Drew University College of Liberal Arts

Investigating the relationship between coral species diversity, most abundant coral growth form, and live coral cover with habitat structural complexity in the Caribbean

A Thesis in Environmental Studies and Sustainability (Science Track)

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ABSTRACT

Recent anthropogenic change is shifting Caribbean coral communities toward reefs dominated by stress resistant coral species, which are often less architecturally complex leading to less productive reefs that are unable support a high diversity of organisms. Coral bleaching, ocean acidification, hurricanes, diseases, and other stressors are leading to decreases in coral species diversity and coral cover along with changes in most abundant coral growth form of reefs throughout the Caribbean region. As these three reef attributes change, architectural or topographic complexity of Caribbean reefs may change as well. The architectural complexity of reefs can greatly influence their ability to support biodiversity and provide ecosystem services. By analyzing the three-dimensional structure of coral reefs, topographic complexity measurements, linear rugosity indices (R) and fractal dimensions (D) at five resolutions were derived. An examination of field data on the effect of coral species diversity and most abundant coral growth form in South Caicos, Turks and Caicos Islands revealed that high topographic complexity may be correlated with high coral species diversity. From a literature review of the relationship between live coral cover and topographic complexity in the Caribbean, my study found, in general, mixed results. While coral cover is an important reef attribute in some cases, the corals' identity plays a bigger role than the amount of cover considering topographic complexity in the Caribbean. In regards to coral species diversity, I found that linear rugosity increased as coral species diversity increased and fractal dimension increased as coral species diversity increased for all resolutions except for the smallest, $D_{0.01}$. By using the highest relative coral species abundance, most abundant coral growth forms were determined (plate, plume, and plate/plume). My study showed a significant relationship between fractal dimensions at larger resolutions and dominant coral growth form in which higher fractal dimensions occurred on plate/plume-dominated reefs than plume-dominated reefs. This may be due to increased diversity in growth form given that there are two different morphologies dominating the area. Coral species diversity seemed to have a stronger overall relationship with topographic complexity than with dominant coral growth form or overall coral cover, thus management and restoration strategies should be sure to ensure high diversity of structurally complex coral species in Caribbean reefs. Understanding the components underlying topographic complexity can help increase effectiveness of strategies for marine ecosystem conservation now and in the coming decades.

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CHAPTER 1

BACKGROUND

1.1 Coral-*Symbiodinium* Relationship, Coral Anatomy, & Threats To Reefs

Coral reefs are the largest living structures on the planet and are located across the globe from deep, cold waters to shallow, tropical waters (Goreau and Goreau 1973; Bak et al. 2005). Reefs brim with life and are often called the “rainforests of the ocean” as they support a wide array of organisms as well as provide numerous ecological services and goods for human communities (Moberg and Folke 1999). Yet coral reefs only cover a minuscule portion (less than 1%) of the ocean surface (Spalding and Brown 2015). Coral reefs encompass several different coral types. Soft and hard corals are comprised of small invertebrate animals, polyps. Hard coral polyps, which have reef-building capabilities, secrete a rigid skeleton of calcium carbonate, $CaCO_3$, in a crystal form called aragonite. Soft corals, such as gorgonian corals, do not produce a rigid calcium carbonate skeleton nor do they form reefs, though they may be present in a reef ecosystem. Polyps have a very basic structure consisting of an epidermis layer, a gastrovascular cavity, and tentacles that surround the mouth (Barnes 1987; Figure 1).

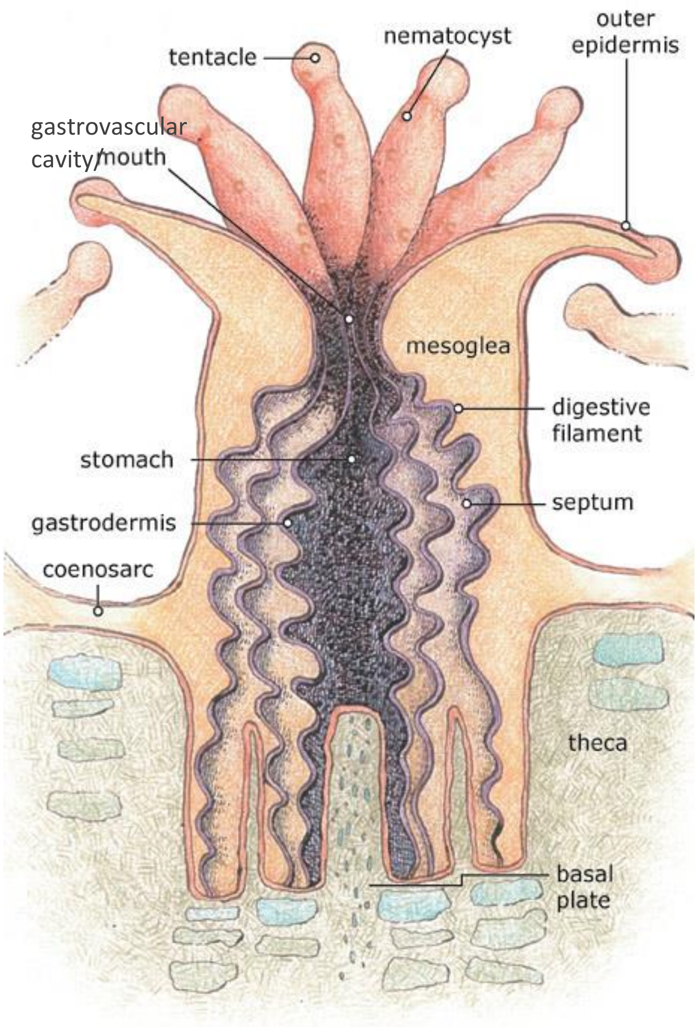

Figure 1. Diagram depicting typical coral polyp anatomy (Gini Kennedy/ NOAA 2011).

Tentacles help the coral capture plankton and are corals' only defense against predators. Nematocysts, within the tentacles, are triggered by tactile stimuli and puncture predators (Hayes and Goreau 1998). Since reef-building corals require an abundant supply of energy to thrive, the energy derived merely from digesting plankton is insufficient for survival (Brown and Ogden 1993). Thus, most corals have developed a mutualistic relationship with endosymbiotic dinoflagellates of the genus *Symbiodinium* in their gastrodermal cells. *Symbiodinium* provides the coral with as much as 90% of its energy (Sumich 1996; Hoegh-Guldberg et al. 2007; Oakley and Davy 2018).

Coral provides the dinoflagellates with a protected environment and compounds needed to perform photosynthesis. In exchange, the *Symbiodinium* produce glucose and glycerol that corals consume (Colombo-Pallotta et al. 2010). As long as *Symbiodinium* are making the corals' food, the coral has energy to make proteins and carbohydrates for the synthesis of calcium carbonate (Knowlton 2001). Because of the endosymbiosis between coral polyps and *Symbiodinium*, coral reefs are most abundant and diverse in relatively shallow tropical waters. The placement in shallow, tropical waters allows sunlight needed for photosynthesis to reach the *Symbiodinium* (Knowlton 2001). Besides *Symbiodinium*, the community of metazoans, protists and microbes associated with corals makes up the coral holobiont (Rohwer et al. 2002).

To make calcium carbonate for shells and other structures, marine animals such as corals, clams, oysters, and some plankton use carbonate ions (CO_3^{-2}). A polyp will create a cup-shaped skeleton, called a calyx, to sit in. This hard skeleton of calyx clusters is the strong foundational structure that protects the coral colony from the harsh force of waves and allows the corals to live together and form the reef structure (Barnes 1987).

Coral reefs are threatened by natural phenomena such as hurricanes and diseases but, unfortunately, some human activities negatively impact ecosystems as well. These activities include emitting carbon, waste dumping, and unintentional physical damage to coral. Coral reefs around the world have been, and are still being, threatened by an array of factors including ocean acidification, unsustainable overfishing, pollution, damage caused by vessels, coastal development, coral bleaching, and invasive species (Hoegh-Guldberg et al. 2007). Not only are coral reefs being affected, but marine life dependent on reefs is being threatened. As mentioned before, reefs display astonishingly high biodiversity. They are often referred to as biodiversity hotspots being home to approximately 25% of the oceans' fish species (Spalding et al. 2001). The resulting impacts of the threats to coral may cause devastating changes to the growth, development, and larval settlement in several species (Kleypas and Langdon 2006; Randall and Szmant 2009; Cantin et al. 2010).

Coral reefs benefit humans by being a source of food for millions of people worldwide, supporting fishing and tourism industries, and providing chemicals used for medicinal purposes (Hoegh-Guldberg 1999). Tourism is a major foreign exchange earner in the Caribbean basin and in some countries ocean-related tourism makes up to half of the GDP (Hoegh-Guldberg et al. 2007; Bryant et al. 1998). Thus, as coral reefs perish, humans will experience negative repercussions as well (Hoegh-Guldberg 1999; Moberg and Folke 1999).

1.2 Ocean Acidification

Ocean acidification is the decrease in the pH and aragonite (crystalized form of $CaCO_3$) saturation state of oceans caused by the absorption of atmospheric carbon dioxide (Zeebe et al. 2008). Over the past two centuries, oceans have absorbed approximately 40% of carbon dioxide emissions (Zeebe et al. 2008). Even though the ocean is immense, a high abundance of carbon dioxide can have a major impact. Carbon dioxide dissolves in seawater to form carbonic acid (H_2CO_3). When carbonic acid breaks down, hydrogen ions (H^+) and bicarbonate ions (HCO_3^-) are released from carbonate acid dissolved in the water. This causes the concentration of carbonate ions in seawater to decrease (Orr et al. 2005; Hoegh-Guldberg et al. 2007). As the availability of carbonate ions decreases, the production of coral skeletons slows. Coral skeletons form at a lower density than normal, causing a weak reef structure (Gattuso et al. 1998; Orr et al. 2005; Zeebe et al. 2008). As aragonite concentrations in ocean water decreases the calcification rate of reef-building coral decreases (Orr et al. 2005). Calcification is essential to the survival and development of coral reefs. Without the calcium carbonate skeleton, coral become weakened by erosion (Kavousi et al. 2015). As corals weaken, some may die which results in many unique marine species, which depend on the coral reef, to relocate or die as well. Acidified seawater has negative impacts on the growth of young coral, including the early life stages and polyp larvae (Albright et al. 2010). Global ocean acidification is predicted to lower ocean pH by approximately 0.3 units from its current value of ~8.1 to a value of ~7.8 by the end of the century (Gattuso et al. 2014). A decrease of 0.2 to 0.3 units in seawater pH inhibits or slows calcification in organisms such as corals and calcareous plankton (Kleypas et al. 1999; Wolf-Gladrow et al. 1999; Riebesell et al. 2000).

Out of all the marine life, one of the most vulnerable ecosystems to ocean acidification is coral reefs because the main framework of reefs is reliant on calcifiers. Besides the loss of biodiversity, acidification will be detrimental for fisheries, negatively impacting food supplies for millions of people, as well as tourism and other sea-related economic activities (Moberg and Folke 1999; Hoegh-Guldberg et al. 2007; Suwa et al. 2010). The change in ocean chemistry is critical given that most modern genotypes and phenotypes of corals do not have the capacity to adapt fast enough to sudden environmental change in the Caribbean (Hoegh-Guldberg et al. 2007). Ultimately, ocean acidification is expected to enhance calcium carbonate dissolution with negative consequences, first for coral growth and accretion and then for the entire reef framework (Hoegh-Guldberg et al. 2007).

1.3 Coral Bleaching

As stated previously, corals have a mutualistic relationship with intracellular dinoflagellates of the genus *Symbiodinium* (Sumich 1996; Oakley and Davy 2018). Coral bleaching occurs after *Symbiodinium* is expulsed out of coral tissue from stress (Brown 1997). The environmental stresses linked to coral bleaching include long exposure to sunlight and high sea surface temperatures (Brown 1997). The visible bleaching of coral is caused by the loss of *Symbiodinium*, which give coral its vibrant color (Witze 2015; Figure 2).

Figure 2: Extensive bleaching of *Acropora palmata* at Buck Island Reef National Monument, November 2005 (Photo: E. Muller; Rogers et al. 2008)

Once *Symbiodinium* leave the polyp's tissue, the coral lose their color and turn white, as seen in Figure 2, which can happen within months of a heat rise (Witze 2015). Exposure of *Symbiodinium* to visible radiation, elevated temperatures, and ultraviolet radiation causes protein damage in *Symbiodinium* photosystem II, which is the protein structure that absorbs radiant energy during photosynthesis (Warner et al. 1996; Warner et al. 1999; Lesser 2011). Additionally, during photosynthesis, the thermally stressed *Symbiodinium* may produce a large concentration of oxygen (Leser 2011). When oxygen levels drastically increase, reactive oxygen species, or ROS, form inside coral tissue. ROS are toxic to coral tissue and cause lipid, protein, and DNA damage, which is the reason coral expel the *Symbiodinium* (Lesser 2011). Once the *Symbiodinium* are no longer present, most of the corals do not obtain enough nutrients to survive. The ones that do survive and recover their *Symbiodinium* normally show reduced growth, calcification, and fecundity (Hoegh-Guldberg 1999). In addition, corals that survive bleaching are often more susceptible to other stresses such as coral disease (Bruno et al. 2007). Importantly, widespread mortality of hard corals that occur after severe bleaching events, moves the balance towards net reef erosion (Sheppard et al. 2002).

1.4 Coral Bleaching & Ocean Acidification In The Caribbean

As the temperature increases, more and more coral are subject to the effects of bleaching. Coral bleaching poses a great danger to coral survival especially in the Caribbean. There have been exponential increases in the extent and intensity of coral bleaching with increasing sea surface temperature anomalies in the Caribbean

(McWilliams et al. 2005). Goreau et al. (1993) found that at seven Caribbean sites, bleaching occurred when temperature was a mere 1º C above the long-term average for the warmest month. According to McWilliams and colleagues, an increase of 0.18 º C in regional sea surface temperature produces a 35% increase in the number of reports of bleached corals (McWilliams et al. 2005).

Ocean acidification has severely impacted Caribbean coral reefs in the past few decades. The fertilization, settlement, and growth of *Acropora palmata,* an important and structurally complex Caribbean coral, is negatively impacted by acidified water (Albright et al. 2010). Although there is spatial variability in the changes in sea-surface carbonate mineral saturation state throughout the Caribbean region due to ocean acidification (Gledhill et al. 2008), the impact is consistently negative (Kroeker et al. 2010). Interestingly, a recent study of two threatened Caribbean reef-building corals, *Orbicella faveolata* and *Acropora cervicornis*, found that the two species were effected by different stressors. *Acropora* was more sensitive to heat stress, while *Orbicella* was more sensitive to high CO_2 levels (acidification stress; Langdon et al. 2018). This, along with the other previously mentioned research, suggests that rising temperatures and ocean acidification pose great threats to specific important corals and the general reef frameworks throughout the Caribbean region.

CHAPTER 2

REEF ATTRIBUTES

2.1 Introduction To Reef Traits

A fundamental interest in ecology is to understand biodiversity and its influence on ecosystem structure and function. Biodiversity, the variety and relative proportion of living species that can be found in an ecosystem, affects marine ecosystem services and processes across temporal and spatial scales. Biodiversity is linked to ecosystem productivity, stability, and recovery potential (Loreau et al. 2001, Palmer et al. 2004, Hooper et al. 2005; Worm et al. 2006). Loss of biodiversity leads to resource collapse and decreased water quality (Bellwood and Hughes 2001; Hughes et al. 2002). Thus, understanding the causes and changes in biodiversity is important. A primary factor that establishes and controls biodiversity within the tropical reef ecosystem is species diversity of coral, the primary habitat-forming organism (Hughes et al. 2002; Hoegh-Guldberg et al. 2007; Messmer et al. 2011; Richardson et al. 2017).

2.2 Coral Species Diversity

Generally, corals vary in physical structure which suggests greater coral diversity provides a variety of habitats and shelter sites for a wide range of species (Messmer et al. 2011; Komyakova et al. 2013). It is important to monitor changes in coral species diversity as it alters reef structure and the diversity of reef communities, especially fish communities (Hughes et al. 2002; Hoegh-Guldberg et al. 2007; Messmer et al. 2011). In the Caribbean, the white-band disease outbreak in the late 1970s and hurricane damage to shallow water branching species, such as *Acropora* spp., led to a huge decline in the populations of these dominant habitat-creating species (Aronson and Precht 2001; Aronson et al. 2002). Since some coral species were wiped out, this diminished reef diversity (Aronson and Precht 2001; Bellwood et al. 2004). Coral disease, ocean acidification, and climatically induced coral bleaching will likely cause further declines in coral species diversity the future (Harvell et al. 2002, Gardener et al 2003; Hoegh-Guldberg et al. 2007; Fabricius et al. 2011).

2.3 Most Abundant Growth Form

The dominant growth form, the most common morphological growth type, of coral is an equally crucial reef factor to study. This is especially true in the Caribbean since Caribbean corals have relatively low diversity and redundancy when compared to other regions of the world (Alvarez-Filip et al. 2011a). Differences in the dominance of particular corals within reef ecosystems may lead to differences in associated biodiversity and ecosystem services (Alvarez-Filip et al. 2011a). There are several organisms that are coral-associated (including commercially important species; e.g. snapper, lobster and grouper) and thus varying coral growth forms can lead to variations in fish community structure (Komyakova et al. 2013). Quantifying the relative contribution of different corals to the architectural complexity of the reef is particularly important in order to understand the trajectory of coral reefs under changing environmental conditions.

Similar to the change in coral species diversity, dominant coral growth form in reefs has been altered due to anthropogenic change. There are a wide variety of common growth forms including encrusting, branching, massive, plume, plate, columnar and more. Stress-resistant species are now dominating reefs (Alvarez-Filip et al. 2011a). In the Caribbean, there has been a loss of reef-building coral species such as *Acropora* spp. (branching) and *Montastraea* spp. (massive) which are less stress-tolerant, and an increase in the stress-tolerant corals, *Porites* spp. (digitate or massive) and *Agaricia* spp. (encrusting or plate), which are often less topographically complex (Aronson et al. 2002; Green et al. 2008; Alvarez-Filip et al. 2011a). See Figure 3 for representative pictures of these species.

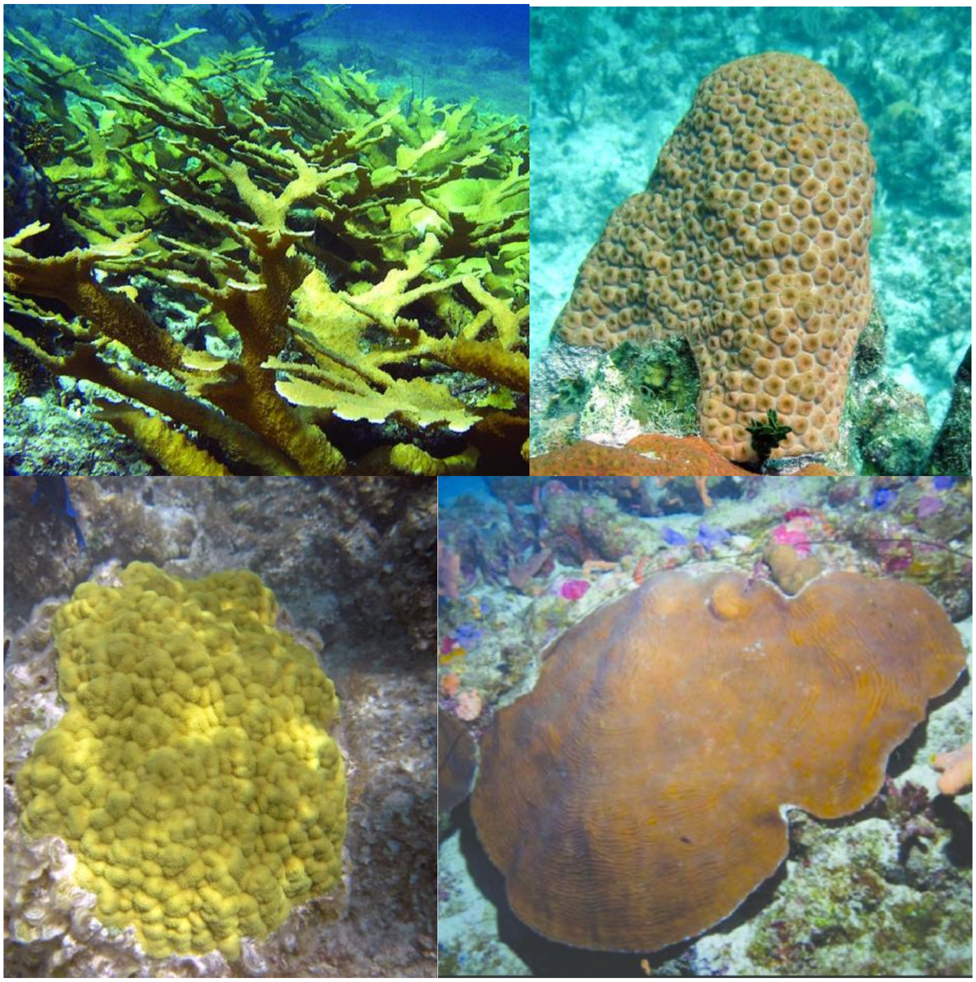

Figure 3: Various coral species of the Caribbean. *Acropora palmata* (top left; from Baums et al. 2014; photography by Geoff C. Chilcoat), *Montastraea cavernosa* (top right; photography by Rosa Rodríguez), *Porites astreoides* (bottom left; photography by James St. John), and *Agaricia* sp. (bottom right; photography by Nicole Helgason).

2.4 Live Coral Cover

Multiple factors have caused a significant decline in live coral cover over the last 40 years (Bellwood et al. 2004). In addition to the ocean warming and acidification discussed earlier, *Diadema antillarum* die off in the Caribbean in the 1980s due to disease greatly reduced urchin populations (Bak et al. 1984; Lessios, Robertson, Cubit 1984; Hughes 1994). With mass mortality of *Diadema*, fleshy macro-algal blooms occurred which caused a major decline in coral cover, especially of the massive coral *Montastrea*, an important reef framework building species (Bak et al. 1984; Hughes 1994). Higher coral cover increases habitat area for obligate coral-dwelling species, corallivorous fishes, and species reliant on coral habitat for recruitment (Komyakova et al. 2013). Low coral cover leads to demographic changes including reduced reproductive output of brood stocks, lower recruitment rates, and species-level changes in coral composition (Bellwood et al. 2004).

CHAPTER 3

ANOTHER REEF ATTRIBUTE: TOPOGRAPHIC COMPLEXITY

3.1 Defining Topographic Complexity

Topographic complexity refers to the physical three dimensional structure of an ecosystem, encompassing the assembly provided by corals and other hard surfaces (Zawada et al. 2010; Graham and Nash 2013; Graham et al. 2015). The defining feature of topographic complexity on a coral reef is foundation taxa (e.g. corals; Ellison et al. 2005; Bryson et al. 2017). Topographic complexity drives biodiversity in tropical coral reef ecosystems because within topographically complex reefs, increased niches and habitat availability encourages high diversity and abundance of organisms (Hixon and Menge 1991; Johnson et al. 2003; Knudby and LeDrew 2007; Alvarez-Filip et al. 2011a; Graham and Nash 2013).

3.2 Flattening Of Caribbean Coral Reefs

By the early 1980s, it was apparent that Caribbean reefs were flattening (Alvarez-Filip et al. 2009). The temporal pattern of declining architecture coincides with major recent Caribbean events that were mentioned previously: the loss of structurally complex *Acropora* corals, the mass mortality of the grazing urchin *Diadema antillarum* which led to macroalgal blooms and multiple warming-induced coral bleaching events. The consistently low estimates of current architectural complexity suggest regional-scale degradation and homogenization of reef structure (Alvarez-Filip et al. 2009). Structurally complex reefs have been virtually lost from the Caribbean region. There has been a nonlinear loss of architectural complexity over the past four decades which suggests that different drivers have influenced components of the reef community (Alvarez-Filip et al. 2009). The major Caribbean-wide event that likely had a role in the steep decline in reef architecture was the outbreak of white-band disease, which started in the 1980s but has continued into the present, that destroys the coral tissue due to a bacterial pathogen (Kline and Vollmer 2011). Approximately 90% of structurally dominant acroporid corals have collapsed due to this disease exposing their fragile branching skeletons to erosion and hurricanes (Aronson and Precht 2001; Aronson et al. 2002). In the late 1990s, Caribbean reefs had another period of structural decline after a widespread coral bleaching event caused by high sea surface temperatures (McWilliams et al. 2005). After the bleaching event, coral mortality rates increased and growth rates declined, both of which contribute to the loss of complexity (Alvarez-Filip et al. 2009). The low levels of coral cover in the Caribbean in the late 1990s may also have increased rates of erosion of underlying geological structures that were no longer shielded by actively growing hard corals, which led to less open substrate for future corals (Gardner et al. 2003). Since that major bleaching event, the Caribbean has faced other mass bleaching events that have contributed to the loss of topographic complexity seen today (Gardner et al. 2003). The increasing prevalence of disturbance and degradation of tropical coral reefs, especially in the Caribbean, has brought the importance of structural complexity to the forefront.

3.3 Importance Of Reef Structural Complexity

Topographic complexity has been found to play a role in reef resilience and influence other important factors such as water flow and nutrient uptake (Zawada et al. 2010; Graham et al. 2015). In regards to ecosystem services, reef structural complexity is also strongly related to the availability of shelter and habitat, which influences fish and invertebrate richness, abundance, and biomass (Idjadi and Edmunds 2006; Wilson et al. 2007; Graham et al. 2009; Graham and Nash 2013). Structurally complex reefs recover more quickly and more fully than less complex reefs (Hoegh-Guldberg et al. 2007; Graham and Nash 2013). Another service provided by reefs with high topographic complexity is coastal protection since the wave energy transmitted over reefs is significantly dissipated by bottom roughness (Sheppard et al. 2005; Hoegh-Guldberg et al. 2007). The flatter the reef is from erosion, the higher the wave energy reaching the shores (Sheppard et al. 2005). This can lead to greater destruction of vegetation and human settlements.

Moreover, reef complexity may play an important role in increasing fish herbivory since there is evidence of an inverse relationship between topographic complexity and total algal cover on reefs (Graham and Nash 2013). In regards to relevance to humans, there is a positive effect of high topographic complexity on tourism (Graham and Nash 2013). Reef complexity enhances the abundance of fishes on reefs, which is an important ecological interest for dive tourists. Therefore, the widespread loss of architectural complexity is likely to have serious consequences on reef habitat quality and biodiversity, ecosystem functioning, and human services (Hoegh-Guldberg et al. 2007; Alvarez-Filip et al. 2009; Graham and Nash 2013).

Over the past few decades, studies have investigated the relationship between topographic complexity and certain reef characteristics (Graham and Nash 2013; Komyakova et al. 2013; Bryson et al. 2017). In regards to coral growth form abundance, reef topographic complexity is highest when corals are low in taxonomic evenness and dominated by morphologically complex reef-building coral (Alvarez-Filip et al. 2011a). However, other reef characteristics including coral species diversity have not been studied thoroughly.

3.4 Measuring Complexity

Topographic complexity can be measured in a variety of ways including rugosity, vector dispersion, and fractal dimension (Young et al. 2017). The structural measures that my study focuses on are linear rugosity (R) and fractal dimension (D). Topographic complexity is commonly represented by a linear rugosity index which is the ratio of the distance of the line following the reef contour (R_D) to the flat, linear distance (R_N; Young et al. 2017; Figure 4). Rugosity is typically measured using the “chain-and-tape method” which is measured as the length the chain reaches as it falls over the reef contour/topography divided by the total length of the tape when held taut over that same area (Young et al. 2017). Less invasive methods are more common now such as the use of underwater 3D modelling software.

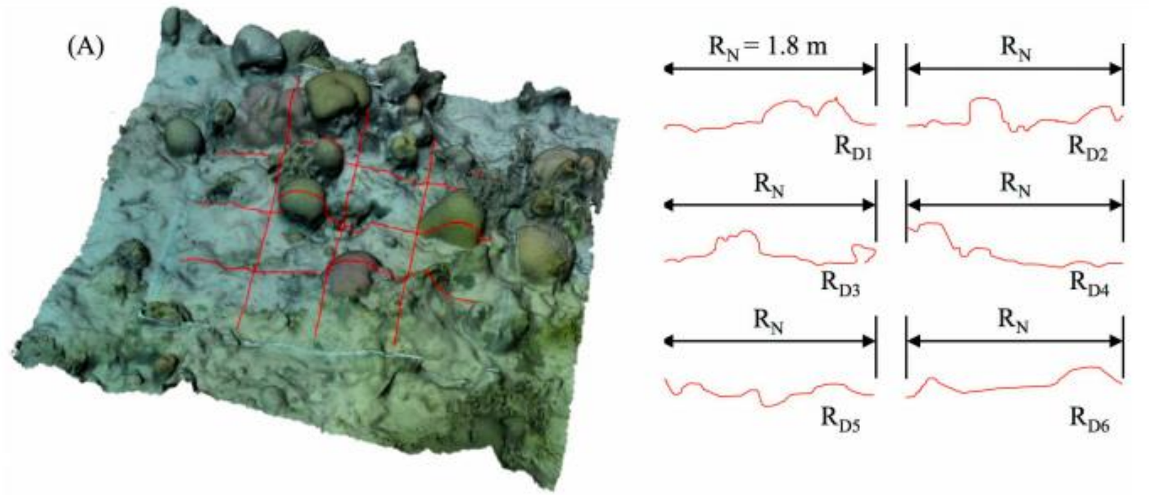

Figure 4. Methods for quantifying linear rugosity using virtual chains (red) in a grid on Rhino 3D model. Rugosity is the ratio of the distance of the line following the reef contour (R_D) to the flat, linear distance (R_N) (Figure from Young et al. 2017).

Fractal dimension is a ratio providing an index of complexity comparing how minutely a surface changes with the scale that it is measured (Zhou and Xie 2003; Young et al. 2017). Fractal dimension is an accurate means of assessing surface complexity that has been shown to be well suited to describing coral reefs (Mark 1984; Young et al. 2017). Fractals, described and illustrated by Mandelbrot (1982), are a class of mathematical functions which are continuous and undifferentiable. Fractal dimension is a morphometrical method to characterize and quantify coral complexity using a ratio comparing how detail in fractal patterns change with the scale at which it is measured (Martin-Garin et al. 2007; Young et al. 2017). Simply, fractal dimension provides a measurement of *roughness* of fractal curves (Martin-Garin et al. 2007). As a rough curve continues on a plane, it may become so close that it fills the plane on which it lies. Thus, increase in roughness is considered to be also an increase in dimension and the dimension of a fractal curve characterizes how the measured length between given points increases as scale decreases (Martin-Garin et al. 2007; Figure 5). To define the dimension of a structure, it is necessary for it to include fractal squares of every possible distance between two points (Martin-Garin et al. 2007). For this study, D indicates how surface area changes with resolutions. It is the slope of a model's resolution versus surface area (Young et al. 2017).

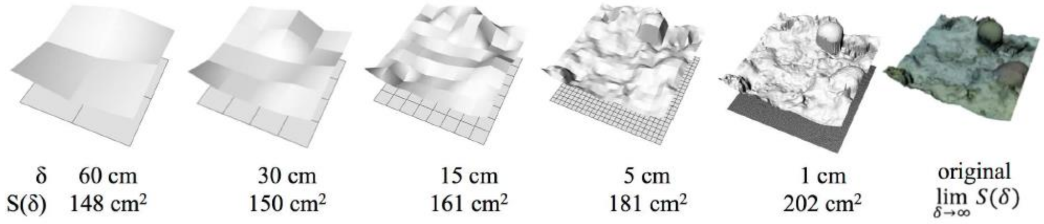

Figure 5. Methods for quantifying fractal dimensions at different resolutions (60, 30, 15, 5, 1 cm) for the same reef transect. The grid above is composed of squares, each of width δ, that are laid on top of the reef transect (Figure from Young et al. 2017).

The use of fractal dimension as a measure of reef topographic complexity is newer and less common than rugosity, which is why it has received less attention in biology in the past (Martin-Garin et al. 2007). My study is comparable to previous studies using rugosity measurement, while creating a baseline for fractal dimension data for future studies to compare.

Threats to Caribbean coral reefs, such as ocean acidification and coral bleaching, have and will continue to impact or change reef attributes such as coral diversity, most abundant growth form, and live coral cover which may all cascade into impacting reef topographic complexity. Given the recent flattening of Caribbean reefs and the importance of topographic complexity, it is crucial to investigate the relationship between reef attributes and topographic complexity. It is known that coral species diversity and topographic complexity are positively correlated with each other. Although it is poorly understood why this relationship exists, it has been speculated that coral diversity and reef topographic complexity may be closely linked because coral species differ greatly in their growth form and branching structure (Veron 2000; Komyakova et al. 2013). However, to date, not many studies have been conducted to determine how topographic complexity and the three reef attributes influence each other. The aim of my honors research was to determine whether coral species diversity, dominant coral growth form, and live coral cover affect topographic complexity.

The following hypotheses were tested: (1) linear rugosity increases as coral species diversity increases; (2) fractal dimension increases as coral species diversity increases; (3) out of three growth forms (plume, plate, and plate/plume mix), plume-dominated reefs would have the highest rugosity followed by plate/plume; and plate-dominated reef having the lowest values (on the basis that plume corals often have higher height- perpendicular to the sea floor- than plate types, thus having more plume than plate types, in theory, would lead to higher rugosity values); and (4) fractal dimensions at large resolutions will be highest for plume dominated reefs and lower for plate and plate/plume dominated reefs since larger dimensions will likely be highest for plume dominated reefs due to largest resolution measure on plume’s perpendicular direction from the sea floor. For small resolutions, the values will be highest for plate-dominated reefs than plume and plate/plume dominated reefs due to the plate corals acute angle from the sea floor, where smaller resolutions are the highest; for visual perspective, see Figure 6.

Figure 6. Examples of plume (left) and plate (right) coral shapes.

CHAPTER 4

MATERIALS AND METHODS

4.1 Study Area

From 29 October 2018 to 23 November 2018, I collected data at a dive site named the “Arch” located off the southern coast of South Caicos, in Turks and Caicos Islands, British West Indies (21°28'59.8"N 71°31'03.7"W; Figure 7 and Figure 8). The Arch is on a shelf-edge situated on the edge of a wall that drops to a 2,000 meter deep ocean drop off. A permit was obtained [D2001 Scientific and Research License] in order to conduct research for this study.

Figure 7. The “Arch” formation at the dive site.

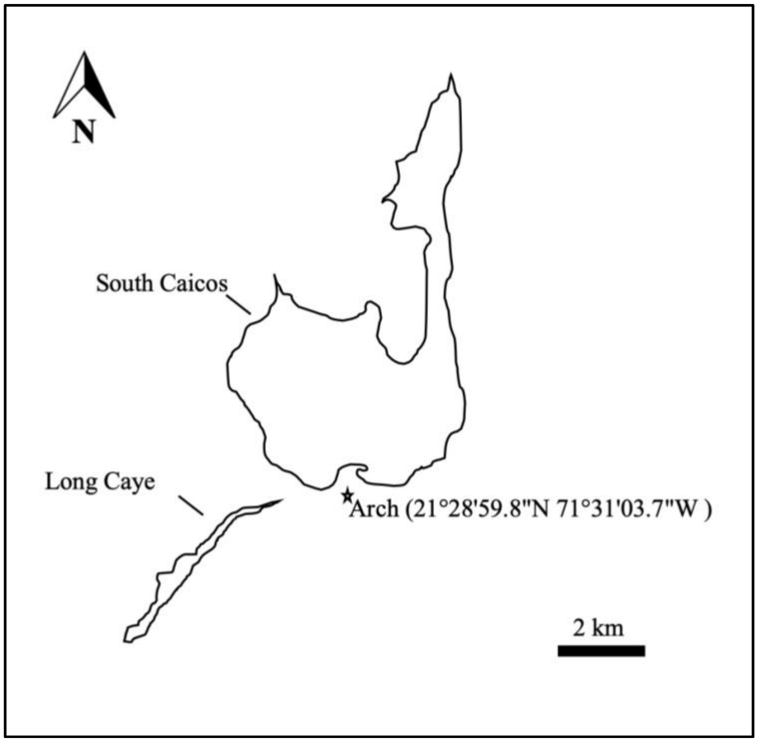

Figure 8. Map of Long Caye and South Caicos, Turks and Caicos Islands. The star represents the Arch, the study site.

4.2 Field Surveys

In total, I conducted 18 coral surveys at the Arch. At each survey area, 10 m-long belt transects were laid with 0.5 meters on either side. A T-bar was used to estimate the width of the transect. Hard and soft coral species were identified that were bigger than 10 cm in diameter or 10 cm in height for columnar-shaped species and counted in the 10 m^2 area. Transects were laid at varying depths. I had 7 transects at 10 m depths, 6 transects at 20 m, and 5 transects at a depth of 30 m. Transect placement was based on permanent benthic markers laid by the School for Field Studies. Transect layout is shown in Figure 9.

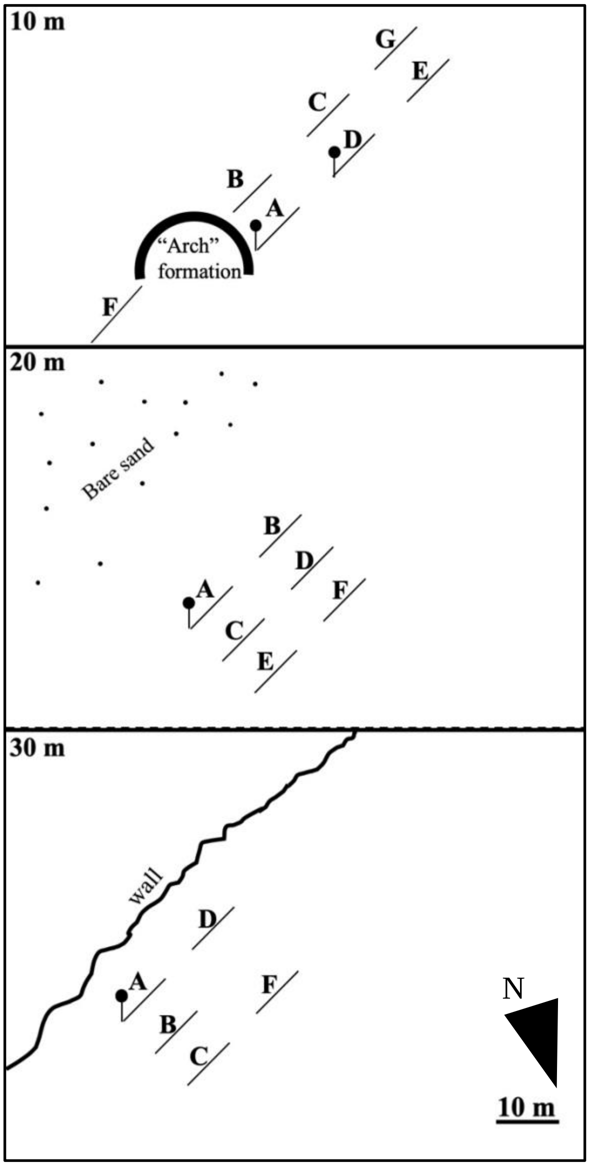

Figure 9. Transect layout at depths 10m, 20m, and 30 m. Lateral distance between transects was 6 m and medial distance was 10 m. Pin signifies dive markers at different depths.

4.3 Underwater Filming

In a lawnmower pattern (Figure 10), a diver filmed over a 10 x 1 meter area with weighted-markers placed on all four corners (the same area used for the coral survey). The diver recorded a video of the transect area going back and forth from one end of the transect to the other (five times in total) as the camera was at a constant height of 1.0 m above the reef and remained pointed straight down at the reef. To ensure that the video encompassed the entire desired area of study, the diver started on the outside of the markers and then with each pass of the length of the transect moved widthwise towards the other side to cover the entire length and width of the transect with some overlap. The swimming pace while recording the video was slow and steady for optimal model quality. The orientation of the camera did not change because the diver held the camera stationary while rotating the body upon reaching the end of the transect before turning back around. This study’s method required approximately six to eight minutes of in-water filming time per transect.

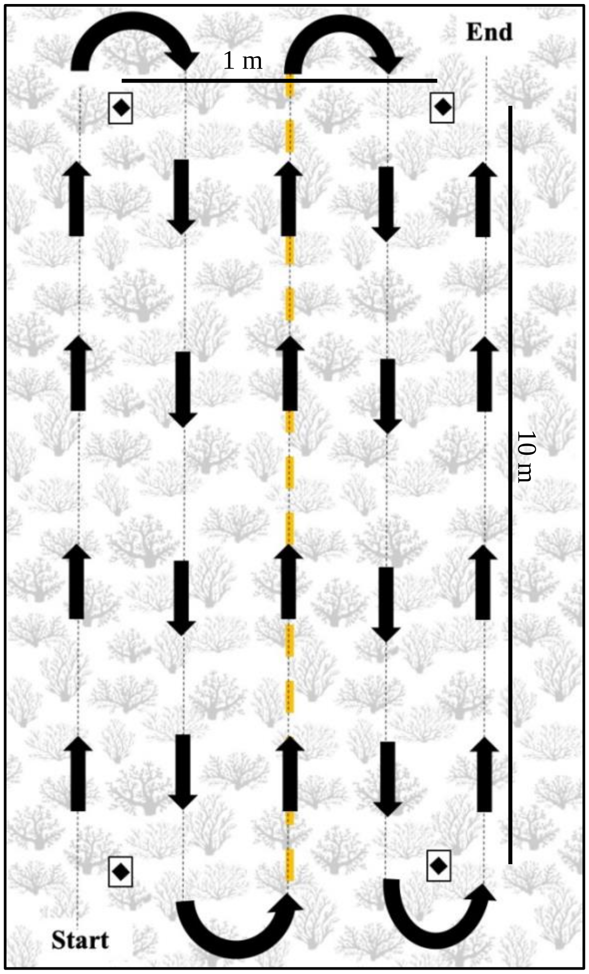

Figure 10. Lawnmower method for filming 10 x 1 m underwater transect area. Dotted lines with arrows signify the filmer/diver's movement. Yellow dotted line represents the transect tape. The squares with black diamonds in the center represent the four markers.

4.4 3D Modeling

The methods for this study's 3D modeling and 3D model analyses follow portions of Young et al.'s (2017) procedure. In order to construct a model from the video, the video was converted to images (JPGs) using Free Video to JPG Converter (version 5.0.101), extracting at 15 frames per second, except two transects (10M_A and 10M_B) which had pictures extracted at every 10 frames to maximize clarity of the model. The software PhotoScan Standard (Agisoft LLC) was used to render models. Images loaded into PhotoScan were rendered into a 3D model by (1) aligning photos, (2) optimizing alignment (3) building a dense point cloud, (4) building mesh, and (5) building texture. The settings were set with default settings, except meshes' maximum face counts were set to 3,000,000. A rendered model was then exported as a wavefront (.OBJ) file and imported into the modeling software, Rhinoceros 3D (“Rhino”; Robert McNeel & Associates).

4.5 3D Model Analysis Preparation

The first step while working within Rhino was scaling the model by using a drawn square on a weighted-marker that measured 4 cm from the center to the corners of the square using the Rhino “Scale” command. Using the Rhino “Point” command, four points were added to the center of the square for each of the four markers in each corner of the transect area. Subsequently, the model was oriented such that a corner of the model rested squarely on the origin between X and Y axes (using Front view) with the entire model located in the positive Z-axis. The model was also set on “Meter” for dimension units. These settings were necessarily applied in order to run the topographic complexity measurements.

4.6 Fractal Dimension

In order to find the fractal dimension (D) values, an edited version of a custom Rhino Python script “FD.py” (https://github.com/gracecalvertyoung/Rhino-Python-3D-Coral-Reefs/tree/master/Fractal_Dimension) made by Young et al. (2017) was run using the “RunPythonScript” command. The edited versions of the Python script allowed for nine 1.2 m x 1.2 m fractal dimension quadrats to be placed along the transect area (9.6 m x 1.2 m) right next to each other, from one end of the reef mesh, indicated by two markers, to the other end. Each quadrat had D values for five resolutions (δ) : 0.01, 0.05, 0.15, 0.3, and 0.6 m. This study’s D values describe the relationship between the reef models’ resolution (δ) and surface area S (δ). The formula below is how the 3D-model derived fractal dimension values were calculated:

$$2 - slope\,\frac{logS(\delta)}{\log(\delta)} = D$$

4.7 Rugosity

To find the linear rugosity values, a custom plane-grid created from “rugosity_helper.3dm” (100 squares of 0.5 m x 0.5 m) was uploaded and pasted onto the model once the model was scaled and set on “Meter” for dimension units. The meshes (reef and cube) were converged using the “MeshIntersect” command once the reef was completely overlapped by the cube mesh. Once the lines of the grid and the reef were intersected, the lines were ungrouped and rotated in the same direction, so that they all faced one direction. A Python Script “rugosity.py” found at https://github.com/gracecalvertyoung/Rhino-Python-3D-Coral-Reefs/blob/master/Rugosity/rugosity.py (also made by Young et al. 2017) was run using "RunPythonScript" command by selecting all of the lines individually. Once the Python script computes the rugosity value of each of the lines in the Command History, those values can be extracted into excel to obtain averages and standard deviation. The formula below is how rugosity values were calculated. The farther the value is to zero, the more rugose and thus topographically complex that area is, as seen in Figure 4.

$$\frac{Distance\ of\ virtual\ chain\ (contour)\ on\ the\ reef\,(R_D)}{Total\ length\ of\ the\ chain\ (flat\ line)\ (R_N)} = Rugosity$$

4.8 Diversity And Abundance

Shannon diversity index (H'), which takes into account species richness and evenness, was calculated for each transect using the formula below.

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

To determine abundant coral growth form for each transect, percentages of each coral species were calculated. The abundant coral growth form was determined as the coral with the highest relative abundance on the transect.

4.9 Data Analysis

Linear regressions were run to determine the correlation between the topographic complexity measures, fractal dimension (D values) and linear rugosity (R), and the Shannon's Diversity Index H'. Considering the data for fractal dimension and linear rugosity were normally distributed within each group of dominant coral growth form, analyses of variance (ANOVA) and the Tukey-Kramer HSD post hoc test were run on JMP statistical software to test the effect of dominant coral growth form on fractal dimension and rugosity.

4.10 Live Coral Cover

For this analysis I qualitatively assessed the literature regarding live coral cover and reef topographic complexity in Caribbean coral reef ecosystems. An analysis of the available peer-reviewed data was conducted using ISI Web of Science database (1972–2019) and GoogleScholar using keywords: coral cover AND structural complexity OR rugosity OR fractal dimension OR topographical complexity. The relationship between topographic complexity and coral cover was extracted from each study or if both coral reef 'traits' were the independent variables within the study, the outcome/impact on other coral reef attributes studied was considered.

CHAPTER 5

RESULTS

In the 18 transects that were studied, there were a total of 1216 corals identified from 28 different species (Table 1). Some species, such as *Siderastrea siderea* and *Porites astreoides,* were present throughout the majority of the transects and some appeared in every transect, such as *Pseudopterogorgia* spp. and *Agaricia* spp. There was a range of growth forms including branching, plate, and massive for stony corals, and branching, fan, and plume for soft corals. The diversity within massive species (*Diploria stokesii, D. clivosa, D. labyrinthiformis, Isophyllia rigida, Leptoseris cucullata, Montastraea cavernosa, Orbicella annularis, P. astreoides*) was higher than any other growth form, but benthic communities at this site were dominated by plate coral (*Agaricia* spp.) and soft corals (*Pseudopterogorgia* spp.; Table 1). Out of the 28 species present, 21 had relatively low species abundance (less than ten per each transect throughout all 18 transects). However, some species had generally low species abundance overall but had a higher number of individuals at one or two transects (*Orbicella faveolata, O. franksi,* and *Pterogorgia* spp.). On four transects, *Pseudopterogorgia* spp. and *Agaricia* spp abundances were within 3% of each other, being the two most abundant growth forms on these transects, plate and plume. When determining coral growth form abundance, those sites were deemed plate/plume dominated reefs. Nine transects were dominated by plume forms, four transects were dominated by plate/plume forms, and five transects were dominated by plate forms.

Table 1. Coral species recorded with corresponding growth form and number of individuals per transect. Bolded values indicate greatest abundance at that transect. 10, 20, and 30 indicates the depths of the transects. The letters correspond to the transect labels at those depths (see Fig 7 for visual reference).

Species	Growth form	10A	10B	10C	10D	10E	10F	10G	20A	20B	20C	20D	20E	20F	30A	30B	30C	30D	30F
Acropora cervicornis	Branching										1								
Agaricia spp.	Plate	**18**	**20**	5	12	10	**12**	9	**13**	**8**	**12**	8	16	15	**12**	16	**8**	**21**	15
Dichocoenia stokesii	Massive										2		1						
Diploria clivosa	Massive														4				
D. labyrinthiformis	Massive				1			1				2	1	2		1	1	1	1
Diploria strigosa	Massive	1								1									
Eusmilia fastigiata	Tubular			1	1		1				2					1	1		
Favia fragum	Hemispherical	3					1				2				1	1	2	3	
Gorgonia spp.	Fan	11	10	2	2	1	7	2				1	2					1	
Isophyllastrea rigida	Massive			1			2		1										
Leptoseris cucullata	Plate														1				
Madracis spp.	Branching		3		1						6		2	1			1		
Meandrina spp.	Massive		2		1					1	3	1	1	1	1	1	1		
Millepora spp.	Branching	5	5	2	4	5	2								4	2			
Montastraea cavernosa	Massive		1				2			1					3	2		1	3
Mycetophyllia spp.	Plate														1		1		
Orbicella annularis	Massive							5			1						3	7	
Orbicella faveolata	Massive		3	1	2	1	1		2			1		6	1	6	6	4	15
Orbicella franksi	Massive			1	1	2	2	1							5	16	2	3	6
Plexaura spp.	Branching (soft)		3								3						2	2	
Porites astreoides	Massive	10	5	2	4	2	6	5				1	6	5	5	5			5
Porites porites	Branching			1	1	1		1			3		2					2	
Pseudopterogorgia spp.	Plume	**19**	13	**24**	**27**	**41**	**12**	**57**	6	4	9	**41**	**45**	**74**	**11**	**26**	**8**	2	**24**
Pterogorgia	Branching (soft)							2	1				6	21					4
Siderastrea radians	Encrusting	11	2		2	2	5				3				7	4	2		
Siderastrea siderea	Massive	3	2	2	1	2	4	3	3	2	5	4	2	4	8	4			1
Solenastrea bournoni	Massive									1					2				
Stephanocoenia intersepta	Plate			2			1	1			4			2	1	3	1	5	8
																	Total: 1216		

5.1 Coral Species Diversity & Topographic Complexity

A significant relationship was found between coral species diversity and fractal dimension ($D_{1.2-0.6}$, $D_{1.2-0.3,}$ $D_{1.2-0.15,}$ $D_{1.2-0.05}$; subscripts refer to the resolution). As diversity increased, fractal dimensions increased (Figure 11). The rate at which fractal dimension increased differed between resolutions. For instance, $D_{1.2-0.6}$ increased at a higher rate than $D_{1.2-0.05.}$ However, for the fractal dimensions at the lowest resolution, $D_{1.2-0.01,}$ there was no significant relationship between coral species diversity and the D values according the regression analysis (linear regression, $n = 18$, $R^2 = 0.04$, $p > 0.05$). Another significant relationship was found between coral species diversity and rugosity (linear regression, $n = 18$, $R^2 = 0.50$, $p = 0.001$). The statistical analysis was run on inverse rugosity as linear/reef contour which was significant. The relationship that the rugosity increased as coral species diversity increased is shown as reef contour/linear (Figure 12). In other words, diversity increased as a function of rugosity.

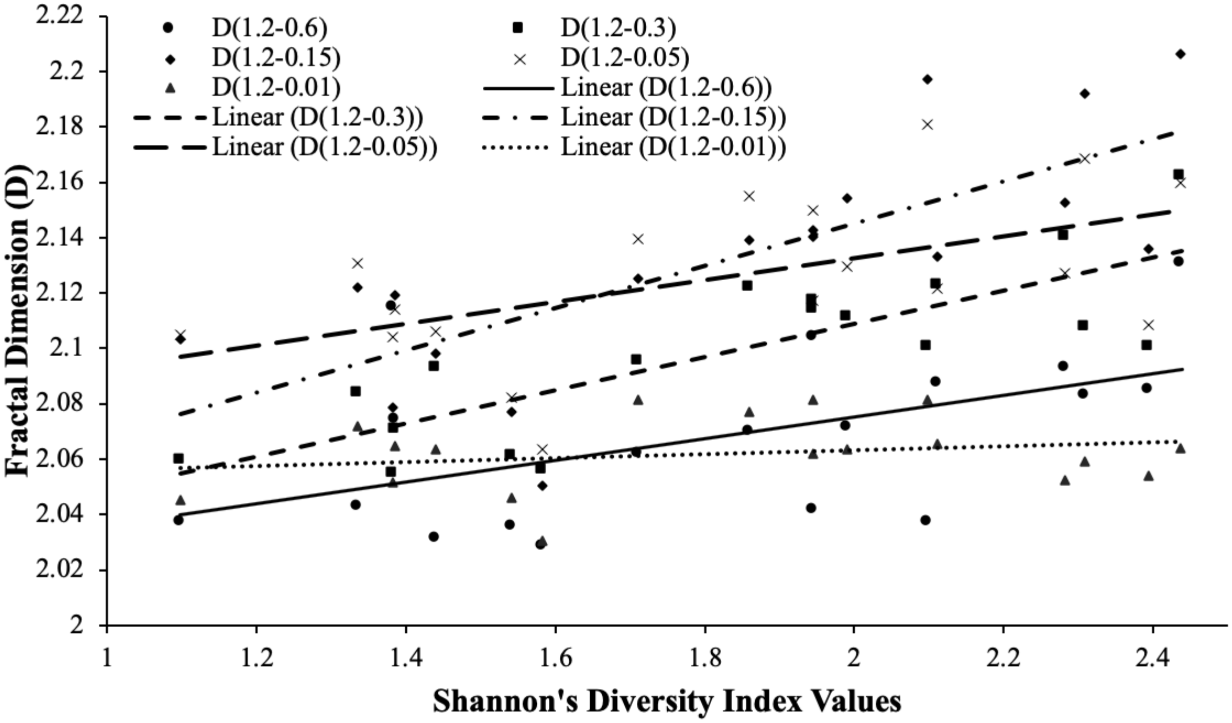

Figure 11. The relationship between Shannon Diversity Index values and fractal dimension values for each resolution ($D_{1.2\text{-}0.6}$, $D_{1.2\text{-}0.3}$, $D_{1.2\text{-}0.15}$, $D_{1.2\text{-}0.05}$, $D_{1.2\text{-}0.01}$). Linear trendline and R^2 value were calculated for each $D_{resolution}$. $D_{1.2\text{-}0.6}$ (n = 18, $R^2 = 0.56$, y = 0.04x + 1.99, p = 0.03). $D_{1.2\text{-}0.3}$ (n = 18, $R^2 = 0.28$, y = 0.06x + 2.00, p = < 0.001). $D_{1.2\text{-}0.15}$ (n = 18, $R^2 = 0.65$, y = 0.08x + 1.99, p = 0.0004). $D_{1.2\text{-}0.05}$ (n = 18, $R^2 = 0.27$, y = 0.04x + 2.05, p = 0.02). $D_{1.2\text{-}0.01}$ (n=18, $R^2 = 0.04$, y = 0.007x + 2.05, p = 0.401).

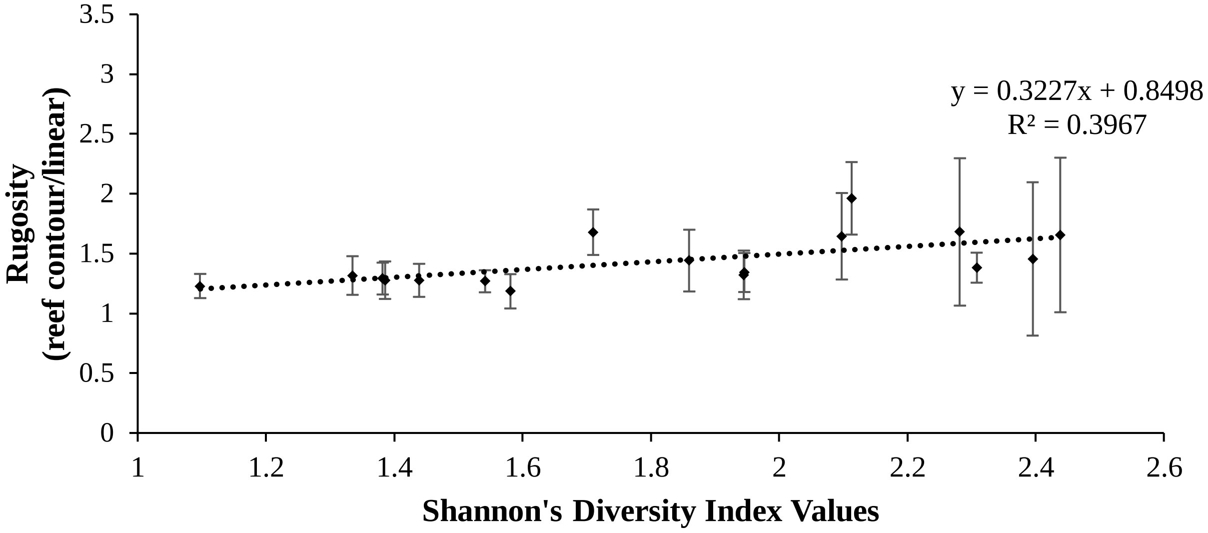

Figure 12. The relationship between Shannon Diversity Index values and rugosity values (reef contour/linear) ($n = 18$, $R^2 = 0.3967$, $y = 0.3227x + 0.8498$).

5.2 Most Abundant Coral Growth Form & Topographic Complexity

From an ANOVA, statistically significant differences between the mean D values for each coral growth form were found for $D_{1.2\text{-}0.3}$ and $D_{1.2\text{-}0.6}$. At both resolutions, values for plate/plume dominated reefs appear as the highest fractal dimension (Figure 13). There were significant differences in fractal dimension at resolutions $D_{1.2\text{-}0.3}$ and $D_{1.2\text{-}0.6}$ among the three dominant growth forms (ANOVA, $n = 18$, $D_{1.2\text{-}0.6}$: $F(2) = 8.97$, $p = 0.003$; $D_{1.2\text{-}0.3}$: $F(2) = 4.10$, $p = 0.04$), with LSD post hoc tests revealing that plate/plume had higher fractal dimension values than plume-dominated reefs. There were no statistically significant differences between plate/plume and plate, or between plate and plume for both resolutions. The means of remaining fractal dimensions and rugosity were not statistically different between plate/plume, plate and plume (ANOVA, n = 18, $D_{1.2-0.15,}$: F(2) = 3.54, $p > 0.05$; $D_{1.2-0.05}$: F(2) = 2.15, $p > 0.05$; $D_{1.2-0.01}$: F(2) = 2.26, $p > 0.05$; R: F(2) = 2.24, $p > 0.05$). To reiterate, for both $D_{1.2-0.3}$ and $D_{1.2-0.6}$, the only difference that was statistically significant was between plate/plume-dominated reefs and plume-dominated reefs.

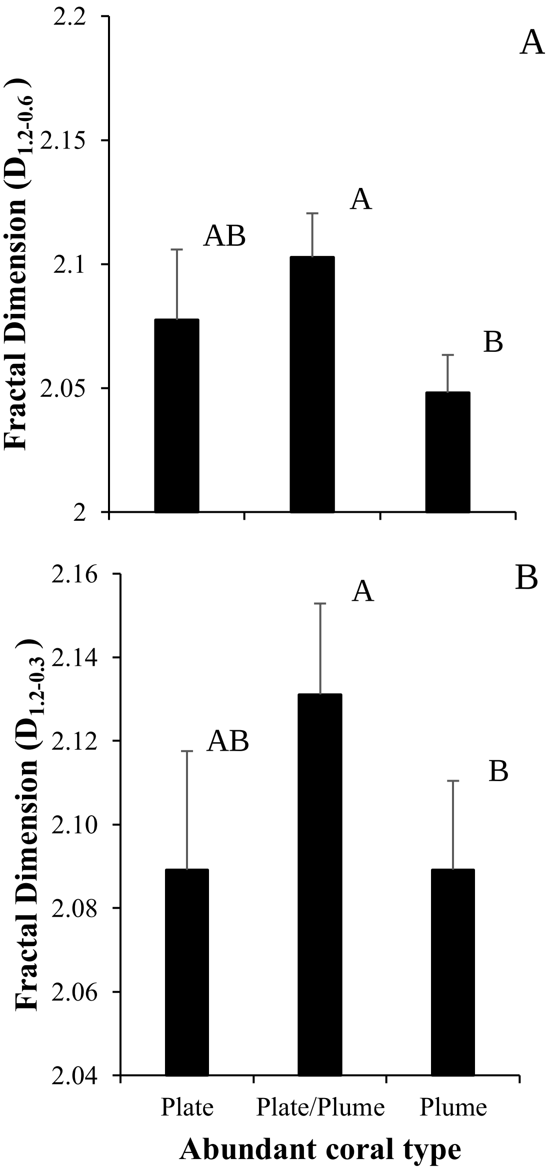

Figure 13. (A) Most abundant coral type and average fractal dimension ($D_{1.2\text{-}0.6}$). **(B)** Most abundant coral type and average fractal dimension ($D_{1.2\text{-}0.3.}$). Bars sharing a letter are not statistically significantly different according to an ANOVA. Error bars signify standard deviation.

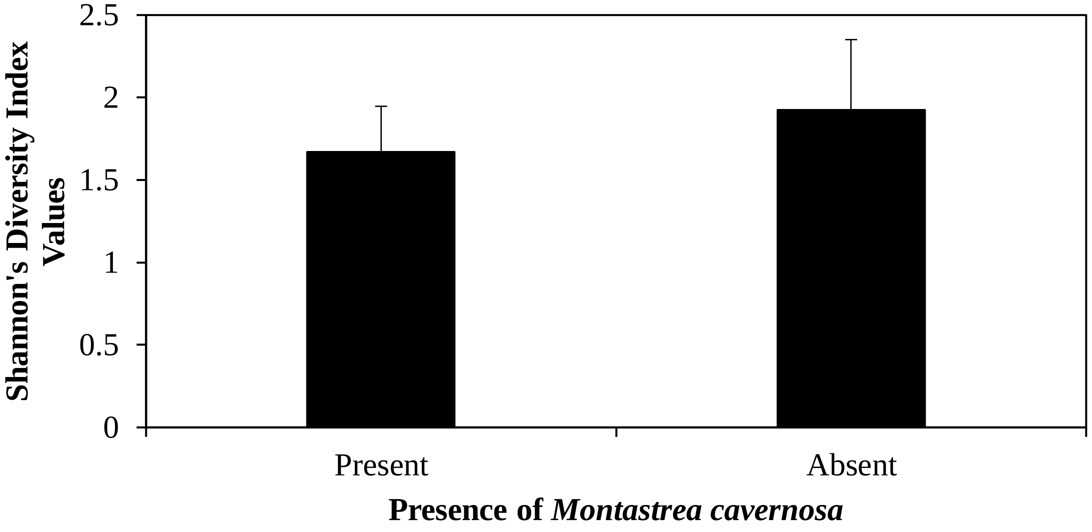

Figure 14. Mean Shannon's Diversity Index Values in transects where *Montastrea cavernosa* was present or absent. Error bars signify standard deviation.

Out of 18 transects, seven had at least one *Montastrea cavernosa*. From taking the average of Shannon's Diversity Index Values of the transects that did and did not have *M. cavernosa,* I found that transects that had *M. cavernosa* tend to have lower Shannon's Diversity Index Values than transects where *M. cavernosa* was absent however these values are not statistically different from each other (n = 18, t(16) = 1.307, $p > 0.05$; Figure 14).

5.3 Live Coral Cover & Topographic Complexity

There is mixed evidence of collinearity between measures of structural complexity and live coral cover. Evidence from multiple sites in the Caribbean suggest that even though coral cover and structural complexity have declined significantly in the past two decades, they have declined at different rates (Alvarez-Filip et al. 2011b). The difference in declines in coral cover and complexity region-wide are likely a consequence of coral disease and bleaching which results in coral mortality but not immediate erosion to the reef framework (Aronson and Precht 2001; Sheppard et al. 2002). The weak relationship between rates of change in coral cover and architectural complexity suggests that complexity is not solely a function of coral cover; changes in other reef attributes have likely influenced the response of reef complexity to the loss of coral cover (Alvarez-Filip et al. 2011b). Another study in the Caribbean by Alvarez-Filip et al. (2013) investigated the changes in coral-assemblage composition and structural complexity and found that as reefs became dominated by species with substantially reduced capacity to produce and maintain reef framework such as *Porites astreoides*, reef structural complexity continued to decline.

In addition to different rates of decline between coral cover and topographic complexity, changes in topographic complexity and coral cover impact the invertebrate community differently (Idjadi & Edmunds 2006). It is the timing between loss of coral cover and loss of topographic complexity that matters. For coral reefs with a low percentage of live coral cover (e.g. < 10%), the skeletons that are left behind after the coral tissue dies and the structural diversity they create are important in determining the diversity and structure of the invertebrate communities (Idjadi & Edmunds 2006). For example, *Acropora palmata* populations that were severely affected by white-band disease in the 1980s had coral cover decrease (Aronson & Precht 2001). The dead *A. palmata* colonies continued to support a rich invertebrate community while their skeletons remained, but when this framework was later damaged by hurricanes, the invertebrate community severely declined (Aronson & Precht 2001).

When multiple studies in the Caribbean involving coral cover and topographic complexity were analyzed, there was no significant correlation between the two (Graham and Nash 2013). In contrast, there have been a small number of studies that have found a significant positive correlation between coral cover and structural complexity (McClanahan and Shafir 1990; Mangi and Roberts 2007). Alvarez-Filip et al. (2011a) found that reefs with greater coral cover had greater architectural complexity; but the variance in complexity also increased with coral cover. The variance in complexity at high levels of coral cover was due to dominance by a particular coral genus. For instance, Alvarez-Filip et al. (2011a) found that sites dominated by species from the genus *Montastraea* had greater architectural complexity for a given coral cover, followed by *Agaricia* and *Porites*. They also found that at sites with relatively low coral cover (<20 %), complexity varied little which may be due to the dominant species not being abundant enough to contribute significantly to the reef framework or that there was not that much coral following erosion. Assuming that this also applies elsewhere in the Caribbean, their findings may help to explain the shift toward flat reefs reported in recent decades (Alvarez-Filip et al. 2009, Alvarez-Filip et al. 2011a). Consequently, the findings of Alvarez-Filip et al. (2011a) suggest that assemblages with species such as *Montastraea spp*. would be expected to facilitate more biodiverse and functionally important coral reefs in the Caribbean. *Montastraea* historically ranked high in importance along with *Acropora palmata* and *A. cervicornis* in overall contribution to Western Atlantic reef structure (Alvarez-Filip et al. 2011a). Therefore, coral cover is an important attribute that may be related to topographic complexity, but the coral cover of certain species may hold more significance than overall coral cover.

There has been an increase in relative abundance of *Porites astreoides* on Caribbean reefs; *Porites astreoides* forms rapidly growing, small colonies that are short lived and quickly replaced (Green et al. 2008). The increase in this less-complex species is important in regards to coral cover and architectural complexity since the increase is mediated by an overall decline in coral cover of other scleractinians (Green et al. 2008). Although percentages of live coral cover were not recorded in South Caicos, there is some evidence that *Porites* is common since it was found in the majority of this study's transects. *P. astreoides* may become a dominant coral on all Caribbean reefs in shallow waters in the future.

Studies in other parts of the world. In other parts of the world, studies have found that low coral cover and low topographic complexity do not significantly impact reef communities. Results from Coker et al.'s (2012) study on Lizard Island, Great Barrier Reef, suggest that declines in coral cover and structural complexity will not necessarily lead to declines in overall fish abundance and species diversity. In addition, fishes will recruit and settle to degraded reefs in high numbers and high diversity following coral degradation, but those fish communities will be significantly different in size and type compared to healthy complex reefs (Coker et al. 2012). The loss of architectural complexity following declines in coral cover in the Caribbean differs from the pattern reported in the Indo-Pacific region, where a lagged response in the aftermath of widespread coral mortality following mass bleaching events was apparent (Graham et al. 2008). Reduction in the structural complexity of the reef matrix due to biological and physical erosion of dead coral skeletons is associated with the decline in coral cover created by bleaching (Sheppard et al. 2002; Graham et al. 2006). Evidence has been found that supports this claim in Chagos Archipelago, Indian Ocean (Sheppard et al. 2002; Graham et al. 2008), as well as Seychelles, Kenya, Maldives, and Tanzania (Graham et al. 2008).

CHAPTER 6

DISCUSSION

6.1 Coral Species Diversity and Topographic Complexity

The aim of this study was to assess the influence of coral species diversity and most abundant coral growth form on topographic complexity using analyses of rugosity and fractal dimension. In addition, I sought to assess the relationship between coral cover and topographic complexity from a literature review of related research. Supported hypotheses include linear rugosity increased as coral species diversity increased and fractal dimension increased as coral species diversity increased (for all except the lowest resolution $D_{0.01}$). In addition, the rate at which fractal dimension increased differed between resolutions.

There was a positive relationship between both measures of topographic complexity (fractal dimensions larger than 0.01 resolution and linear rugosity) and coral species diversity. High coral diversity provides a wider variety of habitats and shelters (higher complexity) for invertebrates compared to low coral diversity, based simply on the morphological diversity of coral species. These findings are in accordance with Alvarez-Filip et al.’s (2011a) study which found topographic complexity to be positively associated with number of coral species. That study showed that sites with fewer than five coral species tended to be relatively flat, while more diverse sites had the greatest topographic complexity. Alvarez-Filip et al. (2009) states that as of 1990, the flattest reefs (rugosity less than 1.5) comprise approximately 75% of the Caribbean region which, when compared to the highest rugosity value of 1.96±0.30 at my study site, shows that the reefs in my study are all relatively flat. An interesting notion is topographic complexity's effect on coral diversity. The direction of the topographic complexity-biodiversity relationship can be described using the phrase "reciprocal causation" because the organisms that create complexity often require complexity to settle as larvae (Torres-Pulliza et al. in-prep). A study that used topographic complexity as a measure of disturbance found that coral species diversity was highest at an intermediate topographic complexity (Aronson and Precht 1995). That study used the same diversity index that I used but utilized linear point-intercept which is another way of measuring complexity. This also is in accordance with the fact that reefs in the Caribbean have become flat, less rugose and more structurally uniform following regional declines in live coral cover (Gardener et al. 2003; Alvarez-Filip et al. 2009).

6.2 Most Abundant Coral Growth Form And Topographic Complexity

In regards to dominating coral growth forms (based on the highest relative abundance), this study found no statistically significant relationships between any dominant coral growth form and rugosity. This may be due to the small number of different dominant coral growth forms. This study only had three different dominant coral growth forms which were comprised of two distinct growth forms and one mix of the two. Some studies in the literature however had a wider of range of up to five different growth forms (Richardson et al. 2017). The lack of significant differences in my study could also possibly be attributed to the 3D modelling software not including plume-shaped species when measuring linear rugosity. Since the analysis runs horizontal and vertical mesh lines over the reef, if plume-shaped individuals weren’t exactly under those mesh lines, they may not have been evaluated. From an above perspective, the area that plume individuals take up is relatively small, thus, they are less likely to be measured in the rugosity index.

I found highest fractal dimension values at largest resolutions on plume/plate dominated reefs followed by plume and lowest for plate-dominated (fractal dimension values for plume/plate-dominated reefs were highest at the largest resolution, followed by plate and plume). I found no statistical difference between fractal dimension values at small resolutions on plate-dominated reefs, plume-dominated reefs and plate/plume dominated reefs. This finding goes against my original hypothesis that the values would be highest for plate-dominated reefs than plume and plate/plume dominated reefs. Topographic variability of the surface at scales that matched our smallest fractal dimension resolutions may be similar for both plume and plate shaped individuals due to their relative shape. Plume and plate shaped species are oriented differently but have similar structures which may explain the lack of significant difference between the coral dominance growth forms measured at the smallest scales. In other words, plume and plate growth forms are structurally similar in that plumes are flat and vertical while plate are flat and horizontal. Or, this may be explained due to reduced accuracy at smaller scales. Small differences are more difficult to obtain for multiple reasons including particulate matter in the water interfering with image resolution (Young et al. 2017). This reduced accuracy at smaller scales can also be applied to this study's lack of statistically significant relationship between coral species diversity and fractal dimension at the smallest scale ($D_{1.2-0.01}$).

Another finding was that fractal dimensions at the largest resolutions ($D_{0.6}$ and $D_{0.3}$) on plume/plate was highest, followed by plate and plume. This does not match the hypothesis of fractal dimensions at large resolutions being highest for plume dominated reefs and lower for plate and plate/plume dominated reefs. The reasoning behind the hypothesis is that the presence of *Pseudopterogorgia* spp. individuals would lead to higher D values since soft coral habitats can have greater topographic complexity at large scales (Richardson et al. 2017). A logical explanation for the results contradicting this would be that not all plumes counted during field surveys were measured in the model. Movement of plumes because of currents during filming may have caused them to not be included in the model or any analyses. Also higher topographic complexity in plume/plate reefs may be due to having two growth forms both relatively abundant in an area.

6.3 Live Coral Cover and Topographic Complexity

The literature on live coral cover and topographic complexity in the Caribbean presents mixed results. The coral cover of certain species such as *Montastraea* spp. may hold more significance than overall coral cover in determining reef's topographic complexity (Alvarez-Filip et al. 2011a). When comparing transects where *Montastraea cavernosa* was present versus absent to test Alvarez-Filip et al.'s claim, I found that transects where *M. cavernosa* was absent actually had higher Shannon's diversity index values on average. Although this may not be indicative of low structural complexity due to presence of *M. cavernosa*. This may be due to small sample size overall; most transects where *M. cavernosa* was present had a single individual.

In comparison to the other reef attributes from my study's evaluation, coral cover had the weakest relationship with topographic complexity according to past research in the Caribbean. My field results provide evidence that topographic complexity is influenced by coral species diversity and in part, by dominant coral growth form. As coral species diversity increases, rugosity and fractal dimension increases (except for the smallest scale). Furthermore, plate/plume dominated reefs had higher fractal dimension values (at large scales) than plume-dominated reefs.

6.4 Notable Observations

I found a relatively large number of *Agaricia* spp. (212 individuals) and a small number of *Acropora* spp. (1; Table 1). This is important to note since *Acropora* used to be the dominant coral species in the Caribbean. A justification could be the two major hurricanes that struck the Turks and Caicos Islands in 2017. Studies found that brooding Agaricids and *Porites* had successful recruitment after hurricanes while *Acropora* was not successful (Hughes 1994; Green and Edmunds 2011), which would explain the low abundance of *Acropora* and high abundance of *Agaricia*. In addition, disease could be a factor playing into low branching coral growth forms. Aronson and Precht (2001) found that in the Caribbean, if *Acropora* spp. do not recover, macroalgae will dominate reefs, accompanied by increased abundances of brooding corals, particularly *Agaricia* spp. and *Porites* spp. Also in the Caribbean, there has been a loss of reef-building coral species such as *Acropora* spp. and *Montastraea* spp. with an increase in the stress-tolerant corals, like *Agaricia* spp., which are often less topographically complex (Aronson et al. 2002; Green et al. 2008). This helps explain the high abundance and dominance of *Agaricia* spp. and low abundance of *Montastraea* spp. and very low abundance of *Acropora* spp. at my study site.

There were limitations within this study which can be eliminated with several modifications in the future. Although this study did take less rigid biota like soft corals into account for topographic complexity, the effect of sponges and other three-dimensional benthic species were not evaluated, which have been measured within rugosity and fractal dimensions. Integrating structural complexity of sponges would be beneficial since there has been very little research on that in the Caribbean. Sponges with structural complexity also offer refuge to species just as corals do. Future studies are needed to determine the impact substantial changes in sponge species diversity has on topographic complexity. Having more studies dedicated to understanding the structural components underlying this complexity, such as the influence of sponge diversity, would be beneficial. Further studies in different reef habitats and different sites are necessary to complete the picture of the relationship between different reef attributes and reef architectural complexity. The density and diversity of corals and reefs are likely to decline globally, leading to vastly reduced topographic complexity and loss of biodiversity (Loya et al. 2001; Hoegh-Guldberg et al. 2007); thus, it is important to continue research on effects of coral species diversity, dominant growth form, and coral cover on topographic complexity.

CHAPTER 7

STRATEGIC CONSERVATION AND RESTORATION METHODS

Within the last two decades, non-profit organizations, scientists, and researchers at coastal universities around the globe have been developing methods for protection, conservation, and reconstruction of coral reefs to promote growth and resilience against changes to the oceanic environment. There is a delay in our attempts to mitigate CO_2 emissions which is a huge issue. However we, reef managers and coastal resource policies must address immediate local stressors such as declining water quality, coastal pollution, and overexploitation of key functional groups such as herbivores (Hughes et al. 2002; Hoegh-Guldberg et al. 2007). Currently, restoration and conservation strategies for Caribbean coral reefs are of utmost importance. Time, effort, and costs are sometimes high in restoration efforts so ensuring strategies are effective is crucial.

7.1 Applications From This Study

In my study, I found that coral species diversity was strongly correlated with topographic complexity. This may suggest that high coral species diversity leads to high topographic complexity and the other way around (reciprocal causation; Torres-Pulliza et al. in-prep), thus strategies should ensure reefs have both high coral species diversity and high topographic complexity. While maximizing the amount of coral present (i.e. high live coral cover), for long term reef condition, topographically complex reefs (with complex growth forms) with high diversity is vital. Since topographically complex reefs are considered more healthy (due to the fact that complex reefs support fish and invertebrate richness, abundance and biomass), coral reef conservation efforts should focus on protecting already complex reefs and promoting richness of coral species, and coral reef restoration efforts should focus on ensuring coral reefs have structurally complex species, especially *Acropora* and *Montastraea*. Another key strategy for restoration efforts is to strengthen reef resilience.

7.2 Reef Resilience And Outplanting

Resilience is the ability of reef communities to regenerate after stress and damage through growth and reproduction of surviving corals and through larval recruitment. By promoting regeneration, coral reefs may reach a state (or close to a state) that the reef was in prior to the stress (West and Salm 2003). Reef communities consisting of diverse adult corals with high fertilization success and high larvae survivability before and after recruitment may benefit its resilience and increase the chance of recovery of adjacent or down-current coral communities, thus, restoration and outplanting efforts of species with high fertilization success and high larvae survivability are spreading (West and Salm 2003; Hoegh-Guldberg et al. 2007). Outplanting and other new techniques for the mass culture of corals from fragments may assist local restoration or the culture of resistant varieties of these key species (Hoegh-Guldberg et al. 2007). Specifically for *Acropora* populations in the Caribbean, low-cost methods such as coral gardening and fragment stabilization were ranked as the most effective activities for reef restoration (Young et al. 2012). Coral gardening consists of removing a small amount of tissue and skeleton from healthy wild coral populations and propagating a stock within *in situ* or *ex situ* coral nurseries (Rinkevich 2005; Young et al. 2012). Once those nursery-grown colonies produce a sustainable amount of corals, those corals can then be transplanted to reefs in need (Rinkevich 2005). Both acroporid species (*A. palmata* and *A. cervicornis*) have particularly high growth rates relative to other corals, therefore, direct planting of coral fragments are logical for restoration (Goreau and Goreau 1959).

7.3 Marine Protected Areas (MPAs)

The major coral reef management measure practiced by NGOs, conservationists, scientists, managers and decision making authorities has been marine protected areas (MPAs; Sale 2008; Rinkevich 2008). MPAs restrict human activity for a conservation purpose in a particular area, typically to protect natural marine resources. Presence of sufficient grazing fish populations may also increase recovery since herbivorous fish consume the macroalgae that may otherwise have out-competed coral recruits for space on the reef (West and Salm 2003; Norström et al. 2009). This can easily be implemented by establishing a MPA over a desired reef. Near this study's dive site was the East Harbor Conch and Lobster Reserve which, with more restrictions in place for the future, may assist in the recovery of the coral reefs by promoting the presence of grazing fish. However, the effectiveness of MPAs has been debated. In the Caribbean, some weaknesses of MPAs are the lack of adequate administration and the failure of the MPA program to evolve with the changes in government and community involvement (Cho 2005). Overall, the main conditions in regards to MPAs are that the restrictions in place at the time of implementation should be constantly revised to current management protocols, rationales and to include active reef restoration as the main part of routine management (Rinkevich 2008).

7.4 Artificial Reefs

Artificial reefs have been used as a tool for reef conservation and rehabilitation for a few decades and have been presented in media worldwide (Clark and Edwards 1999; Perkol-Finkel et al. 2006). Besides increasing the amount of substrate available for benthic organisms such as coral, artificial reefs serve other purposes including increasing the convenience and efficiency of harvesting reef-associated species (Carr and Hixon 1997). The effectiveness of artificial reefs has also been debated and studied. A study found that artificial reefs will mimic its adjacent natural reefs communities only if the artificial reef has structural features similar to those of the natural surroundings; seen in Figure 15 (Perkol-Finkel et al. 2006).

Figure 15. Artificial reef structure placed on reef flat with *Acropora cervicornis* and other species growing on top (photography by Gareth Stingler).

When establishing artificial reefs, coral recruitment is usually higher on inclined surfaces as compared to horizontal because there are increased water circulation and lower sedimentation levels (Clark and Edwards 1999). The structural complexity of artificial reefs play a very important role in the coral community structure in the Caribbean (Carr and Hixon 1997). In fact, structural complexity is more important than age in determining how close the community structure is to a natural reef (Perkol-Finkel et al. 2006). High structural complexity of artificial reefs in the Caribbean drive high fish abundance as well, which reiterates the importance of having structural complexity in reefs, natural or artificially (Hixon and Beets 1989).

As more studies are done, scientists are expanding knowledge about the stressors of reefs, which will assist in saving the world's reefs by influencing conservation and restoration strategies. In saving the world's reefs, not only are some of the marine organisms depending on the reef being saved, but also humans who depend on the protection and food supply from reefs.

CHAPTER 8

CONCLUSION

The architectural complexity of reefs can greatly influence their ability to support biodiversity and provide ecosystem services which may be impacted by different reef attributes. This study integrated methods that were used often in previous topographic complexity studies but also newer methods and techniques whose results can be used as a baseline for future studies. In regards to coral species diversity, this study found that both measures of topographic complexity (rugosity and fractal dimension) increased as coral species diversity increased. While coral cover is an important reef attribute in some cases, the corals' identity plays a bigger role than the amount of cover considering topographic complexity in the Caribbean. My study showed a significant relationship between fractal dimensions at larger resolutions and most abundant coral growth form in which higher fractal dimensions occurred on plate/plume- dominated reefs than plume-dominated reefs. This may be due to increased diversity in growth form given that there are two different morphologies dominating the area. Understanding the reef attributes relating to topographic complexity can help increase effectiveness in the development of strategies for marine ecosystem conservation including coral reef restoration efforts. Therefore I hope that this honors research can be applied to future studies and conservation efforts in the Caribbean and elsewhere moving forward.

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