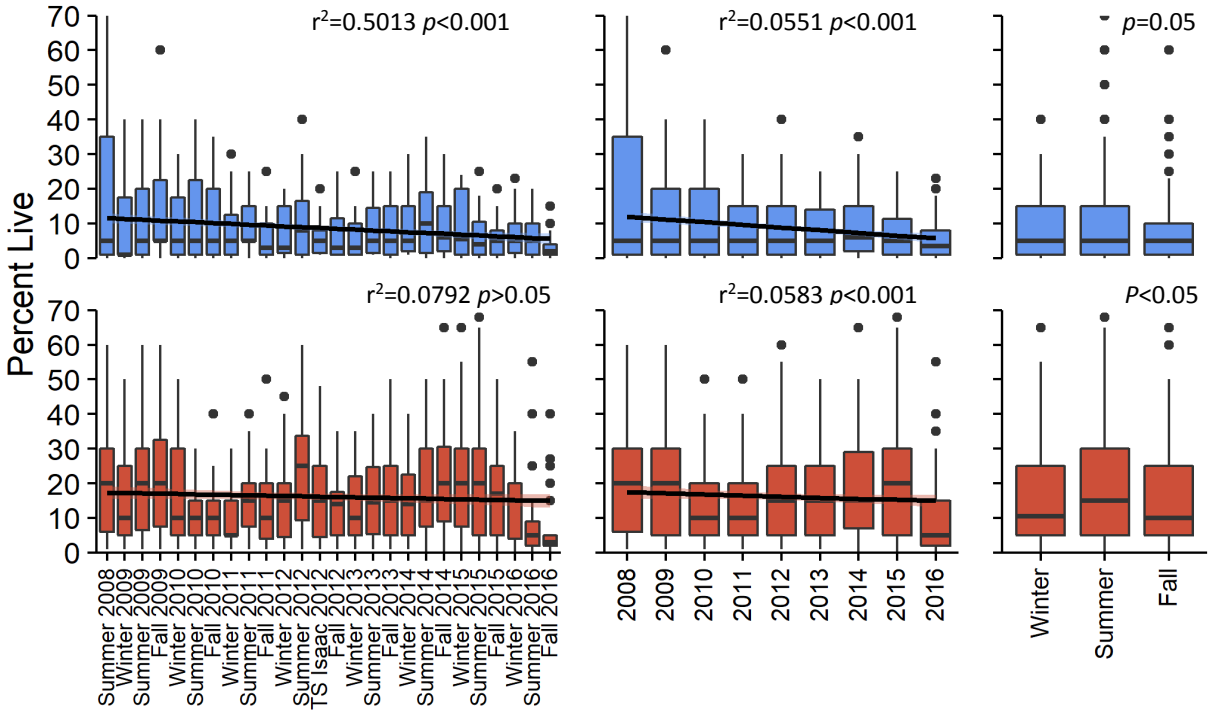

Figure 1. Mean percent living Acropora cervicornis cover per plot for BCA- blue and Scooter- red across monitoring periods, annually, and seasonally.

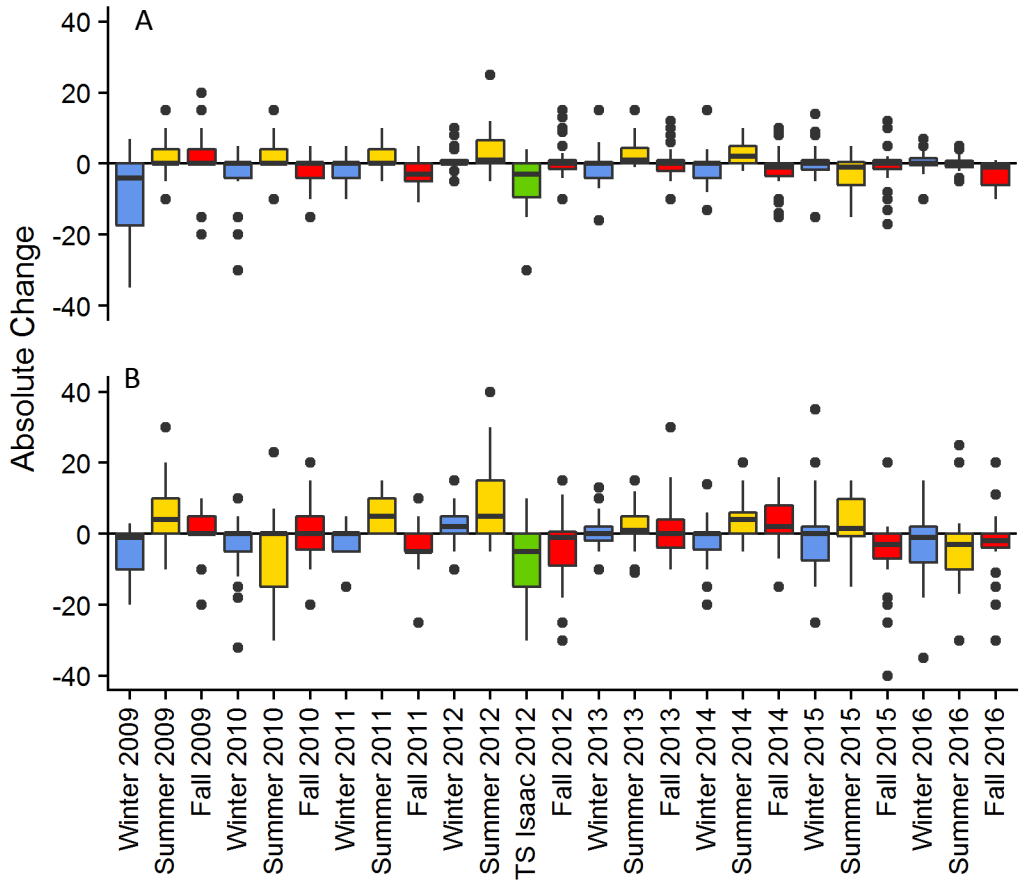

Figure 2. Absolute change in percent cover between monitoring events by site BCA (A), Scooter (B). Colors represent seasonal changes from Fall to Winter- blue, Winter to Summer-yellow, and Summer to Fall-red, the green bar represents change in cover between the Summer 2012 and the TS Isaac monitoring event.

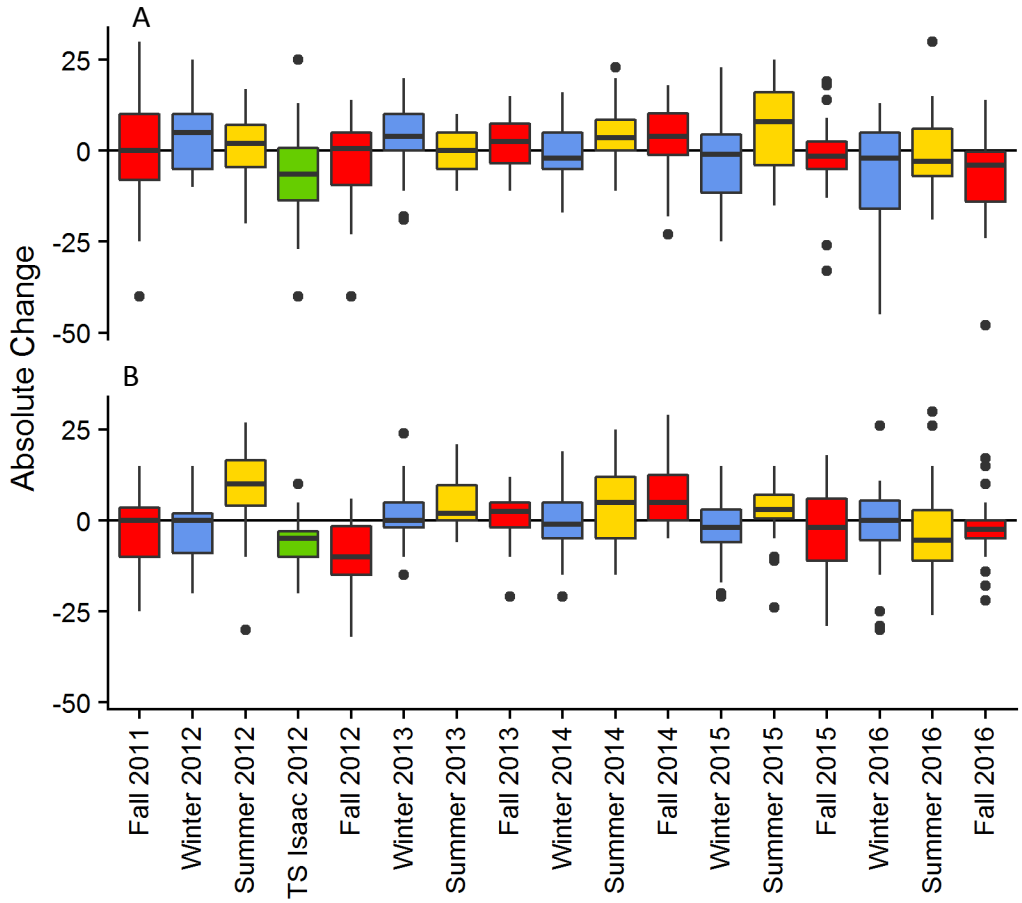

Figure 3. Absolute change in canopy height between monitoring events of living Acropora cervicornis by site BCA (A), Scooter (B). Colors represent seasonal changes from Fall to Winter- blue, Winter to Summer-yellow, and Summer to Fall-red, the green bar represents change in cover between the Summer 2012 and the TS Isaac monitoring event.

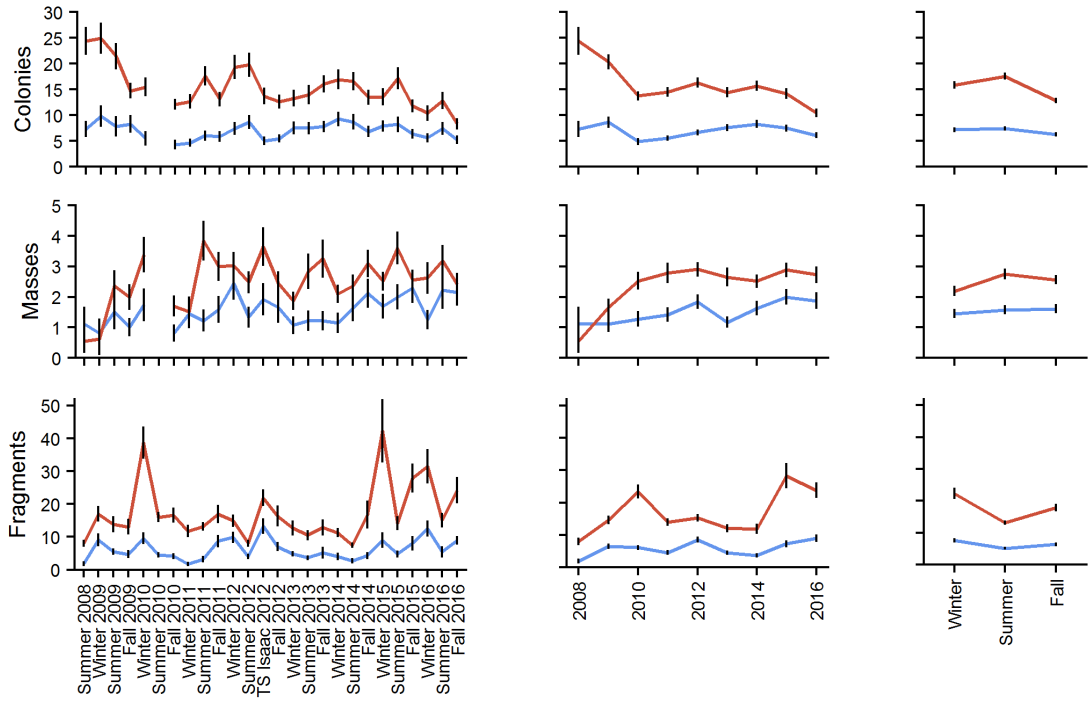

Figure 4. Mean number of colonies, masses, and fragments by plot for BCA (blue) and Scooter (red). Error bars indicate ± 1 SE.

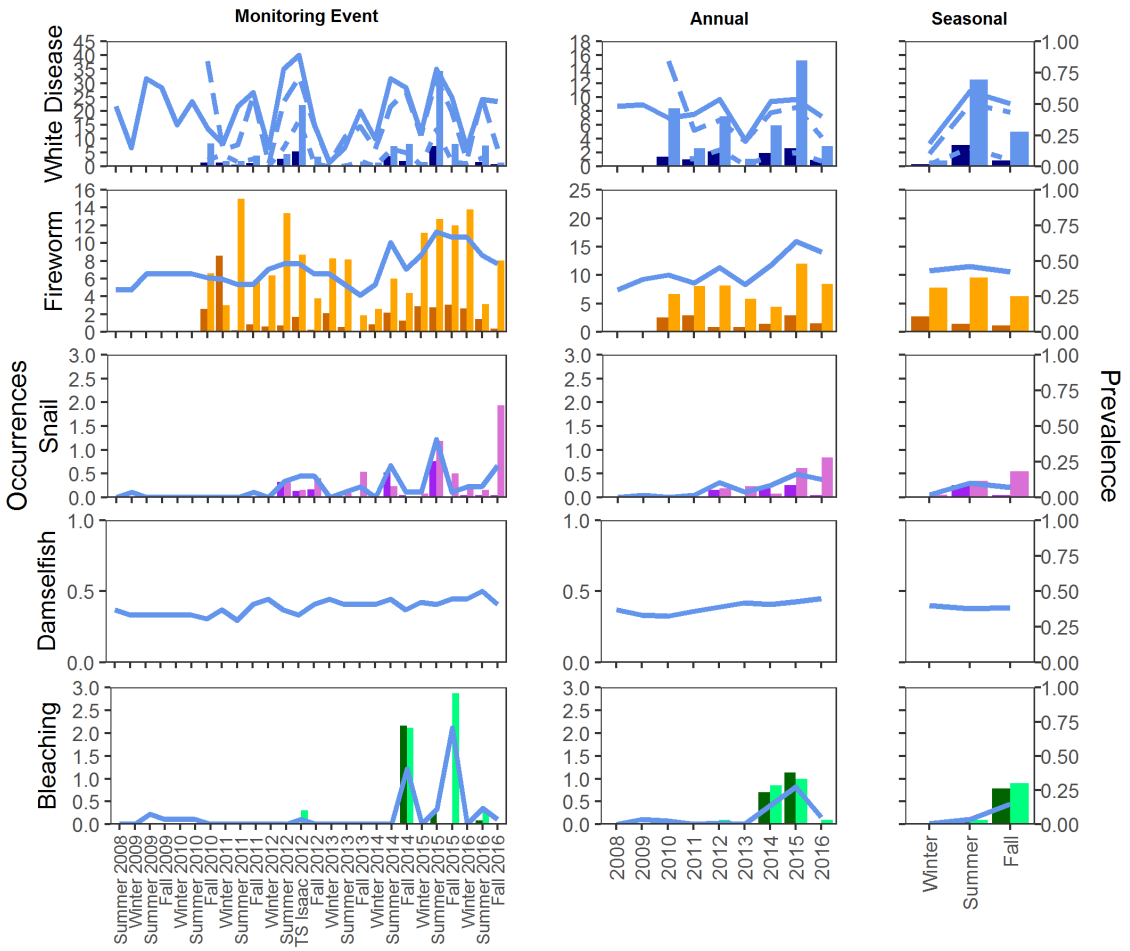

Figure 5. Mean prevalence and occurrence of disease, predation and bleaching by plot at BCA. Prevalence is indicated by the lines on each graph, solid lines represent prevalence of plots with condition, for disease dotted and dashed lines represent prevalence on colonies and masses, respectively. Occurrences of each condition were counted on both colonies (dark bars) and masses (light bars) for each condition.

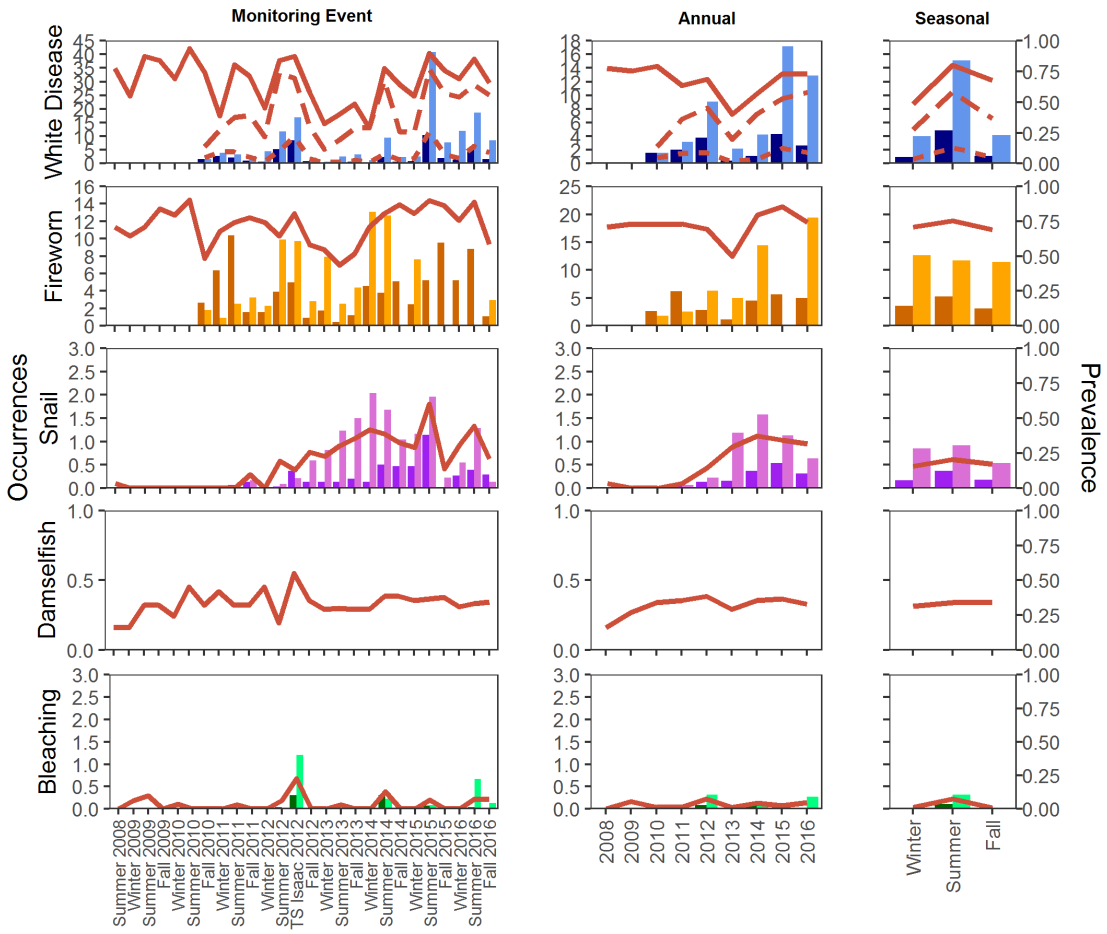

Figure 6. Mean prevalence and occurrence of disease, predation and bleaching by plot at Scooter. Prevalence is indicated by the lines on each graph, solid lines represent prevalence of plots with condition, for disease dotted and dashed lines represent prevalence on colonies and masses, respectively. Occurrences of each condition were counted on both colonies (dark bars) and masses (light bars) for each condition.

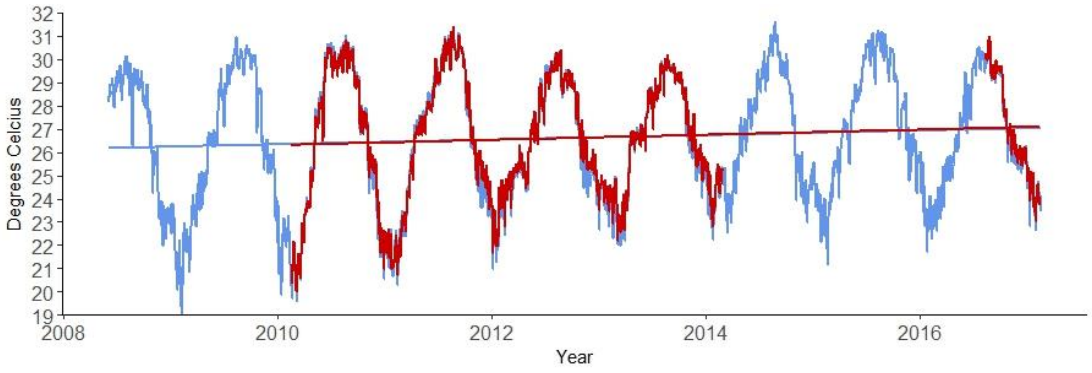

Figure 7. Daily mean water temperature at BCA- blue and Scooter- red. Missing data for Scooter from 2014 to 2016 is due to faulty loggers.

Chapter 2: Spatial and temporal differences in *Acropora cervicornis* colony size and health

Abstract

Acropora cervicornis populations suffered a significant decline in the 1970s and 1980s due to a widespread disease event, reducing populations to spatially isolated populations of low densities. Over the last 4 decades, little to no recovery has been documented and the presence and impact of disease and predation still exist. However, demographic and health characteristics of *A. cervicornis* have not been described temporally or spatially. *Acropora cervicornis* populations in three sub-regions (Broward County (BWD), Middle Keys (MDK), and Dry Tortugas (DRTO)) of the Florida Reef Tract were surveyed from 2011-2015. Multiple sites in each sub-region were surveyed up to three times per year evaluating temporal and spatial differences in colony size, live tissue volume, and prevalence and impact of disease and predation. Colony maximum diameter and volume of live tissue were variable between sub-regions and sites, with significantly larger colonies [both diameter (49.8 ± 30.8 cm) and volume (approximately 29,000 cm^3)] recorded in the BWD sub-region and deeper or more protected sites. Disease and predation were consistently present in all sub-regions, but prevalence of each were significantly different across space and time. Patterns of temporal variability can vary between sub-regions or sites. Disease prevalence was the most variable condition (ranging from 0-28%) increasing after periods of elevated temperatures and environmental disturbances. Disease caused significantly more partial mortality (mean = 3–21%) than fireworm (3-7%) or snail (1-6%) predation in all sub-regions. Recovery potential and long-term persistence of this population may be limited due to the persistent presence of disease and predation, and reproductive limitations at MDK, DRTO (small colonies), and BWD (at the northern most limit of the species range). However, of the sites we surveyed, those of deeper depth and more protection hosted larger and healthier colonies, creating populations that may be acting as refugia for this species.

Keywords: Coral demography, restoration, management, disease, predation, fate-tracking

Chapter Citation: Goergen, E.A., Lunz, K.S., and Gilliam, D.S. (In Prep). Spatial and temporal differences in Acropora cervicornis colony size and health. Coral Reefs.

Introduction

Acropora cervicornis, staghorn coral, once dominated the fore reefs of many Caribbean, Florida, and Gulf of Mexico reefs (Davis 1982; Bruckner 2002; *Acropora* Biological Review Team 2005). Its ability to reproduce through asexual fragmentation and its fast growth rate enables the species to quickly spread across habitats, forming dense structures known as patches or thickets capable of covering hectares of reef habitat. These expansive areas played a significant role in the reef community creating a complex three-dimensional structure providing protection to a multitude of vertebrate and invertebrate species that is irreplaceable by any other coral (Goreau 1959; Adey and Burke 1977; Neigell and Avise 1983).

The health and survival of corals and coral reefs throughout the world and particularly, *Acropora cervicornis* in the Caribbean, are affected by many environmental factors such as nutrient loading, pollution, increased hurricane frequency, and temperature stress (Hoegh-Guldberg et al. 2007; van Hooidonk et al. 2013; Ortiz et al. 2014; Hughes et al. 2017). In addition, the persistence of *A. cervicornis* was affected by biological factors like disease, predation, and colony fragmentation (Gilmore and Hall 1976; Shinn 1976; Highsmith et al. 1980; Tunnicliffe 1981; Knowlton et al. 1990). Unfortunately, by the late 1980's much of this species had been killed by an unprecedented white band disease outbreak leaving only a few remnant populations behind (Davis 1982; Aronson and Precht 2001). The populations that remained were spatially isolated and in relatively low abundance or cover (Miller et al. 2002; *Acropora* Biological Review Team 2005), with a few large patches persisting (Vargas-Ángel et al. 2003; Keck et al. 2005; Lirman et al. 2010; Walker et al. 2012; D'Antonio et al. 2016). These remnant populations have been unable to facilitate natural recovery, and decades later populations remain in low abundance and with no signs of recovery (Miller et al. 2008; Miller et al. 2016). By 2006, *A. cervicornis* was listed as threatened under the United States Endangered Species Act (National Marine Fisheries Service 2006) and in 2008 it was listed as critically endangered on the International Union for Conservation of Nature (IUCN) Red List (Aronson et al. 2008).

In response, numerous restoration programs have been established across the species' range to facilitate recovery by raising *A. cervicornis* colonies in common nurseries and then outplanting them to natural reef structure. However, data gaps still exist in describing species demographics and identifying the current drivers of both population recovery and decline. The biological threats, such as white band disease (Antonius 1981; Gladfelter 1982; Peters et al. 1983) and rapid tissue loss (Williams and Miller 2005), and predation by the bearded fireworm, *Hermodice carunculata*, (Marsden 1962; Antonius 1977; Knowlton et al. 1990; Miller et al. 2014a), the corallivorous gastropod, *Coralliophila abbreviata*, (Hayes 1990; Knowlton et al. 1990), and the three-spot damselfish, *Stegastes planifrons* (Brawley and Adey 1977; Kaufman 1977,1981; Knowlton et al. 1990), have not changed since its decline, but it is still unknown which of those threats is most eminent, nor are the spatial and temporal characteristics fully understood.

Restoration practitioners and resource managers need knowledge about how each of these stressors affect the persistence of *A. cervicornis* across its range to appropriately devise recovery and conservation plans. The main objectives of this study were to compare colony size and colony live tissue volume, and describe the prevalence and impact of major conditions affecting the health of *A. cervicornis* amongst three sub-regions on the FRT. Results of this project can also be used to fulfill the disease and predation criteria in the Threat-based Recovery section of the Recovery Plan for Elkhorn Coral (*Acropora palmata*) and Staghorn Coral (*A. cervicornis*) (National Marine Fisheries Service 2015).

Methods

Wild *A. cervicornis* populations were surveyed in three sub-regions on the Florida Reef Tract: Broward County, the northernmost extent of the species range and towards the northern end of the FRT, the Middle Keys, mid-way along the FRT, and the Dry Tortugas, a remote National Park 60 nautical miles from Key West, at the western end of the FRT. Within each sub-region, permanent monitoring plots (3.5 m radius) were established at multiple sites (Table 1). Each plot was marked by a center pin and

identification tag. Temporary transect lines, 7 m in length were laid perpendicular across the center of each plot defining the survey area during monitoring events. Broward County (BWD) and Middle Keys (MDK) sites were monitored three times per year: winter/spring (February-April; WS), summer (June- August; SM), and fall (October-November; F), however due to logistics Dry Tortugas (DRTO) was visited during the summer (June) and fall (September) between 2011 and 2015, and only during one winter/spring monitoring event in 2012. In the MDK sub-region, site SP2 was added in Fall 2012 and U59 was not monitored during the final event, SM15. The original goal of this study was to compare similar sites (density and cover) across all three sub-regions; however, during reconnaissance and site selection, high cover patch sites could not be found in the MDK and DRTO sub-regions that were comparable to the patches in BWD (Vargas-Ángel et al. 2003; Walker et al. 2012). Therefore, minimum criteria for site and plot selection were established: at least 10 individual *A. cervicornis* colonies were present in at least two 3.5 m non-overlapping radial plots. In the BWD sub-region, plots for colony tracking were not established in high cover areas where >50% of the plot had living *A. cervicornis* in order to maintain a level of similarity between sub-regions.

Up to ten colonies were identified in each plot every monitoring event by starting due North at the plots center pin and working clockwise around the plot (Fig. 1). A colony was defined as a secure individual with living tissue, continuous skeletal structure, and a distinct boundary edge. Colony dimensions (length, width, and height), estimation of percent recent and old mortality, and cause of recent mortality were documented during each event.

Recent mortality, defined as stark white skeleton on which turf algae had not colonized, was estimated attributed to one of the following conditions: rapid tissue loss, white band disease, fireworm predation (*Hermodice carunculata*), snail predation (*Coralliophila spp.*), and "other". Because the distinction between rapid tissue loss and white band disease is unclear they were grouped as white disease for analyses. The category of "other" included conditions that were not frequently recorded or the cause of mortality could not be confidently identified. Damselfish predation (*Stegastes*

planifrons) and bleaching (including partial bleaching) were only noted as present or absent.

Colony fragmentation, dislodgement, and re-attachment are a natural part of the life history of this species, yielding the reliance of tracking individual colonies over the long-term impractical (Tunnicliffe 1981; Smith et al. 2005; Williams et al. 2006; Bruckner et al. 2009; Garrison and Ward 2012). In addition, its branching growth form complicates traditional data collection techniques such as planar percent cover of living tissue, which is unsuitable for this species. A planar estimate of percent cover could be an underestimation of tissue as it misses the living tissue on the undersides and overlapping branches. Therefore, our demographic approach to monitoring *A. cervicornis* individuals focuses on surveying colonies within a designated area with the likelihood that some colonies are repeated across monitoring periods, but are not sought out. By using this approach, we obtained a consistent sample size to describe the temporal and spatial patterns.

Temperature loggers, HOBO © Pendant Temperature and Light Data Loggers, were deployed at each site recording temperature every two hours. These data were used to determine daily averages by sub-region. Loggers were deployed in the BWD sub-region June 2011- July 2015, MDK sub-region July 2011-November 2014, and the DRTO sub-region April 2012-June 2015.

Data analysis

Colony diameter and volumetric index

Measurements were taken of a maximum of 10 colonies per plot up to three times annually (Table 1). Two colony metrics were evaluated, maximum colony diameter (d) and colony volumetric index (CVI), an index corresponding to the percent live tissue (PL) of the colony. CVI was calculated using the shape of an ellipsoid [((4/3) π * d/2 * w/2 * h/2) * PL], where w is the width of the colony perpendicular to d, and h is the maximum height of the colony measured through the axis of growth (Huntington and Miller 2013). Both metrics were evaluated at the plot level yielding an average colony

maximum diameter and CVI by site and sub-region. One-way analysis of variance (ANOVA) were used to assess the differences in colony maximum diameter and CVI amongst sub-regions and between sites within sub-regions. Colony diameter and CVI were Log(x+1) transformed to meet normality (Kolmogorov-Smirnov) and homogeneity assumptions (Levene's Test). Post-hoc comparisons between groups were performed using Tukey's HSD tests. Relative change in colony maximum diameter and mean CVI per plot was calculated for each monitoring period and for the overall project (SM11-SM15). To evaluate the reproductive potential of the each of the sub-regions, colonies were separated by size class: <10 cm diameter (recruit), 11-30 cm diameter (non-reproductive size), 31-89 cm diameter (reproductive size), or over 90 cm diameter (massive reproductive colonies). Sites SP2 and U59 were not included in temporal analysis of colony diameter or CVI because these sites were not surveyed during all monitoring events.

Colony health

The impact of each condition causing recent mortality (white disease, fireworm predation, and snail predation) was evaluated using percent recent partial mortality and was averaged by site or sub-region. Only those colonies affected were included in the condition average, representing the mortality caused by each condition when present. Kruskal-Wallis test by ranks were used to explore percent recent mortality caused by each condition across monitoring event, year, season, and sites within each sub-region to identify patterns in tissue loss. When significant, a Dunn's test with a Bonferroni correction (*p* values were multiplied by number of comparisons) were performed post-hoc to determine significance between factor levels. Prevalence, defined as the number of colonies identified as having a condition divided by the total number of colonies assessed during that event per plot, was analyzed for spatial (site and region) and temporal differences (year, season, and monitoring event). If colonies had more than one condition, each condition was included in the count. Binomial generalized linear models were used to describe the temporal variation in prevalence of each condition, using monitoring event, year, season, and site as factors. Region was also used as an interaction term with monitoring event to evaluate if temporal changes were similar

between regions. When the model identified significant factors, post-hoc multiple comparisons with a Bonferroni correction were employed to define specific contrasts of factor levels. All analyses were performed in R Studio 3.3.1 (RStudio Team 2016) using the multcomp (Hothorn et al. 2008) and dunn.test packages (Dinno 2017).

Results

Colony diameter and volumetric index

A total of 5,515 colonies were surveyed across 11 sites in three sub-regions of the Florida Reef Tract (Table 1). Mean colony maximum diameter for the project varied significantly between sub-regions, with the largest colonies in the BWD sub-region at 49.8 ± 30.8 cm (Tukey HSD MS=0.3956, $p<0.001$). Mean colony maximum diameter by site ranged between 30.5 ± 19.4 cm and 69.3 ± 41.3 cm which was significantly different between sites within all sub-regions (Tukey HSD, $p<0.05$ for all comparisons; Figs. 2 & 3). All sub-regions showed substantial change in colony diameter during 2012, with some of the largest decreases in colony diameter from SM12 to F12 in BWD and MDK (Fig. 4). Plots in the BWD sub-region exhibited the widest range (200%) of change in colony diameter, while the change in DRTO sub-region plots were within ± 35% (Fig. 4). Mean relative change in colony diameter by site ranged from -20 to 19% between monitoring events. Overall, mean colony maximum diameter for the project, from SM11 to SM15, increased for MDK and DRTO sub-regions, 4 ± 21% and 15 ± 1%, respectively, but decreased for BWD -16 ± 12%.

Colony volumetric index (CVI) was significantly different between sub-regions when all sites were grouped, with BWD colonies having the largest CVI ($F_{2,5512}= 37.58$, $p<0.001$; Fig. 5). Mean CVI by site ranged between 7,700- 68,800 cm^3 and varied significantly between sites within each sub-region (Tukey HSD, $p<0.05$; Fig. 5). Mean relative change in CVI by plot was highly variable ranging from -100 to 455% in BWD (two plots had extreme changes of 1,400 and 3,100% increase), -100 to 370% in MDK, and -70 to 170% in DRTO per monitoring event (Fig. 6). While a majority (59%) of the changes in plot CVI were positive for BWD, this sub-region experienced an overall net loss of 411,453 cm^3 of tissue. MDK sub-region lost 1,038,334 cm^3 of tissue; only three

plots increased. The DRTO sub-region had a net increase in tissue volume of 271,715 cm^3. The DRTO sub-region increased towards the end of the project whereas BWD and MDK decreased.

All size classes were recorded in all sub-regions (Fig. 7). The BWD region had substantially more massive colonies (>90 cm diameter) than MDK or DRTO, and a majority (60-80%) of colonies measured during each monitoring event in BWD were of size capable of reproduction (>30 cm diameter; Soong and Lang 1992). The frequency of colonies of reproductive size in the MDK sub-region was 43-60% of the colonies per monitoring event. Between 45-65% of the colonies were of reproductive size during each of the monitoring events in the DRTO. When using CVI as a proxy for reproductive potential a majority of the colonies both the MDK and DRTO had a substantial decrease in the frequency of colonies with the potential to reproduce.

Sites SP2 and U59 were not included in calculations for change in colony diameter and CVI because they were not included in all surveys (Table 1). However, both sites experienced declines in mean CVI per plot across the period they were surveyed; SP2 -48 ± 40% and U59 -81 ± 7%; however, only SP2 had a decrease in mean maximum colony diameter -22 ± 14%, whereas U59 had a 16 ± 27% increase.

Colony Health

Recent mortality affected a total of 18.7% of all colonies surveyed causing 8.5 ± 0.38% tissue loss per colony. The MDK sub-region had significantly more colonies (19 ± 0.7%) affected by recent mortality than BWD (16 ± 0.8%) and MDK (11 ± 1%) ($p<0.05$). Site prevalence ranged from 10 to 32%, but only in the MDK were sites significantly different, U59 (32 ± 3%) had significantly more mortality than all other sites in the MDK ($p<0.05$). Seasonal changes in the frequency were only observed in the BWD sub-region (Table 2), where significantly more colonies exhibited recent mortality in the summer and fall than the winter/spring ($p<0.05$). Recent mortality was more prevalent in colonies during 2014 than 2013, in all sub-regions although only significant

for BWD and DRTO ($p<0.05$), and 2015 was significantly greater than all years in BWD (Tukey, $p<0.05$).

All conditions were present in all sub-regions, but not at all sites (Fig. 8). Prevalence of each condition was variable between sub-regions, and sites in MDK and DRTO (Fig. 8). The influence of year, season, and site were variable amongst conditions and sub-region (Table 2). Year then season were the most significant factors in explaining the prevalence of disease and predation in BWD, whereas site drove differences in the MDK, and in DRTO year or site influenced prevalence depending on condition (Table 2). White disease was the most variable condition with models indicating significant influence of year in all sub-regions, season in BWD and DRTO, and site in MDK (Table 2).

Temporal patterns in the prevalence of all conditions were apparent and varied by sub-region (Fig. 9). The average prevalence of white disease was 6%; however occasional increases were observed, resulting in elevated prevalence during individual monitoring events (Fig. 9). In BWD summer events had significantly more disease than the fall or winter/spring events ($p<0.05$). When all monitoring events were grouped by year, 2013 was a significantly low year for white disease prevalence in all sub-regions and 2015 was a significantly high year in BWD and MDK ($p<0.05$). Prevalence of fireworm predation in the MDK sub-region was consistently higher (8-15%) than BWD and DRTO across the project, but increased during the last two years of the project in the BWD sub-region ($p<0.05$- Fig. 9). Snail predation had consistently low prevalence across all sub-regions, but was showing signs of increase in BWD the last two years of the project. Damselfish predation did not have any significant change over time in any of the sub-regions ($p>0.05$).

Percent recent mortality (when all conditions and events were grouped) was highest in MDK, followed by DRTO then BWD. It was similar amongst seasons ($p>0.05$), but 2011 was significantly higher than 2013 and 2015 in BWD and 2015 in MDK ($p<0.05$; Fig. 10). In BWD, site level differences were apparent: Scooter had

significantly less recent mortality than BCA (p<0.05), and sites within all other sub-regions were similar (p>0.05). When present, white disease caused 13.1 ± 0.89% (SE) partial colony mortality (all sub-regions and monitoring events grouped) and was the leading cause of colony partial mortality in all sub-regions (Fig. 11). The average amount of tissue loss per colony from white disease was highly variable between monitoring events ranging between 1-24% in BWD, 7-29% in MDK, and 5-17% in DRTO. Kruskal-Wallis tests indicate year influenced percent tissue loss by white disease in both BWD (χ^2 = 9.8182, p=0.04) and MDK (χ^2= 25.508, p=0); however, post-hoc analysis only indicate 2015 being significantly less than 2012 in the MDK sub-region (p<0.05). Snail and fireworm predation caused similar levels of colony partial mortality (4.9 ± 0.25% and 4.6 ± 0.35%, respectively; p>0.05) and were significantly less than white disease (p<0.05) amongst all sub-regions. Mortality caused by fireworms was significantly lower in BWD, ranging from 1-7.4% mortality per monitoring event, than MDK (3.3-7.4%) and DRTO (1-16.8%) (Fig. 10; p<0.05). There was no seasonality to the amount of tissue lost to fireworm predation, but year was a significant factor in BWD and MDK (p<0.05). Site level differences were few because the number of colonies affected by each condition at each site were highly variable, but were observed in the BWD and MDK sub-regions (Fig. 10). The amount of tissue lost to snail predation did not fluctuate by season or year, but was significantly higher in the MDK sub-region (p<0.05).

Temperature variation within each sub-region indicates that disease prevalence may be influenced by temperature. Lower mean maximum temperatures for all sub-regions in 2013 are associated with low disease prevalence and higher mean maximum temperatures in 2014 are associated with elevated disease prevalence and mean colony partial mortality (Figs. 9 & 12). Bleaching was mostly recorded in low prevalence, apart from Fall 2011 when 42 ± 7.6% of the colonies were bleached in the DRTO sub-region; however, temperature loggers had not been deployed at these sites yet. Bleaching was more commonly recorded during the Fall monitoring events, following peak temperatures in each sub-region. The warmest year, based on number of days where daily mean temperatures were above 29.5°C, was 2011 in BWD (n=89 days) and 2014 for MDK

(n=108 days) and DRTO (n=113 days), but data were not recorded for 2011 in DRTO and MDK began in mid-2011.

Discussion

In this study, we documented the spatial and temporal variability of *A. cervicornis* in terms of colony size and volume, and predation and disease prevalence across the Florida Reef Tract (FRT). Environmental characteristics (depth, protection from wave energy) of each region and site influenced colony diameter and volume, resulting in larger colonies at deeper sites. The MDK and DRTO sub-regions were composed of mainly small immature colonies, with little indication of change in size class structure across 5 years. Disease and predation were constantly present (18% of colonies were affected each monitoring event) and exhibited a wide range of prevalence and partial mortality on *A. cervicornis* populations. These continuous background levels with intermittent high rates of disease could be devastating for the long-term survival and recovery of this species because colonies were constantly battling adverse health conditions that are stunting their growth and affecting their reproductive capabilities. Similar temporal patterns in disease prevalence were observed in all sub-regions with increases during the Summer and Fall events, whereas seasonal trends were not observed in predation prevalence. As the frequency of thermal anomalies and disturbance events increase (Hoegh-Guldberg et al. 2007; van Hooidonk et al. 2013; Ortiz et al. 2014; Hughes et al. 2017), disease is likely to become more widespread, and potential recovery periods with lower prevalence will become more infrequent.

Colony diameters measured at all sub-regions were larger than what has previously been reported for these sub-regions (Dustan and Halas 1987; Vargas-Ángel et al. 2003; Williams and Miller 2006; Huntington and Miller 2013; Lidz and Zawada 2013; Huntington et al. 2017), but smaller than colonies in the Dominican Republic (Lirman et al. 2010) and Venezuela(Agudo-Adriani et al. 2016). However, the ambiguity of defining a ‘colony’ (entire skeletal unit (Dustan and Halas 1987) to live area units on a larger skeletal unit (Miller et al. 2008; Huntington and Miller 2013)) and the variability in

reporting methods of colony size (maximum diameter, live tissue area, length of live tissue, total linear extension, and volume) are problematic when comparing studies.

Acropora cervicornis is prone to frequent fragmentation due to its fragile skeleton. Fragmentation of colonies (evident through a decrease in colony size) was observed following tropical disturbances or elevated seas states, which for the FRT commonly occurs during the fall. Increases in colony diameter aligned with the summer, a time where calmer sea states are more frequently observed and have been documented as the growth and branching period for this species (Shinn 1976). Furthermore, the frequency and intensity of change in colony size may be due to colony morphology and skeletal density which are likely adapted to each sub-regional hydrodynamic regime (Chamberlain Jr and Graus 1975; Bottjer 1980; Schumacher and Plewka 1981; Gladfelter 1984; Kuffner et al. 2017). Although colony morphology was not measured, casual observations indicate differences in colony morphologies with more compact, densely branched colonies in DRTO than in BWD. Morphological differences were also apparent at a few of the MDK sites. A more compact growth form and possibly denser skeleton may be less prone to colony fragmentation, whereas a less dense skeleton (likely in more protected areas) would be more prone to fragmentation during high energy events. A less dense skeleton in BWD colonies may explain the high variability (75-125%) in change in colony diameter. The range of change in CVI can be similarly explained, but because it was a metric of colony health, patterns also emerged with the prevalence of disease. This pattern was most evident in the BWD sub-region where the highest prevalence recorded resulted in negative changes in CVI.

The structural complexity of an *A. cervicornis* colony is irreplaceable on Atlantic and Caribbean reefs; it provides shelter for small fishes and invertebrates, and coastal protection from high energy events. Colony size and morphological differences, such as branch frequency and length, will inherently affect complexity, habitat creation (space available for protection), and direct the size structure of the fish community inhabiting a colony (Wilson et al. 2010; Huntington et al. 2017). Therefore, the role that *A.*

cervicornis colonies play may vary amongst sub-regions and sites with theoretically higher fish abundance and diversity surrounding larger colonies.

The observed colony size class composition amongst sub-region indicates reduced reproductive potential for the MDK and DRTO sub-regions as less than half the colonies surveyed in these sub-regions were of reproductive size (Soong and Lang 1992). This potential is further reduced when accounting for colony partial mortality using the CVI. The higher abundance of large colonies (>90 cm) in BWD suggests a higher reproductive potential, but contribution to population growth may be limited due the regions northern location on the FRT.

Overall disease prevalence (<6%) was similar to what others have reported for the FRT (Vargas-Ángel et al. 2003; Miller et al. 2014a) and the Dominican Republic (Lirman et al. 2010). Disease prevalence was relatively low for most of the project with increases during the summer months (up to 28% of colonies) influenced by water temperatures and disturbance events. Tropical Storm Isaac passed west of the DRTO sub-region on 26 August 2012 (Berg 2013) just prior to the Fall 2012 DRTO monitoring event and resulted in the highest disease prevalence for that sub-region. Miller et al. (2014a) also reported temporal and spatial variability in disease prevalence with increases surrounding a disturbance event; however, elevated temperatures did not have an effect during their study. Disease was more prevalent at sites with larger colonies, and although they are more capable of overcoming adverse conditions, such as disease (Loya 1976; Sato 1985; Forsman et al. 2006), it is still of concern for reproductive potential as disease was most commonly seen in colony centers where colonies are most fecund (Soong and Lang 1992).

Colony partial mortality (amount of tissue lost) and prevalence (how widespread) were both good indicators of disease impact on a population. However, describing the impact using just one of these indicators is inadequate since variation in these metrics does not always follow the same pattern and prevalence rates can vary wildly over short periods of time (Miller et al. 2014a; Miller et al. 2014b; Goergen et al. In Prep). The

instances in which rates did not correlate may be due to spatial or temporal characteristics such that the data collection period may be at the beginning or end of an event (high prevalence/ low mortality), or that the condition is not widespread and is heavily impacting a few colonies. A good example of this is Summer 2015, when there were extremely high prevalence rates for almost all conditions especially in the BWD sub-region, but the amount of recent mortality per colony is on the lower end of the spectrum. During this same period, decreases in relative change in CVI for both the BWD and MDK sub-regions were evident, which indicate that while recent mortality was no longer extensive, mortality had occurred since the last monitoring event.

Chronic predation by fireworms (ranging from 0-52% of colonies per site per monitoring event) pose a major threat to *A. cervicornis* growth and production. Previously reported fireworm predation prevalence in the BWD sub-region of 4.8-65% of quadrats surveyed indicate that 8 years prior to this study the presence of predation was already widespread (Vargas-Ángel et al. 2003). Similarly, in the MDK sub-region Miller et al. (2014a) reported wide range in prevalence, 4-43% of colonies, with significant changes between years and sites. Snail predation was difficult to quantify because snails typically reside and predate in cryptic locations on the colony, like the underside of branches, around the bases or in branching junctures (Johnston and Miller 2014). When predation was observed, percent of tissue loss was similar to fireworm predation, typically less than 5% and no more that 30%, which is substantially lower than a manipulative feeding behavior study where 70% of transplanted colonies were completely consumed by snails within 23 weeks (Johnston and Miller 2014). While the direct mortality caused by predation was minimal both have been associated with increased disease prevalence, disturbance events, and as vectors of disease (Knowlton et al. 1990; Miller et al. 2014a; Bright et al. 2016). Furthermore, predation reduces a colony's ability to contribute to population growth, reproduction, and recovery due to the typical location of predation on a colony, apical ends (fireworm) and central portions of the colony (snail). Therefore, management of predators within a site could decrease the prevalence or impact of coral disease.

Large colony diameters in the BWD sub-region are likely due to local environmental conditions (depth, location on the reef, hydrodynamics) that have been supportive of faster growth (Bliss 2015), broad distribution (D'Antonio et al. 2016), and long-term persistence (Vargas-Ángel et al. 2003; Walker et al. 2012). Given the location of these populations, at the northernmost extent of the species range, and the dominant Florida Current running north, the likelihood of these populations contributing to population growth through sexual reproduction is limited, and would depend on a countercurrent (Lee 1975; Soloviev et al. 2017).

There is also evidence that the impact of environmental conditions is also supported at the site level within each sub-region. Sites in the BWD sub-region may be thought of as more protected because of their depth and location leeward of the nearshore ridge complex, a shallow habitat that attenuates offshore wave energy, whereas most of the MDK and DRTO sites (except for U59 and Marker 7) could be considered unprotected. Sites with more protection (BCA, Scooter, U59, and Marker 7) had larger colonies, but higher disease prevalence; however, percent mortality caused by disease was highest at the sites with the smallest colonies. This pattern is concerning, especially for the MDK and DRTO where most of the colonies are of smaller sizes. Site depth also contributed to differences in colony diameter; the deepest site U59 (12.5 m) had significantly larger colonies than any other site, which were similar to colony sizes Lidz and Zawada (2013) reported at depths greater than 7 m in the DRTO sub-region, although protection from wave energy at shallow sites lead to increases in colony size (Marker 7). Meanwhile shallower depths and lack of protection from hydrodynamic forces may cause more frequent fragmentation limiting colony growth (Hughes 1994; Meesters et al. 1994; Hughes and Connell 1999; Bright et al. 2016; Hughes et al. 2017).

As restoration practices continue to expand these data will be valuable for gauging success through comparison of what could be expected of a restoration program in terms of disease and predation presence and the impact that each may have. It could also provide insight into site selection and suggestions from this study are to seek out locations that have protection (deeper or protected from strong wave energy), low

predator abundances, or have an active management plan for predators (in particular for *H. carunculata* and *C. abbreviata)* and use larger colonies.

This study provides a multi-year look at the size, growth, and health of numerous *A. cervicornis* populations across the FRT. Data provided herein show that change can be experienced within a population (site or region) over a short period of time and that these changes do not always occur similarly across the entire reef tract. The impact of environmental conditions, likely influenced by the site location, played an integral part in colony size, growth, and health. Site depth or protection allowed for larger colony growth. Sites with larger colonies had higher prevalence of disease and predation, but lower colony partial mortality. Conditions were not unique to one sub-region. However, the consistent presence of both disease and predation and it relationship with larger colonies/densities across the entire range of this study is a concern for the future persistence of this species and may be suggesting a cyclic population, but this needs further investigation.

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Table 1. *Acropora cervicornis* colony survey schedule, site depth, and number of plots per site.

Sub-Region	Site Name	Depth (m)	# of Plots	Total Colonies	SM11	F11	WS12	SM12	F12	WS13	SM13	F13	WS14	SM14	F14	WS15	SM15
Broward County	BCA	6.3	10	735	X	X	X	X	X	X	X	X	X	X	X	X	X
	Scooter	4.8	10	1174	X	X	X	X	X	X	X	X	X	X	X	X	X
Middle Keys	Stag Party 2 (SP2)	4.6	4	305					X	X	X	X	X	X	X		X
	Stag Party(SP)	6.1	2	212	X	X	X	X	X	X	X	X	X	X	X		X
	U11	4.3	4	463	X	X	X	X	X	X	X	X	X	X	X		X
	U55	5.2	10	1200	X	X	X	X	X	X	X	X	X	X	X		X
	U59	12.5	3	251	X	X	X	X	X	X	X	X	X	X	X		
	U9	6.1	4	370	X	X	X	X	X	X	X	X	X	X	X		X
Dry Tortugas National Park	Marker 7 (M7)	3.7	3	265	X	X	X	X	X		X	X		X			X
	Off Ramp (OR)	4.6	3	270	X	X	X	X	X		X	X		X			X
	Perfection(PF)	4.6	3	270	X	X	X	X	X		X	X		X			X

Table 2. Results of generalized linear models by sub-region and condition using Year, Season, and Site as factors. N= number of colonies affected by each condition, D= model deviance, RD= residual deviance, and *p*= factor significance α= 0.05.

			White Disease				Fireworm				Snail				Damselfish				Recent Mortality			
Region	Factor	df	N	D	RD	*p*	N	D	RD	*p*	N	D	RD	*p*	N	D	RD	*p*	N	D	RD	*p*
BWD (1908)	Year	4	140	39.77	961.1	0.000	123	25.40	886.93	0.000	31	18.66	338.52	0.001	17	5.91	188.44	0.206	308	41.74	1645	0.000
	Season	2		83.31	877.79	0.000		1.27	885.67	0.531		8.41	330.1	0.015		2.36	186.07	0.307		35.53	1609.5	0.000
	Site	1		3.05	874.74	0.081		2.22	883.45	0.136		0.00	330.1	0.997		1.57	184.5	0.210		2.34	1607.2	0.126
MDK (2802)	Year	4	139	39.71	1066.3	0.000	303	6.96	1913	0.138	141	5.29	1130	0.259	69	12.77	634.67	0.012	541	5.01	2744.6	0.286
	Season	2		0.89	1065.4	0.641		2.45	1910.5	0.294		1.39	128.7	0.500		3.26	631.41	0.196		0.03	2744.6	0.988
	Site	5		28.69	1036.7	0.000		19.91	1890.6	0.001		44.10	1084.6	0.000		319.50	311.91	0.000		28.27	2716.3	0.000
DRTO (805)	Year	4	36	11.56	282.53	0.021	33	17.92	257.53	0.001	5	3.67	57.11	0.452	99	4.66	595.59	0.324	88	14.56	541.03	0.006
	Season	2		6.44	276.09	0.040		1.42	256.11	0.491		5.08	52.032	0.079		0.62	594.97	0.733		3.56	537.47	0.169
	Site	2		0.33	275.77	0.848		6.18	249.93	0.046		1.46	50.57	0.481		101.20	493.77	0.000		0.41	537.07	0.816
Overall	Region	2		14.17	2401.00	0.001		53.27	3107.70	0.000		70.21	1495.50	0.000		177.80	1442.00	0.000		34.70	4992.00	0.000

Figures

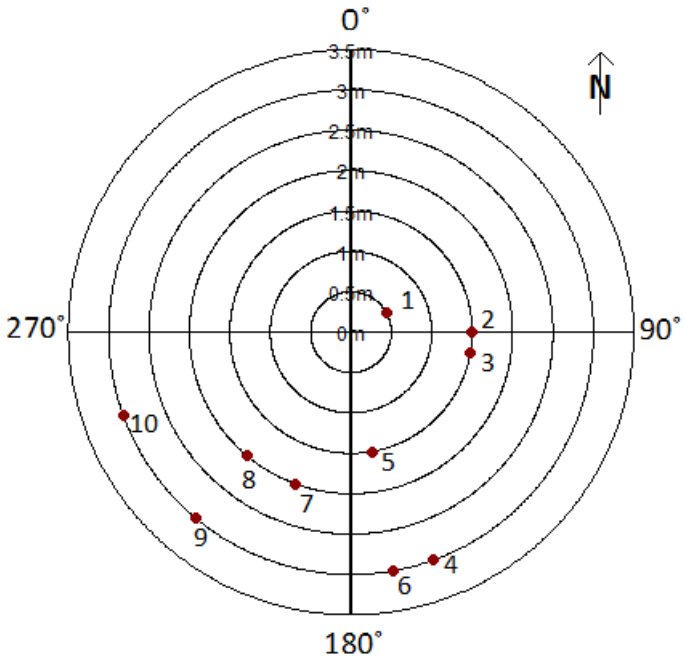

Figure 1. An example of a 3.5 m radial monitoring plot. Colonies (red dots) within the plot were surveyed by starting due North and working clockwise around the plot until up to 10 colonies were identified.

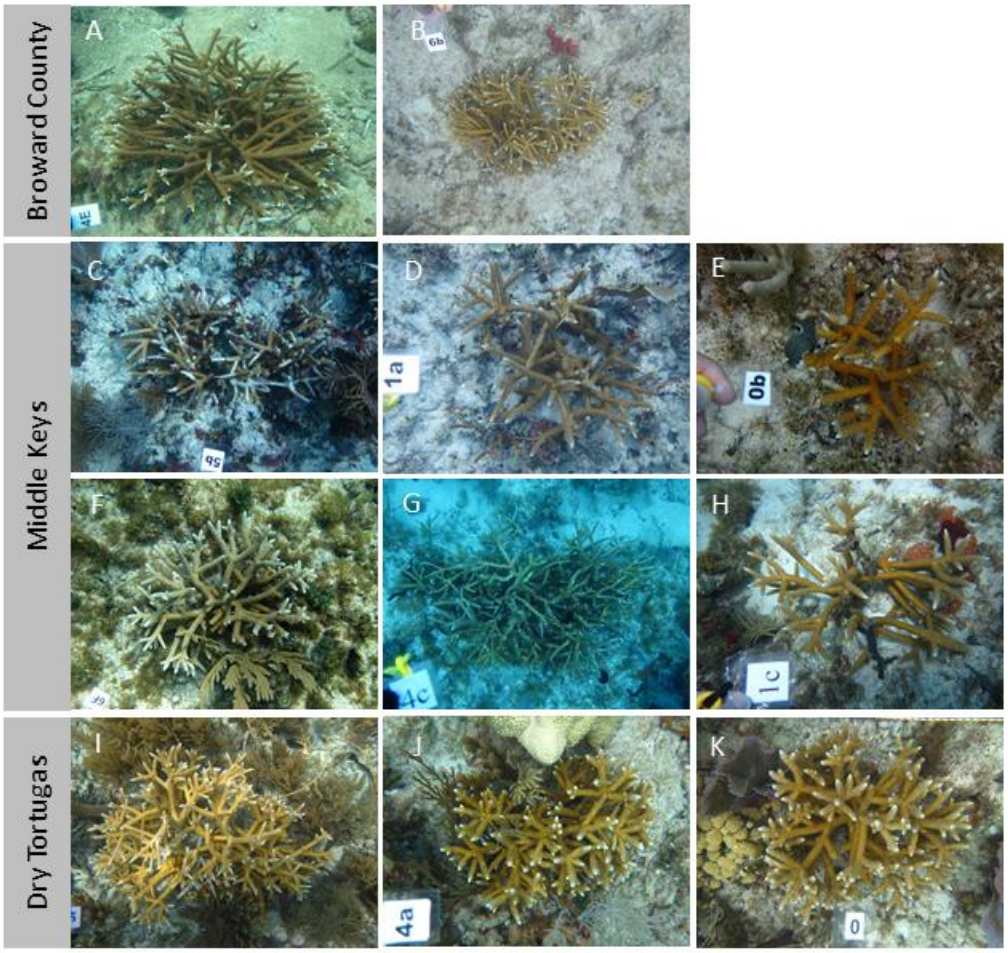

Figure 2. Example images of typical colonies surveyed within each sub-region and site. Broward County sites: BCA (A) and Scooter (B), Middle Keys sites: Staghorn Party 2 (C), Staghorn Party (D), U11 (E), U55 (F), U59 (G), and U9 (H), and Dry Tortugas sites: Marker 7 (I), Off Ramp (J), and Perfection (K).

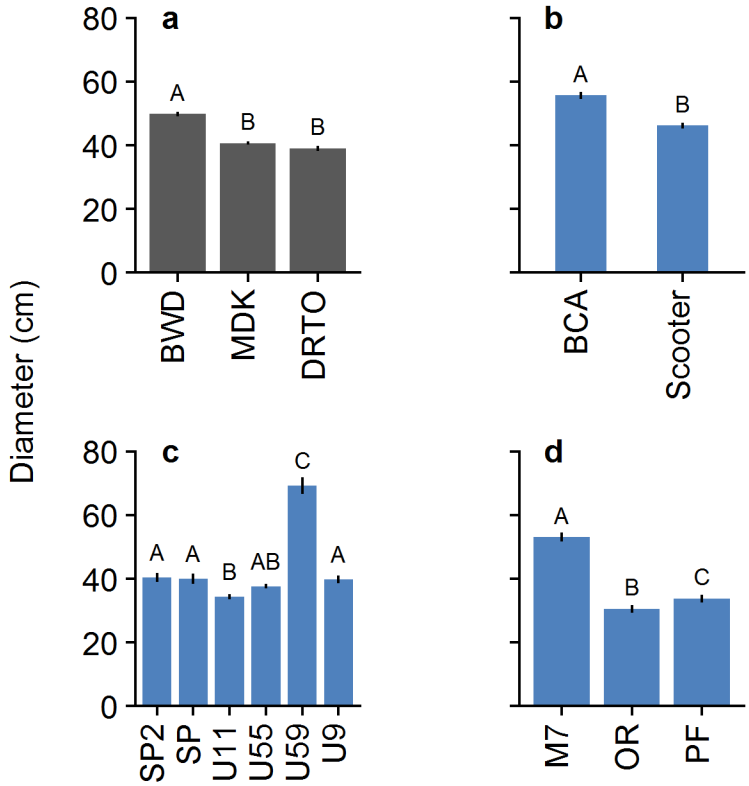

Figure 3. Mean colony maximum diameter by sub-region (a) and site within sub-region, Broward County (b), Middle Keys (c), and Dry Tortugas (d). Letters over bars indicate significant differences within groups, Tukey HSD $p<0.05$. Error bars indicate ± 1 SE.

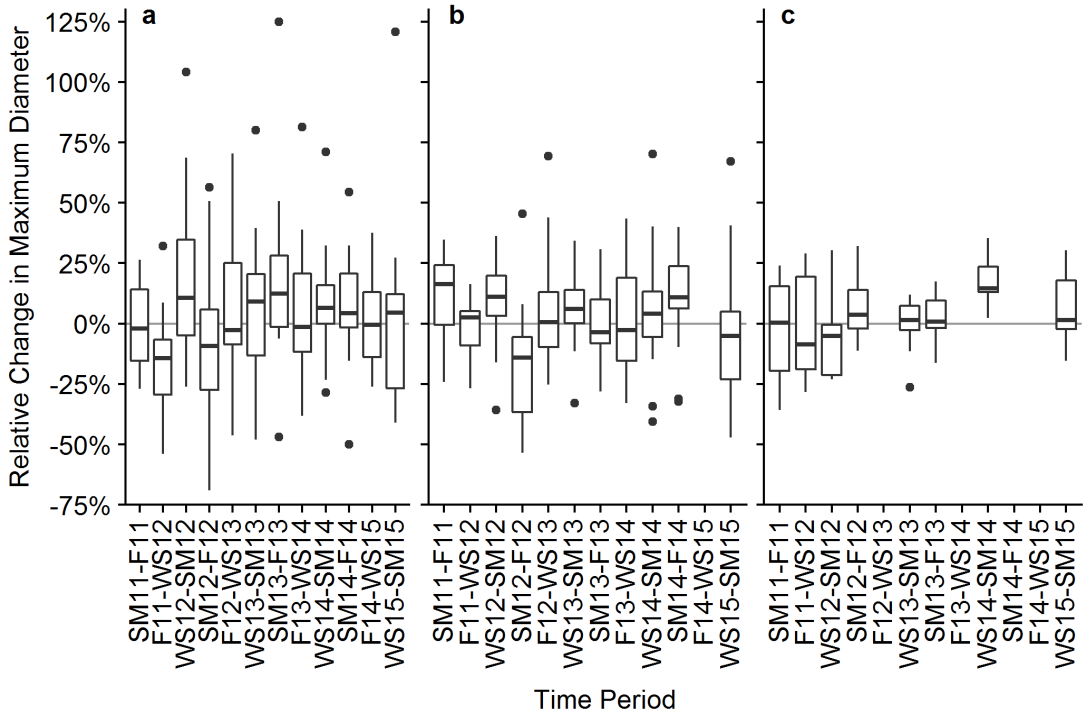

Figure 4. Relative change in mean maximum colony diameter between monitoring events by sub-region: Broward County (a), Middle Keys (b), and Dry Tortugas (c). SM11-F11 indicate the time period between monitoring events Summer 2011 and Fall 2011.

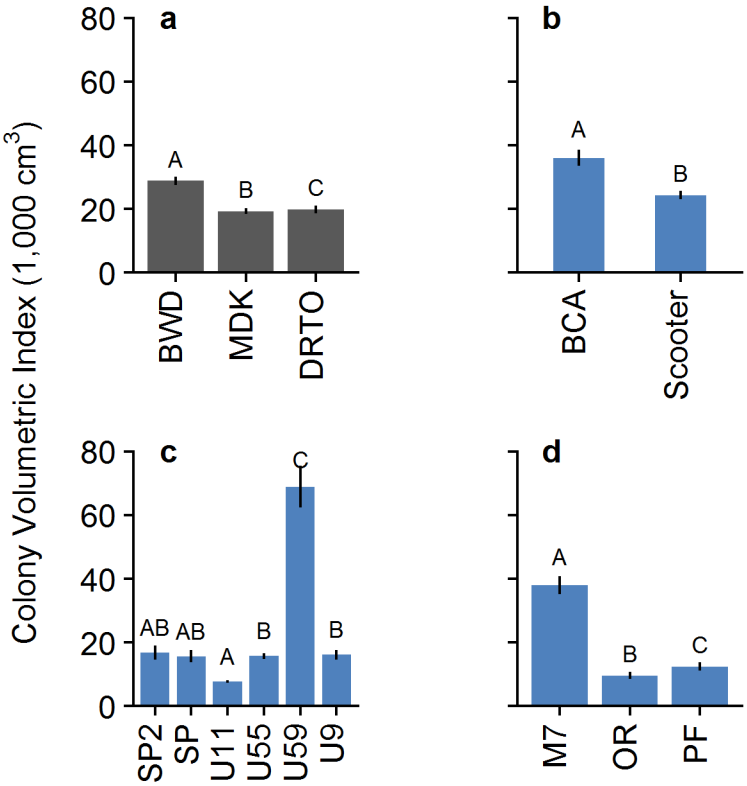

Figure 5. Mean colony volumetric index by sub-region (a) and site within sub-region, Broward County (b), Middle Keys (c), and Dry Tortugas (d). Letters over bars indicate significant differences within groups, Tukey HSD $p<0.05$. Error bars indicate ± 1 SE.

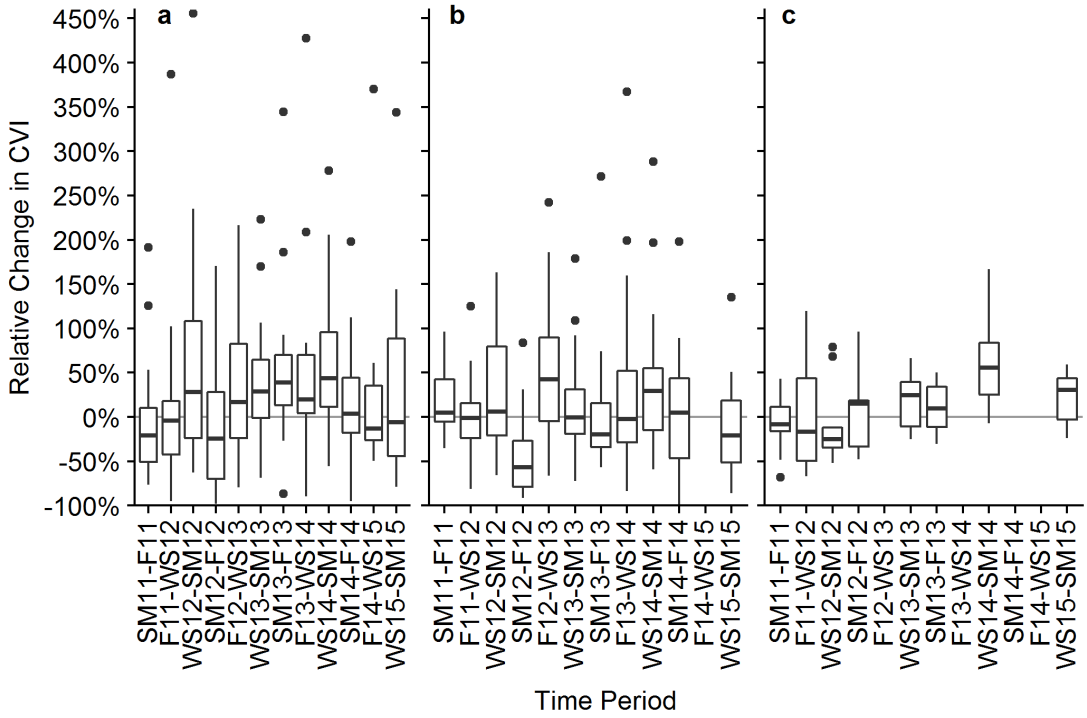

Figure 6. Relative change in mean colony volumetric index between monitoring events by sub-region: Broward County (a), Middle Keys (b), and Dry Tortugas (c). SM11-F11 indicate the time period between monitoring events Summer 2011 and Fall 2011.

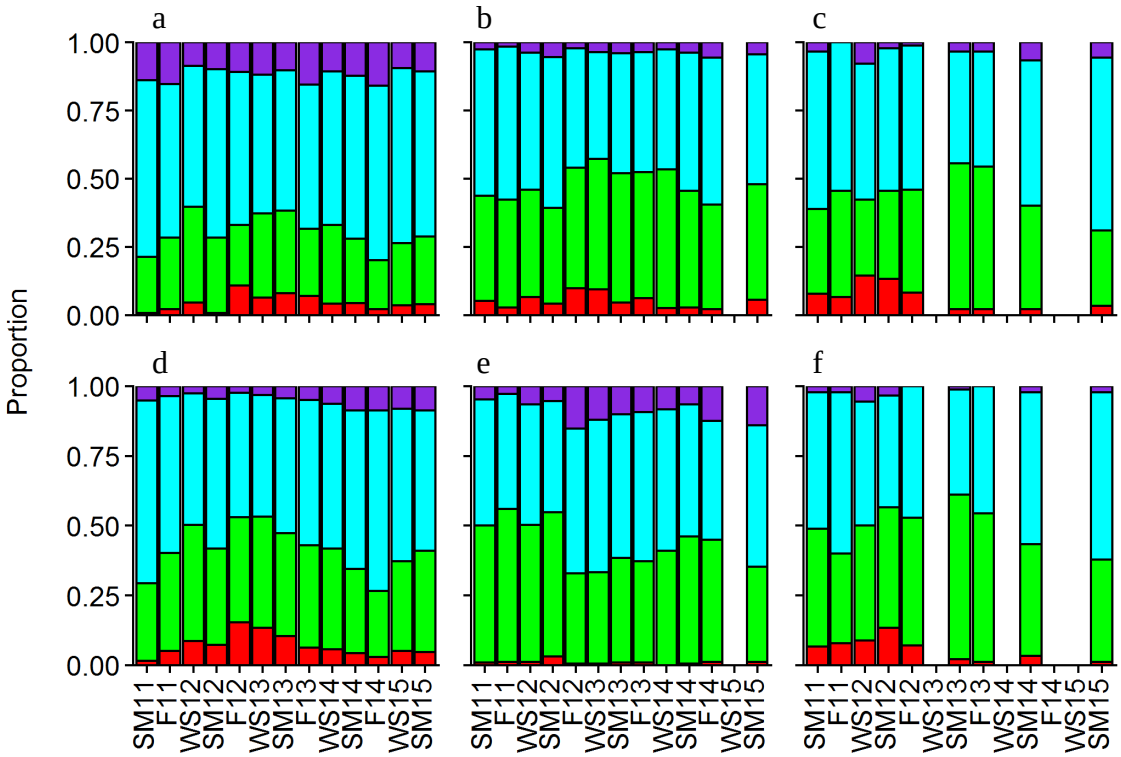

Figure 7. Distribution of colony sizes based on mean maximum diameter (a-c) and colony volumetric index (d-f) within 4 classes by sub-region: Broward County (a & d), Middle Keys (b & e), and Dry Tortugas (c & f).

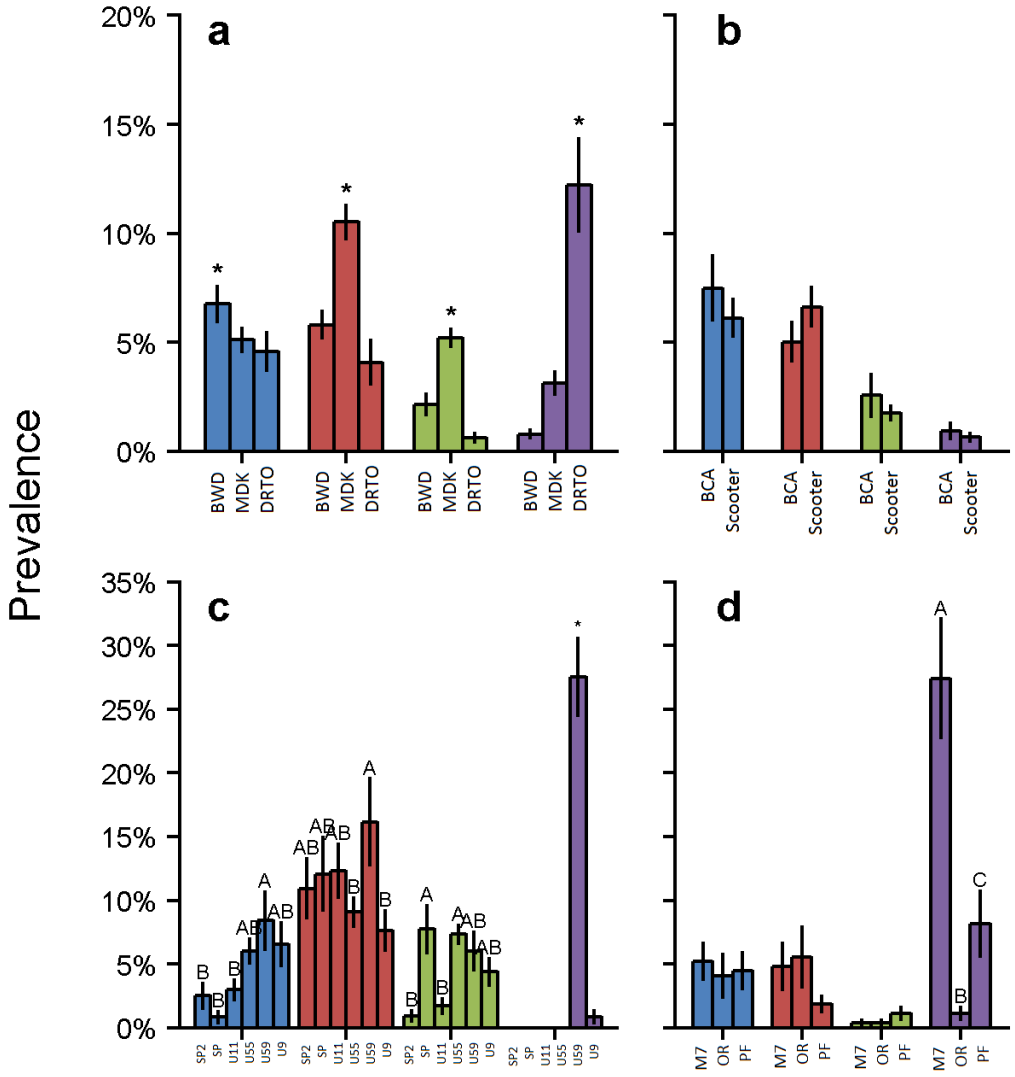

Figure 8. Mean prevalence of white disease (blue), fireworm predation (red), snail predation (green), and damselfish predation (purple) by sub-region (a) and site within sub-region, Broward County (b), Middle Keys (c), and Dry Tortugas (d). Letters or asterisk over bars indicate significant differences within groups, Tukey HSD test $p<0.05$. For clarity letters were removed from groups where there were no significant differences. Error bars indicate ± 1 SE.

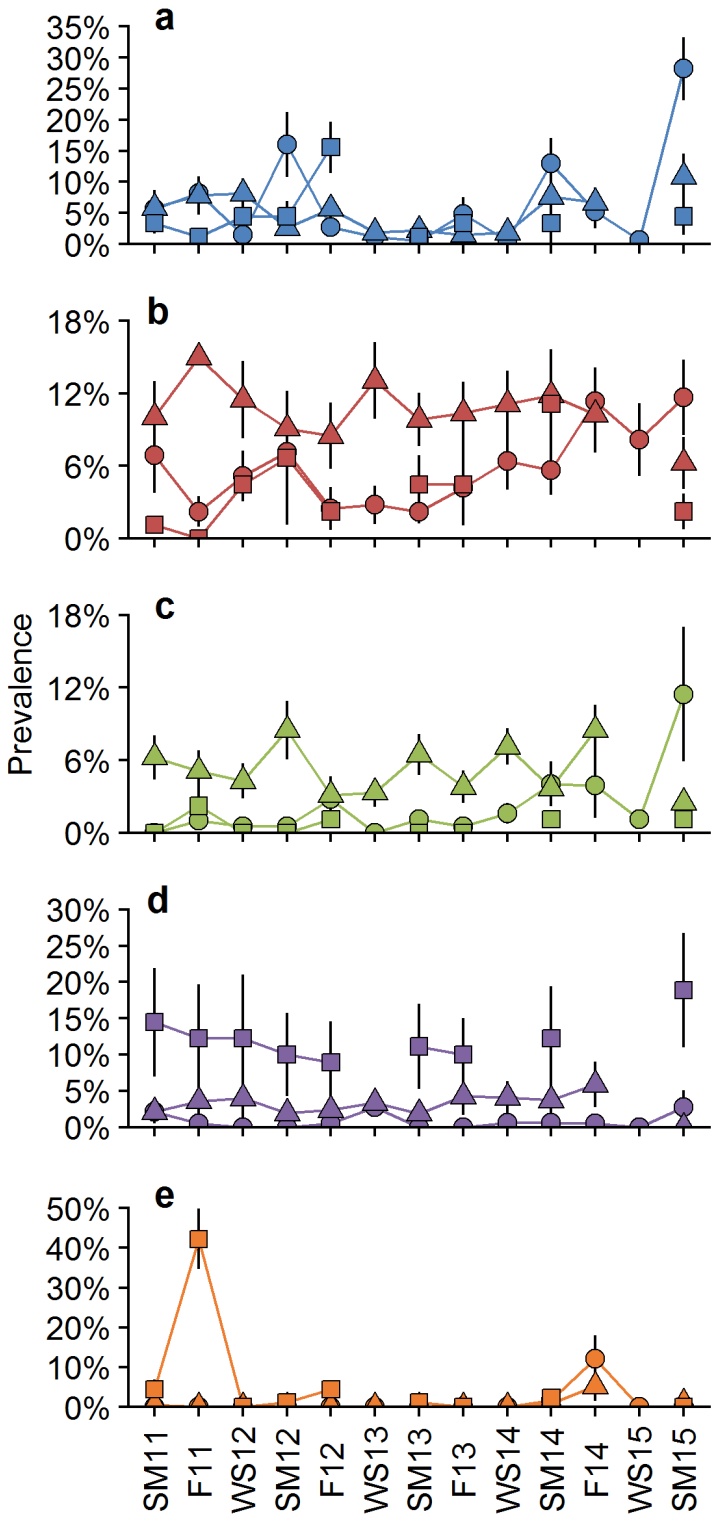

Figure 9. Temporal patterns in mean prevalence of white disease (a), fireworm predation (b), snail predation (c), damselfish predation (d), and bleaching by sub-region, Broward County (circles), Middle Keys (triangles), and Dry Tortugas (squares). Error bars indicate ± 1 SE.

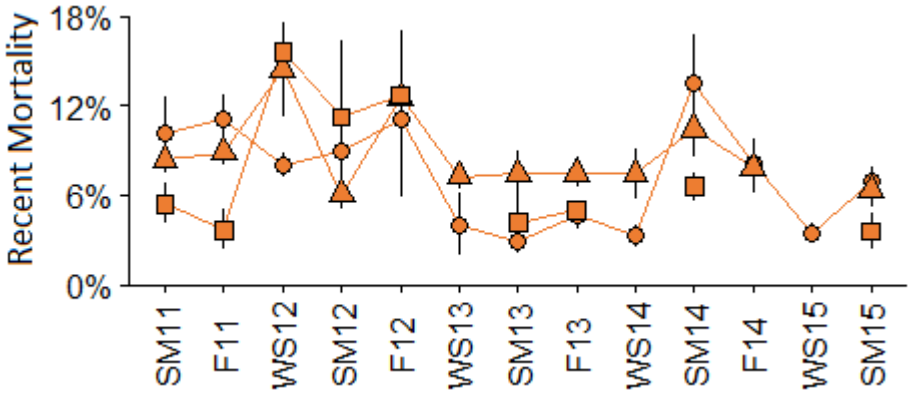

Figure 10. Temporal pattern in mean recent mortality by sub-region, Broward County (circles), Middle Keys (triangles), and Dry Tortugas (squares). Error bars indicate ± 1 SE.

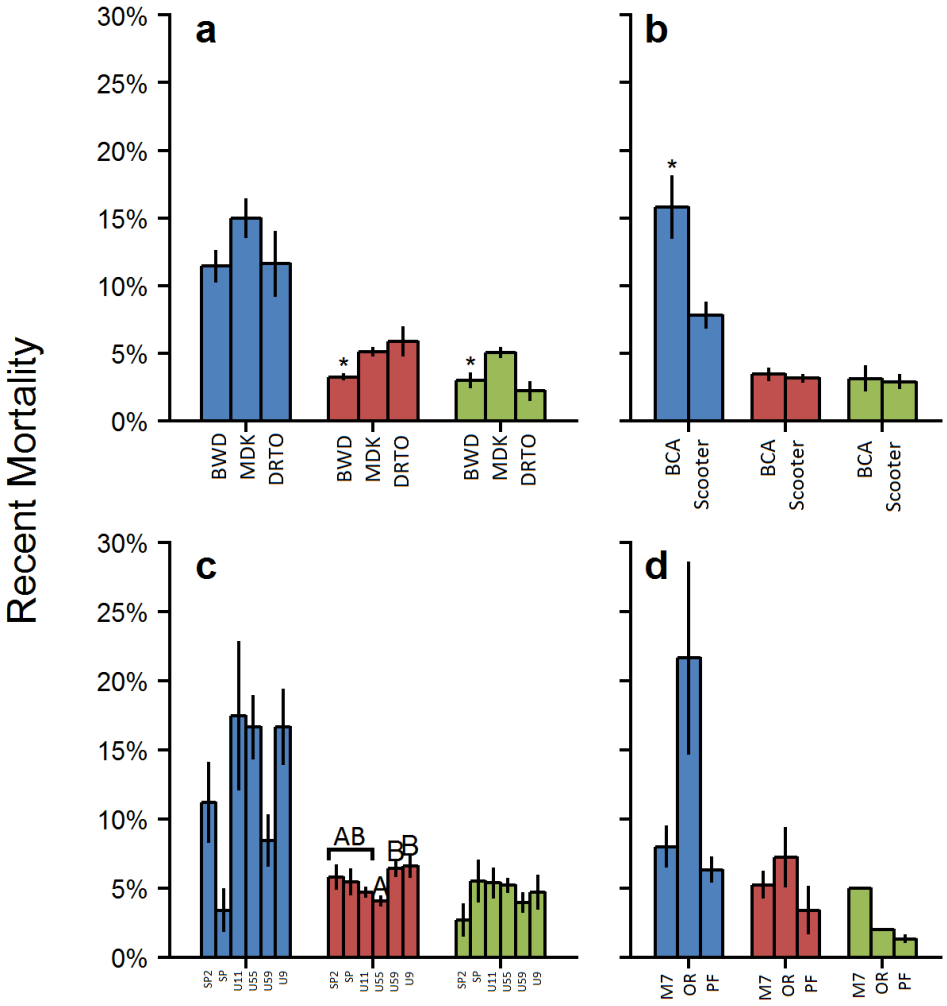

Figure 11. Mean percent recent mortality caused by white disease (blue), fireworm predation (red), and snail predation (green) by sub-region (a) and site within sub-region, Broward County (b), Middle Keys (c), and Dry Tortugas (d). Letters or asterisk over bars indicate significant differences within groups, Dunns test $p<0.05$. For clarity letters were removed from groups where there were no significant differences. Error bars indicate ± 1 SE.

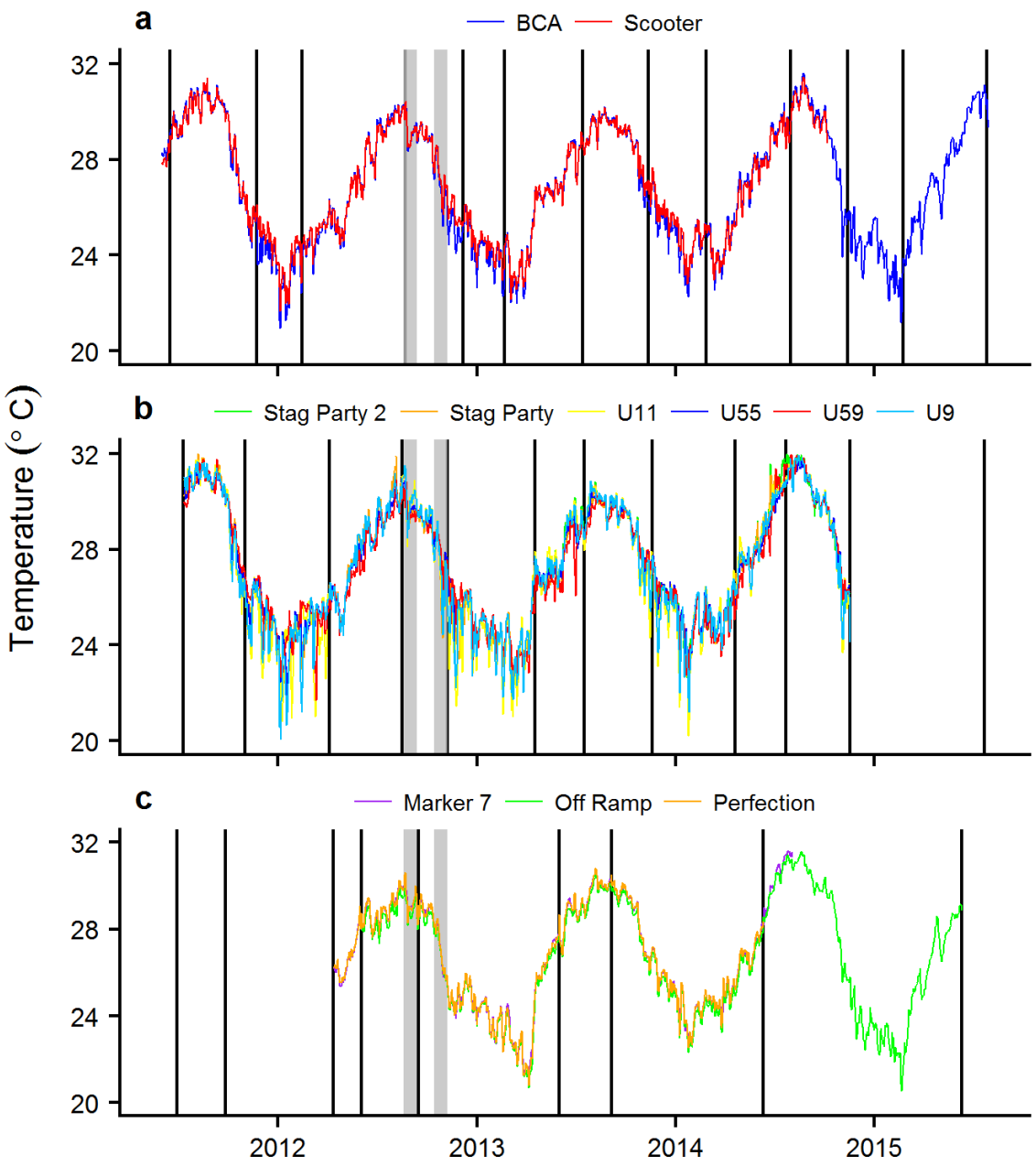

Figure 12. Daily mean in situ water temperature by sub-region, Broward County (a), Middle Keys (b), and Dry Tortugas (c). Black lines represent monitoring events and grey bars represent Tropical Storm Isaac and Hurricane Sandy from left to right, respectively.

Chapter 3: *Acropora cervicornis* colony residence time and retention rates: implications for long-term monitoring

Abstract

Monitoring of individual ephemeral coral species such as *Acropora cervicornis* is difficult because they can fragment or become displaced, yielding individual colonies nearly impossible to track long-term. However, much of the remaining *A. cervicornis* exist as low density populations comprised of individual colonies, and we must understand individual colony dynamics of the species in order to develop proper monitoring guidelines and success metrics for population enhancement programs. In this study, the spatial and temporal components of *A. cervicornis* colony residence and retention were explored by 1) measuring changes in colony abundance, 2) evaluating two methods for colony fate tracking (tagging vs a non-tagging systematic approach, 3) estimating colony residence times (how long a colony will stay in the survey area) and retention rates (likelihood of a colony remaining till the next survey period), and 4) determining if colony size effects colony residence. All parameters were measured within 3.5 m radial plots (n=56) established between numerous sites (n=11) in three sub-regions of the Florida Reef Tract (Broward County, Middle Keys, and Dry Tortugas) from June 2011 to July 2015. Colony residence times were similar between methods used for fate tracking and less than 16% of colonies remaining after two years. A majority of colony loss came from complete colony dislodgement and not mortality. Mean colony abundance by sub-region did not change significantly between survey events; however, median colony residence time was less than one year, and three month retention rates were between 29-88% for all sub-regions, indicating significant and frequent colony movement within sites. The probability of a colony remaining through the end of the study was over three times greater in the Dry Tortugas (0.12) sub-region than Broward (0.03) and Middle Keys (0.04). Residence and retention rates changed by season and monitoring event; however, patterns were not consistent amongst sub-regions. Colony size had a positive effect on retention time although the relationship was weak (between 9 and 19%). The high rates of colony fragmentation and dislodgment presented here are problematic for the long- term survival of this species, as continuous fragmentation does not allow for recovery and growth and reduces fertility rates. Furthermore, our data show that fate tracking of tagged colonies is likely underestimating population growth, propagation, survival, and health of the species, ultimately suggesting the need to modify how *A. cervicornis* are being monitored to describe long-term success and species recovery.

Keywords: Fate-tracking, residence, transient corals, survival, monitoring

Chapter Citation: Goergen, E.A., and Gilliam, D.S. (In Prep). *Acropora cervicornis* colony residence time and retention rates implications for long-term monitoring.

Introduction

Acropora cervicornis is a dynamic coral species that has a temporal component to its distribution. This dynamic characteristic along with its fast growth rate indicate that this species can shift across or even skip life history stages from isolated colony to larger patches to fragments, re-defining the reefscape under the right conditions. The opposite is also true, high energy events or disturbances can cause widespread fragmentation reducing populations to loose fragments that can travel 10's of meters, and unless conditions, substrate, and fragment health are suitable for re-attachment populations could quickly be lost. Similar losses can occur following disease and predation events.

Current monitoring metrics do not accurately describe long-term survival of *A. cervicornis* due to its dynamic characteristics (Smith et al. 2005; Williams et al. 2006). Monitoring methods have long existed for other sessile benthic organisms (stony corals, sponges and gorgonians), but none have been able to accurately capture long-term data on *A. cervicornis* colonies or populations (Bruckner and Hourigan 2002). Most long-term monitoring methods use individual colony monitoring (fate-tracking) or permanent transects; however, *A. cervicornis'* ability to frequently fragment and become dislodged, often reattaching elsewhere, makes fate-tracking difficult. Survival has typically been recorded as loss of cover or site abundance. To our knowledge, the only data defining wild *A. cervicornis* colony survival over a long-term period is Knowlton et al. (1990); most studies end at 1 or 2 years (Mercado-Molina et al. 2015; Schopmeyer et al. 2017). Knowlton et al. (1990) reported survival of less than 10% within 4 years, which also included colonies that became dislodged, but could be positively identified through colony drawings or cable ties around branches. One year survival rates depended on the year, colony size, and the location, and were between 40-80 %. There are also a few records of *A. cervicornis* survival from population enhancement programs which report high (57-80%) short term survival (2 years or less) (Bruckner and Bruckner 2001; Hollarsmith et al. 2012; Mercado-Molina et al. 2014; Schopmeyer et al. 2017; Goergen and Gilliam 2018) and low long-term survival ranging from 25% after 5 years (Garrison and Ward 2008) to 0% after 15 years (Garrison and Ward 2012). All of these allude to

colony loss through dislodgement or fragmentation; however, fragment re-attachment was only mentioned as occurring in two studies (Knowlton et al. (1990); Goergen and Gilliam (2018)). By only fate-tracking individuals, large scale ecological benefits, such as expansion and growth through propagation, may be missed in these studies. Because a majority of the remaining populations exist as isolated colonies it is imperative to determine the time colonies can be expected to reside in a given area in order to understand the dynamics of this species, accurately gauge the potential for population persistence and recovery, and have a metric by which population enhancement programs can gauge their success.

The objectives of this study were to evaluate if individual fate-tracking of *A. cervicornis* is appropriate for long-term colony monitoring using two methods, and to determine colony residence and retention time by systematically tracking colonies within a designated area. The influence of colony size and spatial and temporal components will also be compared within each objective as this study took place over a period of 5 years in three sub-regions on the Florida Reef Tract. The data presented here not only help elucidate *A. cervicornis* dynamics through colony monitoring, but also provides important guidelines to describe population status and health and for monitoring population enhancement projects to better define program success.

Methods

Eleven sites were established as part of a large-scale *Acropora cervicornis* monitoring program along the Florida Reef Tract in each of three sub-regions Broward County (n=2; between 26°10.0'N,80°05.4'W and 26°08.9'N; 80°05.8'W), Middle Keys(n=6 ;between 24°59.2'N, 80°27.1'W and 24°45.5'N, 80°45.9'W), and Dry Tortugas (n=3; between 24°40.1'N, 82°54.5'W and 24°38.9'N, 82°53.5'W). Within each site between 2 and 10 pins were installed marking the center of a 3.5 m radial monitoring plot. Broward County (BWD) and Middle Keys (MDK) sites were surveyed three times per year between 2011 and 2015: winter/spring (February-April; WS), summer (June-August; SM), and fall (October-November; F), Dry Tortugas (DRTO) was monitored

twice a year during the summer (June) and fall (September) between 2011 and 2015, and one winter/spring event in 2012. In the MDK sub-region, site SP2 was added in Fall 2012 and U59 was not surveyed during the final event, SM15.

During each event a species census was completed tallying all fragments and colonies within the radial plots following the methods described in Goergen et al. (In Prep). A sub-set of the colonies were used to compare colony fate tracking methods, colony residence, and retention rates following the methods described below. The full census data was used to describe changes in abundance across the study. Kruskal-Wallis rank sum tests were conducted to evaluate changes in colony abundance within each sub-region.

Colony Fate-Tracking

A total of 101 colonies were tagged and mapped and 155 were tracked using the systematic method described below for colony residence at the two BWD sites. Colonies were surveyed three times per year for two years, following the schedule outlined above. Colonies were mapped using distance and bearing from the center pin to the center of the colony. Colony dimensions (length, width, and height) were measured, percent recent and old mortality were estimated, and cause of recent mortality was documented during each monitoring. Top down photos of each colony with a colony identification marker were taken. Abundant fragmentation at each of the sites cause movement within each plot making colony identification difficult, therefore photos were used to positively identify colonies post-hoc. To test for differences in colony survival between tracking methods a Kaplan-Meier Survival analysis was conducted for the 2 year survey time.

Colony Residence and Retention

During each survey the first 10 colonies were assessed starting due North and working clockwise around the plot following the methods described above. Colonies were not tagged nor were colonies sought out (*i.e.*, the collected distance and bearing were not used in the field for subsequent surveys). This was an effort to still achieve assessment of individual colonies with the hopes that some colonies will be assessed

long-term, but without the added field effort of tagging and subsequently identifying repeated colonies. Colony data and images were used post-hoc to identify repeat colonies. Distinct items in the photos, such as sponges and gorgonians, assisted with identification of repeat colonies especially when colonies had been severely fragmented. Each colony in the database received a unique identifier and was used to track repeated colonies over time (Fig. 1). Colonies not previously identified received a new identification code. Before colonies were recorded as new they were checked against all previous survey images.

Retention rates were calculated for each survey period as the number of repeated colonies identified between two surveys over the initial number of colonies identified during that period. For example, 10 colonies were identified in the Summer 2011 (SM11) survey, using data and images from following survey Fall 2011 (F11) 6 of the 10 colonies were found to still be alive and attached resulting in a retention rate of 60%. Residence time for this study is defined as the total length of time a colony was recorded in the study area. Once a colony was entered in the database its residence time began and ended once the colony was no longer identified or the project ended. Survival is not used because the actual fate of the colony is unknown when it becomes dislodged or is no longer found in the survey area. For surveys where data were not collected in the MDK and DRTO sub-regions, rates were calculated from the previous event. New colonies identified during the last two surveys (Winter and Summer 2015) were not included in residence rates, because no meaningful data could be drawn from such a short time frame.

Kaplan-Meier Survival analyses were used to evaluate residence times between regions, site, and survey event colonies were initially added to the database using the survival package (Therneau 2015) in R Studio 3.3.1 (RStudio Team 2016). When significant, post-hoc pairwise comparisons using Log-Rank tests with a Benjamini and Hochberg p-value adjustment were performed. Kendall's tau regressions were used to evaluate the effect colony size had on residence time within each sub-region. Colony retention rates between regions and sites within regions were evaluated using Kruskal-

Wallis rank sum tests, followed by a multiple comparisons test using the pgirmess package (Giraudoux 2017) in R Studio 3.3.1 (RStudio Team 2016) when factors were significant. One-way analysis of variance (ANOVA) were performed to evaluate differences in retention rates between survey periods.

Results

Mean colony abundance per survey in BWD ranged between 10-16 colonies per plot, in MDK ranged between 18-30 colonies per plot, and in DRTO ranged between 12-23 colonies per plot and were all similar amongst survey events ($p>0.05$; Fig. 2).

Colony residence was similar between the two methods used for tracking ($\chi^2=1.3$; df=1; $p>0.05$). The majority of colony loss was observed during the first year resulting in a median time of survival of 358 days for the tagged colonies and 159 for untagged colonies (Fig. 3). Only 16 and 10% of the tagged and untagged colonies remained in their initial location after 2 years, respectively. All but 3 of the tagged colonies lost were due to complete colony mortality. Initial colony diameter of the tagged colonies ranged from 12- 165 cm and had no effect on colony survival ($\tau=0.11935$; $p>0.05$). Initial colony diameter of the untagged colonies had a similar range (2- 210 cm), but did influence residence time ($\tau=0.187487$; $p<0.01$).

A total of 761 colonies were tracked over 1,502 days in Broward, 929 colonies over 1,475 days in MDK and 275 colonies over 1,443 days at DRTO. Colony dislodgement was greatest during the first year and decreased through time in all sub-regions. Residence time was significantly different between sub-regions ($\chi^2=54.9$; df=2; $p<0.001$; Fig. 4), with a median residence time of 189 days in BWD, 269 days in MDK, and 364 days in DRTO. The probability of a colony remaining to the end of the study (~ 4 years) was 0.03 for BWD, 0.044 for MDK, and 0.12 for DRTO. Sites within BWD sub-region had similar residence times ($\chi^2=0.5$; df=1; $p>0.05$), but were significantly different between sites in MDK ($\chi^2=19.4$; df=5; $p<0.05$), where U55 had lower residence than U9 ($p<0.01$), and DRTO ($\chi^2=7.5$; df=2; $p<0.05$) where Off Ramp had a lower residence than Perfection ($p<0.05$).

For all sub-regions the majority of colonies were added during summer surveys. However, patterns are not consistent between sub-regions in seasonal residence time (Fig. 5). Residence times were similar amongst seasons in BWD (χ^2=2.3; df=2; p>0.05; Fig. 5a), winter residence was significantly lower than summer and fall in MDK (p<0.05), and fall residence was significantly lower than summer in DRTO (p<0.05). For all sub-regions, Summer 2012 median residence time was significantly reduced (p<0.05).

Colony size did not play a significant role in colony residence in BWD or DRTO, and while there was a significant association between colony size and residence in MDK it was weak (τ=0.0931; p<0.05; Fig. 6)

The mean retention rate between monitoring events (3 months to 1 year) ranged between 29-88% and was significantly different amongst sub-regions ($H_{2,56}$= 14.731; p<0.001: Fig. 7). The BWD sub-region had significantly lower retention rates than MDK (p<0.05). Sites in the BWD and DRTO sub-regions had similar retention rates (H=2.984 and 5.815, respectively; p>0.05) and in the MDK sub-region U55 had significantly lower retention than U9 (p<0.05). Colony retention rates were mostly similar across survey periods with only a few periods having significantly different retention rates in all sub-regions (p<0.001; Fig. 8). In BWD, the initial survey period and SM12-F12 resulted in significantly lower retention rates (p<0.05). In MDK, retention rates of SM12-F12 and WS15-SM15 were significantly lower (p<0.05) and in DRTO WS12-SM12 and SM13-F13 had significantly higher retention rates (Fig. 8; p<0.05).

Discussion

Our data suggest that individual colony monitoring of *Acropora cervicornis* is not an adequate method for determining long-term survival or species longevity. We show that the median residence time of an individual colony in all sub-regions is less than one year regardless of the method used for tracking colonies. A similar colony abundance across the period of the study indicated that colonies are not necessarily dying but 'moving' out of the survey area. This was also supported in the tagging study where only

3 colonies were reported as 100% dead-the rest were missing. There is a definite possibility that dislodged colonies do not survive, and we are not intending to imply a 100% success rate in re-attachment. In fact, our correlation of number of loose fragments vs change in number of colonies in the next survey is a good indication that the ratio is far from 100%. However, what these results suggest is the need to modify the way that *A. cervicornis* are being monitored, as the common permanent transect or individual colony tagging and tracking do not capture the dynamic life history of this species, likely underestimating the survival, abundance, health, and ecological benefits of the species.

Tagging, mapping, and re-location of colonies underwater can take a tremendous amount of time and effort. We have proven here that systematically tracking colonies through mapping and images, without tagging them resulted in similar outcomes. By utilizing this type of method over a broad survey area at set time points colony movement and population expansion can be captured, providing a more accurate report of colony residence and health. However, because individual colonies are not sought out, it is imperative that collection methods are similar amongst survey periods. The systematic method reduces in-water time but does take a reasonable amount of post-hoc image and data analysis time to match colonies amongst survey periods. In addition, when substantial fragmentation occurred to the colony it was difficult to positively identify the colony through images, if colony branching pattern, gorgonians, sponges or substrate features could not be used to positively identify the colony they were considered new. Whereas if colonies were tagged this type of error may be reduced as the tag could be used as a positive identification; however, this error was minimal as most of the colonies were completely dislodged between survey events leaving no remnants of the colony behind to try and identify.

Population growth for *A. cervicornis* is reliant on successful reattachment of asexual fragments as recruitment through sexual reproduction is very limited (Tunnicliffe 1981; Knowlton 1992; Vargas-Ángel et al. 2003). However, our 3-month retention rates of less than 75% and low long-term residence time (5-20%) indicate that colonies are experiencing high frequency of dislodgement and fragmentation. Both residence time

and retention rates were negatively affected by tropical disturbances (Tropical Storm Isaac and Hurricane Sandy in 2012) and periods of strong winds (typically during the fall and winter in Florida). This poses a challenge for the long-term survival of this species, as recent attachment rates of loose fragments in the BWD sub-region have been reported as only 2% (D'Antonio 2013). While higher re-attachment rates have been reported, up to 68% percent (Tunnicliffe 1983), most literature report low rates and even lower surrounding high energy, bleaching or disease events (Highsmith et al. 1980; Knowlton et al. 1981; Heyward and Collins 1985; Knowlton et al. 1990; Dollar and Tribble 1993; Miller et al. 2016). Therefore, with the likelihood that the frequency of disturbances will continue to increase (Hoegh-Guldberg et al. 2007; Ainsworth et al. 2016; Hughes et al. 2017), survival, and recovery of *A. cervicornis* may be limited.

Alternatively, colony reattachment and population growth may be occurring outside the study area. Low retention rates are not a directly correlated to colony mortality, but a measurement of colony movement and fragmentation. While it was not part of this particular study to observe population movement beyond the monitoring area, additional research conducted at the BWD sub-region sites indicate that the centroid of the populations were moving (Walker et al. 2012), supporting the notion that dislodged colonies and fragments may be moving distances greater than 7 m, propagating across sites where habitat and conditions are suitable.

Variations in environmental and benthic characteristics between sub-regions and sites likely drive the differences in residence time and retention rates. It is possible that the differences in hydrodynamics between sub-regions are affecting skeletal density — influencing fragmentation potential— and colony morphology (Chamberlain Jr and Graus 1975; Bottjer 1980; Schumacher and Plewka 1981; Gladfelter 1984; Kuffner et al. 2017). It was expected that larger colonies would have higher rates of residence and retention because they are known to have higher survival rates (Mercado-Molina et al. 2015). However, larger colonies may also fragment more frequently (Tunnicliffe 1983; Mercado-Molina et al. 2015) due to their height, small base diameter (attachment area) to colony size ratio (Schumacher and Plewka 1981), or because the base of a colony is the

oldest part of the colony and is typically devoid of live tissue possibly causing skeletal weakness.

Acropora cervicornis exists across a spectrum of sizes and forms from small fragments to 10's of meters of continuous cover and unlike other stony coral species in the Greater Caribbean it has the ability to move between these life history stages making common colony monitoring methods unsuitable for determining population status and health. Permanent linear transects likely underestimate survival, because as colonies move out of the transect they will be documented as lost, when they may still remain elsewhere in the site. And as we present herein fate tracking of individual colonies through colony tagging is only suitable for short-term monitoring, our systematic method is easily adaptable to capturing population movement while still evaluating individual colonies. To capture long-term status and trends *A. cervicornis* monitoring is most effective on a broad scale because of its low residence and retention. For short-term studies, individual colony fate tracking may be useful to document colony residence or the success of attachment methods in population enhancement studies but should not be used to describe colony survival because the fate of the colony cannot be determined once it moves out of the study area.

The stress from constant reduction in colony size and reallocation in energy for reattachment may be compromising the reproductive capacity of this species (Szmant-Froelich 1985; Szmant 1986). Following colony fragmentation, fragments may be temporarily infertile (reverse puberty) while energy is allocated toward survival and reattachment (Kojis and Quinn 1985; Szmant 1986; Smith and Hughes 1999; Lirman 2000). Additionally, Soong and Lang (1992), found the minimum reproductive size of *A. cervicornis* is 9 cm (37% of colonies tested were fertile) and fertility rates increase with size, 89% of colonies greater than 17 cm were fertile. This pattern was also observed on fragments of *Acropora* spp. where fertility of fragments was dependent on species and size, but were always lower than intact control colonies (Szmant 1986; Smith and Hughes 1999). Reproduction may be further compromised at these sites because some of the lowest retention rates (periods of high fragmentation and colony dislodgement) were

recorded between Winter and Summer events when *A. cervicornis* are developing oocytes and spermaries (Vargas-Ángel et al. 2006).

The evaluation of long-term success of most population enhancement programs is currently based on individual fate tracking of outplanted colonies, while this is a suitable method for less transient corals it is not so for transient species such as *A. cervicornis*. Outplanted colonies quickly establish themselves behaving similar to wild populations, including high frequency of fragmentation and dislodgement (Goergen and Gilliam 2018). As outplanted colonies fragment and propagate across sites, individual colony monitoring will not capture these benefits. Based on our results, we suggest that population enhancement programs include site monitoring that records colony movement, and changes in total abundance prior to and following enhancement projects to better describe the long-term success and ecological impact of restoration. Furthermore, our results indicate that within each sub-region there may be better times of the year to outplant. For instance, new colonies recorded in the summer in both the MDK and DRTO sub-regions were more likely to be repeated after 1 year than when they were first recorded in either fall or winter, whereas in BWD new colonies recorded in the fall had the highest residence. Calm seas during this period and faster summer growth rates likely contribute to colony stabilization, but because disease and bleaching prevalence are also higher in the summer (Goergen et al. In Prep) we suggest that in the MDK and DRTO population enhancement occur in late spring to early summer, prior to disease and bleaching season.

Acropora cervicornis populations are in constant flux. Presented here are the rates at which colonies remain in a particular location to prove that individual colony fate tracking of this species cannot provide an accurate long-term outlook of survival, status, and health, unless paired with additional techniques that capture colony movement and fragmentation. Individual colony data collection is still important to document population condition; however, due to low residence and the inability to track colonies after fragmentation, there will rarely be long-term data on the same individual. We therefore recommend a systematic tracking method paired with census counts to provide

an accurate long-term description of individual and population abundance, movement and health.

Acknowledgements

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Figures

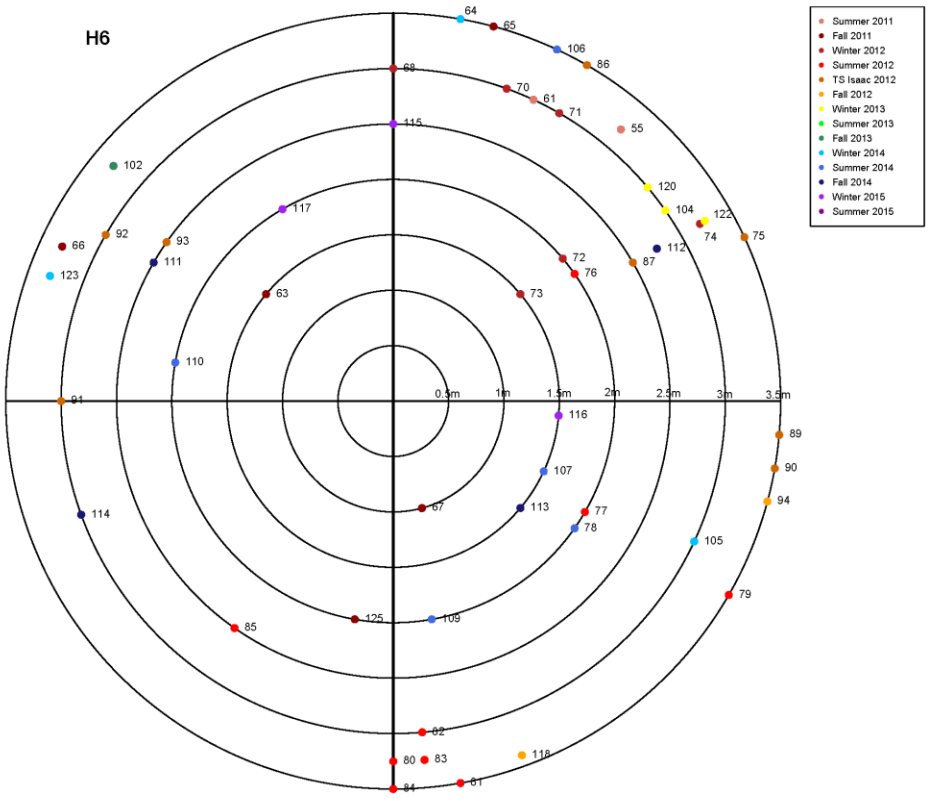

Figure 8. Example of colony movement within a plot. Each point/number represents a colony and the color of the dot represents the initial event the colony was added to the database.

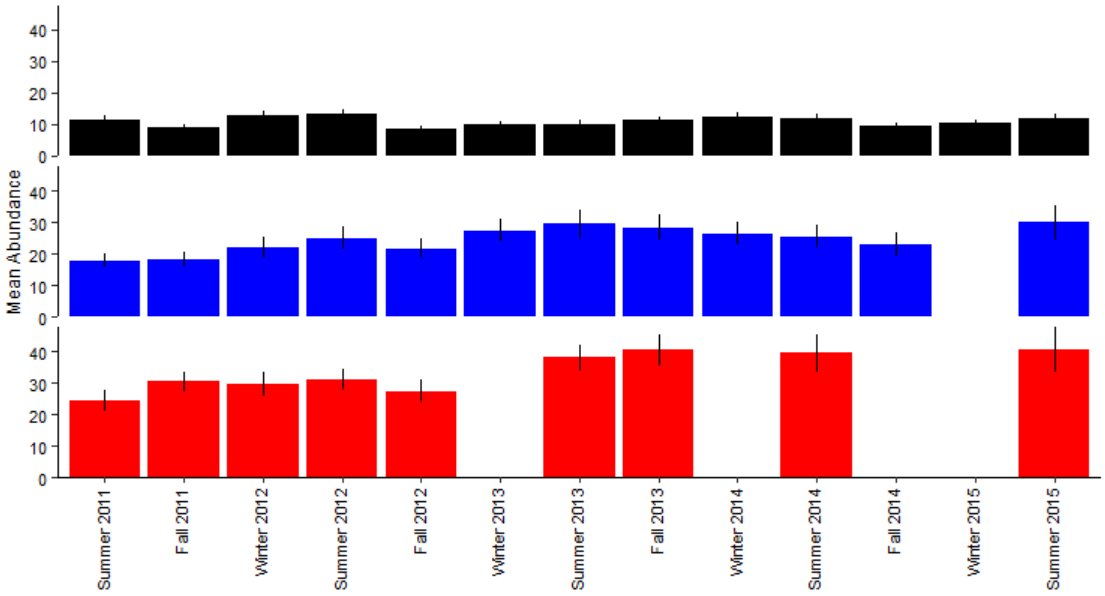

Figure 9. Mean colony abundance by plot for each sub-region, BWD (black), MDK (blue), and DRTO (red). Error bars indicate ± 1 SE.

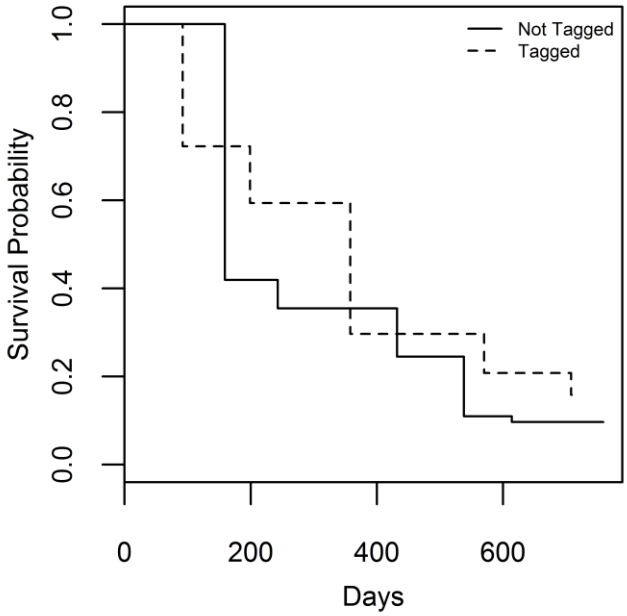

Figure 10. Survival analysis of tagged and non-tagged *Acropora cervicornis* colonies with 95% confidence intervals.

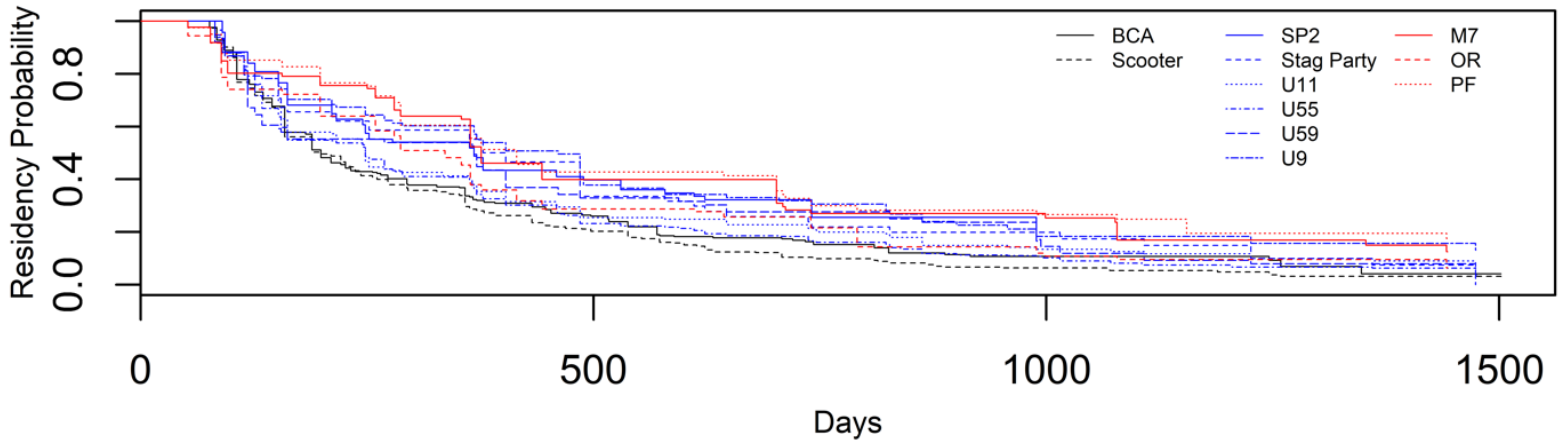

Figure 11. Colony residence probability by site and region

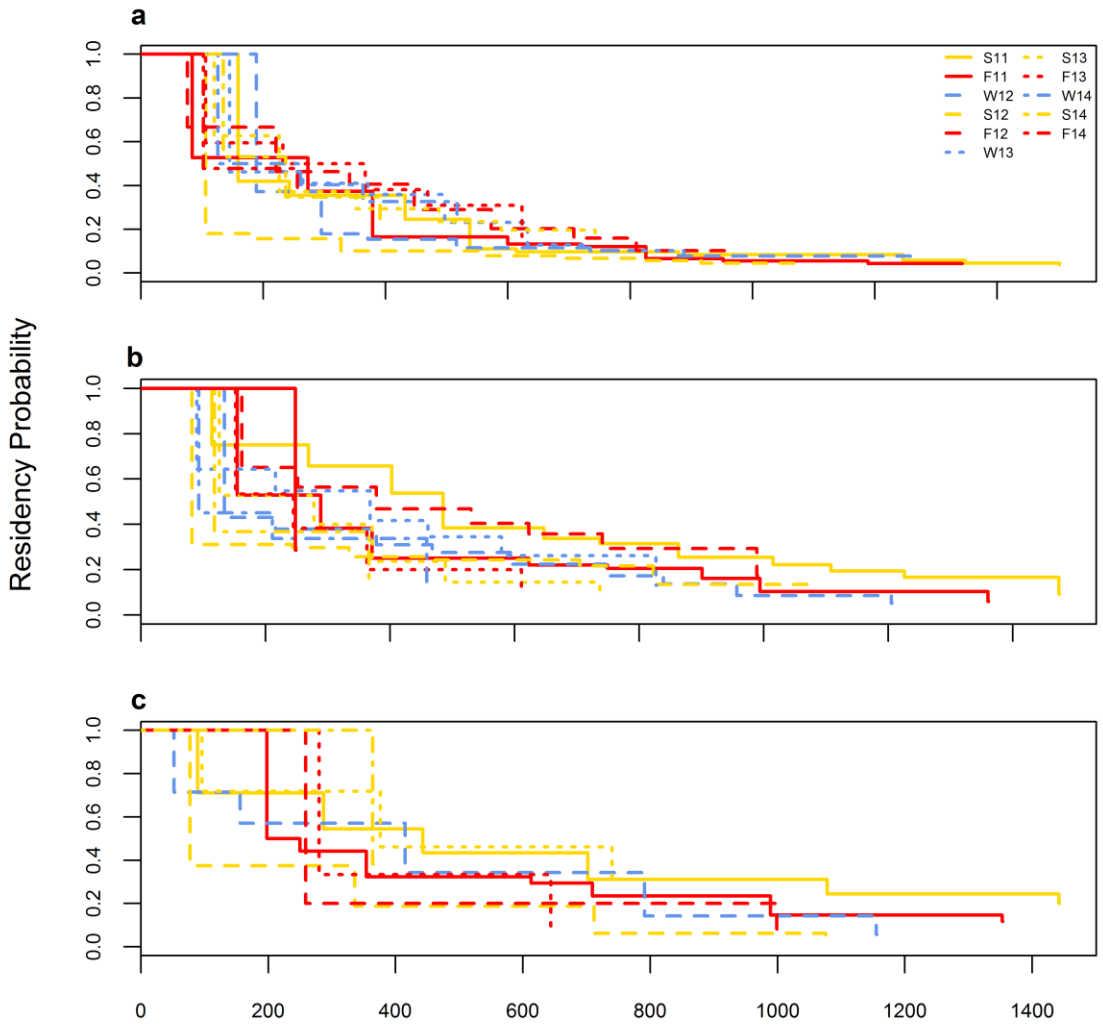

Figure 12. Sub-regional colony residence time by which season a colony was first recorded in, each line represents a survey event for Broward County (a), Middle Keys (b), and Dry Tortugas (c).

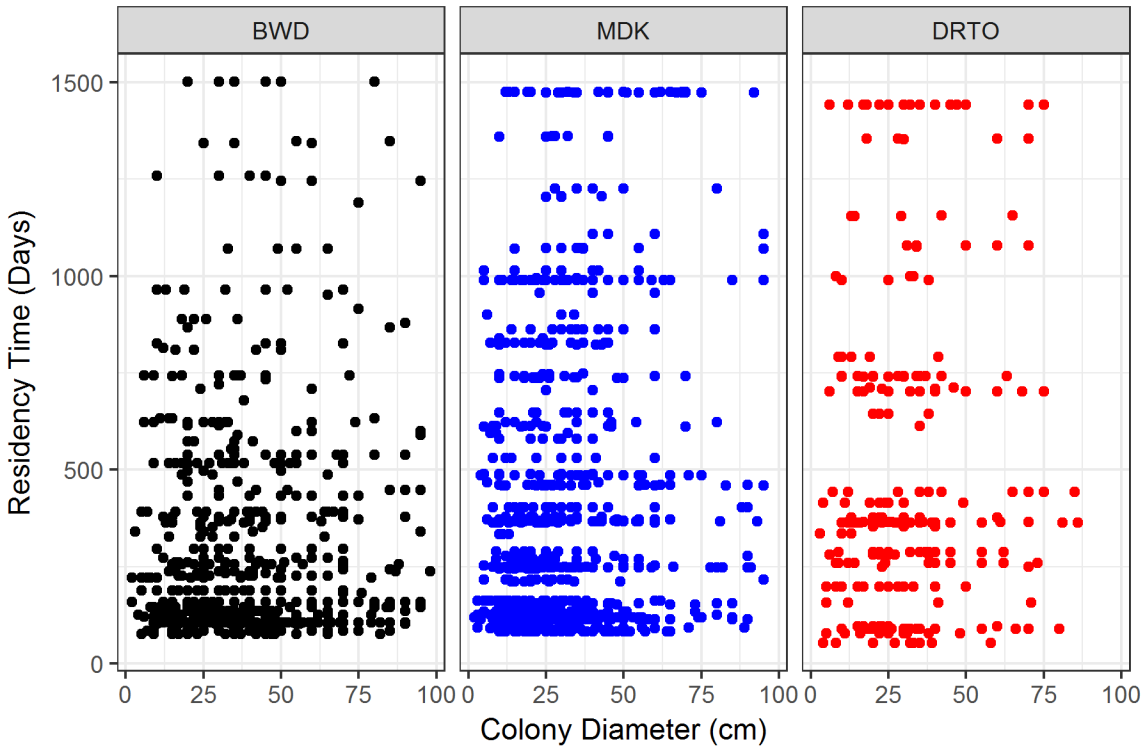

Figure 13. Correlation between colony size and residence time by region BWD (black), MDK (blue) and DRTO (red).

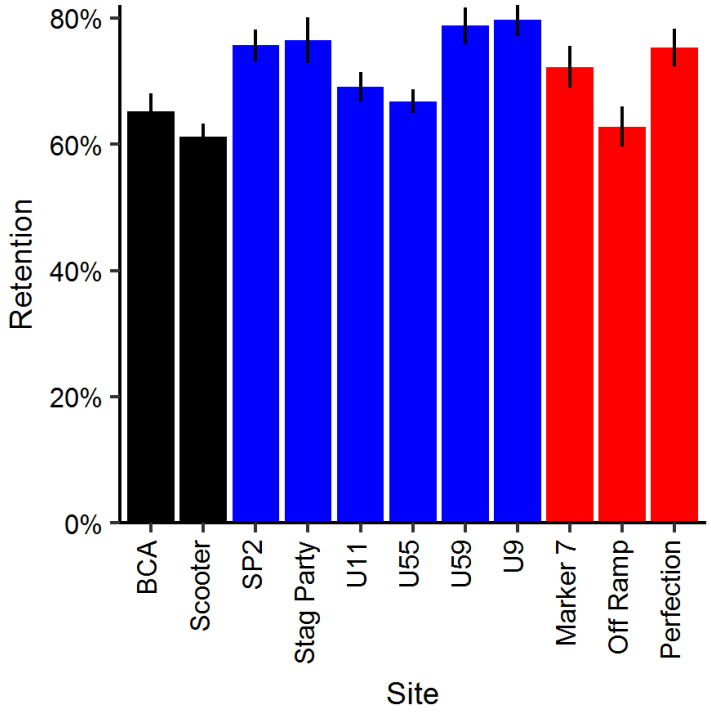

Figure 14. Mean colony retention by site and region, BWD (black), MDK (blue) and DRTO (red).

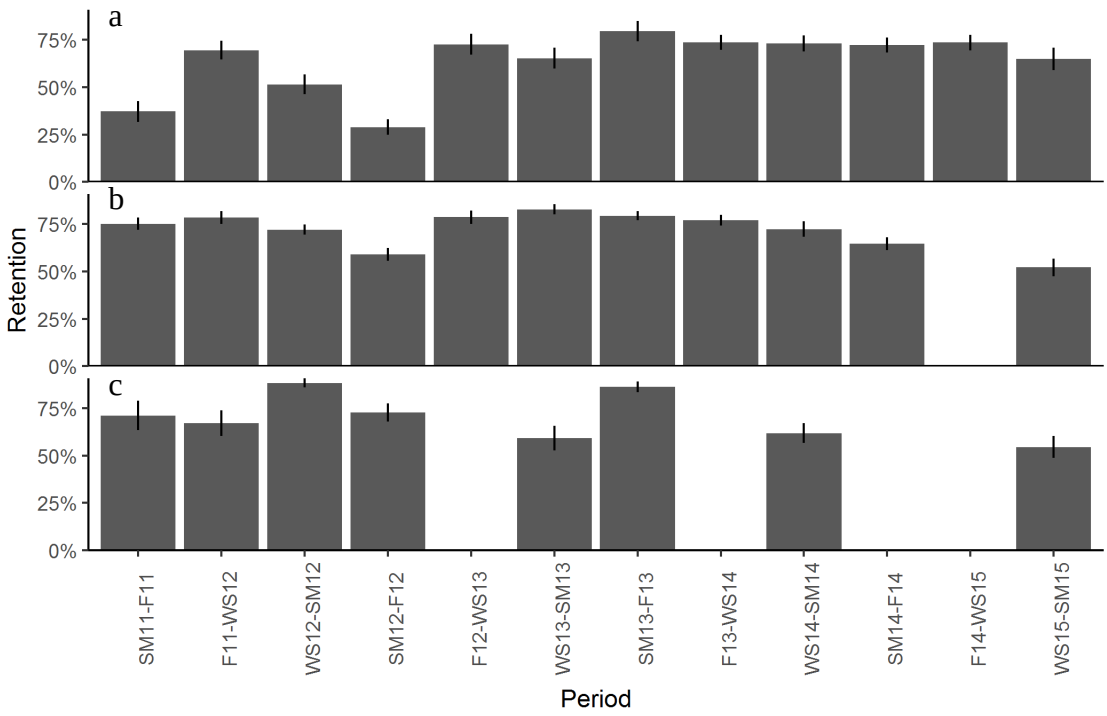

Figure 15. Mean colony retention between survey events for BWD (a), MDK (b), and DRTO (c).

Chapter 4: Outplanting technique, host genotype, and site affect the initial success of outplanted *Acropora cervicornis*

Abstract

Acropora cervicornis is the most widely used coral species for reef restoration in the greater Caribbean. However, outplanting methodologies (e.g., colony density, size, host genotype, and attachment technique) vary greatly, and to date have not been evaluated for optimality across multiple sites. Two experiments were completed during this study, the first evaluated the effects of attachment technique, colony size, and genotype by outplanting 405 *A. cervicornis* colonies, from 10 genotypes, four size classes, and three attachment techniques (epoxy, nail and cable tie, or puck) across three sites. Colony survival, health condition, tissue productivity, and growth were assessed across 1 year for this experiment. The second experiment assessed the effect of colony density by outplanting colonies in plots of one, four, or 25 corals per 4 m^2 across four separate sites. Plot survival and condition were evaluated across 2 years for this experiment in order to better capture the effect of increasing cover. Colonies attached with a nail and cable tie resulted in the highest survival regardless of colony size. Small corals had the lowest survival, but the greatest productivity. The majority of colony loss was attributed to missing colonies and was highest for pucks and small epoxied colonies. Disease and predation were observed at all sites, but did not affect all genotypes, however due to the overall low prevalence of either condition there were no significant differences found in any comparison. Low density plots had significantly higher survival and significantly lower prevalence of disease, predation, and missing colonies than high density plots. These results indicate that to increase initial outplant success, colonies of many genotypes should be outplanted to multiple sites using a nail and cable tie, in low densities, and with colonies over 15 cm total linear extension.

Keywords: Coral nursery, Coral Point Count, Florida, restoration, productivity, propagation

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Introduction

The compounding effects of human population growth, coastal construction, and climate change have caused damage to coral reef ecosystems worldwide (Schopmeyer et al. 2012; Bégin et al. 2016; Bright et al. 2016; Hume et al. 2016; Towle et al. 2016). Historically, the Caribbean staghorn coral, *Acropora cervicornis*, was one of the most important corals in terms of contributing to habitat complexity and reef framework, playing a vital role in the reef community (Goreau 1959; Goreau and Goreau 1973; Adey and Burke 1977; Neigell and Avise 1983). The mainly monotypic stands of *A. cervicornis*, also referred to as thickets, fields, stands or patches, lined the fore and back reefs, spur tops, and octocoral dominated reefs of many Caribbean, Florida and Gulf of Mexico reefs (Davis 1982; Bruckner 2002; *Acropora* Biological Review Team 2005). Its fast growth rate and natural ability to fragment allows it to spread across habitats quickly forming dense patch-like structures providing habitat to a multitude of vertebrate and invertebrate species.

More recently (since the 1980's) populations within the Greater Caribbean have become regionally isolated, existing most commonly as individual colonies or much smaller patches separated by several kilometers or more. The major decrease in the species seen throughout the Caribbean in the 1970's and 1980's was caused by a white band disease outbreak (Gladfelter 1982; Bythell et al. 1989; Bythell et al. 1993; Aronson and Precht 2001; *Acropora* Biological Review Team 2005). Since this dramatic decline, recovery has been limited with few known high cover populations remaining throughout the species range (Vargas-Ángel et al. 2003; Keck et al. 2005; Grober-Dunsmore et al. 2006; Lirman et al. 2010; Walker et al. 2012; D'Antonio et al. 2016). With the loss of these three dimensional structures comes the loss of an unprecedented amount of habitat. In 2006, *Acropora cervicornis* was listed as threatened under the US Endangered Species Act (National Marine Fisheries Service 2006) and in 2008, listed as critically endangered on the World Conservation Union (IUCN) red list (Aronson et al. 2008). While controlling stressors like human population growth, coastal construction, and climate change is difficult, it is as challenging to perform coral reef restoration in the face of these stressors. However, together with effective and active management plans we can

use coral reef population enhancement techniques to attempt to increase resilience of the remaining populations.

Restoration activities specifically for *A. cervicornis* began in 2001 (Bowden-Kerby 2001) and have since increased exponentially (Johnson et al. 2011). Young et al. (2012) reported over 60 programs working on *Acropora* spp. restoration in the Caribbean. Most of these programs are successfully increasing the abundance of *A. cervicornis* on numerous reefs and are now collectively outplanting 10's of thousands of corals a year (Schopmeyer et al. 2017). As mass outplanting becomes more common the best techniques to ensure initial colony survival and growth need to be determined. Outplant designs should incorporate experimentally derived best practices for appropriate colony size, density, attachment technique, site, and host and symbiont genotypes (Griffin et al. 2012; Hollarsmith et al. 2012; Lirman et al. 2014; Mercado-Molina et al. 2015). In this study, we evaluated the effect of host genotype, density, outplant size, and attachment techniques across multiple sites on initial success (within 1- 2 years) of outplanting. It is important that colonies survive and grow large enough during the first year following outplanting so that they can contribute to natural populations through sexual reproduction and fragmentation. It is also important to understand differences amongst genotypes and their growth, survival, and health under the same environmental conditions (same outplant site), as these results could inform restoration practices and improve success. For example, genetic diversity increases the likelihood of successful sexual reproduction, and outplanting slower growing genotypes at larger sizes would allow them to contribute to sexual reproduction more quickly. Therefore, success herein is defined by initial colony survival in the location in which they were outplanted similar to that observed in other population enhancement programs or in the wild (>50%), colonies are exhibiting growth and productivity (increasing abundance and complexity on the reef) and relatively low prevalence of disease and predation.

Methods

Size and Attachment Technique

Corals were outplanted March 2015 to three sites on the nearshore ridge complex of Broward County, Florida at depths between 4-5 m. At each site, corals were outplanted to three arrays using 10 genotypes, three attachment techniques: 1) two-part epoxy ("epoxy"), 2) masonry nail and cable tie ("nail") or 3) cement puck ("puck"), and four size classes: 1) small (5-15 cm total linear extension (TLE)), 2) medium (16-35 cm TLE), 3) large (36-60 cm TLE), and 4) x-large (61-160 cm TLE). Coral host genotype was previously determined by Baums et al. (2010) using microsatellite markers. Forty-five colonies were outplanted to each array with genotype, colony size, and attachment technique randomly assigned within each array at each site (Fig. 1). Small colonies for all attachment techniques and medium nail colonies were outplanted upright, whereas medium puck, medium epoxy, and all large and x-large colonies were transplanted horizontally to ensure colony stability (Fig. 2). Medium and large/x-large epoxy colonies were attached with two and three epoxy points, respectively. Each size class/attachment technique combination was replicated a minimum of 27 times within the three sites for a total of 405 corals (Table S1).

Monitoring occurred at 1, 4, 8, and 12 months post-outplanting. Individual colony survival (alive, dead, or missing), percent tissue mortality, and prevalence of conditions (predation, disease, and bleaching) were recorded. Colonies were considered alive if they were found in the location where they were outplanted and any live tissue was still present. The cumulative prevalence of each condition was calculated by adding the number of colonies affected by each condition during the year divided by the sum of susceptible colonies (colonies with live tissue) during the same period.

Colony growth and productivity analysis was completed using images of each coral taken from the same direction, with a scaling object for calibration, taken upon outplanting and at 1 year post-outplanting. TLE per colony (sum of all branch lengths and central axis) was determined using the tracing feature in Coral Point Count with Excel extensions 4.1 (CPCe)© (Kohler and Gill 2006) (Fig. S1). Multiple images were used per colony for the 1 year monitoring to ensure complete colony coverage because of increased colony complexity (Fig. S1b & S1c). Only colonies that survived the entire

year were included in the growth and productivity analysis. Each colony was traced by three different researchers and the average TLE was used for analysis, when variation between TLE measurements was greater than 15% colonies were re-analyzed by all researchers. Annual productivity was estimated from the sum of length of tissue/coral produced over 1 year divided by the initial sum of length of tissue/coral per colony ($(TLE_{final}-TLE_{initial})/TLE_{initial}$) (Forrester et al. 2011; Lirman et al. 2014) and growth was estimated by $TLE_{final}-TLE_{initial}$.

Colony survival, productivity, growth, partial mortality, and prevalence of conditions were compared among size classes, attachment techniques, genotypes, and sites. Genotype 2 was excluded from this analysis because of a low number of replicates (Table S1). Data for each analysis were tested for normality using the Shapiro-Wilk test, normality assumptions were not met for survival, partial mortality, and prevalence of conditions data and therefore non-parametric tests were performed. Attachment success was evaluated using Kaplan Meier survival analysis with log rank tests (Survival Package- RStudio 2016). In order to evaluate success of attachment technique, missing colonies were considered dead in the survival analysis, because although missing colonies may not have died, they did not successfully attach and their fate was unknown. Kruskal-Wallis tests by ranks were used to explore the prevalence of conditions and partial mortality between size classes, attachment techniques, genotypes, and sites. Post-hoc multiple comparisons of mean ranks between groups with a Bonferroni adjustment were employed when significant differences between groups were found. The Bonferroni correction was calculated by $p=2*(1-Pr(Z<z'))*k*(k-1)$, where k is the total number of groups in the comparison (Statistica 13.0 ©). One-way analysis of variance (ANOVA) were used to assess the differences in colony productivity and growth (log(x+100) transformed data) between colony size, attachment technique, genotype, and site. Post-hoc comparisons between groups were performed using Tukey's HSD tests. All analyses were performed using Statistica 13.0©.

Density

Outplanting occurred in May 2013 at four sites on the nearshore ridge complex of Broward County, Florida at depths of 3-6 m. Colonies were outplanted to 4 m^2 plots in three density treatments: 1) low - 1 colony, 2) medium - 4 colonies (2 m spacing), and 3) high - 25 colonies (50 cm spacing) (Fig. 3). Three replicate treatments were installed at each site and arranged using a random block design with a minimum of 15 m between treatments. Wild *A. cervicornis* colonies within 5 m of each treatment were relocated within the site in order to avoid interference with the treatments. Outplant colonies of approximately 30 cm TLE from 11 genotypes were attached to the substrate using a masonry nail, cable tie and two-part epoxy. Multiple genotypes (randomized across all treatments and sites) were used to control for the effect of genotype and in turn represent a natural population, therefore genotype was not used as a factor in the analyses for this experiment.

Individual colony survival, partial mortality, and condition data were collected quarterly for 2 years, following the methods outlined above for the size and attachment technique experiment. These data were used to calculate plot survival, colony partial mortality, and prevalence of conditions. Data were divided into 0-1 year post-outplanting and 1-2 years post-outplanting to evaluate the effects that increasing colony size and cover of the treatments had on colony survival, partial mortality, and condition. Plot survival and conditions were compared among treatments, between years, and between sites. Survival of each plot was calculated at the end of 1 and 2 years by dividing the number of colonies alive by the total number of colonies at the start of each year. Kruskal-Wallis tests by ranks were used to explore plot survival, the prevalence of conditions, and partial mortality between treatments and years. Post-hoc multiple comparisons of mean ranks between groups with a Bonferroni adjustment (see above) were employed when significant differences between groups were found.

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Results

Size and Attachment Technique

Survival for all treatments combined after 1 year was 77%. Colonies outplanted using a nail and of larger size classes had the highest survival (Fig. 4A & 4B). Colony survival differed significantly between attachment techniques (X^2=6.47; *df*=2; p<0.05), size classes (X^2=18.52; *df*=3; p<0.05), within the small size class between techniques (X^2=11.74; *df*=2; p<0.05), and within epoxy and puck techniques between size classes (X^2=19.74; *df*=3 p<0.05 for all comparisons). Genotype and site did not have a significant effect on the survival of outplanted colonies (Fig. 4C & 4D; X^2=4.87; *df*=8; p>0.05; X^2=1.35; *df*=2; p=0.51). A majority of the mortality was observed during the 8 month monitoring event (Fig. 4). Seventeen percent of the colonies became dislodged and were recorded as missing. All size classes, techniques, sites, and genotypes (except Genotype 15) had missing colonies. However, the number of missing colonies was only significantly different among attachment techniques and size classes (Kruskal-Wallis; H=9.65 and 10.41; p< 0.05).

Mean percent partial mortality, not including colonies that died, was 5.7 ± 0.93 SE% and was attributed to disease, predation, sediment burial, or unknown causes. Total prevalence of disease (rapid tissue loss and white band disease) and predation, by *Coralliophila abbreviata* (corallivorous snail), were lower than 1.5% during each monitoring event (Fig 5A). Predation by fireworms (*Hermodice carunculata*) was not observed. Mean partial mortality was significantly different amongst size classes, genotypes, and sites (Fig. 5B; Kruskal-Wallis; H=15.22, 14.33, and 9.13; p<0.05 for all comparisons). Treatment did not have a significant effect on the prevalence of disease or predation (Fig. 5; Kruskal-Wallis; p>0.05).

Mean colony productivity (sum of all branch lengths) was 3.03 ± 1.5 SE cm/cm initial tissue length, with 32,533 cm of new coral produced from the 12,643 cm coral

initially outplanted. Mean growth rate was 111.15 ± 5.4 cm/year. Productivity was similar across all three attachment techniques (Fig. 6A; F=1.92; *df*= 2; p>0.05). Small colonies had significantly higher mean productivity (4.37 ± 4.5 cm/cm initial tissue length) than any other size class (Fig. 6A; F=9.71; *df*=3; p<0.05). Productivity varied significantly among genotypes ranging from 2.2 to 4.5 cm/cm of initial tissue length (Fig. 6A; F=3.68; *df*=8; p<0.05). Colonies outplanted at Staghorn City had a significantly higher productivity than the other two sites (F= 13.714; *df*=2; p<0.05). There were no significant differences in productivity within a size class between attachment techniques (F=1.49; *df*=6; p=0.18). Colonies attached with epoxy or pucks had significantly higher survival with larger colonies (Fig. 7A; Tukey HSD p<0.05 for both comparisons). Small colonies attached with nails and pucks had significantly higher mean productivity than medium and x-large colonies, respectively (Fig. 7B; Tukey HSD p<0.05 for both comparisons). Colony growth or the amount of coral produced per fragment increased significantly with colony size (Fig. 6B; F=7.45; *df*=8; p<0.05) and between genotypes and sites (Fig. 6B).

Density

Survival between treatments was similar after 1 year (Fig. 8A & Table S2; Kruskal-Wallis; H=4.76; *p*>0.05), but significantly different after 2 years (Kruskal-Wallis; H=15.96; *p*<0.05). Low density treatments had the highest survival (Fig. 8A). Mean number of colonies missing was significantly higher in the high density treatments than the medium and low densities (Table S2; Kruskal-Wallis; H=16.48; *p*<0.05).

Predation by *H. carunculata* and *C. abbreviata* and disease (rapid tissue loss and white band disease) were the most commonly recorded conditions across 2 years (Fig. 8B). Prevalence of disease and predation were significantly higher in the high density treatments during the second year than the first year (Fig. 8B & Table S2; Friedman test; X^2= 5.44 and 8.33; *p*<0.05). The only condition reported in the low density treatments was predation during year 2, which was significantly less than observed in the high density treatments in both years (Kruskal-Wallis; H=12.13 and 6.75; *p*<0.05). Disease

was never recorded in the low density treatment and was significantly less than the high density treatment during year 2 (Fig. 8; Kruskal-Wallis; H=10.58; $p<0.05$).

Mean partial colony mortality increased significantly from the first to the second year for high density treatments (Fig. 8C & Table S2; Friedman test; $X^2= 5.33$; $p<0.05$). Colony partial mortality was significantly different between treatments within both years (Fig. 8C & Table S2; Kruskal-Wallis; H= 9.06 and 15.99; $p<0.05$). During the second year partial mortality of colonies in high density treatments was significantly higher than the medium and low density treatments (Fig. 8 & Table S2; Multiple Comparisons; $p<0.001$).

Discussion

Our results suggest that outplanted colonies should be at least 15 cm TLE, spaced 1-2 m apart and attached using a nail and cable tie. Outplant efforts spread across multiple sites with a variety of genotypes will also increase the overall success of a restoration program. While there were a few genotypes that performed better (no disease and faster productivity and growth) this was only based on one year of data and could change between sites and years. The techniques used here maximize survival, ecological impact (creating habitat faster), the potential for cross-fertilization, and minimize the prevalence of disease.

Small colonies had higher productivity, but result in a lower ecological impact due to their lower growth rates, survival, morphologic simplicity (1-2 secondary branches), and sexual immaturity compared to colonies in the larger size classes. Differences in productivity and survival between size classes may be attributed to changes in energy allocation, in addition larger colonies are able to overcome adverse conditions, such as sedimentation, disease, algae interaction and predation (Loya 1976; Sato 1985; Forsman et al. 2006). As corals age and grow, reaching the size capable of sexual maturity, their energy allocation changes (Sebens 1982; Meesters and Bak 1995; Okubo et al. 2007). Corals in the small size class were not yet of the reported size of being sexually mature (Soong and Lang 1992) and consequently all their energy may

have been allocated to growth and regeneration, whereas the three other size classes are of a size capable of producing oocytes could be the cause of decreased productivity (Okubo et al. 2005). Productivity trends of our outplanted colonies was similar to that previously described for *A. cervicornis* outplant and nursery colonies (Lirman et al. 2014) as well for Pacific corals (Loya 1976; Yap et al. 1998). Productivity of small colonies during this experiment was similar to those reported by Lirman et al. (2014) for outplants in Florida, but our medium colonies were more similar to the outplant colonies in the Dominican Republic.

Differences in productivity and prevalence of conditions were seen amongst genotypes being raised in similar environments, reflecting what others have found (Osinga et al. 2011; Bowden-Kerby and Carne 2012; Griffin et al. 2012; Lirman et al. 2014; Drury et al. 2017). However, the observed variability in prevalence of disease amongst genotypes does not necessarily indicate genotypic resistance. For example, two genotypes (15 and 17) used in both experiments revealed variable results; depending on site and year, survival ranged from 40-100% and prevalence of disease, predation, and bleaching ranged from 0-3.5%, 0-2.3%, and 1.2-4.4% respectively within one genotype. These results support that caution should be used when selecting "best performing" genotypes for restoration, as evidence suggests that in addition to survival and prevalence of conditions, growth, productivity, and thermal resilience may vary between region, site and years (Tunnicliffe 1981; Harriott 1998; Lirman et al. 2014; Miller et al. 2014; Drury et al. 2017). As many unknown factors can influence initial outplanting success (e.g., unpredictable storm events, temperature anomalies, regional disease outbreaks), restoration efforts should diversify outplant arrays across multiple sites, using a variety of genotypes. If genotype is not taken into consideration in restoration projects or if they are lumped together conditions maybe masked or exaggerated. In addition, maintaining genotypic diversity within restoration programs is imperative for successful sexual reproduction. Slower growing genotypes will not contribute as quickly to sexual reproduction if outplanted as small colonies, as sexual maturity of *A. cervicornis* has been linked to colony size (Soong and Lang 1992). Therefore, it may be beneficial for

restoration programs to initially outplant colonies of or close to reproductive size to increase the likelihood of cross fertilization.

In 2015, a Recovery Plan for Elkhorn and Staghorn Corals was published by the United States National Marine Fisheries Service outlining objectives necessary to reach the ultimate goal of delisting these species as threatened under the United States Endangered Species Act (National Marine Fisheries Service 2015). Under the first objective ("Ensure Population Viability"), a staghorn coral abundance criteria was defined as: thickets (≥0.5 m diameter colonies at a density of $1/m^2$ or live staghorn coral cover of ~25%) present on 5% of the consolidated reef habitat in the fore reef zone throughout the species range and maintained for 20 years (National Marine Fisheries Service 2015). As restoration programs grow, practitioners are moving towards massive high density outplanting projects focusing on meeting this criterion. However, our results indicate that outplanting at this density (1 colony/m^2) or higher, while it may create habitat complexity more quickly, decreases the survival of the colonies and increases the prevalence of disease and predation over time. Ladd et al. (2016) reported this same trend although colony health in their study didn't significantly deteriorate until a density of 3 colonies/m^2. Although this tradeoff seems counter intuitive as historical populations of *A. cervicornis* were recorded in high densities, recall that disease killed these high density populations leaving behind remnant individuals which have continued to exist as isolated colonies and are now the material for the recovery of this species. While there are still high density populations in existence today they are few and far between and have the propensity to die or experience a great reduction in live tissue within years (personal observations). While the etiology and process of disease-induced mortality is still being explored, we have demonstrated that disease may spread more quickly and have a bigger impact on outplanted colonies which are relocated within very close proximity (<0.5 m) to each other supporting the theory that for this species disease can be spread by contact, vectors such as *C. abbreviata* or *H. carunculata* (Williams and Miller 2005; Miller and Williams 2007; Vollmer and Kline 2008; Kline and Vollmer 2011) or currents and that predators may be drawn to higher density populations for more protection or increased abundance of prey (Berkle 2004). This pattern of increased

disease and predation was not unique to outplanted colonies and was observed on wild populations surrounding the outplant sites; affecting areas of congregated colonies or patches more commonly than isolated colonies (personal observation). Furthermore, the frequency of disease reported on Arabian Gulf and Australian Reefs was greatest at high coral cover sites that had a high frequency of sea surface temperature anomalies (Riegl 2002; Bruno et al. 2007) so as the oceans continue to warm this trend could be even further exacerbated in high density populations.

The biggest cause of colony loss during this study was colonies which were displaced from their place of outplanting. While colony attachment by nail and cable tie reduced the number of colonies going missing by at least 10%, when compared to the other methods, fate tracking of colonies after 2 years was difficult (Bruckner and Bruckner 2001; Bruckner et al. 2009; Garrison and Ward 2012; Hollarsmith et al. 2012; Mercado-Molina et al. 2014). High frequency of missing colonies may not be indicative of outplanting failure, but is simply a characteristic of *A. cervicornis* life history, as missing colonies were often found attached to the reef meters away from the location they were outplanted. In addition, the rate of wild colony dislodgement (50% loss after 2 years (unpublished data)) and control colonies (Garrison and Ward 2008) was similar to what we report for outplanted colonies. The impact of outplanting corals can be seen beyond the outplanting areas and is missed by tracking each individual where it was outplanted, especially for ephemeral coral species that are known to propagate easily through fragmentation. To quantify the site impact of coral restoration through population enhancement, prior to outplanting, wild colony abundance assessments should be made and repeated periodically following outplanting. These periodic assessments would determine the natural propagation rates of this species and aid in defining the long term success of population enhancement of an ephemeral species.

The methods presented here were successful in terms of survival, over 70% after 1 year, increasing local abundance of *A. cervicornis*, and creating habitat complexity. These were just three attachment techniques that were available to our outplanting program and used by other outplanting programs within Florida and the Greater

Caribbean. At the time of this project, the cost of materials to outplant approximately 100 corals using epoxy was $60 USD, nail and cable tie $15 USD, and puck $190 USD. Not only did the puck technique cost more in supplies, it was also the most time consuming in terms of creating and deploying the pucks at the outplant site. It took two people about three hours to make 100 cement pucks, which had to cure at least 24 hours. They also must be attached to the substrate, at a minimum the amount of time it takes for the epoxy (or cement) to set, before outplanting to ensure attachment. If this is not done the weight and drag of the coral may dislodge the puck from the substrate before it has the time to attach. Outplanting colonies with epoxy took about 2-3 minutes each and depended on the size and how many attachment points were needed. Pounding in nails depended on substrate type, but was a quick process taking about 1-2 minutes to pound in the nail and attach the colony. In one day, with an experienced crew of five divers, colonies were collected from the nursery (1-hour dive) and outplanted to one site (2- 2 hour dives). This process would be accelerated if experimental design was not a factor and sites were closer. There are many other costs involved that will influence the total cost of outplanting program and were not included here because they are very dependent on diver experience, nursery to outplant site distance, outplanting design, site condition, and availability of resources and supplies. However, from our experience herein the added cost and time of making and deploying pucks for outplanting is not countered with greater success or colony performance and therefore should be used as a last resort. There is not one single solution to successful outplanting, but we present a number of factors that will influence and increase the success of an outplanting program especially as restoration efforts continue to scale up.

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Figures

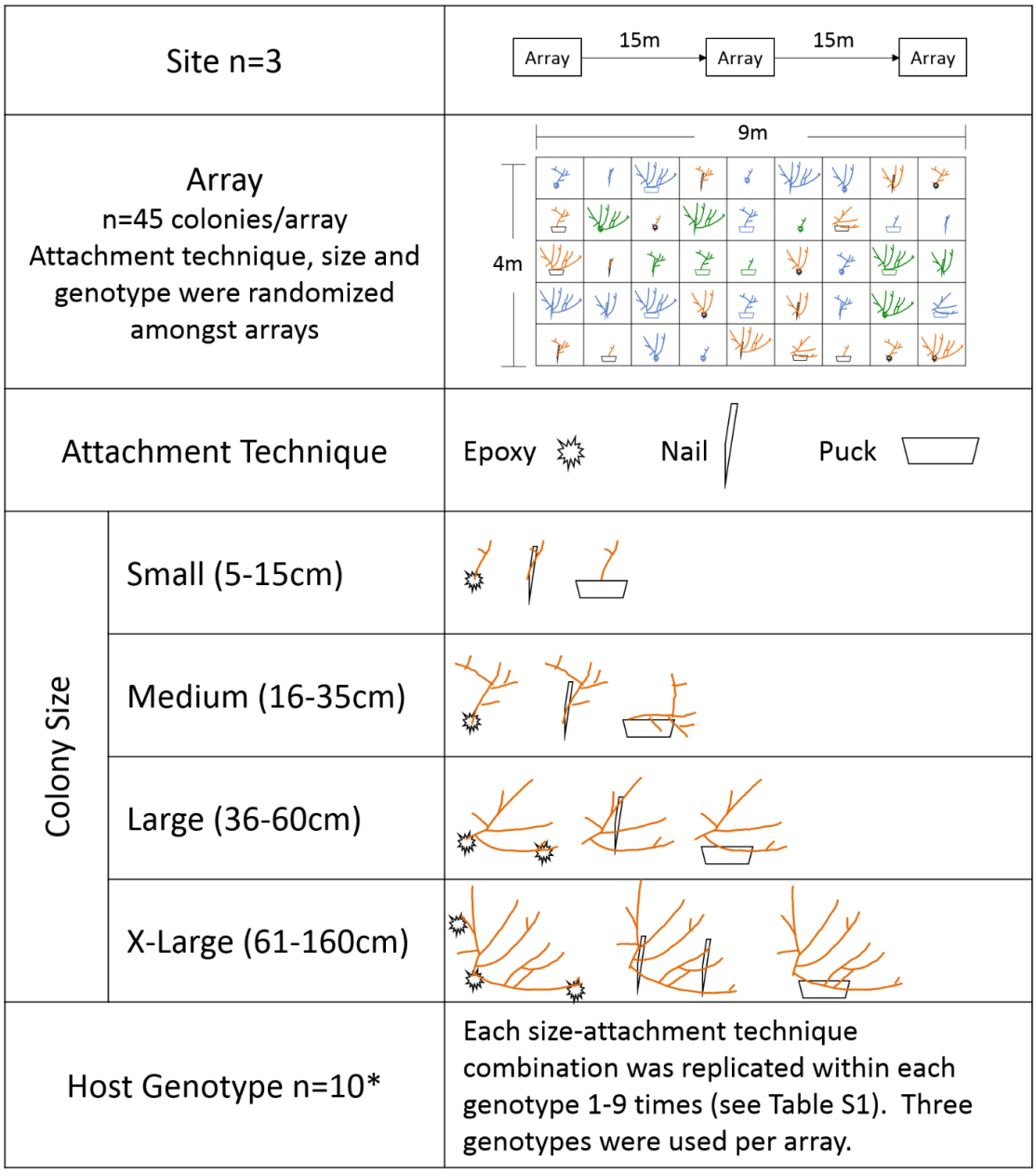

Figure 1. Schematic of experimental design of the size and attachment technique experiment. Different colors in the array diagram represent genotypes. * 10 genotypes were used, however because of the low number of replicates for Genotype 2 it was removed from genotype analyses.

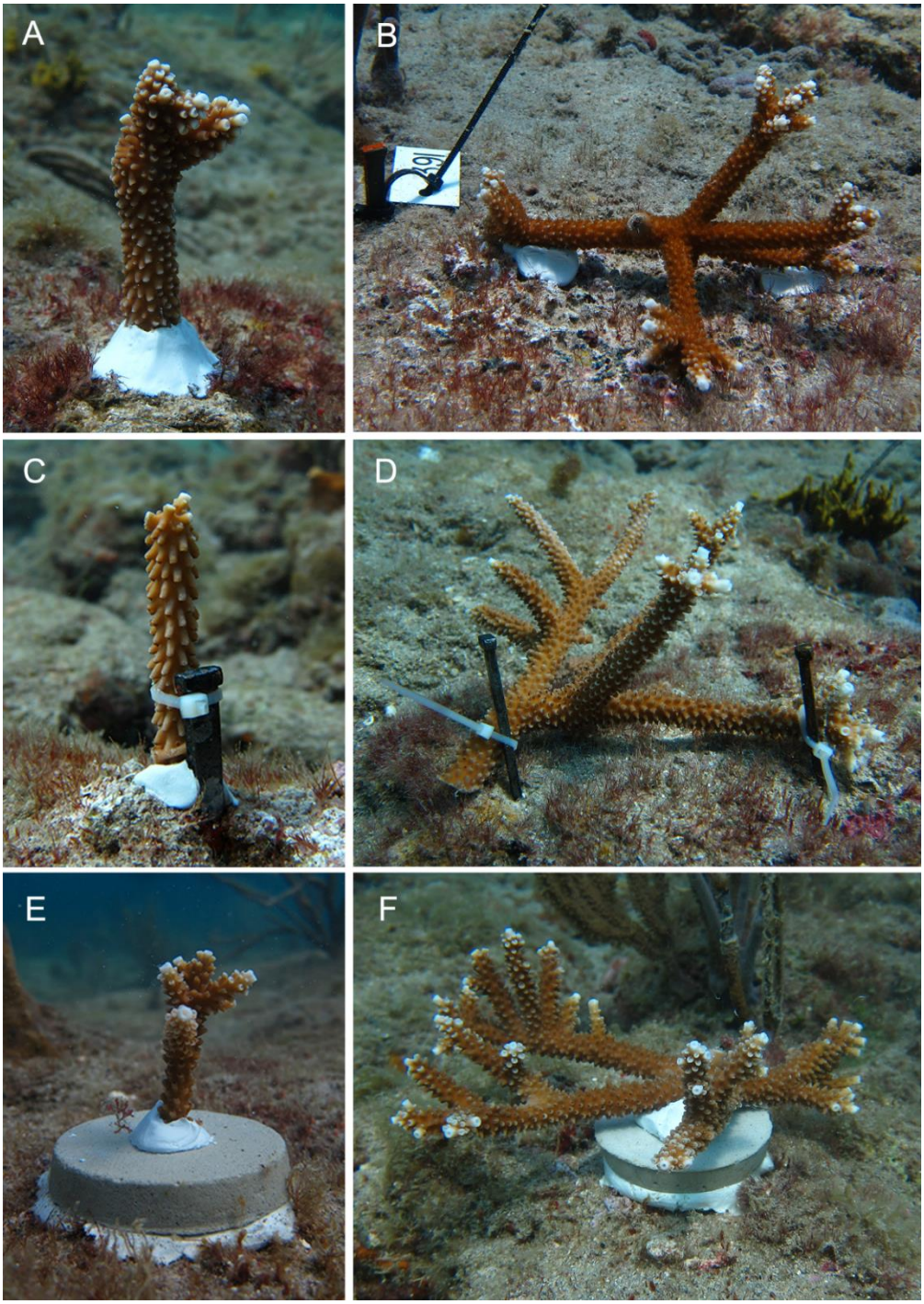

Figure 2. Outplanted *Acropora cervicornis* colonies using three attachment techniques: two part epoxy (A, B), masonry nail and cable tie (C, D) or cement puck (E, F) and four colony size classes: small (5-15 cm), medium (16-35 cm), large (36-60 cm), and x-large (>60 cm), pictured here are small, vertically outplanted (A, C, E) and x-large, horizontally outplanted colonies (B, D, F). To better ensure colony stabilization the small size class was outplanted vertically and the larger size classes horizontally.

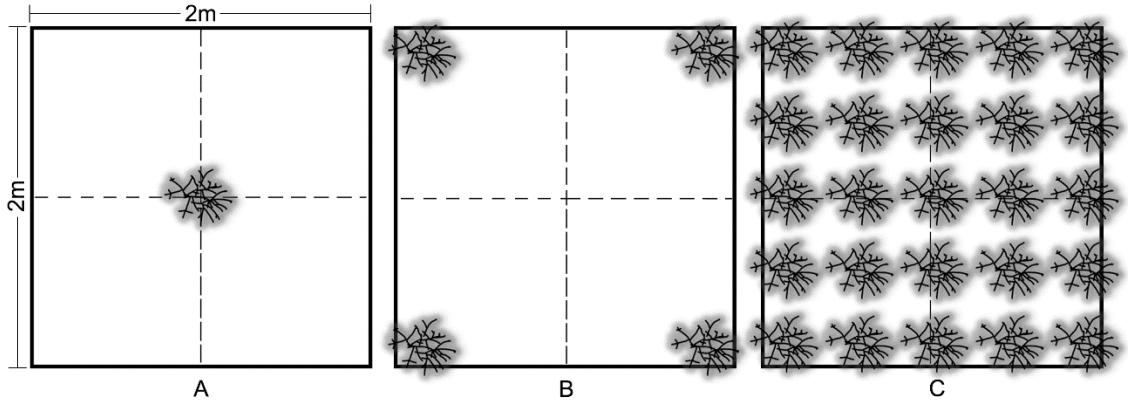

Figure 3. *Acropora cervicornis* outplant colony arrangement in 2 m x 2 m density treatments: A) low (1 coral/ 4 m^2), B) medium (4 corals/ 4 m^2), and C) high (25 corals/ 4 m^2). Colonies were approximately 30 cm TLE and outplanted using a nail, cable tie, and epoxy.

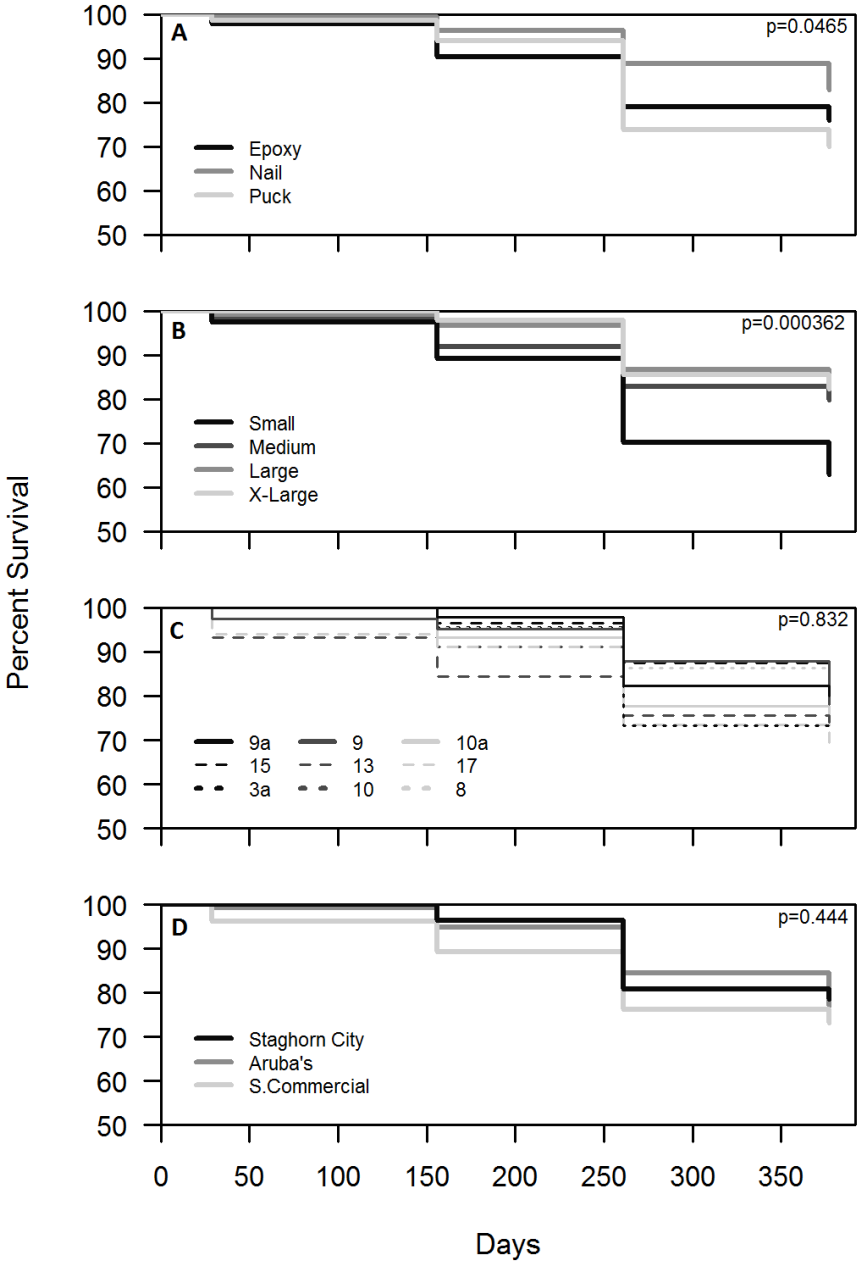

Figure 4. Survival analysis (Kaplan Meier $p < 0.05$) of outplanted *Acropora cervicornis* colonies after 1 year by attachment technique (A), size class (B), genotype (C), and site (D).

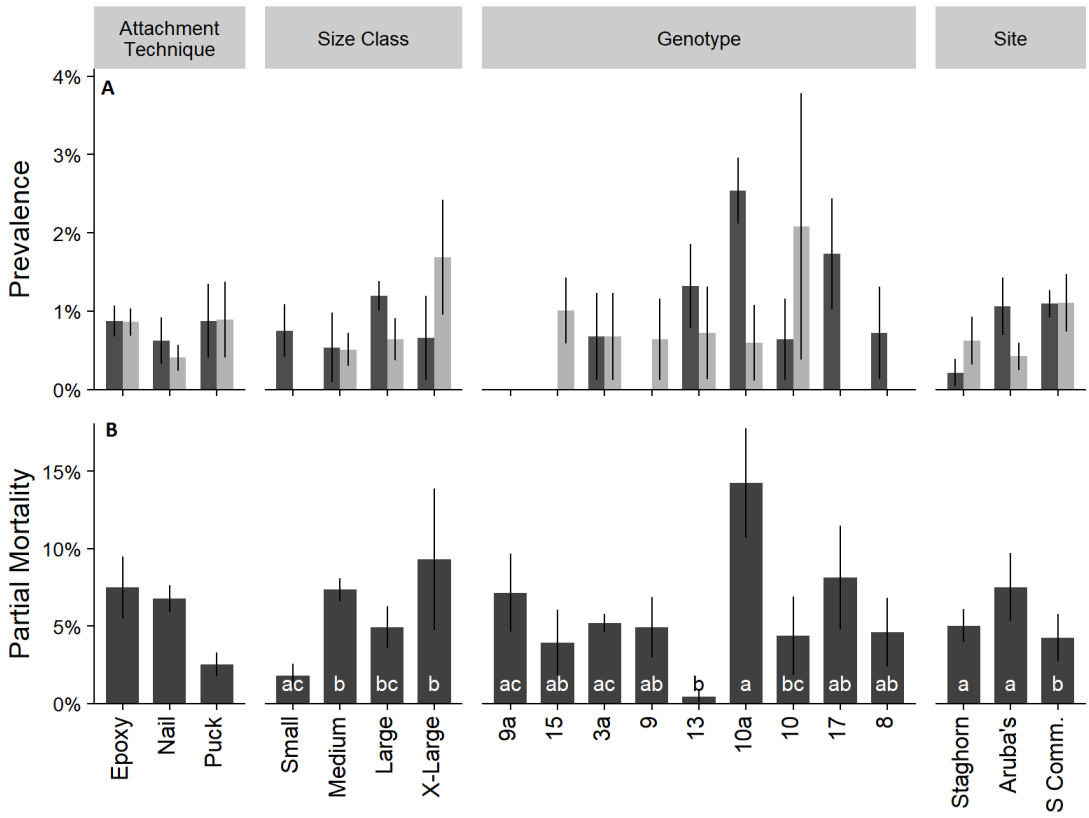

Figure 5. Cumulative prevalence of conditions on outplanted *Acropora cervicornis* colonies after 1 year by attachment technique, size class, genotype, and site. Panel A- mean cumulative prevalence of disease (dark gray), and predation (light gray). Panel B- mean partial mortality. Different letters within groups indicate significant differences between factors $p<0.05$, Kruskal-Wallis Multiple Comparisons. Where there were no significant differences letters were removed for clarity. Error bars indicate ± 1 SE.

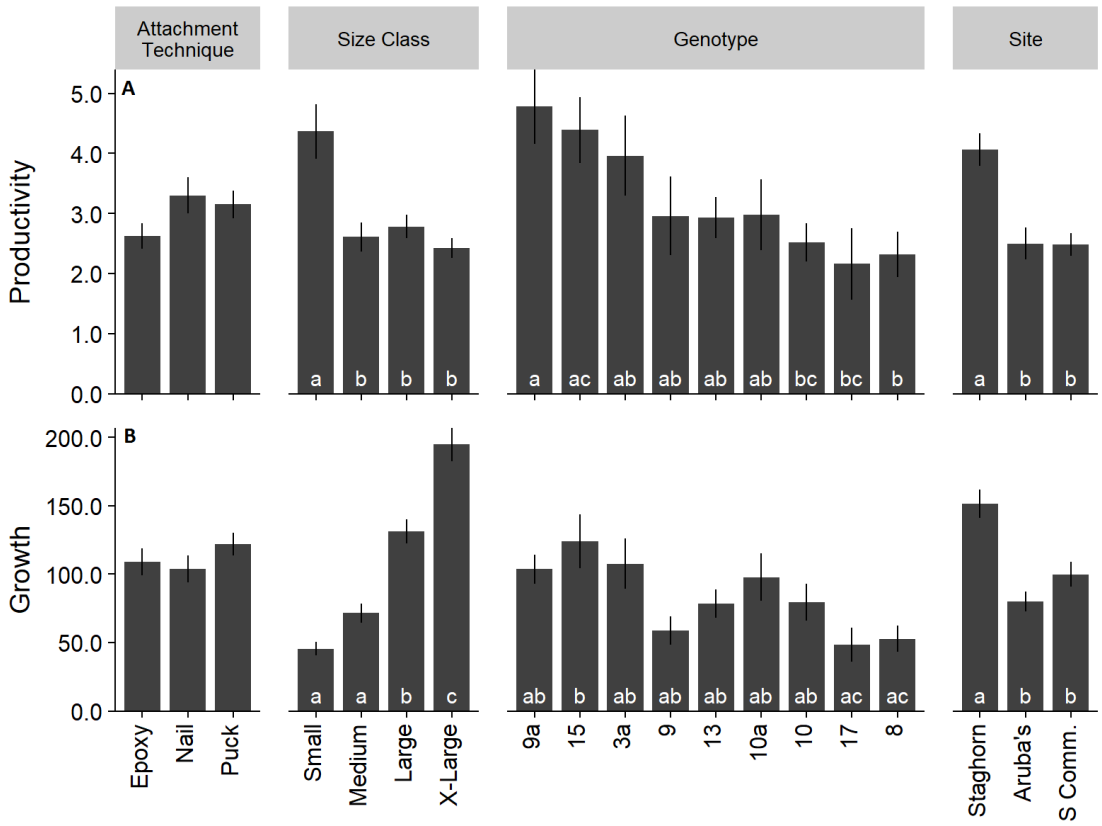

Figure 6. *Acropora cervicornis* outplant colony productivity (A) (cm/cm of initial tissue) and growth (B). Letters on bars indicate significant differences within groups $p<0.05$, Tukey HSD. Where there were no significant differences letters were removed for clarity. Error bars indicate ± 1 SE.

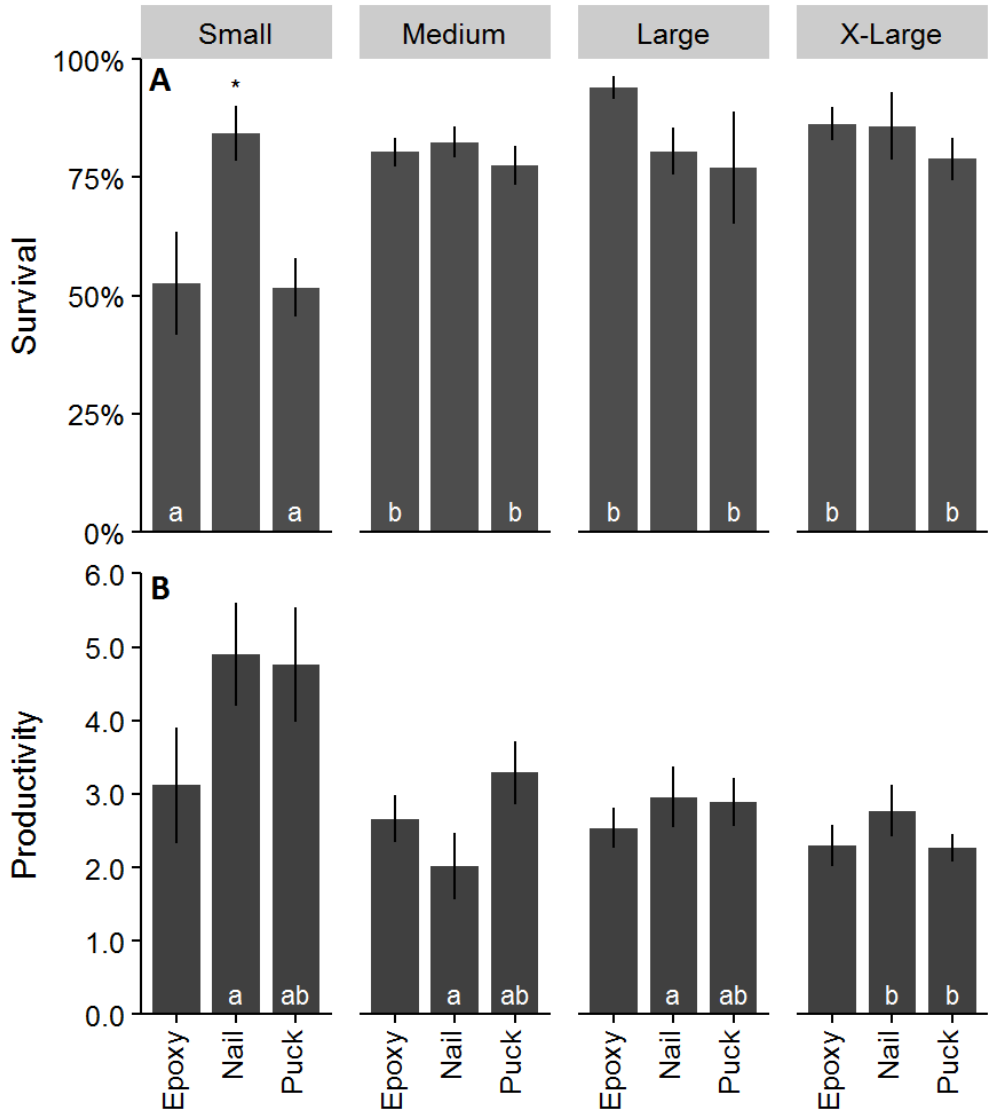

Figure 7. Survival and productivity of outplanted *Acropora cervicornis* colonies after 1 year. These data show the combined effect of colony size and attachment technique. Mean survival per colony (A) and mean productivity per colony (B). Letters on bars indicate significant differences within attachment techniques across size classes and within size class differences are indicated by an asterisks $p<0.05$, Kruskal-Wallis and log rank tests for survival and Tukey HSD for productivity. Where there were no significant differences letters were removed for added clarity. Error bars indicate ± 1 SE.

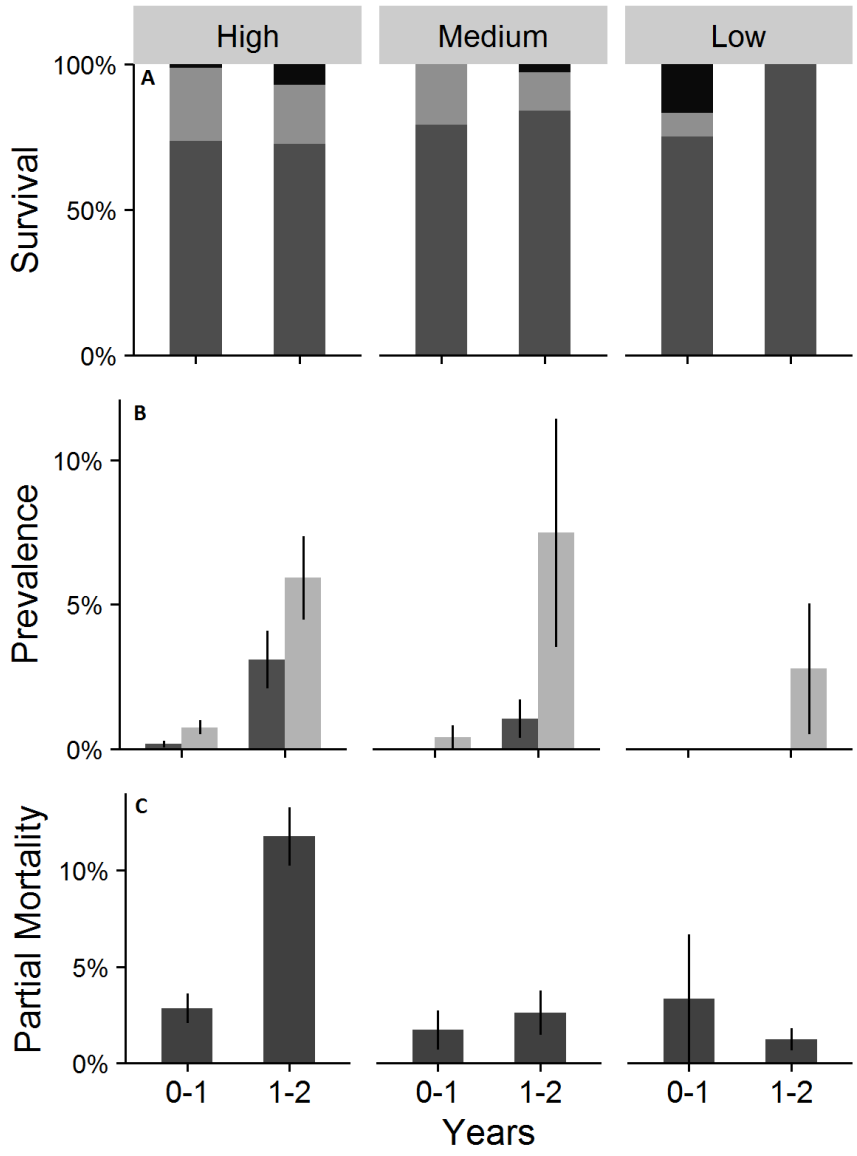

Figure 8. Survival (A), cumulative prevalence of conditions (B), and partial mortality (C) on outplanted *Acropora cervicornis* colonies. In A-survival dark grey is alive, light grey is missing and black is dead. In B-prevalence of disease is dark grey and prevalence of predation is light grey. Data are separated by 1 (0-1) and 2 years (1-2) for colonies outplanted in three densities: High (25 colonies/4m2), Medium (4 colonies/4m2), and Low (1 colonies/4m2). A table indicating significant differences is found in the supplemental materials Table S2. Error bars indicate ± 1 SE.

Supplemental Materials

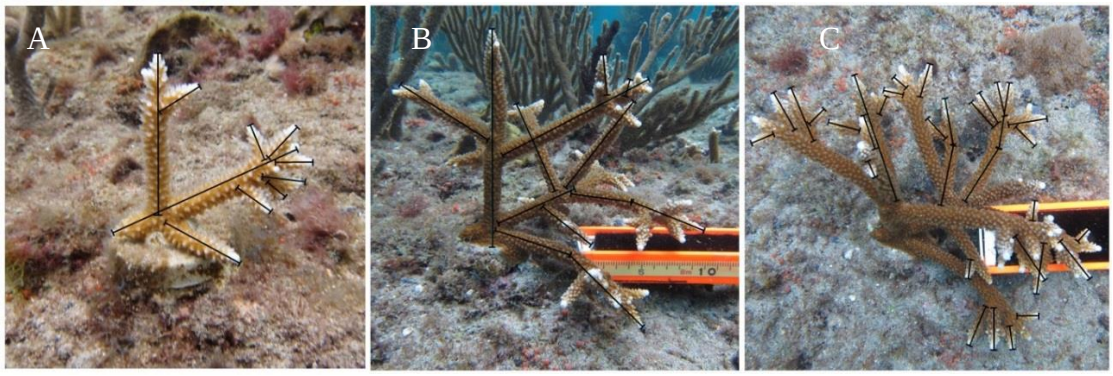

Figure S16. Outplanted *Acropora cervicornis* colony images were analyzed using Coral Point Count with Excel extensions 4.1© to determine change in colony size. A change in total linear extension (TLE) was estimated by tracing the length of every colony branch (denoted by the black lines on the images) initially (A) and at one year post-outplanting (B and C).

Table S1. Number of outplanted *Acropora cervicornis* colonies by genotype, attachment technique, and size class.

Size Class	Technique	2	8	9	10	13	15	17	3a	9a	10a	Total
Small	**Epoxy**		5	4	4	5	5	5	3	5	4	40
	Nail		2	7	5	9	5	6	3	6	1	44
	Puck		4	4	5	5	5	4	5	2	3	37
Medium	**Epoxy**		3	7	4	5	1	5	2	5	2	34
	Nail		9	4	2	1	2	4	4	4	5	35
	Puck		3	3	4	4	3	6		5	2	30
Large	**Epoxy**		3	3	4	2	5	1	3	4	5	30
	Nail			3	4	4	4		6	4	4	29
	Puck		5	5	2	4	3		2	4	6	31
X-Large	**Epoxy**	2	4		3	3	6	1	7	1	4	31
	Nail	1	3		4	1	9	1	2	1	5	27
	Puck	2	3	1	4	2	8	1	8	4	4	37
Total by Genotype		5	44	41	45	45	56	34	45	45	45	405

Table S2. Significant differences in colony survival, missing, disease, predation, and partial mortality. ns= no significant difference, H, M or L indicates which density is significantly different from the row density for each condition; Post-hoc multiple comparisons of mean ranks (p<0.05). If a significant difference was found between years within a condition the relationship is shaded (Friedman Test (p<0.05)).

	Survival		**Missing**		**Disease**		**Predation**		**Partial Mortality**	
	0-1	1-2	0-1	1-2	0-1	1-2	0-1	1-2	0-1	1-2
High	ns	L	L	M,L	**ns**	**L**	**ns**	**L**	**L**	**M,L**
Medium	ns	L	ns	H	ns	ns	ns	ns	ns	H
Low	ns	H,M	H	H	ns	H	ns	H	H	H

Concluding Remarks

Acropora cervicornis proved to be a very difficult species to work with, its dynamic character allows it to grow exceptionally well, propagating across a site, creating habitat, and reproducing sexually one year to nearly complete devastation the next. If enough healthy tissue remains following a devastation year and conditions are supportive, recovery is likely. Unfortunately, all signs indicate that recovery occurs over a much longer period than loss, however the potential still remains.

Key findings from my research on *Acropora cervicornis* dynamics and potential for species recovery are:

Acropora cervicornis is a highly dynamic species that is heavily and chronically affected by both environmental and biological factors. There are spatial and temporal components to most of the factors driving population decline.

- The largest losses of tissue came following tropical storms or extended periods of high wind energy.
- Shallower 'unprotected' sites are likely to have smaller colonies, whereas deeper and/or 'protected' sites had larger colonies; however, these colonies had the propensity to have a higher rate of fragmentation and lower colony residence time.
- Disease prevalence was seasonal, increasing with water temperature and high energy events and fragmentation.
- Predation by fireworms was consistently present and is associated with increased disease periods.
- 2013 was a recovery year for all regions, this year was void of storms or any major thermal event. Further investigation into reasons why this year was supportive of reef recovery is warranted.

Environmental characteristics within each sub-region or site are likely key factors driving differences in colony size, fragmentation, residence, and retention. Areas of shallower depth and stronger hydrodynamic forces had smaller compact colonies. A

more compact growth form and possibly denser skeleton may be less prone to colony fragmentation, whereas a less dense skeleton (likely in more protected areas) would be more prone to fragmentation during high energy events.

Disease, predation, and colony loss were all observed more on larger colonies. Tissue loss from disease typically occurs in the center of colonies and the subsequent loss of tissue allows for settlement and overgrowth of algae, bio-eroding sponges, and other organisms causing weakening of the skeleton leading to colony fragmentation. Similarly, high density outplants had high prevalence of disease and colony loss. In contrast, larger colonies outplanted at low density had high survival and low disease prevalence. Although the larger colonies were much smaller than the wild colonies referred to in the wild populations this supports the need to outplant in lower densities.

The effect of fireworm predation goes beyond the small amount of tissue removed. Fireworms typically predate on the branch tips of colonies removing the growing end, consequently stunting the growth of the colony, as regrowth and repair over the predated area is infrequent. Fireworms have been a proven vector of a bleaching pathogen, which could be of great concern because colonies with predation lesions may be more likely to become diseased. Therefore, it may be advantageous to manage fireworm populations to increase the health and growth of *A. cervicornis*.

Acropora cervicornis is greatly affected by extreme environmental conditions, disease, and predation and unfortunately, data are also indicating that prevalence and frequency of these events are increasing and having an even greater detrimental effect on the long-term persistence of this species. These results emphasize the continued need to address the larger scale problems affecting our reefs, such as climate change, ocean warming, and coastal construction. Without time for recovery and growth between major disease and storm events this species will not recover naturally, unless major changes are made to mitigate the negative effects of disease, climate change, and predator control.

An overall concern for the future of this species is the potential for sexual reproduction. Even though sexual reproduction for this species has never been documented as the primary mode of reproduction it is a necessary component to maintaining or increasing genetic diversity of the population. The constant fragmentation, colony dislodgement and chronic disease and predation create a reproductive road block across much of the Florida Reef Tract. A majority of the colonies that were observed were just reaching or below reproductive size and the multi-year study showed no signs of increase in colony health or size. Furthermore, the largest populations observed (those with the highest reproductive potential) were at the northern most extant of the Florida Reef Tract, with the typical northward flow of the Florida Current repopulation of the Reef Tract from these populations is unlikely. Although, further research is needed this supports the need for increased restoration efforts in areas which can act as source populations.

Species restoration through population enhancement has great potential to aiding in species recovery if completed at low density and with larger colonies. By increasing species abundance, we are lessening the risk of further loss and decreasing the distance between existing wild populations in turn increasing the potential for sexual reproduction.

Acropora cervicornis exists across a spectrum of sizes and forms from small fragments to 10's of meters of continuous cover and unlike other stony coral species in the Greater Caribbean it has the ability to move across these life history stages making common colony monitoring methods unsuitable for determining population status and health. It is therefore recommended to use the methods described herein, such as a systematic tracking method that when paired with census counts can provide an accurate long-term description of individual and population abundance, movement, and health.

In terms of management these data give us a better perspective on the dynamics of *A. cervicornis* and the fluctuations that they may have over time. Specific management actions may include the management of fireworm populations, this may not only lead to improved growth of colonies by reducing the number of damaged growth ends, but could

also lead to a reduction in disease, if it is found that fireworms are a vector. Furthermore, supporting population enhancement by advising practitioners to outplant at lower densities may also improve the health and longevity of *A. cervicornis.*

I have been fortunate to work across the spectrum that *A. cervicornis* exists including impressive, breathe taking expanses as far as the eye can see, isolated colonies of up-and-coming populations, deteriorated rubble fields, to newly outplanted reefs. All of which have provided insight into their existence and potential for recovery and conservation. I have been witness to both population boom and fall within the decade that my research has spanned, which give me hope for the future of this species that if we can make changes in our everyday life to better the environment they will recover. *Acropora cervicornis* is unlike any other species found on Atlantic, Gulf of Mexico, and Caribbean reefs creating a complex 3-D structure that provides habitat to a large portion of reef associated fishes and invertebrates, is a key component to reef health and sustainability, and deserves our attention.

Published Papers Relevant to this Dissertation

Drury C, Dale KE, Panlilio JM, Miller SV, Lirman D, Larson EA, Bartels E, Crawford DL, Oleksiak MF (2016) Genomic variation among populations of threatened coral: Acropora cervicornis. BMC Genomics 17

Drury C, Schopmeyer S, Goergen E, Bartels E, Nedimyer K, Johnson M, Maxwell K, Galvan V, Manfrino C, Lirman D (2017) Genomic patterns in Acropora cervicornis show extensive population structure and variable genetic diversity. Ecology and Evolution

Goergen EA, Ostroff Z, Gilliam DS (2017) Genotype and attachment technique influence the growth and survival of line nursery corals. Restoration Ecology:10.1111/rec.12545

Larson EA, Gilliam DS, López Padierna M, Walker BK (2014) Possible recovery of Acropora palmata (Scleractinia:Acroporidae) within the Veracruz Reef System, Gulf of Mexico: a survey of 24 reefs to assess the benthic communities. Revista de Biología Tropical 62:299-308

Lunz K, Shea C, Ames K, Neely K, Goergen E, Williams D, Gilliam D, Whittle A (2016) Acropora palmata's last stand in Florida? Proceedings of the 13th International Coral Reef Symposium:2-22

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Schopmeyer SA, Lirman D, Bartels E, Byrne J, Gilliam DS, Hunt J, Johnson ME, Larson EA, Maxwell K, Nedimyer K, Walter C (2012) In situ coral nurseries serve as genetic repositories for coral reef restoration after an extreme cold-water event. Restoration Ecology 20:696-703

Supplemental Material- *Acropora cervicornis* Monitoring Protocol

Included in this *A. cervicornis* monitoring protocol is a layout of the sampling design with detailed methodologies and procedures, and materials needed. Suggested data analysis is found in the previous chapters of this dissertation. Example datasheets and images to help support data collection (such as examples of predation, disease, and measurement techniques) are included throughout the document and at the end as appendices.

Site Selection and Installation

Site installation depends on the density of populations being studied. During initial site selection draw a site map including the locations of colonies to aid in selection and installation of plots, especially when populations within a site are spread out (Appendix 1). The center of each plot should be marked with a pin and identification tag (Figure 1). During monitoring, the plot (7m circular area) will be temporarily denoted by placing two 7 m transect lines, centered on the plot pin, placed perpendicularly across the substrate (Figure 1).

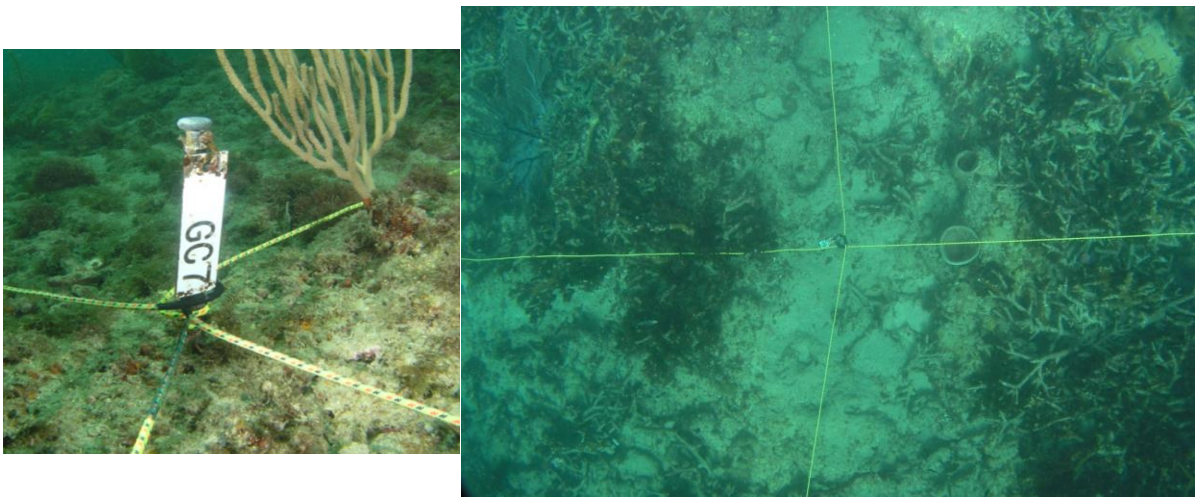


Figure 17. Example center pin with tag and temporarily deployed transect lines.

Isolated colonies

A site should have at least two non-overlapping areas of 7 m diameter that have a minimum of 10 colonies.

High cover

At sites where cover of *A. cervicornis* is semi-continuous (i.e., a patch), plots could be installed in a grid with spacing appropriate to cover the patch or portion of patch, depending on the size of the patch (Appendix 2). By using a gridded layout, movement and growth of the patch can be tracked. Total number of colonies in each plot is less of a concern as data collection will be more focused on cover than individual colonies.

Condition Characteristics- The purpose of this type of data collection is to obtain changes in percent cover and presence or absence and the rank of disease, predation, and bleaching within the plot boundary. Within the plot boundary, an estimate of percent cover (live and dead), presence or absence of disease (WBD and RTL), predation (fireworm, three spot damselfish, and corallivore snail), and bleaching (pale, partial bleaching, complete bleaching), and a ranking of severity of the causes of recent mortality will be recorded. Example datasheet is found in Appendix 4.

1. Percent cover
    a. Estimate percent live and dead *A. cervicornis* coverage within each plot boundary (Fig. 2).
        i. Percent live includes living tissue within the 7 m diameter radial plot boundary. Only the living portions of each individual within the plot are included in this estimate.
        ii. Percent dead includes standing dead and dead rubble within the plot boundary

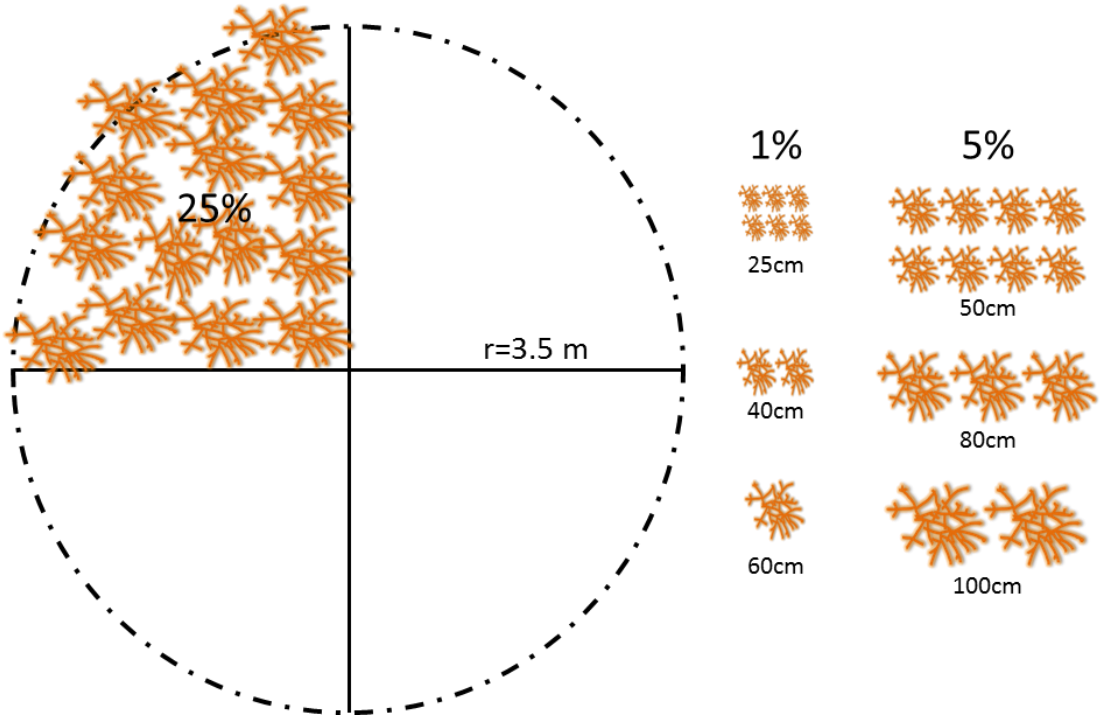


Figure 18. Example plot demonstrating percent cover. The right side of the figure depicts what makes up 1 or 5% of a 3.5 m radial plot base on area. For example 6- 25cm in diameter colonies cover approximately 1% of the plot

2. Disease and predation
    a. The presence or absence of recent disease and/or recent predation within the plot is recorded. Mortality is considered recent if, the skeleton is stark white and turf algae do not appear to have settled on the skeleton. Corallites are still intact (Fig. 3).
        i. Disease- Examples in Figure 4
            1. White Band Disease (WBD)
            2. Rapid Tissue Loss (RTL)
        ii. Predation- Examples in Figures 5-7.
            1. Fireworm *(Hermodice carunculata)*
            2. Three spot damselfish *(Stegastes planifrons)*
            3. Snail (*Coralliophila abbreviata)*
        iii. Unknown or other. If there is a condition present that cannot be positively identified as one of the above categories mark it as unknown and take notes and images if possible
    b. If disease and/or predation are present they are ranked based on severity.
        1° - Primary cause of mortality within the plot

        2° - Secondary cause of mortality within the plot

        3° - Tertiary cause of mortality within the plot

    c. Bleaching is also recorded as present or absent and ranked as bleached, partially bleached or pale.

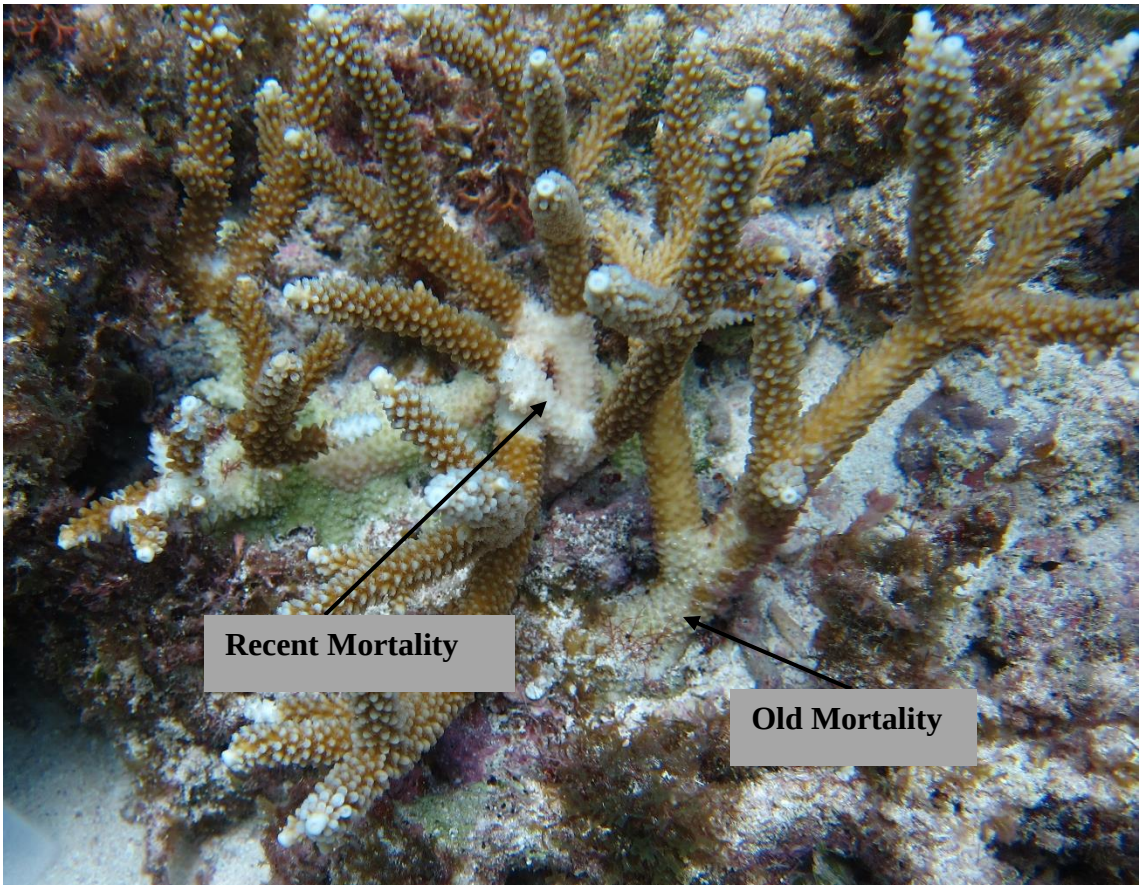


Figure 19. Example of recent and old mortality.

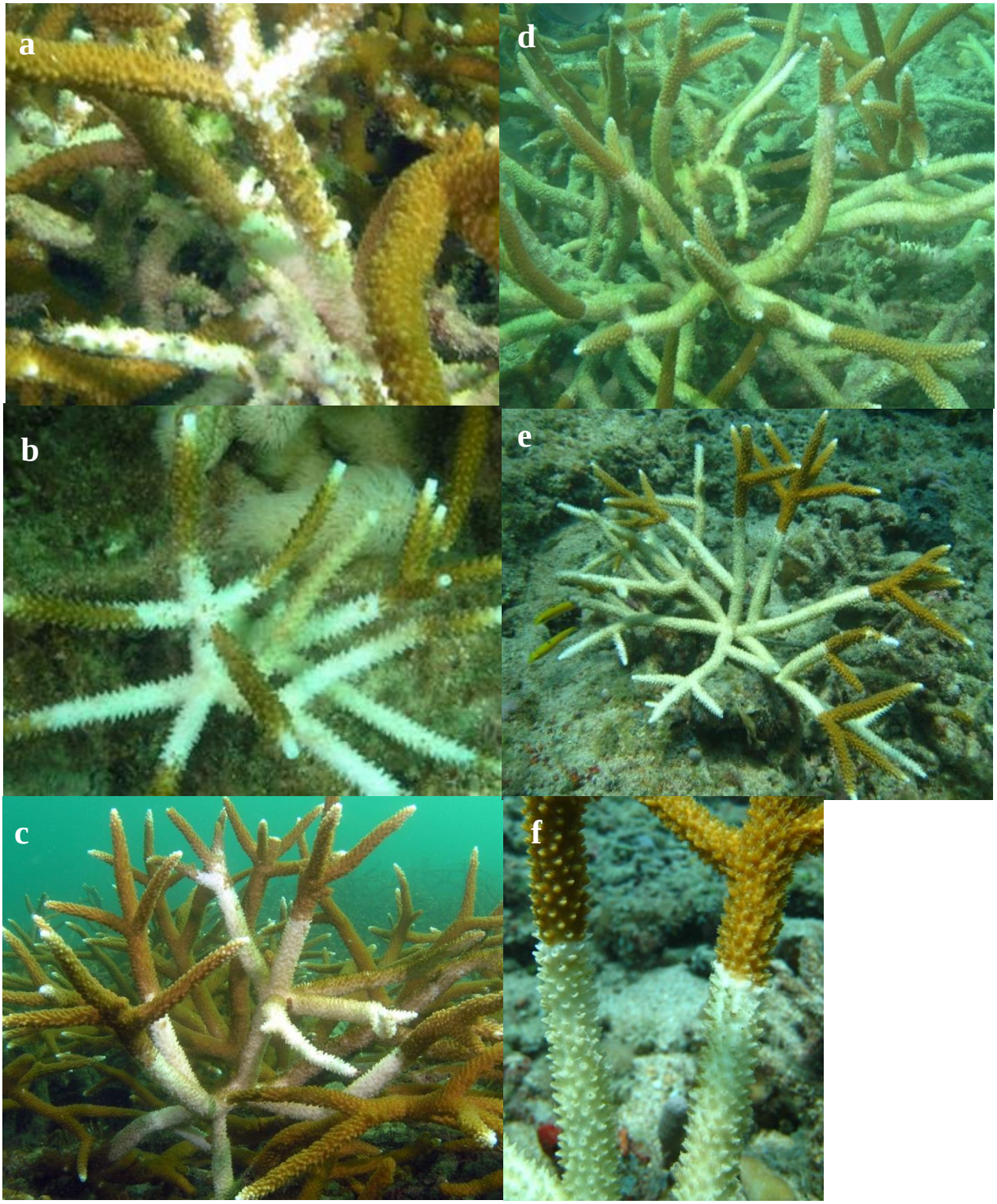


Figure 20. Examples of Rapid Tissue Loss (a-c) and White Band Disease (d-f)

Figure 21. Examples of feeding behavior of the bearded fireworm *Hermodice carunculata*

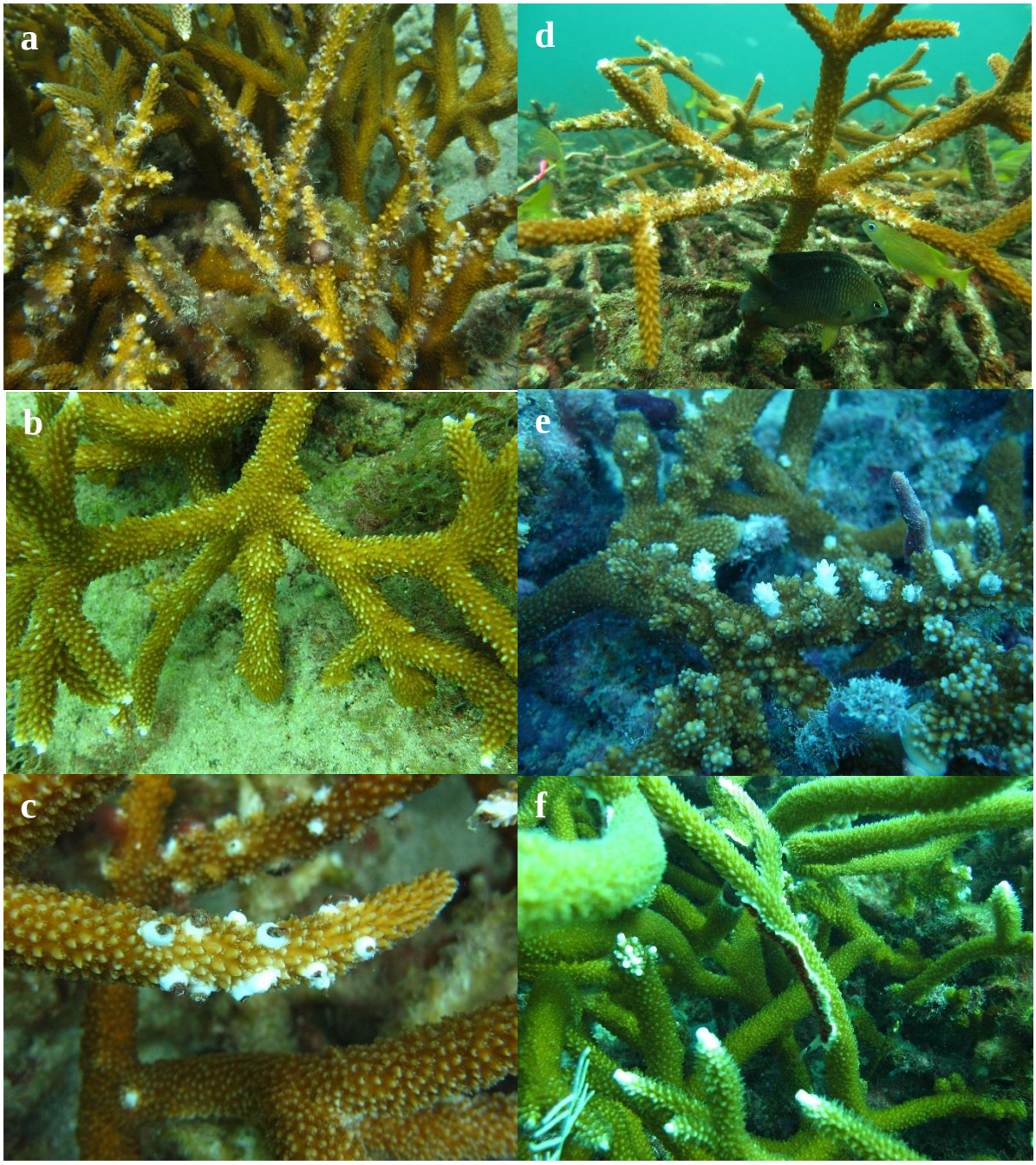


Figure 22. Examples of threespot damselfish predation. Images a,c, and d are the most common looks of a garden. The small white spots in b are the beginning phases of a garden. Image e is a garden no longer maintained, the chimneys have closed over and were predated upon by fireworms- white tips. Damselfish can also create gardens on the undersides of branches, creating an algal law instead of chimneys (f).

Figure 23. Examples of feeding behavior of corallivorous snail *Coralliophila abbreviata*

Species Census- The purpose of the species census is to obtain size frequency data of *Acropora cervicornis*, relative level of disease and predation on *A. cervicornis* and number of predators (fireworm, three spot damselfish, and corallivore snail) in the plot. During the census all *A. cervicornis* individuals will be counted within the plot boundary, and appropriate size class bins will be evaluated through this process. Individuals that show signs of disease will also be quantified to obtain disease prevalence in the plot. Each area of recent disease and predation will be counted based on the cause (i.e., counts will be separated by cause: RTL, WBD, fireworm, damselfish, and snail). All predators (fireworm, three spot damselfish, and corallivore snail) will be counted. The census will provide a count and condition (disease, predation, and bleaching) of *A. cervicornis* within the plot boundary. These data over time give an indication of succession and peaks of disease and/or predation. Example datasheet is found in Appendix 5.

1. Within each plot a census is taken of all masses, colonies, and fragments (Fig. 8).
    a. Mass. A mass is considered a very large colony typically greater than 1.5 m in diameter with no maximum size as long as it is continuous skeleton, live or dead. Large areas joined by continuous standing dead skeleton with multiple living areas are considered one mass as long as the live tissue is connected by continuous skeleton. If a large colony (> 1.0 m) fused (branches are growing together) with a neighboring colony, it is considered a mass.
    b. Colony. A colony has a well-defined boundary edge, typically 1.5 m or less in diameter and attached to the substrate. There is no minimum size to a colony.
    c. Fragment. Fragments are loose *A. cervicornis* not associated with a mass or colony. There are no size limitations to fragments; if a colony is loose it is considered a fragment. If a branch within the boundary of a mass or colony is loose it is considered part of that colony or mass and not counted separately as a fragment. Only those that are isolated are counted as fragments.

2. Occurrence of disease or predation (Fig. 9)
    a. Prevalence. A count of the number of colonies with visual signs of recent mortality from disease.
    b. Occurrence. This includes a count of every occurrence of disease (WBD, RTL) or predation (snail or fireworm) on all colonies or masses. This count does not include recent mortality on fragments. An occurrence includes only areas that are recently affected by disease or predation. Recently affected areas that are separated by healthy tissue are considered separate occurrences. One colony may have multiple occurrences. For fireworm predation, each affected tip is a separate occurrence.
        i. Occurrences on masses- count recent predation or disease that occurs within the plot boundary. The portion of the mass within the plot boundary is the only portion included in the count; portions of the mass outside the plot boundary are not included.
        ii. Occurrences on colonies- if a portion of the colony is within the plot boundary count any recent disease or predation on that entire colony, even if the portion of the colony is outside the boundary.
        iii. Damselfish predation is difficult to quantify and once the garden is established it does not appear to cause additional recent mortality to the colony, therefore it is only identified as present or absent in the condition characteristic data.
3. Count all the predators within the plot boundary (Fig. 10)
    a. Fireworm *(Hermodice carunculata)*
    b. Three spot damselfish *(Stegastes planifrons)*
    c. Snail (*Coralliophila abbreviata)*
4. During the Fall monitoring event all individuals are size classed in to 10- 20 cm size increments. An example datasheet is found in Appendix 7.

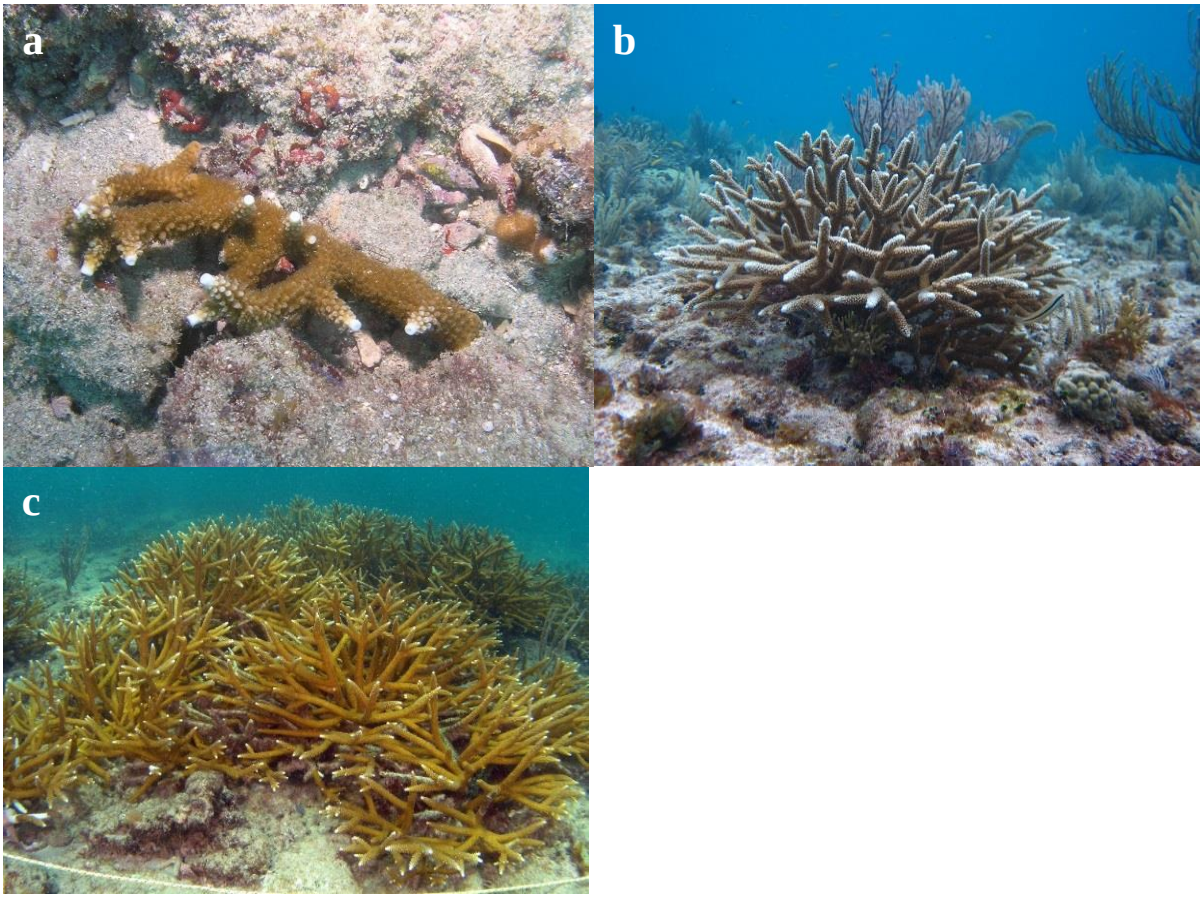


Figure 24. Examples of a fragment (a), colony (b), and mass (c)

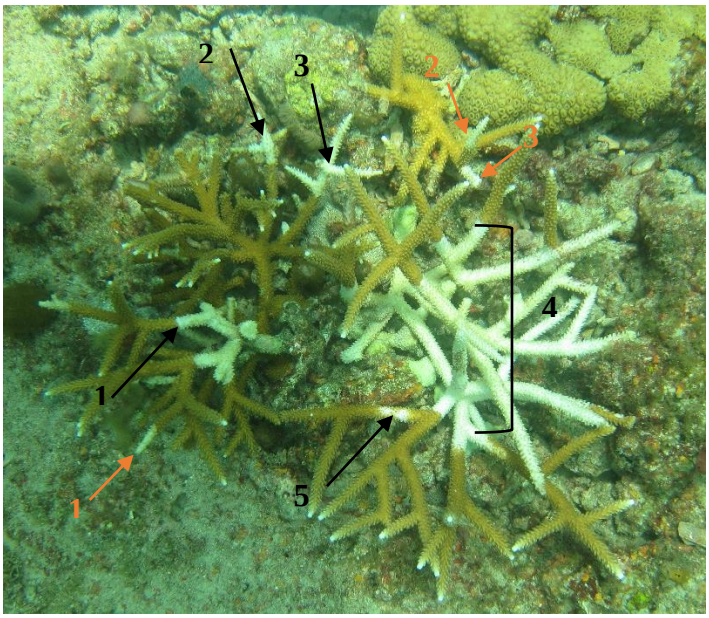


Figure 25. Occurrence of conditions on a colony. Occurrences are separated by living tissue or old dead skeleton. This colony has 5 occurrences of disease as indicated by the black arrows and bracket and 3 occurrences of fireworm predation as indicated by the red arrows.

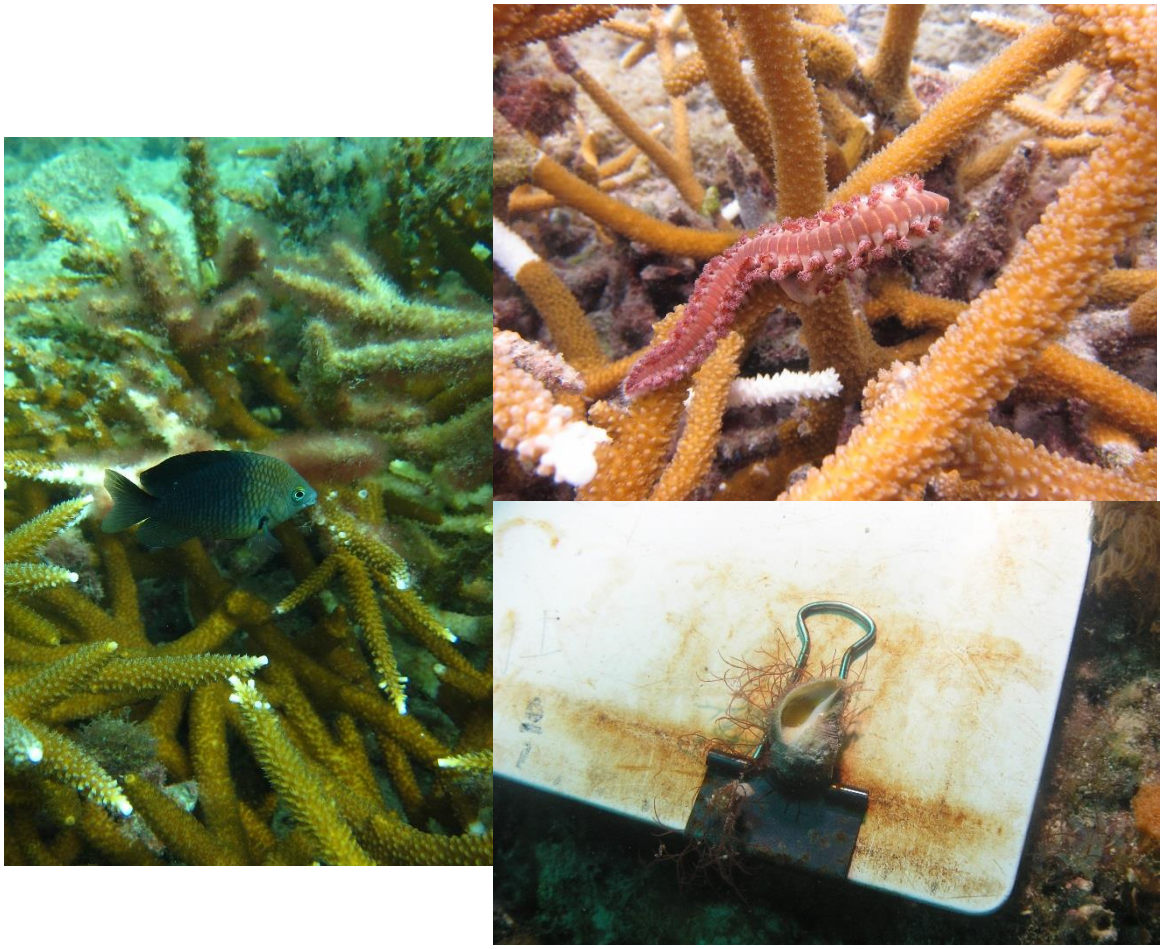


Figure 26. Threespot damselfish, bearded fireworm, and corallivorous snail.

Colony Assessment- This data collection is best suited for areas of definable colonies, not masses or patches. Therefore, this type of data collection is not applicable in high cover areas where there are no definable colonies. The purpose of the assessment is to collect data on size and condition of a subset of the colonies within a plot, which will provide an indication of disease and predation impacts, growth, movement, and overall colony characteristics in a specific region over time. Example datasheet is found in Appendix 6.

For each plot, starting north and proceeding clockwise, data is collected on the first 10 colonies (Fig. 11).

a. Colony mapping and imaging (Fig. 12)
    i. Colony markers are placed next to each colony.
    ii. Distance and bearing from the plot center pin to the front of the colony is taken.
    iii. Planar image of colony with marker for reference is taken (Fig. 13).
b. Colony measurements
    i. Planar length
    ii. Planar width
    iii. Height from the base through the growth axis to the tallest point
    iv. Branch diameter and length (3 measurements per colony)
c. Colony condition
    i. Percent live
    ii. Percent old and recent dead
        1. Record the percent of the recent mortality caused by each condition(s)
            a. White Band Disease (WBD)
            b. Rapid Tissue Loss (RTL)
            c. Fireworm predation
            d. Snail predation
            e. Unknown
    iii. Presence or absence of bleaching
    iv. Presence or absence of damselfish gardens

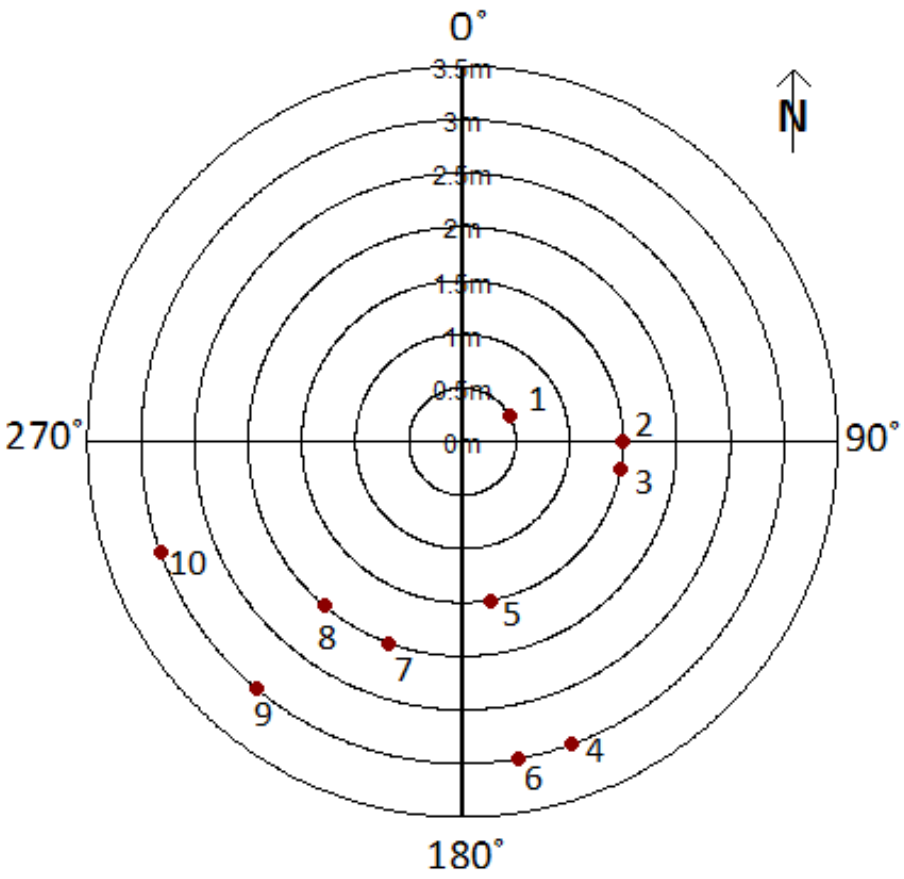


Figure 27. Diagram of choosing colonies within the plot

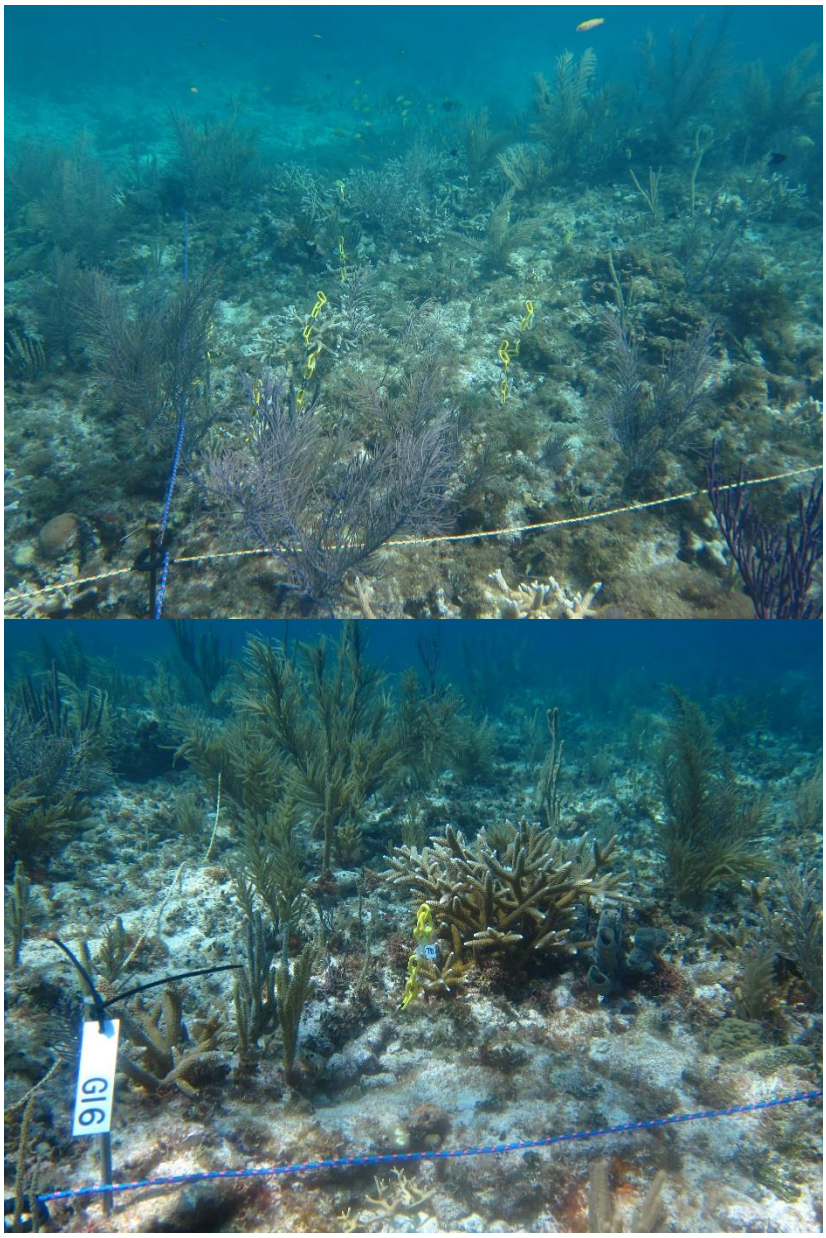


Figure 28. Examples of marking colonies in a monitoring plot

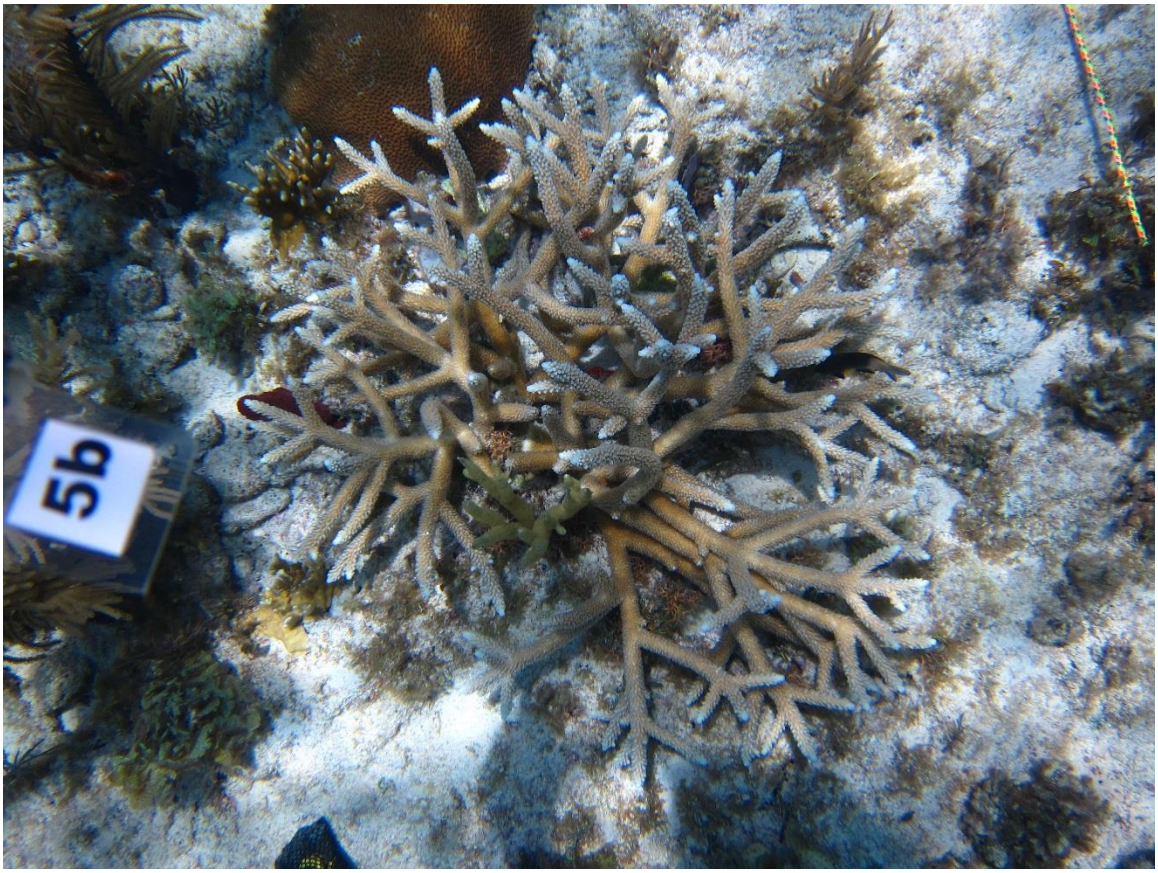


Figure 29. Representative colony image with colony marker.

Appendix 1: Supplies List

Site set-up

Permit

Slates

Datasheets (XXXXX)

Marker Buoys

Handheld GPS

12” nails

Tags

Cable ties

Hammer

Compass

Camera

50m tapes

Data Collection

Permit

GPS point of site and plots

Map of site

Slate

Datasheets

Transect lines

Colony markers

Camera

Compass

2m flexible tape

Photoboard

Tags for photoboard

Extra supplies (tags, cable ties, pencils, clips, rubberbands)

Appendix 2: Site Set-up Datasheet

Site name:_____

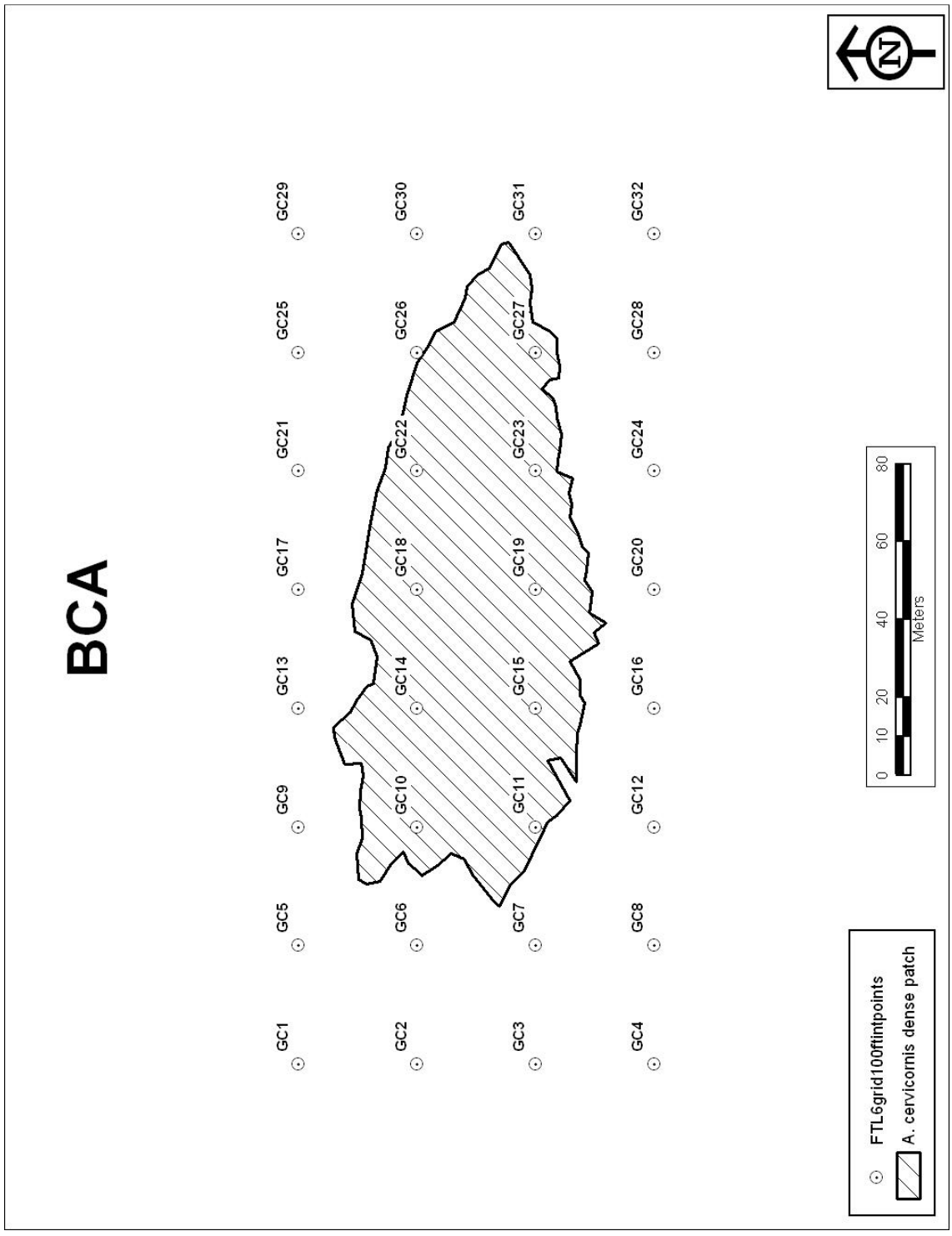
Depth:_____

Site Map: Include: distinguishing features, plot locations, direction

N

Tag #	Distance	Bearing	To Tag #

Appendix 3: Example of Grid Layout across a High Cover Site



***Acropora cervicornis*: Monitoring**

Condition Characteristics

Site:_____

Diver_____

Date:_____

****If conditions are present rank order of severity**

PLOT #	% of PLOT Acerv		PRESENCE/ABSENCE RBD RANK (1°, 2°, 3° or A) cause of recent mortality**							Measurements (cm)			Species Count			NOTES *** describe 'other'
	Live	Dead (including rubble)	White Band	Rapid Tissue Loss	Hermodice Predation	Damselfish Impact	Snail	Other***	Bleaching	Maximum Canopy Height	Branch Diameter x3	Branch Length x3	3-Spot Damselfish*	Hermodice	Snails	

*** Three Spot- yellow eyebrow, dark spot on base of pectoral fin, dark saddle on upper base of tail. Yellow Tail- yellow tail, bright blue dots along dorsal , juveniles dark blue with bright blue dots over body**

Canopy Height: From substrate to highest living A.cerv point in plot
Branch Diameter: Anterior to the last branching point
Branch Length: From the last branching point to second to last branching point

Appendix 5: Species Census Datasheet

Acropora cervicornis Monitoring

Species Census

Site____________________

Diver____________________

Date____________________

Colonies / Masses

*****Remember: if you count occurrence of RTL or WBD there needs to be a count of diseased colonies and/or masses and vice-versa

Plot #	Quad	# of Colonies	# of Masses	# of Loose Fragments**	# Colonies Diseased	# Masses Diseased	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice
	1										
	2										
	3										
	4										

Plot #	Quad	# of Colonies	# of Masses	# of Loose Fragments**	# Colonies Diseased	# Masses Diseased	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice
	1										
	2										
	3										
	4										

Plot #	Quad	# of Colonies	# of Masses	# of Loose Fragments**	# Colonies Diseased	# Masses Diseased	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice
	1										
	2										
	3										
	4										

Plot #	Quad	# of Colonies	# of Masses	# of Loose Fragments**	# Colonies Diseased	# Masses Diseased	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice
	1										
	2										
	3										
	4										

Colonies are attached and have a defined edge- no minimum size

Masses do not have a well defined edge, often look as though multiple colonies have fallen together- typically >1.5m. Can span across multiple quads but only count once

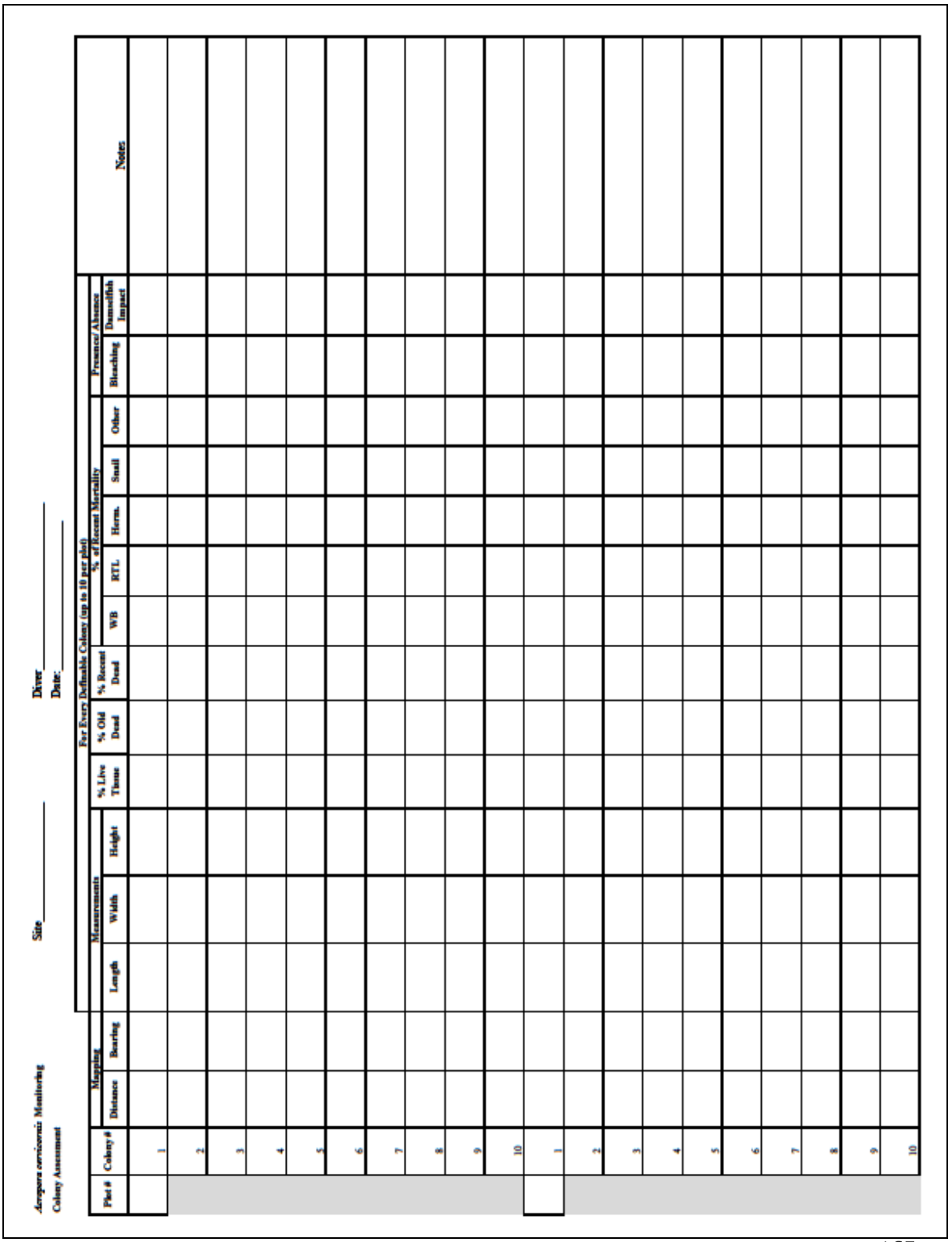
** Loose Fragments are not associated with colonies and/or masses and are their own entity

Colonies and Masses Diseased- of the colonies or masses how many are showing signs of recent disease (does not include predation)

Do not count incidences on Loose fragments

Count the number of times colonies or masses are diseased or predated. Diseased or predation portions on the same colony seperated by healthy tissue are counted as separate occurrences

Appendix 6: Colony Assessment Datasheet



Acropora cervicornis Monitoring
Colony Assessment

Site_____ Diver_____
Date:_____

Plot #	Colony #	Mapping		Measurements			For Every Definable Colony (up to 10 per plot)													Presence/ Absence		Notes
		Distance	Bearing	Length	Width	Height	% Live Tissue	% Old Dead	% Recent Dead	% of Recent Mortality										Disease/Ish Impact	Bleaching	
										WB	RTL	Herm.	Snail	Other								
	1																					
	2																					
	3																					
	4																					
	5																					
	6																					
	7																					
	8																					
	9																					
	10																					
	1																					
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	4																					
	5																					
	6																					
	7																					
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	9																					
	10																					

Appendix 7: Colony Size Frequency Datasheet

Acropora cervicornis Monitoring
Colony Size Frequency Data

Diver
Date___________

Colonies / Masses

Plot #	1-10	11-30	31-50	51-70	71-90	91-110	>110	Loose Frags	CD	MD

Plot #	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice	Plot #	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice

Plot #	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice	Plot #	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice

Plot #	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice	Plot #	Bleached	White Band	Rapid Tissue Loss	Snail	Hermodice

Colonies are attached and have a defined edge- no minimum size

Masses do not have a well defined edge, often look as though multiple colonies have fallen together- typically >1.5m. Can span across multiple quads but only count once

** Loose Fragments are not associated with colonies and/or masses and are their own entity

Colonies and Masses Diseased- of the colonies or masses how many are showing signs of recent disease (does not include predation)

Do not count occurences on Loose fragments

Count the number of times colonies or masses are diseased or predated. Diseased or predation portions on the same colony seperated by healthy tissue or dead skeleton are counted as separate occurrences

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