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Cayman Islands Marine Protected Areas, their status, effects and future

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Abstract

Caribbean coral reefs in the1950s through to the early 1970s were viewed as robust and stable ecosystems, and not considered threatened in any way by a human-dominated world. However, in 1982-1983, in the western Atlantic region including the Caribbean basin, the sea-urchin *Diadema antillarium,* a keystone grazer, died off suddenly. This event, coupled with over-fishing of herbivores and multiple coral-bleaching episodes in the Caribbean region dating back to the 1970s triggered a phase shift from a coral-dominated to an algal-dominated environment. The decline of coral reefs, including fisheries, in the Caribbean region, had fuelled much debate, as several scientists had hypothesized that, by the time humans started studying the coral reefs in the 1950s, the reefs were already overfished and in a degraded state. However, concerns were raised mainly on noticing the gradual loss of the goods and services provided by the coral reefs. With >275 million people in the global tropics living at <30-km distance away from coral reefs, of which >43 million of those people residing in the Caribbean basin has raised the alarm about the loss of coral cover from ~50% average 4 decades ago to a mere regional average of ~12% presently. Though this decline can be attributed to several factors, including the consequences of climate change, over-fishing, ocean acidification, and destructive cyclones, it has spurred and driven coral reef researchers to understand the ecology and biology of these ancient animals better. Furthermore, in the last few decades, coral reefs' ability to function while facing these threats has prompted additional research to understand the ecological and biological attributes of coral reefs and their associated organisms, such as reef fish populations, to ascertain what drives their relationship. However, those underpinning biological and ecological metrics have seemingly eluded coral reef scientist over the past four decades. In September 2009, the Cayman Islands coral reefs experienced a localized acute coral bleaching event with water temperature > 30^{C} for six weeks. This event was caused by a whirlpool of hot water originating off of the island of Cuba southern shelf. Bleaching was observed down to a depth of 100 m using a remotely operated underwater vehicle (ROV). Furthermore, satellite water temperature data from the National Oceanic and Atmospheric Administration (NOAA) showed that water temperatures extended to a depth of 450 m. The coral reefs of the Cayman Islands recovered without any measurable coral mortality; however, there was a notable decline in algal mortality for the island of Grand Cayman. Furthermore, in both 2015 and 2016, the global marine heatwave, the longest ever on record that effected greater than one-quarter of the ocean surface, with devastating consequences for marine ecosystems globally had a negligible effect on the coral reefs of the Cayman Islands. Data was collected on the Benthos and their fish assemblages over years (2009–2012), islands, coast (North, South and West) habitats (deep and shallow) and protection status (MPA and non-MPA) at 55 sites across the 3 Cayman Islands; Grand Cayman (GCM, n=27), Little Cayman (LC, n=16) and Cayman Brac (CB, n=12). Total fish biomass differed significantly over the years, showing an overall strong reserve effect ($p = 0.001$). A significant spill-over effect for the shallow terrace reef on the northern boundary of the MPA in GCM was detected in the years 2009 ($P<0.01$) and 2011($P<0.01$) No spill-over was evident on the deep terrace reef of any the islands, possibly due to residents able to fish anywhere beyond the 24 m depth contour. With more than 50% of the total variance explained, the analysis of principal coordinates (PCO) showed that the functional differences between MPA and non-MPA regarding fish assemblages across the habitats and islands were highly correlated ($p = 0.8$) indicative of a positive linear relationship with 4 species of fish: (1) *Holacanthus tricolour*, (2) *Sparissoma aurofrenatum*, (3) *Anisotremus Surinamensis* and (4) *Kyphosidae* spp. The community structure of fish significantly differed across years on all islands ($p < 0.001$). The fish communities were found to be most similar between the years 2009 and 2010. However, their differences in community structure increased over time, indicating that MPA's effects were not consistent across years on all islands. The temporal and spatial changes in the benthic community structure documented during the period of study were complex, and their trajectories depended on a combination of factors such as the habitat type, coast, and island, including protection. SIMPER analysis revealed the largest average dissimilarities to be GCM for the years 2011 and 2012 (54.4%, driven by macroalgae, dead coral and pavement), whereas the lowest was found between the years 2009 (30.9 %, turf, and macroalgae) and

2012 (40.5 %, turf algae) in Little Cayman. Differences between turf and macroalgae consistently explained 61% to 79% of the average similarities recorded across the Cayman Islands during the study period. The results clearly show that 2011 was a particular year that introduced significant variation to the benthos community structure, particularly for the island of GCM and CB. Higher values of live coral cover (15–20%) was noted in the deeper and shallower habitats of LC and CB, with no evident trends recorded between the areas with different levels of protection. Lower coral cover was found in the shallow habitats around the GCM, regardless of protection status. There was a clear spatial pattern for macroalgae, showing higher cover in the deeper habitats of LC and CB (50–70%), as compared to the shallow habitats of GCM (34–46%). Higher cover of turf algae was normally associated with the shallower habitats of all three islands, but more so LC and CB. Results from Bio Env analysis clearly showed that both benthic and the fish community assemblages were significant, but weakly correlated (BEST, Rho = 0.26, p = 0.01). Variation of the three combined benthic variables: zoanthids, tunicates, and dead gorgonians better fit with the documented changes in the fish community structure across coasts, islands, habitats, years, and protection status. Additionally, the linear model supported that only the zoanthids, dead gorgonians and the cover of other benthic organisms were significantly correlated with changes in the fish community structure, possibly because they were being used as a food resource. However, the DbRDA plot illustrated that changes in the benthic community structure did not fully explain the observed variation in the fish community structure, suggesting some other metric not studies in this thesis is responsible. Results indicate that the MPA's of the Cayman Islands are playing a central role in increasing the biomass of key herbivores and carnivores over time. Data collected indicate that the benthic community structure was extremely variable between habitats; this factor explaining more variation compared to the level of protection and suggest that the benthic community structure was a poor predictor for explaining the differences of the fish communities associated to MPAs and non-MPA's across the Cayman Islands. This study aimed to assess the status and evaluate the effects of protection on the benthos and their fish assemblages of the marine protected areas in the Cayman Islands after 26 years of being actively enforced. It represents an important step in addressing and understanding the Marine Protected Area's ecological function and performance. It is the intent that the results from this study be used to address the present human usage and increasing pressures on the coral reefs of the Cayman Islands. This includes making recommendations based on results for a new network of MPAs, as the current model has become obsolete, making the MPA's of the Cayman Islands more " fit for purpose" in the 21st century for the people of the Cayman Islands.

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Chapter 1. General Introduction

We exist and live in an epoch of a rapidly changing environment, more so for the coral reefs that exist in the global tropics. These organisms mostly can only function within a small window of environmental parameters such as temperature and water clarity, with the health mostly reliant on the protection from overexploitation by human beings. One such location in the Caribbean region that offers up such underpinning complementary factors to study coral reefs organisms are the Cayman Islands, a British Overseas territory, geographically located in the central NW Caribbean Sea. This British three island archipelago are some of the most isolated of all Caribbean islands, with crystal clear waters due to lack of riverine systems amounting to negligible sediment run-off and have a low population density when compared to other countries in the region (Burton, 1994). Additionally, these islands have had a world-class network of actively enforced Marine Protected Areas in place since 1986, with strict marine no-take Legislation dating back to 1978 protecting coral reefs (Turner *et. al*. (2013).

The decline of coral reefs in the global tropics over the past 40 years have seen the emergence of Marine Protected Areas as a spatial tool to protect and conserve them. Coral reefs are recognized as one of the most biologically diverse and productive ecosystems on earth. They are the also one of the most valuable of marine ecosystems and the lifeline of millions of humans globally that depend on them for the goods and services they provide such as shoreline protection, as a food source, cultural significance, and recreational tourism activities to name a few (Richmont, 1993; Moberg and Folke 1999).

Coral reefs have existed for >240 million years (Veron *et al*., 2009), but are considered one of the most critical and exquisite of marine ecosystems on earth (Crabbe, 2009), and bio-diverse, home to an estimated one third of all described marine species (Reaka-Kudla, 1997, 2001; Veron *et al.,* 2009). With predictions that by 2030, more than 60% of coral reefs globally will be destroyed (Hughes et al., 2003), many countries globally have adapted and put in place protective measures such as Marine Protected Areas (MPAs). The Cayman Islands have had a long history of Marine Protected Areas (MPAs), established in 1986 under the Cayman Islands Marine Conservation Law of 1978. These establishments were further strengthened in 1988 with the addition of No Diving Zones, protection of Nassau grouper (*Epinephelus striatus*) spawning sites, and more recent, Wildlife Interaction Zones to manage the feeding of southern rays (*Dasyatis americana*) at the sand bar and Stingray City locations. To date, this British Overseas Territory still possesses a rich marine environment when compared to the rest of countries in the Caribbean region, conceivably due to >2.5 decades of effective management of their Marine Protected Areas combined with active enforcement of their rules and regulations. Additionally, these islands are the driest and amongst the lowest elevation of all Caribbean islands have negligible run-off due to no riverine systems (Burton, 1994). Commercial fisheries are absent, while artisanal and recreational fisheries exist throughout the islands. The population density is considered

low, with far less anthropogenic impacts than other counties in the region (Creary *et al.,* 2008; Turner *et al*., 2013). These properties, in addition to the small landmasses of the Cayman Islands, make them an appropriate location to conduct coral reef resiliency studies. This thesis will investigate what effect >20 years of active enforcement of Cayman Islands MPAs have had in promoting, fostering and maintaining reef fish populations and coral reef resiliency over spatial and temporal scales across Grand Cayman, Little Cayman, and Cayman Brac between the years 2009 through to 2012. The coral reefs and fish assemblages were assessed within the MPAs and outside of Cayman Islands MPAs in order to document changes in total fish biomass of 48 target reef fish species, considered economically and ecologically important to the Cayman Islands along with coral reef benthos. Coral reef benthos was surveyed using a video transect method (Lam *et al.,* 2006) annually during June through to August. Fish biomass sampling was be carried out annually during January through to March between the hours of 0900 and 1500 hours, at two depths, the shallow terrace reef (10-12 m) and the deep terrace reef (16-18 m). Fish data were collected by underwater visual census (UVC), using belt transects, (Samoilys and Carlos, 2000). Findings were further used to suggest placement of MPAs to enhance the effects and performance of the Cayman Islands coral reefs and fish assemblages that are fit for purpose considering the anthropogenic and natural stressors coral reefs are facing into the 21st century.

1.1 Coral reefs

Reef-building tropical coral reef ecosystems have existed for >240 million years (Veron *et al.*, 2009) and are mostly restricted within the global tropics from ~30° North to 30° South. Notably, their geological structures have been constructed by secreting skeletons of calcium carbonate ($CaCO_3$) using the ocean as a resource. According to estimates by Burke et al., (2011), >850 million people globally live within 100 km of reefs whom most likely derive benefits from goods and services that they provide. Furthermore, ~275 million of those individuals live within 10-30 km of the coast (Burke *et al*., 2011) where food, coastal protection, and livelihoods and dependent on coral reef resources. Burke *et al*., (2011) further stated, of 108 countries and territories studies, most dependent on coral reefs were small islands states located in the Pacific and Caribbean regions. Though difficult to estimate, Smith (1978) had estimated that globally, coral reefs cover 600,000 km^2 to a depth of 30 m, with 26,000 km^2 located in the Caribbean basin (Burke and Maidens, 2004). However, 33 years later, from satellite imagery, Burke *et al.,* (2011) estimated coral reefs to cover ~250,000 km^2 and represent 0.01% of 1% of the marine environment as a whole; however, they are home to ~25% of known species of animals. Coral reefs are not only considered as one of the most diverse ecosystems on earth but also one of the most fragile and critical ecosystems on the planet (Crabbe, 2009). However, as the human population rises exponentially, coral reefs seem to be in an inverse relationship with it, declining at an alarming rate. Most of this decline can be attributed to a change that negatively affects them owing to growing man-made interventions such as pollution, climate change, coastal development overfishing, destructive

fishing practices, nutrient loading, bleaching events, disease, recreational activities and an overuse of its resources (Jackson, 1997; Nyström *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Bellwood *et al.,* 2004; Folke *et al.,* 2004; Hughes *et al.,* 2005; Jackson *et al.,* 2014). These issues and pressures have changed coral reefs over the past fifty years, and more so in the Caribbean basin where a phase shift from a coral-dominated environment has changed to a less desirable macro algal environment (Done, 1992; Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al*., 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al*., 2014).

According to Burke *et al*. (2011), more than 60% of the world's coral reefs are under direct threat from localized pressures such as overfishing, destructive fishing, coastal development, point source pollution or some marine-based pollution and damage. They added that overfishing and destructive fishing practices are the most pervasive of all activities, affecting >55% of coral reefs globally. Additionally, Burke *et al*. (2011) further stated that approximately 75% of coral reefs globally are threatened when combining all local and global threats such as thermal stress. Events such as the die-off of the sea urchin *Diadema antillarium* in the Atlantic basin (Lessios *et al.,* 1984), global phenomena such as ocean acidification (Mora, 2008; Mumby and Steneck, 2008), and other climate-changing effects (Hughes *et al.,* 2003; Lubchenco *et al*., 2003, Hughes *et al.,* 2007) have only served as a catalyst in this downward spiral of coral reefs. With approximately 43 million people in the Caribbean region living <30 km from coral reefs (Burke *et al.,* 2011) coupled with the fact that coral reefs and accompanying fisheries provide food and livelihood to the majority of these individuals, the current situation is alarming. Good and services of coral reefs are often a major component of national product in the global tropics (Costanza *et al*., 1997; Costanza *et al.,* 2014).

1.2 Value of Coral Reefs

It is almost impossible to put a value on coral and its allied organisms because as a resource, humankind keeps finding innovative uses for them, thus constantly increasing their value. According to the estimates of Cesar *et al.* (2002), and Costanza *et al*. (1997), coral reefs in the global tropics provide goods and services worth 30 billion USD annually, which equates to about USD 8,384 per/ha/year. However, Costanza *et al*. (2014) further put the value of coral reefs (globally) in goods and services at USD 352,259 per/ha/year in 2011. In the Caribbean region, Burke and Maidens (2004), estimated a net annual economic value for Caribbean coral reefs in the year 2000 to be in the range of USD 3.1-4.6 billion. Analogously, Costanza *et al*. (1997) put the total cost of goods and services of ecosystems worldwide at USD 33 trillion in 1995, updating that figure in 2011 to 125 trillion USD annually (Costanza *et al.,* (2014), noting the fact that some reefs are worth a lot more than others due to geographic locations where the adjacent population are reliant on those reefs for food and commerce. However, Chaisson (2002) asserts that the value of global ecosystems is inestimable because human existence could not continue if they were lost. A contrarian viewpoint in estimating the value of coral

reef is perhaps, that it is unachievable, given that if humans did not exploit them, we would not have been able to put an estimated value on coral reefs. Besides being on the frontline as the first line of defense against hurricanes and typhoons in the tropics (Villanoy *et al.,* 2012), coral reefs supply millions of people globally with their daily dietary needs of protein (Salvat, 1992). Supporting that assumption, Hughes *et al.* (2003) and Pomeroy *et al.* (2004) estimated that coral reefs deliver more than six million tons of fish per annum mostly to developing nations in the global tropics. Meanwhile, the value of the intangible goods and services provided by coral reefs' has been estimated by Veron *et al.,* (2009) to be between 172 and 375 billion USD a year. Furthermore, Brander (2007) states that the Caribbean region as a whole avails more financial benefits from the recreational usage of coral reefs than any other region globally. Despite their irreplaceable status as storm barriers, tourism economic value and a carbon sink (Moberg and Folke, 1999), including the immensely useful cultural role they play globally in deep-rooted traditions, such as subsistence fishing, they have been coming under severe threats from human influences (Bellwood *et al., 2004*). As a result, their reduced functionality has led to compromised health, raising disturbing questions over their ability to survive under mounting human pressures (Hughes *et al.,* 2003; Bellwood *et al*., 2004; Nyström *et al.,* 2008; Hughes *et al.,* 2010). Despite the pressures exerted by humans on coral reefs over the past 200,000 years, fossil records reinforce the fact that they have persisted for more than 240 million years (Veron *et al.*, 2009) and should continue to persist in some form in the foreseeable future, perhaps on a much smaller scale and extent globally.

1.3 Geography, geological setting and demographics of the Cayman Islands

The Cayman Islands are a three-island British overseas-territory archipelago consisting of Grand Cayman (GCM), Little Cayman (LC) and Cayman Brac (CB). They are centrally located in the north-west Caribbean Sea between 19º 15' and 19º 45' N latitude and 79º 44' and 81º 27' W longitude, between 160 km (CB & LC) and 260 km (GCM) south of Cuba, and 230 km (CB & LC) and 310 km (GCM) west of the island of Jamaica. As oceanic islands, they are situated on the peaks of a submerged ridge, what is known as the Cayman Ridge, that runs westwards from the Sierra Maestra mountain range of Cuba (figure 1).

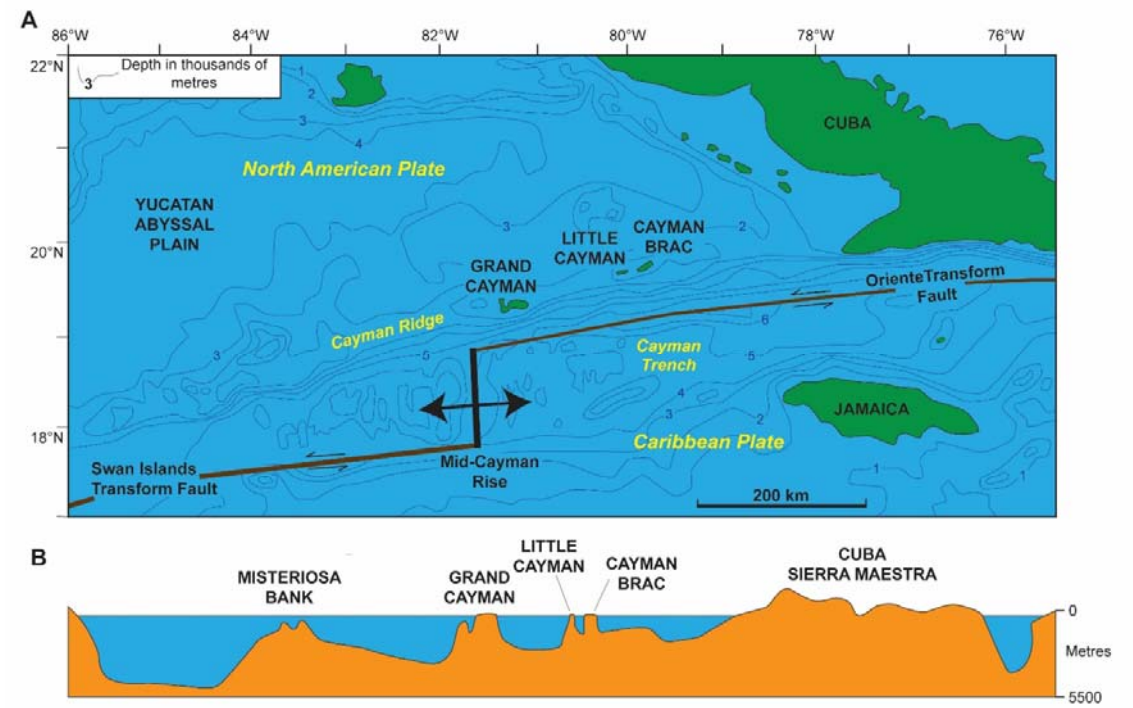


Figure 1. The Cayman Islands tectonic and geographic position; courtesy Dr. Brian Jones, University of Alberta, Canada; https://www.ualberta.ca/science/about-us/contact-us/faculty-directory/brian-jones

They are considered as the most remote of all Caribbean islands, unusually flat and formed entirely from calcareous marine deposits (Davies and Brunt, 1994). This ridge forms the northern margin of the Cayman Trough, located on the south and reaching >7000 m (Rigby & Roberts 1976; MacDonald & Holcombe 1978; Stoddard 1980, Jones 1994; Blanchon 1996). Perfit & Heezen (1978) suggest that the Cayman Ridge was a shallow carbonate reef until the Miocene era after which it began to subside at 6 cm / 1000 years. Horsfield (1975) suggested that all the Cayman Islands were perhaps located on separate fault blocks that were then elevated above the Cayman Ridge. Analogously, Stoddard (1980) thought that all the Cayman Islands move independently of each other, with respect to the sea-level over the past 100,000 years. As of December 2016, the population of the Cayman Islands was 61, 361 (Cayman Islands economic and statistics Office, 2016), with GCM, being the largest and the most populous island (196.8 km²) having 60,413 inhabitants, LC (28.5 km²) and 328 residents, lastly and the easternmost island, CB (38.8 km²) and 1,868 residents.

1.4 Economic and developmental history

The Cayman Islands were considered as "The islands time forgot" owing to their oceanic isolation, including the absence of trade and dependable transport to and from neighboring nations. Additionally, in the absence of fresh water source, it is the aridest of all West-Indian Islands (Burton, 1994). The

Cayman Islands have a long history of Maritime Heritage beginning in the 1700s, with a primary means of a trade by trapping sea turtles and selling their meat as well as other turtle products to neighboring Jamaica and manufactured goods for visiting Mariners (Smith, 1981). The turtle fishery developed into selling to European and North American markets, which resulted in a depletion of turtle stocks and required the islanders to go further afar and capture turtles for this lucrative trade. This was the birth of these islands' maritime legacy, which became the only pillar of the island's economy and supported the well-being of islanders for well over the next century before they eventually collapsed (Smith, 1981). However, in just a few decades, the Cayman Islands evolved into an important tourism and financial hub; tourism began in the early 1960s (Gigliolo, 1976) and the offshore financial center in the 1980s. This rapid developmental success caused major issues for the marine environment, with hotels constructed along the West Bay 7-mile beach peninsula and the dredging of "marl" for construction and infrastructure. Coastal dredging continued until the Government of the Cayman Islands put a moratorium in place in 1996, stipulating that there will be no more dredging within the waters of the Cayman Islands, which continues to exist until now. In the late 1970s to the early 1980s, these islands went through another tourism economic boom due to the evolution of the cruise ships industry, and Grand Cayman became a regular stop, bringing enough tourists onshore to nearly double the local population of ~20,000 residents in the mid-1980's. This cruise ship industry continues to exist today with some six ships carrying as many as 4,000 passengers each visiting the island of Grand Cayman daily.

1.5 Climate

The three Cayman Islands are geographically situated within the north-east trade wind system between 19º 15' and 19º 45' N latitude and 79º 44' and 81º 27' W longitude. They withstand a humid tropical marine climate with distinct seasonal variation (Burton, 1994). Data from the Cayman Islands National Weather Service (www.weather.gov.ky) shows a hot, humid, wet summer season (mid-May to October) as well as a mild winter dry season (November to April)(figure 2.; figure 3). Due to these islands' location in the NW Caribbean Sea, they are far enough north to experience the polar blast of cooler air in the winter months originating off the North American continent which brings in cold fronts and rainfall, with strong winds and rough seas from the north. During the summer months, these islands are also subjected to low-pressure systems that move west-ward, usually developing in the Atlantic, ranging from tropical waves, tropical depressions, and tropical storms. These tropical storms sometimes further manifest in dangerous and damaging tropical cyclones, with heavy rains causing flooding and extremely damaging wind and waves (see Appendix 1.1 for historical record of hurricane / tropical cyclone frequency and intensity for the Cayman Islands). According to Blanchon (1997), when these severe storms affect the Cayman Islands, it is evident that they are the primary agent impacting these islands' marine environment. However, under normal conditions, weather winds are dominated by

moisture loaded North-east Trades, with 71% of observations being made in the 030º-090º sector, and wind speeds during normal conditions being approximately 5 ms^{-1}, (Stoddard 1980).

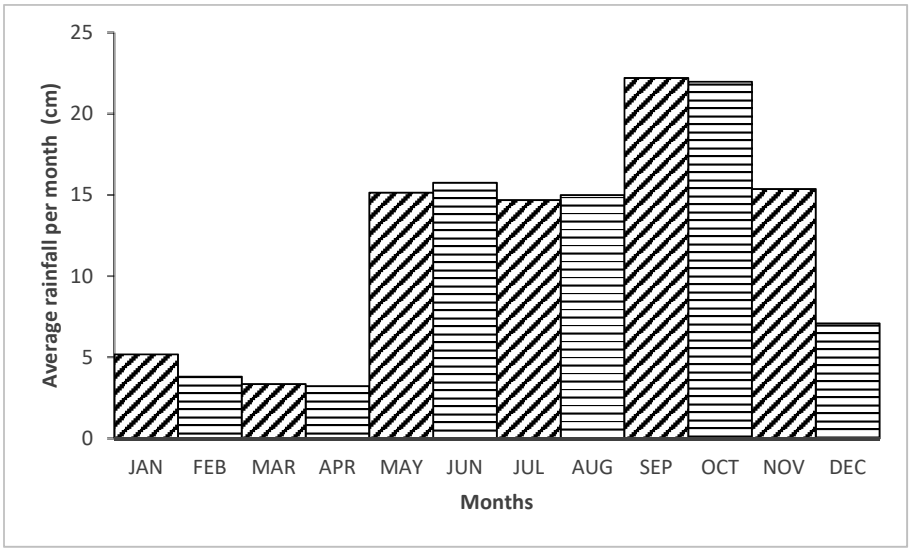


Figure 2. Thirty-year average monthly rainfall totals (cm), courtesy The Cayman Islands National Weather service (www.weather.gov.ky).

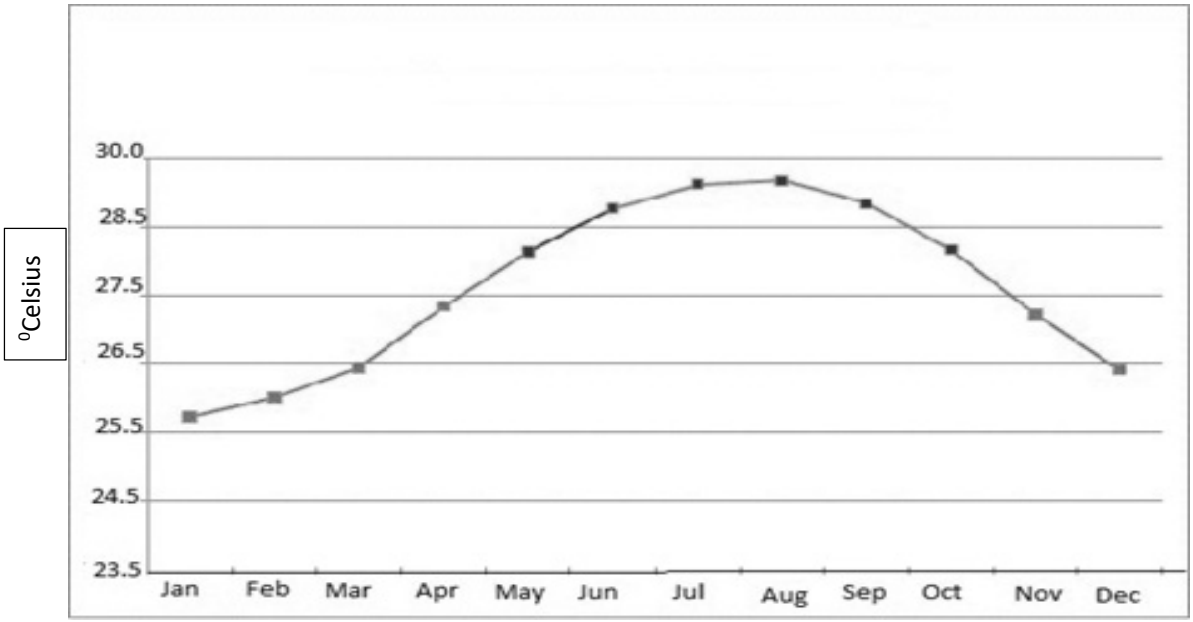


Figure 3. Average monthly temperature (º C) between 1981 and 2010 (37 years), source; The Cayman Islands National Weather service (www.weather.gov.ky).

1.6 Hydrology and Oceanography

The Cayman Islands do not possess any watershed or riverine systems; therefore, they are renowned in Caribbean region for their water clarity, which can exceed >60 m at times (C. McCoy, personal observation). These crystal-clear waters, coupled with an average annual water temperature of 28 ° C (figure 4), make the Cayman Islands appealing as a tourism destination.

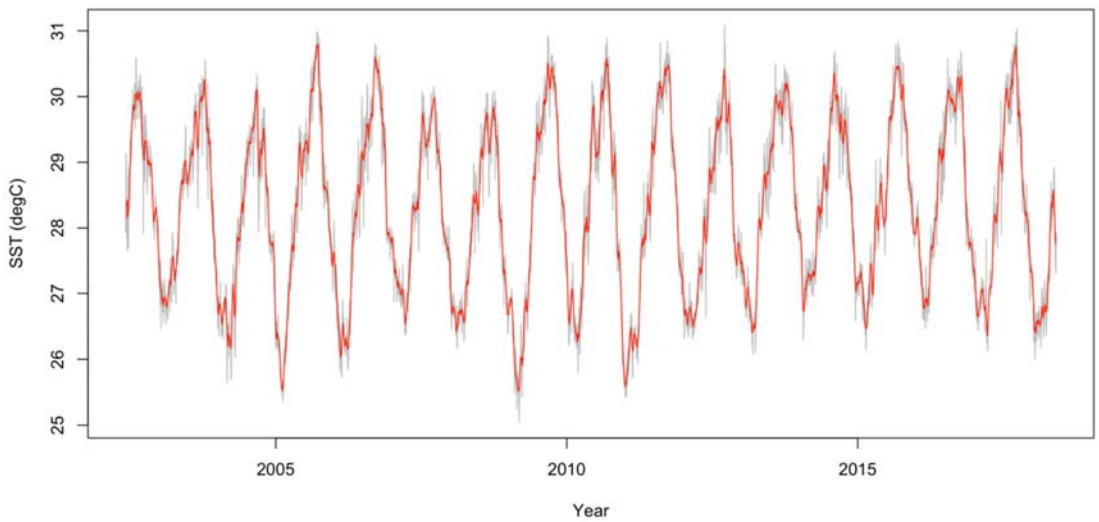


Figure 4. Sea surface temperature (SST) for the Cayman Islands from 2002 to 2018. The grey line depicts the daily average SST, and the red line shows the 14-day moving average, both calculated over 19.6-19.8°N and 79.70-80.15°W. Data courtesy JPL (http://dx.doi.org/10.5067/GHGMR-4FJ04).

According to Burton (1994), the tidal regime of the Cayman Islands comprises of a mixed semi-diurnal tide with an average amplitude of 26 cm. Burton (1994) suggested that with this small amplitude, tidal currents are weak and usually modified by more dominant wind-driven currents. However, localized currents at the eastern and western ends of the islands can exceed 1.5 $ms^{-1,}$ often up to 2 ms^{-1} on occasions(C. McCoy, unpublished data). In 2013 through to 2014, Lagrangian current drifters (40-day tracks) were released every month five days after the full moon at the western Fish Spawning Site in Little Cayman. Drifters released showed a mixed current regime, with some drifters grounding on the island. However, the majority of them exhibited persistent movement south-east towards Jamaica, before returning close to the Cayman Islands after which, they continued towards Cuba, with a total of 5 drifters grounding in the Cuban Isle of Pines area (C. McCoy, unpublished data). Historical oceanic current data showcased a predominantly northwesterly movement of currents (Stoddard, 1980) with velocities recorded on the largest island, Grand Cayman averaging 0.3 ms^{-1} and exceeding 0.35 ms^{-1} for close to 20 percent of the time while being monitored (Darbyshire *et al*., 1976). However, the currents around the Cayman Islands are variable in terms of spatial scales, duration, intensity, velocity, and

stratification. This variability is attributed to the geographic location of the Cayman Islands in addition to the oceanography properties of the Caribbean region in which the generally westerly bound flow from waters entering the Caribbean basin pass through gaps between the Lesser Antilles islands and the Windward and Mona passages, before flowing westward, known as the Caribbean main-stream current. However, this is interrupted from about 75°W due to the seabed topography of the northwest Caribbean being disrupted by the Nicaraguan Rise, the Cayman Ridge, and the Cayman Rise, respectively. Due to the geographic position of the Cayman Islands, they are situated where the Caribbean mainstream current flowing westward. It is then forced through a trough within the basin between Jamaica and the Nicaraguan rise; thereafter, it encounters the deepest depths of the Caribbean basin, and the Cayman Trench, which exceeds 7000 m, merely 8 km to the South of the island of Grand Cayman. All these attributes contribute towards making ocean currents difficult to ascertain, as they are convoluted and inconsistent to a certain degree.

1.8 Coral Reef resiliency

As coral reefs decline due to the growing human activities, there is a growing list of collaborative studies (Hughes *et al.,* 2010; McClanahan *et al.,* 2012; Jackson *et al.,* 2014; Graham *et al.,* 2015; Heron *et al*., 2017 Maynard *et al.,* 2017) documenting their degradation in terms of cover and functionality, which catalyzed the concept of "coral reef resiliency". Subsequently, coral reef scientists, including the scientific community at large, have focused on this concept. However, studies go back decades where scientific investigations have attempted to quantify this by measuring coral reef attributes along with their biological metrics, including their ability to recover after an event or disturbance (Connell 1978; Connell 1997; Vitousek *et al*., 1997; Pearson 1981). Although this term is seemingly redefined with the passage of each decade, coral reefs are facing new threats that erode their health and challenge their ability to cope with detrimental environmental changes. Grimsditch and Salm (2005) defined resilience as the ability of a coral reef system to absorb or recover from disturbance and change while maintaining its functions; for example, the ability of a coral reef to recover from a bleaching event. The most fitting definition describes "coral reef resiliency" as the ability of a coral reef community to return to their original state following a phase of perturbation characterized by significant change and/or mortality whilst maintaining key ecological function and services (Pearson 1981; Nyström *et al*., 2000; Carpenter *et al*., 2001). However, in the wake of ever-changing environmental parameters, including climate change (Hoegh-Guldberg, 1999; Hughes *et al,.* 2010) and ocean acidification (Edmunds *et al.,* 2014), the term "coral reef resistance" has been introduced, redefining it most recently as the ability of a coral reef to resist and recover from recurrent disturbances (Hughes *et al.,* 2007; Hughes *et al.,* 2010; Rogers, 2013; Maynard *et al.,* 2015).

Human beings have long exploited the resources of coral reefs and their associated organisms, primarily for food, medicine, or financial gains. Coral reefs are comparable to the tropical rainforests in that natural changes and exploitation may alter their ecological function. Natural and anthropogenic disturbances such as climate change, coastal development, and overfishing severely compromise coral reef resistance and resilience, thereby disrupting ecological function and lowering resiliency, which usually triggers other damaging events, including coral bleaching and subsequent coral diseases, including algal proliferation (Palumbi *et al*., 2009; Hughes *et. al,*. 2010; Harborne *et al,*. 2017). Odum (1989) defined resistance as the ability of an ecosystem to withstand disturbance without undergoing a phase shift or losing its structure/function, such as a coral colony's capacity of withstanding bleaching and disease mortality. Both these concepts are being tested owing to a wide range of issues in most cases, caused by ever-increasing pressures from human activity (Jackson *et al.,* 2001). Corals in the 21st century need to possess resiliency attributes if they are to survive the stressors that are predicted to be an annual event, such as bleaching by 2020 in the Caribbean basin (Crabbe, 2008) and avoid shifting to an alternate less desirable state. Furthermore, some of the most important resiliency factors, as studied by Bellwood and Hughes, (2001) Nystrom and Folke (2001), McClanahan *et al*. (2002), West and Salm (2003) and Bellwood *et. al*. (2004) (herbivorous fish grazing) such as functional diversity, functional groups, species redundancy, reef connectivity, and recruitment success, including herbivorous grazers (McClanahan *et al.,* 2006) will determine whether coral reefs will be able to survive after disturbances and into the next epoch.

1.9 Caribbean coral reefs

According to Smith (1978), coral reefs cover 600,000 km^2 to a depth of 30 m, with 14% being located in the Caribbean basin. Brian (1992) estimated that approximately 84,000 km^2 of coral reefs are distributed throughout the Caribbean region. However, according to the global estimates of Burke *et al*. (2011), of250,000 km^2, this amounts to ~35,000 km^2 for the Caribbean region, signifying a big disparity in estimates, however as noted, Burke et al., (2011) calculations were from satellite imagery which gives a plan view estimate at best. Starting from the late 1970s, coral cover on coral reefs declined from an average cover in the Caribbean of ~50% to just 10% in the early 2000s, as reported by Gardner *et al.* (2003). Many different factors have contributed to this decline, including destructive hurricanes (Woodley *et al.,* 1981; Woodley *et al.,* 1989; Rogers *et al.,* 1989; Woodley, 1992; Gardner *et al.,* 2005). These include the die-off of a keystone herbivore, *Diadema antillarium* (Lessios, 1984), white-band disease of the *Acroporid* corals (Gladfelter, 1982), over-fishing of herbivorous fish stocks (Jackson, 1997; Jackson *et al,*. 2001; Jackson *et al,*. 2014), and ocean acidification (Edmunds *et al.,* 2014), among several others. However, despite the ever-increasing demands put on reefs along with a continuous barrage of impediments that affect coral reefs negatively, such as bleaching and disease outbreaks (Carpenter *et al.,* 2008; Bruckner and Hill, 2009; Miller *et al.,* 2009; Weil and Cróquer, 2009; Hooidonk

et al,. 2012), the Darwinian theory of 'survival of the fittest' appears to hold true for coral reefs, as mounting evidence suggest that corals that do manage to survive seemingly have greater resilience (McClanahan *et al*., 2009). Caribbean reefs are considered species poor and lack functional redundancy when compared to the Indo-Pacific region (Bellwood and Hughes, 2001), making them more susceptible to anthropogenic impacts (Gardner *et al*., 2003). Additionally, Nybakken (2001) categorized Caribbean reefs as much less diverse that Indo-Pacific coral reefs, containing only a small fraction of the species being traced there. For this reason, Bellwood *et al*. (2004) describe Caribbean reefs as "functionally compromised assemblages", making them more vulnerable to human impacts. He went on to add that they lack functional groups within ecosystems, noting that coral reef resiliency strongly depends on a collection of species performing similar functions within the ecosystem. However, corals in the region have encountered a gamut of natural and anthropogenic impacts over the past century; perhaps, only the ones that have adapted to those repeated impacts have survived. Against this backdrop, Caribbean coral reefs harbor some of the most resilient corals globally as they have persisted in the wake of the global coral reef crisis which has proven devastating for other geographic locations including the Great Barrier Reef and the Indian Ocean reefs.

1.10 Coral reefs of the Cayman Islands

The structures of Caymanian coral reefs are principally constituted by 41.03 km^2 of "spur and groove" formations across the 3 Cayman Islands. A geomorphic feature, the coral formations "spurs" typically have a high vertical relief relative to substrate separated by "grooves" which vary in width and usually covered by sand or hard-bottom. They typically are perpendicular to the shoreline, fore reef, and shelf edge. Grand Cayman (GCM) has 20.85 km^2, Little Cayman (LC) 8.28 km^2 and Cayman Brac (CB) 11.9$km^{2,}$ of this habitat type (figure 5.). However, they differ greatly in topographical rugosity based on the exposure of the coast, including the width of the grooves, with the more sheltered coast having less vertical relief. The southeasterly approach of storms and fair-weather wave fields' results in three margin types: high energy exposed-windward eastern and southern coast; a semi-exposed, moderate energy north coastline; and a low energy leeward western coastline, found only in GCM. These islands have two very distinct reef terraces: the shallow terrace reef (5— 12 meters) associated with two environments, lagoons and a fringing-reef complex, (predominantly GCM and LC), and a deep terrace reef (16—25 meters). Thereafter plunging vertically to abyssal depths, with the exception of Bloody Bay in LC, which is a small < 4km section of reef where the deep terrace is missing and the shallow terrace extends out to the deep terrace, before plummeting vertically to abyssal depths. These two terraces, according to Blanchon and Jones (1995), are attributed to the rise in sea levels during the Holocene epoch. The reefs of the Cayman Islands are dominated by submarine topography, much like other islands within the Caribbean (Rigby and Roberts, 1976; Roberts, 1977; Logan, 1981; Roberts, 1983; Roberts, 1988; Fenner, 1993; Roberts, 1994; Logan, 1994; Blanchon, 1995; McCoy, 2004). All

three islands have a narrow reef-shelf measuring 1.5 km maximum in width and are as narrow as 200 m at some locations; the total shelf area for GCM, LC and CB are 49.4 km^2, 18.81 km^2 and CB 20.72 km^2 respectively (figue 5). The coral community structure is dominated by massive corals such as *Orbicella annularis*, *Orbicella faveolata*, *Montastraea cavernosa,* and *Orbicella franksi* on the deep terrace reefs. Other abundant species found around the Cayman Islands include *Siderastrea siderea*, *Colpophyllia natans* and *Diploria strigosa*. Octocoral communities comprised of large colonies of *Pseudoplexaura porosa*, *Pseudoterogorgia americana,* and *Eunicea* spp., among others. Tubular, barrel and encrusting sponges are common, varying in size and form, depending on depth and coast. A total of 48 of the known 65 species of corals in the Caribbean are found in the Cayman Islands (C. McCoy, unpublished data). Fenner (1993), found a total of 39 species in the Jackson's Point area of the Marine Park in Little Cayman, However, and Logan (1994) in the same area found 16 taxa in six 10 m transects (see chapter 2 for more information).

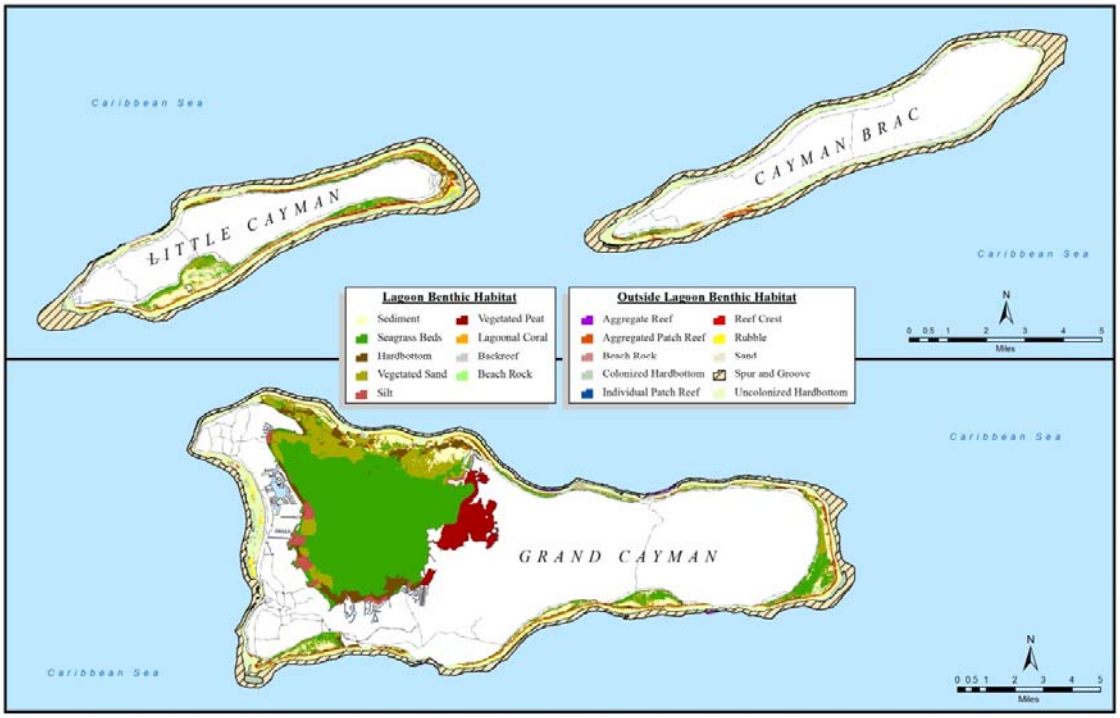


Figure 5. Benthic map of the Cayman Islands; Grand Cayman, Little Cayman and Cayman Brac illustrating their various marine habitat and locations. Source: Dept. of Environment, Cayman Islands Government.

The main benthos category in the Cayman Islands is macroalgae (Gall 2009; Barton 2010; Bruckner and Bruckner 2010; Campbell 2010; Looker 2011; Hillyer 2011; Warrender, 2013; Price, 2015; Sannassy-Pilly, 2016; Sibley 2017). However the coral cover varies, more so with depth and coast, with the highest coral cover recorded located in the south MPA of the island of Little Cayman (site LCS03, figure 2.2, chapter 2).

1.10.1 Bleaching events affecting Caymanian coral reefs

Coral bleaching was first observed in the Cayman Islands in 1983 (Smith and Ghiold, 1989, Turner *et al*., 2013). Though there has been numerous bleaching events effecting Caymanian reefs (1983, 1987, 1991, 1994, 1998, 2003, 2005, 2009; see chapter 3 for full details and records), the most recent and severe episodes occurred in 1998 and 2009 (Turner *et al*., 2013). The 1998 mass bleaching resulted in a 10% absolute loss in coral cover in Grand Cayman (25% coral cover reduced to 15%; C. McCoy unpublished data). In Little Cayman, McCoy (2004), recorded a loss of 50% absolute coral cover at some sites with the Bloody Bay-Jackson Point Marine Park (52% coral cover reduced to (26%). In addition, a regional bleaching event occurred in 2005 (Wilkinson and Souter, 2005; Turner *et al.*, 2013); however no measurable mortality was recorded for Caymanian reefs (C. McCoy and P. Bush, unpublished data). In October 2009, Caymanian reefs underwent a localized mass coral bleaching event due to a deep hot water gyre that originated from the southern shelf of the island of Cuba. This event mainly affected the island of Grand Cayman, where >90% of corals bleached (C. McCoy, unpublished data), however, this event was less severe for the sister islands of Little Cayman and Cayman Brac (van Hooidonk *et al.,* 2012), which were geographically located on the periphery of the gyre. The longest and most intense global heat wave of 2014-2017 (Skirving et al., 2019) as defined by Hobday *et al.,* (2016), devastated coral reefs globally (Eakin et al., 2017; Eric *et al*., 2017), strangely did not affect Caymanian coral reefs (C. McCoy and P. Bush, unpublished data).

1.11 Marine Protected Areas

Marine Protected Areas (MPAs) globally are credited for increasing the resiliency of coral reefs by reducing anthropogenic impacts on a local scale on coral reefs, increasing biomass, size classes, diversity and abundance, which further nurtures a higher reproductive output complementing ecosystem support maintenance (Gell & Roberts, 2002; Grimsditch & Salm, 2005; McCoy *et al.,* 2010; Drommard *et al,*. 2011). Additionally, most are implemented with successful outcomes of increased fisheries biomass, size, density and species richness (Lester *et al*., 2009; Pollnac *et al.,* 2010; McCoy *et al.,* 2010). Conversely, Selig and Bruno (2010) did a meta-analysis of 310 MPAs looking at changes in coral cover of protected areas vs. non-protected areas and found that there were no measurable changes in mean coral cover for reefs located within MPAs over 38 years for any region globally. According to Gell and Roberts (2002), the success depends on its geographic location, size of MPA, level of protection, proximity to adjacent MPAs and most importantly, its management, sharing Hargreaves-Allen et al., (2011) viewpoint that MPA performance could be greatly enhanced by better design, including targeted management activities in the context of integrated coastal zone management.

Laffoley (2008) defined a Marine Protected Area (MPA) as "a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural value." However, the most commonly cited definition is given by the International Union for Conservation of Nature (IUCN), which specifies it as: *"any area of inter-tidal or sub-tidal terrain, together with its overlying water and associated flora, fauna, historical, or cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment."* (Kelleher and Kenchington, 1992) MPAs are being increasingly used to protect coral reefs along with their associated organisms from over-exploitation, but also as a means of preserving biodiversity and maintaining key functional ecology in addition to the biological processes that are beneficial to humanity. De Silva *et al*. (1985) listed 430 MPAs globally and by the year 1995, Kelleher *et al.* (1995) reported 1,306 MPAs, with a median size of 1,584 hectares (15.8 km^2). Correspondingly, Kelleher *et al.* (1995) suggested that they were becoming the new staple of coastal countries in the global tropics, with the majority of these countries implementing an MPA in some form or fashion. However, according to the United Nations Environmental Program (UNEP), there has been a 10-fold increase in MPAs globally since the year 2000. Currently, MPAs cover 23 million km^2 (6.5%) of the ocean, increasing from 2 million km^2 (0.7%) just eight years ago, with a coverage of the ten largest ones exceeding 50%, driven mostly by an expansion of the currently established MPAs (https://www.unep-wcmc.org/). However, of the approximately 5000 coastal MPAs established globally, less than 10% of them are designated as strict "no take" Marine reserves (http://www.protectplanetocean.org), thus leaving more than 90% of them exposed to some form of "managed extraction" by humans or perhaps for different purposes such as food security and the livelihood of fishers. This exponential growth of MPAs was possibly attributed to the fact that they are suggested to increase resiliency by restricting localized anthropogenic pressures, and ensuring a safe refuge for fish by increasing their size, density, and biomass whilst promoting increased fecundity, aiding reproductive success, preserving genetic diversity helping maintain marine ecosystems and in some instances, facilitating their restoration (Polunin & Roberts, 1993; Côté *et al.*, 2001; Roberts *et al.*, 2001; Gell &Roberts, 2002; Halpern *et al.*, 2003; Grimsditch & Salm, 2005; Newman *et al.*, 2006; McCoy *et al.,* 2010). However, most MPAs lack the financial resources and enforcement that are necessary to manage them for those intended purposes effectively. In a study conducted by Burke & Maidens (2004), of the 285 known MPAs established at the time in the Caribbean region, merely 6 % had the resources to effectively manage them, thus rendering > 90% of them vulnerable to continued exploitation, deemed as "paper parks" Bustamante *et al.* (2014) reported similar findings and pointed out that only a quarter of MPAs reported enforcement staff, and there was a heavy reliance on other means of surveillance as well as enforcement such as coast guard, marine police and armed forces. However, the success and failure of MPAs are sometimes predicated on multivariate social interactions with stakeholders involvement, facilitating the compliance of rules and regulations

as opposed to the level of enforcement levied by governments (Pollnac *et al.,* 2010), which can have more effective management outcome, where MPAs meet their intended objectives.

1.12 Marine Protected Areas of Cayman Islands

The Cayman Islands were one of the few countries worldwide to have recognized the value of their marine resources at an early stage of their history. Accordingly, they put laws and legislation in place in order to safeguard these invaluable assets. The Marine Conservation Law of 1978 laid down the foundation of the MPA system that the islands have to date. The law set size and catch for marine life, set open and close seasons, regulated the use of spear-guns and fishing nets. Most importantly, it banned the collection of all forms of sessile marine life (dead or alive) and the discharge of raw sewage within its territorial waters. In addition, the legislation controlled activities, such as anchoring and fishing, whilst facilitating the protection of sea turtles. It also saw the creation of the Marine Conservation Board; an independent organization empowered the Cayman government to make additional regulations prescribing Marine Parks, restricted areas, change or set new catch size, limits and closed seasons. Most pertinently, the Law of 1978 protected all corals and made it an offense to damage corals in any manner, regardless of whether they are located in MPAs. It also controlled vessels anchoring, curtailing them only to designated anchoring areas (sacrificial, i.e. Port anchorages, and sanded areas) if the vessel was less than 18 m, and to do so in a manner that does not damage any marine life.

In August 1986, the MPAs of the Cayman Islands was established across the three Cayman Islands under the Marine Conservation (Marine Parks) Regulations as a response to the rapid coastal development experienced by the islands, most notably, Grand Cayman, along with the West Bay 7-mile beach peninsula. Three distinct zones were created to protect and conserve marine life within the coastal waters of the Cayman Islands (figure 6.); in addition, heavy fines of up to $500,000 Cayman Islands dollars and up to 1 year imprisonment, including confiscation of equipment involved were levied for breach of the Law (figure 6.):

a) Marine Park: created primarily to protect the coral reefs and their associated organisms.
b) Replenishment Zone: created with an aim to protect breeding and nursery habitats, particularly the queen conch (*Strombus gigas*) and Caribbean spiny lobster (*Panulirus argus*) fishery.
c) The Environmental Zone: created specifically to protect the fringing mangroves on the Eastern locality of the Central Mangrove wetland, North Sound of Grand Cayman (no in-water activities).

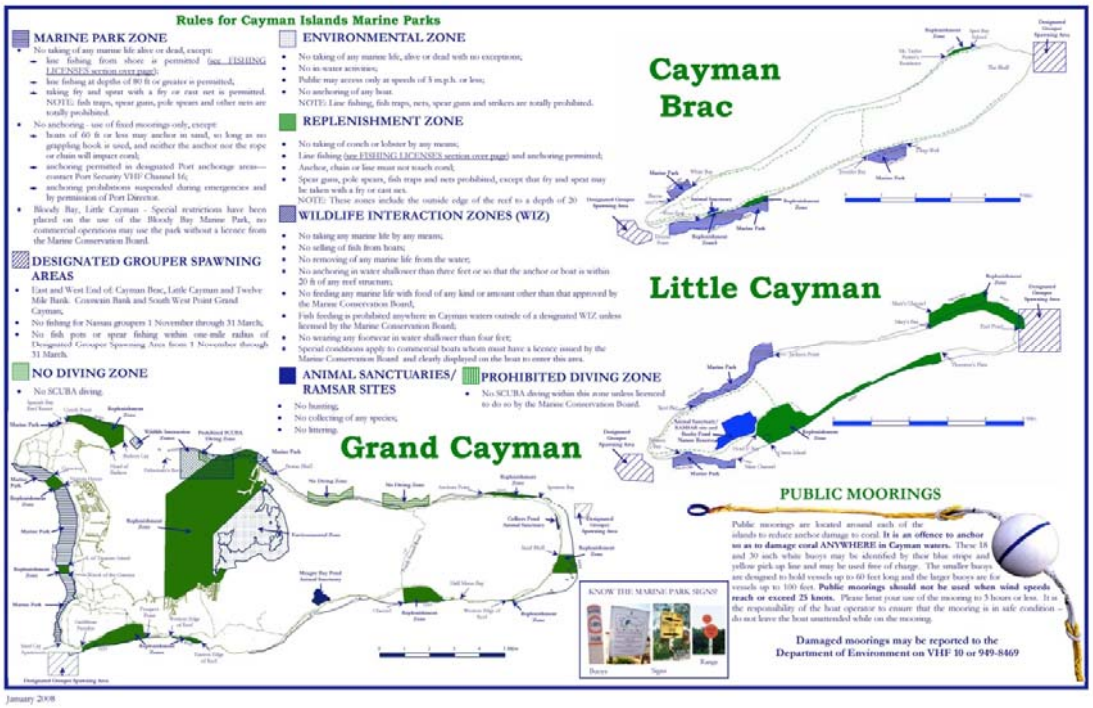


Figure 6. Map of Cayman Islands Marine Protected areas, the different types, general rules and location. Source: Department of Environment, Cayman Islands Government.

The MPA in GCM is located on the leeward western shore of that island (figure 6; chapter 2, Figure 2.2) encompassing 9.2 km² of the coastal shelf, which comprises 5.72% of the total shelf area of GCM. However, upon the inclusion of Replenishment and Environmental zones (additional managed areas), ~18% of GCM was afforded some degree of protection. Little Cayman has two MPAs, one each on the north and the south totaling 2.78 km², representing 10.63% of the island's shelf area. Meanwhile, Cayman Brac has three MPAs, one on the north and two on the south coast of that island, encompassing a total of 3.27 km², which comprises 15.37% of that islands shelf area.

In November 2016, the National Conservation Bill was passed after ten years of revisions and public consultation. This comprehensive piece of legislation replaced all prior laws while galvanizing the rules and regulations governing the MPAs of the Cayman Islands. It added two new zones:

a) Designated Grouper Spawning area (Fish spawning aggregation site)
b) Wildlife Interaction Zone (A locality where tourist go to feed southern stingrays)

This new legislation strengthened the Marine Conservation Laws putting strict liability (full legal responsibility, whether accidental or intentional) on any perpetrator who contravenes any Marine Conservation Laws while mandating Environmental Impact Assessment for all major coastal developmental activities.

Fishing Pressure and Regulations in the Cayman Islands

Traditionally, Caymanian fishers relied on fishing as a food source using methods such as cast netting, fish traps, including hook and line (Burgess *et al.,* 1994). With no obligation or legislation to report fishery landings in the Cayman Islands, it is largely unregulated. Historically, fin fisheries were always subsistence or small-scale artisanal (Harper, *et at*., 2009). However, according to Henshall (2009) and Mier *et al*., (2011), substantial recreational and artisanal fishing does occur. Furthermore, fishers are allowed to fish within marine protected areas, as long as they fish from the shoreline and beyond the 24 m depth contour. Although local fishers perceive sport fishing and recreational fishing as sustainable, Henshall (2009) reported catches of 11,140 fish over a one month period, of which 87% were reef fish species, including important herbivorous species. Meir *et al*., (2011) report mirrored those findings, reporting 14,968 fish caught during one month, of which 88% were reef fish species. This is in agreement with Burgess *et al*., (1994) assessment that the single largest potential threat to reef fish species in the Cayman Islands is overfishing. The only single species of fish that is regulated via legislation is the Nassau Grouper (*Epinepheleus striatus*) , which has a closed season of 1st December through to 30th April annually. During open season, five per person or five per boat, whichever is less can be taken per day. Only Nassau Grouper between 40 cm and 60 cm (inclusive) may be taken. Additionally, no one may take, purchase, receive, permit or possess Nassau Grouper from the waters of the Cayman Islands during the closed season.

1.13 Aims and objectives

The Cayman Islands have a long history of actively enforced MPAs. This prestigious status is flanked by factors such as negligible terrestrial runoff due to no riverine or watershed systems with one of the lowest population densities in the region. Furthermore, they are considered as one of "Hot spots" in the Caribbean with abundant healthy coral reefs and fish assemblages.

Although there have been multiple studies concerning the coral reef benthos and fish assemblages over the past few decades (Fenner, 1993; Manfrino *et. al.,* 2003; McCoy, 2004; Gall, 2009; Barton, 2010; Campbell, 2010; Looker, 2011; Hillyer, 2011; Warrender, 2013; Cloake, 2015; Price, 2015; Sannassy-Pilly, 2016; Sibley and Fish assemblages (Pattengill-Semmens and Semmens, 2001; Henshall, 2009; McCoy *et al.,* 2010; Drommard *et. al.,* 2011; Marlow, 2012; Balsalobre, 2013; Manfrino *et. al.,* 2013; Oliver, 2014; Hall, 2014; Ward, 2015; Sibley, 2017) among others, very few studies have engaged on a spatial and temporal scale in order to address the performance of Cayman Islands' MPAs. Prior studies offered a "snapshot" picture of the status of the coral reefs, fish assemblages of the Cayman Islands, and the performance of these MPAs.

Because coral reef and their associated fish assemblages are inherently variable, studies over space and time are necessary to account for natural perturbations, to test the real effect of protection that is necessary after implementation of MPAs to prove success or failure of any MPA. In the Cayman

Islands, this haphazard pattern of investigations, coupled with the lack of baseline data collected before the MPAs were created in summer 1986, has created a knowledge gap that warrants a comprehensive analysis to ascertain whether they are still fit for that purpose. As a conservation tool, the MPAs of Grand Cayman was implemented out of the then governments' concerns over the rapid and uncontrollable development taking place along the 7-mile beach, West Bay peninsula. In terms of the MPAs established in LC, the placement selection signified an effort to protect the Bloody Bay / Jackson Point reef area. This small section of coral reef on the Southwestern part of the island local people thought was worthy of protection as it was particularly known for sheltering healthy coral reefs and thriving fish stocks (P. Bush, personal communication). There were no initial plans for the island of CB; however, when its residents became aware of Marine Parks on the other islands, they too wanted to get included in the National MPA system (P. Bush, personal communication). Advice for placement was ascertained, with residents wanting to protect areas that were thought to be depleted of fish stocks to restore it to their prior state (G. Ebanks-Petrie, personal communication).

Additionally, since their establishment, the coral reefs of the Cayman Islands have endured multiple hurricane hits (see Appendix 1.1), and coral bleaching events (see chapter 3, section 3.1.3), including subsequent coral disease outbreaks and recreational usage pressures from an increasing stream of visitors. In 1986, as many as 437,031 individuals visited the Cayman Islands; this number soared to 1,829,042 in 2012, representing a four-fold increase (data courtesy Cayman Islands Economics and Statistics Office). Furthermore, the resident population of the Cayman Islands increased from 21,325 to 56,732, which amounted to more than doubling the population and when viewed in entirety, more than five times the amount of human population that the MPAs of the Cayman Islands were originally designed to accommodate. However, the coral reefs and associated reef fish assemblages of the Cayman Islands have persevered; they are still considered as one of the healthiest coral reefs in the Caribbean region, including a trophic fish structure system that continues to be considered intact. In the Cayman Islands, though the MPAs were originally established to mitigate against coastal development (Ebanks and Bush, 1990), they have succeeded in increasing coral size classes (Barton, 2010), more coral recruits (Looker, 2011), increasing coral cover/reef recovery (Manfrino *et al*., 2013; Price, 2015; Sannassy-Pilly, 2016), including the recovery from bleaching (McCoy, unpublished data). Additionally, Cayman Islands MPAs have demonstrated increasing fish biomass and size classes (McCoy *et al.,* 2010; Drommard *et al,*. 2011, Ward, 2015), herbivore density and biomass (McCoy *et. al,*. 2010; Hall, 2014; Hughes, 2017), carnivore density (Oliver, 2014), including reserve effect (McCoy *et al.,* 2010; Drommard *et al,*. 2011, Ward, 2015). Much pressure has been put on scientists to study coral reef ecosystems in order to understand better what metrics confer coral reef resiliency with a view to either reverse or halt the worldwide decline in coral reefs decline, more so in the Caribbean region by preventing them from shifting from a coral-dominated state to an algal-dominated state (Done 1992; Goreau, 1992; White *et al*., 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al*., 2003;

Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014). There are much debate and a knowledge gap about the underlying mechanisms that confer coral reef resilience and how MPAs may or may not enhance resiliency in the face of extreme over-fishing and climate change, which pose the gravest threats to the existence of coral reefs now, as well as in the future.

1.14 Synopsis of Thesis

We exist in an epoch with widespread concerns about the survival of coral reefs (Bellwood et, al., 2004; Hughes et, al., 2010), concerns about compromised health (Hughes, 1994; Gardner *et al.,* 2003; Mora, 2008), including the perils of overfishing (Hughes, 1994; Roberts, 1995; Chabanet *et al.*, 1997; Jackson *et al.,* 2001; Jackson *et al.* 1997; Jackson *et al.* 2014) with Marine Protected Areas (MPAs) increasingly implemented in an effort to save coral reefs by focusing on what constitutes and promotes healthy coral reefs ecosystems. MPAs are usually implemented with specific purposes that mitigate against present threats at that particular time while managing the resources with a precise human population living adjacently that exploit them. Human population increases exponentially, however coral reefs and its associated organisms do not (Baum *et al*., 2015). This mismatch often leads to increasing pressures on a limited and finite resource. It further places increasing demand on coral reefs ecosystems and organisms, without any further mitigating or management changes that would increase their plasticity whereby dampening the added negative effects and increasing the resiliency in a world of increasing anthropogenic and natural events that inhibit coral reef resiliency. It has been more than a quarter of a century since the Marine Protected areas of the Cayman Islands have been implemented with no change to their size, geographic position or management. Contrary, the population has increased three-fold, with marine-based tourism evolving as one of the two main pillars of the Cayman Islands economy, the other being the Financial Industry.

The current thesis aims to address those (science-based) knowledge gaps of the benthos and coral assemblages of the Cayman Islands over space and time between the years 2009 through to 2012. It will review the performance of the Marine Protected Areas (MPAs) in an endeavor to evaluate their effectiveness on the coral reefs and associated fish assemblages and to ascertain whether they are still fit for that purpose. Furthermore, it will try to decipher the correlated variables of the benthos that possibly contribute to fostering healthy fish assemblages in the Cayman Islands. Data and research findings will be used to make recommendations for a future network of new MPAs that are optimally placed geographically to confer coral reef resiliency well into the 21st century in the Cayman Islands. I hope that this Cayman model can be used in other small island nations within the Caribbean region to facilitate the decision-making processes on the most desirable placement of MPAs to optimize coral reef resiliency. The four main chapters comprising this thesis aim to contribute to the understanding of management needs to address Marine Protected Areas in the Cayman Islands, considering the nations increasing population and human pressure on its marine resources. Based on the results of this thesis,

suggestions for an enhanced MPA system for the Cayman Islands will be put forward for consideration. These new enhanced MPAs for the Cayman Islands will be drafted in 2 different forms.

The first will be based on a combination of results of this thesis and input sourced from resource users, including the local recreational and artisanal fishing community. The second alternate version will be recommendations based purely on applied research results that were derived from this thesis specifying a geographic location for healthiest habitats, distances to adjacent MPAs, reserve effect, the spillover of fish from MPAs to adjacent non-MPAs and the sustainable use of the marine resources of the Cayman Islands.

Chapter 2. Coral reef structure, coastal types and reef fish assemblages around the Cayman Islands

Abstract

The Cayman Islands are a UK Overseas Territory located centrally in the Caribbean (Grand Cayman 19° 20′ 0″ N, 81° 13′ 0″ W; Little Cayman 19° 41′ 0″ N, 80° 02′ 0″ W; Cayman Brac 19° 43′ 0″ N, 79° 48′ 0″ W; Figure. 1), with robust financial and tourism sectors. Their coral reefs boast a rich marine environment, benefiting from over three decades of world-class in situ conservation through the active enforcement of zoned Marine Protected Areas (MPAs). Additionally, they have had legislation in place to protect their coral reefs since 1978. While the Marine Protected Areas (MPAs) of the Cayman Islands have been in place since 1986, and are considered some of the most protected coral reefs in the Caribbean region, a limited number of studies have been carried out on their coral reef benthos and reef fish assemblages to describe them in detail. All three islands have a narrow, reef-shelf characteristic for isolated oceanic islands in the Caribbean region measuring 2 km maximum in width and slender as >0.5 km at some locations before reaching abyssal depths. The structure of their coral reefs principally constituted of "spur and groove" formations, greatly differing in reef development types and topographical rugosity according to the exposure of their coast. In this chapter, every aspect of each of the three Cayman Islands, their reef profiles, habitats, coral, and fish assemblages are described. The main coastal profiles and habitats found from the shoreline to the deep terrace reef found in each island are sketched to scale and displayed in this chapter. The island of Grand Cayman (GCM) is the largest of the three Cayman Islands, with a land mass of 196.8 km² a shelf area of 161.4 km^2, and 23.3 km^2 of spur and groove coral reefs. Little Cayman (LC), has a land mass of 28.5 km², a shelf area of 26.1 km^2 and Cayman Brac (CB) with a land mass of 38.8 km² and a shelf area of 21.2 km^2, each with 9.1 km^2 and 12 km^2 of spur and groove respectively. Similar to most other islands in the Caribbean region, the Cayman Islands coral reef profiles illustrate that two significant reef types surround them. A shallow wave dominated fringing reef and a deeper reef that circles each island, with two seaward facing reef terraces; the shallow terrace reef and the deep terrace reef. Differences in the size of each island, their orientation and exposure to prevailing winds and wave action have manifested itself in reef development and associated fish assemblages, with scarids being the dominant fish family across islands. Other respective fish biomass family varied according to coast and depth.

Aim

This chapter is in its entirety completely descriptive of the coral reefs and fish assemblages in and around the 3 Cayman Islands; Grand Cayman, Little Cayman, and Cayman Brac. It will also include a description of methods used for data collection and data analysis. An important aspect of understanding differences reef types, reef topography, habitats and their associated fish assemblages around islands and between islands is knowing the differences in coastal types and their exposure on spatial scales. Though the coral reefs structures of the Cayman Islands are considered highly developed when compared to other Caribbean islands, the shelf can be considered similar to the rest of the islands in the region. Past attempts to describe coral reef structures and their associated fish assemblages have concentrated on the larger island of Grand Cayman, mostly the exposed southern

margin and western leeward coast of that island. Each of the 3 Cayman Islands varies in shape, size, and orientation, giving various degrees of exposure and reef development profiles. The main aim of this chapter is to accurately display all of the different coastal profiles that are found in each of the Cayman Islands from the shoreline to the deep terrace reefs. This will include scaled three-dimensional artistic sketches. Coral reef benthos composition and their reef fish assemblages are described as a precursor to aid explaining the findings and differences in reef composition, fish assemblages, and their association for chapters 3 through to chapter 6. All survey methods used, including experimental design, and site locations, will also be detailed and explained in this chapter.

2.1 Introduction

The islands of Cayman Brac and Little Cayman are oval-shaped, with the eastern and western ends of their land masses more pointed than the largest island, Grand Cayman. Their orientation lies in a northeast/southwest direction contrary to Grand Cayman, which is orientated east/west (Figure 2.1). The south-easterly approach of storms and the fair-weather easterly wave fields for their geographic positions results in two margin types for Cayman Brac and Little Cayman: a very high energy southern exposed-wind ward margin and a moderately-leeward northern aspect. The largest island, Grand Cayman, is orientated east/west and is more rectangular shaped. It results in four exposure types: an exposed southern margin, a fully exposed eastern margin, a semi-exposed northern margin and a low energy leeward western margin, which is only found on the island of Grand Cayman (Figure. 2.2). (see Table 2.2, Appendix 2.1 and Appendix 2.2 for all classification that comprises each island including metrics on habitat sizes and percentages that comprises each island).

In GCM, the Marine Protected Area (MPA) is located on the western leeward area of the island (Figure. 2.2) covering 9.2 km² of the coastal shelf which is 5.72% of the total shelf area of GCM. LC has 2 MPA's, one in the north and one in the south (Figure. 2.2) totaling 2.78 km², 10.63% of that islands shelf area. CB has three MPA's; one located in the north and two in the south, covering a total of 3.27 km², which is 15.37% of the islands shelf area.

The Cayman Islands have been studied sporadically for over thirty years. However, comprehensive studies that address the various habitats and fish assemblages across the Cayman Islands spatially and temporally do not currently exist. Moreover, there are no studies to date that address, in detail, the various aspects of each island, or the profiles of the coral reefs along each aspect. Most published literature has addressed the Islands of Grand Cayman (Roberts 1971, 1974, 1976**,** 1977**,** 1983, 1994; Rigby and Roberts, 1976; Swain and Hull, 1977; Burgess *et. al* 1994; McCoy et al 2010; Pattengill-Semmens & Semmens 2003) and Little Cayman (Fenner, 1993; Drommard *et al* 2011; Manfrino *et al.*

, 2003, 2013), mostly generalising each aspect and providing a broad description of their exposure aspect and habitats.

In this chapter, the various coral reef structures, reef profiles and their associated fish family assemblages of each island and aspect will be graphically displayed for the three Cayman Islands of Grand Cayman, Cayman Brac, and Little Cayman. This includes various marine habitats found around each island from the shoreline to the deep terrace reef that slopes into abyssal depths.

2.3 Cayman Islands reefs

The Cayman Islands have extensive and well-developed coral reef structures with 2 major reef terraces, dominated by spur and groove and a narrow near-shore (<1 km) shallow fringing reef, absent in some instances. Where found, the latter is a narrow band, once dominated by the high surge and wave tolerant corals such as the Acroporids as well as other massive boulder-type scleractinian corals such as *Siderastrea sidera,* diplorids and the hydrocoral, *Millepora*, the former is found mostly on the exposed windward south coast and the latter on the semi-exposed northern and western coastlines. The shallow terrace reef ranges in depth from 5m to 12 m, then extends seaward, and in some instances forming buttresses that extend out to the deep terrace reef at a depth of 18 m to 22 m, which then plummet into the abyss. The only exception is the Bloody Bay area on the island of Little Cayman. In this location, the deep terrace reef is unusually absent. This location is approximately 2 km in length and the shallow reef terrace reef ends abruptly ranging from as shallow as 4.5 m at the easternmost part to 8.5 m on the westernmost part before plunging vertically into the abyss. This area of the Bloody Bay / Jackson Point Marine Park, has historically had low coral cover, typically including a patchy distribution of small *Orbicella* coral heads, *Siderastrea sidera* and diplorids at the seaward edge, possibly due to the heavy surge experienced during the winter months from polar cold fronts that dissipate in the NW Caribbean. The vertical wall is dominated by barrel sponges (*Xestospongia muta*), tube sponges (*Callyspongia* sp.), octocorals and sea whips including black corals (*Antipathes* sp.), that are known to grow as shallow as 12 m in this particular location. Like many neighboring Caribbean Islands, the deep and shallow reef terraces consist of a variety of scleractinian corals, forming spurs and grooves, including coral patches which are, in some instances, different sizes along the different depth gradients moving seaward from the shoreline. The coral reef communities are dominated by the large and massive *Montastraea cavernosa, Orbicella faveolata*, *Orbicella franksi* and *Orbicella annularis,* complex on the shallow and deep reef terraces. Other common species found include *Siderastrea siderea, Colpophyllia natans* and *Diploria Strigosa*. Octocoral communities are composed of large colonies of *Pseudoplexaura porosa, Pseudoterogorgia americana, Gorgonia ventalina, Gorgonia flabellum, Eunicea* spp. among others. Sponges are

common in different reef locations varying in size and growth forms (i.e., encrusting, erect, and massive) depending on depth and wave exposure.

Presently, in terms of coral cover, the reefs of the Cayman Islands have intermediate to high levels in some locations (12-30%) as compared to other countries in the Caribbean region. However, some areas in the sister islands of Little Cayman and Cayman Brac, particularly on the south, have above average coral cover of >30%. Anecdotal evidence suggests that the Cayman Islands had a much higher percentile coral cover, upwards of >50% as compared to the Cayman Islands national average of approximately 11% (data pooled) measured on their reefs. This slowl declined and can be traced back to two major Epizootic events of the 1980s that triggered the decline of their shallow and deeper reefs. These two events coupled with sporadic bleaching events (i.e., those of 1979, 1983, 1987, 1991, 1994, 1995, 1998, 2005, 2009) and the proliferation of coral diseases over the past three decades have been the major contributor towards the decline of the coral reefs on both a local and regional scale to varying degrees. The bleaching event of 1998 that affected coral reefs throughout the global tropics including the coral reefs of Cayman Islands, was the worst on record, demonstrating a >60% loss of coral tissue at monitoring sites located on the north coast of Grand Cayman on the shallow reef terrace (C. McCoy, unpublished data), with coral cover declining from 25% to 15% at the northern sites. On the coral reefs of Little Cayman, McCoy, (C. McCoy 2004, unpublished theses), measured a 38% mortality in coral cover attributed to this event at one site in Little Cayman, dropping from 52% coral cover to 32%, with a concomitant increase in macroalgae. The bleaching event of 2005, in which thermal stress exceeded 16 degree heating weeks (DHW) of +1.2°C vs. the long-term average temperature for the Caribbean region, was much longer than any observed records in the prior 20 years (Eakin, *et.al.,* 2010). This event was much more severe in the eastern Caribbean in duration and intensity, observations recorded at coral reef monitoring sites located on the north and south coast of Grand Cayman during that event in 2005 demonstrated bleaching at the community level were 15% and 11% of colonies, respectively (McCoy, unpublished data). However, corals subjected to the bleaching event in 2005, fully recovered by the year 2006 according to bleaching surveys with no measurable mortality (C. McCoy, unpublished data). The acute global bleaching event in 1998 in the tropics was unprecedented. Remnants of old mortality of corals can still be seen over large colonies of the *Orbicella* complex throughout all three islands to date (Croy McCoy, personal observation). However, since the 1998 mass bleaching event, the coral reefs of the Cayman Islands have been stable, including demonstrating the ability to resist and recover from bleaching events such as the 2009 acute localized bleaching event.

2.4 Coral Reef fish assemblages of the Cayman Islands

The coral reefs of the Cayman Islands support a rich and diverse population of fishes (see chapter 4). This is likely the result of almost three decades of actively enforced Marine Protected Areas (MPAs), a low human population and the absence of commercial fisheries. In this study, 48 target reef fish species, representing different biological and ecological roles on the coral reefs of the Cayman Islands, were sampled at 55 sites across the three Cayman Islands (Figure 2.2). These fish were further grouped into five trophic groups; Herbivore (HB), a diet consisting predominantly of algae, Omnivore (OM), a diet consisting of algae and fish, Predators (P), a diet consisting of 100% fish, carnivores 1 (C1), a diet consisting of invertebrates (inverts feeders) and carnivores 2 (C2), a diet consisting of invertebrates and other fish species (Appendix 4.1). In a fish survey conducted by Pattengill-Semmens and Semmens (2003) they documented approximately 18% more fish than the first ever records of fish surveys, which was done by Burgess *et al*. (1994). This lends merit to the fact that Caymanian reefs support a healthy reef fish population. Caymanian coral reefs fish populations are dominated by the Scarids (parrotfishes). However, they also comprise a healthy biomass of *Serranids* (groupers, more so the Cayman Brac and Little Cayman), *Lutjanidae* (snappers), *Carangidae* (Jacks) and *Balistidae* (triggerfishes). See chapter 4 for the composition of fish families per island

2.5 Methods

2.5.1 Study area.

The Cayman Islands are located between 19º 15’ and 19º 45’ N latitude and 79º 44’ and 81º 27’ W longitude (Figure 2.1). They are the peaks of a submerged ridge, which runs westwards from the Sierra Maestra mountain range of Cuba. The three islands, a British overseas territory archipelago are located in the NW Caribbean between 160 km (CB & LC) and 260 km (GCM) south of Cuba, 230 km (CB & LC) and 310 km (GCM) west of the island of Jamaica.

Figure 2 .1. Location of the three (3) Cayman Islands, Grand Cayman, Little Cayman and Cayman Brac in the NW Caribbean Sea between 19o 15' and 19o 45' N latitude and 79o 44' and 81o 27' W longitude.

2.5.2 Data collection methods

Benthos

Benthos video transect data were collected at 55 survey sites around the 3 Cayman Islands at locations inside and outside of protected areas; Grand Cayman (GCM, n = 27; 9 MPA, 18 non-MPA), Little Cayman (LC, n = 16; 8 MPA, 8 non-MPA) and Cayman Brac (CB, n = 12; 6 MPA, 6 non-MPA) (figure. 2.2); with Sites distributed between the shallow and deep reef terraces (figure 2.2).

Self-contained underwater breathing apparatus (SCUBA) was used to survey the benthos along four 20 m transects at each of the 55 sites using a Sony Handycam HDR-CX550 video camera contained within a Stingray Light & Motion housing. Transects were permanently marked using rebar stakes during the survey years 2009 through to 2012. A fiberglass measuring tape was then laid between the 20 m rebar stakes to use as a guide to follow.

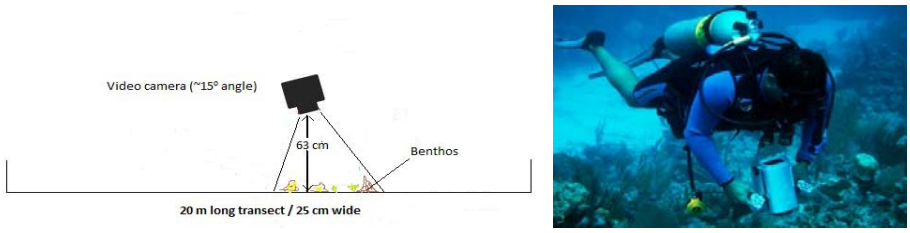


Figure 2.2. Diagram illustrating benthos survey method (left), C. McCoy with video camera starting to video 20 m benthos transect (right).

Fish

Fish biomass data was collected by Underwater Visual Census (UVC), using a belt transect method (Samoilys and Carlos, 2000) at 55 sites across the 3 Cayman Islands (Figure 2.2) for the years 2009 through to 2012. Sites were distributed within protected and outside of protected areas; Grand Cayman (GCM, n = 27; 9 MPA, 18 non-MPA), Little Cayman (LC, n = 16; 8 MPA, 8 non-MPA) and Cayman Brac (CB, n = 12; 6 MPA, 6 non-MPA) (figure. 2.2). Fish counts were conducted along three belt transects per site; each transect was 50 m long, 5 m wide and 5 m vertically from the substrate, with a gap of 30 m minimum to avoid spatial autocorrelation and kept at a constant depth (+/- 1m). The diver swam with a 50 m long transect tape attached to diver with a graduated PVC T-bar with 5 cm marked increments as a size scale identifying and recorded the number of individual target fish species (Appendix 4.1) within defined area for each transect (50 m long, 5 m wide, 5 m high). Fish were estimated to the nearest 5cm forked length and recorded. This was replicated three times per site. Biomass of fish per unit area was calculated using the allometric length-weight conversion (Bonsack, 1988) and expressed in g/m2 using surface area sampled:

$W = a\mathrm{TL}^{b}$

Where W is weight in grams, parameters *a* and *b* are constants obtained from the literature (Froese and Pauly, 2005) and TL is the total length in centimeters.

2.5.3 Study Sites

A total of 55 sites were surveyed across the three Cayman Islands, 27 in Grand Cayman, 16 Little Cayman and 12 in Cayman Brac (figure 2.3), see Appendix 2.3 for latitude and longitude coordinates. This comprised of 24 sites on the deep terrace reef and 31 sites on the shallow terrace reef across the three Cayman Islands (figure 2.3).

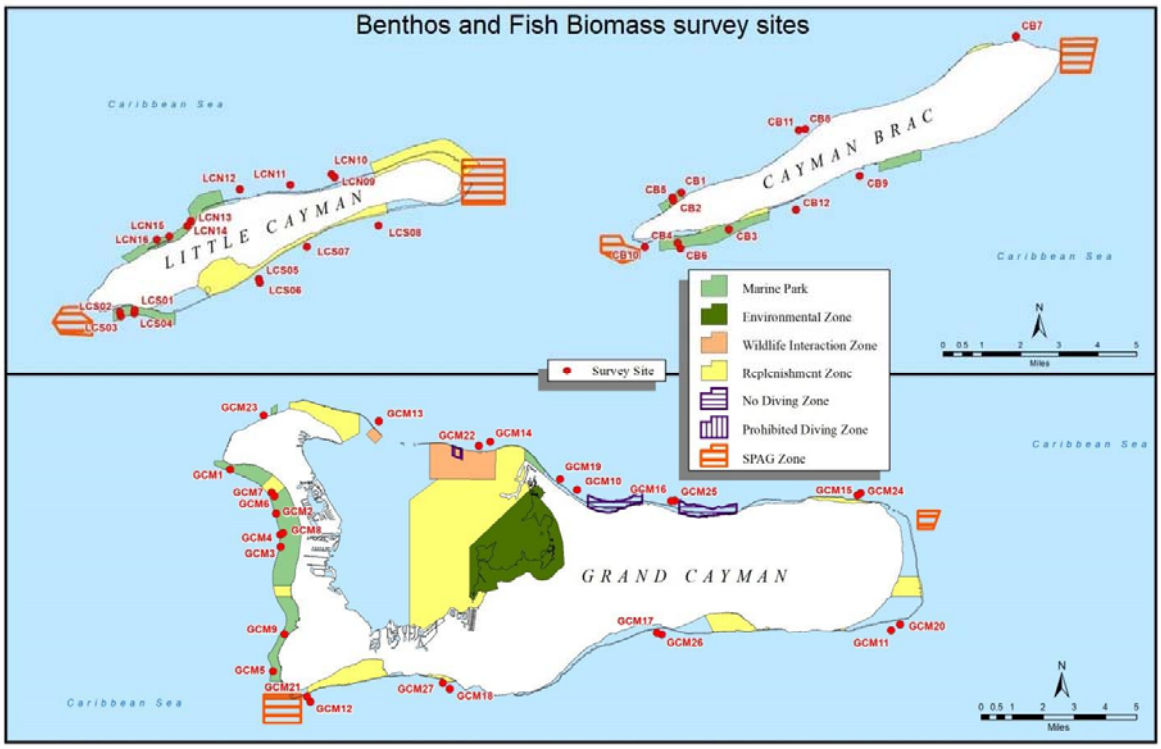


Figure 2. 3. Location of study sites in Grand Cayman (n= 27), Little Cayman (n=16) and Cayman Brac (n=12). See Appendix 2.3 for geographic Lat/Lon GPS positions for sites.

2.5.4 Experimental design

A five factor multivariate design (year, depth, protection, coast, and Island) was used, with the year (2009-2012), depth (shallow terrace reef; deep terrace reef) and protection (MPA, non-MPA) being fixed factors (table 2.1). Twenty-three sites in total were located within existing MPA (GCM = 9, 5 deep, 4 shallow; LC = 8, 2 deep, 6 shallow; CB = 6, 2 deep, 4 shallow) and 32 were located outside (GCM = 18, 9 deep, 9 shallow; LC = 8, 2 deep, 6 shallow; CB = 6, 2 deep, 4 shallow) for a total of 55 sites across islands. The random factors were coast (north, south, west) and Island (Grand Cayman, Little Cayman, Cayman Brac), with coast nested in the island to test if marine protected areas were the main factor driving benthos changes and target reef fish species biomass over time and space in the Cayman Islands (see table 2.1).

With the only MPA in Grand Cayman located on the entire western Leeward coast, it made it not possible to have a balanced experimental design for that island. To counter this confounding factor, double the amount of sites were distributed outside of MPA on the north and south coasts to compare variation and composition of that island benthos and fish assemblages. Additionally, the Northern shelf on the island of Little Cayman in its entirety is shallow, more so within the Bloody Bay / Jackson Point MPA, with some areas <6 m before dropping vertically to abyssal depths. To account for this factor, all sites located on the north coast of Little Cayman are shallow.

Table 2.1 Study design showing factors and levels.

Factors	Abbrev.	Type	Nested in	Levels	
year	yr	Fixed		4	(2009, 2010, 2011, 2012)
depth	de	Fixed		2	(Shallow terrace reef, 9-12 m; Deep Terrace reef,18-20 m)
Protection	P	Fixed		2	(Marine Protected areas, non- Marine Protected Areas)
Coast	Co	Random		3	(North, South, West)
Island	Is	Random	Coast	3	(Grand Cayman, Little Cayman, Cayman Brac)

2.5.6 Methods for aerial imagery, marine habitats, and three-dimensional sketches of coral reef profiles.

Aerial images: 2013, 10cm resolution aerial photography were sourced from Cayman Islands Government Lands and Survey Department (http://www.gov.ky/portal/page/portal/cighome/find/organisations/azagencies/lsu). Marine habitat maps: Benthic habitats classification maps that were developed by the Cayman Islands Department of Environment for the Cayman Islands National Biodiversity Action plan (2009) were used. Those habitat maps were then overlaid using ArcGIS 10.3.1 mapping software to the exact geographic location of matching georeferenced 2013 aerial imagery.

Table 2.2 Categories and classification scheme used for shallow coastal marine habitats of Cayman Islands.

Category	Classification scheme
Aggregate reef	Areas where hard coral cover (alive & dead) exceeds 70% substrate coverage. Usually found in the bank/shelf area, and/or the escarpment. Some soft corals/sponges may also be present.
Spur and groove	Defined as feature, typically hard coral cover (alive & dead), exhibiting a high vertical relief relative to the surrounding pavement/sand channels. Spurs" are usually formed by accreting hard corals. "Grooves" usually comprise sand and/or hard bottom. Spur and groove features are usually associated with the seaward edge of the reef crest, and with the edge of the fore reef, near the escarpment, orientated perpendicular to shore and escarpment. Some soft corals/sponges may also be present.

Rubble	Unstable coral rubble and rocks. Reef rubble is often colonized with filamentous or other macroalgae.
Sand/sand plain	an expanse of un-colonized sediment (ranging from course sand to silt) located between the shallow and deep terrace reefs.
Uncolonized hard bottom	pavement, often dominated by algae but exhibiting a hard coral, soft coral, and sponge cover of <10%.
Beach rock	Cemented sand. Beach rock is derived from calcite precipitating out of seawater; resulting in the formation a flat rock-like substrate
Colonized hard bottom	Pavement exhibiting coral cover within the range of 10-70% of the substrate. Dominant features are low-relief pavement or rubble, or low-relief rock and sand grooves, colonized by algae, soft corals, and sparse hard corals, which are dense enough to partially obscure the underlying rock. Where coral cover >70%, areas fall within the *aggregate reef* category.
Back reef	Dead, unstable coral rubble and rocks located on the landward side of the fringing reef/reef crest. Reef rubble is often colonized with filamentous or other macroalgae.
Seagrass beds	Defined as areas where seagrass species represent the dominant substrate coverage. In cases where algae and seagrass co-exist, coverage is designated as seagrass beds if seagrass is dominant, and to the lagoons, vegetated sand category if algae is dominant.
Reef crest	semi-emergent to emergent high points of coral reef.
Sediment	Unvegetated mud and / or sand.
Vegetated sand	vegetated sediment ≥1 mm in diameter.
Hard bottom	low-relief pavement or rubble, or low-relief rock, often colonized by algae.
Lagoonal coral	Corals heads (alive schleractin corals), within a lagoon, usually solitary and isolated from reef crest and aggregate reef. The corals generally exhibit a higher vertical relief relative to the surroundingrubble/pavement/ sand.

2.5.7 Three-dimensional reef profiles from shore to deep terrace reef

Bathymetric map data was sourced from the Cayman Islands Lands and Survey Department (https://my.caymanlandinfo.ky/). Bathymetry maps were then overlaid using ArcGIS 10.3.1 mapping software to the exact geographic location of matching georeferenced 2013 aerial imagery and habitat map. Further using ArcGIS 10.3.1 mapping software, a line was drawn from the shoreline to the deep terrace reef, which displayed the exact bathymetry profile below line to scale as an image profile scale reflecting the depth and habitat profiles. Image profile obtained was then imported into Microsoft powerpoint software, rotated 45° and adding a duplicate profile to the right side of the image to give a three-dimensional view. The image was then traced and transposed on sketching paper for further manipulation by drawing and sketching. Initial reef structures were done using a fine point Sharpie marker. Sketches were further scanned as a .jpg image file and imported into Microsoft paint image

software where further manipulation of colour and coral structures were done to complete the coral reef profile diagrams.

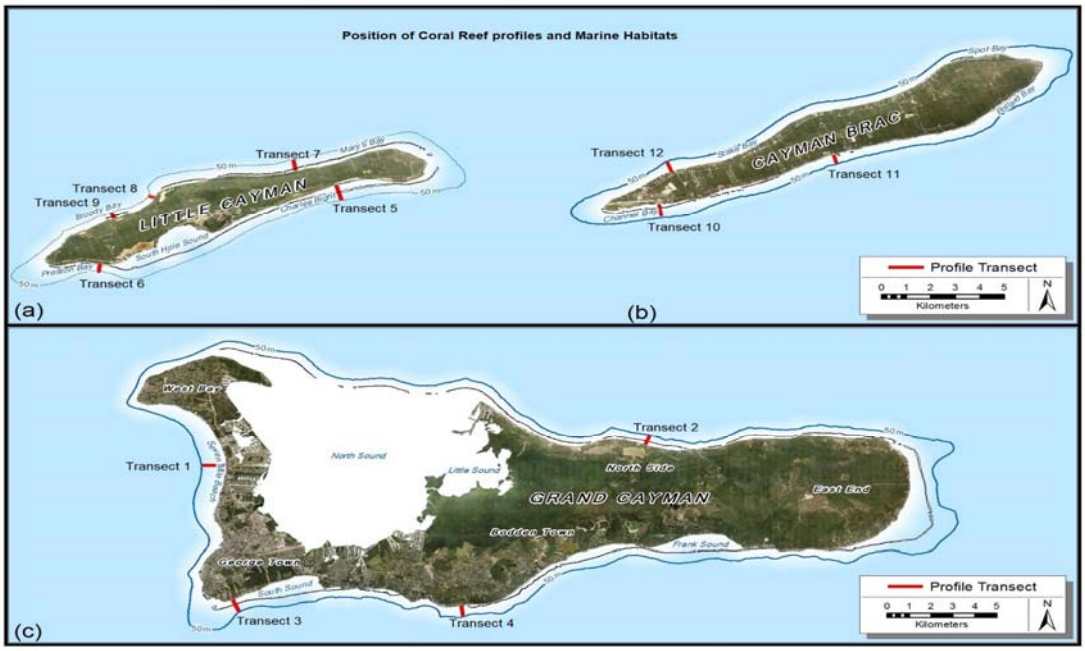


Figure 2. 4. Map showing the position of transect lines of each island where aerial images, marine habitats and the various reef depth profiles from the shoreline to deep terrace reef were taken from. a= Little Cayman (LC) N190 18.985 W810 15.151, b= Cayman Brac (CB) N 190 43.091 W790 48.287, c= Grand Cayman (GCM) N190 18.985 W810 15.151. Transect 1= GCM western leeward, fringing reef absent. Transect 2= GCM north, semi-exposed, fringing reef present. Transect 3= GCM south, exposed, fringing reef present. Transect 4= GCM south, exposed, fringing reef absent. Transect 5= LC south exposed, fringing reef present. Transect 6, LC south exposed, fringing reef absent. Transect 7= LC north, moderately leeward, fringing reef present. Transect 8=LC north moderately leeward, fringing reef absent. Transect 8=LC north, moderately leeward, fringing reef present, Bloody Bay locality. Transect 10= CB south, exposed, fringing reef present. Transect 11= CB south, exposed, fringing reef absent. Transect 12= CB north, moderately leeward, fringing reef absent. See Appendix 2.4 for geographic Lat/long GPS positions of transects.

2.6 Results

2.6.1 Coral reef benthic community structure, Western Leeward aspect of Grand Cayman, MPA

The dominant benthos category is macroalgae, equally distributed between the shallow and deep terrace reefs, followed by calcareous algae and scleractinian corals (figure. 2.5 a; figure. 2.5 b). This particular transect (figure 2.4, transect 1) measuring from shore to the deep terrace reef is at a geographic position halfway along the 7-mile beach (figure.11 a). The shoreline is sandy and gradually progresses to a rocky, uncolonized hard bottom, across a rubble plain. (figure. 11 b; figure. 12). After which some

uncolonized and colonized hardbottom is found before reaching the Shallow terrace reef, then sloping to a spur and groove with valleys filled with sand leading out to the deep terrace reef. In some places, thin low relief spurs connect the shallow terrace reef with the deep terrace reef (figure. 11 a; figure. 2.12)

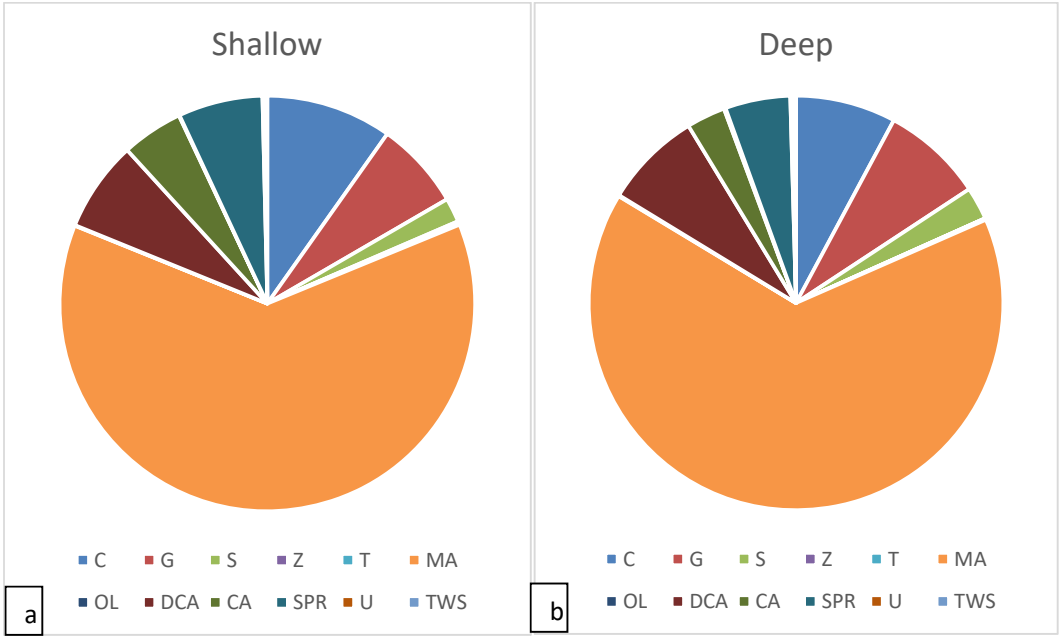


Figure 2. 5. Percentage make-up of the major benthic categories across years (2009-2012) for the Western Leeward aspect of Grand Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled). C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (shallow n= 4; deep n= 5)

2.6.2 Coral reef benthic community structure, north semi-exposed aspect

The northern semi-exposed coast of Grand Cayman's shallow and deep terrace reefs share similar benthos make up. These are six dominant benthos categories: macroalgae, scleractinian corals, gorgonians, dead coral with algae and sand/pavement/rubble in that order for both (figure. 2.6 a; figure. 2.6 b). At the start of this transect onshore, it is sandy with small limestone outcropping which moves across a mix of seagrass and uncolonized hard bottom, with occasional small corals such as diplorids. It then travels over fringing reef dominated by dead *Acropora palmata* rubble to a sediment plain, then colonized hard bottom, mainly consisting of gorgonians before the shallow terrace reef where the spur and groove coral reefs start. (figure. 2.13 a; figure. 2.13 b). It then slopes down to a sand plain at a depth of ~12 m with the occasional spur that connects from the shallow terrace reef to the deep terrace reef (figure. 2.14). The north, deep terrace reef is much more developed than the western leeward margin. The northern semi-exposed aspect of Grand Cayman also has the shallowest deep terrace reefs, some as shallow as 12 m and then plummeting to abyssal depths.

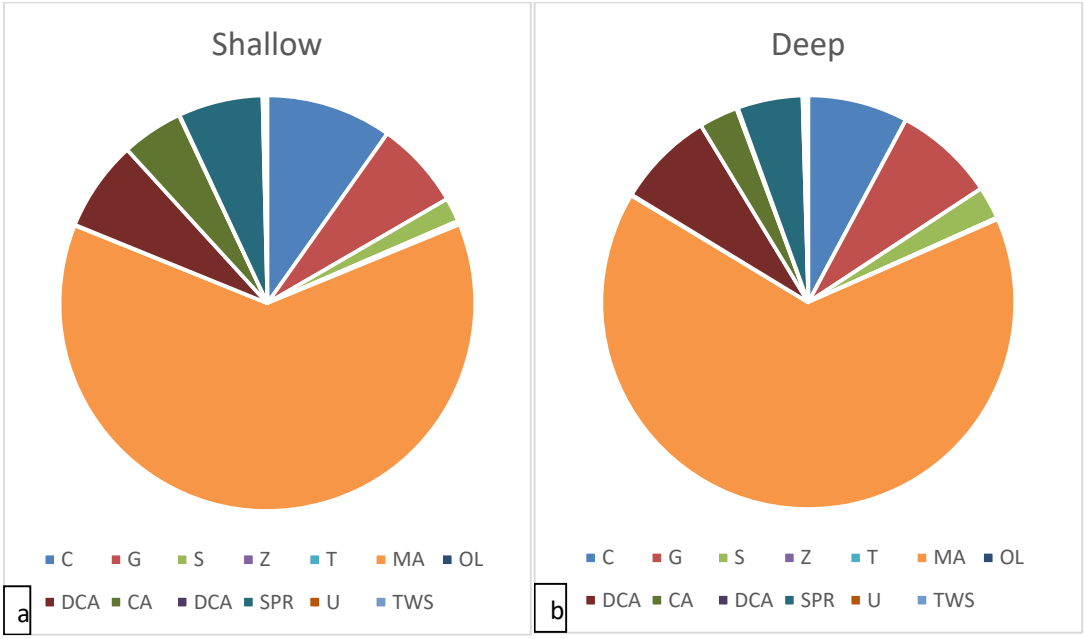


Figure 2. 6 Percentage make-up of the major benthic categories across years (2009-2012) for the northern semi-exposed aspect of Grand Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled). C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, DC= diseased coral, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (shallow n= 5; deep n= 5)

2.6.3 Coral reef benthic community structure, south, exposed aspect.

The southern aspect benthos of Grand Cayman constitutes the highest percentage of macroalgae over the course of study. The four most abundant benthos categories found in the south are macroalgae, scleractinian corals, dead coral with algae and gorgonians with gorgonians found mostly on the deep terrace reef (figure. 2.7 a; figure. 2.7 b).

The southern aspect of Grand Cayman has two very different types of shorelines, one with an outer fringing reef comprising of *Acropora palmata* ramparts, including the new growth of *Acropora palmata* and *Acropora cervicornis* (figure. 2.15 a; figure 2.16). The other is where the fringing reef is absent (Appendix 2.5). The former starts from a high energy sandy beach, across a seagrass bed to a sandy sediment rocky mix with small pebbles (figure. 2.15 a; figure. 2.15 b), It is in this back reef area that the sea urchin, *Diadema antillarium*, can be found in great abundance. Transect then moves across the fringing reef after which rubble is the main benthos type. After that, some colonized hard bottom can be found before reaching the shallow terrace reef. The southern aspect shallow terrace reef is highly developed, with some coral heads reaching 4-5 m in height. Additionally, the interconnecting spurs are a high topographical relief, usually connecting the shallow terrace reef and

the deep terrace reef with sandy valleys in between. The deep terrace reef usually slopes off very steep to abyssal depths at 20 m, with the valleys being about 4 m deeper (figure. 2.16). The latter coastal margin usually starts at a sea cliff or a limestone outcropping known as Ironshore. This particular transect (Appendix 2.5) starts from a rocky limestone coastline, with no fringing reef present. It travels across a 100 m rocky uncolonized hard bottom before reaching the shallow terrace reef at a depth of ~10 m before sloping down to 15 m. Contrary to the other shoreline found in the south, there is very little sand in between the shallow terrace and deep terrace reef, mainly dominated by spur and groove from the shallow terrace reef to the deep terrace reef (Appendix 2.5).

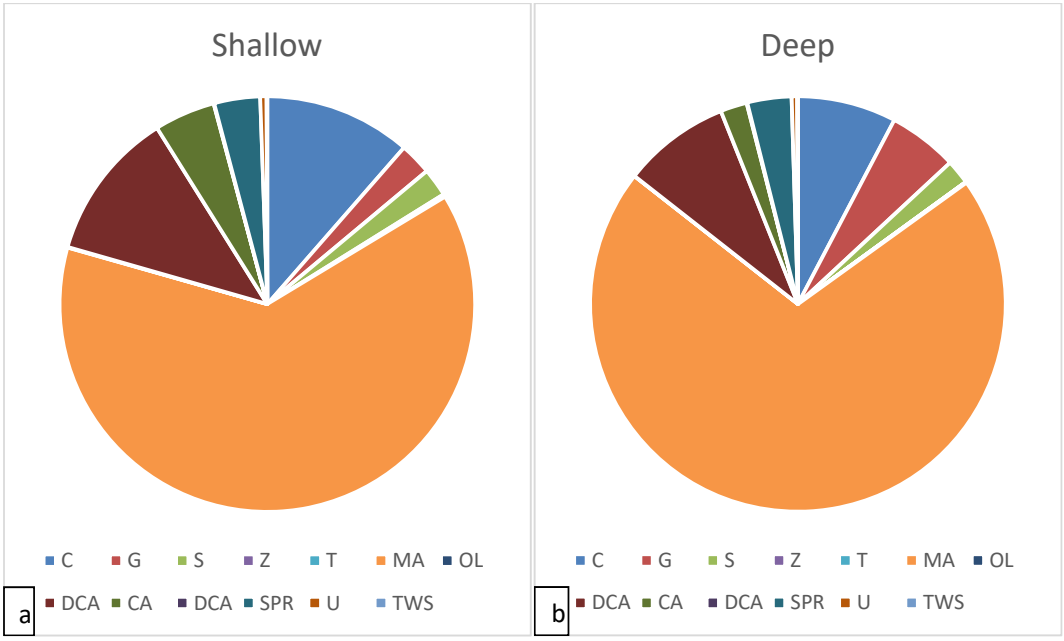


Figure 2. 7. Percentage make-up of the major benthic categories across years (2009-2012) for the southern windward exposed aspect of Grand Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled). C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, DC= diseased coral, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (shallow n= 4; deep n= 4)

2.6.4 Reef fish assemblages, Western Leeward aspect of Grand Cayman.

Herbivores dominate the western leeward shore where the 7-mile beach MPA is located, more so from the family *Scaridae* (figure. 2.8 a; figure. 2.8 b), There is a notable absence of fish from the *Mullidae* family across years and depths. Fish from the *Lutjanidae* family, though found on both the shallow and deep reef terraces, have a preference for the deep terrace reef. *Serranids, Acanthuridae, Sparidae,* and fish from the *Carangidae* are found equally distributed across both the shallow and

deep reef terrace on the western leeward aspect of Grand Cayman (GCM). (figure. 2.8 a; figure. 2.8 b).

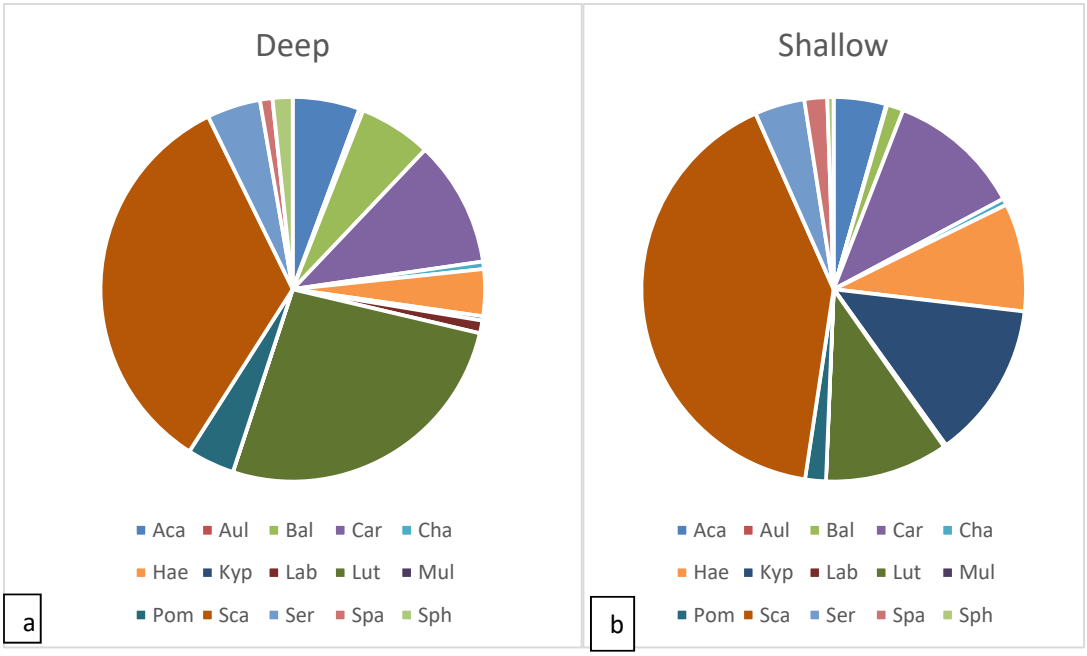


Figure 2. 8 Percentage make-up of the 15 family assemblages along the Western aspect of Grand Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae.(shallow n=4; deep n= 5)

2.6.5 Reef fish assemblages, north semi-exposed aspect

The northern shores of Grand Cayman are also dominated by Scarids (parrotfishes). The four dominant fish families are the Scarids, Haemulidae (grunts), Balistidae (triggerfishes) and Acanthuridae (surgeonfishes) and on the shallow terrace reef (figure. 2.9 a). Whereas, the four dominant fish families on the deep terrace reef are the Scarids, followed by the family Lutjanidae (snappers), Balistidae (triggerfishes) and Acanthuridae (surgeonfishes) on the deep terrace reef (figure 2.9 b).

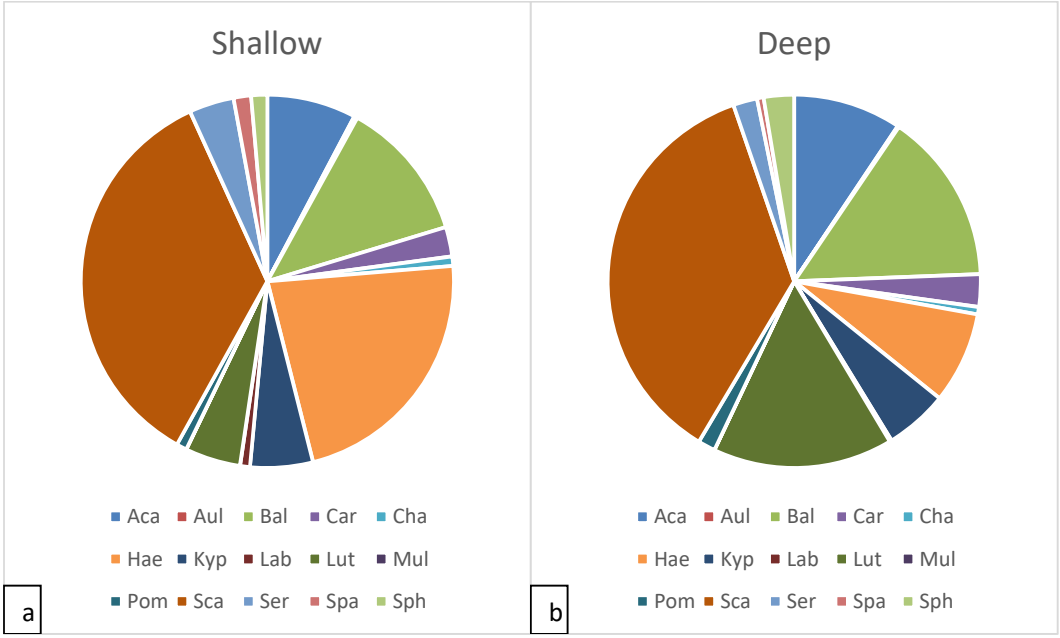


Figure 2. 9 Percentage make-up of the 15 family assemblages along the northern aspect of Grand Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae. (shallow n= 5; deep n=5)

2.6.6 Reef fish assemblages, Grand Cayman south exposed aspect.

The make-up of the southern exposed aspect of Grand Cayman fish family varies slightly from the western leeward margin and the northern semi-exposed coast. Though the Scarids dominate, this is where the Kyphosidae (chubs) and Balistidae (triggerfish) can be found in greater abundance on the shallow terrace reef around Grand Cayman. The five most dominant fish families are the Scarids (parrotfish), Haemulidae (grunts), Balistidae (triggerfishes), Acanthuridae (surgeonfishes) and Kyphosidae (chubs). (figure. 2.10 a; figure. 2.10 b),

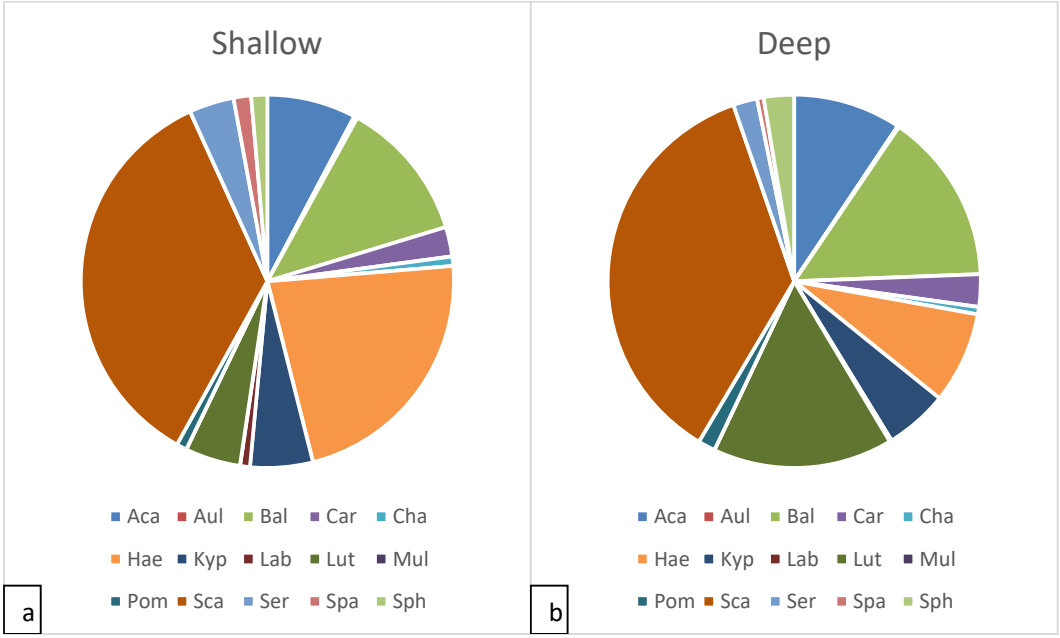


Figure 2. 10 Percentage make-up of the 15 family assemblages along the southern aspect of Grand Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae. (shallow n=4; deep n=4)

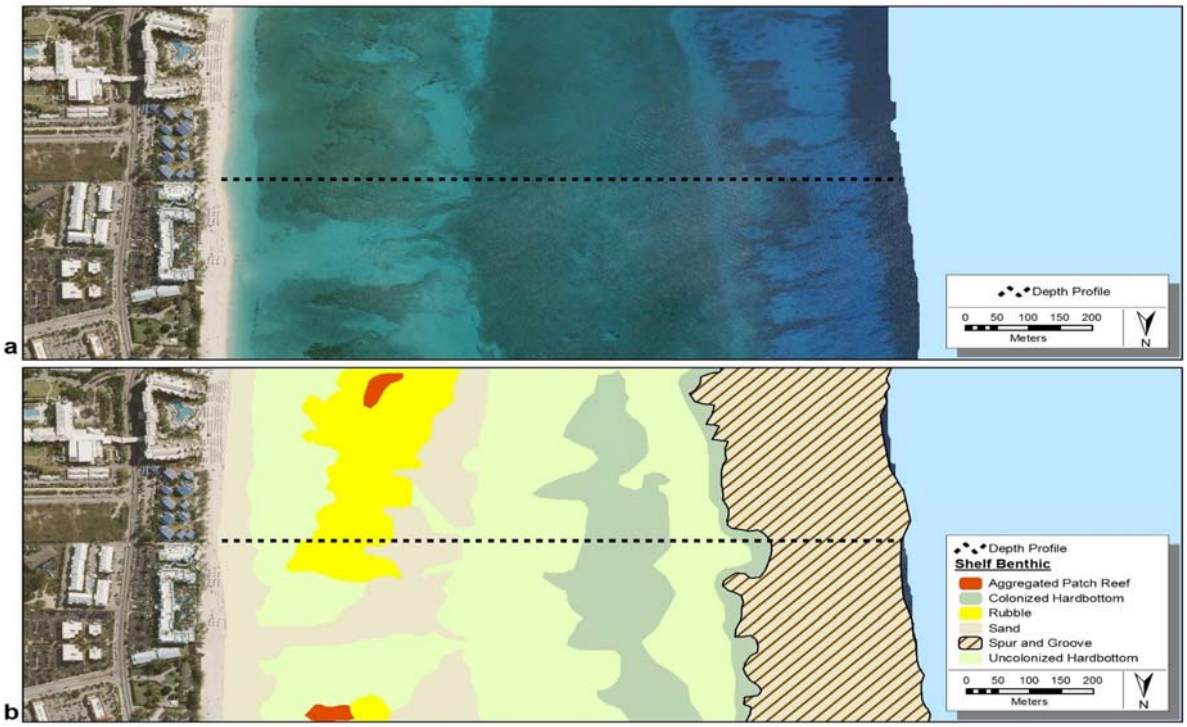


Figure 2. 11. 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the low energy, west leeward aspect of Grand Cayman.

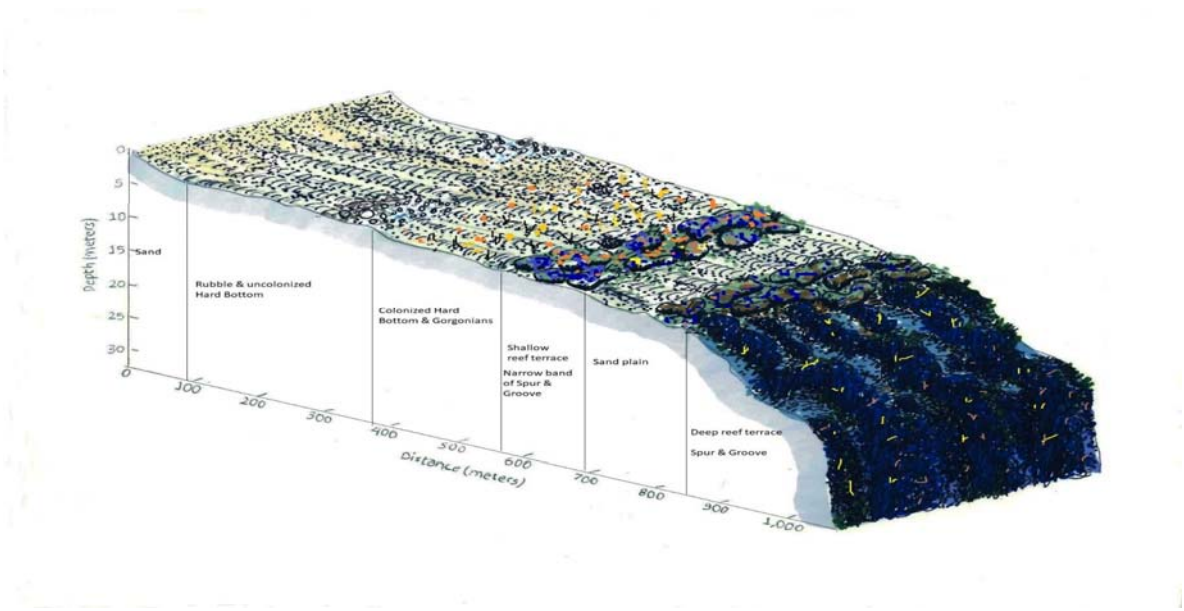


Figure 2. 12. 10 cm resolution, three- dimensional image of depth profile for the west leeward coast of Grand Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters.

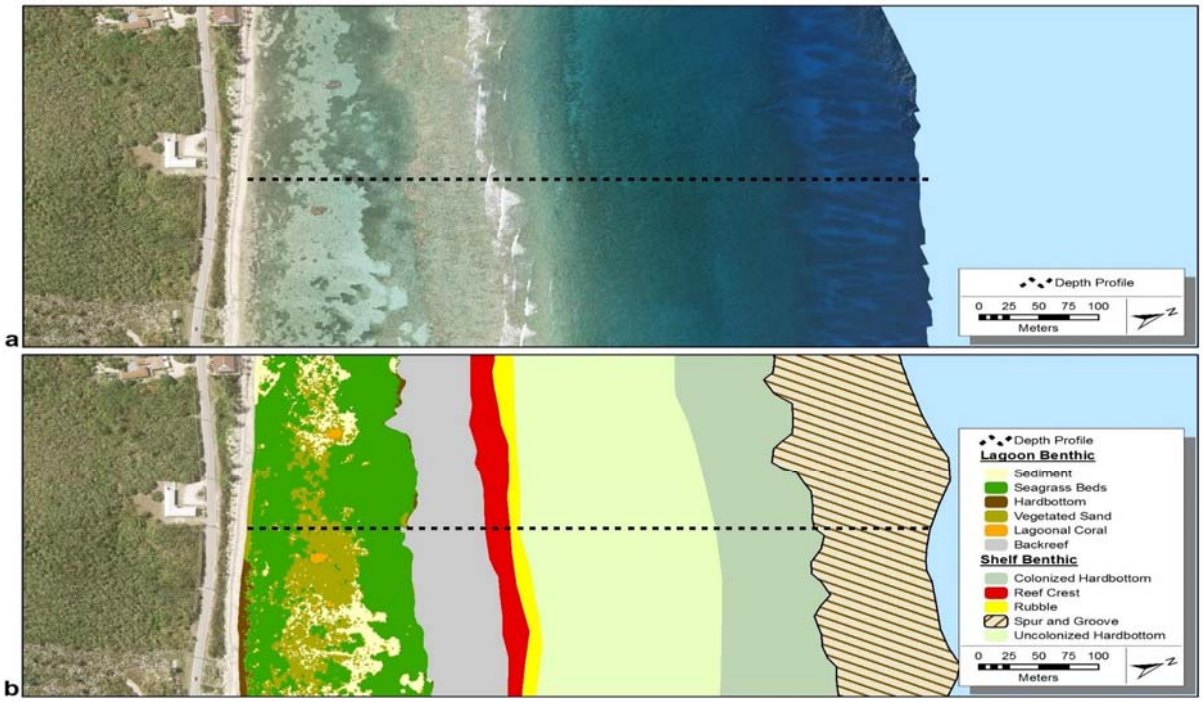


Figure 2. 13. 10cm resolution aerial photography (a) and benthic habitat classification map of the aerial image, (b) for the semi-exposed northern coast of Grand Cayman.

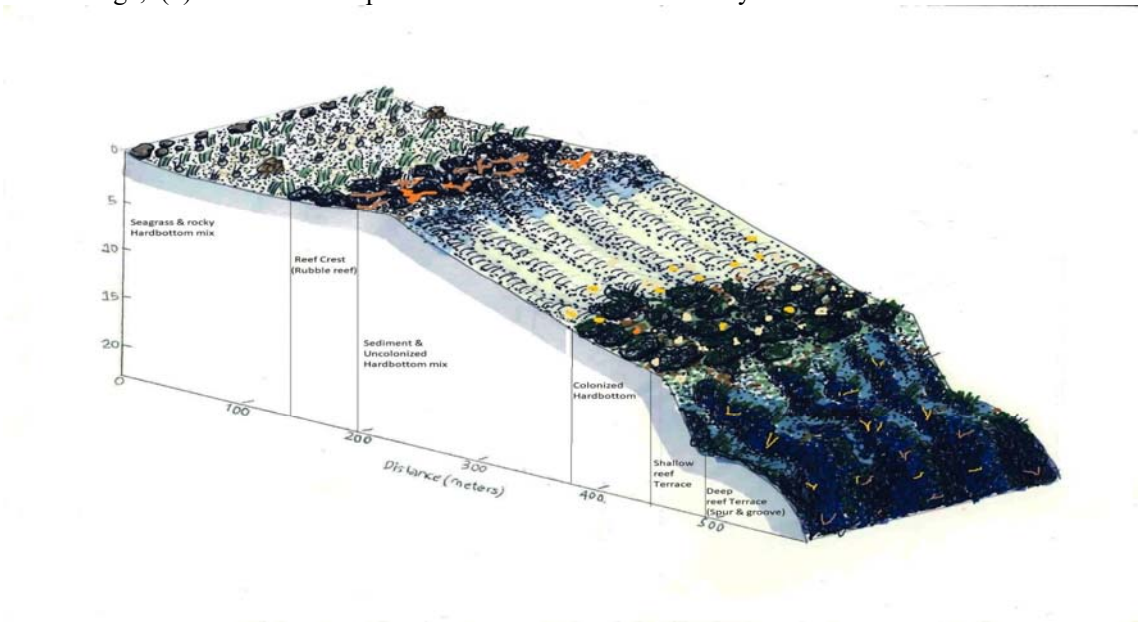


Figure 2. 14 10 cm resolution, three- dimensional image of depth profile for the north semi-exposed coast of Grand Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters. Fringing reef present.

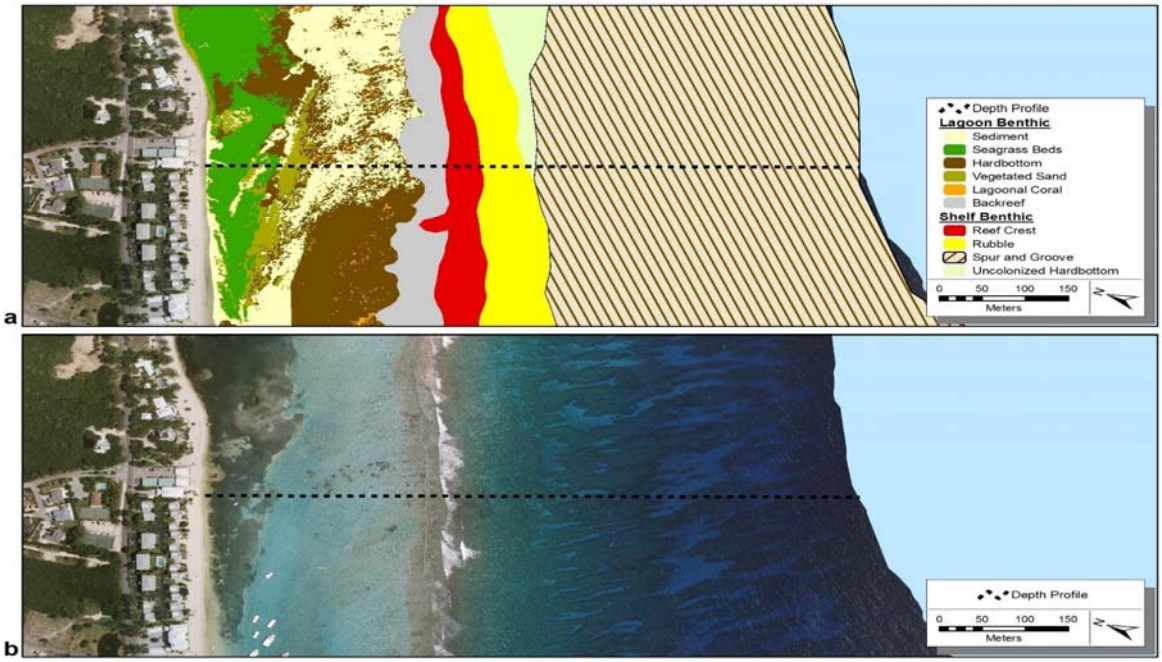


Figure 2. 15. 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the exposed southern coast of Grand Cayman with Fringing reef.

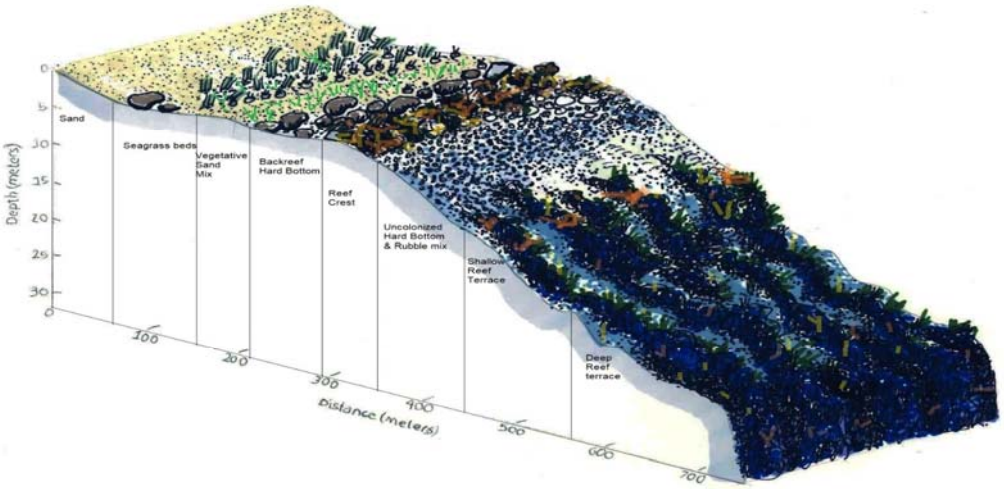


Figure 2. 16. 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Grand Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters.

2.6.7 Coral reef benthic community structure, south exposed aspect of Little Cayman, fringing reef present.

The southern aspect benthos of Little Cayman is dominated by the macroalgal cover which constitutes the highest percentage category over the course of study. The four most abundant benthos categories found in the south are macroalgae, scleractinian corals, calcareous algae and gorgonians (figure. 2.17 a; figure. 2.17 b), with gorgonians found in greater abundance on the deep terrace reef (figure. 2.17 b).

The southern aspect of Little Cayman has two very different types of shorelines, one with an outer fringing *palmata* reef comprising of *Acropora palmata* ramparts, including the new growth of *Acropora palmata* and *Acropora cervicornis* amongst a mix of *diplorids*, *hydrocorals* and *siderastreidae* species (figure. 2.21 a; figure. 2.21 b, figure 2.22), the other is where the fringing reef is absent (Appendix 2.7). The former starts from a low energy sandy/rocky mix lagoonal beach, across a thin band of seagrass bed to a sandy sediment rocky mix with small pebbles (figure. 2.21 a; figure. 2.21 b). It is in this back reef area that the sea urchin, *Diadema antillarium* can be found in greater abundance as it seems to be a preferred habitat, which in particular, is found on the southern aspect of the three islands. The transect then moves across the reef crest, which is a fringing rubble reef comprising of dead *palmata* stumps and ramparts forming a rocky barrier that is visible in low tides. After that, a mix of uncolonized and colonized hard bottom can be found before reaching the shallow terrace reef. The southern aspect shallow terrace reef is highly developed, with some coral heads reaching >4 m in height (figure 2.22). Additionally, the interconnecting spurs are a high topographical relief, usually connecting the shallow terrace reef and the deep terrace reef with sandy valleys in between occupied mostly by the gastropod, *Strombus gigas*. The deep terrace reef usually slopes off to abyssal depths at ~20 m, with the valleys being about 3-4 m deeper (figure. 2.22). The latter coastal margin usually starts at a limestone outcropping known as Ironshore. This particular transect (Appendix 2.7) starts from this rocky limestone coastline, with sandy onshore pockets with no fringing reef present. It travels across a 100 m rocky uncolonized hard bottom and ~50 m of colonized hardbottom before reaching the shallow terrace reef at a depth of ~10 m, after which it abruptly slopes down to 15 m (Appendix 2.7; Appendix 2.8). This particular area has a highly developed coral reef with some heads reaching 4-5 m in height from the substratum, with interconnecting tunnels between coral heads. Thereafter, a vast sand plain is encountered with low relief (<2 m) interconnecting spur and groove with sandy valleys before reaching the deep terrace reef ~300m from the shoreline at a depth of ~20m (Appendix 2.7; Appendix 2.8).

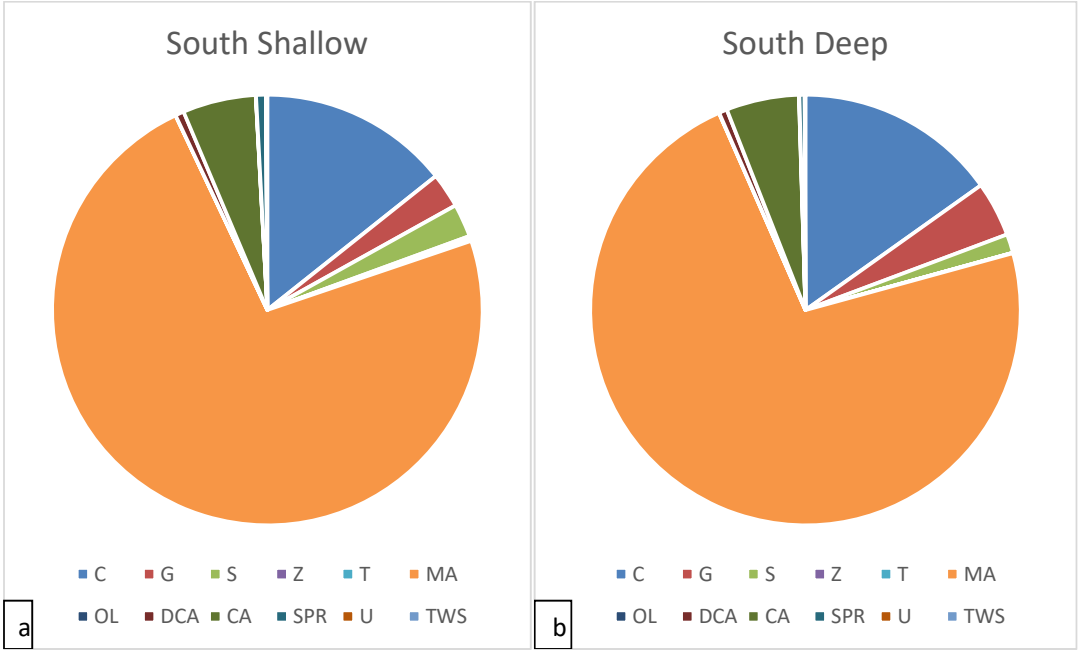


Figure 2. 17. Percentage make-up of the major benthic categories across years (2009-2012) for the southern exposed aspect of Little Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled). C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (shallow n= 4, deep n= 4)

2.6.8 Coral reef benthic community structure, north moderately leeward aspect of Little Cayman

The northern moderately leeward aspect of Little Cayman entire shelf area is much shallower than its sister islands of Cayman Brac and Grand Cayman. For this reason, with depth being a factor in benthos distribution, all sites on the north aspect of Little Cayman were categorized as shallow (9-12 m). Its benthos comprises much like its southern counterpart, dominated by a macroalgal cover which again constitutes the highest percentage category throughout study. The most abundant benthos categories found in the north aspect of the island are macroalgae, scleractinian corals, gorgonians calcareous algae and sponges (figure. 2.18), with the latter two found in equal abundance. The most striking difference between the benthos in the north and south aspect of Little Cayman is the sponge populations, which are found in higher abundance on the northern aspect of Little Cayman.

The north aspect of Little Cayman has three very different types of shorelines. The most common one has an outer fringing *palmata* reef comprising of *Acropora palmata* ramparts, including the new growth of *Acropora palmata* and *Acropora cervicornis* amongst a mix of *diplorids*, *hydrocorals*, *siderastreidae* species and gorgonians, mainly *flabellum* species (figure. 2.23 a; figure. 2.23 b, figure 2.24). The transect starts from a low energy sandy lagoonal shoreline across a thin band of seagrass bed to a rocky mix of hardbottom and sediment (figure. 2.23 a; figure. 2.23 b). The transect then moves across the hardbottom to the reef crest, which is a fringing reef comprising of dead *palmata*

stumps and ramparts forming a rubble reef barrier of which new growth of which acroporids mix with *diplorids*, *hydrocorals*, *siderastreidae* species including gorgonians can be found. After that, a mix of uncolonized and colonized hardbottom comprising of Octocoral communities are composed of large colonies of *Pseudoplexaura porosa, Pseudoterogorgia americana, Gorgonia ventalina, Gorgonia flabellum, Eunicea spp*., among others, can be found before reaching the shallow terrace reef (figure. 2.23 a; figure. 2.23 b). The north aspect shallow terrace reef is not as highly developed as its southern sibling, with most coral heads reaching only 1-3 m in height per most part. The interconnecting spurs are of topographical relief, connecting the shallow terrace reef and the deep terrace reef with sandy valleys in between. The deep terrace reef usually slopes off abruptly to abyssal depths at ~10-12 m, with the valleys being about 2-3 m deeper (figure 2.24).

The two other transects are located within the Bloody Bay/Jackson Point Marine Park (Appendix 2.9; Appendix 2.10). At the Jackson Point location, within the MPA, the fringing reef is absent (Appendix 2.9). The latter coastal margin usually starts at a high energy sloping sandy shore in between limestone outcropping. This transect (Appendix 2.9; Appendix 2.10) travels across ~100 m rocky uncolonized hard bottom and ~25 m of colonized hardbottom before reaching the shallow terrace reef at a depth of ~8 m, after which it abruptly slopes down to 10 m . This particular area has an unusually highly developed coral reef with some coral heads reaching 4-5 m in height from their base in the sand and known for their interconnecting tunnels between each coral heads, a well-known and beloved area for scuba divers. After that, a sandy plain is encountered with high relief (>4 m) spur and groove topography before reaching the shelf edge ~225 m. At this location, the coral buttresses rise to within 9 m of the surface before abruptly plummeting to abyssal depths (Appendix 2.9; Appendix 2.10). The shelf edge in this location has many sand chutes and tunnels starting from the sandy plain on out through gaps through the coral heads to the nearly vertical wall. The former is, is known as the western locality of the Bloody Bay/Jackson Point Marine Park. It is highly unusual as the deep terrace reef is missing and the shallow reef terrace extends out to the deep shelf where it vertically plummets to abyssal depths while also being as shallow as 6 m in some places (Appendix 2.11; Appendix 2.12).

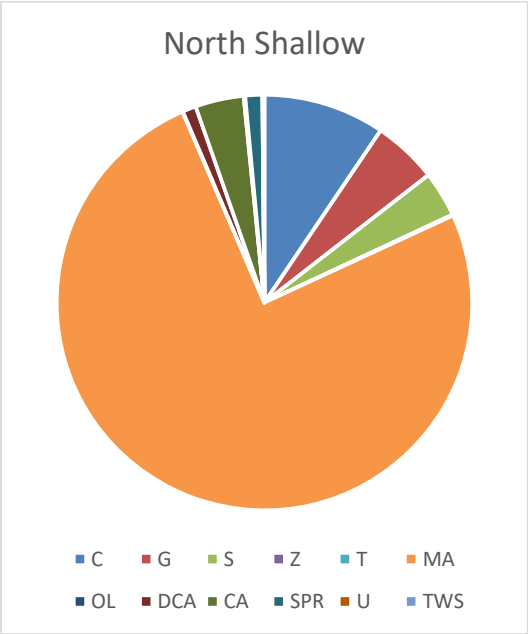


Figure 2. 18. Percentage make-up of the major benthic categories across years (2009-2012) for the north, moderately leeward aspect of Little Cayman for the shallow terrace reef. C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (n=8)

2.6.9 Reef fish assemblages, south exposed aspect of Little Cayman

The south exposed aspect of Little Cayman fish assemblages are dominated by scarids (parrotfishes), haemulidae (grunts), kyphosidae (chubs), Acanthuridae (surgeon fishes), lutjanidae (snappers), balistidae (trigger fishes), and serranidae (groupers) (figure. 2.19 a; figure. 2.19 b). Populations of the fish families' haemulidae, lutjanidae and kyphosidae are much higher on the shallow terrace reef than the deep terrace reef of the south aspect of Little Cayman (figure. 2.19 a). However, the families of scaridae, serranidae and sphyraenidae are found in greater abundances on the deep terrace reef, with the scarids dominating the deep terrace reef fish assemblages (figure. 2.19 b), which perhaps is a dietary or habitat preference.

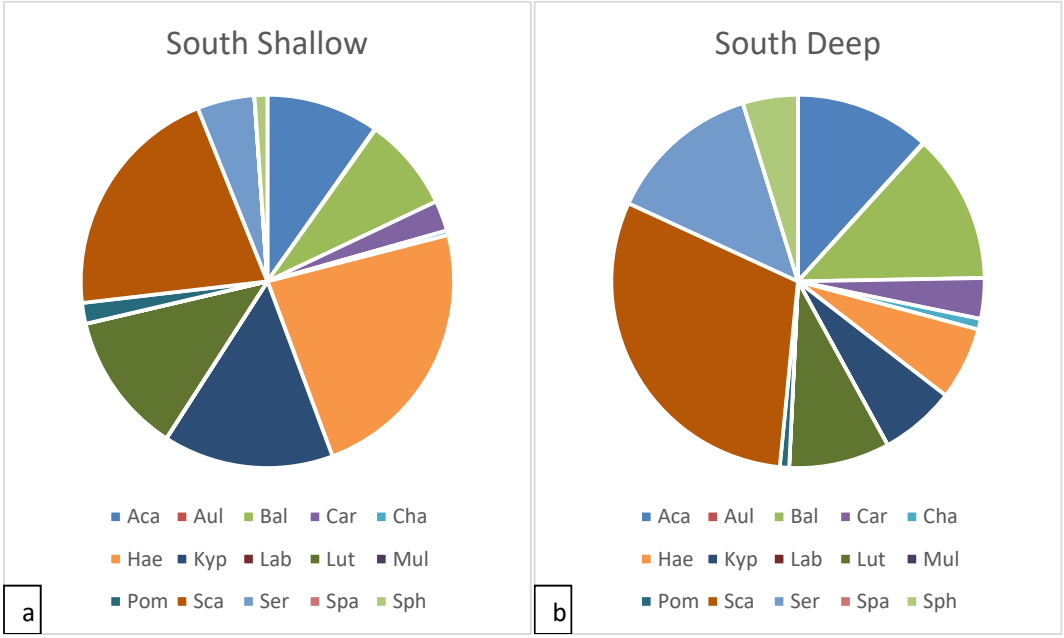


Figure 2. 19. Percentage make-up of the 15 family assemblages along the southern aspect of Little Cayman on (a) the shallow reef terrace (b) the deep reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae. (shallow n=4, deep n=4)

2.6.10 Reef fish assemblages, north moderately leeward aspect of Little Cayman

The north moderately leeward aspect of Little Cayman shallow terrace reef fish family make-up is similar to its southern aspect counterpart, with the family haemulidae (grunts) leading the reef fish assemblage (figure 2.20). The five most prominent fish families found on the north aspect of Little Cayman are haemulidae (grunts), scarids (parrotfishes), lutjanidae (snappers), balistidae (trigger fishes) and Kyphosidae (chubs) (figure 2.20), with the families of Acanthuridae and serranidae found in near equal distribution (figure 2.20). However, when compared to the southern aspect, the family scaridae and Kyphosidae are found in lesser proportions.

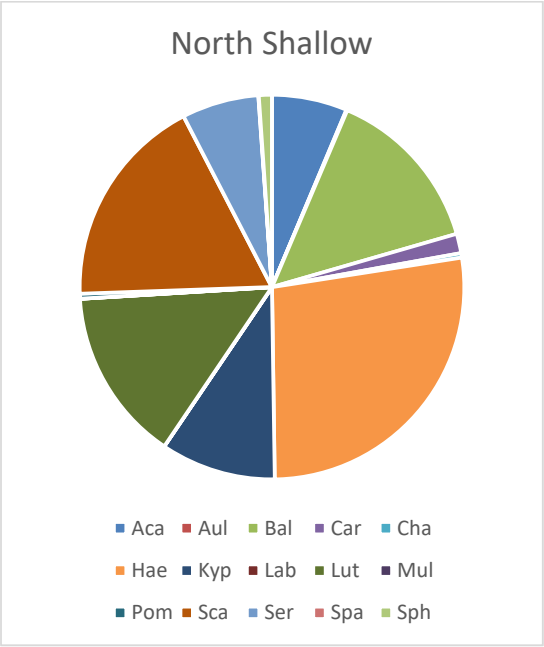


Figure 2. 2. Percentage make-up of the 15 family assemblages along the northern moderately leeward aspect of Little Cayman on the shallow reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae. (n= 8)

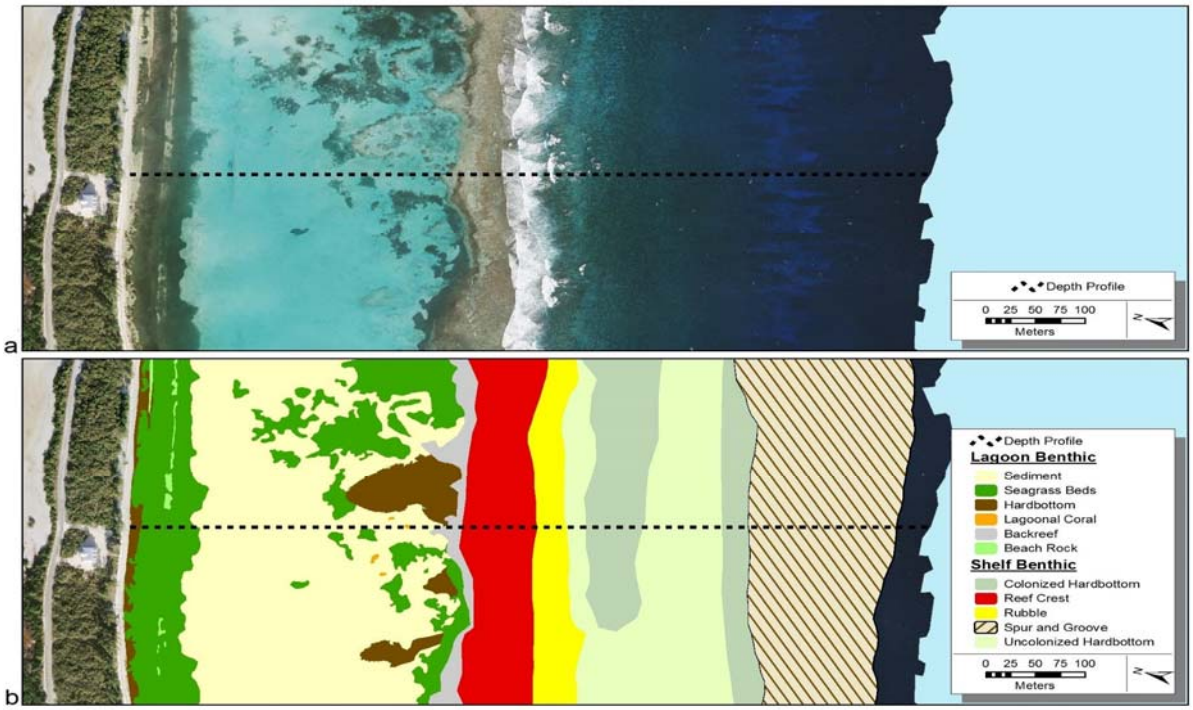


Figure 2. 21. 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the exposed southern aspect of Little Cayman, fringing reef present.

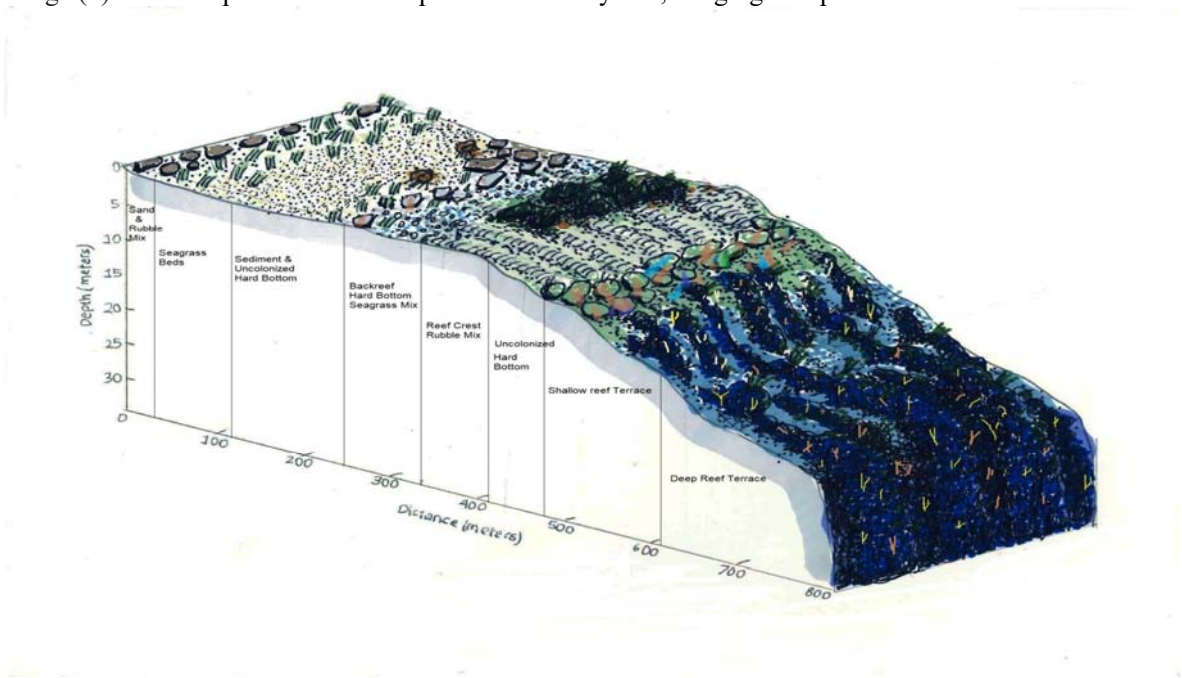


Figure 2. 22. 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Little Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef present.

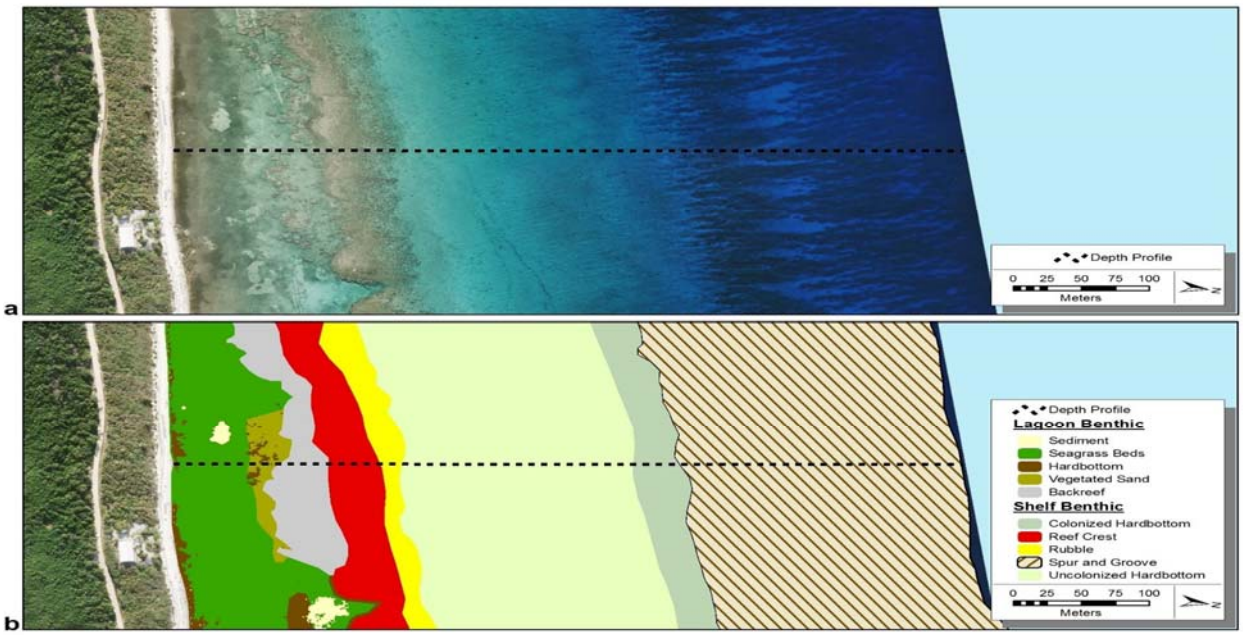


Figure 2. 23. 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the moderately-leeward northern aspect of Little Cayman, fringing reef present.

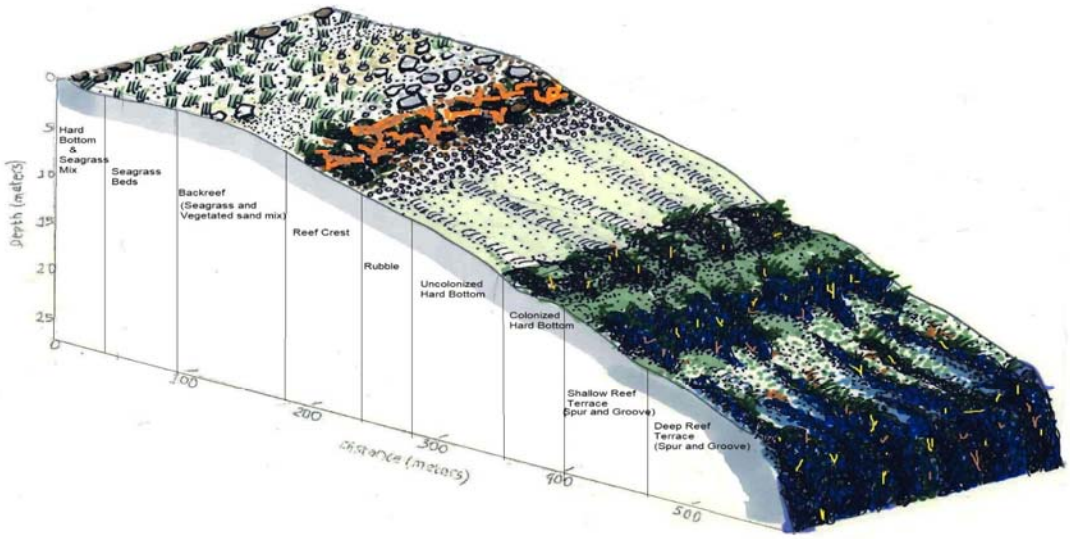


Figure 2 24. 10 cm resolution, three- dimensional image of depth profile for the moderately leeward north coast of Little Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef present.

2.6.11 Coral reef benthic community structure, south exposed aspect of Cayman Brac

The southern aspect benthos on the island of Cayman Brac is dominated by the macroalgal cover, more so than its sister islands of Little Cayman and Grand Cayman and constitutes the highest percentage overall for the Cayman Islands during the study period. The five most abundant benthos categories found in the south are macroalgae, scleractinian corals, calcareous algae, gorgonians and sponges respectively (figure. 2.25 a; figure. 2.25 b), with sponges found in greater abundance on the shallow terrace reef. The shallow and deep terrace reefs on the southern margin of Cayman Brac seemingly have those five benthos categories almost equally distributed across both terraces.

The south exposed aspect of Cayman Brac has two very different types of shorelines, one with an outer fringing *palmata* rubble reef located on the southwestern geographic location (Figure 2.3; Transect 10), This is the only location on that island that has a sandy beach. The other is a rocky limestone outcropping known as " Ironshore" which comprises the majority of the south shoreline of Cayman Brac (figure. 2.3; transect 11). The former fringing reef comprises of rubble based *Acropora palmata* ramparts, including the new growth of *Acropora palmata* and *Acropora cervicornis* amongst a mix of *diplorids* and *hydrocorals* (figure. 2.29 a; figure. 2.29 b). The other is where the fringing reef is absent (Appendix 2.13; Appendix 2.14). The former starts from a high energy sandy/rocky mix lagoonal beach, across a thin band of seagrass bed to a back reef environment of sediments and a rocky mix with boulder ramparts (figure. 2.29 a; figure. 2.29 b). The transect then moves across the reef crest, which is a rubble reef comprising of dead *palmata* stumps and ramparts forming a rocky boulder barrier that is visible, even in high tides and unusually protrudes noticeably during low tides. Thereafter, a mix of uncolonized colonized hard bottom and isolated dead *Acropora palmata* stumps can be found before reaching the shallow terrace reef at ~400 m. Upon reaching the shallow terrace reef, the usual slope to the sand plains found on the south aspects of the Cayman Islands is missing. Instead, it is replaced by tall (>4 m), mostly dead *Orbicella* coral heads of which expanses of dead thickets of *Acropora Palmata* stumps and cervicornis are resident upon (figure. 2.30). It can be envisioned that prior to the white plague disease outbreak of the 1980's, the south coast of Cayman Brac was home to some of the most rugous and developed reefs in the Cayman Islands.

Thereafter, high topographical relief (3-4 m) with finger-like interconnecting spurs linking the shallow terrace reef and the deep terrace reef with a mix of rocky, sandy valleys in between occupied mostly by gorgonians. The deep terrace reef on Cayman Brac is usually from the other islands as it slopes off deeper to abyssal depths at ~25-30 m, with the valleys being much deeper (4-6 m deeper) (figure 2.30).

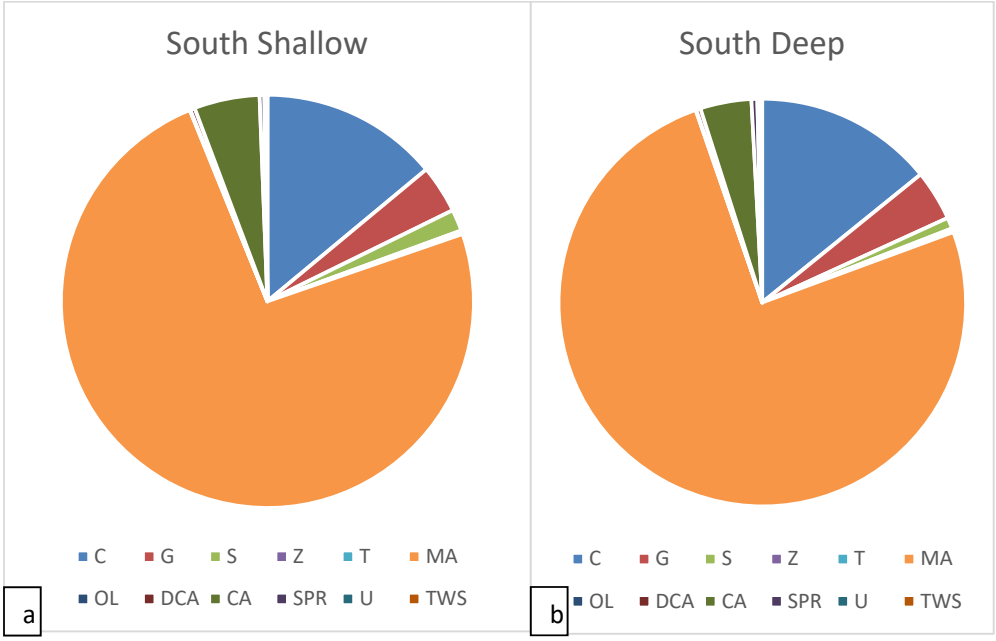


Figure 2. 25. Percentage make-up of the major benthic categories across years (2009-2012) for the southern windward exposed aspect of Cayman Brac on (a) the shallow reef terrace (b) the deep reef terrace (data pooled). C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (shallow n= 3, deep n= 3)

2.6.12 Coral reef benthic community structure, north moderately exposed aspect of Cayman Brac

The northern moderately leeward aspect of Cayman Brac benthos composition is much the same as the south exposed aspect; however, coral cover is much lower (<10%). Its benthos is dominated by a macroalgal cover which, again, constitutes the highest percentage category throughout study. In particular, the north aspect of Cayman Brac is covered by algal genus, *Microdicyton*. Immense beds of this particular alga can only found on the northern aspect of Cayman Brac (C. Mccoy, unpublished data). The most striking difference between the benthos in the north and south aspect of Cayman Brac is the acute prevalence of *microdicyton* algal species and is found nowhere else in the Cayman Islands. The five most abundant benthos categories found in the north aspect of the island are macroalgae, scleractinian corals, sponges, gorgonians and calcareous algae (Figure. 2.26 a; Figure. 2.26 b), with the latter two found in approximately equal abundance across both terrace reefs. The north moderately leeward aspect of Cayman Brac has no fringing *palmata* rubble reef barrier, with only isolated dead thickets of *Acropora palmata* colonies found occasionally. The transect starts from a high energy rocky limestone shoreline across hardbottom and sediment (figure 2.3, transect 12). The transect then travels across 200 m of hardbottom and sediment mix before reaching colonized

hardbottom of comprising of Octocoral communities such as large colonies of *Pseudoplexaura porosa, Pseudoterogorgia americana, Gorgonia ventalina, Gorgonia flabellum,* including *Eunicea spp*. to name a few before reaching the shallow terrace reef. The north aspect shallow terrace reef is not as highly developed as its southern counterpart, with most coral heads reaching only 2-3 m in height per most part. The interconnecting spurs are of low topographical relief, usually <1 m, connecting the shallow terrace reef and the deep terrace reef with sandy valleys in between occupied with mats of the algae from the genus *Microdicyton*. The deep terrace reef usually slopes off abruptly to abyssal depths at ~20-25 m, with the valleys being about 2-3 m deeper (figure. 2.31 a; figure. 2.31 b; figure. 2.32).

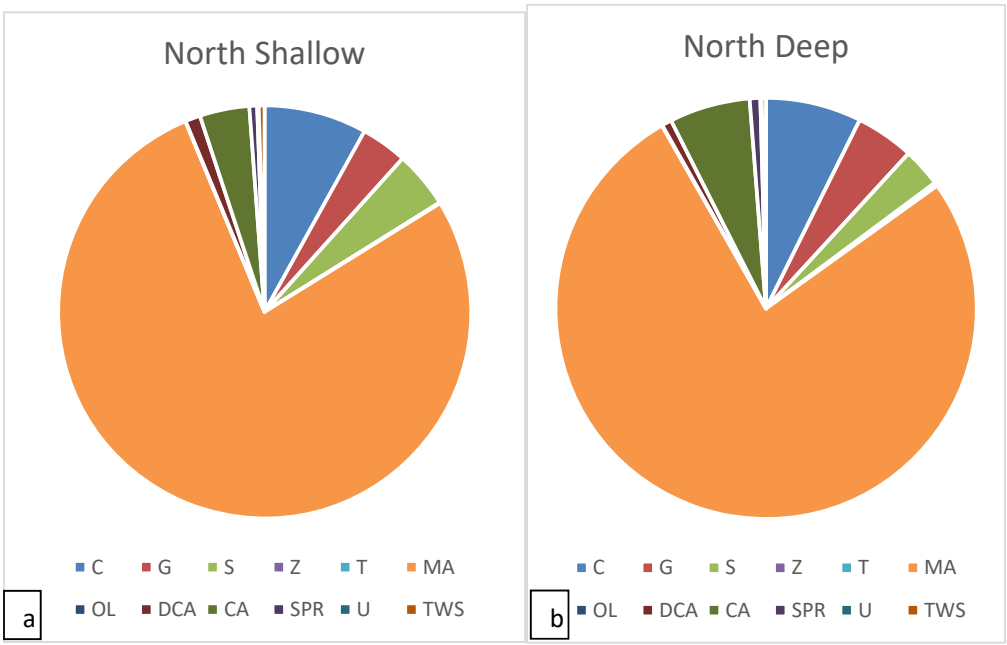


Figure 2. 26. Percentage make-up of the major benthic categories across years (2009-2012) for the north moderately exposed aspect of Cayman Brac on (a) the shallow reef terrace (b) the deep reef terrace (data pooled). C=coral, G=gorgonians, S=sponge, Z=Zoanthids, T=tunicates, MA=macroalgae, OL=other live coral, DCA=dead coral with algae, CA=coralline algae, DC= diseased coral, SPR=sand, pavement, rubble, U=unknown, TWS=tape, wand, shadow. (shallow n= 3, deep n= 3

2.6.13 Reef fish assemblages, south exposed aspect of Cayman Brac Cayman.

As expected for the region, the south exposed aspect of Cayman Brac fish assemblages are dominated by scarids (parrotfishes). The fish assemblage on the southern aspect of Cayman Brac is quite diverse, its make-up consists of a mix of scarids, haemulidae (grunts), kyphosidae (chubs), acanthuridae (surgeon fishes), lutjanidae (snappers), balistidae (trigger fishes), serranidae (groupers), carangidae (jacks), Cheatodontidae (butterfly fishes), Pomacanthidae (Angel fishes) and sphyraenidae (Barracudas) (figure. 2.27 a; figure. 2.27 b). The populations of the fish families' Acanthuridae,

balistidae, kyphosidae, haemulidae and lutjanidae and are much higher on the shallow terrace reef (Figure. 2.27 a) than the deep terrace reef of the south aspect of Cayman Brac Figure. 2.27 b) However, the families of serranidae are found in greater abundances on the deep terrace reef, with the scarids equally distributed between the shallow and deep terrace reefs (figure. 2.27 a; figure. 2.27 b). There is a noticeable near-absence of the genus kyphosidae on the deep reef on the south of that island; however, the shallow terrace reef boast of the healthy and thriving population.

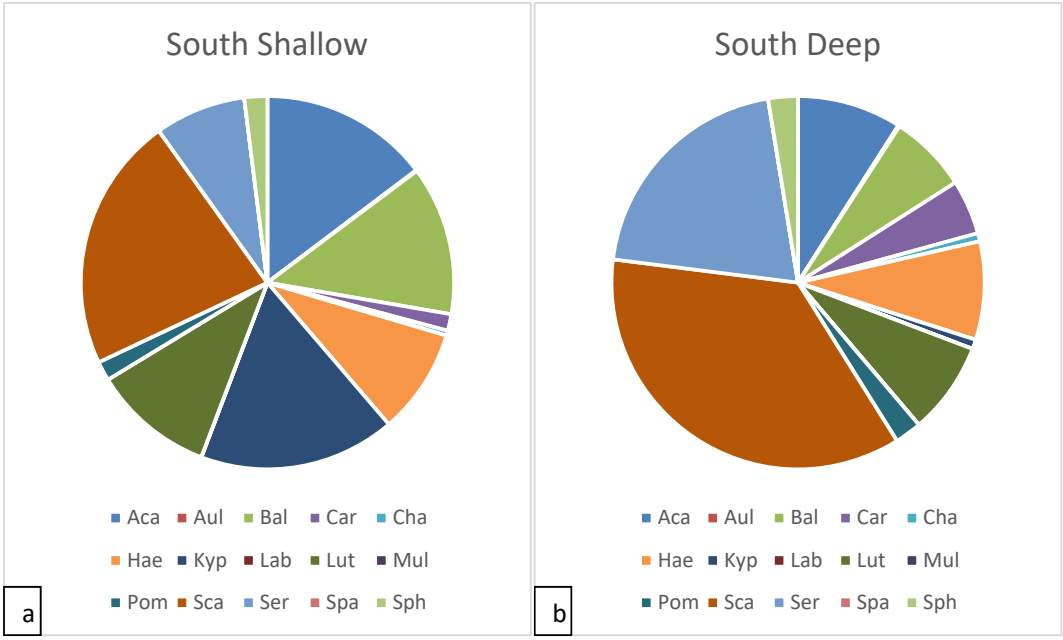


Figure 2. 27. Percentage make-up of the 15 family assemblages along the exposed southern aspect of Cayman Brac on (a) the shallow reef terrace (b) the deep reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae. (shallow n= 3, deep n= 3)

2..6.14 Reef fish assemblages, north moderately leeward aspect of Cayman Brac Cayman.

The north moderately leeward aspect of Cayman Brac shallow terrace reef fish family make-up is different when compared to its southern margin. The genus Kyphosidae (chubs) dominates the reef fish assemblages on the shallow terrace reef and scarids (parrotfishes) dominate the deep terrace reef (figure. 2.28 a; figure. 2.28 b). The five most prominent fish families found on the northern aspect of Cayman Brac on the shallow terrace reef are Kyphosidae (chubs) haemulidae (grunts), scarids (parrotfishes), lutjanidae (snappers), with acanthuridae (surgeon fishes) and serranidae (groupers) almost equal in distribution on the shallow terrace reef (figure. 2.28 a). The five most prominent fish families found on the deep terrace reef are scarids (parrotfishes), haemulidae (grunts), serranidae (groupers), balistidae (trigger fishes) and acanthuridae (surgeon fishes). Other families such as

carangidae (jacks), Kyphosidae (chubs), Labridae (wrasses), lutjanidae (snappers), Sparidae (porgies), Sphyraenidae (barracudas), Cheatodontidae (butterfly fishes), and Pomacanthidae (Angel fishes) are found in lesser amounts that make-up the reef fish assemblages on the north moderately leeward aspect of Cayman Brac.

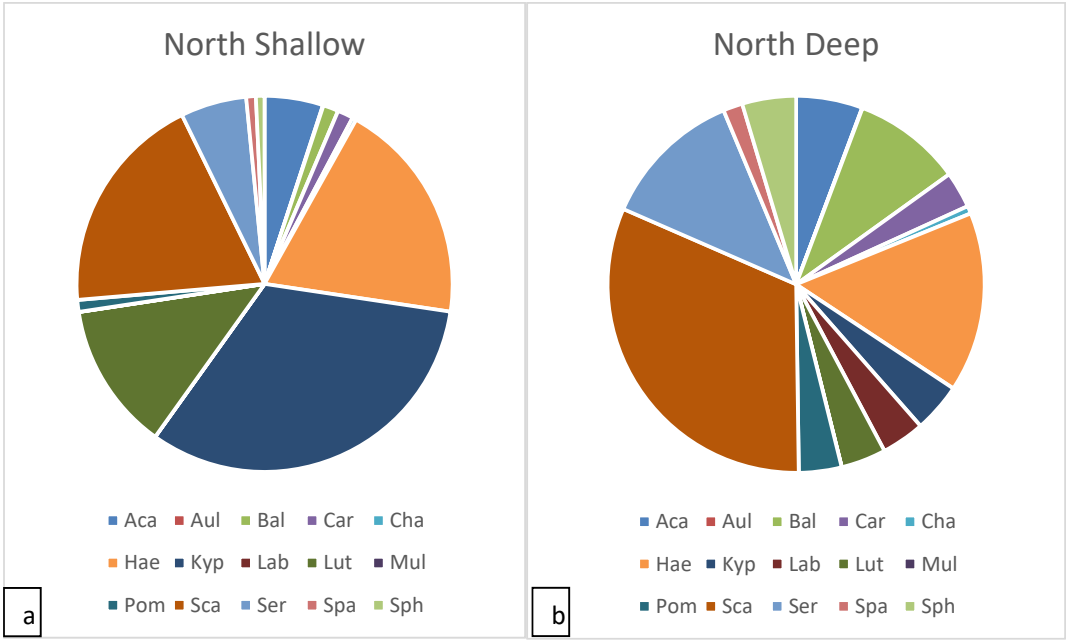


Figure 2. 28. Percentage make-up of the 15 family assemblages along the north moderately leeward aspect of Cayman Brac on (a) the shallow reef terrace (b) the deep reef terrace (data pooled, 2009-2012). Aca= Acanthuridae, Aul= Aulostomidae, Bal= Balistidae, Cha= Cheatodontidae, Hae= Haemulidae, Kyp= Kyphosidea, Lab= Labridae, Lut= Lutjanidae, Mul= Mullidae, Pom= Pomacanthidae, Sca= Scaridae, Ser= Serranidae, Spa= Sparidae, Sph= Sphyraenidae. (shallow n= 3, deep n= 3)

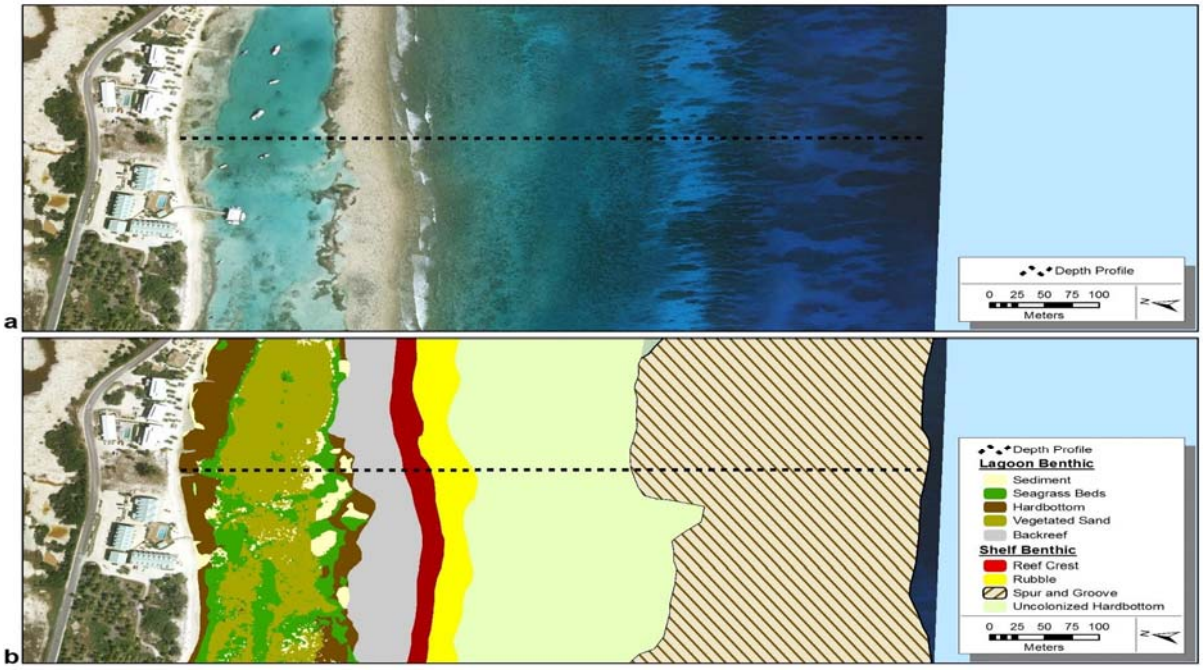


Figure 2. 29. 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the exposed southern aspect of Cayman Brac with Fringing reef.

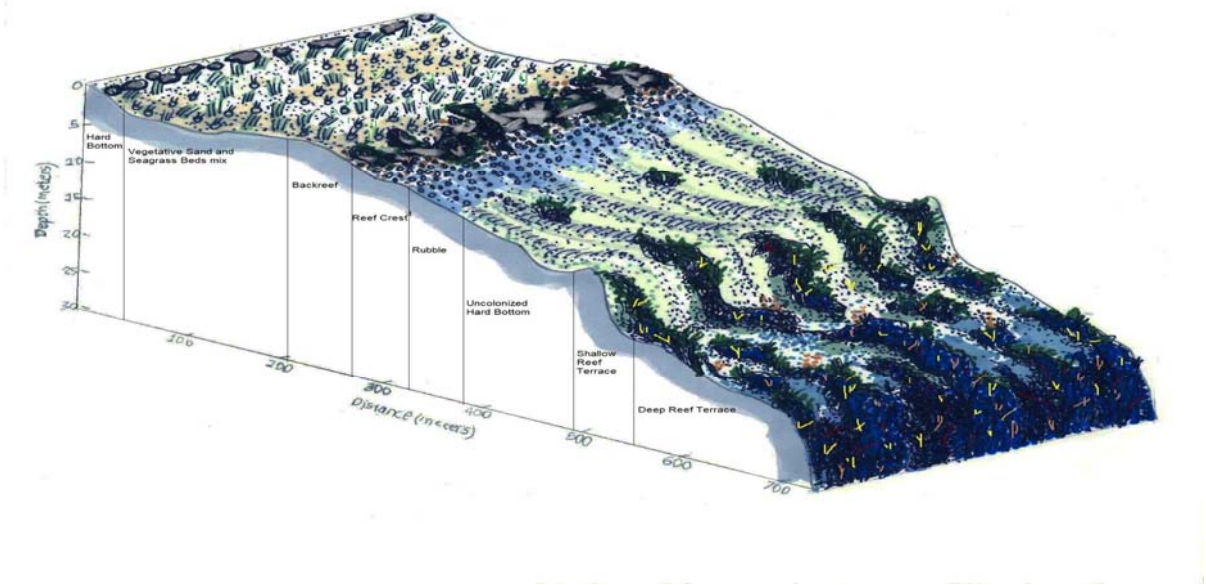


Figure 2. 30. 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Cayman Brac depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef present.

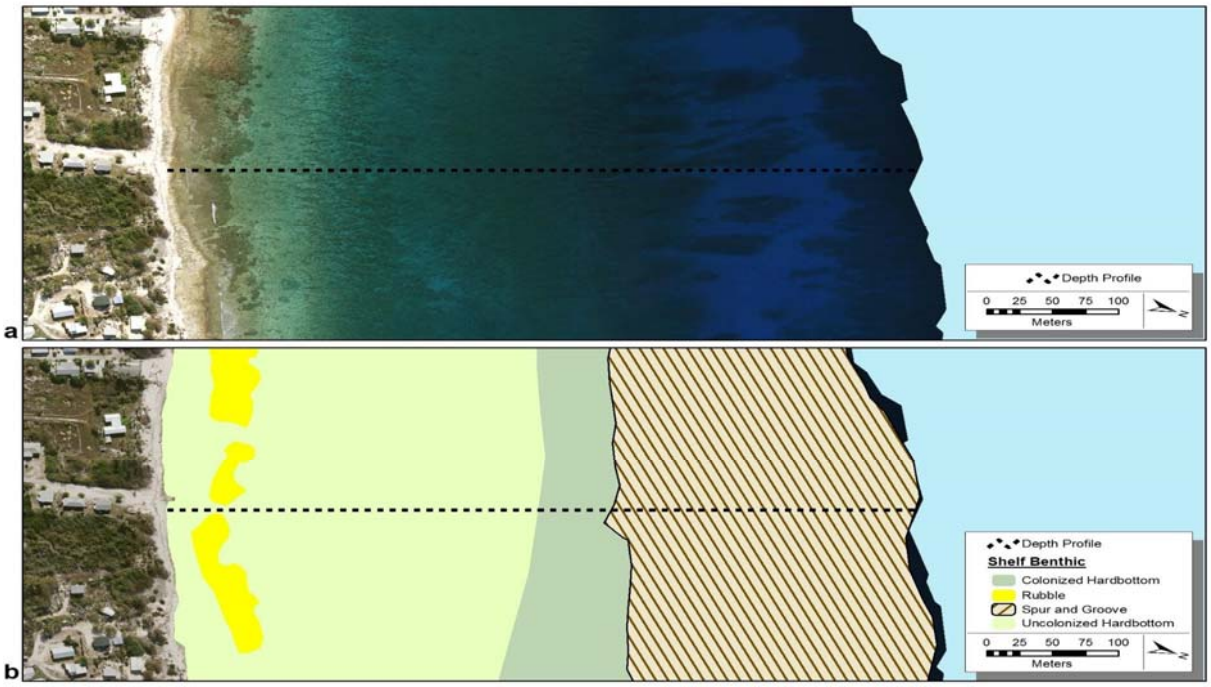


Figure 2. 31. 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the moderately leeward exposed aspect of Cayman Brac. Fringing Reef absent.

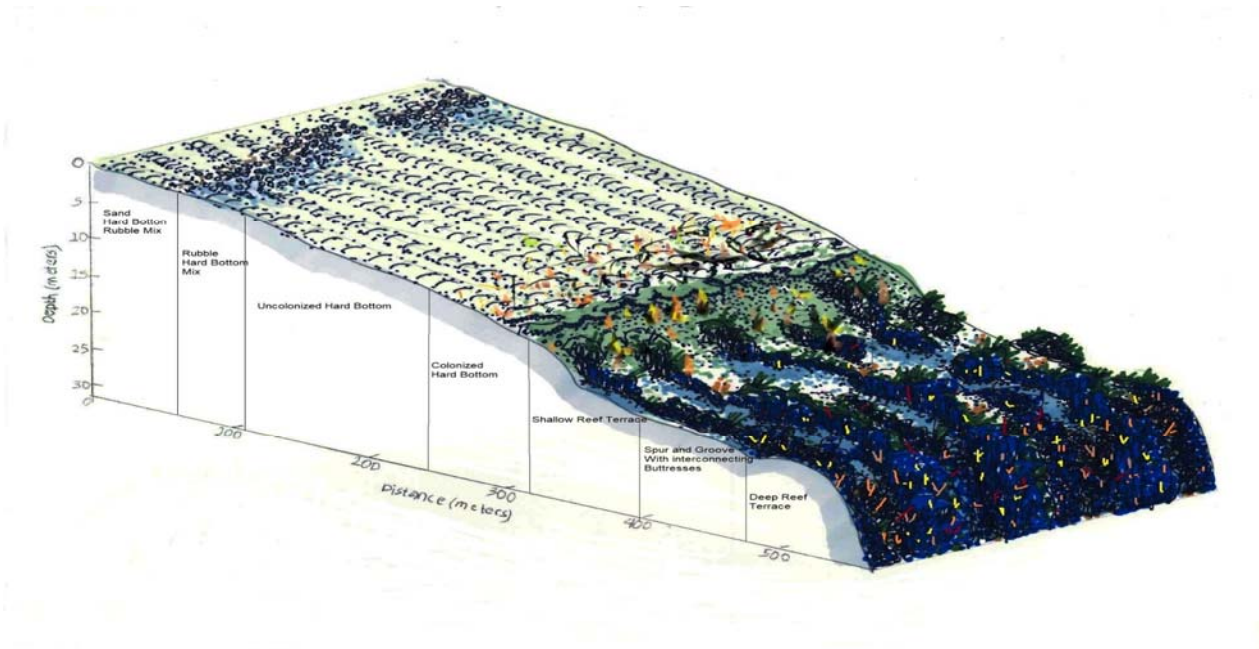


Figure 2. 32. 10 cm resolution, three- dimensional image of depth profile for the moderately leeward coast of Cayman Brac depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef absent.

2.7 Discussion and Conclusions

The main aim of this chapter was to assess and describe the benthos and fish composition of each of the 3 Cayman Islands. This included maps and sketches to detail the different types of coast found on each island habitats from the shoreline to the deep shelf which has never been done to date. Synonymous to most other islands in the Caribbean region, (Rigby and Roberts, 1976; Roberts, 1977; Logan, 1981; Roberts, 1983; Roberts, 1988; Fenner, 1993; Roberts, 1994; Logan, 1994; Blanchon, 1995; McCoy, 2004), the Cayman Islands coral reef profiles illustrate that 2 significant reef types surround them. A shallow wave dominated fringing reef that's found mostly on exposed coast and a deeper submerged reef that circumnavigates each island, with 2 seaward facing reef terraces; the shallow terrace reef and the deep terrace reef/shelf edge. The only variation in these two submerged reef development architecture is within the Bloody Bay / Jackson Point MPA area on the NW coast of Little Cayman, where the deep terrace reef is missing over a 2 km distance (Appendix 2.11 & Appendix 2.12). The variation in the different size landmasses of the 3 Cayman Islands, their orientation and exposure to prevailing winds and wave action have manifested itself in reef development and associated fish assemblages found on and around each island.

Both the shallow and deep terrace reefs as depicted on sketches are characterized by "spur and groove" submarine topography as described by Blanchon and Jones (1997), with valleys covered in sand and or rubble. The varying topographical rugosity of reef profiles from shore to shelf edge is driven by coastal exposure, with the southern coast reef topography more developed in the sister islands of Little Cayman and Cayman Brac than its northern moderately leeward siblings. In Grand Cayman reef profiles on the southern coast was much more rugose with much higher reef topography than the north. The western leeward coast of that island reef profile was much less flattened as expected for sheltered coastlines. Composition of the major benthic categories across islands mostly mirrors each other with macroalgae being the dominant benthos category, as in most islands in the Caribbean region (Graham *et al.,* 2013), on both their deep and shallow terrace reefs.

Fish families found across islands were also similar, with scarids being the dominant fish family, albeit with other respective fish biomass family differing depending on coast and depth. In Grand Cayman, however there was a notable low fish biomass for the fish family of Serraindae as compared to Little Cayman and Cayman Brac, with Little Cayman has the highest fish makeup of that fish family in its fish assemblages, possibly due to low fishing pressure (Henshall, 2009; Meir *et al*., 2011). Fish family make up for the Cayman Islands mirrored McCoy *et al.,* (2010), and Drommard *et al*., (2011) for the sister islands of Little Cayman and Cayman Brac and similar to findings of Pattengill-Semmens and Semmens (2002), and in a broader context, Valles and Oxenford's (2014) findings of the herbivore trophic group constituting the largest biomass in the Caribbean region.

Chapter 3. Protection effects on the coral reefs in and around the Cayman Islands.

Abstract

Coral reef protection and conservation in the Cayman Islands had its birth in 1986 with the establishment of a network of Marine Protected Areas (MPAs) across the Cayman Islands. However, since the establishment of the MPAs, Caymanian coral reefs are far from pristine, being subjected to a plethora of factors such as repeated catastrophic impacts of hurricanes, coral bleaching episodes and subsequent coral disease outbreaks. Regionally, these series of events have led to a "Phase shift" in which macroalgae now dominate the coral reefs. In the year 2009, the Caymanian reefs experience an acute localize mass coral bleaching event. This study aims to investigate the effect of that event, including protection effects on their coral reefs benthos and community structure. Benthos data were collected and sorted into 16 categories using four twenty meters underwater video transects at 55 sites across the Cayman Islands on the deep terrace and shallow terrace reef habitats between June to August for the years 2009 through to 2012. That data was then tested and explored between MPA and non-MPA sites for those 16 categories to access differences and effects of protection on those metrics, including their coral communities and structure over space and time. The benthic community structure amply demonstrated spatial and temporal trajectory patterns in regards to protection effects on the benthic habitat. Two meaningful interactions were found between factors underpinning the protection effects of MPAs on the benthos, which varied across Depth habitats, Coasts, Islands, and Years. The first was between factors; Depth and Coast nested within the factors Year, Island, Depth, and Protection status. The second significant interaction was between factors Year and Islands. *Post hoc* comparisons for this interaction revealed that the benthic community structure of Grand Cayman (GCM) and Cayman Brac (CB) differed between the years 2009 and 2011, with Little Cayman (LC) differing between all years of study, suggesting high variability amongst the coral community structure driving the changes documented. Correspondingly, SIMPER analysis demonstrated that the greatest dissimilarities in GCM were between years 2011 and 2012 (54%), with the lowest found in LC between the years 2009 and 2012 (39.9 %-40.5%). Macroalgae consistently accounted for between 61% and 78% of those similarities during the study period across the three Cayman Islands. Other substrates, such as sponge, octocorals, milliporids, and coral cover did not explain the observed patterns. This indicated that changes unfolding within the benthic community during the period of study were complex, comprising a combination of Depth, Coast, Island and Protection status. When islands benthic community structure were compared, the SIMPER analysis showed the largest dissimilarities between GCM and LC (40%), whereas the lowest was found between CB and LC (21.7%). A confluence of correlating factors such as Depth, Coast, Island, Year, and Protection status accounted for >98% of the total variance for the benthic community structure changes during the study period. Overall, results show that protection has had very little influence of the benthic community structure, possibly due to all benthos being protected, whether located inside or outside of pf protected areas in the Cayman Islands since 1978. The changes in the major benthos categories accounting for the variation of the benthic community structure and patterns documented across the three Cayman Islands over the years of this study, occurred irrespective of protection status, suggesting that protection status had no effect. However, results did indicate that the coral reefs of the Cayman Islands demonstrated resistance by no measurable mortality during the 2009 coral bleaching event, more so, the island of Grand Cayman.

Keywords: Marine protected areas, coral reefs, shallow terrace reef, deep terrace reef, phase shifts, resiliency, community structure.

3.1 Introduction

Coral reefs contain an abundance of biologically diverse ecosystems and habitats (McClannahan *et al.,* 2002; Hoegh-Guldberg *et al.*, 2007; Brander *et al.*, 2007), including one-third of all known marine species (Veron *et al.,* 2009). Also, they are home to >30 animal phyla of the 34 known globally, as compared to tropical rain forests, which according to the World Wildlife Federation (2009) contain only nine of the recognized animal phyla. Despite their richness of species and ecosystem niche abundance (Small *et al*., 1998; Roberts, 2003; Bouchet, 2006), they are mostly valued for the goods and services that they provide, including coastline protection (Spalding *et al.,* 2001; Villanoy *et al.,* 2012), food security and livelihoods in the context of tourism trade. Given the fact that more than 100 countries globally have their coastlines fringed by coral reefs, they are pivotal in driving the economies of many nations in the global tropics (Moberg & Folke, 1999; Costanza *et al*., 1997; Costanza *et al.,* 2014). Wilkinson (2004) indicated that >20% of coral reefs globally have already been destroyed; 24% are in grave danger; with a further 26% predicted to collapse over time, leaving < 50% to remain in the category of low risk. Furthermore, Hughes et al., (2003) predict that by 2030, 60% of reefs globally will have been destroyed. However, despite the grim outlook concerning the survival of coral reefs, they have existed over the past 240 million years (Veron *et al.*, 2009).

3.1.1 Coral Reef resilience

As coral reefs decline due to the growing human activities, there is a growing list of collaborative studies (Hughes *et al.,* 2010; McClanahan *et al.,* 2012; Jackson *et al.,* 2014; Graham *et al.,* 2015; Heron *et al*., 2017 Maynard *et al.,* 2017) documenting their degradation in terms of cover and functionality, which catalyzed the concept of "coral reef resiliency and resistance". Subsequently, coral reef scientists, including the scientific community at large, have focused on these concepts. However, studies go back decades where scientific investigations have attempted to quantify these by measuring coral reef attributes along with their biological metrics, including their ability to recover after an event or disturbance (Connell 1978; Connell 1997; Vitousek *et al*., 1997; Pearson 1981). Although this term is seemingly redefined with the passage of each decade, coral reefs are facing new threats that erode their health and challenge their ability to cope with detrimental human-induced environmental changes.

3.1.2 Threats to Coral Reefs, Globally, Regionally and locally

Although coral reefs have existed for the past 240 million years (Veron *et al*., 2009), their precipitous decline over the past century is seemingly attributed to the evolution of human beings, paralleling observations documented in the Caribbean region. However, the past half-century has witnessed a progressive decline in coral reefs, with climate change, bleaching and subsequent coral disease being the most protuberant factors accelerating this decline (Bruno *et al.,* 2003; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Pandolfi *et al.,* 2005). Carbon production of Caribbean reefs was predominantly due to corals from the genus *Acropora*; however, since the emergence of White Band Disease (WBD), they have all but diminished to <10% of what existed during the late 1970s (Aronson and Precht, 2001; Bruckner, 2003). This problem was exacerbated by

dangerous and destructive hurricanes (Woodley *et al.,* 1981; Woodley *et al.,* 1989; Rogers *et al.,* 1989; Woodley, 1992; Gardner *et al.,* 2005). According to Woodley *et al.,* (1981), "hurricane Allen" caused widespread and extensive damage to the shallow reefs, including the *Acropora* thickets on the north coast of Jamaica. Additionally, coupled with the historical records of overfishing of that island (Jackson *et al*., (1997; 2001), it became the "poster child" for boom and busted the coral reefs for the region. Although the coral reefs of the Cayman Islands did not escape the plethora of factors and disturbances other neighboring islands experienced, including hurricane Allen in 1980 and hurricane Gilbert in 1988 (P. Bush, unpublished data), it is still considered one of the positive examples of resilient reefs, showing evidence of resiliency (Gall 2009; Barton 2010; Bruckner,2010; Campbell 2010; Looker 2011; Hillyer 2011; Warrender, 2013; Price, 2015; Sivajyodee, 2016; Sibley 2017).

3.1.3 Coral Bleaching

Global climate change that has spurred coral bleaching and subsequent coral disease outbreaks have been recognized as the most major threat to reef health, causing mortality. Owing to rising sea surface temperatures, Crabbe (2008) expects the frequency of bleaching in the Caribbean to increase to an annual event by 2040. The first reports of coral bleaching go back as far as 1911, encapsulating the observations of L.R Cary on Bird Key in the Florida Keys, USA. Similar reports were recorded in 1929.

Timeline of Known Coral Bleaching Events

1911: Bird Key Reef, Florida

1929: Great Barrier Reef

1961: Key Largo, Florida USA

1979: Caribbean region, including the Florida Keys USA

1980: Localized bleaching in 1980 (Caribbean region)

1983: Global bleaching

1987: Caribbean region

1988: Hawaii and then other reefs

1991: Caribbean region

1994: Caribbean region

1995: Caribbean region

1998: Acute global bleaching, mass bleaching in Caribbean region

2002: Great Barrier Reef

2005: Eastern Caribbean Region, mass bleaching

2009: Localized mass coral bleaching, Cayman Islands region, NW Caribbean

2010: South-east Asia and Indian Ocean territories

2015 & 2016: Worst global bleaching on record (Great Barrier Reef, Indian Ocean territories)

Hooidonk *et al*. (2012), Berkelmans *et al*. (2004), Goreau and Hayes (1994), CARICOMP, (1997), Gold and Smith (1990) Williams and Bunkley-Williams (1990). Bush and McCoy (unpublished data).

According to Hoegh-Guldberg, (1999) and Hughes *et al.* (2010), the single largest threat to coral reef resiliency is temperature-induced coral bleaching brought on by climate change. However, with different coral species exhibiting different tolerance levels to cope with climate change, the structure of coral reefs species community will most certainly change rather than disappear, with the most temperature tolerant ones emerging as the frontrunners (Hughes *et al.* 2003). Perhaps, those changes will become permanent (Gardner *et al.* 2003), as coral reefs adapt. Furthermore, as coral bleaching events are expected to become an annual event between the year 2020 and 2050, (Hoegh-Guldberg, 1999), at the very least every six years as proposed by Hughes *et al.,* (2018) it is highly likely that some coral species will disappear from the Caribbean reefs. This will only compound the problems Caribbean reefs are facing, which is already considered to be species poor and compounded by the challenges of low species diversity, low functional redundancy and lower resilient capacity, as compared to other regions like the Pacific and Indian ocean locations (Hughes *et al,*. 2005).

3.1.4 Coral Algal Phase Shift

Until the late 1970s/ early 1980s, coral reefs in the Caribbean region were dominated by scleractinian corals; after that, a transition manifested with a shift from coral dominated to an algal dominated reef environment. This phase-shift is well chronicled in the global tropics (Done 1992; Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014) and in the Caribbean, it is believed to be brought on by the disappearance of the main grazer on Caribbean reefs, the sea urchin *Diadema antillarium* (Lessios, 1984) and the outbreak of coral diseases, particularly the white-band disease of the *Acroporid* corals (Gladfelter, 1982) that dominated the shallow reefs of the Caribbean. Aggravating this problem and acting as a catalyst was the widespread over-fishing of herbivorous fish stocks (Jackson, 1997; Jackson *et al,*. 2001; Jackson *et al,*. 2014), which stripped coral reefs of their full capacity to function ecologically, (Russ, 1991; Jennings and Lock, 1996; McClanahan *et al.*, 2000; Micheli *et al.,* 2014). These "man-made" problems further lowered their resiliency by creating a trophic imbalance of fish on Caribbean coral reefs.

3.1.5 Reef structure of the Cayman Islands

Of the 65 different species of scleractinian corals found in the Caribbean region, 48 are found in the Cayman Islands (C. McCoy, unpublished data). The Cayman Islands has extensive and well-developed coral reef structures of classic Caribbean spur and groove formations. Grand Cayman is home to a total of 2,085 hectares of spur and groove reef area, with 293 hectares located within that islands Marine Protected area, Little Cayman 827 hectares, 84 hectares in its Marine Protected areas and Cayman Brac has 1189 hectares with 179 hectares of its spur and groove reef within its Marine Protected areas. Their reef architecture is very similar to neighboring islands in the western Caribbean, dominated by submarine topography (Rigby and Roberts, 1976; Roberts, 1977; Logan, 1981; Roberts, 1983; Roberts, 1988; Fenner, 1993; Roberts, 1994; Logan, 1994; Blanchon, 1995; McCoy, 2004). A shallow terrace reef is located at a depth of 5-10 m, which Shinn (2011) suggests is an old sea cliff, which is a common feature to coral reefs globally, often referred to as the global 10 m notch attributed to wave cut notch at that depth. With a deep terrace reef at 15-20 m, the reef architecture at that depth is indeed dominated by some spur and groove, but mostly by impressive massive coral buttresses orientated perpendicular to the shelf edge with frequent sand channels interspersed between them, terminating in a deep fore-reef with a precipitous drop-off at an average depth of ~20 meters. Exceptions include the eastern and western locations of each island where, in some instances, the shelf's fore-reef is known to extend much further off-shore to a depth of 45-60 m before tapering off into abyssal depths; the islands' shelf widths average ~500 m, with some locations being <200 m. However, the shelf extends much further towards the east and west ends of each island, reaching 1500 m in some instances. The coral reef community structure is similar to other areas of the western Caribbean, dominated by massive *Orbicella annularis*, *Orbicella faveolata*, *Montastraea cavernosa,* and *Orbicella franksi* on the deeper reefs. Other relatively abundant species that are commonly found around the Cayman Islands include *Siderastrea siderea*, *Colpophyllia natans* and *Diploria strigosa*. Octocoral communities are made up of large colonies of *Pseudoplexaura porosa*, *Pseudoterogorgia americana,* and *Eunicea* spp., among others. Meanwhile, sponges are common, varying in size and form, depending on depth and wave exposure. (See chapter 2 for additional information). It is assumed that Caribbean reefs including the reefs of the Cayman Islands lack functional redundancy when compared to their Indo Pacific cousins due to low diversity amongst coral and fish species (Nybakken, 2001, Bellwood *et al.,* 2004), having less than half the amount of species of each when compared. According to Gardner *et al.* (2003), between the late 1970s and the year 2003, coral cover in the region decreased from 50% to a mere 10%, representing an 80% reduction in coral cover. However, the coral reefs of the Cayman Islands have exhibited their tenacity to survive despite withstanding multiple stressors such as coral bleaching and disease outbreak events (Carpenter *et al.,* 2008; Bruckner and Hill, 2009; Miller *et al.,* 2009; Weil and Cróquer, 2009; Hooidonk *et al,*. 2012), including the mounting evidence that corals that survive seemingly have greater resilience (McClanahan *et al*., 2009), in addition to coping with a lowering pH (Edmunds *et al.,* 2014), it is highly probable that Cayman reefs will continue to survive and flourish well into the next millennia.

This chapter aims to explore their effects of the Marine Protected Areas (MPAs) in the Cayman Islands in enhancing coral reef benthos within their MPAs as compared to their non-MPAs. Their current status will be assessed and quantified over space and time across the 3 Cayman Islands as to MPA effectiveness, including the ability of Cayman Islands coral reefs capacity to resist and or recover from disturbances. The factors depth (deep and shallow reef terraces), coast (north, southwest) and individual islands (Grand Cayman, Little Cayman, Cayman Brac) benthos will be assessed to determine if protection has had any effects on benthos community structure and composition.

3.2 Hypotheses and Objectives

H_{01} : Protected Areas (MPAs) of the Cayman Islands will have no effect on benthic community structure within their MPAs.

Objective 1: This question will be addressed using data collected for 16 benthos categories. Benthos coral community structure within and outside of Marine Protected Areas will be statistically tested over space and time to determine protection effect.

H_{02}: The benthic community structure across Habitats (Deep & Shallow) and Years (2009-2012) will not differ after the 2009 localize acute coral bleaching event.

Objective 2: To address this question, benthos data collected between the years 2009 and 2012 on the deep and shallow reef terraces of Marine Protected Areas and non-Marine Protected Areas of Grand Cayman, Little Cayman, and Cayman Brac. Benthos data will be analyzed testing for effect of the acute localized bleaching on benthos across islands.

H_{03}: There will be no significant differences between benthos located within Marine protected Areas when compared to outside of marine protected areas across spatial and temporal scales during the period of study.

Objective 3: To assess and test for significant differences, data collected for years of study will be analyzed by coral point count with excel extensions and tested for significant differences for 16 benthos categories and compared between areas of protection, coast, island, year and depth.

3.3 Methods (see chapter 2 method for map details)

3.31 Study sites:

Video transect data was collected from a total of 55 survey sites; Grand Cayman (GCM) n = 27, Little Cayman (LC) n = 16) and Cayman Brac (CB) n = 12, between June and August 2009 (see Chapter 2, Figure. 2.2). The sites were selected for their similar geomorphological characteristics. Twenty-three sites were located within existing MPAs (GCM = 9, LC = 8, CB = 6) and 32 were located outside (GCM = 18, LC = 8, CB = 6). To account for Depth, sites were distributed between the shallow and deep reef terraces. The only Marine protected Area in Grand Cayman is located on the western leeward coast. To account for this fact, sites were distributed across all aspects for that island (northern, southern and western). With more sites deployed on the outside of that islands MPA in an effort to account for this confounding factor in this study and to test for protection effects.

3.3.2 Data Collection. SCUBA diving was used to survey the benthos along four 20 m transects at each of the 55 sites using a Sony Handycam HDR-CX550 video camera contained in a Stingray Light and motion housing. The start of each transect was randomly selected, with the first transect always laid nearest to the GPS location of the site and transects laid parallel to the shoreline with a minimum gap between them of 20 m. Transects were permanently marked using rebar stakes during the survey years. A fiberglass measuring tape was then laid between the stakes to mark the transect and to use as a guide to follow. The camera was held at the height of 0.63 m above the substrate, giving coverage of 0.25 m^2 of the substrate in the frame. The video camera was held at a 15° angle to minimize the loss of the 3D structure of the reef and consequently taxonomic resolution. A speed of 0.08 ms^{-1} was identified as optimum filming speed during preliminary testing, giving an approximate total time per transect of four minutes depending on rugosity. Depth was recorded at the beginning and end of each transect.

3.3.3 Data analysis:

3.3.3.1 Video data: 200 images per video transect were frame grabbed using Adobe Elements version 10.0 frame grabbing software, of which 50 images per transect were randomly chosen for analysis using Minitab 17.1.0 statistical software calculation function, make pattern data, a simple set of numbers, randomly sample from the column. Images were modified using Adobe Photoshop to enhance images for clearer benthos identification. The analysis of the images was conducted using Coral Point Count with Excel extensions (.cpce) image analysis software (Kohler and Gill, 2006). This software was chosen due to the effectiveness of processing a large number of high-quality images. It projected a selected set of numbers randomly on the image on the computer screen with an identification code file containing all known Atlantic species of benthos, including categories and population estimates as outputs. A cumulative frequency curve was plotted which determined that the optimum number of points to use was 20 per frame, after which additional counts provided little gain in species number. Points were distributed randomly on images, giving a total of 1000 points per transect and 4000 points per site resolution. Benthos located directly below points were identified to

species level whenever possible, classified into one of the 16 assigned categories including the morphological shape of the coral colony and substrate categories (table 3.1).

3.3.3.2 Statistical Analysis: Output data from .cpce was imported into Primer 6 + Permanova in 2 forms, one summarizing the major categories for multivariate analysis and one with all benthos species for univariate/descriptive statistics. Data were first square root transformed to down-weight occurrence of highly abundant species, whereby normalizing data and increasing homogeneity before any statistical analyses were conducted. PRIMER (Plymouth Routines in Multivariate Ecological Research) v6. + PERMANOVA. Multidimensional Scaling (MDS), Analysis of similarities (ANOSIM) and Similarity Percentage Analysis (SIMPER) was used to test if sites belonging to each coast were different across the years. Bubble plots on the MDS were used to visualize this in time and space. Parametric tests using PRIMER v6. + PERMANOVA were used and displayed in a PERMANOVA table and represent the interactions and displayed as a series of Principle component analysis (PCO's) demonstrating patterns and ordinations of sites. *Post-hoc* analysis using t-test based on permutations provided pairwise comparisons for every combination of factors for significant differences. For coral cover and macro algal cover per island per year (MPA vs. non-MPA), one-way ANOSIM test were used.

3.3.4 Coral community structure:

To investigate coral community structure of each island, benthos was grouped into the following 16 categorical variables (table 3.1)

Table 3.1 Benthic and subject categories that the benthos was categorized into for analysis.

Category Variables	
1) SCLR	Corals, (Hard Corals)
2) GORG	Gorgonians, Soft Coral
3) SPON	Sponges
4) ZOAN	Zoanthids
5) TUNI	Tunicates
6) MALG	Macroalgae
7) TURF	Turf
8) CCA	Coralline algae
9) OTHR_BI	Other Biotic
10) DCOR	Dead Coral
11) DGOR	Dead Gorgonian
12) PAV	Limestone Pavement
13) RUBB	Rubble
14) SAND	Sand
15) GAPS	Gaps, holes, shadows
16) OTHR_AB	Other abiotic

These categories were further separated to protected and non-protected sites on the deep and shallow terrace reefs on each of the three islands (n=55). Sites distributed across the shallow and deep fore reef terraces of the Cayman Islands were sampled between June through to August annually during the study period.

3.4 RESULTS

3.4.1 General findings of coral/algal distribution around the Cayman Islands:

This chapter aimed to assess the benthos community and structure across the 3 Cayman Islands, with an emphasis on protection effects offered by their Marine Protected Areas (MPAs). Firstly graphs (figure 3.1, a-f) are presented to set coral cover and macroalgae abundances in context for Grand Cayman (GCM), Little Cayman (LC) and Cayman Brac (CB), of those two metrics over space and time (figure 3.1). Thereafter effects of protection on depth, coast, and island will be explored. Species community structure ranged from 33 species found in 2009 which belonged to 10 families to a maximum of 36 species in 2011 from 20 families of scleractinian corals during this study. One way ANOSIN results (years / protection status) showed that coral cover between Marine Protected Areas (MPAs) and non Marine Protected Areas (non-MPAs) for GCM and CB did not differ over the years of study one way ANOSIM (year/protection); Global R= 0.011, P= 0.19 ; Global R= 0.02, P= 0.07 respectively (figure 3.1 a-e). Conversely, significant differences were observed for the island of Little Cayman between MPAs and non-MPAs for years 2009, 2011 and 2012, one-way ANOSIM (year/protection status); Global R= 0.001, P= 0.001. Further pairwise comparisons showed that 2009 MPA differed from 2009 MPA (R= 0.091, p=.007), 2011 MPAs differed 2011 non-MPAs (R= 0.19, p=.001), 2012 MPAs differed from 2012 non-MPAs (R= 0.155, p=.001) (figure 3.1 c, table 3.2 a). When coral cover over the years were compared for LC, (one way ANOSIM, year / Island/ coral) 2009 differed from 2012 (R= 0.14, p= 0.013), 2009 differed from 2012 (R= 0.036, p= 0.03), however the year 2011 did not differ from year 2012 (R=- - 0.005, p= 0.05) (figure 3.1c, table 3.2 b)

For macroalgal cover, protection effect was significant between MPAs and non-MPAs for Grand Cayman and Little Cayman for year 2011, one way ANOSIM (year / island / protection status), R= 0.162, P= 0.001 ; R= 0.054, P= 0.027 respectively (figure 3.1 b, d; table 3.3 a, b) . No significant differences were detected for Cayman Brac. Further pairwise comparisons for macroalgal cover across years for Grand Cayman showed that the year differ 2009 differed from 2011 (R= 0.585, P= 0.001), 2009 differed from 2011 (R= 0.241, P= 0.001) and the year 2011 differed from 2012 R= 0.32, P= 0.001) (table 3.3 c). For the island of Little Cayman 2009 differed from 2011 (R= 0.685, P= 0.001), 2009 differed from 2011 (R= 0.536, P= 0.001) and the year 2011 differed from 2012 R= 0.992, P= 0.001), (table 3.3 d).

Table 3.2 (a) Pairwise test comparisons for Marine Protected Areas (MPAs) vs. non-Marine Protected Areas (non-MPAs), Little Cayman scleractinian coral cover for years (2009, 2011, 2012). (b) Pairwise test comparisons for Little Cayman scleractinian coral cover between years (2009, 2011, 2012). Red indicates significant differences.

	Years	R statistic	P value	Permutation	Island
(a)	2009 MPA / 2009 non-MPA	0.091	**0.007**	999	Little Cayman
	2011 MPA / 2011 non-MPA	0.19	**0.001**	999	
	2012 MPA /2012 non-MPA	0.155	**0.001**	999	
(b)					
	2009, 2011	0.041	**0.013**	**999**	Little Cayman
	2009, 2012	0.036	**0.03**	**999**	
	2011, 2012	-0.005	**0.5**	**999**	

Table 3.3 Pairwise test comparisons for Marine Protected Areas (MPAs) vs. non-Marine Protected Areas (non-MPAs), Grand Cayman (a) and Little Cayman (b) for macroalgal cover, years (2009, 2011, 2012). Pairwise test comparisons for GCM macroalgal cover between years (2009, 2011, 2012) Grand Cayman (c) Little Cayman (d). Red indicates significant differences.

	Years	R statistic	P value	Permutation	Island
(a)	2009 MPA / 2009 non-MPA	0.031	0.16	999	Grand Cayman
	2011 MPA / 2011 non-MPA	0.162	**0.001**	999	
	2012 MPA /2012 non-MPA	0.217	0.06	999	
(b)	2009 MPA / 2009 non-MPA	-0.017	0.79	999	Little Cayman
	2011 MPA / 2011 non-MPA	0.054	**0.027**	999	
	2012 MPA /2012 non-MPA	0.024	0.0132	999	
(c)	2009, 2011	0.585	**0.001**	999	Grand Cayman
	2009, 2012	0.241	**0.001**	999	
	2011, 2012	0.63	**0.001**	999	
(d)	2009, 2011	0.685	**0.001**	999	Little Cayman
	2009, 2012	0.536	**0.001**	999	
	2011, 2012	0.002	**0.001**	999	

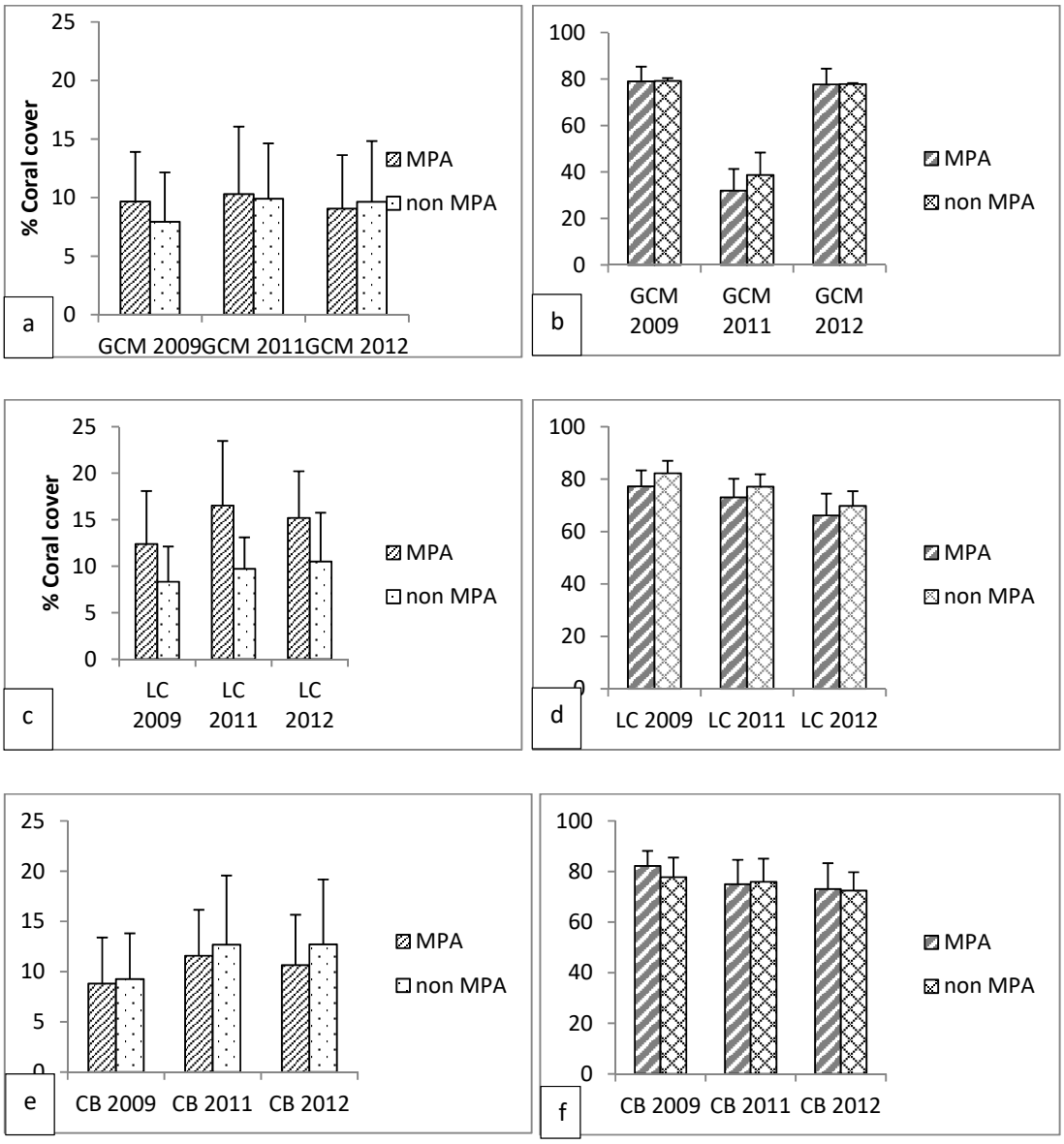


Figure 3.1 Mean percentage cover +/- SE for coral cover and macroalgae of MPAs and non-MPAs across year and islands (a) Grand Cayman (GCM) coral cover (b) GCM macroalgal cover (c) Little Cayman (LC) coral cover (d) LC macroalgal cover (e) Cayman Brac (CB) coral cover (f) CB macroalgal cover for years of study (2009-2012). n=55 (Grand Cayman MPA, n=9, non-MPA, n=18; Little Cayman MPA n=8, non-MPA n=8, and Cayman Brac MPA, n=6, non-MPA n=6,

3.4.2 Main Effects of Marine Protected Area's on Benthic Community Structure

The PERMANOVA partitioning analysis of the benthic community structure illustrated clear spatiotemporal patterns as regards to protection effects of MPAs on the benthos. Two meaningful interactions were found amongst the factors be significant, with each suggesting that the effect of the MPA on the benthos varied across depth, coasts, islands, and years (table 3.4). The first significant interaction was found between depth and coasts nested within the factor Year, Island, Depth and Protection status (Permanova, F = 73.1, df = 24, p = 0.001, coefficient of variation = 12.6 %; table 3.4). According to the finding, the temporal and spatial changes recorded

in the benthic community structure during the period of study were complex and their trajectories were predicated on a combination of factors such as depth (habitat type), the particular coast, island, and protection status. Partition of the variance indicated that 12.6 % of the total variability was attributed to this complex interaction between fixed and random factors (table 3.4). A combination of concurrently interacting factors such as the depth (shallow and deep habitats), coast (geographical position of sites within an island), island (Grand Cayman, Cayman Brac and Little Cayman), years (2009, 2011, 2012) and level of protection (MPAs and Non-MPAs) explained more than 98 % of the total variance recorded for the benthic community structure during study period (table 3.4). The importance of each island in determining the temporal variation within the benthic community structure was further supported by a significant interaction between the factors year and islands (Permanova = F = 20.7, df = 4, p = 0.001, coefficient of variation = 24.54; table 3.4). However, protection status alone was non-significant, illustrating that factor was not an important driver of changes in the benthos community over space and time (Permanova = F=16.3, df=1, p=0.18; table 3.4)

Table 3.4 PERMANOVA partitioning (Permutation) Analysis of Variance based on Bray Curtis similarity for major benthic categories Factors are: Yr= Years (2009-2012, De = Depths (shallow and deep reef terraces), P = Protection (MPA), Co = Coast (north, south, west, nested in island), Is = Islands (Grand Cayman, Little Cayman, Cayman Brac). Text in **red** indicates significant differences.

Source	df	SS	MS	Pseudo-F	P(perm)	perms	CV%
Yr	**2**	**83055**	**41527**	**26,173**	**0.001**	**999**	**16.08**
De	**1**	**6388**	**6388**	**40.261**	**0.019**	**998**	**44.80**
P	1	2593.7	2593.7	16,347	0.18	999	20.71
Is	**2**	**35580**	**17790**	**10,609**	**0.001**	**998**	10.11
Yr*De	2	7928.2	3964.1	24.984	0.069	997	54.52
Yr*P	2	520.13	260.06	0.16391	0.97	997	0.39
Yr*Is	**4**	**1.39E+09**	**34779**	**20.741**	**0.001**	**999**	**24.54**
De*P	1	2657.2	2657.2	16.747	0.186	999	3.36
De*Is	2	3455	1727.5	10,302	0.393	998	1.16
P*Is	2	8080.2	4040.1	24,094	0.062	998	52.49
Yr*De*P	2	981.05	490.52	0.30916	0.893	999	0.39
Yr*De*Is	4	2290.3	572.57	0.34146	0.946	998	0.39
Yr*P*Is	4	7187.6	1796.9	10,716	0.392	999	2.45
De*P*Is	2	2007.2	1003.6	0.59851	0.707	998	0.39
Yr*De*P*Is	4	524.13	131.03	7.81E+02	0.999	998	0.39
Co(Yr*Is*De*P)	**24**	**42015**	**1750.6**	**73.191**	**0.001**	**997**	**12.62**
Res	600	1.44E+09	239.19				15.85
Total	659	5.52E+09					

According to *post hoc* comparisons for this interaction, the benthic community structure in Grand Cayman (GCM) and Cayman Brac (CB) only differed between 2009 and 2011, whereas in the case of Little Cayman (LC), significant differences were found between all years (table 3.5). This indicates that protection status on that island was perhaps driving those changes As regards to the benthic community structure, SIMPER analysis highlighted the biggest average dissimilarities between the years 2011 and 2012 in GCM (54.4%), whereas the lowest was found in LC between the years 2009 and 2012 (39.9% - 40.5%, table 3.6). The underlying differences between turf and macroalgae consistently explained 61 % to 79% of the average similarities recorded across the Cayman Islands during the study period (table 3.6).

Table 3.5 Post hoc comparisons for Year * Island Interaction. Text highlighted in red indicates significant.

Brac Years	t	P	Permutation	Island
2009, 2011	**65.781**	**0.001**	**998**	Cayman Brac
2009, 2012	13,179	0.209	999	
2011, 2012	**41.741**	**0.004**	**999**	
2009, 2011	**92.207**	**0.001**	**997**	Grand Cayman
2009, 2012	16,999	0.137	999	
2011, 2012	**45.233**	**0.002**	**998**	
2009, 2011	**88.314**	**0.001**	**999**	Little Cayman
2009, 2012	**39.744**	**0.004**	**998**	
2011, 2012	**72.133**	**0.001**	**996**	

Table 3.6 Similarities percentage analysis for the Interaction Year * Island Text in red indicates significant.

Benthic category	2009	2011	Contribution (%)	Commulative (%)	Average Diss (%)	Island
TURF	32.47	0.05	39.99	39.99		
MALG	47.53	75.46	35.08	75.07		
SCLR	9.03	12.13	7.83	82.9		
CCA	1.73	4.79	5.29	88.19		
SPON	3.12	2.37	4.03	92.22	40.5	
Benthic category	2011	2012	Contribution (%)	Commulative (%)	Average Diss (%)	Brac Cayman
MALG	75.46	45.72	40.75	40.75		
TURF	0.05	26.58	33.2	73.95		
SCLR	12.13	11.68	8.17	82.12		
CCA	4.79	7.55	6.67	88.79		
GORG	2.86	4.08	3.36	92.15	39.9	
Benthic category	2009	2011	Contribution (%)	Commulative (%)	Average Diss (%)	
DCOR	1.07	27.6	26.36	26.36		
MALG	47.73	25.4	22.94	49.29		
TURF	31.35	11.18	20.54	69.84		
PAVI	0	9.52	9.46	79.29		
SCLR	8.51	10.03	5.17	84.46		
CCA	1.23	5.72	4.77	89.23		
GORG	6.22	4.6	4.28	93.51	50.3	Grand Cayman
Benthic category	2011	2012	Contribution (%)	Commulative (%)	Average Diss (%)	
MALG	25.4	61.26	33.52	33.52		
DCOR	27.6	0.28	25.11	58.63		
TURF	11.18	16.25	14.8	73.43		
PAVI	9.52	0.51	8.42	81.85		
SCLR	10.03	9.44	4.88	86.73		
GORG	4.6	4.34	3.8	90.53	54.4	
Benthic category	2009	2011	Contribution (%)	Commulative (%)	Average Diss (%)	
TURF	26.9	0	39.56	39.56		
MALG	52.83	75.37	33.55	73.11		
SCLR	10.35	13.12	9.68	82.79		
CCA	1.11	4.68	5.57	88.36		
GORG	4.84	2.68	4.73	93.09	34	
Benthic category	2009	2012	Contribution (%)	Commulative (%)	Average Diss (%)	
MALG	52.83	29.54	38.52	38.52		
TURF	26.9	38.16	23.1	61.62		
CCA	1.11	8.1	11.62	73.24		Little Cayman
SCLR	10.35	12.84	10.34	83.58		
GORG	4.84	5.09	5.37	88.95		
SPON	1.85	2.95	3.76	92.7	30.5	
Benthic category	2011	2012	Contribution (%)	Commulative (%)	Average Diss (%)	
MALG	75.37	29.54	43.63	43.63		
TURF	0	38.16	36.33	79.96		
SCLR	13.12	12.84	6.16	86.12		
CCA	4.68	8.1	4.66	90.78	52.5	

An analysis of principal coordinates clearly illustrates these results. For instance, for the interaction at the highest level (i.e., Coast (Island x Year x Depth x Protection Status), the ordination depicted clear patterns (figure. 3.2 a). With a total of 88.2% of the variance being explained by the two first PCO axes, samples corresponding to each year for all three islands ordinated along these two PCOs (figure. 3.2 a). The first PCO

was highly correlated (ρ = 0.8) with two variables: turf and macroalgae, whereas the second PCO was correlated with the percentage of dead corals. Unpredictably, other substrates like sponge, octocorals, milleporids, and live coral cover did not corroborate the observed patterns. As per these findings, the samples ordinated along the PCO1 in accordance to their differences in either macroalgae or turf, whereas the samples ordinated along the PCO2 had different percentages of dead coral cover (figure. 3.2 a).

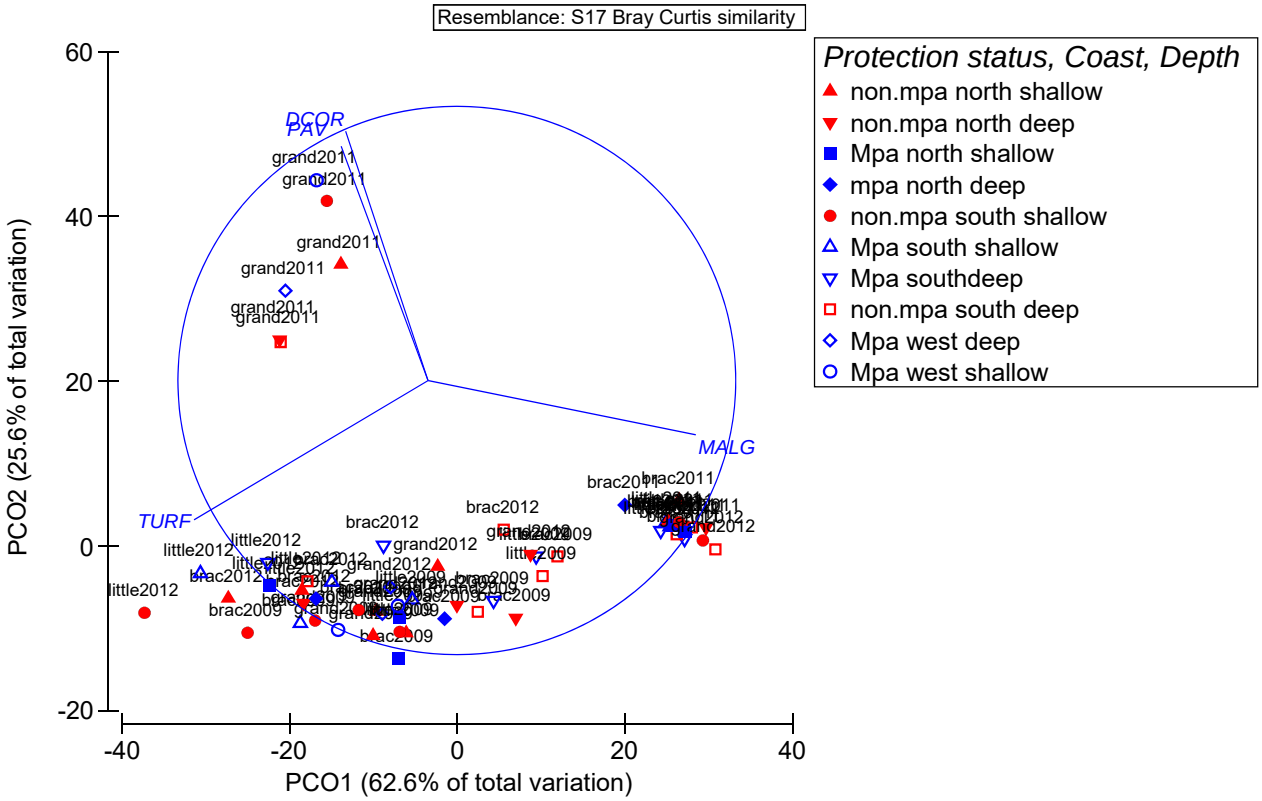


Figure 3.2 a. Analysis of Principal Coordinates (PCO) illustrating spatial and temporal patterns of the community's major benthic categories across years (2009, 2011 and 2012), Islands (Brac= Cayman Brac, Grand = Grand Cayman, Little= Little Cayman), Habitats (deep and shallow), Coast (north, south, west) and Protection status (MPA vs. non-MPA). DCOR= dead coral, TURF= turf algae, PAV= limestone pavement.

For example, dead coral cover reached up to 40% on GCM, particularly during 2011, regardless of the protection status (figure. 3.2 b). During this year only, the north non-MPA area of GCM remained with dead coral cover values below 16% (figure 3.2 b). For other islands, it remained below 10% during the entire study period. This trend was consistent between coasts and across islands (Figure. 3.2 b).

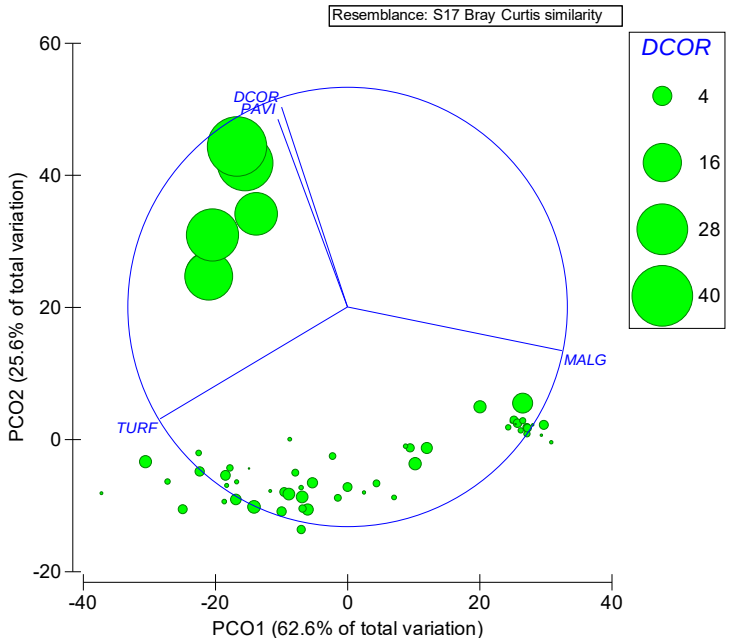


Figure 3.2 b Analysis of Principal Coordinates (PCO) demonstrating spatial and temporal patterns of dead coral across the years (2009, 2011 and 2012), islands (Cayman Brac, Grand Cayman and Little Cayman). DCOR= Dead coral, TURF= Turf Algae, MALG= Macroalgae, PAV= Limestone pavement. Bubbles represent the year, island and abundance of dead coral.

Data showed that macroalgae were particularly abundant outside of the protected area in GCM; however, its cover was extremely variable in time (figure 3.1 b, Figure. 3.2 c). Additionally, the results suggest that macroalgae have been marginally decreasing in LC and CB, regardless of protection or coast in those two islands (figure. 3.1 d, figure. 3.1 f, figure. 3.2 c). Notably, low dead coral cover recorded in GCM after 2011 and an increase of cover of macroalgae may be an indicator of these overgrown, dead corals (figure. 3.2 b-c). The opposite trend was observed in LC, characterized by a lower cover of dead coral and macroalgae but a higher cover of turf algae (figure. 3.2 c-d). During the study period, the benthic community structure in LC remained very similar regardless of the level of protection status and the coast, at least for the level of resolution of major substrate types (figure. 3.2 b-d).

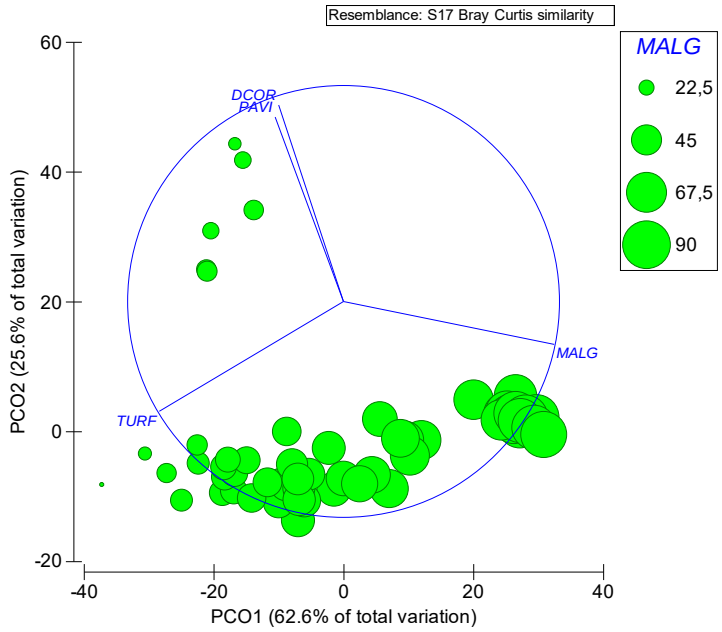


Figure 3.2 c Analysis of Principal Coordinates (PCO) depicting spatial and temporal patterns of macroalgae algae across the years (2009, 2011 and 2012), islands (Cayman Brac, Grand Cayman and Little Cayman). MALG= macroalgae. Bubbles represent the year, island and abundance of macroalgae.

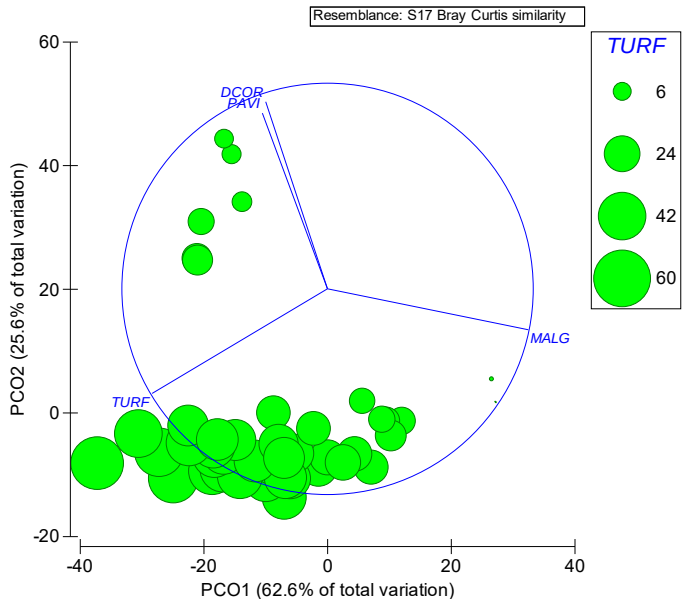


Figure 3.2 d Analysis of Principal Coordinates (PCO) illustrating spatial and temporal patterns of turf algae across years (2009, 2011 and 2012), islands (Cayman Brac, Grand Cayman and Little Cayman). TURF= turf algae. Bubbles represent year, island and abundance of turf algae.

Cayman Brac (CB) meanwhile presented an interesting case. When the study began in 2009, MPAs and Non-MPAs in this island were very similar in terms of the abundance with regard to the major benthic reef organisms to Little Cayman (figure. 3.2 b-d); however, in 2011 the abundance of macroalgae increased and became very

similar to the protected and non-protected coasts of GCM in 2012. Conversely, during the last year of this study, it was observed that the benthic community structure in CB had become substantially different to Grand Cayman and more similar to Little Cayman, as was the case in 2009 (figure 3.2 b-d). These results undoubtedly indicate that 2011 did introduce significant variation into the community structure, particularly in GCM and CB. After 2011, the GCM's benthic community has remained stable. On the other hand, an increase in macroalgae was recorded in 2011 in Cayman Brac; however, since then, the benthic community has moved away from that state. The results clearly show that the role of Cayman Islands MPAs in preventing and/or building opportunities for recovery was ambiguous, with regard to the benthos changes occurring through time, regardless of whether it was protected or not.

3.4.3 Benthic Community Changes across depth and Islands; Variation across Years

With regard to the depth, the results from an analysis of principal coordinates indicate significant variation (in the benthic community structure) between Depths, Islands, and Protection Status (figure. 3.3 a). With more than 80% of the total variances explained by the two first PCOs, samples ordinated along the PCO1 in accordance to their differences in dead coral and macroalgae, whereas the samples ordinated along PCO2 differed in their percentage of scleractinian coral cover and turf algae (figure. 3.3 a). Importantly, higher values of live coral cover (15-20%) were found in deeper and shallower depths (habitats) of Little Cayman and Cayman Brac; no obvious trends were recorded between areas with different levels of protection (figure. 3.3 b).

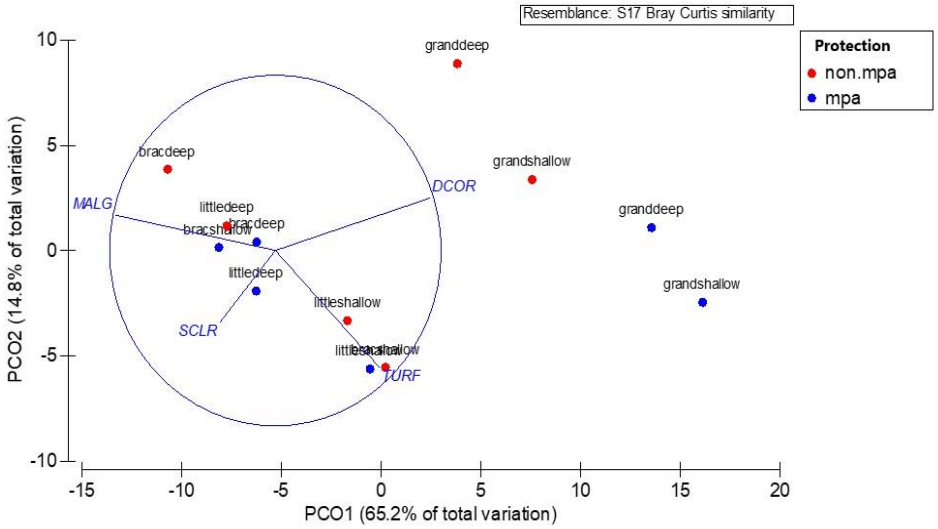


Figure 3.3 a Analysis of principal coordinates (PCO) illustrating spatial patterns across habitats (deep and shallow), islands (grand= Grand Cayman, Little= Little Cayman, Brac= Cayman Brac) and protection status. SCLR= scleractinian corals, TURF= turf algae, DCOR= dead coral, MALG= macroalgae.

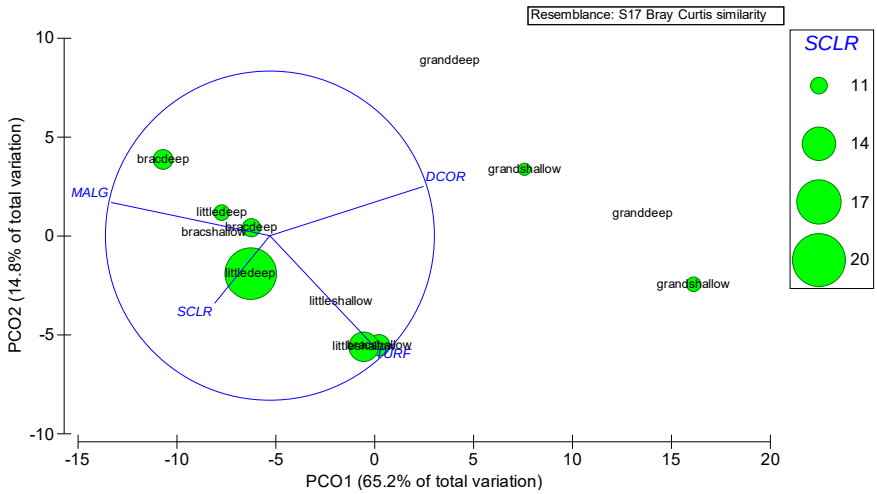


Figure 3.3 b Analysis of principal coordinates (PCO) demonstrating spatial patterns of samples in accordance with habitats (deep and shallow), islands (grand= Grand Cayman, Little= Little Cayman, Brac= Cayman Brac) and protection status. SCLR= scleractinian corals, TURF= turf algae, DCOR= dead coral, MALG= macroalgae. Bubble plots represent the composition of scleractinian corals explaining distribution across depths (habitats).

Dead coral cover was common across habitats in GCM, regardless of coast and the level of protection, ranging from 2-13% (figure. 3.3 c). There was a clear spatial pattern for macroalgae, showing higher cover in deeper habitats of LC and CB (50-70%) as compared to the shallow habitats of GCM (34-46%, figure. 3.3 d). Meanwhile the turf varied from 15 % to 25 % across all depths (habitats), regardless of the protection level, the coast or island (figure. 3.3 e). Higher cover of turf algae was normally associated with shallower depths at all islands, but particularly across coasts of LC and CB (figure. 3.3 e).

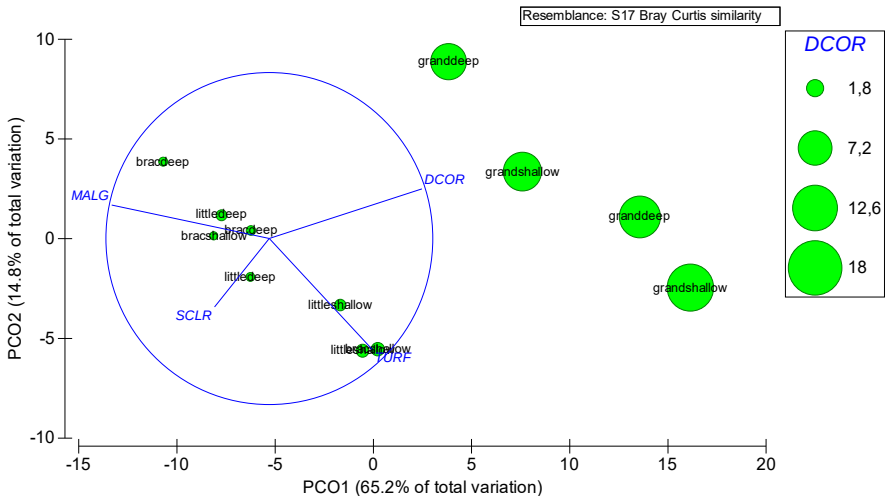


Figure 3.3 c Analysis of principal coordinates (PCO) illustrating spatial patterns of samples according to habitats (deep and shallow), islands (grand= Grand Cayman, Little= Little Cayman, Brac= Cayman Brac) and protection status. SCLR= scleractinian corals, TURF= turf algae, DCOR= Dead coral, MALG= macroalgae. Bubble plots represent the composition of dead corals explaining distribution across depths (habitats).

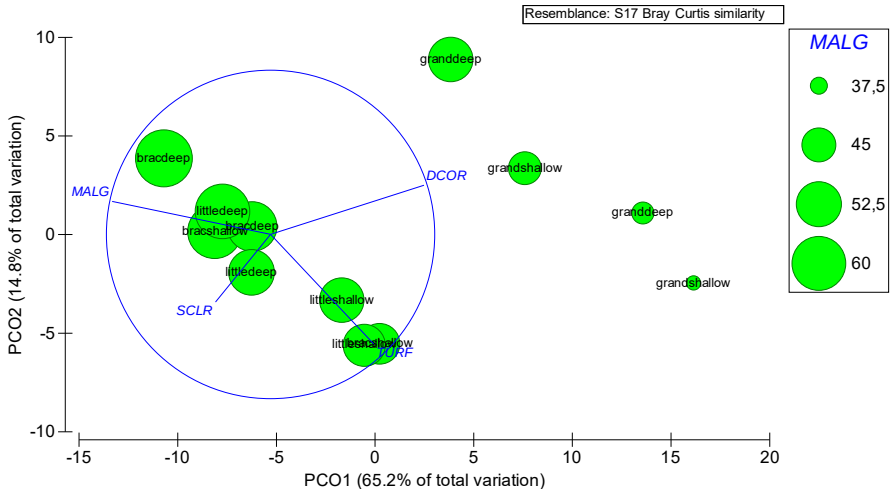


Figure 3.3 d Analysis of principal coordinates (PCO) illustrating spatial patterns of samples in accordance with habitats (deep and shallow), islands (grand= Grand Cayman, Little= Little Cayman, Brac= Cayman Brac) and protection status. SCLR= Scleractinian corals, TURF= Turf algae, DCOR= Dead coral, MALG= Macroalgae. Bubble plots represent the composition of macroalgae explaining distribution across depths (habitats).

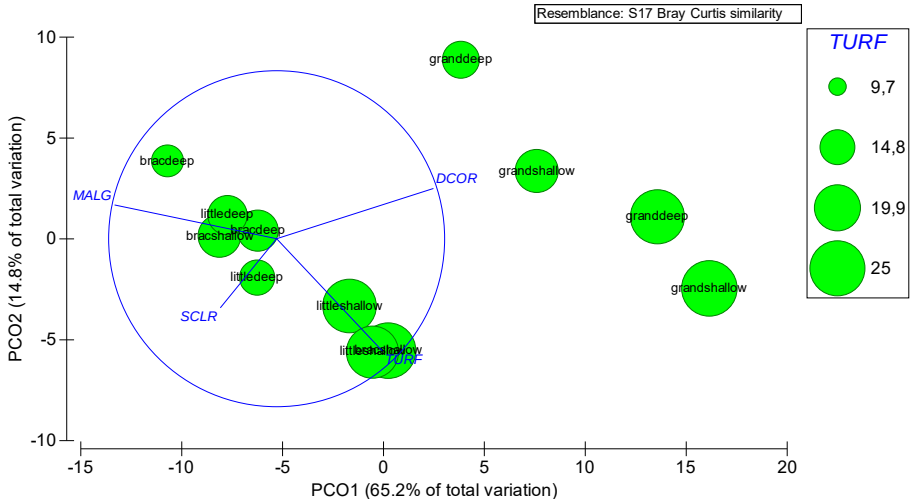


Figure 3.2 e Analysis of principal coordinates (PCO) depicting spatial patterns of samples according to habitats (deep and shallow), islands (grand= Grand Cayman, Little= Little Cayman, Brac= Cayman Brac) and protection status. SCLR= scleractinian corals, TURF= turf algae, DCOR= dead coral, MALG= macroalgae. Bubble plots signify the composition of turf algae explaining distribution across depths (habitats).

3.4.4 Patterns in Benthic Community across Island and Years

Results from the analysis of principal coordinates clearly indicate a significant variation in the benthic community across the islands and years, with GCM clearly exhibiting a marked difference in benthic community structure for the year 2011 (figure. 3.4 a). With a total of >95% of the variance explained by the two first PCO

axes, samples corresponding to each year for each island ordinated along these two PCOs (figure. 3.4 a). The first PCO was strongly correlated with two variables: turf algae (figure. 3.4 b) and macroalgae (figure. 3.4 c) for the years 2009 and 2012; meanwhile the second PCO was correlated with a high abundance of dead corals for 2011. The year 2011 clearly demonstrated separation of the islands in addition to a distinct shift in the benthic community structure for GCM with a high abundance of dead corals for the year (figure. 3.4 d), and a much lower abundance for LC and CB. This was indicative of an event that mostly affected the island of GCM.

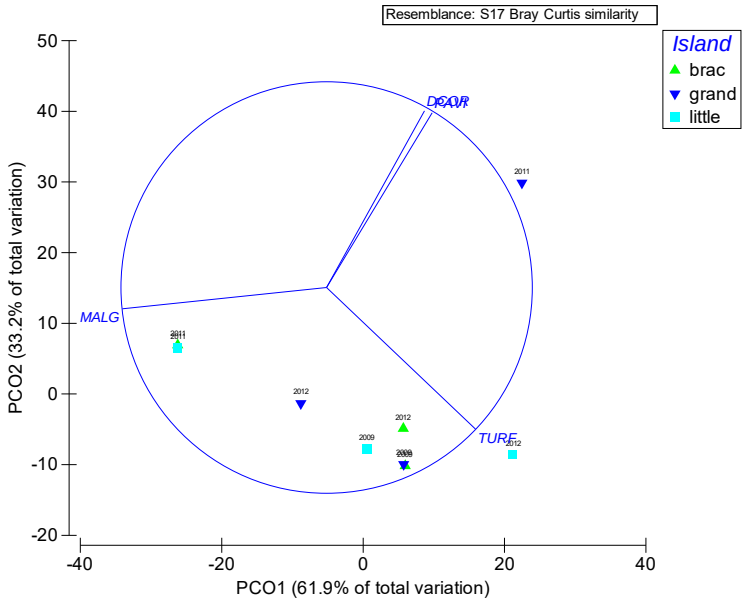


Figure 3.4 a Analysis of principal coordinates (PCO) demonstrating temporal patterns in the benthic community structure across islands, brac= Cayman Brac, grand= Grand Cayman, little= Little Cayman. TURF= turf algae, DCOR= dead coral, MALG= macroalgae.

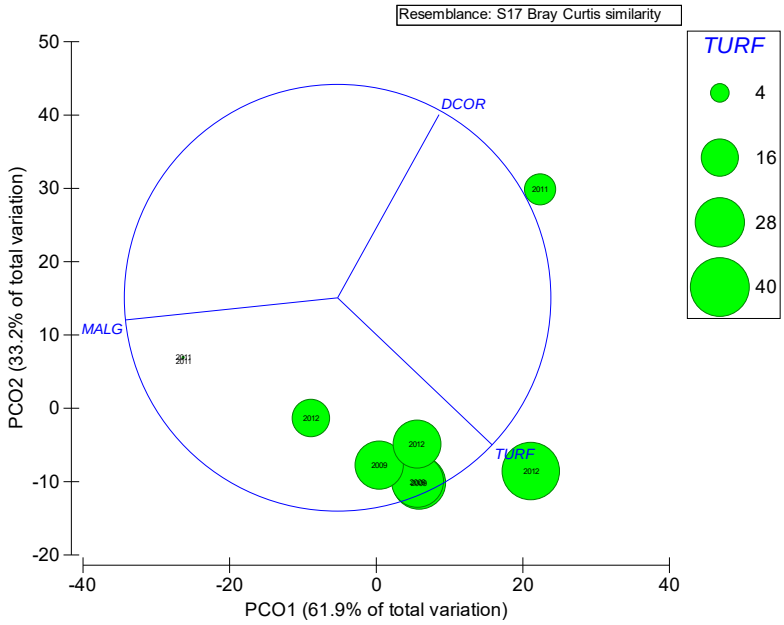


Figure 3.4 b Analysis of principal coordinates (PCO) illustrating temporal patterns in the benthic community structure across islands. TURF= Turf algae, DCOR= Dead coral, MALG= Macroalgae. Bubble plots denote the composition of turf algae explaining its distribution across the years (2009, 2011 and 2012)

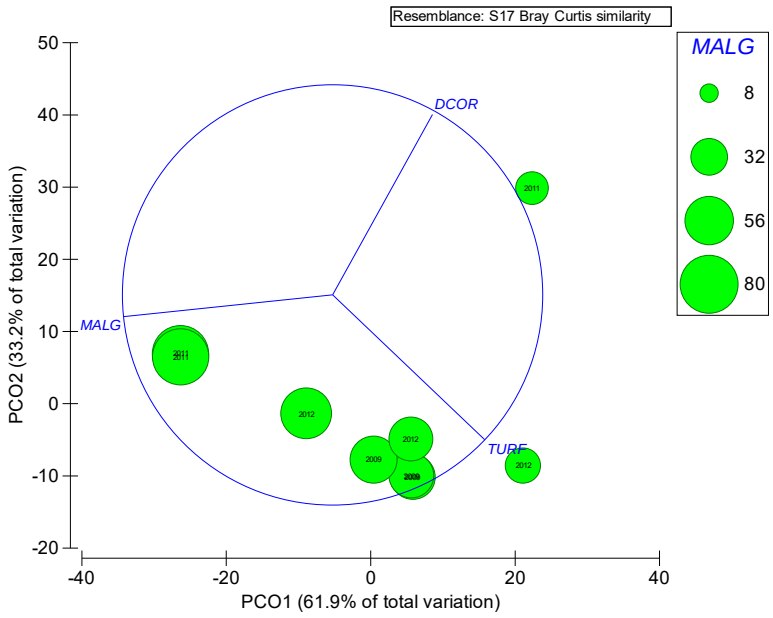


Figure 3.4 c Analysis of principal coordinates (PCO) showing temporal patterns in the benthic community structure across islands. TURF= Turf algae, DCOR= Dead coral, MALG= Macroalgae. Bubble plots depict the composition of Macroalgae explaining its distribution across years (2009, 2011 and 2012)

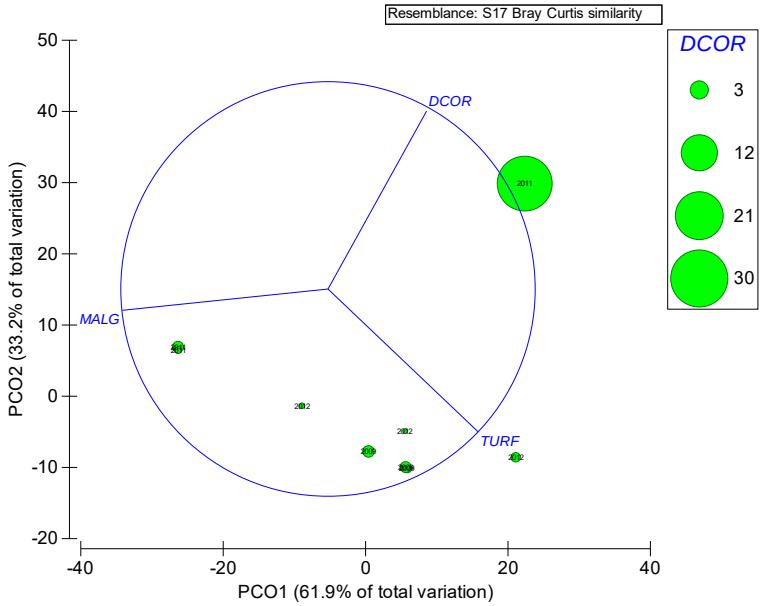


Figure 3.4 d Analysis of principal coordinates (PCO) illustrating temporal patterns in the benthic community structure across islands. TURF= Turf algae, DCOR= Dead coral, MALG= Macroalgae. Bubble plots denote the composition of dead coral explaining distribution across years (2009, 2011 and 2012)

Findings suggest that the benthic community structure was extremely variable between depths (habitats); this factor explained a greater variation (Permanova, F=40.2, df=1, p= 0.019, coefficient of variation = 44.80%; table 3.3) as compared to protection status, which was non-significant. During the study period, data showed a lower coral cover in the shallow habitats across the coasts of GCM, regardless of protection status. This indicates that corals in the shallow-water habitats in GCM's coral reefs were more vulnerable to changing environmental conditions resulting in a declining coral cover as compared to the sites that are located at deeper habitats. This pattern was observed for both MPAs and non-MPAs located on different coasts of that Island.

3.5 Discussion

3.5.1 Protection Effect on Benthic Community Structure

The community composition of Cayman Islands coral reefs recorded during this study clearly illustrates an algal dominated reef environment, well documented by other scholars (Done 1992; Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014). Results demonstrate that the protection effects of Cayman Islands MPAs on the benthos were negligible, irrespective of protection status, except for the island of Little Cayman (LC), where the higher coral cover was found with that islands protected areas. The benthos varied across depths (deep /shallow), coasts (north, south, and west), island (GCM, LC, CB) and years (2009, 2011, 2012). These significant interactions demonstrated that the temporal and spatial changes taking place within the benthic community during the period of this study were multifaceted, with a mix of random factors

(coast & island) and fixed factors (protection status, depth and year) driving their different trajectories. This is not surprising as the shifts in the benthic composition are well documented across the Caribbean region (Garner *et al*., 2003: Hughes *et al.,* 2010). However, they are mostly driven by bleaching events and subsequent outbreaks of coral disease (Aronson & Precht, 2001; Jones *et al.,* 2008; Jackson *et al.,* 2014), which can further trigger disruption of the benthos community (Croquer & Weil, 2009). These complex interactions explained >98% of the total variance recorded over the study period, with each island determining the temporal variation within its benthic community; this is further supported by a significant interaction between the factors year and islands explaining 24.54% of variation observed, with depth alone accounting for 44.8% and year 16.08%. Possible explanations for this observation could include the population status of each island, the anthropogenic activities and impacts on the benthic communities of each island. The localized mass bleaching event in 2009 experienced mostly by GCM (C. McCoy, unpublished data) and Little Cayman (Hooidonk *et al*, 2012) may have played a pivotal role in shaping the trajectory of the benthic communities across the period of this study and each island. This is congruent with the findings of McCoy *et al.*(2010) and Drommard *et al.* (2011) that each island fish assemblages were possibly attributed to the different fishing pressures experienced by each island due to the population status of each island. However, post hoc comparisons showed that the benthic community structure only differed between the years 2009 and 2011 in Cayman Brac and GCM, whereas significant differences were found in Little Cayman between all years. Furthermore, the recorded differences across the Cayman Islands during this study period explained 88.2% of variance and consistently accounted for the differences between turf algae, macroalgae and dead coral (Figure 3.2 a);the 2 former categories explained 62.6% of the variance and were highly correlated (p=0.8), thus indicating the shift in benthic composition from being coral dominated to algal dominated reefs as per the findings of Done (1992); Goreau, (1992); White *et al*. (2000); Jackson *et al. (*2001); Gardner *et al.* (2003);Hughes *et al*. (2003); Bellwood *et al.* (2004); Hughes *et al.* (2005); Graham *et al,* (2006); Jackson *et al.* (2014) and as a direct result of the erosion of keystone algal grazer *Diadema antillarium* in 1983/1984 (Lessios et al, (1984), compounded by the overfishing of herbivorous fishes (Hughes, 1994; Roberts, 1995; Chabanet *et al.*, 1997; Jackson *et al.,* 2001; Jackson *et al.,* 2014). Though factors like euthrophociation and nutrient input from establishments such as golf courses may be the primary drivers of algal blooms, the Cayman Island has no riverine systems or agriculture. As a result, it's nutrient input from land base point sources is negligible. The latter, dead coral accounted for 25.6% of the variation (Figure 3.2 d). One striking observation was that dead coral increased to >40% on GCM, particularly for the year 2011, regardless of protection status (figure 3.2 d). However, the presence of dead coral is a short term variation as will most likely be

removed during subsequent storms. This result parallels the observations noted by C. McCoy (unpublished data) that bleaching was more severe on GCM than on the sister islands of Little Cayman and Cayman Brac, despite observations documented by Hooidonk *et al*. (2012) for Little Cayman. Additionally, for the year 2011, only the non protected areas on the north coast of GCMshowed dead coral values below 16%, whereas Little Cayman and Cayman Brac demonstrated dead coral cover <10 % for the entirety of the study period and underpinned a pattern that was consistent between coasts and across islands (Figure 3.2 a). This observation adds further evidence to the fact that GCM experienced an unprecedented localize bleaching event, far greater in severity than Little Cayman or Cayman Brac, which was congruent with the observations of C. McCoy (unpublished data), including the presence of dead coral on that island. However GCM's live coral tissue sampled for the year 2011 did not reveal a decline in live coral tissue (Figure 3.2 a); instead, it surprisingly demonstrated an increase, which was a positive signal of coral reef resiliency, possibly a byproduct of the acute bleaching in 1998 or the mild 2005 episode, whereby the corals repopulated themselves with more heat tolerant zooxanthellae. Macroalgae meanwhile decreased to its lowest level throughout the study period in Grand Cayman for the year 2011 (figure 3.2 c). This was contrary to expectations, possibly attributed to the water temperatures exceeding the upper limit of macroalgae tolerance and causing severe macroalgae mortality on the island. This suggests that macroalgae cannot tolerate high water temperatures for extended periods, leading to denuding the reef of macroalgae in extreme conditions. This observation might prove to aid the recovery of Caribbean corals by stripping macroalgae from the reef and freeing up space for new corals to settle. The observation of coral bleaching and recovery without measurable mortality, paralleling a reduction and subsequent mortality of macroalgal cover possibly suggests that corals have a much more robust capacity to adapt to higher than normal oceanic water temperatures as compared to macroalgae. This seemingly has enabled the reefs of GCM to resist and recover fully after the localized mass bleaching event of September 2009, with no measurable mortality of its scleractinian corals, unlike the case of the macroalgae. The 2.5 times (MPA) and 2 times (non-MPA) reduction in macroalgae for the year 2011 in GCM (figure 3.1 b / figure 3.2 c) and the rise in dead coral (Figure 3.2 d) is analogous to Looker's (2011) findings of MPA 28.03% +/- 2.08 SE and non-MPA 45.48% +/- 2.93 SE macroalgae, and similar to the findings by Cambell (2010) of MPA 30.65% ±11.64% SE and non-MPA of 44.86% ±16.06% SE macroalgae in GCM. This observation suggests that coral mortality from a previous event was overgrown by the macroalgae, then becoming exposed when it suffered mortality during the bleaching event of September 2009. However by 2012, this low macroalgae cover had re-established itself, increasing to values observed prior to the bleaching event of 2009 of MPA 78 % +/- 6.33 % SE, and non-MPA of 79 %, +/- 5.6% SE macroalgae

coverage in GCM (figure 3.1 b / figure. 3.4 c). An analysis of macroalgal data for Little Cayman and Cayman Brac showed quite a different trajectory, showing a high and consistent amount on macroalgae on their respective reefs throughout the study period, with protection status not showing any effect (figure 3.2 c). However, this could partly be attributed to the fact that the two islands had experienced two hurricanes within a 2-week period in November 2008, with the latter belonging to the high category 4. According to Mumby & Steneck (2008), hurricanes are a major contributor that usually causes the domination of degraded reefs by macroalgae; this hypothesis is supported by the findings of Roger *et al.* (1991) who observed that the Hurricane Hugo had impacted the US Virgin Islands in 1989, causing a 40% decrease in coral cover and triggering a phase-shift from coral dominated to algal dominated reefs. Since the Cayman Islands is considered to be in the path of "Hurricane Alley", it confronts hurricanes rather frequently, in which then causes their reefs to have a high macroalgal cover (Turner *et al.,* 2013). Additionally, hurricane damage to reefs has been recorded to depths >20 m and can play a pivotal role in shaping the coral community structure (Sheppard *et al.,* 2009). Moreover, hurricanes are forecasted to be more frequent and stronger in the future (Wilkinson, 2008); the outlook does not look encouraging for Cayman Islands coral reefs. Furthermore, the findings from a study by Gardner *et al.* (2003), demonstrated that coral reefs which had experienced hurricane damage showed no decrease in macroalgae levels eight years later as compared to the previous lower levels.

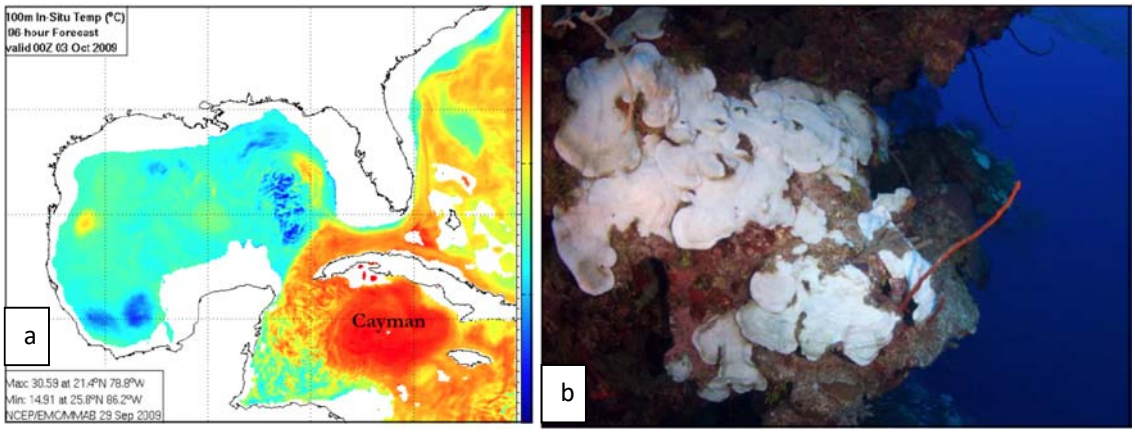


Figure 3.5 (a) Map of Caribbean illustrating a pool of hot water that engulfed the Cayman Islands (Grand Cayman located in the center) for six weeks with temperature >30°C (courtesy NOAA) (b) *Agaricia grahamae* coral colony bleached on the deep wall, (30 m) on North coast of Grand Cayman. GPS Position: N19^0 22.852 W81^{0}17.973

3.5.2 Effects on Benthic Community Structure across Deep and Shallow Terrace Habitats; Variation across Years of Study

Results clearly indicated a significant variation in the benthic community structure of deep as well as shallow terrace reef habitats between the islands and their protection status, with Little Cayman showing higher values of live coral cover in deep and shallow habitats than GCM and Cayman Brac. Differences in dead coral, macroalgae, turf algae, and scleractinian corals accounted for >80% of the total variance (figure 3.3 a). Unsurprisingly, the protection status did not show any obvious or measurable effect. This result could be explained by the fact that all corals have been protected in the Cayman Islands since 1978, regardless of whether they are located within an MPA.

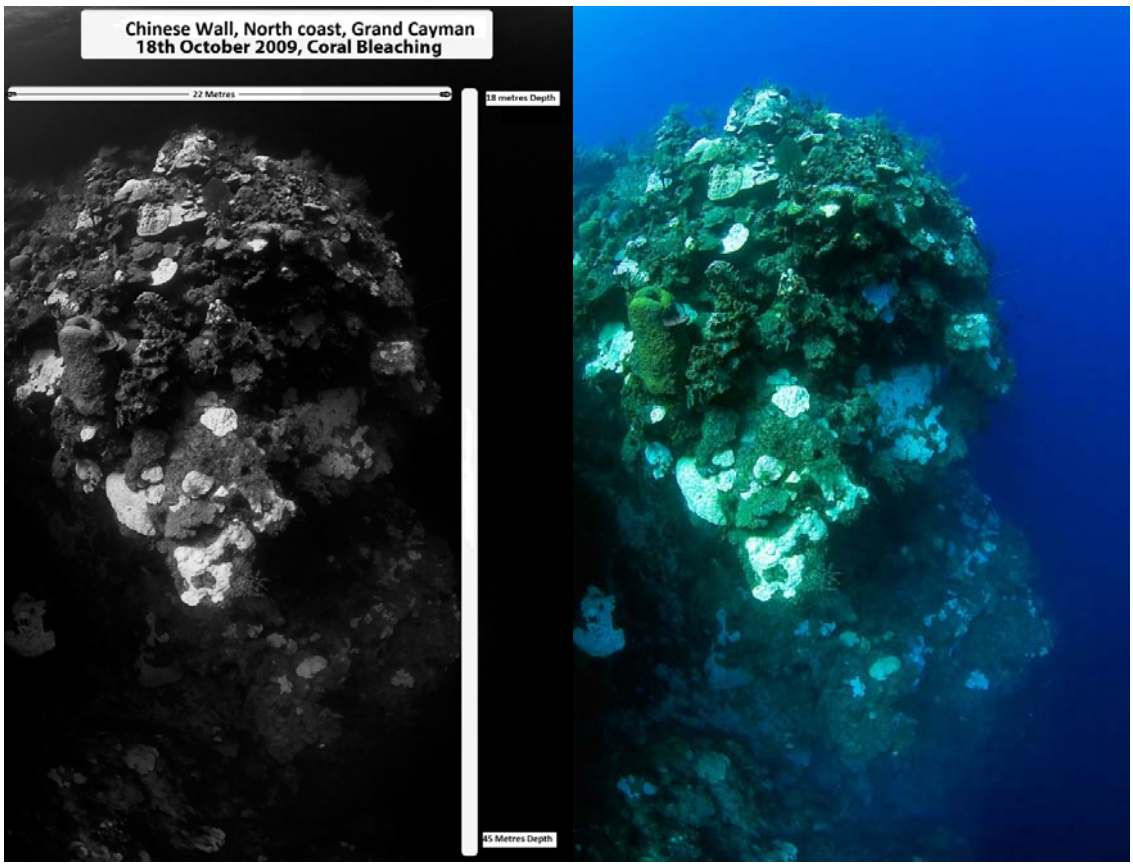


Figure 3.6 Photo of deep terrace reef and deep wall from 18 m on deep shelf edge to a depth of 45 m depth om the deep wall, North Coast Grand Cayman, October 18th 2009 (a) Black & white image with scale (b) Color image. (Photo credit: Patrick Weir) GPS Position: N19^0 22.852 W81^0 17.973

Additionally, dead coral was found in high abundance on shallow and deep reef terrace reefs, regardless of coast or protection status on GCM, which was indicative of an event that affected the marine benthos equally across habits, coast, inside as well as outside the islands' MPAs. Since the hard-coral cover did not show a significant decline (figure 3.3 b), the theory as per which, a prior event had caused widespread coral mortality, possibly the acute global bleaching event of 1998, is supported. Macroalgae colonized the dead coral colonies;

however, in light of the high mortality of macroalgae and subsequent reduction in biomass, those dead coral colonies were exposed as a consequence of the bleaching event of September 2009, which was documented by a striking increase in dead coral on GCM. In the sister islands of Cayman Brac and Little Cayman, macroalgae show clear patterns with a higher abundance in the deeper habitats. This suggest that the event which resulted in mortality of the macroalgae and the subsequent exposure of the underlying dead coral from a previous mortality event had affected the sister islands, albeit to a lesser extent. They exhibited an average of 50-70 % versus 34-46% in Grand Cayman for the year 2011, which was congruent with the findings of Barton (2010), Campbell (2010) and Looker (2011) of higher macroalgae in Little Cayman and Cayman Brac. All the three Cayman Islands showed similar variation in turf algal coverage of 15-25% across islands, irrespective of the deep terrace reef, shallow terrace reef, protection status, coast or island. However, as expected, turf algae % cover underpinned an association with the shallow terrace reef habitats across islands, especially the shallower reef habitat of Little Cayman and Cayman Brac. This demonstrates the robustness of turf algae (Figure 3.2 b) in that it is more temperature tolerant than macroalgae, given that it did not suffer the high mortality as macroalgae did in the sampling data for GCM for the year 2011 (figure 3.2 c). This finding might prove to aid the recovery of Caribbean reefs where bleaching is suggested to become more frequent (Wilkinson, 2008), thereby clearing the substrate of macroalgae and fostering settlement of coral larvae without affecting the more favorable turf algae, which is favored by herbivorous grazers (C. McCoy, personal observation).

3.5.3 MPA's Resiliency Effect on Benthic Community Patterns across Islands and Years

According to data analysis, the year 2011 was distinctly different from other years of this study, clearly indicating a significant difference in the benthic community structure across the three Cayman Islands and over the study period (figure 3.4 a). These differences were highly correlated with two benthos categories - turf Algae and macroalgae for the years 2009 and 2012 (figure 3.4 b-c). The significant differences in the benthic community structure during the year 2011 can be attributed to the high abundance of dead coral for that year in GCM (figure 3.4 d). This fact clearly distinguished the island from its sister islands of Little Cayman and Cayman Brac (figure 3.4 a) and is further explained graphically (figure 3.4 d). The profusion of dead coral in GCM and lower abundance for Little Cayman and Cayman Brac explained the greater variation in the benthic community structure as compared to the effect of protection status, which was negligible. This result further illustrates and underpins the fact that the acute localize bleaching event of 2009 was more intense in severity and extent and intensity on the reefs of GCM, although coral in the sister islands did bleach as well, albeit to a much lesser extent (C. McCoy, unpublished data). The differences in the severity and intensity of bleaching, including how it affected the benthos communities may be the driving force behind the patterns observed in this study. Overall, the results show that protection has had very little influence on the benthic community structure, demonstrating no effect during the period of study. This conclusion is based on the fact that regardless of changes in the major categories that account for the variation in the benthic community structure and patterns across the three Cayman Islands over the years of this study, irrespective of protection status, they were affected equally. However, that result is not surprising as corals are sessile

animals and are correspondingly affected regardless of whether they are located in a protected area or not. The surprising fact that the shallow terrace reef habitats in GCM did exhibit a lower coral cover than the deep terrace reef is indicative that the deeper reef corals of GCM are more robust and have been able to adapt to the changing environmental parameters as compared to their shallower counterparts. Tagged and photographed corals that were 100% bleached at a depth of 30 m recovered over a course of two years with zero mortality (C. McCoy, unpublished data); this demonstrates how robust corals can be and their ability to survive by shifting back and forth between a heterotrophic diet and an autotrophic diet; again, the protection status was negligible. Additionally, the severity of the variation that the reefs of GCM underwent between September 2009 and summer 2011 demonstrated an event that impacted it across habitats, coast, and coral community structure and years. However, by the year 2012 sampling season, post hoc comparisons of the coral reef benthos showed no significant differences between 2009 and 2012. This demonstrated the ability of that island coral reefs to adapt and resume its original coral community structure, albeit with a high macroalgal cover. Data collected across the islands between 2009 and 2012 suggest that the coral reefs of the Cayman Islands are resistance (Little Cayman and Cayman Brac), but are also capable of conferring resiliency, as in the case with GCM, where that islands reefs demonstrated the capacity to emerge from the coral bleaching event of late 2009 with negligible mortality. It is perhaps a result of all corals in Cayman Islands waters being protected since 1978, regardless of whether located within MPAs or outside of MPAs, whereby mitigating against anthropogenic factors.

Chapter 4. Reef Fish assemblages of the Cayman Islands; their status and protection effects.

Abstract

Due to the lack of commercial fisheries and the lack of legislation to report fishery landings in the Cayman Islands, very little information is known about the composition and structure of reef fish communities across the three island British archipelago. Though the Cayman Islands has had legislation governing marine resources since 1978, Marine Protected Areas (MPA's) were not implemented until 1986 as a means to mitigate the rapid development of the tourism industry. In this investigation, 48 target fish species from 15 families considered to be of commercial and ecological importance were surveyed at 55 sites using Underwater Visual Census (UVC) around Grand Cayman (GCM), Little Cayman (LC) and Cayman Brac (CB) from January to March in 2009, 2010, 2011 and 2012. The relationship between fish assemblages and Marine Protected areas was explored, including the spillover effect, fish community structure, trophic, and trophic groups over space and time. Overall, a significant reserve effect was detected. In GCM, post hoc analysis for the comparisons of protected areas and non-protected showed significant differences in the fish assemblages between the shallow reef habitats. No significant effects were found in the deep habitats. In LC, significant differences were found in fish assemblages between the shallow and deep reefs. Regression analysis showed a significant linear relationship for spillover effect for the shallow terrace reef on the northern boundary of the MPA in GCM for the years 2009 and 2011, with the years 2010 and 2012 being non-significant. No spillover effect was detected for the southern boundary of the MPA on GCM, or any of the deep terrace reefs of any of the three islands during the period of this study. Analysis of principal coordinates (PCO) showed that functional differences between MPA and non-MPA regarding fish assemblages across depths (habitats) and islands correlated significantly with four species of fish (*Holocanthus tricolor, Sparisoma aurofrenatum*, *Anisotremus Surinamensis,* and *Kyphosidae* sp). Similarity profile analysis (SIMPER) revealed that the fish assemblages of the MPA and non-MPA areas across the 3 Cayman Islands had different structures in their fish assemblages, this pattern changing from one island to another. Furthermore, the fish community structure differed significantly across all years on all islands. Fish communities were most similar for the years 2009 and 2010, with their differences increasing over time. Significant protection effect on fish biomass was detected for the shallow and deep habitats for the island of LC, and on the shallow reef habitat in GCM. Contrary, no significant protection effect of fish biomass was detected for the shallow or deep habitats in CB. Though the MPAs of the Cayman Islands were successful in increasing some key carnivores and herbivorous species of fish, results suggest that their design, purpose, and goals were not defined properly when implemented in 1986.

Keywords: Marine protected areas, coral reef fish, shallow terrace reef, deep terrace reef, reserve effect, spill over.

4.1 Introduction

Marine Protected Areas (MPAs), Marine Reserves, Marine Parks aim to mitigate the loss of marine life and biodiversity. MPAs were one of the first mechanisms developed and used to protect reef fish stocks including reef fish populations, and they are still the backbone of management tools used in managing and protecting fish stocks, mostly because fishes are one of the first marine organisms to respond to protection. Reef resilience became an important topic in the discipline of coral reef science in the late 1990s, more so after the acute global mass coral bleaching event in 1998 (Buddemeier & Smith 1999; Hughes & Connell 1999; Nyström *et al*., 2000;Carpenter *et al*., 2001; Halpern & Warner 2002, Hughes *et al.,* 2003; Bellwood *et al*., 2004). However, resiliency studies attempting to quantify which biological metrics and their attributes reflect coral reef recovery dates back to over three decades (Connell 1997; Connell 1978; Pearson 1981; Vitousek *et al*., 1997). Through the years, coral reef resiliency has been defined in many ways, however the most fitting describes the ability of a coral reef community to return to their initial state after a perturbation where significant change and or mortality has occurred, while at the same time being able to maintain key ecological function and services (Pearson1981; Nyström *et al*., 2000; Carpenter *et al*., 2001). The status of key species of fish and fish functional groups such as herbivores, pivotal to ecological function, is often overlooked (Jackson *et al.,* 2001) even though they play a key role in top-down macro algal control (Mumby *et al.,* 2001; Green & Bellwood 2009; Poore *et al.,* 2012). Carnivores are argued by Hawkins & Roberts (2004) to be key, setting the trophic structure and reef fish conFigureuration with any changes in predator to prey relationships modifying the reef fish community structure. Mumby *et al.* (2012) documented that where herbivorous extraction was high, there was an increase in concomitant macroalgal cover leading to a well-documented phase shift from a coral-dominated reef environment to an algal dominated reef environment (Jackson *et al*., 2014). Furthermore, Mumby *et al.* (2012) suggested that less pressure from apex carnivores due to extraction is likely to have a trickle-down effect on the mesopredator population whose population would increase and result in an unbalanced trophic hierarchy system. This finding parallel conclusions drawn by Bellwood *et al.* (2004), Mumby (2006), Hughes *et al*. (2007) and Green & Bellwood (2009) who note that a decrease in the herbivores influences and reshuffles coral reef fish community structure.

4.1.1 Global peril of reef fish exploitation

Reef fish stocks, on a global scale are facing ever increasing pressures from human activity (Jackson *et al*., 2001), thereby leading to precipitous declines in fish biomass with a deteriorating chance of recovery in the foreseeable future due to fishing pressure (Jackson *et al*., 2001; Pauly *et al*., 2002; Myers and Worm 2005; Froese *et al.,* 2012). In regards to the capacity of fishing pressure to reduce fish biomass, Pauly *et al.* (2002) noted that over time, there had been a consistent decline of the mean trophic levels of global fish landings. This term, he called "fishing down food webs" and further suggested that fish with life history strategies that make them susceptible to exploitation are in most cases the first to be affected and subsequently decline. According to Burke *et al.* (2011), globally >275 million people

live <30 km of coral reefs, with approximately 43 million of those in the Caribbean region. Most alarming, of the 108 countries and territories studied by Burke *et al*. (2011), the most reef-dependent countries were developing small island nations, with many of them located within the Caribbean region. Additionally, reef fisheries provide livelihoods and food globally to the majority of these individual countries and in some cases; it is a major part of their economy (Costanza *et al*., 1997; 2014). Over-exploitation of reef fisheries does not only reduce the fish population, but changes the trophic balance of the community which can affect the functional ability of the ecosystem (Russ, 1991; Jennings and Lock, 1996; McClanahan, 2000; Micheli *et al.,* 2014), resulting in a modification of the abundance and structure of the fishery which further leads to lower catch rates and eventual collapse and loss of the fishery (Pauly *et al*., 2002). However, the actual tipping point, according to Jackson *et al.* (1997) occurred in the Caribbean region in the late 1950s, with little or no management action taken until the 1980s which perhaps, only served to exacerbate the problem.

4.1.2 Marine protected areas effects on fish assemblages

Coral reefs and their associated organisms have important economic, biological, and aesthetic value (Costanza *et al.,* 1997). It has been estimated that globally, coral reefs generate 8,384 USD per/ha/ year, equivalent to 30 billion USD annually in tourism, fishing, and coastal protection from storms. However, the value of goods and services arising from coral reefs was further increased to 352,259 USD per/ha/year in 2011 (Costanza *et al*. 2014). Over-fishing is considered to be one of the primary threats to the health of coral reef functionality and is considered to be the primary cause of phase shifts from a coral-dominated reef environment to a macro-algal reef environment (Done 1992; Goreau, 1992; White *et al*., 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al*., 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014).

Marine Protected areas are becoming an increasingly common management tool used by countries globally to manage these valuable and limited resources, mostly by offering protection from degradation primarily caused by humans. In addition to the management of fisheries, Lubchenco *et al.* (2003) suggested that we preserve and conserve marine ecosystems as a whole, including the protection of vital species of animals and biodiversity. Additionally, MPAs slow down the possibility of exploitation of marine resources by humans while providing a refuge for spawning stocks. Furthermore, they also provide resources to adjacent areas via migration of fish out of MPAs, often referred to as "spillover effect" (Dugan & David 1993). This mechanism enables MPA's to maintain and contribute positively to the local fish stocks over time (Alcala, 2005). The potential benefits of MPA's in recent times have gained considerable attention as a key conservation instrument in the management of coral reefs and its associated organisms such as fish populations. The success of MPA's globally in recent years has fostered studies documenting and measuring positive changes to fish assemblages after their implementation (Coté *et al.,* 2001; Halpern, 2003; Lester *et al*., 2009).

Consequently**,** reserves are widely advocated to reverse trends of declining coral reef health where a range of factors, including over-exploitation of algal grazing fish, has caused substantial declines in coral cover and increase in macro-algal abundance (Gardner *et al*., 2003). Despite a wealth of empirical data, evidence for some of the expected effects of marine reserves remains oblique and limited by a lack of definitive targeted investigations at appropriate spatio-temporal scales (Russ, 2002)., Willis *et al*., (2003). Both concluded that to demonstrate reserve effects clearly, studies should not be confounded by factors such as insufficient spatial or temporal replication, including the absence of suitable control sites outside of reserves to validate their effectiveness on the coral cover or associated organisms such as coral reef fish assemblages.

4.1.3 Spillover effect

The net migration of adult fish out of MPAs to adjacent fished areas, or the "spillover effect" (Dugan & David, 1993; Rowley, 1994; Alcala, 2005), is usually one of the goals of an MPA. This trait combined with evidence of actual positive effects on local fisheries yield are surprisingly few (Alcala & Russ, 1990; Yamasaki & Kuwahara, 1990). Several studies have used tag-recapture techniques and reported the movements of target species from the reserve to fished areas, e.g. lobsters (David & Dodrill, 1980, 1989), shrimps (Gitschlag, 1986), snow crabs (Yamasaki & Kuwahara, 1990) and reef fish (Beinssen, 1989; Rutherford *et al*., 1989, Davies, 1995). Additionally, some studies have modeled the potential effects of movements of adult fish from a marine reserve to fished areas, using yield per recruit of target species (Russ *et al*., 1992). Russ & Alcala (1996) provide evidence for export of adult large predatory coral reef fish from reserve to adjacent fished areas derived from underwater visual census. The significant positive correlation of increasing mean density and species richness of large predatory fish with a duration (from 1 to 11 years) of reserve protection were observed in both the reserve and non-reserve areas surveyed. For the period of 9 to 11 years of protection combined, there were significantly higher densities of fish in the area that was mostly close to the reserve (about 200 m to 300 m area). Therefore, spillover and recruitment effects are likely to take a long time to develop fully (McClanahan &Mangi, 2000).

The recovery period for exploited species inside no-take marine reserve area depends on a large number of factors, including initial population size, intrinsic rate of population increases, the success of individual recruitment events, rates of immigration into reserves and the extent of reduction of mortality in reserve (Jennings, 2001). For reef fish assemblages, we now know that maximum potential longevities are in the order of 10 to 40 years for many species (Choat & Axe, 1995). However, few studies explicitly demonstrate the spillover effect (net export of adults) from a marine reserve, partly because of the lack of appropriate experimental designs such as lack of information on spatial abundance, spatial catch rate and movement patterns of targeted species before and after reserve establishment. Russ *et al.* (2003) present some of the most convincing evidence for spillover to date.

They showed that the biomass of the surgeonfish, *Naso vlamingii,* tripled inside a reserve at Apo Island, the Philippines, over 18 years (1983-2001). This result is consistent with those of Roberts *et al.* (2001) who studied long-lived reef fishes at Merritt Island Reserve in Florida and with those of Kelly *et al.* (2002) who studied lobsters at the Leigh Marine Reserve in New Zealand. Demonstrating the spillover effect of a reserve is of importance to the successful establishment of reserves in building resilience.

4.1.4 Reserve effect of Marine Protected areas on Reef Fish assemblages

Marine Protected Areas (MPAs) are expected to benefit adjacent fisheries through two main mechanisms: net emigration of adults and juveniles across borders termed spillover and export of pelagic eggs and larvae. Inside reserves, because of no extraction, fish populations increase in size, live longer, grow larger and develop an increase in reproductive potential (Bohnsack, 1998). Higher production of eggs and larvae inside reserves is predicted to lead to net export and increase the settlement of juvenile animals outside the boundaries (Gell & Roberts, 2003). Several other studies demonstrated this reserve effect by studying changes in fish biomass. For example, in the study of Harmelin-Vivien et al. (2008), a reserve effect showed higher values of fish species richness (x 1.1), abundance (x 1.3) and biomass (x 4.7) recorded inside MPAs compared to the adjacent fished areas. The mean fish weight of all fish species recorded was estimated to be 3.4 times higher inside MPAs than in fished areas. More significant effects were observed for fish biomass than for abundance. Overall, 70% of the linear correlations of fish biomass with distances moving away from MPA boundaries were significantly negative, implying that in most cases fish biomass decreases in the distance away from MPAs boundaries to fished areas. McCoy *et al*. (2010) also demonstrated spillover effect on the northern boundary of the MPA in Grand Cayman in addition to noting a strong and significant reserve effect of 1.6 times higher biomass within the MPA of Grand Cayman. Adding further evidence to reserve effect, Lenfant (2003) demonstrated that the distribution of individual size classes is correlated with the degree of protection afforded in his study on the White Seabream, *Diplodus sargus,* individuals were significantly larger and older in the marine reserve. The model also demonstrated that reserve effect could drive demographic structures and sex distribution, finding evidence that *D. sargus* shared similar genetic structure, with younger and smaller females outside of reserve when compared to within reserve.

4.1.5 Coral Reef resiliency

The ability of a system to absorb, resist or recover from disturbances or to adapt to changes while continuing to maintain vital essential functions and processes is the principle of ecological resilience (Holling, 1973; Nystrom and Folke, 2001). When speaking of coral *reef resilience*, we almost always refer to coral reefs that can bounce back or recover after experiencing a stressful event such as bleaching caused by elevated water temperatures. Paralleling that, when we refer to coral reef *resistance*, we are

often referring to coral reef communities that remain relatively unchanged in the face of a significant disturbance event such as bleaching from elevated sea temperatures. Though the true definition of ecosystem resiliency, more so coral reef resiliency has been debated for decades, Hodgson *et al.* (2015) describes it best from the argument of the overall stability of the system, including the rate marine organisms recover from disturbances

4.1.6 Reef fish trophic structure; their significance and vulnerability

Coral reefs in the Caribbean basin do not have the redundancy of reef fish communities in the Pacific and Indian Ocean territories, which have multiple species performing similar ecological roles. Caribbean reefs are usually referred to as species limited with a few key organisms occupying critical ecological role and functions, with high demands of them to maintain a healthy trophic structure amongst biological systems that are not only complex but poorly understood to date. One such example is the case of the sea urchin *Diadema antillarium,* which suffered an epizootic event leading to mass die-off of this keystone herbivore in 1983/4 in the Caribbean and Atlantic basin (Lessios *et al.,* 1984), with no definitive cause (Lessios, 1988). This event triggered a phase shift from a coral-dominated environment to an algal dominated environment (Done, 1992; Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al*., 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al*., 2014). Caribbean reefs are still recovering from this event, whilst faced with other challenges such as overfishing (Roberts, 1995; Chabanet *et al*., 1997; Jackson *et al.,* 2001; Hughes, 1994) Ocean acidification (Mora, 2008; Mumby and Steneck, 2008), including climate change (Hughes *et al.,* 2003; Lubchenco *et al*., 2003, Hughes *et al.,* 2007) amongst other factors. The trophic structure of reef fish assemblages' depends on a delicate balance of a top-down control by carnivorous fish and apex predators (Hairston *et al*., 1960; Miller *et al*., 2001). These control the biomass of other carnivores, omnivores, and herbivores which control other organisms of the reef system such as invertebrates and algae. There is little plasticity in this structure, and an imbalance caused by factors such as overfishing (Jackson *et al*., 2001; Hughes *et al*., 1994) usually results in an unbalanced trophic system (Bellwood *et al.,* 2004; Mumby 2006; Hughes *et al*., 2007; Green & Bellwood, 2009; Mumby *et al*., 2012).

Thought Cayman Islands MPAs were established in 1986, few temporal studies on the effectiveness of protection on their fish assemblages have been carried out. This chapter will investigate the effects of MPAs in the Cayman Islands on 48 target reef fish species considered ecologically and commercially important. Fish assemblages, community structure, biomass, reserve effect, and spillover was surveyed over a 4 year period for the islands of Grand Cayman, Little Cayman, and Cayman Brac at sites located within and outside of their protected areas. Data collected will then be tested for protection effects on those attributes through time and space.

4.2 Hypotheses and Objectives

H_{01} : Marine Protected Area effect has had no effect on reef fish assemblages and community structure across the 3 Cayman Islands.

Objective 1: Differences in biomass of 48 target reef fish species between protected and non-protected locations in Grand Cayman, Little Cayman and Cayman Brac were documented on the deep and shallow reef terrace habitats at 55 sites (32 MPA and 23 non-MPA) across the 3 Cayman Islands using underwater visual census (UVC) annually between January 2009 through to March 2012. Comparisons will be made between protection status and amongst islands testing for differences.

H_{02}: There will be a no decrease in target reef fish species biomass with increasing distance away from marine protected areas boundaries, termed "spillover effect."

Objective 2: The biomass of 48 target reef fish species was accessed in 1 km increments moving from the boundaries of MPAs of the Cayman Islands to a distance of 5 km and to investigate the export of individuals from the MPAs to outlying fished areas for the years 2009 through to 2012.

H_{03}: Protection effect has not increased the biomass of the 48 target reef fish species and their trophic groups between the years 2009 and 2012 in the Cayman Islands.

Objective 3: Species and community trophic structure data were collected from 55 sites across the 3 Cayman Islands on 48 target reefs fish species. Each species of fish will then be grouped into five trophic groups according to their feeding habits. The trophic structure data was then be explored, measured and compared.

4.3 Methods

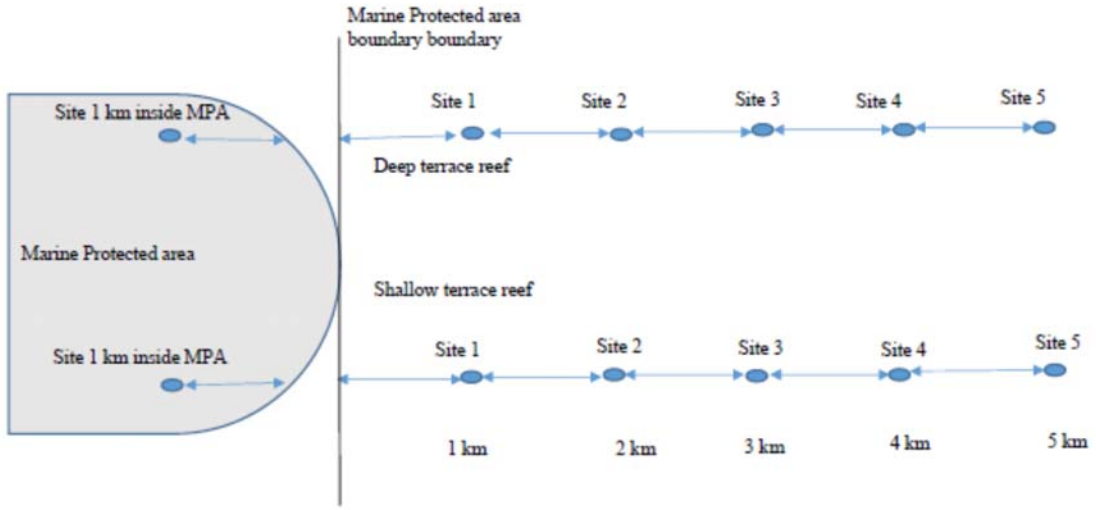
4.3.1 Data collection (see chapter for more detailed methods and map)

These data were collected by Underwater Visual Census (UVC), using a belt transect method (Samoilys and Carlos, 2000). Sampling was done during January through to March at a total of 55 sites across islands (Figure 3.2) between the hours of 0900 and 1500 hours for consistency, for the years 2009 through to 2012. Fish counts were made at two depths: the shallow terrace (10 - 12 m) and the deep terrace reef (16 - 18 m). At each site, the fish were censused along three transects 50 m x 5 m sampling 750 m^2 of reef per site. Each transect was deployed with a minimum of a 30 m gap in between the

transects. The diver swam along transects with a graduated PVC T-bar and recorded the number of individuals, species and the total length of the fish (in 9 size classes of 5-cm increments), within 2.5 m on either side of the transect line and 5 m above it. Target fish crossing the transect belt were identified and counted, with 48 coral reef species, belonging to 16 fish families, constituting the list of targeted fish species (Appendix 4.1). Bell's (1985) method of using artificial fish of various sizes and shapes were used to train the size class estimates during simulated practice surveys. The observer conducted this training until size class estimates were with 1 cm of the actual measured length of artificial fish (>95% estimates).

4.3.2 Spillover effect

To address the spillover effect in the 3 Cayman Islands, six additional sites on the deep and five sites on the shallow terrace reefs were chosen and surveyed. The 1st site was located within the MPA; five additional sites were located ~ 1 km apart starting at the MPA boundary moving away from MPA for a total distance of 5 km (figure 4.3.1). The biomass of the 48 reef species of fish surveyed at sites was then tested to measure the extent of exportation of reef fish biomass along the shallow and deep reef terraces at MPA boundaries.



Survey design to investigate Spillover of fish biomass at boundaries of MPAs in the Cayman Islands.

4.3.4 Reserve effect

To test for reserve effect, fish biomass data was surveyed at sites located inside and outside of protected areas in Grand Cayman (9 protected sites and 18 non-protected), Little Cayman (8 protected and 8 non-protected) and in Cayman Brac (6 protected and 6 non- protected), (figure 3.2). Biomass of the 48 target reef fish species of Marine Protected Areas (MPAs) and non-Marine Protected Areas (non-MPAs) was then compared to ascertain if they were any significant differences.

4.3.5 Data analysis

Fish census data were first square root transformed to down-weight extremely abundant species as to not skew the data results before analysis. Multivariate statistical analyses were conducted using PRIMER (Plymouth Routines in Multivariate Ecological Research) v6. + PERMANOVA. Multidimensional Scaling (MDS), Analysis of similarities (ANOSIM) and Similarity Percentage Analysis (SIMPER) were used to test if sites belonging to each Aspect were different across the years. Bubble plots on the MDS were used to visualize this in time and space. Parametric test using PRIMER v6. + PERMANOVA were used and displayed in a PERMANOVA table and represent the interactions and were displayed as a series of Principle component analysis (PCO's) demonstrating patterns and ordinations of sites. Post-hoc analysis using t-test based on permutations provided pairwise comparisons for every combination of factors for significant differences. To test for differences in total fish biomass of Marine Protected areas and non protected areas, ANOVA test was carried out using IBM SPSS v22 (Statistical Package for the Social Sciences).

4.3.6 Fish community trophic structure and biomass

To investigate the fish community structure of each island, selected groups of fish families and species were grouped into the five trophic guilds, according to Randall (1967), (Appendix 4.1).

(HB) Herbivore, a diet, consist predominantly of algae.

(OM) Omnivore, a diet consisting of algae and other animals.

(P) Predator, a diet consisting of 100% fish.

(C1), carnivores 1, a diet consisting of invertebrates (inverts feeders).

(C2) carnivores 2, a diet consisting of invertebrates and other fish species.

These trophic groups were further tested against protected and non-protected sites on the deep and shallow terrace reefs on each of the three Cayman Islands.

4.4 RESULTS

4.4.1 General distribution of fish

In the year 2009, a total number of 10,578 fish were counted across the Cayman Islands, 16,677 in the year 2010, 17,153 in the year 2011 and 12,019 in the year 201. Total fish biomass data significantly differed across the years for marine reserves of the 3 Cayman Islands. Data demonstrated an overall strong reserve effect ($F = 6.0218$, $df = 3$, $p = 0.001$, CV% 8.94, table 4.1). For the island of Grand Cayman, one-way ANOVAs determined that mean fish biomass was significantly higher within its protected areas in the year 2009 (ANOVA, $F = 11.137$, $p = 0.001$). However, for the year 2011, fish biomass was significantly higher outside of protected areas (ANOVA, $F = 5.844$, $p = 0.016$), (figure 4.1 a, table 4.1). In Little Cayman, significant differences were found for year 2009 (ANOVA, $F = 15.601$, $p = <0.001$) and year 2012 (ANOVA, $F = 6.004$, $p = 0.014$), (figure 4.1 b, table 4.1). For the Island of

Cayman Brac, significant differences were only found for the year 2010 (ANOVA, F = 4.941, p = 0.027) (figure 4.1 c, table 4.1)

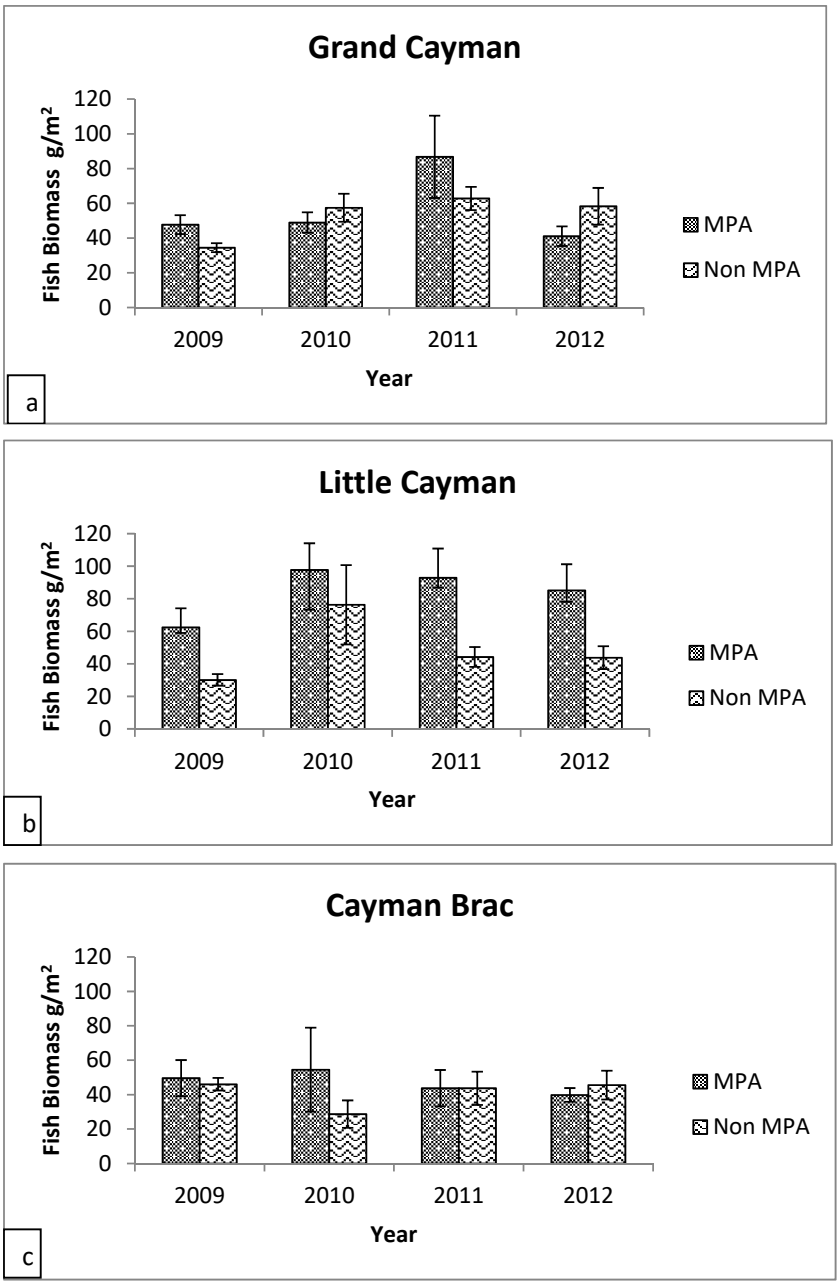


Figure 4.1. Interval plot of Biomass g/m2 vs years of total fish Biomass for the 48 target species of fish across the 3 Cayman Islands (a) Grand Cayman (MPA n=9; non-MPA n=18), (b) Little Cayman (MPA n=8; non-MPA n=8), (c) Cayman Brac (MPA n= 6; non-MPA, n=6) for years of study (2009, 2011, 2012), +/- SE.

Table 4.1. Summary of ANOVA results for total fish biomass inside Marine Protected Areas (MPAs) and non-Marine Protected Areas of Grand Cayman, Little Cayman, and Cayman Brac for years 2009, 2010, 2011 and 2012. n=55 (Grand Cayman MPA, n=9, non-MPA, n=18; Little Cayman MPA n=8, non-MPA n=8, and Cayman Brac MPA, n=6, non-MPA n=6.

Island	Year	statistical test	F-value / Z	p-value
Grand Cayman	2009	ANOVA	11.137	**0.001**
Grand Cayman	2010	ANOVA	0.524	0.4969
Grand Cayman	2011	ANOVA	0.027	0.869
Grand Cayman	2012	ANOVA	5.844	**0.016**
Cayman Brac	2009	ANOVA	0.086	0.769
Cayman Brac	2010	ANOVA	4.941	**0.027**
Cayman Brac	2011	ANOVA	0.091	0.894
Cayman Brac	2012	ANOVA	1.168	0.224
Little Cayman	2009	ANOVA	15.601	**0.001**
Little Cayman	2010	ANOVA	0.068	0.794
Little Cayman	2011	ANOVA	0.136	0.712
Little Cayman	2012	ANOVA	6.004	**0.014**

4.4.2 Spillover

In Grand Cayman (GCM), a significant negative correlation for the northern boundary on the Marine Protected area (MPA) shallow terrace reef was found in the year 2009, ($R2 = 93.3\%$, $p < 0.001$) (Figure 4.2). The family of fish that contributed to most of this exportation was Lutjanidae (snappers). In the year 2011, there was also a significant correlation, ($R2 = 65.0\%$, $p < 0.05$) (Figure 4.3), with the family Haemulidae (grunts) contributing the most to this migration out of the MPA. Other years of this study were non-significant (year 2010, $R2 = 27.3\%$, $p = 0.3$, year 2012 $R2 = 73.1\%$, $p = 0.06$). There was no correlation and evidence of spillover effect on the southern boundary of the Grand Cayman MPA for any year of study. Additionally, for the sister islands of Little Cayman and Cayman Brac, no spillover evidence was found (non-significant) for the years of this study. Furthermore, no spillover evidence was apparent for any of the deep terrace reefs on the boundaries of any of the MPAs of the 3 Cayman Islands.

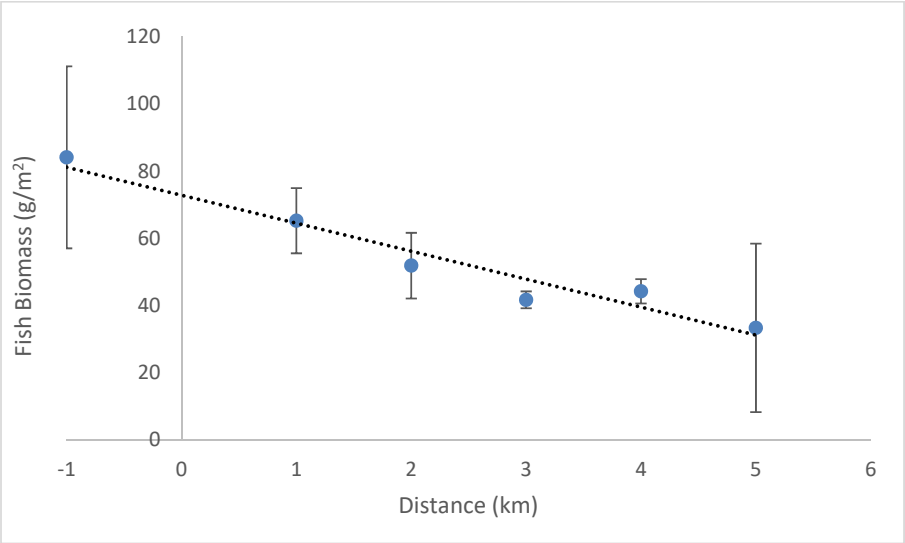


Figure 4.2 Linear regression of total biomass for fish species for the shallow terrace reef sites and their distance from the northern MPA boundary of Grand Cayman for year 2009, (R2 = 93.3%, p = <0.001, slope = -9.192) (n = 6)

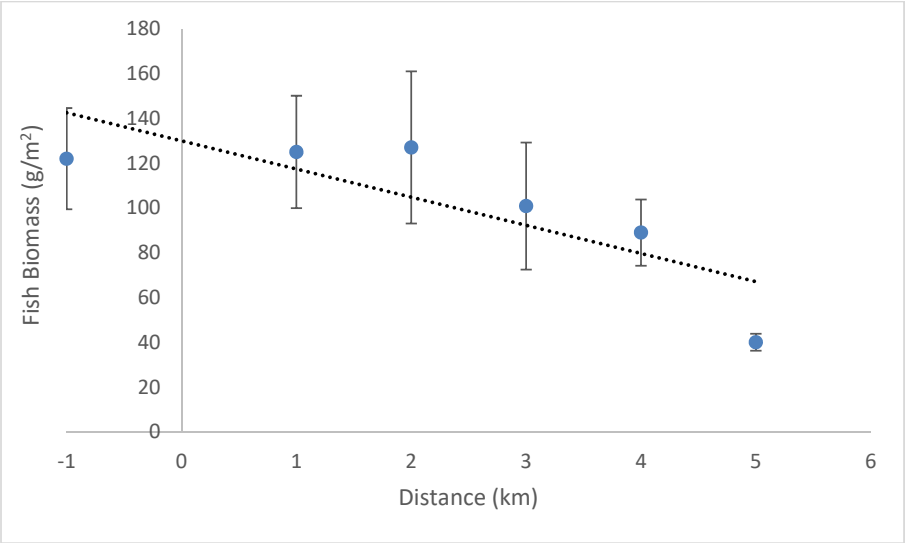


Figure 4.3 Linear regression of total biomass for fish species for the shallow terrace reef sites and their distance from the northern MPA boundary of Grand Cayman for year 20011, (R^2 = 65.0%, p = < 0.05, slope = -13.83) (n = 6)

4.4.3 The effects of marine protected areas on fish assemblages and community structure

Results showed that fish community assemblages were extremely variable in time and space over the years of this study. The results demonstrated that the changes associated with the community structure of the fish assemblages within the Marine Protected Areas (MPAs) across the 3 Cayman Islands were not consistent (table 4.2). A significant interaction between depth (deep and shallow terrace reefs),

and protection status (MPAs and non-MPAs) across islands was also found and further indications show that the effect of MPAs was not always consistent for all depths and islands during the period of this study on the targeted fish species assemblages (Permanova, F = 1.85, df = 2, p = 0.033, coefficient of variation = 6.31, table 4.2). Additionally, a similar trend was found when the fish species were grouped into functional trophic groups (Figure 4.4 a).

Table 4.2 Multivariate analysis of variance based on permutations (PERMANOVA) on Bray-Curtis Similarities of major functional groups of fish. Factors are: yr = years (2009-2012, de = depths (shallow and deep reef terraces), P = protection (MPA), Co = coast (north, south, west, nested in island), Is = Islands (Grand Cayman, Little Cayman, Cayman Brac). Text in **red** indicates significant.

Source	df	SS	MS	Pseudo-F	P	perms	CV (%)
yr	**3**	**45566**	**15189**	**6.0218**	**0.001**	**997.00**	**8.94**
P	**1**	**14796**	**14796**	**5.8661**	**0.001**	**999.00**	**6.22**
Is	**2**	**34592**	**17296**	**6.6302**	**0.001**	**999.00**	**8.15**
de	**1**	**29392**	**29392**	**11.653**	**0.001**	**998.00**	**9.20**
Yr*P	3	5498.6	1832.9	0.72667	0.859	998.00	0.00
Yr*Is	6	17698	2949.7	1.1307	0.272	998.00	2.45
Yr*de	3	6415.8	2138.6	0.84789	0.727	999.00	0.00
P*Is	**2**	**14841**	**7420.7**	**2.8446**	**0.001**	**999.00**	**6.57**
P*de	1	3124.8	3124.8	1.2389	0.285	999.00	1.93
Is*de	2	17418	8709.1	3.3385	0.003	999.00	7.41
Yr*P*Is	6	7798.6	1299.8	0.49824	0.998	998.00	0.00
Yr*P*de	3	5684.5	1894.8	0.75124	0.805	998.00	0.00
Yr*Is*de	6	9499.8	1583.3	0.60693	0.975	998.00	0.00
P*Is*de	**2**	**9661.2**	**4830.6**	**1.8517**	**0.033**	**999.00**	**6.31**
Yr*P*Is*de	6	8599	1433.2	0.54938	0.992	999.00	0.00
Co(yr*Is*de*P)	**32**	**85740**	**2679.4**	**2.1762**	**0.001**	**995.00**	**12.09**
Res	580	7.141E5	1231.2				30.74

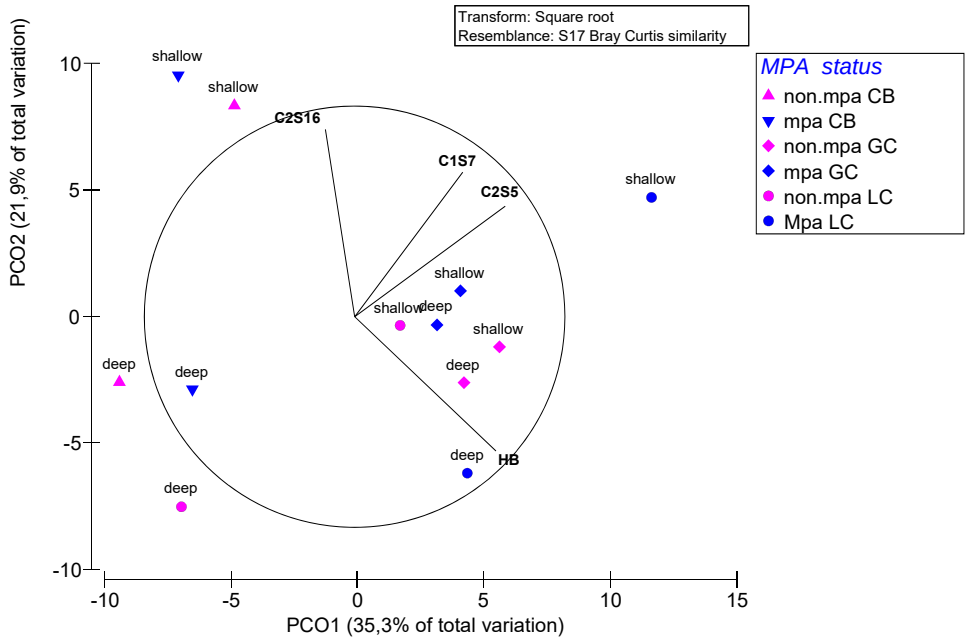


Figure 4.4 a Analysis of Principal Coordinates (PCO) showing ordination of sampling according to factors Depth, Level of Protection, and Islands using functional trophic groups as variables. GC=Grand Cayman, CB= Cayman Brac, LC=Little Cayman. HB = herbivores, C1= carnivores 1, a diet consisting of invertebrates (inverts feeders), C2 = carnivores 2, a diet consisting of invertebrates and other fish species.

In Cayman Brac, post-hoc comparisons showed that the level of protection had no significant effect for the shallow ($t = 1.3$, $p > 0.05$,) or deeper habitats ($t = 1.08$, $p > 0.05$), (table 4.3, Figure 4.4 b).

In Grand Cayman, post hoc comparisons for protection status showed significant differences in fish assemblages between the shallow reef habitats only ($t = 1.88$, $p < 0.05$), whereas in the deeper habitats, the level of protection did not have a significant effect (table 4.3, Figure 4.4 b). In Little Cayman, the MPAs had very different fish assemblages with significant differences being found in both, deep ($t = 2.55$, $p < 0.05$), and shallow reef habitats ($t = 2.28$, $p< 0.05$), (table 4.3, Figure 4.4 b).

Table 4.3 Post-hoc comparisons for the interaction level of Protection x Island x Depth. Numbers highlighted in red indicates a significant interaction.

Level of protection	t-statistic	permutations	p-level	
		Shallow		
MPA-NonMPA	1.3	994	0.18	Cayman Brac
		Deep		
	1.08	996	0.32	
		Shallow		
MPA-NonMPA	**1.88**	**879**	**0.01**	Grand Cayman
		Deep		
	1.05	874	0.05	
		Shallow		
MPA-NonMPA	**2.28**	**999**	**0.02**	Little cayman
		Deep		
	2.55	**999**	**0.001**	

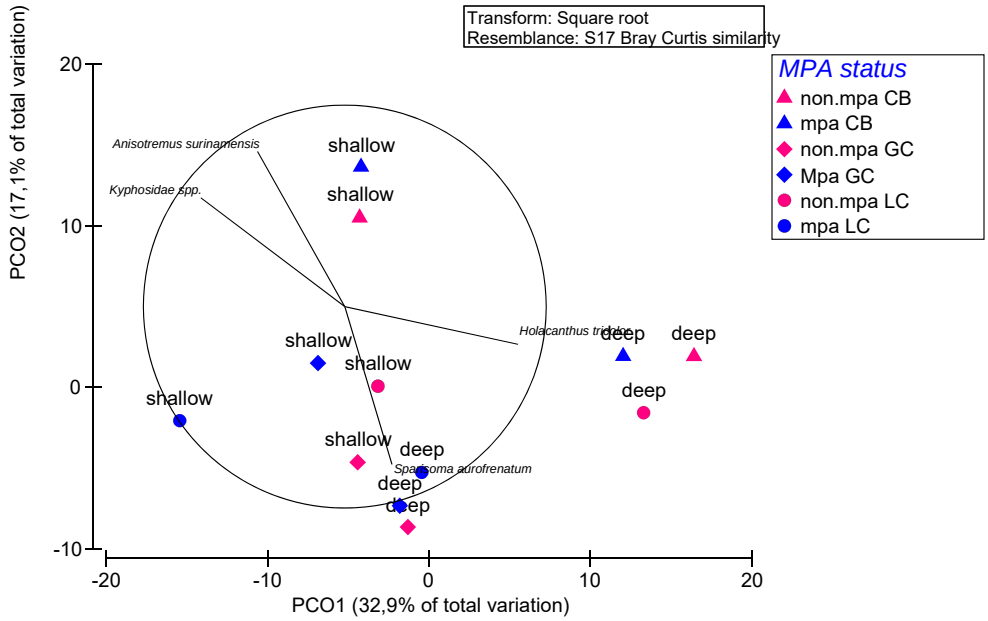


Figure 4.4 b Analysis of Principal Coordinates (PCO) of islands (CB= Cayman Brac, GC= Grand Cayman, LC= Little Cayman) using species composition as variables showing ordination of samples according to factors; Depth (deep and shallow sites), Protection status (MPA vs. non-MPA). species: (1) *Holacanthus tricolor* (Rock beauty), (2) *Sparissoma aurofrenatum* (Redband parrotfish), (3) *Anisotremus surinamensis* (Black margate) and (4) *Kyphosidae* sp (Sea chubs)

4.4.4 Effects on functional trophic groups and species; variation across spatial scales

With more than 50% of the total variance explained, the analysis of principal coordinates (PCO) showed that the functional differences between MPAs and non-MPAs of fish assemblages across habitats (deep and shallow reef habitats) and islands were highly correlated (ρ=0.8) with 4 species: (1) *Holacanthus tricolor* (Rock beauty), (2) *Sparissoma aurofrenatum* (Redband parrotfish), (3) *Anisotremus surinamensis* (Black margate) and (4) *Kyphosidae* sp (Sea chubs) (figure 4.4 b). The first species (*H. tricolor*) was more abundant in deeper habitats as compared to shallower reef habitats, regardless of their protection status ANOSIM ; Global R= 0.045, P= 0.001 (figure 4.4 c). The parrotfish *S. aurofrenatum* was widely distributed but more abundant on the shallower and deeper reef habitats of Little Cayman when compared across islands (ANOSIM ; Global R= 0.024, P= 0.004) (Figure 4.4 d). The grunt *A. surinamensis* was found to be more abundant in the shallower reef habitats of Cayman Brac regardless of their protection status ANOSIM ; Global R= 0.033, P= 0.007) (Figure 4.4 e). Finally, the herbivore, *Kyphosidae* sp that usually feeds in intertidal areas was found to be very abundant in the shallower reef habitats irrespective of their island or protection status ANOSIM ; Global R= 0.022, P= 0.006) (figure 4.4 f).

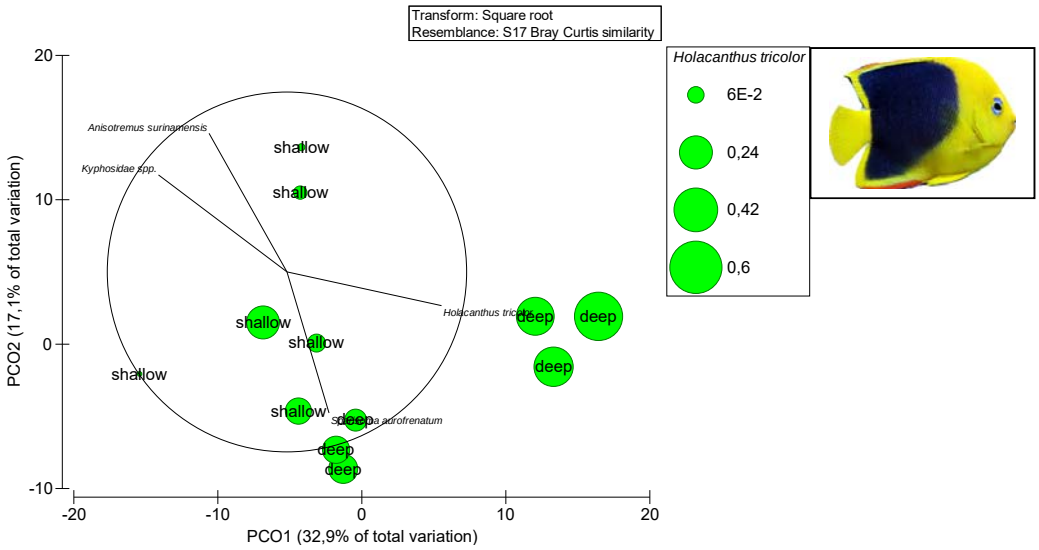


Figure 4.4 c Analysis of Principal Coordinates (PCO) showing ordination of samples according to factors; Depth and species composition. Bubbles plots represent the composition of *Holacanthus tricolor* (Rock Beauty) explaining species distribution across habitats (depth).

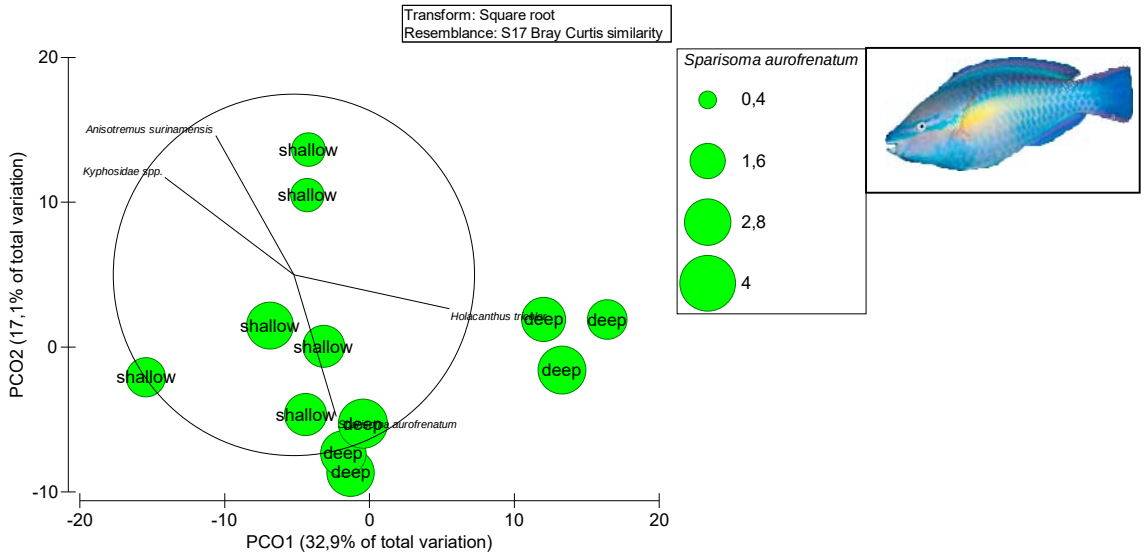


Figure 4.4 d Analysis of Principal Coordinates (PCO) showing ordination of samples according to factors; Depth and species composition. Green bubbles plots represent composition of *Sparrisoma aurofrenatum* (Red Band parrotfish) explaining that species distribution across habitats (depth).

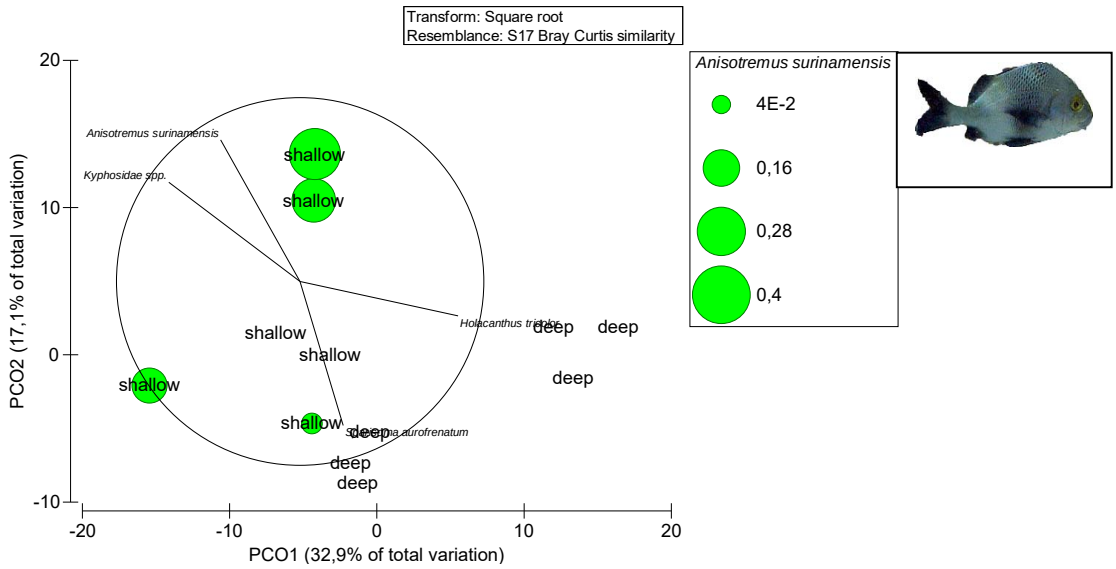


Figure 4.4 e Analysis of Principal Coordinates (PCO) showing ordination of samples according to factors; Depth and species composition. Bubble plots represent Anisotremus surinamesis (Black Margate) explaining that species distribution across habitats (depth)

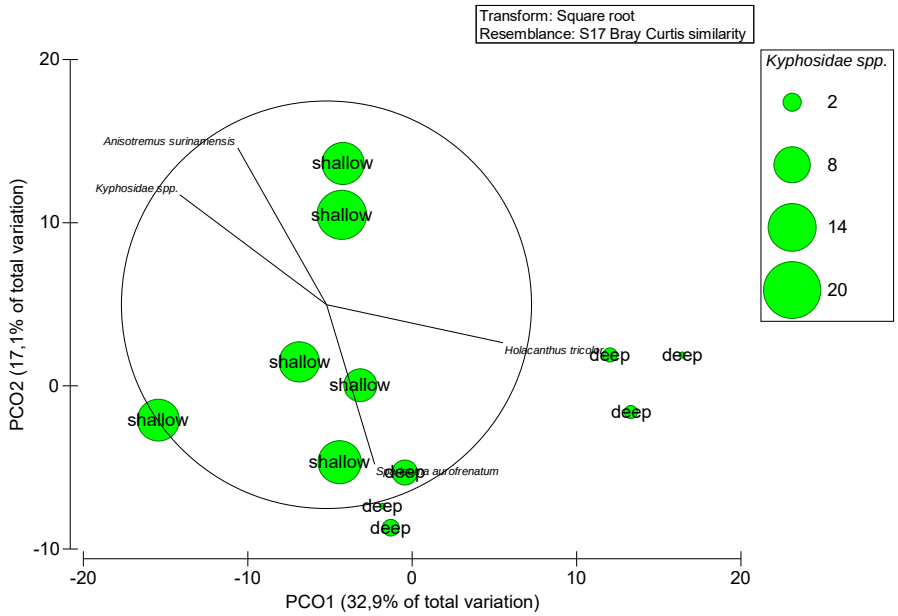


Figure 4.4 f Analysis of Principal Coordinates (PCO) showing ordination of samples according to factors; Depth and species composition. Bubble plots represent Kyphosidae spp. (Chubs) explaining that species distribution across habitats (depth).

The similarity profile analysis (SIMPER) showed that the fish assemblages of the MPA and non-MPAs of the Cayman Islands had very different structures, this pattern changed from one island to another (table 4.4). For instance, despite no statistical differences found between MPA and non-MPA on shallow reef habitats in Cayman Brac, the average dissimilarity was 45.4%; with five species contributing to more than 70% of the average dissimilarity (table 4.4). Both MPA and non-MPA shallow reef sites were characterized by a high abundance of *Kyphosidae* sp*;* a species that reached 14.9 g/m^{2}and 10.4 g/m^2, respectively. Perhaps, the species that better explained the differences between MPAs and non-MPAs in Cayman Brac for the shallow reef habitats was the carnivore *Lutjanus apodus* (Schoolmaster snapper), being 2.5-fold and significantly more abundant ($t = 1.96$, $p < 0.05$, table 4.5), demonstrating 7.11 g/m^2 in the former as compared to the latter of 2.48 g/m^2. This result seems to suggest that the MPAs are seemingly increasing the biomass of *L. apodus*. However, the results showed no significant differences in the structure of the reef fish community as a whole between MPAs and non-MPAs in the shallow reef habitats of Cayman Brac. The average dissimilarity between MPAs and non-MPAs in deeper habitats of Cayman Brac were also low (48.33%, table 4.4). A total of 5 species contributed up to 70% of this average dissimilarly, with the carnivore *Haemolon flovolineatum* (French

grunt) being the most important contributor. The biomass of this particular species was 2-fold in MPAs (4.17 g/m^2) compared to the non-MPAs (2.18 g/m^2, table 4.4) in the deeper reef habitats at Cayman Brac. However, this trend was not statically significant (table 4.5).

The average dissimilarity between MPAs and non-MPAs shallow reefs habitats in Grand Cayman was 69.32% with the two species, *Melichthys niger* (black durgon) and; particularly, the parrot fish *Sparissoma viride* (stoplight parrot fish) contributing with more than 40% of this dissimilarity (table 4.4). In fact, the biomass of this species was significantly higher ($t = 2.23$, $p < 0.05$, table 4.5) in the shallow reef habitats of Grand Cayman MPA's (10.71 g/m^2, table 4.4) compared to that islands non-MPAs (7.8 g/m^2, table 4.4). In this case, the MPAs seemed to be effective by increasing 1.5-fold the biomass of at least one species of herbivore during the period of this study. Fish communities associated with the deeper reef habitats in Grand Cayman were very similar, regardless of their protection status; showing the lowest average dissimilarity recorded in this study (33.26%, table 4.4). Among all species, only 4 (*Sparissoma viride, Melichthys niger, Acanthurus coeruleus* and *Sparissoma aurofrenatum*) contributed with more than 60% of average dissimilarity (table 4.4). Among these four species, the largest and the only significant difference in biomass was found for *Melichthys niger* ($t = 3.37$, $p < 0.05$, table 4.5). The biomass of this planktonic omnivore was 4-fold higher in the deeper reef habitats of non-MPAs (11.25 g/m^2) as compared to the biomass recorded within the MPAs of Grand Cayman (3.07 g/m^2, table 4.4).

The largest average dissimilarities between MPAs and non-MPAs were found in the fish communities in Little Cayman. This pattern was consistent for both the shallow and the deep reef habitats of Little Cayman (table 4.4). In the shallow reef habitats, fish community structure between MPAs and Non-MPAs differed on average of 72.63% (table 4.4). Demonstrating that the biomass of key herbivores such as *S. viride* and *A. coeurelus* was 1.5 to 2.2 times higher within that island MPAs (table 4.4). The MPAs located in the shallow reef habitats of Little Cayman had a significant and noticeable effect ($t = 1.995$, $p < 0.05$, table 4.5) increasing the biomass of the carnivore grunt *Haemolon sciurus* from 3.89 g/m^2 to more than 18 g/m^2 (table 4.4). Finally, the average dissimilarity between MPAs and non-MPAs in deep reef habitats of Little Cayman was 67.2% (table 4.4). Only a few species contributed with more than 70% of this average dissimilarity, with the most important one being the Nassau grouper (*Epinephelus striatus*, table 4.4). The biomass of this top carnivore varied from 4.1 g/m^2 inside MPAs to 2.96 g/m^2 in areas with no protection (table 4.4); however, the changes in biomass were not significant (table 4.5).

Table 4.4 Two-Way-Crossed Similarity percentage analysis (SIMPER) showing average similarities of fish assemblages of MPAs and non-MPAs across islands. Text highlighted in **red** indicates significant contribution.

Species	Av.Abund	SD	Contrib%	Cum.%	Depth-Protection-Island	Average dissimilarity (%)
Sparisoma viride	4.74	0.79	21.2	21.2	Shallow-NonMPA-Brac	45.4
Acanthurus coeruleus	3.75	1.02	17.22	38.42		
Kyphosidae spp.	14.91	0.42	15.70	54.12		
Lutjanus apodus	**2.48**	**0.32**	**14.14**	**68.26**		
Sparisoma aurofrenatu	1.44	0.77	7.43	75.7		
Sparisoma viride	5.33	0.9	26.65	26.65	Shallow-MPA-Brac	
Acanthurus coeruleus	4.07	1	26.33	52.98		
Sparisoma aurofrenatu	1.46	0.93	8.9	61.87		
Lutjanus apodus	**7.11**	**0.43**	**8.33**	**70.2**		
Kyphosidae spp.	10.89	0.34	6.97	77.18		
Sparisoma aurofrenatu	2.04	1.52	19.23	19.23	Deep-Non-MPA-Brac	48.33
Scarus taeniopterus	2.03	1.27	16.74	35.97		
Sparisoma viride	3.68	0.67	15.08	51.05		
Haemulon flavolineatu	**2.18**	**0.65**	**11.27**	**62.33**		
Acanthurus coeruleus	1.38	1.13	9.41	71.73		
Sparisoma viride	3.72	0.9	19.34	19.34	Deep-MPA-Brac	
Sparisoma aurofrenatu	2.51	1.31	16.99	36.33		
Haemulon flavolineatu	**4.17**	**0.54**	**11.7**	**48.03**		
Scarus iseri	1.99	0.97	10.99	59.02		
Acanthurus coeruleus	1.92	1.33	10.3	69.32		
Scarus taeniopterus	1.27	1.3	8.98	78.3		
Melichthys niger	9.06	0.84	22.66	22.66	Shallow-NonMPAGrand	69.32
Sparisoma viride	**7.8**	**0.99**	**22.62**	**45.28**		
Acanthurus coeruleus	4.07	1.04	9.63	54.92		
Sparisoma aurofrenatu	2.3	1.11	8.38	63.29		
Scarus iseri	2.66	0.87	8.07	71.37		
Sparisoma viride	**10.71**	**1.39**	**33.34**	**33.34**	Shallow-MPA-Grand	
Scarus vetula	6.02	0.91	12.84	46.18		
Scarus iseri	3.37	1.19	11.71	57.89		
Sparisoma aurofrenatu	2.85	1.15	7.7	65.6		
Acanthurus coeruleus	2.38	1.24	6.64	72.24		
Sparisoma viride	8.27	1.29	28.75	28.75	Deep-NonMPA-Grand	33.26
Melichthys niger	**11.25**	**0.7**	**16.98**	**45.73**		
Acanthurus coeruleus	3.68	1.29	12.1	57.83		
Sparisoma aurofrenatu	2.92	1.28	10.07	67.89		
Scarus iseri	3	1.03	9.43	77.32		
Sparisoma viride	10.73	1.53	40.97	40.97	Deep-MPA-Grand	
Sparisoma aurofrenatu	2.67	1.43	10.47	51.44		
Acanthurus coeruleus	2.61	1.28	10.2	61.64		
Melichthys niger	**3.07**	**0.63**	**7.87**	**69.52**		
Scarus taeniopterus	1.83	1.25	6.75	76.26		

Table 4.4 continued. Two-Way-Crossed Similarity percentage analysis (SIMPER) showing average similarities of fish assemblages of MPAs and non-MPAs across islands. Text highlighted in **red** indicates a significant contribution.

Species	Av.Abund	SD	Contrib%	Cum.%	Depth-Protection-Island	Average dissimilarity (%)
Acanthurus coeruleus	4.04	1.29	17.94	17.94	Shallow NonMPA Little	72.63
Melichthys niger	5.33	0.84	14.85	32.78		
Sparisoma viride	4.25	0.81	14.79	47.57		
Scarus iseri	3.23	1.02	11.41	58.98		
Sparisoma aurofrenatu	2.26	1.09	9.35	68.34		
Haemulon sciurus	**3.89**	**0.54**	**7.13**	**75.47**		
Melichthys niger	11.55	0.87	22.95	22.95	Shallow-MPA-Little	
Sparisoma viride	9.19	1.02	18.22	41.17		
Acanthurus coeruleus	6.03	0.94	10.35	51.52		
Ocyurus chrysurus	5.79	0.59	7.38	58.9		
Kyphosidae spp.	10.79	0.39	6.72	65.62		
Haemulon sciurus	**18.38**	**0.28**	**6.51**	**72.13**		
Ephinephelus striatus	**2.96**	**1.37**	**20.18**	**20.18**	Deep-NonMPA-Little	67.2
Sparisoma viride	4.74	0.8	17.95	38.13		
Scarus iseri	2.38	1.24	15.81	53.94		
Melichthys niger	4.28	0.86	14.59	68.53		
Ephinephelus striatus	**4.1**	**1.81**	**17.12**	**17.12**	Deep-MPA-Little	
Sparisoma viride	4.33	1.3	14.86	31.97		
Sparisoma aurofrenatu	3.13	1.88	14.05	46.02		
Lutjanus apodus	3.23	1.05	10.82	56.84		
Scarus iseri	2.65	1.13	9.91	66.75		
Melichthys niger	4.08	0.65	6.11	72.86		

Table 4.5 Univariate permutation of variance for relevant variables determining dissimilarities between MPA and Non-MPAs according to SIMPER analysis for the interaction Level of Protection x Depth x Island. Text highlighted in **red** indicates significant interaction.

Habitat/level of protection		Species: *Lutjanus apodus*			Island
Shallow non-MPA	Shallow MPA	t	p	permutations	Cayman Brac
		1.9678	0.046	998	
Habitat/level of protection		Species: *Haemolon flavolineatum*			
Deep non-MPA	Deep MPA	t	p	permutations	
		1.4517	0.153	985	
Habitat/level of protection		Species: *Sparissoma viride*			
Shallow non-MPA	Shallow MPA	t	p	permutations	Grand Cayman
		2.2304	0.026	996	
Habitat/level of protection		Species:*Melichthys niger*			
Deep non-MPA	Deep MPA	t	p	permutations	
		3.3781	0.002	996	
Habitat/level of protection		Species: *Haemolon sciurus*			Little Cayman
Shallow non-MPA	Shallow MPA	t	p	permutations	
		1.9952	0.038	999	
Habitat/level of protection		Species:*Epinephelus striatus*			
Deep non-MPA	Deep MPA	t	p	permutations	
		0.07	0.934	557	

4.4.5 Effects of MPAs on the community structure of fish assemblages and functional groups; variation across years

Though community structure of fish differed significantly across years (F = 6.0218, df 3, p = 0.001, 8.94, table 4.2), no interactions between factor year and all other factors in the analysis were found. Regardless of the island, the structure of fish communities significantly differed across years following a similar pattern. *Post-hoc* comparisons showed that all years were significantly differed (table 4.6), fish communities were more similar during 2009 and 2010 and their differences increased over time (figure 4.5 a).

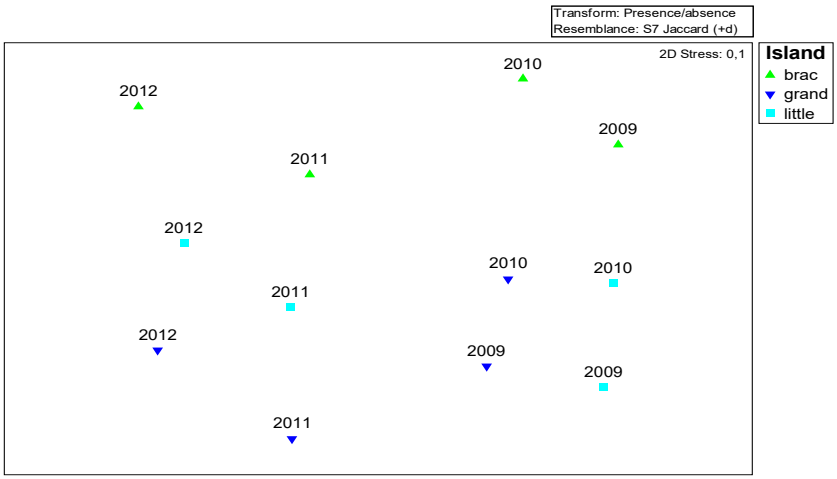


Figure 4.5 a Non Metric Multidimensional scaling showing temporal changes across years and islands for relevant species (*Melichthys niger, Kyphosidae* sp., *Sparissoma viride, Lutjanus apodus and Haemulon. sciurus*) explaining temporal changes according to SIMPER analysis. Brac=Cayman Brac, grand=Grand Cayman, little=Little Cayman.

Table 4.6 Post Hoc comparisons for the factor year. Text in red indicates significant findings between years.

Groups	t	P	perms
2009, 2010	1.672	**0.017**	999
2009, 2011	2.2672	**0.002**	997
2009, 2012	3.1223	**0.001**	999
2010, 2011	2.0179	**0.008**	999
2010, 2012	2.3947	**0.002**	998
2011, 2012	1.6224	**0.028**	997

The SIMPER analysis showed that average Bray-Curtis dissimilarities in fish community structure varied from 67 to 70% (table 4.7). Three species: the omnivore *Melichthys niger,* the herbivores *Sparissoma viride* and *Kyphosidae* spp and the carnivores *Lutjanus apodus* and *Haemolon sciurus* consistently contributed with 31 - 36% of the average dissimilarity across years (table 4.7).

The biomass of the omnivore species *Melichthys niger* significantly increased with time, this trend being consistent across the islands (figure 4.5 b, table 4.8). The herbivores in the genus *Kyphosidae* sp (figure 4.5 c), as well as the parrotfish *Sparissoma viride* (figure 4.5 d), showed that there are no apparent temporal patterns of their biomass which changed inconsistently from one year to another. In fact, the biomass of *Kyphosidae* sp was significantly different only when years 2009 and 2010 were compared (table 4.8), whereas in the case of *Sparissoma viride,* statistical differences were only found between the years 2010 and 2012 (table 4.8). The key coral reef carnivores such as the snapper (*Lutjanus apodus*) and grunts (*Haemolon sciurus*) significantly increased over time (figure 4.5 e-f).

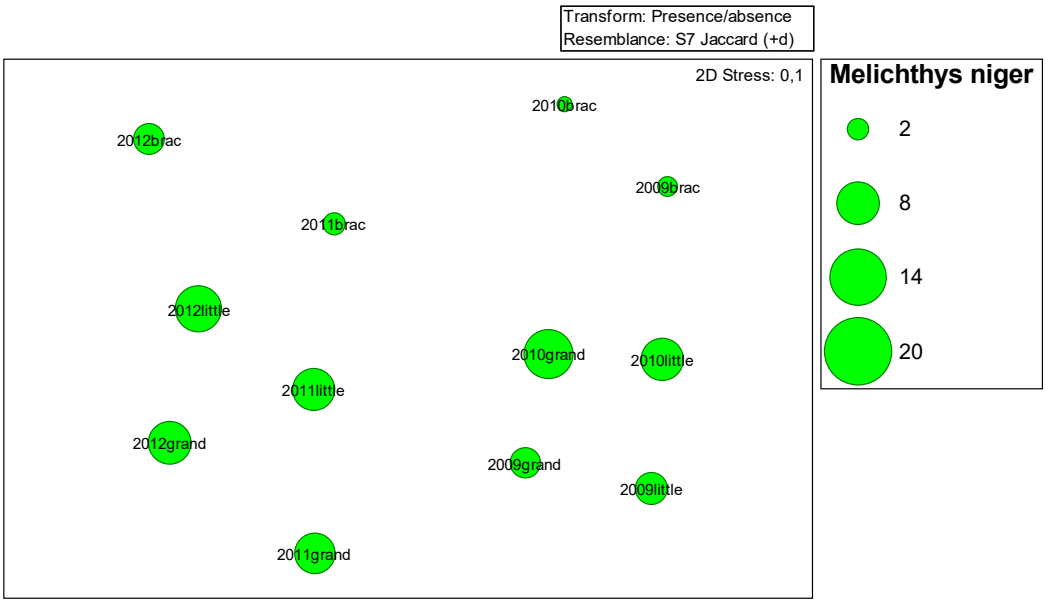


Figure 4.5 b Non Metric Multidimensional scaling showing temporal changes across years and islands. B-F bubble plots of *Melichthys niger* (black durgon) species explaining temporal changes according to SIMPER analysis. Brac=Cayman Brac, grand=Grand Cayman, little=Little Cayman

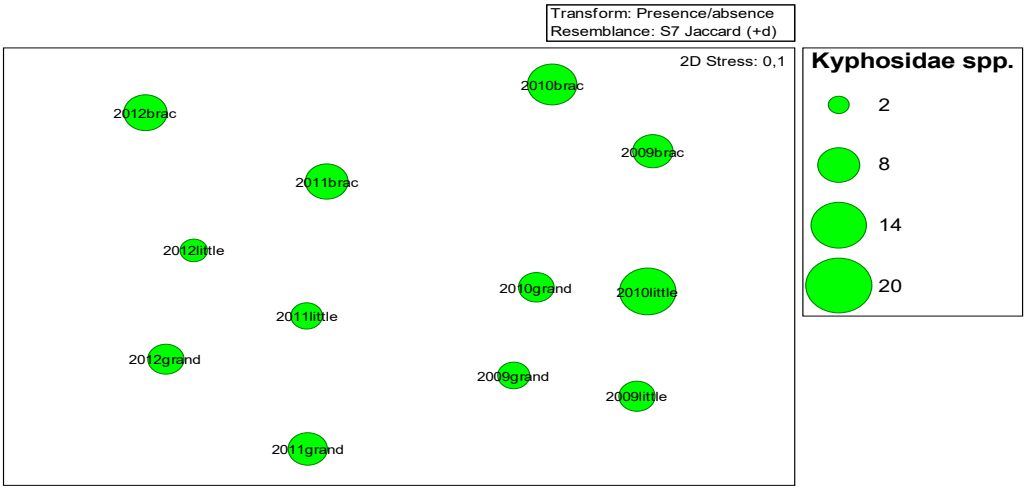


Figure 4.5 c Non-Metric Multidimensional scaling showing temporal changes across years and islands. B-F bubble plots of *Kyphosidae* sp. (chub) species explaining temporal changes according to SIMPER analysis. Brac=Cayman Brac, grand=Grand Cayman, little=Little Cayman

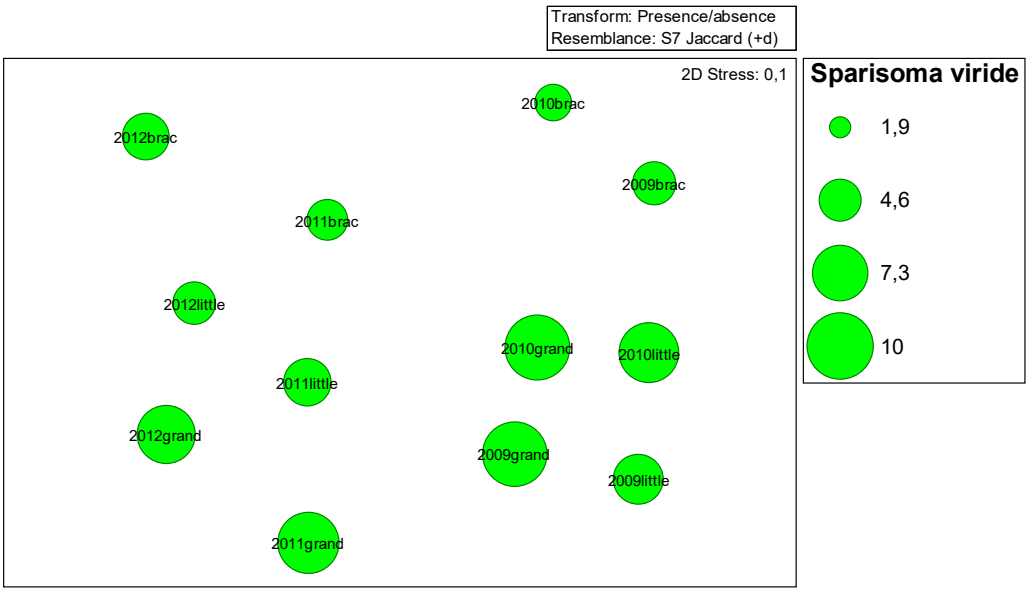


Figure 4.5 d Non-Metric Multidimensional scaling showing temporal changes across years and islands. B-F bubble plots of Sparissoma. viride (Stoplight parrotfish) species explaining temporal changes according to SIMPER analysis. Brac=Cayman Brac, grand=Grand Cayman, little=Little Cayman.

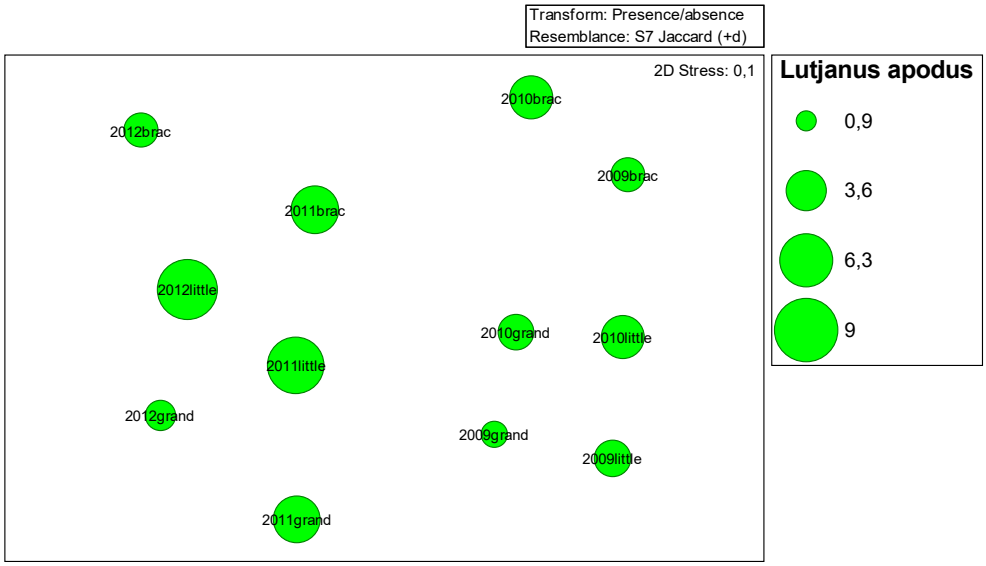


Figure 4.5 e Non-Metric Multidimensional scaling showing temporal changes across years and islands. B-F bubble plots of Lutjanus apodus (Schoolmaster) species explaining temporal changes according to SIMPER analysis. Brac=Cayman Brac, grand=Grand Cayman, little=Little Cayman.

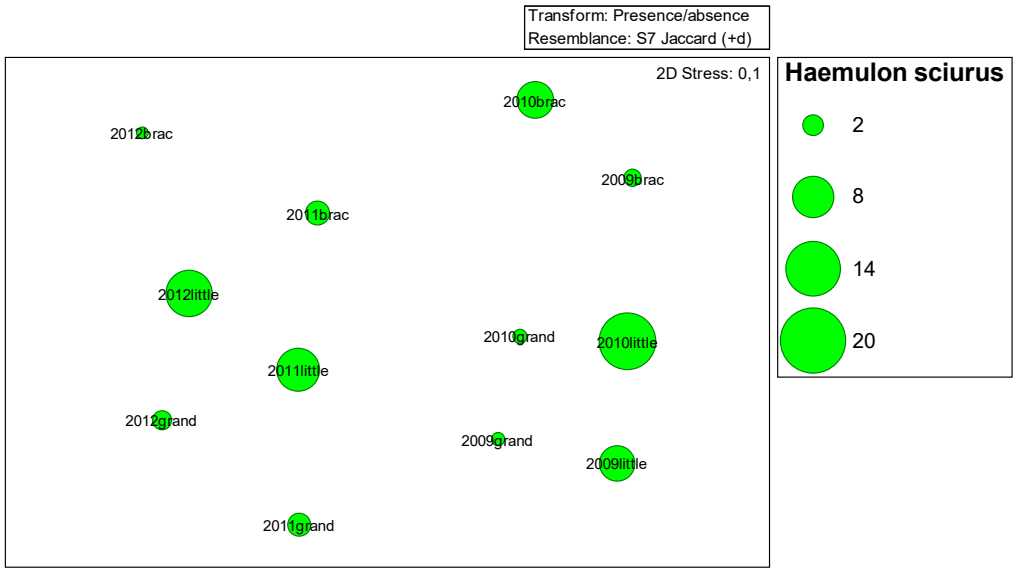


Figure 4.5 f Non-Metric Multidimensional scaling showing temporal changes across years and islands. B-F bubble plots of Haemulon sciurus (Blue stripe grunt) species explaining temporal changes according to SIMPER analysis. Brac=Cayman Brac, grand=Grand Cayman, little=Little Cayman.

Table 4.7 Species that better explained temporal changes in fish community structure from similarity percentage analysis (SIMPER).

Year	Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%	Average Disimilarity (%)
2009-2010	*Melichthys niger*	3,66	7,69	8,79	0,82	12,77	12,77	68.86
	Sparisoma viride	7,49	7,96	8,74	1,13	12,69	25,46	
	Kyphosidae spp.	5,66	9,50	7,90	0,58	11,48	36,94	
	Haemulon sciurus	2,42	6,21	3,90	0,43	5,66	42,60	
	Lutjanus apodus	2,18	3,50	3,65	0,54	5,31	47,90	
	Ocyurus chrysurus	2,20	2,12	3,37	0,56	4,90	52,80	
2009-2011	*Kyphosidae spp.*	5,66	6,59	7,49	0,59	10,76	10,76	69.58
	Melichthys niger	3,66	6,26	6,96	0,83	10,01	20,77	
	Sparisoma viride	7,49	6,84	6,92	1,12	9,95	30,72	
	Lutjanus apodus	2,18	5,59	4,40	0,69	6,32	37,04	
	Haemulon sciurus	2,42	4,30	3,75	0,50	5,39	42,42	
	Acanthurus coerule	2,04	4,58	3,59	0,75	5,16	47,58	
2009-2012	*Melichthys niger*	3,66	7,59	8,56	0,90	12,42	12,42	68.88
	Sparisoma viride	7,49	6,44	8,11	1,12	11,78	24,20	
	Kyphosidae spp.	5,66	5,79	7,20	0,56	10,45	34,65	
	Acanthurus coerule	2,04	5,58	4,73	0,82	6,87	41,52	
	Lutjanus apodus	2,18	3,92	4,05	0,68	5,88	47,39	
	Haemulon flavoline	0,89	3,99	3,84	0,71	5,57	52,97	
2010-2011	*Melichthys niger*	7,69	6,26	8,63	0,85	12,30	12,30	70.19
	Kyphosidae spp.	9,50	6,59	7,20	0,55	10,26	22,56	
	Sparisoma viride	7,96	6,84	6,83	1,11	9,72	32,28	
	Lutjanus apodus	3,50	5,59	4,59	0,59	6,54	38,82	
	Haemulon sciurus	6,21	4,30	4,48	0,49	6,38	45,20	
	Acanthurus coerule	2,72	4,58	3,49	0,78	4,97	50,17	
2010-2012	*Melichthys niger*	7,69	7,59	10,05	0,89	14,66	14,66	68.55
	Sparisoma viride	7,96	6,44	7,79	1,10	11,36	26,02	
	Kyphosidae spp.	9,50	5,79	6,83	0,50	9,96	35,98	
	Acanthurus coerule	2,72	5,58	4,48	0,81	6,54	42,52	
	Haemulon sciurus	6,21	3,91	4,28	0,46	6,25	48,76	
	Lutjanus apodus	3,50	3,92	4,19	0,56	6,11	54,87	
2011-2012	*Melichthys niger*	6,26	7,59	8,53	0,89	12,65	12,65	67.47
	Kyphosidae spp.	6,59	5,79	6,52	0,52	9,66	22,31	
	Sparisoma viride	6,84	6,44	6,11	1,13	9,05	31,36	
	Lutjanus apodus	5,59	3,92	4,84	0,68	7,17	38,53	
	Acanthurus coerule	4,58	5,58	4,24	0,73	6,29	44,82	
	Haemulon flavoline	3,20	3,99	4,13	0,71	6,12	50,94	

However, *post-hoc* comparisons of these two species (*Lutjanus apodus* and *Haemolon sciurus*) only showed statistical differences in the years 2009 - 2011, 2009 - 2012 and 2009 - 2010, respectively (table 4.8). This result seemed to support that MPAs might be playing a central role in building up resilience and resistance by increasing the biomass of a crucial herbivore and carnivores over time. Nevertheless, the fish community structures were extremely variable in space and time, which makes it extremely difficult to address the actual effect of level of protection (MPAs vs. non-MPAs) across islands and habitats (depths).

Table 4.8 Post Hoc comparisons based on permutations for most relevant variables explaining temporal differences according to SIMPER analysis. Text in **red** indicates significant findings between years for fish species.

Species: *Melichthys niger*				Species: *Lutjanus apodus*			
Years	t	P(perm)	perms	Years	t	P(perm)	perms
2009, 2010	**3.7407**	**0.001**	**997**	2009, 2010	1.3996	0.168	998
2009, 2011	**2.8374**	**0.005**	**995**	**2009, 2011**	**2.5988**	**0.005**	**999**
2009, 2012	**3.9385**	**0.001**	**999**	**2009, 2012**	**1.9375**	**0.043**	**996**
2010, 2011	1.095	0.274	998	2010, 2011	1.3514	0.193	998
2010, 2012	$7.5396E^{-2}$	0.946	995	2010, 2012	0.34372	0.749	999
2011, 2012	1.0699	0.284	996	2011, 2012	1.1019	0.266	996
Species: *Kyphosidae* sp.				Species: *Haemolon sciurus*			
2009, 2010	**2.3746**	**0.01**	**999**	**2009, 2010**	**1.9279**	**0.042**	**997**
2009, 2011	0.49382	0.633	996	2009, 2011	1.4502	0.15	996
2009, 2012	$5.8802E^{-2}$	0.961	997	2009, 2012	1.017	0.344	998
2010, 2011	0.99326	0.359	999	2010, 2011	0.91378	0.368	998
2010, 2012	1.2051	0.262	998	2010, 2012	1.0428	0.298	999
2011, 2012	0.35149	0.725	998	2011, 2012	0.23667	0.832	997
Species: *Sparissoma viride*							
2009, 2010	0.58384	0.568	999				
2009, 2011	1.0281	0.299	995				
2009, 2012	1.5819	0.121	997				
2010, 2011	1.4293	0.154	997				
2010, 2012	**1.8759**	**0.043**	**998**				
2011, 2012	0.63083	0.512	995				

4.5 Discussion

4.5.1 Fish assemblages / distribution

Although mean fish biomass was grouped into five trophic groups, the reef fish community structure of the Cayman Islands is dominated by herbivores, constituting the largest biomass of the reef fish community across the four years of this study. As expected, herbivorous fish (predominantly Scaridae) represented the dominant trophic guild within the Marine Protected Areas (MPA's) as well as non-protected areas of the Cayman Islands, conforming to the findings of Pattengill-Semmens and Semmens (2002), McCoy *et al*. (2010), Drommard *et al.* (2011). The results were also in agreement with Valles and Oxenford's (2014) findings and conclusions of a broad study on Caribbean reefs that densities and biomass of herbivores (parrotfishes) were of highest density and biomass of all guilds, with no relationship to human population densities. Though fish assemblages across the islands changed through space and time, the biomass of herbivorous fish remained consistent.

4.5.2 Algal Grazing Regime

This fact brings into question of the algal grazing regime on Caribbean reefs and gives much thought about which organism are responsible for cropping and keeping macroalgae in check. Bellwood (2006) found that one single species (the batfish, *Platax pinnatus*) on Australian reefs was predominantly responsible for algal control, with 43 other herbivorous fish species only playing a minor part.

The percentage makeup of the herbivore community across the years for all islands within their MPAs (data pooled) ranged from 48% to 67% with an average of 61% over the course of this study, similar to McCoy et al. (2010) finding of 67% and Drommard et al. (2011) of 65.5%. Whereas, the non-MPAs herbivore biomass ranged from 74% to a high of 81%, with an average of 75% across the 4 years, much higher than inside MPAs and again similar to the investigation by McCoy et al. (2010) of 79% of the island of Grand Cayman (GCM) and Drommard et al. (2011) of 76% for the sister island of Little Cayman (LC). On average, herbivore biomass was higher outside the MPAs of the Cayman Islands by a factor of 1.2. This observation is perhaps attributed to the lower biomass of carnivorous fish found outside of MPAs in the Cayman Islands.

The vital role that carnivores play in the marine trophic ecosystem in controlling and manipulating other marine organisms' populations, including fish populations in the trophic hierarchy is well documented (Hairston *et al*., 1960; Miller *et al*., 2001; Williams *et al.*, 2004; Kulbicki *et al.*, 2005) from a top-down approach. Removal of carnivores can also have negative impacts and in some cases lead to an increase in lower trophic animals which further control other organisms in the trophic hierarchy as suggested by Pinnegar *et al.* (2000). This might be the case in GCM and CB where large-bodied carnivores' populations are limited in abundance and total biomass, more so on the island of GCM throughout this

study. Further management intervention to protection of the reef fish populations on those two islands may be necessary to avoid a "trophic cascade" where over time, their ecosystem eventually enters a phase where algal totally dominates the reef (Jackson *et al*., 2001; Bellwood *et al.,* 2004; Hughes *et al.*, 2007), which perhaps has results of this study support. Findings were similar to conclusions drawn by Gall (2009), Barton (2010) and Campbell (2010) studies of Caymanian reefs of an algal dominated environment. The percentage make-up of the carnivore dominance across the years for all islands within their MPAs ranged from 33% to 52% with an average of 39% over the course of this study. While at the same time their non-MPAs carnivore percentage community structure ranged from a low of 19% to a high of 30%, exhibiting an average of 24% across this four years of study. Data showed that on average, carnivore biomass averaged 1.6 times more within the MPAs of the Cayman Islands, similar to McCoy *et al.* (2010) findings of the biomass of carnivores in the MPA of GCM of 2 times higher inside that islands` MPA when compared to outside of the MPA. This finding suggests that the protected areas of the Cayman Islands are perhaps playing a central role in building up coral reef fish by fostering a more balanced reef fish community structure within the MPAs of the Cayman Islands of a higher carnivore biomass when compare non-MPAs, with the island of Little Cayman the healthiest reef fish community structure, at least for the course of this investigation.

4.5.3 Spillover

The net migration of fish out of Marine Protected Areas (MPA's) is a critical function of successful MPAs and known as "Spillover effect" whereby replenishing and restocking adjacent fished areas (Russ and Alcala, 1996; McClanahan and Mangi, 2000; Gell and Roberts, 2003; Abesamis *et al.,* 2006; McCoy *et al.,* 2010; Hall, 2014; Oliver, 2014; Ward, 2015). When the Marine Protected Areas (MPA's) were introduced in 1986, no thought was given to the benefits outside of protection as a precaution for the 7-mile beach peninsula from coastal development due to the growing dive tourism industry, mitigating anthropogenic stressors to the leeward margin of Grand Cayman (GCM) coral reef ecosystem (Ebanks and Bush, 1990). Part of this study was to investigate the presence of spillover at the boundaries of the MPA's of the Cayman Islands. Though it is a broad assumption that once in place, MPA's will provide such benefits, Palumbi (2004), and Kerwath *et al.,* (2013) argued that there is a lack of concrete, convincing evidence. However, quite similar "spillover" evidence found in this study on the northern boundary of the MPA in GCM were equally found by other studies conducted in different MPAs globally (Kelly *et al.,* 2002; Maypa et al., 2002; Russ and Alcala, 2003; Russ *et al.,* 2003; Alcala *et al.,* 2005) . Also, contrary conclusions were drawn by Westera *et al.* (2003), Palumbi (2004), Sale *et al.,* (2005) and Fabian *et al.* (2014) that spillover evidence from MPAs is scarce and contradictory. For 2 years of this study (2009 & 2011), a significant and definitive negative correlation was found on the northern boundary of the MPA in GCM as distance increased away from the northern boundary of GCM MPA, with the genus Lutjanidae (snappers) and Haemulidae (grunts) contributing

most to the "spillover" effect. Henshall (2009) and Meir et al. (2011) studies demonstrated that this particular area along the northern boundary of the MPA in GCM is one of the most fished areas, subjected to high fishing pressure from the local recreational, subsistence and artisanal fishers. This evidence suggests that this spillover effect is indeed happening at this location, producing a negative gradient in fish biomass with increasing distance from the MPA boundary. No spillover evidence was found for the herbivores suggesting perhaps some other factor was inhibiting their migration out of MPA. However, Pitman *et al.,* (2014) documented daily movement for the carnivores *Haemulon scirus* (blue stripe grant) and *Lutjanus analis* (mutton snapper) of travelling as much as 11.7 km and 42.2 km respectively, suggesting that carnivores home ranges are much larger than herbivores, making spillover over effect more likely to be detected for that guild of reef fish.

This MPA management tool, by default design, was based on the fact that it would benefit the local fishermen and fisheries per se. This "spillover effect" is well known to the local Caymanian fishermen and is exploited almost daily, mostly referred to globally as "Fishing the line", in which fishermen fish just outside of the MPA to optimize catch per unit effort (personal observation). In well managed MPA's that are actively enforced, there is a buildup of densities and biomass within the MPA's, and in most cases, it gives certain species of fish that are over-exploited, the chance of recovery as they usually reach a larger size class and density (Lester *et al.,* 2009). This finding is consistent with the results here and data collected for the northern boundary of the MPA in GCM. According to Russ (2002), adjacent fisheries are supposed to benefit from the larger body size within the MPA, which transfers to increased production of eggs and larvae, consistent with the results and findings by McCoy *et al*., (2010), giving merit that at least one of the MPA's of the Cayman Islands is displaying spillover effect on it's MPA boundary. Though there are very few studies that try to quantify spillover, Goni *et al.* (2010) in a study of the Columbretes Islands Marine Reserve (CIMR) off the coast of Spain in the Mediterranean Sea demonstrated net spillover benefits using a decade (1997–2007) of tag-recapture data for the lobster *Palinurus elephas*, similar to my findings for at least 2 years of this study (2009 and 2011). For the years that spillover was not detected, one possible explanation may be the fact that there are clear differences in the total biomass of fish as compared to outside of MPA (figure 4.1). On the southern boundary of the MPA in GCM, no correlation in biomass and distance from MPA was found, the southern boundary borders a channel that is >500 m wide. This disrupts the reef topography due to a high volume of water exiting from the upstream South Sound bay enclosure and creating strong currents, including a less rugose reef environment. Reef fish migrates across complex three-dimensional coral reef habitats to avoid predators. This lack of habitat may be an impediment whereby limiting the transgression of fish out of the reserve on the southern boundary of GCM MPA to adjacent areas. Overall, the data collected suggest that any MPA boundaries in the Cayman Islands should have a contiguous reef environment to facilitate net migration out of the MPA's to adjacent fishable areas if

this management tool is to be effective and be utilized in their MPA network across the islands. Though this aspect of Cayman Islands MPAs design was not considered when their MPA systems were set up, this adjustment would be beneficial to all users, including the local fishing population. Additionally, data collected demonstrated that the net movement and migration out of the MPA in Grand Cayman (GCM) were fish predominantly of the genus *Lutjanidae* (snappers) and *Haemulidae* (grunts), this observation is consistent with McCoy *et al.* (2010) and Ward (2015) Hughes (2017) findings. Carnivores such as these are known to have a much larger home range and are aggressively territorial (Pitman *et al.,* 2014). One possible explanation for these particular species being responsible for the observed gradient maybe that these traits transfer into a higher pressure amongst the population in defense of territory and food resources driving this net migration out of the MPA. Lastly, data showed that the net migration was only documented along the shallow reef terrace. This observation was consistent across years, even when data were non-significant. One noted caveat is that Legislation governing the MPA's implemented in 1986, allows local fishers to fish the 24 m depth contour (80ft) and beyond anywhere in the Cayman Islands, including within the MPAs. According to Burgess *et al.* (1994), the deep shelf around GCM had the most abundance and diversity of fish as compared to the shallow terrace. However, this is no longer the case, possibly due to this fact, whereby fishers can remove these targeted carnivores on the deep terrace reef. Furthermore, Meier *et al*. (2011) demonstrated that fish from the genus *Lutjanidae* were the most targeted fish across the 3 Cayman Islands, which manifested itself in this study, demonstrating a shift from the deep terrace reef to the shallow terrace reef for total biomass of all fish species and demonstrating a highly variable and haphazard non-significant effect for spillover on the deep terrace reef of the Cayman Islands. When migratory fish species data is examined over the period of this study, it is evident that the grouper/snapper complex is the group of fish responsible for the gradient of fish biomass away from the boundary of the MPA in Grand Cayman. Additionally, where these species of fish are found in abundance coincides with the presence of the local fishers as they are the most sought-after fish (Meier *et al.,* 2011), further making evident that the "spillover effect" aspect of the MPA in GCM on the northern shallow terrace reef is working as intended. In regards to non-detection at other MPA boundaries, in this study, spillover over locations were only 1 km apart over a 5 km distance. One possible reason for non-detection of spillover as suggested by Pittman *et al*. (2014), that to detect spillover effect, a large spatial scale has to be used to detect a correlation of biomass and distance from MPA boundary.

4.5.4 Resiliency effects of Marine Protected Areas on Fish assemblages and community structure

No take Marine protected areas as a fishery management tool are designed in most cases to foster not only protection of fish assemblages but also to promote a robust resilient fish community structure including serving as a larval source. This robust community structure is therefore supposed to model the actual reef fish assemblages and community structure in its natural state, when left undisturbed and zero extraction regarding exploitation. However, in this study, the fish assemblages and community structures were variable in time and space, with data showing that changes across the islands and marine protected areas were not consistent and each island exhibiting a different trajectory. This observation is consistent with findings by (McCoy *et al*,. 2010; Hall 2014; Oliver 2014; Ward 2015; Hughes 2017) and similar to findings by McClanahan *et al,* (2006) of fish assemblages in Kenya, Africa. This might be due to the population differences between island and the difference in fishing pressure, including choice of target fish supporting Henshall (2009) and Meier *et al.,* (2011) findings. Additionally, the fish assemblages and community structure of the deep and shallow terraces are entirely different across each island and not homogenous supporting McCoy *et al.* (2010) and Drommard *et al.* (2011) findings. In the Cayman Islands, fishers are permitted to fish within 24 m (80 ft) depth contour where MPA's are located. Therefore, this allows fishers to extract fish on the deep shelf, possibly manifesting itself in total fish biomass on the deep shelf and with varying fishing pressure, causing differences in the fish assemblages and community structure. This fact perhaps also contributed to the inconsistencies observed in the trophic structure over the years of study and opposite of finding by Burgess *et al.* (1994) of higher fish biomass on the deep shelf vs. shallow terrace reef. One obvious observation of differences in Cayman Brac, was that protection had no effect on the fish assemblages of the deep and shallow terrace reefs, with some other factor causing those differences, possibly habitat structure. In Grand Cayman (GCM), post hoc comparisons showed significant differences in that islands fish assemblages for the shallow reef terrace, but not the deep reef habitat, this observation may be due to being accessible to fishers at the 24 m depth contour inside and outside of its MPA. Little Cayman demonstrated differences across its deep and shallow terrace reefs similar to Drommard *et al*. (2011) findings. One possible explanation for this observation was perhaps due to the low fishing pressure on that island (Henshall, 2009; Meir *et al.,* 2011). Dive tourism is the only economic pillar of LC economy, therefore support and compliance for the MPAs on that island by the < 300 residents is considered highest of the 3-island archipelago (personal observation).

4.5.5 Resiliency effects on functional trophic groups and species; variation across spatial scales

Grouping functional trophic clusters of reef fishes, and especially herbivorous fishes based on their diets, is increasingly the option used to get an index of resiliency (Heenan and Williams, 2013). The conservation benefits of Marine Protected Areas (MPA's) on fish biomass, densities, biodiversity,

including an increase the reproductive potential (larger fish) have been well documented (Gell and Roberts, 2003; Halpern *et al.,* 2003, Lester *et al.,* 2009; Babcock *et al.,* 2010). Though each of the 3 islands demonstrated a different trajectory in their reef fish assemblages and community structure, a similar trend was observed in their functional trophic groups and species over time and space. The diversity of the different trophic guilds of coral reef fishes is important to ensure ecological processes continue, especially with reference to herbivores to prevent phase-shifts from a coral-dominated environment to an algal dominated one (Done, 1992; Goreau 1992; White *et al.,* 2000; Gardner *et al.,* 2003; Graham *et al.,* 2006) and subsequent depletion of the reef fish assemblages (Done, 1992). Though the functional differences of reef fish assemblages between the MPAs and non-MPAs across habitats and islands were highly correlated, only 4 species accounted for this disparity (*H. tricolor* (Rock beauty), *S. aurofrenatum* (Redband parrotfish), *A. surinamensis* (Black margate) and *Kyphosidae* sp (Sea chubs)(figure 4.4 b). According to Randal (1967), *S. aurofrenatum* and *Kyphosidae* sp (Sea chubs) dietary analysis showed 97% and 99.5% algae consistency respectively. This finding is important in that it may indicate that these 2 coral reef fish species may be very important in cropping and reducing algae across the 3 Cayman Islands.

The similarity profile analysis (SIMPER) demonstrated that the fish community structures were very different throughout this study, changing from island to island. Though ecological data are highly variable, this observational trend is perhaps reflective of the degree of fishing pressure in and around each island (Henshall, 2009; Meier *et al*., 2011) and perhaps correlated with each of the island's population. Even with the island of Cayman Brac (CB) showing no measurable differences between MPA and non-MPA on the shallow reef habitat, 5 species were responsible for >70% of the dissimilarity, with the intertidal herbivore *Kyphosidae* sp (chubs) reaching 14.9 g/m^2 and 10.4 g/m^2 respectively, however, this particular species of fish are known to gather in large schools as they travel along reef terraces. Additionally, they are not targeted by residents on that island (Meier *et al*., 2011). Quite striking was the observation of the carnivore *Lutjanus apodus* (Schoolmaster snapper), being 2.5-fold more abundant on the shallow reef habitat within that island MPAs (7.11 g/m^2 and 2.48 g/m^2 respectively) giving merit to the fact that protection was increasing the biomass of that species.

Nevertheless, the differences were negligible and non-significant for the structure of the reef fish community when MPA and non-MPA was compared, suggesting that the island's MPA's are failing to build up abundance and biomass of its reef fish assemblages on the shallow reef terrace within their protected areas. A similar trend also manifested itself on the deep terrace reef of Cayman Brac, with just 5 species accounting for >70% dissimilarity. Again, one species of carnivore *Haemulon flovolineatum* (French grunt) contributed the most demonstrating a 2-fold increase in biomass within its MPAs (4.17 g/m^2) as compared to that island non-MPAs (2.18 g/m^2), but this apparent increase was again non-significant. This finding is a cause for concern as not only the abundance and biomass of that island's reef fish assemblages are the lowest of the 3-island archipelago, but its MPAs did not generate any significant positive results in fish assemblages during the period of this study. This suggests that

the MPAs of Cayman Brac do not work, resulting in no effect or differences between that island MPAs and non-MPA's fish community structure, which will further be compromised as that island human population increases putting increasing demands on its marine resources. This will further only reduce any chances of increasing that islands reef fish population.

The average dissimilarity between MPA and non-MPA on the shallow reefs of Grand Cayman (GCM) was ~69% with 2 species making the most contribution to those differences. One of those species was the Caribbean keystone herbivore *S. viride* (stoplight parrotfish) which was responsible for >40% of the dissimilarity (table 4.2). Additionally, the biomass of *Sparisoma viride* was significantly higher on the shallow reef terrace within that islands MPA showing 1.5 times more biomass than the shallow reef terrace of that island non-MPA. This result demonstrates that the MPA of that island is exhibiting positive results for that particular species, more so the fact that it is building up higher biomass of a keystone herbivore species (Mumby 2014), suggesting that protection it is fostering ecological resilience within the MPA of GCM, during this study. However, the fish communities on the deep terrace reef of GCM were similar within that islands MPA as compared to its non-MPA, therefore revealing the lowest dissimilarity found during this study (33.26%). Four fish species accounted for this dissimilarity, with *Melichthys niger* (Black Durgeon) being the one species demonstrating a significant difference in biomass between MPA and non-MPA for GCM. This planktonic omnivore biomass was 4 times greater in the deep habitats of GCM in that islands non-MPA (11.25 g/m^2 vs. 3.07 g/m^2, table 4.2). This, however, comes as no surprise as the MPA is located on the leeward margin of GCM, *Melichthys niger* mostly planktivorous diet requires an exposed coastline that has adequate current flow such as the Southern exposed margin of GCM and the semi-exposed north coast of GCM. Additionally, the deep terrace reef abruptly drops to abyssal depths, therefore possibly deep nutrient-rich water is forced upon the shelf providing a food source for this particular species. In particular, this species is well established on the south coast of GCM, most likely due to the SE trade winds which dominate for most of the year (Burton, 1994), perhaps causing upwelling of deep nutrient-rich oceanic waters that they are using as a food source.

Very different from CB and GCM, the island of Little Cayman (LC) fish community structure showed quite striking results. Not only were the largest average dissimilarities found on that island (Shallow terrace reef >72%; deep terrace reef >67%), but the biomass of *Sparisoma. viride* (Stoplight parrotfish) and *Achanturus coeurelus* (Blue Tang) two key Caribbean reef herbivores were 1.5 to 2.2 times higher within that island MPAs (table 4.2). These two particular species of herbivores are considered a keystone species, whereby their biomass and abundance in large numbers aids in preventing a shift from a coral-dominated state to an algal-dominated state (Done, 1992; Goreau, 1992; White *et al.*, 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Bellwood *et al.*, 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.*, 2014).

Results for the shallow reef habitats within the MPAs of Little Cayman (LC) also demonstrated success in increasing the biomass of the carnivore grunt *Haemolon sciurus* >4.5 fold, from 3.89 g/m^2 to more than 18 g/m^2 (table 4.2). However, these ecologically important carnivore show high site fidelity and are found in large schools (Beets *et al.,* 2003), which might explain the large biomass observed. Though only a few species contributed to the 67.2% dissimilarity on the deep reef habitats of LC, it is not to any surprise that *E. striatus* (Nassau Grouper, table 4.2) contributed the most. LC is home to the largest known Nassau grouper aggregation in the Caribbean basin (Whaylen *et al*., 2004; Bush *et al.,* 2006; Whaylen *et al.,* 2006; Archer *et al.,* 2012; Heppell *et al.,* 2012; Egerton *et al.,* 2017). This iconic Caribbean top reef predator biomass was ~2-fold inside LC MPAs. This might be imparted to due not only to protection, but also management strategies of this species implemented by the Cayman Islands Government during spawning months, including catch numbers during open season and catch size limits (see figure 6, chapter 1). Having an abundance of this top predator is imperative for Caribbean reef ecological functionality (Stallings 2008, 2009; Archer *et al.,* 2012; Egerton *et al.*, 2017) and indicative of a healthy ecosystem promoting coral reef fish by manipulating and shaping prey structure by feeding on a wide range of echinoderms, molluscs, crustaceans and worms (Williams *et al.,* 2004; Kulbicki *et al.,* 2005), in addition to top-down control of other carnivores by preying upon them (Miller *et al*., 2001).

4.5.6 Resiliency effects of MPAs on the community structure of fish assemblages and functional groups: variation across years

The management strategy of using functional groups as indicators of vulnerability before disturbances and as a resiliency measure (Nyström *et al*., 2008), is a tool commonly used by coral reef managers globally to prevent or reverse a phase shift from a coral-dominated environment to an algae-dominated environment. With these data showing very different reef fish community structure over time and space, reef fish functional trophic groups can be compared whereby managers can make decision that will impact and possibly confer and promote resiliency in the different trophic groups, especially in the herbivory guild, much like Hoey and Bellwood (2008), Green and Bellwood (2009) findings. Though the presence, size, and densities of reef fish are usually linked to coral cover, as purported by Graham *et al*. (2006) and Williams *et al*. (2008), no clear pattern was observed throughout this study. However, the opposite was found by Bonaldo and Bellwood (2011), and Cheal *et al*. (2012): their findings, at least for the herbivores guild were variable in abundance and distribution across reef habitats and similar to the findings of this study. Furthermore, Heenan and Ivor (2013) found that when further grouping large-bodied parrotfish (bio-eroders/large excavators) it serves as a good predictor of high hard coral cover.

In this study, though no significant interactions between years and all factors in the analysis of the data were found, results show that the fish community structure changed over time for each of the three

island archipelago. It is not surprising that each island followed quite similar trends due to the proximity to each other. The *post-hoc* comparisons (table 4.4) showed that fish communities for each year were significantly different, however a multidimensional scaling plot (figure 4.5 a) showed that they were most similar for the years 2009 and 2010. Thereafter differences gradually increased suggesting that some common factor amongst islands was driving permanent changes other than natural perturbations such as habitat changes over time and or fishing pressure, which Meier *et al.* (2011) findings show that fishing pressure was different amongst islands. Not surprising, SIMPER analysis varied from 67 - 70% along with eight species of reef fishes mostly responsible for these changes in fish community structure; the omnivore *Melichthys niger* (black durgeon) the herbivores *Sparisoma viride* (stoplight parrotfish), Acanthurus coeruleus (blue tang), *Kyphosidae spp* (chubs) and the carnivores *Lutjanus apodus* (mangrove snapper), and *Haemulon sciurus*, (blue stripe grunt) *Haemulon flavolineatum* (French grunt) and *Ocyurus chrysurus*, (yellowtail snapper) consistently contributed with 31 - 36% of the average dissimilarity across years (Table 4.5). These eight species are quite common across the 3 Cayman Islands and the region as a whole. The observation of a significant increase of *Melichthys niger* (Black durgeon) over the course of this study and across all 3 islands is quite consistent with other findings and its life history strategy; highly abundant on reefs of remote oceanic islands (Osbeck, 1771; Lubbock, 1980; Kathryn *et al.,* 2006), and swarming (Lubbock, 1980; Lubbock and Edwards, 1981; Randall et al., 1985; Gasparini and Floeter, 2001; Katryn et al., 2006). Most striking is the study by Katryn *et al.* (2006) findings which demonstrated that they have an exceptionally long pelagic stage, fast growing (35 - 40% in the first year), live long (>11 years), high plasticity feeding mode, able to control aggressive interspecific and intraspecific depending on its population to make the best of resource use making this fish particularly a very successful colonizer able to increase its population status consistently. This is a cause for concern as at some point; population numbers might tip the intricate ecological balance for habitat and food resources for other ecologically important reef fish species. The biomass of the genus *Kyphosidae spp* (chubs) pattern was neither consistent nor showed any clear temporal trajectory, following a haphazard pattern over the years of this study, only exhibiting differences when the years 2009 and 2010 were compared (Table 4.6). This same pattern is also consistent with the reef fish community structure similarities over the years, possibly suggesting that the population of this species might be a controlling factor of the reef fish community structure in the Cayman Islands. According to Green and Bellwood (2009), these intertidal browsers continually feed on macroalgae and its associated epiphytes with the potential of helping keep algal growth in check and possibly playing a pivotal role in coral-algal phase shift reversal. This particular species of reef fish is one of the least targeted across the Cayman Islands (Meier *et al*., 2011) and mostly released when caught (Hall, 2014). Those two circumstances should allow for a consistent increase or stability in their biomass throughout this study, which is not the case. This observation suggests that some other factor or a combination of factors are controlling their population, causing the variability in biomass of the genus *Kyphosidae spp* on Caymanian reefs, possibly an apex predator. The biomass of the keystone grazer

Sparisoma viride (stoplight parrotfish) only showed temporal differences in the years 2010 and 2012 (Table 4.6), and much like the *Kyphosidae spp* did not show any clear temporal pattern, with total biomass changing inconsistently for the years of this study. This is a concerning observation for the herbivore regime within the Cayman Islands for this species as they are considered the most dominant among Scarid species (Mumby, 2006), and one of the most abundant large herbivorous fish of the Caribbean reefs (Burkepile and Hay, 2011). Furthermore, herbivores are the biological drivers of the community structure of coral reefs, controlling the proliferation of macroalgae (Carpenter, 1986; Hay, 1991; Burkepile and Hay, 2006; Mumby, 2006) and promoting coral reef resiliency.

However, the biomass of the carnivores *Lutjanus apodus* (schoolmaster snapper) and *Haemulon sciurus* (blue stripe grunt) increased over time (Figure 4.5 e-f), demonstrating significant differences for the years 2009 - 2011, 2009 - 2012 and 2009 - 2010, respectively (Table 4.6). These results are very encouraging as these two species are key Caribbean coral reef mesopredators and the MPAs of the Cayman Islands seem to be building up their biomass in addition to increasing the biomass of key carnivores and herbivores whereby creating a robust fish community structure representing each of the different trophic promoting ecological function. Ecological data are by nature, variable and difficult to address and separate cause and effect over time and space. Lastly, the fish community structures across the three Cayman Islands were extremely variable during this investigation; however, data collected, exhibited clear signs that the MPAs of the of Little Cayman has been to a large extent successful in promoting robust and resilient coral reef fish assemblages

4.4 conclusion

This study brings to attention how variable ecological data can be through space and time and demonstrates how selective recreational fishing pressure (Henshall, 2009; Meir *et al.,* 2011) can shape the fish assemblages and community structure which can have domino effects on ecological resiliency. If the trophic hierarchy of fish species, their biomass, and associated trophic groups defines the balance between reef fish ecological resiliency status and a compromised system, then the MPAs of the Cayman Islands are seemingly helping to define and shape how each island MPAs performed during the years of study. However, if complex ecological processes are to be maintained and function properly, the functional roles of each species contribution to the ecosystem as a whole have to be present (Nyström, 2006), which was not always the case for all islands, more so the carnivores population on the island of Grand Cayman. The lack of large apex predators in Grand Cayman perhaps lends merit to the increased abundance of lower trophic functional species such as omnivores and herbivores. The reverse is manifested in Little Cayman, where a higher abundance of apex predators is perhaps responsible for the lesser biomass of the lower trophic level fish species when compared, suggesting that they are controlling their population, which further suggests a robust trophic structure. The island of Cayman Brac reef fish assemblages and community structure is seemingly in a steady state position; however,

its MPAs functionality for the intended purpose is seemingly compromised. Algal grazing by herbivorous fishes is an integral and of paramount importance on any reef system in the global tropics to prevent phase-shifts from a coral-dominated reef to an algal dominated reef (Jackson *et al*., 2001; Bellwood *et., al* 2004). This balance is even more important on Caribbean reefs where humans have modified the marine environment from centuries ago by overfishing (Jackson *et al*., 2001; Hughes., 1994) coupled with destructive hurricane damage (Woodley *et al.,* 1981; Woodley *et al.,* 1989; Rogers *et al.,* 1989; Woodley, 1992; Gardner *et al.,* 2005) and the epizootic event causing the complete die-off of the keystone herbivore *Diadema antillarium* across the Caribbean region in the mid 1980's (Lessios *et al.,* 1984). However, these successive events, whether natural or anthropogenic, have all shaped Caribbean reefs to what they are today, including the reef fish community structure across the three Cayman Islands.

The benefits of fish " spillover" effect, though debatable by some scholars (Westera *et al.,* 2003; Palumbi, 2004; Sale *et al*., 2005; Fabian *et al.,* 2014; Kerwath *et al.,* 2013) is very evident on the northern boundary of the GCM MPA for carnivores. However, the lack of spillover on the deep reef terrace is a cause for concern and a possible explanation could be either a disruption of habitat as in the southern boundary of the MPA or the high fishing pressure along the deep terrace reef shelf as fishers are allowed to fish the 24 m contour and beyond. Results suggests that Cayman Islands should be repositioned so that all their MPAs boundaries have a contiguous reef habitat whereby fostering the migration of fish out of their MPAs to adjacent fish areas on the shallow and deep terrace reefs if spillover benefits are one of their objectives to benefit the local recreational and artisanal fishing population.

With the observed trend that the protection of reef fish assemblages and community structure in Cayman Brac had no effect on the shallow or deep terrace is a real cause for concern. According to Ebanks and Petrie (1991), MPA placement in Cayman Brac was chosen by residents at a public meeting, with no define criteria or purpose, whereas in Grand Cayman and Little Cayman, they were chosen due to their high biological to mitigating against coastal development. However, data suggest that the reef fish assemblages in Cayman Brac seemingly to be in a "steady state," with protection not offering any real benefits. In Grand Cayman, effects of protection of their fish assemblages and community structure were evident on the shallow reef terrace. Again, this observed trend may be the result of fishers being allowed to fish the 24 m contour and beyond within its MPA. However, contrary to the shortcomings of the two other islands, the reef fish assemblages on the deep and shallow reef terraces of Little Cayman seem to be benefiting positively throughout this study. With dive tourism being the only economic pillar of that island, it would be a wise move to expand its MPAs whereby ensuring that islands economic growth. When trophic groups over time are considered across the islands, the different trajectories in their reef fish assemblages and community structure trends seem to parallel fishing pressure

assessments by (Henshall, 2009; Meier *et al*., 2011), manifesting itself with extraction rates of each trophic guild. With no mandate to report fishery landings, small island nations such as the Cayman Islands have no means of documenting any decline in fish stocks. If the observed trend documented by Henshall, (2009) and Meier *et al.* (2011) continues of high recreational and artisanal fishing pressure, targeted fisheries could be overexploited before any plausible legislation could be put in place to manage at-risk species such as their herbivores and the grouper-snapper complex. Therefore a needed and necessary fisheries management tool for the Cayman Islands should be considered whereby having the capacity to manage their fish stocks. This action would assist building coral reef fish biomass and safeguard their fish assemblage's, community trophic structure, and functional trophic groups.

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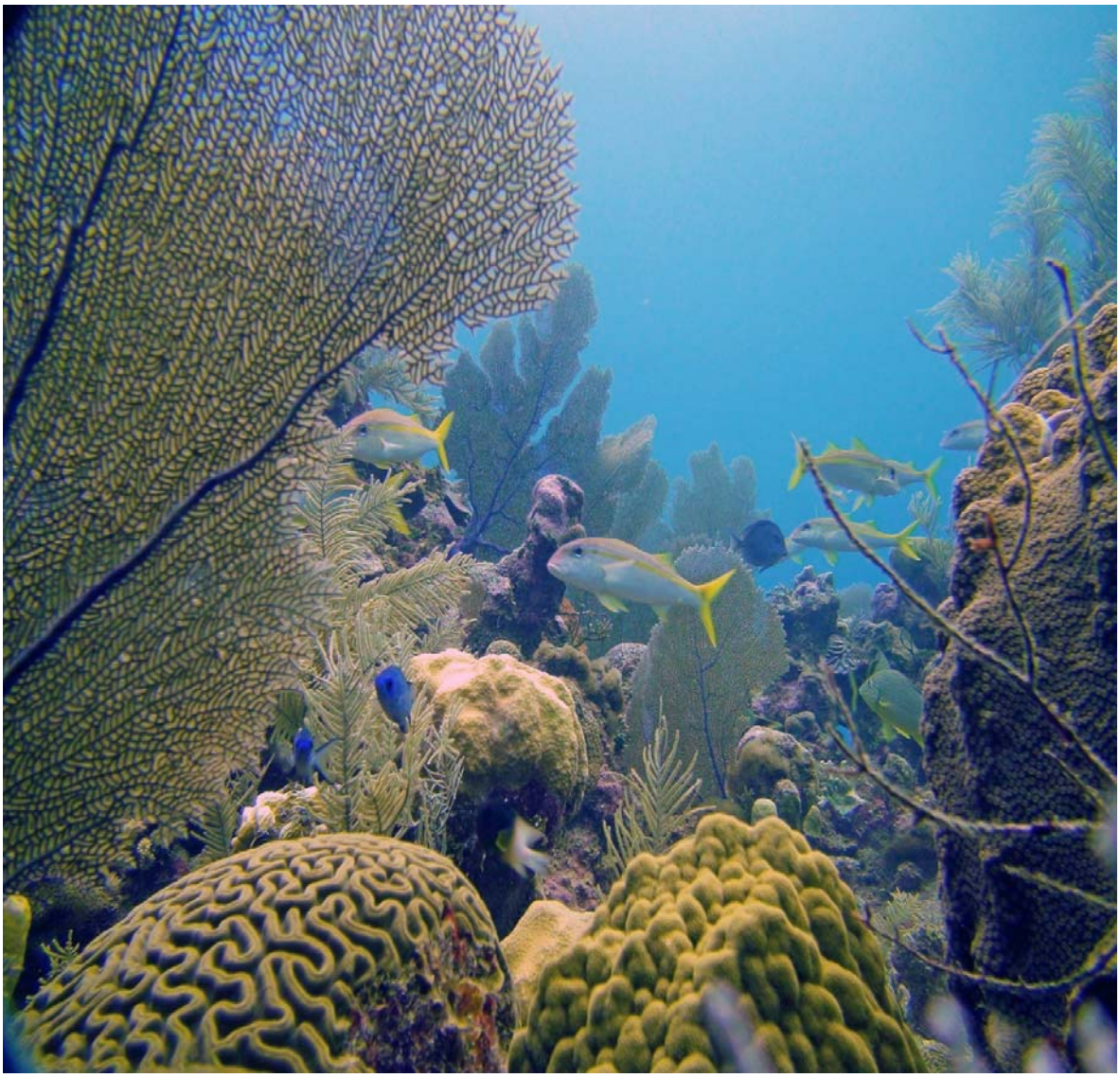
Chapter 5. Relationships between the coral reef benthos and reef fish community structure; Protection effects.



Abstract

Reef fish assemblages and how they relate to the benthos, including reef complexity, have been studied extensively for more than four decades. However, most lack spatial and temporal data to test this intricate affiliation that they share and conclude a predictable as well as the measured association between fish assemblages and benthos, whether biotic or abiotic. Marine Protected Areas (MPAs) are often implemented as part of a strategy regionally and globally without well-defined goals and objectives. Additionally, most MPAs in the Caribbean are implemented in lieu of complaints from the resident population of a declining catch per unit effort (CPUE) of a fishery and loss of tourism revenue because of a degraded reef. In general, the most common objective is to restore a degraded ecosystem and, in some situations, entails an effort to manage multiple conflicting usages of the area. Most do not undergo rigorous scientific evaluation on the best area to place MPAs in order to meet those goals and objectives, a prerequisite for determining placement, size and ascertain whether no-take or some sort of managed extraction is applicable. In this study, the biomass of 48 target fish species from 15 families considered to be of commercial and ecological importance were surveyed at 55 sites across the three Cayman Islands, Grand Cayman (GCM), Little Cayman (LC) and Cayman Brac (CB) between January and March 2009 to 2012 on their deep terrace and shallow terrace reefs using Underwater Visual Census (UVC). They were then grouped into five trophic groups according to feeding habits. Benthosvideo data was collected at the same sites across the three Cayman Islands between June and August for the same years. Benthos data were then grouped into 16 benthos categories for further analysis. Fish biomass trophic groups and benthos variables were analyzed across years, depth, aspect, island, and protection status to test the correlations and ascertain what benthos variables were driving target reef fish communities on spatial and temporal scales, including the effect protection status on this relationship. Results from BioEnv analysis demonstrated that the benthic community and the fish communities were weakly correlated (BEST, Rho = 0.26), though significant ($p = 0.01$). Variation of the three combined benthic variables: zoanthids, tunicates, and dead gorgonians best explained documented changes in the fish community structure across aspects, islands, habitats, years, and protection status. The model supported that only the zoanthids, dead gorgonians, and the cover of other benthic organisms not surveyed were significantly correlated with the changes occurring in the fish community structure. However, the Distance-Based-Redundancy-Analysis (DbRDA) plot illustrated that the changes in the benthic community structure did not fully explain the observed variation within the fish community structure. Data collected indicated that the benthic community structure was extremely variable between habitats; this factor explained a greater variation as compared to the protection status and suggests that the benthic community structure was a poor predictor for explaining the differences of the fish communities linked to both MPAs and non-MPA's across the Cayman Islands. The association of dead gorgonians within the reef fish community structure is an encouraging finding as all three Cayman Islands all have an abundance of gorgonians from their back reefs environment to the deep terrace reefs. The correlation of zoanthids to fish assemblages suggested that these Anthozoans must offer some food resource. The results of this study make it clear that trying to predict the variability of coral reef fish communities and the relationships with their associated benthos communities is complicated and that the relationship is not always linear.

Keywords: Marine protected areas, coral reef benthos, reef fish, shallow terrace reef, deep terrace reef, resiliency, community structure.

5.1 Introduction

This chapter explores the relationship between coral reef benthos and targeted fish assemblages in and around the Cayman Islands and the effect that their MPAs have possibly had in promoting resiliency by making them robust and healthier in comparison than their counterparts in the neighboring Caribbean region. The association and rank between coral reef complexity and reef fish communities have been recognized and studied for quite some time (Risk 1972; Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Grigg 1994; Chapman & Kramer 2000, Friedlander et al. 2007, Komyakova *et al.,* 2013). A few studies have reflected on the association between architectural reef complexity and coral cover (Graham and Nash, 2013), suggesting which benthos category drives this positive association such as sclerantinian coral cover (Sano, 2000). Furthermore, the findings of Garpe and Öhman (2003) demonstrated that live coral was the strongest determinant for fish abundance and species, something that was corroborated by the findings of previous studies by Carpenter *et al.* (1981), Bell and Galzin, (1984), Chabanet *et al.* (1997), Öhman and Rajasuriya, (1998). While the relationship with topographic, architectural complexity have been explored in detail; much work needs to be done on other benthos that could potentially be affecting reef fish community structure on spatial and temporal scales. The coral reef crisis that we are currently experiencing globally, including in the Caribbean region, has reached a tipping point where all investigations seem to be reporting slow death of coral reefs, such as the shift from a coral-dominated reef environment to a less desirable environment, dominated by macroalgae (environment (Done 1992; Goreau, 1992; White *et al*., 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003;Hughes *et al*., 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014). Furthermore, this shift has resulted from a multiple causal factors such as overfishing (Jackson *et al.,* 1997; Jackson *et al.,* 2001; Pandolfi *et al.,* 2005; Jackson *et al.,* 2014), Hurricanes (Kaufman , 1983; Woodley *et.al*., 1981; Woodley *et al*., 1989; Rogers *et al.,* 1989; Gardner *et al.,* 2005), climate change and subsequent coral bleaching (Hoegh-Guldberg, 1999; Bruno *et al.,* 2003; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Pandolfi *et al.,* 2005; Hughes et al., 2010), disease outbreaks (Carpenter *et al.,* 2008; Bruckner and Hill, 2009; Miller *et al.,* 2009; Weil and Cróquer, 2009; Hooidonk *et al*,. 2012), eutrophication (Nyström *et al*., 2000; Wilkinson, 2008; Selman et al., 2008; Graham et al., 2013), among others. Costanza *et al.* (2014) estimate that coral reefs and its associated organisms are valued at $352,915 per hectare per year in terms of the goods and services they provide, with an ever-increasing value, as humankind finds new and innovative ways to exploit them further. To humans, the most commonly associated organism with coral reefs is their fish communities since coral reef fish are an important food source globally in addition to providing livelihoods (Wilkinson, 2008). Additionally, coral reef fishes play an important role in the maintenance of reef ecosystems (Green and Bellwood, 2009), with their removal triggering negative consequences (Mumby and Steneck, 2008) and being pivotal in the regeneration of coral reefs after disturbances (Bellwood et al., 2004).

5.1.2 Importance of fish

As the human population increases exponentially and is on the verge to surpass 7.5 billion, there is an ever-increasing pressure on coral reefs and their fish assemblages, particularly, the demand for protein. This demand has given rise to several technological advances (Sonar, Global Positioning systems, etc.) including larger and more capable fishing fleets with a distinct impact on the overexploitation of marine resources on Caribbean coral reefs and allied fish assemblages (Hughes et al., 2007, Jackson et al., 2014). This led Chabanet *et al.*, (1997) and Swartz & Pauly (2008) to conclude that over 2/3 of wild fish stocks can be categorized as being exploited at maximum sustainable yield, thus posing a threat of fishery collapse, at the very least, causing an imbalance of the trophic structure by altering the species make up of fish communities (McCoy *et al*., 2010; Mumby *et al.*, 2011; Jackson *et al*., 2014). The herbivory on coral reefs are one of the most important guilds of fish ecologically; they act synchronously, much like gardeners tidying up a yard, stripping the reef of algae and turning dead limestone coral debris into sand, thus making way for new coral larvae settlement. They also limit the establishment and growth of algal communities, keeping them in check, something that has been documented to limit coral recruitment, establishment and growth (Green and Bellwood, 2009), a pivotal role in halting, and in some cases, even causing the reversal of the coral-algal phase shift, thus promoting coral reef resiliency (Green and Bellwood, 2009). With a loss in the form of keystone echinoderm herbivore, the Long-spined Sea urchin *Diadema antillarium* in the Caribbean basin in 1983/84 (Lessios *et al.,* 1984), the protection of herbivorous coral reef fishes became a priority to fill this void; their abundance is expected to aid in the recovery of coral reef in the region, thus promoting resiliency (Adam *et al.,* 2015).

The carnivory / predatory guild of coral reef fishes within the global tropics is one of the most important reef fishes commercially and recreationally, as they support many livelihoods globally, including those in the Caribbean region. Many predatory fishes are targeted commercially, such as the *Lutjanids* (Snappers) and the *Serranids* (Groupers), who are far more susceptible to over-exploitation owing to their predictable aggregating behavior observed annually at a particular site to spawn and release their eggs. These large-bodied apex predators are slow growing, late maturing, and follow predictable migratory pathways to Fish Spawning Aggregation sites (FSA) yearly (Coleman *et al.,* 2000). According to Williams *et al.* (2004) and Kulbicki *et al.* (2005), they are pivotal in manipulating prey populations using a varied diet that comprises of crustaceans, echinoderms, mollusks and marine worms. An example of the importance of this predator/prey relationship control has been demonstrated by Pinnegar *et al.* (2000) on Kenyan reefs in the Indian Ocean where the removal of predators such as triggerfish resulted in an overabundance of the echinoderm, *Echinometra mathaei*.

5.1.3 Fish/Benthos relationship

A literature search revealed that very few studies have explored the relationship between benthos and fish assemblages, other than the association of fish and reef architectural complexity, as most investigations primarily focused on the latter (Risk 1972; Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Grigg 1994; Chapman & Kramer 2000, Friedlander et al. 2007, Komyakova *et al.,* 2013). According to Barbault, (1992), highly complex reef environments allow an abundance of fish to co-exist together, including offering shelter to a great number of smaller fish due to the many gaps and holes that help them hide from predatory fish. The findings of Lorenzo *et al.* (2009) suggest that the Caribbean region has been actively losing architectural complexity for over 40 years, with a short period of "stasis" between 1985 and 1998, after which, it resumed its downward spiral to date, a termed he referred to as "reef flattening". This reduction in reef complexity often results in a reduction of fish assemblages such as herbivore abundance (McClanahan, 1999; Almany, 2004; Lee, 2006), given that fish densities tend to be higher in more complex reef environments (Friedlander *et al.,* 2007). Coral reefs that lose structure over time can lead to devastating consequences for those who consume the resources, socially, economically, and culturally. Furthermore, intact structural complexity with high coral cover is often associated with higher biodiversity (Rogers *et al*., 2014), including healthier fish assemblages and biomass. To that end, Mumby and Steneck (2008) suggested that even as a coral reef declines the critical role that reef complexity plays in reef ecosystems remains evident. The resumption of the "reef flattening" scenario since 1998, (Lorenzo *et al*., 2009), has underpinned the importance of discovering other benthos that shares similar associations and supports healthy fish communities. In this chapter, data from the previous two chapters on Coral Reef Benthos and Coral Reef Fish assemblages of MPAs and non-MPAs will be used to test this relationship looking for any correlations to best explain changes in the coral reef fish assemblages of the Cayman Islands over spatial and temporal scales. This will include protection effect. Results will then be used to recommend enhancements to the current Marine Protected Areas network across the three Cayman Islands.

5.2 Hypotheses and Objectives

This chapter investigates the correlations between the benthos community and the fish community structure across years, depth, coast, island and protection status to gauge which benthos variables have been driving reef fish composition on spatial and temporal scales. This includes the effect of protection status.

H_1 There will be no correlation relationship between fish assemblages and coral reef benthos.

Objective 1: Benthos and fish data from 55 sites located within and outside of protected areas across the three Cayman Islands were collected. Benthos data from the 16 benthos categories (Chapter 3, Table 3.1) and the biomass of 48 target fish species (Appendix 4.1) will then be analyzed and tested using PRIMER (Plymouth Routines in Multivariate Ecological Research) v6. + PERMANOVA BEST routine procedure to evaluate the relationship between the benthos and fish assemblages to test for correlations.

H_2: Protection will have no effect on the correlation between benthos categories and fish trophic assemblages across the three Cayman Islands.

Objective 2: Using the best correlating benthos variables with fish biomass from objective 1, data will be tested using PRIMER (Plymouth Routines in Multivariate Ecological Research) v6. + PERMANOVA. A DstLM (distance-based linear model) will be used to test the relation between the benthic and fish assemblages between MPAs and Non-MPAs. Results from this linear model will be presented in a Distance-Based-Redundancy-Analysis (DbRDA) model with sites sorted by MPAs and Non-MPAs to visualize protection effects.

5.3 Methods

5.3.1 Study sites:

A total of 55 survey sites (Appendix 2.3); Grand Cayman (GCM) n = 27, Little Cayman (LC) n = 16) and Cayman Brac (CB) n = 12 were monitored between June and August (Chapter 2; Figure 2.2), for the years 2009 through to 2012. Multiple exploratory SCUBA dives were conducted before the study started inside and outside of protected areas across the three Cayman Islands. Sites were then selected for their similar geomorphological characteristics for comparison. Twenty-three sites were located within existing MPAs (GCM = 9, LC = 8, CB = 6) and 32 were located outside (GCM = 18, LC = 8, CB = 6). To account for depth habitat, sites were distributed between the shallow (9-12m) and the deep reef terraces (18-20 m). To account for aspect, sites were distributed across the northern, southern and in the case of Grand Cayman, it's western shore. Due to the MPA being located on the entire leeward western shore of Grand Cayman, double the amount of sites were selected outside to that islands MPA to account for this confounding factor and to give adequate statistical power in reference to protection effect on that island.

5.3.2 Data Collection.

Benthos: SCUBA diving was used to survey the benthos along four 20 m transects at each of the 55 sites using a Canon ZR850 miniDV with Ikelite housing. At each site, the start of each transect was randomly selected, with the first transect always nearest to the GPS location (Appendix 2.3) of the site. Transects were laid perpendicular to the reef wall along with the spurs where possible. Where the reef was too narrow to set a full 20 m transect, transects were laid parallel to the wall with a minimum gap of 10 m between the end of one and the beginning of the next for consistency. Note: See chapter 3 for further explanations of Benthos data analysis.

Fish communities: These data were collected by Underwater Visual Census (UVC), using a belt transect method (Samoilys and Carlos, 2000). Sampling was done during January through to March at a total of 55 sites across islands (Chapter 2, Figure 2.2) between the hours of 0900 and 1500 hours for consistency, for the years 2009 through to 2012. Note: See chapter 4 for further explanations of Fish data analysis.

5.3.3 Experimental Design: A five-factor multivariate design (year, depth, protection, coast and Island), with year, depth and protection as fixed factors, random factors were coast and Island with coast nested in island to test if marine protected areas were the main factor driving the resiliency of Cayman Islands coral reef over time and space in the Cayman Islands. (Chapter 2, table 2.1).

5.3.4 Data analysis:

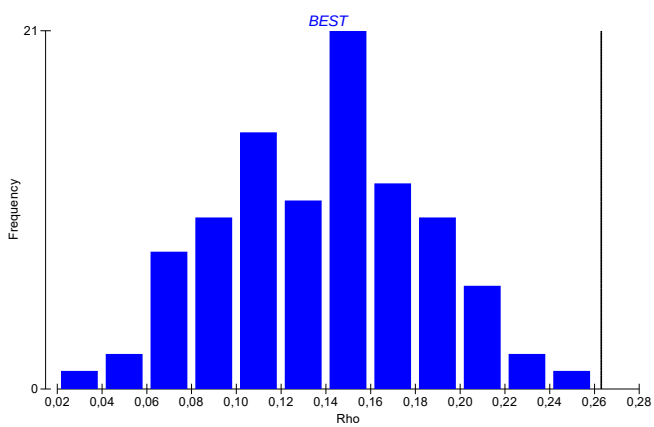
In this analysis, fish and benthos data were used from chapter 3 (fish) and chapter 4 (benthos). Both data sets were first square root transformed before Multivariate statistical analyses were conducted using PRIMER (Plymouth Routines in Multivariate Ecological Research) v6. + PERMANOVA. To link the fish data with the 16 environmental benthos variables (chapter 3, table 3.1) a BEST routine procedure was performed. This random BIOSTEP procedure selected the best environmental benthos variables that best correlated with the fish assemblages. Results from this analysis were then used as a qualitative criterion to select a set of variables that were then used for the DstLM (distance-based linear model) analysis. Using the selected variables from the BEST routine procedure that showed a correlation, a DstLM (distance-based linear model) procedure was performed to (1) evaluate the relationship between fish and benthic assemblages between MPAs and Non-MPAs including all sites and (2) to determine the significance level and variance explained (for the fish community structure) by each benthic variable. The linear model is represented in a Distance-Based-Redundancy-Analysis (DbRDA) in which the sites are sorted by MPAs and Non-MPAs to test for protection effects and to visualize it with vectors

to show most important variables, the longer the vector the greater the importance to explain differences in the fish community structure across sites and years. In this visual model, samples are ordinated according to their similarities in terms of the fish community structure and the importance of each benthic variable to explain these differences.

5.4 RESULTS

5.4.1 Relationship between the benthic and fish community structure across the Cayman Islands: evidence of protection effect

Results from BioEnv analysis demonstrated that both the benthic and the fish community assemblages were significant, albeit weakly correlated (BEST, Rho = 0.26, p = 0.01, number of permutations = 999, figure 5.1). The variation of the three combined benthic variables; zoanthids, tunicates, and dead gorgonians best fit with the documented changes within the fish community structure across coasts, islands, habitats, protection status and years (table 5.1). All other benthic variables such as the scleractinian coral cover, the turf algae and macroalgae did not contribute significantly towards explaining the changes in fish assemblages, at least during the study period (table 5.1). This result is indicative of the fact that the structure of fish communities in the Cayman Islands was not only determined by the structure of their habitats, but also by other factors that have not been addressed in this study



Global Test			
Sample statistic (Rho): 0.263			
Significance level of sample statistic: 1%			
Number of permutations: 99 (Random sample)			
Number of permuted statistics greater than or equal to Rho: 0			

Figure. 5.1. Frequency distribution of Rho values from 99 permutations for the test of null hypothesis between the benthic and the fish community structure across the 3 Cayman Islands during period of study (2009- 2012)

Table 5.1. Best environmental variables selected to explain the correlation between the benthic and the fish communities across islands, habitats, and years. Variables: 3= sponges; 4= zoanthids; 5= tunicates; 8= coralline algae; 9= other biotic; 11= dead gorgonian; 14= sand; 15= gaps, holes shadows; 16= other abiotic). Text in **red** indicates significant.

Number of variables	Correlation (p)	Variables
5	0.263	4,5,11,15,16
4	0.262	4,11,15,16
3	0.252	4,11,16
5	0.254	3,5,8,11,14
5	0.254	3,5,8,14,15
5	0.254	3,5,8,14
5	0.253	3,5,8,11,15
4	0.253	4,511,16
5	0.253	3,4,5,8,15
5	0.251	4,9,11,15,16

The DistLM further corroborated a significant but weak relationship between the benthic and fish assemblages for the entire study period (table 5.2 a). Overall, less than 16% of the total variance of the fish community structure was explained by the changes in the habitat's features. Moreover, they only explained about 2-6% of the total variance each (table 5.2 a). According to DbRDA plot, changes in the benthic community structure were unable to fully explain the observed variation in the fish community structure (figure 5.2 a). With more than 80% of the total variance retained in the first two RDA axes, less than 15% of the total variance recorded for the fish community structure across MPAs as well as unprotected sites located at different islands, habitats and years was explained by the variables signified in these two ordination axes. Overall, the date results demonstrated that zoanthids were mostly found in the shallower habitats (figure 5.2 b), regardless of the island and protection status.

Table 5.2 Distance-Based Linear model to test the significance of selected benthic variables to better explain the variance in fish community structure in the Cayman Islands. Text in **red** indicates significance.

A	**Model including all years**			
$R^2 = 0.168$				
Variable	SS(trace)	Pseudo-F	P	Prop.
SPON	844.43	14.402	0.171	2.42E+02
ZOAN	2145.8	38.053	0.001	6.16E+02
DGOR	1148.3	19.761	0.026	3.29E+02
OTHR_AB	1499.4	26.075	0.007	4.30E+02

B	**Model including 2009 only**			
$R^2 = 0.013$				
Variable	SS(trace)	Pseudo-F	P	Prop.
SPON	844.43	14.402	0.171	5.64E+03
SCLR	2145.8	38.053	0.122	8.42E+03
DGOR	1148.3	19.761	0.443	1.24E+03
GAPS	1499.4	26.075	0.112	1.11E+04

C **Model including 2011 only**

$R^2 = 0.33$

Variable	SS(trace)	Pseudo-F	P	Prop.
SPON	844.43	14.402	0.171	4.92E+02
TURF	2145.8	38.053	0.001	1.57E+01
DGOR	1148.3	19.761	0.026	6.78E+02
OTHR_AB	1499.4	26.075	0.891	4.80E+02

D **Model including 2012 only**

$R^2 = 0.25$

Variable	SS(trace)	Pseudo-F	P	Prop.
SCLR	844.43	14.402	0.001	1.03E+01
ZOAN	2145.8	38.053	0.012	6.16E+02
DGOR	1148.3	19.761	0.443	3.29E+02
OTHR_AB	1499.4	26.075	0.331	4.30E+02

The omnivore fish *Melichthys niger* and the snapper *Lutjanus apodus* were seen to be highly associated with these shallow-zoanthid-dominated habitats (figure 5.2 c-d). Meanwhile, the deeper habitats were dominated by dead gorgonians (figure 5. 2 e) as well as other reef organisms, including the fish species, *Melichthys niger* (figure 5.2 f), possibly due to the deep terrace reef current up-wellings as this particular species has a planktivorous diet component (Randall, 1967). The parrotfish *Sparisoma viride* was widely distributed across islands and habitats, regardless of the level of protection status (figure 5.2 g). Lastly, fish communities showed no clear pattern in terms of sponge distribution and were dispersed amongst habitats with no preference based on protected or non-protected areas (figure 5. 2 h).

5.4.2 Temporal variation of fish and benthic communities

According to the findings for the study period, the benthic community structure was a poor predictor for explaining the differences of the fish communities associated with MPAs and unprotected areas located situated at each of the three islands (figure 5.2 a). This further suggests that the temporal

variability of fish communities across islands and habitats does not necessarily match with the temporal variation recorded for the benthos. When analyzing the trends for each year alone, the DIstLM showed a non-significant correlation between any of benthic explanatory variables used within the linear model and the variation recorded for these fish communities in 2009 (table 5.2 b). However, in 2011 and 2012, MPA linear predictive models were observed to have improved (table 5.2 c; table 5.2 d).

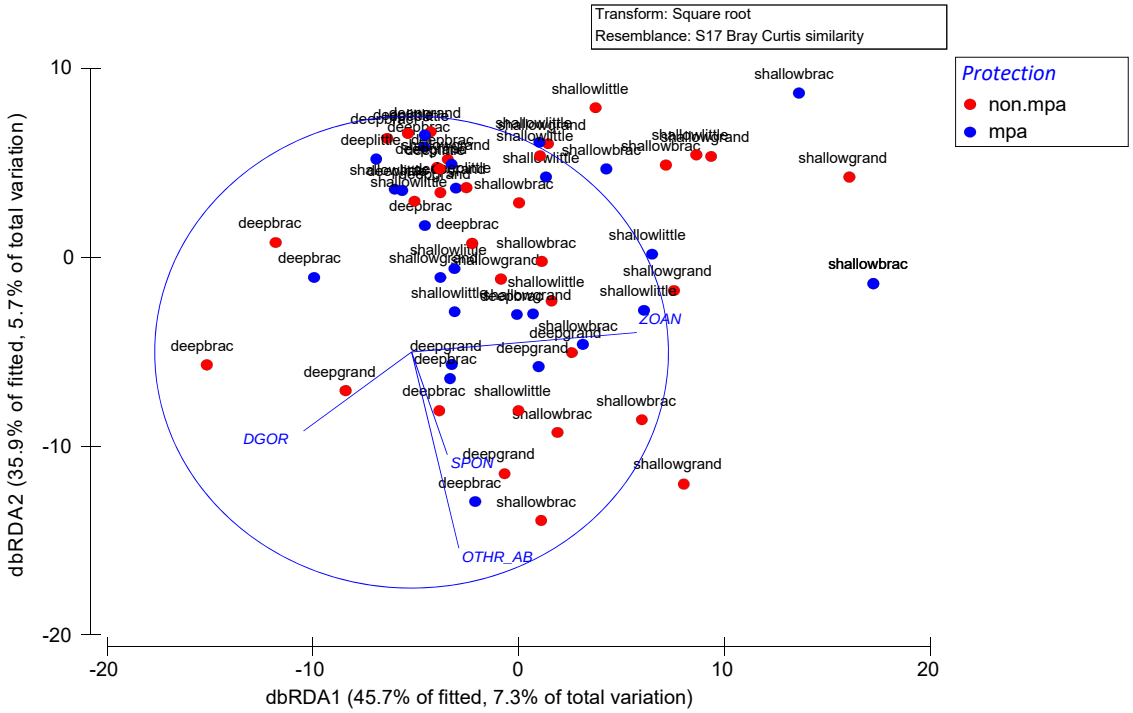


Figure. 5.2 a.Distance-Based Redundancy Analysis which shows the ordination of sampling across habitats of different islands and sites with different levels of protection (MPA and non-MPA) and the contribution of zoanthids, dead gorgonians, sponges and other abiotic factors In the DISTLM model in order to explain the variation of the fish communities. ZOAN= Zoanthids, DGOR= Dead Gorgonians, SPON= Sponges, other AB= other Abiotic**.**

5.4.3 Habitat and fish Benthos relationship; variability across spatial scales

There was a stronger and significant relationship between the structure of the benthic habitat and the variability recorded for the fish communities across different spatial scales in MPAs and unprotected areas in 2011; however, more than 74% of this variance was unexplained by each linear model (table

5.2 c). Only two of the four variables used in this model (turf algae and dead gorgonians) were significant enough to explain the changes occurring within the fish communities; a combination of these changes explained up to 22% of the total variance signified by the linear model (r2 = 0.33) for the fish community structure across both protected and unprotected sites located at different aspects and islands for that given year (table 5.2 c). In 2012, the scleractinian coral cover was seen to be the most important benthic variable that explained the changes in the fish community structure across habitats, protected and unprotected sites, explaining 10% out of 25% of the total variance (table 5.2 d). Changes in the cover of zoanthids were also known to play a significant role in determining the spatial variability of the fish assemblages across habitats, islands, and areas with different protection levels (table 5.2 d).

Collectively, the results indicate that predicting the variability of fish communities is extremely complex; moreover, the structure of the habitat is not necessarily linked with these changes. Furthermore, the effects of MPAs on the benthos as well as their associated fish communities, might not be essentially equivalent to the communities in space and time in different ways.

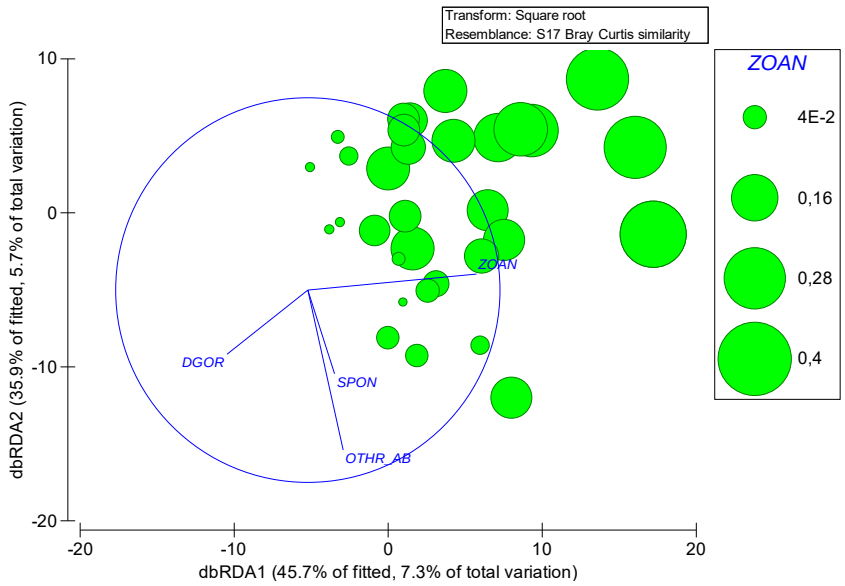


Figure. 5.2 b. Distance-Based Redundancy Analysis showing the ordination of sampling across habitats of different islands as well as sites with different protection levels (MPA and non-MPA). ZOAN= Zoanthid. Bubbles denote the year, island, and the contribution of Zoanthids to the DISTLM model to explain the variation of fish communities (see Figure 5.2 a).

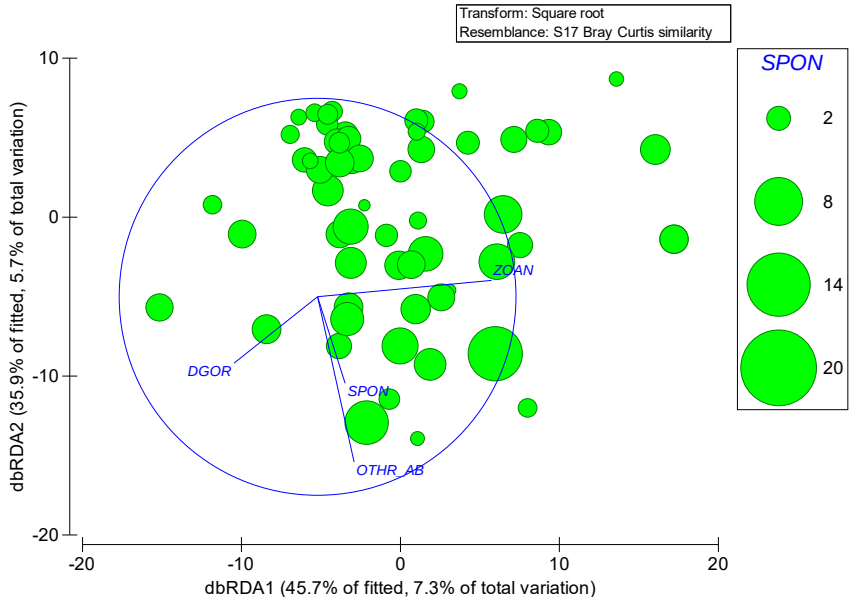
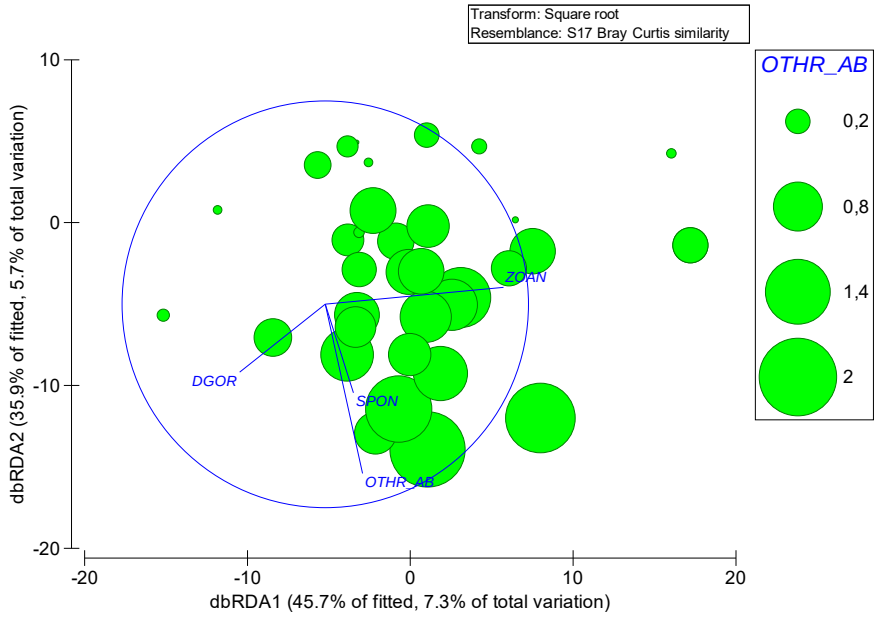


Figure. 5.2 c. Distance Based Redundancy Analysis showing the ordination of sampling across habitats of different islands and sites with different protection levels (MPA and non-MPA). SPON = Sponges. Bubbles denote the year, island and the contribution of sponges to the DISTLM model to explain the variation of fish communities



(d)

Figure. 5.2 d. Distance Based Redundancy Analysis showing the ordination of sampling across habitats of different islands and sites with different protection levels (MPA and non-MPA). OTHER_AB = other abiotic organisms. Bubbles represent the year, island and the contribution of Other Abiotic organisms to the DISTLM model to explain the variation of fish communities.

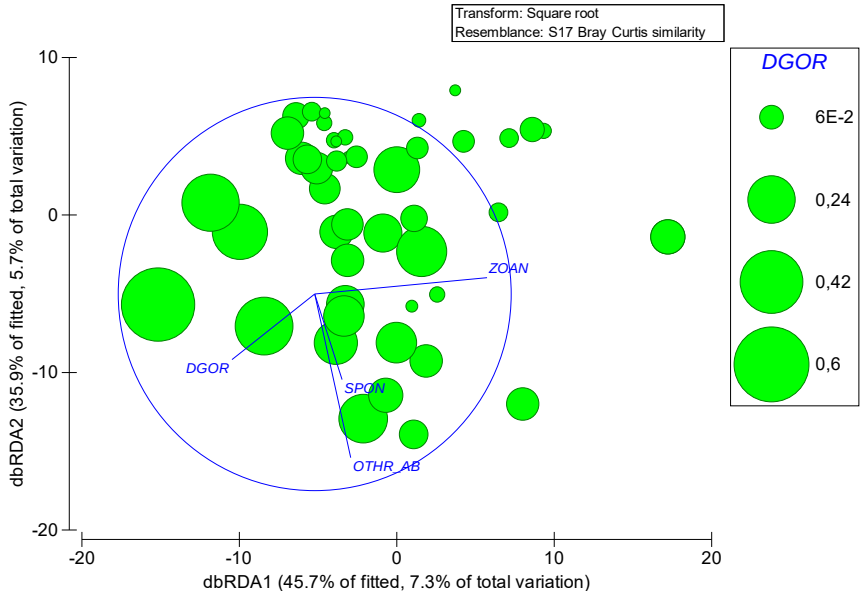


Figure. 5.2 e. Distance-Based Redundancy Analysis, which shows the ordination of sampling across habitats of different islands and sites with different protection levels (MPA and non-MPA). DGOR= Dead Gorgonian. Bubbles represent the year, island, and the contribution of Dead Gorgonians to the DISTLM model to explain the variation of fish communities.

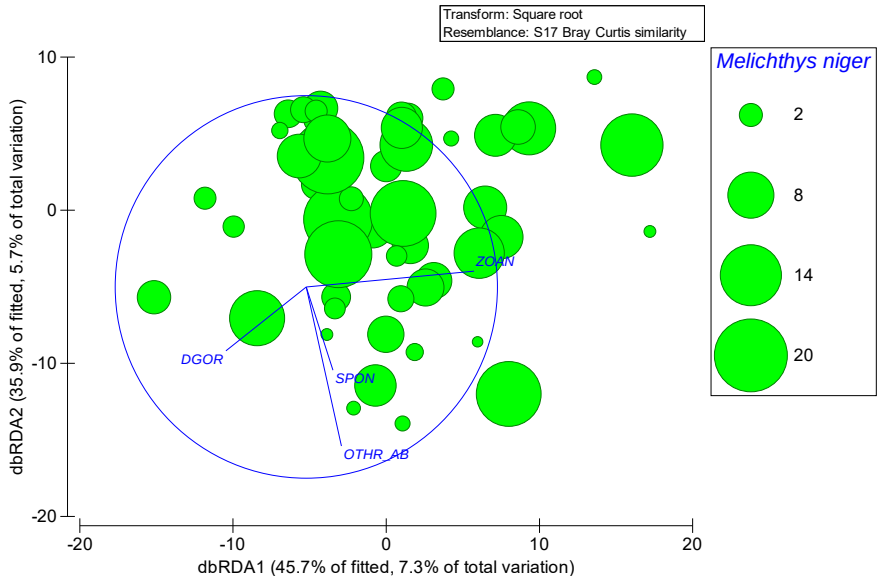


Figure 5.2 f. Distance-Based Redundancy Analysis which shows the ordination of sampling across habitats of different islands and sites with different protection levels (MPA and non-MPA). Bubbles represent the year, the island as well as the contribution of fish species, Melichthys niger to the DISTLM model to explain the variation of fish communities

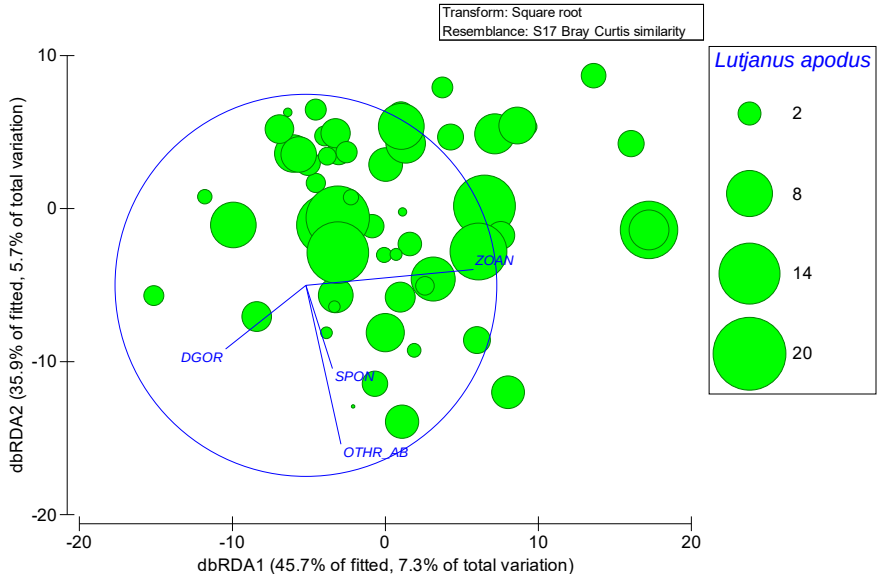


Figure 5.2 g. Distance-Based Redundancy Analysis showing the ordination of sampling across habitats of different islands and sites with different protection levels (MPA and non-MPA). Bubbles represent the year, island, and the contribution of fish species, Lutjanus apodus to the DISTLM model to explain the variation of fish communities.

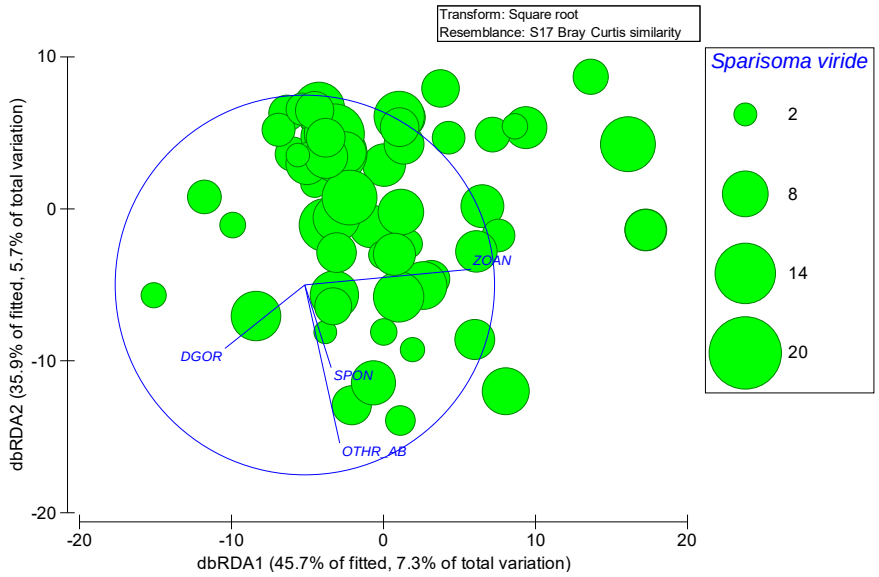


Figure 5.2 h. Distance-Based Redundancy Analysis which shows the ordination of sampling across habitats of different islands and sites with different protection levels (MPA and non-MPA). Bubbles represent the year, island and the contribution of fish species, Sparisoma viride to the DISTLM model to explain the variation of fish communities.

5.5 Discussion

In chapter 3 and chapter 4, fish assemblages and benthos across the three Cayman Islands, their habitats, as well as benefits of protection status, were discussed in detail. In this chapter, those metrics are overlaid in order to test the relationship between the benthic community and fish community structure including protection effects across the three Cayman Islands. Reef complexity is a well-documented to play a major role in driving healthy reef fish assemblages (Risk, 1972; Luckhurst and Luckhurst, 1978; Syms and Jones, 2000; Friedlander *et al.,* 2003; Bozec *et al.,* 2005; Gratwicke and Speight, 2005; Komyakova *et al.,* 2013). In this study, the direct measurement of reef complexity as a variable has been ignored in an effort to quantify 16 other benthic categories on the reefs of the Cayman Islands that might drive the changes in spatial and temporal scales, inside and outside of Cayman Islands Marine Protected areas.

5.51 The benthic and fish community, structure across the Cayman Islands: evidence of protection effect.

According to an analysis from the BioEnv, the fish and benthic community have a weak but significant correlation. Out of the 16 possible benthic variables, the combination of zoanthids, tunicates, and dead gorgonians was the best model fit to explain the changes in fish community structure, which was quite surprising given that visually, dead gorgonians offer limited refuge in the form of three-dimensional versus an upright vertically orientated structure. Dead gorgonians prevalence also suggest low currents and a lull in wave action during the period of this study, as most winter storms are known as "norwesters" (Burton 1994) remove unconsolidated loose material. The significant correlation of dead gorgonians does bring a valid point to the forefront and underpins the importance of these abundant soft corals in the Caribbean as important fish habitat, particularly in consideration of the continued loss of rugosity and reef structure (Lorenzo *et al.,* 2009). A study by Wolff *et al*. (1999) on trap fishing effectiveness in adjacent coral reef and gorgonian habitats in St. John, USA Virgin Islands revealed that after a comparison of visual census data, parrotfishes and surgeonfishes were observed to contribute over 86% of the fish in the gorgonian habitat as compared to 51% in coral reef habitat. One interesting observation was the fact that both parrotfishes and surgeonfishes had higher catches and abundances within the gorgonian habitat, which can only be interpreted that this was a preferential habitat for those two families of fish. It was concluded that the catch rate for most exploitable fishes was higher in the gorgonian habit than the coral reef habitat on magnitudes of up to two times more. This perhaps was due to the associated food resources and prey animals associated with gorgonians that were being targeted. However, they did caution that the fish traps in the gorgonian habitats offered structure; therefore, the results could be confounded by this fact. Further corroborating their results on preferential gorgonian habitats versus coral reef habitat are two other studies conducted in Puerto Rico. The findings

of Recksiek *et al.* (1991) and Acosta *et al.* (1994) also concluded that fish catchability was much higher for several species groups across gorgonian habitats. This finding is important for the future prospect of critical fish habitat for the Cayman Islands. All three islands have extensive gorgonian beds across all habitats, from the patch reef environment of the North sound in Grand Cayman to the shallow and deep reef terrace at a 30 m depth (figure 5.3).

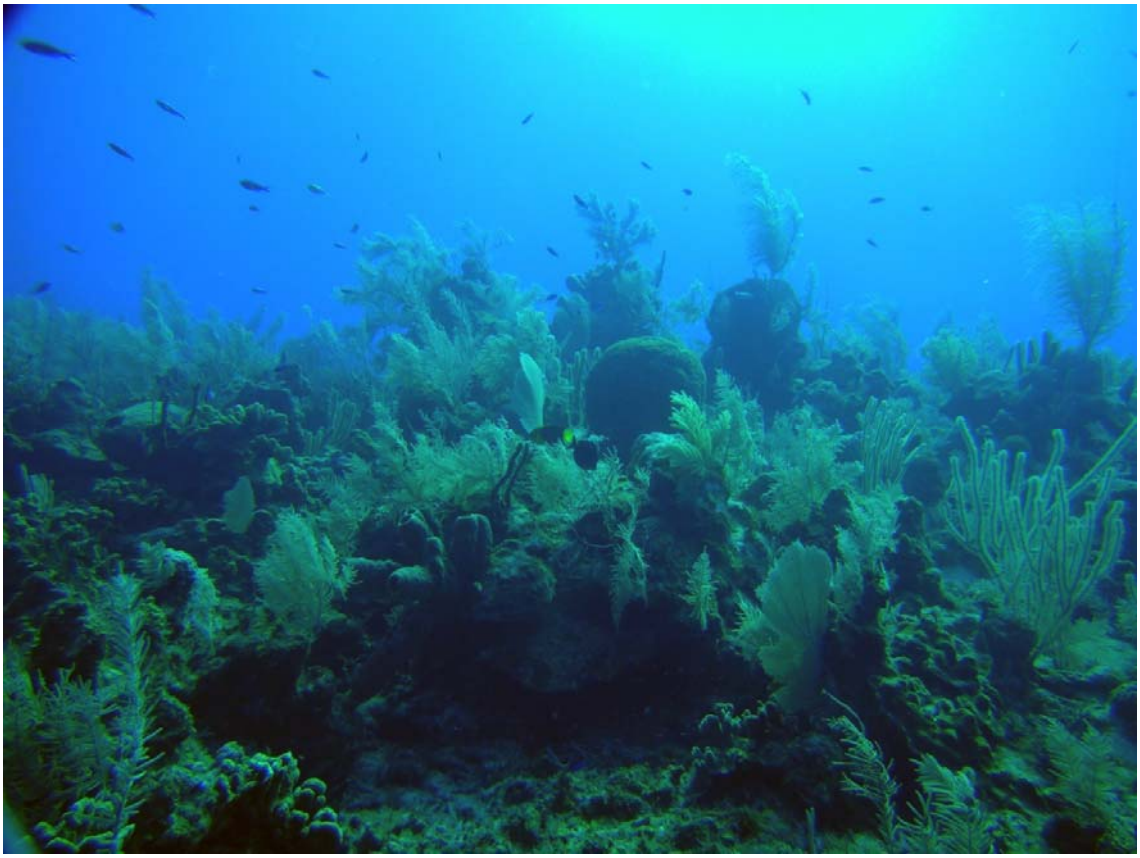


Figure 5.3 Gorgonian bed, north side of Grand Cayman, site GCM24 at 10 m depth.

The importance of gorgonian habitats is also emphasized by DeLoach (1999), who pointed out that the trumpetfish, *Aulostomus maculatus* are dependent on cylindrical sponges and branching gorgonians for camouflage in order to stalk their prey. With regard to the association of fish assemblages and zoanthids, Sergio *et al*. (2007) report a correlation with reef fish assemblages and zoanthids along the reefs of southeastern Brazil, including the fact that the herbivore guild (mainly pomacentrids) were able to thrive in this turf algae, zoanthids, and coral dominated environment. Additionally, at the inception of this study, one of the first survey sites was randomly selected for the southeast coast of the island of Cayman Brac, and the habitat was mainly comprised of a gorgonian dominated environment as opposed to rugous scleractinian coral structures. Subsequent fish surveys conducted in this site revealed very high total fish biomass. However, due to the vast differences in benthos species and topographic makeup

which were very different from all other sites, including a rather large fish biomass component, would prove to be an outlier for both parameters and hence, therefore was not used in this study and a subsequent other randomly selected site was selected and used in this study analysis. Adding further to the importance of gorgonians being a habitat refuge for fish, the findings demonstrated that MPA management might perchance be playing a role in possibly producing inconsistent results across years, each island and protection status, particularly for the benthos community. This perhaps could be attributed to the level of enforcement each island receives, given that Grand Cayman has a ratio of approximately 1 Marine Enforcement officer per 10,000 residents, with Cayman Brac and Little Cayman having 1 per 900 residents and 1 per 300 residents, respectively. Overall, despite these differences over space and time, both the benthic community and fish assemblages showed quite a similar variation, which seem to suggest that they might be correlated, with similar pressures exerting similar effects through space and time. The finding that scleractinian coral cover was not strongly associated with fish assemblages to be able to influence the reef fish communities is contrary to the observations of Bell and Galzin (1984); Sano *et al*. (1984); Chabanet *et.al*. (1997); and Jones *et al*. (2004) Munday (2004), all of whom showed strong linkages of coral cover not only with regard to fish abundance, but to diversity as well; however that might be a function of coral cover, owing to the fact that a higher coral cover means higher rugosity, which is intricately linked to a higher fish abundance (Risk, 1972; Luckhurst and Luckhurst, 1978; Syms and Jones, 2000; Friedlander *et al.,* 2003; Bozec *et al.,* 2005; Gratwicke and Speight, 2005; Komyakova *et al.,* 2013). Another study by Friedlander *et al.* (2007) found a negative correlation with macroalgae, which exhibited a negligible weight to the variation found across years, islands and protection status. The results of these investigations suggest that the benthos metrics used here were possibly not ideal for determining the changes in fish assemblages, structure and their association with benthos over time, indicating that other more important benthos metric might be driving these changes across islands, years and protection status, such as coral reef architecture and rugosity. Although the Distlm showed a weak relationship between the fish and the benthos community (table 5.2 a), merely 16% of the total variance in the fish community was explained by the habitat. More crucially, none of the selected benthos categories explained more than 2-6% each (table 5.2 a), with the DbRDA (Figure 2a) illustrating that the observed changes in the benthos over time and space did not explain the variation recorded in the structure of the fish community. Furthermore, >80% of the total variance was retained during the first two axes of the DbRNA , leaving <15% of the total variation documented for the reef fish community structure across habitats, islands, years and protection status, as explained by the factors in the two ordinations (figure 5.2 a). Although protection status did not have any weight on the distribution of zoanthids, the finding that they were more dominant in the shallower reef habitats is unexpected as in the Cayman Islands; these animals are visually evenly distributed from lagoonal habitats to the deep terrace reef habitats depending on species (C. McCoy, personal observation). However, the linkage of common Yellow Tail snapper, *Lutjanus opodus* to these shallower, zoanthid-dominated habitats (Figure 5.2 g) suggests that

the association is perhaps related to a food resource specific to zoanthid-dominated habitats that they perhaps feed upon and excludes any other attributes, such as shelter. This association should be considered when the placement of MPAs is being negotiated. Throughout this study, a considered keystone species of parrotfish in the Caribbean, *Sparisoma viride* (Vallès and Oxenford, 2014) was distributed widely across all habitats and islands, regardless of protection status. This suggests that this species does not necessarily have any preferences with regard to the metrics recorded in this study; it is a concerning that offering protection did not seem to have any measurable effect (Figure 2h), further suggesting that whatever is driving their populations need to be further investigated as they are pivotal in building reef resiliency on the Caribbean reefs particularly since the loss of major algal controlling herbivore, the long-spined sea urchin, *Diadema antillarium* in 1983/4 (Lessios *et al.,* 1984).

5.52 Temporal variation of fish and benthic communities

The benthos metrics used in this study indicate that they were seemingly poor choices as a predictor for explaining the differences in reef fish communities with regards to the MPAs of the Cayman Islands (figure 5.2 a). However, ignoring the benthic community structure as a predictor for explaining these changes, the data further suggest that the changes across fish communities over time in islands and habitats (deep /shallow) did not particularly follow the temporal variation that was documented for the benthos community. When looking at for each year of study, DIstLm analysis showed no correlation amongst any of the benthic factors included in the model and variation documented for the reef fish communities in 2009 (table 5.2 b). Surprisingly, this changed with the passage of time, as the model fit appeared to improve in 2011 to show a significant correlation between turf algae and dead gorgonians (table 5.2 c); in the year 2012, there was further improvement in the model, showing a significant relationship between scleractinian corals and zoanthids (table 5.2d). This association with scleractinian coral cover with the fish assemblages has been well documented by authors such as Bell and Galzin (1984); Sano *et al.* (1984); Chabanet *et.al*. (1997); Jones *et al*. (2004); Munday (2004), to name a few. However, this finding in the current study is contentious as there is generally a consistent and significant correlation in most investigations when scleractinian coral cover is used as a predictor to drive the variation in fish assemblages over space and time.

5.53 Habitat and fish Benthos relationship

As the models improved between 2009 and 2012, a stronger and significant correlation was observed between the benthos community structures; the variability in terms of the fish community structure over

spatial scales and protection status was documented (table 5.2 c). However, the results show that approximately 74% of the variance of each linear model remains unexplained (table 5.2 a). Nevertheless, for the year 2011, (across islands, coast, protected and unprotected sites) only two out of the four variables used in the linear model were significant enough to explain the changes in fish assemblages, with merely 22% of the total variance being accounted for by the linear model (r2=0.33, table 5. 2 c). This haphazard linearity and non-linearity of the benthos and fish assemblages suggest that separate drivers are operating at different times across spatial and temporal scales. One probable key event/disturbance that could be driving the changes in the benthos community separately from the fish community was the severe localization of the coral bleaching event in late 2009. Some of this variation is possibly attributed to the fact that this event affected each island differently in terms of severity, duration, and intensity (C. McCoy, unpublished data). The model further improved in the year 2012, with results suggesting that the scleractinian coral cover was the most important benthic variable which explained the changes in the fish community structure across habitats (depth) and protection status, taking into consideration 10% of the 25% variability (table 5.2d). This association of scleractinian cover and reef fish assemblages is well documented (Bell and Galzin, 1984; Sano *et al.,* 1984; Chabanet *et.al.,* 1997; Jones *et al.,* 2004; Munday (2004). High scleractinian coral cover transfers to higher reef complexity, which is considered as the most important factor in driving reef fish assemblages (Risk, 1972; Luckhurst and Luckhurst, 1978; Syms and Jones, 2000; Friedlander *et al.,* 2003; Bozec *et al.,* 2005; Gratwicke and Speight, 2005; Komyakova *et al.,* 2013). Changes in the cover of the zoanthids were also found to be significant in shaping the spatial variability of the reef fish assemblages across islands, habitats and protection status (table 5.2 d), much like the findings of Sergio *et al.* (2007) concerning zoanthids being one of the main drivers of the relationship between the herbivores on a reef located in southeastern Brazil.

The association of dead gorgonians (table 5.2 c) within the reef fish community structure is a positive phenomenon. The three Cayman Islands all have an abundance of gorgonians from their back reefs environment, across the depths to their reefs at a depth of 30 m (C. McCoy, personal observation). In the wake of continued reef flattening (Lorenzo *et al.,* 2009), gorgonians, whether dead or living, can offer a three-dimensional habitat because reef fishes depend on the structure not only for food but also shelter (Beukers and Jones, 1997). However, that association of soft corals and fish assemblages contrasts the findings of Craig and Jones (2000), who found no relationship; however that was on a patch reef, as opposed to a contiguous reef system. The correlation of zoanthids (table 5.2 a) was an unexpected result and suggested that they must offer some resource to the structure of the fish community, such as being included in their dietary needs. The results of this study make it evident that trying to predict the variability of coral reef fish communities and the relationships with their associated benthos community structure is an extremely complicated proposition. It suggests that deep and shallow habitats do not necessarily forecast associated changes and that this relationship is not necessarily linear.

Additionally, it highlights the fact that the effects of protection do not necessarily produce equal results for fish and benthos communities since both varied over time and space (independently) in very dissimilar trajectories.

Lastly, the significant association of turf algae with the structure of the reef fish community in the year 2011 was interesting. The model indicated that turf algae contributed ~15.7% to the variation, which is quite similar to findings of Kajsa and Öhman (2003) in Mafia Island Marine Park, Tanzania, where 17% of the variation in total fish abundance was attributed to turf algae. However, they also indicated that the amount of turf algae recorded is often fairly difficult to quantify due to the planar view in addition to the fact that almost every surface that is not covered by any of the benthos groups is occupied by turf algae or macroalgae, which is often difficult to differentiate between benthos categories, such as dead coral. Furthermore, when turf algae colonize a recently dead coral, the choice of the category it becomes difficult and can be confounding factor. With studies demonstrating that turf algae can attract herbivores (McClanahan *et al.,* 2000) and that herbivores abundance increases after the colonization of turf algal on dead coral (Lindahl *et al.,* 2001) this does not come as a surprise following the acute localized bleaching event in the Cayman Islands during late 2009 (Hooidonk *et al.,* 2012; C. McCoy, unpublished data).

Chapter 6. General Discussion and recommendations

This study is about protection effects on coral reefs, reef resiliency, and the drivers behind it, investigated through the benthic and fish communities inside and outside protected areas of the Cayman Islands. "Coral reef resilience" is best described as the ability of a coral reef community to return to their initial state after a phase of perturbation, where a significant change and/or mortality has occurred, whilst still maintaining key ecological function and services (Pearson1981; Nyström *et al*., 2000; Carpenter *et al*., 2001). One of the most striking results of this study was the resiliency demonstrated by Caymanian reefs after the localized mass coral bleaching event that affected the Cayman Islands in September 2009. A whirlpool of hot water came off of the Cuban shelf and seemingly engulfed the Cayman Islands, keeping them in the center of it and raising the water temperature above 30^0 C for more than six weeks from the sea surface to a depth of ~450 m (Dr. James Hendee, NOAA, personal communication). By the time the sea surface temperatures started lowering in late October 2009, >99% of the corals on the shallow reefs, deep terrace reef, and deep wall showed signs of bleaching (colonies pale, partially bleached, or fully Bleached, C. McCoy, unpublished data). According to ROV surveys conducted by the Department of Environment, Cayman Islands Government staff, bleached corals reached depths exceeding 100 m. Although GCM was most severely affected by this event, coral cover across the three Cayman Islands did not suffer mortality as expected, with corals demonstrating a full recovery and a combined higher coral cover for the Cayman Islands by the year 2011. Clearly, this demonstrates a positive sign of resilience, more so for Grand Cayman, as the bleaching event was particularly severe on that Island, contrary to the Bruckner, (2010) report on Cayman Islands Coral Reef Health and resilience; however Bruckner (2010) did report negligible tissue loss associated with bleaching, which was congruent with the observations of this study.

6.1 Recap of chapters

In the preceding chapters of this research study, the general setting of the Cayman Islands was described (Chapter 1), followed by a detailed description of the different reefs, including all coast and benthos habitats of each island, including their fish assemblages and coral communities (Chapter 2).

Chapter 3; Was fully dedicated to describing the fish communities across islands, habitats, coasts, and protection status in space and time. According to the key findings, the fish community's make-up changed significantly across islands, habitats, and protection status between the years 2009 and 2012. Results also showed that the fish communities inside the Marine Protected Areas (MPAs) of Little

Cayman (LC) were more dissimilar than non-MPAs, a pattern that was persistent across habitat depths. The findings also illustrated that several key herbivores (such as *Kyphosidae* Sp. and the parrot fish *Sparisoma viridae*), omnivore (*Melichthys niger*) and carnivores (*Lutjanus apodus* and the grunt *Haemulon scirurus*) were significantly more abundant inside the MPAs of Cayman Brac (CB) and LC. However, the results from Grand Cayman (GCM) were not as positive since the island's MPAs seemed less effective in increasing fish biomass over the years of study. The community structure of fishes was found to be most similar in the years 2009 and 2012.

Chapter 4; was dedicated to temporal and spatial changes occurring in the benthic community structure across islands, habitats, aspect as well as protection status. Results demonstrated that the changes over the study period were complex and that the trajectories were predicated on a multifaceted confluence of factors such as the habitat type, aspect, island, including protection status. Differences between turf and macroalgae consistently explained 61% to 79% of the average similarities that were recorded across the Cayman Islands; additionally, turf algae were associated with a shallow reef terrace habitat, but it was more evident in the sister islands of CB and LC.

In chapter 5; fish data (Chapter 3) and benthos data (Chapter 4) were used to test the correlations between the benthic and fish communities in order to evaluate which variables of the benthos community best fitted into the documented changes (in the fish community structure) across aspect, islands, habitats, years and protection status. According to the findings, the fish and benthic community were statistically significant, albeit weakly correlated, with three combined variables of the benthos fitting the model to explain the changes best that occurred over time and space, across aspect, islands, habitats, years and protection status throughout this study period.

The overall aim of this study was to investigate the protection effects offered by the MPAs in the Cayman Islands to their coral reefs and related reef fish assemblages. In addition, the correlation of protection status, reef fish communities, and benthic variables across aspect, islands between the years 2009 and 2012 was investigated. In this final chapter (Chapter 6), these keys findings will be explained in order to fill the knowledge gaps in not just the Cayman Islands' MPAs, but also regional and global MPAs. Additionally, based on this study's findings, suggestions will be proposed about new and fit for purpose enhanced MPAs that will further confer coral reef resiliency going forward and arguably, well into the next century.

6.2 Human threats

Humans have transformed their surroundings, whether terrestrial or marine, to suit their existence, creating a plethora of chronic and acute anthropogenic factors, flanked by natural perturbations such as repeated hurricane impacts affecting coral reefs that are threatening their existence in the global tropics.

These issues include ocean acidification (Mora, 2008; Mumby and Steneck, 2008), uncontrolled coastal development (Munday, 2004), overfishing (Roberts, 1995; Chabanet *et al.*, 1997; Jackson *et al.,* 2001; Hughes, 1994), to name a few. However, one of the most time-critical issue facing the scientists in the 21st Century are the implications, and possible disastrous outfall of climate change (Hughes *et al.,* 2003; Lubchenco *et al*., 2003, Hughes *et al.,* 2007), including the ramifications of coral bleaching and subsequent coral diseases on coral reefs and their accompanying organisms over the next 50-100 years. All of these global coral reef issues are bound to amalgamate at some point, eventually causing an ecological shutdown of coral reefs in the global tropics where functionality ceases, possibly resulting in further economic difficulties and social unrest. With an estimated 275 million people living globally <30 km of coral reefs, 43 million of those are situated in the Caribbean basin (Burke *et al.,* 2011), the loss of coral reef ecosystems would have more far-reaching negative consequences. This includes a protein deficit (food source), loss of tourism revenue and livelihoods (economic GDP), and medicine (medical compounds source), including wave dampening properties that offer protection from damaging hurricane and cyclone wave action, among others.

6.3 Emergence of conservation

Taking a step back and looking at the big picture, many countries have decided to conserve these valuable, irreplaceable assets from as far back as the early 20th century (Johannes, 1978); Beverton and Holt (1957) provided the first official account describing the management of fisheries through fishery closures. However, it was not until the 1980s that MPAs emerged as a more prominent tool for fisheries management, habitat protection, and biodiversity, paralleling closed areas, fishing net sizes and quotas to name a few, the latter in more temperate regions. De Silva *et al*. (1986) listed 430 MPAs by 1985, and by 1995, Kelleher et al., (1995) purported >1,306 sub-tidal MPAs and 5,000 all over the world. According to Protect our Planet (2018), there are >15,000 MPAs globally, covering 7.26% of the ocean (26,302,971 km^2) That leads us to the big question of timely interventions to prevent the reduction of coral reefs globally; they have continued to travel on the path of shifting to an alternate undesirable state, a well-documented phenomenon depicting a shift from a coral-dominated coral reef environment to an algal dominated one (Done 1992; Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.*, 2003; Bellwood *et al.,* 2004; Hughes et al., 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014). Due to this "coral reef crisis" (Bellwood et al., (2004), countries all over the world, including the Caribbean region, have reassessed their current MPA management strategies. This new approach has grassroots in the scientific community in order to grasp a better understanding of coral reef ecological processes over the past two decades, such as the role of apex predators, carnivores, herbivores and omnivores on coral reefs. This has been done in an effort to better manage their coral reefs, mostly by making reserves no-take areas (Hughes et al., 2007), thus preserving the diversity, and species density of the ecosystem, therefore greater biological functionality of the ecosystem as a whole (Halpern, 2003; Lester *et al*., 2004).

6.4 Disruption of functional groups

The importance of herbivores, at least with regard to Caribbean reefs, emerged after the keystone grazer, *Diadema antillarium* suffered an epizootic outbreak in 1983/84 (Lessios *et al.,* 1984) that wiped out the entire population in the western Atlantic basin. To date, this herbivore is still struggling to re-establish itself at anywhere near the densities that are commonly found regionally before the epizootic spread (Highes *et al.,* 2010). Though herbivores/omnivore guilds constitute the majority of fish biomass on Caribbean reefs (Vallès & Oxenford 2014), a finding corroborated by the current study, they seemingly were not up to the task of filling the deep ecological void left behind by this echinoderm disappearance. This is perhaps attributed to low numbers of grazing fish, as Jackson *et. al.* (2001) hypothesized, that by the late 1950s, overfishing of fish stocks in the Caribbean region was already in motion, if not critically low. A similar study by Jackson *et al*. (2014) corroborated his findings in 2001 in addition to that of Jackson *et al*. (1997) and Hughes *et al.* (2007). Using the Caribbean island of Jamaica, the relationship between herbivores and herbivory regimes, if disrupted most slightly, can have dire consequences and negative outcomes on coral reefs (Jackson, 1997; Jackson *et al,*. 2001; Hughes *et al*., 1994; Jackson *et al,*. 2014). It is this balance that influences the coral reef community structure so prominently by exerting a top-down control of macroalgae (Mumby *et al.* 2007), and removing algae to make space for coral recruits, thus influencing coral settlement success and coral reef recovery (Mumby and Hapborn, 2010). According to global calculations, 2/3 of wild fish stocks are considered as fully exploited (Chabanet *et al.*, 1997; Swartz & Pauly, 2008), posing a grave threat to the intricate balance that has existed for centuries. This synopsis bears very little hope as the human population of ~7.5 billion continues to grow exponentially and the demand for protein parallels that demand. This perilous trend is corroborated within the results here, as the human population increases across islands, there was an equally disruptive balance of the trophic regime, with the least populated island of LC reported to have the most balanced trophic system of the three Cayman Islands (McCoy *et al.,* 2010; Drommard *et al.,* 2011). Equally important are the carnivores on the coral reefs of the Cayman Islands. Their population patterns follow the same trajectory of an increase in carnivores on the Cayman Islands' coral reefs, with a declining population across the islands. This is a cause for concern as *Lutjanidae* and *Serranidae* are mostly large-bodied, long-lived, slow-maturing and low reproductive success species. Additional evidence of this trend is depicted in the results of Henshall (2009) and Meir *et al*. (2011), where results pertaining to fishing pressure show a preference across the three Cayman Islands, for lutjanids (snappers) as being preferred fish for consumption amongst the people of the Cayman Islands. Although the overall biomass of lutjanids did fluctuate spatially and temporarily if did not reflect any gross loss of biomass during the study period.

An additional suggestion evolving from the documented decline of reefs across the globe is for coral reef managers to identify areas that have resisted and demonstrated their ability to cope and thrive under

conditions that have reduced other nearby reefs to rubble and practically collapsed the fishery/fish communities (Hughes, 1994). Though global drivers of change such as climate change are beyond the scope of coral reef management (Obura, 2005), two popular schools of coral reef management have emerged over the past few decades, one of which is termed " Managing for resilience" by The Nature Conservancy (http://www.reefresilience.org/) and ecosystem-based approach. The former is a process that deploys five principles:

1) Effective management where community benefits are provided and local threats are reduced.

2) Replication, where a percentage of all habitats is selected and replicated to ensure the inclusion of key biodiversity elements.

3) Selection of critical areas that have been identified to naturally be more resistant toward climate change and other stressors like coral bleaching.

4) Connectivity, where connections between populations are provided, larval exchange seed /sink scenario is ensured, and the management creates a network of MPAs whereby ecological connectivity is provided amongst and between habitats.

5) Socioeconomic criteria, where social, cultural, economic and governence aspects of the adjacent community are considered and managed, which include incorporating or adapting the opinions of stakeholders into the management plan (Kaiser, 2005).

The latter and second school of coral reef management refers to an "ecosystem-based approach"; it is a proactive form of strategic management, (Hughes *et al.,* 2007), basically being managed in lieu of uncertainty such as climate change, involving the management of functional groups i.e. herbivores and carnivores, including incorporating the strategy of integrating the management of adjacent lands. Coral reef resiliency is predicated on the presence of "functional groups" within the ecosystem that perform similar functions, irrespective of their taxonomic affinities (Bellwood *et al.,* 2004). The role of the functional group "herbivores" was quite overlooked until the loss of the keystone grazer in 1983/4, which pushed the Caribbean region on a catastrophic shift from a coral-dominated reef environment to an algal dominated one. Their pivotal role and their benefit imparted to marine ecosystems, along with the irreplaceable role that they played in coral reef resiliency, were mostly unnoticed (Bellwood *et al.,* 2007). Findings by Mumby *et al.* (2007) of parrotfishes in a Bahamian reserve exhibited a strongly negative relationship between grazing intensity and macroalgal cover, including a positive correlation between grazing intensity and recruitment densities using parrotfish bite rates and body size. These findings underpin the importance of herbivory in the Caribbean region to maintain a healthy coral reef ecosystem *and* are a driving force behind the resilience of coral reefs in a changing climate. According to Holbrook *et al*., (2016), a drop in herbivore biomass can have negative consequences whereby the

top-down control of macroalgae is weakened significantly, leading to a phase shift from a coral-dominated environment to an algal dominated environment one (Done 1992; Goreau, 1992; White *et al*., 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003;Hughes *et al*., 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014). This one guild of coral reef fishes can define the plasticity within a system to absorb changes by preparing the marine real estate for new coral recruits and facilitating the continued growth of a coral reef to create a positive carbon budget (Murphy *et al.,* 2015).

The importance of carnivores in maintaining the health of marine ecosystems has been widely recognized by researchers (Hairston *et al*. 1960; Miller *et al*., 2001). They formulated a top-down control trophic structure by preying on other carnivores, herbivores and omnivores (Miller *et al*., 2001) that further controlled other benthos as well as organisms on the coral reef (Williams *et al.*, 2004; Kulbicki *et al.*, 2005). Comparing the biomass of carnivores across islands, Grand Cayman seems to be much lower than the sister islands of Little Cayman and Cayman Brac. Future efforts on MPA management and species management per se should focus on that island to aid the recovery of carnivores, including protection of the larger size class of carnivores. According to Miller *et. al* (2001), the larger size carnivores are more important than smaller size carnivores for ecosystem control and functionality. An example and lending weight to carnivore removal causing an ecosystem shift, McClanahan, (1995) showed that removing triggerfish from a marine ecosystem in Kenya resulted in an overabundance of the sea urchin *Echinometra mathaei*. The current MPAs of the Cayman Islands are quite small and give very little movement of fish to forage before they encounter open fishable areas. This is contrary to the purpose of MPAs, as Pittman *et al*., (2014) demonstrated in a study, that species such as the blue stripe grunt *(H. scirus*) and the mutton snapper (*L. analis*) were documented to travel 11.7 and 42.2 km respectively in one day. Even the latter of 11.7 km is longer than the largest and longest contiguous MPA in the Cayman Islands, located in Grand Cayman. This fact further lends merit and galvanizes the need to expand the current MPA system in the Cayman Islands to achieve a more balanced trophic structure, possibly increasing the carnivore population and their size classes.

6.5 Emergence of Marine Protected areas

Though the concept of MPAs first emerged during the early 20th century (Johannes, 1978), the concept seemingly did not gain momentum globally until the latter part of the 20th century (De Silva *et al.,*1986; Kelleher *et al.,*1995). Herbivores were the dominant trophic guild of the reef fish across the Cayman Islands, especially species of the family *Scaridae*. This is not surprising as previous local studies have corroborated those results (Pattengill-Semmens and Semmens, 2002; McCoy *et al*., 2010; Drommard *et al.,* 2011), and are consistent with the findings of Valles and Oxenford (2014) as well as the

conclusions of a broad-based study by Valles and Oxenford (2014) on Caribbean reefs that measured the densities and biomass of herbivores. A notable observation was that the higher densities and biomass had no bearing on human population densities, which is again congruent with the findings of this study. This observation can possibly mean that they are not an exploited species in the Cayman Islands; however, the study of Meir et al., (2011) revealed that parrotfishes were second only to snappers as the most heavily fished family across the Cayman Islands. However, that finding by Meir et al., (2011) may be biased due to the fact that local fishermen in the Cayman Islands mainly target the deepwater snappers such as the *Rhomboplites aurorubens*, which could potentially polarize the *Lutjanidae* family, lending further credence to their dominance across the Cayman Islands during the period of that study.

This fact also illuminates two questions: 1) is the fish trophic guild dominated by herbivores across the Caribbean region; and 2) why is the macroalgae dominance so persistent? With a number of studies documenting a shift of coral-dominated to macroalgal dominated one (Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006), and the causal factor mostly purported to be overfishing of herbivores (Jackson, 1997; Jackson *et al,.* 2001; Jackson *et al,.* 2014), this suggests that the capacity of coral reefs has been reduced in biological and ecological function (Russ, 1991; Jennings and Lock, 1996; McClanahan, 2000; Micheli *et al.,* 2014), thereby lowering resiliency by creating a trophic imbalance (Bellwood *et al.,* 2004; Mumby 2006; Hughes *et al*., 2007; Green & Bellwood, 2009; Mumby *et al*., 2012). Data seems to point more towards the disappearance of the echinoderm, *Diadema antillarium* (Lessios, 1984), and the poor recovery of this echinoid, possibly due to a marked increase in the Balistidae family, at least in and around the Cayman Islands, which feeds predominantly on echinoids (Randall, 1967). Exacerbating this recovery problem is the fact that echinoderms such as *Diadema antillarium* are a dietary preference when they are available to the majority of parrotfish species in the Cayman Islands, more especially the juveniles <2 cm (C. McCoy, personal observation).

The finding that herbivores and specifically the Scaridae family dominated the reef fish community is not surprising as it is consistent with the observations of Valles and Oxenford (2014) and local studies conducted by McCoy *et al*. (2010) and Drommard *et al.* (2011). The island of GCM is dominated by herbivores and lacks large bodied apex predators like groupers and snappers. This observation of the herbivory regime of the Cayman Islands, and especially Grand Cayman, contradicts the suggestion by Jackson *et al.* (1997; 2014) that herbivores are overfished in the entire Caribbean, although Jackson *et al*. (2001) did mention that fishing pressure on the Cayman Islands is low when compared to other neighboring Caribbean Islands. It also challenges the observations of Mumby et al. (2007) in a Bahamian MPA where there was a strong negative relationship with grazing intensity and macroalgal cover. Therefore, the Cayman Islands would be an exception and not the norm for the region, in terms of low macroalgal cover, particularly GCM, which is dominated by herbivores and there must be something else that can explain the persistent macroalgal cover in the Cayman Islands. That elusive

driver may perhaps be a functional group different from scarids that is in low numbers, much like the findings of Bellwood *et al.* (2006) that the batfish (*Platax* sp.) which was categorized as a planktivore, turned out to be an important herbivore that ended up removing the most macroalgae in competitive exclusion experiments.

In most cases, the ability of a marine reserve to produce "reserve effect" usually signals that some form of fish extraction is quite high, usually manifesting itself in smaller size classes of species and densities, regardless of whether it is taking place in a commercial or recreational fishing activity (McCoy *et al.* 2010). It also demonstrates that protection is effective in situations where fishing pressure is high. The overall significant reserve effect-related finding of this study agrees with the views of McCoy *et al.* (2010), Drommard *et al.* (2011) and Ward (2016), albeit not due to increased density, but because of the larger size class of reef fish within the MPAs of the Cayman Islands. However, this is somewhat debatable as no prior studies were conducted to define the fish biomass status before the MPAs of the Cayman Islands were designated. Arguably, results on fish biomass may have been the " status quo" before the protection was put in place. However, the positive increase in fish biomass, including increases in size classes of fishes within the protected areas, is well supported by strong empirical data over the past few decades (Coté et al., 2001; Halpern, 2003; Lenfant, 2003; Russ *et al.,* 2003; Claudet *et al*. 2008; Harmelin-Vivien *et al.,* 2008; McCoy *et al.,* 2010; Bohnsack, 2011).

6.6 Spill-over

The lack of evidence for the spillover on the deep shelves across islands is a cause for concern and should be addressed in any review of MPAs in the Cayman Islands. Fishers are allowed to fish at the 24 m depth contour and beyond. This creates a situation whereby fishers are allowed to fish the deep terrace reef of any of these islands, which perhaps results in such high extraction levels that this effect is negated, resulting in a compromised system. Furthermore, the boundaries of the Cayman Islands' MPAs do not always have a contiguous coral reef structure. This seems to be the only commonality that defines whether or not a spillover signature is detected. Reef fish species require habitat to avoid predation; therefore, the presence of structure at MPA boundary is a positive attribute that entails the capacity to promote resiliency. The term "spillover effect" is largely highlighted by studies in which there is a net migration of fish out of MPAs (Russ and Alcala, 1996; McClanahan and Mangi, 2000; Gell and Roberts, 2003; Abesamis *et al.,* 2006; McCoy *et al.,* 2010; Hall, 2014; Oliver, 2014; Ward, 2015) and often do not identify that there are typically few fish families that explain this net migration. In this study, the Haemulidae and Lutjanidae fish families were observed to be the major contributors responsible for the net "spillover effect." This leaves 12 other important fish families such as Scaridae, Serranidae, Acanthuridae, Kyphosidae that are not managed to the point where the MPA system fosters a "spillover" of these fish family species to adjacent fished areas. These species will have to be managed via different strategies, such as bag limits and slot sizes, although it is a broad assumption on a global

level that once in place, MPAs will provide such benefits to all fish families, making some studies skeptical of the existence of such effect owing to lack of tangible evidence of its existence (Palumbi, 2004; Kerwath *et al.,* 2002). Studies in the Caribbean region and globally offer empirical evidence in support of this study's findings of "spillover effect" (McClanahan and Mangi, 2000; Kelly *et al.,* 2002; Maypa *et al.,* 2002; Gell and Roberts, 2003; Russ and Alcala, 2003; Russ *et al.,* 2003; Alcala *et al.,* 2005; Abesamis *et al.,* 2006; McCoy *et al.,* 2010; Hall, 2014; Oliver, 2014; Ward, 2015).

6.7 Trophic group differences across islands and habitats

The trophic differences of Cayman Islands' MPA and non-MPAs were significantly correlated across islands and habitats. This illustrates that there were common fish species between habitats and the three Cayman Islands, pointing towards homogenous functional groups; however, four species of fish were most responsible for this effect. These species are not targeted across islands; two of these are important herbivores on Caribbean coral reefs: *Sparissoma aurofrenatum*, and *Kiphosidae* spp. Having an abundance of these two widely distributed species and the fact that they were growing regardless of protection is significant, considering they are targeted as a food source throughout the Caribbean region.

Although the fish community structure changed both spatially and temporally, the effects of MPAs on the fish community structure is apparent. This is perhaps a direct result of the size-related differences of the MPAs across islands, as all fish species entails a different behavior, foraging and home ranges. This pattern is also evident when species are organized into their functional groups. Protected areas in the Cayman Islands should be reassessed with well-defined parameters to exactly pinpoint which species and more so, the functional groups that the end objective is to manage. This would define a purposeful MPA, including "managing for resiliency," which will impact many ecological, biological, and social benefits to the Caymanian society. The most striking findings across years and habitats was the fact that protection status had no effect on Cayman Brac, which suggests that habitat (deep/shallow) has a greater importance in determining species distribution and any functional differences in the islands fish community structure, also suggesting that the MPAs are located in an inappropriate geographic location.

The findings also demonstrated no differences in fish community structure between MPAs and non-MPAs, suggesting that the relocation of the island's MPAs to more suitable habitats may improve the performance of the MPA network. Not surprisingly, the greatest dissimilarities between MPAs and non-MPAs were found in the fish assemblages on the island of Little Cayman, across all habitats (deep and shallow). These MPAs housed the biomass of key herbivores, such as *Sparissoma viride* and *Acanthurus coeurelus*, 1.5 to 2.2 respectively, which represent a definite sign of building up resiliency within the MPAs. However, the problem of algal profusion was still very evident, facilitating the

conclusion that the drivers of macroalgal persistence are not of a global origin, such as climate change, which unfortunately is not likely to change for the better any time soon.

6.8 Importance of protection

The clear, definitive differences in biomass of Nassau grouper *Epinephelus striatus*, between MPAs and non-MPAs in Little Cayman, is an example of how important protection is in safeguarding the extraction of apex predators. This top carnivore varied from 4.1 Kg/m^2 inside MPAs to 2.96 Kg/m^2 in areas having no protection; however, this regionally targeted iconic species has been managed separately since the year 2003, building resiliency within the MPAs of Cayman Islands. Due to management intervention, this small island is home to the largest aggregation of this species of fish known in the region. A model that countries would do well to adapt regionally, as a healthy population status of this iconic Caribbean predator species is vital for optimal ecological functionality (Stallings 2008, 2009; Archer *et al.,* 2012; Egerton *et al.*, 2017). In most Caribbean countries, this may not be possible in the wake of low numbers of *E. striatus*. Fishery closure of the Nassau grouper in the Cayman Islands took over a decade (2003-2015) to double the population on Little Cayman (1500-3500), exhibiting an ~10% growth per year (C. McCoy, unpublished data). Recent population assessment for this species of fish in February 2019 illustrated the continued growth of the *Epinephelus striatus* population, numbering > 8000 fish at the Fish Spawning Site (FSA) on that island (C. McCoy, unpublished data). However, fishery-dependent data for the other islands suggests that they are not responding to the protection and management strategies. Across the years of study, the fish community structure, regardless of the island, has changed significantly, by following a similar pattern in time and space. Data indicated that the fish communities were more similar during 2009 and 2010 and broadened their differences as time progressed, albeit in a similar pattern. Furthermore, the role of *Kiphosidae* spp may have a greater effect on fleshy macroalgae than the *Scaride* spp, although they are considered to be browsers (Randall, 1967), whether singular or schooling (C. McCoy, personal observation) and fleshy macroalgae is seemingly less in quantity wherever they are found in high biomass across the Cayman Islands.

The haphazard distribution of trophic groups such as herbivores surfaces in the data for the genus *Kyphosidae spp*. as well as the stoplight parrotfish *Sparissoma viride,* showing no clear, consistent temporal patterns in their biomass over the years of this study. This raises genuine concerns as they were two of the five species that consistently contributed 31-36% to the average dissimilarity across the years. Data also indicated that key coral reef carnivores, such as the Yellowtail snapper (*Lutjanus apodus*) and the Blue stripe grunt (*Haemolon sciurus*), significantly increased over time. This finding is meaningful as they were once found abundantly across the entire Caribbean region, but their population has been steadily reducing due to trap fishing. Although each of the islands has taken a slightly different path in terms of fish community structure, functional groups followed suit on spatial

and temporal scales. This observation illustrated that although reef fish community and functional groups are intricately linked, they can exhibit very different results. Algal biomass, at least for 2009 and 2012, was found to be very similar across spatial and temporal scales; yet, the fish community structure changed, clearly indicating the involvement of other more persistent drivers of coral reef changes, which in turn makes the study of what exactly drives reef changes even more complex.

The high herbivore biomass across islands and years refutes most studies which proclaim that the overfishing of this guild has been driving a wedge into the ecological balance in order to keep algal profusion in check. Considering the fact that ecological data is variable and extremely complex, the Cayman Islands serve as a clear example that even under proactive management, well-funded and staffed enforcement, those factors cannot offset and balance the perils of global climate change. This manifest itself in the form of coral decline followed by its associated marine organisms, such as reef fish assemblages, although the latter could be a combination of local recreational fishing pressure, which is quite significant (Henshall, 2009; Meir *et al.,* 2011).

6.9 Coral cover

Coral cover in the Cayman Islands seemingly follows regional trends, but in the wake of mitigating management strategies and protection efforts, it does so at an overall higher percentage level. During this study, coral cover for non-MPAs demonstrated an average low of 10% in 2009 to a national (average) high of 12.79% in 2011 (data pooled), during this study. Though negligible, the lower national average of 11.6% in 2012 during this study may have been the result of localized coral bleaching during 2009, possibly manifesting itself at a later date, as noted by Obura (2009); the effects of full bleaching can linger for a long time after the event had occurred. The coral community structure data illustrated clear patterns over the study period. Further analysis revealed that these changes were complex, causing each island to take different paths due to several factors, including habitat (depth), exposure, island, and protection status, which explained 47% of the variance during the period of study. The temporal variation of the benthic community structure of each island was further corroborated by a significant interaction of years and islands, with *post hoc* analysis showing which years were different, and macroalgae consistently explaining those differences. This model fits into the 'Caribbean Story' (Done 1992; Goreau, 1992; White *et al.,* 2000; Jackson *et al.,* 2001; Gardner *et al.,* 2003; Hughes *et al.,* 2003; Bellwood *et al.,* 2004; Hughes *et al.,* 2005; Graham *et al.,* 2006; Jackson *et al.,* 2014) of a phase shift from coral to macroalgae dominated reefs within the region. In GCM, the macroalgal prominence was higher outside of the protected areas, which was quite predictable as herbivores dominate its community structure; however, large-bodied predators such as the lutjanids and serranids complexes are missing from the trophic structure. Efforts to manage these top carnivores, particularly in Grand Cayman, needs to be addressed, such as a larger protected area. Additionally, because these animals are mass spawners, and their reproductive cycle is very predictive, including their migratory times and patterns with regards

to their respective aggregation sites, they are very vulnerable to overexploitation (Whaylen et al., 2006; Heppell et al., 2012; Archer *et al.,* 2012; Egerton *et al.*, 2017).

6.10 Temporal and spatial patterns of benthos categories

In this study, the temporal and spatial patterns documented within the benthic community structure were complex, their paths depended upon a combination of factors, such as habitat type, aspect, and island, including protection status. The benthos metrics that accounted for most of these changes were by macroalgae cover and turf algal communities. The benthic changes noted in Grand Cayman demonstrated that the benthic community of that island are readily capable of adjusting to temperature extremes, a positive sign of resiliency. Furthermore, the algal mortality after the bleaching event in late 2009 exposed dead coral cover, possibly from prior bleaching events such as 1998 or 2005, thus exposing the surface area to be occupied by juvenile corals. A shorter duration of extreme temperature events might be a developing resiliency aspect for coral reefs, not only in the Cayman Islands but also regionally, whereby the macroalgae suffers from high mortality - an explanation of resiliency that is quite misaligned with the scientific literature on coral bleaching. The macroalgal reduction caused by this extreme temperature variation for a short duration can bring the high algal profusion levels to lower manageable limits which can then enable the current reef herbivores, in the absence of the keystone herbivore *Diadema antillarium,* to crop and keep the macroalgae under control. According to Williams and Polunin (2001), the effects of reef herbivores capacity to keep the algae in check can be negated by approximately 60% algal cover and above. Crabbe, (2008) noted that bleaching is forecasted to be an annual event by 2040, causing the demise of coral reefs not only regionally, but also globally in the tropics, while adding that this trend is likely to be witnessed sooner in the Caribbean. Hughes *et al*. (2003) predicted that by 2030, >60% of coral reefs globally will disappear. The negligible difference in coral cover for the year 2011; however, is very encouraging after undergoing such a massive bleaching event and challenges those predictions. Notably, the bleaching event in 2009 was for a short duration, rather than the long degree heating weeks (Figure 6.1) witnessed in other episodes of coral bleaching, such as the acute coral bleaching event in 1998, which exhibited a 60% loss of coral cover, from a Cayman Islands national average of ~25% before the event to 15% post-event (C. McCoy, unpublished data).

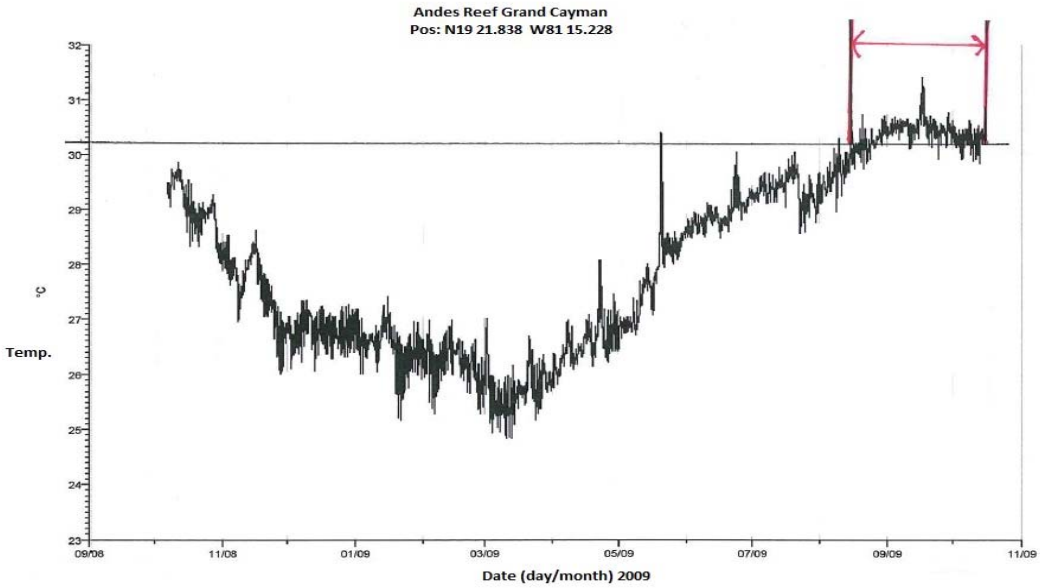


Figure 6.1. Graph of Andes Reef, North coast of Grand Cayman (POS: N19 21.838 W81 15.228) at 10-meter depth depicting the extremely high temperatures experienced in October 2009 for a short duration, highest temperature gap in **red**.

6.11 Benthic community structure; variation between years

Results clearly show that significant variation in the benthos community structure occurred in the year 2011, notably in GCM; however, this island regained stability after 2011, also showing signs of constancy of the coral reef benthos community structure in 2012 surveys. This resilience is indicated by the ability of a coral reef to show recovery after such an event while still carrying out ecological and biological functions (Pearson1981; Nyström *et al*., 2000; Carpenter *et al*., 2001). The higher values of live coral cover (15-20%) found in the deeper and shallower habitats of LC and CB, without any measurable differences between protected and non-protected, is perhaps a combination of actions that have been protecting corals since 1978 by the Cayman Government. This 30-year status protection status was further reinforced by making it illegal to anchor in a manner that damaged or destroyed any corals in 1986, imposing heavy financial fines, including jail time and confiscation of any equipment or vehicles involved. However, lower coral cover was found in the shallow habitats around GCM when compared to deeper habitats, regardless of protection status, paralleling Burgess (1994) findings, but contrary to the findings by Gall (2009) that shallow sites had a higher coral cover and Looker (2011) whose findings showed no difference. These varying results are no surprise considering how variable ecological data is; however, in the Cayman Islands, the coral community structure is more vulnerable to stressors such as the higher temperature at the surface layer of water, including higher UV light penetration. Therefore, change is expected when compared to the deeper habitats

6.12 Correlations of benthos and fish

The weak but significant BioEnv results clearly showed that the fish community was correlated (BEST, Rho = 0.26, p = 0.01), with zoanthids, tunicates and dead gorgonians best explaining the changes in fish community structure across the Cayman Islands. These findings are quite surprising as reef fish assemblages are usually associated with large complex high rugosity structures (Risk, 1972; Luckhurst and Luckhurst, 1978; Syms and Jones, 2000; Friedlander *et al.,* 2003; Bozec *et al.,* 2005; Gratwicke and Speight, 2005; Komyakova *et al.,* 2013). The finding on Caymanian reefs that their gorgonians densities can drive fish assemblages is quite significant. The Cayman Islands has vast gorgonian beds, ranging from the back-reef environment to a deep terrace reef. Considering the fact that these are found in prime reef fish habitats is encouraging, and can possibly mitigate the loss of three-dimensional structure of scleractinian coral habitats that have been proven to be on the decline, lowering reef complexity and ultimately, the overall structure (Lorenzo *et al.,* 2009). Findings by Wolff *et al*. (1999) on trap fishing of fish effectiveness in adjacent coral reef and gorgonian habitats in St. John, USVI corroborated this observation by tracking abundances in the gorgonian habitat as compared to coral reef habitat for several exploitable species of reef fish. Additional findings by Recksiek *et al.* (1991) and Acosta *et al.* (1994) support the fact that fish catchability was much higher for several species groups across gorgonian habitats. Any changes to the MPAs of the Cayman Islands should include and protect as much gorgonian habitat as possible to mitigate against this threat of loss of structure on the Cayman Islands coral reefs. The association of zoanthids and fish community structure found in this study was further supported by Sergio *et al*. (2007), who also found an association of coral reef fish community structure as well as zoanthids. The most common zoanthid on the coral reefs of the Cayman Islands is *Palythoa caribbaeorum*, (C. McCoy, personal observation), and that this particular zoanthid commonly forms mats covering dead coral reef structures, explaining how this affiliation drives changes in the fish community structure across aspect, islands, habitats, years and protection status. The linear model only supported zoanthids, dead gorgonians, and benthos category of other benthic organisms that were the significant drivers of change in the fish community structure. However, the DbRDA plot illustrated that these changes could not fully explain the observed variation in the fish community structure; therefore some other metric that was not captured in this study could be triggering the observed changes in the Cayman Islands' reef fish community structure across aspects, islands, habitats, years and protection status.

Data collected between 2009 and 2012 indicated that the benthic community structure was extremely variable between habitats, thus explaining more variation as compared to the level of protection. This seems to suggest that the benthic community structure was a poor predictor for explaining the differences in fish communities associated with MPAs and non-MPA's across the Cayman Islands. The spillover phenomenon result suggests that the migration of fish out of MPAs to adjacent areas requires an MPA boundary that is homogenous and a contiguous coral reef structure in order to be effective.

Furthermore, the fish families most migrating out of MPAs are Serranids and Lutjanids, which primarily occur along the shallow terrace reef of 10-12 meters.

Though the loss of coral reef resiliency can be attributed to a combination of global, regional, and local issues, the one aspect of control that each country has is on the local anthropogenic stressors. Tackling global issues have seemingly been a wild card as leaders of countries change, and political successors do not necessarily have the same environmental consciousness, which often makes environmental problems take a lower priority on the political agenda. Global warming (leading to climate change) is one of the most treacherous issues facing coral reefs in the global tropics. Multiple mass bleaching has been going on for a long time, with the worst on record being in 1998; however, back to back 2016/2017 seems to be competing for that status, which will be decided when the full ramifications are tallied over the next few years in total coral loss in the wake of the subsequent disease that follows. This phenomenon is very alarming as the projections of frequency suggest that by the year 2020, coral bleaching will be an annual event.

The daunting task of undertaking regional environmental issues, whether in the Caribbean or elsewhere globally, largely poses the same challenges, albeit on a smaller scale. One of the major environmental problems that are common to many countries is overfishing. As pointed out by Jackson *et al*. (1997), by the time countries and governments in the Caribbean recognized that oceans have finite fishery resources, the overfishing problem would already begin to take its toll both socially and economically. One merely needs to review the fishery landings of the Island of Jamaica. According to Jackson *et al.* (1997) and Jackson *et al.* (2014), the island of Jamaica fisheries was overexploited from the 1950s. In actuality, the Caribbean region has a disastrous record of fishery management, usually accepting the collapse of a fishery before any management intervention is made by the majority of countries, most of which depend on fisheries for a livelihood.

Historically, the emergence of MPAs in the Caribbean region was mostly a reaction to dwindling fishery resources and a hope to replenish the resource. However, conservation has to be well thought out in reference to the target species or ecosystem, including any person or organization, which the management practices of the particular area might affect. The MPAs of the Cayman Islands emerged first in GCM by the Government of the Cayman Islands, Natural Resource Unit (NRU) as the risk of coastal development turned into a reality. This was a proactive approach; however, no real science went into properly designing or selecting a geographic area due to its ecological or biological traits. Presently, MPAs regionally and globally are deployed as a means to protect rare species, critical habitat, and species in order to develop resilient ecological and biologically traits, amongst other criteria. Most MPAs are intertwined with land-based areas and activities that are intricately linked ecologically and biologically to promote an increase in the chances of survivorship of coral reefs and associated organisms such as reef fishes. The MPAs of the Cayman Islands has served them well, considering the

criteria that were used to designate them. However, that took place in the mid-1980s, an era when coral reefs (in the Caribbean region) were still considered healthy, and accompanying reef fish trophic structure remained intact. More so, the population was less than half of what it is at this moment.

The effort to keep coral reefs in the Caribbean region healthy and functional, especially the Cayman Islands, is an ongoing process. Coral reefs are not only facing global issues such as a warming ocean and ocean acidification; with each passing year, humans are finding new ways of utilizing and extracting its finite resources for necessities such as food and medicine. Though protected areas are the main tool deployed in the Cayman Islands as part of the national marine conservation system, including bag limits and closed season, it is not enough to exhibit a net positive gain annually for the coral reefs as well as related fish community assemblages. In a global study conducted by Selig and Bruno (2010) on the effectiveness of MPAs, coral cover declined for approximately 14 years after protection status in the Caribbean region. They further stated that after 14 years, reef decline ceased before increasing again with a number of years since implementation, with change rates leveling off as years since the time of protection increased; this finding is consistent with that and the observations of McClanahan *et al.* (2007) and Abesamis and Russ (2005) for reef fish.

The finding that reef fish predominantly migrated out of Cayman Islands' MPAs via the shallow terrace is striking. Where there is a break in the reef topography, spillover from adjacent MPA is not detectable. Of all the MPAs in the Cayman Islands, only one boundary has a contiguous reef structure, the northern boundary of the GCM MPA. The inability to detect spillover elsewhere perhaps accounts for a major flaw in the inefficiency of the Cayman Islands' national MPA network. One of the most important attributes that make an MPA effective at achieving their goals is compliance and enforcement. Most MPAs of small island nations within the Caribbean region lack both and those that have a Coast Guard become reliant on that sector for patrolling and enforcing regulations, including warding off poachers (Bustamante *et al.,* 2014). Unlike most other Caribbean countries, the Cayman Islands have a small population with a limited coastline with a narrow shelf which can be patrolled from land-based vehicular transport per most part. The Cayman Islands and its people have a deep-rooted maritime history, and this factor trades off to high compliance amongst marine resource users, which is quite different when compared to neighboring countries.

The findings of this study suggest that merely making adjustments to foster "spillover effect" at each boundary of the Cayman Islands' MPAs would not suffice; there is a need for careful consideration concerning placement. A contiguous coral reef habitat must be adhered to. The absence of spillover on the deep terrace reef might be the result of fishers who able to fish the shelf edge at 24 m. This should be extended to beyond the shelf edge to abyssal depths, which is < 500 M in most areas. A more favorable concessionary fishing slot of at least 5km would allow spillover overlap across a network of MPAs. As the data clearly showed a spillover distributed over a 5 km distance, a network of MPAs

would have them strategically placed no more than 8 Km apart, giving an overlap of 1 km either direction, at least for the new enhanced MPA network. The current system of MPAs in the Cayman Islands (figure 6, chapter 1) has served the country well; however, the demands on the coral reef environment have increased exponentially over the past three decades, and the "human impact factor" is becoming increasingly evident (C. McCoy, personal observation).

6.13 Darwin Initiative

This exponential increase in human usage of the Marine Environment spurred the Department of Environment (DoE) Cayman Islands Government (lead Host-country partner), School of Ocean Sciences, Bangor University (lead UK institution) and The Nature Conservancy USA (project partner) to initiate an in-depth review of the marine protected areas of the Cayman Islands in 2009, title "Darwin Initiative to Enhance an Established Marine Protected Area System". This comprehensive project aimed to identify social and ecological gaps that underpin effective MPAs ensuring coastal protection and tourism income for the residents of this British Overseas Territory (BOT) by enhancing protection of marine habitats and biodiversity, including building a network of MPAs fostering increased resilience to climate change and human impact. The main achievements and highlights of this Darwin Initiative project were as follows;

(1) **Assessment of resilience**: reef health measured at 63 permanently established monitoring sites inside and outside of the current MPA system, shows that MPAs generally provide local resilience. (Higher cover and coral recruitment, lower coral bleaching, disease prevalence, and macroalgal cover).

(2) **Assessment of benefit**: overspill of fish into surrounding waters is evident at some MPA boundaries. Number, size, and biomass of 53 target fish species are greater in many MPAs than outside, and proportions of herbivorous and carnivorous fish are more balanced. However, invasive lionfish threaten fish communities.

(3) **Assessment of fisheries impact**: recreational, artisanal and illegal fishing are significant on Cayman reefs, and fishers exploit MPA boundaries. Fishing is an important part of Caymanian culture and understanding the incentives to fish legally and illegally must be included in conservation planning. Fish spawning aggregation sites (FSAs) have been identified as being vulnerable to overexploitation.

(4) **Stakeholder consultation:** survey data and protected area planning tools have been used to plan an enhanced MPA system which increases No-take protection from 15% to ~50% of representative reef habitat, but provides access to fishable areas (Grand Cayman from 15.73% to 46.63%; Cayman

Brac 15.31% to 41.23% and Little Cayman from 10.43% to 64.67%). A campaign of public awareness, education and consultation is maximizing understanding and support for the new MPA system.

(5) **Wide and varied communication:** including 50 scientific reports, 81 stakeholder meetings, 43 press articles, 40 TV and 8 radio programs, 16 online items, and 10 other outputs (eg. school information packs, MPA promotions).

The Darwin Initiative to Enhance an Established Marine Protected Area System project also produced new maps for a network of MPAs for the 3 Cayman Islands upon completion of the project (Appendix 6.1, Grand Cayman, Appendix 6.2 Little Cayman, and Appendix 6.3 Cayman Brac). The recommendations for a new and enhanced marine protected area system for the Cayman Islands have been approved by the Cayman Islands National Conservation Council and it currently with the Ministry of Environment, Cayman Islands Government for approval and implementation. The full report can be found here: http://www.darwininitiative.org.uk/project/18016/ .

6.14 This Study

This thesis concentrated on the coral reefs benthos and their associated reef fish assemblages. The focus of this study is to assess and evaluate what impact the marine protected areas of the Cayman Islands have had potentially had after 26 years of the MPAs being actively enforced, on the benthos and their fish assemblages, more so the attributes that have promoted coral reef resistance, resilience, and recovery. The ultimate goal of this thesis was to produce a network of MPAs as an alternative to the Darwin Initiative to Enhance an Established Marine Protected Area based on a rigorous scientific assessment of their performance in fostering "spillover" effect, reserve promoting healthy fish assemblages. It also concentrated on their performance on promoting healthy benthos and their complex relationship to fish assemblages to encourage resilience and recovery. It ignored many social aspects and concentrated more on the science of MPA performance based on the performance of their current MPA system on the benthos and fish assemblages, including fish community structure between the years 2009 and 2012.

According to the findings of this study, the MPAs of the Cayman Islands should be expanded to accommodate the ever-increasing demands of human usage and pressure, as the current model (figure 6, chapter1) has become obsolete. Additions to the current Cayman Model of MPA system should include;

1) A network of MPAs that is strategically placed 8 km apart with 1km overlap and be referred to as "fishing concession slots" in order to accommodate the local artisanal and recreational fishery.
2) Fishing from shore should be allowed.
3) Boundaries of MPAs should end at a contiguous and homogenous reef so to aid migration of fish out of MPAs to adjacent areas
4) Fishing should not be allowed at the deep shelf edge, extended in the MPA from the current 24m to 60m.
5) Seasonal closures of Fish Spawning Aggregations (FSAs) locations should be extended to offer protection all-year round.
6) MPAS should protect 30-50% of all coastal habitats, including the sounds and nursery habitats, the ecological heart of the Cayman Islands.

Since it has been found that the MPAs in small island nations like the Cayman Islands do not necessarily increase density, and primarily lead to larger size classes (McCoy *et al*, 2010; Drommard *et al* 2011), consideration should be given to adopting further bag limits of coral reef fish catches. The ability of islands within the Caribbean region to support fisheries is linked to shelf area; islands such as the Cayman Islands have a very narrow shelf, which becomes a limiting factor. Any form of small or large scale commercial fishing should, therefore, be discouraged as a livelihood. Lastly, the concluding message of this thesis is that the MPA's of the Cayman Islands are playing a key role in fostering resilience through an increase of the biomass of key herbivores and carnivores over time while stabilizing coral loss and reducing the pace of decline. However, with thriving tourism industry and a growing population, the suggestions and maps produced which consider all the findings should be adopted. These suggested recommendations for a new and improved design of MPAs (figure 6.2; GCM, figure 6.3 LC; figure 6.4) should be able to confer coral reef resistance and resiliency, thus serving the people of the Cayman Islands well even in the distant future.

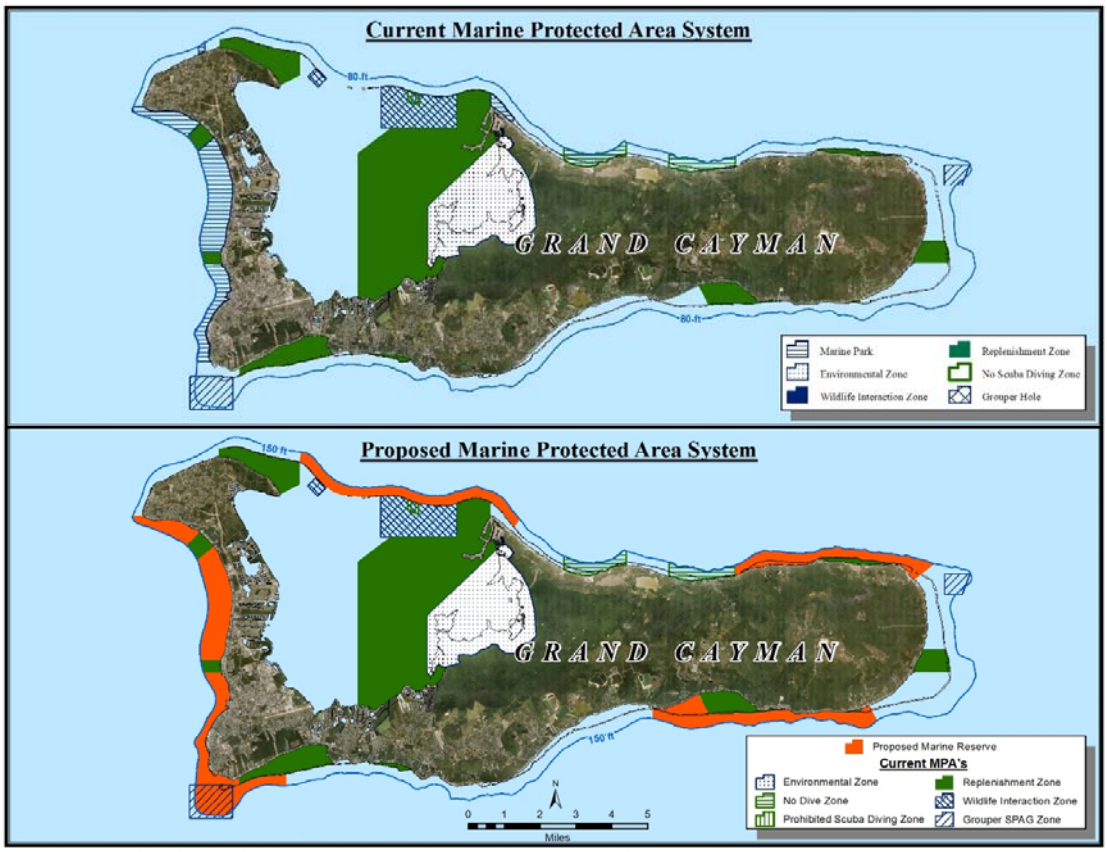


Figure 6.2 Map showing current Marine Protected Area system for Grand Cayman (top) network of MPAs for Grand Cayman as an alternative to the Darwin Initiative to Enhance an Established Marine Protected Area based on a rigorous scientific assessment of their performance in fostering spillover effect and reserve effect promoting healthy coral reefs and associated benthos including fish assemblages. GSP position: N190 18.985 W810 15.151

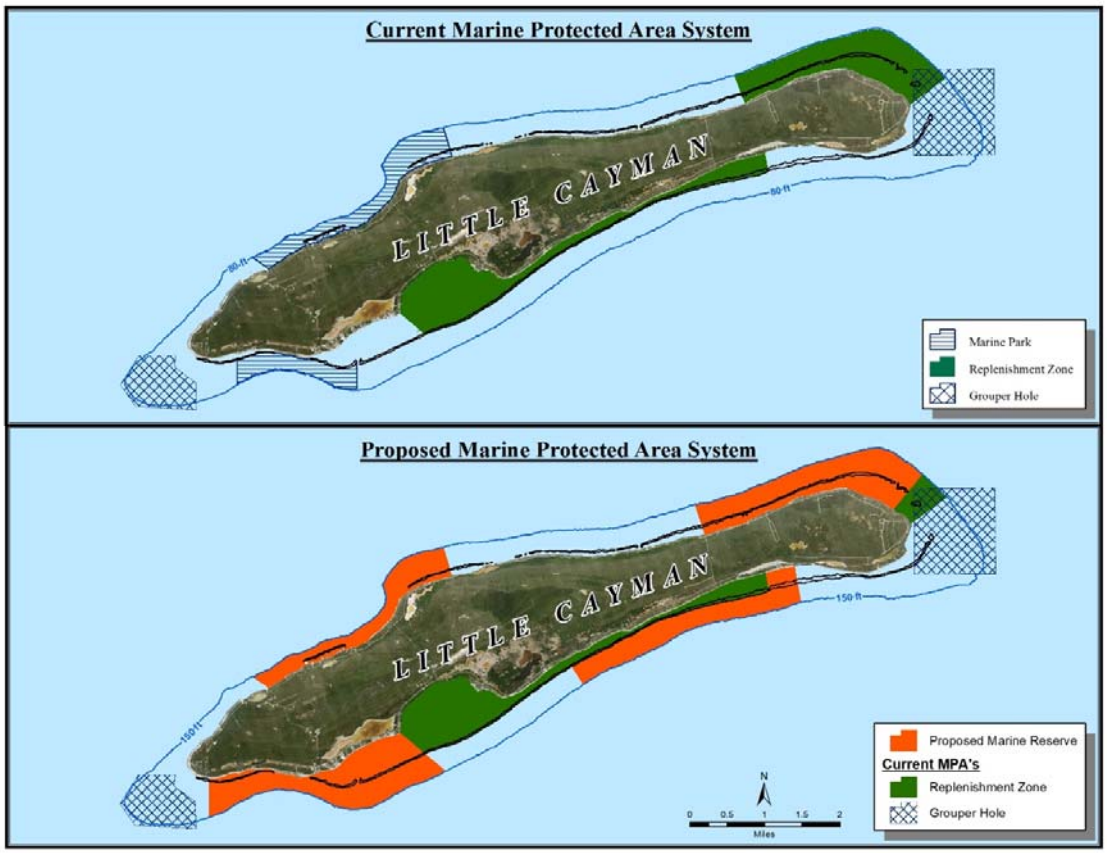


Figure 6.3 Map showing current Marine Protected Area system for Little Cayman (top) Network of MPAs for Little Cayman as an alternative to the Darwin Initiative to Enhance an Established Marine Protected Area based on a rigorous scientific assessment of their performance in fostering spillover effect and reserve effect promoting healthy coral reefs and associated benthos including fish assemblages. GPS position: N190 41.249 W800 02.709

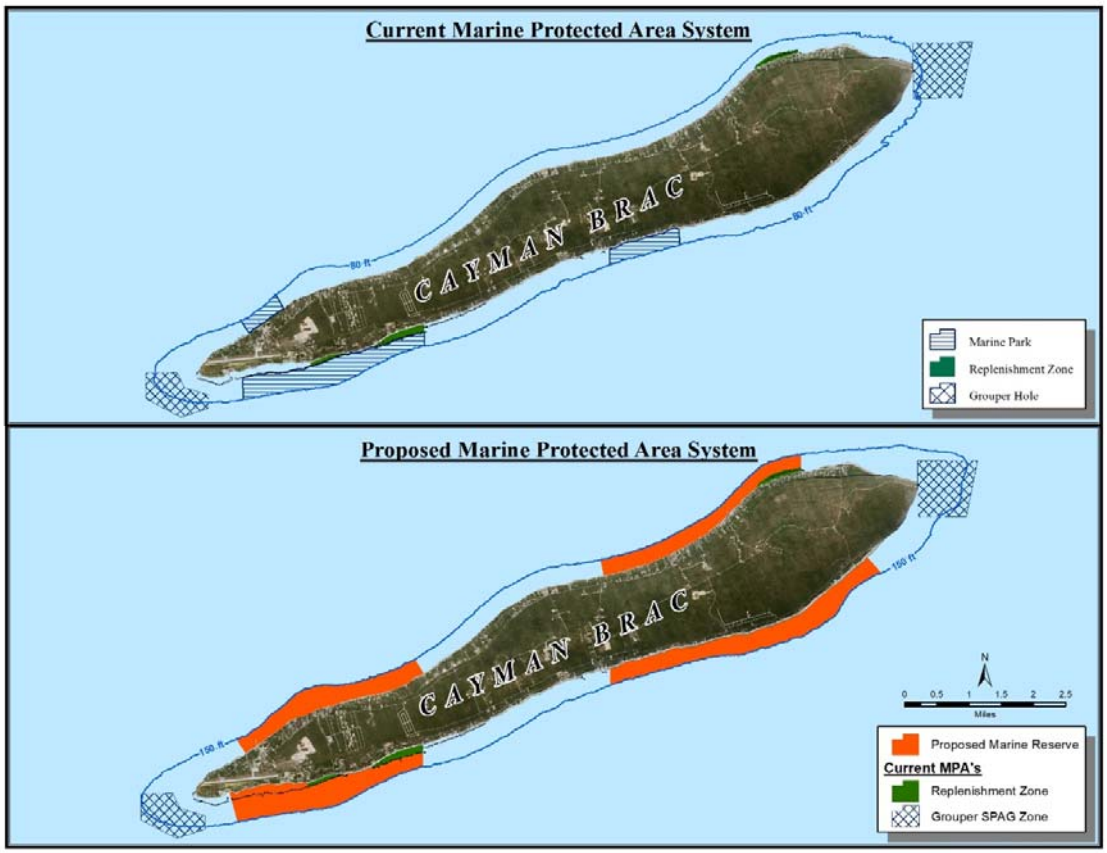


Figure 6.4 Map showing current Marine Protected Area system for Cayman Brac (top) Network of MPAs for Cayman Brac as an alternative to the Darwin Initiative to Enhance an Established Marine Protected Area based on a rigorous scientific assessment of their performance in fostering spillover effect and reserve effect promoting healthy coral reefs and associated benthos including fish assemblages. GPS position: N 190 43.091 W790 48.287

Appendices

Appendix 1.1: Table showing historical tropical cyclone / hurricane frequency and intensity for the 3 Cayman Islands of Grand Cayman, Little Cayman and Cayman Brac from 1852 through to 2018. Kph= Kilometers per hour, CPA= Closest point of approach, TS= tropical storm (63-118 Kph), Category I (119-153 Kph), Category II (154-177 Kph) Category III (178-209 Kph), Category IV (210-250 Kph), Category V (≥251Kph).

Indicates major cyclone.

Date	Storm	Storm category at CPA	CPA Grand Cayman	CPA Little Cayman	CPA Cayman Brac	Max winds at CPA (Kph)
07/10/1852	Storm 5	II	119			167
27/09/1857	Storm 4	II	108			155
09/10/1865	Storm 4	II	0	23	11	167
10/06/1870	Storm 6	I	0	82	66	124
30/09/1873	Storm 5	TS	82	47	44	74
17/10/1876	Storm 5	II	52			155
13/08/1878	Storm 2	TS				93
19/10/1878	Storm 11	I	13			111
04/10/1879	Storm 6	TS	64	56	77	93
13/10/1879	Storm 5	TS	74			74
07/08/1880	Storm 2	I	111			167
27/06/1886	Storm 3	TS		18	32	93
08/07/1887	Storm 5	TS		105	85	64
10/12/1887	Storm 13	I		74	63	138
05/10/1891	Storm 7	TS	45			84
26/08/1895	Storm 2	I	48			158
20/10/1895	Storm 5	I	66			167
26/09/1896	Storm 4	I	40			164
16/10/1897	Storm 5	TS	71			100
08/10/1898	Storm 9	TS	34			93
28/10/1899	Storm 8	TS		34	6	118

7/6/1901	Storm 2	TS		8	19	111
14/09/1901	Storm 7	I		26	15	121
12/8/1903	Storm 2	III	**19**	68	85	195
14/10/1904	Storm 3	TS		31	3	93
17/7/1909	Storm 4	TS	69			100
7/8/1909	Storm 5	TS	24			60
16/09/1909	Storm 8	I	53	39	53	105
9/10/1909	Storm 6	II		97	84	161
9/9/1910	Storm 3	I	55	42	55	130
21/11/1912	Storm 6	TS	45			66
14/08/1915	Storm 2	III	89	**15**	26	188
2/9/1915	Storm 4	I	13			138
16/08/1916	Storm 4	I	35	58	72	179
27/09/1917	Storm 3	III		50	**35**	185
4/8/1918	Storm 1	TS	89			101
18/10/1927	Storm 7	TS	64			66
31/10/1927	Storm 6	TS	19	39	34	74
3/9/1928	Storm 3	TS	77			76
13/09/1931	Storm 8	TS	103			74
11/8/1932	Storm 10	IV	95	**6**	32	212
2/7/1933	Storm 18	I	89	58	85	134
17/07/1933	Storm 15	TS	114			134
17/08/1933	Storm 6	TS	16			74
21/09/1933	Storm 3	I	53	45	56	84
3/10/1933	Storm 2	I	61			137
27/09/1935	Storm 4	III		35	**23**	195
8/12/1938	Storm 2	I	89			148

31/10/1939	Storm 5	I	13	55	58	145
21/08/1944	Storm 11	I	11	71	93	148
15/10/1944	Storm 4	I	52			138
10/12/1945	Storm 11	I	121	11	35	122
20/09/1947	Storm 6	TS		5	24	64
19/09/1948	Storm 7	I	11			143
16/10/1950	King	I			109	148
18/08/1951	CHARLIE	II	93			167
14/10/1951	ITEM	I	32			130
3/10/1953	Storm 10	TS			106	64
23/08/1955	Storm 5	TS	6			64
5/9/1955	HILDA	II	26	8	11	148
23/05/1970	ALMA	TS	26	11	34	64
20/09/1973	GILDA	TS	90	24	5	77
20/09/1975	ELOISE	TS	58	24	21	64
6/8/1980	ALLAN	IV		37	**18**	229
7/5/1981	ARLENE	TS	61	32	18	74
5/11/1981	KATRINA	TS	34	58	74	134
13/09/1988	GILBERT	IV	**39**			241
19/09/2002	ISIDORE	I	84	29	15	111
30/09/2002	LILI	TS		15	6	118
8/12/2004	CHARLEY	I	52	71	93	148
9/12/2004	IVAN	IV	**35**			249
17/08/2008	FAY	TS			118	84
30/08/2008	GUSTAV	I	84	35	53	151
11/7/2008	PALOMA	IV	53	21	**15**	217

Appendix 2.1: Table showing area in square meters and fractions of the various benthos and habitats for each of the 3 Cayman Islands within each islands respective lagoon.

GRAND CAYMAN					
Description	**Total Area (square meters)**	**Fraction of total area**	**Total area protected (square meters)**	**Fraction of total protected area**	**Fraction of habitat protected**
Sediment	8546148.2	0.08	5430429.6	0.09	0.64
Seagrass Beds	63449281.2	0.58	31219111.1	0.54	0.49
Hardbottom	9015557.0	0.08	4801839.3	0.08	0.53
Vegetated Sand	16270252.7	0.15	7085749.8	0.12	0.44
Mud	10006057.6	0.09	7971887.6	0.14	0.80
Lagoonal Coral	581975.4	0.01	278130.2	0.00	0.48
Backreef	1294457.6	0.01	591662.0	0.01	0.46
Beach Rock	43623.5	0.00	8557.9	0.00	0.20
TOTAL	**109207353.2**	**1.00**	**57387367.5**	**1.00**	**0.53**

LITTLE CAYMAN					
Description	**Total Area (square meters)**	**Fraction of total area**	**Total area protected (square meters)**	**Fraction of total protected area**	**Fraction of habitat protected**
Sediment	2188566.4	0.30	1389899.3	0.29	0.64
Seagrass Beds	1830885.5	0.25	1146417.3	0.24	0.63
Hardbottom	1260668.2	0.17	825851.7	0.17	0.66
Vegetated Sand	1361337.3	0.18	1022370.9	0.21	0.75
Lagoonal Coral	102702.4	0.01	93207.8	0.02	0.91
Backreef	623524.7	0.08	380094.1	0.08	0.61
Beach Rock	30621.8	0.00	18473.9	0.00	0.60
TOTAL	**7398306.3**	**1.00**	**4876315.0**	**1.00**	**0.66**

CAYMAN BRAC					
Description	**Total Area (square meters)**	**Fraction of total area**	**Total area protected (square meters)**	**Fraction of total protected area**	**Fraction of habitat protected**
Sediment	56206.8	0.09	2258.2	0.02	0.04
Seagrass Beds	147036.1	0.23	11223.8	0.09	0.08
Hardbottom	244297.7	0.38	73178.0	0.61	0.30
Vegetated Sand	47351.1	0.07	227.4	0.00	0.00
Backreef	141142.0	0.22	33403.5	0.28	0.24
Beach Rock	3310.2	0.01	195.0	0.00	0.06
TOTAL	**639343.8**	**1.00**	**120485.8**	**1.00**	**0.19**

Appendix 2.2: Table showing area in m^2 and fraction of the various benthos and habitats for each of the 3 Cayman Islands outside each islands respective lagoon to deep shelf.

GRAND CAYMAN

TYPE	Total Area (square meters)	Fraction of total area	Total area protected (square meters)	Fraction of total protected area	Fraction of habitat protected
Aggregate Reef	497231.8	0.01	250028.9	0.02	0.50
Aggregated Patch Reef	150161.0	0.00	138146.7	0.01	0.92
Beach Rock	25764.1	0.00	25764.1	0.00	1.00
Colonized Hardbottom	4819589.6	0.10	1963938.8	0.12	0.41
Individual Patch Reef	3380.5	0.00	0.0	0.00	0.00
Reef Crest	2010054.8	0.04	826563.4	0.05	0.41
Spur and Groove	20853941.4	0.42	5655138.9	0.35	0.27
Rubble	3400687.8	0.07	1316791.3	0.08	0.39
Uncolonized Hardbottom	16719012.8	0.34	5554441.1	0.34	0.33
Sand	878564.8	0.02	588535.9	0.04	0.67
TOTAL	**49358388.5**	**1.00**	**16319349.1**	**1.00**	**0.33**

LITTLE CAYMAN

TYPE	Total Area (square meters)	Fraction of total area	Total area protected (square meters)	Fraction of total protected area	Fraction of habitat protected
Aggregate Reef	31747.4	0.00	31747.4	0.00	1.00
Aggregated Patch Reef	39631.6	0.00	39631.6	0.01	1.00
Beach Rock	1162.7	0.00	1162.7	0.00	1.00
Colonized Hardbottom	2475657.7	0.13	1042188.5	0.14	0.42
Reef Crest	1070745.4	0.06	629515.3	0.08	0.59
Rubble	1140159.0	0.06	708960.2	0.09	0.62
Sand	38156.6	0.00	37478.6	0.00	0.98
Spur and Groove	8276403.0	0.44	3282493.8	0.44	0.40
Uncolonized Hardbottom	5646954.3	0.30	1764954.8	0.23	0.31
TOTAL	**18720617.7**	**1.00**	**7538132.8**	**1.00**	**0.40**

CAYMAN BRAC

TYPE	Total Area (square meters)	Fraction of total area	Total area protected (square meters)	Fraction of total protected area	Fraction of habitat protected
Aggregated Patch Reef	278089.4	0.01	216966.0	0.04	0.78
Colonized Hardbottom	1946370.1	0.09	348953.5	0.06	0.18
Individual Patch Reef	244.6	0.00	244.6	0.00	1.00
Reef Crest	159306.1	0.01	78436.1	0.01	0.49
Rubble	222453.3	0.01	102662.9	0.02	0.46
Sand	59851.6	0.00	59850.9	0.01	1.00
Spur and Groove	11899142.2	0.58	3656241.7	0.65	0.31
Uncolonized Hardbottom	6048122.4	0.29	1186851.0	0.21	0.20
TOTAL	**20613579.7**	**1.00**	**5650206.8**	**1.00**	**0.27**

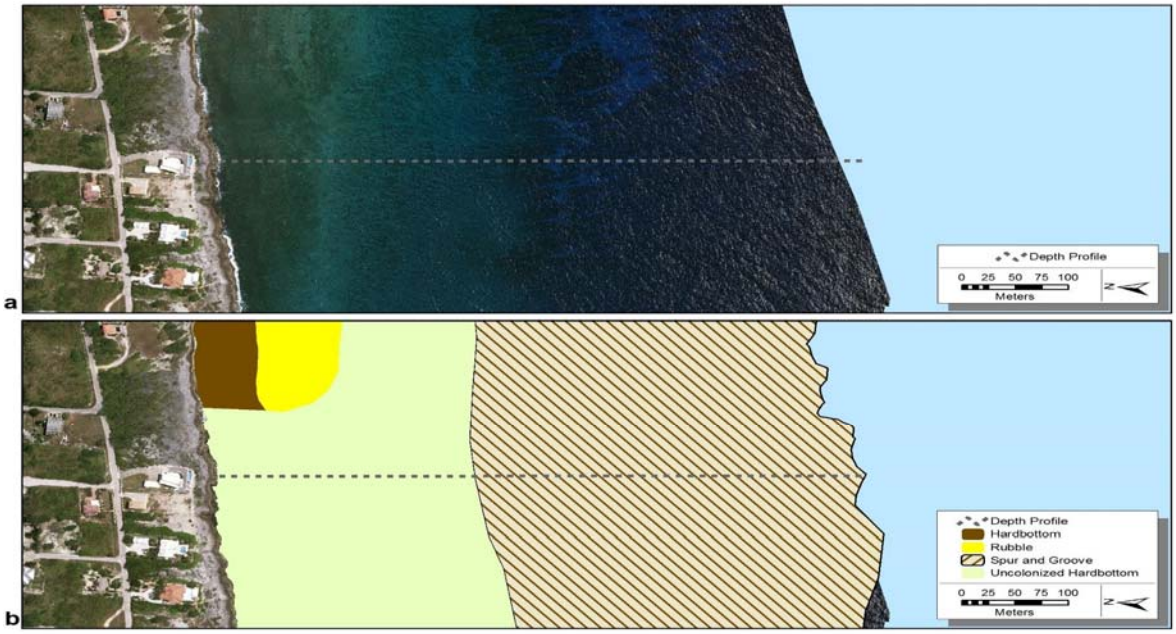
Appendix 2.3: Table showing Lat / Long GPS positions of study sites across the Cayman Islands. GCM=Grand Cayman, LC= Little Cayman, CB= Cayman Brac.

Grand Cayman			Little Cayman			Cayman Brac		
Site	**Lat**	**Long**	**Site**	**Lat**	**Lon**	**Site**	**Lat**	**Long**
GCM1	19.36828	-81.41653	LCS01	19.65658	-80.09781	CB1	19.70019	-79.87428
GCM2	19.34778	-81.39389	LCS02	19.65506	-80.09744	CB2	19.69731	-79.87767
GCM3	19.33213	-81.39167	LCS03	19.65600	-80.09206	CB3	19.68628	-79.85561
GCM4	19.33777	-81.39185	LCS04	19.65731	-80.09189	CB4	19.68139	-79.87603
GCM5	19.27407	-81.39520	LCS05	19.66883	-80.04244	CB5	19.69847	-79.87797
GCM6	19.35578	-81.39467	LCS06	19.66736	-80.04217	CB6	19.67931	-79.87489
GCM7	19.35754	-81.39607	LCS07	19.68075	-80.02331	CB7	19.75819	-79.74094
GCM8	19.33857	-81.39048	LCS08	19.68853	-79.99478	CB8	19.72381	-79.82494
GCM9	19.29133	-81.38967	LCN09	19.70683	-80.01219	CB9	19.70617	-79.80350
GCM10	19.35895	-81.24530	LCN10	19.70803	-80.01339	CB10	19.67986	-79.88911
GCM11	19.29343	-81.09037	LCN11	19.70406	-80.02973	CB11	19.72344	-79.82761
GCM12	19.25972	-81.37670	LCN12	19.70260	-80.04984	CB12	19.69349	-79.82884
GCM13	19.39088	-81.34327	LCN13	19.69072	-80.06942			
GCM14	19.38143	-81.28830	LCN14	19.68886	-80.07081			
GCM15	19.35760	-81.10542	LCN15	19.68492	-80.07800			
GCM16	19.35395	-81.19702	LCN16	19.68378	-80.08297			
GCM17	19.29154	-81.20350						
GCM18	19.26583	-81.30801						
GCM19	19.36397	-81.25381						
GCM20	19.29628	-81.08598						
GCM21	19.26215	-81.37842						
GCM22	19.37942	-81.29390						
GCM23	19.39362	-81.40012						
GCM24	19.35675	-81.10697						
GCM25	19.35383	-81.19901						
GCM26	19.29224	-81.20589						
GCM27	19.26862	-81.31138						

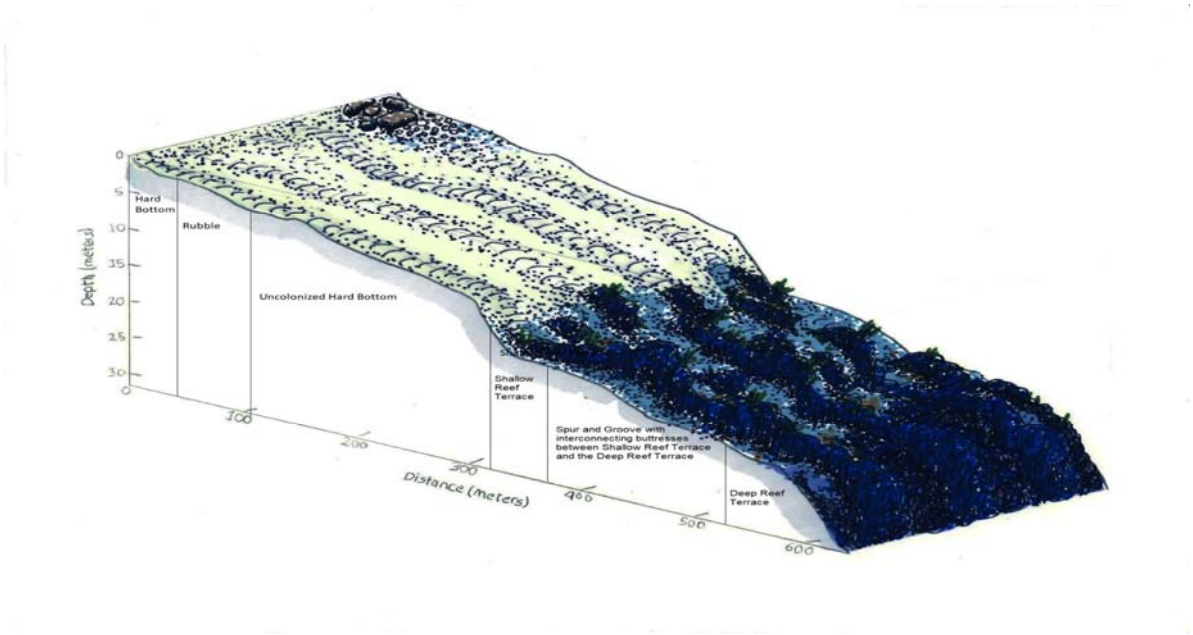
Appendix 2.4: Table showing Lat / Long GPS positions of transect lines of each island where aerial images, marine habitats and the various reef depth profiles from shoreline to deep terrace reef were taken from. GCM=Grand Cayman, LC= Little Cayman, CB= Cayman Brac.

Transect #	Island	coast	Lat_	Long
Transect 1	Grand Cayman Western leeward (typical)	western leeward, fringing reef absent.	19.33815	-81.38170
Transect 2	Grand Cayman South (typical)	north, semi exposed, fringing reef present.	19.26663	-81.37829
Transect 3	Grand Cayman Bodden Town	south, exposed, fringing reef present.	19.26365	-81.27913
Transect 4	Grand Cayman North (typical)	south, exposed, fringing reef absent.	19.34954	-81.19948
Transect 5	Little Cayman South (typical)	south exposed, fringing reef present.	19.70287	-80.01289
Transect 6	Little Cayman South	south exposed, fringing reef absent.	19.69027	-80.06775
Transect 7	Little Cayman North (typical)	north, moderately leeward, fringing reef present.	19.68043	-80.08332
Transect 8	Little Cayman north (Jacksons Point locality)	north moderately leeward, fringing reef absent.	19.65831	-80.08921
Transect 9	Little Cayman north (Bloody Bay locality)	north, moderately leeward, fringing reef present, deep terrace reef absent	19.69578	-79.99720
Transect 10	Cayman Brac south	south, exposed, fringing reef present.	19.70147	-79.86717
Transect 11	Cayman Brac south (typical)	south, exposed, fringing reef absent. Transect	19.68620	-79.87231
Transect 12	Cayman Brac north (typical)	north, moderately leeward, fringing reef absent.	19.70898	-79.80423

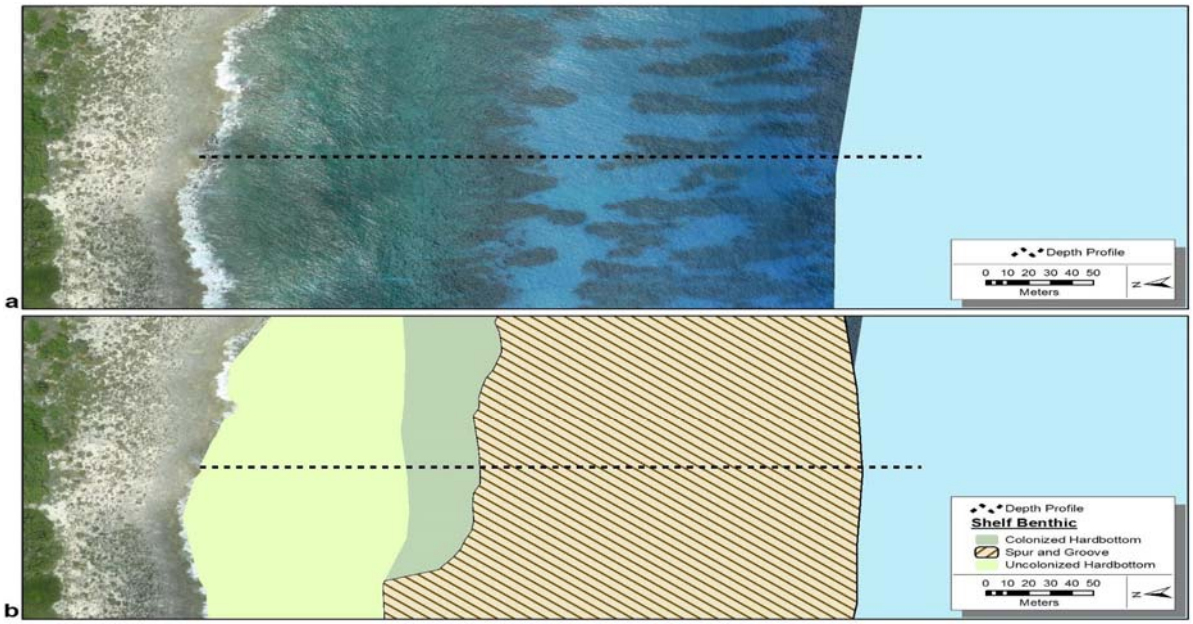
Appendix 2.5: 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the exposed southern aspect of Grand Cayman, Fringing Reef absent



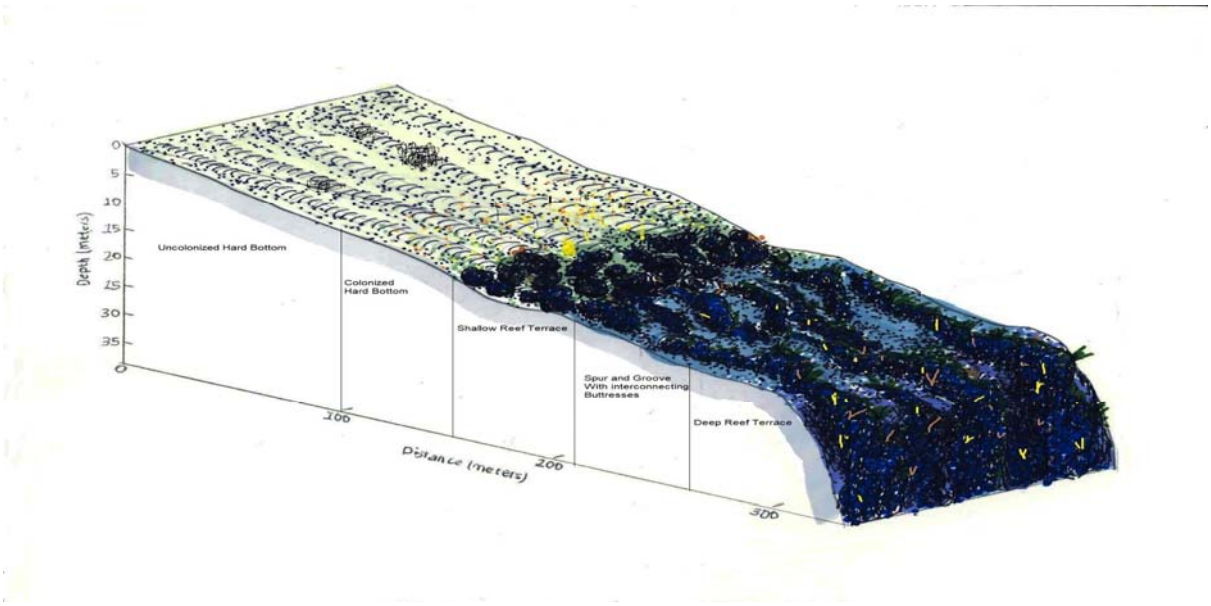
Appendix 2.6. 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Grand Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef absent.



Appendix 2.7: 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the exposed southern windward aspect of Little Cayman, fringing reef absent.



Appendix 2.8: 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Little Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef absent.



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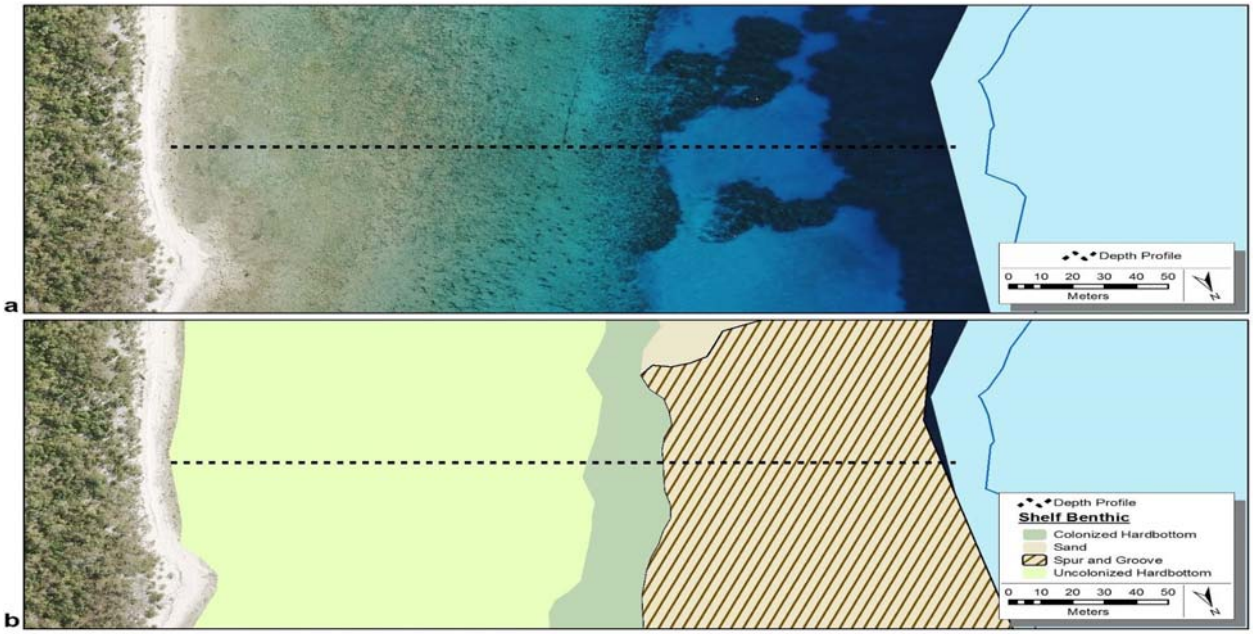
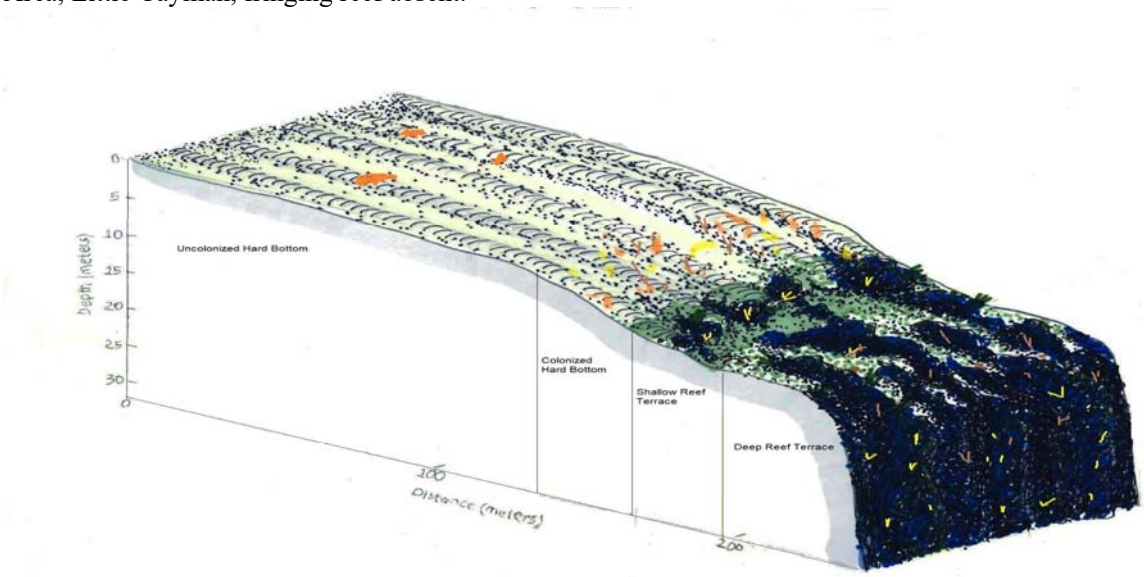
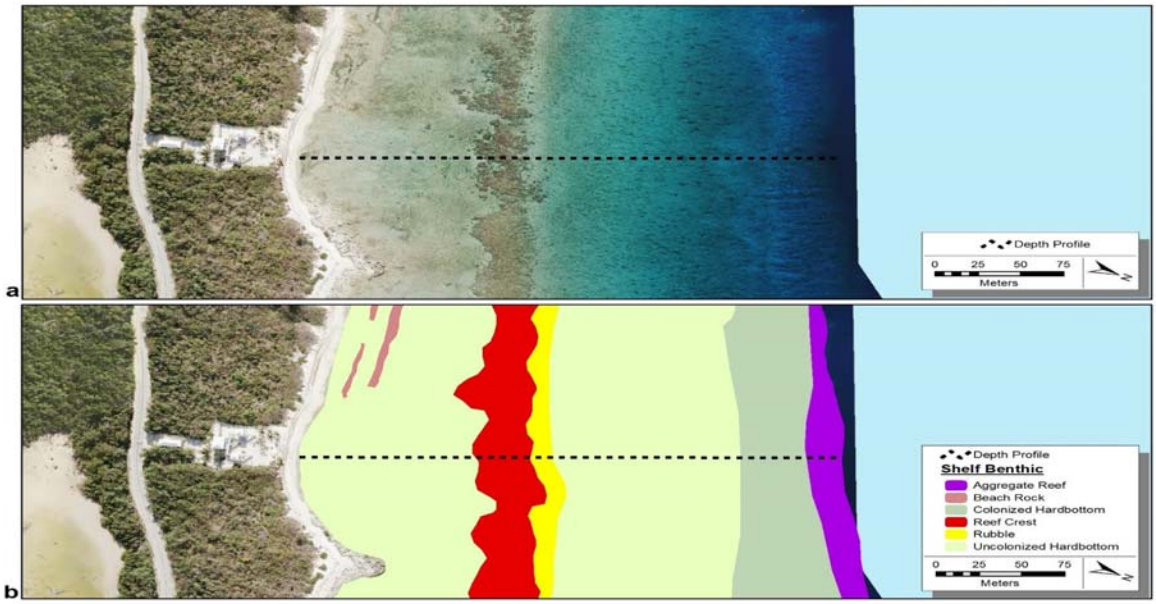
Appendix 2.9 :10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the moderately-leeward northern aspect of Little Cayman within the Bloody Bay / Jackson Point Marine Protected Area, easternmost location, fringing reef absent.



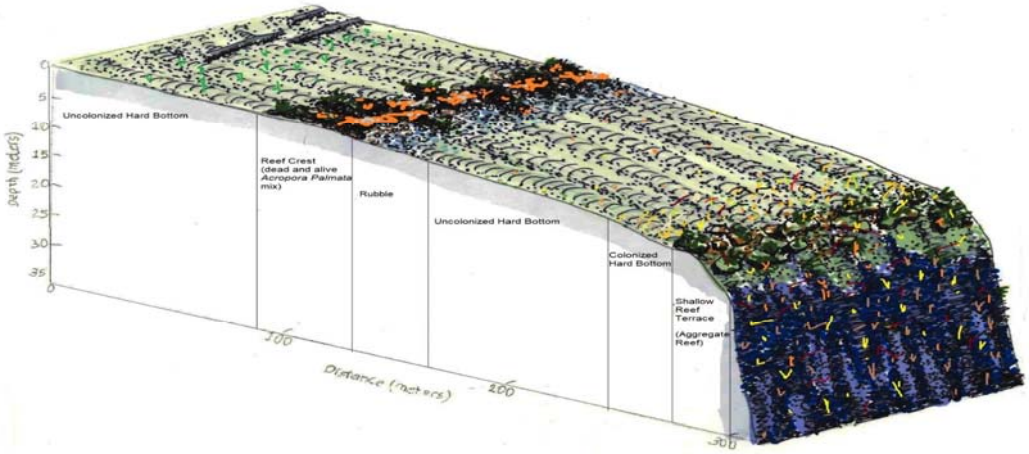
Appendix 2.10: 10 cm resolution, three- dimensional image of depth profile for the moderately-leeward northern coast of Little Cayman depicting habitats from the shoreline to the deep terrace reef. Profile sketch is the easternmost of section within the Bloody Bay / Jackson Point Marine Protected Area, Little Cayman, fringing reef absent.



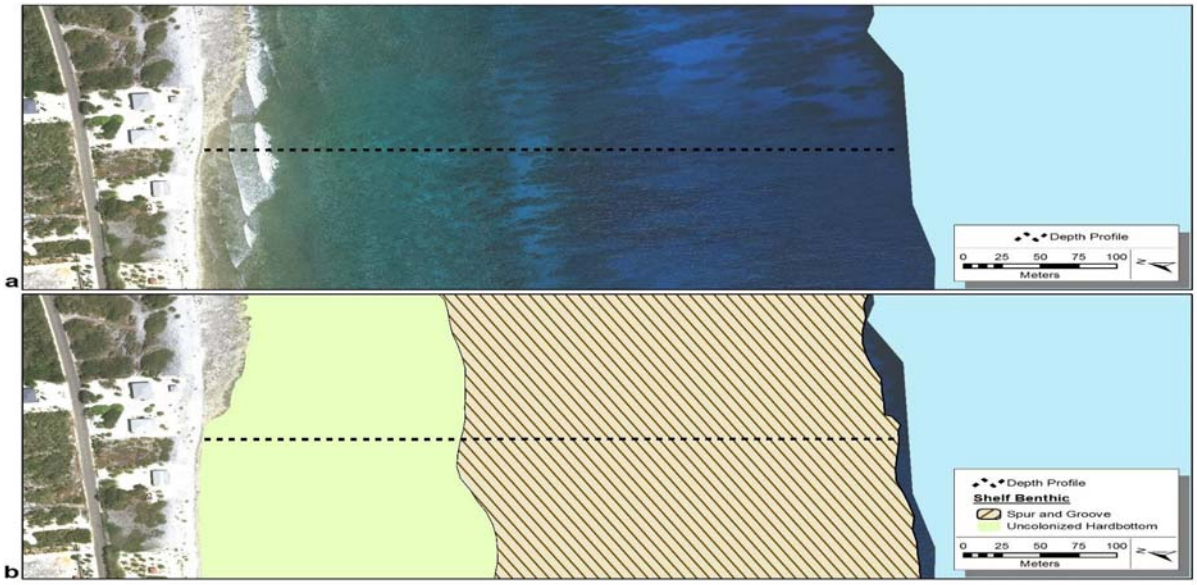
Appendix 2.11: 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the moderately-leeward northern aspect of Little Cayman within the Bloody Bay / Jackson Point Marine Protected Area, western location, fringing / rubble reef present. This area represents the only area within the Cayman Islands where the Shallow Reef Terrace extends out to the Deep Reef Terrace and plummets into the abyss.



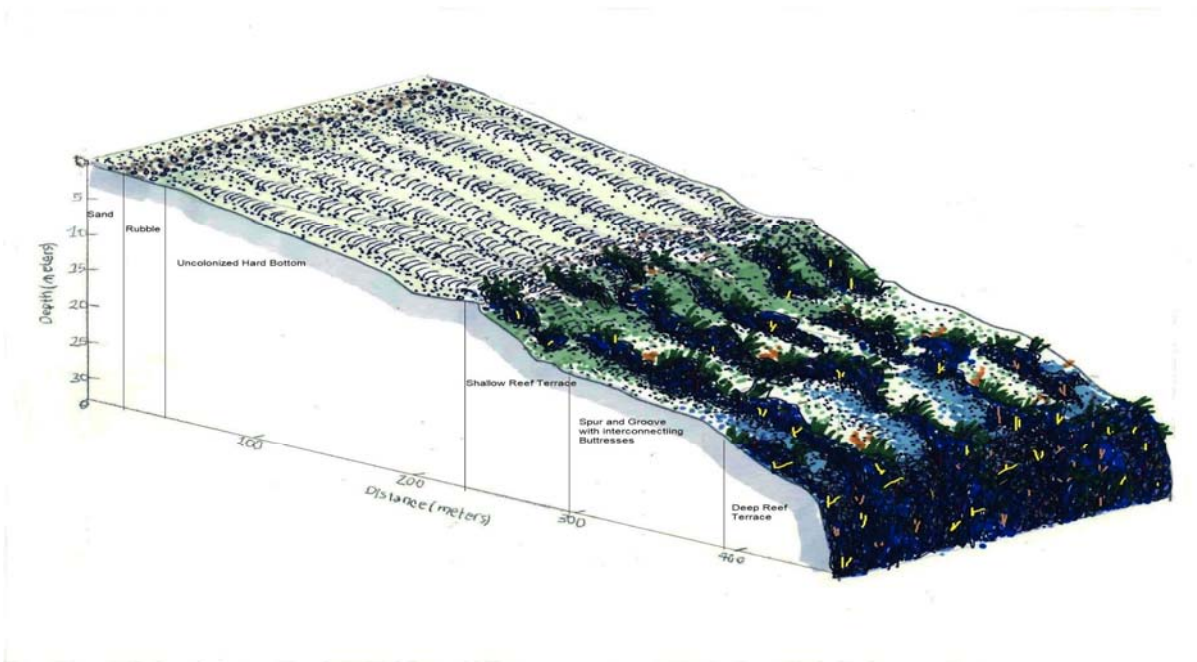
Appendix 2.12: 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Little Cayman depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing/rubble reef present. This area represents the only area within the Cayman Islands where the Shallow Reef Terrace extends out to the Deep Reef Terrace and plummets into the abyss.



Appendix 2.13: 10cm resolution aerial photography (a) and benthic habitat classification map of aerial image (b) for the exposed southern aspect of Cayman Brac. Fringing Reef absent.



Appendix 2.14: 10 cm resolution, three- dimensional image of depth profile for the south exposed coast of Cayman Brac depicting habitats from the shoreline to the deep terrace reef. Distance in meters, fringing reef absent.



Appendix 4.1. List of the fish families and species censused and their respective trophic group. HB: Herbivores, OM: Omnivores, P: Predators, C1: carnivores 1 (inverts feeders) and C2: carnivores 2 (inverts and fish feeders).

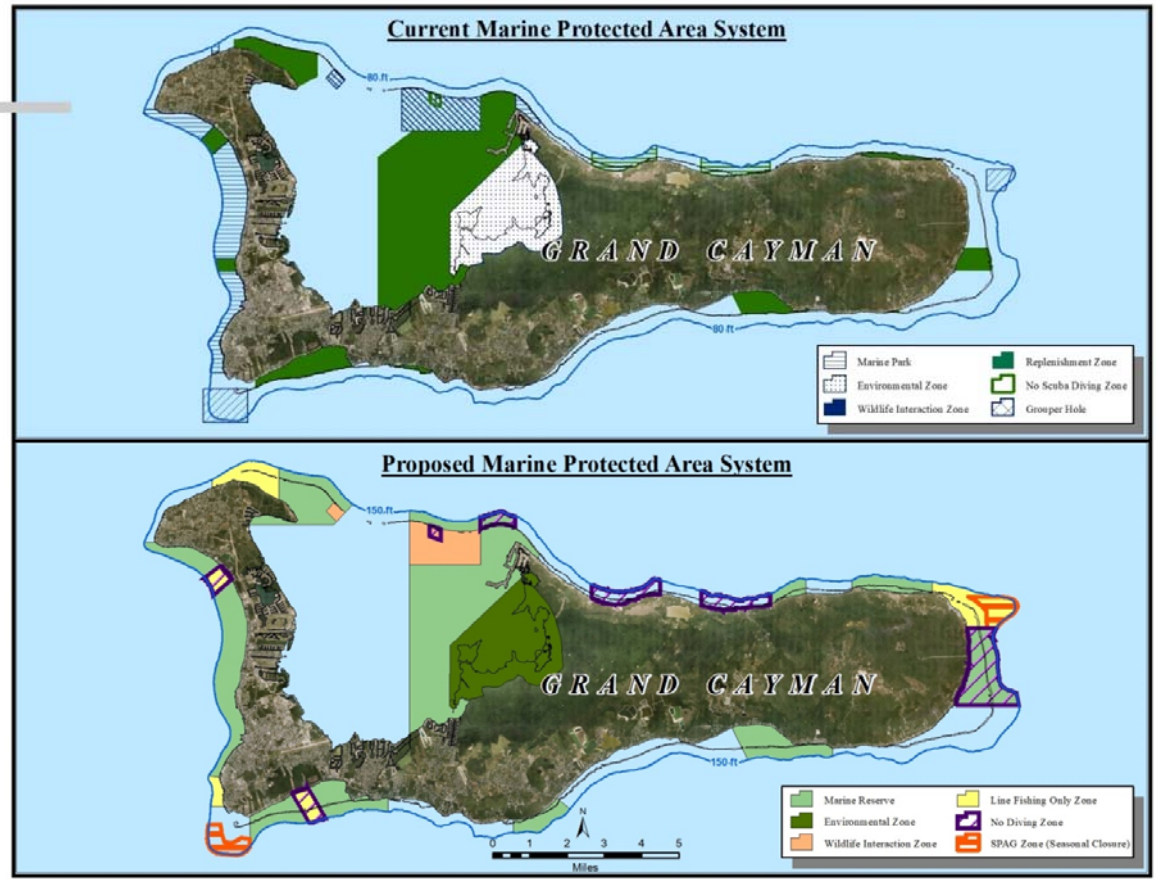
Species	Common name	Trophic group
Serranidae	**Groupers**	
Epinephelus itajara	Goliath Grouper	C1
Epinephelus striatus	Nassau Grouper	C1
Cephalopholis cruentata	Graysby	C1
Epinephelus guttatus	Red Hind	C1
Cephalopholis fulva	Coney	C1
Mycteroperca bonaci	Black Grouper	C1
Mycteroperca tigris	Tiger Grouper	P
Lutjanidae	**Snappers**	
Lutjanus analis	Mutton snapper	C2
Lutjanus jocu	Dog Snapper	C2
Ocyurus chrysurus	Yellowtail Snapper	C2
Lutjanus apodus	Schoolmaster	C2
Labridae	**Wrasse**	
Lachnolaimus maximus	Hogfish	C1
Bodianus rufus	Spanish Hogfish	C1
Halichoeres radiatus	Puddingwife	C1
Thalassoma bifasciatum	Bluehead	C1
Scaridae	**Parrotfish**	
Sparisoma viride	Stoplight Parrotfish	HB
Scarus vetula	Queen Parrotfish	HB
Scarus taeniopterus	Princess Parrotfish	HB
Scarus iserti	Striped parrotfish	HB
Sparisoma aurofrenatum	Redband parrotfish	HB
Acanthuridae	**Surgeonfish**	
Acanthurus coeruleus	Blue tang	HB
Acanthurus chirurgus	Doctorfish	HB
kyphosidae	**Sea Chubs**	
Kyphosus sectatrix	Bermuda Chub	HB
Sphyraenidae	**Barracuda**	
Sphyraena barracuda	Great Barracuda	P
Carangidae	**Jacks**	
Caranx ruber	Bar Jack	P
Caranx latus	Horse-eye Jack	P
Haemulidae	**Grunts**	

Haemulon flavolineatum	French Grunt	C1
Haemulon sciurus	Bluestriped Grunt	C1
Haemulon plumierii	White Grunt	C1
Haemulon macrostomum	Spanish Grunt	C1
Anisotremus surinamensis	Black Margate	
Sparidae	**Porgies / Sparidae**	C1
Mullidae	**Goatfish / Mullidae**	C1
Chaetodontidae	**Butterflyfishes**	
Chaetodon striatus	Banded Butterflyfish	C1
Chaetodon capistratus	Foureye Butterflyfish	C1
Chaetodon ocellatus	Spotfin Butterflyfish	C1
Prognathodes aculeatus	Longsnout Butterflyfish	C1
Pomacanthidae	**Angelfishes**	
Holacanthus ciliaris	Queen Angelfish	C1
Holacanthus tricolor	Rock Beauty	C1
Pomacanthus paru	French Angelfish	C1
Pomacanthus arcuatus	Gray Angelfish	C1
Balistidae	**Triggerfishes**	
Balistes vetula	Queen Triggerfish	C1
Melichthys niger	Black Durgon	OM
Cantherhines macrocerus	Whitespotten Filefish	C1
Aluterus scriptus	Scrawed filefish	OM
Aulostomus maculatus	Trumpetfish	C2
Muraenidae	**Morays**	
Gymnothorax funebris	Green Moray	P
Gymnothorax moringa	Spotted Moray	P
Mullidae sp.	Goatfish	C1

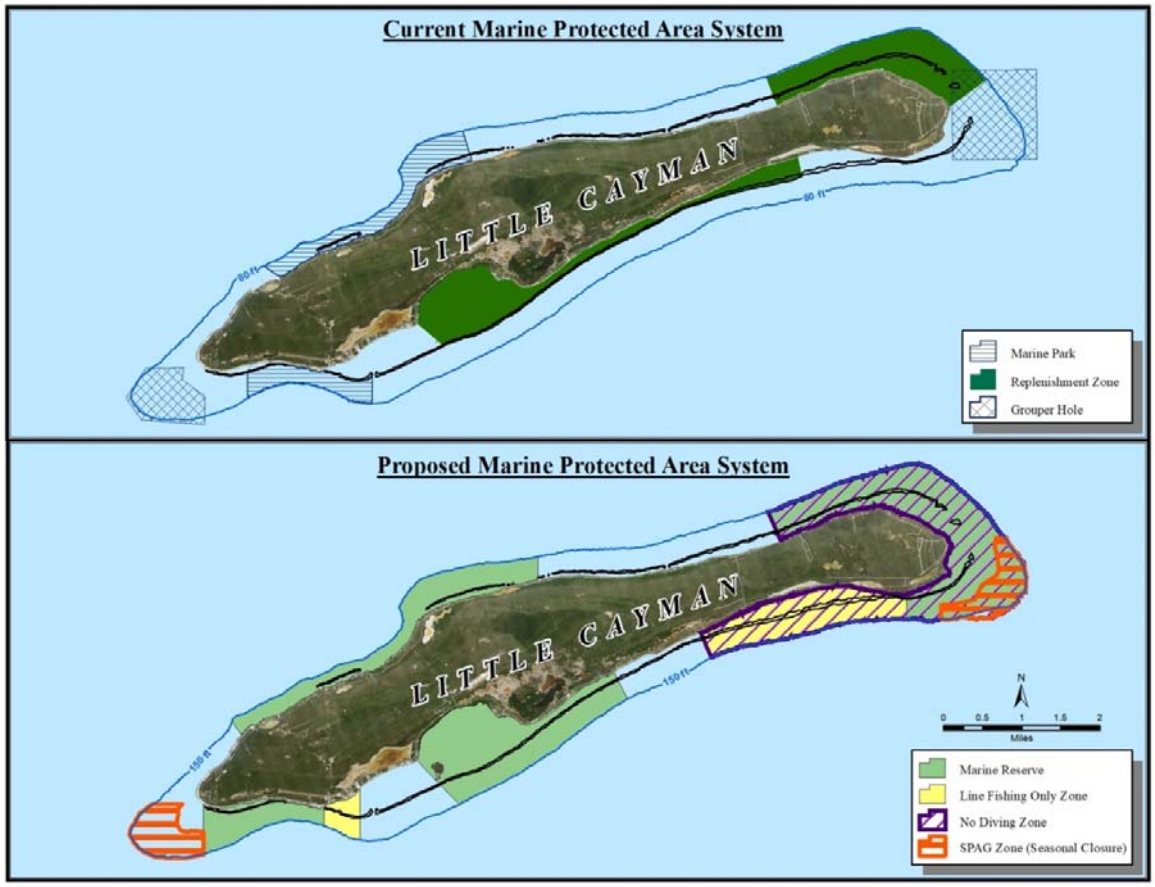
Appendix 4.2 Total fish censused for years of study; 2009, 2010, 2011, 2012 across islands. CB= Cayman Brac (n=12), GCM= Grand Cayman (n=27), LC = Little Cayman (n=16).

Year	Island	Fish counts	Total
2009	GCM	5,272	
2009	LC	3,207	
2009	CB	2,099	
			10,578
2010	GCM	8,815	
2010	LC	5,774	
2010	CB	2,088	
			16,677
2011	GCM	9,494	
2011	LC	4,768	
2011	CB	2,891	
			17,153
2012	GCM	6,192	
2012	LC	3,643	
2012	CB	2,184	
			12,019

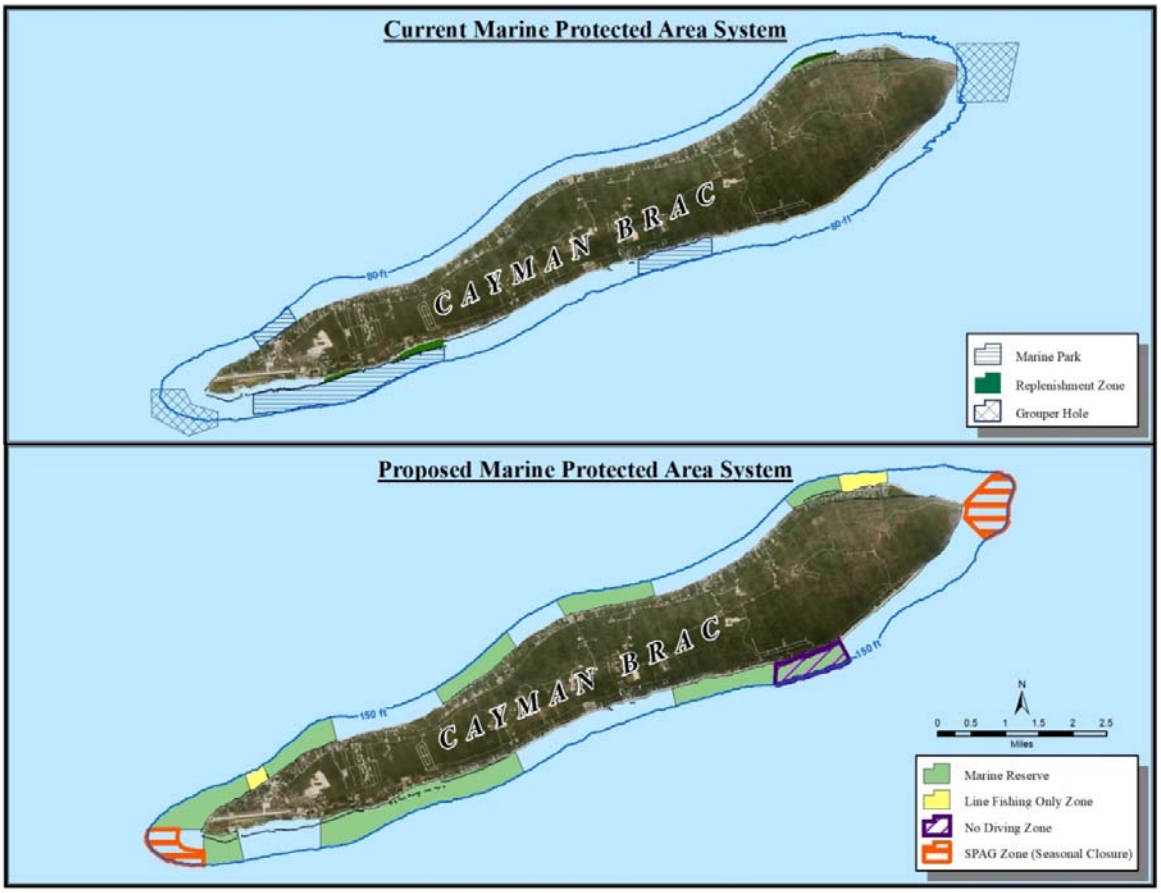
Appendix 6.1 Map showing current Marine Protected Area system for Grand Cayman (top) and the new The Darwin Initiative to Enhance an Established Marine Protected Area System map for the island of Grand Cayman based on survey data and protected area planning tools, increasing No-take protection from 15.73% to 46.63%. Grouper Hole= Known fish aggregation site. SPAG= Fish spawning aggregation site.



Appendix 6.2 Map showing current Marine Protected Area system for Little Cayman (top) and the new The Darwin Initiative to Enhance an Established Marine Protected Area System map for the island of Grand Cayman based on survey data and protected area planning tools, increasing No-take protection from 10.43% to 64.67%. Grouper Hole= Known fish aggregation site. SPAG= Fish spawning aggregation site.



Appendix 6.3 Map showing current Marine Protected Area system for Cayman Brac (top) and the new the new The Darwin Initiative to Enhance an Established Marine Protected Area System map for the island of Grand Cayman based on survey data and protected area planning tools, increasing No-take protection from 15.31% to 41.23%. Grouper Hole= Known fish aggregation site. SPAG= Fish spawning aggregation site.



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1) **An Evaluation of Grand Cayman MPA Performance: A Comparative Study of Coral Reef Fish Communities.**

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2) **Measuring the Performance of Marine Protected Areas: The Case of Little Cayman and Cayman Brac, Cayman Islands.**

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