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Spatial and Temporal Trends of Southeastern Florida's Octocoral Comunity

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Thesis of
Alexandra Hiley

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Spatial and temporal trends in Southeastern Florida’s octocoral community

By

Alexandra Hiley

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

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Table of Contents

List of Tables

List of Figures

Abstract

In the Caribbean, local and global stressors have driven significant declines in scleractinian coral cover up to 80% in only three decades. Following these declines, phase shifts in benthic community composition have been reported. Shifts towards macroalgal dominance has been the most widely observed case, however, shifts towards octocoral and sponge dominance have also been reported. In Florida, USA, the Florida Reef Tract is an extensive barrier reef system that contains diverse assemblages of corals, sponges, fish, and other taxa. The Southeast Florida Reef Tract (SEFRT) within the Southeast Florida Coral Reef Conservation Area is the northern portion of this system and lies adjacent to the highly urbanized and populated South Florida coastline. Long-term decreases in stony coral cover have been reported for this region, as well as more recent and drastic changes resulting from the Stony Coral Tissue Loss Disease outbreak. With this recent significant loss in stony corals, octocorals have become a more abundant constituent of the SEFRT. Although multiple studies highlight the community composition of local stony corals as well as spatial and temporal changes in their cover, the same has yet to be investigated for the octocoral community. This study investigates spatial and temporal trends in octocoral density, community composition, colony height, and colony condition (i.e. bleaching and disease) from 2013-2018 on the SEFRT. Analyses indicate an increase in density and a decrease in colony height throughout the study period. Both bleaching and disease prevalence remained very low, likely at background levels, during a time period when high levels of bleaching and disease were reported in the stony coral community. Finally, significant spatial variation of the community was observed throughout the SEFRT as density, colony height, and community composition of the outer reef was different from both the inner and middle reefs. These changes do not appear to correlate with events that resulted in the significant decline of stony corals (e.g. thermal anomalies, disease outbreak), suggesting that its drivers may not be similarly impacting the octocoral community. Evidence suggests that this high-latitude reef system can support a high-density octocoral community, but significant spatial variation in density and composition exists. With reefs experiencing dramatic phase shifts, it is imperative to understand the contribution of seemingly resistant organisms, like octocorals, to reef community dynamics.

Keywords: Octocorals, Gorgonians, Coral Reefs, Florida, SEFRT, Phase Shift

1. Introduction

The tropical Western Atlantic region, encompassing southern Florida, the Bahamas, the southern Gulf of Mexico and the Caribbean, supports diverse coral reef communities. Scleractinian coral cover has been declining across this region (by up to 80%; Gardner et al. 2003) as a result of global and local stressors such as climate change, over-fishing, nutrient influx, sedimentation, disease, and hurricanes (Hughes and Connell 1999; Hoegh-Guldberg 1999; Porter et al. 2002; Hughes et al. 2003; Harvell et al. 2004; Jackson et al. 2014; Kemp et al. 2016). Following these declines, phase shifts in benthic community composition are becoming more widely observed, with shifts towards macroalgal dominance (highest percent cover relative to other taxa or functional groups) perhaps the most observed case (McCook 1999; Norstrom et al. 2009; Bruno et al. 2009; Graham et al. 2015). Thermal anomalies and disease outbreaks have been primarily contributing to large-scale declines of primary reef-building corals in the Caribbean (Aronson and Precht 1997), and macroalgae now occupies much of the available substrate (Done 1992; Shulman and Robertson 1996; Maliao et al. 2008). In some areas of the Caribbean, such as coral reefs in Jamaica, reefs that once supported 50% coral cover have shifted towards macroalgal-dominated communities of up to 90% macroalgae cover (Hughes 1994). Increases in macroalgal cover appear to be the result of a combination of factors, including increases in available substrate for colonization, decreases of herbivorous organisms due to disease and overfishing, and increases in temperature and nutrient input (Hughes 1994; Adam et al 2015; Graham et al. 2015). In addition to shifts towards macroalgal-dominated coral reef communities, shifts towards “alternative stable states” resulting from increases in other major benthic taxa are becoming more prevalent (Norstrom 2009). Norstrom (2009) reported shifts to octocoral, corallimorph, and sponge-dominated reefs, although the ramifications of these changes on community dynamics are less understood. With such wide-spread declines in scleractinian coral cover, better understanding of the ecology and functionality of other major benthic taxa that are becoming dominant on reef habitats is needed to further maintain effective reef conservation practices.

Members of the anthozoan subclass Octocorallia are abundant constituents of coral reef communities in the tropical Western Atlantic region. The group includes the soft corals and gorgonians, most of which do not produce hard calcium carbonate skeletons like scleractinian corals. They provide multiple essential ecological functions to reefs, including three-dimensional habitat (which serves as shelter and nurseries) and food sources (Weil et al. 2017) for the myriad of other reef organisms. In this region, octocoral communities are primarily composed of members of the order Alcyonacea (often informally referred to as gorgonians), which typically have a supportive proteinaceous axis surrounded by tissue filled with calcareous sclerites. They form a variety of branching colonies that attach to the substrate via a holdfast and extend upwards into the water column, although a few species form encrusting mats. Some species may reach over 2m in height and dense aggregations can form a nearly closed canopy (Sanchez 2017). Coral reefs in this region host highly diverse assemblages of octocorals. Above 30 m depth, almost all species are zooxanthellate (Sánchez and Wirshing 2005; Sanchez 2017). Populations range from 1-10 colonies m^{-2} and most species belong to the families Plexauridae and Gorgoniidae (Sanchez 2017). Their three-dimensional structure combined with that of sponges and other sessile benthic cnidarians (e.g. fire corals, stony corals) and invertebrates (e.g. bryozoans) form “animal forests” (Rossi et al. 2013). The organisms comprising these animal forests are considered ecosystem engineers, which directly and/or indirectly contribute to and modulate resources and physical factors to nearby individuals (Jones et al. 1994; Rossi et al 2013). The more complex or mature an animal forest, the greater its contributions to its constituents, as they can act as carbon sinks, promote stock recruitment, and provide a greater nursery effect and general habitat than smaller communities (Marliave et al., 2009; Orejas et al., 2009; Baillon et al., 2012; Miller et al., 2012; Rossi et al. 2013; Privitera-Johnson et al. 2015; Sanchez 2017).

As principal contributors to the animal forest concept of coral reefs, it is important to understand how octocoral communities are changing in conjunction with known stony coral decline and reef degradation. In the US Virgin Islands (USVI), Tsounis and Edmunds (2017) and Lenz et al. (2015) have reported increases in octocoral abundance following declines in scleractinian coral populations. Each study reported increases in octocoral density at two study sites from 1996 and 2002 to 2013. One site experienced a threefold increase in octocoral density with a concurrent decline in scleractinian coral cover, while the other experienced a six-fold increase in octocoral density, with an initial 50% decline in stony coral cover followed by a slight increase (Tsounis and Edmunds 2017). Increases in octocoral density were also noted at similar, nearby sites after 2002 (Lenz et al. 2015). In the Florida Keys, Ruzicka et al. (2013) reported an increase in octocoral cover following a long-term decline in scleractinian coral cover. More recently, Sanchez et al. (2019) reported an almost threefold increase in octocoral density at an atoll in the Seaflower Biosphere reserve in Colombia from 2003 to 2015, accompanied by large-scale declines in stony coral cover and reduced benthic complexity.

Although more studies are highlighting changes in benthic community composition towards octocoral dominated habitats, few have highlighted temporal changes, spatial patterns, and functional contributions of dense octocoral aggregations in coral reef communities. In south Florida (USA), the Southeast Florida Reef Tract (SEFRT) and Florida Keys comprise the Florida Reef Tract (Duane and Meisburger 1969a; 1969b) within the South Florida Coral Reef Conservation Area. The SEFRT extends from Miami-Dade County in the south to Martin County in the north (Macintyre 1988; Moyer et al. 2003) and is considered a high-latitude reef system. Such marginal coral reef systems present different challenges in understanding reef dynamics, as high-latitude reefs exist near environmental limits of coral growth (Kleypas et al. 1999), thus supporting coral reef growth in areas of thermal and environmental extremes (Kleypas et al. 1999; Thompson and Frisch 2010). The SEFRT encompasses four shore-parallel topographic features: a nearshore hard-bottom ridge complex and three non-accreting linear limestone ridges (herein referred to as the nearshore, inner, middle, and outer reefs) that occur progressively from shore, increasing in depth. The SEFRT also exists adjacent to the highly urbanized and populated south Florida coastline, exposing it to a variety of local stressors. On the SEFRT, octocorals have previously been reported as comprising over 20% of the coral reef benthos whereas stony corals comprise typically less than 5% (Moyer et al. 2003). Observations of other high-latitude reef habitats, such as Sodwana Bay, South Africa (Schleyer et al. 2003; Schleyer et al. 2008), have reported similar or greater percentages of octocoral cover compared to that of scleractinians in their coral reef communities.

As in other areas of the tropical Western Atlantic region, stony coral cover on the SEFRT is declining (Walton et al. 2018; Jones et al. 2019, submitted). Long-term monitoring projects have reported declines in species diversity and stony coral cover in the nearby Florida Keys (Donahue et al. 2008; Ruzicka et al. 2013) and a similar significant decreasing trend in scleractinian coral cover has been observed on the SEFRT (Gilliam et al. 2017; Jones et al. 2019, submitted). In recent years, the SEFRT has experienced multiple thermal anomalies with resulting bleaching and disease events. It has also been estimated that a recent, multi-year disease outbreak of Stony Coral Tissue Loss Disease (SCTLD) resulted in approximately a 60% loss of stony coral live tissue area (Walton et al. 2018). However, the effects of these events have yet to be investigated for other prominent members of the local benthic reef community, such as octocorals. Octocorals are capable of suffering similar fates as stony corals with regards to thermal anomalies, predation pressures, storm events (hurricanes), and disease outbreaks. In Florida (USA) and the Caribbean, more than 10 octocoral diseases have been identified and reported, many of which have significantly impacted local communities (Weil et al. 2017). Known mass mortalities from disease epizootics have been reported affecting a variety of species, including the sea fans *Gorgonia ventalina* and *G. flabellum*, the encrusting octocorals *Briareum* spp. and *Erythropodium caribaeorum*, and other branching octocoral genera (Weil et al. 2017). Outbreaks of the fungal sea fan disease Aspergillosis were reported in the 1980s and again in the mid-1990s, spreading throughout the Caribbean and causing mass mortality into the mid-2000s (Smith et al. 1996; Nagelkerken et al. 1997; Smith and Weil 2004; Weil et al. 2017). Another sea fan disease, Multi-focal Purple Spot disease, was first reported in 2005 in Puerto Rico, Mexico and in Florida, USA, increasing in prevalence in Puerto Rico and other areas of the Caribbean into the 2010s (Weil and Hooten 2008; Weil and Rogers 2011; Weil et al. 2014; Ivanenko et al. 2015; Weil et al. 2017). A newer sea fan disease, *Gorgonia* wasting syndrome, was described offshore Puerto Rico during the thermal anomaly of 2010 and continues to affect colonies in the region, although no putative pathogen has been identified (Weil et al. 2014; Weil et al. 2017). Diseases that have affected other genera of octocorals include Red Band Disease, Black Band Disease, *Erythropodium* Wasting Syndrome, *Briareum* Bleaching Necrosis and *Briareum* Wasting Syndrome, in addition to some other unidentified wasting conditions (Weil et al. 2017); each have been observed at various locations throughout the Caribbean and Florida Keys from the 1990s to the 2010s, in association with warmer months of the year or following specific thermal anomalies (Weil et al. 2017). With regards to bleaching (loss of symbiotic zooxanthellae, often a response to thermal stress), bleached octocorals have been reported in Puerto Rico (Prada et al. 2009), Panama (Lasker et al. 1984), and the Florida Keys (Harvell et al. 2001) following thermal anomalies. In each of these studies, partial or whole colony mortality was observed in association with the bleaching, with the study in the Florida Keys culminating in a mass mortality of *Briareum asbestinum* colonies. However, Prada et al. (2009) indicated a strong difference in the degree of bleaching and mortality among species, with some species experiencing no bleaching or mortality, and others experiencing >50% bleaching and mortality. These data were reported for an event that resulted in >75% bleaching of all scleractinian corals, with bleaching in the octocoral community reported following the initial bleaching of the scleractinian community, suggesting a greater thermal tolerance in some octocorals (Prada et al. 2009).

Since 2003, the reefs of southeastern Florida have been altered significantly with the changing environment (Gilliam et al. 2017). To fully understand the current status of the SEFRT, all components of the benthos need to be considered. Although multiple studies highlight the community composition of the local stony corals as well as spatial and temporal trends in their cover and bleaching and disease prevalence, the same has yet to be investigated for the octocoral community on the SEFRT. The Southeast Coral Reef Evaluation and Monitoring Project (SECREMP) has been established as a long-term monitoring effort to monitor the stony and octocoral populations throughout Southeast Florida, although only the scleractinian coral data has been examined in detail to date. This study utilizes this dataset to identify any long-term spatial or temporal trends in the octocoral populations of southeastern Florida. This information will provide local managers, conservationists, and restoration scientists with a better understanding of contributions by other major taxa to reef ecosystem health, by investigating community trends for potentially resistant and resilient organisms such as octocorals. It will also contribute to the knowledge base regarding stable, high-density octocoral communities, which is the current state of some coral reef ecosystems in the Caribbean and tropical Western Atlantic and may be the future of many more.

2. Objective

2.1 Overview

This project proposes to identify temporal and spatial patterns in octocoral density, colony height, and the prevalence of diseases and bleaching in the octocoral community. It will contribute to the understanding of coral reef community ecology by investigating spatiotemporal trends of an important and prevalent constituent of local coral reefs, concomitant with known shifts in scleractinian benthic cover and community structure.

2.2 Research Questions

- Does octocoral density, colony height or disease and bleaching prevalence vary temporally?
- Does the octocoral community vary by spatially by reef?
- Has the local octocoral community been affected by any major disturbances that have significantly impacted the stony coral community (e.g. thermal anomalies, diseases outbreaks, storm impacts)?

3. Methods

3.1 Survey Methods

This project utilizes data from the Southeast Coral Reef Evaluation and Monitoring Project (SECREMP), which was initially established in 2003 to assess stony coral cover and species richness at 10 sites along the SEFRT from Palm Beach County to Miami-Dade County. It has since expanded to a total of 22 sites along the SEFRT from Martin to Miami-Dade Counties (Table 1) and as of 2013 has included octocoral abundance and demography surveys. The current study omits four of these sites (MC1, MC2, PB1, BCA); octocorals were never recorded at MC1 or MC2; PB1 is an inner reef site likely buried by nearby beach re-nourishment activities prior to 2013 where few, if any, octocorals have been recorded since; BCA, offshore Fort Lauderdale, FL, was established specifically to monitor a dense *Acropora cervicornis* patch and has supported a very low abundance of octocorals.

The reefs of the SEFRT (nearshore, inner, middle, and outer) run parallel to shore, increasing in depth from the nearshore reef to the outer reef (Fig. 1). The 18 sites occur across all four of these reefs (Table 1; Fig. 2). However, due to sample size constraints and similarities in depth and habitat, the nearshore reef and the inner reef were analyzed collectively as one group - the inner reef. This analysis begins in 2013 when octocoral abundance and demography surveys were added to the protocol.

Table 1: SECREMP site locations and depth.

Site	Year Established	Depth (m)	Latitude	Longitude	Habitat
MC1	2006	5	27° 07.900’	80° 08.042’	Nearshore Ridge Complex
MC2	2006	5	27° 06.722’	80° 07.525’	Nearshore Ridge Complex
PB1	2003	8	26° 42.583’	80° 01.714’	Nearshore Ridge Complex
PB2	2003	17	26° 40.710’	80° 01.095’	Outer Reef
PB3	2003	17	26° 42.626’	80° 00.949’	Outer Reef
PB4	2010	17	26° 29.268’	80° 02.345’	Outer Reef
PB5	2010	17	26° 26.504’	80° 02.846’	Outer Reef
BC1	2003	8	26° 08.872’	80° 05.758’	Nearshore Ridge Complex
BC2	2003	12	26° 09.597’	80° 04.950’	Middle Reef
BC3	2003	17	26° 09.518’	80° 04.641’	Outer Reef
BC4	2013	9	26° 08.963’	80° 05.364’	Inner Reef
BC5	2013	12	26° 18.111’	80° 04.090’	Middle Reef
BC6	2013	18	26° 18.064’	80° 03.654’	Outer Reef
BCA	2003	8	26° 08.985’	80° 05.810’	Nearshore Ridge Complex
DC1	2003	8	25° 50.530’	80° 06.242’	Inner Reef
DC2	2003	14	25° 50.520’	80° 05.704’	Middle Reef
DC3	2003	17	25° 50.526’	80° 05.286’	Outer Reef
DC4	2010	12	25° 40.357’	80° 05.301’	Outer Reef
DC5	2010	7	25° 39.112’	80° 05.676’	Inner Reef
DC6	2013	6	25° 57.098’	80° 06.545’	Nearshore Ridge Complex
DC7	2013	18	25° 57.511’	80° 05.627’	Middle Reef
DC8	2013	8	25° 40.712’	80° 07.117’	Nearshore Ridge Complex

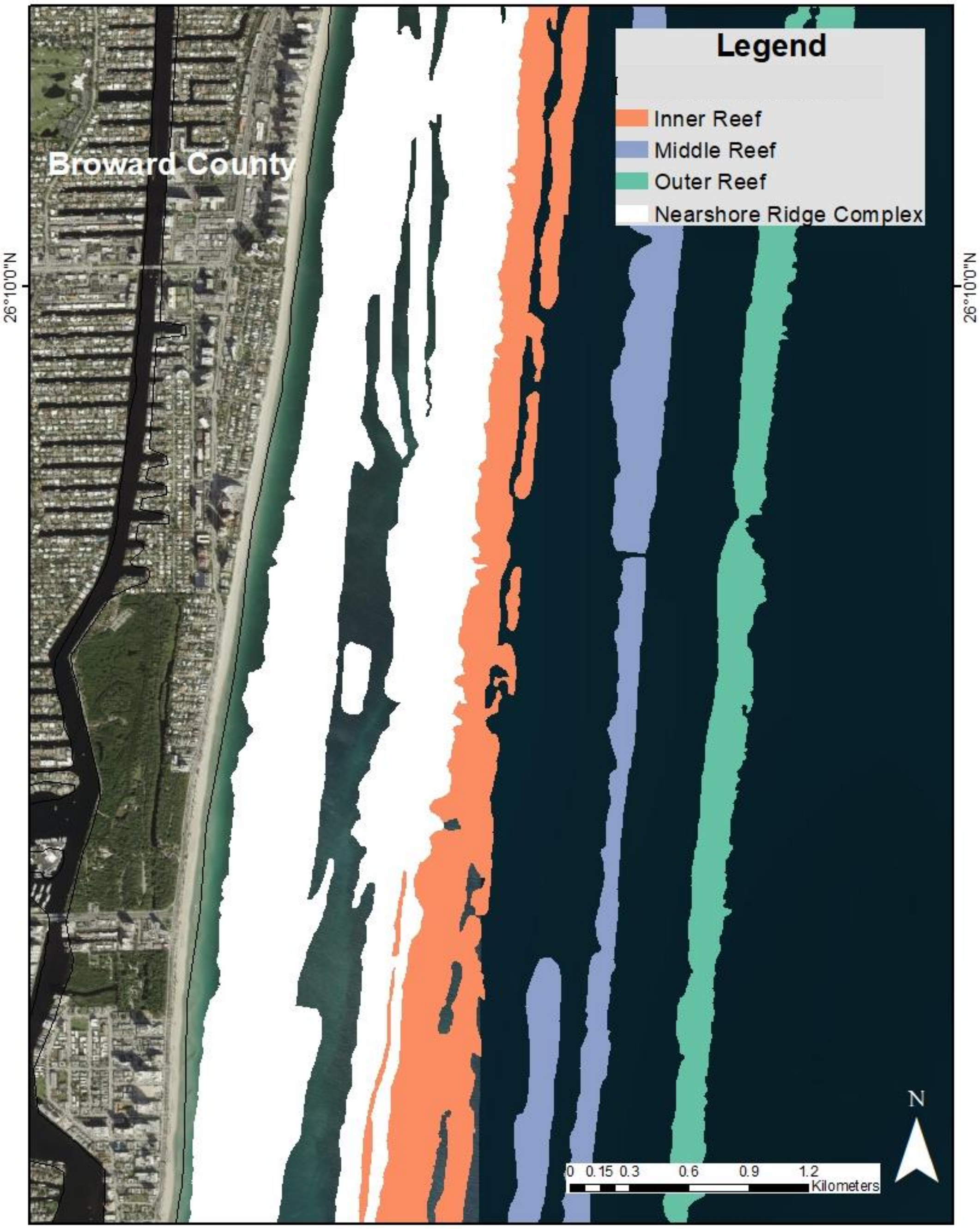

Figure 1: Three reef tracts and nearshore hardbottom ridge complex of the SEFRT, offshore Broward County, Florida: nearshore (white), inner (orange), middle (blue), and outer (green).

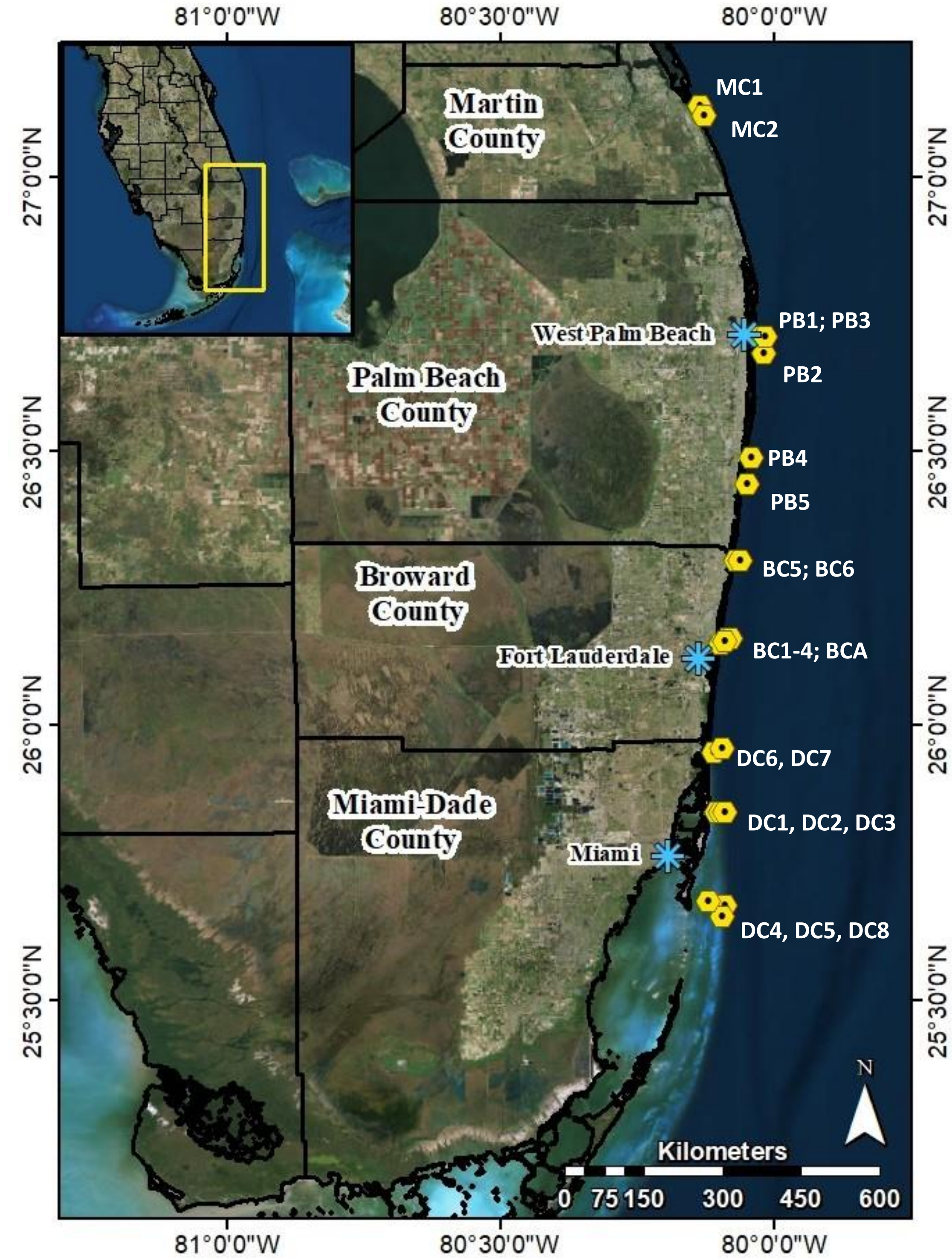

Figure 2: Location of the SECREMP sites along the SEFRT. Yellow dots indicate site location, and the blue asterisks indicate major metropolitan cities along the coastline.

At each site, four permanent 10 x 1m belt transects were established, extending north to south. Along each transect, all octocorals were counted via SCUBA surveys, regardless of size, condition, or species. Maximum colony height and general colony condition (i.e. presence of diseases or bleaching) were recorded for three target species: *Antillogorgia americana* (Gorgoniidae), *Gorgonia ventalina* (Gorgoniidae), and *Eunicea flexuosa* (Plexauridae) (Fig. 3). These species were chosen based on their presence at all sites, abundance across a range of habitats and depths, as well as relative ease of identification in the field simply with morphological characteristics. These target species provided a potentially accurate and easily identifiable representation of the local octocoral community, as many octocoral species require microscopic examination of sclerites for proper identification (Bayer 1961). The total octocoral counts were used to calculate density at each site and to identify temporal trends in abundance. Colony condition data were used to model temporal variation in bleaching (BLH) and diseases prevalence of previously observed diseases in Florida or the Caribbean for our target species: Aspergillosis (ASP; *G. ventalina* only), Multi-Focal Purple Spot disease (MFPS; *G. ventalina* only), Red Band disease (RBD), and Black Band Disease (BBD). Finally, the three target species were used to represent the octocoral community throughout the monitoring period, to identify differences among sites and reef habitats on the SEFRT.

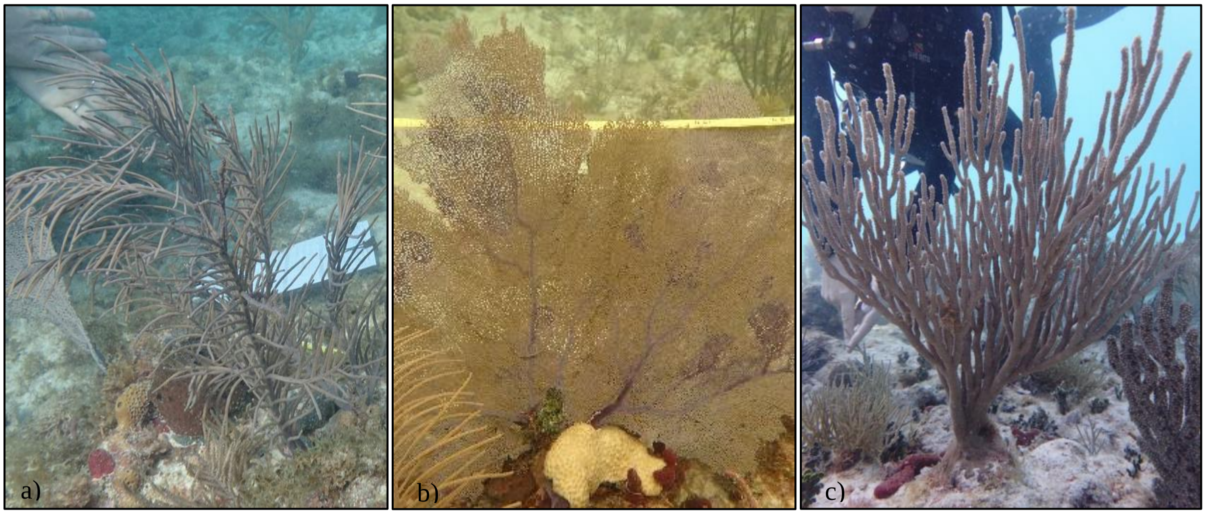

Figure 3: Target species: a) *Antillogorgia americana* d) *Gorgonia ventalina* and c) *Eunicea flexuosa.*

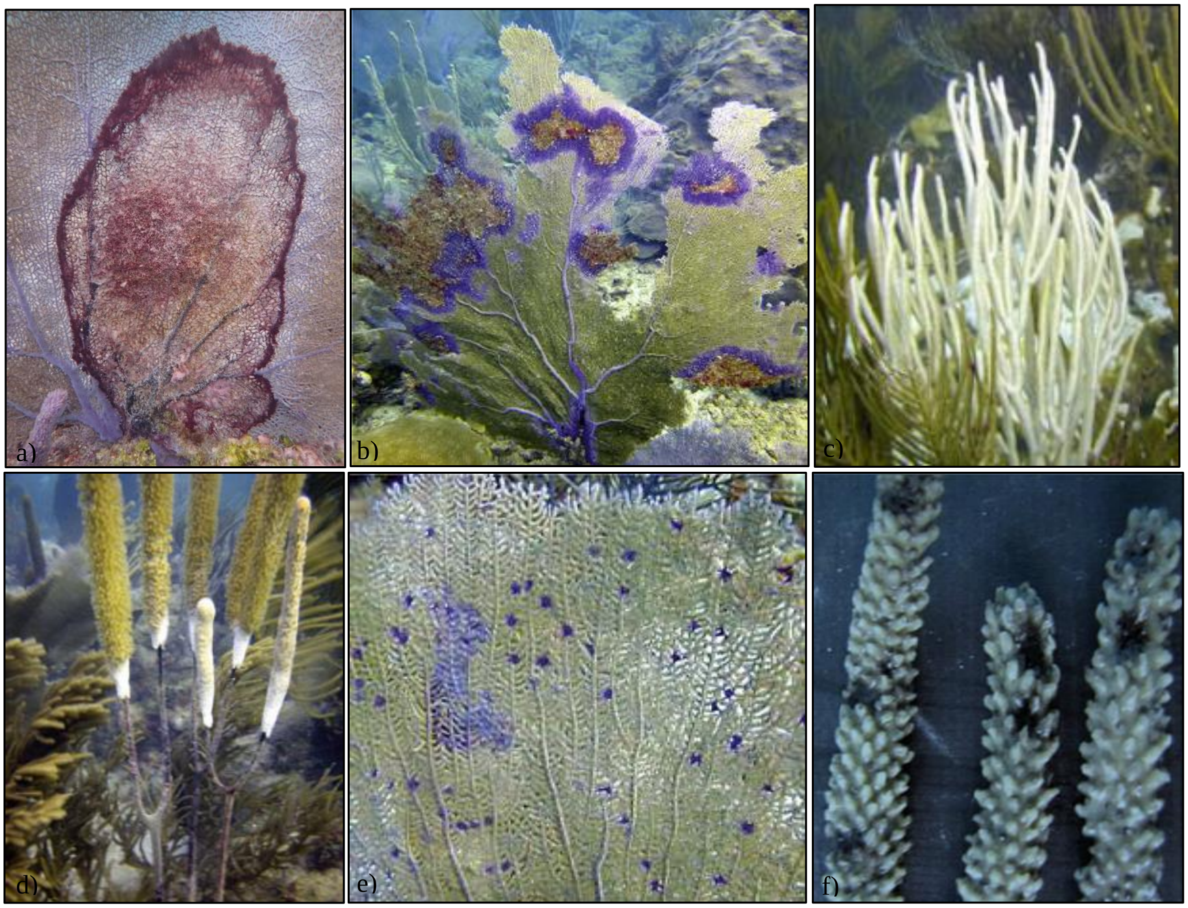

Figure 4: Lesions of octocoral diseases and bleaching: a) Red Band Disease b) Aspergillosis c) Bleaching d) Unknown wasting syndrome e) Multifocal Purple Spot Disease, and f) Unknown disease with black lesions (Photos b-f by E. Weil from Weil et al. 2017).

3.1 Statistical Analysis

Because the temporal relationships for density, target colony height, and bleaching/disease prevalence were all non-linear, generalized additive mixed effects models (GAMM) were used, which allow for non-linear relationships between the response and explanatory variables to be modelled using smoothing functions (Zuur 2009). The mixed effects model accounts for the repeated measures throughout the study period, as well as the nested structure of the experimental design (Zuur 2009). They were created using the Generalized Additive Model for Location, Scale, and Shape (GAMLSS; Stasinopoulos and Rigby 2007) package in R (R Core Team 2013), which allows for the fitting of semi-parametric regression type models that fit a wider range of distribution families (Stasinopoulos and Rigby 2007).

Analyses were completed to identify temporal patterns in colony density, colony height, and the prevalence of diseases (ASP, MFPS, RBD, BBD) and bleaching (BLH), to model changes in each dependent variable throughout the study period against the independent variables of time, reef (inner, middle, outer), and species (where applicable). The "full" models containing all terms were fitted as follows: density was modelled as individual colony counts (integer values) with reef as the only interactive term with time; colony height was modelled with measurements (continuous) of the target species colonies with both reef and species as interactive terms with time; diseases and bleaching prevalence were modelled as presence/absence on the target colonies for each condition, with reef and species as interactive terms with time. Because both ASP and MFPS have only previously been reported locally on sea fan colonies (including *G. vetalina;* Weil et al. 2017), models of these diseases were built with datasets containing only the observations for this target species to gain a more accurate view of the impact to the species. To incorporate spatial correlation among samples within a study site, site was included as a random effect in the models. The full models are defined as:

a) *counts = time x reef + random(site)*
b) *height = time x reef x species + random(site)*
c) *disease = time x reef x species + random(site)*
d) *bleaching = time x reef x species + random(site)*

Penalized Beta-splines (pb) were used for the smoothing of time (Eilers and Marx 1996). The appropriate distributions and explanatory variables were chosen by checking for heterogeneity of the residuals and comparing the Akaike's Information Criterion (AIC) of the various models for each of the dependent variables (abundance, height, disease, and bleaching). If the differences in the AIC scores were between -4 and 0, the effect of the factor in question (reef or species) was considered nonexistent or only marginal and the simpler model was chosen (Burnham and Anderson 2002). To model octocoral density, a negative binomial distribution was used instead of a Poisson distribution (both typical of count data), as the Poisson residuals suggested over-dispersion and the AIC was lower (Table 2). Because the colony height observations (continuous), were skewed from the Gaussian distribution, a log-normal distribution was chosen which produced a lower AIC and homogeneous residuals (Table 2). A binomial distribution was most appropriate for the ASP, MFPS, and BLH models (lower AIC scores, homogeneous residuals) compared to a zero-inflated binomial distribution (Table 2). Models were ultimately not constructed for RBD and BBD as they were not observed during the study period.

Table 2: AIC values and degrees of freedom (df) for distribution selection process for each analysis. The chosen distributions are bolded.

Analysis	Distribution	AIC	df
Density	Poisson	7439.2	28
	Negative Binomial	**4565.2**	**29**
	Zero-Inflated Poisson	7356.9	30
	Zero-Inflated Negative Binomial	4580.6	28
Colony Height	Normal	140497.1	78
	Log-Normal	**131917.0**	**79**
ASP	**Binomial**	**118.8**	**18**
	Zero-Inflated Binomial	129.2	8
MFPS	**Binomial**	**192.9**	**13**
	Zero-Inflated Binomial	372.2	16
BLH	**Binomial**	**467.6**	**48**
	Zero-Inflated Binomial	797.3	51

To further investigate spatial variation and to understand differences in the community composition of the SEFRT and its four reefs, the distributions of the three targeted species were used to determine similarities among sites and reef tracts using an Analysis of Similarity (ANOSIM) and a Similarity Percentage (SIMPER) analysis in PRIMER version 6 (Clarke & Gorley 2006). Data were square-root transformed prior to constructing a resemblance matrix using Bray-Curtis similarity. The ANOSIM was conducted on the resemblance matrix, while the SIMPER was conducted on the transformed data. Clusters of study sites by target species composition were determined with a cluster analysis and the data were visualized using an nMDS plot created using the Bray Curtis-similarity resemblance matrix. Nested ANOVAs were additionally conducted to identify differences in density and colony height among each reef in 2018, to gain a better understanding of the current state of the octocoral community on the SEFRT.

4. Results

4.1. Density

According to the minimum adequate model, octocoral density increased from 2013 to 2017, but decreased from 2017 to 2018 (Fig. 5). The mean (± SE) density of octocorals (all sites pooled) increased from 10.9 ± 0.8 colonies m^{-2} in 2013 to 15.3 ± 1.0 colonies m^{-2} in 2017, then declined slightly to 12.6 ± 0.8 colonies m^{-2} in 2018. The model that explained changes in the density of octocorals only included time as an explanatory factor, suggesting that the temporal trend of octocoral density on the SEFRT did not vary by reef tract (Table 3). The density of octocorals, however, did differ by reef in 2018. In 2018, the mean density of octocorals was significantly greater on the outer reef than on the middle and inner reefs (Nested ANOVA, p= 0.01). The mean density (all sites pooled by reef) was 9.8 ± 1.1 colonies m^{-2} on the inner reef, 9.1 ± 1.1 colonies m^{-2} on the middle reef, and 16.4 ± 1.1 colonies m^{-2} on the outer reef. The density on the outer reef was also consistently greater than the density on the middle and inner reefs throughout the study period (Fig. 6).

Table 3: AIC and df values for total octocoral density. The model that includes all variables is highlighted in grey, and the minimum adequate model is bolded.

Factors Included	AIC	df
Reef tract and time	4565.2	29
Time	**4556.6**	25

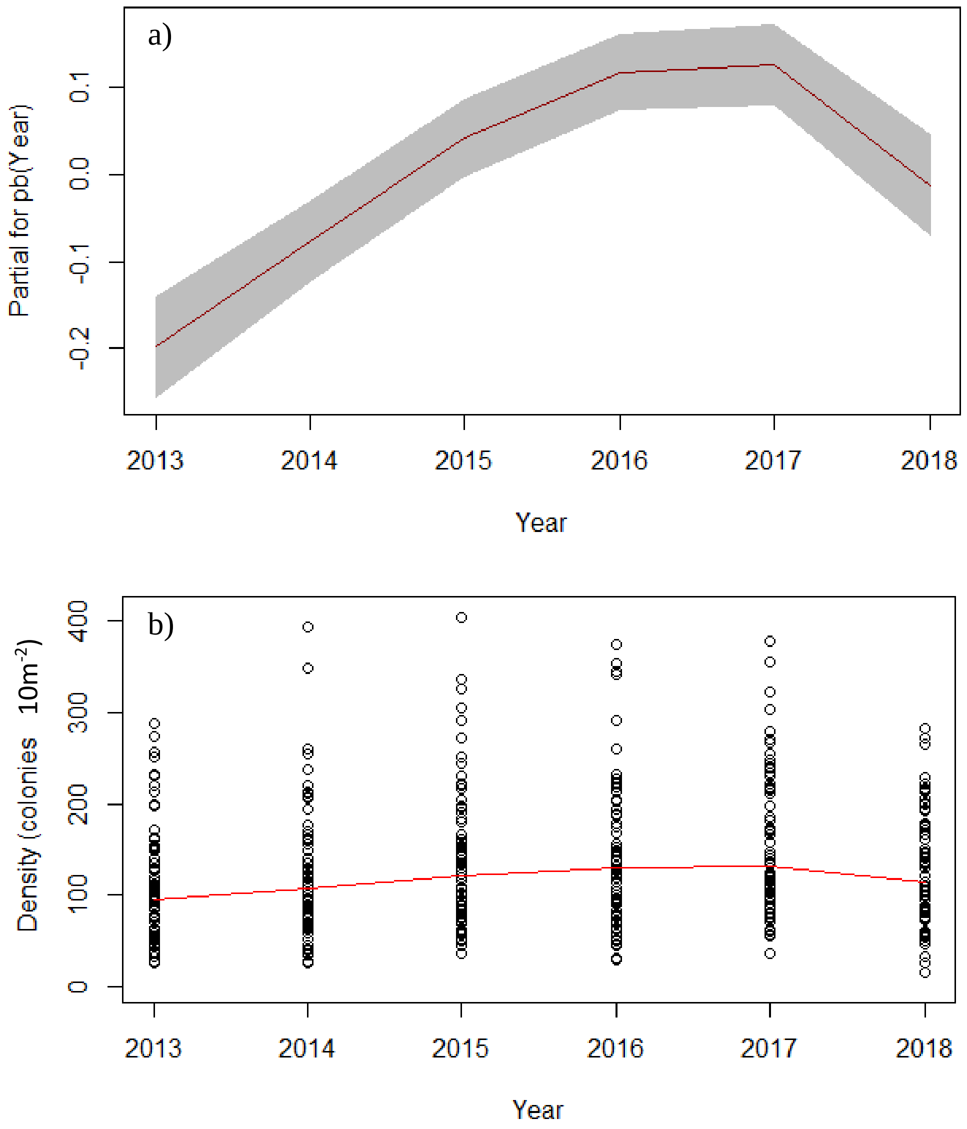

Figure 5: Octocoral density throughout the study period: a) term plot produced from the GAMLSS model, depicting trend and error b) trend from model predictions over actual site density values

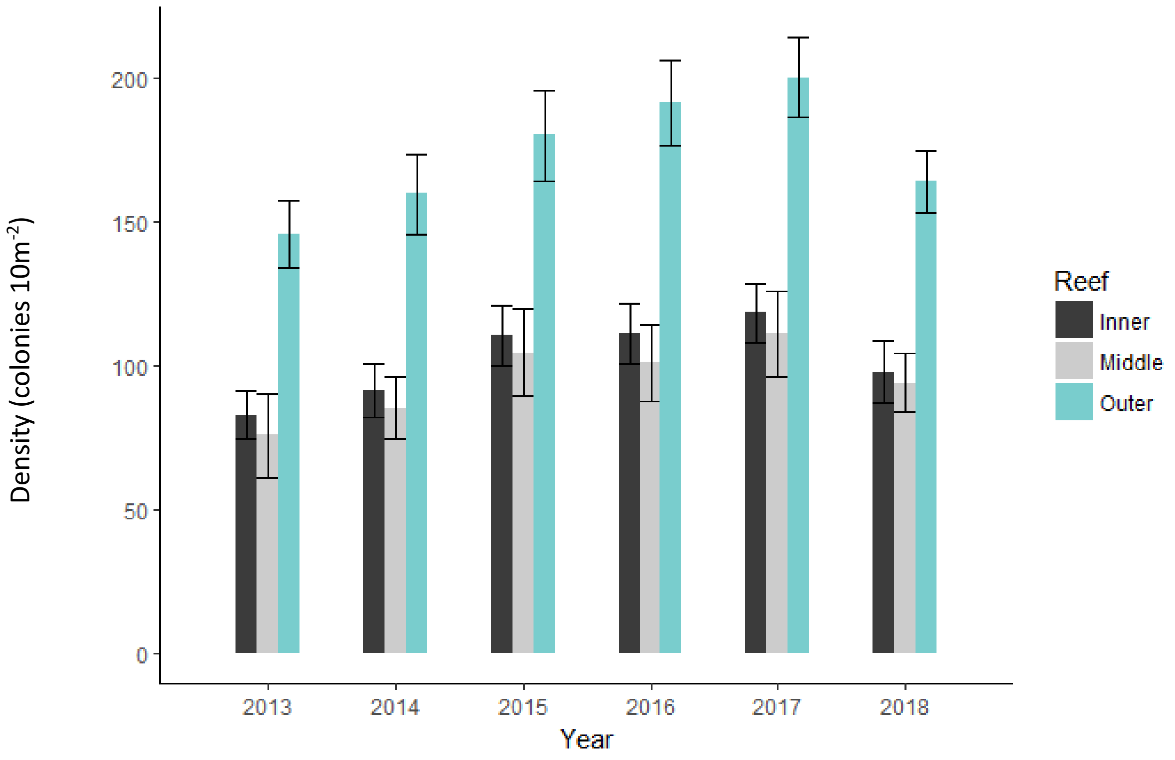

Figure 6: Mean density of octocorals per transect (colonies $10m^{-2}$ ± SE; sites pooled) by reef in each sample year.

4.2 Colony Height

The minimum adequate model indicated a decline in target colony height throughout the study period (Fig. 7). Mean (± SE) colony height (all sites pooled) decreased from 25.7 ± 0.4 cm in 2013 to 21.5 ± 0.3 cm in 2018 (Fig. 8). The mean height (all sites and years pooled) was 23.9 ± 0.2 cm for *A. americana*, 23.1 ± 0.2 cm for *E. flexuosa*, and 16.4 + 0.4 cm for *G. ventalina* (Fig. 8). The model included only species as a factor, however, species did not interact with time (Table 4). This suggests that colony height varies by species, but temporal trend does not. Colony height also does not vary by reef. Including species and reef as interactions with time in the model had the lowest AIC, but the estimates were unstable (Table 4). Modelling species as an interaction with time, with and without reef as an additional factor had the second and third lowest AIC scores, but they both also had unstable estimates (Table 4). Despite the exclusion of reef from the model, colony height significantly differed among reefs in all study years (Nested ANOVA, $p<0.05$) except for 2018 (Nested ANOVA $p=0.95$). From 2013 to 2017, mean colony height (all sites pooled) decreased from 27.2 ± 0.05 to 23.4 ± 0.5 cm on the outer reef, from 22.5 ± 0.8 to 20.4 ± 0.8 cm on the middle reef, and 23.4 ± 0.7 to 22.2 ± 0.6 cm on the inner reef. In 2018, the mean height of target colonies (all sites pooled) was 21.4 ± 0.7, 20.6 ± 0.8, and 22.4 ± 0.5 cm on the inner, middle, and outer reefs respectively.

Table 4: AIC and df values for target colony height. The model that includes all variables is highlighted in grey, and the minimum adequate model is bolded.

Factors Included	**AIC**	**df**
Time, Reef Tract, and Species	130947.8	52
Time and Reef Tract	132222.2	27
Time and Species	**131192.8**	**29**
Time	132218.6	25

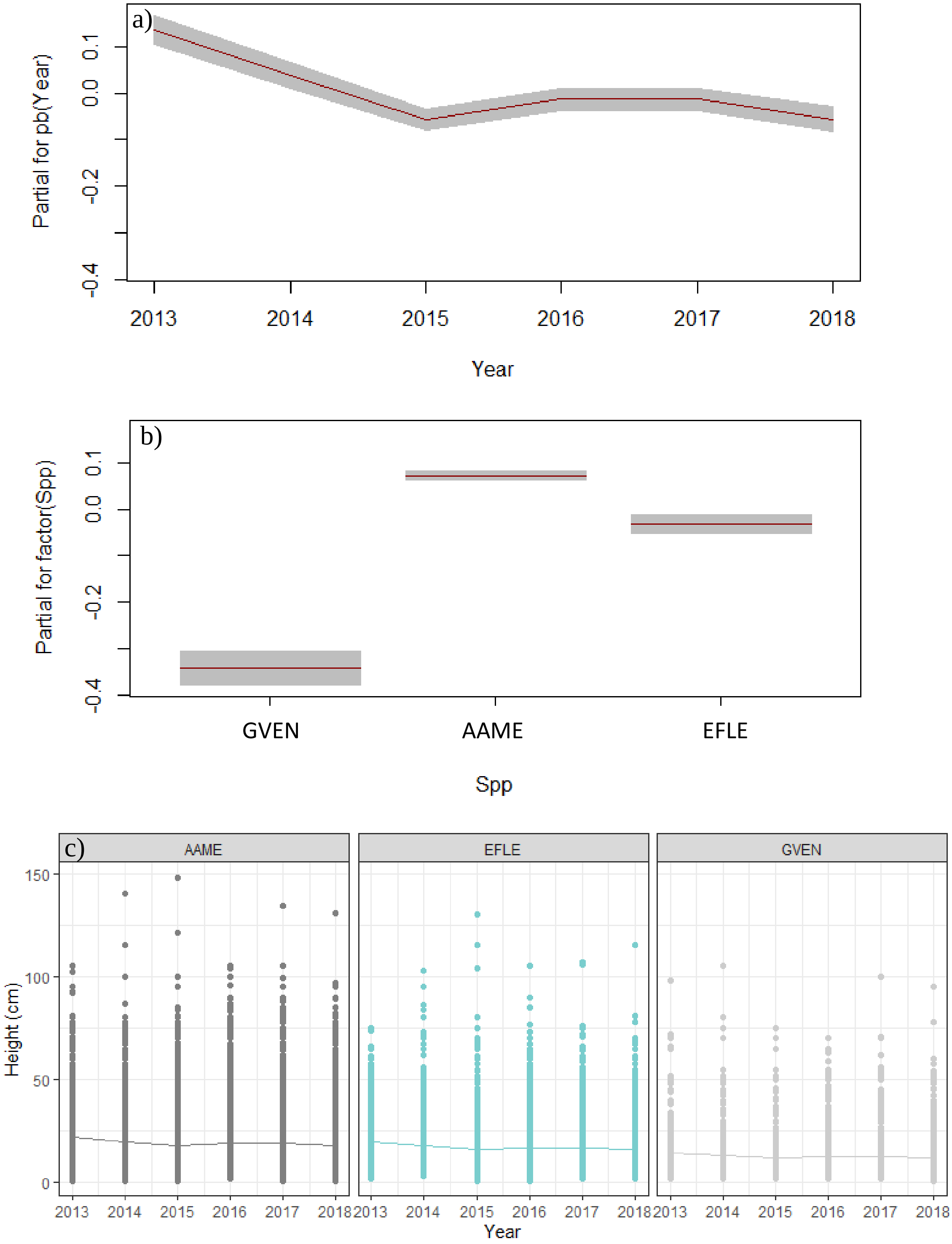

Figure 7: Colony height from 2013-2018 for target species *A. americana* (AAME), *E. flexuosa* (EFLE), and *G. ventalina* (GVEN): a) term plot produced from GAMLSS model depicting change in colony height over time b) term plot produced from GAMLSS model depicting differences in colony height by species c) trend from model predictions plotted over actual colony height values for each target species

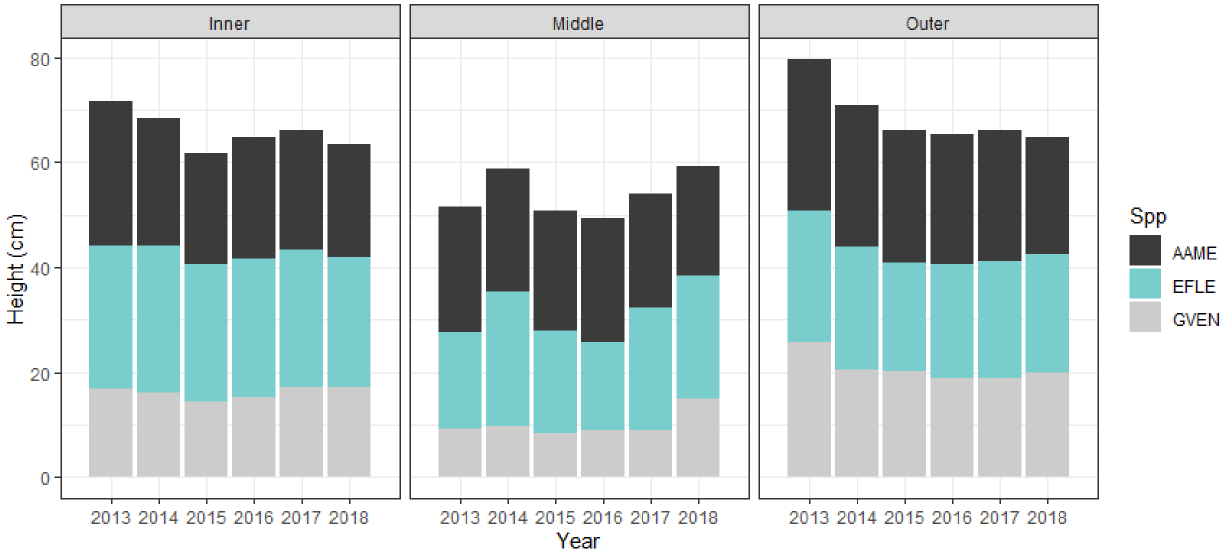

Figure 8: Mean height (cm) of target species colonies *A. americana* (AAME), *E. flexuosa* (EFLE), and *G. ventalina* (GVEN) from 2013-2018 (sites pooled by reef).

4.3 Disease and Bleaching

Only occurrences of ASP, MFPS, and BLH were observed during the demographic surveys of the target species. Other unidentified lesions were also observed throughout the study period, although they have yet to be described as symptoms of disease, so they were not included in this analysis. The minimum adequate model for ASP only included time as an explanatory factor, suggesting that the prevalence of ASP throughout the study period did not vary by reef (Table 5). Its prevalence declined throughout the study period (Fig. 9a), however, the model also indicated a large margin of error (Fig. 9b). At its peak (2013), ASP was only observed on seven *G. ventalina* colonies out of 187 and declined from there. This yielded a 0.37% prevalence of ASP in 2013 and less in the following study years (Table 6). The large margin of error in the model indicates that the constructed GAMMs were unable to properly fit the data, as the number of affected colonies, if any, were very low. The minimum adequate model for MFPS also only included time as an explanatory factor, indicating that its prevalence did not vary temporally by reef (Table 5). MFPS also declined throughout the study period (Fig. 9c). The error in this model was much smaller than that of the ASP model, indicating a more appropriate fit (Fig. 9d). MFPS was recorded on a maximum of six *G. ventalina* colonies (2015), yielding a peak prevalence of 0.29% (Table 6). Similar to both the ASP and MFPS models, the minimum adequate model for BLH only included time as an explanatory factor, suggesting that the prevalence of BLH did not vary temporally by reef or species. The two models with the lowest AIC scores included reef and species, or just species as factors, but the estimates were unstable. Therefore, the model with the third lowest AIC (only time as explanatory factor) was selected as the minimum adequate model, as its estimates were stable. However, like the ASP model, the error in the BLH model was too great, suggesting the inability of a GAMM to properly fit the extremely low prevalence of BLH, which was observed at 1.0% or less in all study years (Fig. 9e and 9f; Table 6).

Table 5: AIC and df values of disease prevalence models (ASP, MFPS, RBD, and BLH), with time, reef and species (where applicable) as explanatory factors. The models that include all variables are highlighted in grey, and the minimum adequate models are bolded.

Analysis	**Factors Included**	**AIC**	**df**
ASP	Time and Reef Tract	118.8	18
	Time	**111.9**	**15**
MFPS	**Time and Reef Tract**	**192.9**	**13**
	Time	194.4	10
BLH	Time, Reef Tract, and Species	467.6	48
	Time and Reef Tract	458.5	22
	Time and Species	452.2	28
	Time	**457.8**	**18**

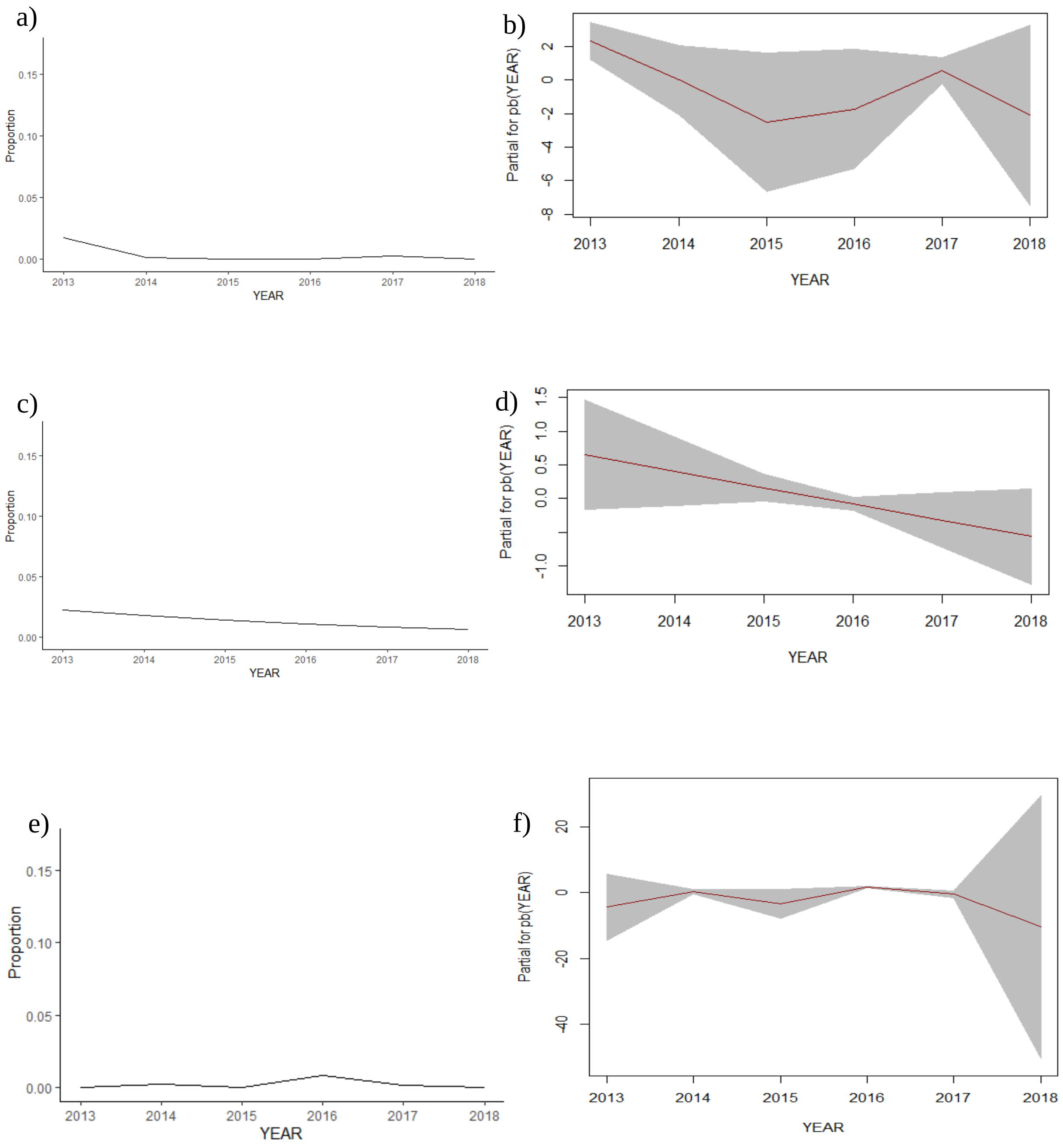

Figure 9: Proportion (all sites and species pooled) of target colony conditions throughout the study period: a) model predictions of ASP prevalence throughout the study period, b) GAMLSS term plot for ASP prevalence, c) model predictions of MFPS prevalence throughout the study period, d) GAMLSS term plot for MFPS prevalence, e) model predictions of BLH prevalence throughout the study period, f) GAMLSS term plot for BLH prevalence.

Table 6: Bleaching and disease prevalence on colonies from 2013 to 2018 (all sites and species pooled).

	ASP	MFPS	RBD	BBD	BLH	Colonies Surveyed
2013	0.37%	0.05%	0.00%	0.00%	0.00%	Total: 1890 GVEN: 187
	n=7	n=3	n=0	n=0	n=0	
2014	0.05%	0.29%	0.00%	0.00%	0.29%	Total: 2072 GVEN: 216
	n=1	n=6	n=0	n=0	n=6	
2015	0.00%	0.00%	0.00%	0.00%	0.0%	Total: 2503 GVEN: 266
	n=0	n=0	n=0	n=0	n=0	
2016	0.00%	0.16%	0.00%	0.00%	1.00%	Total: 2518 GVEN: 256
	n=0	n=4	n=0	n=0	n=25	
2017	0.08%	0.12%	0.00%	0.00%	0.11%	Total: 2542 GVEN: 285
	n=2	n=3	n=0	n=0	n=3	
2018	0.00%	0.04%	0.00%	0.00%	0.00%	Total: 2262 GVEN: 243
	n=0	n=1	n=0	n=0	n=0	

4.4 Spatial Distribution

The distribution of the target species differed significantly among the reefs (inner, middle and outer) throughout the study period (ANOSIM, p=0.001, R=0.2). The outer reef significantly differed from both the inner (ANOSIM, p=0.001, R=0.2) and middle reefs (ANOSIM, p=0.002, R=0.2), but the inner and middle reefs did not differ significantly from one another. Differences in target species distribution drove the differences among the reef tracts. *Antillogorgia americana* was the most abundant target species at sites on both the inner and middle reef tracts and its distribution contributed the most (SIMPER, 49%) to dissimilarities between the inner and middle reefs. Throughout the study period, its mean density (sites pooled by reef) ranged from 1.5 ± 0.3 to 2.4 ± 0.4 colonies m^{-2} on the inner reef and 2.1 ± 0.3 to 2.5 ± 0.3 colonies m^{-2} on the middle reef, while densities of *E. flexuosa* and *G. ventalina* remained <1.0 colony m^{-2} on both reefs (Fig. 10). The outer reef significantly differed from the inner and middle reefs due to the distribution of *E. flexuosa*, which contributed the most to dissimilarities between the outer reef and inner (SIMPER, 39%) and middle reefs (SIMPER, 52%) instead of *A. americana* (SIMPER, 37% and 30%). The mean density of *E. flexuosa* (1.1 ± 0.2 to 1.9 ± 0.3 colonies m^{-2}; Fig. 10) was comparable to the density of *A. americana* (1.5 ± 0.2 to 1.9 ± 0.2 colonies m^{-2}; Fig. 10) on the outer reef and much greater than those of *G. ventalina* (0.5 ± 0.03 to 0.6 ± 0.4 colonies m^{-2}; Fig. 10).

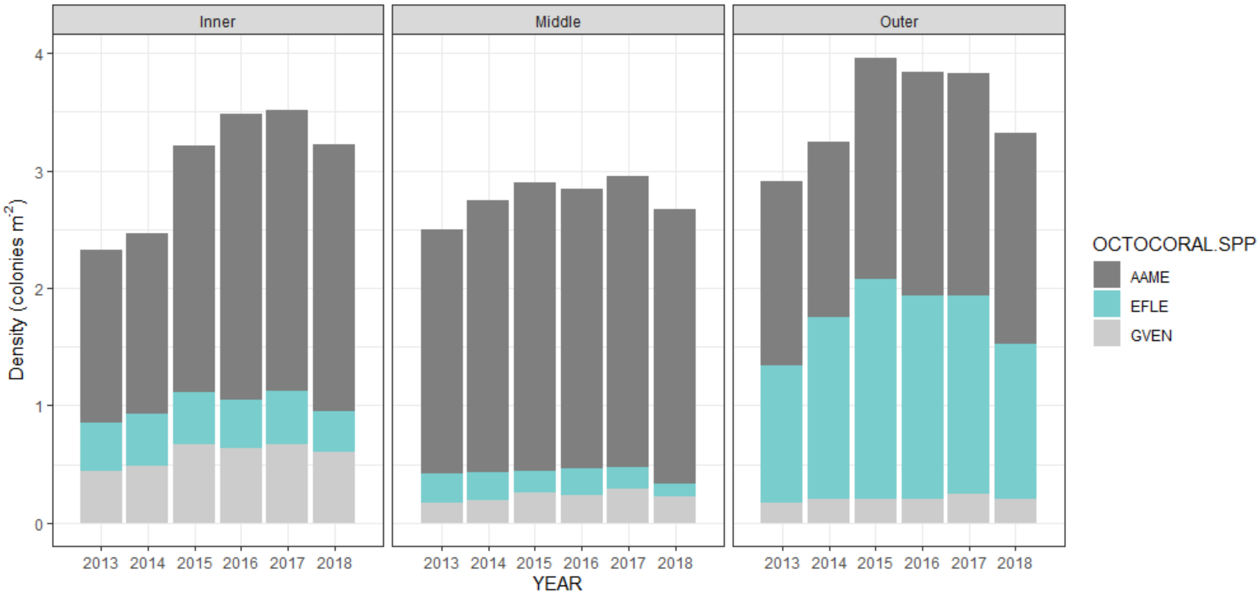

Figure 10: Mean density (colonies m^{-2}) of target species *G. ventalina* (GVEN), *E. flexuosa* (EFLE), and *A. americana* (AAME) throughout the study period on each reef tract of the SEFRT (all sites pooled)

Site within each reef were all 77-79% similar to one another (SIMPER). *Antillogorgia americana* contributed most to these similarities, contributing 44%, 69% and 50% respectively to the sites on the inner, middle and outer reefs (SIMPER). The cluster analysis did not indicate any significant clusters of study sites, however, some study sites did appear to differ from others according to the nMDS plot. When visualized by reef, some of the outer reef sites returned as a small cluster, but most of the site intermingled (Fig. 11, stress=0.14). When visualized by year, it becomes clear that some sites did form independent clusters across all sample years, but most did not. All the PB (PB2-5) sites formed one cluster, with BC1 and DC7 each forming another (Fig. 12, stress=0.14). The remaining 13 sites did not appear to differ in the nMDS plot with respect to the target species distributions.

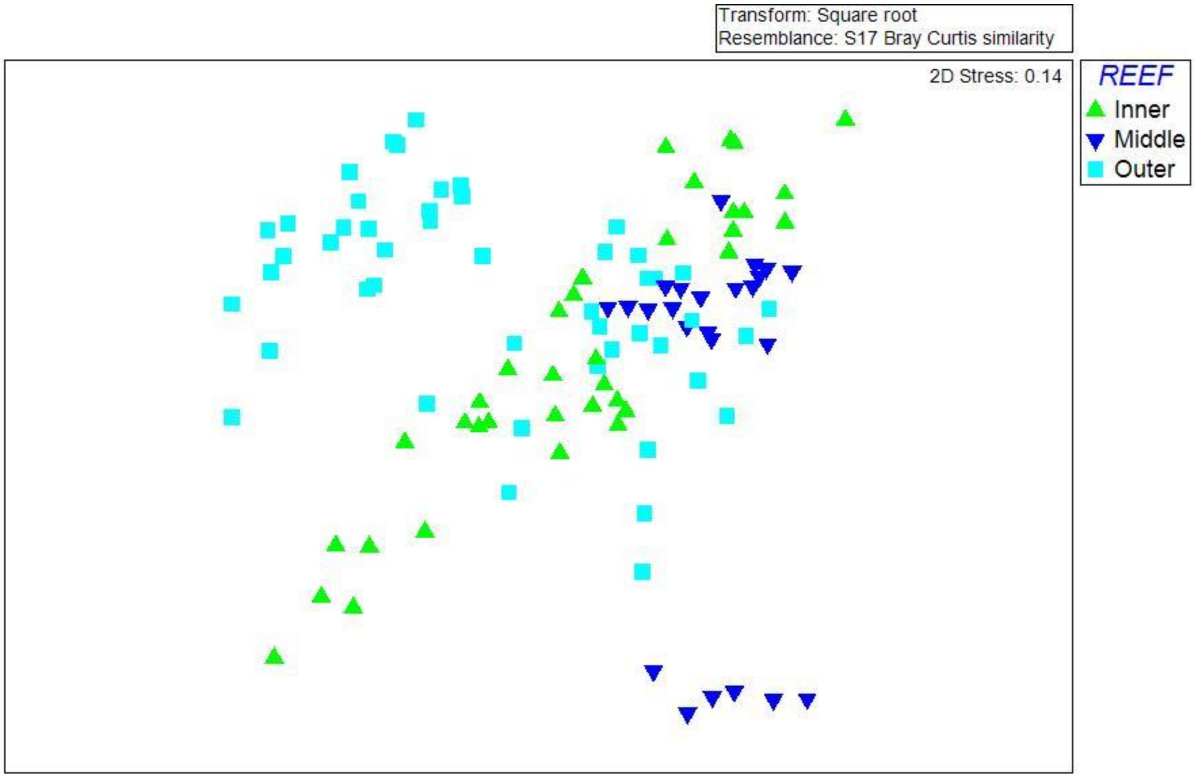

Figure 11: nMDS plot of differences among study sites based on target species distributions, visualized by reef (inner, middle, and outer) across all sampling years (2013-2018).

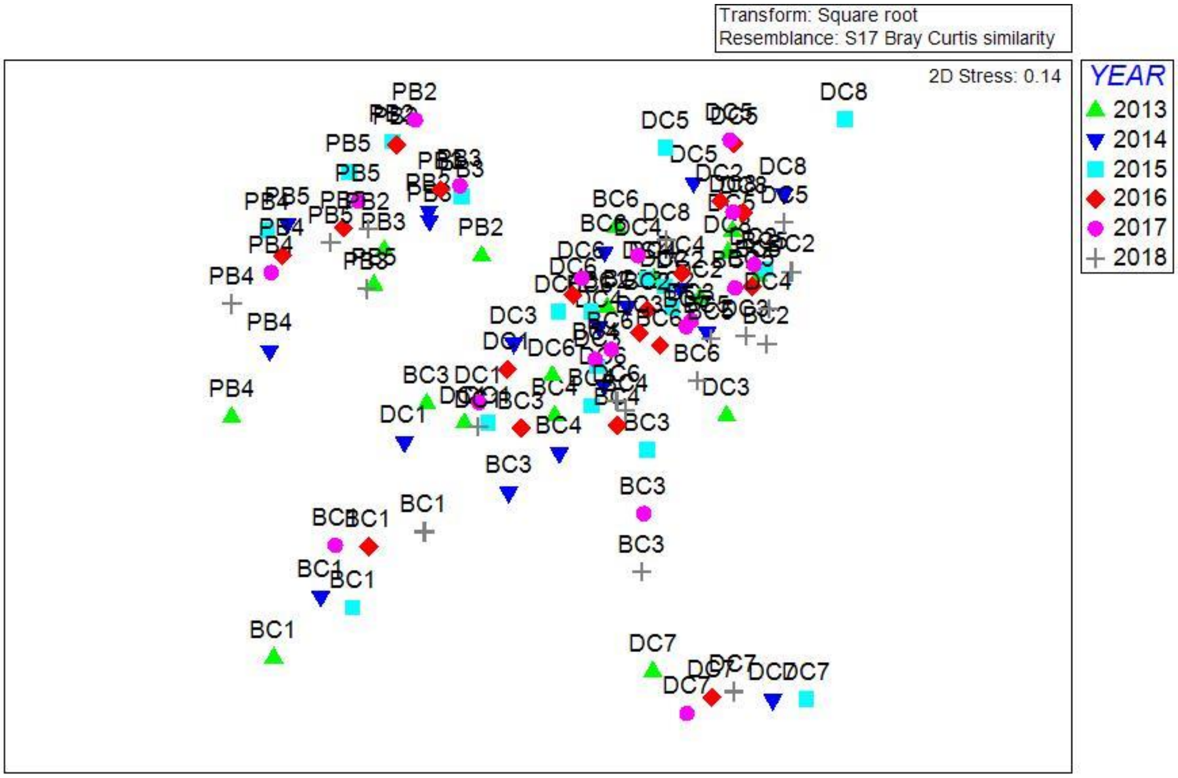

Figure 12: nMDS plot of differences among study sites based on target species distributions, visualized by sampling year (2013-2018).

5.0 Discussion

To characterize recent temporal and spatial patterns in the octocoral community of southeast Florida, total octocoral density and demography (height, presence of bleaching and disease) of three target species (*A. americana*, *E. flexuosa*, and *G. ventalina*) was recorded at 18 sites along the SEFRT from 2013-2018. Octocoral density significantly increased from 2013-2017 but declined in 2018. Reef was not a factor in the GAMM, suggesting that octocoral density varied similarly on each reef (inner, middle, and outer) throughout the study period. Total octocoral density was highest on the outer reef compared to the middle and inner reefs. Colony height of the target species decreased throughout the study period. The GAMM for colony height included species as an additive factor with time but not reef, suggesting that the height of the target colonies varied by species but the temporal trend in colony height did not. Despite the exclusion of reef as a factor in the model, mean colony height was significantly greater on the outer reef from 2013-

2017, but not in 2018. Heights of *A. americana* and *E. flexuosa* were comparable throughout the study period and greater than the heights of *G. ventalina* colonies. The greater density and height of octocorals on the outer reef is consistent with Cary's (1916) observations that deeper reef sites in the Dry Tortugas supported greater abundances and larger colonies, likely due to better protection from wave action during storms. Only two diseases were recorded throughout the study period: ASP and MFPS. Prevalence of these diseases and bleaching varied throughout the study period, but none exceeded 1% in any study year. The low prevalence of these conditions contributed to the inability of the GAMMs to properly fit the data, and spatiotemporal trends in prevalence were not properly identified. RBD and BBD were not observed on target colonies throughout the study period, although RBD was noted on two non-target colonies in 2015. In terms of target species distribution, the outer reef differed significantly from both the inner and middle reefs, which did not significantly differ from one another. The distribution of *E. flexuosa* drove the dissimilarity of the outer reef from the inner and middle reefs, where it occurred at its greatest densities. Conversely, the distribution of *A. americana* contributed the most to similarities between the inner and middle reefs, as well as to similarities among the sites within each reef. The study sites did not differ significantly based on the distribution of the target species, however, a few of the study sites differed when visualized with an nMDS plot; the PB sites (West Palm Beach, outer reef) formed one grouping, with two others formed each by DC7 (North Miami, middle reef) and BC1 (Fort Lauderdale, inner reef, Fig. 2). The West Palm Beach sites have had the highest density of octocorals throughout the study period (>150 colonies m^{-2}). BC1 was the only inner reef site that had a comparable density of *E. flexuosa* to *A. americana*, as all other inner reefs sites had greater abundances of *A. americana* and low abundances of *E. flexuosa*. DC7 was the only site that did not support any *G. ventalina* colonies throughout the study period.

The 2018 sampling event occurred following Hurricane Irma, a category 5 hurricane that made landfall in south Florida late in 2017. It was the first monitoring event to capture the local impacts of the hurricane as the sampling season had been completed prior to landfall of the hurricane in 2017. Anecdotal evidence from surveys immediately following the storm noted mass mortalities of octocoral colonies, which had either been ripped from the substrate or buried in sediment. Many octocorals had also washed up onto the local beaches. The decline in density observed in the model from 2017 to 2018 was likely a result of this event, as colonies were clearly removed from the substrate in the region. This is also supported by the decline in colony height during the same time period, which likely reflects the removal of larger colonies which may have been more exposed to wave action. Similar results were reported for the giant barrel sponge (*Xestospongia muta*) population of the SEFRT, which suffered declines in volume and density during the same 2017-2018 monitoring effort (Waldman 2019, unpublished master's thesis). These impacts also agree with other studies that have investigated the impacts of hurricane disturbances on reef habitats; Tsounis and Edmunds (2017) reported declines in octocoral abundance in the USVI following Hurricane Hugo in 1989 and Hurricanes Marilyn and Luis is 1995. Prior to this event, octocoral density had increased while colony height declined which likely reflects successful recruitment of octocorals and population growth with each study year.

In 2014 and 2015, thermal anomalies were recorded that resulted in bleaching events for the local stony coral population. Bleaching prevalence for stony corals on the SEFRT during these events ranged from 6.07 ± 1.54% to 17.43 ± 3.19% (Gilliam et al. 2015), whereas octocoral bleaching in the same time period was 1.0% or less. These thermal anomalies are also considered to have contributed to the unprecedented outbreak of Stony Coral Tissue Loss Disease (Manzello 2015; Eakin et al. 2016; van Woesik and McCaffrey 2017; Walton et al. 2018; Florida Keys National Marine Sanctuary 2018). The disease, which was first observed in 2014 on the SEFRT in Miami-Dade and Broward Counties (Precht et al. 2016; Walton et al. 2018), peaked in 2016 (Walton et al. 2018; Hayes 2019, unpublished master's thesis). Disease prevalence for the octocoral community remained less than 1% for any of the conditions (BLH, ASP, MFPS, RBD, and BBD) recorded in this study during the same time frame. Similarly, Prada et al. (2009) reported the absence of octocoral bleaching during a thermal stress event that significantly impacted the stony coral community, suggesting a greater thermal tolerance. Furthermore, with thermal stress events (and possible bleaching) often preceding coral diseases (Bruno et al. 2007; Miller et al. 2009; Eakin et al. 2010), the low prevalence of octocoral diseases throughout the study period may be correlated with the near absence of bleaching observed.

Octocorals of the SEFRT appear to be existing as a stable community relative to the stony coral community, as they have increased in density and resisted bleaching and disease throughout the study period. Alternative stable states in coral reef communities, such as an octocoral dominated benthos, may influence ecosystem processes, functions, and feedback mechanisms (Scheffer et al. 2001; Mumby et al. 2007b; Norstrom et al. 2009). However, it is possible that this analysis does not fully reflect features and changes in the SEFRT octocoral community, which may support as many as 39 species (precise number awaits taxonomic revisions; Goldberg 1973). Shallow-water tropical Western Atlantic octocoral communities are typically quite diverse, with over 40 species of octocorals having been identified on reefs offshore Colombia (Sanchez et al. 1998; Velasquez and Sanchez 2015), and 26 species offshore Costa Rica (Breedy 2009). In the most recent monitoring event (2018) for the SEFRT, the three target species only comprised 24.7% of all octocoral colonies observed. Studies of nearby sites in Miami, FL have reported differences in species richness and diversity of the octocoral assemblages by site location (Opresko 1973). Given the possibility of such small-scale differences in distribution and diversity within the octocoral community, the low percentage of the community included in the current study, and lack of significant difference among study sites that are anecdotally visually different (e.g. topography, community structure), the target species may not have accurately represented the octocoral community. Additionally, Prada et al. (2009) reported differences in bleaching severity by species: >50% bleaching for *Muricea spp.*, *Plexaurella spp.*, *Pseudoplexaura spp.*, *Pterogorgia spp.*, and *Briareum spp*, versus low bleaching prevalence for *E. flexuosa*. Similarly, few to no observations of bleaching have been reported for the target species *A. americana*, *E. flexuosa,* and *G. ventalina* on the SEFRT or in the wider Caribbean. Disease prevalence has also been reported to vary by species, with the diseases reported in this study affecting colonies of *Gorgonia* spp., *Plexaurella* spp., *Briareum* spp., *Erythropodium* spp., *Antillogorgia* spp., *Eunicea* spp., and *Plexaura* spp (Weil et al. 2017). Such extreme differences in bleaching severity and disease prevalence among octocoral taxa suggest that higher levels of both bleaching and disease may have existed during the thermal anomalies, but was not captured in the dataset as not all species were investigated in detail. Despite these possibilities, anecdotal evidence further supports an absence of bleaching and/or disease outbreaks in the local octocoral community, as largescale mortalities or conditions were not observed on colonies during the total abundance surveys or outside of the transects.

The stability of the octocoral community throughout multiple disturbance events that have severely impacted the stony coral community suggests that octocorals may be a resistant reef constituent. The coral reefs of southeast Florida have not experienced a phase shift, as stony coral cover has remained <5% in the region since 2007 (Jones et al. 2019, submitted) and octocoral density has only marginally increased. The increase in octocoral density is similar to elsewhere in the region, with increases in abundance observed in recent years in the Florida Keys, the USVI, and Columbia (Ruzicka et al. 2013; Lenz et al. 2015; Tsounis and Edmunds 2017; Sanchez et al. 2019). However, each of these were associated with significant and large-scale declines in stony coral cover. With octocoral abundance increasing in southeast Florida independent of stony coral cover decline, other factors may be influencing the octocoral community. This suggests that octocorals may be more resistant or resilient to the stressors affecting the local stony coral community (e.g. thermal anomalies, disease outbreak). They do, however, remain susceptible to physical disturbances such as storm impacts.

To properly manage declining ocean ecosystems, we must first consider their present state (Sarda, 2012; Rossi 2013). However, this becomes challenging for the many reefs experiencing phase shifts toward alternative stable states, such as octocorals. With octocorals already a long-standing, major constituent of the SEFRT compared to stony corals, this study can provide baseline information for reefs shifting towards dominance by octocoral communities. Rossi (2013) stated that coral reef communities are akin to terrestrial forest ecosystems, regarding that they fell under the umbrella of the term “animal forests.” Understanding the dynamics of the engineering species (e.g. stony corals, sponges, octocorals) that make up these forests will further elucidate the ecosystem services they provide and the functional niches they fill. Shifting reef ecosystems are likely to experience shifts in ecosystem services, so it becomes imperative to understand the functional roles of the different benthic taxa to fully comprehend changes to the communities.

The long-term stability of the octocoral community on the SEFRT suggests continued stability and success in future monitoring events as other communities in the region have reported concurrent increasing octocoral populations (i.e. Columbia, Florida Keys, USVI). Additionally, octocoral recruitment has been positively correlated with mature colony abundance, specifically following disturbance events (Lasker 2013). Therefore, it is expected that sites with high octocoral density successfully recruited in the year following the hurricane, and an increase in juvenile abundance is anticipated for the 2019 monitoring event. Current hypotheses for causes of coral reef community declines include the idea that disturbance events are becoming too frequent, compounding their effects and making it difficult for populations to recover (Belwood et al., 2004; Knowlton and Jackson, 2008; Falkenberg et al., 2010, Rossi 2013).

The success of the local octocoral community not only suggests resistance to the many stressors affecting stony coral populations, but the successful recruitment of octocorals noted by Lasker (2013) further suggests their resilience to physical disturbance events. To fully understand octocoral community dynamics, the local community needs to be investigated in greater detail. This is challenging as the SEFRT octocoral assemblage may be diverse and distinguishing species in the field is often very difficult (Bayer 1961). As a result, other studies have chosen instead to investigate their local communities at the genus level (Lenz et al. 2015; Tsounis and Edmunds 2016; Edmunds and Lasker 2019). Furthermore, little is known about species-specific influences of octocorals on reef environments. Investigating them in a simpler capacity by identifying to genus may be more beneficial in the short term to capture more information about the community until the importance of species-specific identification is elucidated. With less than 30% of the community being represented in the dataset, future studies should attempt to include additional prominent species on the reefs, characterize octocorals by genera for some survey metrics, or group by colony morphologies (e.g. pinnate, mono-planar, encrusting). The majority of the local octocoral community is still unidentified and understudied. In order to fully understand the dynamics of the coral reef community on the SEFRT and to best advise management practices more research needs to be done with regards to the influence of octocorals and ecosystem services they may be providing in this degraded environment.

6.0 Conclusion

Octocorals are increasing in density on the SEFRT. This change appears to be independent of declines in stony coral cover, which have historically occupied a low percent cover of the SEFRT benthos (<5% cover since 2007; Jones 2019, submitted), despite recent declines in the region (Walton et al. 2018). The stony coral disease event and the preceding bleaching events have not similarly affected the octocoral community, suggesting that octocorals may be more resistant to the stressors contributing to declines stony coral cover. Octocorals have previously exhibited resilience following large-scale physical disturbances (Lasker 2013) and increases in juveniles are expected following Hurricane Irma. Additionally, octocorals have exhibited resistance to bleaching, ocean acidification, and disease events, as well as resilience following disturbances (Prada et al. 2009; Gabay et al. 2014; Tsounis and Edmunds 2017). As some coral reefs have experienced phase shifts in the wake of stony coral decline (Norstrom 2009; Ruzicka et al. 2013), it is imperative to understand the ecology of other dominant constituents, such as octocorals, and the ecosystem services they provide. Reef communities such as the SEFRT and other high-latitude reef systems with historically high octocoral cover can clarify the expectations of other reef communities facing phase shifts towards octocoral dominance. Understanding the long-term dynamics of the octocoral community lays the groundwork for elucidating its influence on the local reef ecosystem and discerning its contributions to ecosystem services and functions. However, with only 30% of the local community represented in this analysis, further studies are needed to appropriately investigate these facets. Furthermore, it is possible that prevalence of bleaching and disease was more severe than captured in the data, due to species-specific differences among octocorals, although anecdotal evidence supports the low prevalence observed in the target population. Octocoral monitoring efforts could be expanded on the SEFRT to include other genera, allowing us to gain a better understanding of the distribution and effects of local and global stressors. Improving our knowledge of this high-latitude, octocoral dominated reef system will contribute to our understanding of how coral reef communities function and support their diverse constituents, as octocorals are considered ecosystem engineers, directly and indirectly modulating resources and physical factors to co-occurring reef-dwelling organisms (Jones et al. 1994; Rossi et al 2013). It will also further contribute information to researchers and managers working to protect changing coral reef ecosystems in the face of great local and global stresses. With octocorals functioning as ecosystem engineers and having the potential to support a variety of other organisms, the increase in octocoral abundance noted in this study offers hope for the south Florida reef community. Octocorals may be able to support other aspects of the ecosystem, while managers and researchers work to uncover causes of stony coral decline and restore local coral communities.

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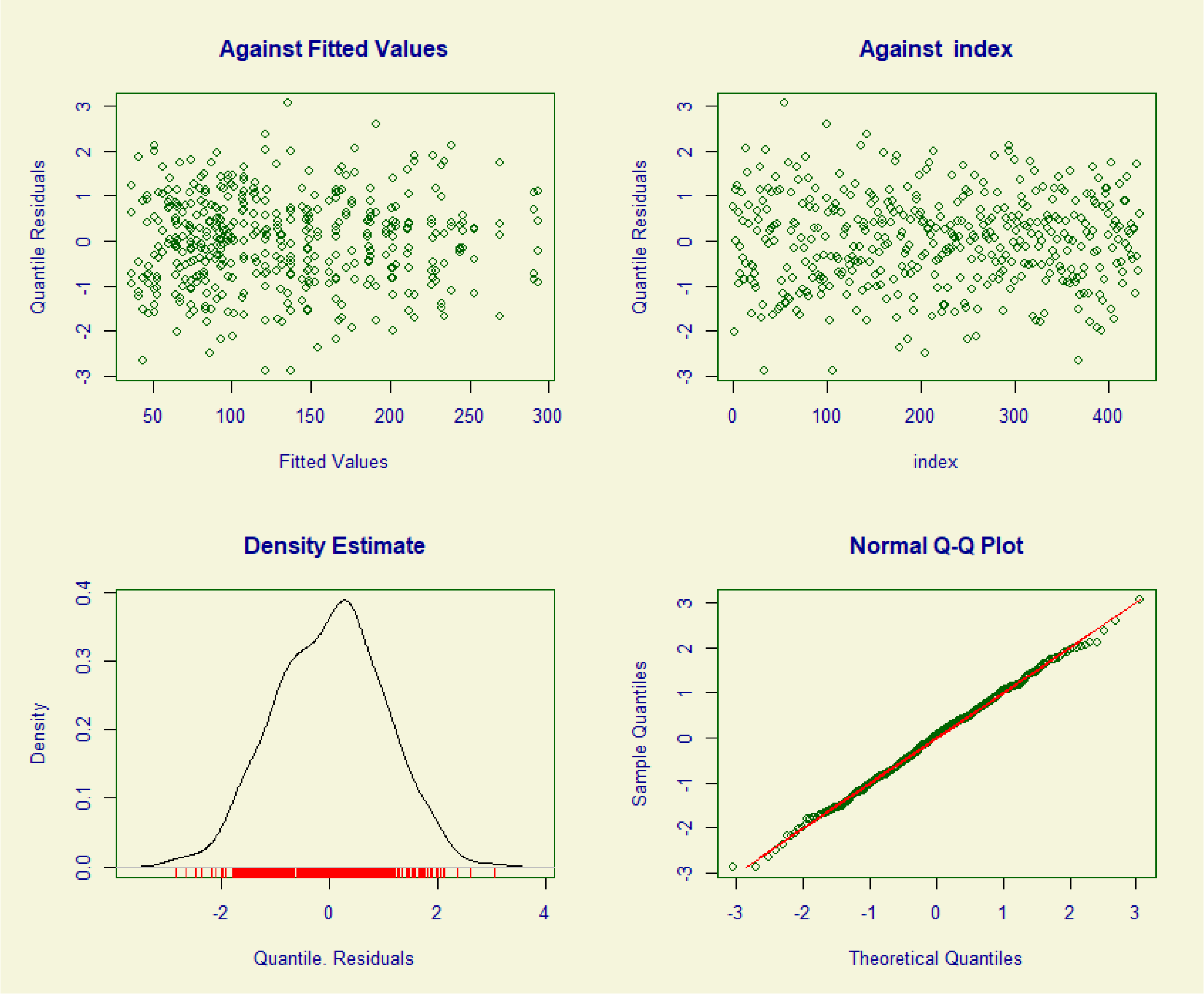
8.0 Appendices

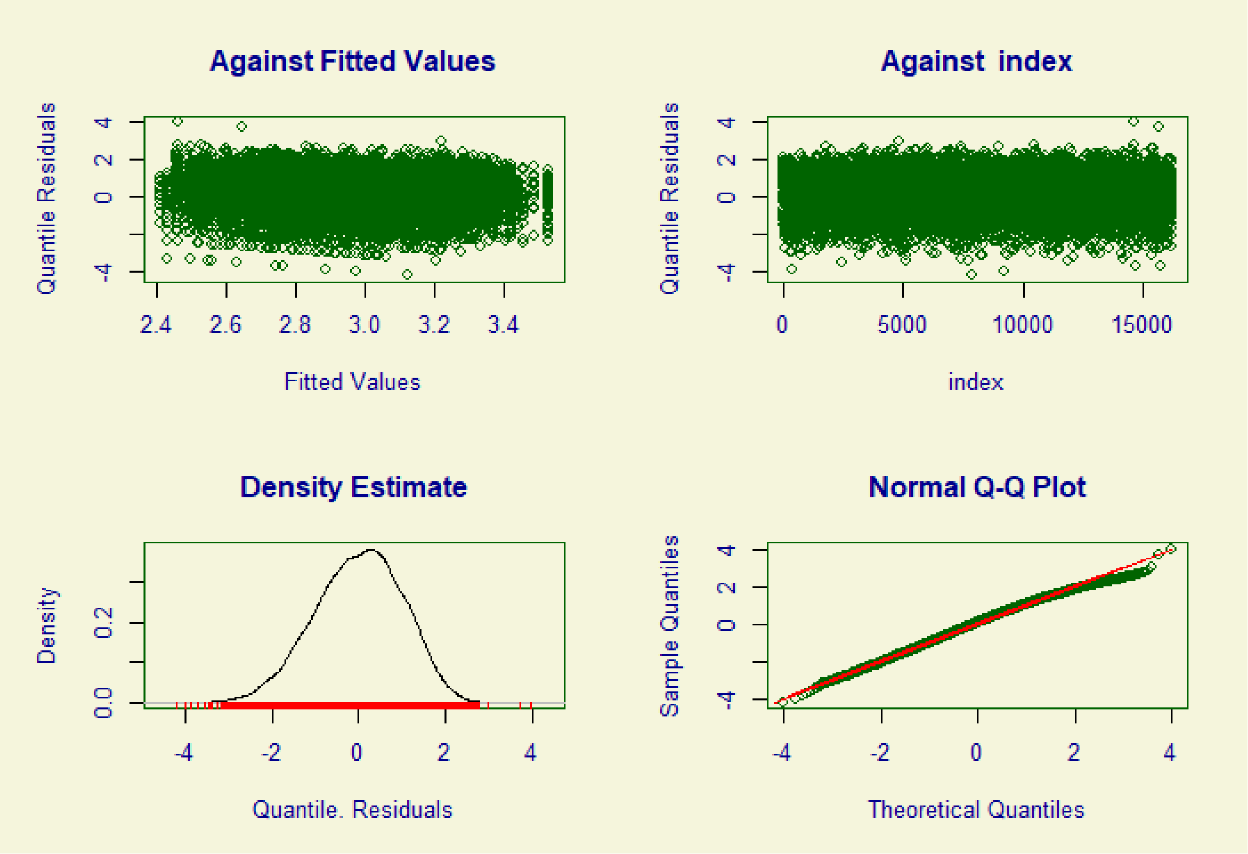
Appendix A: Site densities of octocorals (m-^{2}) by year.

Site	Reef	2013	2014	2015	2016	2017	2018
BC1	Inner	4.89	5.06	5.07	5.31	5.02	6.17
BC 2	Middle	3.36	3.93	3.92	4.22	4.63	4.27
BC 3	Outer	5.86	1.08	5.24	6.50	6.92	5.58
BC 4	Inner	1.69	1.80	2.38	1.85	3.02	1.49
BC 5	Middle	2.60	3.39	2.98	2.81	3.50	3.07
BC 6	Outer	9.44	5.80	9.63	10.67	11.73	9.38
DC 1	Inner	3.15	3.72	5.27	6.02	5.17	4.83
DC 2	Middle	6.25	6.48	8.86	8.17	9.06	6.68
DC 3	Outer	2.81	8.76	3.43	4.24	4.61	4.18
DC 4	Outer	5.10	3.28	6.57	5.42	6.77	6.36
DC 5	Inner	2.99	3.25	4.07	3.92	4.41	3.22
DC 6	Inner	3.14	3.69	4.33	4.49	4.93	3.15
DC 7	Middle	1.56	1.74	3.24	3.16	3.05	3.07
DC 8	Inner	6.77	7.40	9.05	8.76	9.69	7.83
PB 2	Outer	7.74	5.65	10.66	10.67	10.60	7.94
PB 3	Outer	5.84	9.34	6.43	7.88	8.43	6.49
PB 4	Outer	7.10	5.66	10.67	10.82	10.19	9.09
PB 5	Outer	9.00	8.02	12.84	13.33	13.56	10.59

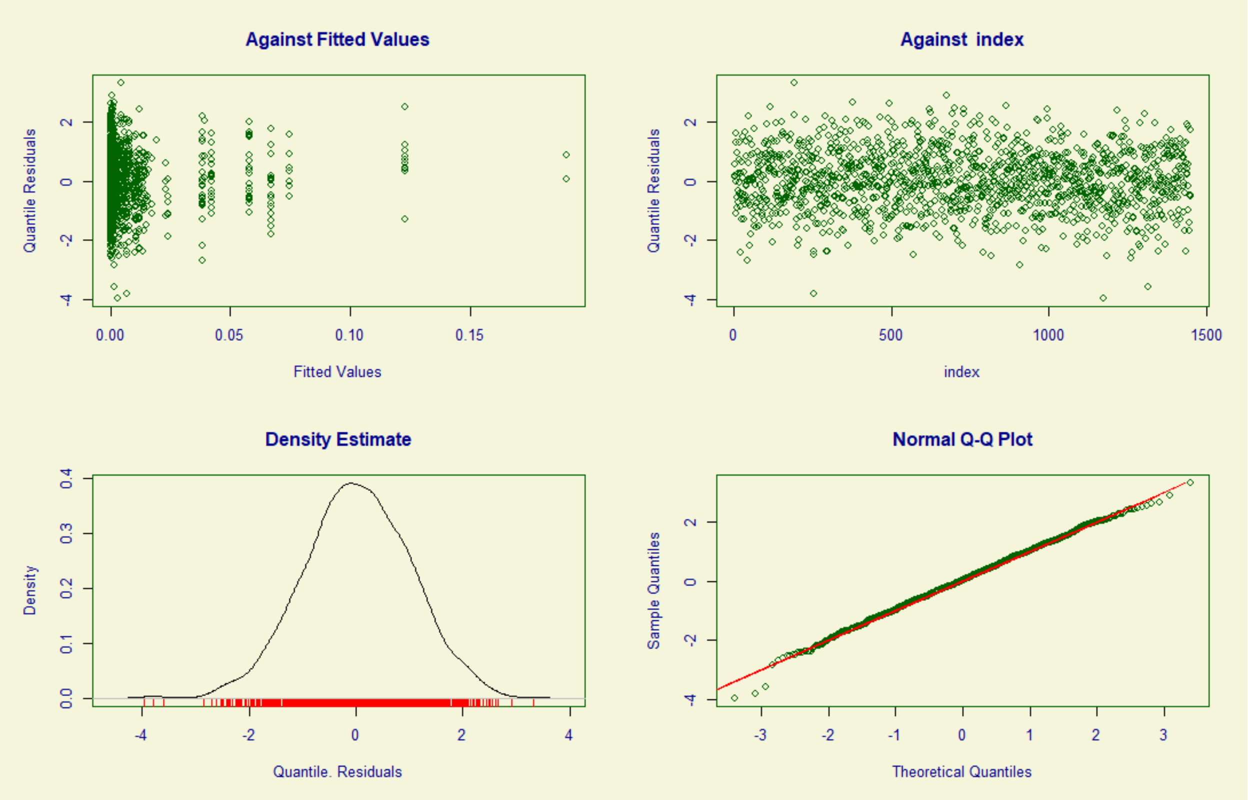
Appendix B. Residual values for the chosen negative binomial distribution for the generalized additive mixed model for octocoral density throughout the study period.



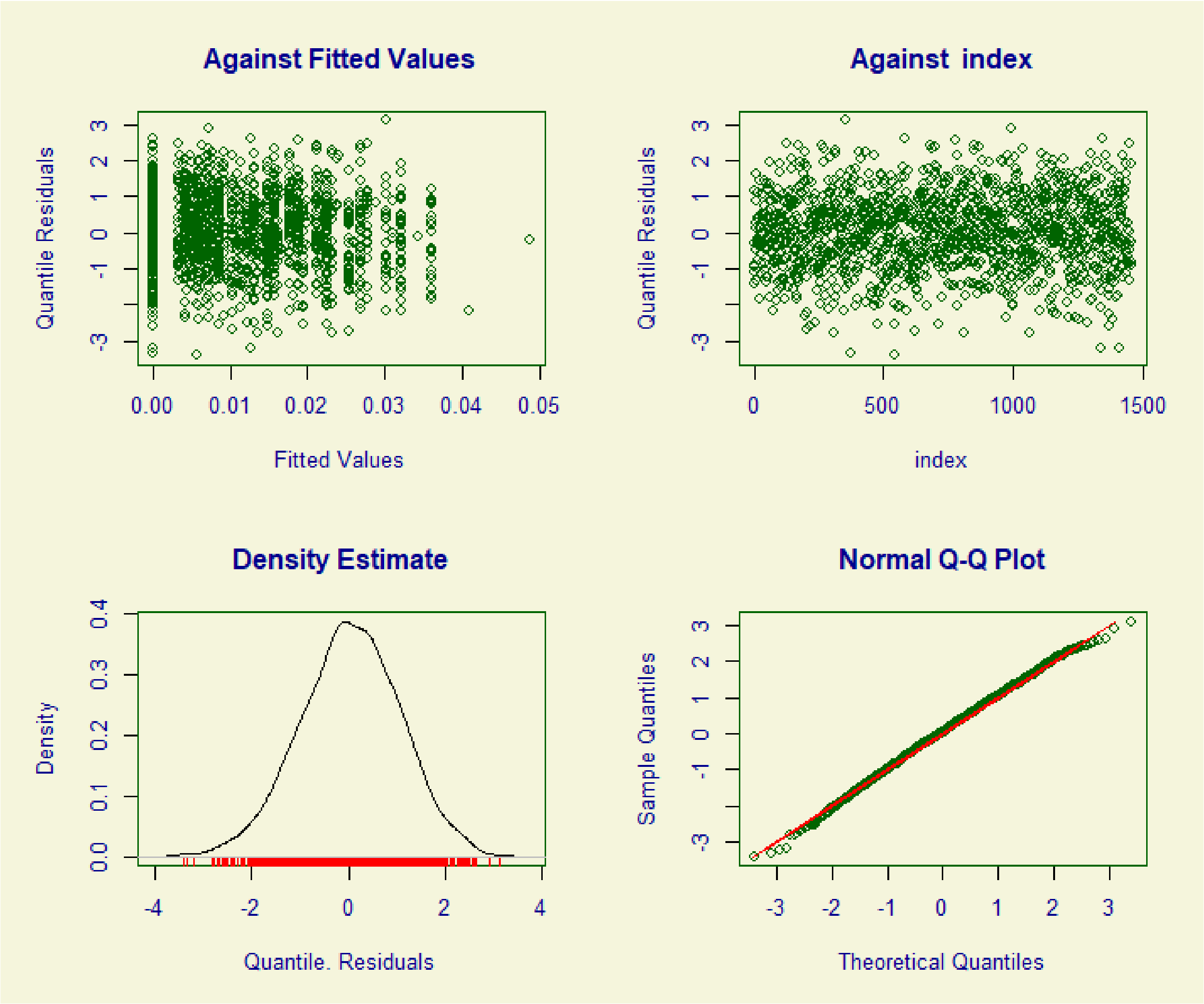
Appendix C. Residual values for the chosen log-normal distribution for the generalized additive mixed model for target colony height throughout the study period.



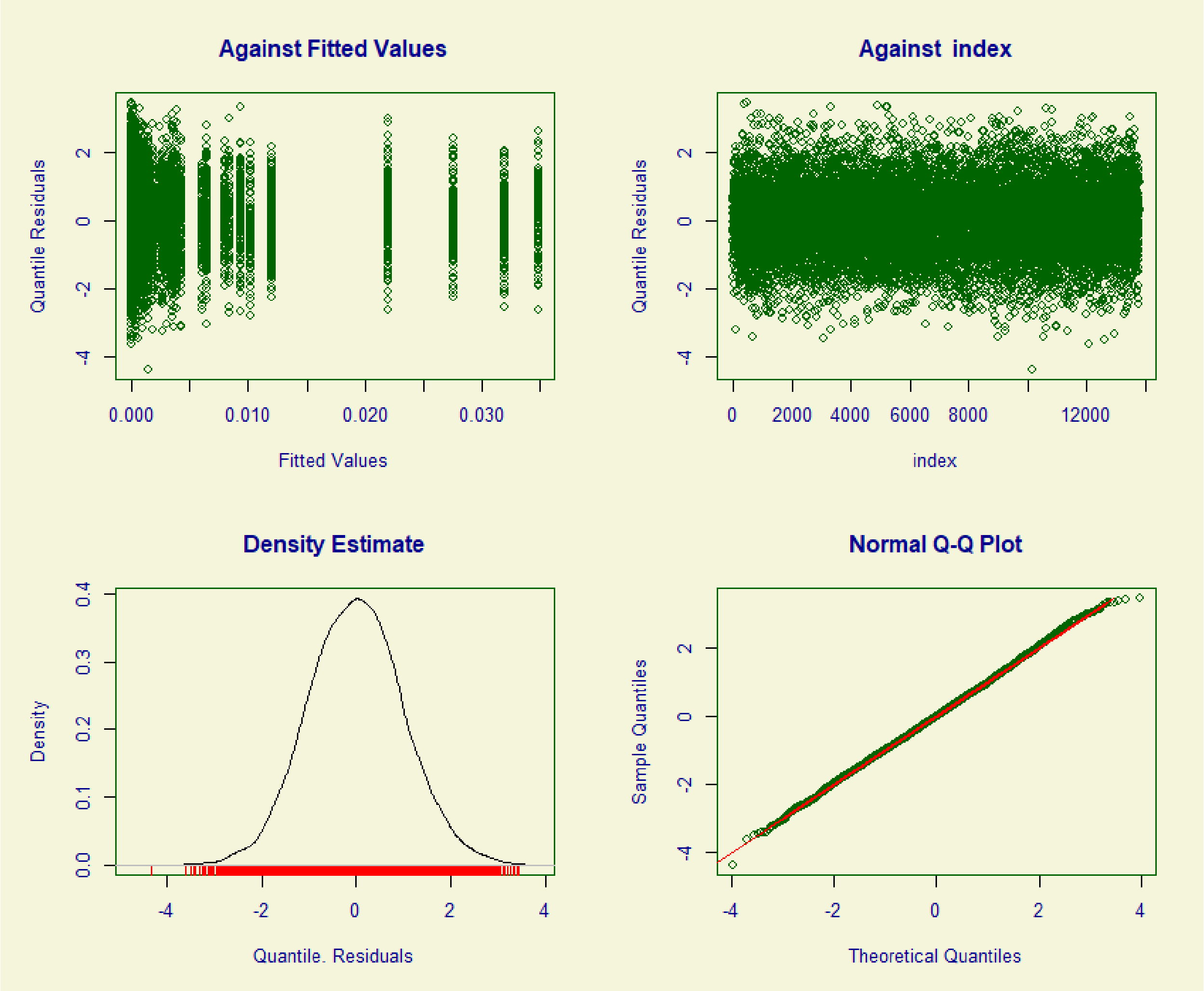
Appendix D. Residual values for the chosen binomial distribution for the generalized additive mixed model for the prevalence of ASP throughout the study period.



Appendix E. Residual values for the chosen binomial distribution for the generalized additive mixed model for MFPS prevalence throughout the study period.



Appendix G. Residual values for the chosen binomial distribution for the generalized additive mixed model for BLH prevalence throughout the study period.


Against Fitted Values
Quantile Residuals
Fitted Values
-4
-2
0
2
0.000
0.010
0.020
0.030
Against index
Quantile Residuals
index
0
2000
4000
6000
8000
12000
Density Estimate
Density
Quantile. Residuals
0.0
0.1
0.2
0.3
0.4
Normal Q-Q Plot
Sample Quantiles
Theoretical Quantiles
4