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Factors in Long-Term Algal Composition of Cayman Reefs: Determining Effects of Natural Disturbance and Grazer Pressures

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by
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Abstract. Current research shows a worldwide shift in the population dynamics of reefs attributed to increasing human disturbance. With increasing nutrient additions, competitive populations of turf and macroalgae bloom and dominate coral reefs leading to decreased health of the reef as a whole. Unfortunately, few studies have been done showing the long-term changes in algae composition on reefs. In order to find the significant factors in the long-term composition of algae on reefs, algae and fish abundance data were collected through the Lawrence University Marine Program and analyzed for this study. Algae were split into three functional groups: encrusting, turf and macroalgae, and relative abundance for each was compared for significance against fish and level of natural disturbance at a site. This study found that the level of natural disturbance was likely an important factor in long-term algal abundance with the highly protected sites hosting high levels of macroalgae and less protected sites hosting high levels of turf algae. Two herbivores, blue tangs (*Acanthurus coeruleus*) and stoplight parrotfish (*Sparisoma viride*) were also found to significantly control turf algae. Future studies on fishing pressures in the region could more fully assess the long-term effects of herbivores on reef algae composition.

Introduction

The Caribbean coral reefs, like the many other reefs on Earth, are mysterious environments capable of hosting a vast diversity of life. The communities here are highly interconnected, and competition for space and resources is a constant battle for the species residing there. Much of what we currently know about reefs came with the advent of SCUBA which provided the general public and researchers with better access to the underwater world. As SCUBA is a historically recent development reef ecology is still a budding field with much left to learn. Aside from internal reef interactions, we know that reefs interact with the ocean on a larger scale, providing shelter and food for oceanic fish species. Understanding this broader interaction is crucial to understanding the status of fish stocks and should be important to anyone who consumes seafood and wishes to continue doing so. With anthropogenic disturbances like ocean acidification, nutrient loading, ocean warming and overfishing becoming increasingly prevalent issues, changes in the historical species dynamics of fish and algae are occurring worldwide. To understand the alterations, it is imperative to have a long-term data set to assess how a reef responds over time. This study analyzes fish and algae abundance data collected biyearly since 1998 on Grand Cayman, BWI to identify the factors behind changes in species composition of fish and algae. In doing so it is our hope to predict the factors influencing the changes in population dynamics the world sees today.

Reef History

A. Long-Term Reef History

1. The Reef Builders

The process of building reefs by deposition of calcium carbonate is a long and slow process and has been carried out by a number of unique reef communities over time. The first reef builders were not corals but rather algal stromatolites, a calcifying algae dating back roughly 2.5 billion years (Newell, 1972). The earliest animal reef builders were archaeocyathids, a group of cup-like sponges which appeared in the early Cambrian period, roughly 600 million years ago (Ma) during the same explosion of life that produced amphibians, reptiles and bony fish (Newell, 1972). These sponges died out after 70 million years, marking the first community collapse. Soon after, a successor community rose up in the mid-Ordovician period. This community included coralline algae, communal bryozoans, stromatoporoid sponges and the first true corals-Rugosa and Tabulata (Newell, 1972). This group lasted until the end of the Devonian period about 350 Ma when the sponges and corals died out in the second community collapse. Roughly 13 million years later, a third community containing chambered sponges, green algae, foraminifera, brachiopods, and crinoids developed (Newell, 1972). This reef-building community thrived until the third collapse at the end of the Paleozoic era, 250 Ma. The following succession occurred throughout the Mesozoic era and saw the appearance of modern scleractinian and hydrozoan corals as well as a new group of mollusks, the Rudists, which died off in the fourth collapse 65 Ma. The draining of shallow seas in the Cenozoic era by glacial formation is thought to be the reason behind the absence of a fifth successor community (Newell, 1972). Today, scleractinian and hydrozoan corals, coralline and green algae, and foraminifera are the major producers of reefs around the world.

2. *Cayman Island History*

The Cayman Islands, located just south of Cuba and northwest of Jamaica, are a series of three islands: Grand Cayman, Little Cayman and Cayman Brac. These islands were uplifted above sea level due to fault-blocking by a transform fault between the North American and Caribbean tectonic plates in the Miocene epoch (~23 to 5.3 Ma) The islands were still connected to Cuba at that time (Roberts, 1977; Jones, 1988). Further fault-blocking in the Pliocene (5.3 to 2.6Ma) and Pleistocene (2.6 Ma to 11,700 years ago) epochs separated the islands from Cuba as well as each other while simultaneously forming the Cayman Ridge. This sub-marine ridge extends from the Sierra Maestra mountain range in southeast Cuba to the Gulf of Honduras. Two deep cuts border the ridge: the Yucatan Basin borders the north with depths exceeding 4,500 meters, and the Cayman Trench borders the south with depths exceeding 7,600 meters.

During this time of uplifting and movement, coral reefs were growing on and shaping these islands. Much of the base "bluff" layer of the Grand Cayman is composed of limestone derived from coral, molluscan and foraminiferal skeletal remains dating back to the Oligocene and Miocene epochs (Roberts 1977). Above this sits a layer known as Pedro's Castle, which formed in the Pliocene epoch during a highstand when water broke down the irregular base limestone and reformed it in a new deposit (Jones et al., 1994). On top of this rests the "Ironshore" formation composed completely of a black, jagged, tough limestone formed in the Pleistocene epoch. Fifteen to nineteen thousand years ago, the last glaciation event caused sea level to fall more than 130 meters. This and the erosion by the subsequent Holocene transgression formed several new horizons throughout the Caribbean (Milliman, 1973). Though the islands above sea level continue to weather away, the deposition of new material by today's reef communities continues.

B. Reef Characteristics

1. Reef Types

There are three different morphological categories of coral reef: fringing reefs, barrier reefs and atolls. Fringing reefs are continuous with the shoreline, leading directly onto the reef flat or in some cases may include a shallow channel or lagoon between a reef flat and shoreline (Pichon, 1995). Barrier reefs are situated a distance from the shoreline with a lagoon separating the two. Fringing reefs are occasionally found on shores or in lagoons as "midshelf reefs" in areas with a barrier reef farther out to sea (Pichon, 1995). An atoll is an offshore reef formation that surrounds a central lagoon and lacks any land not created by the reef. For volcanic islands, each of these categories represents a stage in the island's life cycle. A newly formed island will first gain a fringing reef around its edge. As the island recedes from years of erosion or subsidence, the old fringing reef stays in its original position and becomes a barrier reef (Pichon, 1995). Once the island drops below sea level, a shallow lagoon surrounded by an atoll is all that remains.

2. Reef Zones

Caribbean reefs tend to follow similar patterns in terms of depth, morphology and dominant species with regard to distance from shore. Goreau (1959), after observing Jamaican fringing reefs, was the first to divide sections of reef into identifiable zones (Figure 1). These zones follow a consistent sequential pattern with increasing distance to shore and all the world's reefs adhere to this model to some extent. Variance occurs on barrier reefs, which for instance have larger lagoon zones than fringing reefs, and the lagoon zones of atolls completely replace the inshore zone found on fringing reefs. Overall, these zones and their dominant species are

highly variable due to external factors such as land composition, protection from wind or waves, nutrient availability etc., but reefs still tend to follow Goreau's reef pattern.
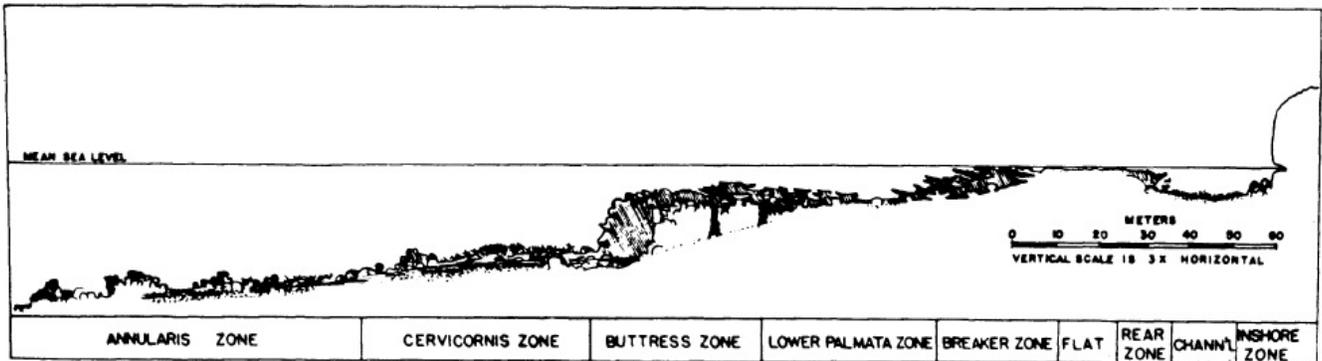

Figure 1. *Traditional Goreau pattern of zonation from Goreau (1959).*

Inshore Zone

The inshore zone is found where the land meets the sea and is highly variable based on whether the shore is alluvial, rock, sand, mangrove, etc. In general, this area is home to a large variety of scleractinian corals, the most prevalent being *Acropora palmata, Montastraea annularis, Montastraea cavernosa, Diploria strigosa, Porites astreoides, Porites porites, Siderastrea siderea* and *Manicina areolata* (Goreau, 1959). Hardier coral species that can endure living on wave-swept rocks can better withstand shallower areas in this zone, and so they exist in greater numbers. In some cases, algae will grow abundantly to form an algal ridge, though this can depend on how protected the shoreline is from waves. In other cases, greater wave action intensity will select for *Millepora* as it is better adapted to wave stress (Glynn, 1973).

Channel/Lagoon Zone

The channel/lagoon zone is located between the shore and the reef flat. It ranges between 10 to 300 meters in width and is usually 2 to 15 meters deep (Goreau, 1959). Lagoon benthic composition is highly dependent upon shore composition. Volcanic rock or ancient coral shores, for instance, tend to produce a sandy bottom whereas a soil-fringed coastline will result in a muddy bottom. If the bottom is sandy, gorgonians, mollusks and echinoderms occur in abundance. Corals in sandy lagoons are rare, but in deeper areas, some corals like *M. annularis* or *P. porites* will form isolated heads or small clusters. Turtle grass (*Thalassia testudinum*), a marine plant, is common in lagoons and is often found growing in large patches. Corals cope poorly with mud, and as a result, areas with large amounts of sediment host very few corals (Goreau and Goreau, 1973).

Rear Zone

The rear zone is identified as a sharp rise from the sandy lagoon zone up to the reef flat. It receives protection from the offshore waves and contains a wide variety of coral. The prominent corals found in this zone are *M. annularis, M. cavernosa, D. strigosa, S. sidearea,* and *P. astreoides* (Goreau, 1959). Branching species such as *A. palmata, A. cervicornis, A. prolifera, P. porites and P. furcata* are very common in this zone but do not make up much of the total biomass.

Reef Flat/Zoanthus Zone

The reef flat is the shallowest zone and is marked by high turbulence and sunlight (Goreau and Goreau, 1973) as well as exposure to air during low tide (Glynn, 1973). In most

cases, the dead coral framework plays host to large populations of calcareous algae.   The few corals that survive here are impoverished and survive mostly in interstitial cracks. On occasion, these corals are replaced by large colonial aggregates of zoanthids belonging to the genera *Zoanthus* and *Palythoa* (Goreau and Goreau, 1973).

Breaker/Upper Palmata Zone

The breaker zone is the section of reef exposed to the greatest wave pressure. As a result, this zone is completely dominated by species which can bear the brunt of the waves, most notably *A. palmata* and *Millepora complanata* (Goreau and Goreau, 1973; Goreau 1959). Dead coral and other rubble break away from this zone during storms or other periods of high wave activity and fall into the lower palmata zone.

Lower Palmata Zone

The lower palmata zone descends from the upper palmata zone and is characterized by a lower abundance of coral (Goreau and Goreau, 1973). The coral community found here consists mostly of *A. palmata* and other corals fragmented and displaced from the upper palmata zone. The majority of rubble and open space is encrusted with crustose algae but gorgonian sea fans are a common sight, with their fans angled to move with the current.

Buttress Zone

The buttress zone contains the greatest amount of diversity of any zone (Goreau and Goreau, 1973). This diversity is primarily due to this zone's unique buttress structures. The buttresses (spurs) are roughly 30 meters long and 3 to 12 meters high, intersected at regular

intervals by deep trenches filled with sand and coral debris. These trenches act as chutes for debris moving to deeper water under the pressure of gravity and wave-induced currents (Goreau and Goreau, 1973). Despite this natural movement, the buttress formations are less due to erosional forces than to differences in coral growth suppression. Trenches are seen as "no growth" areas because the movement of sediments prevents coral construction, whereas buttress tops grow unhindered. This unhindered growth causes the buttresses to grow to be tall with steep sides. In some cases, two buttresses can completely overtop a trench and fuse, forming a cavern-like swim-through (Goreau and Goreau, 1973). The high coral diversity of this zone comes from the resulting wide gradient of microhabitats found on the buttress structure, and many corals have adapted to slough off excess sediment buildup.

The Seaward Slope (Annularis and Cervicornis Zone)

The seaward slope is the last zone before the "final drop off" from the offshore shelf into deep water. It is found just beyond the buttress zone descending from 20 meters down to between 55 and 70 meters in depth (Goreau and Goreau, 1973). The first section of this is the fore reef terrace, which has a similar structure to the buttress zone but has a distinct reduction in coralline algae and deeper "V"-like trenches. Coral here grows directly over lower corals in a plate-like formation to maximize surface area exposed to the sun while shading out competitors. The edge of the terrace is rimmed by a sill, which dams the sediments above. This sill terminates in a steep escarpment, which drops to the fore reef slope below (Goreau and Goreau, 1973). The growth of corals on the escarpment is slowed due to low light levels at such great depth, and as a result, most corals are found in plate-like formations growing out into the open ocean. Notches, believed to be ancient shoreline, protrude into the open ocean and form overhangs, which harbor

their own unique communities (Goreau and Goreau, 1973). The escarpment ends at the fore reef slope, which gradually descends deeper into the ocean. The key feature of this slope is the deep accumulation of sediment swept down from the upper portions of the reef. Coral growth in this area is rare, and that which does occur is restricted to scattered rocks and rubble cleaved from upper portions of the reef. The fore reef slope ends in a shift from the gradual sandy slope to an environment that falls at an angle of 80 degrees to roughly vertical. This area is dubbed the deep fore reef or more commonly referred to as "the wall". Corals here are unusually rich and diverse but grow at an exceedingly slow pace in plate-like formations and are highly fragile.

Reef Ecology

A. Reef Benthic Composition

When thinking about a coral reef, one might expect it to be composed primarily of coral, but in reality, it hosts a wide variety of taxa including gorgonians, sponges, zoanthids, mat tunicates and most importantly, algae. Coral and algae are by far the chief contributors to reef cover, and both constantly struggle among themselves and each other for space and resources. This struggle led to the evolution of multiple strategies to outcompete rival organisms.

1. Determining Abiotic Factors

Common abiotic determining factors for coral and algae growth are light, sedimentation, disturbance and nutrient availability. The majority of corals contain symbiotic zooxanthellae as a source of energy, giving them a competitive advantage over other sessile creatures (Sheppard et al., 2009). Zooxanthellae are single-celled dinoflagellates located in the endodermic tissue of coral and, like other algae, on the reef require sunlight to produce energy. Since sunlight is

necessary to the survival of both corals and algae, species have adapted multiple strategies to obtain it. These strategies primarily come down to shading out or growing over competitors and finding ways to prevent being shaded out or grown over, by physically harming competitors, employing allelopathy, or preventing spores or larval stages from settling nearby (Chadwick and Morrow, 2011; Kim, 2002; Paine, 1980; Huston, 1985).

Sedimentation also poses a problem to both corals and algae by directly blocking out sunlight. In areas with high sedimentation, the species that survive are those that can endure the reduced light or can eliminate sediment build up. To this end, all corals are able to produce mucus to alleviate sediment. Coral can only deal with a finite level of sedimentation, however, until energy lost to mucus production outweighs total energy produced and this tipping point varies by species (Sheppard et al., 2009).

Disturbance comes in the form of waves, tropical storms (Connell, 1997) or anthropogenic destruction (Berkshire, 1997) and results in the removal of biomass leading to empty reef space. This selects for species that are better able to withstand such pressures and those that can quickly recuperate losses (Airoldi, 2000). Reefs with greater disturbance from wave and storm action are dubbed high-energy sites, whereas more protected areas are dubbed low-energy sites (Milliman, 1973).

Nutrient availability, unlike the above factors, is selective in favor of either corals or algae (Chadwick and Morrow, 2011). This stems from seawater, which is traditionally low in nitrogen (Howarth et al., 1988) and the fact that coral reefs do not receive substantial nitrogen inputs from land or sea. Corals thrive in these low-nutrient conditions because they recycle nutrients with their symbiotic zooxanthellae and take up nitrogen whenever possible (Sheppard et al., 2009) including through ingestion of zooplankton (Porter, 1974), a process which algae

cannot accomplish. When nitrogen levels are high, fast-growing nitrogen-inefficient algae are able to outcompete corals and dominate the reef because they are no longer limited by nitrogen (Vermeij et al., 2010). This process has major consequences for ecosystems where nutrients have been added from anthropogenic sources (Barrot et al. 2012b).

2. Algae

Globally, about 2000 to 3000 species of macroalgae reside on reefs with all the major groups represented: Phaeophyta (brown algae), Chlorophyta (green algae), and Rhodophyta (red algae) (Sheppard et al., 2009). Due to evolutionary convergence, algae of multiple taxonomically-distinct species can be categorized into specific functional groups. Members of these groups tend to "behave" similarly due to mass-specific productivity, canopy height, and tallus longevity (Steneck and Dethier, 1994). Grouping algae this way is useful for examining the reef on an ecological level, as herbivorous fish will have similar impacts on algae within functional groups regardless of taxonomic affinities (Steneck and Dethier, 1994), making it an appropriate technique for this study. This is explained in greater detail in the next section. In this study, three functional groups were identified: encrusting, turf and fleshy macroalgae (Figure 2). Encrusting algae, commonly called crustose coralline algae due to its resemblance to coral and ability to form calcareous deposits, is a primary reef builder (Sheppard et al., 2009). Encrusting algae has a range of colors from green to pink and lies flat against the substrate, making it easy to differentiate from other forms. Common genera of encrusting algae in the Caribbean include *Porolithon*, *Neogoniolithon*, and *Paragoniolithon* (Steneck, 1983). Alternitively, turf algae grows up out of the substrate in thin diverse filaments. Common Cayman genera include *Polysiphonia* and *Sphacelaria* (Steneck, 1983). Fleshy macroalgae, hereafter referred to simply

as "macroalgae," has larger, more rigid and more complex forms than turf algae. Common genera for this group include *Laurencia, Jania* and *Lobophora* (Steneck, 1983). For our study, *Dictyota* was also included in turf algae though it is usually grouped with macroalgae (Steneck, 1983).

Figure 2. *Functional groups of algae studied- encrusting (left), turf (middle), and macro (right). Pictures from www.reeffrontiers.com, footage.shutterstock.com, and www.flickr.com*

Within these three functional groups there are a number of competitive interspecific interactions as each species fights for space in the sun. Encrusting algae has higher growth rates than the other two and is usually the first to colonize empty spaces (Airoldi, 2000). Since encrusting algae lies flat against the surface of the reef, it is subject to overgrowth and shading by taller turf and macroalgae. Encrusting algae prevent this by slowing the growth rates of other algae. Ecologists debate how this is accomplished but leading hypotheses include thallus shedding (Keats et al., 1997), providing habitat for herbivorous fish that consume other algae (Morse et al., 1979 as cited in Paine, 1980), release of antifouling compounds (Vermeij et al., 2011), or the physical smoothness of the encrusting algae surface preventing root establishment by turf algae (Airoldi, 2000). Although slowed, turf and macroalgae eventually colonize over encrusting algae, which has traditionally been thought to perish (Paine, 1980) though a more

recent study found that it survives in many cases unharmed (Airoldi, 2000). Although both will colonize over encrusting algae and empty space, turf algae grows faster (Littler et al., 2006), colonizes space faster (Airoldi, 1998), and is resistant to wave pressure (Cheroske et al., 2000 as cited in Vermeij et al., 2010). This allows turf algae to ultimately respond to disturbance faster than macroalgae, giving it a distinct advantage (Airoldi, 1998; Vermeij et al., 2010). The taller, slow-growing macroalgae, on the other hand, can outcompete turf algae in more undisturbed environments through shading and scouring (Kim, 2002).

3. Coral-Algae Interactions

Although algae have evolved strategies to compete within their own taxa, they also compete with coral. The type of interaction coral will have with algae is generally based on which functional group the algae is a part of, but some interactions are unique to a single species. Encrusting algae, as stated above, is often the first colonizer when an area of coral or algae is removed (Airoldi, 2000). It is unique among the other groups in that it does not compete well with corals (Barott et al., 2012b) and has paradoxically been found to enhance coral larva establishment (Vermeij et al., 2011). Turf algae and macroalgae actively compete with coral as reviewed by Chadwick and Morrow (2011). In close proximity the algae takes part in basal encroachment and taller algae cause shading and physical abrasion if brushed against the coral (Coyer et al. 1993, Lirman 2001, Box and Mumby 2007, Titlyanov et al. 2009 as cited in Chadwick and Morrow, 2011). Algae in large numbers have been found to decrease water flow and increase sedimentation on the coral (Nugues and Roberts 2003 as cited in Chadwick and Morrow, 2011). Allelopathy is also used; some algae will release chemicals to directly kill coral tissue or attract coral larvae to the algae, thereby interfering with establishment (Maypa and

Raymundo 2004, Birrell et al. 2005, Mumby 2006, Box and Mumby 2007, Miller and Hay 1996, Littler and Littler 1997, Nugues and Szmant 2006, Vermeij et al. 2009 as cited in Chadwick and Morrow, 2011). Some species of algae reduce bacterial diversity on corals while others promote virulent bacterial strains which cause hypoxic conditions around coral (Barrot, et al., 2012a). Between turf and macroalgae, turf algae is the better competitor against coral (Vermeij et al., 2009) and is found in higher abundance in areas where coral has been degraded (Vermeij et al., 2010).

Studies have found that coral does actively defend against turf and macroalgae (Vermeij et al., 2010; Nugues and Bak, 2006). Methods proposed by Nugues and Bak (2006) include allelopathy, involvement of grazers, and physical damage using mesenterial filaments and sweeper tentacles, which are known to be used primarily in fending off invading corals (Chadwick and Morrow, 2011). Of course, these interactions only tell half of the story. To better understand the reef ecology, we also need to look at reef fish.

B. Reef Fish

Like coral and algae, fish are also highly adapted to the reef and play key roles in the community. Due to the wide variety of food resources and competition, species of fish have adapted behaviorally and morphologically to fill many different niches. This wide variety of specialization, leads to preferential selection of a fish species based on its preferred food sources. This, coupled with the sheer number of fish on the reef, makes fish a driving ecological factor for algal and coral species compositions. We can therefore assume from this interconnectedness that changes in fish species compositions should be reflected in the algae and coral compositions and vice versa.

1. Morphology and Niche

Jaw morphology and size are two of the simplest ways of determining a fish's diet since jaws are commonly specialized for capturing a certain type of prey. The first selecting factor for the jaw is its size relative to prey (Wainwright and Richard, 1995). Simply put, a fish is unable to consume prey that has a greater diameter than its mouth. This rule, however, can be slightly underestimated when looking at soft-bodied prey, which are more malleable than an exoskeleton of hard-bodied prey and can be molded to fit the mouth diameter. Prey size is normally a greater issue for fish that consume prey whole and less for fish that graze on sessile coral or algae, which can tear prey into smaller pieces. The second selecting factor comes from the angle at which the mouth feeds. Benthic fish tend to have downward-facing, inferior jaws that are efficient at grazing and capturing prey found in the sediment or benthos, whereas pelagic fish tend to have upward-facing, superior jaws which are better suited to capturing zooplankton suspended in the water column (Helfman et. al., 2009). Fish with straight, terminal mouths tend to be a mix of both extremes, which allows for opportunistic feeding. Aside from these general cases, there is a whole spectrum of specialized mouths found on the reef. For example, *Chaetodon multicintus*, a species of butterflyfish, has an elongated mouth and small teeth perfect for biting off extended coral polyps. Similarly, parrotfish sport beak-like jaws which they can use to scrape algae off rocks. Fish with less specialized mouths are less likely to selectively prey on any single food source but rather will feed on the most beneficial food source available that meets their current demands.

Some fish are entirely herbivorous, and they are highly influential to reef algal structures. These herbivores are categorized by Steneck (1983) based on what they are able to eat as

follows: non-denuding, denuding, and excavating. Non-denuding herbivores are unable to denude the algal substrata by stripping it from the substrate but rather graze on the younger more vulnerable parts of the algae. Organisms in this group include some damselfish but are mostly limited to polychaete worms and amphipods. Denuding herbivores are able to denude the substratum of smaller turf and macroalgae, removing them from the substrate but are unable to consume encrusting algae. Denuding herbivores include yellowtail damselfish (*Microspathodon*) , tangs (Acanthurus) and some gastropods. Excavators are herbivores that can not only denude macro and turf algae but can also feed on encrusting algae. Excavators include parrotfish (*Scarus* and *Sparisoma*), limpets, *Diadema* and chitons. In applying this to the functional groups of algae, we know that denuding herbivores are able to consume and remove small turf and macroalgae, and excavators are able to consume and remove all functional groups.

2. Fish-Algae Interactions

With the added effects of herbivorous fish, the interaction of algae and coral is regulated. Macro and turf algae are the primary functional groups fed upon by denuders (Steneck, 1983). However, studies have found that denuding species will selectively feed on one functional group over another, and turf algae is the most popular choice (Hall, 2011; DeLoach and Humann, 2007). One explanation for this is the use of chemical deterrents by macroalgae, though this varies depending by species (DeLoach and Humann. 2007). Hay (1981) suggested that this selectivity was because macroalgal species such as *Laurencia, Dictyota and Halimeda*, have basal sites that are shielded by "tightly packed uprights" making the algae "difficult for herbivores to manipulate". Excavators, on the other hand, have less difficulty eating these species. Parrotfish gut contents, for instance, show high levels of both turf and macroalgae

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(Randall, 2004). The same study found little-to-no encrusting algae in the gut contents, suggesting that parrotfish will preferentially feed on macro and turf algae. However, this observation could also be due to rapid digestion of encrusting algae in the gut, artificially skewing results. If we assume parrotfish eat little encrusting algae, then we can conclude that herbivorous fish excavators and denuders have little direct effect on encrusting algae, but they can have a substantial indirect effect through removal of competitors (Paine, 1980). Similarly, this selective feeding also indirectly decreases encroachment on coral, which would normally lower coral growth rate and damage tissue (Lirman, 2001).

Areas like the above with high grazing pressures are often coral-dominated and considered healthy (Mumby, 2006). In unhealthy areas, low herbivorous pressures lead to turf and macroalgae dominance. In this environment, bioerosion by weathering exceeds bioconstruction by corals and encrusting algae (Hutchings, 1986 as cited in Mumby, 2006) resulting in loss of rugosity (Scoffin et al., 1980 and Glynn, 1997, as cited in Mumby, 2006). This together with a filling-in of crevices by algae, (Hay, 1981) leads to a decrease in habitat for small fish and lowers overall fish diversity and abundance (Mumby 2006). In healthy environments, much the opposite occurs: corals and encrusting algae create a wide array of habitats for small fish, supporting higher abundance and diversity of all fish, including those that are not grazers.

3. Fish Selected for Study

Blue Tang (*Acanthurus coeruleus*)

Blue tangs were classified as denuding grazers by Steneck (1983). They are specialized algae-browsers with a diet primarily consisting of turf algae and some macroalgae (DeLoach and

Humann, 2007) including *Dictyota* (Hall, 2011; Randall, 2004). Tangs feed during the day, forming large feeding aggregations which provides them with increased protection from predation and increased foraging success through the ability to overcome the food protection behavior damselfish (Morgan and Kramer, 2004).

Stoplight Parrotfish (*Sparisoma viride*)

Stoplight parrotfish belong to the genus *Sparisoma* and therefore are one of the few excavating herbivores (Steneck, 1983) meaning they can denude both turf and macroalgae. Due to their size, abundance, and continuous feeding, they are usually considered the most significant grazer on Caribbean reefs (Mumby, 2006).

Bar Jack (*Carangoides ruber*) and Tarpon (*Megalops atlanticus*)

Unlike the fish listed above, neither bar jacks nor tarpon are herbivorous. Bar Jacks generally swim above the reef and prey on smaller fish, which make up 90% of their gut content by volume, and they occasionally feed on shrimp and other invertebrates (Randall, 2004). Tarpon similarly feed on a wide variety of small fish, crabs and shrimp while hunting in various habitats (Randall, 2004).

Materials and Methods

Lawrence University Marine Program (LUMP)

Lawrence University, located in Appleton, Wisconsin, began a program in 1986 to send students interested in marine biology to Grand Cayman B.W.I. These trips took place during a two-week period in mid- to late-spring typically after a 4-week preparatory course. Continuing on a bi-yearly basis, Marine Program students have studied the biological and structural features of the reefs surrounding Grand Cayman. The data collected continue to be used to examine differences in coral reef species diversity, population trends and relative coverage between sites across years.

Data Sampling

A. Transect Video Recording.

The majority of data collection done at each dive site is through chain transect video analysis. This process starts with each student buddy pair stretching segments of buoyant yellow chain over randomly chosen spurs in the site's buttress zone. One instructor then progressively presses segments of the chain against the spur, being careful not to damage the organisms underneath, while a second instructor films the chain from directly above until each chain is filmed in its entirety. By filming this way, it becomes possible to count what is underneath each chain and to then calculate the relative species coverage and diversity of each spur as well as the overall site.

B. Video Analysis

Video analysis takes place in lab following the return from the diving trip. Each buddy pair is tasked to analyze their own chain for each site independent of other groups. To analyze a chain transect, students carefully look frame-by-frame through the recorded video and count what lies under each link by category for an entire chain. In the event a link covers multiple categories, it counts toward whichever is most abundant. Categories include coral (by species), dead coral, algae (by functional group), sponge, gorgonians, zoanthid and mat tunicate.

Marine Term followed this procedure from 1986 through 2010. In 2012, the procedure was altered to take account of differences in types of algae that, up until then, had all been lumped into a single category. This meant that the chain transects from the years leading up to 2012 had to be re-analyzed in order to take account of the differences in algae type. Since the earlier analyses were scrutinous in coral species type, the re-analysis followed the previous procedure but differentiated the algae by functional group and lumped coral into one large group. The percentage of each coral species found relative to total number of coral links in old analyses was applied to the total number of coral links in the re-analysis. In this way, the relative percentage of each coral species to total coral was preserved while algae coverage by type could be added. This re-analysis also had the secondary effect of normalizing the data through a team of only two members working together.

C. Fish Sampling

Beginning in 1998, fish surveys were included in data collection to gain a better understanding of the reef ecology. Sampling followed the species and abundance survey method put forth by the Reef Environmental Education Foundation (REEF, 2007). This survey method

records the species seen and the abundance category determined for each. The abundance

categories measure the number of individuals sighted during the survey using a geometric scale:

Single = 1, Few = 2-10, Many = 11-100, and Abundant = over 100. For our analysis, the terms

single, few, many and abundant were replaced with ranks 1, 2, 3, and 4 respectively for

simplicity. In order to record data accurately, each student utilizes underwater paper with

clipboard and pencil to tally up sightings. Counting for each dive begins on the swim out to the

dive site and continues for the duration of each dive. This count is done on every site to

understand how fish assemblages vary between sites and years.

    1. Sites Sampled

Of the eleven sites recorded in the history of the program, we selected four for more

detailed analysis in this study: Beach Bay, Spanish Bay, Smith's Cove, and Parrot's Reef

(Figure 3). These were selected based on quantity of data, location, human impact and

differences in exposure to wind and waves. Sites on the northern and southern windward sides

of the island were labeled "high-energy" due to high exposure to wind and waves whereas sites

on the western leeward side of the island were labeled "low-energy" due to their relative
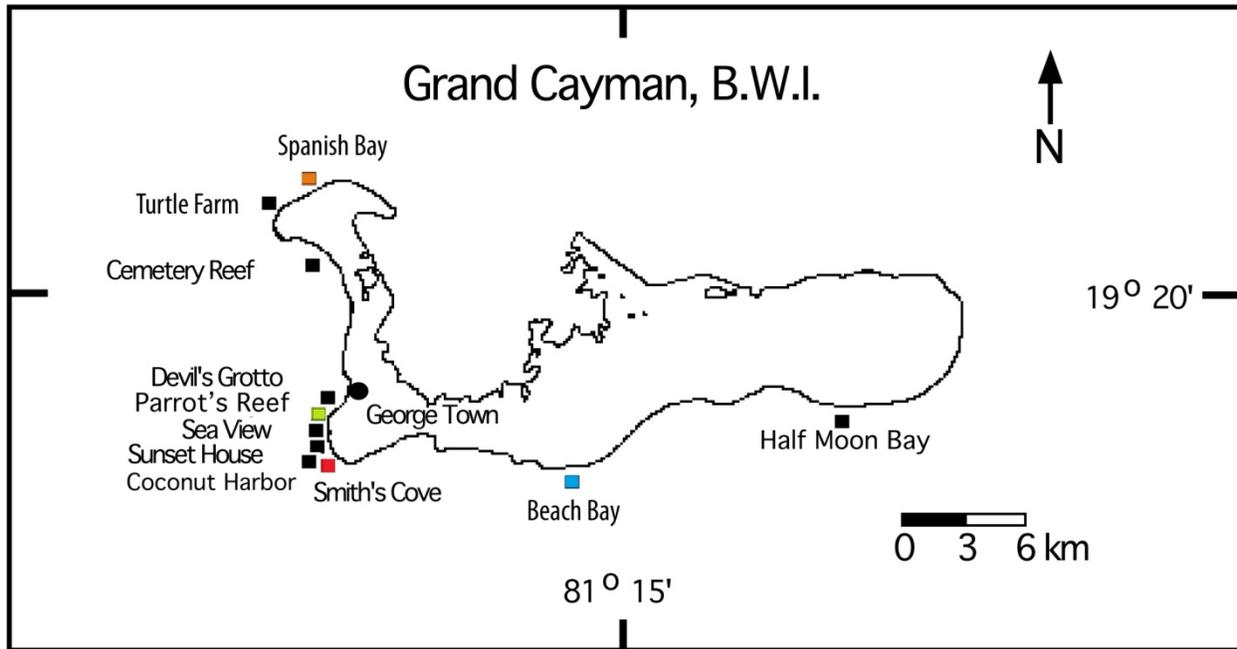
protection.

Figure 3. *Map of all dive sites from which data were obtained across all years by the Lawrence University Marine Program.*

Beach Bay:

Beach Bay is located on the south side of the island where wave pressure is greatest making it a high-energy site. It is far from any major settlements and tourist activity, lessening impacts from human activities. The level of wave activity also makes entry difficult, further dissuading human impact.

Spanish Bay

Spanish Bay, like Beach Bay, is a high-energy site but is located on the northern side of the island which receives comparable yet lower intensity wind and waves. It is located closer to 7 mile beach, a tourist hot spot, than Beach Bay but is on a less inhabited section of the island making human impacts minimal.

<u>Smith's Cove</u>

Smith's Cove is located on the border between the leeward and southern windward side of the island, but is considered low-energy due to the partial protection it receives. The entrance for Smith's Cove is a sandy beach frequented by locals and tourists alike. This, along with the site's close proximity to developed areas makes human impact significant.

<u>Parrot's Reef:</u>

Parrot's Reef is well protected within the leeward side of the island making it a low-energy site. Parrot's Reef is one of a number of sites exploited and maintained through a dive company. Diving pressure and proximity to civilization make human effects significant and comparable to Smith's Cove.

2. *Data Analysis*

To understand relative functional algal abundance temporally, abundances of each algae by functional group, relative to entire chain lengths, were averaged and compared across years and sites using simple line graphs.

To assess similarity between sites and years based on either fish species or algae functional group data we used PAST programs to generate Cluster Analysis Dendrograms and Principal Component Analyses (PCA). Cluster analysis dendrograms were calculated using a paired group algorithm and Euclidian distance measurements to find levels of dissimilarity between sites and years. The variables for each site by year for the algae cluster analyses were average relative abundance of algae on the reef for each functional group. The variables for site by year for fish cluster analyses were average rank abundances for each species. When looking

at cluster analyses for both fish and algae, it becomes possible to see if fish or algae are more or less dissimilar based on the year or the site where they were observed. PCA was similarly done using the same fish and algal data to attribute whether algal or fish similarities are affected by year or site but also to attribute which algal functional group or fish species were most responsible for that pattern. By using covariance measures to standardize the data and then plotting each site with its corresponding year based on the significant common differences in either algal functional types or fish species, coordinates can be explained by relative distance to the center. Factors are most related to a given point with distances further from the center indicating high influence from significant factors. Loadings explain the factors most responsible for the coordinate position and loading values with the greatest absolute values indicate the most influential factors.

To assess significant correlations between fish and algae functional groups irrespective of year, a correlation table was made using Spearman's rank correlation coefficient in PAST programs. This non-parametric method was chosen over linear correlation as the data were highly variable and in geometric form due to the nature of the roving diver collection method. Correlations with P-values <0.1 were considered significant and <0.05 more significant. Significant correlations were selected for further analysis based on prior knowledge of the fish in question and herbivorous importance of the fish. Further analysis for pairs with significant correlations included plotting the rank abundance of the selected fish against the proportion of reef coverage by the functional group(s) of algae. The abundance of the selected herbivorous fish and the algae with which it was significantly correlated were also plotted against time for high- and low-energy sites in an attempt to explain algae functional group variability over years and between sites of differing energy levels.

Results

In 1998, we added fish surveying to our data collection protocol but not all of the selected sites had the combined data sets for every year (Figure 4). This method was test run the first year so only a handful of sites, including Spanish Bay and Smith's Cove, were measured for fish abundance. Since then, the only sites that have lacked fish data were those that were not visited due to harsh weather or time constraints and therefore also lack coral and algae data. These cases include Smith's Cove and Parrot's Reef in 2000, Beach Bay in 2006 and 2010, and Spanish Bay in 2008.
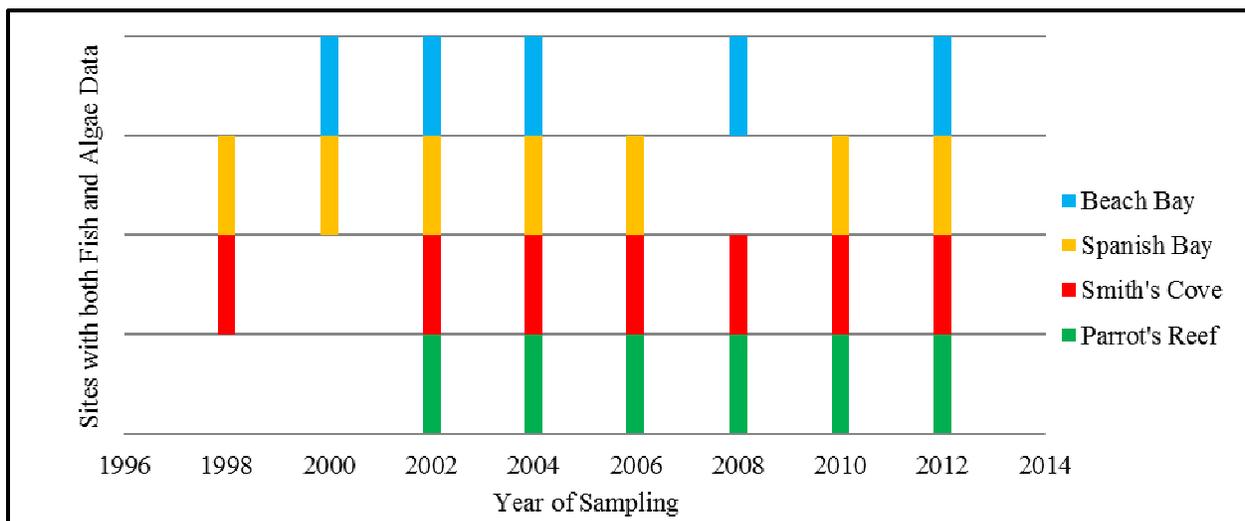

Figure 4. *Select sites of each program year for which both fish and algae data were collected.*

The composition of algae types varied across the selected time period but followed distinct patterns based on whether the reef was located on a high-energy or low-energy site. For high-energy sites like Beach Bay and Spanish Bay, encrusting algae was the most prevalent in the earliest years but has recently become dominated by turf algae (Figure 5). Macroalgae, on average, was the least abundant form composing both sites.   This changed in 2004, however, when Spanish Bay experienced a sharp increase in macroalgae mirrored by an equal decrease in turf algae. In 2006, the turf algae of Spanish Bay rebounded at the cost of encrusting algae.
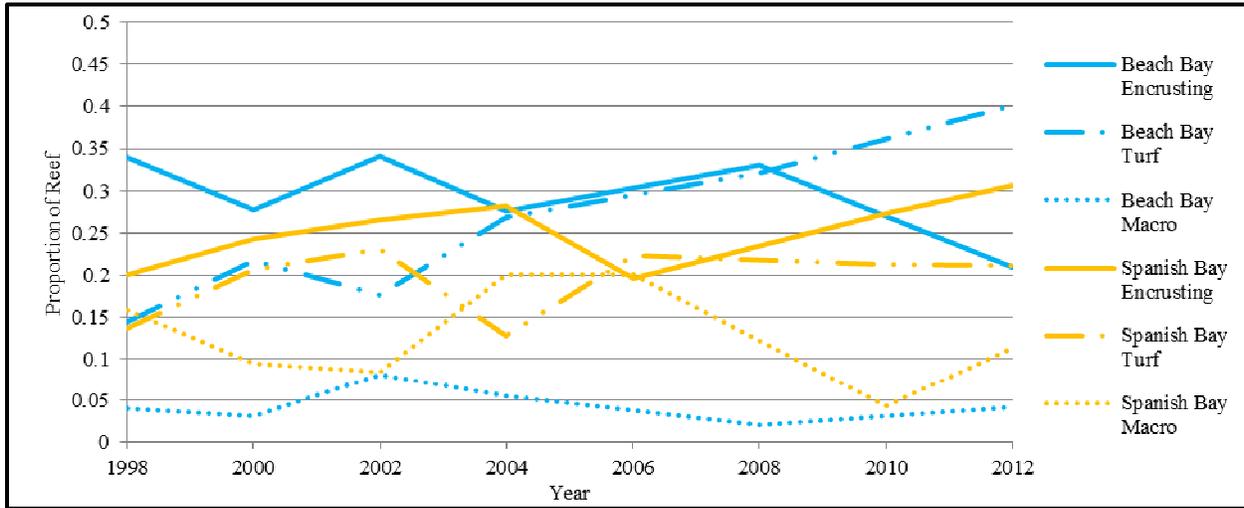
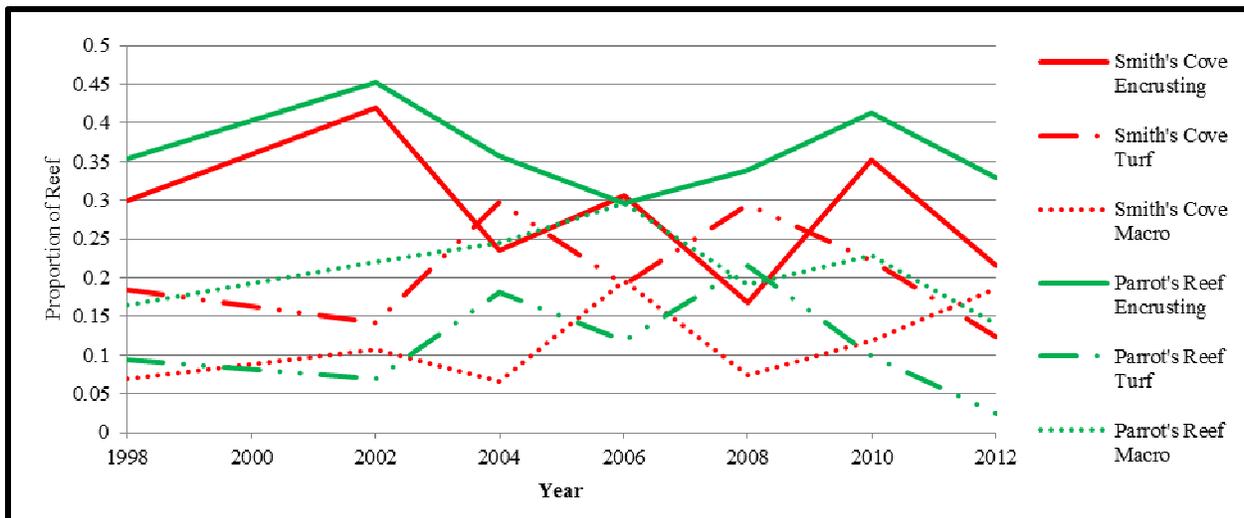**Figure 5**. *Proportions of high-energy reef sites composed of each algae type over selected years.*

Figure 6. *Proportions of low-energy reef sites composed of each algae type over selected years.*

By 2010, the majority of the macroalgae was replaced by encrusting algae, which, in Beach Bay, turf algae overgrew by 2012. In the low-energy sites, encrusting algae was similarly the most abundant for the majority of years (Figure 6). The primary differences between the sites are seen in turf and macroalgae abundance. Smith's Cove, in general, had high turf algae and low macroalgae levels whereas Parrot's Reef had the opposite. Although both sites had different

abundances, turf algae and macroalgae followed almost identical trends. Between 1998 and 2002 turf algae decreased as both encrusting and macroalgae increased. Turf algae sharply rose by 2004, lowering encrusting algae populations. By 2006, turf algae again decreased and was replaced by macroalgae at both sites and encrusting algae at Smith's Cove. Turf algae again displaced this encrusting algae and newly added macroalgae in 2008 only to go into decline until 2012 allowing encrusting and macroalgae levels to rebound.
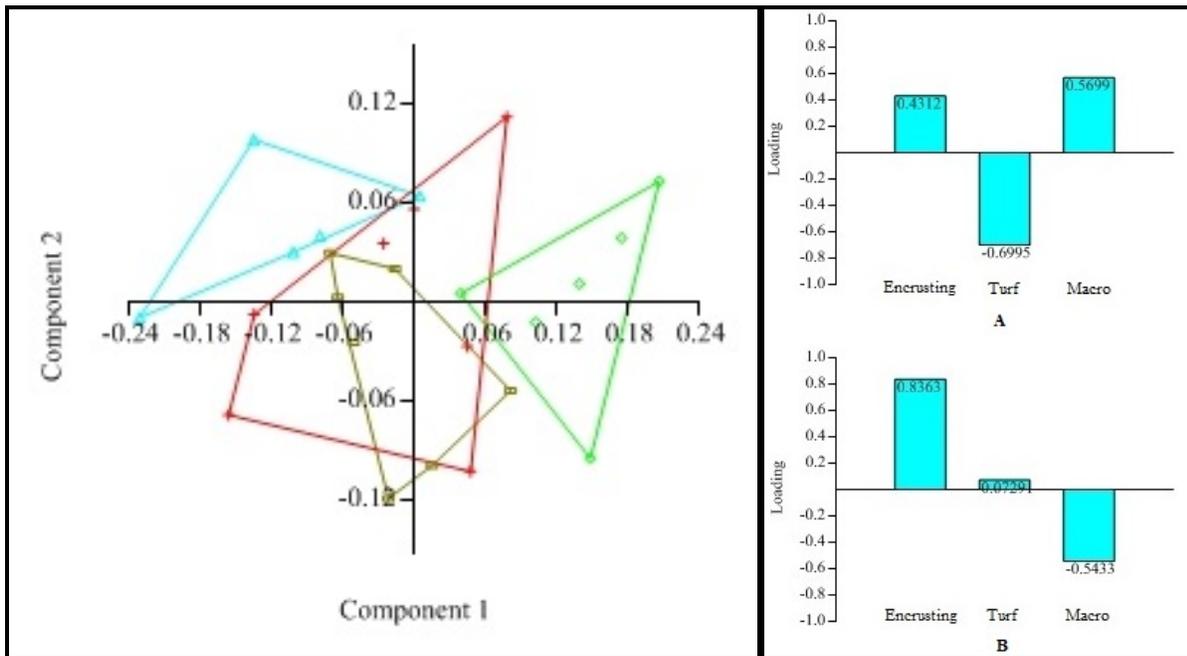

Figure 7. *Principal component analysis of algae type between sites (left). Convex hulls enclose all years for a given site. Sites denoted by color: Blue = Beach Bay, Dark Yellow = Spanish Bay, Red = Smith's Cove, Green = Parrot's Reef. Loadings **A** and **B** (right) indicate algae types responsible for position along the component 1 and 2 axes respectively.*

Patterns of algal compostion over the entire time period can only partially be seen when comparing high and low-energy sites (Figure 7). Beach Bay and Parrot's Reef are highly distinct in their compositions. Beach Bay, a high-energy site, had very high turf algae levels with the remainder based in encrusting algae. Parrot's Reef, a low-energy site, on the other hand, had very low turf algae levels with varying levels of encrusting and macroalgae. Spanish Bay and

Smith's Cove fall between the ranges, with the former having average turf values with slightly higher macro populations and the latter being highly variable. These patterns can further be seen in a cluster analysis (Figure 8), in which both Beach Bay and Parrot's Reef are highly distinct while Spanish Bay and Smith's Cove are less so. Of important note, however, is that the algae assemblages did show distinct similarities when compared between sites but no pattern appears when looking for clustering between years.
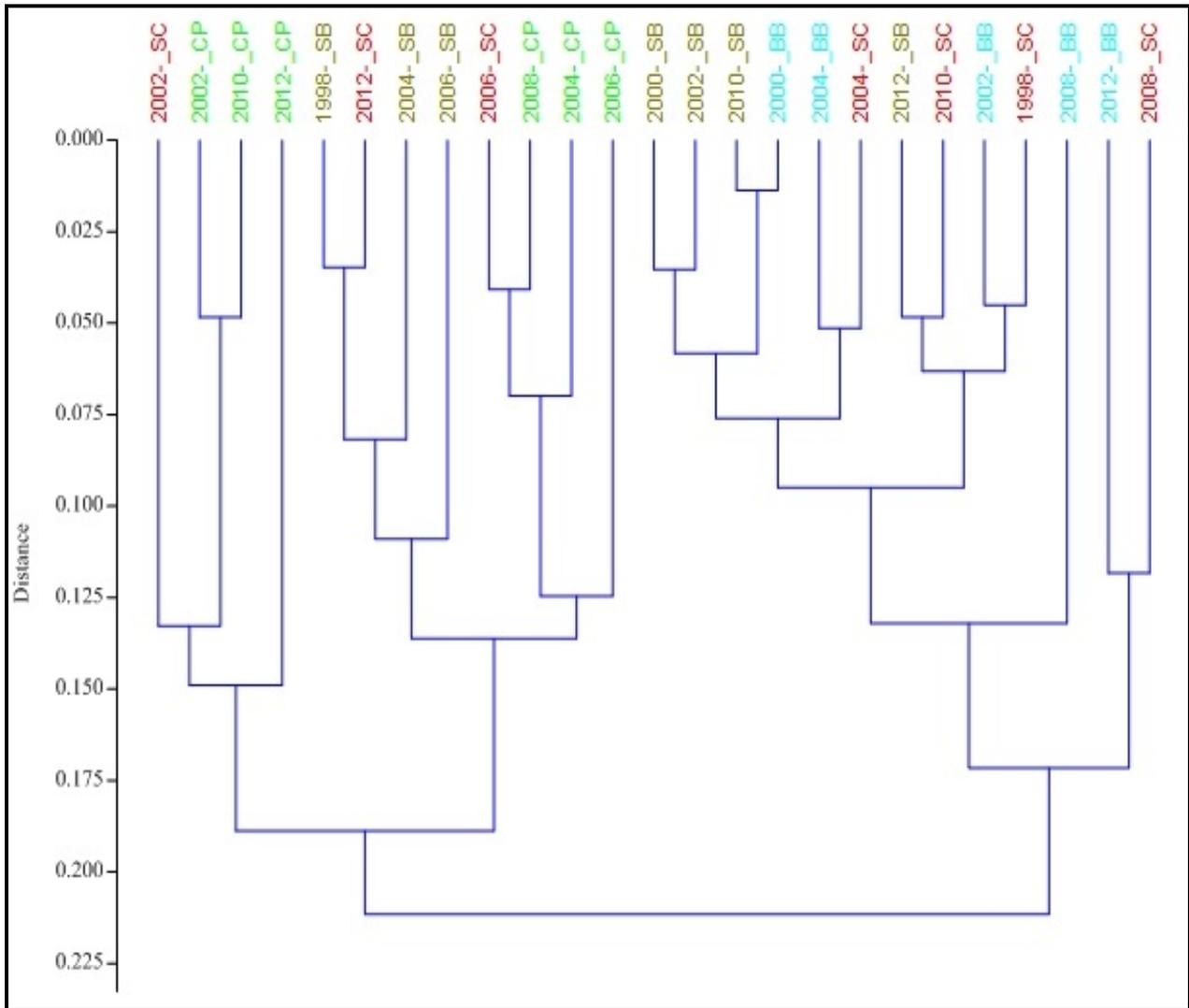

Figure 8. *Cluster analysis of algae assemblage similarity by sites and years. Samples are colored by site. Sites denoted by color: Blue = Beach Bay, Dark Yellow = Spanish Bay, Red = Smith's Cove, Green = Parrot's Reef (CP).*

Unlike algae, fish assemblages are highly conserved within years. This is made very clear in the cluster analysis shown in Figure 9, which found that when fish assemblages from all sites and years are compared, sites within the same year have the most in common with one another. This is further portrayed in Figure10, where 4 major groupings are distinguished based on abundant fish species that were extensively present in some years but absent in others (Table 1). 1998 and 2002 are one pairing where blue tangs, stoplight parrotfish, chromis and bicolor damselfish are common. In 2000, the blue tangs and parrotfish disappear with species like blackear wrasse and reef squirrelfish taking their place. In the years 2004, 2006, and 2008, the chromis and bicolor damselfish become less common and sunshinefish, cubbyu and jolthead porgys are found. In 2010 and 2012, the blue tang and stoplight parrotfish return to levels similar to those in 1998 and 2002.
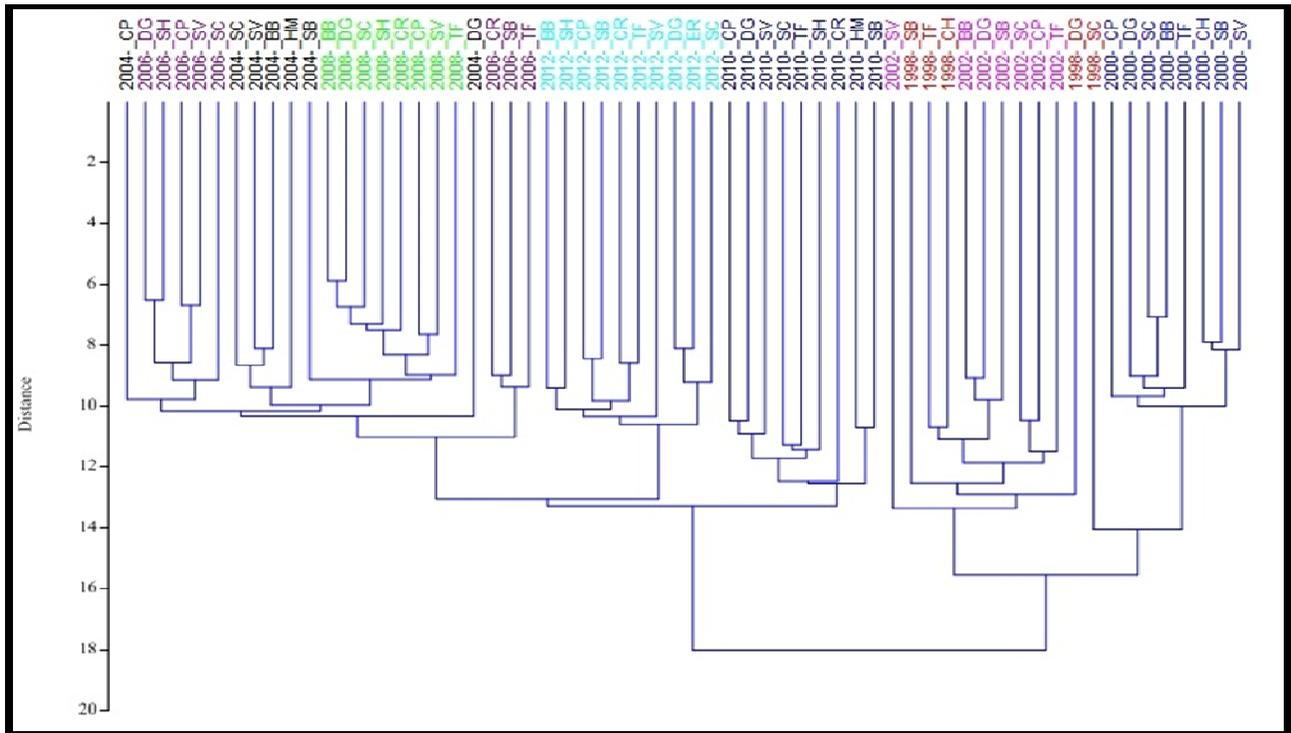

Figure 9. *Cluster analysis of fish assemblage similarity by sites and years. Samples are colored by year. Sites included : Beach Bay (BB), Coconut Harbor (CH), Cemetery Reef (CR), Devil's Grotto(DG), Half Moon Bay (HM), Parrot's Reef (CP), Sea View (SV), Smith's Cove (SC), Spanish Bay (SB), Sunset House (SH), Turtle Farm (TF).*
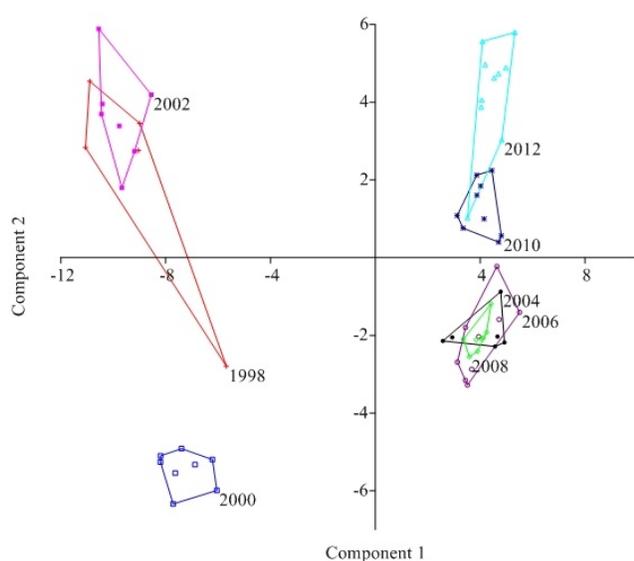
Figure 10, (above). *Principal coordinate analysis of fish between all sites and years. Convex hulls enclose all sites within a given year.*

Table 1, (right). *Loadings for the principal coordinate analysis of fish between all sites and years. Axis 1 and 2 determine component 1 and 2 axes of Figure 6 respectively. Low negative values (red) and high positive values (blue) indicate the fish influential to placement on the corresponding axis.*

Axis 1		Axis 2	
Blue_Chromis	-0.24	Blackear_Wrasse	-0.13
Brown_Chromis	-0.2	Reef_Squirrelfish	-0.12
Bicolor_Damselfish	-0.18	Rainbow_Parrotfish	-0.11
Foureye_Butterflyfish	-0.17	Mojarra,_Yellowfin	-0.11
Sergeant_Major	-0.15	Blue_Tang_	0.32
Squirrelfish	-0.13	Stoplight_Parrotfish	0.26
Schoolmaster	-0.13	Yellowtail_Snapper	0.26
Brown_Garden_Eel	-0.13	Creole_Wrasse	0.19
Bluehead	-0.13	Longspine_Squirrelfish	0.18
Midnight_Parrotfish	-0.11	Indigo_Hamlet	0.18
French_Grunt	-0.11	Blackcap_Basslet	0.17
Princess_Parrotfish	-0.1	Scrawled_Cowfish	0.17
Sunshinefish	0.23	Striped_Parrotfish	0.17
Cubbyu	0.2	Graysby	0.16
Jolthead_Porgy	0.19	Lane_Snapper	0.15
Longfin_Damselfish	0.19	Peacock_Flounder	0.15
Longjaw_Squirrelfish	0.18	Black_Durgon	0.14
Shortstripe_Goby_	0.17	Yellowtail_Reeffish	0.14
Barred_Cardinalfish	0.16	Barred_Hamlet	0.14
Queen_Triggerfish	0.16	French_Grunt	0.13
Redband_Parrotfish	0.15	Bluehead	0.13
Yellowtail_Reeffish	0.15	Spanish_Hogfish	0.12
Margate_(White)	0.15	Dragonet,_Lancer	0.12
Doctorfish	0.14	Blue_Runner_	0.11
Mahogany_Snapper	0.14	Bar_Jack	0.11
Littlehead_Porgy	0.13	Blackbar_Soldierfish	0.11
Reef_Squirrelfish	0.13	Butter_Hamlet	0.11
Jackknife_Fish	0.12	Sergeant_Major	0.1
Green_Moray	0.12	Red_Hind	0.1
Highhat	0.11		
Longsnout_Butterflyfish	0.11		
Dusky_Cardinalfish	0.11		
Redfin_Parrotfish	0.1		

When compared over all the sites, some fish species correlate highly with specific types of algae. Table 2 shows the most significant pairings as well as their correlations. Encrusting algae was found to be significantly positively correlated with Bar Jacks (*Caranx ruber)*, Redspotted Hawkfish (*Amblycirrhitus pinos)* and Tarpon (*Megalops atlanticus*) to a lesser degree, while negatively correlated with Sheepshead Porgy (*Calamus penna),* Rosy Razorfish (*Xyrichtys martinicensis*), Balloonfish *(Diodon holacanthus)* and Graysby (*Cephalopholis cruentata*). Turf algae was positively correlated with Blue Angelfish

Encrusting	Correlation	P-value	Turf	Correlation	P-value
Bar_Jack	0.49	0.013	Blue_Angelfish	0.45	0.025
Hawkfish,_Redspotted	0.47	0.018	Bar_Jack	-0.42	0.035
Sheepshead_Porgy	-0.44	0.026	Blue_Tang_	-0.42	0.035
Rosy_Razorfish	-0.41	0.042	Barred_Hamlet	-0.42	0.037
Balloonfish	-0.40	0.045	Highhat	0.42	0.038
Graysby	-0.40	0.048	Green_Razorfish	0.40	0.046
Lantern_Bass	0.39	0.057	Shy_Hamlet	0.39	0.053
Tarpon	0.37	0.065	Caesar_Grunt	-0.39	0.054
Spotted_Eagle_Ray	-0.37	0.067	Stoplight_Parrotfish	-0.39	0.055
Coney	0.37	0.070	Tarpon	-0.38	0.057
Spanish_Hogfish	0.36	0.073	Black_Grouper	-0.37	0.072
Red_Grouper	-0.36	0.078	Yellowline_Goby	-0.36	0.081
Hogfish	-0.36	0.078	Purple_Reeffish	-0.35	0.085
Dusky_Squirrelfish	-0.36	0.079	Whitestar_Cardinalfish	0.34	0.097
Orangespotted_Filefish	0.35	0.085	Goldspot_Goby	-0.34	0.097
Bluestriped_Grunt	0.35	0.085	White_Grunt	-0.34	0.097
Dog_Snapper	0.35	0.088	Tobaccofish	-0.34	0.097
Beaugregory	0.34	0.097			
Gray_Triggerfish	-0.34	0.097	**Macro**		
Clown_Wrasse	0.34	0.097	Shortstripe_Goby_	0.44	0.026
Rainbow_Wrasse	0.34	0.097	Highhat	-0.36	0.081
Chub_(Bermuda/Yellow)	0.34	0.097	Blue_Angelfish	-0.34	0.091

Table 2. *Significant correlations of fish abundance by species to algae abundance by type over all sites and years. Red text indicates P-value<0.05, Gray text indicates P-value<0.1.*

(*Holacanthus bermudensis*), Highhats (*Equetus acuminatus*) and Green Razorfish (*Xyrichtys splendens*), while negatively correlated to Bar Jacks (*Caranx ruber)*, Blue Tangs (*Acanthurus coeruleus*), and Barred Hamlets (*Hypoplectrus puella*) as well as Stoplight Parrotfish (*Sparisoma viride*) and Tarpon (*Megalops atlanticus*), though less significantly. Macroalgae did not correlate with many fish but had significant positive correlation to Shortstripe Gobies (*Elacatinus chancei*).

Bar Jacks, Tarpon, Blue Tangs and Stoplight Parrotfish were further analyzed for their trends with different algae. Bar Jacks and Tarpon exhibited highly similar trends in comparison to algae abundance.
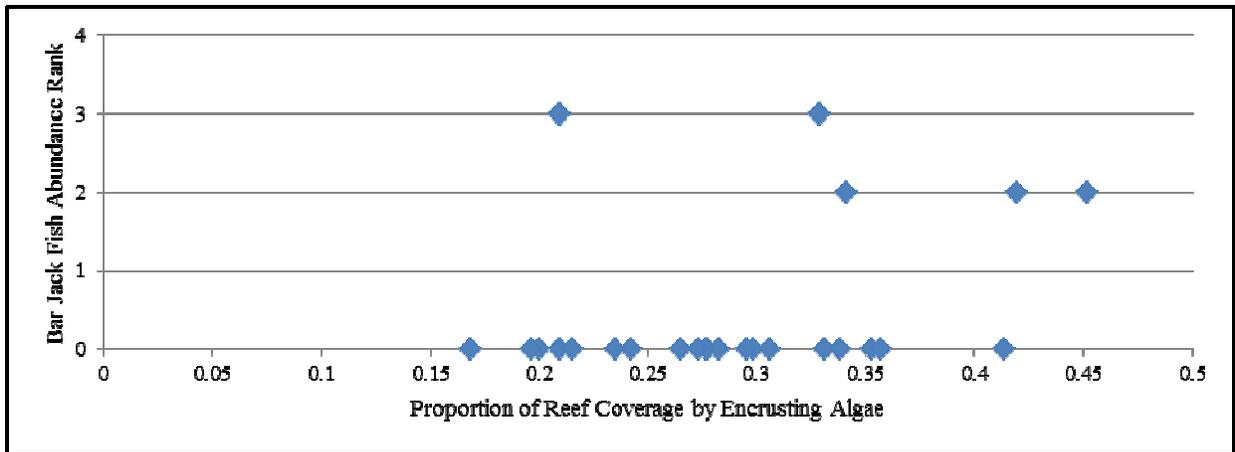
Figure 11. *Trend of Bar Jack abundance and proportion of reef composed of encrusting algae for all sites and years.*
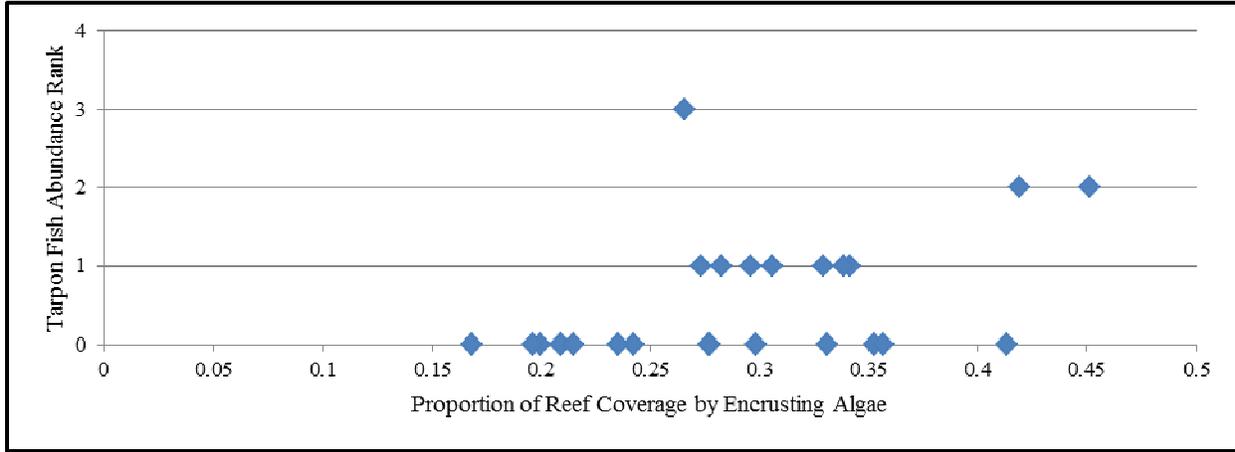

Figure 12. *Trend of Tarpon abundance and proportion of reef composed of encrusting algae for all sites and years.*
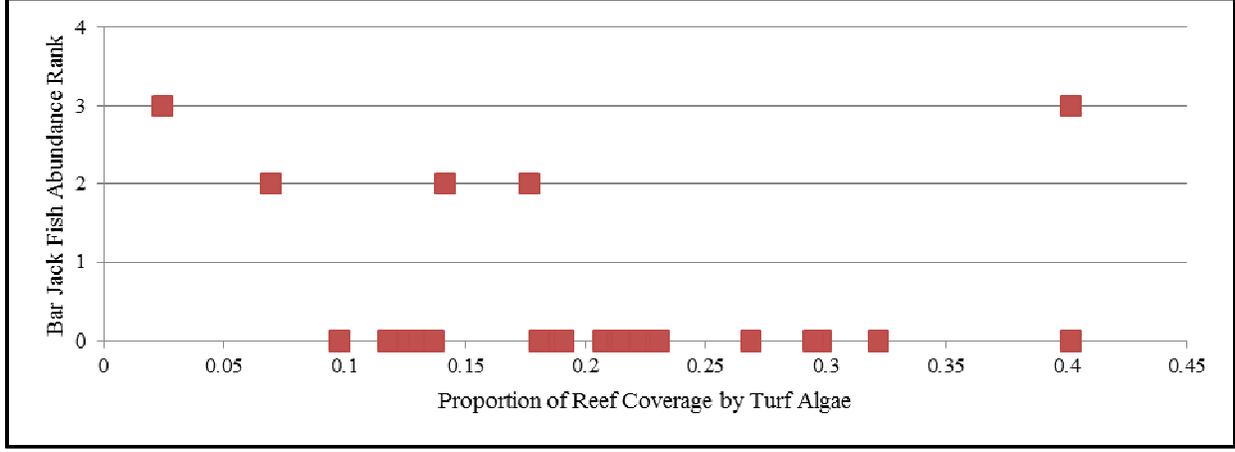

Figure 13. *Trend of Bar Jack abundance and proportion of reef composed of turf algae for all sites and years.*
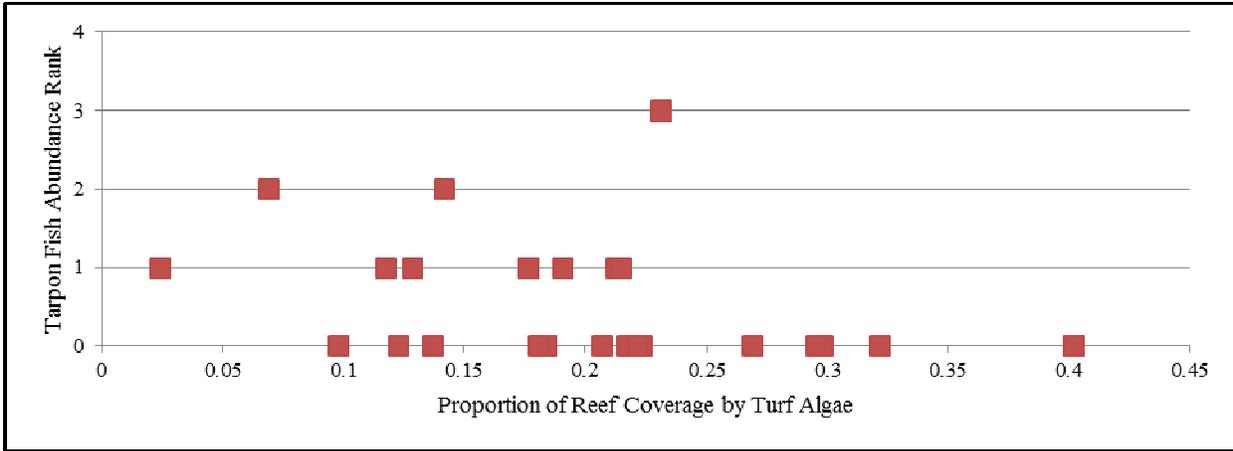
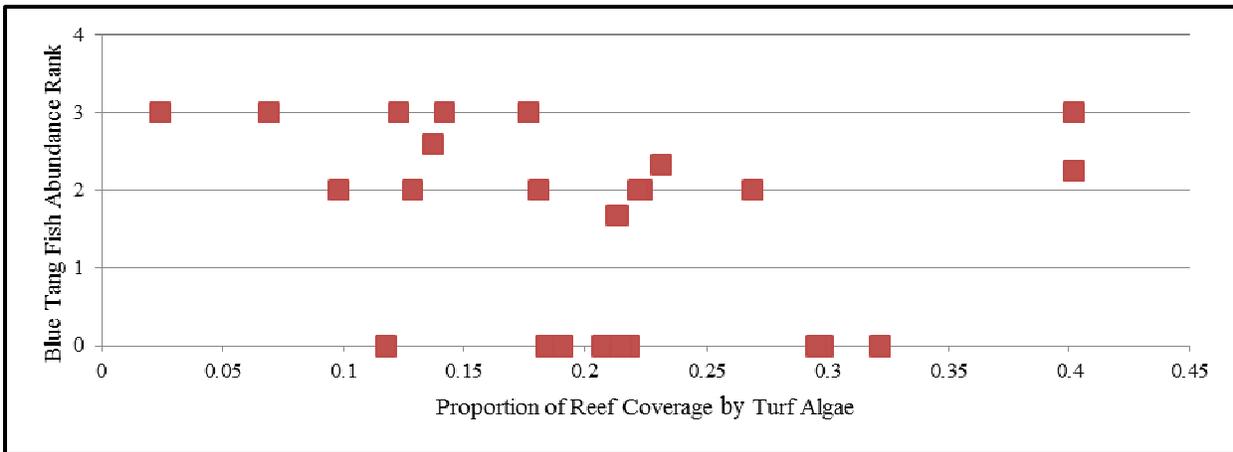**Figure 14**. *Trend of Tarpon abundance and proportion of reef composed of turf algae for all sites and years.*

Figure 15. *Trend of Blue Tang abundance and proportion of reef composed of turf algae for all sites and years.*
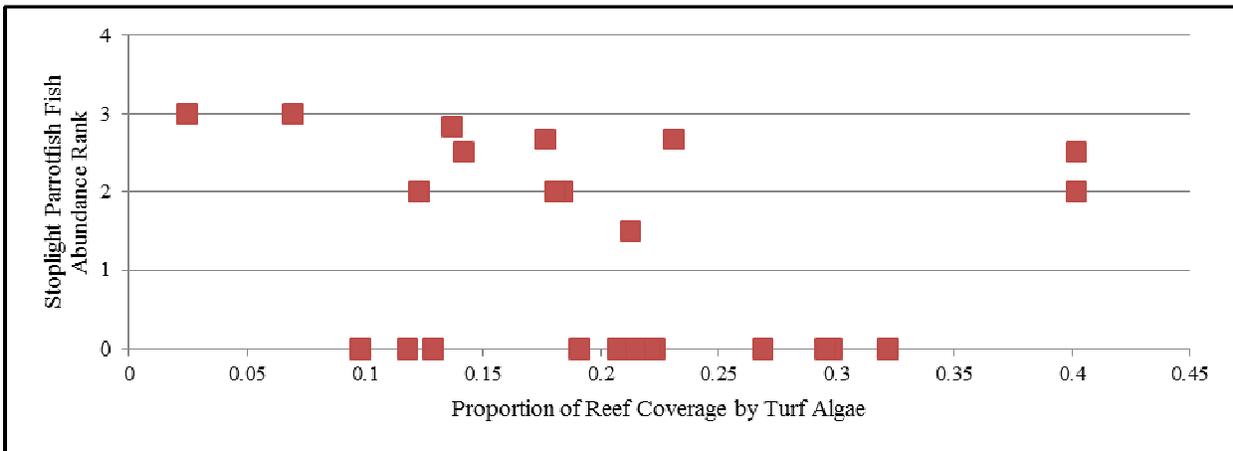

Figure 16. *Comparison of Stoplight Parrotfish abundance to the proportion of reef composed of turf algae for all sites and years.*

Both had significant positive correlations to encrusting algae (Figures 11 and 12) and significant negative correlations with turf algae (Figures 13and 14). Blue Tangs and Stoplight Parrotfish, consumers of turf algae, both held significant negative correlations with turf algae (Figures 15 and 16). For both graphs, the two outlying points of high fish and turf abundance occurred at Spanish Bay and Beach Bay in 2012. Not only were these overall trends similar between Blue Tang and Stoplight Parrotfish, but so were the temporal abundance patterns found at each site.

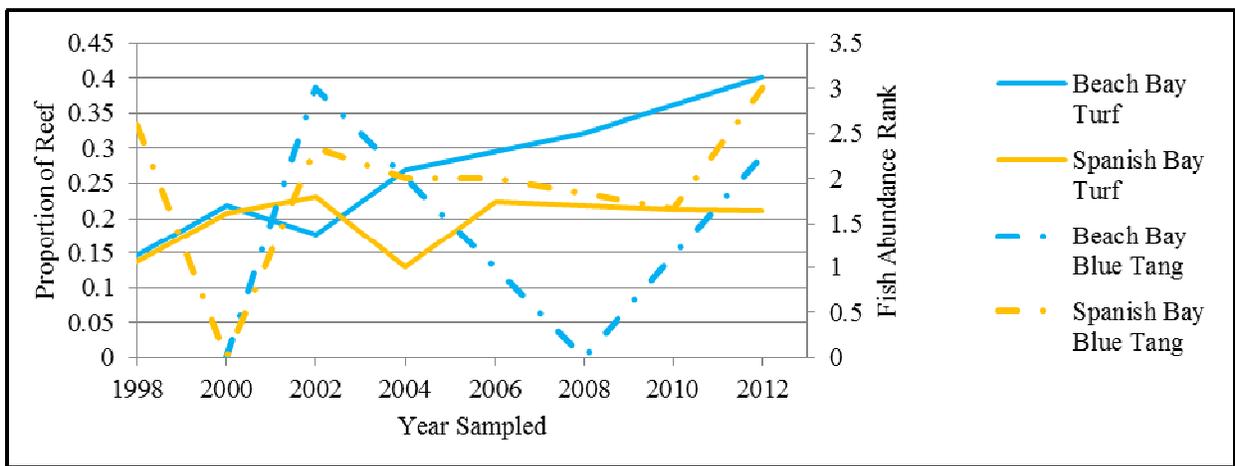**Figure 17**. *Long term trends in Blue Tang abundance and relative reef coverage by Turf algae for high-energy sites.*
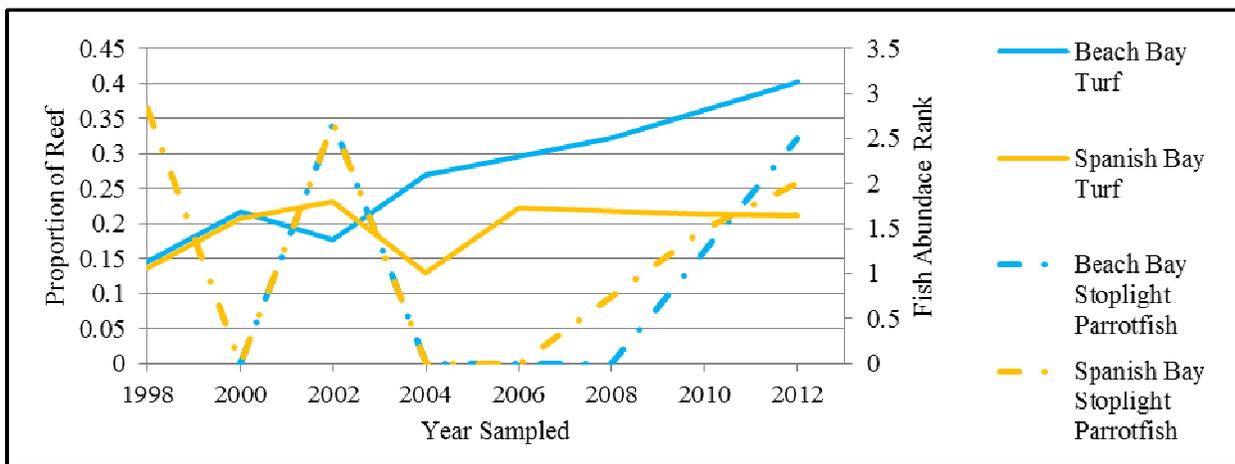

Figure 18. *Long term trends in Stoplight Parrotfish abundance and relative reef coverage by Turf algae for high-energy sites.*

At the high-energy sites, Blue Tang (Figure 17) and Stoplight Parrotfish (Figure 18) abundance was high in 1998 but dropped in 2000. The turf algae expanded during this time but receded with a second spike of both fish in 2002. At Beach Bay between 2004 and 2008, both species began a downward trend and turf algae slowly rose. At Spanish Bay during the same time period, Stoplight Parrotfish diminished while Blue Tangs only decreased slightly. The turf algae at this time dipped slightly in 2004 but held a steady proportion of reef space. By 2010 and 2012, both species began rising in number to values similar to those found in 2002. Turf algae did not show a marked response to this increase but held a relatively similar rate compared to recent years.

At the low-energy sites, Blue Tang (Figure 19) and Stoplight Parrotfish (Figure 20) differed in the early years. At Smith's Cove in 1998, tangs were absent and Stoplight Parrotfish were plentiful, but both rose to a peak in 2002. This peak occurred at both sites and was mirrored by a decrease in turf algae coverage. In a similar fashion to the high-energy sites, both low-energy sites saw a decrease in both herbivorous fish with a two year delay by Parrot's Reef. During this period, turf algae abundance on both sites reached a peak, though they dipped slightly in 2006 during a peak in macroalgae (Figure 6). In 2010, Blue Tangs began returning to both sites marking a decrease in turf algae that was further lowered in 2012 with the return of the Stoplight Parrotfish and increased abundances of Blue Tangs.

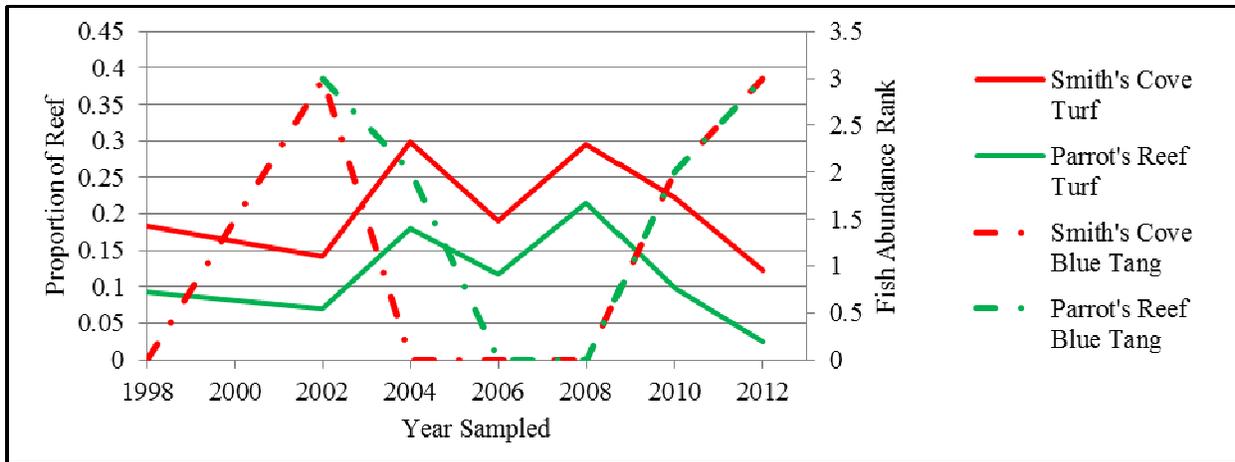**Figure 19**. *Long term trends in Blue Tang abundance and relative reef coverage by Turf algae for low-energy sites.*
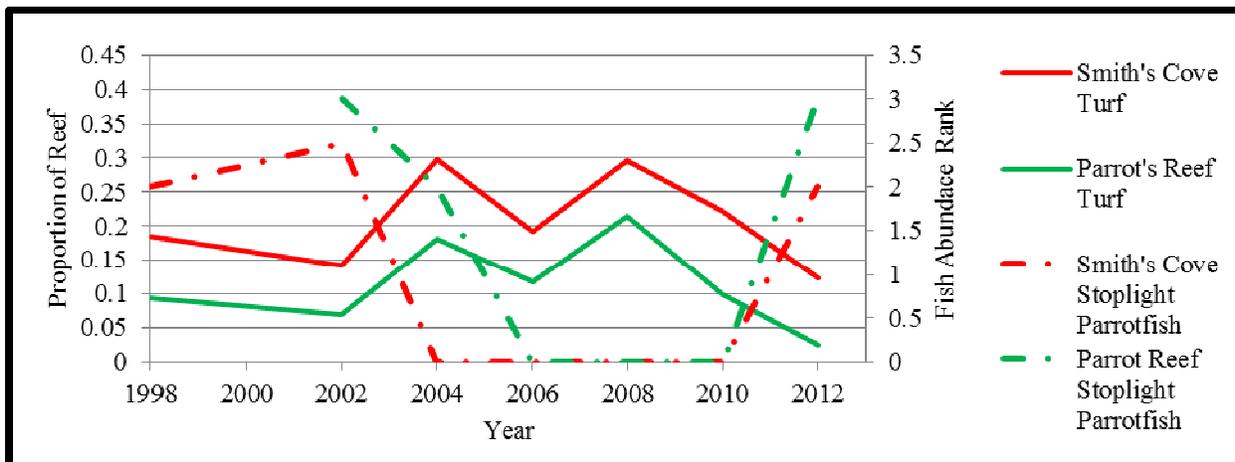

Figure 20. *Long term trends in Stoplight Parrotfish abundance and relative reef coverage by Turf algae for low-energy sites.*

Discussion

In ecology, the systems studied are large and complex, so ecologists regularly reduce questions to a smaller, measureable scale in order to gain insight on how the entire system functions.   An unfortunate consequence of this reduction is the potential to overlook significant processes that are necessary to understanding the system, and to make incorrect assumptions as a result. The analyses in this study were chosen to best describe the relationships found when making comparisons of the reef communities, but none are free from possible error. For this reason, it is important to be mindful of the limitations of each analysis and to make rational predictions.

Summary

The purpose of this study was to determine how functional groups of algae changed over time at sites differentiated by contrasting levels of natural disturbance and if these changes could be attributed to particular species of fish. In order to fulfill the purpose of this overarching question, the study was broken into smaller parts. These included looking at relative algae functional group abundance patterns with varying levels of disturbance, similarity of fish and algal groups between sites and years, and examining significant fish populations and their correlation with algal functional groups.

A. Algal Abundance Patterns and Disturbance

On coral reefs, algae constantly compete with each other and with other attached organisms for space. If the algae were left to compete among themselves without disturbance or

grazing, we would expect the most competitive group –macroalgae- to dominate the reef (Kim, 2002) at the expense of the other groups. We instead see a wide range of variability over the years for all functional groups with no visible pattern for any one group's decline consistently leading to another's rise (Figures 5 & 6). This suggests that the reason for these shifts is multifactorial, as expected, and requires identification of the related factors for explanation.

Disturbance is one possible factor with the ability to remove living matter and free up space. When comparing algal abundances in high-energy environments with greater wave pressures to the more protected low-energy environments, we find that Beach Bay, the site most highly exposed to winds consistently had the highest proportion of turf algae, whereas Parrot's Reef, the most protected site, had the highest proportion of macroalgae (Figure 7). The pattern of turf algae in high-energy areas makes sense when considering that turf algae are relatively well-adapted to wave stress (Cheroske et al., 2000 as cited in Vermeij et al., 2010) and can quickly regrow over disturbed areas. Low-energy areas are rightfully higher in macroalgae, which does well in less-disturbed areas (Kim, 2002). Additionally, nutrient loading from proximity to urbanized land and pressure from diving could be additional factors specific to dive sites like Parrot's Reef (Lawton, 1998). The two sites that showed intermediate pressures, Smith's Cove and Spanish Bay, also had intermediate algal compositions. Based on these data, levels of disturbance is a factor that determines long-term algal composition, but does not provide much explanation for short-term variation.

B. Similarity of Algae and Fish by Year and Site

When clustering fish and relative algal abundance by year and site for similarity, results were highly polarized. Fish diversity and abundance was relatively similar within years

irrespective of site (Figure 9), whereas algal composition was relatively similar within sites irrespective of year (Figure 8). The logical reason for this is that algae are immobile and so their composition will vary only slightly between years at a given site. This also means that sites with highly conserved clusters were unique to other sites. Beach Bay and Parrot's Reef, for example were highly dissimilar, whereas sites from Smith's Cove and Spanish Bay showed similarity to both Beach Bay and Parrot's Reef. Fish, on the other hand, are much more mobile and are therefore not bound to a single site. The similarity of fish at all sites for a given year is intriguing as it suggests that fish populations are highly variable across years and that changes in population are seen simultaneously all across the island (Figure 10 and Table 1). Unfortunately, this could partially be attributed to sampling error as collectors of these data varied between the years and some species may have been overlooked.

C. Significant Fish

1. Herbivores

Blue tangs and stoplight parrotfish showed significant negative correlations with turf algae (Figures 15 and 16), meaning that on sites where these fish were present turf algae was relatively low. This brings up three possible causal relationships - either these fish are choosing to avoid areas with turf algae, turf algae are responsible for lowering fish abundance or fish presence is enough to significantly decrease levels of turf algae. Based on previous evidence of herbivorous predation from these fish on turf algae (DeLoach and Humann, 2007; Hall, 2011; Randall, 2004), it is safe to assume the latter. Observing changes in the turf abundance with changes in herbivore abundance over time further supports this relation; turf abundance tends to decrease with higher herbivore populations and increases when herbivores are absent (Figures

17-20). Rapid growth in turf algae between 2002 and 2004 on low-energy sites, for instance, was accompanied by declines in the herbivores. The turf algae was then subsequently removed after an herbivore resurgence in 2008. Since blue tang and stoplight parrotfish presence is highly variable between years and both fish have the ability to induce rapid changes on relative turf algae abundance, they are very likely a significant short-term factor determining overall algal composition.

2. *Piscivores*

Both bar jacks and tarpon had similar yet unexpected correlations. Based on the concept of top-down trophic interactions, a high abundance of piscivorous bar jacks and tarpon should correlate with a reduction in their food source, small fish. If these small fish were denuding herbivores, we would expect to measure an increase in their food source - turf algae - in turn. This would lead to an overall positive relation between bar jacks/tarpon and turf algae. Instead, we find that both fish have a significant negative correlation with turf algae (Figures 13 and 14) and a significant positive correlation with encrusting algae (Figures 11 and 12). Though the reason for this may seem unclear at first, gut content analysis reveals that bar jacks and tarpon incorporate a wide variety of small fish in their diets and that these small fish, in turn, have a wide variety of diets, often favoring zooplankton and small invertebrates over algae (Randall, 2004). This reduces plausibility of a top-down trophic interaction, but the trends still stand. The answer likely lies in how the composition of algae functional groups affects habitats for small fish. As mentioned above, high populations of turf and macroalgae lower rugosity in reefs by reducing bioconstruction (Mumby, 2006). This, plus turf algae's affinity for filling in crevices and blocking out fish (Hay, 1981), logically results in significant habitat reduction for small fish,

which should become less abundant. Based on this evidence, small fish should be more likely to inhabit areas with higher levels of encrusting algae and lower levels of turf algae where suitable habitat can be found. As both bar jacks and tarpon feed on these small fish, they should frequent areas where their prey is most abundant in order to maximize feeding success. Our trends support this conclusion.

Conclusion

Based on the results of the study it seems that there are multiple factors affecting the benthic composition of the reef. These include levels of disturbance and presence of the herbivorous fish blue tang (*Acanthuru coeruleus)* and stoplight parrotfish *(Sparisoma viride)*. Disturbance appeared to have long-term effects on the composition of algae with protected areas hosting higher abundances of macroalgae and areas exposed to greater wave and wind pressure hosting higher abundances of turf algae. Herbivore abundance, on the other hand, affected composition in the short run by substantially reducing turf algae. Understanding these interactions is integral to understanding the overall health of the reef.

As high percentages of coral and encrusting algae are necessary to reef health, nutrient loading poses a serious hazard to reefs. Nutrient loading enhances the growth rates of turf and macroalgae increasing their competitive edge against corals (Vermeij et al., 2010) and encrusting algae. Since herbivorous fish in this study were found to only have significant correlations with turf algae, it is likely that both preferentially feed on turf when it is available, a behavior proven in blue tangs by Hall (2011). If this is the case, sites protected from natural disturbance should be more vulnerable to the deleterious effects of nutrient additions as the less-preferred, more-competitive macroalgae are expected to overtake the reef. This problem is irreversible assuming

that an herbivore remains that has the capacity to control macroalgae.   An excess of either turf

or macroalgae remains problematic, however, since herbivores have a limit on what they can

graze (Mumby, 2006). In either case, protection of denuding herbivores that consume turf and/or

macroalgae is essential to maintaining health of the reef through algal control.

Possible options for building on this study include incorporation of historical catch limits

on piscivorous fish known to consume important herbivores and of herbivores themselves,

measurements of anthropogenic nutrient inputs at various locations on the island, and

continuation of the study into the foreseeable future to further our understanding of the long-term

changes in reef structure.

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